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The Electric Organ of the Skate. The Electric Organ of Raia radiata

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XX. *The Electric Organ of the Skate.—The Electric Organ of* Raia radiata.

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[Plates 79, 80.]

The Structure of the Electric Organ of Raia radiata.—The development of the electric discs of *Raia batis* and the structure of the electric cups of *Raia circularis* having been already described,* I shall now give an account of the organ of *Raia radiata*, partly by way of indicating in what respects it differs in structure from the organ of the species *batis* and *circularis*, and partly by way of describing the development of electric cups.

In considering the organ of *Raia radiata* it is necessary to bear in mind that the species *radiata* differs greatly in size from both *batis* and *circularis*. While *Raia batis* sometimes reaches a length of 6 feet (180 cm.), and *Raia circularis* may be over 3 feet (90 cm.), *Raia radiata* seldom exceeds 18 inches (45 cm.) from tip to tip.

The largest of many specimens of *R. radiata* sent to the laboratory was only 19 inches (48 cm.) in length. In this specimen the tail, which was thick and broad at the base, measured 9½ inches in length (24 cm.), and the electric organ was in the form of a narrow band (Plate 79, fig. 1) pointed at both ends, which measured only 13 cm. (5⅛ inches) in length and 2 mm. in thickness at the central portion, where the circumference was 9 mm.

In a large *R. batis* the electric organ may be 2 feet (61 cm.) in length, and nearly 3 inches (7 cm.) in circumference at the centre. There is thus a marked difference in both the absolute and relative size of the organ. This difference, however, seems to depend on the difference in the development of the tail in the two species. In *R. batis*, when the organ first appears the tail (Plate 66, fig. 1) is relatively long, and the caudal muscles form a considerable mass at each side of the vertebral column. In *R. radiata*, on the other hand, the adult form is reached before the conversion of the muscular fibres into electric elements sets in. Plate 79, fig. 3, represents (natural size) a young *R. radiata*, in which certain muscular fibres (*o.*, fig. 2A) in the region of the tail were in process of developing into electric clubs. In this sketch it will be

* 'Phil. Trans.,' B, 1888, pp. 399–416, Plates 66–68.

observed that the tail, though thick at the base, rapidly tapers towards the extremity. In transverse sections it was ascertained that this tapering was chiefly due to a reduction of the lateral muscles, more especially of the portion (*m.m.*, fig. 2A) at each side of the tail, from which the electric organ of the Skate is derived. Owing apparently to this reduction of the tail of the young *R. radiata*, the electric organ, when it eventually appears, differs greatly from that of *R. batis*, both in size and position. While in the species *batis* the posterior three-fourths of the organ extends from the skin covering the outer aspect of the tail to the vertebral centra, in *radiata* it occupies a long narrow space or cleft running parallel to the lateral line, and is completely separated from the vertebral column by a relatively thick layer of muscles —the superior and inferior divisions of the caudal muscles. The form and position of the organ are indicated in figs. 1 and 2B, Plate 79. Fig. 2B, shows the organ (*o.*) in contact with the skin, the nerve (*n.*) of the lateral line, and portions of the muscles (*m.*), which lie between the organ and the vertebral column.

But not only is the organ of the species *radiata* relatively extremely small; the elements of which it consists are likewise small and far less highly elaborated structures than either the discs of *R. batis* or the cups of *R. circularis.* The difference in size between the cups of large specimens of *R. radiata* and *R. circularis* will be readily ascertained by comparing Plate 80, fig. 12, with Plate 68, fig. 2, which represent the respective cups drawn with the same lenses (Zeiss AA, and ocular No. 12) and camera.

But the difference in the external size of the cups in the two species does not represent the principal difference. Two cups having the same external size may, owing to the difference in the thickness of their walls, differ greatly in their capacity. In *R. circularis* (Plate 68, figs. 2 and 4) each electric cup is well moulded, has a deep cavity and thin uniform walls; while in *R. radiata* (Plate 80, fig. 12) the cups, as already mentioned, are not only smaller than in *R. circularis*, but, owing to the great thickness of their walls, they are also very much shallower.

By studying sections and teased preparations, it is at once evident that, while the cups of *R. radiata* generally resemble those of *R. circularis*, they differ from each other considerably in detail, more especially in the structure of the walls of the cups and the thickness of the cortex.

The electric layer in *R. radiata*, owing to the shallowness of the cups, is necessarily limited in extent; and, although it seems to extend slightly over the rim of the cup, it probably presents only about one-eighth of the surface provided for the terminal nerve fibres by the electric layer in the cups of *R. circularis.* Further, although the electric layer contains distinct oval and round nuclei, it is extremely thin, and does not seem to consist of two distinct laminæ, as is the case in both *R. batis* and *R. circularis.* In connection with the electric layer of each cup there is an extremely rich bunch of nerve fibres (fig. 10). The nerves which supply the respective cups, as indicated in Plate 80, fig. 10, begin to branch a considerable distance in front of the electric plate, and by dividing again and again they give rise to a complex nerve cone, the terminal branches of which appear to form a continuous network immediately in front of the electric layer.

