

Origin of the electric tissues of *Gymnarchus niloticus*.

Contributors

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Publication/Creation

Washington, D.C., 1914.

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ORIGIN OF THE ELECTRIC TISSUES OF GYMNARCHUS
NILOTICUS.

BY ULRIC DAHLGREN

Professor of Biology, Princeton University.

Nine plates and nine text-figures.

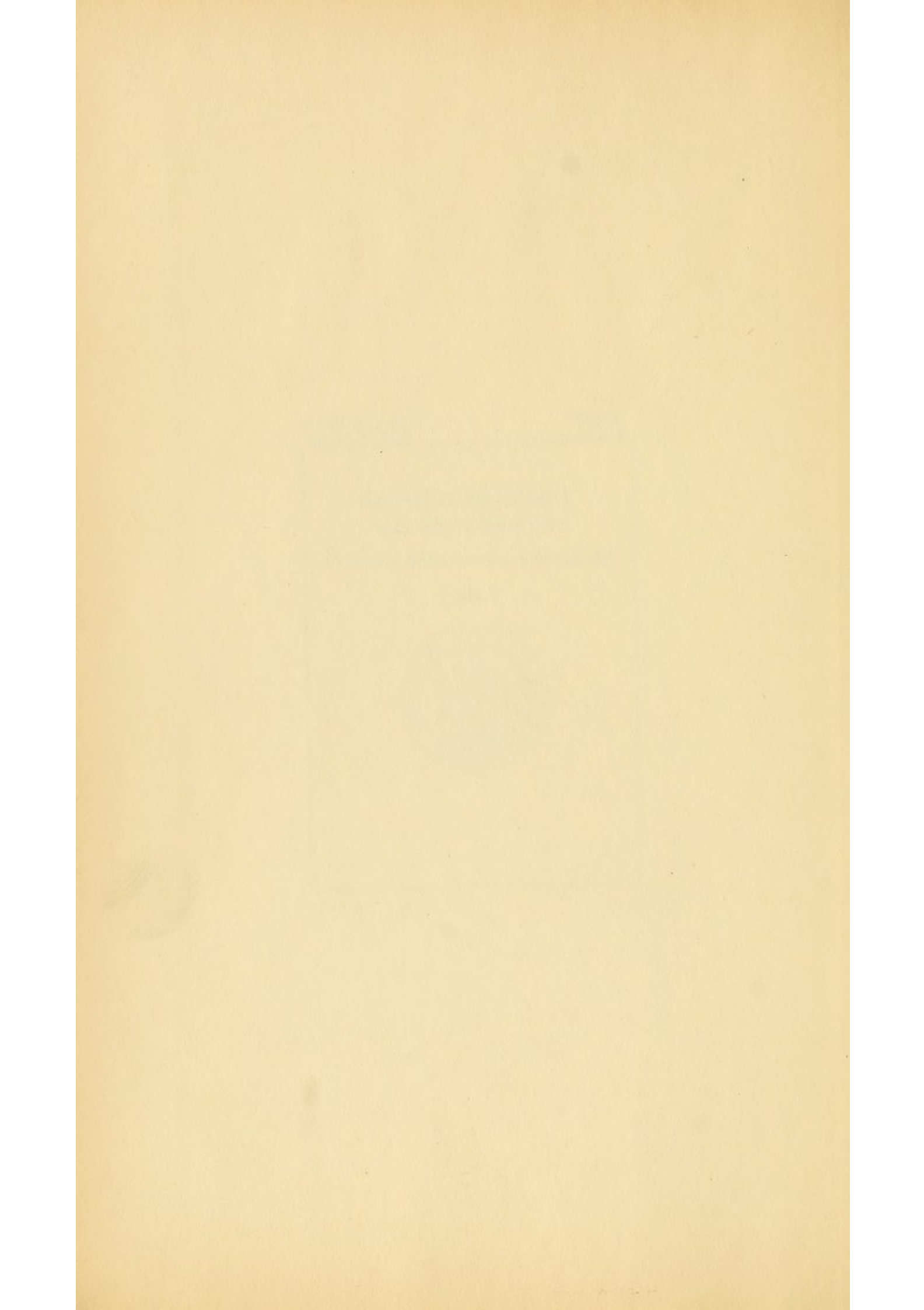
[Extracted from PUBLICATION No. 183 OF THE CARNEGIE INSTITUTION OF WASHINGTON,
pages 159-194. 1914.]

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In the seven types of electricity-producing fishes the exact development by which the electric organs and tissues are produced during the creature's life is known in only two, leaving the other five unknown. It also happens that the two forms which have been studied as to the histogenesis of their electric organs are the only two elasmobranch fishes among the seven, so that we have not as yet seen how the remarkable electric tissues in *Malopterurus*, *Gymnotus*, *Astroscopus*, the mormyrids, and *Gymnarchus* are developed. Also, of the five teleost types we know the structure of the full-grown electric organs in all of them pretty well, except in *Gymnarchus*. This fish is found in Africa and has been rather rare, so that but two workers have published observations on it, both of them a long time ago and from poorly preserved material.

It was, therefore, with great pleasure that the writer came into possession of some embryos of this rare form through the kindness of Dr. J. Graham Kerr, Dr. Arthur Shipley, and Dr. Richard Assheton, to whom he wishes to express his most sincere thanks. This material was collected in Africa by Dr. Samuel Budgett some years ago and was in most excellent condition, owing to the great care and skill with which Dr. Budgett put it up and cared for it. The collecting was done unflinchingly and faithfully, under conditions of hardship and sickness that few white men could stand, and Dr. Budgett lost his life from exposure and illness incurred in part by this work. A full account of his trip and of the scientific results should be read in the Budgett memorial volume issued by Dr. Shipley, Dr. Kerr, Dr. Assheton, and others in 1907, through the Cambridge University Press (24).¹

It is somewhat unfortunate that the structure of the electric organs in the adult fish could not be worked up at the same time that this paper was written, but the writer has material on the way from Khartoum and hopes to publish a second paper shortly.

But three papers have been published on the electric organ of this interesting fish, one by Erdl (15) in 1847 and another by G. Fritsch (19) in 1885. Rüppel's publication on the subject could not be found, but Fritsch states that Rüppel mentioned the peculiar structures which we are considering, and so he stands at present in the writer's knowledge as the first one to have seen and reported to science the electric organs of this fish, although he was in doubt as to their significance. Erdl used a specimen which was so

¹ The figures in parenthesis refer to the literature cited, p. 193.

poorly preserved and so soft that when he cut the animal across its body, the electroplaxes and connective tissue ran out of the muscle in which they are embedded. Nevertheless Erdl stated that it was probably an electric organ, coming to this conclusion by a comparison, of such features as he could make out, with the structures found in the tails of the other electric fishes, as *Raja*, *Mormyrus*, and *Gymnotus*.

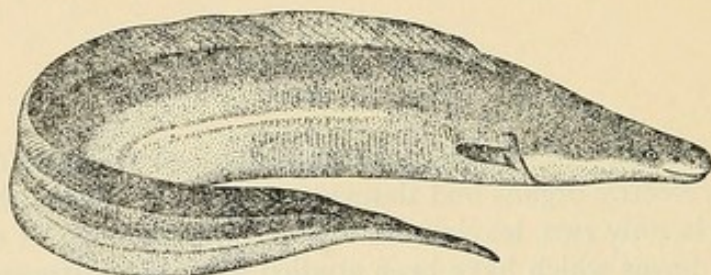


FIG. 1.—General view of *Gymnarchus niloticus*. (Drawn from a lantern slide made from a figure in Jordan's "Guide to the Study of Fishes," New York, 1905.)

Fritsch (19) in 1885 worked on better material and gave a more complete account of the anatomy of the organ, especially of the histology of the electroplax; but he came to the rather strange conclusion that it was not an electric organ at all, assuming the erroneous position that, on account of the large blood-supply, the organ acted in some way as a storage for oxygen during the period of hibernation made necessary by the drying of waters at certain seasons. Fritsch was also mistaken in calling the fibrous

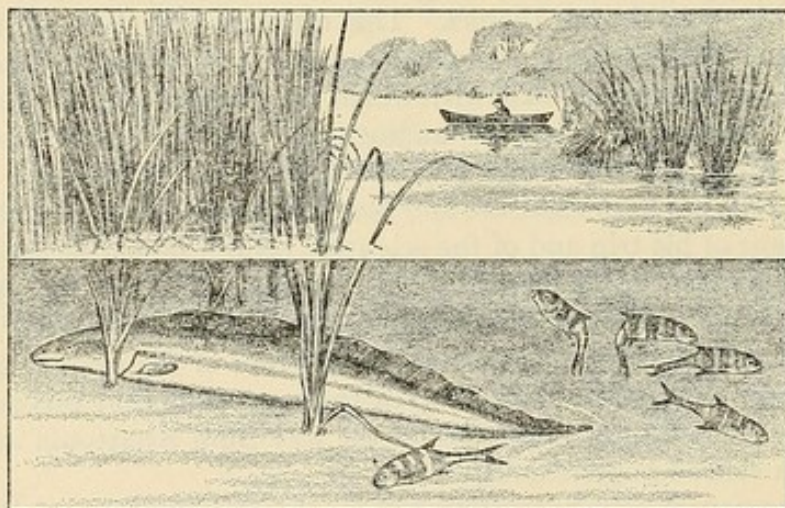


FIG. 2.—Scene drawn from descriptions to illustrate the habitat of *Gymnarchus* and its manner of swimming. (Drawn from lantern slide made from a drawing, by Bruce Horsfall.)

contents of the electroplaxes "connective tissue." He went a great deal farther than Erdl, however, in describing the gross anatomy of the electric organs and surrounding tissues.

Not having full-grown material, the writer must rely on Fritsch's figures and descriptions for the adult gross anatomy, although the oldest embryos

(about 42 days) used for this paper represent practically adult material so far as the histology of the electroplaxes is concerned. A short résumé of the adult anatomy will make a good basis for the embryological descriptions to follow.

The fish (see text-fig. 1) is a mormyrid of elongate form, so much so as to make it almost eel-shaped, although not quite so much so as the *Gymnotus* of South America. It possesses an extensive development of the dorsal fin, which extends from forward on the neck to within a short distance of the tip of the tail, where it suddenly stops, leaving the tip of the tail naked of fin; whence the name of the fish, *Gymnarchus niloticus*. This heavy fin, well provided with a series of lateral ray-muscles, is used extensively by the fish as a means of propulsion, by holding the body straight and stiff and causing a series of lateral undulations to pass from behind forward, thus driving the body backward (see text-fig. 2) or, from front to rear, which causes the fish to move with its head forward. I have not heard, but I presume that in moments of unusual effort the animal can swim by means of the common sinuous body-movements used by other elongate fishes, as is well illustrated in the eel.

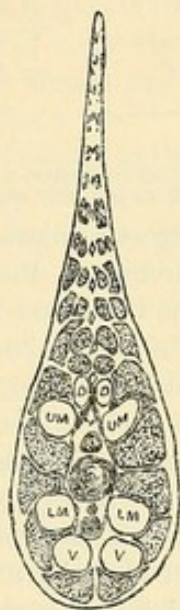


FIG. 3.—Section through mid-tail region of body of an adult *Gymnarchus*, showing position of the eight electric spindles and their relations to surrounding muscular and bony structures. *D*, dorsal spindles; *U.M.*, upper median spindles; *L.M.*, lower median spindles; *V*, ventral spindles. (After Fritsch.) $\times$ unknown.

The posterior tip of the creature's body is interesting. As has been mentioned, this end is free from the fin for some distance (see text-fig. 2). Also it is round in section and ends bluntly. When swimming backwards the animal uses it like a finger to feel its way. The peculiar round and blunt end may be explained by the fact that this tip contains the largest and best-developed portion of the electric organ, which fills the lateral parts of the body at this point almost to the exclusion of the ordinary muscle.

As Erdl and Fritsch have described, the electric organ consists of eight long "tube-like" or cylindrical structures, four on each side, embedded in the muscle tissue as close to the median bony parts as a little connective tissue in between will permit. Four of these are present on each side (see text-figs. 3 and 4), and they may be called in order from above downward, the *dorsal*, the *upper middle*, the *lower middle*, and the *ventral* cylinders, or spindles, of the electric organ. In a section cut through the body at a point midway between tail-point and anus (see text-fig. 3) the dorsal spindles are to be found, just above the union of the neural spines of the vertebræ, and set closely together with only the dorsal spine and some connective tissue between them. The upper median spindles are more widely separated by

the neural canal and its contained spinal cord. This second pair of spindles are at the level of the upper part of the spinal cord. The lower median spindles are found much below, on each side of the ventral processes of the vertebra. They lie at about the level of the caudal artery and almost as widely separated as the upper median pair. Lastly, the ventral pair of spindles are found just below the latter pair and slightly below the level of the caudal vein, which lies between them. They are separated a little less than the lower median pair by the narrower bony structures at this point.

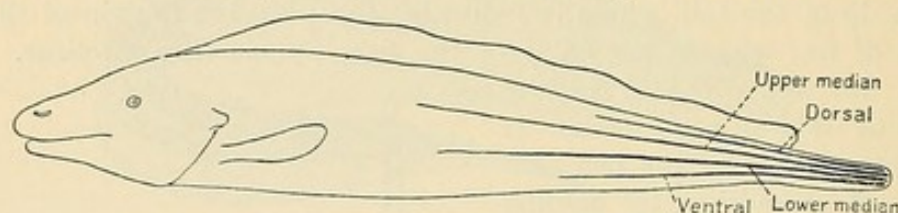


FIG. 4.—Diagram showing longitudinal position and extent of electric spindles in *Gymnarchus*. Those of one side only can be shown in figure.

The four spindles are largest in diameter in the tail, especially out in the thick, finger-like, naked extremity. From this part they taper to a smaller size as they go forward in the body and they finally become thin and end at points in the neighborhood of the anal opening (see text-fig. 4). All are not of equal length. As Fritsch has shown, the dorsal organ is the shortest and extends for about 20 cm. in a fish of 89 cm. length. The ventral pair reach for about 5 cm. further, or 25 cm. in length in a fish of the same size. The two median spindles reach for about 40 cm. from the tip of the tail.

Each spindle is marked off clearly from the neighboring muscle, and other tissues which are found next to it, by a distinct connective-tissue covering. In my largest specimen, which is a young fish of 40 days, this is well shown and is exactly like other dividing connective-tissue sheaths that surround the various muscle divisions. Like them, it often contains pigment cells which show golden-brown pigment granules.

The important contents of these spindles are alternate, cylindrical segments of a denser, deeper-staining, muscle-like substance, the electroplaxes; and a connective tissue of jelly-like, grayish transparence which in all ways appears to be similar to the "electric connective-tissue" found between the electroplaxes in the other electric fishes. In this tissue are found the blood-supply, which is largely in contact with the ends of the electroplaxes, principally the anterior end; and the nerve-supply of thick, medullated fibers which run towards, and are attached to, the posterior ends of these organs. In this case, according to both Pacini's law and the fish's relationship to *Mormyrus*, the direction of the current at time of discharge should be from tail towards the head. I have been unable to learn, from the literature of travelers and scientific collectors and observers, if the electric discharge is strong enough to be felt by the hand. Budgett does not mention it, and no other does, so I conclude that it is not a strong shock and that the organ must be classed with the weak electric organs,

as is the case with its relatives, the various mormyrids. The natives of Africa are much afraid of the creature, especially at nesting time, and one of its Arabian names, "Abu rhad" meaning "father of thunders," might seem to indicate perceptible electric powers.

The embryos and young fishes put at my disposal by Dr. Kerr and Dr. Assheton were five in number, and of these three were the suitable stages from which this paper was worked out. The significant development of the electric tissues in *Gymnarchus* takes place between the ninth day of embryonic life, at which time the embryo possesses a fully formed and complete musculature in the tail with no sign of an electric organ, and the fortieth day of development, at which time it can be seen that the embryo has developed its electric organs, out of a certain part of the previous musculature in the tail, to a degree that shows the farthest advanced electroplaxes in a practically adult condition.

The most interesting and critical stages in this metamorphosis of muscle into electroplax appear to take place within much closer limits, and stages from the eleventh to the fifteenth day would include them. These significant changes have been studied and drawn principally from an embryo 12 days of age, fixed in sublimate-acetic, and showing the changes very much to my satisfaction. A point of interest and importance in this study is that, in earlier embryos, the myotomes and electric spindles are youngest, least developed, and growing fastest in the posterior part of the body or nearest the tip of the tail; while in older embryos and in the adult the greatest, most complete, and most characteristic development of the electroplaxes is to be found in the end of the tail or at the posterior end of the spindle. Thus the adult structures in the anterior part of the spindles represent a somewhat inferior and less complete change of the muscle tissue into electric tissue than the posterior parts of the same organs do.

The same importance attaches to the fact that the rates of development of the several spindles seem to vary. The lower median spindle starts first to differentiate, extends farthest forward in the body, is larger than the others when developed, and during early development is always in advance of the corresponding parts of the other spindles. The upper median spindle closely follows the lower. The ventral spindle is much behind the two median ones, while the dorsal spindle represents the latest and weakest development and is shorter than any of the others. These facts have made it possible in the present study to get many stages of development from very few embryos.

STUDIES OF AN EMBRYO NINE DAYS OF AGE.

This little fish was 26 mm. in length and, while the egg-membrane had been ruptured and cast away, the animal was still forced to remain in its nest because of its huge, elongate yolk-sac, still unabsorbed, and because of its otherwise undeveloped organs of alimentation, locomotion, etc. The posterior part of the body was carefully cut into four portions (see

text-fig. 5) to be sectioned as follows: First, from in front of the anus to a point about 26 vertebral segments posteriorly. The last three segments of this portion were sectioned transversely and serially (region A_1) while the remaining anterior part was sectioned vertically and longitudinally (region A). Another portion of 19 vertebral segments further caudad was removed and its posterior two segments sectioned transversely (region B_1), while the anterior part was cut as before in vertical, longitudinal sections

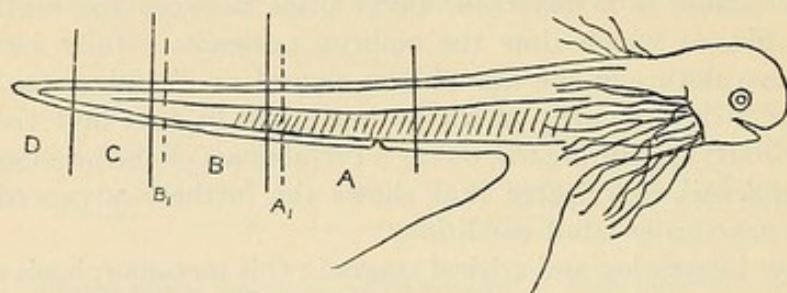


FIG. 5.—Outline of body of an embryo of *Gymnarchus* nine days old. Transverse lines and letters indicate parts sectioned for study. For explanations see text. (Copied from Assheton in "The Work of John Samuel Budgett.") $\times 5$.

(region B). A third part, of 18 more vertebral segments, was treated in the same way, except that no transverse sections were taken and the entire piece was cut vertically and longitudinally (region C), while the remaining portion or tail-tip was cut serially in transverse sections and forms a series (region D).

Figure 1, plate I, shows a transverse section through the body a rather short distance from the extremity of the tail or at a point where we are sure that the electric organ will be well developed a little later in life. It may be thought that such a section could be taken for study to better advantage in a more anterior position on account of the earlier anterior development just discussed, but it must be taken into account that the tail segments are being added and are still growing rapidly at this age, that they are very short and very crowded, and therefore the location of this section is, in reality, fairly well forward in the future electric spindles. Conditions were much the same in region C .

This section shows a good development of muscle fibers as indicated by the shaded area. As is usual in vertebrates, the most advanced stages of muscle-cell development are to be seen at the lateral periphery of the myotome. Here, at the point indicated in figure 1, plate I, by the dotted line, a layer of the outer muscle cells, two or three deep, has acquired an average of about 26 myofibrils (an average of 14 counts). These are grouped in one (fig. 2, plate I, B and C) or sometimes two bundles in the cell (fig. 2, plate I, A) and their correct spacing and their thickness and staining power indicate muscle cells of normal development and good functional activity. The remaining and inner muscle cells of the myotome, forming its larger bulk, show, as one examines them successively farther inward (toward the median line), a series of earlier stages, until at many points on the inner edge of the

myotome the smallest cells are seen with large nuclei and no myofibrils at all (fig. 2, plate 1, C). These youngest cells are particularly abundant at the dorsal and ventral edges of the myotome.

