

1975

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### Recommended Citation

Guest, William C. (1975) "Somatic Pairing in *Drosophila virilis* Mitosis," *Journal of the Arkansas Academy of Science*: Vol. 29 , Article 14.

Available at: <http://scholarworks.uark.edu/jaas/vol29/iss1/14>

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# Somatic Pairing in *Drosophila virilis* Mitosis

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## ABSTRACT

In neuroblast cells homologous chromosomes tend to pair during prophase of mitosis. Heterochromatic elements of homologous chromosomes are widely separated in very early prophase, at which time the euchromatin is poorly stained. Pairing is intimate for euchromatic portions of chromosomes in early and middle prophase with chiasmata frequently present. Homologous chromosomes most commonly lie side-by-side in late prophase and metaphase. Statistical data are presented to show the frequency of intimate pairing in prophase and side-by-side pairing in metaphase.

## INTRODUCTION

Somatic pairing of the chromosomes in Diptera first was reported by Stevens (1908) who described this process in *Drosophila*. Further studies of somatic pairing in *Drosophila melanogaster* and other Diptera have been made by Metz (1916), Kaufman (1934), Cooper (1948, 1948) and Grell and Day (1970). Studies indicate that synapsis of homologous chromosomes during mitosis is a common phenomenon with chiasmata formation occurring during some stages of pairing but without the occurrence of crossing over. Descriptions of somatic pairing have come primarily from observations of neuroblast cells prepared by sectioning or squashing.

This study was undertaken to determine the frequency of somatic pairing in *Drosophila virilis* where pairing was described by Metz (1916), and to determine the sequence of events in somatic pairing in mitotic prophase.

## MATERIALS AND METHODS

*Drosophila virilis* was used for the study. The stock used was obtained from the University of Texas (Stock No. 1801.1). The flies were maintained in the laboratory on standard *Drosophila* growth medium.

Neuroblast cells in mitosis were prepared according to a technique modified from that of Guest and Hsu (1973). The brains of 20-30 third instar larvae were dissected out in physiological saline, treated briefly with distilled water, then fixed in one part glacial acetic acid in three parts absolute methanol. The brains were dissociated into single cells in 60% glacial acetic acid and dropped from a Drummond pipette onto a slide preheated to 40C. The preparations were air dried. The slides were stained in 2% Giemsa prepared in 0.15 M phosphate buffer. Slides were stained for 10 minutes, rinsed in distilled water, air dried and mounted in Eukitt.

## RESULTS AND DISCUSSION

In *Drosophila* the heterochromatin appears distinct in prophase in contrast to the euchromatin which stains very lightly. Usually, the heterochromatin will stain intensely in interphase and very early prophase, at which time the euchromatin cannot be seen. This is particularly true when nuclei are stained with Giemsa.

For this study, if the whole chromosome could be seen with the euchromatin extended but distinct, the nucleus was considered to be in early prophase (Fig. 1). Middle prophase was that stage where euchromatin had condensed to some degree as seen in Figure 2, whereas in late prophase the euchromatin was condensed but it was still possible to



Figure 1. Early prophase showing pairing of euchromatin of homologous chromosomes.



Figure 2. Middle prophase showing pairing of euchromatin of homologous chromosomes with chiasmata in two of the pairs.

distinguish between the euchromatin and heterochromatin (Fig. 3). In metaphase the chromosomes stained uniformly (Fig. 4). In every early prophase it was difficult to determine whether or not the euchromatin was paired. Usually the heterochromatic portions of the chromosomes would be distinct and widely separated, the euchromatin appearing as a mass of poorly defined strands. These very early prophases were not counted.

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Nuclei in air dried preparations are well spread and flattened, and the chromosome structure is observed more readily than in conventional squash preparations. Thus, large numbers of nuclei in various stages of mitosis were available for study.

In early prophase 17 of the 22 nuclei examined showed intimate pairing and one nucleus was observed showing chromosomes with side-by-side pairing. Approximately 82% of early prophase chromosomes showed evidence of pairing of homologues.

