II—On the Nervous System of the Starfish *Marthasterias glacialis* (L.)

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I—INTRODUCTION AND HISTORICAL

In the year 1815, TIEDEMANN observed on the oral surface of the disk of the starfish *Astropecten aurantiacus* (L) a circumoral band of tissue continuous, in the mid-line of each arm, with a radial band. To these bands he ascribed a vascular function. JOHANNES MÜLLER (1850), however, indicated that the radial and circular bands were more properly to be regarded as nerve cords, an observation which OWSJANNIKOW (1871), GREEFF (1871, 1872, *a*, 1872, *b*), HOFFMANN (1872), and TEUSCHER (1876) subsequently confirmed.

LANGE (1876), while not accepting the findings of previous authors as to the nervous nature of the circumoral and radial cords, discovered two ridges of tissue above each of the " V "-shaped radial cords, one lying to the right and the other to the left of the mid-line. These are constituted by thickenings of the coelomic epithelium which lines the radial perihaemal canals, and were considered by LANGE to represent nervous tissue. This opinion has been substantiated by LUDWIG (1878), HAMANN (1883, 1885), and CUÉNOT (1891) among others ; but these and all recent investigators agree that the radial and circumoral cords must also be regarded as constituting part of the asteroid nervous system. CUÉNOT (1891) therefore distinguishes between the part of the nervous system derived from the ectoderm, such as the circumoral and radial cords, and the part—presumably of mesodermal origin—situated in the coelomic epithelium.

HAMANN (1883, 1885) is mainly concerned with the histology of the ectodermal system. He describes both sensory cells and supporting cells as occurring in the nerve ring and radial cord of the asteroid. In thus distinguishing between the nervous and non-nervous elements HAMANN's contribution is of great value as compared with the earlier findings of GREEF (1871, 1872, *a*, 1872, *b*), OWSJANNIKOW (1871), HOFFMANN (1872), and TEUSCHER (1876), who mistook the fibres of the supporting cells for sensory fibrillae. HAMANN makes a further addition to our knowledge of the asteroid nervous system by demonstrating the presence of bipolar and multipolar ganglion cells within the fibrillar substance of the subepithelial nerve plexus.

CUÉNOT's (1891) most important contribution to the study of this subject is concerned, in the main, with the coelomic nervous system. The motor nature of Lange's nerve is established in that twigs from this part of the coelomic system are figured as innervating the inferior transverse muscle. The five pairs of radial ridges, of which Lange's nerve is composed, are represented in the disk by inter-radial hyponeural thickenings, developed on the internal face of the circumoral nerve. CUÉNOT finds, moreover, that there is a separate concentration of nerve fibrils in the coelomic epithelium bordering the apical longitudinal muscle of the arm, and that by virtue of its position this nerve—the apical nerve—must be regarded as being motor in function.

MEYER (1906) gives an excellent account of the histology of the radial nerve cord in which much is added to the description given by HAMANN both with regard to the nervous and non-nervous elements. MEYER, however, can find no evidence of CUÉNOT's apical system in *Asterias rubens*—the subject of his investigation.

The generally accepted view of the distribution of the nervous elements in the Asteroidea, as stated in modern textbooks, is that of CUÉNOT. The nervous system is described as consisting of three parts, of which the ectoneural system, of ectodermal origin, is sensory, while Lange's nerve (hyponeural) and the apical nerve, of presumed mesodermal origin, are regarded as discrete parts of a motor system. CUÉNOT's account, however, requires confirmation in many respects. In the first place, no morphological demonstration of the continuity of the sensory and motor systems has been made, although a separation of the two parts is, of course, impossible. Secondly, the histology and distribution of the nervous elements of Lange's nerve require further study. Thirdly, the apical motor system discovered by CUÉNOT in *Marthasterias glacialis*, *Asterias tenuispina*, *Echinaster sepositus*, and *Astropecten aurantiacus* has been shown by MEYER (1906) not to be present in *Asterias rubens*. In view of this fact, the presence of a separate apical system in the asteroids would appear to be a matter of doubt. Moreover, even if an apical system be present in some or all of the Asteroidea, its connexions with other parts of the motor system or with the sensory system require to be demonstrated. Finally, the histology of the ectoneural system, although described in great detail in MEYER's excellent account, needs verification in some particulars. The present work has been directed, in particular, to the elucidation of the points in question.

The work, the results of which are embodied in the following account, was carried out in the Departments of Zoology of the Universities of Manchester and Sheffield and at the Laboratory of the Marine Biological Association, Plymouth.

I am particularly indebted to Professor H. GRAHAM CANNON, Dr. E. J. ALLEN, and Professor L. E. S. EASTHAM for their help during the various stages of the work, and to the Universities of Manchester and Sheffield for the use of tables at the Plymouth Laboratory.

II—MATERIAL AND METHODS

Most of the material used during the course of this work was collected at Plymouth. The following account is based on sectioned material of *Marthasterias glacialis*, but for confirmation of many points I have had occasion to section a number of other asteroids including *Asterias rubens*, *Solaster papposus*, *Astropecten irregularis*, *Palmipes membranaceus*, *Asterina gibbosa*, and *Leptasterias mülleri*. A few specimens of the last named were collected in the Gullmar Fjord during a visit to the marine biological station of the Swedish Academy at Kristineberg in the autumn of 1933.

Previous investigators have made it clear that the difficulty of examination of the nervous system lies in the application of suitable methods of fixation and staining—a difficulty which applies more particularly to the demonstration of the sensory elements and their fibrillae. It has seemed natural, therefore, in the first place to test the possibility of employing the more specific nerve stains such as methylene blue and the silver impregnation methods of CAJAL. The presence of a large amount of calcareous material within the connective tissue of the echinoderm renders impracticable the application of intra-vitam methods to large pieces of material. Accordingly, for the purposes of experiment, the radial nerve cord was dissected out from large specimens of *M. glacialis* and immersed in various concentrations of methylene blue in sea water for varying periods of time. No real success was obtained, however, because of the large amounts of mucus exuded on to the surface of the cord during its removal from the ambulacral groove. Sections of cord in which the stain had been fixed by fluids containing ammonium molybdate indicate, moreover, that the nervous elements do not react readily to the stain.

Silver impregnation of the radial nerve cord, tube feet, and pieces of arm by the methods of CAJAL and BIELSCHOWSKY's modifications of CAJAL has also been found to be unsatisfactory, although recently ZIRPOLO (1930) claims to have been successful in the application of the Cajal method to the study of the nervous system of *Asterina gibbosa*.

I have found that very good results can be obtained by using less specific methods. In the first place, pieces of nerve cord were used for testing the efficacy of the various fixatives and stains. Good general pictures of the epithelial cells, ganglion cells, and fibrillar system can be obtained with non-osmic fixatives; of these, corrosive-acetic in sea water and Heidenhain's Susa fixative in sea water are undoubtedly the best. For good cytological detail and for demonstration of the sensory elements, however, osmic fixatives must be employed. A variety of these has been tried, but none gave better results than strong Flemming solution without acetic acid.*

Small pieces of nerve cord, about 3–5 mm. long, were fixed either with corrosive-acetic, Susa fixative, or F.W.A. In the latter case the pieces have been bleached with chlorine in 70% alcohol before staining.

Sections of nerve cord and tube feet have been cut 6–8 μ thick and stained with Delafield's haematoxylin (with or without eosin as counterstain), Heidenhain's iron-alum haematoxylin, Mallory's phosphomolybdic acid haematoxylin, or with Mallory's triple stain. F.W.A. fixation, followed by staining with Delafield's haematoxylin, provides the best combination for the demonstration of sensory cells and fibrillae, and has given better results in this respect than Mallory's phosphomolybdic acid haematoxylin, the stain which MEYER (1906) recommends for this particular purpose. With Mallory's triple stain a useful colour differentiation between nervous and non-nervous tissue is obtained, while for the study of nuclei material stained with Heidenhain's iron-alum haematoxylin has been found the most reliable.

In order to study the general distribution of the nervous elements within the body of the starfish, sections have been made of the arm and disk of small animals with a disk diameter of 1·0–1·5 cm. After fixation in corrosive-acetic or Susa solution (F.W.A. not having been found suitable when dealing with large pieces of arm or

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* Referred to subsequently as F.W.A.

disk) the pieces have been decalcified in a mixture of 70% alcohol and nitric acid in the proportion of 100 : 3. The fluid has been changed daily, and decalcification continued for 4–9 days according to the size of the object. Cedar wood oil has been the clearing agent most frequently employed and paraffin wax of 57° C. melting-point has usually been used for imbedding.

Sections cut at 6–10 μ were stained with Mallory's triple stain, Delafield's haematoxylin, or Heidenhain's iron-alum haematoxylin. Of these, the preparations stained with Mallory's stain are of the most general use, in that the colour differentiation between nervous and non-nervous tissue so obtained aids considerably in tracing the neurofibrillae of the sensory and motor systems.

The drawings of the sections have all been made with the aid of a squared net micrometer eye-piece and have been based, in many instances, on a number of comparable sections.

III—General Plan of the Nervous System

There is very good reason to believe, as will be shown in the following account, that the present view of the subdivision of the nervous system of the asteroid into three separate parts, namely the ectoneural, hyponeural, and apical systems, does not adequately portray the real distribution of the nervous elements within the body of the animal. That the ectoneural system represents at least part of a general sensory system cannot be doubted, but, as will be shown, the hyponeural and apical systems ought not to be regarded as the only components of the neurofibrillar system which is developed in connexion with the coelomic epithelium. In the description which follows I have therefore preferred to use the term " sensory system " in describing the nerve elements associated with the ectoderm and with the gut wall. The entire coelomic nervous system, wheresoever placed, is referred to as the " motor system ", for such is its function.

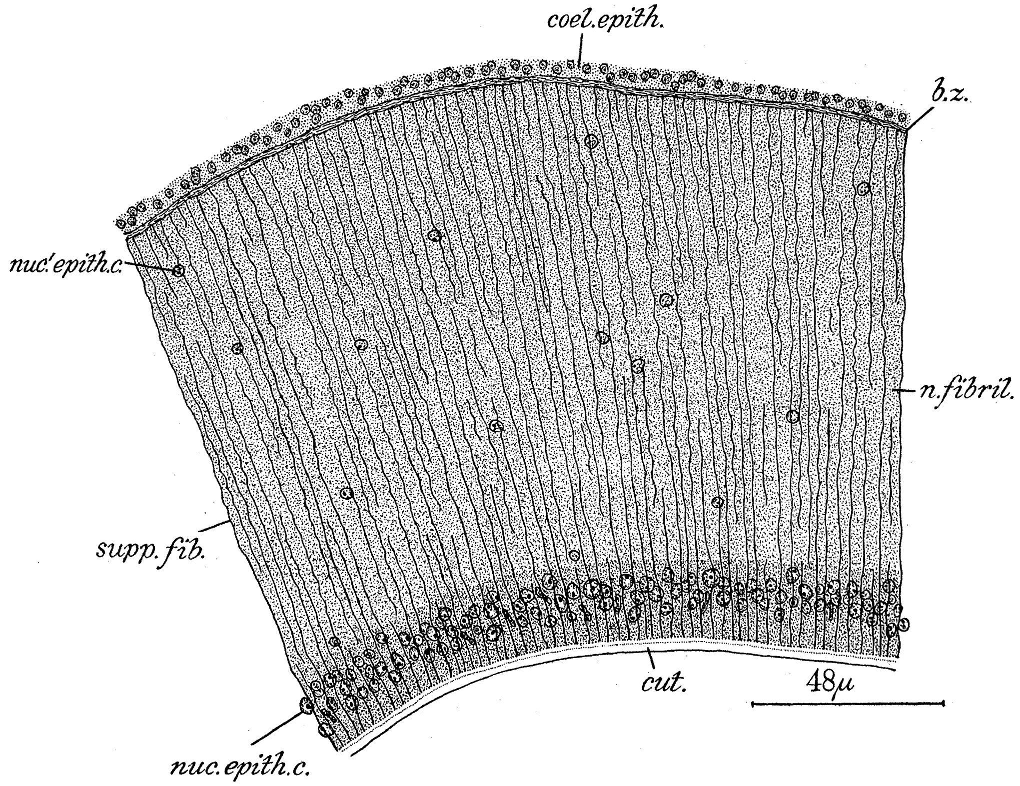
Certain parts of the starfish possess a degree of autonomy. The tube feet (Paine, 1929) and probably the pedicellariae are to be included among the organs which have an independent action system, and therefore their own reflexes. In the pedicellariae there are morphological evidences of the reflexes, and these organs, in possession of an independent sensory-motor system, are therefore separately described.

An account of the nervous system of an asteroid would be incomplete without reference to experimental work on the subject. Much morphological and physiological investigation remains to be done before the behaviour of the starfish can be expressed at all adequately in morphological terms, but many of the more simple reflexes can even now be explained on such a basis. In the discussion, at the end of this paper, reference has been made to experimental work wherever the latter assists in the interpretation of the morphological findings.

IV—The Sensory System

1—*The Radial Cord*

General Description—The radial nerve cord of *Marthasterias glacialis* is in the form of a " V "-shaped thickening of the ectoderm in the mid-line of each of the arms. The angle formed by the sides of the " V " is dependent on the state of contraction of the animal but, in general, tends to be less acute in the proximal part of the radial nerve than distally, and may approach 180° at the point where the radial nerve enters the circumoral nerve ring.



Oral surface

FIG. 1—Portion of a transverse section through the radial nerve cord of *Marthasterias glacialis*. Fixed corrosive-acetic, stained Heidenhain's iron-alum haematoxylin. *b.z.*, boundary zone of connective tissue ; *cut.*, cuticle ; *coel. epith.*, coelomic epithelium ; *n. fibril.*, neurofibrillae of sub-epithelial zone ; *nuc. epith. c.*, nucleus of epithelial cell; *nuc'. epith. c.*, nucleus of migrant epithelial cell ; *supp. fib.*, supporting fibre.

In section (fig. 1) the nerve cord is seen to be made up of three distinct layers. Covering the surface of the cord is a thin cuticle, which in cords dissected out from large *Marthasterias* of arm length about 15 cm. is some 4–5 μ thick. Immediately below the cuticle is a layer containing the numerous nuclei (*nuc. epith. c.*) of the cellular elements which are to be found in this zone. These latter are represented by epithelial supporting cells (the " Stützzellen " of German authors), glandular elements, sensory cells, and association ganglion cells. The total thickness of the layer is about 17 μ.

By far the greater part of the thickness (*ca.* 120 μ) of the cord is constituted by the third layer, underlying the nuclear zone. This is the subepithelial fibrillar zone (*n. fibril.*) made up of the neurofibrillae of the association ganglion elements and the central fibrillae of the sensory cells. In transverse section of the cord most of the fibrillae are cut transversely and the subepithelial plexus has, in consequence, a finely punctate appearance.

Internal to the subepithelial neurofibrillar plexus is a thin layer of connective tissue (*b.z.*), of mesodermal origin, forming a boundary zone which separates the ectodermal elements from the cells of the coelomic epithelium (*coel. epith.*) lining the radial perihaemal cavity. Numerous fibres (*supp. fib.*) traverse the entire depth

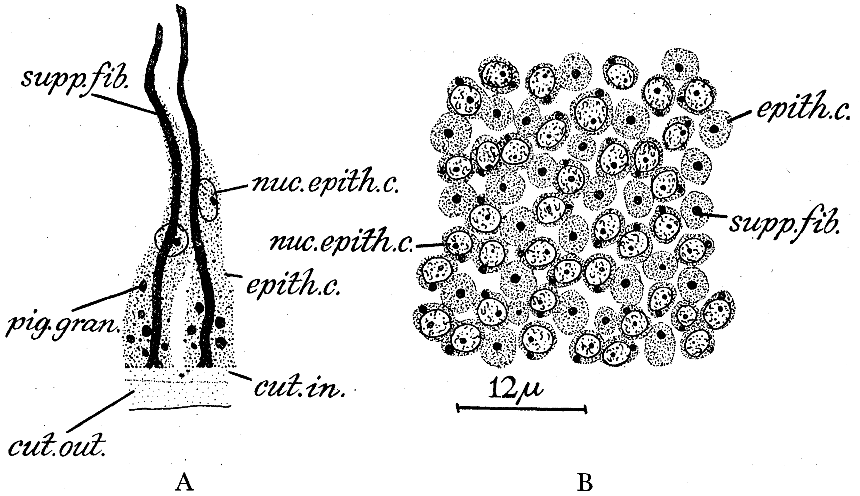


FIG. 2—A, epithelial supporting cells of the radial nerve cord in longitudinal section. B, the same, in transverse section. Fixed in strong F.W.A., stained Delafield's haematoxylin. *cut. in.*, inner layer of the cuticle ; *cut. out.*, outer layer of the cuticle ; *epith. c.*, epithelial cell ; *nuc. epith. c.*, nucleus of epithelial cell ; *pig. gran.*, pigment granule ; *supp. fib.*, supporting fibre.

of the nuclear and fibrillar zones of the nerve cord. Their peripheral ends abut on to the internal surface of the cuticle and their inner ends on to the boundary zone.

These fibres—the supporting fibres (" Stützfasern ")—are the products of secretion of the supporting cells and form the framework through which are threaded the longitudinally running neurofibrillae.

(*a*) *Non-nervous Elements*

The Supporting Cells and Fibres—The supporting cells constitute the epithelium which underlies the cuticle. Their cell boundaries cannot be distinguished after fixation with non-osmicated fixatives, but with material fixed in strong F.W.A. and subsequently stained with Mallory's triple stain or Delafield's haematoxylin they appear (figs. 2A, 2B, 5, *epith. c.*) as cells with an ill-defined border and with finely granular cytoplasm. The vesicular nucleus (*nuc. epith. c.*), which is either round or oval in section, is from 2–5 μ in diameter and usually has a single well-marked nucleolus and a delicate threadwork of chromatin material.

At their extreme bases, where they lie in contact with the cuticle, the cells are crowded together and, in consequence, are roughly hexagonal in cross-section (fig. 3, *epith. c.*). Internally (fig. 2B, *epith. c.*), the supporting cells are less closely pressed together and have a more rounded form. There is evidence that the cells extend the entire distance from the cuticle to the boundary zone, but the cell body proper is never more than 30 μ in length and is greatly attenuated at its inner end. The supporting cells bear cilia, and contain the basal granules typical of ciliated cells. The cilia project beyond the cuticle but are seen only with difficulty in non-living tissue. MEYER (1906) finds pores in the cuticle through which the cilia pass, but no pores have been visible in the preparations examined during the course of this work. Pigment granules are found in the basal part of the supporting cells (fig. 2A, *pig. gran.*) and impart to the cord its characteristic pale yellow colour. Some of the supporting cells appear to have lost their original peripheral position and to have migrated into the neurofibrillar zone, even to the extent of being found just below the boundary zone of connective tissue (fig. 1, *nuc'. epith. c.*). The cells occupying this position are usually of a rounded form.

The most characteristic product of the supporting cells are the supporting fibres which together constitute the framework of the radial cord. Each fibre (figs. 1, 2, *supp. fib.*) is the product of secretion of a single cell and extends from the internal face of the cuticle to the boundary zone. There are no anastomoses of neighbouring fibres, and except at their extreme peripheral ends the fibres are unbranched. They may be, but are not always, slightly expanded internally where they abut on to the boundary zone. The fibres are secreted intracellularly, as can be seen in horizontal sections through the cord. Sections in this plane cut the epithelial supporting cells transversely to their long axes and the supporting fibres are seen to lie entirely within the cytoplasm of the mother cells (figs. 2A, 2B, *supp. fib.*). Each fibre passes close to the nucleus of its parent cell and is bounded by cytoplasm throughout its length, for even beyond the limit of the cell body of the supporting cell the cytoplasmic sheath, although excessively thin, can be discerned in transverse sections of the fibre. The presence of this thin sheath gives to the fibre a double contour which cannot be entirely attributed to refraction.

PFEFFER (1901) describes the supporting fibres as being intracellular in position, but MEYER (1906) maintains that only seldom does the fibre traverse the substance of the cell and is usually to be found running along the outer surface of the latter, in which case it would be regarded as a product of extracellular secretion. Preparations made of the nerve cord of *Marthasterias glacialis* and *Asterias rubens* entirely confirm PFEFFER's findings on this point, in that the supporting fibres are always to be found within the cytoplasm of the parent cell.

The fibres, of a general diameter of 0·5–1·2 μ, are slightly thickened within the body of the epithelial supporting cell. They appear, often (fig. 2A), to be branched at the end adjoining the cuticle. Horizontal sections of the cord show that, in the deeper parts of its substance, the fibres exhibit a characteristic and definite arrangement. Figs. 4A, 4B, and 4C represent three horizontal sections taken at different levels in the subepithelial plexus. Fig. 4A is taken at a level just internal to the nuclear zone; the supporting fibres (cut transversely) are arranged in a rather haphazard manner, but deeper down within the fibrillar plexus (fig. 4B) they are ordinated in linear series, the rows being orientated along the length of the radial cord. This regular arrangement is accentuated in the deepest parts of the plexus, near the boundary zone (fig. 4C). As will be shown later, each of these three zones exhibits, in addition, a characteristic arrangement of the longitudinally running fibrillae.

The supporting fibres would appear to be elastic in nature, for in portions of the nerve cord which have shrunk as a result of fixation they become waved and coiled. They have very definite staining reactions and stain readily with Victoria blue, acid fuchsin, and iron-alum haematoxylin, but less readily with eosin.

The Cuticle—The radial nerve cord, and indeed the whole of the ectoderm of the starfish, is covered by a thin cuticle of a thickness, where it overlies the cord, of 3–5 μ. The cuticle is, without doubt, a secretion of the epithelial supporting cells, but opinion differs as to the way in which it is laid down. CUÉNOT (1887) and PFEFFER (1901) regard the cuticle as being composed of a series of platelets, each platelet being, presumably, the product of secretion of a single epithelial cell. MEYER (1906), however, considers the cuticle to be a homogeneous mass laid down as a single sheet and not as a series of platelets. These authors are also at variance in their accounts of the number of layers present in the cuticle. CUÉNOT (1887) considers it to be single layered, PFEFFER (1901) finds two layers, while according to MEYER (1906) the homogeneous mass is divisible into three zones which, although having different optical properties, are not separable by maceration.

My preparations show quite clearly that the cuticle is two layered, there being an inner zone about 1·5 μ thick and an outer zone about 3 μ in thickness. An oblique horizontal section through this region (fig. 3) illustrates the essential difference between the two cuticular zones. On the left of the figure the bases of the epithelial cells are shown in section. They are roughly hexagonal in form and correspond in size and shape to the platelets which make up the basal layer of the cuticle (fig. 3, *cut. in.*). The outer layer of the cuticle (*cut. out.*), on the other hand, is perfectly homogeneous in structure, and shows no indication of having originated from separate polygons. One must conclude that, initially, the cuticle is composed of closely set platelets, each of which represents the secretion of a single cell, but that the platelets ultimately flow together to form the homogeneous outer, and first formed part of the cuticle. The cuticle may be readily stripped away from the ectoderm, and on such treatment becomes crinkled, a circumstance which suggests that it is pliable in nature. It does not react strongly to many stains—Victoria blue is a notable exception—and in this respect it offers a marked contrast to the other secretory product of the supporting cell, namely, the supporting fibre.

The Glandular Elements—Interpolated between the epithelial cells of the radial cord and of the ectoderm generally, are numbers of glands which, in the nerve cord, are restricted almost entirely to the region at the base of the " V ". HAMANN (1883) first described glandular elements in the ambulacral cord, and more recently MEYER (1906) has given a more detailed and fuller description of them.

The gland cells, unlike the epithelial cells, do not secrete a supporting fibre, and there is no evidence that the secretion is in any way comparable with that of the epithelial cell. MEYER finds two types of gland. The first, the goblet cells (" Becherzellen "), occurs in two modifications both of which, however, contain a mucous secretion and have a well-marked vesicular nucleus. The second type of gland—the " mulberry " cell (" Körnchendrüsenzell ")—contains numerous rounded refringent droplets and occurs in fewer numbers. MEYER was unable to find any opening of this latter type of gland to the exterior.

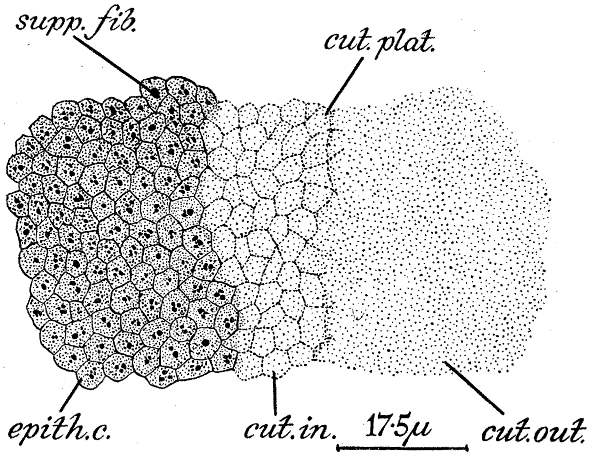


FIG. 3—Oblique horizontal section through the radial nerve cord passing through the base of the epithelial cells and the cuticle. Fixed corrosive-acetic, stained Mallory's triple stain. *cut. in.*, inner layer of the cuticle ; *cut. out.*, outer layer of the cuticle ; *cut. plat.*, cuticular platelet ; *epith. c.*, epithelial cell ; *supp. fib.*, supporting fibre.

