ON THE ORIGIN OF THE ELECTRIC NERVES IN THE TORPEDO, GYMNOTUS, MORMYRUS AND MALAPTERURUS.

THE subject of this communication may seem remote and uninteresting, but it will not be difficult to show that questions of the highest importance for physiology, anatomy, and the Darwinian theory are closely related to those touching the structure of the electric organs of certain fishes and the laws of their functions.

The fact that the body of an animal should become a complete electrical apparatus acting at the will of its owner induces us to inquire how this extraordinary result has been attained; that is, to investigate the origin of the electric organs of fishes, and the manner in which the animal throws them into action. We shall see that in pursuing both lines of enquiry we open far-reaching views into regions as yet unknown.

According to the present state of our knowledge there can be no doubt that most of the electric organs hitherto discovered are of muscular origin. It is not my intention to dwell on this transformation of muscular tissue, but it may nevertheless prove interesting to cite an example of the completeness with which such transformation can take place; I refer to the Mormyrus—the so-called pike of the Nile—a fish which has only of late been sufficiently known to possess electric power. A transverse section of the tail of any ordinary fish shows scarcely anything more than the vertebral column, muscles and their tendons, attached to the bones. On the other hand, a transverse section of the tail of Mormyrus (Fig. 1) shows no conspicuous muscles, but in place of them electric tissue filling up the entire space occupied by muscles in ordinary fishes. Of the muscular apparatus there is nothing left except the longitudinal tendons passing outside the electric organs from muscles placed anteriorly. If these tendons were cut across the Mormyrus would be unable to move its tail.

FIG. 1.—Transverse section of the tail of *Mormyrus cyprinoides*.

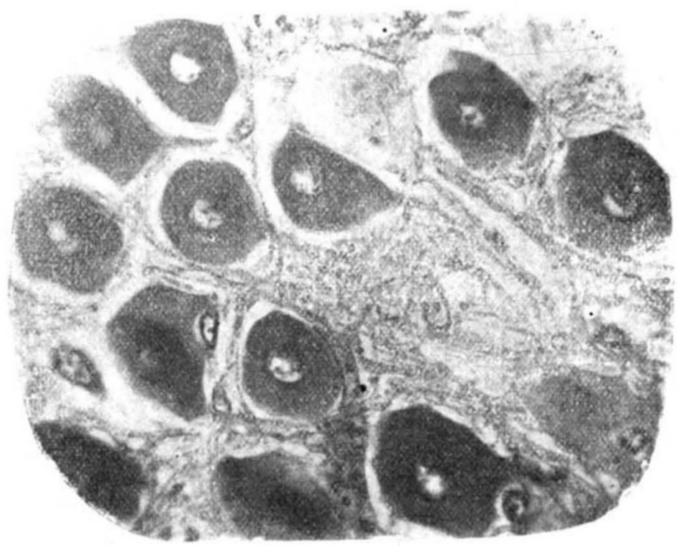

FIG. 2.—Ganglion cells from roots of electric nerves of Torpedo.

Omitting the complicated arrangement of histological elements in this modified muscular tissue in the different electrical fishes—which could not be sufficiently explained without a large number of illustrations—it may be sufficient to state that a kind of swelling loosens the molecular elements of the muscles and allows them to be settled again in a very regular but quite new form.

The well-known electric eel of America, *Gymnotus electricus*, has only the external shape of an eel, and is in reality a very short fish, carrying very powerful electric organs in a long tail springing from a very short rump. A transverse section of the tail shows that a part of the muscle is changed into electric organs, while another remains unchanged.

In the different kinds of electric skates—Torpedinidæ—the electric organs are developed from muscles, which originally belong to the branchial arches and the arch of the lower jaw.

When we look to the nerve apparatus which enables the fish to throw the electric organs into action by a voluntary impulse, we find in every case wonderfully developed ganglion cells from which the impulse is transmitted directly to the electric batteries. Such a coincidence certainly cannot be the result of mere chance. But beyond the invariable presence of large ganglion cells as the starting points of electric nerve fibres there is very little uniformity in the arrangement of these elements in the different sorts of electrical fishes; on the contrary, there are most remarkable and striking differences not only in the position but also in the number and in the appearance of these nerve centres. It is to be hoped therefore, that some important views regarding the character and functions of ganglion cells in general may be suggested by their study.

