# THE STRUCTURE AND DEVELOPMENT OF BIDDER'S ORGAN IN BUFO LENTIGINOSUS.

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At the anterior end of the testis in all of the Bufonidae is the rounded body to which Spengel gave the name "Bidder's organ." Although many of the investigators who have worked on the germ-cells of the Anura have examined this organ and ventured a conjecture as to its nature and probable function, Knappe (18) is the only one who has studied its development in any detail. In his paper, which appeared over twenty years ago, Knappe gives but a brief account of the early development of this body and he pays but little attention to the nuclear changes in the cells. Those who have more recently worked on Bidder's organ believe, with Knappe, that this body is a rudimentary ovary, and they have been more interested in studying the maner in which the cells degenerate than in trying to determine the reasons for this degeneration. As an investigation of the nuclear and cytoplasmic changes occurring in the cells of Bidder's organ during its early development might possibly give some clue to the function of this body and to the causes for the degenerative processes which occur in it, I have studied the structure and the formation of this organ in Bufo lentiginosus in connection with my other work on the germ-cells of this amphibian. Especial attention has been given in this study to the behavior of the chromatin and to the differences between the germ-cells in Bidder's organ and those in the ovary which become functional eggs. For this investigation I have made use of material prepared for a study of the spermatogenesis and oögenesis of Bufo lentiginosus. Methods of fixation and of staining are given in detail in preceding papers.

The formation of Bidder's organ is first apparent when a tadpole is from fifteen to eighteen days old. Transverse sec-

tions through an embryo in this stage of development show that the anterior portion of each genital ridge has developed much more rapidly than the rest and that this region contains from five to eight large primordial germ-cells (Fig. 2), while the middle and posterior regions never contain more than three of these cells at this time. The anterior part of the genital ridge, which has begun to develop into Bidder's organ, is continuous with the part which later becomes the sex-gland, and the cells in one region appear exactly like those in any other (Cf. Fig. 2, Plate V and Fig. 5, Plate I). At the beginning of its development, therefore, Bidder's organ is composed of two kinds of cells: large rounded primordial germ-cells which have a faintly staining polymorphic nucleus; and small peritoneal cells in which the nucleus stains very deeply and is usually elongated. There are no intermediate stages between these two kinds of cells, and in Bidder's organ, as in the sex-gland proper, the primordial germ-cells must arise from undifferentiated embryonic tissue.

Bidder's organ develops much more rapidly than the sex-gland, and it has attained a considerable size long before it is possible to ascertain the sex of the individual. During the very early stages in the development of Bidder's organ the large germ-cells divide by mitosis; the stages in this process being similar to those taking place in the cells of the sex-gland. In the prophase of mitosis twenty-four deeply staining chromatin segments are formed which condense into V-shaped chromosomes (Fig. 3, X). The spindle has a small centrosome at each pole which is devoid of radiation (Fig. 3, Y).

It is only the early generations of germ-cells in Bidder's organ that are able to divide by mitosis; in later development the division of the cells is invariably by amitosis. In a series of papers dealing with the germ-cells of Moniezia, Child (8, 9) has maintained that amitosis is the usual method by which the germ-cells in this form increase in number, and he is inclined to believe that amitosis occurs much more frequently in normal development than most investigators admit. Amitosis is the normal method by which the germ-cells in Bidder's

organ increase in number after a certain period in the development of this organ, but the cells so dividing are not capable of becoming functional eggs. In Bufo, amitosis in the germ-cells is undoubtedly correlated with degeneration since the germ-cells which become functional always divide by mitosis (King, 16).

Hoffmann (14) is, I believe, the only investigator who has found the cells of Bidder's organ dividing by mitosis. Knappe states that from the beginning the increase in the number of cells in this organ is solely through amitosis. In tadpoles of Bufo lentiginosus it is possible to find amitosis and mitosis occurring simultaneously in Bidder's organ (Fig. 3, A and Y), but a cell dividing amitotically is always older than one dividing by mitosis, since the nucleus of a cell has to undergo a definite series of changes before amitosis occurs. After a cell has once divided directly it is not capable of again dividing by mitosis.

The resting germ-cells in Bidder's organ appear similar to the resting germ-cells in the sex-gland, as they are large round or oval cells with polymorphic nuclei which contain a faintly staining granular reticulum and several nucleoli (Cf. Fig. 4, Plate V and Fig. 18, Plate II). Owing doubtless to the rapid growth of Bidder's organ the yolk spherules disappear from its cells much sooner than from the cells of the sex-gland, and they are rarely to be found in the anterior part of the genital ridge after the tadpole has attained a length of 7-8 mm. When the yolk has disappeared the cytoplasm of the germ-cells appears granular, and it is found to contain one or two vitelline bodies (Fig. 4, V) and a centrosome (Fig. 3, C). At this stage of development there is nothing to indicate that these cells differ in any way from the germ-cells in the other portions of the genital ridge.

After the last mitotic division the cells take on the character of young oöcytes and they usually have several peritoneal cells flattened against their outer surface (Cf. Fig. 5, Plate V and Fig. 21, Plate II). The nucleus of the cell is no longer polymorphic but rounded in outline and it contains a faintly stain-

ing chromatin reticulum in the meshes of which there are several nucleoli. The nucleus maintains its rounded form during the later development of the oöcyte and it only becomes irregular when the cell degenerates. I cannot confirm Knappe's observations that the nucleus of the cells of Bidder's organ sometimes sends out amœboid processes by which it moves about to accelerate the taking up of nourishment. At the stage of Fig. 5 the cells are usually collected in cell nests, as are the young oöcytes in the ovary. All of the cells of a nest are in practically the same stage of development, and doubtless all have arisen by the repeated division of one primordial germ-cell. During the early stages of its development Bidder's organ has no outer membrane, but shortly before the tadpole undergoes its metamorphosis this body becomes surrounded by a capsule which is formed by the peritoneal cells in a manner similar to that by which the outer ovarian wall is formed.

The development of the young oöcytes in Bidder's organ parallels that of the ovarian oöcytes. After the stage of Fig. 5 the cell body and the nucleus enlarge very rapidly and the chromatin forms an apparently continuous spireme which stains rather faintly (Fig. 6). When the nucleus has attained a diameter of about 0.013 mm., the chromatin shows a marked increase in its capacity for staining and the spireme, which has become much thicker and somewhat jagged in outline, begins to condense (Fig. 7). This condensation continues until practically all the chromatin is collected in the centre of the nucleus where it forms a loose mass of fine fibres in which are imbedded several nucleoli (Fig. 8). This is the synizesis stage in the oöcytes of Bidder's organ. It corresponds approximately to the stage in the contraction of the nuclear contents in the ovarian oöcytes shown in Plate II, Fig. 24, since the meshwork of fibres is considerably looser and the fibres themselves are much coarser than those in the synizesis stage of the egg shown in Plate II, Fig. 25.

Slight as the differences appear between the synizesis stage in the ova of Bidder's organ and that of the ovarian oöcytes,

their effects on the latest development of the cells of Bidder's organ are far reaching since, after the stage of Fig. 8, the nuclei of these cells appear, as a rule, very different from the nuclei of the same size in the ovarian ova. The development of the ova in Bidder's organ is similar to that of the germ-cells in the ovary only until the synizesis stage. During the time that the chromatin forms a contracted mass in the centre of the nucleus changes occur which check normal development and eventually bring about a degeneration of the cells. Just what these changes are it is impossible to determine. A comparison of the early post-synizesis stages in the cells of Bidder's organ with similar stages in the ovarian ova indicates that during the contraction period in the cells of Bidder's organ the chromatin does not become arranged in a normal manner, since in later stages there is no separation of the chromatin that is normally used for the chromosomes from the chromatin that has other uses in the cell, as is the case in the ovarian ova. The turning point in the development of the ova in Bidder's organ is, therefore, the synizesis stage. Since normal development is not possible beyond this period, except in rare instances, it is evident that the causes which bring about the degenerative processes in the cells of Bidder's organ manifest themselves during synizesis and that they act in such a way as to prevent a normal arrangement of the chromatin granules. Since the amount of chromatin in the nucleus is apparently not affected by these changes it must be that it is the arrangement of the chromatin granules that is the important thing in synizesis. The fact that the cells of Bidder's organ show degenerative changes and divide by amitosis soon after synizesis strengthens my belief that synizesis in the egg of Bufo is a means by which the chromatin which bears the hereditary qualities is separated from the chromatin which has other uses in the cell. This separation is not effected during the synizesis stage in the ova of Bidder's organ, consequently these cells are not capable of developing into functional eggs.

