ANALYSIS OF VARIANCE OF HUMAN HEAD MEASUREMENTS

TRAIT	MEAN SQUARE VARIANCE BETWEEN FAMILIES	MEAN SQUARE VARIANCE WITHIN A FAMILY	F VALUES
Chances under 1 per 100 that F values are due to sampling			
Bizygomatic width	155.02	12.50	12.40
Interpupillary dist.	42.71	4.38	9.85
Minimum frontal width	123.77	14.54	8.51
Head width	98.63	13.41	7.36
Head girth	711.30	107.42	6.62
Dist. bet. inner eye ang.	17.47	2.78	6.29
Trichion to gnathion	254.19	46.59	5.46
Nasion to gnathion	129.45	24.80	5.22
Head length	80.94	16.95	4.78
Head height	54.44	12.62	4.32
Chances 1 to 5 per 100 that F values are due to sampling			
Bigonial diameter	70.44	18.23	3.87
Nasion to stomion	43.38	14.66	2.96
Chances over 5 per 100 that F values are due to sampling			
Trichion to nasion	47.77	18.01	2.65
Stomion to gnathion	31.55	13.14	2.40

TWO X-RAY INDUCED MOSAICS IN DROSOPHILA PSEUDOÖBSCURA

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The mechanism of the origin of chromosomal aberrations is still an open question. The so-called contact hypothesis, advanced originally by Serebrovsky,[1] assumes that translocations and other gene rearrangements are formed due to chance union of chromosomes accompanied by the development of new associations between genes, somewhat in the manner of "illegitimate" crossing-over. According to this view, the breakage of the original chromosomes and the reattachment of the resulting fragments occur practically simultaneously. The alternative hypothesis assumes that chromosomes are broken first, and that some time may elapse before the points of fracture either reunite to restore the original situation or form new attachments.[2,3] Unfortunately, the problem is such that critical evidence has been difficult to obtain.[4, 5, 6, 7] The mosaic translocations described below may possibly shed some light on the question.

Normal males of race *A* of *Drosophila pseudoöbscura* were treated with x-ray (5000) units, and outcrossed to normal untreated females. The

salivary glands of the F_1 larvae were taken, stained in aceto-carmine, and permanent smear preparations were made with the aid of the usual technique. Each slide contained only the two glands of a single individual. In the course of study of these slides, two very remarkable aberrant sets of glands were found. Instead of having the customary single type of tissue, either completely normal or having all cells containing the same aberration, these two sets of glands were mosaics of more than one kind of tissue. Several facts show that this result cannot be due to contamination (i.e., mixing the glands of several individuals in the same slide). In the first place each slide contains two and only two glands; in these particular slides the two glands lie separately. Secondly, both glands of each set are of the same sex. Thirdly, and this is the main argument, both glands of each set contain mixtures of tissues, the same cytological condition being observed in some cells of either gland.

The more complex of the two sets of mosaic glands apparently contains four different tissues. An analysis was made of each of the glands of this mosaic. In one gland, a total of 42 cells proved to be satisfactorily analyzable; the precise status of 8 cells was in doubt and the rest were not clear enough to attempt a classification. The four types of cells are as follows. The first, and by far the most frequent type, observed in 58% (24 out of 42) cells examined, departs from normal in having a translocation between the third and probably the *Y*-chromosomes (Fig. 1*a*). In terms of the maps published by Dobzhansky and Tan,[8] the third chromosome is broken in section 80, between the first and the second dark discs distal to the "bulb." As the *Y*-chromosome in salivary glands is not a distinct body, being simply a part of the heterochromatic chromocenter, it is impossible to determine the position of the break in this chromosome. The second type of cells (11% of the total analyzed) contains a translocation involving the third and the fourth chromosomes (Fig. 1*b*). The third is broken at about the middle of section 66, and the fourth is broken in section 97, the major part of the third being exchanged for the distal end of the fourth chromosome. The third type of cell (19%) is a combination of the preceding two, i.e., the III–*Y* translocation is present together with the III–IV one (Fig. 1*c*). Finally, the fourth type (11%) are normal cells, apparently free from any cytologically detectable abnormality. The second gland of this set contained 15 analyzable cells, 12 doubtful ones and the rest too poor for classification. Again the most frequent type of cell was that having the III–*Y* translocation (11 out of 15). There was only one clear-cut example of the III–IV translocation, none of the III–*Y*, III–IV; and three examples of normal third chromosomes.

