

XXXVI. *Researches on the Development of the Spinal Cord in Man, Mammalia, and Birds.* By J. LOCKHART CLARKE, F.R.S.

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IN the Philosophical Transactions for 1859, I showed that, in the adult spinal cord of Man and all vertebrate animals, the white columns as well as the grey substance are everywhere interspersed with granular nuclei, of which some are attached to the sheaths of the primitive nerve-fibres, while others are imbedded in the intervening connective tissue. In the grey substance these nuclei are more abundant than in the white, and have much resemblance to many of the free nuclei or cells, which are certainly in connexion with nerve-fibres, and with which they are freely intermixed. With the hope of throwing some light on the histological relation between these and the other elementary tissues of the cord, the following inquiries into their development were undertaken.

The histology of the development of the spinal cord in Birds and the higher animals had already been begun by BIDDER and KUPFFER*, and pursued a little further by KÖLLIKER. The results of their investigations are comprised in the following statements:

1. After the closing of the laminæ dorsales, the cord at first consists of a canal, the walls of which are composed of cells of one uniform kind, and disposed in a radiating form.

2. In the next place, this wall of cells divides into two layers, of which the outer forms the grey substance, while the inner one appears as the lining of the central canal.

3. The white substance makes its appearance later than the grey, by the cells of which it is without doubt furnished as an outer layer or covering. The white columns are four in number, two on each side; and to these a white commissure is added. There are no lateral columns; those which are so called are subsequently formed as an extension of the anterior columns†.

The investigations of which I now communicate the results were made on embryos of the domestic fowl, of the Sheep, Pig, Ox, and Man. The fluid employed in the process of hardening was at first a weak solution of bichromate of potash, and then a similar solution of chromic acid. When sufficiently young, the embryos were immersed in the solution without mutilation; but in the more advanced states of development the spinal cord was previously uncovered.

* Untersuchungen über die Textur des Rückenmarks, und die Entwicklung seiner Formelemente. Leipzig, 1857.

† KÖLLIKER, Entwicklungsgeschichte des Menschen und der höheren Thiere. Leipzig, 1861, pp. 259, 260. MDCCCLXII.

In a foetal sheep nine lines in length, a transverse section was made through the spinal column and cord, at the upper part of the lumbar enlargement. The section of the cord was of an ovoid form, with its longer axis before-backward, but was somewhat broader at its anterior than its posterior half (see Plate XLV. fig. 1). The grey substance occupied nearly the whole of its area, but formed an irregular outline which was not concentric with the surface of the section. The central canal was a mere slit or fissure extending backward and forward to near the surface of the grey substance, particularly at its posterior end. Around this fissure was a somewhat dark layer, which was broad along the sides, as well as in front, where it formed a nearly semicircular projection beyond the rest of the grey substance, and was covered externally by the rudiment of the anterior commissure (fig. 1, *a*). Posteriorly it reached quite to the surface of the cord, being hitherto uncovered by the white columns, and was joined to its fellow of the opposite side by a shallow bridge of the same kind of substance. When examined by means of high magnifying-powers, this layer was seen to consist of closely aggregated nuclei connected together by a continuous network of short fibres. The nuclei in size were a little unequal, but their average diameter was about equal to that of the blood-globules. In shape, also, they were somewhat diversified from the round to the oval, the pyriform or the variously angular; but were all intermingled without regularity or order. From the inner border of the layer, that is, from the verge of the canal, the fibres, although they formed an irregular network with the densely aggregated nuclei, had nevertheless a tendency to radiate outward to the rest of the grey substance. From the outer side of the layer, at its posterior extremity, a somewhat dark and curved process (*b*), forming the lateral boundary of the posterior grey substance, extended outward and terminated in a roundish but imperfectly defined mass (*b'*), midway between the anterior and posterior extremity of the section. This mass, however, was uninterruptedly continuous with the outer border of the layer surrounding the canal, as well as with the anterior grey substance, by means of a paler portion composed of similar material. The surface of the mass and concave surface of the process which joined it to the posterior extremity of the section were overlaid with the rudiments of the posterior white column (*c*, fig. 1). In section this column had an oval figure, and covered only about the two anterior thirds of the posterior grey substance, leaving the other convex third entirely uncovered, except by the rudimentary integuments. By means of a sufficient magnifying-power, it was clearly seen that at the surface of the grey substance the fine network of fibres between the closely aggregated nuclei was directly continuous with the fibres of the white column with which it was overlaid. Fig. 2 represents a portion of a transverse section of the posterior grey and white substances at their points of junction, magnified 420 diameters: *a* is an inner part of the white column, and *b* is an outer part of the grey substance, consisting of nuclei and a [close network of fibres continuous with *a*. Through the same network nuclei were connected with some of the fibres of the posterior nerve-roots (*d*), which ran obliquely outward and forward, and made their exit at the anterior border of the posterior column, to enter the intervertebral ganglion (*e*).

The anterior grey substance (*f*, fig. 1) was of a somewhat triangular form, with one of its angles behind and the other two in front. The posterior angle, which projected a little into the lateral part of the antero-lateral column, consisted of a very distinct and dark group of nuclei, and was separated from the posterior grey substance (*b'*) by a much paler structure, composed chiefly of longitudinal and radiating fibres, which formed the rudiments of the lateral column. The anterior and outer angle was more obtuse (like a right angle rounded off), and consisted also of a distinct and dark, but larger group of nuclei, from which the majority of the anterior nerve-roots (*g*) originated, and then proceeded outward and forward, to join the posterior roots which escaped in the same direction from the intervertebral ganglion. At its inner side, the triangular mass, like the posterior grey substance, was continuous with the layer surrounding the central canal by a nucleated network of the same kind.

Throughout the whole of the *posterior* grey substance there was no diversity in the appearance either of the nuclei or of the close network of fibres by which they were connected. In the *anterior* grey substance, however, there was a slight diversity in the appearance of both. The nuclei contained in the separate groups already described were not *larger*, but they were less round or oval, or more irregular in shape, than those of any other part of the section, either anterior or posterior. They had also some tendency to aggregate into small, irregular and imperfectly isolated clusters, which were interspersed with granules and united by a looser and also irregular network, so that the entire structure had more or less the appearance of a sponge-like arrangement. In the central layer surrounding the canal, and of which the inner portion constitutes the epithelium, the nucleated network had a radiating tendency, which decreased on extending outward. In the parts between the separate groups or masses of grey substance, the nuclei were densely but uniformly aggregated, and the network of fibres was less distinct.

The antero-lateral white columns (*h*) were very small in proportion to the quantity of grey substance. Behind, where they joined the posterior columns, they were much shallower, and reduced, indeed, to a mere fringe on each side, sunk in the depression between the anterior and posterior grey substance, from which they were developed as the rudiments of the so-called lateral column. Hitherto the anterior median fissure had no existence, but fibres proceeding from the anterior nerve-roots on each side could be seen to cross each other transversely in front of the epithelial layer which surrounded the canal. These transverse fibres were the rudiments of the anterior commissure.

Surrounding the white columns and enclosing the intervertebral ganglia, there was a quantity of loose tissue, which in front formed a deep layer (*i*), connecting the cord with the body of the vertebra (*jj*), and consisting of a nucleated network, the meshes of which were transversely extended. The nuclei of this network, although much less numerous than those of the grey substance of the cord, differed from them but little in general appearance. Their connecting fibres, however, were thicker, coarser, less granular, and directly continuous, at the surface of the anterior commissure, with

similar fibres which radiated forward from the epithelium (*a*) surrounding the front of the canal. At its opposite or anterior border—or rather anterior part, for it had no distinct border—this nucleated tissue became directly continuous with that which formed the body of the vertebra (*j j*). This body consisted of a dense mass of closely aggregated nuclei, similar at its circumference to those of the connective tissue, but somewhat different in shape toward the centre, where they were round, oval, elongated, angular, and often curiously crescentic. They were all connected by fibres which, nearer the circumference, where the structure was looser, could be very easily distinguished; but in the centre they were less distinctly seen between the densely-crowded nuclei. Near this centre was a circular spot (*k*), the section of a longitudinal cylinder, surrounded by a thick wall resembling the wall of a cartilage-cell and enclosing several closely aggregated nuclei, connected by short fibres. These nuclei were round, oval, pyriform, or otherwise irregular in shape, and rather larger and more granular than those by which they were surrounded.

The spinal cord and vertebral column of the Sheep at this period of development have a considerable resemblance to those of the chick on the fifth day of incubation. In the latter, however, the different parts of the grey substance are more distinctly marked. Fig. 19, Plate XLVII. represents a transverse section of the vertebral column and spinal cord, in the sacral enlargement of the chick, on the fifth day, and magnified 60 diameters. The section of the *cord* was nearly a perfect oval. There was no trace of the rhomboidal sinus or ventricle which in the adult bird separates its posterior lateral halves*. The epithelial layer (*a*) immediately surrounding the canal was clearly defined and easily distinguishable from the rest of the grey substance. It was somewhat broader behind, where it reached the surface in the form of an arch. On each side of it the posterior grey substance (*b*) consisted of a pyriform mass, nearly covered by the rudiments of the posterior white column (*c*), and separated by a triangular and much lighter space from the anterior grey substance (*f*), which had a nearly quadrangular form, but was separable into two different masses, of which the outer was greyer and of an oval shape. From both of these the anterior nerve-roots (*g*) originated and escaped from the anterior and outer angle of the grey substance. Along the posterior half of the epithelial layer (*a*), its nucleated network was arranged in a connected series of arched radiations, which extended into the pyriform mass of grey substance on the same side (*b*). From this substance another very evident series of separate fibres ran directly forward to that part of the *anterior* grey substance (*f*) from which its nerve-roots chiefly arose. Neither these nor the arched fibres just mentioned as radiating from the epithelium could be seen so distinctly in the Sheep. Although the grey substance consisted of the several separate masses above described, yet there was but little diversity in the appearance of its structural elements. Its nuclei, generally, were rather smaller than in the section of the foetal sheep represented in fig. 1.

The cylindrical column (*k*) in the centre of the body of the vertebra (*j j*), and corre-

* See Philosophical Transactions, 1859, Plate XXIII. figs. 34, 35, and 36.

sponding to the *chorda dorsalis* of fishes and reptiles, was at least five times as large in diameter as that of the Sheep, and somewhat different in the arrangement of its elementary parts. It consisted of a loose honeycomb structure with large vacant spaces, formed by a coarse network of fibres, with a nucleus at each point of their junction (see fig. 45, *a*, Plate XLVIII.). Around the cylinder, elongated nuclei giving off fibres in a circular direction were arranged in concentric layers.

