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CHROMOSOME STUDIES

I. TAXONOMIC RELATIONSHIPS SHOWN IN THE CHROMOSOMES OF TETTIGIDAE AND ACRIDIDAE: V-SHAPED CHROMOSOMES AND THEIR SIGNIFICANCE IN ACRIDIDAE, LOCUSTIDAE, AND GRYLLIDAE: CHROMOSOMES AND VARIATION

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FOUR TEXT FIGURES AND TWENTY-SIX PLATES

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INTRODUCTION

In a study of the germ cells of the Tettigidae, concerned chiefly with the problem of synapsis, I have found such a surprising uniformity of numbers and size relations among the chromosomes throughout the eight species of the three different genera examined, that it seems advisable to present the evidence I have on the taxonomic value of the chromosomes and to make my observations on synapsis a second paper, Chromosome Studies. II.

For purpose of comparison with the Tettigidae, and also to emphasize the constancy of numbers and general size relations in three of the subfamilies of the Acrididae, I have worked out the complexes of Syrbula acuticornis Bruner, and of Chorthippus (Stenobothrus) curtipennis Harr., two species of the Truxalinae. Stenobothrus has been described by Davis ('08), Gerard ('09), and Meek ('10, '12) as having seventeen chromosomes. I believe, however, this genus in reality has twenty-three chromosomes, like other genera of the subfamily.

For the chromosome conditions in the Oedipodinae and Acridiinae, I have depended on the figures of Davis ('08).

In order to show that phenomena similar to those in Chorthippus may possibly occur in the Locustidae and Gryllidae, I have given figures from Buchner ('09), Davis ('08), and Baumgartner ('04) and from a paper by one of my students, Miss Carrie I. Woolsey. Here, again, I believe that the great amount of variation in chromosome numbers hitherto described may be due largely to the intimate association of certain chromosomes in some genera or species which in others may remain separate.

TAXONOMY

According to Handlirsch ('08), the order Orthoptera includes five families, Acrididae, Locustidae, Gryllidae, Gryllotalpidae and Tridactylidae. Systematists divide Acrididae into nine subfamilies. Of these, five are found in North America: the Tettiginae (Tettigidae) (figs. 1–6, 9–13, 17, 19, 21), Eumastacinae, Truxalinae (figs. 7, 8), Oedopodinae (figs. 14, 18, 20, 22), and Acridiinae (figs. 15, 16a, 16b). Representatives of all but one have been used for chromosome study; in addition the Pamphaginae have been studied in Europe. In the present work I have studied more particularly the chromosomes of the first group. For reasons which will be stated further on, I rank the Tettiginae on a par with the Acrididae, rather than as one of its subfamilies, and shall therefore use for them the term *Tettigidae.*

1. Taxonomy and chromosomes

McClung ('05, '07) has advanced to a very considerable extent the contention, first advocated by himself, that a certain degree of parallelism exists between chromosome structure and those characters of the body which systematists recognize as of use in determining the relationships of species, genera, and families. He contends that the degree of relationship may be recognized just as precisely in germ-cell structure as in any other part of the body. As the number of species of Orthop-

tera examined for chromosome conditions increases from year to year, the results tend to confirm the correctness of this view. In the chromosomes of Orthoptera we seem to be dealing with morphological structures possessing a definite relative size and constitution as permanent as the cell itself. Their size relations and their behavior are probably constant, not only for all cells of an individual, but for every individual of the species. These size relations may vary, it is true, to a slight extent in the different species of a genus, as would be expected, and still more when the species of different genera are compared; but they may be reasonably constant within these limits for the subfamily, and, in many cases, for the family. Thus the degree of relationship is expressed as accurately in the nucleus as in any of the external body characters. A distinguishing feature in a germ-cell is, however, of much more importance than any character of the rest of the body, since it is located in a structure which may be considered the starting point of a new organism, and accordingly has an important rôle during the development of the body in the formation of *all* distinguishing characteristics of the individual—thus influencing not one part or organ, but many.

McClung held that for the Acrididae there are twenty-three chromosomes $(2N-1)$[1] in the male and for the Locustidae and Gryllidae each thirty-three. He did not make the count in the female, which has since been found to be $2N$; i.e., one more than in the male. So far as the Acrididae are concerned, these numbers will have to be modified to this extent. The subfamily Pamphaginae has 19 (♂) and 20 (♀) (Granata, '10). This is a decided exception. Possibly a multiple chromosome may be involved, as in some Truxalinae and Acridiinae. Barring the Pamphaginae, McClung was correct, for the Tettigidae (figs. 1–6, 9–13), which have 13 (♂) and 14 (♀) as the $2N-1$ and $2N$ numbers respectively, are possibly not related to the Acrididae as a subfamily (Tettiginae) and so might be expected to have peculiar chromosome conditions.

[1] The designation N is used to indicate single or haploid number of chromosomes, $2N$ thus being the formula for the diploid or somatic number.

The fundamental number in the Locustidae seems to be somewhat in doubt. Miss Stevens ('12) found thirty-seven in Ceuthophilus. In Jamaicana subguttata, unicolor, and flava (Woolsey, '15) the number is thirty-five. McClung ('02, '08) and Otte ('07) found the number in five genera to be thirty-three. Buchner ('09) found thirty-one in Decticus. Other cases (Steiroxys, Davis, '08) may be shown to have thirty-one, owing to the presence of compound chromosomes. The numbers most frequently found seem to be thirty-three and thirty-one. The extremely large number in Ceuthophilus may indicate a subfamily difference; in Jamaicana, a tribal difference.

Opinion as to the number of chromosomes in Gryllidae is unsettled. The most frequent is thirty-one or thirty-three (♂). It is quite possible that in Gryllidae also occur cases of compound chromosomes, since eight or ten **V**'s are present in species with low numbers (Baumgartner, '04; Gutherz, '09; Payne, '12). The tree-crickets (Baumgartner, '11) have 13 (♂) and 14 (♀); Stenopelmatus (Stevens, '05), forty-six. Such large variations as the last may indicate wide taxonomic difference.

2. Taxonomic characters compared

Before describing chromosomes, it is best to compare taxonomic characters of Tettigidae with those of three subfamilies of the Acrididae, also the characters of the genera and species I have studied within the Tettigidae.

The Tettigidae are more distinctly marked off from the subfamilies of Acrididae than these are from one another (compare figs. 1–6, 9–13 with figs. 7, 8, 14–16). The dividing line is not clearly marked between the Oedipodinae (fig. 14) and the Truxalinae (figs. 7, 8), and is but slightly more marked between either of these and the Acridiinae (fig. 15).

The chief distinguishing characters of Tettigidae are the extremely developed apical process of the pronotum (figs. 1–6, 9), the absence of pulvillus (fig. 12), and extreme reduction or absence of elytra (*ely.*, in figs. 1, 3, 4, etc.). Over against this in the subfamilies of the Acrididae the pulvillus is present (fig.

16), pronotum not extended over the abdomen (figs. 7, 8, 14–16, *ms'thx.*), and elytra are present and elongated (figs. 7, 8, 14–16, *ely.*) except in cases of brachypterism. It is easy to see the much closer resemblance in all these characters among the subfamilies represented in figures 7, 8, and 15 than between any of these and the Tettigidae. Thus, on the basis of these body characters the Tettigidae are clearly marked off from the Acrididae.

Internal structures present equally distinguishable characters. No organs illustrate this better than the gastric caeca. In the Acrididae the five caeca (fig. 18) have each a large anterior and a smaller posterior extension (pouch). The crop (fig. 18, *iglv.*) is relatively larger and more rectangular anteriorly than in the Tettigidae (fig. 17). In the latter the caeca have only an anterior prolongation. There are, however, two circular ridges, which may possibly serve for posterior caecal pouches.

In the reproductive organs also are characters distinguishing the two groups. In the usual acrididean testis the follicles are long, sac-like structures joining the vas deferens close together (fig. 22). This gives the testis a tassel-like appearance. Figure 22 is of Dissosteira carolina, an oedopodine, and is representative also of the Truxalinae and Acridiinae. In the Tettigidae the plan of structure is more primitive. The follicles are connected with the vas deferens at considerable distances apart in regular order (fig. 21), as in the typical acrididean ovary, except that ovarioles are not nearly so numerous as testicular follicles.

In histological characters there are also the same two types. The appearance of the tettigidean testicular follicle in longitudinal section (fig. 19) differs much from that of the Acrididae (fig. 20). It may even be said to look more like that of Gryllidae or Locustidae. The cell cysts extend completely across the follicle (fig. 19). This is not true of the Acrididae (fig. 20), but is true of Gryllidae and Locustidae. The cytoplasm of spermatogonial and spermatocyte cells is more compact, and the meshes of the cytoplasmic network are much smaller than in the Acrididae. This is also a gryllid character. These facts

do not necessarily indicate close relationship with Locustidae and Gryllidae, but they do show the wide divergence of the Tettigidae in these respects from what we find commonly in the subfamilies of Acrididae.

Upon the basis of these visible external and the grosser internal characters, we would at once separate what was formerly known as the Acrididae into two groups, on the one hand the Tettigidae and on the other the Truxalinae, Oedopodinae, and Acridiinae.

The Tettigidae are in turn divided into four subfamilies, the Cladonotinae, Metrodorinae, Tettiginae, and Batrachidinae. Of these we have represented in the United States only the last two. Of the genera which I have studied, two (Acridium [Tettix] and Paratettix) belonging to the former group and one (Tettigidea) to the latter. We should, therefore, expect to find among these three genera two more nearly related to each other in chromosome characters, than either of them is to the third. Before taking up chromosome characters, we shall consider the body characters.

The subfamilies Tettiginae and Batrachidinae may be distinguished from each other by the following points:

Tettiginae	*Batrachidinae*
1. Anterior femora compressed, carinate above.	1. Anterior femora broadly sulcate above.
2. Vertex, viewed from the dorsal side (figs. 3, 4, 5b, 13a), extends either scarcely to, or slightly beyond, the eyes.	2. Vertex large and projects much in front of the eyes (figs. 10, 11).
3. Antennae composed of twelve to fourteen segments.	3. Antennae composed of twenty-two segments (in Tettigidea).
4. Pronotum in front truncate (figs. 1b, 2b, 3, 4, 5b, 6).	4. Pronotum in front not truncate, but produced above the head; anterior dorsal margin angulate (figs. 10, 11).
5. Dorsum flat, may be at same time slightly carinate or cristate. Median carina inconspicuous.	5. Dorsum not flat, but obtusely tectiform. Median carina conspicuous.
6. Humeral angles of pronotum obtuse (fig. 3, *ang. hum.*).	6. Humeral angles of pronotum angulate.

7. Lateral lobes rounded, not angular (figs. 3, 5, *lob.1*).	7. Lateral lobes angulate (fig. 9, *lob. 1*).
8. Eyes rounded rectangular, long diameters almost parallel (figs. 3, 4, 13a, 13b).	8. Eyes elongate-triangular (figs. 10, 11), long diameters forming an angle of 90° (figs. 10, 11).
9. No supra-ocular lobe of vertex extending over eyes.	9. Eyes partly covered by small supra-ocular lobes of vertex (figs. 10, 11, *lob. su'oc.*).

Within the subfamily Tettiginae the genera Acridium and Paratettix differ in the following respects:

Acridium (Tettix)	*Paratettix*
1. Vertex much broader than one of the eyes, projects beyond them (figs. 3, 4), angulate anteriorly.	1. Vertex as narrow as, or very slightly wider than, one of the eyes (figs. 13a, 13b), does not project beyond, truncate anteriorly.
2. Eyes small.	2. Eyes large, bead-like.
3. Pronotum does not project far overhead, does not reach posterior margin of eyes (figs. 3, 4).	3. Pronotum projects far overhead, reaches posterior margin of eyes (figs. 5b, 6, 13a, 13b).
4. Anterior margin of pronotum slightly angulate.	4. Anterior margin of pronotum decidedly truncate (figs. 5b, 6).
5. Body between shoulders not so wide as in Paratettix.	5. Body between shoulders wide (figs. 5b, 6).

Within Acridium (Tettix) I have studied four species. As in the case of the genera compared above, two of these species are more closely related to each other than either of them is to the third, obscurus. Of ornatus I have not a sufficient number of drawn cells to justify comparison of body characters with those of the other species. (See opposite page.)

By studying these characters it will be seen that granulatus and incurvatus usually agree more closely with each other than with obscurus.

THE CHROMOSOMES

Within the cell, the varying degrees of relationship which we have been looking at from a taxonomic point of view are again shown to a surprising extent by chromosomes. This is found in the constancy of numbers and in differences between size

	ACRIDIUM GRANULATUS (Figs. 1-3) (a)	ACRIDIUM INCURVATUS (fig. 4) (b)	ACRIDIUM OBSCURUS (figs. 2a, 2b) (c)
1. Integument.	Granulate or little rugose.	Granulate.	Arenose.
2. Vertex viewed from above	Nearly twice as wide as one eye (figs. 2b, 3).	Nearly twice as wide as one eye.	Fully twice width one eye, little more depressed than (a) and (b).
Front margin	Obtuse angulate.	Obtuse angulate.	Sub-truncate or scarcely convex.
Advanced beyond eyes	Considerably.	Considerably.	Little.
Occiput	Naked (fig. 3).	More covered.	Naked.
Crown of head in profile.	Above.	Above.	Level with superior margin of eyes.
3. Frontal costa advanced beyond eyes	Strongly.	Strongly.	Only one-fourth diameter of eye. At junction with median carina of vertex projecting as angulate eminence with apex.
Apex	Quite acute (figs. 1a, 3).	Acute.	Obtuse.
4. Pronotum, anteriorly	Truncate.	Truncate.	Truncate, strongly constricted before shoulders.
Posteriorly	Long extenuate; apex acute (fig. 1b).	More or less abbreviated.	Long; not so acute.
Antero-dorsal margin	Indistinctly obtuse, angulate.	Indistinctly obtuse, angulate.	Truncate.
Dorsum, transversely between shoulders	Narrow.	Wider.	Moderately broad.
	Tectiform.	Wider, more tectiform.	Flattened or sub-convex.
Median carina	Distinctly elevated percurrent.	Distinctly elevated percurrent.	Not elevated.
In profile	Nearly straight (figs. 1a, 1b, 3).	Arched (not straight).	
Humeral angles			Much more strongly prominent.
5. Eyes	Small.	Small.	Moderately large.
Viewed from above	Elliptic.	Elliptic, kidney-shaped.	Especially prominent.
Longitudinal axes	Parallel.	Not parallel.	
6. Antennae	Short, stout.	Short, stout.	Slender, long.

gradations. The differences depend upon degree of remoteness in relationship.

First of all, our short-horn grasshoppers may be divided into two large groups on the basis of number of chromosomes: the family Tettigidae having 13 (♂) and 14 (♀), and the family Acrididae with its three subfamilies having 23 (♂) and 24 (♀).

Within each of these groups the chromosomes present certain general size relations, which are fairly constant, but there are minor variations. The larger variations are found between different genera. More distantly related genera are less likely to be similar. The smaller variations between species of a genus, though more difficult to recognize, follow the same principle. The greater are likely to be found between more distantly related species, the lesser between those more closely related. This does not mean that more distantly related species may not occasionally be found with chromosomes more nearly alike than those of less distantly related species. Observations have not been extended far enough to determine that point.

1. Tettigidae

1. Acridium granulatus Scudd. a. Chromosomes of the male germ cells. Spermatogonial and somatic chromosomes of this, and of all other species of the family thus far studied, are of the rod-shaped type, and the spindle fibers are attached at the proximal end; i.e., the end which points toward the center of the cell plate at the time of cell division (figs. 23–28). Great extremes in the relative sizes of different chromosome pairs are characteristic of all the Tettigidae, but are most marked in this genus. Compare chromosomes 1, 1 or 2, 2 with 6, 6 (figs. 23–28). The chromosomes may be readily arranged into a series of six pairs besides the accessory chromosome. The latter is so nearly the size of the smallest pair that it would be difficult to distinguish between them, were it not that frequently the sex chromosomes show the 'woolly' surface texture (no. 2*x* in figs. 23, 25, 26, 27) often seen in other acridiidaean spermatogonial stages (Sutton, '02; McClung, '05; Pinney, '08). Of

these six pairs, two (nos. 6, 6 and 5, 5) are more than twice the length of any other pairs. Nos. 4, 4 and 3, 3 are the intermediate pairs, the larger being about one-half that of no. 5 and less than one-half that of no. 6. Nos. 1, 1 and 2, 2, the smallest pairs, are easily distinguishable from nos. 3, 3 and 4, 4 and usually from each other. The sex chromosome is designated by $2x$ in this species because it ranks second in the total series. It is distinguished from the ordinary chromosomes numbered 2 by the addition of x. In general we have among the ordinary chromosome pairs three distinguishable size-groups: one embracing the largest (nos. 6 and 5), another the intermediate nos. 4 and 3), and a third the smallest (nos. 2 and 1). These three groups may be recognized in all the species of the family here studied. There is noticeable, as the measurements will later indicate, considerable difference in size between the two largest pairs, very little between nos. 4 and 3, but again quite an appreciable difference between nos. 2 and 1.

The size relations are more evident, though not as accurately shown, in the maturation divisions, and are best seen in views of division figures perpendicular to the axis of the spindle. In the Tettigidae the first maturation division is reductional. The members of each pair of chromosomes appear on the first maturation spindle attached to each other by distal ends only. This gives, exclusive of the accessory chromosome, six rods somewhat constricted, or even pulled apart, in the middle (figs. 29–34). Here again the six pairs may be grouped into three sizes, the extremely large (6 and 5), the intermediate (4 and 3), and the smallest (2 and 1).

The inequality in the size of 6 and 5 is well marked, shown by the 5's usually being more advanced in the act of separation than the 6's (figs. 29, 30, 31, 33). This character holds for the species of Acridium in distinction from those of Tettigidea, where it is only slightly marked. It also holds in Parattettix, though not to so great a degree.

The 3's and 4's are more nearly alike in size than the 5's and 6's, sometimes hardly distinguishable (figs. 30, 32, 34). The pairs of the smallest group are unequal in size, though frequently

it is difficult to distinguish them. In size the sex chromosome falls between 1 and 2, often so nearly like 1 that it is a question which to call it, $1x$ or $2x$. This, again, is a character of the genus Acridium. The sex chromosome passes undivided to one pole of the nucleus in the first maturation division. It always lies outside the plate (figs. 35, 36).

At the second division (figs. 37, 38) the inequality in the size of the two largest chromosomes is especially marked and the size relations of all are clearly shown.

b. Chromosomes of the male somatic cells. The same size relations appear in somatic cells though it is more difficult to pick out the members of the smallest and intermediate pairs. In animals taken before the last moult, dividing cells in large numbers were found in the following organs: mesenteron, proctodaeum, hypodermis, fat body, follicles of testis and ovary, and possibly in intestinal muscles. Of these tissues the columnar epithelium of the mesenteron showed the clearest cases of mitosis (figs. 39, 40). The cells were too long to be shown complete; accordingly only that portion which contains the dividing chromosomes was drawn. In figure 40 the two large pairs and their characteristic inequality are especially evident. One of the 4's and one of the 3's are seen foreshortened. These cells are of entodermal origin and their chromosomes resemble very much those of spermatogonia and oogonia.

Figures 41 and 43 show cells from the posterior part of the alimentary canal, probably of ectodermal origin. The size relations of the chromosomes are the same as before.

Figures 44, 45, and 47 represent cells from the hypodermis, the layer which secretes the cuticula. These cells contain pigment granules, which probably bear an important relation to the pigmentation of the cuticula. The number of chromosomes and the size relations are the same as in other tissues. The chromosomes are much shortened and thickened and have a tendency to clump together more than usual.

Figures 48a, 48b, 50a, and 50b are possibly nuclei of fibers from the outer muscular wall of the intestine. The number of chromosomes and the size relations are the same as usual. Fig-

ures 46 and 49 are of cells from the fat body; 49 of a normal cell, but 46 of a giant cell, in which were found not thirteen but twenty-six chromosomes. The fact that there were twenty-six chromosomes and that among these there were four of each of the six sizes indicates that this is probably a double cell with a double set of cell organs. It may have arisen by fusion of two cells, or by failure of the cell to divide after the nucleus had divided. Cells with multiple numbers of chromosomes occur frequently in this tissue.

c. Chromosomes in the female. Oogonial or oocyte divisions were not obtained, owing to incompleteness of material, but abundant mitoses were found in the walls of ovarioles. In every case they showed fourteen chromosomes. The *x* chromosome was distinguishable in over-decolorized cells by its 'woolly' appearance (figs. 51, 53, 55, 58), as was true in spermatogonia.

At this point it will be well to explain the Tables (I–XX) of chromosome lengths (pp. 193–196), prepared for comparison of the several chromosomes in the following genera and species. These show the relative lengths of the six autochromosomes and the relation that the length of the sex chromosome bears to their combined length. In preparing the tables the length of the image of each chromosome, as drawn at 3900 diameters magnification, was measured in millimeters. The measurement from the longer member of each pair was used in most cases, since it was evident, by focusing carefully, that apparent difference in length of the members of a pair was due to a fore-shortening of one of the members. When a chromosome appeared in end view, of course its length could not be obtained, and either the chromosome or the whole cell had to be discarded.

The chromosomes of somatic cells, spermatogonia, oogonia, and second spermatocytes are rod-shaped and may be measured with little difficulty. Those of first spermatocytes are either cross-shaped or rod-shaped. Here the members of pairs are joined at their distal ends and pulled out in opposite directions at their proximal ends, giving a cross or rod; in the latter the chromosome has double the length of a spermatogonial chromosome. To allow a comparison of spermatogonial and somatic

rod-shaped chromosomes with those of the first spermatocyte, all measurements of the former have been doubled. Most dependence is to be placed upon results from simple rod-shaped chromosomes of spermatogonia and second spermatocytes. The double chromosomes in the first spermatocyte divisions are less reliable (figs. 29, 31, 33, etc.), because the members of some pairs are more completely separated than others, which affects unequally the apparent lengths of the chromosomes. The diameters also vary. For this reason length measurements do not always accurately represent the size of chromosomes. But the differences in size are so evident to the eye that it is not difficult to decide where each chromosome belongs in the series.

To find the 'relative lengths' of the chromosomes, the actual length of each of the six pairs of autosomes was found for all available cells. Then the average length of all the chromosomes in each group (no. 1, no. 2, etc.) was found and the sum of these six averages, for the six groups of autochromosomes, was taken as 100 per cent, this being the average total length of the autosomes in all the cells of a given class studied. The 'relative length' of any given chromosome was found by comparing its length with the average total length of all six autosomes and is expressed in per cent. The sex chromosome was not included in making up the 100 per cent, but the percentage relation that it bore to the average sum of the autosomes was found in each case. It was kept separate from the other chromosomes because of its great variation in size in different genera, which ranged from no. 1 to no. 5. The autosomes were more uniform in size in this respect and afforded, therefore, a more suitable basis for comparison.

Explanation of Tables I to XX

The tables show by horizontal bars the average relative lengths of the six autosomes and the relative length that the sex chromosome bears to these in germ cells and in somatic cells for each species of Tettigidae studied. Measurements were made from camera lucida drawings of cells illustrated in the plates and from additional cells, not drawn. The intended length of each bar is indicated in millimeters at the right of the bar. The upper edge of the bar representing chromosome 6 is marked at centimeter intervals in each table. Consult also the text for further explanations.

ACRIDIUM GRANULATUS

TABLE I *Spermatogonia*

FIGURES	NUMBER OF THE CHROMOSOMES	LENGTH IN MM. = × 3900	RELATIVE LENGTHS	1 2 3 4 5 6 7 8 cm.	mm.
23, 24, 25, 27, 28	1	12.26	10.48		29.7
	2	13.44	11.49		32.5
	3	15.56	13.31		37.6
	4	16.46	14.08		39.9
	5	26.28	22.48		63.7
	6	32.9	28.14		79.6
	2×	13.98	11.95		34.0

TABLE II *Second spermatocytes*

37, 38	1	10.05	11.03		31.0
	2	10.25	11.25		32.0
	3	12.25	13.44		38.0
	4	13.33	14.63		41.4
	5	19.2	21.08		59.8
	6	26.0	28.54		80.8
	2×	10.13	11.1		31.5

TABLE III *Spermatogonia and second spermatocytes*

	1		10.6		30.0
	2		11.41		32.3
	3		13.33		37.7
	4		14.24		40.2
	5		22.15		62.9
	6		28.24		79.9
	2×		11.77		32.6

TABLE IV *Follicle cells of female*

51, 54, 55, 57, 56, 58	1	12.8	10.28		29.2
	2	15.2	12.21		34.6
	3	17.27	13.89		39.4
	4	18.98	15.26		43.4
	5	26.45	21.20		60.1
	6	33.83	27.14		76.8
	2×	13.05	10.48		29.8

TABLE V *Average of all except first spermatocytes*

	1	11.7	10.4		29.5
	2	13.33	11.89		33.7
	3	15.14	13.50		38.3
	4	16.38	14.61		41.4
	5	24.48	21.83		61.8
	6	31.06	27.70		78.5
	2×	12.64	11.27		32.0

TABLE VI *First spermatocytes*

29–33	1	10.7	11.07		31.4
	2	11.9	12.3		34.9
	3	13.7	14.18		40.2
	4	14.9	15.42		43.6
	5	21.1	21.84		61.8
	6	24.3	25.15		71.4
	2×	13.0	13.45		38.6

ACRIDIUM INCURVATUS

TABLE VII — *First spermatocyte*

FIGURES	NUMBER OF THE CHROMOSOMES	LENGTH IN MM. × 3900 =	RELATIVE LENGTHS	1 2 3 4 5 6 7 8 cm.	mm.
61–64	1	13.3	11.0		31.0
	2	14.0	11.6		32.9
	3	16.2	13.4		38.0
	4	17.3	14.3		40.5
	5	27.2	22.5		63.8
	6	32.8	27.15		77.1
	1×	13.3	11.0		31.0

ACRIDIUM ORNATUS

TABLE VIII — *First spermatocyte*

65–66	1	18.0	8.55		24.3
	2	25.1	11.92		33.7
	3	30.8	14.63		41.4
	4	33.4	15.86		45.1
	5	45.2	21.47		60.9
	6	58.0	27.55		78.2
	1×	16.7	7.9		22.4

ACRIDIUM OBSCURUS

TABLE IX — *Spermatogonia*

67–68	1	14.6	10.0		28.3
	2	16.2	11.1		31.5
	3	19.4	13.3		37.7
	4	20.5	14.1		40.0
	5	32.1	22.1		62.6
	6	42.8	29.4		83.3
	1×	12.6	8.7		24.7

TABLE X — *First spermatocyte*

69, 77	1	9.63	10.43		29.5
	2	10.33	11.19		31.7
	3	12.5	13.32		37.7
	4	13.46	14.58		41.3
	5	19.08	20.67		58.6
	6	27.33	29.60		83.9
	1×	11.16	12.09		34.3

PARATETTIX CUCCULATUS

TABLE XI — *Spermatogonia*

78–82	1	13.58	11.4		32.3
	2	14.98	12.6		35.7
	3	17.62	14.8		41.9
	4	18.9	15.9		45.0
	5	26.1	22.0		62.3
	6	28.0	23.6		66.8
	3×	16.5	13.9		39.4

PARATETTIX COCCULATUS (Continued)

TABLE XII *First spermatocyte*

FIGURES	NUMBER OF THE CHROMOSOMES	LENGTH IN MM. = × 3900	RELATIVE LENGTHS	1 2 3 4 5 6 7 8 cm.	mm.
83, 84 and three others	1	7.47	12.2		34.6
	2	8.43	13.8		39.1
	3	8.9	14.6		41.4
	4	9.75	15.9		45.1
	5	12.5	20.4		57.8
	6	14.1	23.0		65.2
	3×	10.52	17.2		48.8

PARATETTIX TEXANA

TABLE XIII *Second spermatocyte*

90 + others	1	8.4	11.4		32.3
	2	9.1	12.4		35.1
	3	11.2	15.2		43.1
	4	12.0	16.3		46.2
	5	15.4	20.9		59.2
	6	17.4	23.7		67.2
	3×	9.5	12.9		36.6

TABLE XIV *First spermatocyte*

85, 87, 89	1	10.1	13.3		37.7
	2	10.6	14.0		39.7
	3	11.3	14.9		42.2
	4	11.7	15.4		43.6
	5	15.1	19.9		56.4
	6	17.0	22.4		63.5
	3×	13.5	17.8		50.4

TETTIGIDEA PARVIPENNIS PENNATA

TABLE XV *Spermatogonia*

91	1		11.6		32.9
	2		12.9		36.6
	3		14.2		40.2
	4		14.3		40.5
	5		22.3		63.2
	6		24.6		69.7
	5×		15.3		43.4

TABLE XVI *First spermatocyte*

94, 99	1		11.2		31.7
	2		12.5		35.4
	3		13.7		38.8
	4		14.9		42.2
	5		21.95		62.5
	6		25.6		72.5
	5×		16.3		46.2

TETTIGIDEA PARVIPENNIS

TABLE XVII *Spermatogonia and secondary spermatocyte*

FIGURES	NUMBER OF THE CHROMOSOMES	LENGTH IN MM. = × 3900	RELATIVE LENGTHS	1 2 3 4 5 6 7 8 cm.	mm.
104, 105, 107, 122, 124, 125	1	10.13	10.49		29.8
	2	10.8	11.19		31.7
	3	13.23	13.71		38.8
	4	14.88	15.42		43.6
	5	23.16	24.0		68.0
	6	24.3	25.18		71.4
	5×	17.57	18.2		51.6

TABLE XVIII *Fat body*

108–110	1	11.7	9.8		27.8
	2	13.7	11.5		32.6
	3	15.8	13.3		37.4
	4	18.6	15.6		44.2
	5	28.7	24.2		68.6
	6	30.5	25.7		72.8
	5×	19.7	16.6		47.0

TABLE XIX *First spermatocyte*

111–119, 121	1	11.7	10.9		30.9
	2	13.2	12.3		34.9
	3	14.6	13.6		38.5
	4	16.0	14.9		42.2
	5	25.0	23.3		66.0
	6	27.1	25.2		71.4
	5×	20.5	19.1		54.1

TABLE XX *Oögonia and follicle cells,* (♀)

101–103	1	15.6	10.6		30.0
	2	17.0	11.6		32.8
	3	19.9	13.6		38.5
	4	22.6	15.4		43.6
	5	32.4	22.1		62.6?
	6	39.6	27.0		76.5?
	5×	26.1	17.8		50.4

In the tables giving first spermatocyte lengths the sex chromosome appears longer than in the tables of other cells. This is due to the peculiar behavior of the sex chromosome in these cells, where it is relatively longer and narrower than in other kinds of cells. Its length according to the diagram is therefore greater than it should be.

An examination of the tables will show considerable variation in the length of each chromosome for cells of different tissues. Some of this variation, no doubt, is due to faults in the measurement or drawing of the chromosomes, as well as to cases of fore-

shortening. The results are, therefore, not so satisfactory as desired. Nevertheless, there is a certain amount of agreement in the results which cannot be overlooked; it is fundamental and of use in comparing genera and tribes.

The arranging of the autosomes in three groups—nos. 1 and 2, nos. 3 and 4, and nos. 5 and 6—is best brought out in the tables of spermatogonia and second spermatocytes. The extreme inequality of the two largest pairs may also be seen in the same tables. There is one exception to this; viz., in the tables of first spermatocytes. An examination of the figures of the cells used, however, will show that this is due to variation in the thickness of the chromosomes not expressed in the length measurement. The small size of the 'accessory,' which ranks between nos. 1 and 2 or close to no. 2, is evident from Table V of the average of rod-shaped chromosomes. It is much too long, as already explained, in the first spermatocyte cells.

The slenderness of the sex chromosomes in the follicle cells of the ovary (Table IV) is noticeable. They are 'woolly' and smaller than usual. There may be some connection here with their duality in the female sex.

d. Summary for Acridium granulatus. Acridium granulatus possesses the family number of chromosomes—six pairs and either one or two sex chromosomes, according to the sex—and shows a grouping of these pairs according to the size relations which are characteristic of the family: two extremely large pairs, two intermediate pairs, and two very small pairs. It further bears the subfamily characters: first, in having the sex chromosomes near to the smallest pair of the complex in size; secondly, in having a marked inequality between the two largest pairs; and thirdly, in having very small cells. It bears the generic character of small sex chromosomes and nearly an extreme of inequality between the two largest pairs. The chromosomal relations here summarized may be readily seen in Table I for rod-shaped chromosomes.

2. Acridium incurvatus Hanc. Acridium incurvatus (figs. 4, 59–64; Table VII) taxonomically is closely related to granulatus. The chromosomes also show this close relationship. It possesses

the number characteristic of the family—six pairs and one (♂) or two (♀) sex chromosomes, the pairs being in three groups according to size relations characteristic of the family. The subfamily character is also shown by a sex chromosome that in size is near to the smallest of the complex, by a marked inequality between the two largest pairs, and by small cells. It has the generic characters: nearly the extreme of inequality between the two largest pairs and smallness of the sex chromosome. These similarities serve to put incurvatus into the same family, the same subfamily, and the same genus as granulatus.

According to the systematic descriptions of the species one would expect the chromosomes to be more nearly alike in these two species than in any others. The measurements are not sufficiently accurate to be of use in specific relations. Attention, however, should be called to the *differences* between the chromosomes of the two species.

The difference in length between the 5's and 6's of incurvatus (22.50 to 27.15) is not quite as great as in granulatus (21.83 to 27.70). The gap between the 3's and 4's is only slightly less, being 13.40 to 14.30 compared with 14.18 to 15.42. The same may be said of the smallest pairs (1's and 2's). There is a wider gap between the smallest and the intermediate groups than in granulatus (Tables VI, VII). The sex chromosomes is slightly smaller (11.95 to 13.45). Finally the cytoplasm of the cells is considerably more dense in the former. These differences might be spoken of as specific. However, they cannot yet be said to be satisfactorily established.

The zygote number ($2N$) of chromosomes has been shown in follicle-cell mitoses, no spermatogonial mitoses being available. These mitoses show that numbers and size relations may be readily followed even in somatic cells.

According to Table VII, the length ratios of the autosomes in incurvatus are nearer to the average rod-shaped chromosomes of granulatus (Table V) than to the first spermatocyte chromosomes (Table VI). This is due to the fact that the chromosomes in the first spermatocyte of incurvatus (figs. 61–64) are still in the late prophase, not pulled out unequally as in granulatus

(figs. 29–33). It is true that there is here some abnormal lengthening of some of the double chromosomes, as may be seen by comparing 5 and 6 of figure 62, but this is not so great as in some cases of first spermatocyte chromosomes in granulatus. It seems safe to say that there is a striking similarity in the chromosome ratios of the two species (compare Table VII with I and V), although there are enough differences to serve as a basis for specific distinction.

