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On Some Histological Features and Physiological Properties of the Post-Oesophageal Nerve Cord of the Crustacea

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IV. *On some Histological Features and Physiological Properties of the Post-Œsophageal Nerve Cord of the Crustacea.*

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[Plates 10-13.]

About two years ago, at the suggestion of Dr. W. H. Gaskell, F.R.S., I undertook the examination of the minute anatomy of the nervous system of the Crustacea. Certain of the results of the investigation are incorporated in the following paper.

The nervous systems of *Branchippus*, of *Astacus*, and of the Zooea larva have been examined, but the following pages are limited, almost exclusively, to the two first-mentioned.

I have to thank Dr. Gaskell and Mr. Langley for the many suggestions with which they have aided the work, and Professor Foster, Secretary, Royal Society, for the kindly interest he has shown in my investigations from their commencement, an interest which is extended to all those who have the good fortune to assist him in his professional duties. I am indebted to Mr. Bateson, of St. John's College, for some carefully preserved specimens of *Branchippus* and *Artemia*.

Part I.—The Post-Œsophageal Nerve Cord of *Branchippus*.

The central nervous system of *Branchippus* is of special interest as an example of the conditions found in the most primitive Crustacea. It consists of a well-developed supra-œsophageal ganglion, or brain, connected with a small dorsal median simple eye, and a pair of laterally placed compound eyes. This ganglion also innervates the first pair of antennæ. From the brain a pair of longitudinal ganglionated nerve cords pass backwards. These are connected with one another in each segment by a pair of transverse commissures, except in the most posterior part of the animal. The whole nervous system shows many primitive features, it is connected with the ectoderm in many places, shows little trace of fusion in the mid-ventral line, and has nerve cells very diffusely scattered about it. Generally speaking, both the brain and the nerve cords arising from it consist of a central fibrous core, the fibres of which form an exceedingly fine plexus. This is the "Punktsubstanz" of LEYDIG,* and the nerve cells lie wholly on its surface.

Posterior to the œsophagus there are sixteen well-marked ganglia. These are respectively one mandibular, two maxillary, eleven corresponding to the eleven foliaceous swimming appendages, and lastly, two closely approximated ganglia, situated posterior to the appendage-bearing region, and related to the genital organs. Posterior to these again, in the abdominal region, are two very slightly developed ganglia. The œsophagus is surrounded by a ring of nervous tissue which forms a single remarkable ganglion connected with the sensory surfaces of the lips and from it a pair of nerves pass to the second pair of antennæ. There are thus posterior to the brain nineteen ganglia, as follows :—

1. The circumoral ganglion connected with the sensory surfaces round the mouth and the second pair of antennæ.
2. The mandibular ganglion.
3. The ganglion of the first pair of maxillæ.
4. The ganglion of the second pair of maxillæ.

5 to 15. The ganglia of the eleven pairs of swimming appendages.

16, 17. The genital ganglia.

18, 19. The abdominal ganglia.

The ganglia are separated from one another by portions of the cords absolutely unconnected by transverse commissural fibres.

In the *inter-ganglionic regions* each cord is rather rounded in transverse section (fig. 1.), and free from the ectoderm, but as the ganglia are approached a continually closer connection with the ectoderm obtains. In its free or inter-ganglionic part a delicate sheath with small deeply staining nuclei invests the cord. Passing from the middle region towards the ganglion above or below, nerve cells become more numerous, always immediately underlying the investing sheath. One striking fact thus becomes evident in this primitive nervous system, namely, that there is no sharp line of demarcation between ganglionic and inter-ganglionic, or strictly conducting regions. Further, the fibrous core in this latter region is seen in longitudinal sections to consist of longitudinally arranged fibres which stain well with carmine stains. Connecting these, however, in many cases are more delicate filaments which run obliquely, so that the whole instead of being merely a bundle of parallel fibres, may be more exactly described as a plexus of which the longitudinal strands have been relatively exaggerated.

The shallow groove on the ventral surface of the animal and between the nerve cords deepens considerably just posterior to the mouth, and is there lined by elongated sense cells, and abundantly supplied with nerve filaments, thus forming a sensory pit

* LEYDIG, 'Handbuch d. vergleich. Anatomie,' vol. 1, Tübingen, 1864.

between the mandibles. In the thoracic region the groove is very shallow in the inter-ganglionic regions, but deepens between the ganglionic enlargements. In this groove is a line of sense cells on either side of the mid-ventral line. They are especially prominent near the ganglia. We may, therefore, say that there exists on the ventral surface a pair of almost continuous sense lines, situated on the ridge bounding the ventral groove, and perfectly segmented in correspondence with the ganglionic segmentation of the cords. They meet just posterior to the mouth in a deep sense pit or groove (fig. 2), which again, in its turn, may be regarded as a backward continuation or thickening of the sense ring round the mouth. The arrangement of these ventral sense cells will be seen to have an important bearing on the disposition of the sensory elements of the cord. In the inter-ganglionic, as well as in the ganglionic regions, filaments pass from these ventral sense cells to the cells of the cord.

Structure of a Typical Ganglion.

For purposes of description I will choose the ganglion related to the third pair of swimming appendages. It consists of a double thickening of each nerve cord, so that on either side are anterior and posterior swellings, each connected with its fellow of the opposite side by a transverse commissure. Seen in transverse section (figs. 4, 5, and 6), each of these thickenings is oval, the long axis being horizontal, and from the outer border of each a distinct nerve passes. Each ganglionic swelling, besides being intimately connected with the subjacent ectoderm, abuts dorsally against the gut.* Between the anterior and posterior swellings on each side, and lying partly wedged in between the lateral extension of the oval nerve cords and the ectoderm, are a pair of large vacuolated cells with large granular deeply-staining nuclei (fig. 6). These are the peculiar segmental excretory glands described and figured by Professor CLAUS.† The anterior and posterior portions of the ganglion present profound differences in the arrangement of their elements, and these differences are constant throughout the entire thoracic region.

The Anterior Half of the Ganglion (figs. 4 and 5).

At its anterior end the ganglion commences by an increase in the number of the cells on the internal edge of the cord; these rapidly expand into a well-marked group of multipolar cells. The delicate membrane previously described as enveloping the cord becomes discontinuous over these cells, allowing them to extend themselves both underneath the cord, and also beyond the cord laterally, always in most intimate

* Similarly, the pre-œsophageal ganglion or brain lies beneath and in close contact with a pair of anteriorly directed diverticula of the mesenteron.

† CLAUS, "Untersuch. über d. Organisation u. Entwickel. v. *Branchippus* u. *Artemia*." 'Arb. aus Wien,' vol. 6, p. 267.

connection with the ectoderm. There is thus formed a *plate of cells* which extends under the entire ganglion, dying out at either end only when the inter-ganglionic cord loses its close and immediate connection with the ectoderm. From the most external of these cells delicate processes pass, which branch and end in various ectoderm cells on the ventral surface external to the ganglia, and furnished with sense hairs, and we have here every intermediate condition between ectoderm cells which are almost continuous with nerve cells, to ectoderm cells connected with the ganglion cells by comparatively long processes (fig. 4). From their connections with the ectoderm this ventral group of nerve cells would appear to be sensory in character, and to form a sensory system which does not give origin to a definite sensory nerve. They are connected with the imperfectly segmented series of sense cells which occur on the ventral surface in close connection with the nerve cords.

On the inner dorsal angle of each of the anterior ganglionic swellings is a cell group (figs. 4 and 5, int. dorsal cells), the cells of which give off processes to the anterior commissure, and are also connected by a dorsal series of arcuate fibres with a third group of cells on the outer dorsal edge of the anterior ganglionic swelling (*ibid.*, ext. dorsal cells). These external dorsal cells, though abutting on the external cells of the ventral sense plate, yet differ from them in size and in the fact that from them a bundle of fibres passes through the ganglionic plexus to form the anterior part of the anterior commissure (fig. 4). The posterior part of the anterior commissure is composed of fibres which traverse the ganglionic plexus and pass directly out as part of the outgoing nerve bundle (fig. 5). These decussating fibres thus divide the plexus of each anterior swelling into dorsal and ventral portions, of which the latter is finer and denser in character.

We can therefore distinguish in each half of the anterior portion of the ganglion three cell groups: (1) the ventral group, which extends under the entire ganglion; (2) the external dorsal group, from which decussating fibres pass, forming the anterior portion of the anterior commissure; (3) the internal dorsal group. The external and internal dorsal groups are connected by a bundle of dorsal arcuate fibres.

The *anterior pair of nerves* plunge immediately into the lateral mass of muscles, and, turning dorsalwards and outwards, pass into the upper part of the appendage, giving off motor fibres to the various muscles as they pass them. These end immediately in the neighbourhood of one of the nuclei of the curious granular protoplasmic sheath which, more or less completely, envelopes the transversely striated contractile portion of the muscle fibre (fig. 7). The anterior pair of nerves thus are mainly, if not entirely, motor. Careful searching with a $\frac{1}{15}$th objective failed to discover a case of undoubted connection with the ectoderm. Fibres can be traced into each anterior nerve from both the external and internal dorsal cell groups of its own side. These arise either directly from the cells, or as lateral branches from processes of the cells which are lost in the plexus. A bundle of fibres also passes directly from the posterior portion of the anterior commissure directly across the plexus into each of the anterior nerves.

We have already seen that the fibres of the anterior commissure not only contribute to the formation of the anterior nerves, but also pass to the two dorsal cell groups. It is thus possible that the directly decussating fibres of the anterior nerves are in part connected with the dorsal cell groups of the opposite side.

Some of the fibres of each anterior nerve may be traced directly into the more dorsal portion of the ganglionic plexus. These probably are connected with nerve cells by lateral branches, but the connection cannot be seen in sections. It is probable from the fact that a large number of the fibres of the anterior commissure end in the plexus, that a crossed connection exists between each anterior nerve and the plexus of the opposite anterior ganglionic enlargement.

The following, then, are the central connections of each anterior nerve :—

1. With both external and median dorsal cell groups of each side, but mainly with those of the same side.

2. With the dorsal plexus of each side.

Finally it should be remembered that the dorsal cell groups of the same side are connected by the dorsal arcuate fibres.

These dorsal cells and the dorsal coarser fibrous reticulum I regard as the motor portion of the anterior half of the ganglion.

It may be well here to emphasize the fact that the elements of the entire ganglion are placed in the most intimate connection by means of the complex central plexus. No conception of this primitive nervous system will be an adequate one which does not realize the fact that it is throughout a cell and fibre plexus condensed along certain lines. Even the well-marked bundle of fibres passing from the commissure direct to the anterior nerve is, in its course through the ganglionic plexus, intimately related to, and obviously a part of, that structure, being connected with it by filaments.

The *posterior half of the ganglion* (fig. 6) is very different in its arrangement from the anterior part just described. It consists, like the former, of a swelling on each nerve cord, which is oval in transverse section, and of a pair of nerves, one on each side, arising from their lateral aspects. The posterior ganglionic enlargements, like the anterior swellings, are connected by a transverse commissure. But while the anterior commissure lies in close contact with, and is intimately related to the ventral ectoderm (fig. 4), the posterior commissure arches freely above it.

The cells of the posterior ganglionic swelling on each side form three groups :—

1. A median group placed at the junction of the commissure with the cord (fig. 6, median group). Each cell gives off a strongly marked process to the commissure, while, on the external side, it contributes processes to the ganglionic plexus. The commissure stretches between these cells, and appears to communicate only with

them, neither contributing directly to the formation of the posterior nerves, nor sending fibres directly into the plexus, as is the case with the anterior commissure.

2. An external lateral group of cells which give off marked cell processes into the plexus, while on their outer side they give origin to part of the outgoing nerve.

3. The ventral cells before mentioned which are continuous with the ventral cells found beneath the anterior portion of the ganglion and have the same connections.

The *posterior nerves* pass outwards, but take a course much more ventral than that of the anterior nerves. They pass below the muscles and immediately over the large excretory cells. Each is composed of two bundles (fig. 6) which are respectively dorsal and ventral. The ventral and larger ramus curves downwards and is distributed to the ectoderm of the ventral lobe of the appendage; the dorsal ramus passes outwards and upwards to be distributed to the more peripheral ectoderm. The fibres of the ventral ramus arise from the lateral cell group. The dorsal ramus arises directly from the ganglionic plexus. Within the plexus the processes from the median (commissural) cell group passing outwards, and those from the nerve direct, and from the external cell group radiating inwards, almost meet (fig. 6).

Those fibres of the nerve which pass to the more peripheral ectoderm, that is, the fibres forming the dorsal ramus of the posterior nerves, do not go direct to their destination, but enter, at any rate in some cases, multipolar cells, the processes from which radiate to the ectoderm cells. Such a cell is shown in fig. 8. This relation is extremely interesting and suggestive when taken in connection with the known relations of sporadic nerve cells in Vertebrates, where such cells are regarded as being distributing or multiplying centres for centrifugal impulses. In this case, however, the contrary occurs, for these cells in *Branchippus* act as *condensing centres for centripetal impulses*. Similar "condensing" cells form a distinct layer in the optic ganglion of *Branchippus*, one process passing from each cell to the brain while several enter the cell from the eyes. Yet another consideration is suggested by these condensing sensory cells, which are mostly suspended in the body cavity by their processes. The dorsal ramus of the posterior nerve, which is characterised by the possession of such cells, passes to parts more removed from the central nervous system than does the ventral ramus. At the same time, its fibres, instead of being given off from cells, arise directly from the ganglionic plexus. Thus we may regard the ganglion cells from which the fibres of the ventral ramus take origin, as having travelled inwards from positions more remote from the nerve cords, and this process has led to their becoming an integral part of the central nervous system. Such a view has this advantage, that it accords with the many features of the primitive system of *Artemia*, which point to a derivation from a much more diffuse cell and fibre plexus by a process of condensation.

Each of the posterior nerves is therefore composed of two parts (1) a dorsal bundle, which springs directly from the central ganglionic plexus, and has ganglion cells on the course of its fibres; and (2) a ventral bundle, which arises from the lateral group of nerve cells.

There is yet another group of nerve cells which, like the ventral sensory cells, cannot be said to belong specially to either the anterior or posterior divisions of the ganglion. In describing the anterior part of the ganglion I mentioned a group of cells, the internal dorsal cells, situated on the median dorsal surface and connected with the anterior commissure on the one hand, and with the external dorsal cell group on the other, and contributing directly to the formation of the motor nerves. With this internal dorsal cell group a column of cells is connected (fig. 6), at any rate in point of position. They extend backwards over the region between the anterior and posterior ganglionic thickenings, and over the latter, to finally die away posterior to the ganglion. From this group of cells scattered fibres pass which are lost amid the body muscles. The latter are situated internal to the muscles of the appendages, and form masses closely applied to the sides of the gut (fig. 6). I often suspected the connection of some of these fibres with the gut itself, and am inclined to believe that a few, at any rate, form the nerve supply of the mesenteron. However that may be, they mainly constitute the motor supply of the body as opposed to the appendage muscles, and form a motor system comparable in its antero-posterior extension to the sensory system connected with the ventral lines of sense cells. I stated above that the ventral sensory system owed its antero-posterior extension to the fact that it is related to longitudinal lines of sense cells. Similarly, this dorsal diffuse motor system appears to me to owe its antero-posterior extension to the fact that it is connected with a group of muscles, the flexors and extensors of the body, which extend from end to end in almost unbroken series, and are not clearly divided into disconnected myomeres related to the successive body segments.

Summary.

1. The central nervous system of *Branchippus,* taken as a whole, consists of two cords of nervous tissue running the length of the body, and connected anterior to the mouth by the brain, in the region of the mouth by the circumoral ganglion, and posterior to the mouth by the transverse commissures which connect the various ganglionic enlargements.

2. Each nerve cord is comprised within a delicate nucleated sheath, and consists of a mass of fine nerve fibres invested more or less completely by nerve cells. The investment of nerve cells is most complete in the brain, and more or less wanting in the inter-ganglionic regions of the cords.

3. The ganglionic regions differ from the inter-ganglionic regions chiefly in the development of a very fine plexus on the ventral aspect of the cords. The dorsal portion of the cords in each ganglion is mainly a direct continuation of the inter-ganglionic fibres, and is, therefore, largely conducting in character. The ganglionic regions are also characterised by the large number of nerve cells.

4. The inter-ganglionic and ganglionic regions are not sharply distinct from one another. Nerve cells extend from the latter to a considerable distance along the former, and a plexiform arrangement of the fibres is not wholly wanting in the inter-ganglionic regions.

5. The nerve cells have the following connections :—

(*a*) They send their processes wholly into the plexus. These cells occur mainly in the brain and pre-œsophageal cords. They give off one or several processes into the central plexus. In fig. 3 we have a section through a cord in the pre-œsophageal region, and it will be seen that the cells have a rounded external surface, and give off numerous processes into the central plexus. Where the cell layer thickens, however, those most removed from the plexus fuse, as it were, all their processes into one, and thereby become unipolar cells with one thick process which ultimately breaks up in the plexus.

(*b*) They give off an axis-cylinder filament to a peripheral nerve on the one side, while on the other side they are connected with the central plexus, either by branching filaments, or by a single process which breaks up into that structure. Such cells appear to lie on the course of afferent fibres. Cells belonging to this group are, in many cases, pyramidal in shape, and give off from the base of the pyramid several processes to the skin, while from the apex of the pyramid only one process passes to the central plexus. Such cells act as "condensing centres" for centripetal impulses.

(*c*) They give off a peripheral axis-cylinder process to end in a muscle, while from the principal process, or from the cell itself other finer processes arise which end in the central plexus. Such cells are disposed dorsally in the central nervous system, and are connected with the outflow of efferent fibres.

(*d*) Pyramidal cells giving off on the one side a single fibre to the posterior commissure, while from the other side filaments pass into the central plexus.

6. The distribution of the elements in a typical ganglion is as follows :—

(*a*) On the ventral surface of the ganglion is a group of sensory ganglion cells, the fibres from which are connected with a line of sense cells on the ridges bounding the mid-ventral groove, and which form an almost continuous linear series exaggerated beneath each ganglion. These two lines of sense cells are a backward extension of the folded sense ring which encloses the mouth, and they meet just posterior to the mouth, where the otherwise shallow ventral groove narrows and deepens to form a sense pit.

(*b*) On the internal dorsal angle of the cords is a group of cells, from which are derived the motor fibres to the body muscles. These, like cell group (*a*), extend over both the anterior and posterior portions of the ganglion, and for some distance along the inter-ganglionic cords.

(*c*) On the internal, and external dorsal angles of the *anterior* half of the ganglion are two cell groups which are connected with the fibres of the anterior pair of nerves passing to the appendage muscles.

(*d*) On the external angle of the *posterior* half of the ganglion is a group of cells which give origin to the fibres of the short ventral ramus of the posterior nerves. Similar cells lie scattered on the course of the fibres of the longer dorsal ramus. These cells are connected with afferent fibres.

(*e*) On the internal angle of the *posterior* half of the ganglion is a group of cells from which the fibres of the posterior commissure arise.

The anterior and posterior halves of the ganglion present the following striking structural differences :—

1. The anterior commissure is closely connected with the skin. The posterior commissure arches freely above the skin.

2. The anterior commissure does not lie stretched between two cell groups. Its fibres mainly plunge directly into the "Punkt" substance, and many of them continue as a well-defined bundle across that structure to pass out in the anterior nerves. The posterior commissure lies stretched between two cell groups (group *e*.)

3. A large number of the fibres of the anterior commissure continue as a well-defined bundle across the central plexus, to form part of the anterior nerves. Or, in other words, a considerable number of the fibres of the anterior nerves directly decussate. The fibres of the posterior nerve do not decussate.

The identification which has been made above of certain elements as the afferent and efferent mechanisms of the nervous system of *Branchippus* finds further support if we turn to the structure of the circumoral ganglion, or ganglion of the stomodæum and second pair of antennæ. A complete description of this ganglion would lengthen this communication unduly, and, moreover, would be mainly of morphological interest. The facts which lead to the identification of the motor and sensory elements may, however, be briefly set down.

The circumoral ganglion consists of a double ring of nervous matter enclosing the œsophagus and uniting the nerve cords. The double ring is displaced so that it lies at a considerable angle with the horizontal plane of the body, this displacement being due to the very great hypertrophy of the upper lip and the continuation of the œsophagus as a horizontal and posteriorly directed tube which ends posteriorly in the mouth. The double ring is especially developed posterior to the œsophagus, where it lies stretched as a double commissure between a ganglionic enlargement on each nerve cord. In this, the commissural portion of the ring, the outer part runs across from nerve cord to nerve cord, as a bundle of regularly arranged parallel fibres, resembling the commissures of the typical ganglion. The fibres of the commissural portion of the inner ring also run for the most part regularly, but still a plexiform arrangement is very obvious. This inner ring is very closely connected with the sensory surfaces of the mouth, and it also shades off into a plexus of filaments connected with the epithelium lining the œsophagus. In point of fact, it may be very accurately described as a local hypertrophy or condensation of this œsophageal sensory nerve plexus. The outer ring, on the other hand, is connected with the innervation of the well-developed muscles of this region, and may similarly be described as a local development of a nerve-plexus connected with the musculature of the œsophagus. Having thus established the fact that the inner ring is sensory and the outer motor, can we proceed a step further and identify the two rings with the two parts, anterior and posterior, of the typical ganglion? The connections of the commissural portions, that is, those thicker portions which lie on the posterior surface of the œsophagus stretched between the ganglionic enlargements on each nerve cord, enable us to do this with certainty. The anterior and posterior commissures of the typical ganglion present, as we have seen, certain well-defined structural characters. The anterior commissure, unlike the posterior commissure, does not lie stretched between two cell groups. On the contrary, its fibres plunge directly into the ganglionic plexus. The commissural portion of the external ring of the circumoral ganglion presents this feature. On the other hand, the posterior commissure of the typical ganglion does lie stretched between two cell groups, and a similar connection characterizes the commissural portion of the inner ring of the circumoral ganglion. Thus the outer motor ring of the circumoral ganglion presents the same structural features as the anterior portion of the typical ganglion, and a similar structural agreement is found between the inner sensory ring and the posterior portion.

If we turn to the nerves arising from the circumoral ganglion further confirmatory evidence is obtained. The circumoral ganglion gives origin to the nerves of the second pair of appendages, the second antennæ. Two nerves pass to each second antenna, and they arise from the cords a short distance anterior to the ganglion. CLAUS,* in his account of the anatomy of *Branchippus stagnalis*, describes these nerves, and traces the anterior nerve on each side to the muscles of the second antennæ, and the posterior nerve to the sense cells of those organs, and I am able to confirm him in this respect. Tracing these two nerves centrally we find that the motor pair are connected with the motor, or external, commissure, in a way precisely similar to the direct connection which we have seen to exist between the anterior commissure and anterior nerves of the typical ganglion. Similarly there is evidence that the fibres of the posterior or sensory nerves to the second antennæ are connected with those portions of the ganglionic enlargements of each cord which correspond in structure to the posterior swellings of the typical ganglion, and which are placed in connection by the inner sensory commissure.

PART II.—THE POST-ŒSOPHAGEAL NERVE CORD OF *Astacus fluviatilis*.

The abdominal region of the central nervous system of *Astacus* contains six ganglia, related respectively to the six metameres into which the abdomen is divided. The

* C. CLAUS, 'Zur Kenntniss d. Baues u. d. Entwickel. von *Branchippus stagnalis* u. *Apus cancriformis*,' Göttingen, 1873.

first five of these ganglia differ from one another only in certain small details, and a description of one will serve as a description of the whole.

The *Second Abdominal Ganglion* forms a marked enlargement on the cord, the bulging being most prominent ventrally. There arise from it two pairs of nerves which I propose to distinguish respectively as the anterior and posterior nerve pairs. From the external dorsal aspect of the cord just posterior to the ganglion, a nerve arises on each side, thus forming a third pair to be distinguished as the posterior dorsal nerves.

Distribution and Character of the Nerves.—The *anterior pair* pass directly outwards beneath the great flexor muscles of the abdomen (fig. 9). Their point of origin is not only more ventral than that of the other nerves, but they also pursue a more ventral course. They run outwards almost at right angles to the longitudinal axis of the body, in the groove formed by that thickened portion of the sternal carapace which extends transversely under the ganglion, and between the bases of the second pair of abdominal appendages. Immediately anterior to these nerves is a vertical slip of muscle passing down from the great flexors of the abdomen to be inserted into the thickened carapace (fig. 9*a*). Very shortly after leaving the ganglion each nerve divides into two branches, which, however, continue in the same sheath for some distance. They separate from each other just before the appendage is reached (fig. 9). The posterior and smaller then turns downwards into the appendage, the anterior and slightly larger divides into three main branches on the anterior border of the base of the appendage. These again divide into smaller branches which are distributed to the appendage muscles, pleuron, and dorsal skin. The posterior branch is distributed to the comparatively small muscles which lie within the terminal part of the appendage, but by far the greater number of its fibres pass to the skin which, in the males, is extremely sensitive, the first and second pairs of abdominal appendages being modified to form copulatory organs. On their course the anterior nerves give off a few fine branches to the sternal skin.

Fibres.—The anterior nerves are composed of two markedly different classes of fibres (figs. 11 and 13).

(1.) Large bold fibres with nucleated sheaths, and

(2.) Fine filaments.

The large fibres may be again divided into (*a*) large fibres with thin sheaths, (*b*) small fibres with thick sheaths. In a section through the nerve (fig. 11), it will be seen that these different classes of fibres are segregated into distinct bundles. Each of the large fibres is bounded by a distinct nucleated sheath, which, as was pointed out by KRIEGER,* encloses a substance of such extreme fluidity, that under the influence of preserving agents its shrinks into small clots here and there in the course of the fibre. There is no trace of a sheath resembling the medullary sheath

* KRIEGER, "Centralnervensyst. d. Flusskrebses," 'Zeits. f. wiss. Zool.,' vol. 33.

of Vertebrate nerve fibres, either in preparations treated with osmic acid, or in those stained by WEIGERT'S method.

In tracing the anterior nerves into the ganglion a curious point is noticed, namely, that the transverse sectional area of the whole nerve on each side is much reduced, thus forming a narrow neck just before the nerve plunges into the ganglion. If the fresh nerve is examined under the microscope, or if individual fibres are carefully followed in a series of sections through this part, the sudden increase in the bulk of the nerve which takes place a fraction of a millimetre from the ganglion, is found, as has already been shown by HAECKEL,* to be due to the fact that the large fibres there divide into large and medium-sized fibres (fig. 12). In the example figured it will be seen that while the smaller branch is conspicuously smaller than the nerve fibre before the branching, the large branch is of much the same size.

Both branches of each anterior nerve contain fibres of each of the two classes, as will be seen on reference to fig. 11.

The *posterior ventral nerves* arise directly from the ganglion posterior to, and slightly above the origin of the anterior nerves. Instead, however, of passing outwards at right angles with the cord, and at a level anterior to the appendages, they trend outwards and backwards (figs. 9 and 10), running on the ventral surface of the great flexor muscles to the region immediately posterior to the attachment of the appendages. Their position in this part of their course is not so ventral as that of the anterior nerves. They lie at a level between the slips of the flexor muscles which pass to the sternum in each segment and the main mass of those organs. Each nerve, shortly after leaving the ganglion, divides into two branches which run in the same sheath for some distance. The anterior and smaller branch separates from the main trunk of the nerve where the latter curves abruptly round the belly of the flexor muscles to pass dorsalwards. It then turns upwards and outwards, to run along the infolding of the carapace, which forms the joint between abdominal segments 2 and 3, and is lost in the extensor muscles (figs. 10, 10*a*, 10*b*). The main trunk of the nerve passes sharply backwards along the outer surface of the belly of the flexor muscles and appears on the dorsal surface of those muscles about the middle of the *third* abdominal segment. It gives off the following branches :—

(*a*) To a thin sheet of the external extensor muscles which spreads out into the pleuron of the third segment, and to the dorsal skin in that region.

