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The Idiochromosomes of the Mantis¹⁾

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(With 3 Figures and 3 Tables)

Since GIARDIANA ('97)²⁾ published the results of his study on the chromosomes of *Mantis religiosa*, there has been no attempt made, so far as I am aware, to study the chromosomes in any species of Mantidae. It is evident that our present knowledge is in this respect not yet perfect. The present study was undertaken years ago with a view to the advancement of the cytology of the Mantidae, on the one hand, and to that of the Orthoptera in general, on the other.

The Mantidae are represented in Japan by several common species, but all are confined to the southern parts of the empire; no species is hitherto known to exist in Sapporo and practically throughout the whole area of the island of Hokkaido³⁾. The material of the present study consists accordingly of the eggs of two species, *Tenodera superstitiosa* and *Paratenodera aridifolia*, from Kyoto and Gifu, collected by Messrs. A. NOHIRA, M. SUZUKI, Y. NAWA and late K. NAGANO, to whom I am greatly indebted.

¹⁾ A part of this study has been published in the Zoological Magazine (written in Japanese) ('18).

²⁾ To my regret, I have been unable to get access to his original paper, and am compelled to limit myself to referring to the data cited in Harvey's review ('16).

³⁾ A mantid, which may probably be regarded as *Tenodera superstitiosa*, is recorded only from Hakodate, the southern extremity of Hokkaido.

The eggs hatched out from the middle of June to the end of July. The larvae on leaving the egg-clusters were set free at once in our college meadow to be reared under natural conditions. The observations in the three years past show that the first named species, *Tenodera superstitiosa*, is not difficult to be reared in our rather cold climate up to the adult stage which was attained at about the end of August; with the latter, *Paratenodera aridifolia*, it seems, on the contrary, to be by no means easy to do this, because its adolescence was not attained before the autumn set in, so that I could procure only a few specimens of it.

HERMANN'S mixture and CARNOY'S fluid were appropriately employed for fixation, and iron hämatoxylin with counterstaining of light green, safranin, and methylgreen acid fuchsin mixture respectively was applied for staining. All the material was imbedded in paraffin and sectioned.

In the present study, the author believes to have succeeded in making out not only the number of chromosomes, but also three peculiar idiochromosomes which can certainly be looked upon as the sex-determinants. The present paper is, however, devoted chiefly to the elucidation of the latter.

Here I wish to express my deepest thanks to Prof. S. HATTA for the courtesy shown by him during the course of the present study.

I. FACTS REGARDING *TENODERA SUPERSTITIOSA*.

(Figure 1)

1. *The Chromosomes in the Primary Spermatocytes.*

A primary spermatocyte possesses thirteen chromosomes as a haploid number. *Fig. 1, g* represents all the chromosomes, arranged in the metaphase equatorial plate of the first maturing division and divided into two consecutive sections of a nucleus. Of these thirteen chromosomes, twelve are represented by bipartite bodies which are ring- or dumbbell-shaped and provided with a central swelling, — features characteristic to bivalent chromosomes. But the one remaining, i. e. the third from the left in the figure, shows a quite peculiar form in addition to its magnificent size. It is tripartite in form, being composed of three different parts, of which two are strikingly large and directed to one and the same pole of the spindle, while the third

is much smaller as compared with the former and directed to the opposite pole of the spindle. The larger two parts of the chromosome are nearly similar in shape though different in magnitude: they are bent like L or V, one arm of which lies parallel, and the other at an acute angle, with the axis of the spindle; it is this latter arm which is always remarkable for thickness. The third (and smaller) element of the tripartite chromosome shows likewise a V-shape, but the two arms of it differ greatly in length, and are nearly the same in thickness throughout its entire extent. Both its arms are connected by their free ends with the extremities of the respective slender arms of the two larger components by means of linin fibres, while both the thicker arms of the latter are free. In this respect the larger elements are distinguished not only from the smaller component, but also from the bivalent chromosomes, the arms of which stand in similar relation to the linin connection as those of the smaller component of the tripartite chromosome.

In all the three component parts of the tripartite chromosome, the spindle fiber is invariably attached to the bent point of each; in other words, the attachment is median or subterminal, or what may be called atelomitic in CAROTHER's terminology.

The chromosome in question is to be distinguished from an auto-some bivalent, and regarded as an idiochromosome complex, which is composed of three components so linked as to make up a trivalent chromosome during the growth period of the first maturing division. For the convenience of description, I designate the larger components as *Ia* and *Ib* respectively, and smaller one as *i*. The metaphase of the first maturing division is characterized by *Ia* and *Ib* which are invariably not linked together in a direct fashion, but by means of *i* being interposed between them; in particular the linkage is so arranged that the short arm of *i* is connected with the arm of *Ia* and its long arm with that of *Ib*.

The polar view of the equatorial plates is shown in *figs. 1, e* and *f*. In *fig. 1, f*, the trivalent idiochromosome complex is seen as two separate thick rods which represent the horizontally stretched arms of *Ia* and *Ib*, the chromosome *i* is not seen, lying completely out of focus, so that there are revealed fourteen separate chromosomes instead of thirteen as found in the lateral view of the spindle (*fig. 1, g*). But when we trace by focussing *Ia* and *Ib* downwards to their inner ex-

tremities, these two chromosomes, united with the *i*-chromosome, come into view, so as to represent a complete tripartite figure. I have endeavoured to show such a case in *fig. 1, e*, in which the idiochromosome complex is to be seen as a Y-shaped body.

At the same time, when the twelve bivalent chromosomes are divided in anaphase of the present division into their daughter halves, the tripartite idiochromosome complex is disconnected into three component parts, viz. into *Ia*, *Ib* and *i*, of which the two *I*'s run together to one pole, while the single *i* goes to the opposite pole (*figs. 1, h, i*), as one expects already from their arrangement on the metaphase equatorial plate. It follows that the first maturation division causes the chromosomes to be distributed in the daughter cells which represent the secondary spermatocytes, in such a way, that one of them involves the two separate *I*'s, whereas the other contains the single *i*. One of the most remarkable processes carried out by the first maturing division consists then, in the present case, in the operation, by which the two unequivalent classes of the secondary spermatocytes are brought about.

On arrival at the pole, the chromosomes *Ia* and *Ib* undergo occasionally a longitudinal splitting along their long axes, — the preparatory occurrence for the next division. This is doubtless also the case in the chromosome *i*, even though I am unable to distinguish it.