From what we know of the position of the future electroplexes and their relation to the muscle-masses, we can be sure that it is from the inner edge of the myotome that the electric tissue is to come, and a close scrutiny of the cells which form this edge shows that at two points only is there any indication of such a development.

One of these points, marked with a circle ($\oplus$) in figure 1, plate 1, is where the two myotome segments (dorsal and ventral) meet and close in against the notochord. Here we see, in some of the sections, several especially large and strongly developed fibers, somewhat detached from the rest of the myotome and resting against the vertebral disk. Several reasons exist, however, why these fibers do not represent the future electric organ. First, they are in the exact median position which remains constant during growth and in which no electric tissue is to appear. Second, they are very short and are not attached to each other longitudinally, as other fibers are, by means of connective tissue, but are attached to the bodies of the future vertebra. They may be called the vertebral fibers.

A second point can be seen where some muscle-tissue shows unusual development. At this point (marked with a circle ($\circ$) in fig. 1, plate 1) are several muscle cells which show from 10 to 18 myofibrils each, and a degree of development almost equal to the cells in the outer layer. These cells are represented as seen under high magnification in figure 3, plate 1. They are, I believe, destined to be the future electric cells, several of which will unite and form one of the electroplexes of the lower median spindle of the electric organ. I base this assertion only on their position and their somewhat advanced development as muscle fibers, for they show at this time no indication, other than their size, of developing into electric tissue.

Their position is slightly too far dorsal for the lower spindle, in an adult *Gymnarchus*, but when we examine the 12-day-old and 42-day-old stages, we find that the normal growth of the muscle-mass will carry this point to exactly the proper position for that spindle to lie at, in the grown fish.

An important point in studying these cells in figure 3, plate 1, is to note that they are separated from the rest of the myotome and from one another by other muscle cells of weak or of earlier development and containing only a few myofibrils. These weaker cells, and even some of the more advanced ones, are destined to degenerate during the development and growth of the electroplex. In figure 3, plate 1, 7 cells are present that will probably take part in the formation of the electric spindle at this point. Some of them are contiguous and others are widely separated.

In figure 4, plate 1, we have a fortunate longitudinal section from the adjacent region of this same embryo. The section shows in longitudinal view, and under low magnification, the same group of muscle cells marked with the circle ($\circ$) at both ends. Also, it shows a portion of the ventral

part of the myotome with its strongly developed outer layer (*o.f.*). The vertebral fibers mentioned above are not visible, but their position in a few following sections is indicated by a line one can imagine to be drawn between the points marked with the figure $\oplus$. It has been considered unnecessary to figure the myofibrils longitudinally under large magnification. The cross-striation is very plainly visible and is the same in all parts. Each of several regions of this embryo was examined and in all its parts were the same conditions found. We may sum up by stating that the embryo of 9 days age shows no electric tissue and but a very weak indication of the development of such a tissue, all of the myotome cells being decidedly of the muscular type. Our only evidence is drawn from future stages, as to the position of such electric tissues and from the otherwise unexplained precocity of the fibers in our 9-day embryo, in that same position.

STUDIES OF AN EMBRYO TWELVE DAYS OF AGE.

This animal (text-fig. 6) showed a considerable increase in size, not so much in length as in thickness. The posterior part of the body of this specimen was divided into the following pieces: First, from a short distance behind the anus to 14

vertebral segments further caudad. Two-and-one-half segments were cut off of this by serial, transverse sections from the posterior end (region A-1) and the remainder was cut into vertical, longitudinal sections from right to left (region A). Second,

15 segments more were removed and 3 segments of the posterior end were again

cut as serial, transverse sections (region B₁) and the remaining 12 segments were cut serially in horizontal, longitudinal sections (region B). Third, 14 segments were again cut off and the posterior 3 segments were cut transversely (region C₁), while the remainder was cut in vertical, longitudinal sections (region C). The next 18 vertebral segments formed a piece that was cut in vertical, longitudinal sections (region D), without any transverse sections being made, and this left a small bit of somewhat curled tail-tip, which was so young in development that its segments could not be easily counted. This is cut transversely in series (region E).

Study of this embryo may best begin by examining a transverse section through the posterior part of the body (fig. 5, plate 2) to see what has become of the inner parts of the myotomes. Looking first for the point *L.M.* as seen before in figure 1, plate 1 (marked with O), we can see at once that it is present as a compact mass of muscle-like tissue now clearly

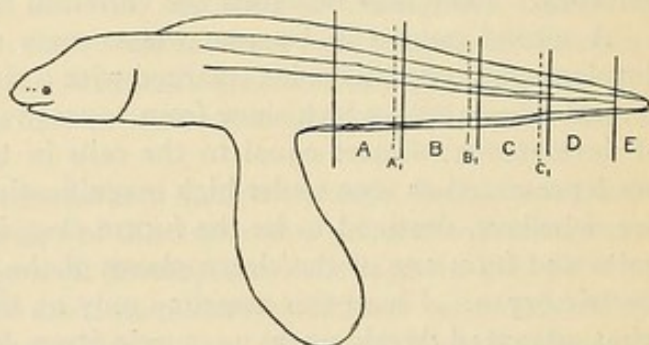


FIG. 6.—Diagram of body of an embryo of *Gymnarchus* 12 days old. Lines and letters indicate the regions studied. For explanations see text. (Copied from the same source as fig. 5.) $\times$ about 3.25.

separated from the rest of the myotome. Further, there are to be seen on each side three other similar sections of the same muscle-like tissue, all more or less also separated from the main mass of the myotome. The most important part of our study now consists on the one hand in proving that this mass *L.M.*, in figure 5, plate 2, is derived from the undoubted muscle-fibers (marked with $\bigcirc$), as seen in figure 1, plate 1, and on the other hand in showing that this same structure is to become the finished electric tissue as seen in such advanced development as in figure 21, plate 8, for instance.

In tracing it back to the muscle, we are much assisted by the fact that the dorsal and ventral spindles are always in an earlier or in a less complete stage of development than the upper middle spindle, or, particularly, the lower middle spindle under consideration. And, since in this embryo of 12 days the development has gone to considerable length, and since a slightly younger stage, say a 10- or 11-day embryo, was not included among the embryos at my disposal, this fact is of much importance, because it will be fair to take the left ventral spindle as an intermediate step in the comparison. Figure 9, plate 3, is a highly magnified section of the locality of the left ventral spindle from region *C* in the embryo of 12 days, and in it we can see a mass of muscle-like cells, closely associated and lying at the inner edge of the myotome. Certain changes clearly differentiate them from the rest of the muscle, however. One change is the fact that the myofibrils have shown a large diminution in size or thickness and have also suffered in power to take the stain; particularly on the periphery of some of the muscle-columns they almost refuse to take it. Their spacing is also irregular and they show a distinct tendency to clumping together and, in some cells, to get close to the nucleus or even to surround it. They can be readily compared in figure 9, plate 3, with the well-developed young muscle cells just outside and to the left of them. The dotted line marked *XX* indicates a separation of the two. All of those to the right of this line show the condition of the myofibrils mentioned above; those to the left show the usual condition of muscle cells of this age in fishes.

A second characteristic of the changing muscle cells under discussion is in their cytoplasm. It appears more abundant, although this may be due to the smaller fibril bundles. But it also stains more heavily with such stains as eosin, erythrosin, and orange G. With the eosin, for example, it also shows a more yellowish tinge than the cytoplasm of the usual muscle cells in the same sections. And lastly, some of the muscle cells seem to have entirely disappeared or to have greatly shrunk. This latter fact causes a loose and separated condition to obtain among the metamorphosing cells which shows in sharp contrast (fig. 9, plate 3) to the compact condition seen in the typical muscle cells to the left of or outside of the line *XX*.

Another important fact can be seen among the changing cells in figure 9. Those near the center of the group show a tendency to touch or coalesce with each other. Already at this early stage this marks a difference in the group. Those cells within the dotted circle are destined to

unite with one another in a compact bundle to form the future electroplax; while those of the group which lie outside of the dotted ring are to degenerate and atrophy altogether, in order to make room for the growing electroplax. Just mediad of, or to the right of, the dotted ring is seen a cell that has entirely lost its myofibrils and whose cytoplasm is vacuolated and about to be absorbed. At other points, to the left, still other cells can be seen that have dwindled to a smaller size than any of the normal muscle cells. The cells within the ring are judged by the writer to be those which will form the electroplax at this point, because they are starting to unite and, also, because they occupy the position at which the electroplax will lie. Another reason is that their myofibrils are weakening and clumping. Some of those cells lying inside of the ring may also atrophy. This can not be infallibly judged; but certainly all of those outside of it and to the right of the line *XX* are about to degenerate and are not found in later stages.

The connective tissue creeps into the neighborhood of and among these metamorphosing muscle cells at this time, and good mitotic figures can be seen, showing that it is increasing the number of its cells. It does not, however, penetrate the groups of future electric cells inside the dotted line. Also blood, pigment, etc., are to be seen in characteristic positions.

A transverse section of the body at region *B*₁ need not be illustrated at this point by a low magnification figure, because it is so like figure 5, plate 2, in general appearance. But it happens that in such a section several very interesting stages, forming a sequence of which figure 9, plate 3, can be taken as the first member, were noticed, and figure 10, plate 3, is the second in this series. This drawing represents the right ventral spindle in region *B*₁, and a number, five to be exact, of the transforming cells can be seen here in closer union than the corresponding cells were in figure 9, plate 3. One or possibly two of these may disintegrate a little later. A dotted ring is not necessary, because the connective-tissue cells have partly marked off the electric cells, and outside of this incomplete ring and above it can be seen two muscle cells which are atrophying. A third cell is shown in a final stage of disintegration. Its cytoplasm is almost clear, or all gone, and its myofibrils have united in a single lump, which will soon become a round droplet or cell-inclusion that will afterwards disappear.

Moving to the right upper middle spindle (fig. 11, plate 3), we need very little explanation to see how the four or more muscle cells that first composed this structure have come into a still closer union. Below and to the right (outer) are still seen some of the degenerating muscle cells—five in this figure.

Several important points must be discussed in connection with this figure; the component cells, as seen here, are not simple, single muscle fibers. The lower one can easily be seen to have two myofibril bundles as well as two nuclei. The presence of two widely separated fibril bundles, as well as the large size of the cell, makes it nearly certain that the structure was formed by the coalescence of two muscle fibers. In the upper region

of the future electroplax, however, a large cell is seen which has only one fibril bundle and four nuclei. It is possible here that this was one cell and that it is growing in size and multiplying its nuclei by amitotic division. As this is the same process which goes on in ordinary muscle cells of this age, it is not surprising to find it going on here, and in older specimens we shall find it the rule. The cytoplasm of all these electric cells is abundant at this stage and is dense staining with the acid dyes.

As compared with figure 11, plate 3, the next illustration, figure 7, plate 2, is most interesting and is a step of some magnitude in the development of the electroplax. The cytoplasm of such cells as compose this young electroplax is all united into a single mass and the relation of nuclei to fibril bundles is completed. The nuclei are always peripheral and the fibril bundles appear to form a single central mass. This is the permanent condition which will obtain throughout the life of the organ, and is also the condition common to some other electroplaxes, as, for instance, *Raja* and *Mormyrus*.

Just how the several fibril bundles become massed as a single bundle is not to be positively stated at this time. The individual bundles can hardly be imagined as moving together through the cytoplasm. It is probable that some of the several bundles as seen in figure 11, plate 3, are lost and absorbed, but it is not probable that all but one are so removed. The central bundle in figure 7, plate 2, looks large enough to be composed of several, such as are seen in figure 11, plate 3. The best explanation is that several remaining bundles are moved toward each other by growth currents in the cytoplasm, or by the absorption of material which lies between them. At the same time, of course, the peripheral cytoplasm is growing in mass and all nuclei tend to remain in this external layer. We shall see later that a very few nuclei are left behind in the central fibrous mass in some electroplaxes.

In figure 7, plate 2, we see, plainly and indubitably, the first form of the electroplax as found in older fishes.

The connective tissues which surround the electroplax are becoming more decided in figure 7, plate 2. Also blood-vessels and pigment-cells are oftener seen as in this drawing. One muscle cell, with its myofibrils clotted into several irregular masses and its nucleus in an advanced stage of disintegration, is seen just between the lower end of the pigment-cell and the electroplax.

It will be well at this point to examine some of the longitudinal sections of these early stages, in order to make clear several points which can not be so well studied in the transverse views.

Figure 12, plate 4, is a low magnification picture ($\times 140$) of 6 segments of the caudal part of the body at region *D* in this 12-day embryo. Only the dorsal part of the body is shown, where a fortunate slant of the section has permitted the knife to pass through both the dorsal and the upper median spindles at the same time. The drawing is an accurate projection from three different sections, so that all parts of each spindle might be

shown, as well as their relations to the rest of the myotomes. Bracket No. 1 (zone 1) in this figure indicates the inner tips of the ventral halves of the myotomes. Zone 2 shows a mass of connective tissue and nerve which runs between these two halves (compare fig. 5, plate 2, *Conn T.*). Zone 3 embraces the inner tips of the dorsal myotomes where they lie between the upper median spindle and the horizontal connective-tissue septum. It will be noticed that this set of muscle fibers appears to be very short, much shorter than the connective-tissue regions between them (not filled out in this drawing). The reason can be seen at once when these same muscle cells are examined under the high power (fig. 15, plate 5, bracket 3; and fig. 6, plate 2), where it is apparent that they are degenerating fibers. Parts of four of these fibers are shown in figure 15, plate 5, and that one nearest the electric tissue which is represented in figure 15, plate 5 (brackets 4 and 4₁), is the farthest gone, having lost its myofibrils altogether. The nuclei are also distorted and, besides the single large nucleolus, are noticeably empty of any chromatic matter or even of linin (notice the nuclei of healthy muscle and electric tissue). The next fibers to the left in this figure serve well to show how the degeneration takes place from the ends, where the cytoplasm is gathered in heavy lumps which stain light and yellowish with eosin. In fact, there is a singular similarity between the process of degeneration of these muscle cells and the transformation of the others into the electric tissue. Above, in zone 3, is a rounded cell which I take to be a muscle cell in a final stage of dissolution. It contains large granules of a chromatic substance, which appear to be the remains of myofibrils. Figure 6, plate 2, also represents three fibers from this same region in another myotome and shows three stages of the degeneration of the muscle. Two of them indicate that the degeneration begins in the middle of the fiber.

Zones 4 and 5 in figure 15, plate 5, as well as in figure 12, plate 4, show the young electric tissue of the upper median spindle. Let us first consider this tissue in figure 12, plate 4, where we can get a larger, low-powered view of it. In the first place, the most noticeable feature of the electric tissue here is that it shows scarcely any signs of a division into the original myotomes. A trace of this is seen in zone 4, but in a careful and systematic search through a number of the spindles of this stage very few instances could be noted. Even the myofibril bundles of successive myotomes seem to have united, and these bundles were most carefully examined under a Zeiss 2 mm. 1.40 ap. lens. I have no doubt that each spindle does constitute a continuous reticulum of muscle cells at this period. Laterally, the various muscle cells are not continuously united, but, as is shown in figure 15, plate 5, they are united at a number of points much in the way that some heart-muscle fibers are.

The myofibrils are best seen, of course, in these longitudinal sections, and it can be seen that they are typical. The transverse striation is as perfect as in the functional muscle, but owing to the slighter fibrils they are not quite so dark. In the upper median spindle of figure 15, plate 5, some

points were found where this striation was slightly weakened. Cases of relaxation and semi-contraction uniformly characteristic of the normal muscle prevailed. The distances between the bands, as well as the length of the anisotropic parts, was the same as in ordinary muscle and remains as long as striation can be seen. This same fact does not hold true in *Raja* or in *Astroscopus*, where it is much shortened. It does hold, however, in *Mormyrus*, which is closely related to *Gymnarchus*.

The longitudinal sections, shown in figure 12, plate 4, and figure 15, plate 5, correspond to the spindles before it has become possible to see that they have segmentally divided into electroplices and before a central core of fibrous material has become definitely differentiated from a superficial layer of cytoplasm containing all of, or nearly all of, the nuclei.

We will now advance toward the head of this same specimen, to find material in a more advanced stage of development, in order to study the segmentation of the embryonic spindle into its individual electroplices (this segmentation has just been described as absent in fig. 12, plate 4), and to study further the differentiation of the inner fibrous core from the outer layer, and lastly to see how the myofibrils lose their transverse striation (muscle striation). The reader will remember that at this stage the anterior electroplices are in advance, developmentally, of the posterior ones. Figure 13, plate 4, shows four vertebral segments, taken from the region C of this same embryo, under low magnification. Bracket 1 embraces the zone of the epithelium. No connective tissue is shown. Between the muscle-zones 2 and 4 lies the zone of the long, narrow, embryonic electric spindle, marked by bracket 3. It is the lower median spindle which is shown, one which is always in advance of all the others in development. In this figure it becomes quite plain that, while the muscle tissue is arranged segmentally to correspond to the vertebra, the electric organ is not. In this case the electric spindle is separated transversely by connective tissue into three segments, instead of four. Nor is this proportion always maintained among the several electric spindles themselves.

In some cases, as will be seen later, a single electroplice corresponds to as many as five vertebrae. Even the electroplices do not correspond with each other. A subsequent figure will also demonstrate this (fig. 23, plate 9). Just what factors do determine the length of the electroplice I am unable to say. A closer study of the nerve distribution and blood-supply may throw some light on the matter.

The transverse sections of the stages represented in figure 13, plate 4, do not show anything of interest over and above what was discussed in connection with the conditions seen in figures 9, 10, and 11, plate 3, and figure 7, plate 2. We will, therefore, advance toward the head one step further in this embryo and examine a longitudinal section from the region marked B in text-figure 6. Here (fig. 17, plate 6) the electric tissue is seen in what may be considered as its maximum development in this 12-day embryo. The electroplices are distinct from each other and have grown considerably in

size. The one selected for illustration is from a lower median spindle and shows an actual length of 0.9 mm. It appears with smooth, well-defined boundaries and good separation of core and outer layer. The myofibrils are shown in the core as several closely associated bundles, only to be distinguished from one another by a slight curving and twisting in their course. This would not be visible in a transverse section at most levels in the electroplax, and it gives strength to the view, expressed before, that the fibril bundles of a number of young muscle cells combine to form the single fibrous core of each electroplax. At the levels examined it would appear that a group of from 4 to 7 cells from each myotome is concerned in the formation of any electroplax and that these same groups of from 2 or 3 myotomes are likewise united end to end, thus making it possible that from 12 to 21 muscle cells are united to form each electroplax.

The beginning of the loss of transverse striation is quite visible in figure 17, plate 6. This striation merely fades or loses its staining power, beginning at several points, but usually at the middle of the electroplax. The ends retain the staining power of the *M* stripes longest.

The multiplication of nuclei must be spoken of at this point. It is well known that the nuclei of future muscle tissue divide by mitosis with a consequent and subsequent division of the cell-body as long as the cells are in the young myoblast stage. As soon as muscle differentiation begins to take place, the mitotic division of nuclei is changed to an amitotic type of division and the cell-body ceases to divide and begins to lay down myofibrils. Some few observations against this view are recorded, but it seems to hold in *Gymnarchus*.

In figure 15, plate 5, one can readily see many cases of amitotic nucleus division. The few cases of mitosis visible in the figure are of connective-tissue cells. Such cells, it is known, always divide by mitosis during their whole existence. As the electroplax grows, more nuclei are needed, and they are supplied by the amitotic divisions above mentioned. Just how long this process keeps up is not known, but it is probably mostly done before the first 15 or 20 days of development are passed. It is evidently going on fast in the 12-day embryo, and it is possibly finished in the 42-day stage. The nuclei are typical muscle nuclei in appearance and are not to be distinguished from the nuclei of real and active muscle in the same preparations, except, perhaps, they are slightly larger and have a somewhat heavier chromatic content (larger nucleolus and chromatic granules). This does not hold, of course, for the degenerating nuclei, whose differences have already been described. Connective-tissue nuclei can at once be distinguished by their delicate outline and small chromatin content, which is distributed as very small granules.

STUDIES OF A LARVA FORTY-TWO DAYS OLD.