3. Acridium ornatus Harris. Only two cells (figs. 65, 66) from this species are shown. They are unfavorable for determining accurately the relative lengths of the chromosomes, since the latter are in prophase and differ in the degree of condensation to which each has advanced. This probably accounts for the extreme difference between the two smallest pairs (Table VIII, 1, 2). Chromosome no. 1 (figs. 65, 66) is much more contracted than either 2, 3, or 4. A similar precocious condensation is seen among the smaller tetrads in Syrbula and Chorthippus (figs. 149, 163). The sex chromosome is precociously condensed and therefore appears shorter (Table VIII) than it otherwise would be. Chromosomes 2, 3, and 4, on the contrary, appear more slender (fig. 66) than nos. 1, 5, and 6, and therefore relatively longer than they otherwise would be, while the latter are relatively shorter (Table VIII). In spite of these discrepancies, the sizes characteristics of the family, subfamily, and genus may be readily recognized. It seems justifiable to say that here, again, the ratios are sufficient to put this species into the genus Acridium rather than Paratettix or Tettigidea. The material is too scant to warrant going into specific differences.

4. Acridium obscurus Hanc. This species (figs. 2a, 2b, 67–77; Tables IX, X) is not so closely related to granulatus as is incurvatus. The germ cells of the male have thirteen chromosomes. I have not examined those of the female nor the somatic cells.

The chromosome size relations, as in ornatus and incurvatus are sufficiently similar to those of granulatus to place obscurus within the genus Acridium. They agree with the other species

(figs. 67–77; Tables IX, X) in having autosomes with a great range of sizes between the smallest and largest, an exceedingly large gap between 4's and 5's, a large difference between 5's and 6's, and a sex chromosome ($1x$) in length near the smallest autosome.

The differences from granulatus are greater than from incurvatus. The two largest pairs in obscurus differ more in length than in any other species of the genus. This is most evident in first spermatocytes, the lengths being respectively 20.67 and 29.60. This difference cannot be far from correct, since in spermatogonia the lengths are 22.1 to 29.4. The ratio of these chromosomes in the first spermatocytes of incurvatus is 22.5 to 27.15, and in granulatus, 21.84 to 25.15. The last number (25.15), however, is not normal, as comparison with the spermatogonial chromosomes (22.48 and 28.14) will show. Comparing measurements of the spermatocytes in incurvatus with those of the spermatogonia in granulatus and obscurus, it appears that incurvatus is more nearly like granulatus than is obscurus. In the last species the 6's are relatively the longest (29.4) and the gap between the 5's and 6's the largest yet found (figs. 69–77).

The intermediate pairs (3's and 4's) are almost indistinguishable from each other, especially in spermatogonia, though measurement shows them to be slightly different. In this respect they are similar to those of the other species of the genus. However, the difference in size between the no. 3's and the no. 2's is greater in obscurus than in granulatus or incurvatus (Tables I, VII, IX).

In the spermatogonia of obscurus the 2's are slightly larger than the 1's and the sex chromosome. But in the spermatocyte the sex chromosome appears larger than either 1's or 2's. This is due to the fact that in the spermatocyte the diameter of the sex chromosome is less than that of the other chromosomes and its length therefore greater than it should be. The more correct measurement is probably that of the spermatogonia, where the sex chromosome is the smallest of the series (figs. 67–70). For this reason it has been numbered $1x$. It is 'woolly' in appearance (figs. 67–68). Here, again, is clear evidence of the 'differential chromosome' in spermatogonia.

Another difference shown by obscurus is that both soma and germ cells are smaller than in any other species studied; possibly a specific difference.

Obscurus shows conditions of chromosome size sufficient to place it in the genus Acridium; it differs from granulatus and incurvatus in having a greater difference of length between the 5's and 6's, a slightly wider gap between the 2's and 3's, a slightly smaller sex chromosome, and smaller cells.

In the spermatogonia of obscurus both resting and dividing nuclei (figs. 67, 68, *c*) frequently contain a spherical body (sometimes two) which stains like chromatin. At mitosis it passes undivided to but one of the daughter cells. Its presence in so many spermatogonia indicates that it may divide at some of the divisions or at intervening stages. However, when two are present, they are unequal in size. This suggests only transitory bodies. In both the prophase and metaphase of the first spermatocyte, from one to three unpaired bodies occur which may represent one or both spermatogonial bodies (figs. 69–74). One, of course, is the sex chromosome (fig. 69). Of the other two, one (*con.*) is small and loose; its staining capacity varies, though it never stains deeply, and frequently is almost indistinguishable. It is cone-shaped (figs. 69–74, *con.*), but sometimes appears partly divided (figs. 72, 73). A third one (*c*) of the unpaired bodies may be present in either nucleus or cytoplasm. It appears like a chromatoid nucleolus, and may be the sort of structure encountered in the spermatogonia. It is always spherical (figs. 73, 74) and passes undivided to one pole in the first maturation division. These structures behave somewhat like chromosomes in staining and in sometimes being drawn into the equatorial plate (figs. 72, 74) at division. It seems possible that the cone-like body (figs. 69–74, *con.*) may be a chromosome fragment, the result of an unequal division at some previous time.

5. Paratettix cucculatus Morse. In Paratettix cucculatus (figs. 78–84) the cells are decidedly smaller than in Acridium, and the histological appearance is different. In external characters the genus is nearer to Acridium than to Tettigidea, which will be taken up after Paratettix. Systematists recognize this fact by

placing Acridium and Parattetix in one subfamily and Tettigidea in another. These relationships are shown in the chromosomes, and in the size of cells. The 5's and 6's are very large and differ considerably in size. The inequality between them (22.0 to 23.6, Tables XI, XIII) is, however, not nearly so marked as in Acridium (22.48 to 28.14, Tables I, VIII). Again, the range of size from largest to smallest is not nearly so great as in Acridium (29.4 to 10.0, Table IX; compare also figs. 78 to 82 with 67, 68).

The sex chromosome in Paratettix cucculatus ($3x$) is slightly larger (13.9) than in Acridium (11.9). In length it comes nearest the 3's, so is designated by $3x$ instead of $1x$ or $2x$, as in Acridium. However, it is, like Acridium, near the size of the smallest group (1's and 2's). It may, as in Acridium, be distinguished in spermatogonia by its 'woolly' appearance (fig. 82). The measurement (17.2 is too high, as usual in first spermatocytes.

6. Paratettix texanus Hanc. This species (figs. 85–90)[2] is similar to cucculatus, but the range in size of chromosomes (first spermatocyte) is somewhat less. This may be due to the greater diameter and consequent shortening of the 5's and 6's. In the second spermatocyte the range is about the same as in the spermatogonia of cucculatus, though the 5's differ (22.0 in cucculatus; 20.9 in texanus).

The sex chromosome is about third in size and slightly larger than in the preceding genus. Its rank, according to length in first spermatocytes, is not correct, since it is longer and of less diameter, compared with autosomes, than it is in the spermatogonia or in the second spermatocytes. The measurements of first spermatocytes were, therefore, not used.

Paratettix is, therefore, distinguished from Acridium by smaller cells; by a less range in extreme lengths of chromosomes; by slightly larger sex chromosome; and by a smaller difference in the length of the two largest chromosomes.

7. Tettigidea parvipennis pennata Morse. Tettigidea is in body structure much farther from Acridium than is Paratettix, so far, in fact, that it is placed in a different subfamily, the Batra-

[2] Figures 88 to 90 are from a slide of Paratettix texanus leucocephalus Nabours, kindly furnished me by Dr. Mary T. Harman.

chidinae. Cell structure and chromosomes likewise show this relation. The cell has a diameter one-fourth to one-third greater than that of Acridium or Paratettix. The network of the cytoplasm is much looser.

Figures 91 and 92 show thirteen chromosomes (♂), arranged as usual in six pairs plus the sex chromosomes: two large (6's and 5's), two intermediate (4's and 3's), and two small pairs (2's and 1's). The sex chromosome (5*x*) ranks fifth in size. The 5's and 6's are more nearly equal than was true in any of the other genera (Tables XV–XIX). Table XX (oogonia and follicle cells) shows a much greater difference between the 5's and 6's. Possibly some error may be the cause of this, as only three cells were used.

Figures 93 to 99, prophases and metaphases of the first spermatocyte, show the number and size relations more perfectly than the spermatogonia do. Figure 99 lacks a single pair of chromosomes (4's), due probably to loss in sectioning. It will be seen from these figures and Table XVI that a greater interval in size (8.6) occurs between the 5's and the 4's in Tettigidea than in Acridium (7.8) or Paratettix (5.1). Also the gap between the 2's and 3's is not so great as in these genera. In other words, the intervals which separate the four largest autosomes are more nearly equal in Tettigidea than in either of the other genera. These relations may be most readily appreciated from Tables I–XX. Figure 100 shows an oogonium. The number of chromosomes is, as usual, fourteen. Size relations are well shown.

8. Tettigidea parvipennis Morse. This species, in chromosomes, is so much like Tettigidea parvipennis pennata that it is impossible to tell them apart. Figures 101 to 103 are of oogonia. The number is fourteen (six pairs plus two sex chromosomes). The slight inequality of the two largest pairs (6's and 5's) is evident, especially in figure 101. In figures 102 and 103 no. 5 is foreshortened. This affects the results in Table XX. The 4's and 3's show the usual gradation in size.

Figures 104, 105, and 107 are spermatogonia with the usual thirteen chromosomes. In figure 106 a large chromosome (no.

6) is drawn from each of several cells showing the split and especially the large knobs, at the distal end, so common in this species. Sometimes the constriction is so great that one could imagine the knob to be a small attached chromosome. Is it possible that this knob corresponds to one of the smaller of the twenty-three or twenty-four chromosomes of the Acrididae? It might thus help to account for the smaller number, thirteen or fourteen, of the Tettigidae.

Figures 108 to 110 are of mitoses in male somatic cells from fat-body tissue. Here the chromosome numbers and their relative sizes are the same (Table XVIII) as in germ cells.

Figures 111 to 119, and 121 are metaphases of first spermatocytes showing number and size relations of chromosomes as before. Figure 121 lacks one pair (5's) due to sectioning. The slight inequality of 5's and 6's and the absence of as large a gap between the 2's and 3's as exists in Acridium and Paratettix are very evident.

Figures 122 and 123, representing two anaphase stages of the first spermatocyte, show that all chromosomes except $5x$ divide. This is probably the reduction division. The sex chromosome tends to drop behind the others in the latter part of its passage to the pole (fig. 123), though it starts ahead of them (fig. 122).

Figures 124 to 127 are metaphases of second spermatocytes. There are two sorts of cells, some containing seven, others only six chromosomes. The relative sizes (figs. 124, 125) are accurately shown. Nos. 5 and 6 are almost alike; $5x$ is clearly between 4 and 5. Further, 4 and 3 are nearly alike, as are also 1 and 2. One of the latter (no. 2), however, is always more slender than the other. This is seen even in first spermatocyte divisions, and it may be this autosome that condenses before the others in the first spermatocyte prophase stages (no. 2, figs. 65, 66). Figure 126 represents a cell sister to that seen in figure 127. These show that all chromosomes, including $5x$, are split in the second spermatocyte division.

The metaphases and anaphases of the first spermatocyte, shown in figures 128 to 135, are from young specimens belong-

ing to Tettigidea (probably parvipennis). They repeat and emphasize what has been found in parvipennis and p. pennata. In figures 132 and 134 tardy divisions of certain chromosomes are seen, which may be of significance in the question of reduction and Mendelian segregation, and may have some bearing upon the question of unequal tetrads. They demand further study.

9. Unequal homologous chromosomes. A female Acridium granulatus was found, in which there were five long chromosomes among the fourteen instead of the expected four. Later, the same condition was found in a male in first spermatocytes, where homologous chromosomes were separating from each other. This, fortunately, gave a clew as to what the long chromosomes paired with, for, with one exception, all the chromosomes were present, of normal size, and paired normally. The exception was in the no. 1's, which were represented by only a single member, and this paired with the fifth long chromosome (figs. 141–145). Anaphase figures (146, 147) showed this small chromosome separating from the abnormal mate (no. 1) and going to the opposite pole.

After seeing this condition of pairing in the chromosomes of the male, those of the abnormal female were easily paired as follows: two 6's, 5's, 4's, 3's, 2's, two 2*x*'s, one no. 1, and the abnormally large no. 1. For the female the counts were made in the cells of the walls of ovarioles.

In the male individual the abnormal no. 1 shows a constriction (figs. 142, 144, 147) at a distance from its distal end equal to the length of the normal no. 1, with which it had been paired. This may possibly be the no. 1 portion of the abnormal chromosome. (See Chromosome Studies. III.)

The members of the unequal pair bear no constant relation to the sex chromosome in their distribution to either the second spermatocytes or the sperm cells, as figures 141–147. show. The abnormal chromosome (1) passes as frequently to the pole receiving the sex chromosome as to the pole lacking it. This has nothing to do with the unequal tetrad reported by Baumgartner ('11) for Gryllotalpa, for that unequal tetrad has since been shown by Payne ('12) to be a group of sex chromosomes.

In T. parvipennis one individual found showed the no. 4 chromosomes unequal. In all dividing first spermatocytes these (united) formed an unequal tetrad (figs. 115, 118, 119, 120, 122). I infer that the no. 4 chromosome, which came from one of the parents, was originally deficient in size. This character seems persistent enough to be preserved in all the cells of the first spermatocyte found dividing. Moreover, the same deficiency occurs in all the somatic cells studied—the fat-body cells (figs. 104, 105, 108).

The bearing which these unequal tetrads have upon questions of synapsis and reduction has been discussed in Study III, but will also be considered later in this paper.

2. *Truxalinae* (*Acrididae*)

In contrast to the family Tettigidae,[3] the three subfamilies, Truxalinae, Oedipodinae, and Acridiinae, of the Acrididae, have in general 23 (♂) and 24 (♀) chromosomes. Exceptions to these numbers have been found in Chorthippus (Stenobothrus) by Davis, Meek, and Gerard, and in Hesperotettix and Mermiria by McClung ('05). McClung found Hesperotettix to have 23 in the spermatogonia and 11 in the first spermatocyte, and Mermiria to have likewise 23 in the spermatogonia, but only 10 in the first spermatocyte. He believed that "the reason for the deviations is due to unusual associations of the spermatogonial chromosomes in the spermatocytes." I believe that likewise in Chorthippus we have not 17 chromosomes, but 23, and that here there is a *permanent* association of certain non-homologous chromosomes, such as no. 11 with 7, no. 10 with 8, or no. 9 with 5, which are not associated in the majority of genera. To show how this may explain the peculiar numbers, I describe first the conditions in Syrbula acuticornis, an example of the 24–23 chromosome genera, in which no such association occurs.

[3] The subfamily Tettiginae should be removed from the family Acrididae and raised to the rank of a family (Tettigidae) coördinate with the Acrididae.

1. Syrbula acuticornis Bruner. In the spermatogonia there are (fig. 148) twenty-three chromosomes, consisting of eleven pairs and the sex chromosome. I have numbered the autosomes in sequence, according to size, from smallest to largest: two 1's, two 2's, two 3's, etc. The sex chromosome ranks tenth from the smallest and is therefore marked 10*x*. The 9's, 10's, and 11's are large. There is a considerable gap in size between the 8's and 9's. The 4's, 5's, 6's, 7's, and 8's form an almost uniformly graded series. A more considerable gap occurs between the 3's and 4's. The 1's, 2's, and 3's form the small series, although a much wider gap occurs between the 2's and 3's than between the 1's and 2's.

The chromosomes are all of the rod-shaped type and at metakinesis lie at right angles to the long axis of the spindle. In this plane they are arranged in radial fashion around the center of the plate (fig. 148), their pointed proximal ends, to which the spindle fibers attach, turned inward; the large blunt distal ends turned outward. It is important to note this arrangement in making comparison with what is found in Chorthippus.

I have drawn a series of stages from the prophase to the metaphase of the first maturation division. Figure 149 is of a nucleus coming out of parasynapsis. There are eleven first-spermatocyte autosomes, each split and more or less twisted spirally, and one sex chromosome (10*x*). The latter is also split and may be recognized by its condensed condition. The other chromosomes, except nos. 1 and 4, are alike in having reached about the same stage of unwinding and condensation. No. 1 is farther along than the others, and no. 4 exceeds no. 1, as indicated by its condensed condition, which approaches that of the sex chromosome. There is a difference between the ends of these conjugated chromosomes. One end usually has two dark knobs (x, x), from which the attraction fibers arise, whereas the other lacks any such knobs. These knobs are probably the 'polar granules' described by Pinney ('08).

In figures 150 to 152 a and 153 (later stages) the separation along the split, which was present in the spirally twisted chromosomes (fig. 149), is much more conspicuous. The spiral twist-

ing has disappeared, probably due to an unwinding process. Each chromosome consists of four parts and may be considered as being split in two longitudinal planes, one at right angles to the other (figs. 151, 152 a–c, 154.) This is more evident in some chromosomes (fig. 149, nos. 1, 4) than in others (fig. 149, nos. 5, 10, 11), and usually more pronounced in later prophases (fig. 150) than in earlier ones (fig. 149). Figure 154 represents chromosome no. 4 in five stages of the process of splitting leading up to the metaphase condition.

In figure 155 the twelve chromosomes are shown in a stage just preceding the breaking up of the nuclear wall. The four parts and the more or less characteristic shape for each chromosome (tetrad) are now evident. No. 11, however, is not in its typical form. This may be seen in figures 156 d and 156 f. Figures 156 a–f show a number of forms assumed by prophase chromosomes. Their form depends much upon the length of the spermatogonial rods which conjugated to produce them. Figures 156 a and 156 b are views of two conditions which are assumed by a no. 1, 2, or 3 pair. The attraction fibers probably arise at x, x, for in the metaphase of this division such chromosomes are rods, frequently constricted in the middle, to whose ends the attraction fibers are attached. During the preceding prophase stages the chromosome has become split in one plane (fig. 156, *I, I*) and the halves thus produced have separated at the end which bears the knobs and have rotated around the opposite end as a fixed center, each through an arc of 90° until the two halves, still attached to each other at the end opposite the knobs, form a nearly straight rod. While this separation and rotation of the halves resulting from the first split is going on, each half begins to show its secondary split (*II, II*, fig. 156b), or else has already acquired it before the rotation begins. Without giving my reasons here, I will simply say that I believe the first or primary split (*I, I*) produces the reductional division; i.e., separates homologous spermatogonial chromosomes, and that the second split (*II, II*) is an equational division of the now end-to-end conjugated spermatogonial pair. This four-part chromosome

(figs. 156a, 156b), after condensing, enters the metaphase plate in this extended condition.

Figure 156c is typical of the so-called cross form. The four parts are visible. The proximal knobs (x, x) appear similar to those of figure 156b. The arms of the cross extending along the axis of the primary split (*I*, *I*) may be bent about until their ends are almost in contact, as in no. 6, figure 150b, or even in contact, giving a ring-shaped chromosome, as in nos. 4, 6, and 9, figure 155.

The condition shown in figure 156d may be produced from that of figure 156c by a lengthening of the arms along the axis of the primary split and by so bringing their distal ends into contact that the whole chromosome forms a ring. With the fusion of the distal ends to form the ring, the components in that region begin to separate along the *primary* plane of division. At the proximal part of the chromosome, where this stage has been reached, the primary split (*I*, *I*) prevails; in the middle part, the secondary split (*II*, *II*) prevails; and at the distal end, the primary split again prevails, giving two knobs slightly smaller than the proximal knobs (x, x). By decreasing the extent of the secondary split (thus lessening the diameter of the ring) and increasing the primary split (thus increasing the length of both proximal-knob [x, x] and distal-knob ends), we get as a result the conditions of figures 156e, 155 no. 10, and 152a. Starting again with the ring-like stage, by increasing the length of the distal-knob ends and then bringing these knobs into contact again at the extreme distal ends (thus forming a second ring whose plane is perpendicular to that of the first ring), and by then decreasing the length of the proximal-knob ends (x, x) and the extent of the first ring, we obtain a condition like that of figure 156f. I do not say that a continuous change takes place along the axes of the 'splits' so as to produce all these different forms in one chromosome, but rather that as the conjugated chromosome—split in two longitudinal planes, the primary and secondary (*I*, *I* and *II*, *II*), at right angles to each other—comes out of the synapsis period, its four parts present one or the other of these conditions, separating most along the primary or second-

ary plane according as the one or the other happens to predominate. During these changes of form the chromosomes are undergoing rapid condensation (fig. 155). As they reach the metaphase stage, we at first get conditions such as are seen in figures 157 and 158.

Figure 157 is a nearly polar view of an early metaphase. The no. 11 chromosome is similar to 156d; no. 10, to figure 156c, except that it must have had very much longer arms than the latter; no. 9, to no. 9 of figure 155a; and nos. 6, 7, and 8, to nos. 7 and 8 of figure 155 and to 156c. Whereas no. 6 in figure 155 is a ring, it apparently is not so in figure 157; but in Syrbula admirabilis it has been shown (Robertson, '08) that chromosomes which usually form rings do not always do so. No. 5 is a ring similar to no. 5 in figure 155, while nos. 1, 2, and 3 are rods similar to the corresponding numbers in figures 155 and to figures 156a and 156b.

Figure 158 is a lateral view with all chromosomes shown. No. 11 is a ring in side view; nos. 1 and 2 are rod-like; no. 4, a cross approaching a rod; and nos. 3 and 8, rings. All others are crosses. The sex chromosome is a rod. In the second spermatocytes (figs. 159, 160) there are two sorts of cells, depending upon the presence or absence of the sex chromosome. The size relations and rod-like character of the chromosomes can readily be made out here.

I have given a detailed description of Syrbula to prepare for a better understanding of the chromosomes in

2. Chorthippus (Stenobothrus) curtipennis Scudd. Chorthippus is unique among Acrididae in having apparently seventeen chromosomes. Three pairs of the chromosomes are V-shaped, each with arms of unequal length. This suggests possible compounding in chromosomes. These V's have the apices turned toward the center of the metaphase plate. At the apex is a thin place, seemingly a point of union, over which the deeply staining material is not continuous. If we assume that each of the six unusual V's embraces two chromosomes, the number seventeen is increased to twenty-three. If this assumption be correct, the chromosomes may be numbered according to

size as in Syrbula, with which the size relations are almost identical. For in Chorthippus there are two large 11's (designated as 12's in Robertson, '08), each linked with a no. 7; two 10's (11's in '08), each linked with a no. 8; and a sex chromosome, 10*x*, as in Syrbula. Further, the two large 9's are linked each with a no. 5. The 6's, 4's, 3's, 2's, and 1's are separate, as in Syrbula. The gap in size between 8 and 9 is possibly larger, between 3 and 4 not so great, and between the 1's and 2's a little greater than in Syrbula; between 2 and 3 it is wide, as in Syrbula (figs. 184–187). In general, then, the size relations of chromosomes in Chorthippus are very similar to those in Syrbula.

As in Syrbula (fig. 149), conjugating chromosomes come out of the diffuse stage in parasynapsis (figs. 163, 164). In each of these cells all conjugated chromosomes (eight) and the sex chromosome are accounted for and drawn. In figure 163 nos. 2 and 4 have been drawn as though moved out radially from their positions; the real position of 10*x* is indicated by a plus sign (+). In figure 164 chromosomes 1, 2, 4, and 10*x* have likewise been transferred outward. I wish to call attention to the three long chromosomes (7–11, 8–10, 5–9) in these two cells. All of the chromosomes show a longitudinal split, and in parts, or all, of each, a second such split at right angles to the first is evident (figs. 163, 164). In figure 163 an accidental (?) interlocking of the two largest chromosomes (7–11, 8–10) seems to have taken place. Both show the primary split farther advanced than the secondary. In 7–11 the halves gap apart in the middle region (x‴, x⁗) and include between them one of the halves (x′) of 8–10, which is gaping apart similarly in its middle region (x′, x″). The two chromosomes are interlocked like the links of a chain. This phenomenon may be of importance in the question of the continuity of the chromatin thread during parasynapsis.

The no. 4 chromosome in Chorthippus, as in Syrbula, is much condensed and deeply stained. Frequently this chromosome, or the end of one exconjugating limb of it (x in fig. 168), lies near one end of the sex chromosome (figs. 164, 165, 168, 170, 173, 174, 178b, 179, 180). In this respect it behaves similar to Mc-

Clung's chromosome in Hesperotettix and Mermiria, which likewise was associated with the sex chromosome, but more permanently than in Chorthippus.

The long chromosome (7–11) in figure 165 is clearly split into two strands and optical cross-sections at favorable points (a and b) show that each of the halves is again split. In the middle at the points x, x, the halves gape apart. These points correspond to what would be the proximal points of chromosomes 7 and 11, were they going through this pairing process separately, as they do in Syrbula (fig. 149).

In figures 166, 167a and 167b are chromosomes in the same stage as figure 164, which show clearly the four longitudinal parts. The black points at the ends are probably the polar granules. In figure 168 is a still later stage where the chromosomes are more condensed, but still show their two longitudinal splits and the resulting four strands. At any point along the chromosomes the strands are usually more closely apposed in one direction than in the other, according as the primary or the secondary split is farther advanced. The letters "x, x" mark the points where the attraction fibers were destined to spring forth, for at these points there is a constriction in the long chromosomes (7–11, 8–10, 5–9). In figure 164 nos. 10*x* and 4 have been drawn outside the nucleus for convenience. Figure 173 is of a still later stage. Chromosomes nos. 3, 6, and 7–11 (173a) have been drawn outside the nucleus (173b) for clearness. The sex chromosome, as usual, lies near no. 4.

In the next older stage (fig. 174) the chromosomes have become more condensed. No. 4 takes on its usual shape, a modified cross. Nos. 1, 2, and 3 are rods, which have already opened out by rotation so that the primary split is represented solely by the region of contact where the distal ends of the halves resulting from this split still meet. The compound nature of nos. 7–11 is evident. The proximal points (x, x) are marked by constrictions. The smaller of the two chromosomes, no. 7, forms an almost complete ring in the plane of the drawing paper. The larger (no. 11) part forms a ring similar to that of figure 156d. The ring perpendicular to the plane of the paper is the link in

the middle formed by the junction of the proximal knobs of 7 and 11. In 5–9 the middle, perpendicular ring is much increased in extent at the expense of the horizontal[4] portion of no. 9, which is a cross, and of no. 5, the halves of which are merely in contact. But in 8–10 the separation is such that we have three rings. The middle, perpendicular ring has constrictions (x, x) near the middle of each part, the points of junction between 8 and 10. The plane of the terminal rings is at right angles to that of the middle ring. They may be referred to as horizontal rings.[4] Their distal parts have split so as to form crosses, the planes of which are parallel to that of the middle ring. No. 6 clearly has the form of a cross. In all of the autosomes the four longitudinal parts are evident in places. I believe that they have originated from conditions like those shown in figures 164, etc., where each of the eight ordinary chromosomes consists of four longitudinal strands lying close together.

Still later prophases of the 7–11 and 8–10 chromosomes are shown in figures 175 and 176. In figures 176 and 177 especially the points of junction (x, x) between chromosomes 7 and 11 is very evident on each of the four strands of the middle ring. Here, too, the four longitudinal parts of the chromosome may be very readily made out. An unusual occurrence is illustrated in figure 177. One of the two compound chromosomes in conjugating has evidently at some time, probably during parasynapsis, enclosed the other. Here, at the end of the period, they are still in the same relation to each other and neither seems to have been affected by it.

Figures 178a and 178b are of a late prophase showing all nine chromosomes. The constrictions at x, x indicate the compound character of the three largest pairs, which is also shown, even more distinctly, in the early metaphase of figure 179.

A careful comparison of this figure (179) of Chorthippus with the corresponding figure (157) in Syrbula is very instruc-

[4] I use the term 'perpendicular ring' to show that this portion of the chromosome, when the latter takes its position on the spindle at metaphase, will be perpendicular to the plane of the metaphase plate, and 'horizontal ring' to designate the portions parallel with this plane.

tive. Keeping in mind that in figure 157 the chromosomes are viewed in a direction (nearly parallel with the spindle axis) almost at right angles to that in which they are seen in 179 (nearly perpendicular to the spindle axis), it will not be difficult to imagine the results of bringing together in twos, by means of attachments at x, x, the separate chromosomes 7 and 11, 8 and 10, 5 and 9 of figure 157. The results would be chromosomes like those in figure 179. It is perhaps necessary to explain further the condition in some chromosomes of figure 179. No. 9 is a ring seen edgewise, with the distal region turned toward the observer; no. 5 is seen edgewise, but instead of forming a closed ring (fig. 157) its distal ends are free. The uncombined chromosomes (1, 3, 4, 6) are sufficiently alike to render their identification in the two figures reasonably certain. It will be observed, however, that there is no chromosome in figure 179 corresponding to the no. 2 of figure 157. This is probably due to the removal of that chromosome in an adjacent section, for there is present no other very small chromosome comparable in size with no. 1.

Figure 180 shows clearly the compound nature of chromosomes 5–9 and 7–11 in the fact that at the junctions (x, x) the deeply staining chromatin material is interrupted.

Figure 181, a late metaphase, shows the compound chromosomes, 5–9 and 7–11, in final stages of division. They give the familiar **E**-shaped picture, so often seen in Chorthippus and other species having **V**-shaped chromosomes, in which one arm of each **V** is longer than the other.

Figures 182a, 182b, 182c are lateral views of successive stages of a compound chromosome during the metaphase of the first spermatocyte division. The horizontal arms of the no. 7 part continue to get shorter. The perpendicular arms of 11, seen in 182a, have disappeared, or do not occur in 182b and 182c. Probably they never existed here; but there is a decrease in the proportionate size of the horizontal part of 11. The vertical ring drawn in figure 183 is probably an 8–10 compound, for the arms of each **V** are more nearly equal in length (compare with figs. 184, 185). The 8's are in contact by their distal ends only,

whereas the 10's are still broadly in contact along their horizontal arms, which thus still retain the familiar cross-shaped tetrad appearance of late metaphases, such as we find in species like Syrbula, where only rod chromosomes are found.

The second spermatocytes in Chorthippus are illustrated by figures 184 to 186, in one of which (fig. 185) the sex chromosome is wanting. An anaphase stage, showing the sex chromosome, is given in figure 187. In each of these four cells are three large **V**-shaped chromosomes. If each arm of a **V** be counted as a single rod-chromosome, there are readily seen to be 11 or, with the sex-chromosome, 12 chromosomes, which may be arranged in a graded series according to size, as in the case of the 11 (or 12) rod-chromosomes of Syrbula (figs. 159, 160). Believing that this is the true condition of the chromosomes, I have given them here corresponding numbers. It will be seen that no. 11 is attached to 7, 10 to 8, 9 to 5. The points of attachment are constricted and show clear spaces, as usual, where the two chromosomes have become united. The size relations of **V**'s, and of all the other chromosomes, are the same as in first spermatocytes and spermatogonia.

3. Chorthippus biguttulus Linn. For sake of comparison with C. curtipennis I have copied two of Gerard's ('09, p. 582) figures of C. (s.) biguttullus, and have attempted to number the **V**-chromosomes (my figs. 188, 189) like those in curtipennis. From the lengths of the limbs of the three **V**'s shown here, one would conclude that probably the same chromosomes are concerned in forming the **V**-compounds in biguttullus, a European species, as in curtipennis.

4. Résumé on Chorthippus and Syrbula. (1) The study of tettigidean chromosomes has shown that the same numbers and, within certain limits, the same size relations are found among all the genera of a family. Syrbula and Chorthippus are closely related genera of the acrididaean subfamily Truxalinae. They differ *apparently* in the number of chromosomes. Both have one (♂'s) or two (♀'s) sex chromosomes. Syrbula has eleven pairs of rod-shaped autosomes; Chorthippus has three pairs of **V**-shaped and five pairs of rod-shaped autosomes.

(2) In Syrbula these rod-shaped autosomes and the sex chromosome may each be recognized in a group by their relative lengths. Almost the same size relations may be seen in the sex chromosome, the five pairs of rods and the six pairs of limbs of the three pairs of **V**'s of Chorthippus.

(3) A constriction, a clear, non-staining bridge, and an attraction fiber occur at the apex of each of the **V**'s in spermatogonia. These conditions may be traced in spireme stages, the prophases, metaphases, and anaphases of first spermatocytes, in second spermatocytes, and in spermatids. Such constrictions divide the members of each pair of **V**'s into two pairs of rods, equivalent in length in each case to the 5's and 9's, the 7's and 11's, and the 8's and 10's of Syrbula.

(4) The limbs of the paired **V**'s in late synapsis stages, prophases, and metaphases of the first spermatocytes behave like the 5's, 7's, 8's, 9's, 10's, and 11's of Syrbula, in that they form, during these stages, rod-shaped, cross-shaped, horseshoe-shaped, and ring-shaped tetrads, depending, as in the rods of Syrbula, upon the lengths of the pair of limbs in each case. They agree also in the characteristic appearance that each such tetrad gives in the late metaphase and in anaphases. The diads resulting from these behave similarly in the second spermatocytes of both genera.

(5) In conclusion, therefore, I believe that the three pairs of **V**-autosomes of Chorthippus are the equivalent of the six pairs of rod-autosomes of Syrbula,—the 5's, 7's, 8's, 9's, 10's, and 11's, —and that the remaining five pairs of rod-autosomes and the sex chromosome of Chortippus are likewise the equivalent of the 1's, 2's, 3's, 4's, 6's, and sex chromosome of Syrbula. If this be so, then we may consider each of these three pairs of **V**'s to be a compound chromosome, and that, therefore, the Truxalinae have the number twenty-three, characteristic of Acrididae.

3. Oedipodinae (Acrididae)

The third subfamily of the Acrididae is here represented by Chortophaga viridifasciata and Dissosteira carolina (figs. 190,

191, after Davis, '08, p. 72). As in Syrbula, there are twenty-three rod-shaped chromosomes. Among these are the usual three large pairs. The sex chromosome does not rank as 10, but as 8 (Dissosteira) or 9 (Chortophaga). As in Syrbula, there are three very small pairs in Chortophaga; in Dissosteira two of the three are exceedingly small, one (no. 3) being, however, considerably larger, as in Chorthippus, though still worthy of being grouped among the three small pairs. The 4's, 5's, 6's, 7's, and in Dissosteira the 8's form a continuously graded series of sizes similar to the conditions in Syrbula.

4. Acridiinae (Acrididae)

In this, the fourth subfamily of Acrididae (fig. 192), we again have twenty-three chromosomes. The size relations differ considerably from those of the oedipodines and truxalines, though there are agreements. There are, as usual, two very large pairs, but the third largest (9's) is smaller than in these subfamilies. The sex chromosome ranks 10. There is a considerable gap between $10x$ and the 9's, but the 9's, 8's, 7's, 6's, and 5's form a graded series with less differences in size than in the truxalines and oedipodines. The 4's are much smaller than usual, though still noticeably larger than the 3's. We can therefore say that for these three subfamilies of the Acrididae the number of chromosomes is twenty-three (♂).