2. Chromosomes in the Secondary Spermatocytes.

Now let us follow the fates of the idiochromosomes in the second maturing division undergone by the secondary spermatocytes. In the course of the metaphase of the second maturing division one cannot fail to note that on the equatorial plate two chromosomes are quite distinct from the remaining twelve rod-shaped ones owing to their considerably large size and markedly crooked shape (*figs. 1, j, k*); these two can be identified with nothing else but *Ia* and *Ib* respectively, whereas the remaining twelve represent the autosomes. The cell with its contents just referred to constitutes, of course, one of the two classes of the secondary spermatocytes.

In other instances, the equatorial plates show only *thirteen* rod-shaped chromosomes (*figs. 1, l, m*). There is practically no distinction among the thirteen chromosomes in size and shape; nevertheless I do not hesitate to take one of them as equivalent of the *i*-chromosome,

from which the twelve autosomes are, in this respect, by no means easily distinguishable, because the *i* and the largest autosome differ hardly at all in length. The cell containing these thirteen chromosomes constitutes, therefore, the second class of the secondary spermatocytes.

An interesting point is the further destiny of the idiochromosomes: all three are divided equally into equal halves; the splitting plane of each chromosome has already become obvious at the close of the preceding division, as has been stated above. The *Ia* and *Ib* contained in the secondary spermatocytes of the first class undergo, for the first instance, the second maturing division, by which the larger idiochromosomes *Ia* and *Ib* are divided like the autosomes into two equal parts (*fig. 1, n*), each of which enters together with the proper group of the autosomes in the formation of each daughter nucleus, so that the two spermatids involve in their nuclei equally *Ia* and *Ib* together with autosomes; the spermatids of the second class are likewise all alike provided in each with the single *i*-chromosome instead of the two *I*'s in the preceding class of the spermatids.

3. *Chromosomes in the Spermatogonia.*

To determine the diploid number of chromosomes and to distinguish idiochromosomes from the autosomes in the diploid group, the spermatogonia come first under notice. A spermatogonium possesses twenty seven chromosomes, as is quite obvious in the mitosis of the nucleus (*fig. 1, a, b*). The chromosomes are all rod-shaped, and varying in length, as is the case with those in the secondary spermatocytes. But, as it appears, two chromosomes of about equal size are coupled, and every couple lies always not only close, but to a certain extent parallel with, the rest, so that it can certainly be said that twenty four out of all the chromosomes are nothing else but twelve pairs of the autosomes. We have thus three remaining which differ from one another in a marked degree in length and are scattered in position and cannot be arranged in pairs. The longest of them grows, in fact, more than twice as long as the largest of the chromosomes which we distinguished above as the autosomes, and the shortest is about equal to or hardly exceeds the autosome just referred to in length, while the intermediate one is about three fourths the length of the largest.

In addition to this, with regard to their position, the three heterogeneous chromosomes are in metaphase always located in the peripheral

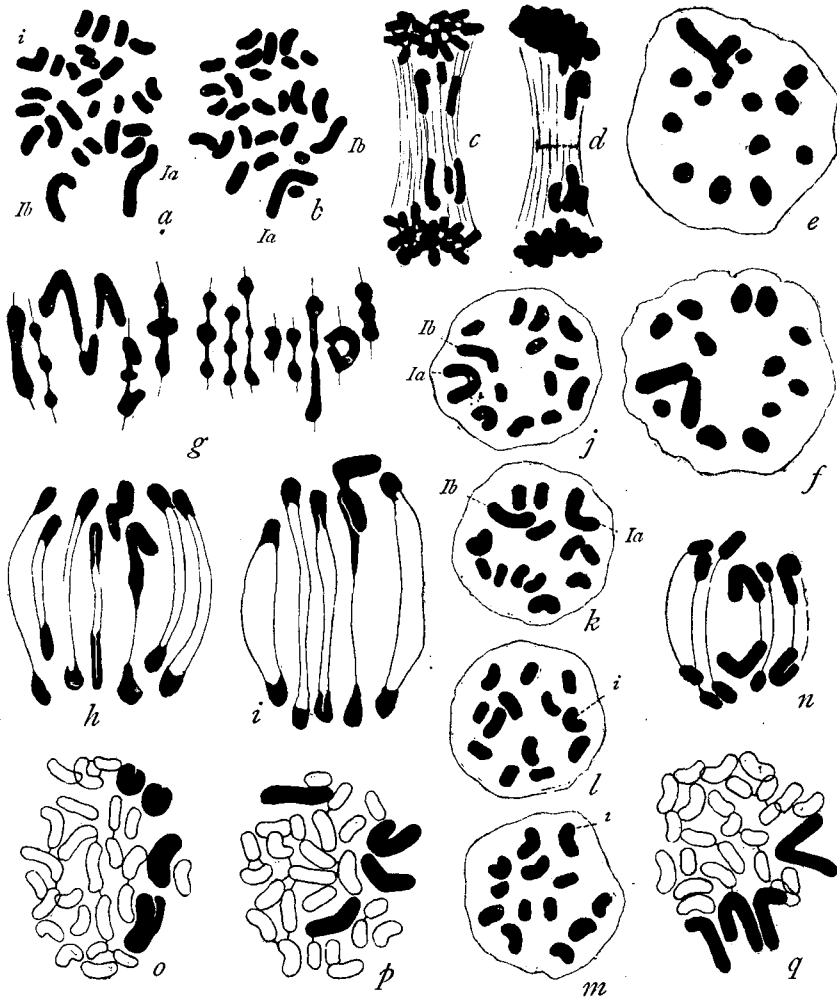


Figure 1.

Tenodera superstitionosa

Figs. a to n, Zeiss 1.5 Apochr. \times Comp. Oc. 12; t. l. 160 mm.