In order to continue tracing this history of the development and growth of the electric tissue, we will now be obliged to pass to an embryo of some

considerable size and one in which the oldest tissues are almost the same, for an understanding of the adult structure as those of a fully grown fish would be. Text-figure 7 gives an outline of this specimen, which was about 63 mm. long and whose tail part was cut off and divided and sectioned as follows: Beginning at about the level of the anus, a portion composed of 6 vertebral segments was sectioned in a vertical and longitudinal direction (region *A*); then passing caudad, the next 2 segments were cut transversely (region *A*₁); then the next 12 were cut longitudinally and horizontally (region *C*); then the next 6 were cut transversely (region *C*₁); then 13 others were cut longitudinally and vertically (region *D*); then 7 more were cut transversely (region *D*₁); then the next 14 were cut longitudinally and approximately vertically (region *E*), while the tip of the tail, composed of some 12 or more segments, was sectioned transversely (region *E*₁).

In the embryo of 12 days the youngest developmental stages of the electric tissue were found in the most distal portion of the tail, which at that time had but recently been extended by growth from the body and was still in process of extension. The oldest and consequently the most-developed electroplexes were to be found in the anterior or cephalic end of the spindles.

In the present embryo, or larva, of 42 days, the conditions are reversed, and the electroplexes in the extremity of the tail have passed those farther up in the body in their differentiation, and have reached a much greater and more complete development. Accordingly we will select for study one of the most anterior and least developed examples and compare it with that electroplex last studied, which is represented by figure 17, plate 6.

Figure 18, plate 6, is drawn from one of the ventral electroplexes of the region *C*, as shown in text-figure 7. This position makes it fairly well forward in the spindle, although portion *B* would have shown slightly younger stages.

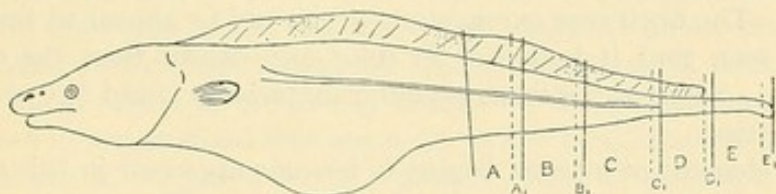


FIG. 7.—Diagram of body of an embryo, or larva, of *Gymnarchus*, about 42 days old. Lines and letters indicate regions studied. For explanations see text. (Copied from the same source as text-fig. 5.) X about 1 and 1.5.

The fibril core will first attract our attention. The first noticeable feature is that this core is growing in mass and volume all through the electroplex, but also far faster in its center than at either end. Throughout its course it has assumed a unified appearance which shows no trace of the several fibril bundles which have gone to compose it. In the narrower ends the mass is straightest and its component fibers appear most parallel, being but slightly wavy. As we follow them from either end towards the middle it can be seen that their course becomes more and more wave-like, until, in the middle, they have been thrown into decided folds. Their actual

course can be somewhat better followed with thicker sections and deep eosin staining than with preparations of the usual kind.

As to the fibrils themselves, they have lost the transverse striation altogether. By this I mean that it is no longer stainable. It seems that, in the straight ends, with a good immersion lens one can see traces of this striation, left as a thickening of the fibrils, at points that may represent the previous position of the anisotropic *M* spindles.

Whether the increase in the mass of the fibrillar core, which goes on as the electroplax grows, is due to the thickening of the individual fibrils or to the laying down of more and new fibrils or to the deposit of an interfibrillar substance between them, was not decided. The first two conditions seemed the most probable, because of the apparent absence of much interfibrillar substance in the oldest and largest electroplaxes.

The cytoplasm of the outer layer begins to be of interest at this stage. Its most particular point of interest lies in the fact that it is decidedly different in structure at its anterior end from its posterior end. This is shown in its staining capacity as well as in its actual structure. In the specimens stained in iron hæmatoxylin and eosin the cytoplasm at the posterior end stains deeper than that at the anterior end, with both dyes. It can also be seen to be granular in structure—a sort of general granulation with a few larger granules of a substance which stains somewhat like chromatin. In particular, its cytoplasm is darker than the fibrillar core at this posterior end.

As the cytoplasmic layer is examined in an anterior direction, it is seen to stain lighter and at the same time to contain an occasional vacuole. This condition increases until, at the anterior end, about one-fifth of the length of the entire structure is covered with a cytoplasm which is so much vacuolated that it appears as a delicate reticulum in the meshes of which the nuclei lie. The fibril core extends out to the end or almost to the end, and it can be seen that it is darker in color and denser than the cytoplasm covering it. Some of the finer, granular material is found out as far as the reticulated tip.

A new element of interest begins to become apparent in this stage, and that is the point of attachment of the nerve. The strong medullated fibers come from the cord, pass through the spinal ganglion, and enter the connective-tissue "tube" of the spindle at the level of the posterior third of each electroplax. The fibers wind and turn considerably, in this vicinity, and are finally applied to the surface of the electroplax over an area which may be described in this specimen as its second sixth part from the posterior end. Thus the extreme posterior end does not receive any nerve-endings at this period.

The cytoplasm shows a number of indentations where the nerve is applied and the axis-cylinders of the nerve can be traced into these spaces, which they apparently fill with a club-shaped nerve-ending. This ending can not be satisfactorily described until some of the special nerve methods can be used to elucidate it.

Another and more simple step in development is indicated in figure 19, plate 6, which was taken from an electroplax in a dorsal spindle of this embryo at the region *E* (see text-fig. 7).

Two points of interest will be spoken of in connection with this stage. The shape has changed as follows: The middle part has both actually and comparatively widened over the breadth shown by the middle part of the electroplax seen in figure 18, plate 6, and this increased width is due to a broadening of the fibrous core alone, the outer nucleated layer remaining the same.

Accompanying this widening is also an actual shortening of the structure. Thus, part of the increased bulk of the middle is due to an absorption of the two ends. Apparently the anterior end suffers the greater amount of absorption, for it is usually shorter and thinner than the posterior. In this connection we must remember the previous vacuolization of this anterior end as seen in figure 18, plate 6. It would appear that the vacuolization was part of an absorption, or rather of an atrophic process. Considerable traces of it remain in figure 19, plate 6, and it is also still noticeable that the anterior end does not stain deeply. The posterior end retains its length and vigor to a greater degree. It seems to become considerably narrowed, however.

The form of the electroplax also begins to show a marked change through the development of spurs, branches, or papillæ which begin to protrude from both its ends, particularly from its posterior end. Some indication of this was visible already in figure 18, plate 6, as small lumps or "shoulders" that marked the organ roughly into three parts—anterior, middle, and posterior thirds. These growing spurs begin to give the middle third a distinct truncate or cylindrical form. The nerve fibers also attach themselves to the sides of the growing papillæ, particularly to their bases. The papillæ show an inclination to grow out of the sides of the posterior third.

We will now pass to the last and oldest stage of the electroplax which can be found in the embryos which Budgett collected in Africa. This is found in the *E* region of the 42-day embryo or larva of *Gymnarchus* and is represented in longitudinal sections under a low magnification by figure 23, plate 9, which shows parts, or the whole, of about 11 electroplaxes lying in place in the ventral, lower middle, and upper middle electric spindles of this region. Figure 21, plate 8, also shows a transverse section just cephalad of this point, in the *D* region, where cross-sections of the 8 electric spindles reveal partial or complete transverse sections of 7 electroplaxes, but only the electric connective tissue which fills the tube at this point, in the eighth.

Figure 20, plate 7, represents a longitudinal section of one of the electroplaxes shown in figure 23, plate 9, and will serve as a basis for our last study of this series.

The form has continued to follow the development which was indicated in figure 19, plate 6. The total length of the structure has shortened somewhat more, while its width in the middle part has increased twofold. These

statements are the result of averages of about 15 measurements. The papillæ on the posterior surface have increased in length and some of them have begun to rival the posterior portion of the organ in length. We have no suitable figures of the adult electroplax, but from Fritsch's (3) descriptions, and from the tendencies shown by these embryos, it would seem that, as Ewart describes in *Raja*, the original posterior portion of the electroplax shortens and the new papillæ lengthen until they all form approximately similar structures. This can only be completely studied when we have secured suitable sections of the grown fish.

The development of papillæ is noticeably weak on the anterior surface. The figure does not show as many as some of the electroplaxes in figure 23, plate 9, but it is a fair illustration. Neither does it show well the usual condition of the main anterior process of the cell at this time, which can be better seen, in some electroplaxes of figure 23, plate 9, to be still in evidence and of considerable length, but of very weak development. This anterior process shows no trace at this age of the general vacuolization of its cytoplasm which we saw in an earlier stage, and the fibrils extend as a very thin and uncertain core through its length.

The fibrillar mass which forms the core of the electroplax has now assumed what appears to be its permanent condition. The fibrils are very fine and, after having passed straight down through the posterior process, are thrown into flat waves by the process of packing them into the shortening and widening middle part which now constitutes the principal bulk of the structure. This causes the larger part of the fibrils to lie nearly at right angles to the longitudinal axis of the organ, and this appearance was first taken by the writer, who examined the oldest embryo first, to be a trace of the transverse striation of muscle from which the organ is formed. We now know it to be the myofibrils, lying at right angles to their original course. No conclusion was arrived at, in this stage, concerning the growth of this mass, as to whether the number of fibrils was increased, or whether the larger size was due to a thickening of the original fibers, or to the deposit of interfibrillar substance. The fibrils seemed to be as fine if not finer than in the earlier stages; certainly they are much finer than functional myofibrils. Since muscle tissue increases the number of its myofibrils long past this age, I see but little reason why this modified muscle should not also do so.

A closer study of the cytoplasm and nuclei of the peripheral layer was next undertaken in this oldest stage. Beginning on the posterior surface and on the papillæ, we find the layer thickest here and composed of at least three distinguishable materials. One was a dense material which was reticular in structure and stained with chromatic stains deeper than almost any other pure cytoplasm that I know of. This material was one constituent, while the other substance composing the general field at this point was a far lighter staining material which was homogeneous and clear. This latter seemed to bear the same relation to the denser material that the "nuclear sap" does to a linin alveolum or reticulum in the nucleus. Like

the linin reticulum, this denser material was more refractive and took more of the chromatic as well as more of the acid counterstains than the homogeneous material did. I shall adopt Schneider's (31) name of "Linom" for the denser substance and his name of "Hyalom" for the clearer and more homogeneous material. It seems probable from the works of Bütscheli (9), Rhumbler (27), Hardy (35), Wilson (34), Andrews (1), Strasburger (32), and others that these structures of cytoplasm, as seen under the microscope in fixed material, do not represent the exact condition as it exists in life. After reading the pages of my recent work on the electric-motor cells of *Torpedo*, one can more easily see that the cytoplasmic linom is a structure which depends upon the fixative used as one factor and upon the chemical and physical peculiarities and the contents of this plasma at the time that the fixative is applied, as another set of factors. Its reticular or alveolar arrangement can most certainly be immensely varied, and all these artificial conditions must be very much different from that which obtains in life. Since I have only a few fixed specimens to discuss, over whose earlier preparation I had no control, I shall not try to solve the question of what the structure was during life, but will merely describe the present specimen as it appears.

The linom of the cytoplasmic layer on the posterior end is very fine and can only be seen with the best lenses and under the best conditions. This holds particularly for the outer portion of the layer, for as we examine the inner portion the reticulum grows larger meshed until, at its point of contact with the fibrillar core, the meshes are quite easily seen.

The same is true as we examine this layer in a more anterior position. Here all the meshes are proportionately larger, until in the layer, as found covering the extreme anterior surface, the meshes of the linom are visible with ordinary high powers. I do not refer to the vacuoles which are found at various points, for there is a great difference between the largest meshes and the vacuoles, although the vacuole may be derived from, or originate in, an overgrown mesh. The meshes always contain the hyalom, while the vacuoles do not. My definition of a vacuole in this case will be a space in the linom into which the hyalom does not extend. Also, the rounded outline of a vacuole shows a surface tension between its content and the cytoplasm, which does not seem to exist between a mesh of the linom and its contained hyalom. These vacuoles appear to have contained a soluble substance during life, and the hyalom is not soluble in fluids used to prepare the specimen. Such vacuoles are found at various points in the cytoplasmic layer, most often at its outer edge, while the large meshes appear at the inner edge and around the nuclei. The vacuoles become so large and numerous at the anterior end of a stage such as figure 18, plate 6, that the cytoplasm looks like foam containing the nuclei and surrounding the unchanged fibrillar core.

In addition to this structural basis of linom and hyalom, another very prominent content of the cytoplasm is a series of granules of some material

that is denser and somewhat more stainable than either of the others. These granules are very numerous and fine at the periphery, where they cause the outer part of the layer to stain deepest with eosin, and they lie in the finer-meshed linom, and grow larger and fewer as one examines the inner parts of the layer. They are of a slightly more refractive quality than the linom and stain deeper with chromatic dyes the larger they get. The largest also have some color of their own, a slight golden-brownish color, somewhat like that of pigment granules. While the smallest granules seem to lie in or attached to the strands of linom, the larger seem to lie in its meshes in the hyalom. They remind the observer of the granules found in certain other cells, particularly in the electric-motor cells of *Torpedo*, as well as in other nerve-cells. In figure 16, plate 5, these finest granules are seen in the outer part of the layer stained with eosin, while the inner part does not show the larger ones that lie there.

The larger granules are prone to gather about the nuclei and about the inner part of the electric layer, as seen in figure 22, plate 8, where they took the iron hæmatoxylin stain well. The larger, chromatic-staining granules are also found, in groups or singly, in many parts of the fibrillar core. While the larger ones found in the core, around the nuclei, and at the inner edge of the cytoplasmic layer seem to stand in sharp contrast to the more numerous and finer ones found in the outer part of the cytoplasm, one can trace steps between the two kinds.

The writer believes these granules to be the secreted or prepared nitrogenous material used by katabolic processes to produce electricity, either directly or indirectly. They must be, physiologically, the same granules described by Ballowitz (5) in the cytoplasmic layer of the electroplax of *Raja*, and by Schlichter (30) in the cytoplasmic regions on both surfaces of the electroplax of *Mormyrus*. In this latter they were very large and not easily demonstrated. The writer has seen some indication of them in *Astroscopus* (12), but they would seem to be noticeably absent in other forms, as *Torpedo* (although they have been figured here by Fritsch (20)), and in *Gymnotus* (3) and *Malopterurus* (6), where such granules as Ballowitz has described or figured would seem to be inadequate in size and number for so heavy a duty. It will be noted in the above list that the weak-electric fish seem to have these cytoplasmic granules best developed, while the strong-electric fish show least of them. It is possible that these latter possess them, or their equivalent, in a more fluid and less visible form.

The cytoplasmic layer is marked off from the fibrillar core by a very definite and sharp line. It can not be said that a definite membrane exists here, although one may exist. The boundary between the outer layer and the core is not an even or a straight one, but shows a wandering course, especially at the two ends. At some points strands of the linom seem to branch into the core (fig. 16, plate 5). At the anterior end in particular it shows many extensive and complicated invaginations of its granule-containing substance into the fibrillar core. Certain small portions

of it also have been permanently left in the main body of the core, usually near its anterior end. These inclusions (fig. 20, plate 7) may or may not include the nuclei. They always contain some of the largest of the granules.

The nuclei do not show any internal peculiarities which would distinguish them as electric nuclei from some of the other tissue nuclei, particularly from muscle nuclei, which they much resemble. They have a large chromatic content and a particularly large plasmosome which stains deeply. They can be sharply distinguished from some other nuclei, as connective-tissue nuclei for instance, where the more delicate outline and different chromatic pattern is discernible at a glance.

Each nucleus shows some sign of a surrounding differentiated layer of cytoplasm. This consists of larger granules and a zone in which the hytoplasm seems to be in greater proportion than elsewhere. At different places in a preparation one may see more or less of a contraction zone around the nuclei. While this may be a physiological condition, it is more probably an artifact due to the fixing or hardening.

One interesting condition is to be seen in most of the few nuclei which become detached from the outer layer and included with some small portion of the outer cytoplasm in the fibrillar core. These nuclei probably become so placed during a very early stage, and the further they are separated from the layer to which they rightly belong, the larger they grow and the more diffuse their chromatin becomes. The plasmosome diminishes in size and the whole structure looks more like a connective-tissue nucleus, except that it is very much larger. I have seen this same condition in the electroplax of *Raja*.

It was not possible to find a real electrolemma or cell-membrane covering this electroplax. A connective-tissue covering, more or less closely applied to the surface, was always present, but the fact that this covering possessed its own nuclei seems proof that it was a real connective-tissue covering and not any product of the activity of the electroplax tissue. At such points, as this connective tissue did not actually touch the electroplax, a careful examination was made to see if some actual cell-membrane did exist. Beyond the fact that the outer edge of the electric layer was sharply defined and that its surface was rounded and even as if some membrane was present, no real membrane could be demonstrated, either by its refractive properties or by its color.

INNERVATION.

A general survey of the innervation is desirable, as too little exact topographical work has been done on those fishes in which the electric-motor centers are thinly distributed in character over large areas of the cord, as, for instance, in *Gymnotus*, *Raja*, and the mormyrids. Regions *D* and *E* were selected in the 42-day-old embryo as the most favorable parts to study. The work was not as exact as it could be if the investigator had had plenty of live material, especially adult material, on which to use some of the well-known neurological methods. But even in this embryo, which was well

fixed in sublimate-acetic, much could be accurately made out, and it is hoped, too, that the description will prove suggestive.

The motor cells were first looked for in the spinal cord, especially that region which was posterior and in the neighborhood of the electric organs. Assuming for the present, as a law, that electric-motor cells are larger than muscle-motor cells which innervate an equal weight of muscle, it was very easy to find groups of large, heavy nerve-cells scattered through the substance of the spinal cord from near the anterior beginning of the spindles to the very last point in the tail to which they extend.

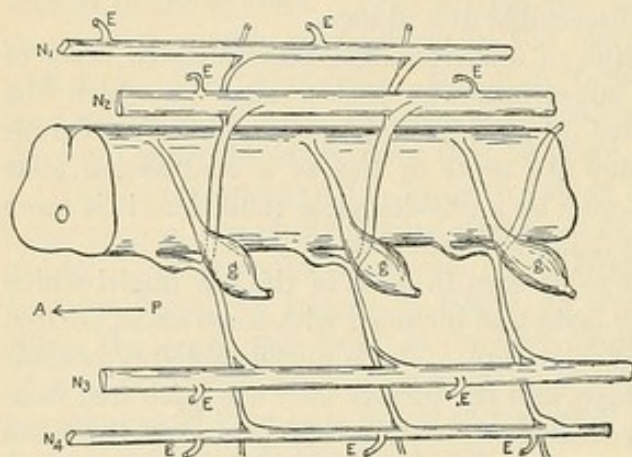


FIG. 8.—Side view of reconstruction (semi-diagrammatic) of spinal cord and motor electric nerves of a larval *Gymnarchus* 42 days old. Arrow indicates anterior and posterior directions. N_1 , N_2 , N_3 , and N_4 are the four electric nerves formed by branches from motor roots of spinal nerves. E indicates small branches from electric nerves that innervate posterior surfaces of electroplaxes. g marks spinal ganglion, whose afferent nerves have been cut off.

These cells were situated just above the central canal and from 1 to 4, or even 5, could be seen in every transverse section in most of this length (fig. 14, plate 4, *A*, *B*, and *C*). They did not appear to be divided into two symmetrical groups, but rather to lie in one median group. On the one hand, their dorsal position might appear to be evidence that they were not motor-cells or that they were not to be considered as modified muscle-motor cells. On the other hand, the presence of real ventral muscle-motor cells (fig. 14, plate 4, *D* and *E*) in the whole length of the cord, the correspondence of the cells under discussion with the position of the electric spindles, and the fact that Fritsch describes similarly placed cells in the same position in mormyrids as the motor-nerve cells of the electric organ, all seemed to constitute very strong indirect evidence that these were the nerve cells which innervated the posterior ends of the electroplaxes.

In addition, the writer was able to trace, in a number of cases, the course of the neuraxons through the cord, out into the ventral roots of the nerves, and finally into special bundles of nerve fibers that undoubtedly innervated the electric tissue. No one nerve process was actually traced for the whole distance unbroken, but the various parts and regions were so pieced together that the course was well established and corresponds in many ways with Fritsch's observations on *Mormyrus*. Text-figure 9 shows a semidiagrammatic cross-section of these courses as seen from in front, while text-figure 8 shows the same thing sketched in relief from the side. This topography will presently be described.

