THE ELIMINATION OF CHROMOSOMES IN THE MEIOTIC DIVISIONS OF BRACHYSTETHUS RUBRO-MACULATUS DALLAS

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The occurrence of meiotic abnormalities is anything but rare. However, in almost every instance it is the result of mechanical or physiological accidents and therefore sporadic and irregular. Hence, if in a certain species a departure from the normal process always takes a very particular form and is restricted to a certain region of the gonad, it is likely that it is not entirely accidental. If, furthermore, every male or female in the species is affected, it is safe to assume that we are dealing with a basic and well regulated condition, unorthodox though it may be.

The case in question is that of *Brachystethus rubromaculatus*, one of the pentatomid Hemiptera. It holds for all the males of the species. The testis here is composed of four lobes and in the fourth of these (counting from the side where the sperm duct makes its exit) the meiosis follows an abnormal but very definite course. In a way, this is analogous to the case of Loxa (Schrader, 1945a and b), but that is only in the sense that in both the exceptional development takes place in a certain lobe of every testis. The nature of the abnormality is quite different in the two species, as will appear in the account below. My chief interest lies in the possibility that such irregularities may be of use in the analysis of the ordinary mechanism of mitosis and in this as well as several succeeding studies I hope to show that they may throw some light on certain puzzling aspects of the division cycle.

Material and Methods

The gonads of four males and one female were used in the investigation. The insects were collected near Turrialba, Costa Rica, during April and May, 1944. The material was fixed in Sanfelice and sectioned at 5 to 10 μ. Gentian violet, haematoxylin and the Feulgen reaction were used in staining, the haematoxylin being especially useful in the analysis of spindle conditions whereas the Feulgen reaction is indispensable in following the maneuvers of the chromosomes. The main manifestations of the mitosis are so clear that they are well shown by pen and ink drawings—a method which in most other cases does not give a just presentation of spindle conditions.

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Normal Spermatogenesis

The testis has only four lobes of which the first three show an orthodox spermatogenesis differing in no essential from that described in so many other pentatomids.

The fourth or "harlequin" lobe has about the same proportions as the rest and does not differ in any discernible way in its general organization.

The size differences among the chromosomes as seen in the spermatogonia are not very great. But it is possible to recognize one large, four medium and one small pair of autosomes. The X is a trifle larger than one of the small autosomes while the Y is the smallest chromosome of the complement (Fig. 1). Identification of the sex chromosomes was checked by examination of oogonial metaphases in the female.

The normal meiosis shows the usual prophase conditions, with the leptotene, synaptotene, pachytene, and diplotene stages followed by the confused period in which chromosomal behavior is difficult to analyze. This is succeeded by a diakinesis marked by the appearance of beautiful tetrads which, as they condense, are distributed around the nuclear periphery. Just before the breakdown of the nuclear membrane this rather even distribution begins to disappear and the chromosomes may even come in contact with each other in small groups of two or three each (Fig. 2). This collocation reaches its height when the membrane disintegrates. All of the chromosomes then huddle together in the middle of the nuclear space only to separate again almost at once to form the equatorial plate. In the latter they follow the characteristic pentatomid arrangement of the first metaphase, with one or both sex chromosomes taking a central position within a ring of autosomal tetrads (Fig. 3).

The sex chromosomes are marked by their heteropycnosis from the leptotene period on. Until the synaptic period they are well separated from each other, but then tend to come together. During the confused period they form a single, rounded chromatin nucleolus and it is not until after the early diakinesis that they once more become independent of each other. They divide equationally in the first, and segregate in the second division, so that the spermatids carry 6 + X or 6 + Y chromosomes (Figs. 3–5).

There is no interkinesis and the two centrioles at each pole have already separated to assume their position for the second division before the chromosomes have completed the anaphase movement of the first. This precocious behavior of the centrioles is however also encountered in several other pentatomids and does not interfere with the normal meiotic distribution of the chromosomes except in such extreme cases as Peromatus (Schrader, 1941b).