Of the glands which are to be found in the radial cord of *Marthasterias glacialis*, by far the greater number are not the goblet cells as MEYER found in *Asterias rubens*, but the " mulberry " glands. These (figs. 7A, 7B, 7C, and 5) are typically flask-shaped, about 30 μ in length, and of greatest width about 15 μ. The gland opens by a narrow duct opposite a pore in the cuticle, the latter representing an area where no cuticular platelet has been laid down. The " mulberry " glands are to be found in various secretory phases. In the initial stages of secretion (fig. 7A) the cytoplasm of the gland is packed with small refringent droplets. An older gland (fig. 7B) contains larger droplets, produced by the flowing together of the smaller spheres ; in later phases (fig. 7C) the droplets expand, finally to coalesce, so that the cytoplasm is completely filled with a clear liquid which escapes to the exterior through the cuticular pore.

Although in the earlier stages of secretion the contents of the gland can only be stained with difficulty, in later phases the liquid reacts readily with acid fuchsin, eosin, and Victoria blue, but not with the haematoxylins.

The nucleus of the " mulberry " gland (fig. 7A, *nuc.*) fits like a small cap over its expanded end and differs from the nucleus of the epithelial cell in that its chromatin is aggregated into a deeply staining mass.

The goblet cell occurs much less frequently than the " mulberry " gland. It has only been seen in sections stained with Mallory's triple stain. The fluid contents are, in such preparations, of a pale blue colour blotched with slightly darker patches. This type of gland (fig. 7D), longer and more slender than the " mulberry " gland, is never more than 10 μ in width, but may attain a length of 40 μ, in which case it projects far into the fibrillar substance of the nerve cord ; its opening to the exterior is through a short duct, placed opposite a pore in the cuticle. Nuclei, definitely attributable to the goblet cells, have not been seen in any of the preparations examined.

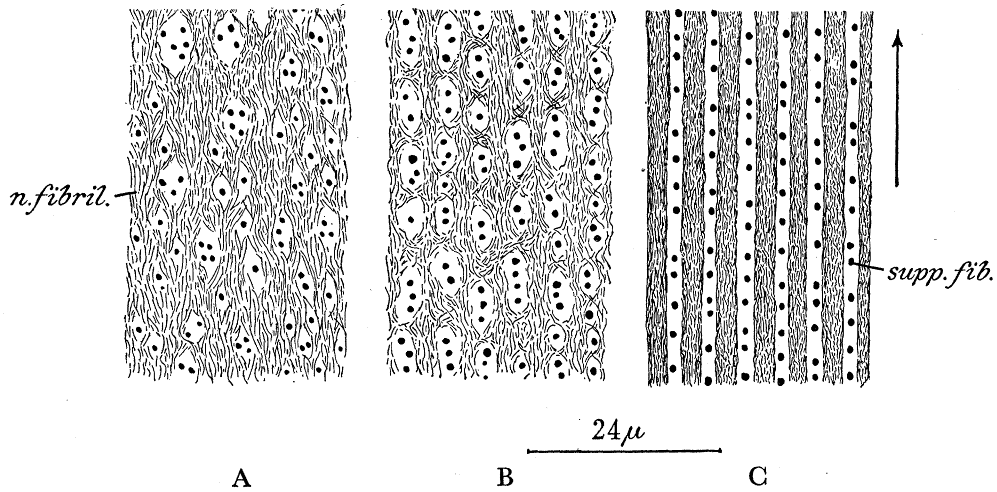


FIG. 4—Horizontal sections through the subepithelial neurofibrillar plexus of the radial nerve cord showing the fibrillar zoning at successive levels. Fixed corrosive-acetic, stained Mallory's triple stain. A, outer zone ; B, middle zone ; C, inner zone. The arrow indicates the longitudinal axis of the cord. *n. fibril.*, neurofibril ; *supp. fib.*, supporting fibre.

The goblet cells have been described as mucus glands, and it is possible that in the living nerve cord they are present in larger numbers than would appear to be the case from an examination of fixed material alone. When stimulated by touch, or by irritation with chemicals, the surface of the nerve cord becomes covered with mucus. Most of the mucus glands would, in consequence, be emptied of their contents, and would only be recognized with difficulty in sections of fixed material. MEYER's (1906) observation that the goblet cells exceed the " mulberry " glands in number may therefore be well founded, although in my preparations the " mulberry " glands constitute a majority of the total number of undischarged glands present.

b—Nervous Elements

The Sense Cells—One of the most difficult problems associated with the study of the asteroid nervous system has been the identification of the ectodermal sensory elements. Much of the confusion has arisen as the result of faulty interpretation by earlier workers of the real nature of the supporting cells and fibres which were described as constituting the sensory and association elements of the nervous system.

We are indebted to HAMANN (1883) for distinguishing between the sensory cells and ganglion cells with their fibrillae, on the one hand, and the supporting cells and fibres on the other, and for showing that the sensory elements are not restricted to the radial nerve cord but are to be found in all parts of the ectoderm.

The sensory elements which HAMANN figures are epithelial or subepithelial in position. The spindle-shaped cell body is continued at its narrow inner end into a delicate fibre which runs into, and merges with the neurofibrillae of the subepithelial plexus of the cord. In addition to this central fibre there may also be a centripetal fibre* which, originating from the outer end of the cell body, runs outwards to end just below the cuticle ; this fibre is to be regarded as the perceptor fibre. In many instances, however, when the body of the sense cell is epithelial in position, there is no centripetal fibre, in which case the stimulus is perceived directly by the cell body.

CUÉNOT (1887), although finding cell bodies comparable to those which HAMANN figures, was unable to find any central fibre, "—j'ai constaté nombre de fois que ces cellules ne continuaient pas avec les fibrilles nerveuses ". The implication would be that the receptor cell transmits its impulse to the fibrillae of the subepithelial plexus not through a central fibre but directly through the fibrillae of the association ganglion cells which would be considered to surround the primary sense cell. MEYER (1906) disagrees with this interpretation and shows that the receptor elements are bipolar nucleated sense cells with a receptor fibre and a central discharging fibre which latter merges, as a rule after branching, with the fibrillae of the plexus.

The following account of the sensory elements, based on a study of sections of the nerve cord of *Marthasterias glacialis* fixed in strong Flemming solution without acetic acid, and stained with Delafield's haematoxylin, differs only in certain details from the account given by MEYER (1906).

The primary sense cells of the radial cord are histologically similar. Their spindle-shaped bodies (figs. 5 and 6, *s.c.*) are always situated below the surface of the ectoderm and, in consequence, have a centripetal as well as a central fibre. The whole of the cell body stains readily with haematoxylin, but with Mallory's triple stain it exhibits a finely granular appearance. It would appear, therefore, that the cell body is composed for the most part of chromatin material, bounded by a thin layer of cytoplasm. Although attaining a length of 10 μ, the sense cell is never more than $1 \cdot 5$ μ in greatest width and tapers rapidly at either end to be

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* The term " centripetal fibre " indicates the direction of discharge of the nervous impulse relative to the cell body, and is used synonymously with the terms " perceptor " and " receptor fibre ".

continued peripherally (fig. 6, *centrip. f.s.c.*) into the centripetal fibre and centrally (*c.f.s.c.*) into the central fibre. In most instances the longitudinal axis of the cell body is inclined at an angle to the surface of the ectoderm, whereas the axis of the epithelial supporting cell is set almost at right angles to the surface.

The centripetal and central fibres are excessively fine and difficult to demonstrate. Only occasionally is it possible, in the thickness of a single section, to follow the course of either over any distance, and it is probably on this account that MEYER has stated that in several instances the centripetal fibre does not extend to the surface of the ectoderm. In my opinion, the centripetal fibre always ends in contact with the cuticle but does not penetrate this layer. MEYER describes and figures a vesicular swelling at the free end of some few of the perceptor fibres of the sensory elements of the radial cord of *Asterias rubens*. The centripetal fibre of the sense cell of *Marthasterias glacialis* has no such enlargement at its termination below the cuticle ; its free end exhibits in no single instance any modification of the unexpanded and unbranched fibre.

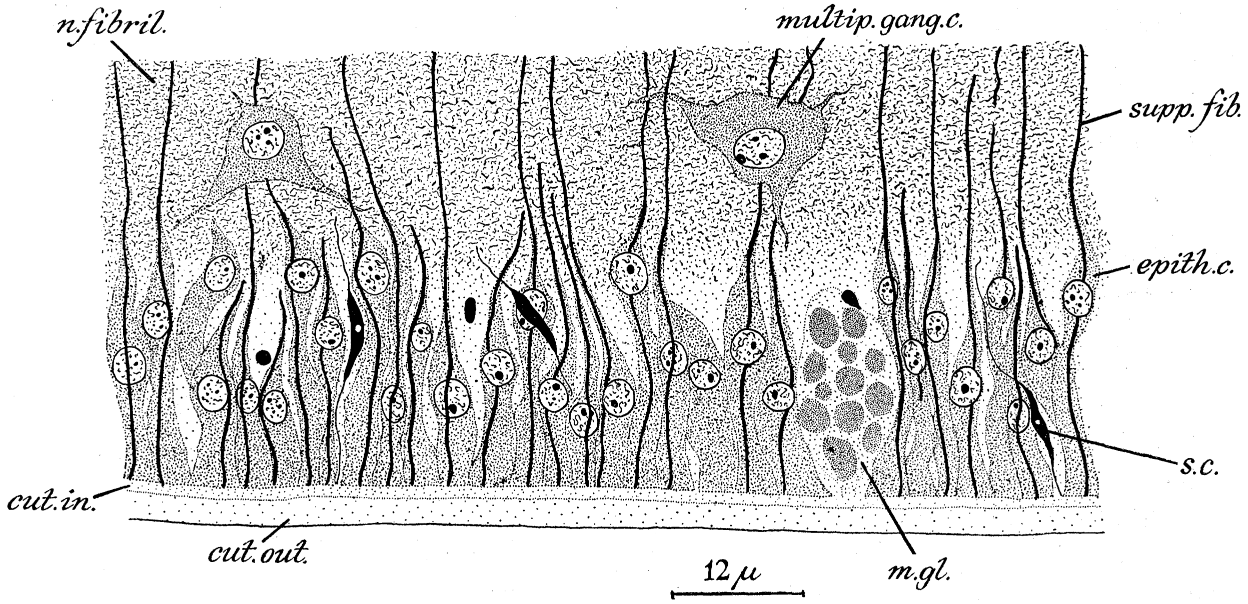

FIG. 5—Portion of a longitudinal section through the epithelial and subepithelial layers of the radial nerve cord. A composite drawing based on material fixed in F.W.A. *cut. in.*, inner, and *cut. out.*, outer, layer of the cuticle ; *epith. c.*, epithelial cell ; *m. gl.*, " mulberry " gland ; *multip. gang. c.*, multipolar ganglion cell ; *n. fibril.*, neurofibrillae of the subepithelial plexus ; *s.c.*, primary sense cell ; *supp. fib.*, supporting fibre.

It is not difficult to understand how tactile stimuli could be perceived by pressure of the cuticle on the nerve endings, but the cuticle must form a bar to the reception of chemical stimuli. There must, of course, be cuticular pores through which the cilia project, but no special openings have been seen opposite the terminations of any of the centripetal fibres.

The central fibre may be branched or unbranched ; in the latter case never, apparently, into more than two fibrillae. Although directly in the first part of their course transversely to the longitudinal axis of the cord, the fibril or fibrillae later bend round so as to run in a direction parallel to the surface and along the length of the cord. Neither the central fibre nor its branches shows any varicosity, and on this point no confirmation of MEYER's statement that the fibre has a beaded appearance can be given.

The sensory elements are fairly evenly distributed over the surface of the cord. Calculations based on several counts of sense cells over circumscribed areas indicate that the number of sensory endings is never less than 4000 per square millimetre of surface, in which area there are about 75,000 supporting cells and fibres.

Although histologically undifferentiated, the primary sense cells of an asteroid such as *Marthasterias glacialis* are capable of the perception both of tactile and chemical stimuli and must therefore either be physiologically differentiated or possess a plurisensibility enabling them to respond to stimuli of different types.

The Association Ganglion Cells—The presence of association elements within the fibrillar substance of the radial nerve cord and tube feet was first demonstrated by HAMANN in 1883. The ganglion cells are described by him as falling into two size groups ; the larger are rounded cells without obvious dendritic processes and with a relatively large nucleus ; the smaller are figured as having a less obvious nucleus. These latter cells are drawn out into two or more dendrites and assume a bipolar or multipolar form. CUÉNOT (1887) does not acknowledge the presence of multipolar cells, and says that such elements are more properly to be considered as belonging to the connective tissue, a point which MEYER (1906) questions on the ground that it would indeed be extraordinary if connective tissue, of mesodermal origin, were found imbedded within the ectodermal substance of the radial nerve cord. MEYER finds both multipolar and bipolar ganglion cells in the radial cord of *Asterias rubens* but, although they may vary in size from 5–20 μ, these cells do not fall into two distinct size groups.

In the nerve cord of *Marthasterias glacialis* both bipolar and multipolar ganglion cells are present in large numbers—the bipolar being the form most frequently occurring. The multipolar association elements are entirely restricted to the area lying at the base of the nuclear zone of the epithelial cells (fig. 6, *multip. gang. c.*). They are usually from 6–18 μ in diameter with cytoplasm finely granular in appearance and tingeing only slightly with cytoplasmic stains. The rounded vesicular nucleus, of diameter about 4 μ, has a well-defined nucleolus and its chromatin is in the form of short coiled threads. A characteristic of the multipolar ganglion cell is that at least two of the dendrites (fig. 6, *long. dend. gang. c.*) are orientated so as to run along the length of the cord, in the same direction as the fibrillae of the subepithelial plexus. One or more of the remaining dendrites (*centrip. dend. gang. c.*) is intruded between the epithelial cells of the cord, in which position it is best able to make contact with the central fibres of the primary sense cells. Frequently, these latter fibres are seen to be contiguous, or nearly contiguous, with a longitudinally oriented process of the ganglion cell rather than with the peripherally directed dendrite (fig. 6, *c.f.s.c.*). The dendrites of both the multipolar and bipolar ganglion cell are drawn out into exceedingly fine fibrillae, which latter make up the greater part of the substance of the subepithelial plexus of the cord. These fibrillae, which run longitudinally along the cord, do not show any " beading " along their length such as MEYER (1906) has figured. It is impossible to trace them any distance from their cell of origin, but it is highly probable that the fibrillae are of an immense length in comparison with the width of the ganglion cell. The fibrillae are not united to, but are contiguous with, the fibrillae of other association elements.

The ganglion cells which lie in the deeper parts of the cord (fig. 6, *bipol. gang. c.*) are all of the bipolar type. Of a length varying from 5–32 μ, they are spindle-shaped cells, each end of which tapers to a fibrilla. The longitudinal axis of the cell is orientated along the length of the cord and, hence, the fibrillar continuation of each dendrite is similarly disposed. The bipolar ganglion cell of the type just described differs considerably in form from the few bipolar cells present with the multipolar elements at the base of the nuclear zone of the cord. This latter type of cell (fig. 6, *multip'. gang. c.*) is never spindle-shaped, but is more obviously allied to the rounded multipolar elements.

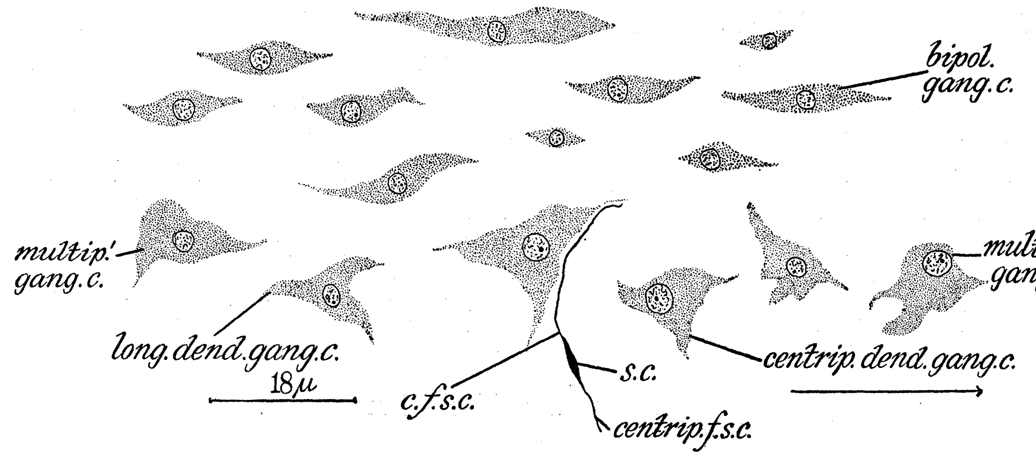

FIG. 6—Multipolar and bipolar association ganglion cells from the radial cord of *Marthasterias glacialis*. A composite drawing based on material fixed in F.W.A. and Susa fixative, stained with Mallory's triple stain. A primary sense cell is figured in relation to one of the multipolar ganglion elements. The arrow indicates the longitudinal axis of the cord. *bipol. gang. c.*, bipolar ganglion cell ; *c.f.s.c.*, central fibrilla of the sense cell ; *centrip. dend. gang. c.*, centripetal, dendrite of the ganglion cell ; *centrip. f.s.c.*, centripetal fibre of the sense cell ; *long. dend. gang. c.*, longitudinal dendrite of the ganglion cell ; *multip. gang. c.*, multipolar ganglion cell ; *multip'. gang. c.*, bipolar derivative of the multipolar ganglion cell ; *s.c.*, body of the sense cell.

The bipolar and multipolar ganglion cells differ one from the other so markedly in their form, disposition, and orientation that one cannot doubt that such differences are associated with functional dissimilarity. It seems clear from their form and disposition that the function of the multipolar ganglion cells is to discharge the stimuli received from the primary sense cells into the longitudinally running fibrillae of the subepithelial plexus. The presence of a centripetal dendrite and of the characteristically orientated pair of dendrites suggests very strongly a polarization of the ganglion cell, the impulses travelling from the centripetal to the longitudinal dendrite to be discharged into the fibrillae of the radial cord. In the deeper parts of the cord, the function of the association ganglion cell is more restricted. There is no longer any necessity for the development of a centripetal fibre, for the body of the ganglion cell is far removed from the primary sense cells. The sole function of the bipolar element is to transmit impulses along the length of the cord, for which purpose bipolarity of the cell would be induced.

The Neurofibrillae—Reference has already been made to the fact that the greater part of the thickness of the radial nerve cord is made up of the subepithelial plexus of neurofibrillae. Most of these fibrillae belong to the association ganglion cells, but the central fibres of the primary sense cells contribute, to some extent, to the total fibrillar substance.

One may say, in general terms, that the fibrillae of the radial cord run in a longitudinal direction although, as has been seen, the central fibres of the sensory cells, in the first part of their course, run at right angles to this axis. A series of horizontal sections through the cord (figs. 4A, 4B, 4C) shows quite clearly that there are three distinct zones within the fibrillar substance. We may distinguish these as follows :—

(*a*) the outer zone ; (*b*) the middle zone ; (*c*) the inner zone.

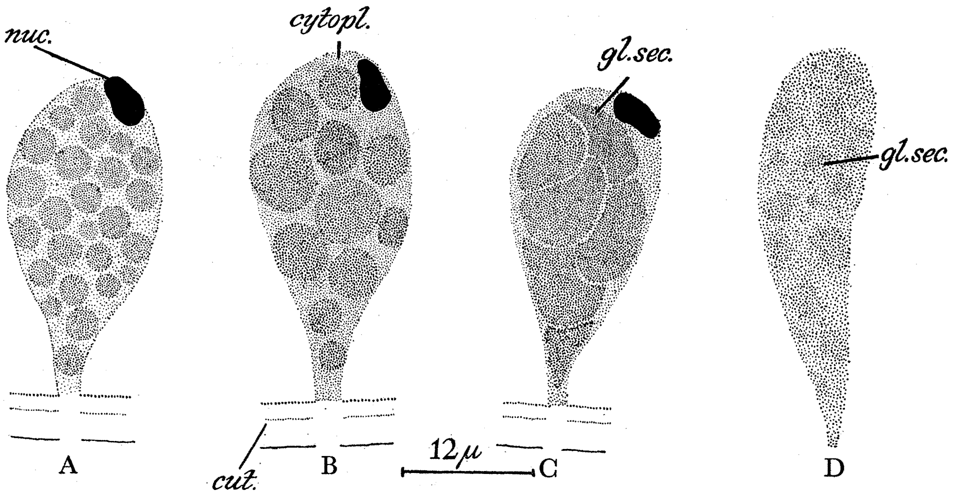

FIG. 7—Glandular elements from the radial cord of *Marthasterias glacialis*. A, B, C, " mulberry " glands in successive secretory stages. D, a goblet cell. Fixed corrosive-acetic, stained Mallory's triple stain. *cut.*, cuticle ; *cytopl.*, cytoplasm of the gland ; *gl. sec.*, glandular secretion ; *nuc.*, nucleus.

The outer zone extends from the inner limit of the nuclear layer of the epithelial supporting cells (*i.e.*, from the level of the multipolar ganglion cells) into the cord, to the extent of about one-third of its depth. In this zone (fig. 4A) the longitudinally running fibrillae (*n. fibril.*) pursue a sinuous course between the supporting fibres—here cut transversely and arranged in an indefinite manner. The supporting fibres, in other words, form the warp into which is threaded the fibrillar woof. The middle fibrillar zone (fig. 4B) is of about the same extent as the outer zone, but here the supporting fibres assume a linear arrangement. The fibrillae, although showing some indication of an arrangement into longitudinal bundles, are interwoven with the supporting fibres in much the same way as in the outer zone.

In the inner zone (fig. 4C), which occupies the inner third of the cord and extends up to the boundary layer of connective tissue, there is a regular linear arrangement of the neurofibrils into longitudinal bundles. The bundles alternate with the palisade-like rows of supporting fibres, but there is no trace of interweaving.

Both the zoning of the neurofibrils and the disposition of the multi- and bipolar ganglion cells reflect with equal clearness a functional differentiation of the superficial and deeper parts of the cord. The fibrillae of the outer and middle zones collect and distribute the impulses received by the primary sense cells, and no doubt transmit them along the length of the cord, but for the rapid transmission of impulses, necessary for the coordination of motor response, the impulses are discharged through the cable-like bundles of the deeper parts of the cord.

2—*The Circumoral Nerve Ring*

The circumoral nerve ring is a thickening of the peripheral part of the buccal membrane. Rather more pentagonal than circular in form, it gives rise, at each of the angles of the pentagon, to a radial nerve cord the structure of which has been described.

In transverse section (fig. 20) the nerve ring is seen to be in the form of an asymmetrical "V", the outer limb (*circum. n.r.o.*) of which is very much longer and more horizontally disposed than the short, almost vertical inner limb (*circum. n.r.i.*). The epithelium and subepithelial plexus of the circumoral ring is continuous peripherally and interradially with the general ectoderm of the disk, and radially with the radial nerve cord. Centrally, the fibrillar substance of the ring is continuous with that of the buccal membrane (fig. 20, *bucc. memb.*).

The histology of the circumoral nerve ring differs but little from that of the radial cord. The cuticle, epithelial cell layer—composed of supporting cells with their attendant fibres—glandular elements, sensory cells, and association ganglion elements are all present, but the main mass of the ring consists of compacted fibrillae. Any differences in the composition of the nerve ring, as compared with the radial cord, are concerned with the ganglion cells and the neurofibrillae. There appear to be fewer multipolar ganglion cells at the base of the nuclear zone, a circumstance difficult to account for in view of the fact that sensory elements are present in almost the same numbers as in the radial nerve cord. Bipolar ganglion cells, on the other hand, are present in larger numbers than in the radial cord and are particularly numerous in the deeper parts of the ring, in the neighbourhood of the connective tissue layer. They are elongate, spindle-shaped cells, 10–36 μ in length (most commonly about 15 μ), and of $3 \cdot 5$–4 μ greatest diameter. The rounded vesicular nucleus is of the usual type.

The neurofibrillae pursue a circular course in conformity with the shape of the ring. There are two fibrillar zones in place of the three to be found in the radial cord, for the inner zone of fibrillae is not represented in the ring. Moreover, the inner zone is only present to the extent of about one-third of the total thickness, so that by far the greater part of the nerve ring substance is composed of fibrillae arranged as in the outer zone of the radial nerve cord. In both the outer and middle zones the supporting fibres exhibit their characteristic arrangement, haphazard in the former, linear in the latter.

It appears, perhaps, at first sight, rather extraordinary that the inner zone of fibrillae should not be present in the nerve ring. If, however, the ring is to be regarded as being in the nature of a central nervous system where impulses received from the arms are sorted out and coordinated, it can well be seen that the necessity for rapid conduction, as represented morphologically by the defined tracts of the inner fibrillar zone, would be subordinated to a more amorphous arrangement of fibrillae, better able to elicit a greater variety of response. On this supposition only can a reasonable explanation of the fibrillar arrangement within the nerve ring be given.