In the Torpedo the electric ganglion cells—being in vast numbers—form a bean-shaped mass in the medulla constituting the well-known electric lobe. It represents modified motor centres of the vagus nerve; anteriorly it is covered by the cerebellum, but emerging from beneath that organ, the lobe increases rapidly where the largest electric nerve leaves the medulla. Lower down its size again diminishes, where it gives rise to the fourth electric nerve and terminates quite free in a blunt point on each side. On counting the ganglion cells in a complete series of sections one finds the number to be about 54,000—a number that can be found to nearly correspond with the fibres in the electric nerves that arise from them. A transverse section of the medulla, close to the spot where the roots of the electric nerves are gathering, shows the so-called axis cylinder processes of the cells entering the roots to form the nerves. This is seen in Fig. 2—a photogram taken from nature like all the other illustrations of this paper.

Even the first and smallest of the electric nerves shows a great number of nerve fibres collected into bundles which on transverse section appear as if perforated by numerous small openings—each apparent aperture being a nerve fibre. I counted about 8039 fibres in the first electric nerve, in the second or largest about 23,770; in all four nerves about 58,318 fibres. This total exceeds that of the ganglion cells by at least 4000, but the disparity of number is probably to be accounted for by the impossibility of getting an exact total from a series of sections where the cells are very often dragged away by the knife.

The ganglion cells of the Gymnotus, or electric eel, are disposed in a different manner. Behind a short portion at the anterior end of the spinal cord where ordinary cells are found, the grey substance contains large rounded ganglion cells, the most anterior of them forming a semicircle around the central canal of the cord. Since these first cells extend in front of the most anterior electric nerves, a transverse section of this region shows no axis cylinders leaving the grey substance, all being directed downwards to the gathering place of the first electric nerve roots, and therefore must be cut off. If, however, a transverse section be made in the middle portion of the cord the whole grey matter is seen to be packed with electric cells and their axis cylinders are seen passing very straight and undivided to join the electric nerve roots at once. The other processes of the cells are so pale and fine that it is impossible to recognize them sufficiently well in a complete section. Since the electric batteries extend along both sides of the tail to its very end, the electric nerves and their ganglionic centres have a similar extension. The electric cells form a continuous column in the spinal cord, but it is very slender, therefore, notwithstanding the great longitudinal extent of the electric centre, the number of cells is not so very great. I estimated the total number of cells to be about 60,000—not many more than the estimated number in the Torpedo.

The genus Mormyrus, whose electric power was doubted until quite recently, resembles the Gymnotus in the structural arrangement of its electric apparatus. I was fortunate enough to find the ganglion cells for the electric nerves in the spinal cord, where the tail is endowed with the electric batteries, as seen in Fig. 1. The cells are very soft, and must be very carefully preserved to show all their details. Their regular undivided axis cylinders leave the cord-like motor roots, and form a sort of plexus before leaving the vertebral canal. It is to be considered as a very important fact, that broad processes of the cells regularly intercommunicate on so large a scale that their union into a complete system for simultaneous action cannot be doubted.

Fig. 3 shows such cells in the grey substance of the spinal cord; the intercommunicating processes can be seen much more distinctly in the microscopic slide and even in a photogram, than they appear in that figure.

The axis cylinder of each cell being a well-defined undivided process, the intercommunicating processes must be regarded as protoplasmic in the sense expressed by Deiters. Their general intercommunication cannot have any other significance than to insure equality of action in giving the impulse to the electric batteries. If that statement be admitted *the protoplasmic processes of the cells must have a conducting function.* If that be true in the Mormyrus there is no reason whatever why it should be otherwise in other vertebrates. Yet Golgi maintains that the protoplasmic processes of nerve cells are to be regarded as having a simply nutritive and therefore a non-nervous function.

