

On out-lying nerve-cells in the mammalian spinal-cord / by C.S. Sherrington ; communicated by M. Foster.

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[PLATES 3, 4.]

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ON OUT-LYING NERVE-CELLS IN THE
MAMMALIAN SPINAL-CORD.

BY

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II. *On Out-lying Nerve-cells in the Mammalian Spinal-Cord.*

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Communicated by Professor M. FOSTER, Sec. R.S.

Received and Read, Jan. 30, 1890.

[PLATES 3, 4.]

To describe the ganglion-cells of the Mammalian spinal cord as confined to the grey substance of the cord is not quite strictly correct. BEISSO* was the first to draw attention to the fact, that apart from axis-cylinder processes which pass into the ventral roots from cells of the ventral cornu, there project also from those cells of the cornu which lie next the white column other branches to mingle with the fibres of the bundles of the ventral nerve-roots. The ganglion-cells of the grey matter often, by one or more of their processes, jut partially into the white matter. The descriptions of BEISSO,† PICK,‡ and SCHIEFFERDECKER§ have further shown that in certain situations in the anterior and lateral columns, ganglion-cells lie outside the grey substance in the surrounding white matter.

Since GASKELL,|| in 1885, drew attention to the ganglion-cells in the cord of Alligator, lying at the periphery of the antero-lateral column, and, of course, quite removed from the central grey matter, I have often searched in the cord of the Mammalia for evidence of similarly situated cells; always, however, without success. The search has, however, persuaded me that isolated ganglion-cells are no infrequent constituents of the white columns. The cords examined by me have been chiefly those of Man, the Monkey (Bonnet, Jew, and Rhesus), and the Dog. A number of sections have also been prepared from the Cat, Lion, Calf, Rat, Mouse, Rabbit, and Guinea-pig. The out-lying ganglion-cells in the white matter may conveniently be considered in three sections, according as their situation is within the anterior (ventral), the lateral, or the posterior (dorsal) white column respectively.

* TORQUATO BEISSO, 'Del Midoll. Spinal,' p. 37, 1873.

† *Loc. cit.*

‡ 'Archiv für Psychiatrie,' vol. 4.

§ 'Archiv Mikrosk. Anat.,' vol. 10.

|| 'Proceedings of the Physiol. Soc.,' Dec., 1885.

Out-lying Cells in the Anterior Column.

Among the bundles of transverse fibres slanting from the mesial edge of the ventral horn toward the depth of the ventral fissure and the white commissure can, not infrequently, be found multipolar ganglion-cells. The cells somewhat resemble in form the cells of the ventral cornu itself, but I have not found them quite so large as are the latter. They are, in my specimens, obviously triradiate. The largest I have measured is 38μ in diameter, from the middle of one side across the cell body to the base of the opposite cell-process. Fig. 1, Plate 3, shows the position and form of one of these out-lying individuals, from the cervical cord of the Dog between the points of exit of the first and second nerves. The section is in the transverse plane of the cord. Fig. 2, Plate 4, gives an example of another such cell from the lower part of the lumbar enlargement of the Human cord. The cell does not lie far out from the limiting edge of the grey cornu. It is much smaller than a neighbouring cell belonging to the superficial region of the cornu. The cornual cell can be seen to give a branch into the same bundle of transverse fibres as harbours the smaller and out-lying cell. Similar cells I have observed to occur in both the cervical and in the lumbar regions of the cord, and have seen examples in the Monkey and Cat, as well as in Man and in the Dog. They have somewhat the appearance of being aberrant members of a group of cells which occurs scattered in more or less broken fashion along the deeper part of the mesial edge of the ventral grey horn, and best seen just above the lumbar enlargement. This group was called attention to in the Human cord by PICK,* and is characterised, according to him, by the fact that the cells give off large processes into the fibre-bundles of the white commissure.

The references to out-lying cells in the anterior column which I have been able to discover are three. The earliest by TORQUATO BEISSO in 1873; he figures a specimen, which was obtained from the cord of the Ox. He writes,† “La figura dimostra come una grossa cellula bipolare contenuta nell'intrecciamento della commissura mandi un prolungamento che ripiegando si perde fra le fibre più mediane della sostanza grigia.” A second reference is by SCHIEFFERDECKER.‡ In speaking of the structure of the cord in the lumbar region of, apparently, the Canine cord, he writes that he has found occasional cells in the white commissure, sometimes bipolar, but more often “shaped like arrowheads.” He was, it would seem, not aware of the observation by BEISSO. A third reference is by PICK,§ who, after describing the cells of the ventral cornu which give off processes from the mesial edge of the cornu, goes on to speak of the occasional occurrence in the white commissure of the Human cord of cells similar to those noted by SCHIEFFERDECKER in the lumbar cord of the Dog. He concludes by

* *Loc. cit.*† *Loc. cit.*, p. 37.

‡ VIRCHOW'S 'Archiv,' vol. 67, p. 598.

§ *Loc. cit.*

adding that such cells probably exist not merely in the lumbar region but in other regions as well. My own preparations confirm the description of SCHIEFFERDECKER. In them the cells are like arrow-heads in shape; one of the cell-processes, occasionally two, disappears into fibre-bundles in a direction toward the adjacent grey horn, and one process is directed toward the bottom of the ventral fissure, as if to pass with medullated nerve-fibres into the white commissure. One cell process may project, as, for instance, in fig. 2, in a median direction, neither toward the grey cornu nor the white commissure. This may pass into a fibre-bundle lying further ventrally than that which contains the parent cell, and in that may turn either toward the grey cornu, or, and more probably, toward the white commissure. It is to be remembered, however, that the direction at first taken by it is the same as that of numerous bundles of fine medullated fibres which radiate into the anterior white column from the ventral part of the mesial border of the ventral cornu, as if to reach the angle of white matter forming the lip of the ventral fissure. I have found the cells in the cervical as well in the lumbar region of the cord. It is difficult not to think that these isolated cells as in the anterior column are connected with the fibres among which they lie. Most of these appear certainly to pass between the mesial portion of the ventral horn and the opposite side of the cord in the white commissure. In bundles starting from the cornu further ventrally, it is not usual in one and the same section to see that the bundles pass actually into the commissure, although they slant in the required direction. It is possible that they take a longitudinal course within the white column. The view of BIDDER* and his pupils† that the fibres of the white commissure run to nerve-cells in the ventral cornu, although opposed by STILLING‡ and untrue in the sense in which GERLACH§ advocated it, has much in its favour. In the white commissure are collected together fibres from and for manifold end-stations, and that some of these fibres are of the kind described by BIDDER is rendered all the more probable by the presence of the outlying cells above-mentioned.

Out-lying Ganglion-Cells in the Lateral Column.