The electric-motor cells at this age must of course be considered as still very young, and descriptions from the adult are desirable. We will begin by examining the 9-day-old embryo once more to see if they have started. In this cord (fig. 8, plate 2) there are but very faint traces of any nerve-

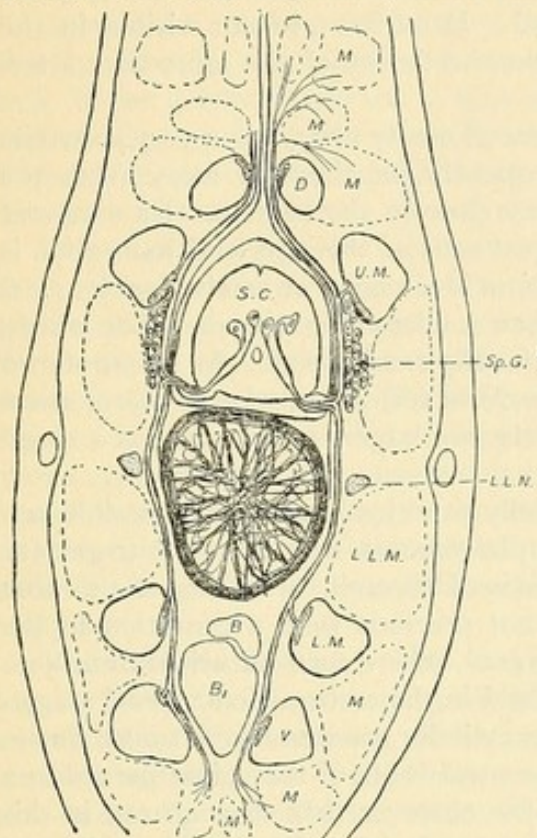


FIG. 9.—Diagram to show position and relations of nerve elements to electric spindles. S.C., spinal cord, showing central canal and four motor electric nerve-cells. Processes from these cells pass out through ventral roots, and distribution of these roots to electric spindles and muscle-masses is indicated. M, some of the muscle-masses. D, U.M., L.M., and V show electric spindles on one side. Sp.G., spinal ganglion; L.L.N., lateral line nerve.

cell development, and some neuroblast mitosis is still going on. In the position to be later occupied by electric cells a little enlargement of nucleus and cell-body is visible. One cell here is of great interest, and that is one of the now well-known "Hinterzellen" or giant cells, first described by J. Beard (37), Rohon (29), Studnitzka (33), and others, in the embryos of *Salmo* and *Raja*, and later by Fritsch (21), as a different sort of cell, in the adult *Lophius*. Still later, such cells were described by the writer (36) in the embryos and adults of various *Pleuronectidae* and in *Pterophryne*, where he showed it to be the same cell in both embryo and adult, and described the relations of anterior and posterior branches of the neuraxon. From its size, shape, and position in the present specimen, it seems that this dorsal cell might be, in some way, related to the electric-motor cells, but that question is easily settled when one examines the 12-day embryo and finds that all of the dorsal cells have effectually disappeared before the electric-motor cells begin to differentiate. Besides, the well-known fiber courses of the dorsal cells as worked out by Fritsch in *Lophius*, the writer in *Pterophryne*, Harrison in *Salmo*, and Johnson in *Catostomus* are sufficient proof that the two have nothing in common.

The 42-day larva shows the best development of these electric-motor-nerve cells until an older fish can be described. Here we find a heavy, rounded, cytoplasmic body of about 40 microns in diameter (fig. 14, plate 4, A, B, and C). Its outline is usually pear-shaped, with the axis-cylinder process given off at the pointed end. Dendrites are not visible in the specimen at hand. While most of these cells are of the same size, a few are noticeably smaller.

The nucleus is large, round, and placed nearly always in a very eccentric position. This position is most frequently on the side away from the neurite, but sometimes it may be very close to the neurite. Its diameter is about 16 to 19 microns in the largest cells of this age, and its outline is hard and round. The nucleolus consists of a single, or rarely double, plasmosome, which is a very little less than 5 microns in diameter, but which, when double or multiple, is of proportionally smaller size. As I have shown in the nucleus of the electric cells of several torpedoes, when a plasmosome is multiple its several parts, collectively, are larger in mass than is a single normal or usual plasmosome.

Of course, the nucleus was carefully examined as to any possible orientation of its nuclei, particularly the plasmosome, with reference to gravity or to the electric current or to the axis of the cell. Nothing of this sort could be found, although this does not preclude such a condition in the grown fish. It is known that in *Torpedo*, where such an orientation does exist, this same orientation is not found in the embryonic or larval stages.

From these cells thin, delicate axis-cylinder processes were traced down, as has been described, and into the ventral roots of the spinal nerves in a sufficient number of cases to assure the observer that they all ran in this direction. The process was thinnest shortly after leaving the cell, and became thicker as it approached the nerve-root. When it once entered the root it again became very thin, although now invested with a connective tissue and a medullary sheath. A large number of connective-tissue nuclei, nerve-sheath nuclei, and some unknown elements cause the motor-root of the nerve to swell to some size just after leaving the cord. It decreases again in size before it enters the foramen and leaves the vertebral canal in company with the much smaller dorsal root.

Just outside the canal the dorsal root ends in the spinal ganglion, and the motor-root traverses the inner side of the ganglion, from which it emerges on the lower edge, and at once divides into a dorsal and a ventral branch.

The ventral branch passes backward and downward (see text-figs. 8 and 9) to a point at a level with the lower middle spindle, and here it gives off a considerable group of fibers which pass caudad just inside of the spindle capsule. These fibers are joined by similar groups from others of the spinal nerves and the whole mass forms the lower middle electric nerve (text-fig. 8, N_3). At the posterior level of each electroplax this nerve gives off a few fibers (text-fig. 8, E) which branch out and innervate the posterior surface of this electroplax.

The remainder of the ventral branch passes farther down and again gives off a branch which goes to form part of the ventral electric nerve (text-fig. 8, N_4). This latter sends off little branches to furnish the posterior surfaces of the ventral electroplaxes with motor-fibers (text-fig. 8, E).

Going back to the anterior root, we find that its dorsal branch leads directly upward and, passing between the spinal ganglion and neural arch, slopes gently backward to give off a large branch which becomes a part of the upper median electric nerve (text-fig. 8, N_2). Its remaining fibers reach upward and furnish the dorsal spindle with a part of the fibers that form its dorsal electric nerve (text-fig. 8, N_1).

Of course, there are muscle-motor elements in both these branches of the anterior nerve-root, the number depending upon the position, backward or forward, at which we examine the arrangement. Two examples of the motor-nerve cells of the muscle-tissue from the cord in region D are shown in figure 14, plate 4, D and E . At the level of the anterior parts of the electric organ, when there are large quantities of muscle and the electroplaxes are very small, the muscle branches are large, particularly the dorsal branches, which have to supply the muscle-bundles for the large dorsal fin. In the posterior region of the tail, on the other hand, the muscle is almost entirely absent and the muscle-branches of the anterior roots are not even easily seen.

The eight (four on each side) longitudinal electric nerves are interesting in that they form a morphological buffer between the conflicting segmentation of the nervous, skeletal, and muscular systems, and the independent segmentation of the electric system. Were the electric segmentation to correspond with that of the others, we should not find these nerves in this recognizable form. In fact, in the anterior part of the electric organ we do not find them as continuous nerves, in many places, for more than two or three neuromeres at a time. And even posteriorly where they do form continuous nerves, the fibers that enter them from any given spinal nerve do not pass very far back in them before leaving to innervate one of the electroplaxes. Each nerve cell probably lies but a very short distance in front of the electroplax which it supplies. This was decided upon by plotting the relative positions of all motor-electric cells and all electroplaxes in the larger part of the organ.

While doing this it was also determined how many nerve-cells sent their nerve-processes to each electroplax. Thus, in region E of the 42-day-old larva there were easily counted 414 of the electric-motor cells, while in the same part there were 81 electroplaxes. This makes it quite sure that, on an average, about 5 of the nerve-cells were used for each electroplax. It was attempted to count the nerve-fibers as they left the electric nerve to branch out over the electroplax, but the elements were too small and the fixation not just what was needed to do this. It could be easily done in a grown specimen.

I shall now take up the structure of the nerve-fibers as they leave the

electric nerves to pass to the electroplaxes, assuming that they have no peculiarities of interest during their course through the nerve-tracts between the cord and the electric chambers. (The electric chambers are not divided as in *Mormyrus* by a transverse septum of heavy, opaque, white connective tissue; this can be explained by the fact of their secondary segmentation.)

As the few fibers destined for any particular electroplax first leave the electric nerve they are directed caudad and are very small in diameter and invested with a fine connective-tissue sheath. This covering is probably medullated in the grown fish. They quickly turn in a gentle curve whose diameter is about half that of the spindle and pass forward through the electric connective tissue to the posterior surface of the electroplax. At the beginning of this curve, or just after leaving the electric nerve, the axis cylinder or neuraxon enlarges to a considerable diameter and becomes very wavy and irregular in diameter. Its course is no longer straight, and it is not possible to find a section of any considerable part of its length, except in some very few cases. Its sheath of connective tissue is loose fitting and the inner side shows a loose reticulum of fine fibrils and plates that form a weak connection between the axon and sheath.

It is at once apparent in the maze of fibers which approach the electroplax that the few neuraxones which first entered the compartment are now many in number. Still, it is difficult to see where they branch in the thin sections, owing to their sinuous and irregular courses and to the large numbers of transverse and oblique sections present. In several places this branching was seen, however, and recognized as the same multiple branching which has often been described in the terminal part of nerve-paths and, in particular, in the same comparative region of the electric tissue of *Raja* by Ballowitz (5) and Retzius (26), in *Torpedo* by several authors, and especially in *Malopterurus* by Ballowitz (4), who refers in this article to many other cases. The writer has also seen and figured it in the electric tissue of *Astroscopus* in a paper soon to appear. In the present case, one section, as can be seen in figure 16, plate 5, exhibits two cases of this branching, one of them showing a single fiber dividing into at least three or four branches; also, figure 25, plate 9, in which there is to be seen a well-defined single fiber dividing into two branches just before they end in two club-shaped nerve-endings in the electric layer of the posterior surface of an electroplax. The abundant nodes of Ranvier, described by Schlichter (30) in the case of *Mormyrus*, were not observable here, probably on account of the lack of osmic-acid fixation. I have no doubt that they are present and they must be present at the points at which the fibers divide.

As has already been stated, the fibers now approach and end on the posterior surface of the electroplax, as well as on the lower sides of some of the papillæ that arise from it. The mode of ending is not difficult to see, apparently, although this much studied and controverted question should not be approached lightly, especially where the material is merely a sublimate-acetic fixation stained with iron-hæmatoxylin and eosin.

The nerve-process, carrying its connective-tissue sheath until it actually reaches the surface of the electroplax, ends in a blunt and somewhat thickened knob which is embedded in a hollow or invagination in the substance of the posterior cytoplasmic or electric layer of that structure (see figs. 18 and 19, plate 6; also fig. 16, plate 5; also figs. 24 and 25, plate 9). This knob may be quite elongate in form and in some cases appears to be branching. The nerve fiber becomes very narrow and apparently dense just before entering the cavity, but it quickly broadens out, to as much as or more than its previous width, to fill the cytoplasmic cavity of the electroplax. Its substance becomes very light-staining, more so than any other part of its length is, and this light-staining quality is most apparent at its extreme distal end in the cavity. The nerve-fibrils, faintly visible in the outer courses of the axon and rather more so in the denser neck just before entering the cavity, can be seen in the light-colored club-shaped ending to be running in an irregular reticulum instead of in their previously almost straight and parallel manner. They could not be traced into the protoplasmic bridges between the club-shaped nerve-ending and the surface of the protoplasmic cavity in which it lies. In very few instances did the nerve-substance fill the recess in the electric layer tightly, probably owing to some shrinkage in both of the tissues. The small space between the two surfaces is crossed by the numerous fine processes or strands, mentioned above, of some of the nerve-tissue remnants, probably of an original closer contact.

The question now arises as to whether the cavity or depression which the nerve-ending occupies is to be considered as an invagination of the surface of the electric layer or as a real penetration of the electroplax by the nerve. I shall consider it as the former, because the surface of the electroplax appears not to be interrupted by the opening but to continuously follow the inner edge of the cavity all the way around.

The presence of a perceptible cell-membrane or electrolemma would assist in the solution of this question, but such an organ could not be demonstrated. The edge of the cytoplasm was sharp and definite, but no membrane was visible, either by its staining properties or by refrangibility. It possibly will be found in the adult organ. Nor was it possible to see the "Stäbchen" or rodlets which have been described in other electric organs by Ballowitz (3, 5) and his pupils (30). Some striated arrangement of the granular electrochondria or granules described previously was observable, but this constituted a fibrillar secretory striation, such as is seen in the surfaces of most cells that are undergoing exchanges of any kind. Here, again, we must await examinations of the adult electroplax before we can say if such "Stäbchen" are present; also if they are homologous with the well-defined rodlets found by Ballowitz in *Torpedo* and in *Raja*, and whether they are specific structures of any importance in the production of electricity.

Returning to the relation of nerve-ending to electroplax, we have practically decided that the nerve-club is embedded in an invagination of the surface rather than in a cavity in the substance of the electric layer.

In doing this it has formed a much more intimate connection than may be seen in other places where the nerve-fibers touch the electroplax very closely, even being partly embedded in it, or running through the fundus that lies between two papillæ, where the fiber is closely pressed on three sides by the surface of the electroplax. In these fiber contacts the connective-tissue sheath persists, while in the club-shaped or heavily rounded endings the connective-tissue sheath is lost, left at the surface, and the little protoplasmic bridges, shown when slight shrinkage has taken place, testify to the intimacy of the contact. In addition a slight amount of fine, golden-colored granules surrounds the nerve-ending, lying on its surface, between it and the substance of the electroplax (figs. 24 and 25, plate 9). These granules are not found on any other part of the nerve surface.

Naturally the paper of Schlichter (30) was carefully examined to see what he had found as to the ending of the electric nerves on the related form, *Mormyrus oxyrhynchus*. He had adult material, but otherwise was no better off than the writer in the possession of material which had been treated especially for neurological study. He describes the nerve-fibers with their medullary sheaths as coming in contact with the large process of the electroplax and then suddenly ending just as they reach certain large indentations of the surface of this electroplax. He found in these indentations only a little coagulated material and some nuclei.

The writer has no doubt that the slight coagulum represents what remains of a club-shaped nerve-ending similar to that which he finds in *Gymnarchus*. The nuclei, from their position in Schlichter's picture, are evidently the nuclei of terminal connective-tissue coverings. If this idea be correct we will have a very simple but interesting form of nerve-ending, much larger in size than that found on any muscle or any other electric organ and one in which it will be, apparently, easier to study the intimate contact of nerve-substance with motor-substance from a cytological point of view than in any other form. In particular, we should try to stain these endings with the nitrate of silver and methylene blue methods devised for neuro-cytological studies. This work, however, can be undertaken only on the ground, with good laboratory facilities and with an abundance of fresh material.

The writer has published observations on some peculiar horizontal, pointed rods, or pointed threads, found imbedded in the electric layer of the electroplax of *Astroscopus*. At that time he suggested that they might be in some way homologous with or related to the "Stäbchen" because of the absence of any other well-defined "Stäbchen" in this fish. Such structures are not found in the present *Gymnarchus* larva, but they have been seen and described in *Raja*, in a paper soon to be published. Their presence in *Raja*, in addition to the "Stäbchen," proves them to be entirely different cell organs.

One word in regard to certain possibilities for the physiological study of the electric organ in *Gymnarchus*. A recent paper by Bernstein and

Tschermak and another by Bethe go to show that the electric discharge of *Torpedo* and other fishes is produced by different concentrations of sodium chloride in the electroplaxes and in the intervening electric connective tissue. Since there is a long series, theoretically, of these alternate segments of higher and lower degrees of concentration of the electrolyte, and since all the higher concentrations are presumably equal, and all the lower concentrations are equal, we would have a series of equal potentials alternately opposed to each other, and the result would be zero or else only the strength of one concentration current, in case there was one more or one less of either of the concentrations.

To obviate this difficulty a membrane has been imagined, on one surface of each electroplax, presumably the electric or nerve-ending surface (posterior surface in this case), which will be permeable only to one kind of the ions, either negative ions or positive ions, and by which the current is thus rendered integral in one direction.

Two things remain to be proved in connection with the above theory—the fact of different concentrations and the presence of such a membrane. This can be done in any fish in which it is possible to effectively separate the segments in a fresh state, so as to submit them to delicate chemical tests. In *Gymnarchus* we have a fish whose elements are larger than those in any other one of the seven electric types—large enough to be cut apart, I believe, and analyzed separately in the chemical laboratory; also large enough to submit anterior and posterior surfaces to physical tests that may show its permeability to either positive or negative ions and its impermeability to the other kind in one direction. This experimental work can most certainly be done if the proportion between the bulk of electric connective tissue and electroplax remains the same in the adult as in the larva (see fig. 23, plate 9). Fritsch shows much less of the electric connective-tissue segments in his figures of the adult organ.

Numerous other anatomical features of *Gymnarchus* have caused it to be classed with the other mormyrid fishes. This fact makes it of interest to compare its electroplax with the very different electroplax in these fishes.

That found in *Mormyrus oxyrhynchus* will serve as a type and its general plan has been well shown by Ogneff (25) and Schlichter (30). Here it is evident that a number of consecutive and entire myotomes have been converted into electroplaxes and that the middle layer of each electroplax is composed of unaltered and clearly striated myofibril bundles. The large number of these fibril bundles, and their distribution, indicate that the whole electroplax in *Mormyrus* is a syncytium composed of all or most of the cells which would otherwise have gone to make up the single myotome. In this we find an agreement with the electroplax of *Gymnarchus* which is also formed from several cells. In the one case, however, all the cells in the myotome have been used (*Mormyrus*); in the latter only those lying in eight particular localities (*Gymnarchus*). (See paper by Dahlgren (36).)

Further homology is seen in the disposition of the probably superfluous myofibrils. In both forms they are relegated to a middle position in the electroplax, while the apparently more important cytoplasm forms layers on the anterior and posterior surfaces of the structure. Also, in both, the now useless myofibril bundles are packed out of the way at right angles to the axis of the electroplax, which remains the same as the former axis of the muscle-cells that were used to form it.

The only difference lies in the fact that the striation of the fibrils is retained in the *Mormyrus* forms, while it is lost in *Gymnarchus*, the dark-staining anisotropic substance apparently dissolving away.

From what little can be predicted concerning the possible origin of the electric tissue in the other teleost forms, it is probable that the Mormyridæ (including *Gymnarchus*) are the only fish in which the electroplax is formed as a syncytium from more than one cell. In *Astroscopus*, *Electrophorus* (formerly *Gymnotus*), and *Malopterurus* the structures show every evidence of having been developed from single myoblasts with the exception of *Malopterurus*, where it is a question as to whether they are not evolved from gland-cells instead.

SUMMARY.

In conclusion it may be stated that—

(1) The electric tissues of *Gymnarchus* are developed by the differentiation of certain portions of its normal, striated muscle-tissues during an embryonic or larval period extending from the ninth day to the forty-second day of embryonic life. The critical period of this change takes place in the neighborhood of the eleventh, twelfth, to fifteenth days.

(2) The muscle fibers which go to form the electric tissue give up their usual segmentation into myotomes, and first form eight long and continuous spindles which afterward segment, each into a lesser number of masses, the electroplaxes.

(3) The myofibrils lose their transverse striation and form a large inner core for each electroplax. They lie in a wavy mass, mostly at right angles to their former course. The active cytoplasm forms an outer layer which is denser and stains deeper on the posterior than on the anterior surfaces. It contains granules.

(4) Each electroplax is made up of several muscle cells, 12 to 20 or more. This is different from the two elasmobranch fishes, in which each muscle cell forms only one electroplax.

(5) The nerve is distributed on the posterior surface and ends in blunt knobs that lie in cavities formed by the invagination of the surface of the electric layer. The current probably runs from tail toward head, as in *Mormyrus*.

(6) The development of the tissue gives a strong clew to the probable development of the electric tissues in the other mormyrid fishes.

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EXPLANATIONS OF THE PLATES.

PLATE 1.