Figs. o to q, Zeiss 2 mm Apochr. \times Comp. Oc. 12; t. l. 200 mm.

a, b, Chromosomes in spermatogonia., c, d, Chromosomes at a late anaphase of the last spermatogonial division., e, f, Chromosomes of the primary spermatocytes., g, Side view of the chromosomes of the same., h, i, Chromosomes in the anaphase of the first maturing division., j-m Chromosomes in the metaphase of the secondary spermatocytes., n, Chromosomes in the anaphase of the second maturing division., o, p, Chromosomes in the cells of follicle. epithelia in female., q, Chromosomes in the cell of oviduct. The lines enclosing chromosomes in e, f, j, k, l, and m, indicate not the nuclear membranes, as one might mistake for, but represent the outlines of the spindle.

part of the equatorial plate, and lie, moreover, often far apart from the other members of the chromosomes (*fig. 1, a*). It is, therefore established that these three chromosomes are not susceptible of arrangement in pairs as is the case with the autosomes.

From the indisputable facts above mentioned, we have no alternation but to identify these three chromosomes of different size with the idiochromosomes, of which the characteristic behavior shown in the maturing divisions has already been dealt with in detail. It needs not to say that the two larger idiochromosomes correspond respectively with *Ia* and *Ib*, and the shortest with *i*. The *Ia* and *Ib* are curved or crooked in most cases like U or V, while the *i* is sometimes straight (*fig. 1, b*).

4. Chromosomes in the Somatic Cells of Female Individuals.

The determination of the significance which attaches to the idiochromosomes is accessible only when these are brought into view in the cells on the female side. Our next subject-matter consists, from this point of view, in the examination of cells taken from the female individuals; I took the somatic cells as the material on account of the facility with which the work could be carried on.

In the epithelium of the follicle as well as of the oviduct several cells are in process of division, and some of them are available for the purpose of counting the complete set of chromosomes contained. In the follicle cells (*figs. 1, o, p*), they are distinctly twenty eight in number, therefore one more than the diploid number in the male germ-cells (*vide supra*). All the chromosomes are short, simple and rod-shaped, except four which are enormous in length (shown black in the figures). From their size and shape these four may safely be taken as two pairs, each of which is represented by a couple of homologous mates. In (*fig. 1, o*) we recognize that the chromosomes of the longer pair show a slight curvature and in one of them, moreover, a longitudinal splitting, to be followed by its division in coming anaphase, while those of the other pair are crooked so markedly that both ends of each rod come together. In *fig. 1, p* the short pair represented is rather stretched, and one chromosome of the long pair is considerably bent. Finally in *fig. 1, q*, which was drawn from a cell of the oviduct, we likewise find four chromosomes of remarkable size amongst the twenty eight. In contrast to the preceding cases, these four are pro-

longed and slender and cannot otherwise be distinguished from those shown in the preceding figures, so that we are justified in taking them as two pairs of chromosomes identical with those dealt with above.

It is self-evident that these two pairs of chromosomes are the equivalents of the idiochromosomes which I have pointed out in the spermatocytes, and are in particular identical with *I*'s. The idiochromosomes *I*'s shown in *fig. 1, q* are likely to prove to be their full-grown form, and are thereafter thickened at the cost of a diminution in length (*fig. 1, p*), to be ultimately split (*fig. 1, o*) as the indication of the approaching next anaphase. There is represented in the present case no chromosome corresponding to the *i*; for the remaining twenty four chromosomes must be regarded as the twelve pairs of autosomes. Accordingly it is indisputable that the somatic cells of the female individuals are provided with the two pairs of larger idiochromosomes representing the two *I*'s according to our nomenclature, one half of which is carried over no doubt from the spermatids, *viz.* spermatozoa, containing in their nuclei the two large idiochromosomes in question.

5. *Idiochromosomes in the Growth Period and Prophase of the Primary Spermatocyte Division.*

(*Figure 2*)

The primary spermatocyte is very peculiar, inasmuch as its nucleus contains in every stage of its growth period a conspicuous chromatin nucleolus (*fig. 2, a, chn*), which is remarkable and is distinguished, as well by its enormous size and peculiar outline, as by its intense colour affection with haematoxylin or methylgreen, from the plasmosome (*p*), which is stained a little or remaining not affected by the reagents at all. Our problem ultimately consists in elucidating the origin and destiny of the body in question.

It is obvious that in *fig. 1 (c and d)* at the close of the last spermatogonial division the three idiochromosomes, *1a*, *1b* and *i*, are always still lagging on the way while the autosomes have arrived at the poles. Moreover, the three are at first separated from each other; in the course of division they are gradually drawn together, to coalesce at last into a single body which is nothing else than the chromatin nucleolus of the primary spermatocyte above referred to. How the coalescence is brought about, I can not tell; it can, however, be nothing



Figure 2.

All figs. Zeiss 1.5 mm Apochr. × Comp. Oc. 12, t.l. 160.

a-m. *Tenodera superstitionosa*.

n-o. *Paratenodera aridifolia*.

a, A primary spermatocyte after synaptic stage., b, Chromatin nucleoli from the primary spermatocytes in still later stage., c, Chromatin nucleoli in the prophase of the first division., d, chromatin nucleoli in still later stage., e, A nucleus of the same stage, shown all the chromosome elements and plasmosome., f, A nucleus in a still more later prophase., g, A nucleus at the end of prophase., h, Idiochromosome complex of various forms found in the same stage., i, Idiochromosome complex at the metaphase., j-o, Abnormal forms of idiochromosome complex at the metaphase and anaphase of the first division.

more than a simple mechanical fusion.

The chromatin nucleolus thus brought forth is, at the leptotene stage and in the synaptic stage, oblong in form and pointed at one of its poles, which is directed to the pole of the nucleus where the leptotene threads come in contact with one another to form a mass (*fig. 2, a*). Later in the confused stage, however, it becomes much shortened (*fig. 2, b*) and is then closely applied to the nuclear membrane.

Rarely, two smaller chromatin nucleoli can be detected in a nucleus instead of a large one. It is highly probable that in this case one of the idiochromosomes is delayed in fusion, or has failed, as it were, to be fused. I was, however, unable to follow the fates of this disconnected chromatin nucleolus.

At the commencement of the prophase, while autosomes begin to condense into more compact bodies with vague contour, the chromatin nucleolus sends out a pair of chromatic threads which appear as if budded out from it (*fig. 2, c*). The threads gradually grow longer, probably drawn out from the main body of the chromatin nucleolus, so as to attain a considerable length (*fig. 2, d, e*). At first they are nearly equal in length and easily confounded with the leptotene threads of the autosomes, showing an imperfectly defined contour and a number of deeply stained knobs at intervals; later one of the threads becomes somewhat longer than the other (*fig. 2, e*). In contrast to their terminal parts which are thickened into clavate shape and usually placed close together, the threads themselves are separated and very often apart from each other. The main part of the chromatin nucleolus from which two threads are produced, grows by stages smaller in size so as to be reduced so small as to be compared with the *i* of idiochromosome complex and yet it retains its sharp contour throughout these stages.

