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Contributors

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Some Anomalies in the Genital Organs of Bufo Lentiginosus and their Probable Significance

By HELEN DEAN KING

Assistant in Anatomy, Wistar Institute

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SOME ANOMALIES IN THE GENITAL ORGANS OF BUFO LENTIGINOSUS AND THEIR PROBABLE SIGNIFICANCE.

BY

HELEN DEAN KING,

Assistant in Anatomy, Wistar Institute.

WITH 26 FIGURES.

During the course of a series of investigations on the germ-cells of the common American toad, Bufo lentiginosus, I have had occasion to examine a large number of these amphibians at various stages of their development, and I have found many individuals in which the genital organs showed marked deviations from the normal type. The most striking of these anomalies are described in the present paper. Many cases of this kind have a direct bearing on the question of the existence of hermaphroditism in the primitive vertebrates, and but few of them have as yet been recorded for any amphibian other than Rana.

I. ANOMALIES IN THE GENITAL ORGANS OF YOUNG TOADS.

Anomalies occur much more commonly in the sex-glands of young toads than in those of adults, and at least two per cent of the young individuals that I have examined showed more or less marked irregularities of this kind. As most of the toads in which abnormalities were found were reared in the laboratory, one might infer that the anomalies were the result of pathological changes produced in the genital organs by abnormal environmental conditions. That such is not the case, however, is shown by the fact that eleven individuals in which the sex-glands were anomalous in some respect were found in a lot of 500 young toads that had completed their metamorphosis under natural conditions.

Although in Bufo sex is probably determined at or before the time that the egg is fertilized, the gonads are often in an apparently

indifferent state even at the time of metamorphosis, and in many instances the genital glands must be examined histologically before the sex of an individual can be ascertained. The toad grows very rapidly after completing its metamorphosis, and then, except in very rare cases, the sexes are readily distinguished by an examination of the sex-glands under a dissecting lens. At this period of development the testes are long, cylindrical bodies with a smooth contour (Figs. 3 and 6, Left); the ovaries, although they are of about the same length as the testes, are relatively broader and they have an irregular, jagged outline (Figs. 5 and 7, Left). At the anterior end of each genital gland is a large rounded body, Bidder's organ (Fig. 1, B. O.), to which the corpora adiposa are attached (Fig. 1, C. A.). In young toads Bidder's organ is of the same size and structure in both sexes: it persists throughout the lifetime of the male, but it disappears in the female towards the end of the second year. A study of the structure and development of Bidder's organ (King, '08 a) has shown that this body is undoubtedly a rudimentary ovary in which the cells have marked characteristics which readily distinguish them from the eggs developing in the ovaries.

As a rule there is but one Bidder's organ at the anterior end of a sex-gland, and it usually measures about 0.4 mm. in diameter. In many young toads Bidder's organ shows considerable deviation from the normal size and shape. In some instances this structure is very large, measuring 0.6 mm. in diameter (Figs. 1, 2, 7); in rarer cases it is less than one-half of its usual volume (Fig. 13). Examined histologically such Bidder's organs are found to differ from those of normal size only in the number of ova that they contain.

Not infrequently a Bidder's organ is found that is greatly elongated (Figs. 7, 9, 12). In such cases this body is usually indented in the middle region (Figs. 7, 9), although sometimes it has a perfectly smooth contour (Fig. 12). Anomalies of this kind indicate clearly the steps by which the one Bidder's organ becomes divided into two; and the presence of two of these structures at the anterior end of an ovary or of a testis is probably the most common abnormality occurring in the genital organs of young toads. Usually, in cases like this, one Bidder's organ lies directly behind the other (Figs. 1, 10, 11,

14); more rarely these bodies are separated as shown in Fig. 3. I have found one instance only in which there were three Bidder's organs at the anterior end of a sex-gland (Fig. 16). Abnormalities of this type can doubtless be ascribed to the mechanical effect of pressure exerted by some structure on Bidder's organ at a very early period in its development.

In many individuals one or more rounded bodies, similar in appearance to the normal Bidder's organ although usually much smaller, appear along the course of the sex-gland (Figs. 1, 2, 5, 8, etc.). Structures of this kind may occur on any part of the gland, and they are found in both sexes, although they are, perhaps, more common in males than in females. The probable origin of these bodies will be considered later.

Fig. 12 shows in outline the most interesting of the anomalies found in the genital organs of young toads. On the left side Bidder's organ appears much enlarged and greatly elongated; on the right there are four rounded Bidder's organs lying one behind the other. Sections of these bodies show that each has the structure typical of a normal Bidder's organ. As in this individual the ovaries were not more than one-half of their normal length, it is evident that some of the germ-cells in the anterior part of each ovary became incorporated with Bidder's organ and assumed the characteristics of rudimentary ova. A somewhat similar case in which the anterior part of a testis has been changed into a Bidder's organ is shown in Fig. 16. Abnormalities of this kind can hardly be due to any mechanical cause, although possibly a lessening of the normal blood supply to the anterior part of a sex-gland might induce such changes which undoubtedly must be considered as degenerative in their character.

In all of the cases so far described, and in many others of the same general character, sections were made of the genital glands and the anomalies appearing in them carefully studied. All enlargements of the sex-glands, no matter what their position or their size, were found to contain large cells having all of the characteristics of the rudimentary ova of which the normal Bidder's organ is composed. If there are two Bidder's organs at the anterior end of a sex-gland,

each has the structure typical of the normal Bidder's organ. Most of the large bodies found along the course of the sex-glands (Figs. 6, 13, 16) also appear similar in structure to Bidder's organ, and they are directly connected above and below with germ-cell tissue that appears normal in every respect.

