

X. *The Electric Organ of the Skate.—Observations on the Structure, Relations, Progressive Development, and Growth, of the Electric Organ of the Skate.*

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[PLATES 26–30.]

IN my previous papers on the ‘Electric Organ of the Skate,’ I considered the development of the organ in *Raia batis*,\* the structure of the organ in *R. circularis*,\* and the structure and development of the organ in *R. radiata*.† I propose now to consider the relations, structure, and progressive growth of the organ in *R. batis*, to contrast the organ of *R. batis* with that of *Torpedo*, and to refer to the various modifications of the electric organ I have found in the Skate genus.

I. THE RELATIONS AND STRUCTURE OF THE ORGAN OF *R. batis*.

(1.) *Historical.*

The electrical apparatus of the Skate was discovered, in 1844, by Dr. STARK, who published a short account of its structure in the ‘Proceedings of the Royal Society of Edinburgh.’‡ Dr. STARK described the organ as follows:—“On removing the skin from the tail of a Flapper Skate, an organ was discovered occupying the place of the lateral muscles, extending from near the base to the very tip of the tail, and possessing all the anatomical characters of the electrical apparatus of fishes. It was about 14 inches in length, and about half-an-inch in diameter for nearly one half of its length, was composed of columns, or four-sided membranous tubes about  $\frac{1}{12}$ th of an inch in diameter, divided by cross membranous septa into compartments varying from  $\frac{1}{20}$ th to  $\frac{1}{30}$ th of an inch in diameter. These compartments were filled with a transparent gelatinous matter. The columns were so arranged as to form layers

\* ‘Phil. Trans.,’ B., 1888, p. 399.

† ‘Phil. Trans.,’ B., 1888, p. 539.

‡ On the Existence of an Electrical Apparatus in the Flapper Skate, and other Rays. ‘Edinb. Roy. Soc. Proc.,’ 1844–45, Vol. 2.

which on transverse section were seen to have a concentric arrangement, but on a longitudinal section were seen to form hollow cones placed one within the other. This arrangement allowed about  $\frac{3}{4}$ ths of the wide extremity of every cone-shaped layer to come into contact with the skin."

After referring shortly to the microscopic structure of the organ, and mentioning that in most Rays it was merely rudimentary, consisting of only four or five columns, he gave his reasons for considering the organ as an electrical apparatus.

Early in January, 1845, Dr. STARK made a further communication to the Ed Royal Society on the Electrical Organs of Rays,\* and, at the same time, M GOODSIR submitted observations on the same subject,\* pointing out that the organ consisted of "the posterior part of the middle mass of the caudal muscles," and "that the evidence educed of its electrical properties appeared to him to be insufficient."

Shortly after the discovery of Dr. STARK, Professor CHARLES ROBIN (without knowing of STARK's discovery†) made a careful study of the Skate's electric organ, and as early as 1846 presented a communication on the subject to the Academy of Sciences ('Ann. Sci. Nat.,' vol. 7), and in 1865 he published a second paper in the 'Journal de l'Anatomie et de la Physiologie.‡

Since the appearance of ROBIN's Memoir various biologists have examined the Skate's electric organ, notably LEYDIG,§ REMAK,|| ECKER,¶ KÖLLIKER,\*\* SCHULTZE,†† BABUCHIN,‡‡ and, quite recently, BURDON-SANDERSON and GOTCH.§§ The first four investigators mentioned directed their attention chiefly to the minute anatomy, more especially to the terminations of the nerves in the electric discs. BABUCHIN, who made the important discovery that the electric organs were derived from muscular tissue, described some of the more important stages in the development of the Skate's organ, while SANDERSON and GOTCH have dealt chiefly with its physiology. The last authors, however, in their first paper give a short but valuable account of the structure of the organ, and point out that it corresponds, both in *R. batis* and *R. clavata*, in structure and functions with other electrical organs in fishes.||||

\* 'Annals and Magazine of Natural History,' Vol. 15, p. 122.

† That ROBIN's work was fully appreciated by GOODSIR, who for some time continued to work at electric organs in fishes, may be inferred from his stating in a lecture in 1855, that ROBIN had "rediscovered and most minutely and accurately described" the Skate's electrical apparatus. 'Edinburgh Med. Journ.,' August, September, 1855, p. 278.

‡ 'Journ. de l'Anat. et de la Physiol.,' vol. 2, 1865.

§ 'MÜLLER's Archiv,' 1854, p. 314, *et seq.*

|| 'MÜLLER's Archiv,' 1856, p. 471, *et seq.*

¶ 'Zeitschrift f. wissenschaftliche Zoologie,' 1849, p. 41.

\*\* 'Verhandl. der Physik.-Medicin. Gesellschaft in Würzburg,' 1857.

†† 'MÜLLER's Archiv,' 1858, p. 193.

‡‡ 'Centralblatt f. d. med. wissen.,' 1872, and 'Archiv f. Anatomie und Physiologie,' 1876, p. 538.

§§ 'The Journal of Physiology,' vol. 9, Nos. 2 and 3, and vol. 10, No. 4.

|||| 'The Journal of Physiology,' vol. 9, p. 140.

I ought, perhaps, to add, that in 1801 GEOFFROY ST.-HILAIRE\* gave it as his opinion, that the mucous ducts of the Skate were the analogues of the electrical organs of the *Torpedo*. A similar mistake was made in 1858 by M. JOBERT DE LAMBALLE,† and in 1861 by McDONNELL,‡ who considered (what I have elsewhere§ described as) the hyoid group of ampullæ, as corresponding to the *Torpedo's* batteries.

## (2.) *Relations of the Organ.*

Although, as pointed out by SANDERSON and GOTCH,|| the essential elements of the Skate's organ may be said to belong histologically to the nervous, and not to the muscular system, there can be no doubt that the structure of the organ can only be understood when its relation to the muscular system is considered. ROBIN states that the organ is formed out of the *sacro-lumbalis* muscle of CUVIER, and lies between the *supra-* and *infra-spinous* muscles, and GOODSIR describes it as the posterior part of the middle mass of the caudal muscles. It was, however, only after BABUCHIN¶ discovered that electrical organs were derived from muscular tissue, that the actual relation of the Skate's organs to certain caudal muscles could be accurately determined. In order to make out exactly which muscular fibres take part in the development of the organ of the Skate, I have found it necessary to examine the arrangement of the muscles in the tail of some of the less specialised Selachians. In the Dogfish (*Scyllium*) the muscles of the tail consist of myotomes bent zigzag fashion (Plate 26, fig. 1) so as to form at each side of the body five rows of muscular cones, three lying above and two below the transverse connective tissue septum (Plate 26, fig. 2, s.), which extends outwards from the vertebral column to reach and unite with the skin on a level with the lateral sensory canal. The myotomes, by the folding of which these cones are produced, are made up of short fibres (Plate 26, fig. 1, f.) which run obliquely between the nearly parallel metamerically arranged connective tissue septa—the myocomma (Plate 26, fig. 1, m.). When the skin is removed, or still better, when a longitudinal section is made at the root of the tail, the zigzag arrangement of the septa, between which the muscular fibres extend, is easily observed (Plate 26, fig. 1); while in a transverse section three of the rows of cones are seen to lie above the transverse septum and two below (Plate 26, fig. 2). These rows of cones may be known as the dorsal (*d.*), dorso-lateral (*d.l.*), lateral (*l.*), ventro-lateral (*v.l.*), and ventral (*v.*) (Plate 26, figs. 1 and 2). The apices of the dorsal, lateral and ventral cones project forwards, while the apices of the dorso-

\* 'Ann. du Mus.,' I., 1801, p. 392.

† 'Des Appareils Electriques des Poissons Electriques,' Paris, 1858.

‡ 'Nat. Hist. Review,' 1861, p. 59.

§ "The Lateral Sense Organs of Elasmobranchs," 'Edinburgh Roy. Soc. Trans.,' vol. 37, 1892.

|| 'Journal of Physiology,' vol. 9, p. 144.

¶ 'Archiv f. Anatomie und Physiologie,' 1876.

lateral and ventro-lateral project backwards, and the muscular fibres which make up the several cones have always the same relation to their apices. The cones vary in length, and are often incomplete where they come into contact with the vertebral column; and, further, each cone is more or less notched at its base. Partly owing to this imperfection of the cones, and partly owing to their being flattened, the conical arrangement is not so apparent in horizontal as in vertical sections.

Turning now to the Skate the question at once arises: To which of the muscular columns of the Dogfish does the electric organ correspond? This question is at the outset not so easily answered. The tail of the Skate has been flattened and otherwise modified, and while some of the rows of cones are relatively larger than in the Dogfish, others have been displaced and reduced in size. When, however, a series of sections of embryo and young Skates is examined, the interpretation of sections of large Skates becomes somewhat easier, and all the difficulties are removed when a series of sections from the tails of *Scyllium*, *Lamna*, *Myliobatis*, and *Raia* are examined side by side.

In *Lamna cornubica* the tail for some distance in front of the caudal fin has undergone considerable flattening, and at the same time there has been a reduction of the dorso-lateral and ventro-lateral muscular cones, and, compared with *Scyllium*, an increase in size of the external row of muscular cones (Plate 26, fig. 3). As a result of these changes the sections through the tail of *Lamna* present a remarkable resemblance to those through the root of the tail of *Myliobatis* and *R. batis* (Plate 26, figs. 4 and 5).

In all three cases the external or lateral row of cones (Plate 26, *l.*, figs. 3 and 4) is large and pear-shaped, the cones being rounded externally, and, except in *Myliobatis*, somewhat pointed internally. Further the outer cone seen in a transverse section comes into, or all but into, contact with the vertebral centra at the inner side, and with the subcutaneous tissue by its rounded outer surface. The dorsal and ventral rows (Plate 26, *d.* and *v.*, figs. 3, 4 and 5), though smaller and less rounded, are equally distinct in all three, but the dorso-lateral and ventro-lateral are only represented in *Lamna* and *Raia* by thin wedge-shaped masses (Plate 26, *d.l.* and *v.l.*, figs. 3 and 5), which gradually diminish in size as the tip of the tail is reached in *Lamna*, and completely disappear before the middle of the tail is reached in *R. batis*. In the figure (Plate 26, fig. 5) showing a section of the root of the tail of *R. batis*, the dorsal (*d.*), lateral (*l.*), and ventral (*v.*) rows of cones are easily recognised, the dorso-lateral (*d.l.*) is seen to be relatively small, while the ventro-lateral (*v.l.*) is so reduced in size that it can only with difficulty be detected lying below the transverse septum in a small space between the lateral and ventro-lateral rows. The dorso- and ventro-lateral rows are relatively still smaller in *Lamna*, but larger in *Myliobatis* (figs. 3 and 4). That the large row of cones in *Lamna*, *Myliobatis*, and *Raia* corresponds to the lateral row in *Scyllium* is evident when its relation to the transverse septum is considered, and this homology is confirmed by examining vertical sections.

From this comparison it becomes evident that while the large middle or outer



muscular row of cones in *R. batis* corresponds to the lateral row in *Scyllium*, the upper and lower rows of the Skate correspond respectively to the dorsal and ventral rows in *Scyllium*, while the wedge-shaped mass (Plate 26, *d.l.*, fig. 5) between the dorsal and lateral cones corresponds to the dorso-lateral, and the few fibres (Plate 26, *v.l.*, fig. 5) between the lateral and ventral cones to the ventro-lateral row of cones in *Scyllium*.

When a series of transverse and longitudinal sections is made through the tail of *R. batis*, it becomes further evident that the electric organ is a direct continuation backwards of the large mesially placed lateral row of cones (the middle caudal muscle of GOODSIR), and that the two lateral and two ventral rows gradually diminish in size, and either disappear, or are represented by delicate tendons which lie immediately under the skin.

A comparison of the tail of *Scyllium* with that of the Skate not only shows that in the Skate the lateral row of cones is relatively large, while the dorsal and ventral rows are relatively small, but also that the cones which make up the lateral row are relatively much longer than in *Scyllium*, more especially at the base of the tail. This difference is obvious when *Scyllium* (Plate 26, fig. 1) is compared with *Raia* (Plate 27, fig. 6), in which the cones are seen to be nearly four inches in length.

A comparison of the muscles of the tail in *Selachians* with very different results was made by McDONNELL, who evidently failed to make out that the electric organ of the Skate occupied the position of the middle row of muscular cones in the Sharks. Had McDONNELL made out this relationship, he would not, in all probability, have been led to make the following statement:—"The tail electric organ, which is found largest in the common Skate, is seen to be smaller in the more spiny Rays, and at last in the Angel-fish (*Squatina angelus*), the Dog-fish (*Squalus galeus*), the Porbeagle (*Squalus cornubicus*), the Basking Shark (*Squalus maximus*), it exists as a ridge along the sides of the tail which, in transverse section, shows more or less of a structureless substance between the layers of the corion."\* None of the Sharks mentioned by McDONNELL, nor any others I have examined, have a vestige, or do they show any signs of ever having had any rudiment of, an electric organ. The middle row of cones which, in the Skate, give rise to the electric organ are in all the Sharks perfectly distinct, but in no case have I found any of their fibres transformed, or in process of transformation, into electrical elements. The structureless substance between the layers of the corion referred to by McDONNELL consists of the connective tissue, which in all cases extends as a more or less distinct band parallel and internal to the canal of the lateral line. What is true of the Shark is equally true of the Rays and Skates, with the single exception of the genus *Raia*. But while in the Sting- and Whip-Rays there is no indication of an electric organ in the adult, there may be rudiments of an organ in the embryo. I have not yet obtained material to settle this point, which is obviously of considerable importance, as it may throw some light on the present stage reached by the organ in the Skate genus.

\* McDONNELL, 'Trans. Roy. Irish Acad.,' vol. 24.

(3.) *Structure of the Electric Organ.*

STARK\* described the organ as consisting of four-sided membranous tubes, divided by septa into compartments filled with a transparent gelatinous matter. ROBIN\* described the organ as a spindle-shaped structure, divided by septa into lozenge-shaped compartments, each containing a polygonal disc, the discs forming columns or piles separated by longitudinal septa. SANDERSON and GOTCH\* speak of the organ as consisting of "spindle-shaped tubes, imperfectly divided into loculi placed one above the other, and each holding a disc," the tubes being "so arranged that the axes are either parallel, or very slightly diverge backwards," and the discs suspended in the tubes by the connective tissue which supports the blood vessels. They point out that the compartments are not lozenge-shaped, as stated by ROBIN, "but, as a rule, oblong and rectangular in section."

By referring to Plate 27, figs. 7 to 12, an idea will be obtained as to the form of the organ as a whole and at various parts of its length, and from fig. 6 it will be seen that it has a general resemblance to the muscle (*i.e.*, the lateral row of muscular cones) with which it is continuous, and by which it is, in part, completely invested. It will be especially noted that, like the lateral muscle (*l,m*, fig. 6), the organ consists of a series of cones (*c*, fig. 6) separated from each other by septa still practically identical with the septa (myocomma) between the myotomes. When the structure of the electric organ in the various members of the Skate genus hitherto examined is taken into account, the organ may be described as consisting of a series of cones composed of more or less completely metamorphosed muscular fibres—of fibres which, while retaining their original position, have completely lost, in most cases, their original structure, and (with the possible exception of *R. radiata*) their original function. This being the case, instead of describing the organ of *R. bat's* as made up of piles or columns of discs, it will be better, when dealing with its structure, to speak of it as consisting of electric cones, each cone being composed of discs having essentially the same arrangement as the fibres that make up the lateral row of muscular cones in Lamna and other Selachians.

Owing to the organ being spindle-shaped, the cones of necessity vary considerably in length and also in the diameter of their open distal ends. In an organ which measured 46 centims. in length, twenty-eight distinct cones were counted, to which must be added several (6 to 8) incomplete cones which formed the pointed terminal portion. The first electric cone, which fitted accurately within the last muscular cone (Plate 27, fig. 6), measured along its upper surface 5 centims. in length.† From the first to the tenth the cones gradually increased, until a length of 6·8 centims. was reached. The apex of the tenth cone was 21 centims. from the anterior end of the organ. The eleventh cone agreed with the tenth, but from the eleventh backwards

\* *Loc. cit.*

† The cones were measured along their sides, as seen in a longitudinal sagittal section.

they gradually diminished in length. The twelfth measured 5·7 centims.; the fourteenth, 4·6 centims.; the sixteenth, 3·5 centims.; the eighteenth, 3 centims.; the twentieth, 2·5 centims.; the twenty-second, 1·75 centims.; the twenty-fourth, 1·25 centims.; the twenty-sixth, ·75 centim.; and the twenty-eighth, ·5 centim. The terminal cones could only with difficulty be distinguished—the anterior ones each consisted of several discs which formed minute concave plates; beyond these the organ was completed by a few discs having no very definite arrangement. The anterior half of the organ contained fewer cones than the posterior, *e.g.*, the apex of the fifth cone was 9 centims. from the anterior end of the organ; the space between the apices of the fifth and tenth cones was 11·75 centims.; between the tenth and fifteenth, 10·5 centims.; between the fifteenth and twentieth, 8 centims.; between the twentieth and twenty-fifth, 5 centims.; and between the twenty-fifth and thirty-third, only 2 centims. The apex of the eleventh cone lay nearly at the centre of the organ, *i.e.*, nearly 23 centims. from either end, while the base extended to within 16 centims. of the distal end of the organ; in other words, while the anterior 30 centims. contained only eleven complete cones, the posterior 16 centims. contained parts of twenty-two cones in addition to the indistinct terminal cones.

Transverse sections were equally instructive. In a section about 7 centims. from the anterior end of an organ which measured 60 centims. in length, the apex of the fourth cone was seen lying within the fifth and sixth cones (Plate 27, fig. 8). A section, about 15 centims. from the anterior end, showed five cones (Plate 27, fig. 9), three completely surrounding the apex of a fourth, and surrounded by the incomplete base of a fifth consisting of small irregular discs. It will be observed that in fig. 9 the spindle-like form is still maintained, and that the outer electric cone is not, as in fig. 8, invested by muscular cones. About the middle of its length, however, the organ loses its oval contour and projects inwards by a keel-like ridge as far as the vertebral column (Plate 27, fig. 10). In sections near the middle of the organ only portions of the base of the fifth cone are as a rule visible, and the dorso-lateral and dorso-ventral rows of muscular cones can no longer be detected.

For some distance beyond the middle of the organ the concentric arrangement so well marked in front is still evident (Plate 27, fig. 11); but as the posterior end is reached it becomes obscured, partly owing to the shortening of the cones and partly owing to the relation of the organ to the vertebral column. It is important to note that the outer portions of the bases of all the cones come into contact with the skin, and this notwithstanding the fact that the anterior part of the organ is completely invested by the lateral row of muscular cones (Plate 27, fig. 6). But while the outer part of the base of each cone reaches the skin, the inner part is in contact first with the dorsal and ventral rows of muscular cones, and beyond the middle of the tail with, in addition to the muscles or their tendons, the centra of the caudal vertebræ (Plate 27, figs. 10 and 11), with which it comes into more intimate relation as the tip of the tail is reached.

For the purposes of description the Skate's organ has been frequently described as spindle-shaped. It should, however, be borne in mind that while a portion at each end is rounded and tapering (Plate 27, fig. 11), the middle segment—considerably over a third—is distinctly irregular in section. This irregularity is chiefly due to the organ coming into contact with the vertebral column, and having its upper and lower surfaces grooved by the dorsal and ventral muscles and their tendons, and the muscles of the dorsal fin (Plate 27, figs. 10 and 11). The groove is most marked in the dorsal aspect—the dorsal muscles being the larger—a short distance beyond the middle of the organ. In this position a keel-like ridge, nearly .5 centim. in width in large Skates, projects inwards, and is only separated from the centra of the caudal vertebræ by a thin layer of connective tissue.

*The Electric Discs.*—The walls of the muscular cones, in a full-grown Skate, consist of numerous short, slender, muscular fibres, which run obliquely between the septa (Plate 27, fig. 6), the individual fibres being separated from each other by connective tissue, nerves, and blood vessels. This is the case with all the caudal cones in embryos of *Raia batis* under 6 centims. in length; the fibres having their long axes nearly parallel with the long axis of the tail. But in a Skate 7 centims. in length the anterior ends of the fibres of the laterally-placed cones throughout over two-thirds of the tail have assumed a rounded form, each fibre having its expanded end covered by the already slightly enlarged motor plate. In a Skate of 9 centims. in length the club-shaped bodies have begun to assume the form of discs having their long axes at nearly right angles to the long axis of the tail.\* This difference between the direction of the fibres and the discs at once marks out the transformed from the unaltered fibres. These discs, when fully developed, vary very considerably in shape, their form depending largely on their position in the cone; at the apex they are small and irregular; a short distance from the apex they approach a hexagonal or polygonal form, while throughout the greater part of the cone they are nearly quadrangular; but as the base of the cone is reached the discs gradually diminish in size and become extremely irregular in contour. The discs of each cone are separated from each other by well-marked septa, developed from the connective tissue that invested the muscular fibres in the embryo. These septa are so arranged that they, together with the walls of the cone, form a series of nearly parallel tubes (Plate 28, *t* and *t'*, fig. 13), which extend from the apex to the base of the cone, and they further give rise to transverse partitions which divide the tubes just referred to into numerous small compartments or loculi (Plate 28, *l.*, fig. 13), each of which contains an electric element—the disc proper.

While it is possible to enumerate with a sufficient amount of accuracy the number of cones in the electric organ, it is practically impossible to determine the number of discs which make up the several cones. I have, however, endeavoured to estimate the number of discs in the entire organ. I at first divided the organ into sections,

\* 'Phil. Trans.,' 1888 B, Plates 66, 67, figs. 2 to 10.

and endeavoured to make out the number of discs in each ; but more accurate results were obtained by a plan suggested by Dr. PURVIS.\* At the best, probably only a rough estimate has been arrived at, but it may be of some use when a comparison comes to be made between the electric organs of the Skate and Torpedo.

Altogether I have estimated that each organ contains about 10,000 discs, *i.e.*, the two organs would have about 20,000 discs. According to this estimate the Skate's organ compares very unfavourably with the organ of the Torpedo, and still less favourably with the organ of *Malapterurus*. In *T. marmorata* there are in each organ about 250,000 electric elements each several times larger than the discs of the Skate, while in the large Torpedo of America (*T. gigantea*) there are in the two organs about 1,000,000 electric elements or discs, and the electric battery of *Malapterurus* is said to contain about 2,000,000 electric elements.

Various observers have already directed their attention to the minute structure of the electric discs. In a recent paper† I described the discs as consisting essentially of three layers :—the electric, striated, and alveolar. SANDERSON and GOTCH speak of these layers as the nucleated, striated, and alveolated laminae. Of these laminae or layers the first is the most important.‡ This, the anterior or electric layer, extends over the entire anterior surface of the disc and bends round the margin to become continuous with the posterior or alveolar layer.

The electric layer (Plate 28, *el.*, fig. 14) may be described as consisting of two laminae, an anterior (the nervous) (*n.l.*, fig. 14) in which the nerve fibres seem to terminate, and a posterior (the nuclear) (*nuc.l.*, fig. 14) which contains numerous nuclei. The nervous lamina, which consists of fine granular protoplasm, is best understood when considered along with the nerves which reach it. The nerves of the electric organ, as pointed out by ROBIN, come from the ventral root of the spinal nerves in the region of the electric organ (Plate 29, *e.n.*, fig. 15). On reaching the organ they enter its substance between the cones, the main stems running first forwards to the apex, and then backwards towards the base of the cone in the substance of the myocomma.

On the way, they give off numerous branches which enter the loculi (Plate 29, *l.*, fig. 15) and break up into a countless number of twigs§ which occupy a considerable space between the anterior wall of the chamber and the electric layer of the disc. This space (the anterior part of the chamber traversed by the nerves) contains a peculiar gelatinous tissue, having simple and branched connective tissue corpuscles

\* This consisted in first finding the exact weight of an entire organ, and next the weight of a small piece (about an inch from near the centre) of the same organ, counting the number of discs in the piece, and then calculating the number in the entire organ.

† 'Phil. Trans.,' vol. 179 (1888), B.

‡ In support of this statement it may be mentioned that in the powerful organ of the Torpedo the discs have been so reduced in thickness that little more than the electric layer is left.

