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The Motor Nervous System of the Starfish, Astropecten irregularis (Pennant), with Special Reference to the Innervation of the Tube Feet and Ampullae

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THE MOTOR NERVOUS SYSTEM OF THE STARFISH, *ASTROPECTEN IRREGULARIS* (PENNANT), WITH SPECIAL REFERENCE TO THE INNERVATION OF THE TUBE FEET AND AMPULLAE

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[Plate 27]

CONTENTS

The motor nervous system of *Astropecten irregularis*, lodged within the mesothelial linings of the coelomic body cavities, has a bilateral and metameric arrangement in conformity with the longitudinal seriation of the tube feet and of the ossicles and muscles of the ventral wall of the arm.

Bilateral and metameric groups of central distributory motor neurons, lodged above the radial nerve cord in the floor of the radial perihaemal sinus, have long axon processes which extend outwards on either side of each body segment through the lateral perihaemal canals to circumscribe the base of the foot. The central distributory axons may be regarded as pre-ganglionic fibres since they terminate in one or other of two ganglionic complexes: (*a*) the lateral motor complex on the outer side of the foot in the perihaemal cavity and (*b*) the foot complex within the foot cavity. The former is interposed into the tracts which supply the arm musculature, the latter serves as a relay to the several muscle systems of the foot and ampulla.

The post-ganglionic innervation of the arm musculature is effected through chains of distributory internuncial neurons linked in series. They form clearly defined tracts, each of which terminates in ultimate motor neurons. The axons of these neurons, initially of small diameter (*c.* $0{\cdot}5\,\mu$) and circular in section, expand distally into broad ribbons (20 to $30\times 0{\cdot}5\,\mu$) which invest the muscle fibres and have a continuous surface of synapsis with them. Some of the fibres of each muscle system are supplied by collateral branches of the ribbon axons.

The neurons of the foot complex are lodged in two more or less bilaterally disposed bulbs of supporting tissue within the base of the foot. One is lateral, the other (bilobed) medial. There are three component series of neurons in each bulb complex. α neurons synapse with and are in receipt of excitation from the central distributory axons external to the foot in the adjacent perihaemal canals. They transmit excitation to a β neuron complex which functions as a relay to the foot and ampulla musculature. Chain neurons conduct excitation from the β neurons to the ampulla. They terminate in ultimate motor (ribbon axon) neurons whose ribbon axons and axon collaterals innervate the ampulla musculature. The ultimate neurons serving the retractor muscles are in direct contact with the relay neurons of the β complex. Those supplying the postural muscles connect with the β complex through radially arranged fibres. The latter provide, in all probability, for the sectorial contraction of the musculature by which a 360° range of pointing and stepping can be effected. Circular fibres connecting the ultimate neurons of the various muscle sectors are thought to play a role in the display of autonomous and individual patterns of pointing.

The fine structure of the unique ribbon axons is described. Of particular interest is the presence of an axiolemma sheath.

Comparison is made of the echinoderm nervous system with that of other invertebrates.

INTRODUCTION

Experimental analysis of the nervous mechanisms which underlie locomotory and other behavioural activities of starfishes has, in the past, been gravely handicapped by an inadequate knowledge of the nervous anatomy of these animals and by misconceptions concerning the relations of the different parts of their nervous system. Cuénot (1887, 1891), to whom we owe the first detailed account of the nerve tracts within the starfish body, described the system as consisting of the following divisions: (*a*) an ectoneural system comprising sensory cells and association tracts best developed in the ectoderm of the radial nerve cords and circumoral ring; (*b*) a hyponeural motor system (Lange's nerves), situated in the mesoderm lining the floor of the perihaemal sinus above the cords and ring, and innervating the inferior ambulacral musculature; and (*c*) an apical motor nerve, also within the mesoderm, accompanying the longitudinal apical muscle of the arm in the roof of the perivisceral cavity.

In a paper describing the anatomy and histology of the nervous system of *Marthasterias glacialis* (Smith 1937) it was shown that Cuénot's apical system is part of a more extensive system of tracts which take their origin from nerve cells lodged in the wall of the perivisceral body cavity lateral to the tube feet. These lateral motor centres are bilaterally disposed in respect to the longitudinal axis of the arm and have metameric correspondence with the feet. The tracts to which they give rise extend as half-hoops around the two sides of the internal wall of the arm to end on the apical muscle, innervating, in their passage, other muscle systems within the body wall.

Intra-vitam staining with methylene blue (Smith 1946) confirmed the view that the starfish motor system consists essentially of the two series of bilaterally and metamerically arranged hyponeural and lateral motor neurons, both of which were found to have connexion with the subepithelial association tracts of the ectoneural system by way of fibres which penetrate the substance of the body wall. The tube feet and ampullae, the mode of innervation of which had not previously been known, were moreover shown to have both hyponeural and lateral motor connexions. Owing, however, to the fact that observations were made on whole mounts of pieces of tissue made opaque by the calcite contained within them, it was not possible to trace either the anatomy of the connexions nor the nature of the motor endings on the muscles in any detail.

Meanwhile (Smith 1945, 1950) experimental studies on the nervous control of the movements of the foot had suggested a scheme of innervation which would provide for the protraction, retraction and 360° range of co-ordinated directional locomotory stepping.

This scheme, while consistent with the known anatomical picture, presupposed certain additional details of arrangement and interconnexion of the hyponeural neurons with neurons seen to be contained within the cavity of the foot for which there was no anatomical justification. These suppositions related, in particular, to the innervation of the postural muscles by which the step is directionally oriented. In order to test their validity and the more surely to interpret the experimental data it has become necessary to work out the motor innervation of the starfish arm and feet in greater detail. The further investigation has been made possible by the successful application of the ammonium molybdate colour-fixation technique to starfish tissues and by finding it practicable to cut serial sections of arms without first decalcifying them. The concealed nervous elements have thus been revealed in some detail and in their normal anatomical relations. The present account divides into three main sections. The first deals with the technique employed and with the criteria adopted for the recognition of the nervous elements. There follows a section illustrating the anatomical principles underlying the motor innervation of starfishes based on a description of the nerve supply to one or two selected muscles within the starfish arm. These principles are then applied in the succeeding and main part of the paper to a clarification of the motor complex of the foot. Especial attention is paid in this part of the account to the form, fine structure and distribution of the axons which run in conjunction with and excite the musculature. These axons appear in many ways to be different from any motor elements that have previously been described.

Preparation of the material

The animals examined during the course of this work were freshly caught, small to medium-sized *Astropecten irregularis* (Pennant). Prior to staining, the arms were cut longitudinally along the midline and then divided into 3 to 4 mm. lengths by transverse cuts. Two or three of the half-sections of arm were placed in a Petri dish containing 50 ml. of sea water of about 35 *per mille* salinity to which had previously been added 0·5 ml. of 1 % methylene-blue (Grübler) leucobase, prepared by reduction of the dye with rongalit white (Unna 1916; McConnell 1932). The following observations on the use of the stain and the treatment of stained material summarize the experience gained since notes on the technique, as applied to starfishes, were last published (Smith 1946).

The staining solution

If the reduced solution of methylene blue is stored in a closed container it remains in the reduced state for some 3 to 4 weeks. Successful staining has been effected with solutions varying in age from 18 hr. to 25 days, though the solution stains most rapidly and effectively from about the fifth to the tenth day. When staining material daily over a period of some weeks it has been customary to make up several stocks of the leucobase, each of 20 ml. volume and to use them, in succession, over the period of their maximum efficiency. As soon as any one solution began to develop a blue colour the leucobase was regenerated by adding a pinch or two of rongalit white to the solution and gently warming it until it became colourless again. Solutions that had been regenerated several times did not appear to suffer any impairment of their staining properties.

The progress of staining

In order to assess the progress of staining, sections were made of tissues previously immersed in a well-aerated 1 % methylene-blue leucobase solution (1:10,000 concentration of the original dye) for periods varying from 1 to 12 hr. Staining begins towards the end of an hour, the sensory and subepithelial ectodermal nerve cells and fibres which are the most accessible to the dye and to oxygen being the first to take the colour. It is usually (though not invariably) complete in respect to all the elements of the foot by the fifth hour and may gain in intensity by further immersion. The tissues begin then, however, to show abnormalities such as 'beading' and their subsequent fixation is less satisfactory. Material stained for 5 to 6 hr. has in general provided the most successful combination of intensive staining with adequate tissue fixation.

Stain and tissue fixation, dehydration

Pieces of arm after removal from the stain were usually exposed for about a minute to the air or subjected to a stream of air from a compressor. It was hoped thereby to intensify the colour in the more deeply lying neurons to which oxygen is less readily available, but it was doubtful whether any advantage was gained by this treatment. The dye was made fast by immersing the tissues in a freshly prepared ice-cooled 8 % solution of ammonium molybdate in sea water. Ammonium molybdate is not a satisfactory tissue fixative, but in most instances the fixation was found to be adequate if the period elapsing between the excision of the pieces of arm and fixation was cut down to the minimum time compatible with good staining. The material after removal from the fixative was washed in running tap water for not more than 5 min. and taken at 0° C through numbers 6, 8, 9, 10 and 11 of Lang's series of graded water—95 % ethyl alcohol—N-butyl alcohol mixtures (Lang 1937).*

Storage of stained material

Dehydrated, stained pieces of arm were taken directly from N-butyl alcohol (Lang 11) to liquid paraffin, cedar-wood oil, or methyl benzoate. Specimens have been kept for more than two years in paraffin and cedar-wood oil without visible fading or loss of stain. Methylene blue leaches out fairly rapidly in methyl benzoate which was used merely as a medium for transfer to celloidin.

Embedding and cutting†

Pieces of arm later to be sectioned were transferred from N-butyl alcohol, liquid paraffin or cedar-wood oil to methyl benzoate for half an hour, thence to a 1·5 % solution of celloidin in methyl benzoate. Here they remained for from 12 to 48 hr., according to the size of the piece, to allow of complete penetration. The impregnated specimen was then lifted from the celloidin and dropped into a tube containing benzol. Within about half an hour the celloidin congeals into a rubbery mass which was doubly imbedded for 4 hr. in two changes

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* I am indebted to Dr H. P. Whiting for suggesting, on the basis of his experience with the vitally stained larvae of *Lampetra* (Whiting 1948), the omission of the more aqueous mixtures of the Lang series. Transfer from water direct to Lang 6 lessens the loss by solution of the precipitated dye and does not engender significant shrinkage.

† The ester-wax embedding technique (Steedman 1947) which should lend itself well to the cutting of calcified tissues came to my notice after the bulk of the material had been sectioned and has not been tried.

of 54 to 60° C wax with 1 % of ceresin added. Although the calcareous ossicles of the arms felt stony to the touch the great majority of the blocks cut perfectly well on a Cambridge Rocker microtome providing that the sections were not less than 20μ thick and that the knife was restropped after every fifth or, at the most, tenth section. Sections were usually cut at 40 to 50μ. Thick sections have the great advantage over thin ones of rendering the pattern of cell bodies and the course of their fibres relatively easy of reconstruction. It was, in fact, found impossible in thinner sections to be sure of the identity of any one fibre within a complex when attempting to trace its course from one section to another. Occasionally, for the purpose of checking the reconstructions from 40 to 50μ sections, blocks were cut into 100μ slices. This can be done on a Rocker microtome if a bunsen burner is placed close to the block in order to soften it and so prevent cracking and curling of the wax.

Counterstaining

Serial sections were usually mounted in balsam without previous counterstaining. Some few slides, however, were counterstained with 1 % eosin or 0·5 % orange G in 90 % alcohol. No perceptible fading of any of the permanently mounted sections has yet been observed, though many of the preparations are at the time of writing more than two years old.

All drawings of sections have been made, in the first place, on squared paper against a squared eyepiece grid.

IDENTIFICATION OF THE NERVOUS ELEMENTS

Methylene blue when used as a vital dye stains certain non-nervous tissues in addition to the neurons. Although it is not usually difficult to distinguish between the two it may be well briefly to state the criteria adopted for the identification of the neurons.

Cell bodies which are drawn out into long thin fibres (e.g. figures 1, 5 and 11) appear, in starfishes, always to be nervous in function. The grounds for this generalization are that: (*a*) in non-vitally stained preparations of starfish tissues neither muscle nor collagen (the only other fibrous elements present) remotely resemble the nerve cells. Their fibres are much thicker, more markedly birefringent and their nuclei have different relations to the fibre; (*b*) the neurons stain more intensely and well in advance of collagen and muscle; and (*c*) the neurons have anatomical relationships one with another and with the muscles which would be meaningless if they were to function as anything other than conductors of excitation.

While therefore the nervous nature of the long thin-fibred cells may be assumed, blue staining cells which lack fibres or have only short processes are more difficult to interpret. A cell of this kind may be: (*a*) a neuron whose cell body (1) stains in advance of its fibre or fibres, or which (2) remains coloured after the stain has faded from the fibre; (*b*) a neuron whose fibre is so excessively tenuous at its origin from the cell body as to be invisible or only doubtfully perceptible; (*c*) a neuroblast whose cell processes have not developed; or (*d*) a non-nervous cell.

The condition (*a*1) is normally met with in the early stages of staining of most neurons. A further period of immersion in the stain will, however, always show whether or not cell processes are present. The condition (*a*2) has not been observed, though the disappearance of colour from the cell body after prolonged immersion is of common occurrence. Cell bodies with exceedingly fine fibres (*b*, above) are frequently found, as, for example, those of figure 1 (*f*) and figure 13 *A* and *C*, *c.b.*, in which latter instances the cell body gives rise to a scarcely visible fibre (*f.fib.*) which, in its more distal course, expands into a broad ribbon (*rib.ax.*). Here again, though in any one preparation the cell bodies may appear as isolated structures, their fibre connexions usually become apparent when the appropriate period of staining is ascertained. There are, however, a few remaining instances (figures 6, 7, 20, *c.b.*) where possible fine fibre connexions between cell bodies (*c.b.*) and axons (*rib.ax.*) still require to be demonstrated. Some non-nervous elements (*d*, above) are easy to identify as such. This is true of the integumental mucus cells and of the large amoeboid wandering cells of the coelomic cavities. Smaller cells sometimes to be found in the neighbourhood of nerve fibres (figure 1, *x*) are of a more puzzling character. They may perhaps be connective tissue cells or neuroblasts, but as they do not appear to have determinate nervous linkages they have been omitted from the account and, except in the instance cited, from the figures.

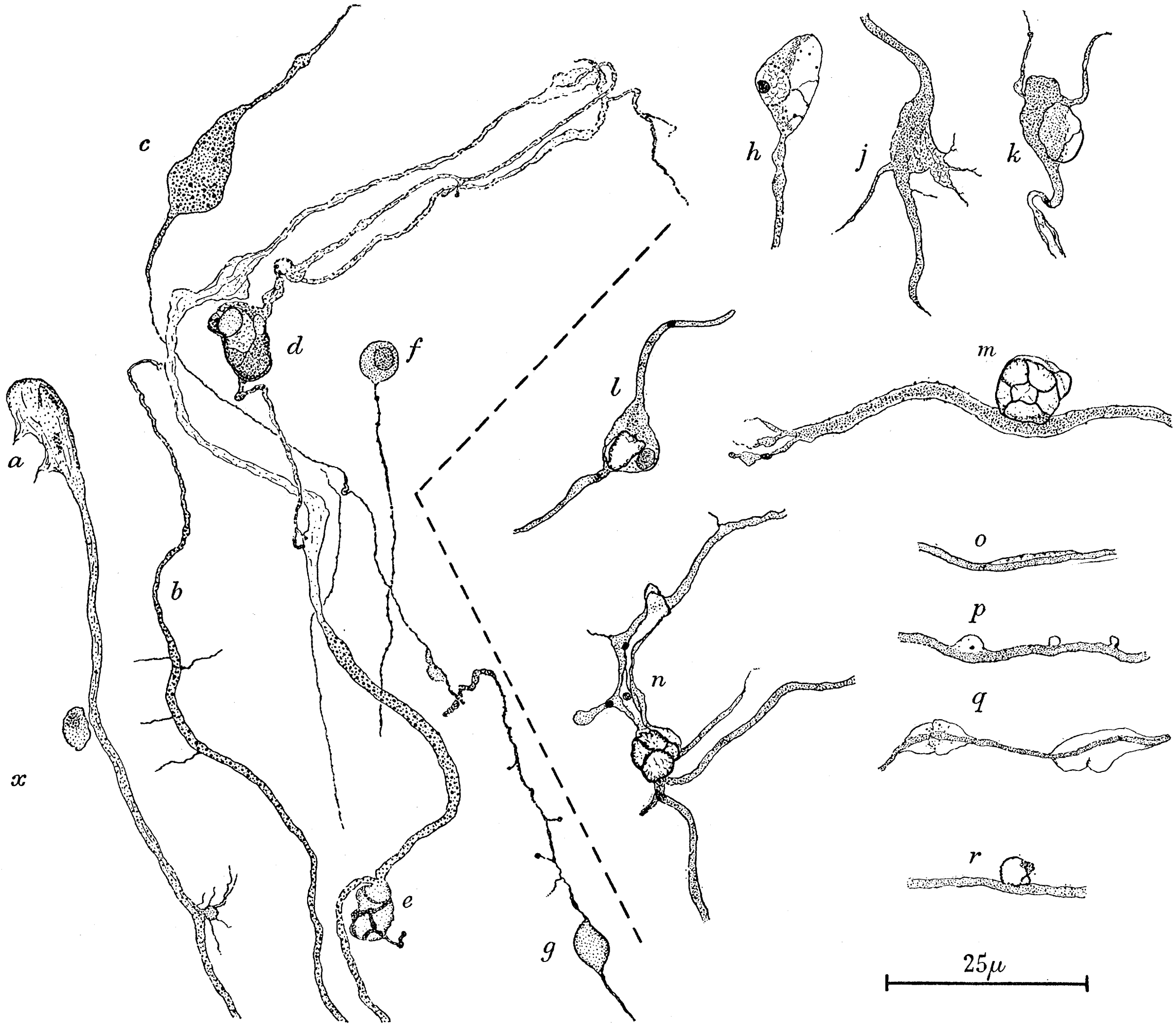

Figure 1. *a* to *r*, motor neurons and fibres from the bulb complex of the foot showing normal conditions of staining and some of the more commonly occurring artefacts. The neurons to the left of the broken line are drawn in their observed relations, those to the right of the line are selected examples of individual neurons and fibres. *x*, cell body of a problematical character.

Interpretation of the structure and interrelations of the motor neurons

A neuron which has been stained for some hours in methylene blue, fixed in ammonium molybdate and subsequently dehydrated, differs markedly from the living neuron both in respect to its individual appearance and its relations to other neurons. Even while staining is in progress pathological changes in the form of the cyton and of its fibres are made manifest. Beading of the smaller fibres is but one of many such changes. The validity of any judgement concerning the form and relations of the living neurons must therefore depend on the extent to which the more commonly occurring artefacts can be recognized and allowed for.

Artefacts may be reviewed under two headings, the first affecting individual neurons, the second their spatial relationships. Figure 1 illustrates the points at issue, all types of motor neuron except the ultimate (ribbon axon) neurons (see below, p. 545) being shown, and many kinds of abnormality as well as supposedly normal conditions being represented.

