The Giant Nerve Fibres and Epistellar Body of Cephalopods.

By

John Z. Young, M.A.

Magdalen College and the Department of Zoology and Comparative Anatomy, Oxford.

With 20 Text-figures.

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INTRODUCTION.

AT the hind end of the stellate ganglion of Eledone moschata there is a small yellow spot, about the size of a pin's head, which can be seen on examination of serial sections to consist of a closed vesicle. On account of its position it has been named the epistellar body (Young, 1929). It has been found in all the Octopods examined, though it is not always coloured yellow. Search was made for a similar organ in the same position in Decapod Cephalopods but no trace of it could be found. However, during the search certain extremely large nerve fibres were noticed in the stellate ganglion of Loligo, and study of these showed them to originate not from giant nerve cells, but by the fusion of the axons of a very large number of small cells which are congregated together in a separate lobe situated at the hind end of the ganglion. This lobe lies in a position which corresponds exactly to that of the epistellar body present in Octopods, and these latter have no giant fibres. The conclusion which has been drawn as a result of study of the two systems is that the epistellar body of Octopods is derived from the cells of the giant fibres of Decapods; and, since the former is probably secretory, we have here a case of the formation of gland from nerve cells parallel to that of the adrenal medulla of Vertebrates. The many curious features of this peculiar transformation are described in this paper, beginning with a preliminary account of the giant fibres themselves, which present several points of very great interest.

The material described has been collected over several years, during visits to the Stazione Zoologica di Napoli and the Marine Biological Station at Plymouth.[1] Nearly all the observations have been made on sections fixed in various ways, which are detailed in the text. The silver methods used for the study of the details of the nervous connexions have been described elsewhere (Sereni and Young, 1932). The formol-Cajal method gives particularly good stains of the finest branches of the giant fibres.

Giant Nerve Fibres in Decapods.

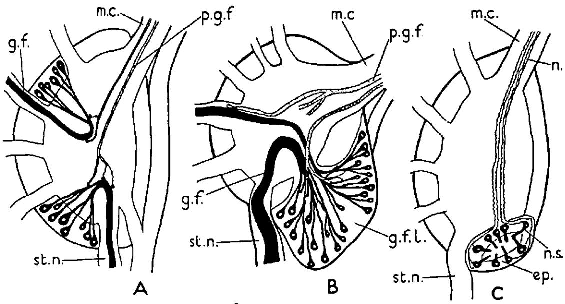
Giant nerve fibres have been found in several groups of cold-blooded animals, their function being apparently the conduction of impulses for the performance of some rapid action of advance or retreat involving the synchronous contraction of large numbers of muscles. Thus it is by means of their giant fibres that Earthworms are enabled to retract rapidly when touched either at the head or tail end (Stough, 1926).

To the best of my knowledge the only mention of giant fibres in Cephalopods, or indeed in any Mollusc, is the very brief account of Williams (1909), who noticed the giant fibres in the central nervous system of Loligo pealii. He believed that these ran straight into the pallial nerve and thence through the stellate ganglion into the stellar nerves. In Loligo forbesi this is certainly not correct. The giant fibre system begins with a pair of giant cells lying at the hind end of the pedal ganglion. The processes of these cells pass backwards into the pallio-visceral ganglion, in which the two axons actually fuse across the middle line, instead of merely crossing as described by Williams. They then separate again and each breaks up into several branches which end in synaptic junctions with other giant fibres arising from cells in the palliovisceral ganglion and

[1] I am grateful to Dr. E. J. Allen and to Dr. R. Dohrn for their help, also to Professor E. S. Goodrich for criticism of the MS.

passing out in the posterior infundibular, visceral, and pallial nerves.

