A STUDY OF THE GERM CELLS OF CERTAIN DIPTERA, WITH REFERENCE TO THE HETEROCHROMOSOMES AND THE PHENOMENA OF SYNAPSIS

BY

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WITH FOUR PLATES

INTRODUCTION

In connection with previous work on the spermatogenesis of the Coleoptera ('05, '06), the germ cells of the common fruit-fly, Drosophila ampelophila, were examined in the autumn of 1906. The difficulties encountered in handling this material led to the study of the spermatogenesis of several other flies. The results will be presented in accordance with the following scheme:

Calyptrate Muscidæ.
- Muscinæ.
  - 1 Musca domestica.
  - 2 Calliphora vomitoria.
  - 3 Lucilia cæsar.
- Sarcophaginæ.
  - 4 Sarcophaga sarraciniæ.
- Anthomyiinæ.
  - 5 Phorbia brassica.

Acalyptrate muscidæ.
- 6 Scatophaga pallida.
- 7 Tetanocera sparsa.
- 8 Drosophila ampelophila.
- Syrphidæ.
  - 9 Eristalis tenax.

METHODS

With this material it was found that the best results could be obtained from fresh tissue mounted in Schneider's aceto-carmine.

The testes (or ovaries) of adult flies were dissected out in physiological salt solution and immediately transferred to a drop of aceto-carmine on a slide. The cover-glass was pressed down with a needle to break the capsule of the testis and spread the cells. All excess of stain was removed with filter paper, and after ten or fifteen minutes, the preparation was sealed with vaseline. Such preparations may be studied to the best advantage after twenty-four hours, as the chromatin gradually acquires a deeper tint. They remain in good condition for several days, but are, of course, not permanent. The method has several advantages besides that of enabling one to examine a large amount of material in a limited time. The aceto-carmine fixes and stains instantly without the shrinkage incident to the usual treatment with fixing fluids, alcohols, xylol and paraffin, necessary in order to obtain sections. Then, one is able to study the whole cell with all of the chromosomes present and uncut, which is an obvious advantage for work of this kind. The chromatin stains much more deeply than any other cell element, but the achromatic structures are not always well brought out, and they have been omitted from most of the figures, as this investigation is concerned primarily with the heterochromosomes and the method of synapsis. In favorable preparations of this kind, with good light, it is possible to get as accurate camera drawings as from sections stained with iron hæmatoxylin.

RESULTS OF INVESTIGATION

1 *Musca domestica*

In many respects the spermatogenesis of this fly resembles that of Tenebrio molitor (Stevens '05), Odontata dorsalis (Stevens '06) and the other Coleoptera which have an unequal pair of heterochromosomes. There are, however, no synapsis, synizesis or spireme stages in the spermatocytes, nor are tetrads ever formed.

In the prophase of spermatogonial mitoses one finds five pairs of long slender chromosomes, the members of each pair either lying parallel to each other or twisted together (Fig. 1). The members of the additional unequal pair are usually separate

(Fig. 1, h_1 and h_2). Apparently a side-to-side pairing or conjugation of homologous chromosomes, with the possible exception of the unequal pair, occurs preliminary to each spermatogonial mitosis. The twelve chromosomes separate, and each divides longitudinally in metakinesis. Whether they pair again in the telophase or not until the prophase of another cell-division is not evident.

The heterochromosomes remain condensed and are found side by side during the whole growth stage, while the other chromosomes pass into a more or less diffuse condition (Fig. 2). In the prophase of the first spermatocyte mitosis there are five thick V-shaped chromosomes and a pear-shaped mass of chromatin which in metakinesis proves to be the unequal pair of heterochromosomes (Fig. 3). The V-shaped chromosomes all divide longitudinally and the larger and smaller heterochromosomes separate as seen in Fig. 4. In the interval between the first and second divisions a nuclear membrane forms, but the chromosomes do not change greatly. Figs. 5 and 6 show the two kinds of daughter nuclei, one containing the larger, the other the smaller heterochromosome. In the second spermatocyte mitosis the V-shaped chromosomes again divide longitudinally and the heterochromosomes divide as shown in Figs. 7 and 8, so that in all stages they are clearly distinguishable from the ordinary chromosomes. The resulting spermatozoa fall into two equal classes, dimorphic as to the heterochromosomes, as in similar cases among the Hemiptera and Coleoptera. In most of the flies studied there was no difficulty in finding oögonia in which the number and relative size of the chromosomes could be determined. Only one such was found in Musca, that shown in Fig. 9. Here a part of the chromosomes are still paired; others have separated, but the members of each pair of ordinary chromosomes are not far apart; while the two equal heterochromosomes are on opposite sides of the group (h). Here again we have what may be regarded as a partial synapsis of homologous chromosomes. The relation of the heterochromosomes in the two sexes is the same as in many of the Coleoptera (Stevens '05 and '06) and the Hemiptera heteroptera (Wilson '05 and '06), an unequal pair (large and small) in

the male and an equal pair of large heterochromosomes in the female. An egg which is fertilized by a spermatozoön containing the smaller heterochromosome produces a male, while one which unites with a spermatozoön containing the larger heterochromosome produces a female.

Although there is no distinct synapsis stage visible in the development of the spermatocytes of Musca domestica, the method of synapsis is without doubt indicated by the side-to-side pairing of chromosomes of equal length in the prophases of both spermatogonial and oögonial mitoses. The final synapsis is a closer union of the homologous chromosomes, and the first spermatocyte division separates the members of each pair instead of dividing each chromosome as in the spermatogonia.

