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FURTHER RESEARCHES

ON

THE GREY SUBSTANCE OF THE SPINAL CORD.

BY

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XXII. *Further Researches on the Grey Substance of the Spinal Cord.*
By J. Lockhart Clarke, *Esq., F.R.S.*

Since the appearance of my second series of investigations on the structure of the Spinal Cord, certain modifications in the method I employ have enabled me to carry my inquiries to a still greater extent, and in many respects beyond the limits of what was actually known on this important subject. By this modified method the elementary nerve-tissues undergo less alteration from their natural state; for the most minute nerve-cells and their processes, as well as the finest fibres, are permanently preserved, and display a sharpness of outline unattainable by any other mode of preparation employed at the present day; while sections the one-twelfth of an inch in thickness may be rendered perfectly transparent*.

Many of the older anatomists, from Bartholinus downwards, had observed that the grey substance of the spinal cord is softer, more delicate and more vascular than the surrounding white columns; but Rolando was the first to point out a diversity in its structure. He observed, chiefly in quadrupeds, that on each side the posterior third of the grey crescent consists of a peculiar cineritious substance, which presents a different aspect from that which forms its two anterior thirds: it is different in colour, darker, and less red†. Rolando, however, assigned too large a space to this "new substance," which does not comprise so much as the posterior third of the grey crescent, but forms only a comparatively narrow and curved lamina or band around the extremity of each cornu, and, when viewed in a thin section by transmitted light, is found to be actually much paler and more transparent than the rest of the grey crescent. That this lamina is the part indicated by Rolando appears evident on examining his plates‡.

Now I propose, also, to make a primary but different division of each posterior cornu

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* See Appendix.

† "Non è molto difficile il vedere nel midollo spinale di bue, di maiale e di pecora, che le corna posteriori della sostanza cinericcia, che in questi si mostrano molto più spesse e più grosse che nell' uomo, sono formate in gran parte da una sostanza cinericcia particolare, che presenta un aspetto diverso da quello, che si osserva nella porzione che forma i due terzi anteriori della mezza luna. Questa nuova sostanza è più gelatinosa, ciò che fa sì che prende eziandio un colore diverso, e che in generale è meno rossigno, e di un colore più oscuro." *Ricerche Anatomiche sulla Struttura del Midollo Spinale* (con figure), 1824, Torino, p. 60. He states that it was only in quadrupeds that he succeeded in distinctly seeing this new substance, partly because in them the spinal cord may be obtained in that state of freshness which is more favourable for observation, and partly because this substance is found there in greater abundance; but that, nevertheless, in Man, unequivocal traces of it may be seen in the lumbar region.

‡ Some authors, however, seem to think that the *gelatinous substance* comprises a larger portion of each

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into two parts, namely, the *caput* cornu and the *cervix* cornu*. The *caput* consists of
the broad or expanded extremity of the cornu, and is separated from the *cervix* by an
imaginary line drawn across from the opposite anterior extremities of the arched lamina
of *gelatinous substance*. In some regions of the cord a line of somewhat paler substance
partially marks the separation. The *cervix* comprehends the remaining portion of the
cornu as far forwards as the level of the central canal. This distinction is grounded
on the facts,—1, that in ascending the *medulla oblongata*, the part which I designate the
caput cornu is thrown aside from the rest, as a distinct mass which is traversed in
succession by the vagus and glossopharyngeal nerves, and then becomes the principal
nucleus of the sensory root of the trifacial; and 2, that, independently of the *gelatinous
substance* which surrounds it, it differs in structure from the *cervix*, or remaining part of
the cornu, which, in the *medulla oblongata*, supplies the grey substance of the *posterior
pyramid* and *restiform body*†. This distinction is not only consistent with anatomical
facts, but will be the means, I think, of adding clearness and precision to the description
of these parts.

The *caput cornu posterioris* varies in form in different regions of the cord. In the
upper part of the cervical region it is long and pointed, or pyramidal; broader and more
rounded in the lumbar enlargement and in the conus medullaris; and again pointed,
or somewhat pyramidal, through the whole of the dorsal region in Man (see fig. 12,
Plate XXV.; fig. 15, Plate XXI.; fig. 17, Plate XXIII.; figs. 5 & 6, Plate XXI.).
From its border a network of blood-vessels, accompanied by nerve-fibres, extends outwards
through the posterior and lateral columns (see fig. 1, Plate XIX.), and in the lumbar
region especially is very conspicuous around its pointed extremity, at the bottom of the
lateral fissure, where it divides the white columns into a number of separate fasciculi of
different shapes and sizes.

posterior cornu,—an opinion which is perhaps founded on the statement of ROLANDO, that it forms the
posterior *third* of the grey crescent.

* In my memoir on the Medulla Oblongata I have written "caput cornús posterioris." As I have heard
that this has been objected to by an "eminent classic," on the ground that the noun *cornu* is indeclinable
in the singular number, I may here take the opportunity of informing any one who has made or may make
a similar objection, that the expression is perfectly grammatical and correct; for there is another and more
ancient form of the same noun, which makes both the nominative and genitive singular to end in *us*. This
ancient form may be found in several of the Latin classics—in CELSUS, CICERO, LUCAN, and the elder PLINY.
In PLINY it occurs frequently: see *Historia Naturalis*, lib. viii. 29; lib. x. 90; lib. xiii. 51 and 52; lib. xxviii.
42, 46, and 64. I find that it has also been used by METZLER in his dissertation *De medullæ spinalis avium
textura*. Dorpat, 1855. I employed it on account of the distinctive character of its genitive; but as it appears
necessary at times to use the words *cornu* and *cornua*, because they are so generally known, I shall confine
myself to the more modern form of the noun.

† See the author's "Medulla Oblongata," Philosophical Transactions, Part I. 1858, figs. 12, 15, 16, 19,
and 23. The grey tubercle of ROLANDO, which reaches the surface on each side of the *medulla oblongata*, is
generally considered to consist of the *gelatinous substance*, but in fact it includes the whole dilated extremity
of the posterior cornu, or caput cornu.

Structure of Caput Cornu Posterioris.

The *caput cornu* may be seen even with the naked eye to consist of two different portions: 1, an outer and comparatively transparent portion—the *gelatinous substance*; 2, an inner and more opake portion, or base.

1. The *outer* portion or *gelatinous substance* consists of—

> A. Nerve-fibres.
> B. Nerve-cells.
> C. Blood-vessels.
> D. Connective tissue with nuclei.

A. *The nerve-fibres are transverse, longitudinal, and oblique.*—The *transverse* fibres, proceeding from different parts of the grey substance, run backwards across the *gelatinous substance* in a kind of radiating series of bundles, and in planes at right angles to the axis of the cord (fig. 1, Plate XIX.). The bundles near the middle line (as seen in a transverse section) are straighter and more parallel than the rest, but partly join or cross each other near the posterior border of the *gelatinous substance*, from which they run out through the posterior columns as radiating fibres and posterior roots of the nerves. The bundles on each side take a curved direction towards the middle line, but before they pass out, their fibres describe a series of arcs of different lengths within the margin of the *gelatinous substance*: along the inner side of the latter there is always a large bundle which subdivides and runs out towards the posterior median fissure; and from the outer side of the *gelatinous substance* a smaller number of fibres proceed through the posterior part of the lateral column. The primitive fibres composing these bundles, as I showed on a former occasion, are not grey fibres, but tubules of small average size, the larger kind possessing double contours. By far the greater number vary from about the $\frac{1}{5000}$th to the $\frac{1}{20,000}$th of an inch in breadth, but are intermixed with others of about the $\frac{1}{1700}$th of an inch in diameter. The marginal fibres within the posterior border of the *gelatinous* substance are more often of the latter kind.

The *longitudinal* fibres of the *gelatinous substance* are very numerous, and resemble the finer tubules of the transverse bundles*.

The oblique fibres, which are found in different planes, are in various degrees intermediate in direction between the two former sets, and, as I formerly stated, are apparently continuous on the one hand with the longitudinal, and on the other with some of the fibres of the posterior roots†.

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* These fibres were more fully described in my first communication, Philosophical Transactions, 1851, Part II. p. 610.

† In his first treatise on the Spinal Cord, STILLING described all the fibres of the grey substance as *grey* fibres, but in his recent work they are shown to be tubules. He seems to think that I was not acquainted with the fibres which take an oblique course through the gelatinous substance. It is true that I gave no separate description of them, but in the explanation of fig. 2, Plate XX., Philosophical Transactions, 1851, Part II., when speaking of the bundles which project into the substantia gelatinosa from the grey substance, I observed that "this appearance is caused by oblique sections of bundles of nerves and blood-vessels which

B. *Cells of the Gelatinous Substance* *.—The cells of the gelatinous substance, in regard to size, may be described as (*a*) large, (*b*) small, and (*c*) intermediate.

(*a*) The *large* cells are almost exclusively found amongst the semicircular fibres which run within the external border of the *substantia gelatinosa*, and never extend beyond the middle of its depth (fig. 1, Plate XIX., and fig. 47, Plate XXII.). They are more or less oval, pyriform, fusiform, crescentic, triangular, or otherwise irregular, and contain distinct nuclei. They all give off processes from two to five or six in number. The *fusiform* and *oval* variety are elongated transversely, longitudinally, and in planes intermediate or oblique. Sometimes a *fusiform* cell tapers at each end into a broad process, which attenuates in its course, and either remains single or subdivides into two or more; or it bifurcates at once into two processes at each extremity or only at one. In a transverse section of the cord, some of these processes appear to terminate in one or more of the semicircular or marginal fibres; some run backwards through the posterior columns, or forwards across the *gelatinous substance*; others pursue a longitudinal course with the *fibres* of the *gelatinous substance*, or along the verge of the posterior columns. From a cell of another shape three or more processes may be seen to extend in different directions—backwards, forwards, laterally, obliquely, or longitudinally. Frequently a *triangular* cell, resting on the verge of the gelatinous substance, sends a process right and left, and a third through the posterior column along the side of a bundle of the poste-

enter the grey substance in a more or less longitudinal direction, or with various degrees of obliquity." And in my second communication, Philosophical Transactions, 1853, p. 353, it is stated, "I believe that they (the longitudinal fibres of the gelatinous substance) are all derived from the fine fibres of the posterior roots," which must therefore cross the gelatinous substance in an oblique direction.

* The cells of the gelatinous substance have been described by KÖLLIKER, SCHRÖDER VAN DER KOLK, and by STILLING in his late work. In my first communication I only incidentally mentioned them in the following passage: "All (the nerve-cells of the grey substance), except those peculiar to the gelatinous substance, have remarkably delicate processes issuing from their sides." Upon this passage STILLING takes the opportunity of remarking, that by my peculiar method of preparation the sections are rendered too transparent, so that the finer elementary structures escape observation. This objection is without sufficient foundation. In the first place, I described the gelatinous substance, as I then stated, from examination of the *fresh* cord, treated with acetic acid, and not by means of my "peculiar method" of preparation, which, however, shows the cells and processes in the most perfect manner; secondly, to see these preparations to advantage, the illumination must be adapted to their degrees of transparency. But they may be made of all degrees of transparency and of thickness up to the one-twelfth of an inch. If STILLING has given but a hasty trial to this method and only messed with a little turpentine and Canada balsam, he is not prepared to offer an opinion worth notice. I may add that the few of my preparations that have found their way to the Continent are some of the first that I made, and are very inferior to those I have since made, especially by my modified method. The great thickness, also, of some of these preparations renders them exceedingly valuable for tracing the course of fibres, which must often be inevitably cut across in the very thin sections required by other methods. This is evident in STILLING's large wall-diagram, where the grey substance, particularly of the cervix cornu posterioris, appears chopped up like chaff; so that it is impossible to form any idea of the destination of the fibres. It may not be out of place to state that all the observations described in this communication have been carefully repeated on sections of the cord hardened simply in chromic acid, and without further preparation.

rior roots, or through a fissure containing a blood-vessel; or two contiguous bundles of the posterior roots, as they pass out from the gelatinous substance, are accompanied by the processes of a *crescentic* cell, which occupies the curve between them (see fig. 1. Plate XIX.). And beyond the *point* of the cornu, a variable number of others, of different shapes and sizes, may be seen amongst the *network* of blood-vessels and fibres, which is formed, as already stated, around separate fasciculi of the posterior and lateral columns. They occupy the angular interspaces or partially embrace the fasciculi, and send between them their processes, which contribute to form the network (*b, b*, fig. 1).

(*b*) The *small* cells abound in every part of the *gelatinous substance.* They are round or oval, somewhat pyriform, fusiform, or angular, and give off two processes or more. Fig. 46, Plate XXII. *a, b, c*, represents them magnified 350 diameters. They vary considerably in size, and many are nearly as minute as blood-disks*. The largest of them contain distinct nuclei. Near the border of the posterior columns, the oval and fusiform variety, like those of the first set, are elongated transversely, longitudinally, and obliquely; but through the rest of the gelatinous substance the longer axes of many, as well as their processes, are parallel to the antero-posterior fibres that form the posterior roots of the nerves, with which they are apparently continuous (fig. 1, Plate XIX.).

(*c*) The cells of *intermediate* size, like the first set, which they closely resemble in shape, are found chiefly near the verge of the posterior columns. Some are so exceedingly fusiform that they appear like gradual dilatations in the course of the fibres, but still they are true cells.

There can be no doubt whatever that a great number of the *smallest* cells of the gelatinous substance belong to the connective tissue. This tissue extends as a fine network from the border of the grey substance, through the white columns as far as the surface of the cord, where it forms a layer of variable thickness, in which its fibres run circumferentially, and return at intervals to rejoin the network in the white substance. Now in very delicate preparations which I lately made of the spinal cord of the Calf between three and four months old, I discovered that in every part of the *white columns* the connective tissue between the primitive nerve-fibres abounds with both *nuclei* and small *nucleated cells*, many of which are quite equal in size and similar in character to numbers of those which are found in the gelatinous substance; but on account of their position, some of them are more diversified in shape. They are more or less round or oval, pyriform or club-shaped, angular, fusiform or crescentic, and lie in the interspaces between the nerve-fibres, sending out fine processes in different directions to join the network of connective tissue. Frequently a crescentic cell half encircles a primitive nerve-fibre, and forms a swelling or knot around one side of its sheath. Fig. 48, Plate XXII. represents the appearance of some of these nucleated cells and free nuclei. There is no difference in structure between them and the smallest of those in the grey substance; indeed from this substance an *uninterrupted* layer of cells and nuclei, of an apparently

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* Care must be taken not to confound these minute cells with the cut ends of small blood-vessels: a mistake not at all unlikely to occur where they are not very distinct and well-defined.

identical character, may be traced through the *white columns* between the fibres, as far as the surface of the cord. The nuclei are more or less round or oval, and contain a number of delicate granules. In a free state (see fig. 48 *e* and fig. 46 *c*) they abound in every part of both the grey and white substance, but sometimes they are partially or wholly surrounded by a kind of shaggy, flocculent, or finely filamentous mass (fig. 48, below the letter *e*), while in other instances they are attached to the surrounding parts only by a few fine fibres. Now there is reason to believe that this flocculent or filamentous substance is really the remains of the cell in process of development into the surrounding tissue and sheath of the nerve-fibre; for on examining the cord of an adult animal, I found that the *nucleated cells* had disappeared, while in the midst of the filamentous tissue between the nerve-fibres, the same kind of *nuclei* were still present[*].

