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The Electric Organ of the Skate

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XV. *The Electric Organ of the Skate.*

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Communicated by Professor J. Burdon Sanderson, *F.R.S.*

On the Development of the Electric Organ of Raia batis.

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[Plates 66, 67.]

There are few, if any, structures in the animal kingdom the origin of which is more difficult to account for than the electric organs of Fishes. Darwin recognised in the electric organs one of the "special difficulties of the Theory of Natural Selection;"* and, although we now understand their structure and development, it is still "impossible to conceive by what steps these wondrous organs have been produced." Although the structure and development of the electric organ of the Torpedo has been determined, we are as ignorant as before of its phylogeny.

Almost the only chance of our obtaining a hint as to how the organ passed through its initial stages, as to the causes which were at work while the muscular fibres were in process of conversion into electric cells or discs, seems to be by turning to the so-called "pseudo-electric"† organ of the Skate.

The organ of the Skate has hitherto received comparatively little attention from biologists. We are mainly indebted for what we know of its structure to Robin,‡ while the limited information we possess as to its development is entirely due to the inquiries of Babuchin.

In turning to the common Gray Skate (*Raia batis*), one is at once struck with the remarkable fact that, while the organ has not yet been proved to have any special use, it is apparently as structurally perfect as the organ of the Torpedo. The presence of an extremely complex apparatus, having no evident function, is difficult to understand; and, before venturing any explanation of this unusual circumstance, it is desirable, if possible, to enquire whether the organ of the Skate is on the up or the

* 'Origin of Species,' 6th edit., p. 150.

† "Pseudoëlektrisches Organ bei einem Gymnotinen?" 'Untersuchungen am Zitteraal, *Gymnotus electricus*,' von du Bois-Reymond, Leipzig, 1881, p. 66.

‡ 'Ann. Sci. Nat.' (*Zool.*), vol. 7, 1847, p. 193.

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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.

To determine the present condition of the Skate's organ is by no means a simple matter. To start with, it is desirable to make out not only its development, but also 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. Further, it will be equally necessary to make a comparative study of the organ in the various members of the Skate family. Having, through the kindness of Professor BURDON SANDERSON, had the opportunity of making a very complete examination of the electric organ of the Torpedo, I was able some time ago to direct my attention to the organ of the Skate, with a sufficient appreciation of the difficulties to be overcome and of the points which deserved especial attention.

With a view to arriving at some general conclusions as soon as possible, I first, with the help of one of my assistants (Mr. G. C. PURVIS, M.B.), made a preliminary examination of the electric organ at various stages of development in eight different species of Skate. This done, I next proceeded to make as thorough an investigation as possible of the development of the organ of the Gray Skate (*R. batis*). Before referring at length to the comparative anatomy of the organ in the various members of the genus *Raia*, I have thought it desirable to prepare a paper dealing almost exclusively with its development in *Raia batis*. I have already ascertained that there is considerable diversity in the time of appearance and development of the organ in the Skate genus, as well as a marked difference in its form and structure. In the Gray Skate, as is well known, the organ consists of numerous discs, but in some other forms (*e.g.*, *R. radiata*), instead of large complex discs, we have small simple cup-shaped bodies provided with long or short striated tails, each cup being lined with an enlarged motor (electric) plate, and coated with a richly nucleated layer of protoplasm. The form and character of these cup-shaped organs seem to indicate that they have been retarded in their development; but the question still remains—Are they advancing or receding? Are these electric cups degenerated discs, or are they the primitive ancestral elements out of which the discs have been evolved? Do these characteristic cups ever develop into discs, or do they, after having persisted for a time, finally disappear, or are they distinct and independent structures?

These and various other questions at once suggest themselves for solution, but in the meantime I need only say that I believe the large discs of the common Skate have been derived from cup-shaped structures, such as still persist in certain adult forms—that, in fact, the electric plate of the disc in *Raia batis* is the greatly expanded lining of a simple cup-shaped structure, such as exists in *Raia radiata*, while the accessory portions of the disc have been derived from the muscular substance composing the body of the cup.

To make the account of the development intelligible it will be desirable to shortly describe the structure of the hitherto imperfectly described organ of the Gray Skate. While in the Torpedo the electric elements are arranged to form numerous vertical columns, in the Skate they give rise to numerous hollow cones, which are fitted within each other to form two elongated electric spindles, one at each side of the tail.

Each of the discs of which the electric cones of the Gray Skate are composed consists essentially of three distinct layers, exclusive of the nerves and vessels distributed to it and the connective tissue in which they are embedded. The first layer, beginning from the anterior side, may be known as the electric plate, which consists of a layer of protoplasm, containing large nuclei (*a.*, figs. 10 and 13). Extending to end in this plate (which probably corresponds to the motor plate of muscles) are numerous nerves (*g.*, fig. 13) which divide dichotomously as they pass backwards through a supporting connective tissue framework.

The second layer may be known as the striated or meandriform layer (*b.*, figs. 8, 10, and 13). It consists of a compact mass of lamellæ, which, though they often present an extremely sinuous appearance, are seemingly continuous from one end of the disc to the other. This striated layer is easily separated from the electric plate in front, and it can also, though less readily, be detached from the third layer lying immediately behind it. This third layer may be known as the alveolar layer (*c.*, figs. 10 to 13). Its anterior surface is smooth and even, while the posterior is extremely irregular, and presents a number of spaces or alveoli (figs. 11 and 12) which somewhat resemble the sacculations in a Frog's lung. From this alveolar layer a funnel-shaped projection (*d.*, fig. 13), which ends in a long narrow process, is sometimes seen extending obliquely backwards.

Behind these three layers, which form the disc proper, there is a thick cushion of gelatinous tissue (*f.*, fig. 13), which fills up the space between the alveolar layer and the septum (*s.*, fig. 13) that forms the posterior wall of the chamber in which the disc lies.

Enclosing the disc, with its nervous layer in front and the gelatinous cushion behind, there is a complete fibrous investment, which is continuous with the fibrous septa that lie between the adjacent discs and the connective tissue that lies between the electric cones. Each disc (when the nerves and gelatinous tissue are included) may hence be said to lie in a cell or chamber, to the walls of which it is chiefly attached by the nerves and their accompanying connective tissue fibres in front, and by the blood-vessels which enter the chambers from behind.

From a general consideration of the electric organs of the Torpedo and Gray Skate, it seems evident that the essential structure is the electric plate; and that, in order to have an efficient organ it is necessary to provide a large superficial area for the terminations of an incalculable number of nerve fibres.

This is gained with the greatest economy of space when numerous small insulated plates are piled above or in front of each other, and held in position by a delicate framework. A structural homologue of the electric plate on a small scale already exists in the motor plate of muscles. In the production of the electric organ of the

Skate advantage has been taken of this already existing structure, which has been in fact enlarged to form the essential part of the organ, while the muscular fibre to which the motor plate belonged has been utilised in the formation of certain accessory portions of the organ.

Previous to the researches of BABUCHIN the development of electric organs was practically as obscure as their origin, and even now many biologists are unable to understand the relation between muscular fibres and electric columns and discs. BABUCHIN, in addition to working out the development of the Torpedo organ, has on several occasions referred to the organ of the Skate. The material at his command, however, seems to have been limited, and it was impossible to identify the species of some of the embryos examined. From the figures accompanying BABUCHIN'S most important paper, it is probable that his observations were made, in part at least, on the Flapper Skate (*Raia macrorhynchus*). Apparently, neither *R. batis* nor any of the forms having cup-shaped organs were subjected to examination. BABUCHIN* describes the now familiar "clubs," and refers to the more important stages of development, including the formation of the alveolar and striated layers; but his clubs seem to have passed directly into flattened discs, and the stems or processes were not found after the Skate had reached a length of 15 cm.

While in the Torpedo the electric organ appears at a very early stage of development, and begins to discharge feeble shocks before the young escape from the oviduct, in the Skate the rudiments of the organ are late in appearing, and development is, in some cases, extremely slow.

In very young embryos of *R. batis* there is no indication of an electric organ, the position of the organ being occupied by unaltered muscular fibres; but in an embryo about 7 cm. in length the rudiments of the future organ are easily recognised, both in teased preparations and sections.

I have figured the embryo (Plate 66, fig. 1) in which the earlier stages were studied, so that the period of development may be the better understood. It will be observed that the so-called external gills (fig. 1, *g.*) still persist, and that the tail is relatively long and powerful. The large yolk sac is not represented in the figure.

In this embryo the rudiments of the organ were in the form of long slender clubs (fig. 2) which occupied the vertebral or inner portion of the muscular band lying next the notochord. In transverse sections through the middle of the tail, where the clubs are most numerous and most advanced, they are seen to be few in number and to occupy a very small and indistinctly defined area, being still surrounded, except on the side adjoining the notochord, by unaltered muscular fibres. Transverse sections are, however, especially interesting in demonstrating the existence of muscle nuclei in the substance of the head of each club and between the head and the sarcolemma, and in showing a marked increase of embryonic connective tissue cells between and around the various clubs. They also in some cases point to the existence of a channel at or

* For titles of BABUCHIN'S papers see p. 407.

near the centre of the stem of the club, which may have resulted from the migration forwards of the muscle nuclei. In longitudinal sections (fig. 2) the gradual change from an ordinary muscular fibre to an electric club can easily be traced.