The remarkable group of nerve-cells discovered by BERGER|| in the cord of Alligator and allied forms still remains, so far as I am aware, an unexplained fact. I have, as already stated, never seen any unequivocal trace of it in the Mammalian cord. It may be that a vestige of it does really exist in the shape of a thickened rib in the sub-pial

* In a letter to R. WAGNER in 1854. See WAGNER'S 'Neurolog. Untersuchungen,' 1854.

† KUPFFER, 'De Medullae Spinalis Textura in Ranis,' 1854, p. 30; OWSJANNIKOW, 'Disq. Microsc. de Med. Spin. textur. imprimis in Piscibus fact.,' 1854, p. 36.

‡ 'Neue Untersuch. ü. d. Bau des Rückenmarks,' 1859; also FROMMANN, 'Untersuch. ü. d. Normal. Anat. des Rückenmarks,' 1864 and 1867.

§ STRICKER'S 'Handbuch,' vol. 2.

|| "Ueber ein eigenthümliches Rückenmarks band einiger Reptilien und Amphibien." 'Sitzungsb. der Mat. Class. der Kaiserlich. Akademie zu Wien,' Feb., 1878.

membrane over the lateral column at a point which in the cervical cord lies nearer the exit of the ventral than that of the dorsal nerve-root, and in the lumbar and lower thoracic cord, is nearer to the dorsal than to the ventral nerve-root. This thickening occupies a shallow fissure, and is better seen in young animals than in adult. It is particularly evident in the lower thoracic and upper lumbar regions. In fully-grown Dogs, in the Monkey, and, to a less extent, in the Human adult, a small septum, more marked than any of the neighbouring, projects into the lateral column at the level of the ventral extremity of the area of the crossed pyramidal tract; it has repeatedly seemed to me that this septum is identical with the thickening of the sub-pial membrane found in the still imperfectly developed cord of the young animal. In cords in which the crossed pyramidal tract comes to form a large portion of the lateral column, it would seem that with the growth of the tract the shallow bay containing tissue continuous with the sub-pial membrane becomes, so to say, unfolded and more shallow, even to disappearance. But a septum thrusting itself into the lateral column at the spot records the site of its existence. That the septum is of real morphological significance, I believe, from the fact that it divides from one another two masses of nerve-fibres, which offer a strong contrast in their appearance. On the dorsal aspect of the septum lie coarse fibres of fairly equable size (cerebellar); on the ventral exists an admixture composed largely of fine fibres (ascending antero-lateral). In the Monkey, in which animal, as I have indicated,* a portion of the pyramidal tract lies outside the cerebellar along the surface of the lateral column, the fibres of the pyramidal tract, as marked out by the degeneration method, generally, when followed along the surface in the ventral direction, cease abruptly at the little septum in question. In some instances, especially in the upper cervical region, a few scattered fibres belonging to the pyramidal tract may be found on the ventral side of the septum; but this appears to be quite exceptional for the cord as a whole. But I have never found nerve-cells either in the septum or in the sub-pial band.

Into relation with the deeper region of the lateral column come cells of the lateral cornu, especially where that cornu is well developed. The small fusiform cells of the lateral horn are for the most part situate in that part of the horn which abuts upon the white substance of the column. Cells can very frequently be found not far within, but yet distinctly within,† the limits of the white matter surrounding the horn, most frequently on the dorsal aspect of the horn. There seems no room for doubt that these are out-lying members of the lateral cornu group. A certain number of nerve-cells, evidently, I think, also out-lying members of the same group, lie further out still separated by a much greater distance from the grey matter. They are in every case placed upon fine strands of connective tissue which cross the white column (fig. 3, Plate 3), and in these strands are to be found fine medullated nerve-

* 'Journ. of Physiol.,' vol. 10, p. 429.

† These are seen in CLARKE'S fig. 2, from thoracic cord of Ox, 'Phil. Trans.,' 1859.

fibres. That these distant cells are to be considered as belonging to the group of the lateral horn is to be inferred from the similarity of them to those in shape and size. They are of oval figure, with the long axis in the transverse plane of the cord. They are of the same size as, or slightly larger than, the lateral horn-cells. Five of them, taken without selection, measured respectively 32, 30, 34, 33, and 29 μ , giving the average of 31.6 μ . Five cells taken from the lateral cornu in the same preparations measured respectively 30, 35, 26, 28, and 31 μ , giving an average for the five of 30 μ . They are, moreover, arranged with their long axes upon lines which radiate backwards and outwards from the lateral cornu, suggesting a common origin from that point (fig. 4, Plate 3). They appear to be more numerous in the Human cord than in the other of the cords examined. The vertical fibres of the white matter in which they lie embedded belong to the area of the lateral column, called by FLECHSIG the lateral limiting layer; but it may well be that those lying furthest out are beyond this layer, and within the area of the crossed pyramidal tract. The arrangement of the cells in the transverse plane, and the coincidence of the longer axis of the cell-body with the direction of the medullated fibres running horizontally in the same connective tissue septa as contain the cells, suggest, however, that the cells are connected with the horizontal fibres radiating between the grey matter and the white column, rather than with the vertical fibres of the column. But the horizontal fibres must be in turn continuous with certain of the vertical; with which of these, however, is a question that at present there is no possibility of deciding.

To the dorsal side of the lateral horn, and often continuous with it, *e.g.*, in the lower part of the cervical enlargement, is the processus reticularis. It merges dorsally in the lateral portion of the cervix and caput cornu dorsalis. In the bars of its reticulum made up of many interlacing horizontally and vertically running bands of fibres, numerous ganglion cells exist. For the most part, the cells seem attached to those bands of the interlacement which are horizontal. They present more variety of form than do the previously mentioned groups, and they seem to be equally numerous upon frontally running, and upon sagittally running bands of the formation. Many are small and fusiform, and many are somewhat larger and triangular. The triangular cells resemble closely the cells above-described in the bands of the white commissure, and likened by SCHIEFFERDECKER* to arrow-heads in their shape. The cells of the reticularis may, one must imagine, be related to the numerous small ganglion cells, chiefly fusiform, but often triangular, which occupy the grey matter bordering on the processus. These, as CLARKE stated,† lie for the most part with their length parallel to the nearest portion of free edge of the grey substance, except that the deeper lying of them are mostly directed outward, as if belonging to continuations of the cross-running transverse fibres of the commissures. These cells point into the bars of extension of the grey matter which form the roots of the processus reticularis, and

* *Loc. cit.*

† *Loc. cit.*

the frontally directed cells in the reticularis may be considered to belong to part of the same system as do they.