These observations, then, render it apparently impossible to point out the exact distinction between the connective and the true nerve-tissue, and *might* suggest the question, whether there is any actual and essential difference between them, 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.

2. The *anterior* or *inner* and more *opake* portion of the caput cornu is continuous with the *grey substance* of the *cervix*, and surrounded behind and on each side by the arched lamina of the *substantia gelatinosa*, with which it varies in shape at different regions of the cord (figs. 5 to 17, Plates XXI. XXV. & XXIII.). In some parts of the cervical and in the dorsal region, as seen in a transverse section, it projects into the gelatinous substance in the form of a cone, while in other regions its posterior border is more or less angular or rounded. Its elementary structure, in addition to blood-vessels and connective tissue, consists of—

    a. Longitudinal fibres.

    b. Transverse and oblique fibres.

    c. Cells.

a. The longitudinal fibres are collected into bundles, and are the principal cause of the opacity of this portion of the *caput* cornu. They are broader and coarser than the fibres of the *gelatinous substance*, which, however, they immediately adjoin. Sometimes, as in the neck, they form round the extremity of the cone a kind of arched band or roof, of the same shape and about the same depth as the *substantia gelatinosa*, which rests

* I find that precisely similar nuclei are abundantly scattered throughout both the white and grey substance of the cerebrum and cerebellum. In the convolutions of the cerebellum, the nuclei, which in a dense layer form the internal portion of the grey substance, and into which the fibres of the white substance first penetrate, are for the most part a little different from those in the immediate neighbourhood. They are *generally* round or globular, are more uniform in size, and mostly contain a distinct and clear circular or globular nucleolus (as in fig. 46, Plate XXII., below the letter *a*), surrounded by fine granules. Nuclei like these, but frequently of larger size and sometimes containing two globular nucleoli, are very numerous in the *gelatinous substance* (see the two above *a*, fig. 46), but are not peculiar to this substance. They are also found in all parts of the grey substance of the cerebrum.

upon it*; while in the cervical and lumbar *enlargements* they also extend, but in smaller numbers, through deeper parts of the cone. The bundles themselves are of different sizes and not exactly parallel, even in the same plane, but intersect each other at acute angles, and extend obliquely, at intervals, into the *gelatinous substance*; so that in a transverse section some of their divided extremities are more or less oval or elongated, and give to the posterior border of the cone, or lamina, an irregular or jagged outline, like the worn extremity of a brush (see fig. 2, Plate XX. D, on left side).

b. The transverse fibres are continuous with the posterior roots of the nerves and longitudinal columns, and cross each other and the longitudinal fibres in a great variety of ways. Some of the roots, on reaching the base of the cone or *caput cornu*, return through it in loops to the posterior columns (see fig. 2, Plate XX. P, on right side); some become continuous with the longitudinal bundles, particularly on the outer side; others cross them obliquely in opposite directions and run out on the one side through the lateral, and on the other through the posterior, columns; while the rest proceed forwards through the cervix cornu, and in part escape through the posterior commissure to the opposite half of the cord.

The oblique fibres, as may be inferred from the descriptions just given, are only continuations of the transverse and longitudinal, at different angles and in different planes.

c. Most of the cells are of the smallest and intermediate size. The majority are oval and fusiform—sometimes to a remarkable degree, and lie with their longer axes and their processes in the direction chiefly of the oblique and horizontal nerve-roots, but also in the direction of the longitudinal fibres, with which they appear to be continuous.

Amongst these, a few larger cells, from three to five in a transverse section of moderate thickness, are scattered at unequal intervals. They are more or less oval or fusiform, or irregular in shape, and give off from three to five processes, or perhaps more. Frequently one of these cells is found nearly as far back as the verge of the gelatinous substance; but they mostly lie deeper. Sometimes they bifurcate around longitudinal bundles, which are probably accompanied by *some* of their processes, while the *others* may be traced to a surprising distance and in different directions, backwards, forwards, and laterally to the white columns.

Having given the structure of the *caput* cornu posterioris, I shall next describe the *cervix*, or rest of the posterior grey substance, as it appears in the dorsal region, and then proceed to trace it both upwards and downwards, through the remaining length of the cord. In the dorsal region I shall describe it in considerable detail, and illustrate it by drawings of the greatest possible exactness, not only on account of its great interest and apparent importance, but in order that we may recognize its parts as the *same* during the *changes* which they undergo in passing through other regions.

About the middle of the dorsal region in the spinal cord of the higher Vertebrata, the inner sides of the posterior cornua are in close contact along the middle line, or are

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* This layer of fibres I pointed out in my first communication on the Spinal Cord, Philosophical Transactions, 1851, Part II. p. 611.

separated only by blood-vessels which descend from the median fissure ; so that together they form but a single mass, along the posterior part of which the *gelatinous substance* is uninterruptedly continued from side to side *. Fig. 2, Plate XX. represents a transverse section of the grey substance in the dorsal region of the Calf, magnified 60 diameters. The *caput* cornu posterioris, on each side, would be marked off by an imaginary line extending across from the *antero-lateral* extremity of the *gelatinous substance* to the bottom of the posterior median fissure (*l*); while the *cervix* is included between this line and another drawn nearly horizontally across from the anterior border of the transverse commissure which arches over the pellucid space (H) surrounding the central canal.

The inner or median half of the *cervix* is occupied by a remarkable longitudinal column, which in this part of the dorsal region is nearly cylindrical or oval. These bodies I described in my first communication, and named them the *posterior vesicular columns—columnæ vesiculosæ posteriores*; but their highly interesting structure and connexions have induced me to examine them again with more attention.

Each *posterior vesicular column* (M, M, fig. 2, Plate XX.) consists of a somewhat dark cylinder of fibres interspersed and surrounded by cells and their processes. The fibres are in great part derived from the posterior roots of the nerves, and are much finer than those of the white columns. They are more or less longitudinal, transverse, and oblique, and interlace each other in bundles in the most intricate manner, as may be seen in a longitudinal section.

The cells in the cylinder or opake portion of the column are oval, pyriform, or more or less fusiform, and variously stellate (see also Plate XXII. figs. 49 & 50). They differ considerably in size; some are very small, but the largest are quite equal to those of the anterior cornu. Their *number*, also, varies in different sections of the same thickness, and even in the opposite columns of the same section. Sometimes only a few small cells, with perhaps a single large one, appear at irregular intervals; and occasionally they are all absent. Their processes extend *transversely*, *obliquely*, and *longitudinally*: *transversely* they intersect the cylinder in various ways (M, M, Plate XX. fig. 2), in a kind of network formed by their subdivision, and in irregular curves, which sometimes suddenly change their course to become *longitudinal*, and sometimes escape *directly* to surrounding parts, or after running for some distance round the cylinder. In sections made *longitudinally* all the cells are seen to be elongated in that direction (Plate XXII. fig. 50), and are frequently quite fusiform; it would therefore appear that each cell is prolonged in different planes. They lie imbedded in the plexus of bundles, and branch into many processes, which run *transversely* backwards and forwards, *obliquely* and *longitudinally*. Sometimes longitudinal processes extend to a surprising distance, and then become transverse, and often again longitudinal.

* In the Rodentia—at least in the *Guinea-pig*, *Rat*, and *Rabbit*—the posterior cornua, as in Man, remain separate in all regions of the cord. It is curious, also, that in these animals the *caput* cornu is remarkably large in the *dorsal*, but particularly in the *cervical* region, and is thronged, as indeed is every other part of the grey substance, with small cells.

Around the whole of the cylinder, and partly encroaching on its border, other cells are disposed, that contribute to form, by their *collective* processes, an irregular circle of fibres; but these *individually*, after describing parts of the circle, run off tangentially in different directions (fig. 2, Plate XX.).   On the outer side of the cylinder they cross each other obliquely from before backwards and *vice versâ*, extending in opposite directions to the anterior and posterior cornua.   They also contribute with the posterior roots to form the transverse commissure behind the central canal.   The cells are of all sizes, and mostly fusiform—often to a remarkable degree; but some are triangular and stellate.   Many are curved and elongated circumferentially; others are inclined at a tangent, and send off their processes, on the one hand, within or around the circle, and, on the other, to distant parts.   Sometimes an irregular or stellate cell sends two of its processes round the circle, one longitudinally or obliquely, and the rest in other directions, but mostly towards the anterior parts, or towards the lateral column.

When the posterior roots of the nerves are traced inwards, they are found to be most intimately connected with all parts of the *posterior vesicular columns.*   One large bundle is generally observed proceeding from near the middle of the caput cornu to the outer side of the cylinder, where its fibres diverge or separate: some of them partly enclose it, apparently in connexion with the cell-processes; while the rest interlace within it, or form a series of tortuous curves, as may be seen best in a longitudinal section; or after running *longitudinally* backwards and forwards, in a kind of looped or zigzag course, escape into the lateral white column*.   Another large bundle (P) invariably enters along the inner side of the caput cornu near the posterior median fissure; some of its fibres return backwards towards the point and outer side of the gelatinous substance, partly to form loops with other roots, and partly to escape through the lateral white columns; some interlace through the cylinder; some sweep round on its outer side and join both the posterior and anterior commissure, while others are prolonged forwards through the lateral portion of the cervix cornu.

A band of fibres from the posterior transverse commissure, after curving round the front of the vesicular cylinder, runs nearly horizontally outwards (as seen in a transverse section) to the lateral border of the grey substance and lateral column (see figs. 2, 3 & 4).   These fibres, which are more conspicuous at the upper and lower parts of the dorsal region, are joined by others, which proceed from the inner side of the cylinder, and from a *different plane*; for at this point they are cut across in the section, and terminate abruptly in divided extremities†.   The *lateral* portion of the *grey substance* which is

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* It is difficult, however, to determine whether these tortuous and zigzag fibres are directly continuous with the posterior roots, or with the processes of the cells, for their diameters are often considerable.

† This appearance is observable chiefly in the upper and lower parts of the dorsal region, but particularly the latter; it is also to be seen in some degree in the cervical and lumbar enlargements; in the upper part of the latter it is very conspicuous.   At the point where these fibres are divided in the transverse section, that is, at the inner side of the *posterior vesicular column*, and a little behind the spinal canal, they appear to be continuous with the tortuous and zigzag fibres seen in a longitudinal section, as above described.

traversed by this band, and near the level of the canal, may be considered as intermediate between the anterior and posterior cornua. At the border it forms a small and more or less pyramidal projection (F, figs. 2 & 4, Plate XX.; and figs. 3, 5, 6, Plate XXI.). which is very transparent, and in colour resembles the *gelatinous substance*. In some parts of the dorsal region, as we shall presently see, it extends inwards as a somewhat conical layer, and becomes less transparent towards the point, which reaches nearly to the front of the posterior vesicular column (fig. 3, Plate XXI.; and fig. 4, Plate XX.). This tract, which I intend to follow through other regions of the cord, was first pointed out by myself in 1851*. I shall call it, on account of its position, the *tractus inter-medio-lateralis*. It consists for the most part of oval, fusiform, or pyriform and triangular cells, which are somewhat smaller and of more uniform size than those of the anterior cornu. Figs. 51 and 52, Plate XXII., represent them magnified 220 diameters. In the *middle* of the dorsal region they are less numerous than in some other parts. and found only near the verge of the grey substance. They are elongated as well transversely as longitudinally,—*transversely* both in a lateral and antero-posterior direction, in which they send their processes, on the one hand, to the transverse commissure and the lateral column, and on the other, to the anterior and posterior cornua. Sometimes a few lie beyond the border of the grey substance, where their processes accompany nerve-fibres and blood-vessels which radiate through the lateral column (fig. 51 *b*. Plate XXII.; and fig. 2, Plate XX. F).

The outer or lateral portion of the *cervix* cornu posterioris (Plate XX. fig. 2, *n*, and corresponding part on the opposite side of the figure), between the *tractus intermedio-lateralis* and the *caput* cornu, is composed of fibres and cells. The fibres descend from the roots of the nerves, and run partly outwards to the lateral column, and partly forwards to the anterior cornu, passing through the *tractus intermedio-lateralis* (F). The cells, which are often of considerable size, are mostly fusiform in the same direction as the fibres, and taper into processes of remarkable length, which seem to be continuous with them. But *some* of the cells are stellate or irregular in shape, and send out their processes in all directions. These are generally observed near the outer border of the posterior vesicular column, with which they are partly connected by their processes, and near the *edge* of the *cervix* and the *base* of the *caput* cornu, where *some* of their processes contribute with blood-vessels and fibres to form a network around several longitudinal bundles, with which *others* are *probably* continuous. At N (fig. 2) are three of these longitudinal bundles, the most anterior of which is partially embraced by a multipolar cell, and the most posterior by another of a crescentic form. The outer cells of the posterior vesicular column are so gradually intermixed with this lateral layer, that it seems almost impossible to determine their exact limits.