(*b*) Branches which pass above and end in the external extensor muscles, but also give off fibres to the dorsal skin.

(*c*) Branches which pass beneath the external extensors to end in the coiled internal extensors.

The extensor muscles consist of four distinct bands situated on each side of the

* HAECKEL, "Ueber d. Gewebe des Flusskrebses," 'MÜLLER'S Archiv,' 1857, Taf. XVIII., figs. 2 and 8. *Cf.* also KRIEGER, *loc. cit.*, fig. $9n^3$.

mid-dorsal line. The two median bands, or internal extensors, as I have called them, are coiled on themselves so as to form roughly a spiral of muscle; the external extensors, on the contrary, are flat band-like muscles with slips passing off to be inserted into the tergum in each body segment (fig. 29).

The posterior ventral nerves of the second abdominal ganglion, therefore, are distributed to the extensor system of muscles in the posterior two-thirds of the third abdominal segment, and the anterior third of the fourth segment. Professor CLAUS* describes a similar distribution of the nerves to the body muscles in the abdominal region of Nebalia.

The different branches when they reach the extensor muscles divide continuously, forming horizontal fan-like tufts of fibres, thus forming a plexus which spreads through a considerable length of the muscles.

The posterior ventral nerves are composed of two sizes of fibres like the anterior pair, but the small fibres form only a small part of each nerve (fig. 14).

The *dorsal nerves* are of extraordinary interest. They spring from the dorso-lateral portions of the cord just posterior to the ganglion (fig. 16), and turning backwards are distributed to the great flexor muscles (fig. 26).

Each of the dorsal nerves near its origin, and before any branching has taken place, is composed of only a few, generally ten, very large tubular fibres, about 30 to 60 μ in diameter.

In order to adequately realize the size of these fibres, it should be remembered that they have only a thin sheath. The dimensions given above should therefore be compared with those of the axis cylinders of vertebrate medullated fibres rather than with the whole fibre. Each fibre is distributed to a relatively enormous mass of muscle by a process of continuous branching. No small fibres occur in the main nerve, but there is usually a small bundle composed wholly of a few of the small thick sheathed class of tubular fibres (fig. 15) which leaves the main trunk immediately after its exit from the cord and curves abruptly ventralwards. I have not followed it further.

The fibres when they enter the cord form ascending and descending columns, seven of the ten fibres passing upwards to the second abdominal ganglion, and three passing downwards to the third ganglion. In other words, the dorsal nerves of the second ganglion, though belonging mainly to that ganglion, yet derive part of their elements from the ganglion next below.

Like the posterior ventral nerves the dorsal nerves branch very extensively and irregularly, and pass to a part of the flexor muscles which lies mainly in the third abdominal segment.

We thus see that the body muscles, both flexors and extensors, have been displaced posteriorly, the relation of the second abdominal ganglion to the second pair of abdominal appendages affording us a fixed point for reference. And this displacement has taken place to such an extent that the main branch of the posterior ventral

* CLAUS, "Ueber d. Organismus der Nebaliden," 'Arbeit. Wien,' vol. 8, 1889.

nerves of the second abdominal ganglion courses on the dorsal surface at the junction of the *third and fourth segments* on its way to the extensor muscles (figs. 10A and 10B).

The same posterior displacement of the muscles is shown when we examine the nerves of the remaining abdominal ganglia. In connection with the general question of metamerism, it is interesting to notice that the very definite blood supply of these muscles does not appear to have suffered a similar displacement. The dorsal aorta gives off at about the middle of each segment two pairs of arteries, one on each side to the extensor muscles, and one passing ventrally on each side of the flexor muscles.*

Motor and sensory fibres.—Before turning to the ganglion itself it will be advisable to discuss the question of the identification of motor and sensory fibres in the nerves.

Evidence derived from the distribution of the different classes of fibres.—The chief tactile organs possessed by *Astacus* are long hair-like filaments, each composed of a special expansion of the general cuticle jointed to the carapace, and containing a filamentous process of an ectoderm cell in its axis. These lie mainly on the appendages, but also occur on the edges of the pleura, the telson, and the posterior edge of the tergum in each segment. The general surface elsewhere is covered by a thick and, for the most part, hard lamellated horny cuticle, which in sections is seen to be traversed by comparatively infrequent delicate pores in which fine processes of certain elongated ectoderm cells lie. These are especially well seen in sections through the skin near the anus (fig. 17). The tergal surface, where the carapace is especially thick, is relatively insensitive, while the swimmerets, on the contrary, with their numerous tactile hairs, are especially sensitive. In correspondence with this we find that the nerves supplying the swimmerets contain a very large number of fine fibres, while the nerves to the tergal surface contain relatively fewer; and that the branch of the anterior nerve which passes *into* the appendage and to the small muscles therein contained contains relatively fewer large fibres than does the larger branch which innervates the larger muscles of the appendage (fig. 11). Further, the nerves passing to the telson, which contains no muscular elements, and to the sensitive region round the anus, are entirely composed of fine fibres. On the other hand, the nerves passing solely to the flexor muscles, that is, the posterior dorsal pair in each segment, contain only the large tubular type of fibres.

Evidence derived from direct experiment.—Seeing that the anterior nerves of the abdominal ganglia contain a considerably larger number of the fine nerves than do the posterior ventral nerves, I determined to try the relative effects of stimulation.

The abdominal cord was laid bare from the ventral surface, the operation requiring great care to avoid injuring the very delicate and superficial anterior nerves. The anterior and posterior nerves were then stimulated with an interrupted, or tetanizing current, and the following points noticed :—

* Compare also MILNE-EDWARDS' 'Histoire Nat. d. Crustacés,' Paris, 1834, vol. 1, Plate 7.

(1.) The anterior nerve of the left side was stimulated at a point about midway between the ganglion and the appendage. The effects were double, (*a*) flexure of the limb, and, (*b*) enormous reflex disturbance of the animal generally, every appendage being moved. In other words, the main effect of stimulating this nerve was to produce very great sensory disturbances.

(2.) The posterior ventral nerve on the same side was stimulated with the same strength of current, and the only effect was a faint sensory disturbance and feeble movement of the second abdominal appendage of the same side.

The difference between the central effects produced by stimulating these nerves is very obvious when the animal is exhausted. Then, when stimulation of the anterior nerve on one side will produce reflex movements of all the appendages, stimulation of the posterior nerves leads to no such result.

The movement of the appendage which resulted from stimulation of the posterior nerve I regarded as being due to reflex action, and to settle this point the following experiment was made :—

(3.) The posterior ventral nerve was cut and its peripheral end stimulated. No movement of the appendage resulted, but, on applying the electrodes to the central end, results occurred similar to those described under (2).

(4.) With respect to the posterior ventral nerves, MARSHALL* states that on stimulating the peripheral end of one of them (in the Lobster) no effect was produced. Hence he concluded that "the anterior nerve would seem to be mixed, but the posterior nerve purely sensory." This result was due to the fact that, in his experiments, the animal was fixed in such a position that it was impossible to observe any contraction of the extensor muscles. If, however, the animal be placed in such a position that the extensor muscles can be observed while the posterior nerve is being stimulated near the ganglion, and therefore on the ventral aspect of the body, a marked tetanus of the extensor muscles is found to follow stimulation.

(5.) The posterior dorsal nerves in the case of *Astacus* are so delicate and deep lying, and their unbranched free portion is so extremely short, that it is impossible to directly stimulate them without escape of the current into the muscles. The experiment was therefore carried out in the following manner :—The anterior and posterior ventral nerves were cut on both sides and in each segment of the abdomen. Thus only the posterior dorsal nerves were left intact. The nerve cord was then cut in the thoracic region and lifted on to the electrodes. On opening the circuit the abdomen was sharply flexed.

The facts both of dissection and stimulation thus lead to the conclusion that the anterior nerves are of mixed function, and contain both afferent and efferent fibres. But they mainly supply sensory surfaces. The posterior ventral nerves are also of mixed function, but they supply a relatively larger mass of muscles, and a much more

* MARSHALL, "Some Investigations on the Physiology of the Nervous System of the Lobster." 'Studies from Owens College, Manchester,' 1886.

insensitive region of skin. In correspondence with this difference between these two pairs of nerves, we find that the anterior nerves are relatively poor in the large tubular fibres, but contain a very great number of the fine fibres. The posterior ventral nerves, on the other hand, are relatively much richer in large tubular fibres.

The posterior dorsal pair differ from the anterior and posterior ventral nerves, in being solely efferent in function, and we find that they contain only the large tubular fibres.

We may thus, I think, conclude that the large tubular nerve fibres of *Astacus* are efferent, while the fine nerve fibres are afferent in function; and these two classes of fibres are not only sharply marked off from one another in point of size, but also the gulf between them is unbridged by intermediate forms within the limits of the somatic system.

Summary.—Three pairs of nerves arise from each of the first five abdominal ganglia:—

(1.) An anterior pair, which arise directly from the ganglion, and contain a large number of the fine, or afferent fibres, and comparatively few of the large, or efferent fibres. These supply the appendages with motor and sensory fibres, and also the skin of the sternum and pleura.

(2.) The posterior ventral nerves containing relatively more large fibres. These supply the dorsally placed extensor muscles and the dorsal skin in the third segment, or segment next following.

(3.) Posterior dorsal nerves which are purely motor and innervate the flexor muscles.

The General Relations and Structure of the Second Abdominal Ganglion.

Only a very general mention of the main features of the ganglion itself need be made, since KRIEGER has so fully dealt with them in his paper on the "Central-nervensystem des Flusskrebses" ('Zeit. f. Wiss. Zool.,' vol. 33, p. 527). The ganglia appear as "small knot-like swellings on an apparently single longitudinal commissure." Each ganglion is surrounded by a tough lamellated membrane, which is separated from the nerve substance by a loose reticulum, especially abundant on the ventral face of the ganglion. The spaces in this connective tissue reticulum are large and are filled with blood. We thus have two distinct sheaths, a point not sufficiently insisted on by KRIEGER (fig. 18), of which the inner one is practically a system of blood spaces bridged by connective tissue, and is only slightly developed in the inter-ganglionic regions (fig. 23).

Owing to the continuity of the investing membrane, the nerve cord at first sight appears to be single, but the nervous elements in reality form two perfectly distinct cords which are united only in each ganglion by a thick transverse bridge. In the inter-ganglionic regions the two halves are separated by a median vertical lamella of connective tissue. As they enter a ganglion either above or below they diverge from one another, and the inner sheath at the same time becomes thicker. There is thus formed at each end of the ganglion a vertical cleft-like space between the lateral masses of nervous tissue, and filled by the inner sheath of the cord; and the anterior cleft, or *anterior fissure*, is separated from the *posterior fissure* by the transverse bridge of nervous tissue which was spoken of above.

The outer sheath.—This sheath is composed of one or more lamellæ, each of which is built up of fine fibrils which appear to be bound into bundles (fig. 19). These may either run parallel to one another, or interlace. The lamellæ appear to be entirely free from cellular elements in their substance, but on the surface of the sheath flattened plate-like cells occur (figs. 19 and 20), with large, flattened, deeply-staining nuclei.

Quite on the inner face of this sheath these cells are more numerous and their plate-like extensions often overlap one another (fig. 19). Supporting filaments are seen to arise from the outer sheath which are continuous with the inner sheath (fig. 20).

The inner sheath appears in sections as a coarse reticulum, largely cellular in nature. It closely resembles in structure the tissue surrounding the sternal artery, and lying beneath and about the nerve cord. The inner sheath is essentially a blood-containing investment, and into its spaces the arteries supplying the ganglion open. In the inter-ganglionic regions of the cord this sheath is very thin. The branched cells of the inner sheath are continuous, on the one hand, with the flattened cells on the inner face of the outer sheath; and on the other, with the variously modified cells which form the intimate supporting structure of the nervous elements.

The *supporting tissue of the nervous structures* appears to be mostly, if not entirely, cellular in character, and is best seen by teasing out the fibres of the inter-ganglionic commissures where they diverge into bundles on entering the ganglion. If these have been preserved with FLEMMING's fluid mixed with an equal volume of ·5 per cent. solution of osmic acid, and afterwards stained with hæmatoxylin, the individual bundles will be seen to be covered by an imperfect sheath of flattened cells with large, oval, deeply-staining nuclei (fig. 21). Cells of this type represent the imperfect attempts at endothelium building found so widely in *Astacus*. They occur, only of much larger individual size, lining certain of the large body spaces, and similar cells have been already noticed in connection with the outer sheath of the ganglion. Within the substance of the ganglion, where the nerve fibres branch and become much finer, similar supporting cells occur. Each consists of a small cell body, from which arise short plate-like processes which branch into the wildest tangle of exceedingly delicate filaments (fig. 22), thus recalling the neuroglia cells of the Mammalia. There is thus formed a supporting tissue composed, like the neuroglia of Vertebrates, of the delicate processes of much modified cells. Both plates and filaments are of an optically structureless and non-staining character, very different from the finely granular and staining cell substance of the nerve cells. Their nuclei also stain more deeply than the nerve cell nuclei, and are not so coarsely granular.

Blood supply.—The ganglion is supplied with blood by four arteries which arise by a short common stem, which springs from the posterior sternal artery, immediately under the middle of the ganglion. After penetrating the external sheath, two of the arteries curve round the sides of the ganglion between the roots of the anterior and posterior nerves, and, running in the inner sheath, finally end in the dorsal portion of an enlargement of that sheath on the lateral face of the nervous tissue, and above and between the two nerve roots. These may be called the *lateral arteries*. The other two arteries run respectively anteriorly and posteriorly for a short distance, and then make their way upwards through the anterior and posterior fissures to the dorsal surface, where they open into a dorsal median thickening of the inner sheath. They may be called the *anterior and posterior arteries*.

Thus, in the intact ganglion, there must be a stream of blood flowing through the interstices of the inner sheath from the dorsal to the ventral side, where it drains into a large ventral sinus situated in the inner sheath, and incompletely divided into four longitudinal sinuses by septa. The blood finally leaves the ganglion by apertures placed in the mid-ventral line at the posterior end of the ganglion, and leading from the ventral sinus of the ganglion into the ventral abdominal sinus. The arrangements for the nutrition of the large nerve cells which occupy the ventral, and, to a less extent, the lateral surfaces of the nervous tissue of the ganglion, are most interesting. These cells are of the unipolar, pear-shaped type, and are quite removed from the dense nerve substance of the ganglion. Each is covered by a delicate cellular sheath, and this alone separates the cell substance from the blood; for they may be said to hang in bundles suspended by their processes, and steadied by the reticulum of the inner sheath, in blood spaces of that tissue. Between them, in the mid-ventral line, and below them, in the posterior region of the ganglion, are the venous sinuses mentioned above.

The mass of the ganglion is composed of a fibrous reticulum, coarse in some places, fine in others, and the fibres in the finer reticulum appear to touch one another, so that blood spaces are conspicuous by their absence. In the case of nerves and of commissures the same fact strikes one, whether they are viewed in the fresh condition, or examined by means of sections—the sheathings of the nerve fibres are contiguous with one another, and, at first sight, no provision appears to have been made for their nutrition. This may, I think, explain the prevalence of "tubular fibres" in the central nervous system and peripheral nerves of *Astacus*. Each of these fibres in section appears as a tubular nucleated sheath, and little more. The contents of the tube, or what corresponds to the axis cylinder of the nerve fibres of Vertebrates, have shrunk into small clots gathered here and there at long intervals on the course of the fibre. In other words, the contents of such a tubular fibre are exceedingly fluid. If they are examined in the fresh state bubbles of air may often be seen, which may be made to move about in the almost fluid contents, as though one were dealing with a fine tube filled with fluid. If these fibres are isolated and watched, their contents will, as was pointed out by KRIEGER,* be seen to undergo a change comparable with *rigor mortis*. Clotting takes place, the clot appearing in the form of granules, which outline delicate fibrils, which I regard with KRIEGER as the true axis-cylinder fibrils. These, I take it, are suspended in life in an extremely fluid substance, protoplasm or plasma, by the aid of which the transportation of nutritive material or the removal of waste matters can be managed through considerable lengths of these tubular fibres. It is therefore possible that each efferent fibre is the morphological equivalent of a considerable number of afferent fibres, each one of the latter being, without doubt, a single axis cylinder.

Be this as it may, it is, at any rate, abundantly clear that the disposition of the nerve cells on the surface of the dense nervous tissue of the ganglion, and their relation to the blood streams, lends no support to the idea that they are nourished, even in part, by their processes. The distinction of the processes of nerve cells into "nutritive processes" and true nerve or axis-cylinder processes has been advocated by NANSEN† for the Crustacea, and by GOLGI for Vertebrates. In the latter case the distinction is based upon histological facts which appear to me to be adequately explained by the effect of the shrinkage of the tissue in occluding the lymph lacunæ which, we must suppose, surround the nerve cells of the central nervous system and their processes during life.

Arrangement of the Nervous Elements of the Ganglion.

These consist of cells, fibres, and fibrillar plexus. The relation of the cells and fibrous elements is the same as that which is found in the nerve cord of *Branchippus* where the former lie wholly on the surface of the latter. In the cord of *Astacus*, however, cleft-like spaces filled with the inner or blood-containing sheath penetrate the nerve substance, and the cells to a certain extent occupy these (fig. 34, *c*). The nervous tissue of the ganglion is composed of fibres and fibrillar plexus and nerve cells. The fibres are of the same tubular character as those already noticed in the nerves. They run in the ganglion for the most part in longitudinal bundles, which, penetrating the ganglionic plexus, divide it up into regions. Many of these fibres, especially in certain of the bundles, run straight through the ganglion without effecting connection with its elements. The other tubular fibres in the ganglion are either commissural between the lateral halves, or derived from the large unipolar cells which occur in the ventral cell-plate mentioned above.

In passing up the cord towards the brain one finds, as in Vertebrates, that the number of fibres passing straight through the ganglia to regions below continuously increases. Such fibres are limited to the more dorsal portion of the cord, and in the

* *Loc. cit.*

† NANSEN, 'Bergen's Mus. Aarsberet,' 1886.

upper portion of the thoracic cord they may be readily separated by simple dissection from the ventral bundles of fibres which pass to and through the ganglionic substance. This is well seen in fig. 24, which is a drawing of the ganglion of the chelæ, as seen from the ventral surface.

The ganglionic plexus is separated into regions distinguished both by the size of the fibres forming the plexus and the complexity of their arrangement. We may distinguish two grades:—

(*a*) A coarser plexus, the elements of which, though much smaller than the tubular fibres of the inter-ganglionic cord or nerves, yet show the marked tubular appearance (fig. 36).

(*b*) A fine plexus, comparable in the extreme tenuity of its elements to that of the nerve-cord of *Branchippus* (fig. 32). The fine plexus and the coarse plexus are, respectively, ventral and dorsal, and related, the former to the fine nerve fibres, and the latter to the large nerve fibres. The fine plexus may be said generally to form an irregular plate on the under surface of the fibrous portion of the ganglion.

The large tubular nerve fibres pass at once to the coarse plexus, and we may regard the latter structure as being formed by their branching. I do not, however, regard the coarse plexus as constituting the final ending of the large nerve fibres, but merely as the place where those fibres subdivide before passing to various regions of the more ventral fine plexus. The fine nerve fibres, on the contrary, run in bundles directly to the fine plexus (figs. 32 and 34). The fine plexus, as will be seen later, is not a homogeneous structure, but presents differences in density in its different parts.

The Internal Connections of the Anterior Pair of Nerves.

Each of the anterior nerves, as it enters the ganglion, divides into a dorsal and a ventral root, each of which contains both large and small fibres (fig. 35). In each root the large and small fibres form quite distinct bundles, and in the section through the trunk of this nerve, figured in fig. 13, it will be seen that a short distance from the ganglion the fine and large fibres are still arranged in distinct bundles.

The *dorsal root* passes to a distinct mass of plexus which lies in the outer, or more lateral, part of its own half of the ganglion in the anterior region, at the level of the entry of the anterior nerve, and immediately above the ventral root (fig. 33, *d, c*). This mass of plexus is very definitely divided into a small rounded and ventral mass of fine plexus, and a dorsal mass of coarse plexus, which extends to the lateral surface of the ganglion above the entering nerve. (Fig. 33, *d, c*. The dotted line bifurcates, and ends respectively in the coarse and in the fine plexus.) The fine fibres of the dorsal root pass to the ventral fine plexus, the large fibres to the dorsal coarse plexus.

I regard this root as being of mixed function, motor and sensory, and its centre as being composed of two parts: (1) a dorsal coarser portion, formed by the first branching of the large efferent fibres; and (2) a ventral, very much finer portion, to which the fine afferent fibres pass directly.

Connection with Cells.—By far the greater number of the fibres, both large and small, pass directly to break up in the fibrous reticulum. Where the large fibres arch round the ventral ball of "punkt" substance on their way to their own coarser reticulum, I found several distinct T-shaped junctions. One limb of the T could be traced to the most external of the ventral unipolar cells in the region of the entering nerve. These form a distinct group of cells of fairly uniform size, and averaging from 30 to 40 μ in the shortest axis.

In addition to these, there are cells situated between the bundles of entering nerve fibres, where they diverge. These are much smaller. Each gives off one process which proceeds to strike the entering bundles at right angles. I think I may say positively that nerve fibres do not end in these cells, though their processes are connected by T-shaped junctions with certain of those fibres—probably the fine ones (fig. 35, *a*, *a′*).

In longitudinal vertical sections it is seen that these cells lie chiefly in two masses anterior and posterior to the entering nerve, and that their fine processes pass in two main bundles to join the fine fibres before they break up into the "punkt" substance (fig. 35, *a*, *a′*). There is a third very distinct group of cells related to the dorsal root, and lying on the dorsal side of the entering nerve, and on the lateral surface of the coarse nerve network (fig. 36). Each cell receives an axis-cylinder process, and gives off from its internal face processes into the plexus of the ganglion. The small tubular fibres, with thick neurilemma, pass to these cells. This cell group is continuous with the more dorsal cells of the lateral extension of the ventral plate of cells between the point of exit of the anterior and posterior ventral nerve, and, from them, fine tubular processes pass, which curve round as dorsal arcuate fibres (fig. 36).

The *ventral root* also consists of large tubular and fine fibres. It passes in beneath the centre for the dorsal root, and the fine fibres break up in a large mass of fine plexus in the most ventral part of the ganglion near the middle line (fig. 33, *v.c.*). The large fibres pass up anterior to the fine fibres to break up in a mass of coarse plexus dorsal and anterior to the above-mentioned fine plexus (the region it will occupy is indicated by the upper limb of the dotted line in the figure). This root, therefore, also contains motor and sensory elements connected respectively with a coarse and fine plexus.

Cells.—The large fibres appear to be connected by short branches given off at right angles, with a group of the ventral unipolar cells immediately underlying them, just after their entrance into the ganglion (fig. 35, *b*). The fine fibres are connected with the group of small nerve cells lying between the divergent roots (fig. 35, *a*, *a′*).

To sum up the internal connections of the anterior pair of nerves, we see that each nerve divides into two parts on entering the ganglion. Each part, or root, is composed of large tubular and fine fibres which pass respectively to a coarse and fine ganglionic plexus. There are thus two distinct centres related to the two roots. These centres are connected with one another by zones of plexus, and by unbranched fibres in such a way that the coarse plexus of the external centre (that of the dorsal root) is connected with the coarse plexus of the more median centres, and, similarly, the fine plexus of the external centre is connected with the fine plexus of the median centre. Further, the centres of the two sides of the ganglion are placed in communication with each other by two commissures, one of which consists of the finest fibrous elements, and stretches between the median masses of fine plexus. The other consists of coarser elements and connects the median coarse plexus of the one side with that of the other. The completely dual nature of the internal connections of the anterior pair of nerves, that is, the nerves to the appendages, I take to be of especial significance. In the thoracic region, where the nerves to the appendages are large and predominate, the dual nature of their internal connections is even more strikingly shown. In the thoracic region, also, the two roots of the appendage nerves, instead of being fused in the neighbourhood of the ganglion, and only diverging within its sheath, form two long roots which remain quite distinct as far as the second joint, *i.e.*, a considerable distance into each appendage (fig. 25).

These two roots differ markedly in size, and, as a result of experiments carried out on the Lobster, MARSHALL (*loc. cit.*) states that (1) "the small nerve contains motor fibres which supply the extensor muscles of the limb, and especially the divaricator muscle of the claw;" and (2) "the large nerve contains the motor fibres to the muscles which raise the limb and close the claw." Also the small nerve contains "afferent fibres which cause reflex contraction of the claw through the large nerve which supplies the occlusor muscle," while the large nerve contains "afferent fibres which cause opening of the claw by reflex action through the small nerve which alone supplies the divaricator muscle." These experimental results I have been able to substantiate in the case of the nerves to the chelæ of *Astacus*. I have further found that the small nerve passes to a median centre, the large nerve to an external centre in its ganglion.

In contradistinction to the posterior ventral and dorsal nerves the fibres of the anterior nerves do not appear to directly decussate in any case. RETZIUS failed to find any decussating fibres;* but, as has been pointed out, bilateral connection is made by fibres large or small between the various centres.

Concerning the cell connections of the fibres of the anterior nerves we find that:—

(1.) The large tubular efferent fibres are connected with large nerve cells.

(2.) The fine fibres, afferent in function, are connected with small nerve cells. The connection with the cells is, as RETZIUS (*loc. cit.*) has already shown, by lateral branches. The nerve cells, therefore, do not lie in the direct path of the nervous impulses to or from the ganglionic plexus. Exceptions to this appear, however, to occur in the case of the small tubular fibres with thick neurilemma.

* RETZIUS, 'Biologische Untersuchungen.' Stockholm, 1890.

Internal Connections of the Posterior Pair of Nerves.

The first and most striking facts in connection with the posterior nerves is that they do not pass to two distinct centres, and that a certain number of the fibres, as Retzius also found, do directly decussate.

On entering the ganglion the fine fibres of each nerve take up a position posterior to the large fibres, and form a well-defined single stream which passes to a single mass of fine plexus on the ventral surface and towards the median line (fig. 34, *f.pl.*). This centre, therefore, occupies the same relative position as the internal centre, or centre for the ventral root, of the anterior nerve. Sometimes the fine fibres enter the nerve tissue of the ganglion at a point higher up than the large fibres, and arch round to pass to the ventral-lying fine plexus. They may be said generally to take a more or less arched course through the nerve substance of the ganglion and to enter their centre from above. Certain of these fine fibres directly decussate and pass to the centre of the opposite side. This, however, does not always occur.

The large fibres form two sets, some ascend, and after passing for a short distance as external arcuate fibres, plunge into the nerve substance of the ganglion and either—

(*a*) Break up in a zone of coarse plexus lying at the junction of the upper and middle third of the ganglion; or

(*b*) They directly decussate, passing to a similar region on the opposite side (fig. 34, *a*).

The second stream of large fibres (fig. 34, *b′*) passes in more ventrally and anteriorly, and communicates with a cell group lying on the ventral surface of the ganglion and extending round the entrance of the posterior nerve (figs. 34 and 35, *b*). Some of the fibres, however, break up directly in a mass of plexus, lying anterior and external to the fine plexus related to the fine fibres of the posterior nerves.

We thus see that the fine fibres or sensory elements of each posterior nerve pass to a single centre, while the large fibres or motor elements are distributed to two regions of coarse plexus. I take it that we may correlate this dual character of the central connections of the motor elements with the fact that the nerve supplies two sets of muscles—the external and internal extensors, differing enormously in their general arrangement, and in the position of their fibres. At the same time these two masses of plexus are intimately connected by unbranched fibres and bridges of plexus.

Retzius (*loc. cit.*) has shown that a certain number of the fibres of the posterior nerves have no connection with the elements of the ganglion, but turn directly backwards to descend in the longitudinal commissure. A similar arrangement, as will be seen, obtains in the case of the posterior dorsal nerves. On the other hand, fibres have not been traced directly from the commissures to the anterior nerves.

Internal Connections of the Posterior Dorsal Nerves.