The cell bodies of the individual neurons are from 4 to 12μ in diameter, spherical, pear-shaped or more or less irregular in outline, the shape in general being related to the number of processes emerging from the cyton. The nucleus is sometimes visible (*f*, *h*) but not always (*a*, *c*). On occasions the cytoplasm stains with a uniformly blue punctation (*c*, *j*), but parts of the cell are frequently devoid of colour and apparently vacuolated (*h*). The vacuole is often dilated to form a blister (*k*, *l*), in which event the thin bounding membrane becomes patterned by a blue-staining reticulum which is most apparent when the blister is large and seemingly devoid of cytoplasmic content (*m*). The reticulum somewhat resembles the superficial Golgi network described by Bethe (1903) and other workers. Tiegs (1926) questions the reality of Bethe's Golgi network. He finds that nerve cells often have a frothy appearance after methylene-blue staining, and he regards the network as a product of coagulation for 'all intermediate stages between such a network and undoubted surface coagulations may readily be observed'. My observations and conclusions accord with those of Tiegs. The superficial network on the motor neurons of starfishes is an undoubted artefact, and there is no reason to suppose that it is related either to pre-existing structures in the living cell or to synaptic endings on the cyton that might have evaded staining. The observed synapses are almost always between one nerve fibre and another (figure 1*b*,*e*), a condition which, as Holmes (1942) has remarked, is probably common among invertebrates and which Bodian (1942) also reports in vertebrates.

Nerve fibres (other than the large ribbon axons) vary in diameter from about 0·2 to 4μ. The finest fibres almost always bead after an hour's staining and, as Allen (1894) noted in crustacean fibres, the rapidity of beading is inversely related to the fibre diameter. One may add that in asteroid fibres there is a critical diameter of about 1μ above which beading does not readily occur. The coarser fibres, on the other hand, tend to blister by the elevation of an extremely thin colourless membrane from the central core of blue-staining axoplasm (figure 1,*o*,*p*,*q*,*r*). Except for the giant fibres of cephalopods (Bear, Schmitt & Young 1937), annelids (Nicol 1948) and crustacea (Holmes 1942), to cite some of the more recent papers on this subject, invertebrate fibres are usually regarded as unmyelinated and naked. The unmyelinated giant fibres of balanoglossids, for example, which at 2·5 to 5μ are comparable in diameter to the larger fibres of asteroids, appear to be without a sheath of any kind (Bullock 1944). It would be unwise to come to a definite conclusion concerning the nature of the delicate investing membrane of the asteroid nerve fibre without further investigation, but the indications are that here, as in the ribbon axons (see below, p. 547), the membrane is a part of the neuron itself and not, like the myelin sheath, an adventitious layer.

Axon swellings even when large (figure 1*q*,*r*) can usually be distinguished without difficulty from cell bodies, and their presence is unlikely to lead to misrepresentation of the relations of neurons. Artefacts of the nerve fibre terminals, on the other hand, are very troublesome. As Bodian (1942) has remarked '...many axon terminals are...minute and their post-mortem change is often very rapid. The uncertain staining qualities of many axon endings, because of these and many other factors, constitute the most common obstacle in the determination of normal anatomical relations as well as of experimentally induced changes.' One is vividly aware of this difficulty when examining methylene-blue preparations of starfish tissues. The fibre terminations are sometimes club-shaped (figure 1, *e*), more often finely tapered (*c*), and are frequently branched (*d*), while more often than not they appear to be unconnected with other nerve cells or muscles. In most instances however, one of which is later discussed in detail (p. 541), the terminals have a general direction which, if continued for a very short distance (10 to 20μ), would place them in connexion with other cells and fibres, and one has the impression that the gap may be bridged in the living system by fine fibres which either fail to stain or have suffered regression during staining and fixation. Herein lies the principal assumption that has been made in the interpretation of the spatial relationships of neurons and the patterns of their connexion during the course of this work. It may be explicitly stated as follows: where undoubted synapses appear to be absent, continuity of conduction has been assumed if the orientation and appositional tendencies of fibres one to another are such as to make synapsis or physiological continuity probable.

THE MOTOR INNERVATION OF THE ARM

(*a*) *General features*

The motor nervous system of the starfish may be defined, for the purposes of this account, as the system of neurons interposed between the association nerve tracts of the ectoderm and the muscles and other effector systems of the body. All the motor neurons lie within or upon the mesothelia which line the various coelomic body cavities, and their fibres, in their course to the muscles, tend to adhere to the walls of the sinuses.

The first, and functionally perhaps the most important, feature of the motor innervation of the arm is the bilateral and metameric arrangement of the nervous pathways. Metamerism*

* The term metamerism is here used in the sense defined by Lankester (1904) as indicative of the repetition of structural units in line. The units repeated are metameres. In the starfish arm, where there are two alternating systems of serially repeated structures, we might speak of one series as metameres or meres and the other as intermeres, or the alternating systems might be grouped together in pairs, each pair constituting a metamere. The development of the calcareous plates of the starfish arm (Gordon 1929) lends some support to this latter view, for the rudiments of the paired ambulacral plates are laid down at much the same time as those of the adambulacral ossicles proximal to them. The seriation of the motor nerves does not, however, correspond to the metameres so defined. The hyponeural (central) and lateral motor neurons are adambulacral in position and extend proximally and distally to the adjacent areas of the ambulacral ossicles. I have preferred therefore, for convenience of description, to call the transverse slices of the arm which contain the adambulacral ossicles and the tube feet the metameres, and to regard the transverse slices containing the ambulacral ossicles as intermeric.

is exhibited in respect to a number of the constituent parts of the arm including the tube feet, the adambulacral and ambulacral ossicles, and the muscles of the ventral (oral) body wall. Some of these, as for example the tube feet and adambulacral ossicles, have a strictly transverse correspondence *inter se* while alternating with other bilaterally correspondent structures such as the ambulacral ossicles and supra-ambulacral muscles, new parts being added during growth by the proliferation and differentiation of tissues within a subterminal growth zone. It will be convenient, for the reasons given in the footnote, to term the transverse slice of the arm within which is contained a pair of tube feet, one on either side of the midline, as a metamere. A half of such a metamere, together with an ambulacral ossicle of an adjoining intermere, is drawn in figure 2. The various motor cells and fibres shown in the figure are bilaterally arranged in each metamere and are serially repeated throughout all the metameres of the arm. The metameric pattern of the motor system is, moreover, definitive, in that none of the nervous pathways appear to extend from one metamere to another.

Every motor pathway that has so far been traced within the arm originates from groups of neurons (*c.dist.*) lodged above the nerve cord (*n.c.*) in the floor of the radial perihaemal sinus. The axons of these motor neurons extend outwards into the lateral canals of the sinus along the proximal and distal faces of the tube foot (*t.ft.*). Lateral to the podium and still within the canal they converge to terminate within a system of neurons which may be termed the lateral motor complex (*lat.mot.*). During their course along the lateral perihaemal canals the axons of the central distributory neurons come to lie very close to a motor complex contained within the cavity of the foot from which they are separated by a thin layer of connective tissue, some 5μ thick. The foot complex is omitted from the figure, its constitution and relations with the central neurons being considered in some detail later (p. 543). For the moment we will be concerned with the extension of the axon tracts beyond the lateral motor complex and the distribution of the nervous pathways which supply the various muscles of the arm.

Two main fibre tracts diverge from the lateral motor complex. One runs for a short distance along the length of the arm in the farthermost extension of the lateral perihaemal canal towards the longitudinal adambulacral muscle (*b*). The second traverses the substance of the lateral transverse muscle (*a*) beyond which it divides into two branches. One branch terminates near the apical muscle (*e*), the other mounts the lateral face of the ambulacral ossicle (*amb.oss.*) and, after running medially, forks at its extremity into two branches ending respectively in the neighbourhood of the supra-ambulacral (*d*) and longitudinal ambulacral (*c*) muscles. Each of the four series of tracts is made up of chains of serially arranged bipolar neurons, the multisynaptic pathways efferent to the lateral motor complex thus differing markedly in constitution from those on its afferent side which are made up of the extended single-fibre axons of the central motor neurons.

The chain neurons were described in the previous paragraph as ending in the *neighbourhood* of the arm musculature. They do not, in other words, directly innervate the muscle fibres. Junction with the muscles is effected through neurons of an entirely different character from those of the main supply tract. Their cell bodies, when they can be identified, are disposed in groups around each muscle, a condition represented in figure 2 by the small arrows projecting into the areas circumscribed by the dotted circles. The axons of these neurons may best be likened to ribbons many times broader but not noticeably thicker than the thread-like fibres of the nerve chain. They are applied along the length of the muscles, many fibres of which are served by collateral branches of the ribbon axons.

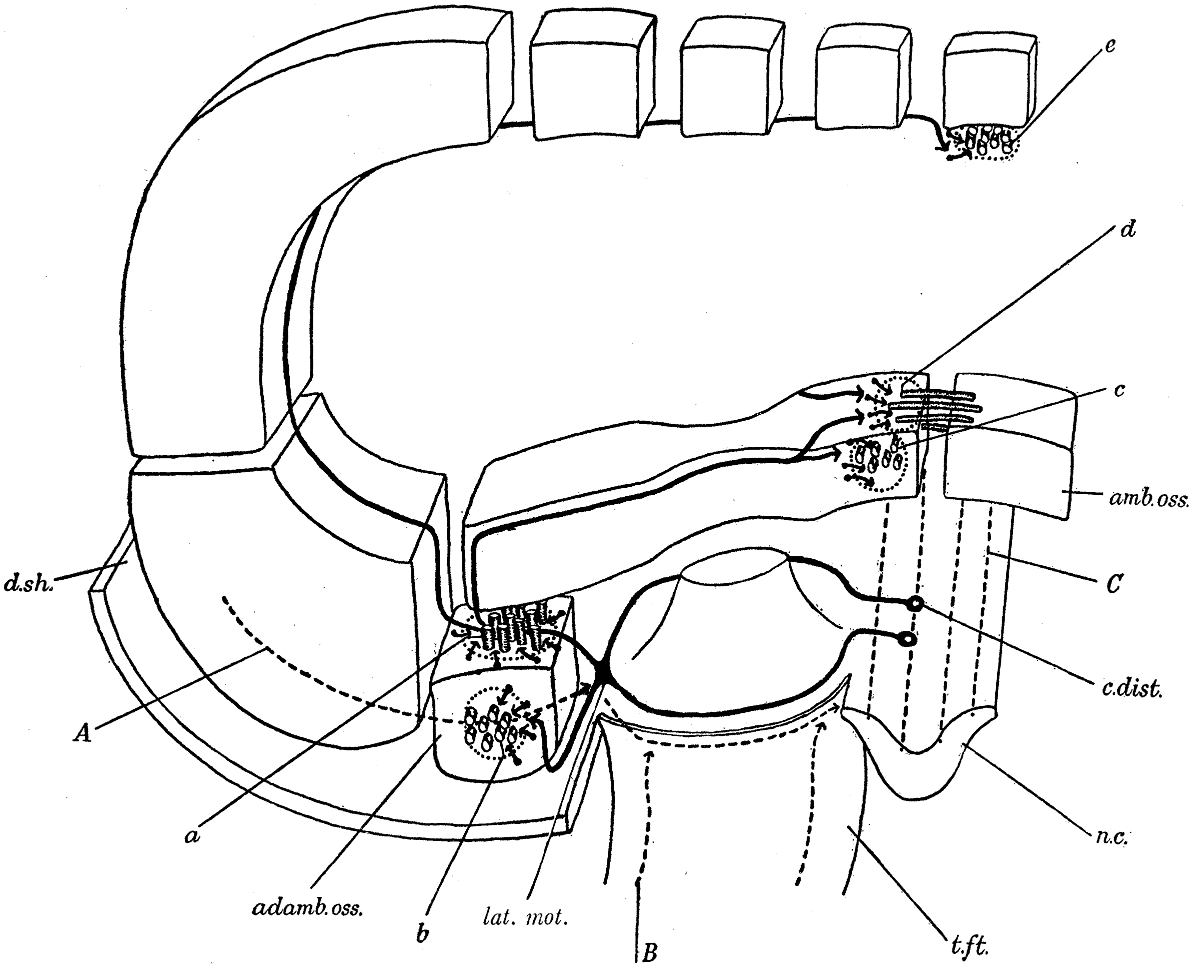

FIGURE 2. Schematic half-section of a transverse slice of an arm showing the position and distribution of the principal metameric motor nerves. The intrinsic (bulb) motor complex of the foot is omitted from the figure. *A*, *B* and *C*, deep tracts of the ectodermal subepithelial nerve plexus of the dorsal integument, tube foot and nerve cord respectively. *a* to *e*, the lateral transverse, longitudinal adambulacral, longitudinal ambulacral, supra-ambulacral and apical muscle, respectively. *adamb.oss.* adambulacral ossicle; *amb.oss.* ambulacral ossicle; *c. dist.* central distributory motor neuron; *d.sh.* dorsal integument; *lat.mot.* lateral motor complex; *n.c.* nerve cord; *t.ft.* tube foot.

The motor arcs supplying the different systems of muscles, though rather variable in respect to the number of neurons contained within them, are nevertheless similar in their basic constitution. They have in common the central distributory neurons the axons of which connect, in every instance, with a ganglionic neuron complex—either the foot or the lateral motor complex. The one serves as a relay to the foot and ampulla musculature, the other to the several muscles of the arm. Excitation is transmitted from each complex to the musculature through nerve tracts made up of chains of neurons linked in series, the final element in every chain being the ultimate motor neuron whose ribbon axon overlies a muscle fibre. In presenting the evidence for these generalizations concerning the motor innervation of the starfish arm it will be convenient to refer to the component elements of the motor tracts, in the order of their excitation, as the central distributory, internuncial, and ultimate (ribbon axon) neurons, the internuncials being further distinguished as neurons of the complex and distributory (chain) neurons.

A survey of the motor innervation of the arm would not be complete without some reference to the tracts through which the motor nerves are excited. The starfish arm is richly supplied in all its parts with integumental sensory cells which conduct excitation by way of internally directed fibres to subepithelial neurons. The fibres of these association neurons form a plexus which, in its deeper parts, is organized into linear tracts, the distribution and general direction of conduction of which are indicated in figure 2 by the broken lines, *A*, *B* and *C*. In order that the excitatory state shall be transmitted from the afferent pathways to the motor arcs provision must be made for the synaptic continuity of the motor neurons of the internal face of the body wall and the association fibres of its outer surface. Such contiguity is impossible over the greater part of the wall where the heavily calcified stroma is many hundreds of microns thick and apparently devoid of penetrating fibres. In two zones only, both on the ventral (oral) side of the arm, is the body wall sufficiently thin to allow of the apposition of the two parts of the nervous system. The one is in the roof of the nerve cord (*n.c.*), the other below the lateral motor complex (*lat.mot.*); in both places the boundary is uncalcified and a mere 1 to 3 μ thick. In the former instance fibres have been seen to penetrate the boundary and to run in conjunction with fibres on the farther side (see below). An anatomical connexion of the two systems in the region of the lateral motor complex is not so well established, but the responses of the tube feet and arm under experimentally defined conditions of innervation (Smith 1945), show that excitation can, in fact, be short-circuited through the lateral motor centres, and that in consequence the motor arcs can be excited either centrally (through the radial cord) or peripherally.

(*b*) *The detailed anatomy of the motor supply to the arm musculature*

The detailed constitution and fine anatomy of the motor tracts supplying the arm musculature may be exemplified by a description of the fibre systems which extend (figure 2) from the radial nerve cord (*n.c.*) to the lateral transverse (*a*), longitudinal ambulacral (*c*), and supra-ambulacral muscles (*d*).

The cell bodies of the central distributory neurons (figures 2 and 3, *c.dist.*) lie in the floor of the radial perihaemal canal. Each group is confined within an area roughly bounded by the proximo-distal width of a foot and the middle third of one side of the V-shaped nerve cord. Methylene blue is a capriciously selective stain, but in the many preparations that have been made of the *Astropecten* cord not fewer than fifteen and not more than twenty-four cell bodies have been made visible by staining in any one group. It seems probable therefore that each segment of the arm has approximately the same number of central distributory neurons and that the number is not large.

The individual cell body is pear-shaped (*c.* 12 by 9 μ) and unipolar. Its axon (figure 3, *c.dist.*) originates from the pointed end and extends outwards to the margin of the cord, giving off in its course four or five short collateral processes. The collaterals are oriented at right angles to the main fibre and dip through the underlying lattice of connective tissue (*c.t.*)

to run for a short distance in company with the longitudinal tracts of the deep plexus of association fibres (*pl.deep*).

The techniques employed have not allowed of a more precise determination of the pattern of connexion of the motor axon collaterals and the longitudinal association tracts of the cord. Methylene blue picks out the axon collaterals satisfactorily but stains, as a rule, only about ten fibres of the association tracts. Sections of the cord fixed in F.W.A. and stained with Mallory's triple stain, while failing, on the other hand, to show the axon collaterals, represent the association system as made up of about 90 to 100 separate bundles each containing several fibres. There are thus about 80 to 100 axon collaterals, as shown by one technique, available for connexion with some 90 to 100 longitudinal bundles, as shown by another. The numerical correspondence is interesting in view of the fact that the scheme of innervation put forward (Smith 1945, figure 4) as a possible basis for the observed patterns of movement of the feet embodied, as one of its principal features, a precise numerical and

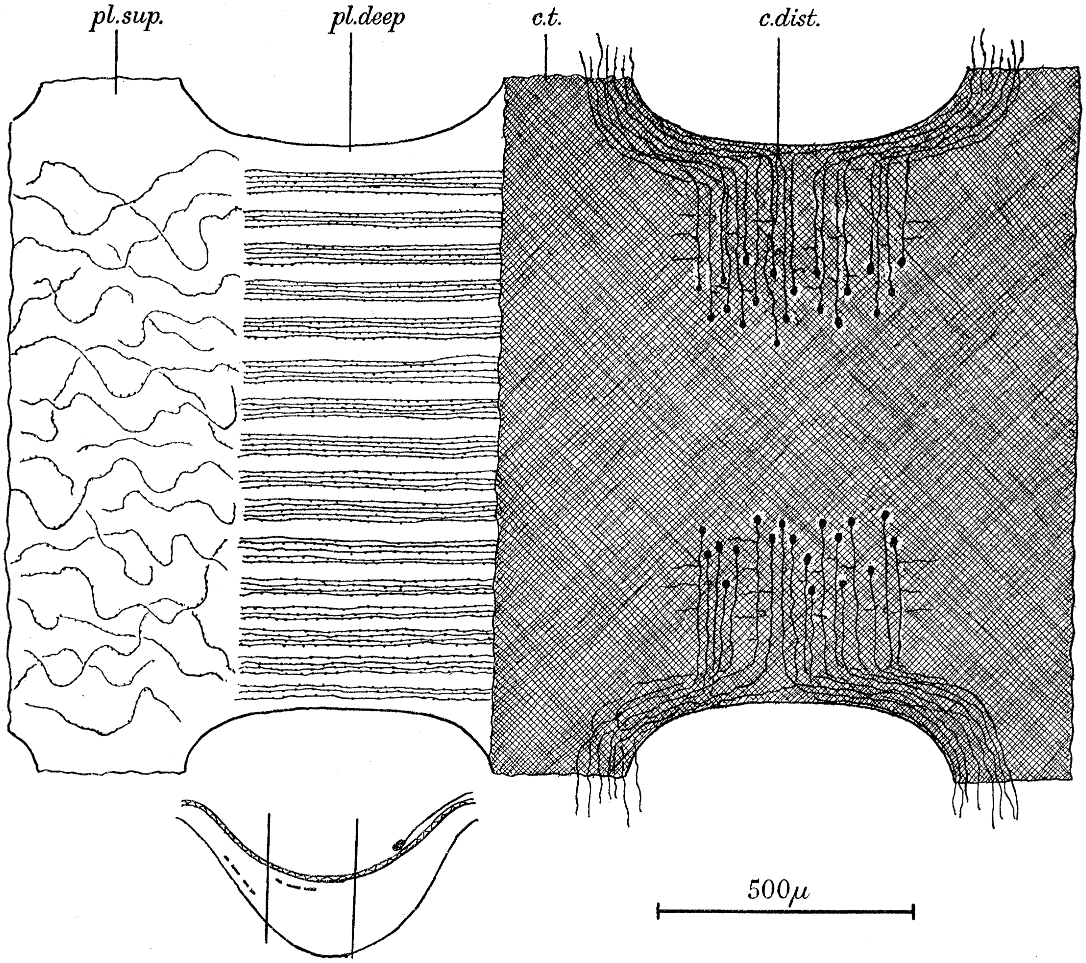

FIGURE 3. A portion of the radial nerve cord stained intra-vitam with methylene blue, flattened out and viewed with its internal surface uppermost. The small diagram of the cord as seen in transverse section shows the levels of the neurons and fibres included in the main figure. *c.dist.* central distributory motor neurons; *c.t.* connective tissue lamella flooring the radial perihaemal canal; *pl.deep*, deep fibre system of the association plexus; *pl.sup.* superficial fibre system of the association plexus.

spatial relationship between the motor neurons and the underlying tracts of the cord. It is therefore the more to be regretted that the spatial characteristics of the pattern have not been more accurately resolved.

