The early History of the cellular elements of the Ovary of a Phryganid, Platyphylax designatus Walk.

By

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(From the Zoological Laboratory, University of Berlin.)

With Plate XV and XVI.

The larva of *Platyphylax designatus* can be obtained throughout the year in some springs in the vicinity of Madison, Marshall and Vorhies (26); the pupae are very easy to get, and the imagoes may readily be caught if one visits the springs during the few days they are alive. My material was all obtained at this place and the work on the following paper done in the Zoological Laboratory of the University of Berlin. I desire to thank Prof. F. E. Schulze for the use of the laboratory and library of the Zoological Institute.

The principal preserving fluid used was Flemming's, both weak and strong; a modification of Gilson's and Hermann's solution were also used. Flemming's triple stain and Heidenhain's iron-haematoxylin I made use of more than any other stains, but sections were stained with a number of the commoner fluids, and with safranin alone; this last, when well washed out, gave very beautiful results.

The question concerning the origin of the cellular elements of the ovary has been discussed by many who have worked with the ovaries of different insects; such good reviews can be found in the works of Korscheit (22), Gross (11) or Henneguy (17) that it seems superfluous to repeat the subject here. The discovery of nuclei and cells within the ovarian tubule occurred long ago; then came the question as to the origin of the different cellular elements, a question on which nearly every one who has worked on the subject has had something to say. Workers like Huxley (20), Lubbock (25) and

Claus (6) gave, many years ago, a clear solution of the problem; to this short list might be added many more. These views have not been held by all and there have also been many who have given different ones as to the origin of oöcyte, nurse and epithelial cells. At present the question is that concerning the origin of the epithelial cells; do the cells, as many believe, all have a similar origin, or do these originate differently than do the oöcytes and the nurse-cells, Heymons (18), Giardina (8), Gross (11).

It seems hardly necessary to enter here into a review of the work which has been done on the later maturation of the egg and the subject of tetrad formation. In neither of the cells which here in *Platyphylax* form paired chromosomes and have a rather doubtful tetrad formation, has the work been carried on to the following division. This in the nurse-cells would of course be impossible as they do not again divide, and their history, where we leave it, is almost ended. With the oöcyte one would have to carry on the observations through the formation of the polar bodies, a work we have not undertaken. The tetrad formation is in *Platyphylax* rather doubtful, some of the paired chromosomes undoubtedly breaking up without passing through this stage or, if reached, it is only one step in their disintegration. Our account of their formation is, in general, similar to that of Rückert, Häcker and vom Rath.

Historical.

Very few groups of insects have received less attention from entomologists than have the Phryganeidae, and when one endeavors to find papers treating of the anatomy or histology of the reproductive organs, there is very little to be found. The only papers I have been able to find which, in this group of insects, would be of any comparative interest with our subject are those by Brandt (3), Stuhlmann (36) and Stitz (34).

Brandt's (3) work has here and there a mention of the ovary of *Holostomis phalaenoides*, the principal caddis-fly he studied; he was unable to find an epithelial layer around that part of the chamber in which were the nurse-cells, and noted, correctly, that these same cells become spindle shaped around the old oöcyte. His figure of an ovarian tubule of *Holostomis* shows very little cellular structure. At one place he says »An den voluminösen und grobkörnigen Dotterbildungskeimbläschen von *Holostomis* konnten die Keimflecke weniger überzeugend zur Anschauung gebracht werden.«

Stuhlmann (36) figures (Plate VII, Fig. 113 and 114) two chambers of the ovary of *Anabolia*; one of these a young and the other an old one. The structure of the nuclei is not well given, but in the younger oöcyte, »Im Keimbläschen ist ein größerer Nucleolus und einige Granulationen sichtbar, welche wohl als Reste des Kerngerüstes anzusehen sind«. In the oldest oöcyte the nucleus is represented by a small irregular mass in one corner. The nurse-cell nuclei are all regular in outline. He called attention to the similarity of these tubules to those of the Lepidoptera.

Stitz (34) has very little to say about those parts of the ovary with which we are most interested. In the end chamber of *Phryganea striata* he found two kinds of nuclei; »Die Endkammer jeder Eiröhre zeigt im Innern zwei Arten von Elementen: eiförmige, oft gekrümmte Kerne, welche hell und feingranuliert sind, und kugelförmige homogen aussehende mit dunklem Nucleolus.« The first of these two kinds, becomes, further down the tubule, spindle-shaped, and they later become the nuclei of the epithelial cells; the second kind become the nuclei of the oöcytes and nurse-cells. In the terminal filament of *Molanna augustata* there were, near its end, both small and long nuclei, but further down these changed and were shorter and nearly round in outline.

Observations.

Ovary A. This ovary was taken from the youngest larva I had, and, while not as early a stage as I wished to commence with, it was impossible, without waiting at least an entire year, to procure any younger ones. A study of the many tubules of which this ovary is composed, shows that there is quite a variation in the development reached by the cells in different ones. As in *Polistes*, each ovarian tubule showed that the cells in its proximal end or in the middle, were more advanced than those at the distal end. When two tubules, one showing a further development than the other, were compared, it was noticed that the more advanced cells which the older tubule contained, were always present at or near its proximal end. Thus in the youngest tubule of this ovary no nuclei were found in which the spireme-thread was present; in the older ones on the contrary such a stage was found but never in the distal part of the tubule. Some of the youngest tubules showed, in each section, two to six cells in the nuclei of which the spireme-thread was forming; in all such sections these few cells were in the proximal end.

Any tubule (Fig. 1) from ovary A shows distally a well formed terminal filament, the cells of which, except at its very tip, are elongated and lie across the filament Leydig (24), Paulcke (28). The nuclei within these cells are also much elongated; each contains a small nucleolus and a number of chromatin granules which are connected by achromatin strands (Fig. 2). Following the terminal filament is a large chamber, oval in outline, in which cells are found in different stages of development. These chambers differ somewhat in shape, due to the pressure of the neighboring ones, and we find them long and narrow, or shorter and thicker. Along the margin lie most of the smallest cells; they may show an epithelial-like arrangement, or, in many tubules, this may to a great extent be lost. It is not true that all marginal cells are small and have small nuclei, for we find, here and there, some on the margin as large as any in the central part of the chamber (Fig. 4 *c*). Tönniges (37) has found that in Myriopods some of the epithelial cells of the wall of the ovary, grow to form undifferentiated cells, which may later develop to oöcytes, nurse- or follicle cells. Proximal to this chamber is a stalk which connects it to the long oviduct common to all the tubules of each ovary. In this early stage the stalk has a small lumen but the oviduct itself (Fig. 1 *odt*) is still solid. Of these latter parts no further notice will be taken, this account being confined entirely to the cells which lie between the terminal filament and the basal stalk, and from which develop the oöcytes, nurse- and epithelial cells. In both the stalk of the tubule and the oviduct there are many mitotic figures.

From this ovary, A, we shall select two tubules, one of the youngest (Fig. 1) and one of the oldest (Fig. 8), and describe the different kinds of nuclei the cells in each contain. In most, but not all, of the sections through any of the tubules are a few mitotic figures; they may occur in any part but are more numerous near the margin.