2 *Calliphora vomitoria*

The chromosomes in this species are similar to those in Musca domestica. Both members of the unequal pair of heterochromosomes are smaller, as may be seen in a spermatogonial metaphase (Fig. 10). Pairing of homologous chromosomes is also evident here. In the growth stage (Fig. 11) the heterochromosomes are associated with a plasmosome as in many species of Coleoptera Two views of the metaphase of the first spermatocyte mitosis are shown in Figs. 12 and 13, and an anaphase in Fig. 14. Two metaphases and an anaphase of the second division appear in Figs. 15, 16 and 17. The equal pair of heterochromosomes in the female is clearly shown in two oögonial metaphases (Figs. 18 and 19). In this case we have further evidence of the side-to-side pairing of homologous chromosomes in the spermatogonia and oögonia.

3 *Lucilia cæsar*

Only a few specimens of this species were captured and the series of stages is incomplete. No spermatogonial or oögonial metaphases were found. In the growth stage a pair of *m*-chromosomes is present with an enormous heterochromosome bivalent

(Fig. 20). The metaphase of the first spermatocyte division is shown in Figs. 21 and 22, and prophases of the two kinds of second spermatocytes in Figs. 23 and 24. The spermatozoa would evidently be dimorphic as in the other species.

4 *Sarcophaga sarraciniæ*

The three species of Diptera whose spermatogenesis has already been described belong to the sub-family Muscinæ, while Sarcophaga is a member of the sub-family Sarcophaginæ. The number of chromosomes in Sarcophaga is the same as in the other species, 12 somatic and 6 reduced, and the heterochromosomes closely resemble those in Calliphora. The spermatogonial plate (Fig. 25) shows the 12 chromosomes paired, but separated ready for metakinesis, and one chromosome shows the division line. In the growth stage (Fig. 26) the pair of heterochromosomes comes out clearly in the midst of diffuse and irregular masses of faintly stained chromatin. In these flies the ordinary chromosomes become much branched or diffusely granular in the growth stage but do not unite to form a spireme of even width as in so many forms. Whether or not they unite end-to-end at any stage before or after synapsis I cannot say. A prophase and an equatorial plate of the first spermatocyte mitosis may be seen in Figs. 27 and 28, and the metaphase and anaphase in Figs. 29, 30 and 31. The polar views of the metaphase of the second mitosis (Figs. 32 and 33) of course show dimorphism as to the heterochromosomes (h_1, h_2). Equal division of all of the chromosomes follows as in the three preceding species. Figs. 34 and 35 were drawn from adjacent oögonia in metaphase to show the close longitudinal pairing of the chromosomes and their later separation before metakinesis. The equal heterochromosomes are usually found together in the middle of the plate and each one is evidently equivalent in size to the larger heterochromosome of the spermatogonia and spermatocytes (Figs. 25 to 33). Fig. 36 is from an ovarian follicle cell. The four figures, 25, 34, 35 and 36 show the pairing of homologous chromosomes in spermatogonia, oögonia and somatic cells.

5 *Phorbia brassica*

Only one male of Phorbia was obtained and only four stages drawn; but these indicate precisely the same conditions as in the other species examined. Phorbia belongs to the sub-family Anthomyiinæ. Fig. 37, a growth stage; 38, a prophase; 39, a metaphase; and 40, an anaphase, show clearly the presence of an unequal pair of heterochromosomes resembling those of Musca domestica.

6 *Scatophaga pallida*

7 *Tetanocera sparsa*

The chromosomes of Scatophaga and Tetanocera resemble each other so closely in number, form and behavior that they will be considered together. Fig. 41 is a spermatogonial prophase of Scatophaga; and Figs. 42 and 43, spermatogonial prophase and metaphase of Tetanocera. All show equally paired ordinary or V-shaped chromosomes and unequally paired heterochromosomes. Figs. 44 and 45 are prophase and metaphase of the first spermatocyte of Scatophaga, Figs. 46 and 47 the corresponding stages for Tetanocera. In both species it will be seen that there is a close resemblance between the paired condition of the chromosomes in the prophases of a spermatogonial division and of a first spermatocyte mitosis. In general the chromosomes were larger in the spermatogonia (Figs. 41, 42, 43) than in the spermatocytes (Figs. 44, 45, 46, 47), but frequently prophases of spermatocyte mitoses could be certainly identified as such only by the metaphases in the same cyst and the growth stages in the neighboring cysts. The only actual observable difference between the synaptic condition in the spermatocytes and the spermatogonia is the behavior of the pairs in the following mitosis: in the spermatogonia the members of the pairs separate in metaphase (Fig. 43), and each divides in metakinesis; while in the spermatocytes the members of each pair remain closely associated in metaphase (Figs. 45 and 47) and separate in metakineses (Fig. 48), but do not divide until the

second spermatocyte mitosis, though they frequently show the preparatory split in the anaphase (Fig. 49). We have here an unusually clear demonstration of the essential facts of synapsis and reduction, together with the rather unusual phenomenon of conjugation of homologous chromosomes in cells outside the sphere of maturation. Prophases of the second spermatocyte mitosis in Scatophaga appear in Figs. 50 and 51, and metaphases in Tetanocera in Figs. 52 and 53. An oögonial prophase and anaphase are given in Figs. 54 and 55, and a late prophase for Tetanocera in Fig. 56.

These two species as well as the one following belong to the Acalyptrate Muscidæ.