In a foetal sheep a little larger than that first examined, and measuring exactly 1 inch in length, a section of the spinal cord from the same region as before (the upper part of the lumbar enlargement) presented the appearances seen in fig. 3, Plate XLV. The canal, as a sword-shaped slit, extended behind-forward through nearly the whole of the grey substance. Immediately surrounding it was a bulbous or club-shaped layer of nuclei, with its bulbous end (*l*) posterior and reaching the surface in the middle line, but partially covered on each side by a portion of the posterior column (*c*). At this latter part it was less clearly defined, and gave off a process of grey substance, which extended outward and forward beneath the rest of the white column (*c*), and terminated in a rounded but imperfectly circumscribed mass (*b*). From about its middle to its anterior extremity the narrower portion of the club-shaped layer consisted of a nucleated meshwork of epithelium with an outwardly-radiating tendency; but on passing backward to the bulbous end, this appearance was confined to the wall of the canal, and moreover became less distinct, while at the same time it was gradually lost amongst the densely aggregated nuclei in the lateral part of the bulb.

The anterior grey substance presented nearly the same aspect as in the section represented in fig. 1. There was a very evident decussation, or crossing of fibres from the opposite roots of the nerves, in front of the canal; but, as in the last section, there was no anterior median fissure.

In the elements of the grey substance there was scarcely any perceptible advance in development. Some of the nuclei in the anterior masses seemed in a trifling degree to have increased in size, become more irregular in shape, and to be connected by a network which had rather more of the sponge-like arrangement.

The antero-lateral columns had somewhat increased in depth. Behind, where they joined the posterior columns, they were much shallower than elsewhere, and formed, on each side, the so-called lateral column (*h'*), which was sunk in a depression between the anterior and posterior grey substance.

The posterior white columns (*c*, *c*) were also deeper than in the previous sections. Behind, they were bevelled on to the exposed surface of the central club-shaped layer; and in front, where they joined and overlapped the lateral columns, they terminated in prominent but rounded edges, to which the posterior roots of the nerves (*d*) were attached.

There is every reason to believe that the fibres of the white columns are developed from the grey substance as prolongations of the network by which its nuclei are connected.

In foetal sheep of exactly 2 inches in length, it was found that the different parts of the spinal cord already described had become more or less modified in form, size, and relative arrangement, that new parts had been superadded, and that the structural elements of the grey substance had undergone considerable alterations. Fig. 4, Plate XLV. represents a transverse section of the cord from the same region as before, viz. the upper part of the lumbar enlargement. Here we at once perceive that each lateral half of the grey substance is fashioned into very distinct anterior and posterior cornua (f , & $l\ b$), which are partially separated from their fellows of the opposite side by an anterior and a posterior median fissure (m , n), both of which were absent in the former sections, and now come into existence, as we shall presently see, as a *consequence* of the development of the cornua. We also observe that the anterior half of the central slit represented in the preceding figures has dilated into an oval canal (o), which is near the centre of the section. Moreover it will be seen that two new portions of the posterior white columns (p, p) have made their appearance on each side of the posterior median fissure. Let us now consider the course of the developmental growth by which these changes have been gradually effected. First, then, it may be remarked that in fig. 4 the anterior cornua are formed by a growth of the grey substance forward and inward, in front of the canal, from the imaginary line (f'), which corresponds to the line of limit of the anterior grey substance (f) in fig. 3. The anterior white columns (h, h) extend in the same direction around the growing ends of the cornua, until only a narrow space or fissure is left between their inner borders in the mesial line. In this way is formed the anterior median fissure (m) in front of the commissure, which projects into it as a conical process. During these changes in the anterior part of the cord, the posterior grey substance ($l\ b$, fig. 3) grows obliquely outward and backward ($l\ b$, fig. 4); while its anterior angle (at b) becomes further removed from the posterior angle of the anterior cornu (f'), and is separated from it by a broader and deeper indentation, which is the rudiment of the neck or cervix cornu posterioris. This space or indentation is filled up and overlaid with the lateral column (h'), which has reached the level of the posterior column (c) and assumed a convex surface. This so-called lateral column differs from the rest of the white substance in being subdivided into a much greater number of small but separate fasciculi of various shapes, by means of a remarkable system of radiating fibres which proceed both from the grey substance between the cornua and the epithelium surrounding the canal. A radiation of fibres, however, but of much less extent, takes place from the whole circumference of the grey substance.

At the commencement of these changes, the central fissure or canal represented in fig. 3 reaches the surface of the posterior grey substance. The growth of this substance is then continued not only backward, but *outward*, or divergent from the mesial line, while in the intervening angular and gradually increasing space between it and this line (fig. 4, n) there are developed on each side two new pyramidal columns of longitudinal fibres (p, p'), which increase in depth in a corresponding proportion. Of these, the outer one (p), which is much the larger, rests on the back of the cornu, over which it ultimately

blends with the *outer* portion (*c*) of the posterior column previously developed. The inner and smaller column (*p'*) is in general more conspicuous and distinct in the dorsal and cervical than in the lumbar region, as shown in figs. 5, 6, & 7. The opening of the original canal or slit between these additional columns constitutes the posterior median fissure (*n*), which is now occupied by blood-vessels and pia mater in connexion with radiating fibres from the central epithelial layer.

We see, then, that the direction taken by the developmental growth of the posterior grey substance is just the reverse of that which is followed by the anterior. The changes which occur in the former, and the consequent production of new columns, have much resemblance to some of those that take place in the upper part of the cord during its transition and development into the medulla oblongata. In the course of those changes the central canal retreats further and further to the posterior part of the medulla, until at length it opens on the surface in the form of the fourth ventricle. In a corresponding proportion the posterior cornua diverge, while from their roots on each side of the mesial line the posterior pyramid is developed *. The cases, however, are not exactly parallel.

Returning to the interior of the grey substance, we find that a variety of changes, more or less important, have occurred,—first, in the disposition and destination of some of its parts; secondly, in the structure and arrangement of its constituent elements. First, then, we may observe that the club-shaped layer surrounding the central fissure or canal, as represented at *l*, fig. 3, has lost its defined outline and become very much diffused. Behind the oval canal, on each side of the mesial line (at *q q*, fig. 4), it forms the inner half of the cervix cornu posterioris, which subsequently contains the posterior vesicular column, or nucleus of the cervix. Hitherto, however, it consists only of a closely aggregated mass of nuclei, which become gradually more diffused on its outer side, where it joins the rest of the grey substance. Passing backward and outward and then forward in the direction *l b*, as an arched layer near the posterior border of the cornu, it terminates in the dark mass (*b*) within its outer angle or point. In the space between this arched layer and the posterior border of the cornu, the nuclei are less closely aggregated, and thus constitute, with their intervening network, a paler lamina (*r r*), which is the rudiment of the *gelatinous* substance. In the adult cord, as I showed on former occasions, the space occupied by the above-described arched layer of nuclei contains numerous bundles of nerve-fibres continuous with the posterior roots. On its inner side, near the centre of the cornu, there is a somewhat paler space, which is continued forward and outward, in a curve, to the border of the grey substance at the bottom of the lateral column. This is more conspicuous in the dorsal region, as shown in figs. 5 & 6.

On tracing the club-shaped layer forward along the side of the median line, we observe that its outer part has lost the defined outline which it possessed in section 3,

* See my memoir on the "Medulla Oblongata," Philosophical Transactions, 1858, Plate XII. figs. 13 & 14, *b* Plate XIII. fig. 16; Plate XIV.; and Plate XV. fig. 19.

and has gradually blended with the anterior grey substance; while its inner border forms the epithelial layer (*s*) surrounding the central canal. Along the *sides* of the canal, the epithelium, as regards its constituent elements, differs but little in appearance from the rest of the grey substance. The only apparent differences are, that its nuclei are less closely aggregated; that the fibres radiating through their interspaces from the verge of the canal, and which are thicker, are consequently *seen* to be more continuous and branched; and that a few of its nuclei are larger, while others are more elongated or fusiform at right angles to the axis of the canal. Nor is it bounded externally by any definite line, but is continuous, as a nucleated network, with that of the anterior cornu. From the posterior margin of the elliptical canal its radiating fibres extend outward and backward into the posterior cornua, and directly backward between them into the posterior median fissure. In *front* of the canal, however, the epithelium has a somewhat different arrangement. At this part it forms a deeper and more distinct layer, containing more of the fusiform nuclei, which are elongated in a direction forward, and terminate at each extremity in a fibre. At the sides of this layer the nuclei with their fibres are curved inward, but become progressively straighter as they approach the middle line (see figs. 4 & 8). Posteriorly their processes or fibres are thicker, and attached by their extremities to the margin of the canal; while anteriorly they converge across the anterior commissure, as a conical network, into the anterior median fissure, where they become directly continuous with the fibres of the pia mater and connective tissue enveloping numerous blood-vessels and derived from the circumference of the cord (*m*, figs. 4 & 8). In many cases the epithelium in *front* of the canal differs but little in appearance from the rest of the layer, except that the principal fibres of the network converge forward to join the process of pia mater in the anterior median fissure. In such cases it has a general resemblance to that seen in fig. 9, Plate XLV., which exactly represents a portion of the canal and surrounding grey substance of a human foetus of nine weeks, magnified 420 diameters. It was taken from the same foetus as the section represented in fig. 8, Plate XLVI. *o* is the anterior part of the canal; *s, s*, between the canal and the outer line, is the layer of epithelium, which on each side, however, is seen to be gradually continuous with the anterior grey substance, *f*; while in front it terminates in a conical network of connective tissue interspersed with nuclei, and continuous (at *m*) with the pia mater of the surface.

