

THE CHROMOSOMES OF ANASA TRISTIS
AND ANAX JUNIUS.

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WITH 5 FIGURES.

ANASA TRISTIS.

The material for the study of the chromosomes in the spermatogenesis of *Anasa tristis* was obtained at Columbia, Mo., and was examined by means of sections. A careful investigation has completely confirmed Wilson's results, 05, 06, 07, respecting the number of spermatogonial chromosomes in this insect and the presence of an accessory or heterotropic chromosome, as well as the asymmetrical distribution of this chromosome, at the second maturation division. The observations here presented are, on the other hand, at absolute variance in all important points with the recently published investigation of Miss Foot and Miss Strobell, 07, who have studied and photographed smear-preparations of the testis of *Anasa tristis*.

Wherever an accurate count of the spermatogonial chromosomes can be made at full metaphase, the number has been found to be 21, as discovered by Wilson, and not 22, as originally determined by Paulmier, 99, and recently confirmed by Foot and Strobell. No exception to this result has been encountered, although the count has been made with certainty in scores of cells, and not a single case showing 22 chromosomes has ever been observed. Many of the spermatogonial groups have been drawn under high power, six of which are reproduced in Fig. 1, A-F, and in every instance both the number and form of the chromosomes are seen with diagrammatic distinctness, conforming in all respects with the groups as figured by Wilson. The two *m*-chromosomes and the three large ones appear in all, while one of the latter is usually bent upon itself, sometimes nearly at right angles, as in Fig. 1, F'. It is not at all improbable that in smear-preparations this chromosome might be pulled apart at the angle, and thus account for the observations of Miss Foot and Miss Strobell. This explanation, moreover, is in a sense justified by their photographs of the spermatogonial groups, especially photos. 47

and 50, 07b, which show only two large chromosomes, while in each case two other chromosomes are lying with their ends in contact and at an angle to each other, as if they might well be portions of the large bent chromosome which has become partially severed, but which is seen intact in sections.

Side views of the spermatogonial spindles clearly prove that all of the chromosomes at metaphase lie in a flat plate and preclude the possibility, as Wilson has pointed out, that some of the chromosomes may be outside the plate at this time, and hence fail to be included in a transverse section. The spermatogonial groups, therefore, show in this material not only the same number but precisely the same form-relations of the chromosomes as described and figured by Wilson, and afford a detailed confirmation of his results.

Our sections, furthermore, lend strong support to Wilson's view that the "chromosome-nucleolus" of the growth-period is the persistent odd chromosome of the spermatogonia, and not merely a chromatin nucleolus, as maintained by Foot and Strobell. They also furnish the most indisputable evidence of the asymmetrical distribution of the heterotropic chromosome at the second division. There is not the faintest indication that it is merely a "lagging chromosome" which divides at a late period of the anaphase, as is believed to be the case by the latter observers, but, on the contrary, every stage in its passage without division to one pole of the spindle can be followed. If any doubt as to this fact should remain from an examination of side views, two of which are given in Fig. 1, *G* and *H*, it is at once removed by seeing sections of the daughter plates of the same spindle which show ten chromosomes in one and eleven in the other, as figured by Wilson. *I* and *J* of Fig. 1 represent polar views of the daughter groups of the second division, the former lacking, the latter including the odd chromosome. These two groups belong to the same spindle and were drawn from the same section at different focuses, as one was lying immediately above the other in the same cell. The odd chromosome in *J* is easily recognized at *h*; it lies just below the others, while the remaining chromosomes in the two groups correspond exactly in size and relative position. It by no means always lies on the periphery of the group, but may be found in any position. The designation "eccentric," which Miss Foot and Miss Strobell apply to this chromosome is, therefore, a misnomer, for its position outside of the group at the second division—an occurrence upon which they lay much stress—is far from being a constant one.

Several such instances as that figured in *I* and *J* have been found, and

when the two groups can be observed in the same cell, they furnish an absolute demonstration of the inequality of the distribution of the chromosomes at this division, with the result that the heterotropic chromosome passes into one of the spermatids and not into the other.

The evidence presented by a study of the chromosomes of *Anasa tristis*, obtained in a locality widely separated from the places where other observers who have examined this form have secured their material, would seem to indicate that Wilson's description, especially with regard to the behavior of the heterotropic chromosome, holds good throughout the species.

In view of the important bearing which these facts have upon the chromosome-theory of sex-determination, it has seemed advisable to add a confirmatory note to the already clear and convincing observations of Wilson on this and other hemipterans.

ANAX JUNIUS.