The details of the anatomy of this giant fibre system will be published later, here it is sufficient to say that the fibres running backwards in the pallial nerve do not, as supposed by Williams,



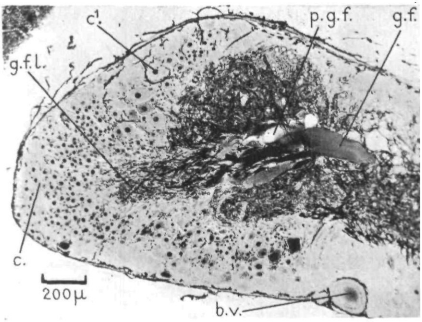
TEXT-FIG. 1.

Diagrams of stellate ganglia of Cephalopods. In Sepia (A) the giant fibres arise from cells scattered throughout the ganglion, and in Loligo (B) from cells collected into a giant fibre-lobe. In Octopods (C) there are no giant fibres, but in the position of the giant fibre-lobe are the cells whose axons end blindly in the epistellar body.

LETTERING FOR TEXT-FIGURES 1–20.

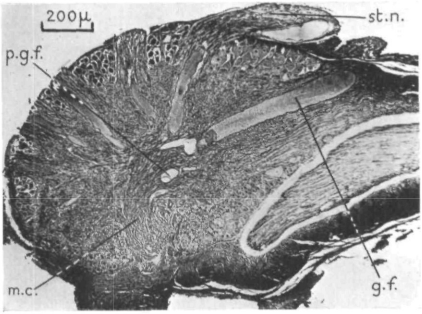
am., amoebocyte; *b.*, terminal bouton; *b.v.*, blood-vessel; *c.*, cell of giant fibre-lobe; *c′.*, ordinary cell of stellate ganglion; *cav.*, cavity of epistellar body; *c.ep.*, epithelial cells of epistellar body; *ep.*, epistellar body; *f.*, connective tissue fibrils; *g.*, osmiophil granules; *g.f.*, 'post-ganglionic' giant fibres; *g.f.l.*, giant fibre lobe; *h.*, homogeneous substance at centre of epistellar body; *l.*, isolated masses at centre of epistellar body; *m.c.*, mantle connective (pallial nerve); *m.ret.*, musculus retractor capitis; *m.m.*, mantle muscles; *n.*, nerve to epistellar body; *n.am.*, nucleus of amoebocyte; *n.conn.*, nucleus of connective tissue; *n.s.*, neurosecretory cell; *n.n.s.*, nucleus of neurosecretory cell; *p.n.s.*, process of neurosecretory cell; *p.g.f.*, 'pre-ganglionic' giant fibre; *st.g.*, stellate ganglion; *st.n.*, stellar nerve.

run right through the stellate ganglion, but end there in synaptic junction with another set of giant fibres, which we may call 'post-ganglionics', running out in the stellar nerves to innervate the mantle muscles (Text-fig. 1). The giant synapses in the stellate ganglion, by which the pre- and post-ganglionic fibres communicate, are of the greatest interest and will be described fully in a later paper; here we are concerned only with the post-ganglionic fibres themselves. These are of extremely large size, up to 600μ in diameter in Loligo forbesi and 150μ in Sepia officinalis. In Loligo forbesi there is one



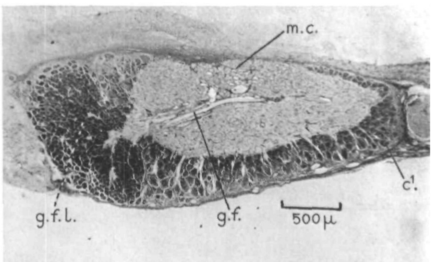
TEXT-FIG. 2.
Loligo forbesi. Sagittal section of stellate ganglion showing giant fibres. Formol-Cajal.

of them in each of the stellar nerves, and if any one fibre is traced into the ganglion it is found to branch many times until the finest branches can be followed back to their origin as the axons of single cells situated in a separate lobe at the hind end of the stellate ganglion (Text-figs. 1, 2, 3, and 4). These giant fibres are therefore syncytia, each formed by the fusion of the processes of very many small nerve cells. It is not easy to say exactly how many cells go to the making up of each giant fibre. The number of post-ganglionic giant fibres varies in different individuals of Loligo forbesi between nine and fifteen, and estimates of the number of cells in the giant fibre lobe, obtained by counting the cells in a small area, vary between 5,000 and 15,000. It would appear, therefore, that the processes



TEXT-FIG. 3.