Since Bidder's organ develops much more rapidly than the sex-gland, it is possible, perhaps, that the rapid growth of the

cells may in a measure be responsible for the deviations from the normal processes which occur during synizesis. On this assumption to determine the causes for the rapid growth of Bidder's organ would be to determine also the reason for the degeneration of its cells. These causes must be sought through experimental work; they cannot be determined from a morphological study of this body.

Occasionally, in later development, I have found nuclei in the cells of Bidder's organ which were very much like nuclei of ovarian eggs of the same size (Cf. Plate V, Fig. 20 and Plate III, Figs. 40-43). In such cases it can only be supposed that the nuclear changes which took place during synizesis were nearly like those occurring in the ovarian ova and, consequently, that the cells could continue for a longer time to develop in a normal manner.

Stages in the development of the young oöcytes of Bidder's organ through the synizesis stage shown in Fig. 8 are to be found in young tadpoles in which the sex-glands are still in an apparently indifferent state. Soon after the synizesis period the cell nests are broken up and the ova, which are surrounded by follicle cells, become separated by the connective tissue stroma which develops throughout the organ. The formation and development of the ova proceeds from the periphery centripetally; the oldest and largest cells lie towards the center of the organ, the youngest cells towards the periphery.

In tadpoles killed at the time of metamorphosis and also in young toads one frequently finds at the periphery of Bidder's organ nests of young ova in various stages of synizesis. It is doubtless such cell nests that Hoffmann and Cerruti (5) have considered as cysts containing sperm-cells, since the cells at this time bear but little resemblance to the later stages in the development of the ova and they appear somewhat like certain stages in the development of the spermatocytes. I have never found sperm-cells in the ova of Bidder's organ. Oblique sections passing through the posterior part of this organ may show the sperm-cells of the upper part of the testis

in close contact with the large ova of Bidder's organ, but as von Wittich (34) states, Bidder's organ is always clearly marked off from the testis; one never passes gradually into the other as Knappe and Ognew (24) maintain is the case in Bufo vulgaris. The sharp distinction between Bidder's organ and the sex-gland is not maintained in the female of Bufo lentiginosus after the first year, since at about this time the cavity of Bidder's organ becomes continuous with the central cavity of the ovary. Knappe asserts that he has found mature spermatozoa in the cells of Bidder's organ that have begun to degenerate, and he believes that these spermatozoa have developed from follicle cells that have entered the cytoplasm of the ova. In a recent paper (King, 17) I have shown that the structures considered by Knappe as spermatozoa are very probably parasites, since the figures which he gives of these bodies are very similar to certain stages in the life cycle of a sporozoan parasite which infects the cells of Bidder's organ in the American toad, Bufo lentiginosus.

As the nuclei in the cells of Bidder's organ emerge from synizesis the nuclear contents does not become arranged in a manner similar to that found in the nuclei of the ovarian ova in early post-synizesis stages. In the great majority of cases practically all of the chromatin goes into a continuous spireme (Fig. 9), while the greater portion of the plasmosome substance is collected into one or two rounded masses which lie in the meshes of the spireme or against the nuclear membrane (Figs. 10, 14). In some few nuclei the plasmosome masses have a smooth outline and they color uniformly red when preparations are stained with safranin and gentian violet (Fig. 14). In such cases it is evident that all of the chromatin, except that found in the few small karyosomes which are scattered about the nucleus, has gone into the spireme. In other nuclei a small amount of chromatin remains attached to the outer surface of the plasmosomes, giving these bodies a slightly irregular outline (Figs. 9, 10). Nucleolar masses of this kind correspond in structure to the compound-nucleoli found in the ovarian ova, and their subsequent fate is the

same since they undergo a resolution into plasmosomes and oxychromatin granules (Figs. 21-25).

The continuous spireme found at the stage of Fig. 9 appears granular and somewhat irregular in outline. It does not undergo a longitudinal splitting at any stage of development, but it divides transversely into a number of segments which are of various lengths (Figs. 10-14). These segments are scattered throughout the nucleus and they are never found in pairs. Camera drawings of all of the sections of a nucleus in this stage of development show that the number of chromatin segments is greater than the somatic number (24). All of the chromosomes appear granular, as a rule, and numerous fine projections extend out from either side (Fig. 16); only in rare instances (Fig. 20) do any of the chromosomes assume the feathery appearance which characterizes the chromosomes in the later growth stages of the ovarian ova. In later development all of the chromosomes break up into minute granules which are dissolved in the karyoplasm when the egg degenerates.

Usually the cells begin to divide by amitosis soon after the spireme has broken into segments. Nuclear divisions sometimes follow each other rapidly, and a cell may contain several rounded nuclei before the cytoplasm divides (Fig. 31). As a rule, the largest nucleolus divides once or twice before the nucleus itself divides. A constriction appears in the middle of the nucleolus (Fig. 11), and it subsequently breaks into two rounded portions which are nearly equal in size (Fig. 12). The two nucleoli thus formed usually move to opposite sides of the nucleus before the nucleus divides (Figs. 10, 13). The nucleus elongates considerably previous to amitosis (Fig. 15), and it is constricted into two nuclei of approximately equal size (Figs. 16, 17, 19). Each nucleus contains at least one large nucleolus and apparently half of the chromosomes (Fig. 19); and one or both of the nuclei may divide again before the cytoplasm of the cell shows any evidence of a division (Fig. 31). Amitosis is frequently seen in the cells of Bidder's organ in tadpoles killed at the time of metamorphosis, and it can be

found in practically every section of Bidder's organ taken from young toads or from adult males.

By the time that the nucleus has reached the stage of Figs. 10-13 the follicle cells have formed a membrane around each egg, the zona pellucida (Figs. 27, 28, 30). Not infrequently a blood corpuscle is to be found among the follicle cells which lie inside of the zona pellucida in contact with the outer surface of the cell (Fig. 19, B. C.).

In the early stages of the development of Bidder's organ the cytoplasm of the young oöcytes contains a single vitelline body which is sometimes surrounded by a clear area as it is in the ovarian ova (Fig. 7, V). About the time of synizesis this vitelline body divides repeatedly, and by the time that the egg has attained a diameter of 0.035 mm. there are a number of these bodies of various sizes scattered throughout the cytoplasm (Fig. 16). Will (33) and Leydig (20) maintain that the rounded bodies in the cytoplasm of the egg of Rana (which are similar to the vitelline bodies in the egg of Bufo) are nucleoli which have migrated from the nucleus into the cytoplasm in order to form the yolk. Such an origin for the vitelline bodies in the cells of Bidder's organ is impossible, since these bodies are increasing in number at the time that the nucleus rarely contains more than three or four small nucleoli. As is the case in the ovarian ova, the vitelline bodies bring about the formation of granular yolk-nuclei in the cells of Bidder's organ, and, at the stage of development shown in Fig. 19, the cytoplasm of the cells sometimes contains a large number of these structures. The arrangement of the yolk-nuclei in the cells of Bidder's organ differs from that found in the ovarian ova, since these bodies are always scattered irregularly throughout the cytoplasm and are never collected in a zone midway between the nucleus and the periphery of the egg. In many cases the yolk-nuclei form in a very abnormal manner, and a cell, instead of containing a large number of small yolk-nuclei, will contain only two or three of these structures which are very large (Fig. 18). In such ova one of the large yolk-nuclei almost invariably forms

a cap over one side of the nucleus, thus appearing very similar to the yolk-nuclei which, in many kinds of eggs, originate close to the nuclear membrane.

Knappe states that in Bufo vulgaris about one year old the cytoplasm of the cells of Bidder's organ contains a large, rounded, refractive body which is sharply marked off from the cytoplasm. He maintains, furthermore, that the nucleus puts out processes like pseudopodia which engulf this body; afterwards the pseudopodia are slowly withdrawn and the nucleus again becomes rounded, while the ball of substance is gradually dissolved in the karyoplasm. I have not observed this remarkable phenomenon in the cells of Bidder's organ in Bufo lentiginosus. In this species of Bufo, at certain stages in the development of Bidder's organ, the cytoplasm of the cells contains many granular yolk-nuclei which are more or less rounded in form and sharply defined (Fig. 19), but I have never seen anything that would indicate that these masses are ever taken into the nucleus.