§ See also 'Phil. Trans.,' 1888, B., Plate 67, fig. 13.

scattered through its substance. Some of these corpuscles lie in close contact with the nerve fibres, and are apt to be mistaken for the nuclei belonging to the sheaths of the smaller nerves. The nerves on entering a loculus first approach its centre, keeping near the anterior wall; they then usually bend backwards dividing dichotomously on the way to form an immense number of delicate twigs which reach the anterior surface of the disc. On entering the chamber the nerves are medullated, but after a time only the grey sheath persists, and the axis cylinder becomes extremely slender. Numerous nuclei occur on the nerve sheaths. On the sheath of the non-medullated nerves in close proximity to the electric plate the nuclei are often relatively extremely large, and sometimes irregular in shape (Plate 23, *n.*, fig. 14). ROBIN\* described multipolar nerve cells in front of the disc. The large connective tissue corpuscles just mentioned, with the slender nerve fibres that lie over and above them, often resemble nerve cells; this resemblance probably misled ROBIN. As pointed out by SANDERSON and GOTCH,\* there are no branched nerve cells in front of the electric disc.

How the nerve fibres actually terminate has not been definitely settled. I have devoted much time endeavouring to find out what becomes of the terminal twigs when they reach the disc, without any very satisfactory result. The terminal branches are so numerous that even in thin sections but little can be made out. In many preparations each nerve seems to terminate in a loop, while in others the terminal branches seem to form a network. ROBIN\* asserted that the primary fibres anastomosed to form a network; ECKER\* speaks of net-like ramifications; LEYDIG\* pointed out that ROBIN was mistaken in describing a network, but fell into a still graver mistake himself in figuring the nerves as entering the disc from behind through the posterior gelatinous tissue. KÖLLIKER\* says the nerves either end in knob-like swellings or (as suggested by fresh sections) give rise to a horizontally placed network. He, however, was quite clear that no nerve fibres penetrate, as asserted by LEYDIG, into the substance of the disc. SCHULTZE\* describes two networks, a somewhat coarse network immediately in front of the disc, and a fine network in contact with the granular protoplasm of the electric layer, and BABUCHIN\* favoured the network theory of SCHULTZE.

From an examination of a large series of sections of the discs preserved with different reagents and cut in different directions, it is readily understood how SCHULTZE and others believed in the existence of a network. The nerve-fibres are not only numerous but they frequently come into contact with each other as they run obliquely backwards, some in one direction, some in another, to the electric layer. In thick longitudinal sections the nerves seem to form several networks immediately in front of the disc. With care, however, it becomes evident that the nerve-fibres never actually communicate with each other before reaching the electric plate. In vertical sections of the disc it is clear beyond doubt that the nerves

\* *Loc. cit.*

continue to divide, until they reach and lose themselves in the nervous lamina of the electric layer (Plate 28, *n.l.*, fig. 14). What becomes of the axis cylinder, I have been unable to make out. Recently Dr. PURVIS, who has devoted much time to this question, states that in one series of preparations he found the nerves terminating in very minute enlargements on the surface of the electric layer.\* Whether the axes cylinders terminate abruptly in minute swellings, as is the case according to FRITSCH in the Torpedo,† or form a network so delicate that it escapes detection, I am not in a position to say. There seems no doubt, however, that, as pointed out in a former paper, the terminal twigs of the nerves form immediately in front of the electric layer a nearly regular series of loops.‡ These loops (Plate 28, *l.*, figs. 14 and 14*a*), which are very characteristic, stand at nearly right angles to the surface of the disc; as the terminal twigs reach the nervous lamina, the protoplasm is, as it were, heaped up around the axes cylinders thus forming an almost continuous series of minute cones.

In oblique and sometimes in horizontal sections of the discs the anterior surface of the electric layer presents a pitted appearance, the margins of the pits suggesting a delicate network. These shallow depressions which lie between the terminal nerve-fibres may result from the heaping up of the protoplasm of the nervous lamina around the limbs of the terminal nerve-loops. In conclusion, I need only add that every part of the electric layer is equally rich in nerves—everywhere all over the surface the extremely delicate terminal loops are equally abundant. There is no other organ, as far as I am aware, in which it is so easy to demonstrate the presence of a countless number of nerve-fibres terminating in a thin layer of protoplasm.

It may here be mentioned that in the case of *R. circularis*, the nuclear lamina is in some respects more highly differentiated than in *R. batis*. It presents a striated appearance (*n.l.*, fig. 14*a*), and thus resembles the corresponding lamina in the Torpedo, which is especially characterised by the “palisade” of REMAK—the “nerve hairs” of RANVIER. The resemblance between the nervous lamina of the Skate and the Torpedo will be at once evident if fig. 14*a* is compared with figs. 55 and 56 (Plate 19) in FRITSCH’s recent monograph.§

The striation of the nervous lamina is probably of little significance, but the fact that in one of the Skates (*R. circularis*) there is a palisade-like arrangement, helps to show that while a complete electric element in the Skate differs greatly from a complete element in the Torpedo, the essential parts are practically identical.

The nuclear lamina of the electric layer (Plate 28, *nuc.l.*, figs. 14 and 14*a*) consists of a layer of granular protoplasm, in which numerous large oval nuclei are imbedded at nearly regular intervals. The protoplasm immediately around the nuclei seems to be

\* Thesis for Degree of M.D., 1889. MS., Library, University of Edinburgh.

† ‘Die Elektrischen Fische.—Die Torpedineen.’ Leipzig, 1890.

‡ See also Plate 68, fig. 5, ‘Phil. Trans.,’ 1888, B.

§ *Loc. cit.*

non-granular, for it is left unstained in gold chloride and other preparations. The nuclei of the electric lamina of the Skate closely resemble the nuclei of the electric plates of the Torpedo, and in a less degree the nuclei in the motor plates of muscles. As to the origin of the nuclei it is difficult to determine, but it is extremely probable that, as suggested by Dr. BEARD,\* they are derived from nerve cells which found their way to the developing muscle during the formation of the nerves and the motor plate, and, while the nervous lamina of the Skate corresponds to the "stratum granulosum" and the "sogenannter Palisadensaum" of the Torpedo, the nuclear lamina corresponds to the "stratum moleculare."†

*The Alveolar Layer.*—This layer being continuous with the electric layer, and, like it, developed in intimate relation to the sarcolemma, will be described before the striated layer. It is at first represented by a thin nucleated layer of protoplasm which covers the posterior surface of the developing discs and surrounds the base of its stem.‡ After a time a remarkable change sets in—prong-like projections of the nucleated protoplasm grow backwards, with the result that the posterior surface of the disc appears to be studded with numerous villi.§ From these primary outgrowths secondary projections spring, and unite with each other to form a complex irregular network, the spaces of which open freely posteriorly (Plate 28, *a.l.*, fig. 14).||

As the trabeculæ develop, the nuclei increase in size, and eventually closely resemble the nuclei of the electric layer, many of them being surrounded by a broad zone of translucent protoplasm (Plate 28, *a.n.*, fig. 14). As the discs increase, the alveolar layer becomes more complex. In macerated specimens, a fine network is seen occupying the deeper portions of the pits or alveoli.¶ This fine network, which lies immediately behind the striated layer, is formed by the union of slender outgrowths from the primary and secondary projections. It is somewhat remarkable that this complex arrangement of vertical prongs and horizontal connecting beams (Plate 28, *p.* and *b.*, fig. 14) of various sizes is entirely absent in the Torpedo, in which, besides the layers already mentioned, there is only in addition a thin limiting membrane—the 'dorsale bindegewebige Grenzschrift' of FRITSCH and dorsal lamina of RANVIER. There may be some relation between the presence of a complex alveolated layer and the position of the electrical elements. In the Torpedo the discs are arranged to form columns that extend from the skin on the dorsal to the skin on the ventral surface. In the Skate and in *Gymnotus* (in which the electrical elements present numerous papillæ), the columns or piles formed by the discs run nearly parallel with the long axis of the trunk. The difference, however, may be due to the

\* 'Anat. Anzeiger,' Nos. 9 and 10, pp. 297 and 298, 1892.

† FRITSCH, *loc. cit.*, Plate 19, figs. 55 and 56.

‡ 'Phil. Trans.,' 1888, B, Plate 66, fig. 5.

§ 'Phil. Trans.,' 1888, B, Plate 66, fig. 6.

|| 'Phil. Trans.,' 1888, B, Plate 66, fig. 7.

¶ 'Phil. Trans.,' 1888, B, Plate 67, fig. 11.



difference in the arrangement of the muscular fibres which are utilised in the formation of the respective electric organs, or more likely to the Torpedo's battery having undergone greater specialization.

*The Striated Layer.*—While the electric and alveolar layers are being developed in more or less intimate connection with the sarcolemma, the striated layer is formed by a remarkable transformation of the anterior end of the club. Up to a certain stage the muscular striation persists, but, after a time, the ordinary transverse markings disappear, and the peculiar and comparatively broad lamellæ, represented in fig. 14, make their appearance. How the change is effected, I am unable to state. When the wavy lamellæ are further examined, they may be found to be related more closely to connective than to muscular tissue, and to be the products of connective tissue rather than of muscle cells. The lamellæ have a granular appearance, and seem to extend right across the disc. Those shown in fig. 14 are from a photograph of a longitudinal section of a well-grown Skate.

Unlike the other two layers, the striated layer is, except in rare cases, devoid of nuclei. Nuclei were described as occurring in this layer by SCHULTZE, but their presence was denied by BABUCHIN. At first, while the process of conversion from the muscular fibre is in progress, numerous nuclei are present, but one by one they disappear; only in one out of numerous sections has a nucleus been found by Dr. PURVIS.\* This striated layer on which the electric plate rests is usually concavo-convex, and, as already explained, around its recurved margin the electric layer becomes continuous with the alveolar layer (Plate 30, fig. 21). It may be added that when the posterior part of the original muscular fibre persists, it is directly continuous with the striated layer.

Turning from the layers to the disc as a whole, it will be observed that in longitudinal sections (Plate 28, fig. 13) it only occupies, at the most, one-third of its compartment.† It looks as if it were suspended from the anterior wall of the chamber by the rich nerve plexus terminating in the electric plate. The space behind the disc is occupied by gelatinous tissue which extends into and fills up all the spaces in the alveolar layer.‡ Through this tissue nuclei are scattered at irregular intervals, some of which seem to be in connection with the fibres described by LEYDIG as nerves.

This tissue, which may serve to insulate the discs, is traversed by small blood-vessels and capillaries. The blood-vessels, as fully described by ROBIN, enter the electric organ along with the nerves, and run at first parallel with the zig-zag septa (myocomma); they afterwards leave the nerves and penetrate the chambers to reach and form a plexus in the gelatinous tissue lying in the spaces of, or behind, the alveolar layer. In no instance have vessels been found amongst the nerves that traverse the gelatinous tissue in front of the electric plate or in the substance of the disc proper, *i.e.*, in or between any of the three layers of the disc.

\* *Loc. cit.*

† 'Phil. Trans.,' 1888, B, Plate 67, fig. 13.

II. PROGRESSIVE GROWTH OF THE ORGAN IN *R. batis*.

In my first paper on the Skate's organ I pointed out that, before attempting to account for the existence of an organ structurally as perfect as that of the Torpedo, and yet, as far as had been ascertained, useless to its possessor, it was desirable to inquire whether the organ is "on the up or down grade—whether, having reached a high state of elaboration, it is now increasing in functional importance, or whether, its days of usefulness being over, it is slowly undergoing retrogressive changes." I also pointed out that it was desirable to make out its development, the period at which it first appears, the rate at which development proceeds, and the changes, if any, which set in after development has been completed. Having previously given an account of the time of appearance and development of the organ, and having considered at some length its relations and structure, it is now possible to discuss the changes which take place after development has been accomplished. In *R. batis*, although the process of conversion of the muscular fibres into discs does not begin until a length of 6 or 7 centims. is reached, the development of the discs is practically completed when the young Skate measures 12 centims., before it leaves the egg capsule.

It may now be asked, does the organ, immediately or soon after development has been completed, begin, either as a whole or in any of its essential parts, to degenerate; or does it continue to grow as the Skate increases in size, keeping pace at least with the growth of the tail of which it forms a part? These questions will best be answered by comparing the organ in Skates of different sizes, say from 12 centims. upwards.\* To admit of this I have had the fresh organs from over a hundred Skates carefully exposed and measured, and afterwards removed and weighed, the size of the Skate in each case being duly noted.

In Skate from 10 to 12 inches ( $25\frac{1}{2}$  to  $30\frac{1}{2}$  centims.) in length, the organ measured from 5 to  $5\frac{1}{2}$  inches ( $12\frac{3}{4}$  to 14 centims.) and weighed from .5 to .6 gm. In Skate measuring from 1 ft. 3 in. to 1 ft. 6 in. (38 to  $45\frac{1}{2}$  centims.) the organ varied from  $5\frac{1}{2}$  to 7 in. ( $14$  to  $17\frac{3}{4}$  centims.) and weighed from .7 to 1.5 grms. In Skate from 1 ft. 6 in. to 1 ft. 9 in. ( $45\frac{1}{2}$  centims. to  $53\frac{1}{4}$  centims.) in length, the organ varied from 6 to 8 in. ( $15\frac{1}{4}$  to  $20\frac{1}{4}$  centims.) and weighed from .8 to 1.8 grms. In Skate from 1 ft. 9 in. to 2 ft. ( $53\frac{1}{4}$  to 61 centims.) in length, the organ varied from 7 to 9 in. ( $17\frac{3}{4}$  to

\* It may be mentioned that the tail in the adult is relatively smaller than in the embryo. In a nine to ten months' embryo, 14 centims. in length (Plate 29, fig. 16), the tail is more than half the length of the entire fish, and the dorsal fins near its tip are some distance apart; but after a time the tail is less than half the length of the entire fish, and, except at the base, relatively much thinner than in the embryo. The arrest of the growth of the tail is doubtless associated with the habits of the fish, for, while the Skate uses its tail freely for lashing about in the water, it is never used as an organ of progression, as it probably was in the less specialised ancestors. In sections through the Skate's tail the rapid tapering is seen to be due partly to the diminution of the vertebral column, but chiefly to the reduction of the dorsal and ventral and the dorso-lateral and ventro-lateral muscles.

to 23 centims.) and weighed from 1·3 to 3 grms. Twenty out of the thirty weighed were at or close upon 2 grms., and only three at or more than 3 grms. In Skate from 2 ft. to 2 ft. 3 in. ( $61$  to  $68\frac{1}{2}$  centims.) the organ measured from  $8\frac{1}{2}$  to 11 in. ( $21\frac{1}{2}$  to 28 centims.) and weighed from 2·3 to 5 grms., the majority being under 4 grms. In Skate from 2 ft. 3 in. to 2 ft. 6 in. ( $68\frac{1}{2}$  to 76 centims.) in length, the organ measured from  $10\frac{1}{2}$  to  $12\frac{1}{2}$  inches ( $26\frac{1}{2}$  to  $31\frac{3}{4}$  centims.) and weighed from 4·8 to 7 grms. In Skate from 2 ft. 9 in. to 3 ft. ( $83\frac{1}{2}$  to  $91\frac{1}{4}$  centims.) in length, the organ varied from 12 to  $13\frac{1}{2}$  inches ( $30\frac{1}{2}$  to  $34\frac{1}{4}$  centims.) and weighed from 6 to 8 grms. In Skate just over 3 ft. (95 centims.) in length, the organ averaged 1 ft. 3 inches (38 centims.) in length, and weighed 8·5 to 11 grms. In a Skate 4 ft. 6 in. (137 centims.) in length, the organ measured 1 ft.  $5\frac{1}{2}$  in. ( $44\frac{1}{2}$  centims.) in length, and weighed 16·8 grms. In a Skate 5 ft. 2 in. (157 centims.) in length, the organ measured 1 ft. 7 in. ( $48\frac{1}{4}$  centims.) in length, and weighed 25 grms. In Skate about 6 ft. ( $182\frac{1}{2}$  centims.) in length the organ measured 1 ft. 9 in. ( $53\frac{1}{4}$  centims.) and weighed 70·75 grms., while in Skate which measured from 7 ft. to 7 ft. 4 in. in length (213 to 225 centims.) the organ measured from 2 ft. to 2 ft. 4 in. (61 to 70 centims.), and weighed 145 to 156 grms.\*

It is generally held that vestigial organs reach their highest development in the embryo, and that they afterwards either (1) only slightly increase in size, or (2) are arrested in their development or growth and retained in a more or less imperfect condition, or completely, or all but completely, disintegrated and removed. From the figures given above it is evident that the organ of *R. batis*, if judged by this law, cannot well be considered a vestigial structure. Up to a certain stage—to the time when a length of five feet (157 centims.) is reached the growth and increase in weight are gradual and constant, and though there is a certain amount of variation the range is not such as one would expect in an organ in process of degenerating.

But the most remarkable result brought out by the above figures is that while the

\* The rate of increase in the length and in the weight of the organ is brought out more clearly in the following table:—

Length of fish.	Length of organ.	Weight of organ.
centims.	centims.	grms.
25·50–30·50	12·75–14·00	0·50– 0·60
38·00–45·50	14·00–17·75	0·70– 1·50
45·50–53·25	15·25–20·25	0·80– 1·80
53·25–61·00	17·75–23·00	1·30– 3·00
61·00–68·50	21·50–28·00	2·30– 5·00
68·50–76·00	26·50–31·75	4·80– 7·00
83·50–91·25	30·50–34·25	6·00– 8·00
95·00	38·00	8·50–11·00
137·00	44·50	16·80
157·00	48·25	25·00
182·50	53·25	70·75
213·00	61·00	145·00
225·00	70·00	156·00

Skate is increasing from 5 to 6 feet (182·5 centims.) in length, the organ, while only increasing two inches (about 5 centims.) in length, increases from 25 grms. to 70·75 grms., *i.e.*, it weighs nearly three times more in a 6-foot than in a 5-foot Skate, and although the difference in the length and weight of the tail, minus the electric organs, between a 6-foot and a 7-foot Skate is but slight, the organ in a 7-foot (213 centims.) Skate is more than double the organ in a 6-foot Skate. Consequently there is no escape from the conclusion that the growth of the Skate's organ does not progress at the same relative rate as the growth of the tail, but at an independent, and, after a time, far higher rate, more in keeping with the growth of the entire fish. This is scarcely what one would expect in a degenerating organ, but what might be expected in a functional and useful organ which happened to be lodged in a part of the body which, under the influence of natural selection, was being gradually reduced in size. It is worthy of note that while the rate of growth of the organ is greater after a time than that of the tail, it seems to bear some relation to the growth of the claspers. These organs are late in developing; in a *R. batis* 2 feet in length, I have found them measuring  $1\frac{1}{2}$  inches, while in a large Skate they are sometimes nearly 18 inches in length. On the other hand, in *R. clavata*, which reaches maturity when comparatively small, the claspers of a 3-foot fish measure from eight to nine inches.

It might, however, be advanced that the increase in size and weight of the organ is not necessarily the result of growth of the electric elements, as is the case in the Torpedo, but due either to a gradual conversion of new muscular fibres, or to an increase of the connective and gelatinous tissues, and that the increase might even be accompanied by degeneration of the electric nerves or other essential structures. These various possibilities I have fully considered. In the first place, when a certain number of muscular fibres in the embryo have been converted into electric elements, the process of transformation abruptly ceases. HUNTER\* and others believed that in the Torpedo the number of electric columns increased as the fish grew larger, but FRITSCH,† after enumerating the number of columns in the several species of *Torpedo*, arrived at the following conclusions, viz. (1) that the number was the same in the embryo and adult; and (2) that the number of the columns varied considerably in the different species of *Torpedo* (*e.g.*, *T. marmorata* had usually under 500, while *T. gigantea* had over 1000 columns). In the same way in the Skate genus I have found a considerable variation in the size and number of the electric cones in the different species, but (as far as it was possible to estimate) nearly the same number of cones and discs in the members of the same species. In sections through the centre of the organs from fish of different lengths, the same, or approximately the same, number of discs were invariably found, and estimates made of the entire number of discs in the organs of large and small Skates were sufficiently close to indicate that the number of elements was practically the same in organs which differed greatly both

\* 'Phil. Trans.,' 1775.

† *Loc. cit.*

in size and weight. By examining a series of sections from organs measuring from 6 inches (15·25 centims.) to 2 feet (61·75 centims.) in length, it was evident, first, that the increase in size was due to an enlargement of the individual discs, and, second, that, as the discs increased, the various layers, the nerve layer included, continued to present the same histological characters as were found in the young fish—that, in fact, the discs of the Skate were, from a structural point of view, as perfect from first to last as the corresponding structures in the Torpedo. In the Torpedo, as life advances the discs gradually increase in diameter but diminish in thickness, while the thickness of the gelatinous insulating tissue between the discs is considerably augmented. Practically the same changes take place in the Skate. While the Skate is increasing from 1 to 7 feet (30·5 to 213 centims.) the organ increases about four times both in length and in diameter. The increase in length is chiefly due to an increase in the gelatinous and connective tissues, but in part to an increase of the striated layer. The increase in diameter is accompanied with an expansion of all the layers of the disc, and of a corresponding increase of the chamber or locus and the contained gelatinous tissue.\*

To illustrate the increase in size of the electrical elements, a point of considerable importance, I have introduced four figures (Plate 29, figs. 17–17c), which represent four discs from fish varying from 45·5 centims. to 182 centims. in length. Fig. 17 represents one of the largest and best-formed discs from the organ of a Skate (*R. batis*) 45·5 centims. (18 inches) in length; fig. 17a, from a fish 61 centims. (2 feet) in length; fig. 17b, from a fish 91 centims. (3 feet) in length; while fig. 17c represents a disc from a fish 182 centims. (6 feet) in length. All the figures were drawn to the same scale, with the aid of a camera, and in each case the posterior or alveolar aspect is represented. The increase in size between the 18-inch and the 6-foot fish is very striking.

Taking all the facts given above into consideration, it appears that, as already stated, from a morphological point of view the electric organ of *R. batis* is as complete and elaborate as the organ of the Torpedo, and that, as in the Torpedo, it increases in dimensions as the fish increases in size. Further, from the observations of SANDERSON and GOTCH, the Skate's organ is, from a physiological point of view, as perfect as the Torpedo's organ; this does not imply that the Skate's organ is as useful as the Torpedo's, or even that it is of any service whatever. The electromotive force of the shock, *i.e.*, the electromotive force corresponding to 1 centim. of the Skate's organ has been "roughly estimated to be about half a volt. In Torpedo it is probably ten times as much."† This difference, I believe, from a comparison of the two organs, is sufficiently accounted for by the difference in the size and

\* For example, the area of typical discs in a Skate 61 centims. (24 inches) in length, is from ·8 to 1·0 square millims., while in a Skate 167 centims. (5½ feet), they measure from 1·4 to 1·6 square millims., and in Skate over 182 centims. (6 feet), they have an area of more than 2 square millims.

† SANDERSON and GOTCH, *loc. cit.*

arrangement of the electric plates. When due allowance is made for the structural differences, there seems no escape from the conclusion that the organ of the Skate is not only physiologically as perfect as that of the Torpedo, but further that, taking the plate as the unit, the value per square millimetre in the Skate is equal to, if not greater than in the Torpedo.

### III. THE MODIFICATIONS OF THE ELECTRIC ORGAN IN THE SKATE GENUS.

I have found two distinct forms of electrical elements in the Skate genus—the *disc-shaped* and the *cup-shaped*, the latter occurring in three well-marked modifications. In seven of the ten British species of Skate, the organ is made up of discs; in the remaining three it consists of cups. Those having discs are—*R. batis* (LINN.), *R. macrorhynchus* (RAFF.), *R. alba* (LACEP.), *R. oxyrhynchus* (LINN.), *R. clavata* (LINN.), *R. maculata* (DONOV.), and *R. microcellata* (MONTAGU); those with cups are—*R. radiata* (DONOV.), *R. circularis* (COUCH.), and *R. fullonica* (LINN.). Through the kindness of the United States Fish Commission, I have had an opportunity of examining a number of Skate from the West Atlantic, and I have also examined several species taken in Simon's Bay, S. Africa.\* In all the foreign species examined, the organ consisted either of discs or cups; one, which I identified as *R. eglanteria*, a species, according to GÜNTHER, allied to *R. circularis*, had cups extremely like those of *R. circularis*. In all the species having disc-shaped elements, there seems to be a complete agreement in the structure, extent of elaboration, and arrangement of the discs. But, while all the disc type of organs agree in structure, they undoubtedly differ in the time of appearance, rate of development, relation to the spinal column, and especially in the size ultimately reached. In *R. alba* the organ closely agrees in size with that of *R. batis*, and in *R. macrorhynchus* it also reaches a considerable size; but in the other British species I have no evidence to show that it ever measures over 40 centims. (16 inches) in length, or weighs more than 11 grammes, *i.e.*, about, at the most, one-twelfth the weight of the organ of a large *R. batis*. This being the case, it may be inferred that the shock from the electrical apparatus of the majority of the British species of Skate would be much weaker than the shock from a large *R. batis* or a *R. alba*, most probably so weak that it would be impossible to detect it without the use of the electrometer or some other instrument. Hence, should it be afterwards shown that the electric organ of a large *R. batis* is of use, it will not necessarily follow that the much weaker batteries of the smaller species are also useful.