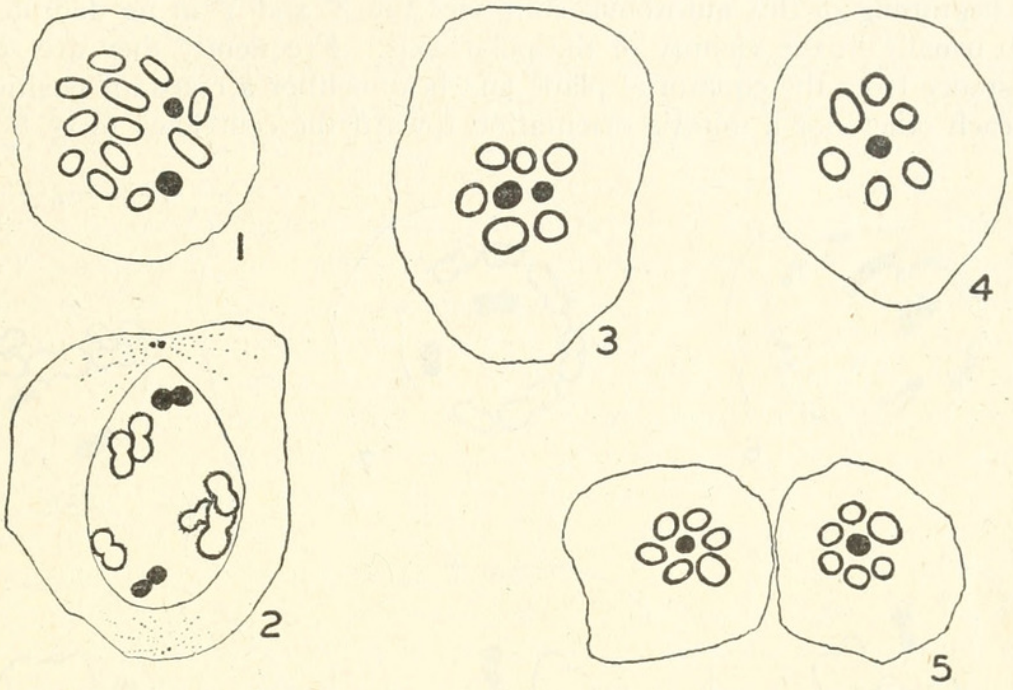
Abnormal Spermatogenesis

First division

Neither in the spermatogonial nor the meiotic behavior up to the late diakinesis does the harlequin lobe differ from the other three. Six autosomal tetrads are formed which resemble in every way those seen in the normal lobes (Fig. 6). Again, as these tetrads condense into the characteristic dumbbell shaped bodies, they and the sex chromosomes are well distributed around the nuclear periphery.

But then arises a difference in behavior from the normal. Here, too, the last phase prior to membrane disintegration witnesses a coming together of the chromosomes. In this fourth lobe, however, the collocation is both more regular and more pronounced. In nearly all cells the six tetrads form a single chain whose constituents maintain contact with the nuclear periphery. This chain is always more

or less equatorially placed (Fig. 7 and 8). The configuration is evidently the resultant of several different forces. Just as in normal cells, the tendency to collocate begins to manifest itself in late diakinesis. But in this fourth lobe the autosomal tetrads are also repelled by the two opposite poles at this early stage. Since the chromosomes are still confined within the nuclear membrane they consequently move into the middle region. The combination of polar repulsion, the tendency to collocate, and adhesion to the still intact nuclear membrane must perforce result in the formation of an equatorial chain.



Drawings were made from haematoxylin preparations, except for Figures 12 and 24. All figures magnified approximately 1400 ×. Autosomes drawn in outline, and sex chromosomes in solid black throughout.

FIGURE A. Normal spermatogenesis. 1. Spermatogonial metaphase; 12 autosomes and X (large) and Y. 2. Late diakinesis; beginning of autosomal clumping. 3. Metaphase of Division I; X and Y in middle. 4. Metaphase of Division II; X superimposed on Y. 5. Telophases of Division II showing two types of spermatids: 6 autosomes + Y, 6 autosomes + X.

As one might expect, there is no constant seriation in such a chain. When the nuclear membrane disintegrates, the chain is converted into an irregular clump just like the clump formed by the tetrads of normal cells that have undergone no such maneuvers (Fig. 9 and 10). Much less frequently is there a formation of two smaller aggregates instead of the single large one. The two sex chromosomes are included in such groupings only by accident and sooner or later they always separate from the autosomes and assume an independent position. This is not necessarily an equatorial one at first (Fig. 8–10).

It is, however, in the establishment of the first metaphase that the most striking departures from an orthodox behavior are evinced. As already stated, the breakdown of the nuclear membrane is followed immediately by the clumping of the autosomal tetrads in the midregion. In many cells this may, however, be halted temporarily if a central core of spindle fibers is formed quickly between the poles. The clumping autosomes may then be applied to these central fibers in a half moon

configuration for a moment (Fig. 11). But in any case, before the metaphase spindle has assumed final shape, the autosomal aggregate is shifted out of this general middle region. Almost always this movement seems to be a sudden one and frequently the aggregate comes to rest rather close to the lateral wall of the cell, the direction of the shift being toward the side and never toward the poles. The cell frequently bulges out on the side on which the aggregate is located (Fig. 14). If instead of one aggregate, two smaller ones have been formed, they undergo similar reactions and often become displaced toward opposite sides of the cell (Fig. 13).

The beginning of this autosomal shift sees the X and Y in no definite position although usually in the vicinity of the polar axis. Frequently they are situated at some distance from the equatorial plane and bear neither a constant positional relation to each other nor a mitotic orientation toward the centrioles (Fig. 9 and 10).