In receding from the middle of the dorsal region towards either extremity of the cord. the posterior cornua gradually separate from behind forwards, receiving between them the deep encroaching layers of the posterior columns, until in the middle of the cervical

* Philosophical Transactions, Part II. p. 613.

and lumbar enlargements they are joined only by a narrow band of the transverse commissure, immediately behind the canal.   During these changes, the posterior vesicular columns undergo certain modifications in form, size, and structure.   As they approach the cervical enlargement, the cylinder or opake portion of each is gradually reduced in size, but the whole inner half of the cervix is still occupied by the surrounding layer of cells.   Sometimes the cylinder is intersected, and divided into smaller portions, by fibres of the transverse commissure, in continuity with the processes of some of its own cells, which are more or less intermixed with those of the surrounding layer: other fibres of the transverse commissure, in their passage outwards, enclose it in front and behind, and after partly reuniting on its outer side and running backwards through the caput cornu, where they are also continuous with cells, they diverge and traverse the gelatinous substance as posterior roots of the nerves.   Some of those fibres which enclose it in front, in company with processes or fibres from the inner side of the vesicular column, proceed, as already stated, with a gentle curve, or in a slightly serpentine course, to the lateral border of the grey substance, where they are partly continuous with the cells of the *tractus intermedio-lateralis* (F, figs. 2 & 4, Plate XX.), while the rest escape through the lateral column.   Behind, and at the sides of, the canal, the fibres of the transverse commissure are connected with many small oval and fusiform cells,—sometimes with others of larger size,—and are separated at intervals by blood-vessels which run longitudinally and obliquely and communicate with one of considerable size, which proceeds transversely, with the commissure, to the lateral grey substance, where it divides into numerous branches.   In the middle of the cervical enlargement, the circumscribed cylinder of the posterior vesicular column has entirely disappeared, but the whole inner half of the cervix cornu is filled with cells, and contains a somewhat dark and imperfectly-defined mass, which is traversed by the fibres of the transverse commissure and interlaced by the posterior roots.   In the Ox many of these cells are very much branched, and send out their processes in all directions: some are fusiform in various degrees; others are apparently riband-shaped, and sometimes not much broader than the processes into which they gradually taper.

In the upper part of the cervical region, near the origin of the third pair of nerves, a darker and more defined mass (M, fig. 12, Plate XXV.) reappears at the base of the cervix cornu.   It is composed of cells both large and small, and of bundles of the posterior roots which interlace amongst them.   This mass is not distinctly circumscribed like that of the posterior vesicular column in the dorsal region, but is somewhat triangular, with one of its angles directed towards the point of the posterior cornu, another towards the transverse commissure, and the third obliquely forwards and outwards towards the antero-lateral column.   It gradually diminishes upwards, and disappears near the first pair of nerves.

The *tractus intermedio-lateralis* is larger at the *upper part* than in the *middle* of the dorsal region.   On the one hand it projects further into the lateral column, and on the other tapers inwards across the grey substance to near the front of the *vesicular cylinder*

(see F, Plate XX. fig. 4; Plate XXI. fig. 3). *Transversely* its *outermost* or marginal vesicles lie, for the most part, with their longer axes and processes in an *antero-posterior* direction, as in fig. 2, Plate XX.; while those more internal are elongated in the direction of the transverse commissure, with the fibres of which, as already stated, their processes are continuous.   As it ascends, however, through the cervical enlargement, it gradually disappears; but, as in the dorsal region, the lateral portion of the grey substance is still traversed, from behind forwards, by numerous fibres apparently in connexion with branched and with very elongated cells of all sizes, amongst which are scattered a few that resemble those of the *tractus intermedio-lateralis*.   Through this lateral portion of the grey substance the *lowest* roots of the *spinal-accessory* nerve bend *forwards* to the cells of the *anterior cornu.*

In the region of the upper cervical nerves, there reappears a vesicular tract in the same position as the *tractus intermedio-lateralis*, and composed of the same kind of cells, which are elongated in a lateral direction and send their processes, on the one hand, outwards through the lateral column, and on the other, inwards to join the fibres of the transverse commissure behind the central canal (see F, fig. 11, Plate XXI.; and fig. 12, Plate XXV.).   It is traversed by the roots of the spinal-accessory nerve (*r*) as they bend forwards on their way to the anterior cornu.

In *descending* the cord from the *dorsal* to the *lumbar* region, the posterior grey substance undergoes a series of changes nearly similar to those which are observed in *ascending* to the cervical enlargement.   The posterior cornua become gradually more separate, or thrown aside from each other, in a direction obliquely backwards.   At the *upper* part of the *lumbar* enlargement, the posterior vesicular columns are decidedly larger than in any other region of the cord (M, fig. 13, Plate XXI.).   In a transverse section each presents the appearance of a dark oval mass, lying along the whole inner half of the cervix cornu, the border of which it renders convex against the deep strata of the posterior column.   Its larger cells are more numerous than in the dorsal region.   They do not form in the centre of the column a circumscribed group, but lie scattered irregularly through the whole inner half of the cervix, which their processes traverse in different directions and envelope in different planes. Many of the oval variety are elongated in the direction of the cornu, and their processes are continuous, on the one hand, with the transverse commissure, and on the other, with the posterior roots of the nerves. Some stretch along the convex border of the cervix; and sometimes a crescentic or triangular cell, in the same situation, sends one of its processes through the posterior column with a bundle of radiating fibres.   Part of the fibres of the transverse commissure run out in front of the mass, as already stated, in company with processes or fibres which proceed from its inner side; of these some are continuous with the cells of the *tractus intermedio-lateralis*, while others escape through the lateral column.

The *tractus intermedio-lateralis* is prominent at the border of the grey substance, between the anterior and posterior cornua, but its cells are not so numerous as in the upper *dorsal* region.

Through the remaining half of the lumbar enlargement, the *posterior vesicular columns* are gradually less encircled and enveloped by the processes of their cells, which also diminish in number, but are still traversed by the divergent fibres of the transverse commissure and by a plexus of the posterior roots which sweep round on their outer sides. In the Ox two or more of these cells are often very large and wonderfully branched into six or seven processes, which radiate in all directions. I think there can be no reason to doubt that they form a part of the *posterior vesicular column* which has just been traced from above.

In descending through the lower portion of the lumbar enlargement, the border of the grey substance between the posterior cornua is gradually drawn backwards, so that in the same proportion the space behind the canal, containing the transverse commissure, becomes deeper (compare fig. 15, Plate XXI., with figs. 16 & 17, Plate XXIII.). Some of the posterior roots of the nerves cross the cornu from without inwards to the side of the *anterior* commissure, and a large number converge to form the *posterior* commissure behind the canal. From the inner side of the caput cornu several large bundles sweep round through the cervix, where they interlace with the others and separate in different directions. Some of them descend to the anterior grey substance; others curve inwards to the side of the canal; and amongst the plexus which they form with the transverse commissure are a few scattered cells, which may be regarded, I think, as the remains of the posterior vesicular column. These cells are scattered in front as far as the border of a peculiar group which, near the level of the second pair of sacral nerves, begins to make its appearance on each side and a little behind the spinal canal. This group was first pointed out by myself in 1851, and considered as the commencement of the posterior vesicular column. I think, however, that STILLING is right in considering it as a distinct group, although it is reached by the posterior roots; but, as I shall presently show, its connexions with the anterior roots are more direct and intimate than in the case of the *posterior vesicular column.* It is more or less round or oval, but not entirely isolated from the surrounding cells, nor circumscribed by fibres. It increases in size through the level of the second pair of sacral nerves, below which it gradually disappears. The cells are oval, fusiform, irregular in shape, or stellate, and all of the larger kind. Some of their processes cross over to the opposite side behind the canal; others run out towards the lateral column; some join the anterior and posterior roots, and others form a system of longitudinal fibres, the cut extremities of which, in a transverse section, are seen scattered amongst the group. The oval and fusiform cells are in part elongated transversely towards the anterior roots, but chiefly in a lateral direction, and a continuous layer or tract of these elongated cells may be frequently seen to extend from the outer side of the group to near the border of the grey substance, in company or in connexion with fibres which proceed in the same direction, and escape through the lateral column. But the *principal part* of the group is most intimately connected with the *anterior roots* of the nerves; for a large number of these roots, frequently side by side, run directly backwards to reach it, through the middle and inner part of the

cornu: some of them are seen to be continuous with the cells, especially with those which are elongated towards them; others wind about them in a series of curves, which, like the processes themselves, are frequently divided in a transverse section *.

In the spinal cord of Man, the form of the grey substance differs in some respects from that of Mammalia. Throughout the whole of the dorsal region, the posterior cornua stand completely apart, and are joined only at their bases by a narrow transverse commissure. Fig. 5, Plate XXI. represents a transverse section of the entire grey substance about the middle of this region. Each posterior vesicular column (M) occupies nearly the whole inner half of the cervix cornu. It is more or less oval, and, in structure and appearance, closely resembles that of Mammalia in the upper parts of the lumbar enlargement. Its large cells are more numerous than in the dorsal region of Mammalia. They are not accumulated near the centre, but scattered at unequal intervals to the very border of the cervix, from which some of their processes run out with blood-vessels and fibres to the posterior white column. Most of the oval variety are elongated in the direction of the cornu, and are continuous by their processes with the transverse commissure, on the one hand, and on the other, with the posterior roots of the nerves, which also interlace through the mass and sweep round on its outer side.

Towards the upper end of the dorsal region the dark oval masses diminish in size, as may be seen in fig. 6, Plate XXI. They are frequently divided or broken into smaller portions by bundles of the posterior roots in their course to the transverse commissure, and in connexion with some of their cells. In ascending through the cervical enlargement they continue to decrease, and at length disappear; but the spaces which they occupied along the inner halves of the cornua are still interspersed with a multitude of cells and traversed by the posterior roots, which also sweep round as usual, on their outer sides, in bundles of considerable thickness (see figs. 8 & 9, Plate XXI.). The cells, however, are very much smaller than in the dorsal region; the majority are scarcely larger than those in the middle of the gelatinous substance; but a few of superior size are unequally scattered amongst them. Many are oval, round, and fusiform, especially in the direction of the fibres; others, particularly the larger kind, and nearer the centre of the cervix, are triangular or irregular in shape, and send out their processes on all sides.

Above the cervical enlargement, the dark masses present nearly the same appearance as in Mammalia; but they are rather paler, and the cells they contain are of smaller size.

The *tractus intermedio-lateralis*, also, in Man, closely resembles that of Mammalia, and contains cells of the same kind, but rather smaller (figs. 51 & 52, Plate XXII.). In the upper part of the cervical region, a similar but somewhat larger tract reappears in the same situation, and projects in the same way into the lateral column (see fig. 11, Pl. XXI. F). It increases in ascending to the third pair of nerves (fig. 12, Plate XXV. F), where the form of the entire grey substance presents a very striking resemblance to

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* As there are no traces of these groups of cells in the *human* cord, and I have not found them in the *Guinea-pig*, it is probable that they supply the nerves of the *tail*.

that in the upper part of the dorsal region (compare with fig. 6, Plate XXI.). This tract is traversed by several roots of the *spinal-accessory* nerve, in their course forwards to the *anterior* cornu, and contributes, with the edge of the posterior cornu, to form a beautiful network (N, N, N) in the lateral column, through which the nerve enters. Its cells are triangular, oval, and fusiform in different directions: some of them are elongated in the direction of the transverse commissure and towards the front of the posterior vesicular column; others extend outwards with radiating fibres through fissures of the lateral column. There is reason, therefore, to believe that this tract forms a part of the *tractus intermedio-lateralis*. In the Sheep and Ox, and probably in all Mammalia, a *peculiar* group of cells, which is traversed by the roots of the spinal-accessory nerve, is found in the same situation; and this group, in ascending the medulla oblongata, retires inwards to the space behind the canal, and there contributes to form the nucleus which gives origin to the highest roots of the nerve. It has also been seen that the cells of the *tractus intermedio-lateralis* are elongated with their processes in a longitudinal direction, and reached by both the *posterior* and *anterior roots* of the *spinal* nerves, and perhaps by the *spinal-accessory*; that the latter nerve extends *forwards* to the cells of the *anterior cornu*, which also send some of their processes *longitudinally*, and are reached by the *posterior* roots. Moreover, I have in another memoir shown that, while *one* portion of the *upper* roots of the *spinal-accessory* nerve and *one* portion of the *vagus roots* proceed *inwards to their respective nuclei behind the canal, other* portions of *both bend forwards to the vesicular network into which the anterior cornu has become resolved* *. Again, I have shown, in the same memoir, that some of the roots of the *trifacial nerve descend longitudinally through the caput cornu*, between the transverse roots of the *vagus*; in which course they are probably brought into connexion with the *respiratory centres*, and perhaps also, like the *vagus*, with the anterior grey substance of the medulla. These extensive and intimate connexions seem to afford an explanation of the mechanism by which impressions made on the vagus and on the incident fibres of the trifacial and spinal nerves, may call into action the whole class of respiratory muscles; and if the tract which I have just described in the upper part of the cervical region be continuous, as it probably is, with the *tractus intermedio-lateralis*, which is reached by the dorsal nerves supplying the intercostal and other respiratory muscles of the trunk, the explanation in question will be still more complete†.

I shall now briefly trace the posterior vesicular columns of the human cord from the dorsal region downwards. At the upper part of the lumbar region, as in Mammalia, they are larger than in any other portion of the cord (see fig. 13, M, Plate XXI.). They have the same form and dark appearance as in the dorsal region, but contain more large cells. As they descend, however, the dark masses diminish, and are frequently broken into

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* See the author's "Medulla Oblongata," Phil. Trans. Part I. 1858, pp. 252, 253, figs. 19 and 36.

† Both in this communication and that on the Medulla Oblongata, I have abstained from drawing any physiological conclusions, except on this one occasion, where so *many different* facts required to be brought together while fresh in the memory of the reader.

parts; their larger cells, also, are gradually reduced in number, but others of a smaller kind are scattered through the spaces which they occupied.   In the middle of this region, the lumbar (fig. 15, Plate XXI. M), there is still, near the centre of the cervix cornu, a some-what dark and irregular mass, which in a moderately thin section may be very distinctly seen even with the naked eye.   Each of these masses is interlaced and surrounded, as usual, on its outer side by bundles of the posterior roots, and traversed by the transverse commissure. They present no traces of the large, strongly-marked cells which are found higher up, but, when examined under a sufficiently high magnifying power, they are seen to be interspersed and surrounded by cells of a smaller and more delicate kind, like those contained in the corresponding part of the cervical region.   In descending through the conus medullaris, the posterior cornua, by the retreat of the border between them, become gradually shortened and approach each other towards the middle line, so that the grey substance on the inner side of each *cervix* is brought nearer the central canal (compare figs. 16 & 17, Plate XXIII. M).   This grey substance, which, I think, must be considered as the remains of the posterior vesicular column, is still interspersed with a multitude of small and delicate cells, which lie amongst the fibres of the transverse commissure and posterior roots of the nerves.   But there is scarcely any trace of the peculiar group which is found in Mammalia on each side, and a little behind, the canal.   Sometimes, however, two or three cells rather larger than the rest may be seen at this spot in connexion with a few fibres of the anterior roots, but they are not distinguishable as a separate group.