As already mentioned, I have recognized three distinct modifications of the cup-shaped elements. These three variations are illustrated by the three British species having electric cups, *viz.*, *R. radiata*, *R. circularis*, and *R. fullonica*. One of the most interesting facts about the cups in these three species is that they seem to

\* For the specimens from Simon's Bay I am indebted to Surgeon ANDREW F. BALFOUR, M.B., of H.M.S. "Stork."

represent three important stages in the evolution of the disc-like electrical elements out of muscular fibres—the cups in *R. radiata* being at the best only modified muscular fibres, while the cups in *R. fullonica* approach, in many respects, the discs of *R. batis*. The structure and development of the organ of *R. radiata* I have previously described.\* Since writing the account of the organ of this species I have examined the organs of *Gymnotus*, *Malapterurus*, and *Mormyrus oxyrhynchus*, and re-examined the organ of *Torpedo*, with the result that I am convinced that *R. radiata* possesses the most primitive form of electric organ that we are at present acquainted with. While in the newly-hatched *R. batis* the electric organ is completely developed (the development is completed still earlier in *R. clavata*), the organ does not begin to appear in *R. radiata* for some time after hatching, probably not sooner than six months after hatching, *i.e.*, probably not less than eighteen months after the development of the fish commenced. Hence it cannot be said that in *R. radiata* the electric organ makes its appearance early, or reaches its highest stage of development in the embryo. But not only is the organ late in appearing, its rate of development is extremely slow, being only completed about the time maturity is reached, and when at its maximum only measuring 13 centims. ( $5\frac{1}{2}$  inches) in length. What is perhaps still more remarkable is that, in the largest specimens of *R. radiata* hitherto recorded,† each electric element consisted of a muscular fibre which, though altered to support a large electric plate, retained its characteristic striations.‡ Further, although the cups are arranged to form cones which correspond to the electric cones of *R. batis*, the electric elements in *R. radiata* are not provided with distinct loculi or chambers, but are simply separated from each other by the myocomma and the intermuscular connective tissue. Through this tissue extend the nerves and blood vessels, the latter often running side by side with the nerves in front of the cups. These electric elements, therefore, while presenting on the one hand the characters of an electrical apparatus, present on the other the structure of muscular tissue. Further experiments may show that, in addition to discharging electric shocks, the altered fibres are still capable of contracting. When the electric cups of *R. radiata* (Plate 30, fig. 18) are contrasted with the discs of *R. batis* (Plate 30, fig. 21), their rudimentary (in an embryological sense) condition is at once evident. Though the electric plate is distinct enough, and has numerous nerve twigs proceeding to its anterior or free surface, it is thinner than in *R. batis*, and not distinctly differentiated into nervous and nuclear laminæ. This thin and relatively small plate (which in *R. batis* rests on an extensive striated layer of equal thickness throughout, and devoid of nuclei) simply lines a shallow, thick-walled, muscular cup. The cup, formed originally by the expansion of a muscular fibre, presents throughout the entire thickness of its wall distinct striation, and, in addition, retains all through its substance numerous muscle nuclei. Further, the

\* 'Phil. Trans.,' 1888, B.

† They were from 45·5 centims. to 48 centims. (18 to 19 inches) in length.

‡ 'Phil. Trans.,' 1888, B, Plate 80, fig. 12.

only representative of the thick alveolar layer, with its complex network of beams, is a thin membrane, apparently the only slightly altered sarcolemma.\* Taking these and other facts into consideration, there seems little escape from the conclusion that in *R. radiata*, either comparatively little progress has yet been made in the evolution of an electric organ, or, for some reason or other, at a comparatively early stage the development of the electric organ has been arrested. The question as to whether the organ in *R. radiata* is or is not in a vestigial condition was considered in a previous paper. All the facts that have been recently accumulated seem to me to point to *R. radiata* being one of the most primitive members of the Skate group. If this is established, it will support the view that the electric organ of Skates does not belong to vestigial structures. In discussing the place of *R. radiata* in the phylogeny of its group, various questions require consideration. From what we know of the ancestral history of Mammals, Birds, and Reptiles, it seems probable that the smaller (dwarfed and degraded forms excepted) rather than the larger species of any given genus are most likely to present ancestral characters. In the case of the Skate genus, the probability is that the smaller species (e.g., *R. radiata* or *R. circularis*) found in our waters more closely resemble the ancestral forms than the large *R. batis* or *R. alba*. In other words, it is more likely that the Skates have sprung from small generalized Selachians than from extinct forms as large, e.g., as *Læmargus*, which implies that *R. batis*, and other still larger species, do not owe their great size to the fact that they are large Sharks flattened out, but rather that they are Skate whose ancestors have continued to produce large varieties, which have best succeeded in the struggle for existence. If this is the case, if the ancestors of the Skates were comparatively small forms, it will, it appears to me, be impossible to account for the existence of the electric organ by looking upon it as a vestige of a large useful ancestral structure—a view which neither seems to be warranted by the developmental history nor the behaviour after development. From an embryological standpoint, *R. radiata* appears to be in various aspects more Shark-like than either *R. batis* or *R. clavata*.† Further, according to the observations of HOWES, recently communicated to the Zoological Society,‡ *R. radiata* is, in structural points, more primitive than other Skate. It appears that there is a continual increase in the mesopterygeal area of the skeleton of the pectoral fin as one passes from the *Rhinobatidæ* through the *Raiadæ* to the *Myliobatidæ* and *Trygonidæ*; and especially that while in the *Rhinobatidæ* the number of rays represented is 10 to 14, in *Raiadæ* (with the exception of *R. radiata*) 12 to 18, and in the *Trygonidæ* as many as 26, in *R. radiata* the number is only 10 to 11.

The second modification of the cup-like electric elements is found in *R. circularis*,

\* 'Phil. Trans.,' 1888, B, Plate 80, fig. 12.

† This conclusion is based partly on the size of the egg and partly on the appearances assumed during the early stages of development.

‡ 'Proc. Zool. Soc. Lond.,' December 2, 1890.



a species which is nearly double the size of *R. radiata*, often reaching a length of over 3 feet (90 centims.). Although I am not yet in a position to state when the transformation of the muscular fibres begins in this species, I know that the rate of development is much more rapid than in *R. radiata*. Further, the organ, though relatively smaller than in *R. batis*, reaches a considerable size. In the young *R. circularis* the muscular fibres destined to form electric elements soon reach a stage resembling the cups in the full grown *R. radiata*. This stage once reached, further changes take place which result in the formation of large, deep, well-moulded cups with delicate rounded stems (Plate 30, fig. 19). The wall of the cup consists of a relatively thick striated layer of delicate wavy lamellæ,\* similar to those of the corresponding layer in *R. batis*. Surrounding this layer is a thick nucleated cortex, which evidently takes the place of the alveolar layer in *R. batis*, and forming a complete lining for the cup is the electric layer to which proceeds a countless number of nerve fibres.† The striated layer in *R. circularis* differs from the corresponding layer in *R. batis*, in having a number of nuclei scattered through its substance, and in being unequal in thickness. The electric layer only differs from that in *R. batis* in being slightly thicker (Plate 28, fig. 14a). It is as richly nucleated and has as many nerve fibrils reaching it, and the loops and pits in connection with the nervous lamina are even more distinct than in *R. batis*. The inner surface of the electric layer presents, as stated above, numerous delicate lines which occupy the same position as, and seem to correspond to, the “nerve hairs” of RANVIER, and the “palisade” of REMAK (Plate 28, fig. 14a). This striated appearance I have not yet detected in *R. batis*, though the organ was treated in exactly the same way as that of *R. circularis*, showing the palisade-like striation. The cortical layer which is of a considerable thickness, consists of dense protoplasm, containing numerous nuclei, closely resembling those in the electric plate.‡ The thickness is nearly uniform, but on the outer surface, more especially around the base of the stem, there are frequently delicate, short, blunt, projections, which evidently correspond to the rudiments of the processes of the alveolar layer, seen in the late club-stage of *R. batis*. The inner part of the cortex is granular, while the outer is distinctly striated. The nuclei enveloped in a layer of clear protoplasm, lie in the granular protoplasm immediately within the striations. This remarkable layer, which is continuous round the margin of the cup with the electric layer, is developed in connection with the sarcolemma, and corresponds to the complex alveolar layer of *R. batis*, and the thin indistinct investing membrane of the cups of *R. radiata*. It is on an average four times thicker than the electric layer, and many times thicker than the sarcolemma-like investment of the cups in *R. radiata*. At the base of the stem it becomes continuous with the sarcolemma of the stem of the cup—the distal portion of the original muscular fibre.

\* ‘Phil. Trans.,’ 1888, B, Plate 68, figs. 3 and 4.

† For an account of the organ of *R. circularis*, see ‘Phil. Trans.,’ 1888, B.

‡ ‘Phil. Trans.,’ 1888, B, Plate 68, fig. 5.

The third, and only other form of electric cups hitherto discovered, is found in *R. fullonica*. This Skate, though frequently larger than *R. circularis*, never approaches in size either *R. batis* or *R. macrorhynchus*. The organ, however, is relatively larger than in *R. circularis*. In a 3-foot fish it measured 43 centims. ( $1\frac{3}{4}$  inches) in length, and nearly 1 centim. in diameter at the thickest central portion. While the organ of *R. circularis* resembles a flattened spindle, the organ of *R. fullonica* forms a nearly perfect circular spindle, the keel-like ridge which in *R. batis* and others projects inwards towards the vertebral column, being absent.

The cups in *R. fullonica* (Plate 30, fig. 20), except in one respect, are almost identical in structure with those of *R. circularis*. They are usually well moulded and deep, and provided with a distinct stem. The stem, however, varies more than in *R. circularis*. In some cases it is short and thick and in others long and slender, or slender near the cup, and expanded at the distal end. The electric and striated layers will probably be found, when sections of carefully preserved organs are obtained, to be identical with the corresponding layers in *R. circularis*. The great difference between the cups of the two species is in the outer or cortical layer. In *R. circularis*, as stated above, there are extremely short, rounded projections from the outer surface of the cortex, but in *R. fullonica* the entire outer surface of the cup presents numerous simple and compound nucleated processes (Plate 30, fig. 20), similar to those found in the half developed discs of *R. batis*.\* In transverse sections these processes give the outer surface of the cups an extremely irregular appearance, which at once distinguishes them from those of *R. circularis*, and indicates an approach to the conditions which obtain in *R. batis*. But even in full grown specimens of *R. fullonica* these projections, though sometimes provided with secondary processes, never seem to unite to form a network, hence in surface views instead of seeing several layers of beams with spaces diminishing in size from without inwards, only a series of irregular pits or depressions are visible.

When figs. 18 to 21 are compared, we seem to have an excellent illustration of progressive development. All the figures are from adult members of the four species under consideration, viz., *radiata* (18), *circularis* (19), *fullonica* (20), and *batis* (21), and they were all drawn, with the aid of the camera, to the same scale. From *radiata* it is no great step to *circularis*, from *circularis* it is a still easier step to *fullonica*, in which, although the form is different, the electric layer seems to be identical with that of *batis*, while the cortical layer has developed a long way in the direction of the alveolar layer of *batis*.

From the observations made up to this point, it appears that there is not only abundant evidence of progressive growth in the electric organ of *R. batis*, but also evidence of progressive development of the electric organ in the Skate genus. In *R. radiata* the electrical elements have been shown to be extremely simple, little

\* A short account of the organ of *R. fullonica* will be found in Dr. PURVIS' Graduation Thesis, MS., the University Library, Edinburgh.

more than muscular fibres, each with a large motor plate at its expanded anterior end. This simple condition of the electric elements, which cannot, it appears to me, be accounted for by saying that in *R. radiata* the organ has undergone retrogressive changes, is accompanied with a more primitive condition of the pectoral fin than is found in other Skates and Rays, and with certain affinities to generalised Selachians during development. In *R. circularis*, although the electrical elements are still in the form of cups, a decided advance has taken place. The elements are larger—instead of shallow, thick-walled cups, there are deep, well-moulded cups, lined with a highly differentiated electric layer, and provided with a thick, dense, nucleated cortex, in place of the thin sarcolemma-like investment found in *R. radiata*. Further, the development is more rapid, the anterior ends of the original muscular fibres instead of retaining their characteristic striations have been modified to form a thick, non-nucleated, striated, or meandriiform layer, similar to the middle layer in *R. batis*. In fact the muscular fibres have been so profoundly altered that without a knowledge of the development of the cups in *R. circularis*, it would be impossible to make out that they were in any way related to muscular tissue.

In *R. fullonica* a still further advance has been made towards the conditions found in *R. batis*, and the other Skate having disc-like electrical elements. Evidence of this advance is especially found in the alveolar layer, which in structure stands midway between *R. circularis* and *R. batis*—there being outgrowths larger and more complex than in *R. circularis*, but not so complex as in *R. batis*.

I may add, by way of conclusion, that my investigations have not yet enabled me to offer any opinion as to the method by which the electric organs of fishes have been produced. Until it is possible to show that during the initial stages, that during the generations while the muscular fibres were being slowly transformed into electrical elements, the developing organ was of some real use to the species, it is impossible to account for its appearance by the direct influence of natural selection. It might be supposed that the muscular fibres during the process of transformation retained their ordinary function, until their greatly overgrown motor plates were able to discharge shocks sufficiently powerful to tell in the struggle for existence, and that, this stage being reached, natural selection stepped in and, while neglecting the muscular fibres, carefully attended to the further elaboration of their motor (electric) plates. When the unique condition of the electrical elements in *Raia radiata* is considered, some such argument as the above might be maintained. But even if it were shown that a given number of muscular fibres retained their power of contracting until their combined overgrown motor plates were able to discharge serviceable shocks, no explanation of the increase in size of the motor plates would be given.

It is doubtless possible that electric organs are intimately related to some other structures, that correlation of growth may account for their presence. Taking into consideration the complexity of electrical organs, and especially their richness in nerve tissue, I am inclined to think that it will be found as difficult to discover the structure

or structures that served as a foster-brother to the electric batteries, as it has been to discover their independent origin. I am unable to think of any structures in any of the electrical fishes which, as they developed, could induce muscular fibres in various parts of the body to transform themselves into electric batteries.

It seems to me that we must look to physiologists for an explanation of the transformation of muscular fibres into electrical elements, and that the secret of the origin of electrical organs will only be revealed when the physiology of muscles and nerves is better understood.

#### SUMMARY OF OBSERVATIONS ON THE ELECTRIC ORGAN OF THE SKATE.

The electric organ of the Skate was discovered in 1844 by Dr. STARK of Edinburgh, and a valuable account of its structure was published by ROBIN in 1846. This was supplemented by further observations by ROBIN, published in 1865, and in 1872 BABUCHIN shortly described its development, while the physiology has recently been considered at great length by BURDON SANDERSON and GOTCH.

In the common Skate (*R. batis*), specimens of which, over 7 feet in length, are frequently taken in British waters, the first indication of an electric organ is found in embryos from 6 to 7 centims. in length.\* At first the muscular fibres of certain muscular cones at each side of the vertebral column, in the region of the tail, become club-shaped. The clubs, after increasing considerably in length, and having their rounded anterior ends enlarged, assume an indistinct cup form, and each then gradually expands transversely to form a large electric disc, while the remainder of the muscular fibre is reduced to a delicate, often ribbon-shaped, stem, which retains few, if any, indications of the original striation.

When the development is complete, each disc is found to consist of three distinct layers and to occupy a connective tissue chamber (*loculus*), which also contains gelatinous tissue, nerves, and blood vessels. The layers of the disc from before backward are, (1) the electric layer, (2) the striated layer, and (3) the alveolar layer. The electric layer is made up of (1) a nervous lamina, consisting of granular protoplasm into which the nerves enter and terminate, and (2) of a nuclear lamina, containing nearly regularly disposed nuclei, each surrounded by a zone of clear protoplasm. The electric layer is developed in connection with the sarcolemma and may be looked upon as a greatly enlarged motor plate. The striated layer consists of numerous delicate lamellæ, which often present a wavy or contorted appearance in section. This layer, which, except in rare cases, is devoid of nuclei, seems to be formed by the direct modification of the anterior end of the original muscular fibre. The attenuated posterior portion of the muscular fibre extends backwards from the striated layer in the form of a slender ribbon-like stem, presenting granular nuclei at irregular intervals, and here and there faint striation.

\* A length of 6 centims., Dr. BEARD informs me, indicates that an embryo is about 7 months old.

It has been estimated that well-formed discs in a large fish (180 to 210 centims., 6 to 7 feet in length) have a superficial area of 2·08 square millims., and that there are about 10,000 discs in each organ. The majority of the discs have a quadrangular form, but, as a rule, at the apex of the cone, and especially near the base, the discs have an irregular outline, sometimes presenting an elongated appearance, and at other times being small and nearly hexagonal in outline.

The alveolar layer consists of a complex network, the trabeculæ of which are formed from prong-like outgrowths that make their appearance at a comparatively early stage around the base of the stem. The alveoli vary in size and are occupied by gelatinous tissue, traversed by capillaries, which, though in close proximity to the disc proper, never penetrate its substance. Each locus is formed partly out of the original inter-muscular septa (myocomma) between which the muscular fibres extended, and partly from the connective tissue surrounding the fibres. In longitudinal sections, each disc appears to be suspended from the anterior wall of its locus by the numerous nerve fibres which proceed through the anterior gelatinous tissue to terminate in the electric layer, while from the alveolar layer of the disc prong-like projections are seen to extend backwards into the thick layer of gelatinous tissue that occupies the posterior and largest portion of the locus. In some cases the degenerated posterior part of the original muscular fibre is seen proceeding obliquely backwards, to lose itself in the intercolumnar tissue. The loculi or chambers in which the discs lie are arranged to form a series of honey-combed cones having their apices directed forwards. These electric cones, which, with the exception of the first, fit accurately within each other, vary in length. After increasing slightly from before backwards they, first gradually, and then rapidly, diminish in length, the terminal cones consisting of only a few discs. The united cones thus form a spindle-shaped organ which, throughout the greater part of its length, extends from the skin on the outer side of the tail to the side of the vertebral column. On the inner aspect, however, the rounded form is lost through the presence of the dorsal and ventral rows of muscular cones and the muscles of the dorsal fin, which together, by, as it were, compressing the organ, produce a keel-like ridge that extends inwards and abuts against the sides of the caudal vertebræ. The first electric cone is invested by the last of the muscular cones with which the electric organ is continuous, which implies that the anterior part of the organ (about one-third) is provided with a complete muscular investment, which increases in thickness from behind forwards as the muscular cones increase in number.

In the tail of the embryo Skate, as in less specialised Selachians, there are five rows of more or less complete muscular cones, three above and two below the transverse septum that extends from the vertebral column to reach the skin on a level with the lateral line. Of these rows, the middle and largest one, which lies immediately above the transverse septum, contains the fibres by a transformation of which the electric organ is formed. The nerves and vessels of the organ resemble in their origin and arrangement the vessels and nerves which supply the corresponding muscular cones in

Sharks and Dogfishes; they run along between the electric cones, the nerves penetrating the loculi in front of the discs, while the vessels enter behind the disc and ramify in the thick posterior layer of gelatinous tissue.

The development of the organ is practically complete when the Skate has reached a length of 12 centims., *i.e.*, before it leaves the egg capsule. Further changes consist in the increase in size of the various parts of the organ, not in the addition of new elements by the further transformation of muscular fibres. In fish about 60 centims. (24 inches) in length the tail measures about 28 centims. (11 inches), the organ 22·5 centims. (9 inches), and the well-formed discs have an area of from 0·8 to 1 square millim. In fish about 165 centims. (about 5½ feet) the tail measures 60 centims. (24 inches), the organ 45 centims. (18 inches), and the discs have an area of from 1·4 to 1·6 square millims., while in still larger Skate, about 225 centims. (7½ feet), the tail is about 85 centims. (32 inches), the organ 70 centims. (28 inches), and the discs have an area of about 2·08 square millims. The increase in the area of the discs is accompanied not only with an increase in the circumference of the entire organ, but also with an increase in its length and weight as the following table shows :—

Length of fish.	Length of organ.	Weight of organ.
Centims.	Centims.	Grms.
25·5 to 30·50	12·78 to 14·00	0·5 to 0·6
45·5 to 53·40	15·25 to 20·25	0·8 to 1·8
61·0 to 68·50	21·50 to 28·00	2·3 to 5·0
83·5 to 91·25	30·50 to 34·25	6·0 to 8·0
137·0	44·50	16·80
157·0	48·25	25·00
182·5	53·25	70·75
213·0	61·00	145·00
225·0	70·00	156·00

There is no evidence that the increase in size is accompanied with any retrogressive change in any of the essential parts of the disc.

SANDERSON and GOTCH concluded that the Skate's organ corresponds in function as well as in structure with the electrical organs in fishes, but that a piece of the Torpedo's organ would be about ten times more powerful than a corresponding piece of the Skate's organ.

From a comparative study of the electric organ in the Torpedo and the Skate it appears that the most essential part, the electric layer, is similar in both, but that the striated and alveolar layers, together with the thick posterior layer of gelatinous tissue of the Skate, are only represented in the Torpedo by a thin layer of connective tissue, the dorsal lamina of RANVIER and others. The absence of these layers in the Torpedo is accompanied with (when compared with the Skate) a great increase in the number of the electrical elements and with an increase in area of each electric layer,

with the result that any given piece of the Torpedo's organ would contain a larger number of elements than a corresponding piece of the Skate's organ. A centimetre of the Skate's organ, for example, would contain about 680 electrical elements or discs, each with an area of about 1.64 square millims., while a corresponding piece of the Torpedo's organ would contain about 1680, each having an area of about 9 square millims.

Further experiments may show that the individual electric plates of the Skate are, when allowance is made for their size, at least as powerful as the corresponding structures in the Torpedo.

In all the other British Skate, with the exception of *R. fullonica*, *R. circularis*, and *R. radiata*, the electric organ resembles that of *R. batis*. In each case the electric elements are in the form of discs, but only in two of them, *R. alba* and *R. macro-rhynchus*, is there any evidence that the organ reaches a large size. The organ is, in fact, so small in most of the members of the Skate genus that it is difficult to imagine what useful purpose it can serve; but as to its utility some light may be thrown when we understand the use (granting there is any) of the large organ of full-grown specimens of *R. batis*, say of specimens 7 feet in length, with an electrical apparatus weighing about 300 grms.

The more important stages through which the relatively large and complex electrical elements of *R. batis* have passed during their evolution seem to have been, as it were, stereotyped in the three British species of Skate in which the electric organ consists of electric cups, *i.e.*, in *R. radiata*, *R. circularis*, and *R. fullonica*.

The small and apparently primitive species, *R. radiata*, possesses the most primitive form of electrical organ that can well be imagined; instead of complex discs or greatly specialised plates the organ of *R. radiata* consists of structures which, though no longer resembling muscular fibres in appearance, present the characteristic muscular striation as well as the large protoplasmic plate, with its countless nerve fibres, so characteristic of electric organs. In the larger species, *R. circularis*, the relation of the electrical elements, even in comparatively young fish, to muscular fibres is no longer evident. The organ is relatively much larger than in *R. radiata*, and chiefly differs from that of *R. batis* (1) in having cups instead of discs, (2) in possessing instead of a complex alveolar layer a thick cortex with only the merest rudiments of processes (prongs) projecting from its outer surface, and (3) in being separated from the vertebral column by the dorsal and ventral rows of muscular cones or their tendons.