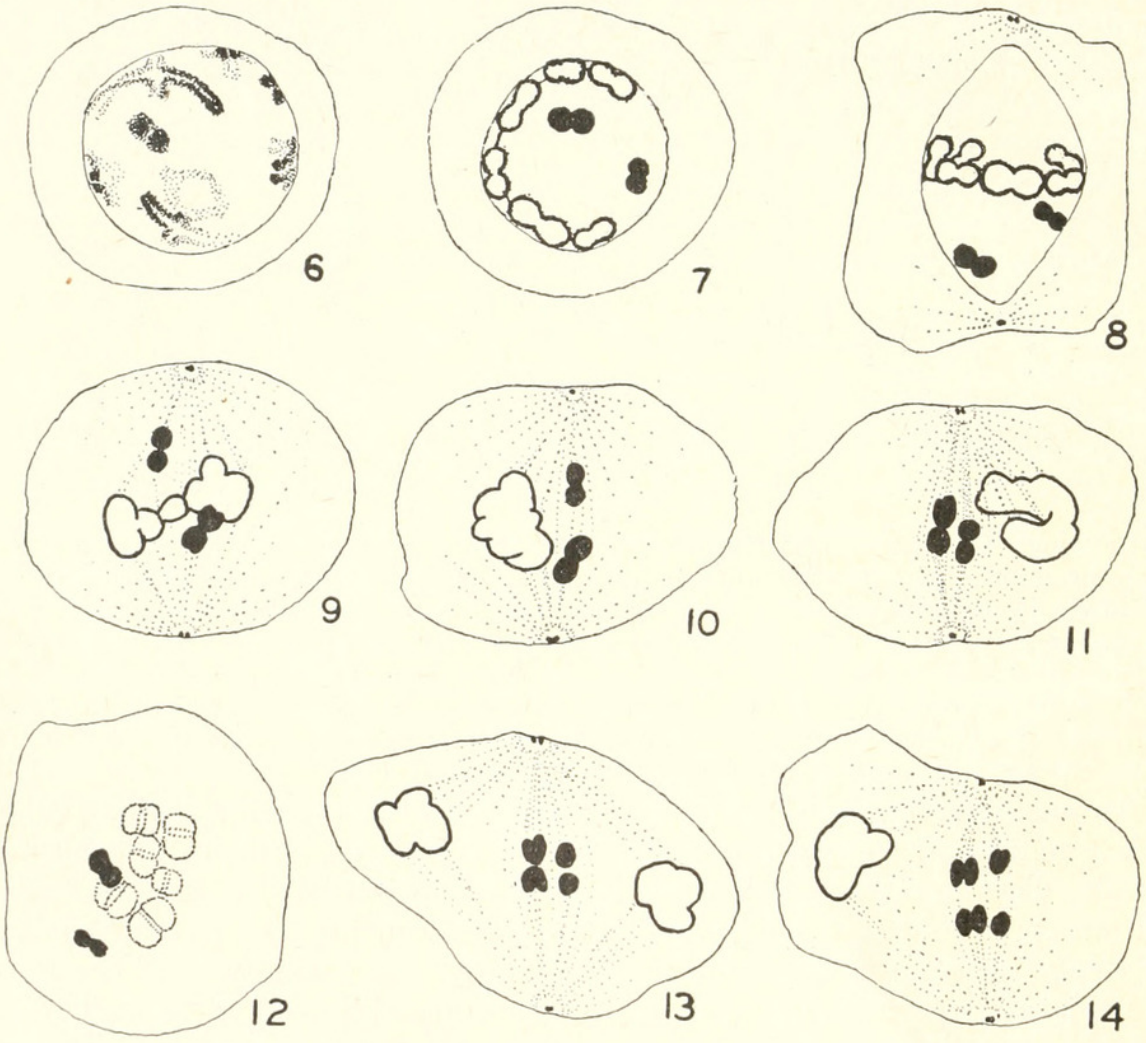


FIGURE B. Abnormal spermatogenesis. Division I from diakinesis to early anaphase. 6. Mid diakinesis showing tetrads of normal appearance. 7. Late diakinesis in polar view; autosomal tetrads forming equatorial chain. 8. Late diakinesis in side view. 9. Early stage in clumping of autosomal tetrads. 10. Beginning of movement of autosomal aggregate away from polar axis. 11. Displaced autosomal aggregate applied to central portion of spindle in half moon form; X and Y assuming equatorial position. 12. Feulgen preparation corresponding to Figures 9 or 10 showing that tetrads retain their individuality in the aggregate. 13. Autosomes in two aggregates, both shunted out of polar axis. 14. Early anaphase, with X clearly showing "tertiary" split; characteristic displacement of autosomal aggregate.

However this situation is quickly altered and as the autosomal aggregate moves toward the side of the cell, the X and Y approach very close to the polar axis and assume a position in the equator with a definite orientation toward the poles (Fig. 11 and 13).

In all of the hundred or more cells observed at this stage, such a configuration of autosomes and sex chromosomes is always maintained. Since in the prometaphase the two types of chromosomes form one general group albeit not always in contact with each other, it is clear that the later separation is not an accidental one. The unusual shift of the autosomes is equivalent to an actual extrusion from the mid-region of the cell.

Despite their distance from the polar axis, the autosomes continue to be connected with both poles by chromosomal spindle fibers. This is at first glance rather surprising since with ordinary stains like gentian violet and haematoxylin the autosomal aggregate appears as a solid, structureless mass which plainly suggests degeneration. In good Feulgen preparations, however, it becomes clear that the autosomal tetrads have by no means lost their individuality. All six of them can be easily distinguished, lying in a substance which does not stain with Feulgen and thus reveals the individual chromosomes (Fig. 12). This substance, which with other stains becomes just as dark as the chromosomes themselves, resembles the material surrounding the sex chromosomes of certain reduviid Hemiptera (Troedsson, 1944) and may also be akin to the "flocculent, whey-like coagulum" which envelops some regions of the chromosomes in Olfersia (Cooper, 1944). In Brachystethus it is evidently formed when the chromosomes clump at prometaphase and it persists through both meiotic divisions.

In the middle of the cell, between the two poles, there is a well-formed spindle of normal length, which however is smaller in diameter than the spindle of normal cells. This accommodates the two sex chromosomes, which are located in the middle of the spindle substance just as they would be if the autosomes were free to form a ring around them.