In the youngest tubule (Fig. 1) are a number of cells with nuclei showing different structures but there are not so many kinds as will be found in later stages. In the distal region we find the greatest amount of similarity in their structure, but even here the cells differ much in size and also in the contents of their nuclei. Some of the cells lying at this region along the margin show, from their nuclear structure, a great similarity to the cells of the terminal filament; these represent the youngest stage. In *Polistes* we have shown that the gonads of the embryo and youngest larvae contain nuclei which are all similar (HENKING [16]). We believe that in *Platyphylax* the same would be true and that this kind of nucleus would be the only one found in the very young larvae. These undifferentiated cells (Figs. 3, 4 and 5 *a*) have either an oval or sperical nucleus; in this there is a single achromatin nucleolus, a number of small chromatin granules connected by achromatin strands. These cells and their nuclei grow; the first change we notice in their structure is an increase in the size of the chromatin granules which become very prominent (Figs. 3 and 4 *b*). Cells with such nuclei are mostly in the distal half of the tubule. The chromatin granules become in many so prominent as to appear, from a surface view, to nearly fill the nucleus. They are mostly peripheral in position and are nearly square in shape. The large achromatin nucleolus is present, the strands are not so noticeable but a little achromatin matter lies around each chromatin granule and can be seen extending some little distance from many of them. Whether the strands really in part disappear or are hidden by the large chromatin granules I am unable to say. There are many nuclei with both large chromatin granules and prominent achromatin strands, but these we believe to be the next stage. Such nuclei (Fig. 5 *c*) we find at almost any place, except the proximal end, in this tubule. They show quite distinctly a small achromatin mass around each chromatin granule and these are all distinctly connected to each other by strands of the same material (Figs. 4 and 5 *c*). Any of these nuclear structures we can find in cells at the margin or in the center of the tubule, although certain of them, *a* and *b*, are more abundant in the former region. In fact these two stages we never find at any distance from the margin except in the distal part of the tubule. In most of these early stages the nucleolus is quite prominent, and in many (Fig. 6) reaches, relatively, a very large size. We find that nuclei of the same size may have a large or a small nucleolus, but we were unable to distinguish any relation between relative size of nucleus and its nucleolus, to the stage of development. In darkly stained slides the nucleolus would be dark, but when the stain had been well washed out of the section, it either had no color at all or a very slight tinge; in all these sections the chromatin granules were dark.

With the increase in distinctness of the strands we find a decrease in the size of the chromatin granules, they become small and loose their regularity of position within the nucleus. This tubule also shows a more advanced stage, represented however by few cells and these at the proximal end. In these (Fig. 7) the former large chromatin granules have entirely disappeared and the strands have become quite regular. In these nuclei are seen a number of dark and of light granules; the former are the ends of the strands, seen in real or optical section, the latter represent the beginning of a beaded structure which becomes more noticeable in older stages.

The second, more advanced, tubule from ovary A (Fig. 8) shows, even under a low power, quite a difference from the one we have described. At the distal end, and along a part of the margin, are a number of cells with nuclei very similar in structure to those we found present in the younger tubule. We find some which are similar to those we have designated as the youngest, undifferentiated, stage; others are also present with large prominent chromatin granules (Fig. 9 *b*) and some in which these have begun to disappear and the chromatin strands to become more distinct. As development goes on the chromatin granules decrease in size and regularity of position and the strands, which before this were prominent, begin to show a beaded appearance (Fig. 9 *c*). In larvae of *Bombyx* Grünberg (12) observed that the oogonia lying nearest the oviduct, changed the original arrangement of their chromatin and form a spireme. After the disappearance of the chromatin granules, beaded strands are all that we notice, except the nucleolus, within the nucleus (Figs. 11, 12 and 13). Along the margin some cells show, by the structure of their nuclei, that they are not so far advanced.

In all the tubules of this ovary there are found a few cells which are larger than any of the others (Fig. 14). These apparently pass through the same stages as the others and can be found in any of those we have so far described. At first it seemed possible that these were the oöcytes, which, in the later stages, will be seen to be larger than the nurse-cells, although their nuclei show but a slight, if any, difference in size. This explanation seemed very good but when we came to study the older stages we failed to find a few cells larger than the others. It seems more likely that there is a considerable difference in the size of the cells, and that the few largest are, from their size, more noticeable than the others.

We notice, in this youngest larva, that there are many different nuclear structures but that they are all very similar to some one of the several we have described. The first differentiation of the cells has here taken place, and we find that they all come under one of two groups; 1st, cells with nuclei similar to those of the terminal filament; 2nd, those with nuclei very different from this in structure, but which we believe have come from nuclei similar to the first group. Of the first group there is little to be said. We meet them again in all the stages we study, and, in the pupa, cells with similar nuclei form the epithelial layer. These undifferentiated cells show no further change in nuclear structure but, increasing in number by mitosis, form the follicle around the oöcyte and the thin epithelial layer of the nurse cells. While the second group shows many different nuclear structures the cells all pass through the same development; as yet they show no indication of their future fate.

Mitosis occurs throughout this ovary and the question at once arises, do these cells, in their development from undifferentiated ones and after they have reached the second group mentioned above, pass through one or two divisions, or, are the dividing cells only the undifferentiated ones increasing in number. This is a difficult question to answer. From our study of *Polistes* we found that at one time all nuclei within the gonad were similar in structure; as the gonad grew these nuclei increased in number, dividing mitotically. The same is undoubtedly true for *Platyphylax* at corresponding stages. In the older larvae and pupae of *Platyphylax* we fail to find nearly so many dividing cells as in this stage. If the cells we have just been describing, those of the second group, passed through one or more divisions we must have found in some of the many ovaries examined, a zone containing many cells in mitosis, or else some region, as that of synapsis, where a number of dividing cells would occur together. This we do not find, and we hold that after the oöcyte or nurse-cell has started on its development from an undifferentiated cell, it does not divide. This we did not find true for the nurse cells of *Polistes* where a number of divisions take place. In the two insects the conditions however are different. In *Polistes* the number of nurse-cells accompaning each oöcyte is much greater, as is also the number of eggs each ovarian tubule produces. In *Platyphylax* the eggs are all laid in a very short period, but in *Polistes*, this period is very much longer and the eggs in the ovary are continually growing.

Ovary B. This ovary shows a considerable advance over what we found in the last one and its oldest cells are much further developed. If we take any section which passes longitudinally through the center of a tubule, we can trace in it nearly the entire history of the cells, from their first change from an undifferentiated cell, to the stage when they have the paired chromosomes as possessed by all young oöcytes and nurse-cells. All these last mentioned, here the oldest, cells have similar nuclei, and it has been impossible, in this tubule, to distinguish between oöcyte and nurse-cell; at a little later stage this can be done by the size of the former. We shall see later that when the group of oöcyte and accompanying nurse-cells are first formed they show no difference in nuclear structure.

Distally in this tubule (Fig. 15 *a*, *b* and *c*) we find the same nuclear structure present that we found in the younger ovary. Only a few undifferentiated cells (Fig. 15 *a*) are present, and these are, with few exceptions, found on the margin. In most of the cells at this end the nucleus shows a number of large chromatin granules, and this stage is here much more prevalent than any other. These are of exactly the same structure as we found in ovary A (Figs. 3, 4 and 5 *b*); each has an achromatin nucleolus and a number of large, rather square, chromatin granules (Fig. 16 *b*) around each of which lies a small mass of achromatin. The next stage, that in which the achromatin strands become prominent, is found scattered in among these last and also lying proximal to them (Fig. 15 *c*). During this change many of the strands show a beaded structure even before the chromatin granules have decreased very much in size (Fig. 16 *c*). We find that, as the chromatin granules disappear, the beaded strands become more and more prominent until, when the spireme-threads have formed, there is nothing left of the former (Fig. 20). A somewhat similar spireme-thread stage is figured by GRÜNBERG (12) for *Bombyx mori* and he says that all »Keimzellen« nuclei pass through it. He describes the thread as at one time beaded. A beaded spireme-thread has been found by STSCHELKANOVZEW (35) for *Aphis rosae*.