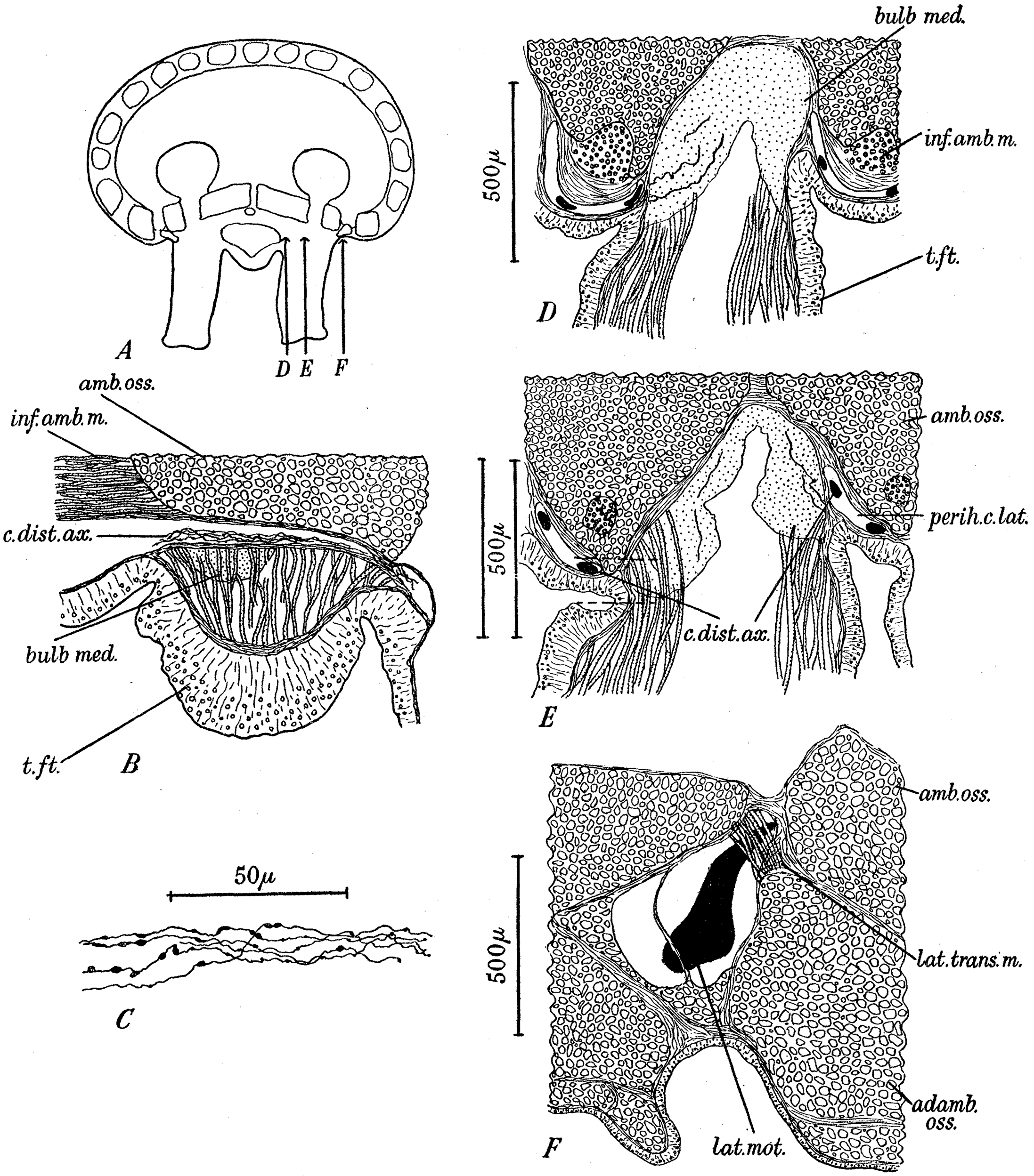

FIGURE 4. *A*, diagrammatic transverse section of the arm to show the levels of the longitudinal parasagittal sections *D*, *E* and *F*. *B*, part of a transverse section of the arm showing the lateral perihaemal canal and the axons of the central distributory motor neurons. *C*, the axons of the central distributory neurons. *D*, *E* and *F*, longitudinal parasagittal sections of the arm to show the relations of the lateral perihaemal canals to the foot and other structures and the course of the central distributory axons to the lateral motor complex. *adamb.oss.* adambulacral ossicle; *amb.oss.* ambulacral ossicle; *bulb med.* medial bulb of connective tissue supporting the motor complex of the foot; *c.dist.ax.* axons of the central distributory motor neurons; *inf.amb.m.* infra-ambulacral muscle; *lat.mot.* lateral motor complex; *lat.trans.m.* lateral transverse muscle; *perih.c.lat.* lateral perihaemal canal; *t.ft.* tube foot.

The axons of the central distributory neurons, on reaching the margin of the nerve cord, enter the lateral perihaemal canal on one or other side of the foot, some axons bifurcating into branches running to either side. A transverse section of the arm cutting the foot tangentially shows the course of the axons in the canal (figure 4*B*, *c.dist.ax.*). They number about twenty fibres and are supported throughout their length by non-nervous tissue. As nearly as can be estimated by measurement against a 9 μ grid and taking into account the resolving power of the microscope used (N.A. of objective 1·32) the diameter of the fibres is not more than 0·5 μ, a thickness comparable to fibres of the association plexus, the nerve fibres of coelenterates (Woollard & Harpman 1939) and the smaller fibres of the balanoglossid plexus (Bullock 1944). Fibres of this size bead very readily (figure 4*C*), but the beads are never large enough to be mistaken for cell bodies. The fact that there are some fifteen to twenty fibres in the canal and that cell bodies are absent makes it almost certain that there are no additional internuncials interposed between the radial nerve cord and the lateral motor complex and that the axons of the central distributory neurons are alone concerned in the preganglionic transmission of excitation through the motor arcs.

The course of the central distributory axons through the lateral perihaemal canal and their relations to the foot and other structures of the arm is seen more clearly in longitudinal parasagittal sections of the arm (figure 4*D*, *E* and *F* and reference figure 4*A*); the distal face of the foot (nearer the arm tip) is to the left of figure 4*D*, *E* and *F*. Each perihaemal channel (*E*, *perih.c.lat.*) contains two fibre systems (*c.dist.ax.*), the one which circumscribes the distal face of the more proximal of two adjacent feet lying in the lower (more oral) part of the obliquely set sinus. It will be observed that where the axon sytems of the distal and proximal faces of the foot converge and meet on the lateral side of the foot (4*F*) the nervous tissue becomes greatly expanded, and that the expansion is almost entirely confined to the proximal channel. This expansion is a consequence of the introduction into the nervous pathways of new neuron systems and marks the position of the lateral motor complex (*lat.mot.*).

Figure 5, a horizontal section through the base of a foot (*t.ft.*) and the lateral margin of the perihaemal canal (*perih.c.lat.*) shows the terminations of the central distributory axons (*c.dist.ax.*) among the neurons of the lateral motor complex (*lat.mot.*). Most of the neurons are bipolar and have 0·5 μ diameter fibres, some of which (*fib.′*) lie against the boundary tissue (*c.t.*) separating the perihaemal sinus from the foot cavity. Others (*fib.″*), more directly concerned with the innervation of the arm musculature, are directed laterally through the gap between adjacent adambulacral ossicles (*adamb.oss.*). They can, however, be traced for only a short distance in horizontal sections on account of their sharply ascending approach to the lateral transverse muscle (figure 4*F*, *lat.trans.m.*). The continuing course of these fibres to the arm musculature may be followed in figures 6 and 7.

The distributory tracts (figure 6, *dist.*) on emerging from the lateral motor complex are re-enforced by the interpolation of further bipolar internuncial neurons. Any resulting tendency towards an increase in the number of fibres in the tracts is, however, offset by the divergence from the main system of individual and groups of fibres which become distributed over the musculature (*lat.trans.m.*) as a plexus (*pl.mot.*).

One of the main difficulties encountered in this work has been the accurate identification of the position and form of nerve-fibre terminals. In the particular instance of the innervation of the lateral transverse muscle the interpretation of interneural relations is made difficult chiefly by reason of the terminal attenuation of the delicate fibres of the motor plexus which can be followed on occasions to the limits of their optical visibility without their appearing to come into contact with other nervous or non-nervous structures. When they do acquire such relationship it may be either with a muscle fibre or with intensely blue staining structure (*rib.ax.*) which overlie the muscles along their length as flat ribbons some 5 to 10μ wide and 0·5μ thick. These structures, which at first inspection might be

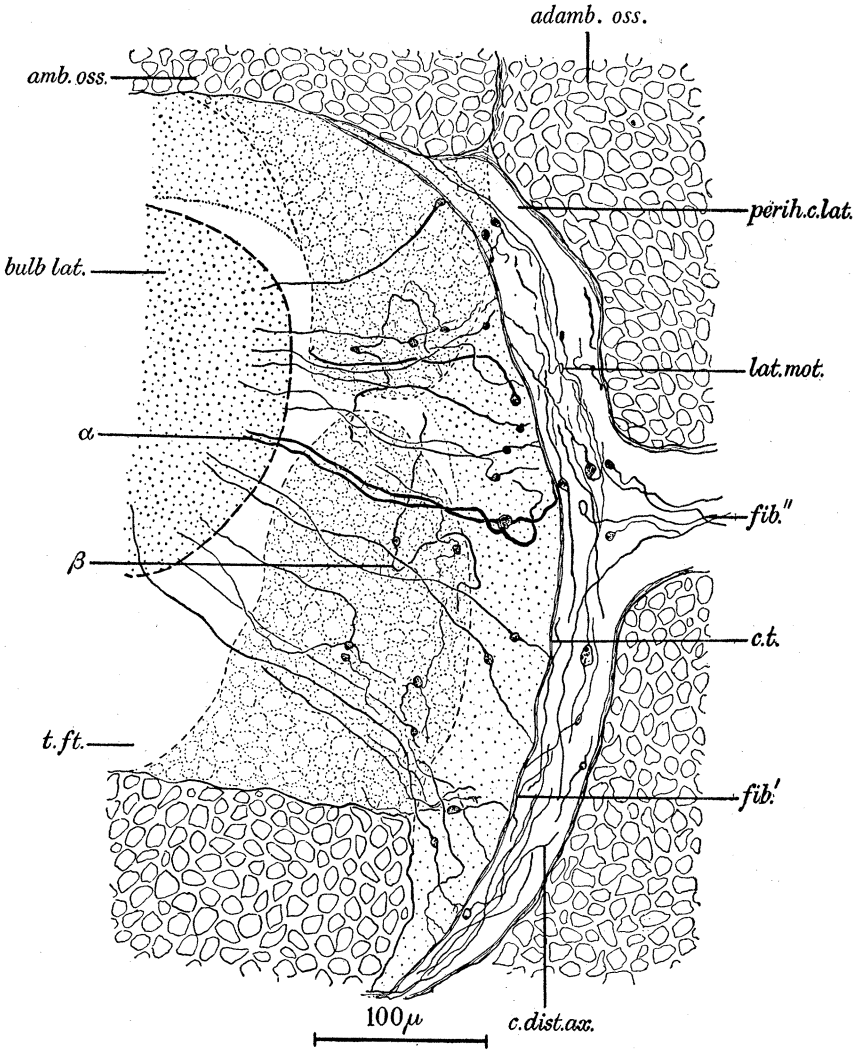

FIGURE 5. A transverse section through the lateral half of the base of a tube foot showing the entry of central distributory axons into the lateral motor complex, the origin from the lateral motor complex of the distributory tracts to the arm musculature, and the relations of the neurons of the lateral motor complex to the α and β neurons within the cavity of the foot. α, β, internuncial neurons of the lateral (intrinsic) foot complex; *adamb.oss.* adambulacral ossicle; *amb.oss.* ambulacral ossicle; *bulb lat.* tissue of the lateral bulb; *c.dist.ax.* central distributory axons; *c.t.* connective tissue of the tube foot wall; *fib.′* fibres of the lateral motor complex adherent to the foot wall; *fib.″* fibres of the distributory tracts to the arm musculature; *lat.mot.* lateral motor complex; *perih.c.lat.* lateral perihaemal canal; *t.ft.* tube foot.

mistaken for muscle fibres, differ from them in a number of important respects, chief of which are their shape, the possession of collateral branches, and the apparent absence of a nucleus. Their nature and function, as will be shown later, are more readily interpreted in preparations of the ampulla, the thin walls of which stain and fix more satisfactorily than calcite-laden pieces of arm. Each ribbon is then seen (figure 13*A* and *C*, *rib.ax.*) to take origin from a somewhat remote cell body (*c.b.*) to which it is connected by an exceedingly fine fibre (*f.fib.*). The cell, or its fibre, is in turn embraced by, or stands in close relation to, the antecedent plexus of distributory internuncial motor neurons. The cell body, fine fibre and ribbon are here parts of a single neuron—the ultimate element in the motor chain—and the ribbon is the distal expanded part of the axon where it overlies and innervates the muscle fibre. In this event the ribbons which accompany the lateral transverse muscle must also be regarded as axons which, however, in the absence of visible fine-fibre connexions, appear to be without parent cell bodies. A number of cells (figure 6, *c.b.*), of the same order of size (5μ) as the cell bodies of the ultimate motor neurons of the ampulla, border the margin of the ambulacral ossicle (*amb.oss.*) to which the fibres of the lateral transverse muscle are attached. They may be neurons or they may be connective tissue stroma cells. Their nervous nature has, however, been assumed in the foregoing more general account of the innervation of the arm musculature (p. 529).

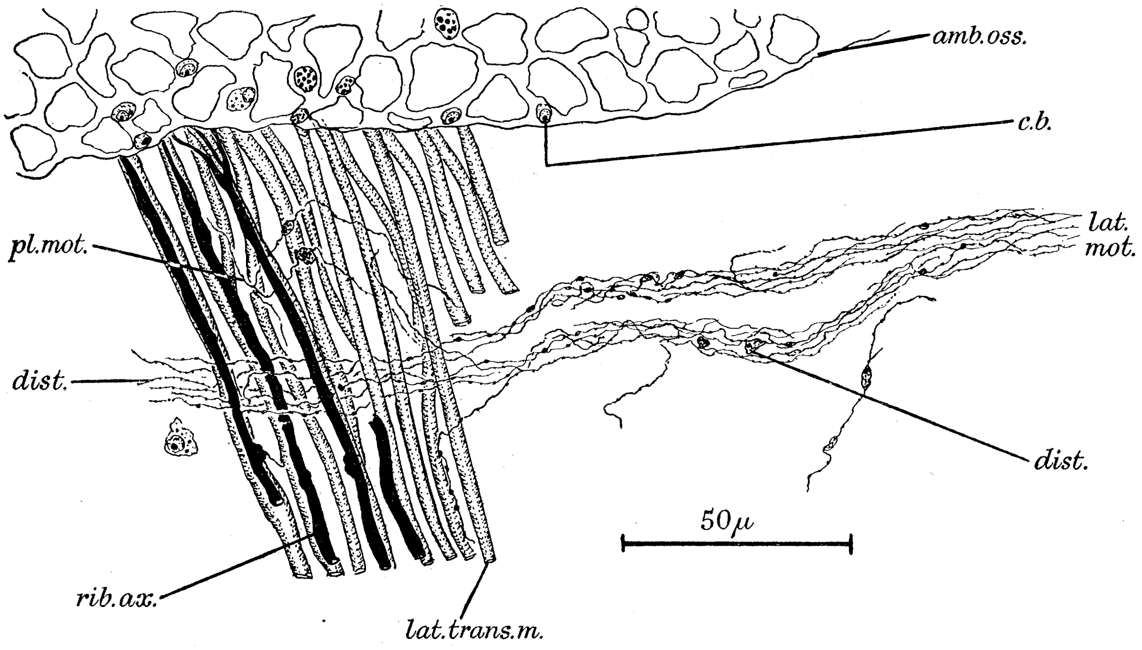

FIGURE 6. Part of a transverse section through the arm to show the course of the distributory motor fibres from the lateral motor complex to the lateral transverse muscle and the mode of innervation of the muscle. *amb.oss.* ambulacral ossicle; *c.b.* cell body, presumed to be the cyton of a ribbon axon neuron; *dist.* distributory (chain) internuncial neurons and tracts; *lat.mot.* the region of the lateral motor complex; *lat.trans.m.* lateral transverse muscle; *pl.mot.* fine fibre motor plexus; *rib.ax.* ribbon axon, the more distal part of the axon of an ultimate motor neuron.

The orientation of the ribbon axons along the length of the muscles contrasts markedly with the rather random configuration of the plexus of distributory fibres. It seems highly probable therefore that the ribbon axons alone are directly concerned with the excitation of the musculature, and that the function of the fine-fibre motor plexus is to make connexion with the ultimate motor neurons and to mediate the transfer of excitation between the system of internuncial distributory fibres and the ultimate elements.

