XVII. *Observations on the Nervous System of* Aurelia aurita.

By Edward Albert Schäfer, *Assistant Professor of Physiology in University College, London.*

Communicated by W. Sharpey, *M.D., LL.D., F.R.S.*

Received October 31, 1877,—Read January 10, 1878.

[Plates 50–51.]

Last August I undertook, at the request of my friend Mr. G. J. Romanes, an investigation with the view of proving the presence or absence of histologically differentiated nervous structures in the Medusæ. Mr. Romanes' experiments* have shown the existence of a central nervous apparatus in the marginal bodies of these animals, and probably also of nervous tracts (lines of discharge) over the lower surface of the nectocalyx or umbrella. But up to the present time the anatomical proof of the existence of a nervous system in this class has rested chiefly upon the authority of Haeckel, who has described† in two genera of the craspedote Medusæ a ring of nerve-fibres lying on the inner side of the marginal canal, and provided with a ganglionic enlargement at the base of each lithocyst. From each of these ganglia four nerves are described as passing—one to the polypite, and the others to the adjacent tentacles and lithocyst.

My observations have been chiefly confined to *Aurelia aurita*, partly because, at the time of year chosen, this species furnished the most abundant material, partly on account of its having been the subject of the greater number of Mr. Romanes' experiments, and also because the nervous structures can be more readily made out in this species than in any other that could be readily got. But preparations of a species of *Chrysaora* make it abundantly evident that ganglion cells somewhat similar to those immediately to be described as underlying the muscular sheet in *Aurelia* are found also in this genus, and it is probable that what is true of these two genera will apply with but little modification to other genera of acraspedote Medusæ. Whether a similar distribution of nerves exists also in the Craspedota, is a matter which must for the present remain undecided; my own observations, which were confined to species of *Thaumantias* and *Tiaropsis*, have so far yielded a negative result.‡

* Phil. Trans., 1876, pp. 269, et seq.; and Phil. Trans., 1877.

† Beiträge zur Naturgeschichte der Hydromedusen.

‡ See postscript.

The nervous system of *Aurelia* consists (1) of the *marginal bodies* or *lithocysts*, the discharging function of which has been clearly demonstrated by Mr. ROMANES; (2) of certain tracts of peculiarly modified epithelium in their vicinity, which we may term the *nerve-epithelium*; (3) of an interlacement of nerve-fibres, which covers the whole of the under surface of the muscular sheet, lying between the muscular fibres and the ectoderm-cells, and partly amongst the latter, and which may be termed the *subumbrellar plexus*.

Subumbrellar Nervous Plexus.

The plexus can be distinctly seen even in the fresh tissue if care be taken to bring the subumbrella flat and uninjured under microscopic observation, and the fibres then have very much the appearance of the sympathetic fibres, or fibres of Remak, of the Vertebrata, and, like these, show an indistinct longitudinal striation. Here and there oval or fusiform swellings occur in the course of the fibres, and in the larger of the swellings a vesicular nucleus, and a distinct bright nucleolus may be detected. These appearances are so obvious as to allow of no question that we have before us undoubted nerve-fibres, and bipolar ganglion-cells. The tissue which they underlie being just as clearly muscular, with well-characterised cross-striæ, it is interesting to observe, even so low down in the metazoic scale as the Medusæ, that the textures, which in the higher animals are generally looked upon as the most highly differentiated, should have already attained a degree of structural complexity and of functional activity in many respects scarcely inferior to the nervous and muscular tissues of Vertebrates.

The subumbrellar nerves. Structure of the nerve-fibres.—The reagents which are ordinarily employed for the demonstration of nervous tissues, and especially the chloride of gold, bring the structures in question to view in the most striking manner possible. As in the higher animals, the nerve-fibres and the substance of the ganglion-cells become stained of a deep violet colour by this reagent, so that the fibres may be followed with ease over large tracts of the surface (Plate 50, figs. 1–7; Plate 51, figs. 11–16). Osmic acid preparations lack this distinctiveness of colouration, so that the nerves are scarcely better exhibited *in situ* than in the fresh preparation. But whereas after treatment by the chloride of gold method the fibres appear markedly smaller than in the fresh tissue, and seem to have become somewhat shrunken, in the preparations made with osmic acid they preserve their original size and for the most part their pristine appearance (Plate 50, fig. 8). If the nerve-fibres which have been stained with chloride of gold be attentively observed, it may be seen that they are surrounded by a clear space which separates them from the tissue in which they lie. This space may have been produced by the expression of fluid from the fibre during its supposed shrinkage, or on the other hand it may represent a previously existing homogeneous sheath, surrounding an axis-cylinder; and, if this were the case, certain small nuclei, which are occasionally seen adhering to the fibres (figs. 13 and 14, *n.*),

might be regarded as belonging to such a sheath. The fact of the distinction between fibre and sheath not being visible in the unstained preparation would be accounted for, if we suppose them to possess much the same index of refraction.

Course and distribution of the nerve-fibres.—The nerve-fibres are not uniformly distributed over the whole subumbrella. They are met with in least abundance near the margin, but are not wholly absent even here, and I have sometimes thought I could trace a delicate fibre into a tentacle. But I have not been able to detect anything of the nature of a marginal ring of nerve-fibres like that described by HAECKEL in the craspedote forms.

At certain parts the fibres come together to form wonderfully intricate interlacements (fig. 7), whilst at other places only a few fibres may be seen crossing the field of the microscope (fig. 3). Neither individually nor collectively do the fibres appear to have any special relation to the nutritive tubes. Nor are they especially numerous in the neighbourhood of the lithocysts, although a certain number of nerve-fibres may generally be traced converging towards each of these structures (fig. 4). I have never been able to follow them directly, either into the marginal bodies or into the nerve-epithelium near; at the same time it is probable that some of these converging nerves, if they do not enter or issue from the lithocyst itself, at least come into relation with the thick nerve-epithelium which is found near the base of that organ. The difficulties of observation are here very considerable, owing partly to the fineness of the converging fibres, and partly to the fact that the tissues near the margin, and especially near the lithocysts, are apt, more than elsewhere, to become uniformly darkly stained by the reagent employed.

At the central part of the umbrella some of the fibres may be observed to sweep round the margins of the four genital sacs, and to pass between these towards the polypite, but it has not been possible to trace them actually into the latter.