In the case of *R. fullonica* the organ is larger than in *R. circularis*, and both in size and structure it more closely approaches *R. batis*. The chief point of interest in *R. fullonica* is that while the electrical elements, as a whole, closely resemble those of *R. circularis*, the outer layer, in *R. fullonica*, stands midway in structure between *R. circularis* and *R. batis*, being thick and dense as in the one, but provided with prongs or processes, simple and complex, as in the case during development of the

other. Further, in *R. fullonica* the arrangement of the electrical elements more closely resembles that found in *R. batis* than is the case in *R. radiata* and *R. circularis*.

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#### EXPLANATION OF PLATES 26-30.

##### PLATE 26.

- Fig. 1. Longitudinal vertical section of *Scyllium*, immediately posterior to second dorsal fin, showing five myotomes, bent zig-zag fashion, so as to form five muscular cones. Of these, three, the dorsal (*d.*), middle or lateral (*l.*), and ventral (*v.*), have their apices directed forwards, while the remaining two, the dorso-lateral (*d.l.*) and ventro-lateral (*v.l.*), have their apices directed backwards. The myotomes consist of fibres (*f.*), which assume a more and more longitudinal direction as the apices of the cones are reached. The fibres extend between connective tissue lamellæ, the myocomma (*m.*), and are so arranged that, if the handle of a scalpel is carried along two rows of cones, the surface of the one row is left smooth, while the other presents a rough appearance. The coloured lateral row of cones corresponds to the row which, in the Skate, is transformed into the electric organ. *s.*, skin of dorsal aspect; *s.v.*, skin of ventral aspect.
- Fig. 2. Transverse section through *Scyllium*, immediately behind the second dorsal fin, showing the five muscular cones represented in fig. 1. The cones vary in shape and size, the dorsal (*d.*) and ventral (*v.*) are small, while the lateral (*l.*) presents the most regular outline. The lateral rests on the transverse septum (*s.*) which extends from the vertebral column to reach the skin on a level with the lateral line (*l.l.*). *d.l.*, dorso-lateral row, and *v.l.*, ventro-lateral row of cones. Fig. 1 was drawn from a section made through the line AB. The electric organ in the Skate occupies the position of the lateral row (*l.*), coloured as in fig. 1.
- Fig. 3. Transverse section through the tail of *Lamna cornubica* (Porbeagle), behind the second dorsal fin. In *Lamna* the root of the tail is considerably flattened, and the flattening has been accompanied by a reduction in the size of the dorso-lateral (*d.l.*) and ventro-lateral (*v.l.*) rows, and with a great increase of the lateral (*l.*) row of cones—the row which is transformed into the electric



organ in the Skate. In *Lamna* the transverse measurement is more than double the vertical, and the number of cones seen in the upper (*d.*), middle (*l.*), and ventral (*v.*) rows is far greater than in *Scyllium*. This is due to the cones being longer.

Fig. 4. Transverse section through the root of the tail of *Myliobatis*. The tail is less flattened than in *Lamna*, and, though the lateral row of cones (*l.*) is large, the dorso-lateral (*d.l.*) and ventro-lateral (*v.l.*) are distinct and nearly as large as the dorsal (*d.*) and ventral (*v.*). By comparing the lateral row of cones in figs. 2, 3, and 4, it will be observed that, while there are only two cones seen in section in *Scyllium*, there are nine complete cones in *Lamna*, and eight in *Myliobatis*.

Fig. 5. Transverse section through the tail of a large specimen of *R. batis*, about 18 centims. behind the pelvic fin, and on a level with the tip of the electric organ (*o.*). The five rows of cones found in *Scyllium*, *Lamna*, and *Myliobatis* are easily recognised, viz.:—the dorsal (*d.*), dorso-lateral (*d.l.*), lateral (*l.*), ventro-lateral (*v.l.*), and ventral (*v.*). The dorso-lateral and ventro-lateral are better developed than in *Lamna*, but the lateral, which only presents six complete cones, is relatively smaller than in *Lamna* and *Myliobatis*. By comparing figs. 3, 4, and 5 it is evident that the tail of the Skate differs considerably from the tails of *Lamna* and *Myliobatis*, agreeing more with the Shark than its ally *Myliobatis*, but differing from *Lamna* in presenting a flatter under-surface, and in having the lateral fold approaching the ventral, instead of the dorsal, aspect. Note that a number of tendons (*t.*) lie embedded in the dorsal (*d.*) and ventral (*v.*) rows of cones.

## PLATE 27.

Fig. 6. Longitudinal vertical (sagittal) section through the anterior part of the electric organ (blue part), and of the unaltered muscular cones (*l.m.*) of the lateral row, that lie immediately in front of and partly invest the organ. The two most anterior electric cones (*c.c.*) are almost completely represented, and there are portions of four others. It will be observed that the electric cones closely resemble the muscular cones in their arrangement, size, &c., but while the muscular fibres have an oblique, and in some cases nearly a longitudinal direction, the electric elements have a nearly transverse direction. The longest limb of the first cone measures over 11 centims. in length. It will be observed that the discs at the apex and near the base of the first cone are small and irregular in outline.

Fig. 7. Ventral view of the electrical organs of the Skate *in situ*. On the right side of the drawing only the skin has been removed, on the left side the entire length of the organ has been exposed by the removal of the skin, muscles,

and tendons, and half of the hæmal arches have also been removed to show better the relation of the organ to the caudal vertebræ. Fig. 7, together with figs. 6 and 8, show that the anterior part of the organ is completely invested by muscular cones, and that the transition from the one to the other is most abrupt. The organ throughout nearly three-fourths of its length is in contact with the vertebral column, and it is only separated from the skin by the wedge-shaped dorsal and ventral muscles. On the ventral, and still more on the dorsal, surface, the organ is grooved for these muscles, and thus, in transverse sections, presents internally, in most cases, a keel-like ridge. From a fish 140 centims. (56 inches) in length.

Figs. 8-12. Transverse sections through the tail of a Skate, 213 centims. (85·2 inches) in length. The organ measured 60 centims. in length, and weighed 145 grms. Fig. 8, which represents the organ (*o.*), 10 centims. (4 inches) from the anterior end, shows three electric cones, the outer one completely invested by a muscular cone; *d.*, the dorsal row of cones; *d.l.* and *v.l.* the greatly reduced dorso-lateral and ventro-lateral rows; *v.*, the ventral row of muscular cones. Fig. 9 is a section through the organ, 20 centims. (8 inches) from the anterior end. The dorso-lateral and ventro-lateral rows of cones are now represented by small wedge-shaped masses (*d.l.* and *v.l.*), while the organ (*o.*) consists of five all but complete electric cones. Fig. 10 gives a section at 30 centims. (12 inches) from the anterior end of the organ. The dorso-lateral and ventro-lateral rows of muscular cones have now disappeared, and the ventral row is considerably reduced in size. The outer row of electric cones is incomplete, and the organ is deeply grooved on its upper surface for the dorsal muscular band. Fig. 11 shows the organ 45 centims. (18 inches) from the anterior end. The organ, which is now much smaller, only presents three complete cones, is nearly oval in shape, and lies in close contact with the vertebral column. Fig. 12 shows the organ 52·5 centims. from the anterior end (7·5 centims. from its termination). The organ, which is now much larger than the combined dorsal and ventral muscles (*d.* and *v.*), is freely in contact with the vertebral column, and nearly circular in outline.

#### PLATE 28.

Fig. 13. Longitudinal vertical (sagittal) section through a portion of the anterior end of the electric organ, and its investing muscular cones. The electric elements (*l.* and *l.*') which form the cones are arranged in piles, and lie at nearly right angles to the long axis of the tail. The unaltered muscular fibres (*f.*) occupy an oblique position. Like the fibres, the electric elements extend between myocomma (*m.*): they are separated from each other by the altered

intermuscular tissue which, together with the myocomma, form chambers or loculi. The discs proper (*d.*) occupy less than a third of the loculi. In the space in front of each disc lie the nerve-fibres; the larger space behind the disc contains gelatinous tissue and blood vessels, and through it the posterior degenerated portion of the altered muscular fibre (*f.*') is sometimes seen. From a Skate 90 centims. in length  $\times 15$ .

Fig. 14. Section through a disc showing the nerves, the electric (*e.l.*), striated (*s.l.*), and alveolar (*a.l.*) layers. The nerves divide as they approach the disc, and after forming numerous loops (*l.*), enter and terminate in the nervous lamina (*n.l.*) of the electric layer; (*n.*) nuclei on the nerve sheaths; (*nuc. l.*) nuclear laminae of the electric layer with large nuclei. Note the absence of nuclei in the thick striated layer (*s.l.*), the well-developed alveolar layer with large nuclei (*a.n.*), long processes (*p.*), connected by secondary processes (*b.*), to form a network. The gelatinous tissue which occupies the spaces between the nerves and the processes of the alveolar layer is not represented. The electric and striated layers copied from a camera drawing; the alveolar layer is semi-diagrammatic. ZEISS, apochromatic, 2; compensating eyepiece, 12.

Fig. 14a. Drawing showing the structure of the electric layer of *R. circularis*. (*n.*), nerve proceeding to electric lamina; (*n.'*), nuclei on nerve sheath; (*l.*), nerve loops in front of electric lamina; (*n.l.*), electric lamina with nerve fibrils entering. This lamina has a striated appearance, and thus resembles the part of the electric layer of the Torpedo characterised by the "nerve hairs" of RANVIER; (*nuc. l.*), the nuclear lamina corresponding to the nuclear lamina (dorsal half) of the electric layer of the Torpedo; (*st.*), two of the lamellæ of the striated layer. Camera drawing; ZEISS, apochromatic, 2; compensating eyepiece, 12.

## PLATE 29.

Fig. 15. Transverse section of the organ of a Skate, 90 centims. in length, to show the various forms assumed by the electric discs, and to indicate the origin of the electric nerves; (*sp.*), spinal cord; (*d.*), dorsal root of a spinal nerve; (*v.r.*), ventral root, giving off a branch (*e.n.*) to the organ before uniting with dorsal root; (*e.n.'*), electric nerve springing from junction of two roots; (*e.n."*), electric nerve springing from nerve trunk beyond ganglion. Each nerve, by dividing dichotomously, breaks up into numerous branches in front of the disc (*l.*).

Fig. 16. Represents the stage of development reached by a *R. batis* embryo about nine months after the fertilised egg was removed from the oviduct. Compared with the adult, the pectoral fins are small, while the tail is long and broad, and has the two dorsal fins some distance from each other and the tip

of the tail. Compare with fig. 7, in which the first dorsal fin is relatively nearer the end of the tail, and nearer the second fin than in the embryo figured.

Figs. 17, 17A, 17B, 17C. Four camera drawings, to show that the discs increase in size as the fish grows larger; fig. 17 shows a disc from a Skate 45 centims. (18 inches) in length; fig. 17*a*, a disc from a fish 60 centims. (24 inches) in length; fig. 17*b*, a disc from a fish 90 centims. (36 inches) in length; fig. 17*c*, a disc from a fish 180 centims. (six feet) in length. In all the figures the pitted appearance presented by the posterior or alveolar aspect is indicated.

### PLATE 30.

Figs. 18–21. Low-power camera drawings to show the four modifications of the electrical elements found in the British members of the genus *Raia*. Fig. 18, one of the modified muscular fibres which form the electric organ in a full-grown *R. radiata*. The expanded cup-shaped upper part presents throughout the ordinary muscular striation, an enlarged motor plate (the electric layer) lines the shallow thick-walled cup. Fig. 19, a still further altered muscular fibre, one of the electric cups from the electric organ of a full-grown *R. circularis*. The muscular striation has entirely disappeared from the cup, which is deep, well moulded, and lined by an extensive electric plate. Fig. 20, a still further modified muscular fibre, representing the form assumed by the cups which make up the electric organ in *R. fullonica*. The cup is larger but shallower than in *R. circularis*, and instead of a nearly simple cortex, numerous simple and compound villous-like projections extend from the outer surface. Fig. 21, a profoundly altered muscular fibre, one of the discs which make up the electric organ of *R. batis*. The electric layer is many times larger than in *R. radiata*, the striated layer is, except in rare cases, devoid of nuclei, and the simple outer layer or cortex of *R. circularis* is represented by long prongs, which, unlike the processes in *R. fullonica*, give rise, by secondary outgrowths, to a complex network. Figs. 18, 19, and 20 may be looked upon as three stages in the evolution of the more complex disc of *R. batis*.

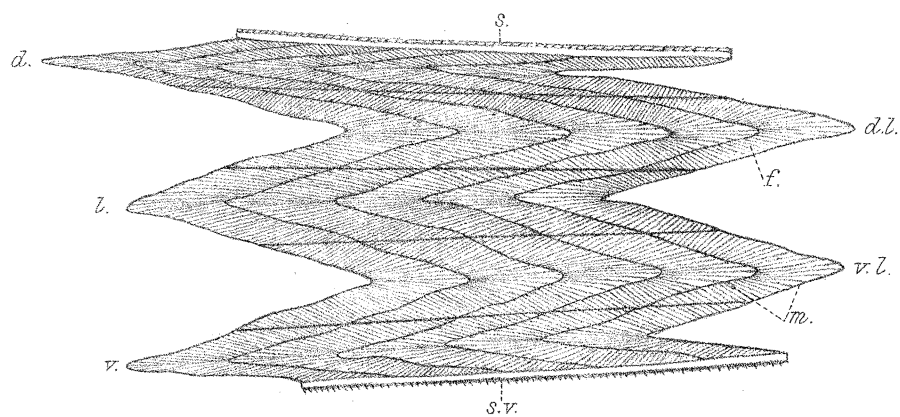


Fig. 1.

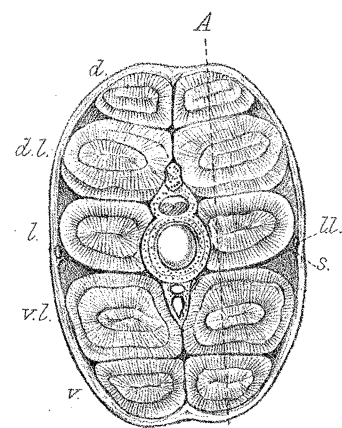


Fig. 2.

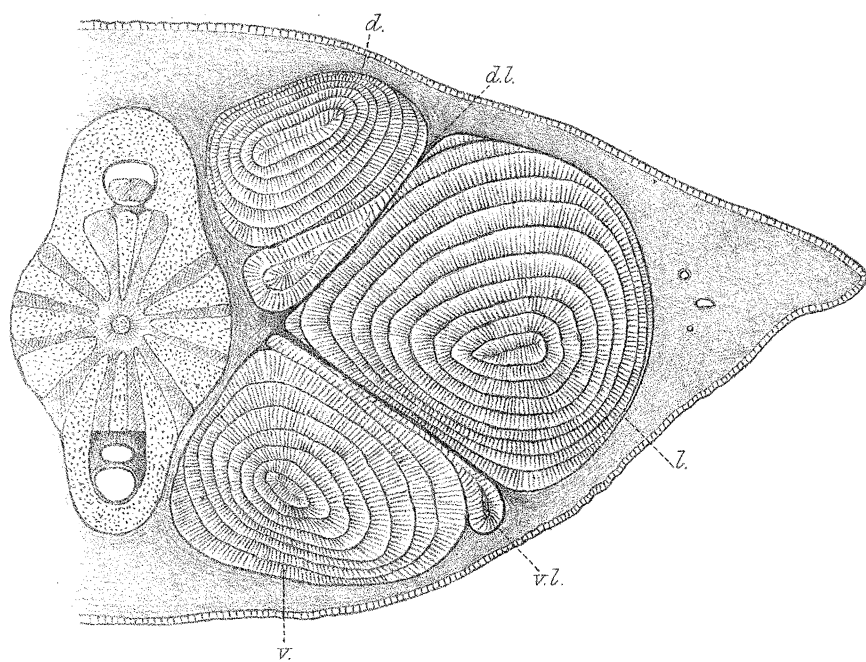


Fig. 3.

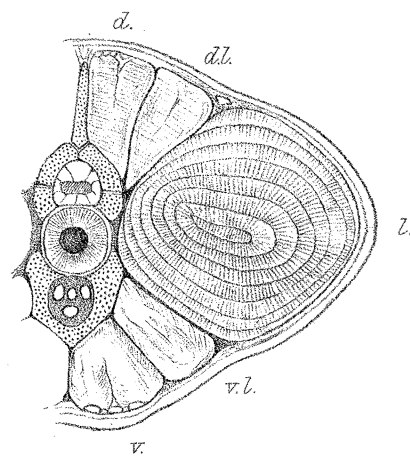


Fig. 4.

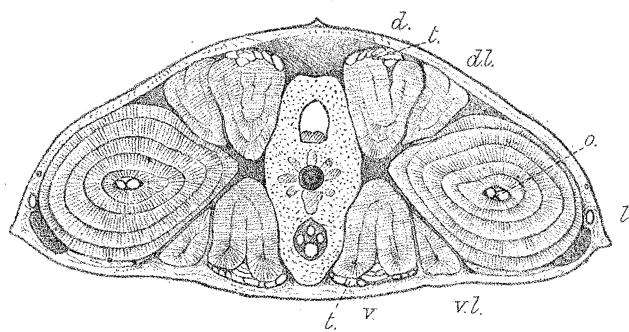


Fig. 5.

*l.m.*

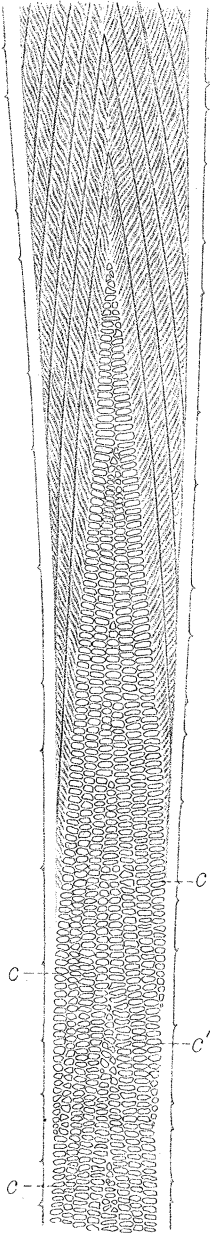


Fig.6.

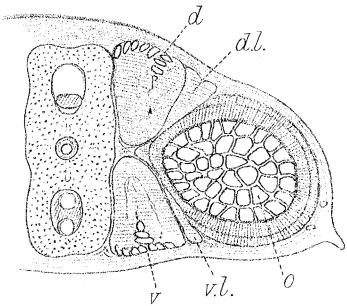


Fig 8.

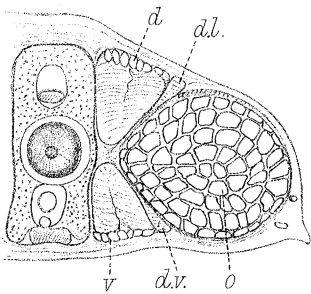
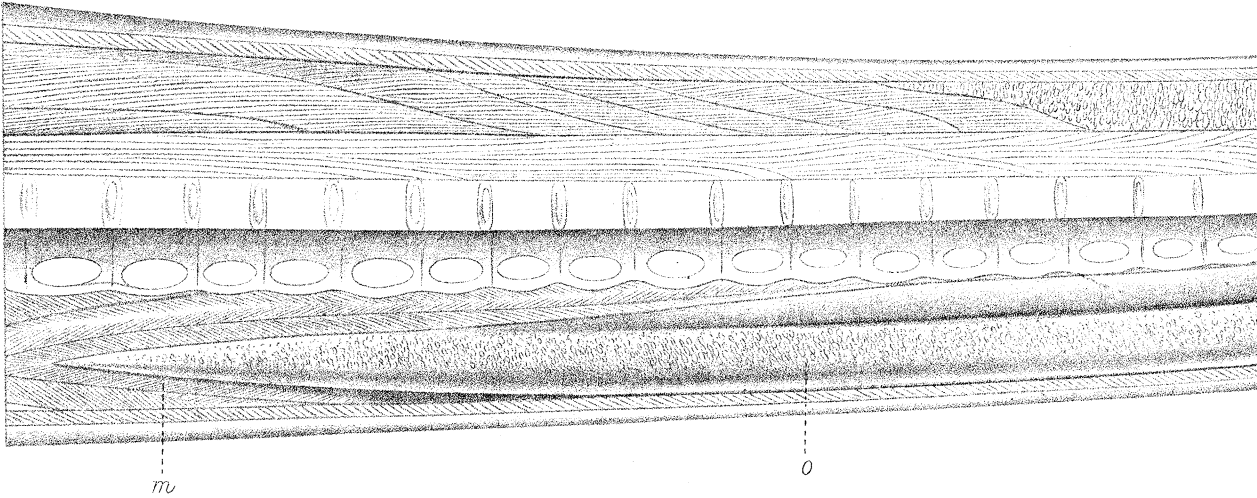


Fig.9.



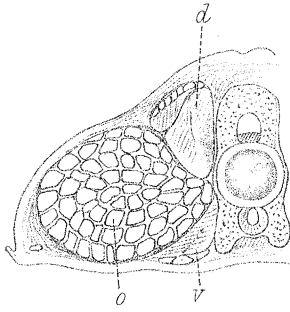


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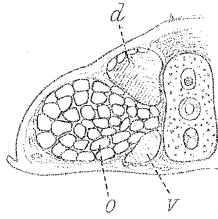


Fig. 11.

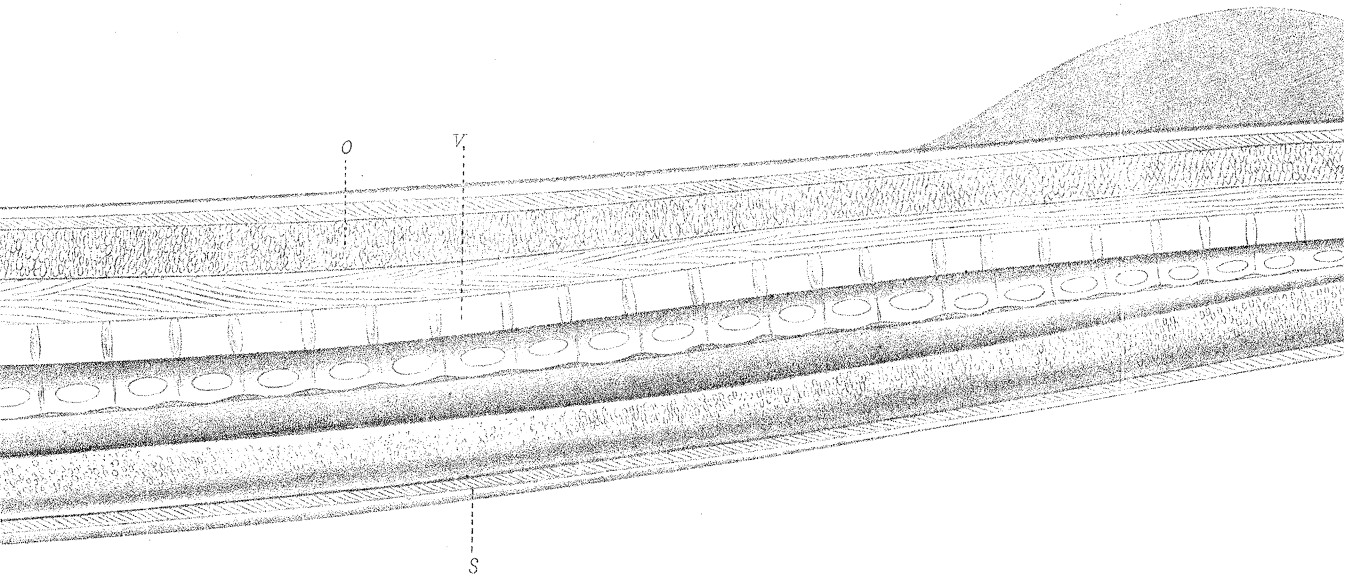


Fig. 7.