At about the middle of the tubule (Fig. 15 *c*) we find a number of nuclei in synapsis; these are at once distinguished by their structure and their staining darker than in the last stage. Neither PAULCKE (28) for *Apis*, nor GRÜNBERG (12) for *Pieris*, could find any cell boundaries during synapsis as we find them here in *Platyphylax*. The nucleolus is still present but generally hidden, it does not always lie at the pole towards which the threads have contracted. It is rather difficult to distinguish any difinite arrangement of the threads; most of them lie closely packed together and do not show such great regularity as GIARDINA (8 and 9) has figured for

Dytiscus and *Mantis*. The threads staining darkly makes it impossible to always distinguish their beaded structure (Fig. 21). After synapsis the threads become again distributed throughout the nucleus; at first they are quite thin and are beaded (Figs. 22 and 23). The cells that come out of synapsis develop to either oöcyte or nurse-cell (Woltereck [41]) but it is yet some little time before we can distinguish between them.

There now occurs a rather sudden change in nuclear structure the transitions to which we have not been able to determine; this is the change from the last stage (Fig. 23) to what we next find (Fig. 24). In this latter we see that the threads have become very much thicker and shorter, and that in each, two long, narrow chromosomes have appeared. These are thin, somewhat curved to follow the shape of the thread, and they stain quite darkly. In diagonally cut threads they naturally appear as two short rods. Contraction of the thread goes on, the chromosomes become shorter and thicker and increase in distinctness (Figs. 25 and 26). The position of the cells having such nuclei is shown (Fig. 15 *g*) and they are seen to lie further towards the proximal end than any we have hitherto described.

At least one quarter, the proximal, of this tubule, is occupied with cells whose nuclei show, that the contraction of the threads and chromosomes, is completed. Each piece of the former thread is now nearly square and contains a pair of short chromosomes (Fig. 27). The nucleolus is still present and remains unstained entirely or only slightly tinged.

Ovary C. This larval ovary shows very distinctly the grouping of the oöcytes with their accompaning nurse-cells; no chambers are yet formed, nor do we find that the two or three oldest oöcytes, are arranged behind each other in the tubule as in older stages. In the section of the tubule (Fig. 28) we have drawn, we see the proximal oöcyte lying in the middle, but other tubules from this same ovary showed, at this region, two lying side by side. The proximal half of the tubule is occupied by groups of oöcytes and nurse-cells, and in the distal half are cells which show the different, earlier stages, of development. Of these latter we will here say nothing the structure being similar to what has been described for ovary B, and nearly the same, as we find in a slightly older stage, ovary D, which we next take up.

The ovary we now describe, C, shows so well the change and breaking up of the paired chromosomes in the nurse-cell nuclei, that we will speak of it at this place. The formation of the dyads, of their assuming a dumb-bell shape, and finally the tetrad formation, is very similar in the nurse-cells of *Platyphylax* to what GIARDINA (8) found in the same cells of *Dytiscus*. GRÜNBERG (12) also notices for *Pieris*, that the tetrads in the nurse-cell nuclei, break up into many small granules which finally fill the nucleus. In about the middle of the tubule each oöcyte has lying distal to it, or slightly at its side, a group of nurse-cells; in the nucleus of both kinds of cells there is, besides a large achromatin nucleolus, a number of small achromatin masses, remains of earlier threads, in each of which lies a pair of chromosomes. In the youngest group we have drawn (Fig. 29) the oöcyte is larger than any nurse-cell, but the structure of its nucleus is the same. As in all the groups the oöcyte nucleus remains unchanged (Figs. 29 to 33 *oö*), we need not speak of it but confine ourselves to that of the nurse-cells. A little older stage shows, that while there are some distinct paired chromosomes present, in the place of many of them there is an apparent tetrad formation (Fig. 30). Some of these are undoubtedly tetrads, but in others the appearance is due to the chromosomes each having the shape of a dumb-bell with a thin, bent handle, which is not always seen. A slightly older cell (Fig. 31) shows about the same structure, but we notice, that instead of paired rods or of tetrads, there are some groups of five or more small chromatin granules which have come from the breaking up of the paired chromosomes. Still a little later (Fig. 32) these paired chromosomes and tetrads entirely disappear, and in their place, we find small groups of chromatin granules, not of five or six, but more in number. Each group is entirely distinct from the others. The granules then spread throughout the nucleus until they occupy a position similar to what we find in the oldest nurse cell (Fig. 33) of this tubule; here the groups have become entirely lost and the chromatin granules spread throughout the nucleus GIARDINA (8), GRÜNBERG (12). They have increased very much in number, but only in part fill the nucleus, leaving in it large, empty spaces. As we have already said the first of these granules come from a breaking up of the paired chromosomes; whether the others come from those already formed or not we do not know. The number seen in older nurse-cell nuclei is too great to all be derived from a breaking up, or a separation, of the paired chromosomes. In the oldest nurse-cell nucleus of the next stage, ovary D, (Fig. 36) we find a nearly similar structure. There are here however two nucleoli instead of one and, as in older stages, we always find them more in number, we judge that here this increase has begun. Here also we find the nucleoli always staining and they become the most prominent structures within the nurse-cell nucleus.

In ovary C, we have for the first time found that oöcytes and nurse-cells have become differentiated and many of them arranged in groups, each one of which will, in still later stages, form a chamber. In the youngest group we can here distinguish as such, we find that the only difference between oöcyte and nurse-cell, is in the larger size of the former; their nuclei are, both as to size and structure, alike. The paired chromosomes which both contain, are at first similar, but here in this larval stage, ovary C, those within the nurse-cell nuclei begin to change and from them come a large number of small chromatin granules. The single achromatin nucleolus of the nurse-cell nuclei persists throughout, but at a little later stage, ovary D, we always find more than one. While the nurse-cell nucleus has passed through these changes that of the oöcyte remains unchanged.

Ovary D. This larval ovary shows (Fig. 34) that it is somewhat older than the last; there are as yet no chambers formed but the three oldest groups of oöcyte and nurse-cells are arranged in the center of the tubule. In the last ovary we described the proximal half of the tubule, and, as in this one nothing different in cellular structure is shown, we shall confine the description to what is found in the distal part.

Here (Fig. 35) we find a more distinct epithelial layer than is generally seen. The cells composing it are in different stages of development: undifferentiated nuclei, *a*; some with large chromatin granules, *b*; and those in which the threads have begun to be formed, *c*. Of these the undifferentiated kind, *a*, are found along the margin and most of them close to the distal end of the tubule; the other two kinds are found both at, and away from, the margin. In the center different stages in the formation of the spireme-thread are seen and some nuclei in synapsis. The most proximal of all the nuclei are seen to have the paired chromosomes already formed. All of these nuclei have an achromatin nucleus.

Ovary E. This tubule (Fig. 7) is from the ovary of a pupa; it has five well developed chambers each with an oöcyte and the accompanying group of nurse-cells. These cells have increased very much in size; the epithelial cells have increased in number, and arranged themselves around the oöcyte and, indistinctly, around each group of nurse-cells. They also separate the chambers from each other, and a few may lie between an oöcyte and the nearest nurse-cells belonging to it.

Distally there is as usual a terminal filament; this is followed by a long, narrow end chamber which, by a slight indentation, is nearly divided into two parts. In this end chamber (Fig. 38) are found a few developing cells and a number of bodies we hold to be dead ones. These latter are of different shapes; each lies in a clear space and consists of a rather homogenous mass in which is a large, darkly staining body that, in most of them, has a distinct outline; in some however this is not so and the stained part goes over very gradually into the unstained mass. A few of these bodies are large and different consisting of a rough unstained mass in which no structure can be made out. The regular cells which are here present, show different stages in development from the undifferentiated cells, *a*, to those with large chromatin granules, *b*, and one, *c*, in which the strands are being formed. Near the proximal end of the tubule are two cells, *d*, in the nuclei of which the spireme-thread is already formed.

