III. *Researches on the Comparative Structure of the Cortex Cerebri.*

By W. BEVAN LEWIS, *L.R.C.P. (Lond.), Senior Assistant Medical Officer, West Riding Lunatic Asylum, Wakefield.*

Communicated by Dr. FERRIER, *F.R.S., Professor of Forensic Medicine, King's College, London.*

Received June 18,—Read June 19, 1879.

[PLATES 6, 7.]

THE object and scope of this paper are to detail the results of a full investigation into the minute structure of the cerebral cortex in the Pig, and to add such notes upon the histology of the same structure in the Sheep and Cat as will suffice for a fair comparative view of those divergencies in fundamental structure which present themselves between the brain of these animals and that of the highest members of the Mammalian series. Attention has been especially directed to the greater mass formed by the parietal, frontal, and upper arc of the limbic lobe,* the inferior arc of the limbic lobe (gyrus hippocampi) and the olfactory lobe being left for subsequent examination. The method adopted has been that of slicing the hemispheres of fresh brain from end to end upon the freezing microtome, and examining each individual section, both in the fresh state and after preservation, by a method already described.† Tables containing details of the dimensions of cells and depth of layers accompany the paper, being collated at the end for convenience of reference.

THE CONVOLUTIONS OF THE BRAIN IN THE PIG.

The regional distribution of ganglionic cells in the cortex of this animal constitutes so important a portion of our inquiry that, in order to avoid any obscurity in the subsequent sketch, it will be advisable to review briefly the arrangement of the convolutions and sulci. In doing so I shall follow the terminology adopted by Professor BROCA, in his late important work on the comparative anatomy of the convolutions in Mammals.‡

* The limbic lobe consists of the convolution of the corpus callosum, together with the gyrus hippocampi (BROCA).

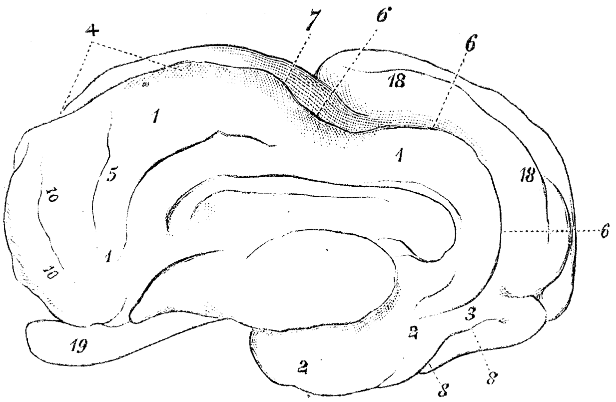
† "Application of Freezing Methods to the Microscopic Examination of the Brain." 'Brain,' part 3, October, 1878.

‡ "Anatomie Comparée des Circonvolutions," par M. PAUL BROCA. 'Revue d'Anthropologie.'

The brain of the Pig presents us with four primary divisions or lobes: 1, the great limbic lobe; 2, the parietal lobe; 3, the frontal lobe; 4, the olfactory lobe.

1. *The great limbic lobe.*—This lobe, seen chiefly on the internal aspect of the hemisphere, consists of a superior arc (convolution of the corpus callosum), fig. 1 (1, 1), commencing in front of the corpus callosum where the internal root of the olfactory unites with it, bends round the anterior extremity or genu of this great commissure, and borders its upper aspect as far as its posterior extremity, where it becomes continuous with the inferior arc of the same lobe, or the gyrus hippocampi, fig. 1 (2, 2), and from which it is marked off by a well-developed retro-limbic annectant (3). The anterior half of the upper arc becomes superficial and exposed upon the surface of the hemisphere, forming here the border of the great longitudinal fissure (4). The limbic fissure, separating this important lobe from the remainder of the hemisphere, may be traced in front as a somewhat obscure sub-frontal sulcus (5), and further back as a

Fig. 1.

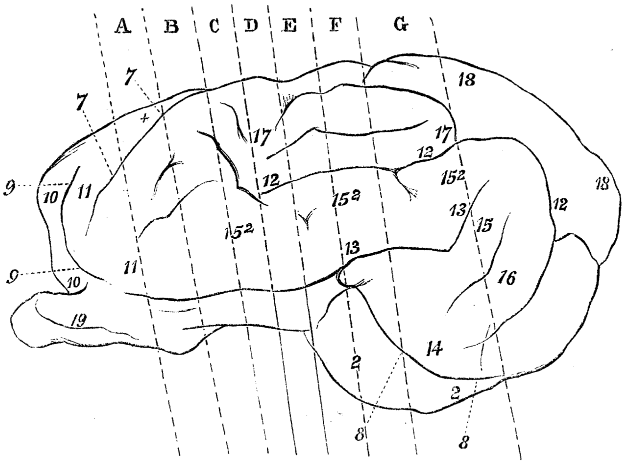


deeply-marked sub-parietal sulcus (6), interrupted posteriorly by the retro-limbic annectant (3). Beyond the latter annectant, it can be traced between the parietal lobe and the inferior arc of the limbic lobe, *i.e.*, the gyrus hippocampi (8). The anterior extremity of the sub-parietal sulcus turns upwards towards the surface of the hemisphere, and is continued obliquely forwards and outwards as a well-marked crucial sulcus, separating the superficial portion of the limbic lobe from the parietal lobe (7). The great comparative depth of the anterior portion of the superior arc, when contrasted with its posterior half, is well marked in this animal—a feature identified by BROCA as of constant occurrence in "Osmatic" Mammals, or those in whom the olfactory apparatus is highly developed.

2. *The parietal lobe.*—Turning our attention to the external aspect of the hemispheres (extra-limbic mass of BROCA), we find by far the greater portion enters into the constitution of the great parietal lobe. In this extra-limbic portion we recognise readily three primary fissures—the crucial, interparietal, and Sylvian. Still further forwards, at the extreme anterior pole of the hemisphere, is a shallow vertical fissure—

that of ROLANDO. The crucial sulcus, figs. 1 and 2 (7), separates the parietal from the anterior exposed part of the limbic lobe, figs. 1 and 2 (4); the fissure of ROLANDO, fig. 2 (9), separates the latter from the frontal lobe, fig. 2 (10); whilst the interparietal, fig. 2 (12), runs between the upper and lower series of parietal convolutions. The Sylvian fissure, fig. 2 (13), is directed obliquely upwards and backwards, the lower parietal gyri arching around the fissure. All the parietal convolutions take origin

Fig. 2.



from a region termed by BROCA the temporal lobule of the parietal lobe, and, after winding around the fissure of SYLVIUS, terminate near the fissure of ROLANDO, in a region corresponding to the ascending parietal convolution of higher Mammals, fig. 2 (11).

Above the interparietal fissure we find the third and fourth parietal convolutions, the latter being also called the sagittal, figs. 1 and 2 (18). The sagittal gyrus is almost invariably split up posteriorly by secondary sulci. The first parietal or Sylvian convolution, although separated from the second parietal behind the fissure of SYLVIUS, fig. 2 (15, 16), is in front of that fissure blended with the second parietal often as far as the gyrus post-Rolandique (11).

3. *The frontal lobe.*—This lobe is limited to the extreme anterior tip of the hemisphere and its inner aspect as far as the sub-frontal sulcus. The portion appearing upon the outer surface of the hemisphere anteriorly is the representative of the ascending frontal convolution (10), and is separated from the parietal lobe by the fissure of ROLANDO. Its inner surface is separated from the great limbic lobe by the sub-frontal sulcus, fig. 1 (5), or anterior extremity of the limbic fissure.

LAMINATION OF THE CORTEX OF THE BRAIN IN THE PIG.

Number and arrangement of layers.—The general arrangement of the varied series of cells, constituting the greater portion of the cortex of the brain, is very similar to

that which we find in animals which rank highest in the Mammalian series. The nerve-cells are distributed either in five or six layers, the five-laminated type being as characteristic of a certain constant area as the six-laminated arrangement is of another region of the brain. As in Primates and Carnivora, we find a limited portion of the cortex organically specialised by its disposition into five layers, and a more extensive realm distinguished by a six-fold lamination, so here in the Ungulata the same characters are impressed upon the cortex. A still more striking resemblance is presented by the character of the individual layers, which are not alone identical in number with those of the brain in higher groups of animals, but are likewise, to a great extent, identical in composition. Thus we find in the cortex of the Pig the first or pale external layer, the layer of small angular cells, the third or large pyramidal layer, the fourth layer of small angular and pyramidal cells (absent in five-laminated areas), the ganglionic series of cells, and, lastly, the sixth or spindle layer. Neither in the number of layers nor in the individual constitution of these layers must we expect to find any great distinctions between these distant groups of the Mammalian class. It is in the essential characters of the individual cells of these layers, in the relationship of these anatomical units the one to the other, and in their general distribution, that we detect divergence from the type normal to the higher Mammalia. These divergencies, we shall find, appear very strongly pronounced as further on we enter into a close examination of the constitution of each individual layer of the cortex. It is important that we bear in mind the homologous constitution of the cortical layers in distant groups of Mammals, and that we are alive to the fact that minute differences in elementary distribution may afford suggestive hints as to any existing analogy in functional endowments. It will be apparent, upon the most superficial examination of this subject, that it is of the highest importance that we define as accurately as possible the regions characterised by these diverse laminar arrangements; and the contrast established between the comparative area of these realms in different orders must be regarded as highly desirable. What is the relative area borne by the five- to the six-laminated region in individual groups of animals, and what is the relative extent of similarly laminated regions in different orders? These are questions which require careful and deliberate consideration, and towards the solution of which the following researches are devoted. As I have elsewhere indicated,* the great distinctions betwixt the two chief laminated types of the cerebral vault centre about the mid-regions of the cortex, and hence the ganglionic layer and the layer superimposed will invite in these investigations especial attention. Let it then be understood at the outset, that the ganglionic cells of the cortex are arranged upon two distinct and readily recognisable plans. These may be termed—1st, the grouped, nested, or clustered arrangement; 2nd, the laminar or solitary arrangement. The first is typical of a more limited area of the cortex than the latter, and is, as far as my investigations lead me, especially characteristic of the motor area of FERRIER—at least, as regards Man, the Monkey, the

* "On the Comparative Structure of the Cortex Cerebri." 'Brain,' part 1, April, 1878.

