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The Cytology of the Sea-Side Ear-
wig, *Anisolabis maritima* Bon.

Part I

SIDNEY I. KORNHAUSER

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THE CYTOLOGY OF THE SEA-SIDE EARWIG, ANISOLABIS MARITIMA BON.

PART I

SIDNEY I. KORNHAUSER

From the Zoölogical Laboratory of Denison University, and the Biological Laboratory of the Brooklyn Institute of Arts and Sciences at Cold Spring Harbor, Long Island

WITH THREE PLATES

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1. INTRODUCTION

The forficulid, *Anisolabis maritima* Bon., which is found under the stones and riff-raff at the high-tide mark, is especially beautiful material for cytological study. The chromosomes are clear and distinct; the cytoplasmic structure, nicely demonstrable; and good preservation is not difficult. The differentiation of the oöcyte and nurse cell and their subsequent growth present many interesting problems which will be taken up in another paper. The origin and distribution of mitochondria in both the sex and the embryonic cells may also be studied profitably in this species. For the present, the author has confined himself chiefly to the chromosome number, and the origin and fate of the sex-chromosomes in the male. The work was begun in the summer

of 1915, suffered many delays due to the World War, but was taken up again in the spring of 1920.

I wish to express my thanks to the American Association for the Advancement of Science, which, through its Committee on Grants for Research, has enabled me to purchase microscopical lenses suitable for cytological study. These lenses have aided greatly in the completion of the paper.

2. HISTORICAL REVIEW

Two of the Forficulidae have been previously worked upon from a cytological standpoint, *Forficula auricularia* and the present species, *Anisolabis maritima*; the bulk of the work having been done upon the former species. The accounts claim a great variability in the diploid and haploid number of chromosomes, and several combinations of sex-chromosomes have been described.

The most recent and detailed contribution to the cytology of the forficulids is that of Payne ('14) on the variability of the chromosomes of *Forficula*. Payne states that the spermatogonial metaphases show from 24 to 27 chromosomes, twenty-four being the most usual number. The spermatocytes were found to have from 11 to 14 chromatic elements present. Zweiger ('06) states that the spermatogonial count was 24 or 26, the latter number being the more prevalent. He states that either 12 or 13 chromosomes may appear in the primary spermatocytes, and 12 to 14 in the secondary spermatocyte metaphase plates.

Stevens ('10) considered 24 the correct spermatogonial number and 12 the haploid number, one of the twelve seen in the primary spermatocytes being an unequal hetero chromosome group, which separated reductionally in the first maturation division.

Pantel ('12), whose work deals mainly with the degeneration of cells due to the presence of protozoan or insect parasites, described a variable number of chromosomes in *Forficula*. Spermatogonia have either 25 or 26 chromosomes; and spermatocytes, 11 to 13 chromosomes. He does not insist, however, that

this variation, which had already occupied the attention of such pioneers as Carnoy, La Valette, St. George and Sinéty, should be produced by parasitism.

Brauns ('12), in his study of the oögenesis of *Forficula auricularia*, believes that the haploid number in the female is 13. He quotes Professor Ludwig Will of Rostock as saying that the male diploid number of *Forficula* is 25, and the female diploid number 26; but that some males show 24 chromosomes in their spermatogonia. It is a striking coincidence that my counts on *Anisolabis* are in very close agreement with the results of Professor Will.

Randolph ('08) worked on *Anisolabis* and described 24 chromosomes as the diploid number in both sexes. In the primary spermatocytes she pictures a pair of almost equal hetero chromosomes which lag in the anaphase of the first maturation mitosis, but her results are not at all in accord with those described in the present paper.

3. METHODS

The material studied consisted of gonads and embryos. Nymphs were found best for the study of the germ cells. The animals were all collected at or near Cold Spring Harbor, Long Island, during June, July and August of several summers since 1915.

The best fixatives were Flemming's fluid (strong), Bouin's fluid and Benda's modification of Flemming's fluid. Various stains were employed. The Flemming material was stained in Heidenhain's haematoxylin, counterstained with Orange G or with safranin and lichtgrün. The Benda material was stained either with alizarin and crystal violet, or with methyl green and acid fuchsin of Bensley. These last two were especially valuable in the study of the xxy-complex.

