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The Abnormal and Characteristic Behaviors of the Sex-chromosome in *Locusta migratoria* (Orthoptera)

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With 2 text-figures

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Locusta migratoria, a grasshopper widely distributed over the world except in the Western Hemisphere, has been well known for the fact that it may exhibit two different forms or phases, migratory and stationary. The two forms, swarming and solitary, were once believed to be two different species, *Locusta migratoria* and *L. danica* respectively, since they differ distinctly not only in color but also in structure. It is now generally recognized, however, that they represent two different phases of the same species, *Locusta migratoria*, under different environmental conditions. Cytological study, on the other hand, has revealed an unusual chromosomal condition in this species, namely numerical variations in the chromosome complex within the individual, due to the presence of supernumeraries from one to five, sometimes six (ITO, '34). It has also been found that many abnormal phenomena, such as fragmentation, elimination, non-disjunction and non-conjugation of the chromosomes, take place in this species in nature. A unique and surprising fact in the present case is that all of the imaginable types of abnormalities are found within a single individual (ITO, '39).

The present paper deals mainly with the abnormal behavior and characteristics of the sex-chromosome in mitosis and meiosis in this species.

I. Non-disjunction and elimination of the sex-chromosome in the multiplication period of the secondary spermatogonia

The phenomenon of non-disjunction of the sex-chromosome in mitosis is one of the most prominent abnormal behaviors of the chromosomes in this material. One could expect as a matter of course this sort of thing in mitosis, but the actual case has never been reported so far as the writer is aware. The instances which have been described in the literature are limited to cases of meiotic division, although the presumed case in somatic mitosis has been reported in a few cases.

Generally the testicular follicle of the Orthopteran insects is made up of a number of cysts and all germ-cells within a cyst are descendants from the

common ancestor, a primary spermatogonium. In the case of this species sixty-four primary spermatocytes are found in a cyst; that means that six divisions take place in the multiplication period of the secondary spermatogonia. The chromosomal complex, on the other hand, normally should be the same for all the cells in the same cyst. Detailed study, however, reveals that deviation is found for the sex-chromosome, as well as for the autosomes, in this species. A few examples will be given here.

In cyst Ga in individual 9948, seven cells are found to lack sex-chromosome, while in five cells there are two sex-chromosomes one of which is apparently supernumerary extra. These twelve aberrant cells are invariably found as a group of two or four lying adjacent to each other, indicating their close relationship