Cat, Dog, and allied animals. In these latter regions the ganglionic cells are clustered one above the other, occupying oval areas forming the well-known "nests" of BETZ, and usually separated by short intervals from one another (Plate 7). The second arrangement, however, reminds one of the characters exhibited by this series of cells at the bottom of a sulcus. Here (in the sulcus) we find solitary cells at great comparative distances apart, arranged irregularly along the floor of the sulcus, forming in vertical sections a well-marked *linear* series (Plate 7). Not unfrequently two cells lie side by side, but no groups of such elements are discoverable in these localities; hence the depth of this layer is far less than the same layer at the summit or side of a convolution. Vertical sections will therefore show at the summit of the gyrus deep oval groups of cells, contrasted with a simple streak of solitary and distant cells at the bottom of the sulcus. In general terms, it may be said that the typical arrangement of the ganglionic series, at the base of a sulcus, is identical with the formation of the same layer over a very extensive area of the vault. When in examining vertical sections of the cortex we find the grouped cells give place at the *summit* and *sides* of a convolution to a shallow streak of distant cells, arranged as solitary cells or in twos or threes at most, we may assure ourselves we have passed from the region which FERRIER considers impressed with motor endowments, and have reached a territory possessing an equally characteristic formation. Further, the *transition* from the grouped arrangement into the solitary or laminar band here referred to resembles what is observed at the sides and base of a sulcus in the motor area. The groups, from being closely aggregated, become more distant and *discrete;* the groups themselves become shallower, include fewer cells, until one or two elements alone reappear at great distances apart, and characterise the region furnished with the solitary or laminar type. I do not mean to infer that the base of a sulcus in the motor area furnishes us with a lamination identical in its characters with that of non-motor realms. The distinctions are as follows: in the region just alluded to as possessing the laminar arrangement of ganglionic cells there is superimposed on it a distinct layer of small pyramidal and angular cells, whilst the horizontal distribution of spindle cells never occurs except at the base of a sulcus. To summarise, then, in a few words, we have two regions of the vault characterised by two very distinct types of lamination:—

A. The five-laminated type with its grouped ganglionic cells, exhibiting a laminar arrangement at the sulcus only.

B. The six-laminated type, with the solitary laminar arrangement of the sulcus *generally* distributed over the summit and sides of the gyrus; and the introduction of a layer of small pyramidal elements immediately above the ganglionic group.

Transition realms.—Every intermediate state is clearly discernible betwixt these two types of lamination in neighbourhoods where they approach each other and blend. Thus, in studying the passage of a five- into a six-laminated region, we meet with territories where the five-laminated cortex presents us with very small ganglionic cells still arranged in nests, and forming but pigmy representatives of those larger groups believed to be

characteristic of motor areas. Again, we come upon regions where a nested arrangement of small ganglionic cells is associated with a six-laminated cortex. In fact, the nested arrangement and size of the individual cells appear to be invariably in inverse ratio to the depth of the small angular formation superimposed, so that, as we approach motor realms, the latter thins out and gradually disappears, whilst the nests become more and more perfect and embrace larger and still larger cells. On the other hand, as we recede from motor regions the nests thin out, become less perfect as groups, include cells of small dimensions, become more widely separated from each other, whilst the superimposed stratum gains in depth and increases in density by the close aggregation of its angular and pyramidal elements. In studying the arrangement of the layers of the cortex the above points appear to me to demand careful attention, and the eye should become perfectly familiarised with the varied appearances presented by transition zones of the cerebrum.

First layer (Plate 6, A).—Over different regions of the cortex this stratum varies somewhat in depth: In the neighbourhood of the limbic lobe it averages ·619 mm., and nearer the Sylvian fissure it becomes ·418 mm. in depth. In all points except the relative proportion borne by the connective to the nervous elements, this layer closely resembles the corresponding layer in the higher Mammalia. The matrix is constituted of a fine areolation of connective fibrils, with which is associated an extremely delicate network of nerve fibrils. The latter are derived from the apex processes of nerve cells in subjacent layers, the long, delicate process of the large ganglionic cell being frequently traced up into this layer, where it is observed to divide into numerous subdivisions. The connective elements include cell-forms of two kinds—the perivascular, and the neuroglia corpuscles, both forms nucleated, and measuring respectively 5μ and 9μ in diameter. The larger elements are especially numerous just beneath the pia mater, and constitute a distinct belt of cells in many situations—irregular in form, and throwing off numerous delicate processes. These cells, known also as DEITER's corpuscles, are found in such vast numbers in the Sheep that attention will be directed to their mode of distribution and significance when describing the first cortical layer of that animal. In all fresh preparations this layer presents us with three distinct regions differing somewhat in appearance and corresponding very nearly to its upper, middle, and lower third. In the upper division we find a band of medullated nerve fibres following the course of the convoluted surface and surrounded on all sides by processes from the cells of DEITER. The lower division shows us a coarse network formed by the division and decussation of the apex processes of the second layer of cells, which are often thrown off at a very oblique angle from the cell.

Second layer.—A shallow belt of densely congregated cells forms the second layer of the cortex (Plate 6, B). Its superficial and deep limits terminate somewhat abruptly, so that a fair estimate may be taken of its depth, which is found to be decidedly less than the corresponding layer in the human brain. The average depth may be given at ·093 mm., increasing, however, in some regions to ·116 mm. or even ·138 mm.

In the human brain, on the other hand, the depth of this layer in the frontal lobes varies between ·139 mm. and ·186 mm., whilst posterior to the fissure of ROLANDO it may increase to ·279 mm. The nerve-cells vary greatly in form, appearing as angular, pyriform, pyramidal, oval, or globose elements, which throw off several delicate processes, one or more thrown off from the apex towards the surface of the cortex being a frequent but *not constant* arrangement. I have elsewhere alluded to a striking character as common to these elements in the human brain,* viz.: the relatively large size borne by the nucleus to the protoplasm of the cell as compared with larger nerve-cells of subjacent layers. We find the same character maintained by these cells in the cortex of the Pig. Another peculiarity is the frequent occurrence of the globose form of cell which throws off an apical process and several very delicate branches from its sides, into which branches, however, the cell protoplasm does not prolong itself as in other cells; hence its contour is wholly unaffected by the branching. This form of cell is peculiar, and I shall allude to its possible relationships further on. In this layer the angular form of cell is most frequent; its peripheral branches diverge obliquely to the radial fasciculi, cross each other in all directions, and by their repeated divisions and ramifications form a dense network of fine fibres quite characteristic of the deeper portions of the first layer. In delicate sections this network can be traced upwards for a distance of ·162 mm.—*i.e.*, one-fourth the whole depth of the superficial layer of the cortex. These angular cells are peculiar in form, and are met with frequently, as we shall see, at deeper levels. The gradual blending of the second and third layers of the cortex as seen in the human brain is far less marked in the Pig, as over most regions of the cortex one layer *abruptly* terminates in the other.

Third layer (Plate 6, C).—The depth of this layer, taken together with the second layer, averages ·913 mm. This average was struck from measurements at thirty-six different points of the cortex of the vault, the variations lying between ·744 mm. and 1·488 mm. The greatest depth is attained immediately below the summit of the convolution, whilst towards the sulci the layer gradually becomes shallower. The gradual increase in size of its constituent cells from above downwards, which is so prominent a feature in the human brain, is not observed here, the deeper cells of this layer being identical in point of size with the more superficial cells bordering upon the second layer. Not only are these cells very constant in size throughout the depth of this layer, but they vary very slightly in magnitude throughout the whole surface of the cortex. An approximate average from a very large number of measurements may be given as 23μ in length by 13μ in breadth, and the longest diameter of their nucleus as 9μ. On reference to the table of measurements we shall find that, whilst the upper series of cells in this layer in Man and the Carnivora do not reach this magnitude, the lower series in Man are far larger, whilst in the Cat the lower series corresponds exactly in size with those of the Pig. It is important to bear in mind the fact that the lowest stratum of the third layer in the Cat is formed of cells identical

* "The Cortical Lamination of the Motor Area of the Brain," Proc. Royal Soc., No. 185.

in size with those which constitute the whole thickness of this stratum in the Pig; whilst none of the smaller cells crowding the upper portion of this layer in Man, the Monkey, and the Cat are here present. The nerve-cells of this layer vary much in contour: we find them oval, oblong, pyriform, and pyramidal, and a few even elongate spindles. By far the more frequent form assumed is that of the pyramidal or a slight modification of the pyramid. The junction of every main branch with its cell is marked by the gradual increase in size of the branch where it blends with the cell, occasioned by the continuation of a funnel-shaped prolongation of protoplasm from the cell into its branch. This *gradual blending* of the cell with its branch is a safe criterion to follow if any doubt arise as to the actual junction betwixt the two. The average number of processes thrown off by these cells (inclusive of basal and apex process), as seen in vertical sections, is six. As many as eight or more are often seen; but, from reasons already adduced,* no approximate knowledge can be obtained of the absolute number of primary branches. The apex arising from the gradual attenuation of the cell lies more or less parallel with the radial fasciculi, and is therefore directed outwards or directly towards the superficial layer of the cortex. The basal process appears to conform in every respect to the corresponding process in the large ganglionic cell. The smaller branches arise from various points of the periphery of the cell, more especially near the base, and radiate outwards, dividing and subdividing into extremely delicate fibrils occupying an extensive zone around the cell. Each cell contains an oval nucleus (deeply stained by aniline and carmine), which is invariably centric in position. The cells of this layer frequently have a number of small nuclei arranged around or upon them: these elements pertain to the pericellular lymph spaces.† As to the general arrangement of the cells of the third layer, no regular grouping is apparent: they are scattered very irregularly through the greater depth of this layer except at its deeper portions, where they lie in dense clusters between the advancing sheaves of apical processes given off from the ganglionic cells of the subjacent stratum. These latter bundles of nerve-fibres consequently occupy somewhat pale spaces almost devoid of cells, forming well marked septa betwixt the cells of the deeper regions of this layer. The peculiar angular cell is found *sparsely* scattered throughout the whole depth of the third layer as in the cortex of higher animals.

Ganglionic layer (Plate 6, D).—We now arrive at a region of the cortex where the most striking and characteristic features develop themselves, and where the distinctive characters impressed upon the architecture of the cortex in Man and the lower Mammalia come out most prominently. Any one accustomed to the microscopic

* "Cortical Lamination of the Motor Area of the Brain," Proc. Royal Soc., No. 185.