3—*The General Ectoderm*

In the account already given of the radial and circumoral nerve cords, attention has been drawn to the fact that these cords are to be regarded merely as thickenings of the general ectoderm, in which the greater part of the thickness is due to the presence of an immense number of fibrillae. It would be expected, therefore, that the ectoderm which clothes the surface of the starfish would be composed of the same elements as are the cords. This is, in fact, so, but the elements of the general ectoderm exhibit such great differences in form by comparison with the equivalent elements of the cord that a separate description of them is necessitated.

The ectodermal covering of the starfish *Marthasterias glacialis* as seen, for example, in transverse section of the arm, is not everywhere of equal thickness. Thickened pads are usually to be found at the base of the spines and pedicellariae, and there is also a thickening in the mid-line of the adambulacral surface of the arm. It is this thickening which is shown in fig. 8A, where the ectoderm may have a maximum depth of 45 μ, although over the greater part of the surface it is usually not more than 10–15 μ thick. As will be seen, the subepithelial plexus (figs. 8A, 8B, *n. fibril.*) does not, as in the radial or circumoral cord, contribute substantially to the substance of the ectoderm, but is everywhere to be found as an extremely thin layer underlying the epithelial cells of the ectoderm. Exceptionally, as, for instance, at points lateral to the tube feet (fig. 27, *n. fibril. exp.*) there are expansions of the fibrillar substance, but these are developed in connexion with the motor nervous system. (*See* p. 152.)

The non-nervous elements of the general ectodermal covering of the starfish are the same as those present in the radial cord and nerve ring. The cuticle is, in all respects, precisely similar and calls for no further consideration. Glandular elements are of the two types already described—" mulberry " glands and goblet cells. The former, occurring much more frequently than the latter, are to be found in all stages of secretion (figs. 8A, 8B, *m. gl.*). The adambulacral surface is much more richly supplied with glands than the lateral and ambulacral surfaces, and while the ectoderm of the pedicellariae contains a few glandular elements these are fewer in number on the papulae and are practically absent on the suckers of the tube feet.

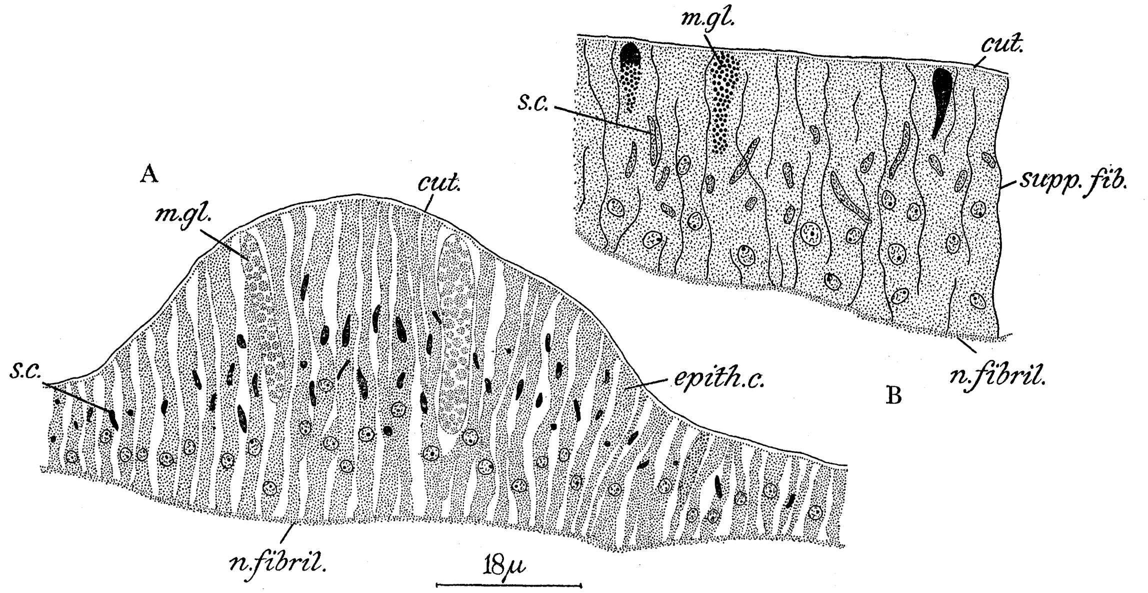

FIG. 8—Transverse sections through the ectoderm of the aboral surface of the arm of *Marthasterias glacialis*. A, from material fixed in F.W.A. and subsequently stained in Heidenhain's iron-alum haematoxylin. B, from Susa fixed material stained with Mallory's triple stain. *cut.*, cuticle ; *epith. c.*, epithelial cell ; *m. gl.*, " mulberry " gland ; *n. fibril.*, neurofibrillae of the subepithelial plexus ; *s.c.*, body of sense cell ; *supp. fib.*, supporting fibre.

It is in the form of the supporting cells of the ectodermal epithelium that the greatest difference is to be seen by comparison with the radial or circumoral cord. Instead of having the conical form with a tapering inner end, as described in the account of the histology of the radial cord, the epithelial cells are almost cylindrical (fig. 8A, *epith. c.*). The thickness of the ectoderm is dependent on the length of the epithelial cells composing it and not at all on the development of the neurofibrillar layer. Each epithelial cell, of length 10–45 μ, is about 2 μ in thickness and has a round vesicular nucleus, situated about one-sixth to one-third of the distance from its inner end. The epithelial cell secretes, intracellularly, a supporting fibre (fig. 8B, *supp. fib.*) which is, however, only poorly developed and not comparable in thickness with the fibre of the radial cord. The greater development of the fibre within the radial cord is, of course, attributable to the necessity for providing a framework strong enough to lend support to the thickened plexus of neurofibrils. In the general ectoderm, where the fibrillar plexus is only feebly developed, no such provision is required.

Primary sense cells are present in large numbers in all parts of the ectoderm (figs. 8A, 8B, *s.c.*), although their distribution is very patchy. Where the ectoderm exists only as a thin layer, some 15 μ in thickness, relatively few sensory elements (about 4000 per sq. mm. of surface) are to be found, whereas the thickened pads at the base of the spines and pedicellariae and in the mid-line of the adambulacral surface of the arm may have a concentration of sensory cells up to *ca.* 70,000 per sq. mm.

Fig. 8A shows sense cells as they appear after staining with Delafield's haematoxylin material fixed in Flemming's solution without acetic acid. The body of the cell consists of chromatic substance reacting homogeneously with the stain, but after treatment of Susa fixed material with Mallory's triple stain (fig. 8B, *s.c.*) the cell body has a granular appearance. The peripheral and central fibres cannot readily be seen in any of the sections of pieces of starfish arm which have been subjected to decalcification before imbedding.

There is no indication of any zoning of the fibrillae at the base of the ectoderm. Ganglion cells have not been seen within the fibrillar zone and, if present, they must occur in very small numbers. The limited extent of the fibrillar plexus at the base of the general ectoderm suggests that its substance may be made up entirely of the central fibres of the sensory cells and that the immense development of the plexus in the radial cord and nerve ring is due to the presence of the fibrillae of the association ganglion elements.

4—*The Tube Feet*

The tube foot of an asteroid such as *Marthasterias glacialis* is, in its nervous organization, a highly developed organ capable not only of the perception of tactile and chemical stimuli but of responding, by the performance of sometimes complicated movements, to the stimuli received. The tube foot is, indeed, an autonomous organ (Paine, 1929) and, as such, must possess its own sensory-motor reflexes. In its normal functioning, however, a podium does not react independently of its fellows and there is, in the starfish, a degree of coordination of movement sufficient for the performance, in conjunction with muscle action within the body of the animal, of the complicated movements necessary for the righting reaction or for the more normal actions of the animal in its everyday life.

The podia of *Marthasterias glacialis* are set in two zig-zag lines, one on each side of the ambulacral groove in the mid-line of the oral surface of the arm (fig. 10, *t.f.*). Each tube foot (fig. 12) is in the form of a hollow tube with a terminal sucker. The central cavity is part of the coelom of the water vascular system and the wall which bounds it is made up of an outer epithelial and sensory ectoderm (*ect.*), a subepithelial neurofibrillar plexus (*n. fibril.*), a layer of connective tissue (*conn. tiss.*), and an internal longitudinal muscle coat (*long. musc.*) lined by coelomic epithelium (*coel. epith.*). In the description which follows, the connective tissue and muscle layer are considered only in so far as their relations with the nervous elements are concerned.

Fig. 9 shows a transverse section through a part of the wall of the middle region of a tube foot. The ectoderm consists of epithelial cells, recognized here by their rounded vesicular nuclei (*nuc. epith. c.*), supporting fibres (*supp. fib.*) (not shown in their entirety in this section), sensory elements (*s.c.*), and glands (*m. gl.*) in large numbers, the whole being covered by a thin cuticle (*cut.*). The histology of the ectoderm of this part of the tube foot is essentially similar to that already described in the account of the general ectoderm, and need not be further considered here.

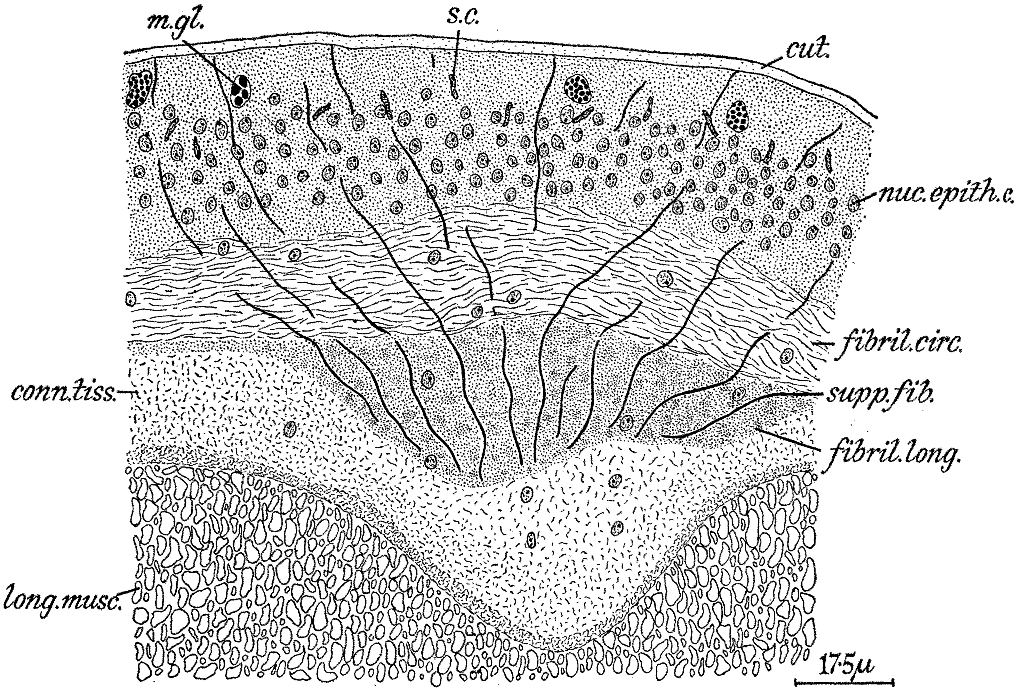

FIG. 9—Part of a transverse section through the middle region of a tube foot showing the longitudinal coordinating fibrillar tract. A composite drawing based on corrosive-acetic fixed material stained with Mallory's triple stain or Delafield's haematoxylin. *conn. tiss.*, connective tissue ; *cut.*, cuticle ; *fibril. circ.*, circular fibrillar zone ; *fibril. long.*, longitudinal fibrillar zone ; *long. musc.*, longitudinal muscle fibres ; *m. gl.*, " mulberry " gland ; *nuc. epith. c.*, nucleus of epithelial cell ; *s.c.*, body of sense cell ; *supp. fib.*, supporting fibre.

Below the epithelial cells lie the neurofibrillae of the subepithelial nerve plexus. The outer part of the plexus (fig. 9, *fibril. circ.*), some 15–20 μ thick, is composed of fibrillae which take a circular course round the internal border of the epithelial cells. Within the fibrillar substance numerous multi- and bipolar ganglion cells, here recognizable by their nuclei, occupy their characteristic positions as indicated in the account of the radial cord. Internal to the circular fibres is a very thin zone of fibrillae which runs longitudinally along the length of the tube foot. This layer is only about 2 μ in thickness over the greater part of the circumference of the podium, but in one particular line—which is always orientated in a definite manner relative to the longitudinal axis of the arm—the longitudinal fibrillar tract (*fibril. long.*) is especially well developed.

The position of the tract is shown in fig. 10, where part of a horizontal section through the arm and disk is figured. The longitudinal fibrillar tract (*long. tr.*) is directed towards the mid-line (*i.e.*, towards the radial nerve cord) and faces in the direction of the circumoral nerve ring (*circum. n.r.*). Its position suggests very strongly that its function is to transmit impulses through the radial nerve cord to the circumoral ring and that it is this tract which carries impulses responsible for the coordination of movement of the tube feet to the coordinating centres of the nerve ring. A more detailed study of the fibrillar tract elicits information which gives considerable support to this suggestion.

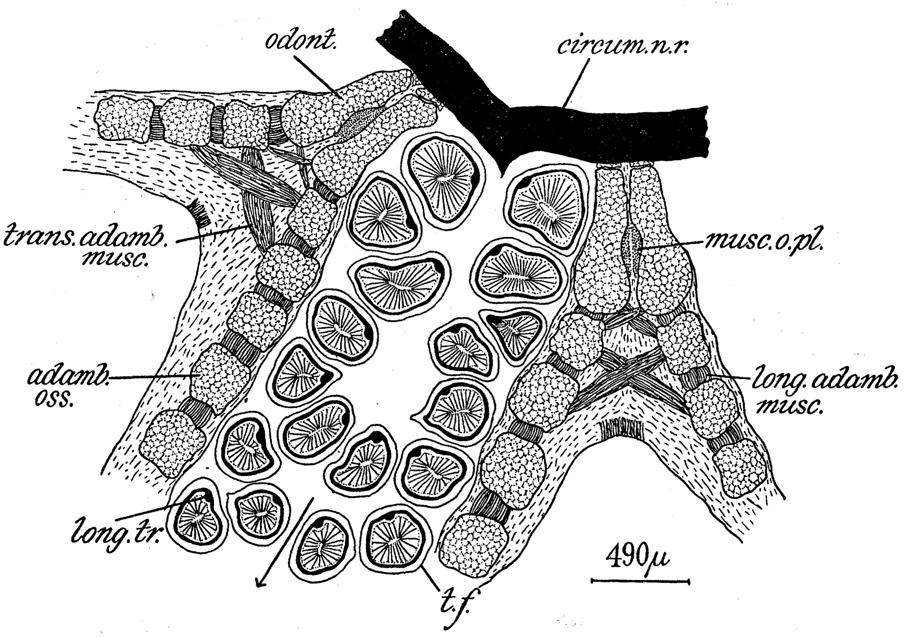

FIG. 10—Horizontal section through part of the disk and an arm of *Marthasterias glacialis* showing the position of the longitudinal fibrillar tract of the tube feet relative to the radial cord and circumoral nerve ring. The subepithelial neurofibrillar plexus is figured in black and the arrow indicates the longitudinal axis of the radial cord. Fixed in Susa solution, stained Mallory's triple stain. *adamb. oss.*, adambulacral ossicle ; *circum. n.r.*, circumoral nerve ring ; *long. adamb. musc.*, longitudinal adambulacral muscle ; *long. tr.*, longitudinal fibrillar tract of the tube foot ; *musc. o. pl.*, muscle running between the odontophore and oral plate ; *t.f.*, tube foot ; *trans. adamb. musc.*, transverse adambulacral muscle.

Five distinct fibrillar zones can be discerned in a tangential section through the tube foot (fig. 11A–E). A and B belong to the circular fibrillar zone, D and E to the longitudinal tract, while C is transitional between the two. The section passes, in fig. 11A, through the base of the epithelial layer. Numerous nuclei of the epithelial supporting cells (*nuc. epith. c.*) are to be seen and the supporting fibres, indiscriminate in distribution, are cut transversely. Such neurofibrillae as are here to be found are the central fibres of the sense cells. These merge (fig. 11B) with the circular fibrillae of the association ganglion cells, which latter constitute the greater part of the circular fibrillar zone. The arrangement of the supporting fibres, in this and the following zone, is still a haphazard one. When the third zone is reached (fig. 11C), the fibrillae, which had previously pursued a circular course, turn through a right angle and run longitudinally along the length of the podium. In this transitional zone, therefore, both circular and longitudinally directed fibrillae are to be found. The outer zone of the longitudinal tract proper (fig. 11D) corresponds almost precisely to the middle fibrillar zone of the radial cord. Here, the supporting fibres, arranged in linear series, form a framework through which the fibrillae are interlaced. Finally, in the deepest zone (fig. 11E), where the fibrillae are arranged in discrete longitudinal tracts, alternating regularly with the lines of supporting fibres, we have a condition in all respects similar to that of the inner fibrillar zone of the radial nerve cord, where paths of rapid conduction are to be found.

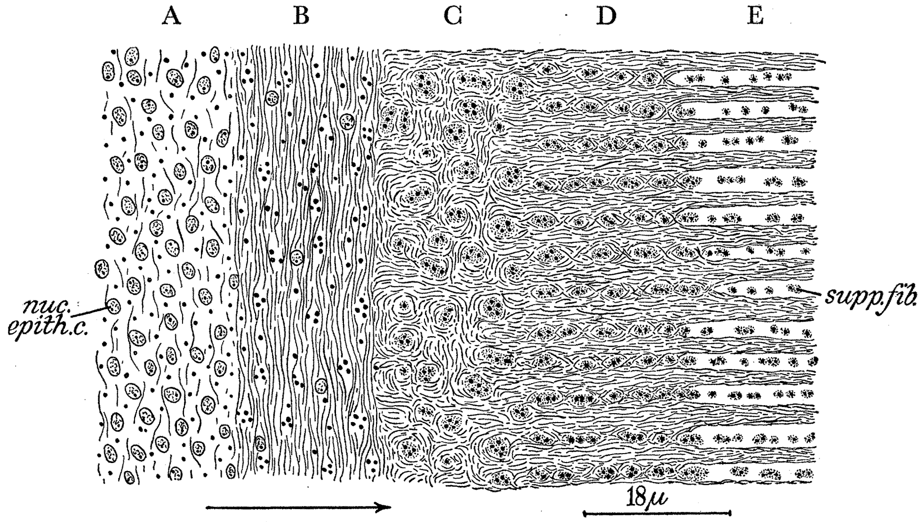

FIG. 11—Oblique parasagittal section through a tube foot passing through the subepithelial neurofibrillar plexus. Fixed in Susa solution, stained Mallory's triple stain. The arrow indicates the longitudinal axis of the tube foot. A, base of the epithelial layer ; B, the circular fibrillar zone ; C, the transitional zone ; D, the outer longitudinal fibrillar zone ; E, the inner longitudinal fibrillar zone. *nuc. epith. c.*, nucleus of epithelial cell ; *supp. fib.*, supporting fibre.

The disposition of the five fibrillar zones would indicate that stimuli perceived by the primary sense cells are brought round to the greatly developed longitudinal tract through the circularly disposed fibrils of the outer fibrillar ring, and that rapid and unidirectional transmission of impulses to the radial cord and circumoral ring is entirely effected through the deep lying fibrillar cords of the longitudinal tract.

The terminal portion of the tube foot is expanded into a sucker, by means of which the podium can be attached to the substratum. The sucker is highly sensitive, owing to the development, within the ectoderm, of large numbers of sense cells. As a result of the special development of primary sense cells, there is present an extensive fibrillar system. The disposition of the nervous elements in this region will be better

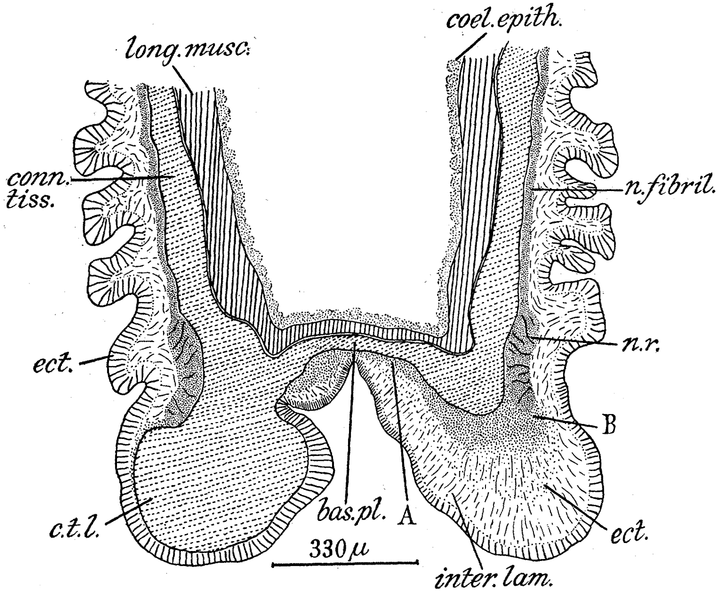

FIG. 12—Diagrammatic figure of a longitudinal section through the terminal portion of a tube foot. The significance of the points indicated by the letters A and B is explained in the text. *bas. pl.*, basal plate of connective tissue ; *c.t.l.*, connective tissue lamina ; *coel. epith.*, coelomic epithelium ; *conn. tiss.*, connective tissue ; *ect.*, ectoderm ; *inter. lam.*, interlaminar area ; *long. musc.*, longitudinal musculature ; *n.r.*, nerve ring ; *n. fibril.*, subepithelial neurofibrillar plexus.

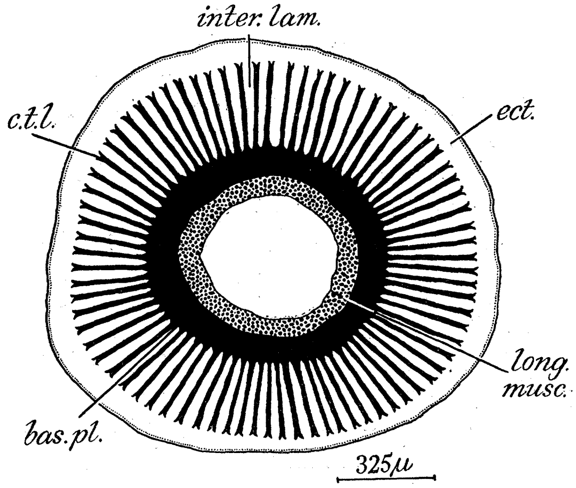

FIG. 13—Diagrammatic figure of a transverse section through a tube foot sucker. *bas. pl.*, basal plate of connective tissue ; *c.t.l.*, connective tissue lamina ; *ect.*, ectoderm ; *inter. lam.*, interlaminar area ; *long musc.*, longitudinal musculature.

understood if the relations of the ectoderm with the underlying connective tissue are first considered.

The connective tissue layer, which in the tubular part of the podium separates the ectoderm from the muscle layer, is expanded at the base of the sucker into a flat plate (figs. 12 and 13, *bas. pl.*) from which numerous radially arranged laminae (*c.t.l.*) extend downwards into the substance of the sucker. In fig. 12—a diagrammatic representation of a median longitudinal section through the tip of a tube foot—a connective tissue lamina (*c.t.l.*) is figured on the left-hand side of the figure, while to the right of the mid-line an area between two adjacent laminae is shown. These interlaminar areas (fig. 12, *inter. lam.*) are therefore occupied entirely by ectoderm which penetrates into the substance of the sucker as a series of ridges, alternating with the connective tissue septa. The arrangement is seen rather more clearly in fig. 13, a diagram of a transverse section through the terminal part of a tube foot. The connective tissue lamina (*c.t.l.*), figured in black, radiates from the central basal plate (*bas. pl.*) like a series of spokes ; between these lies the ectoderm of the interlaminar areas—white in the figure.