Despite the presence of the chromosomal fibers which connect the autosomes with the poles, the autosomal aggregate behaves more or less like an inert mass in the mitosis that follows. While the sex chromosomes undergo an equational division and approach the poles, the autosomes near the periphery of the cell undergo no movement (Fig. 14–17). It is only when the dividing cell elongates and becomes narrow that the autosomal clump is moved toward the midline (Fig. 18). If it there comes in contact with the expanding interzonal region or "Stemmkörper" it may be swept along into one of the two daughter cells, but very often it is not until the cleavage constriction is being completed that the aggregate is definitely included in either of the resulting cells (Fig. 19 and 20). Apparently the chromosomal fibers exert little or no traction at this time. So far as one can tell, the inclusion of the autosomes in either daughter cell occurs entirely at random.

It is of interest to note that although in its essentials the equational division of the sex chromosomes is always accomplished successfully, there are certain features that distinguish it from the corresponding process in normal cells. In the first place, the sex chromosomes and especially the X clearly show a tertiary split already at this first metaphase—a split which is not utilized until the first somatic division in the egg (Fig. 13–15). This is sometimes indicated in normal cells also, but never so strikingly as here where it appears after all three of the stains used. The second

feature lies in the anaphase behavior of the sex chromosomes. Although both start out from an equatorial position, the early anaphase often shows the chromatids of the Y much closer to the poles than those of the X (Fig. 15). In other words, the Y precedes the X in the poleward movement. When there is such a disparity of movement, there is frequently a shift during mid anaphase through which these four chromatids are all brought into the exact polar axis in a single line. Since as just stated, the chromatids of the Y move more quickly, they constitute the extremities in this tandem arrangement, whereas the two X chromatids are in between (Fig. 16). Such a seriation strongly resembles that which characterizes the second di-

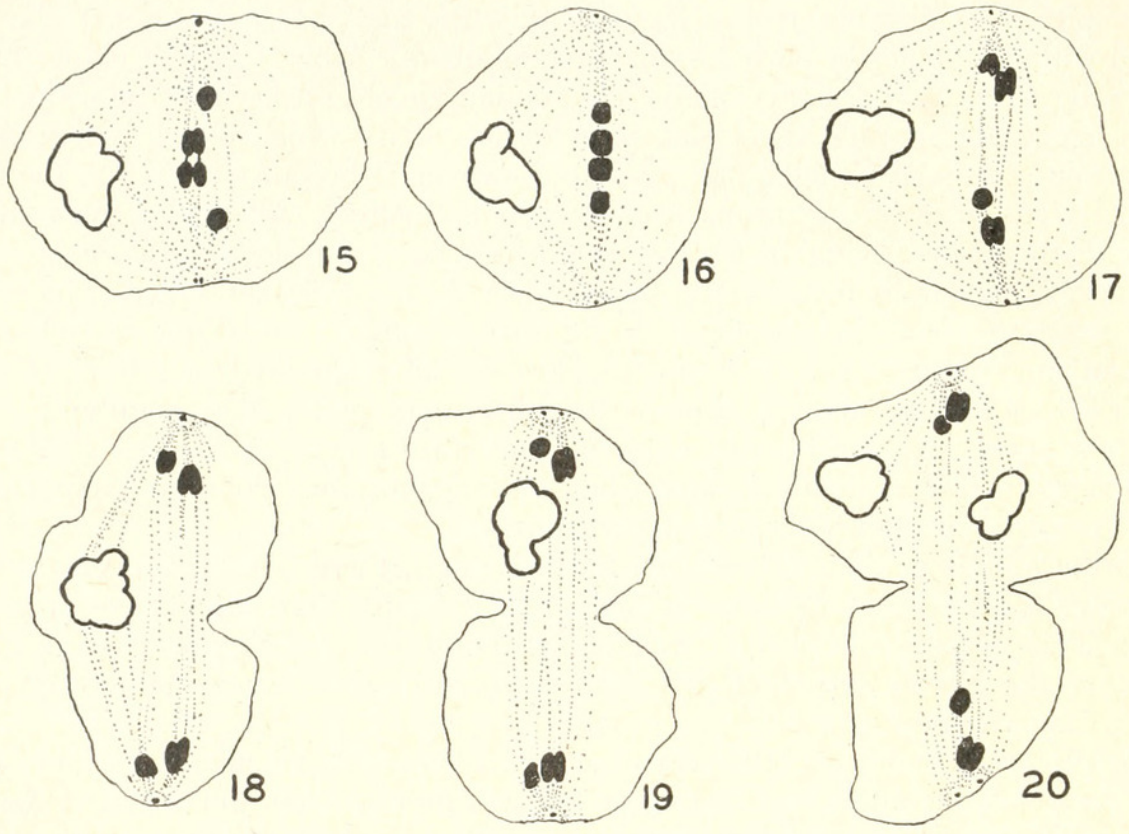


FIGURE C. Abnormal spermatogenesis. Division I, anaphase and telophase. 15. Early anaphase with Y preceding to the poles. 16. Early anaphase; X chromatids have moved into polar axis between separating Y chromatids. 17. Mid anaphase. 18. Late anaphase; autosomal aggregate returning to axial region. 19. Early telophase; an X and a Y at each pole with the autosomal aggregate included in upper cell. 20. Late telophase with two autosomal aggregates both included in upper cell.

vision of the coccid Protortonia (Schrader, 1931), and there is little doubt that similar forces are involved. This anaphasic shift does not affect the result of the division; one X and one Y chromatid go into each of the resulting second spermatocytes.

Thus in the majority of cases, two types of second spermatocytes are produced: one carries an X and a Y, as well as the clumped autosomes; the other contains only the two sex chromosomes (Fig. 19). If the autosomes have been aggregated in two masses before metaphase, these may both go to the same pole or to opposite poles, apparently at random (Fig. 20). In no case is there a division of the individual tetrads.