- FIG. 1. Transverse section through body of 9-day-old embryo of *Gymnarchus* in region *C*. *L.M.*, position of the large muscle cells that will eventually change into the lower median electric spindle; *V.F.*, location of large vertebral fibers; *XXXX*, locations of electric spindles in an adult fish with reference to bony structures, blood-vessels, and spinal cord; *N*, canalis centralis; *B₁* and *B₂*, caudal blood-vessels. $\times 110$.
- FIG. 2. Muscle-tissue in transverse section from 12-day-old embryo of *Gymnarchus* to show typical muscle cells. *A*, one of oldest fibers with two strong fibril bundles; *B*, growing muscle cell with fibrils being laid down in a ring; *C*, extreme upper edge of myotome with youngest cells at top. $\times 1150$.
- FIG. 3. Transverse section through group of larger muscle cells found at *L.M.* in fig. 1. Under greater magnification. For explanations see text. $\times 1150$.
- FIG. 4. Longitudinal vertical section of *C* region in 9-day-old embryo, ventral portion. Between marks $\bigcirc \bigcirc$ are seen same parts of seven myotomes as are shown at *L.M.* in preceding figure in transverse section. Note heavy development of these cells. A line drawn between marks $\oplus \oplus$ would indicate location of seven groups of vertebral fibers in next few mediad sections.

PLATE 2.

- FIG. 5. Transverse section of body of 12-day-old *Gymnarchus* embryo in region *CC₁*. *D*, dorsal electric spindle; *U.M.*, upper median spindle; *L.M.*, lower median spindle; *V*, ventral spindle; *Conn.T.*, connective-tissue septum; *N*, canalis centralis. *B₁* and *B₂*, caudal blood-vessels. $\times 110$.
- FIG. 6. Three degenerating muscle cells from another (3) zone in fig. 12. $\times 1440$.
- FIG. 7. Electric spindle showing first stage where electric muscle cells can be called an electropilax. Complete coalescence has taken place. Nuclei are in peripheral layer. Myofibrils are concentrated in middle to form central fibrillar core of structure. $\times 1150$.
- FIG. 8. Transverse section of upper dorsal part of spinal cord in a *Gymnarchus*, embryo 9 days old. Neuroblasts, in region that will later show electric motor-cells, show some little differentiation and growth. Near, and above, this region is one of the transitory giant ganglion cells. $\times 940$.

PLATE 3.

- FIG. 9. Transverse section of left ventral spindle from region *C* in embryo of 12 days. To left of dotted line are normal muscle cells, to right are degenerating muscle cells, in the midst of which, and surrounded by dotted circle, are a group of muscle cells going through the first steps of transformation into electric tissue. $\times 1150$.
- FIG. 10. Transverse section of ventral electric spindle in process of formation in region *B*, of 12-day-old embryo of *Gymnarchus*. At left of figure two muscle cells begin to degenerate, while just to right of upper one of this pair a muscle cell is seen in advanced stage of atrophy. Connective-tissue capsule beginning to form. Electric muscle cells rather more coalesced than in fig. 9. $\times 1150$.
- FIG. 11. Transverse section of upper middle electric spindle in same section as fig. 10. Rapidly degenerating muscle cells to left. Further coalescence of electric muscle cells than in fig. 10. Myofibrils weakening but still in separate groups. $\times 1150$.

PLATE 4.

- FIG. 12. Longitudinal vertical section of dorsal part of region *D* of 12-day-old embryo of *Gymnarchus*, showing relations of muscle tissue and electric tissue. Bracket 1 indicates zone of degenerating muscle fibers on inner median edge of five myotomes, on ventral side of median connective tissue; zone 3 shows atrophying muscle fibers on inner median edge of myotomes, dorsal of median connective tissue; zone 4, rudiment of upper median electric spindle; zone 5, same of dorsal electric spindle; zone 6, muscle tissue from ventral spindle to dorsal outer edge; zone 7, connective tissue; zone 8, dorsal epithelium. $\times 140$.

FIG. 13. Longitudinal vertical section of ventral part of region C of 12-day-old embryo of *Gymnarchus*. Zone 1 indicates ventral epithelium; zone 2, ventral outer portions of five myotomes; zone 3, lower median electric spindle which is dividing into three parts in five vertebral segments; zone 4, inner degenerating muscle fibers of five myotomes; zone 5, projected outline of vertebral segments. $\times 140$.

FIG. 14. Motor nerve cells from spinal cord of 42-day-old larva of *Gymnarchus*. A, B, and C, three electric motor nerve cells. D and E, two muscle motor nerve cells. From region E. $\times 1500$.

PLATE 5.

FIG. 15. More highly magnified part of fig. 12. Brackets indicate same zones. $\times 760$.

FIG. 16. Highly magnified part of transverse section through an electroplax from C region of 42-day-old larva of *Gymnarchus*. Curving bundles of modified myofibrils are seen in core and cut at various angles. Outer or electric layer is fixed and stained to show finer outer granules or electrochondria. Vacuoles as well as larger meshes of the linom are visible on inner edge of electric layer. Electric nerves are cut in sections at many angles and show medullary or connective-tissue sheath and its nuclei. At two points branching of these nerve fibers is visible and at four points its contact with electric layer of electroplax is to be seen. $\times 1500$.

PLATE 6.

FIG. 17. Longitudinal section of a young electroplax from B region of 12-day-old embryo. Segmentation of electric tissue is now complete into unit electroplaxes of which figure is good example. Central fibril bundle beginning to lose its transverse striation. Structure is as long as three muscle segments or bony segments, as near-by spinal processes show. This represents oldest stage in embryo of this age. $\times 210$.

FIG. 18. Longitudinal section of young electroplax from C region of 42-day-old larva of *Gymnarchus*. Fibrils have lost all striation and become waved in middle part. Cytoplasm shows strong differentiation at two poles (ends). Anterior end strongly vacuolized. Papillae begin to grow from ends of middle part and nerve-endings have become established at junction of posterior third with middle third. This shows youngest stage in 42-day-old larva and is a successively later step in differentiation than fig. 17. $\times 210$.

FIG. 19. Longitudinal section of an electroplax from E region of 42-day-old larva of *Gymnarchus*. Fibril bundle much "waved" in middle third, which now begins to show form of electroplax. Papillae more developed. Nucleus and some cytoplasm inclosed in fibrillar core. $\times 210$.

PLATE 7.

FIG. 20. Longitudinal section of another electroplax from further caudad in E region of same larva of *Gymnarchus*. This represents oldest stage accessible and is regarded as almost adult in its histological characteristics. Two nuclei shown in fibrillar core; one of these shows characteristic swelling.

PLATE 8.

FIG. 21. Transverse section of body of 42-day-old embryo of *Gymnarchus* from D region. Greater part of muscle tissue is here transformed into electric tissue. Section passes through very last part of dorsal fin. Electroplaxes cut at different levels and in one case section passes through right ventral spindle showing only electric connective tissue. D, dorsal spindles; U.M, upper middle spindles; L.M, lower middle spindles; V, ventral spindles; B₁ and B₂, caudal blood-vessels; N, neural canal. N₁, N₂, N₃, and N₄, electric nerves; N₅, lateral line nerve. $\times 110$.

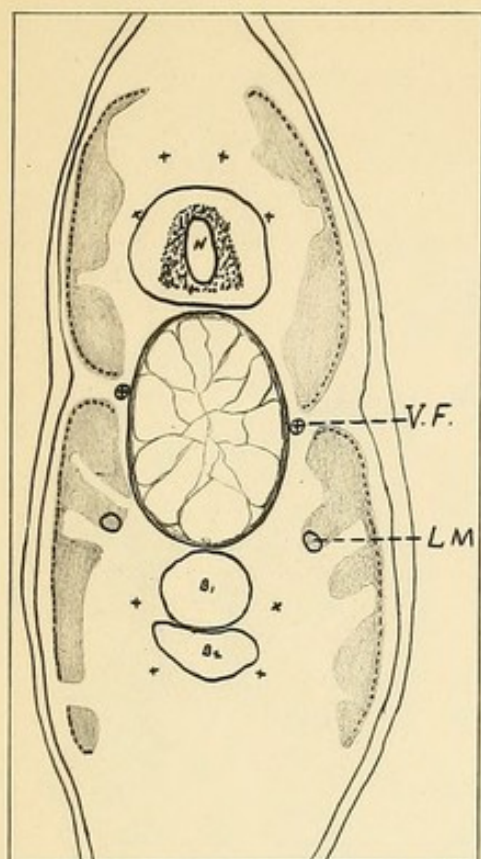
FIG. 22. Part of transverse section from middle part of an electroplax in E region of same larva of *Gymnarchus*. This figure serves well to show larger granules that lie deeper in electric layer, also connective-tissue sheath or wall of electric spindle. $\times 1500$.

PLATE 9.

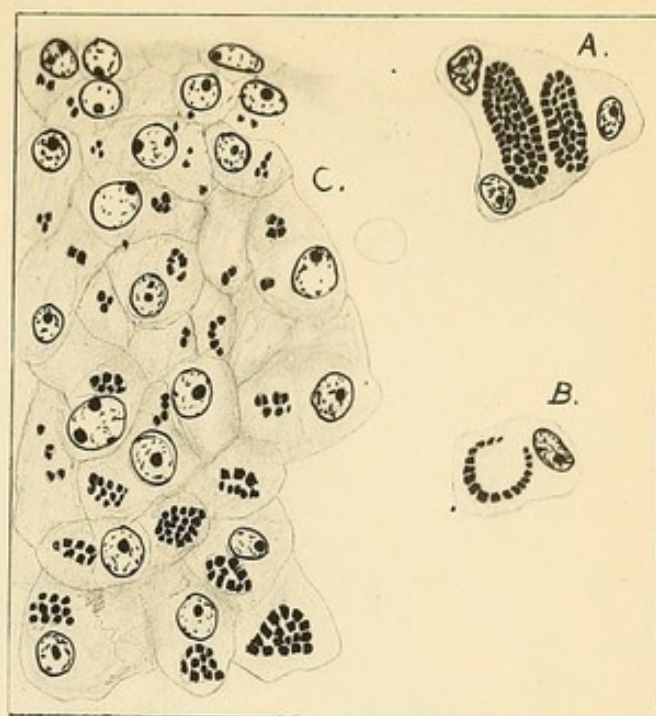
FIG. 23. Longitudinal section from E region, showing parts or whole of 11 electroplaxes lying in dorsal, upper middle, and lower middle spindles. Some remaining muscle fibers are visible at sides. Figure serves to show that there is no heavier, transverse connective-tissue wall lying in electric connective tissue, as is found in *Mormyrus*. This emphasizes secondary segmentation found in *Gymnarchus*. $\times 110$.

FIG. 24. Small part from edge of basal part of a papilla on posterior surface of an electroplax from *C* region of 42-day-old *Gymnarchus*. Shows a single nerve, ending in a somewhat elongate and branched end-plate in electric layer. Outer crowded mass of granules stained deeply with eosin; larger inner granules not stained. $\times 1500$.

FIG. 25. Small part of edge of another part of anterior surface of same electroplax. Shows a nerve fiber dividing and each branch ending in typical club-shaped nerve ending of *Gymnarchus*. $\times 2200$.



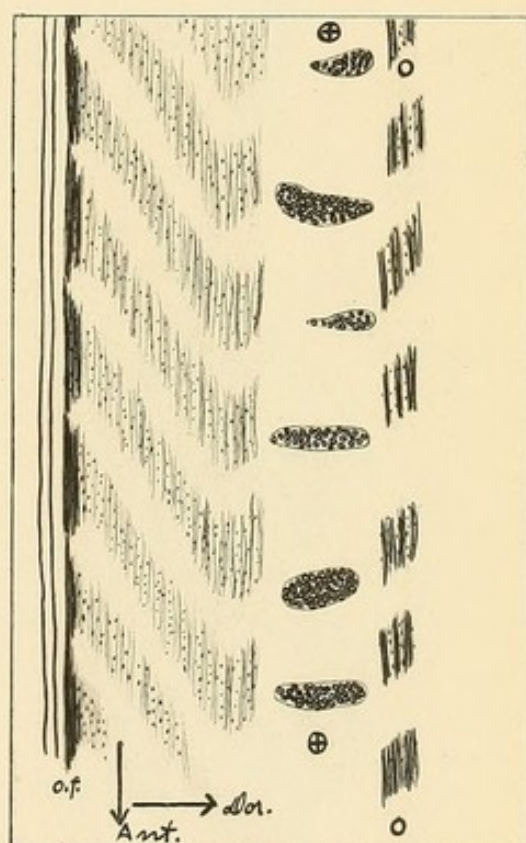
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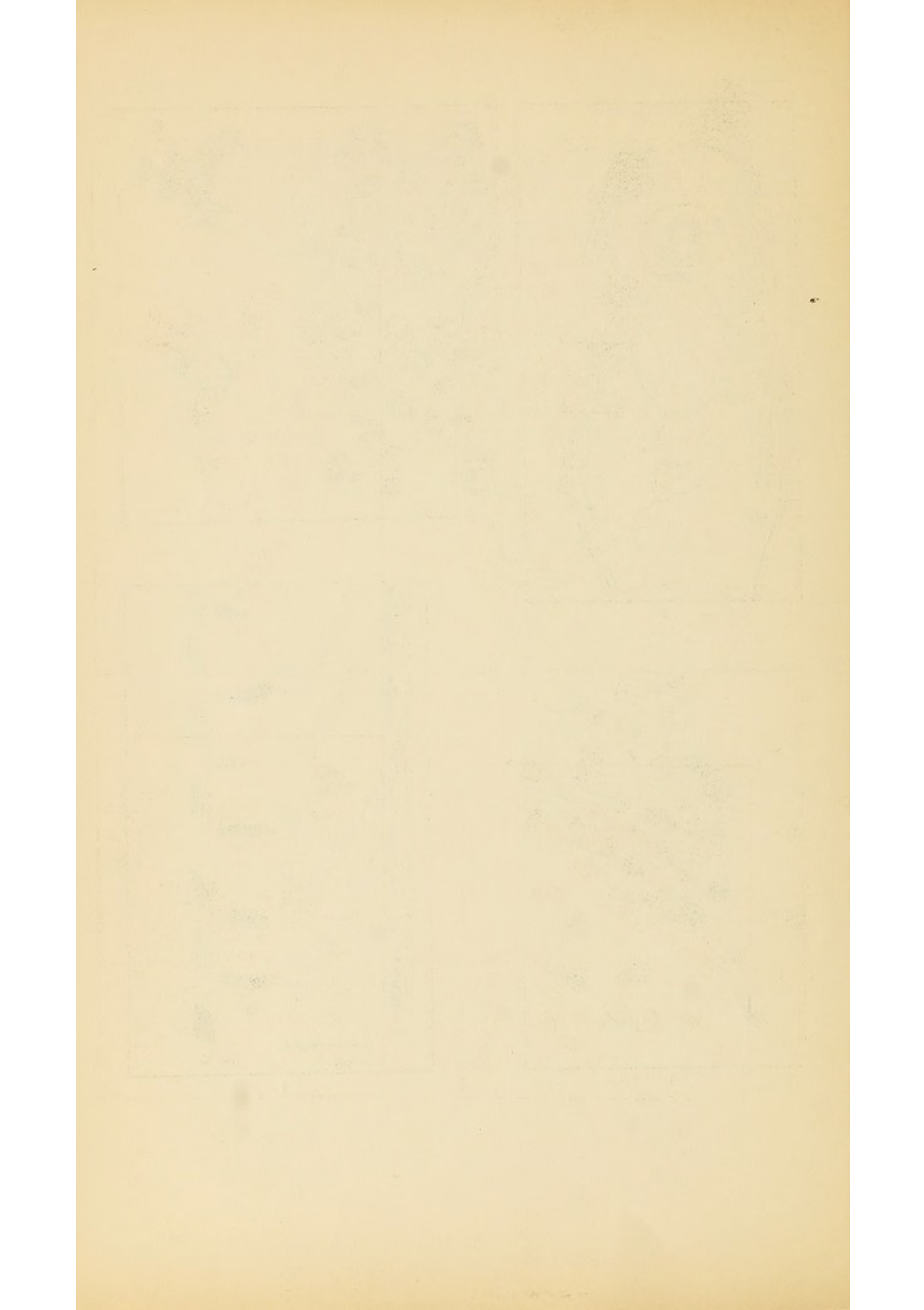
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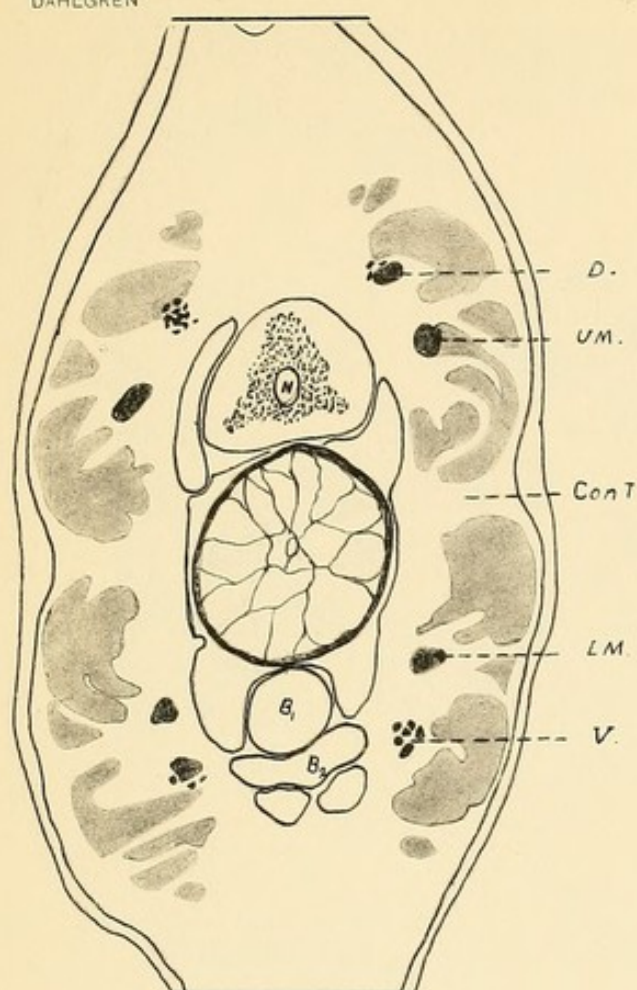


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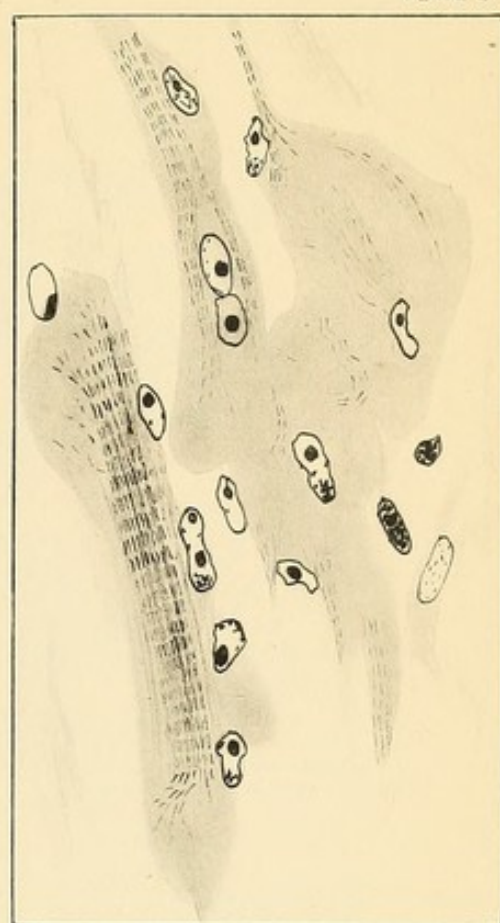


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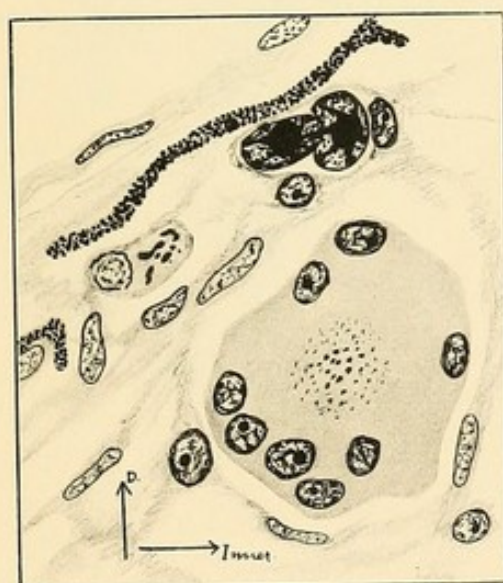