I have endeavoured to show all the formative contents, autosomes, chromatin nucleolus and plasmosome as a complete set, in *fig. 2, e*, drawn from three consecutive sections.

The autosomes attain their final condensation into the bipartite or quadripartite bodies, when the plasmosome disappears; meanwhile the transformation before explained is still going on in the chromatin nucleolus, although it is already about to assume the form characteristic to the idiochromosome complex. After attaining their full growth

in length, the chromatic threads, which are provided with clavate extremities, now begin to be shortened and condensed, until they are converted into short, thick and peculiarly bent threads with the specially dense knob at its middle point (*fig. 2, f*), which represents the main part, easily discernible by its sharp demarcation from the remaining parts of the threads imperfectly defined. The threads accordingly admit of distinction into three parts, of which the middle knob is, as the later history shows, transformed into the *i*, while the two other parts are destined to be converted into the *I*'s. It is only with the latest prophase of the first division, that the two rudiments of *I*'s with vague contour become as compact and are contoured as sharply as the *i*; arrived at the stage named, however, the three rudiments are expressed clearly and discriminated distinctly from one another by two constrictions (*fig. 2, g*). The idiochromosome complex assumes, when it acquires its characteristic feature, a ring shape, putting both the extremities of the thread into close contact; the threads are, however, stretched, as it afterwards happens (*fig. 2, h*). The chromosome complex is exceedingly distinct among the autosomes, not only because of its enormous size, but also of its tripartite structure. The *Ia* and *Ib* may or may not in either case be straight, but in the majority of cases they have already assumed the L- or V-shape at the stage spoken of.

When the nuclear membrane fades away, the metaphase of the first division sets in, and the three elements of the idiochromosome complex are brought at the same time to the equatorial plane in such an arrangement as shown in *fig. 2, i*.

What the history of the peculiar body contained in the nucleus of the primary spermatocyte and known as the chromatin nucleolus, shows, interests us very much, because the history is nothing than the historical cycle of the idiochromosomes regarded as the sex-determinants. The chromatin nucleolus is nothing more than the idiochromosomes that fused together, as we learn from its history above given. It is curious enough that the middle segment (*i*) of the three, of which the nucleolus is composed, is permanently in repose, while the two segments (*I*'s) manifest, at every prophase in the first division of the spermatocyte, being drawn respectively into threads. In the second place, the threads thus produced run parallel with each other and exhibit double nature and, in this respect, a great resemblance to the threads of the auto-

somes; but the former are essentially distinguishable from the latter: the threads of the idiochromosomes are made double by the two single threads of unequal length drawn out respectively from the two sides of the chromatin nucleolus and consequently not identical with each other; the threads of the autosomes are doubled, on the contrary, by two identical threads being brought together. In the former case, moreover, the double threads are permanently in a state of non-coalescence, in contrast to the latter, in which the double threads are brought at the proper stage into the complete fusion, leaving traces of the double nature. It is therefore evident that the idiochromosomes are in their nature quite distinct from the autosomes. I cannot but suppose that the whole phenomena displayed by the history of the idiochromosomes must be full of great significance, but I can at present form no conclusions about it.

In the transformation above mentioned I had the opportunity of observing some forms of the idiochromosomes deviating in form from the ordinary ones. In the case shown in *fig. 2, j* one of the *I*'s is spiral in form and the other is shovel-shaped; in the latter the terminal thickened portion is so deeply constricted as to give the impression of two distinct parts serially combined. In the second case (*fig. 2, k*), one of the *I*'s appears as an undulating rod with a globular head, while the other is rather normal in form. In spite of my efforts, I could not make out how the bodies are related to the spindle fibers. These are, of course, abnormal forms and it is highly probable that they are converted at last into normal forms of U- or V-shaped brought about by atelomitic attachment of the spindle fibres.

II. FACTS REGARDING *PARATENODERA ARIDIFOLIA*.

(*Figure 3*)

Another species of Mantids, which comes next under notice, is *Praratenodera aridifolia*; in this species we find again the idiochromosomes homologous to those detected in *Tenodera superstitiosa*, and their relation to the autosomes does not differ from that observable in the latter species so far as the present observation goes.

A primary spermatocyte possesses thirteen chromosomes, of which one assumes a tripartite form, as is quite obvious in the black representation in *fig. 3, e*. The tripartite form is in a so close resemblance

to that in the last species, that one can hardly distinguish them from each other, when *fig. 3, e* is compared with *fig. 1, g* and *fig. 2, i*. This represents the idiochromosome complex. On the equatorial plate shown in *fig. 3, c* the idiochromosome complex is conspicuous and quite distinct from the twelve rod-like autosomes owing both to its extreme size and to its tripartite structure, in which the middle segment *i* is revealed faintly, because it lies not exactly in the plane of focus; in the next figure (*fig. 3, d*) this is totally out of focus and does not come into view, inasmuch as the two other segments *l*'s are represented as apparently disconnected.

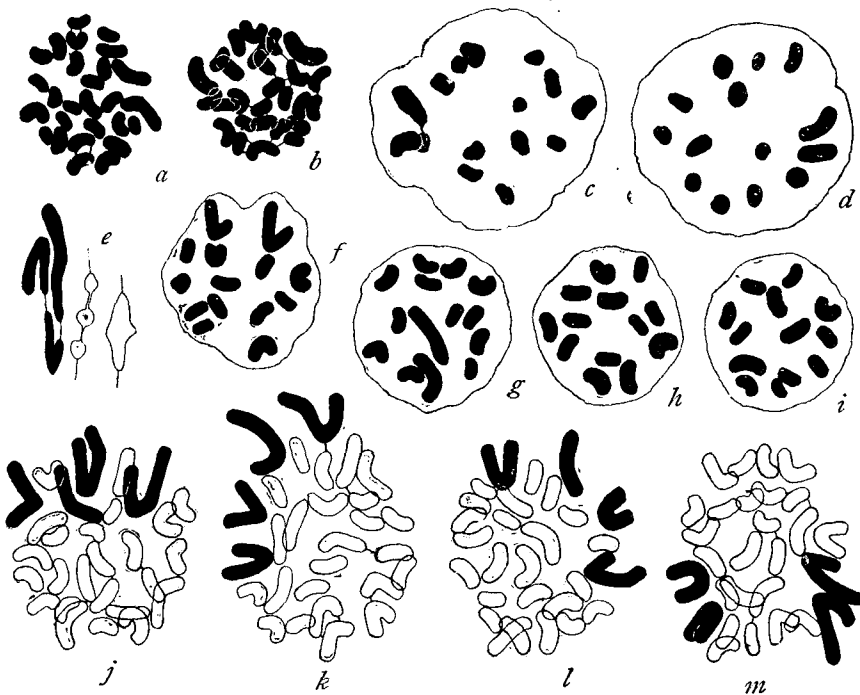


Figure 3.