8 Drosophila ampelophila

Drosophila has been placed at the end of the list of Muscidæ because of the peculiarities which occur in the behavior of its chromosomes and the difficulties which have been encountered in their interpretation. While in Sarcophaga all the stages necessary for a description of the behavior of the heterochromosomes of both sexes were found in the course of a few hours' work on perhaps ten or twelve preparations, satisfactory results in the case of Drosophila have been obtained only after a prolonged study extending over more than a year and involving the dissection and examination of some two thousand individuals. Sectioning the material has never given satisfactory results. Hermann's platino-osmic solution and Worcester's formal-sublimate gave the best fixation, but the division stages are so scattering that permanent preparations, even if good fixation were secured, seemed less practical than the aceto-carmine method, which is much quicker and gives clearer pictures of the mitotic phenomena when they are present.

Spermatogonial mitoses are not abundant, and cells in which perfectly clear equatorial plates can be studied are exceedingly rare. The chromosomes in prophase are paired and twisted together in such a manner that it has been impossible to make an intelligible drawing of them in an early prophase. In Fig. 57, a

late prophase, two small spherical chromosomes and four larger elongated ones are distinctly paired while the members of the unequal pair (h_1, h_2) are separated. For a long time it was impossible to be sure that an unequal pair was present, as foreshortening in the case of one chromosome (h_2) was possible, but recently a comparatively large number of good spermatogonial plates has been secured in which the inequality in length of one pair is clearly demonstrated. No case has been found in which the members of this pair appeared to be equal. Figs. 58, 59 and 60 show exceptionally clear cases, and Fig. 61 shows a peculiar folding of the chromosome h_1, whose significance may be apparent as we proceed to consider the unequal heterochromosome bivalent of the first spermatocyte.

In Drosophila the heterochromosomes cannot be demonstrated in the growth stages of the first spermatocyte. In some sections from Hermann material stained with thionin the plasmosome (p) and some of the chromosomes appeared as in Fig. 62 in cysts adjacent to the spermatogonial cysts. In later growth stages nothing definite, except the immense plasmosome, can be made out in regard to the contents of the nucleus. The earliest prophase of division is the appearance of the chromatin massed together, usually on one side of the nucleus, while the plasmosome may be in the middle or on one side of the nucleus (Fig. 63). In aceto-carmine preparations the chromosomes first appear in early prophase, scattered through the nucleus, faintly stained and irregular in outline (Fig. 64). The plasmosome may be broken up at this time or it may appear intact in the spindle. Figs. 65 and 66 are later prophases in which the chromosomes are completely condensed. The unequal heterochromosomes are h_1 and h_2. Fig. 67 shows the three equal bivalents, and the unequal heterochromosome pair in its simplest form, in the metaphase of the first spermatocyte mitosis. Fig. 68 shows slight modifications of this form from other cells of the same cyst. The most common form of this pair is seen in Figs. 69 and 70, where there are two equal V-shaped elements and a third portion (x) which in many cases looks like a separate element, and for a time the group was thought to be trivalent; i. e., made up of two equal V-shaped

chromosomes and a smaller odd chromosome. This belief was strengthened by the appearance of many metaphases and anaphases (Figs. 70, 71, 72) where the third portion of the figure (x) seemed to be on the point of separating from the V-shaped element next to it. This opinion was not confirmed however by the composition of the spermatogonial or oögonial equatorial plates, nor was it possible to demonstrate with certainty a separate element corresponding to x in the polar plates of the first spermatocyte mitosis or in the second spermatocyte. Fig. 72 is one of several cases where the portion x seemed to be separated from the two other elements of the group, but the separation must have been only apparent, for one much oftener finds an anaphase like Fig. 73 where the separation of the heterochromosome group into two unequal parts is certain (h_1, h_2). Sometimes the anaphase is like Fig. 74, where more or less spherical masses replace the usual V's of the heterochromosome group. Often all of the chromosomes except the smallest pair show in the metaphase that they are elongated and V-shaped (Fig. 75), and in late anaphases (Fig. 76) the elements of the two largest bivalents are usually divided and the daughter chromosomes separated, often crossed. Both here and in the second spermatocytes it is often difficult or impossible to distinguish the heterochromosomes from the others. In the telophase the chromatin forms a dense mass which loses none of its staining quality and is soon resolved into the already divided chromosomes of the second spermatocytes (Figs. 77, 78, 79). A greater or less degree of elongation together with twisting and fore-shortening makes it impossible to measure or even estimate with any accuracy the relative length of the chromosomes, so as to distinguish the two classes of second spermatocytes as to size of heterochromosomes. Figs. 78 and 79 are two equatorial plates from the same cyst where the corresponding chromosomes are probably a—a, b—b, and h_1—h_2. All of the chromosomes divide in this mitosis.

The oögonial metaphases are perfectly clear, and four equal pairs of chromosomes are always present (Figs. 80, 81, 82). In the metaphase they are usually grouped in pairs, and in the prophase they are closely approximated and twisted. In fact this

prereductional pairing of homologous chromosomes was first noticed in the oögonia and ovarian follicle cells of Drosophila. An attempt was made to ascertain whether such a pairing occurs in embryonic cells. Very little evidence was obtained. In the prophase of one mitosis paired chromosomes were found (Fig. 83). Fig. 84 is the equatorial plate of a segmentation stage. In both cases the pairs appeared to be equal.