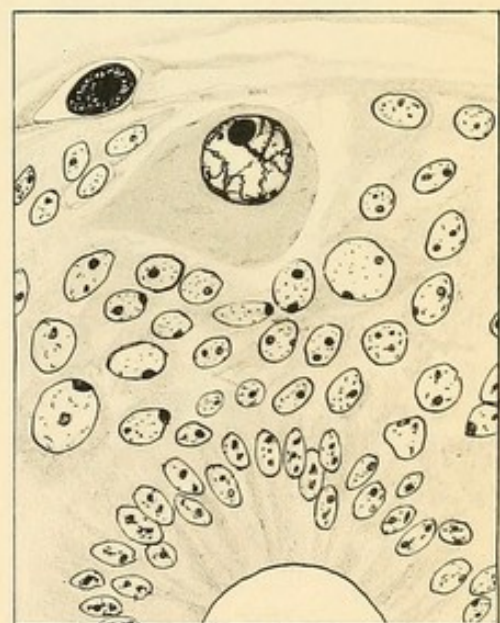
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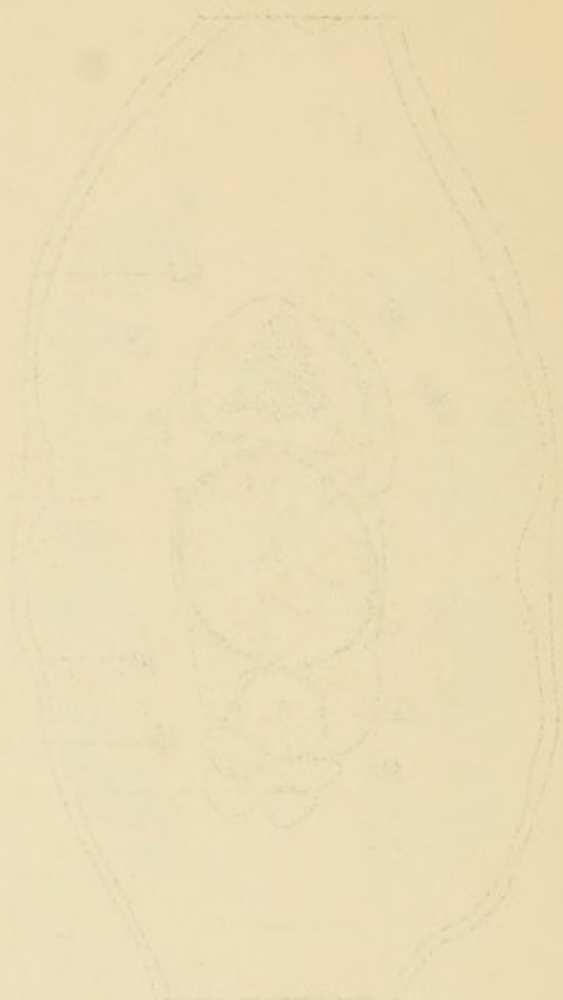
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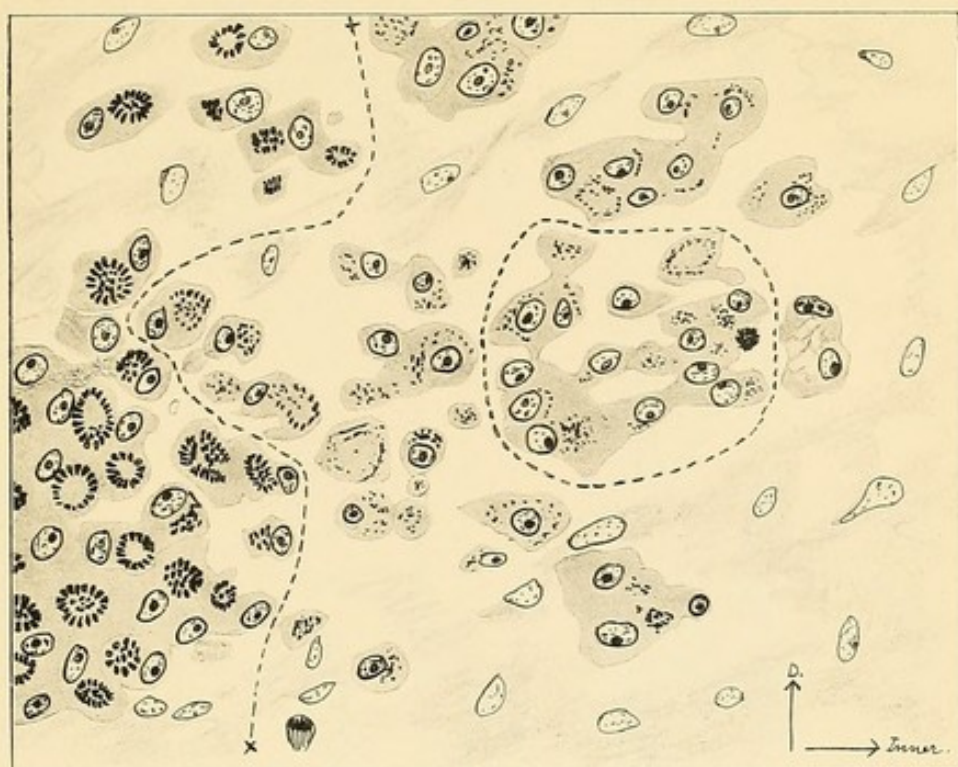


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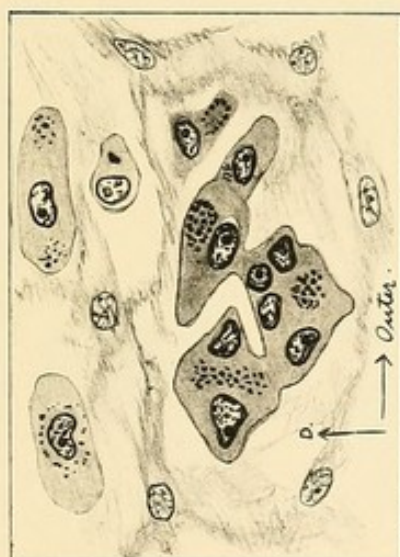


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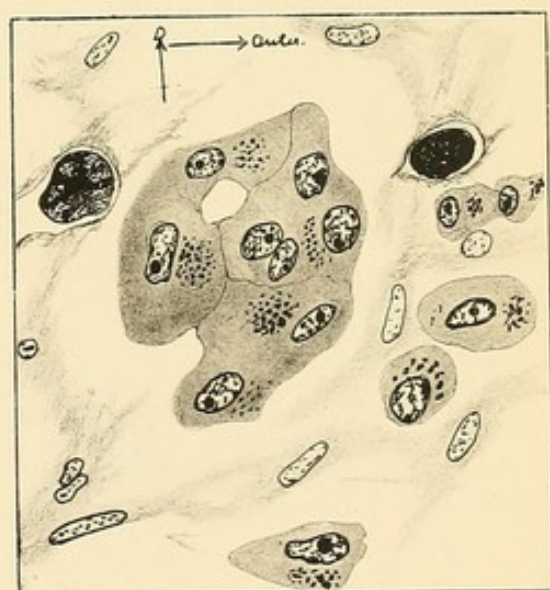




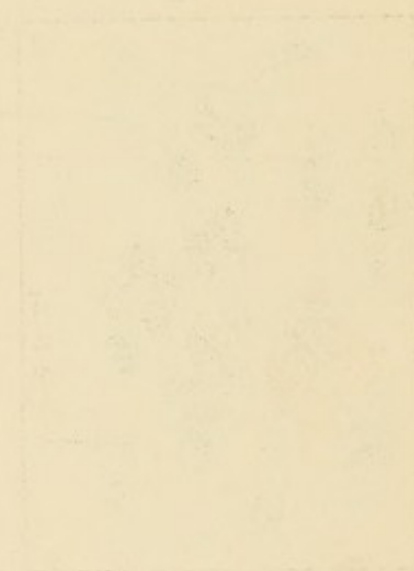
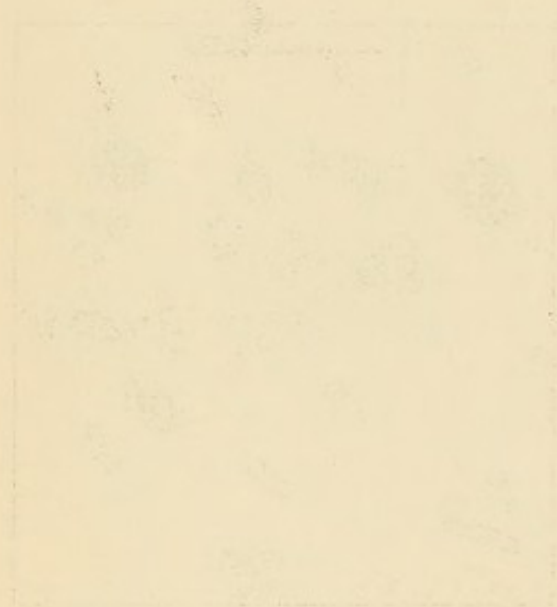
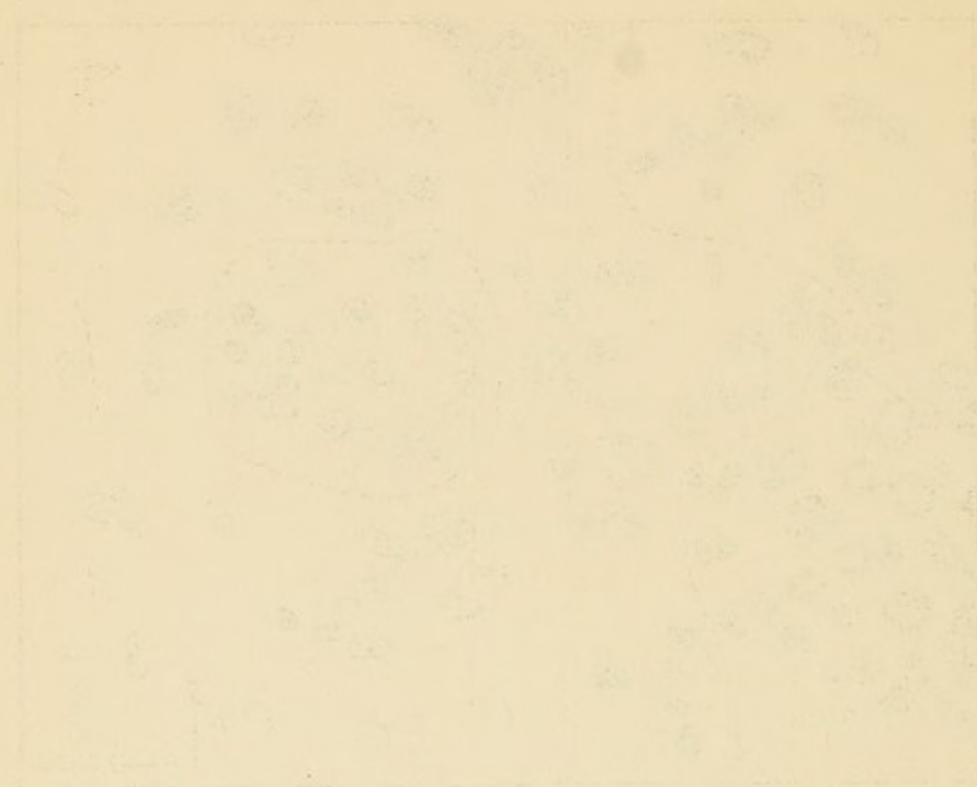
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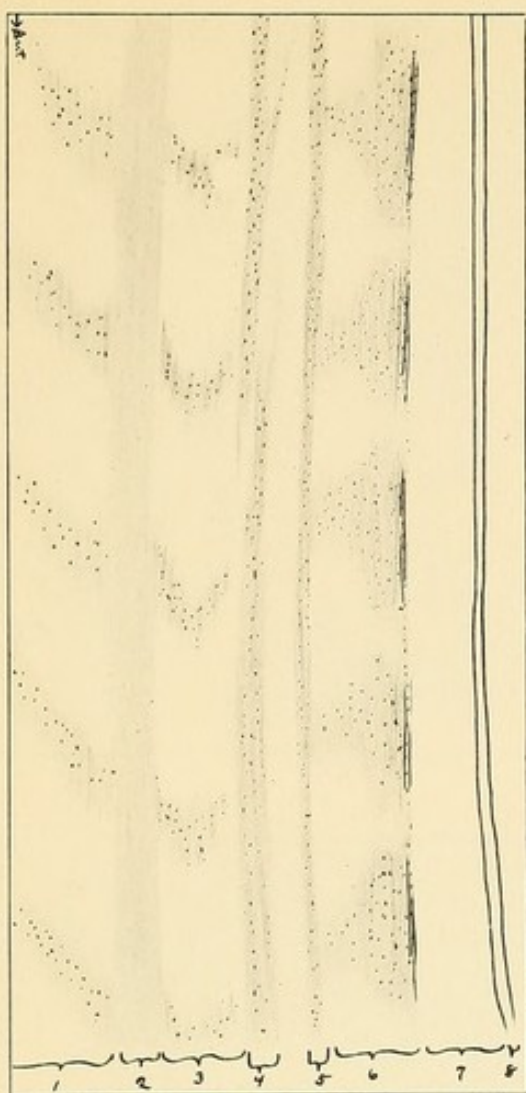


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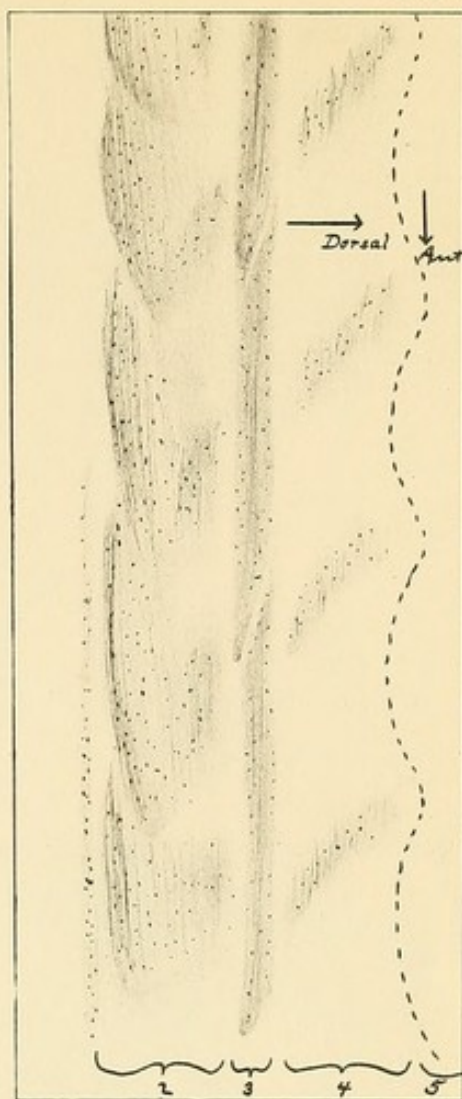


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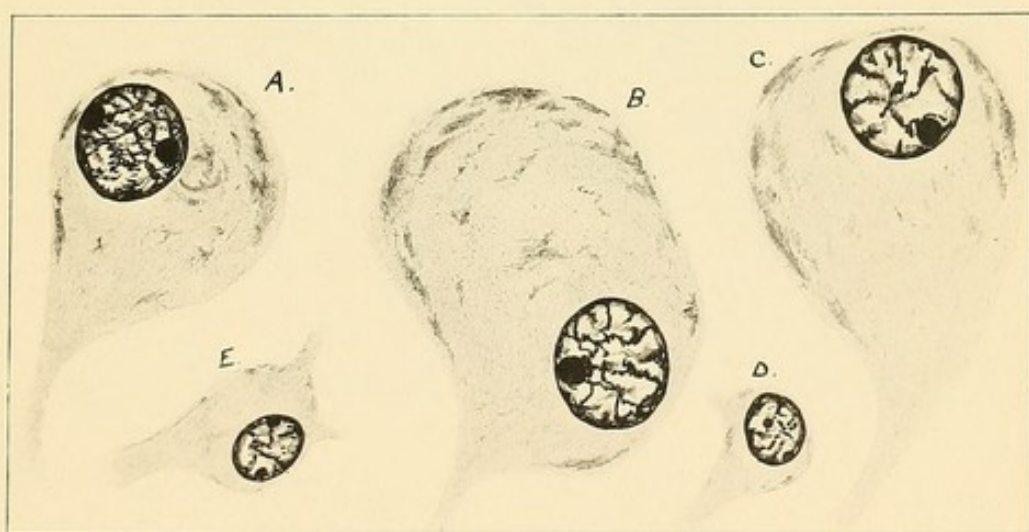




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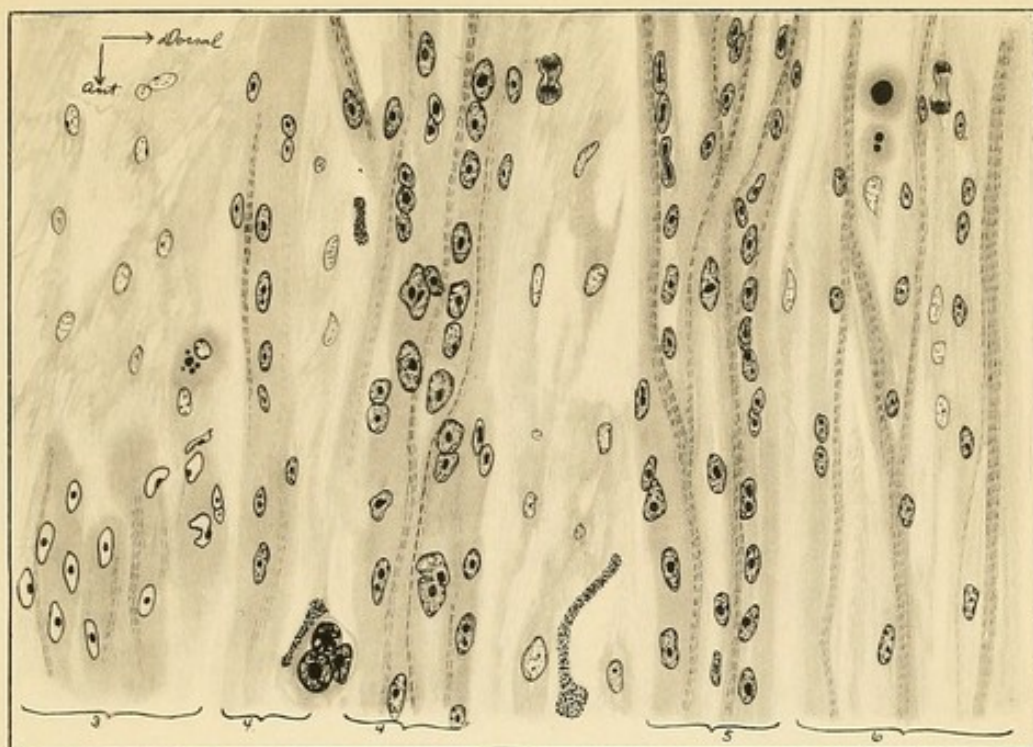


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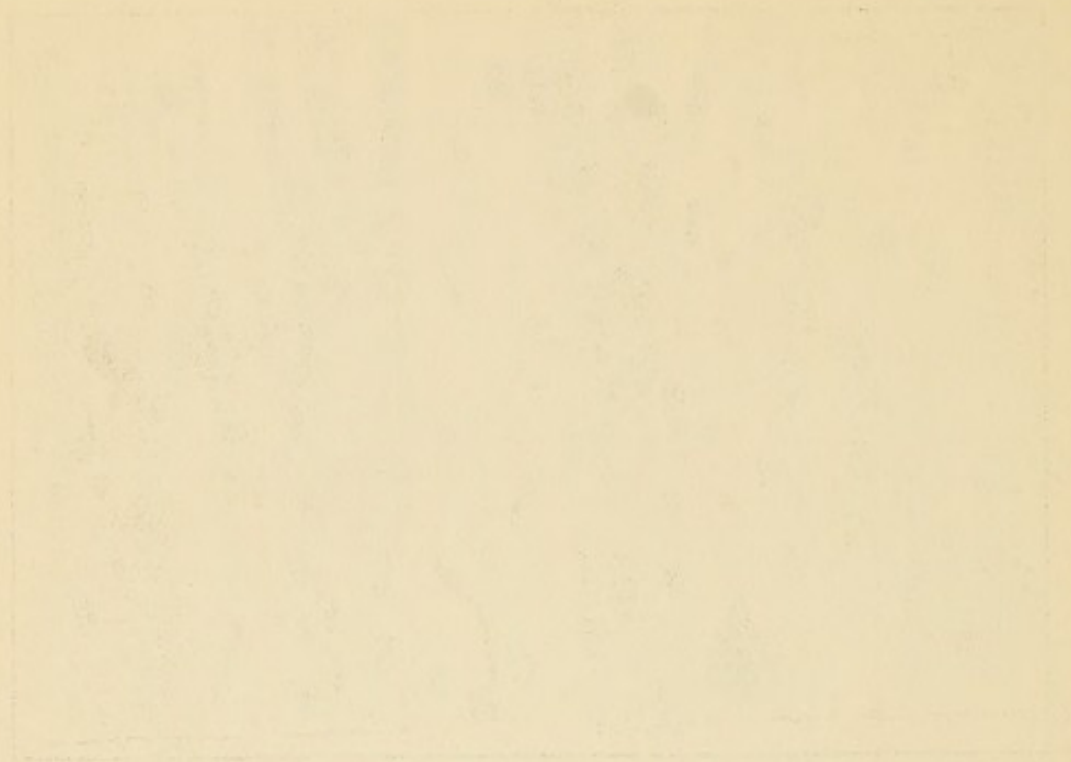