Besides the smaller nerve cells in the processus reticularis are some much larger, indeed, quite to be reckoned among the large ganglion cells of the cord. These are multipolar, and never, so far as I have seen, of bipolar form. They may measure 50μ across, but it is the size of the cell-processes rather than of the cell-body, which is characteristic. On this account they contrast more strikingly with such cells as compose, for instance, the posterior vesicular column of CLARKE, than do even the multipolar cells of the ventral cornu. Lying well out in the reticularis the appearance they offer invites the idea that in them may be provided a nodal junction for the fibres that are there arriving along various planes. But it is difficult to adduce evidence for such a view. SCHIEFFERDECKER,* who has furnished what appears to be the only definite reference to the cells of the processus reticularis, considers the cells typical representatives of his "conducting ganglion-cells" (Leiter-zellen) as distinguished from "reflex ganglion-cells" (Reflex-zellen), the latter being such, for instance, as the multipolar cells grouped in the ventral grey horn. He does not advert to the existence of any large multipolar cells in the reticularis, and although the smaller spindle-shaped and triangular elements would obviously agree with the characters he describes for his "conducting-cells," it is not so obvious that he could attach the same meaning to the large-sized multipolar individuals that one not rarely finds. Examples of these appear, however, in the reticularis of all regions of the cord.

Where the beams of the processus reticularis are thrust backwards towards the dorsal angle of the lateral column, and enclose a finer meshwork than they do more ventrally, ganglion-cells elongated in the direction of the length of the beams exist within them. Many are fusiform, and occur near or on bundles of medullated fibres which sweep laterally round the caput cornu dorsalis toward the base of the cornu. In the sacral cord, of the Monkey and Dog at least, nerve-cells are to be found lying considerably distant from the caput cornu within the dorsal part of the lateral white column, as represented in fig. 5, Plate 4. The arrangement of these tends to show a curvilinear grouping parallel with the outer edge of the lateral limb of the substantia gelatinosa. Those that are within the strands continuous with the processes of the reticularis may, it would seem reasonable to conjecture, be connected with medullated nerve-fibres from the dorsal spinal nerve-roots, which curve round the dorsal horn on its lateral side. The individuals lying further out it is difficult to suggest connections for. Their extension in the transverse plane of the cord must, one would think, mean that they communicate mainly with fibres that are taking a horizontal course in the lateral column at their level, but there is no evidence of more than sparsely scattered horizontal fibres in the neighbourhood.

* VIRCHOW'S 'Archiv,' *loc. cit.*

Out-lying Ganglion-Cells in the Posterior Column.

As in the antero-lateral, so also in the posterior column of the cord out-lying ganglion-cells exist. And it would seem that the anatomy of the out-lying cells in the posterior column is less complex than that of the former classes. In the first place, the cells appear to be confined to one portion of the posterior column, namely, the extero-posterior division of it, and in that division to one particular area, namely, the radicular zone. In the second place, one has obtained definite evidence of their existence from a certain region only of the length of the cord, namely, from that which is especially characterised by the large dimensions assumed by the posterior vesicular column of CLARKE.

The out-lying cells appear to be situated in the root-zone exclusively upon certain of the horizontal radiations of the root-fibres from the white column into the grey cornu. These radiations are among those which in transverse sections through the cord can be seen to pass from the dorso-median limit of the root-zone in a ventral and lateral direction to enter the grey substance in the neighbourhood of CLARKE'S column, often describing as they do so bold curves with the convexity turned toward the postero-median fissure. They are radiations consisting of root-fibres, which belong to the median division in KRAUSE'S* classification of the bundles of the dorsal roots. They enter the grey matter without previously passing through any part of the mesial limb of the gelatinous substance. BECHTEREW† has shown that they are composed of fibres which already are possessed of the medullary sheath in the human foetus of 25 cm. length, and are therefore among the earliest of the fibres of the cord to be developed. It is also to be remembered that their fibres are among those of largest calibre in the whole of the dorsal spinal nerve-root.

The form of the out-lying cells found in these radiations of the dorsal root may be described as oval (figs. 6, 7, 8, Plate 4); one end is usually considerably the less pointed. A nucleus, which is large and contains a very obvious nucleolus, is fairly centrally placed within the cell, though often somewhat nearer the blunter of the two extremities. The cells have not been observed isolated in teased preparations, but they may really be of a more symmetrically bipolar figure than the foregoing description would suggest. Although they are certainly chiefly extended in the plane at right angles to the long axis of the cord, a very slight inclination in such a plane, either of themselves or of the section in which they lie, would suffice to truncate one end of the spindle-shaped cell-body. In such a case the nucleus, if centrally placed, would appear nearer to the more rounded pole. That this does actually happen and frequently explains the somewhat unipolar appearance of the cell, is suggested by the fact that the more pointed end, continued into an obvious cell-process, is sometimes turned with the fibres of the dorsal root in the direction of the grey substance of the

* 'Allgemeine u. Mikroskop. Anatomie,' 1876, p. 389.

† 'Archiv f. Anat. u. Physiol., Anat. Abth.,' 1887, p. 126.

cornu, and sometimes reversely, the blunter end, devoid of any obvious cell process, is directed centrally, while the tapering extremity mingles with root-fibres on the distal side, and is turned away from the grey matter of the cornu.

In rare instances is observable a deviation from the usual shape, which is less easy to reconcile with a belief that the cells are all of fairly regular bipolar form. Such an instance is represented in fig. 8, Plate 4. The impression is given of possession by the cell of two processes issuing from the cell-body in somewhat close juxtaposition, and both turned in a direction absolutely away from the grey matter of the dorsal horn. A little eminence rising from the ventrally-directed edge of the cell, is all that can suggest the giving off of a process toward the grey cornu. This very slight suggestion is perhaps strengthened by the fact that nerve-fibres (of the roots) in their centripetal path sweep by the little eminence in question, and the direction in which the eminence is set is certainly the same as theirs. As will have been gathered, the outlying cells strongly resemble in form the cells of CLARKE'S column. This may be easily seen by a comparison of the two in one and the same section, especially in the lowest portions of the column, where, in Man, as pointed out by MOTT,* the arrangement of the component cells so as to have their longer axes parallel to the long axis of the cord is not so marked as is the case higher up. There, where cells of CLARKE'S column may thus be viewed lengthwise in the same transverse section as contains the out-lying cells, the similarity in shape between them is too obvious to be overlooked.