In my first description of the posterior vesicular columns, it was stated that in the Calf they commence small at the lower extremity of the cord, increase in size in lumbar and cervical enlargements, and terminate at the upper part in the medulla oblongata. This statement, though in many respects true, must be modified by the descriptions above given.   It is true that they are actually largest, and contain the greatest number of large cells in the lumbar region, but only at its upper part; it is also true that both in the Calf and Sheep the large cells scattered through the inner half of the cervix cornu are at least as numerous in the lower part of the cervical enlargement as in the dorsal region. STILLING, however, while agreeing in the main with my first description of these columns and of their connexion with the posterior roots, denies their existence at the upper part of the cervical enlargement; for he does not consider the cells scattered through the inner half of the cervix cornu as part of the vesicular columns; and in the two lower thirds of the lumbar enlargement, he denies the existence of cells altogether: under low powers of the microscope they are certainly not visible*.

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* In discussing the causes which have led to this difference of opinion between himself and me, he adopts a very singular kind of argument.   1. He *assumes* that I made the sections thicker at one part of the cord than at another.   2. He *assumes* that I *squeezed* cells, lying at different depths, into one layer, in consequence of the *necessary* pressure resulting from the employment of Canada balsam and thin covering glass. The Canada balsam which I always use is fluid; everyone covers his preparations with thin glass; and if, as he asserts, my preparations are already too transparent, there is no need of pressure.

I was desirous to know whether the posterior vesicular columns are present in the spinal cord of the lower Vertebrata. I found that in Birds, as in the larger Mammalia, the posterior cornua, near the middle of the dorsal region, are united along their inner borders, and form but a single mass, around which the *gelatinous substance* extends without interruption. Each on its outer side, where the *caput* cornu joins the *cervix*, is very much constricted, but again dilates as it extends forwards to be continuous with the anterior cornu, so that the entire grey substance has nearly the form of an hour-glass or goblet (see fig. 32, Plate XXIII.). Numerous cells of various shapes and of moderate size are scattered on each side and behind the canal, and are traversed by the posterior roots proceeding through the constriction; but there are no dark masses at all corresponding to those of the posterior vesicular columns. In receding from the dorsal region, both upwards and downwards, the posterior cornua gradually separate, and the anterior cornua become enlarged. In Mammalia, and especially in Man, it has been seen that, through the middle of the cervical and lumbar enlargements, the cells on the inner side of the cervix cornu are reduced in size. In Birds, on the contrary, they are much larger than in any other region. This is particularly the case in the lumbar enlargement, especially near its middle, where they form a distinct group, which is traversed and surrounded by the posterior roots of the nerves (see M, figs. 34, 35, and 36, Plate XXIII.). They are mostly oval and round, with large nuclei, and send out their processes in different directions. In the corresponding part of the cervical region the larger cells are less numerous, but are mingled with others of a smaller kind.

In Reptiles, it is only in the *conus medullaris* that the posterior cornua are united into a single mass. In a transverse section they present no dark masses resembling those of the posterior vesicular columns, but only a few cells, of various shapes, at their bases. A distinct stratum, however, of small fusiform cells, in connexion with the fibres of the posterior roots of the nerves, extends diagonally from the point of each cornu to the posterior commissure, which is also interspersed with numerous nuclei, like those of the epithelium which lines the canal. In the cervical and lumbar enlargement, the cells, as well as the stratum which they form, are larger than in the dorsal region. (See figs. 44 & 45, Plate XXV.).

On the Grey Substance of the Filum Terminale.

In the *conus medullaris* of the *human* cord, as soon as the posterior cornua have united at their inner sides in a single mass (fig. 19, Plate XXIII.), the *gelatinous substance* (*g*) becomes continuous from side to side in a curve with its concavity backwards, in which the posterior columns (A) are included *; but, as it descends through the *filum*

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* The continuity of the gelatinous substance across the middle line was asserted in my first communication, and has since been found in birds by METZLER, 'De Medullæ spinalis Avium Textura,' p. 14 (1855). STILLING, however, in his late work, denies the fact, and maintains "that the middle portion is *grey,* and not *gelatinous,* substance" ("das Mittelstück ist graue Substanz, und nicht gelatinöse"); and adds that my method of preparation rendered these two substances too transparent to perceive any difference between

terminale, it rises to the surface in the middle line and extends directly across (see fig. 20, Plate XXIII.); meanwhile the posterior columns (A, A) become gradually shallower and at length disappear, *except* at the *sides*, so that the *gelatinous substance* behind is covered only by the pia mater (*m*) of the cord, with which it is immediately connected. The deep posterior strata of the lateral columns obliterate it at the sides, by encroaching in bundles on the grey substance which forms a continuous network around them. Still lower down (see fig. 21, Plate XXIII.) the canal is prolonged backwards as far as the gelatinous substance, and dilates in a lateral direction behind the dark bundles (D), which in the preceding sections occupied the interior of each caput cornu. (See explanation of Plates.)

In Mammalia a series of nearly similar changes may be observed, except that the posterior columns are not interrupted in the middle line.

Fig. 22, Plate XXIV. represents a transverse section of the *conus medullaris* of the Ox, near the third pair of coccygeal nerves, magnified 60 diameters. Multitudes of fibres are observed to radiate from the grey substance and form a beautiful network through the white columns. From the extremities of the anterior cornua considerable offsets of the grey substance are prolonged through the anterior columns, rejoining each other around masses of longitudinal fibres, and reaching the surface to be continuous with the layer of connective tissue. Amongst these offsets, and even *in* the masses of longitudinal fibres, several large cells are scattered very nearly to the surface of the cord; some of their processes *appear* to reach the connective tissue at the surface.

Through the lower part of the conus medullaris the canal continues to enlarge. It nearly reaches the anterior fissure, and extends backwards to the *gelatinous substance*, in front of which it dilates in a lateral direction (see fig. 23, Plate XXIV.). The grey substance, as it descends through the *conus*, gradually decreases in quantity, and is encroached upon more and more by the antero-lateral columns, around the bundles of which it radiates outwards as a network. Numerous small oval and fusiform cells, with one or two others of superior size, are scattered through it. The filum terminale, in its natural state, appears to be a nearly cylindrical tubule, but, when hardened in spirit or chromic acid, is more or less flattened at the sides, so that the canal becomes compressed and sometimes completely collapsed (see figs. 24 & 25, Plate XXIV.). The grey substance is at length reduced to a mere border or fringe (fig. 25), from the edges of which a series of tapering processes (*a, a*) extend through the white substance to the pia mater at the surface. The larger kind of cells have entirely disappeared, but a number of small fusiform cells, or nuclei, resembling those of the connective tissue, are observed in continuity with fibres which run along it and form arches from one process of the grey substance to another, as they pass out to the white columns.

them ("CLARKE's Preparations-methode zeigte ihm aber beide Substanzen zu hell, als dass er einen Unter-schied hätte finden können "); but, if he had taken the trouble to read the explanation of the figure in question, he would have seen that it was drawn from a section of the conus medullaris, treated *only by acetic acid*. The continuity of the gelatinous substance is so apparent at this part, both in a fresh state and when hardened with chromic acid, that STILLING's denial of the fact seems to me unaccountable.

Of the Epithelium of the Central Canal.

In the Ox, the *epithelium* which lines the central canal consists not only of *columnar* or cylindrical cells—as I first described them*, and as they have since been described by other observers—but also of cells which are more or less *fusiform*.   Fig. 53, Plate XXII. (*a*) is an exact representation of some of their forms, magnified 400 diameters. In the *columnar* variety (the first three on the left of *a*) the nucleus is large, sometimes spheroidal, but generally oval, and contains apparently from two to five large, brilliant, globular granules or nucleoli, which powerfully refract the light.   Between this and the verge of the canal the free ciliated end of the cell is broad and short like the end of a cylindrical brush, and *appears* to be made up of granular fibres; but in the *fusiform* epithelium (the four on the right of *a*), the corresponding free portion consists only of a long and narrow kind of stalk extending from the tapering end of the cell, which latter in this case is similar to what forms the *nucleus* of the *columnar* variety, and contains several brilliant granules, which are frequently arranged in a row.   Between these two kinds of epithelium there are different grades of transition.   They are all beautifully packed in close apposition, so that the convexity of each is applied to the concavity of those which surround it, and by reason of its peculiar shape, it exactly occupies the intervening space (see fig. 53 *b*, Plate XXII.).   In the *human* spinal cord, the canal is often completely filled up by what would appear to be the *débris* of the epithelium; for nothing is to be seen but a confused heap of *nuclei*, which are here mostly large and round: but sometimes in the midst of this heap there remains a small opening or canal, which, strange to say, is still lined or surrounded at its *margin* by the *usual regular* layer of columnar cells; and what is still more curious, I occasionally find, particularly in the cervical region, *two* such secondary canals, each lined in the ordinary way (see fig. 55, Plate XXII.).

The cilia of this epithelium are much coarser and less numerous than those in the larynx and trachea (fig. 53 *b*).   In the *conus medullaris* they may be very well seen around the entire circumference of the canal, but in other regions of the cord they are very sparingly found.   If this be the result of accident in manipulation, it is difficult to say why they are always preserved in the one place and not in the others.

The light-coloured space immediately surrounding the canal is interspersed with nuclei or small cells.   Some of these are round or oval, finely granular, and exactly resemble those in the connective tissue of the white columns (see fig. 46, Plate XXII. *c*); others are similar to the *nuclei* of the epithelium, and have the same kind of large brilliant granules, or nucleoli, but are themselves rather smaller.   These latter nuclei, which are frequently elongated in different directions, are connected with the processes of the epithelium (see fig. 53, Plate XXII. *b*), and also with the fine fibres which surround the canal, and which are precisely similar to the fibres of connective tissue at the circumference of the cord †.   They are not, however, confined to the neighbourhood of the

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* Philosophical Transactions, 1851, p. 614.

† In 1851, I described the light-coloured part immediately surrounding the canal, as composed of fila-

canal, for they may be found in different parts of the grey substance, and in the posterior fissure. The only difference between them and the *nuclei* found in the *white columns* and *pia mater*, is, that in the *latter* cases the *granules* or *nucleoli* are *smaller*; but in the Tortoise I have found that nuclei which, in every minute particular, *exactly* resemble those of the epithelium, may be traced continuously from the edge of the canal through the *whole* of the grey substance and the *white* columns of the cord *. Indeed, the spinal canal appears only to be the part where they are more thickly accumulated in layers; and even there they are not enclosed in cells, but are connected only by a variable number of fibres with the verge of the canal (see fig. 54, Plate XXII. G, and explanation of Plate). There is good reason, then, for believing that both the epithelium and the small cells or nuclei by which it is surrounded, are allied to the connective tissue.

The outer ends of the epithelial cells taper into delicate fibres, of which those proceeding from the columnar variety are the thickest (fig. 53, Plate XXII.). These fibres radiate in all directions, and either run side by side, or cross each other in various ways and subdivide to join in an intricate network. For a considerable distance around the canal they may be frequently seen, as already stated, to be continuous with the small cells or nuclei above described. Some of them run directly backwards across the posterior commissure and along the posterior median fissure; some extend forwards across the *anterior* commissure to the inner edges of the anterior *columns*, and may be traced in part to blood-vessels and pia mater contained in the median sulcus; while others run off in a lateral direction and are lost in the grey substance. In the *filum terminale*, where this substance, as already remarked, is reduced to a narrow fringe (figs. 24 & 25, Plate XXIV.), their actual destination may often be very satisfactorily traced by means of my method of preparation. Here they may be seen, sometimes at right angles, and sometimes more obliquely to the axis of the cord, to pass *through* the *grey substance* and then through the *white columns* to join the connective tissue, every part of which is interspersed with nuclei like those in continuity with the fibres *in the central fringe*, which *here* evidently consists of the same kind of tissue as the light-coloured space surrounding the canal in other regions of the cord.

HANNOVER regards the cells which line the cerebral ventricles as true *nerve-cells*, and BIDDER takes the same view of those round the spinal canal; while STILLING considers them as epithelium, but, nevertheless, believes that the fibres which they give off form elementary parts of the primitive *nerve*-fibres and *nerve*-cells, with both of which, according to him, they are directly continuous. He professes to have seen the peripheral ends of two epithelial-cells unite with each other after a shorter or longer course, and then enter a *nerve*-cell; or the process of a *nerve*-cell divides into two or three branches, which end in two or three epithelium-cells†. By the most careful examina-

mentous or connective tissue, in opposition to STILLING, who considered it to consist of *grey nerve-fibres*, and called it the circular *commissure*, but now calls it the "substantia gelatinosa centralis" (see Philosophical Transactions, Part II. p. 614, 1851).

* I have found the same in the Cat.

† "Zuweilen sieht Man die peripherischen Enden zweier Epithelialcylinder in kürzerer oder längerer

tion of some hundreds of preparations, I have never been able to perceive that the epithelial-processes are connected with any other than the *small* cells or nuclei which I have already described. I have sometimes seen the process of a *large nerve*-cell extend close up to the epithelium, but I have generally succeeded in tracing it round the canal to the *opposite side* of the cord*. If the processes of the epithelial-cells were directly continuous with, and formed elementary parts of, *nerve*-cells and *nerve*-fibres, we might reasonably expect to find the number of the former always in proportion to that of the latter; but the very reverse is the case; for, as we have just seen, in the *filum terminale*, where both *nerve*-cells and *nerve*-fibres have *entirely disappeared*, the *canal* is much *larger*, and the *epithelial-cells* are consequently much more numerous than in any other region; while, as I have already shown, their processes may be traced through the surrounding white substance as far as the surface of the cord.