Paratenodera aridifolia.

Figs. a to i, Zeiss. 1.5 mm Apochr. × Comp. Oc. 12, t. l. 160 mm.

Figs. j to m, Zeiss. 2 mm Apochr. × Comp. Oc. 12, t. l. 200 mm.

a, b, Chromosomes in spermatogonia, c, d, Chromosomes of spermatocytes, e, Idiochromosome complex (black) and two autosomes in the same stage (side view), f-i, Chromosomes of the secondary spermatocytes, j, k, Chromosomes in the cells of oviduct, l, m, Chromosomes in the cells of follicle epithelia of female. The lines seen in c, d and from f to i are the same thing as those in Fig. 1.

There are consequently two kinds of secondary spermatocytes: one contains fourteen chromosomes including the two *I*'s (*fig. 3, f, g*), and the other thirteen including the single *i* (*fig. 3, h, i*).

The spermatogonial group of the chromosomes is composed of twenty seven, of which three are represented by the idiochromosomes, *Ia*, *Ib* and *i* (*fig. 3, a, b*). *Ia* and *Ib* are quite easy to make out amongst the autosomes, as shown in the figures, by their markedly large size. The idiochromosome *i* is, on the contrary, by no means easy to detect among the autosomes, the largest of which is about equal to it in size and shape. But from the total number of chromosomes, one of these ought to be taken as the idiochromosome *i*.

In the present species I have also not failed to observe the occurrences displayed in somatic cells of the female individuals. First of all in the epithelia of the oviducts (*fig. 3, j, k*) and follicles (*fig. 3, l, m*) a nucleus of the cells contains always twenty eight chromosomes, i. e. one more than in the spermatogonium, of which four (represented black in the figures) are conspicuous by their large size. It is these four which correspond to the idiochromosomes *I*'s, each being doubled, i. e. into the two *Ia*'s and two *Ib*'s.

There has been detected no outstanding fact to be added to our statements made on the chromosomes of the preceding species, so far as the scope of the present study is concerned.

III. IDIOCHROMOSOMES AS THE SEX-DETERMINANTS.

From the results obtained in the present observation, the sexual difference between the chromosomes is quite obvious, so far as concerns the Mantis observed. The cells of one sex are in sharp contrast with those of the other both in the quantity and the quality of the chromosomes contained in them. The difference is due to the number and the kinds of idiochromosomes: both the male and the female cells alike constantly contain twenty four autosomes, but of the idiochromosomes concerned, four (of two varieties) are found in the female, as worked out in its somatic cells, while all the three varieties are represented in the genital cells of the male.

Now let us designate the autosomes by *A* and the three idiochromosomes with *Ia*, *Ib* and *i* respectively, as above given, the

following formulae will be valid to denote the chromosomal elements contained in each kind of cells.

In the male cells :

Spermatogonium	$24A + Ia + Ib + i = 27$
Primary spermatocyte	$12A + (Ia + Ib + i) = 13$
Secondary spermatocyte of the 1st class	$12A + Ia + Ib = 14$
Secondary spermatocyte of the 2nd class	$12A + i = 13$
Spermatid and spermatozoon descended from the 1st class of spermatocyte	$12A + Ia + Ib = 14$
Spermatid and spermatozoon descended from the 2nd class of spermatocyte	$12A + i = 13$

In the female cells :

Somatic cell (from the epithella of the follicle and the oviduct)	$24A + Ia + Ia + Ib + Ib = 28$
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The facts just given justify the following assertion. The male cells possess *twenty seven* chromosomes in total as the diploid number, instead of *twenty eight* in the female. The respective diploid group of chromosomes is certain to be reduced through the two successive maturing divisions into just half a number by re-union of each two homologous mates separated beforehand. There is, therefore, expected no case in which the dimorphism of eggs is brought forth, thus :

Reduced chromosomes of an egg cell	$12A + Ia + Ib = 14$
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Drawing the fertilization into consideration, suppose that an egg is fertilized by a spermatozoon of the first kind, loaded with the chromosomes $12A + Ia + Ib$, the combination of the chromosomes must be $24A + Ia + Ia + Ib + Ib$, — a combination identical with that of the diploid group in the female. It follows that an egg fertilized in this way will develop into a female insect. If, on the other hand, an egg is fertilized by a spermatozoon of the second kind with the chromosomes $12A + i$, the resulted progeny is expected to be formed of the cells containing the chromosomes in such a combination as $24A + Ia + Ib + i$: this is quite same combination of chromosomes found in the spermatogonium, as seen in the above table, and the animal brought forth must be the male. The sex is, therefore, determined, at least in Mantids, by whether an egg is fertilized by a spermatozoon having the idiochromosomes *I*'s or by that containing the *i*. The consequence is that the idiochromosomes perform, or at least play an important *role* in, the dertermination of sex.

IV. LENGTH OF THE IDIOCHROMOSOMES
RELATIVE TO AUTOSOMES.

The measurement of chromosomes, which is exceedingly tedious work, has been undertaken with two objects: firstly, to detect the length-difference of them as between the two kinds of spermatids, i. e. the male producing and the female producing, and secondly, to know whether any constant difference exists between two species of the Mantids, as regards the length of the chromosomes. For these purposes I have selected chromosomes from the metaphase equatorial plates of the second maturing division, on which they are arranged all together horizontally at full length. The chromosomes are in this stage invariably and approximately equal in thickness, varying only in length. The measurement has been carried out by the aid of Abbe's apparatus with all possible accuracy, and given in mm. under magnification of 2000 times.