It will be instructive to compare the nerve cone of *R. radiata* (Plate 80, fig. 10) with the nerve layer in *R. batis* (Plate 67, fig. 13) and *R. circularis* (Plate 68, fig. 4). It is easy to understand how the cone of *R. radiata* might assume the form which obtains in *R. circularis*, and how by an expansion of the electric plate the arrangement in *R. circularis* would pass into that of *R. batis*. In fresh sections, and in sections fixed with osmic acid, the nerves and the numerous nuclei on their sheaths are readily made out. As in the other species referred to, the smaller branches retain only the grey sheath, and the spaces between the nerve fibres are occupied by gelatinous tissue. In *R. radiata* capillaries wind in and out amongst the nerves in front of the electric plate, while in the species *batis* and *circularis* capillaries seem to be entirely absent from the nerve layer. Immediately behind the electric plate in the species *batis* and *circularis* there lies the striated layer, made up of characteristic sinuous lamellæ. In *circularis* this layer supports the electric plate and forms the chief portion of the walls of the well moulded cup. In *R. radiata*, on the other hand, the striated layer can scarcely be said to exist. In its place, as represented in Plate 80, fig. 12, supporting the electric plate and forming the great bulk of the shallow thick-walled cup, is a mass of apparently only slightly altered muscular tissue, with nuclei scattered through its substance. The difference between the walls of the cups of *R. radiata* and those of *R. circularis* and the striated layer of *R. batis* will be best understood by comparing Plate 80, fig. 12, with Plate 68, fig. 5, and Plate 67, fig. 13. As shown in Plate 80, fig. 12, the entire thickness of the walls of the fully developed cup of *R. radiata* is composed of distinctly striated tissue (containing numerous nuclei), which more closely resembles ordinary muscular fibres than does the head of the clubs (Plate 66, fig. 3) of *R. batis*. This resemblance to a muscular fibre is equally well marked in the centre and at the periphery of the cup in question.

In *R. circularis* the striation of the striated layer differs decidedly from the transverse striation of a muscular fibre. Instead of presenting simple parallel lines, as in ordinary muscular fibres, the striated layer (Plate 68, fig. 5) presents a series of extremely sinuous lines, which makes it difficult, at first sight, to believe that the striated layer consists of altered muscular tissue. In *R. batis* the striated layer very closely resembles that of *R. circularis;* the contortions are often quite as well marked, but apparently it has departed further from ordinary muscular tissue, in as far as the muscle nuclei have entirely disappeared. Whether the striated layer retains any of the contractile properties of muscular tissue in any of the three species of Skate referred to has not yet been determined; but, from the appearance presented by the cups of *R. radiata*, one might almost expect that it would respond (though, perhaps, very feebly) to stimulation like an ordinary muscular fibre.

Extending backwards from the cup of *R. radiata* is a long tapering stem, sometimes flattened, sometimes bayonet-shaped, but seldom rounded or symmetrical in the fully formed cups. The shape seems to depend chiefly on the amount of compression the adjacent cups produce on one another. In many cases the base of the stem forms an irregular triangle, while the terminal portion is oval or ribbon-shaped. In all cases the stem consists of more or less altered muscular tissue. Sometimes the striations are distinct throughout the whole length; at other times they are obscure in at least the middle portion, while the terminal portion may be crowded with nuclei—thus suggesting degenerative changes. Surrounding the cup and its stem there is a thin nucleated membrane, which, while it seems to represent the thick cortex of *R. circularis* and the alveolar layer of *R. batis,* differs but little from the sarcolemma of an ordinary muscular fibre.

The cups are invested by connective tissue, which further fills up the spaces between them, and forms for them a delicate framework. This connective tissue consists partly of fine fibres and partly of gelatinous material. In addition to binding the cups together, so as to form the long narrow electric spindle, the connective tissue serves as a highway for the nerves passing to the cups, and for the blood vessels from which they derive their nourishment. Scattered through the connective tissue are a number of nuclei.

The Development of the Electric Organ of Raia radiata.—As in *Raia batis,* the electric elements are developed out of muscular fibres. In the species *batis,* as already pointed out, some of the muscular fibres at each side of the caudal portion of the notochord have assumed the form of clubs when the embryo is 7 cm. in length, and before it escapes from the purse the electric discs are often well advanced towards completion. In *R. radiata,* although the rate of the development of the embryo seems to be slower than in *R. batis,* I have been unable to detect any change in the muscular fibres until the development of the Skate was completed. The youngest specimen of *R. radiata* in which a rudiment of the electric organ could be detected is represented (nat. size) in Plate 79, fig. 3. This Skate measured nearly 9 cm. across the pectoral fins, and was over 12 cm. in length. Hence, it may be presumed that it was three or four times the age of the embryo *R. batis* (Plate 66, fig. 1) from which the electric clubs represented in Plate 66, fig. 2 were drawn, and that the electric organ is very much later in appearing in the species *radiata* than in the species *batis.*

As already pointed out, the reduction of the tail (and more especially of the middle section of the caudal muscles on each side) has proceeded further in *R. radiata* than in *R. batis* before the organ appears. For this reason, the space available (Plate 79, fig. 2A) for the electric organ to develop in is far more limited than in *R. batis.** Probably, for this reason also, only a limited number of muscular fibres are altered in *R. radiata* (about one-third of the number in *R. batis*); and it may be for the same reason that instead of forming large discs they give rise to small cups.

* The amount of raw material out of which the organ is developed is also limited; but this is probably of secondary importance.

The first evident step in the conversion of the muscular fibres destined to form electric elements consists, as in *R. batis,* in the expansion of their anterior ends so that each assumes the appearance of a club (Plate 79, fig. 3A). This process seems to occupy a considerable time, and it takes place without causing any marked change either in the position or structure of the fibres concerned. Further, all the fibres are not enlarged simultaneously; while some of the fibres have expanded into distinct clubs, others differ from the adjacent muscles only in having their anterior ends slightly rounded and retracted from the intermuscular septum. As the comparative lateness of the conversion of the muscular fibres would lead one to expect, the clubs of *R. radiata* are at the outset nearly double the length of the clubs of *R. batis.* In other words, the muscular fibres in *R. radiata* are nearly double the length of the fibres in *R. batis* when the process of conversion first sets in. This difference in the size of the newly formed clubs in the two species will be made evident on comparing Plate 66, fig. 2, with Plate 79, figs. 4 and 5. In fig. 2 the clubs of *R. batis* are represented, while figs. 4 and 5 represent on the same scale the clubs of *R. radiata.* The form of the clubs of *R. radiata* is represented in Plate 79, fig. 3A, in which *a* represents a fibre with the anterior end only slightly expanded, and *b* a fibre which is distinctly club-shaped. As already stated, the clubs are only in process of formation when the young *R. radiata* has reached a length of 12 cm., and measures 9 cm. across the pectoral fins. In *R. batis* the clubs appear long before the embryo is hatched, while there is still a large yolk sac, and when the measurement across the pectoral fins is only 2·5 cm. Further, not only does the conversion of the muscular fibres set in sooner in *R. batis* than in *R. radiata*, but the development proceeds so rapidly that before *R. batis* reaches a length of 12 cm. (the length at which the clubs first appear in *R. radiata*) the electric elements are in some respects more fully developed than they are in the adult *R. radiata.*