These, as will be remembered, arise from the dorsal and external surface of the inter-ganglionic cord, a variable but short distance posterior to the ganglion. As was pointed out before, they each consist of two parts derived respectively from the ganglion above and the ganglion below. This fact is only demonstrable by sections, since simple dissection merely reveals the fact that they arise a very short distance posterior to, but in very close connection with the second abdominal ganglion. I have examined these nerves in detail in the first five abdominal ganglia. Each nerve is composed of from ten to thirteen tubular fibres, which vary in size from 12 to 13 μ.

On entering the nerve-cord, or a little distance before entering it, each nerve divides into two unequally sized roots, of which the smaller, containing generally three fibres, passes down the inter-ganglionic commissure to the ganglion next below. It at first lies on the external dorsal angle of the cord, but soon makes its way obliquely over the external giant fibre* to a more median position, and then curves ventrally to run in the external region of the dorsal group of longitudinal fibres. These I propose to call the *descending root*. The remaining fibres, eight to ten in number, turn sharply upwards and form a column of fibres external to the external giant fibre. These form the *ascending root* (fig. 23).

Tracing the whole bundle in its upward course to the second ganglion, it is found to assume a more dorsal position until it overlies the external giant fibre. Almost before any indications of ganglionic structure have appeared in the cord, the most median and largest fibre (a, 35 μ) detaches itself from its fellows and passes obliquely forwards and inwards immediately under the internal giant fibre. It continues its course across the middle line to the opposite half of the ganglion, where it divides into two main branches. One is given off ventrally immediately after the decussation has been completed. It runs downwards and backwards, at first in the dorsal sulcus between the lateral halves of the cord in this region, and then plunging into the nerve substance ends in or rather forms the single process of one of the largest giant cells, situated in the external and anterior part of the posterior division of the ventral plate of nerve cells (fig. 33, a). It will thus be seen that the most internal fibres of each side, after decussating, each give off a branch which runs forwards for a considerable distance before passing to its cell.

The rest of the fibre, or the other branch, continues horizontally across, under the internal giant fibre of the opposite side, to finally break up in a small mass of dorsally situated plexus which overlies the nerve substance between the two giant fibres. This plexus is intimately related to a small group of small nerve cells on its dorsal surface.

Continuing anteriorly, a second fibre (b, 18 μ) next detaches itself from the bundle

* In each lateral half of the inter-ganglionic cord are two large giant fibres which are respectively external dorsal and internal dorsal. They lie completely dorsal to all the other fibres.

and runs inwards under the internal giant fibre, then curves downwards and decussates by the dorsal motor commissure, which is largely composed of the decussating motor fibres of the posterior pair of nerves (fig. 34, *c*). It breaks up in the dorsal coarse plexus of the opposite side.

Two fibres, one 18 μ (*c*) the other 15 μ (*d*), are the next to leave. They take different courses. The first arches close round the external giant fibre and runs inwards a short distance towards the median line. It then turns downwards and forwards, running in a sulcus or fissure between two columns of longitudinal fibres which I will call the internal dorsal and median dorsal columns (*cf.* later). It then appears to divide into two branches, of which one turns inwards towards the median line, and breaks up in the dorsal plexus of its own side, in the region corresponding to that of the opposite side in which fibre (*b*) is lost.

Fibre (*d*) leaves the bundle at the same time that fibre (*c*) does and curves *outwards* over the external giant fibre, then passes forwards and downwards on the external surface of the nerve tissue, and breaks up in the most lateral portion of the dorsal plexus of its own side, and at a level lying between the points of origin of the anterior and posterior nerves. It is the only fibre which passes laterally instead of mesially, and from its superficial and isolated course can be easily traced.

Two fibres (*e*, 12 μ, and *f*, 12 μ) leave next and turn inwards and downwards, to curve under the external giant fibre and pass to the same lateral-dorsal region as fibre (*d*).

The three last-mentioned fibres (*d*), (*e*), and (*f*) thus take the same course.

Two fibres (*g*, 20 μ, and *h*, 20 μ) alone remain, and they turn abruptly downwards and outwards to curve down ventrally between the entering anterior and posterior nerves, and end in two large unipolar cells of the ventral cell-plate on the same side corresponding in position to the cell of the opposite side in which fibre (*a*) ended. Each gives off a branch to the dorso-lateral plexus as it passes near it. They thus completely resemble fibre (*a*) in their connections, except in the fact that they do not decussate.

The following table summarizes the connections of the descending column of the posterior dorsal nerve on each side.

It will be seen that the fibres fall in three groups defined by distribution and size.

Group 1.—Three large fibres which break up in the coarse plexus on most dorsal aspect of the ganglion.

Fibre	*a*	decussates . . .	35 μ.
"	*g*	do not decussate .	20 μ.
"	*h*		20 μ.

Group 2.—Three fibres, of which one, the largest, arches above and others below the external giant fibre to pass to the lateral portion of the dorsal plexus.

Fibre *d* passes above external giant fibre 15 μ.
,, *e* } pass below external giant fibre . { 12 μ.
,, *f* } { 12 μ.

Group 3.—Two fibres which break up in the more lateral portion of the dorsal plexus.

Fibre *b* decussates . . . . 18 μ.
,, *c* does not decussate . 18 μ.

The table shows that there is a close agreement in size between fibres having the same connections.

The Motor System of Nerves.

When we consider together the central origin and mode of distribution of the motor fibres, we see that they present certain features of remarkable interest. Their relations are most clearly shown, because the peculiarities are most exaggerated in the case of the motor system of the flexor muscles just described.

The unit of the system is a large unipolar cell, characterised by the abundance and solidity of its cell substance, which is loaded with granules of a basophile nature. Like basophile granules generally, they colour more or less intensely with osmic vapour. The cell is enclosed in a nucleated sheath, and suspended by its process in the blood stream of the ganglion.

The single process from this cell runs for a considerable distance without giving off branches. The first branches leave the main process in the ganglion, and break up in the general plexus of that structure. These relations are very clearly shown in the figures illustrating RETZIUS's work (*loc. cit.*). The cell process then leaves the nerve cord in one or other of the nerves and, on its course to the muscle, it branches *into a great number of fibres which pass to a large mass of muscle fibres.* In the case of the nerves to the very large flexor muscles each myomere (fig. 26) may be innervated by as few as ten nerve fibres, which arise from the same number of nerve cells.

The fibres branch dichotomously, but one of the branches is smaller than the other, while the larger branch is equal in size to the fibre before the branching. This is shown at fig. 12, and, as it occurs in the more peripheral parts of the system, in HAECKEL's beautiful drawings (*loc. cit.*). By this method of branching *the transverse sectional area of the unit of the motor system continuously increases as one passes from the nerve cell to the final ending in the muscles.**

* These connections have been traced by RETZIUS (*loc. cit.*) with the aid of methylene blue; and by myself in sections and dissections.

The whole structure, which we may call the unit of the motor system, is enclosed in a continuous nucleated sheath which forms the capsule of the nerve cell, and the "tube" of the tubular process.

The substance of the processes is very different from the substance of the cell. The latter is solid and granular, the former is extremely transparent (compare HAECKEL, *loc. cit.*, figs. 6, 8, 10, 11, 12), and consists of two parts :—

(1.) Fine filaments running longitudinally; and suspended in

(2.) A more or less fluid plasm (KRIEGER, *loc. cit.*). The junction between cell substance and process substance is extremely abrupt. Similar tubular fibres enclosing filaments are described by SCHIEFFERDECKER and KOSSEL in *Petromyzon*,* and the facts at present at our disposal warrant the suggestion that the filaments are the structures which convey the nervous impulses.

The unit of the motor system of *Astacus* thus consists of the following parts :—

(1.) A single nerve cell which, from its histological characters, and relation to the blood stream, appears to be a highly metabolic structure; and which is removed by a considerable length of nerve from the direct track of the nervous impulses.

(2.) A single nerve process from this cell which branches in a characteristic fashion, and consists of a number of filaments, presumably processes of the cell, which are suspended in a plasma.

(3.) The branches of this process, and, therefore, of the single nerve cell. These are very numerous, are distributed to the plexus of the ganglion and to a very large mass of muscle fibres.

If the prevailing conception of the trophic functions of the central nervous system is correct, we must regard this single nerve cell as the trophic centre for this large mass of muscle fibres.

Though at first sight the motor system of the flexor muscles, consisting, as it does, in each metamere of only a few fibres and cells, seems a simple one, yet a consideration of the arrangement of the flexors themselves shows that we must regard it as a simple contrivance arranged so as to secure a complex result. Figs. 26, 27, and 28 represent dissections of the flexor muscles, and it is there seen that each myomere extends over three metameres. The contraction of the muscles produces flexure of the abdomen, and, if we define the terms "origin" and "insertion" to mean respectively the fixed points from which the muscle pulls and the point of attachment which is moved by the contraction, then we may say that each myomere has three origins and one insertion. Taking the myomere, the main mass of which lies in the fourth abdominal segment, for description, its most anterior origin is from the transverse thickening of the sternum in the second abdominal segment, and it is inserted into the anterior edge of the transverse thickening of the sternum in the fifth abdominal segment (figs. 9, 26, and 28). From the anterior origin to the insertion the muscle runs as a mass of tissue, with a great thickening in the fourth abdominal segment, and with an S-shaped curl, arranged

* SCHIEFFERDECKER u. KOSSEL, 'Gewebelehre d. Menschlichen Körpers,' figs. 129 and 130.

in such a way that the fibres in the thickest part of the muscle run almost transversely to the long axis of the animal (figs. 10A, 10B, 26, and 28). The other two origins are situated in the fourth abdominal segment and serve to steady the muscle. They are (*a*) a tendinous attachment to the similar muscle of the opposite side by means of a ventral sheet of fibres springing from the most superficial aspects of the belly of the myomere (fig. 28), and (*b*) an origin from the pleuron of the same side by a dorsal sheet of fibres (figs. 26, 27, and 28). The ventral sheets of fibres are best developed in connection with the myomeres of the second and fifth abdominal segments.

It is thus clear that we are dealing with a muscular machine of very great complexity, and one the proper working of which must depend upon the coordination of the contraction waves in different regions of the large mass of tissue in respect to the time when they occur.

The mode of innervation of the electric apparatus of the Torpedo helps us to form a first mental conception of how this correlation is accomplished. In the electric organ the correlation is the simplest possible, namely, the discharge of the individual batteries at the same instant. This, as WAGNER has pointed out, is accomplished by the agreement in the length which intervenes between the first branching of the fibre and the final end of each filament. In the case of the flexor muscles of *Astacus* the correlation is a threefold one—

(1.) A sequence in the time of contraction of the large and distinct masses of fibres which in sections are seen to compose each myomere;

(2.) The contraction at the same instant of time of the fibres of any one mass, and

(3.) The serial contraction of the separate myomeres from before backwards.

In case (2) the simultaneous contraction of a large number of fibres receives the simplest explanation, if we suppose that they are innervated by one unit of the motor system, and in this connection I would again draw attention to the constant relation which obtains between the size of the fibres and their morphological relations, and that the distance along the nerve fibre from the central origin of the impulse to where it breaks on the individual muscle fibres is the same. In other words, the explanation would exactly resemble that put forward by WAGNER to account for the simultaneous discharge of the batteries of the electric organ. The sequence in the time of contraction of the various fibre masses of the myomere would receive the simplest explanation if we referred it to *differences* in the length of fibre interposed, in the case of each unit of the motor system, between the central origin of the impulses and the muscle fibres.

Lastly, the sequence in the contraction of the different myomeres we might regard as a phenomenon of central origin and to be referred to the time occupied in the transmission of the disturbance from the higher centres down the abdominal nerve cord.

It will be remembered that in describing the motor arrangements of a typical ganglion of *Branchippus* allusion was made to a diffuse motor system connected, not with the purely metameric appendage muscles, but with the longitudinal body muscles which simply send slips to the skin in each segment. And it was there pointed out that this diffuse system consisted of a column of cells on the median dorsal aspect of the cord, from which fibres passed to these muscles. One cannot fail to see in the motor system of the abdominal body muscles of *Astacus* a distinct reproduction of these conditions in *Branchippus*, for the nerves, both to the extensor and flexor muscles of the abdomen, that is, to the body muscles, each arise from two ganglia.

The Inter-ganglionic Regions, or Longitudinal Commissures of the Cord.

The longitudinal commissural parts of the cord are composed solely of tubular fibres running parallel to one another and of very various sizes. As has been already noticed, the two lateral halves in the inter-ganglionic regions are clearly marked off from one another by a median vertical septum of connective tissue. There is absolutely no admixture of what may be called ganglionic elements, that is, of nerve cells or plexus, with the commissural fibres; on the contrary, the inter-ganglionic regions correspond, accurately and solely, to the white matter of the spinal cord of Vertebrates (fig. 23). As has been mentioned previously, many of the fibres continue straight through the ganglion to regions below. In the abdominal region, and in sections passing through those parts of the inter-ganglionic cords more removed from the ganglia, a grouping of the fibres into columns is not very obvious, owing to the slight development of the inner sheath. On approaching the ganglia, however, whether from below or from above, a distinct division into columns is very apparent. The fibres in different regions diverge from one another, while at the same time the median fissure widens, and the inner sheath becomes thicker, in order to fill the spaces thus formed, which appear in transverse sections as fissures, or sulci, occupied by an inward extension of the inner sheath (fig. 18). It should be distinctly stated that there is no confusion of the columns of fibres along the whole inter-ganglionic tract; there is no decussation or branching of fibres into this column or that, but, on the contrary, they maintain a parallel course without branching, the different columns simply diverging from one another at the upper or lower limits of the ganglia.

The result of this divergence is that the transverse sectional area of the cord rapidly increases as the ganglion is approached. This increase, however, is also due to another cause, namely, that in each column some of the fibres branch. In one case the fibres were counted in one lateral half of the cord about a quarter of the distance between the first and second abdominal ganglia away from the latter; and again, in a section taken through the region where the divergence of the columns passing to the second ganglion had taken place.

The number of fibres of all sizes found in the hemisection furthest from the ganglion was 613, in the hemisection near the ganglion 815; while in the former case the large fibres numbered 161, and in the latter 225. The division of the fibres may be readily observed in longitudinal sections, or teased preparations, and it is then seen to take place *wholly without the intervention of cells.* Passing on into the ganglion the division of certain of the fibres in each bundle is continued until they form tufts of fine fibres, which, just before they enter the ganglionic tissue, form a plexus, the fibres of which lie mainly in the general direction of the bundle. The transverse or obliquely running filaments also are rather finer, so that, at any rate near where it merges into the parallel bundles of fibres of the inter-ganglionic cord, it may be described as a *nerve plexus, the longitudinal fibres of which are the more prominent.*

In describing the inter-ganglionic region of the ventral chain of *Branchippus* in the first part of this paper, I said that it consisted of a fibrous core of longitudinally arranged fibres with oblique filaments, and a study of the primitive nervous system strongly impressed me with the idea that it is derived from a nerve plexus by the condensation of that plexus along certain lines and in certain places. The connections between the nerve fibres and plexuses described above I regard as suggesting this phylogenetic origin in the case of the nervous system of *Astacus.* In the Zooea of a Crab (one of the Paguridæ) which I have examined, the ganglia in the thoracic region are practically continuous. There is no inter-ganglionic cord, but a continuous internal plexus. Here and there in this are delicate strands composed of only a few fibres, and traceable right up to the brain. These represent the great longitudinal columns of the Mammalian cord, and appear to end in the thick sheath of nerve cells surrounding the fibrous core. The longitudinal commissural columns or fibres between ganglion and ganglion have not yet appeared. In other words, the general plexus still performs the functions carried out in the Mammalian cord by the root zones of white matter, and probably, in part, by the grey matter itself, and in *Astacus* by the parallel fibres of the inter-ganglionic regions.

As the growth of the Zooea proceeds, the ganglionic masses, the cells and fibrous elements of which are at first quite continuous, are, as it were, pulled apart from one another, to remain connected by an inter-ganglionic zone of parallel fibres.

We may, with RETZIUS, distinguish three connections for the longitudinal fibres of the ventral cord:—

(1.) Directly with the plexus of the ganglion.

(2.) Directly with the plexus of the ganglion, but with a T-shaped junction, with cells.

(3.) With cells whose processes merge in the plexus of the ganglion (fig. 30). The connection through cells is more common in the higher parts of the cord.

Paths of Conduction in the Cord.—In transverse sections through the cord just above or below the ganglion, the fibres in each half of the cord are clearly seen to lie in three main columns—dorsal, median, and ventral. Each of these again is divisible into three regions—internal, median, and external (fig. 18). The ventral columns are related chiefly to the centres of the anterior nerve, the median to the centres of the posterior ventral nerves, and the dorsal to the dorsal nerves. The divisions of the respective columns which abut on the median fissure contain a larger proportion of fibres, which run through the ganglia without change. Thus the great conducting columns, that is, those fibres which correspond in the cord of *Astacus* to the fibres of the pyramidal tracts, and GOLL's column in the cord of Vertebrates, form, in the abdominal region, a mass of fibres, wedge-shaped in transverse section, and disposed symmetrically on each side of the median fissure. The base of the wedge is dorsal. Higher up the cord, in the thoracic region, these fibres occupy a still more dorsal position (fig. 24). Further, these fibres are stratified according to their connections, those related to the appendages being most ventral; while of the fibres related to the body muscles, the flexor system is dorsal to the extensor system.

The more lateral and ventral longitudinal fibres of the cord are commissural between one metamere and another.

Minute Structure of the Fine Plexus.

The fine plexus is added to the cord on its ventral side in the abdominal ganglia, and is itself composed of a most complex and dense plexus of filaments which, in teased preparations, and under a high power, sometimes appear faintly moniliform. Teased preparations or sections show that the plexus varies in the fineness of its elements, and in the complexity of their arrangement in different portions. Here and there one sees in the general mass of plexus regions of the most extraordinary delicacy and density (fig. 32). These are often connected with one another by bars of equally dense material, and the masses and bars are embedded in a plexus, the elements of which are larger and more loosely arranged. The appearance is very striking in hæmatoxylin or gold-stained preparations. Into the fine plexus of the ganglion may be traced bundles of fine fibres derived from the nerve bundles, from longitudinal columns, or from the coarse plexus in which the large tubular nerve-fibres break up, and each bundle ends in one of these dense masses (fig. 32). The fine plexus is strikingly free from cells of any description. We may thus distinguish in the fine plexus what we may call "centres," each of which forms the immediate termination of a bundle of fine fibrils. Some of these are placed in immediate connection by bars of a similarly dense nature, while all are connected by the general mass of *relatively* less dense plexus.

I have already pointed out that there are regions of the ganglionic plexus to which the fibres of the various nerves may be traced. These we may speak of as the "centres" for the different nerves, and each comprises a coarse plexus of interlacing tubular fibres and a fine plexus. The former structure is merely the expression of the first branching of the large nerve fibres, while to the latter may be traced bundles of fine fibres derived (a) directly from the fine nerve fibres or, (b) from the coarse plexus. Also by means of serial sections or teasing one can follow a tubular nerve fibre from the inter-ganglionic commissure to where it breaks up into a bundle of fibrils which are lost in the fine plexus. We must therefore look upon this structure as the place where the fibres of the nervous system ultimately communicate with one another.

Lastly, the nerve fibrils passing to the fine plexus enter it in well-defined bundles which go to histologically distinct regions, and this structural feature we may correlate with the fact that each nerve contains different groups of fibres which supply either different muscles, or regions of the sensory surface supplied by the nerve as a whole, which differ in the fact that stimulation of the one region or the other does not produce quite identical disturbances in the central nervous system.

Description of Figures.

Part I.—*Branchippus.*

PLATES 10–13.

Fig. 1. Transverse section through ridge bounding the ventral groove in an inter-ganglionic region. The inter-ganglionic cord also shown. Oc. 4, Ob. E, Zeiss, Cam. Luc.

Fig. 2. Transverse section through mandibular region and just posterior to the mouth showing the deep post-oral groove lined by sense cells. The long posteriorly directed upper lip is seen in the lower part of the figure. Oc. 4, Ob. D, Zeiss, Cam. Luc.

Fig. 3. Transverse section through the right-hand cord between the circumoral ganglion and the brain. Oc. 2, Ob. $\frac{1}{15}$, Cam. Luc.

Fig. 4. Transverse section through the anterior commissure and just before the exit of the anterior nerve of the right-hand part of the third thoracic ganglion. Oc. 4, Ob. E, Zeiss, Cam. Luc.

Fig. 5. Transverse section of the right-hand half of the same ganglion passing through the exit of the anterior nerve. Oc. 4, Ob. E, Zeiss, Cam. Luc.

Fig. 6. Transverse section of the right-hand half of the same ganglion, and showing the posterior commissure and exit of posterior nerve. Oc. 4, Ob. E, Cam. Luc.

Fig. 7. A portion of a fibre from one of the appendage muscles, showing the termination of a nerve fibre in the protoplasmic sheath. Oc. 4, Ob. E, Zeiss, Cam. Luc.

Fig. 8. A group of ectoderm cells connected with a single (condensing) ganglion cell, which is suspended freely in the body cavity. Oc. 2, Ob $\frac{1}{15}$, Cam. Luc.

Part II.—*Astacus*.

PLATES 11–13.

Fig. 9. Dissection of the second abdominal ganglion from the ventral surface. The tissue, which lies on the ventral face of the cord and between it and the posterior sternal arteries has not been disturbed. The course of the anterior nerve on the right side is shown, and the two main branches may be traced, the anterior to the pleuron and more dorsal appendage muscles, the posterior to where it divides into two and curves down into the appendage.

Fig. 10. Dissection of that portion of the posterior nerve of the left side which runs along the ventral aspect of the flexor muscles of the abdomen.

Fig. 10A. Drawing of the same dissection from the side. The posterior nerve is still seen to be running on the surface of the flexor muscles.

Fig. 10B. The same dissection seen from the dorsal side, showing the breaking up of the branches of the posterior nerve into fan-like tufts of fibres, which pass into the extensor muscles.

Fig. 11. Transverse section through one of the anterior nerves of the second abdominal ganglion a short distance away from the ganglion. Osmic vapour, and FLEMING's fluid. Right-hand and smaller branch passes into the appendage. Oc. 2, Ob. E, ZEISS, Cam. Luc.

Fig. 12. Large nerve fibre dividing shortly after its exit from the ganglion. Fresh preparation.

Fig. 13. Transverse section through an anterior nerve of the second abdominal ganglion, before it has divided into the two main branches. Oc. 2, Ob. E, ZEISS, Cam. Luc.

Fig. 14. Transverse section through one of the posterior ventral nerves of the second abdominal ganglion close to its exit from that structure. Oc. 2, Ob. E, ZEISS, Cam. Luc.

Fig. 15. Transverse section through the posterior dorsal nerves of the second abdominal ganglion shortly after their exit from the cord. Oc. 2, Ob. E, ZEISS, Cam. Luc.

Fig. 16. Part of a transverse section through cord, showing the exit of the posterior dorsal nerves. Oc. 2, Ob. D, ZEISS, Cam. Luc.

Fig. 17. Section through the skin near the anus, showing the process of a sense cell traversing the cuticle.

Fig. 18. Transverse section through the most anterior portion of the second abdominal ganglion, showing divergence of columns. Oc. 4, Ob. A, ZEISS, tube 16·8 centims.

Fig. 19. A piece of the external sheath, or perineurium, of the ganglion isolated by teasing, and viewed from its internal surface. Oc. 2, Ob. $\frac{1}{15}$, Cam. Luc.

Fig. 20. Optical section through the external or perineurial sheath of the ganglion. Oc. 2, Ob. $\frac{1}{15}$, Cam. Luc.

Fig 21. A bundle of fibres isolated by teasing from the interganglionic cord where it enters the ganglion, showing an imperfect sheath of flattened cells. Oc. 2, Ob. $\frac{1}{15}$, Cam. Luc.

Fig. 22. Supporting or "neuroglia" cell from the ganglion. Isolated by teasing. Oc. 2, Ob. $\frac{1}{15}$, Cam. Luc.

Fig. 23. Transverse section through the inter-ganglionic cord just below the second abdominal ganglion, showing the ascending roots of the posterior dorsal nerves. From a micro-photograph.

Fig. 24. Dissection of the ganglion of the chelæ to show the relative positions of the fibres which are going to regions below, and of the fibres passing to and through the substance of the ganglion. Viewed from below.

Fig. 25. Dissection, showing the long double roots of the nerves to the chelæ and walking legs. Viewed from below.

Fig. 26. Dissection, showing the flexor muscles and the origin of the nerves of the second and third abdominal ganglia. The extensor muscles and gut have been removed, and the preparation is viewed from the dorsal surface. Thin sheets of muscle fibres arise from the belly of the great mass of the flexors in each segment, and stretch across to be joined in the middle line and above the nerve-cord by tendinous tissue. These are shown intact in Segment II., and cut in Segments V. and VI., and completely removed in Segments III. and IV.

Fig. 27. Dissection, showing the most superficial aspect of the flexor muscles. The extensor muscles of the right-hand side have been removed.

Fig. 28. Dissection, showing two myomeres of the flexor muscles. On the left, the dorsal muscle sheet, which extends outwards into the pleuron, has been removed. Diagrammatic.

Fig. 29. Dissection of the extensor system. Viewed from above.

Fig. 30. Group of nerve-cells from ganglion of chelæ, isolated by teasing from the ending in the ganglion of a bundle of fibres from the longitudinal commissures. Oc. 2, Ob. $\frac{1}{15}$.

Fig. 31. Teased preparation of "Punkt Substanz" with two nerve cells. From ganglion of chelæ. Oct. 2, Ob. E., ZEISS, Cam. Luc.

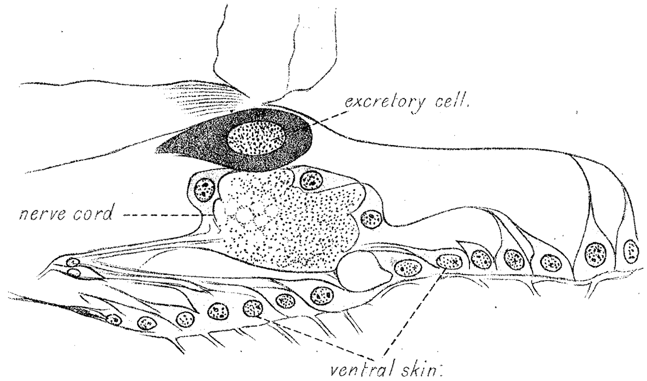
Fig. 32. Section through "Punkt Substanz," showing the entrance of a bundle of fine fibres from the posterior nerve. From section next in series to Fig. 34. Oc. 4. Ob. $\frac{1}{12}$, Cam. Luc.

Fig. 33. Section (slightly oblique) through region of entrance of anterior nerves, showing external and median centres, and the fine fibres of dorsal and ventral roots passing to them. From a micro-photograph.

Fig. 34. Section through entrance of posterior ventral nerves. Oc. 4, Ob. D, Zeiss.

Fig. 35. Longitudinal vertical section, showing the entrance of the anterior and posterior nerves into the ganglion. (Figures 32, 33, 34, and 35, are from the serial sections through the second abdominal ganglion.)

Fig. 36. Part of transverse section through the ganglion, showing the coarser and more dorsal ganglionic plexus. The nerve cells, and those of the lateral group, which are connected with the thick-sheathed tubular fibres of the interior nerves. Oc. 2, Ob. $\frac{1}{15}$, Cam. Luc.