The general direction of the fibres over the whole subumbrella is radial, but this direction is greatly obscured by bendings and intercrossings. Moreover, a few nerves pass in the direction of the muscular fibres, and therefore parallel with the circumference of the swimming-bell.

If we trace out the course of the individual nerve-fibres more closely (as has been done with the fibre marked *xx.* in figs. 11–16), we are struck with certain remarkable facts. In the first place, each fibre is entirely distinct from, and nowhere structurally continuous with, any other fibre. Secondly, each fibre is provided with a bipolar nerve-cell (fig. 13), which is interpolated in or near the centre of the fibre, each end of the fibre representing the prolongation of one of the poles of the nerve-cell. Thirdly, each nerve-fibre is of limited length (seldom exceeding 4 millims. from end to end), and in most cases tapers at either extremity to a gradual termination. Lastly, it may be mentioned that the fibres are rarely branched; and where they are so (as in fig. 12) the branches do not join with other nerve-fibres, but after a longer or shorter course end in a tapering extremity like the unbranched fibres.

It seemed at first sight almost incredible that with such a prodigious number of nerve-fibres, exhibiting so close an interlacement, there should be no actual junctions of the intercrossing nerves. And it was especially difficult of credence because some of the experiments of Mr. ROMANES, performed with the view of testing the amount of section which the tissue could endure without loss of nervous (or excitational) continuity, seemed to point to the existence of a structurally continuous network of nerve-fibres. Nevertheless, there can be no doubt that the fibres do not come into anatomical continuity. On the other hand, it can readily be seen that each nerve-fibre comes at one or more points of its course into very close relations with other nerve-fibres. Two fibres, for example, may sometimes be observed to bend towards each other out of their previous course, in order to run closely side by side for a greater or less distance, and in such cases one fibre may hook round the other (fig. 6), or they may even be two or three times intertwined. At other places a number of fibres come together from different parts and join in a very close entanglement, the fibres in which run for the most part parallel (figs. 7 and 15), and it is only with difficulty that the individual fibres can be followed. So that although there is no actual anatomical continuity, abundant opportunity is afforded for inductive action, whether electrical or of some other kind. That physiological continuity is thus maintained it seems as yet premature to conjecture.

Mode of termination of the nerve-fibres.—Most of the fibres end, as already mentioned, in a gradually tapering extremity, which is sometimes bifid (fig. 16, x^{vi}.). This, so far as could be seen, does not actually enter a muscular fibre, although since there is no sarcolemma it comes in close contact with the muscular substance. In some instances the nerve-ending takes the form of a fusiform dilatation (fig. 11, *x*.), which may contain a small nucleus; in other cases the dilatation is more marked, and may even form a triangular flattened expansion within which a number of nuclei can be detected (fig. 8, *p*.). These expansions of the end of the nerve appear to represent a primitive form of the motorial end plate.

The nerve-cells.—The cells vary in size, but for the most part are roundly fusiform bodies, averaging ·05 millim. in length, and ·015 millim. in diameter. As stained with gold they are of characteristic appearance, and present a marked resemblance to the bipolar cells which are met with in the spinal ganglia of fish, or to those which are found interpolated in the course of the nerves distributed to the ciliary muscle in the human eye. The cell-substance is granular in the gold preparation, but extraordinarily clear and pellucid when examined fresh; in this respect resembling the ganglion cells of the human retina. An appearance of striation radiating from the poles into the substance of the cell is sometimes faintly visible. The nucleus, which is not coloured by the gold salt, is either spherical or ovoid: it is clear and vesicular, and contains a very characteristic nucleolus. The nucleus is generally situate nearer to one of the extremities of the cell, rarely in the centre. The cell itself is not always evenly fusiform, but is often bulged out at one

end; it passes at either pole sometimes abruptly, but more often gradually into the nerve-fibre.

Cells are frequently met with, especially in young specimens, which closely resemble the nerve-cells just described, with the exception that the nerve-fibre processes are of much more limited length, or even, in some cases, altogether absent. They are, no doubt, ectoderm cells, in process of development into nerve-cells and nerve-fibres: they are usually more abundant in the neighbourhood of the polypite than elsewhere (fig. 3). The arms of the polypite itself generally show a number of cells of this description, but they are entirely destitute of nerve-fibre prolongations.

Function of the subumbrellar nerves.—Each nerve-fibre may be regarded as serving to connect a part of the muscular sheet nearer the circumference with other parts nearer the centre of the swimming-bell, and thus to bring the contraction of different zones of muscle more nearly in correspondence. Further, as a result of the interlacements which occur, and the closely parallel course which the fibres take in them, it is reasonable to conclude that nervous impulses are transmitted by some means or another from fibre to fibre. If so, the result would be the same as if an actual net-work of nerves existed, viz., the production of a general co-ordination in the contractions—not absolute, it is true, but often nearly so. Lastly, since the nerve-cells are brought into close relation with the exterior of the body through the medium of the ectodermic epithelial cells, amongst which they lie, any stimulus affecting these is communicated by means of the nerve-fibre processes to the parts of the muscular sheet to which these fibres themselves are distributed, and, if there is any means of transmission from fibre to fibre, it will rapidly spread over the general subumbrellar plexus to the whole of the contractile tissue.

The Lithocysts and Tracts of Nerve-epithelium.