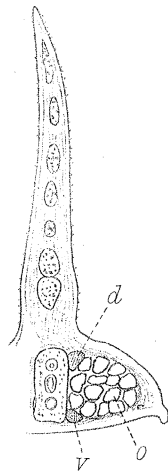
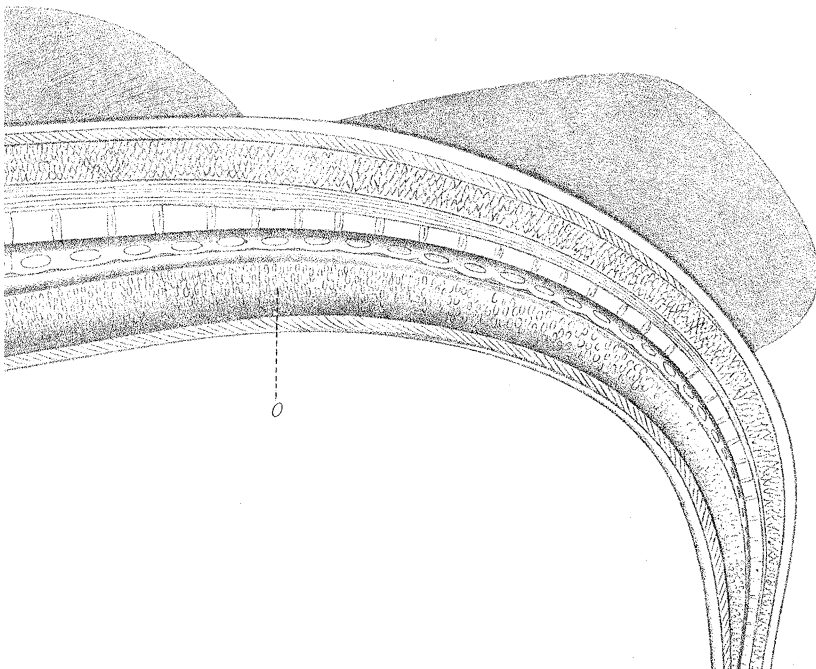


Fig. 12.



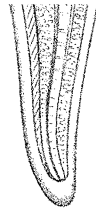


$m$

$0$

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Fig. 7.



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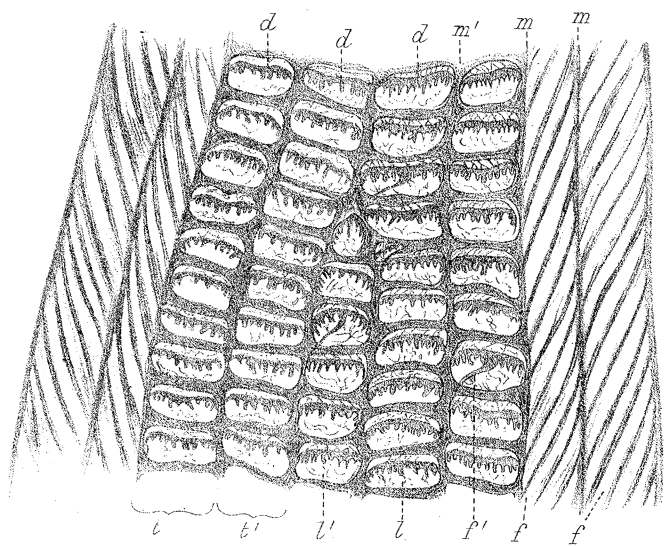


Fig. 13.

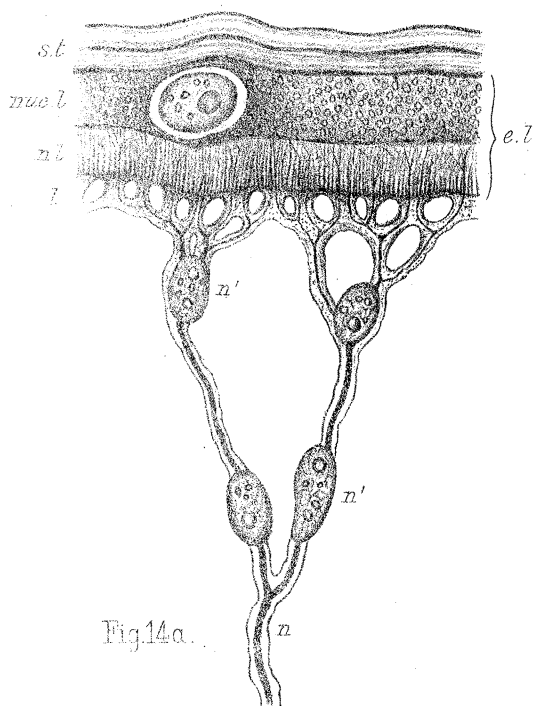


Fig. 14a.

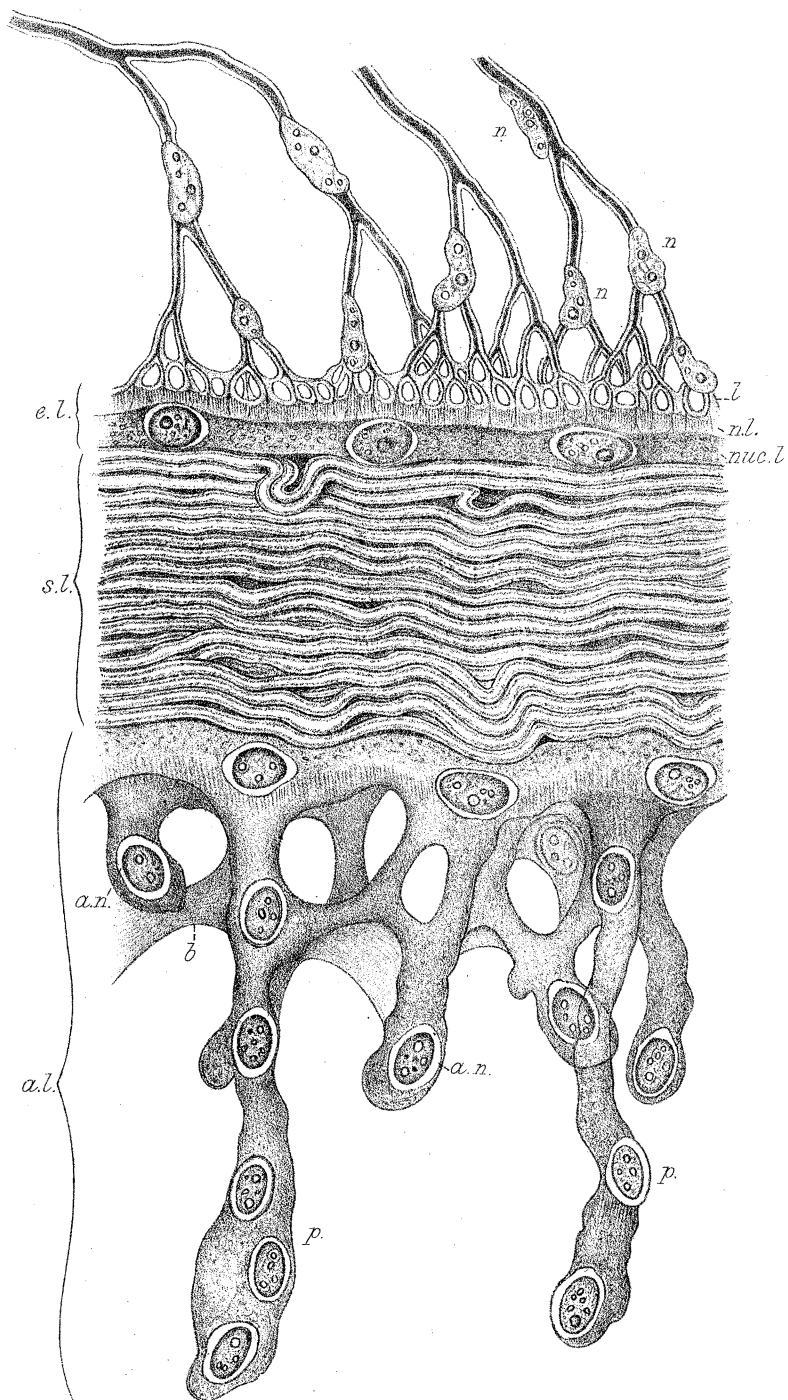


Fig. 14.

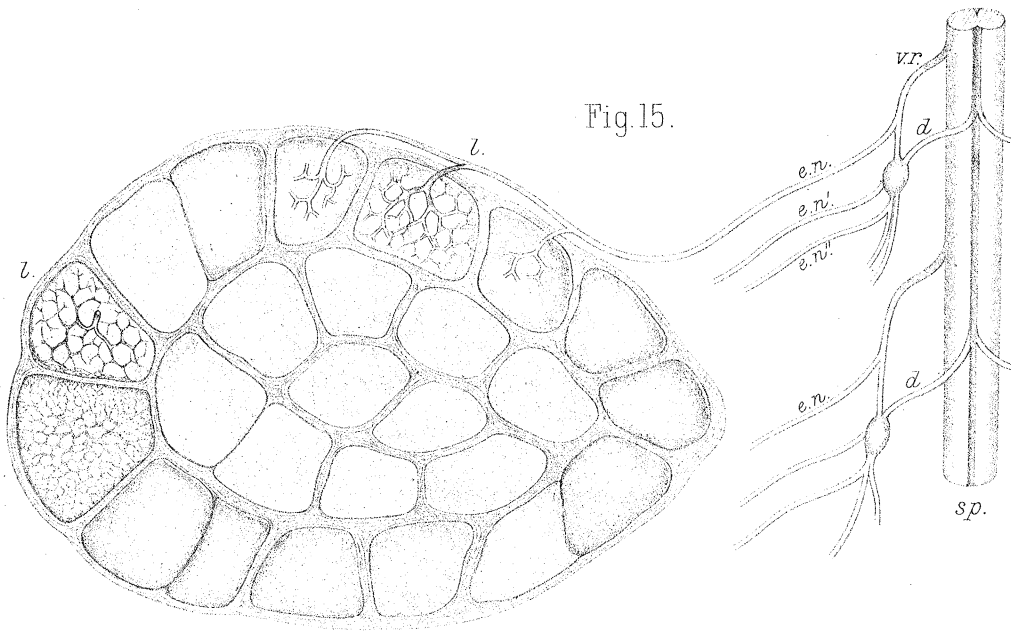


Fig. 17.

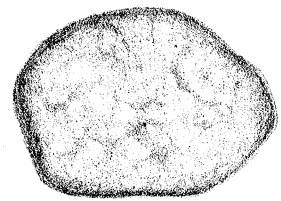


Fig. 17a.

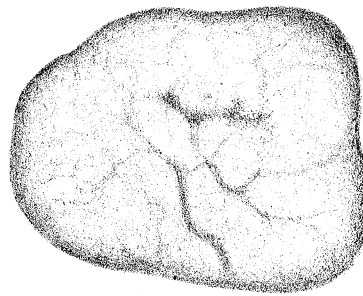


Fig. 17b.



Fig. 17c.

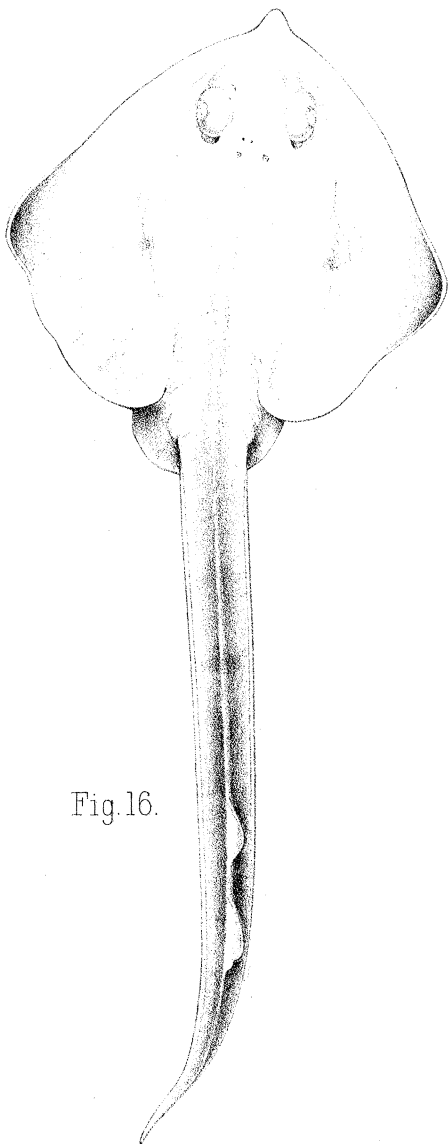


Fig. 16.

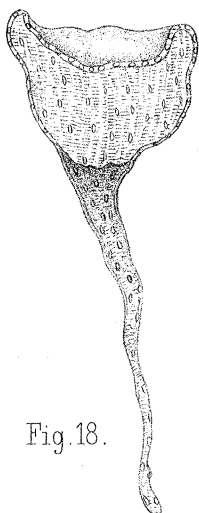


Fig. 18.

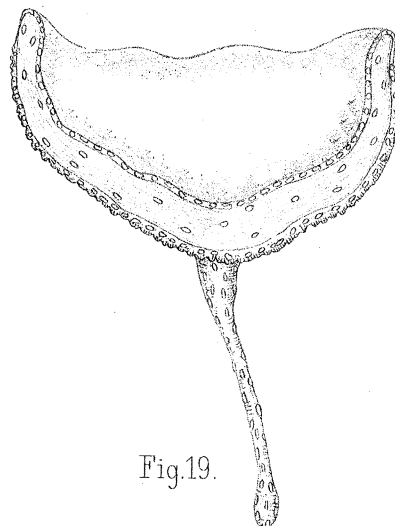


Fig. 19.

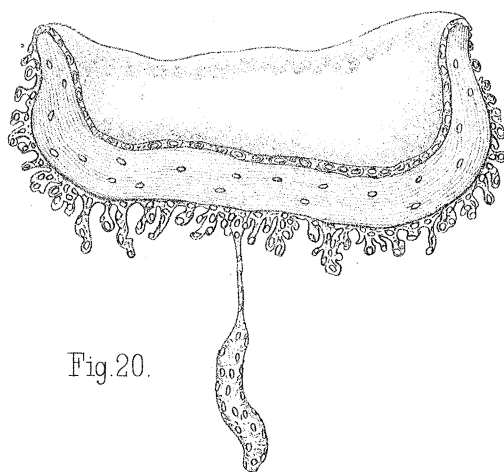


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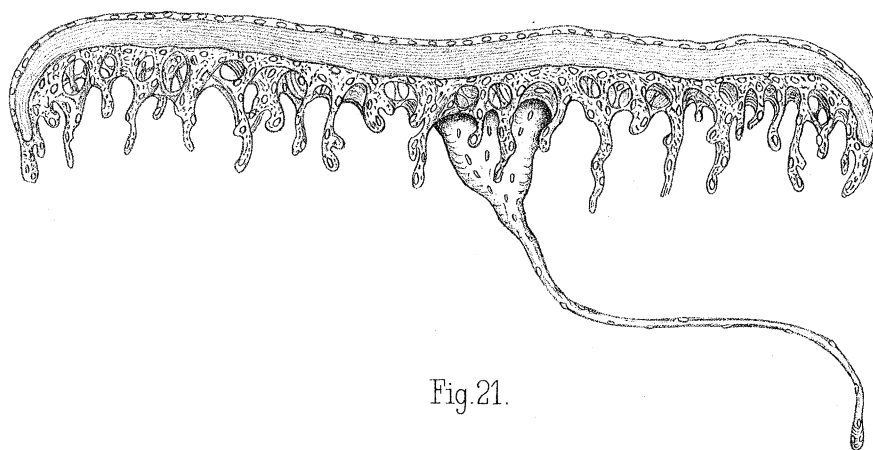


Fig. 21.



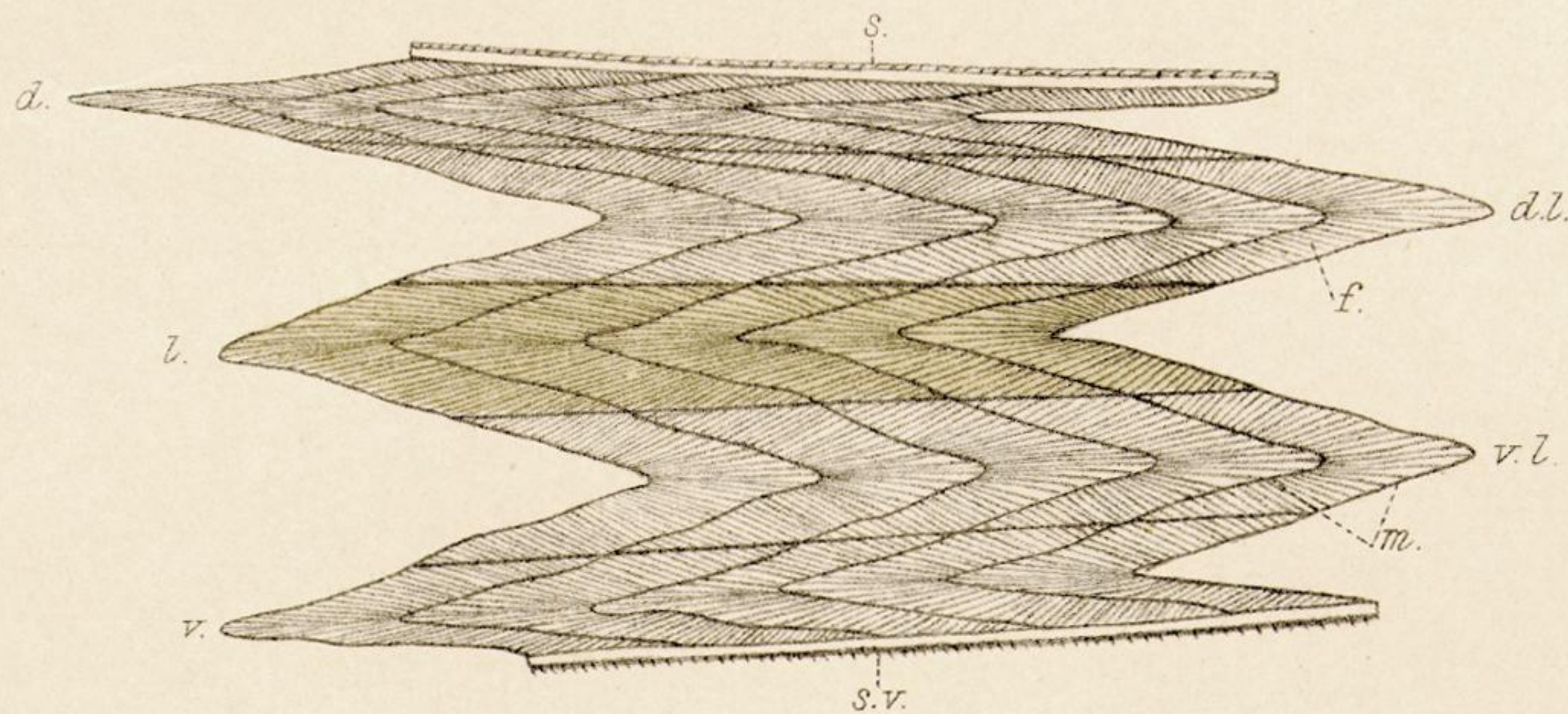


Fig 1.

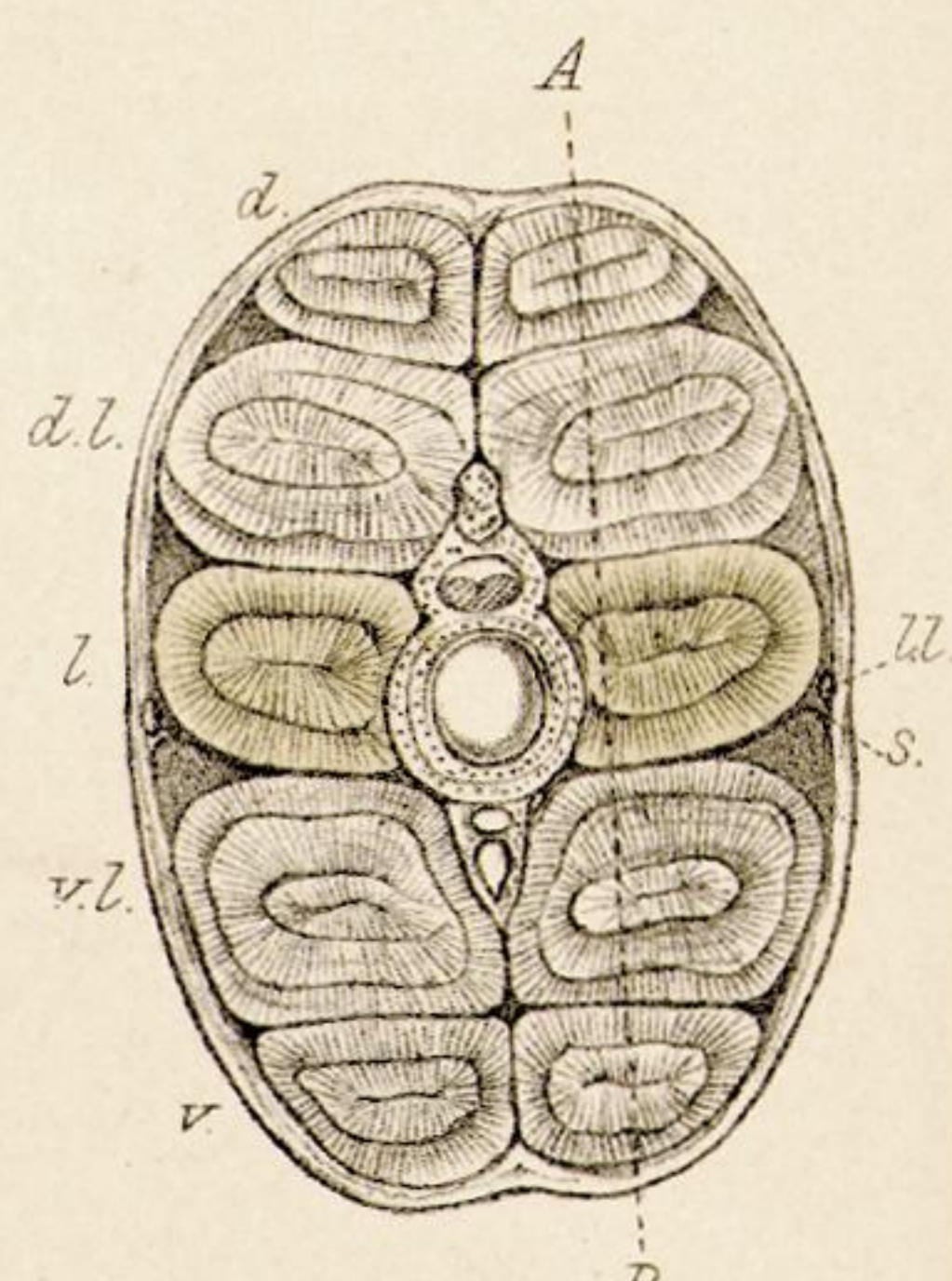


Fig 2.