9 *Eristalis tenax*

A considerable number of these flies were captured on some late blooming mustard plants in October. The material was in exceptionally favorable condition, and a complete series of drawings was obtained. The outer wall, or capsule, of the testis was thinner and more permeable to fixing fluids than in most of the other species studied and it was therefore possible to work with both sections and aceto-carmine preparations. This fly belongs to the family Syrphidæ, but the chromosomes in most respects resemble those of the Muscidæ. The heterochromosome bivalent is different in form from that of any of the Muscidæ described above; it however consists of a larger and a smaller component united in a somewhat different way from the corresponding elements in Drosophila.

Among the spermatocytes, several follicle cells were found in mitosis; the chromosomes of one such is shown in Fig. 85. The spermatogonial chromosomes are paired in prophase but separate and form a flat plate in the metaphase as seen in Fig. 86, where the two heterochromosomes (h_1, h_2) are conspicuously unequal in size. In this form there is a distinct synizesis stage, as shown in Fig. 87, from a section of material fixed with Gilson's mercuro-nitric fluid and stained with thionin. The cysts in which this stage occurs border upon the spermatogonial region of the testis. The outline of the chromosomes is visible and in the next stage the chromosomes are distinctly bivalents. Later they become more diffuse, but do not appear to form an even spireme at any stage. Fig. 89 is a growth stage, showing the heterochromosome group (h), a pair of m-chromosomes and the other chro-

mosomes in a loosely branched condition. Fig. 90 is an early prophase in which the heterochromosome pair is very compact and deeply stained, while the other chromosomes are granular and denser in some parts than in others. A later prophase (Fig. 91), from a section, shows the heterochromosome pair assuming the cross-shape which we find in the later metaphase. Fig. 92 is a polar view of the equatorial plate of the first spermatocyte; and Figs. 93 and 94, side views of the spindle to show the cross-shaped heterochromosome bivalent in two positions. Here the cross (Fig. 94), instead of having opposite arms equal, as in cross-shaped tetrads composed of equal elements, has one of the vertical arms longer. It is evident from Figs. 93 and 95 that the longer arm is the smaller heterochromosome, while the remainder of the cross is the larger member of the pair. The larger element is folded in the same manner as in Drosophila (Figs. 66 and 67) but the smaller element is attached by one end instead of by the middle as in Drosophila. The second spermatocyte mitosis proceeds as in the other forms and presents nothing of especial interest. Dimorphism of the spermatozoa is foreshadowed by the first spermatocyte anaphases (Figs. 96 and 97). In the female the clearest figures were obtained from ovarian follicle cells (Figs. 98 and 99). The pairs are equal and comparison with the spermatogonial chromosome group (Fig. 86) indicates that the equal heterochromosome pair is one of the two longest.

The general results for the nine species of flies are the same; i. e., an unequal pair of heterochromosomes in the male leading to dimorphism of the spermatozoa, and a corresponding equal pair in the female, each equivalent to the larger heterochromosome of the male: also a prereductional pairing of homologous chromosomes in the prophase of mitosis in spermatogonia, oögonia, and ovarian follicle cells.

DISCUSSION

1 *Sex Determination*

So far as I know there is no published work on the heterochromosomes of the Diptera. The literature on the heterochromo-

somes in other orders of insects has recently been so fully discussed in a paper by A. M. Boring ('07) that it seems hardly necessary to go into the subject exhaustively here. The dimorphism of the spermatozoa resulting from the maturation of the male germ cells of the nine species of Diptera considered in this paper is of the same character as that described by the author for 36 species of Coleoptera (see note, p. 49, Stevens '06), and by Wilson ('05 and '06) for several species of Hemiptera heteroptera. The dimorphism is brought about by the presence in the spermatogonia and spermatocytes of an unequal pair of heterochromosomes, while in large numbers of other insects such dimorphism is due to the presence of an odd chromosome in the male germ cells. These flies have proved to be exceptionally favorable material for demonstrating the occurrence in the female germ cells and somatic cells of a pair of chromosomes, each equivalent to the larger heterochromosome of the male.

Here, as in similar cases previously described, it is perfectly clear that an egg fertilized by a spermatozoön containing the smaller heterochromosome produces a male, while one fertilized by a spermatozoön containing the larger heterochromosome develops into a female. The material does not, however, throw any further light on the question whether the dimorphic spermatozoa are themselves in some way instrumental in determining sex in these insects; or whether sex is a character borne by the heterochromosomes and segregated in the maturation of the germ cells of each sex. If the latter supposition is true, sex is probably determined by the dominant heterochromosome of the egg, and fertilization is selective as has been shown in previous papers (Wilson '05, '06; Stevens '06, p. 54; Nowlin '06; Boring '07).

The only hope of determining whether sex is a Mendelian character seems at present to lie in breeding experiments with forms that may be shown by cytological study to be favorable. It is probable that in some cases at least, other characters may be so correlated with sex that their behavior in heredity may throw light on the sex question.

As to the proportion of sexes in these flies, a few figures may be given for Drosophila ampelophila. In the autumn and winter

of 1906–07, Drosophila was bred in the laboratory on two kinds of food, grapes and bananas. As the flies were dissected for the cytological work, a record was kept of the numbers of each sex; 1551 were so recorded. Of these 759, or 48.94 per cent were males; 792, or 51.06 per cent females. The records of the grape-fed and the banana-fed flies were kept separately. The total number of grape-fed flies dissected between November 1 and March 19 was 787, 404 or 51.33 per cent being males, and 383 or 48.67 per cent females. The banana-fed flies between October 30 and December 3 numbered 764, 355 or 46.47 per cent males, and 409 or 53.53 per cent females. In the total number there were 2.02 per cent more females than males, in the grape-fed 2.66 per cent more males than females, and in the banana-fed 7.06 per cent more females than males. These differences are probably not significant, but if sex is a Mendelian character, the numbers for the two sexes should of course be equal unless food produces some discriminating effect on the development of either individuals or eggs of the different sexes. It has always been a noticeable fact that the banana-fed flies were larger and more robust than those fed on grapes; this however applies to both sexes. In mass cultures it is not possible to tell whether failure of many of one sex or the other to reach the adult stage in different cultures might account for the discrepancies in numbers observed with the two kinds of food.