There is also a correspondence between the two in size. Measurements made of ten of the out-lying cells, taken at random, gave them an average dimension of 68.7μ . This is larger than the average diameter assigned by some authorities (GERLACH, HENLE†) to cells of CLARKE'S column, but agrees fairly with the measurements given by SCHWALBE‡ and MOTT:§ and the average size obtained by measurements of ten cells of CLARKE'S column from the same sections as furnished the out-lying cells measured, is 73μ .|| The actual measurements run as follows:—

* 'Journ. of Anat. and Physiol.,' 1888. "Microsc. Exam. of CLARKE'S Column in Man, the Monkey, and the Dog," by FRED. MOTT, M.D., B.S. Lond., M.R.C.P., Lect. on Physiol. and Med. Regist., Charing Cross Hospital.

† 'Handb. der Nervenlehre,' 1879.

‡ 'Lehrb. der Neurologie,' 1881.

§ 'Journ. of Anat. and Physiol.,' 1888.

|| [GASKELL has recently ('Journ. of Physiol.,' vol. 10, 1889, p. 157) referred to the cells of CLARKE'S column as "divisible into two groups, of different-sized cells," and on that ground exception might be taken to the method of measurements for comparison employed above. I must confess, however, I have not been able to convince myself of the division of the cells into two groups, nor do I interpret the observations of MOTT ('Journ. of Anat. and Physiol.,' *loc. cit.*) to be in support of the division of the cells into two groups.—June, 1890.]

	Out-lying Cell.	CLARKE'S Cell.
	μ	μ
One specimen, at level of 1st lumbar nerve-root	74	68
" " " " " " " " " " " "	68	79
" " " " " " " " " " " "	65	72
" " between 1st lumbar and 12th thoracic nerve-roots ..	60	68
" " " " " " " " " " " "	76	69
" " at level of 12th thoracic nerve-root	61	63
" " " " " " " " " " " "	61	77
" " between 12th and 11th thoracic nerve-roots	59	73
" " at level of 8th thoracic nerve-root	55	61
" " " " " " " " " " " "	63	55

Another point of similarity between these cells and those of CLARKE'S column is the considerable resistance of both, in comparison with the cells of the ventral cornu, to shrinkage and other damage incident during the ordinary hardening processes. The out-lying cells are well preserved in ordinary bichromate preparations. The degree of depth of tint assumed by them, in hæmatoxylin preparations, varies in various preparations, but not in the same preparation. The differences observable in respect to depth of stain between cells of the ventral cornu on the one hand, and, on the other, the cells of CLARKE'S column, are often extremely striking. When large series of specimens are searched through, these differences are seen to be of capricious nature, and, I think, of little real significance. Although it will often happen that the cells of CLARKE'S column, as has been claimed for them by v. LENHOSSEK* and others, become stained more deeply than, and with an apparently different kind of sepia tint (in, for instance, "WEIGERT" preparations), to the cells of other groups, notably of those of the ventral cornu, yet the reverse is quite frequently the case even in sections from the same levels of the cord. Without, therefore, laying more stress on the fact than the above limitation leaves, it is, perhaps, worthy of note that the out-lying cells in the radicular zone are found tinted in the same degree and manner as are the cells of the vesicular column.

Also, as connecting them with CLARKE'S column is to be mentioned the peculiar distribution of the out-lying cells in the length of the cord. I have not observed them lower than the level of exit of the 3rd lumbar nerve-root nor higher than the level of the exit of the 5th thoracic. They appear, therefore, best seen where CLARKE'S column is best developed. And where, as above stated,† the cells of CLARKE'S column are placed, many of them, at least, with their length in the transverse plane of the cord, so are the out-lying cells themselves. This suggests that perhaps in upper thoracic and other levels where CLARKE'S cells are more segmentally distributed and lie parallel with the length of the cord, out-lying ganglion-cells, if

* 'Archiv Mikrosk. Anat.,' vol. 33, 1889.

† And cf. MOTT, *loc. cit.*

related to them, might also be so arranged and a little difficult of discovery. A cross section of a bipolar cell, imbedded in the fibres of the white column, even when the plane of the section passed through it allowing recognition of the nucleus, might be somewhat hard to detect. In longitudinal sections they should be clearly discoverable. I have not, however, obtained specimens which prove that the cells exist beyond the limits mentioned above. I have not found them in the region of the sacral nucleus of CLARKE* and STILLING, nor in the upper cervical cord where a cell-group, in some respects resembling the posterior vesicular column, is obvious.

As to the particular position in the radicular zone occupied by the out-lying cells, they may be far removed from the limits of the grey matter (*cf.* figs. 9, 10[†]), in the middle of the extero-posterior column, indeed, near the edge of that column where it abuts upon the, in this region of the cord, ill-defined confines of the column of GOLL. The cells far distant from the grey matter appear in my specimens more numerous in the lumbar than in the thoracic cord, although there are many in the latter. The distant cells are not so numerous as others, quite resembling them, which lie in the portion of the root-zone that is nearer to (fig. 11, Plate 3), and close outside (figs. 12, 13, Plate 3), the grey matter of CLARKE'S column. Occasionally the cells are situated far ventrally, near the dorsal commissure. Even from that district of the extero-posterior column, not a few bundles of fibres proceed towards CLARKE'S group; it is presumable that these are root bundles, if so, the radicular zone extends ventrally sufficiently far to include them and the out-lying cells in question. The position of the isolated ganglion-cells upon these bundles favours the supposition.

A point to be mentioned is that just as CLARKE'S group at its lower end is placed well backward in the base of the dorsal horn, considerably behind the *niveau* of the dorsal commissure, and when traced upwards is found to rapidly exchange this position for a more ventral one, so do the out-lying cells in the posterior columns experience a shift of their general position in the same sense. In the lower levels of their distribution they lie nearer the dorsal part of the periphery of the cord than in levels situated higher. A comparison of fig. 9, from near the exit of the 2nd lumbar nerve-root with fig. 10, from the level of the 8th thoracic, shows this difference in general position of the cells within the posterior column.

The proportion of the number of out-lying cells to the number of the cells of CLARKE'S column, varies in different sections from the same level, and at different levels. Two out-lying cells to eight of CLARKE'S cells is a high ratio. In the middle of the thoracic region, several successive sections may not reveal a single out-lying cell, even if the sections be made as thick as is compatible with a satisfactory examination of them, and as many as eight or nine of CLARKE'S cells are to be found in the section of the vesicular column.

* CLARKE latterly did not consider that this nucleus corresponded to his posterior vesicular column of the lumbo-thoracic region.

† The positions of the cells are marked by crosses.