Second division

As in normal cells, the centriole at each pole of the first spindle is divided and the two daughter centrioles separate some time before the division has been finished (Fig. 21). Each moves through an arc of 90° and the new polar axis for the second division is therefore at right angles to the first. Even while still in telophase, the two sex chromosomes often respond to the new poles and move toward them (Fig. 21). However, this precocious movement is soon reversed and the X and Y then come together in the middle of the new spindle in their orthodox "touch and go" pairing (Fig. 22 and 28) and it is only following this that they separate in the regular segregation toward opposite poles. There is no indication of any interkinesis.

The autosomal aggregate may at first remain in the general region where it has entered the cell upon completion of the first division, but in other cases it approaches closely to the two sex chromosomes that are near the new polar axis (Fig. 21). Such an approach is only temporary, however, and before the second division is initiated the aggregate is always extruded from this middle region just as it was in the first division (Fig. 23). The configuration of the second division thus almost duplicates that of the first.

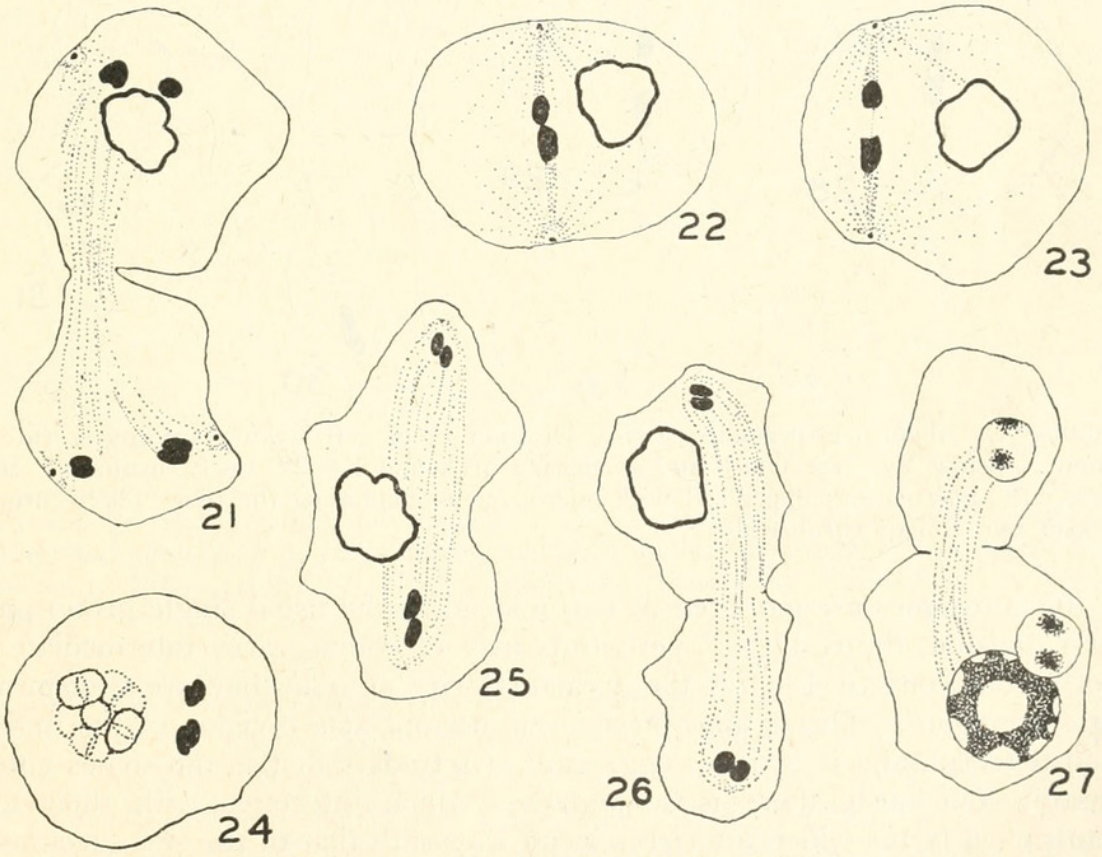


FIGURE D. Abnormal spermatogenesis. Division II of cell containing autosomal aggregate (all drawings except Fig. 21 show X below Y). 21. Beginning of Division II; X and Y reacting to new position of poles. 22. Touch and go pairing of X and Y; autosomal aggregate shunted away from polar axis. 23. Early anaphase; X and Y going to opposite poles; autosomal aggregate in characteristic displacement. 24. Feulgen preparation showing that tetrads still appear unaltered in early phase of Division II. 25. Anaphase; autosomal aggregate returning toward polar axis. 26. Telophase; autosomal aggregate included in cell with Y. 27. Spermatids; upper cell carries only a micronucleus with the Y half chromatids; lower cell with micronucleus containing X half chromatids and autosomal nucleus.

The autosomal tetrads are still intact and are still imbedded in the substance that stains intensely with gentian violet and haematoxylin. However, the aggregate is usually smaller than it was just prior to the first division, a fact that results from a greater crowding of the tetrads, as can be seen in Feulgen preparations (compare Fig. 24 with Fig. 12). Again, chromosomal fibers are formed (Fig. 22), although the aggregate seems to be moved about as a more or less passive body (Fig. 25 and 26). In short, just as in the first division it is only the sex chromosomes that are involved in the regular mitotic mechanism. But now, as in normal second divisions, the process is reductional and the resulting cells receive only an X or a Y (Fig. 26 and 30). The autosomes if present are once more included in either cell as a group, and so far as one can tell, on the basis of chance (Fig. 23–26).