† See on this subject OBERSTEINER'S views, "Ueber einige Lymphräume im Gehirne" (Sitzb. d. k. Akad. d. Wissensch., Abth. i., Jan. Heft, 1870). Also an article by the writer entitled, "The Relationships of the Nerve-Cells of the Cortex to the Lymphatic System of the Brain," Proc. Royal Soc., No. 182, 1877.

appearance of the cortex cerebri in Man in or neighbouring upon the motor area cannot fail, on examining the cortex of the Pig for the first time, to be struck by one great differential character. In Man and the higher Mammalia the cells of the third layer increase in size with their depth, so that the lowest stratum consists of tolerably large cells, and the eye is thus, as it were, prepared for the enormous elements of the ganglionic layer below. In the Pig, however, the transition is most sudden from the small cells of the lowest stratum of the third layer to the dense nests of large ganglionic cells beneath. The transition is so abrupt as to form a characteristic feature in the brain of this group of animals. I will endeavour to give here a general idea of this formation by a description of the nerve-elements under the following heads:— 1. Depth of layer; 2. Form of cells; 3. Size of cells; 4. Processes.

1. *Depth of ganglionic layer.*—The pale band corresponding to this layer in Man, and containing the large cells grouped in nests or clusters, is in the Pig crowded with very dense groupings of cells in certain regions, whilst at other sites, as above mentioned, the laminar or solitary arrangement prevails. The depth of this layer, therefore, varies with these two varieties of lamination. In the clustered arrangement the average depth is ·595 mm.; in the laminar arrangement it may be a simple streak of cells or attain a depth of from ·186 mm. to ·372 mm. The greatest depth in the clustered regions was ·697 mm. Further details respecting absolute depth of individual layers is given in a tabulated form for convenience of reference. (See p. 62.)

2. *Form of cells.*—It has been stated in a former memoir* that a great irregularity in marginal conformation is quite peculiar to these cells in Man. Now we can by no means state that such is the case with the corresponding elements in the Pig; in fact, a striking uniformity in the contour of these cells is observable, by far the greater proportion taking the form of an elongate pyramid, the few exceptions occurring being usually gigantic spindles. They resemble closely, both in size and form, the large pyramidal cells at the *deepest portion* of the third layer in Bimana, Quadrumana, and the large Carnivora, as also the *ganglionic cells* in the parietal and tempero-sphenoidal lobes of Man. Nowhere do we find the irregular, swollen, and at times almost globose cells so frequent in the motor area of the human brain. How is it possible, it may be asked, to discriminate between these cells and those of the third layer if they approach them so closely in size and contour? In the first place, their arrangement in nests is indicative of their true significance; in the next place, their *abrupt* commencement is indicative of a layer distinct from the third; and, lastly, of still greater import to my mind is the fact that in those regions marked by a six-laminated type the belt of angular cells becomes *interposed between this layer of cells and the third layer.* To summarise, therefore, we may state that the ganglionic layer in the Pig consists of cells which, whilst arranged in *clusters* corresponding to the nests of BETZ in the human subject, conform in size and configuration to the lowest pyramidal cells of the third layer in Man (Plate 7).

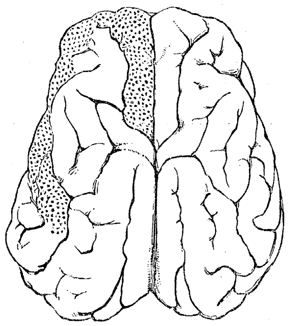
* *Loc. cit.*

3. *Dimensions of cells.*—The largest cells are found anterior to the crucial sulcus in the antero-superior portion of the great limbic lobe, where that lobe becomes superficial on the hemisphere, figs. 1 and 2 (4). Next to them in point of size are the ganglionic cells of the anterior portion of the parietal convolution immediately external to the crucial sulcus. In the exposed portion of the limbic lobe above referred to, the cells attain the dimensions of 48μ in length by 17μ in breadth, their nucleus measuring 15μ long. Such are the dimensions in the middle third of this region, fig. 2 (B C). Towards the frontal extremity of the hemisphere near the fissure of ROLANDO, fig. 2 (9) they decrease to $37\mu \times 16\mu$ (nucleus 11μ), whilst posteriorly at the commencement of the crucial sulcus they average but $25\mu \times 19\mu$. The variations observed in the dimensions of these cells will be further dealt with in our remarks upon regional distribution, and will also be found in a tabulated form at the end of this article.

Regional Distribution.

That portion of the antero-superior arc of the great limbic lobe or convolution of the corpus callosum, which becomes in the Pig and other Mammals superficial on the upper aspect of the hemisphere, and which in this animal bounds the anterior half of the longitudinal fissure, is *par excellence* the region which exhibits the highest development attained by the ganglionic series of cells. From the commencement of the crucial sulcus where this lobe becomes superficial to its termination anteriorly, the five-laminated cortex and nested arrangement of the fourth layer of cells is maintained throughout. Local variations in the distribution of the ganglionic cells occur markedly in this lobe, and will require separate notice further on. For the present it is necessary that we trace the regions over which this characteristic formation is spread. The

Fig. 3.



extreme anterior tip of the hemisphere participates in this formation, both convolutions bordering upon the fissure of ROLANDO exhibiting a five-laminated cortex and distinct clustered cells in the fourth layer. The same fundamental type of structure can be traced along the whole course of the lowest parietal convolutions (first and second), from their union with the ascending parietal (post-Rolandique, BROCA) towards and

around the Sylvian fissure. To speak generally, then, it may be stated that the arrangement of the elements of the fourth layer in clusters is more especially characteristic of the cortex in—

a. The great limbic lobe (anterior half of superior arc).

b. The frontal lobe.

c. The first and second parietal convolutions.

Embraced within this territory we have the third and fourth parietal convolutions lying above the primary parietal sulcus (inter-parietal) extending from the ascending parietal convolution to the opposite pole of the hemisphere. These convolutions, forming the greater mass of the upper and posterior aspects of the hemisphere, present us with an arrangement of the ganglionic series very distinct from that just dealt with: I allude to the solitary or laminar arrangement of cells. This mode of distribution is highly characteristic of this region. When referring to the transition realms of the cortex it was stated that the passage of one form into that of another is never *abrupt;* the change is a *gradual* one, and hence no exact boundary line can be drawn betwixt the clustered cells of the fourth layer in the *limbic* lobe and the solitary elements of the same layer in the adjacent parietal gyri. Vertical sections taken through these adjacent convolutions constantly exhibit the grouped arrangement overstepping the boundary of the crucial sulcus and spreading towards the summit of the uppermost parietal convolution, but thinning out into the stratiform or solitary arrangement beyond. On the other hand, numerous nests of these same elements occupy that aspect of the third parietal gyrus which dips into the inter-parietal sulcus. Bearing this fact in mind, we may state that the crucial and inter-parietal sulci roughly map out the boundary lines between two highly characteristic formations—the clustered and the solitary ganglionic series. We will now deal with the several regions alluded to seriatim, and describe the local variations in the conformation of the mid-regions of the cortex in—1, the limbic lobe; 2, frontal lobe; 3, parietal lobe.

1. *The great limbic lobe.*—We shall limit our examination to the antero-superior arc of this lobe, or the convolution of the corpus callosum, and first inquire into the special arrangement of the fourth layer of the cortex in that anterior portion which lies in front of the *sub-parietal* sulcus, and whose limits extend from the commencement of the crucial sulcus to the internal root of the olfactory nerve, fig. 1 (6–19). The superficial portion of this lobe exposed on the surface of the hemisphere is represented in the diagram as mapped out by several oblique lines into six divisions (fig. 2). The ganglion cells of the fourth layer are most densely grouped in the divisions B and C. At this site the nests are large, oval, and deep, and are rich in densely-packed cells; the groups themselves are so numerous and closely set as to be almost confluent. Reference to the table of measurements will show us that the cells of this immediate locality attain the greatest average dimensions—viz.: $48\mu \times 17\mu$, the largest cell observed being $69\mu \times 32\mu$. At D the dense confluent groups are again met with, but over a limited area, the outer aspect exhibiting chiefly distant or discrete clusters.

At E, and still more at F, the dense confluent groups re-appear, although the tendency to thin out into discrete clusters shows itself towards the crucial sulcus. A gradual reduction in the dimensions of these cells is noticed towards F, so that at the commencement of the crucial sulcus they average but $28\mu \times 17\mu$. Further forwards at A, dense groups appear on the internal aspect of the lobe just where it becomes superficial, but between this and the crucial sulcus the cells are scattered in distant groups, and average in size $37\mu \times 16\mu$. These densely-grouped confluent nests may be traced down along the whole internal aspect of the anterior arc of the limbic lobe as far forwards as the sub-frontal sulcus. In the divisions marked A C great fusiform cells are frequently met with measuring 55μ long $\times 13\mu$ in diameter, or $69\mu \times 11\mu$. In entering thus somewhat minutely into the details of examination of an important region of the cortex, I have been influenced by the desire of pointing out what may prove a significant fact: that these groups of ganglionic cells do not form an *equably* distributed layer, but are associated in dense masses towards various centres with intervening tracts formed by distant or discrete cell groupings. The remaining portion of the convolution of the corpus callosum, viz.: that part lying *beneath the sub-parietal sulcus* and limited posteriorly by the *retro-limbic annectant*, presents us with the most perfect example of the six-laminated cortex and solitary arrangement of ganglionic cells. The band of angular or pyramidal elements separating the third layer from the ganglionic is both deep and dense.

2. *Frontal lobe.*—The extreme tip of the hemisphere anteriorly constituting the frontal lobe presents us with the nested arrangement of cells, the nests being in the ascending frontal convolution thinly supplied with cells and distant in their grouping, whilst throughout the ascending parietal gyrus the nests are formed of densely-congregated cells. These rich nests are, however, invariably discrete and even distant. The inner aspect of the frontal lobe, limited behind by the sub-frontal sulcus, has numerous cell groups which form, however, but ill-defined nests. Throughout the whole extent of the frontal lobe no coalescence of groups or confluent nests were observed.

3. *Parietal lobe.*—The four convolutions constituting this lobe are by no means identical in structure throughout. The convolutions below the inter-parietal fissure will first engage our attention. The first or Sylvian convolution is usually blended with the second parietal in front of the fissure of SYLVIUS; a few faint markings indicating their line of union. Throughout these convolutions the general arrangement of ganglionic cells is in shallow, ill-formed nests, poor in cells, and the nests discrete and often distant. The richer aggregation of cells occurs along what corresponds to the second parietal gyrus bordering upon the inter-parietal fissure, and they thin out into distant nests towards the Sylvian fissure. The groups of cells are dense and almost confluent in the divisions A B C, fig. 2, of the second parietal convolution, as also they are throughout the whole extent of the first and second parietal convolutions at F. Still further back at G we find both gyri possess well-formed distinct nests of from

five to six cells, which groups are invariably distant from one another. Their maximum dimensions are obtained at B ($=40\mu \times 21\mu$) and at F ($=37\mu \times 27\mu$), the minimum at E ($= 28\mu \times 18\mu$).