But the clubs of the two species differ in more respects than in size and time of appearance. The clubs in *R. radiata* are not only longer and thicker; they are, in addition, more distinctly striated, and there is no indication of a forward migration of nuclei towards the anterior end, as is the case in the clubs of *R. batis.* From Plate 79, figs. 4 and 5, it will be observed that, although in *R. radiata* there is no marked crowding of nuclei in front of and around the head of the club, as is the case in *R. batis,* the nerves are extremely abundant, apparently as numerous as they are at the corresponding stages in *R. batis.*

After the clubs have appeared in *R radiata*, they slowly expand and increase in length to form what may be termed secondary clubs (Plates 79 and 80, figs. 6, 7, and 8). These secondary clubs vary considerably in form, and especially in length. Some of them are quite double the length of the primary clubs represented in figs. 4 and 5; but, while the anterior portion has greatly increased in dimensions, the posterior is often reduced to a long slender, though still distinctly striated, process. The difference between the primary and secondary clubs will be seen by referring to Plate 79, fig. 7, where two of the primary clubs (*b.*) are represented alongside a number of secondary clubs (*o.*). By the time the secondary clubs are formed the young Skate has reached a length of about 18 cm., and the unaltered muscular fibres adjacent to the developing clubs have greatly increased in length, being at least double the length of the longest clubs. In a *R. batis* of about the same length (though, probably, somewhat younger) the electric organ is already made up of complex discs (Plate 67, fig. 8) which only essentially differ from the discs of the adult Skate in being of a smaller size. There is thus a striking difference in the club stage of the two species. In *R. batis*, the clubs rapidly enlarge to form shallow cup-shaped bodies, which are as rapidly transformed, first into mushroom-like structures, and then into discs—the cup-stage being reached when the *R. batis* embryo is only some 10 cm. in length, while in *R. radiata*, as already mentioned, a length of 18 cm. is reached before the secondary clubs are completed. In all probability the indistinct cup found in embryo specimens of *R. batis* corresponds to the well marked cups found in the adult *R. radiata* and *circularis*. If this is the case, it may be inferred that, while the process of conversion of a muscular fibre into an electric element is prolonged in *R. radiata*, it is comparatively rapid in *R. batis*, the early stages especially being abbreviated—a state of things advantageous in most cases, but especially so, one would suppose, in an electric organ which is presumably, at the most, of little use during its early stages of development.

But, although in *R. radiata* a considerable time is occupied in converting the muscular fibres into what I have designated secondary clubs—although, as it were, every step in the ancestral history seems to be faithfully reproduced, there is never any indication of the development being arrested nor of retrogressive changes setting in; and this holds for the later as well as the earlier stages, for until the simple electric cup of *R. radiata* is completed (and this only takes place when the Skate is reaching maturity) there is no pause in the process, and when once complete the cup increases in size as the tail of the Skate increases in dimensions.

There is thus a remarkable difference in the history of the muscular fibres which are converted into clubs, and the surrounding fibres which, as it were, become obliterated to make room for the developing electric cups. In fig. 2A it will be observed that less than a third (*o.*) of the fibres (*m.m.*) seen in transverse section are utilised for the production of electric elements. Yet, in fig. 2B, the electric organ (*o.*) occupies the entire space between the skin and the superior and inferior caudal muscles (*s.i.*). It is extremely interesting to study sections between the stages represented in fig. 2, and to note that as the central fibres (*o.*, fig. 2) gradually increase in size until they occupy the whole available space, the fibres at each side (*m.m.*) as gradually undergo degenerative changes, and ultimately completely disappear.

As the primary club enlarges, the rounded anterior end becomes truncated, and, later, slightly concave; and at the same time the motor plate increases in size and forms a lining or the shallow depression towards which the ever-increasing nerve fibres extend. These nerve fibres occupy the trumpet-shaped space left as the developing club retracts from the septum to which it was originally connected (Plates 79 and 80, figs. 6 and 8). This space seems to be enclosed by a layer of intermuscular connective tissue. What becomes of the sarcolemma which surrounded the anterior end of the muscular fibre has not been determined; but, in all probability, it remains in contact with the truncated end of the fibre, and eventually blends with and assists in forming the electric plate. The secondary clubs having been completed, they begin to condense, to form the characteristic electric cups. It is impossible to state what time is occupied in passing from the club to the cup stage: when the young *R. radiata* is about 24 cm. in length the moulding has distinctly begun (Plate 80, fig. 9), but even when a length of 35 cm. is reached it is still imperfect (Plate 80, fig. 10), and the cup proper (Plate 80, figs. 11 and 12) does not seem to be completed until a length of nearly 40 cm. is reached, *i.e.*, until the Skate has all but reached maturity. It is somewhat remarkable that while the anterior end of the club is expanding, as represented in figs. 6, 9, and 10, the narrow posterior portion is still increasing in length. An idea of the extent of the changes which take place in a developing cup during the time required for a *R. radiata* to grow from 11 cm. to 35 cm. will be gathered by comparing figs. 3A and 10, which are both drawn to the same scale.