I have nothing to add to the description which I formerly gave of the anterior roots of the spinal nerves, except that in the *conus medullaris* I constantly find that some of the fibres of these roots terminate *in loops* round the group of cells in the anterior cornu; but whether they be really *nerve*-fibres I have not quite satisfied myself. Sometimes they form loops between two different bundles of roots, and sometimes a fibre from one bundle returns in a loop to the inner or outer side of the anterior column. But in the same region of the cord I have seen the processes of the nerve-cells extend so frequently into the anterior roots, that there can be no doubt that some of the latter arise from them†. In the cervical and lumbar regions of the Tortoise, but especially in the lumbar enlargement, the course and connexions of the processes proceeding from the cells of the anterior cornua are extremely interesting. Fig. 44, Plate XXV. represents a transverse section of one lateral half of the grey substance, through the middle of the lumbar enlargement. From the whole of its lateral border numerous large bundles of fibres proceed outwards and form with each other a beautiful network between fasciculi of the antero-lateral column. Some of these fibres converge from the central parts of the grey substance; the rest proceed from the roots of the nerves, and from the cells of both the posterior and anterior cornua, but particularly from the latter. The large cells of each anterior cornu form a considerable group; they are angular, sigmoid, crescentic and fusiform, and *elongated* to an *extraordinary* degree in a direction obliquely backwards. The processes from their anterior extremities are continuous with the anterior

Entfernung vom Mittelstück mit einander verschmelzen, und in eine Nervenzelle übergehen, resp., den Fortsatz einer Nervenzelle sich dichotomisch oft trichotomisch theilen und in zwei oder drei Epithelial-cylindern endigen." " Es ist mir aber sehr wahrscheinlich, dass diese Ausläufer oder peripherischen Enden der Epithelialzellen als Elementarrörchen der betreffenden Primitivnervenfaser oder Nervenzelle, in welche sie eintreten, bestehen."—Neue Untersuchungen, Erste Lieferung, p. 11 (1857).

* In the coccygeal region of the cord, processes from the nerve-cells in the anterior cornu may be very distinctly seen to cross both in *front* and *behind* the canal to the *opposite* side.

† I never, as SCHRÖDER VAN DER KOLK asserts, *denied* the connexion of nerve-fibres with processes of cells, but simply maintained that the occasional extension of these processes into nerve-roots was not a sufficient proof of such a connexion, for they *might* be distributed to blood-vessels.

roots of the nerves, or escape through the anterior columns; while those from their posterior ends extend backwards to different distances, and form a continuous stratum of fibres along the lateral margin of the grey substance: some of them join the fibres which radiate from the centre, and contribute in succession to form the bundles which escape as a network through the antero-lateral column; others extend as far as the *posterior* cornu, and seem to be continuous with the *posterior* roots which escape through the postero-lateral fissure. The rest of the posterior roots partly descend towards the centre of the anterior cornu, and partly cross the posterior cornu diagonally in connexion with a chain of cells, to be continuous with the transverse commissure. In the cervical enlargement (fig. 45), the cells of the anterior cornu are more numerous and more diversified in shape; some of them send processes towards the anterior commissure, but a great number have no apparent connexion with it.

In my first communication on the *spinal cord*, I stated that the posterior roots of the spinal nerves are attached *exclusively* to the *posterior* white columns. I have since found that the same assertion was made by ROLANDO: he says, "tutti i fili nervosi delle radici posteriori se staccano esclusivamente dai cordoni posteriori del gran funicolo spinale; ciò che può essere comprovato in varie e differenti maniere*." STILLING denies the fact, and maintains that in the lumbar region a few fibres traverse the posterior part of the antero-lateral column. I have again carefully gone over the ground, in the cord both of Man and different animals, and find that my statement is correct. STILLING has probably confounded nerve-fibres with the blood-vessels which traverse the posterior part of the antero-lateral column much in the way that he represents.

APPENDIX.

[Added during the printing of the Paper.]

Convinced of the superiority and value, in many respects, of my method of anatomical research, I will here describe it more fully, together with the modifications which I have lately introduced in some stages of the process, and the precautions necessary to be observed in order to ensure success.

The structure or part intended for examination should be as fresh as possible, and cut into portions as small as is compatible with the end in view. These portions I formerly hardened by means of a mixture of one part of spirit of wine and three parts of water, which at the end of twenty-four hours was replaced by a fresh mixture of equal parts of spirit and water, and this again after the same interval was replaced by pure spirit, which ought to be renewed every five or six days. At the end of ten to fourteen days the medulla is sufficiently hard for making sections, which are then subjected to the following process for the purpose of inducing transparency. The sections are first placed in a mixture of one part of strong acetic acid, and four, five, or six of spirit, for a

* *Op. cit.* p. 82.

period varying from two or three to ten minutes, according to their thickness. They are then washed in pure spirit, after which, if thin, they are floated on the surface of spirit of turpentine, where they remain until they are quite, or nearly transparent, when they are removed to glass slides on which a little Canada balsam has been previously dropped. If now examined under the microscope, they frequently show but little or no traces of cells or fibres,—a circumstance which seems to have *at first* caused SCHRÖDER VAN DER KOLK and some others to abandon the method; but if the sections be set aside for some time and treated occasionally with a little turpentine and Canada balsam, the cells and fibres reappear and present a beautiful appearance. Before they are finally covered with thin glass, they should be examined at intervals by the microscope. If the sections be *thick*, I find it best to place them in a shallow vessel, the bottom of which is kept simply wet with turpentine, which can therefore ascend from below while the spirit evaporates from their *upper* surfaces; for the *principle* of the method is this,—to replace the spirit by turpentine, and this by Canada balsam without *drying* the sections. The method at first presents some difficulties, and practice is necessary to ensure complete success. Experience, also, will suggest, according to circumstances, many little deviations from the exact rules here given, which to a certain extent must be considered as general.

For the last three years I have used chromic acid instead of spirit in the process of hardening. This is one of the modifications mentioned in my memoir "On the Medulla Oblongata"*. The medulla of Man and the higher Mammalia is steeped in a solution of one part of crystallized chromic acid in 200 parts of water, for two or three weeks, and then kept in a solution of about one part of bichromate of potash in 100 or 200 parts of water†. Spirit is used to wet the knife in making the sections, which are first placed in spirit for a few minutes, and then (with or without the previous use of acetic acid) transferred to the turpentine and Canada balsam, as before.

LENHOSSÉK, GERLACH, and quite recently SCHRÖDER VAN DER KOLK, have adopted this method of rendering sections transparent. LENHOSSÉK uses spirit for hardening the medulla, with some slight modification in other stages of the process. An entire series of very beautiful preparations of the cord and medulla oblongata have been purchased of him by the Royal College of Surgeons of London. GERLACH uses bichromate of potash in the process of hardening; then acetic acid, spirit, and Canada balsam‡. He does not *mention* turpentine; but if this be dispensed with, the Canada balsam must be very thin, and the section must be placed on its surface to allow of the evaporation of the spirit, which will not mix with the balsam, but in contact with it becomes turbid and opake.

In his Essay on the Spinal Cord published in 1854, SCHRÖDER VAN DER KOLK says that my (second) method, "which appears to have been extremely successful," did not suc-

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* 1857. Philosophical Transactions for 1858, Part I.

† For the Rodentia, Birds, Reptiles, and Fishes, it is necessary to use the solution much weaker—about one part to 600 of water, and gradually increase the strength at the end of a week.

‡ Mikroskopische Studien, p. 2, 1858. Erlangen.

ceed with him; "the preparation became only partially clear, and the ganglionic cells, from which the fat seemed to be removed, were rendered indistinct *." It is perfectly clear that he had not sufficient practice in the process. He says again, in speaking of LENHOSSÉK, "he follows CLARKE's method with turpentine, which, *according to my expe-rience*, cannot lead to correct results, as the spinal marrow is too much altered by that agent †." After criticising every other method, he describes his own, which consists in the use of concentrated chloride of calcium, and which, according to his experience, "deserves to be preferred to all the others." But now we find that he has abandoned it, and adopted *my* method in conjunction with the colouring process recommended by GERLACH; for in a supplementary paragraph to the English translation which has just been issued by the Sydenham Society (1859), he states that after some trials he finds this mode of making preparations the most satisfactory, and in many respects still better than with *chloride of calcium*. The section, after having been coloured with solution of carmine and washed in spirit, is laid in a watch-glass and allowed to dry a little, after which, "a couple of drops of spirit of turpentine are added. If it is now left for twenty-four or forty-eight hours without a covering glass, but protected from the dust, the spirit evaporates, and the object becomes perfectly clear. It is now covered with Canada balsam and a glass‡." The colouring with carmine is often very useful, but I think it rather interferes with the sharpness of the fibres. I have long used, occa-sionally, a colouring fluid known to painters and wood-stainers by the name of *archel*. When carmine is used, the solution should be previously filtered, otherwise a deposit or crust is apt to form on the object; and for the same reason, the section, after having been coloured, should be washed in water before it is placed in the spirit, which readily precipitates the carmine.

STILLING has given a full, but somewhat inconsistent and incorrect criticism on my method. He concludes by saying, "While it is allowed that by the employment of CLARKE's method many truths indeed in reference to the minute structure of the spinal cord may be brought to light, and that CLARKE's labours must be said to be quite trust-worthy (recht anerkennenswerthe), it must nevertheless be observed that the condition of certain textures, such as the elementary structure of the primitive nerve-fibres and the nerve-cells, are so altered by it, that this method in many respects must be con-sidered as an obstacle to the more exact kind of investigation §."

Now, although I am not so blindly prejudiced as to maintain that preparations made by this method are in every respect perfect, I do maintain that it produces but little alteration from the natural appearance of the nerve-cells, and that almost the only structure that appears to suffer more than from chromic acid alone is the white sub-stance of the nerve-fibre; and even this may be perfectly preserved if the medulla is placed first in a weak solution of chromic acid and then in a solution which is much stronger. Fig. 1, Plate XIX. was drawn from a preparation made in this way, and of

* Translation of Sydenham Society, 1859, p. 30.   † Ibid. p. 28.
‡ *Loc. cit.* p. 33.   § Neue Untersuch., 5 Lief. p. 1071.

which it is as exact a copy as possible.   But even the *loss* of the *white substance* would be of no consequence for tracing the *course* of the nerve-fibres, the axis-cylinders of which in these preparations are rendered unusually strong and distinct.   And if I wish to investigate the *natural* structure of the nerve-fibres and cells, I select a perfectly fresh and unaltered specimen from an animal just killed (as I stated in my first communication to the Royal Society, 1851); for I never think of trusting to any kind of preparation, or even to chromic acid, which STILLING uses, and which coagulates the contents of the nerve-fibres and alters their appearance after a short maceration.   Not that I reject other methods; for I find sections of the medulla, simply hardened in chromic acid, of great service, and use them largely, particularly for drawing figures under low powers, and sometimes for examination under higher powers, when I have been in some doubt as to the nature of the tissue.   In fact, I employ whatever means appears most suitable for the occasion and most likely to lead me to the truth.   But I still contend, that for clearness, sharpness of outline and fine definition under the higher powers,—for the advantage of obtaining *thick* sections of *great transparency*, and for the durability and unchangeableness of the preparations when properly made, I know of no method that will bear any comparison with this.   To confirm this opinion in one respect, I may mention the fact, that although STILLING, in his recent work, has described and represented the spiral structure of the fibres of the white columns of the *Calf* under a power of 1100 diameters, he has failed to detect the nucleated cells and nuclei which are so beautifully seen by means of my method under a power of 350 diameters.

EXPLANATION OF THE ·PLATES.

Fig. 1, Plate **XIX.** represents a transverse section of the *caput cornu posterioris* and part of the *cervix* cornu, with a portion of the surrounding posterior and lateral white columns: from the middle of the cervical enlargement of the Ox; drawn from a preparation magnified 50 diameters:—A, A, A, part of the posterior white column; B, B, part of the lateral column: the small circles and dark spots represent the cut ends of longitudinal and oblique fibres.   These columns are traversed by a beautiful network of blood-vessels and nerve-fibres radiating from all parts of the grey substance.   At *b, b* (the peak of the cornu) may be seen extending outwards the processes of nerve-cells situated in the network between bundles of the white column.   The *darker* portion of the *caput* cornu consists principally of numerous longitudinal and oblique bundles of fibres, with blood-vessels, and of the posterior roots of the nerves, with cells chiefly of the small and intermediate size; the *lighter* space behind and at the sides is the *gelatinous substance*, studded with small cells, and having a stratum of *large* cells and marginal nerve-fibres along its posterior border next the posterior column, into which some of the processes of the cells may be seen to extend.   C, C, part of the *cervix* cornu, containing some

3 P

large cells, and crossed in different directions by the posterior roots of the nerves, and by fibres which radiate to the white columns. At the junction of the *cervix* and *caput* cornu, near the right border of the grey substance, are five large bundles of longitudinal fibres, interlaced by transverse fibres, and more or less encircled by large elongated nerve-cells, which send some of their processes longitudinally.

Fig. 2, Plate **XX.** represents a transverse section of the grey substance from the middle of the dorsal region of the Ox; drawn from a preparation magnified 60 diameters:—D, D, posterior cornua, the points of which are cut off; on the left side, the letter D is in the darker portion of the *caput* cornu. The nerve-cells are shown chiefly on the right side. *g*, the gelatinous substance; E, E, anterior cornua; F, tractus intermedio-lateralis of right side; two of its cells are seen extending into the lateral column towards the letter F; G, central canal, lined with epithelium, from which fibres radiate in connexion with small cells and nuclei, through the surrounding transparent space, H; behind H is the posterior transverse commissure, the fibres of which are in connexion with fusiform cells, and partly extend outwards to the tractus intermedio-lateralis, F; I, two bundles of longitudinal fibres, cut off from the anterior columns by transverse fibres of the anterior commissure, K, K; L, anterior median fissure; *l*, posterior median fissure; P, P, bundles of posterior nerve-roots; M, M, cylinders of the *posterior vesicular columns*; N, three bundles of longitudinal fibres near the margin of the grey substance, and two of which are seen to be partially embraced by nerve-cells; T, fibres of the posterior commissure extending outwards; *n*, outer side of cervix cornu posterioris of left side, where there is a decussation between the fibres of the posterior roots, in connexion with the posterior vesicular columns and the posterior commissure; *o'*, anterior roots of the nerves.

Fig. 3, Plate **XXI.** Transverse section of the grey substance of the Ox, at the upper part of the dorsal region, where the posterior cornua are beginning to separate from each other in the middle line:—F, tractus intermedio-lateralis, extending inwards towards the posterior transverse commissure, and the front of the posterior vesicular column.

Fig. 4, Plate **XX.** A similar section, higher up, near the lower end of the cervical enlargement.

Figs. 5 to 21 are transverse sections of the grey substance of the spinal cord, from a Woman aged 33 years.

Fig. 5, Plate **XXI.** Section near the middle of the dorsal region:—F, tractus intermedio-lateralis; M, posterior vesicular column.

Fig. 6, Plate **XXI.** Another, at the upper part of the dorsal region.

Fig. 7, Plate **XXI.** A similar section through the lower part of the cervical enlarge-

ment; the tractus intermedio-lateralis, F, rests on the lateral projection of the anterior cornu, behind a group of large vesicles, and is connected by a network with the *cervix* cornu posterioris.

