
The Hippocampus

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Phil. Trans. R. Soc. Lond. B 1893 **184**, 389-429
doi: 10.1098/rstb.1893.0006

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VI. *The Hippocampus.**By* ALEX HILL, M.D., *Master of Downing College.**Communicated by Professor* ALEXANDER MACALISTER, M.D., F.R.S.

Received May 4, 1892,—Read June 2, 1892.

[PLATES 23–25.]

NOMENCLATURE.

It is only within quite recent times that anatomists have realized that the comparisons with which they help out their descriptions of parts of the brain are likely to become fixed as the names of the parts. Even in the beginning of this century—indeed the custom has not altogether ceased even yet—they quoted the illustrations used by their predecessors, to replace them at once by new ones, if any, more apposite, occurred to them, without recognising the risk of confusion likely to arise from the multiplicity of names. There is a curious alternation between the use of the simile as an unalterable symbol and as an aid to description. In other words, we strike in quite recent anatomical strata upon stages in word-formation which are deep down in the history of other sciences.

GALEN converted illustrations into cognomens for most of the bones, muscles, and other parts of the body, but the anatomists of the 17th and 18th centuries, when writing of the parts of the brain, considered it as immaterial whether or not they used the same symbols or illustrations as their predecessors; they did not regard its terminology as in any degree fixed, and if a new illustration occurred to them which conveyed a better idea of the form of the part than any as yet current, by all means let posterity make use of it!

Thus we find the region about to be described compared to and named as:—Hippocampus, pes hippocampi, bombyx, appendix bombycinus, vermis bombycinus, baco, processus cerebri lateralis, protuberantia cylindroides, cornu arietis, cornu Ammonis; with innumerable variations in the translation of the foregoing terms into French and German:—hippocampe, corne de bélier, corne d'Ammon, Ammonshorn, Widderhorn, Reil'sche Kolbe, &c.

Nor does the confusion end with the selection of a suitable name. The limitation of the part is as uncertain as its nomenclature. Thus, we find the term “pes hippocampi” applied to the swelling within the descending horn of the lateral ventricle;

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to the anterior part of this swelling only, with a loose use of the term "hippocampus" for the swelling as a whole; to the swelling *plus* its fimbria, or *plus* its fimbria and the fascia dentata. Indeed, the use of the term as including all these parts appears to be the older: "pars longior cum proxime cruribus fornicis interjecta, cerebri medulla unitur et cum hippocampo comparata in arcum flectitur."*

If out of all the terms in use it were open to us to choose the most apposite, "cornu Ammonis" would be the one upon which our selection would fall. This is the term preferred by SCHWALBE,† although he seems to me to overlook its descriptive value when he limits it to the "halbmondförmig gekrümmter Wulst von ungefähr 50 millims. Bogenlänge, der vom Balkenwulst an zunächst dem vorderen concaven Rande des Trigonum ventriculi lateralis folgt." The peculiar applicability of the term is not appreciated until the brain is dissected away from above, as often happens, almost by accident, when the brain is semi-putrid, and the two gently curling horns exposed in their whole extent. Exclude the fimbriæ, and the illustration is almost pointless!

I should have selected the expression "cornu Ammonis" for application to the whole region had it appeared justifiable to neglect the classical expression "hippocampus or pes hippocampi"; but it appears that this name was already fixed before its likeness to the horns of the Horned-Jupiter occurred to any anatomist.

The part was first described and named by ARANTIUS‡ "hippocampi vel bombycini vermis ventriculos appellare libuit."

DIEMERBROEK, writing in 1632, attributes the name "pes hippocampi" to HIPPOCRATES, but I cannot find the reference, and the anatomists of the 17th and 18th centuries who were likely to be deeply read in HIPPOCRATES are unanimous in assigning it to ARANTIUS.

VIEUSSENS, in his 'Neurographia Universalis,' written in 1585, just before the date of ARANTIUS' work, while giving a somewhat elaborate description of the part, uses no name: "crura posteriores corporis callosi seu veri fornicis columnas nuncupamus cruribus intermediam fimbriatam veri fornicis appendicem nominamus."

CASPAR BAUHIN,§ in 1621, says: ". . . parte posteriore fulcra duo obtinet, quæ posterius deorsum reflexa velut novas cavitates constituere videntur, quas ventriculos hippocampi, ab animalis forma, posteriores denominare solent. *Pedes hippocampi nominantur ab Arantio.*"

RIDLEY,|| in 1695: "Hippocampi Arantii or bombyces."

J. and C. WENZEL¶ explain: "Processus cerebri lateralis, vulgo hippocampus ab Arantio qui processum istum primus descripsit."

* HALLER, 'Elementa physiologiæ,' lib. 10, sect. 1, 1762.

† SCHWALBE, 'Lehrbuch der Neurologie,' p. 513.

‡ 'Anatomicarum Observationes,' cap. 3, 1587.

§ 'Theatrum Anatomicum,' lib. 3, cap. 13.

|| 'Anatomy of the Brain.'

¶ 'De penitiori structura cerebri hominis et brutorum.' Tübingen, 1812.

It seems to be clear, therefore, that this region was first described by ARANTIUS, and that his comparison to the "pes equuli marini" was adopted as its name.

I have been unable to trace the origin of the term "cornu Ammonis."

MORAND* terms the region "cornes de bélier"; but, he remarks, "qu'une partie de l'embarras qui se trouve à concilier les anatomistes, vient de ce qu'ils ont donné indifféremment le nom de cornes de bélier aux ventricules et aux parties qui y sont contenues. Ce sont celles-ci qui sont vraiment les cornes de bélier ou l'hippocampus suivant ARANTIUS." The three cornua of the lateral ventricle (first called *lateral ventricle* by MORAND) were named some time later by VICQ D'AZYR; the confusion did not arise, therefore, from the application of the term "corne de bélier" to the descending horn.

GUNZ† uses the term "cornu arietis." "Quæ cornu in modum flexæ sunt, atque rotundulæ, totæque in illo pariete exstant, hippocampi, vel arietis cornua nominantur"; but the first use of the term "cornu Ammonis" which I have been able to trace is in a series of papers "On the Human Brain," laid before the French Academy by VICQ D'AZYR, in 1781. In obs. ix. (p. 518) he treats of "Les cornes d'Ammon ou hippocampes," and says that "une circonvolution recourbée en manière de crochet désigne leur situation et leur forme." From his description it would be difficult to gather his view as to their external boundary, but his figures make it quite clear that the cornu Ammonis, as he understood it, included the floor of the descending horn as well as the fascia dentata. The latter he terms "la portion crénelée ou bord dentelé de la corne d'Ammon." In his 'Vocabulaire,' VICQ D'AZYR defines: "Hippocampi, pedes hippocampi, cornua Ammonis; les protubérances médullaires recourbées qui sont situées dans la partie postérieure et inférieure des ventricules lateraux." He adds, "je distingue deux espèces d'hippocampes. Les grands . . . et les petits ou ergots dit de MORAND."

Perhaps a more thorough search through the literature of the period preceding the French revolution would reveal the origin of the term, or it may be that VICQ D'AZYR transformed "corne de bélier" into "corne d'Ammon" without thinking the change of name worth noticing. The quotation from HALLER, which is given above, is important in this connection, for HALLER, although extremely careful to give synonyms and references, says nothing about cornu Ammonis.

Vulgo "hippocampus" appears to be the established term. The "pes" may be omitted, for it has no meaning when applied to the hippocampus minor, and can hardly be retained without rendering the expression cumbersome when the subiculum (pedis) hippocampi, gyrus (pedis) hippocampi, &c. are referred to.

* 'Histoire de l'Académie,' 1744, p. 6.

† 'Prolusio observationes anatomicas de cerebro continens altera.' Leipsic, 1750.

INTERPRETATION OF THE HIPPOCAMPUS.

By all anatomists with whose works I am acquainted the whole of the hippocampus is regarded as a part of the cortex. "On doit regarder la corne d'Ammon ou grand hippocampe comme une circonvolution cérébrale d'une forme particulière," says VICQ D'AZYR; containing, that is to say, the same elements as are found in other parts of the cortex (although they are differently arranged) and no elements which are not found elsewhere. The hippocampus is always spoken of as a composite of convolutions, the only difference of opinion being as to the number of convolutions represented. Since the time when ZUCKERKANDL* pointed out that the striæ longitudinales lateralis et medialis (the stria obtecta and nervus Lancisii, as they are usually called) belong to the mesial surface of the brain, being developed from the dorsal portion of the outer arcuate convolution of ARNOLD, while the ventral portion of the same convolution becomes the fascia dentata, the problem has altered somewhat in form, but it remains essentially the same as in the days of VICQ D'AZYR. It is taken for granted that the arcuate convolutions of ARNOLD are portions of the mantle, homologous with those other parts which develop into the convolutions of the general surface of the adult brain.

In a recent memoir, HONEGGER† has most laboriously analyzed the literature of this subject, and it would therefore be unnecessary for me to go through it a second time, even if I thought that it would throw any light upon the subject of this paper. The sum of this investigation is that ZUCKERKANDL traces the stria lateralis (seu obtecta) into the fascia dentata; HONEGGER traces the stria medialis into the fascia dentata, while the lateral stria passes, he says, into the superficial layer of the gyrus hippocampi. GANSER‡ denies that the fascia dentata is continued in any way on to the dorsal surface of the corpus callosum. GIACOMINI'S views will be discussed later.

It is doubtless of great importance that these stages in the development of the margin of the porta should be traced with exactitude, but before the facts can be applied to the determination of the homology of the hippocampus certain antecedent questions must be answered, and still earlier stages in the development of ARNOLD'S convolutions must be worked out in order that we may be placed in a position to judge whether they are in any respects comparable to the convolutions of the general surface of the great brain. In particular we need to know the relation which ARNOLD'S convolutions bear to the olfactory crus and bulb. If the external stria of the olfactory tract passed into any part of the hippocampus we should have data from which to

* ZUCKERKANDL, 'Das Riechcentrum.' Stuttgart, 1887.

† HONEGGER, "Vergleichend-anatomische Untersuchungen über den Fornix und die zu ihm in Beziehung gebrachten Gebilde im Gehirn des Menschen und der Säugethiere." 'Recueil Zool. Suisse,' vol. 5, Nos. 2 and 3, pp. 201-435. December, 1890.

‡ GANSER, "Gehirn des Maulwurfes." 'Morphol. Jahrb.,' vol. 7, 1882, pp. 591-725.

speculate; but this is not the case. Although I have cut a great number of sections in all possible planes from the temporal pole of brains of various animals, I am unable to trace the ultimate connection of the external stria, but I can with confidence assert that it does not go, as HERRICK* conjectures, into the lamina nuclearis and superficial bundle of the fascia dentata. Until, therefore, something more is known as to the morphogeny and histogeny of ARNOLD'S convolutions, no light will be thrown upon the morphology of the hippocampus by the study of the relations of the several portions of these convolutions in the adult brain.

Whatever its origin, all anatomists who have written on the subject up to the present time agree in regarding the fascia dentata as a convolution, or as a part of a convolution, and as this is not the view of the writer of this paper, little would be gained by giving an account of the attempts which have been made to homologize it with other convolutions. Such theories as have been published may be classified in three groups:—(a) Fascia dentata *plus* nucleus fasciæ dentatæ constitute one convolution, the small cells of the stratum granulosum being the small pyramids of the gyrus (subiculum) hippocampi collected together in a separate cluster (HENLE, KRAUSE, MEYNERT, HUGUENIN, SCHWALBE, OBERSTEINER, &c.); (b) the fascia dentata is an independent convolution, cells of all layers being represented in its granules (DUVAL); (c) it is an independent convolution, but inverted (GOLGI, SALA).

The view last cited† would appear at the first moment to approach most nearly to my own. GOLGI says that the reflected cortex (strato grigio circonvoluto), and the fascia dentata “non devono essere considerati come due zone di un medesimo strato, ma bensì come due distinti circonvoluzioni . . . che la fascia dentata sia una dritta continuazione anzi un' espansione della lamina grigia circonvoluta.” Such embryological investigations as I have yet been able to make, lead me to believe that the inner margin of the wall of the great brain is folded into a pouch, the mesial wall of which folds back to the fimbria, and is carried into the descending horn of the ventricle as the choroid plexus. As said elsewhere, I lay very little stress upon these observations, which require to be checked by a full examination of the earliest stages in the development of this region, and I should have preferred not to mention them at all except that they confirm GOLGI and SALA'S view that the layers present a “disposizione inversa.”

Certain appearances presented by the hippocampus at its extreme anterior end are highly suggestive of the folding over of the margin of the cortex into a pouch or trough; as is also the arrangement of the small cells in this region in animals in which the fascia dentata is rudimentary or not developed at all (see figs. 2 and 7). It does not necessarily follow, however, that the margin of the general cortex (subiculum hippocampi) rolls over into the trough in the manner imagined by GOLGI. It is clear

* HERRICK, “Cerebrum of Opossum.” ‘Jl. of Comp. Neurology.’ February, 1892, p. 12.

† GOLGI, ‘Sulla fina anatomia degli organi centrali del sistema nervosa,’ pp. 80–112.

that there is one other way in which the fascia dentata might be applied to the subiculum; the nucleus fasciæ dentatæ, or rod of large pyramids, might press against the outer side of the lateral wall of the trough. The fascia dentata would, in this case, be two-layered, and either its inner or its outer wall might be developed into nervous matter. Some appearances which I have seen, have led me to suspect that the fascia dentata is covered by a layer of undeveloped cerebral tissue (ependyma), but, on the other hand, in many cases an observation of the adult tissue favours the idea that the thickened margin of the general cortex has rolled over into the trough of fascia dentata. It is a question which can only be settled by ontological investigations.

SALA* represents the fascia dentata as containing rounded cells, 10 to 20 μ broad by 15 to 30 μ long, which give an abundantly branched process towards the periphery, after the manner of PURKINJE's cells in the cerebellum. The nerve-network formed by the nervous process of the cells (which belong to GOLGI's Types 1 and 2) is in apposition with the nerve-network formed by the processes of the large pyramids of the nucleus fasciæ dentatæ. The small and large pyramids are therefore placed, as it were, back to back. As in many other cases in which portions of the brain are described and figured after the manner initiated by GOLGI, it is quite impossible to know how to harmonize or compare the descriptions with other observations. The beautiful pictures which accompany SALA's description show a single sheet of black cells, placed at considerable intervals apart, and each provided with an elaborately branched black peripheral process, and a single red central process which breaks up into an open network. The protoplasmic process unites with the processes of neuroglial cells. These pictures are, of course, drawn from mercury and silver impregnations. Prepared in any other way, the fascia dentata appears as a layer of "granules" close set in three or four rows, and mixed with a certain number of small fusiform or pyramidal cells (see fig. 1).

I agree, therefore, with GOLGI and SALA in looking upon the fascia dentata as a peculiarly-folded portion of the wall of the fore-brain, independent of the nucleus fasciæ dentatæ in its origin, and I am not disinclined to believe from such imperfect observations as I have been able to make into its mode of origin, that the layers may be inverted. We are not at present in a position to state, however, that an embryological inversion would permanently result in the projection of the processes of the neuroblasts in opposite directions.

I am absolutely opposed, however, to the writers just named, and, indeed, to all anatomists with whose works I am acquainted, in their attempt to homologize the elements found in the fascia dentata with those found in other parts of the cortex; or in other words to prove that the fascia dentata is a convolution comparable with

* SALA, 'Zeitschrift f. wiss. Zool.,' vol. 52, 1, pp. 18-46.

other convolutions of the general cortex. *Firstly*, because in structure it does not appear to me to resemble the general cortex, and, *secondly*, because it does not behave like a convolution. For example, it does not vary in its development with the convolutions of the general surface. In perfectly smooth brains, the fascia dentata is as large, or proportionally larger, than in convoluted brains. As I have pointed out in my paper on the brain of *Ornithorhynchus*,* the brain may be absolutely destitute of convolution, and yet the rhinencephalon be cut off from the general surface with unusual distinctness and the fascia dentata exceedingly broad. In the *Ornithorhynchus*, the fascia dentata lies wholly in the dorsal half of the cerebral hemisphere. It joins the pyriform lobe or rhinencephalon at the back of the porta. It is also interesting to notice that, since in this animal there is no corpus callosum, nothing has happened to destroy the external arcuate convolutions.

If it could be proved that the stria longitudinalis lateralis passes anteriorly into true cortex as the gyrus geniculi, and posteriorly into the fascia dentata, a strong argument in favour of the latter being a convolution would be advanced, but the manner in which the fascia dentata terminates beneath the middle of the corpus callosum in strongly osmotic brains, such as that of the Ox, have led me to doubt the validity of this description, and the views held by VICQ D'AZYR (?), A. RETZIUS, ZUCKERKANDL, HONEGGER, GIACOMINI, *et al.* I fail to see any indication of the return of the fascia dentata to the under side of the splenium, in order that it may round the splenium and sweep forward in the nervus Lancisii in the manner required by the theory.

To label the fascia dentata, gyrus uncinatus, as is sometimes done,† appears to me a gratuitous assumption which does not in the least facilitate the comprehension of the subject. Its development bears no relation to that of the gyrus uncinatus, as can be seen at a glance in the brain of *Monodon monoceros*, in which the uncus and gyrus uncinatus (*seu hippocampi*) are particularly well developed, while the fascia dentata is absent.