The lithocysts of *Aurelia* are eight thumb-shaped projections (fig. 17) at the circumference of the umbrella, each being situate in one of the marginal bodies and having a horizontal direction with a slight upward curvature. They are covered above by a cushion-like prominence (fig. 17, *c.*) of the upper edge of the umbrella, and are further hidden by a tongue-shaped fold on either side, into which a cœcal protrusion of the marginal canal extends.*

At the base of the cushion above referred to, there is seen a deep pit which extends down towards the attached end of the lithocyst. This pit it will be convenient to distinguish by the name of *fovea nervosa superior* (figs. 17, 18, *f.n.s.*). It is lined by a

* These diverticula of the nutritive canal, after passing a certain distance laterally into the substance of the fold, contract abruptly and the narrowed portion then passes a variable distance towards the end of the fold. The larger portions of the diverticula often present, on one or both sides, a solid cellular axis, projecting into the lumen of the canal, and formed apparently by an infolding of the entodermal wall, but its purpose and the precise mode of its formation I have been unable to elucidate.

layer of thickened ectoderm, the ciliated columnar cells of which (fig. 10, A, B) are very narrow and elongated, each having a clear oval nucleus, which causes the portion of the cell where it is situated to be bulged out. For convenience of adaptation, therefore, the nuclei of adjoining cells are on different levels, and this gives an appearance as if there were several layers of nuclei (fig. 18). The upper or free end of the cell is peculiar in presenting a distinct, highly refractive thickened border (fig. 10, A, *b.*), convex outwardly, and from the top of the convexity a single long cilium springs (fig. 10, A, *c.*). The attached ends of the cells rest upon a fibrous stratum, often granular looking in section, which in fact seems to be formed by the interlacement and union of fine fibres prolonged from the branching fixed ends of the columnar cells (fig. 10, A, *f.*). These fibres have a certain resemblance to delicate nerve-fibres; they pass from the cells, at first perpendicularly through the stratum in question (fig. 18), but they then turn abruptly down towards the bottom of the fovea, passing beneath and between the branching processes of the other cells, under which they aid in forming in like manner a fibrous stratum. Towards the upper limit of the fovea the fibrous stratum becomes thinner and at last altogether ceases, and the elongated cells pass by a gradual transition into the small epithelium cells which cover the upper surface of the umbrella.

Immediately beneath and on the oral side of the attached end of the lithocyst is another deep depression of the surface. This, which may be termed *fovea nervosa inferior* (fig. 17, *f.n.i.*), is applied for the greater part of its extent to the process of the nutritive canal which passes to the lithocyst. It is lined by a thick epithelium with a nervous substratum, quite similar in appearance to that found in the superior fovea; towards the lithocyst this epithelium passes into the ectodermal covering of that structure. It is possible that the subumbrellar nerve-fibres, which were before described as converging towards the attachment of the lithocyst, end in the fibrous substratum of this inferior fovea.

The lithocyst itself consists of three parts, which may be distinguished as the *basal* (fig. 17, *b.*), the *intermediate* (fig. 17, *i.*), and the *terminal* portions (fig. 17, *t.*), the last-named projecting freely under the cushion before mentioned. They are marked off from one another by two shallow grooves. The terminal part contains the clump of calcareous crystals which give the name of lithocyst to the whole organ. The intermediate part has a deep brown colour on the up-turned surface, especially in and near the groove which marks it off from the terminal portion, the colour being situated in the ectodermic cells.*

The interior of the lithocyst is occupied throughout its whole extent by a radial prolongation from the marginal nutritive canal (fig. 17, *n.c.*), which is, of course, lined

* The presence of calcareous crystals (otoliths ?) in the marginal bodies of the Medusæ has led to their being commonly regarded as auditory organs, and the presence of pigmented spots (ocelli ?) is supposed to indicate the existence of a dim visual perception, but there has been hitherto no experimental proof of the actual possession of these functions in the case of *Aurelia*.

by entoderm cells. This prolongation remains hollow in the basal and in the intermediate portions, but into the terminal part it is continued as a solid projection, which expands into the clump of otolithic cells. These, therefore, are continuous with, and are doubtless derived from the entoderm, for they have no connexion whatever with the ectoderm, being separated from it by a thin layer of the jelly-like tissue (mesoderm ?). This is a noteworthy fact, for in nearly all animals in which an auditory organ containing otoliths is developed, these particles are, so far as is at present known, formed in connexion with cells derived solely from the ectoderm. The lithocyst consists then (1) of a central part or core derived from the entoderm, and (2) of a covering formed of ectodermic cells, the two being separated from one another by a thin layer of the jelly-like mesoderm.*

Entodermic part or core of the lithocyst.—As already mentioned, the central canal of the lithocyst is prolonged directly from the circular nutritive canal of the margin, and it extends as far as the junction of the intermediate with the terminal portion. It is lined by a columnar ciliated epithelium, the cells of which are much longer than those found in the ordinary nutritive canals. Its lumen is partially filled with rounded cells, which towards its extremity entirely occlude it, so that the canal is prolonged into the terminal portion of the lithocyst by a somewhat narrowed, solid stalk, which widens out as the otolothic clump. Of the cells which form the stalk the external are much elongated, and are disposed in a radiating manner, whilst those in the centre are rounded or polygonal, and the more distal already have small crystals developed in their interior. The peripheral otolithic cells of the clump itself have also a radiate arrangement and an oblong appearance in longitudinal section (fig. 17), whilst the internal ones are more irregularly packed, and many of them almost regularly dodecahedral in shape. In teased (osmic) preparations their flattened sides sometimes are seen to have the bases of columnar cells applied to them, the ends of the latter tapering to fine branching processes (fig. 10, E). These (nerve fibre ?) processes seem to become lost in a network having a granular appearance in section, underlying the tapering ends of the columnar entodermal cells, like the stratum already described as existing under the ectodermal cells of the foveæ nervosæ and that immediately to be described in connexion with the ectodermic part of the lithocyst. Opposite the foveæ the fibrous stratum under the ectodermic cells comes for a certain

* In one specimen of *Aurelia*, sections of which were prepared, there was observed a small supplementary organ (fig. 20, *l'*) a short distance from one of the ordinary lithocysts, remarkable for several reasons. In the first place, it projected from the *upper* edge of the umbrella-margin, and in place of being covered with a cushion it was free superiorly, resting below on the prolonged lower edge of the umbrella. In the second place it was of simple structure, consisting merely of a bell-shaped ectodermal prominence, enclosing a diverticulum of the marginal canal; both its ectodermal and entodermal layers (which were separated by a thin layer of jelly) being distinctly thickened. But the most interesting fact was that the entoderm at the apex of the bell was prolonged *through the ectodermic covering*, in the form of a short stalk, bearing a small bunch of otolithic cells, which could thus project, naked and without an ectodermic covering, into the surrounding medium.

distance into contact with the corresponding stratum just described as underlying the entodermic cells of the lithocystic canal (fig. 18). Moreover, indications can sometimes be obtained of fibres bridging across the mesoderm which separates the ectoderm of the fovea nervosa superior from that covering the base of the lithocyst, so that all the tracts of modified epithelium with fibrous substratum, whether ectodermic or entodermic in their origin, are probably to be regarded as forming collectively a rudimentary nervous centre.