Carrying our observations into the structure of the upper parietal region, immediately above the inter-parietal fissure, we find the solitary or laminar type of the ganglionic layer as most prevalent throughout. We have here, of course, two convolutions to deal with, viz.: the third parietal and the fourth or sagittal convolution. The anterior extremities of these gyri exhibit, as above stated, certain modifications in the immediate neighbourhood of the crucial and inter-parietal sulci; but with this exception the laminar arrangement is maintained. In the regions alluded to, the nested cells may be traced from the crucial and inter-parietal sulci some distance up the adjacent side of the upper parietal convolutions. They frequently reach the summit of these gyri as extremely rich nests, which are invariably discrete and often very distant. The laminar arrangement of the posterior parietal region is highly characteristic. It appears as a pale band, along the upper limit of which a line of solitary cells lie at distances of from ·139 mm. to ·379 mm. apart. Frequently, however, two or three of such cells appear side by side. In this region we recognise the tendency to the accumulation of angular and small pyramidal elements towards the lower limits of the third layer, which tendency becomes more marked the further back we carry our examination of the cortex. It must, however, be distinctly understood that we have here no distinct belt of small angular elements; no accumulation of cells so differentiated from the third and subjacent layers as to merit the name of an additional layer of the cortex. We find over the greater portion of the parietal region but the faint shadowing forth of the six-laminated type—an arrangement met with over a very limited region of the cortex in this animal.

The Cortex Cerebri of the Sheep.

The points of resemblance exhibited between the cortex of the Sheep and the Pig are so numerous that to describe the structure in each separate lobe of the Sheep's brain would be to a great extent a task of recapitulation. I shall therefore content myself with a description of the structure of the cortex in that great fundamental portion of the brain—the limbic lobe, and emphasise more especially those features where points of divergence are indicated.

Lamination of the great limbic lobe.—We have here in the anterior portions of the upper arc to deal with a five-laminated cortex over an area which, as will be pointed out further on, is coextensive with the same formation in the Pig.

First layer (Plate 6, A).—The average depth of this pale stratum is ·550 mm. It embraces the two forms of nucleated cells which are found in this layer in other animals, viz.: the perivascular and neuroglia corpuscles, measuring 5μ and 9μ in diameter. These cells contain large nuclei. Immediately beneath the pia mater great numbers of the

spider-like bodies known as DEITER's cells are met with. They are distributed especially along the course of the blood-vessels which vertically traverse this superficial layer of the cortex. Closely packed beneath the pia mater, their long filaments spread in all directions embracing the nearest blood-vessel. They thin out in numbers below the upper third of this layer, becoming few, and scattered widely apart in the neighbourhood of the small pyramidal layer. It may here be stated that these peculiar bodies are found in *very* scant numbers throughout the various subjacent layers, but towards the lower realms of the spindle layer they again congregate in larger numbers, become especially abundant along the blood-vessels which course through the medullary strands at the confines of the cortex. It is evident from this distribution that they are more especially limited to the regions of the greater vascular channels, and do not intrude upon the regions of capillary distribution. This fact I regard as significant, when we also take into consideration their reappearance in Man as *morbid elements* in those diseases of the brain which are regarded as closely connected by a causal relationship with extensive vascular lesions. The pia mater is not only thickened, but is strongly attached to the cortex by means of these bodies, and over certain regions, as the two lower parietal convolutions, the adhesion is so strong that the pia cannot be separated without destroying the subjacent layer. In these regions of firm adhesions betwixt the pia mater and cortex the processes of these cells are extremely coarse, and often form a dense felt of fibres immediately beneath the pia. Such a condition I have not observed in Man except as the result of retrogressive changes in diseased regions. The depth of this characteristic formation is usually ·134 mm., and varies from $\frac{1}{3}$rd to $\frac{1}{5}$th the depth of the first layer. The other elements of this layer resemble in all essential features those of the corresponding formation in the Pig.

Second layer (Plate 6, B).—In the five-laminated region of the limbic lobe which we are now considering, this formation is peculiarly poor in cells and forms but an insignificant belt of small angular and pyramidal elements associated with larger pyramidal cells. It is often apparently absent, or forms by the closer approximation of its elements a limiting border to the important layer below it. This layer becomes deeper and more decided towards the posterior pole of the hemisphere. Again, in the anterior extremities of the lower parietal convolutions it is a more distinct formation. The cells are oval, angular, or small pyramids possessing a large spheroidal nucleus. The smaller cells average $13\mu \times 6\mu$ in dimensions, their nucleus having a diameter of 6μ.

Third layer (Plate 6, C).—The cells of this layer are remarkably uniform in size throughout, and in the anterior portion of the superior arc of the limbic lobe they are most densely aggregated in the upper half of the layer, their comparative paucity in its lower half gives to this region the appearance of a pale white belt. The whole layer is of fair depth, and presents but few of DEITER's corpuscles above alluded to. The cells vary much in contour, although the majority are pyramidal in form, their nucleus measures 6μ in diameter, and the cells average $18\mu \times 10\mu$. Their apical process is frequently contorted and twisted in its course upwards towards the first

layer. Throughout this layer small pyramidal cells usually measuring 13μ in length by 9μ in breadth are found. These latter elements tend in *certain regions* of the brain to accumulate towards the lower half of the third layer; and the pale zone, poorly supplied by cells in the anterior extremity of the limbic lobe, becomes in its *posterior* half, and at other sites, occupied by these small pyramidal and angular elements which form the *fourth* layer of the *six-laminated* cortex. This layer of angular elements attains a depth of ·186 mm., the cells measuring from 6μ to 9μ in greatest length and breadth. Not only do we miss here the gradual increment in size of these cells with their greater depth which is so noticeable in Man and the Monkey, but we frequently find the largest elements of the series ($27\mu \times 15\mu$) immediately beneath the second layer. This layer is as a rule richly supplied with cells which are densely aggregated.

Ganglionic layer (Plate 6, D).—This important formation attains a depth of ·372 mm. below the superimposed stratum. The nerve-cells of this layer vary much in their conformation. The most frequent form assumed is that of an elongated pyramid, the apical process of which can be traced often as far as the first layer of the cortex. Other cells assume the form of elongated spindles, and a frequent form is that of a horned cell, which bears a striking resemblance to the egg case of the Skate. The apex process may bifurcate close to the cell, giving the latter the form of a horned pyramid, or it may divide into two secondary processes of equal diameter at any distance up the third layer. The apex process is particularly coarse and does not undergo rapid attenuation. The average dimensions of these cells is $46\mu \times 11\mu$, a measurement which reveals clearly the elongated conformation of these elements, in fact, the oval and plump rounded contour so frequent in the corresponding cells of Man, the Monkey, and the Carnivora is very rarely met with in these animals. Occasionally a larger cell than usual is met with, *e.g.*, $65\mu \times 23\mu$. They contain an oval nucleus measuring 13μ in length. These cells are disposed in oval or oblong nests, often covering an area 460μ deep by 110μ broad, and contain as many as twenty cells in some situations. The cells are frequently scattered somewhat irregularly in the anterior portion of the limbus, but they become progressively *larger and more distinctly nested* towards the *exposed portion of the limbic lobe.* The clusters are frequently so closely packed as to become confluent, and in many regions on this account the nests are badly differentiated. It is impossible after close examination of this formation to arrive at any other conclusion than that these cells not only resemble those larger pyramids of the third layer in Man in their general form, but also by their gradual increase in size from above downwards (the largest cell being invariably lowest in the series) claim further affinities to this formation. It is however distinctly differentiated from the third layer in the six-laminated regions by the interposition of the layer of small angular cells.

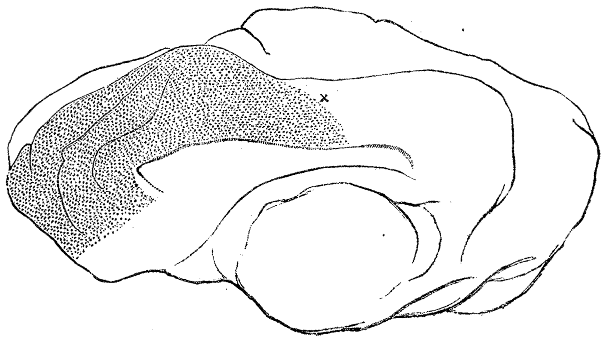
Spindle layer (Plate 6, E).—The lowest formation of the cortex in this region presents no special features demanding notice here. The spindle-cells are large in size and the

stratum deep. Passing now to the subject of regional distribution of the different types of lamination, and the diverse arrangements of the ganglionic series, we shall rapidly glance at each individual lobe.

Regional Distribution.

Great limbic lobe.—The anterior half of the superior arc of this lobe, fig. 4, is distinctly five-laminated, whilst the ganglionic series of cells is arranged in clusters throughout the whole extent of this lobe as far back as the retro-limbic annectant. From the commencement of the crucial sulcus the nested arrangement of these cells becomes a more marked feature the further forward our examination extends, so that in the neighbourhood of the fronto-limbic sulcus the nests are large and richly

Fig. 4.



crowded with ganglion cells. The groupings also in this situation are frequently confluent. Although the nested grouping of this formation is maintained throughout the superior arc of this lobe, a great dissimilarity is seen between sections taken near the posterior extremity of the corpus callosum and those from regions anterior to its genu. The posterior half of this upper arc differs however not only in the mode of grouping of its elementary constituents—a fundamental divergence is observed in its lamination. Beneath the whole extent of the sub-parietal sulcus the limbic lobe is found to be six-laminated (Plate 7). This change in the type of cortical stratification is assumed at fig. 4 (*), a little posterior to the point where the sub-parietal sulcus becomes superficial on the surface of the hemisphere, and is continued as the crucial sulcus. The intercalated series of small angular cells is first observed therefore where the limbic lobe comes close in contiguity with the sagittal gyrus of the parietal lobe at the origin of the crucial sulcus. A similar disposition is maintained in the lamination of the limbic lobe in the Pig, as we have already stated above. From this point the six-laminated cortex is spread downwards and backwards over the whole posterior portion of the superior limbic arc. The intercalated series of small angular elements becomes more and more richly developed towards the retro-limbic annectant, where it forms a dense and deep stratum, which readily characterises this region as wholly differing in important features from realms anterior to the crucial sulcus.