In the five chambers (Fig. 37) we notice, as we pass from the youngest to the oldest, that the proportion of each chamber occupied by the oöcyte increases, and that filled by the nurse-cells, decreases. The first, most distal, chamber shows five nurse-cells, the nucleus of each contains one or two rather large nucleoli and a great many small granules; these latter are connected by delicate achromatin fibrils. The nucleus of the oöcyte contains a few of the paired chromosomes we have already noticed. Epithelial cells lie around the oöcyte and a few are seen at the margin of that part of the chamber in which the nurse-cells lie. In this youngest chamber the cytoplasm of all the cells stains equally, but, in the older ones, the nurse-cells are darker than is the oöcyte.

The oöcyte of the second chamber may have either a round or a pyriform nucleus, the latter shape, when present, being due to a thick process which extends up between the nearest nurse-cells. In the three other chambers, the oöcyte becomes much flattened and is more rectangular in outline. In each of the four last oöcytes the nucleus contains a large nucleolus in which there are a number of vacuoles. The paired chromosomes, present in the earlier stages, have disappeared, but the achromatin masses, former threads, are present and in each are one or more small chromatin granules, or rods; there are also very many smaller achromatin bodies free from these. All these parts are joined by achromatin fibrils. The outline of the oöcyte nucleus is generally irregular but not so much so as are most of the nurse-cell nuclei. Within the basal part of the oöcytes, are generally a number of round, dark bodies, which represent some product of the metabolism of the cell; in specimens preserved in Flemming, these are always black.

In all the four oldest chambers the nurse cell nuclei are very similar. Each contains a few large, irregular nucleoli, which stain darkly, a great many small granules, also staining, and achromatin fibrils connecting these. Many, but not all, of the nuclei are quite irregular in outline.

In the nucleus of each of the two oldest oöcytes, we find that a change has taken place which connects the younger ones we have described in other stages (Fig. 36), with the oldest one of the next ovary (Fig. 49). The nucleolus is present, containing two or three large and a great many small, vacuoles, which almost fill it, Dublin (7). Scattered throughout or occuring in groups are a great many small unstained bodies. A few of the largest of these still show within them a distinct chromatin spot or spots; this is all that is left of the earlier paired chromosomes. In the space left free from these bodies there is a delicate achromatin fibrillar mass.

In ovary C, we found that the paired chromosomes which are at one time similar in both oöcyte and nurse-cell nucleus, broke up into many pieces which became scattered throughout the nucleus. In the oöcyte nucleus this change was not seen but the structure of the oldest oöcyte in that stage was similar to the youngest (Figs. 29 to 33 *oö*). We now find in the pupa that, while the younger oöcyte nuclei still have the paired chromosomes in them, the oldest ones show a different structure. The change is not however similar to what we found in the nurse-cells nuclei. In an old larva one can find that a few of the paired chromosomes in the oöcyte nucleus have changed to tetrads (Fig. 36) but we doubt if they all pass through such a change. Each pair of chromosomes lies, as already described, in a small mass of achromatin, the remains of the contracted thread. As new achromatin bodies appear in the nucleus, some are always to be seen which are larger than the others, and, in each of these, is a distinct chromatin rod or dot (Figs. 39 and 40) which is all that remains of the paired chromosomes or the tetrads. These we find persist through still older stages (Fig. 49). The history of the nucleolus in the oöcyte nucleus differs from that in the nurse-cell. Here in the oöcyte it does not change to a chromatin one, nor do we as a rule find oöcyte nuclei with more than a single one although some are seen with one large and one or two small ones. The nucleolus first changes by becoming filled with vacuoles and then, at a later stage (Fig. 49), decreases in size.

Ovary F. This tubule is from the ovary of a pupa. In a longitudinal section one can distinguish a small terminal filament, followed by an end chamber which, in very many tubules, is divided by a small indentation into two parts. The anterior of these contains a number of nuclei in early stages of development up to the formation of the paired chromosomes (Fig. 42). In the more proximal part are found oöcytes and nurse-cells which are already arranged in groups. Following this are the regular chambers (Fig. 41), small at first, but, as we pass down the tubule, the cells increase considerably in size and consequently the chambers themselves. In this tubule there are five well marked chambers, separated, in an external view, by indentations formed by a narrowing of the tubule. In section the chambers are also seen to be separated by elongated epithelial cells which extend across the tubule. Each chamber is divided into a distal part containing the nurse-cells, and a proximal portion within which lies the oöcyte; between these there is no distinct separating part. In all the chambers a well defined layer of epithelial cells surrounds the oöcyte, but, along the margin of that part in which lie the nurse cells, one sees only a few epithelial nuclei.

To show the relation of the cells to each other three views are given: 1st, (Fig. 42) most of the terminal filament and the distal portion of the end chamber; 2nd, (Fig. 43) the other, proximal, part of the end chamber; 3rd (Fig. 41) the remainder of the tubule showing the five chambers. The second and third of these drawings were from the same tubule, but the first from another one of the same ovary.

The terminal filament (Fig. 42) is composed of a single row of cells, these are nearly square at its tip but they narrow very much towards its base. The shape of the nuclei changes with that of the cells; in structure they are similar to those we described (Fig. 2) from an earlier stage. Distally within the end chamber are a number of cells with undifferentiated nuclei (Fig. 42 *a*); their similarity, both to those occupying a like position in younger tubules (Figs. 4, 15 and 35 *a*) and to nuclei of the terminal filament, is noticeable. Other early stages are found in this region, those in which the chromatin granules are very large (Fig. 42 *b*) and also nuclei in which the achromatin strands are becoming prominent (Fig. 42 c). Whether all the most distally situated nuclei have cell boundaries or not is difficult to determine. Proximal to these cells is a group in whose nuclei the spireme-threads heve been formed (Fig. 42 *d*). These do not here show any variations, the threads stain but lightly, and they belong therefore to a stage previous to synapsis. Following these are some cells whose nuclei have very distinct paired chromosomes. In all these a chromatin nucleolus is present. The paired chromosomes lie in small achromatin masses. To the left in this figure are shown a few abnormal cells which are disintegrating, and have already lost their regular form and structure. Such bodies are found in many of the sections from ovaries of different ages, but not so abundantly in young, as in old ones.

The next part (Fig. 43) shows a few undifferentiated nuclei, which later become epithelial cells, and three groups of oöcyte and accompaning nurse-cells. The proximal of the three groups shows only four nurse-cells, the oöcyte belonging to these, not being in the section from which the drawing was made. Just distal to these three groups are a number of cells (Fig. 42) in whose nuclei are many paired chromesomes; here in the groups we also find a similar structure in the oöcyte nuclei, but see that in the nurse-cells they have begun to break up. This is here similar to what we described for the last stage. The paired chromosomes always disappear from the nurse-cells earlier than from the oöcytes.

The remaining and much the largest part of the tubule (Fig. 41), is composed of five distinct chambers which show a regular gradation in size. The oöcyte of each of the first two chambers sends a large blunt process up between the nearest nurse-cells (Fig. 44). The nucleus of this, the youngest, oöcyte shows the paired chromosomes still present, and with these a large achromatin nucleolus. In the next oldest oöcyte this is not the case (Fig. 46), the paired chromosomes have nearly disappeared as such, and in their place an irregular chromatin rod or small mass is seen. In still the next oldest oöcyte

(Fig. 47) this change is shown more clearly and in each achromatin mass we still find, instead of the paired chromosomes, the small pieces as in the last. Loose achromatin fibrils become, in this stage, more distinct. Here will be noticed a difference in the fate of the paired chromosomes in the oöcytes and in the nurse-cells. In the former we have just learned that, still remaining in the original achromatin mass, they break up into a few small pieces which remain in the original position. In the nurse-cell nuclei we found that this reaking up occurs earlier, and the resultant pieces become scattered throughout the nucleus.

In many of the nurse-cells of these chambers we find that the nucleus shows an irregular form; this may be a general irregularity over the entire surface (Fig. 48), or one or more deep indentations at one place (Fig. 46). This has to do with the secretory activity of the nurse-cells of which we will speak later.