The inability of the cells of Bidder's organ to develop into functional eggs has been ascribed by Knappe to the fact that these cells are not able to form yolk. A study of the early development of Bidder's organ in Bufo lentiginosus shows that in a great many of the cells the first stages in the formation of yolk take place, since yolk-nuclei are formed in a manner similar to that which takes place in the ovarian ova (Fig. 19). Except in the one case to be described later, I have never found the development of yolk in the cells of Bidder's organ progressing beyond the stages shown in Figs. 18-19. Were the processes leading to yolk formation independent of nuclear action it would seem as if they might continue beyond this point, since there is no evidence of cytoplasmic degeneration at the stage of Fig. 19. The degenerate condition of the nucleus at this time is shown by the arrangement of the nuclear contents and by the fact that the cells are dividing amitotically.

Fig. 26 shows a section of a cell taken from the Bidder's organ of a young male toad with a body length of 2 cm. In

this cell, and also in a few others lying near it, the cytoplasm contains a number of yolk spherules of various sizes. These spherules were not formed at the periphery of the egg, as is the case with the yolk spherules that first appear in the ovarian ova, but they were formed in, and from the substance of the yolk-nuclei scattered throughout the cytoplasm of the cell. The cytoplasm appears much vacuolated and the nucleus is in an advanced state of degeneration, while many of the large yolk spherules are disintegrating. The process of dissolution at first affects only a part of the yolk spherule, leaving a crescent shaped structure (Fig. 26, Y) which remains for a time and then disappears. This egg seems to me to furnish convincing evidence that yolk-spherules are formed from the substance of yolk-nuclei, and it also shows that the failure of the cells of Bidder's organ to develop into functional eggs cannot be due entirely to their inability to form yolk, as Knappe claims.

The compound-nucleoli which are found in some eggs during early post-synizesis stages (Figs. 9, 10) begin their resolution, as a rule, soon after the spireme divides into segments. These bodies first become very irregular in outline (Fig. 21), and subsequently several light areas appear in them (Fig. 22). In later stages a differential stain, such as safranin and gentian violet, shows that these structures are composed of a mass of rounded plasmosomes embedded in chromatin granules (Fig. 23). The component parts of these masses are soon separated (Figs. 24-25), and the plasmosomes become distributed throughout the nucleus. Very little chromatin is found in the compound-nucleoli in the cells of Bidder's organ compared with the amount that goes into the formation of the large nucleolar masses in the ovarian ova. Usually, after the resolution of the compound-nucleoli, the chromatin granules become scattered through the karyoplasm, only in exceptional cases (Fig. 20) is enough of the chromatin separated from the spireme after synizesis to form oxychromatin filaments. Nucleolar masses similar to those shown in Figs. 23-24 are evidently present in the cells of Bidder's organ in Bufo vulgaris since Ognew states that he sometimes

finds large nucleoli which have a very complicated structure, being composed of a number of deeply staining balls surrounded by a mass of granules.

No matter how many plasmosomes a nucleus may contain there is usually one of these bodies that is larger than the others (Fig. 29); and one of the first indications of the approaching dissolution of the nucleus is the formation of a fluid space around this large nucleolus (Fig. 17). The nucleolus itself at this time may appear homogeneous (Fig. 18), or it may contain one or many vacuoles (Fig. 17). In either case it stains less intensely than in earlier stages and it gradually decreases in size (Figs. 26-27), while the vacuole around it constantly grows larger (Figs. 18, 26, 29). As the fluid space becomes several times the size of the original nucleolus, its substance cannot be derived entirely from the nucleolus, but it must be obtained in part from the dissolution of the karyoplasm. The vacuole grows until it comes in contact with the nuclear membrane (Fig. 26). It then breaks at some point in its outer surface and the nuclear substance is in direct contact with the cytoplasm, as during the growth of the vacuole the nuclear membrane becomes very irregular in outline and it disappears entirely when the vacuole breaks (Fig. 27). While these changes are taking place the chromosomes gradually break up into granules that cannot be distinguished from the karyoplasm, and by the time the nuclear membrane has disintegrated most of the chromosomes have disappeared (Fig. 27). During the disintegration of the nucleus I have never found the chromatin in the form of irregular clumps as Ognew has found to be the case in the degenerating cells of Bidder's organ in Bufo vulgaris. The degenerative changes just described are not found in the cells of Bidder's organ until the young toad has attained a length of about 2 cm.

Degenerative changes usually appear in the cytoplasm soon after the stage of Fig. 19, since only in rare cases is a cell able to form yolk spherules. If a cell contains a large number of yolk-nuclei at the time that these degenerative processes begin the yolk-nuclei are dissolved in situ, leaving clear fluid spaces

in the cytoplasm which at first have the shape and size of the yolk-nuclei (Fig. 29). Later these spaces are united and the cytoplasm then contains several large vacuoles (Fig. 27). In cases in which the cytoplasm contains only a few large yolk-nuclei instead of a number of small ones (Fig. 18), these masses become sharply marked off from the cytoplasm when degenerative changes begin and they stain much more intensely than before. The appearance of these bodies thus becomes so very different from that of the yolk-nuclei shown in Fig. 19 that it might be thought that they were not yolk-nuclei but the products of a fatty degeneration of the cytoplasm. In order to determine this point definitely several cells appearing much like that shown in Fig. 18 were drawn with the aid of a camera lucida and the preparations containing them were then put in ether where they remained for about two weeks. At the end of this time the slides were remounted and the same cells were again drawn. The irregular granular masses had not been affected in any way by the ether and they were just as large and conspicuous as before. These bodies cannot, therefore, be products of a fatty degeneration of the cytoplasm or they would have been dissolved by the ether. Soon after the stage of Fig. 18 these masses dissolve in situ and several large vacuoles are formed in the cytoplasm which later become connected as in Fig. 27.

Knappe maintains that there are four ways by which the rudimentary eggs in Bidder's organ disintegrate: (1) through the penetration into the cytoplasm of follicle cells which absorb the egg substance; (2) through the development of pigment in the cytoplasm which seems to bring about a gradual collapse of the egg; (3) through the invasion of the cytoplasm by both follicle cells and blood capillaries; (4) through pigment formation combined with the penetration of blood capillaries into the egg. To these Ognew, from his study of Bidder's organ in Bufo vulgaris, adds a fifth method—a peculiar process in which the follicle membrane between two adjacent oöcytes disappears leaving a space which grows in breadth and finally becomes a large spherical vacuole which is

filled with a fluid derived from the disintegration of the oöcytes. Ognew also suggests as a special process of degeneration, the penetration of one cell of Bidder's organ into another.

From the very early stages in the development of Bidder's organ in Bufo lentiginosus the germ-cells are surrounded by follicle cells which are in direct contact with the outer surface of the cytoplasm, since the cells never seem to develop a yolk membrane as do the cells of Bidder's organ in Bufo vulgaris according to the investigations of Ognew. After the stage of Fig. 29 the egg shrinks away from its zona pellucida and its outline appears somewhat irregular (Fig. 27). At this time many of the follicle cells lie in slight depressions in the egg surface as if they were already beginning to enter the egg. It would seem as if the absence of a yolk membrane might make it possible for follicle cells to penetrate into the eggs at any stage of development, but I have never found these cells inside of the egg until the nucleus and the cytoplasm have begun to degenerate. Stages in the penetration of the follicle cells into the egg are shown in Fig. 30. The cells do not show any amœboid processes, but they appear to sink gradually into the substance of the cytoplasm. Fig. 32 shows a late stage in the absorption of the egg by means of the follicle cells; the nucleus has entirely disappeared and all that is left of the egg is a small amount of deeply staining, granular substance.

Sometimes, as shown in Fig. 30, B. C., blood corpuscles enter the cytoplasm with the follicle cells and evidently take part in the absorption of the egg. The zona pellucida becomes very irregular as the egg degenerates, and, owing to the pressure of the surrounding eggs, it collapses after the egg has become partially absorbed and evidently suffers the same fate as the egg itself.