Loligo forbesi. Horizontal section through stellate ganglion, showing the giant fibres. Formol-Cajal.



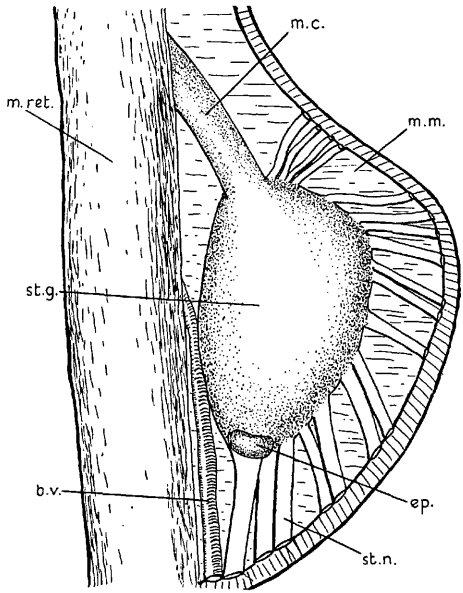
TEXT-FIG. 4.

Loligo forbesi. Sagittal section of stellate ganglion showing giant fibres and the lobe from which they arise. Carnoy, toluidin blue.

of from 300 to 1,500 cells fuse to form each giant fibre. Since the latter are of different sizes it is probable that some arise from more, others from fewer cells.

This arrangement, though certainly very peculiar, is not unique in the animal kingdom. Thus several cell bodies contribute to each of the segmental giant fibres of earthworms Stough (1926), and Speidel (1933) has actually seen the anastomosis of living axons in the tails of frog tadpoles.

In Sepia officinalis the giant fibres of the stellate gang-



TEXT-FIG. 5.

Eledone moschata. Right stellate ganglion seen from below, showing the position of the epistellar body.

lion arise as do those of Loligo, by fusion of the processes of a number of nerve cells which, however, are not all collected together into a single giant fibre-lobe, but are scattered throughout the ganglion (see Text-fig. 1). This is possibly the more primitive arrangement, from which the giant fibre-lobe has arisen by collection together of all the cells which give rise to the giant fibres.

The Epistellar Body of Octopods.

(i) General.

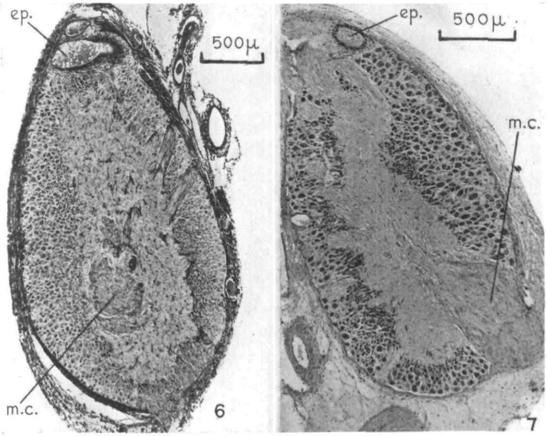
The epistellar body is a closed vesicle which has been found in all the Octopods examined, namely:

Eledone moschata (Leach).
Eledone cirrosa (d'Orbigny).
Octopus vulgaris (Lam.).
Octopus macropus (Risso).
Octopus defilipi (Vérany).
Octopus salutii (Vérany).
Tremoctopus violaceus (delle Chiaje).
Argonauta argo (L.).
Ocythöe tuberculata (Rafinesque).