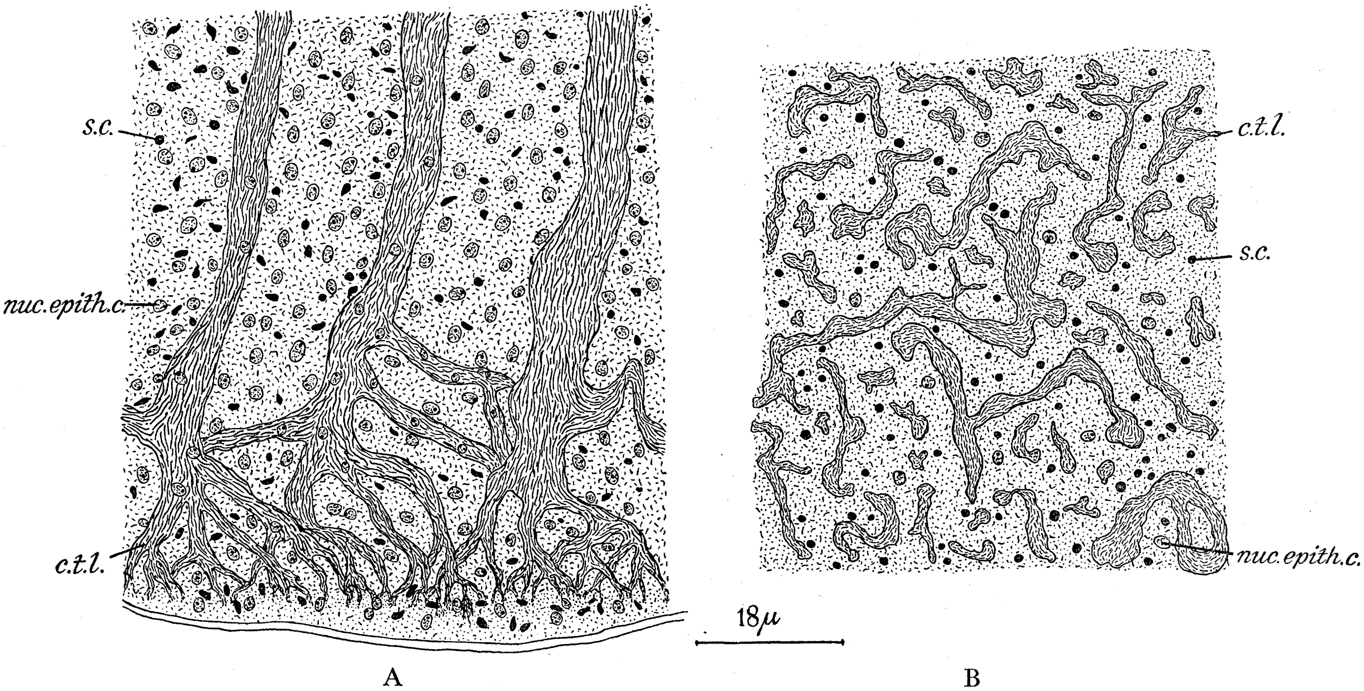

FIG. 14—A, a parasagittal section through a portion of a tube foot sucker showing the arborescent character of the free edges of the connective tissue laminae ; B, a portion of a transverse section through the tip of a tube foot sucker showing the disposition of the sensory and epithelial elements between the branches of the connective tissue laminae. Fixed corrosive-acetic, stained Mallory's triple stain. *c.t.l.*, connective tissue lamina ; *nuc. epith. c.*, nucleus of epithelial cell ; *s.c.*, body of sense cell.

The free edges of the laminae are arborescent (figs. 14A, 14B) with the result that, in the ectoderm below the cuticle, the connective tissue is in the form of fine twigs which together make up a network, in the interspaces of which are the epithelial supporting cells (*nuc. epith. c.*) and sensory elements (*s.c.*). In the sucker of the tube foot the sensory elements are almost as numerous as the epithelial cells, as compared with an approximate 1 : 16 ratio in the radial nerve cord. Figs. 14A and 14B show the sensory cell bodies to be darkly staining elements, contrasting sharply with the rounded vesicular nuclei of the epithelial cells. The histology of the tube foot is figured in more detail in fig. 15—a part of a longitudinal section of the sucker passing through an interlaminar area.

On account of the relatively great depth to which the ectoderm penetrates in this region, the epithelial cells (*epith. c.*) become correspondingly elongate. They

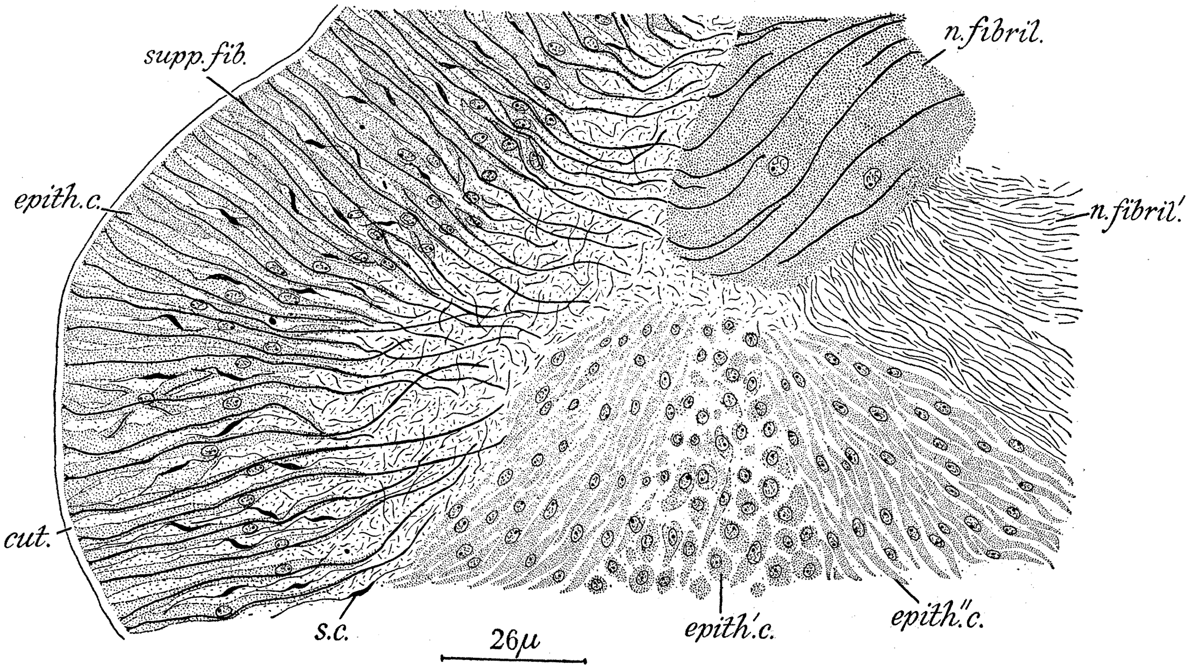

FIG. 15—Longitudinal section through an interlaminar area of a tube foot sucker showing the nature of the epithelial cells of the sucker and the entrance of the fibrillae from below the basal plate of connective tissue into the nerve ring. Fixed corrosive-acetic, stained Mallory's triple stain. *cut.*, cuticle ; *epith. c.*, epithelial cell cut along its longitudinal axis ; *epith'. c.*, *epith''. c.*, epithelial cells cut transversely and obliquely ; *n. fibril.*, neurofibrillae of the nerve ring ; *n. fibril'.*, neurofibrillae of the plexus underlying the basal plate of connective tissue ; *s.c.*, sense cell ; *supp. fib.*, supporting fibre.

resemble the epithelial cells of the radial cord rather than those of the general ectoderm, in that they are drawn out internally into a tapering end. Each of the cells secretes, intracellularly, a supporting fibre (*supp. fib.*), the internal end of which penetrates as far as the connective tissue layer. The fibre, traversing in its path the whole of the neurofibrillar plexus, may attain a total length of 250 μ or more. The primary sense cells (*s.c.*) are of the usual spindle-shaped form with a cell body subepithelial in position and with long centripetal and central fibres. The subepithelial plexus is not continuous round the base of the sucker, under the basal plate of connective tissue, owing to the development of the connective tissue septa, but is divided into interlaminar areas. The fibrillae of the plexus of each interlaminar area run centrifugally (fig. 12, from A to B) to curl round the outer edge of the plate. As a result of this centrifugal displacement, the fibres become massed round the periphery of the basal connective tissue plate and form a well-defined ring of nerve fibrils which pursue a circular course. This is well shown in fig. 15; the centrifugally running fibrillae of the interlaminar plexus (*n. fibril'.*) enter the nerve ring where they bend sharply round to run in a circular direction (*n. fibril.*).

There is no indication of any division of the fibrillar system of the nerve ring into zones. The fibrillae are interwoven between the supporting fibres and correspond in their entirety to the circular fibrillar zone of the middle part of the tube foot (fig. 11B). This is important from the point of view of interpretation of function, for it shows that the nerve ring of the tube foot is nothing more than a local thickening of the circular fibrillar zone consequent on the development, within the ectoderm of the sucker, of enormous numbers of primary sense cells. It is not to be regarded as a coordinating ring with defined tracts for the rapid transmission of impulses. At the top of the nerve ring (towards the tubular part of the podium) the circular fibrillae turn through a right angle and become continuous with the fibrillae of the longitudinal coordinating tract (fig. 16). Impulses received by the sensory endings of the sucker are thus conveyed through the nerve ring and longitudinal tract to the radial cord and coordinating centres of the circumoral nerve ring.

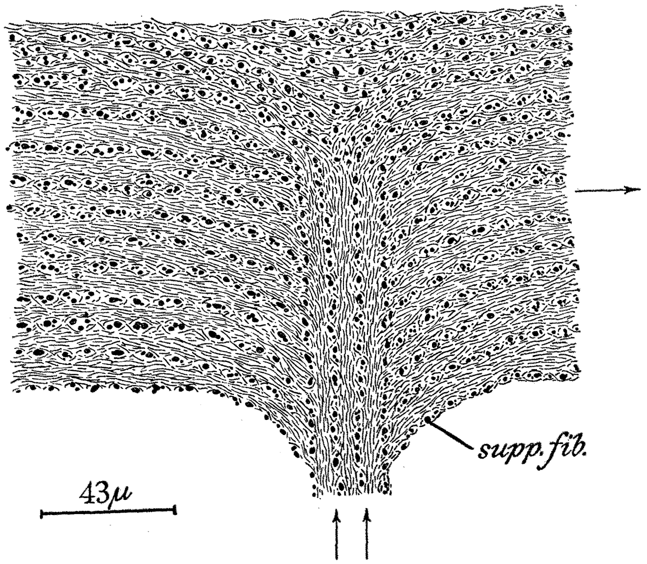

FIG. 16—Parasagittal section through a tube foot passing through the subepithelial fibrillar zone at the junction of the longitudinal fibrillae of the longitudinal tract with the circular fibrillae of the nerve ring. Fixed in corrosive-acetic, stained with Mallory's triple stain. The double arrow indicates the direction of the longitudinal tract, the single arrow that of the nerve ring; *supp. fib.*, supporting fibre.

By way of summary we may say, therefore, that the tube foot is a highly sensory organ with a particularly sensitized sucker. The fibrillar system is divisible into an outer circular and an inner longitudinal zone, the former being concerned primarily with the collection of impulses from the sensory cells, the latter with the transmission of these impulses to the coordinating centres. As a result of the special development of sensory elements within the sucker, the circular fibrillar zone is thickened and forms a ring which is not in itself concerned with the coordination of stimuli, but is connected with the more centralized parts of the nervous system through the longitudinal tract.

It has already been noted that the tube feet are autonomous, and as such must possess their own reflex systems. No trace of any motor system has been seen within the podium, but the probable nature of the muscle innervation is discussed at a later stage of this paper, after the consideration of those organs which are known to have their own sensory-motor reflexes.

5—*The Azygos Tentacle*

Terminally situated, at the free end of each of the arms of the starfish, is an azygos tentacle. It is placed (fig. 17, *azyg. tent.*) so as to overhang the distal expansion of the radial nerve cord—the optic cushion (*opt. c.*)—and its cavity (*rad. w. v.*) represents the end part of the radial water vessel. The azygos tentacle differs from all the other tube feet not only in regard to its position but in the poor development of the sucker and in the feeble musculature of its wall.

In respect to the organization of its sensory system the azygos tentacle shows, except in the asymmetrical development of the ectodermal sensory areas and fibrillar plexus, no great variation in comparison with the other tube feet. Figs. 17 and 18 show, diagrammatically, the morphological relations of the azygos tentacle and the extent of the plexus. The ectoderm of the tentacle is continuous aborally (fig. 17) and laterally (figs. 18A, 18B) with the general ectoderm of the arm, and orally (fig. 17) with the distal end of the nerve cord, where it is expanded into the optic cushion. The aboral and lateral connexions are effected through lappet-like foldings of the ectoderm (figs. 17, 18A, 18B, *ab. lap.*, *lat. lap.*), which form a hood within which the tentacle can be partially retracted.

The ectoderm of the azygos tentacle is made up of epithelial cells with supporting fibres, sensory elements, and glands, and is covered by a thin cuticle. Glands are not numerous on the azygos tentacle and are practically absent from the sucker. The primary sense cells are very asymmetrically distributed, for while the oral and lateral faces of the sucker are supplied with sensory endings in even greater numbers than are the suckers of the ambulatory podia, the aboral ectoderm is practically devoid of them. To this uneven distribution may be related the fact that the starfish, in life, bends the ray aborally and so presents only the oral face of the tentacle for the reception of stimuli, the aboral surface being thus hidden under the hood.

Consequent on the asymmetrical disposition of the sensory elements is an uneven development of the subepithelial fibrillar plexus. The thickness of the epithelium and plexus is indicated by the blackened areas in figs. 17, 18A, and 18B. Fig. 17 clearly shows that the plexus is very much more extensive on the oral than on the aboral face of the tentacle. The nerve ring (fig. 18B, *n.r.*), not so well developed as in the rest of the podia, attains its greatest diameter orally, and is least expanded aborally. The fibrillae are continuous laterally and aborally with those of the general ectoderm through the fibrillar system of the ectodermal hood. Orally, they are in connexion with the fibrillae of the radial cord. Of the two ectodermal folds which together compose the hood (figs. 18A, 18B), the outer has a very much better developed fibrillar plexus than the inner, and is provided with a correspondingly larger number of primary sense cells.

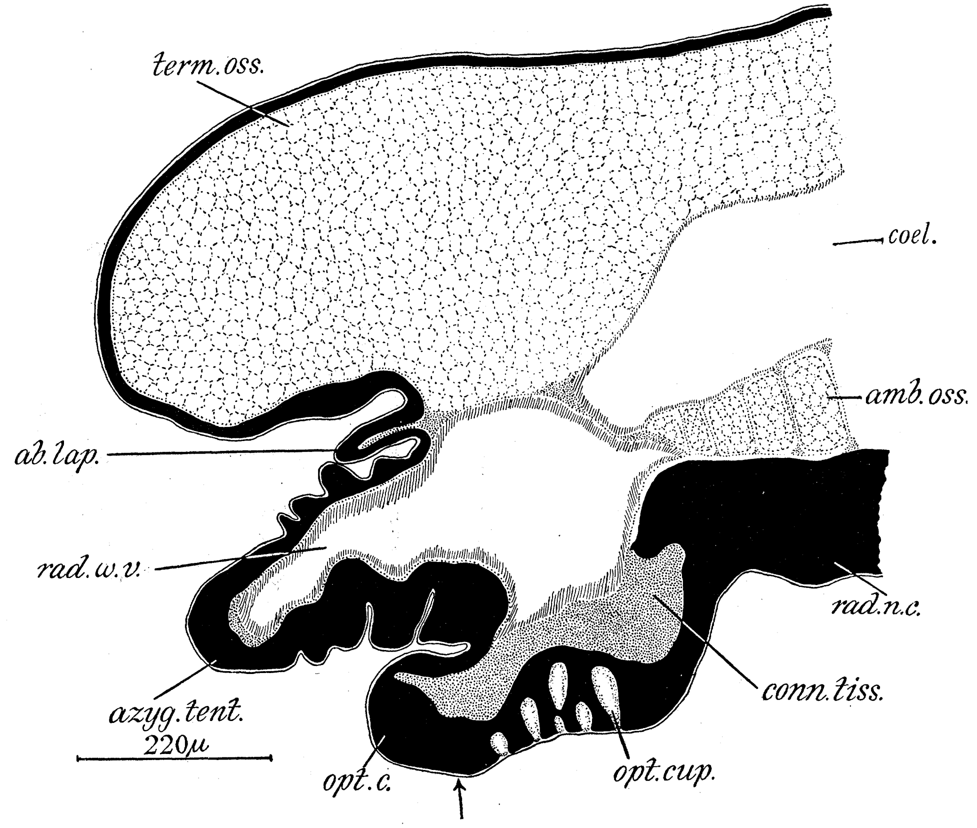

FIG. 17—Diagrammatic figure of a sagittal section through the tip of an arm of *Marthasterias glacialis*. The ectoderm—including the epithelial layer and subepithelial plexus—is figured in black. *ab. lap.*, aboral lappet ; *amb. oss.*, ambulacral ossicle ; *azyg. tent.*, azygos tentacle ; *coel.*, perivisceral coelom ; *conn. tiss.*, connective tissue ; *opt. c.*, optic cushion ; *opt. cup.*, optic cup ; *rad. n.c.*, radial nerve cord ; *rad. w.v.*, radial water vessel ; *term. oss.*, terminal ossicle.

It is characteristic of the azygos tentacle that its neurofibrillae are not arranged along any particular axis, circular or longitudinal, as in the ambulatory podia. In view of this fact, it is noteworthy that the fibrillar zoning of the radial nerve cord, although extending to the distal limit of the optic cushion, does not extend into the narrow strip of ectoderm which unites the cord and the oral surface of the azygos tentacle.

6—*The Optic Cushion and Optic Pits*

We have already seen that at its distal extremity, where it underlies the azygos tentacle, the radial nerve cord is expanded into an optic cushion (fig. 17, *opt. c.*). The " eye-spot ", on the oral surface of the cushion, is rendered visible to the naked eye by virtue of the orange-red pigment lodged within the cells which line the separate optic cups (figs. 17, 18A, *opt. cup.*) of which the " eye " is composed. The pigmented " eye " was noted as long ago as 1780 by VAHL, but the details of the histology of the optic cup still provide some of the most difficult problems associated with the study of the asteroid nervous system.

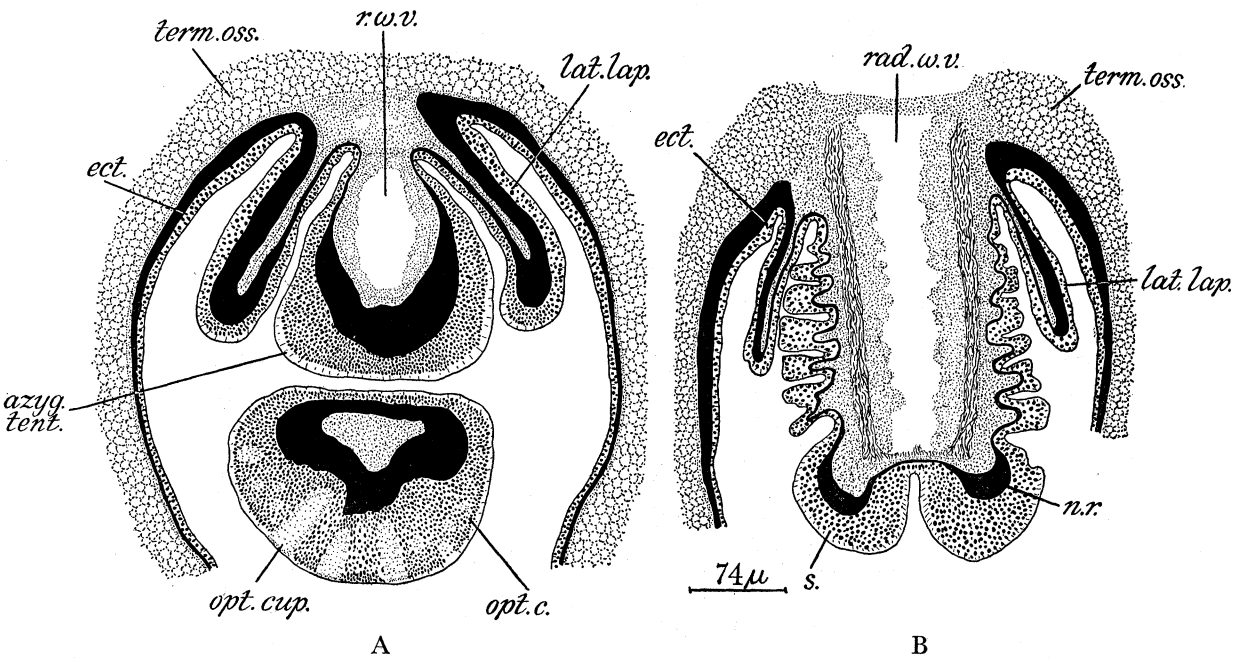

FIG. 18—A, transverse section through the tip of an arm of *Marthasterias glacialis* ; B, horizontal section through the azygos tentacle and its lateral lappets. The subepithelial plexus is figured in black and the black dots represent nuclei of epithelial and sensory cells. *azyg. tent.*, azygos tentacle ; *ect.*, ectoderm of the arm ; *lat. lap.*, lateral lappet ; *n.r.*, nerve ring ; *opt. c.*, optic cushion ; *opt. cup.*, optic cup ; *rad. w.v.*, radial water vessel ; *s.*, sucker of the tube foot ; *term. oss.*, terminal ossicle.

Each of the cups (fig. 19) is formed by an invagination of the superficial ectoderm, which thus comes to enclose a thimble-shaped cavity filled with droplets of a lightly staining fluid. The mouth of the cup is covered by the cuticle below which is a hyaline lenticular structure. Opinion has differed chiefly in regard to the disposition of the cuticle, the nature of the lens, and the identity of the pigmented and sensory cells of the ectoderm lining the optic cup.

Haeckel (1860), Greeff (1872), Hoffmann (1872), and other earlier workers regarded the droplets within the cup as lenses, but they have subsequently been shown not to be of a lenticular nature. Hamann (1883) and Cuénot (1887) do not figure any special lenticular structure in the optic cup. Pfeffer (1901), however, shows that the hyaline thickening, of ectodermal origin, which covers the mouth of the cup must be regarded as a lens, an observation I have been able to confirm.

Cuénot's account differs from that of all other workers in respect to the cuticle which, he says, " descend jusque dans les godets oculaires qu'elle revêt completement ". My sections of the optic cushion of *Marthasterias glacialis* show, on the contrary, that the epithelial cells of the optic cup have no cuticular lining resulting from an invagination of the cuticle ; the latter, in fact, is entirely superficial in position. Finally, there remains for consideration the histology of the cells which line the optic cup. Briefly stated, there are two divergent views as to the nature of these elements of ectodermal origin. Hamann (1883) finds in the cup both pigmented and sensory cells. The former, of the nature of epithelial cells, have their inner ends produced as a long fibre which, extending through the underlying fibrillar zone, terminates on the basal connective tissue layer, while the latter have a central fibre which merges with the fibrillae of the subepithelial plexus. Pfeffer (1901), on the other hand, is of the opinion that the cup is lined by cells which are pigmented and are also sensory in function, *i.e.*, there is only a single type of cell. He says, " Die Sonderung in Pigment- und Stäbchenzellen ist eben bei der Retina des Seesternauges nicht durchgeführt, so dass hier die Retinazellen die Funktion der Ausscheidung einer Hühle sowohl als auch die Funktion der Stäbchenzellen übernehmen müssen, nämlich das Fortleiten des durch das Licht bedingten Reizes. Man muss das Verhältniss, wie es sich bei den Sehzellen der Asteriden darbietet, als der primitivere bezeichen, da hier keine Arbeitstheilung eingetreten ist ". In the following account of the histology of the optic cup of *Marthasterias glacialis* particular attention is directed to the points indicated above.

Fig. 19 is a composite drawing of two optic cups, based on a study of a number of series of longitudinal sections through the optic cushion. The left-hand cup is drawn from a Susa-Mallory triple stain preparation, the right-hand one from F.W.A. fixed material, subsequently stained either with Heidenhain's iron-alum haematoxylin, Delafield's haematoxylin, or with Mallory's triple stain.

The invaginated ectodermal lining of the optic cup is entirely surrounded by epithelial supporting cells (*epith. c.*) and by the neurofibrillae of the subepithelial plexus (*n. fibril.*). The supporting cells are of the type characteristic of the radial cord, and are roughly conical in shape with a long tapering inner end of barely sufficient width, along the greater part of its length, to be visible even under high magnification. The cells secrete an intracellular fibre (*supp. fib.*) which extends from the cuticle to the connective tissue at the base of the plexus. In the neighbourhood of the mouth of the optic cup some few of the supporting fibres bend inwards so that their peripheral ends enter the biconvex hyaline structure (*l.*) which fits into and closes the mouth of the optic cup. This biconvex structure is described by

Pfeffer (1901) as a lens of ectodermal origin, a statement of the accuracy of which there can be little doubt. The fact that the supporting fibres enter its substance shows that the lens cannot be of a cuticular derivation, and that it must be regarded, not as a product of secretion of the epithelial cells but as part of the epithelial cells themselves, and as such must contain a portion of the supporting fibres. The cuticle (*cut.*) remains as a thin covering, closely applied to the outer surface of the lens.