A mystery surrounds the fascia dentata, which is not removed by attempts to homologize its several layers with those found in other parts of the cortex, and it would not serve my purpose to give in this paper a synopsis of the tables of homologies which have been drawn up by SCHWALBE, OBERSTEINER, GOLGI, and others. For purposes of comparison, it may be well, however, to give an account of the view generally held, as expressed, for example, by SCHWALBE, before appending a summary of my own.

SCHWALBE speaks of the fascia dentata as the remains of the gyrus arcuatus Arnoldi: “. . . der rudimentäre hintere untere Theil des Randbogens, der zwischen

* HILL, 'Phil. Trans.,' 1893, p. 367.

† Cf. HERRICK, "Brain of Opossum," *loc. cit.*, figs. 4, 10, &c.

Fimbria und Subiculum cornu Ammonis gewissermassen eingefalzt ist und einen eigenthümlich gekerbten grauen Rand besitzt, als Fascia dentata Tarini."

He treats it as a part of the cortex, and gives a table to show the homology of the constituents of convolutions in general, the subiculum, the cornu Ammonis, and the fascia dentata. In this table the several constituents of the typical cortex are found in the fascia dentata by homologizing the fimbria and alveus with the medullary substance, the pyramids of the nucleus fasciæ dentatæ with the large pyramids, and the stratum granulosum with the layer of small pyramids.

It is easy to follow SCHWALBE in his distinction between the fascia dentata and the "cornu Ammonis," but very difficult to see where he can draw a boundary-line between the latter and the subiculum.

The writer's view of the relation of the hippocampus to the general cortex is entirely different, as he briefly pointed out in his translation of OBERSTEINER'S "Nervöse Centralorgane."* The fascia dentata cannot, he thinks, be homologized with any layer which is to be found in the cortex elsewhere. Instead of the fascia dentata being part of the layer of small pyramids—(1) it consists, as already pointed out, of "granules," and a much smaller number of pyramidal or fusiform cells; (2) it does not shade off into the cortex, but has a pronounced border on either side of the folded strip. Its upper border encloses in some situations a portion of the fimbria instead of its being everywhere (as it would be were it a portion of the general cortex) placed beneath the fimbria; (3) the nucleus fasciæ dentatæ is not the homologue of the layer of large pyramids, but of the whole cortex. As the hippocampus is approached through the subiculum, the many ranks of pyramidal cells arrange themselves in single file, the sheet thus formed enters the hilum fasciæ dentatæ, and, when within the fascia dentata, the pyramidal cells, which are not of exactly the same form or size as those in either of the layers of the cortex, form-up into an irregular crowd.

In certain sections of embryonic brains the cells of the nucleus fasciæ dentatæ are seen to belong to the series of the small pyramids, with which the large pyramids level-up from behind, as it were, and not with the large pyramids—so far as it is justifiable to describe these as forming a separate layer.

In early embryonic brains the thin mesial wall of the lateral ventricle is seen to be doubly folded. The portion of the **S**-fold which is convex towards the ventricle is the subiculum hippocampi, the deep concave part the fascia dentata; but a description of the way in which these structures are formed from these folds, and of how it comes about that they interlock, must be reserved until the matter has been more fully investigated.

The nucleus fasciæ dentatæ must, as I think, be regarded as the edge of the mantle

* 'The Anatomy of the Central Nervous Organs,' by OBERSTEINER and HILL, p. 362, *et. seq.*

proper; the fascia dentata as a sheath, into which this edge is received. In this sense the fascia dentata is a band of grey matter added to the cortex around a portion of its margin. It is useful to make a distinction between the cortex and the fascia dentata for descriptive purposes, albeit it is quite understood that both alike are developments from the wall of the fore-brain. I purposely use the expression "fore-brain," without the qualification "primary" or "secondary," since there are questions with regard to the development of this region which need, as it seems to me, further investigation.

THE HIPPOCAMPUS OF THE OX.

I do not propose in this paper to give an elaborate account of the minute anatomy of the well-developed hippocampus, nor could I do so with advantage without a large number of illustrations. Before, however, describing the hippocampus, or rather the want of hippocampus, in marine Mammalia, it is necessary to call attention to certain points in the structure of a well-developed hippocampus, and it is desirable that the animal selected should be as nearly related to the Cetacea as may be, and that its brain should be of large size. It seemed to me, therefore, that I could not do better than select for my standard of comparison, the brain of the Ox.

In the Ox the outer margin of the slit through which the velum interpositum enters the lateral ventricle is folded over into the structure known as the hippocampus, of which the fimbria and fascia dentata are best regarded as parts. Commencing on the inner side of the temporo-sphenoidal lobe it passes backwards and upwards to the under side of the corpus callosum, which it joins some little distance in front of the splenium. It lies in contact with the corpus callosum to about its centre, when the folding over ends rather abruptly, by a rapid diminution in the extent of the folding, that is to say, the fimbriæ are then for a short distance separated from the corpus callosum by a small amount of grey matter only, after which, as the anterior pillars of the fornix, they sweep downwards along the back of the septum pellucidum.

Except for a distance of about 3 millims. the fimbriæ are separated from the corpus callosum by a considerable interval.

There are no posterior pillars of the fornix in the sense of pillars which intervene between the body of the fornix in contact with the corpus callosum, and the fimbriæ hippocampi.

The hippocampus presents no digitations at its inferior end similar to those which mark the floor of the descending horn of the lateral ventricle in the Human brain, and from which the comparison with the foot of the Seahorse was derived.

The hippocampus can only be described as a folding over of the cortex about the

dentary fissure; its extreme edge ending in the fascia dentata Tarini, and its upper or convex surface bearing the fimbria, which gradually increases in thickness from its commencement at the apex of the ventricular slit.

A typical section through the *middle of the hippocampus* in the Ox has the following characters:—

As the cortex approaches the dentary fissure the arrangement of its cells is changed. If the section is really carried through the middle of the hippocampus, *i.e.*, near the splenium corporis callosi, where the caudex of the rhinencephalon is narrow, the change in arrangement commences at the ectorhinal (collateral) fissure. If it happened that the section was carried through the pyriform lobe a special description of the arrangement of the pyramidal cells would be necessary. On the outer or under side of the ectorhinal fissure, the molecular layer has a uniform thickness of $\cdot 4$ millim., the pyramids are arranged, as everywhere else in the cortex, according to size, the largest being the farthest from the surface, but in a section taken from behind the pyriform lobe, it is sufficient to state that the cortex has its ordinary appearance.

In the gyrus hippocampi (*seu uncinatus* in the wider use of the term) the cells instead of forming a number of layers are pressed together into a sheet some two or three cells thick. The cortex falls rapidly outwards towards the lateral ventricle, from which it is separated by the thin sheet of white fibres known as the alveus. At the summit of the great curve upon which the fimbria rests, the cells are truly pressed into a single layer. Sweeping down for a short distance beyond the fimbria, the sheet of cells enters the hilum of the fascia dentata. As soon as this is entered the single layer gives place to a crowd of cells disposed with great irregularity, but still in most sections showing a tendency to concentration on its upper side (the concavity of the curve). Certain peculiarities in the form of the cells will be mentioned presently.

Where the cortex begins to fall back towards the ventricle its molecular layer is greatly increased in thickness, from $\cdot 4$ millim. to $1\cdot 4$ millim. It is not, however, increased in amount relatively to the superficial expansion of the layer of large cells, since it occupies the inside of a sharp curve. The molecular layer can hardly be said to enter the hilum fasciæ dentatæ.

The number of white fibres on the surface of the molecular layer also undergoes a considerable increase, the fibres lying tangentially for the most part and marking the boundary between the molecular layer of the cortex and the molecular layer of the fascia dentata, where these would otherwise be in contact beneath the bottom of the dentary fissure. Blood-vessels which enter from the bottom of this fissure also limit the two regions in certain sections. The names which have been applied to these several layers do not, as it appears to me, aid the description, but rather introduce a source of confusion by suggesting differences in kind, where there is only a change in

the arrangement of the elements which make up the cortex in the subiculum hippocampi and other parts.

The only essential alteration consists in the disposition of the pyramidal cells in a thin sheet. Between the bases of these cells and the ventricle lie the usual fusiform cells (stratum oriens) very few in number, the medullary substance (alveus), and ependyma. On the concave or mesial side of the curve lie the apical processes of the pyramids (stratum radiatum); the usual molecular layer, very thick, as already mentioned (stratum moleculare—I can see no object whatever in distinguishing the deeper part of it as stratum lacunosum); a sheet of white fibres such as are found elsewhere in the molecular layer, although not, perhaps, in such numbers; and then, as far as the bottom of the dentary fissure, the pia mater or surface-ependyma, from the cells of which remarkably coarse processes radiate into the substance of the cortex.

The fascia dentata I can only regard and describe as something superadded to the reflected cortex. It may, of course, be objected that, if the fascia dentata is a portion of the wall of the fore-brain, it is, *ipso facto*, a portion of the cortex, but this is a very unworkable definition of the term “cortex.” It is far better to limit the name “cortex” to all such parts of the grey matter on the surface of the cerebral hemispheres as have a certain typical structure.

Portions of the wall of the fore-brain remain as “ependyma,” other parts acquire the typical cortex structure, while still another part becomes the fascia dentata. The fascia dentata is a strip of tissue into which the thickened edge of the cortex is received. It is almost uniform in thickness and constitution. Its borders are well defined, and show no tendency to shade off into the superficial layers of the cortex. If it could be stripped off from the border of the reflected cortex, it would be found to be a riband of uniform width and thickness; in the Ox about 9 millims. wide by 50 millims. long. Proceeding from the nucleus fasciæ dentatæ outwards it consists of the following layers:—(1.) The stratum granulosum which appears in most preparations as a sheet of nuclei some three or four deep, lying in clear spaces. The greater number of these nuclei belong to “granules.” The sheet of nuclei comes quite to the surface on the mesial side. On the outer side it ends abruptly, and is in certain situations most clearly marked off from the adjacent molecular layer of the cortex by the fibres which occur in the superficial layer of the latter. (2.) The molecular layer has a thickness of .4 millim. in its centre, but increases in thickness from its mesial to its outer border, and presents, so far as one can see, much the same constitution as in other parts of the cortex, unless it is, as I am inclined to think, somewhat more dense in texture. It is covered by (3.) the pia mater. Beneath the pia mater a few medullated fibres are to be seen running tangentially (stratum marginale).

Fig. 1 was taken from a portion of the fascia dentata of the calf from near the anterior end. The brain was hardened in warm bichromate of ammonia ($2\frac{1}{2}$ per cent.), well washed out in 30 per cent., 50 per cent., 75 per cent. alcohol., stained in carmine-

alum *en bloc* (the excess of carmine being washed out in 30 per cent. alcohol), the tissue embedded in celloidin and cut frozen in gum. Sections were then stained with WEIGERT's hæmatoxylin method. The previous staining in carmine-alum causes the cells and their processes to take a black or grey coloration. It is a modification of WEIGERT's method which I introduced six years ago, and have since used almost invariably in my own work.

It may not be out of place perhaps to call the attention of histologists to the importance of stating how the tissue has been hardened before giving measurements of cells. Great confusion arises in the case of the central nervous system from want of information on this point, since we are often dependent upon accurate measurements of size for the only differentia between cells. Measurements are only comparable when taken from specimens of brains not only hardened in precisely similar ways, but of exactly equal freshness at the commencement of the process. In sections stained according to the manner just described the blood corpuscles are dark and regular in outline, and may serve, therefore, as a test of the amount of shrinkage which the tissue has undergone.

The blood-capillaries are numerous in the fascia dentata. They traverse it vertically or obliquely. The corpuscles in this specimen have an average diameter of 4μ , *i.e.*, about half their size when living.

In examining the fascia dentata we have to look to the nuclei for information concerning the nature of the cells of which it is made up. The section stained as above described shows, in addition to blood corpuscles, four forms of nucleus.

1. Nuclei exactly similar to those found throughout all parts of the brain, 3.6μ in diameter, round, darkly-staining. These are the nuclei of neuroglia cells. They are often seen to occupy the centre of a clear space, which indicates that the ground substance has shrunk away from them. It is important to bear this in mind when examining the granules, as otherwise one might be tempted to believe that the granules, which also occupy clear spaces, are surrounded during life by cell-bodies of exceedingly soft and deliquescent protoplasm which disappears in the hardening process.

2. Dark round or oval nuclei, 7 or 8μ in diameter.

3. Clear dark-bordered nuclei 7, 8, or, in some cases (when oval) 12 or 13μ diameter, with conspicuous nucleoli.

The differences between these two kinds of nuclei have exercised me for a long time past, not only when examining the fascia dentata, but in the cerebellum and elsewhere, but I am inclined to think that the marked contrast in appearance depends upon a different behaviour towards the staining-reagent, which again depends upon the age or state of activity of the nucleus. It will be noticed that a large number of the clear nuclei in this specimen, which was taken, as already stated, from a young animal, are in the act of dividing. I am inclined to think that we may safely conclude that the dark and clear nuclei both belong to granules, but that the former are in a

resting condition, while the latter are either about to undergo or have recently undergone division.

4. Oval or triangular nuclei of 10 or 11 μ in long diameter. They are surrounded by cell-bodies, 18 to 20 μ in long diameter, and resemble very closely the small pyramids of the cortex. Measurements of a considerable number of these cells, as well as of small pyramids seen in the cortex in this section, give their nuclei an advantage in length of 1.5 μ , as compared with the small cortical pyramids; their cell-bodies are also slightly wider and shorter, but I do not think that any conclusions can be drawn from such trifling differences.

Occasionally a much larger pyramid, wide and blunt in form, is to be found in the fascia dentata. Only one such is exposed in the section under description. It measures 22.2 μ by 18.5 μ . It appears to be a displaced cell of the nucleus fasciæ dentatæ.

The ground substance of the fascia dentata constitutes an open network. The method of staining adopted, resolves it, as it does other parts of the cortex, into a soft brown substance, containing blue dots and dashes. I am not prepared, in this paper, to enter into the meaning of this appearance, but will merely point out that within the fascia dentata the brown substance contains more of the indescribably delicate blue tissue than it does elsewhere, and the latter has, in a certain degree, the appearance of lines disposed vertically to the layer.

The Nucleus Fasciæ Dentatæ.

As the sheet of pyramidal cells turns over beneath the fimbria, a notable alteration in the shape of the cells is apparent. In the middle of the subiculum the cells are rather smaller than elsewhere. In its upper part they are long pyramids 14 μ in transverse diameter. As the fimbria is passed they become equilateral or irregular and stellate, with a diameter of 18 or 19 μ .

It becomes in consequence difficult to say in which direction their apical processes, if they have any, point. The longer axis of the most superficial cells is, except at the apex of the nucleus, usually placed tangentially to the fascia dentata.

The nuclei of neuroglial cells are scattered over the section in about the same number as in other parts of the cortex. Of other nerve cells there appear to be none.

The ground substance is very transparent and uniform, and embeds a remarkably rich plexus of nerve fibres, which cross one another in all directions. Between the nucleus fasciæ dentatæ and the fascia dentata a large number of delicate fibres are disposed parallel with the surface.

Termination of the Hippocampus at its Anterior End.

As it approaches the temporal pole the hippocampal formation, considered as a whole, curves inwards towards the median line. It is not sufficient therefore to cut sections in a coronal plane, but the sections must, if they are to be comparable, be gradually inclined forwards on the outer side until they cut the coronal plane at an angle of about 45° . Misleading results have been obtained by continuing to cut the Human hippocampus coronally right up to its anterior end. A section of the "claw" ("digitationen") is obtained in this way. Although it expands in front its true anterior end lies on the surface of the brain and not within the ventricle.

My sections through the anterior end of the hippocampus of the Ox follow one another at varying intervals until the region in which the hippocampus terminates is nearly reached, and then I retain all the sections until the region is passed.

In the way in which the hippocampus progressively decreases in size I can recognize no point which calls for particular comment. Until it is very small it presents all the usual features which mark the folding over of the cortex and its ensheathing in fascia dentata. The mesial and lateral limbs of the fascia dentata are about equal in length. The mesial portion of the granular layer cuts the surface. The layer of pyramidal cells is disposed in the usual manner and shows no indication of a fusion with the fascia dentata.

The hippocampal formation is continued beyond the extremity of the descending horn. It is marked off from the general surface of the temporal lobe by a groove; the continuation forwards of the dentary fissure or the fissure about which the uncinata convolution (of microsmatic animals) curves over into its uncus. This groove is to be seen on the mesial surface of the pyriform lobe for a short distance in front of the termination of the hippocampus. In it lie some small blood-vessels.

At its extreme anterior end the fascia dentata is continued up the mesial surface of the pyriform lobe for about twice as far as it is a millimetre farther back. It loses its outer limb and is, as it were, **DISPOSED FLAT ON THE SURFACE INSTEAD OF BEING DOUBLED UPON ITSELF** around the pyramidal cell-layer. The layer of pyramidal cells is no longer folded upon itself, and it and the fascia dentata fuse at their dorsal borders, and are continued up the surface as a very indefinite sheet of small cells, larger than those of the fascia dentata but small for pyramids. The cells are also rather fusiform than pyramidal, with their long axes disposed tangentially upwards and downwards.

It is to be remembered that we are now in the region of the nucleus amygdaleus which occupies the anterior end of the rhinencephalon, filling up its temporal extremity (the natiform protuberance) and running forward beneath the frontal region as the pyriform lobe, or crus, of the olfactory bulb.

Termination of the Hippocampus behind or above.