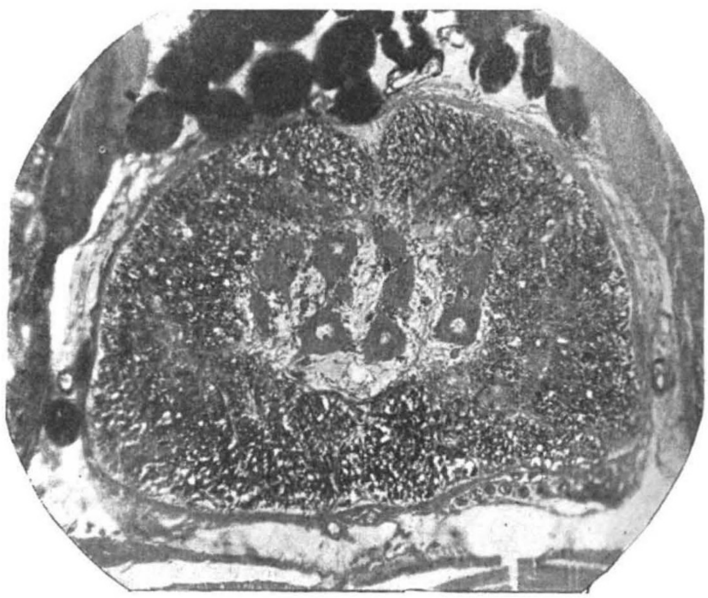

FIG. 3.—Communicating Electric Cells in the Spinal Cord of Mormyrus

There is another most remarkable fact in the organization of the Mormyrus having reference to the combined action of the electric organs on both sides. The upper as well as the lower electric nerves form a decussation outside the vertebral canal resembling the chiasma of the optic nerves. I am not acquainted with any other instance of motor nerves crossing the median plane to the other side of the body outside the cerebrospinal axis. In all other cases they are outside the brain and the spinal cord confined to their own side of the body to insure the isolated action of each muscle or group of muscles on that side. It is therefore stated that in changing the motor into an electric function these nerves at the same time became liberated from the strict rules of their predecessors. Certainly the case of Mormyrus gives a very good idea of the extraordinary power of adaptation to function with which Nature is endowed; but who can say how this particular anatomical arrangement could come about by gradual variation? I consider this difficulty far greater than that relating to the first development of electric organs in general which is so frequently the subject of reference.

Since the celebrated investigations of Prof. E. du Bois-Reymond have shown that the function of the muscular system is intimately associated with electric currents it is permissible to take them into account where muscle and their derivatives are under consideration.

I have shown elsewhere that most of the electric fishes are liable to a degeneration of the muscular system, seemingly caused—in part, at all events—by a certain lazy mode of life (disuse of organs). We therefore find along with fully developed electric tissue in the Gymnotus, nests of muscles which have not arrived at perfection. In the Mormyrus degenerating muscles in the forepart of the electric organ suggest the impression that the process of transformation is still going on. Still more is this the case in the common Raja.

Moreover, we know that the peculiar degeneration of muscular tissue into electric tissue destroys the contractile power of the muscles, but does not interfere with their electromotor properties; on the contrary the loosened and differently arranged elements of the changed muscles are more capable of producing electric currents. In that

FIG. 4.—Transverse section through the body of Malapterurus with a parasite in the electric organ.

state of development which has still quite an occasional character, it seems only necessary to assume that under certain favourable circumstances the fish while trying to catch a prey or to defend itself against an enemy in the sudden excitement becomes aware of its electric power hitherto unknown to itself. On perceiving the advantage of the electric power in the struggle of life the fish might begin to use it regularly and to develop it gradually to perfection in its descendants; just as a man might one day perceive that he is endowed with the power of hypnotism, consequently learns to use it and gradually improves it.

But now it is necessary to consider also the electric Shadfish of the Nile, the *Malapterurus electricus*, a powerful fish of very peculiar structure, which places it in quite a different category from the electric fishes already mentioned. A transverse section of the whole fish (Fig. 4) shows the difference at once. The body of the animal is enveloped in a very thick electric skin, constituting one electric organ. Muscular tissue is nowhere deficient, other histological elements must therefore have furnished the material for the electric plates, which are packed very close in lozenge-shaped compartments of the skin.

In my opinion the plates are nothing else than modified cells of the cutaneous glands which are plentiful in the remainder of the skin. The precise proof of that statement ought to be furnished by a complete investigation of the development of the animal, which as yet is quite unknown. But the differences between the two kinds of electric organs are so great that we are surely entitled to separate the *muscular* from the *cutaneous* electric organs.

Assuming that the origin of these cutaneous batteries differs from those developed from muscle, we cannot wonder that their functions also differ in most important points. The electric current passes through the body in a direction the opposite of that in other electric fishes. There are *only two* electric nerve fibres, one on each side, which divide and subdivide until they give off more than two million branches. We shall see that these two nerve fibres are not true axis cylinder processes of ganglion cells. Before making a more detailed reference to these interesting elements it may not be amiss to point out in the section shown in Fig. 4 the existence of an intruder, a specimen of the so-called *Filaria piscium*, which had taken up its abode in the electric organ itself. This proves that animals can become accustomed to strong electric currents without receiving injury, and it suggests that the immunity of electric fishes against their own currents and that of their young *in utero* (Torpedo) is a faculty acquired by gradual training.