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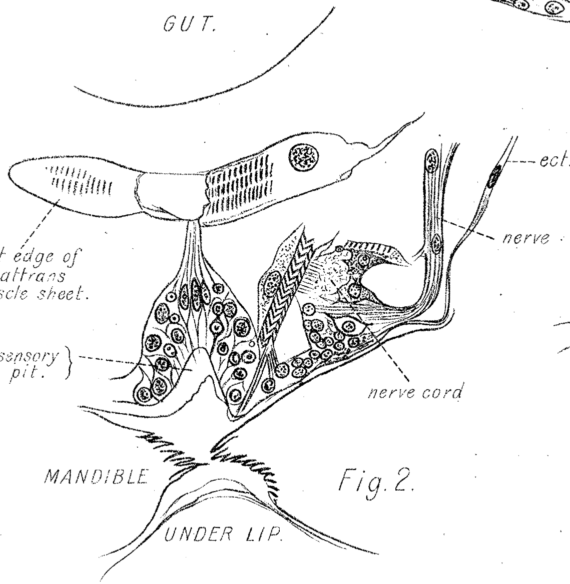

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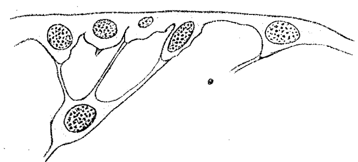

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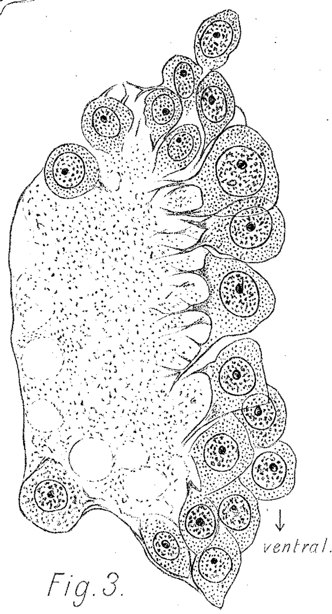

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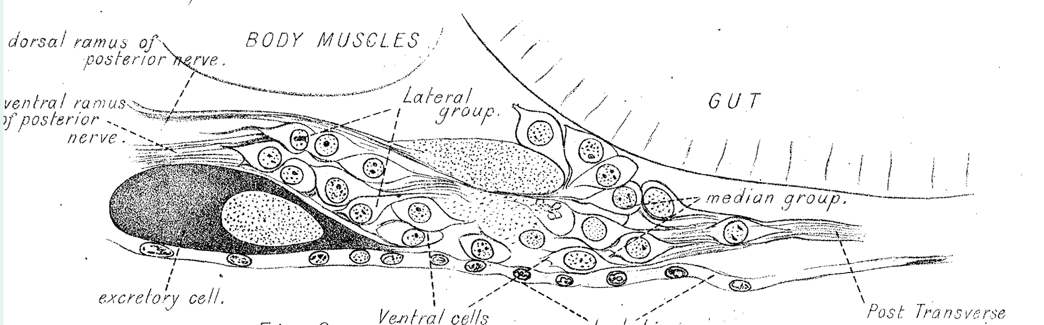

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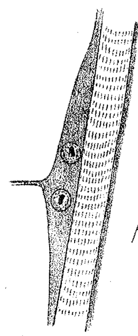

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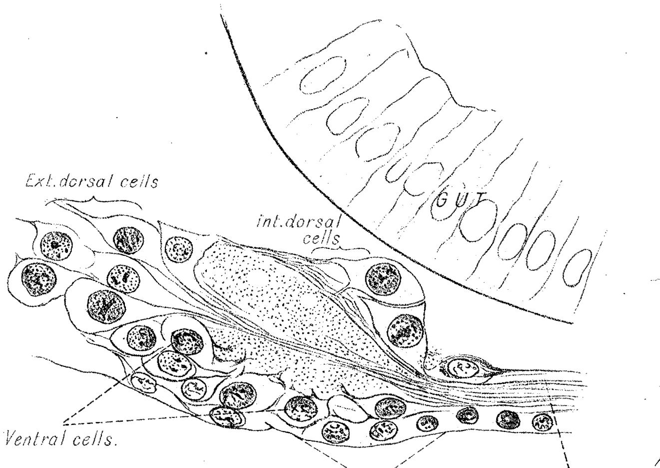

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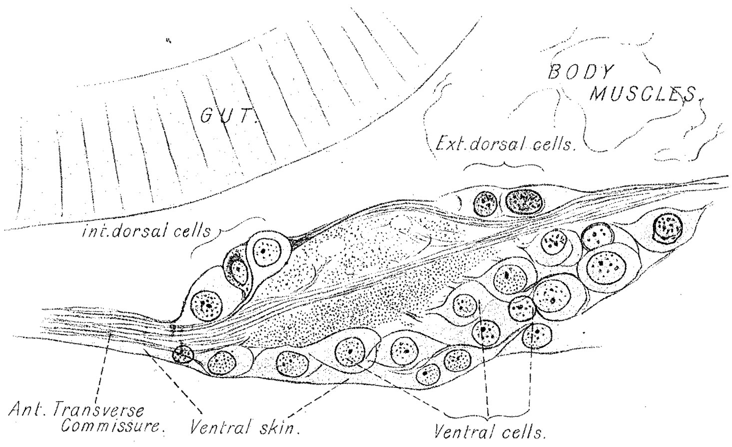

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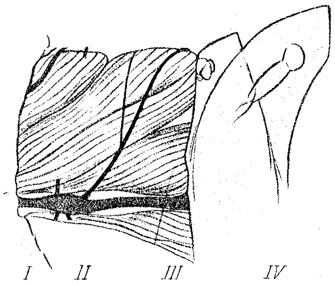


Fig 10.

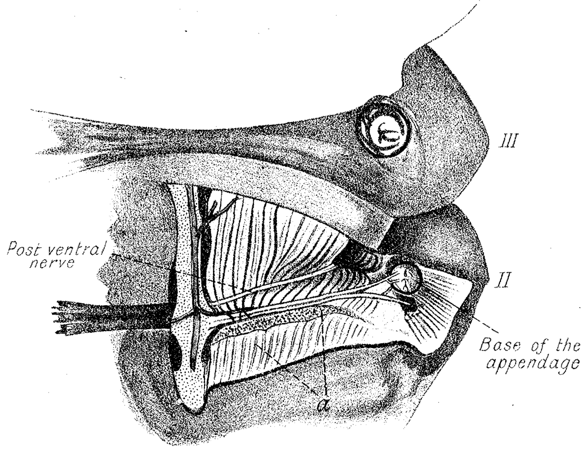
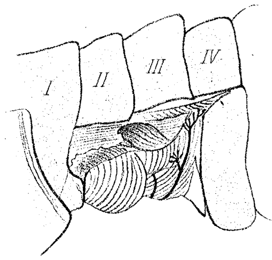


Fig. 9.



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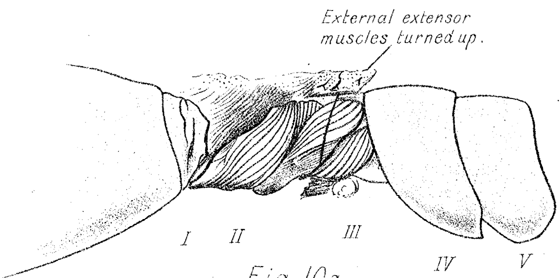

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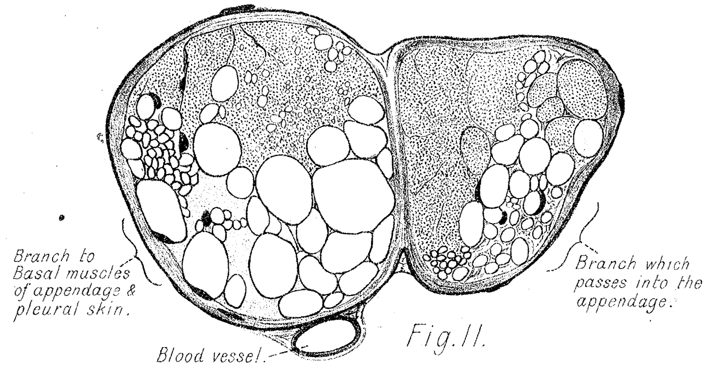
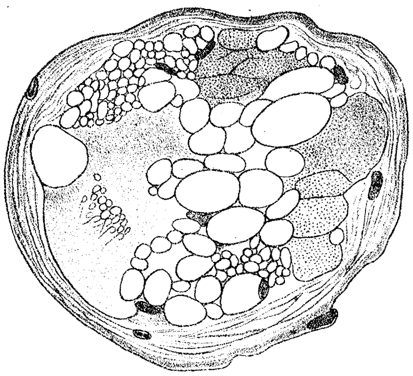


Fig. 11.



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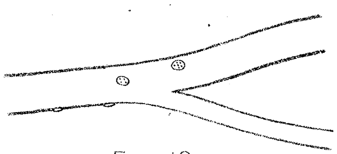

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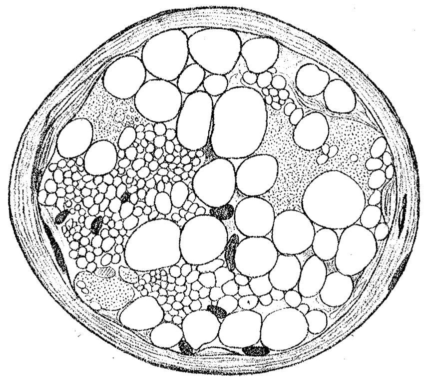

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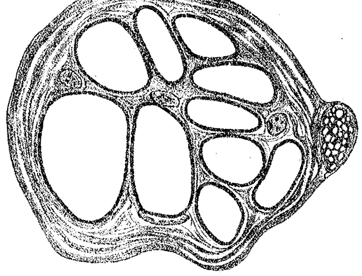

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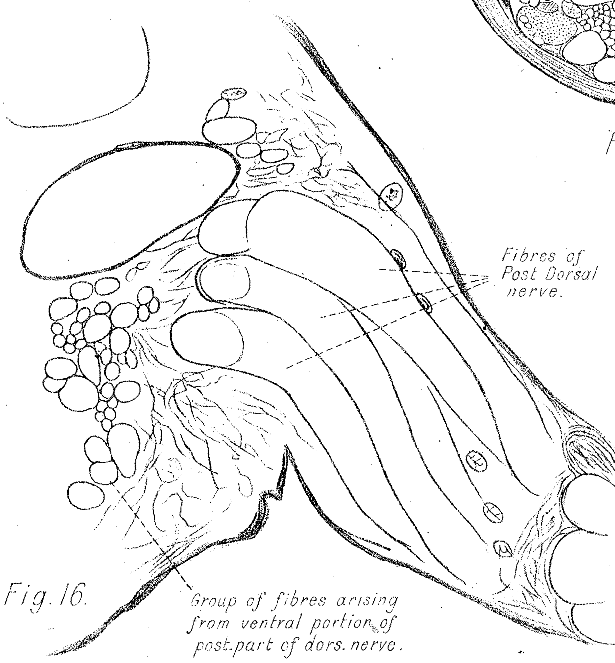

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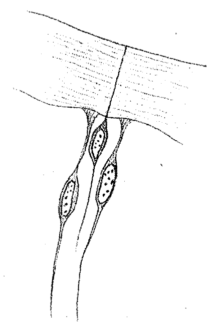

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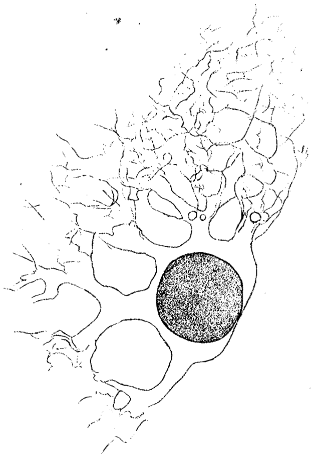

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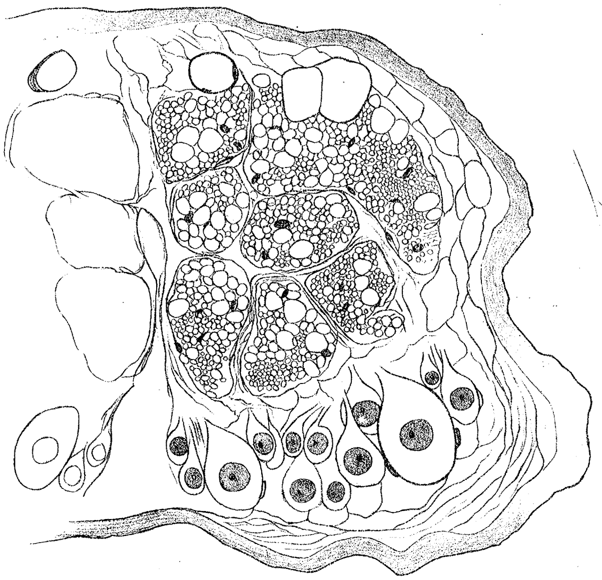

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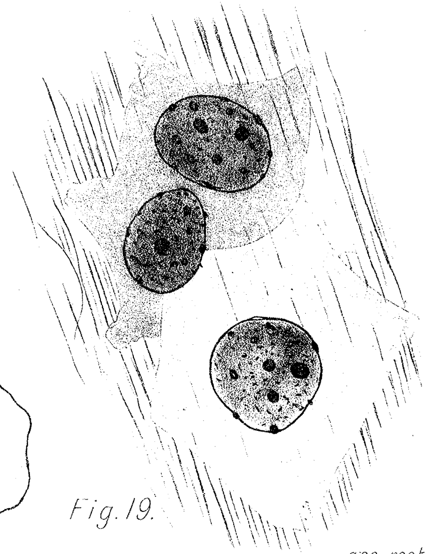

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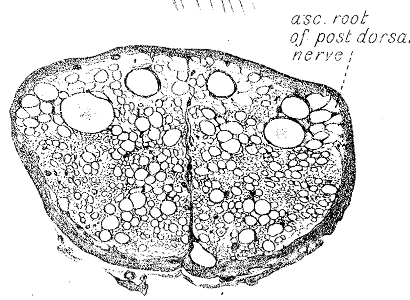

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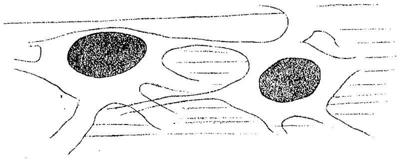

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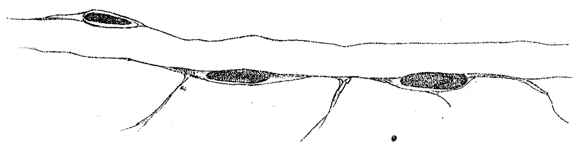

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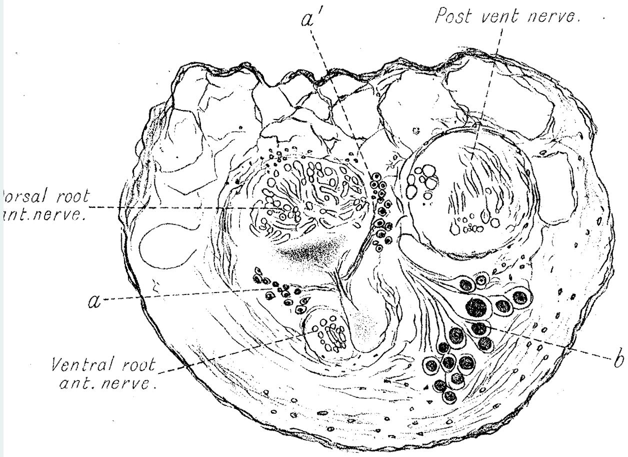
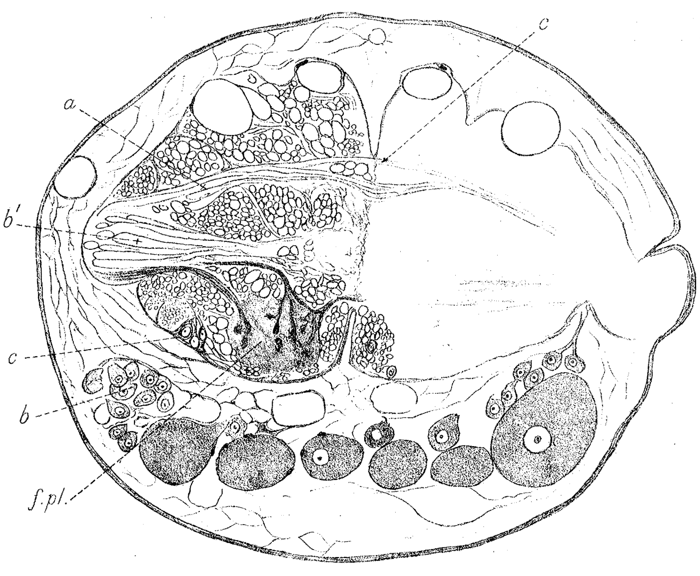


Fig. 35.

Fig. 33.

Fig. 31.



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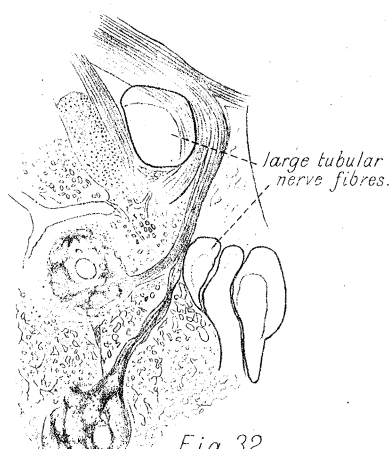

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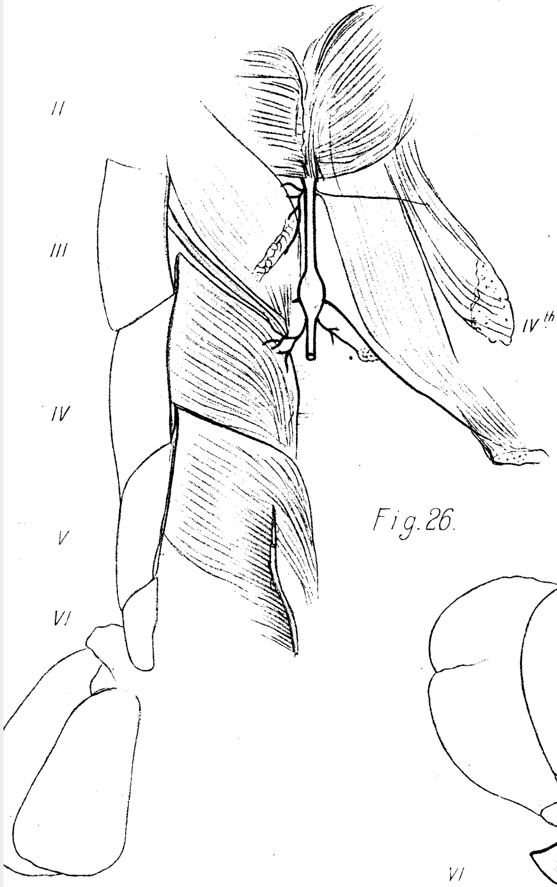

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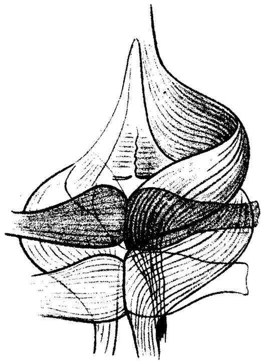

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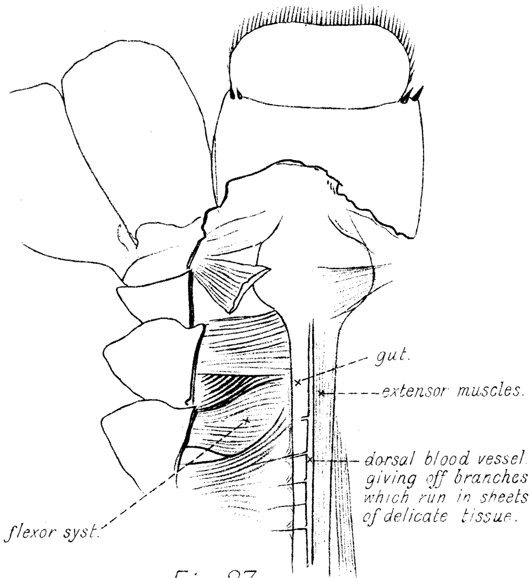

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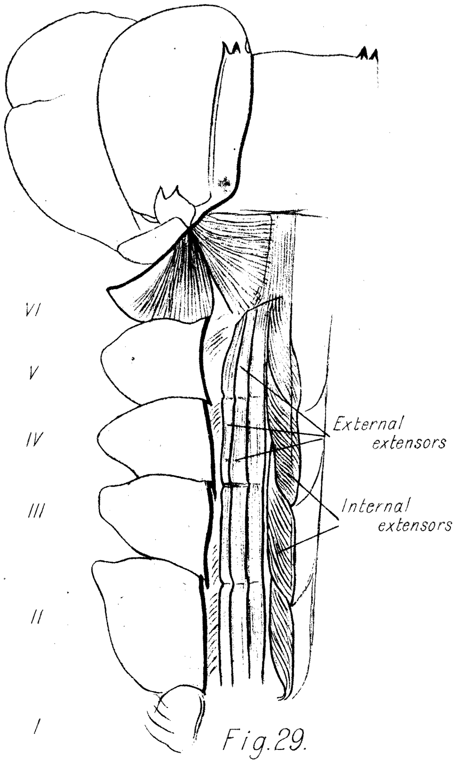

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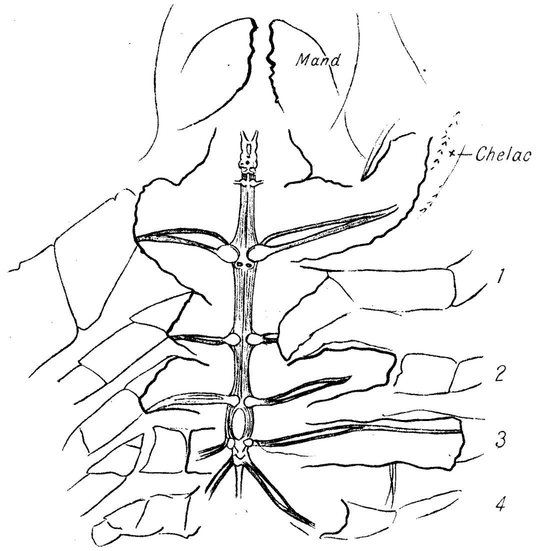
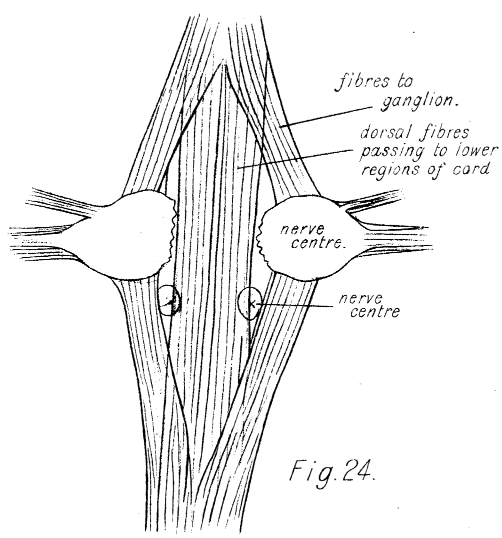


Fig. 25.

Fig. 30.

Fig. 36.



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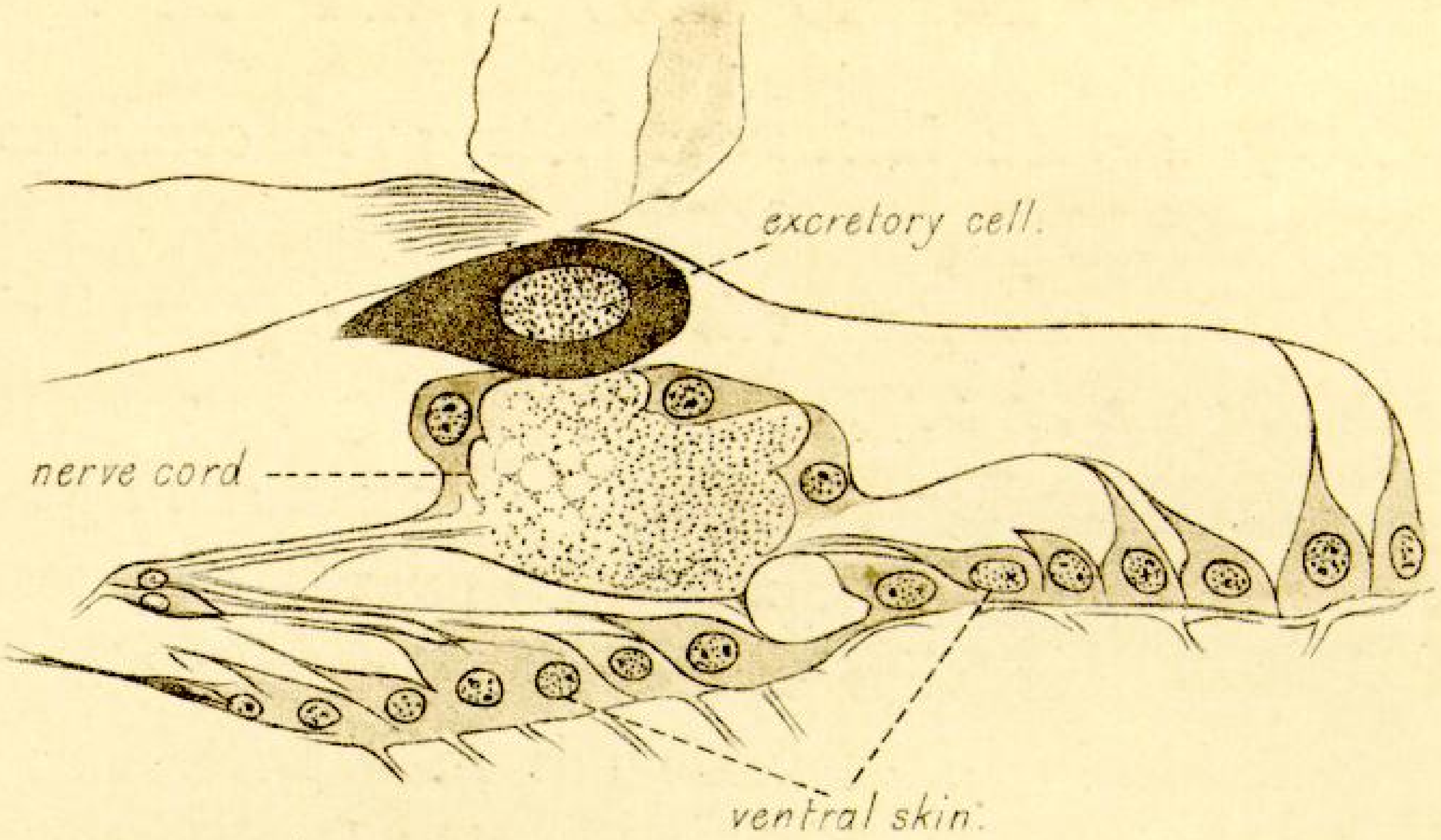