The process described above is the usual method by which the eggs in Bidder's organ disintegrate in all toads under two years old. Sometimes in young toads, more often in adults, a blood capillary breaks through the zona pellucida and forces

its way into the egg, taking with it a number of follicle cells (Fig. 28). In such cases the egg disappears very rapidly, its substance being absorbed directly by the blood. I have never found the cells of Bidder's organ disintegrating as a result of the formation of a large amount of pigment in the cytoplasm. Pigment is rarely formed in the cells of Bidder's organ in Bufo lentiginosus, and then only in adult males. In all of the cases which I have found the pigment was confined to a narrow zone around the periphery of the egg; it did not develop throughout the entire egg as is usually the case in eggs which are degenerating in the ovary. There was nothing in any of these eggs to indicate that the pigment was concerned in any way with the degenerative processes taking place in the cell.

Although I have never found two adjacent oöcytes degenerating as a result of the development of a spherical vacuole between them, I have seen what Ognew considers as degeneration due to the penetration of one oöcyte into another. This phenomenon was first described by Cerruti (6) in 1905. Cerruti states that in Bufo vulgaris the cytoplasm of one oöcyte in Bidder's organ sometimes forces its way into the cytoplasm of another oöcyte. Later the nuclear substance of the entering cell flows towards the place of penetration and eventually one cell is engulfed by the other. Cerruti suggests that this process is analogous to the entrance of follicle cells into the egg, and that the entering cell may be considered as a parasite of the cell into which it penetrates. Ognew considers that this suggestion ventures too much since we would have to assume a subsequent struggle for existence between the two nuclei. Ognew does not think it possible that this phenomenon can be associated in any way with amitosis, and his only suggestion is that it is "a highly original process of degeneration" which requires further study. The figures given by Cerruti and by Ognew seem to me to show unmistakably that both of these investigators were dealing with cases of amitosis in degenerating ova which were greatly distorted in shape on account of the pressure of the surrounding cells. Bidder's

organ never grows beyond a certain size in adult males. During the summer months the cells of this body increase rapidly in number and also in size and they often become so crowded together that one cell forms a decided indentation in the surface of an adjacent cell. In preparing to divide the nuclei of such cells frequently become greatly elongated, much more so than shown in Fig. 17, and before the appearance of the division membrane it might readily seem as if the substance of the nucleus was flowing in a certain direction and that the one egg was trying to force its way into another. Very often, during the division of these cells, currents seem to be set up in the cytoplasm and a portion of the cytoplasm around one nucleus may appear sharply distinct from the remaining cytoplasm. On superficial examination such ova may give the impression that one cell has entered another since the egg contains two separate nuclei; one of them being surrounded by cytoplasm which appears differently from the other cytoplasm in the cell. The cell which has apparently engulfed one of its neighbors is never noticeably larger than the surrounding cells; and both of its nuclei are similar to the nuclei in the adjacent cells, while its zona pellucida appears perfectly intact in all places. These facts seem to me sufficient proof that the egg in question is dividing amitotically and that it has not been entered by another cell. I do not see how it would be possible for one egg to enter bodily into another egg of practically the same size without causing a break in its zona pellucida or without producing a marked increase in the size of the cell and a profound change in its structure.

Friedman (11) has observed that the cytoplasm of the degenerating eggs that are sometimes found in the testis of Rana viridis is often separated into two distinct portions which have no regular outline but dovetail into each other in various ways. One part of the cytoplasm has a granular structure and stains very intensely, while the other part is apparently homogeneous and stains very faintly. This appearance of the cytoplasm is probably due to an abortive attempt on the part of the cell to form yolk-nuclei similar to those shown in Fig.

18. There is the possibility, however, that it may be caused by currents in the cytoplasm of the degenerating eggs which separate the more fluid portion of the cytoplasm from the more granular, as is sometimes the case in the cells of Bidder's organ.

The degenerative changes taking place in the cells of Bidder's organ are very similar to those which occur in mature amphibian eggs which have remained in the ovary after the breeding season, according to the investigations of Bühler (4), Dubnisson (10), Ruge (28), and others. In such eggs the chromatin breaks up into granules and, after the disappearance of the nuclear membrane, the substance of the nucleus mingles with that of the cytoplasm, the egg being finally absorbed through the agency of follicle cells, leucocytes and blood capillaries which have penetrated into the cytoplasm. Eggs which are degenerating in the ovary are always heavily pigmented, however, while pigment is rarely developed in the cells of Bidder's organ and when it is present it never seems to be concerned in the degenerative processes.

Bidder's organ is a permanent structure in the males of all species of the Bufonidae so far investigated. In Bufo variabilis, Bufo cinereus, and Bufo calamita, this body disappears in the female at the end of the second year. In Bufo vulgaris, according to the observations of Knappe, Bidder's organ disappears in the adult female during the winter and a new organ is regenerated during the summer months. According to Ognew, Bidder's organ does not disappear in the adult female of Bufo vulgaris during the winter, but it persists as a small shrunken organ which lies near the fat bodies. Bufo vulgaris is, therefore, the only species so far studied in which Bidder's organ is a permanent structure in both male and female.

In Bufo lentiginosus Bidder's organ disappears in the female at the end of the second year and no traces of it are to be found in older females. During its early development this organ contains no central cavity, although there are a number of intercellular spaces between the rounded ova. After the

metamorphosis of the tadpole the cells of Bidder's organ increase in number very rapidly and, owing to pressure, they are often greatly distorted. The central cavity is formed when the cells in the interior of Bidder's organ degenerate; this occurs when a young toad has attained a body length of about 2 cm. In the female, after the first year, the cavity of Bidder's organ opens into the cavity of the ovary, as Knappe has stated is the case in Bufo vulgaris, and eventually the outer wall of this organ becomes continuous with the epithelial covering of the ovary. Bidder's organ then appears as a small lobe of the ovary which is easily distinguished from the other lobes as the cells never develop beyond a certain stage. Bidder's organ then gradually decreases in size and finally disappears. Although I have several times carefully examined entire ovaries of mature females, I have never been able to find any traces of this body.

In the male toad Bidder's organ varies greatly in size and in appearance at different seasons of the year. In the early spring this body appears shriveled and it is somewhat irregular in shape. Sections of Bidder's organ taken from toads killed at the height of the breeding season in April show that at this time the organ has a very large central cavity and that it contains a considerable number of degenerating ova and only a few young eggs. In the early summer large numbers of new eggs are formed at the periphery of Bidder's organ, and this body increases considerably in size and becomes more rounded. During the latter part of August and in September the large cells begin to degenerate in increasing numbers and only a very few young ova can be found.

Ognew states that the development of Bidder's organ is closely associated with the development of the sex-gland. When the sex-gland is resting, Bidder's organ grows and the number of cells increases, but from the time that the formation of the spermatozoa begins up to the period of sexual activity which occurs in April and May, this organ gradually decreases in size. I cannot agree with Ognew that the sex-gland is "resting" during the summer months when Bidder's

organ is increasing in size. My study of the spermatogenesis of Bufo lentiginosus (King, 16) has shown that early summer is the time when the sperm-cells are most actively dividing and that in August and September, when large numbers of the cells of Bidder's organ are beginning to degenerate, the testes are filled with spermatids and spermatozoa. The growth of Bidder's organ is therefore most rapid during the period when the cells of the testis are most actively developing into spermatozoa. The degeneration of numerous cells of Bidder's organ at the end of the summer is not due to the beginning of a period of sexual activity on the part of the testes, but to the fact that these cells have reached their maximum stage of development and, since they can go no further, they must of necessity degenerate. During the winter there is no active formation of new cells in Bidder's organ, and many of the cells already formed gradually reach their maximum development and then disintegrate. In the spring, therefore, Bidder's organ is only about one-half of its former size. New cells are formed in great numbers in Bidder's organ only at the time that new cells are developing in the testes.

In adult males the nuclei of the cells of Bidder's organ usually contain a number of small nucleoli rather than one or two large ones as is so often the case in the young animals. The cytoplasm of these cells usually appears uniformly granular until it is beginning to be absorbed by the follicle cells and by the leucocytes. Yolk-nuclei are very rarely developed in these cells, and when they are found they always appear like the granular masses shown in Fig. 18. Disintegration of the cells through the agency of blood capillaries which have penetrated into the cytoplasm occurs much more frequently in the Bidder's organ in the adult than in the young toad.