The anterior end of the muscular fibre destined to become a club assumes a rounded form, and the nerve and the motor plate become more distinct, and the muscle nuclei increase in number. As the muscle nuclei increase the head expands and retreats slightly from the septum to which it was originally connected, leaving the intermuscular tissue in the form of a funnel-shaped expansion, within which lie the now enlarged nerve fibre and a number of round and oval embryonic connective tissue corpuscles. These corpuscles gradually increase in number, and eventually form the connective tissue framework which supports the numerous branches of the nerves proceeding to the electric plate. Had there been no interference with the muscular fibres, the muscle nuclei would have ministered to their growth, and probably also to a certain extent to the enlargement of the motor plate. The energy of these nuclei is, however, now largely diverted into new channels; for, while some continue, evidently under unfavourable conditions, to increase the size of the muscular fibre, the greater number migrate in one of two directions—forwards, to assist in enormously increasing the motor plate; or, outwards, to give rise later to the alveolar layer. *They all, however, seem to remain within the original sarcolemma.*

The clubs (as fig. 2 indicates) usually make their appearance from within outwards; but, however they appear, some of them are further advanced than others, and the precedence at first gained is maintained throughout the whole period of development. In somewhat older embryos clubs are found at one part and rudiments of discs at another. Figs. 3, 4, 5, and 6 are all taken from one section from near the centre of the tail of a Skate about 10 cm. in length. The great difference in the size and elaboration of the clubs at the same part of the tail is worthy of special note.

As the size of the head of the club increases the development of the stem is arrested, and after a time the whole club, instead of being as long as the adjacent muscular fibres, is at least one-third shorter; and as development proceeds, the tail or process is reduced to a long, narrow, somewhat ribbon-shaped structure, only partially striated (figs. 3 to 9).

It may hence be taken for granted that the expansion of the anterior end of the original muscular fibre has resulted from a change in the motor plate, accompanied by corresponding changes in the motor nerves and the cells in the spinal cord from which they originate. This seems to be corroborated by the fact that in slightly older embryos the nerve cells around the embryonic neural tube are relatively large and distinct.

As the motor plate, with the help of the rapidly multiplying muscle nuclei (which continue to arrive for some time from the head of the club), increases in size the nerves in connection with the plate develop new branches, which occupy a nearly vertical position in front of the plate. These branches, after reaching a certain size, are provided with a sheath and held in position by the connective tissue network already referred to.

Coincident with the increase of the motor plate there is an enlargement of the head of the club, which gradually loses its rounded form and assumes a truncated appearance, somewhat resembling a mace. In front of the flattened anterior surface of the mace there lies the richly nucleated motor plate. When this stage has been reached the striation of the anterior portion of the mace is observed to be much closer than that of the posterior portion, while at the root of the stem the striation has almost completely vanished.

There is, further, a diminution of the muscle nuclei in the anterior portion, and an increase in and around the posterior portion, of the head of the mace; and in many cases the head of the mace is tilted so as to form an obtuse angle with the stem.

The next stage is an exceedingly important one. The front portion of the head of the mace, in order to support the ever-increasing motor plate (which may henceforth be spoken of as the electric plate), expands transversely, and at the same time projects the whole, or the greater portion, of its margin forwards, and thus forms an extremely shallow cup-shaped structure, which is, of course, lined by the electric plate.

The finely striated anterior portion of the mace is chiefly involved in the formation of this electric cup. The beginning of the cup is indicated in fig. 3, and later stages are represented in figs. 4 and 5.

As the expansion and moulding take place the few nuclei which persist in the striated front part of the mace either pass forwards into the electric plate, backwards towards the unstriated portion, or they disappear; and when all these nuclei have vanished the finely striated portion of the mace has, without any marked change, become the striated layer, while the nuclei behind this layer arrange themselves to form the rudiment of the alveolar layer. The nuclei behind the striated layer very closely resemble the nuclei of the electric plate. They may both be considered muscle nuclei, which have entirely, or to a large extent, lost their muscle-forming properties. The striated layer, having been once established, remains, as far as I have observed, absolutely free of nuclei. We may suppose that it obtains the nourishment required for its further growth from the protoplasm lying in contact with one or both of its surfaces.

The cup stage having been reached, there is apparently a short pause, which is followed by a period of considerable activity in all the three layers.

The electric layer, at first quite within the margin of the shallow cup, gradually increases until the edge is reached. As this takes place the striated layer first increases in thickness and has its margins recurved. It then steadily expands to form the large characteristic striated layer of the fully developed disc. This layer is represented in figs. 4 to 13 (*b*). It is always distinctly striated; but its thickness and the amount of sinuosity of the lamellæ vary with the mode of preparation. In the completed disc the form of the striated layer varies considerably. In front views it presents sometimes a circular, sometimes a nearly hexagonal, outline. In side views of the entire disc the margin is uniformly but unequally curved backwards, while in sections it appears sometimes distinctly concave in front, at other times convex—or it may be concavo-convex, the form again partly depending on the mode of preservation.

The alveolar layer may next be considered. It is at first represented by a nucleated layer of protoplasm lying between the posterior surface of the striated layer and the sarcolemma at the base of the mace. The nuclei multiply, and protoplasmic projections, containing one or more nuclei, begin to grow backwards around the stem of the mace or cup (fig. 6). These projections vary greatly in form; some of them are long and rounded, but in most cases they consist of relatively broad flattened processes, which, as they grow backwards, give rise to irregular pit-like depressions.

As the original processes increase in length they throw out lateral projections, which, by meeting and fusing with each other, give rise to an irregular network (figs. 7 and 9). By the appearance of still more delicate processes, a fine network is formed within the larger pits immediately behind the striated layer.

These processes and pits are represented in figs. 7, 8, 9, and 10, and the network formed by their fusion is shown in figs. 11 and 12. The nuclei of this alveolar layer are from the first large and prominent, and as development proceeds they are surrounded by a clear area of unstainable protoplasm, which in some cases (*h*. fig. 10) reaches a considerable thickness. After a time the nuclei and the surrounding protoplasm are less distinct. In longitudinal sections of the alveolar layer (figs. 10 and 13) the most striking objects are the prong-like backward extensions of the original simple processes.

Having considered the striated and alveolar layers, the electric plate may now be further described. During the club and mace stages the electric plate consists of a layer of protoplasm, which is almost obscured by the numerous large nuclei embedded in its substance (figs. 4, 5, and 6). After a time the multiplication of the nuclei seems to come to an end; hence, as the plate increases, they are gradually separated from each other. Fig. 8 indicates the arrangement in a Skate 20 cm. in length, and fig. 10 the relative proportion of nuclei to protoplasm in a Skate 25 cm. in length. In the last-mentioned Skate, the electric plate was extremely distinct and relatively thicker than at later stages, in which the nuclei are flattened and apparently applied to the surface of the striated layer, while the protoplasm in which the nuclei are imbedded is reduced to a thin and nearly transparent membrane. As figs. 10 and 13 indicate, the electric plate lies in contact with the striated layer, but is not inseparably connected with it, while it becomes continuous with the alveolar layer round the margin of the disc. On the anterior surface of the electric plate there is a delicate nerve plexus (fig. 10, *g*.); but no fibres appear to pass through its substance, either in a vertical or oblique direction.

The general arrangement of the nerve fibres which pass to the electric plate is indicated in fig. 13. It will be observed that to a large extent they lie at nearly right angles to the electric plate, and that they branch dichotomously as they proceed to end in its substance.

Having considered the structures directly or indirectly derived from the head of the original club, we may now refer further to its shaft or stem. This at first is distinctly striated; but as the condensation takes place in the club or mace to give rise to the striated layer, the transverse markings at the base of the stem disappear, and this part of the stem undergoes vacuolation, only a few clear oval corpuscles remaining in contact with the sarcolemma. As the anterior third of the stem is altered the communication between the posterior portion and the developing disc seems to be cut off (figs. 3 to 9); and occasionally, immediately behind the atrophied portion, there is, as it were, a whole detachment of muscle nuclei arrested in their attempt to move forwards to take part in the formation of the disc. The muscle nuclei left in the posterior portion of the stem continue in a feeble way to produce muscular tissue; but they only succeed in forming a long, slender, and apparently useless process.

This process, however, long retains its striated appearance; and, although it has not hitherto been detected in a Skate over 15 cm. in length (and its existence in a fish of this size seems to have surprised BABUCHIN), I have had no difficulty in finding it practically unaltered in Skates over 60 cm., and on several occasions I have found it both in sections and in teased preparations of discs from fully developed organs. I ought to add that the terminal portion of the stem is often enlarged and crowded with nuclei; whether the stem always ultimately disappears has not yet been determined. It is not surprising that it is seldom seen in sections, for it is eventually reduced to form a thin ribbon, which, unless the section runs parallel with its long axis, easily escapes detection; and, further, it gets deeply embedded in the connective tissue framework and is easily obscured by the accompanying blood vessels and nerves. It will be observed in fig. 13 that the stem springs from a funnel-like expansion attached to the under surface of the disc. This funnel consists partly of the remains of the head of the original club, or rather of the electric cup, and partly of the dilated base of the stem—the dilatation having taken place as the cup gradually expanded to form the relatively large flattened disc. In some cases, when there are long projections from the alveolar layer, one or more of them may simulate the stem of the original club; while, on the other hand, when only a short portion of the stem is left in the section it may be mistaken for one of the projections from the alveolar layer.

In concluding the description of the electric disc, it is only necessary to add that there are discs at several stages of development and growth in the same part of the tail, and that the discs continue to enlarge as the fish increases in size. But apparently the organ becomes active (*i.e.*, acquires the power of discharging electric shocks) long before the maximum size is reached, for I understand SANDERSON and

GOTCH* have obtained decided shocks from Skates considerably under 60 cm. in length.

The thick layer of connective tissue which lies behind the alveolar layer is represented in fig. 13 (*f.f.*), which also indicates the connective tissue investment of the entire electric cell or chamber and the connective tissue septa (*s.*) which lie between the various chambers. The walls of the chambers are largely derived from the original septa (*s.*, fig. 2), which lie between the myotomes, while the thick layer of tissue behind the alveolar layer is derived from the embryonic connective tissue corpuscles which are so extremely abundant around the clubs and rudimentary discs.