Figs. 8 & 9, Plate XXI. Sections of the lateral half of the grey substance, successively nearer the middle of the cervical enlargement:—N, large bundles of longitudinal fibres near the lateral edge of the grey substance.

Fig. 10, Plate XXI. Lateral half of the grey substance, through the middle of the cervical enlargement: the tractus intermedio-lateralis is no longer visible, but the lateral projection of the anterior cornu, on which it rested, is still connected by a network with the side of the cervix cornu, which is pierced by several bundles of longitudinal fibres, N.

Fig. 11, Plate XXI. A similar section of the grey substance at the fourth cervical nerves:—N, longitudinal bundles of the lateral column, enclosed in the meshes of a network proceeding from the grey substance, and containing small cells; through this network the roots of the spinal-accessory nerve proceed from behind forwards to the *tractus intermedio-lateralis*, F, and to the cells of the anterior cornu; P, posterior roots of the spinal nerves; M, posterior vesicular column traversed by bundles of the posterior roots, and by the transverse commissure.

Fig. 12, Plate XXV. Similar section at the upper part of the third cervical nerves, magnified 60 diameters:—N, N, N, network proceeding from the side of the posterior cornu and tractus intermedio-lateralis, containing small cells and enclosing bundles of fibres of the lateral column, between which the roots of the spinal-accessory nerve proceed forwards to the *tractus intermedio-lateralis*, F, and to the anterior cornu; the extremity, and particularly the outer portion, of the anterior cornu is pierced by numerous longitudinal bundles (represented by the dark round or oval masses), between which the fibres of the anterior roots (O') cross each other in an intricate plexus; amongst this plexus are several large nerve-cells, which partially embrace the bundles and send some of their processes longitudinally.

Fig. 13, Plate XXI. Transverse section of one lateral half of the grey substance at the upper part of the lumbar enlargement; the posterior vesicular column, M, is larger than in any other region.

Fig. 14, Plate XXI. A similar section, nearer the middle of the lumbar enlargement.

Fig. 15, Plate XXI. Another section, through the middle of the same enlargement: the posterior vesicular column, M, is composed almost entirely of small cells; the lateral part of the cervix cornu is pierced by several bundles of longitudinal fibres.

Fig. 16, Plate XXIII. A similar section, through the lower part of the lumbar enlargement.

Fig. 17, Plate XXIII. Section through the upper part of the conus medullaris.

Figs. 18, 19, 20 & 21, Plate XXIII. Sections through the remaining portion of the conus medullaris.

Fig. 19. The *gelatinous substance*, *g*, is continuous across the middle line beneath the posterior columns, A; D, opake portion of the caput cornu; N, bundles of longitudinal fibres.

Fig. 20. The posterior white columns (A, A) are wanting in the middle line, and terminate by a thin edge on each side of the gelatinous substance (*g*), which rises to the surface in a straight transverse layer, covered only by pia mater, *m*; D, are the dark bundles which in the preceding figures formed the opake portion of the caput cornu; similar, but less numerous, bundles are scattered through the rest of the grey substance anteriorly.

Fig. 21. The spinal canal has extended backwards and sideways in the form of T; its lateral extension is through the *gelatinous* substance, which thus becomes continuous with the space previously surrounding the central canal, while the part corresponding to the opake portion of the caput cornu (D) is now in front and at the side of the canal. The remains of the gelatinous substance are covered and permeated by a quantity of pia mater, *m'*; indeed they now seem to consist of little or nothing else; this pia mater is continuous with that surrounding the cord, *m'*. E, the anterior grey substance, forming a network between longitudinal bundles of fibres.

Fig. 22, Plate XXIV. Transverse section of the *conus medullaris* of the Ox, at the first pair of coccygeal nerves; drawn from a preparation magnified 60 diameters:— A, A, posterior columns; B, B', antero-lateral columns. From the grey substance a beautiful network of nerve-fibres with blood-vessels extends through the white, especially the antero-lateral, columns (B, B'), and encloses in its meshes a multitude of longitudinal bundles. From the extremities of the anterior cornua, considerable offsets of the grey substance extend through the anterior white columns, which are interspersed with large nerve-cells nearly to the surface of the cord. Fibres from around the canal, joined by others proceeding from the epithelium, run forwards along the sides of the anterior median fissure to the circumference. In the posterior cornu are many large bundles of longitudinal fibres; one of these is partially encircled by a cell; several other longitudinal bundles are seen amongst the fibres of the posterior commissure.

Fig. 23, Plate XXIV. Transverse section through the lower part of the *conus medullaris* of the Ox; drawn from a preparation magnified 60 diameters:—A, A, posterior white columns; B, B, antero-lateral columns; G, central canal; *a, a, a,* posterior grey substance; E, anterior grey substance: the whole of the grey substance, on each side of the canal (which is here very large), is pierced by a multitude of longitudinal bundles of fibres of different shapes and sizes (represented by the dark masses), and is interspersed with a number of *small*

cells; a small group of *large* cells is found at its anterior extremity on each side.

Fig. 24, Plate **XXIV**. A similar section, near the end of the *conus medullaris* of the Ox. It appears to be altered in shape by some accidental cause; for in its natural state the canal is nearly of the same form as in fig. 23:—A, A, posterior white columns; B, B, antero-lateral columns. The grey substance around the canal is reduced in quantity, and appears as a kind of network enclosing a multitude of longitudinal bundles; it is also interspersed with small cells, but contains only a few of *a larger kind*, near its anterior extremity.

Fig. 25, Plate **XXIV**. Transverse section of the grey substance of the *filum terminale*, or filiform extremity of the cord, magnified 60 diameters. The canal is collapsed laterally, but is naturally very large, and the epithelium is consequently abundant. The grey substance surrounding it is reduced to a mere fringe, pierced here and there by small longitudinal bundles, and interspersed with small cells or nuclei:—*a, a*, processes of pia mater, and blood-vessels radiating from the border of the grey substance through the white columns towards the surface.

Figs. 26 to 36, Plate **XXIII**. represent transverse sections of the spinal cord of the domestic Fowl.

Fig. 26. Section at the first pair of cervical nerves.

Fig. 27. Section in the middle of the neck.

Fig. 28. Section at the upper end of the cervical enlargement.

Fig. 29. Section through the middle of the cervical enlargement.

Figs. 30 & 31. Sections through the lower half of the cervical enlargement.

Fig. 32. Section through the middle of the dorsal region.

Figs. 33, 34 & 35. Sections through the upper half of the sacral enlargement.

Fig. 36. Section through the middle of the sacral enlargement.

In fig. 34 the posterior median fissure (*l*) begins to widen towards the surface, so as to form the commencement of the sacral ventricle; and through it the pia mater descends and expands into a mass which surrounds the canal, and replaces the posterior transverse commissure. In fig. 35 is seen an extension of the same changes. In fig. 36 the posterior columns, with the grey substance, are thrown widely apart, so that the posterior median fissure dilates into the broadest portion of the ventricle, which is filled by a large mass of the pia mater (*m*). The lateral halves of the grey substance are consequently united only by the anterior commissure (K), in which there is a very evident decussation. Some of the decussating fibres may be traced into the cervix cornu posterioris. METZLER, whose observations are in general in accordance with my own, states, however, that a real decussation is found only in the *sacral* enlargement, and in the upper part of the cervical region;

but I have certainly found a decided but slighter decussation in the *cervical enlargement*.

Figs. 37 to 45 represent transverse sections of the spinal cord of the Tortoise.

Fig. 37, Plate **XXII**. Section at the first pair of cervical nerves. A network (N) is prolonged from the sides of the grey substance into the antero-lateral columns, enclosing bundles of their longitudinal fibres.

Fig. 38. Section through the upper part of the cervical enlargement.

Fig. 39. Section through the middle of the cervical enlargement.

Fig. 40. Section through the middle of the dorsal region.

Fig. 41. Section through the middle of the lumbar enlargement.

Figs. 42 & 43. Sections through the lower part of the lumbar enlargement.

Fig. 44, Plate **XXV**. Transverse section of one lateral half of the grey substance, through the middle of the lumbar enlargement, of the Tortoise, magnified 80 diameters:—D, posterior cornu; E, anterior cornu; O', anterior roots of the nerves; P, posterior roots; B, B', antero-lateral column, divided into separate fasciculi by a beautiful network, formed by nerve-fibres and processes of nerve-cells from the grey substance.

Fig. 45, Plate **XXV**. Similar section through the middle of the cervical enlargement of the Tortoise, magnified 80 diameters. The cells of the anterior cornu present a more varied shape than in the preceding figure; and the network in the antero-lateral column is neither so considerable nor so uniform as in the last figure.

Fig. 46, Plate **XXII**. Cells from the *gelatinous* substance of the Ox, magnified 350 diameters:—a, b, cells of small and intermediate size; c, round, oval, and fusiform nuclei of connective tissue.

Fig. 47, Plate **XXII**. Large cells from near the posterior border of the same, magnified 220 diameters.

Fig. 48, Plate **XXII**. Nucleated cells and free nuclei from the white columns of the spinal cord of a Calf, between three and four months old, magnified 420 diameters:—a, cut end of a nerve-fibre, showing a kind of spiral or concentric arrangement around the axis-cylinder; b, b, nucleated cells partially encircling the nerve-fibres, and attached to their sheaths; c, c, separate nucleated cells, some with ramifying processes; d, two nucleated cells from a longitudinal section; e, free granular nuclei.

Fig. 49, Plate **XXII**. Large cells from a *transverse* section of the *posterior* vesicular columns of the Ox, magnified 220 diameters:—a, one of the processes running in a nearly longitudinal direction.

Fig. 50, Plate **XXII**. Large cell from a *longitudinal* section of the posterior vesicular columns, magnified 220 diameters:—a, process extending towards the posterior nerve-roots; b, another extending towards the anterior cornu.

Fig. 51, Plate **XXII**. Transverse section of the human *tractus intermedio-lateralis*, from

near the middle of the dorsal region, magnified 220 diameters:—*c*, the inner portion, adjoining the grey substance between the anterior and posterior cornua (see fig. 6, F, Plate XXI.); *b*, the free extremity extending transversely across the lateral column; *a, a, a*, fasciculi of longitudinal fibres of the lateral column.   The tractus is interspersed with cells, from some of which the processes escape with nerve-fibres into the lateral column; while others are continuous with nerve-fibres proceeding from the transverse commissure and other deep parts of the grey substance.   At its inner end (*c*), some of the cells with their processes are elongated towards the anterior and posterior cornua (compare fig. 6, Plate XXI.).

Fig. 52, Plate XXII. Cells from a transverse section of the *tractus intermedio-lateralis* of the Ox, magnified 220 diameters.

Fig. 53, Plate XXII. Epithelial-cells from the spinal canal of the Ox, magnified 400 diameters:—*a*, isolated cells (the letter is placed over their free, ciliated end); *b*, same cells packed together *in situ*, and bearing cilia, which project into the canal.

Fig. 54, Plate XXII. Epithelium from the spinal canal of the Tortoise:—*a, b*, separate cells, magnified 400 diameters; G, part of spinal canal, with the cells disposed around it, and a little less magnified; *c*, free nuclei from the white columns: magnified 400 diameters.

Fig. 55, Plate XXII. Human spinal canal from the cervical region.   Its outer parts are filled up with a heap of epithelial-nuclei, in the midst of which are two secondary canals, surrounded by the usual regular layer.