Investigations have shown that Bidder's organ is not found in the amphibians as a class, but that it is confined to the Bufonidae except in rare instances. In 1830, Müller (22) stated that a rounded body is present at the anterior end of the testes in tadpoles of Pelobates fusca and also in those of Rana. These observations have not been confirmed by other

workers and it is probable, as Knappe suggests, that Müller mistook tadpoles of Bufo for those of other species of amphibians. Knappe found a Bidder's organ in a young male Salamandra about two years old, but he gives no details of its structure. As far as I have been able to determine, these are the only recorded cases in which a Bidder's organ has been found in amphibians other than the Bufonidae. The numerous cases of hermaphroditism that have been reported in different species of Rana and the investigations of Pflüger (25) which show that large numbers of tadpoles of Rana temporaria are hermaphroditic would seem to indicate that a body somewhat of the nature of the Bidder's organ in Bufo is not infrequently formed in Rana. I am at present investigating the development of the germ-cells in a number of species of American amphibians, and I hope later to record my observations regarding the presence or absence of Bidder's organ in these forms.

Bidder's organ has been a subject of controversy ever since its discovery in 1758 by Rösel von Rosenhof (27), and a number of different theories have been advanced regarding its nature and probable function. The discoverer of this organ considered it a part of the fat body, while Ratke (28), who examined it in 1825, believed it to be a portion of the testis. Three years later Jacobson (15) came to the conclusion that all toads are hermaphrodites since the body at the anterior end of the testis is a rudimentary ovary. This view was adopted in 1853 by von Wittich (34), after a study of Bidder's organ in Bufo cinereus, and it has since been advocated by La Valette St. George (29), Nussbaum (23), Bourne (3), Cerruti (6) and Ognew. Hoffman (14) believes that Bidder's organ contains both ova and spermatozoa, and he therefore considers that this body is a "rudimentäre Zwitterdrüse." On the other hand, Bidder (1) maintains that the body at the anterior end of the testis is not a rudimentary ovary but an "Abtheilung des Hoden, und zwar eine auf einer niedrigen Entwickelungsstufe stehen gebliebene, welche die Bildung des Sperma und der Spermatozoen nun vorbereitet." Leydig (19)

and Spengel (31, 32) also consider that Bidder's organ is an accessory organ and not an ovary. The latter investigator thinks it highly probable that "dies Organ eine Rolle in den Leistungen der Geschlechtsdrüsen, spielt, etwa in irgend einer Beziehung steht zur Bildung des Materials von der die Entwickelung neuer Ureier ausgeht, im weiblichen wie im männlichen Geschlechte."

Spengel gives three reasons why he does not believe that Bidder's organ is a rudimentary ovary: (1) the anatomical differences between Bidder's organ and the true ovary consisting in a lack of a central cavity in Bidder's organ and the absence of pigment and yolk from the cells themselves; (2) the fact that Bidder's organ is found in the female as well as in the male; (3) the presence of Bidder's organ in hermaphroditic toads. Later researches have rendered the first of these reasons invalid since Bidder's organ has been found to contain a central cavity. Knappe has found pigment in the cells of Bidder's organ in Bufo vulgaris, and I have also found it in Bufo lentiginosus. The formation of yolk-nuclei is a common phenomenon in the cells of Bidder's organ in tadpoles of Bufo lentiginosus, and in one instance (Fig. 26) I have found the cells of Bidder's organ developing yolk spherules. Although Bidder's organ was found in the hermaphroditic toad examined by Spengel it is not present in a most interesting specimen of Bufo vulgaris recently described by Cerruti (7). In this individual there is a well developed testis in front of each kidney, and lying between each testis and the fat body is an ovary which appears to be intermediate in structure between a true ovary and Bidder's organ. In this individual Bidder's organ has been able to develop further than it normally does and it has thus become a part of the rudimentary ovary. This development would probably not have been possible if Bidder's organ were merely an accessory male organ.

The evidence brought forward by the investigators who have more recently studied the structure of Bidder's organ in adult toads has been unanimously in favor of the view that this body is a rudimentary ovary, and the results of my study

of the development of this structure point to the same conclusion. The germ-cells of Bidder's organ arise from primordial germ-cells which are similar in character to the cells which become functional spermatozoa or eggs, and the early development of these cells closely follows that of the ovarian ova up to the synizesis stage. During synizesis the cells of Bidder's organ appear similar to spermatocytes in which the nuclear contents are in a contracted condition, but at no other period in their development do they resemble in any way stages in the development of the spermatozoa; neither are they similar to any cells of the body except the ova. Even when the cells of Bidder's organ are degenerating their resemblance to the ovarian ova is very marked, and the degenerative processes occurring in them are similar to those taking place in the mature eggs which are not expelled from the ovary. There is, therefore, no probability that Bidder's organ is a portion of the testis which has been arrested in its development to serve as an accessory male organ as Bidder, Leydig, and Spengel maintain.

If Bidder's organ is a rudimentary ovary there are three possibilities that may be considered in a discussion of the origin of this body. It is possible, as Haeckel (13) suggests, "dass das älteste und ursprünglichste Geschlechtsverhältniss die Zwitterbildung war und dass aus dieser erst secundär (durch Arbeitstheilung) die Geschlechtstrennung hervorging." This primitive hermaphroditic condition has been lost by most of the vertebrates, although it still persists in many of the lower forms. If the amphibians were originally hermaphrodites then this primitive condition of the sex-glands still exists in the Bufonidae, being indicated by the presence of Bidder's organ. On this assumption Bidder's organ is a degenerate ovary in the male toad and a degenerate testis in the female.

In the female toad the cells of Bidder's organ have no resemblance whatever to the sperm-cells and in their structure and development they resemble the ovarian ova as closely as do the cells of the Bidder's organ in the male; neither is there

any tendency to the development of male organs by the female in any of the Bufonidae. These facts are considered by Marshall (21) to furnish sufficient reason to overthrow the view that amphibians were originally hermaphroditic. In spite of the objections that can be brought against it, this theory seems to me to offer the most satisfactory explanation of the presence of Bidder's organ in Bufo. It is conceded by most, if not by all, zoölogists that the spermatozoa are more highly differentiated than the ova. It is therefore only natural to suppose that in a degenerate sex-gland, such as Bidder's organ, the germ-cells would follow in the course of their development the type of the least specialized germ-cells, the ova, rather than that of the more highly specialized spermatozoa. Such an organ would, therefore, have the same structure in all animals regardless of sex. According to this view it is only necessary to assume that Bidder's organ has degenerated in the female more than it has in the male in order to have the conditions in this body what we find them at the present time. Since Bidder's organ usually disappears in the adult female, although it persists throughout the lifetime of the male, there is good reason to believe that this body is more degenerate in the female than in the male. That the Bufonidae, which are among the most highly differentiated of the amphibians, should retain a primitive hermaphroditic condition of the genital organs when such a condition is not found at the present time in other classes of amphibians, even among forms which are considered as primitive or degenerate types, is not an obstacle in the way of the theory outlined above. A somewhat similar condition is found among certain fishes, and many of the higher vertebrates have retained primitive organs which are at present in a degenerate condition and seemingly of no use to the individual.

Marshall has suggested that the formation of Bidder's organ "may be regarded as due to a further extension backward of that tendency to degeneration and atrophy which has caused the conversion of the most anterior part of the germinal ridge into the fat body." In accounting for the similarity in the

appearance and in the development of the cells of Bidder's organ in the two sexes, Marshall states that the "degeneration of the male genital gland may be regarded as taking the form of a reversion to the more primitive ovarian type." According to the investigations of Spengel (35), Semon (30), Goglio-Tos (12), and Bouin (2), the anterior portion of the genital ridge, which develops into the fat body, is composed entirely of small connective tissue cells. Sections of the young tadpoles of Bufo lentiginosus show that the germ-cells are never found anterior to Bidder's organ in this amphibian. In Bufo the germ-cells are not derived from peritoneal cells but from undifferentiated embryonic tissue. It hardly seems probable, therefore, that a mass of cells having a different origin from the germ-cells and totally unlike them in structure ever belonged to the sex-gland proper at any period in the history of the race. In very young tadpoles the cells which are to develop into the fat body form a forward extension of the genital ridge, but this does not necessarily indicate that they were primarily sex-cells. I am strongly inclined to believe that the peritoneal cells which form the fat body have secondarily come into connection with the anterior end of the genital ridge and that Bidder's organ marks the extreme anterior boundary of the sex-gland. If this be true, then Marshall's theory is untenable since the cells forming the fat body are not germ-cells, and even Marshall himself believes that the cells of Bidder's organ are degenerate ova.