Castle and his co-workers ('06 p. 772) found the sexes about equal in three families of the sixth inbred generation of a grape-fed series, and the remarks which follow the table indicate that they regard the normal proportion as near equality.

Monkhaus' results on sex in Drosophila seem not yet to be in print, except for a brief report in the Year Book of the Carnegie Institution.

An attempt was made to ascertain the normal proportion of the sexes for the adults of Musca domestica. When caught by hand 58.33 per cent were females, but when a wire trap baited with sugar or molasses was used, only 46.53 per cent were females. The results need no comment.

Cuenot states that the normal proportion of males to females

in Lucilia cæsar, Calliphora vomitoria and Sarcophaga carnaria is approximately equal, and his experiments show that neither amount nor kind of food given to the larvæ has any marked effect on the proportion of the sexes in the first or second generation, but here as elsewhere in such experiments the number of eggs that did not hatch is not noted, and this may be the critical point. It is evident that more experiments are needed in which the fate of all of the eggs of isolated pairs of flies is determined.

2 *Synapsis*

In the spermatogenesis of most insects synapsis involves an end-to-end union of homologous chromosomes, and tetrads of various forms are commonly found in the prophase of the first spermatocytes. In these flies no tetrads have been observed and as a rule nothing comparable to the synizesis, bouquet or spireme stages of other forms is apparent. In these respects the germ cells of the Diptera resemble the oögonia of sagitta (Stevens '03 and '05) and the male and female germ cells of the aphids (Stevens '05 and '06). In the oögonia of Sagitta the chromosomes pair side-to-side in an early stage, while in the spermatogonia of the aphids the pairing occurs as a prophase of the first spermatocyte mitosis. The indications are that in the flies the chromosomes are already paired side-to-side at the beginning of the growth stage (Figs. 87 and 88), but the pairs do not appear to unite end-to-end to form a spireme. In some cases the members of the pairs are perfectly fused in the prophase of the first spermatocyte (Figs. 3 and 27); in others the bivalents are clearly such in both prophase and metaphase (Figs. 44 to 46). The first spermatocyte division is without doubt reductional for both ordinary chromosomes and heterochromosomes.

Perhaps the most interesting point in the whole study is the pairing of the chromosomes in cells somewhat removed from the sphere of the reduction process. This was first noticed in the oögonia of Drosophila, and was also found to occur in the ovarian follicle cells, the spermatogonia and some embryonic cells. This is not an occasional phenomenon, but one which belongs to every

oögonial and spermatogonial mitosis. In many cases the prophases of spermatogonia and first spermatocytes resemble each other very closely, the members of each pair being twisted together in both. In the spermatocyte we get complete synapsis and reduction; in the spermatogonium only a foreshadowing of reduction, and abundant proof that synapsis is here a side-to-side pairing of homologous chromosomes, and the first spermatocyte division a separation of univalent chromosomes, and not a longitudinal or quantitative division of two chromosomes united end-to-end. The relation of the heterochromosomes to each other in synapsis varies greatly with differences in form and size.

One is tempted to suggest that if homologous maternal and paternal chromosomes in the same cell ever exert any influence on each other, such that it is manifest in the heredity of the offspring, there is more opportunity for such influence in these flies than in cases where pairing of homologous chromosomes occurs but once in a generation. Possibly experiments in cross-breeding of flies may bring out some interesting facts in heredity.

NOTE. A preliminary statement in regard to the chromosomes of Drosophila was made at the International Congress of Zoölogists in Boston, August 21, 1907. The question as to whether an odd chromosome or an unequal pair of heterochromosomes was present in the male cells was then unsettled.

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DESCRIPTION OF PLATES

With the exception of Figs. 59, 65, 73 and 82 for which a Zeiss 1.5 mm. obj. was used, the figures were all drawn with a Zeiss 2 mm. oil immersion obj. and a Zeiss compensating oc. 12. The magnification was doubled with a drawing camera, and the figures were then reduced one-half, giving a magnification of 1500 diameters.

Lettering on plates

h = a heterochromosome or a pair of heterochromosomes.
h_1 = the larger heterochromosome.
h_2 = the smaller heterochromosome.
m = an m-chromosome (Wilson).
p = plasmosome.
x = middle part of h_1 in Drosophila.

Plate I

Musca domestica

Fig. 1 Spermatogonium, prophase, five equal pairs and one unequal pair of chromosomes.
Fig. 2 First spermatocyte, growth stage.
Fig. 3 First spermatocyte, prophase.
Fig. 4 First spermatocyte, anaphase.
Figs. 5 and 6 Second spermatocytes, prophase.
Figs. 7 and 8 Second spermatocytes, anaphase.
Fig. 9 Oögonium, metaphase.

Calliphora vomitoria

Fig. 10 Spermatogonium, metaphase.
Fig. 11 First spermatocyte, growth stage.
Figs. 12 and 13 First spermatocyte, metaphase.
Fig. 14 First spermatocyte, anaphase.
Figs. 15 and 16 Second spermatocyte, metaphase.
Fig. 17 Second spermatocyte, anaphase.
Figs. 18 and 19 Oögonia, metaphase.