The ectodermic covering of the lithocyst.—The cells which compose the ectodermic covering of the lithocyst form a single layer, which is continuous with the general ectodermic covering of the under surface of the umbrella. But the layer varies very greatly in thickness, in conformity with the varying length of the epithelium cells and with the greater or less development of the granular (fibrous) stratum which lies immediately beneath them. This is by far most strongly marked over the basal and intermediate portions of the lithocyst, gradually disappearing in the terminal portion, where the ectoderm is represented by a layer of small flattened cells covering the clump of entodermal otolithic cells, and separated from them by a very thin mesodermic stratum. Some of these cells contain the brown pigment before mentioned, and near the distal of the two furrows which encircle the lithocyst there are transitional forms between them and the greatly elongated pigmented cells of the intermediate portion immediately to be described.

The epithelium of the basal portion quite resembles that already described as lining the foveæ. The fixed branched extremities of the cells pass as before through the granular-looking sub-epithelial stratum, and having reached its deeper portion turn sharply round to course either peripherally or centrally, and some, it may be, also laterally, within the layer in question. How these and the other fibres of the similar layers before described terminate must for the present remain undecided. They seem gradually to shade off and disappear beneath the neighbouring epithelium cells. They are very much less defined than the fibres of the general nervous plexus of the subumbrella; moreover, they unite as before said into an irregular network, and altogether have far less decidedly the character of nerve fibres. The stratum which they form resembles in its half-granular half-fibrous appearance the neuroglia of the grey matter of the Vertebrate brain; and the tracts in question with their elongated ciliated cells and the granular substratum bring forcibly to mind the appearance presented by the central nervous system of the Vertebrate embryo at the time when differentiation into cells and fibres is just beginning. Altogether there can be very little doubt that we here meet with the first beginnings (in a phylogenetic sense) of a central nervous apparatus. It is interesting to remark that although characteristic nerve-cells are met with on the nerves of the subumbrella, yet in these specialized parts, which may be regarded as the representatives not only of a central nervous system but also of sense-organs, definite nerve-cells are altogether wanting.

The ectodermic cells of the intermediate portion of the lithocyst resemble, on the

whole, the cells of the basal portion. But in those which are pigmented, and which we may suppose to be concerned with visual perception, we meet with some modifications (fig. 10, C D). The outer extremity of the cell is much enlarged, and contains the whole of the pigment, and from the middle of this wide and generally convex free end there extends a very long filament of exquisite fineness. The fixed end of the cell is prolonged from the nuclear dilatation as a straight, very delicate thread, which usually shows one or more minute varicosities. Its branches become lost in the network of cell processes which forms the subjacent fibrous stratum.*

October, 1877.

Description of the Figures.

Fig. 1. Part of the plexus of nerves covering the muscular sheet, taken about midway between the margin and the polypite. Fusiform bipolar nerve-cells are seen on some of the fibres. The direction of the muscular fibres is indicated by the slightly curved lines. Drawn under a magnifying power of about 140 diameters, but not to scale.

Fig. 2. Part of the same plexus, from over a nutrient tube. The vertical striation is intended for shading only; not, like the transverse lines, to indicate the direction of the muscular fibres.

Fig. 3. Part of the same plexus, from near the margin of one of the genital sacs. Three cells are observed amongst the nerve-fibres which somewhat resemble the nerve-cells, but are of irregular shape, and possess no nerve-fibre processes.

Fig. 4. Margin of an *Aurelia* near a lithocyst, showing the manner in which the nerve-fibres of the subumbrellar plexus converge towards the attachment of the lithocyst. The lithocyst has been removed from the place marked *l* in the figure. Less magnified than the three preceding figures.

Fig. 5. Part of the submuscular plexus of *Aurelia*, more highly magnified.

c'. A tripolar nerve-cell. These occur but rarely.

c, *c*. Bipolar nerve-cells.

Drawn under a power of about 300 diameters.

* Since this article was written, a paper ('Ueber das Nervensystem und die Sinnesorgane der Medusen,' Jena. Zeitschr., 1877), by O. and R. Hertwig, has come to hand, which contains a preliminary notice of microscopical observations upon the nervous system and sense-organs of the Medusæ. The authors appear to have chiefly studied these structures in the craspedote forms, but they also record observations upon two or three genera of the acraspedote Medusæ. The extensively distributed nerve-fibres and bipolar cells here described as covering the muscular sheet in the latter seem to have escaped their observation, but their account of the structure of the lithocysts and the modified epithelium in their neighbourhood in other species of Medusæ, so far as can be made out from the brief preliminary statement, corresponds in the main with the observations here recorded upon the similar structures in *Aurelia*.

Fig. 6. Two nerves of the submuscular plexus bending towards and looping round one another. Drawn under a power of about 600 diameters.

Fig. 7. A very dense interlacement of nerve-fibres situate between two of the nutritive tubes. Drawn under a power of about 100 diameters.

Fig. 8. Central part and ends of a nerve-fibre from the submuscular plexus of *Aurelia* (osmic acid preparation). The fibre took a nearly straight course across the direction of the muscular fibres. The whole of the fibre is not given: it was about 3 millims. in length.

a. End of fibre nearest polypite with motorial end-plate enlargement, *p*.

b. Middle of fibre with bipolar ganglionic enlargement.

c. End of fibre nearest to margin of umbrella.

Drawn under a power of about 600 diameters.

Fig. 9. Vertical section through the ectoderm covering the under surface of the umbrella of *Chrysaora hyoscella*.

c. Ganglion-cell.

e. Layer of epithelium-cells.

m. Layer of muscular fibres.

Drawn under a power of about 400 diameters.

Fig. 10. Isolated cells of the nerve-epithelium of *Aurelia aurita*.

A. Three of the long ciliated cells in conjunction.

b. Thickened border.

c. Cilia.

f. Fixed extremity branching into fine fibres.

n. Nuclear dilatation.

B. A single cell, similar to the foregoing.

C D. Isolated cells from the pigmented patch on the intermediate portion of the lithocyst.

h. Fine hairlet.

n. Nuclear dilatation.

p. Enlarged free end of the cell loaded with brown pigment.

v. Varicosities on central end of the cell.