The spermatids that result from these two peculiar divisions thus either carry only one sex chromosome (the X or the Y) or else they contain the autosomal aggregate in addition. In other words, there are four main types of spermatids: X; Y; X + autosomes; Y+ autosomes (Fig. 26 and 30).

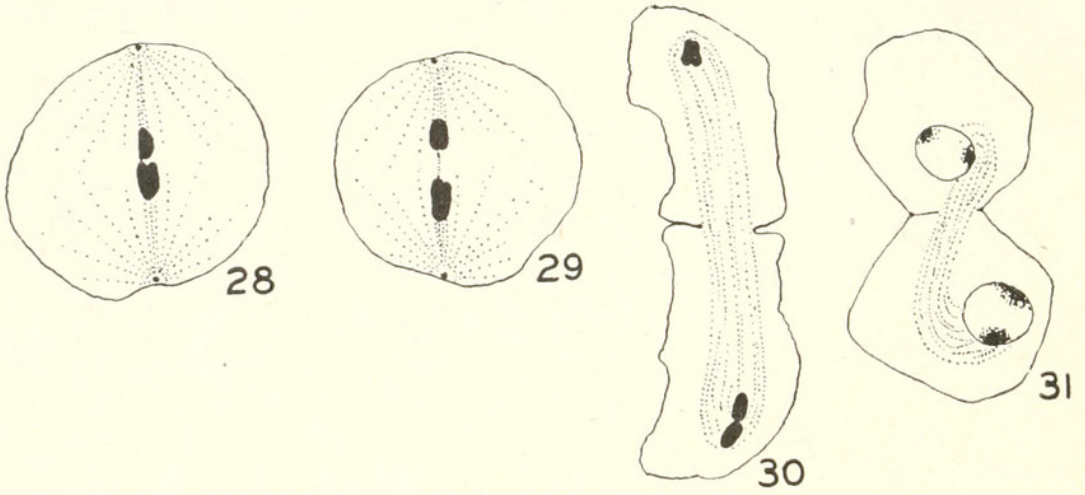


FIGURE E. Abnormal spermatogenesis. Division II of cell lacking autosomes (all drawings show X below Y). 28. Touch and go pairing of X and Y. 29. Early anaphase. 30. Late telophase. 31. Spermatids; upper cell with micronucleus containing the two Y half chromatids, lower with two X half chromatids.

If the autosomes are gathered in two instead of the usual single group prior to the first division, the resulting spermatids may of course carry intermediate numbers of chromosomes. But for the great majority of cells they are transmitted in a single aggregate. Throughout there is no attempt at a division of the individual autosomal tetrad, and it is as an aggregate of tetrads that the autosomes enter the spermatid. Obviously there is some factor which interferes with their mitotic mechanism—a factor which interferes in no way with that of the sex chromosomes. The latter behave just as they do in the normal cells of neighboring lobes of the testis.

Spermateleosis

The first steps after the telophase of the second division parallel the normal course of events. The transformation of the autosomal mass into the spherical nuclear structure shown in Figure 27 is peculiar, though in later stages it approaches

closely the condition seen in the normal spermatid. In these abnormal cells however, the sex chromosome at first forms a micronucleus which is distinct from the larger autosomal nucleus (Fig. 27). But sooner or later, the micronucleus becomes applied to the large nucleus and gradually merges with it.

When, as in most cases, a single sex chromosome constitutes the only chromosomal constituent of the spermatid, its behavior differs in no way from that in cells containing the autosomes as well. In either case a tiny nucleus is formed by each sex chromosome and in this the constituent half chromatids separate to form two distinct chromosomal bodies. (Fig. 27 and 31). This precocious separation is not surprising when it is remembered that already in the first metaphase these half chromatids can be clearly identified as such.

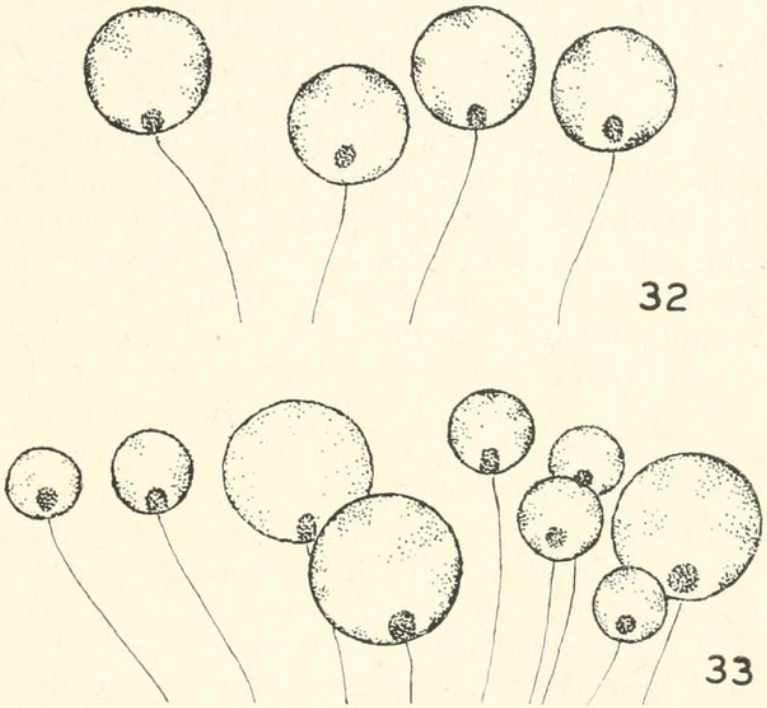


FIGURE F. Spermatids before elongation. 32. Normal spermatids shown to indicate size. 33. Abnormal spermatids at stage corresponding to Figure 32. Largest spermatids contain all autosomes as well as either X or Y. Smaller spermatids carry either X or Y; latter is the smallest.

