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AN EXAMINATION OF
OVOGENESIS IN THE CESTODE, TAENIA PISIFORMIS

by


William Ovide Negherbon
B.A. State University of Montana, 1934.

Thesis presented in partial fulfillment of the
requirements for the degree of Master of Arts.

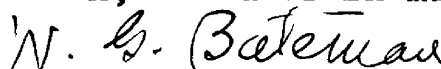
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To my teacher, Doctor Robert Thompson Young,
in whose work I have found help and inspiration .

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My thanks are given also to my friend John Coughill for the reading of the proof and for interest and encouragement throughout the research.

AN EXAMINATION OF OVOGENESIS IN THE CESTODE, TAENIA
PISIFORMIS

I. INTRODUCTION

The little research which has been done in the past fifteen years on the cytology of the cestodes does not mean that the problems which first aroused interest in these forms have been solved.

Three opinions, all quite well documented, exist. Child believes that amitosis is the method of cell proliferation in the tissues of cestodes although he grants the occurrence of maturation in the orderly meiotic manner. Richards finds mitosis and meiosis to be the method of cell division and maturation in cestodes. Young holds that mitosis is degenerating in cestodes in line with their degeneracy or extreme specialisation.

MacBride, in his "Invertebrate Embryology", indicates the uncertainty that exists concerning these forms by leaving them out of consideration on the basis that their organogeny is still to be worked out.

It seems necessary to reexamine the cestodes as a group and to establish the truth of all three views for various forms within the class Cestoda or to bring the class into line with those forms showing orderly mitosis and meiosis and so complete the evidence for the universality of these processes in animals.

The present study concerns itself with the ovogenesis of a cestode variously known as *Taenia serrata* or *Taenia pisiformis* both classifications, in accordance with most cestode literature, being used synonymously in this paper.

A number of positive statements are made throughout the text. It is necessary to understand that these statements grow out of the material worked with. The writer does not propose to have solved all the questions of cestode cell division. Many suggestive figures were seen. On the basis of these figures in this one form, *Taenia pisiformis*, all such statements are based. The writer completely realizes that further work with many genera is necessary at every step.

The figures shown are in simple line form showing only the salient nuclear details. The cytoplasm except where it has bearing on the interpretation of nuclear phenomena has not been shown in detail.

II. HISTORICAL

Much of the cestode literature has been of a taxonomic nature. This need not concern us here. The controversial literature dealing with mitosis and amitosis falls again into a consideration of the writings of the principal investigators of cestode cytology, Child, Richards, and Young.

Child^{1,2,3,4,5,6,7,8} in a series of detailed papers concerning every phase of cestode cytology questions the importance of mitosis in the development of *Moniezia*. He finds that while amitosis is the chief mode of reproduction in the cells of the ovarian anlage, some mitoses do occur. He figures these. Child finds maturation to be typical in all respects with definite spindles, chromosomes and centrosomes. He states that the fate of a cell may be the same whether it divides mitotically or amitotically. He notes that the chromosomes pass to the poles irregularly, that

the spindle is extremely delicate, that a fertilization membrane exists, and that metaphase plates are rare. He figures polar bodies and mitoses in early cleavage. He proposes physiological reasons for the occurrence of mitosis or amitosis in various regions of the cestode body, mitosis being characteristic of regions of slow growth and amitosis being the method of division in highly active tissues. His work is summarized by his affirmation that amitosis is more frequent than mitosis during the development of the testes and ovaries and that a nucleus which has given rise amitotically to many cell nuclei may at any point give rise to the number of chromosomes characteristic of the species.

14,15.

Richards^{14,15.} confining himself to the development of the female gametes in *Moniezia* confirms his earlier work on *Taenia*. He finds no evidence for amitosis and abundant evidence for both mitosis and meiosis. He notes that mitoses in the ovarian anlage occur in the actively growing region at the periphery of the anlage. Richards' figures are positive as to the typical nature of the two maturation divisions and the polar bodies.

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The work of Harman¹⁰ on *Taenia taeniaeformis* is in complete accord with the work of Richards on *Moniezia*. Wilson in his latest edition of "The Cell in Development and Heredity" inclines to the work of Harman and Richards in his views of cestode cytology.

17,18,21.

Young^{17,18,21.} does not attempt to adhere to Child's view that amitosis is the chief method of cell division in cestodes but states that mitosis is a degenerating process in these animals. He poses three methods whereby cell division in cestodes may be accomplished: (1) by amitosis, (2) by de novo development of nuclei in the cytoplasm, (3) by development from chromidial extrusion

of material from preexisting nuclei.

In ovogenesis Young describes the occurrence of an abortive prophase which he interprets as an attempt at maturation. In most cases he finds that the prophase "skein" degenerates and the nucleus returns to a resting state. In some instances abortive metaphases were observed by him. He states that the polar bodies observed by other workers are yolk cells. His views are summarized by his belief that mitosis seldom occurs save in later cleavage stages and that it is abortive in gametogenesis. He believes these phenomena to be a reversion to simpler conditions frequent in the protista.

¹³
Motomura working with *Archigetes appendiculatus* finds typical maturation divisions and a haploid chromosome number of nine, a diploid number of eighteen. He has never observed amitotic divisions.

The state of the cestode problem is clearly indicated by this analysis of the most important researches on the subject and the points in conflict are clearly evident. It has seemed necessary for a reinvestigation of the whole question to be made. The contemporary worker in cestode cytology must sit in judgment on these various viewpoints. The implications of the more radical viewpoints toward modern genetic and cytological ideas are clear.

III. MATERIALS AND METHODS

Five complete worms recovered from a dog immediately after death under ether were used. The worms which consisted of over ninety proglottids each showed in the older proglottids complete embryos indicating that a complete chain had been obtained. Only two scolices were recovered and on the basis of these as well as of other details of structure the taxonomic position of

the specimens was determined. The other worms recovered were complete except for the scolices since they began at the neck region where complete strobilization was not yet evident. It is probable that the scolices of these individuals were broken off in the washing of the intestinal wall which was done in the course of the search for the tapeworms.

The animals were fixed immediately after removal in Allen's B-15 modification of Bouin's fluid, a material which has given remarkable results with the tissues of other forms. The use of this fixing fluid was justified by the results obtained since the cells showed practically no shrinkage and the cytological detail seemed well and sharply preserved. No other fixing fluids were used although the material of Dr. Young fixed in various solutions was available for comparison. For the formula of Allen's B-15 modification of Bouin's fluid, Guyer's "Animal Micrology" may be consulted.

The use of the higher or lower alcohols after fixation was avoided because of their hardening and shrinking effect upon delicate tissues. The use of the fixing fluid just mentioned was perhaps responsible for the very little difficulty which was experienced with the chalk bodies, structures which have given other investigators many puzzling pictures.

The worms were washed in 70% alcohol and then dehydrated and cleared in anilin oil and wintergreen in which liquid they were preserved until the time of embedding. Little difficulty was experienced due to the contraction of the proglottids during fixing, proglottids in a contracted and in an expanded state both being

available, showed under observation no dissimilarities which could be attributed to this factor.

After dehydration and clearing, the worms were divided into pieces of from one to five proglottids - depending on their size and state of maturity - and embedded in a special paraffin containing pure latex and bayberry wax. Through the use of this method no difficulty was experienced with crystallization. The embedded material infiltrated well and the ribbon left nothing to be desired. A warning may be sounded at this point in regard to proglottids containing either mature eggs or embryos in fairly advanced development. These have the habit of falling out of the section during the processes of washing or cutting and the difficulty must be guarded against. The use of a thin celloidin to coat the slide carrying such sections seems to be indicated.

By proceeding in this manner, an entire worm was sectioned from the scolex to the ninetieth proglottid, and sections required for further work and observation were taken from the other material as required. The sectioning of a whole worm in this manner gives a complete view of what is occurring in the chain from the earliest anlage of the female reproductive organs to the end result of gametogenesis, the establishment of the embryo.

Both cross and sagittal sections were cut in the course of the examination. The cross sections have perhaps the advantage over the sagittal sections because it is somewhat easier to orient oneself in the proglottid. The worms were sectioned from anterior to posterior as these terms are commonly accepted in reference to the cestodes. The sections were arranged serially upon thin slides. The sections were cut 5 micra thick.

Several stains were used, among which were Heidenhain's iron-alum haematoxylin, Mallory's phospho-tungstic acid haematoxylin, and Ehrlich's acid haematoxylin. All were satisfactory although this investigator recommends the use of Mallory's phospho-tungstic haematoxylin which stains with great sharpness and pleasing color, stains slowly and thus lends itself admirably to progressive staining and has the advantage of staining the achromatic figure better than either of the two other stains. Ehrlich's acid haematoxylin gives excellent results but uniformity of staining was found to be a bit difficult in this work.

All the haematoxylin of course have the distinct disadvantage in cestode work of staining the yolk, and careful distaining is essential to minimize this obscuring factor.

No counter stains of any sort were used, it being felt that these, in small cells, tended rather to obscure than clarify the structures, especially since little interest in the cytoplasm was indicated by the scope of the investigation.

It may be mentioned here that the Mallory's phospho-tungstic haematoxylin seems to give the sharpest and best results with the small cells involved in the study of spermatogenesis. Fine demonstrations of this were observed in the course of this study.

The completed slides were examined serially under the oil immersion lens of a binocular microscope, using a substage lamp as the source of illumination.

IV. OBSERVATIONS

A clear understanding of the processes involved in the ovo-

genesis of *Taenia serrata* demands that a short explanation of the organization of a typical proglottid be given to permit a clear orientation within the proglottid. The outline drawing which accompanies this material will indicate in graphic form the level of the most productive sections.

At the end commonly accepted as anterior, that is, toward the scolex, in tapeworms the typical proglottid is mostly filled by the many testes which join each other by fine ducts emptying into the common vas deferens leading to the genital pore. Occupying a space in the center of the proglottid is the uterus in which the eggs complete their development. This communicates directly with the oviduct which serves the double ovaries at the posterior end of the proglottid. Near the point where the oviduct joins the uterus, the vagina opens to bring spermatozoa to the eggs. This is sometimes known as the fertilization duct. Posterior to the ovary lies the vitelline gland which in this form is of problematical significance. A small shell gland lying between the yolk gland and the oviduct pours its contents into the oviduct near the opening of the vagina.