Altogether, it appears to me most probable that the cells are to be considered outstanding members of CLARKE'S group; and it appears to me that they suggest a connection between the cells of CLARKE'S column and certain other cells of the dorsal horn. SCHWALBE* creates a class, which he terms "the solitary cells of the posterior horn," to include all the cells in the grey matter of the dorsal cornu, after deduction from it of the substantia gelatinosa and the vesicular column of CLARKE. He groups, therefore, under one title, cells differing greatly from one another in appearance, and of relationships probably widely different. He, further, in his explanatory figure,† indicates as the chief of these "solitary cells of the posterior horn" the comparatively closely-arranged smallish cells at the base of the processus reticularis, which CLARKE described as part of his tractus intermedio lateralis. These cells are certainly anything rather than "solitary" in their distribution (*cf.* fig. 4, Plate 3), and it seems to me that CLARKE was justified in not considering them within the confines of the dorsal cornu at all. But among ganglion-cells, situated undoubtedly within the dorsal cornu, are certain that might more fittingly be termed "solitary" cells, and seem to form a division apart. These resemble strikingly, in some features, the out-lying cells of the radicular zone. If in sections of, for instance, the lower lumbar cord, the fibre-bundles of the dorsal roots be examined where they plunge at intervals through the median limb of the gelatinosa, certain sparse ganglion-cells can be found (figs. 16, 17, 18, 19.) Large and spindle-shaped, they occur in the sections for the most part singly; but also, though rarely, two or even three together. The region of the dorsal horn that extends between the substantia gelatinosa and the longitudinally running bundles of the dorsal root, is very scantily occupied by ganglion-cells. It is in this region, and especially in that part of it adjoining the gelatinosa, that the large ganglion-cells chiefly appear. The longer axis of the cell is, in most instances, set parallel with the lines taken by the bundles of root-fibres that pierce the gelatinosa horizontally. The shape of the cell is that of a broad spindle, tapering to processes at the ends. The constancy with which these cells are seen, lying near or upon the root-bundles, and their direction with the bundles, makes a connection between the cells and fibres of the bundles highly probable. If one of these cells, with the adjacent root bundle, were situated in the white matter of the extero-posterior column, I doubt whether it would be possible to discriminate between it and the out-lying cells, described in this paper as so resembling the cells of CLARKE'S column. May not these cells, therefore, be equivalent to the cells of CLARKE'S column? The more so, that in many cases they lie barely more within the grey substance than do the out-lying cells of the radicular zone, for they are seen on the mesial aspect of the gelatinosa, between it and the white matter of the posterior column. There, also, they lie near to and parallel with certain of the bundles of the

* 'Lehrbuch d. Neurologie,' p. 359.

† Letter c in fig. 221, p. 347.

coarser fibres of the dorsal nerve-root. In this position CLARKE has figured them,* in his fig. 22, Pl. XXIV., Phil. Trans., 1859.†

The chief interest attaching to ganglion-cells lying in the white columns is that it may well be supposed they are connected with the nerve-fibres among which they are placed, and that in this way some knowledge may be gained as to the anatomy of the cells themselves, and of the cell-group of which they may be out-lying members, and of the fibre-bundles containing them.

When the out-lying cell is isolated in position, it is not easy to conceive what becomes of the branched processes of the cell (GERLACH's protoplasmic processes). The axis-cylinder process, if one exist, may be continuous with a fibre of the adjacent fibre-bundle. Are the cells possessed of more than one axis-cylinder process? BEISSO, SCHIEFFERDECKER, and FLECHSIG have at various times urged that cells of such a kind exist. In this connection arises a slight difficulty if the out-lying cells of the radicular zone are considered individuals belonging to CLARKE's column. In the case of the out-lying cells, it is not easy to see that there is evidence of their communicating with any representative of the fine-fibred plexus that constitutes so striking a feature of the vesicular column itself, and with which it is customary to believe that the cells of the column do communicate.

If the out-lying cells of the dorsal root-zone are, as seems most probable, out-lying cells of CLARKE's column, certain suggestions as to the anatomy of that group become obvious. These are: that the cells of that group are connected *directly* with certain of the fibres of the mesial division of the sensory or posterior nerve-root, which, after an upward course in BURDACH's column, plunge into the grey matter of the base of the dorsal cornu: that some, at least, of the cells of the group are interpolated, more or less immediately, into the course of medullated nerve-fibres of large calibre: that other outstanding individual cells to be reckoned as belonging to the group may be present as solitary cells in the near neighbourhood of the substantia gelatinosa of the dorsal horn.

Further, it seems likely that the cells in the root-zone may in the Mammalian cord represent the cells described by FREUD‡ in the cord of *Petromyzon Planeri* as

* From the conus medullaris of the Ox.

† They can be seen also in a figure in VAN DER KOLK.

‡ 'Sitzungsberichte d. Kais. Akad. zu Wien,' vol. 75, III. Abth., 1877, also following year; and Lit. Einleitung, No. 12. See also KUTSCHIN, 'Ueb. d. Bau d. Rückenm. des Neunages,' 1863, abstracted in SCHULZE's *Archiv*, 1887, vol. 2; also KLAUSNER on Proteus. [It may be recalled here that STILLING ('Neue Untersuchungen über den Bau des Rückenmarks,' 1859) suggested that the "grosse runde" cells in the spinal cord of *Petromyzon*, which lie each side of, and dorsal to, the central canal, represent in *Petromyzon* the group of cells described by CLARKE in the thoracic region of the Mammalian cord, and now generally known as CLARKE's vesicular column. STILLING asserted that these cells in *Petromyzon* possess each a cell-process directly continuous with a nerve-fibre of the dorsal nerve-root. KUTSCHIN, in 1863 (*loc. cit.*), confirmed STILLING's description; he found certain fibres of the dorsal root in *Ammonoetes* and *Petromyzon* directly traceable to the large cells, which he spoke of as the inner central cell-

directly connected with fibres of the posterior roots, and named by him "Hinterzellen." It is conceivable that the out-lying cells are really equivalent to cells of the dorsal root-ganglion, although placed in an intra-spinal position. If so, they may help to explain the observation of JOSEPH* that not all the nerve-fibres of the dorsal root degenerate on being cut off from the root-ganglion. JOSEPH's observations were, however, made on an upper cervical nerve-root.