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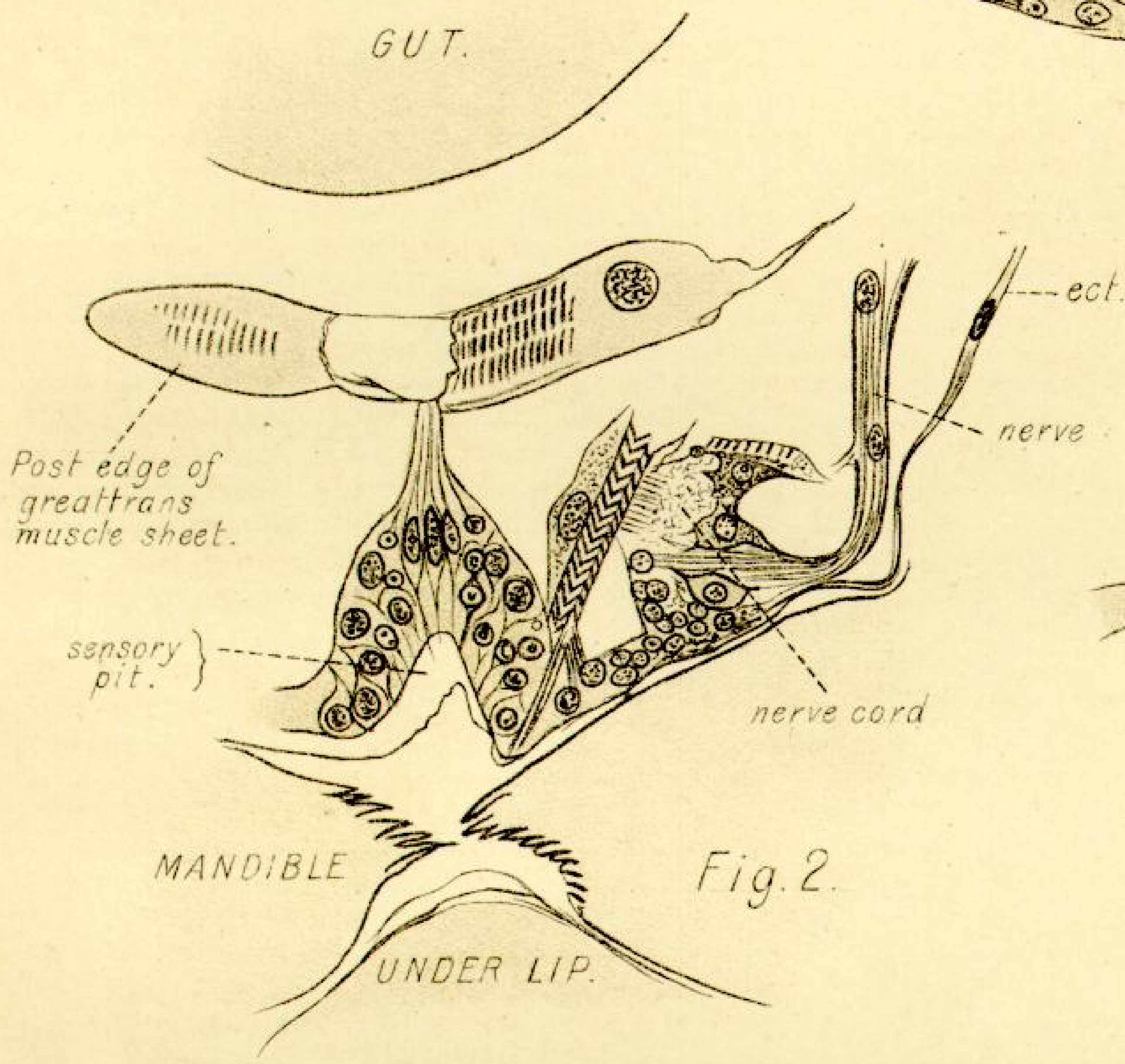

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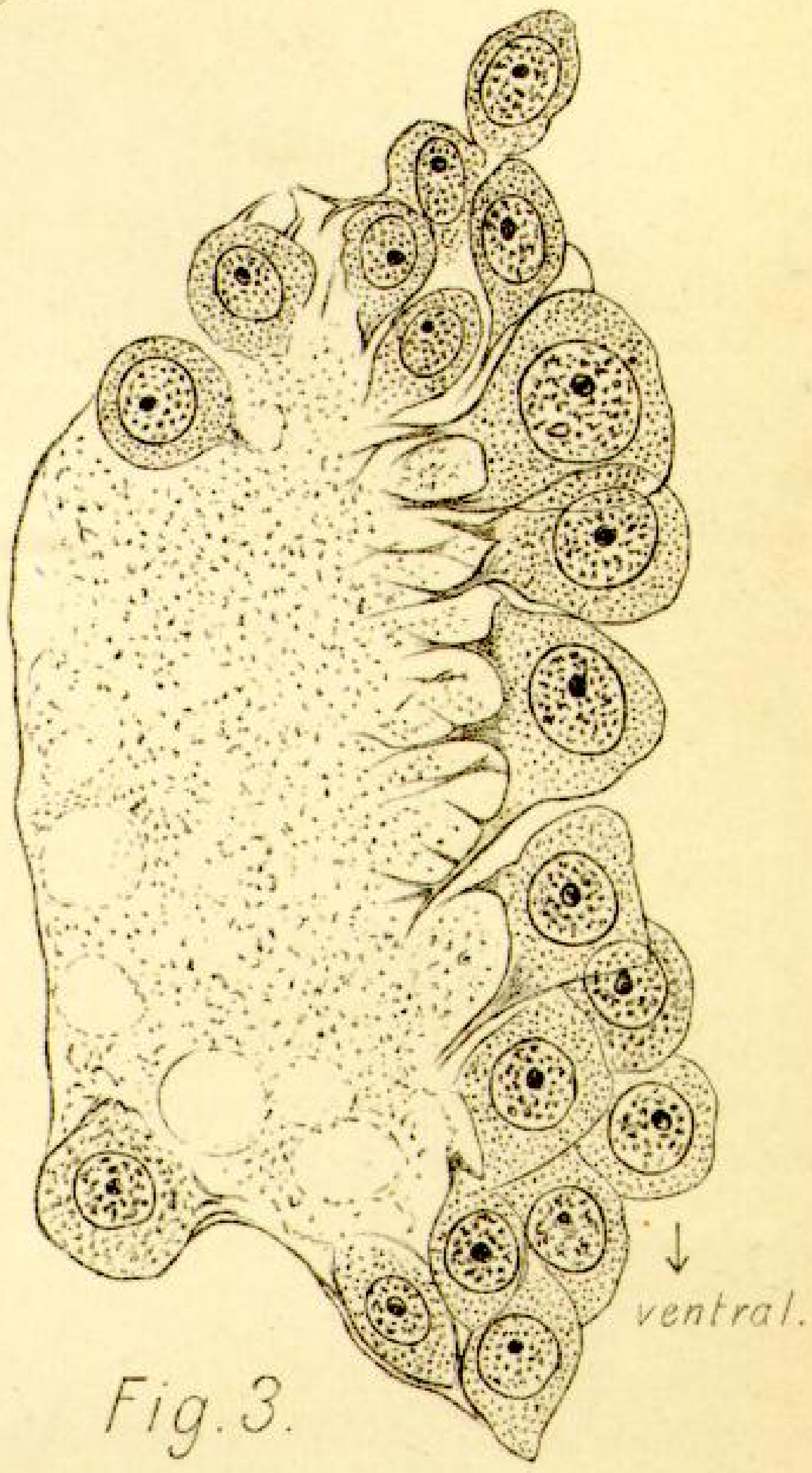

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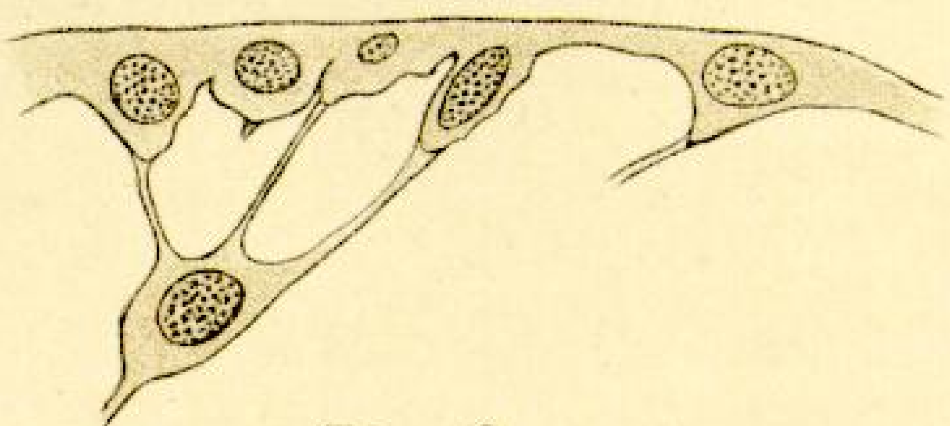

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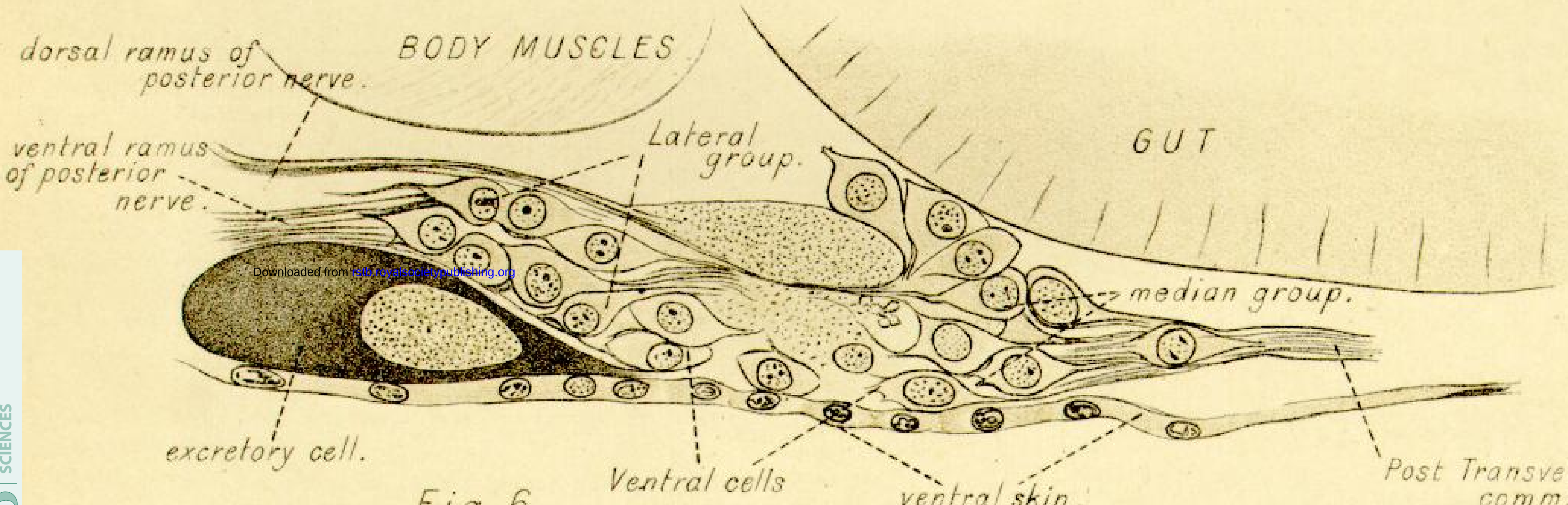

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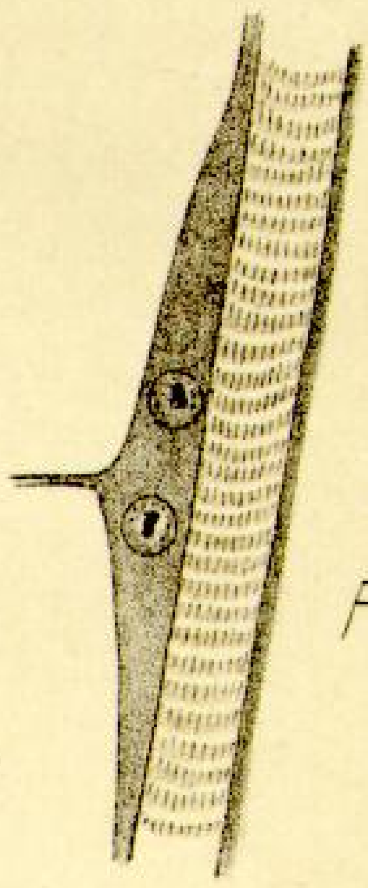

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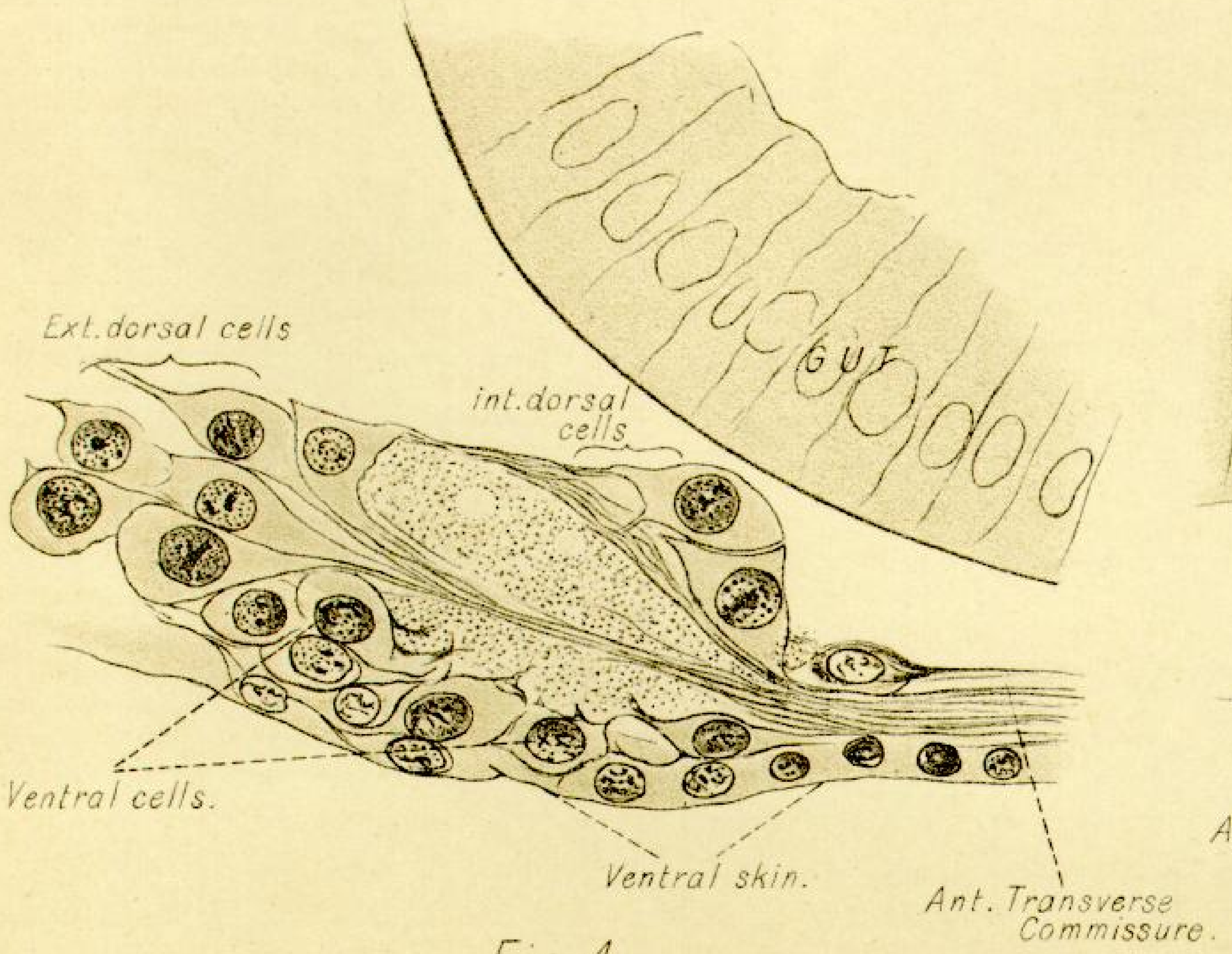

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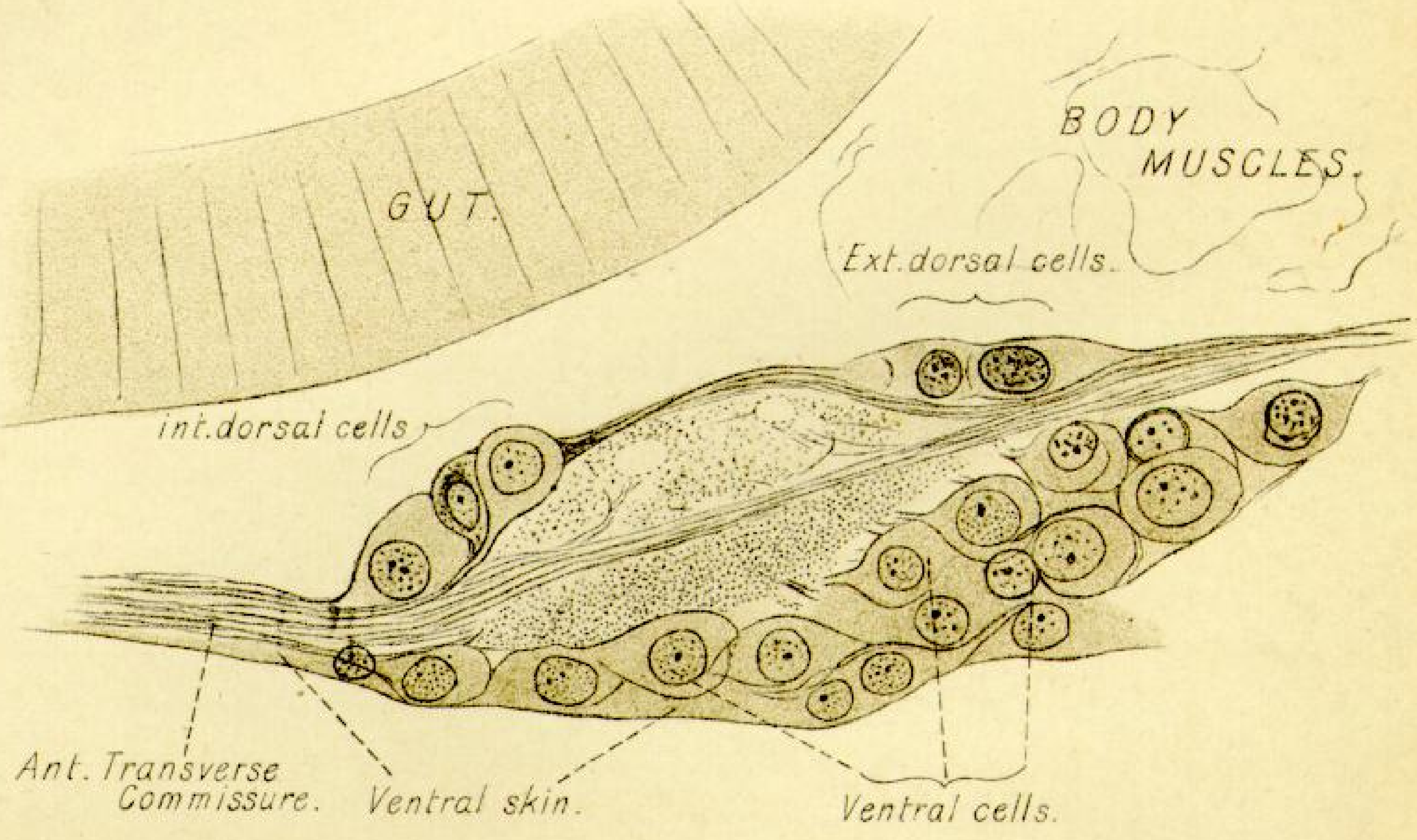

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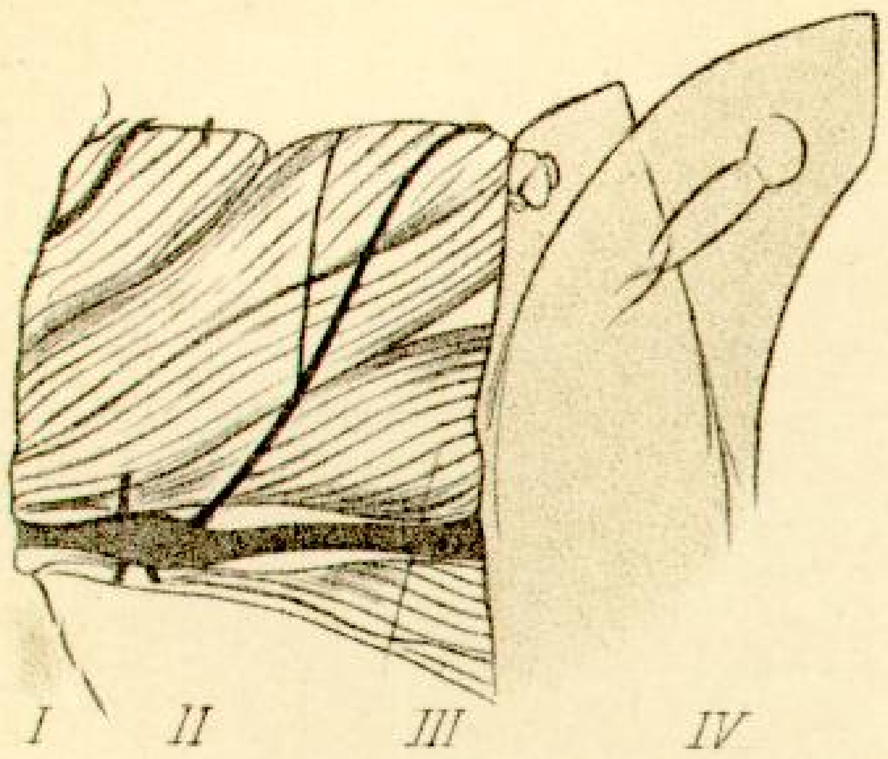

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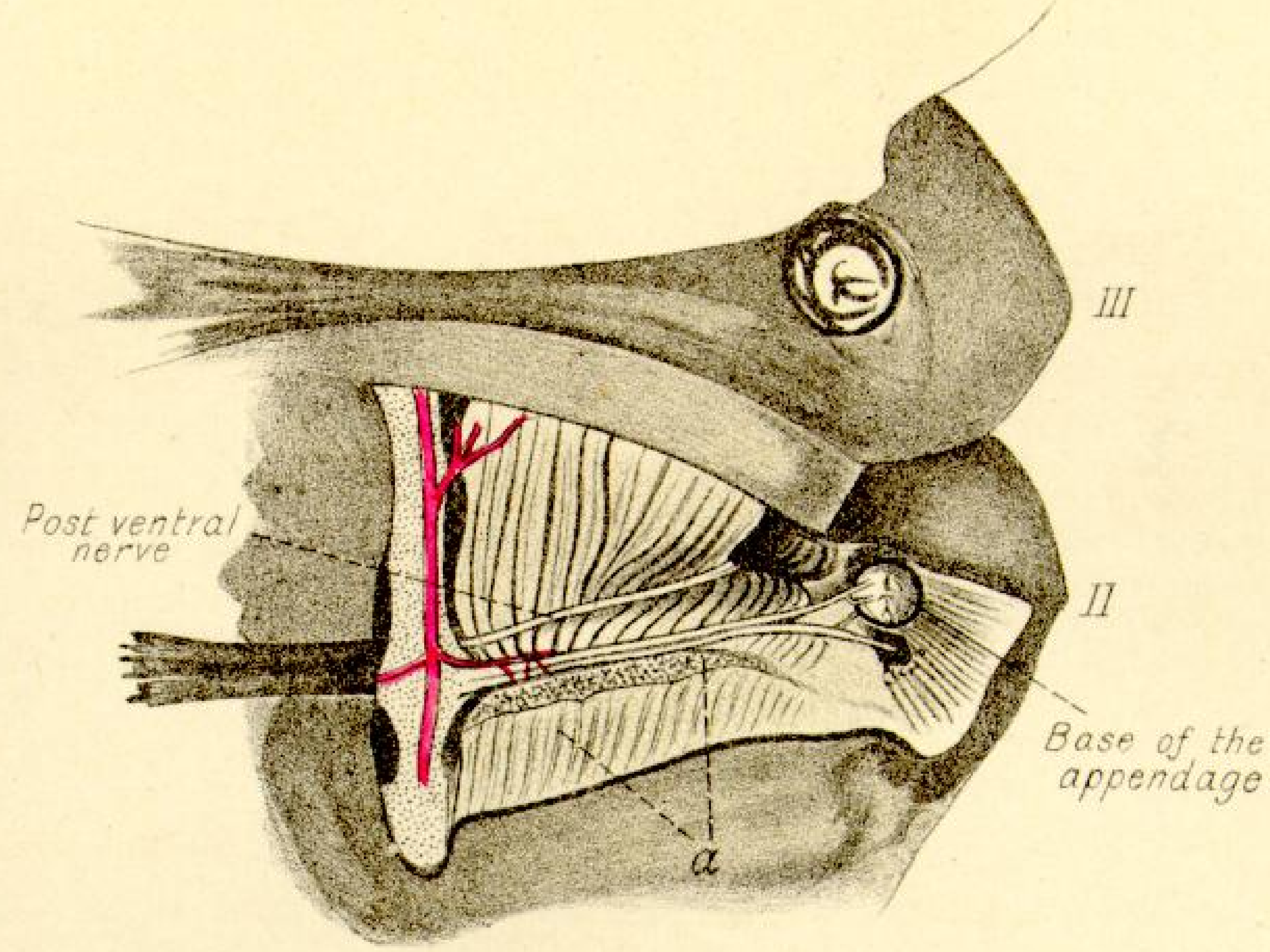

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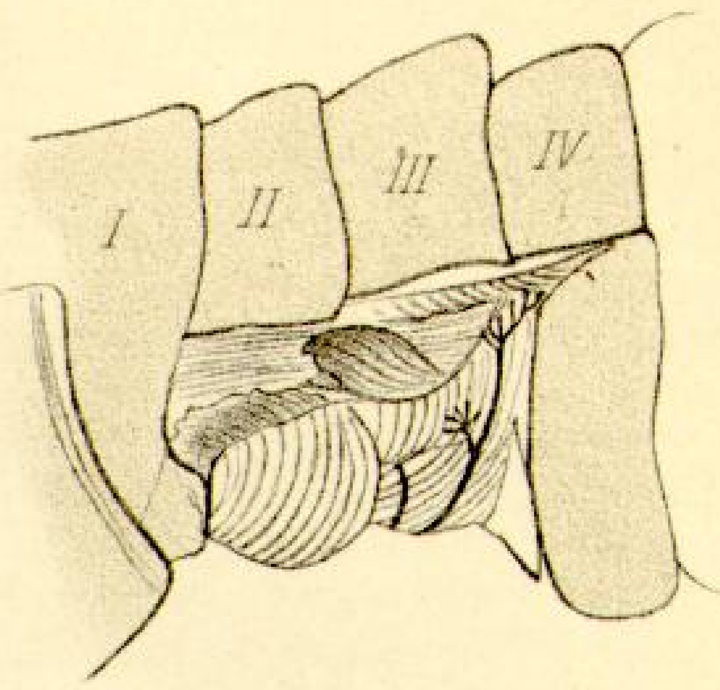