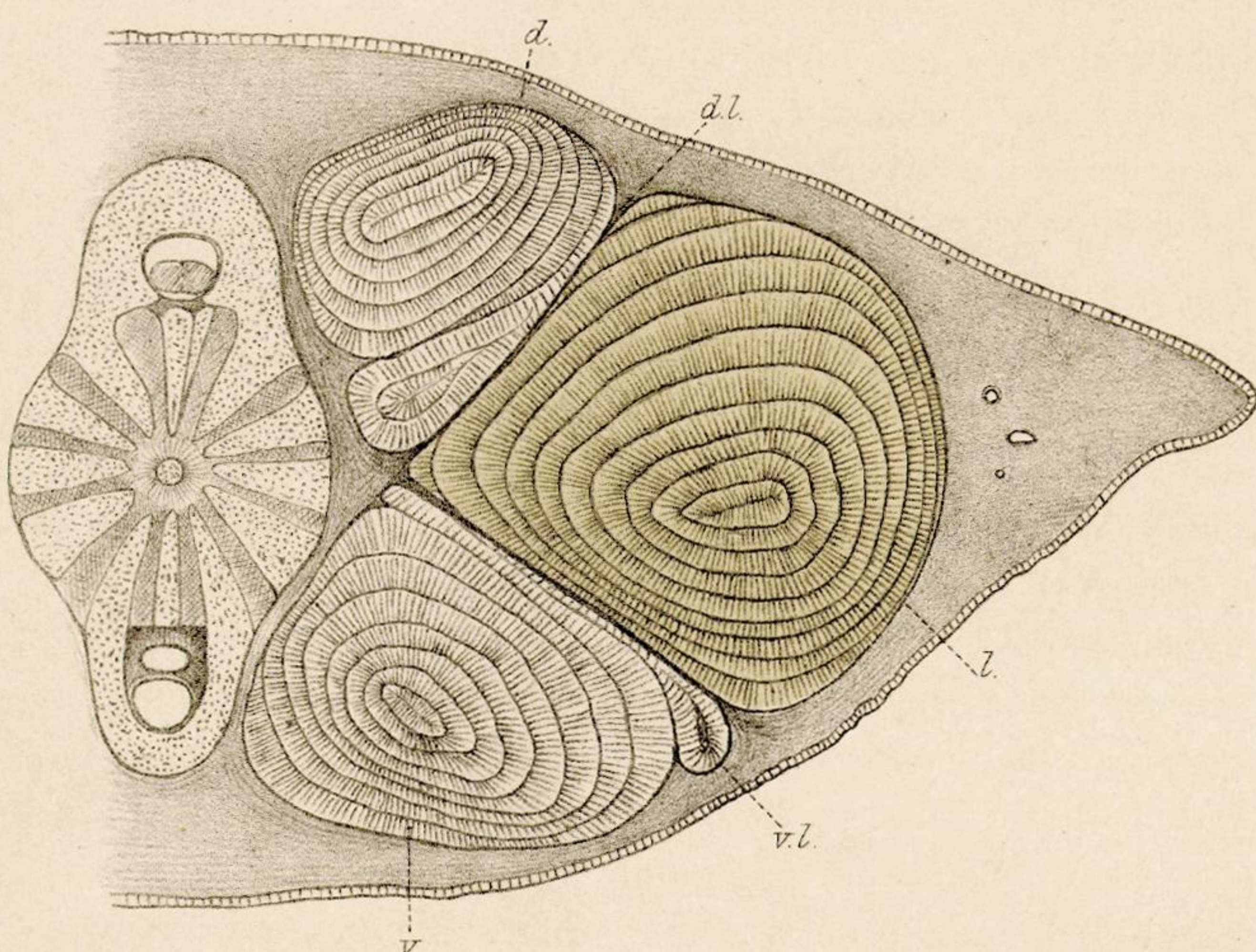


Fig.3.

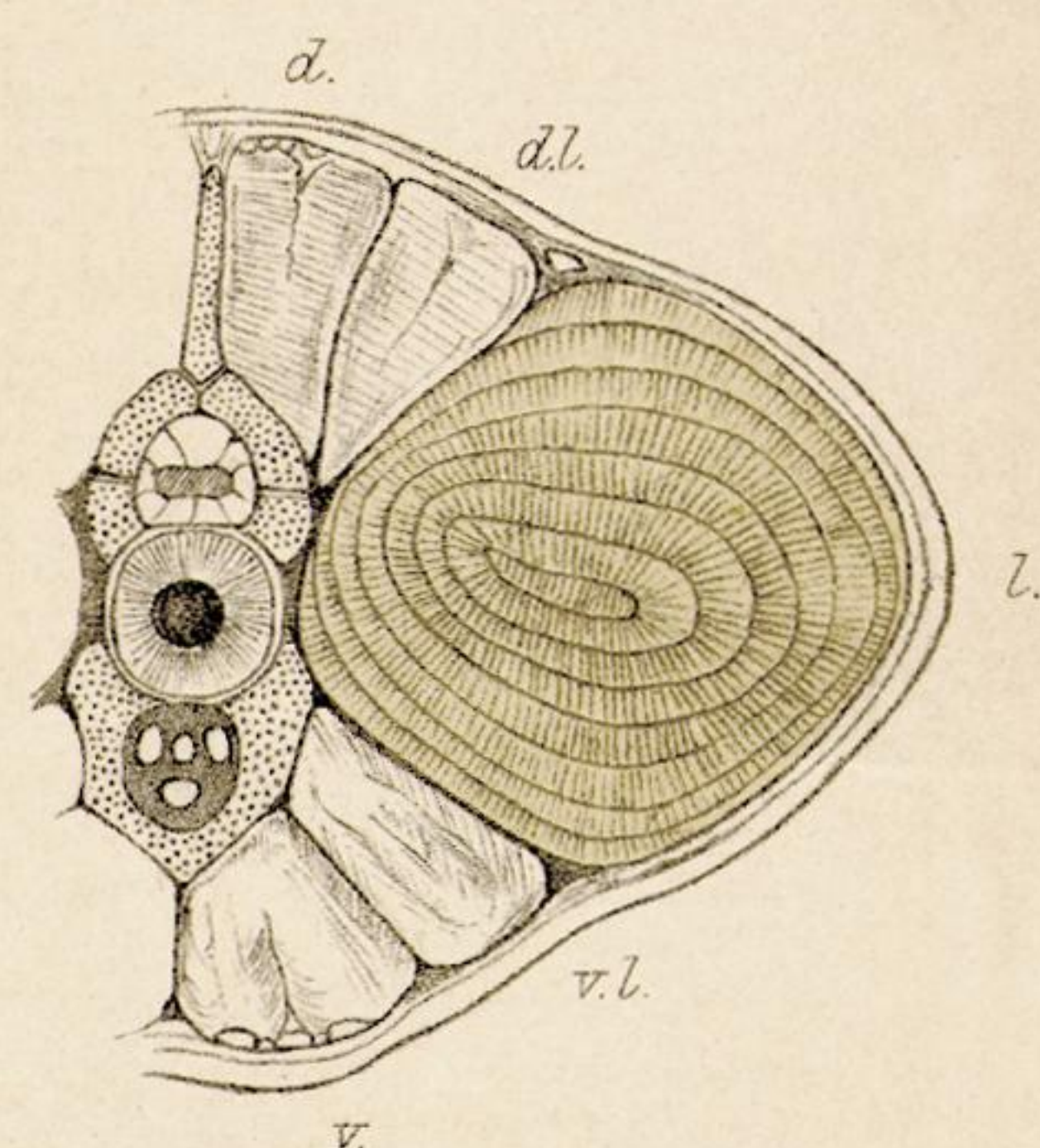


Fig.4.

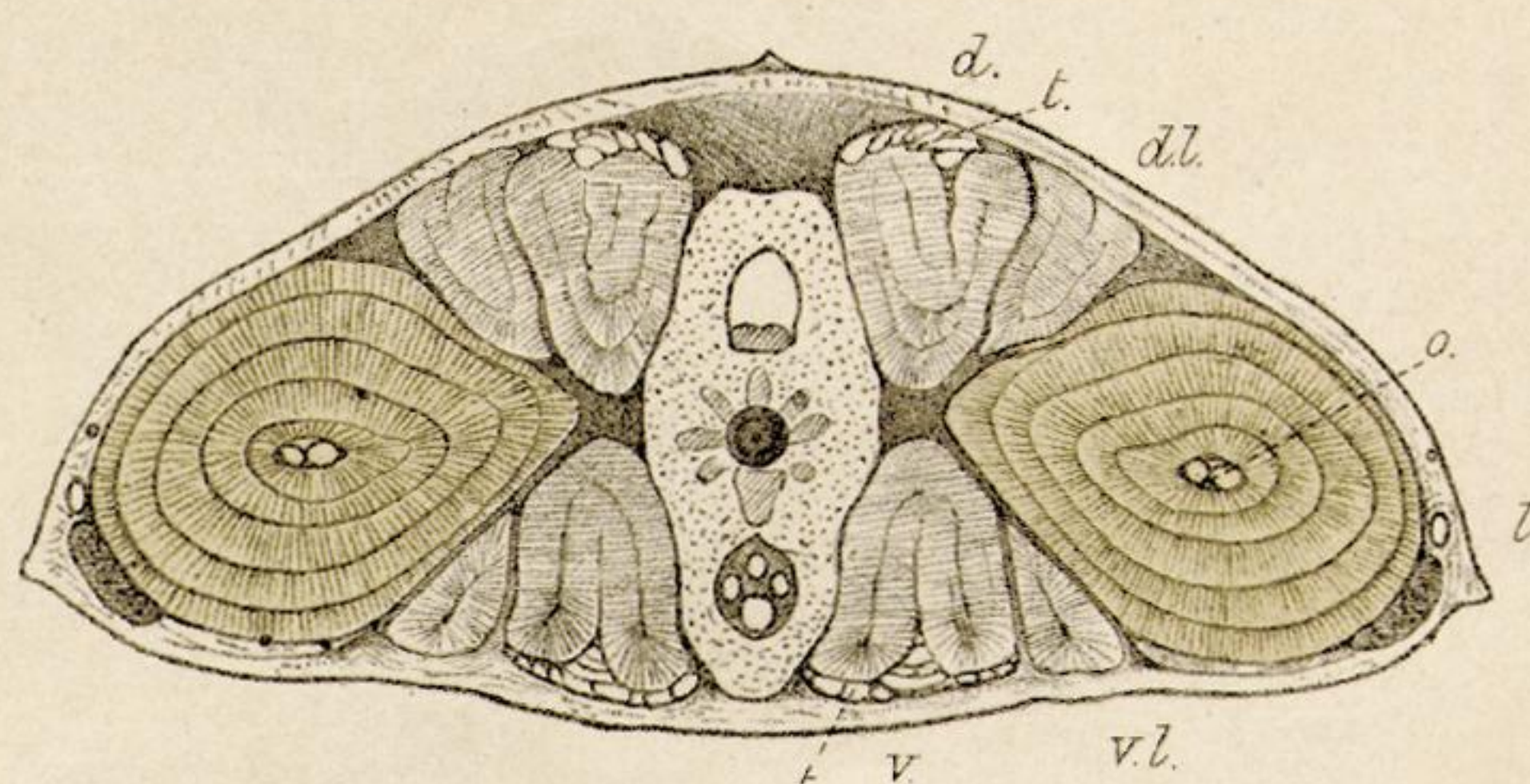


Fig.5.

## PLATE 26.

Fig. 1. Longitudinal vertical section of *Scyllium*, immediately posterior to second dorsal fin, showing five myotomes, bent zig-zag fashion, so as to form five muscular cones. Of these, three, the dorsal (*d.*), middle or lateral (*l.*), and ventral (*v.*), have their apices directed forwards, while the remaining two, the dorso-lateral (*d.l.*) and ventro-lateral (*v.l.*), have their apices directed backwards. The myotomes consist of fibres (*f.*), which assume a more and more longitudinal direction as the apices of the cones are reached. The fibres extend between connective tissue lamellæ, the myocomma (*m.*), and are so arranged that, if the handle of a scalpel is carried along two rows of cones, the surface of the one row is left smooth, while the other presents a rough appearance. The coloured lateral row of cones corresponds to the row which, in the Skate, is transformed into the electric organ. *s.*, skin of dorsal aspect; *s.v.*, skin of ventral aspect.

Fig. 2. Transverse section through *Scyllium*, immediately behind the second dorsal fin, showing the five muscular cones represented in fig. 1. The cones vary in shape and size, the dorsal (*d.*) and ventral (*v.*) are small, while the lateral (*l.*) presents the most regular outline. The lateral rests on the transverse septum (*s.*) which extends from the vertebral column to reach the skin on a level with the lateral line (*l.l.*). *d.l.*, dorso-lateral row, and *v.l.*, ventro-lateral row of cones. Fig. 1 was drawn from a section made through the line AB. The electric organ in the Skate occupies the position of the lateral row (*l.*), coloured as in fig. 1.

Fig. 3. Transverse section through the tail of *Lamna cornubica* (Porbeagle), behind the second dorsal fin. In *Lamna* the root of the tail is considerably flattened, and the flattening has been accompanied by a reduction in the size of the dorso-lateral (*d.l.*) and ventro-lateral (*v.l.*) rows, and with a great increase of the lateral (*l.*) row of cones—the row which is transformed into the electric organ in the Skate. In *Lamna* the transverse measurement is more than double the vertical, and the number of cones seen in the upper (*d.*), middle (*l.*), and ventral (*v.*) rows is far greater than in *Scyllium*. This is due to the cones being longer.

Fig. 4. Transverse section through the root of the tail of *Myliobatis*. The tail is less flattened than in *Lamna*, and, though the lateral row of cones (*l.*) is large, the dorso-lateral (*d.l.*) and ventro-lateral (*v.l.*) are distinct and nearly as large as the dorsal (*d.*) and ventral (*v.*). By comparing the lateral row of cones in figs. 2, 3, and 4, it will be observed that, while there are only two cones seen in section in *Scyllium*, there are nine complete cones in *Lamna*, and eight in *Myliobatis*.

Fig. 5. Transverse section through the tail of a large specimen of *R. batis*, about 18 centims. behind the pelvic fin, and on a level with the tip of the electric organ (*o.*). The five rows of cones found in *Scyllium*, *Lamna*, and *Myliobatis* are easily recognised, viz.:—the dorsal (*d.*), dorso-lateral (*d.l.*), lateral (*l.*), ventro-lateral (*v.l.*), and ventral (*v.*). The dorso-lateral and ventro-lateral are better developed than in *Lamna*, but the lateral, which only presents six complete cones, is relatively smaller than in *Lamna* and *Myliobatis*. By comparing figs. 3, 4, and 5 it is evident that the tail of the Skate differs considerably from the tails of *Lamna* and *Myliobatis*, agreeing more with the Shark than its ally *Myliobatis*, but differing from *Lamna* in presenting a flatter under-surface, and in having the lateral fold approaching the ventral, instead of the dorsal, aspect. Note that a number of tendons (*t.*) lie embedded in the dorsal (*d.*) and ventral (*v.*) rows of cones.



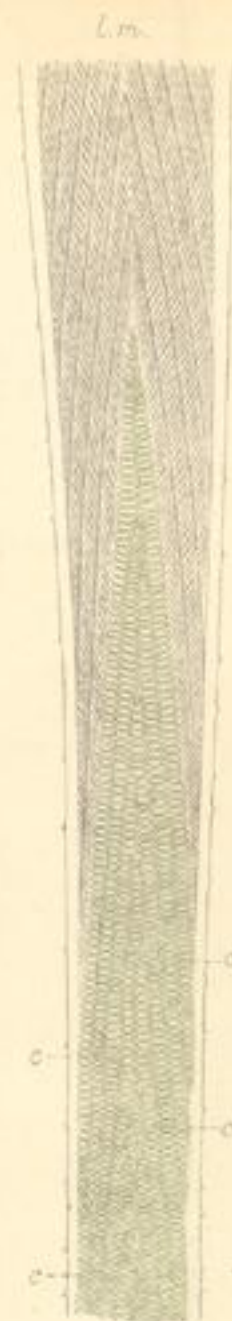


Fig 6.

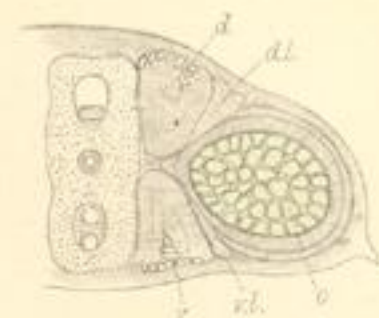


Fig 8.

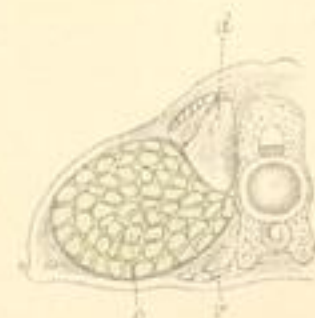


Fig 10.



Fig 9.



Fig 11.

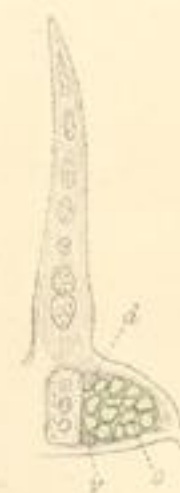


Fig 12.

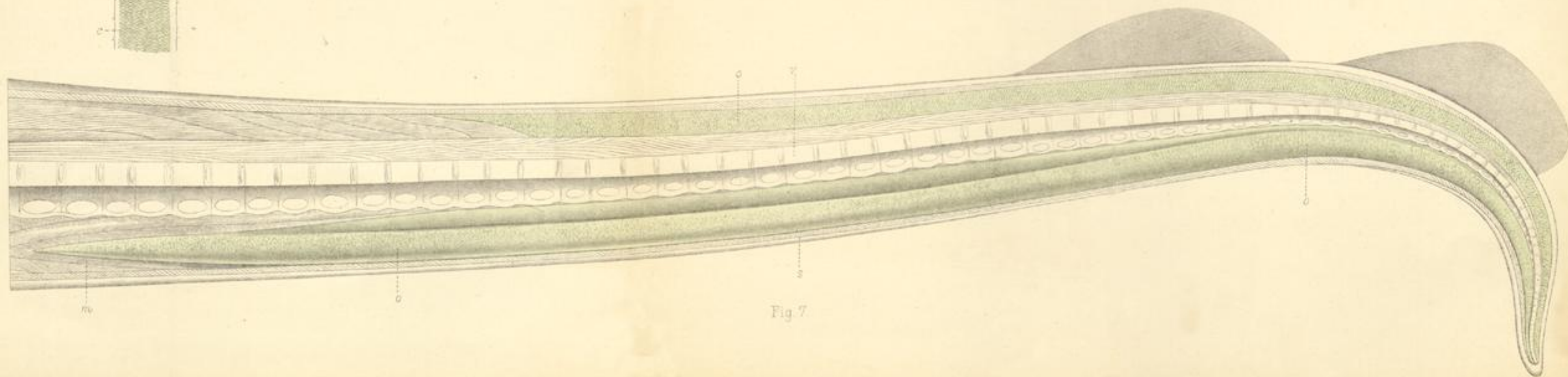


Fig 7.



*l.m.*

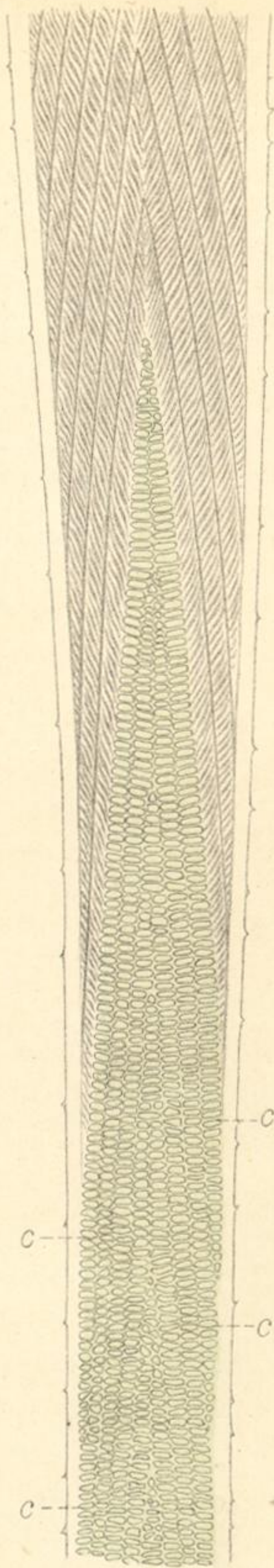


Fig. 6.

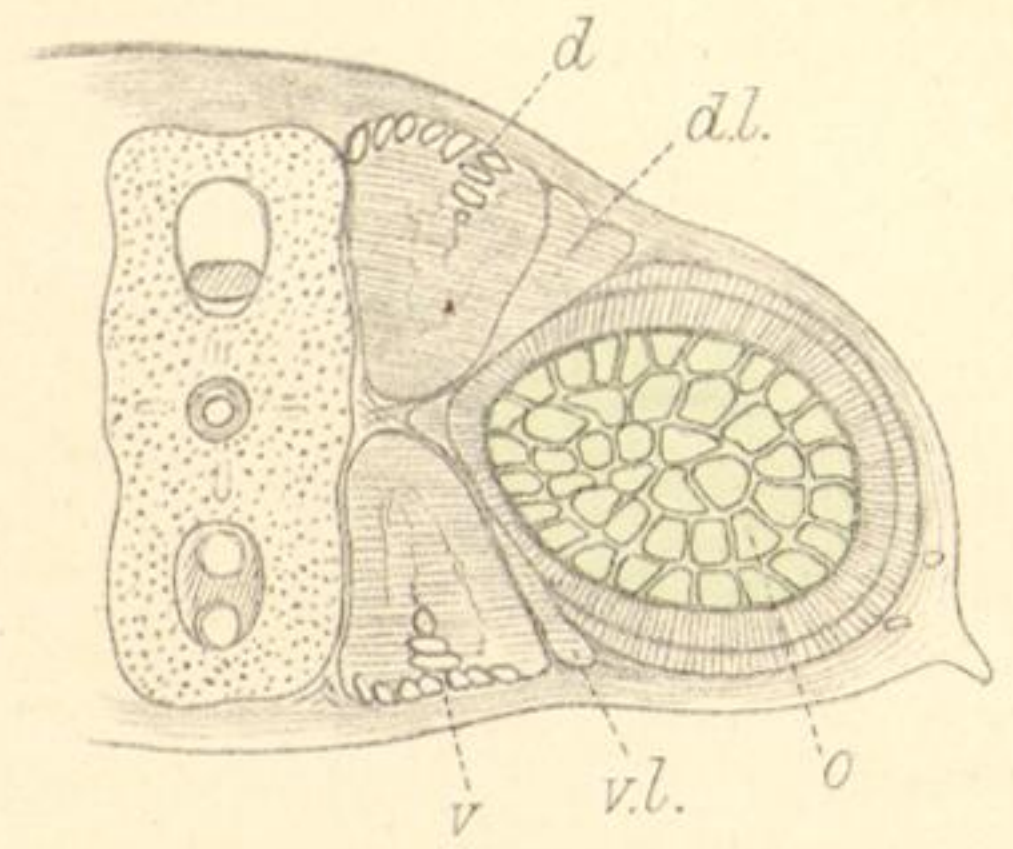


Fig 8.