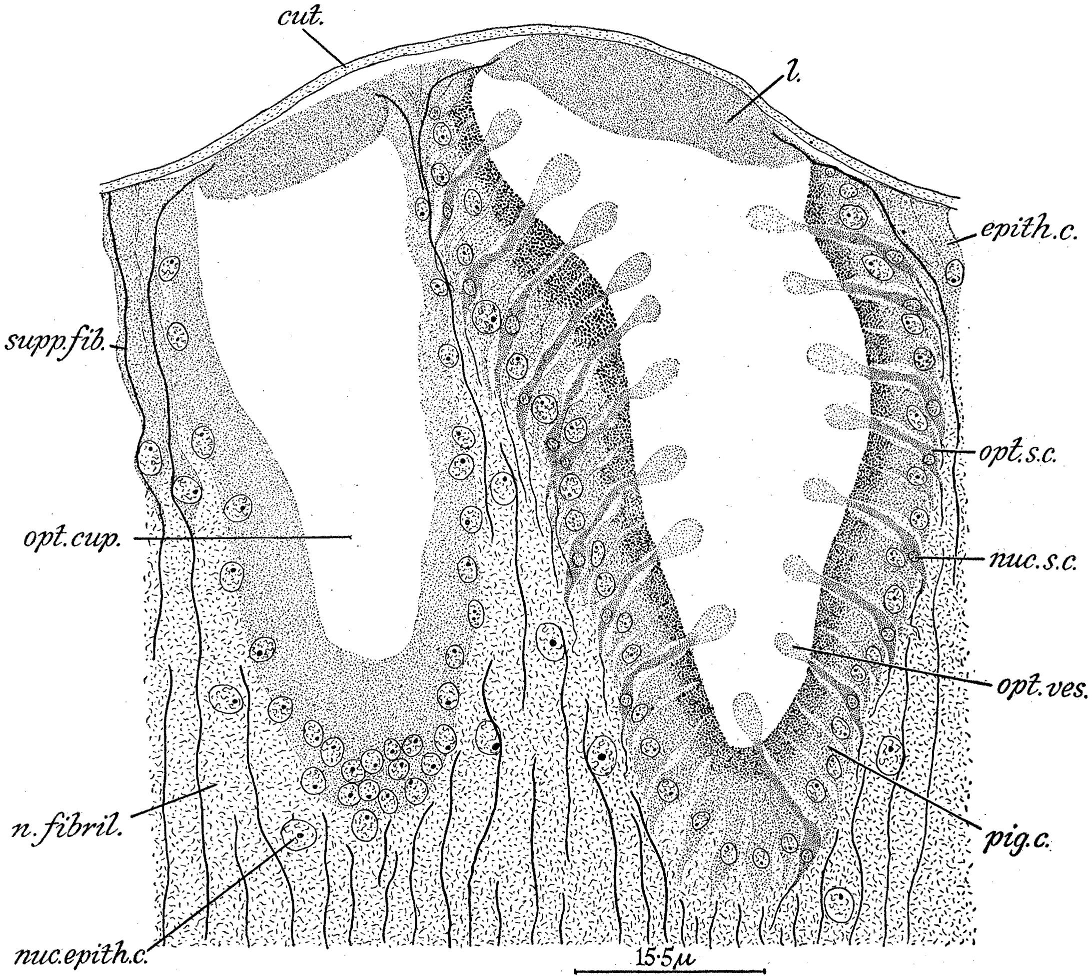

Fig. 19—Longitudinal section through a part of the optic cushion of *Marthasterias glacialis*. On the left is figured an optic cup after fixation with Susa solution, on the right a cup after fixation with F.W.A. *cut.*, cuticle ; *epith. c.*, epithelial cell ; *l.*, lens ; *n.fibril.*, subepithelial neurofibrillar plexus ; *nuc. epith. c.*, nucleus of epithelial cell ; *nuc. s.c.*, nucleus of sensory cell ; *opt. cup.*, cavity of the optic cup ; *opt. s.c.*, visual sensory cell ; *opt. ves.*, optic vesicle ; *pig. c.*, pigment cell ; *supp. fib.*, supporting fibre.

The epithelial lining of the optic cup is composed of two types of cell—the pigmented cell (*pig. c.*) and the sensory elements (*opt. s. c.*). The former are in shape very similar to, but are in length much shorter than, the general epithelial cells of the cord, and can be distinguished from them by the smaller size of their nuclei, for while the nucleus of the epithelial cell is about 4 μ in diameter, that of the pigmented cell is only about 2·5 μ. The outer ends of the pigmented cells form the wall of the cup, and are broader than the inner tapering ends which merge into the subepithelial plexus. Although the main body of the cell is set almost at right angles to the longitudinal axis of the optic cup, the sharply attenuated inner ends bend round so as to lie along its longitudinal axis. Characteristic of the pigmented cell is the development, in the peripheral part of its substance, of pigment in the form of small granules which, though soluble in acetic acid (fig. 19, left-hand side cup), remain visible after treatment with osmic fixatives (right-hand side cup). The pigment is restricted in distribution to the outer third of the cell, the nucleus of which is situated in the non-pigmented portion.

Interpolated between the pigmented cells of the optic cup are numerous bodies which must be regarded as constituting the visual cells of the cup. The visual elements are most difficult to demonstrate, and are not visible at all after fixation with non-osmic fixatives (fig. 19, left-hand cup). They have, in fact, not been seen in their entirety in any one preparation, and it must be pointed out here that the interpretation of their structure, as indicated in fig. 19 (right-hand side cup), has been arrived at by the study of many series of sections of F.W.A. fixed material, after treatment with a variety of stains. The visual sensory cell is divided into two well-defined regions—a peripheral portion (*opt. ves.*), projecting into the cavity of the cup, and a sensory portion (*opt. s.c.*), intruding between the pigment cells. The former is seen to best advantage in iron-alum haematoxylin preparations, after F.W.A. fixation, when it appears as a very lightly staining vesicle, slightly swollen at its free end and projecting for a distance of about 4–5 μ into the cavity of the cup. Although the vesicle is almost transparent, its outlines are well defined, and its shape is not in any way variable. This is important because of the possibility of mistaking the vesicles for droplets of secretion in the process of being exuded into the cavity. The secretion is, in fact, very different in appearance, distribution, and staining properties from the optic vesicles, which latter are only to be found as the peripheral extensions of the visual sensory cells into the optic cup. The central portion of the sensory element (*opt. s.c.*) forms the body of the cell. Its disposition follows that of the pigmented cell in that, although in its middle region the cell is set almost at right angles to the wall of the cavity, its tapering inner end bends round so as to be orientated along the longitudinal axis of the cup. Each cell body is of a narrow cylindrical form, some 12 μ long, and is broadest at the point where the nucleus is situated. The cytoplasm of the cell reacts hardly at all to the usual stains, but the small nucleus (*nuc. s.c.*), not more than 1 μ in diameter, is easily demonstrated. At its base the sensory cell is continued as a fine fibrilla which merges with the fibrillae of the subepithelial plexus.

The separation of the cells lining the wall of the optic cup of *Marthasterias glacialis* into two distinct elements, recalls the condition usually to be found in the eyes of invertebrates. The probability is that the pigmented cells not only reflect the light on to the vesicular portion of the sensory element but also secrete the fluid which fills the cavity of the optic cup. Visual impulses are transmitted through the sensory cells to the fibrillae of the underlying plexus, but whether or not there are association ganglion cells intermediary between the two is a point which must at present be left open.

7—*The Alimentary Canal*

In the centre of the oral surface of the disk of the starfish is the mouth, at which point the buccal membrane is continuous with the oesophagus. The continuity of the tissue involves not only the epithelial cells but the subepithelial plexus of neurofibrils. It has been the custom to apply the term " endoneural " to that part of the nervous system which is developed in the wall of the alimentary canal in contrast to the ectoneural system of the general ectoderm. This distinction appears to be rather an artificial one in view of the continuity and similarity of the two parts of the sensory system, and the nervous elements of the alimentary canal, therefore, are included in this account of the sensory system without further reference to the division which is usually adopted.

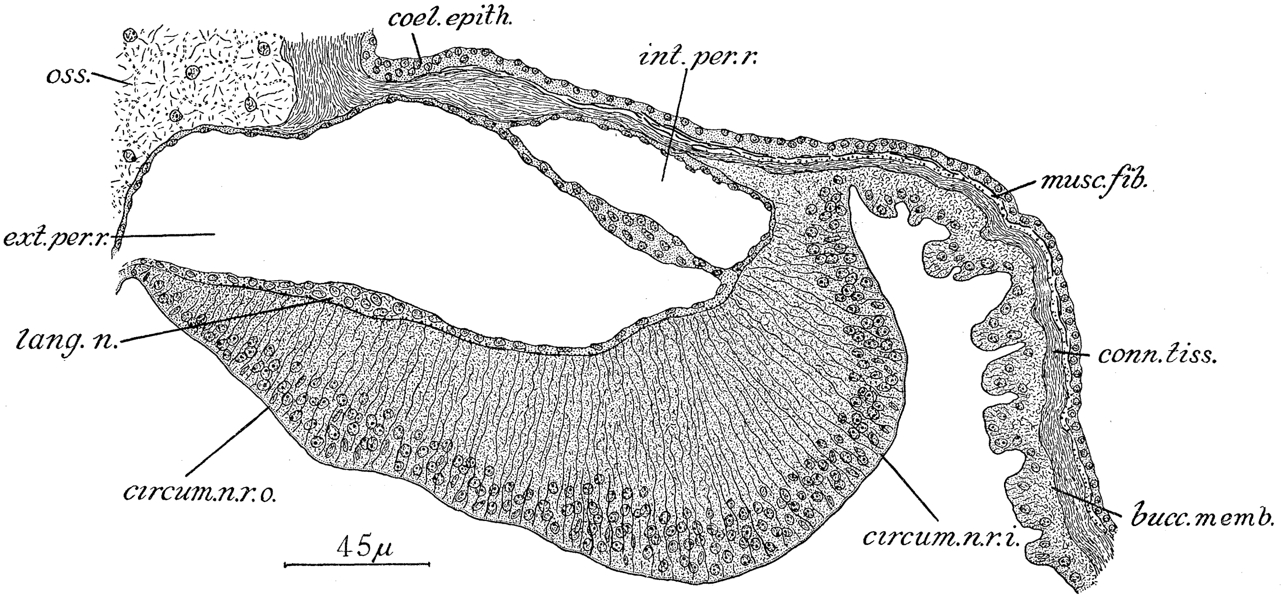

FIG. 20—Transverse section through the circumoral nerve ring and buccal membrane of *Marthasterias glacialis*. Fixed in Susa solution, stained Mallory's triple stain. *bucc. memb.*, buccal membrane ; *circum. n.r.i.*, inner, *circum. n.r.o.*, outer, limb of the circumoral nerve ring ; *coel. epith.*, coelomic epithelium ; *conn. tiss.*, connective tissue ; *ext. per. r.*, outer, *int. per. r.*, inner, perihaemal ring ; *lang. n.*, Lange's nerve ; *musc. fib.*, muscle fibres ; *oss.*, ossicle.

The non-glandular buccal membrane (fig. 20, *bucc. memb.*) is composed of the usual ectodermal elements and has, at its base, a layer of connective tissue (*conn. tiss.*) of considerably greater depth than that which underlies the circumoral nerve ring with which the buccal membrane is continuous. In its nervous organization the buccal membrane is remarkable only in its possession of very few sense cells. The subepithelial plexus is correspondingly limited in extent, and does not appear as a well-defined zone because the fibrils of which it is composed run in all directions and, in section, have an appearance very similar to that of the fibrillated cytoplasm of the epithelial cells.

The oesophagus expands into the globular cardiac portion of the stomach, the two parts, in respect to their sensory system, being almost similar. Fig. 21A shows a part of the cardiac wall in section. The ciliated epithelium has a fibrillated appearance and contains numerous readily staining glandular elements (*m. gl.*), the secretion of which is in the form of spherical refringent droplets, as in the " mulberry " glands of the general ectoderm. The neurofibrillar zone (*n. fibril.*) of the cardiac region of the stomach has a depth of about 6 μ—about one-quarter that of the whole epithelium— and is made up of fibrils which run in all directions. External to the subepithelial plexus are the connective tissue (fig. 21B, *conn. tiss.*), circular muscle (fig. 21A, *circ. musc.*), longitudinal muscle (fig. 21B, *long. musc.*), and coelomic epithelial (fig. 21A, *coel. epith.*) layers, in that order.

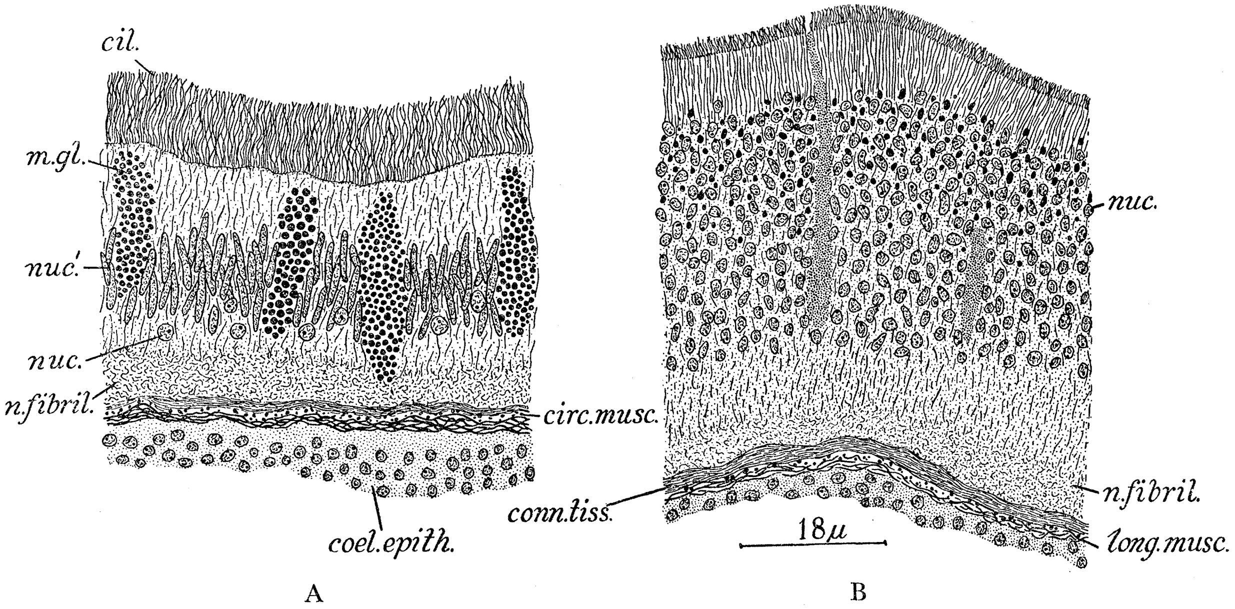

FIG. 21—A, transverse section through a part of the cardiac wall of *Marthasterias glacialis* ; B, transverse section through a portion of the wall of the pylorus. Fixed in Susa solution, stained Mallory's triple stain. *cil.*, *cilia* of the epithelial cells ; *circ. musc.*, circular muscle fibres ; *coel. epith.*, coelomic epithelium ; *conn. tiss.*, connective tissue ; *long. musc.*, longitudinal muscle fibres ; *m. gl.*, " mulberry " gland ; *n. fibril.*, fibrillae of the subepithelial plexus ; *nuc.*, nucleus of epithelial cell ; *nuc′.*, nucleus of sensory cell.

Within the cardiac epithelium two types of nucleus occur. Basally, there are a few round or oval nuclei (fig. 21A, *nuc.*), each with a well-marked nucleolus, while, more centrally placed, there are very many cigar-shaped nuclei (*nuc′*). The chromatin of the latter is distributed as fine granules and there is no nucleolus present. The cigar-shaped nuclei are only to be found in those parts of the gut in which there is developed an extensive neurofibrillar plexus, and one is prompted to suggest, therefore, that some, at least, of them represent the nuclear elements of the sensory cells of the gut epithelium. This suggestion is only made in view of the fact that, although no direct evidence has been obtained of the presence of sensory elements within the gut wall, their presence may be inferred on account of the development of a basal fibrillar plexus. This being so, the nuclei of the sensory elements should be visible in preparations which show, in all other respects, excellent fixation. The rounded nuclei correspond to the rounded nuclei of other parts of the body both in form and number, while the cigar-shaped bodies similarly correspond to the nuclei of the primary sense cells of the general ectoderm (fig. 8B, *s.c.*). There are excellent *a priori* grounds for the suggestion that we have here the visible signs of the presence of numerous sensory elements. Their presence would, indeed, not be unsuspected in an evaginable part of the gut which is capable of being wrapped round the prey during the process of digestion.

The cardiac region of the gut is succeeded by the pyloric sac of pentagonal form, flattened in the oro-aboral plane. In histological detail (fig. 21B), the pyloric sac differs considerably from the cardiac portion of the stomach. Glandular elements are fewer in number, the cilia of the epithelial cells are much shorter and, as regards the nervous system, we find here only a relatively poorly developed subepithelial plexus. The epithelial cells, markedly fibrillated at their ciliated ends, have typical rounded nuclei (*nuc.*), but the cigar-shaped nuclei, so abundant in the cardiac region, are here practically absent. On the basis of the suggestion already put forward, we should regard the wall of the pyloric sac as being less sensitive than the cardiac wall. It has, in consequence, a more poorly developed basal plexus.

The pyloric sac is produced laterally into five radial extensions—the hepatic caeca. Sections through a caecum show that its lateral walls differ considerably from the oral and aboral walls in histological detail. This is clearly shown in fig. 22A, where a portion of the wall of the hepatic caecum, at the junction of the lateral and aboral epithelium, is figured. On the left of the arrow is the lateral epithelium ; its fibrillated cytoplasm, glandular elements, and oval or round vesicular nuclei are essentially similar to the corresponding features of the pyloric wall of the gut. Sensory elements, as represented by the cigar-shaped nuclei, are absent or only few in number, while the subepithelial plexus (*n. fibril.*) is reduced to an extremely thin basal layer or, indeed, may be altogether absent in some parts of the lateral wall of the caecum. The epithelium of the oral and aboral walls (to the right of the arrow), on the other hand, is crowded with the cigar-shaped nuclei (*nuc′.*) and has at its base a well-developed fibrillar plexus. The hepatic caeca are therefore histologically differentiated into extensive laterally placed digestive and absorptive regions and more restricted oral and aboral sensory areas. It is difficult to account for this differentiation on a functional basis. Wolf (1925), as a result of experimental investigation of the righting reaction in *Marthasterias glacialis*, concluded that the mesenteries of the gut and hepatic caeca contain statocysts, and that these are responsible for the initiation of the righting movements. There is, however, no evidence that statocysts do occur in the mesenteries. FRAENKEL (1928) has shown that the removal of the skin and mesenteries does not affect the righting movement, and that the alimentary canal plays no part in the reception of the righting impulses. In view of these findings, no adequate explanation can at present be given of the distribution of the nervous elements within the wall of the caecum.

The remaining part of the gut—the rectum—passes directly aboralwards from the pyloric sac to the anus. Neither the rectum (fig. 22B, *rect.*) nor its lateral diverticulum the rectal sac (*rect. sac.*) calls for much comment. Histologically, the epithelium of this part of the gut is similar to the ectoderm of the aboral surface of the disk, and differs from it only in lacking a cuticle, which latter ends abruptly at the anus (fig. 22B, *an.*). The epithelial wall of the rectum contains few primary sense cells, and has as its characteristic constituent the epithelial cell with its rounded nucleus. The epithelial cells are ciliated, but the cilia are not continued into the rectal sac, the wall of which is otherwise similar to but much thicker than that of the rectum.

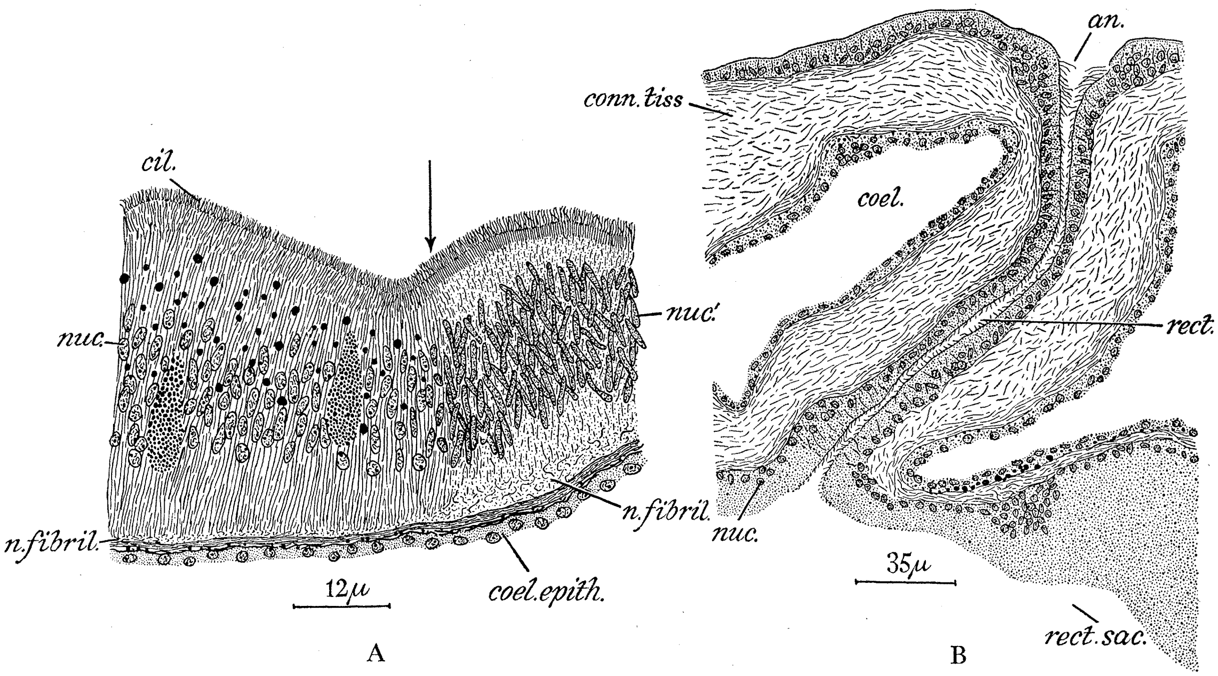

FIG. 22—A, transverse section of a portion of the wall of the hepatic caecum. The part to the left of the arrow is the lateral wall, the part to the right the aboral wall; B, longitudinal section of the disk of *Marthasterias glacialis* passing through the rectum and anus. Fixed in Susa's solution, stained Mallory's triple stain. *an.*, anus; *cil.*, cilia of epithelial cells; *coel.*, perivisceral coelom; *coel. epith.*, coelomic epithelium; *conn. tiss.*, connective tissue; *n. fibril.*, neurofibrillae of the subepithelial plexus; *nuc.*, nucleus of epithelial cell; *nuc'.*, nucleus of sensory cell; *rect.*, rectum; *rect. sac.*, rectal sac.

It may be said, by way of summary, that sensory elements are most abundant in the oesophagus and the cardiac region of the stomach, both of which are eversible and which, in consequence, might be expected to possess a well-developed sensory system. In other parts of the gut, except in the oral and aboral sections of the hepatic caeca, the sensory system is poorly represented both in respect to primary sense cells and subepithelial fibrillae.

V—The Motor System

1—*General Account*

The motor system of *Marthasterias glacialis* is to be identified as local concentrations of neurofibrillae, developed in association with the coelomic epithelium. It will be shown in the following account that there is developed, in addition to the local fibrillar concentrations representing Lange's nerve and the apical nerve of Cuénot (1891), a series of lateral motor nerves, the fibrillae of which extend through practically the whole of the epithelium of the perivisceral coelom, innervating, in their course, parts of the musculature of the arm.

It will be necessary, however, before attempting to describe the distribution of the motor elements in the starfish, to consider, in the first place, the nature of the connexion between the sensory and motor divisions of the nervous system.

Although there is abundant experimental evidence of the continuity of the sensory and motor fibrillae, no morphological evidence has as yet been forthcoming. The sensory and motor elements of the starfish are separated by a layer of connective tissue which, by virtue of its position, has been referred to in this account as the boundary zone. Before the histology and distribution of the motor elements receive consideration it will be necessary to consider whether or not continuity of sensory and motor fibrillae through the boundary zone is possible. For this purpose we have chosen to describe the histology of the part of the boundary zone which lies between the fibrillae of the radial nerve cord and those of Lange's nerve.

A transverse section through the radial cord of *Marthasterias glacialis* (fig. 23) gives the impression that the boundary zone (*b.z.*) is an impenetrable band of connective tissue, effectively isolating the sensory and motor centres one from the other. In horizontal section (fig. 24B), however, it can be seen (*b*) to consist of thickened fibres crossing at right angles, and arranged so as to lie at an angle of about 45° to the longitudinal axis of the cord. The whole arrangement is such as to form a meshwork with large interspaces. On the one side of the net (*a*) lie the longitudinally disposed fibrils of the inner fibrillar zone of the radial nerve cord, and on the other (*c*) the transversely orientated fibrils of Lange's nerve. It has not been possible definitely to establish the existence of a continuous fibrillar system in this region, but it is quite clear that the nature of the boundary zone is such as to permit of communication of sensory and motor fibrils through the meshes of the connective tissue. Moreover, as mingling of sensory and motor fibrillae, by penetration of the boundary zone, can be seen at the point of origin of the lateral motor nerve (*see* p. 153), there is every reason to believe that similar connexions are to be found wherever the sensory and motor systems lie in close proximity.

2—*Lange's Nerve*

Lange's nerve consists of that part of the motor system of the asteroid which is developed in connexion with the radial cord and circumoral nerve ring. Above the radial cord, and divided by the connective tissue septum, is the radial perihaemal cavity (fig. 23, *rad. per. c.*) the wall of which is lined by coelomic epithelium (*coel. epith.*). The fibrillae of Lange's nerve are to be found only in a part of the epithelium and are, in fact, confined to the lateral third of the epithelial tissue overlying the radial cord (fig. 23, *lang. n.*). The cytoplasm of the coelomic epithelium bordering the septum, and overlying the median part of the cord, is granular in appearance, and is clearly demarcated from the fibrillar region of the motor nerve. A longitudinal section through the motor nerve cord (fig. 24A) shows it to consist essentially of a nuclear layer (*nuc.*), adjoining the perihaemal cavity, and a fibrillar zone (*n. fib'.*), at the most 12 μ thick, extending from the basal nuclear layer to the connective tissue of the boundary zone (*b.z.*).