Smears of testes were made in a moist chamber, immediately exposed to osmic fumes for a few seconds, and then immersed in a fixing fluid; care being taken to avoid drying. Such smears were then treated and stained like sections.

Embryos were removed from their chorionic coverings before fixation in Flemming's fluid.

The abundance of material, the large number of preparations made, and the variety of methods employed lead the author to believe that his results are fairly accurate.

All drawings were made with the aid of a camera lucida, using a 1.5 mm. Zeiss apochromatic objective and a 20 $\times$ compensating ocular. This gave an initial magnification of 3300 diameters. The drawings were reduced in the reproductions, plate XXIV about one-third and plates XXV and XXVI about two-fifths.

4. THE GONADS

Each testis consists of two long narrow tubules surrounded by a fat sheath. The length and narrowness of the tubules gives a good seriation of stages from the blind tip to the bottom where the sperm pass into the vas efferens. Near the blind or cephalic end of the tubule is a large apical cell, surrounded by young cysts of spermatogonia. These younger spermatogonial generations are larger cells and better for spermatogonial counts than those in cysts more caudad. The cysts are clearly marked off from one another by distinct walls. The spermatocytes undergo considerable growth in size and their cytoplasm acquires a large amount of mitochondria. The spermatocyte cysts occupy by far the greater part of the tubules in nymphal males. At no time during the growth period do the chromosomes disappear or lose their staining powers. The transition from ultimate spermatogonia to the formation of the spermatids must be rather slow, inasmuch as every stage in the conjugation of the chromosomes and the formation of the tetrads may be found in the testes of a single nymph, previous to the final moult. This is in marked contrast to many insects, in which the syndetic stages are very rare and difficult to find. One fortunate condition in the study of *Anisolabis* is the fact that each testicular tubule contains a large number of cysts and that each cyst shows slight variations in its meiotic phase.

Many testes show a central core of heterogeneous material made up of degenerating cysts. This looks much like the stream of food seen passing from the terminal chamber to the growing oöcytes of telotrophic insect ovarioles. It is not the purpose of the present paper to describe the details of the spermatogenesis or the cytology of degeneration, although the author hopes to attack these questions at another time.

The ovaries are composed of very long, and much attenuated tubules, each fastened at its narrow, cephalic end by a terminal filament reaching to the dorsal body wall. The sheath of each ovariole is composed largely of tracheal tubules, and undergoes rhythmic pulsations. The space between the egg string and this sheath is filled with a coagulable fluid. The cephalic tip of each ovariole, just caudad to the attachment of the terminal filament, is occupied by a Keimpolster; then follow oögonia, showing an occasional mitosis; while a trifle more caudad one may find pairs of oögonia both in the same mitotic phase. About one-tenth of a millimeter from the Keimpolster occur the ultimate oögonial mitoses. Here four cells all in the same stage of mitosis may be found, and each cell gives rise to an oöcyte and a nurse cell which continue in close connection and accompany each other from this time until the end of the growth period. Syndesis occurs immediately after the differential mitosis, the oöcyte here outstripping its sister nurse cell in size. Soon, however, the nurse grows much larger than the oöcyte, and, at about six-tenths of a millimeter from the Keimpolster, they orient in single file (oöcyte, caudad; nurse cell, cephalad), acquire follicular walls, and proceed in the accumulation of yolk material. The large nurse cell with irregular nucleus is surpassed finally in size by the oöcyte, and becomes a small cap on the cephalic end of the ovum.

5. THE DIPLOID CHROMOSOMES

A. The female

Oögonia in their ultimate mitoses show 26 clear, distinct chromosomes, well separated from one another. Numerous drawings were made and the number 26 established without doubt. Fig-

ures 1-4 (Plate XXIV) represent four typical metaphase plates. Subsequent observations lead the author to believe that, of the twenty-six chromosomes, twenty-two are autosomes, and four are two double x-chromosomes, which appear in quiescent oögonial nuclei as two double and almost square karyosomes.