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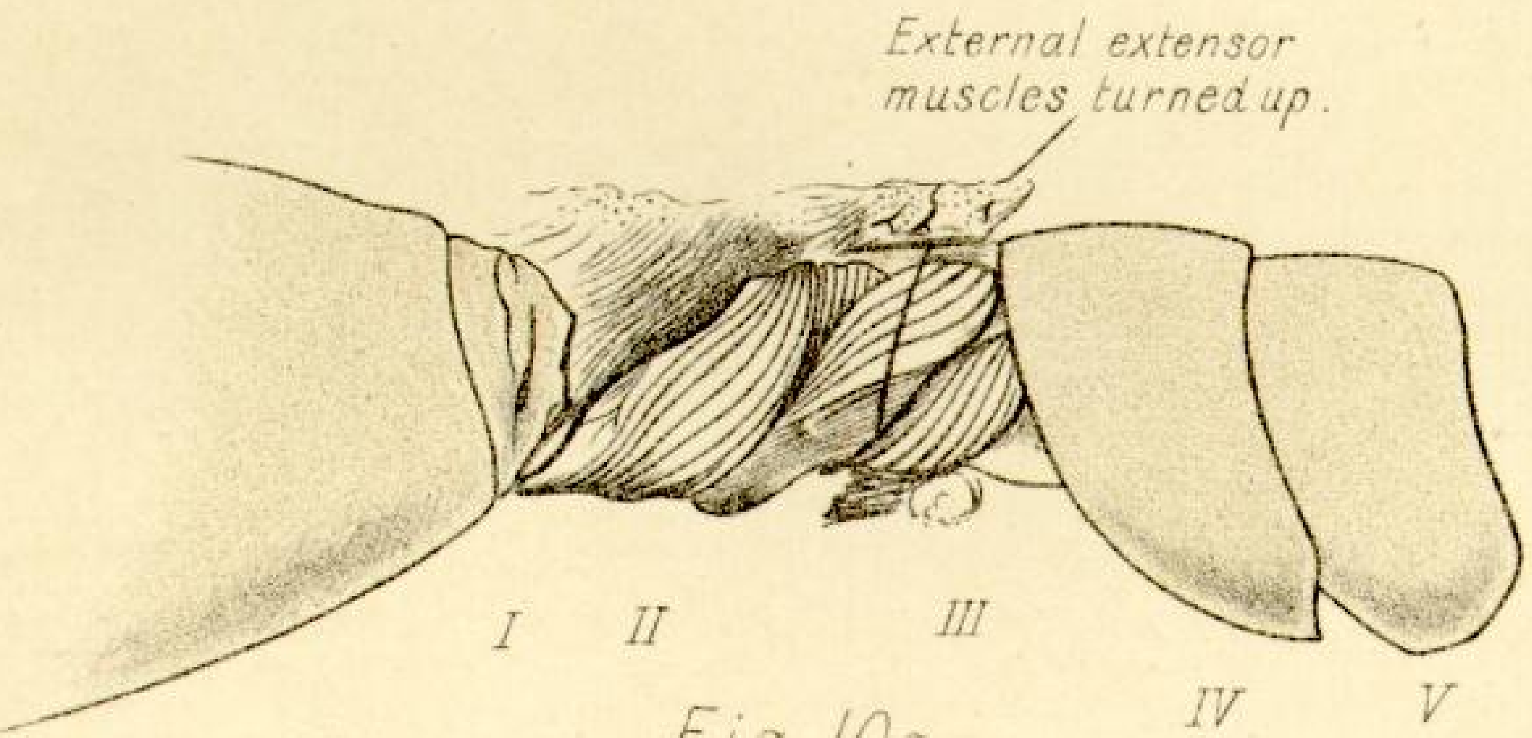

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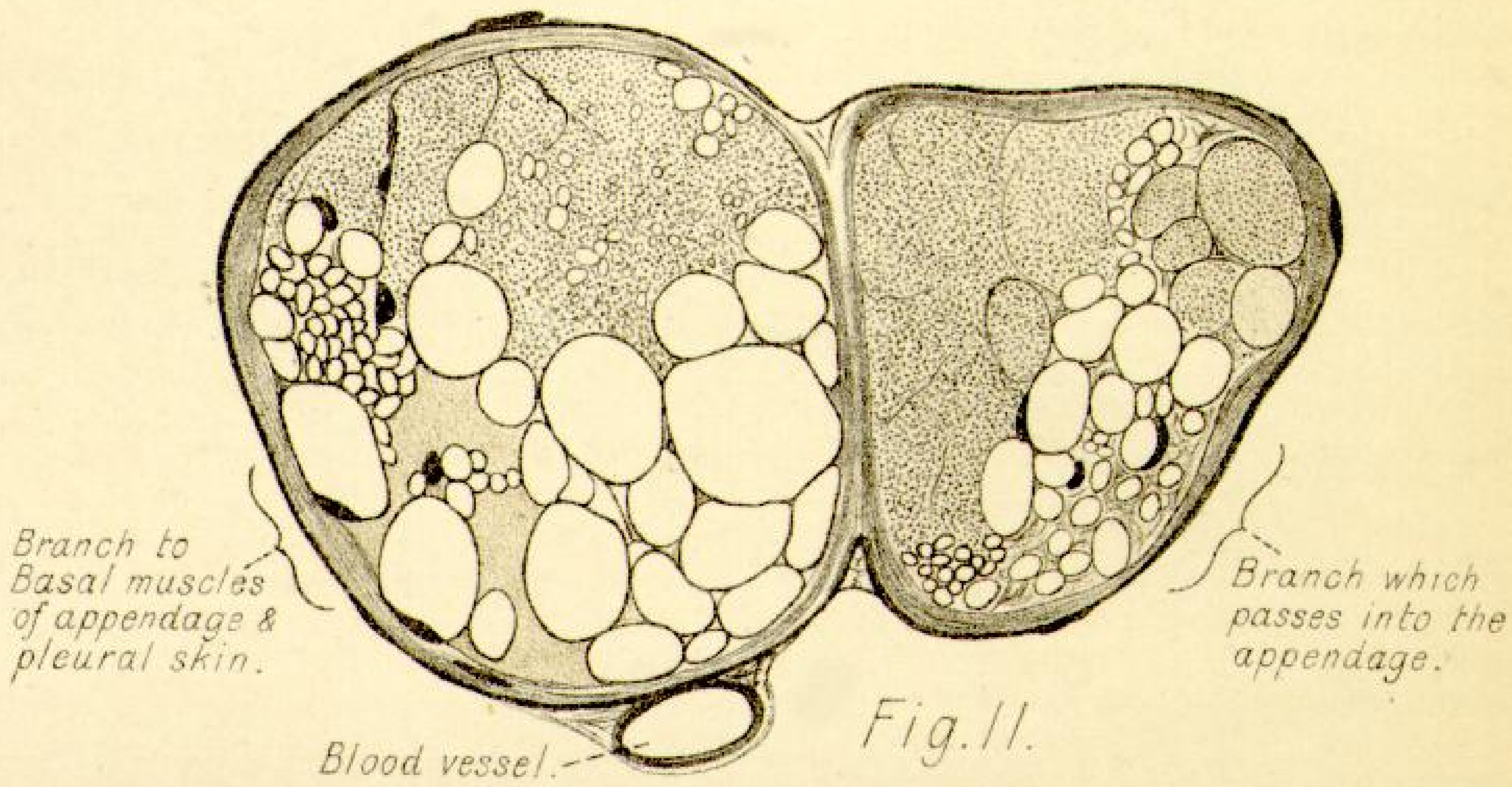

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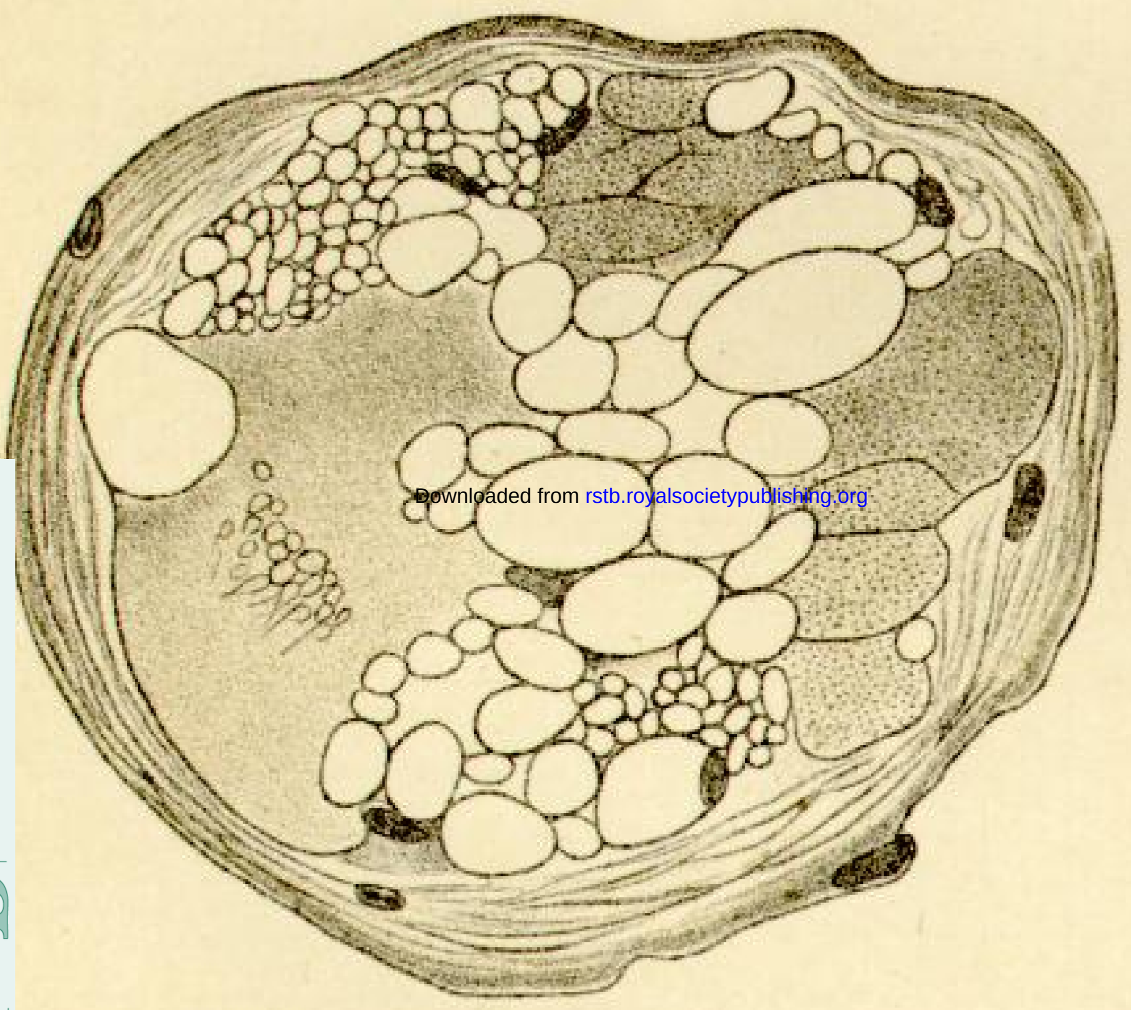

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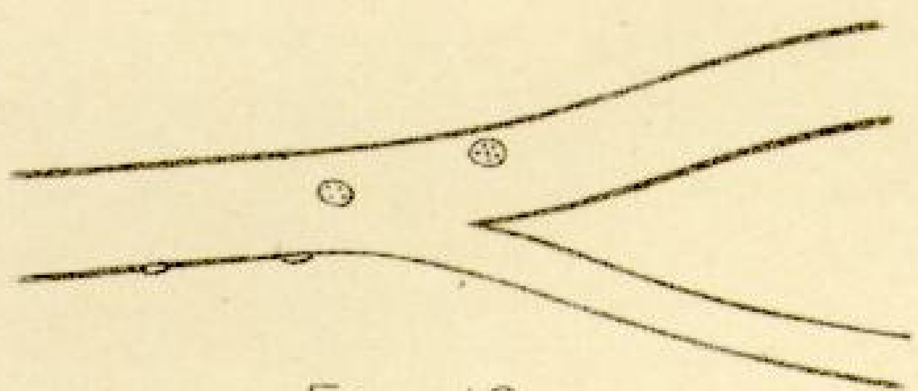

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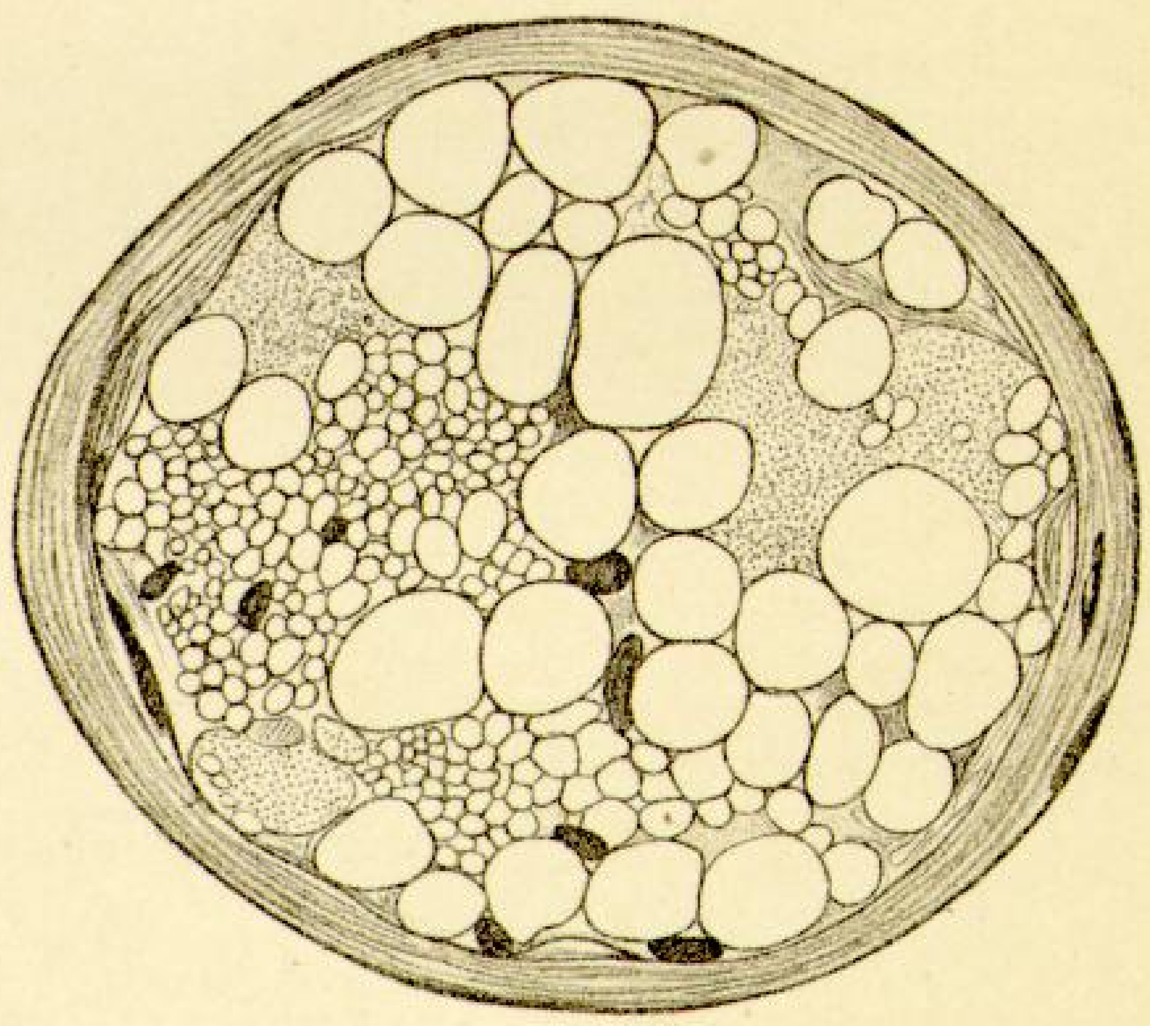

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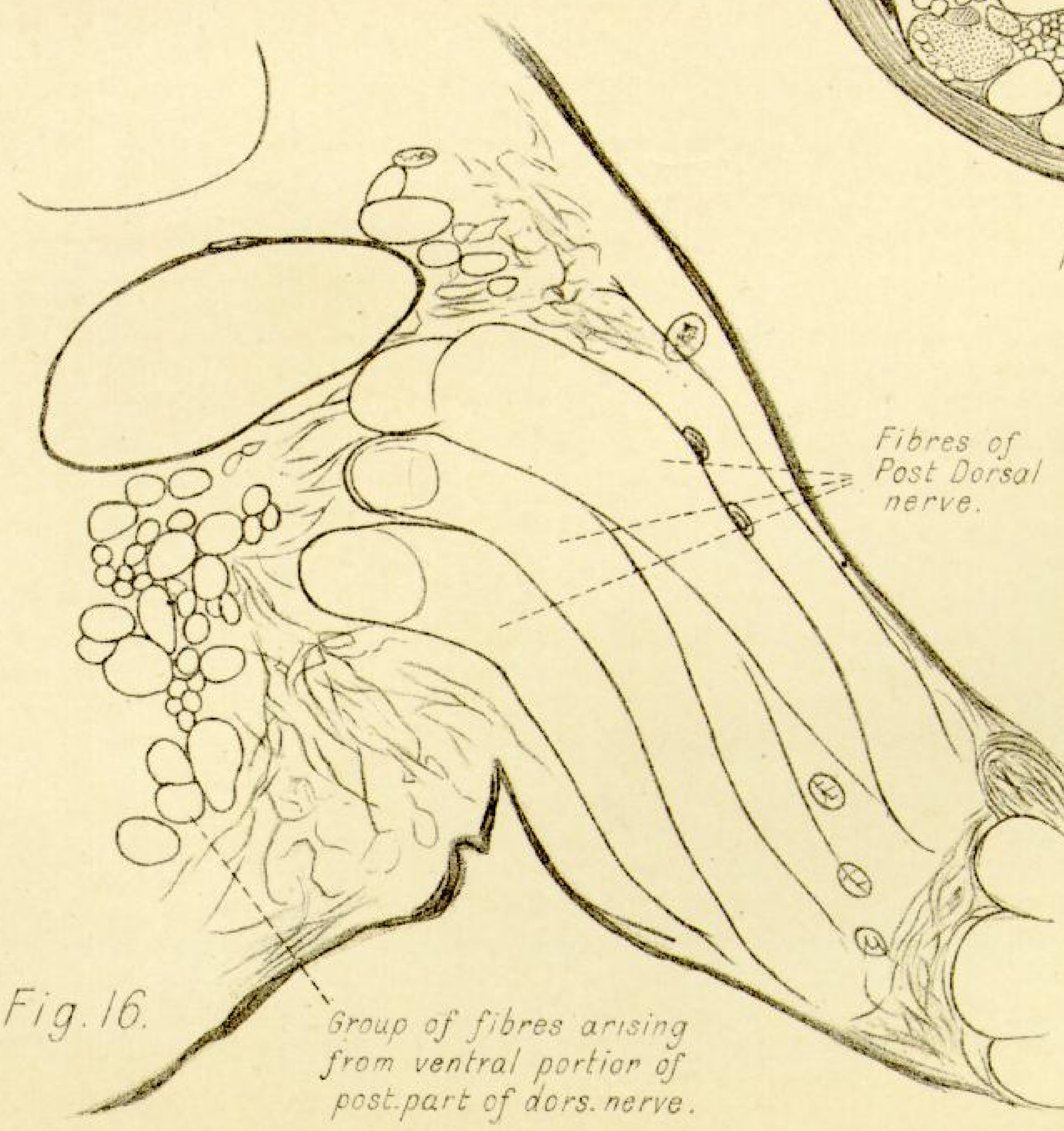

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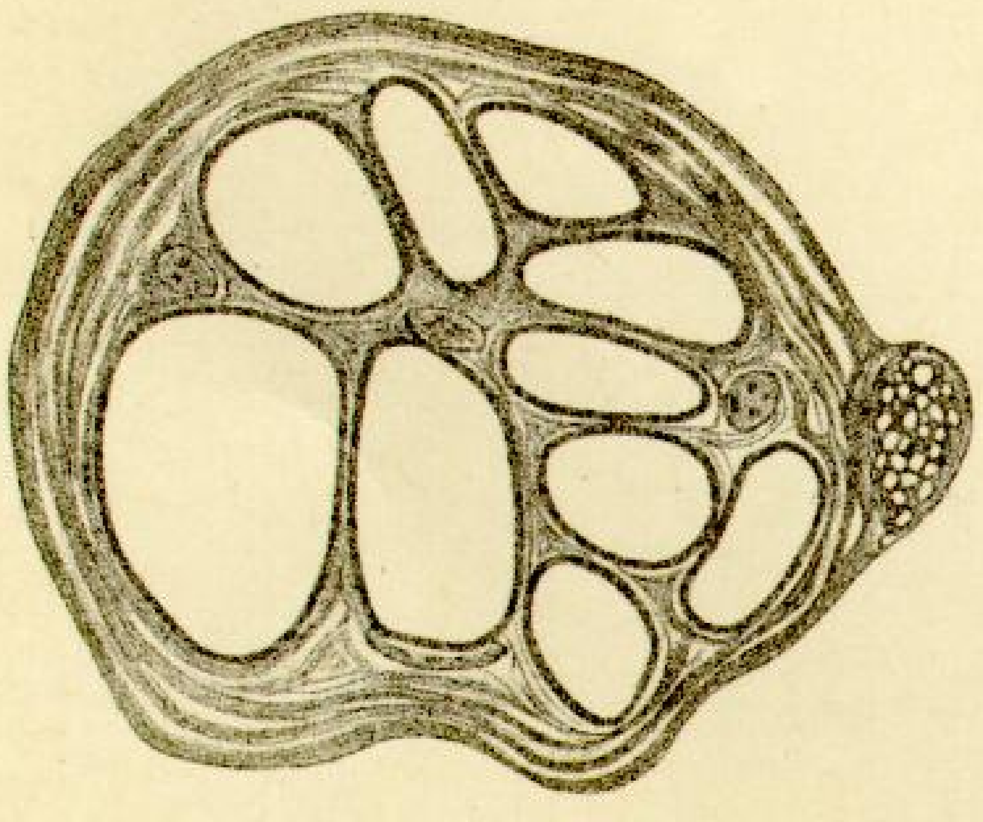

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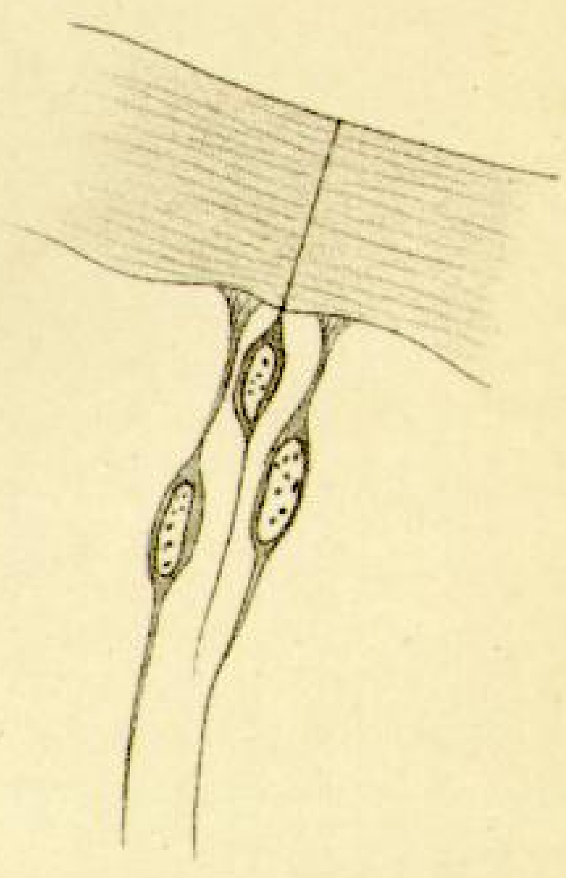

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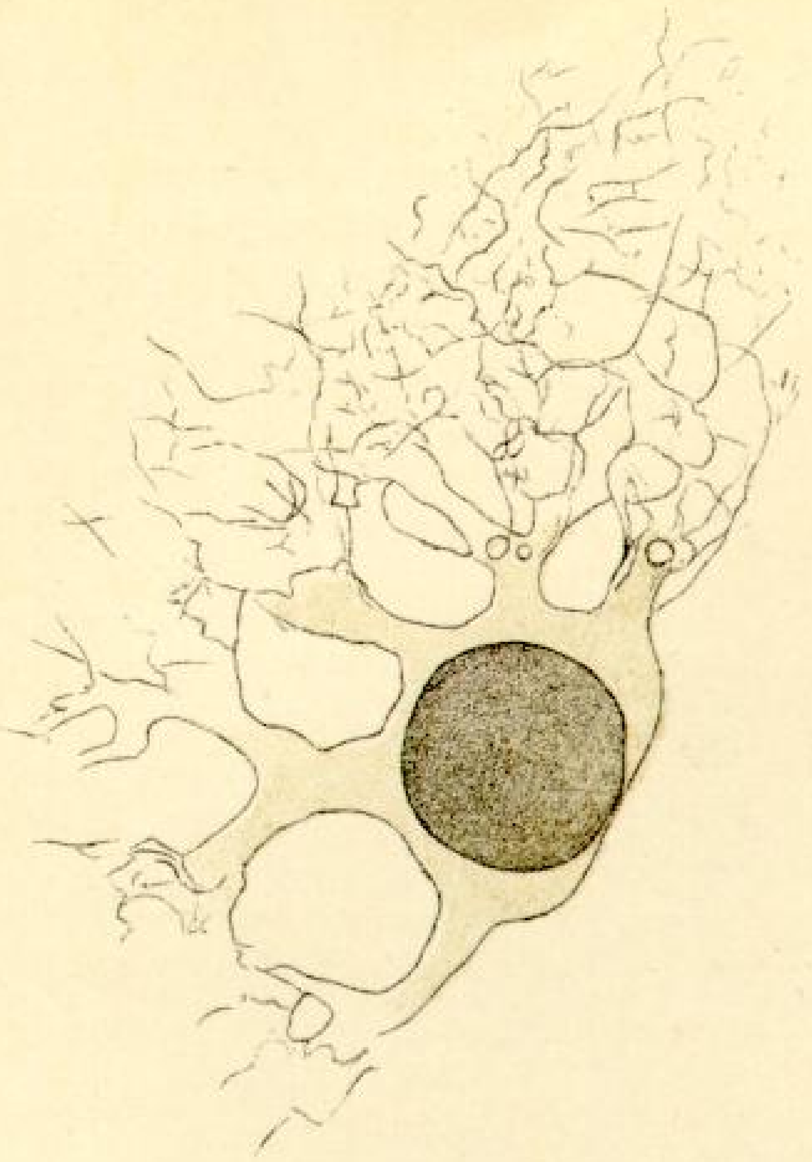

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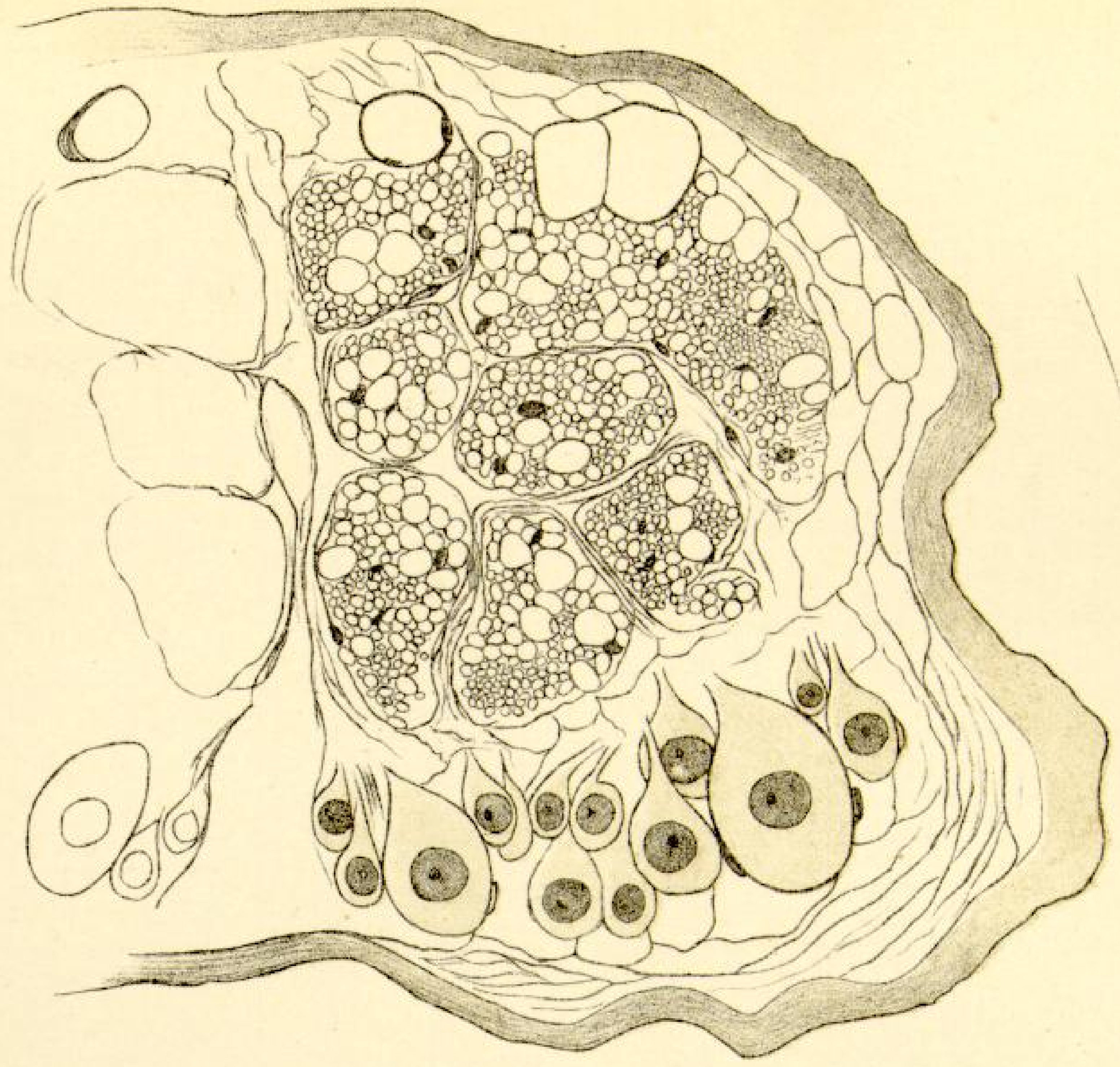