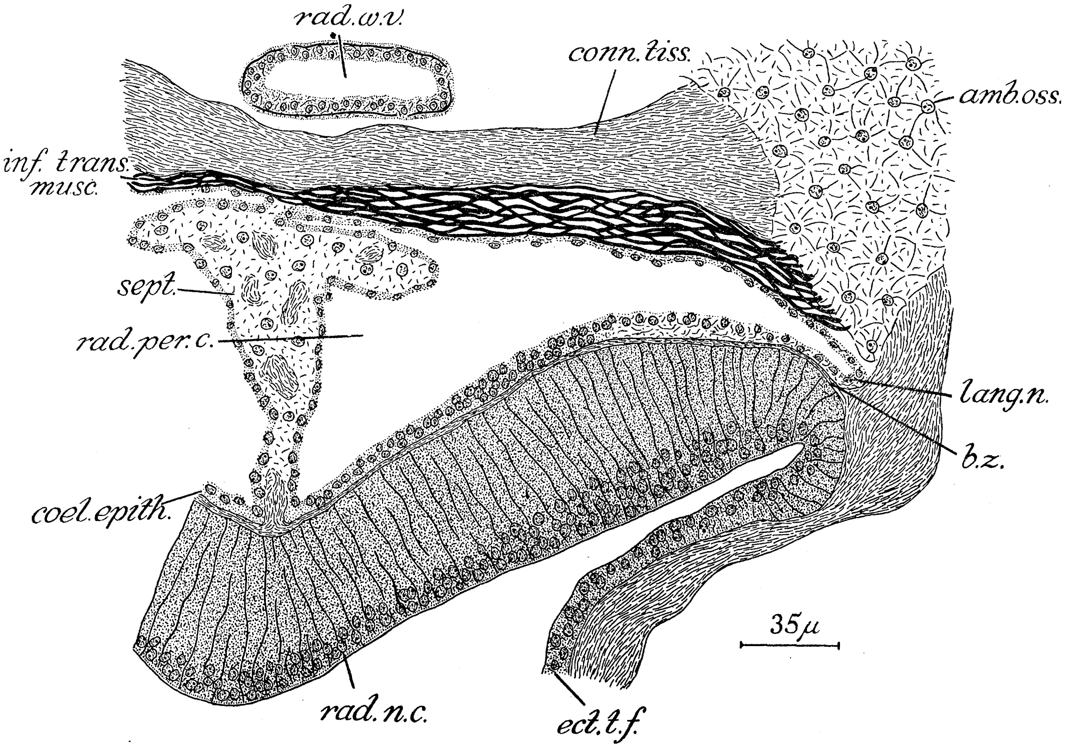

FIG. 23—Transverse section of half of the radial cord of *Marthasterias glacialis* showing the innervation of the inferior transverse muscle by Lange's nerve. Fixed corrosive-acetic, stained Mallory's triple stain. *amb. oss.*, ambulacral ossicle ; *b.z.*, boundary zone ; *coel. epith.*, coelomic epithelium ; *conn. tiss.*, connective tissue ; *ect. t.f.*, ectoderm of the tube foot ; *inf. trans. musc.*, inferior transverse muscle ; *lang. n.*, Lange's nerve ; *rad. n.c.*, radial nerve cord ; *rad. w.v.*, radial water vessel ; *rad. per. c.*, radial perihaemal canal ; *sept.*, septum.

The cellular elements of the coelomic epithelium are of a spherical form ; each contains a rounded vesicular nucleus some 2·5 μ in diameter. The epithelial cell secretes a fibre (*supp. fib'.*) which runs through the neurofibrillae to end at the boundary zone. The fibre has the same staining reactions as the supporting fibre of the sensory system and is probably secreted in much the same way, although it is not possible to determine whether it is a product of extra- or of intracellular secretion. Unlike the supporting fibres of the radial cord, the fibres of Lange's nerve show no definite arrangement, linear or otherwise, when seen in transverse section ; neither do they run at right angles to the surface, but are directed, in most cases, obliquely.

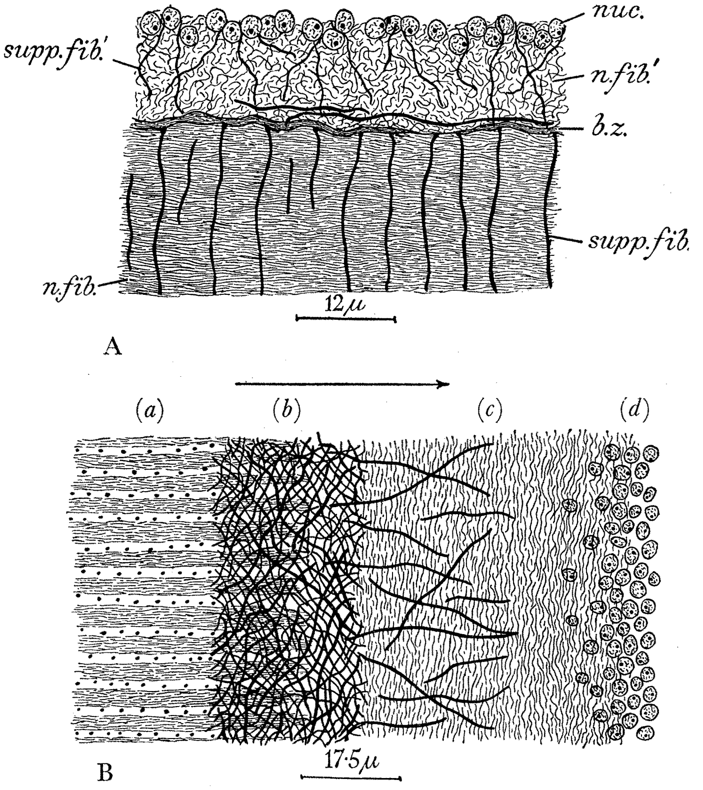

FIG. 24—A, longitudinal section through a part of the radial nerve cord of *Marthasterias glacialis*, showing Lange's nerve (above) separated from the fibrillae of the ectoneural nerve cord by the boundary zone. Fixed in strong F.W.A., stained Mallory's triple stain. *b.z.*, boundary zone ; *n. fib.*, neurofibrillae of ectoneural nerve cord ; *n. fib'.*, neurofibrillae of Lange's nerve ; *nuc.*, nucleus of coelomic epithelial cell ; *supp. fib.*, supporting fibre of ectoneural cord ; *supp. fib'.*, supporting fibre of Lange's nerve. B, oblique horizontal section through the radial ectoneural cord and Lange's nerve. Fixed corrosive-acetic, stained Mallory's triple stain. (*a*) Fibrillae of the inner zone of the ectoneural cord ; the supporting fibres are cut transversely. (*b*) Connective tissue fibres of the boundary zone. (*c*) Fibrillae of Lange's nerve with associated muscle fibres. (*d*) Nuclei of the coelomic epithelial cells. The arrow indicates the longitudinal axis of the nerve cord.

The supporting fibres of the motor nerve are much more fragile than the corresponding fibres of the sensory system, and are coiled and waved to a greater degree. There can, however, be little doubt that they are precisely similar in function to the supporting fibres of the better defined ectoneural system, and that their more feeble development is correlated with the small amount of fibrillar substance present in the motor nerve cord.

The neurofibrillae of Lange's nerve are not orientated as definitely along any one axis as are the fibrillae of the sensory system, neither are they divided into zones. In general, they tend to be set at right angles to the sensory fibrillae (fig. 24B), and are therefore ordinated transversely to the longitudinal axis of the arm. Cellular elements are to be found in some number among the fibrillae, but a definite opinion cannot be given as to whether these are ganglion cells or epithelial cells which have migrated into the fibrillar substance in much the same way as has been seen to occur in the epithelial elements of the ectoneural system.

The only other elements present in the fibrillar zone of Lange's nerve are muscle fibres. They run along the length of the cord and lie almost in contact with the connective tissue of the boundary zone. By their contraction they assist in the flexure of the arm.

At a point opposite the insertion of the inferior transverse muscle (fig. 23, *inf. trans. musc.*) into the ambulacral ossicle there is a lateral extension of Lange's nerve (*lang. n.*). The fibrillae of the nerve twig become flexed in an aboral direction and run in contact with the oral surface of the muscle. The inferior transverse muscles of *Marthasterias glacialis* are thus innervated at their two extremities by segmentally disposed branches of Lange's nerve. It is not possible to follow the fibrils any distance over the muscle fibres, or to see how many of the individual fibres of a muscle are directly innervated. The inferior transverse muscle is the only muscle to receive its nerve supply from the radial cords of the motor nerve. In the disk, Lange's nerve is to be identified as a single fibrillar thickening (fig. 20, *lang. n.*), situated above the outer and longer limb of the " V "-shaped circumoral ring, and present only in the positions of the five interradii. In histological detail it resembles the radial motor nerve, but so far as my preparations show, it does not serve as a source of innervation of any of the disk musculature, consequently it is more probably to be regarded as a centre uniting the radial motor cords of adjacent arms.

3—*The Lateral Motor Nerves*

The ambulacral groove of the starfish arm is supported by the ambulacral ossicles, closely applied one to the other so as to form a solid roof which, when seen in section (fig. 25, *amb. oss.*), is in the form of an inverted " V ".

The ossicles of the two limbs of the " V " adjoin in pairs, medianly, each pair being connected orally by an inferior transverse (*inf. trans. musc.*) and aborally by a superior transverse muscle (*sup. trans. musc.*). Laterally, the ambulacral ossicles abut on to the adambulacral ossicles (*adamb. oss.*) with which they alternate. Paired muscles—the lateral transverse muscles (*lat. trans. musc.*)—run between the adambulacral and ambulacral ossicles of each side of the arm ; they are inserted into the centre of the articulating surfaces of the adambulacral muscles and diverge from this source to be attached, at their upper ends, one to each of the adjoining ambulacral ossicles. At points corresponding to the mid-line of each of the adambulacral ossicles and, therefore, to the adjoining surfaces of adjacent ambulacral ossicles, the ectoderm exhibits a considerable local thickening (figs. 25, 27, *n. fibril. exp.*). Each thickening is placed so as to lie a little to the side of the more laterally placed tube feet on each side of the ambulacral groove and is situated opposite the space between the adambulacral and ambulacral ossicles, across which the lateral transverse muscles run. From each local expansion of the ectoderm there runs inwards into the perivisceral coelom, through the space formed by the divergence of the lateral transverse muscles, a motor nerve, henceforth to be referred to as the lateral motor nerve (figs. 25, 27, *lat. m.n.*). It will be seen (fig. 26, *lat. m.n.*) that the paired lateral motor nerves are segmentally arranged and correspond in position to the adambulacral ossicles and to the ambulacral pores through which run the channels connecting the cavities of the tube feet and their ampullae.

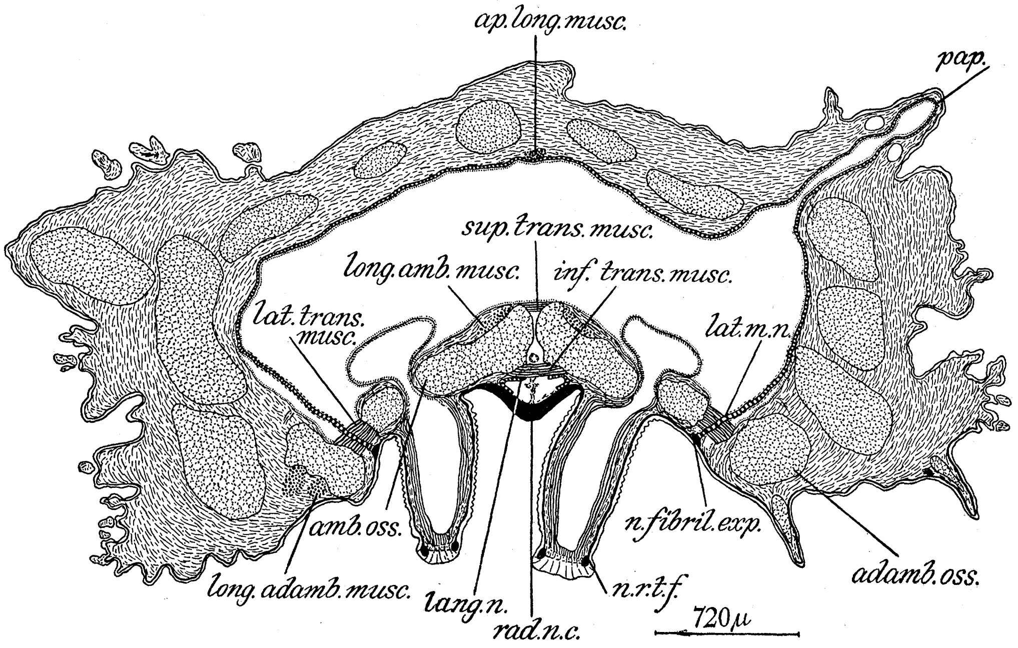

FIG. 25—Diagrammatic figure of a transverse section through the arm of *Marthasterias glacialis*. Much of the detail has been omitted. Black shaded areas indicate expansions of the fibrillar zone of the sensory system ; black and white broken lines represent the motor system. *adamb. oss.*, adambulacral ossicle ; *amb. oss.*, ambulacral ossicle ; *ap. long. musc.*, apical longitudinal muscle ; *inf. trans. musc.*, inferior transverse muscle ; *lang. n.*, Lange's nerve ; *lat. m.n.*, lateral motor nerve ; *lat. trans. musc.*, lateral transverse muscle ; *long. adamb. musc.*, longitudinal adambulacral muscle ; *long. amb. musc.*, longitudinal ambulacral muscle ; *n. fibril. exp.*, expansion of the subepithelial neurofibrillar plexus at the base of the lateral motor nerve ; *n.r.t.f.*, nerve ring of the tube foot ; *pap.*, papula ; *rad.n.c.*, radial nerve cord ; *sup. trans. musc.*, superior transverse muscle.

Fig. 27 shows the local lateral thickening of the ectoderm and the root of the motor nerve in some detail. The thickening is formed entirely by the expansion of the fibrillar substance of the ectodermal subepithelial plexus and not from any special development of the epithelial layer. At the base of the fibrillar expansion, the connective tissue of the boundary zone (*b.z.*) is greatly thickened and some of its fibres bend round so as to run internally in conjunction with the motor fibrillae. In the account of Lange's nerve it was pointed out that the nature of the boundary zone was such as to permit of contact of sensory and motor fibrillae ; such a connexion has been seen to occur at the root of the lateral motor nerve. Some few of the sensory fibrillae of the subepithelial ectodermal plexus penetrate the boundary zone and join the motor fibrils to be directed internally towards the coelomic epithelium of the perivisceral cavity.

Of the detailed histology of the motor nerve itself, one can say very little. The simple non-beaded neurofibrillae are intermingled with connective tissue fibres, and numerous nuclei are to be found both external and internal to the substance of the well-defined nerve tract. It has not been found possible to determine whether these nuclei are to be attributed to ganglion elements or to the non-nervous cells of the connective tissue or coelomic epithelium.

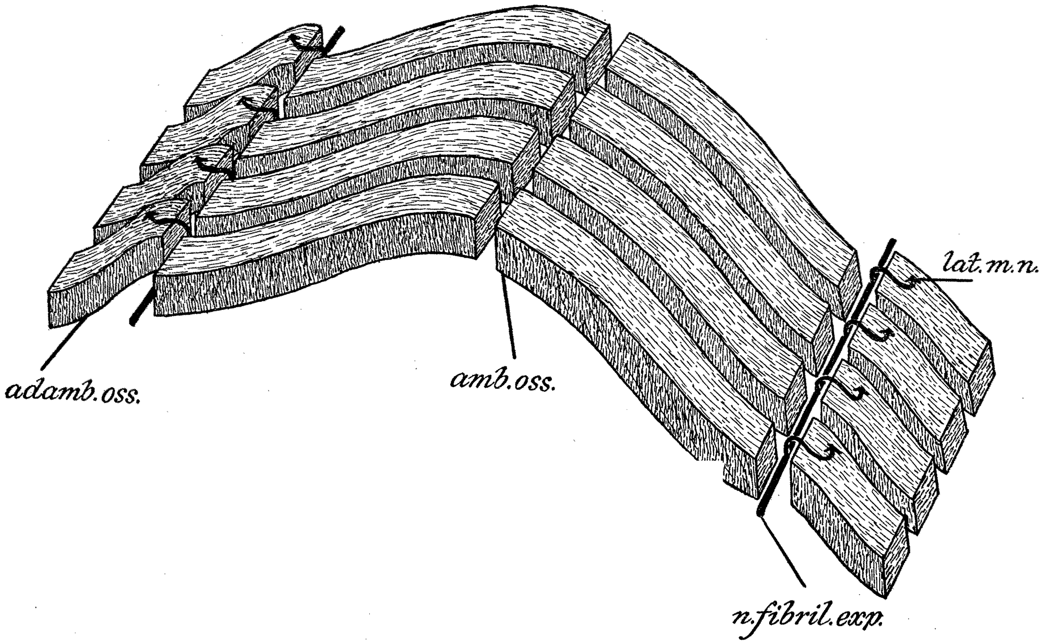

Fig. 26—Diagram illustrating the " segmental " arrangement of the lateral motor nerves and the position of the root of each nerve relative to the ambulacral and adambulacral ossicles. *adamb. oss.*, adambulacral ossicle ; *amb. oss.*, ambulacral ossicle ; *lat. m.n.*, lateral motor nerve ; *n. fibril. exp.*, expansion of the subepithelial neurofibrillar plexus associated with motor nerve development.

The full extent of the lateral motor nerve is best shown in fig. 25—a diagrammatic figure of a transverse section through the arm of *Marthasterias glacialis*. In the first part of its course the nerve is quite separate from the coelomic epithelium, but later it comes to lie within the epithelial lining of the perivisceral cavity. The neurofibrillar substance is to be seen only with difficulty where the nerve is associated with the epithelium, but there is very good evidence, as will later be shown, that the whole of the coelomic wall, except where it overlies the ambulacral ossicles, is innervated by fibrils from the lateral motor nerve.

A short distance from its source the nerve sends out lateral twigs which innervate the lateral transverse muscles (fig. 27, *lat. trans. musc.*), the neurofibrils running along the length of the muscle fibres. As far as can be seen in the preparations studied, no other muscles are innervated by the lateral nerve until its fibrils enter the coelomic epithelium. In this latter part of their course one may reasonably assume that they innervate the outer circular and inner longitudinal muscles of the arm, which muscles are to be found within the epithelial lining of the perivisceral coelom.

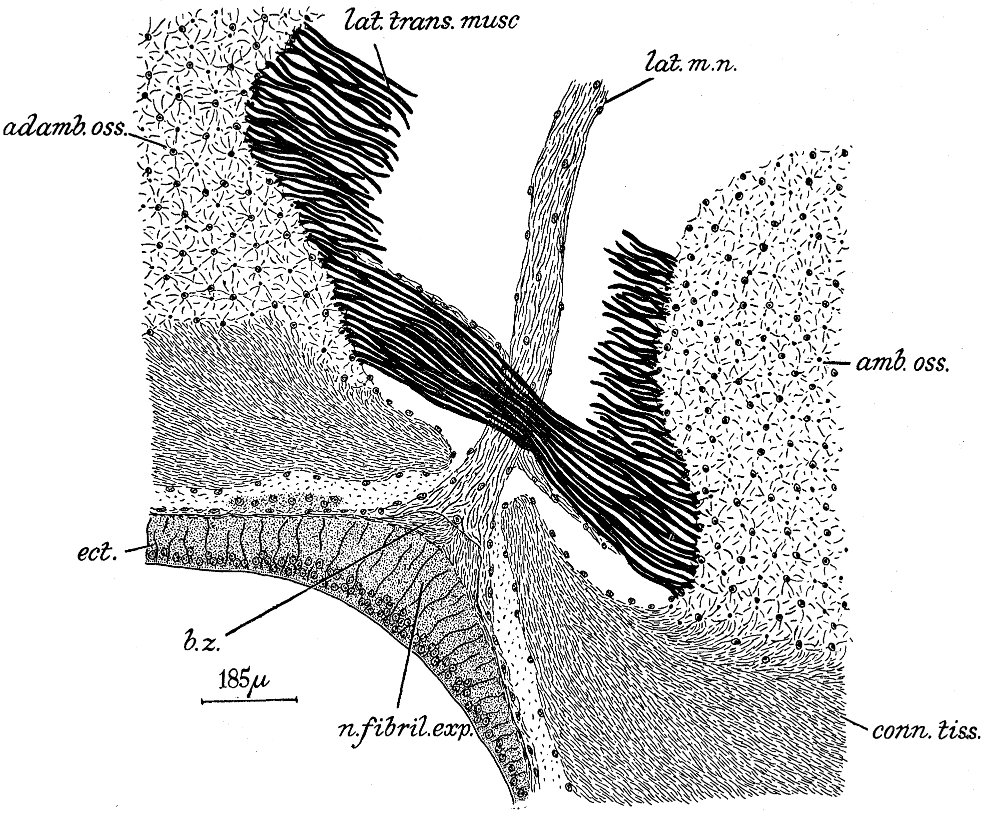

FIG. 27—A part of a transverse section through the arm of *Marthasterias glacialis*, lateral to the tube feet, showing the origin of the lateral motor nerve and the innervation of the lateral transverse muscle. Fixed corrosive-acetic, stained Mallory's triple stain. *adamb. oss.*, adambulacral ossicle ; *amb. oss.*, ambulacral ossicle ; *b.z.*, boundary zone ; *conn. tiss.*, connective tissue ; *ect.*, ectoderm ; *lat. m.n.*, lateral motor nerve ; *lat. trans. musc.*, lateral transverse muscle ; *n. fibril. exp.*, expansion of the subepithelial neurofibrillar plexus at the point of origin of the lateral motor nerve.

Although motor fibrils cannot easily be discerned in all parts of the wall of the perivisceral cavity, they are clearly to be seen in the extreme aboral wall where the longitudinal musculature of the arm is especially thickened as the apical longitudinal muscle (fig. 25, *ap. long. musc.*). Here, as in all parts of the coelomic wall where they are present, the fibrils run between the epithelial layer and the musculature, and pursue a circular course round the arm. These fibrils constitute the apical nerve of CUÉNOT (1890, 1891), the existence of which, in *Asterias rubens*, was denied by MEYER (1906). An apical fibrillar plexus is certainly present in *Marthasterias glacialis*, but there is no reason for assuming that it represents a discrete system. We have, in *Marthasterias glacialis*, a condition where not merely the extreme aboral but the whole of the lateral and aboral walls of the perivisceral coelom are innervated, and in which the apical nerve must be regarded merely as a local condensation of fibrillae developed in consequence of local muscle development. The source of innervation is the lateral motor nerve and the muscles innervated are the lateral transverse muscles, the circular and longitudinal muscles of the arm—including the apical musculature—and the feebly developed muscles which serve for the retraction of the papulae.

No reference has been found in the literature on the subject of the asteroid nervous system to the lateral motor nerve or to any tissue occupying its position ; neither, as far as I am aware, has any previous author referred to the thickenings of the ectodermal subepithelial plexus from which the motor nerves take their origin. Sections have been made of the arm of several species of starfish, including *Asterias rubens*, *Solaster papposus*, *Astropecten irregularis*, *Palmipes membranaceus*, *Asterina gibbosa*, and *Leptasterias mülleri*. The lateral motor nerve is present in them all and has a distribution similar to that described in *Marthasterias glacialis*. There is, it would appear, very good reason to believe that the lateral motor nerve is as characteristic of the asteroid nervous system as is Lange's nerve, and it is certainly a more important constituent if one is to judge by the extent of its distribution.

4—*Other Motor Centres*

From what has already been stated in the accounts of Lange's nerve and the lateral motor nerve, it will have been noted that two of the characteristics of motor nerve development are, firstly, that the fibrillar system is developed in the neighbourhood of the muscles to be innervated and, secondly, that the root of the motor nerve is associated with an expansion of the sensory fibrillar plexus. For Lange's nerve, the muscle to be innervated is the inferior transverse muscle, and the sensory fibrillar system is that of the radial cord ; while the lateral motor nerve arises close to the lateral transverse muscle, and is associated with a local expansion of the subepithelial plexus of the general ectoderm. If, then, we should find other such local expansions, we should be justified in searching for related motor extensions, particularly if the sensory fibrillar expansions were to be found in close proximity to a part of the musculature of the body. This combination of circumstances does actually occur in parts of the body of *Marthasterias glacialis*, other than those already mentioned.

The adambulacral muscles of each side of the arm are connected by paired longitudinal adambulacral muscles (fig. 25, *long. adamb. musc.*). A parasagittal section of the arm (fig. 28), passing through the longitudinal adambulacral muscles, shows that the subepithelial neurofibrillar plexus (*n. fibril. exp.*) opposite the muscles and between the adambulacral spines is especially thickened, and that the muscle fibres, in consequence, abut directly on to the fibrillae of the subepithelial plexus. No definite motor tract has been seen in this region, but as the conditions here are precisely those associated with motor nerve development in other parts of the body the suggestion is made that we may have, at this point, a separate and distinct centre for the innervation of the longitudinal adambulacral musculature.