The structure of many of the smaller bodies found on the sex-glands does not conform strictly to that of Bidder's organ. Fig. 17 shows a longitudinal section of the enlargement on the lower part of the left ovary, which is outlined in Fig. 10. The ovarian wall has a perfectly normal structure here as in other parts of the sex-gland, being composed of cysts of secondary oögonia and of oöcytes in the synizesis stage of development (Fig. 17, S.). In the cavity of the ovary is a mass of large cells inclosed by follicle cells and a thin membrane. These large cells have all of the characteristics of the large rudimentary ova normally found in Bidder's organ; they do not bear the slightest resemblance to the oögonia and oöcytes of which the ovarian wall is composed. A somewhat different arrangement of tissues is shown in Fig. 18 which is a drawing of a transverse section through the smaller of the two bodies on the right testis outlined in Fig. 2. Here the spermatogonial tissue does not inclose the group of cells which appear like rudimentary ova, but is collected together at one side of it and the cells are surrounded in great part only by a thin covering of mesentery. A similar condition of the tissues was found in the enlargements of the testes shown in outline in Figs. 8 and 15.

As a rule only the enlarged portions of the sex-glands contain any of the large cells which appear like rudimentary ova, in all other parts the glands have a normal structure. In but one instance have I found cells of this character among germ-cells when their presence was not shown by an examination of the sex-gland under a dissecting lens. In this case the cavity of one of the ovaries in a young female contained three of these large cells which were separated a considerable distance and thus gave no external evidence of their presence.

During the course of my investigations on the toad (King, '07, '08, '08a) I have made sections of the gonads of a large

number of tadpoles in various stages of development from the time of hatching up to metamorphosis. In no case have I found any abnormalities in the gonads proper, although in several instances Bidder's organ on one or both sides had been divided as shown in Figs. 11 and 14. The large cells resembling rudimentary ova which are found singly or in groups in the genital organs of so many young toads that have recently completed their metamorphosis must, therefore, develop very quickly, presumably just before or during the period of metamorphosis. It is highly improbable that these cells originate in Bidder's organ and subsequently migrate into the sex-gland, as there is never any opening between these structures except in the female toward the end of the second year when the entire Bidder's organ is degenerating. Such cells, moreover, never show the slightest evidence of amœboid movement, and in many instances the membrane surrounding them is continuous with that inclosing the primordial germ-cells themselves. Judging from my previous investigations I am strongly inclined to the opinion that these cells are primordial germ-cells in which, for some unknown reason, the course of development has been changed so that the cells increase in size with unusual rapidity and assume the characteristics of rudimentary ova. Cells of this kind must, therefore, be considered as degenerating cells. Their presence in the sex-gland is apparently not harmful to the individual, since none of the young toads in which they are found seem to differ in any other way from the normal type. In Bufo, with rare exceptions, all cells of this character must become absorbed early in the life history of the individual. I have never found any of them in the sex-glands of toads that were more than three or four months old.

According to Pflüger, '82, there are three kinds of individuals to be found among young frogs killed soon after completing their metamorphosis: males, females, and hermaphrodites. In the course of a few months the hermaphroditic forms become either definite males or females, and in few cases only does the hermaphroditic condition persist until the individual becomes an adult. During the course of a series of investigations on the determination of sex in frogs, Hertwig, '06, '07, has found a number of individuals in which sex

could not be ascertained even after metamorphosis was completed. These individuals, Hertwig believes, correspond to the "hermaphroditic" forms described by Pflüger. Schmitt-Marcel, '08, has recently studied the structure of the sex-glands in young Rana temporaria that appeared to be hermaphrodites. He states that in all cases the sex-glands of such individuals, which he calls "intermediate forms," appear much more like ovaries than like testes, yet they probably all ultimately develop into testes. In accounting for the origin of such forms Schmitt-Marcel assumes that they are derived from young females, and he concludes: "Die Veränderung also, die von einer normalen weiblichen Drüse zu dieser Bildung führt, besteht im wesentlichen wohl darin dass bei einem Wachstum des Organes nicht in der ganzen Keimdrüse ein Heranwachsen von Urkeimzellen zu jungen Eizellen stattfindet, sondern dass ganze Strecken auf dem Stadium der Urkeimzellen stehen bleiben und sich als solche weiter vermehren, während gleichzeitig eine ausserordentliche in der normalen weiblichen Keimdrüse fehlende Vermehrung der Stroma Platz greift." The young ova grow to a considerable size and then degenerate; meanwhile indifferent germ-cell tissue spreads throughout the whole sex-gland and later develops into spermatogonia so that the individual eventually becomes a male. Schmitt-Marcel states that he finds an increasing number of such forms among young frogs killed from the second to the tenth month after metamorphosis, and that the number of these forms gradually decreases after this time. Among adult frogs such "intermediate forms" are not known, males and females being found in about equal proportions.

