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A CONTRIBUTION TO THE MORPHOLOGY OF THE CORPUS STRIATUM

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INTRODUCTION

For a recapitulation of the essential features in the divergent conclusions of investigators who have studied this problem, we are indebted to the recent paper by Elliot Smith ('20) in which he pointed out the nature of the corpus striatum in *Sphenodon*, and indicated the morphological relationships of its several parts.

For some time past I have been studying a series of sections of the brain of the highly specialised Marsupial Mole, *Notoryctes typhlops*, which was very kindly placed at my disposal by Prof. Elliot Smith. As might be anticipated, in this creature devoid of any visual apparatus, the olfactory and closely associated striatal areas play a dominant rôle in its cerebral constitution—features already described by Elliot Smith in his communication to the Royal Society of South Australia ('95). In attempting to elucidate the significance of these structures I have investigated more primitive forms in the biological series; and I have to acknowledge the generosity of Professors A. Dendy of King's College and J. P. Hill of University College for the free access to their important collections, which has made possible an extensive comparative study. It is primarily for the purpose of abbreviating the account of the brain of *Notoryctes* that this preliminary note upon the striatal region is submitted; but the problem of the evolution of the corpus striatum is sufficiently important to call for this separate treatment.

If a transverse section of the brain of *Notoryctes* be studied in the region of the anterior commissure and foramen of Monro (e.g. A. 2. 7. of this series) (fig. 1), the pallial formation is recognisable as a continuous cell layer from the region of the fascia dentata and hippocampus dorso-medially, to the upturned lateral margin of the pyriform lobe ventro-laterally. Medial to this point (where the pyriform area is turned up to become continuous, through a scattered cell zone, with the denser structure of the claustral area lateral to the corona radiata) there are to be seen in section remnants of the lenticulo-striate artery (claustral artery of Shellshear, '20) whose significance as a guide to the morphology in this region has been indicated by Elliot Smith ('19). Medial to this vessel are to be seen the "scattered islands of Calleja" which constitute the "cortical" formation known as the tuberculum olfactorium. Medially this formation becomes continuous without any sharp break with the grey matter of the hypothalamic region—the constricting influence of the optic tract in strongly separating these two formations being absent in this brain.

It is important to recognise that the tuberculum olfactorium is a cap-like structure surrounding the enormously expanded striatal region ventrally.