I have next to show that the elements of the grey substance, which in fig. 3 were nearly uniformly alike, have in fig. 4 become more or less modified both in structure and arrangement. In fig. 3 every nucleus had a plain or smooth appearance, without any trace of granular contents or of a distinct enveloping membrane. In fig. 4, however, both these modifications of structure had taken place; and although the observation of this fine distinction might seem to be trivial and unimportant, it will nevertheless be seen, as we proceed, to be well worthy of attention. It was also observed that in section 3 the nuclei were very nearly of the same size in all parts of the grey substance. In section 4, however, those of the anterior grey substance had everywhere

increased in diameter; while those of the posterior grey substance, as far forward as the posterior level of the canal, had scarcely, if at all, advanced in size. In all the darker parts of the latter they were still very closely aggregated, but less so than in fig. 3; so that the network of fibres by which they were connected was conspicuous in a corresponding proportion. Fig. 10, *b*, Plate XLV., represents some of the nuclei and their connecting fibres, from the arched layer (*lb*) of the posterior cornu in fig. 4, magnified 670 diameters*. In the section, however, although it was exceedingly thin, the nuclei were rather more crowded in that part; but exactly the same appearance is presented where a very thin portion has been shaved to an edge.

Throughout the whole of the *anterior* grey substance the average size of the nuclei is about twice as great as in the *posterior* grey substance, and therefore about twice as great as in every part of section 3. Their increase in diameter begins rather abruptly near the posterior level of the oval canal. They have also become more granular, more distinctly circumscribed by well-defined walls, and lie at greater distances from each other. The tissue which supports them has still a reticular structure, but is looser, more open, and in the central portion of the cornu consists of a sponge-like network of coarser fibres, which are more or less granular and connected with the nuclei by irregular aggregations of granules. Fig. 12, at *v*, Plate XLVII., is a faithful representation of this peculiar arrangement, which can be more intelligibly represented than described. In the middle of the cornu, where it is traversed by the central fibres of the anterior nerve-roots, as they run directly backward, the structure has very much the appearance delineated in fig. 11, Plate XLVII. But in the antero-lateral parts of the cornu (*w*, *w'*, figs. 4 & 7, Plate XLV.), where the groups of large nerve-cells are developed, it has a kind of honeycomb arrangement in the form of circular or somewhat irregular cavities or cells, which are large, but variable in diameter, and frequently in close apposition, but often separated by angular interspaces containing each a nucleus encrusted with granules. Fig. 12, *x x*, Plate XLVII. is a very exact representation of a portion of the outer or lateral group (*w'*, fig. 7, Plate XLV.). The walls of the cavities and the granular network are directly connected with the tissue of the antero-lateral white columns at *y*, *y'*. Within each cavity is a nucleus, which is sometimes in or near the centre, sometimes more excentric, and sometimes close to the wall. The nucleus is imbedded in granules, which are generally seen to connect it to the wall, and which in some instances occupy the whole, in others only part of the cell; in the latter cases they aggregate in a variety of forms†.

Within the posterior angle or shoulder of the anterior cornu is a remarkable dark and nearly triangular group of nuclei (fig. 4, *f'*, Plate XLV.), which differ from the rest only in being rather larger, and more closely aggregated.

The roots of the nerves may be very distinctly traced into the grey substance (see

* By some mistake this figure is marked in the Plate as $\times 420$ diameters.

† The separation of the granular masses from their cell-walls, and the stellate form which they sometimes assume, seem due to the action of the chromic acid.

fig. 8, Plate XLVI.). The anterior roots (*g*) are attached to the anterior column, which they traverse transversely inward to reach the anterior cornu (*f*), within which their fibres diverge and cross each other in different directions. A large number proceed backward along the lateral part of the cornu, some of them running in succession outward to the lateral column (*h'*), while the rest reach the triangular group of nuclei just pointed out, within the posterior angle of the cornu. Another set of fibres run more directly backward, through the central part of the grey substance (*f*), where they join in the general network, and appear as represented in fig. 11, Plate XLVII.; while some curve inward to decussate, in front of the canal, with their fellows of the opposite side, in company with others proceeding forward and inward around the canal from the posterior grey substance. (See also fig. 3, Plate XLV.)

The posterior roots (fig. 8, *d*, Plate XLVI.) have no immediate connexion with the lateral columns, and are attached solely to the posterior, through which they diverge in a direction backward and inward to reach the grey substance (*l b*). On entering this substance many of them evidently become finer by subdivision, and contribute to form the network by which the nuclei are connected. Fig. 10, Plate XLV. is a faithful representation of a very thin transverse section near the extremity of the posterior cornu, through which the roots (*d*) are entering; at *b* they are seen to become continuous with the general network. In the same way many of the fibres of the posterior columns are connected with nuclei of the grey substance. (See fig. 15, I, Plate XLVII.)

In foetal sheep of 3 and 4 inches in length, there was no remarkable alteration in the shape and disposition of the grey and white substances in the region corresponding to fig. 4; nor was there any great difference in the appearance or arrangement of the constituent elements. Fig. 13, Plate XLVI., represents a transverse section of one, and part of the other, lateral half of the spinal cord, near the middle of the lumbar enlargement, of a foetal sheep, 4 inches long; and fig. 14 shows a similar section of the middle of the lumbar enlargement of a foetal ox, 5 inches long. Here we see that nearly one-half of the posterior grey substance still consists of a dark layer of closely aggregated nuclei, which differ but little in size and general appearance from those of section 4, Plate XLV. This dark layer constitutes the *caput cornu posterioris*. Fig. 15, I, Plate XLVII. is a longitudinal section of it near its outer border, or the posterior extremity of the cornu, where it is overlaid and crossed in different directions by the decussating fibres of the white column. As the posterior (*l b*, fig. 14) merges into the anterior grey substance (*f*), the nuclei become larger, while the network which supports them becomes coarser and looser (II, fig. 15, Plate XLVII.). In the posterior part of the section, the very irregular and granular meshwork of fibres appears to extend nearly equally in all directions; but towards the anterior part (opposite II) the meshes have a tendency to elongate in a direction forward; while many of the nuclei are elongated in the same direction, and have tapering granular masses extending from their ends. These latter appearances, however, are more conspicuous on the inner side of the cornu, nearer the median line. On proceeding forward, the network assumes the peculiar

honeycomb structure already observed in section 4, and represented at *x*, fig. 12, Plate XLVII. Here, however, the layer is deeper, but variable in depth. Fig. 15, III, Plate XLVII. is a portion of a longitudinal section, behind-forward, through this layer of large cells of the anterior cornu (*w w*, fig. 14, Plate XLVI.). It will be remarked that these more or less globular cells are closely grouped, and frequently in actual contact; that in many instances they are seen to be filled with the granular material surrounding their nuclei; and that the nuclei themselves are sometimes larger than those in other parts of the anterior grey substance, and contain each either one large globular nucleolus or two. With the general network of this layer the anterior nerve-roots may be seen to be continuous.

In foetal sheep of 6, 7, and 8 inches in length, further changes were observed to take place in the grey substance, but they were limited chiefly to its posterior and middle portions. In the *caput* cornu posterioris, the nuclei, although still aggregated in vast numbers, were comparatively less numerous and more widely separated from each other than in fig. 15, and somewhat larger; the network of fibres by which they were connected was also coarser and looser; while a complete system of transverse, longitudinal, and oblique nerve-fibres were very readily distinguishable.

In the middle portion of the grey substance, that is, between the *caput* cornu (*l l*, fig. 13, Plate XLVI.) and the groups of large nerve-cells (*w, w'*), the coarse network already described and represented in fig. 15, II, Plate XLVII. was now interspersed with a great number of cells, which differed from each other both in size and shape (fig. 16, Plate XLVII.). The majority were fusiform in a direction before-backward, and either more or less wavy and sigmoid, or perfectly straight, with processes which extended occasionally to an amazing distance. In some cases, as at *a*, fig. 16, a fusiform cell was bent into the shape of a crescent, and formed part of the circumference of an oval or circular space. In other cases it was converted into a triangle by giving off two processes from one end, which became broader, and embraced, as before, part of the circumference of an open space (*b*, fig. 16). In many of these cells, especially of the smaller kind, the nuclei were only faintly, or not at all, observable.

The groups of large nerve-cells (*w, w'*) had undergone scarcely any appreciable change, and presented nearly the appearances represented at III, fig. 15.

With regard to the changes which ensue in the structure of the cord on approaching the period of birth, I shall confine my remarks chiefly to those particular points which relate to the development of its constituent elements. During these successive changes, the *gelatinous substance* becomes more and more conspicuous as a distinct lamina around the end of the *caput* cornu. Along its margin the peculiar nerve-cells observable in the adult are gradually developed, after the manner of those already described in the middle of the grey substance (fig. 16, Plate XLVII.); while its arciform, transverse, oblique and longitudinal fibres increase in number in a corresponding proportion. Coincident with this development of the gelatinous substance, the nuclei in the dark and inner part of the *caput* cornu become less numerous, while its transversely-radiating, longitudinal,

and variously-oblique fibres, continuous with roots of nerves, increase in a corresponding proportion and pursue a more definite course. But even at an advanced period of utero-gestation (at the fifth month, for instance, in the human foetus) the *caput cornu* is still very thickly crowded with nuclei, and presents an opaque and uniformly dark mass, like that of the foetal ox of 5 inches long, represented in fig. 14, Plate XLVI. By the end of the *sixth* month, however, it is much less opaque, and contains a much smaller proportion of nuclei, but a correspondingly large proportion of fibres running in the directions already indicated. Fig. 40, Plate XLVIII. represents, under a low power, a transverse section of one lateral half of the grey and white substances of the cord from the upper part of the lumbar enlargement of a human foetus of six months*. Here the *caput cornu posterioris* (*l b*) is at once distinguishable from the *cervix*, not only by its bulbous expansion, but also by its much darker colour. The gelatinous substance, however, and arciform fibres are not very strongly marked, but were readily detected under high magnifying-powers. In the larger and darker portion of the *caput*, the nuclei were imbedded in a fine granular network, and were most numerous at its sides, particularly its outer side. Amongst this network were the longitudinal and oblique fibres, to which in the adult cord the opacity of this part is chiefly due. The majority of the nuclei were round, but some were oval, and a few had an angular form. They were finely granular, were enclosed in distinct envelopes, and differed from each other in size. Their average diameter was rather below that of the blood-globules of the same foetus. Scattered irregularly amongst these were a few others, which, in addition to the fine granules, contained each a larger, central and globular nucleolus. These latter nuclei were identical in appearance with the nuclei of the larger nerve-cells.