The spermatogenesis of this dragon-fly was first described in 1904 by Miss McGill, *o4*, who found a close similarity to Paulmier's account of *Anasa tristis*. Like him, she described an even number of spermatogonial chromosomes, in this case 28, and followed him in identifying the accessory chromosome of the maturation divisions with the two small chromosomes of the spermatogonia which were supposed to have united to form a bivalent at synapsis. The accessory chromosome was correctly observed to divide at the first maturation mitosis and to pass undivided to one pole at the second, as Paulmier had described for the squash-bug.

A recent study, however, of the testis of *Anax* has brought to light the fact that the same error was made as in the case of *Anasa*, since it has been determined beyond any doubt that the number of spermatogonial chromosomes is 27 and not 28. It is, furthermore, clear that the small or *m*-chromosomes of the spermatogonium divide at both maturation mitoses, and hence cannot be identified with the accessory which is one of the larger chromosomes, though not the largest of the spermatogonial group. Miss McGill was also unable to find evidence in the material which she examined of a condensed chromosome-like body persisting throughout the growth-period, but in our more recent study this has been clearly demonstrated at every stage of the resting spermatocyte until it passes on the spindle of the first maturation mitosis. Judging from its size-relations and other considerations, it is unquestionably the odd or heterotropic chromosome.

Our re-examination of *Anax*, therefore, brings this dragon-fly into complete accord with those insects, like *Anasa* and *Protenor*, in which an odd number of chromosomes is found in the spermatogonia and an asymmetrical distribution of the heterotropic chromosome takes place at one of the maturation divisions, resulting in a dimorphism of the spermatids. These observations consequently lend additional support to Wilson's interpretation of the relation of the chromosomes to sex-production.

In the following account, the general course of spermatogenesis in *Anax* will not be traced, as this will be found in Miss McGill's original paper, but only such points will be brought out as require correction or further amplification.

THE SPERMATOGONIAL GROUP OF CHROMOSOMES.—As already stated, the number of chromosomes is 27. This has been determined with perfect clearness in a very large number of cases and has been found to hold true without exception. Whenever the equatorial plate is cut transversely at full metaphase, the chromosomes are seen lying well apart and sharply defined, while the counting of their number is a matter of the greatest ease. It is only in unfavorable cases, as in insufficiently extracted sections or through a close crowding of the chromosomes, that an accurate count is rendered uncertain. In properly stained sections, an unlimited number of cells have been found which show 27 distinct chromosomes, never more.

The size differences in the chromosomes are well marked, although not so strikingly as in many of the Hemiptera. Between the *m*-chromosomes, which are the smallest pair, and the largest pair or macro-chromosomes, which are usually quite perceptibly larger than any of the others, the remaining chromosomes, except the odd one, may be arranged in pairs of intermediate sizes. The differences among the latter, however, are only slight and some pairs are of approximately equal size (Fig. 2, *A* and *B*). After pairing off all the others, one will be left without a mate, and this will be found among those of intermediate size. The exact chromosome cannot be identified as the odd one, as the sizes are not sufficiently differentiated to allow of an accurate pairing of all the remaining chromosomes, and furthermore some of the chromosomes exhibit a certain irregularity of form which increases the difficulty.

In side views, the spermatogonial spindles show a flat equatorial plate at metaphase, with all of the chromosomes lying in the same plane (Fig. 2, *C*), and here, as in *Anasa*, polar views at this stage exhibit without doubt the full number of chromosomes.

The spermatogonial divisions have been adequately described by Miss

McGill, and the details need not be repeated here. All of the chromosomes divide longitudinally and pass in similar daughter groups to the poles, while after the last division the young spermatocytes enter upon the growth period.

THE FEMALE SOMATIC CHROMOSOMES.—An attempt has been made to determine the number of chromosomes in the female germ-cells, and sections of the ovaries of the nymphs have been carefully examined. Although no oögonial divisions have been encountered, possibly because we have not been able to obtain ovaries from young enough nymphs, nevertheless mitosis occurs abundantly among the follicle cells and a detailed search has disclosed several cases where the sections were favorable for counting the chromosomes. It might be remarked that Miss McGill, 06, in her study of the ovarian history of the germ-cells in the same dragon-fly has shown that the follicle cells have the same origin as the oögonia, both being differentiated from cells of the end-filaments of the egg-strings, and there is, therefore, every reason for supposing that their chromosomes are essentially the same. The number of chromosomes in the follicle cells has been determined in several instances, and wherever an accurate count has been possible, it has been found to be 28. Two of these cases are drawn in Fig. 2, *D* and *E*, and show the full number distinctly. The size differences are not as well marked as in the male groups, although the *m*-chromosomes are readily identified in *D*, and a decidedly largest pair is seen in *E*. The chromosomes, however, appear somewhat smaller and show a slightly greater irregularity of form than do those of the male group. This is especially true of *D*, the group *E* being more nearly like the male in the size and shape of the chromosomes. In both of these cases, and also in a few others where an accurate count has been possible, the chromosomes had not quite come to full metaphase. They had, therefore, not reached their complete condensation and were evidently not lying in their final orientation on the spindle, with the result that they appeared in the sections at varying angles. This fact explains their irregularity of form, and, doubtless, a longer search would have revealed more favorable cases showing a closer similarity to the size and shape of the male chromosomes. Still, the cases illustrated exhibit a striking correspondence, and it is a matter of great importance for the theory of sex-chromosomes to know that the female number is 28, while that of the male is 27. It is, furthermore, of interest to find that the same differences among the chromosomes exist in a member of the Odonata as have been shown to occur in the Hemiptera and other groups of insects.