In all these species the body lies at the hind end of the stellate ganglion, but it is pigmented only in Eledone moschata, Eledone cirrosa, Octopus salutii, and Octopus macropus, being difficult to make out with the naked eye in the other species. The organ is built on fundamentally the same plan in all these forms, but there are considerable and characteristic differences between the species. In the case of Eledone moschata and Octopus vulgaris epistellar bodies from numerous individuals were studied and some evidence of a cycle of activity was discovered.

A description will first be given of the conditions in Eledone moschata. It was in this animal that the body was first noticed, on account of the fact that it contains yellow pigment which was observed by Bauer (1908), who refers to a 'pigment-fleck' at the hind end of the stellate ganglion of Eledone. As can be seen from Text-figs. 5, 6, and 7 the body lies on the outer side of the ganglion, close to the origin of the hindermost and largest stellar nerve, and not far from the large artery which runs along the side of the ganglion. The body is of an irregular oval shape, with its long axis transverse to that of the body.

Serial sections show that it is shallow in proportion to its exposed surface area, the dimensions in one specimen being 500μ across and 75μ deep. The form is irregular and shows considerable variation. Usually the organ contains a single main cavity having several diverticula (Text-fig. 8), but occasionally



TEXT-FIGS. 6–7.

Fig. 6.—Eledone moschata. Sagittal section of stellate ganglion, showing epistellar body with two cavities. Bouin, azan. 9.2.29.

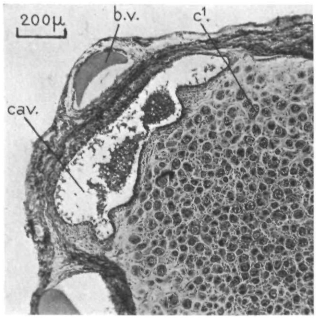
Fig. 7.—Octopus vulgaris. Sagittal section of the stellate ganglion, showing the position of the epistellar body. Bouin, Ehrlich's haematoxylin. 7.1.29.

there are two completely separate cavities (Text-fig. 6). The organ usually lies within the thick connective tissue sheath which surrounds the ganglion, but is isolated from the latter by a thin layer of connective tissue, broken at one place to allow of the entrance of a nerve. Occasionally the body is quite separate from the ganglion and enclosed in its own connective tissue sheath.

(ii) The Neurosecretory Cells.

The walls of the epistellar body may be said to consist of three layers:

(1) The connective tissue referred to above.
(2) An irregular layer of medium-sized cells, having long processes which extend into the cavity of the organ.
(3) An inner layer lining the cavity, and consisting of small epithelial cells between which pass the processes of the cells of the middle layer.

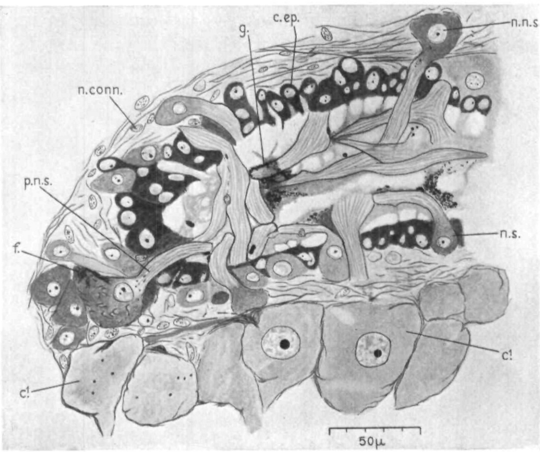


TEXT-FIG. 8.

Eledone moschata. Sagittal section of the epistellar body, showing the irregular shape of the central cavity. Zenker, carmalum, picronigrosin.

It is the second of these types of cells which constitute the most peculiar feature of the body (Text-figs. 9, 10, and 11). They have rather large nuclei with several karyosomes, and a distinct layer of cytoplasm, the latter containing a few rather large granules which stain well with iron haematoxylin after fixation in Flemming's fluid. Round the outside of these cells are numbers of fibrils, apparently of connective tissue, which stain very readily with basic stains (Text-fig. 9). The cells are elongated at right angles to the wall of the organ, having a long process which enters the cavity. Sometimes they also have one or two shorter processes directed away from the centre of the body.