In the Ox the folding-over of the margin which forms the hippocampus extends about half the length of the corpus callosum on its under surface, and then comes to an end somewhat abruptly 3 millims. to 4 millims. before the anterior pillars of the fornix leave the under surface of the corpus callosum. The splenium corporis callosi extends for some distance behind the hippocampus, the interval between the two being occupied by a bulging or tubercle of the gyrus fornicatus (callosal convolution).

A section through the posterior part of the corpus callosum shows the fimbria borne at some distance from the corpus callosum on the surface of the reflected cortex. The alveus is very extensive. Its white fibres sweep outwards and upwards to join the corpus callosum, as well as downwards into the fimbria; about the same number of fibres going apparently in each direction.

The fascia dentata is shaped like an arrow-head, as seen in section, its hilum is comparatively narrow, its nucleus well-developed, the large nerve-cells being uniformly distributed. A thin sheet of fibres separates it from the surface of the subiculum.

The strata granulosum et moleculare end abruptly at the margin of the fimbria, which is, of course, of great size (8 millims. high by 4 millims. wide at its base, as seen in section) in this region. A number of scattered bundles of longitudinal fibres are found inside the sheath of fascia dentata, beneath its upper or mesial limb.

The cells of the nucleus fasciæ dentatæ are considerably larger than any of the pyramids to be found in the cortex of the subiculum. They have an average diameter in the hardened tissue of about 40 μ , and are almost as broad as they are long: whereas the largest cells of the cortex of the subiculum at this level are not more than 12-14 μ in transverse diameter.

The stratum granulosum in this region contains about one pyramidal cell (diameter 8 or 9 μ) to ten granules, only the diameter of the nuclei of the latter can be determined, since their cell bodies are never so distinctly visible as to be clearly defined from their neighbours.

The folding over of the cortex ceases abruptly at the spot indicated, the outer edges of the two folds making an angle of 60° with one another. At neither end, therefore, does the hippocampus show a gradual transition from the general cortex of the brain. Allowing for the shortest distance necessary, so to speak, in ending the fold, the hippocampal formation is well and comparatively evenly developed in its whole extent.

HYPEROODON ROSTRATUS. (Figs. 2, 7, 8.)

I have for some time been acquainted with the peculiarities of the hippocampus in the brains of aquatic Mammals as illustrated by the Porpoise; on which subject I read a paper at the meeting of the British Association, in Manchester, in 1887. The Porpoise, however, has a rudimentary hippocampus, and my investigations would have been incomplete and conclusions uncertain, had not Mr. ROBERT GRAY, of Edinburgh University and Aberdeen, brought me from the Arctic regions five brains of *Hyperoodon* and two brains of *Monodon* in a capital condition, not only for macroscopical, but also for microscopical study. To take out the brain of the Whale and to detach from it the hippocampus are tasks requiring a very considerable knowledge of its anatomy, and I am deeply in Mr. GRAY'S debt for bringing me specimens, removed without injury and so admirably preserved, as to allow of the use of WEIGERT'S staining-method.

Certain peculiarities in the general form of the Cetacean brain as well as in the topography of its hippocampal regions need to be explained before an effective comparison can be made between this absolutely anosmatic and an ordinary osmatic brain.

The Cetacean brain is, as has so often been remarked, extremely convoluted, its fissures being of great depth. This renders the orientation of the brain difficult at first, but a very little study enables one to distinguish the primary and secondary from the tertiary fissures.

A still more remarkable peculiarity of the Cetacean brain is its wide departure in general form from the ordinary type.

The shape of the brain of my three uncut specimens is in each case distorted by the pressure of the muslin in which, as in pudding bags, they were suspended in a tub of spirits. The result was at first sight most perplexing, the whole brain being a blunt cone, its base completely hidden out of view by the orbital region, so that the medulla oblongata seemed to enter the base of the cone between the cerebellum and the frontal region of the cerebral hemispheres. The measurements of the cerebrum were in one specimen: Height, $7\frac{1}{2}$ inches; length, $5\frac{3}{4}$ inches; transverse diameter, $8\frac{3}{4}$ inches.

Unlike any osmatic brain, the length of the Cetacean brain would appear from this specimen to be less than either its height or its width.

When I compared my specimens with the plates in KÜKENTHAL'S 'Walthiere'* I felt convinced that exquisitely as KÜKENTHAL has figured the brain in this sumptuous monograph, he has doubted the possibility of so wide a departure from the ordinary

* 'Vergleichend-anatomische und entwickelungschichtliche Untersuchungen an Walthieren,' von Dr. WILLY KÜKENTHAL. Jena, 1889.

Mammalian type, and has conventionalized the brain by somewhat flattening it down and opening it out. With a view to determining its natural form I prepared casts from the interior of two skulls in the Cambridge Museum, of one of which fig. 8 is a photo-lithograph.

The extreme measurements of this cast are: Length, 183 millims.; height, 160 millims.; transverse diameter, 266 millims.

It shows that the brain has the form of a truncated cone, the apex of the cone being directed upwards and but slightly backwards. Its peculiarity in shape has been considerably exaggerated in my spirit-hardened brains.

Inside the skull-case the cerebro-spinal axis presents the ordinary **S** curvature, but in an unusually marked degree. From the foramen magnum to the pons Varolii the medulla oblongata is directed ventralwards. The plane of the base of the brain, as a whole, makes an angle of 160° with the chief axis of the skull. The long axis of the cerebral cone is vertical to its base.

This is the form of the anosmatic brain exhibited in the highest degree, and is clearly due to two causes (1) the absence of the portion of the brain connected with the olfactory sense, and (2) the closing up of surrounding parts which have not this olfactory portion to displace and support them.

In the long brain of an osmatic animal, as is well seen in the Ox, although it is, of course, still more obvious in the brain of a Carnivore, the convoluted portion of the hemisphere is spread out, as it were, upon the unconvoluted, or almost unconvoluted, rhinencephalon. In the Human brain the rhinencephalon is reduced in size to the comparatively insignificant hippocampo-uncinate convolution. The Seal closely resembles Man, as will be pointed out subsequently, in the reduction of its olfactory brain. Every gradation between the Dog and the Whale, as regards the relative development of the olfactory brain, is to be found in the Mammalian class, and allowing for the total size of the brain, its size relative to the cross-section of the medulla, and other circumstances which have yet to be discovered, it is probable that the relation of breadth to height to length, or, as it might be expressed, the mean of the length-breadth and length-height indices of the brain would give a fairly accurate numerical expression for the development of olfaction in different species of animals.

It must not be supposed, however, that the only parts of the brain unrepresented in anosmatic animals are the rhinencephala. As I have attempted to show elsewhere,* the brain, in its general sense, is a formation of grey matter secondary to the grey matter of the axis or grey matter bordering the central canal. The "peripheral grey tube," as I termed it to distinguish it from the "central grey tube" which contains the primary centres of peripheral nerves, is disposed about the axis, and the loss of a cerebral nerve means the curtailment of both tubes as well as of all intra-cerebral

* 'Plan of the Central Nervous System.' Cambridge, 1885.

connections between the missing parts of the two tubes. The short brain of the Whale is not only devoid of rhinencephalon, but its central grey matter also is shortened; the intervening white matter is absent; the great brain is reduced from an apparatus connected with five senses to an apparatus in which four only are represented, the missing sense being the one which in macrosmatic animals (Carnivora especially) demands the largest share in cerebral organization.

I am not prepared, in this paper, to consider what other parts of the brain are absent in the anosmatic Whale; it is a large subject, which demands extensive and accurate investigation. It is, perhaps, worth while to point out, however, that there is great risk of error in concluding that parts absent in certain brains are directly connected in those animals in which they occur with the missing sensory apparatus; take the anterior commissure as an example.

The anterior commissure is present in the Whale, although extremely thin. It does not, however, follow from this that the anterior commissure is a chiasm between the olfactory nerves or tracts. Its enormous size in Monotremes and Marsupials precludes the possibility of this as a complete explanation of its function. The anterior commissure is certainly the commissure between the temporo-sphenoidal lobes, whatever other sets of fibres it may contain. The sense of smell has its cerebral representation in these lobes.

In the Whale, the temporo-sphenoidal lobes are reduced to a minimal size, and their commissure is correspondingly deficient.

The extreme retraction of the temporo-sphenoidal lobe produces an alteration in the disposition of the parts of the brain, which must be thoroughly understood before an attempt is made to cut a series of sections through the hippocampus which will be comparable with the series cut through this region in the brain of the Ox. The posterior limb of the fissure of Sylvius, instead of sloping upwards and backwards, as in other Mammals, passes almost directly upwards towards the apex of the conical brain. This is due to the fact that the temporo-sphenoidal lobe reaches so short a distance forwards on the basal aspect of the brain that the frontal lobe is allowed to roll round, as it were, into the place on the basal aspect usually occupied by the temporo-sphenoidal lobe. The posterior pillar of the fornix, and its continuation the fimbria, are continued in a very open curve backwards and downwards without any tendency to return. If, therefore, a section of the hippocampal region is to be compared with a coronal section of the brain of a Sheep or Dog, it must be made in a plane extending backwards almost horizontally with regard to the plane of the corpus callosum.

The body of the fornix and its posterior pillar are adherent to the under surface of the corpus callosum. In the middle part of its course it can be detached, for its fibres are here collected into a compact bundle placed at right angles to those of the corpus callosum. At its posterior part the fibres evidently spread out in a fan on the under

surface of the corpus callosum, and the posterior pillar is marked by a groove on either edge, but is otherwise quite indistinguishable from the fan of fibres upon which it rests. If it be compared in this respect with the brain of the Ox already described, the extreme importance of this feature will be at once recognized; for in the Ox no part of the fornix is really in contact with the corpus callosum. As the hippocampus is approached, the rounded inner margin of the forceps posterior crosses the posterior pillar of the fornix very obliquely, passing into the substance of the hemisphere on its outer side.

The length of the hippocampal region is inconsiderable. In a large brain, weighing (in spirit) 1904 grms., in which the longitudinal distance from the genu to the splenium was 36 millims., and the length of the posterior pillar of the fornix (or rather the structure which would be the posterior pillar in an osmatic brain), from the point at which it diverged from its fellow to the attached portion of the fimbria, was 52 millims., the length of the fimbria properly so called—that is to say, of the portion of the fornix which adhered to the hippocampal convolution—was only 11·5 millims. Indeed, this measurement is considerably in excess of the length of the real hippocampal region. The posterior pillar of the fornix never leaves the under surface of the corpus callosum, but adheres closely to its posterior wing or tapetum. Instead of forming, for a considerable part of its course, an independent rounded column, it consists merely of fibres, not very obviously collected into a bundle, which, having begun to diverge from the middle line at some distance in front of the posterior border of the corpus callosum, pursues a long oblique course before it gains the margin of the forceps posterior. The length of the folded portion of the edge of the cortex, the hippocampus properly so called, and therefore the region in which alone the posterior pillar should be named the fimbria, did not exceed 9 millims. Of the exact measurement I am doubtful, for two reasons: *firstly*, as will be explained later on, it is very difficult to determine the exact point at which the cortex ceases to fold over upon itself; and, *secondly*, the measurements depend upon the estimated thickness of the sections. It may, however, be taken as certain, that the length of the border of the cortex which is folded over in the manner which marks the cornu Ammonis, and carries the fimbria, is at the outside 10 millims. Closer measurement is not necessary for purposes of comparison, for, if we compare the dimensions of the region in the anosmatic Cetacean brain with its dimensions in a megosmatic brain, such as that of the Ox, we find the most striking difference. In an Ox brain weighing (in spirit) 315 grms., the length of the cornu Ammonis, properly so called, was 50 millims.

Hippocampus of Hyperoodon rostratus.

Series of sections of this region were made from two separate brains. The second was the more satisfactory and therefore the sections from this series need alone be described. It was not convenient and did not happen to be necessary to make a complete series. The region was however divided into nine blocks, and from each of these a number of sections were taken (*a*) from the front, (*b*) from the middle, (*c*) from the back of the block. It yielded therefore twenty-seven sets of sections by which it may be said to have been completely explored. Some sections from each set were stained in carmine, and others in carmine and subsequently by WEIGERT'S method. Of the WEIGERT-sections some were bleached in ferridcyanide of potassium and others in permanganate of potassium.

The hippocampal convolution commences with a sharp point which is deeply buried in a fissure between the flat posterior pillars of the fornix and the convolution which lies on the mesial side of the collateral fissure. To use any terms other than gyrus hippocampi (or uncinatus) and collateral fissure appears to me pedantic. Although the sense of smell is moderately present in Man, its development is so small as compared with the prominence of the same sense in most other animals that his microsmatic brain approaches in form the anosmatic brain of the whale so closely as to leave no possible doubt as to the homologies of these parts. There is no doubt in my mind as to the homology of the ectorrhinal fissure of the Dog with the collateral fissure of Man, and consequently of the pyriform lobe and natiform protuberance of the Dog with the uncinatus gyrus (or hippocampal gyrus plus the uncus) of Man, but a very large series of brains is needed to help one to realize such an extreme variation in development of corresponding parts.

From its position at the bottom of a deep recess the gyrus hippocampi gradually emerges on to the surface and at the same time steadily increases in width; or in other words the fimbria (posterior pillar of the fornix) inclines outwards into the descending horn of the lateral ventricle. In sections from block 8 the fimbria appears as a broad flat strap constricted in the middle like a Naples biscuit. In section 6 the outer limb of the biscuit is much narrower, the hippocampal convolution reaches as far outwards as the under side of the bay between the two limbs. The ependymal wall of the ventricle is attached to the lateral border of the outer limb so that the whole of the fimbria is outside the ventricle. The two rounded ends of the biscuit give place to ridges triangular in section, the mesial ridge being the first to appear. In block 4 (fig. 2) the gyrus hippocampi lies entirely on the mesial surface, the inner ridge is raised on to the top of its convexity; the outer ridge carries the ependymal wall on its apex. In block 3 the mesial ridge has disappeared, the ependymal ridge is small; in block 2 the fimbria is completely lost, no ridge marks

the attachment of the ependymal wall. At its first appearance in block 8 the gyrus hippocampi is simply the edge of the cortex.

As the gyrus grows, traces of the reflection of the edge of the cortex down its surface are seen, but so extremely indistinct is this reflected portion that it is made out with great difficulty. It consists only of small triangular cells sparsely scattered in a single layer upon the surface of the molecular layer. The sheet reaches almost down to the collateral fissure. A little farther forward a slight condensation of the molecular substance is visible, and it is seen that the boundaries of this area are marked both outside, inside, and below by scattered small pyramidal cells. By block 5 we have therefore the vestiges of a fascia dentata, but so extremely indistinct is this formation that it was only after long searching that I discovered the existence of any differentiation whatever within what seemed at first to be the molecular layer of the hippocampal gyrus. It is not till we reach the front of block 4 that we come across any definite trace of the layer which is in osmatic animals the fascia dentata. In this block the layer begins to ascend the hippocampal gyrus so as to leave a space between its inferior border and the collateral fissure. Its inferior border is in 4A received into a cup of ependyma.

So delicate are these transitions that one would like to reproduce a section from both blocks, but it is as well perhaps, since the number of figures must be limited, to reproduce a section from near the back of block 4, from the region that is to say which lies immediately behind the more definite vestige of a fascia dentata.

4B (fig. 2) is the most posterior of the sections taken from near the middle of this block 4.

While in this section the folding over of the surface is very indistinct, in the sections immediately in front of it the rudimentary hippocampus, or, rather, the part of the cortex which would be hippocampus if ensheathed by fascia dentata, is as strongly developed as anywhere in the Whale's brain.

It shows the mesial wall of the ventricle from the collateral fissure up to the ventricular slit.

The fimbria is divided into two ridges, separated by a groove. To the summit of the outer ridge is attached the ependyma-wall of the ventricle, which is involuted to support the choroid plexus.

The ventricle is lined by a very thick ependyma, and a similar layer of epithelium covers the surface of the brain, although it is only seen in perfection in the fissures, being, as it were, stretched almost out of existence on the convexity of the convolutions.

The cells are conical; their nuclei lie close beneath the surface. The cells constitute a palisade, but, although their bases are in apposition, they do not constitute a membrane in any proper sense of the word; indeed, I am inclined to think that gaps are left between the bases of the cells through which the cerebro-spinal or

subarachnoid fluid is allowed a free communication with the intercellular spaces of the brain-substance. The apex of each ependymal cell is prolonged into a tapering process, usually crooked, and therefore soon lost from the section, but sometimes straight and traceable for a very long distance into the brain tissue.

The greater number of fibres on the ventricular side of the cortex run tangentially, but especially near the surface layers of longitudinal fibres are visible. The layer of fibres is very thick, occupying nearly one-half of the thickness of the ventricular wall.

The layer of pyramidal cells, which has made a wide sweep into the region from beneath the collateral fissure, shows just at the level of this fissure a tendency to break mesially towards the surface. This curve is very pronounced, as will be seen directly, in the more anterior sections, where it constitutes the bottom of a cursive Q, of which the upper curve is formed by the reflected cortex.

For a very short distance the pyramidal cells are condensed into a thin stratum, foreshadowing the single-celled sheet of the subiculum, but above this, again, they are massed together in many layers. The sheet of pyramidal cells is carried mesially beneath the fimbria until it almost cuts the surface, the last of its cells being only 18 millims. from it.

The molecular layer is very broad in the gyrus hippocampi, but shows, as far as I can see, no peculiarities in structure. Near its surface are seen the few small pyramidal cells which undoubtedly represent the fascia dentata; none of them exceed 12μ in diameter, while the pyramids in the subiculum have an average diameter of about 20μ .