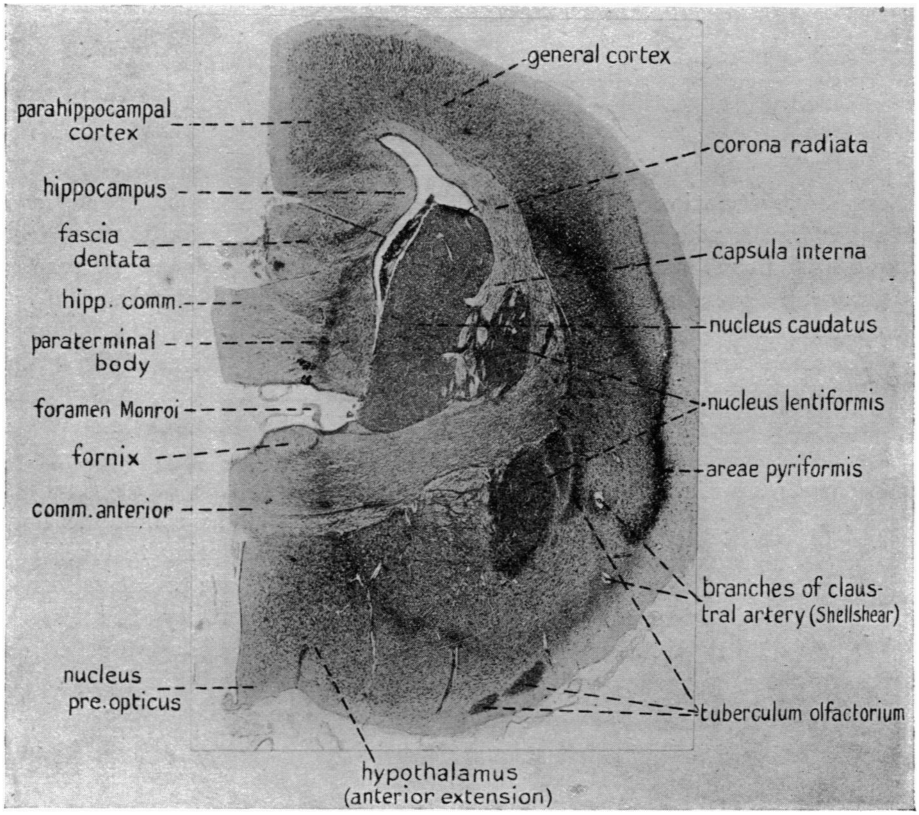

Fig. 1. Transverse section of cerebrum of *Notoryctes typhlops* (A. 2. 7. of this series) to show the scattered islands of Calleja and the lateral relationships of the tuberculum olfactorium.

Laterally this close relationship of Calleja's "islands" to the corpus striatum is preserved into the depth of the section as far as the anterior commissure, and indeed actual remnants of the tubercular cortex appear to be intermingled with the commissure itself. Certainly islets are to be observed deep to the lateral part of the claustral region and the upturned part of the pyriform lobe and the associated lenticulo-striate artery.

Ramon y Cajal (*Histologie du Système Nerveux*, tome II, 1911, p. 730) has remarked concerning this region: "Son aspect varie beaucoup avec l'orientation et la place des coupes ainsi qu'avec l'espèce animale. Cet amas atteint ses plus grandes dimensions chez le chien, chez lui ses bords plongent jusque dans les couches profondes et projettes des cordons et des bandelettes ramifiées et anastomosées." Hence it is not to be wondered at if in a creature much more dependent for its livelihood upon its sense of smell than is the dog, an even more remarkable development of this component should be present.

Sagittal sections corroborate these observations concerning an apparently "inrolled" tubercular cortex: figs. 2 and 2*a* (representing Section V. 2. 5. of this series) portray the same facts, viz., a pyriform cortex turned in above a lenticulo-striate artery to become continuous with the claustrum, while below the artery the tubercular cortex is continued in its characteristic interrupted fashion till it meets the corona radiata and the anterior commissure.

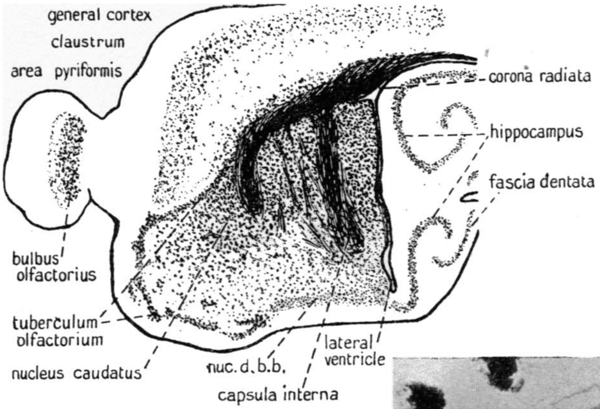

Fig. 2.

Figs. 2 and 2*a*. Sagittal section of cerebrum of *Notoryctes* (Section V. 2. 5. of this series) to illustrate "embracing" relationship of the tuberculum olfactorium to the corpus striatum, and the continuous "cortical cap" of this body.

Fig. 2 *a*.

Not every section illustrates these phylogenetic vestiges so diagrammatically as the two to which reference has been made; but despite the disturbing factors which have influenced the structure of this lowly Metatherian brain, a clear conception can be adduced of the primitive anatomical relationships of the region.

It is definite then that both ventrally, laterally, and anteriorly the tuberculum olfactorium in *Notoryctes* bears a definite "embracing" relationship to the striatal region. The same longitudinal section (fig. 2) shows that this "cortex" is continuous posteriorly with a formation which is equally entitled to the appellation of "cortex," and later in this paper it will be proved to be composed of those elements known as the nucleus of the diagonal band of Broca (*nuc.d.b.b.*) and the amygdaloid nucleus.