Table I shows the results obtained in *Tenodera superstitiosa*. The chromosomes are numbered from 1 to 15 according to their length,

TABLE I. *Tenodera superstitiosa*.

Chrom. No.	Aver. Length from 50 cells of 1st kind.	Aver. Length from 50 cells of 2nd kind.	Aver. Length from 100 cells of both kinds.	Relative Length.	Differ. betw. two indiv. chrom. of appr- ox. size.
1	2.44	2.47	2.45	6.01	0.61
2	2.68	2.74	2.71	6.62	0.54
3	2.89	2.95	2.92	7.16	0.44
4	3.08	3.12	3.10	7.60	0.30
5	3.19	3.35	3.22	7.90	0.32
6	3.34	3.37	3.35	8.22	0.29
7	3.43	3.51	3.47	8.51	0.32
8	3.58	3.62	3.60	8.83	0.37
9	3.73	3.77	3.75	9.20	0.37
10	3.91	3.89	3.90	9.57	0.54
11	4.18	4.09	4.13	10.11	0.56
12	4.42	4.29	4.35	10.67	0.44
13 (<i>i</i>)	—	4.63	4.63	11.11	4.13
14 (<i>II</i>)	6.21	—	6.21	15.24	4.52
15 (<i>Ia</i>)	8.06	—	8.06	19.76	

and arranged in this order; in the first column of the table the first twelve, 1 to 12, represent the autosomes, and the remaining three, 13 to 15, indicate the idiochromosomes. In the second column is given the average length of the chromosomes of the first kind, in the third column that of the second kind, of the spermatids. In the fourth column is shown the average length of two homologous chromosomes found separately in both the kinds of the secondary spermatocytes. The numbers shown in the fifth column represent the average length of the individual autosomes (i. e. the numbers in the above twelve lines of the fourth column) given in percentages of the total sum of all the twelve autosomes (i. e. in that of the total sum of the numbers given in the twelve lines of the fourth column) taken as 100. In the sixth column are given the numbers of difference between two chromosomes most approximate in length (i. e. those two numbers one upon the other in the fifth column compared).

Turning to the idiochromosomes, the difference between the two kinds of secondary spermatocytes is altogether due to the number and the nature of these characteristic chromosomes contained in them. The sum of the length of *Ia* and *Ib*, which are confined to the first kind of secondary spermatocytes, corresponds to 35 per cent, and the smallest idiochromosomes *i* contained in the second kind of the cells shows 11.11 per cent, of the total sum of the autosomes. The difference of these two numbers 23.89, ought, at the same time, to be taken as the difference in the entire length of all the chromosomes combined, of which the head of the spermatozoon is composed. The female producing spermatozoon which is provided with the chromosomes, when taken together, about 24 per cent longer than the male producing, is, therefore, to be regarded as having its head so much bigger than that of the latter.

The results obtained from *Paratenodera aridifolia* are shown in Table II, In this species, an insufficient number of cases were at my disposal, because there were only a limited number of cases, in which the chromosomes were laid approximately horizontally on the equatorial plates, thus facilitating measurement. The numbers given in the table are confined to those obtained from the same example as represented in *fig. 3*. The results can not consequently be expected to be as accurate as those obtained from the last species, yet we find that the difference between the values of the *i* and *I*'s corresponds to about 24 per cent of the total sum of the autosomes. And in this respect, the

two species of Mantids must be recognized as standing in close relation to each other.

This difference in length between the two idiochromosomes interests us, inasmuch as it is of the highest measure ever observed: The highest difference hitherto known is, as ZELENY and FAUST (1914) made out in *Anasa*, 11 per cent—a number obtained from a comparison of the length of the total sum (1) to that of the heterortopic chromosome 0.11.

TABLE II. *Paratenodera aridifolia*.

Chrom. No.	Average Length.	Relative Length	Difference betw. two indiv. chrom. of approx. size.
1	3.91	6.47	0.61
2	3.29	7.08	0.38
3	3.47	7.46	0.20
4	3.56	7.66	0.19
5	3.65	7.85	0.21
6	3.75	8.06	0.22
7	3.85	8.28	0.15
8	4.92	8.43	0.22
9	4.02	8.65	0.80
10	4.40	9.45	0.68
11	4.71	10.13	0.28
12	5.84	10.41	0.56
13 (<i>l</i>)	5.10	10.97	4.91
14 (<i>lb</i>)	7.48	15.88	3.55
15 (<i>la</i>)	9.03	19.43	

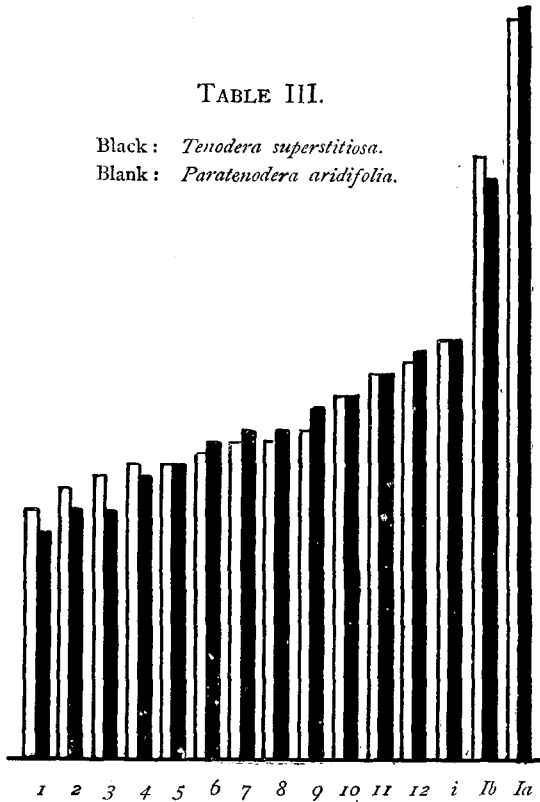
MEEK ('12) states, in his study of five species of *Stenobothrus*, that the length of the chromosomes constitutes consecutive numbers of a series in arithmetical progression. But in the present case, this is not proved, there is no definite relation to be recognized between the chromosomes in length, as shown in the sixth column. In his first study on chromosomes, ROBERTSON ('16) maintains that in Acrididae and Tettigidae the autosomes can be classified into groups according to definite relations in their length. This is also not the case with the Mantids, no relation of length between the chromosomes can possibly

be detected, as the numbers in the sixth column positively prove. What is characteristic of the Mantids is only that some of the *bivalent* chromosomes of approximately equal size are frequently found to lie side by side on the metaphase equatorial plates, like the homologous pairs of univalent often observed in spermatogonia.