In section 3B, which is represented diagrammatically in fig. 7, the hippocampal formation is as well developed as anywhere. The layers of pyramids in the cortex are not concentrated to the same extent as in the subiculum of an osmotic brain, but still they are reduced more nearly into a single sheet in this situation than they are elsewhere. The cortex is folded outwards abruptly towards the ventricle. It then returns upon itself beneath the fimbria, and shows at its edge a little tendency to fall over towards the aborted fascia dentata.

In block 2 the cortex, as well as the aborted fascia dentata, are caught up on to the mesial surface of what would otherwise be the ependyma-wall of the ventricle. The hippocampus is, that is to say, continued forwards beyond the anterior end of the ventricular slit.

In block 1 the hippocampus has disappeared.

The most remarkable result of the examination of the hippocampal region of the brain of this animal is the discovery that at no spot in the region is there any fascia dentata. IN HYPEROODON, IN WHICH THE OLFACTORY BULB AND TRACT ARE COMPLETELY ABSENT, THE FASCIA DENTATA TARINI IS ABSENT ALSO.

It may appear at the first moment as if this result were simply a confirmation of ZUCKERKANDL'S generalizations, which are based upon observations made—not, of

course, upon a series of sections such as I have just described—but upon a superficial examination of the brains of a number of Mammals, including the Dolphin.

This is the case in a very limited sense, however, as will be made clear by an analysis of ZUCKERKANDL'S results. Such an analysis will necessarily include reference to certain large questions which I wish in this paper to avoid as far as possible. The subject to which I wish to restrict myself is the anatomical constitution of the hippocampus, and more particularly an exact determination by means of series of sections of the extent to which the fascia dentata is developed in the marine Mammalia.

ZUCKERKANDL commences his summary of the olfactory lobe as follows :—*

“Die Rindentheile des Gehirnes, welche in dieser Monographie behandelt werden, haben in gesamt Beziehungen zum Centrum des Geruchsorganes. Was bisher als centrale Stätte dieses Sinnesorganes angesehen wurde, ist zum grössten Theile im Gyrus fornicatus enthalten, und indem ich vor Allem über diesen berichte, wird es möglich, zu übersehen, wie weit zur Zeit die Lehre von dem Centralorgane des Geruchsapparates gediehen ist. In der Beschreibung desselben halte ich mich hauptsächlich an BROCA'S ausgezeichnete Schilderungen, welche den Gegenstand erschöpfend behandeln.”

BROCA'S position is extremely clear, but, as I have tried to show elsewhere,† absolutely untenable.

BROCA‡ associates the gyrus fornicatus with the rhinencephalic lobe (pyriform lobe, &c.) in a “grand lobe limbique qui peut donc être comparé à une raquette dont l'anneau entourant le seuil de l'hémisphère, est formé en haut par le lobe du corps calleux, en bas par le lobe de l'hippocampe et dont la queue est formée par le lobe olfactif.” The handle of the racquet is supposed to be formed by the olfactory lobe and its peduncle, while the two striæ diverge to embrace the bat; the mesial stria going to the gyrus fornicatus, the lateral stria to the hippocampal lobe. The great limbic lobe is described and figured as the olfactory region. The proof of this conception is supposed to be based upon comparative anatomy, but the only witnesses whose evidence would be of value (the animals, namely, in which the sense of smell is not developed) are rejected on the ground that “la psychologie des Cétacés est actuellement (et pour longtemps sans doute) trop inconnue pour que l'on puisse savoir ou présumer quelles sont ces fonctions cérébrales qui se sont développées chez eux au delà du degré que l'anatomie permet d'admettre chez les autres animaux.”

BROCA'S great limbic lobe is an anatomical assumption, which is certainly not justified by the relative development of its parts in animals in which the sense of smell is prominent in different degrees. Nor is it supported by the only investigation into

* *Loc. cit.*, p. 32.

† ‘Plan of Central Nervous System,’ Cambridge, 1885.

‡ BROCA. “Sur les centres olfactifs,” ‘Revue d'Anthropologie,’ 2^e série, vol. 2, p. 386, and also “Le grand lobe limbique et la scissure limbique dans la série des mammifères,” *idem*, vol. 1, p. 385.

the functions of the gyrus fornicatus which has been made as yet. HORSLEY and SCHÄFER* assign to this region the several areas for tactile sense; an allocation of function which will, if confirmed, prove that the middle portion of the gyrus fornicatus instead of being a portion of a limbic lobe is really the base of the great Rolandic lobe, which extends outwards across the surface of the brain and includes the paracentral lobule, parallel convolutions, and operculum, together with a portion of the regions adjoining. If this allocation of function is justifiable, the comparatively modest dimensions of the gyrus fornicatus in the limbless Whales is not to be wondered at. The gyrus fornicatus is, however, very far from diminutive in Cetacea.

ZUCKERKANDL endorses BROCA'S view with a qualification,† “Die aufgezählten Resultate erlangen einen erhöhten Werth, weil sie den Rückschluss gestatten, dass wir die Rinde des Lobus hippocampi und des Stirnendes des Lobus Corporis Callosi als centrale Stätte des Geruchsnerven anzusprechen haben.”

ZUCKERKANDL then goes on to describe, as already explained (p. 592), that within the ring of the limbic lobe there lies another convolution which constitutes the true “gyrus marginalis” or edge of the mantle. This marginal convolution is well developed in most animals and also in the Human embryo, but in adult Primates and Whales is partially rudimentary inasmuch as it is represented in its dorsal portion by the nerve of Lancisi only.

It consists of three segments, the fascia dentata Tarini (gyrus dentatus), gyrus supracallosus (“Lancisi'schen Streifen” when atrophied, as in Man), and gyrus geniculi (also included in the striæ Lancisii in Man).

Just in the same way in which BROCA'S speculative union into a great limbic lobe of three lobes or portions of the great brain—lobus olfactorius, lobus hippocampi, lobus corporis callosi—falls to the ground when tested by comparative anatomy, so, also, is ZUCKERKANDL'S association of fascia dentata, nerve of Lancisi, and gyrus geniculi, although attractive as a speculation, opposed to certain facts.

It is extremely desirable that the development of this region which surrounds the foramen of MONRO should be studied with such exactitude as would leave the question quite beyond the reach of doubt. Failing precise embryological and especially histogenetical evidence I feel some unwillingness to refer to the subject at all, but lest it should be supposed that I endorse ZUCKERKANDL'S conclusion with regard to the wider question, I feel bound to point out certain considerations which militate against his association of the fascia dentata, nerve of Lancisi, and gyrus geniculi in a “marginal convolution.” These considerations may be best set forth after a statement of GIACOMINI'S views.

* HORSLEY and SCHÄFER. “Record of Experiments on the Functions of the Cerebral Cortex,” ‘Phil. Trans.,’ 1888, B., p. 1. BROWN and SCHÄFER, ditto, 1888, B., p. 303. FRANCE and SCHÄFER, 1889, B., p. 331.

† *Loc. cit.*, p. 40.

GIACOMINI'S* description of this region agrees with ZUCKERKANDL'S in general outline although differing in certain points. I have not, as already said, had the advantage of seeing the original paper, but TESTUT states that he is giving an account of GIACOMINI'S views in his 'Traite d'anatomie humaine' (pp. 497 and 498), and adds, "J'ai contrôlé sur un grand nombre de cerveaux les recherches du professeur italien ; elles sont exactes." I quote from this book. In the Human brain, according to GIACOMINI, the fascia dentata terminates at its anterior end, after extending to the most anterior part of the fissure between the uncinata gyrus and its uncus, as follows:—" Arrivé là, il s'infléchit en dedans, sort du sillon et devient de nouveau visible à l'extérieur ; il contourne alors de bas en haut le face interne du crochet de l'hippocampe et disparaît, en s'atténuant de plus en plus, sur la face ventriculaire de ce crochet. Cette extrémité antérieure du corps godronné nous apparaît nettement, dans la plupart des cas, sous la forme d'une petite bandelette d'aspect gélatineux, d'une couleur cendrée, large d'un millimètre à un millimètre et demi. Nous l'appellerons, du nom de l'anatomiste qui l'a à la fois découverte et bien décrite, la bandelette de GIACOMINI." At its posterior extremity the fascia dentata is said to join the nerve of Lancisi in the following way:—" Il change d'aspect, de bosselé qu'il était, il devient lisse et uni ; il change aussi de nom et devient le fasciola cinerea. Sous ce nouvel aspect et sous ce nouvel nom, il se porte obliquement en haut et en dedans vers le bourrelet du corps calleux, le contourne de bas en haut, arrive sur sa face supérieure et se continue là avec les tractus longitudinaux de Lancisi, soit avec les tractus médians, soit avec les tractus latéraux."

ZUCKERKANDL and GIACOMINI agree, therefore, in regarding fascia dentata, nerve of Lancisi, and geniculate gyrus as three portions of the same convolution, the most internal of the annular convolutions, the margin of the porta. They differ as to the connection between the fascia dentata and nerve of Lancisi. According to ZUCKERKANDL, the callosal convolution constitutes the intervening segment ; according to GIACOMINI, the intervening segment is the fasciola cinerea, while the callosal convolution is a portion of the general cortex.

I hesitate to give my own views upon this question, because I have not yet investigated the matter, as I hope to do soon, in the only way in which it can be definitely settled, by studying (1) a number of fresh brains, (2) series of sections through this region carefully hardened ; (3) its development ; nor have I paid especial attention to the Human brain. I have, however, made a large number of sections of this region in the brain of the Ox, and also of certain Cetacean brains, and am opposed to the view that the fascia dentata, or tissue which belongs to the ring or convolution, out of which the fascia dentata is developed, is continued on to the dorsal surface of the corpus callosum on the following grounds:—

* GIACOMINI. "Fascia dentata del grande hippocampo nel cervello umano," 'Giornale della Reale Accademia di Torino,' 1883.

1. The little convolutions which rest against the splenium corporis callosi are indubitably continuous with the atrophied convolution which lies at the bottom of the callosal fissure, and is known as the stria longitudinalis obiecta, *seu* lateralis, or nerve of Lancisi, when this last expression is not limited to the stria medialis, or to the white fibres which run along the inner edge of the stria lateralis.

The stria lateralis emerges from the callosal fissure, in many cases in Man, in most cases in animals, in which the corpus callosum is relatively smaller. It appears again on the surface, either above the genu or only in front of the genu, as the geniculate convolution.

These parts, callosal convolution, stria obiecta, supra-callosal and geniculate convolutions are parts of the general mantle, and do not resemble the fascia dentata in minute structure.

2. In the Ox (and many other animals) the callosal convolutions, when not strongly developed, very closely resemble in form the corresponding convolutions in any human brain in which they are unusually well developed; but their size, both in Man and animals, varies considerably. In the Ox, however, instead of the fascia dentata ceasing beneath the splenium at the spot at which fasciola cinerea and subcallosal convolutions appear, it accompanies the fimbria to within a few millimetres of the level at which the septum pellucidum intervenes between the fornix and corpus callosum. In other words, the *fascia dentata continues its subcallosal course* instead of accompanying the fasciola cinerea to the dorsal surface of the corpus callosum, nor can I see, in sections which I have made through this region, the slightest indication upon the under surface of the corpus callosum of any structure which might be regarded as the fascia dentata returning to the splenium to surmount it and join the nerve of Lancisi.

These considerations seem to me to indicate that the corpus callosum in its backward extension breaks through a convolution which lies outside the ring from which fascia dentata, fimbria and fornix are developed.

It is, so to speak, an accident that the fascia dentata terminates at the level of the callosal convolutions in Man.

Turning now to the more special point: ZUCKERKANDL'S observations upon the fascia dentata. In the second edition of his 'Twelve Lectures' (I quote from the English translation),* EDINGER says, "All the convolutions which lie near the margin of the hemisphere—the gyrus fornicatus, the gyrus hippocampi, the stria longitudinalis Lancisi, and the fascia dentata—are very strongly developed in animals having highly perfected organs of smell. In those which, like human beings, have small olfactory lobes, they are somewhat atrophied, and in the Dolphin, which has no olfactory lobe, they are totally undeveloped (ZUCKERKANDL)."

* EDINGER. 'Twelve Lectures on the Structure of the Central Nervous System.' Translated by VITTMUM and RIGGS. Philadelphia, 1890.

ZUCKERKANDL in his paper makes the following references to the brain of the Dolphin, in all of which, except the last, he omits to make any mention of the fascia dentata :

“Cetaceen.—Es wurde nur der Delphin untersucht.

“A. Der verkümmerte lobus hippocampi besitzt einen Haken im Sinne der Primaten; die den Mandelkern enthaltende Rindenpartie liegt über dem lobus hippocampi.

“B. Die Balkenwindung,

“C. Die Randwindung, und

“D. Die Fimbria fehlen” (p. 19).

“Cetaceen.—Untersucht wurde der Delphin. Der gyrus marginalis fehlt bis auf das kurze Stück des dorsalen Schenkels, der in hohem Grade atrophisch ist” (p. 42).

“Bei den Cetaceen, Primaten, vielleicht aber schon bei einzelnen Halbaffen, ist die ventrale Portion der Randwindung relativ schwach, die dorsale hingegen auffallend atrophisch. Die Differenz zwischen den beiden Portionen des Randbogens is demnach auf einen atrophischen Process zurückzuführen. Am meisten atrophisch ist die Randwindung bei den Cetaceen und bei den nicht anthropoiden Affen” (p. 56).

“Cetaceen.—Untersucht wurde der Delphin. Von einer Balkenwindung ist keine Spur vorhanden” (p. 67).

In his chapter, “Ueber die Bedeutung der bisher beschriebenen Rindentheile und über das Gehirn des Delphins,” we find this sentence: “denn hier findet sich sogar ein Rudiment der fascia dentata mit einem dicken stratum granulosum vor, wie aus der schematischen Zeichnung ersichtlich wird, in welcher der ganze Spitzenantheil des Hakens der Fascia angehört.”

From the time of TREVIRANUS both comparative anatomists and pathologists have frequently noted the fact that absence or deficiency of the olfactory bulb is associated with deficiency of the hippocampus, using the term in its wider sense. This relation is confirmed by ZUCKERKANDL, to whom also belongs the merit of correcting the extraordinary errors made by TIEDEMANN,* who mistook the optic thalamus for the hippocampus; and STANNIUS,† who describes and figures (the figures are reproduced by ZUCKERKANDL), a hippocampus in the Dolphin formed upon the ordinary osmatic plan.

ZUCKERKANDL, however, sets out with a case to prove; to wit, that the outer arcuate convolution is developed into (1) the fascia dentata, (2) the gyrus supra-callosus (or Lancisi's nerve), (3) the gyrus geniculi; the inner into the fimbria and fornix. The Dolphin is used as a proof that these three parts are proportionately developed and vary as the olfactory bulb, and the case, as based upon the Cetacea, breaks down on every count.

* TIEDEMANN. ‘Zeitschrift f. Physiologie,’ vol. 2, 1827.

† STANNIUS. “Ueber den Bau des Delphingehirnes.” ‘Abh. a. d. Gebiete der Naturw.,’ Hamburg. Quoted by ZUCKERKANDL.

1st. He says that in the Dolphin the fimbria is absent; it is present in all the marine Mammals which I have examined; the only specimen of the Dolphin's brain which I possess is not sufficiently well preserved for this investigation.

2nd. He says that the callosal convolution (Balkenwindung) is absent. With a brain which is not folded forward beneath the corpus callosum, and in which (more completely than even in Man) the posterior pillar of the fornix is adherent to the corpus callosum, there is no place for this small convolution on the back of the splenium, or between the splenium and the fornix.

3rd. The gyrus arcuatus (Randwindung) is absent. On the contrary, the stria lateralis presents much the same appearance as in other Mammals. It is present in Hyperoodon, Monodon, and Phocaena, and in the former it escapes from the position in which it is hidden at the bottom of the immensely deep callosal fissure and appears on the mesial surface as a narrow supracallosal convolution which ends in front in a gyrus geniculi. In one specimen in my possession, which has been beautifully preserved in bichromate of ammonia, the supracallosal and geniculate convolutions have much the same appearance as in the Ox. These convolutions, as well as the callosal (or subsplenial) convolutions, are subject to great variations in development. In the Anatomical Museum, at Cambridge, there is a large model of the anterior portion of the human cerebrum which I made for the purpose of illustrating a paper at about the time at which ZUCKERKANDL's article on the "Riechcentrum" appeared. I was at the time ignorant of ZUCKERKANDL's researches, and made the model from a fresh human brain in which the geniculate convolution happened to be remarkably well developed and its connection with the stria lateralis very clear. When ZUCKERKANDL's article appeared I abandoned the paper, finding that the work had already been done; but the examination of a considerable number of human brains and the comparison of the brains of Man and animals had shown me that the circumcallosal convolution is exceedingly variable. Its variability is strongly suggestive of alterations in the mesial aspect of the brain, produced by the backward extension of the corpus callosum.

The rudimentary condition of the nerve of Lancisi in Man and in Cetacea appears to me to depend not upon their union with the fascia dentata and association through this with the olfactory apparatus, but upon the large size of the corpus callosum.

4th. ZUCKERKANDL pays but little attention to the only structure which is absent or rudimentary in Cetacea, namely, the fascia dentata.

PORPOISE. (Figs. 4, 5, 6, 9, 10, 11.)

Although less conical than that of the Whale, the brain of the Porpoise (*Phocaena communis*) resembles the Whale's brain in general appearance. It is short, and extremely broad as compared with osmatic brains, being almost globular in form.