5. Locustidae and Gryllidae

V-shaped chromosomes are very common among the Locustidae and Gryllidae. The number of chromosomes in Locustidae seems frequently to be thirty-one or thirty-three. In cases where a smaller number occurs, some of the chromosomes are V-shaped, as in Chorthippus. By counting each of these as two chromosomes, the total number becomes thirty-one. This may be seen by comparing figure 193 of Decticus verrucosus (after Buchner, '09, fig. 82) with figure 202 of Steiroxys trilineata (after Davis, '08). If we assume that the two large V's in the latter are twofold, the number in reality is thirty-one.

Baumgartner ('03) found in the field cricket (Gryllidae) twenty-one chromosomes, whereas in the house cricket (Gryllis domesticus) there were twenty-nine. His figures of the field cricket show similar, though small, V-shaped chromosomes, whose apices are turned inward (figs. 203, 204). By counting each of these V's as two chromosomes, the number here also is twenty-nine.

That my suspicion is well-founded in regard to V-chromosomes, has just been shown by the work of one of my students, Miss Woolsey, upon three species of Jamaicana (Locustidae). Figures 194–201 have been taken from her paper (Woolsey, '15). One species of this genus always has thirty-five (♂'s) rod-shaped chromosomes (fig. 194, spermatogonium). A second species may have thirty-five (♂'s) or thirty-four (♂'s) chromosomes. When the number is thirty-four, one large V-shaped chromosome is always present (spermatogonium, fig. 196, no. 14–16). A third species shows either thirty-five rod-shaped chromosomes or a group of thirty-three in which there are always two equal-sized large V-shaped elements (nos. 14–16, fig. 200, spermatogonium). In prophases and metaphases of the first spermatocyte, individuals of the 35-rod type present seventeen rod-shaped tetrads similar to those of Tettigidae, in addition to a very large sex chromosome (18*x*, fig. 195). In the 34-chromosome individuals, where one V is present, the first maturation division shows fifteen rod-shaped tetrads plus the sex chromosome plus one long V-shaped chromosome (octad), which evidently represents the V-chromosome of the spermatogonium joined to two of the rod-shaped spermatogonial chromosomes (14, 14–16, 16, figs. 197–199). Careful measurements of the length of the limbs of the V in spermatogonia and first spermatocytes and of the chromosome attached to the end of each limb of the V in first spermatocytes show each limb to be of the same size as the chromosome attached to it (figs. 198, 199). Each attached chromosome (14, 16) is therefore probably homologous with the limb of the V-type multiple chromosome to which it is joined.

In figure 198 it is noticeable that one limb of the V is longer than the other. In the pairing which takes place during the first maturation, it is to be expected that the long limb will pair

with a similar long-rod chromosome and the short limb with a similar short-rod chromosome. There would then result in first maturation divisions a long V with unequal limbs, exactly what is found (figs. 198, 199). At the end of this division the limbs of the original spermatogonial V separate from their rod mates and the V, passing to one of the second spermatocytes, has the same size as a spermatogonial V.

In two-V type individuals, first spermatocytes show the sex chromosome, fifteen rod-shaped tetrads, and an elongated ring (fig. 201). This ring evidently results during the exconjugation process of the pair of V-shaped chromosomes. The longer (16, 16) and shorter (14, 14) sides of this ring probably contain the same elements as are present in the longer and shorter limbs of the first spermatocyte V's of figures 197 to 199. I have examined carefully every cell drawn by Woolsey and am reasonably certain that in Jamaicana we have cases of linkage of non-homologous rod chromosomes to form V's, etc., which are entirely similar in their behavior to the V's of Chorthippus. Jamaicana is important because it shows the transition from rod-shaped to V-shaped chromosomes and a corresponding reduction in the number of chromosomes, not only within the genus but within each species. It shows in the individuals studied that two chromosome pairs may exist as four rods, or as two rods, and one V or as two V's. At the same time there are present in each case thirty additional rod-shaped chromosomes and the sex chromosome, making always thirty-five rod chromosomes or their equivalent.

DISCUSSION

1. V-*shaped chromosomes*

1. General. I undertook an examination of the V-chromosomes of Chorthippus in an attempt to find if such V's were not in some way concerned in bringing about the smaller number, seventeen, which all species of this genus seem to have. The number characteristic of the subfamily to which this genus belongs, as well as of the two other subfamilies closely related

to it—the Oedipodinae and Acridiinae—had up to this time been thought to be twenty-three. As a result of the comparisons of chromosomes in this genus with those of the related genus Syrbula and with those of some of the Oedipodinae and Acridiinae, and in view of what I have found to be true of chromosome numbers and sizes among the genera of the Tettigidae, and especially in the light of the relation known to exist between rod- and V-shaped chromosomes in three species of Jamaicana, I am convinced that the smaller number in Chorthippus is due to the presence of V's. I am reasonably certain that these V's, such as we find in Chorthippus and Jamaicana and possibly in other locustids and gryllids, have resulted from the linkage proximally of two non-homologous chromosomes, and that the non-chromatic bridge at the apex of these V's,—sometimes accompanied by a constriction,—from which the spindle fiber springs, is the point at which this linkage has taken place. With these conclusions in mind, I turn to a consideration of V-shaped and segmented chromosomes described by others, and the possible relation of such chromosomes to some of the problems of cytology and genetics.

V-shaped chromosomes are common in both plants and animals. They are referred to in cytological literature as 'equal armed' and 'unequal armed' (caudés) V's or U's, or as being 'hook-shaped' or 'J-shaped' (Grégoire, '05, '10). The spindle fiber springs from the apex of the angle formed by the arms and is referred to as coming from the median, a near-median (intermediate), or a subterminal region. Besides these V's, the only forms of chromosomes we have, except in first-maturation divisions, are straight rods and, possibly, spheres. In the straight-rod type the spindle fiber usually springs from the end and is spoken of as terminal. However, in Copepoda, where the rods show transverse segmentation, the attachment of the fiber may be median or sub-median. But in anaphases such rods appear as V's and therefore may be so classed. For convenience, I use the term V-chromosome in a general sense to include all of these two-armed chromosomes, viz., the V's, U's, and J's, and transversely segmented rods. However, I do not consider

as **V**-chromosomes the '**V** *simples*' of Grégoire ('10, fig. 65a), which occur in both anaphase and telophase of the first and in the metaphase of the second maturation division (Robertson, '08, figs. 37–39; Davis, '08, figs. 65, 93; the present paper fig. 160, nos. 7, 10, and 10*x*). These diads are in reality rod-shaped chromosomes, equivalent to spermatogonial rods split longitudinally, whose halves have a tendency to gape at the distal end. The same appearance is frequently seen in spermatogonial and somatic metaphases in Syrbula, where we are certain of having only rod-shaped chromosomes from which such so-called **V**'s may be derived. Frequently in illustrations of the anaphase of first spermatocytes, or the metaphase of second spermatocytes, the outlines of the halves of these chromosomes are overlooked, especially at the apex, so that the chromosome is made to appear as a true **V** or **U** (Hartman, '13, figs. 33–47). I believe that the failure of authors—Rückert and his followers, who worked on copepods, and Belajeff ('98) and Ishikawa ('97) on plants—properly to distinguish between the '**V** simples,' derived from the rod-type tetrad in anaphases of the first and in metaphases of second maturation divisions, and the true **V**-shaped type of chromosome during these stages, has led to confusion in causing an interpretation of the second maturation division as exhibiting post reduction. Furthermore, I do not include among the true **V**'s the '**V**-tetrads' of insects (nos. 7, 8, and 10 in fig. 157; McClung, '14, figs. 92, 93), whose **V** form I consider to have resulted from the moving apart, along the axis of the secondary split (II, fig. 156c), of the distal ends of the parts of a tetrad which originally consisted of four strands lying side by side (Robertson, '08, fig. 29, *e* and *h*).

In going over the literature on these chromosomes, it has seemed to me that possibly there may be two types of **V**'s. In the first the chromosome may be considered a bent rod having no achromatic bridge nor marked constriction at the apex of the **V** or **U**. Such chromosomes, if short, would tend to be rods, straight or slightly curved; if long, they would be **U**'s. The **U**-shape would be especially brought out in anaphases of division figures. Chromosomes of this type may be seen in

Ascaris, Tomopteris (Schreiner, '06a), in amphibia and, possibly, among the chromosomes of an unidentified acridid described by McClung ('14, figs. 59–62). McClung suggests that "**V**'s may have been derived from straight rods through an altered transverse segmentation of a continuous spireme thread, which would result in chromosomes with fiber attached at a subterminal or median position, instead of a terminal." Such **V**'s might be grouped with the bent-rod type.

In the second group the **V**'s bear at the apex unmistakable achromatic bridges of clear non-staining material. At this point there is also a constriction. Such chromosomes I believe to have been derived in many cases from the linkage proximally of two non-homologous rods (nos. 8 and 10 in Chorthippus, nos. 14 and 16 in Jamaicana unicolor). In this type may also be placed those chromosomes which are loosely linked together, possibly in the stage of forming **V**'s (Browne ['10, '13], in Notonecta insulata; Woolsey ['15, figs. 5–8, *A*], in Jamaicana flava).

As to the validity of the former group, I am unable to say. I merely suggest that such may exist (Agar, '12, fig. 9). By far the larger number of the **V**'s and **U**'s which have been figured have been represented as such, exhibiting neither constrictions nor transverse clear regions and would therefore be grouped with this type. But certainly not all such described **V**'s may be so grouped.

I am certain of the occurrence of the second type of **V**'s. I also believe that this type will be found to be much more frequent than one might suppose, for in the case of the genus Chorthippus (Stenobothrus) alone, de Sinéty ('01), Davis ('08), Gerard ('09), and Meek ('11, '12a) have overlooked the transverse segmentation which I describe here. I should expect to find this linkage type of **V** in those genera which show a smaller number of chromosomes than is characteristic of the family to which they belong, and at the same time a relatively larger number of **V**-shaped chromosomes—conditions which are found in comparing Chorthippus with other genera of the Truxalinae.

2a. **V**-*shaped chromosomes in plant-cell mitoses, not including prophase and metaphase of the first maturation division.* True **V**-shaped chromosomes have been described in Lilium, Allium, Trillium, Helleborus and Podophyllum. In Lilium they have been shown by Grégoire ('99, '10), Strasburger ('00), and Mottier ('03, figs. 6, 8, 16, 41). Only in figures 16 and 41 does Mottier present any indication of transverse segmentation. Grégoire's ('99) figures show **V**'s, but, with the exception of 19*b*, *c*, and d and one or two chromsomes in figures 22 and 23, it is impossible to distinguish between the true **V**'s and his **V**-simples. Mottier describes these chromosomes as straight rods, bent rods, and **U**'s. His figures indicate that for the genus Lilium probably a large number of rods is characteristic. Bonnevie ('11, figs. 12, 13) finds in Allium both **V**- and rod-shaped chromosomes (figs. 55–60). Like Grégoire, she has failed to distinguish between true **V**'s and **V**-*simples*. The former show a split along each arm of the **V** in the anaphase. Mottier found similarly shaped chromosomes in Podophyllum (figs. 22, 23), in Tradescantia (fig. 32), and in Helleborus (seè Grégoire, '09, fig. 19). As to whether any of the **V**'s in the genera described would on re-examination show the segmentation at the apices, I cannot tell, except in the case of Podophyllum, where in root-tips cells I have found segmentation similar to that shown in Chorthippus.

In Trillium, Grégoire et Wygaerts ('04) have observed three cases of segmentation, of which they say,

> Nous observons très souvent dans les chromosomes-filles une ou plusieurs fentes transversales, très précises, comme tailleés au couteau, Fig. 20. Elles se correspondent parfaitement d'un segment-sœur à l'autre, Fig. 20. Il est certain qu'il ne s'agit pas là d'une fente complète; le chromosome en effet ne se disloque jamais; mais nous n'entrevoyous pas d'explication de ce phénomène, que nous ne faisons que signaler.

This transverse segmentation corresponds with what I have found in Chorthippus. Since at least five of the seven pairs of chromosomes in this genus are **V**'s, as figured by Atkinson ('99) and by Grégoire ('09); since many of these chromosomes have unequal arms, almost identical to my no. 7–11's or 8–10's in

figures 162, 186, and 187; and since the number is small compared with that of other genera of the lily family (which possess twenty-four), I believe that Trillium may possibly present a case of compound chromosome formation similar to that of Chorthippus.

2b. **V**-*shaped chromosomes in somatic, spermatogonial, and second spermatocyte divisions and in anaphases of first spermatocytes.* Beginning, among animals, with nematodes, we find Ascaris megalocephala to have in one variety, four; in the other two chromosomes, which appear to be of the **U** type (Boveri, '88, figs. 44b, 60, 61). The spindle fibers are attached not at any one point but along the whole mid-region. The only indication of constriction which has been figured is that of the first maturation chromosome, shown by Tretjakoff ('04, fig. 7).

In annulates the Schreiners ('06a, figs. 2, 6, 8–12) describe **V**-shaped chromosomes of the **U** variety. There is a long narrow constriction in the middle but no indication of segmentation such as exists in Chorthippus or Trillium. In Nereis Bonnevie ('06, pp. 62, 63) has demonstrated **V**-shaped, **J**-shaped, and rod-shaped chromosomes in somatic cells.

After an examination of the cell studies on Copepoda by Rückert ('93), Haecker ('95, '02, '11), Lerat ('05), Krimmel ('10), Braun ('09), and Matscheck ('10), I have come to think that possibly a good deal of the confusion in respect to variation in chromosome numbers, heterotypical mitoses, etc., has been due to the presence of compound chromosomes of the form, either of **V**'s, bent rods or straight rods, possessing a segmentation similar to that which I find in Chorthippus. Lerat ('05, figs. 25–32, 46–50) has shown that three types of chromosomes exist in the copepods as in other groups of animals and in plants; namely, straight rods with terminal attachment of fibers, bent rods or **V**'s with subterminal attachment of fibers, giving **J**'s or hooks, and **V**'s with either median, or submedian attachment of fibers. The occurrence of these three types of chromosomes, especially the straight-rod type, has been overlooked by the other investigators of the group, though Matscheck in his figure 8 gives one rod chromosome occurring along with

three V's, and Haecker himself has also shown V's ('11, figs. 22, 30, 65).

But we do not always find V's in the copepods as described by Haecker, Matscheck and others. This is possibly due to the fact that the limbs of what might be regarded as straightened-out V's are usually so short that they have a tendency to lie in one axis instead of at an angle to each other, and also that in some of these species there may be few compound chromosomes. The V structure, if present, appears in anaphases, whether the limbs are short or long. Lerat's cells were evidently in the right stage to show V's.

The best evidence of the compound nature of the chromosomes in Copepoda is the presence of a constriction, leaving an archoplasmic bridge, median or submedian in position, which gives to the chromosome the appearance of being transversely segmented. Lerat denies the presence of the constriction or break, but admits the presence of a non-staining region. His figures, however, show constrictions at the apices of the V's. This segmentation has been figured by Rückert ('93), Schiller ('09, figs. 7–19), Haecker ('95, '02), Krimmel ('10) and Matscheck ('10). Rückert (see Lerat, '05, p. 181) was the first to describe the phenomenon of segmentation in chromosomes, though probably he did not understand its meaning. Haecker ('11, p. 45) describes this phenomenon when he says, "Seltener ist eine durch helle Querkerben hervorgerufene *wirkliche* Segmentierung wahrzunehmen, so z. B. bei den 'bivalenten' Chromosomen der Kopepoden (fig. 14b) und offenbar auch bei den auffallend langen 'Sammelchromosomen' von Ascaris." He has, however, in my opinion, misinterpreted this bridge as representing a stage in the reduction process, in accordance with his metasyndesis theory, which postulates that at some time during the life cycle of the animal after fertilization of the egg and before the first maturation division takes place, there occurs an end-to-end synapsis of like chromosomes, resulting finally in a fusion during the growth stages of the first maturation cell. It will be seen that, according to Haecker, the transverse segmentation of chromosomes in the Copepoda does not persist as a permanent

region of the chromosome, but must appear and disappear with the life cycle of the animal. He looks upon it as the point of conjugation of two *homologous* chromosomes, the halves of the rod (limbs of the **V**) being homologous chromosomes and, of course, equal in length. That this is not the case, is shown by the fact that the limbs of the V are frequently of unequal length (Lerat, '05), as in Chorthippus and in so many species with **V**-shaped chromosomes.

The variation in chromosome numbers which Krimmel ('10) found in somatic mitosis of Diaptomus—between twenty-eight and fourteen (reduced number)—Haecker ('11, p. 113) explains as follows: "Man wird die intermediären Zahlen auf einen unvollständigen Zerfall bivalenter Elemente, also auf eine Mischung bivalenter and univalenter Elemente zurückführen dürfen." Haecker is probably right in ascribing numerical variation to breaks at points of segmentation, though I believe he is wrong in thinking that the 'univalent' chromosomes making up these 'bivalents' are to be considered as members of homologous chromosome pairs.

Schiller ('09, figs. 7–9) describes tetrads in somatic cells of Copepoda. He probably saw some of these compound chromosomes with transverse segmentation in which the longitudinal split is visible, as in Trillium (Grégoire et Wygaerts, '04, fig. 20). In such a chromosome one might see four parts and thus mistake it for a tetrad (compare fig. 134).

Among the insects **V**-chromosomes have been found in the phasmids by de Sinéty ('01); in five acrididaean genera; in Stenobothrus by de Sinéty ('01), Davis ('08), Gerard ('09), Meek (10', '11, '12) and myself, in Hippiscus, Mermiria, Hesperottix, and Chortophaga by McClung ('05, '14); in the Locustidae by Woolsey ('15), Stevens ('12), McClung ('05), Buchner ('09), Vejdovsky ('11–12), Davis ('08); in the Gryllidae by Baumgartner ('04) and Payne ('12); and in Coleoptera (Coptocycla) by Nowlin ('06).

In the phasmid Leptynia attennuata Pant., de Sinéty shows in spermatogonia (figs. 73, 75) three **V**'s among thirty-six chromosomes. In Stenobothrus three pairs of **V**'s, such as I have found, have been described by all authors who have investigated this

genus (de Sinéty, Gerard, Davis, Meek). With the exception of Davis ('08, figs. 17, 21), none of these authors have seen the archoplasmic bridge or constriction at the apex of the V's. Though Davis's figures (17–21) show it, it is not mentioned in the text. The V's in every case have arms more or less unequal in length.

McClung ('05, figs. 1, 7, 8, 9; '15, fig. 84) has described a single V-shaped chromosome in three species of Hesperotettix (♂) which is made up by linkage proximally of an autosome with the sex chromosome. The sex-chromosome portion may be recognized by the smoothness of its surface. In Mermiria also he has described a V-chromosome; this differs from that of Hesperotettix in that the sex chromosome here seems to be attached to the distal end of one of the two autosomes entering into the V. McClung believes that in this multiple chromosome of the first spermatocyte division two tetrads, as well as the sex chromosome, are concerned, and that in this division whole tetrads separate from each other. It seems to me that, instead of interpreting the multiple body in this way, we may say that Mermiria has a pair of autosomal V's, to the end of one of which is appended the sex chromosome. The presence of the sex chromosome in the V's of both genera is evidence of the compound nature of these V's, since one limb of the V may be identified by its smooth surface as an individual, specific chromosome (viz., the sex chromosome), while the other limb is shown by its roughness to be similar to the autosomes. Also the number of other autosomes present shows that it must be one of them.

The V's of Chortophaga, which McClung (fig. 94) interprets as the result of the precocious synapsis of homologous chromosomes in the spermatogonia, I am inclined to think are not such; they are, instead, V's consisting of non-homologous chromosomes, similar to those of Chorthippus, in which, however, the fusion is more like that of Notonecta (Browne, '13) or Jamaicana (Woolsey, '15) than of Chorthippus. The non-homologous nature of the limbs of the V's in all these cases may be inferred from the fact that they are always of unequal length.

In the Diptera Stevens ('08) describes **V**'s in nine genera. She has not distinguished, however, between the true **V** and the '**V**-simples' of Grégoire. No points of constriction or segmentation at the apices are in evidence except in Drosophila ampelophila (figs. 57–82), in which there are two pairs of **V**'s, a pair of *M*-chromosomes, and a pair of unequal sex chromosomes. Metz ('14) has found in eight species of the genus unmistakable evidence of the compound nature of these **V**'s, since in some species one pair of **V**'s may be replaced by two pairs of rods, and in other species both pairs of **V**'s may be replaced by four pairs of rods.

Among vertebrates the Dipnoi (Lepidosiren) and the Amphibia afford striking examples of **V**-shaped chromosomes. In Amphibia from ten to eleven of the twelve pairs of chromosomes are **V**-shaped, and only one or two pairs rod-shaped; e.g., Flemming ('87, figs. 41, 42, 43a, 44) and Drüner ('94, '95) in Salamandra; Eisen ('03), Janssens et Dumez ('03), and Janssens ('05, figs. 69–71) in Batrachoseps; Carnoy et Lebrun ('99, figs. 103, 104, 118) in Triton; Lebrun ('02, figs. 33–35, 41, 42) in oögenesis of Diemyctilus; Montgomery ('03) in Desmognathus and Plethodon, and Muckermann ('12) in urodeles.

The arms of the **V**'s in Amphibia are seldom of equal length (Janssens, '02), as is clearly shown by Muckermann in somatic mitoses, where (his figs. 1–4) ten pairs are either **V**'s or **J**'s and only two pairs are rods. Three pairs of the **V**'s have sharp-angled apices, and some appear constricted at this point, as was also shown by Eisen ('00, figs. 112, 120h, 120k). The constriction, accompanied by a clear non-staining bridge, was shown by Montgomery ('03) in the chromosomes of the first spermatocyte, which were in synapsis.

That transverse segmentation occurs in Amphibia is clear from the works of Meves ('07) and Della Valle ('07), who describe in somatic cells from various tissues of Salamandra chromosomes thus segmented and showing at the same time the longitudinal split. According to these authors, and others who describe similar figures (Bonnevie, '08, '11; Popoff, '08; Haecker, '07), these are examples of heterotypical (tetrad-like) divisions

in somatic cells. They argue that if such conditions are found in somatic cells, where only longitudinal divisions occur, the similar heterotypical division of the first maturation may likewise be interpreted as longitudinal. The second is like it, therefore no reduction occurs. The question of heterotypical division we shall discuss later. Their observations, however, are evidence that we are dealing with at least some transversely segmented, and possibly compound, chromosomes in Amphibia.

In Lepidosiren Agar ('11, figs. 6, 7) found thirty-eight chromosomes. Of these, thirty-four are clearly either **V**'s or hook-shaped, four are rod-shaped. He notes a transverse constriction across each of the thirty-four univalent chromosomes, as he calls them, and says ('11, '12) that it corresponds in the spermatocyte divisions with the apices of the **V**'s of the somatic or spermatogonial mitoses. This is in exact agreement with my results on Chorthippus. He also shows ('12, p. 291) that for each chromosome this constriction always lies at a certain point, whether the limbs are equal or unequal. This is described for the five largest chromosomes. One pair always has limbs of nearly equal length in all mitoses, while the four pairs next in size are always hook- or **J**-shaped. This resembles Chorthippus, where there are always three pairs with arms of unequal length.

In mammals van Hoof ('12) figures in spermatogonia (figs. 01–2, 03–6, to 03–8) and anaphases of the first spermatocyte (plate III, figs. 026–48d; plate IV, figs. 027–50, 01–65, 01–66) rod-shaped, **J**-shaped, and **V**-shaped chromosomes. A few of his **V**'s have sharp apices, where they show a constriction. I think that in man, according to the work of Wieman ('13), there is evidence of compound chromosomes in the transverse segmentation, which is clearly shown, and in the presence of many short **V**-shaped chromosomes. The great disagreement in the number of chromosomes reported for man may be due, in my opinion, to the extent of this compounding in chromosomes. Winniwarter ('12) reports forty-seven for a Caucasian, while Guyer ('10) and Montgomery give twenty-two (♂) and twenty-four (♀) for the negro. Wieman finds an intermediate num-

ber, about thirty-three to thirty-eight. Among these are a large number of **V**'s with transverse segmentation. He says: "The small chromosomes may be derived by a breaking up or 'diminution' of the larger ones. Likewise the difference between the somatic number and the spermatogonial number (as reported by Duesbug, Guyer, and others) may have a similar explanation."

From the preceding survey it may be seen that **V**-chromosomes, with either short or long arms, are of common occurrence in most families. We are led to suspect that transverse segmentation (not always shown) and constrictions, when they occur, together with non-terminal attachment of fibers may possibly be correlated in many cases with decrease in numbers brought about by a compounding of non-homologous chromosomes. We also are led to think that a **V**-chromosome may break at the apex to form two rods.

3. **V**-*Chromosomes in synapsis and reduction.* A general review of the literature upon these stages has been given, either completely or in part, by Grégoire ('05, '10,) Haecker ('07, '10), Davis ('08), Granata ('10), Wilson ('12), and others. It is necessary, however, to consider the literature which bears upon the **V**-chromosomes, since they are of such wide occurrence and possible importance. I shall try to show where I think others have failed to interpret correctly the behavior of these chromosomes, and wherein my work, together with the work of others on these and other chromosomes, furnishes evidence in favor of parasynapsis, but opposed to a complete fusion of the pairing threads, also in favor of the first division being reductional.

V-shaped chromosomes, since they are of such wide occurrence, have, I believe, played a considerable rôle in the debate over the synapsis stages, for much confusion has resulted from the failure of investigators to appreciate correctly the difference between chromosomes of the **V** or **J** and the straight-rod types during synapsis and following periods. The first stage in which misunderstanding has occurred is the so-called 'bouquet stage.' Janssens ('03, '05), the Schreiners ('06a, '06b, '08), and others have shown conclusively that, following the

parallel arrangement of the leptotene threads, the side-to-side pairing of homologous chromosomes begins at the free ends of the members of each pair; i.e., the ends which lie at the distal pole of the cell, and advances along the pair toward the opposite ends. In the case of **V**'s, pairing should begin at the distal ends of their limbs, and move toward the apices (Schreiners, '06a, figs. 20–26). The distal ends of the chromosomes lie in the distal part of the cell; i.e., that part which contains the interzonal body and is nearest to the plane of the last division (Davis, '08, p. 81). There would then result from **V**-pairs—of which according to Muckermann ('13) there are in urodeles about seven or eight—the familiar loops of the 'bouquet stage,' characteristic of so many species.

In those species where no **V**'s, but only straight rods, occur the loops, such as Janssens ('05, fig. 42) and the Schreiners ('06a, figs. 20f, 20h, 22, 25, 26) have shown in this stage, would not appear. I have found this to be true in the Tettigidae (my unpublished "Study II"), where this stage, from its resemblance to a sheaf of wheat, might appropriately be termed the 'sheaf' stage. Wilson ('12, p. 387) has not been able to find the 'bouquet-stage,' nor the polarization that goes with it, in any of the Hemiptera. Here the chromosomes are short, which may account for the lack of polarization. Davis ('08, figs. 31–34) describes for Dissosteira (a rod-chromosome genus) what he took to be the loops in the 'bouquet-stage;' but I think he has wrongly interpreted as 'loops' what I believe are the much bent, long rod-chromosomes ('10s and 11's of Syrbula) intimately paired side-to-side. The extreme length of the paired thread in such cases has caused it to bend and simulate the loops of Tomopteris or Batrachoseps. But if one look carefully at Davis's figures, it will be noticed that only one limb of each 'loop' lies completely within the region of the distal pole of nucleus and cell. The other end may, in some cases (the longer chromosomes), lie not far from this pole, but more usually it is in the region of the opposite (proximal) pole, or on the right or left side of the nucleus. Many investigators (Montgomery '05, Davis '08, and others) have made this mistake in attempt-

ing to find loops in this stage, where, since they were dealing with only straight-rod chromosomes, there could be none. And in doing this they have attempted to see in these loops, so formed, the evidence of end-to-end synapsis, misled probably by Montgomery's ('03) work on Amphibia. He, it is true, was there dealing with loops, since the Amphibia have ten pairs of **V**'s, and he correctly saw the constriction shown at the apices of these loops; but these constrictions did not mean that telosynapsis had taken place between one of the ends of each of a pair of **V**'s; on the contrary, they probably corresponded to the constriction at the apices of the spermatogonial pair of **V**'s, which were here in parasynapsis.

In those species, however, where some **V**'s occur, as in Chorthippus, one might expect a few of the loops characteristic of the 'bouquet' to appear. This may be seen in Davis's ('08) figure 48 of Stenobothrus. Finally, in those species where all or nearly all the chromosomes are of this **V**-shaped type, we find the nucleus in the 'bouquet-stage' with practically nothing but these loops present, as the Schreiners have shown for Tomopteris ('06a, figs. 20f, 22, 23, 25, 26), and Montgomery ('03, figs. 2, 3, 5), Janssens ('05, fig. 42), and the Schreiners ('06b, fig. 12) for the Amphibia.

I have not studied the 'bouquet' and the earlier synapsis stages in Syrbula or Chorthippus, but only the later synapsis. My first stage (figs. 149, 151, 163–168) corresponds, I believe, to stage '*h*' of Wilson ('12) and stages '*f*' of Davis ('08), since it not only resembles these, but, like them, is immediately preceded by a stage in which no regular spireme can be distinguished, the chromatin being in a fine netlike condition, possibly the 'diffused' stage ('*g*') of Wilson ('12, figs. 66, 67).

As explained in the description (pp. 210–215), each autosome, when it emerges from stage '*g*,' consists of two longitudinal strands in both Syrbula (fig. 149) and Chorthippus (figs. 163–167). These two-strand spiremes resemble very much those of Pamphagus shown by Granata ('10, figs. 25–27); Dissosteira, Steiroxys, Stenobothrus by Davis ('08, figs. 57, 58, 70, 83); Ceuthophilus, by Stevens ('12, figs. 27, 28); Oncopeltus, by Wilson ('12, figs.

107, 108); Tomopteris, by the Schreiners ('06, figs. 22, 23, 25, 26, 29–35); Salamandra, by the Schreiners ('06, figs. 10–13; '08, figs. 13–22); Batrachoseps, by Janssens ('05, figs. 57–60); Amphibia, by Montgomery ('03, figs. 2–4); and Lilium, by Grégoire ('99, figs. 5–8; '07, figs. 12–19). With the exception of Davis, Montgomery, and Granata, these authors have considered this stage to be the result of the side-to-side pairing of homologous chromosomes now beginning the disjoining process, and I agree with them.

In the later stages four strands were seen in each spireme (figs. 164–167). Such spiremes are similar to the tetrads which Carnoy described in 1887 for the nematodes Ophiostomum, Ascaris clavata, and Ascaris lumbricoides as being formed by a double longitudinal division of the single primary maturation chromosome rod, and to those seen in Ascaris megalocephala in the same year by Boveri ('87), who gave the same explanation of their origin. Granata likewise found, in Pamphagus, the early prophase chromosomes of the first spermatocyte to consist of four longitudinal parts, the result of splitting in two longitudinal planes at right angles to each other. I do not agree with him in regard to the origin of tetrads, nor in regard to the time and manner of reduction, but I am able to confirm his figures.

In Syrbula there were eleven of these spiremes, in Chorthippus, eight, corresponding respectively to the number of pairs of autosomes in each species. Polarization of the material in the spiremes was shown by the presence of the polar granules (knobs). These were terminal in Syrbula, a pair for each of the eleven chromosomes. In Chorthippus but five showed terminal knobs. The three remaining (long) spiremes each showed two pairs of the granules or thickenings, located at the point along the chromosome corresponding to the position of the apices of the V's which had conjugated to produce them. The number of knobs in Chorthippus will therefore be seen to be eleven, as in Syrbula, consisting of the five terminal pairs on the short spiremes and the two non-terminal pairs on each of the three long spiremes. In the two-strand condition (fig.

163) only two pairs of these knobs appeared; in the four-strand, four pairs. Between the two thickenings on each strand (figs. 163, 174, 176, 178) is a constriction and segmentation which is identical with the non-staining region at the apex of the **V**-chromosomes of the spermatogonia (fig. 162) and is similar to that which occurs in the **V**'s of Lepidosiren and Trillium and the bipartite rods of Copepoda. This constriction divides each of the three four-strand spiremes into two unequal parts, corresponding in length with the limbs of the three respective pairs of spermatogonial **V**'s. The facts, (1) that the position of these knobs and the constriction of the filament between them corresponds with that of the constriction and apices of the three pairs of **V**'s respectively, and (2) that there is among the three long spiremes but one such *un*equally segmented spireme for every pair of **V**'s, and further (3) that such single segmented spireme cannot have resulted from a pair of **V**'s in telosynapsis (since the segments of each of the three long spiremes are unequal) and (4) that the presence of all other spiremes in these nuclei has been accounted for, lead to the conclusion that in these three long spiremes of Chorthippus we probably have the result of a parasynapsis of each of the three pairs of **V**-chromosomes, which took place at some previous time. The ends of the spiremes represent the distal ends of the limbs of the **V**'s and their knobs the proximal or apical region of these **V**'s. If this be granted, then the autosome spiremes in Syrbula corresponding to the limbs of these **V**'s must also be in parasynapsis, for in each case their behavior is similar to that of the **V**'s. Since the remaining five autosomes in Syrbula and Chorthippus are similar to these three—each of them splitting into four longitudinal parts—I believe that all autosome spiremes, eleven in Syrbula and eight in Chorthippus, have united at some previous time in parasynapsis.

The remaining figures of the first maturation chromosomes of Syrbula and Chorthippus I shall, for convenience, group into four stages, '*i*,' '*j*,' '*k*,' and '*l*,' but will discuss them together. Stage '*i*,' early to middle prophase, includes figures 150, 152, 153 of Syrbula and figures 174 to 177 of Chorthippus; stage '*j*,'

late prophase, includes figures 155, 156 of Syrbula and figure 178 of Chorthippus; stage '*k*,' metaphase, figures 157, 158 of Syrbula and figures 170, 180, 182a, 182b, 183a of Chorthippus; and stage '*l*,' late metaphase or early anaphase, figures 181, 182c, 183b of Chorthippus, but none in Syrbula.