The processes of these cells which enter the cavity very much resemble the axons of nerve cells, having, in fixed preparations, a faintly striated appearance (Text-fig. 9). These processes



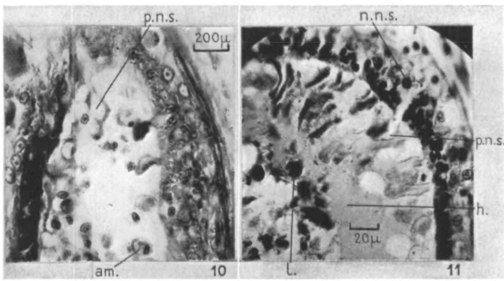
TEXT-FIG. 9.

Ocythöe tuberculata. Sagittal section of epistellar body. Camera lucida drawing with W.W.1/12″ oil imm. Flemming, iron haematoxylin. 20.3.30.

usually end blindly, embedded in a homogeneous substance which fills the cavity.

In preparations stained with Cajal's method it can be seen that small darkly staining knobs, closely resembling the boutons terminaux of the neuropil (Sereni and Young, 1932), lie close to the outer ends of these bipolar cells (Text-fig. 12). These boutons are the terminals of a small nerve which enters the epistellar body from the neuropil of the stellate ganglion (Text-fig. 13). In serial sections this nerve can be traced through the ganglion to the pallial nerve (mantle connective): and in experiments in which the latter had been cut for short periods before death, it was found that the fibres which run to the epistellar body were degenerating.

It will be seen, therefore, that the cells whose processes enter

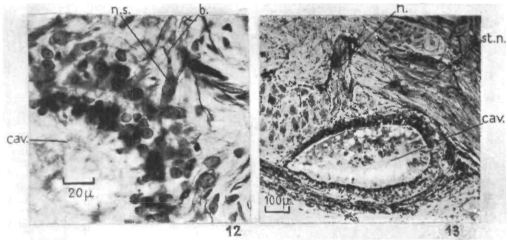


TEXT-FIGS. 10–11.

Fig. 10.—Octopus vulgaris. Epistellar body, showing inner ends of the neurosecretory cells. Flemming, iron haematoxylin. 15.5.29.

Fig. 11.—Eledone moschata. Epistellar body showing neurosecretory cells and contents of the cavity. Bouin, azan. 9.2.29.

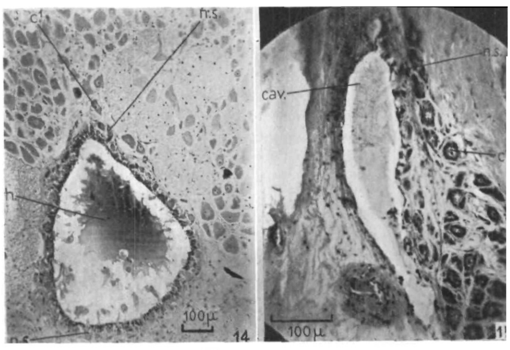
the cavity of the epistellar body have many points of similarity with the neurons of the stellate ganglion. Besides having long processes which immediately recall axons, they also resemble the nerve cells in the structure of their nucleus and cytoplasm and in being innervated from the mantle connective. That they are indeed modified neurons is confirmed by the fact that in some cases there can be seen side by side ordinary neurons of the ganglion and the cells here described, so that it is sometimes difficult to decide which is which. This transition is only rarely visible in Eledone on account of the thick sheath of connective tissue, but it appears very clearly in Tremoctopus (Text-fig. 14). Since these cells appear to be of nervous origin



TEXT-FIGS. 12–13.

Fig. 12.—Eledone moschata. Part of epistellar body, showing nerve ending on outer prolongation of neurosecretory cell. Formol-Cajal. 9.2.29.

Fig. 13.—Eledone moschata. Sagittal section of epistellar body, showing its nerve. Bouin, azan. 4.8.31.