As in the Whale, the front part of the cerebral hemisphere is flexed upon the back part, although the base of the brain is not covered nearly so far as in the Whale. The surface is deeply fissured.

With a view to showing clearly the peculiarities in shape, which appear to me to be characteristic of anosmatic brains, I prepared a cast of the inside of the skull of a young Porpoise (fig. 9). It exhibits the extreme diminution of antero-posterior length with corresponding increase in breadth and height. Since the brain fits close to the skull case, such a cast represents accurately the shape of the brain; as is evident from the appearance of the fissures and convolutions upon all parts of its surface.

Its extreme measurements are: length, 80 millims.; height, 78 millims.; transverse diameter (of the two hemispheres), 132 millims.

General Form of the Hippocampus of the Porpoise.

The fornix is, in the Porpoise, quite distinct from the corpus callosum.

Its anterior pillar is well defined. The body, which is small and oval in section, is fused neither with its fellow nor with the corpus callosum. The posterior pillar is free.

It is difficult to say how far the fimbria reaches forwards, for it seems to die away on the uncus instead of being tucked in beneath it in the usual manner (see figs. 5, A, B, C); but the total distance from the point at which the posterior pillar first touches the cortex to the tip of the hippocampal region, in a large adult brain, was only 18 millims. The fimbria is strap-shaped and, in the greater part of its extent, completely covers the reflected margin of the cortex, but I estimate (from my sections) that the length of the reflected portion is about 10 millims.

Hippocampal Region in the Porpoise studied in a series of sections.

In its general features this region corresponds closely in structure with that of the Whale. The reflected layer of cortex is throughout feebly developed, small in all its dimensions, and pressed flat against the cortex of the gyrus hippocampi.

Section 9A (fig. 10) shows the form of the hippocampus in its posterior part.

The fimbria is flat. It does not, as in osmatic brains, take the form of a distinct rod, but is a flat band which covers the reflected portion of the cortex, and belongs distinctly to the sheet of fibres which lines the ventricle.

The pyramidal cells, which show in the gyrus hippocampi a tendency towards an arrangement in several layers, are collected at the point where the cortex folds over into a single layer, the cells in which are fairly large. In the reflected cortex the cells become fewer and smaller as the edge is approached.

There is no thickening of the layer into a rod (nucleus fasciæ dentatæ). Nor is there any trace, at this level, of the reception of the edge of the cortex into a scabbard of fascia dentata.

Small though it be, the fascia dentata is nevertheless distinct in section 5A (fig. 11). It consists, at this level, of some three or four layers of cells closely packed together. As in other animals the nuclei are of two kinds, nuclei of small angular nerve cells, and "granules," conventionally so called, *i.e.*, nuclei which are somewhat smaller and darker than those of the angular cells, and lie in clear spaces with but faint traces of cell bodies in tissues as ordinarily prepared.

The layer of fascia dentata, with its nuclei and superficial molecular stratum, does not fuse in any way with the layer of pyramidal cells; but there is not, on the other hand, any appearance from which the relation of the fascia dentata to the cortex can be inferred—whether a special development of some part of the cortex or a new formation superadded.

My sections do not, unfortunately, allow me to state with accuracy the length of the fascia dentata; but I can assert that it is found in the Porpoise for a short distance only (at the outside 6 millims.), and that it nowhere reaches a greater development than in the section (5A) which I have drawn.

HIPPOCAMPUS OF MONODON MONOCEROS. (Figs. 3, 12.)

The brain of the Narwhal resembles that of the bottle-nosed Whale so closely in those particulars, upon which in my account of *Hyperoodon* I laid especial stress, that I do not propose to call attention to them again.

Its extreme flexion is well shown in the accompanying rough sketch of the brain (fig. 12), as seen from the under side after cutting through the axis in front of the cerebellum. Looking at the sketch on the right side first, we see, in order, the corpus callosum (its splenium), the anterior right tubercle of the corpora quadrigemina, the posterior tubercle, the brain-stem with the fillet and crusta on its side; and lastly, on the extreme left, the optic chiasm. Owing to its extreme flexion, all these structures can be seen at the same time after the brain-stem has been divided by a single cut.

The uncinata convolution is larger than in *Hyperoodon*. It appears on the surface from beneath the forceps posterior of the corpus callosum, bends round the axis, and curves slightly round the temporal pole into the throat of the Sylvian fissure. The uncus is completely separated from the rest of the convolution (or as it would be expressed in the more usual terminology, the uncinata convolution is separated from the hippocampal convolution) by a deep fissure. It is oval in form.

The fimbria is not seen from the under surface of the brain, nor is it visible when

the temporo-sphenoidal lobe is broken off and looked at from its mesial aspect. It is hidden away within the hiatus ventriculi (choroidal fissure).

Among the treasures which Mr. GRAY brought me from the Arctic regions were two brains of *Monodon*. They were hardened in bichromate of ammonia, and it was therefore possible to stain sections made from them in hæmatoxylin after WEIGERT'S method. Unfortunately, as so often happens, the chromic salt had rendered them extremely friable in texture, brittle almost to disintegration, and great care was therefore needed to fix any part which it was necessary to detach with a syrupy solution of collodion before cutting it.

The larger brain must, as I judge from its size as well as from histological evidence, have come from a young animal. The smaller brain is labelled "foetal Narwhal." From its size, the complexity of its convolutions and the presence within it of medullated fibres and well formed nerve-cells, it is clear that the foetus must have been at full term.

The right hippocampal region was removed from the larger brain and cut into a series of sections. From the smaller brain both hippocampal regions were cut up.

I had hoped to find in the foetal brain evidences of development along the ordinary lines followed in osmotic animals, but could recognize no points which seemed to me to need illustration, and therefore confine my description to the brain of the larger animal.

The hippocampus of this animal was cut into ten blocks. Each block into three sets of sections (A, B, and C).

Section 6B (fig. 3) is a typical section through the region in which the nearest approach is made to the formation of a hippocampus. In order that the whole section might be shown in a figure of practicable size it is magnified only 9 diameters. This necessitates a slight exaggeration in the distinctness of its details; cells and fibres are shown with the same distinctness as when viewed through an objective magnifying 50 diameters. It was necessary also to make slight restorations in the section owing to the extreme tendency of the tissue to split, already mentioned. It is perfectly accurate, however, as a combination-view of three or four sections.

In the upper part of the figure are seen from left to right:—(1.) A part of the optic tract; this is an excellent landmark in all the sections; its fibres are much larger than any others which are cut across in the several sections. (2.) A part of the cerebral peduncle (substantia innominata) with a distinct bundle of fibres lying just above the attached border of the mesial wall of the descending horn; the tænia semicircularis.

In sections a little further forward, block 5, the tænia semicircularis and fimbria form a common sheet of fibres; a good many fibres running up and down the wall in the plane of the section. It is also useful to mention as giving a clue to the exact position of the sections, that from 3B, forwards, the anterior perforated space is

recognizable on the outer side of the *tænia semicircularis* owing to the presence in the tissue beneath it of extremely large oval cells containing a patch of bright yellow pigment on one side of the nucleus. These are the peculiarly characteristic cells of the basal optic ganglion of WAGNER.

The ependyma wall of the ventricle is thick, and affords an excellent opportunity for the study of the modifications which epiblastic cells undergo when reduced in function to connective tissue purposes. On its outer side the connective tissue wall forms a mass of fibrous tissue as thick as a penholder, supporting a considerable number of large and a very great quantity of small tortuous vessels. The appearance which it assumes in all sections through this region, no matter to what animal the brain belongs, are, of course, largely due to contraction in the hardening agents.

The plate of *velum interpositum* is prolonged into two pouches, of which the mesial or lower pouch fits into the angle beneath the fimbria, while the upper or outer pouch fits into the pocket formed at the angle between the *gyrus hippocampi* and cortex, which is dipping into the collateral fissure.

The prolongation of the *velum interpositum*, beneath the fimbria, is a marked feature of all the sections. The fimbria, instead of lying as is usually the case on the summit of the hippocampus, lies altogether in the groove between the *crus* and the hippocampus, and takes the form of a flattened plate which covers over a prolongation of the descending horn. I have several times in this paper called attention to appearances which are suggestive of a deep folding of the cortex inwards and downwards (as the reflected cortex), and its return upon itself as the *fascia dentata*, fimbria, and ependymal wall. In the sections of the hippocampus of the Narwhal, I thought several times that I had come upon this folding, always to find, however, that it was due to the splitting of the section in the line of a blood-vessel which entered the cortex from the *velum interpositum* and traversed it from without inwards parallel with and very near to the surface of the summit of the hippocampal *gyrus*.

The presence of these blood-vessels which enter the cortex from the ventricle and run towards the surface in this region is remarkable, since the plan of blood-supply of the rest of the *gyrus hippocampi*, as of other parts of the cortex, is for the vessels to enter from the pial surface. It seems to point strongly to the existence in the embryo of a ventricular pouch which has closed up in the course of development.

The fimbria increases in transverse sections very rapidly from before backwards; retaining throughout, however, its strap-like form. As already mentioned, it is separated from the *alveus* by a deep groove or pocket. Another small groove marks off the portion of the *alveus* which lies beneath the fimbria as a separate column, more distinct in the sections behind 6 than in the section figured.

The sections show in a very striking manner, owing presumably to the fact that they are taken from a young animal, the way in which the fibres of the *alveus* take origin in the cortex of the hippocampal convolution, pass between its columns of cells,

and sweeping inwards beneath the floor of the ventricle, curve round the groove between the alveus and fimbria into the fimbria, in which eventually they assume a longitudinal direction. In sections of osmatic brains the formation of the fimbria from the alveus is obscured by the origin of large numbers of fibres in the hippocampus proper, if it is allowable to restrict this term to the reflected cortex.* The fibres of the alveus are crossed at right angles by fibres which pass outwards into the white matter which lies beneath the collateral fissure.

A few delicate fibres are seen near the surface beyond the border of the pyramidal cell-layer, close to the fimbria. They are also found in the cortex of the gyrus uncinatus, but none are to be seen at the extremity of the gyrus.

In structure the cortex of the gyrus uncinatus resembles the cortex in other

* As pointed out in the introduction to this paper, the nomenclature of the region is in complete confusion. The term "hippocampus" or "hippocampus major" is used either for the swelling in the descending horn, or for this *plus* the fimbria and fascia dentata, or the terms "pes hippocampi" are used for the swelling and "cornu Ammonis" for the fimbria and fascia dentata, or cornu Ammonis includes the whole region, or again it is limited to the swelling in the descending horn. Some definition of these terms is absolutely necessary, but it is hardly possible without rearrangement to a certain extent. I am very unwilling to make any suggestions which may still further add to the confusion by introducing a new use of the words, but seeing that a certain formation of brain is found in osmatic animals which is absent in anosmatic animals, it appears to me most convenient to term the osmatic structure the "hippocampus," this being, so far as I can make out, the use which would have been made of the term by those who first described the region, had they known of the difference between the two classes of animals in this respect. I imagine that ARANTIUS or HALLER would have said: "the Dog has a very large hippocampus while the Whale has none." If then we use the term for the structure which the Dog possesses and the Whale does not possess, we have, at any rate, a useful anatomical distinction between the two. I should then do away with the term "gyrus hippocampi" altogether, for almost all anatomists confuse it with the gyrus uncinatus, and I should term the whole of the most internal convolution from the isthmus gyri fornicati downwards and forwards, the "gyrus uncinatus," with its hook, the "uncus." The ascent from the gyrus uncinatus to the fascia dentata I should term "subiculum hippocampi." The swelling in the descending horn has been known for three hundred years as "the hippocampus;" but then this term is made to include so much more that it has no definite signification, and there seems no reason against our terming it "pes hippocampi" for the sake of distinction.

The term hippocampus would then mean the reflected cortex, where its cells form a single sheet, with its enlargement into the nucleus fasciæ dentatæ, *plus* the fascia dentata itself, and the fibres derived from this region which pass into the fimbria. It may be objected that I include under the term hippocampus structures which by most anatomists are known collectively as fascia dentata; but my answer is that it seems to me highly misleading to include under this latter name two entirely different tissues—(1) the piece of the layer of large pyramids which is reflected as the nucleus fasciæ dentatæ, and (2) the particularly distinct layer of "granules" and molecular substance which ensheaths this rod of pyramidal cells.

It would be understood that the fimbria is made up of at least two distinct sets of fibres—(1) the fibres of the alveus which are derived from the uncinatæ gyrus; (2) the fibres which take origin in "the hippocampus."

regions. As the hippocampus is approached the pyramidal cells are massed rather more closely together and reduced to a layer three or four cells deep, but no attempt is made to take up an arrangement in Indian file. At its very edge the layer is slightly thickened and turned downwards near the surface. The cells of the reflected portion of the layer are smaller than those in the rest of the cortex. For a short distance downward the cells of the reflected layer are pyramidal, angular and darkly stained; they then give place to cells which do not stain. In these cells, which are placed pretty close together, indications of cell bodies are visible; but as they are not stained, the form of the cell cannot be made out. Their nuclei are large and clear with a distinct nucleolus. They increase in numbers towards the inferior and mesial angle of the convolution. They resemble in appearance the cells, or rather the nuclei of the cells, found in embryonic cortex.

In the Narwhal the cortex is reflected in the hippocampal region; but *no fascia dentata is developed*. Its place is taken by embryonic tissue. In an osmotic animal of the same age the hippocampus is relatively far larger and more conspicuous than it is in the adult.

HIPPOCAMPUS OF PHOCA VITULINA. (Fig. 13).

The brain of the Seal belongs to a strongly microsmatic type resembling in this respect the brain of Man. When it is viewed from the ventral side its general resemblance in form to the human brain is indeed very striking. It is almost as broad as it is long, and the orbital region of the frontal lobe is large, a considerable portion of the frontal lobe having rolled over on to the basal surface.

If the parts in which we are especially interested are examined, it is found that the olfactory bulb and tract are distinct although small. The tract ends in an external "stria" which skirts the outer edge of the anterior perforated space (tuber olfactorium). I was unable to trace the passage, so distinctly seen in macrosmatic brains, of the external stria on to the surface of the pyriform lobe.

The rhinencephalic lobe is small and tapers rapidly at its hinder end. The rhinal fissure joins the fissure of Sylvius, and then skirts the outer margin of the pyriform lobe as a deep posterior rhinal or ectorhinal fissure, which does not, however, run on into the equally deep collateral fissure, but is separated from the latter by transverse or bridging convolutions. So striking, however, is the resemblance to the human type, that there appears to be no sufficient reason for the use of a separate nomenclature for this region. I have already insisted that the pyriform lobe, including its natiform protuberance, is the same part as the uncinata (*plus* the hippocampal) convolution of human anatomy. Difficult as it is to recognize the homology between these parts in the macrosmatic Dog or Ox and microsmatic Man, the aquatic Mammalia supply all the intermediate steps. The crus of the olfactory bulb, or the pyriform lobe, as it is

often termed by writers who distinguish between the pyriform lobe and the natiform protuberance, is represented in Man by the superficial region which intervenes between the internal and external olfactory striæ.

Adopting, therefore, the terminology of human anatomy, we should describe the uncinatè convolution of the Seal as broad in front but bearing no uncus. The dentary fissure has a remarkable disposition, for, instead of ending between the uncus and the rest of the uncinatè convolution, it is carried outwards and forwards around the anterior end of the temporo-sphenoidal lobe as far as the temporal pole. In *Monodon* the isolation of the uncus is still more complete.

When I examined the hippocampal region with the naked eye, I came to the conclusion that the fascia dentata was well developed, that it appeared on the surface beneath the fimbria and was continued forwards beyond the spot at which the fimbria disappears in the ventricular slit. Microscopical examination, however, showed this to be a complete mistake. The fascia dentata does not appear on the surface at all, but lies at the bottom of a deep dentary fissure. I had mistaken, as any one who looks at the surface of the brain is likely to do, the narrow roll of cortex which intervenes between the fimbria and the fascia dentata for the fascia dentata itself. It would be difficult to find a name for this portion of the cortex, which is, so to speak, a convolution turned inside out and exposing its medullary layer on the surface. In the Seal, therefore, the cortex is folded over further than in any other animal I have examined; the upper loop of the S (see fig. 13) almost completing the circle. The fascia dentata is hidden away at the bottom of the upper bay.

In consequence apparently of its position between two convolutions, the fascia dentata is much flatter than usual, its two limbs being pressed together so that they meet at an acute angle.

In my Section 4B, the hippocampal formation is shown at its greatest development. Its anatomical disposition is curious, the cortex making a very wide sweep before ending in fascia dentata. It might almost be supposed that the gyrus hippocampi lay at the bottom of the dentary fissure, but the arrangement of the pyramidal cells shows that this is not the case, since, as soon as the cortex enters the fissure, its cells are pressed together into a thin sheet of large pyramids with very long tapering apical processes, arranged with great regularity. The small pyramids disappear from the cortex at the same point.

This is the part of the gyrus hippocampi which might with propriety be called the subiculum hippocampi,* if the nomenclature of this region ever becomes entitled to claim anything like definiteness. It would be very useful to have a term which might

* The term subiculum cornu Ammonis vel hippocampi is used as synonymous with gyrus hippocampi; which, again, is the name applied by many anatomists to a part of the convolution termed by others the gyrus uncinatus.

belong to the cortex which has not yet entered the fascia dentata, but has undergone this change in the disposition of its layers of cells.