THE GROWTH PERIOD.—The growth period has not been followed throughout in all the detail that is desirable, and the important question of the character of the synapsis must for the present be left undecided. Preceding the contraction-phase a stage is found where the chromatin appears in the form of fine threads scattered throughout the nucleus or more or less massed in loose tangles. Some of these strands are V or Y-shaped, or are seen lying in separate pairs or as irregular crosses (Fig. 2, *F*.) The appearance might readily be interpreted as the result of a longitudinal conjugation of univalent chromosomes which are now opening out to form elongated loops or ribbons. In view of the work of v. Winiwarter, 00, the Schreiners, 04-06, Lerat, 05, Janssens, 05, Bonnevie, 05-07, Stevens, 05, 06, and others, who have brought forward evidence in support of parallel conjugation, it is entirely possible that a more careful study of this and earlier stages in the growth-period of *Anax* might throw light upon the true nature of synapsis in this insect, but at present the evidence is insufficient for a demonstration.

The odd chromosome, as a dense nucleolus-like body, is quite conspicuous at this stage, staining deeply in both hæmatoxylin and safranin, and is frequently found to be constricted into a dumb-bell shape (Fig. 2, *F*, *h*). It does not occupy a constant position in the nucleus, sometimes lying near the membrane, at other times at any point within the nuclear area. Often it is seen close against the plasmosome, while as often it may lie at quite a distance from it.

This stage is followed by the contraction-phase (Fig. 2, *G*), in which, however, the chromosomes never become condensed into a compact mass. The threads now appear much thicker and longer than at an earlier period and are usually arranged in long, loose loops, the ends of which are more or less directed toward one pole of the nucleus, constituting the so-called "bouquet-stage." Curiously enough, the longest and thickest ribbon, which is the one that will give rise to the largest tetrad later on, frequently lies outside the "bouquet" and is seen stretching half-way around the nucleus close against the membrane, as shown in Fig. 2, *G*. This elongated chromosome is often interrupted at its middle point, as are, in fact, some of the looped threads, which consequently exhibit a bivalent nature. The break, moreover, is found to persist from now on to the time when the final condensation of the chromosomes takes place in the formation of the crosses. It may represent, of course, the line of suture between two univalent chromosomes conjugating end to end, or it may be equally well interpreted as the point of contact between the

ends of two chromosomes which have previously undergone a parallel conjugation and subsequently opened out to form a loop or ribbon.

During the bouquet-stage, the chromosome-nucleolus, which we may speak of as the heterotropic chromosome, as it directly passes into this body without ever assuming a thread-like form, is always present and is frequently constricted in the middle or even completely divided into halves. (Fig. 2, *H*).

It is not until after the bouquet-stage is passed and the chromosomes, in the form of bivalent threads of varying length, have scattered through the nucleus, that the longitudinal split becomes visible, while the interruption at the middle of each thread becomes very conspicuous (Fig. 2, *H* and *I*). Delicate strands of linin may be seen bridging across the transverse split and connecting the halves with each other. One of the double ribbons is always much longer than the rest and can be traced continuously back to the long chromosome of the bouquet-stage and forward to the largest tetrad.

The heterotropic chromosome is still seen to be double, although it has lost its dumb-bell form and is now spherical with a distinct line of cleavage dividing it into halves, as if the two rounded portions of the dumb-bell had flattened down upon each other (*H* and *I*).

Late in the growth period and preparatory to the first maturation division, the longitudinally split threads showing their quadripartite character, as seen in the last figure, begin the process of condensation. The longitudinal halves fuse completely and become much shorter and thicker, although the transverse interruption is still present as a clearly marked constriction at the middle point of the chromosomes. This stage is drawn in Fig. 2, *J*, in which the large bivalent is quite easily recognized.