It will be seen that, according to Janssens, the Schreiners, and others, the side-by-side pairing of the leptotene chromosomes begins at the distal ends. In the case of a pair of **V**'s, it begins at the free (distal) ends of the limbs of the pair. From the appearance of the spiremes of the autosomes of Syrbula (fig. 149) and of Chorthippus (figs. 164–167, stage '*h*' of Wilson, '12)—where in at least two cases (figs. 149, 164) all of the autosomes are clearly visible—one is forced to admit that side-by-side pairing has taken place and probably has proceeded from the distal to the proximal part of the chromosome pair. If we grant that side-by-side pairing occurs and that it begins at the distal ends, then, if the process advances regularly, the last region of the two threads to become approximated would be the proximal ends of the rod in the case of rod chromosomes and the apices of the **V**'s in the case of **V**-chromosomes. In unequal tetrads formed by unequal homologous chromosome pairs, in Tettigidea the no. 4's (figs. 115, 120), in Acridium the no. 1's (figs. 141–147), in three genera of Oedipodinae, viz., Arphia, Brachystola, and Dissosteira (Carrothers, '14), in Schistocerca (Hartmann, '14), and in the **V**-rod bi-tetrad of Jamaicana (figs. 197–199), one feels very certain that reduction division is taking place. If this be admitted, then in all of these cases the last region of the pairing chromosome to be in contact with its mate is the distal end. Granting this, and knowing also that the first region to pair is the distal, it may be said that *the proximal regions are the last to pair and also the first to begin the process of disjoining.*

In a very large chromosome, such as 7–11 in figures 163 or 165, it is of course impossible to say whether the gaping in the middle represents the end stages of the approximation of the univalents in parasynapsis or the beginning stages of their separation in the disjoining process. I think it is the latter, because in the follicles furnishing material for figures 163 to 166

there were several cysts of cells which were in earlier stages than those drawn, probably in Wilson's '*g*' or 'diffused' stage, which is known to *follow* the approximation stage of *parasynapsis*, and also because there were no breaks in the stages succeeding figure 165 up to the metaphase. In such a nucleus as is represented at figure 168, I feel still more certain that the gaping apart is the beginning of the disjoining process, because the chromosomes are much farther along in the process of condensation. I therefore believe that in the gaping apart of the **V**-bivalents we may have *the beginning of the process of disjoining.*

In the rod bivalents of Syrbula (fig. 149) the proximal parts (x, x), which are terminal in this species, are probably in the beginning stages of the process of disjoining. This may be claimed for at least those six bivalents (5, 9; 7, 11; and 8, 10) which we have many reasons to believe are the equivalents of the three large chromosomes of Chorthippus (fig. 168). The behavior of the remaining five bivalents of figure 149 is similar to that of the larger bivalents, and therefore they are probably undergoing the same process.

First maturation chromosomes, which are probably in the end stages of approximation, some of them possibly in the beginning of disjoining (Schreiners, '06a, fig. 30), behaving like the 5–9 7–11, and 8–10 compounds of Chorthippus (figs. 163 and 165), have been described in the work of the Schreiners ('06a, figs, 22, 30; '08, figs. 16–18) for Tomopteris. Later stages shown in Salamandra (the Schreiners, '06b, figs. 12–14) are undoubtedly in the disjoining process. The gaping loops of their figures 16 to 18 ('08) are almost duplicates of 7–11's and 8–10's in my figures 163 and 165. Their figures 16 and 17 show, in addition to the loop, the halves of which gap apart in the middle, a short rod with halves gaping apart at the end. This I assume to be a rod pair; the side-to-side approximation, having started at the distal ends, is progressing toward the proximal ends, which in this case are free (not attached to another rod) and thus form a **V**. The large-loop chromosome in the same cell is possibly in the same condition.

I may assume, then, that in my figures of the '*h*' stage parasynapsis has taken place, since they are so much like those which

authors have so interpreted, and since we may be reasonably certain that in the case of the compound chromosomes of Chorthippus such has occurred. The fact that gaping-apart occurs between the two strands at the middle of the compound chromosomes, and that a similar phenomenon occurs in Tomopteris and Batrachoseps, where the Schreiners have shown that parasynapsis takes place first at the free ends of the limbs of the V's, forces one to believe that in Chorthippus likewise we may expect to have parasynapsis beginning at the free ends of each pair of V's. It seems perfectly possible, then, that in this process of simultaneous approximation of the distal ends of each pair of limbs of a V pair there may be accidental interlocking between the members of two pairs of V's, such as we find in figure 163, between the 8–10's and 7–11's, or, as appears to have been the case in the pairs shown in a later stage at figure 177, or, still better, the interlocking which the Schreiners ('06b, figs. 24, 25) have described in Salamandra. It seems to me that such figures can be explained only on the assumption that the phenomena have taken place in the manner I have set forth.

If we admit that the interlockings just described have resulted during approximation side-to-side of pairing V's, then the presence of such conditions in the stage when separation (fig. 163) is evidently beginning, means that the split appearing at the middle of chromosomes 7–11, 8–10, 5–9, must be the split of reduction, and that this stage must mark the beginning of the separation of homologous chromosomes. For, following this split through figures showing these compound chromosomes, it is evident that it gives rise to the space of the middle or perpendicular-ring portion of each compound. This middle ring may, as before said, be thought of as being formed by the four proximal knob-like parts of the two pairs, 7's and 11's, 8's and 10's, etc., which have become linked to form the compound (compare figs. 155–158 with 174–180). The points of constriction, from which the attraction fibers spring at the opposite sides of this ring, are evidence of this. The terminal portions of the compound—forming horizontal rings, if the rod chromosomes involved be long (11's, 10's, or 9's), or horseshoes, crosses,

and tetrad-rods, if the rods involved be short (8's, 7's, and 5's)—may be considered identical with the body or main part of a Syrbula no. 11-, 10-, 9-, 8-, 7-, or 5-tetrad of this stage. As the metaphase passes into the anaphase and the process of disjunction approaches its end, the perpendicular-ring portion increases at the expense of the horizontal portions (figs. 182, 183) until, in the anaphase, the shorter members of a compound (5's and 7's, fig. 181) separate, leaving the longer members still attached, their horizontal rings changing to crosses (figs. 181, 182c) and finally to rods just before the completion of the disjunction. The circular space enclosed by the perpendicular ring in these compound tetrads becomes, in the anaphases of the first maturation division, the space between the **V**-shaped daughter chromosomes resulting from division of these bi-tetrads. Since it is the same space as that seen in parasynapsis between the two gaping-apart strands of these compound chromosomes, *we conclude that the first division must be reductional.*

Turning now to the literature involving **V**-chromosomes of these stages (synapsis and reduction), I find figures of prophases that are comparable with what I have here described for Chorthippus. In the lily Grégoire's ('99) figures 6, 8, and 12 resemble my '*j*' stage (fig. 174). His figure 19a is identical with my figures 183a and 183b, and figures 19b and 19c are similar to my 7–11's and 5–9's in figure 181. The result of the division, if continued, would have been an equal-armed **V** going to each pole (his figs. 19b and 19c), each in turn split longitudinally in preparation for the second maturation division (see my figs. 184–186). In Tomopteris (Schreiners, '06a), which has many **V**'s, I find one of the best series of such chromosomes. Their figures 34–36 correspond to my stage '*i*,' figure 38 to '*j*,' and figures 39, 49 to late '*k*' or early '*l*.' Upon examining their figures it will be noticed that the perpendicular ring of the middle region increases at the expense of the more distal portions until there is a breaking through of the short arm and finally of the long arm of the **V** (figs. 53, 56, 57, etc.). Frequently the long arm of the **V** forms a cross at the junction with its mate, similar to that of my figure 183. In the anaphases (figs. 58–60) the **V**'s in their

split condition pass to the poles as usual. I believe the Schreiners, like most of the workers on Amphibia, have frequently shown incorrectly in Tomopteris these compound chromosomes, owing to a misunderstanding of the conditions. The common error is to represent the loops at the junction between the perpendicular (middle) and horizontal (terminal) rings as though they simply crossed ('06a, figs. 34–38), whereas they split and then contribute to each side of the horizontal ring in the manner I have shown for chromosome 7–11 in figures 173a, 174, and 176. In the early stage '*h*' it is not so easy to see the nature of these junctions, but in the '*i*,' '*j*,' and '*k*,' stages the figures of most authors show very clearly that these crossings have been misinterpreted; e.g., Janssens ('05, figs. 58–60) in Batrachoseps, ('01, figs. 8, 9) in *Triton*; Flemming ('87, figs. 3, 4, 7a, 8) and Meves ('96, fig. 50) in Salamandra; Grégoire ('99, figs. 7, 8) in the lily; Atkinson ('99, figs. 1, 2, 3, 4) in Trillium. In the paper by Agar ('11) on Lepidosiren figure 15 shows this stage, though not very clearly.

In Copepoda the chromosomes are so short that one could not expect to find two- and three-ring structures in the prophases and metaphases of the first maturation, such as are found in species with long **V**'s. But short **V**'s and the transverse segmentation are found, as in Chorthippus. This point of segmentation corresponds, I believe, to the apices of the **V**'s of Chorthippus, even though the chromosome may be a rod. The resemblance to my stage '*i*' may be seen in the prophase figures of Lerat ('05, figs. 18, 19, 39). In his figures 27–30 and 40, (early anaphases of the first maturation) the **V** nature of many of these chromosomes is evident in the longitudinal split of their arms. In the first maturation prophases of Matscheck ('10, figs. 37, 62–64, 75, 78) the paired bivalents may be considered to correspond with those of my figures (163–168) of stage '*h*.' In slightly later stages ('*i*,' '*j*') the transverse segmentations on both rods of each bivalent are similar, I believe, to the constrictions on each of the two strands of my compound bivalents (figs. 168, 176). These paired chromosomes, each transversely segmented and longitudinally split, give rise to four similar

longitudinal rods lying side by side in his 'biseriale Anordnung' (see Matscheck's text figs. 10, 11, etc.). Such transversely segmented, four-strand, rod chromosomes of copepods correspond to the transversely segmented **V** compounds of Chorthippus (my figs. 164, 165, 168, 176, etc.). In anaphase the spindle fibers, evidently attached to the constricted part in the middle, make the daughter chromosomes appear **V**-shaped (his text figs. 7, 8), as in Chorthippus. In synapsis they remain in contact longer than the intermediate parts of the chromosomes. I believe, in short, that the "chromosomes in biserial arrangement" (Haecker and Matscheck) are indeed compound chromosomes.

Those investigators of insects who have worked upon species of Stenobothrus and of the Locustidae have found a few of these chromosomes. Stevens ('12) shows for Ceuthophilus two chromosomes (fig. 29) similar to my figure 176, but, as usual, has misrepresented the relation of the middle to the terminal rings at the points of crossing (figs. 30a, 30b). In the metaphase and anaphase (figs. 31–33) there are evidently **V**'s with unequal arms separating from each other. One of them shows the **E**-appearance. In Stenobothrus (Chorthippus) de Sinéty ('01) has shown, but again wrongly interpreted (figs. 122, 123), these compound chromosomes. Compare *b* in his figure 124 with my no. 8–10 chromosome in figure 178; also *a* in figure 125 with my figure 182c. The latter he has illustrated incorrectly, I believe. Davis ('08, fig. 87) gives two chromosomes similar to my no. 7–11 in figure 174. He is, like others, wrong in showing the loops of the middle ring crossing each other rather than passing into each loop of the terminal rings. What I have found in this species (figs. 181–183) is almost identical with his figures 88, 91. The criticisms I have made of Davis's figures applies to those of Gérard ('09, figs. 37–44, S. biguttullus) and of Meek ('11, figs. 10, 11, 14–16, 18; '12, figs. 276–289) in S. viridulus.

In the works of Baumgartner ('04) and Payne ('12) on Gryllidae, which exhibit a large number of **V**-chromosomes, the peculiar perpendicular rings of their metaphases probably result from the separation of the members of **V** pairs. Nowlin ('06) deals in Ceptocycla with many pairs of **V**-shaped chromosomes.

The loops of the 'bouquet-stage' result from the pairing of **V**'s. The points on these which, following Montgomery ('03), she thought were points of junction of homologous chromosomes in telosynapsis, I believe were constrictions at the apices of **V**'s in parasynapsis. In the metaphase her perpendicular rings and **E**-shaped figures are the result of the separation of **V**'s in reduction, as in Chorthippus.

In Amphibia Flemming ('87) figures (fig. 23), I believe, a three-ring chromosome of stage '*j*,' like my no. 7–11 of figure 174. In the first maturation division the majority of his chromosomes (figs. 21–25) are in the perpendicular-ring condition—a late '*k*' or early '*l*' stage (my fig. 183b). Many show the cross-form on the side of the ring which is derived from the longest arms of the **V**'s concerned in making the ring, as in Chorthippus. In anaphases (stage '*l*') of these chromosomes (figs. 26, 28) the **V**'s—unequal-armed, equal-armed, and hook-formed—are each split longitudinally in preparation for the second spermatocyte division. This phenomenon suggested to Flemming the name 'heterotypical' for this division. For Salamandra the Schreiners ('06b) have shown in figures 13 and 14 the '*i*' stage, though it is incorrectly represented with loops crossing; at figures 15 to 20, the '*j*' stage; and at figures 22 to 25, the perpendicular rings in late '*k*' stage, similar to my figures 183a and 183b. In figure 27, at the left, is a perpendicular-ring chromosome with horizontal ring almost identical to my figure 182c.

Montgomery ('03) saw in Amphibia the constriction at the apex of **V**'s in parasynapsis (stage '*h*') similar to my figures 163 to 165, 168, but interpreted this constriction as the point of junction in telosynapsis of two spermatogonial chromosomes. I believe that he wrongly identified this point of constriction with the point of separation between the *distal* ends of the limbs of the **V**'s, which, in the final stages of disjunction, form, as in Chorthippus, the long perpendicular rings of the first maturation, late metaphase. In other words, he thought the point of segmentation at the apex of the **V**'s in parasynapsis was the same as the ends of the limbs of the **V**'s in the metaphase (see his fig. 8). His final results were correct, but his interpretation of the stages

from the 'bouquet' up to the metaphase was wrong. His mistake has caused no little confusion in the work of younger investigators.

With the exception of the workers on copepod material, and of Agar (Lepidosiren), no one thus far cited has shown in the first maturation chromosomes resulting from **V**-type pairs segmentation at the apices of the separating halves of the perpendicular rings, such as may be seen in figures 174 to 183 of Chorthippus. In Lepidosiren Agar ('11, figs. 27, 28, 30; '12, fig. 13b and c) has illustrated this segmentation in his perpendicular rings of the '*j*,' '*k*,' and '*l*,' stages. The **V**'s of Lepidosiren have such short arms, however, that there results from them (when all parts of the pair of **V**'s except the extreme distal ends have gone through the disjoining process) a four-part ring-tetrad, similar to what vom Rath described for Gryllotalpa. We can now understand the peculiar figures which vom Rath gave, for Payne ('12) has shown that in Gryllotalpa there are many **V**'s.

2. Is there pre-reduction or post-reduction in autosome tetrads?

In a former paper (Robertson, '08, on Syrbula admirabilis) I held that an end-to-end synapsis of homologous chromosomes took place, that the first spermatocyte division was a longitudinal division of each of the conjugating members of a pair, and that the second division was the true reduction division. In that work, so far as the actual observations are concerned, I was correct and the observations will stand. My interpretation of the results, however, was incorrect.

In the first place, I did not make a study of the early stages of the spermatocyte, where parasynapsis has been found to take place. My conclusions in favor of telosynapsis were based, I now find, upon what is really the end stage of parasynapsis. I have been forced to the present position by the study of the **V**-chromosomes in Chorthippus in comparison with those of Syrbula acuticornis. The first spermatocyte metaphase (figs. 179, 180) of Chorthippus shows in the compound chromosomes the 7 and 11, the 5 and 9, and the 8 and 10 parts behaving so much like the same (but independent) tetrads in Syrbula (figs.

157, 158), that one cannot avoid believing them identical, though they are compound in one genus and simple in the other. The connections at the apices of the V's, where the spindle fibers become attached, apparently make no difference in the behavior of the rod limbs of the V's in the processes of conjugation and disjunction. The limbs of the 7–11 pair of V's may form rods, crosses, horseshoes, or rings of various sorts just as readily as if they were separate chromosomes. The compound nature of the large chromosomes was evident. Having this in mind, and knowing that in parasynapsis the first parts of chromosomes to pair are the distal ends (in the cases of V's the ends of the limbs), my opinions in regard to the time of reduction were seriously changed when I found the interlocking that I have described and shown in figures 163 and 177. It was then evident to me that the gaping split between the halves in the middle of paired loops was, most likely, the space between chromosomes which had paired. Following this split through the series of prophase chromosomes up to the first maturation division, I found it to be the primary split and therefore the reductional division. In both species of Syrbula the prophase tetrads, consisting of rods, crosses, horseshoes, and rings, appear and behave just like the 5, 7, 8, 9, 10, and 11 parts of the compound chromosomes of Chorthippus. There is good reason to believe that in Syrbula admirabilis, as in Chorthippus, the first maturation division is reductional. I therefore must admit that in my paper on Syrbula I was wrong in regard to the absence of parasynapsis and to the time of reduction, and that, so far as concerns the time of reduction, I shall have to differ with McClung and those of his students who have taken the same stand upon this question.

A second case in which it seems to me that the first maturation division is clearly reductional is that of the single V-chromosome of Jamaicana subguttata (my figs. 198, 199), which separates from its two unequal rod-mates in this division. Spermatogonia of this animal show thirty-two rod-shaped autosomes in addition to one slightly unequal armed V autosome and the large sex chromosome. The first maturation division (fig.

197) has, in addition to the long sex chromosome, fifteen rod tetrads, plus the **V** (14, 14, 16, 16) with limbs double the length of the spermatogonial **V**. This **V** showed considerable inequality in the lengths of its limbs; moreover, there were constrictions (figs. 198, 199) at the middle of each limb, indicating the points at which separation in the last stage of disjunction is about to take place. It is probably a bi-tetrad, for, counting it as such, we get the seventeen tetrads characteristic of the first spermatocyte. Anaphases (Woolsey, '15, figs. 44–47) proved that separation did take place at the points of constriction on the double-length arms of this **V** bi-tetrad. To one pole went a **V** with unequal arms, similar to the spermatogonial **V**; to the other pole went two rods of unequal length, similar to the limbs of the **V** from which they had separated. I can think of no clearer demonstration than this, that, in so far as these chromosomes are concerned, the first division is reductional. The remaining fifteen tetrads behave in all respects similar to the limbs of the bi-tetrad **V** (figs. 195, 198, 199). In view of the fact that this **V** separates from its rod-mates (fig. 199) and that in the two-**V**-chromosome of the first spermatocytes (fig. 201) of another species (J. unicolor) the **V**'s open out into an unequal-sided ring of the same size as the bi-tetrad **V** of the first species (J. subguttata), there is strong reason for believing (1) that the three **V** pairs of Chorthippus likewise divide reductionally in the first maturation division; also (2) that all *perpendicular* rings of first maturation divisions resulting from **V** pairs of chromosomes are of a similar nature, dividing reductionally. Furthermore, since the limbs of the long **V** bi-tetrad (figs. 197–199; Woolsey, '15, figs. 39–43) are similar in every respect to the other tetrads present, I suspect that this division is reductional for all of the pairs of chromosomes in this genus.

A third case that forces me to take sides in favor of pre-reduction is that of the separation in the first maturation division of the members of unequal homologous chromosome pairs, such as I found (Robertson, '15) in one specimen of Tettigidea parvipennis (figs. 115, 120, 122, no. 4's) and in one specimen of Acridium granulatus (figs. 141–147, no. 1's). From a study

of the chromosomes of a large number of individuals belonging to species of both these genera, I became acquainted with the form, the relative length, and the behavior of what appeared to be the normal chromosomes. I was able with little difficulty to distinguish the members of a pair from each other, by means of their length. When an individual was found showing one chromosome in a pair of slightly abnormal length, I was able to determine to which pair of chromosomes it belonged, whether to the 4's, or 1's, etc. This enabled me to trace its course in the maturation division. As a result I found that it separated from its mate in the first spermatocyte division, and divided equationally in the second. On passing to the pole of the first division these abnormal members showed that they were split longitudinally in preparation for the next division (no. 1 in fig. 147), which was equational. The length of the abnormal chromosome in the late metaphase, as the result of the constriction of the tetrad, or in the anaphase after separation from its mate, agreed in each case, when compared with the rest of its fellows, with the length of the chromosome in the diploid divisions. This may be seen by comparing the deficient 4's (4–) in figures 115 and 104 or 105, and likewise by comparing the abnormally long no. 1's in figures 141 to 147 with those in figures 136 to 140.

The above are not the only instances of unequal homologous chromosomes separating from each other at this division. Hartmann (March, 1913) was the first to recognize—in the primary spermatocytes of Schistocerca—what he termed 'unequal divisions' of tetrads. Carrothers later (December, 1913) likewise described a large number of cases of the unequal division of one tetrad among the three smaller pairs of chromosomes in the twenty-three-chromosome grasshoppers Arphia simplex, Dissosteira carolina, and Brachystola magna. There are probably additional divisions of this kind among the larger tetrads of these grasshoppers, but it will be more difficult to recognize them on account of their greater lengths, a slight variation showing less easily in a long chromosome pair than in a short one.

These unequal tetrads behave very much like the tetrads of the two other small pairs of chromosomes of these twenty-three-chromosome grasshoppers. If we may assume specific individuality for the members of each of the twenty-two pairs of autosomes in the subfamilies of this group of grasshoppers, then we may draw the conclusion that the tetrads of at least seven of the eleven pairs of autosomes divide reductionally in the first maturation division. This number is reached by counting Carrothers' ('14) one small pair and the six pairs associated in the **V**'s of Chorthippus, leaving out of the enumeration the **V**'s of Hesperotettix and Mermiria.

A fourth case which supports my contention is that of the multiple **V**-chromosomes of Hesperottetix and Mermiria, just mentioned, which McClung ('05, '14) found to divide reductionally in the first maturation division. In Hesperotettix one **V** occurs in the spermatogonial divisions. One limb of this **V** is the sex chromosome, the other limb an autosome. In the first spermatocyte the rod-mate of the autosomal arm becomes paired with that arm and may be seen separating from the **V** in this division. Something similar occurs in Mermiria, except that there are two autosomes, instead of one in the form of a **V**, associated with the sex chromosome. The autosomal part of this compound probably separates from its autosomal **V** mate in the first maturation division.

From the many instances which I have here given, it seems to me the inference may possibly be drawn that all autosomal tetrads will be found to divide reductionally in the first maturation division.

3. The question of synapsis

1. Is synapsis a fact? Do chromatin elements actually conjugate or otherwise become associated two by two? I am assured of the occurrence of synapsis from the behavior of the **V**-chromosomes of Chorthippus, of Jamaicana and of Hesperotettix, and from the behavior of the unequal homologous chromosomes of Tettigidea parvipennis, Acridium granulatus and other species.

In Chorthippus my conclusion is based in particular upon a comparison of its total chromosome complex, V's and rods, with (1) the total rod series of its nearly related genus, (2) the series of its subfamily, and (3) the series of two related subfamilies. This comparison enables me to locate certain points upon the members of three pairs of chromosomes in Chorthippus, and by that means to identify them in the bivalent chromosomes of the first spermatocyte, at least from the stage which Wilson has termed '*h*' up to and through the two maturation divisions to the spermatids.

I find that all the genera of the subfamily to which Chorthippus belongs, with the exception of a single species, the identity of which is not certain (McClung, '14), have eleven pairs of autosomes. These autosomes, so far as length is concerned may be arranged in three groups: (1) a series of three very short pairs, (2) five intermediate pairs forming a graded series among themselves, and (3) three very long pairs (Robertson, '08, pls. 21, 22; present paper, figs. 148, 157 to 162, 178 to 180, 184 to 192). I find the same number of chromosomes, and to a certain extent, the same size relations in the Oedipodinae and Acridinae. If, therefore, for these three subfamilies of the Acrididae there is such a constant number of chromosomes and also, to a certain extent, of sizes, then it is reasonable to regard each of the eleven pairs of autosomes as a pair of similar individual organs in the cells of every species belonging to the genera of these subfamilies. That established, it is possible to trace these recognizable pairs of autosomes through different genera, whether they be separate, as in Syrbula and most genera, or linked together, as in Chorthippus. Syrbula and Chorthippus are two closely related genera—one has no linkage in its chromosomes, the other has three pairs of V's. As I have explained at pages 235–237, the only conclusion to be drawn, in the case of the V-chromosomes at least, was that during the synapsis period they had paired two by two.

A second line of evidence that synapsis takes place is afforded by the behavior of the V's in Jamaicana, where one individual showed in its first spermatocyte cells a single unequal-armed

V autosome paired with, and separating from, rod-autosome mates (pp. 221–222, 246–247). In germ-cell divisions preceding synapsis the V autosome existed separate from the rod autosomes, but in divisions succeeding synapsis it separated again from them, passing into one-half the spermatids while the rod autosomes passed into the other half. I can think of no clearer evidence than this that synapsis takes place—that chromatin elements actually become associated two by two.

In the unequal homologous chromosome pairs of Tettigidea parvipennis and Acridium granulatus, we have a third line of evidence for synapsis. In one case an abnormal individual was found having a deficient no. 4 chromosome paired with a no. 4 of normal size (figs. 115, 120); in an other case, an abnormally long no. 1 paired with a normal sized no. 1 (figs. 136–147). I find that the members of these unlike pairs in the two individuals exist apart in diploid series (figs. 136–140), together in synapsis in the first spermatocyte of the germ cell generations (figs. 141–143), and that they again separate from each other at the first spermatocyte division (figs. 144–147).

2. Admitting the fact of synapsis, are the conjugating elements chromosomes, and are they individually identical with those of the last diploid or pre-meiotic division? To prove this, one must be able to trace the individual chromosomes from the telophase of the last spermatogonial division to the prophase of the first spermatocyte division. I have not done this in the cases described in this paper. My evidence must, therefore, be indirect.

Giglio-Tos ('08) and Granata ('10) look upon the chromosomes as being not permanent morphological structures, but only temporary formations resulting from chemical processes of some sort. They therefore believe that the individual chromosomes become disintegrated and disappear after the last spermatogonial division, that the chromosomes of the first spermatocyte are formed anew in half the former number, each split twice longitudinally, thus becoming tetrads for the maturation divisions. Meves ('96, '07a), Fick ('07, '08) and Duesberg ('08) likewise believe that the individuality of the spermatogonial chromosomes is lost during this period. According to

their views, there is no such thing as conjugation two-by-two. A continuous spireme is formed anew in the nucleus, and breaks up into half as many segments as there are chromosomes. These segments divide twice longitudinally and are distributed during the two maturation divisions to the spermatids. Both maturation divisions are considered to be equational.

The theory of the Italians cannot be discussed in this connection, since they deny that chromosomes are morphological structures. According to the views of Meves, Fick and Duesberg, it would be hard to explain how, in a nucleus like that of the one-**V**-type individual of Jamaicana subguttata, a continuous spireme could break up into just half the number of segments, one of which is destined to give rise to the peculiar **V**-bi-tetrad (figs. 197–199). This segment in the first place would have to split longitudinally, the daughter threads separating along their whole extent except at the ends (figs. 201, no. 14–16), which would remain in contact up to the beginning of the anaphase. In the meantime, before separation is completed at the ends, one of the daughter threads would have to divide transversely at a point not in the middle of the strand to give segments in length equal to a no. 14 and a no. 16 chromosome (figs. 198, 199). This would have to be repeated accurately in all cells of the first spermatocyte. It is highly improbable that such could occur. The theory fails to explain the phenomenon of reduction in numbers or the formation of this peculiar type of first maturation chromosome.

In the case of the unequal homologous chromosomes of Acridium and Tettigidea, the fact that the members of the pair separate from each other in the first maturation division and are distributed each to only one-half of the germ cells is proof that the zygotes of the next generation will be formed with varying combinations of these chromosomes in their nuclei. It is difficult to imagine a continuous spireme being formed in the growth period of the first spermatocyte which should become divided so accurately that it would give rise to segments of the exact length of these abnormal chromosomes which are characteristic for this particular combination and seem to be present in *all* cells of the

animal resulting from such a combination. At the formation of zygotes, combinations must have been made having, for instance, either an abnormally long no. 1, and a short no. 1 (figs. 136–140, 141–147) or two short no. 1's (the most usual); and, in the case of the no. 4's, one normal and one deficient no. 4, or two normal no. 4's. While such a segmentation must be uniform for every cell division in this animal as a result of Mendelian segregation and recombination, the same chromosomes in the next generation will have to give rise to an entirely different segmented spireme at each division. This cannot be imagined. The same may be said in respect to the **V**'s and their rod-mates in Jamaicana, where we have undoubted evidence of Mendelian segregation and recombination, since in the same species there were individuals having two pairs of rods, and again two rods and one **V**, or in another species two **V**'s. It seems to me that it will have to be admitted by Meves, Duesberg, and others that these abnormal chromosomes persist from one cell division to the next. In order to do this they must remain independent of each other and of the mates with which they pair, for pairing in this case is proved to take place. They must be identical from cell to cell of the same animal, for in the one-**V** type of Jamaicana subguttata every cell, except one-half the second spermatocytes, possessed this **V**-chromosome. The same may be said of any of the other abnormal chromosomes. These chromosomes persist as entities from one cell division to another and especially from the pre-meiotic to the first spermatocyte division; otherwise how can we explain the repeated appearance of such irregularities in so exactly similar a manner in all dividing cells of the animal in which they happen to be?

3. Do they conjugate side by side (parasynapsis, parasyndesis) or end to end (telosynapsis, metasyndesis) or in both ways? The only evidence I have to offer that is of any force in answer to this question is that afforded by the **V**-chromosome compounds in Chorthippus. As has already been shown (pp. 232–234), they give strong evidence in support of the parasynaptic method of conjugation.

4. Does synapsis lead to partial or complete fusion of the conjugating elements to form 'zygosomes' or 'mixochromosomes,' or are they subsequently disjoined by a reduction division? Bonnevie ('06, '08) and Vejdovsky ('07) believe that parasynapsis occurs and that in this process a complete fusion takes place, which is permanent. As a result, a new chromosome is formed, two longitudinal divisions occur, and a four-strand first-maturation chromosome results. Both first and second maturation divisions are simply equational, not reductional. Haecker in his metasyndesis theory holds a somewhat similar view, with this difference, however, that as a result of incomplete (only half as numerous) transverse segmentations of a continuous spireme, previously formed by the union end to end of the chromosome threads, there appears just half the number of segments (reduction), in which homologous spermatogonial chromosomes find themselves united end to end. This union is conceived to be permanent and evidence of it may be seen, according to Haecker, in the transverse segmentation so often visible in chromosomes of the copepods during both first and second maturation divisions as well as in the division of soma cells. Both maturation divisions are, according to Haecker, equational, merely dividing his two-part rods longitudinally into four similar two-part rods to be distributed to the four spermatids. It will be seen that no reduction or segregation in the usual sense of the term occurs. The germ cells, then, all receive the same sort of chromosomes.

In view of our work upon the transversely segmented chromosomes in Chorthippus and Jamaicana, whose segmentation we have found to be due to the usually permanent association of two non-homologous chromosomes, we have many reasons to believe that Haecker has probably been dealing with similar cases of compound chromosome formation. The work of Lerat ('05), Matscheck ('10), Krimmel ('10) and others has shown the presence in copepods of chromosomes in the form of **V**'s with, in many cases, unequal arms, as well as the usual segmented copepod rod, which likewise in some figures has unequal instead of equal segments. These observations agree with mine upon

the **V**'s of Chorthippus and Jamaicana, in which no pairs have arms of equal length. These conditions make it improbable that the **V** is a pair of homologous chromosomes in telosynapsis. It is self-evident, that neither the separation from each other of unequal homologous chromosomes in Tettigidae nor the separation of the **V** from its rod-chromosome mates in Jamaicana subguttata during the first maturation division, can be explained according to Haecker's metasyndesis theory.

In regard to the complete fusion of homologous chromosomes during parasynapsis, as held by Bonnevie and Vejdovsky, I have again some very important evidence in the unequal homologous chromosomes, and likewise in the **V**'s of Jamaicana and Chorthippus. I have discussed in full with figures (Robertson '15, plate 3) in my Studies III the evidence afforded by the unequal pairs. In Chorthippus the interlockings which I have found between the no. 8–10 and 7–11 compounds (fig. 163) and between the 5–9 and 7–11 compounds during the middle and late synapsis periods, together with two cases that have been illustrated by the Schreiners ('06b, figs. 24, 25), furnish strong, though rare, evidence that these pairing chromosomes during the parasynapsis period have maintained their individuality as chromatin threads. I am convinced by my work upon the Tettigidae (Study II) that parasynapsis is a fact in grasshoppers. The three long asymetrically segmented spiremes in Chorthippus, as I have already explained, furnish indirect evidence that parasynapsis must have taken place. If we accept the evidence of the Schreiners and of Janssens, side-to-side pairing probably begins at the distal ends of the limbs of a **V** pair. This takes place, according to them, previous to, or about the time of, the bouquet period and soon after the last spermatogonial division. It is apparently possible that the interlockings between **V** pairs which I have described might have occurred at this time. Following this period of side-to-side approximation, is a period of intimate side-to-side pairing, which passes into a period, the '*g*' stage of Wilson, in which individual spiremes cannot be made out. Yet we find the spiremes coming out of this period in the reduced number and in the same relative sizes as are the auto-

some series of pairs. Now, apparently, after going through all of these stages, these spiremes exhibit interlockings between pairs of **V**'s, such as the Schreiners and I have described; interlockings which I believe must have been made at the beginning of parasynapsis. This to my mind is of significance, and means that these pairing chromosomes probably maintain their individual identity while passing though these stages, and that there is probably not so intimate a fusion of them as to necessarily result in loss of continuity as a thread.

Further evidence that parasynapsis probably does not result in complete fusion of the pairing chromosomes can be drawn from the **V**-rod pairs of Jamaicana subguttata, providing we assume parasynapsis to have taken place in this double pair (figs. 197–199; also Woolsey, '15, figs. 37–46). If we make this assumption, then in the process of disjunction the proximal ends of the rod-mates have evidently rotated away from the proximal region (apex) of their **V** mate until each of the rods has come into line with its respective limb of the **V**, as is shown in most of the figures (fig. 37 especially). All division figures found in which this **V** bi-tetrad could be studied gave distinct proof that the length of the no. 16 rod corresponded with the length of the no. 16 limb of the **V**, and the length of the no. 14 likewise with its limb of the **V**. In all such divisions this long bi-tetrad **V** with segmented limbs was the only form in which the body appeared. This is evidence to my mind that these rods in separating from their respective limbs of the **V** have separated along the plane in which the side-to-side pairing took place. Otherwise, if a complete fusion of these rods with the limbs of the **V** had taken place with possibly splitting in a new plane, there would have resulted a variety of forms of this compound body ranging from the long bi-tetrad **V** form we have here to an elongated unequal sided ring, such as is found to be constant for the species Jamaicana unicolor (fig. 201; Woolsey, '15, figs. 65–67). The constancy with which this **V** separates from its rod-mates in unmodified form is strong though indirect evidence that parasynapsis, if it occurred, was not as complete a fusion as Bonnevie and Vejdovsky would maintain.

4. On the chiasmatype of Janssens

In the first spermatocyte chromosomes of Syrbula and Chorthippus (figs. 150, nos. 6, 8, 11; 152a; 156b; 174, 7–11; 176; 178) I have bodies similar to those of Triton and Batrachoseps upon whose structure Janssens ('09) bases his 'theory of the chiasmatype.' Morgan ('13, '14) has made much use of this theory in explaining the failure of the linkage of characters usually coupled together in transmission to offspring. Janssens used it to furnish a basis in the germ cells to account for the occurrence of a larger number of allelmorphs than there are pairs of chromosomes by which they may be borne.