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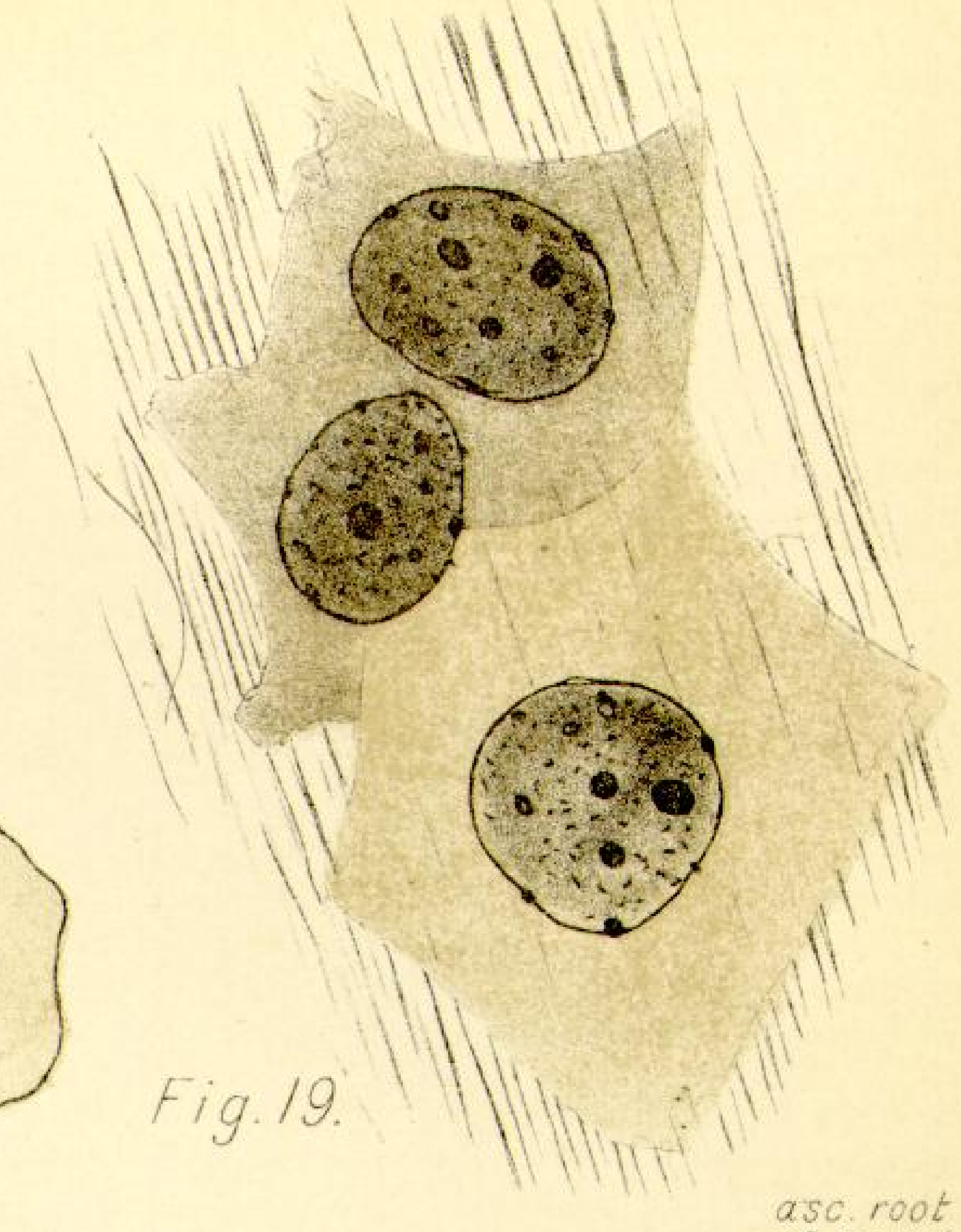

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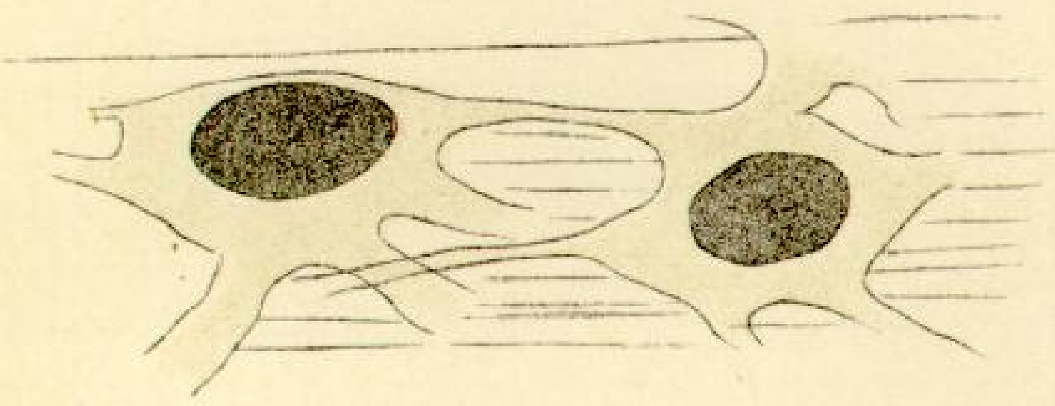

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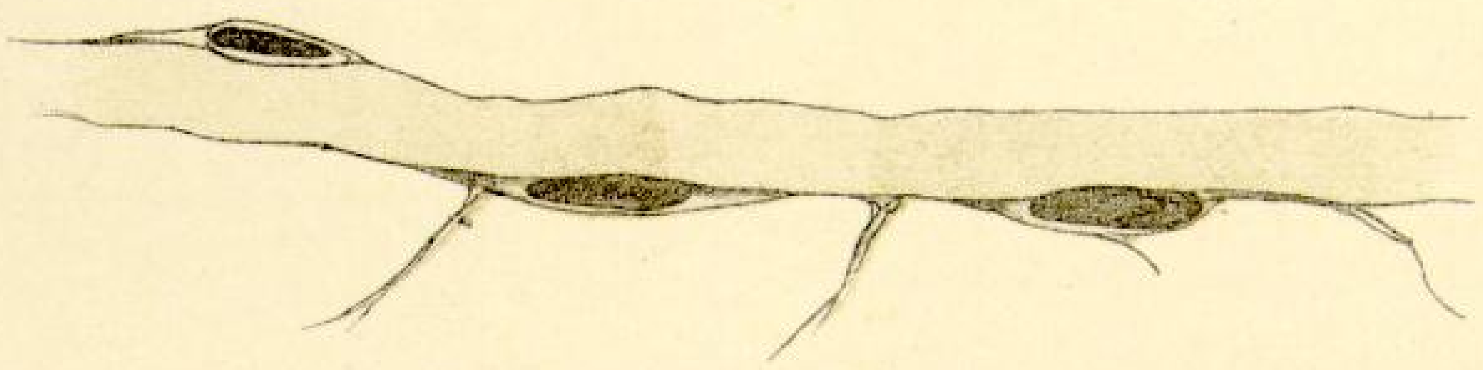

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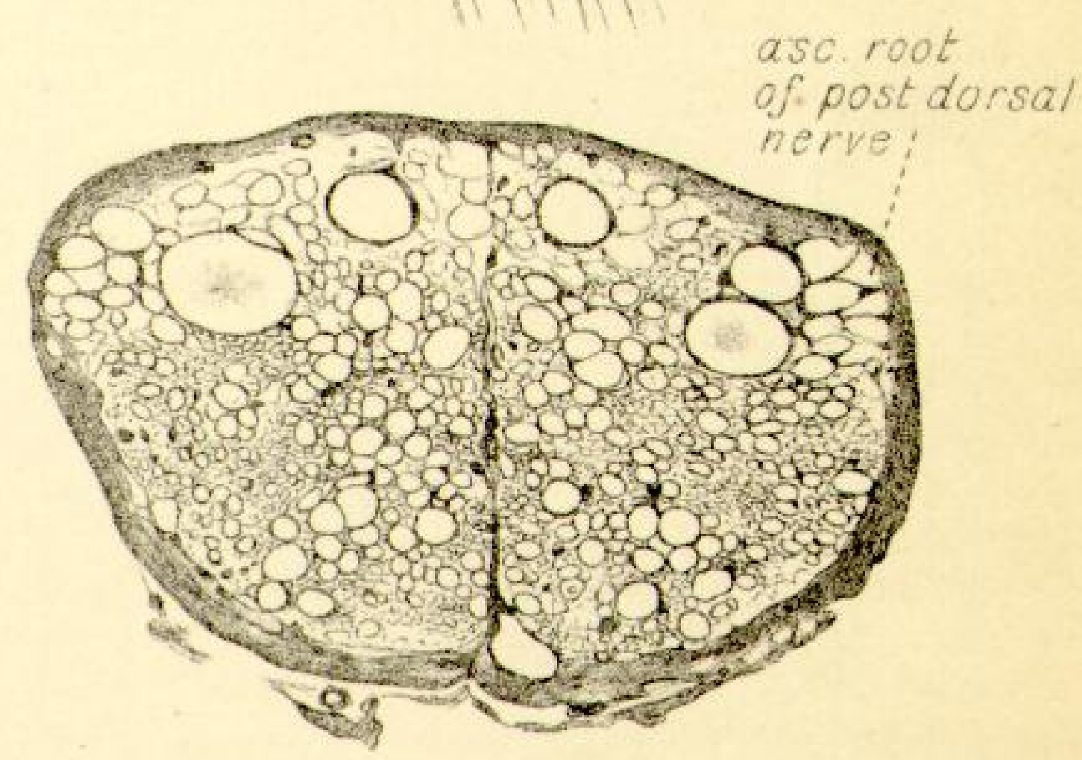

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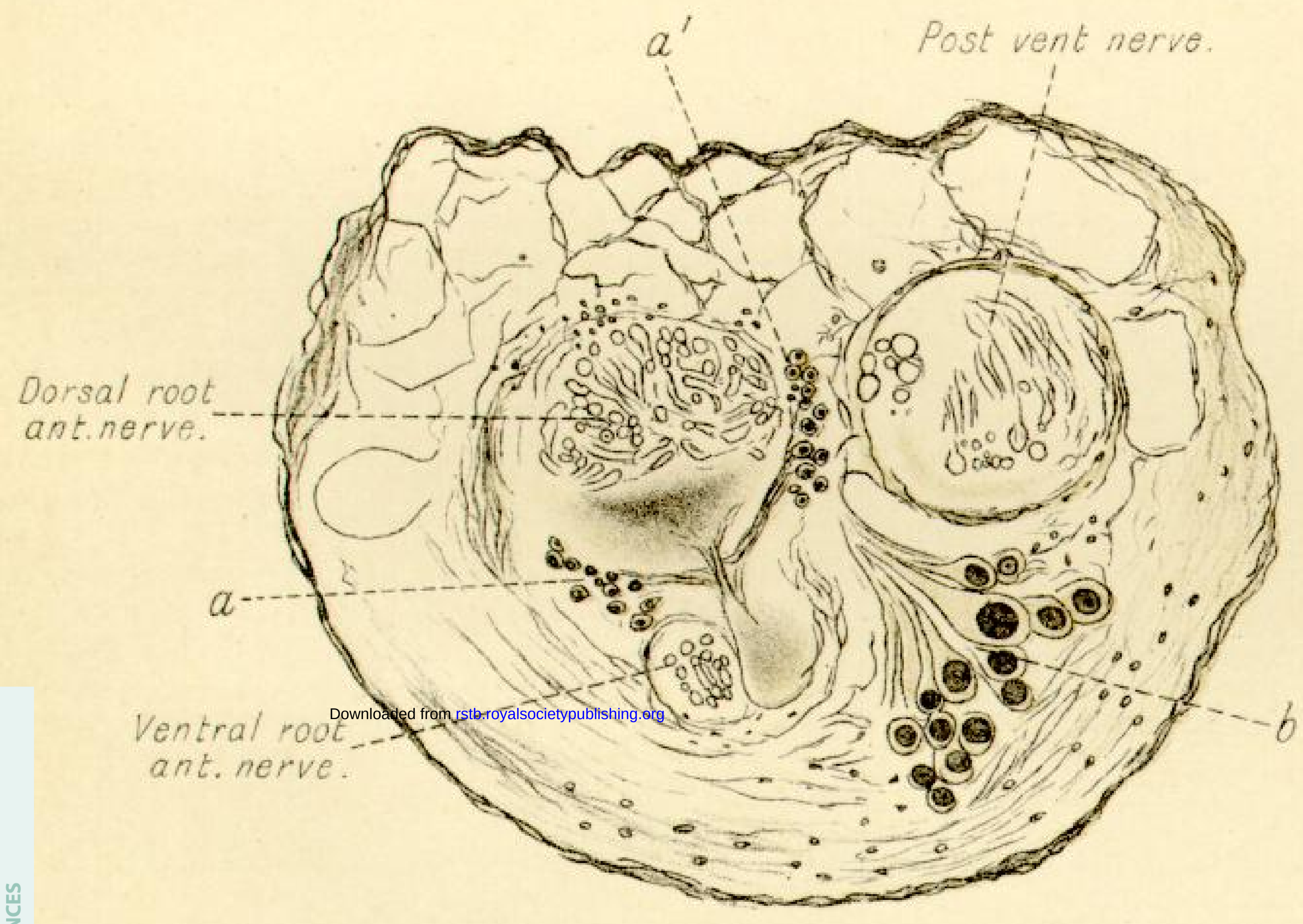

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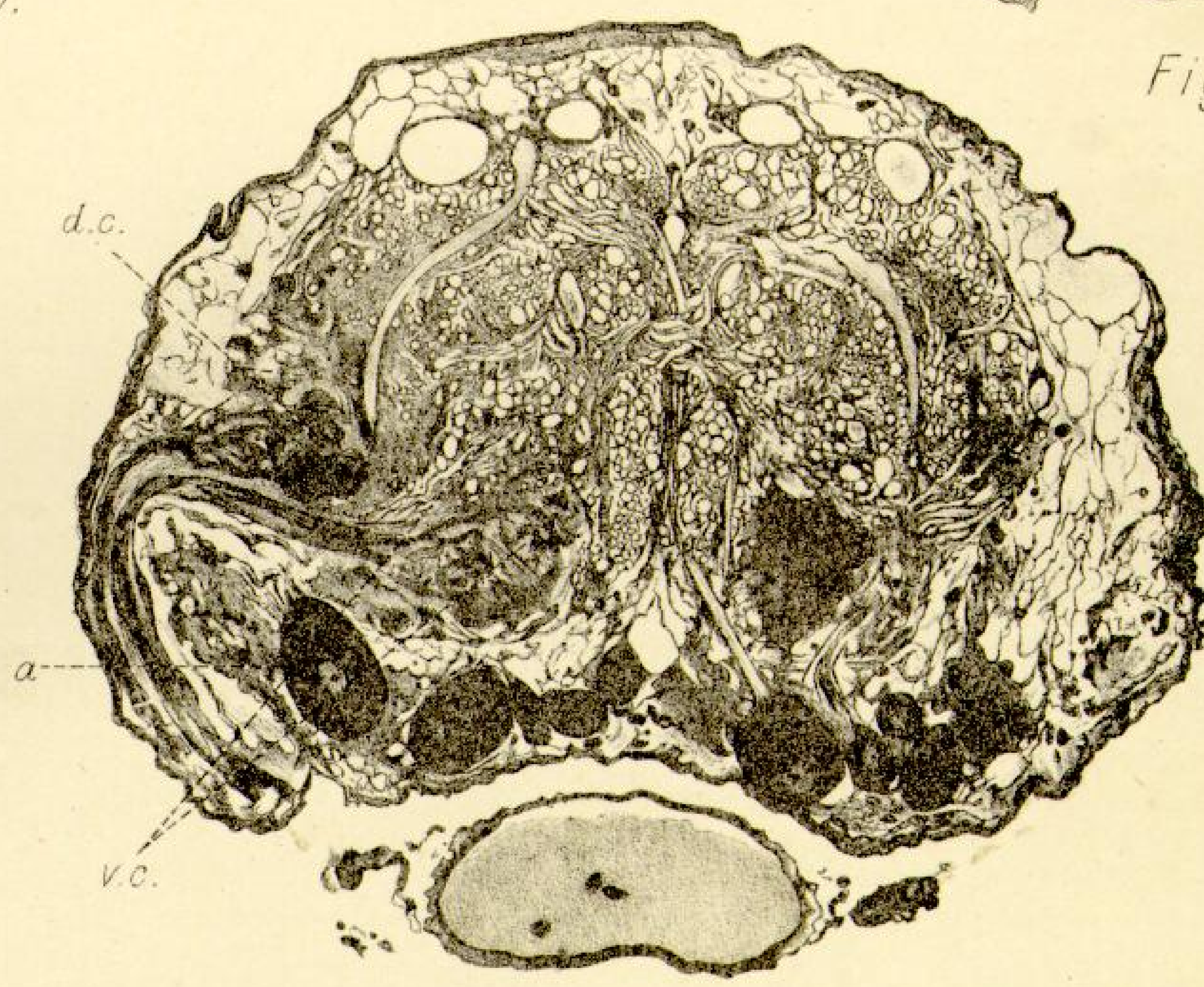

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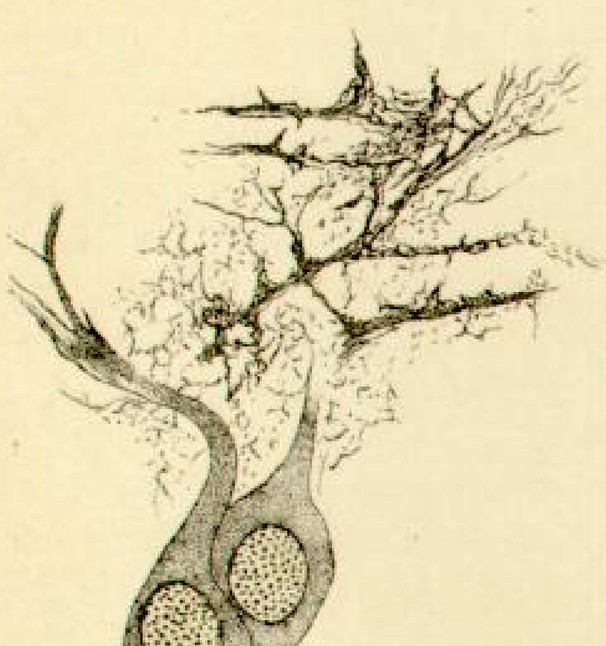

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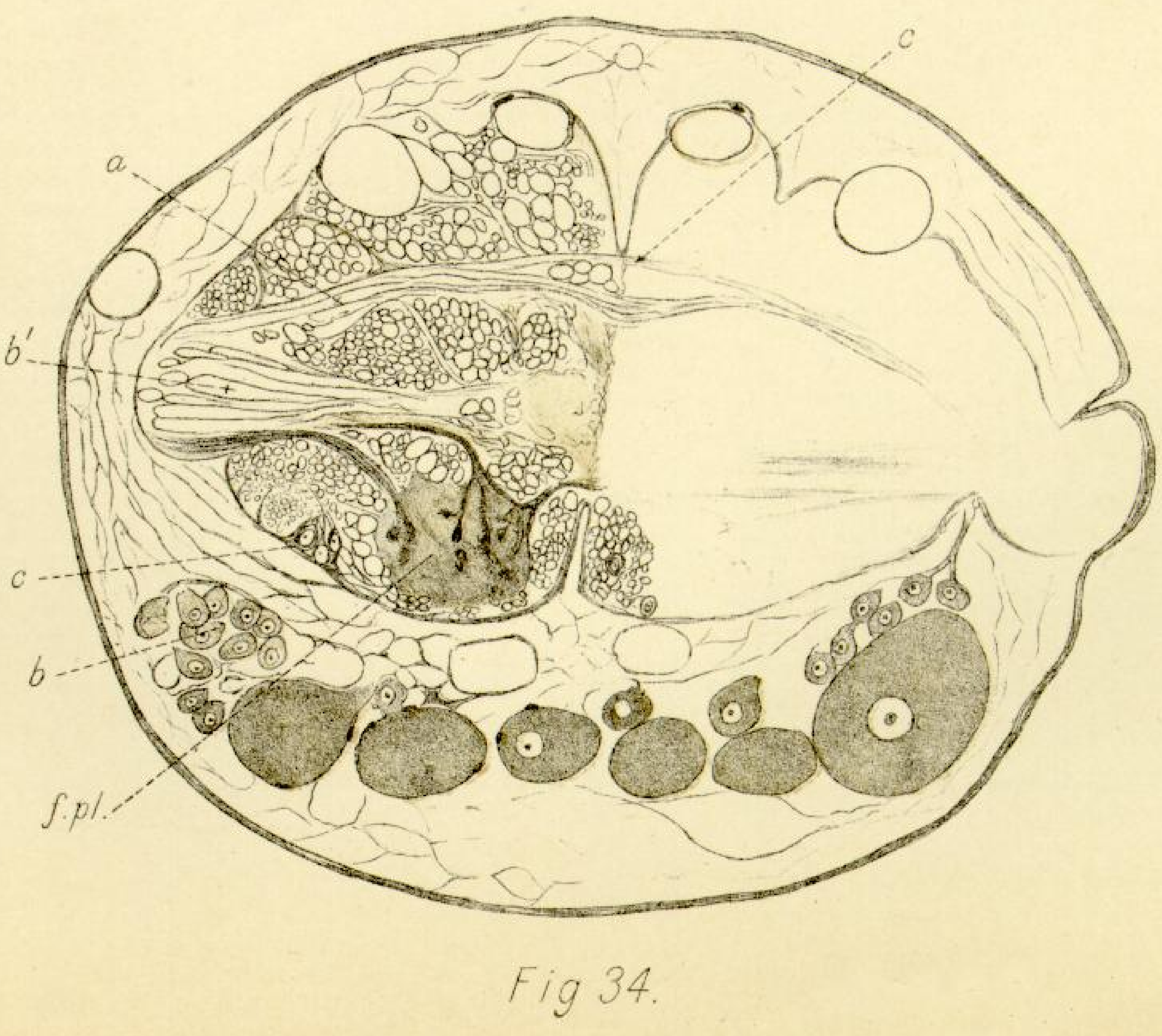

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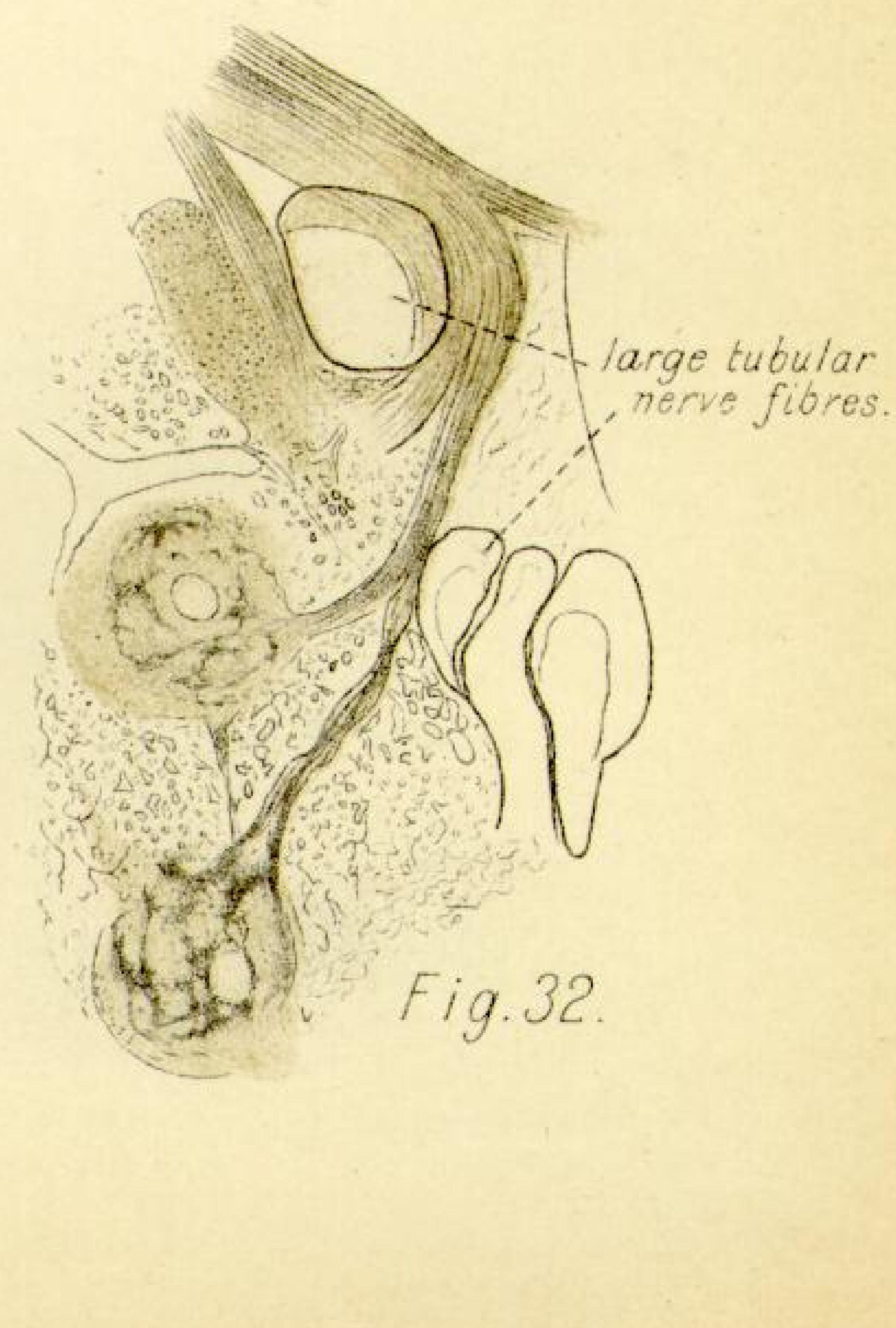