This, in brief, gives an outline of the nature of the morphology of the genitalia in *Taenia serrata* as determined from cleaved whole mounts. With the help of the accompanying sketch, these statements should be sufficiently clear.

Excellent cross sections were obtained during the course of this work showing maturing egg cells in the oviduct and uterus, ovarian eggs in various stages of development in the ovary and the shell gland, yolk gland, vagina and shell gland duct in cross

sections. It was in these sections in the series of proglottids beginning at the forty-third and extending back to the sixtieth that the clearest evidence of maturation was obtained.

1. The Anlage of the Female Reproductive System.

The development of the ducts and the gland accessories of the cestode *Taenia serrata* does not concern us here although Richards presents evidence which indicates that, not only does the vitellarium arise as part of the primordial anlage but consists of undeveloped egg cells whose development has been overlaid by a function other than that of reproduction.

The first anlage of the ovary was observed in my material between the eleventh and twentieth proglottids as cords of cells lying in the parenchyma of the proglottid. These worms are incompletely protandrous and testes in rather advanced development were already present in the region where these observations were made.

The ovarian anlage appeared to arise from the undifferentiated parenchyma, and in this respect my results are in accord with those of Child², Richards¹⁵, and Young¹⁸. Richards¹⁵ points out that there is no marked region dividing the thickening of cells which mark the developing ovary from the parenchyma. Young^{18,21} likewise notes the rise of the anlage of both the male and female genitalia from the parenchyma. Young²⁰ further records as additional evidence of this origin the presence of developing flame cells in the developing testes, and Child² has observed the rise of germ cells from differentiated muscle cells, an observation which has been questioned.

The rise of the ovary from the thickening cells of the parenchyma seemed quite clear in the preparations used during this investigation and the differences existing between the cells of the parenchyma are quite difficult to see. The parenchyma cells in my preparations showed a slightly smaller and more chromatic nucleus than the cells of the ovarian anlage, a more characteristic spindle shape, and a greater distance from one another.

I find this fact difficult to reconcile with Child's⁵ view that the parenchyma of the cestodes is essentially a syncytium, a statement supported in other quarters. My observations are in agreement with those of Richards¹⁵ who not only comments on the distance between the cells of the parenchyma but also notes, as I have noted, the fact that parenchymal nuclei are always surrounded with a well marked cytoplasm lying, to be sure, surrounded by much intercellular material.

The ovarian anlage is, of course, characterized by the presence of less intercellular material and the arrangement of the cells into strands or cords. Accompanying illustrations will easily demonstrate the slight differences that exist between individual cells of the ovarian anlage and individual cells of the parenchyma.

The nuclei of the anlage stain quite lightly in my preparations but show a distinct nucleolus.

The cells of the ovarian anlage are apparently proliferating very rapidly as they grow to occupy their definitive position in the proglottid. Their proliferation beginning in the region of the excretory canals at the sides of the proglottid rapidly sends

strands of cells to the median and ventral region of the proglottid, the growth proceeding quickly in three dimensions.

Mitoses in this region and at this time, although their occurrence in large numbers might be expected, are not as numerous as one would believe. I have found few mitoses in the preoogonia at this stage. It is because of this apparent lack of mitoses at this time that Child^{1,2} finds so much evidence for the proliferation by amitosis. Child² himself shows several figures of mitosis occurring in this region.

¹⁵ Richards, to explain the paucity of mitoses in this region where they are to be expected in abundance, considers the possibility of migration from a region of high mitotic division in the neck region of the scolex. Indirect evidence alone, he suggests, can be adduced in support of the hypothesis of migration. Richards himself has found no region of high proliferation in the neck of the cestodes to account for a point of origin of the presumably migrating cells.

The observations gained in the present work show that the anlage cells are very small, that they do not stain with the ease and clarity of parenchyma cells, and that mitoses, although not as abundant as one would expect a priori, do occur. Some of these divisions are figured and show the occurrence of a rather well marked broad spindle and centrosomes or regions of high activity in the cytoplasm from which radiate the astral lines.

¹⁵ It is quite essential to remember as Richards also points out, that the term "primordial germ cells" is used with qualifications in regard to genital anlagen in the cestodes, since the

rise of the anlagen from undifferentiated parenchyma gives no clear evidence of the existence of a "germ track". With this statement the present observations agree and have comparatively little to add to the already well reported development of the ovarian anlage - reports which have been made by Child², Richards¹⁵ and Young¹⁸.

The evidence gained from this present study indicates that the mitoses in the ovarian anlage occur near the periphery of the growing cell cords where such division would be expected to occur. The cells in this region of the ovarian anlage are drawn out and elongated as though the cell cords were under considerable tension.

Nuclei showing peculiar configurations are not rare at this period, but the peculiarities are explainable in absence of a clear sequence of stages which, in my material, cannot be seen, not as amitotic figures but as peculiar configurations of the nucleus which can be attributed to the stretched out nature of the cytoplasm and the tension under which the cells seem to be. Dumb-bell shaped nuclei were present in considerable numbers in my preparations and figures of these are shown.

The rapid growth of the proliferating anlage and the growth of the oogonia themselves after they come to the end of the period of proliferation is paced by the hollowing out of the parenchyma and the creation of hollows or follicles in which the nests of oogonia lie. In many cases the coalescence of two follicles and the formation of larger follicles may be seen. The follicles push outward and downward in the proglottid forming many finger-like projections in which the cells often show a rather regular

arrangement. Many oogonia I have observed in rather advanced stages of growth which have a characteristic pear-shape and are attached to the follicular wall or limiting parenchyma by the small pedicel-like end. This condition is common in my material.

It may be said that the true oogonial period begins with the development of follicles for it is at this period that the cells destined to become the female gametes begin to show the characteristics that mark them out from all the other cells of the proglottid. The preoogonia are differentiated primarily only by their position since they do not differ markedly in character from the cells of the parenchyma.

Of course in the younger proglottids, the transition is gradually accomplished. The proglottids as they reach maturity in the sense that true gametes are present show various transitional stages in which the cells which have been termed preoogonia exist in the presence of cells which are definitely entering upon the true oogonial state.

The passage of oogonia into the uterus and oviduct as oocytes is undoubtedly progressive since proglottids are found with the female gametes in all stages.

The preoogonial period is purely a period of proliferation, the character of the cells in the anlage retaining their preoogonial character through the many divisions which increase their numbers.

In this regard the character of the parenchyma is somewhat clarified. If the parenchyma partakes, as Richards¹⁵ and Young¹⁸ both indicate, of the character of embryonic mesenchyme and possi-

bly of mesoderm - the rise of the germ cells directly from this tissue is to be expected. In this respect the cestodes would fall clearly in line with the other members of the platyhelminthes.

Many preoogonia in my preparations appear in pairs with nuclei in the same plane of the section. Many also appear in which¹⁵ a strand of cytoplasm seems to connect two cells. As Richards points out, only the absence of spindles or spindle remnants bars one from interpreting these cases as examples of the final stage of telophase.

Carefully as I have examined my materials, I have found no cases showing the fragmenting nuclei or extrusion of chromidial²¹ particles as found by Young .

The nuclei of the preoogonia are definite entities and a clear membrane about the nucleus is visible in all my preparations.

The technique used in staining of course gives rather different pictures. Ehrlich's acid haematoxylin does not stain the nuclei of this stage very densely. Heidenhain's iron alum and Mallory's phospho-tungstic haematoxylin both show the preoogonial nuclei as densely granular. In many cases the small nuclei are so densely chromatic that close observations reveal a dense spireme.

2. The Oogonial and Growth Periods

¹⁵ Richards has suggested, and I believe rightly, that the period of true oogonial activity is marked by the full development of the follicles. Richards uses the term follicular membrane. With this I am in disagreement. The oogonia lie in clear spaces or hollows of the parenchyma, separated from each other in many cases by thin strands of tissue but no definite limiting membrane

of cells marks the boundaries of these spaces. In some cases, and this is not always uniform, the parenchymal cells seem to be a bit more numerous at the periphery of the follicles and show a more regular arrangement. This is true chiefly of some of the small follicles.

The oogonia which lie in the follicles have ceased activity from the standpoint of division. In all the cases examined, only three divisions were found at this time and these were in small cells, which may well have been preoogonia belatedly performing their final division before growth.

The oogonia are of various sizes and shapes, depending upon the stage of their development. At the periphery of many follicles cells of long spindle shape are still evident, many larger cells of oval shape may be seen. In some regions crowding of the cells no doubt accounts for the shape.

Oogonia make their appearance in the material observed in the course of this study in the region of the 25th to the 30th proglottids. The region of preoogonial proliferation is very limited. Growth in the oogonia, as Richards¹⁵ points out, must be very long. Oogonia were found by the writer to be present far back in the region of the sixtieth proglottid.

The oogonia during growth are cells of very characteristic form. The cells are very large with germinal vesicles of great size, the relation of nuclear volume^{to} cytoplasm being easily 3:1. The cytoplasm is very clear and, in cells which can be viewed in isolation, surrounds the nucleus in a uniform band. The huge germinal vesicles of oogonia near the end of growth are extremely clear.

In Ehrlich acid haematoxylin preparations few scattered chromatic granules may be seen on a very light network. Accompanying illustrations will show this condition. In these preparations the chromatin lines the nuclear membrane in an irregular band from which the light strands originate. This condition is not uniform, nuclei are found which show all gradations from nuclei which are apparently achromatic to those showing quite a definite reticulum.

In Herdenhain's haematoxylin and Mallory's phosphotungstic haematoxylin the nuclei of the oögonia show a more granular ground work, but cannot be said to be more heavily charged with chromatin.

The nucleolus which is of large size is usually centrally located and stains very darkly. Some nucleolar detail may be observed but no special staining was tried to examine the internal structure of this body.