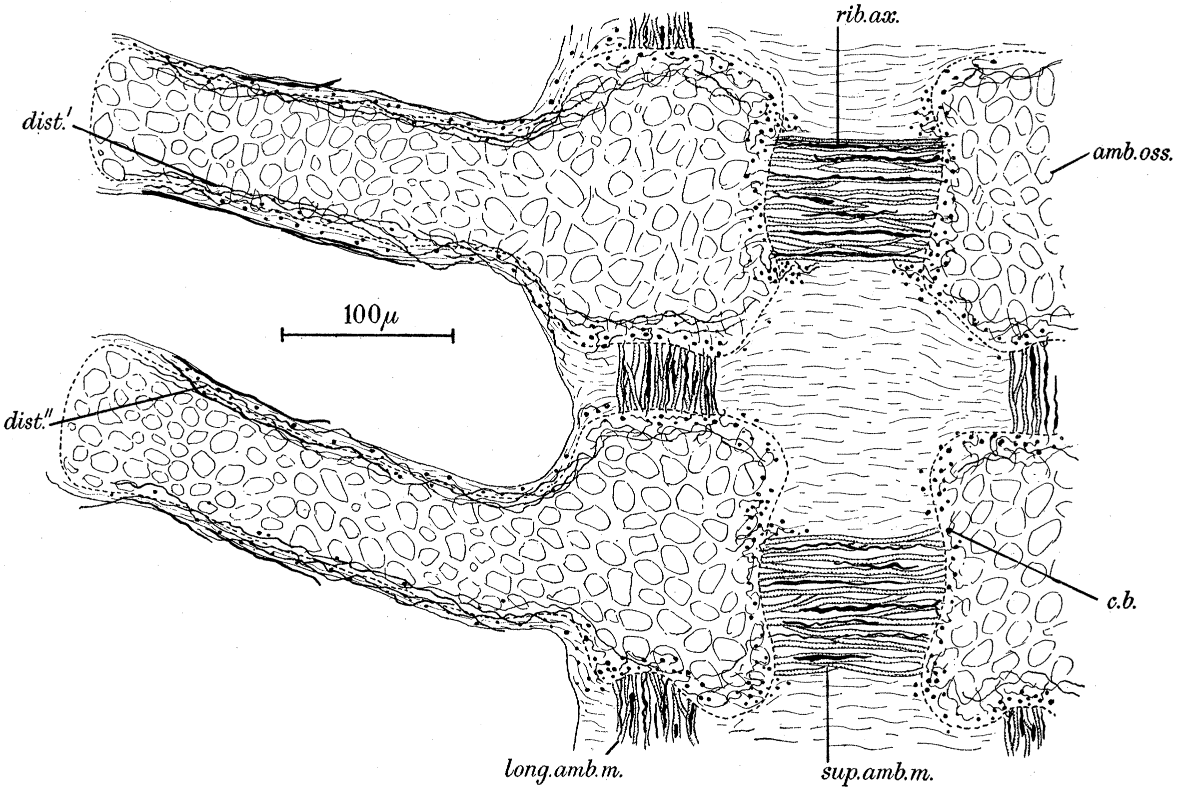

FIGURE 7. Part of a horizontal section through the arm at the level of the ambulacral ossicles showing the more general features of the nerve supply to the longitudinal ambulacral and supra-ambulacral muscles. *amb.oss.* ambulacral ossicle; *c.b.* cell body, presumed to be a cyton of a ribbon axon neuron; *dist.′ dist.″* distributory (chain) internuncial neurons and tracts; *long.amb.m.* longitudinal ambulacral muscle; *rib.ax.* ribbon axon; *sup.amb.m.* supra-ambulacral muscle.

The distributory tracts, after traversing the lateral transverse muscle, enter the perivisceral coelom of the arm to continue their course along the sides of the ambulacral ossicles (figure 2, *amb.oss.*). Figure 7, a part of a horizontal section through an arm at the level of the ossicles (*amb.oss.*), shows the main features of their further distribution. Each tract divides at the lateral extremity of the ossicle and proceeds as two separate systems of fibres (*dist.′*, *dist.″*) which run along the opposing faces of adjacent ossicles to terminate in the middle line of the arm on the crest of the ossicle. The supra-ambulacral (*sup.amb.m.*) and longitudinal ambulacral (*long.amb.m.*) muscles which they there supply have ribbon axons (*rib.ax.*) running along their length, and there are also isolated ribbons associated with the more diffuse muscle fibres bordering the lateral margins of the ossicles. Large numbers of cell bodies (*c.b.*) fringe the ossicles, but as in the case of the lateral transverse muscle their nervous nature remains in some doubt.

The motor innervation of the tube foot-ampulla system

(a) *General features*

The more general features of the motor supply to the foot and ampulla are shown schematically in figure 8. Where, as in the *Astropecten* podium, a terminal sucker is lacking, there are but three systems of muscle fibres. The most extensive is that of the longitudinal retractors (*retr.m.*) which originate basally on the under-surface of the ambulacral ossicles (*amb.oss.*) and extend as a cylindrical sheath along the length of the foot to be inserted, at its tip, into a subterminal plate of connective tissue. The retractor muscles are opposed by circumferential vertically set fibres within the ampulla (*amp.*) which, on contraction, squeeze the ampulla and force fluid through the narrow connecting neck (*nck.*) into the cavity of the podium. The foot is thereby protracted. A sheath of short fibres (*post.m.*) originating on the ambulacral ossicles and having their insertion around the base of the foot column form the third series of muscles. By the reciprocal contraction and relaxation of diametrically opposed fibres of this system the foot is enabled to assume postural pointing attitudes and to undertake directional stepping (Smith 1946).

Each set of muscle fibres is accompanied by ribbon (ultimate motor) axons (*rib.ax.*, *rib.ax.′*, *rib.ax.″*), there being fewer stainable axons than muscle fibres in each system. The cell bodies of the ultimate neurons supplying the retractor muscles are arranged around the periphery of the foot at or near the level indicated in the figure by the broken white line; those serving the postural muscles have a similar disposition but at a higher (more aboral) level within the foot cavity (represented by the dotted line). The *Astropecten* ampulla is bilobed and its wall is thickened mesially and laterally by the insertion of seams of supporting tissue (*amp.sm.*). The cell bodies of the ultimate motor neurons of the ampulla lie within these seams, and their fine-fibre axons diverge from them to either side to expand distally into the ribbon axons (*rib.ax.*) which overlie the musculature.

Excitation of the three systems of ultimate motor neurons of the foot and ampulla and of the muscles which they serve is effected through a somewhat complicated system of internuncial neurons (*intern.n.*), the cells and fibres of which are embedded in a supporting tissue matrix similar to and continuous with the material of the ampulla seams. The main body of supporting tissue is in the form of two bulbous masses lodged in the base of the foot cavity. One, a simple bulb (*bulb lat.*), lies laterally and the other, bilobed (*bulb med.*), medially. Both are set obliquely with their swollen bases pressed against the wall of the podium and their tapering ends extending into the ampulla as the seam tissue. The supporting matrix is an open-fibre lattice with the main ‘grain’ set along the length of the bulbs and seams. The lattice, while sufficiently open to allow the passage through it of muscle (figure 9, *musc.*) and nerve fibres, is, nevertheless, rigid enough to resist deformation during the protraction and retraction of the foot and the compression and dilation of the ampulla. Its principal function appears to reside in this latter property, for without the support of the non-nervous matrix it is difficult to see how the delicate fibres of the internuncial neurons could preserve any kind of constancy of relationship one with another under the conditions of fluid flow associated with the movements of the foot and ampulla.

These relationships are later discussed in some detail. The more immediate inquiry, however, is concerned with the afferent connexions of the internuncials, namely, with the

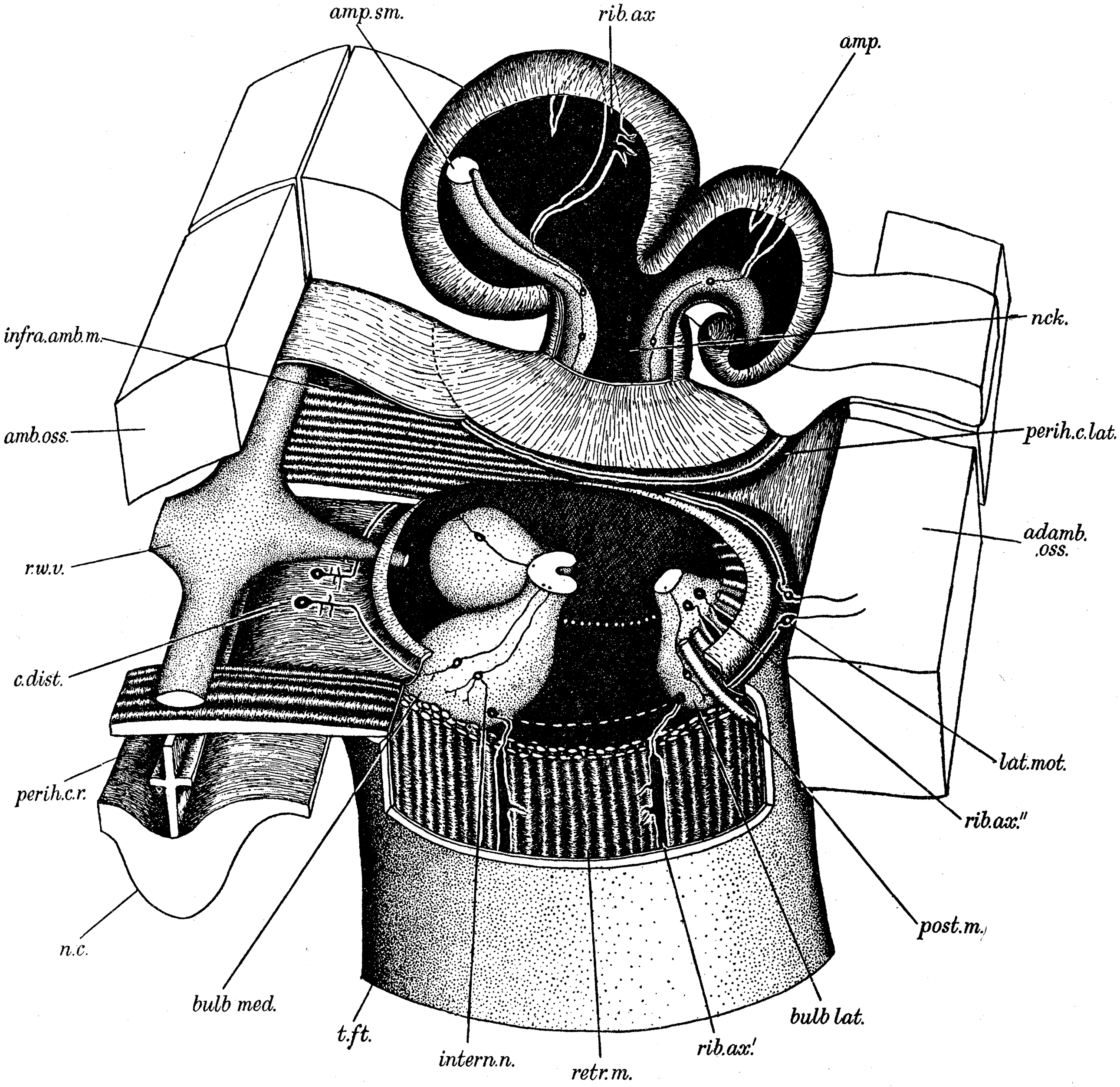

FIGURE 8. Schematic stereogram of a part of an *Astropecten* arm showing some of the principal neuron systems of the intrinsic motor complex of the foot and their relations to the central distributory motor neurons extrinsic to the foot. An ambulacral ossicle and an ampulla have been removed in order to expose the cavity of the foot and the medial and lateral bulbs. The bulbs have an open lattice structure; they support and invest the neurons and fibres of the intrinsic motor complex. Representative neurons included in the figure are the bulb internuncials, distributory chain neurons and the ultimate (ribbon axon) neurons serving the retractor and postural muscles of the foot and the ampulla (foot protractor) musculature. The levels of origin of the two former series are represented respectively by the broken and dotted lines. The latter, connected to the bulb complex by chain neurons, are seen in the bisected ampulla. *adamb.oss.* adambulacral ossicle; *amb.oss.* ambulacral ossicle; *amp.* ampulla; *amp.sm.* ampulla seam; *bulb lat.* lateral bulb; *bulb med.* one of the lobes of the medial bulb; *c.dist.* central distributory motor neuron; *infra.amb.m.* infra-ambulacral muscle; *intern.n.* internuncial neuron of the bulb (α series); *lat.mot.* lateral motor complex; *n.c.* nerve cord; *nck.* ampulla neck; *perih.c.lat.* lateral perihaemal canal; *perih.c.r.* radial perihaemal canal; *post.m.* postural (orienting) muscles of the foot; *r.w.v.* radial water vessel; *retr.m.* retractor muscles of the foot; *rib.ax.*, *rib.ax.′*, *rib.ax.″* ribbon axons of the ampulla, foot retractor and postural muscles respectively; *t.ft.* tube foot.

central distributory axons of the perihaemal canal through which excitation is transmitted from the central tracts of the nerve cord to the foot complex.

(*b*) *The relations of the motor tracts extrinsic and intrinsic to the foot*

Unequivocal synapses between the central distributory axons extrinsic to the foot and the intrinsic internuncial neurons of the foot complex have not been directly observed. The evidence for the functional continuity of the two systems may be stated as follows: (1) A foot deprived of its connexions with the nerve cord is unable, under any circumstances of stimulation, to assume an attitude of oriented pointing or to execute any but the most limited movements of protraction and retraction (Smith 1945). The muscles of the foot must therefore be supposed, under normal circumstances of innervation, to be in receipt of excitation through nervous pathways which involve the tracts of the cord. (2) The only motor connexions between the cord and the foot that have been demonstrated, or which appear on anatomical grounds to be possible, are the central distributory neurons. These alone of the motor elements have connexion with the longitudinal conducting tracts of the cord and have axons which enter into intimate relations with the foot. (3) The dendrites of the internuncial neurons of the intrinsic motor complex of the foot extend towards and

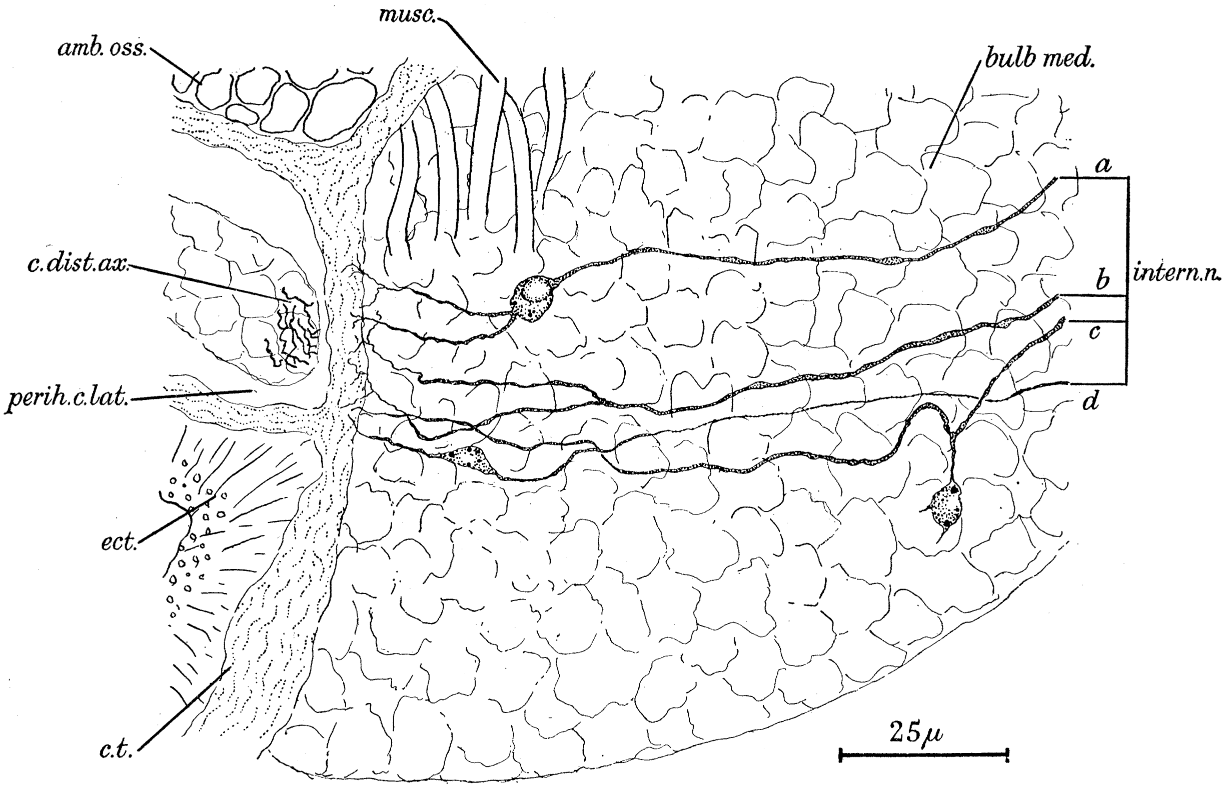

FIGURE 9. Part of a longitudinal parasagittal section through an arm (corresponding to the area bounded by the broken lines in figure 5*E*) to show the relations and possible connexions of the central distributory axons in the lateral perihaemal canal to the internuncial neurons (α series) of the medial bulb motor complex. *amb.oss.* ambulacral ossicle; *bulb med.* medial bulb; *c.dist.ax.* axons of the central distributory neurons; *c.t.* connective tissue investment of the foot; *ect.* foot ectoderm; *intern.n.* (*a*, *b*, *c* and *d*) internuncial neurons of the bulb complex (α series); *perih.c.lat.* lateral perihaemal canal; *musc.* muscle fibre.

arborize over the internal wall of the foot in a zone corresponding exactly in extent and position to that circumscribed externally by the lateral perihaemal canal and by the axon fibres contained within it. The validity and significance of this last and most crucial indication of nervous continuity may be better appreciated by reference to figure 9.

The figure includes a part of a longitudinal parasagittal section of an *Astropecten* arm in a region corresponding roughly to the guide line *intern.n.* of figure 8 and more precisely to the area included within the broken lines of figure 4*E*, though sections cutting the medial or lateral bulbs of the foot and the perihaemal canal at other places around the periphery of the foot would have served equally well to illustrate the points at issue. Central distributory axons (*c.dist.ax.*) are seen within the lateral perihaemal canal (*perih.c.lat.*) to the left of the figure. As the section is not strictly transverse to the length of the axons they appear as short fibres, some of which show traces of lateral twigging. The connective tissue (*c.t.*) which bounds the foot and separates the perihaemal canal from the bulb tissue (*bulb med.*) appears, and is drawn as, about 8μ thick though, if the obliquity and thickness of the section is taken into account, its actual thickness is more nearly of the order of 4μ. Internuncial neurons (*intern.n.*, *a*, *b*, *c*, and *d*) of various types have dendrites which extend from the cell bodies in the bulb tissue to the connective tissue boundary where they branch into a number of exceedingly fine processes. It has not been possible to decide with certainty whether the terminal branches stain and are visible to the limits of their extension or whether they are continued as still finer threads which perforate the connective tissue lattice and acquire contiguous relationship with the axons on the farther side. It is difficult, however, even in the absence of more positive anatomical evidence of such perforation and relationship, to deny significance to the striking appositional tendencies of the two systems. One feels that it is the nature rather than the fact of connexion that is in doubt. If this conclusion, which is amply supported by experimental evidence, is valid the internuncial neurons of both the medial and lateral bulbs of the foot are in receipt of excitation through the central distributory tracts, and the muscles of the foot and ampulla have in consequence a nerve supply which in its superficial aspects at least conforms to a bilateral pattern.

The innervation of the ampulla musculature

As figure 8 shows, the nerve supply to the ampulla, while essentially bilateral in character, deviates from strict bilaterality on account of the division of the medial bulb into two lobes. The asymmetrical disposition of the bulbs, and consequently of the internuncial neurons contained within them, is, however, almost certainly due to the intrusion into the medial side of the foot of the lateral water vessel. It appears otherwise to have no functional significance.

The component elements of the motor tracts supplying the ampulla musculature can be readily identified in excised ampullae vitally stained and viewed as whole mounts (figure 10). Each tract is made up essentially of three systems of neurons linked in series. They are, in the order of their excitation, the internuncial neurons of the bulb (*intern.n.′amp.*), the internuncials of the seams (*intern.n.″amp.*) and the ultimate neurons whose ribbon axons (*rib.ax.*) accompany the muscle fibres. Since the tracts entering the two lobes of the ampulla are, so far as can be ascertained, identical in constitution, it will suffice to limit the description to the tracts serving the lateral lobe.

All the neurons made visible by methylene-blue staining within a 50μ median sagittal slice of the lateral bulb are shown in figure 11, a drawing of a part of a transverse section through the arm of *Astropecten*. Unipolar, bipolar and multipolar neurons are represented, their fibres, up to 2μ in diameter, traversing the substance of the bulb in every direction. Although the arrangement of the fibres seems at first sight to be largely random it is not entirely without order, and three main groupings of neurons can be distinguished (perhaps somewhat arbitrarily) within the complex.