The fascia dentata is ill-developed ; it is relatively less extensive than even in Man. Its under (mesial) limb commences very gradually on the upper border of the dentary fissure, nearer to the mesial surface of the hemisphere than does its upper or external limb. Its granular layer appears to be made up of " granules " and small pyramidal cells in about the same relative numbers as in megosmatic brains.

In the greater part of its extent the hippocampal region presents the same features as in 4B. Slightly behind this level, however (5B), the mesial limb of the fascia dentata reaches the surface of the brain. In the sections behind this it is seen to be sharply folded upon itself and continued up the surface towards the fimbria for a short distance. The course of its folding is, therefore, as follows :—In the front, where it is deeply sunk in the dentary fissure, it is folded into a V. Behind this, the angle of the V gives place to a curve. Behind this again, the mesial limb is folded upon itself in a fresh place.

SUGGESTED TERMINOLOGY.

So much confusion arises from discrepancies in the use of the terms applied to the hippocampal region that I am inclined to suggest, even at the risk of adding to the confusion, a revision of the terminology on the following lines :—

The hippocampus to mean the whole of the region in which the border of the mantle bears fascia dentata.

The most internal convolution, from the inferior end of the gyrus fornicatus (isthmus gyri fornicati) onwards, to be termed gyrus uncinatus ; its hook the uncus.

The homologous region in megosmatic brains to be termed the pyriform lobe ; this term to be synonymous with rhinencephalon, excluding the olfactory bulb. The pyriform lobe to be divided into its crus, the natiform protuberance, and its caudex or posterior tapering portion.

The term gyrus hippocampi to be discarded.

Subiculum to mean the portion of the cortex of the uncinata gyrus in which changes preparatory to the formation of the hippocampus are recognizable, *i.e.*, the concentration of large pyramids and the absence of small ones.

The swelling in the floor of the descending horn to be termed the pes hippocampi ; the sheet of white fibres which covers its surface the alveus.

The reflected portion of the cortex, or portion which returns upon itself, declivus hippocampi ; its thickened border, nucleus fasciæ dentatæ.

The expression fascia dentata to be rigidly limited to the layer of small cells (zona granulosa) and its superficial molecular layer.

The fimbria hippocampi to be reckoned as a part of "the hippocampus" in the general sense suggested above.

Dentary fissure to be the fissure between the subiculum hippocampi and fascia dentata.

The term hippocampal fissure, which at present is sometimes used as synonymous with dentary fissure (in the sense just defined) and sometimes for the slit by which the choroid plexus enters the descending horn, to be abandoned.

Hiatus ventriculi (rather than choroid fissure, or lateral portion of rima transversa cerebri) to be the name for the slit by which the descending horn would be placed in connection with the subarachnoid space, were it not closed by the ependymal wall of the ventricle.

I do not pretend that such a terminology is as satisfactory as it might be made, were it possible to overlook terms the use of which is already more or less fixed by custom, but with the exception of the introduction of the terms caudex and declivus (which are already well-known anatomical words) and the substitution of hiatus ventriculi for the confusing expression fissura choroidea or fissura hippocampi, or misapplied expression fissura dentata, I do not suggest any alteration in the terms now in use, nor any application of these terms in a manner which has not been already adopted by certain anatomists.

As our knowledge of the structure of the body becomes more exact, it is necessary that terms used at first in a vague manner should be exactly defined. It is time for the brain to be treated with the same respect as has been long shown to other parts of the body. Hitherto anatomists have felt that, since so little is known with regard to the specialization of its functions, the accurate delimitation of its regions is of little moment.

SUMMARY OF CONCLUSIONS.

In Chief.—1. The fascia dentata is absent from the brains of *Hyperoodon rostratus* and *Monodon monocerus*. It is but very slightly developed in *Phocæna communis*. In *Phoca vitulina* its size is small.

2. The extension of the fascia dentata in the several members of the Mammalian class varies as the relative development of their olfactory apparatus.

Subsidiary.—*a.* The column of large cells known as the nucleus fasciæ dentatæ is the extreme margin of the general cortex.

b. The granular and molecular layers of the fascia dentata belong to a separate portion of the wall of the fore-brain which has undergone this characteristic development.

c. In osmatic brains the fascia dentata ends on the mesial surface of the brain, slightly in front of the anterior end of the ventricular slit. Towards its anterior

extremity its mesial and external portions or limbs meet below in an acute angle. At its extreme anterior end the two limbs of the V are opened out into a flat band which lies on the surface.

d. At its posterior or upper end the fascia dentata terminates abruptly. It is therefore a long riband, folded into a trough; if laid out flat, the riband would be found to have a nearly uniform width and a very regular and uniform structure.

e. Excluding neurogleial cells, blood vessels, and occasional large pyramids, the stratum granulosum of osmatic brains contains two kinds of cell: (1) "granules," (2) small pyramids. In a typical section from the brain of the Ox I find an average of one pyramid to eight granules.

f. The anterior commissure and the fornix vary in thickness as the relative development of the rhinencephalon, although neither of these structures is absent from anosmatic brains. In anosmatic brains the posterior pillars of the fornix are closely adherent to the under surface of the corpus callosum.

g. There is no reason for associating the fascia dentata with the striæ longitudinales (nervus Lancisii), gyrus supracallosalis, and gyrus geniculi, or for supposing that all these four structures belong to a single organ, which forms a part of the cortical centre for the sense of smell. The fascia dentata is a subcallosal structure; it alone disappears in completely anosmatic animals. The stria longitudinalis lateralis and the minute convolutions (supracallosal and geniculate) into which it enlarges anteriorly are found in animals destitute of olfactory bulb or tract.

h. The relative representation of olfaction in brains of different species is shown by the ratio which the length of the hemisphere bears to its other dimensions.

DESCRIPTION OF PLATES.

PLATE 23.

Fig. 1. A portion of the fascia dentata from the anterior end of the hippocampus of the Calf. *Magnified 500 diameters.*

It consists of some granules with nuclei which stain darkly, and others with nuclei which do not stain; several of the latter are in process of division. Small pyramidal cells are also seen amongst the pyramids. The grey matter exhibits a delicate fibrillation. It contains sparse nerve-cells.

The blood corpuscles are stained darkly; they lie in chains in the capillary vessels.

Fig. 2. The hippocampus of *Hyperoodon rostratus*. Section 4B. Stained with carmine-alum, followed by hæmatoxylin after WEIGERT'S method, slightly modified.

The fimbria is seen as two ridges, from the larger of which springs the ependymal wall of the ventricle.

The cortex almost reaches the surface, where it ends with a blunt border. A blood-vessel is cut across at the edge of the cortex, and beneath this a few small pyramidal cells, which represent the fascia dentata, descend on the surface of the molecular layer of the gyrus uncinatus.

Fig. 3. Hippocampus of a young Narwhal (*Monodon monoceros*). Section 6B. *Magnified 9 diameters.*

This section was carried through the region in which the traces of hippocampal formation are more distinct than in any other part.

O.T., optic tract; *T.S.*, tænia semicircularis; *N.W.*, basal optic nucleus of WAGNER; *E.W.*, ependymal wall of descending horn of the lateral ventricle; *V.I.*, velum interpositum; *F.*, fimbria; *H.*, reflection of the cortex at the hippocampus; *G.H.*, gyrus hippocampi (*seu uncinatus*); *A.G.*, groove for an artery.

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Fig. 4. Right hemisphere of the brain of the Porpoise (*Phocæna communis*) from the basal surface, to show the uncinate convolution (natifiform protuberance,

&c.). The base of the 'tween-brain was injured, and hence details in its structure are not shown.

Fig. 5. Hippocampal region of the Porpoise. *Magnified* $\frac{3}{2}$.

A. As seen from the (mesial) surface.

B. As seen from the lateral ventricle.

C. As seen from behind and mesially.

Fig. 6. Five blocks cut from the hippocampal region of the Porpoise brain. Each of the blocks is drawn as it appears from the front, the four intervening blocks being omitted. *Magnified* $\frac{5}{2}$.

The sections exhibit the want of development of the reflected portion of the cortex.

C.A., the most posterior block, shows the strap-shaped posterior pillar of the fornix as it appears where it first touches the cortex of the uncinatus gyrus. *P.p.f.*, posterior pillar of the fornix; *Ch.pl.*, choroid plexus, collected into a mass.

6C and 6D, the fimbria, *fi.*, reduced to small dimensions, rests on the apex of the reflected portion of the cortex.

6E is carried through the nucleus amygdaleus, in front of the anterior end of the hippocampus.

Fig. 7. A semi-diagrammatic view of a section (3B) of the hippocampus of *Hyperoodon rostratus*, near its anterior end; showing the double curvature of the cortex and the looped layer of minute scattered cells which occupies the place of the fascia dentata.

E., ependymal wall of the descending horn of the lateral ventricle; *V. III.*, lateral ventricle; *F.D.*, vestige of fascia dentata; *G.H.*, gyrus hippocampi, *seu* uncinatus; *F.C.*, fissura collateralis.

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Fig. 10. Transverse section through the hippocampus of a Porpoise. Section 9A, taken from rather behind the middle of the region.

Ch.Pl., choroid plexus; *F.*, fimbria; *R.C.*, reflected cortex.

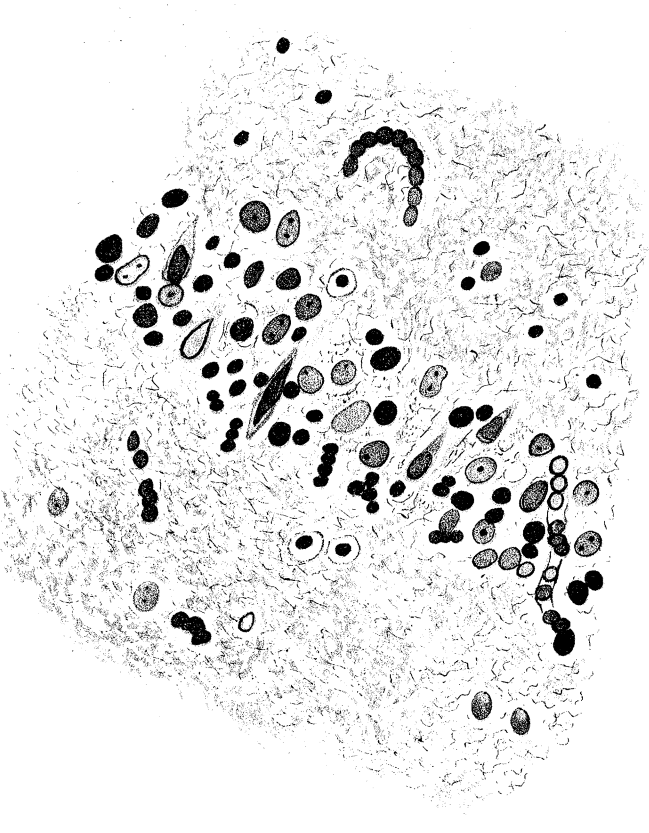
Fig. 11. Transverse section through the hippocampus of a Porpoise. Section 5A,

carried through the very limited region in which the reflected cortex appears on the surface, enclosed in a sheath of fascia dentata.

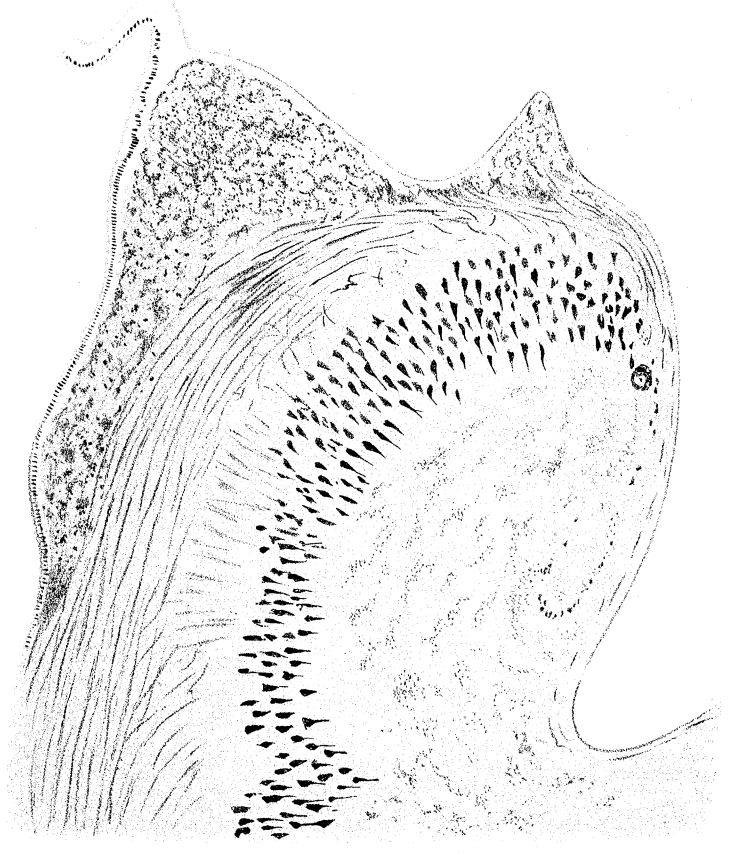
- Fig. 12. The under surface of the brain of *Monodon monoceros* (fœtus at full term), as it is seen after removal of the hind brain, by a transverse section through the front of the pons Varolii. The drawing shows the extent to which the brain is folded upon itself.

O.ch., optic chiasm; *C.C.*, crus cerebri; *F.*, fillet; *P.C.Q.*, posterior tubercle of the corpora quadrigemina; *A.C.Q.*, anterior tubercle; *U.*, uncus, completely separated from *G.U.*, gyrus uncinatus *seu* hippocampi; *Sp.C.C.*, splenium corporis callosi.

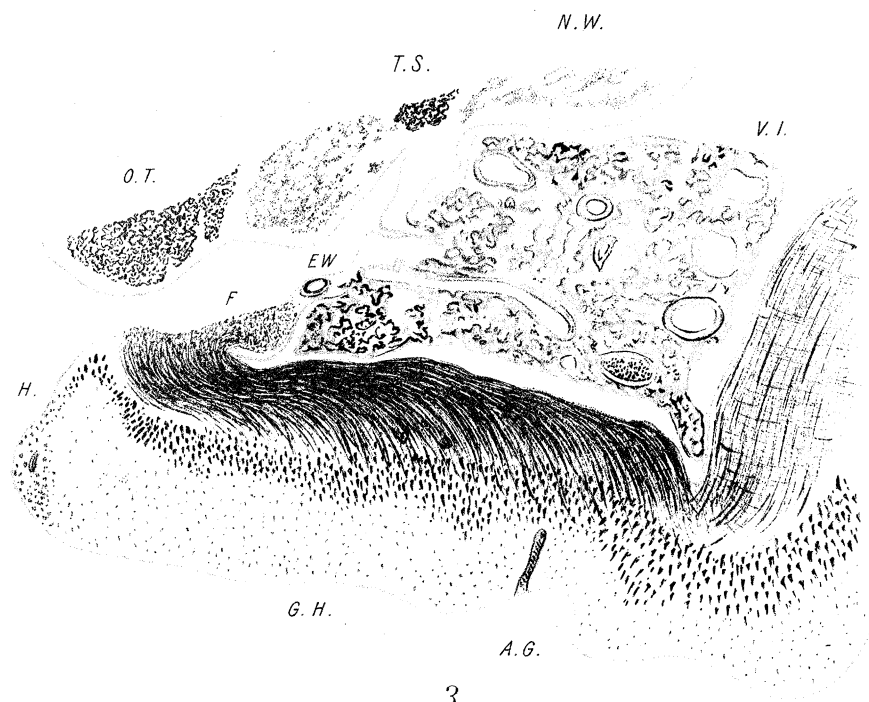
- Fig. 13. Transverse section of the hippocampus of a young seal (*Phoca vitulina*). Section 4B, carried through the region in which the hippocampus is best developed. The fascia dentata is seen lying at the bottom of the dentary fissure.