E. An otolithic cell with two adherent columnar cells. The ends of these, which are turned away from the otolith, are very delicate and branched.

Figs. 11–16 represent a series of views (drawn under a magnifying power of about 600 diameters, but not to scale) of various parts of the same nerve-fibre, but only about half of the whole length of the fibre is represented. Any other fibres that happened to be visible in the same field of the microscope are also delineated. The clear margin around each fibre giving an appearance resembling a sheath is distinctly seen in all. In all the series the fibre is marked *xx*. The direction of the subjacent muscular fibres is in all parallel to the upper and lower margins of the paper, and is sketched in at one or two places.

Fig. 11. End of fibre nearest to margin: near its commencement is seen a fusiform nucleated swelling.

Fig. 12. The next part of the fibre. It exhibits two lateral branches, which take the direction of the muscular fibres, and soon become lost amongst them.

Fig. 13. The central part of the fibre with its interpolated nerve-cell. A small nucleus adheres to one end of the cell, which perhaps belongs to a sheath represented by the clear surrounding of the cell.

Fig. 14. The next succeeding portion of the fibre. Here there are two such nuclei adhering to the sides of the fibre. A nerve-fibre termination, *t*, occurs in this field. Also a nerve-cell, which is only prolonged at *one* end into a nerve-fibre, *c'*.

Fig. 15. The nerve-fibre now comes into relation with a large number of other fibres; it then takes a sharp bend, nearly at right angles, and very shortly after can be traced to its termination in a bifid extremity. This is represented in fig. 16.

Fig. 17. Meridional section through the margin of the umbrella of *Aurelia aurita*, the section passing through the middle of a lithocyst (semi-diagrammatic).

b, Basal; *i*, intermediate; and *t*, terminal portion of the lithocyst.

c. Cushion covering the lithocyst.

ect. Ectodermic covering of lithocyst.

ect'. Ectodermic covering of under surface of umbrella with the cut ends of the muscular fibres, *m.f.*

ect''. Ectodermic covering of upper surface of umbrella.

f.n.i. Fovea nervosa inferior.

f.n.s. Fovea nervosa superior.

m. Jelly-like mesoderm; *m'*, layer of mesoderm between ectoderm and entoderm of lithocyst.

n.c. Nutritive canal passing to the interior of the lithocyst and continuous at its extremity through the stalk *n*, with the clump of the otolithic cells, *o.c*. None of my sections show a communication of this canal with the exterior, as commonly described (see HUXLEY'S 'Invertebrates,' p. 135).

p. Pigmented patch on upper surface of intermediate portion.

Fig. 18. Vertical section (tangential to the margin of the umbrella) through the base of the lithocyst and the fovea nervosa superior. Letters as in previous figure. The fibrous stratum under the ectoderm of the fovea nervosa superior is seen to be in continuity with that under the entoderm of the nutritive canal. In the engraving of the figures this fibrous stratum has been imperfectly rendered, and in some places has been altogether omitted.

Fig. 19. A small portion of entoderm lining the nutritive canal near the fovea nervosa inferior, with two delicate processes of (mesodermic?) cells, simulating nerve-fibres, passing towards the epithelium of the canal.

Fig. 20. Vertical meridional section through the margin of an *Aurelia* near one of the lithocysts, showing the rudimentary organ described in the text (note to p. 569). The extremely dark appearance imparted to it is a mistake of the engraver.

ect. Bell-shaped projection formed of thickened ectoderm and occupied by a prolongation of the nutritive canal, *n.c.*; the thickened entoderm of which is seen to pierce its ectodermic covering and project as an otolithic clump, *o.c.*

ect'. Ectoderm of under surface.

ect'' Ectoderm of upper surface of umbrella.

m. Mesoderm.

r.n.c. Radial nutritive canal cut obliquely. This is seen to be connected to other canals by a layer of entodermic cells, *end.*, indicating an adhesion of originally separated tracts, such as are seen in *Chrysaora*.

Postscript.

(Received October 16, 1878.)

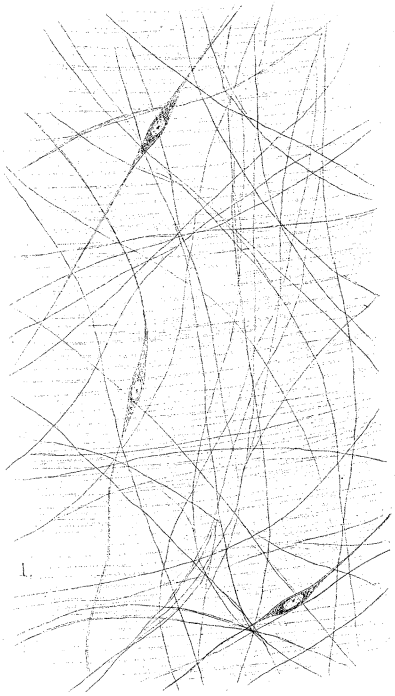
It was not originally my intention, in submitting my observations upon the nervous system of *Aurelia aurita* to the Royal Society, to add to the length of the communication by introducing an account of the general literature of the Medusæ, and for this reason: that in looking through the various papers upon the subject to which I had access I could find no observations (beyond those of Haeckel, referred to at the beginning) that had any direct bearing upon the immediate subject of this article. I was fully aware of the fact that fibres had been described *in the jelly-like tissue*, and, more than this, I was familiar with the aspect of these fibres; but since both from their situation and appearance there could be no idea of their nervous nature, or of their having any connexion with those described in this paper, it seemed to me unnecessary to refer specially to them. And the same with regard to previous observations upon the "marginal bodies," which had not before, so far as I knew, been submitted to the more modern methods of histology, and especially had not been examined by means of sections, which are necessary for throwing light upon the intimate structure of such objects. But my friends thought differently, and, yielding to their advice, I was preparing an account of the literature of the Medusæ to take the form of an Appendix to this article, when the appearance, in the spring of this year,