Johnston ('13) has shown in detail the morphology of the tuberculum olfactorium on the medial side, his work being an extension of Beccari's ('11) results. In *Notoryctes* it is clear that in front of the region where it is continuous with the hypothalamus it forms the lateral boundary of the homologue of the preoptic nucleus (of many writers). Still further anteriorly it again penetrates deeply, separating the so-called paraterminal body (nucleus septalis of some writers) from the nucleus accumbens of Ziehen. This nucleus accumbens is a portion of the palaeostriatum, and it is therefore separated from the paraterminal region by islets of Calleja. This is clearly portrayed in Johnston's ('13) figures one of which I reproduce here as fig. 3 depicting the state of affairs in *Didelphys*. While her specimens obviously (e.g. her diagrams 6, 7 and 8) illustrate this cell grouping, Crosby ('16–'17) does not recognise the patent fact. The confusion which obtains in the nomenclature of this region is a token of the uncertainty concerning its interpretation. The tubercular formation is not well developed in Reptilian forms and it is curious that where its islet formation is clearly marked, viz., in the cortical islets capping the anterior end of the palaeostriatum (the caudate nucleus of Johnston in the turtle, '15), writers (such as Johnston, '15, and Crosby, '17) should choose to dignify it with the distinctive title of anterior olfactory nucleus. No useful purpose can be served by unnecessarily

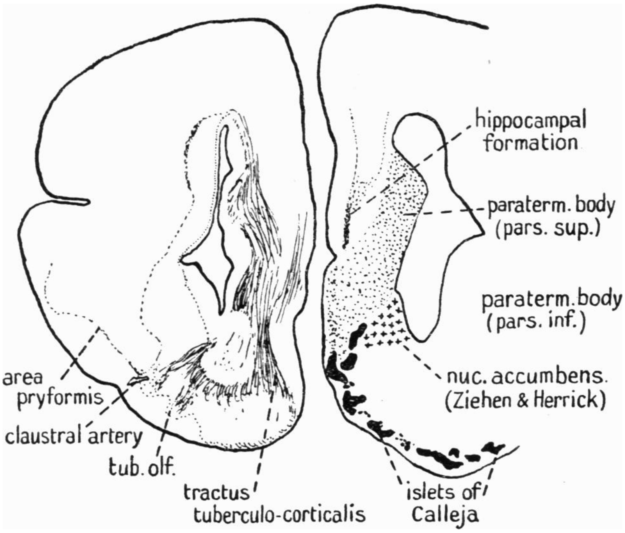

Fig. 3 (after fig. 27, Johnston, '13). To illustrate relationship of tuberculum olfactorium medially, anterior to the commissures.

adding to the already unwieldy and cumbersome accumulation of anatomical terms. The structure in question is merely the most obvious portion of the tuberculum present in Reptiles.

Before entering into the discussion of the morphology it is necessary to refer to a further conclusion insisted upon by Johnston ('13), and previously recognised by Elliot Smith (e.g. '02). This is the careful discrimination between a supra- and infra-foraminal portion of the paraterminal body (or commissure bed) of Elliot Smith (see fig. 5). This discrimination has unfortunately led to the use by Johnston of the term "primordium hippocampi" invented by Elliot Smith for a wholly different structure. Whether, as he contends, there is any justification for this gratuitous transference of terminology and incidental confusion remains to be proved. Apart from the question of priority of usage, the appellation "primordium" as applied to any structure is meaningless unless that structure gives rise later in phylogeny to the tissue of which it is called the primordium. And this Johnston has failed to show. For the purposes of this paper I prefer to use the terminology of Elliot Smith. It will therefore appear that the infra-foraminal portion of the commissure bed corresponds with the medial parolfactory nucleus (so-called) which is stated to meet its fellow of the opposite side in the nucleus of the anterior commissure, and is continuous behind with the nucleus preopticus. I am not wholly in accord with the interpretation of the cell masses found by Röthig ('12) in this region: otherwise I would gladly have utilised his terms "pars dorsalis et ventralis."