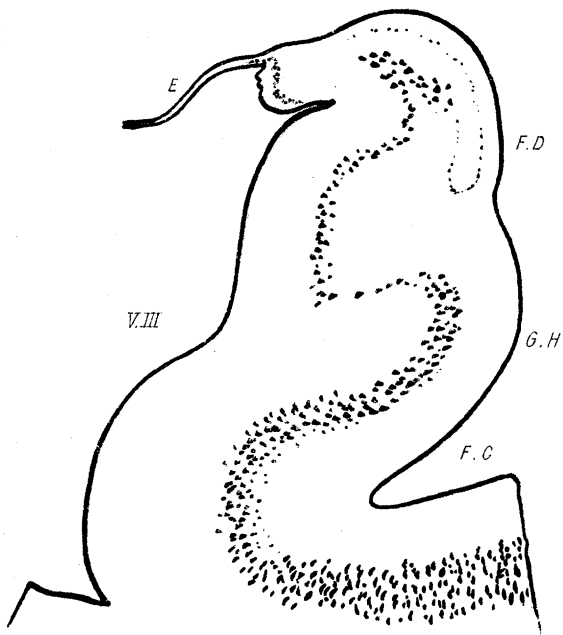
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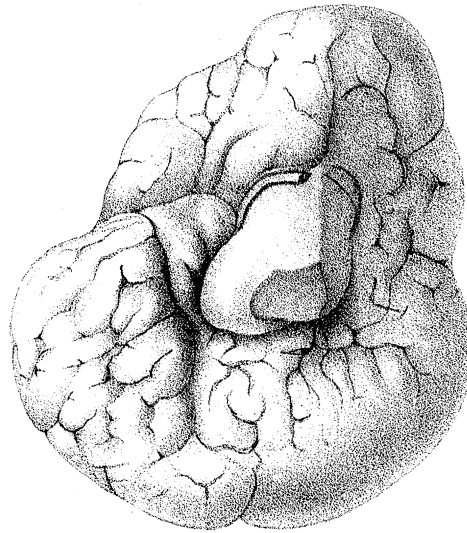
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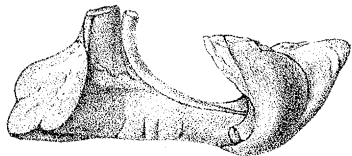
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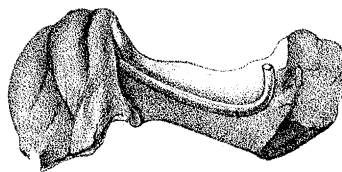
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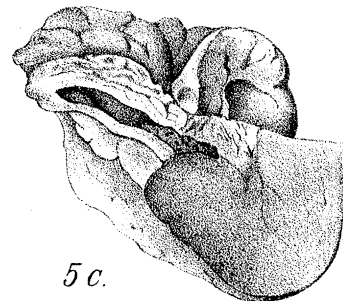
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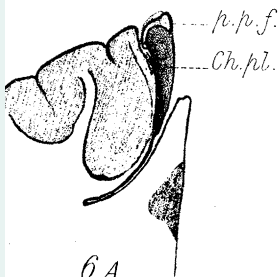
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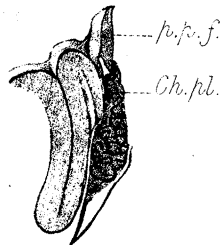
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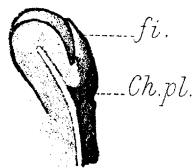
5C.



6A.



6B.



6C.

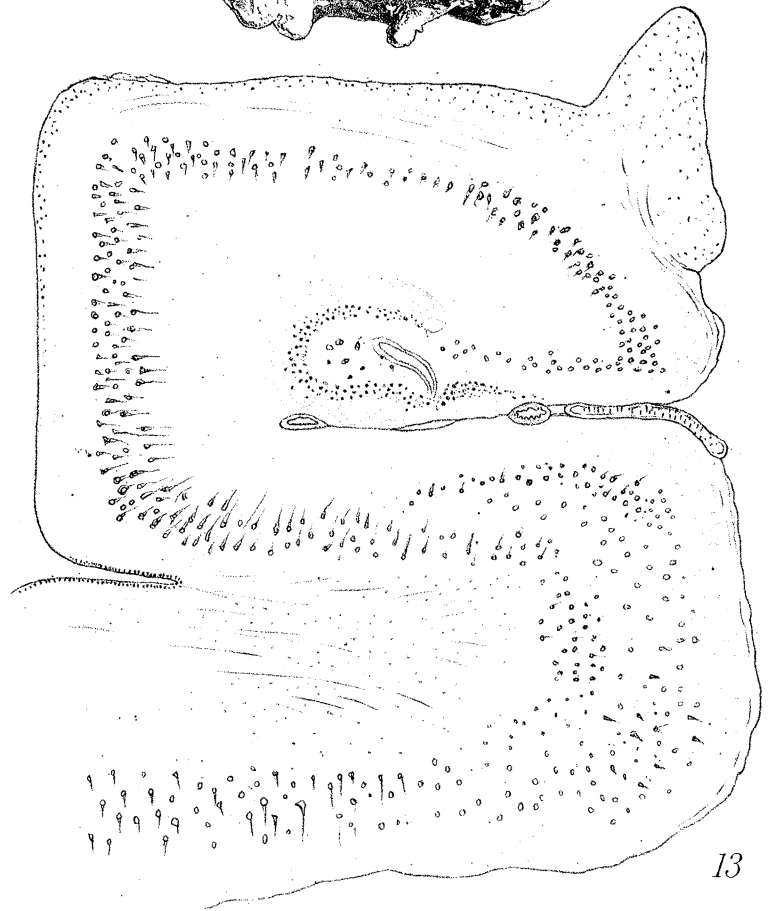
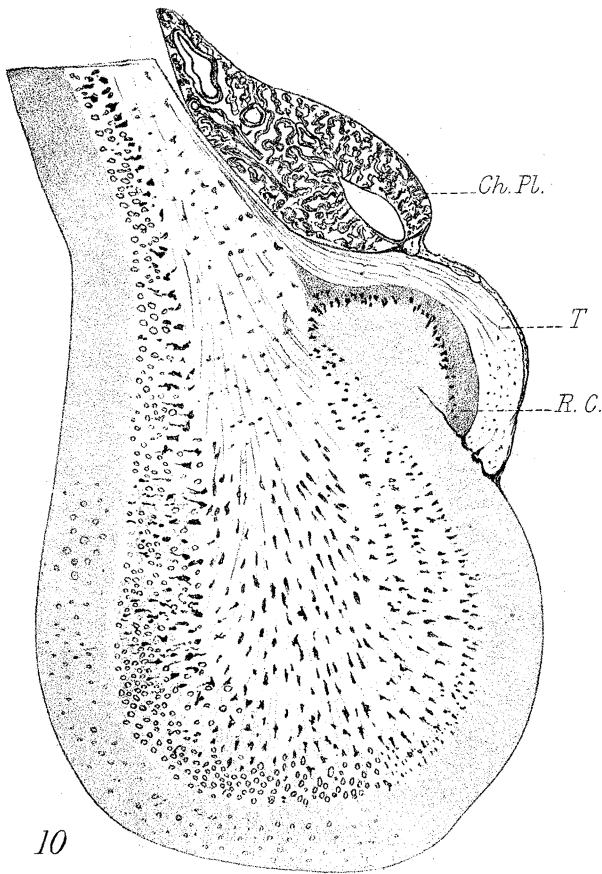
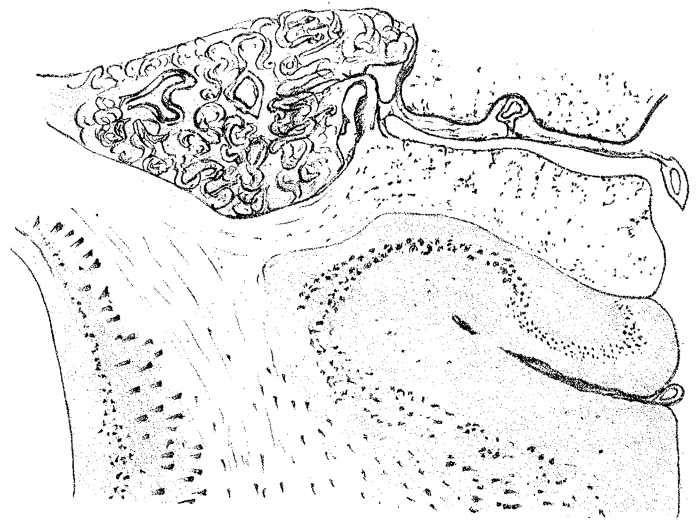
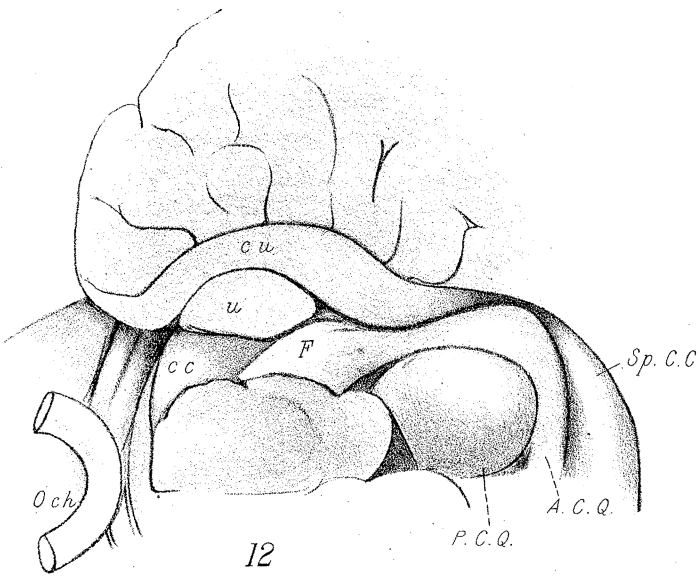


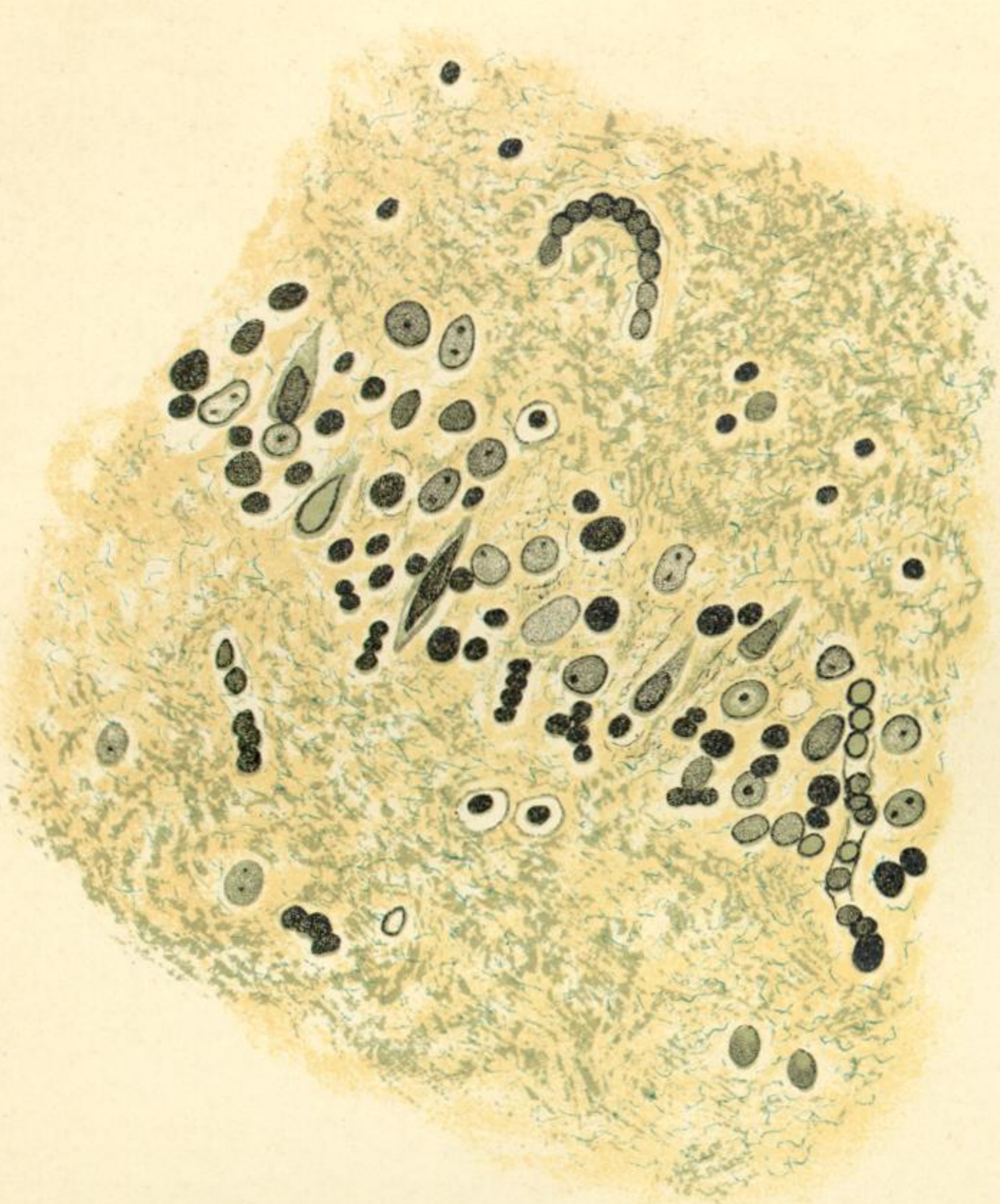
6D.



6E.

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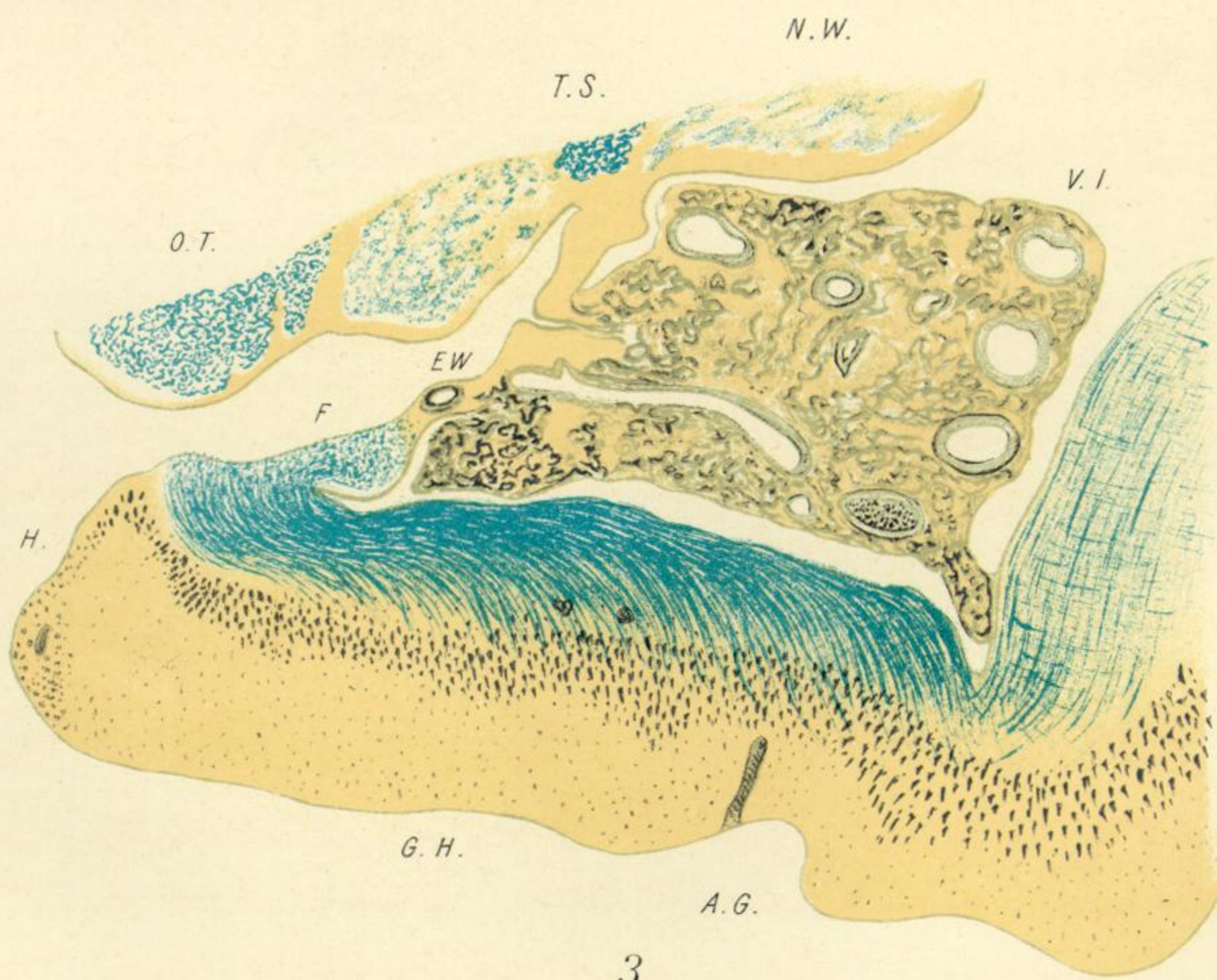




1.



2.