The female somatic number has likewise been established to be 26. The counts were made on well-developed embryos, treated by the same methods as the gonads. Numerous mitoses in the hypodermal cells and in the developing central nervous system offered abundant material for satisfactory counts. A suitable embryo would be selected and then sketches made of every distinct metaphase plate in the whole series of sections. Figures 5-8 (Plate XXIV) represent four groups showing 26 chromosomes each. These are selected from a single embryo in which dozens of clear counts of 26 were made. In the somatic cells, as has been noted by previous investigators, there is a much greater variation in the size of the cells and the form of the chromosomes (whether long and narrow, or short and broad) than there is in the germ cells. The chromosome number, however, remains constant, with the occasional exception of a giant cell with twice the diploid number present.

B. The male

Spermatogonia likewise have clear, clean-cut chromosomes, twenty-five in number, cells near the apex of the tubule serving best for such counts. These spermatogonia have a large amount of cytoplasm and the chromosomes are well separated (Plate XXIV, figs. 9-12). In the cytoplasm one may often encounter bodies, which might be mistaken for chromosomes in deeply stained haematoxylin preparations, especially after Bouin or sublimate fixation. In such preparations these cytoplasmic masses are quite as dark in color as the chromosomes and not greatly different in size from the average *Anisolabis* chromosome. These bodies are shown, light gray in tone, in figures 9, 11, and 12 of Plate XXIV. After Benda fixation these cytoplasmic bodies take mitochondrial stains, and stand out in marked contrast to the

chromosomes, being purple in crystal violet + alizarin, and red in methyl green + acid fuchsin. The use of these stains enables one to establish the number twenty-five for the spermatogonial chromosomes. As will be shown later, twenty-two of these are autosomes, two form an x-complex, and one is a y-chromosome.

The male somatic number was likewise established by the study of serial sections of embryos in which many counts of single individuals were made. Figures 13 to 16 (Plate XXIV) are typical 25 chromosome plates of such male embryos. The following important variation, the only characteristic one so far found in the study of *Anisolabis*, must be noted. In male embryos, with typical 25 chromosome cells, one finds clear metaphase plates with only 24 chromosomes. This happened too often to be purely accidental or due to error or oversight. A probable explanation of the phenomenon will be given in Part 8.

6. THE SPERMATOCYTE CHROMOSOMES

The initial and most fundamental facts to be established were that twelve chromatic elements were uniformly present in primary spermatocyte metaphase plates (Plate XXV, figs. 28-29), and that half the secondary spermatocytes possessed twelve chromosomes and the other half had thirteen (Plate XXVI, figs. 44-47). These facts made necessary the careful study of the origin of the twelve primary spermatocyte chromosomes.

From the 25 spermatogonial chromosomes are formed eleven autosomal tetrads and a heterochromosomal hexad, which I have called the xxy-complex and which may be seen in figures 17-27 (Plate XXV). The autosomal threads and tetrad formation are omitted from these figures. The evidence is rather clear that the tetrads are formed by parasynopsis, and it is hoped that additional smear preparations will enable the author to deal with this point in more detail in another paper. Figures 17-22 show merely the nuclear outline and the xxy-complex, stained in iron-haematoxylin, the relative intensity of the stain being depicted as accurately as possible in the figures.

Figure 17 is an early leptotene stage, the autosomal threads just emerging from the telophase chromosomes of the ultimate

spermatogonial division. Here there is seen a double, rather angular body (xx), and a deeply staining sphere (y). With the establishment of the leptotene threads (Plate XXV, fig. 18), the xx-and the y-element come into close apposition and remain connected, sometimes merely by a small strand (Plate XXV, figs. 19, 20), and also during syndesis they continue this connection. When the zygotene threads are well formed, the xx-element separates from the y-element. Often they come to lie at some distance from each other in the nucleus, but apparently not under control of the centrosome at the positive pole of the nucleus (Plate XXV, figs. 21, 22).