A most noteworthy feature presented by this layer is its tendency to take a higher position than is observed in the same region in the Pig; in other words, it appears to encroach upon the third layer, which becomes unusually shallow, whilst the ganglionic stratum is proportionately increased.

Parietal lobe.—Throughout the greater mass of the parietal lobe the six-laminated type prevails, and the solitary or laminar arrangement of the ganglionic series is found. Exceptions occur, however, near the crucial sulcus, in the ascending and lower parietal convolutions. Along the whole of the first parietal or Sylvian convolution the same structural peculiarities exist that were apparent in the Pig. The five-layered cortex and the clustered ganglion cells reappear here. The nests in this Sylvian convolution are dense in cells, and so closely approximated as frequently to become quite confluent, and especially is this the case towards the lower aspects of this convolution. They usually occupy areas ·325 mm. in depth by ·162 mm. in breadth, and the cells average $40\mu \times 13\mu$, with a nucleus having a diameter of 13μ. The largest cell observed measured $60\mu \times 27\mu$. It will be apparent from the foregoing statement that, as in the similarly stratified portion of the limbic lobe, the elements of this layer are peculiar from their elongated form and their rich dense clustering. Posterior to the fissure of SYLVIUS these nests become thinned out, the lamination assumes the transitional characters, passing eventually into the six-laminated type. The second parietal convolution anterior to the Sylvian fissure presents us with a realm transitional between a five and six-layered cortex. The ganglion cells assume a distinctly laminar arrangement, the angular cells increasing in number but not forming in this region a very distinct layer.

Frontal lobe.—Throughout the whole extent of this lobe the cortex is constituted of five layers. The cells of the ganglionic layer are small, well nested, and often confluent, but do not approach in their development the corresponding series in the exposed portion of the limbic lobe. The third layer in this lobe is constituted of cells maintaining uniform dimensions throughout the depth of this layer; but they approach close to the ganglionic series and fail to exhibit the pale zone betwixt these two layers, which is apparent in realms nearer the six-laminated cortex.

THE CORTEX CEREBRI OF THE CAT.

Taking the great limbic lobe as presenting in its most perfect development the cortical formation characteristic of the motor area, we proceed to note the essential features of its individual layers. For the present we restrict our examination to the anterior half of its superior arc, fig. 5 (*).

First layer.—A narrow, pale, white streak, averaging ·325 mm. in depth, constitutes this stratum as seen by the naked eye. It is found to consist of an extremely delicate meshwork of connective and nerve-fibrils, in which two forms of nucleated cells may be observed—the perivascular following the course of blood-vessels, and

measuring 5μ, with a large spheroidal nucleus, and a true connective corpuscle, averaging 9μ in diameter, having one or more nuclei, and when not altered by reagents seen as a corpuscle of irregular contour with numerous delicate radiating processes. As I have stated elsewhere,* I regard the latter as the origin of DEITER's corpuscle, to which frequent allusion has been made. The coarser connective element recognised as DEITER's cell is present immediately beneath the pia mater, but far less abundantly than in the Pig and Sheep. The nuclei of these cells usually measure 4μ in diameter, whilst the nucleus of the angular cell, which in general conformation sometimes approaches them, measures fully 9μ. The superficial portion of this layer presents us with the usual belt of medullated fibres extending to a depth of ·162 mm. to ·192 mm., the individual fibres of which measure 2μ to 4μ in diameter.

Second layer.—This stratum, far better marked than in the Sheep, is constituted of small angular, ovoid, or pyramidal cells. The angular cell is frequently bifurcate or horned, and branches irregularly. All the cells contain a large oval or spheroidal nucleus, and are imbedded in a matrix identical with that of the first layer. Here we also recognise the large connective cell. The nerve-cells of this layer average $10\mu \times 6\mu$, with a nucleus 5μ in diameter; but amongst them are found larger pyramidal cells, identical in appearance with those of the upper part of the third layer, and which attain the dimensions of $13\mu \times 10\mu$. The depth of this layer varies between ·139 mm. and ·186 mm.

Third layer.—This layer and the one superimposed appears to the naked eye as a dark grey translucent band, and extends to the depths of ·744 mm. to ·790 mm. The pyramidal elements characteristic of this formation increase in size with their depth, as do the corresponding cells in the cortex of Man and Apes. The average dimensions of these cells is $16\mu \times 9\mu$, the larger cells at the lowest levels of this stratum attaining proportions of $23\mu \times 13\mu$. Seven processes are usually seen in vertical sections. In the *immediate* neighbourhood of the crucial sulcus the largest cells of this layer do not extend below the upper half of the stratum, leaving betwixt them and the ganglionic series a paler band, in which are very sparsely scattered a few smaller pyramidal cells and angular elements, the latter being found at all depths of this layer, although in very small numbers. On the *parietal* side of the sulcus, however, the pale band becomes a belt of small angular elements. Thus, although the angular cells are found at all depths from the second layer downwards, they do not constitute a distinct stratum betwixt the large pyramidal and ganglionic layers until the parietal boundary of the crucial sulcus is reached, and the limits of the anterior portion of the limbic arc overstepped. Perivascular and connective cells of the same character as those of superimposed layers appear here. The matrix consists of an extremely delicate connective with a meshwork of the minutest nerve-fibrils given off from the angular elements and the periphery of the small and large pyramidal and

* *Loc. cit.*

ganglionic cells. Through this layer course upwards the apex processes of its cells as also those of the great ganglionic series below.

Ganglionic layer.—The cells of this formation are plump, oval, or pyriform bodies, differing notably from the elongated pyramidal cells of the Sheep and the Pig. Occasionally a fusiform cell occurs, and more frequently a well-formed pyramid. They attain the dimensions of $51\mu \times 23\mu$, with a large oval nucleus, measuring 18μ. The nests are usually large and uniform, and most frequently contain from three to four cells (as seen in vertical sections). One of the larger and richer nests measured ·340 mm. in depth by ·093 mm. in breadth, and showed nine cells. The ganglionic cells are decidedly largest in the gyri bounding the crucial sulcus. In a former investigation into the structure of the gyri in this neighbourhood * the following facts were elicited. The limbic boundary of this sulcus possessed ganglionic cells averaging $39\mu \times 17\mu$, whilst the parietal boundary of the sulcus contained cells averaging $46\mu \times 17\mu$, a large number even measuring $69\mu \times 27\mu$. At the external limit of the crucial sulcus, where the parietal gyrus bends round and unites with the limbic lobe, the largest cells were found ($83\mu \times 37\mu$), whilst an occasional gigantic cell occurred, attaining the dimensions of $106\mu \times 32\mu$.

The spindle layer calls for no special description here.

Parietal lobe.—On the parietal side of the fissure of ROLANDO we come upon a six-laminated type of cortex; and just as we shall find that the crucial sulcus presents us with a different type of structure on its limbic and parietal walls, so here the fissure of ROLANDO separates two typical stratifications of the cortex. In short, the structure of the ascending frontal differs materially from that of the ascending parietal. The difference consists essentially in the reappearance of a distinct layer of angular cells below the large pyramidal series, in the larger dimensions of its ganglionic cells, and the fairly rich and well-formed nests of these elements. We find the average depth of the first cortical layer has decreased to ·232 mm., and that of the next two subjacent layers to ·697 mm. The cells of the ganglionic series attain an average of $37\mu \times 19\mu$, with a nucleus 13μ in diameter. Passing from the ascending parietal gyrus to the four tiers of parietal gyri, we find the laminar conformation and structural peculiarities of this great extra limbic mass to be as follows. The first and second parietal convolutions exhibit various stages of transition betwixt a five- and a six-laminated conformation. The small pyramidal and angular layer above the ganglionic series is but poorly represented, and in the anterior extremities of these convolutions the cells are so few and so thinly scattered that the formation scarcely deserves the name of a distinct layer, whilst in the posterior extremities of the same gyri the layer is more richly developed. The arrangement of the ganglionic cells varies at different sites, but the nested is that which predominates in the first or Sylvian convolution, especially in the immediate neighbourhood of the Sylvian fissure. Towards the inter-parietal sulcus these clusters become more distant, and constituted of fewer cells, until a purely laminar arrangement

* Vide 'Brain,' part 1, April, 1878.

is maintained. The third parietal convolution is six-laminated throughout, its fourth layer of small pyramidal elements being very distinct and richly developed. The ganglionic cells are arranged in clusters towards the anterior half of this convolution, becoming larger and denser nests the nearer they approach the sigmoid gyrus. In this latter region the cells are of *large size.* Towards the posterior extremity of the third parietal convolution the clustered arrangement gives place to the laminar. Passing now to the fourth parietal or sagittal gyrus, we observe at the anterior extremity, where it impinges upon the crucial sulcus, the small pyramidal cells below the third layer are so scanty that nothing beyond a mere tendency to the formation of a separate stratum can here be discerned. The ganglionic cells, however, are very *large* and *globose,* and the nests rich and extensive. Except at the very extreme anterior portion of this convolution, the cortex is distinctly *six-laminated* throughout, and the cell-clusters become thinned posteriorly to a solitary or laminar formation, as far as the posterior pole of the hemisphere.

Frontal lobe.—This lobe forms the extreme anterior pole of the hemisphere, and presents a well-marked fissure directed obliquely downwards and outwards—the fissure of ROLANDO, bounded externally by the ascending parietal, and internally by the ascending frontal convolution. The cortex of this lobe is five-laminated, except in the immediate neighbourhood of the fissure of ROLANDO, where a transition lamination presents itself.

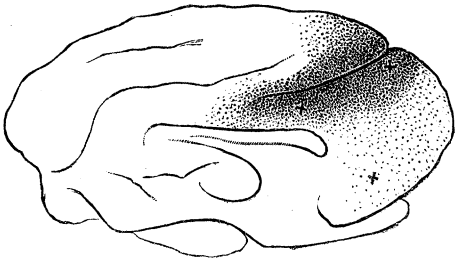
Taking the structure of this lobe in the order of its layers, we notice that the first layer attains a depth of ·325 mm., and differs in no essential points from that of the limbic lobe. The second layer is here scarcely appreciable, always poorly represented, and often absent over limited areas. It becomes distinctly defined towards the ascending parietal gyrus. The second and third layers have a depth of ·930 mm. The pyramidal elements of the third layer increase in size with their depth, are most densely congregated in the upper half of the layer, whilst the lower half is left as a paler zone, in which towards the fissure of ROLANDO we can readily trace the gradual increase of angular and small pyramidal elements, which, as above stated, form in the ascending parietal a distinct belt dividing the cortex into six layers.