There is a great similarity between the sex-glands of the "intermediate forms" found among young Rana temporaria and those of young toads having the anomalies described above. In both cases large cells, having the general appearance of young ova, are found among primordial germ-cells which are still in an apparently indifferent state. These cells develop to a certain size and then undergo processes of degeneration and absorption, leaving the gland male or female as the case may be. The chief differences between such anomalies in Rana and those in Bufo consist in the fact that the large cells which appear in the sex-glands of young toads are, as a

rule, segregated into one or several masses which can be seen under a low magnification before the gland is sectioned, and they have very distinctive characteristics that distinguish them from normal ova; in Rana, according to Schmitt-Marcel, the large cells are scattered throughout the sex-gland, and they appear in every respect like normal ova.

Schmitt-Marcel offers no suggestion as to how or why, in an individual in which the female sex is already determined, the primordial germ-cells can change the course of their development and subsequently alter the sex of the individual. If this phenomenon is of common occurrence in young Rana temporaria, then it would seem as if some clue might be obtained as to the causes which determine sex in this species if an extensive series of experiments was to be made with young individuals that had recently completed their metamorphosis.

Except in rare cases, the sex of young toads in which anomalies appear in the genital organs can readily be ascertained, since, although the primordial germ-cells may appear alike in both sexes at this time, the ovary has a central cavity which is lacking in the testes. There are, therefore, no young toads that can properly be called "intermediate forms," as each individual is at this time definitely male or female, no matter how many cells appearing like rudimentary ova may be present in the sex-glands.

The development of the genital organs must be considerably slower in Rana temporaria than in Bufo lentiginosus, since in the former species it is impossible to ascertain the sex of many individuals until they are nearly a year old. As according to Schmitt-Marcel the germ-cell tissue which spreads throughout the sex-glands in these intermediate forms is still in an indifferent state I can see no valid reason for the assumption that such forms were originally females. In Bufo, as far as I can judge from the number of cases (about 75) that have come under my observation, large cells with the characteristics of rudimentary ova appear somewhat more commonly in the genital glands of young males than in those of young females. Assuming that a similar condition exists in young Rana temporaria, one readily accounts for the fact that the great majority

of "intermediate forms" ultimately become males, and one also avoids the necessity of presuming that sex can be altered after an individual has completed its metamorphosis.

In young toads, and possibly also in young frogs, primordial germ-cells that fail to undergo normal processes of development assume the characteristics of rudimentary ova, regardless of the sex of the individual in which they occur. An explanation of this phenomenon seems to me possible if one accepts for the amphibians Haeckel's, '74, view "dass das älteste und ursprünglichste Geschlechtsverhältniss die Zwitterbildung war und dass aus dieser erst secundär (durch Arbeitstheilung) die Geschlechtstrennung hervorging." In the male amphibian at the present time many of the primordial germ-cells still have the power, under certain conditions, of developing into ova which, since they cannot leave the sex-gland or come to maturity, are destined to degeneration and absorption. Except in very rare cases the primordial germ-cells in the female are no longer able to develop into spermatogonia. When, therefore, these cells fail to develop along normal lines they become rudimentary ova which are similar in structure to the rudimentary ova derived from the primordial germ-cells in the male and they have a similar fate.

In adult amphibians, as a rule, germ-cells which fail to undergo normal processes at any stage of their development disintegrate at once and become absorbed. Some few cases have been found, however, in which germ-cells in adult males have changed the course of their development and become rudimenary ova. Cole, '95, Friedmann, '98, Latter, '90, and Punnett, '00, have noted the presence of rudimentary ova in the testes of various species of frogs, and I also have a preparation of the testis of an adult Rana pipiens which shows this anomaly. Rudimentary ova have also been found in the testes of adult Bufo vulgaris by Spengel, '76, Hoffmann, '86, Knappe, '86, and Friedmann, '98, but as yet no cells of this kind have been found in the testes of the American species, Bufo lentiginosus.

Fig. 4 shows a type of abnormality which is found occasionally in the sex-glands of young toads. The median genital ridge, which is usually divided into two ridges when a tadpole is from twelve to

fourteen days old, has separated only in the anterior region and it still remains undivided posteriorly even after the toad has completed its metamorphosis. Sections of the sex-glands show no other apparent abnormality.

II. Anomalies in the Genital Organs of Adult Toads.

Among the large number of adult toads which I have examined during the past ten years there was but óne individual in which the sex-glands appeared in any way abnormal. This toad, which proved to be a rudimentary hermaphrodite, was brought into the vivarium of the University of Pennsylvania on the morning of March 30, 1907, having been captured in a pond near West Philadelphia. The abnormal character of the sex-glands was noticed as soon as the body cavity was opened, and these organs were removed at once and fixed in Flemming's fluid; the body of the toad being placed in a 4 per cent formalin solution for future examination.