In another communication I hope to give an account of the structure of the cup-shaped bodies of which the electric organ of *Raia circularis* and other forms is composed.

LITERATURE.

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EXPLANATION OF PLATES.

PLATE 66.

Fig. 1. Dorsal view of the smallest *R. batis* embryo in which the rudiments of the electric organ were observed. The large yolk bag is not represented.
g. So-called external gills. Natural size.

Fig. 2. Longitudinal horizontal section through the tail of the embryo figured (fig. 1), showing the muscular fibres developing into clubs.

1. and 2. Well-marked clubs, with numerous muscle nuclei lying in contact with the enlarged anterior end.

3. A club with a pit-like depression at free end, and nuclei apparently in the process of migrating from the interior of the altered muscular fibre.

4. A muscular fibre only very slightly altered, lying in contact with an ordinary muscular fibre.

Observe the oblique position of the clubs, that the muscular striations still persist, even at the expanded portions; note also the intermuscular septa. The connective tissue corpuscles, which are extremely numerous around the clubs, are scarcely represented.

ZEISS' apochromatic 4, eyepiece No. 3. Outlined with ZEISS' camera.

* 'Journal of Physiology,' vol. 9, Nos. 2 and 3 (August, 1888).

Fig. 3. Two clubs from a slightly older Skate embryo (*R. batis*); one (1) a little more advanced than the other: both clubs are considerably larger than those represented in fig. 2.

a. The enlarged motor plate, with numerous nuclei embedded in its substance, and well-defined nerve fibres (*e.*) proceeding towards its anterior surface. Observe the nuclei in connection with the sheaths of the nerves, and the connective tissue corpuscles scattered amongst them.

b. The portion of the club which is altered to form the striated layer of the disc, behind which lie nuclei (*c.*) which give rise to the alveolar layer.

d. The stem or tail of the club, which is still muscular.

ZEISS' apochromatic 4, eyepiece No. 3. Outlined with ZEISS' camera.

Fig. 4. An isolated club which has expanded to form a shallow electric cup. Letters as in fig. 3.

Fig. 5. From a longitudinal section to show one of the first steps towards the formation of the electric disc. Note that the three principal layers (*a.*, *b.*, *c.*) are already represented—the alveolar by a layer of richly nucleated protoplasm.

Figs. 4 and 5 drawn with ZEISS' apochromatic 4, eyepiece No. 3.

Fig. 6. A somewhat more advanced stage, more highly magnified (ZEISS' apochromatic 4, compensating eyepiece No. 12), showing (*a.*) the large nuclei of the electric plate; (*b.*) the striated layer; (*c.*) the alveolar layer, sending out blunt processes; and (*d.*) the long stem.

Drawn with ZEISS' camera.

The stages represented in figs. 3, 4, 5, and 6 were all present in the same Skate.

Fig. 7. Sketch of an isolated disc from a Skate nearly 60 cm. in length, showing the projections and alveoli of the alveolar layer, and the long stem, which still retains some of its striations. Letters as in fig. 6.

ZEISS' apochromatic 4, eyepiece No. 3.

PLATE 67.

Fig. 8. Longitudinal section through a disc, slightly larger than fig. 7, showing the nucleated electric plate (*a.*); the processes of the alveolar layer (*c.*) extending into the posterior gelatinous cushion (*f.*); the connective tissue sheath (*s.*); and the long stem (*d.*) with a trumpet-like expansion (*e.*) where it joins the disc.

ZEISS' apochromatic 4, eyepiece No. 3.

Fig. 9. Sketch of an isolated disc from the same Skate as figs. 7 and 8. Observe that (though the magnifying power is the same) it is larger than fig. 7. The alveolar layer (*c.*) is now extremely complex; the stem (*d.*, *e.*) is ribbon-

shaped, but still striated posteriorly; and the electric plate presents a still larger area for the terminations of the electric nerves. *b.* Striated layer. *d.* Electric plate.

Fig. 10. A portion of a disc from a slightly older Skate, magnified 950 diameters.

a. The electric plate with its large distinct nuclei, and a nerve plexus? (*g.*).

b. The striated layer in the form of a narrow sinuous band.

c. The alveolar layer with (*c.′*) simple and compound (*i.*, *d.*) projections, giving rise to primary and secondary alveoli. Note the large nuclei and the clear protoplasm (*h.*) surrounding them.

Zeiss' apochromatic 4, compensating eyepiece No. 12. Drawn with Zeiss' camera.

Figs. 11 and 12. Two transverse sections through the alveolar layer of a fully developed disc. Fig. 11 shows the fine network formed by the processes of the alveolar layer immediately behind the striated layer, while fig. 12 shows the wider network some distance from the striated layer. The spaces are occupied by gelatinous tissue, containing blood vessels.

Zeiss' AA, eyepiece No. 3.

Fig. 13. Longitudinal section through a disc from a Skate (*R. batis*) about 27 inches in length. This sketch illustrates the general structure of an electric disc in *Raia batis.* The blood vessels are not included.

g. The nerve fibres passing to the electric plate. The fibres, at first large and provided with a medullary sheath, divide dichotomously as they approach the plate, and eventually have only a gray sheath. They all terminate on the anterior surface of the plate, where they seem to form by their terminal divisions a series of delicate loops or rings. The spaces between the nerve fibres are occupied with gelatinous tissue, containing numerous nuclei.

a. The electric plate, consisting of a layer of protoplasm capable of being divided into two lamellæ, the posterior of which contains large nuclei.

b. The striated layer, made up of numerous lamellæ having an exceedingly sinuous arrangement.

c. The alveolar layer, with processes projecting backwards into (*f.*) the gelatinous cushion, and connected together by secondary processes to form an irregular network.

dd. The stem of the disc, which consists of the altered posterior portion of the original muscular fibre, part of which is still indistinctly striated (*e.*). The part of the stem surrounded by the projections of the alveolar layer is considerably dilated. This dilated portion, together with the upper half, or more, of the narrow portion, is embedded in the gelatinous tissue.

s. Septum between two electric chambers.

s′. Part of the original transverse intermuscular septum.

On the Structure of the Electric Organ of Raia circularis.

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[Plate 68.]

In the preceding paper "On the Development of the Electric Organ of *Raia batis*," I mentioned that in some Skates (*e.g.*, *R. batis*) the electric organ consists of rows of discs, while in others it is made up of numerous small cup-shaped bodies. These electric cups (which, as far as I can ascertain, have never been observed before) I first noticed in *R. circularis*, but they are equally well marked in *R. radiata* and *R. fullonica*. In *R. radiata*, however, the electric organ is extremely small (while the individual cups seem to be incompletely developed); and, *R. fullonica* being comparatively rare in our waters, I found it most convenient to study the structure of the cups in *R. circularis*.

This Skate sometimes reaches a length of 3 feet, and the tail is usually a little more than half the length of the entire fish. The dorsal aspect of the tail is studded with numerous large and small denticles, which, however, differ considerably in their distribution in different individuals.

The electric organ in *R. circularis* only occupies a relatively small portion of each side of the tail, in this respect differing decidedly from the organ of *R. batis*, which extends from the inner surface of the skin to the vertebral column, leaving a very small space for the posterior portions of the caudal muscles. Although the electric organ only occupies a small segment of the tail in *R. circularis*, it reaches a considerable length. In a specimen which was nearly 27 inches (68 cm.) in length from tip to tip, the electric organ measured $8\frac{1}{4}$ inches (21 cm.) in length, was 5 mm. in breadth, and nearly 25 mm. in thickness at the thickest central portion. This organ is represented, natural size, in Plate 68, fig. 1. When exposed, it was seen to occupy the posterior two-thirds of the tail, and the posterior portion (three-fifths) lay immediately under the skin, while the anterior portion (two-fifths) was embedded in the caudal muscles.

The exact position of the organ will be at once understood by a reference to fig. 2, which represents a transverse section through a portion of the tail, about 4 inches from its termination. It will be noticed that the nerve of the lateral line (*n.*, fig. 2) is in contact with the outer surface of the organ, and that the organ has a somewhat oval form in section.

When the organ is removed it has, owing to the tapering at the ends, a striking resemblance to a slightly flattened spindle (Plate 68, fig. 1). The posterior end, which reaches to the tip of the tail, is usually more pointed than the anterior end, which is enveloped by muscular fibres.

In thick transverse sections of the fresh organ it is possible to distinguish with the naked eye the nearly circular cups. These vary in number in the different sections, but they are always more abundant in the thick central portion of the organ than near the extremities. When slightly magnified (fig. 2, *c.c.*) the cups become more evident, and the nerve (*n.*) of the lateral line is seen indenting the outer surface.

Fig. 2 also shows the relation of the organ to the skin and the caudal muscles; the outer surface is in contact with the subcutaneous tissue; the inner surface is separated from two well-marked muscular bands by a thick fibrous septum, from which an intermuscular septum projects inwards towards the vertebral column. Along this transverse septum vessels and nerves find their way to the electric organ. Transverse sections made near the ends of the organ only differ from sections of the thick central part in the number of the cups; at the terminations only one or two cups may be found, but they are apparently as perfect as, though less regular in form than, the cups at the centre of the spindle.

The size and form of the cups can be readily determined by means of thick sections of the fresh organ, or by teasing portions of an organ which has been macerated in nitric acid. In teased preparations it is often possible to study completely isolated cups. When a dozen or more cups are under observation, it is at once evident that, although they all resemble each other, there is over all a considerable amount of variation both in shape and size. Some of the cups are comparatively shallow, while others are both wide and deep; it is possible that the shallow ones only differ from the others in being less fully developed. One of the most regular and common forms is represented in fig. 3. It will be noted that this cup is of a considerable size, so large, in fact, that it does not necessarily follow, as I originally supposed when studying the organ of *R. radiata*, that organs made up of cups have been arrested in their development. In describing the development of the organ in *R. batis*, I mentioned that the discs passed through an indistinct cup stage, but the cup in *R. batis*, instead of becoming deeper, has its margin everted to form, first, a mushroom-shaped structure, and, eventually, a large flat disc.