Several mechanisms which may produce such a mosaic may be suggested. If one were to suppose that two sperm fertilized a single egg and that each one had one chromosome aberration in it, a mosaic individual

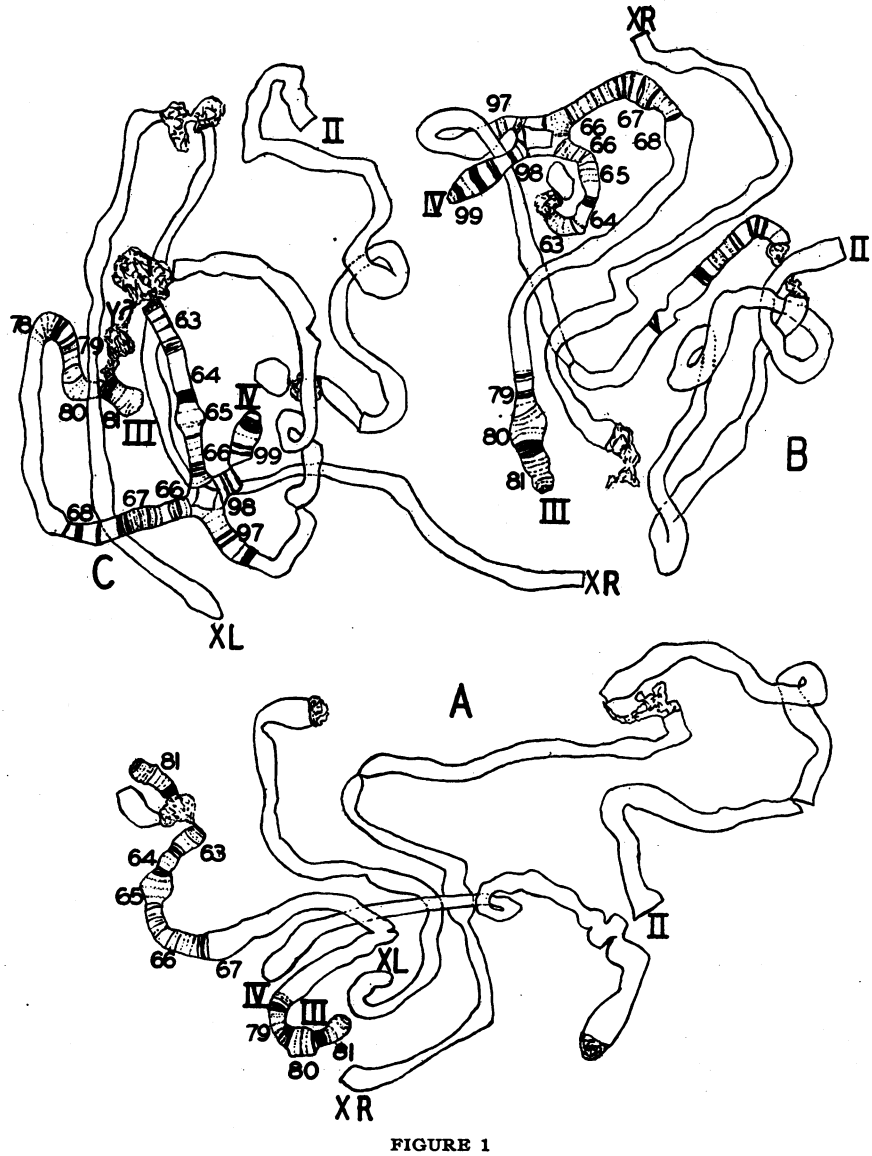

FIGURE 1

Three types of aberrant tissue found in the salivary glands of an F_1 male offspring from a cross between x-rayed males to normal females. *A*—translocation involving the tip of III and the *Y*-chromosome, *B*—translocation between the base of III and the tip of IV, *C*—combination of translocations *A* and *B*.