The process of transformation into the sperm seems at first alike in all spermatids and homologous to that observed in the normal lobes. This is true whether they carry only a single chromosome or the autosomes as well. As might be expected, the former are distinctly smaller than the corresponding normal cells and nuclei (Fig. 32 and 33); the latter on the other hand are markedly larger. It is also interesting to note that it is often possible to distinguish between the small sperms carrying either an X or a Y. The latter are the smaller of the two (Fig. 33). However, when the rounded sperm heads begin to elongate, those which carry only a sex chromosome begin to stain less intensely than either normal or "autosomal" abnormal sperms, and as the elongation into the typical tenuous sperm head continues it becomes more and more difficult to trace their further fate even in Feulgen preparations. It is likely that the "sex chromosome sperms" never attain

the final stages of sperm formation. However, this cannot be made certain without smear preparations for even in very thick sections the long sperm heads are practically always cut and it is impossible to decide whether one is dealing with an abnormally small sperm or only a portion of a larger sperm. The fate of the giant sperms, however, is subject to no such doubt. They continue their development to the fully formed stage, enter the sperm duct, and are there mingled with the normal sperms from the normal lobes.

General Considerations

The cytological features that characterize this abnormal development are thus of the most striking sort. The most obvious one lies in the clumping of the autosomes. A temporary collocation of chromosomes is of course encountered as a normal occurrence in many species, but is there, confined—as it is in the normal lobes of Brachystethus—to a very brief, almost momentary period immediately after the breakdown of the nuclear membrane in prometaphase. In Brachystethus there is some tendency toward a collocation of autosomes even before this event. But in the abnormal lobe, the clump that is finally formed is not resolved again, and this condition is maintained through both meiotic divisions and into sperm formation. Moreover this collocation of chromosomes is so intimate that only a Feulgen preparation reveals that there has not been an actual fusion.

Although the further behavior of this autosomal aggregate suggests strongly that it is shunted about more or less like a passive body during cell division, it nevertheless evinces certain reactions which indicate that it is not completely inert. In diakinesis, these autosomal tetrads duplicate the behavior of normal tetrads in establishing contact with the nuclear periphery; toward the end of the diakinetic period they evince a reaction to the two poles in taking up an equatorial position in contact with the nuclear membrane; after the disappearance of the latter they form chromosomal fibers to the poles; and almost simultaneously they move out of the midregion of the cell with a suddenness that bespeaks a forcible displacement.

It is possible and even likely that this movement toward the side of the cell is due to the same centriolar repulsion which forces the chromosomes into the equatorial plane while they are still held within the confines of the nuclear membrane. An influence of centrioles on the chromosomes prior to the dissolution of the nuclear membrane is observed in certain other forms also (for instance in Anisolabis, Schrader, 1941a). But not often is it exerted so as to bring about an equatorial placement at so early a stage, even though a role in the later final formation of the equatorial plate is frequently assigned to it.

It will be realized, however, that even in normal cases, additional factors must function to restrict the chromosomes to the middle of the equatorial plane. Repulsion from the two poles alone cannot do that. It is possible that the chromosomes are thus confined to the midregion simply because of surface tension conditions that prevail in the spindle body at the time of metaphase. The escape of the autosomes in the present case might then be attributed to abnormalities in the spindle, say to untoward alterations in the timing of the normal viscosity changes. But that is clearly not the entire explanation since the autosomes are not accompanied in their displacement by the two sex chromosomes. The latter remain in the spindle in a quite orthodox position. Since the cytoplasm, the centriolar forces,

and the general spindle conditions are identical for both autosomes and sex chromosomes, it is therefore in the chromosomes themselves that the explanation must be sought. More specifically, the question to be solved is why the autosomes do not respond to the forces which at metaphase counteract the influence of the centers and confine the chromosomes to the middle of the equatorial plane.

The abnormal condition of the autosomes is not indicated by any striking behavior during the prophase. There is only a more pronounced tendency to assume an equatorial position at prometaphase and the formation of chains that are absent in normal cells. Also, after the aggregate has been formed, Feulgen preparations show the component tetrads to be somewhat swollen and less intensely stained than are the prometaphase tetrads. This probably indicates the first step in a return to a diffuse state. Such a regressive condition may in some way be responsible for the special maneuvers of the autosomes, for the X and Y chromosomes which during this time remain fully condensed behave just like the sex chromosomes of normal cells. But it is not certain that this would suffice as an explanation since in addition to the clumping of the autosomes one must also account for their elimination from the midregion and their failure to take the first steps in division. For it must be remembered that the initial separation of daughter chromosomes is an autonomous process which is independent of spindle action. Nevertheless, although the Brachystethus tetrads appear ready for such a step and the line of demarcation between the paired chromosomes is clearly marked and complete, no separation ever occurs. Either there is no mutual repulsion or else the pellicle and the achromatic constituents of the tetrads prevent the normal division. In any case it is clear that some of the basic reactions of the chromosomes have been altered.