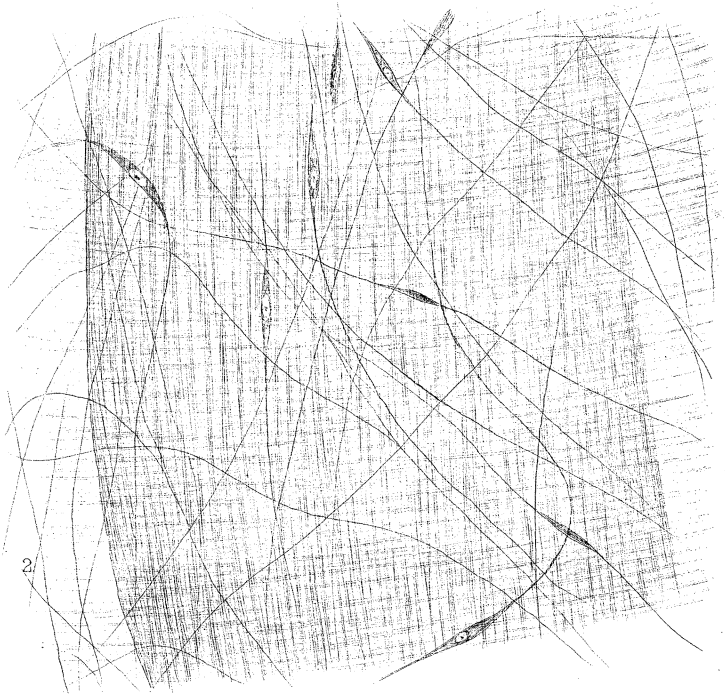
of the monograph by the Brothers HERTWIG,* in which the literature of the whole subject is treated of in an exhaustive manner, rendered superfluous any further action on my part. As to the work of the Brothers HERTWIG it is difficult to do justice to the carefulness of the descriptions and illustrations, and the philosophical way in which the subject is treated. Unfortunately, their supply of *Aurelia* seems to have been limited, and altogether their observations upon the Acraspeda have been comparatively few, although the types studied were well selected. This will probably account for the fact that the subumbrellar plexus which I have described in *Aurelia* has escaped their notice. Moreover, the nervous character of the epithelium of the foveæ near the lithocysts is not alluded to by them, probably because in the acraspedote species which they chiefly examined the epithelium of these parts has not so distinctly the character in question as it has in *Aurelia.* In *Chrysaora hyoscella*, for example, the ectoderm of the superior foveæ is throughout like that of the rest of the upper surface of the umbrella.† I had hoped to have continued and extended my researches this year, and indeed spent some little time on the coast of Brittany with this object, enjoying the hospitality of M. LACAZE-DUTHIER'S experimental laboratory at Roscoff. But my hopes were disappointed by the adverse weather which prevailed during my stay there, and I succeeded in obtaining but few specimens. Nevertheless I was enabled to place one fact beyond doubt—the existence, namely, of nerve-fibres in the velum of some at least of the Craspedota. On page 128 of their work, the Brothers HERTWIG speak of having only by the most careful search been able to make out the existence in two genera (*Trachynema* and *Cunina*) of fine fibrils, *perhaps of nervous nature*, taking a radial direction in the velum beneath the epithelium of the under side. In a specimen of *Thaumantias* (species ?) I observed in the living animal distinct nerve-fibres like those I had seen in the subumbrella of *Aurelia.* They passed outwards from the nervous ring, becoming gradually finer until lost near the free edge of the velum, and since they exhibited no nucleated enlargement I conclude with the Brothers HERTWIG that they spring from ganglion-cells in the ring.

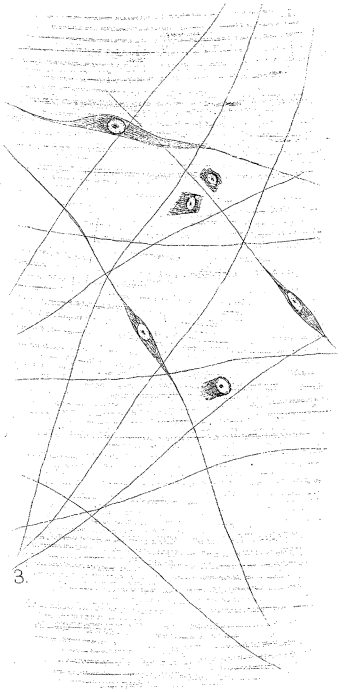
October, 1878.

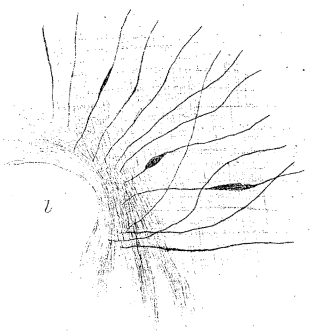
* Das Nervensystem und die Sinnesorgane der Medusen. Monographisch dargestellt von OSCAR HERTWIG und RICHARD HERTWIG. Mit 10 lithographirten Tafeln. Leipzig, 1878.

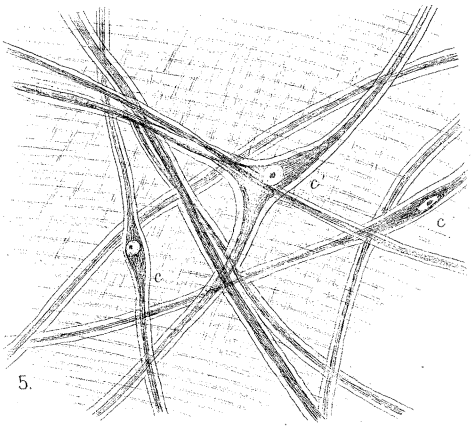
† CLAUS (Studien über Polypen und Quellen der Adria. Denkschriften der Wiener Akademie, 1877) seems to have noticed the peculiar character of the ectodermic cells in this fovea in *Aurelia.* He has advanced the hypothesis that it represents a rudimentary olfactory organ, and has given it a name in accordance with this hypothesis; but it would be difficult to put the opinion to experimental proof. The ganglion-cells in the subumbrella of *Chrysaora* are also noticed by CLAUS, but his statement as to the existence of ganglion-cells under the nerve-epithelium I am unable to confirm.


1.