With the beginning of the strepsinema the xx-element and the y-element again approach each other and are again connected by a narrow strand (Plate XXV, figs. 23, 24). The xx-element reveals its two-fold constitution, when viewed at a favorable angle in well-decolorized haematoxylin preparations, and especially well in crystal violet + alizarin slides. At the establishment of the strepsistene stage we notice the coalescence of the xx-and the y-element. In iron-haematoxylin the y-element has a lighter cortical zone, and a more deeply stained center. The doubleness of the x-portion is no longer so distinct (Plate XXV, figs. 25-26).

When the autosomal tetrads are formed, but are still very granular, there appears on the xxy-complex a highly refractive spherule (fig. 27, *nl*), which separates from its parent mass at about the time the smooth, deeply staining tetrads are established. This nucleolar body may then lie anywhere in the nucleus, even in close apposition to one of the autosomal tetrads. As the centrosome divides and preparation is made for the first maturation spindle, this nucleolar body diminishes in size and finally disappears, leaving eleven autosomal tetrads and the xxy-hexad to enter the metaphase plate.

Not only form but also differential reaction to stains enables one to trace the evolution of the hexad. In safranin + lichtgrün, the y-element is not so deep a red as the xx-component, in stages corresponding to those shown in figures 17-26. The y-element also appears vacuolated, and has a greenish tinge in the early

strepsinema. Finally in the later strepsistene stage, when the chromatic spherule is given off, the y-element stains as deeply as the two x-elements. In crystal violet + alizarin the y-element is purple, and the xx-element brown with small purple granules in it; whereas the nucleolar sphere of the late strepsinema is deep purple. In methyl green + acid fuchsin, the y-element is red, and the xx-element green. As the two fuse, in stages corresponding to figures 25 and 26, the y-element gradually loses its red color and becomes green, while the extruded nucleolar spherule is a deep red. We must, I believe, assume that the extrusion of this nucleolar spherule is in a vital way connected with the change in "stainability" of the y-element.

The twelve chromosomes of the primary spermatocyte metaphase (Plate XXV, figs. 28, 29) are so widely separated that, in lateral views with very high magnification, one may focus sharply on each element in the spindle. Good lateral views of the xxy-hexad may be obtained not only in metaphase plates (figs. 30-33) but also in anaphase stages (Plate XXVI, figs. 37, 38). Figure 34 (Plate XXV) shows the twelve elements of the metaphase plate viewed laterally, the chromosomes of the several foci being here transposed into a single row from the camera lucida drawing. The hexad is on the extreme right. Figure 35 represents a corresponding stage, but taken from a smear slide. The contents of the cell were so spread out that a single focus displayed all the chromosomes with no overlapping. In the smear slides the chromatic elements appear smaller but retain all the features seen in sections, and offer a very good check upon the latter.

The attachment of the y-element and the xx-element seems to be either terminal $\begin{Bmatrix} y \\ x \\ x \end{Bmatrix}$ or lateral $\begin{Bmatrix} y \\ xx \end{Bmatrix}$. Various arrangements of the elements taken from metaphases and anaphases are seen in figures 30-38. Figure 36 (Plate XXV) shows seven separate xxy-hexads, the y-element in all cases being uppermost in the figures.

In the first meiotic division (Plate XXVI, figs. 37-41) the y-chromosome passes to one pole and the double x-chromosome

to the other. Figures 40 and 41 represent two anaphase plates of a single cell, similar to that shown in figure 39, but cut through the equatorial zone so that one section contains one plate and the next section its sister. In both plates eleven of the chromosomes, the autosomes, are similar; and the large xx-element in figure 41 and the smaller y-element in figure 40 occupy corresponding positions.

Following the telophase of the first meiotic division there is a definite interkinetic period with the establishment of a well-defined, nuclear membrane (Plate XXVI, fig. 42). The centrosome of the primary spermatocyte telophase remains visible and establishes the spindle of the secondary spermatocytes. The dyads remain rather distinct, deeply staining, block-like masses in the nucleus of the interkinetic stage.