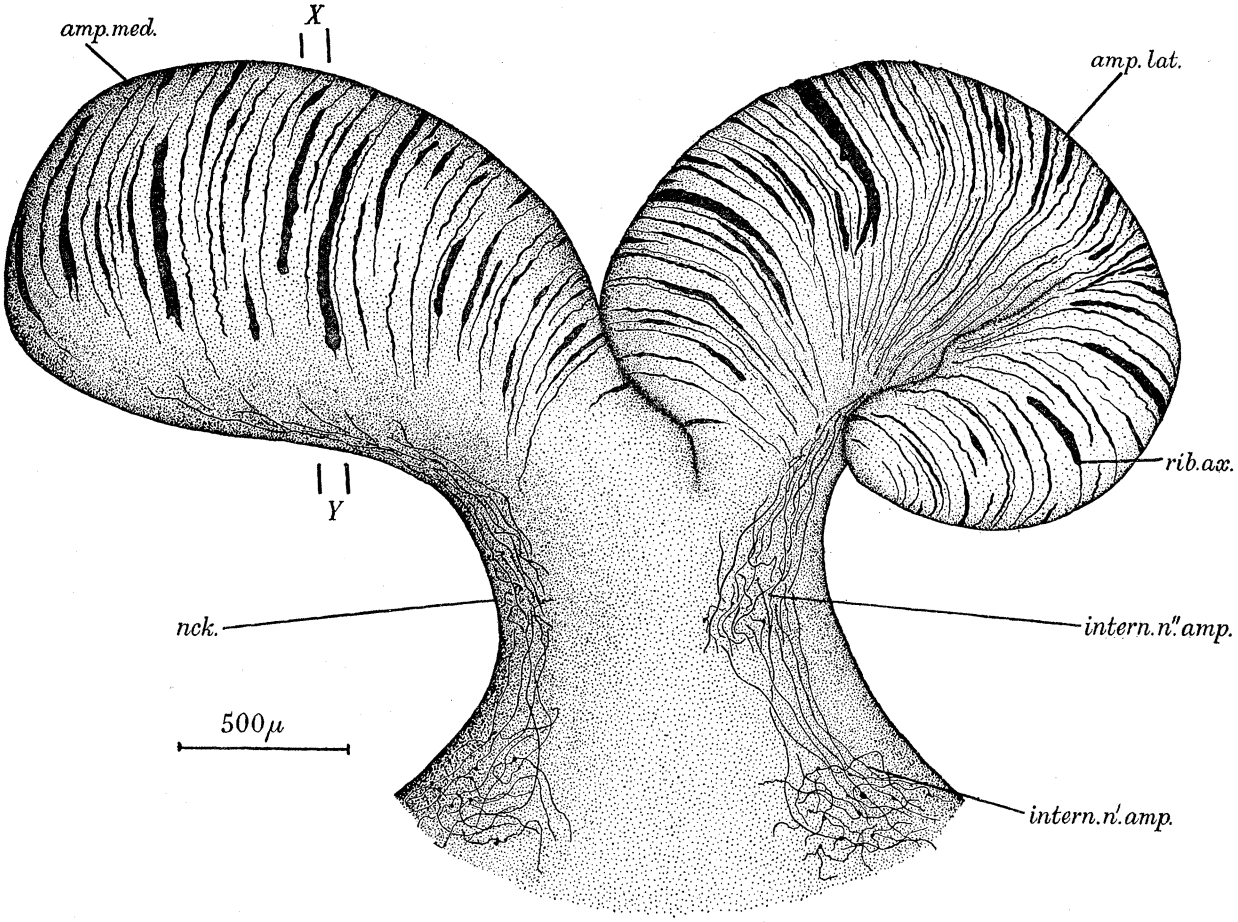

FIGURE 10. An ampulla and part of the base of a foot stained intra-vitam and viewed as a whole mount. *amp.lat.* lateral lobe of the ampulla; *amp.med.* medial lobe of the ampulla; *intern.n.′amp.*, *intern.n.″amp.* respectively the bulb and seam motor internuncials of the ampulla supply; *nck.* ampulla neck; *rib.ax.* ribbon axon overlying the ampulla musculature.

The character common to all the neurons of the first series (α) is that their afferent fibres terminate on the wall of the podium next the lateral perihaemal sinus (*perih.c.lat.*). These are the neurons which have been assumed to make connexion with the central distributory axons extrinsic to the foot. The extent of their association with the wall of the perihaemal sinus and of their implied connexion with the distributory axons is apparent in horizontal sections through the base of the foot (figure 5) where the fibres of this neuron system (α) are seen to converge from a wide arc of the lateral margin of the foot towards the centre of the bulb (*bulb lat.*). Their course within the bulb is not so determinate, but the prevailing orientation is upwards and inwards so that they tend ultimately to reach the apex of the bulb where it narrows into the ampulla seam (figure 11, *amp.sm.*). Very few of the fibres of the α neurons extend beyond this point.

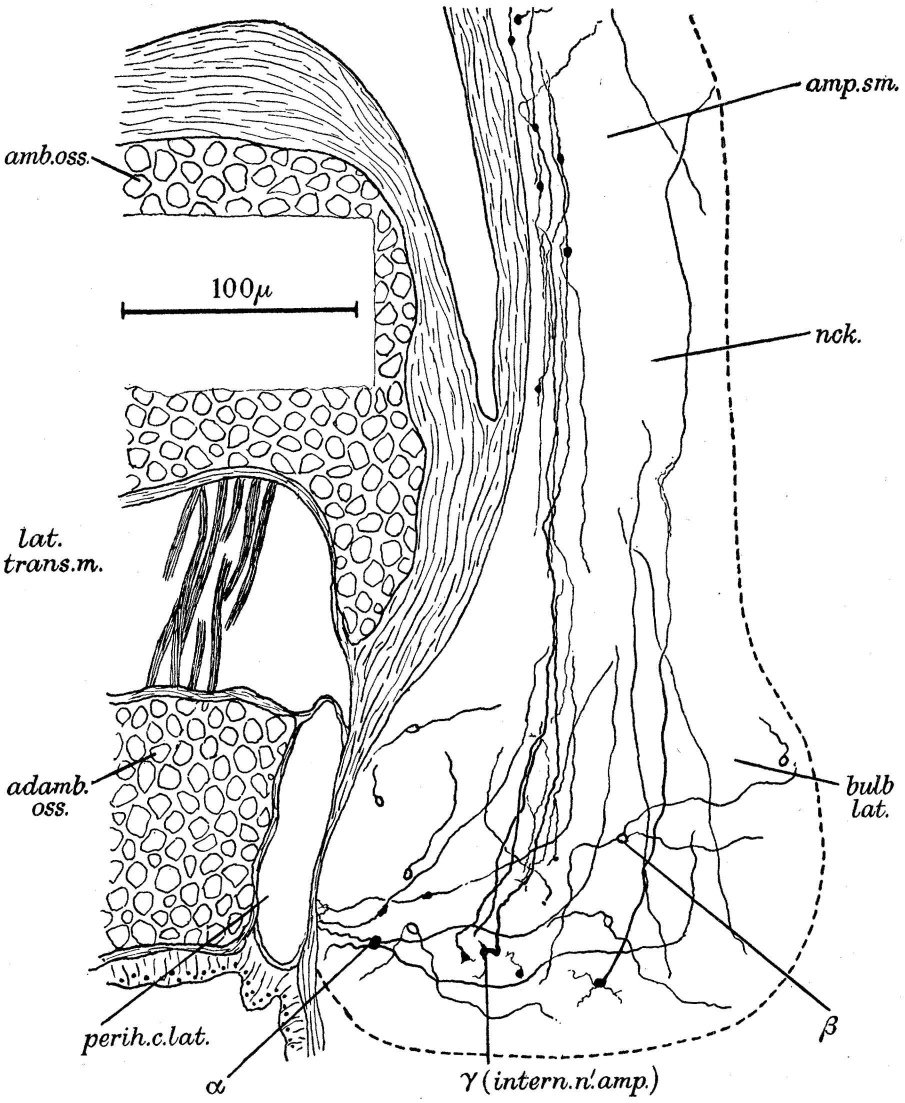

FIGURE 11. Part of a transverse section of an arm of *Astropecten* to show the neuron complex of the lateral bulb as seen in a thick (50μ) median sagittal slice of the bulb. The boundary of the supporting tissue of the lateral bulb and ampulla seam is indicated by the broken line. α, β, γ (*intern.n.'amp.*) neurons of the bulb complex; *adamb.oss.* adambulacral ossicle; *amb.oss.* ambulacral ossicle; *amp.sm.* ampulla seam; *bulb lat.* bulb lateral; *lat.trans.m.* lateral transverse muscle; *nck.* ampulla neck; *perih.c.lat.* lateral perihaemal canal.

The second series (figure 11, β and all other neurons figured with an unshaded cell body) comprises all the neurons which are wholly confined to the substance of the bulb but which, unlike the α series, lack connexion with the wall of the perihaemal canal. The β neurons are multipolar, bipolar and unipolar. They are found in all parts of the bulb and have diverse orientations. The group is without doubt a heterogeneous assemblage, the possible functions of which will be further considered in connexion with the innervation of the foot musculature. The third and last series (γ) is the most homogeneous of the three in respect to the form, position and orientation of its constituent neurons. Their cell bodies, mostly unipolar, are contained within the core of the bulb, and their long axons extend in clearly defined tracts along the axis of the bulb well into the substance of the seam.

In so far as it is permissible to assign functions to the three systems of neurons on the basis of their more general orientations, interrelations and distribution, we may venture on the following suppositions. The α neurons by virtue of their connexions with the perihaemal canal transmit excitation from the central distributory tracts to other neuron systems (β and γ) contained within the bulb complex. The role of these latter neurons is to distribute the incoming excitation into pathways more specifically concerned with the innervation of particular muscles. In the instance of the ampulla innervation it is anatomically possible for the transfer of excitation from the α to the γ neurons to be made either directly by axo-axonal synapses at the base of the ampulla seam or through the complex of β fibres which closely enmesh the centrally situated cell bodies of the γ neurons. The postural and retractor muscles, on the other hand, may provisionally be considered to require the mediation of the β complex, in justification of which latter assumption further data will be presented (pp. 552, 555).

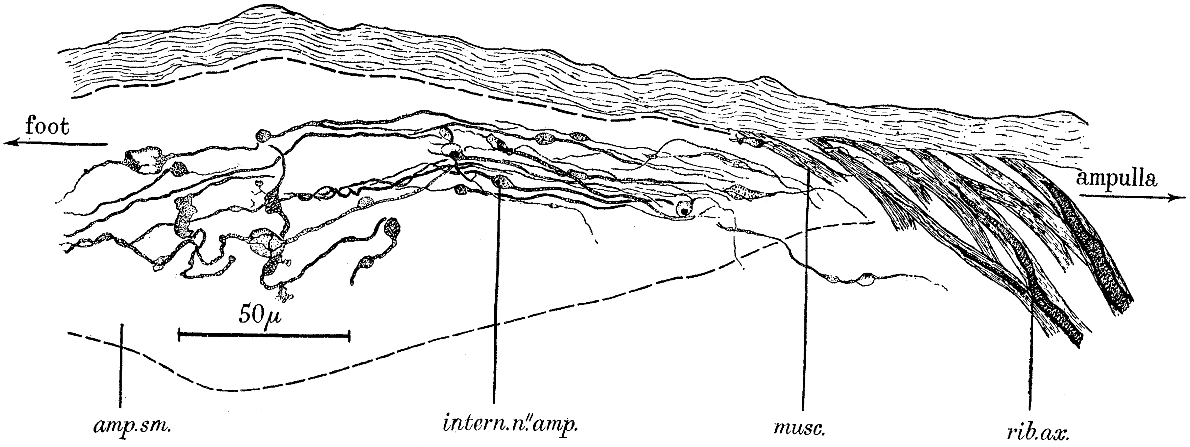

FIGURE 12. A median sagittal section through the neck of an ampulla to show the internuncial (chain) neurons of the ampulla seam. The long axis of the neck is, *in situ*, vertical. In the figure it is set horizontally with the entry from the tube foot to the left and the exit into the ampulla to the right; *amp.sm.* ampulla seam; *intern.n.″amp.* internuncial (chain) neuron; *musc.* muscle fibre; *rib.ax.* ribbon (ultimate motor) axon.

We may now return to the question of the organization of the ampulla tracts with which this section of the account is more directly concerned by noting that the γ neurons can be identified with the first internuncial neurons of the definitive ampulla tracts (figure 10, *intern.n.′amp.*) and that they number some ten to fifteen cell bodies each of which sends out a long axon process into the ampulla neck (figure 11, *nck.*).

Further neurons within the ampulla seam (figure 10, *intern.n.″amp.*) extend the gently curving arc of motor fibres initiated by the first-order bulb internuncials through the ampulla neck and into the free lobe. The seam neurons (figure 12, *intern.n.″amp.*) are always unipolar or bipolar, and their fibres, with very few exceptions, pursue a strictly longitudinal course along the length of the seam. Most of the fibres are about 1 μ in diameter and little more than 1 mm. long. Thus even in the short passage of the ampulla neck excitation is conducted through a chain of two or three neurons, synapsis of the successive neurons being amply provided for by the close and often continuous apposition of their fibres. Counts of the number of fibres at the entrance to and exit from the neck show an approximate threefold multiplication of fibres consequent on the interpolation of the secondary internuncial neurons into the ampullary tracts. An important role of the secondary internuncials thus appears to be the dispersal of excitation, a role which is the more evident when it is observed that there are some 70 ultimate (ribbon) axons distributed over the muscles of each of the ampullary lobes, the ribbon axons being at the end of a motor chain which has its origin in but 10 to 15 first-order neurons of the bulb.

It is a matter of some difficulty to trace within the limits of a single section the entire course of the ultimate motor neurons owing to the obliquity and curvature of their axons relative to the transverse and longitudinal axes of the ampulla (figures 10 and 22, plate 27, *rib.ax.*). Their arrangement and more general anatomical features can, however, be conveniently set out in a composite drawing made to simulate a thick obliquely transverse slice of an ampulla lobe (figure 13*A*).

The cell bodies of the ultimate motor neurons (*c.b.*) lie in the ampullary seam (*amp.sm.*) among the secondary internuncial nerve fibres, from which they are in receipt of excitation. Each cell body gives rise to an exceedingly fine fibre (*f.fib.*) less than 0·5μ in diameter which, diverging from one or other side of the seam, continues in an ascending and forwardly directed course along the internal wall of the ampulla. Having reached a point from one-half to one-third the way up the wall it expands either gradually or abruptly into a broad flat ribbon (*rib.ax.*) which, though no thicker than the original fibre, is 25 to 30μ wide. The ribbon, which sometimes has a short recurrent branch (*rib.ax.rec.*), extends over the dorsal wall of the ampulla far down on to the farther side to terminate in one or more attenuated filaments. The flat faces of the ribbons have a radial alinement, their outer (centrifugal) margins being attached in many instances to the wall of the ampulla by means of a series of short, regularly arranged, conical processes of the axon (*con.*). From the opposite (centripetal) edge of the ribbon, and more rarely from the broad face, there originate a number of much longer and more irregularly disposed collateral branches (*collat.*). These latter, of varying shapes and complexity, reach out in a predominantly radial direction to penetrate and innervate the meshwork of muscle fibres (*musc.*) traversing the ampulla cavity.

A closer examination of the relations of the ultimate axons to the ampulla musculature reveals the significance of their change of form. The fine fibres, in diverging from the seam, tend to cut across the line of the muscles without acquiring intimate contact with them. The axon ribbons (figure 13*C*, *rib.ax.*), on the other hand, lie parallel to and indeed partly ensheath the muscle fibres (*musc.*). This is not, however, to say that they are in contact throughout their entire length with the muscles, for, in many instances (figure 13*B*), a ribbon axon (*rib.ax.*) may cross over once or several times from one muscle fibre (*musc.*) to another, but on the whole the ribbons establish an almost continuous area of synapsis with the more peripherally situated fibres of the ampulla musculature. A similar relationship holds between the axon collaterals (figure 13*A*, *collat.*) and the deeper muscles. The radially directed processes, on leaving the parent fibre, penetrate the muscular meshwork, expanding at intervals along their length and at their distal extremities into plasmodial-like sheets and vesicles which are applied to the surface of the muscles.

Figure 14 and figure 23, plate 27, show a ribbon axon viewed in broad face and (in figure 14) with its dimensions relative to the initial fine fibre (*f.fib.*) indicated. The lobes on the upper edge of the axon (*con.*) are the cones of attachment to the collagen connective tissue of the ampulla wall (*amp.*). The blue coloration of the main fibre has a finely granular consistency, the centre of the ribbon being deeper in colour and less transparent than its margins and collateral branches. In addition to this more homogeneous shading there are locally developed patterns of deeply stained lines and areas of varying form and extension, some of which patterns are illustrated in figure 16 under the general heading of colour reticula (*retic.*). These and other manifestations of differential staining of the ribbon axon

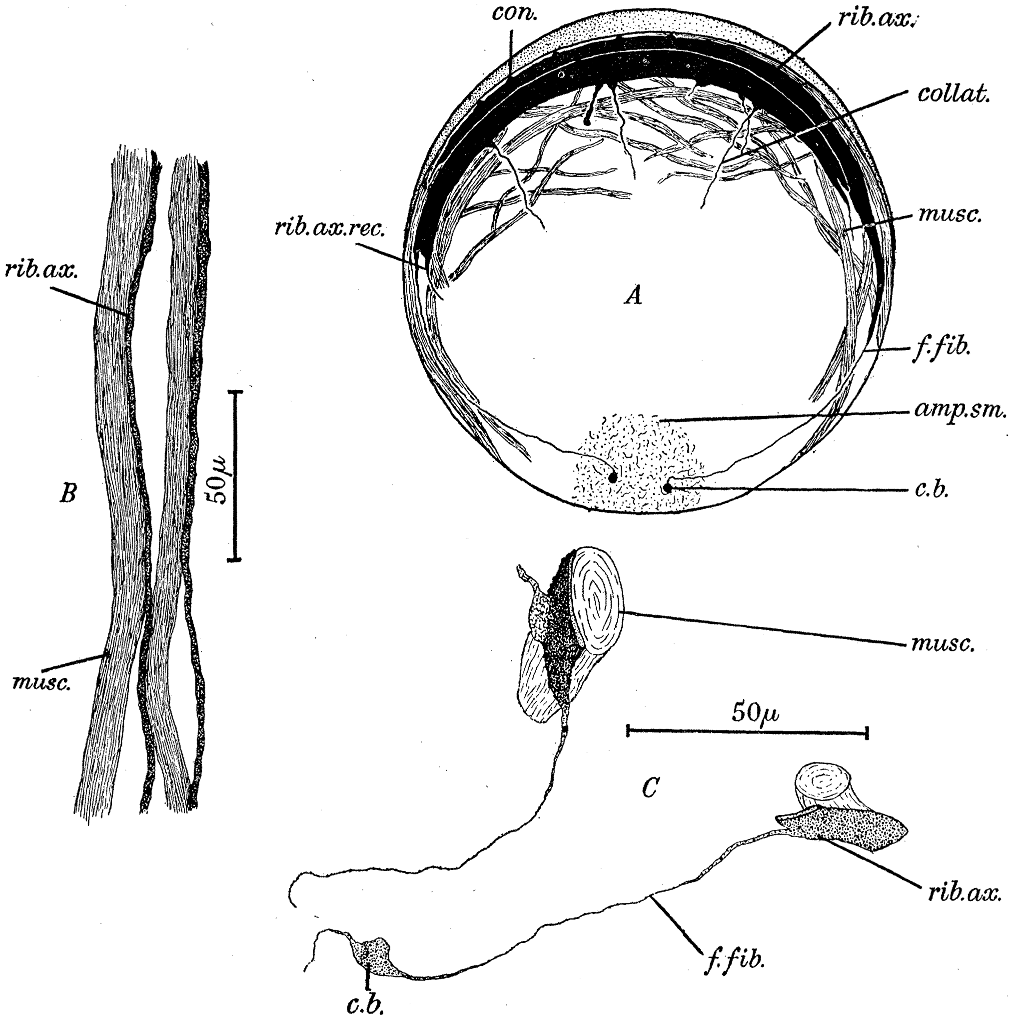

FIGURE 13. *A*, reconstructed oblique transverse slice of an ampulla (axis *XY* of figure 10) showing the more general anatomical features and neuromuscular relations of the ultimate motor neurons. *B*, Ribbon axons (seen edgeways) accompanying muscle fibres. *C*, the cell bodies, fine-fibre axons, and the beginning of the ribbon axons of two ultimate motor neurons of the ampulla. *amp.sm.* ampulla seam; *c.b.* cell body of neuron; *collat.* axon collateral; *con.* attachment process of the ribbon axon to the ampulla wall; *f.fib.* fine-fibre axon; *musc.* muscle fibre; *rib.ax.* ribbon axon; *rib.ax.rec.* recurrent branch of ribbon axon.