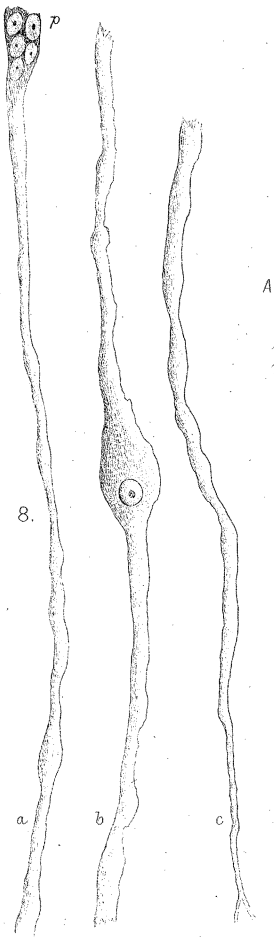

2.


3.

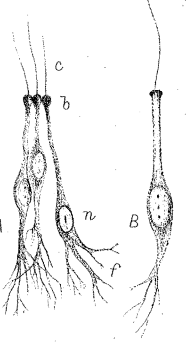

l

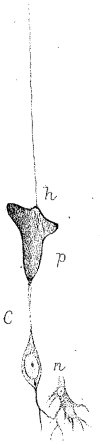


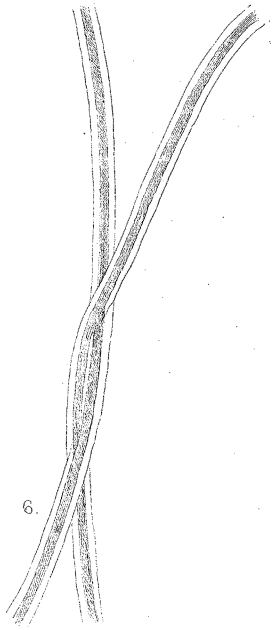
5.

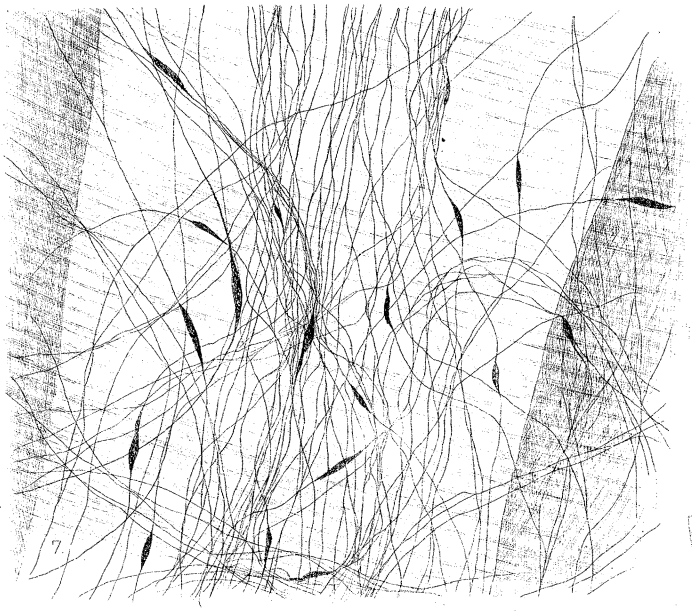


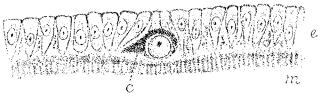
8.



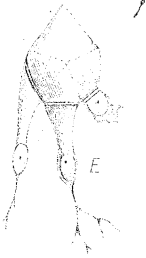



6.

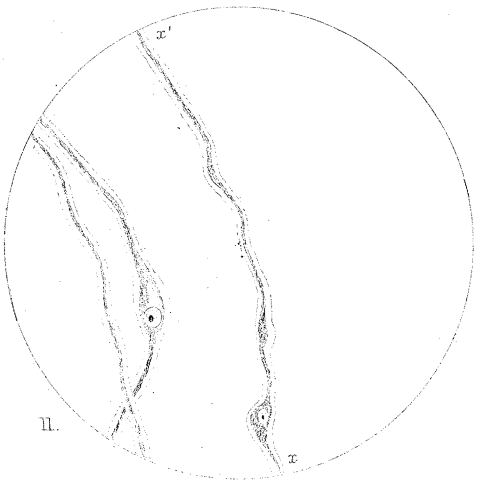

7.

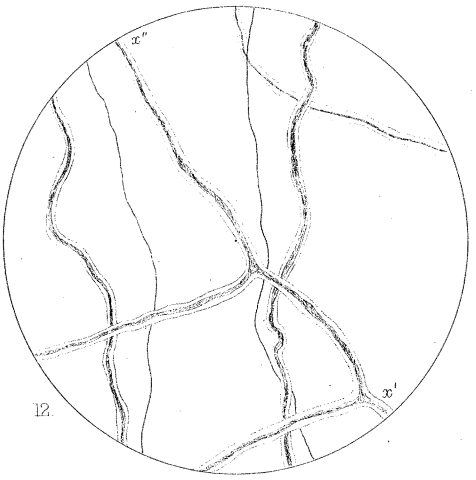


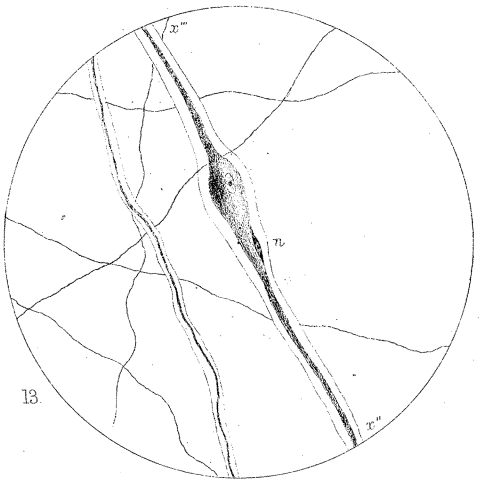
9.