In *R. circularis* and others, however, as will be afterwards described, exactly the opposite changes set in; the head of the original muscular club is moulded as it increases in size to form a thin-walled cup, from which the posterior part of the muscular fibre projects in the form of a long or short stem. At first one is apt to suppose the cups must be far less effective than the discs. Whether this is the case or not has still to be determined, but it does not necessarily follow; for, if the superficial area of such a cup as is represented in fig. 3 is compared with the superficial area of a disc from *R. batis*, it will be found that the extent of the one nearly corresponds to that of the other. Owing to a given number of cups occupying a smaller space than a corresponding number of discs, it is conceivable that it might require an organ composed of discs to be somewhat larger than an organ composed of cups to be equally effective. As to the cups, I ought, perhaps, to mention that in transverse sections those near the periphery are often flattened and irregular. This irregularity is, however, in most cases due to the influence of reagents. In longitudinal sections (2A) the cups are seen to be arranged in oblique rows, so that the adjacent cups, to a certain extent, alternate with each other. This holds for both horizontal and vertical longitudinal sections. By this arrangement a large number of cups can be packed in a comparatively small space.

A reference to fig. 2A will also show that, though the individual cups are usually slightly tilted to one side, the wide open mouth, which always looks forward, is nearly at right angles to the long axis of the organ.

In giving a short account of the discs of *R. batis* in the previous paper, I pointed out that each consisted of three essential layers, viz.: (1) an electric plate, (2) a striated layer, and (3) an alveolar layer; and that a layer of gelatinous tissue supported the nerves in front, while a thick gelatinous cushion lay behind each disc, filling up the alveoli and forming a convenient stratum for the blood vessels. The advantage of recognising that each electric element consists of only three important layers becomes evident when the cup-type of electric organs is considered.

In *R. circularis*, for example, each cup consists of (1) a thin lining, (2) a thick central layer, and (3) a dense cortex, invested with a thin coating of gelatinous tissue. The lining of the cup is practically identical with the electric plate of the disc of *R. batis*; the thick central layer corresponds to the striated layer of the disc, while the cortical layer represents the alveolar layer of the disc. Corresponding to the nervous layer in *R. batis*, we have in *R. circularis* a bunch of ever-dividing nerve fibres, with gelatinous tissue filling up the intervening spaces, and in place of the thick gelatinous cushion there is the thin gelatinous investment of the cup, already mentioned, in which the blood-vessels ramify. The whole organ, as in *R. batis*, is surrounded by a connective tissue sheath, from which fibres extend inwards to lie between the various rows of cups, and provide for each cup a thin, and often indistinct, fibrous investment.

The lining of the cup (the electric plate) consists of a continuous layer of finely granular protoplasm, containing numerous large nuclei, having a remarkably regular arrangement. Having formed a complete lining for the cup, the electric plate extends over the somewhat sinuous margin to melt and blend with the cortical layer in very much the same way as the electric plate unites with the alveolar layer in *R. batis*. The posterior surface of the electric plate lies in close contact with the anterior surface of the striated layer, but it is apparently less easily detached from the striated layer than in *R. batis*. For the purposes of description, this electric plate may be described as consisting of two lamellæ—a thick posterior lamella in contact with the striated layer and containing the large nuclei, and a thin anterior lamella which is inseparably connected with the terminations of the electric nerves. The anterior lamella is sometimes separated at irregular intervals from the posterior lamella, owing, apparently, to tension, the result of shrinkage of the nerve layer. The nuclei of the electric plate are usually oval in form; sometimes they are nearly spherical. Each, surrounded by a layer of difficultly stainable protoplasm, contains numerous small darkly stained points, the significance of which has not yet been determined. The relative size, position, and abundance of these nuclei may be learned by a reference to fig. 5, *e.p.*

The distribution of the nerves to the electric cups is indicated in figs. 4 and 5. The remarkable bouquet of nerve twigs which enters each cup can be readily seen in sections of fresh organs fixed with osmic acid. The larger medullated branches divide dichotomously again and again until a countless number of delicate fibrils are produced, which, as they approach the electric plate, lose their white sheath and are only separated from each other by the gelatinous tissue which assists in holding them in position. Some of the terminal branches, magnified 950 diameters, are represented in fig. 5. Each terminal branch retains its gray sheath until it reaches the electric plate, and at the point of bifurcation of even extremely small branches a nucleus is usually present. Only a few of these nuclei, however, are represented in the drawing, and the connective tissue corpuscles, which are often large and prominent, are entirely left out, to prevent crowding.

How the nerves ultimately terminate it is extremely difficult to determine. Various views have been advanced as to the nerve endings in the electric organ of the Torpedo, as well as of the Skate; but, as the nerve endings will be specially described in a paper on the structure of the organ of *R. batis*, I shall, in the meantime, simply call attention to the peculiar nerve loops represented in fig. 5, in contact with the anterior surface of the electric plate. These loops result from what appears to be the terminal bifurcation of the non-medullated nerve fibres; hence, they have usually a vertical, or nearly vertical, position, and are only distinctly visible where the section happens to run parallel with the loops, and are indistinct or invisible when the section is at right angles to the loops. Sometimes the loops have an oblique or nearly horizontal position, and when this is the case they often assume the form of complete rings, and when several of these rings are seen at one part of the section in contact with each other the loops seem to have given rise to a delicate network with small, nearly circular, meshes. I have never seen any indication of the nerve fibres expanding to form terminal swellings, or of their giving rise to a plexus in the substance of the electric plate.

The striated layer, as in *R. batis*, may be considered as consisting of altered muscular substance. In some sections it still suggests striated muscular fibres (fig. 4, 2.*s.l.*); but in most cases the fibres are extremely contorted, as is indicated in fig. 5 (*s.l.*). This layer has a considerable thickness, and, unlike the corresponding layer in *R. batis*, it retains a few nuclei amongst the lamellæ. In transverse sections a number of clefts or spaces are usually seen at irregular intervals between the fibrillæ. These spaces are greatly exaggerated in frozen sections, in which the striated layer somewhat resembles an irregular network, which might be mistaken for the alveolar layer of *R. batis*. The striated layer is directly continuous with the axis of the stem, which consists of the altered posterior portion of the original muscular fibre. In the fully developed cup, however, the greater part of the stem consists of a nucleated sheath continuous with the cortical layer of the cup.

The two layers described agree in all essential characters with the corresponding layers in the discs of *R. batis,* but the third, or cortical, layer of the electric cup differs very decidedly from the alveolar layer of the electric disc. The nature of this layer may be gathered from figs. 4 and 5 (*c.l.*). It consists of a thick layer of protoplasm, containing large nuclei, each surrounded by a halo of clear protoplasm. The anterior portion of this cortical layer has, in some preparations, a granular appearance, while the outer is finely striated; but whether the striations have any special significance I cannot say. From the cup proper this layer extends, as already mentioned, on to the stem, which it completely invests, diminishing in thickness as it approaches the apex. This cortical layer doubtless agrees with the alveolar layer of *R. batis.* As in *R. batis,* it probably arises from altered muscle nuclei. In *R. batis* the alveolar layer at first consists of a single layer of nucleated protoplasm, but it soon sends out projections, which eventually give rise to a complex network. In *R. circularis,* on the other hand, alveoli are never developed; at the most a few short blunt processes (figs. 3 and 4, *p.*) are thrown out from the outer surface of the cortex, more especially around the base of the stem. It is, however, conceivable that in some other species the outer, or cortical, layer of the cups may develop long complex processes similar to those of *R. batis.* The gelatinous layer, as already indicated, is comparatively unimportant; it surrounds the cups (*c.t.*, fig. 5), and fills up the spaces between the stems; it, in fact, forms a matrix in which the cups are embedded, and in which the blood vessels freely ramify. One of the capillaries is represented in fig. 5 (*c.p.*). The capillaries form an irregular network between and around the cups; but they never appear either to enter the cups with the nerves or penetrate into the substance of the striated layer through the cortex.

In a further communication I hope to give an account of the structure and development of the electric cups of *Raia radiata* and to indicate whether I consider them retrograding or progressive structures.*

* For the material for the above investigations, I am chiefly indebted to the Fishery Board for Scotland. I am also indebted for specimens of various species of Skate to Professor McIntosh, F.R.S., St. Andrews; The Maclaine of Lochbuie; Mr. W. L. Calderwood, Mr. Thomas Scott, and Mr. P. Jamieson (Members of the Scientific Staff of the Scottish Fishery Board); Mr. Sime, Aberdeen, and Dr. P. J. White, Nat. Hist. Dept. Univ. Edin. I have especially to thank Dr. G. C. Purvis, Dem. Zool. Univ. Edin., for much valuable assistance rendered during the progress of the work.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Explanation of Plate 68.

Fig. 1. The entire organ of *Raia circularis*, from a specimen 27 inches (68 cm.) in length. The sketch was made from an organ exposed by removing the skin and portions of the caudal muscles. It measured $8\frac{1}{4}$ inches (21 cm.) in length, and was 5 mm. in breadth at the widest central portion. Note the shallow groove (*g.*) on the surface of the posterior two-thirds, along which lay the nerve of the lateral line, and note also that the organ is spindle-shaped. Natural size.