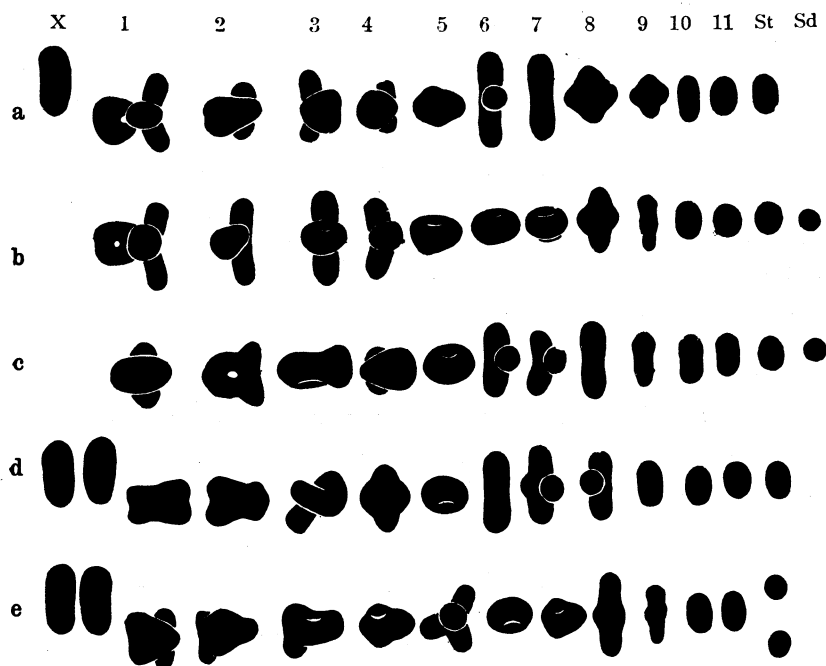


Fig. 1. Heteroploid complexes from a single cyst. They are lateral views of metaphase chromosomes from first spermatocytes. Each horizontal row represents the chromosomes of one cell and each vertical column contains corresponding chromosomes from different cells. The sex-chromosomes are in the first column and St and Sd represent paired and unpaired supernumeraries respectively.

- a A typical complex for the cyst.
- b, c Two hypoploid complexes lacking the accessory.
- d, e Two hyperploid complexes having two accessories. In e two homologous supernumeraries have failed to synapse.

The complexes were drawn with the aid of camera lucida at a magnification of 2400 diameters. The figures have been reduced one-third in reproduction.

in cell lineage. Taking into account their chromosomal organization, together with their relative position in the cyst, one not only can easily imagine the fact that these aberrant forms arise either by non-disjunction or by elimination of the accessory chromosome, but also he can estimate the time when the abnormal behavior took place. Thus it becomes possible to assume that the non-disjunction of the sex-chromosome takes place twice in the fifth spermatogonial division and once in the last mitosis. The remaining two hypoploid cells should be explained by the elimination of the sex-chromosome in one of the last mitoses.

It is quite surprising that non-disjunction is rather a common occurrence in this material. The writer has found indubitable, clear-cut cases in many other cysts. The fact should be stressed that whenever cells are found with an extra accessory, there is a corresponding number which lack the accessory among their neighbours. These facts, it seems, can be explained only by the irregular distribution of the accessory. A remarkable case is found in cyst Ce in the same individual. As a detailed discussion with regard to this cyst will be given elsewhere, here only the fact may be mentioned that presumably non-disjunction occurred twice in the fourth division and twice in the fifth division of the secondary spermatogonia.

A clear-cut case of the elimination of the accessory was found in cyst Ca in which four cells located in the same region as a group of neighboring cells lack the accessory. There is not a single cell, having an extra accessory, to be matched with these deficient cells. The number of the deficient cells is so large that one can hardly regard it as an artificial loss. Accordingly it must be ascribed to the total elimination of the accessory. Considering their relative position and chromosomal organization, it is assumed that the elimination occurred in a cell in the fifth spermatogonial mitosis.

Throughout all the cysts observed it is noted that the irregular distribution of the accessory chromosome takes place only in the last three generations of the secondary spermatogonia. The writer has never found a case in which half or one-fourth of the cell in the cyst are involved nor one in which the entire cells of the cyst are consistent with one of the two aberrant forms. These facts demonstrated that the non-disjunction of the accessory occurs neither in the first spermatogonial generations nor in the early part of the secondary spermatogonial generations. The same is true in the case of the elimination of the accessory. The fact seems to be correlated with the peculiar nature of the accessory in meiotic prophase. The accessory chromosomes of the grasshoppers in general are distinguished not only by their heteropycnotic nature but also by their conspicuous movement through the entire course of the growth period of the primary spermatocyte. In this material the peculiarity in movement of the accessory may

be traced back to the multiplication period of the secondary spermatogonia. As a rule the accessory can be distinguished by its attenuated, weakly stained condition in the metaphase spindle of the primary spermatogonia as well as in the very early generations of the secondary spermatogonia, but it is always arranged in the equatorial plate and no unusual behavior is observed. However in the later generations of the secondary spermatogonia the accessory is ordinarily found out of the equatorial plate, a slight but distinct distance from the rest of the chromosomes of the complex. This peculiar nature of the accessory in spermatogonial mitosis may be responsible for the non-disjunction and elimination of this chromosome, and the writer has interpreted it as the premeiotic movement of the chromosome, that is to say, the meiotic movement of the accessory which is characterized by the precocious nature and unique movement in the meiotic prophase (COREY, '33, McCLUNG, '28), is actually initiated in the multiplication period of the secondary spermatogonia in advance of the autosomes.