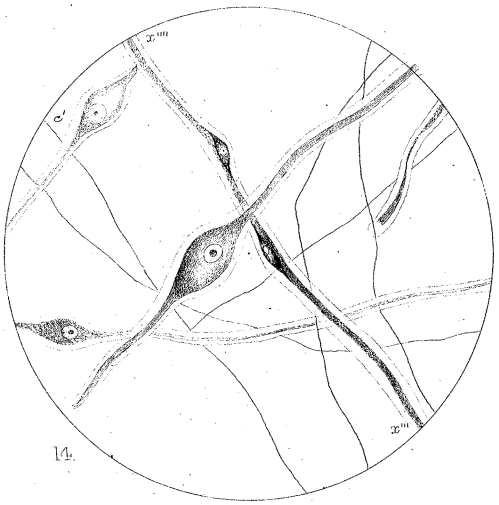


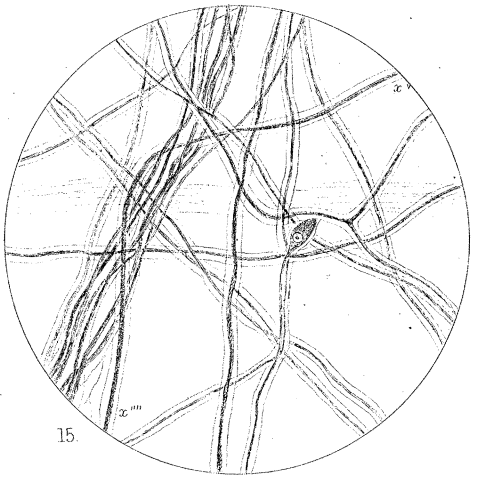
West, Newman & Co. sc.

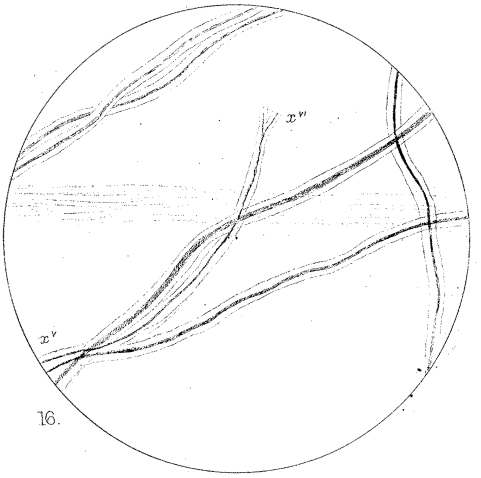


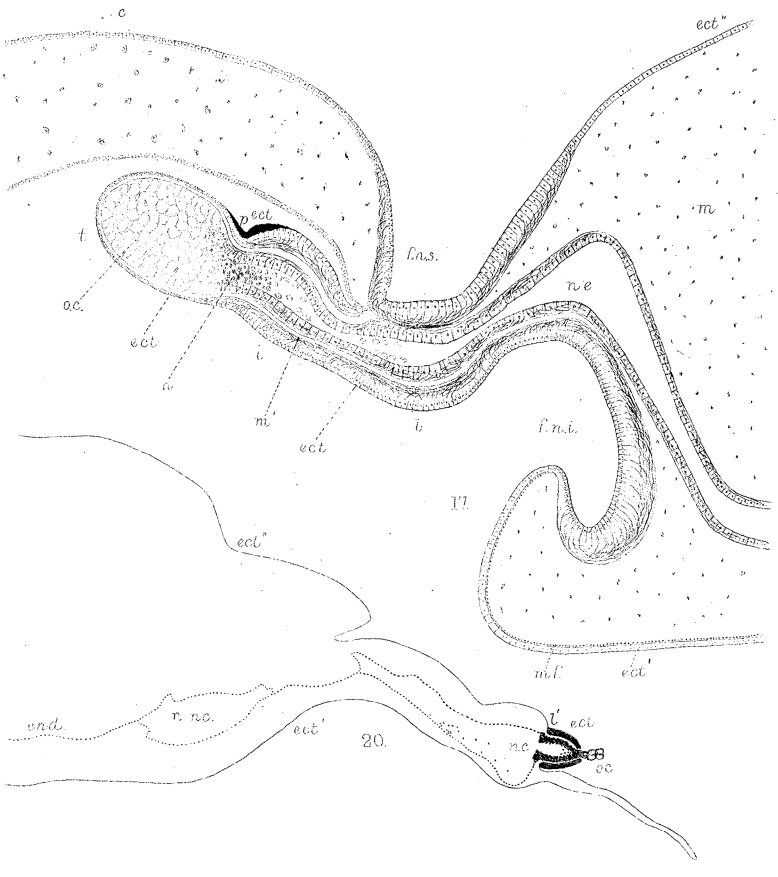


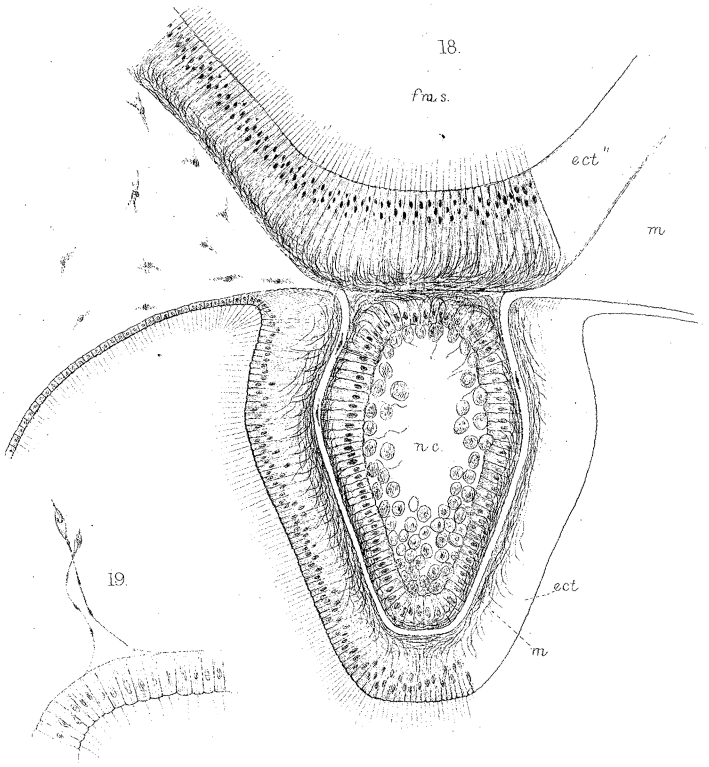












West, Newman & Co. sc.