As growth proceeds to its close the germinal vesicles are at their clearest stage. Only scattered irregular fragments of staining material being lightly visible.

3. Yolk Production

Yolk is produced in the oögonia of *Taenia servata* in large volume. The mechanism of its production is unknown. It is no doubt correlated as
13 2
Young indicates with the degeneracy of the vitellarium. Child observes that no yolk is seen to pass from the yolk gland to the oviduct and uterus. Unless the yolk produced from the yolk gland passes to these structures to nourish the eggs, in a fluid form Child does not find any function for the vitellarium as such.

The onset of yolk production as the illustrations show is heralded by the recollection of the chromatin in the nucleus in heavy clumps and masses with a reticulum supporting them. The nucleolus stains more heavily and be-

comes very prominent. During growth the nucleolus has moved from the center of the nucleus and at the beginning of yolk production becomes increasingly condensed and the nucleus passes into the stage called by Richards and Young "synapsis" or "bouquet." This it would seem is a misuse of terms. Synapsis means but one thing, the apposition of the homologous chromosomes in preparation for tetrad formation. This phenomenon ^{was not observed.} appears in clumps and in some cases a spireme like structure is apparent. But the pairing of the chromosomes and the formation of tetrads has not been observed. In view of the fact that the synapsis or "bouquet" stage passes off long before maturation would indicate that it is not a true synapsis. Additional material in this regard will be cited a little later.

During the period of yolk deposition puzzling structures were observed in the cytoplasm. Some of these correspond quite closely to the yolk nucleus mentioned by Richards. Examples of this are figured. In some cases the yolk center appears as a group of heavily staining granules in the main body of the yolk mass. In at least three cases at the very inception of yolk production a small sphere with dark granules within was observed. What the function of this structure is must be left in doubt until work is done on the mechanism of yolk secretion by the cell.

Yolk in *Taenia serrata* is first produced in scattered small globules which increase in size and finally collect as a large mass at one pole of the oögonium. The yolk globules and masses stain in a homogeneous, hyaline manner which does not permit much confusion with nucleoli, chromatin and other inclusions in well prepared slides.

At the completion of yolk production the cell is at its largest size. The yolk mass may be so great that as the figures show the nucleus is pushed to the edge of the cell and may assume a dumbbell shape. That this appearance has purely a mechanical significance is attested by its occurrence only in

cells with large yolk masses or in cells crowded by adjoining cells. This appearance has suggested amitosis in the past. Child (2), Young (19).

Yolk production does not come into full activity until the period of chromatin recollection has waned and the nucleus has returned to a period of rest in which the nucleus stains very lightly, the nucleolus lies at the cell periphery and the chromatin lies close to the nuclear membrane. Richards¹⁵ has noted that yolk production begins on that side of the nucleus where the "hauguet" was situated. It would seem that this period of high nuclear activity before yolk production, characterized by the high staining power of the nucleus, may be correlated to the intense cytoplasmic activity which follows. At the end of yolk production the cells are in a state of complete rest.

At this point the question of the occurrence of a nuclear membrane may¹⁸ well be considered. Young does not believe the cestodes to possess a nuclear membrane and considers this to accord with his theory of chromidial extrusion of nuclear material. If by a nuclear membrane is meant a definite limiting structure between nucleus and cytoplasm, demonstrable by staining and indicating the integrity of the nuclear content such structures have been constantly observed in the material considered in this work. The very fact that the yolk is able to compress the nucleus without entering its limits gives color to these observations.

Many possibilities of yolk proliferation exist. The egg itself may produce yolk within itself and this by^{ny} mitosis has the bulk of the evidence to support it, since the "yolk nucleus" may well represent a complex of secretory granules. Yolk might be transmitted to the eggs in highly agglutinated form in the general body fluid and stored within the egg. The clearest evidence points to its production by the egg itself.

4. Passage of the Egg from the Ovary to Oviduct ^{and} Uterus
1

With the completion of yolk production the eggs are mature and ready for maturation and may be justly called oocytes. The cells are crowded together and may assume a somewhat polygonal shape. The nucleus as the illustrations show is in a condition of complete rest. The egg is ready for passage from the ovary to the oviduct and uterus.

The process of passage is effected in two ways. The follicles hollow out to permit the eggs to lie distinct from one another. Fluid pressure may push the eggs out through the oviduct toward the uterus where in the lower portion of this structure the eggs collect together. In the oviduct which is more or less convoluted the eggs may be seen packed close to one another in places and lying distinct from one another in others.

15

Richards in the eggs of this stage has figured centrosomes although he does not definitely commit himself to this interpretation of the structures. The writer has also seen several suggestive cases of which one is figured in which dark bodies not identical with the yolk particles may be the centrosomes preparing for maturation.

5. Fertilization

In this investigation no case of a sperm actually entering the egg was observed, indeed, in no unmistakable cases were spermatozoa found lying among the eggs although these are present in great number in the vagina, and are seen in vast clumps in the vasa deferentia ^{of} proglottids at this stage. Several cases were observed in which darkly staining bodies were found within the egg surrounded by clear haloes which have been interpreted as sperm nuclei. These are figured. At least one case was seen in which either a fertilization path, or the sperm tail was seen lying in the cytoplasm of the egg. If this tail was actually within the egg and if it was not the fertilization path an interesting question is indicated. The sperm head in cestodes

and the writer has observed a definite head is extremely small. The male pronucleus is very large. It seems possible that the sperm tail may enter the egg and carry with it materials for the formation of the large male pronucleus.

21

Young describes spermatozoa coiled over the surface of cestode eggs. If the above observed case was of this nature the line which has been considered to be either the sperm tail or path might be the tail lying on the egg surface in a section cut close to the surface of the egg.

Fertilization is undoubtedly effected either in the oviduct as the eggs pass the opening of the vagina, which in these preparations was seen distended with spermatazoa or in the posterior portion of the uterus. In both the uterus and oviduct indubitable pronuclei were seen. Some pronuclei are figured.

Fertilization is further heralded by the appearance of the fertilization membrane which surrounds eggs undergoing maturation as well as those showing pronuclei. One case at least is figured in which the maturation prophase is occurring with the sperm nucleus inside the egg and the fertilization membrane investing the oocyte.

The crowding of the eggs makes the observation of sperm entrance and the fertilization membrane difficult. No observations have been recorded nor were any made in this study to indicate a definite spot of sperm entrance.

15

One investigator, Richards, has mentioned the possibility, in view of several instances observed, of polyspermy.

By the time the eggs have entered the upper oviduct and uterus they have rounded up and many phases of nuclear activity may be observed.

Although it was stated at first that no case of sperm entrance was observed, fertilization undoubtedly occurs since pronuclei make their appearance and structures closely resembling swollen sperm are seen lying in the cyto-

plasm of oocytes.

6. Maturation

In the material under observation many maturation divisions were observed in all sections from the region of the thirtieth to the fiftieth proglottids. The most abundant evidences were obtained from the region of the forty third to the fiftieth proglottids. At least two of these proglottids even to the naked eye before embedding showed a definite distention in the uterine region due to the contained eggs. Maturation divisions appeared in all proglottids from thirtieth to fiftieth proglottid—but were most numerous in the region cited.

As was stated previously under the heading "Materials and Methods," the clearest achromatic figures were observed in preparations stained with Mallory's phosphotungstic haematoxylin.

Difficulty was experienced in many cases in differentiating between the first and second maturation divisions although in a few sections rather definite tetrads seemed to be visible.

The reduced number of chromosomes was almost certainly observed in several instances. Suggestive cases of maturation divisions in various stages and views are figured as evidence for the occurrence of this process.

One very clear case of dyads in anaphase was noted. These general observations are made here to indicate why the nuclear figures observed in this region indicated very early in the investigation that a region rich in meiotic figures had been found.

The onset of maturation is heralded by the occurrence of the spireme of the meiotic figure lying in a dense skin within the degenerating nuclear membrane. Child speaks of the intranuclear nature of the spindles but in no case was this observed.

The chromatin during prophase is concentrated finally in a very dense blob and it is at this point that true synapsis probably occurs. It is necessary to guard in examining for this stage, against mistaking polar views of anaphase for the late prophase and synaptic periods. The spireme in many cases was seen very clearly in both the dense and finely spun stage and in a few cases the fragmentation of the spireme was visible.

During the period of prophase, not only the nucleus is in activity but deep seated changes are occurring in the cytoplasm. The yolk which has lain inert in a large globule becomes dispersed through the cytoplasm and lies principally in the equatorial regions lateral to the meiotic spindle. This dispersal of the yolk gives the maturing oocytes a characteristic appearance in stained preparations. The cytoplasm is darker and more homogeneous in appearance. This is probably due not only to a yolk dispersal but also to the passage of nuclear contents into the cell during late prophase.

In one instance, at least, at the time of the close spireme in prophase, an apparently definite picture was seen of the centrosomes moving to the poles of the spindle. Whether one centrosome had divided to form two, it is impossible to say. This phase of the meiosis would depend upon the finding of all stages for elucidation.

15 10 2 18
Various workers, Richards, Harman, Child, and Young have spoken variously of centrosomes, centrospheres and have questioned or affirmed the presence of asters during this phase of maturation.

15
The observations of the author are in accord with the observations of Richards to a fair extent. Definite centrosomes were observed many times. The ring shaped structure described by Richards was not evident save in a few instances. 15
The centrosomes in the preparations studied, particularly those stained with Mallory's phospho tungstic haematoxylin, were quite large and stained

in a clear hyaline manner. Occasionally a densely staining granule could be seen in the centrosome by carefully racking the microscope up and down. Radiating from the centrosomes the astral rays were clearly visible in several instances. These rays were very long and were seen bending to accommodate themselves to the cell periphery.

The spindle in most cases is very long and delicate with comparatively few fibers. The spindle, as is common in the maturation of most forms, does not in *Taenia serrata* lie near the surface of the egg, but frequently extends from one cell border through to the other. It is possible that an equal division is prevented here, as the nature of the spindle might lead one to suspect, by the inert accumulation of yolk which prohibits equal division and permits the extrusion of a small polar body. A few cases, however, were observed in which the spindles were broad and almost spherical in shape. No reason can be given for this by the writer.