According to this theory the chromosomes which pair side by side in synapsis twist about each other in an irregular spiral manner on coming out of this stage. Before the members of a pair separate each may be seen to be split longitudinally, so that the tetrad is made up of four longitudinal strands. Janssens has noted strands crossing over from one conjugant chromosome to the other (his text, fig. XXII) and upon the basis of this observation concludes that when such paired chromosomes later complete their disjunction they represent combinations different from those present before synapsis due to the establishment secondarily of these 'cross-over' connections.

If Janssens assumes that the breaking and secondary fusion of those crossed-filaments nearest each other (text figs. XIII–XV) takes place after the chromosome has reached the stage represented by his figures 1 to 13 (pl. I) etc. (stage '*h*' or '*i*' of Wilson), I believe that he has been mistaken in his interpretation of the form of the chromosome (text fig. XI) upon which he has based his theory, but if he believes this secondary fusion takes place much earlier, following the amphitene and preceding the pachytene stage, then I have little to say. As will be seen from his figures (text figs. I, IX, XI, XXI, XXVII), he believes that the chromosomes conjugating side by side (each split longitudinally) should normally cross each other entire, i.e., with both filaments, at the nodes (N, text fig. I). He finds, however, that instead of both filaments of a segment

(portion of a conjugant between the nodes) crossing over together to the next segment, only one may cross (text figs. XII, XXII). This he assumes to mean that a single original filament (longitudinal half of a conjugant) of each chromosome has broken at the point of their crossing (text fig. XIII) and that broken ends of one filament have traded connections with the broken ends of the other (text figs. XIII–XV, XXII, XXVII). That it is unnecessary to assume this, is shown by the fact that we are able to trace all steps in the formation of such 'cross-overs' in tetrads of the ring and cross type back to the stage in which the tetrad consists of a rod split in two longitudinal planes, and consisting of four longitudinal filaments lying side by side (figs. 150–156, 164–168, 173–178). The crossing over of filaments results from the tendency of the four-strand rod to split part of the time in the primary plane (*I*), and part of the time in the plane at right angles to it, the secondary plane (*II*). If the chromosome be short, but one cross-over occurs and 'a cross' results (nos. 6 and 8, fig. 150; fig. 156c); if the chromosome be long, two, or, as in the compound chromosomes of Chorthippus, even three cross-overs may occur (figs. 150, 10's and 11's; 155, 6's, 9's, 10's and 11's; 156d–156f; 174, 7–11's, 5–9's, 8–10's; 175, 176, and 178, 8–10's, 7–11's). This formation of the cross-overs as a result of the opening-out process of the four strands does away with the possibility of a "compénétration graduelle de deux chromosomes au niveau d'un chiasma avec la soudure des filaments qui se touchent les premiers," as Janssens has supposed according to his text figures XIII–XV.

Many investigators who have worked upon species in which there occurred tetrads resulting from these long **V** chromosomes (Janssens, '05 among others) have misinterpreted their form, representing them as two spirals twisting about each other (Janssens's text fig. 1, page 391, or Davis's, '08, figure 87), rather than in the way I have shown them in figures 156f, 174 (7–11's and 8–10's) and 176. In like manner, when dealing with shorter chromosomes which give crosses (my figs. 150, 6's and 8's; and '08, figs. 29c, 29h) and simple rings having at one point on the circle (sometimes an additional pair at the opposite point)

a pair of proximal knobs or arms (my figs. 156d, 156e; '08, figs. 29b, 29f, fig. 30, no. 11, fig. 32, nos. 7 and 9), these investigators have represented them as crossing each other in the manner of Janssens's text figure XXI for crosses, or as Davis ('08) has represented at figures 179, 180 for the simple knobbed rings. In some cases I admit that a free crossing resulting from a twisting of the chromosomes, rings, etc., may have occurred, but I am certain, especially in the case of the long chromosomes of Stenobothrus, that many of these so pictured crossings do not occur, and that the chromosomes have been misrepresented in illustrations (e.g., Davis, '08, figs. 86, 87, 183–186; Meek, '11, figs. 10, 14–16, 18; '12, figs. 276–279; de Sinéty, '01; Gerard, '09).

I do not believe that the breaking and secondary fusion of crossing filaments which Janssens has postulated can take place after, or at the time of, stage '*h*.' If they take place at all, it must be in the zygotene or pachytene stage, when the pairing threads twist about each other more or less intimately and for a time appear fused. That such breaking and secondary fusion as he postulates occurs, I am not quite ready to admit, in view of the evidence to the contrary given by the unequal homologous chromosomes of Acridium and Tettigidea ('4s in figs. 115, 120, 122, and 1's in figs. 141–147) and by the V-rod tetrad of Jamaicana (figs. 197–199). In Tettigidae I am certain (Studies II) that parasynapsis takes place. Now, if there be such a fusion as Janssens says occurs in the early strepsitene stage, we should except to have irregularities in the lengths of the exconjugating chromosomes shown at the late metaphase and anaphase of the first maturation division (4's in figs. 115, 120, 122 and 1's and 1's in figs. 141–147). There is, however, no visible variation in the relative length of these separating chromosomes. This matter I have taken up also in Study III.

Something similar may be said of the V in Jamaicana, which, if we assume that parasynapsis occurs, we have every reason to believe must be paired with two rods (nos. 14 and no. 16) during such a stage as the pachytene or strepsitene. If fusions take place of the type Janssens supposes, we should expect the occurrence of irregularities in the form of the exconjugating mem-

bers of such a pair, but apparently no irregularities do occur. The **V** travels to one pole and its rod-mates to the opposite pole. They separate in the form they had on entering the pairing process. However, this is not contending that there is no possibility of a break at the apex of the **V** member of this bi-tetrad and a relinkage of one limb of the **V** with one of the free rods or with a limb of an opposite **V**. If such occurred, it would, of course, be a 'crossing over' carrying a large group of factors.

I wish to call attention to some of the peculiar mitosis figures which Janssens gives in support of his theory. The gaping apart of the distal ends of halves of exconjugants, which be believes to be abnormal (text fig. XXIII, XXIV and figs. 40, 41a, 41b, 47, 48, 50–52), is in reality not unusual for chromosomes of the Tettigidae and Acrididae. The twistings shown in anaphases, such as his figures 17, 18, 24, 30, 31, may be explained as the result of misfortune in the prophase. Frequently I find such a chromosome as figure 17 in various prophase periods from late '*i*' up to the metaphase in the same condition, the only difference being in the degree of condensation. In stages '*h*' and '*i*,' when such a chromosome is in the long-spireme condition, split into four strands and coming out of disjunction, it is to be expected that the four strands composing it will get twisted into all sorts of positions before turgidity (rigidity) sets in as a result of the condensation process. That, however, it seems to me is no argument for the breaking and re-fusing of any two of these filaments. I have similar chromosomes in no. 11 of figure 155b and 7–11 in figure 175.

But my chromosomes 5–9 in figure 178 cannot be explained as the result of a twisting in the disjunction process. Janssens has shown in his figure 14 a chromosome of the same nature. His chiasma-type theory, it seems to me, fails to explain the persistence of such twistings. It seems to me that this might be explained more readily if the splitting of the conjugating chromosomes and a twisting were to occur in each conjugant before side-to-side pairing takes place. Such might be expected in compound chromosomes of the **V** type in which pairing possibly begins simultaneously at the distal ends of both limbs of the

V's. It might also be imagined that only the ends of such split compound chromosomes should conjugate and not the mid-regions. That such *pre*synapsis splitting is possible, we are led to suppose from the reports of Dehorne ('11) and Schneider ('10) in somatic mitoses and Brunelli ('10, '11) in last spermatogonial mitoses, who found that the telophase chromosomes on their way to the poles show longitudinal splitting. Before I knew of any of these works (thus eliminating the chance of error by suggestion), I had found similar conditions in the anaphases of both somatic cells and the last spermatogonial divisions in the Tettigidae. My conclusions from the Tettigidae are, that these spermatogonial chromosomes on entering synapsis are already split. This may be seen, in each of the chromosomes of cells where the full diploid number exists. Before synapsis the split disappears. The twelve autosomal spiremes, pairing two by two, are seen to form six threads. Now, if this be the case it seems to me that we can explain such conditions as Janssens has shown in figure 14 and I in figure 178, no. 9, where one conjugant before conjugating with its mate seems to have twisted, once in mine and several times in his. In my opinion Janssens's chiasmatype theory does not explain satisfactorily this phenomenon, while that of a *presynapsis splitting* does.

This theory appears to me based upon an unnecessary and incorrect interpretation of the first spermatocyte chromosomes. It fails to explain all of the phenomena of twisting in these chromosomes, and there is some evidence to show that it probably could not occur. Until the theory can be established upon a more firm basis cytologically, we are not justified in accepting it unreservedly in our study of problems of heredity.

5. Linkage as shown in V*-chromosomes—a basis for coupling and repulsion*

Such linkage of chromosomes as Chorthippus reveals when compared with Syrbula and as the species of Jamaicana, more especially J. subguttata, show, furnishes a second possibility

of accounting for some of the phenomena of coupling and repulsion and the deviations from this, i.e., failures of linkage. Janssens's ('09) theory of the chiasmatype is the first explanation that has been offered. Phenomena of coupling and repulsion have been observed by Bateson and Punnett ('11), Correns, Baur, Emerson, East, Trow, and especially by Morgan and his students in their bred Drosophila ampelophila. In their experiments the last mentioned authors have found that certain groups of characters, usually carried together, occasionally become broken into two groups. A specific case is afforded by the results obtained when a gray, red-eyed female is crossed with a yellow, white-eyed male (Morgan '13, p. 88). The factors for gray body and red eye are usually carried together with the sex determining chromosome, their allelomorph yellow body and white eye likewise in a sex chromosome. The offspring in F_1 are all gray-bodied and red-eyed in both sexes. In the F_2 generation the expected results, assuming for the moment free interchange of the factors for gray and yellow body and for red and white eye, would be 4GR ♀ : 1GR ♂ : 1GW ♂ : 1YR ♂ : 1YW ♂. But this ratio is not realized. The results obtained are 170GR ♀ :84GR ♂ : 1GW ♂ :1YR ♂ :84WY ♂, which show that there is a tendency for the factors that entered together, gray body and red eye, and yellow body and white eye, to remain together. By these numbers in F_2 it may be seen that coupling was not complete but failed in the proportion of 1:84, in other words the chances are 84:1 that the factors entering together will remain together. Now, it seems possible that such a small departure from normal coupling as 1:84 might be explained by an occasional break in the **V** sex chromosome at the apex. Stevens ('08, figs. 61, 65–73) gives two **V**-shaped sex chromosomes, one a normal **V** and the other carrying attached to its apex a rod-shaped element, the nature of which is not clear. That **V**'s may be formed by the fusion of non-homologous rods by their proximal ends and also that rods may be formed by the breaking of a **V** at its proximal end, the apex, is to be inferred from the presence of a **V** and its rod-mates in one and the same individual (figs. 196–199). The same may reasonably be expected

to occur in Drosophila ampelophila. Is it not possible that the extra rod-like appendage to the apex of one of the V sex chromosomes described by Miss Stevens may be a rod segment of some V that had previously broken at the apex?

Besides these sex-linked factors, Morgan has found "other factors to cross over to various degrees; in the extreme cases the chance is one to one that they cross over." Metz has shown for Drosophila ampelophila two pairs of V-shaped chromosomes in addition to two rod-shaped and two *M*-chromosomes. While he has not shown variation from this configuration in D. ampelophila, he has shown it in other species of the genus, where it is perfectly clear that either one pair of V's may be broken up into two pairs of rods, or, similarly, both pairs of V's, making four pairs of rods. While he has not shown a single V alternating with a pair of rods, as occurs in Jamaicana subguttata, I feel reasonably certain that it will be found. It seems likely that a strain could be built up, having either all rods, as in the all-rod type of J. subguttata, or all V's, as in J. unicolor. I also believe that breaks in the V's may occur at any time and that varying degrees of this tendency to break might exist, ranging from the condition in those compound V's where no break seems to occur, such as we find true of all species of the genus Chorthippus (Stenobothrus), to that where only occasional linkage occurs, as in Chortophaga (McClung '14), or merely irregular association, as in the members of the 14 and 16 pairs in two specimens of Jamaicana flava (compare A, nos. 14 and 16, in Woolsey '15, figs. 1–4 with 5–8). From a comparison of such V's, I think it reasonable to suppose that races might be built up in a species with V's of any grade in respect to this tendency to break. Such, again, might form a basis for the varying degrees of crossovers Morgan obtained in coupling factors.

6. The chromosomes: a mechanism furnishing a basis for variation, heredity and evolution?

The observations presented in this paper seem to be but additional links in the chain of evidence going to show that in

the chromosomes we have structures sufficient in many respects to serve as a morphological basis for the phenomena of heredity, variation and evolution.

In the first place there is a number which may be considered fundamental and constant, not only for all the cells of an individual but likewise of the individuals of a species, the species of a genus, the genera of a subfamily and, if they are sufficiently closely related, even the subfamilies of a family, as may be seen in the Truxalinae, Oedipodinae, and Acridiinae, three of the four subfamilies of the Acrididae or better in the subfamilies of the Tettigidae. In the family Tettigidae, with the exception of three specimens,[5] I have found this number to be 13 (♂) and 14 (♀) for the genera I have so far examined: Choriphyllum (one species) Nomotettix (one species), Acridium (four species), Paratettix (two species), and Tettigidea (two species)

This number I found in all cells, both germ and somatic; in the testis, spermatogonia and first spermatocytes, in the hypodermis, the integument, the proctodeum, the mid-intestine, 'fat body,' muscle tissue, the follicular walls of the gonads (♂ and ♀). In the 'fat body' two cells were seen which showed instead of the usual number (13) the double number (26). This, however, may be the result of failure of the cytoplasm to divide. I have no hesitation therefore in saying that the numbers fundamental for the family Tettigidae are 13 (♂) and 14 (♀), i.e., six pairs of autosomes plus the sex chromosomes.

In the three subfamilies of the Acrididae (Truxalinae, Oedipodinae, Acridinae), over forty genera (McClung '14) so far examined have been found to possess with three exceptions twenty-three chromosomes. The exceptions are in the genus Chorthippus (Stenobothrus), where in five species seventeen chromosomes have been reported, and in material from an unidentified specimen described by McClung ('14, figs. 59–76) as having twenty-one. My work upon Chorthippus curtipennis

[5] The three exceptions were one individual (♂) in which there occurred a deficient supernumerary sex chromosome, and two others (♂ and ♀) in which there seemed to be the one-and-one-half equivalent of supernumerary no. 1. chromosome attached to a normal no. 1 (figs. 136 to 147 and my Studies III).

shows that probably twelve of the twenty-three chromosomes have fused to form the six **V**'s which are always present. If we admit that this may have occurred, the number continues to be twenty-three for this as for other genera. The case described by McClung seems to be an exception I cannot explain. A third exception is that described by Montgomery in 1906 in Syrbula acuticornis, where the number was reported as varying from twenty to twenty-four. This, however, may have been a mistake, since I have shown in the present paper that this species may have twenty-three. For these three subfamilies of the Acrididae, the Truxalinae, Oedipodinae and Acridiinae, the fundamental number therefore seems to be twenty-three.

The phenomenon of linking as shown in the compound **V**-chromosomes of Chorthippus leads us to suspect that fundamental numbers will probably be found for the subfamilies of the Gryllidae and the Locustidae also, where **V**'s are known frequently to be present. A start in this direction has been made for the Locustidae, in the genus Jamaicana, as described by Woolsey ('15) and in this paper. Similar conditions have been found by Metz ('14) for the Diptera in the species of Drosophila. It is to be expected, I believe, that a great deal of the variation in chromosome numbers among nearly related species may be ascribed to this cause.

As the number of the chromosomes is, within certain limits, constant, so too are their sizes. It seems that no group of species or of genera so far studied presents such unmistakable evidence in constancy of size gradations as do the genera of the Tettigidae. There may readily be seen in all cells of the body, both somatic and germinal, a series of relative sizes constant for the six pairs of autosomes and for the single (♂) or paired (♀) sex chromosomes. These size gradations are constant for the individuals of a species and, with slight variation, for the species of a genus; likewise, with somewhat greater variations, for the genera of a family. Of the autosomes there may be recognized two very small pairs, two intermediate ones and two extremely large ones. The two pairs within each of these three groups may in turn be distinguished by slight difference

in size. These size gradations are so dependable that one may follow without difficulty any chromosome pair he chooses through the cells of all of the species and genera I have so far studied. If I see the whole series or, in some cases, even a part of it, I can recognize a no. 6 or a no. 4, for example, as such. An idea of the degree of constancy may be obtained by following any chromosome through the figures from 23 to 147. In Protenor belfragii Wilson ('05) was able to recognize in all cells only the two largest and the two smallest pairs of chromosomes. In the Tettigidae it is possible to recognize every one of the series of six autosome pairs as well as the sex pair.

In the Acrididae[3] again size gradations are recognizable with a considerable precision, as may be seen in the species of Stenobothrus (Meek, '12), Syrbula (Robertson, '08), Melanoplus (Nowlin, '08) and numerous other genera. There may always be readily recognized three small pairs and three large ones with a graded series of intermediates. The sex chromosome ranks from eighth to tenth in the series of twelve pairs. With the exception of the three largest and three smallest pairs and the sex chromosome, it is impossible to trace very definitely individual chromosomes through these three subfamilies unless the chromosomes happen to be in some way linked together as in Chorthippus.

Such constant size gradations recognizable in both germ and somatic cells is evidence against the theory of King ('08) and Haecker ('11) that size gradations are the result of unequally rapid development or growth. The occurrence of these size gradations in somatic cells is also an answer to Haecker's ('11) criticism that such gradations have not been found outside of germ cells.

As in number and in size, so in their behavior, the members of a series of chromosomes are constant to a greater or less degree. In the Tettigidae all spermatogonial, somatic and second-spermatocyte chromosomes are straight rods, pointed at the proximal, and rounded at the distal end. In the prophase and metaphase no rings like those in the Acrididae (Syrbula, fig. 157, no. 10) have thus far been found. There seems to be a

predominating tendency for the four-strand tetrads to divide throughout a large part of their length along the plane of the primary split (*I*), the division beginning at the proximal end, and the halves remaining attached at the distal ends. There results the dumb-bell shaped rods (figs. 29–31, 73–77, etc.) of the late prophase and the metaphase. Frequently in the longer chromosomes of Tettigidea there is a tendency for a tetrad simultaneously to split also from the distal end along the plane of the second division, so that there is formed a cross with unequal arms (figs. 94–99, 112–114), the transverse arms being short, even mere knobs. For the Tettigidae the characteristic form of prophase tetrads in tetrads formed from shorter chromosome pairs is the dumb-bell rod, and in tetrads from longer chromosomes it is the cross with very short transverse arms.

In the species of the subfamilies having twenty-three chromosomes, there is a prevailing tendency in the pure straight-rod type for the longer and intermediate chromosome tetrads to split widely along the plane of the secondary division. If this begins at the distal end and extends almost to the proximal end the result is the **V**-tetrad (fig. 157, no. 10, and Robertson, '08, plate 21, chromosomes 4, 6, 8); if it does not begin at the distal end, but at a point just proximal to it, and extends as before nearly to the proximal end, there results a horizontal ring (11 in fig. 157 and Robertson, '08, plate 21, chromosomes 7, 9–12); or, in the case of the intermediate chromosome pairs, if the widening of the primary split, beginning at the proximal end, is equal to that of the secondary beginning at the distal end, a cross tetrad results. The three smallest tetrads usually form dumb-bell shaped tetrads, as in Tettigidae (Robertson, '08, plate 21, chromosomes 1–3). Chromosomes of the ring-**V**-tetrad-, and cross-type are characteristic for these subfamilies, while those of the dumb-bell-, rod-, and unequal-armed cross-type are characteristic for the Tettigidae. The behavior of tetrads in producing these forms is not such a constant characteristic, however, as is number or size. This may be seen in my chromosome table ('08, plate 21). While there is a tendency to produce tetrads of a certain form, rings for instance, in no. 10,

that tetrad does not always do so, as may be seen in cells 5 and 6 of this table.

While the behavior of chromosomes in forming tetrads is not always constant, as Moore ('06) and Baumgartner ('04) believed, but only tends that way; their behavior, on the contrary, in either forming or refusing to form certain associations resulting in compound chromosomes seems to be constant in some cases (Jamaicana subguttata), only for the individual, in others (Drosophila ampelophila) for the species or in still others (Chorthippus, Syrbula, Hesperotettix, Mermiria) for the genus. In Chorthippus curtipennis, for example, there are present in all individuals of the species so far examined three pairs of **V**'s. These pairs of **V**'s may be distinguished and recognized by the relative lengths of the two arms, which differ enough to enable one to recognize the **V**'s individually, not only in all cells of this species, but—judging from figure 6 of Meek ('12b) and those of Gerard and of Davis—in other species of the genus as well. The lengths of these arms in Chorthippus are almost identical with the relative lengths of the nos. 5, 7, 8, 9, 10, and 11 chromosomes in Syrbula, a nearly related genus, in which no **V**'s are formed. The behavior of these pairs, so far as our knowledge goes, is therefore constant within one genus (Chorthippus) in forming **V**'s, and in another genus (Syrbula) in not forming **V**'s. The same may be said of the sex chromosome and the particular autosome with which it forms a compound (**V**-chromosome) in the species of Hesperotettix, when compared with their behavior in failing to do so in the majority of other genera. Likewise in Mermiria, and especially in the four large pairs of rod chromosomes in Drosophila, as Metz has shown, where in one type of species they remain independent rods, in another type two pairs of the rods unite to form a pair of **V**'s, while in a third type the four pairs of rods unite to form two pairs of **V**'s.

Individual, or at least genetic, continuity and specificity is shown in chromosomes that are traceable. In the Tettigidae the fact that we may trace and recognize any particular pair of autosomes from the no. 1's to the no. 6's, as well as the sex

chromosome, in any cell of the body, and not only for the cells of an individual or a species but even in the different species of a genus and in different genera and subfamilies (though they may have suffered considerable modification), is evidence to my mind that in these structures we are dealing with at least genetically continuous bodies. The same may be said in regard to the V-compound chromosomes of Chorthippus. Here we evidently have six pairs of rod chromosomes, so linking as to form three pairs of V's which may be recognized individually in all cells; for spermatogonia in the diploid relation; for first spermatocytes in the pairing relation in all stages of synapsis from stage '*i*' on to and through the metaphases, and (in disjunction) in the anaphases; and again in the haploid relation in the second spermatocytes and spermatids. This habit of association or linking in the case of these six particular pairs of autosomes is the individually continuous relation which is surprising. In the majority of genera it does not occur, at least not for all six of these pairs of autosomes, but here in a number of species occurring widely distributed in both Europe and America, which systematists have, upon the basis of similarity in external body characters, grouped into a single genus, this habit of association between members of these six particular pairs is constant. This signifies to my mind that there must be more than a genetic continuity; there must be an individual continuity of each specific V-chromosome through the spireme stage from cell division to cell division, for it does not seem likely that the connecting substance in the achromatic bridge between two particular rod chromosomes in the case of each V would be dissolved in a telophase only to be formed again at the next prophase.

If the interlocking which I have figured and described (fig. 163) and the Schreiners ('06b, figs. 24, 25) have likewise illustrated is to be taken into consideration, then we have again very definite evidence not of genetic but of individual continuity through the stages of the first spermatocyte nucleus, where most doubt prevails as to the persistence of the continuity of the chromatin thread.

Again the one-**V**-type individual of Jamaicana has an important bearing on the subject of individual continuity. Here in the same animal one member of each of the pairs 14 and 16 exists as a separate rod in every cell, while the mates of these exist in the same cells linked together. Whether the chromosome in the ancestral species was a **V** or two rods, I cannot say. If the ancestral chromosome was a **V**, then a break has occurred at some time and this break has been handed down generation after generation. On the other hand if a fusion has occurred at some time, then the fusion condition has been handed down. Whichever hypothesis we adopt, this much seems certain, that the thread in the case of the **V** retains its identity from cell to cell and likewise in the case of the rods. If we argue for a fusion of the rods to form the single **V** at each prophase, how can there exist in the same cell homologous rods which do not form **V**'s? This to me is an argument against the 'manouvre hypothesis' of Fick, viz., that chromosomes represent tactical formations produced anew in the cell, and the somewhat similar hypotheses advanced by Meves, Giglio-Tos and Granata.

It seems to me that further strong arguments in favor of the individual continuity of the chromosome thread are the deficient no. 4 of Tettigidea (figs. 104, 110, 115, 119, 120, 122 and Study III) and the no. 1's of Acridium (figs. 136–147, and Study III). Here we have in these animals every cell in the body, both germ and somatic, showing in the one case the defective no. 4 chromosome, in the other case the abnormally long no. 1. That these chromosomes were probably present at the fertilization of the egg, is shown in the first case by their presence in every cell of the body and in the second case by their being distributed as units to half the second spermatocytes. This is also reinforced by the fact that the same abnormal long chromosome has in all probability been found in both male and female animals. That these chromosomes are abnormal, I think no one who reads the description of them will doubt. Now, in the case of the defective no. 4, all cells in division showed it to be of constant relative size. The same may be said of the long no. 1 of Acridium; not only is it true for all cells of one

animal, but likewise for those of another individual, a female taken at the same time and from the same spot as the male. Both chromosomes were probably handed down from preceding generations. The behavior of this chromosome, it seems to me, argues for the persistence of individual continuity in the chromatin thread from cell to cell. Otherwise, how could the constancy of size be maintained, especially in the case of the defective chromosome?

These again are arguments opposed to the views of Haecker ('11) and King ('08) that the differing sizes of the chromosomes are due to unequal growth. If their theory be correct, why these permanent abnormalities in size?

It seems to me that these abnormal chromosomes are even more conclusive arguments in favor of continuity than the behavior of the supernumerary chromosomes, for in the latter we have more or less independent bodies in the cell—in the former, abnormal bodies linked up in one case with a chromosome which we can readily recognize in the cell. We also have the advantage in Tettigidae that we may there recognize all of the chromosomes individually.

Specificity of chromosomes is so closely bound up with individuality and genetic continuity that it is not necessary to discuss it at length. Montgomery has pointed out that specificity of function is at least implied in the permanent size differences in so far as amount of chromatin is concerned, a large chromosome having more with which to maintain a function than a small chromosome. Another case of specificity of chromosomes is shown in the tendency of one pair (no. 4's) to precede the other autosomes in condensation, and also that of at least one member of this pair to associate with the sex chromosome in the first spermatocytes of Syrbula and Chorthippus (figs. 149, 150, 155, 163–165, 168–170, 171–174, 178–180). Another case that might be cited is the occurrence of the **V** and its rod-mates in Jamaicana unicolor (figs. 196–199) within the same cell. This might be cited as exhibiting not only a difference from the rest of the chromosomes in forming **V**'s, but likewise a difference in speci-

ficity between members of the same pairs. The same may be said of the no. 4's in the deficient no. 4 tetrad.

And now it seems to me that in the foregoing data on constancy in number, size and behavior, and in the evidence for genetic—and in some cases individual—continuity of the chromosomes, we have, especially in the Tettigidae, proof of the presence in the germ cells of a structure sufficiently stable and continuous to furnish a physical basis for heredity. Again, this structure, while sufficiently stable to account for heredity, the relationship of species, genera, etc., has evidently been plastic enough to allow of variation in the past sufficient to account for what we find characteristic of at least two subfamilies of the Tettigidae, the Batrachidinae and Tettiginae, and of the genera within these, when compared with each other, and of the respective species of the genera, in so far as we are able to see.

The family Tettigidae itself in its thirteen-chromosome trait is distinctly and clearly marked off from the subfamilies Truxalinae, Oedipodinae and Acridinae of the Acrididae in their twenty-three chromosome trait. This degree of difference, as I have already pointed out, is paralleled in the somatic characters, both internal and external. The degree of difference in relative length of chromosomes between the genus Tettigidea, of the subfamily Batrachidinae, and the two genera Paratettix and Acridium of the Tettiginae is greater than is the difference between the genera Paratettix and Acridium themselves. This may be seen in the tables (I–XX). Among the species of Acridium the same phenomenon may be seen, though to a much less degree. As we descend to the species, the differences between nearly related ones are so little that it is practically impossible to detect them.

The variations I have described are found existing today, permanent for a number of organisms which systematists have grouped into families, subfamilies, genera, and in some cases species. Whether any one of these three genera of the family Tettigidae represents the more ancestral genus of the family, I am not ready to say. This may be determined later. Suffice it to say that from the evidence displayed in the series of chromo-

somes, descent by variation from a common ancestral series of chromosomes may certainly be inferred, and the degrees of variation shown in these chromosomes is paralleled by the degrees of variation exhibited by somatic structures, which systematists have made use of in showing the relationship of species, genera, subfamilies, etc.

Variations which have occurred in the Acrididae and which seem to be of a permanent nature are the fusion of non-homologous autosomes to form compound chromosomes as in the species of the genus Chorthippus. That these are variations is to be inferred from the fact that about nine-tenths of the genera of the twenty-three-chromosome grasshoppers do not possess these **V**'s, while in one-tenth, and especially this one genus Chorthippus, the species so far described (5) all show this variation. It is interesting to note that it occurs in both the American and the European species of the genus. In Hesperotettix McClung ('05) has described a somewhat similar occurrence, though here the sex chromosome is concerned. The variation is constant for all species of the genus that have been examined. Likewise in the genus Mermiria McClung ('05, '14) has described associations similar to Hesperotettix but in which *two* autosomes seem to be linked up permanently with the sex autosome.

In Jamaicana we have a third case of such chromosome variation, which, however, is peculiar in that two variations, each apparently permanent, exist side by side within the same animal, as the compound **V** paired with its rod-mates seems to show. The associated rods evidently remain together through spermatogonial and first and second spermatocyte generations, and are found even in somatic cells, while their rod-mates remain separate. This case is of great importance for it shows that chromosome variations characteristic of two classes of individual animals may exist side by side within the same cell, apparently independent of each other, conditions we should expect to find in the cells of hybrid animals.

These, it seems to me, are permanent variations of a fundamental type; but in addition to these, I have described in the

present paper and in Studies III a class of variations that seem to be of an abnormal type, which, as I have pointed out in Study III, are also probably of a permanent nature. One of these (figs. 136–147) is probably to be placed in the class of 'supernumerary chromosomes.' Up to this time the supernumerary chromosomes described have been either extra sex chromosomes or chromosomes in some way partaking of the properties of sex chromosomes in that they are usually condensed. Here we probably have in the $1\frac{1}{2}$-valent portion of the large abnormal chromosome 1 the remains of supernumerary no. 1's strung out in a row (compound-supernumerary). Just what relation to variation they may have, it is difficult to imagine. A more important representative of this abnormal class for matters of variation, it seems, is the deficient no. 4, whose measurement (Studies III) shows it clearly to be about four-fifths the length of its mate, which has the size normal for the halves of the pair in the species. In such a chromosome we have the basis for the dropping of unit factors from the germ plasm. This, I think, might explain those characters which are evidently due to the lack of something, such as pigment or its producer in albino animals, and come under the class of 'loss' unit characters. But such sorts of variations (mutation) are not, it would appear, to be classed with variations which mark off species from each other, such for instance as distinguish Acridium granulatus from A. obscurus. They are, instead, to be classed as minor variations occurring within a species and possibly of little use in the production of new species. It is not possible to consider them normal, for it might be a question whether a race having such could be permanent until at least some additional compensating variation occurred to supply what is lacking. Possibly there may be some connection in this respect between compound-supernumerary autosomes (1) of one pair and the deficient autosomes of another pair.

Our conclusion is that in the chromosomes of the germ cells variations *have occurred*, as shown by taxonomic relations, and *may again occur*, as shown by deficient and compound-super-

numary chromosomes, and that according to all indications they are *permanent.*

The fact that three genera of Tettigidae show the same general plan of chromosome structure leads us to suppose that within each of these three genera we might look for the same general sort of variations, such as could be dealt with by the Mendelian law. Nabours ('14), in his work upon the inheritance of color markings in Paratettix, has shown that their behavior conforms to this law in one of these genera. He finds nine pure strains showing distinct color patterns, and in addition to this eighteen heterozygous patterns from combinations of these pure strains. It is a striking fact that in collecting specimens of three other genera, Acridium, Nomotettix and Tettigidea, I have found many of the same markings. All of these genera have individuals showing the white spot on the large femora which Nabours has described in his Paratettix punctofemorata (fig. D, plate VI). The spot varies slightly in shape and orientation, but nevertheless it is a white spot on the same region of the rear leg. Likewise I have found all four genera to have individuals with a white band across the thorax, such as he has described in his leucothorax variety (fig. C, plate XI) and as Hancock ('02) has shown for Acridium (Tettix) in the fourth specimen of his figure 1, page 9. I have also found in all four genera the leuconotus variety shown by Nabours at B, plate VI, and by Hancock in figure 1, specimen 6. The variety with a median stripe of the shape of that shown at E (Nabour's fig. VI), but white instead of yellow, I have found in all four genera. Hancock has also pictured this variety for Acridium in his figure 1. The gray variety carrying small patterns of black, like A of Nabours and the first specimen of figure 1 in Hancock, is probably the most common of all patterns in all of the genera.

The genera Nomotettix, Acridium and Paratettix belong to the same subfamily (Tettiginae), while Tettigidea belongs to an entirely distinct subfamily, the Batrachidinae. The germ-cell structure shows Tettigidea to be farther removed from the other three genera than they are from one another. Basing my opinion upon a knowledge of germ cells alone, I should expect to find in

this genus the *same* minor variation (such as Nabours has worked out), but *considerably modified* from the condition found in the three more closely related genera. This seems to be the case in regard to at least the 'punctofemorata,' 'leuconotus' and 'lineatus' characters. Such characters are present in Tettigidea, but apparently widely different from what they are in any of the other three genera.

It appears to me that in the varying behavior of the chromosomes among the genera of this subfamily we have a splendid opportunity, by repeating on other species and genera the work of Nabours, to find out something of the workings of the chromosomes in respect at least to minor, non-vital variations, such as these seem to be.

The chromosome studies which I here present were begun at the University of Kansas in 1908 under the direction of Prof. C. E. McClung. A part of my material was collected at Lawrence, Kans., and also in the course of zoological collecting trips on which he was kind enough to send me to Arizona, Texas, and Puget Sound, Washington. The studies were continued at Harvard University from October, 1909, to June, 1912 under the direction of Prof. E. L. Mark. I am indebted to both of these men, to Professor McClung for starting me upon the work and for his kindly interest afterward, and to Professor Mark for his helpful criticism and guidance and for the encouragement he gave me during the time when the bulk of the work was being done.

April 28, 1915.