Lucilia cæsar

Fig. 20 First spermatocyte, growth stage.
Figs. 21 and 22 First spermatocyte, metaphase.
Figs. 23 and 24 Second spermatocyte, prophase.

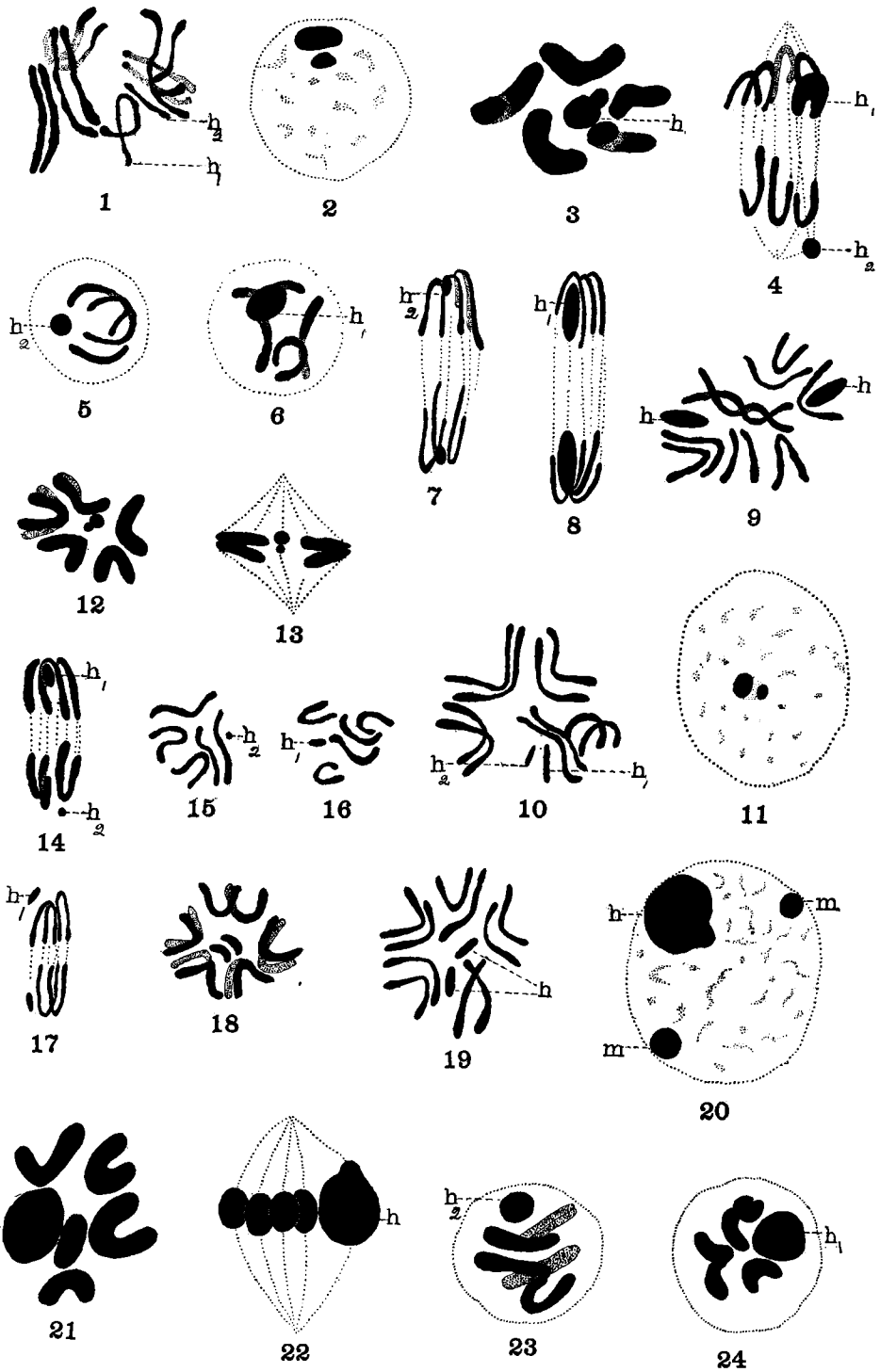
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Plate II

Sarcophaga sarraciniæ

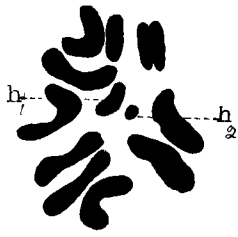
Fig. 25 Spermatogonium, metaphase.
Fig. 26 First spermatocyte, growth stage.
Fig. 27 First spermatocyte, prophase.
Fig. 28 First spermatocyte metaphase.
Fig. 29 First spermatocyte, metakinesis.
Figs. 30 and 31 First spermatocyte, anaphase.
Figs. 32 and 33 Second spermatocyte, metaphase.
Figs. 34 and 35 Oögonia, metaphase.
Fig. 36 Ovarian follicle cell, metaphase.

Phorbia brassica

Fig. 37 First spermatocyte, growth stage.
Fig. 38 First spermatocyte, prophase.
Fig. 39 First spermatocyte, metaphase.
Fig. 40 First spermatocyte, anaphase.

Scatophaga pallida and Tetanocera sparsa

Fig. 41 Scatophaga, spermatogonium, prophase.
Fig. 42 Tetanocera, spermatogonium, prophase.
Fig. 43 Tetanocera, spermatogonium, metaphase.
Fig. 44 Scatophaga, first spermatocyte, prophase.
Fig. 45 Scatophaga, first spermatocyte, metaphase.