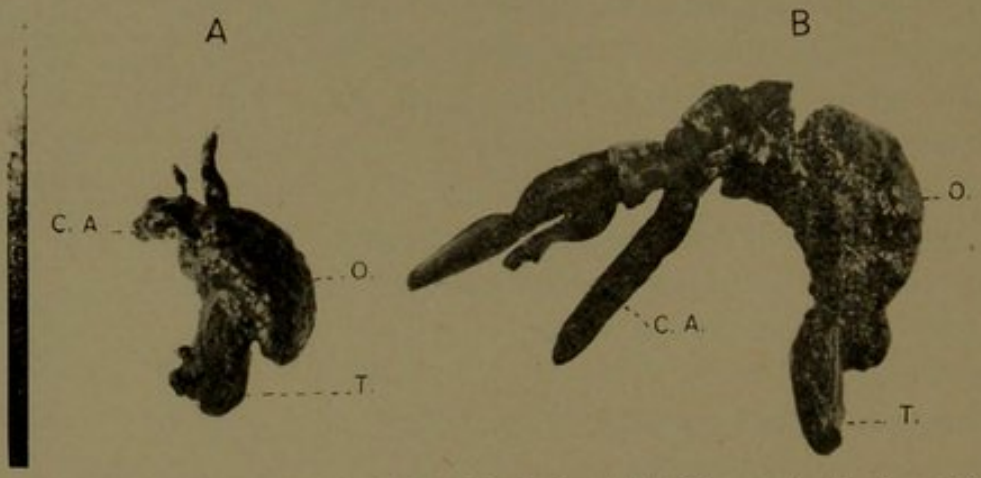
Measurements that were made showed that this toad was somewhat larger than the average male as it had a body length of 8.5 cm. The thumbs were deeply pigmented, and they bore pads similar to those found on the thumbs of all male toads during the breeding season, although these structures were somewhat smaller than normal.

Photographs of the genital organs of this individual are shown in the text-figure. On the left side (B) there is a well developed testis (T), measuring 8 mm. in length and 3 mm. in width. Above the testis is a large, pigmented, irregularly shaped body (O), unquestionably a rudimentary ovary, which is 15 mm. long and 7 mm. across at its widest part. The genital organs on the right side (A) are noticeably smaller than those on the left, although they have a similar structure. The testis (T) is but 7 mm. long; the rudimentary ovary above it (O), which has a much more regular outline than that on the left side, measures 10 mm. in length and 7 mm. in width. There is no Bidder's organ on either side, the fat bodies (C. A.) being attached directly to the anterior surface of the rudimentary ovaries.

Transverse sections through the testes show that these bodies are composed of cysts filled either with ripe spermatozoa or with sper-

matocytes and spermatids in various stages of development. A careful study of many cysts failed to show a single instance in which the development of the germ-cells appeared to be abnormal. The cysts in the centre of the testes are not crowded quite as closely together as are the cysts in the testes of the normal male, and the stroma separating them is unusually thick; in all other respects the testes appear perfectly normal. Each testis was connected with the kidney by vasa efferentia, the genital ducts appearing normal. In this individual the Müllerian ducts were still present; but, although they were quite large and much convoluted, they showed no dilatations either in the anterior or in the posterior region.

Interest in this individual centers in the structure of the rudimentary ovaries lying above and attached to the testis on either side.



Photographs of the right (A) and of the left (B) ovo-testis found in an adult Bufo lentiginosus. O, ovary; T, testis; C. A, corpora adiposa.

The position of these bodies and the fact that no Bidder's organs are to be found indicate that they have been produced, in part at least, from the cells which ordinarily form Bidder's organ. Since in this individual the testes are somewhat shorter than those usually found in adult males, it seems probable that primordial germ-cells in the anterior part of the germinal ridge, which normally would have developed into spermatozoa, joined with the cells of Bidder's organ to form these rudimentary ovaries. The force, whatever its nature, which modified the development of the cells and brought about the formation of these rudimentary ovaries must have acted

at a very early period in the life history of the individual, as in a normal toad the cells which develop into Bidder's organ begin to show characteristics which distinguish them from the other germ-cells when a tadpole is about two weeks old.

Sections show that each ovary contains a well defined central cavity which is lined by epithelial cells, and that the structure of the ovarian wall is the same in each case. In both ovaries the great majority of the ova are practically of the same size and in about the same stage of development. It is not possible, therefore, to trace the various stages in the growth of the cells or to discover any apparent reason for their unusual mode of development. With but a few exceptions the cells in both ovaries have developed uniformly along the same lines, and those in the upper part of each ovary bear no more resemblance to the cells which are typical of Bidder's organ than do the ones lying more posteriorly which were derived, presumably, from primordial germ-cells belonging to the sex-gland proper.

The smaller ova, which usually lie at the periphery of the ovaries, are rounded in outline, and they have an average diameter of 0.14 mm. As a rule, the cytoplasm of these cells appears uniformly granular, although sometimes it contains yolk nuclei, as shown in Fig. 19, Y. N. The nuclei are round, or slightly oval, and they measure about 0.08 mm. in diameter; with but few exceptions, all of them are in the early post-synizesis stage of development (Fig. 22). I can detect nothing in the structure of the great majority of these small cells that would in any way serve to distinguish them from normal young oöcytes of the same size.

In some few cases the smaller cells of these rudimentary ovaries exhibit all of the characteristics of the young ova normally found in Bidder's organ. A section of a cell of this type is shown in Fig. 19. The nucleus contains a number of nucleoli of various sizes and chromatin threads which are composed of a series of deeply staining, rounded granules. Two of the larger nucleoli show degenerative changes that are similar to those taking place in the large nucleoli of the cells of Bidder's organ which are beginning to disintegrate. The body of the cell contains a number of finely granular masses,

sharply distinct from the cytoplasm, which stain very intensely with iron hæmatoxylin (Fig. 19, Y.N.). These are the so-called "yolk-nuclei" which are always present in the normal ova at certain stages in their development, and which sometimes appear in the young cells of Bidder's organ. The arrangement of the yolk-nuclei in the cell shown in Fig. 19 is very similar to that of the yolk-nuclei in the cells of Bidder's organ. I have not been able to find any cells in these rudimentary ovaries that might be considered as intermediate in structure between normal and rudimentary ova.