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EXPLANATION OF PLATES

All figures except those on the first three plates are reproduced at the same scale. The drawings were outlined with an Abbé camera lucida at a magnification of 3900 diameters, obtained with a Leitz 1/12 homogeneous immersion objective and a Zeiss 18 × compensating ocular with draw-tube set at 150 mm. and drawing made at the level of the base of the microscope. Having been reduced one-third in the reproduction, they now show a magnification of 2600 diameters.

ang.hum., humeral angle
ang.p., posterior angle.
apr.prc., apical process of pronotum
c., chromatoid body
cap., head
car.m., median carina
car.vrt., carina of vertex
cav., cavity of intestine
cla.cl.i., (by mistake for) *cta. chi.*
cl.apx., apical cell
cl.tis.co'nt., connective-tissue cell
coe.ga., gastric coecum
coln., colon
con., cone-like body
cta.chi., chitinous cuticle
cul.crc., circular ridges
cys., cyst of testis
dk., darkly stained material
dst., distal
ely., elytron
fem.a., femur of anterior pair of legs
fis., split
foll., follicles
gl.rt., rectal glands
iglv., crop
il., ilium
lob.l., lateral lobe of pronotum
lob.su'oc., supra-ocular lobe
mat.1., first maturation division
mat.2, second maturation division
ms'thx., mesothorax
mu.lg., longitudinal muscle of intestine
nll., nucleolus
occ., occiput
oes., oesophagus
par.cys., cyst wall
par.foll., follicular wall
par.nl., nuclear wall

pli.al., wing folded
pro'nt., pronotum
pro'nt.a., anterior margin of pronotum
prx., proximal
pullv., pulvillus
rt., rectum
seg.tar., segments of tarsus
sn.p., posterior, or elytral, sinus
sn.if., inferior sinus
sp'cy., cyst of first spermatocyte generation
sp'd., cyst of spermatid
sp'go^{7}., cyst of 7th generation spermatogonia
sp'go^{8}., cyst of 8th generation spermatogonia
sp'go.^{9}*pr.*, primary spermatogonia
sp'go.scd., secondary spermatogonia
spi.t., terminal spines of tarsus
sp'zo., cyst of spermatozoa
tb.Mpg., Malpighian tubule
te., testes
tib., tibia
v., ventriculus
va. df., vas deferens
vrt., vertex
x,x., proximal ends of chromosome
x, sex chromosome
I., primary split of chromosome
II., secondary split of chromosome
1, abnormal no. 1 chromosome

PLATE 1

EXPLANATION OF FIGURES

1 to 5b, 9a, 9b are from Hancock ('02). Figure 6 is from Otto Lugger's 'The Orthoptera of Minnesota.' 7 and 8 are from J. McNeill's 'Truxalinae of North America.'

1a, 1b Acridium granulatus Scudd. Female.
2a, 2b Acridium obscurus Hanc. Female.
3a, 3b, and 3c Acridium granulatus Scudd.
3c Lateral view of tarsus of A. granulatus.
4a, 4b Acridium incurvatus Hanc.
5a, 5b Paratettix texanus Hanc.
6 Paratettix cucculatus Burm.
7 Syrbula acuticornis Bruner, male, lateral view.
8 Syrbula acuticornis Bruner, dorsal view.
9a, 9b Tettigidea jalapa Hanc, male.

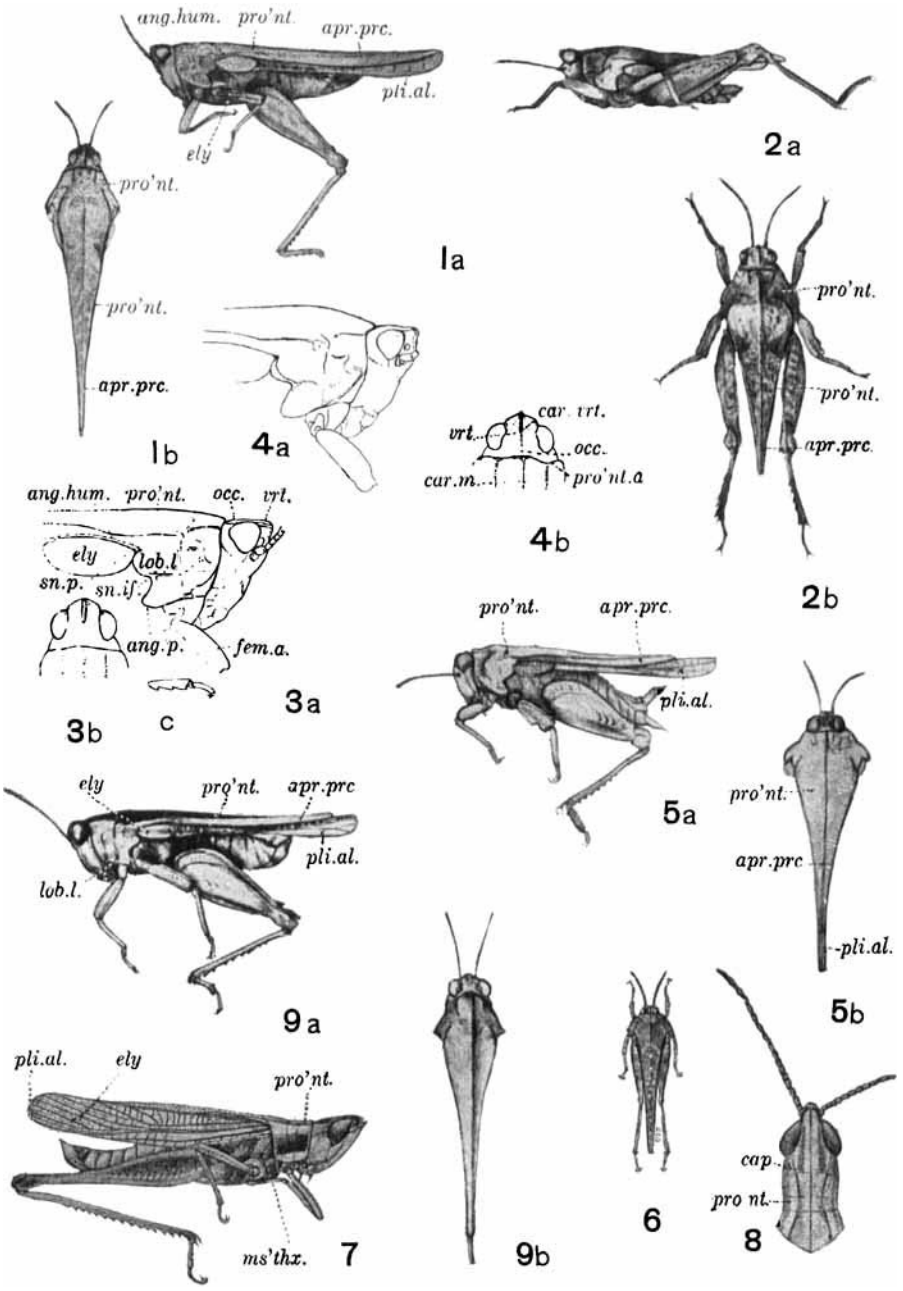

ang.hum.
pro'nt.
apr.prc.
pli.al.
ely
1a
2a
pro'nt.
apr.prc.
1b
4a
car. vrt.
vrt.
occ.
car.m.
pro'nt.a
4b
pro'nt.
apr.prc.
2b
ang.hum.
pro'nt.
occ.
vrt.
ely
lob.l.
sn.p.
sn.if.
ang.p.
fem.a.
3a
3b
c
pro'nt.
apr.prc.
pli.al.
5a
ely
pro'nt.
apr.prc
pli.al.
lob.l.
9a
pro'nt.
apr.prc
pli.al.
5b
pli.al.
ely
pro'nt.
ms'thx.
7
9b
6
cap.
pro nt.
8

PLATE 2

EXPLANATION OF FIGURES

10, 11, 13a and 13b are from Hancock ('02). Figures 14 and 18 are from Snodgrass's 'Anatomy of the Carolina Locust.' Figure 15 is after Packard.

10 Tettigidea parvipennis pennata Morse. Female; dorsal view of head.

11 Tettigidea parvipennis Morse, female.

12a, 12b Foot of a tettigidaean, lateral and ventral views, respectively.

13a Paratettix cucculatus Morse. Dorsal view of head of male.

13b Paratettix cucculatus Morse. Same of female.

14 Dissosteira carolina Linnaeus.

15 Melanoplus femur rubrum. After Packard.

16a, 16b Foot of above species. Ventral and lateral views, respectively.

17 Alimentary canal of Tettigidea.

18 Alimentary canal of Dissosteira carolina.

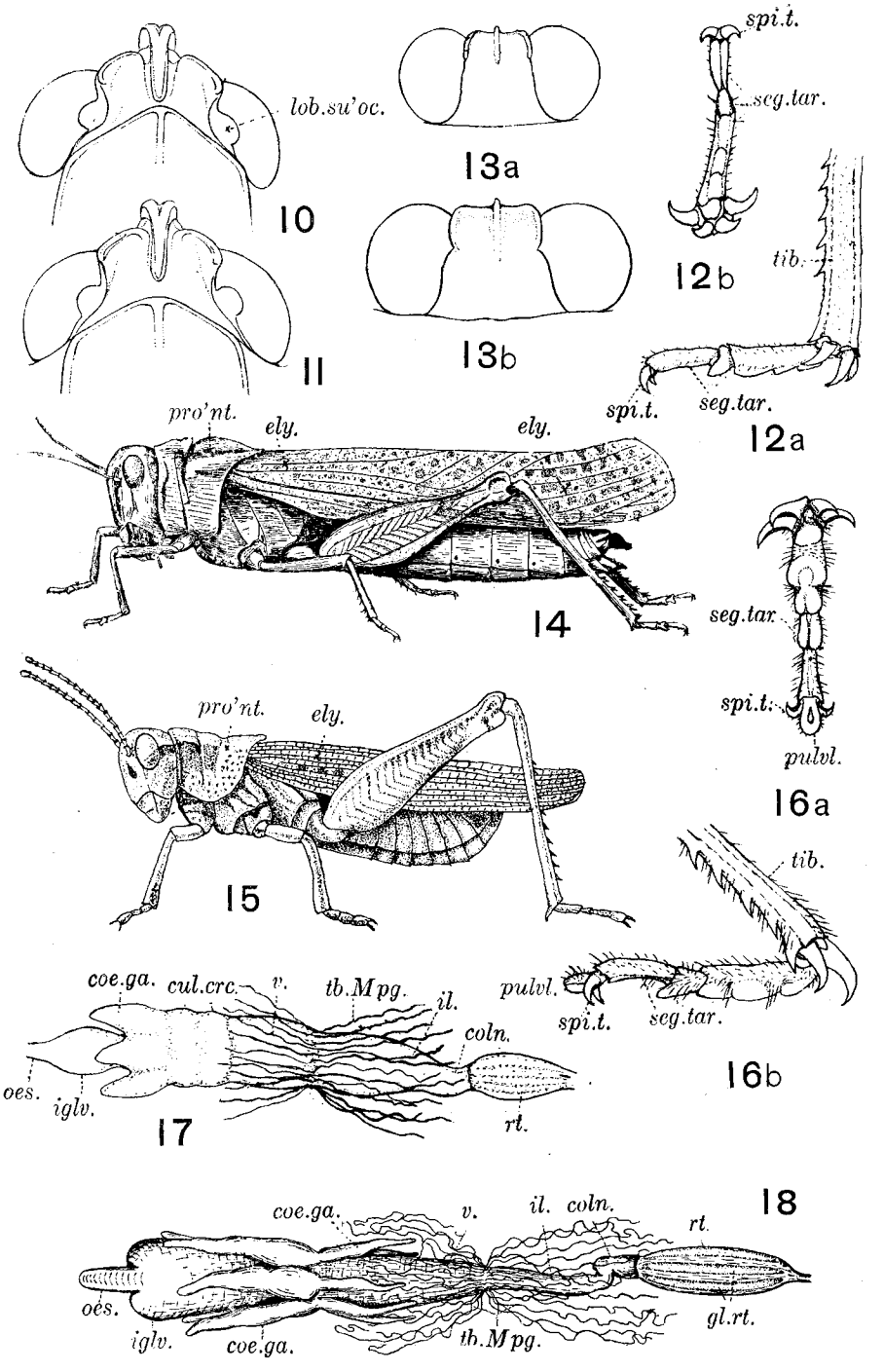

lob.su'oc.
10
11
13a
13b
spi.t.
seg.tar.
12b
tib.
spi.t.
seg.tar.
12a
pro'nt.
ely.
ely.
14
seg.tar.
spi.t.
pulvl.
16a
pro'nt.
ely.
15
tib.
pulvl.
spi.t.
seg.tar.
16b
coe.ga.
cul.crc.
v.
tb.Mpg.
il.
coln.
oes.
iglv.
rt.
17
coe.ga.
v.
il.
coln.
rt.
18
oes.
iglv.
coe.ga.
th.Mpg.
gl.rt.

PLATE 3

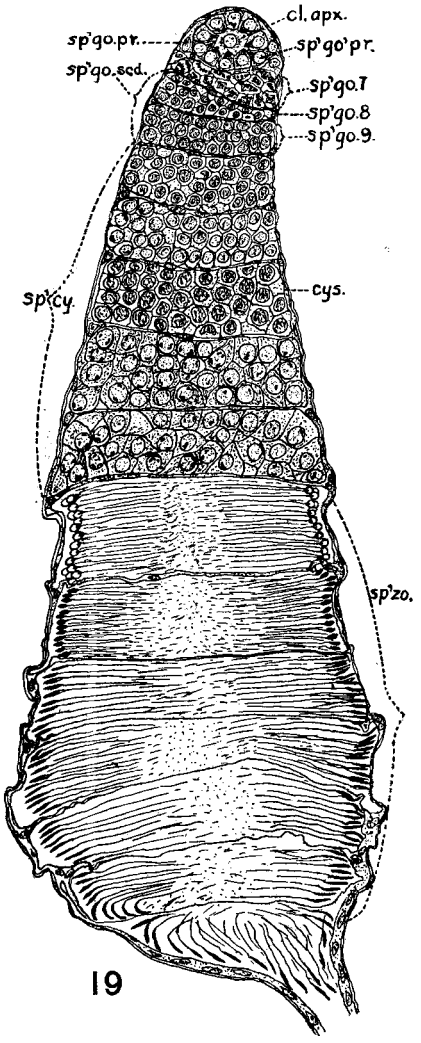
EXPLANATION OF FIGURES

19 Longitudinal section of follicle of testis from Acridium granulatus. A cyst of the seventh generation secondary spermatogonia (*sp'go. 7*) contains 64 cells; one of the eighth generation secondary spermatogonia (*sp'go. 8*), 128 cells; cysts of the first spermatocyte generation (*sp'cy.*), 256 cells each; and cysts of spermatozoa (*sp'zo.*), 1024 cells each.

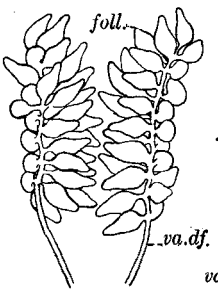
20 Longitudinal section of follicle of testis of Dissosteria carolina. After Davis ('08).

21 Testis of Acridium.

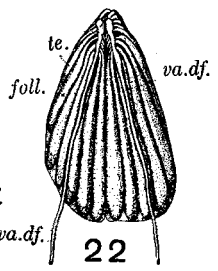
22 Testis of Dissosteira carolina. From Snodgrass's 'Anatomy of the Carolina Locust.'


cl. apx.
sp'go.pr.
sp'go.sec.
sp'go.pr.
sp'go.7
sp'go.8
sp'go.9
sp'cy.
cys.
sp'zo.

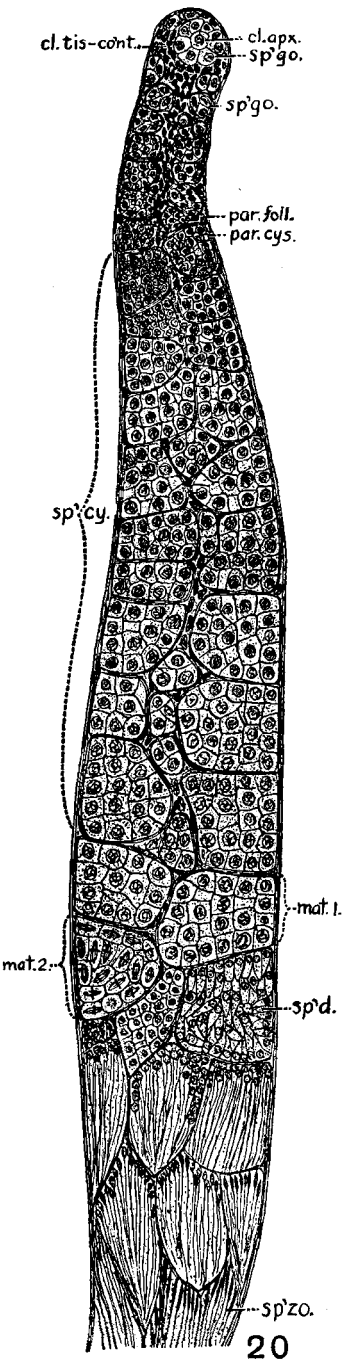
19


foll.
va.df.

21


te.
foll.
va.df.
va.df.

22


cl. tis-cont.
cl. apx.
sp'go.
sp'go.
par. foll.
par. cys.
sp'cy.
mat. 1.
mat. 2.
sp'd.
sp'zo.

20

PLATE 4

EXPLANATION OF FIGURES

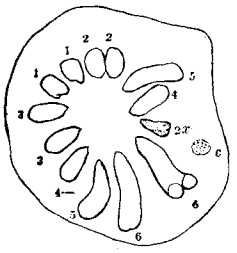
23 to 58 Acridium granulatus Scudd.

23 Secondary spermatogonium from young cyst. Only chromosomes and cell boundary shown. Ordinary chromosomes numbered according to size from 1 to 6. Sex chromosome, 2 x, ranks second in the series between ordinary chromosomes nos. 1 and 2. The number 2, preceding x, indicates this rank. It stains lightly. The deficiency of one no. 4 chromosome (4−) is shown by the minus sign (−) following the no. Sex chromosome lightly stained.

24, 25, 27, 28 Spermatogonia from various animals. Sex chromosomes ($2x$) faintly stained and 'wooly.' Deficient no. 4 in figure 27.

26a, b, c, d 'Wooly' sex chromosomes from different spermatogonial metaphases.

29 to 34 First spermatocyte divisions. Members of pairs in each case are separating from each other. The sex chromosome ($2x$) goes to one pole ahead of the others.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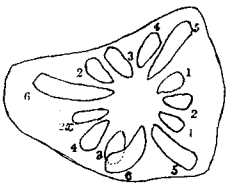
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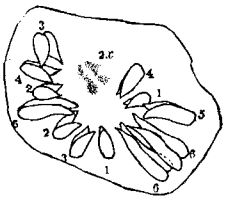
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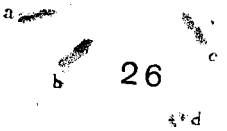
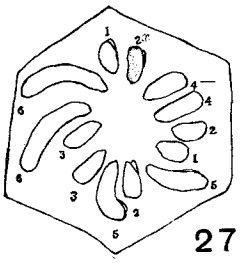

a
b
c
d
26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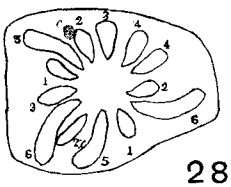
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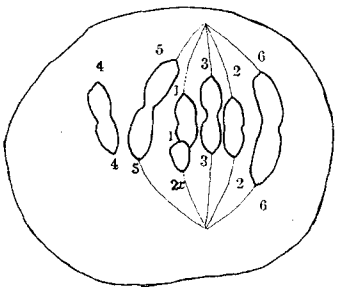
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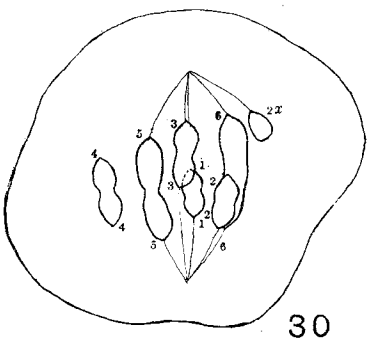
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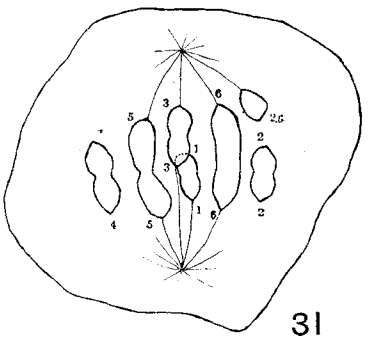
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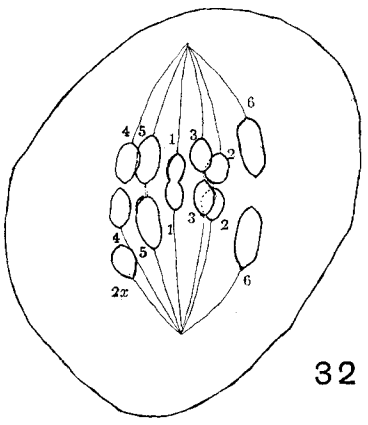
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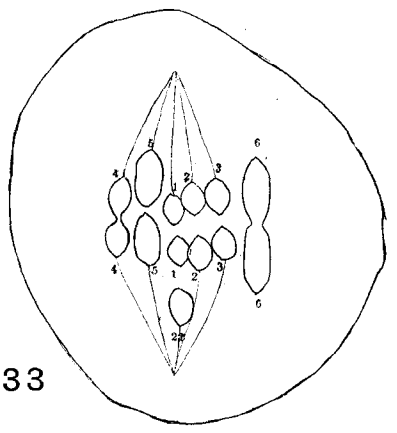

33

PLATE 5

EXPLANATION OF FIGURES

(Acridium granulatus)

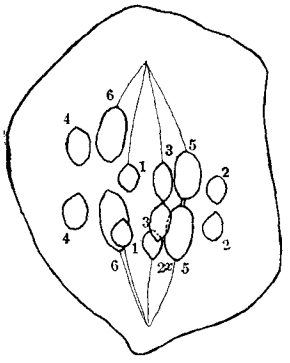
34, 35, 36 Polar views of the same stages as figures 29 to 31. The chromosomes differ in diameter.

37, 38 Second-spermatocyte metaphases, polar views, one containing and one lacking the sex chromosome ($2x$).

39 Intestinal epithelium, mesenteron. The no. 5's are relatively smaller here.

40 Intestinal epithelium, mesenteron.

41 From proctodeal region of intestine, near base of the epithelium.



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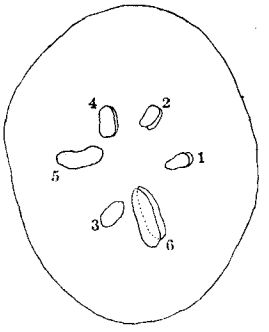

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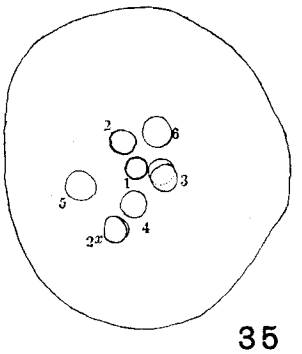

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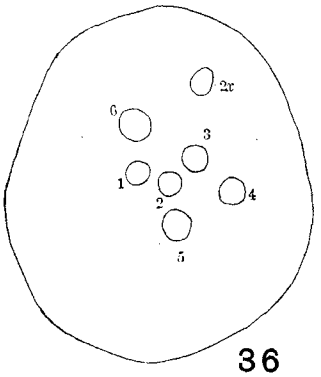

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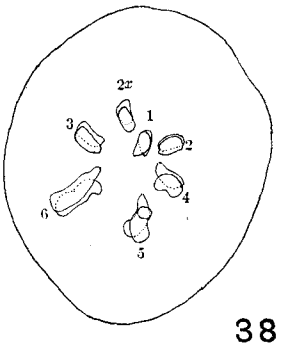

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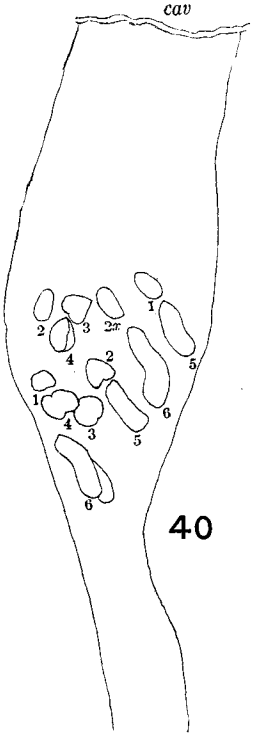

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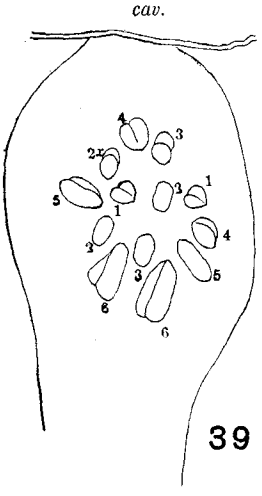

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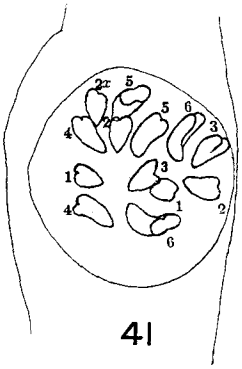


41

PLATE 6

EXPLANATION OF FIGURES

(Acridium granulatus)

42 Proctodeal cell from same animal as figure 23. Deficient no. 4.

43 Proctodeal cell.

44 From the hypodermis. Contains many pigment granules.

45 Hypodermis.

46 Giant cell from 'fat body.' Twenty-six chromosomes.

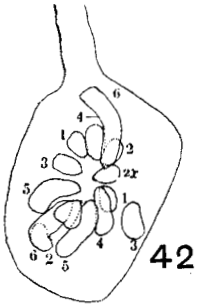
47 Hypodermis cell.

48a and b Proctodeal or connective-tissue cell in contact with muscular coat of intestine.

49 From the 'fat body.'

50a and b From hypodermis.

51 to 54 From female. Ovarian follicle cells. Fourteen chromosomes in each. The two sex chromosomes ($2x$) may be recognized by their looser, more faintly stained character. A precocious synapsis of the no. 1's in figure 51.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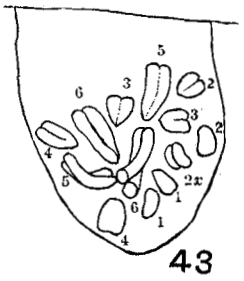
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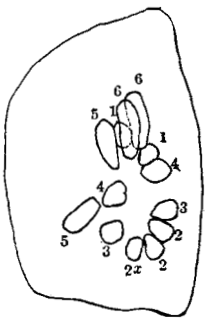
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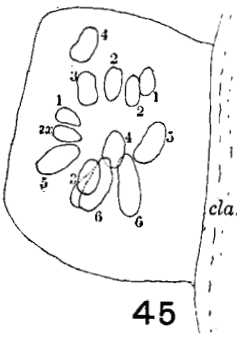
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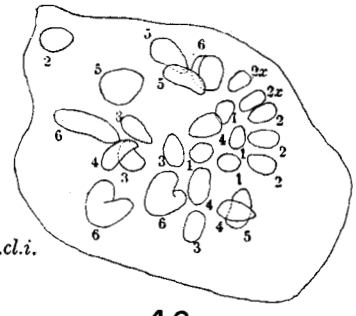
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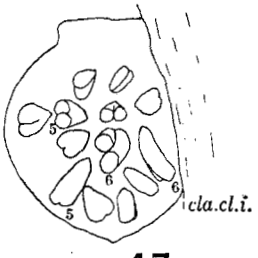
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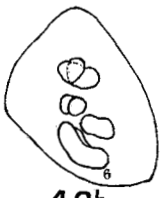
48a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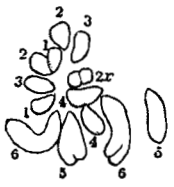
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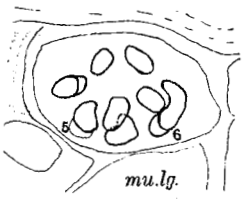
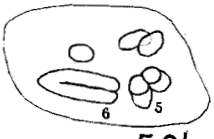

mu.lg.
50a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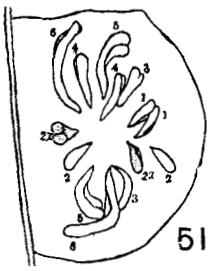
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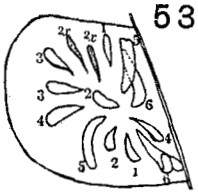
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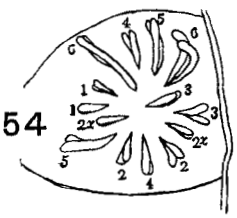

54

PLATE 7

EXPLANATION OF FIGURES

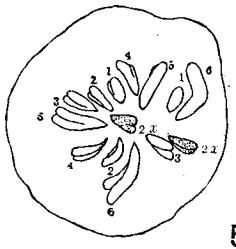
55 to 58 Acridium granulatus. Ovarian follicle cells, continued. Sex chromosomes 'woolly' (fig. 58) and loose in much decolorized cells.

59 to 64 Acridium incurvatus Hanc.

59, 60 From wall of follicle of testis.

61 to 64 First spermatocytes, late prophase. One small pair (no. 2) is stubby, the other is long and slender. In figure 61 the no. 1x has been drawn out of its normal position. In figure 63 nos. 4, 5, and 2 have been treated similarly. 1x is seen in end view in figure 63.

65, 66 Acridium ornatus Harris. Prophase of first spermatocyte.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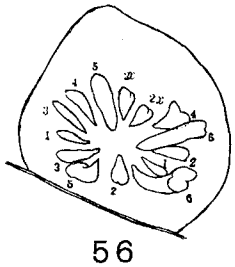
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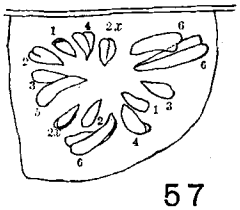
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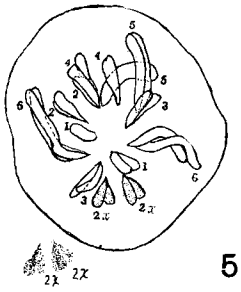
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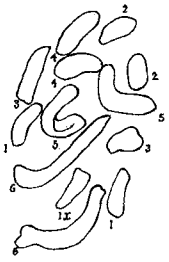
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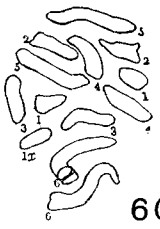
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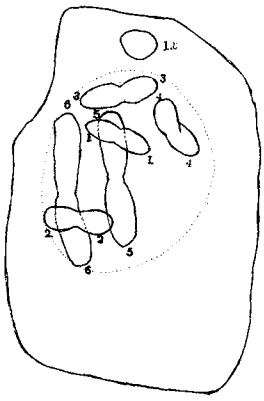
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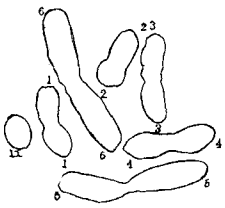
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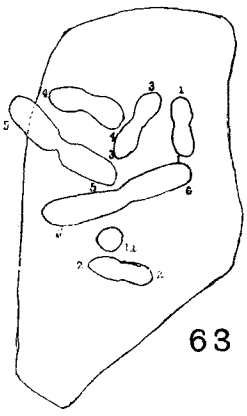
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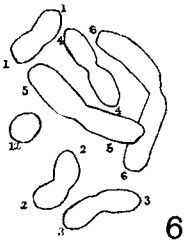
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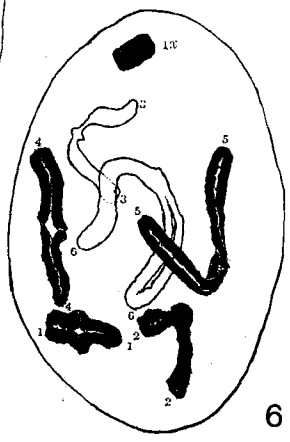
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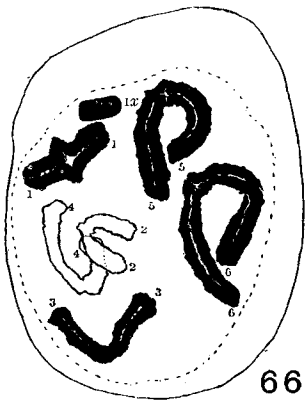

66

PLATE 8

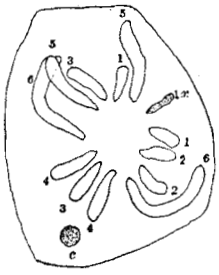
EXPLANATION OF FIGURES

67 to 77 Acridium obscurus Hanc.

67, 68 Spermatogonial cells. Sex chromosome faintly stained. Autosomes black. Chromatoid body (*c*) not always present.

69 to 71 Prophase of first spermatocyte. Homologous chromosomes in synapsis by distal ends only. *con.*, probably a fragment of a chromosome.

72 to 75 First spermatocytes in division. *con.*, split in figures 72 and 73, possibly attempting to divide.



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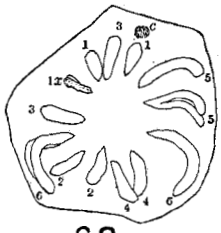

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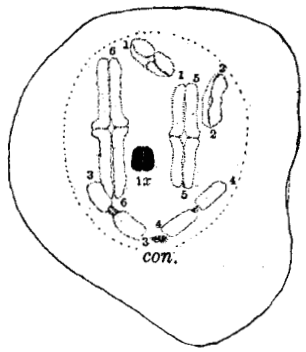

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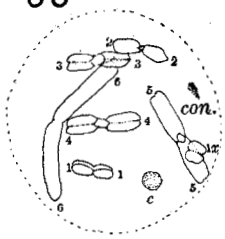

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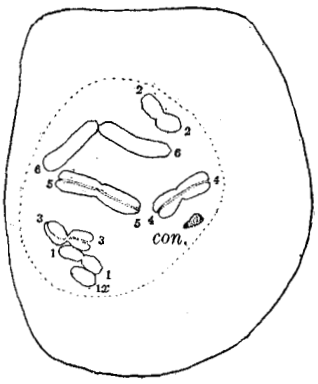

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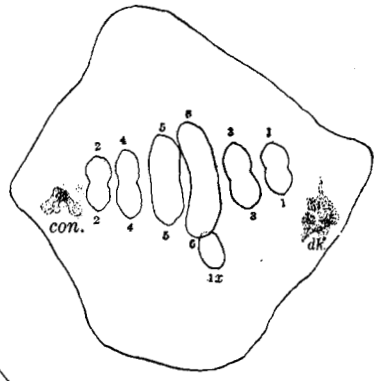

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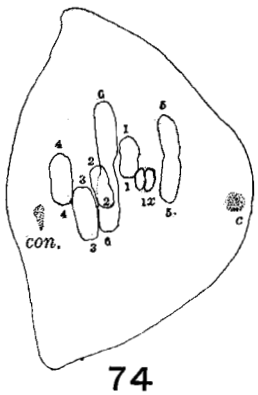

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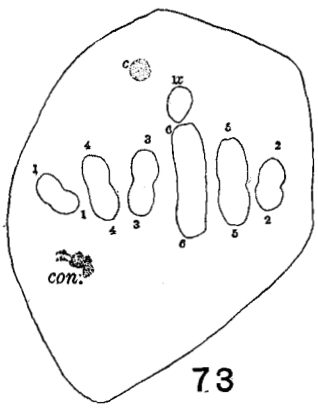

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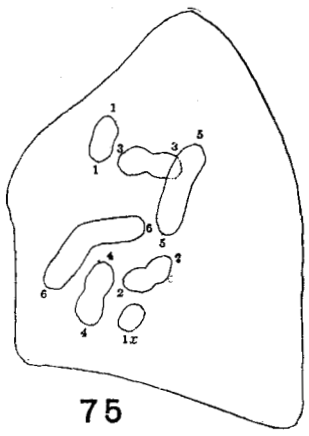


75

PLATE 9

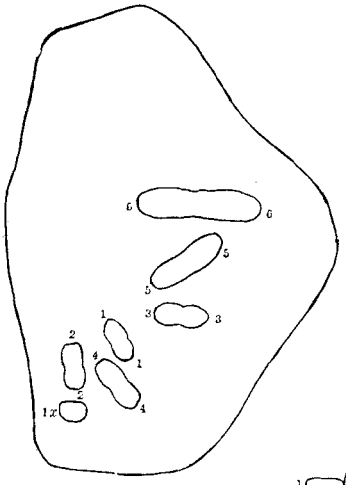
EXPLANATION OF FIGURES

76 and 77 A. obscurus. Late stage of first spermatocytes.