Regional Distribution.

It will be seen that we have in the foregoing description anticipated many of the facts regarding relative areas of different laminations and distribution of the ganglionic series. The whole superior arc of the great limbic lobe, from its origin near the olfactory lobe backwards as far as the retro-limbic annectant, presents us with the best example of the clustered arrangement of the ganglionic cells. These cell clusters are most thickly grouped, and most rich in cells in the *anterior* regions of this upper arc, attaining their *maximum development* in the vicinity of the *crucial sulcus.* The elements of this layer in the latter region differ much amongst themselves in contour

and size according to their local distribution. Thus the cells found in that portion of the parietal lobe dipping into the crucial sulcus are peculiarly *swollen, globose, and of*

Fig. 5.



great size—frequently solitary, or arranged in twos or threes. The cells of the limbic portion of this sulcus are, on the other hand, *smaller, elongated, and thickly grouped.* In front of the crucial sulcus the whole cortex of the limbic lobe is distinctly modelled upon the five-laminated plan, fig. 5. Posterior to the crucial sulcus the small pyramidal and angular cells begin to congregate towards the lower confines of the third layer, and this tendency increases from before backwards, so that towards the posterior end of the corpus callosum these small elements form a distinct layer above the ganglionic series. This six-laminated structure is maintained backwards as far as the retro-limbic annectant, which is also modelled upon the same type. Tracing the five-laminated

Fig. 6.

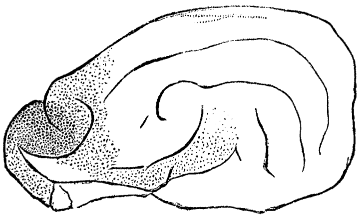
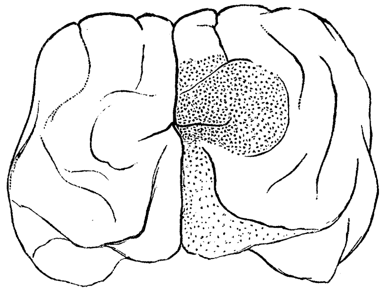


Fig. 7.



type beyond the confines of the limbic lobe, we find it extends through the whole of the frontal lobe, and that it is limited externally by the fissure of Rolando. In the anterior part of the Sylvian convolution we meet with a transitional form of lamination, whilst a more purely five-laminated cortex occupies the anterior extremities of the third and fourth parietal convolutions. The latter or sagittal convolution in the neighbourhood of the crucial sulcus shows an especially rich development of the five-laminated cortex and its clusters of ganglionic cells.

Relative Area of Five-laminated Cortex in different Animals.

When inquiring into the architecture of the human cortex cerebri, it was stated that the five-laminated cortex, conjoined to the clustered arrangement of ganglion

cells, was most highly characteristic of motor areas.* We have acquired from the foregoing examination sufficient data for mapping out approximately the relative areas of the five- and six-laminated cortex in the Pig, Sheep, and Cat; and the subjoined table gives the information necessary for the comparison of such results:—

Area of five-laminated cortex.

The Pig. (Figs. 1, 2, 3.)

1. Anterior portion of superior limbic arc in front of the crucial sulcus. Fig. 1 (7–19).
2. Frontal lobe.
3. Ascending parietal convolution.
4. First and second parietal convolutions united in front of Sylvian fissure.

The Sheep. (Fig. 4.)

1. Anterior portion of superior limbic arc in front of the crucial sulcus.
2. Frontal lobe.
3. Ascending parietal convolution.
4. First parietal convolution (Sylvian).

The Cat. (Figs. 5, 6, 7.)

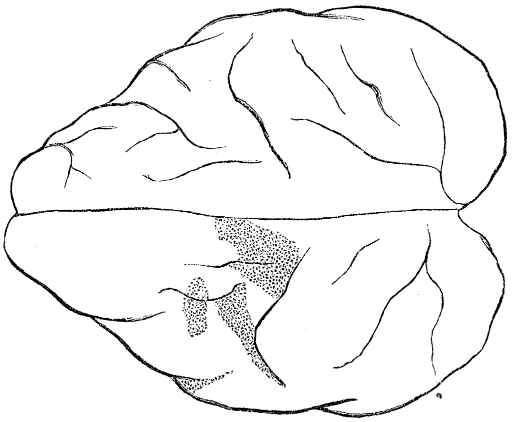
1. Anterior portion of superior limbic arc in front of the crucial sulcus.
2. Frontal lobe.
3. First parietal or Sylvian convolution.
4. Anterior extremity of second parietal convolution.
5. Anterior extremity of fourth parietal or sagittal convolution.

From this summary it is evident that, whilst in all these animals corresponding portions of the limbic and the whole of the frontal lobe are framed upon the same plan, the ascending parietal convolution partakes of this formation in the Pig and Sheep alone; the first and partly the second parietal convolution is (in front of the Sylvian fissure) so constructed in all these animals, whilst a well-developed area of the same formation occupies the anterior extremity of the fourth or sagittal convolution in the Cat. It is interesting to note here the fact that the crucial sulcus forms in all these animals alike a boundary line betwixt the two typical laminar arrangements of the vertex, and marks at its commencement the transition of the one formation into that of the other in the limbic lobe. In summarising, as above, the areas of the five-laminated cortex, with its coextensive nested series of ganglionic cells, due regard must be paid to the varying richness in development of the latter formation. In the diagram accompanying this memoir attention has been paid to this point, the dark shading indicating the rich developments of this formation; the paler shading covers regions where the same formation is poorly developed. Guided by these diagrams, let us summarise for comparison the limits of the richly-developed motor cortex in each animal under consideration.

* *Loc. cit.*

Barbary Ape (fig. 8.)—The most important grouping occupies the posterior extremity of the frontal convolutions, and the upper end of the ascending frontal gyrus.

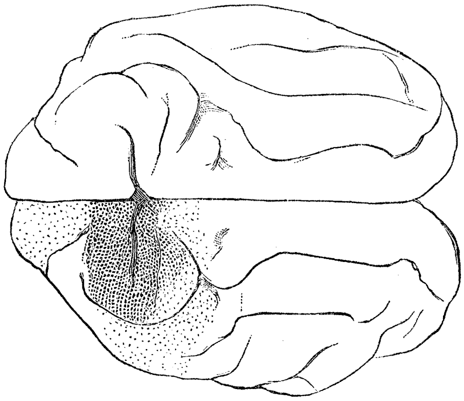
Fig. 8.



At the middle third of the latter convolution two other small areas are represented. The upper and anterior end of the larger group is continuous with a large formation extending over the anterior half of the paracentral lobule. Over all these areas the cells are large and richly clustered. The greater part of the unshaded portion of the figure consists of the transitional and six-laminated realms.

The Ocelot (fig. 9).—Here the great ganglionic nests centre around the crucial sulcus, entering into the structure of its limbic and parietal boundary, and exhibiting cells of large size congregated in rich clusters, and so closely resembling those found in

Fig. 9.



the Cat that a full description would here be out of place. I subjoin, however, a table of measurements of these great cells at different points of the limbic and parietal boundaries of the crucial sulcus :—

DIMENSIONS of ganglionic cells in the Ocelot, from sections taken across the crucial sulcus.

		Limbic boundary.	Parietal boundary.
		μ μ	μ μ
Upper third.	Average . . .	46 × 20	48 × 27
	Largest . . .	88 × 27	93 × 32
Middle third.	Average . . .	51 × 23	48 × 22
	Largest . . .	92 × 27	93 × 41
Lower third.	Average . . .	64 × 29	49 × 27
	Largest . . .	92 × 46	92 × 41

The Cat (figs. 5, 6, 7).—The nested cells extending through the faintly-shaded portion of the Sylvian convolution can bear no comparison, either in size or number, to those seen in the limbic lobe. Throughout the whole limbic boundary of the crucial sulcus the ganglionic cells attain such great dimensions, and are so densely grouped, that they form quite a characteristic area; whilst still greater cells of comparatively gigantic dimensions, although in smaller numbers, occupy the parietal boundary of the same sulcus. The obliquity which the crucial sulcus presents on its deep aspects affords a larger area for distribution than would be imagined from a superficial view of the hemisphere. The faintly-shaded parietal and frontal convolution represents the less richly-developed areas of this formation, but the regions above described we should regard as endowed with the higher manifestations of functional activity.

The Sheep and Pig (figs. 3, 4).—The distribution is so similar in these two animals that a separate description is not required. In the diagram it will be seen that all portions of the five-laminated cortex are equally shaded, to indicate that, in size of cell and complex relationships, the nested ganglionic layer differs but slightly through this wide area. That slight differences in size between the cells do occur has already been indicated, but we fail to discover over this extensive field the extraordinary divergence in these particulars which is presented by the five-laminated cortex of Man, the Ape, and members of the Carnivora. The chief features of interest connected with regional distribution in the brains of these animals appear to be—

1. The wide area of distribution occupied by the five-laminated cortex.
2. The great uniformity observed in the dimensions and complex relationships of the ganglionic cells.

DIVERGENCE IN TYPE OF GANGLIONIC CELL.