The larger cells in the rudimentary ovaries border the central cavity, and, owing to pressure, they are usually greatly distorted in shape. The average diameter of these cells is 0.6 to 0.7 mm.; while the diameter of their nuclei ranges from 0.17 mm. to 0.25 mm. As a rule the nuclei of these cells resemble to a remarkable degree those of young ovarian ova of the same size: they are rounded in outline and contain a large number of scattered nucleoli; the karyoplasm appears uniformly finely granular; and the chromatin threads have the feathery structure characteristic of the chromosomes in the young ovarian oöcytes (Fig. 25).

The structure of the cell body in many of these larger cells differs considerably from that normally found in the ovarian oöcytes of the same size. As a rule the cytoplasm is much vacuolated, as if degenerative processes had already begun in it. In some cases the vacuoles extend radially from the periphery of the cell to the nucleus, giving the cytoplasm a striated appearance when examined under a low magnification; in other cases the vacuolated area extends only around the periphery of the cell and the cytoplasm surrounding the nucleus appears uniformly reticular (Fig. 23). There is a possibility that the vacuolization of the cytoplasm in these cells is due, in part at least, to the way in which the material was preserved. Flemming's fluid, although an excellent fixing agent for the testes at all stages of their development, is but a very indifferent fixative for amphibian ova after they have passed the synizesis stage. The cytoplasm of these large cells would doubtless appear much less vacuolated had some other fluid with greater powers of penetration been used in fixing the ovo-testes.

Many of the ova contain large numbers of yolk spherules which have formed, as in normal ova, at the periphery of the cell. In some few cases I have found two distinct layers of yolk spherules; one lying at the periphery, the other half-way between the surface of the cell and the nucleus (Fig. 24). In cases of this kind it is probable that the inner layer of yolk spherules was derived from yolk-nuclei which appeared in a ring midway between the nucleus and the periphery of the cell and were there transformed directly into yolk spherules. I have found one or two cases somewhat similar to this occurring in the ovarian ova (King, '08).

This hermaphroditic toad was killed at the breeding season when the germ-cells have become mature and the large ova in the normal Bidder's organ have reached the highest stage in development of which they are capable. It seems probable, therefore, that the large cells in the rudimentary ovaries have also attained their maximum development, and that they would have undergone rapid degeneration and absorption to give place to another generation of similar cells, had the individual not been killed. This assumption seems the more plausible since a number of the largest ova in the rudimentary ovaries already show marked degenerative changes.

The processes of degeneration occurring in the nuclei of the large cell found in these rudimentary ovaries are somewhat different from those taking place in the large ova of Bidder's organ, and they differ also from the disintegration processes occurring in mature eggs that for some reason have failed to leave the ovary. The first evidence of degeneration is the migration of the nucleoli to the centre of the nucleus where they lie massed together as shown in Fig. 20. At this time all of the nucleoli are rounded in outline and, with but few exceptions, they stain uniformly black with iron hæmatoxylin. The chromatin threads can sometimes be seen in the nucleus at this stage, although they cannot be found at a later period owing, possibly, to the fact that Flemming's fluid does not fix the chromosomes well in cells of this size. The next step in the degeneration of the nucleus is shown in Fig. 20. Many of the nucleoli appear vacuolated, others stain faintly and are evidently being dissolved. Only that portion of the karyoplasm in which the nucleoli lie is uniformly finely

granular at this time, elsewhere it contains numerous rounded granules, staining very intensely, that are much smaller than the nucleoli and many times larger than the minute granules which normally form the karyoplasm. In a later stage (Fig. 21) the nucleus is filled with numerous short fibres composed of deeply staining, rounded granules which appear similar to those scattered through the nucleus at the stage of Fig. 20. There is no finely granular karyoplasm anywhere in the nucleus at this time, and the fibres, as well as the remaining nucleoli, lie in an apparently fluid space. The immense number of the large granules in the nucleus at this stage of degeneration seems to preclude the possibility that these bodies have been derived from chromatin or from the substance of the relatively few nucleoli that have been dissolved. It seems probable, therefore, that these granules have originated from the granular karyoplasm, since their number increases in proportion as the minute karyoplasmic granules disappear. At the stage of Fig. 21 follicle cells and blood capillaries are beginning to enter the cytoplasm of the cells to complete the processes of disintegration and absorption. The nuclear membrane breaks down at or soon after the stage shown in Fig. 21, and the nuclear contents come in direct contact with the cytoplasm. Unfortunately the rudimentary ovaries contain no later stages in the degeneration of the large ova.

The granular fibres which fill the greater part of the nucleus at the stage of degeneration shown in Fig. 21, bear a very striking resemblance to the "oxychromatin" fibres found in connection with the nucleoli during the early post-synizesis stages in the development of the young oöcytes. It is possible, therefore, that the latter structures are not composed of chromatin but of fused karyoplasmic granules which have great affinity for the chromatin stains. If this interpretation is correct, then the chromatin in the amphibian egg is probably not concerned in any way with the formation of the nucleoli which are doubtless waste products of nuclear metabolism.

Cerruti, '07, has recently given a brief description of two cases of hermaphroditism which he has found in Bufo vulgaris. In one individual the anterior part of each testis had developed into a small rudimentary ovary lying between Bidder's organ and the testis proper:

this case is similar to that found by Spengel, '76, in Bufo cinereus. In the other individual Cerruti found that each Bidder's organ had developed into a rudimentary ovary which contained many large ova in various stages of degeneration and also ova that appeared like normal oöcytes except that they did not have any yolk spherules.