78 to 84 Paratettix cucculatus Morse.

78 to 82 Spermatogonial cells. Sex chromosome ($3x$) is 'wooly,' as usual. In figure 81 the 6's and one no. 5 are foreshortened. Figure 82 is from a cyst of dividing cells which contained an apical cell in the center.

83 First spermatocyte division.



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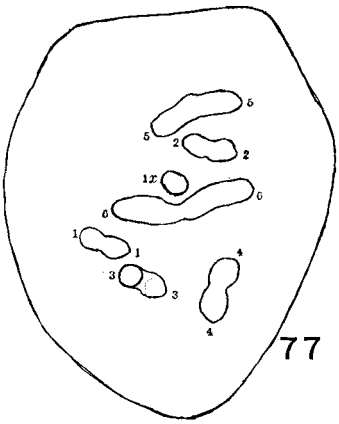

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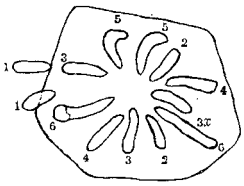

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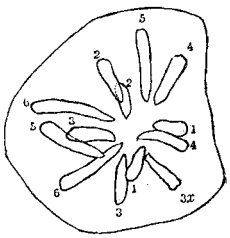

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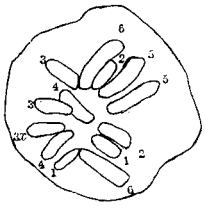

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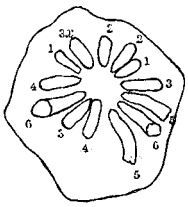

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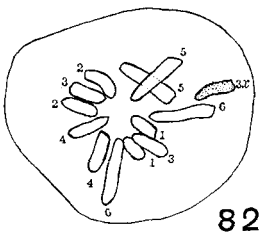

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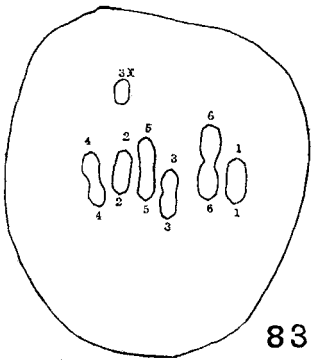


83

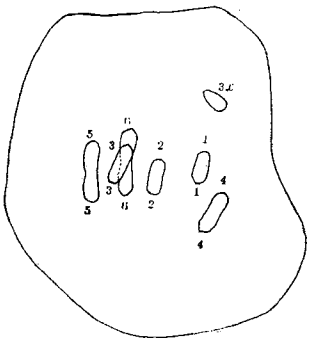
PLATE 10

EXPLANATION OF FIGURES

84 P. cucculatus. First spermatocyte.

85 to 89 Paratettix texanus Hanc. First spermatocyte division.

90 P. texanus. Second spermatocyte metaphase showing relative size of all chromosomes.



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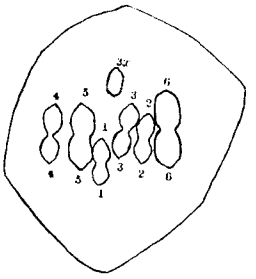

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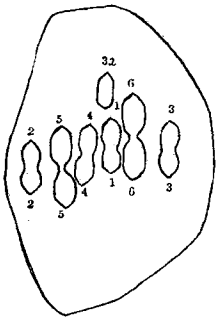

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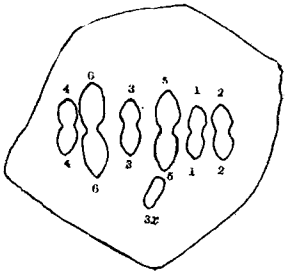

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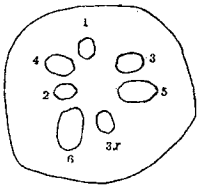

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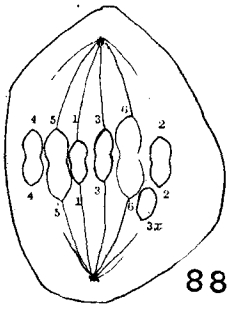

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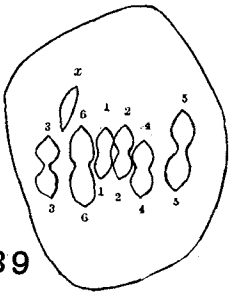


89

PLATE 11

EXPLANATION OF FIGURES

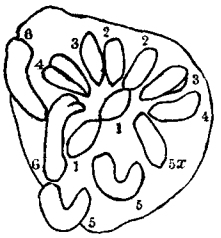
91 to 100 Tettigidea parvipennis pennata Morse.

91 Spermatogonium, 13 chromosomes. Sex chromosome ranks fifth in the series, being between the fourth and fifth autosomes in size.

92 Spermatogonium, 13 chromosomes.

93 to 98 Late prophases of first spermatocyte. Chromosomes in some cases illustrated out of their natural position to provide more room.

99 First spermatocyte division. The no. 4 pair is lacking, lost in sectioning the cell.



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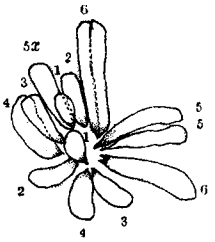

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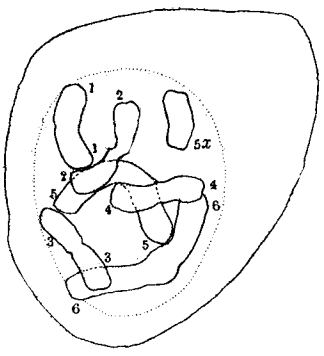

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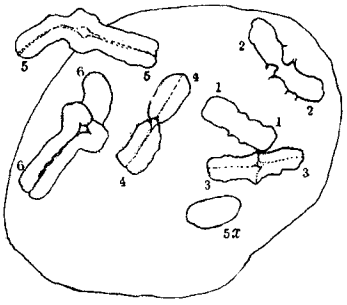

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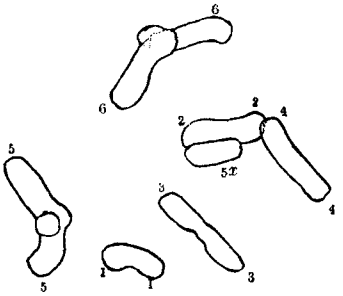

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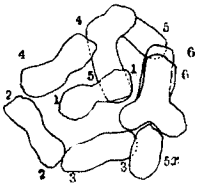

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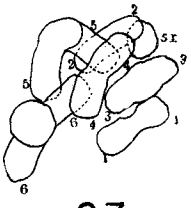

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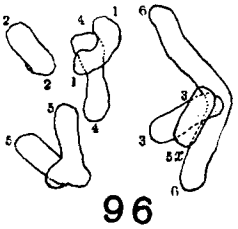

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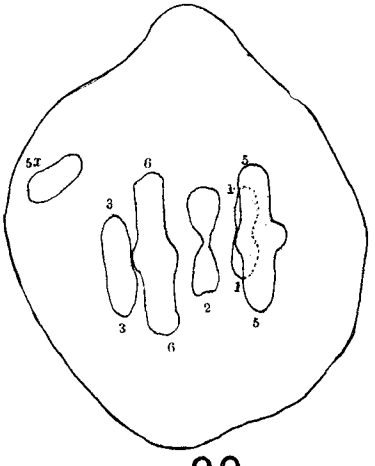


99

PLATE 12

EXPLANATION OF FIGURES

100 T. parvipennis pennata. Oogonium, 14 chromosomes.

101 to 127 Tettigidea parvipennis Morse.

101 to 103 Cells from the ovarian follicle. Fourteen chromosomes; two no. 5x's in each cell. Chromosomes show their split.

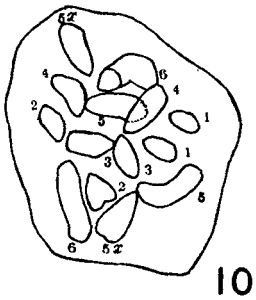
104, 105, and 107 Spermatogonial cells all from same animal but from different cysts of testis; 13 chromosomes. One no. 4 (4−) is deficient in length. Chromosomes show their split.

106 5's and 6's from various cells, similar to those of figure 104, showing the knobs on the ends of the chromosomes.

108 to 110 From dividing cells in the 'fat body' surrounding the testis of same animal from which figures 105 to 107 came. A deficient no. 4 chromosome (4−) present in each case.

108a and b are the parts of one cell from two sections.

110 is in anaphase.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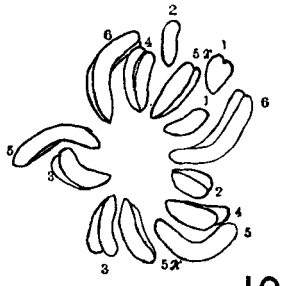
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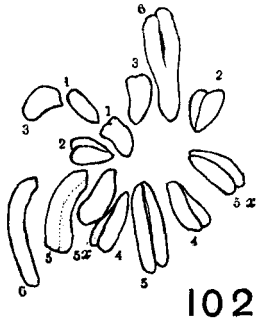
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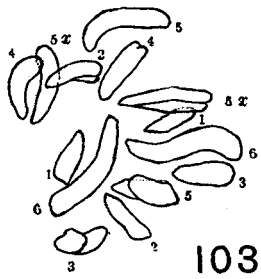
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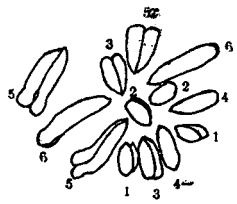
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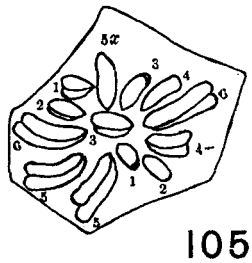
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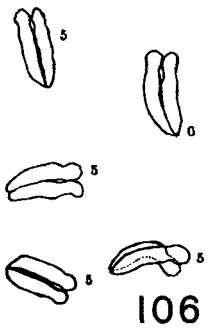
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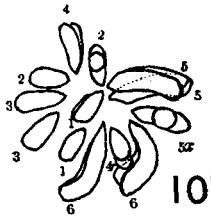
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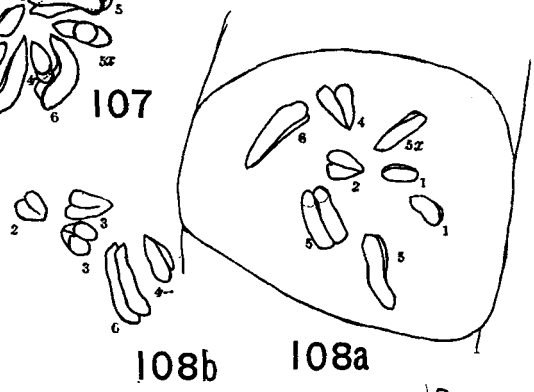
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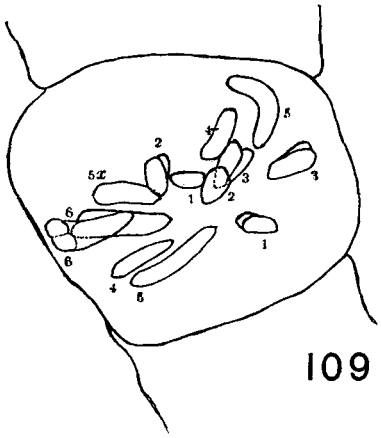
108a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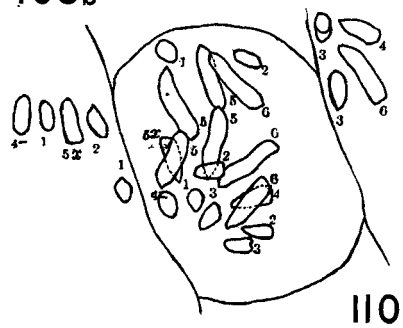
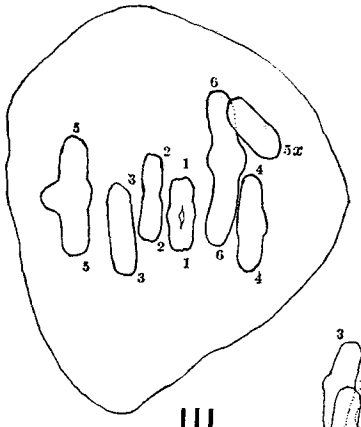

110

PLATE 13

EXPLANATION OF FIGURES

(Tettigidea parvipennis)

111 to 118 First spermatocyte divisions. Full number of chromosomes in each cell. Figures 115, 118, containing the deficient tetrad no. 4, are from same animal as figures 104, 105, 107 to 110. Note inequality of the no. 4's.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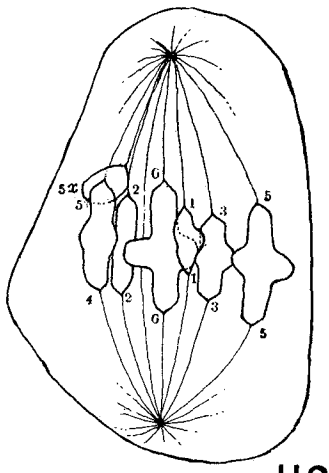
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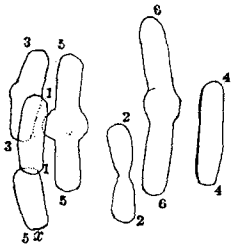
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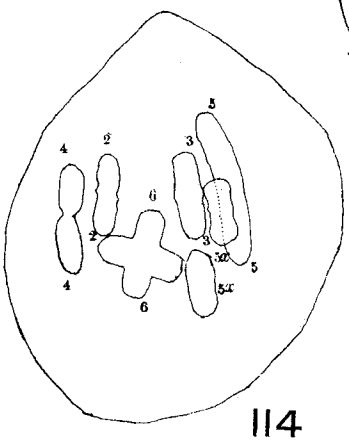
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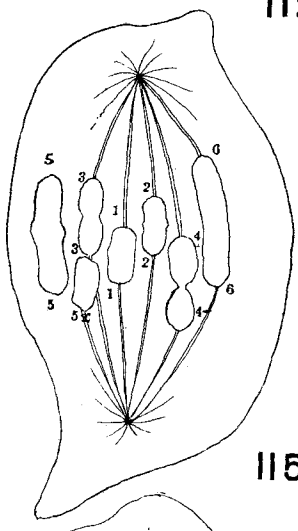
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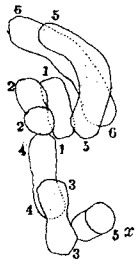
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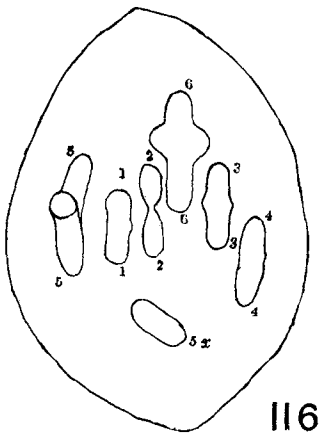
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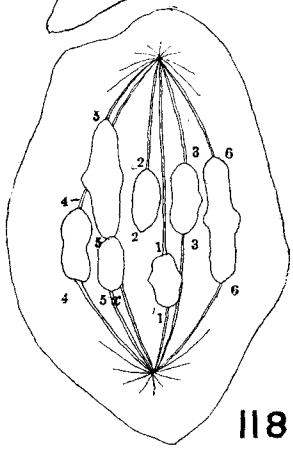

118

PLATE 14

EXPLANATION OF FIGURES

(Tettigidea parvipennis)

119, 120, 122 First spermatocytes from same animal as figures 104, etc.

120 Three of the unequal no. 4 tetrads compared. Note uniformity in sizes of deficient and normal no. 4's; also irregularity in position of points of attachment.

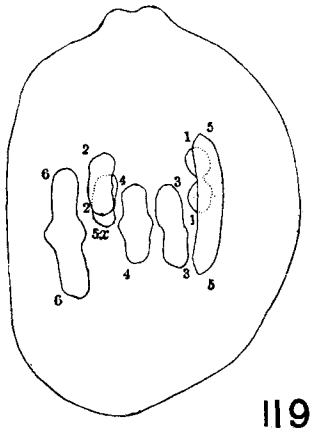
121 First spermatocyte, showing relative sizes of chromosomes except no. 5, which is lacking, lost in sectioning.

122 Anaphase of first spermatocyte.

123 Late anaphase showing lagging sex chromosome.

124, 127 Second spermatocyte metaphases containing the sex chromosomes. Figure 124 is a mate to figure 125.

125, 126 Second spermatocytes lacking sex chromosome. 126 is a mate to figure 127.



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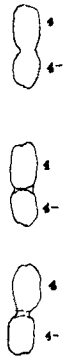

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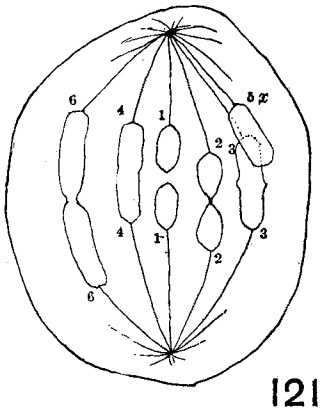

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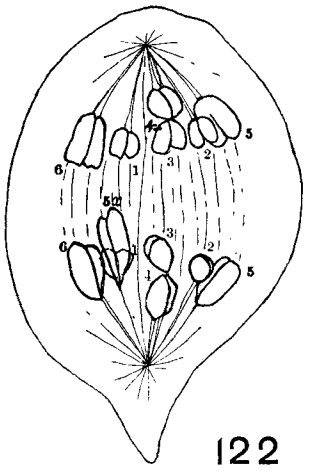

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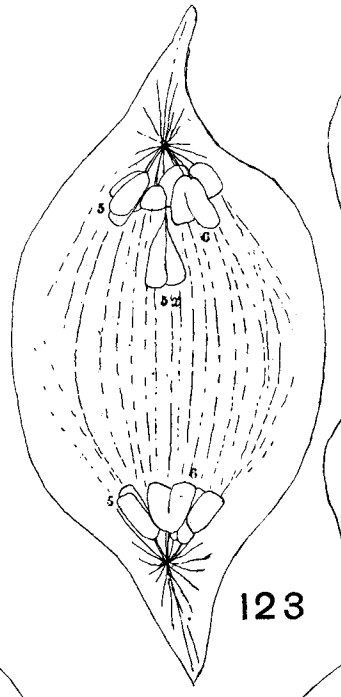

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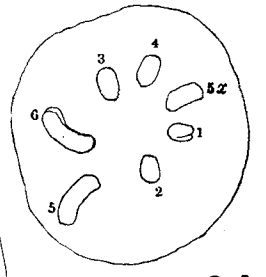

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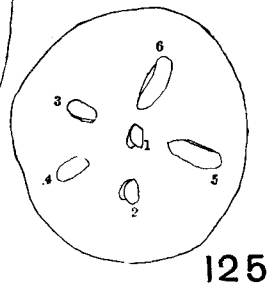

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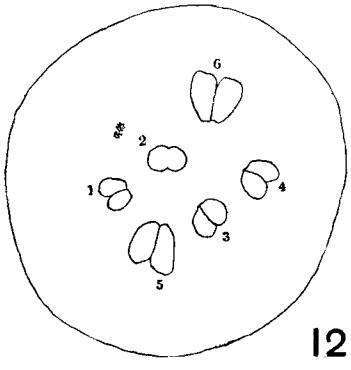

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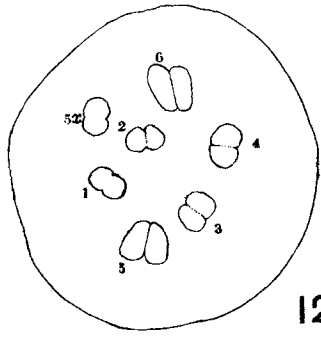
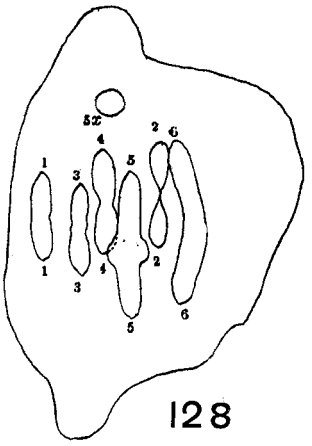


127

PLATE 15

EXPLANATION OF FIGURES

128 to 135 Tettigidea parvipennis Morse or parvipennis pennata Morse. First spermatocytes dividing. Tardiness and inequalities in division of the no. 6 chromosome in figures 132 and 134.



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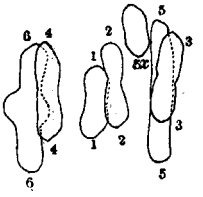

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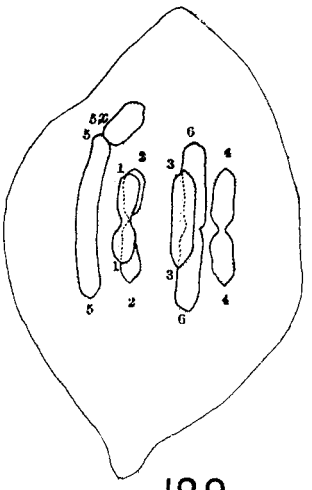

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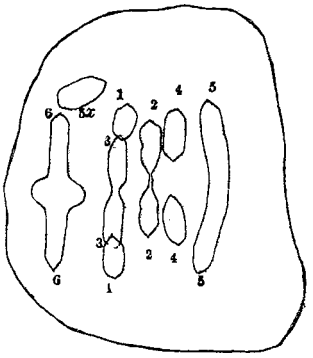

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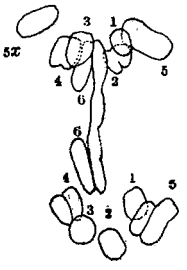

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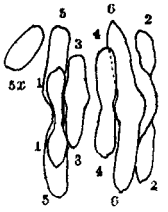

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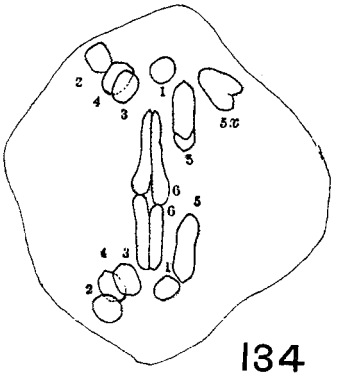

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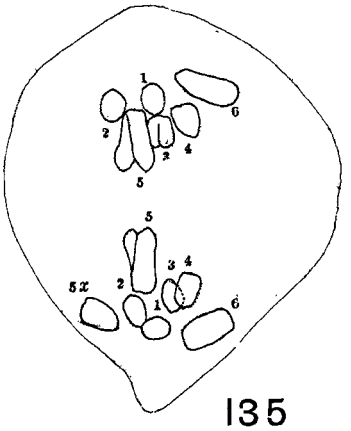


135

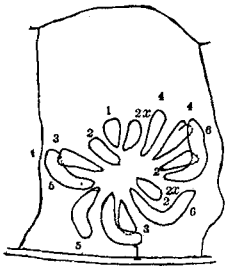
PLATES 16 AND 17

EXPLANATION OF FIGURES

136 to 147 Acridium granulatus Scudd.

136 to 140 From walls of ovariole of ovary of one animal. Fourteen chromosomes present. Five long ones instead of four. One long chromosome (1) is probably a mate to the normal no. 1.

141 to 147 First spermatocyte divisions from one male. Note that all chromosome pairs are present and normal, except the smallest (no. 1), which is made up of a normal no. 1 and an abnormally long mate (1), from which it is separating. The abnormal chromosome is constricted at a point as far from its distal end as the length of its no. 1 mate (figs. 142, 144, 146, 147).



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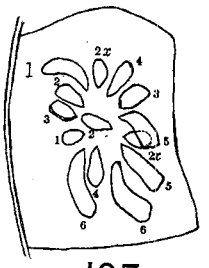

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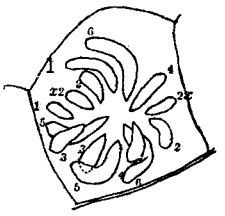

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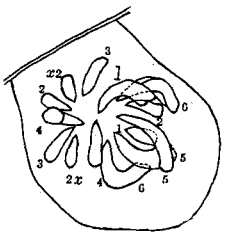

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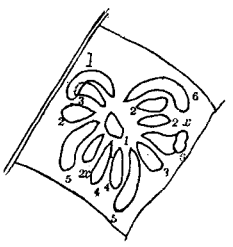

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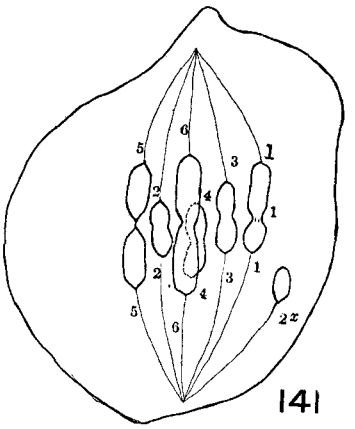

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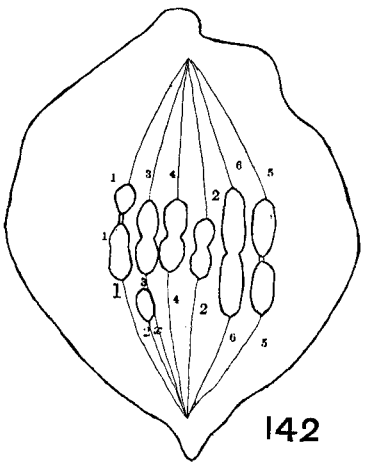

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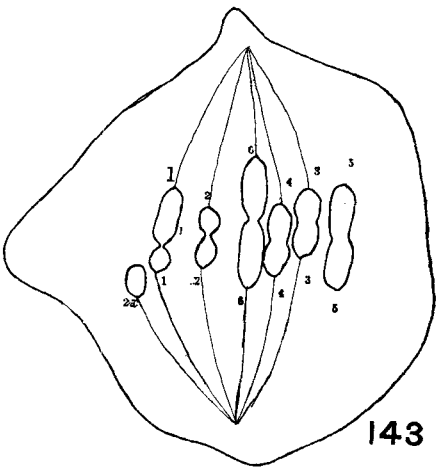

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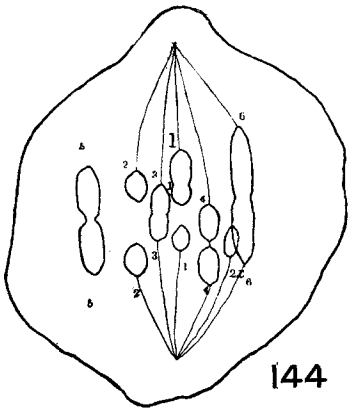
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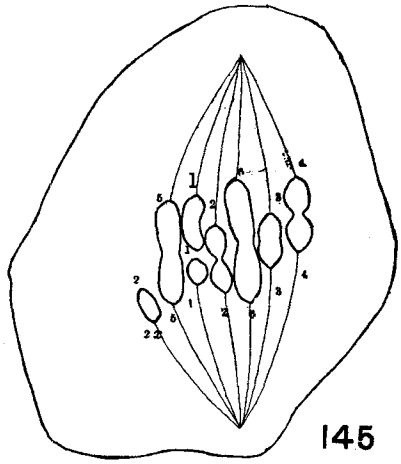
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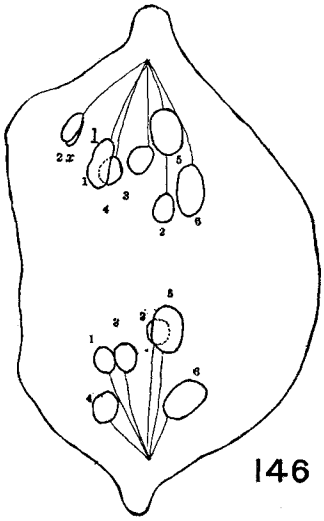
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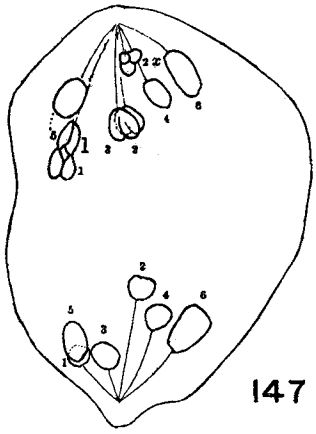

147

PLATE 18

EXPLANATION OF FIGURES

148 to 160 Syrbula acuticornis Bruner.

148 Metaphase of spermatogonium. Autosomes paired from 1 to 11 according to size. Sex chromosome ($10x$) numbered 10 to show that it ranks tenth in size, being between the ninth and tenth autosomes; marked x to indicate its sex determining nature.

149 to 158 First spermatocyte stages.

149a Early prophase of first spermatocyte stage *h*. Four of the paired chromosomes coming out of parasynapsis. x, x, indicate the points from which the attraction fibers will spring in the succeeding reduction division.

149b Remainder of the nucleus of the spermatocyte shown in figure 149a (the following section). In the cell shown in figures 149a and 149b the eleven paired autosomes and the sex chromosomes are all accounted for.

150a and 150b Two successive sections of a spermatocyte at a stage (*i*), later than that shown in figure 149. The four parts of the paired chromosomes are evident. Chromosomes are condensing to enter the metaphase.

151 Portion of a nucleus showing the four parts of paired chromosomes 1, 2, 5, 11, and the continuation of the separation process following parasynapsis. Stage *h*.

152a to 152d Stage *i*. Individual chromosomes from different cells showing further continuation of the process of separation and the structure of the various paired autosomes about ready to enter the condensed metaphase stage. The attraction fiber knobs, i.e., the exconjugating knobs of the tetrad, are indicated by x, x. 152a would have formed a ring, 152b a cross, 152c a V with two knobs at the apex, and 152d a rod chromosome.

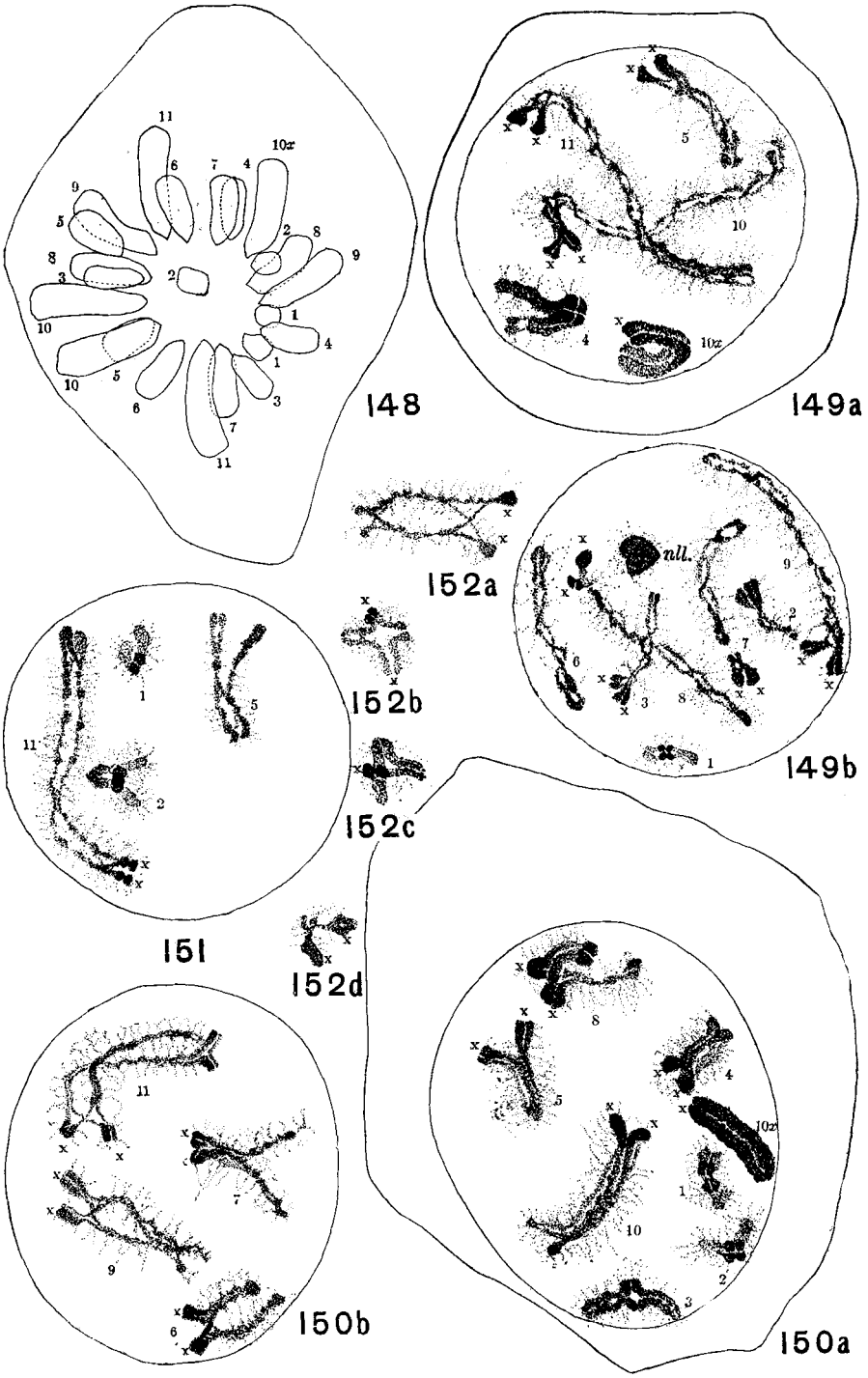

148
149a
152a
nll.
149b
152b
152c
151
152d
150b
150a

PLATE 19

EXPLANATION OF FIGURES

(S. acuticornis)

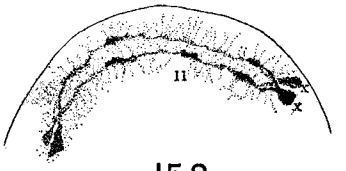
153 A first spermatocyte in prophase. Stage *i*. Chromosome 11 about to form a ring with a pair of knobs at each end. Near the knobs (x, x) the four parts of the chromosomes are easily distinguishable.

