X-RAY AND ULTRAVIOLET STUDIES ON POLLEN TUBE CHROMOSOMES. II. THE QUADRIPARTITE STRUCTURE OF THE PROPHASE CHROMOSOMES OF TRADESCANTIA* 

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Most x-ray data dealing with induced chromosome breakage are interpretable on the basis of a divided or an undivided chromosome. The extensive studies on induced breaks in the microspore chromosomes of *Tradescantia* indicate that chromatid and chromosome breaks result, respectively, from changes occurring within a divided or an undivided chromosome. Data from pollen tube chromosomes in the same plant, where the split nature of the chromosomes can be determined at the time of treatment, agree with the above view, and, at the same time, invalidate beyond a doubt the interpretation of Darlington and LaCour as to the origin of induced aberrations of the isochromatid type. The relative lack of mosaics in x-rayed *Drosophila* suggests that, for the most part, the chromosomes in the sperm head are undivided at the time of treatment, although chromatid breaks are by no means rare in the treated salivary gland chromosomes. It appears, therefore, that, as a general rule, the smallest subdivision of the chromosome to be involved in breakage and rearrangement is the chromatid. This interpretation explains very well similar breakage results obtained from chromosomes treated with ultraviolet, as well as the extensive data of Stadler on endospermal deficiencies in treated maize.

That the chromatid is not the smallest subdivision of the chromosome, however, has long been known (see Nebel and Kuwada for reviews). In addition to earlier observational studies there is much supporting data.
of recent date. Mention may be made of the x-rayed chromosomes of *Tradescantia*⁵,⁶ and *Steatococcus*,⁷ the quadripartite nature of the trabant in the microspore chromosomes of *Tradescantia*,⁸ and the occurrence of half-chromatid exchanges in the pollen tube chromosomes of the same plant.² Carlson¹² has likewise reported the probable occurrence of half-chromatid breaks in the neuroblast chromosomes of *Chortophaga* embryos, as has Marshak¹³ in *Vicia*, but these have been dismissed by some⁸ as irrelevant observations. Similar half-chromatid breaks are frequent in the pollen tube chromosomes of *Tradescantia* following x-ray or ultraviolet treatment,² although they are admittedly difficult to distinguish from the openings between adjacent somatic coils.

Recently a number of aberrations have been found whose interpretation can only be understood in terms of half-chromatid breaks and rearrangements, and it is the purpose of this note to present a consideration of them. Because of their sporadic appearance, no attempt has been made to relate them to dosage, but they are frequent enough to convince the author that the chromosomes in very early prophase (the time of treatment) are quadripartite.

![Figure 1](image)

**Figure 1**

Semi-diagrammatic drawings of *Tradescantia* pollen tube chromosomes. A and B. Half-chromatid exchanges between non-homologous chromosomes. C. Half chromatid exchange between the two chromatids of the same chromosome. D. Half-chromatid deletion which has rotated from an inside to an outside position. E. Metaphase chromosome showing a quadripartite condition in the centric region.

Figure 1 illustrates the types of half-chromatid aberrations found. Figures 1A and 1B are exchange breaks. At the points of exchange, the stretched condition of the threads permitted the split in the individual chromatids to be viewed with clarity even though the portions of the chromatids on either side of the break presented a solid and undivided
appearance. Figure 1C illustrates an exchange break between half-chromatids of the same chromosome. The sister chromatids have moved apart from each other at their centromeres, but they are held in close juxtaposition at the point of exchange.

The exchange type of break has never been found following treatment with ultra-violet. The breakage of a single half-chromatid, however, has been observed, and, in figure 1D, the rotation of the broken piece from an inside to an outside position leaves little doubt as to the interpretation: it cannot be confused with the separation of the gyres of a coiled chromatid. Further evidence of the quadripartite structure is illustrated in figure 1E. The chromosomes, in passing down the pollen tube, are frequently stretched, with the strain being evidenced by an attenuation of the centric region. When so stretched, this portion of the chromosome shows four very thin parallel strands, each possessing one or more coils of small diameter. Whether or not these stretched and coiled strands represent the centromere, or a portion of it, is not known; more likely, they are the half-chromatids pulled free from body of the chromatids. If the latter, it may be pointed out that there is no evidence of a chromomeric differentiation even though the threads approximate the thinness of a leptotene chromosome. The coils, too, are of a much smaller diameter than the usual somatic coil.

The fact that the chromatid is further split into half-chromatids in the early prophase stages poses the problem of "What is the functional unit of the chromosome, and what determines its integrity?" In crossing over, genetical and cytological evidence leaves little doubt that the chromatid is that functional unit. The chromatid also appears to be the smallest functional unit in coiling, and, as pointed out above, most x-ray and ultra-violet data are understandable if interpreted in terms of chromatids or chromosomes, but not in terms of some smaller unit. Since, however, the evidence presented reveals a quadripartite structure which under most circumstances behaves as though it were bipartite, the conclusion is unavoidable that there must be some structural unit in the chromosome other than the chromonemata themselves which preserves the integrity of the chromatid, thus enabling it to react as a single entity in crossing over, coiling, breakage, and reattachment. Occasionally this structure can be broken in such a way by radiation as to permit the formation of half-chromatid exchanges, thus revealing a further subdivision of the chromonemata, but under ordinary circumstances the unitary behavior of the chromatid remains. It is tempting to suggest the matrix as the structural unit which determines the behavior of the chromosome, or chromatid, in breakage and reattachment, but the speculative nature of our knowledge concerning the structure and function of the matrix is such as to make one proceed in that direction with caution. It is only possible to state that
the degree to which the chromonemata is subdivided is not the limiting factor which determines the types of breakage and subsequent recombination found following x-radiation. It likewise follows that ultra-violet, although possessing a localized photochemical action, is capable of breaking a bipartite chromatid. Whether it does so by disrupting some structure other than the chromonema itself remains to be determined.

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ON THE ASYMPOTIC SOLUTION OF THE DIFFERENTIAL EQUATION FOR SMALL DISTURBANCES IN A LAMINAR FLOW*

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The hydrodynamical equation of Orr and Sommerfeld (see C. C. Lin1 for a detailed analysis) is a special case of differential equations of the form

$$\sum_{j=0}^{4} a_j x^{(4-j)} + \lambda^2 \sum_{k=0}^{2} b_k y^{(2-k)} = 0$$

(1)

Here $a_j$, $b_k$ are analytic functions of the complex variable $x$, $\lambda$ is a large complex parameter with constant argument, $a_0 = 1$, and $b_0$ has a zero of first order at some point, say at $x = 0$.

The aim of the present work is to supplement the hydrodynamical theory by a mathematical study of the validity of the formal asymptotic developments used there and, in particular, to shed some additional light on the phenomenon of the so-called "crossing substitutions,"