In the Table III, I have intended to make a comparison of the chromosomes of both species studied, as they are not only the same in number, but approximately parallel in gradation of length. Between the two species there may be recognized a slight difference of the

TABLE III.

Black: *Tenodera superstitiosa*.
 Blank: *Paratenodera aridifolia*.



corresponding chromosomes in length, in particular it is almost even in a great proportion of those of middle size, while it is striking, as we approach both extremes of size. Though the difference is so slight, as is obvious from the Table, yet it can not be said with certainty, whether or not it is deserving of the generic or even specific

value maintained by systematists, because the results are, in this respect, not cogent enough on account of the insufficient number of specimens of *Paratenodera aridifolia* at my disposal. But renewed investigations will, it seems to me highly probable, educe facts by which the difference——i. e. the specific at least generic distinction——will certainly be exploded.

V. HISTORICAL COMPARISON OF LITERATURE.

The unique record on the chromosomes of a Mantid made by GIARDIANA ('97) diverged, in several respects, too far for comparison with my present results. He counted, in *Mantis religiosa*, fourteen chromosomes in a spermatogonium and seven, as the reduced number, in a spermatocyte. Of the occurrence of idiochromosomes nothing is said. The chromosomes vary in number not infrequently, to an great extent, even in two species included in the same genus, as WILSON ('05) pointed out in *Anasa*. A more surprising numerical variation of chromosomes was found in the case of *Gryllotalpa vulgaris*, in which individuals collected from different localities differ, in this respect, widely from one another (VOM RATH, '92, PAYNE, '16). The numerical difference between the case reported on by GIARDIANA and mine may, therefore, be put out of the question. I cannot agree, however, with him without hesitation in assuming a total absence of idiochromosomes in *Mantis religiosa*.

Among the orthopteran insects which have been studied, *Gryllotalpa* affords the case most nearly parallel with the present results, so far as the idiochromosomes are concerned. BAUMGARTNER ('12) found in *Gryllotalpa* an unequal pair of idiochromosomes, which are separated into two unequal parts at the first maturing division, accompanied by an unpaired heterotropic chromosome. A similar fact was reported in the same year by PAYNE ('12) from *Gryllotalpa borealis*. Since their discovery by WILSON ('05) in Hemiptera, a pair of idiochromosomes, unequal in size, has been known not only in several genera and species of the order, as *Notonecta* by BROWNE ('10, '13), *Enchenopa* by KORNHAUSER ('14), but also in some beetles by STEVENS ('08, '11) and METZ ('17), and in the earwig by RANDOLPH ('08) and by STEVENS ('10). On the other hand, the presence of the unpaired heterotropic chromosome, which is present among the paired autosomes in the male germ cells, has hitherto been demonstrated, since its discovery by HENKING ('91) in

Hemiptera, in almost every order of insect. It is worthy of notice that there occur three heterogeneous chromosomes — a pair of idiochromosomes and a heterotropic chromosome — in *Gryllotalpa*. PAYNE ('16) remarks in his paper that such a combination of chromosomes as that just referred to is to be interpreted in three different ways: firstly, as a pair of XY or idiochromosomes and a supernumerary, secondly, as one of the idiochromosome-pair represented by two distinct parts, and thirdly, as XY -pair and an accessory chromosome. The first assumption was soon discarded by him on account of his affirmation that the unpaired heterotropic chromosome passes regularly to the pole to which the larger component of the idiochromosome-pair also goes, while the smaller component turns itself to the opposite pole.

Let us now follow VOINOV's account ('12) of the chromosomes of *Gryllotalpa vulgaris*, in which he also recognized the similar occurrence of the three peculiar chromosomes. According to the author, these peculiar chromosomes are those identical with a pair of idiochromosomes and an accessory; the latter may or may not pass to one pole together with the larger half of the unequal idiochromosome-pair, which is moreover, sometimes united with a bivalent autosome in the first maturing division. This view is denied by PAYNE in his second paper ('16) in which an extensive and comparative study of *G. borealis* and *G. vulgaris* is included. He emphasizes his interpretation of the peculiar combination of chromosomes in *Gryllotalpa* taken as an idiochromosome-pair, one component of which X is represented by two distinct elements, so as to be brought into the same category as the corresponding case in *Conorhinus* and *Fitchia* in Hemiptera (PAYNE, '09).

The difference between these two orders consists in two points: in *Gryllotalpa* one of the X 's never comes into direct connection with Y , which is the case in Hemiptera, and the separation of the XY -pair occurs, in *Gryllotalpa*, in the first division instead of the second as in Hemiptera. This discrepancy between the groups is connected with the difficulty apparently encountered in attacking the problem of the present investigation.

My present results as regard the Mantids, perhaps, suffice to bring the case of *Gryllotalpa* onto the same plane as the Hemipteran examples in which two *real* X 's are actually present. As before mentioned, there is in the Mantids a splendid example of idiochromosome complex constituted of two I 's and an i . It need not absolutely

be assumed in this case that either of the I 's is the accessory chromosome, both behaving quite similarly to each other. But if by reason of accidents disconnection between i and one of the I 's occurs, the separated I may quite possibly behave independently from its partners, so as to be taken as an accessory chromosome. Fig. 2, m probably affords an actual example (observed in *Tenodera superstitiosa*) or the explanation of the supposed accidental case; here it is obvious enough that an I , probably the Ia , is cut off from the i with which it is usually connected. The whole system of the idiochromosome complex is in great resemblance with the case seen in *Gryllotalpa*, when by the Ia is represented the accessory chromosome in the latter group. Suppose the I 's be identical with X , and i with Y in *Gryllotalpa*, then the difficulty above referred to is certainly got rid of; the Mantids, *Gryllotalpa* and Hemiptera are fundamentally the same as regards the idiochromosomes, and diverge apparently on account of the combination of the chromomes more or less modified in each.