bear directly on its structure and especially on the question as to whether the fibre is invested by a sheath or is naked axoplasm. Axons viewed in transverse section yield little information as to their fine structure, partly because of their small diameter but more particularly on account of their close association with the markedly birefringent muscle and connective tissue. It is sometimes possible, however, to obtain longitudinal sections of the ribbons free from underlying muscle and collagen and, if the fibre is cut tangentially, one may on occasions discern an extremely thin and transparent axon membrane (figure 15, *lem.*) patterned by faint striae and delicate tessellations but otherwise devoid of visible

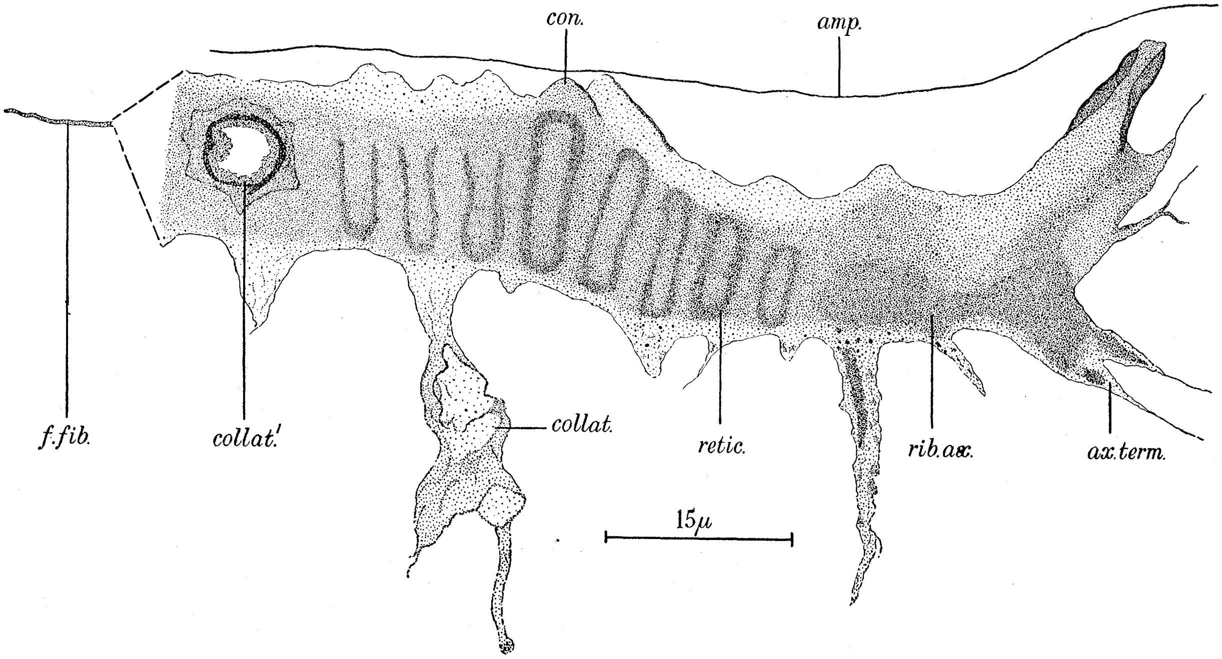

FIGURE 14. An ampulla ribbon axon viewed in broad face. *amp.* ampulla wall; *ax.term.* terminal branch of the axon; *collat.*, *collat.'* axon collaterals; *con.* attachment process of the axon to the ampulla wall; *f.fib.* fine-fibre axon; *retic.* colour reticulum; *rib.ax* ribbon axon.

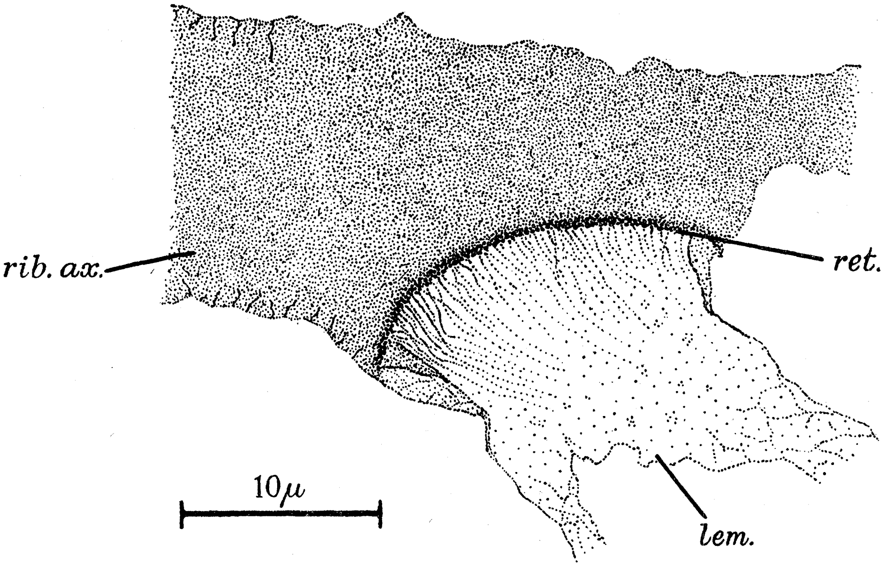

FIGURE 15. The origin of a collateral branch from a ribbon axon. *lem.* axiolemma; *ret.* colour reticulum encircling the base of the axon collateral; *rib.ax.* ribbon axon.

structure or of accreted or incorporated colour. The absence of nuclei or other structures makes it difficult to regard the membrane as other than a part of the fibre itself; it appears, in fact, to be an axiolemma. Myelinated fibres of vertebrates (Maximow & Bloom 1944) and of cephalopods and crustacea among the invertebrates (Young 1936; Schmitt & Bear 1939; Holmes 1942) are said not to have a visible axiolemma though, as Young has observed, they may have a superficial molecular orientation suggestive of a submicroscopical limiting membrane. It is therefore not without interest that in the unmyelinated fibres of the asteroid such a membrane is not only present but is optically visible.

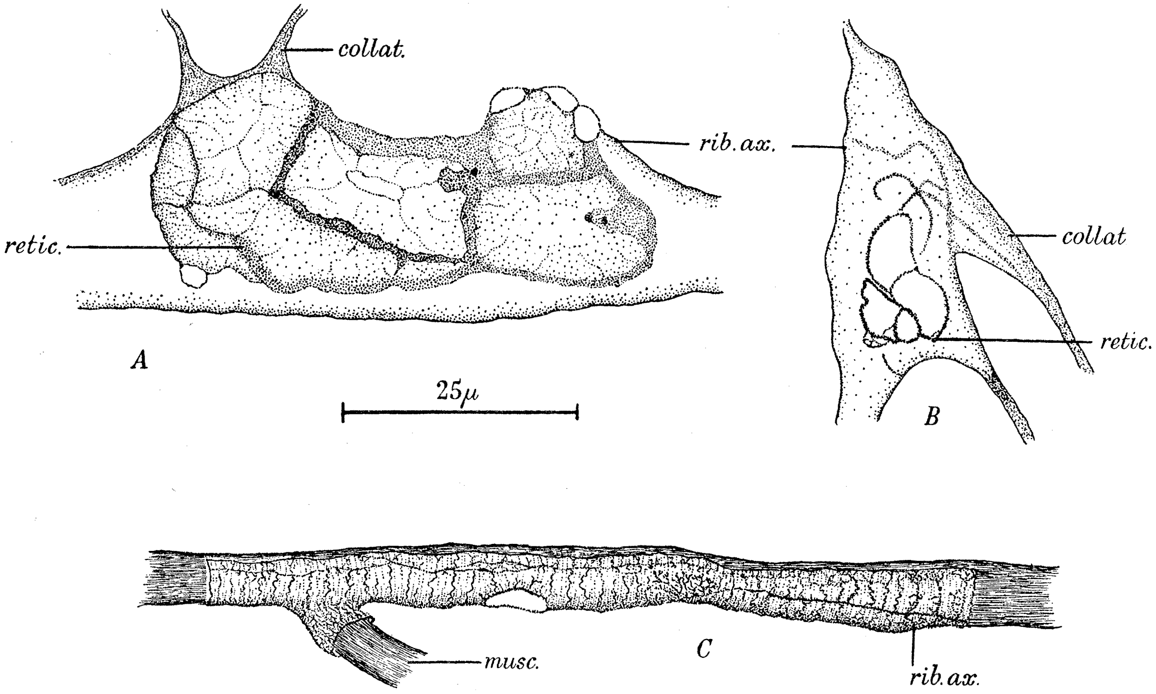

FIGURE 16. Different types of colour reticula commonly visible in vitally stained axons and supposedly due to differential staining of the axoplasm coagulum or to shrinkage of the axiolemma. *A*, coarse reticulum within the axoplasm of the main fibre. *B*, reticulum characteristic of the junctions of the ribbon axon and its collateral branches, and of the endings of the collateral branches on the muscles. *C*, finely reticulate pattern of a ribbon axon which is closely applied to a muscle fibre. *collat.* axon collateral; *musc.* muscle fibre; *retic.* colour reticulum; *rib.ax.* ribbon axon.

Since the axiolemma is not susceptible to staining, the colour of the vitally stained axon must presumably be axoplasmic, a conclusion which accords well with its dilution towards the thinner edges of the ribbon and in the more tenuous collateral branches. Many of the colour reticula (figure 16*A*, *retic.*) would, in this event, be attributable to plasma coagulation, though this in itself would hardly account for the more frequent occurrence of reticula at the origin of the branches (figure 16*B*, *retic.*) than in the main body of the axon. It is possible, therefore, that some of the concentrations of colour may be due to the differential shrinkage of the axiolemma over the more fluid plasma with a consequent creasing and more accentuated staining of the swollen bases of the collaterals. Shrinkage, if general over the entire surface of the ribbon, might indeed account for the complicated patterning shown in figure 16*C*. Whatever be the cause of the reticulation its arbitrary appearance and great variety of form would seem to show that it is not a reflexion of preformed structures within the living fibre. It would not therefore be justifiable to assign to the colour reticula any special significance as end-plate or synaptic structures. The entire surface of the ribbon appears rather to constitute a continuous and morphologically undifferentiated zone of synapsis with the underlying muscle.

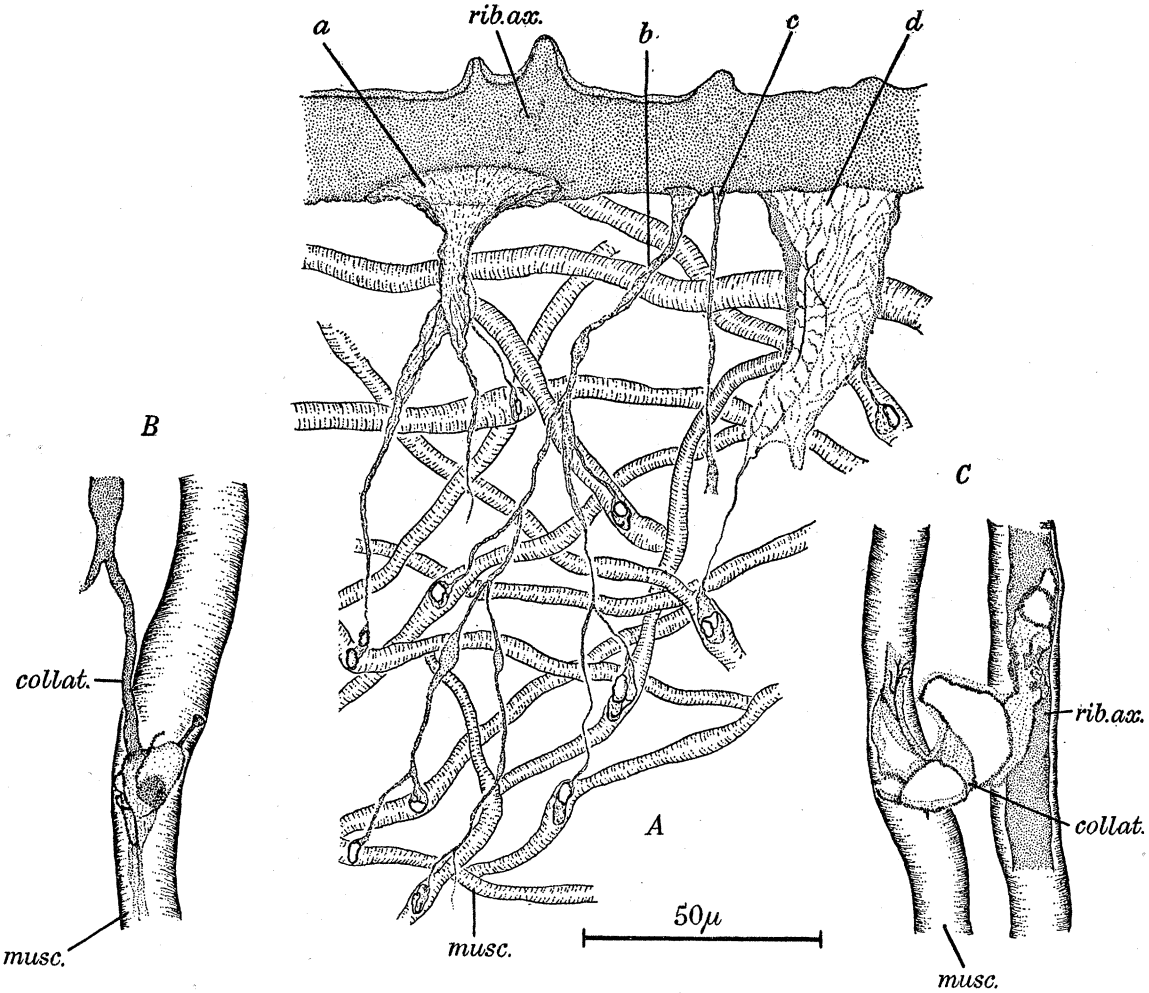

FIGURE 17. *A*, ribbon axon showing the various types of marginally originating collateral branches and the mode of innervation of the deeper muscle fibres of the ampulla. *B* and *C*, two examples of endings of axon collaterals on muscle fibres; the collateral fibre in *C* arises from the broad face of the ribbon axon. *B* and *C* are drawn at twice the magnification of *A*, the scale of which is marked. *collat.* axon collateral; *musc.* muscle fibre; *rib.ax.* ribbon axon.

The collateral branches of the ribbon axons arise from the parent fibre as fine threads (figure 17*A*, *b* and *c*), tapering cones with wide circular zones of junction (*a*), or as plasmodial-like sheets (*d*). They may continue as single fibres or be subject to extensive branching. In traversing the network of muscles the fibres expand at intervals along their length, and finally at their tips, into bulbs and plates which form areas of close contact with the muscles (figures 17*A*, *B* and *C*). The zones of neuromuscular junction are readily identifiable, even in the most faintly stained preparations, by their deep colour reticula which stand out as twisted coloured strands on the otherwise vacuolated and colourless axoplasm (figure 24, plate 27). Every one of the deeper muscle fibres is supplied by several such expansions of the axon collaterals, each muscle fibre thus being innervated at intervals along its length. The mode of supply to the deeper fibres might appear, at first sight, to differ radically from that of the superficial muscles which are overlain for considerable distances by the single structural continuum of the ribbon axon. When, however, it is recalled that the ribbon axon deviates in its course from one muscle fibre to another and that each muscle fibre may be supplied by a number of axons, each accompanying it for a part of its length with uninnervated sections of muscle intervening between the point of dissociation from the muscle of one nerve and the application to it of another, the essential similarity of the two methods is apparent.

It may be appropriate in conclusion to this account of the ampulla innervation to refer to the possible functional significance of the ribbon-shape of the terminal axon. These structures, though most readily studied in the ampulla, are present in all parts of the asteroid musculature and having been found, in addition, in the lantern muscle of echinoids, may be of general occurrence in the phylum. This circumstance makes it improbable that the ribbon is a special adaptation to the conditions of mechanical deformation obtaining during the contraction and dilation of the ampulla, especially as other animals, such as, for example, anemones and flatworms, which can suffer considerable change of shape, possess the more normal cylindrical fibre. Neither does it appear probable that the flattened axon is a device for ensuring a rapid response. Even if the rate of transmission of excitation in the ribbon is 8 to 10 times that of the initial fine fibre, a figure which assumes that the rate of conduction is proportional to the square root of the fibre diameter (Pumphrey & Young 1938) and the further (probably unjustifiable) assumption that the rate is governed by the greatest diameter of the fibre, the interpolation of a ribbon at the end of a chain of otherwise cylindrical-fibred motor neurons would have little effect in reducing the total time of passage of the excitatory state through the motor arc.

We return then, in retrospect, to the most probable of the functions of the ribbon axons, namely, that they are extended motor end-plates ensuring a maximal degree of association between nerve and muscle. On no other basis is it possible to rationalize the congruence of the ribbons with the muscle and the retention of cylindrical fibres in neurons which are not directly concerned with the innervation of muscles. So little is known of the fine anatomy of invertebrate neuromuscular synapses that it is difficult to make adequate comparison of the asteroid and other types of axonal endings, though there is little doubt but that the extreme ribbon flattening is unique among known nervous structures. In invertebrates, where neuromuscular junctions have been described, the cylindrical motor axons on reaching the muscle become attenuated or branch into finer and finer fibres. In many instances however, as, for example, in the coelenterates (Woollard & Harpman 1939) and arthropods (van Harreveld 1939; Wigglesworth 1939), the ends of the fibres are swollen into bulbs or woven into end-plates which increase the surface of contact between the axon and muscle. Here, as in the vertebrates, it would appear that the physical and chemical phenomena associated with muscle excitation require the provision of adequate areas of junction between the two tissues. We are left to speculate as to why the areas should be so peculiarly extensive in the Echinodermata. Bacq's (1947) observation that the nerves of many echinoderms are markedly cholinergic may have relevance to the form of the axon ribbons, but until further anatomical and physiological investigations of invertebrate neuromuscular synapses have been undertaken the question must remain *sub judice*.