Fig. 56, Plate XXII. Longitudinal section of part of the *tractus intermedio-lateralis*, magnified about 200 diameters.   The cells are elongated longitudinally at the verge of the lateral column, the fibres of which are accompanied by their processes.
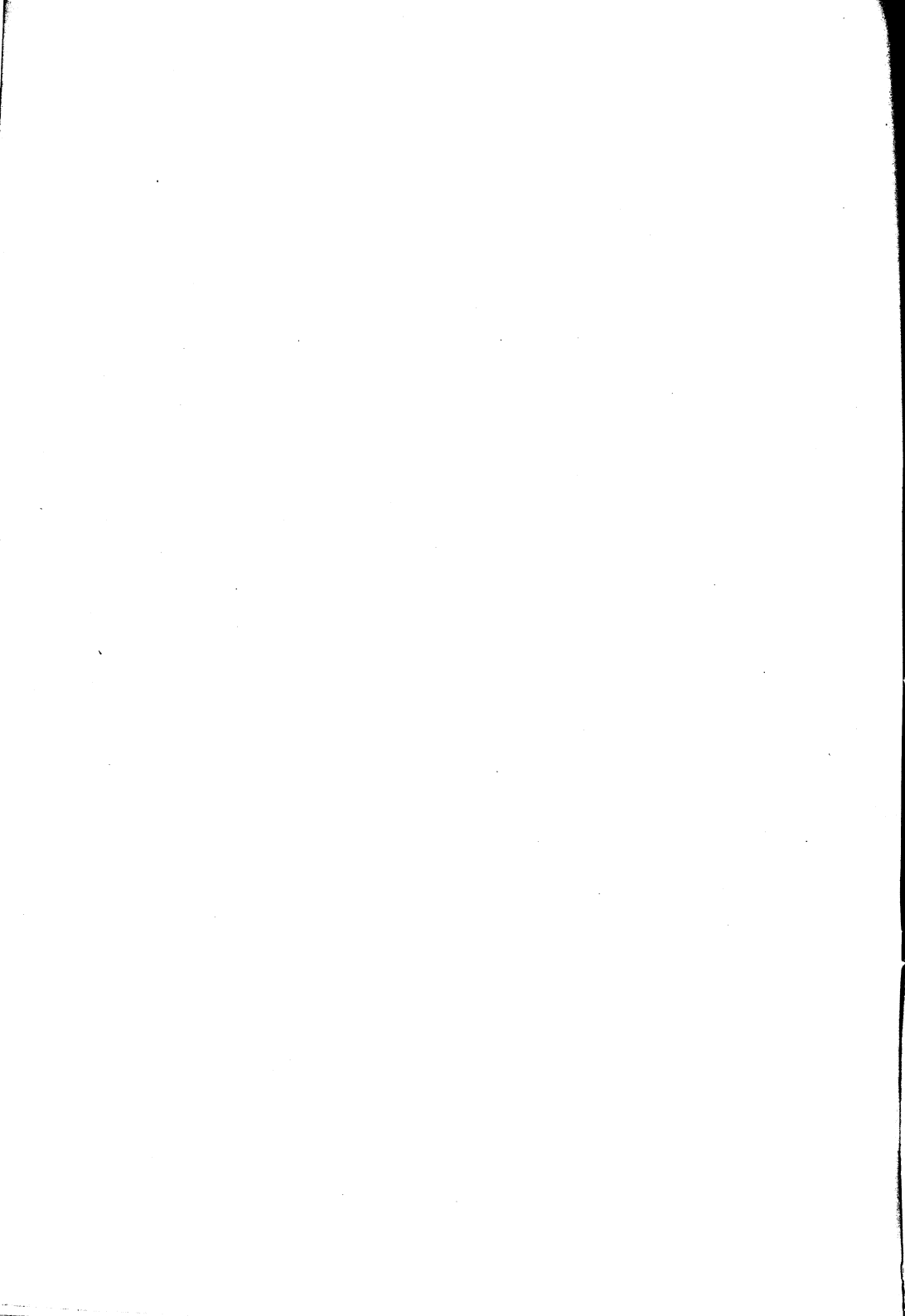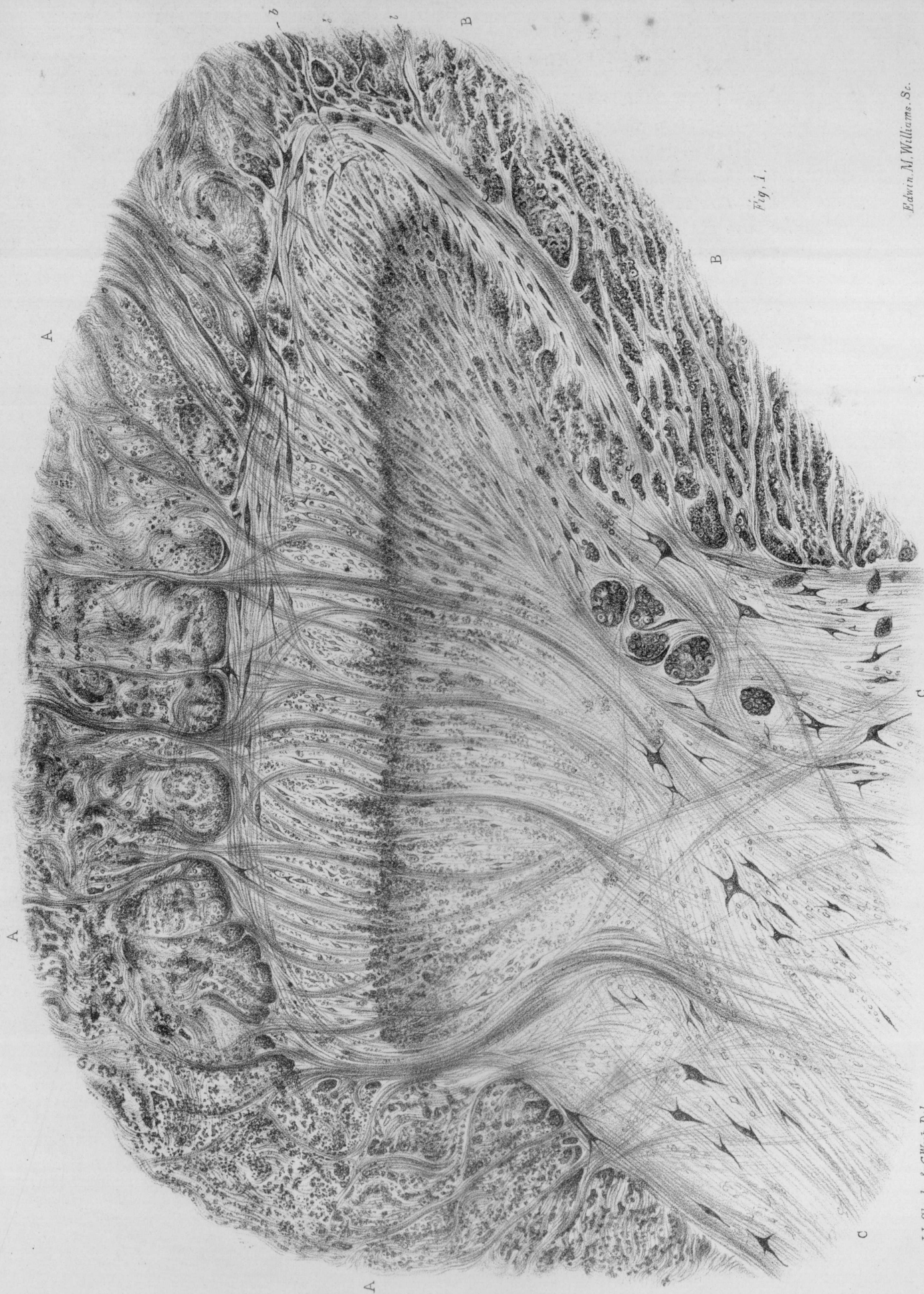
Fig. 1.

Fig. 2. × 60.

Fig. 4.

Fig, 3,

Fig, 8,

Fig, 9,

Fig, 5,

Fig, 14,

Fig, 10,

Fig, 6,

Fig, 7,

Fig, 15,

Fig, 13,

Fig, 11,

J. L. Clarke, Del.

Fig, 46, × 350.

Fig, 37. A

E

Fig, 47. × 220.

a

c

Fig, 38.

Fig, 54.

1 a b c

2 C

Fig, 48. × 420.

e

c

b

a

d

Fig, 41.

E

Fig, 49. × 220.

a

a

b

g Fig, 39.

D

Fig, 55.

Fig, 40.

P

E

Fig, 50. × 220.

b

Fig, 51, × 220.

c

Fig, 43.

D

Fig, 42.

D

Fig, 53,

a

b

Fig, 52. × 220.

Fig, 56.

Fig. 26.

Fig. 17.

Fig. 32.

Fig. 27.

Fig. 33.

Fig. 28.

Fig. 16.

Fig. 34.

Fig. 29.

Fig. 18.

Fig. 19.

Fig. 35.

Fig. 30.

Fig. 20.

Fig. 31.

Fig. 21.

Fig. 36.

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Fig. 22. × 60.