The odd chromosome can be followed continuously from the earliest stages of the growth-period, until it appears as shown at *k* in this figure. The two hemispheres have become rounded out and slightly drawn apart, although not completely separated, and in this condition it is taken up on the spindle which is formed a little later.

The thick bivalent rods next undergo a still further condensation and are converted into crosses by outgrowth of transverse arms at the level of the constriction. These arms, however, do not extend so far as to confuse the original longitudinal axis, a condition which is especially conspicuous in the largest cross where the transverse and longitudinal arms remain quite unequal, although it is more or less pronounced in all. As this inequality in the length of the arms is retained until the crosses are taken up on the spindle, an identification of the long axis of the cross with that

of the threads of the growth-period is made certain, and, furthermore, it is evident that the crosses are placed lengthwise upon the spindle.

The number of chromosomes is now easily observed, fourteen in all, thirteen of which are in the form of crosses, while one, the heterotropic, is a simple, condensed, bipartite body. As the crosses condense, their centers, just before the disappearance of the nuclear membrane, become lighter and soon take the stain only faintly, while by the time the spindle is visible they have become completely hollowed out. The series of changes taking place in the formation of the crosses, and their conversion into the open tetrads may be followed through Fig. 2, *J-L*, and Fig. 3, *A* and *B*, successively. These figures also demonstrate the relation of the long axis of the cross to that of the spindle which are seen to be parallel.

THE FIRST MATURATION DIVISION.—After being taken up on the spindle the open tetrads rapidly undergo a condensation; all traces of the space between the arms disappear, and by the time the prophase is ended they have the form shown in side view in Fig. 3, *C*. Although the quadripartite character of the thirteen tetrads is still indicated by slight depressions or grooves on the surface, there is at this stage no separation of the four elements which have become fused with each other. In side views the broad face of the tetrads shows the demarcation of the four compound parts, while those tetrads which are seen on edge in these views appear as dumb-bell shaped bodies and therefore cannot be distinguished, except in some cases by size, from the heterotropic chromosome which has this appearance when seen in either vertical plane. In order to determine with certainty which chromosome is the heterotropic, one must examine the metaphase groups in polar view, in which all of the tetrads appear as dumb-bell shaped bodies, while the heterotropic is seen as a single chromosome, since its constriction lies in the horizontal plane. Fig. 3, *D*, shows these relations very plainly; there are thirteen double chromosomes which are the thirteen tetrads seen in polar view, while the heterotropic at *h* appears as a single oval body. The range in size from the smallest to the largest tetrad is also clearly indicated. *E* is another polar view, but at a slightly later time when the separation of elements is just beginning in four of the tetrads. This breaking apart of the component parts of the tetrad proceeds rapidly with the beginning of the anaphase, until all four elements are entirely distinct from each other as the opposite pairs advance toward the poles of the spindle (*F* and *H* of Fig. 3). *G* shows a daughter group in the early anaphase before the members of all of the pairs are entirely separated, while *I* is a similar view a little later. In the latter, there is no longer any connection be-

tween the halves of the dyads, which, however, are still lying side by side. In both drawings the heterotropic is recognized at a glance, as it is the only chromosome in the group without a mate.

The divergence of the chromosomes occurs at unequal rates, those on the periphery lagging behind, those in the center taking the lead, while the heterotropic lags most of all and in late anaphases, when the others are grouped about the poles in a dome-shaped mass, the halves of the heterotropic may usually be seen some distance behind in the process (*J* and *K* of Fig. 3).

As the chromosomes reach the poles, they become closely crowded together and partially break up into a reticulum, although to a certain extent their identity is still retained in the nodes of the network. The centrosomes fade out and a new nuclear membrane forms but only to disappear shortly afterwards in preparation for the second division. In fact, there are indications that in some cases at all events this intervening resting stage between the two divisions is practically omitted.

THE SECOND MATURATION DIVISION.—As soon as the nuclear membrane fades away the chromosomes reappear as dumb-bell shaped bodies, and as the new spindle forms they take up their position in the equatorial plate with the constriction at right angles to the long axis of the spindle. There are thirteen of these dyads, and the one single chromosome, the heterotropic. Even before the other chromosomes pass definitely into the equatorial plate, the heterotropic without undergoing division begins usually to move in advance toward one of the poles, as may be seen in Fig. 4, *A* and *B*, and it has nearly completed its journey before the divergence of the other chromosomes is commenced. There is, however, a good deal of irregularity in the movement apart of the chromosomes, especially during the early anaphase, the halves of each pair seeming to diverge at a more or less independent rate. This independence of movement, not only of the heterotropic, but of the other chromosomes as well, increases the difficulty of mechanical or electrical theories of the cause of divergence.