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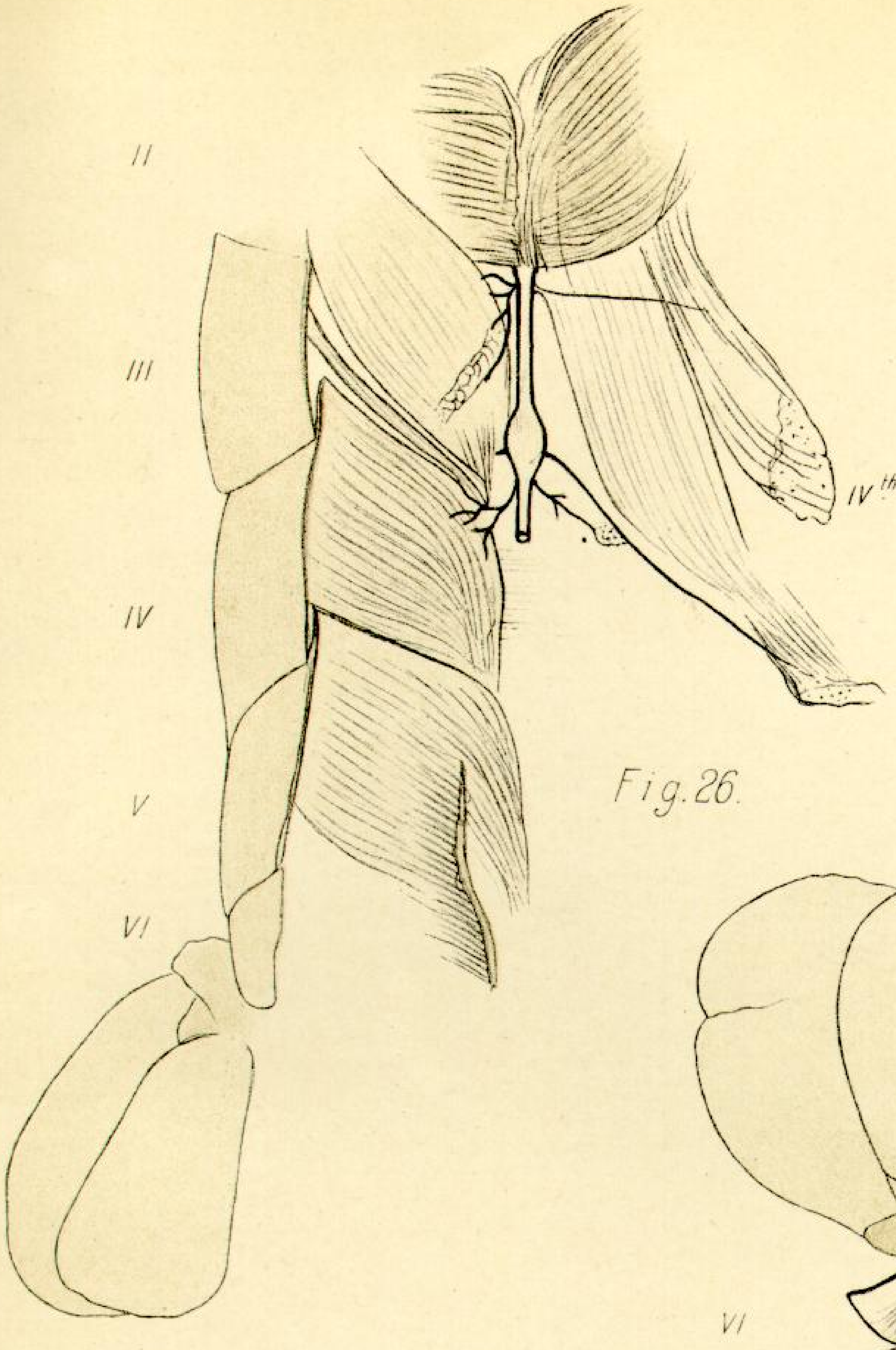

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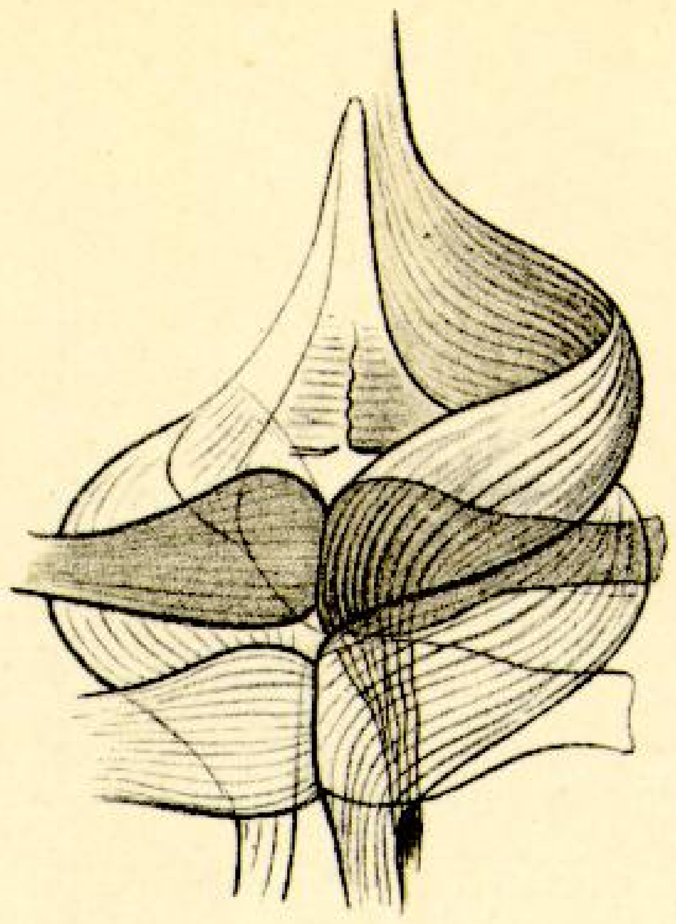

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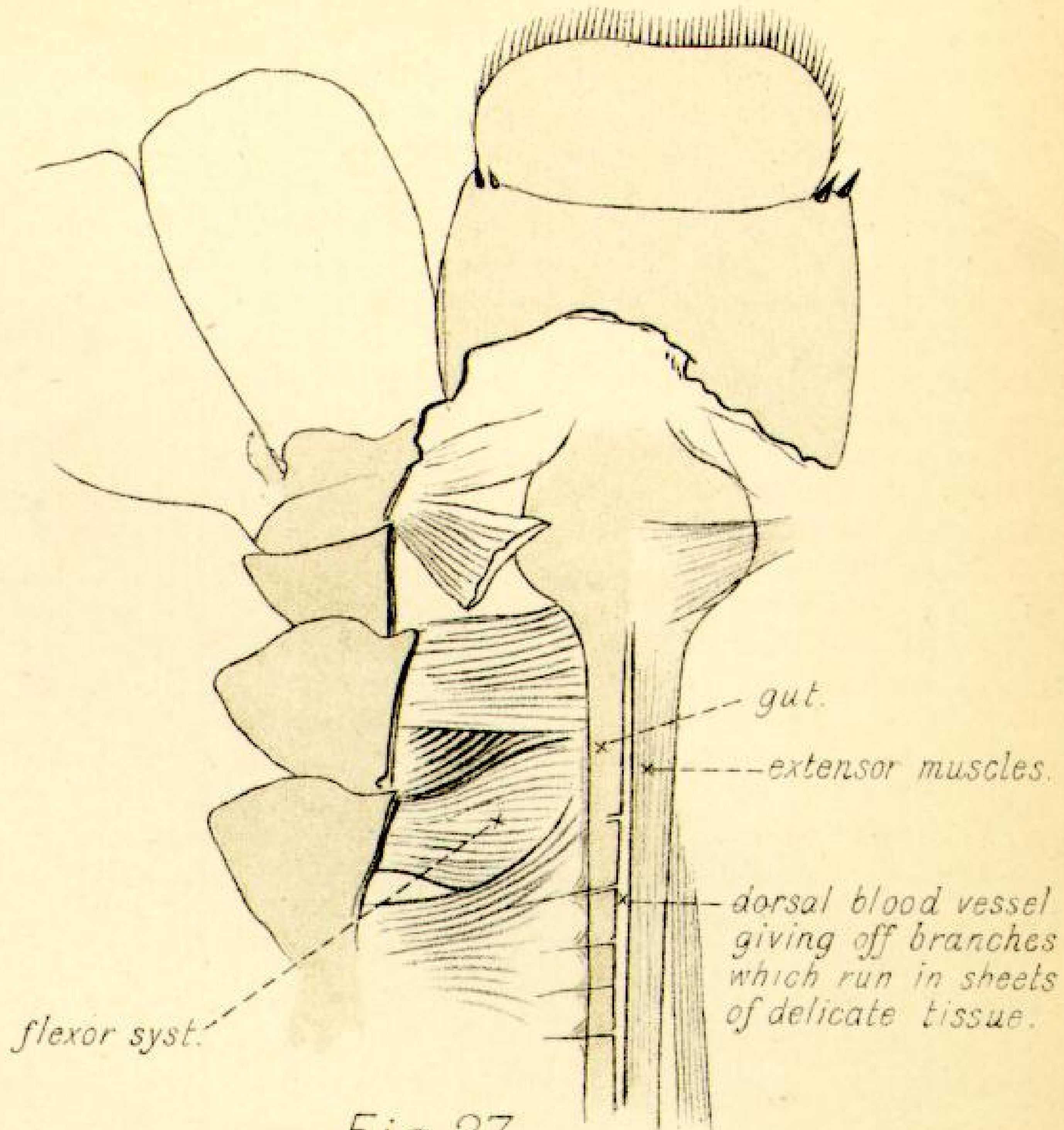

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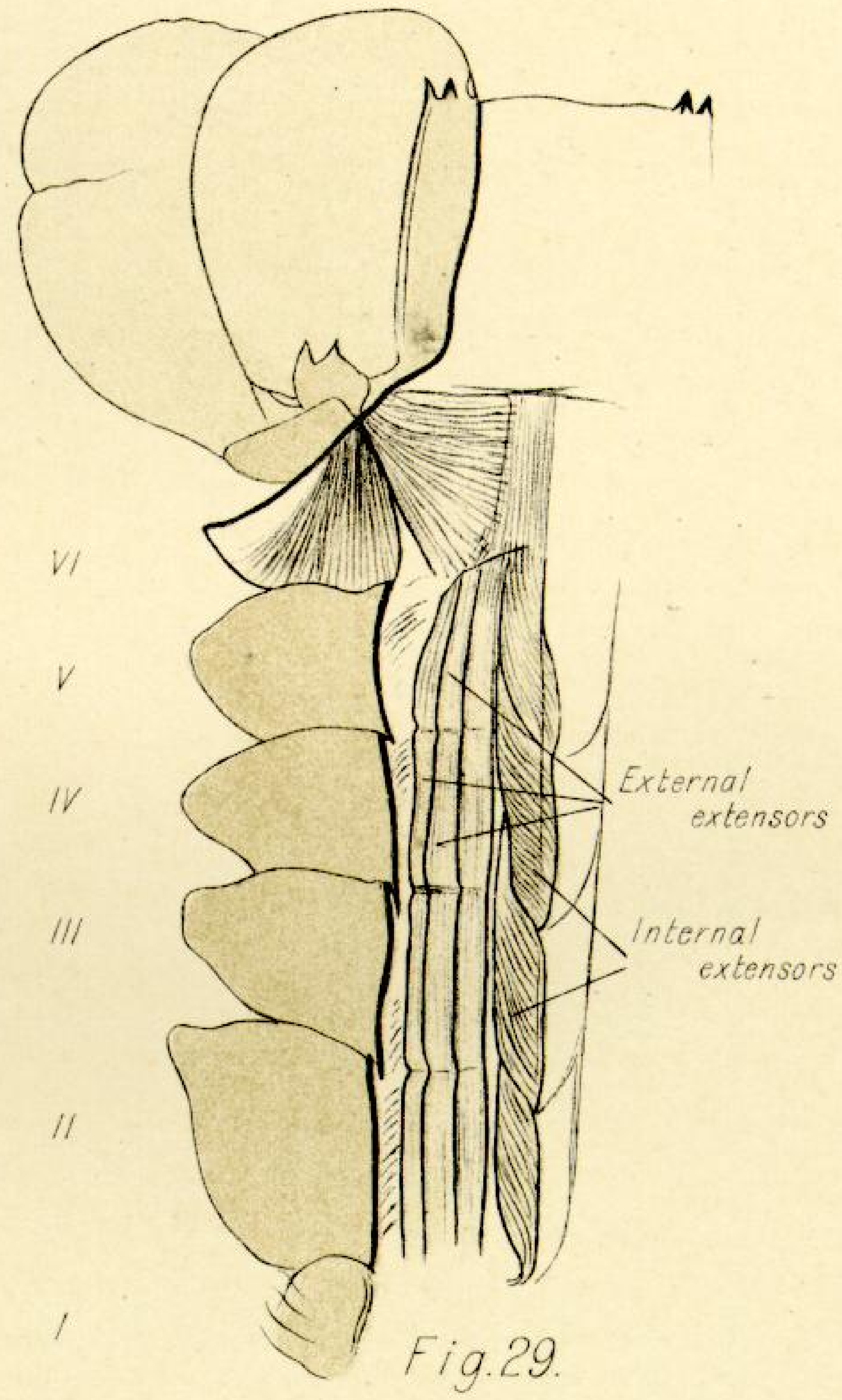

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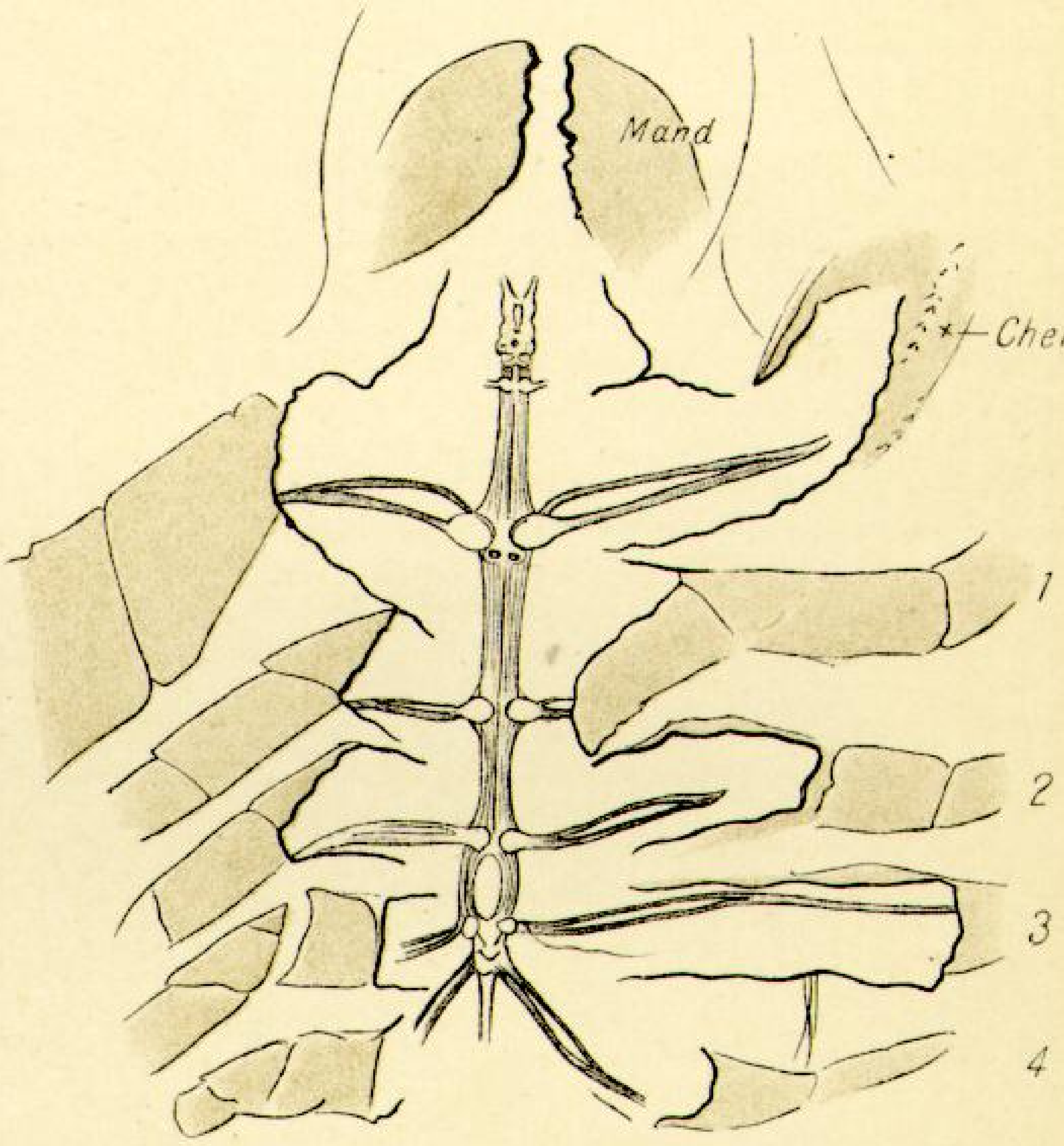

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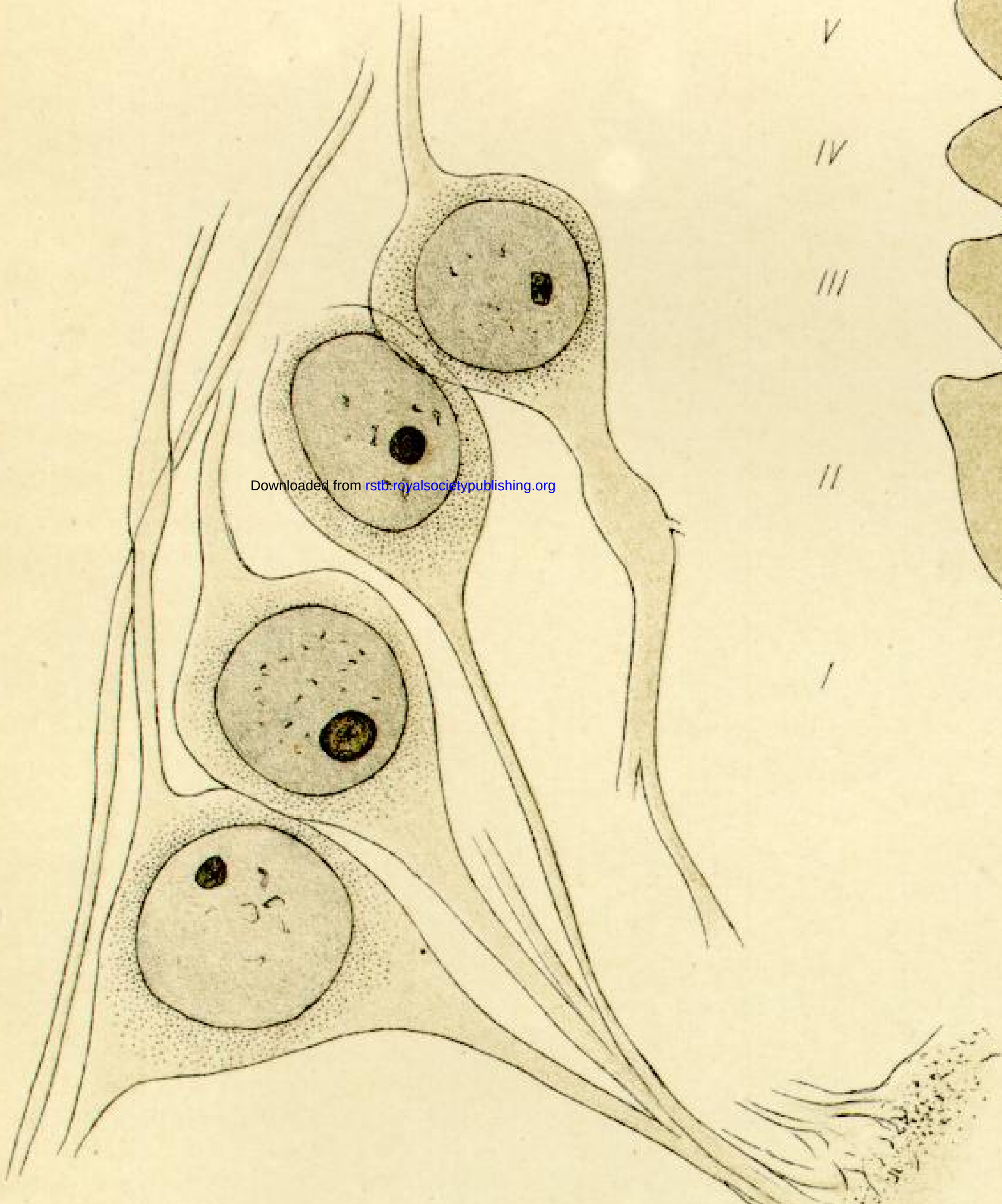

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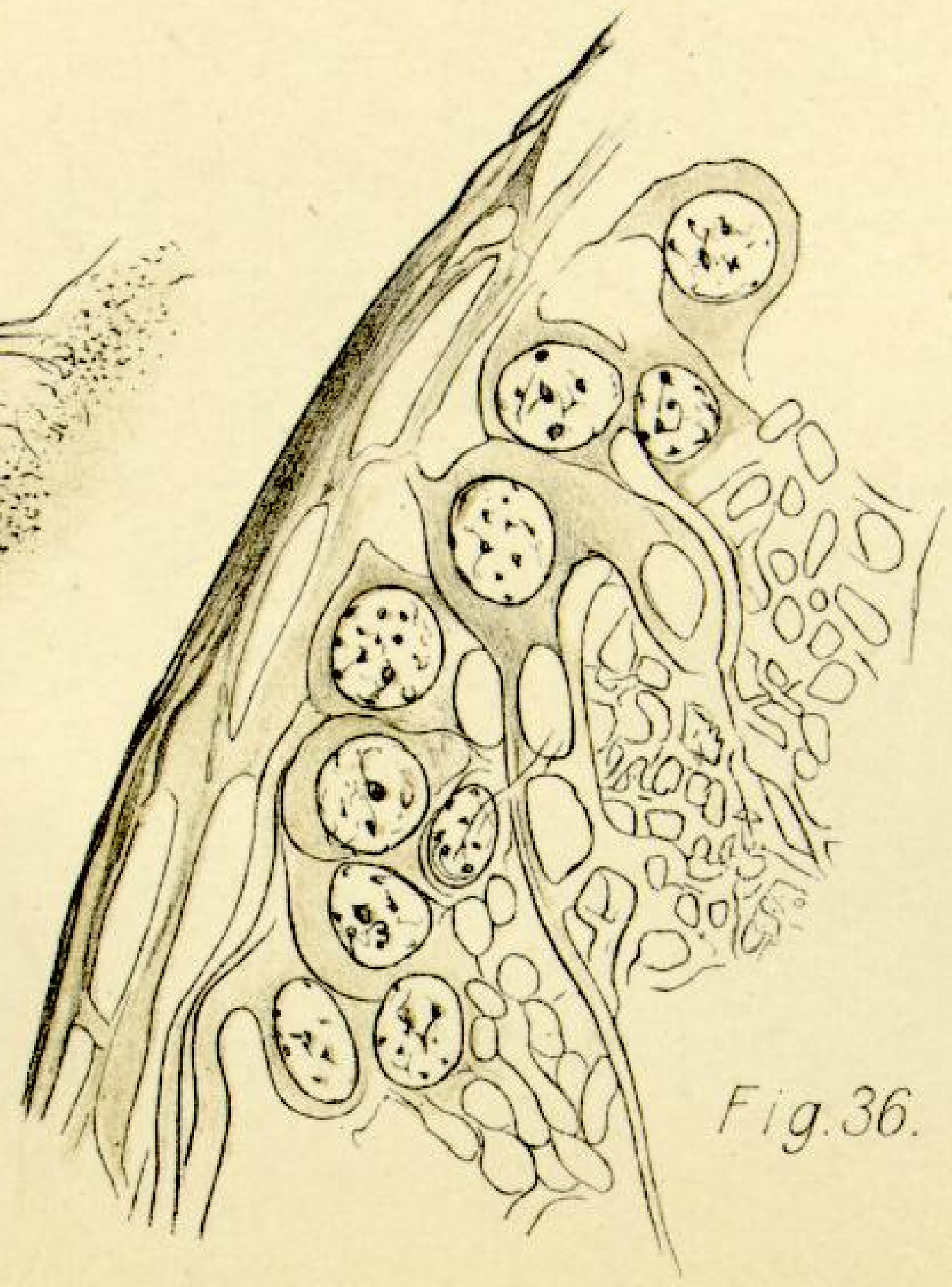

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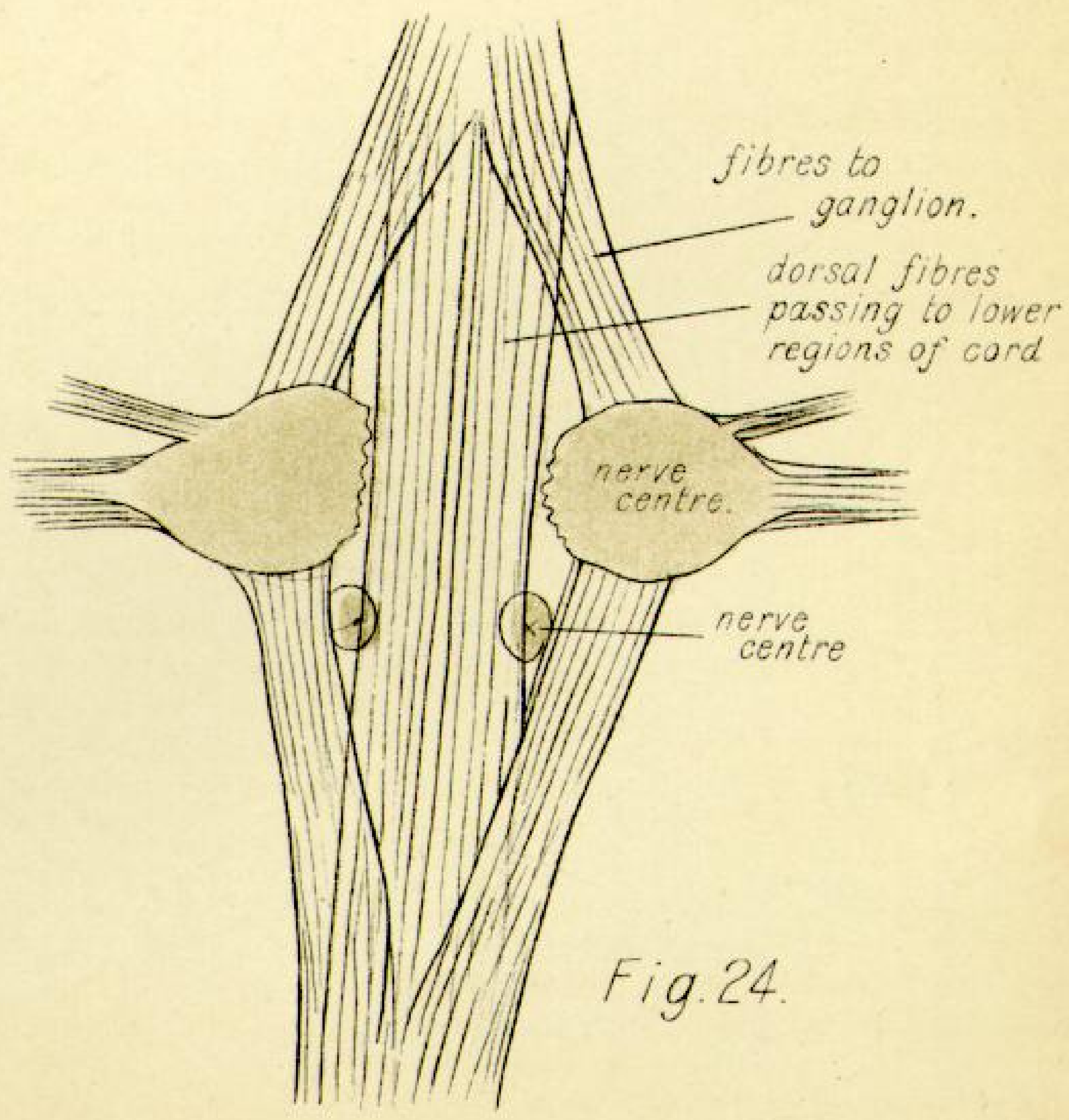

Fig. 24.