The Structure of the Chromocenter

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As has been shown in the already classical work of Painter, the chromosomes in the nuclei of salivary glands of Drosophila melanogaster have the appearance of six cross-striated rope-like structures containing the genes, and these six ropes are all connected together by their proximal ends to a body termed the chromocenter. In his first detailed paper (May, 1934), Painter figured this chromocenter as an element of the nucleus consisting of more or less diffuse or structureless chromatin. In his later papers, Painter does not alter this interpretation, nor add facts which would lead to a different one. That the chromocenter, on this view, is to be regarded as devoid of genes, may be inferred from his assignment of an approximate location even to bobbed and to the point of spindle fibre attachment, upon the rope-like structure which he proved to correspond to the X-chromosome, while in his latest paper (December, 1934) Painter again notes that the chromocenter is built up of inert chromatin.

In the work of Heitz (1934) on Drosophia virilis, a distinction is drawn between the central-most body which he calls “" heterochromatin”, and the proximal portions of the rope-like structures immediately adjacent to that structure. These latter he terms “' heterochromatin” and notes that they are less deeply stained than the “" heterochromatin”, while on the other hand they differ from the bulk of the rope-like bodies in being more deeply stained than the latter and apparently devoid of cross-striations. The length of these segments of “' heterochromatin” is, according to Heitz, different in the case of different chromosomes, but in all cases they are short compared with the remainder of the chromosome. He believes the “inert regions” of the mitotic chromosomes to correspond with the “" heterochromatin” only. In Bridges’ recent work (1935) no new facts or interpretations are added concerning the chromocenter, but his very detailed maps show, in the case of the X-chromosome at least, a rather faintly cross-striated region, adjacent to the chromocenter, which is hardly represented on Painter’s map, and which may probably be considered as corresponding to Heitz’s “' Heterochromatin.” It is not, however, suggested by Bridges that this region
has any special peculiarities, and in fact other regions of more or less similar appearance may be found in other parts of his maps.

Prior to the publication of Bridges' work, a cytogenetic investigation of the inert region of the X-chromosome was carried out by Muller and Prokofyeva (1935), by means of a study of a series of inversions in which the right break had occurred in the inert region. In this work it was found that the inert region of the X ("XI") is identifiable, in the main at least, as a faintly cross-striated region shown to the right of the last striation in Painter's map. It no doubt corresponds with the similar faintly striated region found in Bridges' independent work and there designated as 19 EF, 20 ABCD, and it probably corresponds at the same time with the so-called "β heterochromatin" figured in Drosophila virilis by Heitz. The number of striations in this region is at least as great as seven, but the visible number varies according to the quality of the preparation and the optical conditions. The cytogenetic work of Muller and Prokofyeva further showed that bobbed lies in the distal third or quarter of this region, and probably lies in the portion containing the two most distal faint striations. This work was quickly followed by the finding by Prokofyeva (described in a parallel paper, 1935) that the Y-chromosome in large part at least consists of a small faintly cross-striated body similar to and homologous with the inert region of the X, and conjugating with the latter. These findings have led to a more intensive study, on the part of the present author, of the structure of the chromocenter in general. Preliminary data obtained in this investigation are herewith presented.

Observations

Turning our attention first to the already demonstrated inert region of the X, and the homologous portion of the Y-chromosome, it is to be noted first that the cross-striations there visible (as seen in aceto-carmine preparations) appear to be composed of very fine chromioles, situated relatively far apart from one another; thus these striations appear as interrupted lines. It is possible that these chromioles are simple, corresponding to the loci of individual genes. These chromioles are easily displaced by the crushing of the salivary gland; the striated structure then becomes disturbed and the region seems to be composed of scattered chromioles. This accounts for the unstriated character of such regions in Heitz's figures and for the fact that in Painter's figures these regions were not distinguished from the remainder of the chromocenter. The most proximal of the observable striations definitely attributable to the Y and to the inert
region of the X-chromosome directly enter into the formation of the central part of the chromocenter.