It is natural to seek a parallel in other cases already on record. The investigation of certain echinoderm hybrids by Baltzer (1910) is especially pertinent. Baltzer found that in certain of these crosses, the paternal chromosomes are eliminated during cleavage. There, too, is a tendency for such chromosomes to clump, and there also a formation of chromosomal spindle fibers occurs nevertheless. Likewise there is sometimes a lateral elimination of these chromosomes although they usually simply lag in the middle of the spindle. However, all this does not occur until the anaphase is well advanced and the various configurations are by no means as constant as they are in Brachystethus. After a careful analysis, Baltzer concluded that it is the chromosomes themselves rather than the plasma that is responsible for the elimination. That such a conclusion is warranted for the case of Brachystethus, as well, has already been pointed out. The difference in behavior between the autosomes and the sex chromosomes in the same plasma makes it unavoidable.

The elimination of chromosomes consequent on a loss of their kinetochores is observed regularly in certain molluscs (Pollister, and Pollister, 1943). Such an explanation is worthy of serious consideration in the case of Brachystethus. However, there can be only a partial loss of the kinetochore activity because some chromosomal fibers are evidently still being formed. Since we are dealing here with a diffuse kinetochore, such a partial loss is easily conceivable, but it must be confessed that the akinetic chromosomes of molluscs present very different elimination pictures than those seen in Brachystethus.

The conditions in such coccids as Phenacoccus (Hughes-Schrader, 1935) may also be germane to the present case. There, too, certain chromosomes betray a

tendency to clump, and it is these chromosomes that become inert and degenerate within one or two succeeding divisions. Nevertheless, these chromosomes form normal chromosomal fibers.

But all these other instances are themselves in need of further explanation. The only conclusion that protrudes itself in such an analysis is that the abnormality is to be sought in the basic organization of these forms and is not a superficial and accidental one. The alterations that are involved primarily affect the chromosomes and influence their reactions to each other and to the mitotic mechanism.

Evolutionary Aspects

It is very questionable whether spermatids carrying only an X or a Y chromosome ever develop into mature sperms. That, however, is not true of the giant sperms which in addition to a sex chromosome carry the full set of autosomes unaffected by any meiotic mitosis (i.e., four times the number of autosomes contained in a normal sperm). But though these large sperms enter the sperm duct and mingle with the normal sperms, it is doubtful whether they ever become functional in the hereditary sense. Of the seven specimens of Brachystethus that I have examined, none was marked by unusual morphological features such as confidently might be expected if a sperm nucleus with a quadruple set of autosomes joins the haploid nucleus of a normal egg.

But if these numerous giant sperms play no direct role in the hereditary mechanism of the species, it becomes a matter of wonder that such an extensive development of abnormal gametes could have withstood the effects of natural selection. For it must be remembered that the testis of Brachystethus has only four lobes and if the sperms of one of these do not function in the genetic determination of the embryo, we are confronted with a prodigious waste which is added to that which occurs normally in the reproduction of most male animals.

Such a waste is paralleled in several species of Loxa (Schrader, 1945a and b) where there is likewise an abnormal lobe in every testis. Although the nature of the aberrancy is different in the two cases, they are similar in that both encompass the production of a huge number of sperms which carry many times the normal number of chromosomes. It seems strange that two processes so diverse in their abnormalities should culminate in gametes whose general characters are so similar.

The explanation may lie in the fact that though these large sperms take no part in the direct control of the heredity of the species, they may nevertheless be important in its welfare. Since they are normal in every respect except size, it is more than likely that they enter the egg like the normal sperms. It also must be recalled that polyspermy is almost universal in the fertilization of insect eggs and that in many species the number of supernumerary sperms is very high. The entrance of genetically inert sperms would probably offer no difficulties in the regular fertilization process and a union between two normal pronuclei would proceed as usual.

It is clear from evidence in marine eggs that the breakdown of gamete nuclei releases substances which have a far reaching influence on the reactions in the egg. It is likely that such substances are present in abnormally large quantities in the giant sperms and that therefore their possibly beneficial effects are increased. Again, if the developing embryo utilizes the nucleo-proteins that are brought in by

supernumerary sperms, an advantage might well accrue to a species which has such substances available in the unusually large amounts that are represented in the giant sperms. In short, the latter may play a not inconsiderable role in the embryology.

If that is the case, the harlequin lobe would in no sense be a useless organ. The development of such a lobe in the testes of two genera that are taxonomically as diverse as Brachystethus and Loxa may well have been due to a nongenetic but metabolic advantage that is thereby conferred on the developing embryos.

Summary

1. The fourth lobe in all testes of the pentatomid *Brachystethus rubromaculatus* shows an aberrant meiosis of a very definite character.

2. The first indication of this aberrancy is found in a chain formation and clumping of the autosomal tetrads just prior to metaphase. The two sex chromosomes are not included in this aggregation of autosomes.

3. At metaphase the X and the Y take a normal position in the spindle but the aggregate of autosomes is shunted laterally out of the middle region of the cell, away from the polar axis.

4. The two sex chromosomes divide equationally in the first division while the autosomal aggregate passes unaltered to either pole.

5. In the second division the X and Y again behave as in a normal meiosis and separate to opposite poles. The autosomal aggregate, if present, passes to either pole apparently at random.

6. Since the clumped autosomal tetrads pass undivided through both divisions while the sex chromosomes behave normally, the following four main types of spermatids are produced: X; Y; X + autosomes; Y + autosomes.

7. The mechanics and evolution of so constant an aberrancy are discussed.

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