If, as according to the view of HENSEN† and of SCHENK,‡ the cells of the dorsal root-ganglia are nothing else than nerve-cells that originally were a part of the cord itself, then the out-lying cells in the root-zone suggest that the posterior vesicular column of CLARKE may be composed of cells equivalent to those composing the root-ganglia, that have, however, retained their original position as a constituent of the cord.§ The occurrence of CLARKE's column in the thoracic region would then well agree with other features which show that region to present more primitive characters than, for instance, the regions of the enlargements.

group. FREUD's papers on the subject appeared in 1877 and 1878. He designated the large cells into which he traced the posterior root-fibres *innere Hinterzellen*. The name *äussere Hinterzellen* he reserved for certain cells, similar, he considered, to the *innere Hinterzellen*, which he found placed upon fibres of the posterior root, between the root-ganglion and the posterior horn of grey matter of the cord. According to FREUD, some of the *äussere Hinterzellen* lie at the surface of the cord, upon fibres of the posterior rootlets which run for a distance upward along the surface of the spinal cord. Other individuals of the *äussere Hinterzellen* lie within the cord, upon nerve-fibres of the posterior roots in their intra-spinal course. If this nomenclature be transferred to the Mammalian cord, then the cells of the posterior vesicular column are the *innere Hinterzellen* of *Petromyzon*, and the out-lying cells of the posterior root-zone are the intra-spinal set of the *äussere Hinterzellen*. As judged of from FREUD's figures of *Ammocetes*' cord, the *innere Hinterzellen* do certainly in their position, and fairly in their form also, justify STILLING's view of their identity with CLARKE's vesicular column of the Mammalian cord. The appearance of them in some sections of *Ammocetes*' cord, which I have been permitted to examine through the kindness of Dr. GASKELL, also bears out in this respect the impression obtained from the figures given by FREUD. That the cells of CLARKE's column are connected on their proximal side with the fibres of the cerebellar tract admits of little doubt; as to their distal connections, it may be said that two views are current. The one, which has recently been ably supported by MOTT (*loc. cit.*), is that the cells are connected with afferent fibres, fibres of the posterior root. The other (GASKELL, HILL) is that CLARKE's column is connected with the efferent fibres of anterior roots. Of these views, the former, I think, derives support from the facts observed with regard to out-lying cells in the posterior root-zone of the cord; but it is difficult to believe that these out-lying cells, although they appear equivalent to members of CLARKE's column, can be at all closely connected with any fibres in the anterior root. Indeed, it appears more likely that not only the vesicular group of CLARKE, and the out-lying cells of the external posterior column, but also the cells described above (p. 43) as occurring in and near the gelatinosa, all belong to the afferent system entering by the posterior root.—June 12, 1890.]

* 'Archiv für Physiologie,' DU BOIS-REYMOND, 1888.

† "Beob. über d. Befruchtung u. Entwick. des Kaninch. u. Meerschw." 'Ztschr. f. Anat. u. Entwickl., vol. 1, 1876.

‡ "Die Entwick. der Gangl. u. des Lobus electricus." 'Sitz. d. Kais. Akad. zu Wien,' vol. 74.

§ Interesting in this connection are the small ganglia intercalaria which, as HYRTL was the first to note, occasionally occur on the posterior roots of the human cord, between the main root-ganglia and the cord itself. Cf. HYRTL.

NOTE.

Mention of any out-lying cells in the posterior column is not to be found in the classical monographs by CLARKE, STILLING, FROMMANN, DEITERS and MAX SCHÜLTZE, KRAUSE, &c., nor in the recent admirable papers by LISSAUER, BECHTEREW, DARKSCHEWITZ, MOTT, and v. LENHOSSEK. One reference, however, does occur in a second and very recent paper by M. v. LENHOSSEK, in the 'Archiv f. mikrosk. Anatomie' of November (vol. 34, II., 1889). At the end of a paragraph, in which the writer there contends for a direct connection between CLARKE'S column and the posterior roots, he clearly mentions the fact of the existence of isolated cells in the posterior column. To quote his words: "in der Regel findet man frei gewordenen Zellen an der Grenze zwischen grauer und weisser Substanz (he is speaking of CLARKE'S column), doch begegnet man denselben zuweilen in der Einstrahlungszone der BURDACH'SCHEN Stränge; ja, sie rücken hin und wieder fast bis zur Eintrittsstelle der Hinterwurzeln, halten sich in Lage, auch Richtung ihrer Achse, an den Hinterwurzelfasern." My description above was written before I had read this sentence in LENHOSSEK'S admirable and rather lengthy article.

ADDENDUM.

(June 14, 1890.)

Out-lying nerve-cells, similar to those above described existing along the root-fibre bundles in the external posterior column of the lumbar and thoracic regions of the cord, occur in the region of the bulb imbedded in the funiculus cuneatus. In this situation they lie sometimes two or three together, with the long axis of the cell in the frontal plane, and close to or upon bundles of nerve-fibres of large calibre (posterior root-fibres), which pass through the funiculus on their way to reach the grey matter of the nucleus. The similarity of these out-lying cells to the out-lying cells of the posterior root-zone of the cord is too striking to escape attention. The funiculus cuneatus is, of course, equivalent in the bulb to the external posterior column in the cord; it undoubtedly contains an area which corresponds to the posterior root-zone of the spinal posterior column. The out-lying cells in the funiculus cuneatus appear, in point of position, to hold the same relation to the inner mass of the nucleus cuneatus as is held by the out-lying cells in the external posterior column of the lumbo-thoracic cord to the vesicular column of CLARKE. This seems to indicate that in the bulb the homologue of the vesicular column of CLARKE is to be found in the cuneate nucleus.

It will, perhaps, be urged against this that the upper end of the vesicular column of CLARKE is the vagus nucleus (ROSS, HILL, GASKELL). But although a group of cells

in the upper cervical region appears to represent there the vesicular column of CLARKE, even with this group as a guide to the probable position of CLARKE'S column, I have never been able to satisfy myself that in the redistribution and dislocation of grey matter, that can be followed out in a series of sections passing upward into the bulb, the vagus nucleus is continuous with the upper part of CLARKE'S column, or that its position is that which the upper extremity of CLARKE'S column would assume. Neither does the histological appearance of the vagus nucleus altogether favour, in my opinion, the view that it represents CLARKE'S column. Its cells appear to resemble more closely, in form and arrangement, the smaller fusiform cells of the lateral horn of the cord—such as, for instance, are seen in fig. 4, Plate 3. On the other hand, the cells of the cuneate nucleus do much resemble, in form and arrangement, the cells of the vesicular column of the cord.

EXPLANATION OF PLATES 3, 4.