THE ORIGIN OF THE HYPOPALLIUM

The brain of *Lepidosiren* presents with almost diagrammatic clearness the simplest arrangement of cortical cell groupings in the cerebrum. In the absence of definite knowledge concerning the arrangement of its fibre tracts our interpretation of its forebrain is not yet conclusive. It has been described by Elliot Smith ('08). Figs. 4 and 5 have been taken from his work, in which the double constitution of the commissure bed was pointed out. This conclusion has been questioned by Herrick ('10). Apart from this however, there are two outstanding characteristics of its forebrain which merit special attention in a study of the striatal region. The first relates to the tubercular cortex, which is seen (figs. 4 and 5) completely to surround a cellular area ventral to the ventricle. This cellular mass below the ventricle is the palaeostriatum (of Kappers) and, as has been shown by various authors, its limits are indicated by sulci in the ventricular wall; that is to say, the sulci are opposite the medial and lateral limits of the tubercular cortex.

The primitive morphological relationship for the vertebrate palaeostriatum then, is that it should lie within a cortical structure, which we may term provisionally the "palaeostriatal cortex," a portion of which we recognise as the tuberculum olfactorium. This tuberculum olfactorium is a very obvious

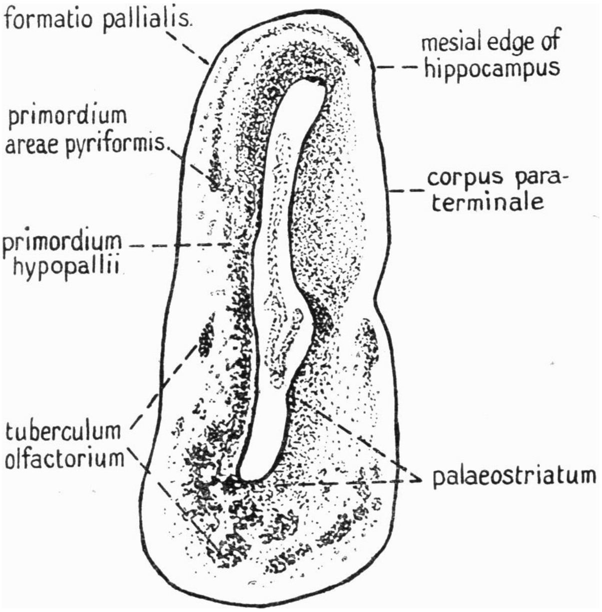

Fig. 4. A coronal section through the left cerebral hemisphere of an adult *Lepidosiren paradoxa* Fitz., a short distance in front of the lamina terminalis (Graham Kerr's section 148 c. 37. 2.). × *circa* 10. (Reproduced from Elliot Smith's paper on "The Cerebral Cortex in *Lepidosiren*.")

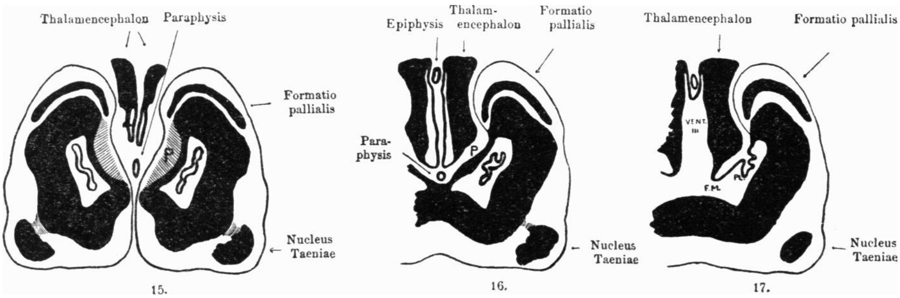

Fig. 5 consists of the three figs. 15, 16 and 17 taken from Elliot Smith's article upon "The Cerebral Cortex in *Lepidosiren*," and here reproduced to reinsist upon his interpretation of the paraterminal region in that form and to show the relationship of the "nucleus taeniae" so-called to the palaeostriatal region. His description of the figs. is appended.

Fig. 15. A diagram of another section (20. 2. 4.) of the same series cut immediately in front of the lamina terminalis. (140 A. 20. 2. 4.) × *circa* 20.