Early stages in the progress of the undivided heterotropic chromosome toward one pole are shown in *A* and *B* of Fig. 4, while still later stages are represented in *C* and *D*. In the former drawings, both the *m*-chromosome and the macro-chromosome are distinctly recognized in side view, while in *D*, although the heterotropic is still visible at one pole, the other chromosomes are closely massed together. As in *Anasa tristis*, polar views at the anaphase of this division clearly demonstrate the dimorphism of the daughter groups, since thirteen single chromosomes appear in one and fourteen in the other, the former being the one that lacks the hetero-

tropic. At about the stage of the anaphase represented in *C*, this inequality in the number of chromosomes composing the daughter plates has been determined in several well marked cases where the groups have been observed in polar view at different focuses on one and the same spindle. *E* and *F* are such anaphase groups drawn from the same section, *E* including the heterotropic which is seen at *h*, *F* lacking this chromosome. In each group the *m*-chromosome and the macro-chromosome are readily picked out, while the two groups, if added together, would exactly reproduce the conditions seen in the spermatogonial plate.

It has been said that the heterotropic chromosome *usually* passes in advance of the others during the anaphase of the second division, as in the majority of cases, where this stage is observed in side view, such a condition is quite evident. But, strangely enough, a few cells are always encountered, often in the same cyst with the others, which show the heterotropic lagging behind instead of preceding the other chromosomes, as in the case of *Anasa*. Of course it cannot be determined with certainty that the lagging one is the same chromosome as the precocious heterotropic of the commoner cases, but there can be little doubt that the two are identical. This conclusion is rendered very probable from their similarity in size and also from the fact that when the heterotropic is seen in advance a lagging chromosome is not observed, and vice versa. It is, therefore, to be supposed that the heterotropic may pass indifferently either in front of the other chromosomes or behind them.

SOME GENERAL CONSIDERATIONS.—As a result of our re-investigation of the spermatogenesis of *Anax junius*, it has been established beyond doubt that this dragon-fly, in the behavior of the chromosomes of the male germ-cells, closely parallels the conditions which have been observed in some of the Hemiptera and other higher groups of insects. In the differentiation of its chromosomes as *m*-chromosomes, macro-chromosomes, and chromosomes of intermediate sizes; in the occurrence of an odd number of chromosomes (27) in the male groups and of this number plus one (28) in the female groups; in the presence of an accessory or heterotropic chromosome which persists as a condensed body throughout the growth-period and passes undivided at the second maturation division into one of the spermatids, a strict parallelism may be recognized between *Anax* and those other insects, of which *Anasa tristis* may be taken as a type, which possess a heterotropic chromosome. In at least one of the Odonata, therefore, a dimorphism of the spermatozoa occurs, and the theory of the determination of sex by differentiated sex-chromosomes receives additional support from this group of insects.

Our observations, however, throw no light upon the important problem of reduction, yet certain conditions in the formation of the tetrads and the distribution of their component elements may be briefly indicated. A slightly schematic representation of the formation of the tetrads, showing also the axial relations of the longitudinally split bivalent threads of the growth-period and of the tetrads on the spindle is given in Fig. 5. In each of the successive figures from *A* to *I*, it is the largest chromosome that is shown, while all are drawn under the same magnification. Many of the chromosomes in this diagram are redrawn with only unimportant modification from the macro-chromosome already represented in previous figures. For example, *D* is taken from Fig. 2, *K*; *H*, from Fig. 3, *F*; etc.

It has already been pointed out that the long axis of the tetrad is identical with the long axis of the chromatin threads of the growth period, and since the figures have clearly shown that the tetrads are placed upon the spindle lengthwise, it follows that the first maturation division must separate univalent chromosomes and be therefore a reducing division on the assumption that an end to end conjugation takes place between individual chromosomes at synapsis. And continuing this assumption, the second division must be equational, since the chromosomes are oriented in such a way as to distribute the halves of the dyads which are separated by the longitudinal split. This conclusion was drawn by Miss McGill in her original paper. If, however, it should prove true of this form that a parallel conjugation occurs, as has been suggested, the first division would still be a reducing one, since the axes of the crosses are not reversed by the drawing out of the transverse arms and the attachment to the spindle fibers is at the end of the longitudinal arms, as seen in Fig. 5, *E*. But in the event of the chromosomes conjugating side to side, it would still have to be shown that they separate after fusion as the originally distinct chromosomes without loss of identity before a real reduction could be established. The crucial problem, then, in the whole question of reduction lies at this point, and until further light is thrown upon it by future investigation, it is futile to indicate possibilities and frame speculations.