- Figure 1, Plate 3. Portion of the anterior column adjacent to the mesial edge of the anterior grey cornu. Tri-radiate nerve-cell lying between the fasciculi of white matter. From a section, stained with carmine, and prepared from the cord of the Dog, between the 1st and 2nd cervical nerve-roots. Camera lucida and apochromatic immersion (ZEISS), with ocular 4.
- Figure 2, Plate 4. Portion of the anterior column adjacent to the mesial edge of the grey cornu. Tri-radiate nerve-cell lying between fasciculi of white matter. A larger nerve-cell belonging to the inner group of the grey cornu is seen. WEIGERT hæmatoxylin preparation, from the cord of a full-term human foetus, at the level of the 5th lumbar nerve-root. Camera lucida and ZEISS apochromatic immersion, with ocular 4.
- Figure 3, Plate 3. Out-lying cells in the lateral column, near the cell-group of the lateral horn. At level of 8th thoracic nerve-root of *Macacus*; stained with aniline blue-black. Camera lucida and ZEISS apochromatic immersion, with ocular 4.
- Figure 4, Plate 3. Out-lying cells in the lateral column in the neighbourhood of the lateral grey cornu. Picro-carmine preparation, from human cord at the level of the 7th cervical nerve-root. Camera lucida and ZEISS objective BB, ocular 2.
- Figure 5, Plate 4. Out-lying cells in the lateral column, outside the formatia reticularis. WEIGERT hæmatoxylin preparation, from cord of young *Macacus*. ZEISS objective α , ocular 4.
- Figure 6, Plate 4. Out-lying cell in the posterior column. Two cells of CLARKE'S column in the grey matter. WEIGERT hæmatoxylin preparation from human cord at level of 12th thoracic nerve-root. Camera lucida and ZEISS apochromatic immersion, with ocular 4.

Figures 7 and 8, Plate 4. Out-lying cells in the posterior column, showing their relation to strands of connective tissue in which are medullated nerve-fibres. These cells are those the position of which is shown by two crosses in the posterior column of figure 9. Camera lucida and ZEISS apochromatic immersion, with ocular 4.

Figure 9, Plate 3. Transverse section of human cord at level of 2nd lumbar nerve-root, showing the posterior horn and CLARKE'S column. The number and position of the cells of CLARKE'S column are shown by crosses, also the two out-lying cells of the posterior column drawn in figures 7 and 8. Camera lucida and ZEISS objective α , ocular 2.

Figure 10, Plate 3. Transverse section of human cord at level of 8th thoracic nerve-root, showing posterior horn and CLARKE'S column. The number and position of the cells of CLARKE'S column are shown by crosses. The position of an out-lying cell is indicated by the cross in the posterior column. Camera lucida and ZEISS objective α , with ocular 4.

Figures 11, 12, and 13, Plate 3. Outlines, taken with the camera from preparations from the human cord at the level of the 3rd lumbar, 11th thoracic, and 9th thoracic nerve-roots respectively, to show the position of out-lying cells relatively to the cells of CLARKE'S column and to bundles of medullated fibres passing through the radicular zone towards CLARKE'S column. From WEIGERT hæmatoxylin specimens. ZEISS A, ocular 4.

Figure 14, Plate 4. The mesial limb of the substantia gelatinosa, showing bundles of root-fibres passing through it, and close to one of the bundles a solitary bi-polar nerve-cell. Human cord, at level of 4th lumbar nerve-root. WEIGERT hæmatoxylin. ZEISS objective A, ocular 2.

Figure 15, Plate 4. The mesial limb of the substantia gelatinosa, with bundles of root-fibres passing through it; two large bi-polar nerve-cells in close relation to the bundles. Cord of Puppy. WEIGERT hæmatoxylin. ZEISS objective A, ocular 2.

Figure 16, Plate 4. Posterior horn, with medullated root-fibres sweeping through the mesial limb of the substantia gelatinosa. In close relation to a bundle of fibres is a large nerve-cell. At level of 6th thoracic nerve-root. Lion cub. WEIGERT hæmatoxylin. ZEISS α , ocular 4.



Fig 1



Fig 9



Fig 3

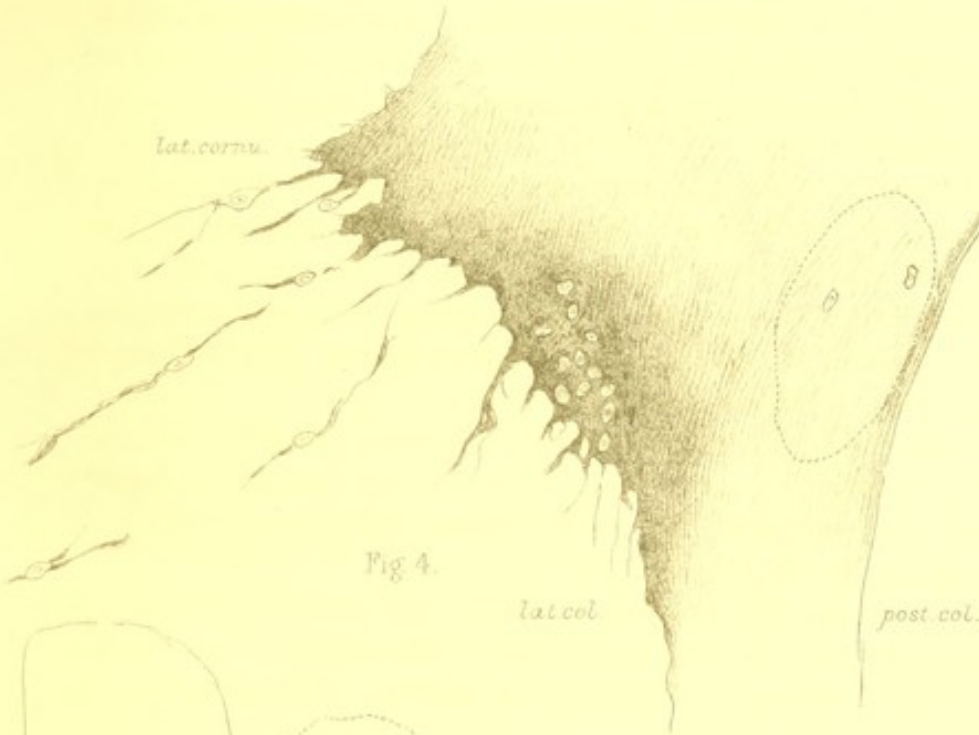


Fig 4.

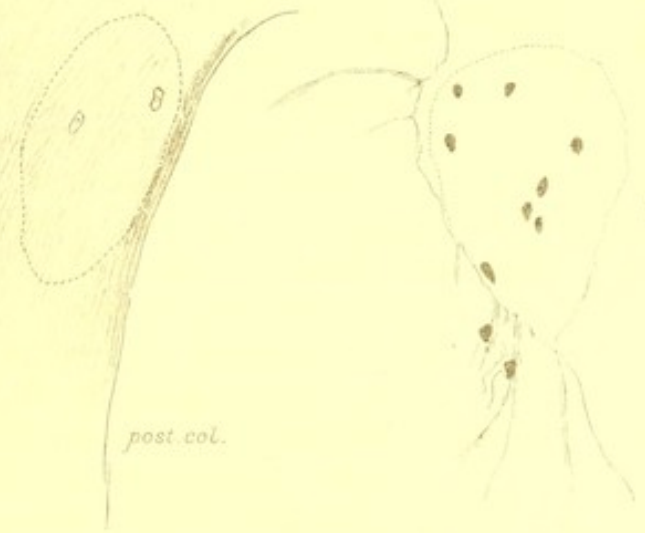


Fig 13.