In middle prophase 46 of 61 nuclei showed chromosomes with intimate pairing, nine of the 61 showing side-by-side pairing. By late prophase the picture had changed significantly, however, with only two of the 59 nuclei examined showing intimate pairing and 25 of the 59 nuclei showing side-by-side pairing. In metaphase 42 of 85 nuclei examined showed side-by-side pairing and none exhibited intimate pairing. These results are summarized in Table I.

There is no statistical difference between the percentages showing intimate pairing in early and middle prophase. Nor is the difference between the percentages of side-by-side pairing in metaphase and total pairing in late prophase significant. It should be pointed out, however, that in the technique for



Figure 3. Late prophase showing separation of homologous chromosomes with several homologues lying side-by-side.



Figure 4. Metaphase showing random arrangement of chromosomes.

preparing the cells for study there is an opportunity for distortion as the cells are flattened by air drying. The difference between late prophase and metaphase may be due to this treatment.

The observations on pairing in mitosis can be interpreted as follows. Intimate pairing of euchromatin of homologous chromosomes is initiated in early prophase or perhaps as early as the preceding interphase. Kaufman (1934) showed illustrations of early prophase showing intimate contact between homologues, and indicated that this complete pairing is found frequently. No cases of complete pairing were observed in this study. Though it was not possible to observe the euchromatin in the very early prophases, the euchromatin appears very elongated and pairing is certainly possible. By early prophase the euchromatin is paired intimately in most cases, with the heterochromatin widely separated. Not all chromosomes in a nucleus show intimate pairing and in many instances the X chromosomes will remain unpaired as Kaufman (1934) noted. The X and the Y are associated randomly; they may lie near each other but are never paired.

The intimate association of the euchromatin of homologous chromosomes continues through middle prophase with chiasmata present in many cases. By late prophase, however, the chromosomes separate and tend to lie side-by-side. Usually the homologues are not in physical contact with one another. Both Kaufman (1934) and Cooper (194) called attention to this side-by-side pairing in late prophase and metaphase, as did Grell and Day (1970). By metaphase all of the homologous chromosomes have separated and about one half of the nuclei show the side-by-side pairing.

Both Kaufman and Cooper studied somatic pairing in *Drosophila*, but did not attempt to determine the frequency of occurrence. Grell and Day (1970), using oögonial cells of *Drosophila melanogaster*, determined the frequency of pairing for both onohomologous and homologous chromosomes at metaphase. In *Drosophila virilis*, as shown in Table I, it was found that approximately 77% of the early prophases studied showed intimate pairing and about 75% of middle prophases showed homologous chromosomes in this condition. In sharp contrast, in late prophase only 3.4% were intimately paired but

Table I. Nuclei in Mitosis Showing Pairing

	Early Prophase	Middle Prophase	Late Prophase	Metaphase
Total counted	22	61	59	85
Intimate pairing	17	46	2	0
Intimate pairing (%)	77.3	75.4	3.4	0
Side-by-side pairing	1	9	25	42
Side-by-side pairing (%)	4.5	14.8	42.4	48.9
Total pairing	18	55	27	48.9
Total pairing (%)	81.8	90.2	45.8	48.9

approximately 42% showed side-by-side pairing. In metaphase about 49% were in the side-by-side pairing. Grell and Day (1970) reported 71.6% pairing of homologous chromosomes in metaphase in contrast to the results reported here.

The behavior of chromosomes in prophase and metaphase indicates that somatic pairing of homologous chromosomes is a common phenomenon in *D. virilis* as it is in *D. melanogaster*. This association involves euchromatin only, with the heterochromatin unpaired. Cooper (1959), Yunis and Yasmineh (1971) and Hsu (1974) outlined some of the suggested functions of heterochromatin. Yunis and Yasmineh (1971) presented evidence that heterochromatin in general forms aggregates between both homologous and non-homologous chromosomes in both mitotic and meiotic mammalian cells. However, the evidence in *D. virilis* indicates that the heterochromatic segments of homologous chromosomes do not synapse even in very early prophases. One function of heterochromatin in *Drosophila*, where somatic pairing commonly occurs, may be to facilitate the separation of homologous chromosomes and insure proper disjunction in mitosis and meiosis.

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