3

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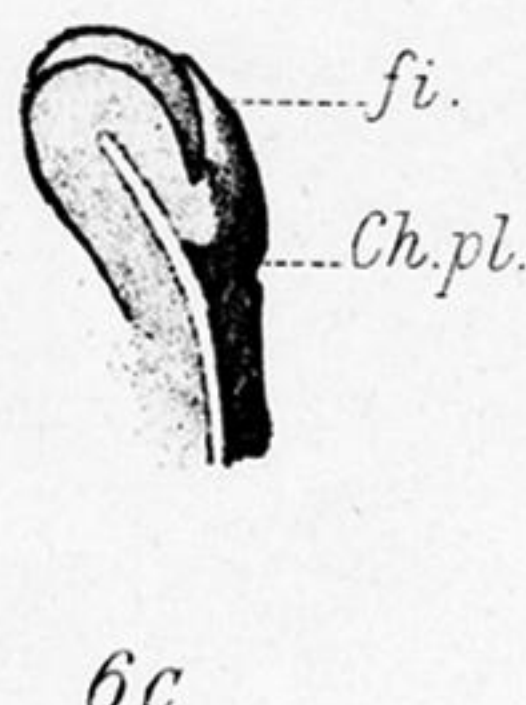
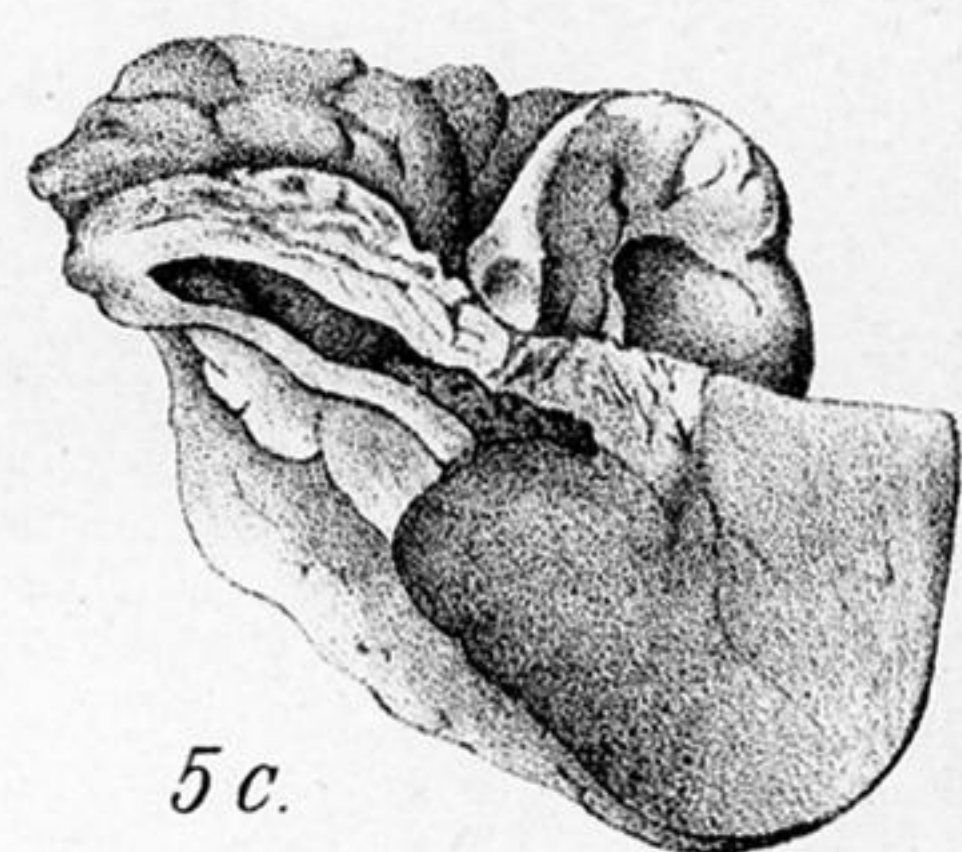
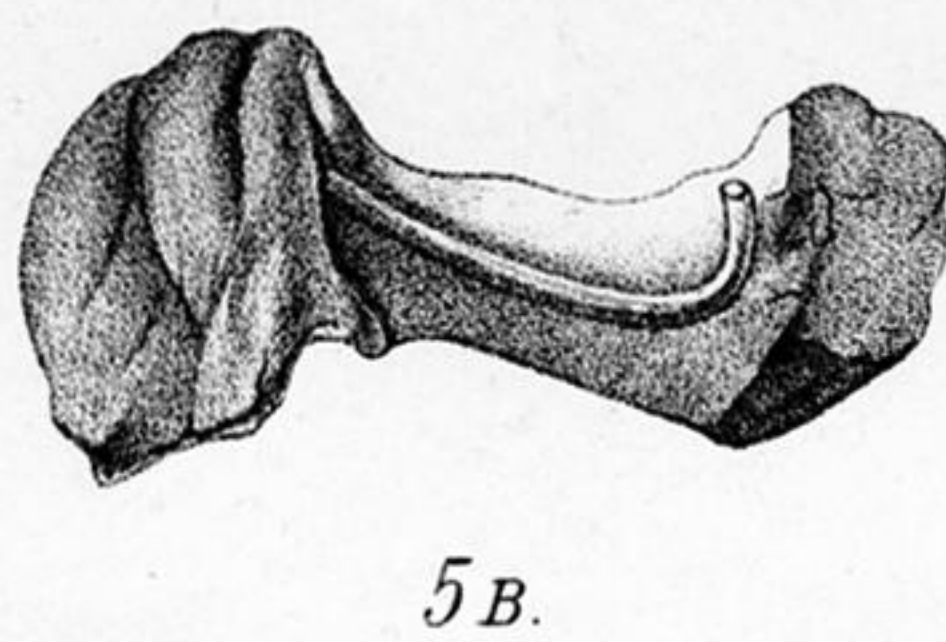
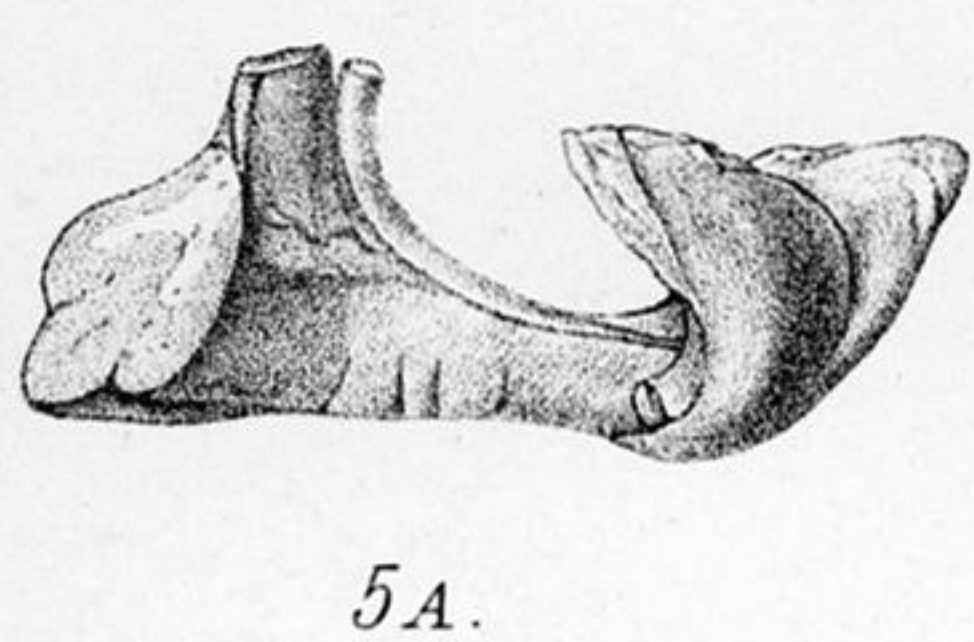
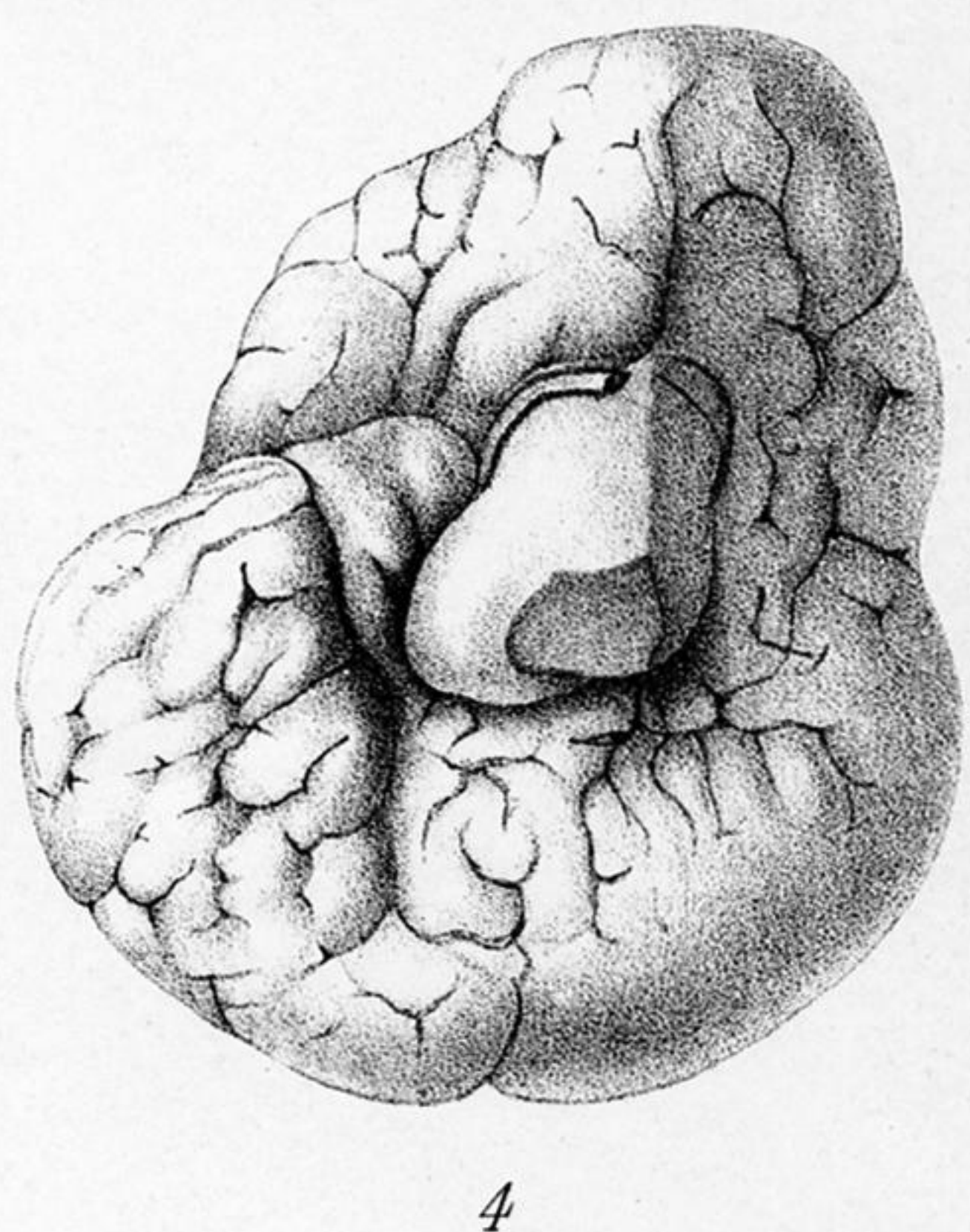
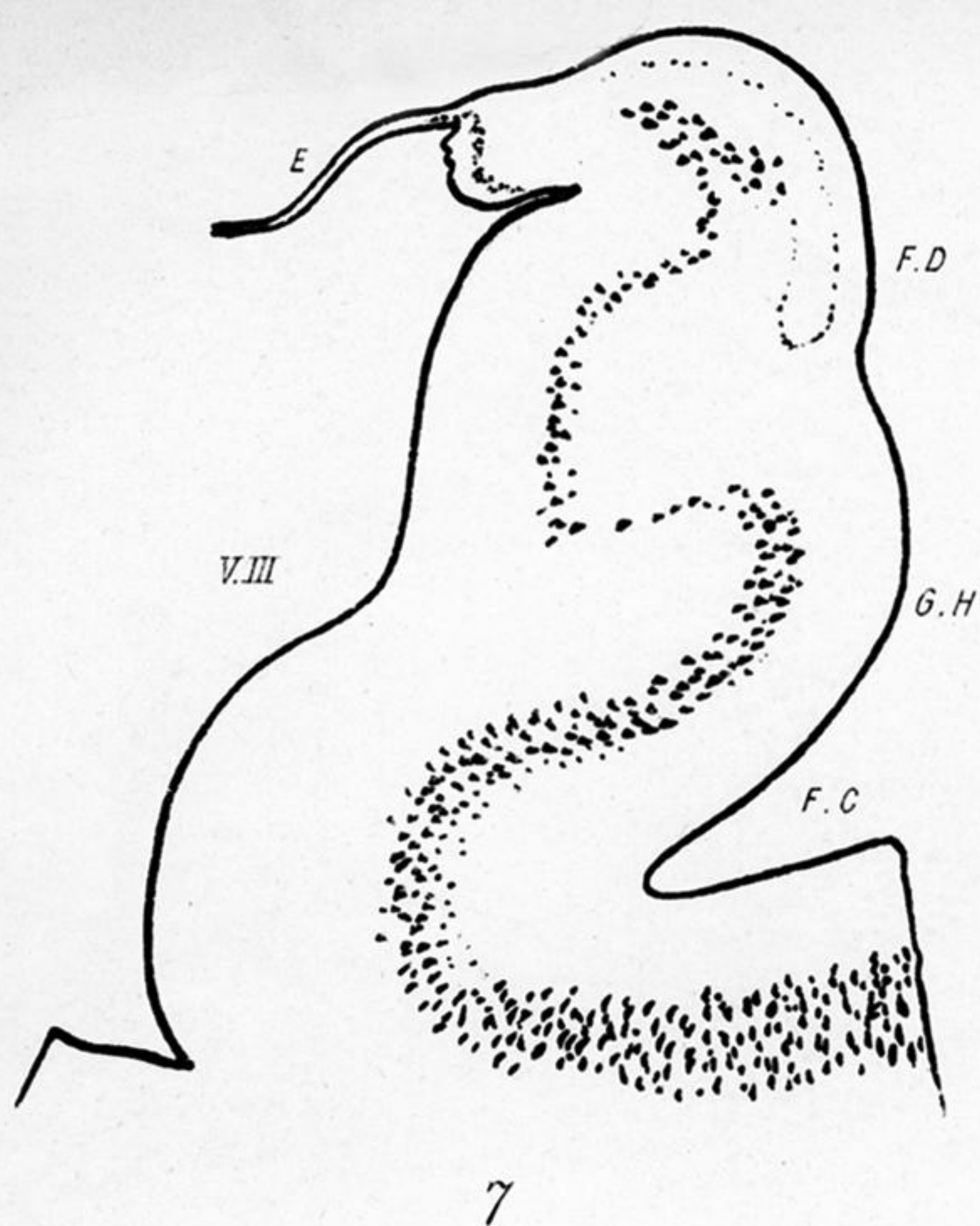


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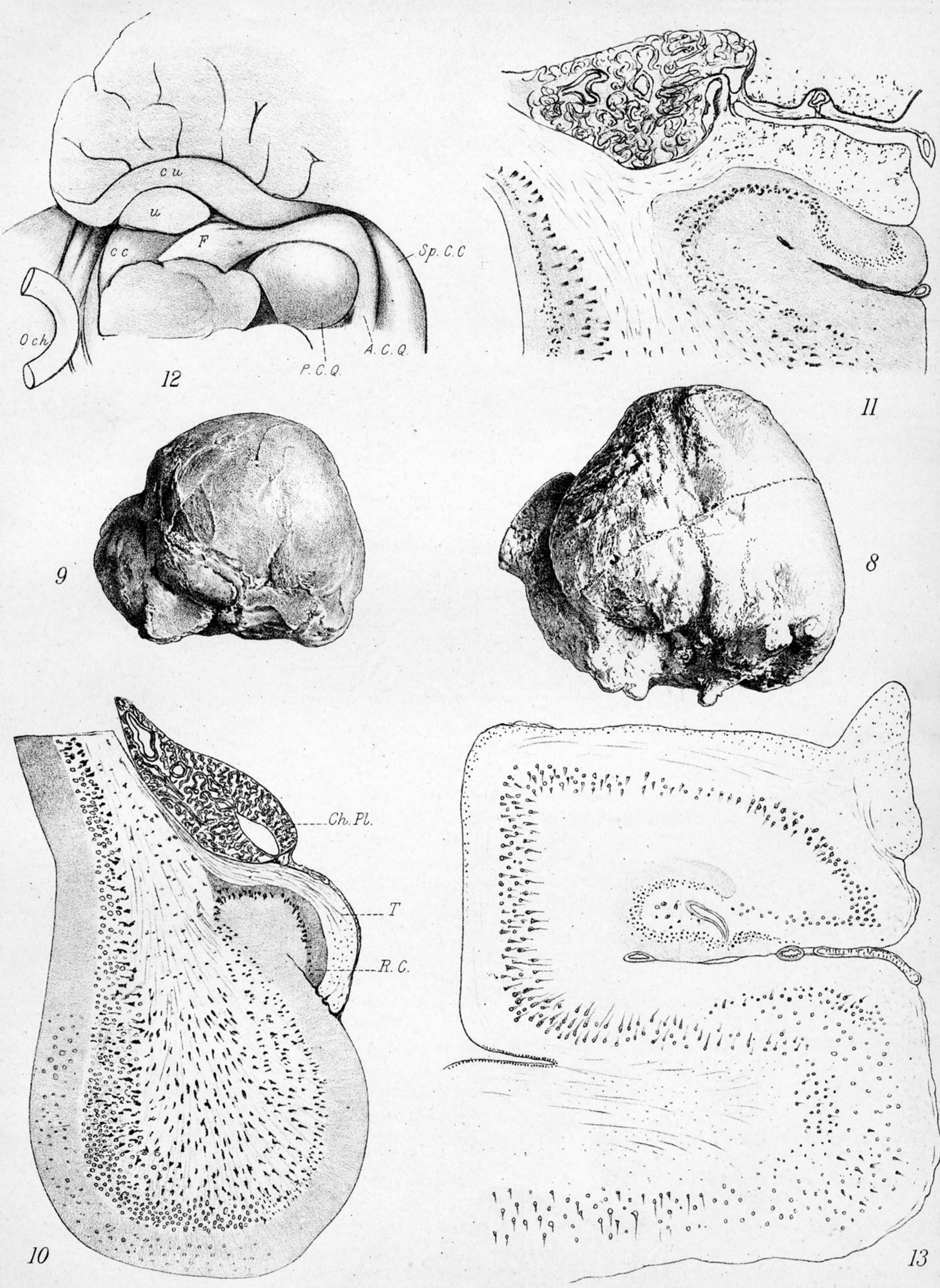


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