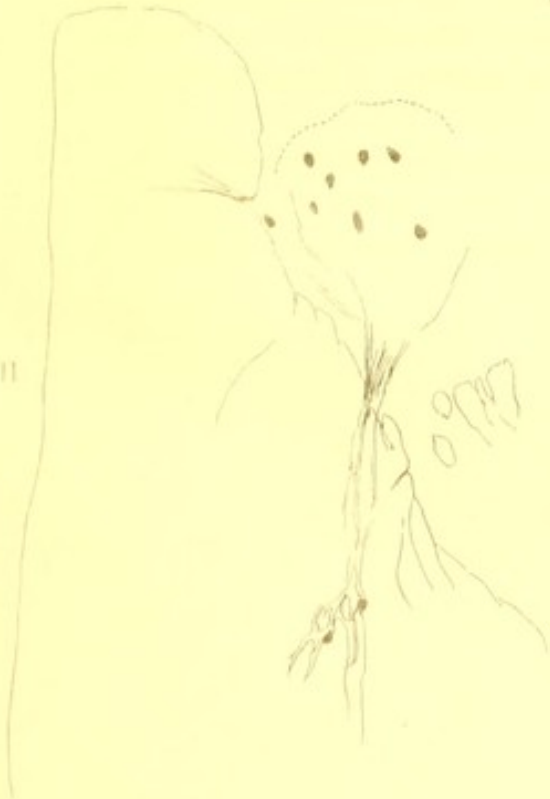


Fig 11



Fig 10



Fig 12

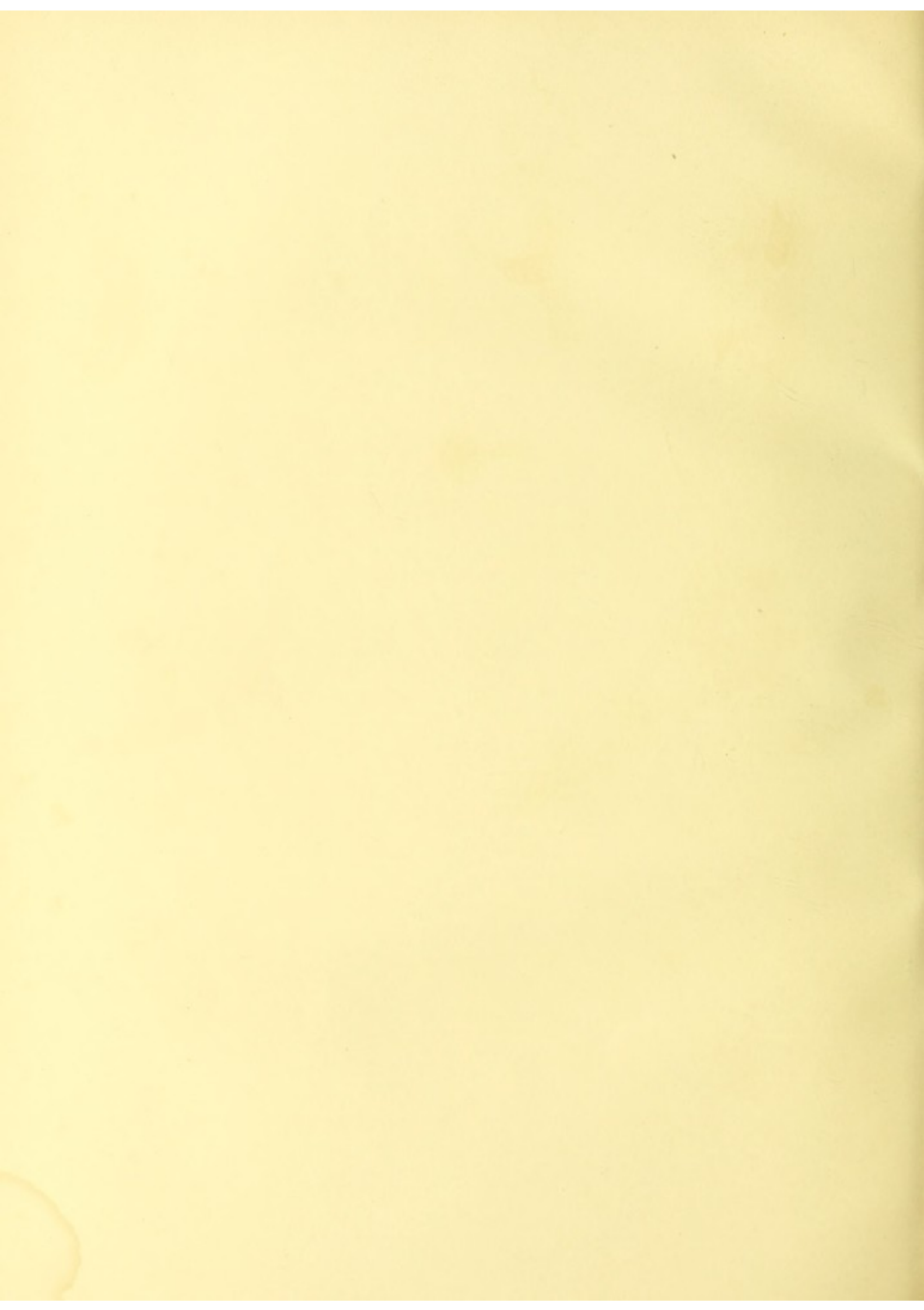


Fig 2.



Fig 7.

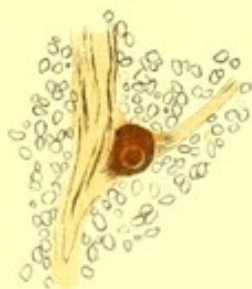


Fig 5



Fig 8.

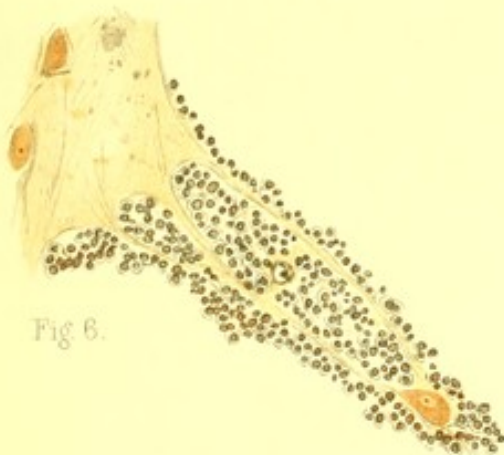


Fig 6.

Fig 15.



Fig 14.



Fig 16.