By referring to the same figure (40), it will be seen that each inner half of the *cervix cornu* (*q*) is occupied and rendered convex by a remarkable group of nucleated cells, which I formerly described very fully under the name of the posterior vesicular column†. In this region of the cord (the upper part of the lumbar enlargement), not only are these columns larger than in any other region, but the cells which they contain are for the most part of the largest description, and similar in appearance to those of the *anterior cornu*: but their development is somewhat later. In the human foetus, at the sixth month, however, they are perfectly developed, and assume a variety of stellate forms, with processes that extend in all directions. They are closely invested by a thin

* Through the kindness of Mr. HATHERLY, of Belgravia South, I was fortunate enough to obtain this fine male foetus within about an hour after death. The brain and spinal cord were immediately removed and hardened in the most gradual and careful manner by immersion, first, in an exceedingly weak solution of bichromate of potash, then in stronger solutions of the same salt, and finally in a solution of chromic acid. The preparations, of which a series of representations are given in Plate XLVIII., are the most beautiful that I have ever succeeded in obtaining from the *human foetus*. I must also acknowledge my obligations to Mr. R. DUNN, of Norfolk Street, Mr. WHITNEY, of Westminster, Mr. PAINTER, of Westminster, and Mr. HUNT, of South Belgravia, for their kindness in providing me with foetuses.

† Probably a better term for this column would be the nucleus of the *cervix cornu*—*nucleus cervicis cornu*.

sheath or envelope, which is prolonged on to the processes and connected with the intervening reticular tissue. It is beyond all doubt (for it was distinctly seen in preparations of this foetus) that many, at least, of the processes, by repeated subdivision, become continuous with the fine network of this intervening tissue. See fig. 17, Plate XLVII.*

In the same foetus the *tractus intermedio-lateralis*, or tract of grey substance (*t*, figs. 41, 42 & 43, Plate XLVIII.) which projects into the lateral column between the anterior and posterior cornua, was in a nearly complete state of formation.

The epithelium, also, surrounding the canal was completely developed, and on no occasion in the *human* cord have I seen it so perfect and beautiful. In the adult human cord it is very difficult to obtain a good view of the exact form and arrangement of its constituent elements, which are often, especially in the cervical region, confusedly heaped together in a mass that entirely fills up the canal†. In the *fœtal* cord, however, the canal is larger, the epithelial layer is deeper, and its elements in general are more uniformly arranged. In the case now under consideration these elements were more than usually distinct. In some regions of the cord they were exactly alike throughout the whole circumference of the layer. In such regions they consisted partly of oval, and partly of still more elongated nuclei or cells, which gave off a process from each extremity, and were arranged with their longer axes at right angles to the axis of the canal. The *nuclei*, however, were placed at *different distances from the canal*, and were so disposed as to lie in nearly close apposition, and form a compact stratum. Their *central* processes, which reached the *inner* margin of the layer, were consequently of *different lengths*; and the length of these processes, in general, was inversely proportional to their thickness. Here and there between the rest of the nuclei, narrow interspaces were occupied by remarkably slender and fusiform bodies, of which the tapering ends reached the verge of the canal, without the intervention, apparently, of any distinct processes. At their *peripheral* or outer ends all these nuclei tapered into fine fibres which crossed each other in every direction, and frequently divided into smaller branches, to be continuous with the network surrounding the epithelial layer. In the lumbar region of the cord the nuclei were *not* exactly alike around the whole circumference of the canal. In the anterior third of the layer they were in every respect similar to those which I have just described; and at the front of the canal, the fibres proceeding from their peripheral ends were seen to cross the commissure, and become directly continuous with the process of pia mater within the anterior fissure. Frequently this process consisted almost entirely of blood-vessels containing numerous well-preserved globules, and at the bottom of the

* This statement is confirmatory of the descriptions which I first gave of the ramifications of the processes of the nerve-cells of the spinal cord.—Philosophical Transactions, 1851, p. 614.

† On a former occasion (Phil. Trans. 1859, Part I. p. 455, and Plate XXII. fig. 55) I showed that the canal in the human cord is sometimes double, or rather that two secondary canals, as it were, are hollowed through the mass of epithelium just mentioned. The same fact has since been made the subject of a paper by Dr. JOH. WAGNER, in REICHERT-DUBOIS's Archiv für Anat. &c. 1861, p. 735. Even in the fourth ventricle, at the calamus scriptorius, in Man I have frequently found on the surface a kind of short supplementary canal formed by a double layer of epithelium enclosing a narrow space.

fissure it gave off a brush-like radiation of fibres that were continuous with those of the epithelium. In other sections, blood-vessels from the same process extended right and left, as well as backward and around the canal. Some of the fibres from the epithelial cells on each side of the front layer, after crossing the anterior commissure, penetrated the anterior white columns, at the sides of the fissure, and were lost in the tissue between its longitudinal fibres. Behind, a narrower portion of the epithelial layer was composed of the same kind of elements as those which were found in front; and in a similar way fibres proceeding from their peripheral ends converged *backward*, to be continuous with blood-vessels and pia mater in the *posterior* median fissure. Other fibres, also, from the same source could be traced into the posterior white columns. Around the remaining portion of the canal the epithelial layer was narrower and somewhat different in structure. It consisted, for the most part, of round and of rather oval nuclei, irregularly disposed, and in connexion with the fibres on the outside of the layer. These nuclei, like the others just described, were finely granular, and in every way similar to a multitude of those which are scattered through the grey substance, and, as I shall presently show, through the tissue between the fibres of the white substance*.

The large nerve-cells of the anterior cornu had assumed the shape and general appearance which they present in the adult cord. Like those of the cervix cornu posterioris,

* This description of the epithelium in the human foetus has a general resemblance to that which I gave of the same structure in the full-grown ox (Phil. Trans. 1859, p. 455, Plate XXII. fig. 53); but I have entered more particularly into details in the present case, on account of the close resemblance of the *oval* cells to the "olfactory cells" of the olfactory mucous membrane as first described by SCHULTZE in the Frog and Pike. It is believed by SCHULTZE and others, that the processes of these "olfactory-cells" are directly continuous with fine fibres of the olfactory nerves. Such a connexion, however, has never, so far as I am aware, been actually *seen*. I have myself traced these nerve-fibres quite into the epithelial layer, but have not hitherto quite satisfied myself of their actual termination. Six years ago I showed that beneath the epithelium of the pharyngeal sac of the common earth-worm, a ganglionic plexus of nerves terminates in a network of single nucleated fibres, resembling in form a capillary network (Proc. Royal Soc. Jan. 1857, No. 24. vol. viii.). It is true that AXEL KEY (Archiv für Anat. &c. 1861, p. 329) has described and figured in the tongue of the Frog, a remarkably conspicuous communication between nerve-fibres and cells which correspond to those of SCHULTZE. But no such communication was observed either by BILROTH or HOYER (Archiv für Anat. &c. 1858 & 1859) in the same organ. On the fibres proceeding from the "olfactory cells" of SCHULTZE, there are slight granular dilatations, which I have found most remarkable in the Pike. On the fine fibres which surround the canal in the human foetus, as above described, and with which the processes of the oval epithelial cells are connected, I have also observed exceedingly minute dilatations. These fibres, as already stated, are evidently continuous, and identical in appearance with the fine fibres of the pia mater on the outside of the cord. Without, therefore, denying the *possible* continuity of the "olfactory cells" with true nerve-fibres, we must be so much the more cautious in admitting their *actual* continuity as an anatomical fact, until confirmed by actual *observation*. That the fibrous structure immediately surrounding the spinal canal is of the nature of connective tissue, was first maintained by myself (Phil. Trans. 1851) in opposition to STILLING, who described it (together with the epithelium, which he had not detected) as a "circular commissure" composed of *grey* nerve-fibres. In the human brain, also, the processes of the epithelium which extends from the aqueduct of Sylvius along the under surface of the posterior commissure, have clearly been seen by myself to pass through fissures in that commissure, to the pia mater on its opposite surface (Proceedings of Royal Society for June 20, 1861).

they were enveloped in delicate sheaths, which, however, were quite distinct from, although in connexion with, the surrounding reticular tissue (see figs. 12 & 15, Plate XLVII.). Many of their processes also were very clearly seen to subdivide, or to break up suddenly, into a multitude of fine branches to form part of the intervening network†.

I shall conclude my remarks on the development of the cord in the human and mammalian foetus, by a few observations on the development of its nerve-fibres. In a very young foetus it is difficult to obtain a satisfactory view of isolated nerve-fibres, and to detect the way in which their formation commences. According to my own opportunities of observation, they are not developed from nucleated cells, but rather by the extension of finely granular substance from round and oval nuclei. On this point, however, I cannot at present speak with confidence, and therefore leave it open for further inquiry. In the early stages—for instance, in a foetal sheep, or human foetus from 1 to 2 inches long—the fibres, in a *fresh state*, consisted of most delicately granular and nucleated bands, without any sharpness of outline or appearance of separate border. But the nuclei were far from being numerous, either in the nerves or in the white columns of the cord. In fig. 8, Plate XLVI. their average number is shown in the white columns of the left side, in a human foetus of about nine weeks. As development, however, advances, their number increases considerably, while the fibres to which they belong acquire a more sharply defined outline or border, which in some parts of its course appears darker and thicker than in others. In fig. 9⁺, Plate XLV., on the left, is an exact representation of a separate fibre in a fresh and unprepared state, from the sciatic nerve of a human foetus of four months, magnified 670 diameters; and in the same figure, on the right, is represented the appearance of several such fibres as they lie side by side in a bundle. Fig. 18, Plate XLVII. shows a small portion of a transverse section of the posterior white columns of a human foetus of five months, magnified 670 diameters. When compared with the same parts in fig. 8, Plate XLVI., which is magnified only 50 diameters, it shows how much the nuclei have increased in number. Some of these nuclei belong to the sheaths of the nerve-fibres, others to the tissue by which their sheaths are connected. As the period of birth approaches, they are again reduced in number; but even in the adult cord, as I showed on a former occasion, they are scattered at intervals between the fibres of all the white columns. In structure they are altogether similar to the nuclei of the foetal epithelium above described, and differ from them only in having a somewhat less average diameter.