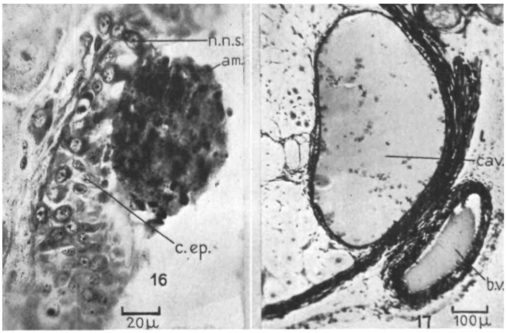
TEXT-FIGS. 14–15.

Fig. 14.—Tremoctopus violaceus. Epistellar body, showing similarity between neurosecretory cells and neurons. Bouin, iron haematoxylin.

Fig. 15.—Argonauta argo. Saggittal section through epistellar body. Bouin, Ehrlich's haematoxylin, eosin. 11.7.30.

and, as will be shown below, they probably have a secretory function, it is proposed to call them neurosecretory cells.

The third set of cells mentioned on p. 375 as forming a lining to the cavity resemble the neurosecretory cells in the structure



TEXT-FIGS. 16–17.

Fig. 16.—Octopus vulgaris. Part of epistellar body, showing fused inner ends of the neurosecretory cells. Flemming, iron haematoxylin. 22.6.29.

Fig. 17.—Octopus macropus. Swollen epistellar body. Bouin, azan. 19.7.29.

of their nuclei, and it is possible that they, too, represent neurons which have become still further modified.

It remains to describe the conditions in the cavity at the centre of the epistellar body. It is here that the greatest differences are seen between individuals of a single species, differences which are perhaps correlated with some cycle of activity. In some animals the wall of the body appears stretched and the cavity large and mainly filled by an optically homogeneous substance (Text-fig. 17). This latter stains readily with nigrosin or anilin blue, but not with basic dyes, or with any of the usual acidic stains such as eosin, orange G, or acid fuchsin. Embedded in the outer edges of this substance lie the inner ends of the neurosecretory cells (Text-figs. 9, 10, and 11). Sometimes there are masses of osmiophil granules collected round the ends of these cells, possibly representing a secretory product. The only other constituents of the cavity in this state are a few amoebocytes which lie near the centre of the homogeneous substance and usually contain large granules which stain readily with osmium tetroxide.

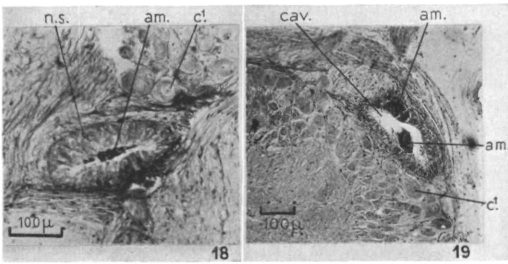
Frequently the contents of the cavity are more complex. The homogeneous substance is broken up and interspersed with large, irregular lumps containing fibrillae which stain deeply with basic dyes, and resemble those seen round the outer edges of the neurosecretory cells (see p. 375). So far as can be ascertained these masses consist of the shrunken inner ends of the neurosecretory cells which have become nipped off from the cell body. Only very rarely is the nucleus of one of these cells seen inside the cavity. The shrunken remnants often occur in large numbers scattered throughout the cavity, and each such mass may be surrounded by one or more amoebocytes, which appear to be devouring it by phagocytosis.

All gradations are seen between this and the third stage, in which the walls are relaxed and the cavity very small. The number of amoebocytes is very much increased, so that they almost fill the cavity. The homogeneous substance has almost disappeared, and the only other contents besides the amoebocytes are the processes of the neurosecretory cells, apparently fusing at the periphery of the mass of amoebocytes to form a syncytium (Text-fig. 16). The extreme of this condition was observed only in Octopus vulgaris taken in June, July, and August (Text-fig. 18). It is impossible to be certain whether it occurs also in Eledone, since this species is not to be found during the summer months in the bay of Naples as it migrates into deep water to breed. In two of the Octopus in question not only was there a mass of amoebocytes filling the cavity, but they could also be seen to be bursting through its wall (Text-fig. 19); whether they were passing inwards or outwards could not be determined.