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NOTE.—All of the drawings were made as carefully as possible with the camera under a 2 mm. Zeiss apochromatic and compensation-ocular 12. They were then enlarged with a drawing camera two and a half times, corrected by comparison with the objects, and reduced by one-third in reproduction. Their final magnification as they appear here is about 3583 diameters. Although the chromosomes are represented as accurately as possible, and are in no sense schematized, an attempt has not been made to show the details of the achromatic structures.

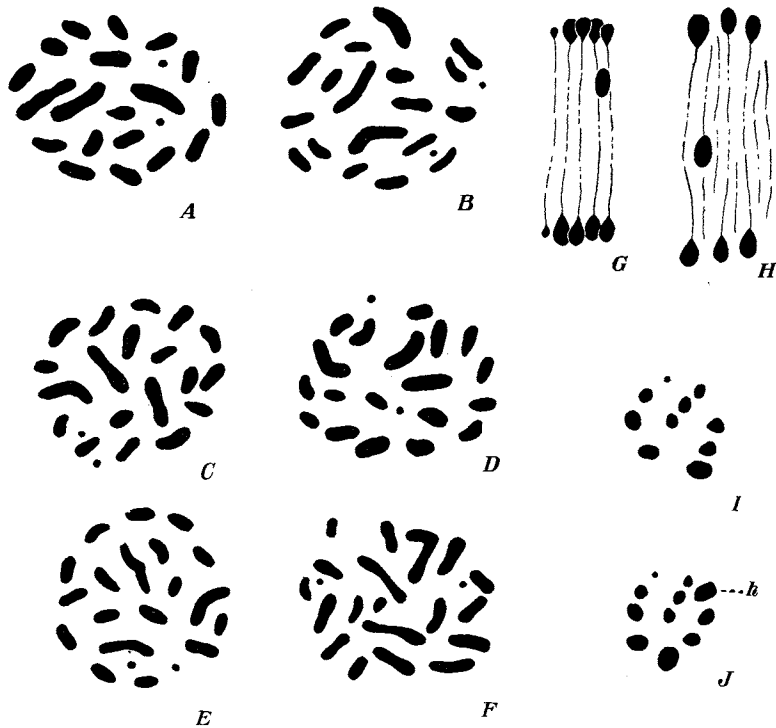


FIG. 1. *Anasa tristis*. *A-F*, spermatogonial groups; *G, H*, anaphases of second division, showing division of *m*-chromosomes in *G* and the undivided heterotropic chromosome on both spindles; *I, J*, anaphase groups from the same spindle, polar view, second division, showing *m*-chromosome and macrochromosome in each and the heterotropic (*h*) in *J*.

FIG. 2. *Anax junius*. *A, B*, Spermatogonial groups; *C*, metaphase of spermatogonial division; *D, E*, chromosome-groups from follicle cells of ovary; *F*, early stage of growth-period of the male, showing heterotropic (*h*) and plasmosome (*p*); *G*, contraction-phase, "bouquet-stage," showing the bivalent macro-chromosome; *H, I*, later growth-period, showing longitudinal splitting of chromosomes and the divided heterotropic (*h*); *J, K, L*, successive stages of the spermatocyte-nucleus, showing condensation of the bivalent chromosomes to form crosses.