The innervation of the foot musculature

(*a*) *The retractor musculature*

Of the two systems of muscles within the *Astropecten* podium—the retractor and postural series—the retractors are by far the more extensive. They originate (figure 8, *retr.m.*) on the under-surface of the ambulacral ossicles and extend as a cylindrical sheath encircling the hydrocoel almost to the tip of the podium. The more superficial fibres are accompanied along a greater or lesser part of their length by ribbon axons, some 250 to 300 of which may be visible in a whole mount of a vitally stained foot (figure 18, *rib.ax.*). The flat surfaces of the ribbons have a radial orientation in respect to the transverse diameter of the foot (figure 19, *rib.ax.*), and from their internal edges there spring numerous collateral branches (*collat.*) which innervate the deeper fibres of the muscle sheath (*musc.*). Shorter centrifugally disposed projections (*con.*) anchor the ribbons to the connective tissue (*c.t.*) of the foot wall. The innervation of the retractor musculature is in all these respects comparable to that of the ampulla.

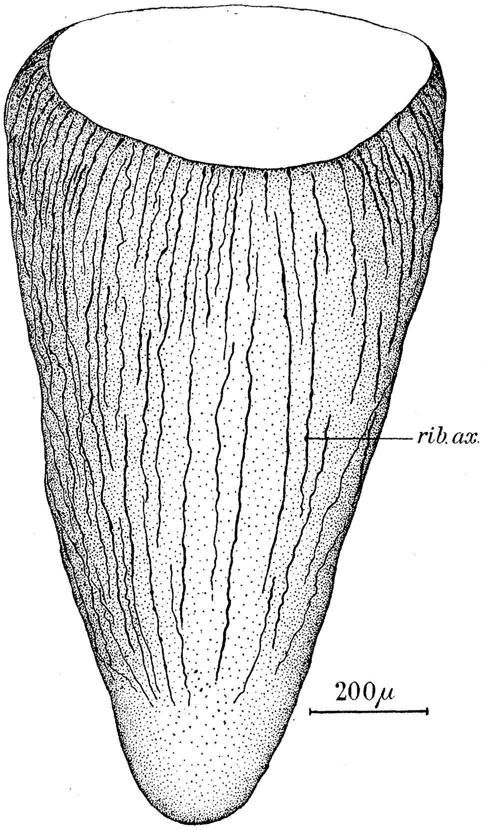

Figure 18. A vitally stained tube foot amputated at its origin on the ambulacral ossicles and with the ectoderm removed so as to show by transparency the distribution of the ribbon axons over the retractor musculature. *rib.ax.* ribbon axon.

In the case of the retractor muscles, however, it is rarely possible to identify with certainty the position and relationships of the ribbon axon cell bodies. Figure 20, a longitudinal section through the lateral bulb complex (*bulb lat.*) and the base of the foot, shows the more apparent of the connexions. The more basally situated ribbons (*rib.ax.′*), when traced back towards the bulb, taper into fine filaments which penetrate and enter the lower margin of the bulb tissue. Within the marginal tissue are a number of cell bodies (*c.b.*), each with one or more delicate processes, which processes, though coming into very close relation with the axon filaments, cannot be said with surety to be continuous with them. If then we incline to interpret the cell body, fine-filament and ribbon axon as parts of the same ultimate motor neuron we do so more by analogy with the similarly constituted neurons of the ampulla and (see below, p. 554) of the postural musculature than by direct observation. On this assumption the ribbon fibres supplying the foot retractor musculature would be regarded as being connected by fine-fibre axons with cell bodies lodged in the periphery of the swollen bases of the medial and lateral bulbs of supporting tissue, the system of cell bodies, as a whole, being disposed in a circlet around the base of the foot at the level indicated in figure 8 by the lower of the two broken lines.

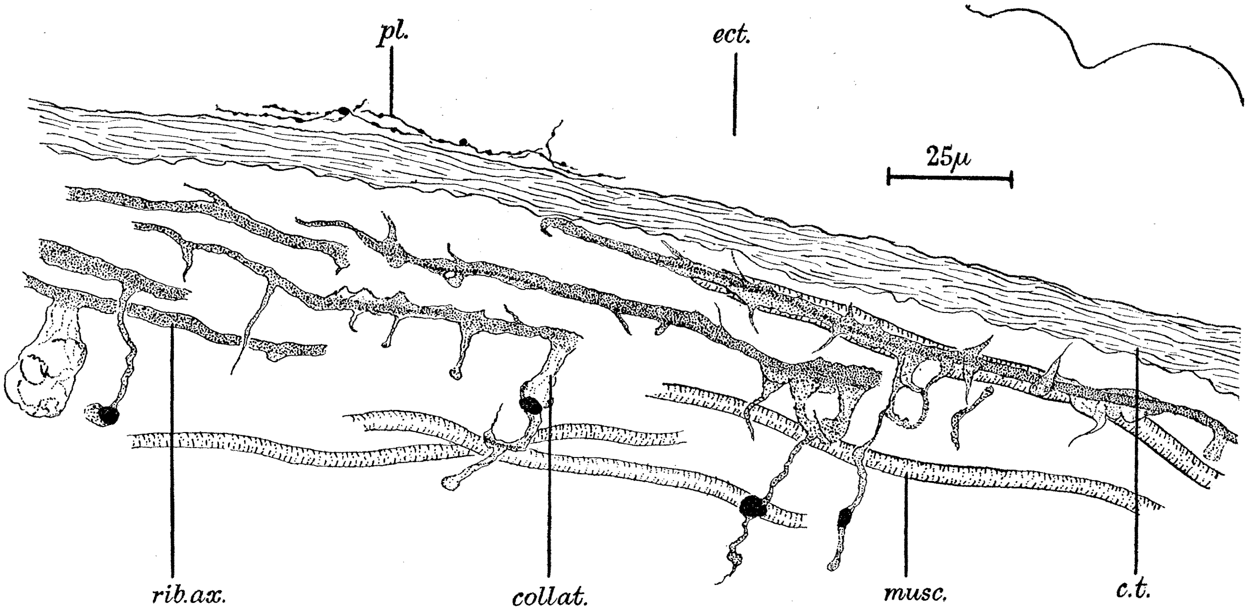

FIGURE 19. A part of a longitudinal section through the upper part of the column of a tube foot showing the orientation, structure and neuromuscular relations of the ribbon axons and axon collaterals to the retractor musculature. *c.t.* connective tissue sheath; *collat.* axon collateral; *ect.* ectoderm; *musc.* muscle fibre; *pl.* subepithelial ectodermal nerve plexus; *rib.ax.* ribbon axon.

It will be recalled that many of the bulb neurons—the β neurons of the earlier account (p. 543 and figure 11, β)—are wholly confined to the substance of the bulb and are without connexion with the extrinsic neurons of the perihaemal canal. Certain of the neurons of this series (figure 20, β) appear to enter into synaptic relationship with the cell bodies of the ultimate neurons of the retractor innervation, this being especially evident in the neurons like the one marked which have long fibre processes oriented along the line of the cell bodies. The β neurons, as we have seen, are in receipt of excitation from the central tracts of the nerve cord by way of the distributory axons of the perihaemal canal and the α neurons of the foot complex. They thus function as a relay both to the ampulla and foot-retractor musculature, and to this extent may be said to furnish the anatomical basis for the observed reciprocation of movement of the foot and ampulla. The random character of the β complex and the apparent absence of any determinate pattern of connexion between the nerve tracts supplying the two systems renders impracticable, however, any further clarification of the neurological mechanisms which underlie the reciprocal excitation and inhibition of the two antagonistic muscle systems and of their mutually opposed movements.

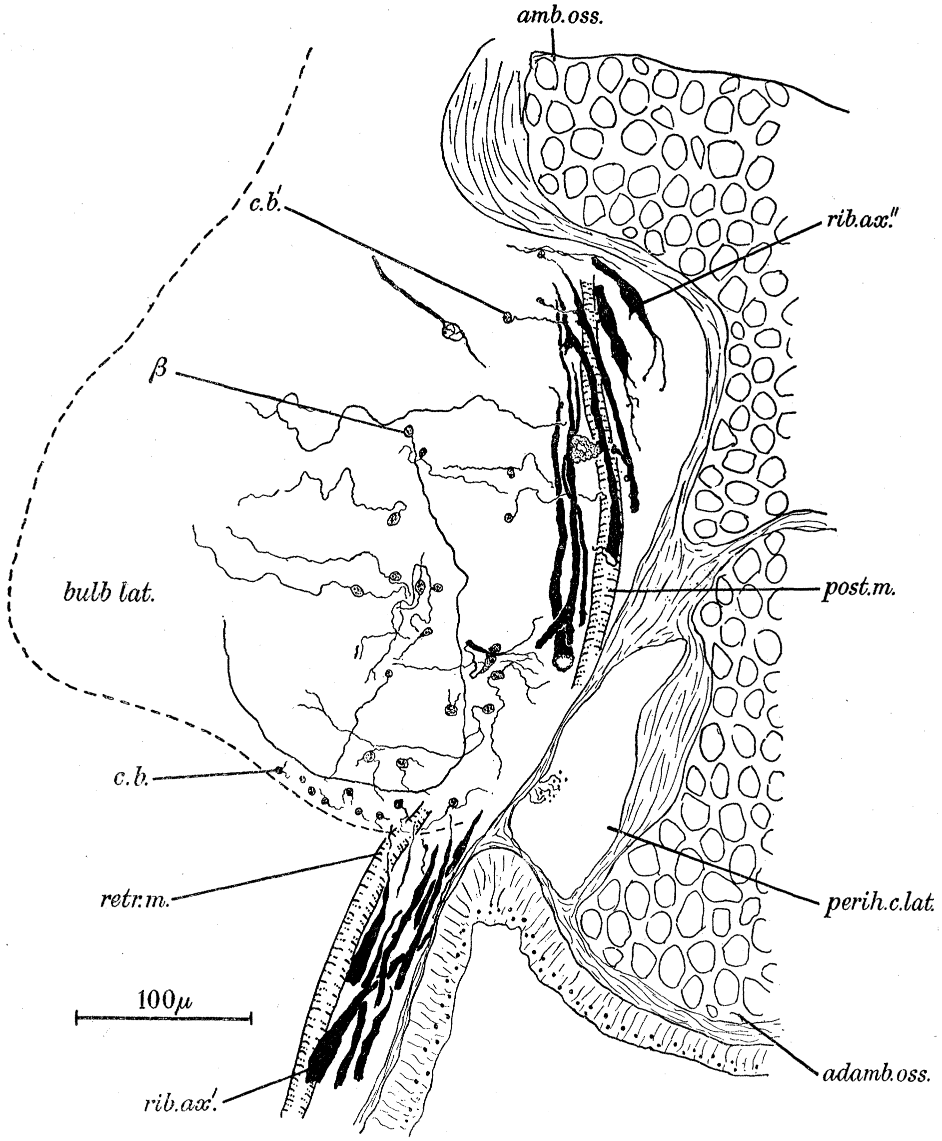

FIGURE 20. A part of a longitudinal section through the base of a foot and lateral bulb complex showing the more general features of the postural and retractor muscle innervation. *adamb.oss.* adambulacral ossicle; *amb.oss.* ambulacral ossicle; *β*, internuncial neuron of the bulb complex; *bulb lat.* supporting tissue of the lateral bulb; *c.b.*, *c.b.'* cell bodies of the ultimate neurons serving the retractor and postural musculature respectively; *perih.c.lat.* lateral perihaemal canal; *post.m.* postural muscle fibre; *retr.m.* retractor muscle fibre; *rib.ax.'*, *rib.ax.''* ribbon axons respectively of the retractor and postural musculature.

(*b*) *The postural musculature*

We turn now to the innervation of the postural muscles of the foot, the cylindrical sheath of short fibres confined to the base of the foot (figures 8, 20, *post.m.*). Two features serve to emphasize the separateness of the motor supply to the postural and retractor muscles. The ribbon axons which overlie the postural muscles (figure 20, *rib.ax.″*) are, in the first place, nearer the base of the foot and rarely overlap the retractor fibre ribbons (*rib.ax.′*). Secondly, the cell bodies of the postural neurons (*c.b.′*) are high up in the substance of the bulb (at the level of the upper broken line in figure 8), and are remote from the retractor neuron cytons (*c.b.*). Transverse sections through the base of the foot, parallel to the under-surface of the ambulacral ossicle (figure 21), show the cell bodies of the postural muscle neurons (*c.b.*) to be arranged around the entire periphery of the podium within the muscle layer (*post.m.*). Each cell body has a fine-fibre extension which in longitudinal sections through the foot (figure 20) can be traced radially and centrifugally for a short distance before it expands into a ribbon (*rib.ax.″*) oriented at right angles to the fine fibre in the line of the muscles (*post.m.*). Centripetally oriented collateral branches of the axon provide subsidiary neuromuscular contacts.

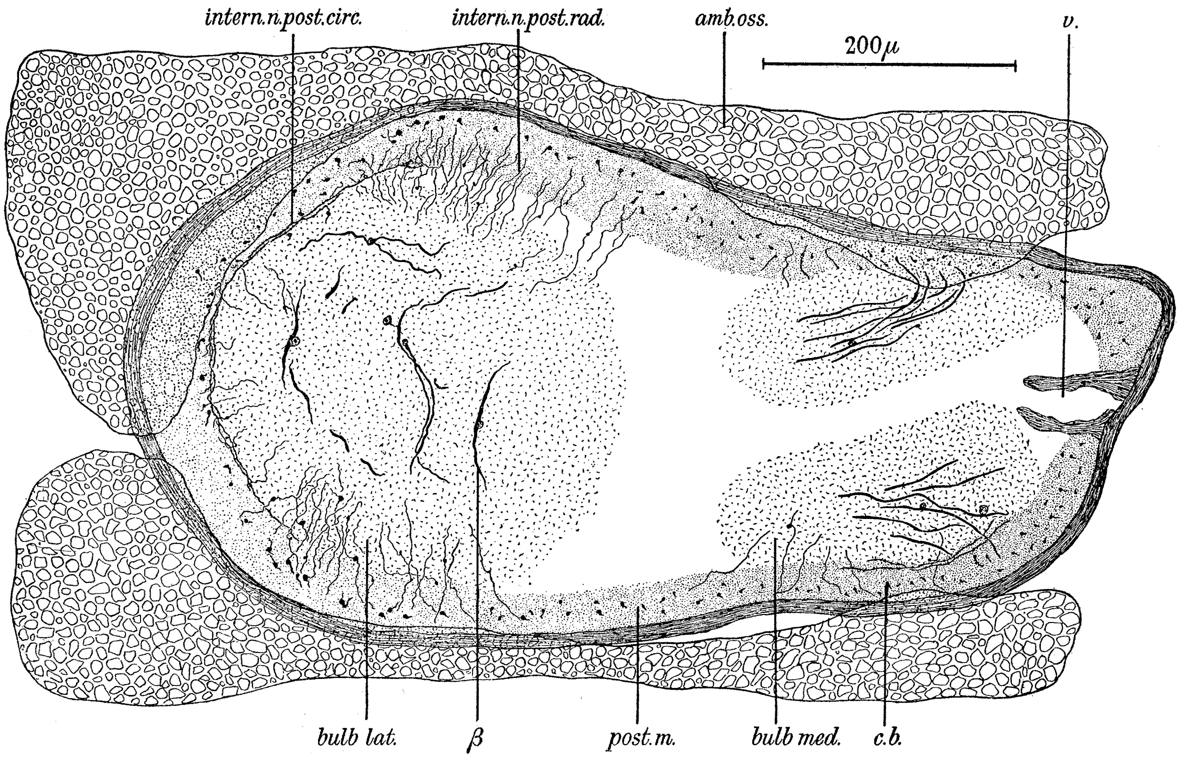

FIGURE 21. A transverse section through the base of a tube foot showing the radial and circular fibre systems associated with the innervation of the postural musculature. Features from a number of sections are included in the drawing. The midline of the arm is to the right and the base of the arm to the lower side of the figure. *amb.oss.* ambulacral ossicle; *bulb lat.* lateral bulb supporting tissue; *bulb med.* medial bulb supporting tissue; *β*, internuncial neuron of the bulb complex; *c.b.* cell body of an ultimate motor neuron; *intern.n.post.circ.* circular fibres of the postural muscle innervation; *intern.n.post.rad.* radial fibres of the postural muscle innervation; *post.m.* postural muscle sheath; *v.* valve of the lateral water vessel.

In commenting elsewhere on the mechanisms which govern the directional co-ordination of the tube feet in starfishes (Smith 1945, 1947 and 1950) it had been concluded that unidirectional pointing and stepping is effected by the contraction, in each foot, of sectors of the postural muscle ring having a like compass orientation, and that changes in the direction of pointing and stepping are initiated by the selection for action, in each foot, of one series of spatially correspondent muscle fibres in the place of another. Experimental evidence seemed further to show that the selector mechanisms are based on a particular patterning and interconnexion of neurons contained (1) within the radial nerve cords and circumoral nerve ring and (2) within the motor complex of the feet. In this latter respect therefore especial interest attaches to the anatomy of the nervous connexions between the internuncial neurons of the foot complex and the ultimate neurons which serve the postural muscle fibres.

Two systems of nerve fibres appear, in vitally stained preparations, to enter into relation with the ultimate postural neurons. The one (figure 21, *intern.n.post.rad.*) comprises a number of extremely delicate processes which can with difficulty be traced out from the central mass of the supporting bulbs (*bulb.lat.*, *bulb med.*) to the cell bodies of the ultimate neurons (*c.b.*) as radially and horizontally disposed strands closely applied to the under-surface of the ambulacral ossicles. It has not been possible, in spite of much careful searching, to identify the cell bodies of the radial fibres, which appear to taper into fine filaments at either end. The most that can be said of them is that they emerge from the fibre complex of the β internuncial neurons and connect peripherally with the ultimate motor neurons supplying the postural musculature. The second series of fibres (*intern.n.post.circ.*) encircle the base of the foot around the margin of the ossicles, and at the level of the ultimate neuron cell bodies, as chains of serially connected relatively short fibres. They, too, show no sign of a cell body.

Such is the picture, so tantalizingly deficient in configurational detail, of the intrinsic motor innervation of the postural muscles. Though it must be admitted at the outset that it yields but little information concerning the mechanisms by which the various sectors of the postural ring are selected for action, the more general significance of the pattern should not be overlooked. The radial and circumferential fibres are, in the first place, the only systems of oriented tracts to be found within the bulb complex, a circumstance suggesting that the postural muscles are subject to a more precise regional grouping of contraction than are the retractor muscles which are served through a diffuse system of internuncials and which are known to act as a single contractional unit. Secondly, the radial distribution of the fibres linking the bulb complex with the terminal elements of the postural muscle innervation is, in its general features, fully consistent with the sectorial contraction of the postural musculature and is in fact a requirement of the hypothetical scheme of innervation that had been put forward (Smith 1945) as a possible explanation of the observed patterns of orientation of the feet. The ring fibres, on the other hand, introduce a new and somewhat unexpected element into the innervation, the functional implications of which may become more apparent on further study of the oriented movements of the podia. A possible role is, however, suggested by the ease with which centrally controlled movements of the feet can be made to yield to other patterns under the influence of particular patterns of peripheral stimulation. *Astropecten*, for example, on moving from a rocky substrate to a sandy bottom ceases to walk and commences to burrow, its feet forsaking the unidirectional line of locomotory advance to act as laterally moving scoops which push the sand outwards from the midline to the sides of the arm, thus causing the animal to sink below the surface. *Asterias* will also exhibit local and peripherally controlled patterns of movement of the feet as in the capture of food and its transference to the mouth. These and similar activities call for a nervous mechanism whereby individual or localized groups of feet can be made to orientate and move independently of the main body of locomotory podia. The ring fibres which connect the various sectors of the postural musculature in each foot may possibly subserve this function.