With regard to the development of the spinal cord in Birds, I need dwell only on those particulars in which it differs from that in Man and Mammals. Fig. 19, Plate XLVII. shows the appearance of the grey and white substance in a transverse

† I have described and figured a similar ramification of the processes of the cells around the base of the peduncle of the olfactory bulb, and in the anterior perforated space, and have frequently observed the same appearance in the convolutions of the cerebral hemispheres. (See *Zeitschrift für Wissensch. Zoologie*, Bd. xi. Hft. 1. Taf. v. fig. 6.)

section of the upper part of the sacral enlargement of the chick, on the fifth day of incubation. The central dark layer (*a*) surrounding the canal is still uncovered by the posterior columns (*c, c*), and forms the posterior surface. The grey substance hitherto is not divided into distinct cornua; there is no trace of a posterior median fissure, and only the first rudiments of an anterior (*m*). In the course of four days we find that rapid and remarkable progress has been made in developmental growth. Fig. 20, Plate XVII. represents the appearances in a transverse section of the same part, at the end of the ninth day of incubation. By a succession of changes similar to those that have been described in the foetal sheep, both the anterior and posterior cornua have become fully developed, with corresponding median fissures. In each anterior cornu (*f*) is a thick cylindrical column of large nerve-cells. These cells, however, for the most part, differ both in shape and mode of formation, from those that are found in the corresponding part of the human and mammalian foetus. The majority are fusiform from before backward, and continuous with the antero-posterior fibres which reach the posterior cornu. They are not formed within large round and oval spaces with thick walls, like those already described in the mammal, but grow side by side in close apposition by the extension of substance from the ends of their nuclei, apparently after the manner of those in the central part of the grey substance of the Sheep and Ox, represented in fig. 16, Plate XLVII. Besides their antero-posterior processes, they send off others both outward and inward. The middle portion of the grey substance between this vesicular group and the posterior cornu contains a few isolated cells of the same kind.

The antero-lateral white columns (*h, h'*) have increased considerably in area, and the anterior median fissure between them is much deeper, while the canal (*o*) is reduced in size and limited to the centre of the section. The caput cornu posterioris (*lb*), on each side, consists of a dark mass of closely aggregated nuclei, which are smaller than those in any other part of the grey substance. It is entirely covered by the posterior white column (*c p*), which, however, does not extend along the inner side of the cervix (*q*). The space between the cervix cornu (*q*) of one side and that of the other, and which, in the corresponding part of the adult cord of both the bird and mammal, is occupied by the inner and deep portions of the posterior columns, is now filled up by a bell-shaped mass of connective tissue (*n'*), which consists of a loose network of fibres connected at intervals with nuclei. The fibres of this tissue are also directly continuous with the connective tissue of the inner part (*p*) of the posterior white column, and with the network in the cervix cornu (*q*), along the inner border; but its fibres are coarser, and its nuclei are larger. Its deep portion, which is divided by a central raphè, forms the posterior wall of the canal (*o*), and constitutes its *epithelium* on that side; while its superficial portion extends on each side over the posterior white column (*p*), and is connected at its convex surface with the *pia mater* which surrounds the cord. In the lower part of the sacral enlargement (fig. 21, Plate XLVII.), the cervix cornu is united along the middle line with its fellow of the opposite side, and forms with it a single mass; so that only the extremities of the cornua surrounded by the posterior columns remain

apart from each other. Between these the space n , which here represents the posterior median fissure, is much shallower and narrower than in fig. 20, and widely separated from the central canal by the coalescence of the cervix (q) of each side. The loose and nucleated tissue (n'), however, with which it is filled is still connected, across this coalesced grey substance, with a number of fibres radiating from the epithelium around the posterior wall of the canal (o). On ascending the sacral enlargement, the posterior cornua become more and more deeply separated, until the division reaches the canal. Fig. 22 represents a transverse section about midway between sections 20 and 21. Here the space n between the cornua has, in section, the form of a deep cylinder filled with the loose nucleated tissue, of which the deepest portion itself constitutes the epithelium around the posterior wall of the canal, instead of being only connected with it, as shown in fig. 21, by a number of radiating fibres. As development advances, the inner part (p , fig. 20) of the posterior column gradually extends over the side of the cervix cornu (q), and replaces a corresponding proportion of the nucleated tissue (n'), until it reaches the median raphè at the back of the canal. On approaching the *middle* of the sacral enlargement, the entire lateral halves of the grey substance are more widely removed from each other, and joined only by the *anterior* commissure; for the *posterior* commissure has no existence. At the same time the canal is lengthened in a lateral direction, and opens behind, through the raphè or median fissure, to form the rhomboidal sinus, which is filled up with the remaining nucleated tissue continuous with the pia mater of the surface*.

I have now to describe the development of the intervertebral ganglia.

In the young foetus, the first thing that strikes the observer on looking at these ganglia, is their enormous size in comparison with the diameter of the spinal cord. Fig. 8, *e, e*, Plate XLVI. represents them as seen in a transverse section of the vertebral column of a human foetus of 9 weeks. In this section each ganglion appears nearly as large as the entire lateral half of the grey substance of the cord itself. It is closely invested by a fibrous sheath, which is prolonged on to the nerve-roots, and is continuous with the surrounding connective tissue, as well as with the denser nucleated tissue that constitutes the lamina (z) of the vertebra. In a foetal sheep of 1 inch in length, the ganglion consisted of a mass of closely aggregated nuclei or cells, connected together by a network of fibres. Fig. 23, *a*, Plate XLVII. represents a small portion magnified 420 diameters. The fibres connecting the nuclei or cells were continuous on the one hand with the nerve-roots which entered the ganglion, and on the other hand with the surrounding connective tissue. Their course was most conspicuous in an antero-posterior direction—that is, in the direction in which the nerve-roots spread through the ganglion. The nuclei or cells were about the same size as those of the grey substance of the cord to which they belonged, but were rather more varied in shape. Like them also, at this period of development, they had a plain and smooth appearance, without any traces of granular contents and of distinct enveloping membranes.

* Compare my figs. 34, 35, & 36, from the adult bird, Philosophical Transactions, 1859, Plate XXIII.

In a foetal sheep of about $1\frac{3}{4}$ inch long, it was found that a considerable proportion of the nuclei or cells had increased in size, but in a variable degree. Many of them were twice as large as those in the foetus of 1 inch, while others were still about the same size. Fig. 24, Plate XLVII. represents a small portion of the ganglion as seen in a transverse section of the spinal column and cord—that is, in the direction in which the nerve-roots enter and leave it. A great number of the nuclei or cells were also more diversified in shape; they were round, oval, triangular, irregular in outline, and variously stellate. By processes of different lengths and degrees of fineness all of them were connected with each other, as well as with fibres of the nerve-roots; and at the circumference of the ganglion this common network was continuous with the surrounding nucleated connective tissue, as at *b*, fig. 23, which represents a portion of the tissue connecting the outer part of the ganglion (*a*) with the lamina of the vertebra. Many of the round and oval nuclei evidently belonged to the connective tissue, and some few to the nerve-fibres which spread through the structure. The nerve-cells, although enlarged, had a smooth homogeneous aspect, and presented scarcely any traces of internal nuclei. Here and there, however, a faintly granular appearance was visible through their surface; and in some cases, as at *a*, fig. 24, a rounded but imperfectly-defined body, resembling an indistinct nucleus, might also be observed.

As development advanced, considerable changes were observed to take place in the appearance of the ganglion. At first, the principal changes consisted in an increase in the size and granular structure of a large number of the cells, while their nuclei remained still indistinct (see fig. 24⁺). Soon after, however, a striking alteration ensued both in the structure and form of the cells: fig. 25 represents a portion of the ganglion of a foetal sheep, about 3 inches long, transformed from those just seen in fig. 24⁺. Here the nuclei in the cells are large, well-defined, round or oval, and contain one, two, and in some instances three globular nucleoli, surrounded by numerous granules. The cells to which they belong vary considerably both in size and shape. The majority, however, are perfectly pyriform or cup-shaped, their tapering ends pointing in different directions, while the broader end of each is occupied, or as it were closed, by its nucleus. According to the position in which they lie, and their different degrees of foreshortening, in reference to the observer, they appear either round, oval or pyriform. Sometimes several of them lie side by side in a similar position, and are continuous by their tapering ends with a corresponding series of branches from one nerve-fibre. Lodged in the spaces between them are a number of small nuclei, of an angular, oval, or elongated form, and resembling those which belong to the sheath of the ganglion (see figs. 25 & 28). When exceedingly thin sections were very carefully examined under a sufficient magnifying-power, it might sometimes be observed that the nerve-fibres, in their course through the ganglion, divided into branches, which became continuous with the processes of the cells; and when the section was carefully broken up into minute fragments by means of fine needles, these appearances were found to be universal. The nerve-fibres were then frequently seen to consist of bundles of delicate fibrillæ, each of

which separated in succession from the rest to be connected with one of the nerve-cells. Fig. 26, Plate XLVII. is an exact representation of a thick fibre giving off a short branch, which immediately subdivided into two and perhaps other fine filaments, to join a corresponding number of cells. The lower and broken end of the fibre seemed to be split up into its constituent parts, and resembled the hairs of a brush. Very frequently a series of pyriform cells, in close apposition, but one in advance of the other, were arranged in a compact group around a common fibre, with a fibril of which each was connected by its tapering end. Fig. 27 represents part of such a group, magnified 420 diameters. The connecting fibrils were of different lengths, and sometimes so short that the small end of the cell seemed to arise from the fibre itself. Where the relative position of the cells forming a compact group is less regular, we have the appearance represented in fig. 28. Through such a group the nerve-fibres pursue a more or less tortuous course, giving off branches or their component fibrils in succession, and in all directions, to the cells between which they pass. In fig. 29, for example, a fibre, after giving off fibrils to be connected with the smaller ends of the two uppermost cells, continued its course between them to be connected by a fibril with the next cell, along the sides of which two other branches ran in a similar way until they reached the points of other cells; and so on in different directions and planes. Between the upper and lower ends of the figure the cells were broken off, and exposed the fibre and its short branches.

When separated from the group, a large number of the cells seemed to have scarcely any investment that might be called a distinct cell-wall; but still they were frequently more or less covered by a shaggy layer of delicate fibres (α , α' , fig. 30, Plate XLVIII.), by which in their natural position they appeared to be connected. This investment seemed to be an extension from the surface of the fibres or processes with which the cells were continuous, and occasionally entangled a small nucleus (α' , fig. 30). In some instances, as at b , it assumed the appearance of a thin, loose, and delicate sheath; while in others, as at c , it formed a more compact investment, to which the nuclei were more closely adherent.