Fig. 2. Represents a transverse section from near the centre of the organ of *R. circularis*. Note that the organ lies immediately within the skin, and has the nerve (*n.*) of the lateral line indenting its outer surface.

a. The skin with four denticles (*a′.*) embedded in the dorsal portion.
b. The lateral fold of the tail.
c. The electric cups.
d. The connective tissue surrounding the organ and extending between the caudal muscles.
n. Nerve of the lateral line.
m. Caudal muscles, cut transversely. About six times natural size.

Fig. 2*a*. Represents a thin longitudinal vertical section of the organ of *R. circularis*. It shows the arrangement and various modifications of the electric cups, some of which retain, almost complete, the delicate stems. Note that the cups form nearly regular oblique rows.

Ocular 3, objective 00. Outlined with Zeiss' camera.

Fig. 3. Shows one of the cups of *R. circularis*, cut somewhat obliquely. Note the depth of the cup, the great extent of its nucleated lining (electric plate) (*e.p.*) the irregular margin, with a spout-like projection (*s.*) at one side, the cortical layer (*c.l.*) and its blunt processes (*p.*), the thick striated layer (*s.l.*), and the long stem (*st.*).

Zeiss' AA, compensating eyepiece No. 12. Outlined with Zeiss' camera.

Fig. 4. Two electric cups, showing the nerves, a portion of the striated layer, the long stems, &c.

n. The nerves proceeding towards the cups.
c.l. The cortical layer, with (in 1.) short blunt projections (*p.*).
s.l. Part of the striated layer.
st. The stem.

Zeiss' AA, compensating eyepiece No. 8. Corrosive sublimate and spirit preparation.

Fig. 5. Longitudinal vertical section through one of the cups of *R. circularis*, showing the three chief layers, the terminal nerve branches, &c.

e.p. Electric plate, with large nuclei at nearly regular intervals.

n. Terminal branches of the electric nerve, forming loops and rings as they reach the electric plate. Only a few of the nuclei of the gray sheath are shown in the sketch, and the gelatinous tissue is not represented.

s.l. Striated layer. Note its great thickness, the irregular arrangement of its fibres, and the presence of nuclei.

c.l. The thick cortical layer, with large nuclei embedded in its substance, each surrounded by a distinct halo of clear protoplasm.

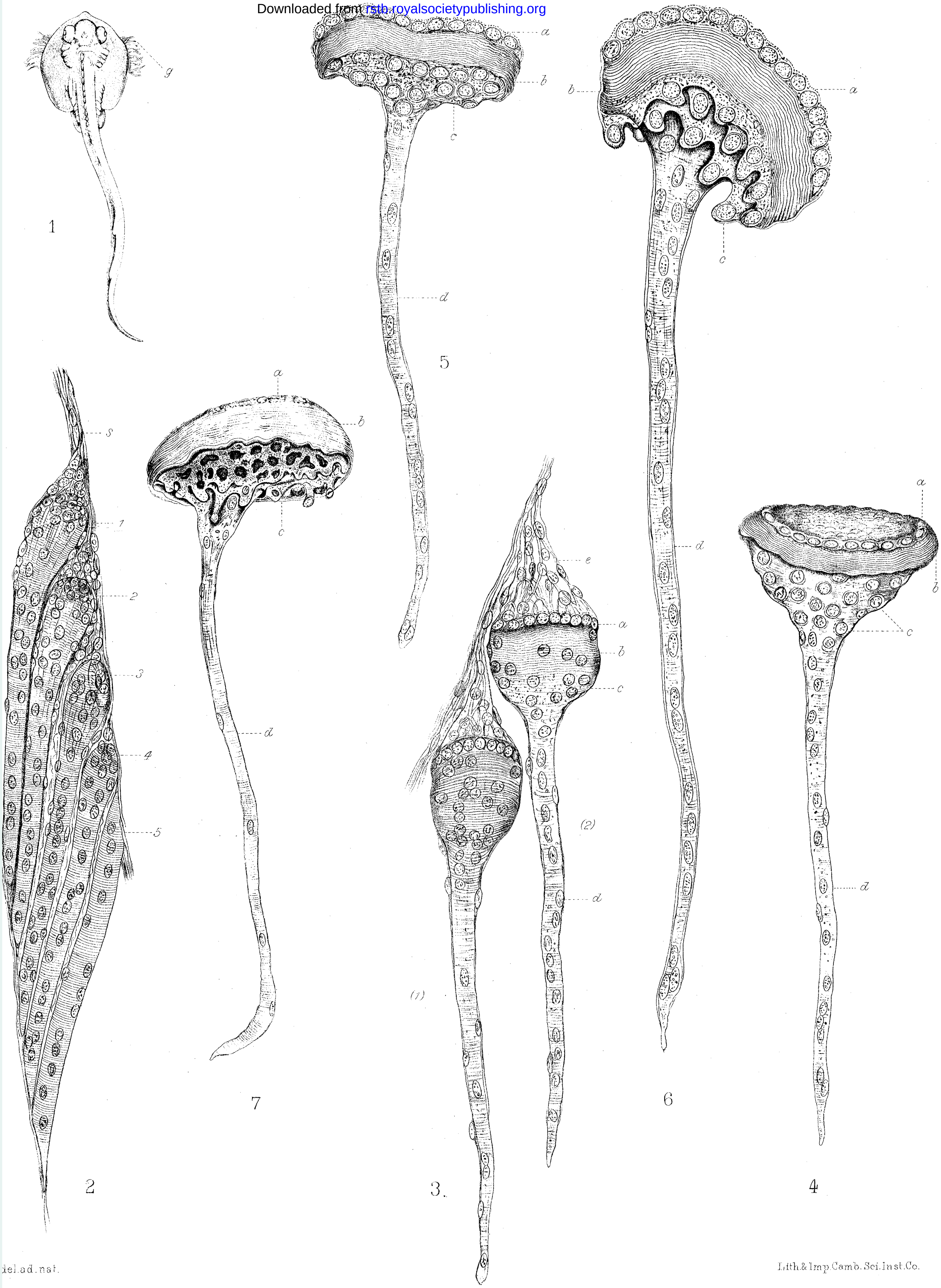
st. The stem, invested by nucleated protoplasm, apparently identical with the cortical layer.

c.t. Gelatinous tissue, investing the cup.

c.p. Capillary, lying in contact with the gelatinous tissue.

Zeiss' apochromatic 4, compensating eyepiece No. 12. Outlined with Zeiss' camera.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



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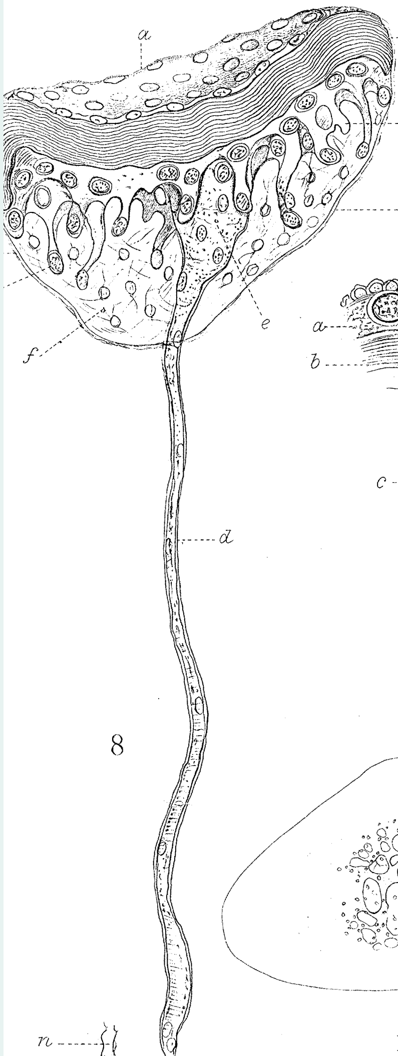

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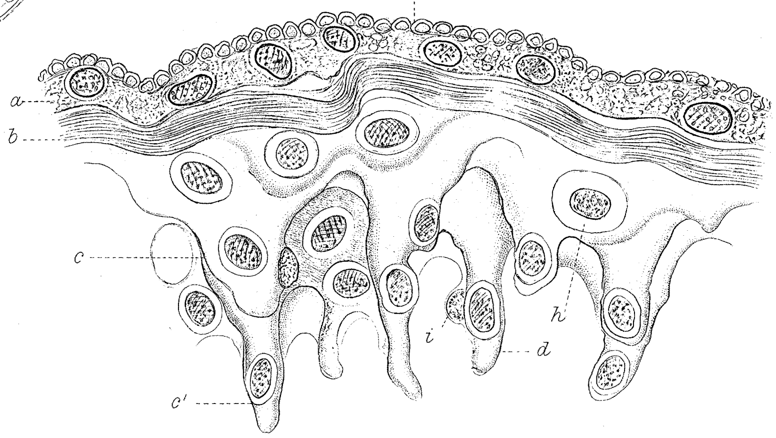

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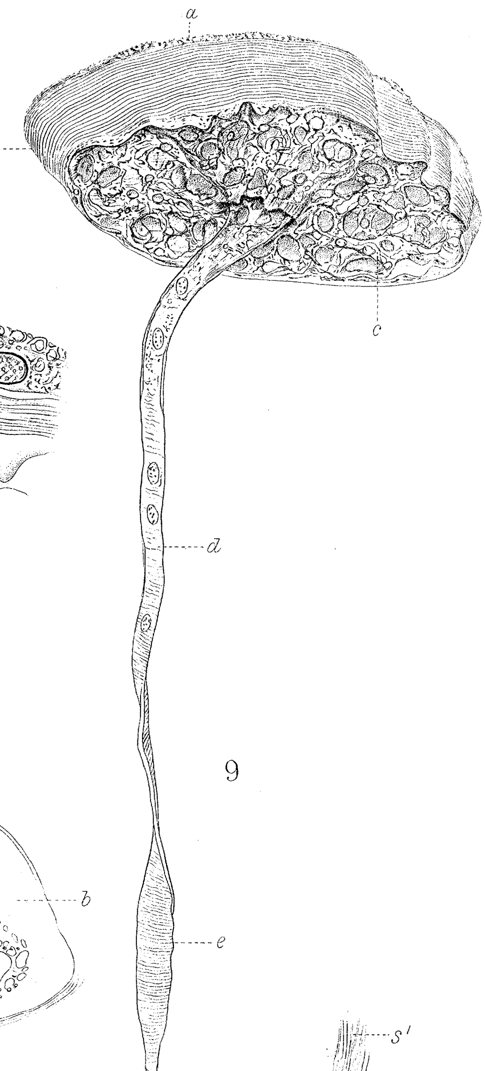