would result. Such an individual might have two different types of salivary gland tissue. That it is possible for both nuclei of the first cleavage division to be incorporated in the salivary gland tissue is supported by recent work of Kaufmann.[9] The points in the present evidence which automatically rule out this hypothesis are that not two but four types of tissues are present, and that one of these contains an aberration combining the properties of the two other aberrant types (Figs. 1*a* and 1*b*). Another possibility is that x-rays as such had no effect on the sperm, but that during the course of the development three types of the aberrant tissues arose spontaneously. A spontaneous translocation has been described in an individual of *Drosophila melanogaster* that has not been treated with x-ray, and this individual has been a mosaic of normal and aberrant tissue.[10] Since spontaneous chromosomal changes are relatively very rare, to suppose that so rare an event takes place three times in the development of a single individual is, however, too improbable. Still another possibility is that one translocation took place due to the irradiation (for example the III–*Y* translocation), and then another (the III–IV translocation) occurred spontaneously after fertilization in a part of the modified tissue. This view is also ruled out because of two securely established facts, namely the presence of cells with the III–IV but without the III–*Y* translocation, and of the apparently normal cells containing neither translocation. A somatic crossing-over would have to be invoked to produce these additional types.

The fourth possibility is one which assumes that the chromosomes in the sperm are in the four-strand stage. Were such the case a workable hypothesis could be developed to account for the formation of a four-tissue mosaic. For example, if one supposed that the breaks induced by the x-ray at any level effect only two of the four strands present, and if in the third chromosome two of the strands are broken in region 80, whereas the other two are broken in region 66, a cross-over occurring between one strand broken at 80 and one broken at 66 would result in one unbroken normal strand, one broken both at 80 and at 66, one broken at 80 and the fourth broken at 66. Reattachment of broken parts might occur before the chromosomes went into the first cleavage spindle. Then, all these suppositions granted, the segregation in the first and the second cleavages must be such that each of the resulting four nuclei contains one of the four types of cells found. The main weakness of this hypothesis is the assumption of crossing-over among the four strands of a chromosome of a haploid group.

The fifth possibility, and the one which seems most probable to the author on the basis of the available evidence, is that the breakage of the chromosomes due to x-rays need not occur at the time of the treatment but may be delayed for one or more cell generations. Let it be assumed that the action of the x-rays has weakened, or actually broken, the third chromosome in two places, in sections 80 and in 66, the fourth chromosome in sec-

tion 97 and the *Y*-chromosome at an undetermined point. Such a sperm has fertilized a normal egg. During the process of the chromosome splitting in the first two cleavage divisions the weaknesses or the breaks in the chromosomes have persisted. In one of the resulting cells the broken ends have become reunited to restore the original gene arrangements, thus giving rise to cells with normal chromosomes. In one of these normal cells, before the weaknesses have become healed, an exchange has occurred between the third chromosome and the *Y*-chromosome. This would give rise to the III–*Y* aberration. In another cell, or cells, an exchange has taken place between the fragments of the third and the fourth chromosomes which is later followed by an exchange between the third and the *Y*-chromosomes. Thus the four types of tissue have arisen containing a III–IV translocation, a III–*Y* translocation and a combination of the two.

The rather involved character of the above explanation must be admitted, but it seems to be the one that best fits the observed facts. It must be noted, however, that it is not entirely unprecedented. Indeed, Lewitsky and Araratian[11] have described a mosaic translocation in a root of a Crepis seed treated with x-ray, in which some cells were normal, others contained a translocation involving certain chromosomes and still others had the chromosomes further modified, with the first modification being preserved. Lewitsky and Araratian's observations, as well as the facts presented in this article, constitute evidence in favor of the view that breakage, or "weakening" of the chromosomes due to irradiation with x-rays precedes the reattachment and formation of aberrations.

The second mosaic pair of salivary glands contained only two types of tissue. The aberrant tissue consisted of an inversion in the second chromosome from the proximal part of region 43 to the distal part of region 45. The other type of tissue was normal. In one of the two glands 32 out of 48 analyzable cells contained the aberration, in the other gland, out of 36 analyzable cells, 15 were aberrant. This mosaic is not critical as an evidence for the "breakage first" hypothesis, since any one of several mechanisms might have produced it.

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