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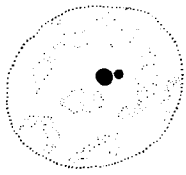

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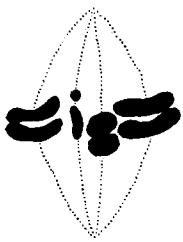

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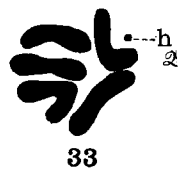

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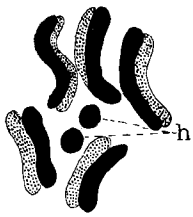

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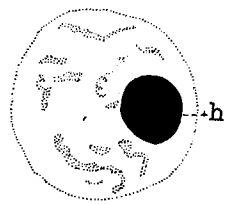

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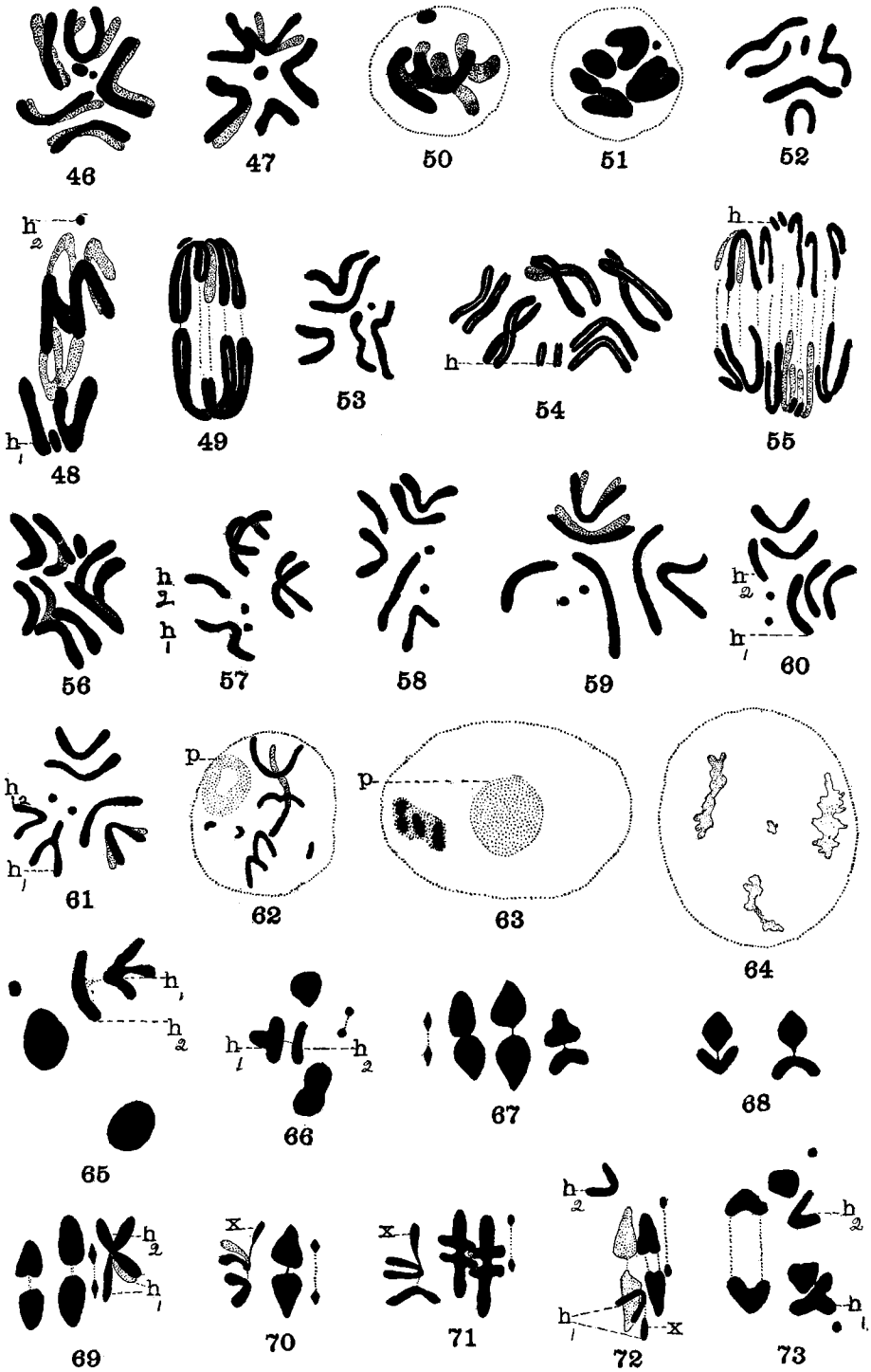
Plate III

Scatophaga and *Tetanocera* (continued)

Fig. 46 Tetanocera, first spermatocyte, prophase.
Fig. 47 Tetanocera, first spermatocyte, metaphase.
Fig. 48 Scatophaga, first spermatocyte, anaphase.
Fig. 49 Scatophaga, first spermatocyte, anaphase.
Figs. 50 and 51 Scatophaga, second spermatocyte, prophase.
Figs. 52 and 53 Tetanocera, second spermatocyte, metaphase.
Fig. 54 Scatophaga, oögonium, prophase.
Fig. 55 Scatophaga, oögonium, anaphase.
Fig. 56 Tetanocera, oögoniaum, prophase.