In passing from the club to the cup stage the changes are less abrupt in *R. radiata* than in the species *batis* and *circularis*. The muscular substance of the head of the club, without being transformed into extremely complex sinuous lamellæ, as is the case in *R. circularis* and other forms, is simply moulded to give rise to a rounded shallow cup, such as is represented in fig. 12, every part of which is striated like an ordinary muscular fibre.

Further, numerous nuclei lie in the substance of the cup (fig. 12), and in frozen sections spaces appear in the walls similar to those seen in frozen muscular fibres. As the cup proper resembles in structure a muscular fibre, its investing sheath, as already stated, resembles ordinary sarcolemma. In *R. circularis* nuclei aggregate around the outer surface of the cup, and give rise to a thick cortex (Plate 68, fig. 5). These nuclei in *R. circularis* seem to migrate from the substance of the muscle as it undergoes transformation, but in *R. radiata* this aggregation of nuclei around the outside of the cup is extremely limited, while the nuclei of the muscular wall of the cup retain their original position. This non-migration of the nuclei may to some extent account, on the one hand, for the cup resembling the last muscular tissue, and, on the other, for the absence of a thick cortical layer. The cups when once formed slowly increase in size as the Skate grows larger, and retain their rounded form, except when subjected to pressure by coming into close contact with each other. As the result of pressure, they may assume an oval or somewhat hexagonal form, and the margins may become irregular or even slightly everted.

As the cup stage is reached the stem becomes more distinctly marked off from the cup proper, and loses its rounded contour. Later, it gets compressed, more especially at the base, and in macerated specimens its base sometimes looks extremely broad and transparent from one point of view, but narrow and opaque from another. As the result of compression, the stem often assumes the form represented in figs. 11 and 12; but, even although the terminal portion may be reduced to a narrow thin band with aggregations of nuclei at one or more points, it is never reduced to a short rudiment, as is the case in *R. fullonica* and, to a limited extent, in *R. circularis*, nor does it ever, as far as I have seen, entirely lose its transverse striations.

The electric plate seems to arise in *R. radiata* in very much the same way as in *R. batis*. As in *R. batis*, there is an aggregation of nuclei in front of each club. As the club expands, the nuclei, together with the protoplasm around them, give rise to a thin lining for the shallow muscular cup.

At the same time nerves increase in number and in length, and form a rich conical bunch of fibres, which terminate by extremely delicate branches (fig. 12) in the electric plate. While the above changes are taking place the intermuscular connective tissue increases, so as to form a thin gelatinous investment for each cup. It also seems to bind the cups together into a number of short, obliquely directed columns. When these columns are further invested by a delicate sheath the long, slender electric spindle is completed.

Without further exhaustive inquiries, it will be impossible to offer any opinion as to whether the electric organ of the Skate is or is not functionless, or to discuss the uses which the organ has served in the past, or, supposing it to be still functional, to consider how it is of service to the Skate at the present day. But, although a discussion of this nature would, in the absence of sufficient data, be somewhat premature, it may facilitate future inquiries if, by way of concluding this paper, I indicate whether the organ in *R. radiata* may be looked upon as a structure in a state of progressive development, or as a structure which, having been arrested in its development, is now undergoing retrogressive changes. At the outset it may be taken for granted that, either in the Skate group or in some of the ancestors of the Skates, certain muscular fibres in the region of the tail were gradually altered to form electric organs. There is no great difficulty in admitting that under certain conditions muscular fibres might be readily transformed into rudimentary electric plates or discs, but it is still difficult to understand how natural selection could, during the initial stages, step in and take advantage of this variation, and gradually build up complex and, in some cases, extremely useful electric organs. Ordinary muscular fibres may be looked upon as incipient electric elements, for, in addition to their power of contracting, they possess the power of discharging feeble electric currents. It is conceivable that under certain circumstances the one function might be developed at the expense of the other—that the power of contraction would gradually fall into abeyance, while the power of discharging electric shocks would be as gradually increased; and, could we discover a motive for this increased output of electricity during the incipient stages—that even the feeblest electric shocks were of some real use from the outset—the whole mystery as to the evolution of electric organs would at once and for ever vanish.

Granted that under certain conditions muscular fibres are converted into electric organs, and that these conditions still exist and are likely to continue, there is no reason why electric organs should not be in process of elaboration at the present day. Mr. DARWIN, in considering electric organs, points out* that "there is no reason to suppose that they have been inherited from a common progenitor," for, he adds, "had this been the case, they would have closely resembled each other in all respects." Hitherto no trace of an electric organ has been discovered in any of the Selachians, not even in the family Spinacidæ, to which the Skates and Rays are supposed by some to be genetically related. Neither is there reason for supposing that electric organs would have been more useful to the extinct than to the recent members of the Skate family. It is thus possible that the electric organs of the Skates have not been inherited from Shark-like ancestors, and that they were neither larger nor more useful in the extinct than they are in the recent species. There being thus a possibility that the electric organ has reached its maximum size in some Skates during recent times, and that in others it is still in a state of progressive development, or at the most only recently arrested in its development, it is desirable to carefully consider the organ of *R. radiata* with a view to determining, if possible, whether it is a progressing or retrograding structure.