Fig. 1. The chromocentral region of the salivary gland nucleus of Drosophila melanogaster. The middle left figure is from a male; the others are from females. The figures are semi-schematic representing only the most distinct pictures seen at certain positions of the micrometer. Cross striations are more stressed than the longitudinal chromonemata.
Further study shows that all the other chromosomes, namely, the fourth and both limbs of the second and third, have, at their proximal ends, segments containing very fine, more or less interrupted striations analogous in their structure to the striations of the inert region of the X-chromosome; hence these segments too no doubt correspond with the "β heterochromatin" of Heitz. Like the corresponding part of the X-chromosome, these finely striated regions of the autosomes enter to a greater or lesser extent (varying with the preparation) into the formation of the chromocenter. Until they shall be shown to be inert regions in the same sense as in the X they may at least be termed "chromocentral regions" The chromosome which appears to have the longest chromocentral region is the X; after this comes the left limb of the third chromosome, with at least five to six striations. The chromocentral region of the right limb of the third chromosome is the shortest, appearing to contain only two or three striations.

The above described portions of the chromocentral regions of the chromosomes form only the periphery of the chromocenter. A study of the deeper lying layers of the chromocenter shows that the most central part of the latter also has a striated structure, fundamentally like that of the above peripheral parts. Following upon the fine striations of those chromocentral regions that can be identified as lying in separable chromosomes, we come upon a region composed of striations common to all of the chromosomes. In other words, the most proximally situated striations of all the chromosomes are connected with one another, forming irregularly coursing striations that take the shape of curved or crooked lines, and it is these that constitute the middle portion of the chromocenter (the "α heterochromatin" of Heitz).

This striational character of the chromocenter is especially well distinguishable in cases in which the most proximal striations definitely attributable to individual chromosomes are distinctly visible. In such cases it can often be observed that these striations conjugate with apparently homologous striations in the adjacent proximal regions of the other chromosomes. In so doing, they tend to become stretched and so to become disintegrated into their separate beadlike chromioles, spaced at rather even intervals along irregular lines that connect the chromosomes with one another. Bordering on, but "distal" to these common lines and obviously forming one system with them, are the striations of the more distal separable portions of the chromosomes. Just "proximal" to the above mentioned common lines, and also obviously part of the same system, are a series of long, irregular striations, coursing through the middle of the chromo-
center, which seem to have no direct relation to any particular chromosomes but only form a part of the middle chromocentral mass.

Analysis of the position of the striations in the chromocenter is made difficult by the fact that the individual chromonemata which are held together in the distal portions of the chromosomes in the form of compact bundles, separate from one another within the chromocenter. This is probably due to a mutual attraction between the loci of all six proximal chromosomal ends. Thus these chromonemata go across the chromocenter as very fine lines in a direction largely at right angles to the direction of the striations formed by the attraction of homologous chromioles.

Despite these difficulties, it is clear that the homologous chromioles of different chromonemata do form continuous ring-like striations in the chromocenter, connecting all the chromosomes together. But the separation of the chromonemata in this region, and the complicated three-dimensional form of the striations compounded of several chromosomes, make it difficult to count the number of ring-like striations that take part in the composition of the central body. Preliminary estimates indicate that this number is not less than ten, and not more than twenty.

The above observations lead us to the conclusion that the chromosomes in the nuclei of the salivary gland cells of *Drosophila melanogaster* are connected at their proximal ends by means of the conjugation of the genes in the inert region of the X chromosome and the Y with those in the proximal regions of the autosomes, and of those in the proximal regions of the different autosomes with one another. This would indicate some sort of homology between these regions in all the chromosomes, a homology, moreover, extending not merely to a single gene, but to a whole linear lot of genes. It would also follow that the arrangement of these homologous genes in the proximal portions of the different chromosomes is similar. But if non-homologous loci in this region can conjugate, as in maize, these inferences would not follow. They represent only preliminary steps in a series of cytological and genetic studies, the way to which has just been opened up. In this connection the suggestion may be recalled (Muller and Painter, 1932, p. 355–6) that the spindle-fibre regions not only of the X and Y but also of the autosomes may be homologous with one another and of the nature of "inert regions", and that by the translocation of these regions both increases and decreases of chromosome number may have occurred in past evolution.

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**Literature Cited**