Drosophila ampelophila

Fig. 57 Spermatogonium, late prophase.
Figs. 58–61 Spermatogonia, metaphase.
Fig. 62 First spermatocyte, early growth stage.
Fig. 63 First spermatocyte, very early prophase.
Fig. 64 First spermatocyte, prophase.
Figs. 65 and 66 First spermatocyte, late prophase.
Fig. 67 First spermatocyte, metaphase.
Fig. 68 Heterochromosome pairs.
Figs. 69–71 First spermatocyte, metaphase.
Figs. 72 and 73 First spermatocyte, anaphase.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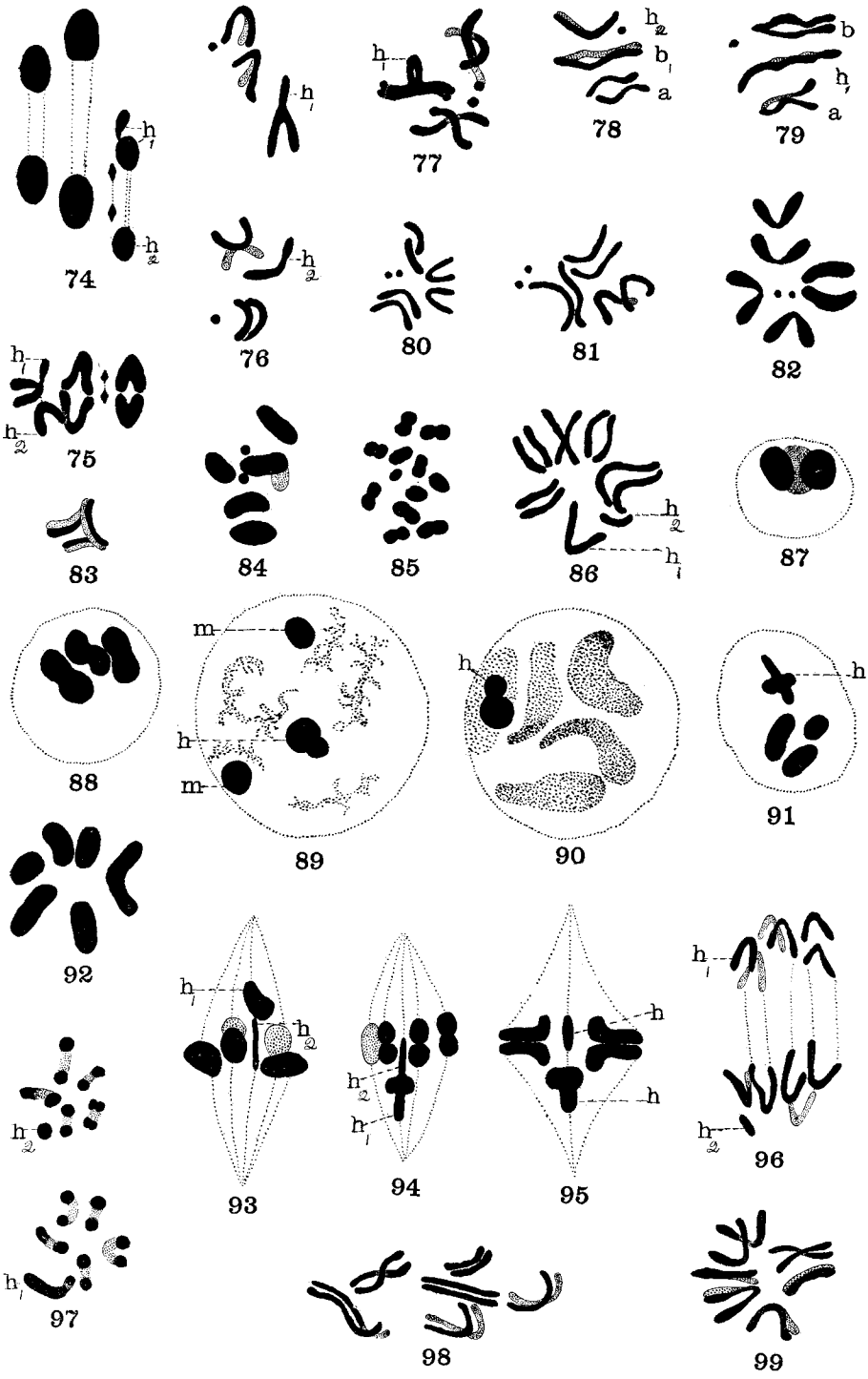
Palte IV

Drosophila (continued)

Fig. 74 First spermatocyte, anaphase.
Fig. 75 First spermatocyte, metaphase.
Fig. 76 First spermatocyte, anaphase.
Figs. 77–79 Second spermatocyte, metaphase.
Figs. 80–82 Oögonia, metaphase.
Fig. 83 Chromosomes from embryonic cell.
Fig. 84 Chromosomes from segmentation stage.

Eristalis tenax

Fig. 85 Chromosomes of follicle cell of the testis.
Fig. 86 Spermatogonium, metaphase.
Fig. 87 First spermatocyte, synizesis stage.
Fig. 88 First spermatocyte, growth stage immediately following synizesis stage.
Fig. 89 First spermatocyte, later growth stage.
Fig. 90 First spermatocyte, early prophase.
Fig. 91 First spermatocyte, late prophase.
Figs. 92–95 First spermatocyte, metaphase.
Figs. 96 and 97 First spermatocyte, anaphase.
Figs. 98 and 99 Chromosomes of ovarian follicle cells, prophase and metaphase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