The elimination of the accessory chromosome does not appear to take place quite so often as the non-disjunction of the same chromosome. However the writer has observed it in a number of different cysts other than the cases referred to here. In all cases the process is strictly limited to the later half of the generations of the secondary spermatogonia. The phenomena would be explained in a way similar to the case of the non-disjunction of the accessory. It is quite conceivable that in the spermatogonial anaphase, in which the spindle as a whole is very much reduced in volume and the chromosome group is crowded on the spindle, the accessory may fail to divide normally and two daughter chromatids may pass to one pole or remain in the equatorial plate resulting in the eventual total elimination of the element.

It must be pointed out here that the cell deficient in the accessory chromosome is viable and can assume the normal activity at least during a few cell generations.

The frequency of non-disjunction and elimination of the accessory is indicated in Table I. Two thousand one hundred and ninety-six cells in thirty seven cysts were counted. Heteroploid cells, in respect to the accessory, are found in rather high percentage in this individual, totaling one hundred and thirty-one, which is divided into forty-three of 2X-class and sixty-one of no-X class. The excess of the latter form is doubtless due to elimination of the accessory as mentioned previously. By comparing the configuration of the heteroploid cells in the cyst and their chromosomal constitution it can be determined in which mitoses these two phenomena occurred for the individual case. Thus non-disjunction of the accessory presumably took place twenty-three times and elimination seven.

TABLE I.

Frequency of non-disjunction and elimination of the accessory.

no. of cyst	no. of cells counted	no. of mitoses in last 3 gener.	no. of hetero-ploid cells		no. of non-dis.	no. of elimin.
			2X	no-X		
37	2196	1920	43	61	23	7
%			2.0	2.8	1.2	0.4

Since these irregularities occur only in the last three generations of the secondary spermatogonia, the percentage of each was calculated for the absolute number of mitoses in those three generations. Non-disjunction takes place at the rate of 1.2 % and elimination at 0.4 %.

II. The sex-chromosome in meiosis.

A distinctive feature regarding the sex-chromosome in this material is that a pair of X-chromosomes in a cell never conjugates to form a tetrad. As described previously, some diploid primary spermatocytes have two accessories owing to non-disjunction in the pre-meiotic mitosis as well as the tetraploid primary spermatocytes. In both cases the two sister accessories behave quite independently of each other and never show the slightest sign of synapsis nor display any modified behaviors throughout the meiotic prophase and metaphase. Subsequently the segregation of the two accessories in the first division is at random; in some cases both elements go to the same pole, while in other cases they segregate to the opposite poles. Thus the formation of the sperm which has two accessories is naturally expected. If such a sperm is functional, then one would expect in the subsequent generation to meet an individual whose chromosome complex consists of three accessories. The individual would be the super-female.

The reason why the two sister accessories do not synapse is not clearly understood. However if the synaptic reaction is primarily due to the attraction between homologous genes, then it may be inferred from the asynaptic behavior of the accessory that the X-chromosome of this species bears only a single or at most a few genes. In view of the fact that the X-chromosome in this species does not affect the viability of the cell either in hyper- or in hypoploid conditions, such a case is not quite improbable.