Now the assumption is justified that the I 's in the Mantids, which are separated always at the first maturation division of the spermatocyte from the i and move together to one and the same pole, are to be taken as the equivalents of the X 's in *Gryllotalpa*, while the i runs to the opposite pole, and is regarded at the same time as identical with the Y in the latter group. Here it is added that the Mantids are in parallel with *Conorhinus*, as pointed out by PAYNE ('90, '12), in the relative size of the three components of the tripartite idiochromosome complex.

Rare though the case may be, there are met with abnormal examples of another kind in both the species of Mantids studied: the I 's are so arranged as to be directed to the opposite poles of the spindle (fig. 2, l and o); it must consequently be expected, that one of the I 's, Ia , is associated with the i instead of the Ib to give rise to one of the daughter cells, the other of which is to contain the Ib alone. If the separation likewise actually takes place in *Gryllotalpa*, the view by VOINOV ('12) may be taken as not incorrect. I can, however, affirm nothing regarding the fates of the idiochromosomes of the arrangement in question.

Let us turn to the L-chromosomes found frequently in Orthoptera, to be compared with the chromosomes I 's and i in Mantids. The L-chromosome is so called because its shape resembles the letter L,

as first noted by SINETY ('01) in the Phasmidae. Later, similar chromosomes have been discovered by McCLUNG ('05) in the Acrididae and by VOINOV ('12) in the Gryllidae. The *I*-chromosomes in Mantids also are often bent like the letter L, as is seen in the metaphase of the first division. The *Ib* and *i* form together an arrangement like the letter L, when the *Ia*, the largest component of the idiochromosome complex, is cut off from them. Certain relations between the so-called L-chromosomes and the *Ib-i* group of the Mantids may therefore be expected. SINETY's case will first be taken into consideration.

According to the author, the L-chromosome comes in the Phasmids into view in the metaphase of the first division and is composed of a tetrad and an accessory chromosome. If this is actually the case, the diploid number of chromosomes in the spermatogonial division must be *thirty seven* instead of *thirty six*, as he says. From this assumption, this fact is explained by WILSON ('11), in his seventh study, as due to the accessory chromosome already united with one of the univalent autosomes maintaining complete union throughout the maturing divisions. Under the light of the observed facts regarding Mantids, the results obtained from the Phasmid by SINETY may be interpreted as follows: according to the author (his *fig. 75*) among the chromosomes of the diploid group there are found two special ones, large and V-shaped, taking the peripheral position in the equatorial plate and lying side by side, in a great resemblance to the *I-i* pair in Mantids. The chromosomes in question owing to their characteristic V-shape are very distinct from the remaining chromosomes, and one of them is much larger than the other. From these facts, I am driven to assume that the two V-shaped chromosomes in the Phasmids represent in fact the idiochromosome pair *I-i* in the Mantids or *XY*. In other words, the diploid group of chromosomes consists of the thirty four autosomes¹⁾ and of the two idiochromosomes are reduced in the first maturing division into seventeen tetrads and *Ii* or *XY* complex. The larger component of the *Ii*, for instance, may be bent like the letter L, as is often the case in Mantis; then the case in the Phasmids pointed out by SINETY and explained by WILSON cannot be distinguished from that of the Mantids.

1) McCLUNG ('14) expected thirty five chromosomes in the spermatogonial group in the SINETY's case, as JORDAN ('08) found the like number in *Aplopus* of Phasmidae to which *Leptynia* and *Dixippus*, the material used by SINETY also belong.

Neither can the multiple chromosomes described by McCLUNG ('05) in Acrididae be distinguished, in their shape, from the L-chromosomes, as the following explanation shows. The chromosomes are recognized in *Hesperotettix* and *Mermiria* and assume clearly the L-shape in the metaphase of the first division. It is maintained repeatedly by McCLUNG ('14, '17) that the chromosome in question is, in fact, a tetrad connected with the accessory chromosome in such a way that it represents the vertical arm of the letter L, the horizontal bar of which is formed by the latter. There is, therefore, no difficulty in bringing it to the same plane as the idiochromosome complex of the Mantids.

The third example of the L-chromosome is that discovered by VOINOV ('12) in Gryllidae. It presents a close resemblance in shape to that of the Phasmidae discovered by SINEY ('01) and is regarded by VOINOV as of the same constitution with the multiple chromosome of the Acrididae discovered by McCLUNG ('05). In his recent work, however, PAYNE ('16) insists that the so-called L-chromosome in the Gryllidae is not composed of a bivalent chromosome and an accessory, but merely of a bivalent, of which one half becomes bent like the letter L. According to the author, in the Gryllidae then occurs a chromosome resembling an L, which is divided into two equal halves at the anaphase of the first division. Quite recently, CAROTHERS ('17) arrived at the same conclusion as that of PAYNE as to the nature of the L-chromosome described by VOINOV and identified with the J-shaped chromosome fully worked out by her.

Finally I have to add a few lines on the origin of the idiochromosomes in the Mantids. As have been observed above, the two *I*'s and the single *i* develop out of a chromatin nucleolus, passing through a mode quite peculiar to themselves and different from what has been observed in Hemiptera by WILSON ('05) or in Coleoptera by STEVENS ('09). In these insects the idiochromosome pair *XY* is separated, according to the authors, into its components *X* and *Y* by simple constriction of the chromatin nucleolus which was brought forth formerly by fusion of *X* and *Y*. Both the *X* and *Y* are, even after the separation, similarly compact in consistence and stained with like intensity, in contrast to the case of the Mantids, in which the *I*'s are drawn into threads of loose texture and less of colour affinity before being condensed, while the *i* remains permanently compact and is always stained accordingly intensely. A case which may be looked

upon as parallel with that in the Mantids is, however, not wanting in the other group of insects. KORNHAUSER ('14) has pointed out that in *Euchenopa binotata* the *X* and *Y* conjugate by their termini in the synaptic period, whereas the part *Y* remains in loose texture and vague outline, until the final condensation takes place at the close of the growth period whilst the other part, *X*, retains a typical appearance of chromatin nucleolus throughout that period.

STEVENS ('06) has suggested the possibility that the *X*-chromosome may have been separated from the *YY* pair, with which it is originally united, and this theory is advocated by WILSON ('11) taking as an example the case of *Thyanta*. This explanation consequently gives further supports to McCLUNG's views on the multiple chromosome in the Acrididae. But the present case of the Mantids can by no means be explained on this assumption, because neither of the halves, into which the *I-i* pair is separated, is the equivalent of the other half.

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