The construction of the single electric nerve fibre in Malapterurus resembles to a surprising extent that of an electric cable on a minute scale. We see the tiny nerve fibre like the central wire of the cable surrounded by a little non-conducting material and held *in situ* by a sort of network; the whole being enveloped in an enormous mass of connective tissue sheaths just like a cable protected externally by numerous layers of strong material. Fig. 5 shows a transverse section of the central part only to render the details of the round fibre and supporting network more distinct. If we follow this single fibre inwards to its origin in the central nervous system we are led to *a single ganglion cell* from which the single fibre arises. There is one cell on each side of the cord, therefore just two cells in all; whereas in Mormyrus, which has the smallest number of electric cells in the fishes with electric organs of muscular origin, the cells must be estimated at more than 1500. The position of the two cells in the spinal cord of Malapterurus reminds one of Clarke's column in the cord of higher vertebrates where the cells differ in certain particulars from the motor cells. As already stated there is only one cell on each side, but

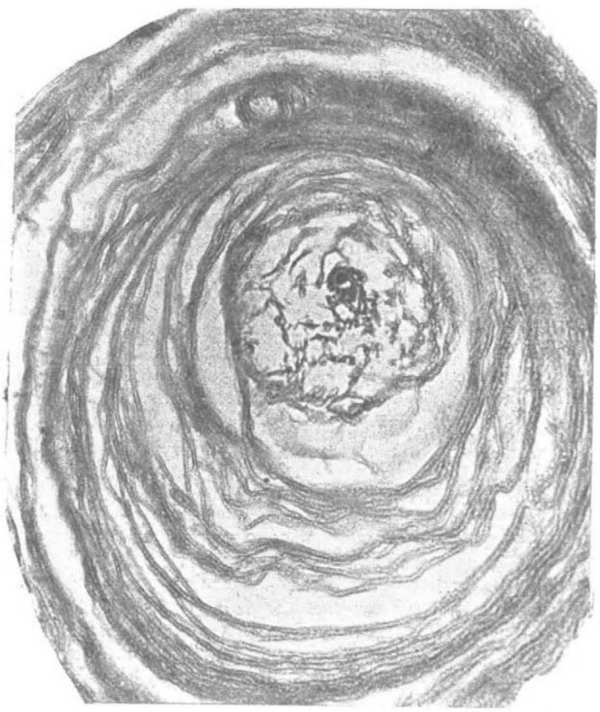

FIG. 5.—Transverse section of the central part of the electric nerve of Malapterurus.

that is a giant of its race. There is no real axis cylinder arising from the cell, but in place of it branched protoplasmic processes join and form a kind of perforated plate beneath the cell, from which the nerve fibre starts with a broad base (Fig. 6). I consider this a chief point of difference between this peculiar cell and all the other afore-mentioned cells of a motor character. Fig. 6 gives a good idea of this magnificent histological specimen with its elegant nucleus showing its network and its nucleolus on one side.

Reviewing from a physiological standpoint the several facts stated above, we must feel convinced that the peculiar ganglion cells which are invariably found in relation to electric organs must play an essential part in bringing the electric organ into action. In my opinion that is tantamount to proof that other ganglion cells must be essential for sending nerve impulses to peripheral organs, and that the idea lately suggested by Nansen that ganglion cells have only a trophic influence on nerve tissue cannot be reasonably maintained in the face of these and similar facts. I may here refer to the well-known peculiar ganglion cells found in the motor region of the brain of higher animals, including man. Betz, who discovered them, searched for them for the purpose of stating anatomically the laws of localization found by Prof. Hitzig and myself.

It may not be out of place to adduce here another piece of evidence taken from the department of pathology. My friend and collaborator Hitzig has lately published the case of a man who died from tetanic cramp of the head. He observed that in the ganglion cells of the motor centre of the fifth nerve presiding the affected muscles there was a very singular change to be observed *in these cells only*. It appears that the bacteria of tetanus caused a granular decomposition of the protoplasm in the cells, which led to a further state of degeneration characterized by the appearance of large holes, while the other ganglion cells and the remainder of the organ appeared quite healthy. I am convinced the case shows that the cramps in the combined muscles resulted from the irritation and gradual disorganization of the ganglion cells.