As development progressed the cells somewhat enlarged, while their walls increased in thickness, and, like the nerve-fibres, were studded with an increasing number of small nuclei. Fig. 31, Plate XLVIII. shows a portion of one of the intervertebral ganglia of a foetal sheep, 8 inches long, magnified 420 diameters. Many of the cells, which had a globular appearance in their natural positions, were found to be pyriform when separated by dissection. Their walls were evidently prolongations from the surfaces of the nerve-fibres; the nuclei on the former were in every respect similar to those on the latter; and in both cases their number increased in the same proportion. Sometimes a nucleus was found at the point where a fibre was continuous with a cell; so that it was impossible to say whether it belonged to the one or the other. Fig. 32 represents a group of cells from the anterior part of an intervertebral ganglion of the chick, on the ninth day of incubation, at the point where the nerve-fibres are escaping to join the anterior roots. The

free surfaces of the walls have a shaggy structure consisting of fine fibres, by which they are connected with the walls of their neighbours, and apparently with the nucleated investment of the nerve-fibres which run between them *. Sometimes, in consequence probably of the action of the chromic acid, the cell-wall is removed to a little distance from the surface of the contained cell, but is still connected with it by fine fibres or processes. Now in the case of the large nerve-cells of the spinal cord, like those represented in fig. 12, *xx*, the thick cell-walls, as development advances, form part of the surrounding reticular tissue, with which the surface of the contained cells, still retaining a thin investment, is in a similar way connected by processes. Sometimes there remains around the stellate cell a more or less circular space enclosed by what seems to be the inner surface of the original cell-wall, of which the outer portion has blended with the surrounding tissue.

In the account thus given of the development of the spinal cord, I have carefully refrained from indulging in any theoretical views, and have confined myself solely to a faithful description of what was actually seen. A few remarks, however, are required in further explanation of some of the observed facts, and in reference to the conclusions that may be drawn from them.

We have seen that in its earliest stage of development, the spinal cord consists of a canal surrounded only by one uniform or homogeneous layer of small cells or nuclei, which are not distinguishable from each other in appearance, and are so closely aggregated as to seem in actual contact. To call this single layer the epithelium of the cord, appears to me about as incorrect as it would be to call the germinal membrane of the ovum the mucous or internal of the two layers into which it immediately separates; for in the second stage of its development, we find that this single and homogeneous layer constituting the entire substance of the cord, while it continues to increase in depth,

* The connexion of nerve-cells with each other by means of prolongations of their sheaths is well seen in many of the Invertebrata. Fig. 33 shows such a connexion between five cells, from one of the groups of ganglia composing the subœsophageal mass of the common Slug. The central space between these cells is occupied by portions of nerve-fibres running in different directions, as well as by connective tissue continuous with prolongations of the cell-sheaths. It is not, however, denied that some of the processes contain prolongations from the *interior* of the cells. These cells differ considerably both in size and shape. Many of them are enormous. In fig. 33, Plate XLVIII. they are magnified only 420 diameters, and in some parts of the ganglion they reach the prodigious size represented in fig. 34 under the same magnifying-power. The nuclei within the cells are also of extraordinary dimensions, and filled with exceedingly coarse granules, amongst which are a variable number of round nucleoli enclosing some finer granules. Between the larger cells are others of a much smaller but variable size, many of them not exceeding one-fourth the diameter of the *nuclei* of those represented in fig. 33. A great number of the cells are pyriform, and lie side by side in regular rows. The cephalic or supraœsophageal ganglion has an entirely different structure. It consists of two lobes, united above the œsophagus by a thick transverse band or commissure. The portion of each lobe on the side of the median line is a globular and finely granular mass, traversed by a multitude of exceedingly fine fibres proceeding from a somewhat hemispherical layer of small and closely aggregated cells, which partially encloses the inner mass, and forms the lateral crust of the ganglion.

undergoes a differentiation into two distinct layers—an inner, constituting the true epithelium, and an outer, constituting the grey substance; and although the former does not undergo the histological and morphological changes which subsequently take place in the mucous layer of the germinal membrane, yet it is probable that *after* the production of the outer or grey substance, it differs in its histological character from the originally homogeneous layer. This differentiation of structure proceeds very gradually, and is not at first marked by any decided line of separation, or by any difference in the appearance of the structural elements. At the same time there is gradually formed around, and apparently secreted from, the small cells or nuclei, a granular substance that forms into processes or fibres, and constitutes a continuous network by which all the nuclei or cells of both layers are uninterruptedly connected. In the grey substance itself there is at first little or no apparent difference in structure between its anterior and posterior portions, although in each portion darker and more-closely aggregated groups of nuclei may be observed in connexion with the roots of the nerves. But as development progresses, a diversity of structure ensues; for while the nuclei of the *posterior* grey substance, although rather more granular than at first, have scarcely advanced in size, those of the *anterior* substance have increased to double their original diameter, and are connected by thicker fibres, which form a coarser and more granular network. At the same time, around the separate groups of the latter substance, the granular network (seen in fig. 35, Plate XLVIII.) between the nuclei assumes a more sponge-like structure, as represented at *v*, fig. 12. Meanwhile, within the group, there are formed from the nuclei a number of large, roundish or irregular but adjacent cells, with thick nucleated walls (*xx*, fig. 12). It is quite evident that the nucleated tissue constituting the walls of these cavities and the network around them is in every respect similar in appearance to that which is very commonly assumed by the connective tissue of parts external to the cord, as may be seen, for instance, at *b*, fig. 23, Plate XLVII., which represents a portion of the connective tissue on the outer surface of one of the intervertebral ganglia, with the substance of which, however, it is directly continuous.

It appears, then, that in these early stages of development there are at least two kinds of free nuclei in the grey substance of the cord. The one kind appear to develop the general network of tissue which pervades the entire structure, but proceed no further; whereas each of the other kind, while connected with this network as well as with nerve-fibres, develops a nucleated cell with a nucleated wall which is still connected, and ultimately blended, with the surrounding reticular structure. In the cells of the intervertebral ganglia, although the process appears to be *essentially* the same, there is some difference in the appearance they present in the earlier stages of development. Fig. 23, *a*, Plate XLVII. is a small portion of one of the intervertebral ganglia of a foetal sheep, 1 inch long. Fig. 35, Plate XLVIII. is a portion of the dark group of nuclei in the anterior grey substance of the cord, destined to be developed into large nerve-cells, from the same foetus. In the former the nuclei are joined by more sharply defined fibres, and there is an absence of the delicate granular network surrounding

the nuclei in the latter. As development advances, these nuclei or small cells of the intervertebral ganglia simply enlarge, at first, but at the same time are connected with each other and with intervening granular nuclei by fine fibres, as shown in fig. 24, Plate XLVII. At a later period a very distinct and well-defined nucleus, surrounded by a variously shaped granular mass, makes its appearance within each cell; while its surface becomes the cell-wall, which at first is thin, but gradually increases in thickness. Now the surfaces of these cells are in connexion not only with the intervening nucleated fibres (as shown in fig. 24) which are continuous with the connective tissue forming the sheath of the ganglion, but also with the walls of the adjacent blood-vessels, as seen at *c, c* in the same figure; and it is probably through the medium of this nucleated tissue that the developing cells are supplied with nutritive fluid. Indeed, if we except the muscular fibre-cells, with which some of them are provided, the walls of the blood-vessels are only a part of the pia mater and connective tissue between them. On examining the layer of pia mater which immediately surrounds the cord, it may be seen to connect the walls of the blood-vessels which it contains with the sheaths of the intervertebral ganglia, and, through this, with the sheaths of their nerve-cells, on one side, and on the other side with the connective tissue or pia mater within the cord itself. In fig. 36, Plate XLVIII., *a a'* represent the outer surface of the cord; *b b* the outer part of one of the intervertebral ganglia; and *c c'* the intervening layer of pia mater, containing blood-vessels, *d, e*. On its left side, the walls of the vessels (*e, d*), containing some globules, are seen to be connected by a continuous and nucleated network with the sheath of the ganglion, *b b*; and from the right side of the walls a series of processes or fibres enter the cord (particularly at *a, a'*), in which they are continuous with the reticular tissue of both its white and grey substance. At *c'* there intervenes, between the transversely-cut vessel (*d*) and the cord, a layer of pia mater, from which similar processes are derived. These processes are not branches of the blood-vessels; and they enter the cord around the whole of its circumference. Now, in the anterior median fissure, it may be seen beyond all question, as already stated, that this layer of pia mater, with the walls of the blood-vessels which it contains, is directly continuous with the processes of the epithelium surrounding the front of the canal (see figs. 4, 8, 9, & 14); and therefore we are warranted in concluding that a similar continuity exists within and around the remaining parts of the cord. But this is only an *à priori* confirmation of what I long ago actually observed and described in the adult cord*. And since the sheaths of the nerve-cells have been shown to be continuous with, and indeed to form a part of, the reticular connective tissue of the cord, which is itself continuous with the pia mater of the surface, it is evident that the processes of the epithelium, the pia mater and connective tissue within the cord, the walls of the blood-vessels, and the sheaths of the nerve-cells must be all uninterruptedly continuous with each other. But the sheaths of the nerve-cells are certainly connected with the surfaces of their granular contents; and in the fully-developed cord, where the cell-

* Philosophical Transactions, 1851 and 1859.

sheaths are much finer and thinner, processes from the cells are continuous by fine subdivisions with the surrounding reticular structure, as shown in fig. 17, Plate XLVII. These observations, then, appear to throw important light on the question which I formerly proposed, as to whether there is any actual and essential difference between the connective and the true nerve-tissue, or "whether the connective tissue of the cord be intermediate in its nature, passing on the one hand into *nerve-tissue*, and on the other into *pia mater*"*. We have seen that the cell-sheath or wall is the product of, and indeed is constituted by, the very surface of the primitive nucleus or cell, and that, while it ever after remains in connexion with its contents, it forms a part of the surrounding connective tissue, which is itself a prolongation not only of the pia mater of the surface, as well as the walls of the blood-vessels, but also of the processes of the epithelium. But although there is this uninterrupted continuity between all the constituent elements of the cord—although, perhaps, the nerve-tissue actually changes by insensible degrees into the tissues with which it is continuous—and although the cell-wall, which forms part of the surrounding reticular structure, is a product of the primitive nucleus, there is yet no ground for believing that the connective tissue, as such, can ever develop itself into nerve-tissue, any more than that any one of the differentiated parts of a fully-developed organ can reproduce the entire structure; for the nerve-cell, although it develops from itself its own sheath, which forms part of the nucleated connective tissue, produces something more than this tissue, viz. the granular contents of the cell†.