Comparison with other invertebrate nervous systems

The five classes of living echinoderms differ but little in the gross morphology of their nervous systems. All possess a peripheral sensory net having connexions with five radial cords united around the mouth by a nerve ring. All but the most localized of responses, which may be mediated through the peripheral net, require the intervention of the radial cords and ring. In the asteroids, the only class in which the motor system has been worked out in detail, excitation is distributed from the radial cord by bilaterally and metamerically arranged groups of neurons with extended axon processes. These neurons lie in the mesothelial floor of the radial perihaemal canal immediately above the nerve cord, and their connexion with the tracts of the cord is effected by axon collaterals which penetrate the intervening boundary tissue. The mesothelial position of the motor cells is a feature peculiar to echinoderms; other triploblastic animals incorporate them in the ectodermal central nervous tissue. It must be remembered, however, in commenting on this peculiarity, that the difference in location of the motor cells, though of great morphological and phylogenetic interest, originating perhaps with the divergence of the Enterocoela and Schizocoela from the ancestral diploblastic stock, has no functional significance. In all animals the transmission of excitation from the integumental receptors to the musculature involves the penetration by the nervous pathways of the boundary membranes which separate the ectoderm from the more deeply seated mesodermal muscles. In echinoderms the penetration occurs centrally at the zone of junction of the association tracts of the cord and the initial (most afferent) motor neurons. Other triploblastic animals, with the association and motor elements contained within the intucked ectodermal nervous tissue, effect the penetration peripherally at the zone of junction of the nerve and muscle.

The echinoderm nervous system embodies, in addition to the features which are peculiar to the phylum both coelenterate and coelomate characteristics. The radial nerve cord and its associated hyponeural motor cells may, for example, be compared directly with the nerve cord of an annelid or arthropod. Both consist essentially of longitudinal connective and transverse commissural tracts which ensure the co-ordination of serially and bilaterally disposed systems of organs; both are in receipt of excitation through afferent metamerically arranged sensory tracts, and both discharge excitation to the body musculature through a metamerically correspondent series of motor tracts. The principal difference between the nervous system of echinoderms and other coelomate animals is that in the echinoderms the sensory and motor pathways are made up of a comparatively large number of short-fibre neurons linked in series, whereas in the vertebrates and remaining coelomate invertebrates the sensory tracts are spanned by a single neuron, and the motor tracts by, at the most, two or three neurons.

The multisynaptic subepithelial sensory system of the echinoderm much resembles, in its fine anatomy, the ectodermal nerve plexus of the coelenterate, and though we find in the echinoderms as in the coelenterates a tendency to achieve through-conduction in the manner of extended fibre tracts, the sensory plexus retains, in both instances, many of the fundamental anatomical and physiological characteristics of a nerve net.

In their motor organization the differences between echinoderms and other coelenterate animals are much less radical. With the exception of the arthropods, where the motor nerves run without interruption from the central nervous system to the musculature, almost all invertebrates include a peripheral relay, often identifiable as a ganglion, between the centrally originating motor fibres and the musculature. The intervention of a motor relay, while not relieving the various parts of the animal from central nervous control, allows of the peripheral adjustment of their activities and for a certain autonomy of movement. In starfishes each of the metameric motor pathways comprises, at its origin, some twenty elongated axons of the central distributory neurons. Further neurons are interpolated between the central distributory fibres and the various muscle systems, the more afferent of which are elaborated into ganglion-like neuron complexes, the more efferent extending in linear series as post-ganglionic distributory tracts. The central distributory axons of each motor nerve discharge into two such ganglia. One, the lateral motor complex situated in the lateral perihaemal canal at the outer margin of the foot, functions as a relay to the arm musculature, the other, the bulb complex within the cavity of the podium, disperses excitation to the several muscles of the foot and ampulla. The motor innervation of the asteroid is thus characterized by (1) a connexion of all the motor trunks with the nerve cord, (2) a metameric and bilateral pattern of supply, (3) a division of the main trunks into branches serving particular groups of organs and muscles and (4) the presence, at the origin of each of the branches, of a peripheral ganglion. Such an arrangement almost exactly duplicates the annelidan system and, except for its metamerism, that of the mollusca and other invertebrate animals.

No one would suppose that the similarity is other than a manifestation of convergence. The echinoderms as a group have pursued a line of evolution independently of the main coelomate stock. This is evident not only in the retention, within their nervous system, of many primitive acoelomate features such as the multisynaptic sensory net, but in the more general relations of the nervous system which, by virtue of its connexions with the radial cords and circumoral nerve ring, is adjusted to the radial symmetry of the animal and to the development of co-ordinated response. Convergence derives from the superimposed metameric and bilateral pattern of the motor supply and from the interpolation within the motor tracts of peripheral ganglia, these features having a functional value in that they permit of a considerable degree of autonomy of the individual parts and of an interplay of peripherally and centrally controlled patterns of movement which is no less restricted in its character and variety than that of other, often more highly organized, invertebrates.

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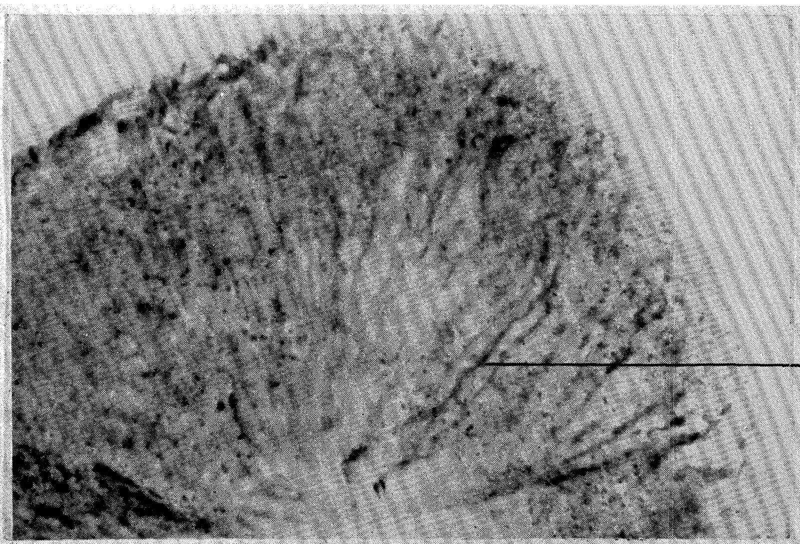
Description of plate 27

Photographs of vitally stained motor nerve fibres from the ampulla of *Astropecten*.

Figure 22. Part of a whole mount of an ampulla showing the circumferential ribbon axons (*rib.ax.*). (Magn. × 150.)

Figure 23. A part of a ribbon axon (*rib.ax.*) with attachment processes (*con.*), the origin of a collateral branch (*collat.*)—mainly out of focus—and a colour reticulum (*retic.*). (Magn. × 1425.)

Figure 24. A colour reticulum at the termination of an axon collateral on a muscle fibre. (Magn. × 1425.)



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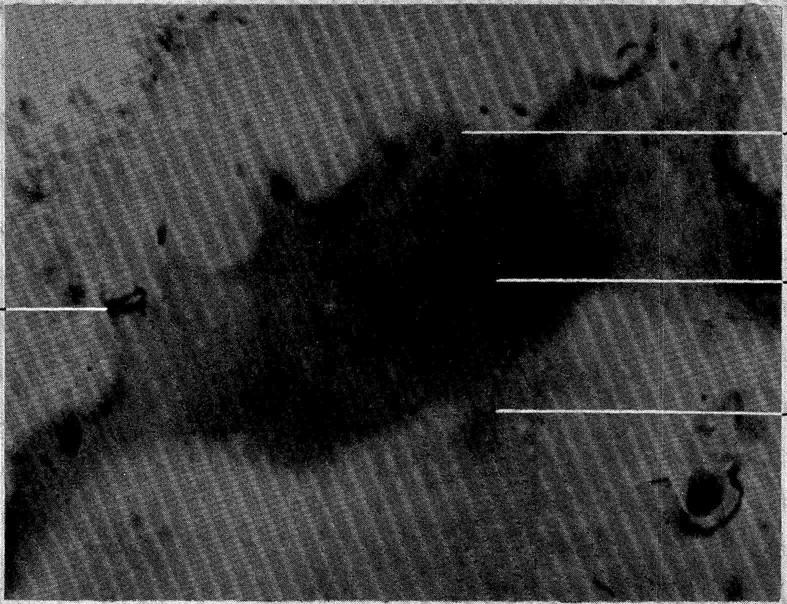

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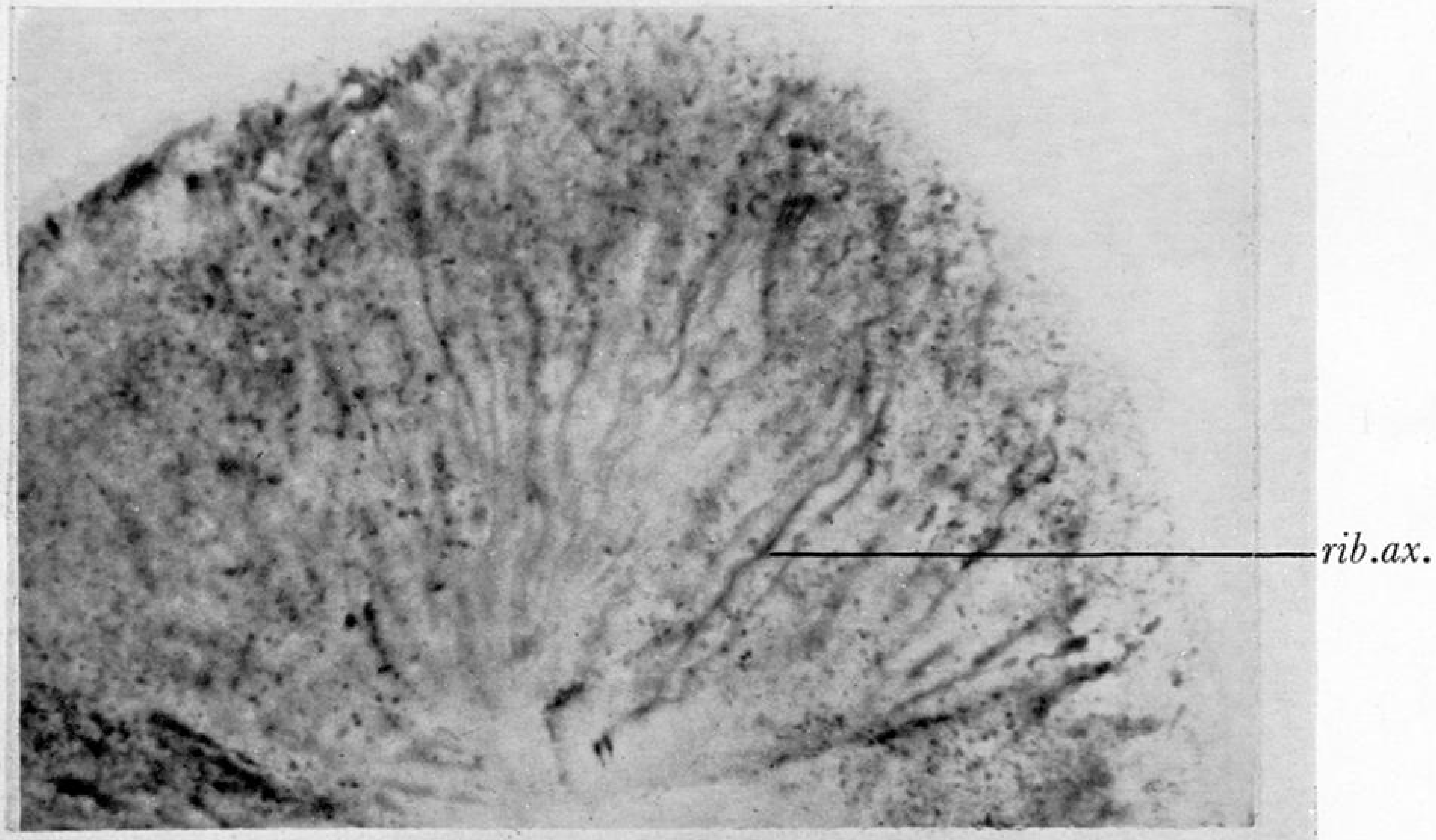

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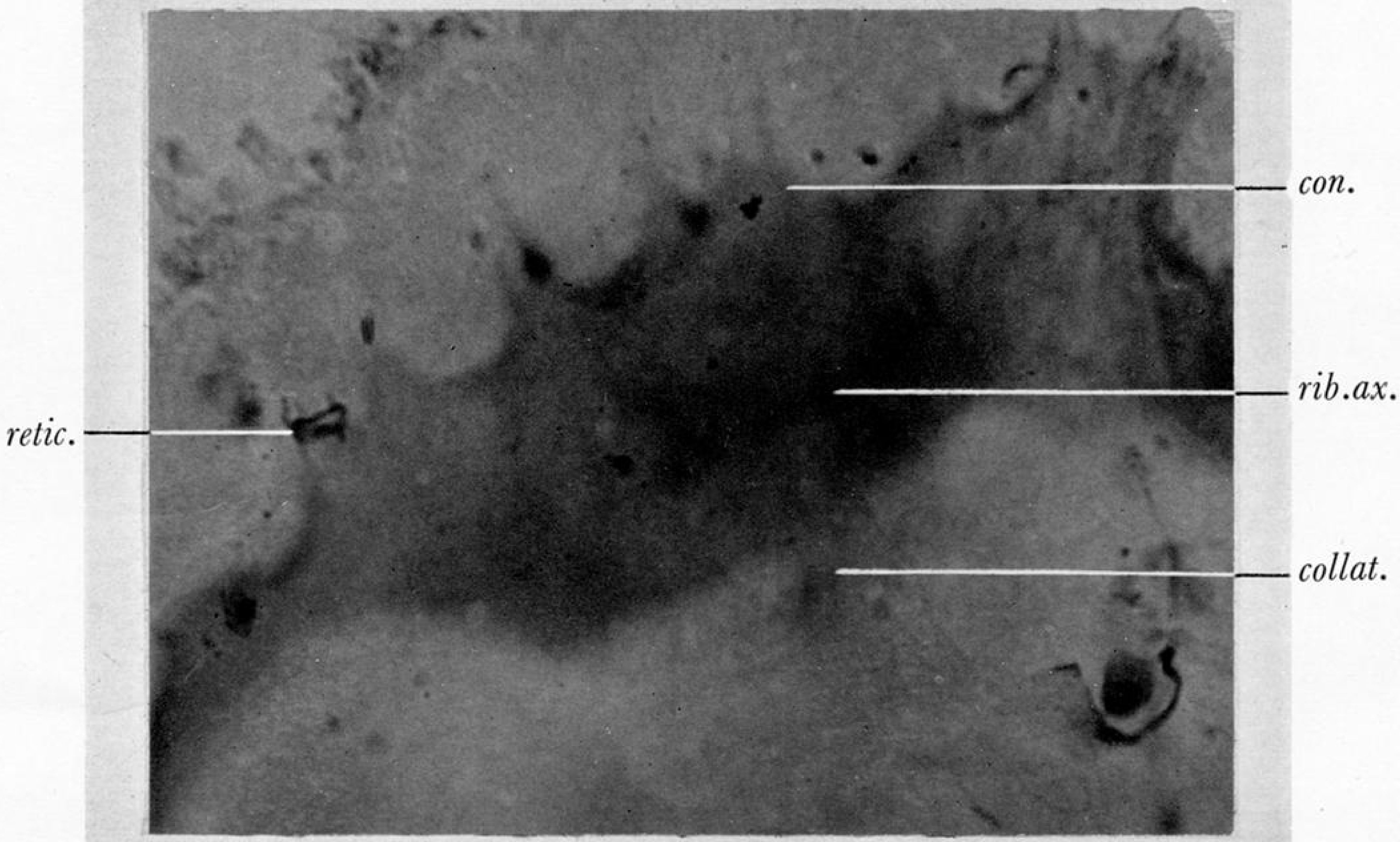

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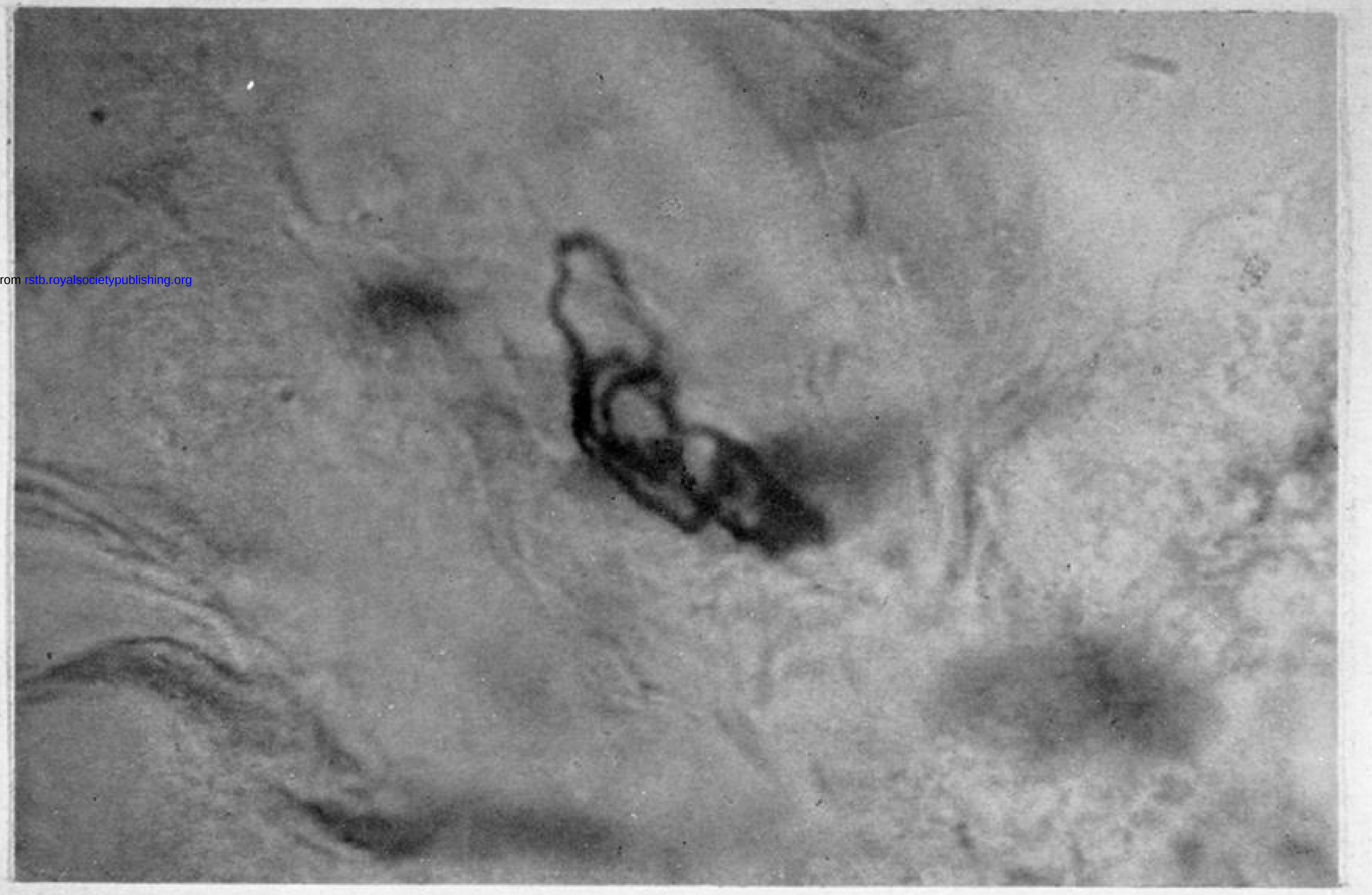

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Description of plate 27

Photographs of vitally stained motor nerve fibres from the ampulla of *Astropecten*.

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