There is a third possibility regarding the origin of Bidder's organ which may be suggested, although little can be said in its favor. Bidder's organ may, perhaps, be the remains of a primitive sex-gland which was functional when the Bufonidae were sexually mature in their larval state, as is the condition of the Axolotl at the present time. On this assumption the ovary and testis are structures secondarily acquired when the reproductive activity became manifested at a later period in the life of the individual. The similarity in the appearance of the cells of Bidder's organ in both sexes and their resemblance to ova can be accounted for on the supposition that, as the

organ is degenerate in both sexes, its cells have taken on the character of the least specialized germ-cells, the ova. The Axolotl is the only known amphibian that reproduces while in a larval condition, and its genital organs are similar to those of other salamanders. Since it is probable that neotenia in this form is a phenomenon of adaptation rather than a primitive condition, there is little ground for a belief that the amphibians as a class were ever sexually mature in a larval state.

The function of Bidder's organ is as yet undetermined. Since this structure is confined chiefly to the Bufonidae it hardly seems as if it could have an important rôle in the development of the sex-cells, as Spengel claims; neither can it be considered as a storehouse of reserve material that is to be used during the hibernation period, since measurements made of this body at different times of the year show that it loses not more than one-half of its volume during the winter months. As a rudimentary ovary Bidder's organ is apparently functionless, although further research, possibly by experimental means, may determine the part played by this body in the life history of the individual.

## LITERATURE.

1. BIDDER, F. H. Vergleichende anatomische und histologische Untersuchungen über die männlichen Geschlechts- und Harnwerkzeuge der nackten Amphibien. Dorpat, 1846.

2. BOUIN, M. Histogenèse de la glande génitale femelle chez Rana temporaria. Arch. de Biol., t. XVII, 1901.

3. BOURNE, A. G. On Certain Abnormalities in the Common Frog (Rana temporaria). Quart. Journ. Micr. Sci., Vol. XXIV, 1884.

4. BÜHLER, A. Rückbildung der Eifollikel bei Wirbelthieren II. Morph. Jahrb., Bd. XXXI, 1902.

5. CERRUTI, A. Contribuzione per lo studio dell' organo di Bidder nei Bufonidi I. Prosenza di spermii nell' organo. Boll. della Soc. di Naturalisti in Napoli, Vol. XVII, 1903.

6. CERRUTI, A. Contribuzione per lo studio dell' organo di Bidder nei Bufonidi II. Di una speciale penetrazione di ovule adiacenti nel Bufo vulgaris, Laur. Atti della Reale Accad. della Sci. Fisiche e matematiche, Vol. XII, 1905.

7. CERRUTI, A. Sopra due casi di anomalia dell' apparato riproduttore nel Bufo vulgaris, Laur. Anat. Anz., Bd. XXX, 1907.

8. CHILD, C. M. Studies on the Relation Between Amitosis and Mitosis. Development of the Ovaries and Oögenesis in Moniezia. Biol. Bull., Vol. XII, 1907.

9. CHILD, C. M. Studies on the Relation Between Amitosis and Mitosis. II. Development of the Testes and Spermatogenesis in Moniezia. Biol. Bull., Vol. XII, 1907.

10. DUBNISSON, H. Contribution à l'étude du vitellus. Arch. de Zool. exper. et gen., t. V, 1906.

11. FRIEDMAN, F. Rudimentäre Eier im Hoden von Rana viridis. Arch. mikr. Anat., Bd. LII, 1898.

12. GIGLIO-TOS, E. Sull' origine dei Corpi Grassi negli Anfibi. Atti R. Accad. Sci. Torino, Vol. XXXI, 1895.

13. HAECKEL, ERNST. Anthropogene oder Entwickelungsgeschichte des Menschen. Leipzig, 1874.

14. HOFFMAN, C. K. Zur Entwickelungsgeschichte der Urogenitalorgane bei den Anamisia. Zeit. wiss. Zool., Bd. XLIV, 1886.

15. JACOBSON, H. Det kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger. Tredje Deel., 1828.

16. KING, H. D. The Spermatogenesis of Bufo lentiginosus. Amer. Journ. Anat., Vol. VII, 1907.

17. KING, H. D. Bertramia bufonis, a New Sporozoan Parasite of Bufo lentiginosus. Proc. Acad. Nat. Sci., Phila., 1907.

18. KNAPPE, E. Das Bidder'sche Organ. Morph. Jahrb., Bd. XI, 1886.

19. LEYDIG, F. Anatomisch-histologische Untersuchungen über Fische und Reptilien. 1853.

20. LEYDIG, F. Beiträge zur Kenntniss des thierischen Eies im unbefruchteten Zustande. Zool. Jahrb., Bd. III, 1888.

21. MARSHALL, A. M. On Certain Abnormal Conditions of the Reproductive Organs in the Frog. Journ. Anat. and Physiol., Vol. XVIII, 1884.

22. MÜLLER, J. Bildungsgeschichte der Genitalien. 1830.

23. NUSSBAUM, M. Zur Differenzirung des Geschlechts im Thierreich. Arch. mikr. Anat., Bd. XVIII, 1880.

24. OGNEW, S. J. Materialen zur Histologie des Bidderschen Organs der Kröten. Arch. mikr. Anat., Bd. LXXI, 1908.

25. PFLÜGER, E. Ueber die das Geschlecht bestimmenden Ursachen und die Geschlechtsverhältnisse der Frösche. Arch. für die gesammte Phys., Bd. XXIX, 1882.

26. RATHKE, H. Beiträge zur Geschichte der Thierwelt III. Neueste Schriften der Naturforscher Gesellsch. in Danzig, Bd. I, 1825.

27. RÖSEL VON ROSENHOF, A. J. Historia naturalis ranarum. 1758.

28. RUGE, G. Vorgänge am Eifollikel der Wirbelthiere. Morph. Jahrb., Bd. XV, 1889.

29. ST. GEORGE, LA VALETTE. Zwitterbildung beim kleinen Wassermolch (Trioton taeniatus). Arch. mikr. Anat., Bd. XLV, 1885.

30. SEMON, R. Studien über den Bauplan des Urogenitalsystems der Wirbelthiere darlegt an der Entwickelung dieses Organsystems bei Ichthyophis glutinosus. Jenais. Zeit. Naturwiss., Bd. XIX, 1892.

31. SPENGEL, J. W. Das Urogenitalsystem der Amphibien. Arbeit a. d. zoolog.-zootom. Inst. in Würzburg, Bd. I, 1876.

32. SPENGEL, J. W. Zwitterbildung bei Amphibien. Biol. Centralblatt, Bd. IV, 1884.

33. WILL, L. Ueber die Entstehung des Dotters und der Epithelzellen bei den Amphibien und Insecten. Zool. Anz., Bd. VII, 1884.

34. WITTICH, DR. VON. Beiträge zur morphologischen und histologischen Entwickelung der Harn- und Geschlechtswerkzeuge der nackten Amphibien. Zeit. wiss. Zool., Bd. IV, 1853.

## EXPLANATION OF PLATES.

All figures were drawn with the aid of a camera lucida. They have been reduced one-third.

FIG. 1.—Outline drawing of the genital organs of a toad killed at the time of metamorphosis. C. A., corpus adiposum; B. O., Bidder's organ; O., ovary; R., kidneys.

FIG. 2.—Section of Bidder's organ taken from a tadpole 17 days old. × 1,000.

FIG. 3.—Section of Bidder's organ taken from a tadpole 35 days old. × 1,000.

FIG. 4.—Resting stage of a primordial germ-cell in Bidder's organ. V., vitelline bodies. × 1,334.

FIG. 5.—Young oöcyte in Bidder's organ. × 1,334.

FIG. 6.—Growth stage of a young oöcyte. ×1,334.

FIG. 7.—Beginning of the condensation of the chromatin spireme leading to synizesis. × 1,334.