When I first discovered that in some Skates the electric organ consisted of cup-shaped bodies, I was inclined to look upon the cups as primitive structures, which, having been arrested in their growth, had failed to develop into discs, such as exist in *R. batis* and *R. clavata*. I was all the more in favour of this view when I made out that the discs of *R. batis* passed through an indistinct cup stage, and that in *R. radiata* not only were the cups small and simple compared with the discs of *R. batis*, but the entire organ was only a few inches in length, and only about 8 mm. in circumference at its thickest central portion. When, however, I found that the cups in *R. circularis* were large well moulded bodies, with an electric plate nearly as extensive as the electric plate of the disc of *R. batis*; that the electric organ of *R. fullonica*, which also consists of cups, was relatively large and well developed; and that the development of the cups in *R. radiata* was extremely slow; and also that, instead of showing signs of degenerating, they continued to increase in size in the adult forms, it was no longer possible to feel so confident that all the electric organs consisting of cups had been arrested in their development.

Further investigation convinced me that the electric cups were quite distinct structures; that, in fact, while in some Skates the electric elements had assumed the form of discs (*e.g.*, *R. batis* and *R. clavata*), in others they had taken the form of cups (*e.g.*, *R. circularis* and *R. fullonica*); and that it was as unlikely that a fully developed

* 'Origin of Species,' p. 151.

cup should be converted into a disc as that a disc should be moulded into the form of a cup.*

In endeavouring to determine the present *rôle* of the electric organ of *R. radiata*, it may be better first to state the arguments in favour of its being a degenerating structure.

In favour of degeneration there is first to be mentioned that it has been impossible hitherto to discover any use which the organ of the Skate subserves. If there is a difficulty in discovering the utility of the large electric organ of *R. batis,* it may be presumed the difficulty will be still greater in suggesting a use for the smaller organ of *R. radiata.* But the small size of the organ in *R. radiata* may, of itself, be considered an argument in favour of degeneration, or, at least, in favour of its having been arrested in its development; and to the absolute smallness of the organ there is to be added, that the cups composing it are not only extremely minute, but, further, they are remarkably shallow, and hence the electric plate (the most essential part of an electric organ) is very limited in extent. But, as already indicated, the small size of the organ in *R. radiata* has, in all probability, been determined by the size of the tail in this species. It may be supposed that the reduction of the tail in the species *radiata* had proceeded further than in the species *batis* before the electric organ succeeded in establishing itself, and that, in fact, the organ in *R. radiata* is as large as the circumstances attending its development hitherto have rendered possible. It is, of course, impossible to say whether the organ in *R. radiata* is now, or in former ages long remained in, or nearly in, a state of arrested development—neither distinctly receding nor advancing.

In a degenerating organ, which appeared at a remote period, we should expect that it would pass rapidly through the early or developmental stages, and that as its possessor continued to increase in size the organ would undergo retrogressive changes, while in an organ that had been simply arrested we should expect that after a certain stage of development had been reached it would remain in a state of comparative quiescence. A reference to the chapter on the development of the organ in *R. radiata* will, however, show that neither of these conditions holds—the development is only completed when maturity is reached, and, once developed, the organ slowly increases in size as the Skate grows larger.

Again, in a degenerating electric organ, we should expect the electric plate to be incomplete, and the nerves passing to it few in number or undergoing retrogressive changes; and one would further expect to find some indication of degeneration of the less essential layers. But in *R. radiata* there is a relatively large bunch of well

* But, although the cups and discs are perfectly independent and distinct, there is no reason for supposing that the Skates with cup-shaped organs have sprung from one ancestor, while the Skates with discs have descended from another. The fact that the disc of *R. batis* passes through an indistinct cup stage points to a common ancestor, in which the electric organ was in all probability made up of slightly altered muscular fibres resembling the clubs of *R. radiata* represented in Plate 79, figs. 4 and 5.

developed nerves proceeding to an electric plate, which is not only complete, but, being apparently in advance of the development of the supporting cup, extends some distance over its margin.

In support of the view that the electric organ of *R. radiata* is a progressive structure, or, if not still advancing, that it has been comparatively recently arrested in its progress, there is, first, the remarkable developmental history. I have already pointed out that, while the electric organ of *R. batis* is late in making its first appearance, the organ of *R. radiata* is very much later; that, in fact, while in an embryo *R. batis* 12 cm. in length the three essential layers of the complex discs have already been established, in a *R. radiata* completely developed and of a considerable size (Plate 79, fig. 3), the muscular fibres (now long and well developed) are only beginning to pass into the primary clubs. I have shown, further, that the clubs pass slowly through a series of intermediate stages before the cup form is assumed, and that the cups when eventually completed slowly increase in size as the Skate increases in length, and that in the largest specimens of *R. radiata* examined there was no indication of degeneration, either in the electric cups or in the nerves passing to them.

In fact, the history of the development of the cups in *R. radiata* seems to be, as far as it goes, a complete record of the more important changes which have taken place in the evolution of electric organs out of muscular fibres. There is at no period any indication of degeneration or any evidence that in *R. radiata* a higher stage of development of the electric organ was ever reached. As one would expect, the electric (motor) plate gradually increases in size, and the muscular fibre is slowly modified to form a suitable support, the fibre retaining, however, its original structure, and, probably, to a certain extent, the power of contracting; and, hence, the transformation is far less complete than in *R. batis*, in which, at the most, only a vestige of the original muscular fibre persists unaltered, the whole of the anterior portion undergoing profound modifications.

Hence, taking into consideration that the young *R. radiata* has reached the adult form before the muscular fibres are converted into clubs, that the clubs are quite double the size of those in *R. batis*, and that, instead of at once giving rise to cups, they form large secondary clubs, and that the cups when they eventually appear in the all but mature Skate retain the characteristic structure of ordinary muscular fibres, and, further, that in the largest specimens examined there was no indication of degeneration in the cups, or of retrogressive changes in the electric plate or its extremely rich supply of nerves, it may, I think, be inferred that in *R. radiata* the electric organ, though relatively extremely small and apparently functionless, is in a state of progressive development.

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Explanation of Plates 79 and 80.

PLATE 79.