In close connexion with the subject just considered are the following points, to which I am anxious to draw attention. It has been shown that the cells of the ganglionic series in the higher development of the motor cortex are *larger* in Man, the

Ape, the Cat, and the Ocelot than in the corresponding series in the Sheep and Pig. This increase in size is chiefly assumed in their short diameter or width, the cell being swollen, ovoid, and often approaching a globular contour. The protoplasmic mass forming these cells is therefore much greater in these higher animals. The important consideration attached to this form is dependent upon the fact that the swollen form is invariably associated with a far more complex branching from all parts of the periphery of the cell, whilst in the pyramidal cell the lateral angles give rise to the greater number of processes. In fact, the oval swollen cell shows numerous angular projections spread over its surface, from which delicate processes arise, and it is presumably the situation and number of these branches which form the chief elements in moulding the contour of the cell. Thus, the simplest cell is elongated, spindle-shaped, and bi-polar; the acquirement of a third process thrown off the centre of the body of the cell gives the spindle an angularity frequently observed in the last layer of the cortex. This appears to be the origin of the pyramidal form of cell and its various modifications and multipolar varieties. Two elementary forms of cell constantly occur in the cortex cerebri, which develop the one into the small pyramidal and angular, and the other into the large pyramidal and ganglionic series. It appears that when the processes arising from the *larger cells are most numerous*, we get the plump ganglionic cell—when *less numerous*, the large pyramidal cells of the third layer; whilst, if the complexity in branching of the smaller cell is great, we have an ovoid, irregular angular cell, or if few branches arise, we obtain the small pyramidal cell. I have stated elsewhere* that the absolute number of branches of these cells could never be determined with any degree of certainty; yet it is important to bear in mind the fact that the irregular contour of the large swollen ganglionic cell depends upon multiplicity of cell branchings, and that therefore this contour in the normal cell may be regarded generally as indicative of greater complexity. We therefore infer what we may approximately ascertain by examination of vertical and horizontal sections—that the cell groups of the ganglionic series have far more branches than those of the third layer. In Man, the Ape, Cat, and Ocelot we found the elements of the ganglionic series possessed this swollen contour, whilst in the Sheep and Pig they were almost universally *elongated pyramids.* The first glance at these cells in the latter animals suffices to establish their peculiar resemblance to the large pyramids of the third layer in higher animals. We therefore may with justice assume that—

1st. The large ganglionic cells of the Pig and Sheep are far less complex in their relationships and connexions than the corresponding cells in the Cat, Ocelot, Ape, and Man.

2nd. The same cells in the Pig and Sheep resemble closely in their general conformation and complexity the large pyramids of the third layer in higher animals.

* *Loc. cit.*

Relative Increase of Connective Matrix.

Examination of the brain of animals below Man in the scale of organization shows in a striking manner that the comparative amount of connective to nerve elements is greatly increased. This fact I have already drawn attention to in discussing the relative and absolute depth of the first layer of the cortex in different animals—a layer which in all cases essentially consists of a larger amount of connective than the subjacent strata.* MEYNERT also gives a table illustrative of this point.† Independent of the increase in relative and absolute depth of this layer, we have by these investigations been taught to recognise a great increase in the quantity of the cellular constituent of this matrix in the form of DEITER'S corpuscles, which crowd the upper regions of this layer. In Man they appear in scanty numbers; in the Barbary Ape they become more frequent; in the Cat and Ocelot they are still more abundant; in the Pig and Sheep so profusely scattered are they that they form a most characteristic stratum immediately below the pia mater, and the meshwork formed by their fibres is dense and coarse, binding the blood-vessels to the cortex and rendering the pia mater strongly adherent (Plate 6). We find these corpuscles more freely in human brain which has undergone senile degeneration and in other diseases attended by reductions in functional activity and vascular affections resulting in retrogressive changes and a reversion to a low type of structure.

The Globose Cell and its Affinities.

It has been already mentioned, when referring to the nerve-cells of the second layer of the Pig, that peculiar *globose* elements occur here with few processes, and no angular projections as in the angular cells which enter into the constitution of the fourth layer. These cells, which are more numerous in some regions than others, are peculiar in that they resemble none of the usual elements described as forming the various layers of the cortex. They look like small pyramidal cells whose angles have been rounded off by the uniform swelling of the cell, and in most of these cells the apex process can alone be seen. It is interesting to note that these cells are found in the third and second layers of the cortex in the *Ape*, and that I have never recognised them in any human brain except in the brain of *idiots* and *imbeciles*, where they appear in abundance.

The most characteristic feature presented in the cortex of idiots which I have had the opportunity of examining, has been the presence of these peculiar elements, which to a great extent take the place of the ordinary pyramidal cell of the second and third layer. Their essential characters consisting in their swollen, globose contour, and great paucity of branches.

* 'Brain,' part 3, October, 1878.

† "Brain of Mammals," by TH. MEYNERT, in STRICKER'S 'Human and Comparative Histology,' Sydenham Society, vol. 2, p. 383.

Summary.

In conclusion it will be well to summarise briefly the chiefs facts of interest which have resulted from these investigations. These may be stated as follows :—

1. A five and a six-laminated cortex is found in all the animals examined.

2. The fundamental structure of the layers is very similar in all.

3. Divergence in type is induced through varied character and distribution of the elementary units of these layers.

4. As in Man so in other animals variations in laminar type centre about the mid-regions of the cortex.

5. The ganglionic series is arranged upon *grouped* and *laminar* type.

6. The five-laminated cortex and nested cells are characteristic of motor areas.

7. Transition realms are readily recognisable in the Pig.

8. The first layer of the cortex in the Pig is deeper than in animals higher in the series and is crowded with Deiter's corpuscles.

9. There is great uniformity in size of the cells of the third layer in the Pig.

10. The six-laminated type is formed by the intercalation of a belt of small angular and pyramidal elements.

11. Great uniformity in contour and complexity of cells is observed throughout the ganglionic series in the Pig and Sheep.

12. The contour of these cells is almost invariably that of an elongated pyramid in these two animals.

13. The ganglionic series is distinguished from the third layer by the interposition in six-laminated realms of a belt of angular cells.

14. The area of five-laminated cortex in the Pig extends over the great limbic and frontal lobes and the first and second parietal gyri.

15. The intimate structure of the brain of the Sheep closely resembles that of the Pig.

16. The crucial sulcus at its origin indicates the transition from the one form of lamination into that of the other.

17. The cells of the third layer in the Cat increase in size with their depth.

18. The ganglionic cells of the Cat are of great size, and closely crowded around the crucial sulcus.

19. Their arrangement in the limbic and parietal boundaries of the sulcus differ.

20. Whilst the limbic and frontal lobes in the Pig, Sheep, Cat, and Ocelot have areas of the five-laminated cortex, greater variation is found in its disposition over the parietal regions.

21. The main feature of importance observed in the regional distribution of the ganglionic series in the *Carnivora* is its concentration around a limited area embracing the crucial sulcus ; in *Man* and the *Ape* its wide-spread area conjoined to great variations in developmental complexity ; and in the *Pig* and the *Sheep* its wide-spread distribution conjoined to a notable uniformity throughout in complex relationships.

22. The ganglion cells of the *Pig* and *Sheep* differ wholly in type from those of higher Mammals, and approach closely in appearance the large pyramidal cells of the third layer in Man and the Ape.

23. The appearance presented by the first layer in all this series of animals indicates very strongly the proportionate increase of the connective element over the nervous in animals lower in the scale of organisation.

24. The globose cell characterised by its contour and great deficiency of organic connexions, and which is found in large numbers in the brain of idiots, reappears as a normal element in the cortex of the Pig and Sheep.

DIMENSIONS of Ganglionic Cells in Cortex of Pig. (See fig. 2.)

Site of section.	Limbic lobe.	Fourth parietal gyrus.	Third parietal gyrus.	First and second parietal gyrus.
	μ μ	μ μ	μ μ	μ μ
A. . . .	47 × 17*	42 × 20	..	37 × 21
B. . . .	48 × 17†	37 × 21	..	37 × 18
C. . . .	41 × 11	36 × 19	26 × 18	28 × 18
D. . . .	38 × 18	39 × 24	31 × 18	37 × 18
E. . . .	28 × 17	40 × 17	26 × 20	37 × 27
F. . . .	25 × 19	25 × 19	33 × 19	21 × 19
G. . . .	..	29 × 17	29 × 17	29 × 17

Note.—μ, or micromillimetre = ·001 millim.

DEPTH of Cortical Layers from before backward.

LIMBIC LOBE.

	mm.	mm.	mm.	mm.	mm.	mm.	mm.
First layer	·790	·558	·558	·511	·651	·651	Average = ·619
Second and third layers .	·930	·837	·799	1·488	·697	·744	,, ·897
Ganglionic layer	·650	·465	·604	·372	·697	·558	,, ·557
Spindle layer	2·604	2·617	1·739	2·604	1·488	1·813	,, 2·144

UPPER PARIETAL CONVOLUTIONS.

	mm.	mm.	mm.	mm.	mm.	mm.	mm.
First layer	·372	·372	·372	·465	·744	·558	Average = ·547
Second and third layers .	·937	·744	·744	1·116	1·116	1·116	,, ·962
Ganglionic layer	·372	·279	·232	·186	·372	·372	,, ·302
Spindle layer	1·600	1·255	1·730	2·139	1·999	1·395	,, 1·689

LOWER PARIETAL CONVOLUTIONS.

	mm.	mm.	mm.	mm.	mm.	mm.	mm.
First layer	·418	·372	·372	·558	·372	..	Average = ·418
Second and third layers .	·930	1·300	1·116	·744	·930	1·116	,, 1·022
Ganglionic layer	·232	·373	·232	·558	·232	·325	,, ·344
Spindle layer	1·860	1·860	2·232	1·488	1·488	2·232	,, 1·860

* Largest cell observed = $69\mu \times 32\mu$.

† Largest cell observed = $70\mu \times 27\mu$.

References to Woodcuts in Text.

Fig. 1. Right hemisphere of Pig. Internal aspect.
1. Superior arc of the great limbic lobe.
2. Inferior arc of the great limbic lobe.
3. Retro-limbic annectant.
4. Superficial portion of the superior arc (great limbic lobe).
5. Sub-frontal sulcus.
6. Sub-parietal sulcus.
7. Commencement of crucial sulcus.
8. Inferior portion of the great limbic fissure.
10. Inner aspect of the frontal lobe.

Fig. 2. Left hemisphere of Pig. External aspect.
9. Fissure of Rolando.
10. Frontal lobe: portion corresponding to ascending frontal convolution.
11. Anterior part of parietal lobe, corresponding to ascending parietal convolution. The tiers of parietal gyri terminate here (gyrus post-Rolandique).
12. Inter-parietal sulcus.
13. Sylvian fissure.
14. Temporal lobule of the parietal lobe.
15. First parietal or Sylvian convolution.
15A. Anterior limb of first and second parietal convolutions united.
16. Posterior limb of second parietal gyrus.
17. Third parietal convolution.
18. Fourth parietal or sagittal convolution.
19. Olfactory lobe.

Fig. 3. Brain of Pig. Illustrative of the distribution of the five-laminated cortex over the limbic, frontal, and parietal lobes.

Fig. 4. Brain of Sheep (internal aspect of right hemisphere). Illustrative of the distribution of the five-laminated cortex over the frontal and great limbic lobes.

Fig. 5. Brain of Cat (inner aspect of left hemisphere). Illustrative of the distribution of the five-laminated cortex over the frontal and great limbic lobes.