FIG. 8.—Synizesis stage. × 1,334.

FIGS. 9-10.—Early post-synizesis stages. The chromatin is in the form of a continuous spireme. × 1,334.

FIGS. 11-14.—Post-synizesis stages showing the division of the spireme into segments. × 1,334.

FIG. 15.—The beginning of amitotic division in the nucleus of a cell in Bidder's organ. × 1,334.

FIGS. 16, 17.—Later stages in the amitotic division of a cell. × 1,000.

FIG. 18.—Section of an oöcyte which has begun to degenerate. A fluid space has formed around the large nucleolus and the yolk material is collected in several masses, one of which lies against the nucleus. × 1,000.

FIG. 19.—Section of an egg in Bidder's organ taken from a toad killed at the time of metamorphosis. Yolk-nuclei are forming in the cytoplasm. × 1,000.

FIG. 20.—Section of the nucleus of a cell in Bidder's organ which is very similar to nuclei of the same size found in the ovarian oöcytes. × 1,000.

FIGS. 21-25.—Stages in the resolution of compound-nucleoli in the cells of Bidder's organ. × 1,334.

HELEN DEAN KING

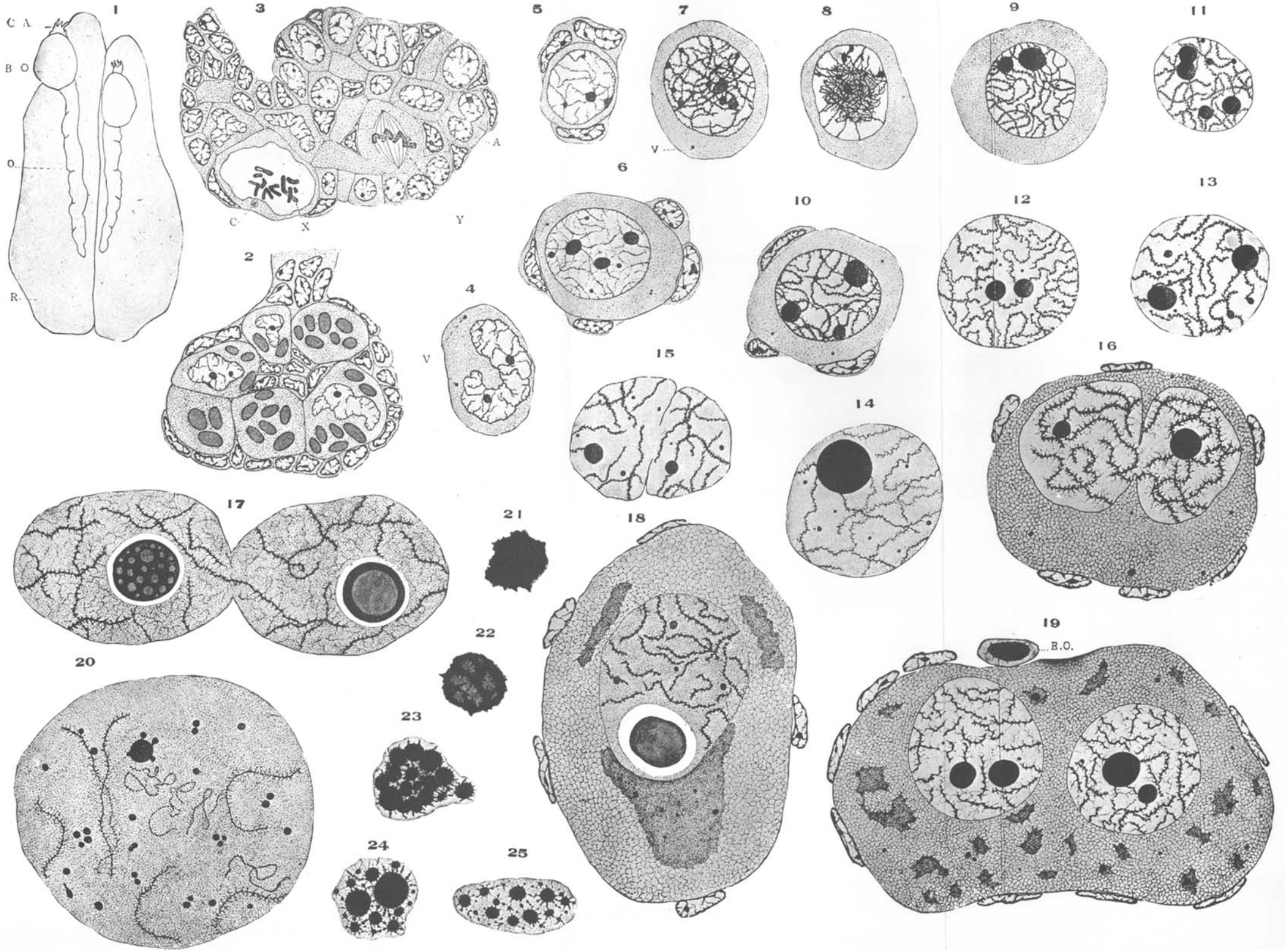


FIG. 26.—Section of an oöcyte in Bidder's organ in which yolk spherules were formed. Taken from a young male toad with a body length of 2 cm. × 1,000.

FIG. 27.—Section of a degenerating egg in Bidder's organ. Taken from a young male toad with a body length of 4.5 cm. × 1,000.

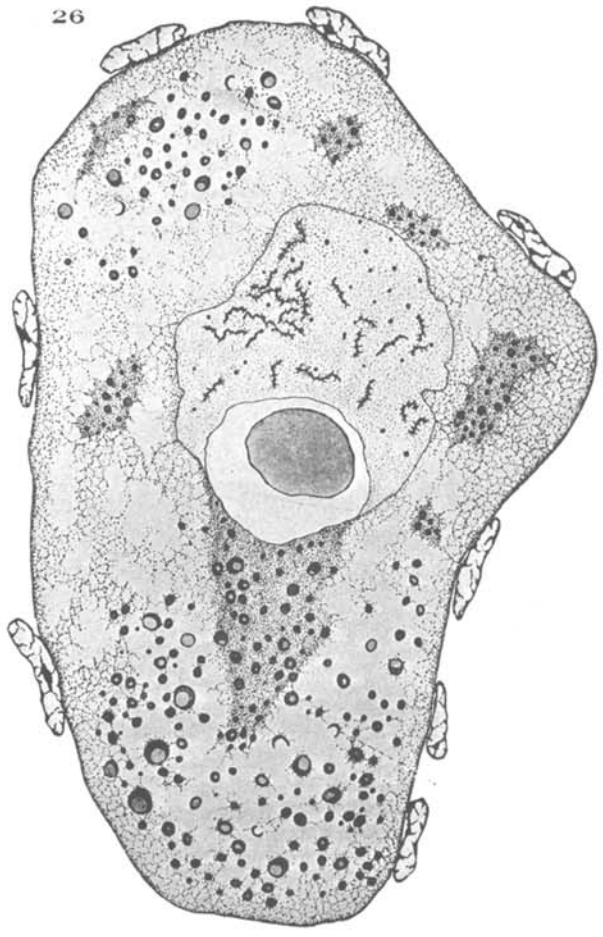
FIG. 28.—Part of a section showing the penetration of a capillary into a degenerating egg. Taken from an adult male toad killed in July. × 1,000.

FIG. 29.—Section of a degenerating egg taken from a young male toad with a body length of 5 cm. × 1,000.

FIG. 30.—Part of a section of a degenerating egg into which blood capillaries (B. C.) and follicle cells have entered. Taken from a young male toad with a body length of 5 cm. × 1,000.

FIG. 31.—Outline drawing of a section of a multinucleated egg in Bidder's organ.