Concerning the epithelial cells there is little to say that cannot be seen from a view of the tubule (Fig. 41). In that part of the chamber occupied by the nurse-cells, they are almost entirely missing, only a few nuclei being found along the margin. We are inclined to the belief that there is here a continuous layer of epithelial cells, but that the pressure from the nurse-cells has so flattened them, that only here and there can they be seen. Between the chambers there are a number of long narrow cells which are much larger than the others, and, excepting near its base, each is nearly empty. Between each oöcyte and its accompanying nurse-cells there are also a few flattened epithelial cells. All these cells have similar nuclei (Fig. 50).

We have already noticed the breaking up of the paired chromosomes of the nurse-cell nuclei into many small granules. After this has occured each nucleus also contains a few irregular bodies, nucleoli, which now stain, and which we believe came from the single unstained one of the earlier stages. It has been continuously present through all of the stages. During the further growth of the nurse-cells there is no change in nuclear structure except an increase in the number of nucleoli. Wether these come from the one already present, or from some other substance within the nucleus, we do not know. The fine achromatin fibrils are much more distinct in the older stages.

The nucleus of the oöcyte, after the breaking up of the paired chromosomes, contains a large, generally vacuolated, nucleolus which is unstained; besides this there are many achromatin bodies in a few of the larger of which the remains of the paired chromosomes may be seen. There are also a number of achromatin fibrils connecting these parts. The changes from here we have spoken of in another stage and will now only call attention to the nucleus of the oldest oöcyte in this tubule. This (Fig. 49) shows a proportionally smaller nucleolus and a great increase in the number of the achromatin bodies which do not as yet entirely fill the nucleus.

Korschelt (21) some time ago called especial attention to the secretory activity of the nurse-cells in insect ovaries, and many others have noted the same fact. This is shown so plainly in *Platyphylax*, that we would call attention to it in this stage where it shows as well as in any other. Before the group of oöcytes and nurse cells have arranged themselves into chambers (Fig. 43) this activity has begun. The cytoplasm around the nuclei, especially along those parts facing other nuclei, is darker and denser than that found in the other part of the cell. This occurs on those sides of the nurse-cell nuclei which face the oöcyte, and in that part of the oöcyte which lies nearest the nurse-cell. These darkened masses may fuse with one another or strands may connect them. As yet the regularity in outline of the nuclei has but slightly changed, if at all. In older groups this is different (Fig. 46) for we find at least one surface of each nucleus becoming very irregular. This is due to a sinking in of the nucleus at one point, and, where this occurs, its surface is exceedingly irregular. This in *Platyphylax* may go so far as to nearly penetrate the nucleus or separate it into two parts. A few cells may be found which at first appear to be binucleate, but this appearance is only due to the partial separation of the single nucleus. In older stages (Fig. 47) this activity is still noticed; the oöcyte nucleus is also irregular but not so markedly so as that of the nurse-cells.

Ovary G. This ovary is from an old pupa; in each tubule there are four or five chambers and a terminal filament. The proximal, oldest, chambers show a great increase in size; they have broadened so much that the last one is nearly round. The difference between these and the others is not in size alone but also in the structure of the oöcyte and its nucleus.

The most distal of all the chambers (Fig. 51 *1*) not only contains a few cells in different stages of development, but, in its proximal part, are to be found an oöcyte and its accompanying nurse-cells. The cells in the distal part do not show a very great variation in structure, and it would be hard, from so old an ovary, to find all the changes in their development. We find both ovoid and spherical nuclei in which there are a number of large chromatin granules, the majority of the cells here being in this stage (Figs. 53 *b* and 54). A few cells are also present in which the strands are becoming very prominent (Fig. 53 *c*). From this stage we pass directly to the group of cells in the proximal part of the tubule, without finding spireme-thread or synapsis stages. It is not likely that the oöcyte in this or even the following chamber ever develops. An examination of the ovary of a mature *Platyphylax* seldom shows more than three chambers containing mature eggs. This means of course the number in an ovarian tubule, not in the entire ovary. As the eggs are all laid soon after the mature insect emerges, and, as its life is very short, it is hardly possible that eggs which are not entirely developed before the mature insect emerges, will ever do so. *Platyphylax* is similar in this respect to the Lepidoptera; the same has been observed by Gross (10) in other forms of insects.

The oöcyte which lies at the base of this youngest, most distal, chamber, has a somewhat flattened nucleus. It contains an achromatin nucleolus (Fig. 55) and a number of paired chromosomes similar to other nuclei we have described. The nurse-cell nuclei are the same as those we have found in the youngest stages. In the entire chamber there were but a few epithelial nuclei some showing a regular arrangement around the oöcyte.

Nothing new is seen in the next chambers. In each the oöcyte nucleus contains a number of paired chromosomes although, in the older one, these are beginning to break up. The nurse-cells of both chambers show a normal structure, the nucleus of each containing a few nucleoli and many of the small granules we have already noted in other stages.

The two oldest chambers show considerable differences from anything we have hitherto found, and they are in a much older stage. This is not true of the nurse-cells which, except in their larger size, are quite similar to the oldest ones we found in the last stage (Fig. 47).

Both of the oldest chambers are similar in structure. All of the epithelial cells that can be seen around the nurse-cells are a few nuclei, which are found along the margin of the tubule. Around the oöcyte they are somewhat flattened and retatively smaller than in the younger chambers. The contents of the oöcytes has changed very much and in the tubule no transition is found between the two proximal and the two distal chambers. We find the two oldest filled with deutoplasm no trace of which was seen in any of the younger tubules, this fills the entire cell in the form of large, round or polygonal, bodies which lie in a granular network. The nucleus of each of these oldest oöcytes is the same (Fig. 56), it is quite irregular in outline with a thick membrane. Within the nucleus are very many irregular bodies with rounded surfaces; these stain not at all or slightly. They are crowded together and leave little space for a non-staining granular mass which is loosely scattered between them. No nucleolus was found in any of the oöcytes of this age.

Summary.

In a fairly old larva, ovary A, the first differentiation of the cells has taken place and we find them either; 1, undifferentiated or; 2, passing through the first stages in the development which is to result in the further differentiation of oöcytes or nurse-cells. Cells of the first group may either remain unchanged and become the epithelial cells, or, they may pass through the same changes as those of group two. Of group one nothing more need be said. Cells of the second group pass from undifferentiated cells through the following forms: with large chromatin granules in the nucleus, *b*; appearance of achromatin strands and disappearance of the chromatin granules, *c*; formation from these strands of beaded spireme-threads, d; synapsis, e. It does not appear that the nucleolus has anything to do with chromatin formation.

In the synapsis nuclei the threads stain more darkly than in the preceeding stage.

In the youngest larvae studied, ovaries A and B, mitosis occurs but is seldom found in the older stages. After the oöcytes and the nurse-cells have started through these changes they do not divide. From synapsis beaded threads appear, these increase in thickness and in each two thin chromosomes make their appearance. The threads shorten and the chromosomes become shorter and thicker.

All oöcyte and nurse-cell nuclei reach a stage in which they have this structure; proximal end of ovary B, but can not yet be distinguished from each other.

The first differentiation of these two kinds of cells is in their

size the oöcytes being the larger- as yet the nuclei are similar in structure. Youngest group in ovary C.

The paired chromosomes of the nurse-cells begin to change, and, some first becoming tetrads, break up into a number of pieces. These at first remain in small groups and then become distributed throughout the nucleus.

In the oöcyte nucleus the paired chromosomes, some first becoming tetrads, disappear as such but at a later stage than in the nurse-cells. They remain within the achromatin mass, former thread, becoming small rods or granules.

The nucleolus of the nurse-cell nucleus persists; at first it does not stain or is very lightly tinged. In older pupal stages it stains darkly and we then find several in each nucleus, their number increasing with the age of the cell.

The nucleolus of the oöcyte also persists. It is always unstained or colored very lightly. In older pupae it fills with vacuoles and finally decreases in size.