With the formation of the secondary spermatocyte spindles we now have two distinct types of metaphase plates: those with twelve chromosomes, and those with thirteen (Plate XXVI, figs. 43-47). The twelve chromosome plates consist of 11 dyads and a y-chromosome. The thirteen chromosome plates consist of 11 dyads and two x-chromosomes, which separated from each other during the interkinetic period and are here represented by two discrete elements. Figures 46 and 47 (Plate XXVI) show two pairs of sister second spermatocytes, one in each pair containing twelve, and the other thirteen chromosomes. The former figure is taken from a section, the latter from a smear slide.

Occasionally giant secondary spermatocytes are formed with all the chromatic elements of the first maturation spindle present, the chromosomes having divided but the cytoplasm having failed to do so. Two such metaphase plates are shown in figures 48 and 49 (Plate XXVI) and each has 25, well-defined chromosomes.

The second maturation mitosis divides all the chromosomes equationally, and they pass to their respective poles without lagging. Figures 50 and 51 represent sister anaphase plates, drawn from a smear slide, and showing an exact correspondence in their chromatic elements. The spermatids (fig. 52) are formed

immediately after the telophase of the second meiotic division and bear a remarkable resemblance to the interkinetic spermatocytes, except that they are smaller and that their chromosomes soon break up into granules.

7. DISCUSSION

The author believes the female diploid number of chromosomes of *Anisolabis* to be twenty-six in both germ cells and soma cells, as against twenty-four claimed by Randolph ('08) for both sexes. The normal male diploid number is twenty-five although somatic mitoses with twenty-four chromosomes are found.

The union of the two x-chromosomes into a single body is probably the explanation of this last phenomenon, and this supposition is strengthened by the fact that, in the growth of the spermatocytes and in the first spermatocyte division, these two x-elements of the xxy-hexad are in close apposition, leading to the assumption that the two parts are intimately related. The x-complex may be considered either as having originated from a single x-chromosome or as now being in the process of the formation of a single x-chromosome out of two previously distinct chromatic elements.

Another view of the 24 chromosome somatic male cells is possible: namely, that after a number of somatic divisions, the y-element undergoes a dissolution. From the behavior of the y-element in the growth of the spermatocytes, one may infer that it is greatly different from the normal chromosomes; for, not until the late strepsistene does it acquire a true chromatic stain, when tested with alizarin + crystal violet or with methyl green + acid fuchsin. Only after giving off the nucleolar spherule, which takes the mitochondrial stains deeply, does its definite chromatic nature appear.

Our interest in the y-chromosome must be again kindled in view of the recent type of inheritance described by Castle ('21) linked with this exclusively paternal chromatic element. We must try to determine whether the y-chromosome is a chromosome in a state of formation or whether it is merely a degenerate x-chromosome.

In regard to the sex-chromosome of the forficulids, the author would maintain that in *Anisolabis* we have neither unpaired accessory chromosomes, nor a pair of unequal heterochromosomes, nor a pair of almost equal heterochromosomes, as previously described by various authors. The following conditions are believed to exist: the female diploid number is 26, consisting of 22 autosomes and 4 x-chromosomes; the female haploid number (inferred) is 13, consisting of 11 autosomes and 2 x-chromosomes; the male diploid number is 25, consisting of 22 autosomes, 2 x-chromosomes, and a y-chromosome; half the second spermatocytes show 13 chromosomes, and the other half 12. The former gives rise to two female determining spermatozoa, containing 11 autosomes and 2 x-chromosomes; the latter gives rise to two male determining spermatozoa, with 11 autosomes and a y-chromosome.

It will be an interesting problem to see if the small mature males, occasionally found in *Anisolabis*, are in some way related to an upset in the normal chromosomal distribution described above.

8. SUMMARY

1. The diploid number of chromosomes in *Anisolabis* is 26 in the female, and 25 in the male both in somatic and germinal cells.

2. The only variation from the above is in the male somatic cells, where only 24 chromatic elements may often be counted. This may be due to a fusion of the two x-chromosomes in the male cells or to the loss of the y-chromosome.

3. Primary spermatocytes show twelve chromosomes: eleven are autosomal tetrads, and one an xxy-hexad.

4. The xx-element together with 11 autosomal dyads pass into one secondary spermatocyte; the y-element and 11 autosomal dyads pass into the sister cell.