The phenomena of maturation are difficult in the extreme to follow in the cestodes, the chromosomes are small and their activities are not always of the most regular type. Certain peculiarities exist which have led investigators, ¹⁸Young, to question the occurrence of a definite number of chromosomes in the cells of these forms. The author also has noted some of these abnormal phenomena--abnormal only because they do not directly fall in line with conceptions derived from the study of other forms.

There is, to be sure, an apparent difference in chromosome number in various oocytes examined. The author has observed however that these peculiarities are to be noted only at the time of early anaphase when the chromosomes are migrating to the poles. There does appear to be a certain amount of fragmentation which gives a misleading picture.

¹³

Motamura, however, working with *Archigetes appendiculatus* has made careful

chromosome counts. He has found the number to be nine in haploid and eighteen in diploid. A definite reduction is indicated.

The writer counting carefully the chromosomes in those meioses where these were distinct in the cytoplasm arrived at a variable number for *Taenia seriata*. The diploid number seems to be between ten and twelve and the haploid number five or six. More extensive work on other material would very likely pin the number down to one of these figures.

The fate of the chromosomes during late prophase and early metaphase could not be followed with the clarity desired in the material under investigation. However a few cases of the fragmentation of the spireme have been noted.

Immediately following the fragmentation of the spireme the chromosomes of the oocytes of *Taenia seriata* arrange themselves in a clearly marked metaphase plate upon the spindle. Several examples gave indication that tetrads were thus arranged upon the achromatic figure of first maturation. The spindle lies in the long axis of the cell which is usually ovoid. Polarity is difficult to establish unless the point of intrusion of the polar body marks, in cestodes, as in other forms, the animal pole of the egg.

Some of the sharpest figures, of mitosis in this material, many of which are 15
figured, were the meiotic metaphases with their typical metaphase plates. Richards 18, 21
and Young, rarely report typical metaphases in the cestodes. Young of course for obvious reasons, since he postulates a degeneration of mitosis.

The metaphase plates were observed in all stages; as heavy chromatic lines in the equator of the spindle in some, as distinct bands of distinct chromosomes in others, with the daughter chromosomes separating in late metaphase in other cases. Not only were many lateral views seen but also many polar views.

Movement to the poles is irregular. Some of the chromosomes lag behind others but with the appearance of the completed anaphase the chromosomes are gathered in two groups at the spindle termini. Two anaphases are figured in which the five

dyads lie in a crescentic figure at the poles of the spindle. In many cases the chromosomes at the poles are not so distinct and in polar view may simulate the synapsis of meiotic prophase.

The presence of dyads in the anaphase of the meiotic figure in several cases, gives clear evidence that chromosome reduction has occurred since the dyads are always one half the number of the diploid state.

Two clear cases of the extrusion of the polar body were seen with spindle fragments evident. Many first polar bodies were observed in which the polar nucleus was in resting stage and the oocyte chromosomes lying naked in the cytoplasm were arranging themselves on the second maturation spindle.

The second maturation demonstrated by the appearance of the second polar body is not essentially different from the first polar division. The spindle is perhaps a little more slender and difficult to demonstrate and the asters and centrosomes not so well marked. This may well have been due to nature of the material.

Little difference between the first and second oocytes can be seen. However a rather evident reduction in the size of the egg was observed after the extrusion of the first polar body which is comparatively large.

In one cell especially the result of maturation was very clear. A polar view of the egg nucleus showed five chromosomes. The sperm nucleus lay near by with a clear area surrounding it.

All stages of maturation were observed and in them all the chromosomes showed a compact densely staining nature and extremely small size.

7. The Polar Bodies

One of the clearest criteria of true maturation divisions in the ovocytes of metazoans is of course the formation of the polar bodies. Young has stated the denial of the existence of polar bodies in cestodes and in the same papers, that the cells found in association with cestode ovocytes are yolk cells. He

points out the absence of these cells and the absence of polar bodies as well in a form which has no vitellarium. It is significant that the "yolk cell" described by Young is not attached to the oocyte until long after yolk production has been accomplished and its functions are not elucidated by Young. No statement is made to indicate that this problematical "yolk cell" serves to nourish or protect the egg in any way.

In this research, the polar bodies have been seen in the actual process of formation. The first polocyte is rather large with a considerable amount of cytoplasm. This condition is made clear in the figures. The second polar body is smaller. The nuclei of the polar bodies are small, quite densely chromatic and sometimes show a reticulum.

The polar bodies in these preparations showed no resemblance to yolk cells either in the nature of their contents or in any way. They lay in some quite clear examples in immediate contact with an oocyte in mitotic activity and were invested by the vitelline or fertilization membrane. Their appearance heralded a slight reduction in the size of the oocyte. Von Janicki working with *Taenia serrata* identified small densely staining bodies at the cell periphery as polar bodies. The structures studied by Janicki are not the same as those here described as polar bodies. No confirmation of his work can be noted.

8. The Pronuclei

Although maturation is finished with the extrusion of the second polar body the appearance of the pronuclei which are form the fusion nucleus may be briefly described.

Many cells showing pronuclei were noted and the reconstruction of pronuclei after maturation was observed several times. In several cells, one of which is figured, the pronuclei were seen in contact with one another while the polar bodies were visible at the cell periphery.

The pronuclei present the appearance of typical resting nuclei, lightly

staining and with delicate strands within. The pronuclear membranes are sharply clear and the pronuclei lie side by side in many cells separated by a band of cytoplasm.

The yola mass in cells showing pronuclei lies at the pole of the cell with its main axis between the two pronuclei. The male pronucleus is characterized by a slightly smaller size compared to the female pronucleus.

With the establishment of the pronuclei ovogenesis may be considered complete. The cleavage stages and their mechanism are beyond the scope of this work and are not considered.

IV. DISCUSSION

Before embarking on a general discussion of the significance of the observations made in the preceding portions of this paper and their evaluations in the light of other researches of a similar nature, the question of the possibility of artifacts in the material should be considered. It was noted at the beginning of this paper that the possibility of artifacts in cestode material during fixation and staining is ever present. In the light of this the nuclear phenomena described in this course of work might be called into question. In forestalling this occurrence a number of remarks should be made.

The phenomena recorded have been consistently found in the material and build into a clear sequence of events typical of maturation figures in other forms. They corroborate closely the work of several investigators in the same field. Moreover the figures described lie in the midst of many cells with typical resting nuclei. If the structures described were artifacts caused in the nuclei by the action of fixing fluids or stains, certainly all nuclei would show the same artifacts. Furthermore the pictures obtained by the use of three different stains and the uniformity of these pictures suggest that actually existent figures were examined.

The review of the literature made at the beginning of this work indicates quite clearly the three main lines of interpretation of the cytology of cestodes--the conclusions of Child, Richards, and Young.

In any living form the occurrence, of as basic a mechanism as cell division and development of gametes of an orderly sequence of events, simple and direct is to be a priori expected. This does not mean that the extraordinary and the seemingly bizarre when they are proven to be actualities are to be passed over and disregarded.

So ever at the present time the method of cell division and gametogenesis in practically all living forms has been reduced, with limitations, to essentially the same processes. This is in direct accord with the great theory of heredity, the constancy of the chromosome body of evidence which today places upon an unshakable foundation the chromosome number within the species and the significance of maintaining the normal chromosome set up in continuing the existence of a species.

The work of Child in this discussion may be passed over rather quickly. In the light of contemporary evidence, his case for amitosis is not strong as he himself might grant. Not only this but the fundamental contradiction in his work becomes increasingly clear: That is that a cell which has divided amitotically through several generations should suddenly give rise to the chromosomes characteristic of the species and undergo a mitotic maturation.

This viewpoint represents the extreme of considering the nucleus from the purely physiological standpoint and is out of accord completely with the evidence of genetics and modern cytology.

From references made throughout this paper it is evident that in the main the observations of the author agree closely with the observations of Richards and Harman who bring the methods of cell division and gametogenesis in cestodes into the fold of mitosis. It was with a view to deciding or helping to decide finally between the conflicting theories of Richards and Young that

this study was undertaken, especially since Young publishing many years after Richards, later brings up additional evidence in support of his contentions.

If Young's idea that mitosis is degenerating in the cestodes is to be tenable some explanation must be offered to clarify the mechanism whereby at least fragments of mitosis are still retained and evidence must be collected whereby the processes of heredity in even these specialized forms is made clear.

In view of the evidence for mitosis presented by this research the view that degeneracy of an extreme parasite is reflected in the breakdown of fundamental cell mechanisms is made at least in the mind of the writer, quite improbable. Because it remains that parasites have cells and that regardless of their loss of organ systems through degeneracy they retain cellular organization and from the evidence collected ordinarily cell processes.

It seems to the writer that the fragmentation of the spireme described
21
by Young in the oocytes of cestodes may well have been a misinterpretation of the clearing of the nucleus after the growth period and the bouquet stage just prior to yolk production and a failure to observe thereafter the completion of the maturation phenomena whose abortive simulacra are at least granted by Young. The very delicacy of these structures in cestode cells lends color to this explanation, although it must be said in all justice to Young that he employed many methods and forms, indeed many more methods and forms than the writer.

There is but one way in which Young's work could be brought into line with what we now know of the universality of the mitotic process in the animal series, and this line has not been considered by Young.

If the degeneration of the prophase spireme in oogenesis and the return of the egg to the resting condition as Young's material indicated to him were

be
true it might be yet possible to bring his ~~idea~~ ^{be} into line with what he believes about the spermatogenesis of these forms, that is, that sperm may arise from individual granules extruded from the spermatocyte nuclei as chromidia. It might be possible to postulate that the cestode egg retains a permanent diploid chromosome number, develops parthenogenetically, and that the spermatozoa are either abortive or supply merely the mechanical stimulus for the development of the eggs. ^{all} Even this in the light of Young's own statement that pronuclei make their appearance in the eggs in the oviduct and uterus cannot be upheld in the light of his own observations.