FIG. 32.—Section of a degeneration egg containing numerous follicle cells. Taken from a young female with a body length of 5 cm. × 1,000.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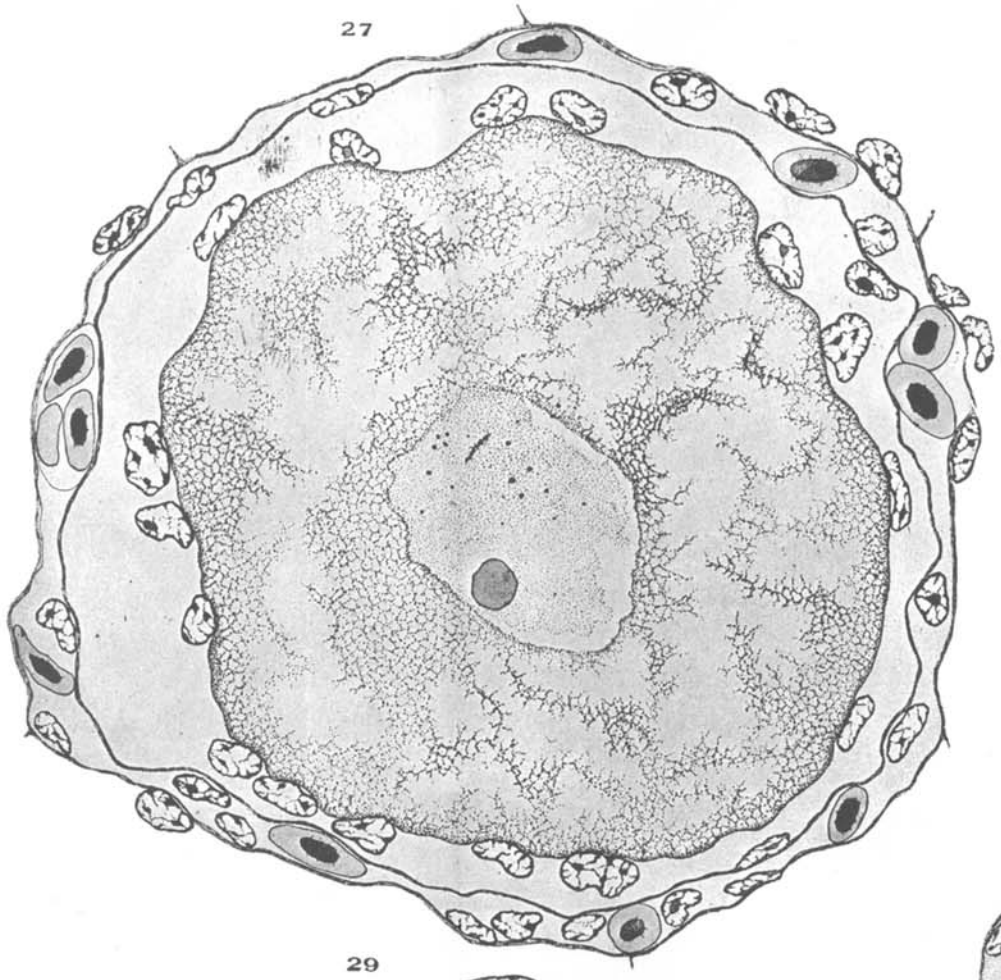
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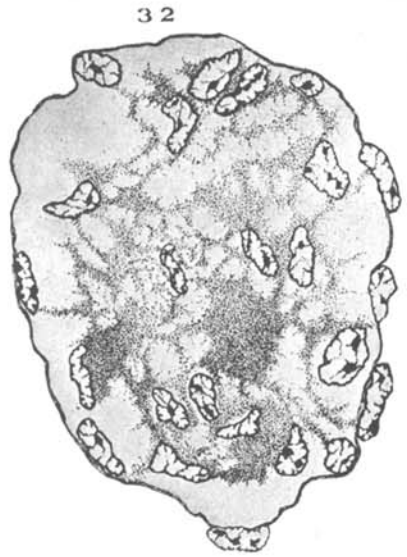
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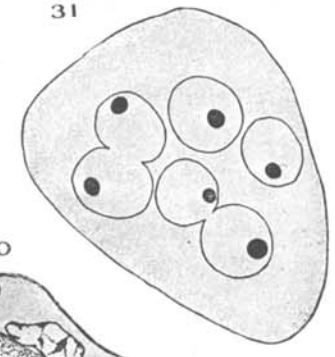
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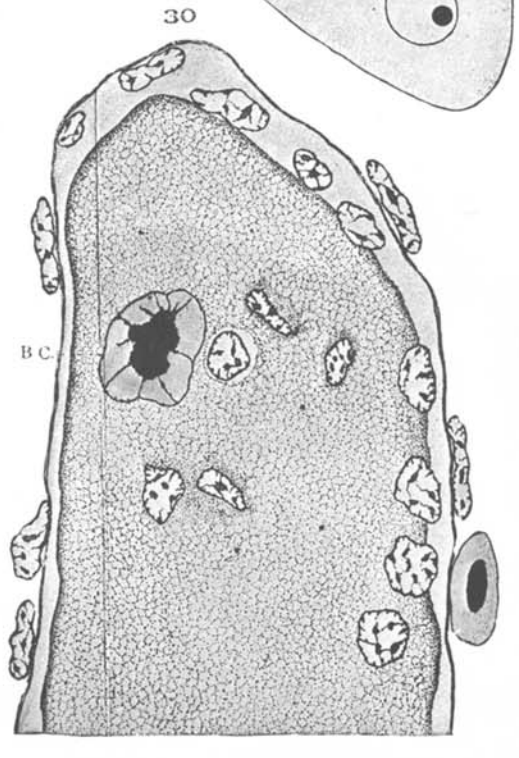
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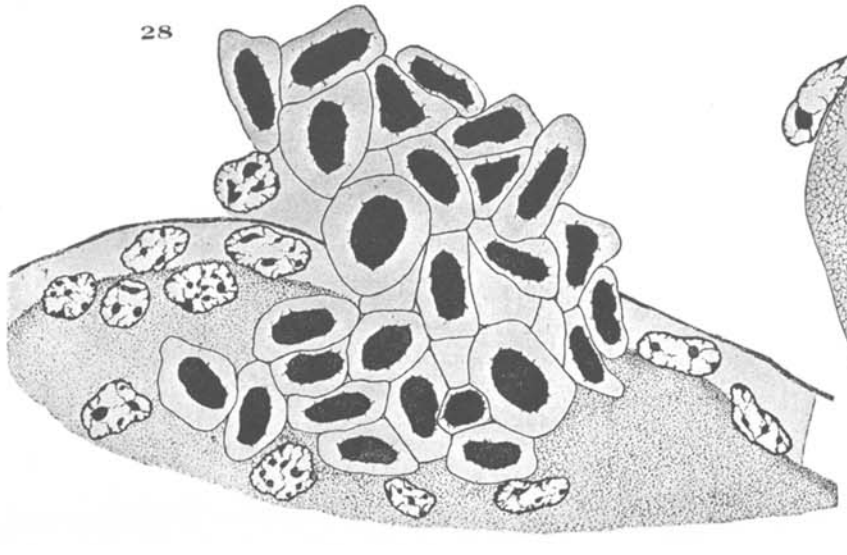
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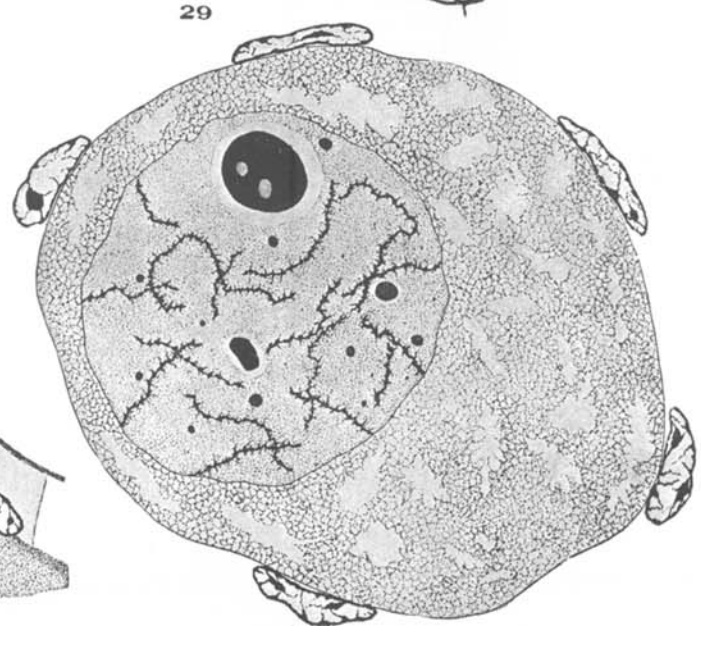
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