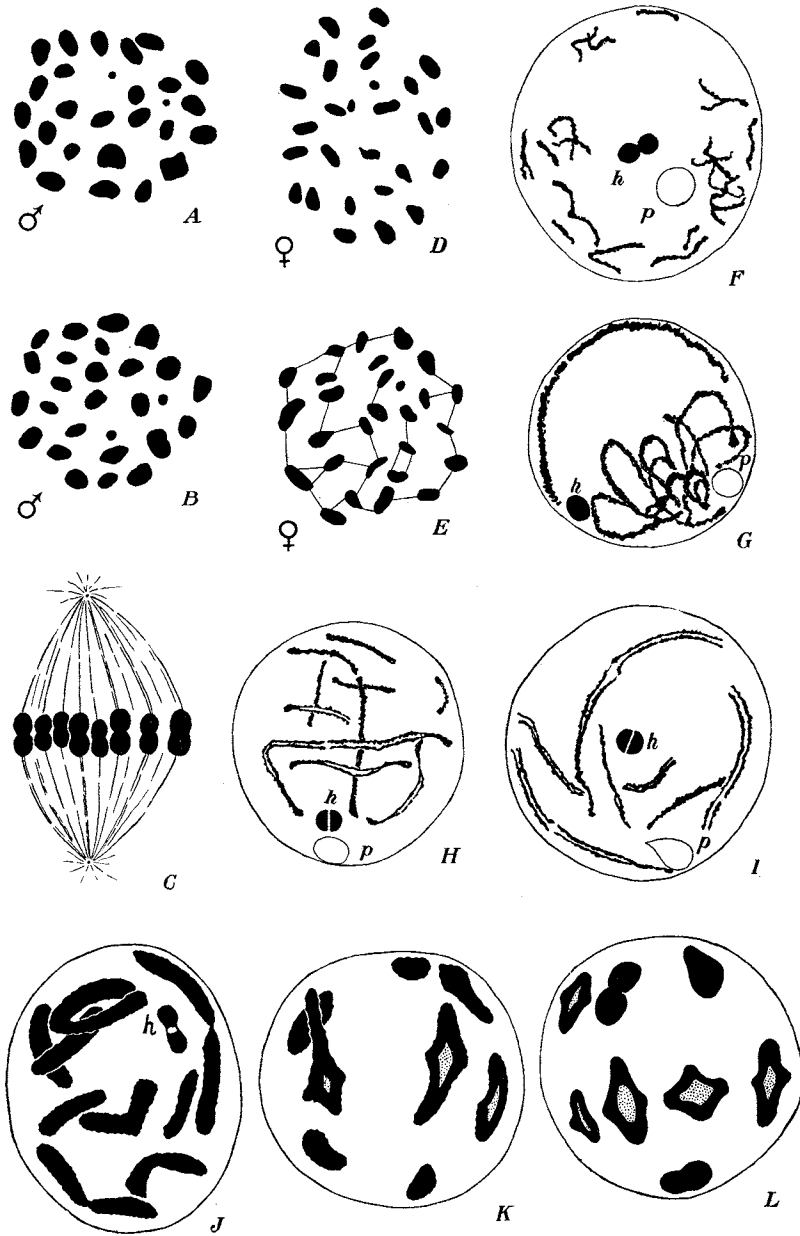


FIG. 2.

FIG. 3. *Anax junius*. *A, B*, Late prophases of first division, showing in some cases the four parts of the crosses; *C*, metaphase, first division, showing condensed tetrads; *D, E*, metaphase groups, polar view, showing the 13 tetrads and the heterotropic (\bar{h}) in each case; *F*, beginning anaphase, first division, showing complete separation of the parts of the tetrads; *G*, early anaphase group, polar view, showing 13 dyads and the single heterotropic; *H*, early anaphase, first division; *I*, anaphase group, polar view, same stage as last; *J, K*, later anaphases, first division, showing the divided heterotropic lagging.