We know that processes of the nerve-cells constitute the axis-cylinders of the vaso-motor nerves distributed to parts external to the cord; and therefore it seems probable that the finer processes which are lost by subdivision in the pia mater or connective tissue within the cord are the means of transmitting nerve-power to that tissue and to the coats of its blood-vessels, from which, by their uninterrupted connexion with them, as already shown, the nerve-cells in return receive their supply of nutriment.

* Philosophical Transactions, 1859, Part I. p. 442.

† There can be no doubt that a considerable proportion of the gelatinous substance and other parts of the posterior cornu are of the nature of pia mater; but amongst this there are numerous small nerve-cells. As I have dwelt, however, on this point in another place (Phil. Trans. 1859), I need not repeat my remarks.

EXPLANATION OF THE PLATES.

PLATE XLV.

- Fig. 1. A transverse section of the spinal column and cord in the upper part of the lumbar enlargement of a foetal sheep $\frac{3}{4}$ inch in length, magnified 60 diameters:—*h*, anterior white column; *f*, anterior grey substance; *g*, anterior nerve-roots; *c*, posterior white column; *b b'*, posterior grey substance; *d*, posterior nerve-roots; *e*, intervertebral ganglion; *a*, epithelial layer surrounding the front of the canal; *j j*, body of vertebra; *k*, chorda dorsalis; *i*, connective tissue uniting the body of the vertebra and intervertebral ganglia to the circumference of the cord.
- Fig. 2. A portion of the outer surface of the posterior grey substance (*b*) in connexion with the inner surface of the posterior white column (*a*); magnified 420 diameters; from the same foetus.
- Fig. 3. Transverse section of spinal cord in the upper part of the lumbar enlargement, magnified 60 diameters, from a foetal sheep 1 inch in length:—*h'*, lateral column.
- Fig. 4. Transverse section of spinal cord in the upper part of the lumbar enlargement, magnified 60 diameters, from a foetal sheep 2 inches long:—*h'*, lateral white column; *r*, gelatinous substance; *p, p'*, inner portions of posterior white column; *l b*, caput cornu; *n*, posterior median fissure; *q q*, cervix cornu; *w, w*, groups of large nerve-cells of anterior cornu; *o*, central canal; *m*, anterior median fissure.
- Fig. 5. Transverse section of the spinal cord of the same foetus, from the middle of the dorsal region.
- Fig. 6. A similar section from the upper part of the dorsal region.
- Fig. 7. Another, from the middle of the cervical enlargement.
- Fig. 9. A portion of the section represented in fig. 8, magnified 420 diameters:—*o*, anterior portion of the canal; *s s*, epithelium surrounding it; *f*, nuclei forming the anterior grey substance; *g*, inner bundle of anterior roots entering the grey substance; *h, h*, inner parts of the anterior white columns; *m*, anterior median fissure between them. The epithelium is seen to be continuous on the one hand with the network of fibres between the nuclei of the anterior grey substance (*f*), and on the other hand with the network of pia mater (*m*) prolonged from the circumference of the cord into the anterior median fissure.
- Fig. 9⁺. Fresh nerve-fibres from the sciatic nerve of a human foetus of four months: on the left is a single fibre; on the right several are seen as they lie together constituting a nerve.
- Fig. 10. A portion of the grey substance near the edge of the posterior cornu traversed by fibres of the posterior roots (*d*). From a foetal sheep $2\frac{1}{2}$ inches long; magnified 670 diameters.

PLATE XLVI.

- Fig. 8. A transverse section through the spinal column and cord of a human foetus of nine weeks, from the cervical enlargement; magnified 50 diameters;—*z*, lamina of vertebra; *z'*, muscular fibres.
- Fig. 13. One, and part of the other, lateral half of a transverse section through the lumbar enlargement of the spinal cord of a foetal sheep 4 inches long:—*lb*, caput cornu posterioris.
- Fig. 14. A similar portion of a transverse section through the middle of the lumbar enlargement of a foetal ox 5 inches long:—*lb*, caput cornu posterioris, consisting of a dark mass of closely aggregated nuclei. From the outer edge of this mass, as well as from that of the rest of the grey substance, nuclei are scattered in smaller numbers through the white columns.

PLATE XLVII.

- Fig. 11. Grey substance from the middle of the anterior cornu, traversed by anterior nerve-roots; from a foetal sheep $2\frac{1}{2}$ inches long; magnified 670 diameters.
- Fig. 12. Portion of the anterior grey and white substances of a foetal sheep $2\frac{1}{2}$ inches long; magnified 420 diameters:—*y y'*, internal part of the anterior white column, bordering the grey substance; *x x*, group of large nerve-cells in process of development; *v*, granular and nucleated network nearer the middle of the anterior cornu.
- Fig. 15. Portions of a longitudinal section of the grey substance of the same foetus, in a direction before-backward; magnified 420 diameters. I. Part of the caput cornu posterioris, intersected by the deep decussating fibres of the posterior roots, and posterior white column. II. Middle portion of the grey substance (between *b* and *f*, fig. 14), in which the nuclei are much larger, and the network between them becomes gradually coarser and looser as it proceeds forward. III. A group of the large nerve-cells of the anterior cornu (*w w*, fig. 14), surrounded by thick walls, with intervening nuclei.
- Fig. 16. Portion of a longitudinal section of the middle of the grey substance (corresponding to II, fig. 15), from a foetal sheep 8 inches long; magnified 420 diameters. Numerous fusiform, triangular, and crescentic cells have become developed in it.
- Fig. 17. Stellate nerve-cell from the nucleus cervicis cornu (posterior vesicular column) of a human foetus of six months; magnified 420 diameters. Some of the processes are seen ramifying and becoming continuous with the surrounding network. It is not often seen so distinctly as in this case.
- Fig. 17*. Cells from the posterior grey substance of a human foetus of four months; $\times 670$.

- Fig. 18. A portion of one of the posterior white columns of the spinal cord of a human foetus of five months, showing the numerous nuclei with which it is interspersed; magnified 670 diameters.
- Fig. 19. A transverse section of the spinal column and cord of the chick at the end of the fifth day of incubation; magnified 60 diameters.
- Fig. 20. A similar section of the cord at the end of the ninth day of incubation:—*n'*, large mass of nucleated connective tissue replacing the inner portion of the posterior columns.
- Fig. 21. A transverse section of the cord of the same, through the lower part of the sacral enlargement.
- Fig. 22. A similar section a little higher up, between figs. 20 & 21.
- Fig. 23. Part of an intervertebral ganglion and surrounding connective tissue of a foetal sheep 1 inch long:—*a*, nuclei or small cells of the ganglion; *b*, connective tissue on its outer surface; magnified 420 diameters.
- Fig. 24. The same from a foetal sheep $1\frac{3}{4}$ inch in length. The nerve-cells have enlarged and are connected by a continuous network with each other, with the nerve-fibres, with intervening granular nuclei, as at *b'*, and with nucleated fibres connecting the ganglion with the lamina of the vertebra, at *b*. At *a* indistinct nuclei are seen in the interior of the cells; magnified 420 diameters.
- Fig. 24*. Cells from the same at a little later period of foetal life; $\times 420$.
- Fig. 25. Portion of a transverse section of the intervertebral ganglion of a foetal sheep about 3 inches long. The cells have increased in size, are pyriform, a well-defined nucleus has made its appearance in each, and between the cells the interspaces are occupied by small angular or elongated nuclei.
- Fig. 25*. Cells from the intervertebral ganglion of a human foetus of nine weeks; from one of the ganglia represented at *e, e*, fig. 8, Plate XLVI.
- Fig. 26. A nerve-fibre dividing into branches to be connected with cells. From the intervertebral ganglion of a sheep 3 inches long; magnified 670 diameters.
- Fig. 27. Another fibre connected with cells by division.
- Fig. 28. A group of cells in their natural position connected with ramifying nerve-fibres; small nuclei occupy the spaces between them; magnified 420 diameters.
- Fig. 29. Portion of such a group, showing the manner in which the nerve-fibres are connected with it.

PLATE XLVIII.

- Fig. 30. Isolated nerve-cells from the same.
- Fig. 31. Group of cells from the intervertebral ganglion of a foetal sheep 8 inches long; magnified 420 diameters: each cell is enveloped in a thick nucleated sheath.
- Fig. 32. Group of cells, with nerve-fibres, from the anterior part of one of the intervertebral ganglia of the chick at the end of the ninth day of incubation; magnified

fied 420 diameters. At *a* the cells are in an earlier state of development, neither their walls nor their nuclei being yet very distinct.

- Fig. 33. Five large and two small cells from one of the group of subœsophageal ganglia of the common slug; magnified 420 diameters.
- Fig. 34. An enormous cell from the same; magnified 420 diameters.
- Fig. 35. Group of small cells or apparent nuclei, destined to be developed into the large cells of the anterior cornu, from a foetal sheep 1 inch in length. The cells are surrounded and connected by a delicate granular network.
- Fig. 36. Part of the spinal cord, intervertebral ganglion, and intervening pia mater from a foetal sheep 3 inches long:—*a a'*, outer surface of the cord; *b b*, sheath and outer portion of intervertebral ganglion, with some of the marginal cells; *c c'*, intervening pia mater; *d*, a blood-vessel cut transversely and full of blood-globules; *e*, another blood-vessel, running round the cord: at *a* transverse processes are seen proceeding from the nucleated wall of the vessel to the surface of the cord; at *a'* similar processes are given off from the pia mater, which is merely a continuation of the nucleated walls of the vessels. On the other side, the pia mater and walls of the blood-vessels are seen to be continuous with the nucleated investment of the intervertebral ganglion, *b b*.
- Figs. 37 to 44 are exact representations of transverse sections of the spinal cord of a human foetus, all magnified about 34 diameters. The actual and relative quantities of the grey and white substance are well seen in each.
- Fig. 37. A transverse section of the conus medullaris:—*l b*, caput cornu posterioris; *f*, anterior cornu; *o*, canal; *c*, posterior white column; *h'*, lateral white column; *h*, anterior white column; *m*, anterior median fissure; *n*, posterior median fissure.
- Fig. 38. A transverse section through the lower third of the lumbar enlargement:—*d*, posterior nerve-roots; *q*, posterior vesicular column; *w*, increasing groups of large nerve-cells in the anterior cornu.
- Fig. 39. A similar section through the middle of lumbar enlargement. The posterior vesicular column (*q*) forming the inner half of the cervix cornu has enlarged, but hitherto consists chiefly of a multitude of *small* cells. Through it and on its outer side several curved bundles of the posterior roots sweep forward and inward, and separate it from the outer half of the cervix, at the border of which are several dark spots, representing the cut ends of longitudinal bundles. In front of the canal (*o*) are the decussating fibres of the anterior commissure, and behind it is the posterior commissure. The group of nerve-cells in the anterior cornu has much enlarged.
- Fig. 40. Similar section through the upper third of the lumbar enlargement. Here the *cells* of the posterior vesicular column (*q*) or nucleus of the cervix cornu have increased considerably in size: they are nearly all equal to those of the anterior cornu. The groups in the anterior cornu are much diminished.