As a rule the accessory chromosome in the male Acridian insects precedes

the autosomes to the pole in the first meiotic division. According to BELAR's observation on living spermatocytes of a grasshopper the X-chromosome lines up in the equatorial plate in the metaphase, but as soon as it gains the spindle fiber it begins to move towards the pole so that it is always found in advance of the autosomes in the beginning of the anaphase. In this species, however, the degree of this precocious movement of the accessory is usually very slight and the movement appears to be somehow retarded as the process proceeds, since in the anaphase no sign of precocious movement of the accessory is found. On the other hand the movement of the accessory in meiotic metaphase and anaphase appears to be affected by the physiological condition of the cells. In cyst Na, where the developmental synchronization has been lost and many cells manifest extreme abnormalities, the accessory becomes thick, stained deeply, and markedly advanced to the poles, sometimes in their vicinity. Here the situation somewhat resembles what is found in Locustidae in which the thickened X-chromosome never attains the equatorial seat throughout the first meiotic mitosis.*

In her recent paper on components of the mitotic spindle, CAROTHERS ('36) described and figured the sex-chromosomes in several Acridian species which might be said to be in a dilemma (p. 473, Figs. 1-5). In those a few or many fibers or processes are put out from the different regions of the chromosomes. The chromosomes are distorted as though subjected to conflicting stresses. A count of 115 first spermatocytes gives such a conflicting figure in 25.

In this material there has been found, although with rare occurrence, the sex-chromosome showing the similar feature as described above. Fig. 2 indicates them. In all these cases, the X-chromosome lies paralld to the equatorial plane, and at a right angle to the ordinary position, and projects several fibers in different directions. In a single exceptional case, two distinct fibers, passing towards both poles, attach to each end of the sex-chromosome. In such a case the anaphasic movement would not be free as it is in the normal case.

Another characteristic of the X-chromosome in this species is strong resistance to the effects of agents which cause chromosome fragmentation. WHITE ('35) finds in the irradiated germ cells of the same species that the frequency of fragmentation in the X-chromosome is much less than that in the autosomes and concludes that the difference in reaction to irradiation between the X-

* The behavior of the X-chromosome which is a large telomitic rod in Locustidae in the first meiotic division is quite interesting. In the metaphase it is usually found near the pole in the shape of a V folded at the middle region; sometimes as an unfolded long rod. In the anaphase when the divided autosomes advance to each pole, the X-chromosome stays in the same position or even moves backward to the equatorial plane. After the daughter chromosome groups reached to the poles it passes to one of the poles (unpublished observation). In this respect the meiotic behavior of the X-chromosome strikingly resembles that of the unpaired chromosomes in hybrid plants.

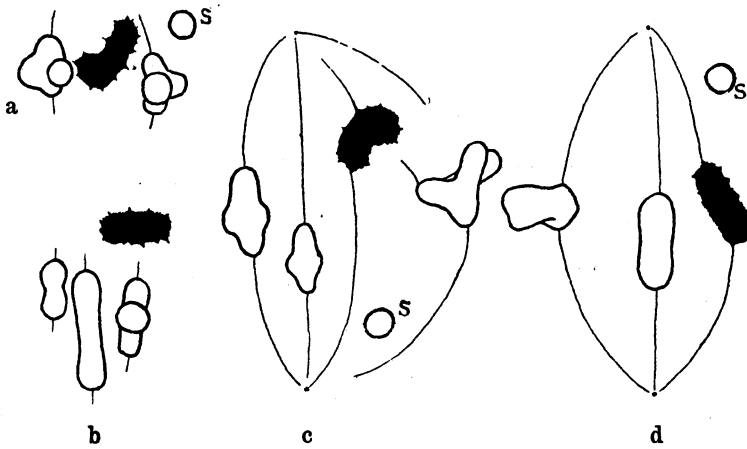


Fig. 2. Partial complexes of four first spermatocyte metaphases, lateral views. X-chromosome, solid black. The dyad supernumerary is indicated by S.

chromosome and the autosome is far greater in *Locusta* than in *Drosophila*. In writer's observation the actual breakage of the X-chromosome is found in only two cells, except for a few doubtful cases, in thousands of cells examined. There is evidence that X-rays have almost no effect on the X-chromosome in *Circotettix* (HELVIG, '33). It seems, therefore, that the strong resistance of the sex-chromosome to X-rays and some other agents is of specific nature in Acrididae.

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