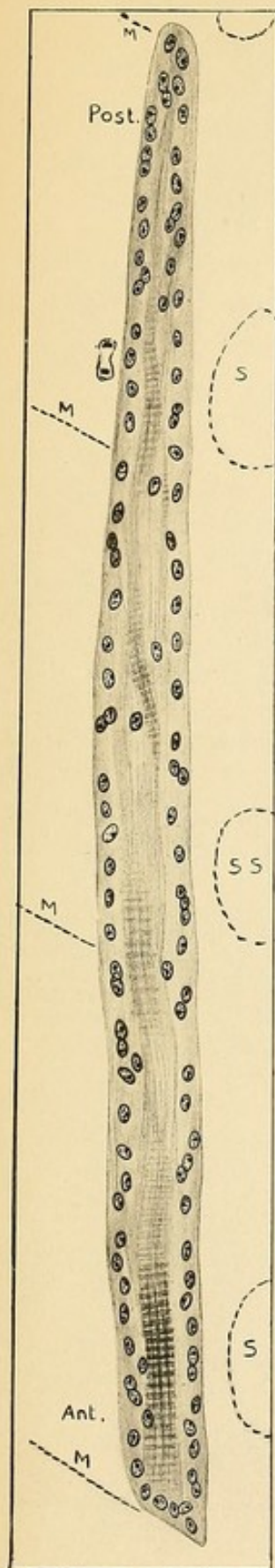


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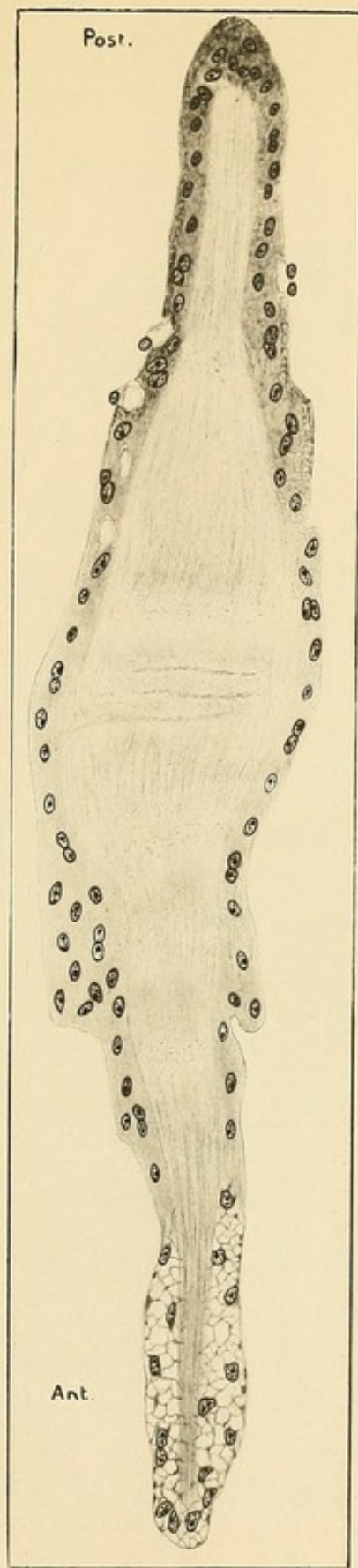


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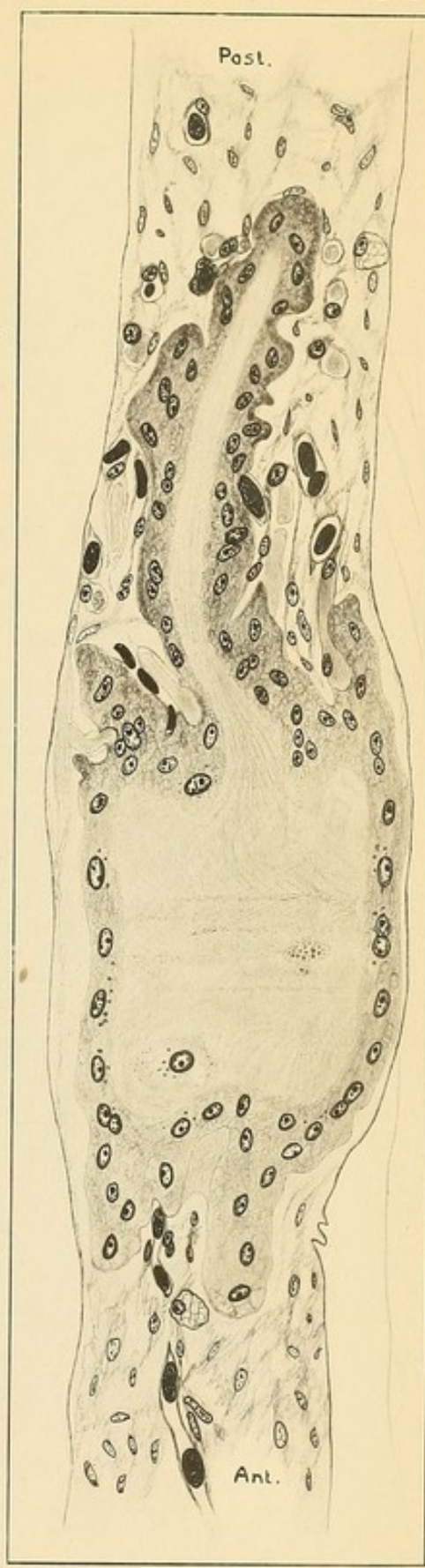




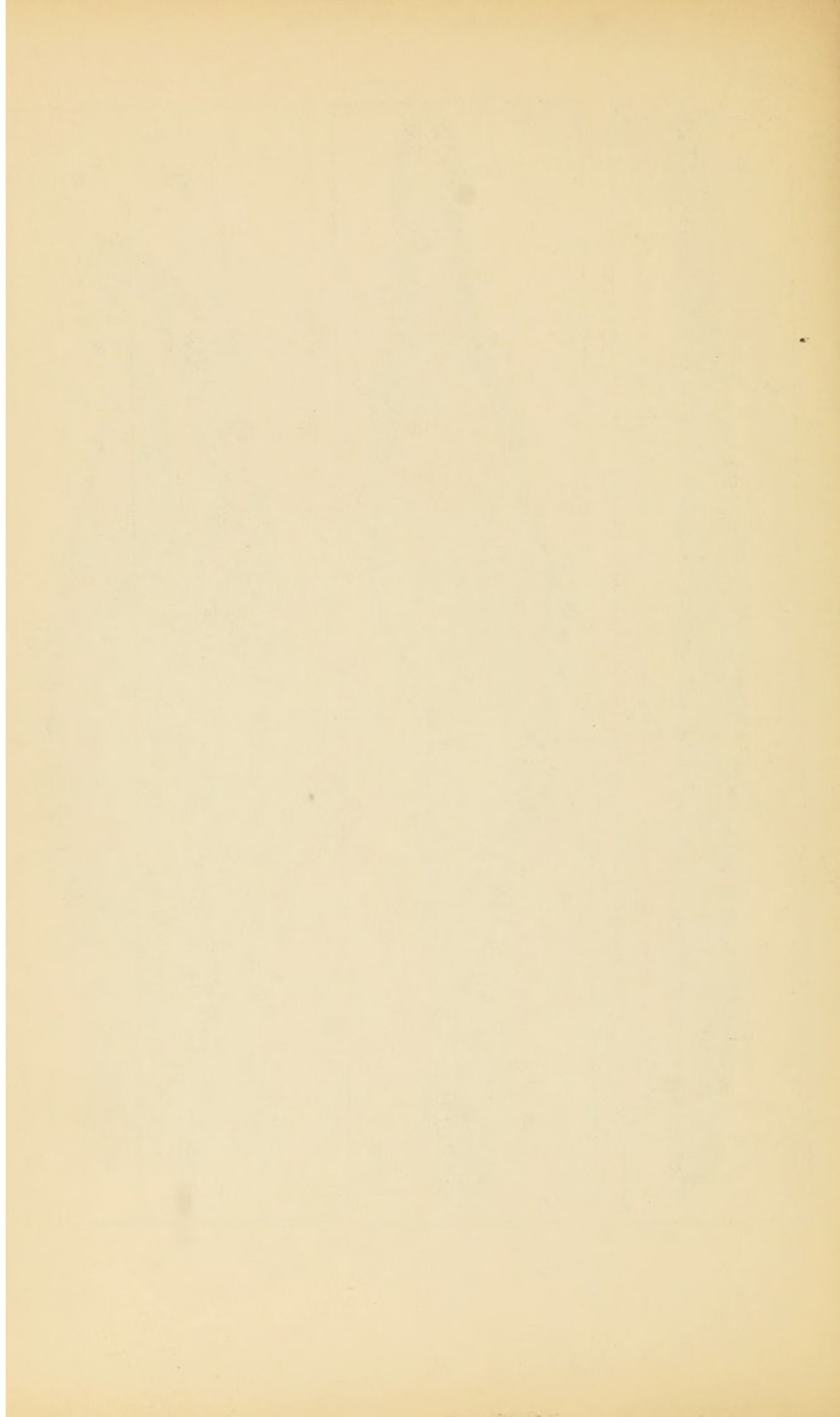
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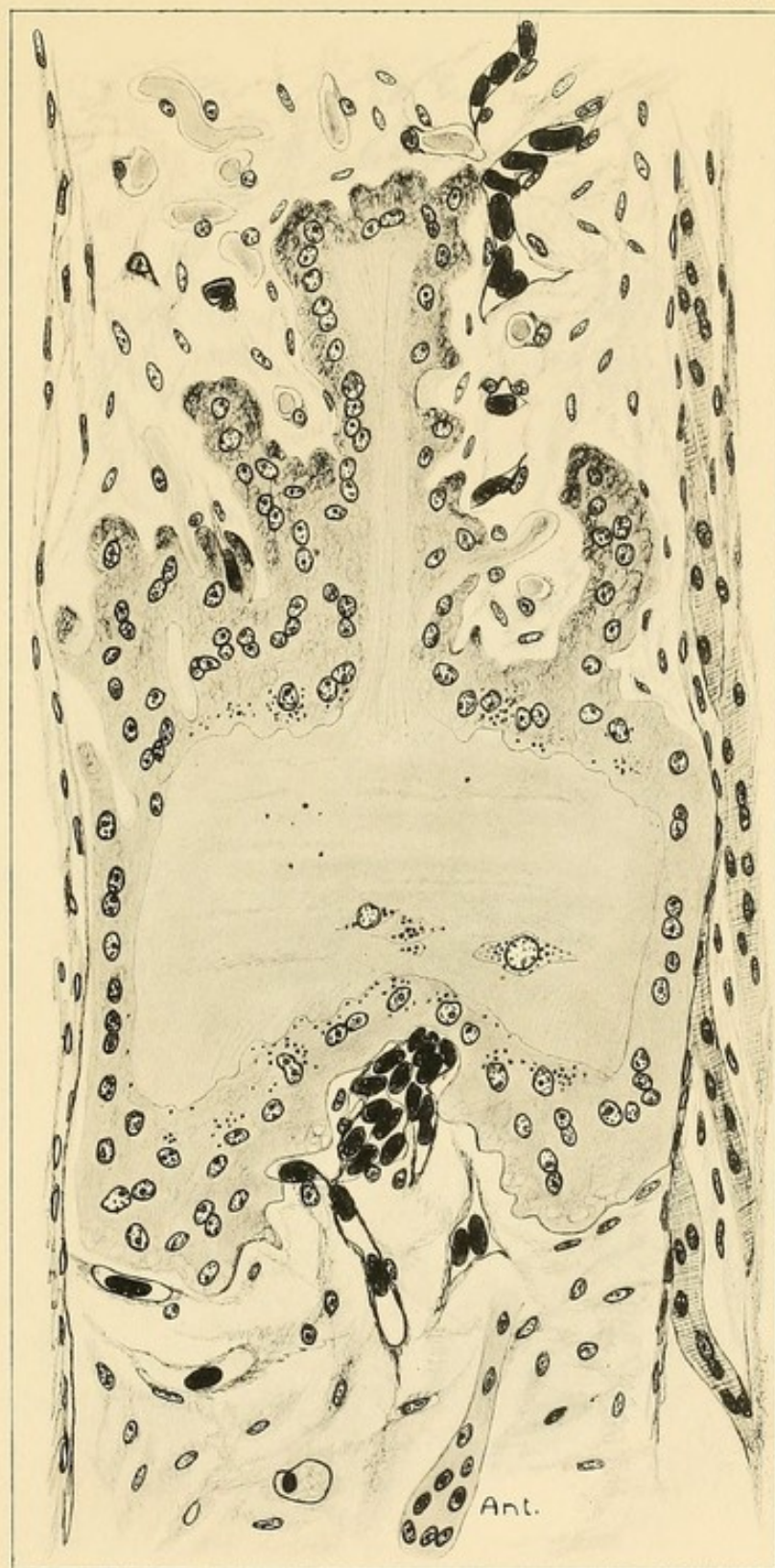


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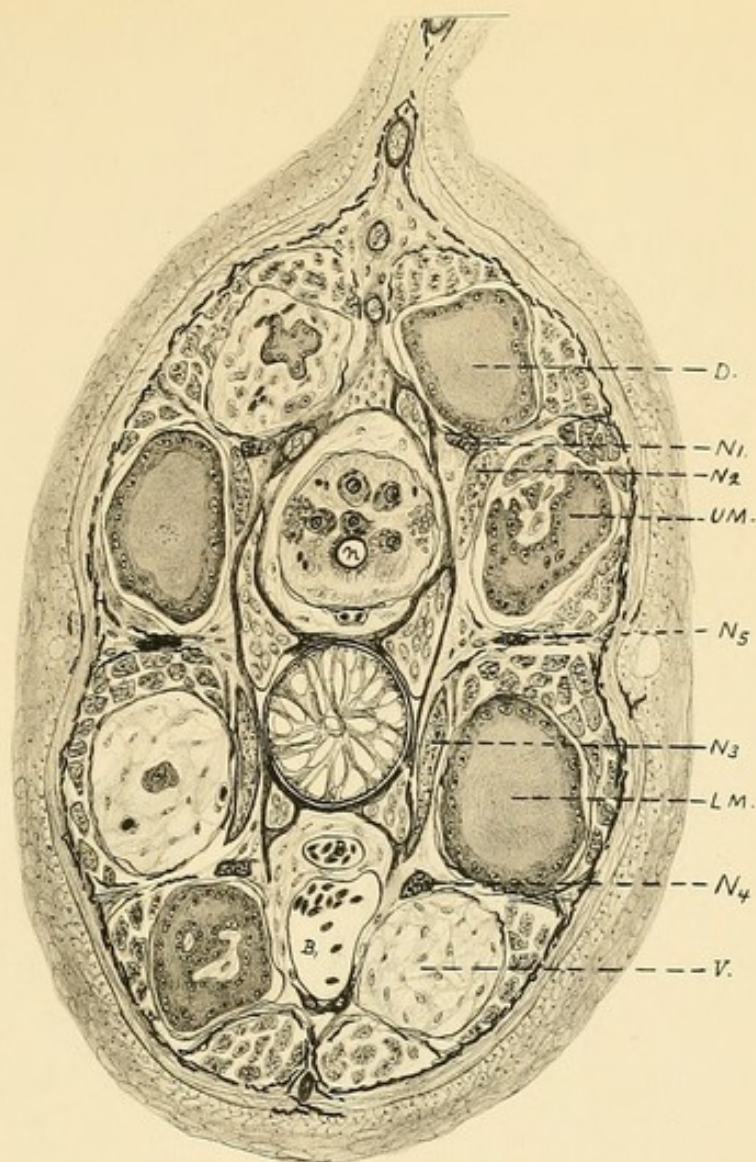


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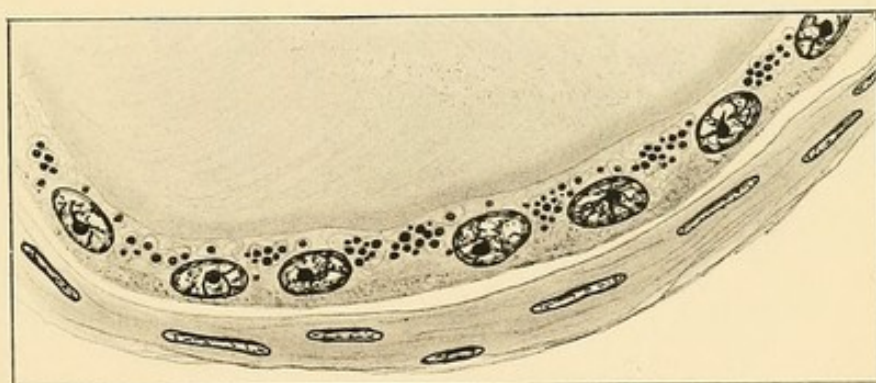