- Fig. 41. Section through the lowest part of the dorsal region, or upper end of the lumbar enlargement. Here the posterior vesicular column (*q*) is larger than in any other part of the cord, and consists chiefly of large, oval and stellate cells. Here also we first distinctly see the *tractus intermedio-lateralis* (*t*), a tract of smaller cells between the anterior and posterior cornua, and projecting in a conical form from the border of the grey substance into the lateral white column.
- Fig. 42. Another section, through the *middle* of the dorsal region. The posterior vesicular column diminishes in size.
- Fig. 43. A section through the *upper* part of the dorsal region; the *tractus intermedio-lateralis* (*t*) is very prominent.
- Fig. 44. Another, through the middle of the cervical enlargement:—*e'*, the posterior lateral fissure, through which the outer fibres of the posterior roots (*d*) are seen to reach the dark spots or longitudinal bundles on the outer side of the cervix cornu, with which they become continuous. These longitudinal bundles are more numerous here than in any other region of the cord. On the inner side of the cornu, other fibres of the roots are seen sweeping both around and within the posterior vesicular column (*q*). This column is here again large, but consists chiefly of a multitude of *small* nerve-cells. The groups of nerve-cells in the anterior cornu have again increased in size. These groups, and indeed the whole of the anterior cornu, as well as the outer part of the cervix of the posterior cornu, are supplied, as represented, on the left side, by a beautiful branch of a large blood-vessel (*v*), which enters through the anterior median fissure (*m*), and bifurcates right and left, at its bottom, through the anterior commissure. The parts behind the canal are supplied by other vessels running transversely and derived in part from a larger longitudinal vessel on each side of the canal, and of which the cut ends are seen in the figure. In the lateral white column is a somewhat oval space (*g'*) occupying nearly the whole of its area, and of a lighter and greyer colour than the rest. This is apparently due to a greater abundance of blood-vessels and pia mater. It is limited chiefly to the cervical and dorsal region. The wedge-shaped column (*p'*) on each side of the posterior median fissure, and forming part of the posterior white column, is very strongly marked in this figure. Its tapering end is gradually lost in the deep part of the column on its outer side. At this period they are limited almost entirely to the cervical enlargement; at an earlier period they may be traced lower down (see figs. 4, 5, 6, & 7).
- Fig. 45. Part of the chorda dorsalis of the chick at the end of the ninth day of incubation, with some of the surrounding cartilage-cells:—*a*, chorda dorsalis, consisting of a nucleated network of fibres, having precisely the appearance of connective tissue; *b*, cartilage-cells around its circumference, in different stages of development: in one the nucleus is seen undergoing division.

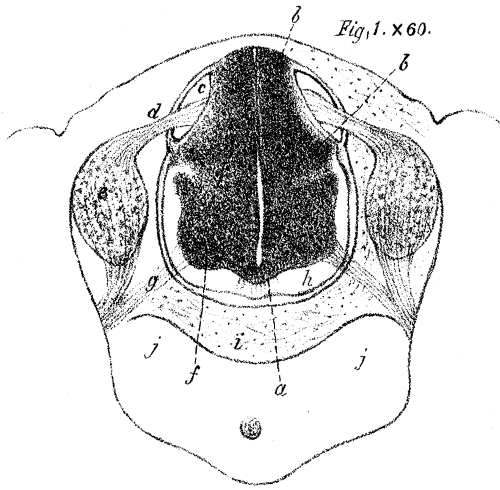


Fig. 10. x 420.

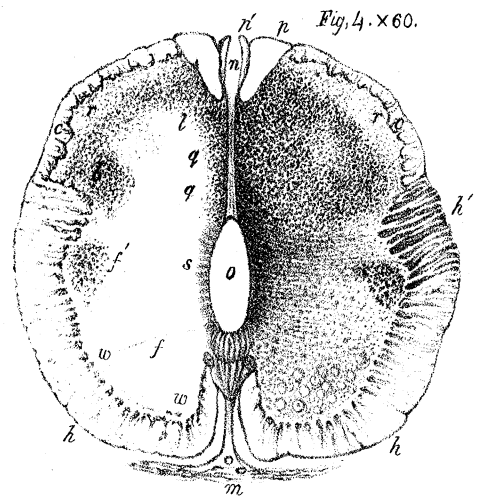
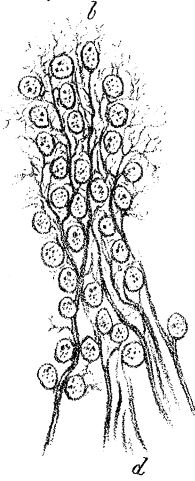


Fig. 3. x 60.

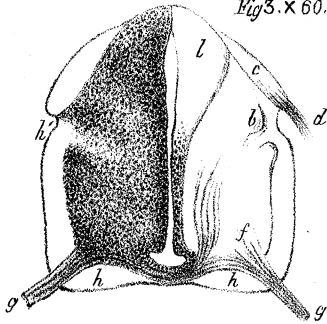


Fig. 2. x 420.

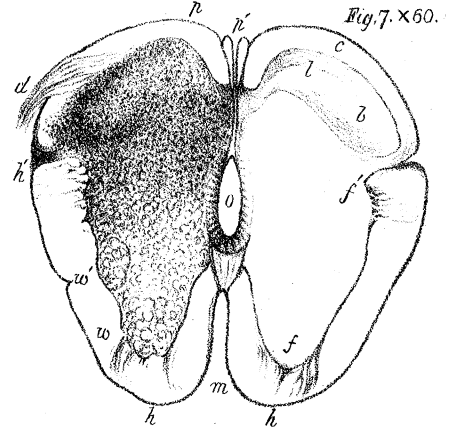
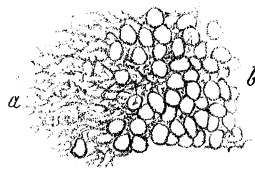


Fig. 5. x 60.

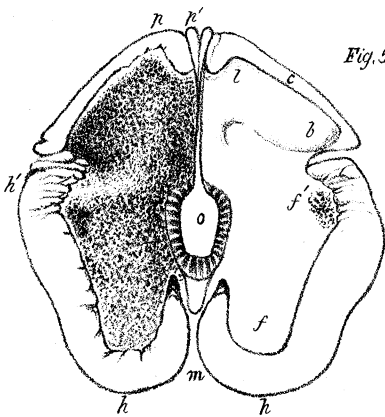


Fig. 6. x 60.

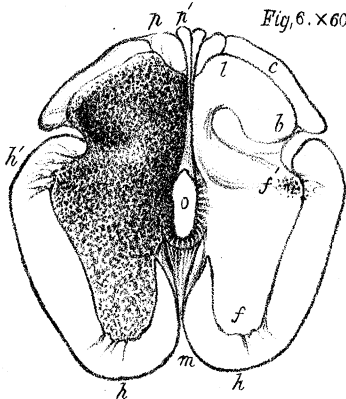


Fig. 9. x 420.

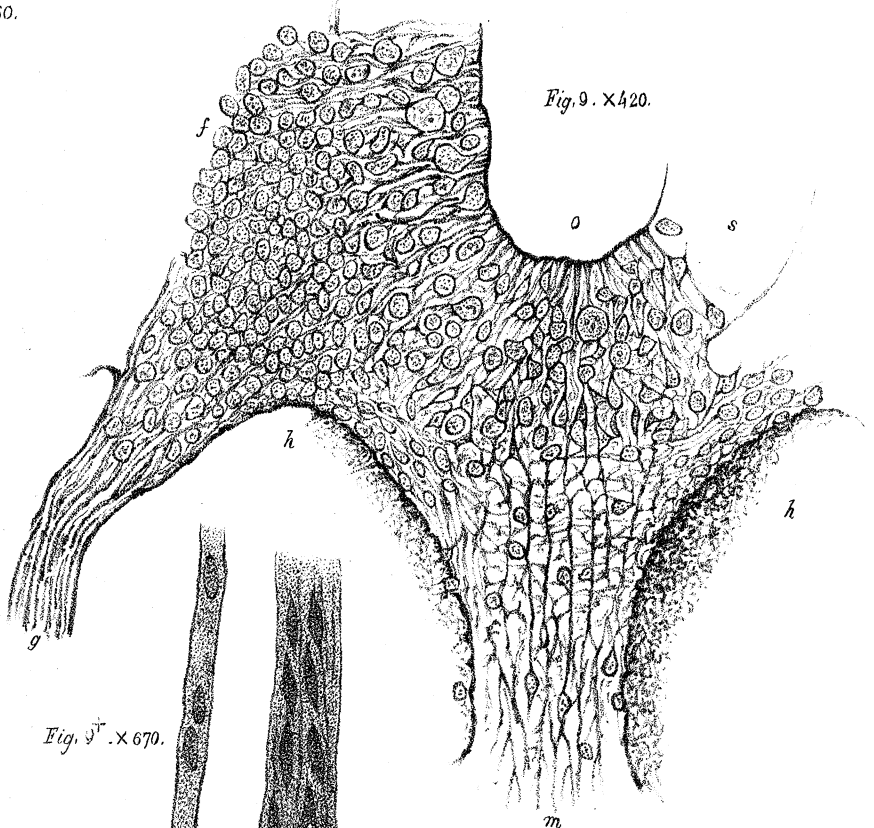


Fig. 8. x 670.