The present research in the course of its development recorded some interesting phenomena in the spermatogenesis of *Taenia serrata* which in themselves, although they were cursory, further weaken Young's case. Spermatids were noted in all stages of development and cytoplasmic reduction. Although structures resembling Young's cytophores were seen their syncytial character was not convincing to the author—there being too much possibility of mistaking cytoplasmic debris extruded from the spermatids as a cytophore and the possibility that a nurse or sertoli type cell may be established for cestodes. These suggestions would bear a careful and detailed examination.

The status of the question of chromidial development of nuclei is no longer as generally tenuous as formerly, and Young has drawn many of his analogies from the conditions described by Briggs, in the fungus *Synchytrium*.⁹

Young's interpretations like those of Child seem to be too much dominated by the idea that the nucleus is primarily a "physiological unit." All contemporary evidence denies this except when one considers that cell structures and activities are primarily based on physiological grounds. We know all too well from the studies of *drosophila* and many more forms what happens when chromosomes or parts of chromosomes are lost or altered, and if Young believes as he seems to

that the sperm brings something to the egg in cestodes as is evidenced by pro-nuclei and his own observance of mitosis in early cleavage the implications of his chromidial spermatozoa arising from single granules from broken down nuclei are evident without further elucidation.

It is evident how basically this research differs from the conclusions of Young and Child merely by studying the figures which accompany the text-- but some specific points of difference may well be brought out here.

Not a little of Young's case rests on his failure to find polar bodies and his interpretation of the structures observed by Harman, Child, Richards, and the writer to be yolk cells. It may justly be asked how do these yolk cells get into the oviduct and uterus and why has no investigator described their migration?

What is their function if as Young himself states the yolk gland in cestodes is degenerate? How does this hold with the proliferation of yolk by the egg itself? Why does not every oocyte carry a yolk cell and why if it is a yolk cell does this structure make its appearance coincidentally with maturation? How does Young explain the spindle fragments which so often connect the polar body nucleus with the oocyte? Why is there no yolk in this yolk cell? Is similarity of the polar body nucleus to a yolk cell nucleus sufficient evidence for pronouncing them the same--or even logical evidence in view of the possibility of similarity between any two small nuclei. Certainly the yolk gland in this writer's preparations was very compact and showed no evidence that cells were breaking away to attach themselves to oocytes. All these questions must be answered before Young's position is tenable.

There remains even as Richards points out in these very words the possibility of periodic mitosis which Young's observations themselves might hint in his statement concerning the differing frequency of mitosis in various proglottids and various chains. Of this the writer can say nothing realizing that he has

not examined sufficient material to make any claim concerning this possibility whose proof would depend upon much material collected under all circumstances and on the observation of living material. Mention might well be made here concerning the evidence presented by Harman, Young, and Morse. All of them while able to keep cestode material alive for greater or lesser periods were unable to find any growth. Additional researches may disclose a method for cultivating these tissues.

It is of theoretical importance that the division and maturation phenomena in cestodes be definitively worked out because of their bearing on our theories of the role and activity of the chromosome in development and heredity.

This study with all its deficiencies is offered as a contribution to the evidence already existing, but which is yet too meager, that mitosis is the method of gametogenesis in the female sex cells of *Taenia serrata*, a cestode.

V. SUMMARY AND CONCLUSION

Evidence is presented to show that the method of gametogenesis of the female germ cells in *Taenia serrata* occurs by mitosis.

The anlage of the ovary arises from the undifferentiated parenchyma.

Polar bodies are formed.

There are two maturation divisions.

The occurrence of tetrads and dyads is shown.

The presence of centrosomes and astral figures is demonstrated.

The phenomenon of yolk production is described.

The chromosome number has been determined as 10 or 12 in diploid, 5 or 6 in haploid.

A review of the literature is presented.

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EXPLANATION AND PLATES

Prefatory Note to the Plates.

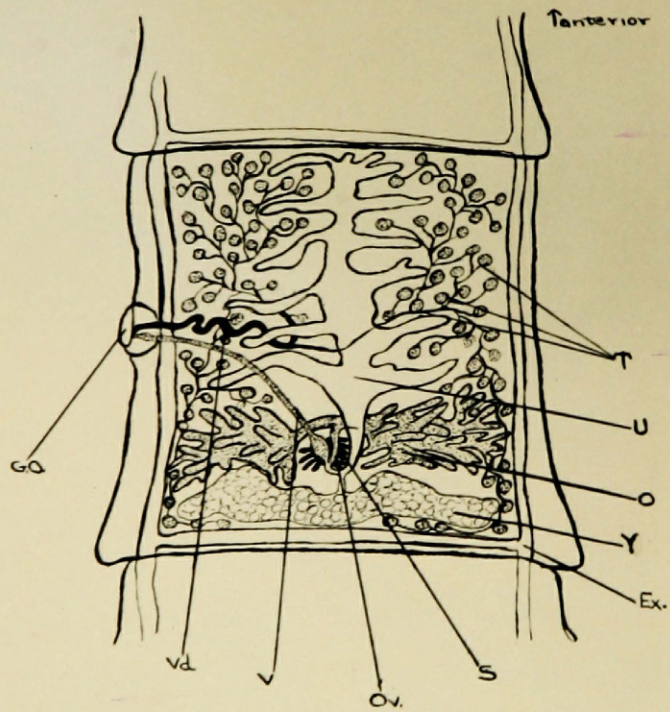
The figures shown were drawn from fixed and stained material. The occurrence of mitotic activity is quite clear. Concerning the controversial subjects of polar bodies in the cestodes and the presence of asters and centrosomes as well as the occurrence of reduction divisions they contribute suggestive evidence which is not by any means diagrammatically clear. The figures are subject to interpretation. Long and careful study of material which is extremely difficult to stain and which is frequently not as clear as one might wish have lead the writer to suggest the interpretations suggested in the explanations to the plates. The astral figures especially are very difficult to demonstrate in an unmistakable fashion. The writer is convinced that they exist and that he has seen them clearly enough to warrant figuring them as clearly as they are shown here. It must be kept in mind that these figures are taken from but one form a fact which does not permit any generalisation. They are offered as suggestive figures. Final interpretation must await further study of a greater mass of material drawn from various genera and species of cestodes.

Explanation of plate I

A semi-diagrammatic view of a proglottid of *Taenia serrata* drawn to show the arrangement of parts.

G O	-----	genital opening
Vd	-----	vas deferens
V	-----	vagina
Ov	-----	oviduct
S	-----	shell gland
Ex	-----	excretory canal
Y	-----	yolk gland
O	-----	ovary
U	-----	uterus
T	-----	testes

Plate
I



W.O.N.

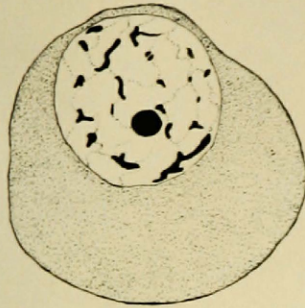
Explanation of plate II

Figure 1. An ovogonium at the end of growth. Nucleolus large and centrally located.

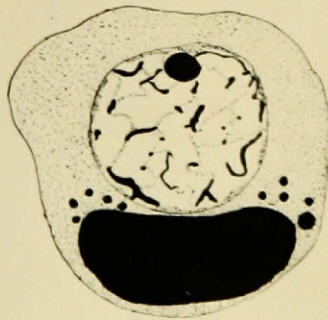
Figure 2. An ovocyte in the resting stage at the close of yolk production. The nucleolus has moved to the edge of the nucleus. The yolk is concentrated at one end of the cell.

Plate
II

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2.

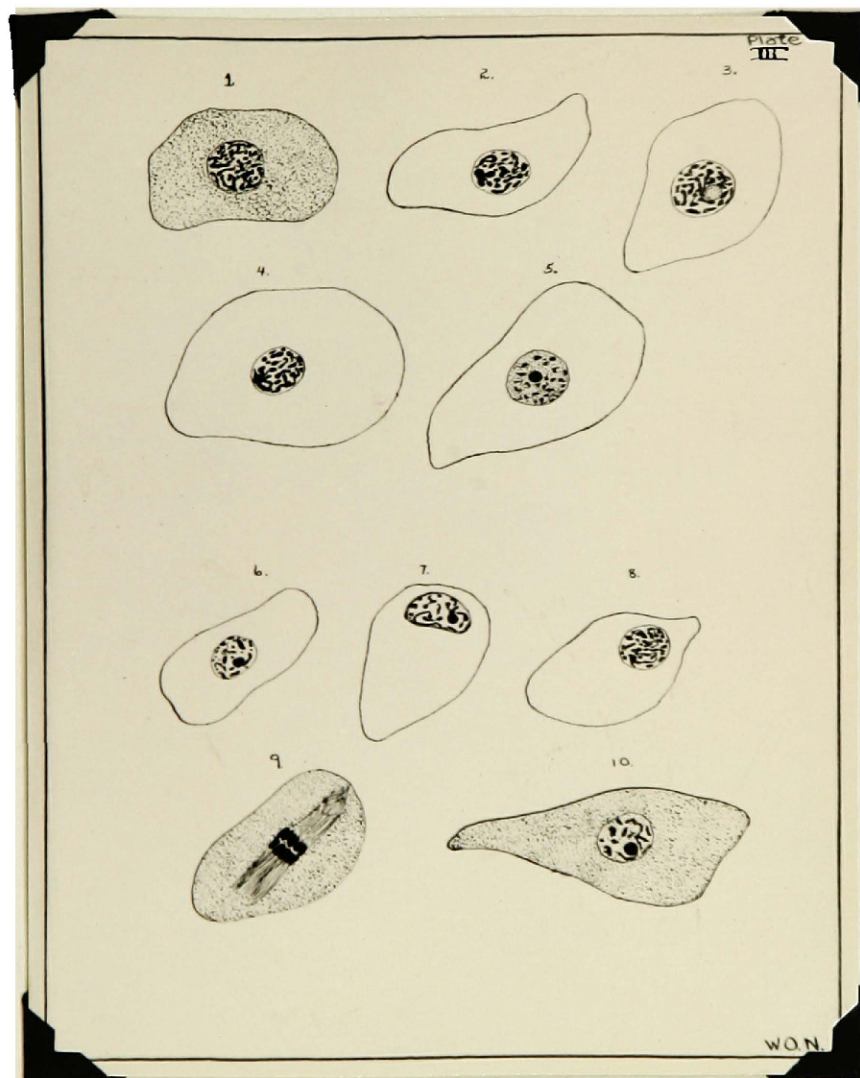


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Explanation of plate III

Figures 1,2,3,4,5. Parenchyma cells selected at random from the sections to show the chromatic nature of the nucleus and the characteristic spindle shape.