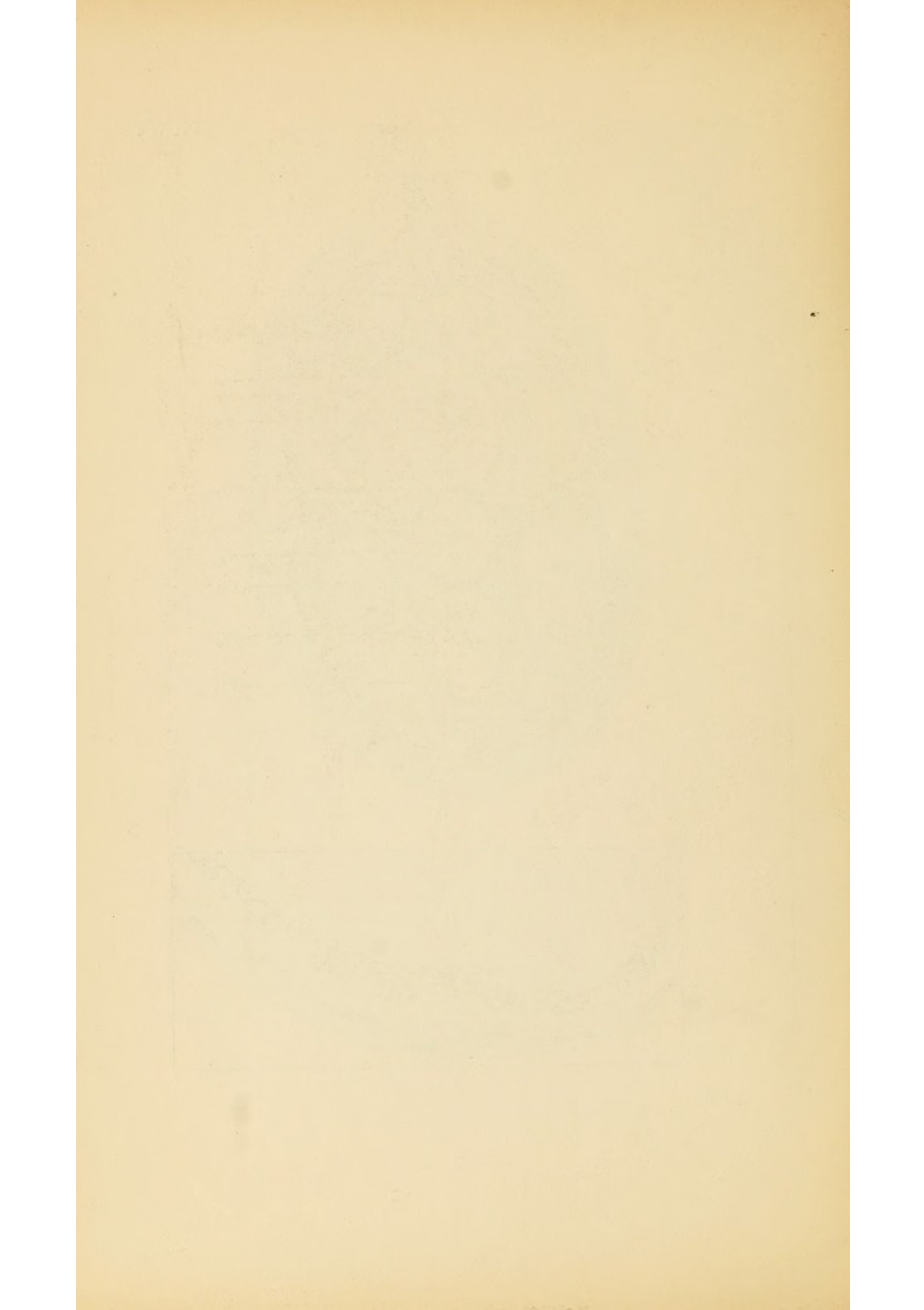


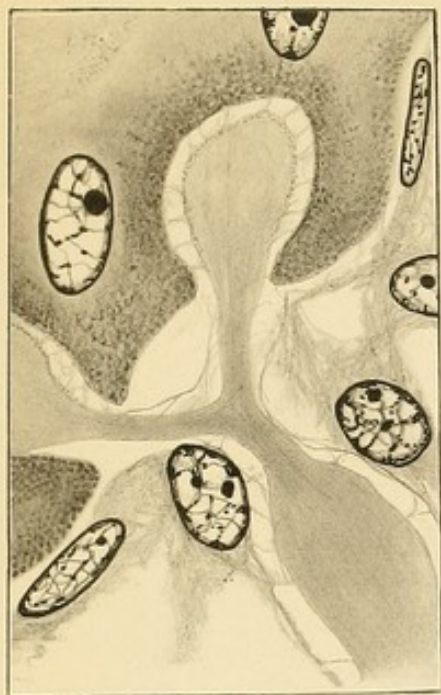


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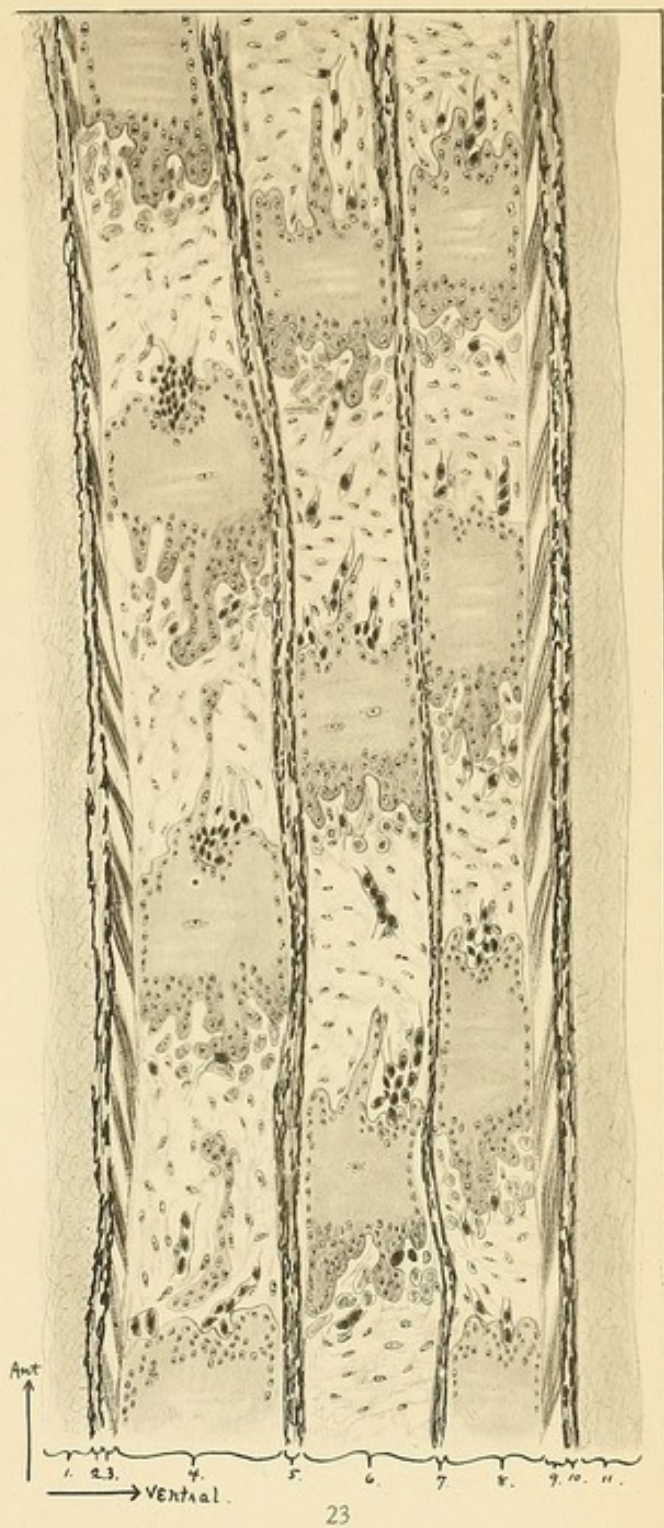




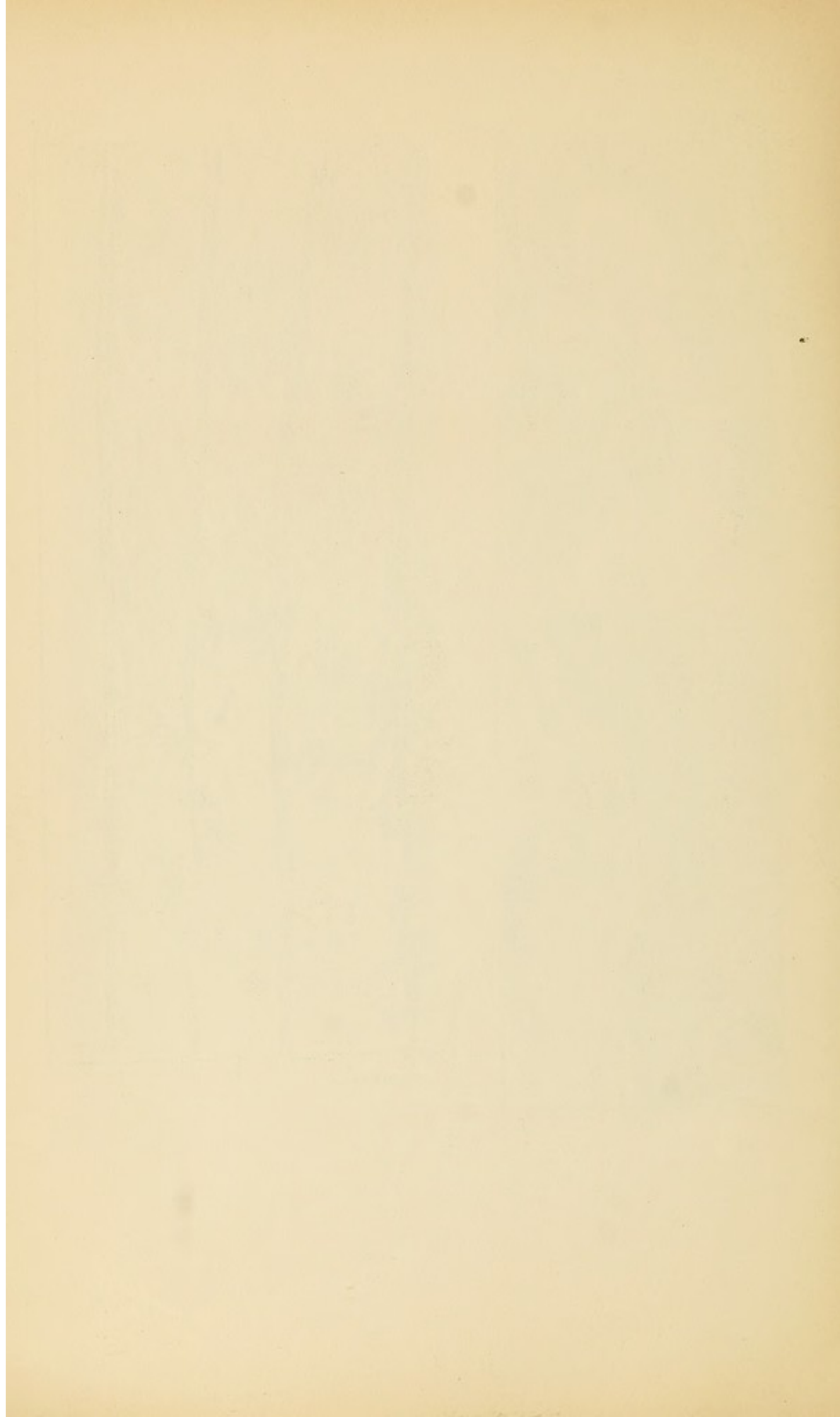
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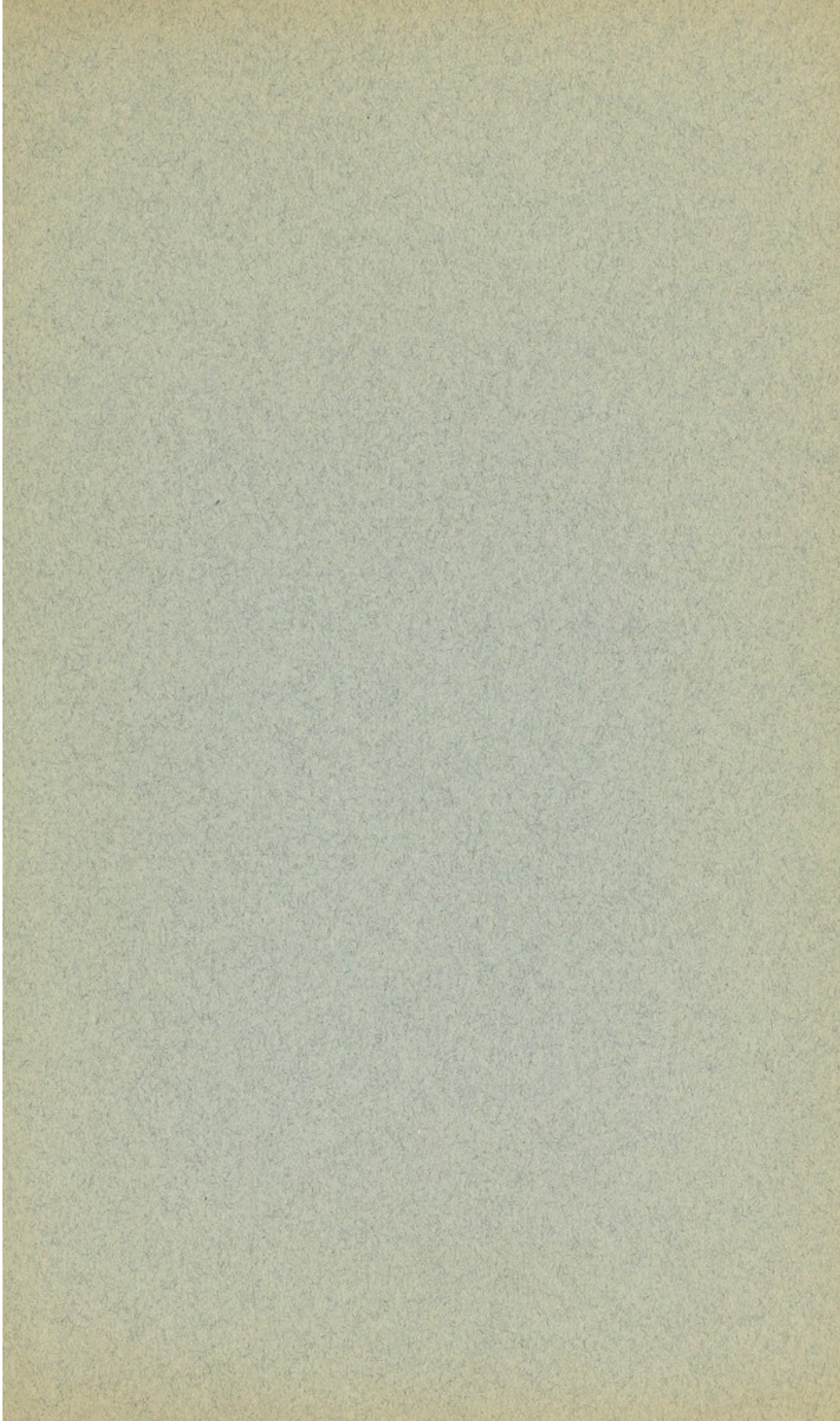


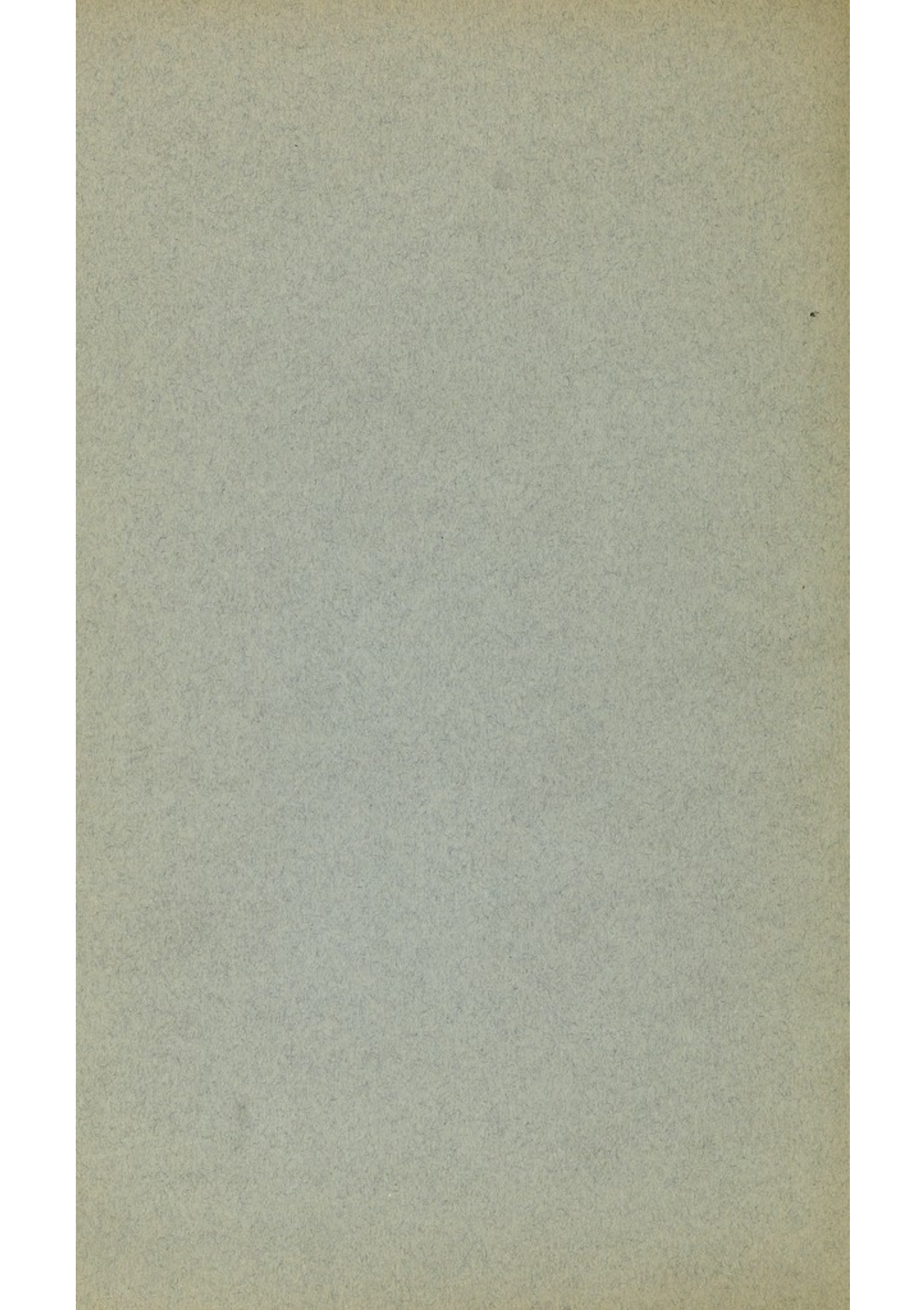
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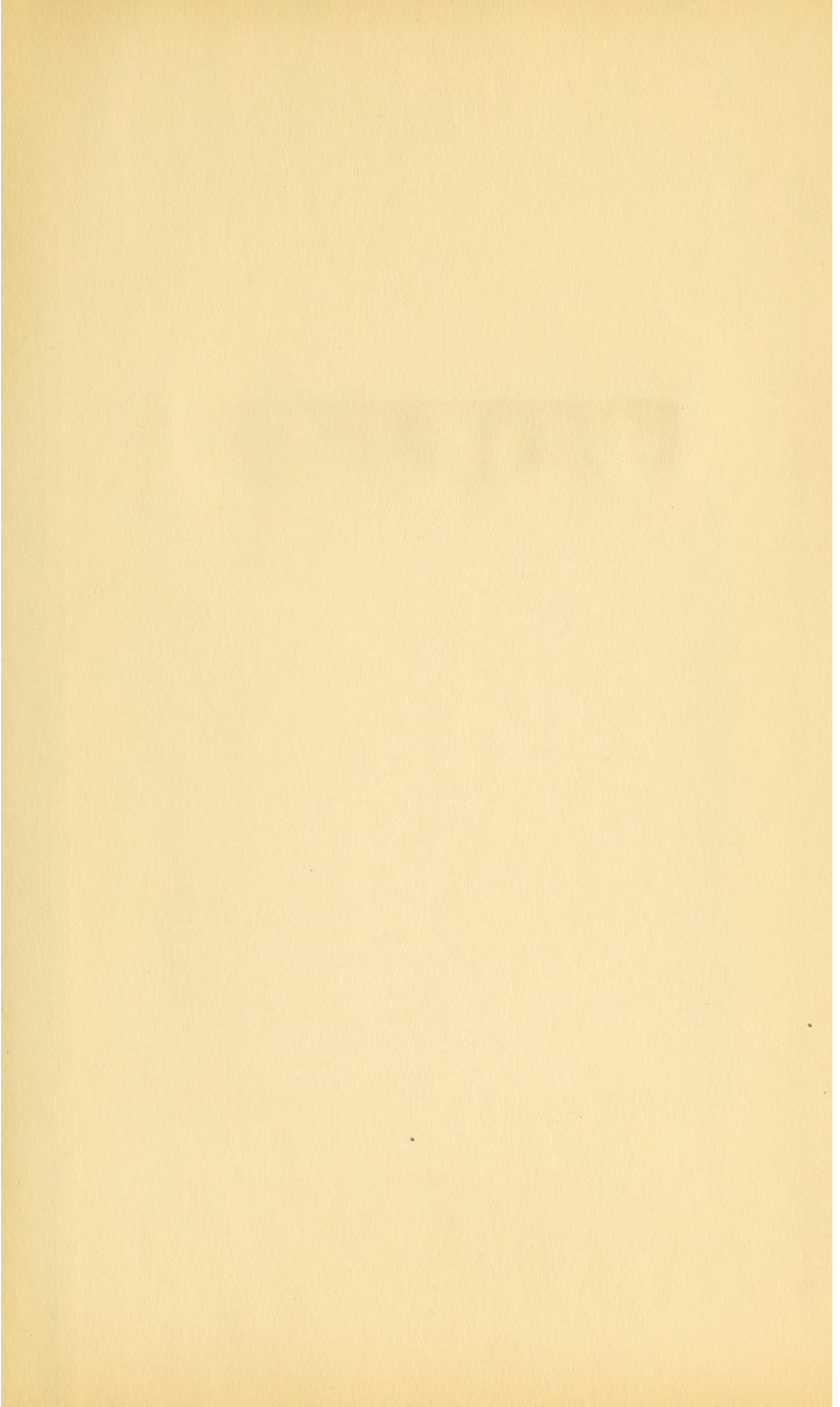


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