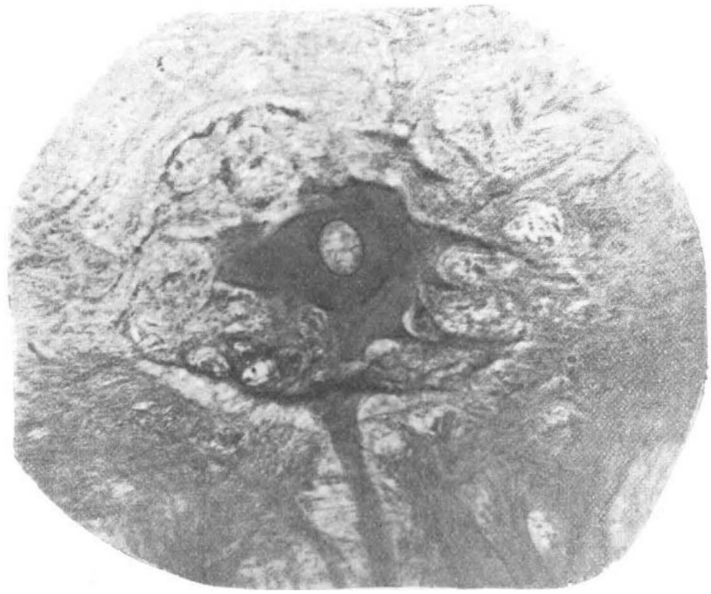

FIG. 6.—The right giant ganglion cell with the origin of its electric nerve from spinal cord of Malapterurus.

The above statements may suffice to show that the electric fishes and their nervous elements are really not such outsiders in science, and that the observations made on them should be brought into comparison and correspondence with those gathered from other sources. Indeed the histological elements in their organs are so instructive, that I would strongly recommend that the conclusions deducible from their study should be employed in maintaining well-founded former notions regarding the organization of the nervous system in vertebrates against certain revolutionary ideas of some modern authors.

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AUSTRALIAN TRAVELS.[1]

ON opening this work, one is at once struck by the beauty of the illustrations, particularly those of the New Zealand Alps. The double-page plate opposite p. 248, drawn from a photograph taken by the author, is especially worthy of remark. For effect this view may well compare with some of the most picturesque parts of Switzerland. Some of the photographs, however, have a familiar appearance to the travelled reader; one recognizes in the beautiful picture "Off the West Coast of Ceylon" (p. 300) an old friend, none the less worthy of reproduction.

The work makes no pretensions to a virgin freshness its professed object being to gather together the already published observations of the author, and to present them in a popular form. This it does very successfully, though the English reader could have dispensed with a good deal of the very apparent "padding." Thus the first twenty pages of this book of travel are devoted to the history of Australia, and remind one of Coghlan's opening chapter in the "Wealth and Progress of New South Wales": the next twelve pages on gold differ from Coghlan's second chapter, particularly in giving greater prominence to Count Strzelezki's discovery, and one regrets that n mention is made of James McBrian, who certainly ha prior claims. The author is candid in his criticisms and condemns both the theatres and University of Sydney, as being, from the German standpoint, decidedly bad. On p. 34 we come to a "Journey into New South Wales," and here commences an interesting medley of natural history, traveller's tales, and geographical investigation. In this vacation ramble Von Lendenfeld claims to have discovered the culminating point of the Australian continent in Mount Townsend, to which he assigns (by aneroid) the height of 2241 metres. The doggerel verse on p. 82, in which a red sunset is taken to indicate approaching rain, must be wrong in its meteorology, so at least it proved, a red sunset being followed, much to Lendenfeld's surprise, by a fine day. It is satisfactory to find that the signs of the weather are not inverted at the Antipodes.

The author's familiarity with glaciers and ice-action in Europe served him in good stead in the southern hemisphere. Several interesting pages are devoted to his discovery of the former existence of glaciers in the Australian Alps; though there seem to have been contemporaries in this matter, for while Von Lendenfeld's observations proved the existence of *moutonnéed* and striated surfaces down to a level of 1500 metres above the sea—Mr. James Stirling claimed to have found signs of ice-action at lower levels still, as in the neighbourhood of Omao, where they occur at 800 metres above sea-level. The historical conscience is strong in the author, or he would scarcely have troubled to recall the

[1] "Australische Reise," by R. von Lendenfeld, pp. 325, with Illustrations. (Innsbruch: Wagner, 1892.)