Figures 6,7,8,9,10. Primordial germ cells from the ovarian anlage to illustrate the similarity between the cells of the anlage and the parenchyma. Figure 9 is in the early anaphase of mitosis.



Explanation of plate IV

Figures illustrating mitoses in cells of the ovarian anlage.

Figures 2,3,5. Metaphase in lateral view.

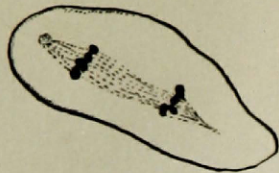
Figure 4. Metaphase in polar view with ten chromosomes visible.

Figures 1,6. Anaphases.

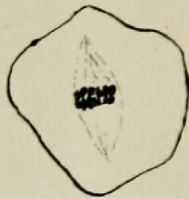
Figure 7. A figure suggestive of late telophase.

Plate
IV

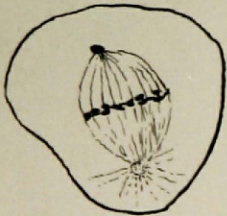
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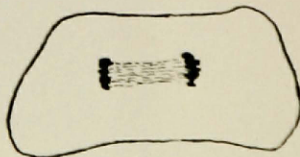
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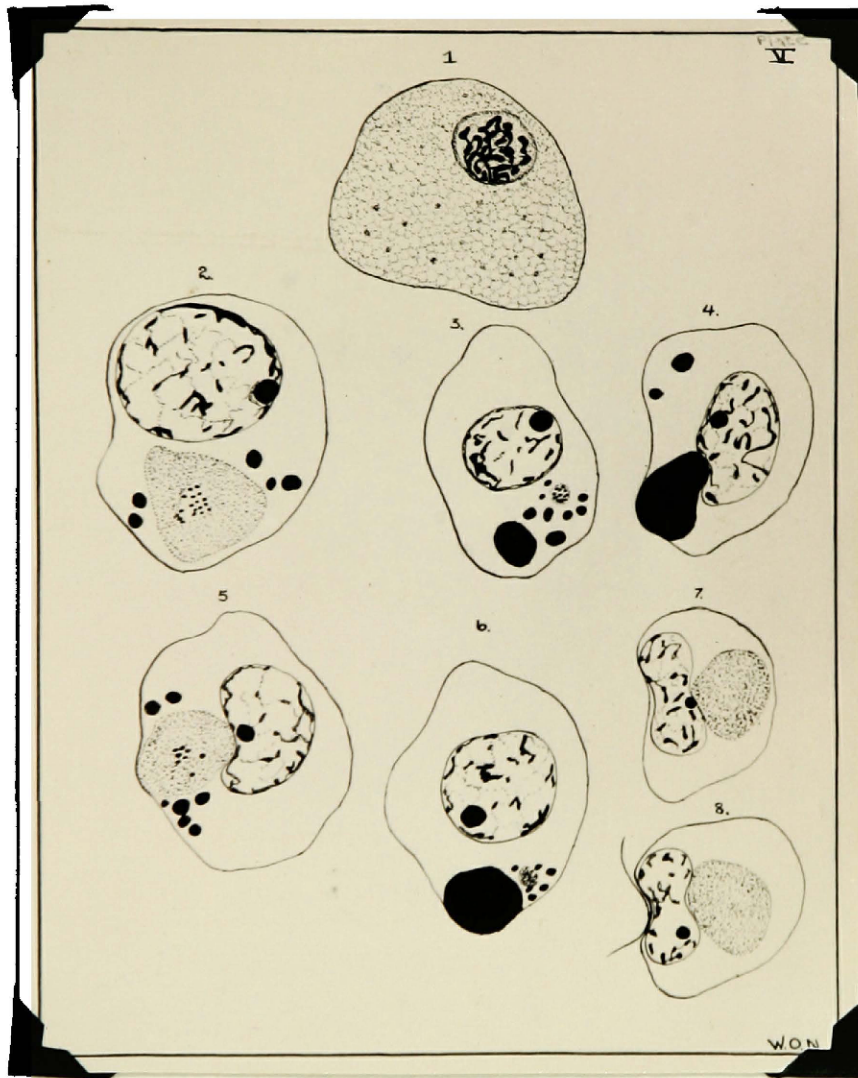
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Explanation of plate V

Figure 1. An ovogonium with the nucleus in "bouquet" before yolk production.

Figures 2,3,4,5,6. Illustrating various phases in yolk production by the ovocytes. Figures 2 and 5 show the "yolk nucleus" in the center of the growing yolk mass.

figures 7,8. Showing the "dumb-bell" nucleus produced by the crowding of the nucleus produced by the yolk mass and by adjacent cells.

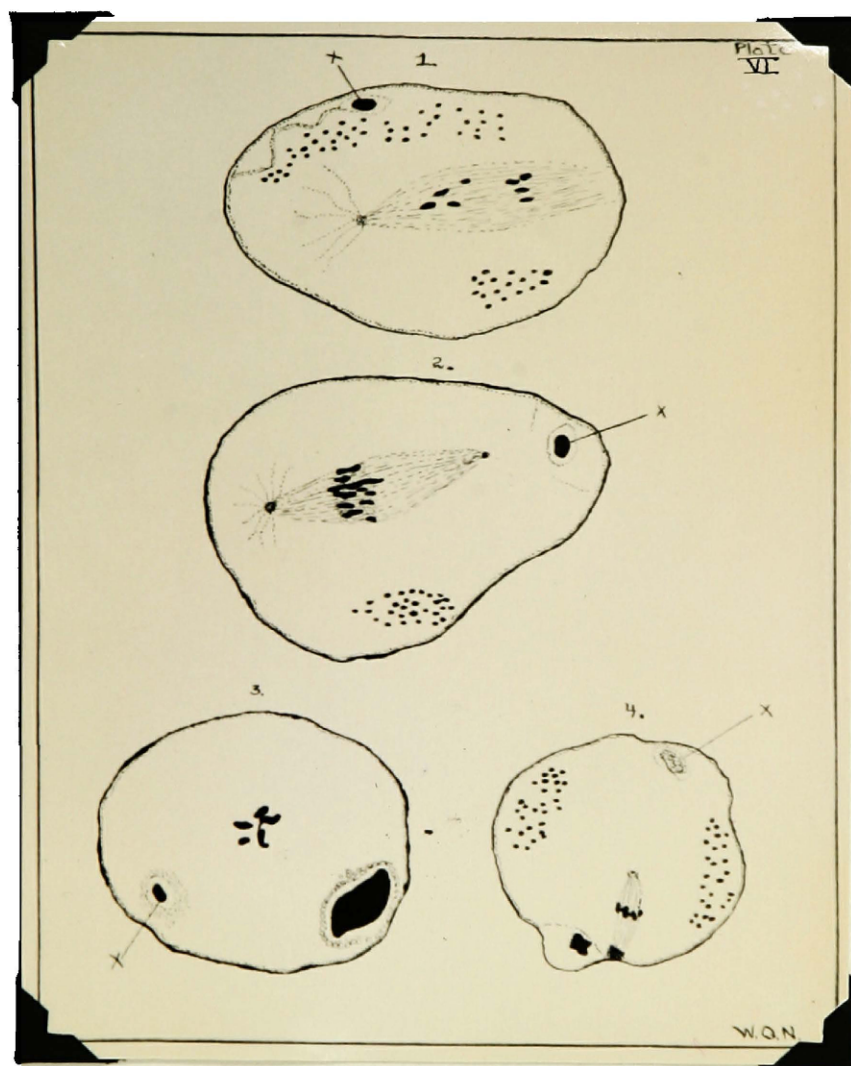


Explanation of plate VI .

Figures of maturing ovocytes with sperm nuclei in the cells.

Figure 1 shows the sperm path.

X marks the sperm nucleus.



Explanation of plate VII

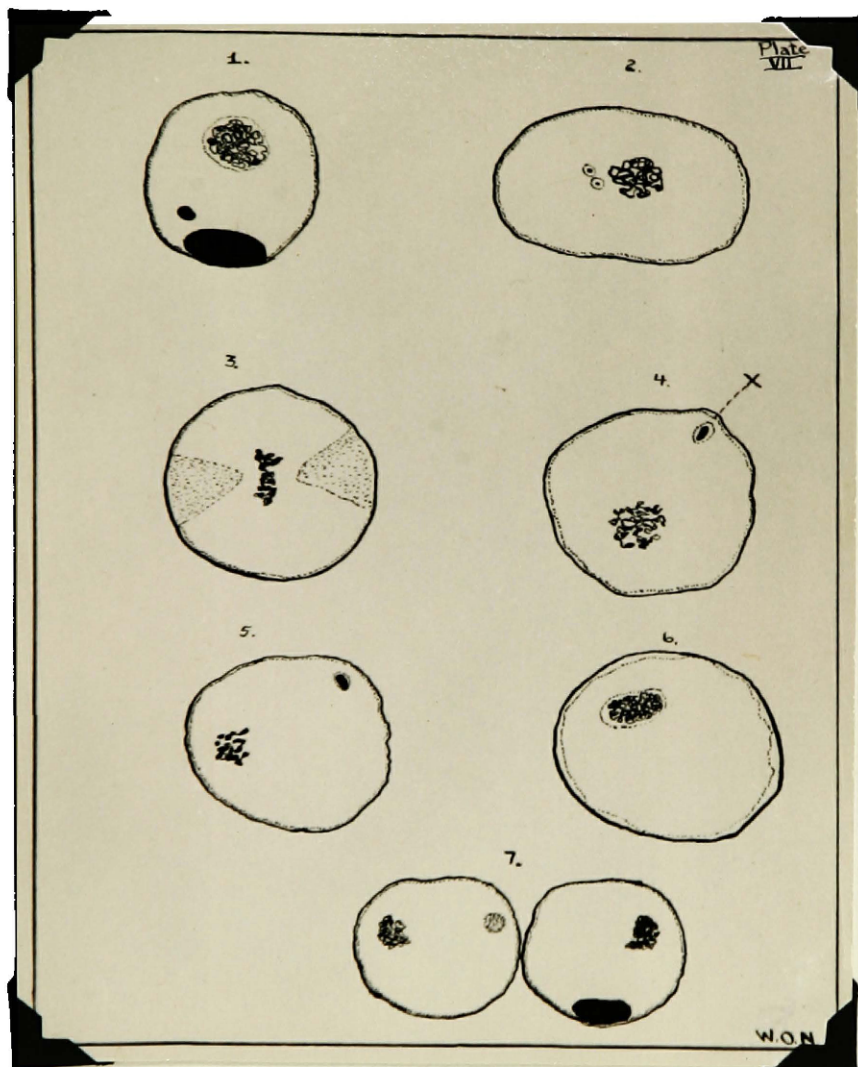
Maturation prophases.