In the second cases noted by Cerruti the condition of the sex-glands is much like that in the hermaphroditic Bufo lentiginosus described above. In both of these individuals it is evident that the rudimentary ovaries were derived from cells which normally would form a Bidder's organ. In young toad tadpoles, as shown in a previous paper (King, '08a), the cells which are destined to form Bidder's organ are directly continuous with the primordial germ-cells that later form the sex-gland; they are similar to the germ-cells in structure, and they develop like the germ-cells up to the synizesis stage. These facts seem to me to prove conclusively that the cells which form Bidder's organ are degenerate germ-cells. It is not surprising, therefore, that occasionally these cells develop into ova which apparently have a normal structure.

Many instances of hermaphroditism have been recorded for various species of frogs. Cases similar to those found in Bufo, where a rudimentary ovary has developed at the anterior end of a testis, have been described by Marshall, '84, Kent, '85, and Ridgewood, '88; the reverse condition, with the ovary below the testis, has been found by Bourne, '84, in Rana temporaria. Marshall, and also Smith, '90, have reported cases in which one of the sex-glands in an individual was an ovary and the other a testis. This latter form of hermaphroditism is extremely rare among amphibians, and it has not yet been found in Bufo. Evidently hermaphroditism occurs much less frequently among the Urodela than among the Anura, as only two cases have as yet been reported for this group of amphibians. La Valette St. George, '93, has given a brief description of a case of hermaphroditism in Triton tæniatus, and Knappe, '86, has noted the presence of a Bidder's organ in a young salamander; neither investigator gives any details regarding the structure of the ovo-testes in these forms.

Abnormalities of the kind described above, whether they occur

in the sex-glands of young or of adult amphibians, seem explicable only on the assumption that the primitive amphibians were hermaphroditic, and that in the course of their evolution this primitive hermaphroditic condition has given place to the bi-sexual condition found at the present time. Although a rudimentary sex-gland (Bidder's organ) is found only among the Bufonidæ at present, traces of the primitive hermaphroditic condition still exist in other forms, as is shown by the fact that in some individuals the genital glands contain both ova and spermatozoa. Such individuals, however, are only rudimentary hermaphrodites, since apparently only one kind of germ-cell ever becomes functional. The spermatozoa are probably a much more specialized type of cell than the ova, and it might be expected, therefore, that the male germ-cells would assume the characteristics of ova more frequently than that the female germ-cells would be able to develop into spermatozoa. This is doubtless the reason that, with but very few exceptions, all of the anomalies found in the sex-glands of adult amphibians occur in individuals which must be considered as males since only the sperm-cells are able to reach maturity.

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EXPLANATION OF FIGURES.

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

FIGS. 1-16.—Outline drawings showing the various types of anomalies found in the genital organs of young toads killed soon after completing their metamorphosis. C.A, corpora adiposa; B.O, Bidder's organ; T, testis; O, ovary; N, kidney. × 26.

FIG. 17.—Longitudinal section through the enlargement in the lower part of the left ovary which is outlined in Fig. 10. × 250.

FIG. 18.—Transverse section through the enlargement in the lower part of the right ovary which is outlined in Fig. 2. × 250.

FIG. 19.—Section of an ovum found in the rudimentary ovary of an hermaphroditic toad. This cell has all of the characteristics of the young ova normally present in Bidder's organ. Y.N, yolk-nuclei. × 1000.

FIG. 20.—Section of the nucleus of a rudimentary ovum which is just beginning to degenerate. × 333.