5. In the interkinetic period the two x-chromosomes separate and appear as discrete bodies in the second maturation spindle. We therefore find 13 chromosomes in one half the metaphase plates, and 12 chromosomes in the other half.

6. All chromosomes divide equationally in the second spermatocyte division, giving rise to female determining spermatozoa with 11 autosomes and two x-chromosomes, and male determining spermatozoa with 11 autosomes and a y-chromosome.

7. The y-chromosome of the spermatocyte is chemically and morphologically rather unlike the x-chromosomes during the growth period up until the late strepsinema, when it gives off a nucleolar spherule which takes mitochondrial stains.

Granville, Ohio, June 28, 1921.

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10. EXPLANATION OF PLATES

All drawings were made with the aid of a camera lucida. A 1.5 mm. Zeiss apochromatic objective and a 20X compensating ocular was the optical combination used. All figures were drawn at 3300 diameters magnification and subsequently reduced, in Plate XXIV the reduction being about one-third and in Plates XXV and XXVI the reduction being about two-fifths.

PLATE XXIV

Figs. 1-4. Oögonia, metaphase plates, polar view, 26 chromosomes.

Figs. 5-8. Somatic metaphase plates, polar view from female embryo, 26 chromosomes.

Figs. 9-12. Spermatogonia, metaphase plates, polar view, 25 chromosomes.

Figs. 13-16. Somatic metaphase plates, polar view from male embryo, showing 25 chromosomes.

KORNHAUSER: CYTOLOGY OF ANISOLABIS MARITIMA BON.

PLATE XXV

PRIMARY SPERMATOCYTES

- Fig. 17. Early leptotene nucleus, showing xx and y
Fig. 18. Trifle later stage than Fig. 17, xx and y in close apposition.
Figs. 19-20. Nuclei of syndetic cells, xx and y connected.
Figs. 21-22. Diplotene nuclei, showing separation of xx and y-elements.
Figs. 23-24. Early strepsistene nuclei, showing reunion of xx and y.
Figs. 25-26. Later strepsistene nuclei, showing fusion of xx and y.
Fig. 27. Late strepsistene, showing the formation of the nucleolar spherule
(nl)
Figs. 28-29. Primary spermatocytes, metaphase plates, polar view, showing 12 chromosomes.
Figs. 30-33. Primary spermatocytes metaphase, lateral view, showing xxy-hexad
Fig. 34. The twelve chromosomes of a primary spermatocyte metaphase. xxy on extreme right, taken from a section.
Fig. 35. Same stage as figure 34, except that it was taken from a smear slide.
Fig. 36. Various forms of the xxy-hexad, as seen in metaphases and anaphases of primary spermatocytes viewed laterally. y-element shown above in each case.

PLATE XXVI

Figs. 37-38. Anaphases of primary spermatocytes, showing separation of xx and y. In figure 37, the hexad is in linear arrangement; in figure 38, the two x-chromosomes are placed side by side and the y-chromosome is above.

Fig. 39. Late Anaphase of primary spermatocyte, the xx-element passing to the upper pole in the figure.

Figs. 40-41. Sister anaphase plates of cell corresponding to figure 39. In figure 40, the y-element is included; in figure 41, we see the xx-element.

Fig. 42. Interkinesis.

Fig. 43. Metaphase secondary spermatocyte, lateral view.

Fig. 44. Metaphase secondary spermatocyte, polar view, showing 13 chromosomes.

Fig. 45. Metaphase secondary spermatocyte, polar view showing 12 chromosomes.

Fig. 46. Sister cells, secondary spermatocytes, metaphase, polar view: one showing 12, the other 13 chromosomes.

Fig. 47. Same stage as figure 46, but taken from a smear slide.

Figs. 48-49. Giant secondary spermatocytes, metaphase, polar view, showing 25 chromosomes

Figs. 50-51. Sister anaphase plates of a secondary spermatocyte (12 chromosome type), showing exact distribution of chromatin to spermatids.

Fig. 52. Spermatid, shortly after second meiotic division.

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