There appears, therefore, to be some seasonal change in the contents of the body, especially in the sense that there are more amoebocytes during the summer months. But at no time is the cavity quite devoid of amoebocytes, and it seems more than likely that the differences observed are due, not to a cycle of activity, but simply to the much more rapid course of all processes during the summer months.

(iii) Function of the Epistellar body.

The only evidence at present available as to the function of the epistellar body was collected in 1929 before morphological



TEXT-FIGS. 18–19.

Fig. 18.—Octopus vulgaris. Epistellar body with very small cavity, filled with amoebocytes. Flemming, safranin. 19.6.29.

Fig. 19.—Octopus vulgaris. Epistellar body, showing amoebocytes passing through the wall. Flemming, safranin. 22.6.29.

studies had provided the suggestion that it consists of modified nerve cells. The late Professor Sereni was kind enough to assist me in removing both epistellar bodies from nineteen Eledone moschata. The operation itself, performed under urethane anaesthesia, is a very slight matter for the animal,[1] and yet after it abnormalities were seen, which may best be described as a state of general muscular atonia. Instead of moving actively about the tanks the operated animals remained attached to the sides, with the tentacles hanging limply, giving a striking picture

[1] Other minor and major operations, such as section of the stellar nerves and gonadectomy, served as controls in this respect.

of depression. Since the chromatophores of Cephalopods are kept expanded by muscles they provide an excellent index of the muscular tone. The animals from which the epistellar bodies had been removed became abnormally pale in colour, indicating a lack of tone in the muscles of the chromatophores.

This state of affairs lasted for about a week and then gradually passed off, the animals returning to an apparently normal condition in which they remained for as long as observed (up to 186 days). Histological examination, however, showed that no regeneration of the epistellar body had occurred.

From these results it is suggested as a working hypothesis that the epistellar body produces a secretion which assists in the maintenance of the muscular tone of the animal. It is natural to look for this product among the varied contents of the cavity. Perhaps the secretion is produced at the inner ends of the neurosecretory cells and diffuses away thence to the blood-stream. The granules surrounding the ends of the 'axons' of these cells, or the homogeneous substance which fills the cavity, suggest themselves as being perhaps the actual secretory product, but further evidence is required on this point.

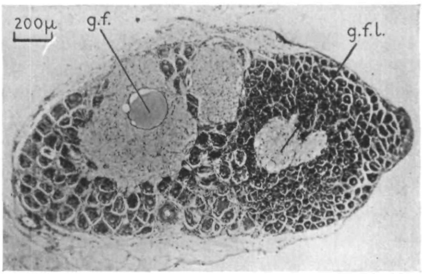
The role played by the amoebocytes in the epistellar body is uncertain. They may assist in the transport of active secretion to the blood-stream, or simply in the removal of exhausted portions of the cells.

Discussion.

Origin of the Epistellar Body from Giant Fibres.

The evidence on which it is suggested that the epistellar body is derived from the cells of the giant fibres may now be summarized. The epistellar body lies in the same morphological position as the giant fibre lobe of Loligo. The Decapods have giant fibres but no epistellar, whereas the Octopods have epistellar but no giant fibres. The giant fibre lobe is already partly cut off from the rest of the ganglion and the neuropil at its centre consists of fused processes of the cells of its walls; so that seen in certain aspects it is not at all unlike the epistellar body, in which the centre may also be filled by the fused processes of cells (Text-fig. 20). If the giant fibre lobe became completely cut off it would resemble the epistellar body in all essential points. That the conducting function of the giant fibres should be lost in Octopods is in accordance with the general reduction which has taken place in the respiratory and locomotor functions of the mantle, these activities being performed more and more by the arms (Robson, 1931).