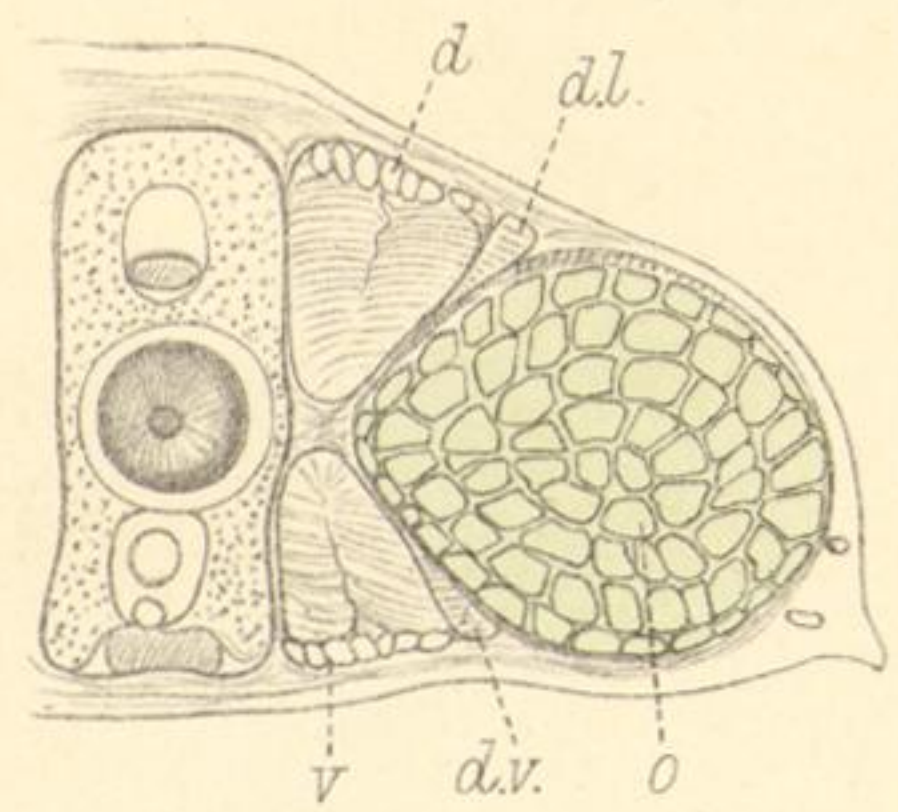
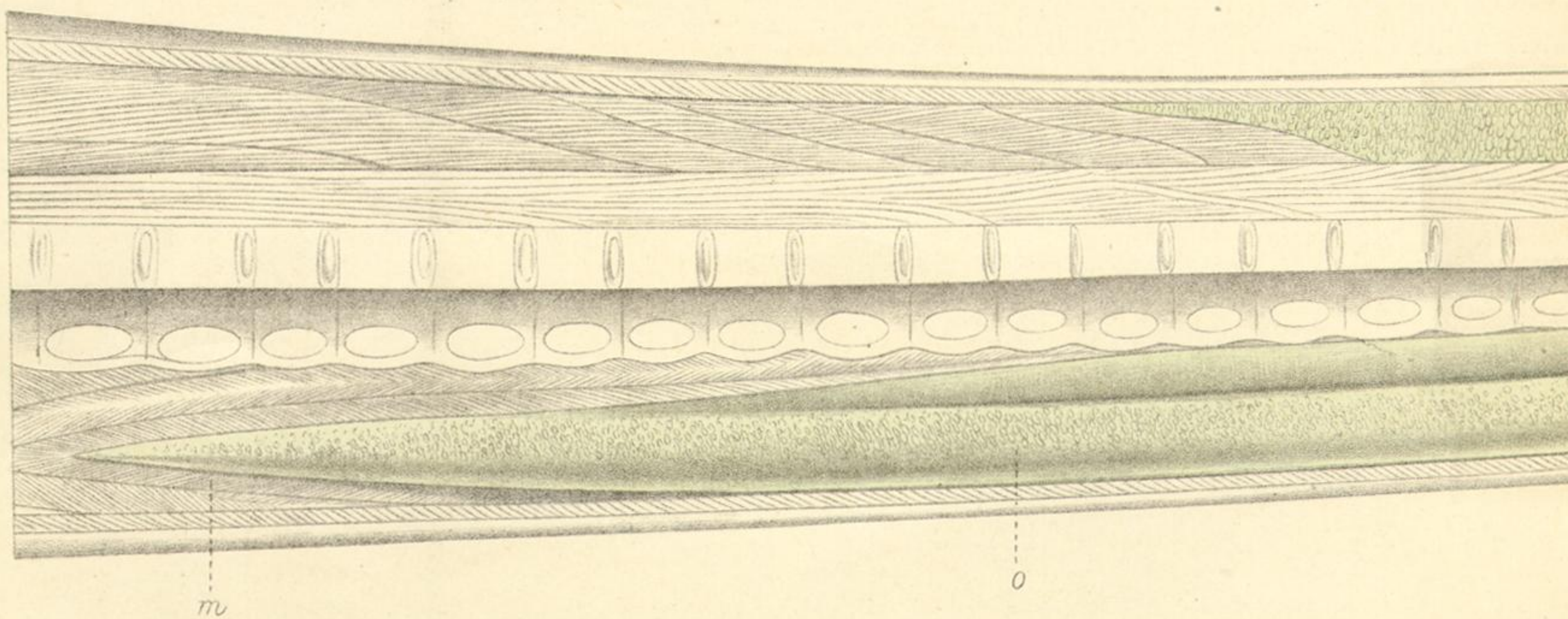


Fig. 9.





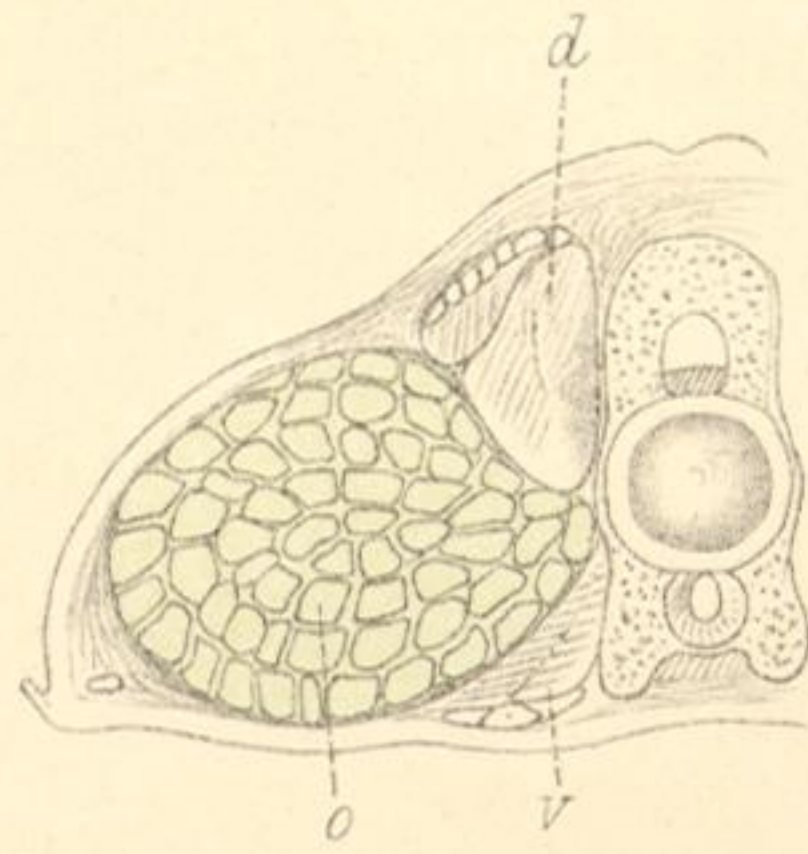


Fig. 10.

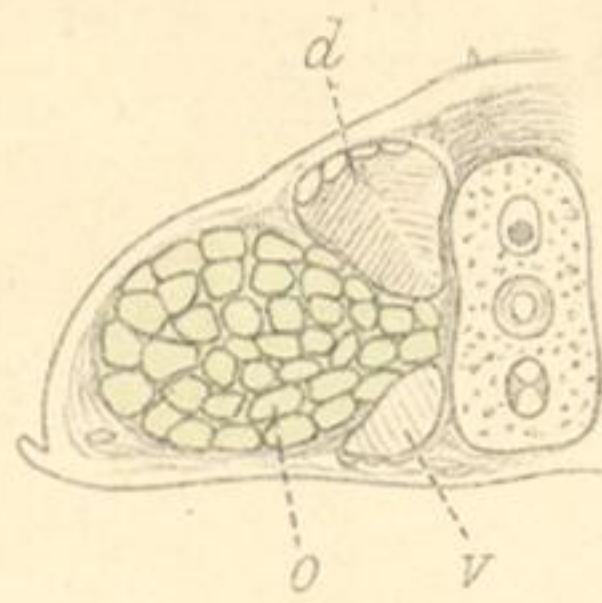


Fig. 11.

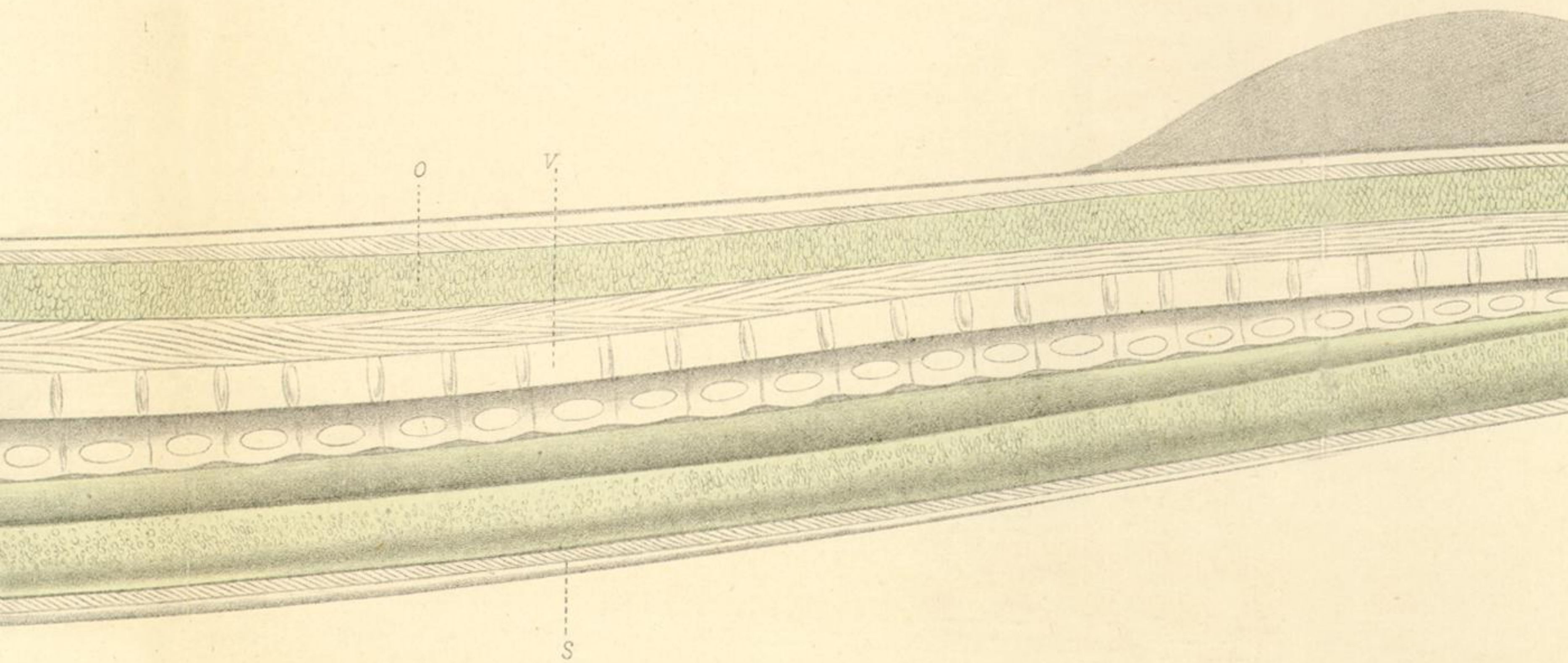


Fig. 7.



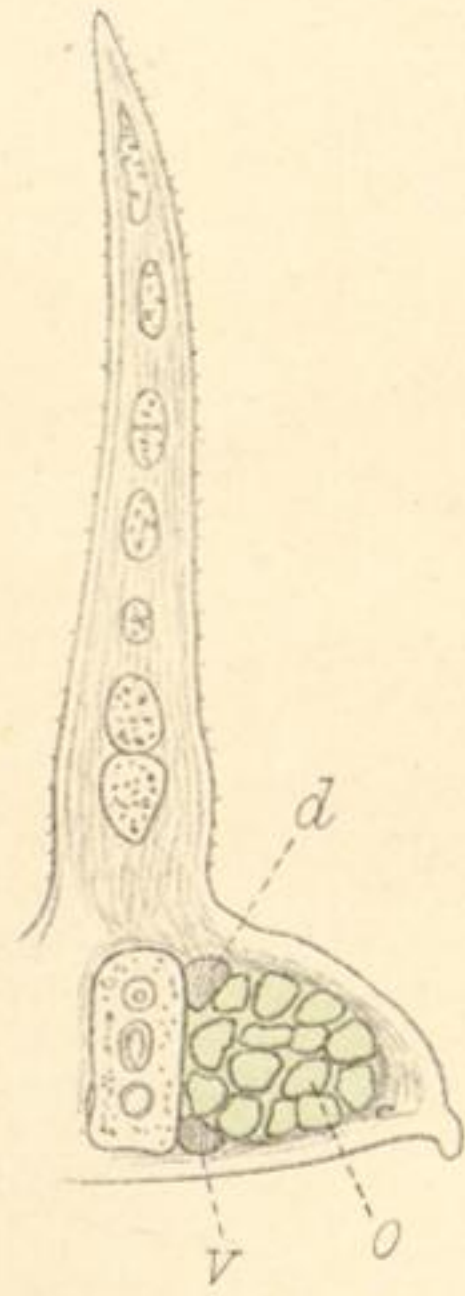
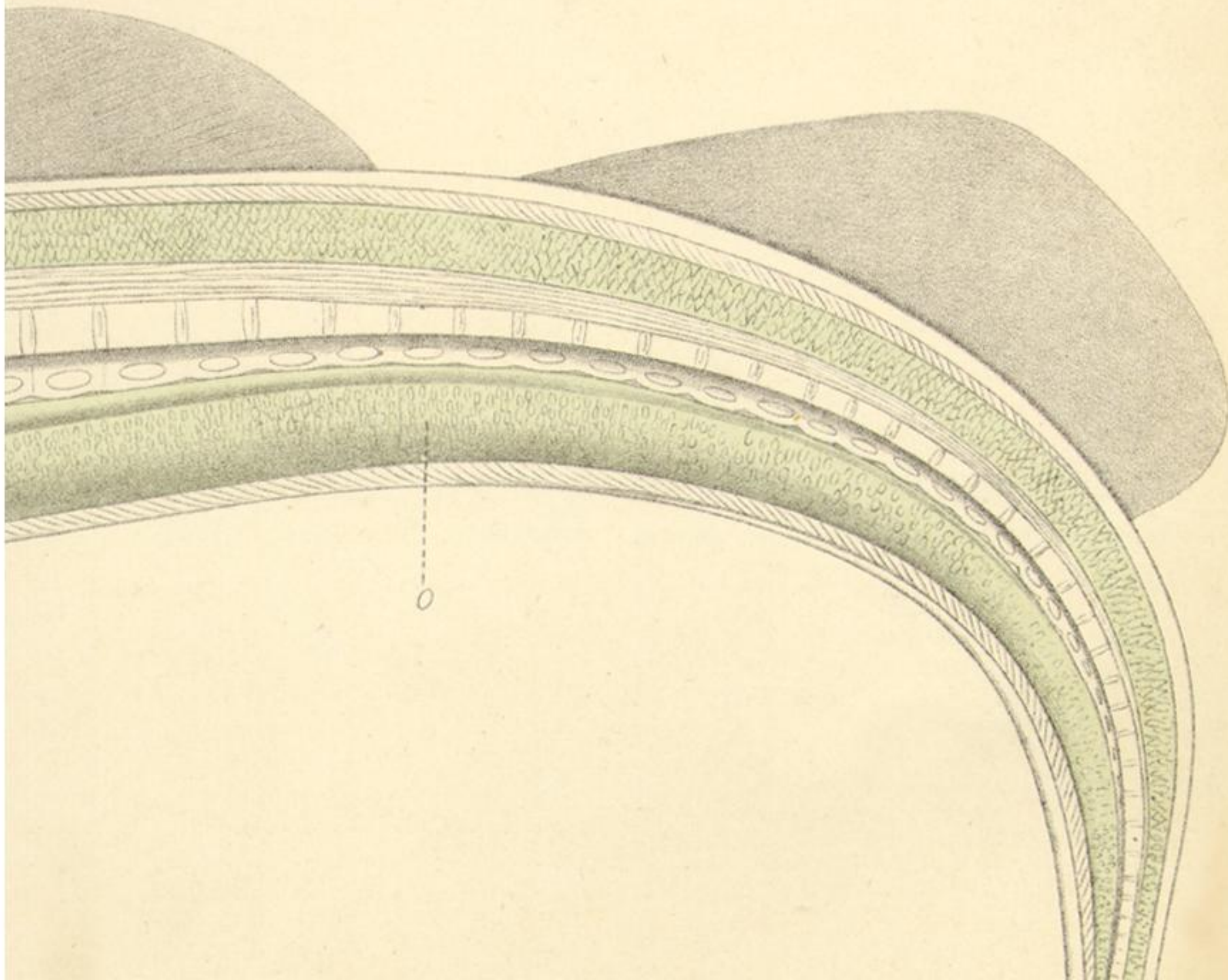
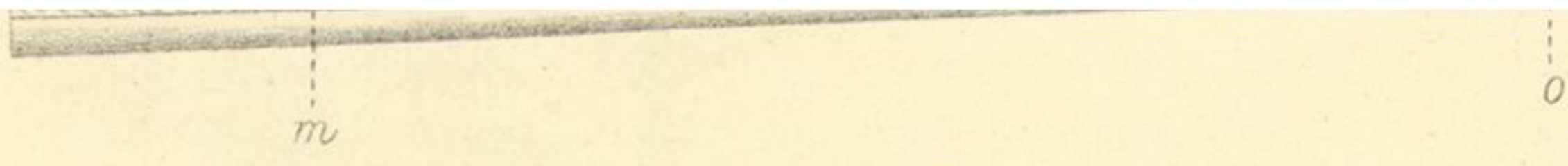


Fig. 12.

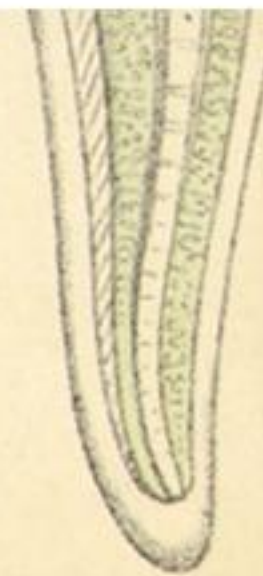




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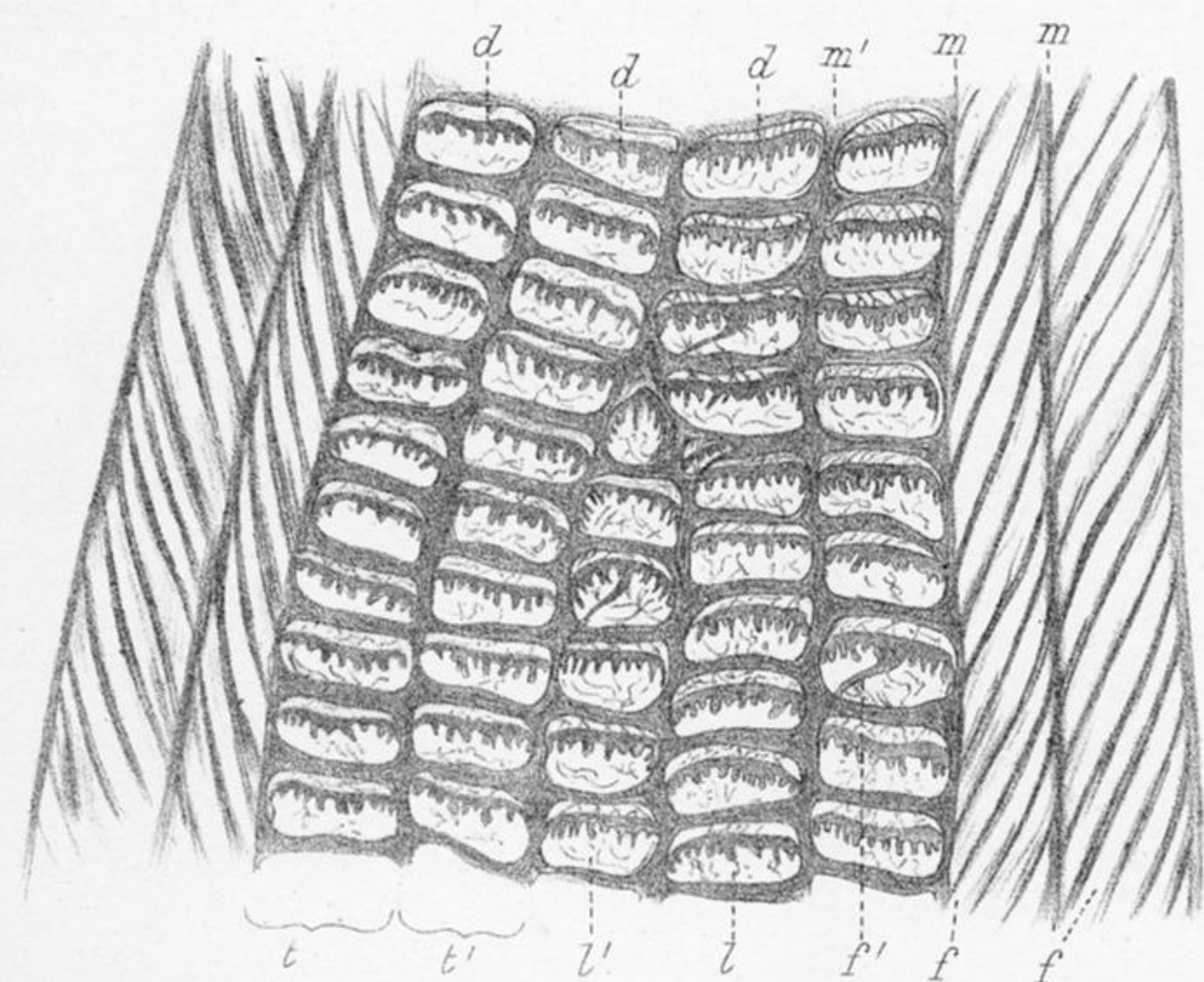


Fig. 13.

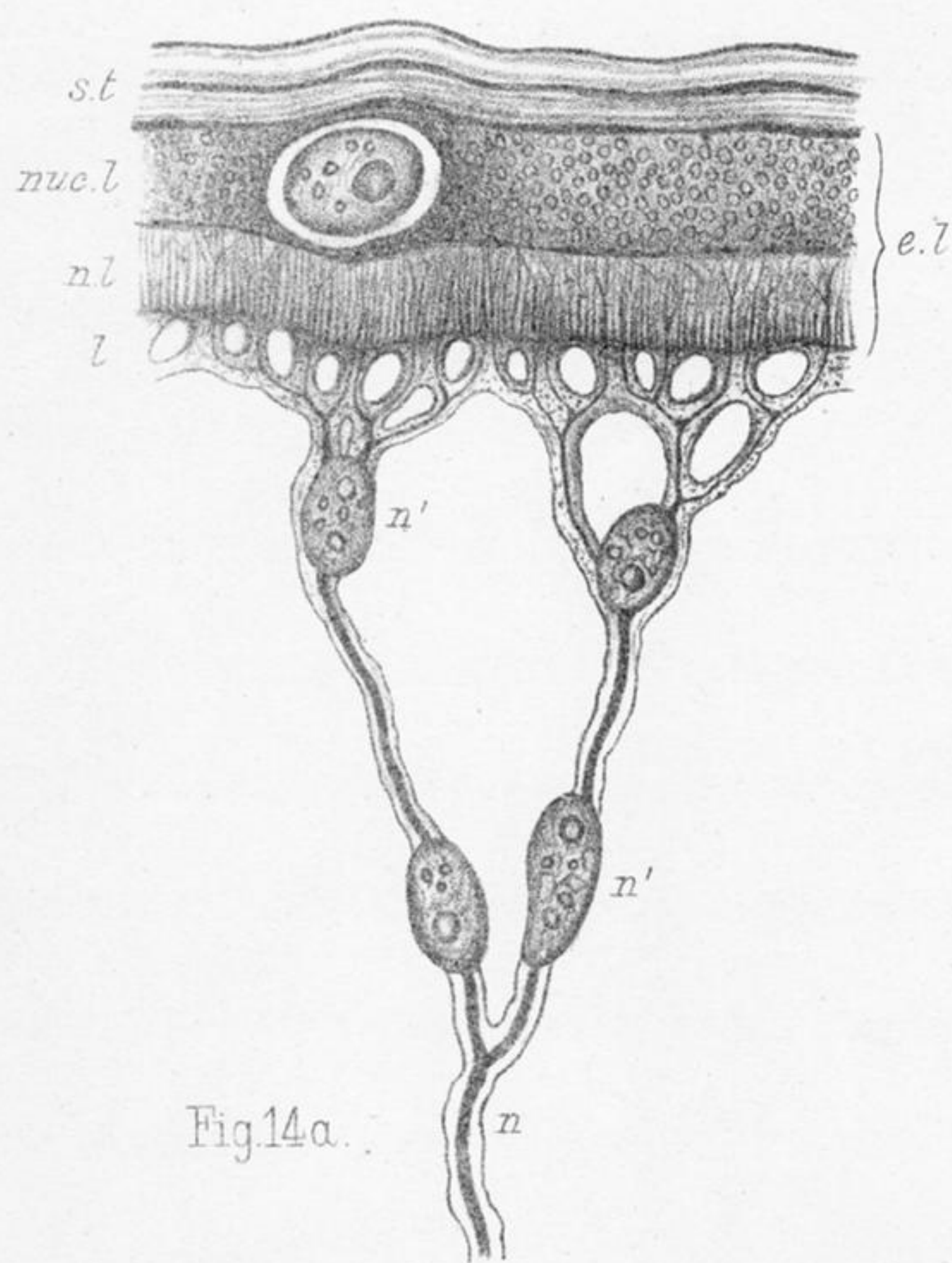


Fig. 14a.