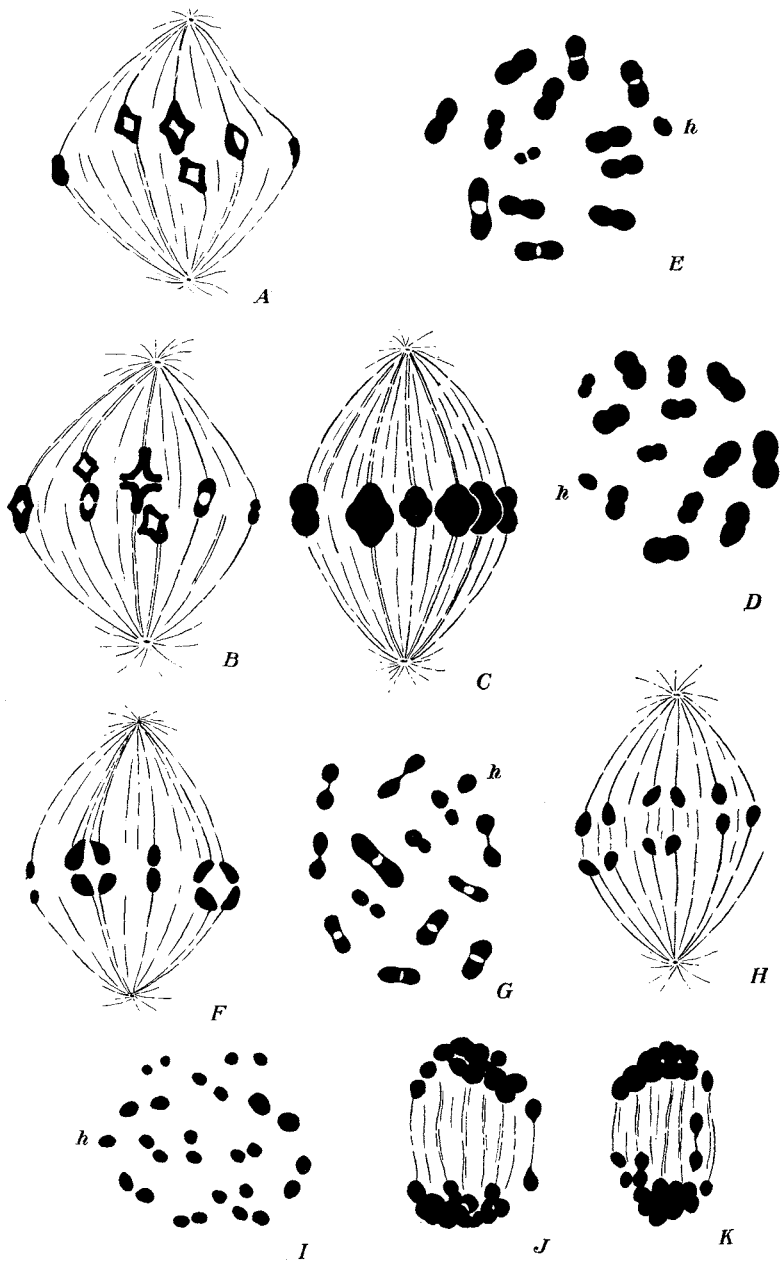


FIG. 3.

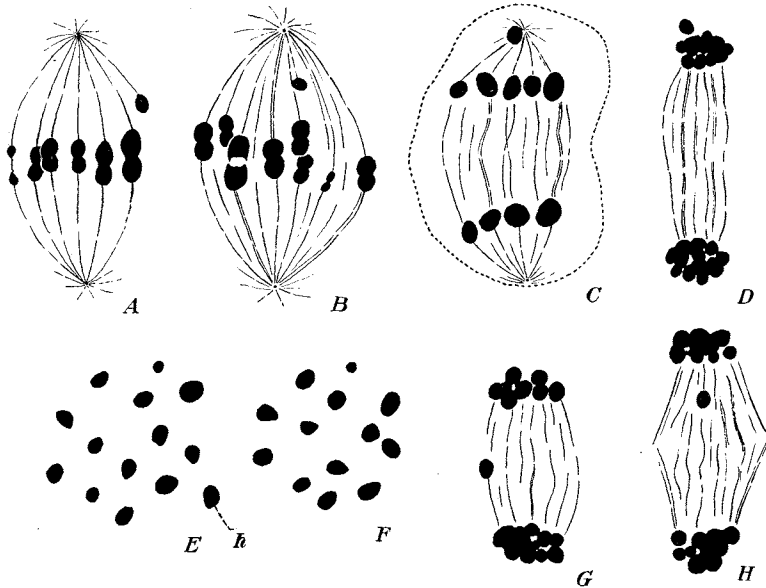


FIG. 4. *Anax junius*. *A, B*, Second spermatocyte-division, showing undivided heterotropic passing to one pole and the *m*-chromosome dividing in *A*; *C, D*, later anaphases, second division, still showing undivided heterotropic in advance of other chromosomes; *E, F*, anaphase groups from same spindle, polar view, second division, showing the *m*-chromosome and macro-chromosome in each and the heterotropic (*h*) in *E*; *G, H*, late anaphases, second division, showing the heterotropic lagging behind instead of advancing in front of the other chromosomes.

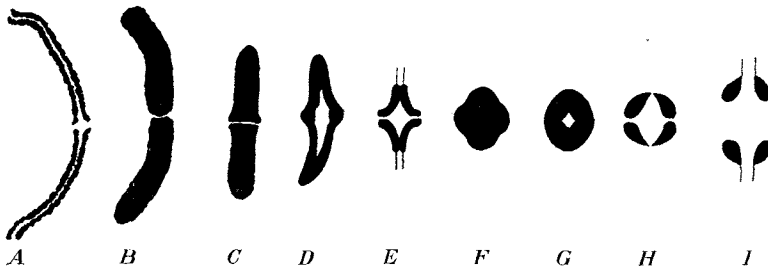


FIG. 5. *Anax junius*. Slightly schematic representation of successive stages in formation of tetrads and axial relations of same; *A*, longitudinally split bivalent from late growth-period; *B, C*, condensation of bivalents; *D*, formation of cross; *E*, cross with the four parts distinct, oriented on spindle with original long axis placed lengthwise; *F*, condensation of tetrad; *G*, tetrad beginning to open; *H*, tetrad completely separated into 4 parts; *I*, divergence of the divided dyads in anaphase of first maturation mitosis.