All divisions are mitotic.

Berlin, im August 1906.

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Explanation of Plates.

All figures drawn with a camera-lucida.

oö, oöcyte.
ec, end chamber.
tf, terminal filament.

Plate XV and XVI.

Fig. 1. Ovary A. Longitudinal section of one of the youngest tubules of this ovary. The terminal filament, *tf*, is here proportionally larger than in the older ovaries. The stalk which connects the tubule with the oviduct has already a small lumen; only part of the common oviduct, *odt*, has been drawn, its width should be a little greater than the widest part of the tubule. × 500.

Fig. 2. Nucleus from one of the cells of the terminal filament; taken from position 2 of the preceding figure. × 1600.

Fig. 3. Four marginal cells from ovary A, taken from place 3 in figure 1. × 1600.

Fig. 4. Four marginal cells from another tubule of the same age in ovary A. × 1600.

Fig. 5. Four cells from ovary A, taken from position 5 in figure 1. × 1600.

Fig. 6. Cell from same tubule showing the disappearance of the large chromatin granules and formation of the distinct achromatin strands. × 1600.

Fig. 7. Two cells from the proximal end of this same tubule; their position is shown by figure 6 in the first figure. × 1600.

Fig. 8. An older tubule of ovary A, drawn without terminal filament, membrane or stalk. *D*, distal end. The numbers 8 to 12 represent the position from which the five following figures have been drawn. × 500.

Figs. 9, 10, 11, 12 and 13. Five cells (figure 8 has two cells) from the preceding tubule. The position from which each is taken is represented by the corresponding number in figure 8. × 1600.

Fig. 14. One of the largest cells in the ovary. × 1600.

Fig. 15. Ovary B. Longitudinal section through a tubule of a larva. *D*, distal end. The letters a to *g*, represent different stages in the development of the cells, *a*, undifferentiated cell; *b*, those with large chromatin granules; *c*, the

formation of the achromatin strands which become, *d*, the spireme-threads; *e*, synapsis; *f*, thread which comes out of synapsis; *g*, shortened threads now with paired chromosomes. $\times$ 850.

Fig. 16. Three cells from the distal part of this tubule. Letters same as last. $\times$ 1600.

Figs. 17, 18 and 19. Three cells from same tubule showing formation of the beaded threads. $\times$ 1600.

Fig. 20. Cell from same ovary. $\times$ 1600.

Fig. 21. Three synapsis nuclei from near the center of figure 15. $\times$ 1600.

Figs. 22 and 23. Cells from same tubule directly following, proximal to, synapsis. The position of one of these is shown at point *f*, figure 15. $\times$ 1600.

Fig. 24. A cell from the same tubule, its position indicated by *g*, in figure 15. The paired chromosomes have appeared. $\times$ 1600.

Fig. 25 and 26. Two cells from the same tubule showing the shortening of the threads. $\times$ 1600.

Fig. 27. Two cells from the proximal part of the same tubule. In figure 15 it will be seen that this quarter of the tubule is filled with similar cells, but as yet no distinction is noticeable between oöcyte and nurse cell. $\times$ 1600.

Fig. 28. Ovary C. Longitudinal section through an ovarian tubule of an older larva; in the proximal part are several groups of oöcyte and accompanying nurse-cells. At this same end part of the stalk is drawn. $\times$ 850.

Figs. 29, 30, 31, 32 and 33. Five oöcytes from the proximal half of this tubule, each with two or three of the accompanying nurse-cells. Commencing with figure 29 these are successiveley older stages and show the breaking up of the paired chromosomes in the nurse-cell nuclei, and their persistance, thus far, in the oöcytes. Only enough of the boundary of each oöcyte has been drawn to show that it is larger than any nurse-cell. Cytoplasm not filled in. $\times$ 1600.

Fig. 34. Ovary D. Longitudinal section of a tubule from a slightly older larva. No chambers have yet been formed. $\times$ 500.

Fig. 35. Distal part of an end chamber from another tubule of the same ovary. $\times$ 1600.

Fig. 36. The oldest oöcyte and one accompanying nurse-cell from figure 34. $\times$ 1600.

Fig. 37. Ovary E. Longitudinal section through a tubule of a pupal ovary. The terminal filament and end chamber are not drawn. $\times$ 200.

Fig. 38. Section of the end chamber of preceding tubule. The disintegrating cells, »corps residuels«, — many labelled x — are more abundant than is generally the case. $\times$ 850.

Fig. 39. Nucleus from the oöcyte in chamber 4 of ovary E. $\times$ 850.

Fig. 40. Same from chamber 5. $\times$ 850.

Fig. 41. Ovary F. Longitudinal section of an ovarian tubule from an older pupa. $\times$ 200.

Fig. 42. Section of part of the terminal filament and distal half of the end chamber from another tubule of the same ovary. $\times$ 850.

Fig. 43. Section of the proximal part of an end chamber. From the same tubule as figure 41. $\times$ 850.

Fig. 44. Oöcyte from the first, youngest, chamber of ovary F. This shows the process which is often present in oöcytes of about this age, it extends between the nearest nurse-cells. $\times$ 850.

Fig. 45. A nurse-cell from the nearest chamber. × 850.

Fig. 46. A chamber from another tubule of ovary F; this is about the same age as chamber 2 of figure 41. × 500.

Fig. 47. Oöcyte and one nurse-cell from a chamber, same ovary, corresponding in age to chamber 3 of figure 41. Only part of the oöcyte is shown. × 850.

Fig. 48. A nurse-cell nucleus from the oldest chamber, number 5, of figure 41. × 850.

Fig. 49. Nucleus from the oldest oöcyte of ovary F. × 850.

Fig. 50. Two epithelial cells from those surrounding the oldest oöcyte of the same ovary. × 850.

Fig. 51. Ovary G. Longitudinal section of a tubule from the ovary of an old pupa. × 100.

Fig. 52. Terminal filament and first three chambers of the same tubule. × 400.

Fig. 53. Two cells from position bc, in figure 52. × 1600.

Fig. 54. Cell from position b, in figure 52.

Fig. 55. Oöcyte nucleus from first chamber of ovary G. × 1600.

Fig. 56. Same from the fifth chamber. × 850.