There can therefore be little doubt that the cells of the epistellar body are homologous with those which in Loligo



TEXT-FIG. 20.

Loligo forbesi. Transverse section of hind end of stellate ganglion, to show similarity of giant fibre lobe to epistellar body. Carnoy, toluidin blue.

give rise to the giant fibres, and since the evidence given above seems to show that the epistellar produces a secretion, this means that neurons have been converted into secretory cells. However, it must be remembered that the evidence as to the function of the epistellar body is still very incomplete, and it is possible that it represents simply a rudimentary vestige of the giant fibre lobe.

Such a transformation of nerve into gland is by no means unlikely on general grounds. The cells of the adrenal medulla of Vertebrates are derived from nerve cells, and nests of accessory chromophil cells occur in sympathetic ganglia. Gaskell (1914) claimed that in Annelids certain large neurons of the ventral ganglia contain pressor substances, revealed by the chromophil reaction which they give with bichromates. Recently

Hanström (1931, 1934) has described cells in the eye-stalks of various Crustacea which, though secretory, are probably of nervous origin. There is considerable evidence that nerve endings, in smooth muscle, exert their effects by the liberation at their ends of some stimulating substance (see Parker, 1932). There is no positive evidence that this is the case in Cephalopods, but it is perhaps significant that a betain is found in considerable quantities in the mantle muscles (Henze, 1910), and that this substance has been shown to have effects on the smooth muscles of the chromatophores similar to those of choline and its esters (Sereni, 1928).[1] It is tentatively suggested that in Decapods the giant fibres may exert their effects on the muscles by the liberation of some substance at the periphery, whereas in Octopods the fibres no longer run to the muscles but end blindly in the cavity of the epistellar body, where they produce a stimulating substance which is carried away in the blood-stream to the muscles. The evolutionary change necessary would not be a very large one, since the enzymatic or other system necessary for the synthesis of the stimulating substance would presumably be present at the peripheral endings of the giant fibres and thus be able to continue its work even when the fibres came to end in a closed vesicle.

However, this suggestion is clearly speculative, and needs the support of further experimental evidence, which I hope to collect as soon as material is available. The evidence in the present paper shows that the epistellar body contains cells of nervous origin which probably function by the production of secretion, but have yet retained something of their characteristic form as elongated neurons. They may thus be regarded as having reached a stage intermediate between ordinary motor-nerve fibres which liberate an active substance at the periphery, and the secretory cells of the adrenal medulla which though of nervous origin no longer bear any resemblance to neurons.

SUMMARY.

1. In Decapod Cephalopods there is a system of giant fibres probably serving to produce the rapid contractions of the mantle

[1] Bacq ('Nature', **136**, 1935) has recently shown that acetyl choline is present in large amounts in the C.N.S. of Octopus.

muscles and ink-sac by means of which the animal shoots backwards behind a cloud of ink.

2. The giant fibres in the stellar nerves arise in the stellate ganglion, not from single giant cells, but as syncytia, by the fusion of the processes of a large number of cells. In Loligo forbesi all the cells giving rise to the giant fibres of the stellate ganglion are connected together into a giant fibre lobe.

3. In Octopods there are no giant fibres, but in the position of the giant fibre lobe there is a small closed vesicle, pigmented yellow in some species, and named the epistellar body.

4. In the walls of this body there are curious cells, the neurosecretory cells, whose general structure resembles that of neurons, but whose inner processes (axons) end blindly, embedded in a homogeneous substance which fills the cavity.

5. The neurosecretory cells are innervated by a small nerve which reaches them from the mantle connective.

6. After removal of both epistellar bodies from Eledone moschata the animal shows general muscular weakness for some days.

7. It is suggested that the epistellar body has arisen from the giant fibre lobe, and that the neurosecretory cells produce at their inner ends a secretion which is poured into the blood-stream.

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