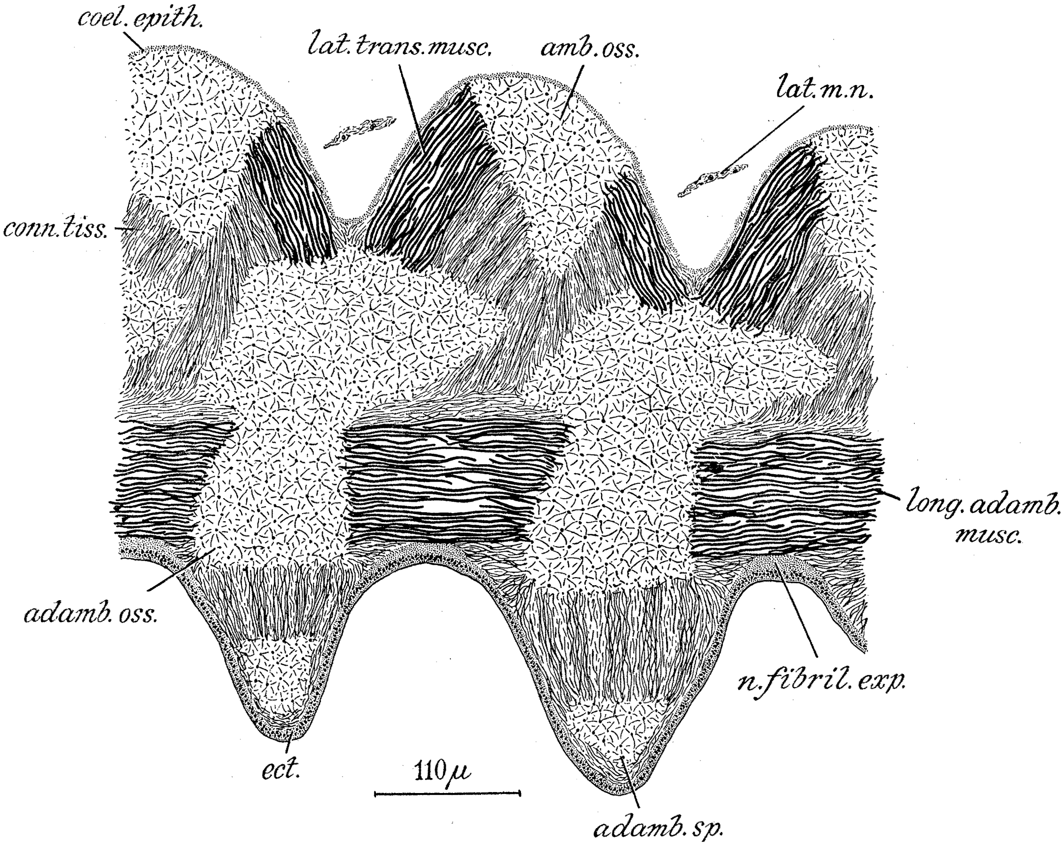

FIG. 28—A part of a parasagittal section of an arm of *Marthasterias glacialis* through the line of junction of the adambulacral and ambulacral ossicles. Fixed in Susa solution, stained Mallory's triple stain. *adamb. oss.*, adambulacral ossicle ; *adamb. sp.*, adambulacral spine ; *amb. oss.*, ambulacral ossicle ; *coel. epith.*, coelomic epithelium ; *conn. tiss.*, connective tissue ; *ect.*, ectoderm ; *lat. m.n.*, lateral motor nerve ; *lat. trans. musc.*, lateral transverse muscle ; *long. adamb. musc.*, longitudinal adambulacral muscle ; *n. fibril. exp.*, expansion of the subepithelial fibrillar plexus, probably associated with the innervation of the longitudinal adambulacral musculature.

Apart from this postulated local innervation of the longitudinal adambulacral muscles and a similar, but better defined, direct innervation of the muscles of the pedicellariae, there appear to be no indications of local fibrillar development in the neighbourhood of other sets of muscles either within the arm or disk of *Marthasterias glacialis*. There are, in fact, many muscles the centres of innervation of which cannot even be conjectured. Among these we may include the superior transverse and the longitudinal muscles of the ambulacral ossicles, the muscles of the tube feet, the circular muscles of the disk, and the muscles connecting the odontophore and oral plate. It is certain that no well-defined motor tracts innervate any of these muscles, but the possibility of innervation by tracts composed of but few fibrillae which would not easily be demonstrated by the less specific staining methods must not be overlooked.

At present, however, we must limit the number of motor centres in the arm of the starfish *Marthasterias glacialis* to the three described above, namely, Lange's nerve, the lateral motor nerve, and the local centre for the innervation of the longitudinal adambulacral muscles. Of these, only the lateral motor nerve is at all extensive and of more than local significance.

The disposition of the motor centres is such as to suggest that stimuli perceived by the *aboral* surface of the starfish arm will be conveyed as impulses through the *lateral motor nerves*, while response to stimulation of the *oral* surface will be effected through the *sensory motor reflexes of the tube feet*, and through *Lange's nerve* via the radial nerve cord. Without attempting more accurately to define the principal reflex arcs, we may distinguish, therefore, between the " aboral reflex ", through the lateral motor nerves, and the " oral reflex ", as effected through a number of motor paths, including Lange's nerve.

VI—The Sensory-Motor System (The Pedicellariae)

We have included in our account of the motor system of the asteroid only those centres which are concerned with the innervation of the general musculature of the body of the animal. An isolated arm or even a piece of a starfish arm is capable of autonomous and purposeful movement, but the motor reactions of a single arm of an uninjured animal are subject to inhibitory impulses which may modify the behaviour of the part for the better coordination of movement of the whole animal. For the most part it is the tube feet which are subject to these inhibitory impulses. The tube feet must therefore be innervated by neurofibrillae which are in connexion with the coordinating centres of the radial cord and nerve ring. Paine (1929), however, has shown that the tube feet of the asteroid are autonomous organs. As such they must have sensory-motor reflexes independent of the central nervous system. It has not been found possible during the course of this work to establish the presence of these sensory-motor neurofibrillar arcs on a morphological basis. In the pedicellariae, however, definite indications of a motor system are to be seen.

Jennings (1907) has analysed the behaviour of the straight and crossed pedicellariae of the starfish *Asterias forreri* in some detail. He finds that, occasionally, a single mechanical stimulus and, invariably, repeated stimuli applied to a spine or to the neighbouring ectoderm will cause an uprising of the pad of tissue at the base of the spine. The crossed pedicellariae, which are grouped on the pad, open and wave about, the valves snapping repeatedly without the application of further stimuli. As soon as a pedicellaria touches the object which is causing mechanical stimulation, it snaps its valves on it and retains the foreign body within its grasp. Neighbouring pedicellariae bend towards the cause of the disturbance and, after touching it, seize it by closure of the jaws. The impulse to open the valves can, apparently, be transferred to neighbouring pedicellariae, while the impulse required to close them and to keep them closed is not so conducted. In this latter case, in fact, in order for closure to occur, each valve must be separately stimulated. There is then, in the " opening " reaction and its transference to neighbouring pedicellariae, evidence of nervous connexions outside the body of the pedicellaria, while in the " closing " reaction, which is not transmitted from one pedicellaria to another, there is evidence of an independent sensory-motor system within the body of the organ. JENNINGS (1907) found, moreover, that in the absence of inhibitory impulses stimulation of the inside of the valve caused closure, while stimulation of the outer surface caused opening of the valves. As a result of JENNING's work it is established that while many of the movements of the pedicellaria are coordinated with those of its neighbours, each individual pedicellaria is capable of a functional autonomy ; which autonomy, we may add, is determined by the independent sensory-motor system of the organ. We are aided in our search for the nervous reflex arcs by the knowledge that closing or opening are respectively conditioned by stimulation of the inside or outside of the valve. With these facts in mind we are in a position better to appreciate the morphological features of the straight and crossed pedicellariae of *Marthasterias glacialis*, particularly as regards the musculature and its innervation.

1—*The Straight Pedicellariae*

The straight pedicellariae are usually solitary, and are restricted in their distribution to the sides of the disk and to the margins of the ambulacral grooves, where they are borne on the adambulacral spines. In specimens of *Marthasterias glacialis* with an arm length of 25 mm., the straight pedicellariae, which are sessile, may attain a length of one-third of a millimetre. In longitudinal sagittal section (fig. 29A), the pedicellaria is seen to consist of two equal and similar blades, each of which is supported by an ossicle (*bl. oss.*)—the calcareous material of which has been dissolved away during the process of decalcification—while at the base of the two blades there is a median ossicle, the basal piece (*bas. oss.*). The ossicles of the blades of the pedicellariae lie, in their basal extremities, one on each side of the basal piece, and such muscles as are to be found within the pedicellaria have their insertions, at one end, in the basal piece and, at the other, in the ossicles of the blade.

The whole of the external surface of the pedicellaria is clothed with an ectodermal layer (*ect.*), composed for the most part of epithelial cells but containing, in addition, sensory and glandular elements. Three pairs of unstriped muscles are responsible for the opening and closing of the blades ; two pairs act as adductors, a single pair as abductors. The inner adductor muscle (*in. add. musc.*) of each blade is inserted, basally, into the median portion of the basal piece and has its distal attachment on the inner surface of the blade ossicle, about one-third of the way from its base. Just lateral to the inner adductor is the outer adductor muscle (*out. add. musc.*). Its basal insertion is lateral to that of the inner adductor, but on account of its greater length by comparison with the latter muscle, the outer adductor has its distal attachment at the extreme free end of the blade. The abductor muscle (*abd. musc.*) is distinguished from the adductors by the greater fineness of its fibres. It is attached to the outer surface of the blade ossicle, near the base of the latter, and to the edge of the basal ossicle, laterally to the outer adductor muscle. In addition to these muscles there are isolated fibres running from the ossicles of the arm or disk to the ossicles of the pedicellariae. By their contraction they effect the waving movements of the pedicellariae.

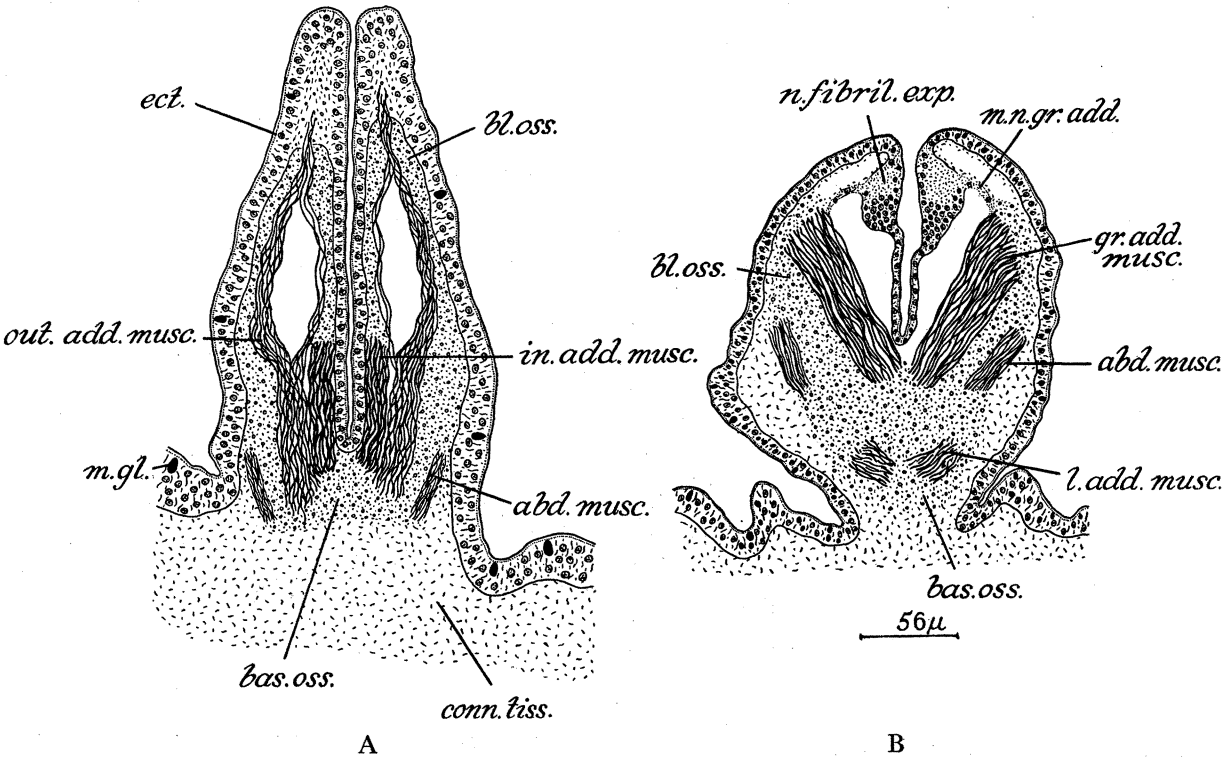

FIG. 29—Longitudinal sections through A, a straight pedicellaria, B, a crossed pedicellaria, of *Marthasterias glacialis*. Fixed in Susa solution, stained Mallory's triple stain. *abd. musc.*, abductor muscle ; *bas. oss.*, basal ossicle ; *bl. oss.*, ossicle of the blade ; *conn. tiss.*, connective tissue ; *ect.*, ectoderm ; *gr. add. musc.*, greater adductor muscle ; *in. add. musc.*, inner adductor muscle ; *l. add. musc.*, lesser adductor muscle ; *m. gl.*, " mulberry " gland ; *m.n. gr. add.*, motor nerve innervating the greater adductor muscle ; *n. fibril. exp.*, expansion of the subepithelial neurofibrillar plexus associated with motor nerve development ; *out. add. musc.*, outer adductor muscle.

Each individual muscle fibre is unbranched and runs without a break between its points of insertion. In transverse section (fig. 30) the inner adductor muscle (*inn.*

add. musc.) is roughly dumb-bell shaped, the outer adductor (*out. add. musc.*), oval in section, fitting into its outer concave surface. The fibres of the inner adductor are much thicker and more compacted than those of the outer adductor muscle and, moreover, have a rounded outline, whereas the individual fibres of the outer adductor are roughly cuboid in section. These differences are constant whether the blades are open or closed and are not, therefore, dependent on the degree of contraction of the muscle. It is possible that the morphological differentiation is reflected functionally in a difference in tone of the two sets of muscles, and that one set represents rapidly contracting muscle of the tetanus type and the other, slowly contracting tonus muscle, enabling the blades to retain a grip on captured prey for relatively long periods.

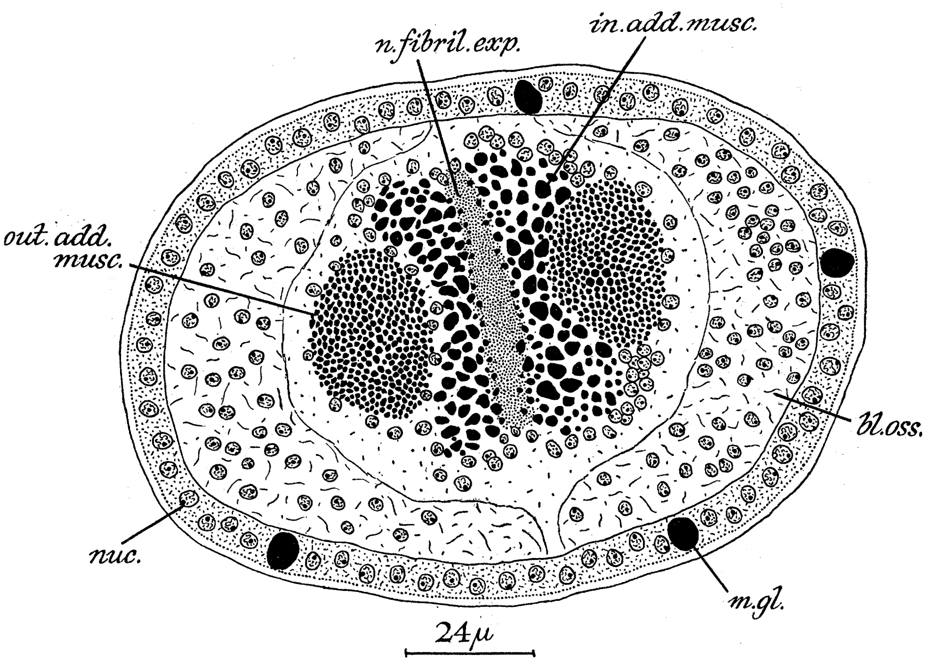

FIG. 30—Transverse section through a straight pedicellaria near the base of the blade ossicles. Fixed in Susa solution, stained Mallory's triple stain. *bl. oss.*, ossicle of the blade ; *in. add. musc.*, inner adductor muscle ; *m. gl.*, " mulberry " gland ; *n. fibril. exp.*, expansion of the subepithelial neurofibrillar plexus associated with the innervation of the inner adductor muscles ; *nuc.*, nucleus of epithelial cell ; *out. add. musc.*, outer adductor muscle.

Transverse sections through a straight pedicellaria at the level of the inner adductor muscle (fig. 30) show that in this region the fibrillar plexus at the base of the ectoderm of the inner surface of the blade is particularly well developed (*n. fibril. exp.*) and that the fibrillae are in contact with some, at least, of the fibres of the inner adductor muscle. A similar expansion of the subepithelial fibrillar plexus is to be seen at the base of the outer side of the blade, opposite the abductor muscle (fig. 31, *n. fibril. exp.*).

Fibrils from this plexus enter the substance of the abductor muscle and run parallel and in contact with the individual fibres. It has, unfortunately, not been found possible to discern any neurofibrillae within or near the outer adductor muscle, although it is possible that the nerve supply to this muscle is in the form of isolated fibrils which would not readily be demonstrated by the methods of staining adopted during the course of this work. As far as can be made out, therefore, each straight pedicellaria has four centres for the innervation of its musculature. The two supplying the inner adductor muscles are situated on the inner surface of the blade, the two innervating the abductors are on its outer surface. It may reasonably be assumed that impulses resulting from stimuli received by the sensory elements of the ectoderm of the outer surface of the pedicellaria would be conveyed to the adjacent motor centre ; contraction of the abductor muscle and opening of the blade would follow. Similarly, stimulation of the inner surface of the blade would cause contraction of the inner adductor muscle and the blade would be closed. This inference is in accord with the experimental findings of JENNINGS, to which reference has already been made, and there can be little doubt that the four local nerve centres comprise the sensory-motor system responsible for the autonomous reactions characteristic of the pedicellariae.

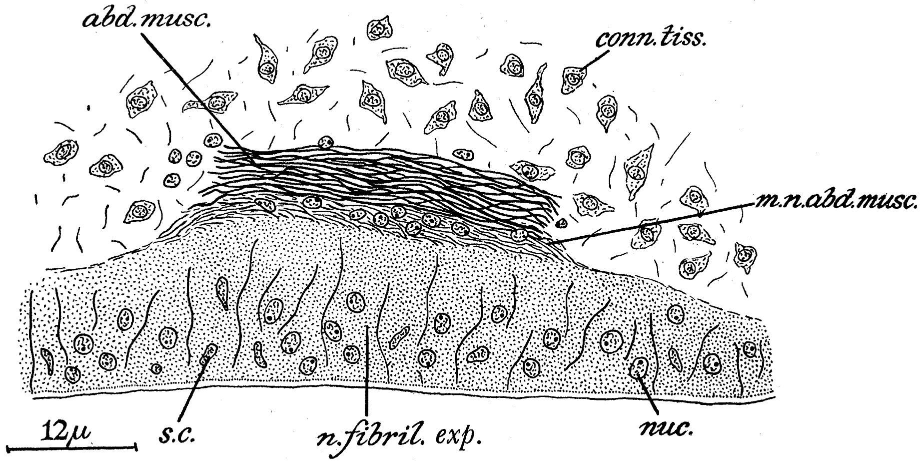

FIG. 31—A part of a longitudinal section through a straight pedicellaria showing the innervation of the abductor muscle. Fixed in Susa solution, stained Mallory's triple stain. *abd. musc.*, abductor muscle ; *conn. tiss.*, connective tissue ; *m.n. abd. musc.*, motor nerve innervating the abductor muscle ; *n. fibril. exp.*, expansion of the subepithelial neurofibrillar plexus associated with motor nerve development ; *nuc.*, nucleus of epithelial cell ; *s.c.*, nucleus of sensory cell.

2—*The Crossed Pedicellariae*

Crossed pedicellariae are present in much greater numbers on the surface of the disk and arms of *Marthasterias glacialis* than are the straight pedicellariae. Unlike the latter they are not isolated, but are aggregated at the base of the spines of the lateral and aboral surfaces of the animal. They are sessile and are only of about two-thirds the length of the straight pedicellariae (fig. 29B). The skeletal elements of a crossed pedicellaria are three in number, there being one ossicle (*bl. oss.*) to each blade and a single basal piece (*bas. oss.*), to either side of which the base of the blade ossicle is applied. The proximal ends of the latter are produced into " handles " which cover and project beyond the opposite sides of the basal piece. The arrangement has been compared to a pair of scissors, in which the blade ossicles represent the separate blades and the basal piece the fulcrum, about which the blades are pivoted. Movement of the blades is effected by three pairs of muscles which have a disposition rather different from that of the musculature of the straight pedicellaria. As in the latter, there are two pairs of adductor muscles and a single pair of abductors. The abductor muscles (*abd. musc.*) are placed, as in the straight pedicellariae, so as to run from the outer face of the blade ossicle to the lateral margin of the basal ossicle. One pair of adductors—the greater adductors (fig. 29B, *gr. add. musc.*)—have their proximal insertions almost in the mid-line of the basal ossicle and their distal attachments in the distal ends of the blades. The lesser adductor muscles

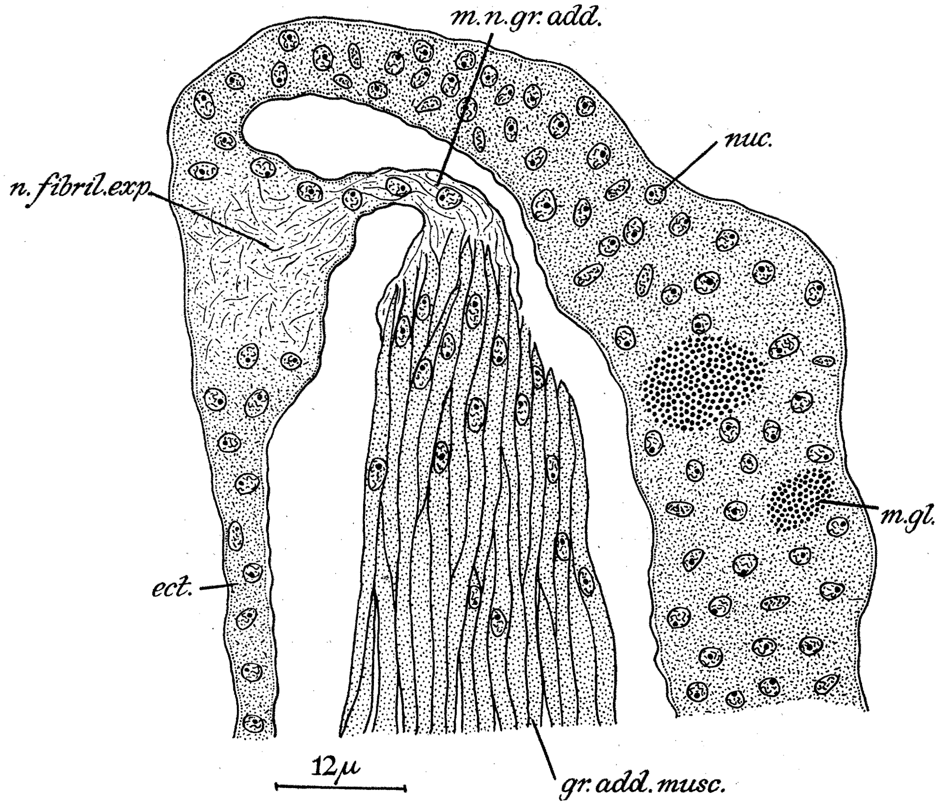

FIG. 32—A part of a longitudinal section through a crossed pedicellaria showing the innervation of the greater adductor muscle. Fixed in Susa solution, stained Mallory's triple stain. *ect.*, ectoderm ; *gr. add. musc.*, greater adductor muscle ; *m. gl.*, " mulberry " gland ; *m.n. gr. add.*, motor nerve innervating the greater adductor muscle ; *n. fibril. exp.*, expansion of the sub-epithelial neurofibrillar plexus associated with motor nerve development ; *nuc.*, nucleus of epithelial cell.

(*l. add. musc.*) are inserted into the substance of the basal ossicle and run almost at right angles to the longitudinal axis of the pedicellaria to be attached to the " handle " of the blade covering the opposite side of the basal ossicle. By their contraction they bring the " handles " of the blades together and therefore close the blades.