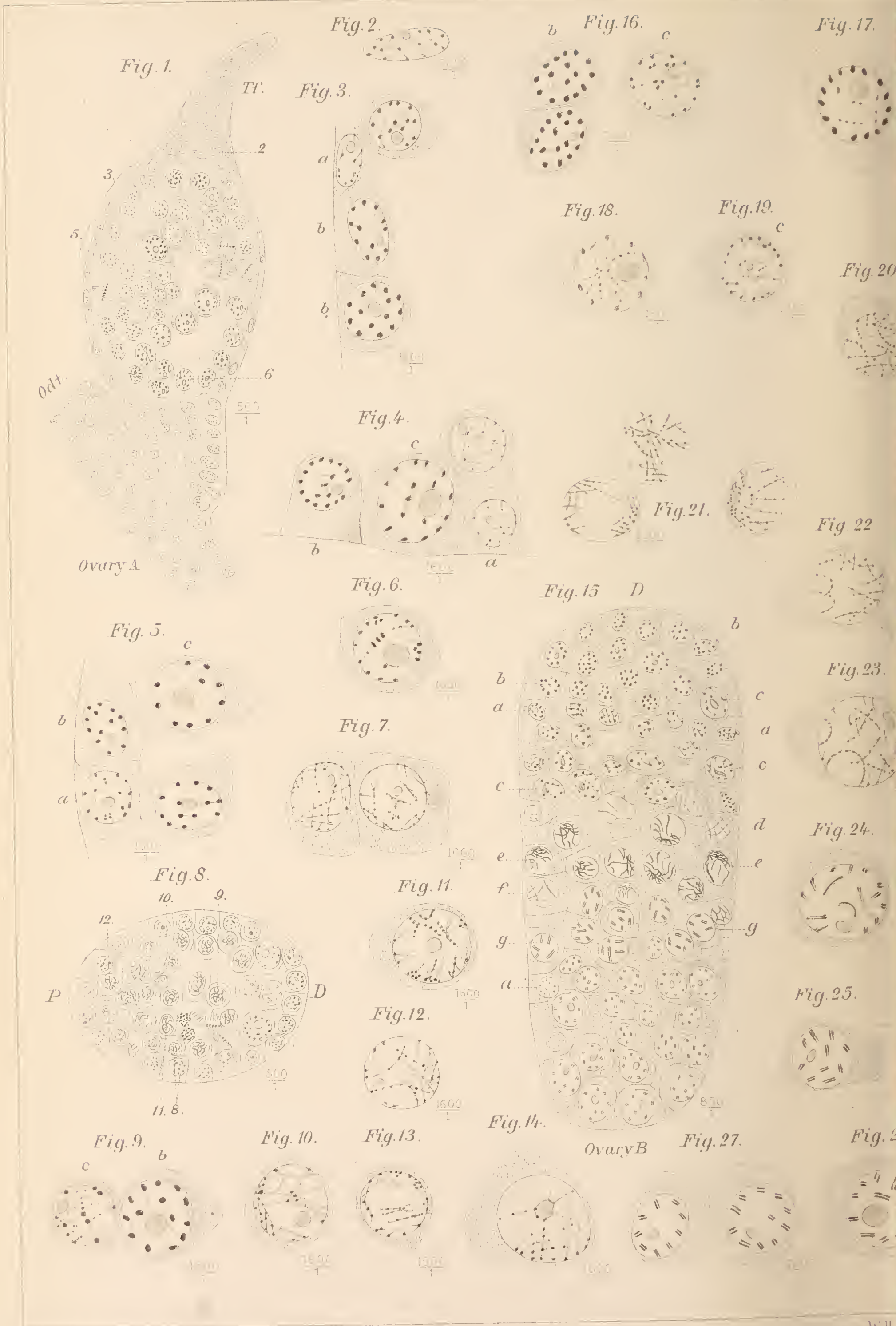
Fig. 1.
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2
3
5.
Od+.
6
500/1
Ovary A.
Fig. 2.
Fig. 3.
a
b
b
Fig. 4.
c
b
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Fig. 5.
c
b
a
Fig. 6.
Fig. 7.
1600/1
Fig. 8.
10.
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P
D
500/1
11. 8.
Fig. 9.
c
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Fig. 11.
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Fig. 12.
1600/1
Fig. 13.
Fig. 14.
Fig. 15
D
b
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850
Ovary B
Fig. 16.
Fig. 17.
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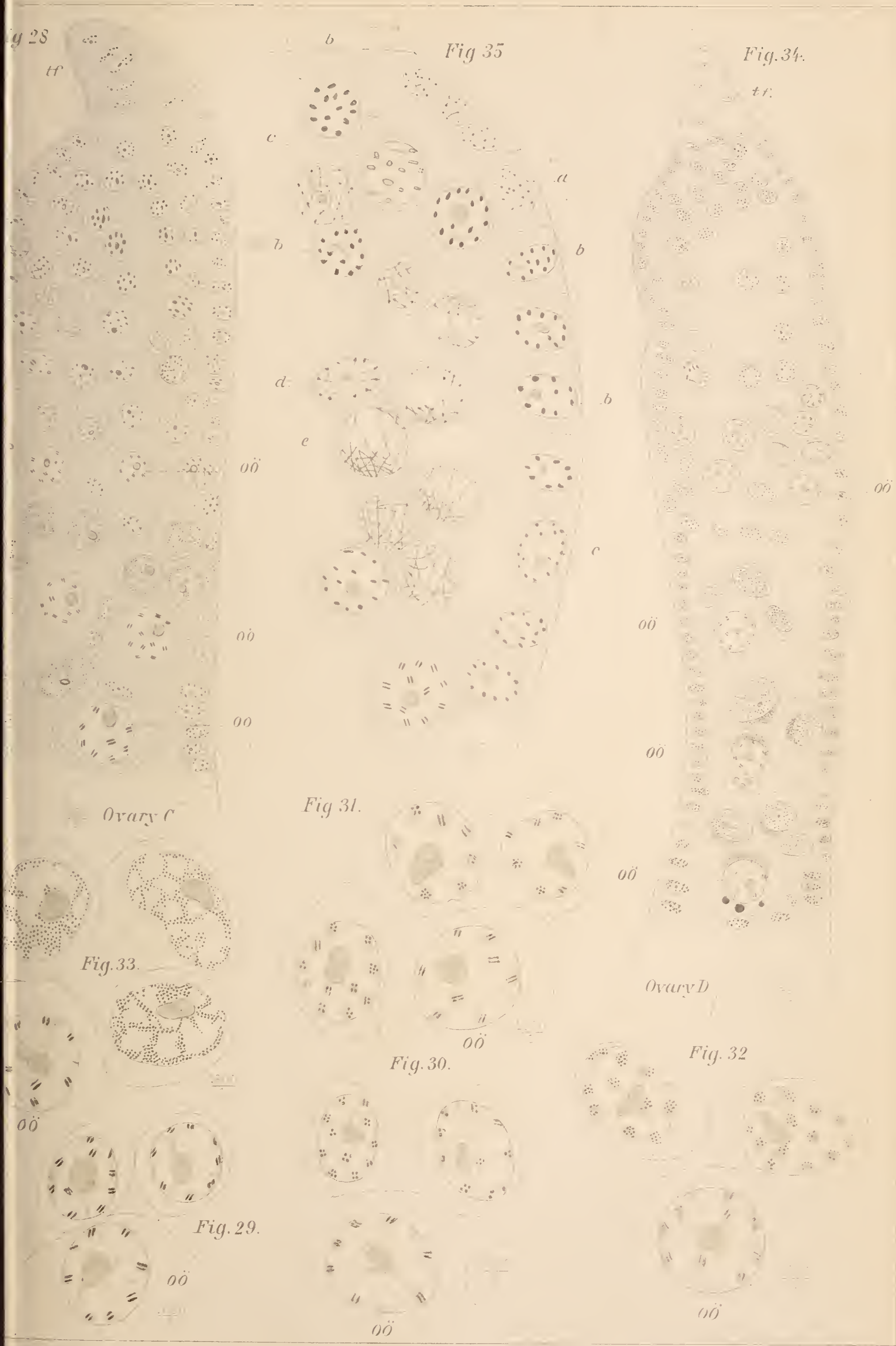
Fig 28
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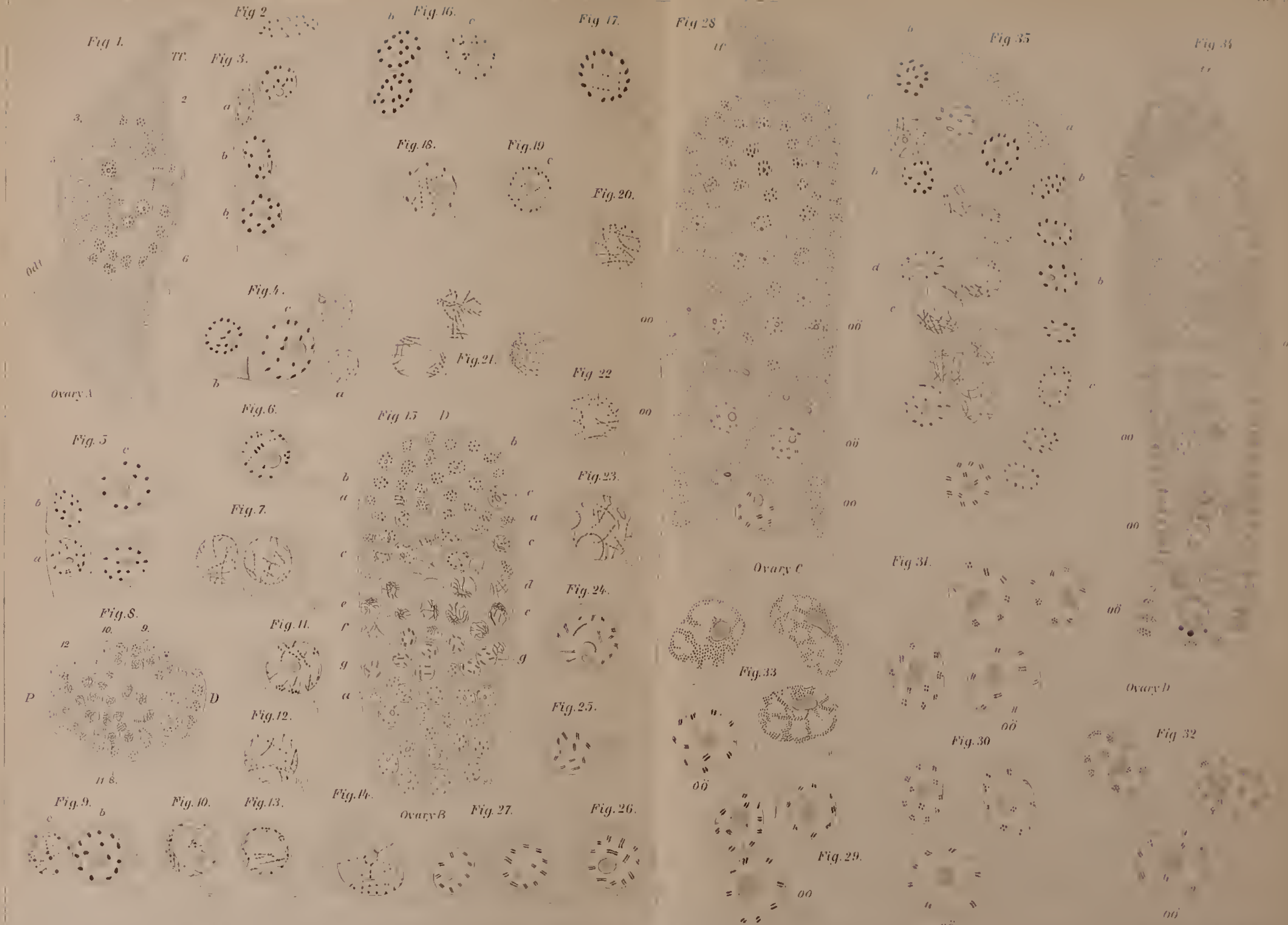
Fig. 29.