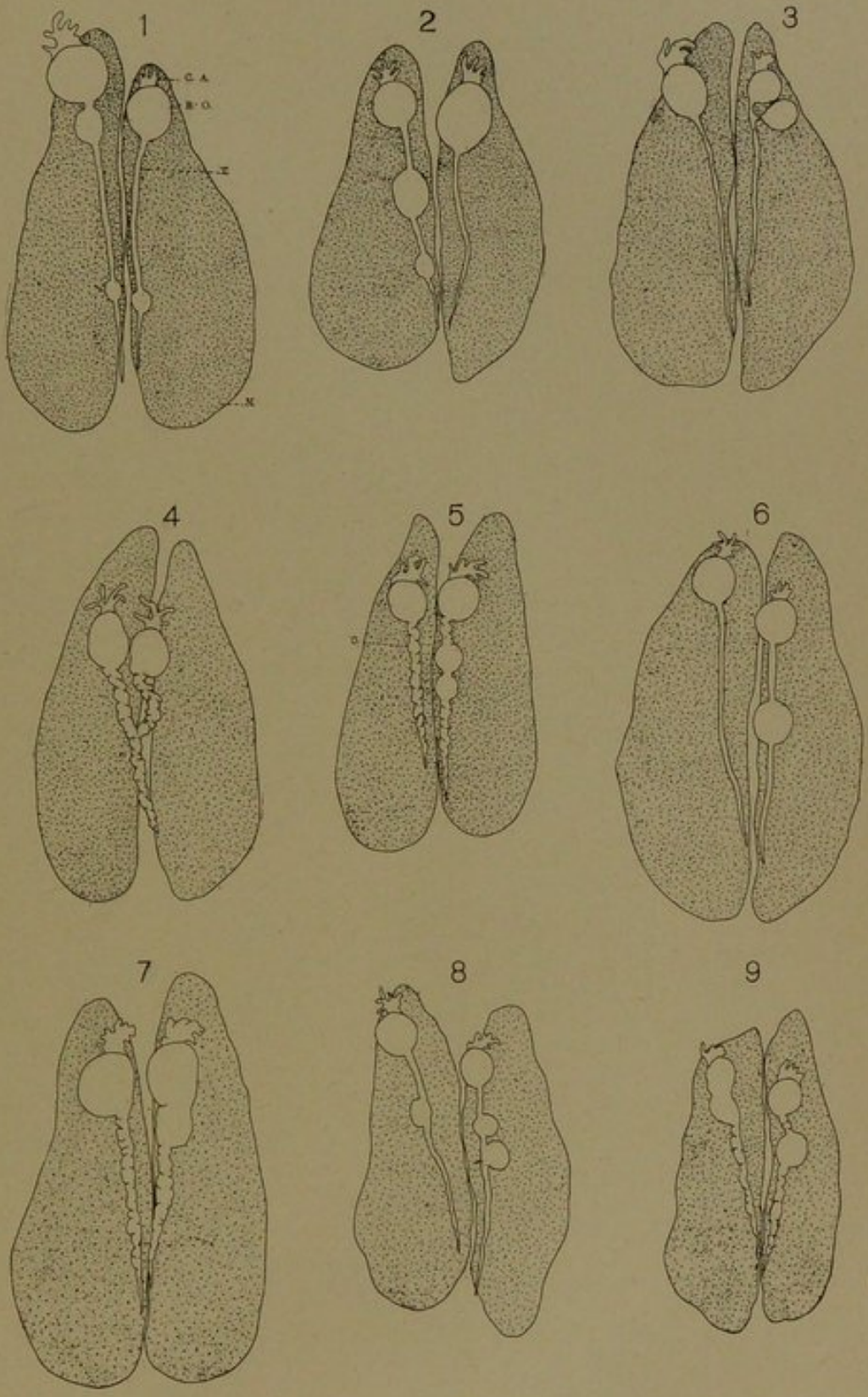
FIG. 21.—A later stage in the degeneration of the nucleus of a rudimentary ovum. × 333.

FIG. 22.—Section of the nucleus of a young oöcyte which appears normal. × 1000.

FIG. 23.—Part of a section of a large ovum showing vacuolization of the cytoplasm. × 333.

FIG. 24.—Part of a section of a large ovum having two distinct layers of yolk spherules in the cytoplasm. × 333.