The innervation of the musculature of the crossed pedicellaria has been determined only very incompletely. No special centres for the innervation of the abductors or for the lesser adductors have been found, but an expansion of the subepithelial plexus of the ectoderm of the inner surface of the blade, in its distal extremity (figs. 29B, 32, *n. fibril. exp.*), has been identified as the centre from which fibrillae run to the muscle fibres of the greater adductor muscle. Fig. 32 shows this centre in some detail. The ectodermal thickening in which the motor fibrillae have their origin is produced internally into a strand of tissue (*m.n. gr. add.*) within which the fibrillae run. The latter enter the substance of the adductor muscle at its distal extremity and are the sole visible source of innervation of the muscle, the individual fibres of which, each with an oval vesicular nucleus, are figured.

Since the crossed pedicellariae exhibit a behaviour essentially similar to that of the straight pedicellariae in regard to their opening and closing reactions by stimulation of the outer and inner surfaces of the blades respectively, it would seem probable that there is, in addition to the centre responsible for the transference of impulses to the adductor muscle, a nerve centre on the outside of the blade the purpose of which would be, as in the straight pedicellaria, to innervate the abductor muscle.

Even though morphological evidence of the presence of more than one motor centre in the crossed pedicellaria is, at the moment, lacking, enough has been discovered to indicate that the similar behaviour of the two types of pedicellaria is to be correlated with similar methods of innervation of the musculature, and that the powers of functional autonomy of the pedicellariae, as defined by JENNINGS, are to be ascribed to the possession of these centres.

VII—RÉSUMÉ AND DISCUSSION

The generally accepted view of the morphology of the echinoderm nervous system, as stated in present-day textbooks, is that the system is divisible into three distinct parts—the ectoneural, the hyponeural, and apical divisions. Although from a purely morphological standpoint the three parts would appear to exist as discrete fibrillar systems, it is recognized both by morphologists and physiologists that there can be no real separation, for the ectoneural system, of a sensory nature, must necessarily be in connexion with the hyponeural and apical systems which are motor, or predominately motor, in function.

Of the three divisions, the ectoneural is the most constantly occurring, for it appears in its entirety in all classes save the crinoids where the circumoral ring is lacking.

The hyponeural fibrillar system (Lange's nerve in the asteroid) is not so constant in its form or degree of development as is the ectoneural system. It is best developed in the crinoids and ophiuroids where it consists of a closed ring from which the radial nerves to each arm emerge in the form of paired ridges. In the asteroid the hyponeural nerve ring is incomplete, being developed in the interradial positions only, while in the Holothuroidea it is altogether absent, and although the ring is present in the Echinoidea, there are no radial extensions along the ambulacra.

Still more variable is the apical system. In the crinoid it is greatly developed and constitutes the most important nerve centre of the body. Emanating from the nervous wall of the chambered organ are five or ten interradial nerves which branch to form a complicated plexus. Radial nerves extend distally from the plexus into the arms and pinnules. The Asteroidea are the only other echinoderms in which an apical strand, definitely to be identified as consisting of nervous tissue, is present, but the apical nerve of the asteroid, as will later be shown, is not in any way homologous with that of the crinoid.

The question now arises as to the extent to which comparison of the sensory and motor divisions of the nervous system of the various classes of the phylum can be made. Little difficulty is to be found in tracing the homologies of the sensory (ectoneural) system. The circumoral ring and radial nerves are found in all echinoderms except the crinoids, where the nerve ring may be poorly developed or entirely lacking, in which latter case the fibrillae of the radial cord innervate the oesophagus directly. In the crinoids the apical system provides the functional sensory system, the radial ectoneural cord being purely subsidiary, as witness the fact that its removal does not in any way interfere with the normal functioning of the animal. The apical system of the crinoid is not, therefore, directly comparable to that of the asteroid where the nerve is entirely motor in function. The apical nerve of the asteroid, which has been regarded by many authors as constituting one of the fundamental divisions of the motor nervous system has, consequently, no homologue among the rest of the Echinodermata. Furthermore, although the hyponeural system is a more constant feature of the echinoderm nervous system, its variable constitution in the different classes of the phylum further demonstrates the variable nature of the motor system generally. The conclusion to be drawn is that while the functional sensory system is comparable in all groups except the crinoids, the motor system, both in respect to its apical and hyponeural divisions, exhibits varying degrees of development and is not strictly comparable throughout the phylum. It is clear, therefore, that before comparison of the motor system of the various classes can be attempted, it will be necessary to consider the conditions which determine motor nerve development.

It has been shown in this account of the nervous system of *Marthasterias glacialis* that the motor fibrillae are not restricted to the hyponeural system (Lange's nerve) and the apical nerve. The latter represents, in fact, a condensation of the fibrillae of the lateral motor nerve, which condensation is associated with the innervation of the apical longitudinal muscle. In the same way, Lange's nerve must be regarded as a local centre serving for the innervation of the inferior transverse muscle. The motor nervous system of *Marthasterias glacialis*, as far as it can be traced, is, in fact, developed where it is most required, *i.e.*, in the neighbourhood of the muscles of the arm and disk. Comparison of the motor systems should be made with this fact in mind, and not merely by reference to the hyponeural and apical systems which, from the evidence provided by the study of *Marthasterias glacialis*, are only parts of a generally distributed neurofibrillar plexus.

The hyponeural system is, on this account, best developed in the ophiuroid where it undertakes the innervation of the four intervertebral muscles responsible for the lateral and oro-aboral flexure of the arm. In the Holothuroidea it is precisely this centre of innervation which supplies fibrillae to the circular and longitudinal musculature of the body wall. In the crinoids the hyponeural nerve is both sensory and motor, its motor fibrils serving for the innervation of the muscles of the wall of the water vascular vessels, while in the asteroid, where it is purely motor, the hyponeural radial nerve supplies branches to the inferior transverse muscle. Only in the Echinoidea, where the development of a calcareous test has rendered the presence of body wall muscles superfluous, is the radial hyponeural nerve entirely absent. All that remains of the system is the circumoral nerve on which are developed five ganglia which are said to provide nerves for the innervation of the musculature of Aristotle's lantern.

We have seen, in *Marthasterias glacialis*, that the conditions for the development of a motor nerve are, firstly, that in order that the sensory-motor reflexes may be established, there should be, in its vicinity, an expansion of the sensory fibrillar plexus and that, secondly, there should be, in its neighbourhood, muscles to be innervated. The multiplicity of function and the varying degrees of development of the hyponeural radial cord in the various classes of echinoderms can best be explained on this basis ; its position is determined by the fibrillar plexus of the radial ectoneural nerve and its degree of development by the extent of the musculature to be innervated.

It is on these grounds that we have accounted for the various motor centres of the asteroid *Marthasterias glacialis*. Lange's nerve, the lateral motor nerves, and the nerves innervating the longitudinal adambulacral muscles have arisen in response to the requirements of the neighbouring musculature and are associated with expansions of the neurofibrillar system of the sensory system. The lateral motor nerve, alone, is of more than purely local significance, for its fibrillae extend throughout almost the whole of the wall of the perivisceral coelom and are especially thickened in the aboral wall where the longitudinal musculature is greatly developed as the apical longitudinal muscle. A discrete apical nervous system is therefore absent in the Asteroidea as well, apparently, as in the Ophiuroidea, Echinoidea, and Holothuroidea.

The sensory system of the asteroid, while exhibiting primitive characteristics in that it is entirely superficial in position, and is composed of simple sensory cells, the central fibrillae of which are contiguous with the fibrillae of the morphologically undifferentiated association ganglion cells, nevertheless shows some indications of morphological and physiological differentiation.

The subepithelial neurofibrillar plexus contains ganglion cells which, in the deeper parts of the radial cord and circumoral nerve ring, are bipolar and are orientated in a way suggestive of a definite polarity. In the radial nerve cord the ganglion cells are directed along the length of the cord and in the nerve ring are so disposed that the fibrillar continuations of their tapering ends pursue a circular course. Moreover, the fibrillar system of the radial cord exhibits zoning in that, although almost all its fibrils are directed along the length of the cord, the deeper lying fibrillae are arranged in definite cable-like tracts which have been interpreted as providing paths for the rapid conduction of impulses from the sensory elements of the ectoderm to the circumoral nerve ring. This zonation is visible not only in the radial cord but also in the subepithelial plexus of the tube feet. These organs are highly sensitive and the stimuli which they perceive produce impulses which are conducted to the radial cord through a single longitudinal tract of fibrils. This coordinating tract is always situated in a definite position relative to the radial cord and nerve ring, and is placed so as to face the radial cord on the side of the tube foot nearest the circumoral nerve ring, a disposition which suggests that the cord receives the impulses from the tube foot and transmits them to the nerve ring. The latter would be regarded as the centre responsible for the maintenance of coordinated movement of the tube feet and arms and for the regulation of the responses required for the performance of complicated movements such as are involved in the righting reaction.

Impulses are transmitted from the sensory fibrils to the motor fibrillae which communicate one with the other through the interspaces of the boundary zone. There are, as we have seen, at least three distinct motor centres in the arm of *Marthasterias glacialis*, each innervating a different set of muscles. Experimental corroboration of the existence of more than one centre has been given by Moore (1920). The starfish *Asterias forbesii*, if placed in a 0·0001% solution of strychnine sulphate in sea-water, flexes its arms dorsally. If the dorsal myodermal sheath be cut out from all five rays, dorsal flexure still takes place and, moreover, the excised pieces of the dorsal myodermal sheath, when treated with strychnine, show the same direction of flexure. Moore concludes that, in the intact animal, muscles responsible for the dorsal flexure of the arm are present both in the dorsal sheath and in the floor of the ray.

Nicotine, on the other hand, in a concentration of 0·00002 % causes ventral flexure of the arm and therefore excites muscles antagonistic in action to those excited by strychnine. When the dorsal myodermal sheath is excised, ventral flexure still takes place, but the excised portions, when treated with nicotine, exhibit dorsal flexure. As a result of these observations Moore is able to show that the dorsal part of the starfish arm contains muscles responsible only for dorsal flexure, while in the floor of the arm there are antagonistic muscles responsible both for dorsal and ventral flexure. This independent action of the limited parts of each muscle system can only be accounted for on the assumption that they have an independent innervation.

We are not, at the moment, in a position to say which of the motor centres of *Marthasterias glacialis* are concerned with the transmission of impulses for dorsal flexure and which for ventral flexure, but the possession of discrete centres does at least provide a morphological basis for the interpretation of the experimental findings. This much may, however, be conjectured. Since the dorsal myodermal sheath of the starfish arm contains only such muscles as are capable of causing dorsal flexure and since this flexure must result from the contraction of the apical longitudinal muscle, the lateral motor nerve, which innervates the apical muscle, cannot supply any of the muscles of the floor of the ray which by their contraction cause ventral flexure. These latter must be supplied by fibrillae either from Lange's nerve or from the local centre for the innervation of the longitudinal adambulacral musculature or from some centre or centres which have, so far, escaped observation.

By way of summary we may say that the starfish in its behaviour exhibits movements explicable only on the assumption (experimentally confirmed) that antagonistic sets of muscles are involved. This antagonism implies independent innervation of the antagonistic muscles. In *Marthasterias glacialis* this is provided for by the development of at least three distinct motor centres which transmit to the muscles impulses of a tactile, chemical, or visual nature.

There remain for consideration those organs of the starfish which are capable of a degree of autonomy, and which must necessarily possess nerve centres independent of the neurofibrillar plexus of the general ectoderm of the animal. Paine (1929) has shown that the tube feet, if excised with their ampullae, exhibit autonomous movement, and Jennings (1907) has demonstrated that the pedicellariae are capable of a functional autonomy in that, although many of their reactions are made in coordination with those of neighbouring pedicellariae, the " closing " reaction is not so transmitted and is dependent on the possession of an independent nerve centre.

The sensory-motor reflexes of the pedicellariae have already been considered in some detail (pp. 161, 163), and it is only necessary to state here that the motor centres are developed, as in other parts of the starfish, in conjunction with the muscle to be innervated, and that they have their origin adjacent to a local expansion of the ectodermal fibrillar plexus, the fibrillae of the two parts being in connexion one with the other through the interstices of the medianly situated boundary zone. The adductor and abductor muscles are antagonistic in action, the excitation of the one inhibiting the excitation of the other. This reciprocal inhibition is explicable only on the assumption that there are separate centres of innervation, a condition which has been shown to exist in the straight pedicellaria of *Marthasterias glacialis*. Although only one centre has been found in the crossed pedicellaria, there is good reason to believe that the innervation of its musculature is similar to that of the straight form.

The coordination of movement of the tube feet and their power of autonomy together imply that the muscles of these organs are innervated, like those of the pedicellariae, both by fibrillae, which are in connexion with the plexus of the radial cord, and by fibrils of local sensory-motor arcs. A careful study of many series of sections of tube feet has failed to reveal any motor fibrils within the muscle fibres, and one is forced to the conclusion that here, as with many of the muscles of the starfish arm, the nerve supply is in the form of isolated fibrils in communication with the sensory elements through the interspaces of the meshwork of the connective tissue fibres of the boundary zone.

This résumé cannot be concluded without reference to a few other points in the morphology and histology of the asteroid nervous system which require further elucidation. The innervation of the greater part of the musculature of the arm and disk is still unknown and may remain so until one of the special techniques for demonstrating neurofibrils is successfully applied to echinoderms. The identity of the association ganglion cells of the motor system has yet to be determined, while certain details of the histology of the sensory system, more particularly of the optic cup, require confirmation.

For the proper understanding of the behaviour of the starfish, the nature of the nervous reflexes must be established. An attempt has been made, in this paper, to explain, as far as possible, some of the simpler reactions of the starfish on a morphological basis. This has been made possible by the location of some of the motor centres, more particularly the lateral motor nerves. The fact that only the simplest reactions are at all explicable on this basis is sufficiently demonstrative of the limited extent of our present knowledge of the asteroid nervous system.

VIII—Summary

The foregoing account includes a description of the histology and distribution of the nervous and non-nervous elements associated with the nervous system of the starfish *Marthasterias glacialis*.

As an introduction to the histology of the ectoneural sensory system, the radial nerve cord has been studied in some detail. The cord is composed of nervous elements in the form of primary sense cells, association ganglion cells, and neurofibrillae, the latter representing delicate extensions of the sensory and association elements. Epithelial cells, supporting fibres, glands, and cuticle constitute the non-nervous elements of the cord (fig. 5).

The cuticle overlying the ectoderm is in the form of a hyaline lamina, some 4–5 μ thick, secreted by the epithelial cells. Two cuticular layers can be discerned. The inner layer is composed of closely apposed hexagonal platelets, each platelet representing the product of secretion of a single cell, while the other layer is homogeneous and results from the flowing together of the separate platelets (figs. 1, 3).

The epithelial elements are elongate cells, broad at their bases where they abut on to the cuticle, but with tapering inner ends extending inwards through the subepithelial plexus of neurofibrils to the basal connective tissue layer. The epithelial cells are ciliated and contain, in their basal portions, granules of yellow pigment (figs. 2, 5).

Each epithelial cell secretes, intracellularly, a supporting fibre which traverses the depth of the cord and lends support to the longitudinally running fibrillae. In

the deeper parts of the cord the fibres are ordinated in longitudinal linear series (figs. 2, 4, 5).

Glands are most numerous at the base of the limbs of the " V "-shaped cord. They are of two kinds—" mulberry " glands and goblet cells. The former are the more numerous and are distinguished, in the early stages of secretion, by their readily staining contents in the form of spherical refringent droplets, while the latter, of a mucous nature, contain a fluid which stains but lightly with most of the reagents used (fig. 7).

Primary sense cells are present in large numbers in the radial cord. Each consists of a spindle-shaped cell body and a centripetal and central fibre. The centripetal fibre ends in contact with the cuticle while the central fibre frequently branches into two fibrillae which become orientated along the length of the cord and merge with the fibrillae of the subepithelial plexus (figs. 5, 6).

The association ganglion cells are subepithelial in position. Multi- and bipolar forms are to be found, the former situated just internal to the nuclear zone of the epithelial cells and the latter in the deeper parts of the cord. The fibrillar extensions of the ganglion cells constitute the greater part of the subepithelial fibrillar plexus. By virtue of their form and position, the multipolar elements are considered to serve the purpose of transmitting impulses received from the sense cells to the fibrillae of the bipolar cells, which latter are orientated along the length of the cord and conduct impulses to the circumoral nerve ring (fig. 6).

A definite zoning of the fibrillae of the subepithelial plexus has been noted. Three zones are to be observed. The outer (nearest the cuticle) consists of fibrillae which are interwoven with the irregularly disposed supporting fibres of the epithelial cells. In the middle zone, the supporting fibres are ordinated in linear series, but still form a weft into which the longitudinally running fibrillae are interwoven, while in the inner zone the cable-like longitudinal neurofibrillar tracts alternate with the linear transverse rows of supporting fibres (fig. 4).

In histological detail the circumoral nerve ring differs but little from the radial cord. There are, however, only two fibrillar zones, corresponding to the outer and middle zones of the cord.

The histology of the general ectoderm of the starfish is essentially similar to that of the nerve cord. Sensory elements are particularly numerous in the mid-line of the aboral surface and at the base of the spines and pedicellariae. The subepithelial plexus is only poorly developed in consequence of the absence or comparative absence of association ganglion cells and their fibrillae (fig. 8).

The tube feet are highly sensitive organs. Sense cells are found in greatest numbers in the sucker and on this account the subepithelial plexus is especially thickened, at the base of the sucker, as a nerve ring (fig. 12).

In the middle part of the tube foot the plexus is divisible into an outer zone of circularly disposed fibrils and an inner zone in which the neurofibrillae are directed along the length of the podium. The latter exhibit a zonation similar to that of the fibrillae of the radial cord. The longitudinal fibrillar system is especially developed as a tract so placed as to lie on the side of the tube foot nearest the radial cord and facing towards the circumoral nerve ring (figs. 9, 10, 11, 12, 16).

Because of the constant position of the longitudinal tract of the tube foot and of the presence, in the radial nerve cord, of fibrillar tracts in which bipolar ganglion cells, orientated along the length of the cord, are to be found, a polarization of the nervous system is presumed, the circumoral nerve ring serving as the centre for the coordination of impulses.

In its nervous organization the azygos tentacle differs from the other tube feet only in the fact that the sensory elements and subepithelial plexus are more or less confined to its oral surface—the surface which is normally in a position to receive stimuli (figs. 17, 18).

The " eye " is composed of numerous invaginations of the ectoderm of the optic cushion, *i.e.*, the swollen end of the radial nerve cord. Each invagination or optic cup is provided with a lens, derived from the basal portions of the surrounding epithelial cells, and over the lens there is a cuticular covering. Lining the cup are pigmented cells, containing granules of an orange colour, and sensory cells. The sensory elements consist of an almost transparent optic vesicle projecting into the cavity of the cup and a cell body drawn out into a central fibre, which latter merges with the fibrillae of the underlying plexus (fig. 19).

At the base of the epithelial lining of the alimentary canal is a neurofibrillar plexus continuous, at the mouth, with the fibrillae of the buccal membrane and circumoral ring. Sensory elements are most abundant in the oesophagus and cardiac portion of the stomach and in the oral and aboral walls of the hepatic caeca, but are absent or are only few in number in the pyloric sac, the lateral walls of the hepatic caeca, and in the rectum and rectal sac (figs. 20, 21, 22).

The motor nervous system consists of separate fibrillar centres closely associated with the coelomic epithelium, but in communication with the subepithelial plexus of the sensory system through the interspaces of the boundary zone of connective tissue which lies between the sensory and motor divisions of the nervous system.

Lange's nerve is developed in the epithelial wall of the radial perihaemal canal as paired cords lying to the right and left of the mid-line. Its fibrillae, which run transversely to the axis of the radial cord, innervate the inferior transverse muscles and are supported by non-nervous fibres, presumably derived from the epithelial elements of the coelomic wall. In the disk, Lange's nerve is only to be found interradially, above the outer limb of the circumoral nerve ring (figs. 23, 24).

The lateral motor nerves originate at the base of thickenings of the subepithelial plexus of the ectoderm just lateral to the outer row of tube feet. Their fibrillae run inwards into the perivisceral coelom innervating, in their passage, the lateral transverse muscles. In the distal part of its course the lateral motor nerve is in intimate connexion with the coelomic epithelium and innervates the circular and longitudinal muscles of the arm, including the apical longitudinal muscle. In the vicinity of the latter there is a concentration of fibrils constituting the " apical nerve " of CUÉNOT (figs. 25, 26, 27).

There is evidence that the longitudinal adambulacral muscles are innervated from separate motor centres, which latter are marked by thickenings of the ectodermal plexus at the base of the adambulacral spines (fig. 28).

Pedicellariae of the straight and crossed types have their own motor centres for the innervation of the adductor and abductor muscles of the blades. Separate centres innervate the inner adductor and the abductor muscles. The source of innervation of the outer adductor muscles has not been traced. An attempt has been made to explain the simpler reflexes of the pedicellariae on the basis of the morphological findings (figs. 29, 30, 31, 32).

IX—Abbreviations Used in the Figures

ab. lap.,	aboral lappet.
abd. musc.,	abductor muscle.
adamb. oss.,	adambulacral ossicle.
adamb. sp.,	adambulacral spine.
amb. oss.,	ambulacral ossicle.
an.,	anus.
ap. long. musc.,	apical longitudinal muscle.
azyg. tent.,	azygos tentacle.
b.z.,	boundary zone of connective tissue.
bas. oss.,	basal ossicle of pedicellaria.
bas. pl.,	basal plate of connective tissue.
bipol. gang. c.,	bipolar ganglion cell.
bl. oss.,	ossicle of blade of pedicellaria.
bucc. memb.,	buccal membrane.
c.f.s.c.,	central fibre of sense cell.
c.t.l.,	connective tissue lamina.
centrip. dend. gang. c.,	centripetal dendrite of ganglion cell.
centrip. f.s.c.,	centripetal fibre of sense cell.
cil.,	cilia.
circ. musc.,	circular muscle fibres.
circum. n.r.,	circumoral nerve ring.
circum. n.r.i.,	inner limb of circumoral nerve ring.
circum. n.r.o.,	outer limb of circumoral nerve ring.
coel.,	perivisceral coelom.
coel. epith.,	coelomic epithelium.
conn. tiss.,	connective tissue.
cut.,	cuticle.
cut. in.,	inner layer of cuticle.
cut. out.,	outer layer of cuticle.
cut. pl.,	cuticular platelet.
cytopl.,	cytoplasm.
ect.,	ectoderm.
ect. t.f.,	ectoderm of tube foot.
epith. c.,	epithelial cell.
epith'. c.,	
epith''. c.,	

ext. per. r.,	outer perihaemal ring.
fibril. circ.,	circular fibrillar zone.
fibril. long.,	longitudinal fibrillar zone.
gl. sec.,	glandular secretion.
gr. add. musc.,	greater adductor muscle.
inf. trans. musc.,	inferior transverse muscle.
inn. add. musc.,	inner adductor muscle.
inn. per. r.,	inner perihaemal ring.
inter. lam.,	interlaminar area.
l. add. musc.,	lesser adductor muscle.
lang. n.,	Lange's nerve.
lat. lap.,	lateral lappet.
lat. m.n.,	lateral motor nerve.
lat. trans. musc.,	lateral transverse muscle.
long. amb. musc.,	longitudinal ambulacral muscle.
long. adamb. musc.,	longitudinal adambulacral muscle.
long. dend. gang. c.,	longitudinal dendrite of ganglion cell.
long. musc.,	longitudinal musculature.
long. tr.,	longitudinal fibrillar tract of tube foot.
m. gl.,	" mulberry " gland.
m.n. abd. musc.,	motor nerve of abductor muscle of pedicellaria.
m.n. gr. add.,	motor nerve of greater adductor muscle of pedicellaria.
musc. fib.,	muscle fibre.
musc. o. pl.,	muscle running between odontophore and oral plate.
multip. gang. c.,	multipolar ganglion cell.
multip'. gang. c.,	bipolar derivative of multipolar ganglion cell.
n. fib.,	neurofibrillae of ectoneural system.
n. fib'.,	neurofibrillae of Lange's nerve.
n. fibril.,	neurofibrillae of subepithelial plexus.
n. fibril'.,	neurofibrillae of the plexus underlying the basal plate of connective tissue.
n. fibril. exp.,	expansion of the subepithelial neurofibrillar plexus associated with motor nerve development.
n.r.,	nerve ring.
n.r.t.f.,	nerve ring of tube foot.
nuc.,	nucleus.
nuc. epith. c.,	nucleus of epithelial cell.
nuc'. epith. c.,	nucleus of migrant epithelial cell.
nuc'., *nuc. s.c.*,	nucleus of sense cell.
opt. c.,	optic cushion.
opt. cup.,	optic cup.
opt. s.c.,	visual sensory cell.
opt. ves.,	optic vesicle.
oss.,	ossicle.
out. add. musc.,	outer adductor muscle of pedicellaria.
pap.,	papula.
pig. c.,	pigment cell.
pig. gran.,	pigment granule.
rad. n.c.,	radial nerve cord.
rad. per. c.,	radial perihaemal canal.

rad. w.v., radial water vessel.
rect., rectum.
rect. sac., rectal sac.
s., sucker of tube foot.
s.c., primary sense cell.
sept., septum.
supp. fib., supporting fibre of the ectoneural system.
supp. fib'., supporting fibre of Lange's nerve.
sup. trans. musc., superior transverse muscle.
t.f., tube foot.
term. oss., terminal ossicle.
trans. adamb. musc., transverse adambulacral muscle.

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