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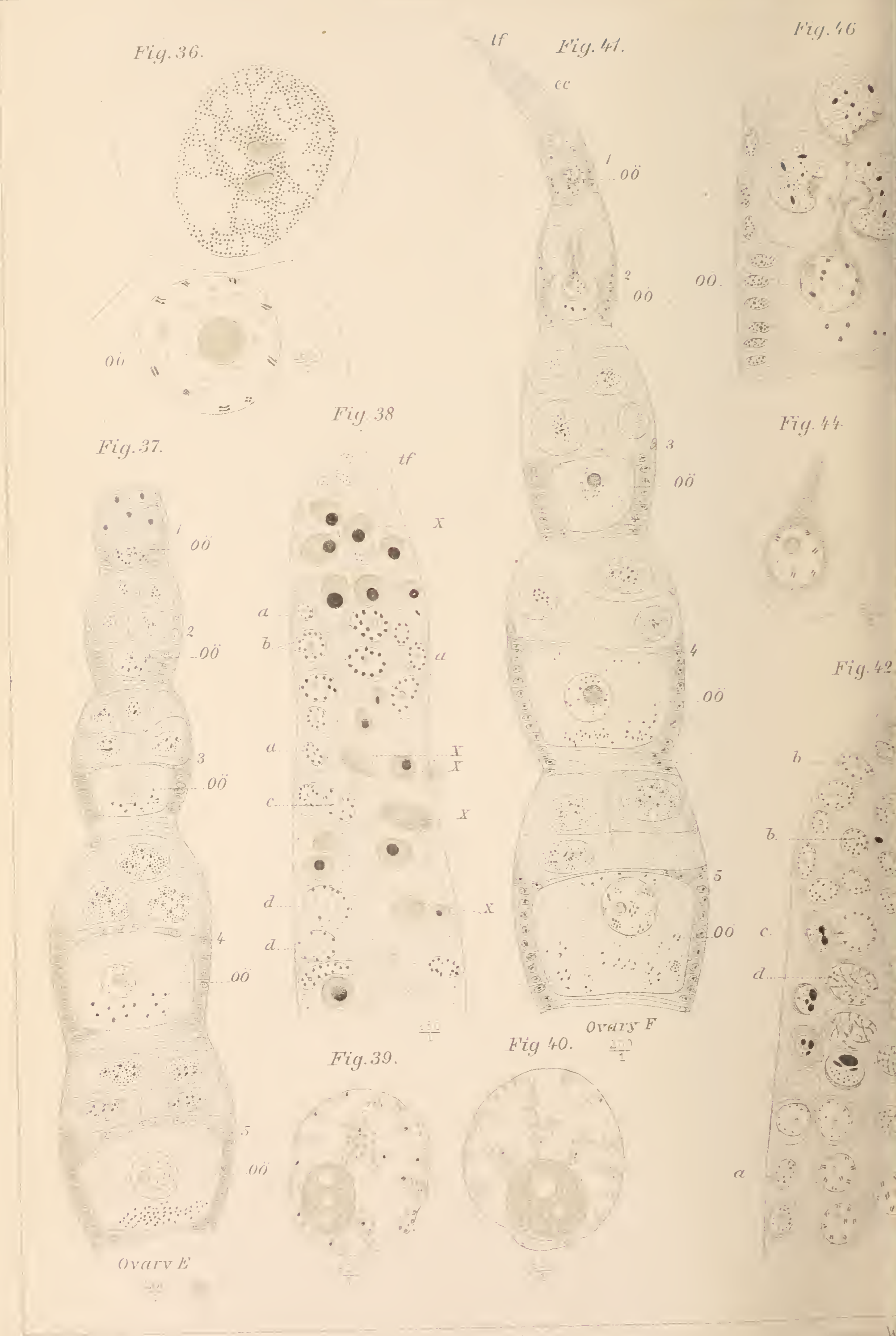
Fig. 36.
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Fig. 37.
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2
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3
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5
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Ovary E
Fig. 38
tf
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a
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d
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Fig. 39.
Fig 40.
tf
Fig. 41.
ec
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3
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Ovary F
Fig. 46
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b
b.
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Fig. 47.

Fig. 49.

Fig. 51.

Fig. 48.

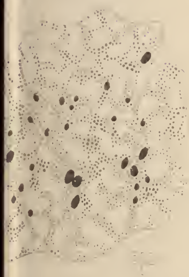

Fig. 53.

Fig. 45.

Fig. 43.

Fig. 50.

Fig. 54.

Fig. 52.

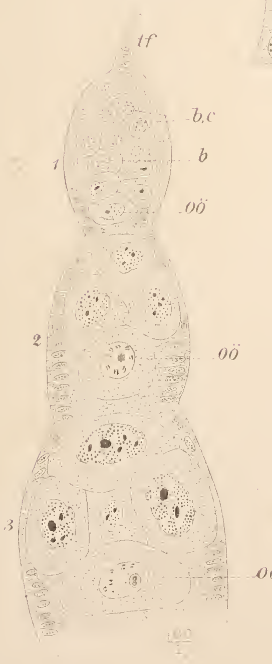

Fig. 55.

Fig. 56.

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