154 Five stages in the exconjugation of chromosome pair no. 4: a, the members are in parasynapsis; b, separation of the members has begun, and a second split, at right angles to the first, is now evident; c, separation almost complete; e, lateral view of same.

155a, 155b Nucleus of later prophase, stage *j;* drawings of two successive sections. All the chromosomes (complete) contained in the two sections. Nos. 1 and 2, crosses; 3, a rod probably; 7 and 8, wide **V**'s with knobs at their apices; 4, 5, 6, 9, rings; 10, a four-knobbed ring; 11, a double ring.

156a to 156f Stage *j*. Showing the primary (first maturation division) split (*I*, *I*), and the secondary (second maturation division) split (*II*, *II*) in various first spermatocyte chromosomes. The proximal exconjugating portions of each pair are indicated by x, x.

157 Stage *k*. First spermatocyte in metaphase; slightly oblique polar view; chromosomes in outline. Nos. 1 to 3 rod-shaped tetrads similar to figures 156a and 156b, and possibly to no. 3 in figure 155b. No. 4 is a cross, like no. 1, figure 155b, or no. 2, figure 155a. Nos. 5, 9 are rings similar to 4 or 5, figure 155. Nos. 6, 7, 8, 10 are knobbed **V**'s, like nos. 7, 8, figure 155, or figure 156c, or nos. 6, 8, figure 150. No. 11 is a ring resembling figure 152a, or no. 11, figures 150, 151, or 153, or nos. 6, 9, figures 155, 156a.



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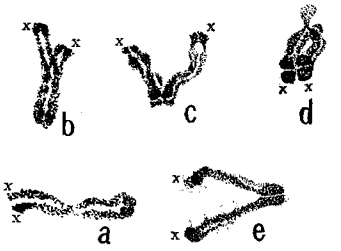

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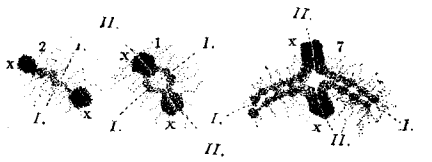
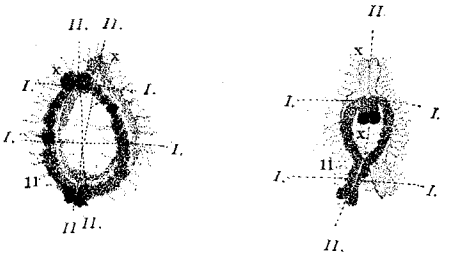
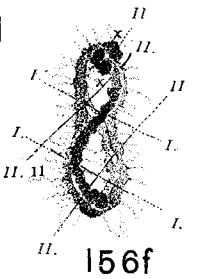


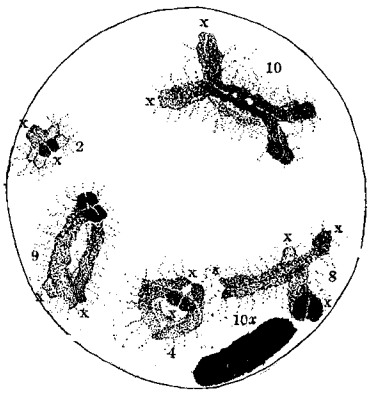
156a 156b 156c



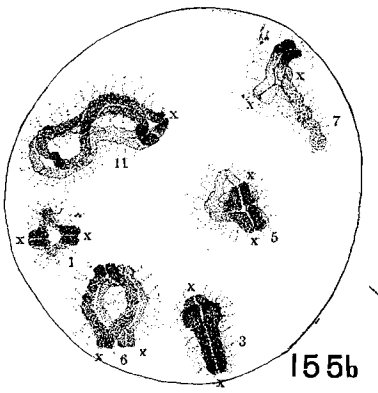
156d 156e



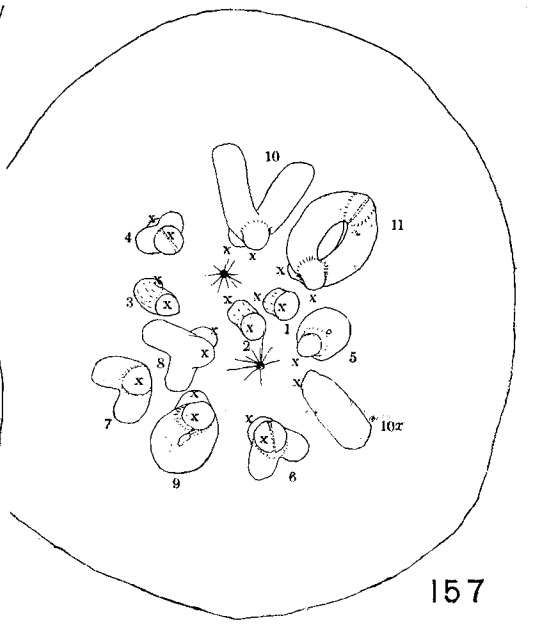
156f



155a



155b



157

PLATE 20

EXPLANATION OF FIGURES

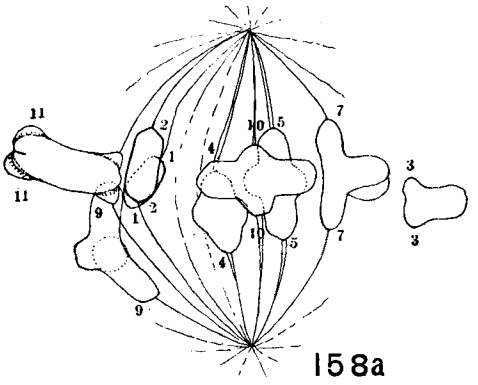
158a, 158b S. acuticornis. Stage *k*. Lateral view of spindle and chromosomes in metaphase, similar to figure 157, from two successive sections. Nos. 1, 2 are rods; 3 approaches a ring in shape; 4, 5, 6 and 9 are crosses; 7 and 10, knobbed V's, similar to no. 7, figure 155, or to figure 156; 8 is a view of the distal end of a knobbed ring similar to 10 in figure 155a; 11, side view of a ring similar to figure 156d.

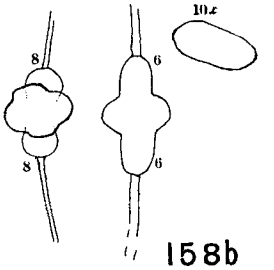
159 S. acuticornis. Second spermatocyte in metaphase showing the relative lengths of the eleven autosomes. Sex chromosome absent from this cell. All chromosomes are split, though both parts do not always show.

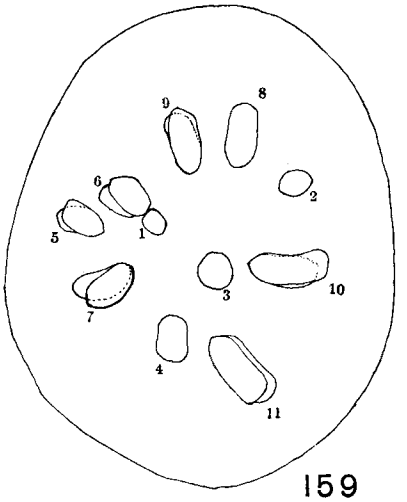
160 S. acuticornis. Second spermatocyte in metaphase showing twelve chromosomes. The halves of 3, 7, 10, and 10*x* have begun to separate.

161 to 187 are from Chorthippus (Stenobothrus) curtipennis Bruner, one of the Truxalinae.

161, 162 Nuclei of spermatogonia in metaphase. The same size relations appear as in figure 148. The 5's are linked at their proximal ends with the 9's, the 7's with the 11's, and the 8's with the 10's.


11
11
9
9
158a


10x
8
8
6
6
158b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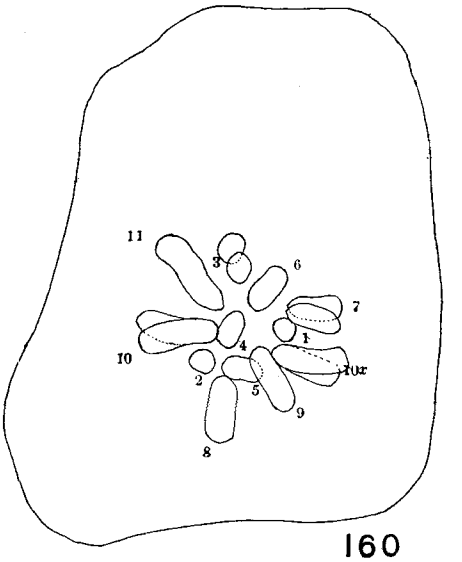
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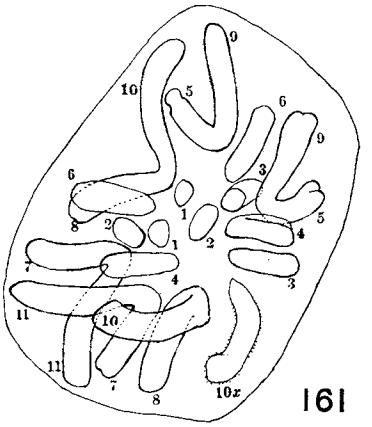
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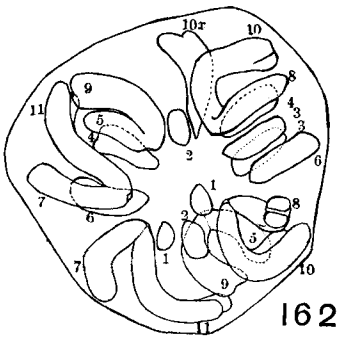

162

PLATE 21

EXPLANATION OF FIGURES

(C. curtipennis)

163 to 183 First spermatocyte.

163 Early prophase, stage *h*, parasynapsis still occurring. All chromosomes (nine) are present. To prevent confusion, nos. 2, 4, and 10*x* have been drawn outside the cell boundary, nos. 2 and 4 being moved out radially; no. 10*x* is from the nuclear-wall region at + near the figure 6. Distal and proximal ends are indicated by *dst.* and *prx.* respectively. x′ to x‴ are points at which spindle fibers become attached; they also indicate the proximal end or region. The numerals 5–9, 8–10 and 7–11 indicate the linked chromosomes 5 with 9, 8 with 10, etc. One-half (exconjugant portion) of the 7–11 in the proximal region (x′ to x‴) is included between the similar parts (x′ to x″) of the 8–10 chromosomes. The remaining parts of each chromosome are still in parasynapsis.

164 A slightly later stage. All chromosomes present. The autosome pairs still in parasynapsis. End views show each chromosome spireme to be split in two planes mutually perpendicular.

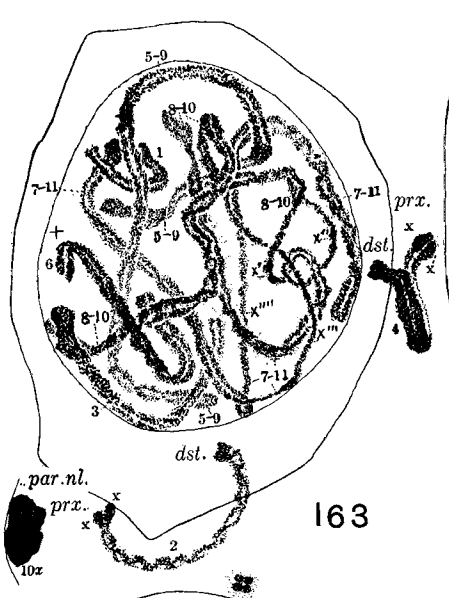
165 Stage *h*, similar to figure 163, also showing the nature of the 7–11 compound. At a and b, just outside the nuclear membrane, are drawn cross-sections of this chromosome at the two points opposite a and b. No. 4 lies near 10*x*, and, as in figures 149, 163, 164, 168, etc., is more condensed than the other autosomes.

166 Stage *h*, similar to figure 164, showing the four parts of a first-spermatocyte chromosome before exconjugation sets in.

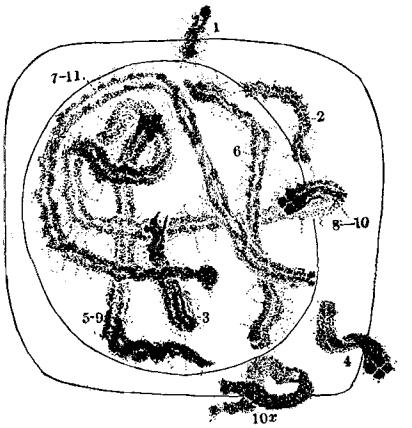
167a and b similar examples. Stage *h*.

168 Prophase (stage *h*) approaching that of figure 150. The three multiples and all other chromosomes present. The proximal regions (x, x) are beginning the exconjugation process. The proximal part of one exconjugation portion of no. 4 is in contact with one end of the sex chromosome.

169, 170 Show association of one end of the no. 4 pair (still in parasynapsis) with one end of the sex chromosome (10*x*).

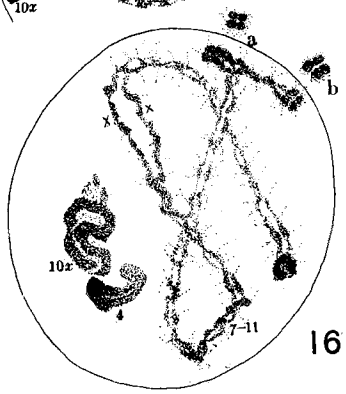


163



164

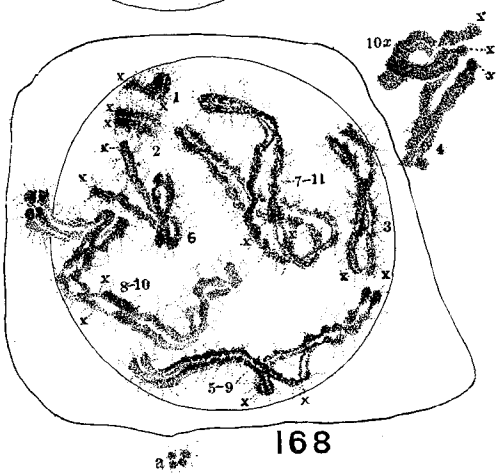
166



165

167b

167a



168

169

170

PLATE 22

EXPLANATION OF FIGURES

(C. curtipennis)

171 Shows conditions similar to those of figures 169 and 170.

172 Showing the same association, also the relative condensation of the no. 4 and 10*x* chromosomes and that of the other autosomes (no. 6) in the same cell.

173a, 173b A prophase similar to figure 150, showing a complete set of chromosomes. 7–11 is displaced and drawn as 173a to make room for the other chromosomes. Note the position and the stage of condensation of nos. 4 and 10*x*.

174 Stage *i*. Prophase similar to figure 155. The junction of 7 with 11, 5 with 9, and 8 with 10 is shown by constriction at x, x in each case.

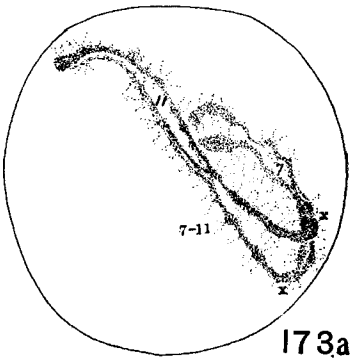
175 Stage *i*. The 7–11 multiple-chromosome.

176 Stage *i*. Junction of 8 with 10 shown at x, x by constrictions. x, x correspond to the apices of the 8–10 V's of figures 161, 162.

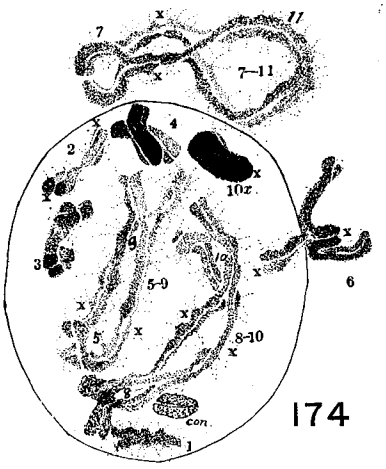
177 A 7–11 pair enclosing a 5–9 pair. Stage *i*.

171

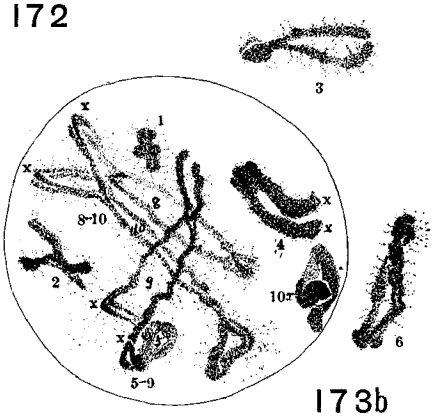
172



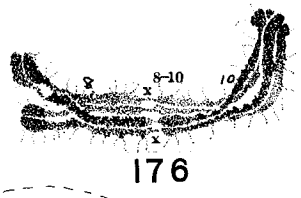
173a



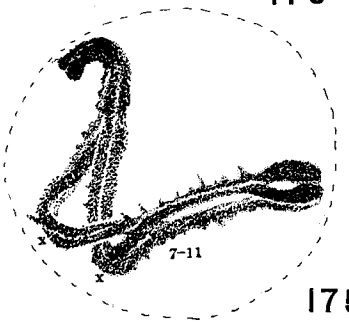
174



173b



176



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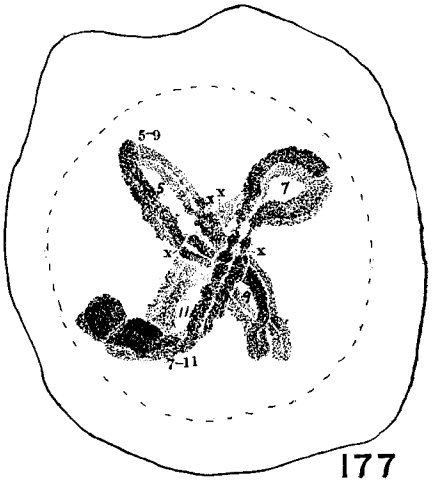


177

PLATE 23

EXPLANATION OF FIGURES

(C. curtipennis)

178a, 178b Stage *j*. Complete set of chromosomes from a late prophase. Compare each chromosome with those of figure 155. The four parts of each are apparent.

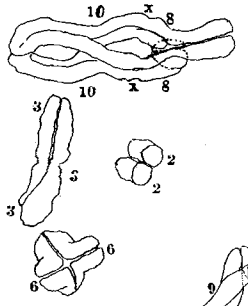
179 Stage *k*. Lateral view of metaphase similar to figures 157 and 158. The tetrad no. 2 is lacking from the section. No. 1 is a rod; no. 4, a **V**; no. 5, a **V**; no. 6, a two-knotted ring; nos. 7 and 8, similar to no. 8 of figure 157; no. 9, a ring; no. 10, similar to no. 10 of figures 157 and 158; no. 11, a four-knobbed ring similar to no. 11 of figures 157 and 158.

180a, 180b Stage *k*. A similar stage, all chromosomes present obtained from two sections. Note constrictions at x, x in 180b.

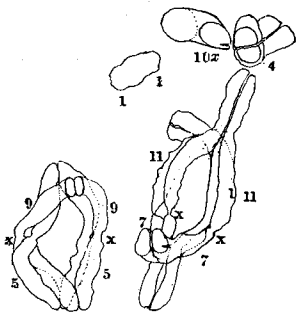
181 Stage *l*. E-shaped figures resulting in the separation of the members of the 7–11 and 8–10 pairs in the first maturation division. The no. 7 components, shorter than the no. 11 components, separate before the longer companions (no. 11) do. The same is true for chromosome 5–9.

182a, 182b, Stage *k*, 182c Stage *l*. Stages in the separation of the chromosomes 7–11 from their mates in the 7–11 multiple during the first spermatocyte division.

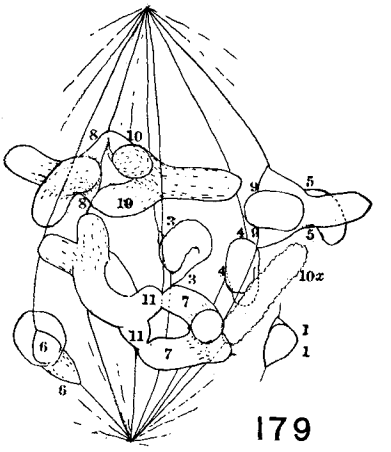
183a (stage *k*) and 183b Similar stages in the 8–10 multiple.



178a



178b



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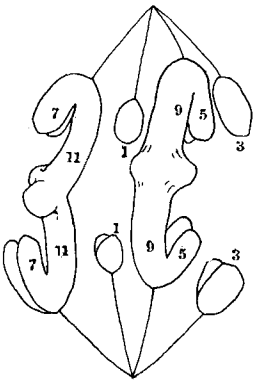
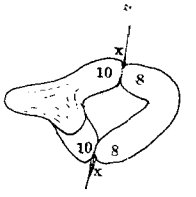
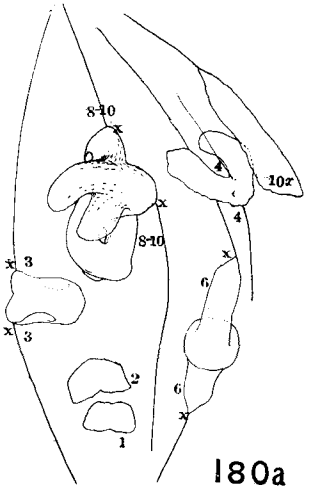


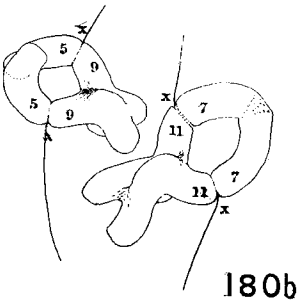
181



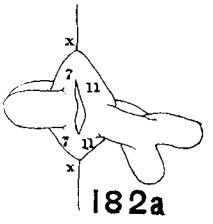
183a



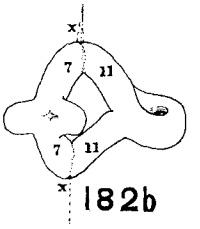
180a



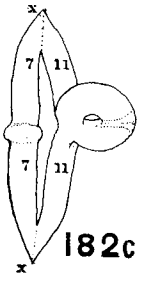
180b



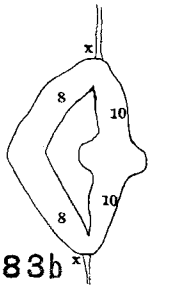
182a



182b



182c



183b

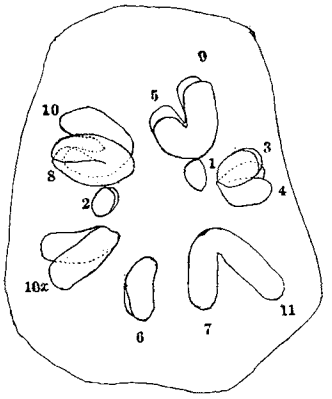
PLATE 24

EXPLANATION OF FIGURES

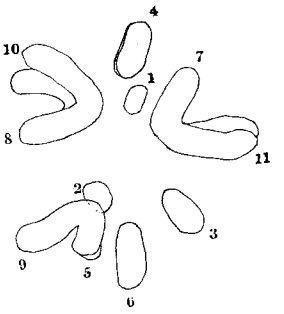
184 to 186 C. curtipennis. Three second spermatocytes in metaphase. Each chromosome consists of an upper and a lower half. The 10*x* is present in two cells. Three unequal-armed **V**'s present in each cell. Size relations same as in figures 159, 160.

187 C. curtipennis. Second spermatocyte in anaphase.

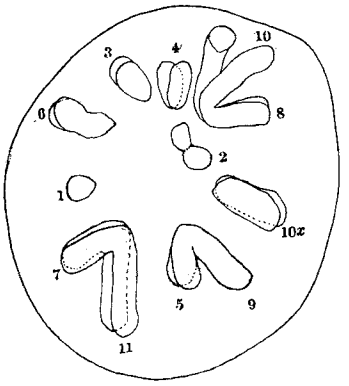
188, 189 Second spermatocyte from Chorthippus (Stenobothrus) biguttulus after Gerard ('09). Numbers (mine) show similar size relations (except in case of sex chromosome) and association to form three **V**'s as in curtipennis. At no. 11 the halves of this part are probably gaping apart, as in no. 10 of figure 186.



184



185



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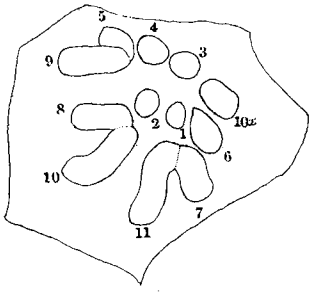
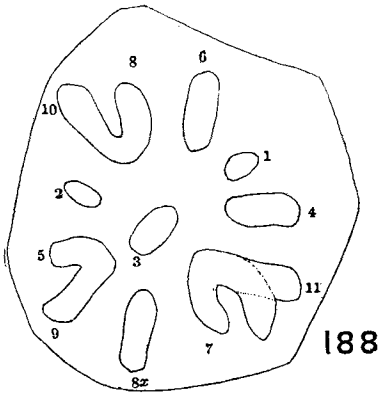
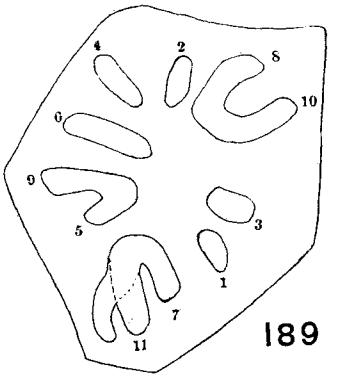


187



188



189

PLATE 25

EXPLANATION OF FIGURES

190 Spermatogonium of Chortaphaga viridifasciata, one of the Oedipodinae, after Davis ('08). Same number of pairs of autosomes. Sex chromosome ranked $8x$.

191 Spermatogonium of Dissosteira carolina, one of the Oedipodinae, after Davis ('08). Eleven pairs of autosomes plus one sex chromosome ($9x$).

192 Spermatogonium of Melanoplus femoratus, one of the Acridiinae, after Davis ('08). Eleven pairs of atuosomes plus sex chromosome ($10x$).

In figures 148, 159 to 162, 184 to 192, note that all subfamilies have three extremely small chromosomes or pairs, and three extremely large ones with a somewhat similarly graded series between.

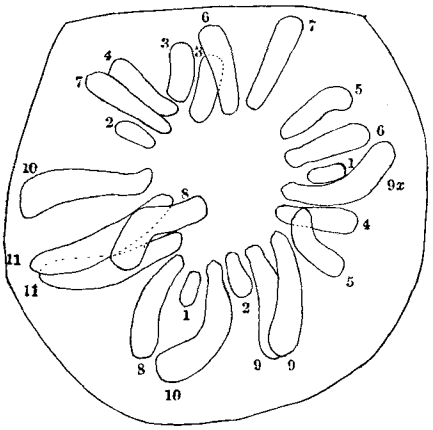
193 to 202 from Locustidae.

193 Spermatogonium of Steiroxys trilineata after Davis ('08). Thirty-one rod-shaped chromosomes.

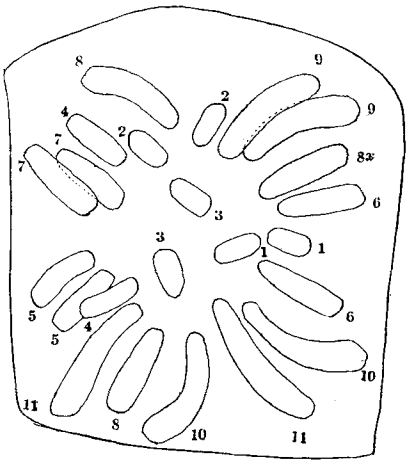
194 to 201 After Woolsey ('15).

194 Spermatogonial chromosome group from Jamaicana subguttata Walker. Thirty-five rod-shaped chromosomes, paired. Sex chromosome is $18x$.

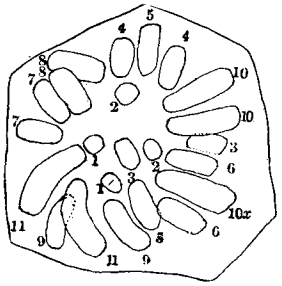
195 First maturation division of same species, showing seventeen first spermatocyte pairs of autosomes in the process of reduction. Sex chromosome ($18x$) going over undivided to one pole.



191



190



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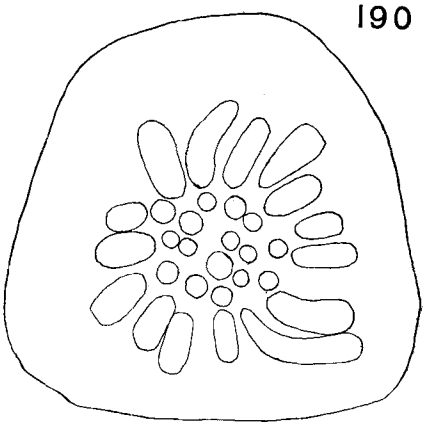
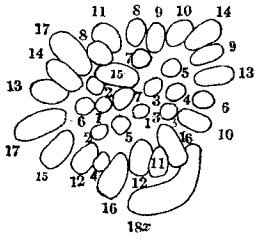
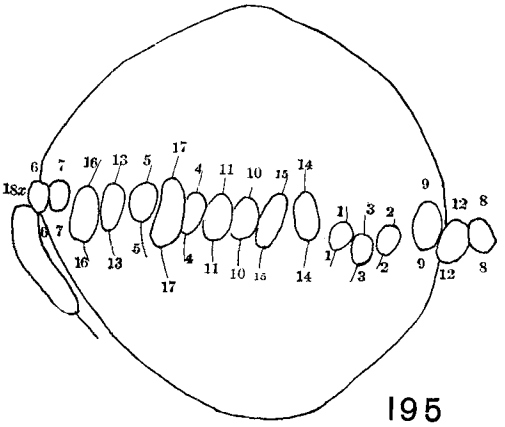


193



194



195

PLATE 26

EXPLANATION OF FIGURES

196 Spermatogonium of Jamaicana subguttata Walker, showing one member of the no. 14 pair linked with one member of the no. 16 pair. Thirty-two rod-shaped chromosomes, plus one V-type, plus the sex chromosome, are present.

197 Prophase of first spermatocyte of same animal showing fifteen tetrads plus the V bi-tetrad plus the sex chromosome.

198, 199 Lateral views from same animal showing the separation of the short no. 14 and long no. 16 limbs of the V from their no. 14 and no. 16 rod mates. Points of separation marked by the constrictions.

200 Spermatogonium from Jamaicana unicolor Bruner, showing two V's of equal size. Thirty rod-shaped chromosomes, plus two V's, plus the sex chromosome, are present.

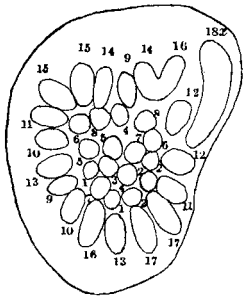
201 Prophase of first spermatocyte from same animal showing the sex chromosome ($18x$), the fifteen rod-tetrads, and the large ring-shaped bi-tetrad resulting from the separation of the V's in exconjugation. Note the unequal length of the 14, 14 and the 16, 16 sides of the ring.

202 Spermatogonium of Steiroxys trilineata, after Davis ('08), showing the presence of twenty-six rod-shaped chromosomes plus one sex chromosome. Compare with figure 193 in number.

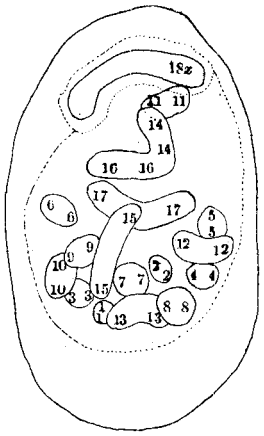
203, 204 Of Gryllis domesticus, after Baumgartner ('04).

203 Spermatogonium, showing twenty autosomes plus one V-shaped sex chromosome (x). Eight of the autosomes are V-shaped with apices turned toward the center of cell plate.

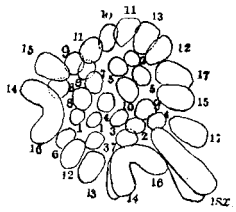
204 Second spermatocyte, ten autosomes plus the sex chromosome. At least four of the autosomes are V's with apices turned toward the center of the plate.



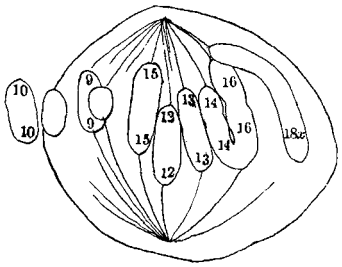
196



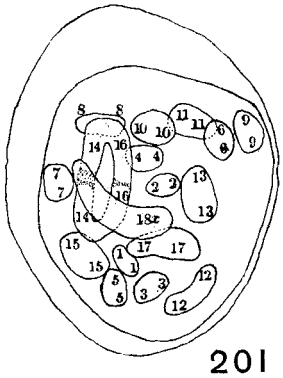
197



200



198



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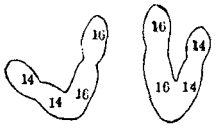
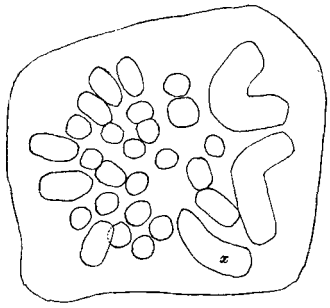
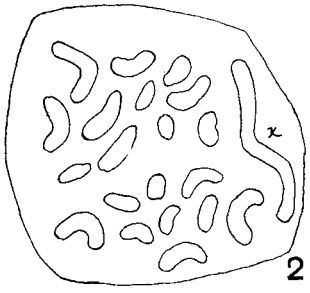


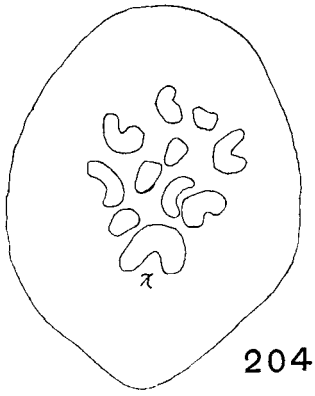
199



202



203



204