Figure 1. Spireme with nuclear membrane still intact.

Figure 3. Late prophase with fragmenting spireme.

Figures 4,5. Fragmenting spiremes. X points to the sperm nucleus.

Figures 6,7. Prophases in various stages.



Explanation of plate VIII

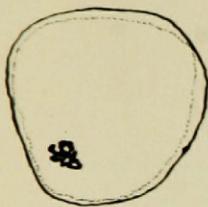
Figures 1,2. The close spireme stage.

Figure 3. Late prophase with spindle formed.

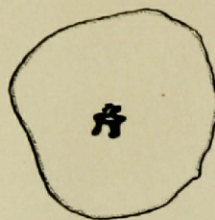
Figure 4. Loose spireme with structures suggestive of a dividing centrosome.

Figures 5,6. Close spiremes. Figure 5 shows a centrosome.

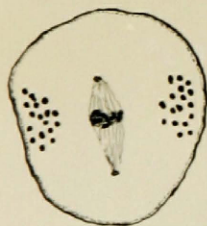
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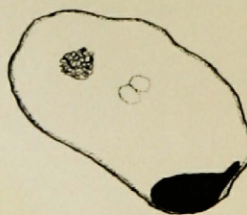
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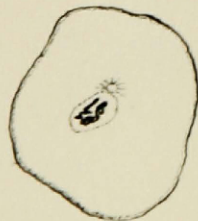
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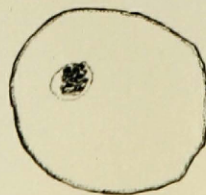
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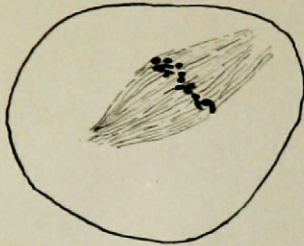
Explanation of plate IX

Maturation metaphases

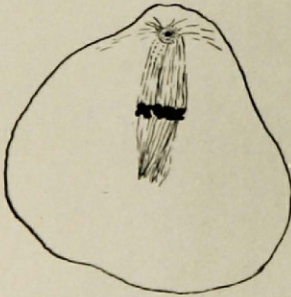
Figures 1,2,3. Metaphase plates.

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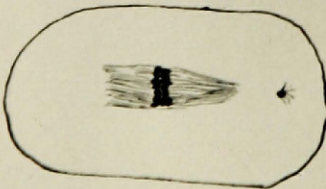
Plate
IX



2.



3.



W.C.M.

Explanation of plate X

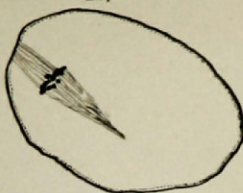
Maturation metaphases

Figures 1,3,4. Lateral view of first maturation metaphase.
Metaphase plates are clearly visible.

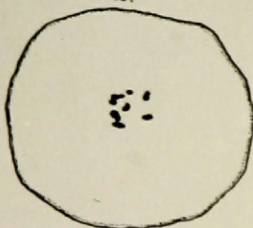
Figure 2. Polar view of metaphase.

Plate
X

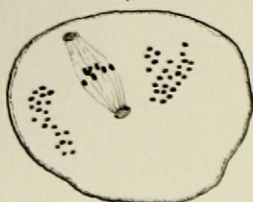
1.



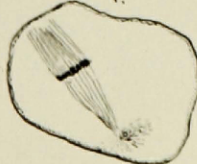
2.



3.



4.



WON

Explanation of plate XI

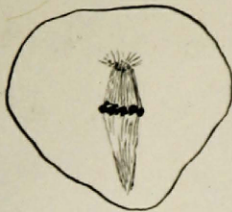
Maturation metaphases

Figure 1. The arrangement of the chromosomes in this figure is suggestive of tetrads.

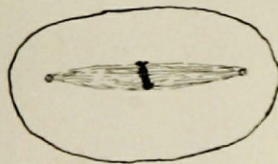
Figures 2, 3, 4. Typical metaphases.

Plate
XI

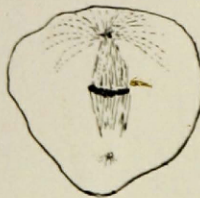
1.



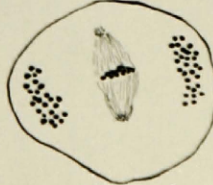
2.



3.



4.



W.A.N.

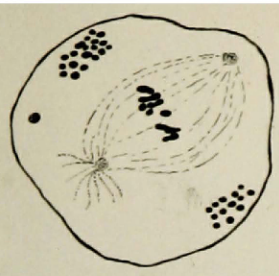
Explanation of plate XII

Maturation metaphases

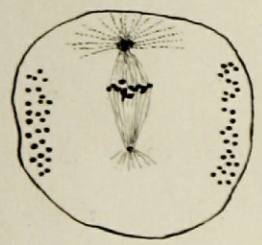
Figure 1. This figure suggests the separation of the dyads.

Figures 2 and 3. Showing the arrangement of the yolk at the sides of the meiotic figure in small globules. Structures which may be interpreted as centrosomes and asters are present.

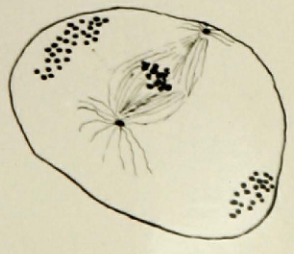
1.



2.



3.



WON.

Explanation of plate XIII

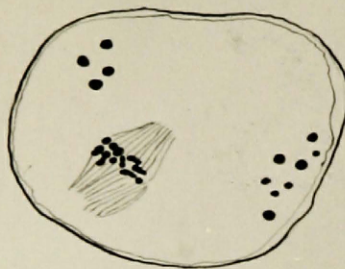
Maturation metaphases

Figure 1. Five bodies which may be dyads are shown in this figure.

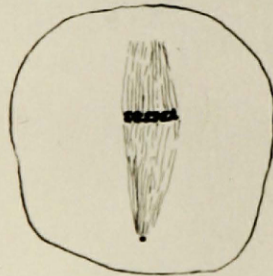
Figure 2. Figures which suggest tetrads. The small size of the chromosomes makes a definite interpretation difficult.

Figure 3. A polar view which shows nine masses of chromatin.

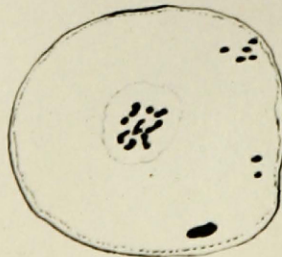
1.



2.



3.



Explanation of plate XIV

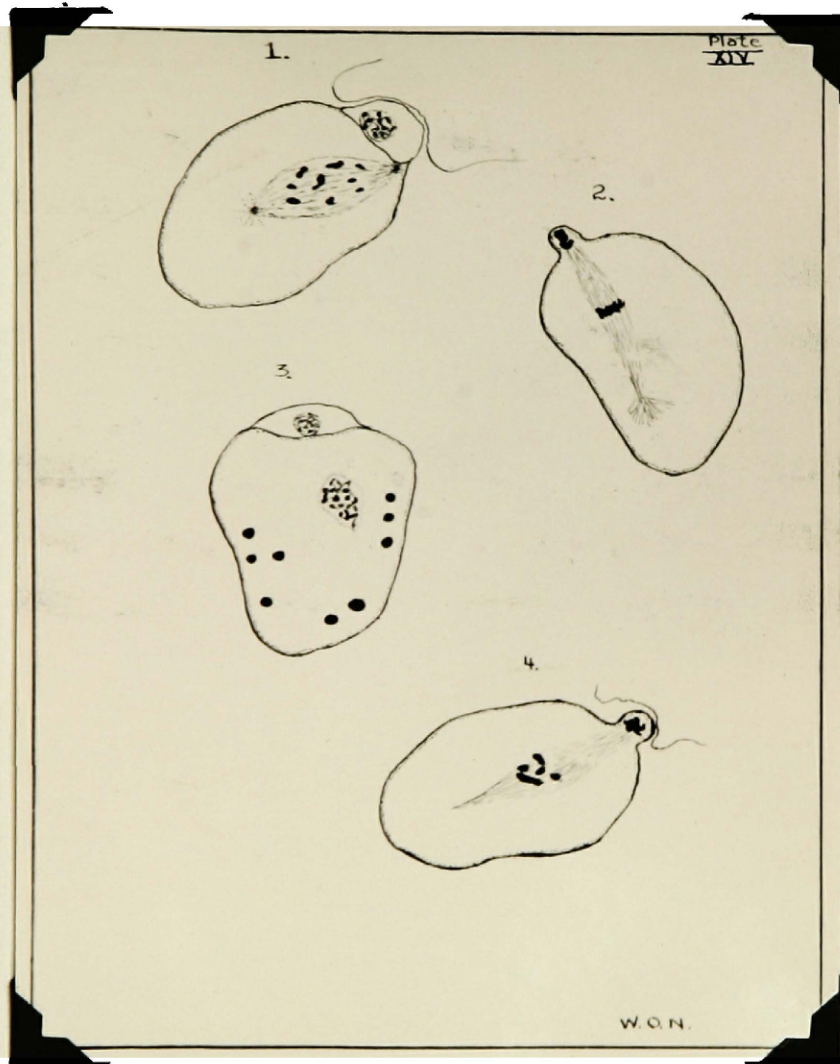
Figures suggestive of polar body formation.