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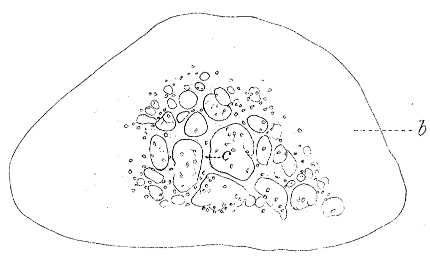

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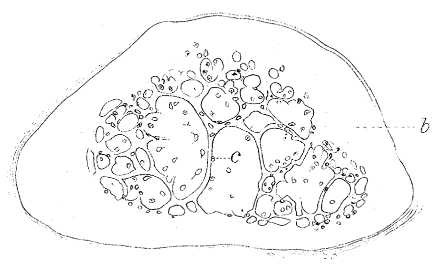

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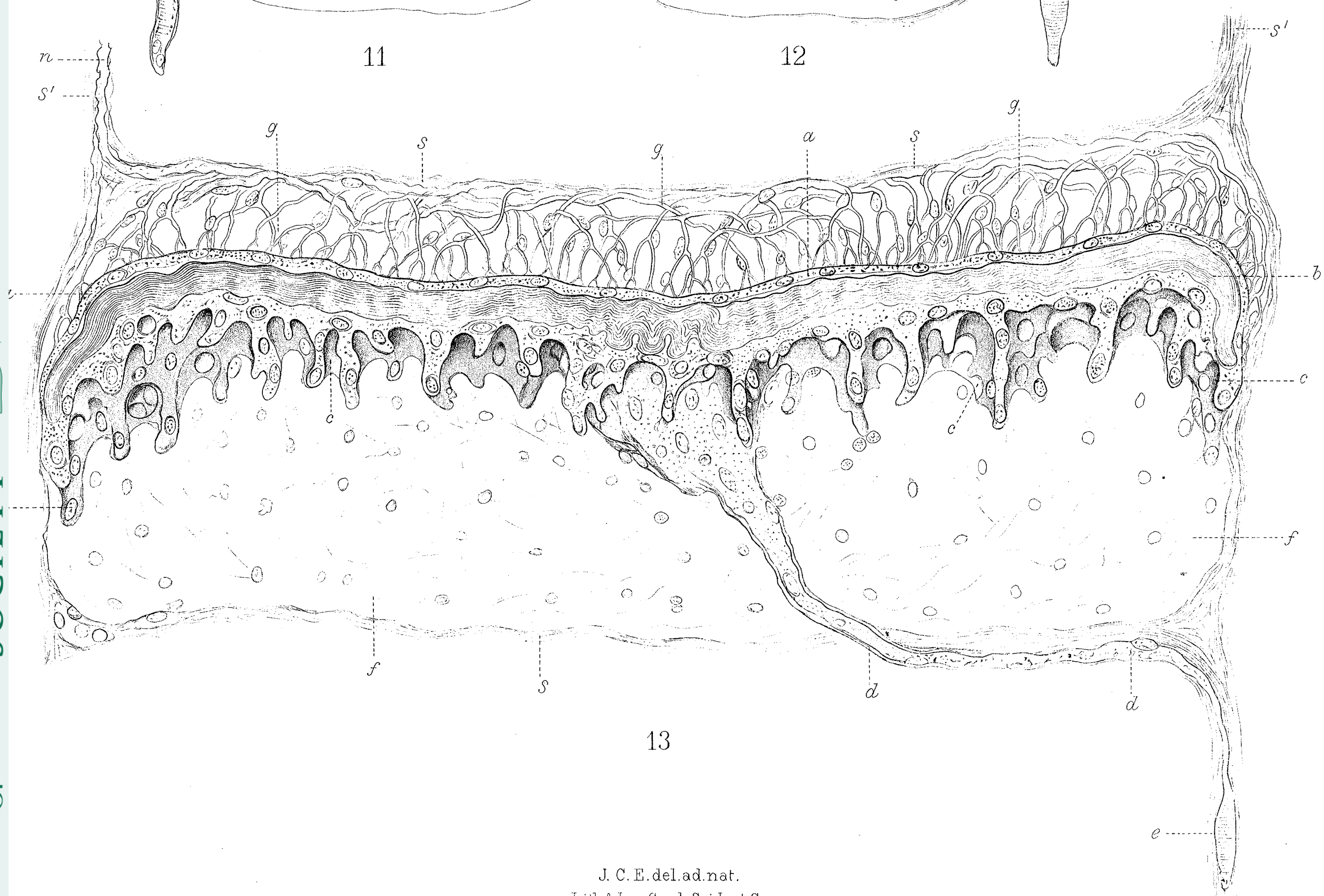

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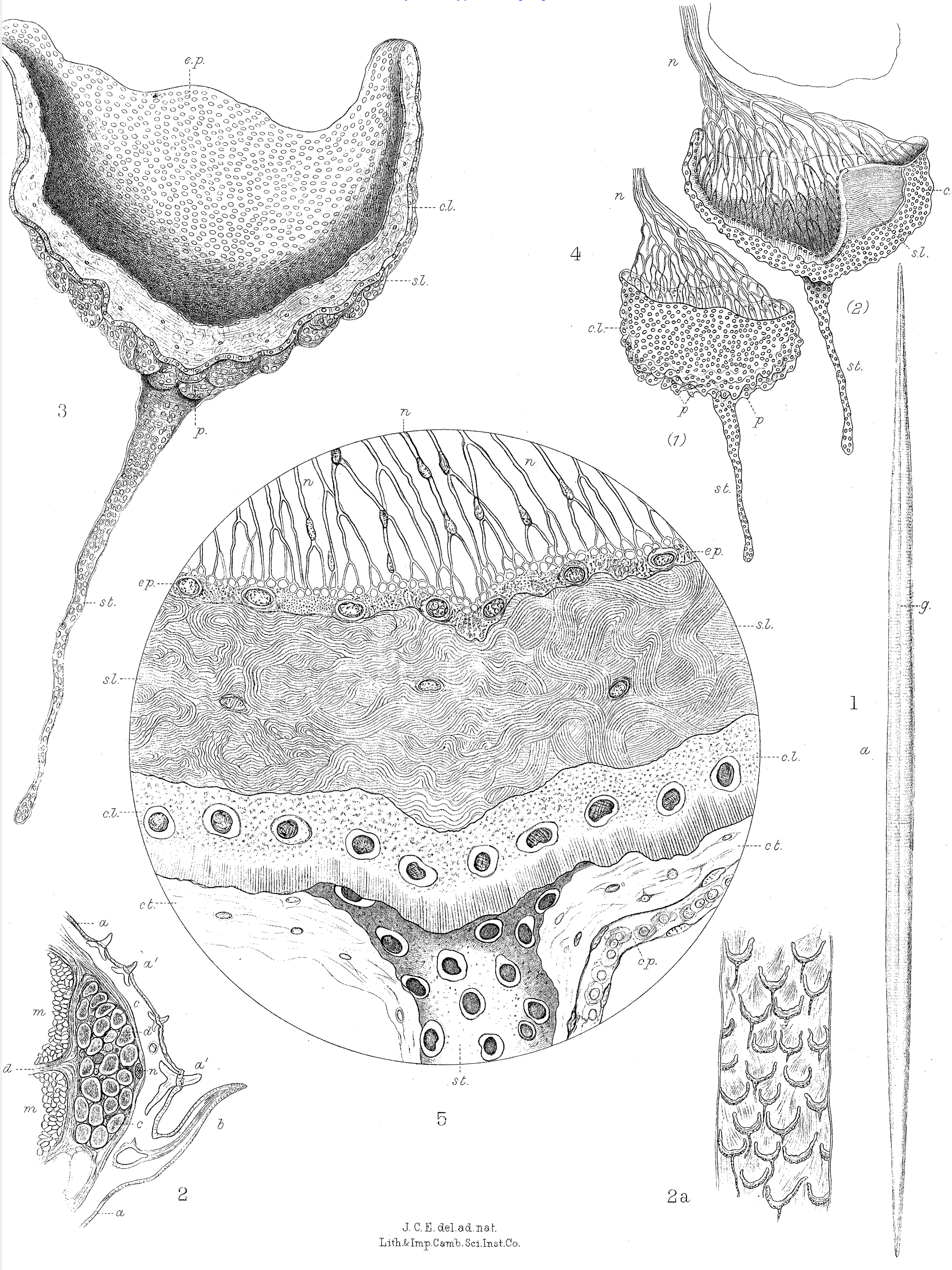