Fig. 1. Sketch of the electric organ of *Raia radiata*, in a specimen which measured 48 cm. in length. The nerve of the lateral line occupied the groove (*n.*) which indents the posterior two-thirds of the outer surface of the organ. Natural size.

Fig. 2. *A*. Transverse section showing the first indication of the electric organ in a young *R. radiata* (fig. 3) 12 cm. in length.

o. The group of slightly enlarged muscular fibres from which the electric cups are developed.

m. The unaltered fibres of the lateral muscular band, most of which, as the organ increases in size, gradually atrophy and disappear.

n. The nerve of the lateral line still separated from the rudimentary organ by a row of muscular fibres.

B. Transverse section of the fully developed electric organ from an adult specimen of *R. radiata* which measured 45 cm. in length.

o. The electric organ lying between the skin and the superior and inferior caudal muscles.

m. Muscular fibres in transverse section.

n. Nerve of the lateral line lying in direct contact with the sheath of the electric organ.

Leitz 00, ocular 3. Outlined with Zeiss' camera.

Fig. 3. Sketch of the smallest *R. radiata* in which muscular fibres were found in process of developing into clubs.

Fig. 3a. Three muscular fibres in process of developing into clubs from the Skate represented in fig. 3. *a.* A fibre with the anterior end only very slightly enlarged. *b.* A fibre which has become distinctly club-shaped and has an enlarged motor plate.

Zeiss AA, compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 4. A muscular fibre from a *R. radiata* (fig. 3) 12 cm. in length, in which the motor plate and the nerves in connection with it have been considerably enlarged, while the fibre is only very slightly club-shaped.

Zeiss apochromatic 4·00 mm., compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 5. A muscular fibre which has reached the club stage, from the same Skate as fig. 4. The anterior enlarged end is slightly concave and completely covered

by the motor plate in which the nerve fibres terminate. The striation in this fibre was identical with that of the adjacent muscles.

ZEISS apochromatic 4·00 mm., compensating eyepiece 12. Outlined with ZEISS' camera.

Fig. 6. Two muscular fibres, which resemble Indian clubs, from a Skate (*R. radiata*) measuring 18 cm. These may be known as secondary clubs. The truncated end, which is slightly concave, supports the motor plate, in which numerous nerve fibres terminate. Note that a considerable portion of the muscular fibre takes part in the formation of the club.

ZEISS AA, compensating eyepiece 12. Outlined with ZEISS' camera.

Fig. 7. Sketch of a longitudinal section through part of the tail of a Skate (*R. radiata*) 18 cm. in length, showing from without inwards the skin (*s.*), the nerve of the lateral line (*n.*), the electric organ (*o.*), and portions of muscular fibres (*m.*). Note the oblique arrangement of the secondary clubs, their relative length, and compare them with the two primary clubs (*b.*) from a specimen 12 cm. in length.

ZEISS AA, eyepiece 3. Outlined with ZEISS' camera.

PLATE 80

Fig. 8 shows the secondary clubs, from a specimen 18 cm. in length, more highly magnified than in fig. 7. Observe the difference in the length and diameter of the clubs figured, the nuclei of the motor plate in *A.*, the nerves passing to the motor plate in *B.*, and that the striation of both the head of the club and stem of *B.* resembles the striation of the altered muscular fibre *m.* Had the club *A.* been drawn to the same scale as the clubs represented in figs. 4 and 5, it would have been nearly double the length.

ZEISS DD, ocular 3. Outlined with ZEISS' camera.

Fig. 9. Two muscular fibres in process of changing from clubs into cups from the electric organ of a Skate (*R. radiata*), 24 cm. in length, macerated in nitric acid. Observe that the altered muscular fibres, though nearly double the width of those (fig. 6) from a Skate 18 cm. in length, are only very slightly longer. In some of the developing cups the striation was distinct, and a large bunch of nerves remained in connection with the motor plate.

ZEISS AA, compensating eyepiece 12. Outlined with ZEISS' camera.

Fig. 10. Two fibres which almost reached the cup stage from a Skate 35 cm. in length. The bunch of nerves passing to the motor plate has been represented in *A.*, and their mode of ending in delicate loops and the depth of the cup are indicated in *B.*