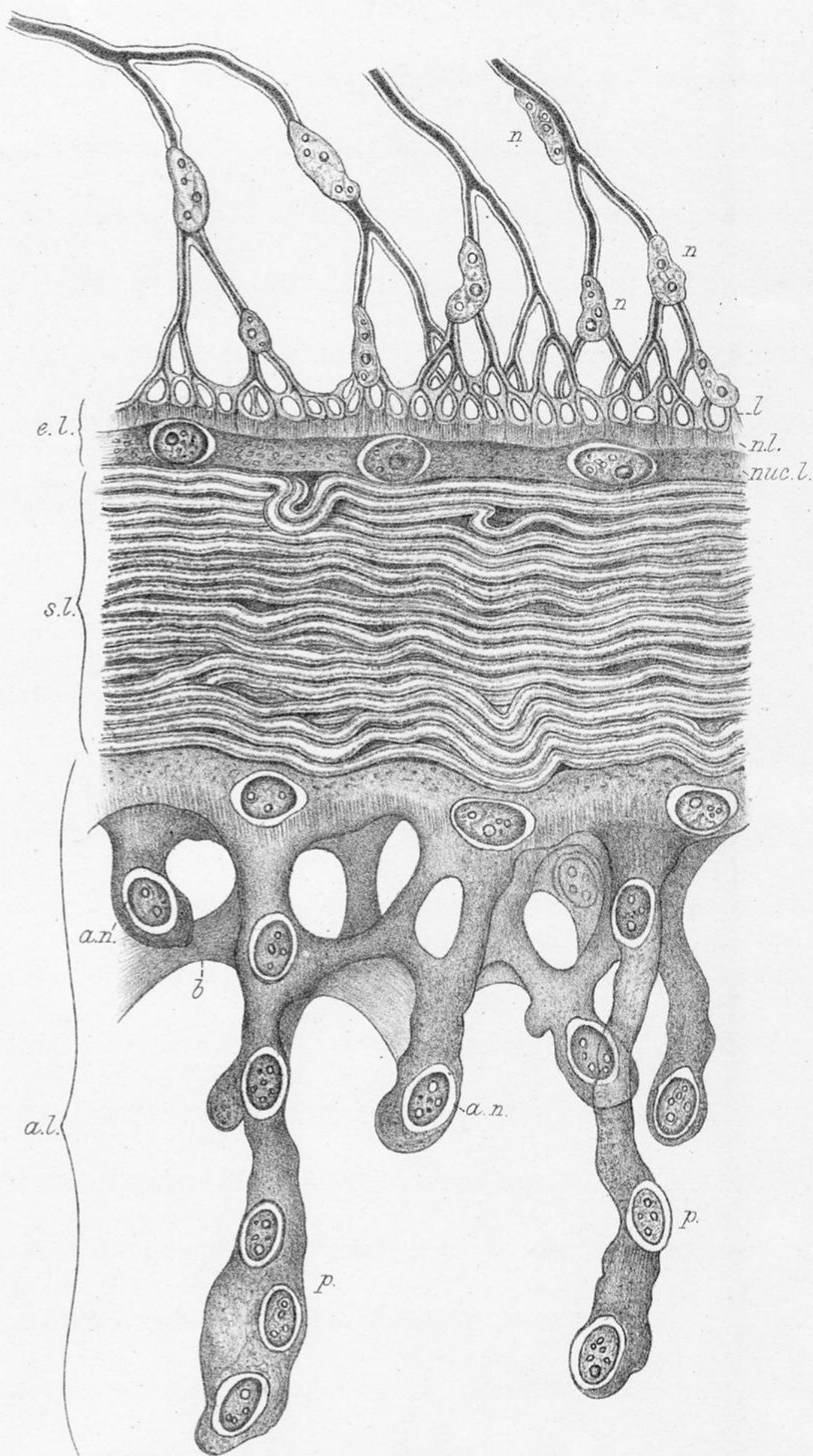


Fig. 14.

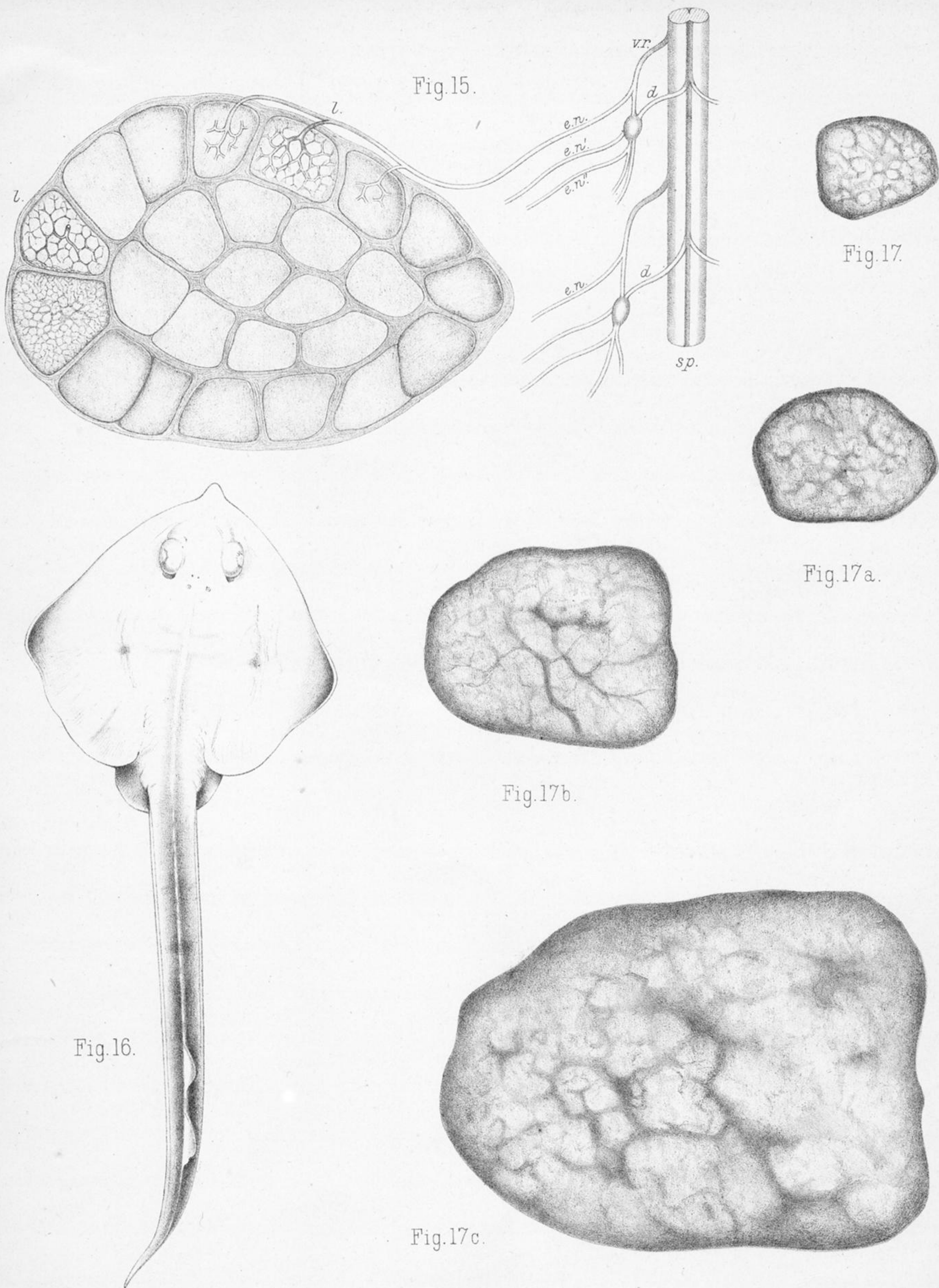
## PLATE 28.

Fig. 13. Longitudinal vertical (sagittal) section through a portion of the anterior end of the electric organ, and its investing muscular cones. The electric elements (*l.* and *l'*) which form the cones are arranged in piles, and lie at nearly right angles to the long axis of the tail. The unaltered muscular fibres (*f.*) occupy an oblique position. Like the fibres, the electric elements extend between myocomma (*m.*): they are separated from each other by the altered intermuscular tissue which, together with the myocomma, form chambers or loculi. The discs proper (*d.*) occupy less than a third of the loculi. In the space in front of each disc lie the nerve-fibres; the larger space behind the disc contains gelatinous tissue and blood vessels, and through it the posterior degenerated portion of the altered muscular fibre (*f'*) is sometimes seen. From a Skate 90 centims. in length  $\times 15$ .

Fig. 14. Section through a disc showing the nerves, the electric (*e.l.*), striated (*s.l.*), and alveolar (*a.l.*) layers. The nerves divide as they approach the disc, and after forming numerous loops (*l.*), enter and terminate in the nervous lamina (*n.l.*) of the electric layer; (*n.*) nuclei on the nerve sheaths; (*nuc. l.*) nuclear laminae of the electric layer with large nuclei. Note the absence of nuclei in the thick striated layer (*s.l.*), the well-developed alveolar layer with large nuclei (*a.n.*), long processes (*p.*), connected by secondary processes (*b.*), to form a network. The gelatinous tissue which occupies the spaces between the nerves and the processes of the alveolar layer is not represented. The electric and striated layers copied from a camera drawing; the alveolar layer is semi-diagrammatic. ZEISS, apochromatic, 2; compensating eyepiece, 12.

Fig. 14a. Drawing showing the structure of the electric layer of *R. circularis*. (*n.*), nerve proceeding to electric lamina; (*n'*), nuclei on nerve sheath; (*l.*), nerve loops in front of electric lamina; (*n.l.*), electric lamina with nerve fibrils entering. This lamina has a striated appearance, and thus resembles the part of the electric layer of the Torpedo characterised by the "nerve hairs" of RANVIER; (*nuc. l.*), the nuclear lamina corresponding to the nuclear lamina (dorsal half) of the electric layer of the Torpedo; (*st.*), two of the lamellae of the striated layer. Camera drawing; ZEISS, apochromatic, 2; compensating eyepiece, 12.





# PLATE 29.

Fig. 15. Transverse section of the organ of a Skate, 90 centims. in length, to show the various forms assumed by the electric discs, and to indicate the origin of the electric nerves; (*sp.*), spinal cord; (*d.*), dorsal root of a spinal nerve; (*v.r.*), ventral root, giving off a branch (*e.n.*) to the organ before uniting with dorsal root; (*e.n.'*), electric nerve springing from junction of two roots; (*e.n''*), electric nerve springing from nerve trunk beyond ganglion. Each nerve, by dividing dichotomously, breaks up into numerous branches in front of the disc (*l.*).

Fig. 16. Represents the stage of development reached by a *R. batis* embryo about nine months after the fertilised egg was removed from the oviduct. Compared with the adult, the pectoral fins are small, while the tail is long and broad, and has the two dorsal fins some distance from each other and the tip of the tail. Compare with fig. 7, in which the first dorsal fin is relatively nearer the end of the tail, and nearer the second fin than in the embryo figured.

Figs. 17, 17A, 17B, 17C. Four camera drawings, to show that the discs increase in size as the fish grows larger; fig. 17 shows a disc from a Skate 45 centims. (18 inches) in length; fig. 17*a*, a disc from a fish 60 centims. (24 inches) in length; fig. 17*b*, a disc from a fish 90 centims. (36 inches) in length; fig. 17*c*, a disc from a fish 180 centims. (six feet) in length. In all the figures the pitted appearance presented by the posterior or alveolar aspect is indicated.





Fig. 18.

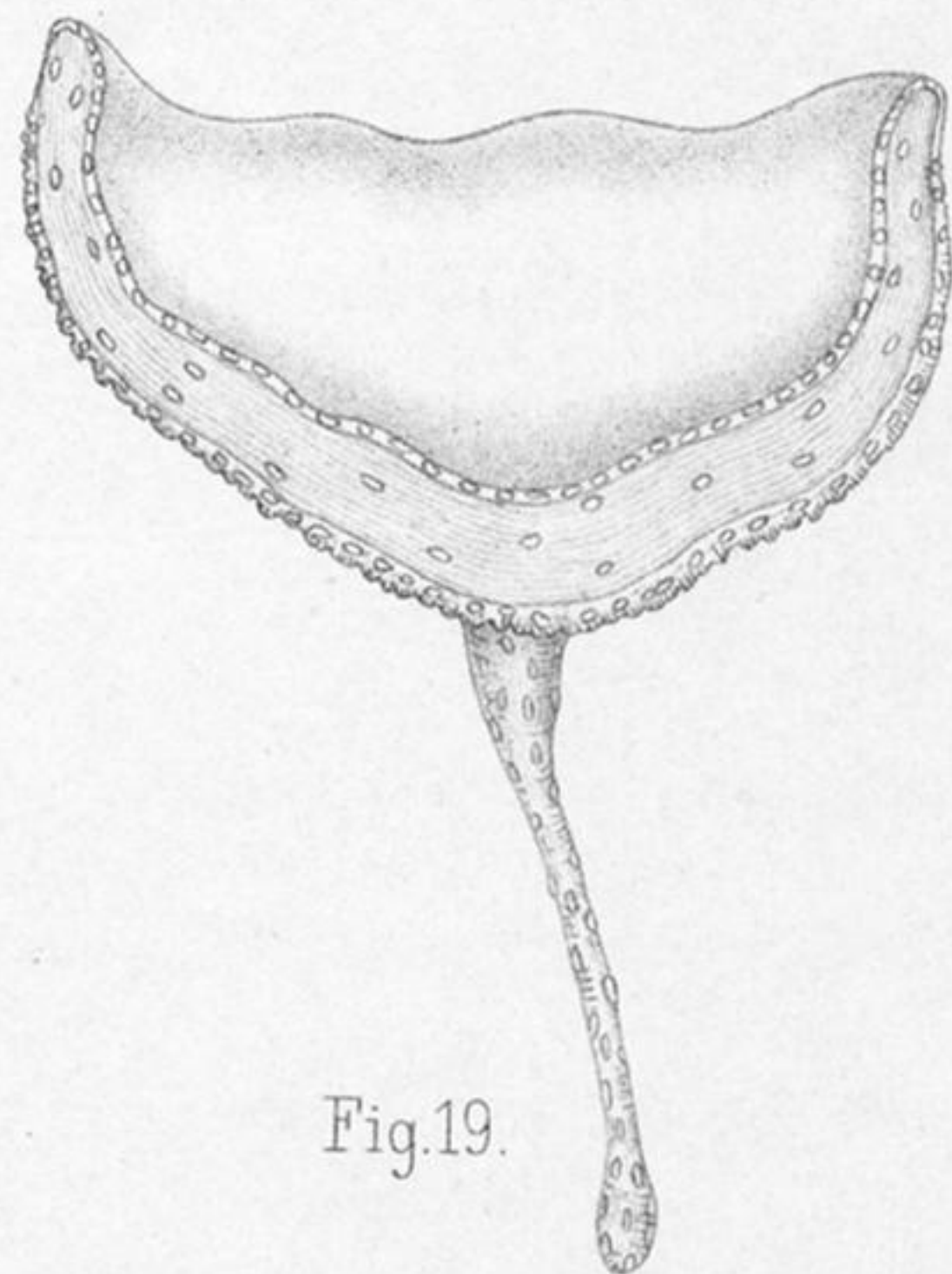


Fig. 19.

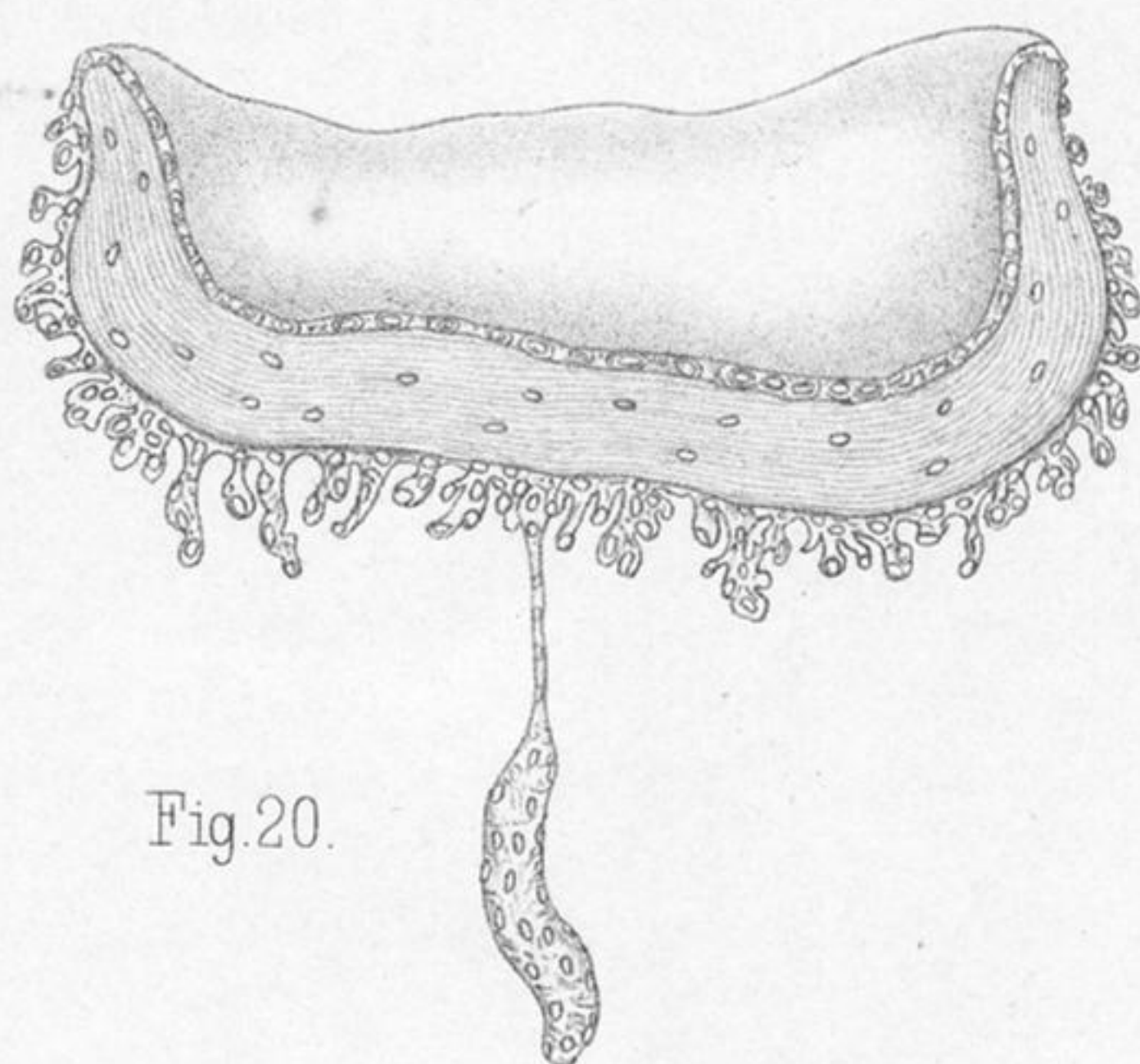


Fig. 20.

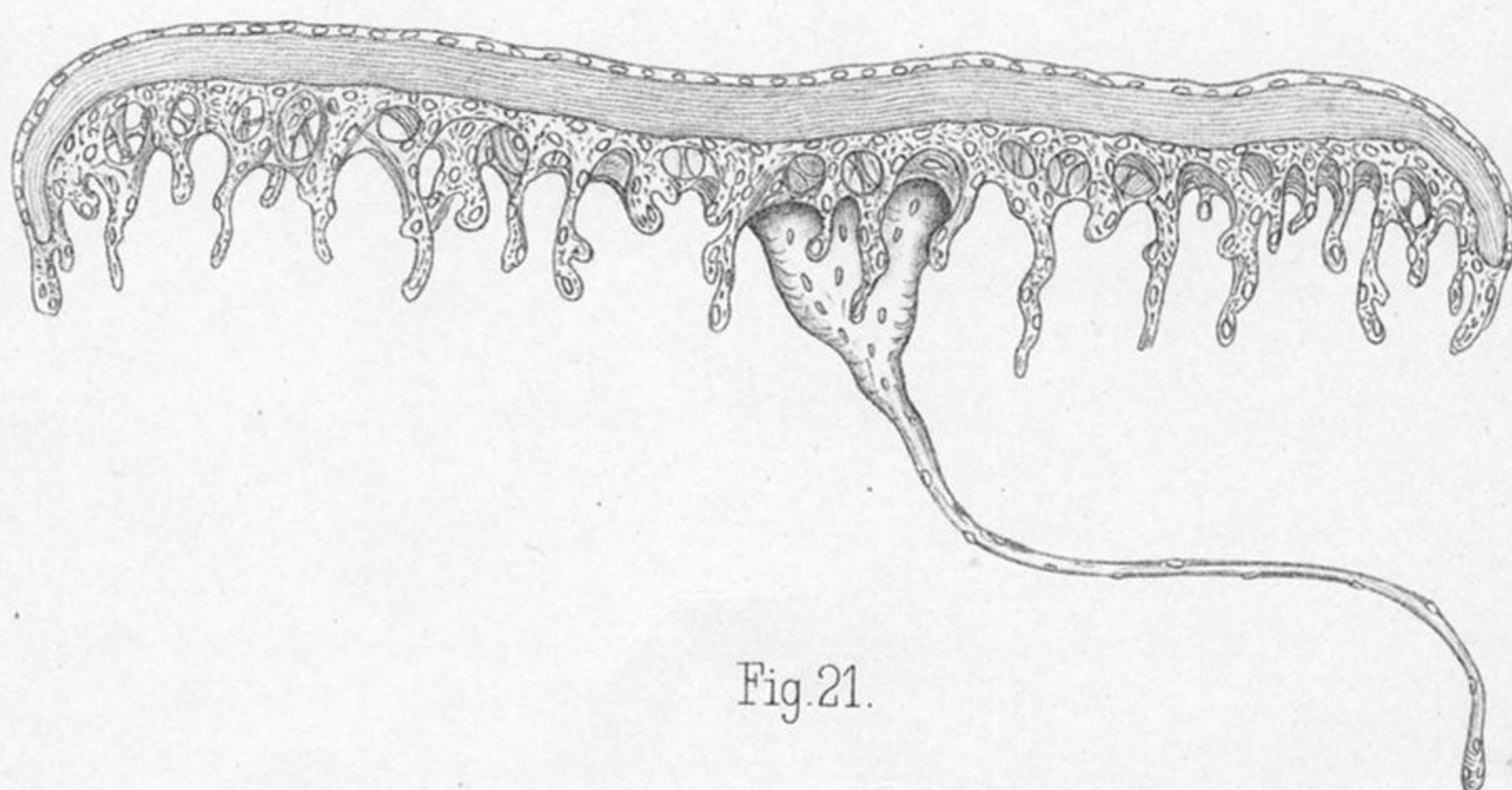


Fig. 21.

### PLATE 30.

Figs. 18–21. Low-power camera drawings to show the four modifications of the electrical elements found in the British members of the genus *Raia*. Fig. 18, one of the modified muscular fibres which form the electric organ in a full-grown *R. radiata*. The expanded cup-shaped upper part presents throughout the ordinary muscular striation, an enlarged motor plate (the electric layer) lines the shallow thick-walled cup. Fig. 19, a still further altered muscular fibre, one of the electric cups from the electric organ of a full-grown *R. circularis*. The muscular striation has entirely disappeared from the cup, which is deep, well moulded, and lined by an extensive electric plate. Fig. 20, a still further modified muscular fibre, representing the form assumed by the cups which make up the electric organ in *R. fullonica*. The cup is larger but shallower than in *R. circularis*, and instead of a nearly simple cortex, numerous simple and compound villous-like projections extend from the outer surface. Fig. 21, a profoundly altered muscular fibre, one of the discs which make up the electric organ of *R. batis*. The electric layer is many times larger than in *R. radiata*, the striated layer is, except in rare cases, devoid of nuclei, and the simple outer layer or cortex of *R. circularis* is represented by long prongs, which, unlike the processes in *R. fullonica*, give rise, by secondary outgrowths, to a complex network. Figs. 18, 19, and 20 may be looked upon as three stages in the evolution of the more complex disc of *R. batis*.