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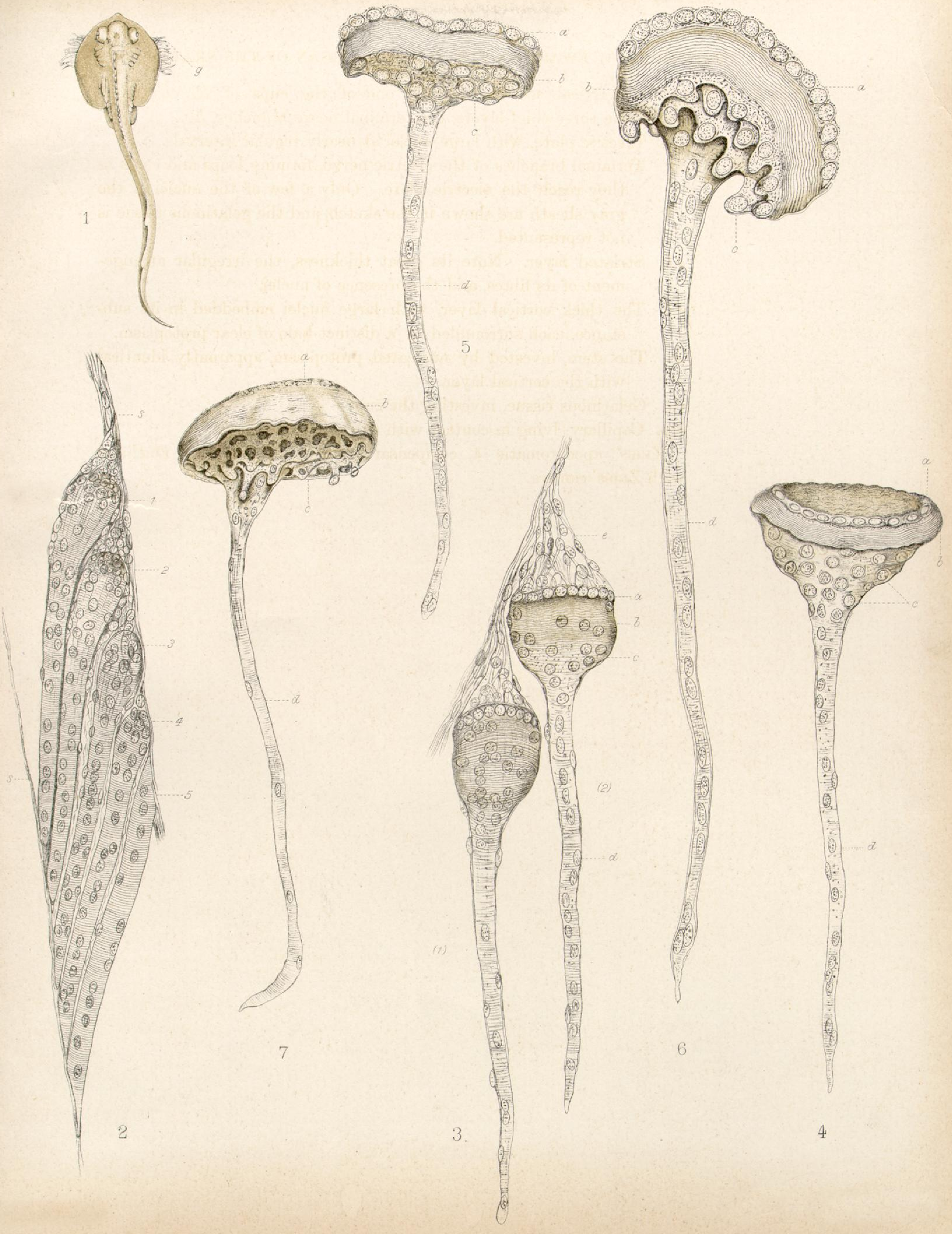


PLATE 66.

Fig. 1. Dorsal view of the smallest *R. batis* embryo in which the rudiments of the electric organ were observed. The large yolk bag is not represented. *g*. So-called external gills. Natural size.

Fig. 2. Longitudinal horizontal section through the tail of the embryo figured (fig. 1), showing the muscular fibres developing into clubs.

1. and 2. Well-marked clubs, with numerous muscle nuclei lying in contact with the enlarged anterior end.

3. A club with a pit-like depression at free end, and nuclei apparently in the process of migrating from the interior of the altered muscular fibre.

4. A muscular fibre only very slightly altered, lying in contact with an ordinary muscular fibre.

Observe the oblique position of the clubs, that the muscular striations still persist, even at the expanded portions; note also the intermuscular septa. The connective tissue corpuscles, which are extremely numerous around the clubs, are scarcely represented.

Zeiss' apochromatic 4, eyepiece No. 3. Outlined with Zeiss' camera.

Fig. 3. Two clubs from a slightly older Skate embryo (*R. batis*); one (1) a little more advanced than the other: both clubs are considerably larger than those represented in fig. 2.

a. The enlarged motor plate, with numerous nuclei embedded in its substance, and well-defined nerve fibres (*e*.) proceeding towards its anterior surface. Observe the nuclei in connection with the sheaths of the nerves, and the connective tissue corpuscles scattered amongst them.

b. The portion of the club which is altered to form the striated layer of the disc, behind which lie nuclei (*c*.) which give rise to the alveolar layer.

d. The stem or tail of the club, which is still muscular.

Zeiss' apochromatic 4, eyepiece No. 3. Outlined with Zeiss' camera.

Fig. 4. An isolated club which has expanded to form a shallow electric cup. Letters as in fig. 3.

Fig. 5. From a longitudinal section to show one of the first steps towards the formation of the electric disc. Note that the three principal layers (*a*., *b*., *c*.) are already represented—the alveolar by a layer of richly nucleated protoplasm.

Figs. 4 and 5 drawn with Zeiss' apochromatic 4, eyepiece No. 3.

Fig. 6. A somewhat more advanced stage, more highly magnified (Zeiss' apochromatic 4, compensating eyepiece No. 12), showing (*a*.) the large nuclei of the electric plate; (*b*.) the striated layer; (*c*.) the alveolar layer, sending out blunt processes; and (*d*.) the long stem.

Drawn with Zeiss' camera.

The stages represented in figs. 3, 4, 5, and 6 were all present in the same Skate.

Fig. 7. Sketch of an isolated disc from a Skate nearly 60 cm. in length, showing the projections and alveoli of the alveolar layer, and the long stem, which still retains some of its striations. Letters as in fig. 6.

Zeiss' apochromatic 4, eyepiece No. 3.

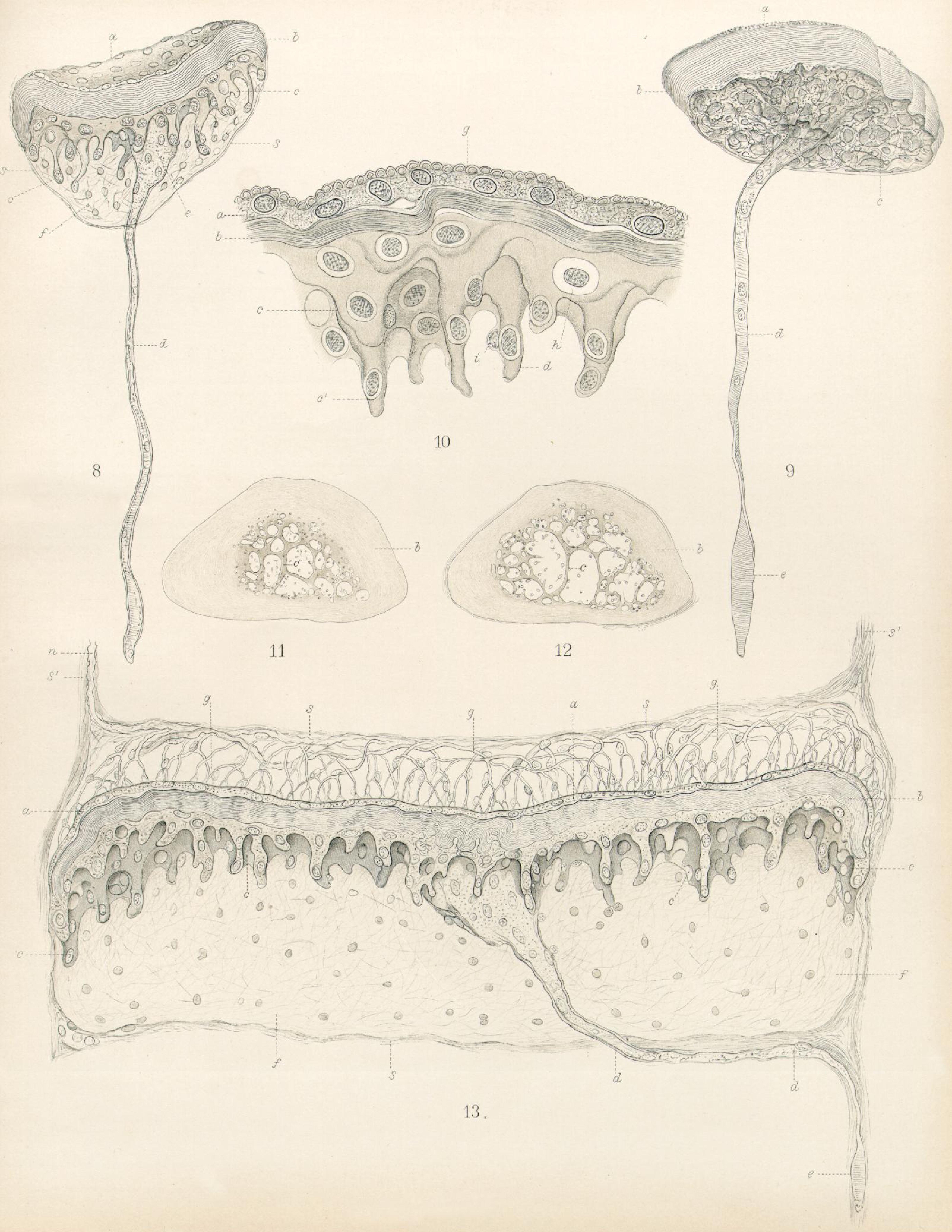


PLATE 67.