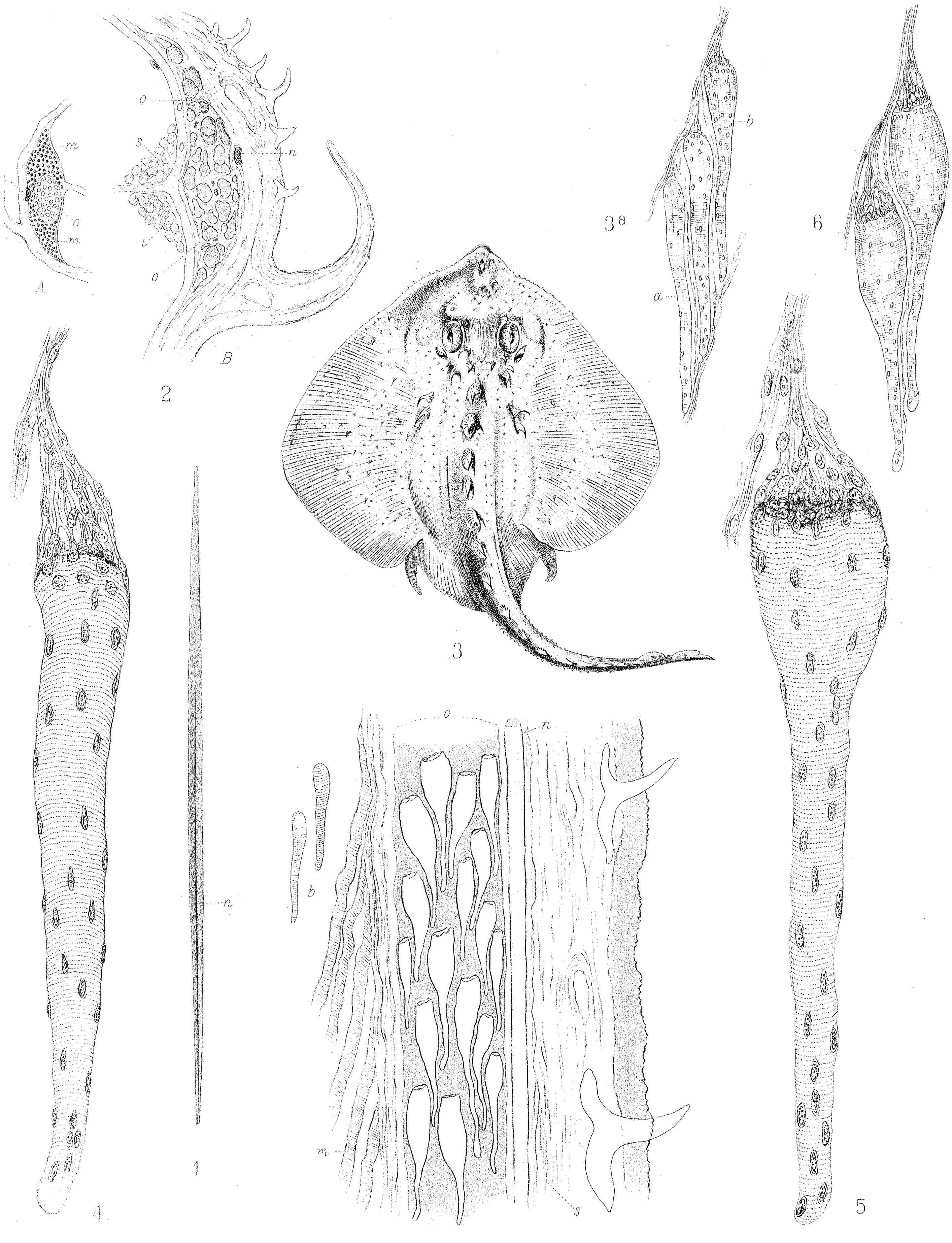
ZEISS AA, compensating eyepiece 12. Outlined with ZEISS' camera.

Fig. 11. Sketch showing two cups from the electric organ of a Skate (*R. radiata*) which measured 40 cm. in length. Note that the cups, though well moulded, are shallow, and that they lie in close contact with each other. Note, also, that the stems have lost their rounded contour, and that, apparently owing to compression, the anterior part of each has been altered so as to present in front a prominent ridge (*r*). By comparing this figure with figs. 6, 9, and 10, an idea will be gained as to the increase in length which has taken place in the stem.

ZEISS AA, compensating eyepiece 12. Outlined with ZEISS'camera.

Fig. 12. Sketch showing two completely developed cups from an adult Skate (*R. radiata*) which measured 45 cm. in length. Compare these with the incompletely formed cups represented in fig. 10, and also with the cup of *R. circularis* (Plate 68, fig. 3) which, though drawn to the same scale, is considerably larger, and has a far more extensive lining (electric plate) and a thick cortex. Observe (1) the thick wall of the shallow cup *A.*, composed of muscular tissue still distinctly striated, with a few muscle nuclei scattered through its substances; (2) the thin electric plate extending over the rim of the cup; (3) the nerves (of which only a few fibres are introduced) which form a continuous series of loops over the electric plate; (4) the thin outer layer (thickened sarcolemma); and (5) the long striated irregularly compressed stem.

ZEISS AA, compensating eyepiece 12. Outlined with camera from cups isolated by maceration.



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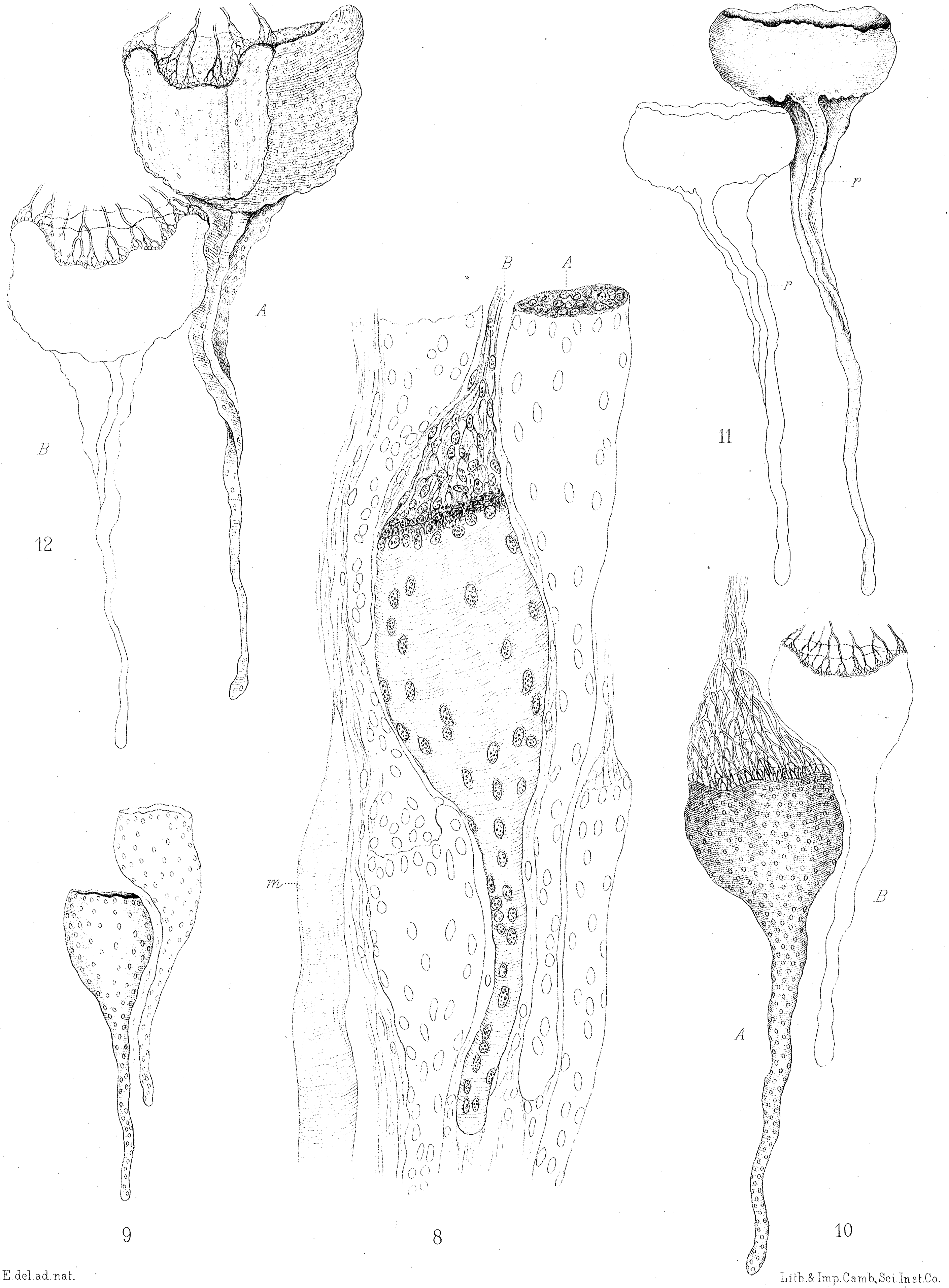