Fig. 24. × 60.
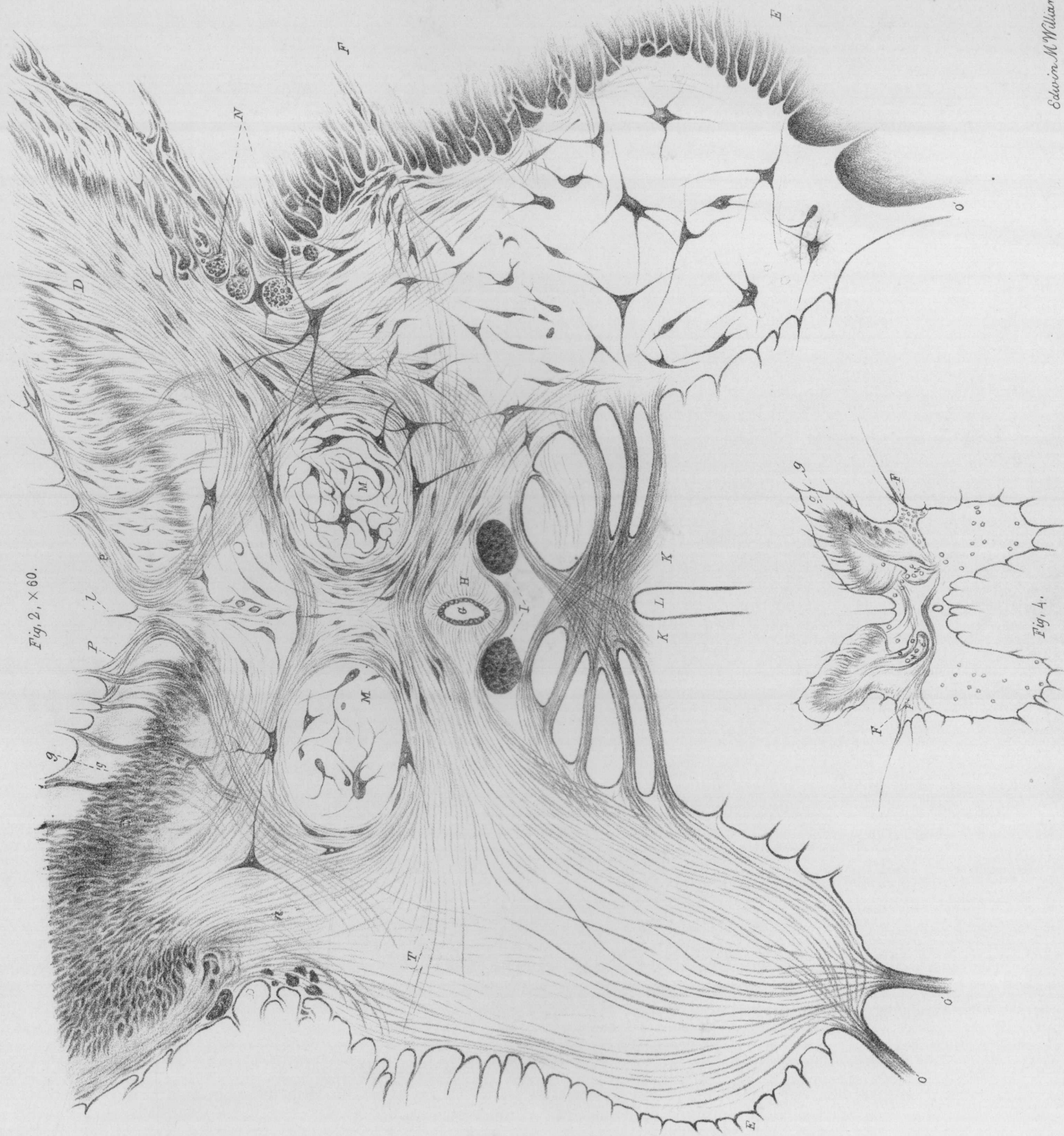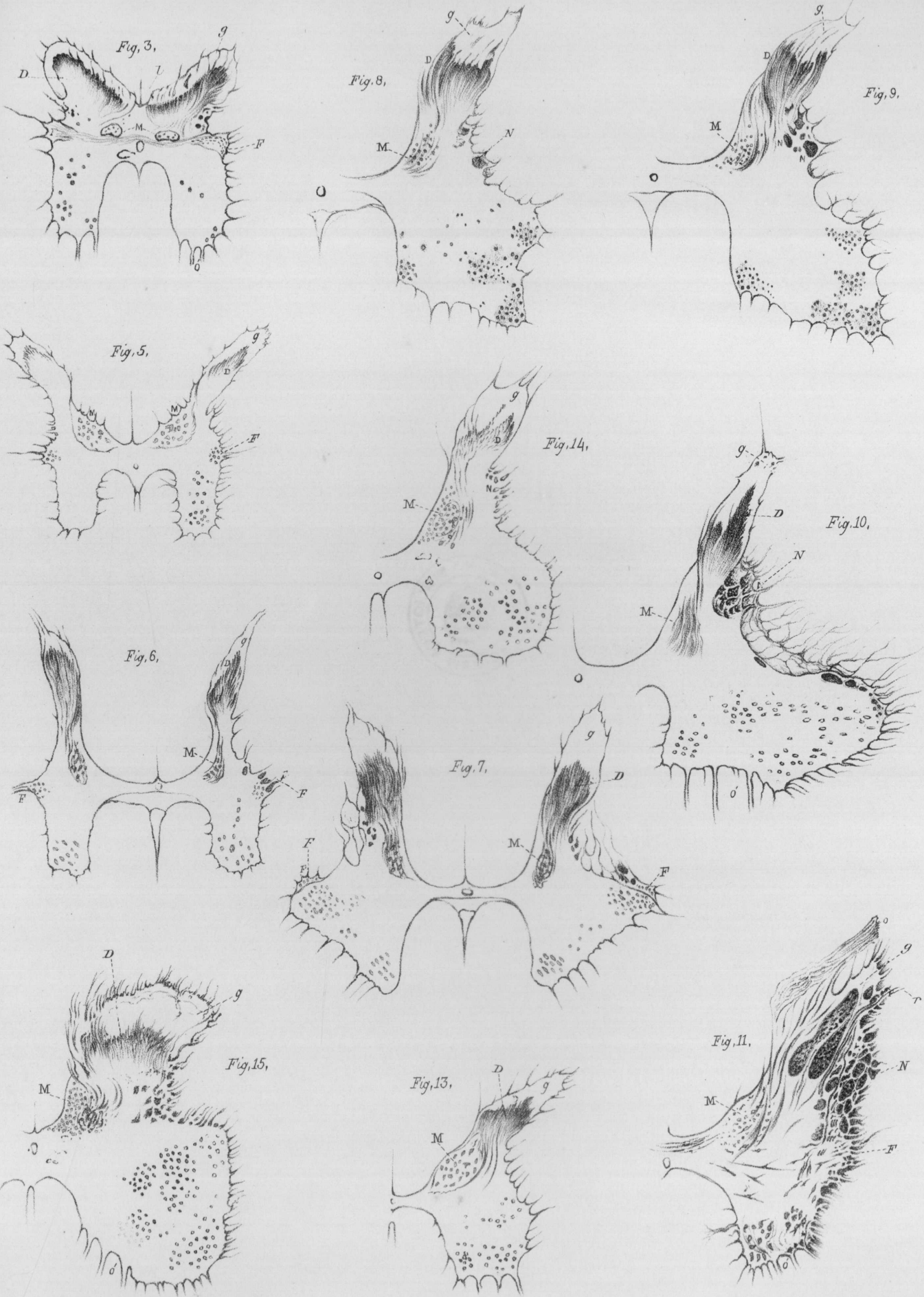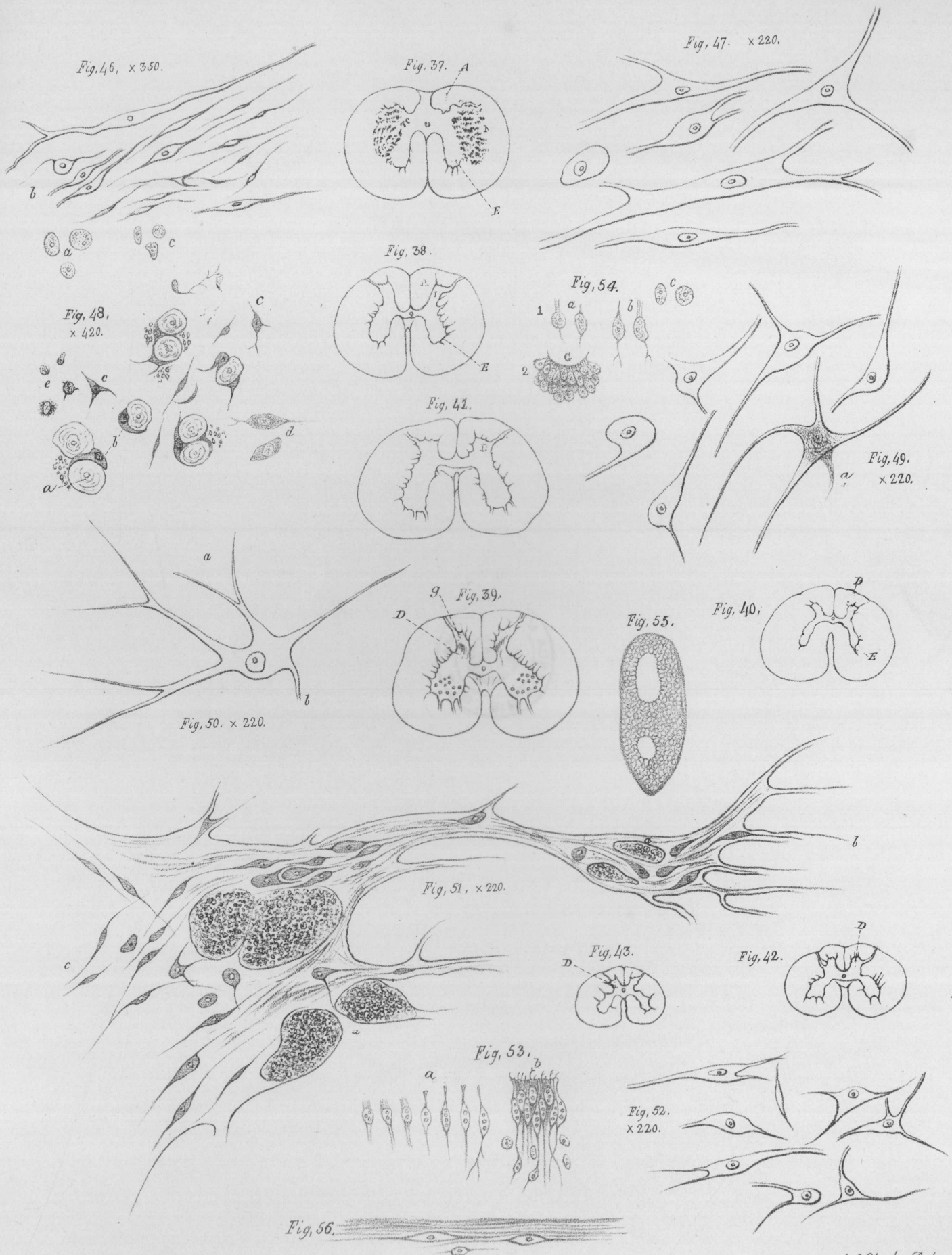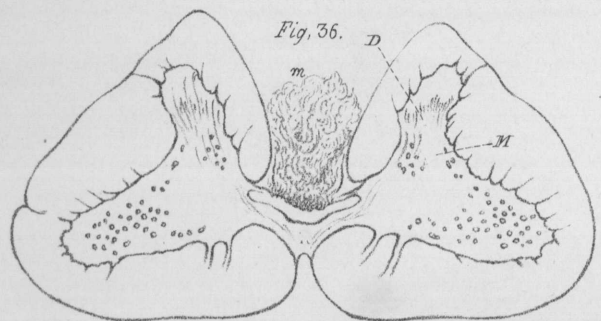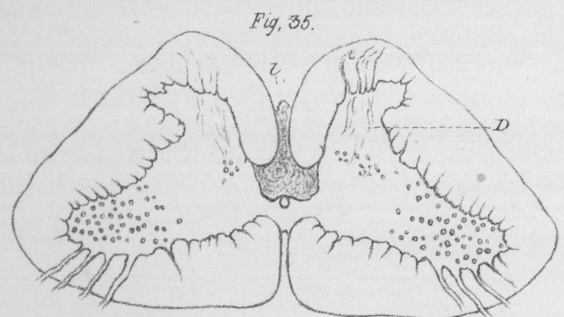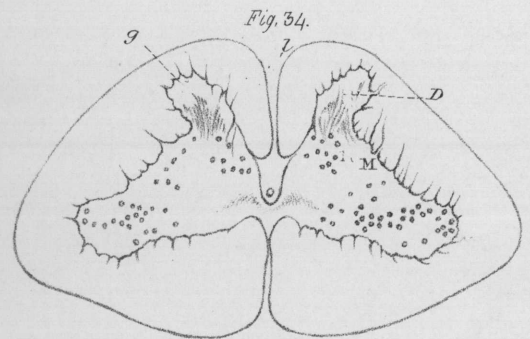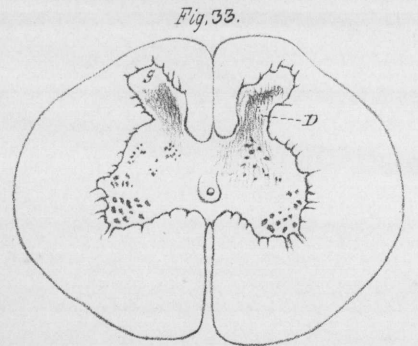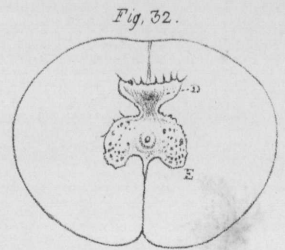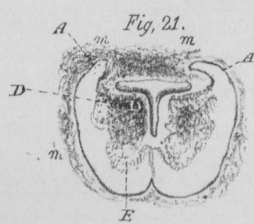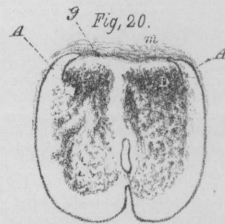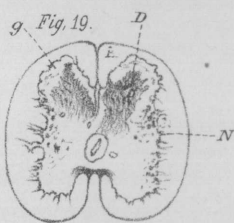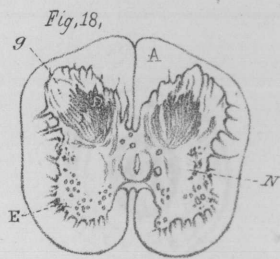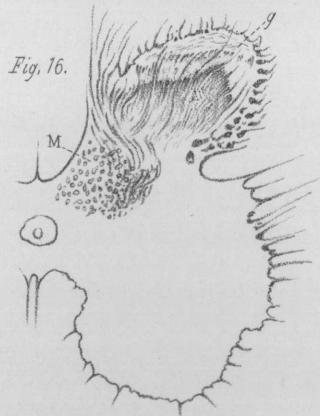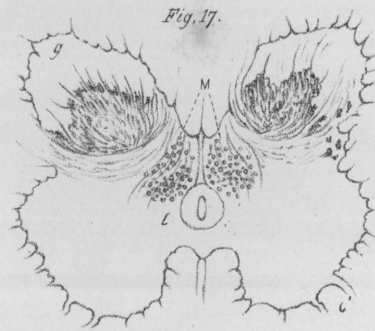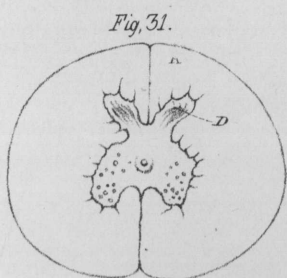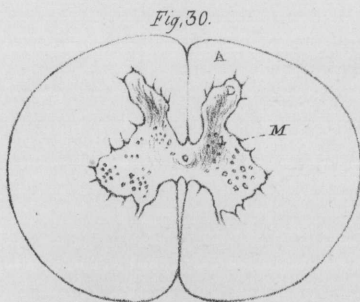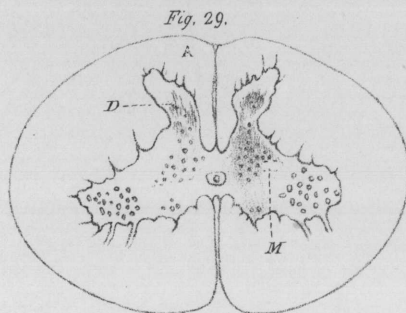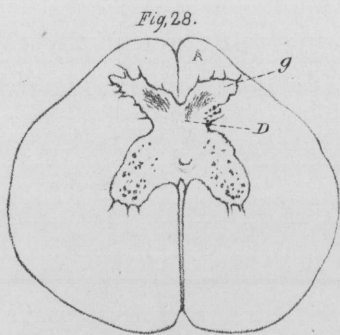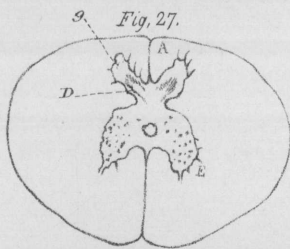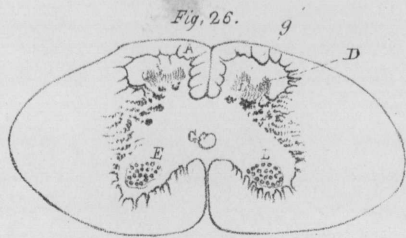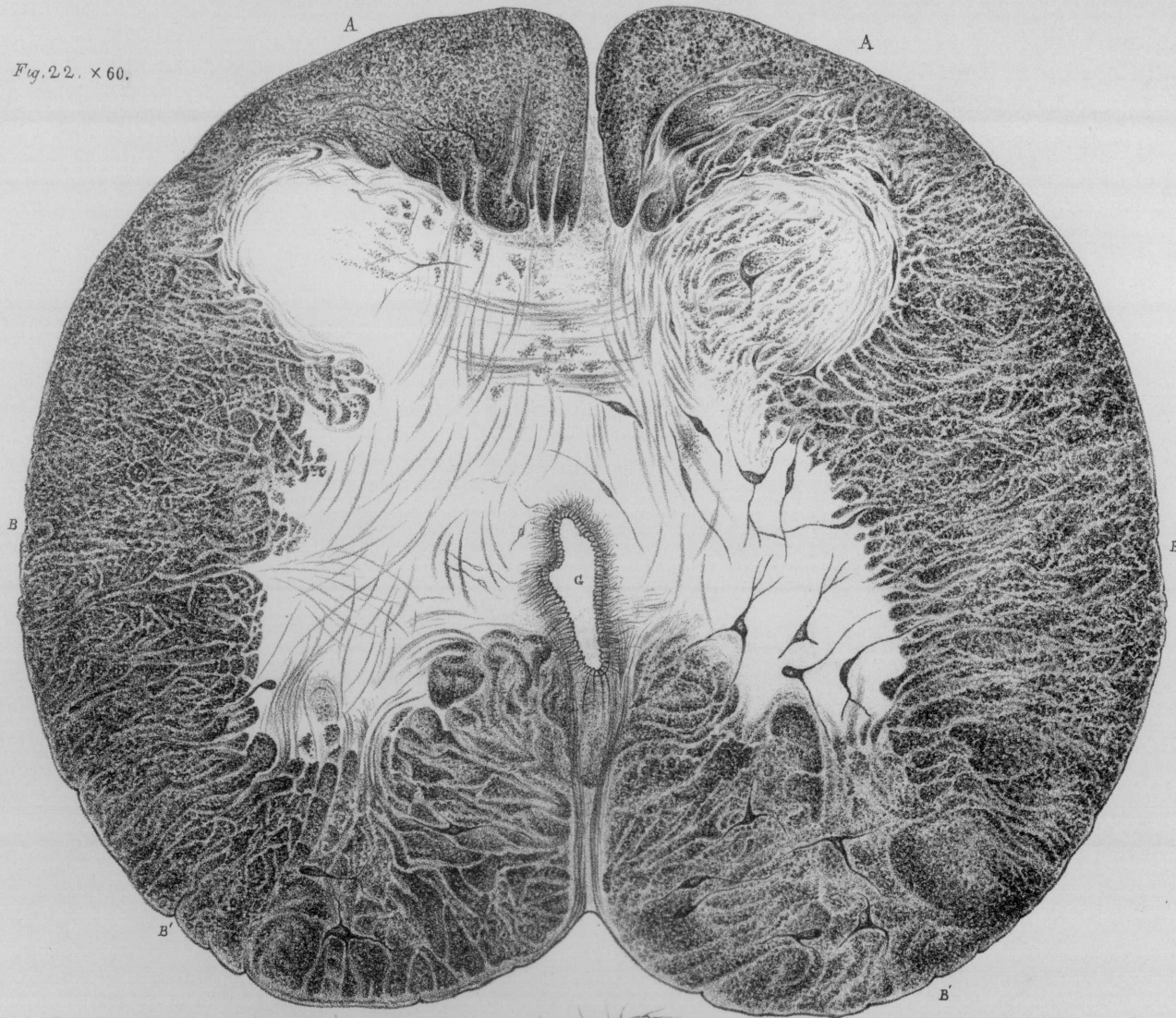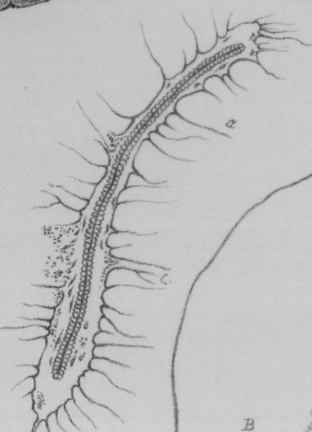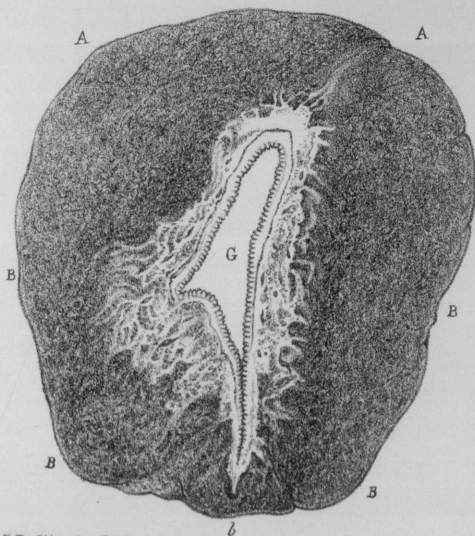
Fig. 25.
× 60.

Fig. 23. × 60.

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Fig. 44. ×80.

Fig. 12. ×60.

Fig. 45. ×80.