Figure 1. Possible second polar spindle.

Figure 2. Figure which may be interpreted as a first polar body.

Figure 3. The second maturation prophase.

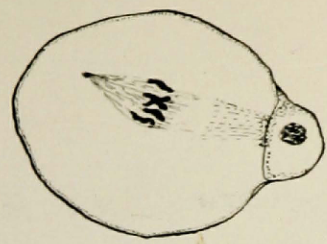
Figure 4. A possible first polar body. The chromatin in the ovocyte is in five clumps resembling dyads.



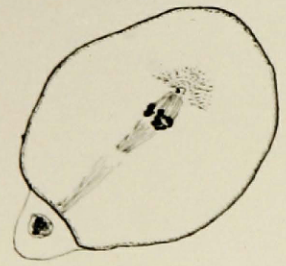
Explanation of plate XV

Three figures taken from cells in the uterus of the forty third proglottid which suggest maturation divisions and polar body formation.

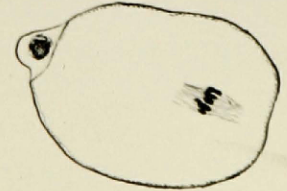
1.



2.



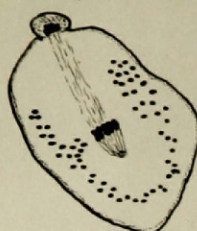
3.



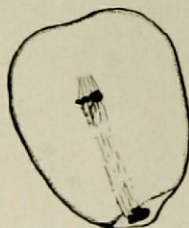
Explanation of plate XVI

Three figures of maturation divisions with structures suggestive of polar bodies in formation.

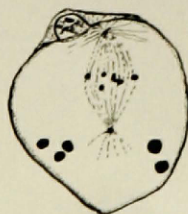
1.



2.

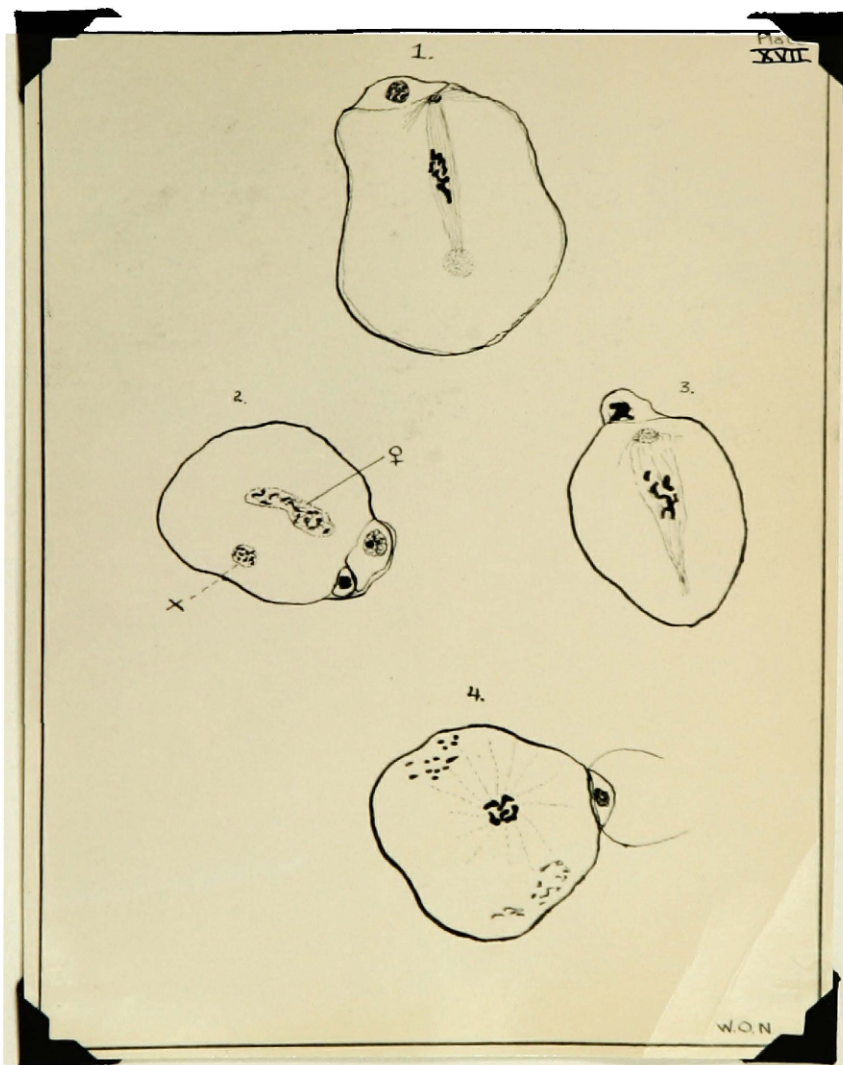


3.



Explanation of plate XVII

Four figures which show structures which may be interpreted as polar bodies. In figures 1 and 3 a spindle may be seen. Figure 4 is a polar view of a cell in which the chromatin is clumped into five bodies which may be dyads.



Explanation of plate XVIII

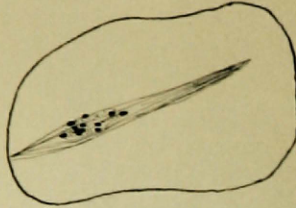
Maturation anaphases

Figure 1. A long, slender spindle showing chromosomes moving to the poles singly.

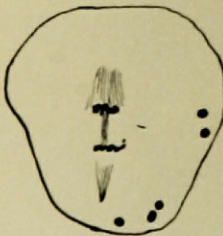
Figures 2,3,4. Chromosomes clumped in late anaphase.

Figure 5. Chromosomes moving to the poles.

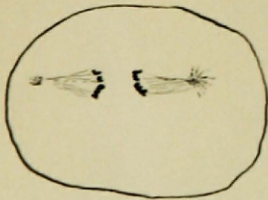
1.



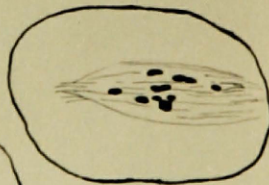
2.



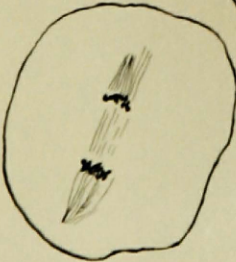
4.



5.



3.



Explanation of plate XIX

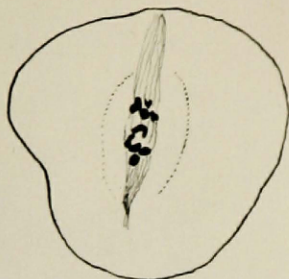
Maturation anaphases

Figure 1. Early anaphase showing dyads.

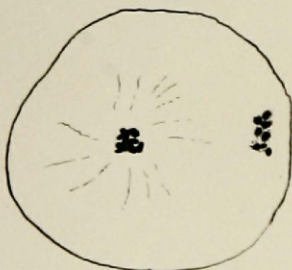
Figure 2. Polar view of anaphase clump of chromosomes.

Figure 3. Late anaphase showing five dyads at each pole.

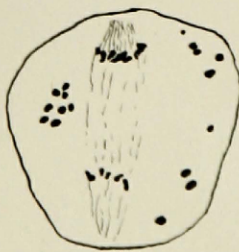
1.



2.



3.



Explanation of plateXX

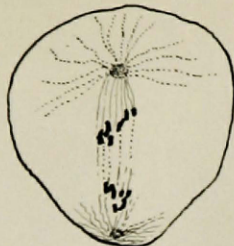
Three cells drawn from the uterus of a proglottid in which many maturation divisions appeared to be in progress.

Figure 1 shows a fairly late anaphase.

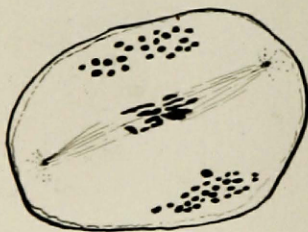
Figures 2, 3. Figures suggestive of early anaphase.

Plate
XX

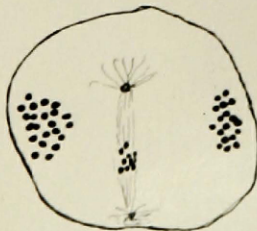
1



2



3



W. O. N.

Explanation of plate XXI

Maturation anaphases

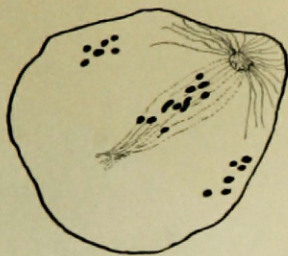
Figure 1. Chromosomes moving to the poles of the spindle.
Large centrosome is shown.

Figure 2. Early anaphase.

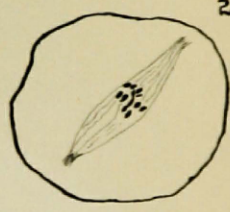
Figure 3. Dyads at the poles of the spindle in anaphase.

Figure 4. Late anaphase.

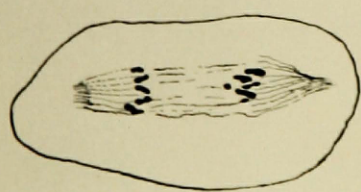
1.



2.



3.



4.



Explanation of plat. • XXII

Pronuclei

Five figures showing the male and female pronuclei.
Figures 1 and 4 have structures suggestive of polar bodies at the cell surface.

