PROPHASE CHROMOSOME BEHAVIOR IN TRIPLOID INDIVIDUALS OF *DROSOPHILA MELANOGASTER*

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One feature of chromosome behavior characteristic of the Diptera is the paired association of homologous chromosomes in the somatic cells as well as in the germ cells. This is indicated by the side-by-side arrangement of homologues in the metaphase plate (STEVENS 1907, 1908), which is in turn due to an intimate association in the prophase when the chromosomes are drawn out into long threads (METZ 1916). It has been found that this same principle of association of homologues applies in the case of tetraploid cells (somatic) in flies (HOLT 1917, METZ 1916, 1922). Here the association is in fours, and apparently all four members of a set are associated with equal intimacy (METZ 1922). In octaploid cells it is probable that a similar association occurs, the sets being composed of eight members (METZ 1916, HOLT 1917), but the evidence is not so clear here since only metaphases were identified as octaploid.

These results seem to indicate that the association is due to the attraction of homologous materials in corresponding chromosomes, and not to a simple positive-negative type of attraction which would become "balanced" when two members came together. In all of the above cases, however, homologous chromosomes have been present in even numbers. No flies have hitherto been available in which odd numbers were present. Such flies are now provided, however, by the triploid "race" of *Drosophila melanogaster* obtained by Doctor C. B. BRIDGES, who has kindly furnished material for the present study.

An examination of this material has shown that here also homologous chromosomes are not only associated in metaphase (cf. figure 4, and also figures in a forthcoming paper by BRIDGES), but undergo an intimate association during somatic prophases, the association being in threes, and all three members being associated with equal intimacy, as far as can be determined visually. The inferences drawn from previous observations thus apply to this case in which homologues are present in odd numbers.

Explanation of Plate 1

All figures are from sectioned material, fixed in strong Flemming. They were drawn with the aid of the camera lucida, at table level, using Zeiss 1.5 mm objective and number 12 ocular, and are reproduced without reduction.

All figures are from *Drosophila melanogaster* Meigen.

Figures 1 to 3 are from diploid specimens; the remainder are from triploids.

Figures 1 to 3 represent the metaphase and prophase conditions in ordinary diploid specimens.

Figure 4 is a typical triploid metaphase with an extra Y chromosome ($3n+Y$). The larger of the small bodies in the center is probably double, representing two of the three "m chromosomes." All of the other chromosomes are obviously in threes, except the extra Y at the top of the figure.

Figures 5, 6, 7, 10 and 11 are prophases from adjacent cells near the tip (distal end) of an ovary (slide 2165-2). These are undifferentiated cells. Figure 5, and probably figures 6 and 7, represent entire or practically entire nuclei, although in 7 part of one or two chromosomes may be cut off. In each of these figures the triads are slightly transposed to prevent overlapping. No good metaphases were obtained in this ovary, but the prophases have an extra small body which presumably is a Y chromosome. This body appears to be close to the X's in the drawings (figures 5, 6, 7), but the appearance is somewhat misleading, for in figure 5 the X's are transposed and should be farther from the Y-like body, and in 7 the body is at a higher level than the X's. In figure 6 the relative positions are correctly represented.

Figures 8 and 9 are from ovarian follicle cells. Here again the Y chromosome may be present, although no good metaphases were obtained to check the point. In figure 9 only the large autosomes are clear. The sex chromosomes are either cut or broken apart or otherwise disturbed, so that their relations are not clear.

Figures 10 and 11 represent single triads from triploid prophases to show the intimacy of association of the three homologues.

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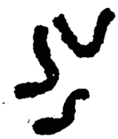

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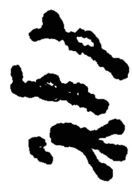

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A detailed discussion of these earlier cases in the flies, including theoretical considerations and also a comparison with analogous conditions in other organisms, has been given in earlier papers (METZ 1916, 1922). The present paper will, therefore, be mainly a descriptive account.

The nature of the prophase association in triploid cells is best shown by the figures, and needs little discussion. In the following account a résumé of the general features is given first, followed by notes on the individual figures.

Typical prophase figures are shown in the accompanying camera lucida drawings, which were made from somatic and ovarian cells of females,[1] including follicle cells and undifferentiated cells whose descendants become nurse cells and oöcytes. Chromosome behavior is not visibly different in these different types of cells.

Figures 1 to 3 are typical diploid figures, the latter two showing the close approximation of homologues in prophase. The remainder are triploid figures. These are from specimens identified as triploids by their external appearance and (in some cases) by metaphase chromosome groups, as well as by the prophase figures shown here; so it is safe to assume the presence of the triploid number even when the association is so close that a direct count cannot be made.

In some, if not all, of the accompanying triploid figures an extra Y chromosome is present. This is shown clearly in the metaphase group of figure 4. Such groups, therefore, are $3n+Y$. Apparently the Y does not associate with the three X's in prophase, although it may be near them (see below). The very small "m" or "fourth" chromosomes are not, as a rule, distinguishable in the prophases, either in triploid or diploid cells.

Most of the accompanying prophase figures represent a fairly late stage in prophase, and in most cases some of the triads are transposed in drawing so that they will not overlap. In the actual figures they usually lie at different levels and overlap. It was found impracticable to draw earlier stages because the threads were so elongate and intertwined that they could not be represented clearly. From analogy with conditions in diploid cells of other Diptera (METZ 1916), however, it is assumed that the association of homologues is more intimate in the earlier prophase stages than in those figured here.

The autosomes appear to associate uniformly throughout their length, but the X chromosomes seem to behave differently. In most figures the latter are closely associated for about half their length, and then diverge,

[1] All of the triploids are females. See forthcoming paper of BRIDGES.

finger-like, as shown by the drawings. This may be due to a precocious separation of the homologues at one end, preceded by a stage of close association throughout. An attempt is being made to study this feature further. The figures thus far examined indicate that the behavior is constant and that the end at which the association remains intimate is probably the one at which the spindle fibres become attached. In any case, the phenomenon is sufficiently definite to suggest that it is a reflection of the process in oögenesis which is responsible for the unusual crossover values given by the X chromosome in triploid flies, as is pointed out by BRIDGES in a later paper. In such flies BRIDGES has found that crossing over near one end of the X is greater, and near the other end less, than in ordinary diploid flies.

In late prophase, as the chromosomes separate and go on the spindle, the X's (which are rod-like and have a terminal spindle-fibre attachment) tend to retain their positions with respect to one another, usually remaining parallel. The large autosomes, however, are apparently disturbed in their arrangement. These are V-shaped, and have a median spindle-fibre attachment. Instead of remaining parallel and going on the spindle "three deep," as might be expected, they frequently, or usually, separate. Judging from the available figures one of the most frequent shifts results in the condition shown in figure 4, in which one member of each set has moved to one side,—the other two remaining parallel as in diploid figures.

This behavior suggests that the equator of the spindle is restricted in size, and that the autosomes cannot remain "three deep" without either extending beyond the margin of the equator or else crowding too closely together in the center. In other words, it suggests that the chromosomes move, or are drawn, to within a definite distance of the center, but are at the same time held apart so that they are not crowded. Apparently, an equilibrium cannot, as a rule, be reached if the autosomes all remain parallel and three deep.

If, as suggested by observations on other Diptera (METZ and NONIDEZ 1922, 1924), each chromosome is enveloped in a transparent gelatinous sheath or rind, these sheaths may hold them apart and may account for the apparent absence of crowding near the center of the figures,—which in turn may account for the shifting of some chromosomes out of alignment.

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