Fig. 8. Longitudinal section through a disc, slightly larger than fig. 7, showing the nucleated electric plate (*a.*); the processes of the alveolar layer (*c.*) extending into the posterior gelatinous cushion (*f.*); the connective tissue sheath (*s.*); and the long stem (*d.*) with a trumpet-like expansion (*e.*) where it joins the disc.

Zeiss' apochromatic 4, eyepiece No. 3.

Fig. 9. Sketch of an isolated disc from the same Skate as figs. 7 and 8. Observe that (though the magnifying power is the same) it is larger than fig. 7. The alveolar layer (*c.*) is now extremely complex; the stem (*d.*, *e.*) is ribbon-shaped, but still striated posteriorly; and the electric plate presents a still larger area for the terminations of the electric nerves. *b.* Striated layer. *d.* Electric plate.

Fig. 10. A portion of a disc from a slightly older Skate, magnified 950 diameters.

a. The electric plate with its large distinct nuclei, and a nerve plexus? (*g.*).

b. The striated layer in the form of a narrow sinuous band.

c. The alveolar layer with (*c.'*) simple and compound (*i.*, *d.*) projections, giving rise to primary and secondary alveoli. Note the large nuclei and the clear protoplasm (*h.*) surrounding them.

Zeiss' apochromatic 4, compensating eyepiece No. 12. Drawn with Zeiss' camera.

Figs. 11 and 12. Two transverse sections through the alveolar layer of a fully developed disc. Fig. 11 shows the fine network formed by the processes of the alveolar layer immediately behind the striated layer, while fig. 12 shows the wider network some distance from the striated layer. The spaces are occupied by gelatinous tissue, containing blood vessels.

Zeiss' AA, eyepiece No. 3.

Fig. 13. Longitudinal section through a disc from a Skate (*R. batis*) about 27 inches in length. This sketch illustrates the general structure of an electric disc in *Raia batis*. The blood vessels are not included.

g. The nerve fibres passing to the electric plate. The fibres, at first large and provided with a medullary sheath, divide dichotomously as they approach the plate, and eventually have only a gray sheath. They all terminate on the anterior surface of the plate, where they seem to form by their terminal divisions a series of delicate loops or rings. The spaces between the nerve fibres are occupied with gelatinous tissue, containing numerous nuclei.

a. The electric plate, consisting of a layer of protoplasm capable of being divided into two lamellæ, the posterior of which contains large nuclei.

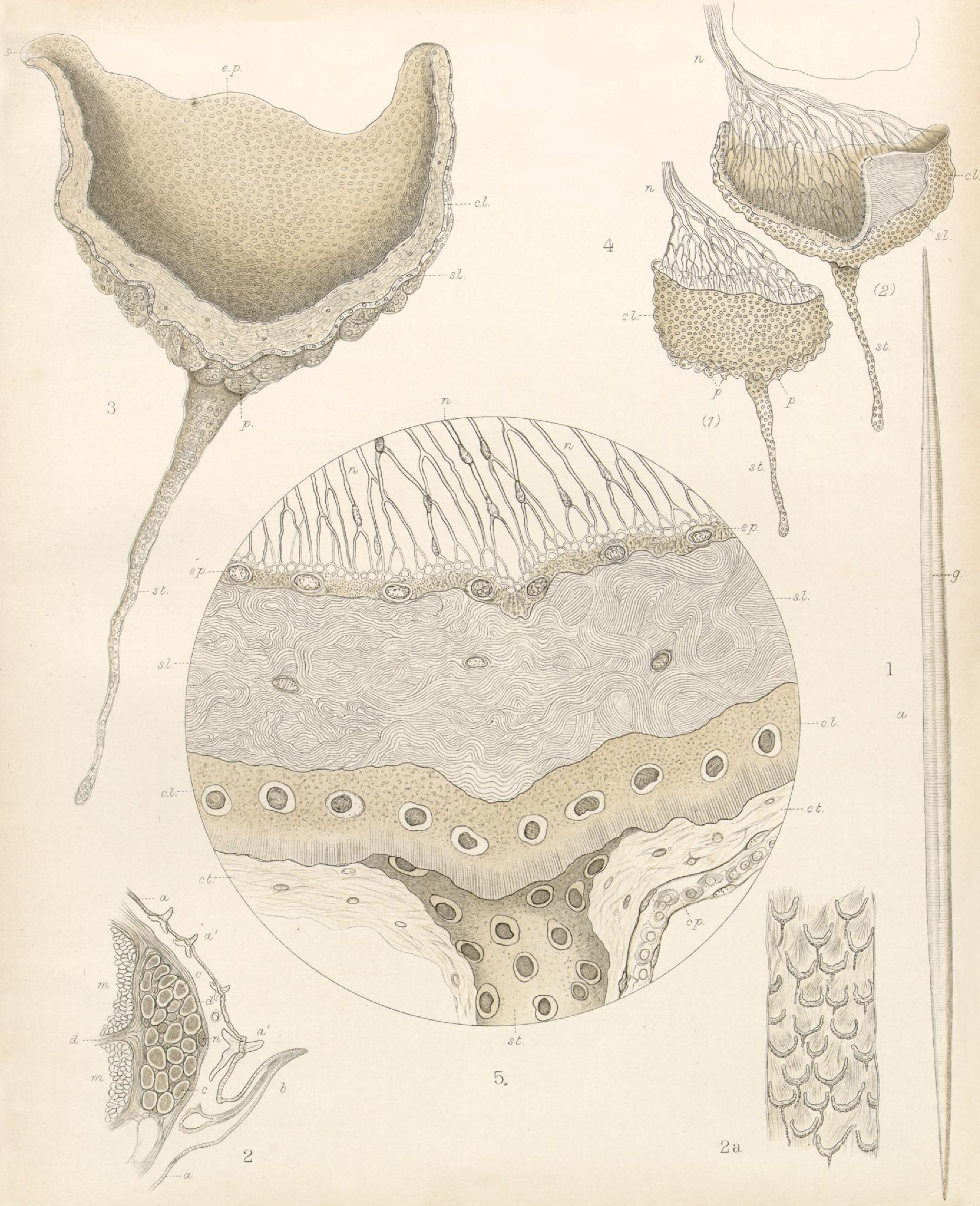
b. The striated layer, made up of numerous lamellæ having an exceedingly sinuous arrangement.

c. The alveolar layer, with processes projecting backwards into (*f.*) the gelatinous cushion, and connected together by secondary processes to form an irregular network.

dd. The stem of the disc, which consists of the altered posterior portion of the original muscular fibre, part of which is still indistinctly striated (*e.*). The part of the stem surrounded by the projections of the alveolar layer is considerably dilated. This dilated portion, together with the upper half, or more, of the narrow portion, is embedded in the gelatinous tissue.

s. Septum between two electric chambers.

s'. Part of the original transverse intermuscular septum.



Explanation of Plate 68.

Fig. 1. The entire organ of *Raia circularis*, from a specimen 27 inches (68 cm.) in length. The sketch was made from an organ exposed by removing the skin and portions of the caudal muscles. It measured $8\frac{1}{4}$ inches (21 cm.) in length, and was 5 mm. in breadth at the widest central portion. Note the shallow groove (*g.*) on the surface of the posterior two-thirds, along which lay the nerve of the lateral line, and note also that the organ is spindle-shaped. Natural size.

Fig. 2. Represents a transverse section from near the centre of the organ of *R. circularis*. Note that the organ lies immediately within the skin, and has the nerve (*n.*) of the lateral line indenting its outer surface.

a. The skin with four denticles (*a'.*) embedded in the dorsal portion.
b. The lateral fold of the tail.
c. The electric cups.
d. The connective tissue surrounding the organ and extending between the caudal muscles.
n. Nerve of the lateral line.
m. Caudal muscles, cut transversely. About six times natural size.

Fig. 2*a*. Represents a thin longitudinal vertical section of the organ of *R. circularis*. It shows the arrangement and various modifications of the electric cups, some of which retain, almost complete, the delicate stems. Note that the cups form nearly regular oblique rows.

Ocular 3, objective 00. Outlined with Zeiss' camera.

Fig. 3. Shows one of the cups of *R. circularis*, cut somewhat obliquely. Note the depth of the cup, the great extent of its nucleated lining (electric plate) (*e.p.*) the irregular margin, with a spout-like projection (*s.*) at one side, the cortical layer (*c.l.*) and its blunt processes (*p.*), the thick striated layer (*s.l.*), and the long stem (*st.*).

Zeiss' AA, compensating eyepiece No. 12. Outlined with Zeiss' camera.

Fig. 4. Two electric cups, showing the nerves, a portion of the striated layer, the long stems, &c.

n. The nerves proceeding towards the cups.
c.l. The cortical layer, with (in 1.) short blunt projections (*p.*).
s.l. Part of the striated layer.
st. The stem.

Zeiss' AA, compensating eyepiece No. 8. Corrosive sublimate and spirit preparation.

Fig. 5. Longitudinal vertical section through one of the cups of *R. circularis*, showing the three chief layers, the terminal nerve branches, &c.

e.p. Electric plate, with large nuclei at nearly regular intervals.
n. Terminal branches of the electric nerve, forming loops and rings as they reach the electric plate. Only a few of the nuclei of the gray sheath are shown in the sketch, and the gelatinous tissue is not represented.
s.l. Striated layer. Note its great thickness, the irregular arrangement of its fibres, and the presence of nuclei.
c.l. The thick cortical layer, with large nuclei embedded in its substance, each surrounded by a distinct halo of clear protoplasm.
st. The stem, invested by nucleated protoplasm, apparently identical with the cortical layer.
c.t. Gelatinous tissue, investing the cup.
c.p. Capillary, lying in contact with the gelatinous tissue.

Zeiss' apochromatic 4, compensating eyepiece No. 12. Outlined with Zeiss' camera.