Fig. 6. Brain of Cat (outer aspect of left hemisphere). Illustrative of the distribution of the five-laminated cortex over the frontal, limbic, and parietal lobes.

Fig. 7. Brain of Cat (frontal aspect). Illustrative of the distribution of the five-laminated cortex over the frontal, limbic, and parietal lobes.

Fig. 8. Brain of Barbary Ape. Illustrative of the distribution of the five-laminated cortex over the upper surface of the hemisphere.

Fig. 9. Brain of Ocelot (*Felis pardalis*). Illustrative of the distribution of the five-laminated cortex, as seen from the vertex.

REFERENCES TO PLATES.

PLATE 6.

The five-laminated cortex cerebri of the Sheep and Pig, as seen in vertical sections taken from the limbic lobe.

A. First layer exhibiting large numbers of DEITER's cells beneath pia mater.

B. Second layer of small pyramidal and angular elements which in the Pig form by their branches a dense meshwork in the lower regions of the first layer.

C. Third layer of large pyramidal cells.

D. Fourth layer or ganglionic series.

E. Spindle cells of fifth layer.

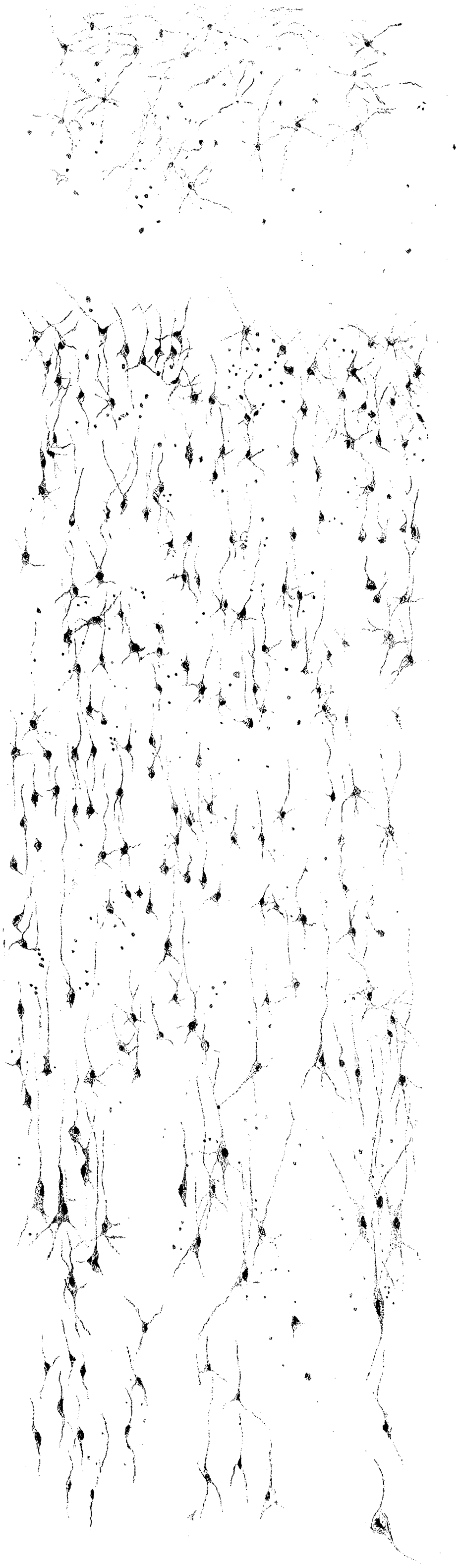
PLATE 7.

From the six-laminated cortex of the Sheep. The five upper layers are alone seen, the spindle or sixth layer being excluded. A belt of small angular elements is seen at D, interposed between the large pyramidal (C) and the ganglionic layers (E). × 55.

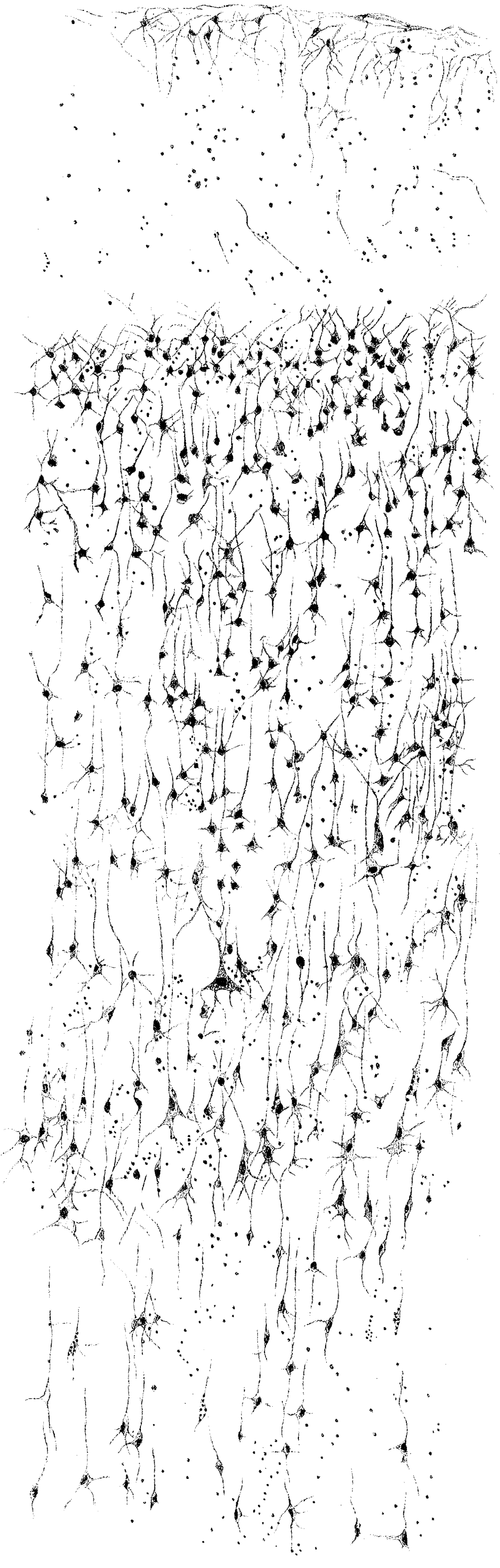
A group of ganglionic cells from the five-laminated cortex of the Pig. × 270.

Section through the cortex cerebri of the Pig. This section having been taken from a sulcus in the limbic lobe exhibits the laminar or solitary arrangement of the ganglionic cells, as contrasted with the appearance of the "nests" of BETZ seen in the group above. × 98.

Note.—All the above have been sketched under high powers, and reduced subsequently by photography.

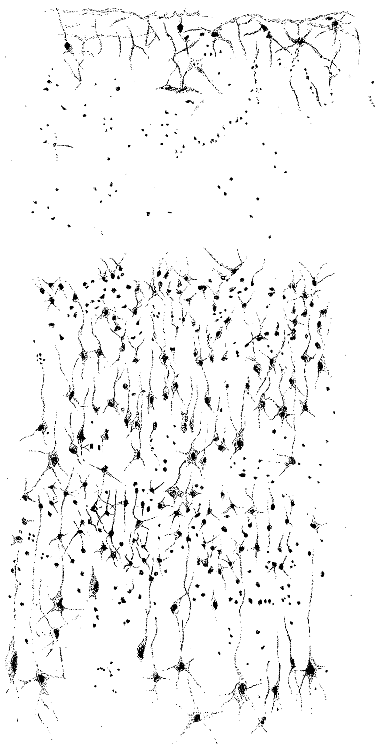


Section through Cortex Cerebri of Sheep.
From the Limbic Lobe.
x 78



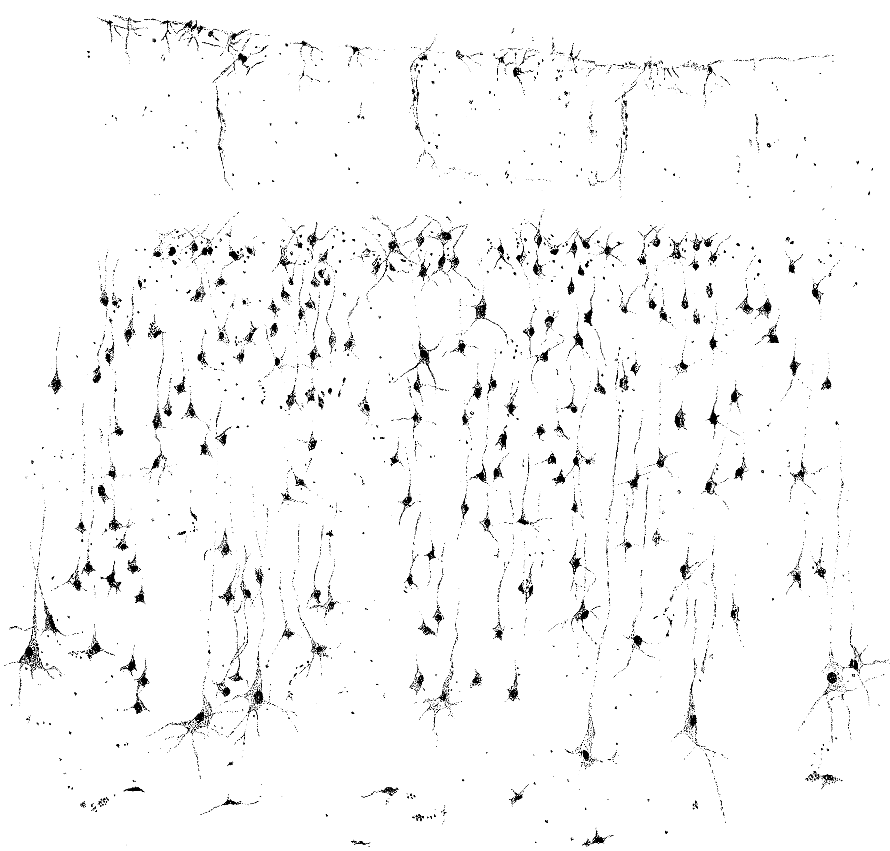
Section through Cortex Cerebri of Pig.
From the Limbic Lobe.
x 93

West, Newman & Co. sc.



From Six-laminated Cortex of Sheep.
Section carried down to fifth layer.
x 55

Ganglionic Cells as grouped in the
Limbic Lobe of the Pig.
x 270



Section through the Cortex Cerebri of Pig.
From a Sulcus in the Limbic Lobe.
x 98

West, Newman & Co. sc.