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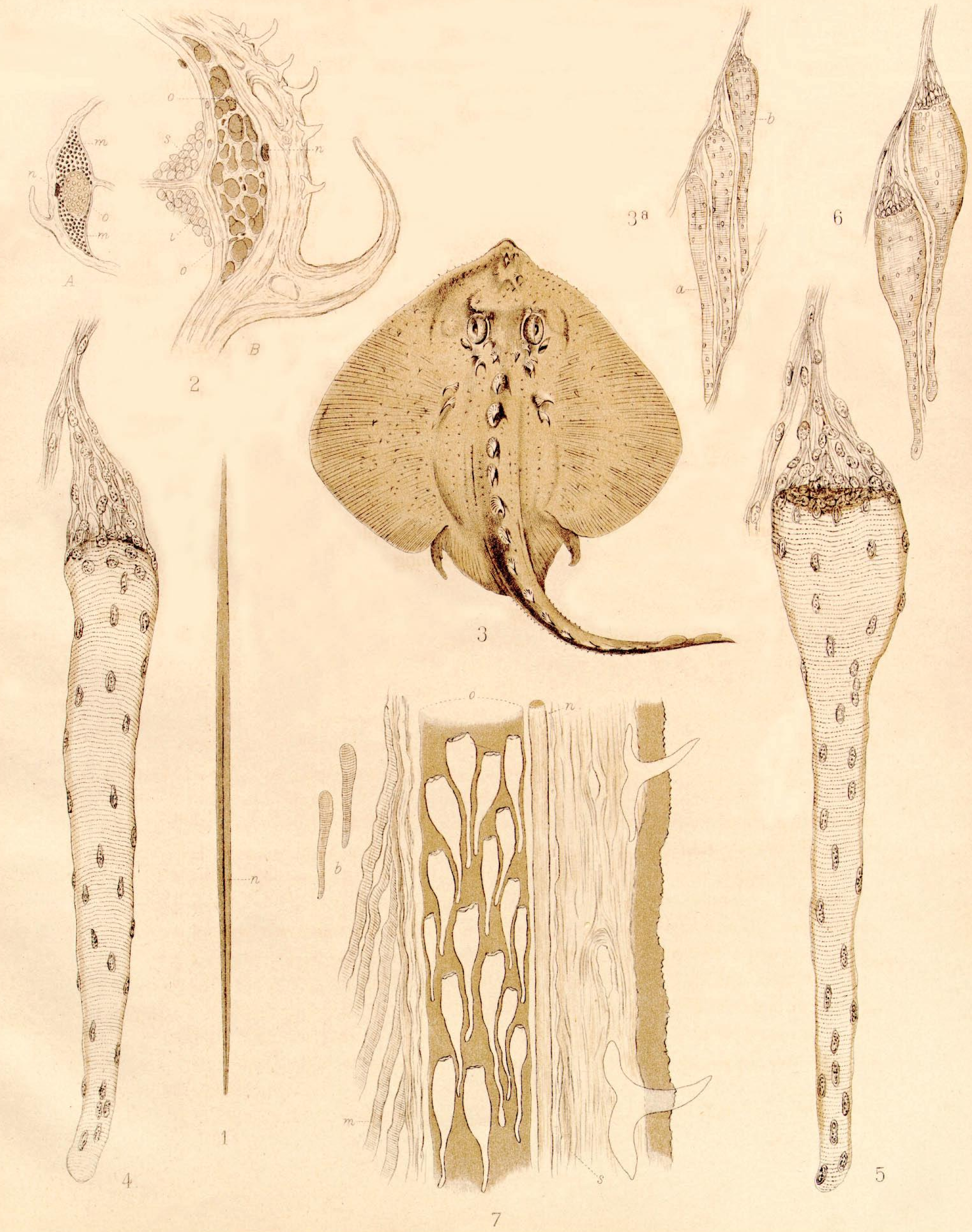

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