FIG. 25.—Section of the nucleus of a large ovum which appears normal. × 333.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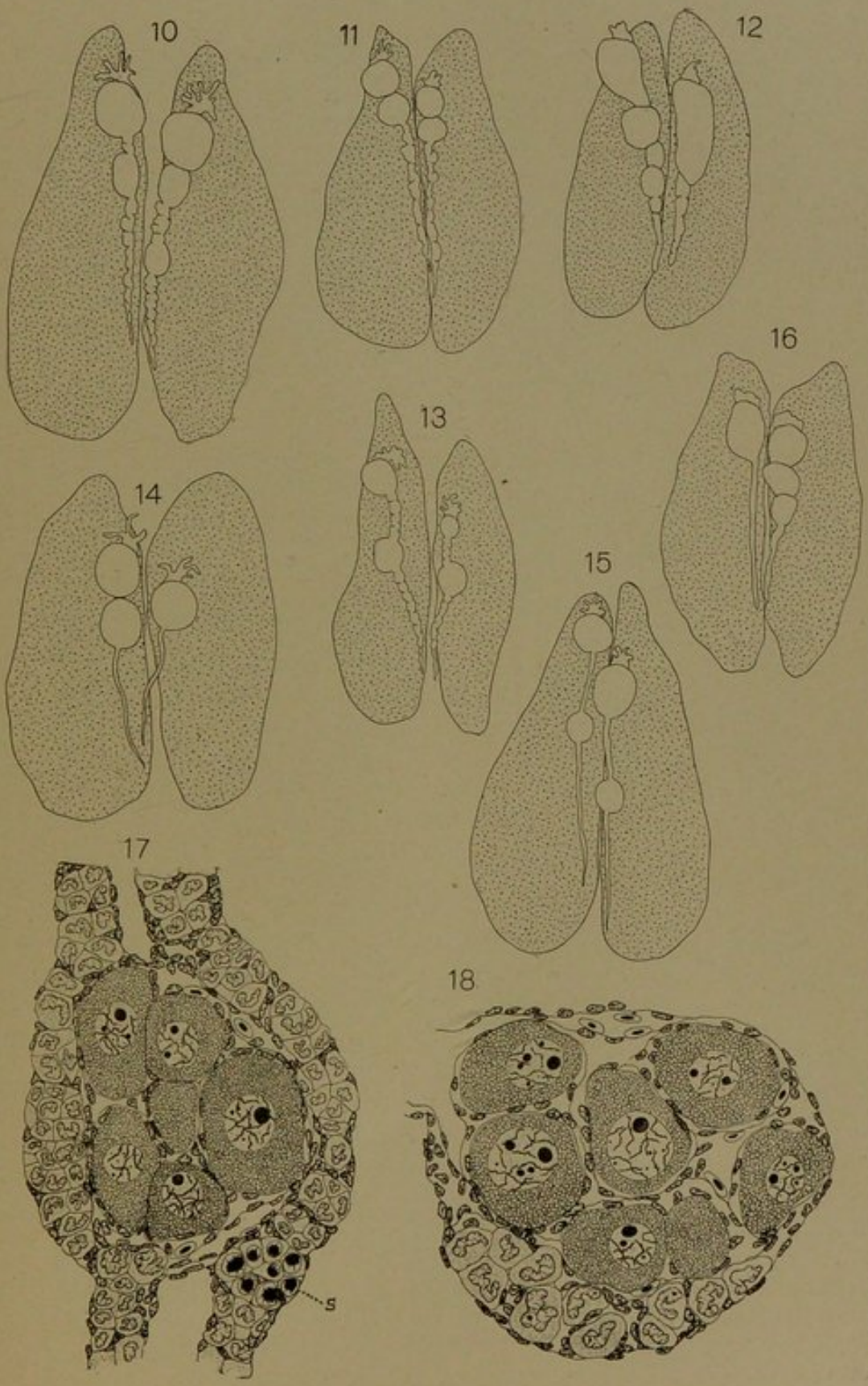
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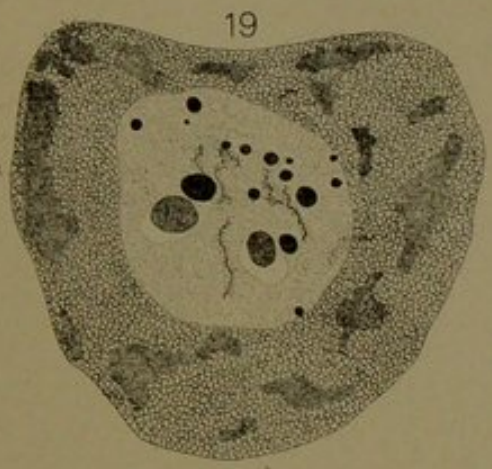
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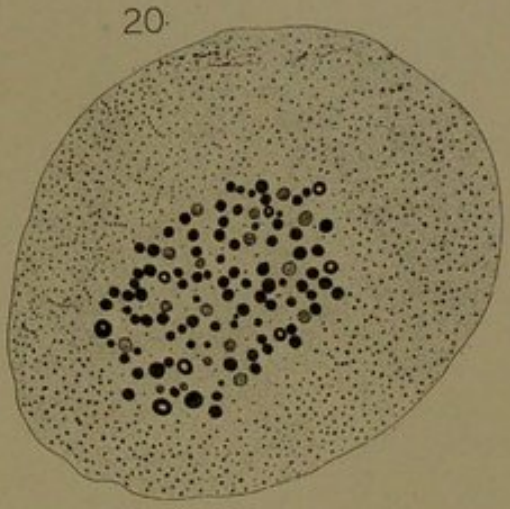
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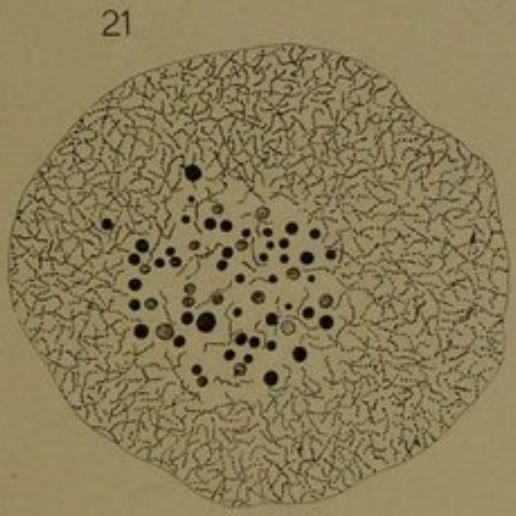
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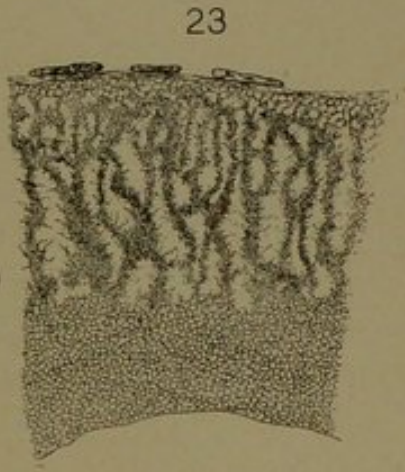
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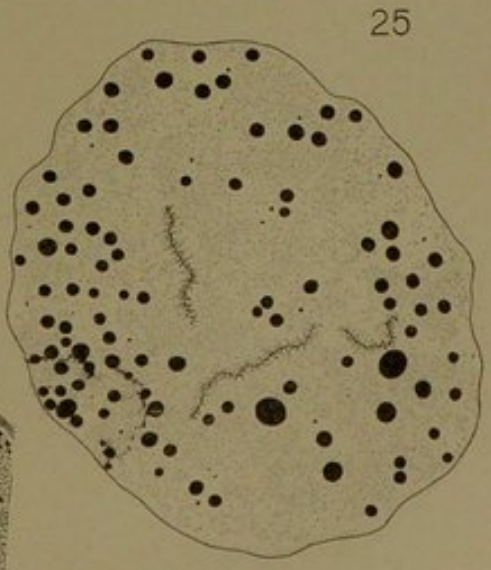
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