Fig. 16. Here the lower parts of the paraterminal bodies have fused to form the commissure bed or matrix for the cerebral commissures. The dorsal portion of the paraterminal body, marked *P* in fig. 15, has now become attenuated to form an epithelial membrane *P*. (140 A. 20. 3. 6.) 70 μ behind the section represented in fig. 15.

Fig. 17. Diagram of a section 40 μ behind that shown in fig. 16. (140 A. 21. 1. 2.) The paraterminal lamella (*P* in fig. 16) has now given place to the lamina chorioidea, which is invaginated into the lateral ventricle to form the choroid plexus (*PL.*).

F.M. Foramen of Monro. *vent. III* third ventricle.

feature in certain fishes, and also as we have seen in Mammalia, but may be inconspicuously developed in certain reptilian forebrains. But the palaeostriatum is always enclosed by a cortex of some kind; and I find myself in strong disagreement with the statements of certain authors (e.g. Johnston, '15) who find that the striatal areas are sometimes covered by, and sometimes free from, a migrating olfactory area. The palaeostriatum presents a typical arrangement throughout the vertebrate series, it is encapsulated by a "palaeostriatal cortex." Hence it is apparent that the tubercular cortex found in *Notoryctes* represents the remnants of that completer arrangement shown in primitive vertebrates such as the Dipnoi.

A second characteristic to be noted in the Dipnoan cerebrum (cf. fig. 4) is a certain area of cortex lying between the lateral boundary of the so-called "formatio pallialis" of Elliot Smith and the lateral boundary of the tuberculum olfactorium. It conforms to all the known criteria of the region called "hypopallium" by Elliot Smith in reptilian forms: for it lies between the above-stated regions and already shows a "bending-in" which has affected the contour of the ventricular wall. It is the part of the primordial cortex first to be affected by the stimuli arriving from diencephalic centres, and by neurobiotactic influence comes to assume a deeper position. It may be regarded as the forerunner of the claustrum and part of the corpus striatum of still higher forms, and is therefore the "primordium hypopallii."

In this communication I have deliberately refrained hitherto from discussing the Elasmobranch forebrain (which is perhaps the most unspecialised primitive vertebrate form known to us) because that structure has been analysed by Johnston ('11). I intend at a later date to give an account of the Selachian forebrain in which I shall enter into a detailed criticism of that author's conclusions, but in this communication I shall refer only to certain points directly relevant to the matters under discussion here. *Lepidosiren* presents us with an indubitable homology on account of the macroscopical clearness of its tuberculum olfactorium, its definite relation to the simple palaeostriatum and the obvious meaning of the remaining cell masses.

Exactly the same formations are, however, to be seen in the Selachii and even in the specialised and retrogressive Amphibia. A comparison of Johnston's own figures ('11 and '13), and the distribution of the cell areas as depicted by J. Stuart Thomson ('18–'19), with fig. 6 will disclose this fact unappreciated by either of these authors, which is all the more remarkable since Röthig had pointed out this "rudiment of the epistriatum" in 1912. After discovering this rudiment as figured in his paper ('12), it is surprising that Röthig himself should have had any doubt concerning the cortical nature of the epistriatum (cf. his figures for *Hynobius*, *Cryptobranchus*, etc.). Prior to my examination of the *Lepidosiren* cortex I was quite unaware of Röthig's facts, and although there is not in the Amphibia (owing to its retrograde development) the same degree of cortical differentiation that one finds in the Dipnoan, the homology of the several parts is precise and unquestionable.

Preparations of the Selachian forebrain stained by the Weigert or Bielschowsky methods exhibit the nature of the factors actually at work in the production of this so-called "Epistriatum-Anlage" or as I have already named it "primordium hypopallii." In a transverse section (stained by the Weigert method) through this brain in the region of the distribution of the lateral olfactory tract (fig. 7) it will be seen that, medial to this nucleus of the lateral olfactory tract (*nuc.lat.olf.tr.*) there is a mass of fibres which have a different direction, for they course upwards and laterally, as if issuing from the main forebrain bundle, and are distributed to an area abutting upon the ventricular wall and forming the hypopallial ridge.

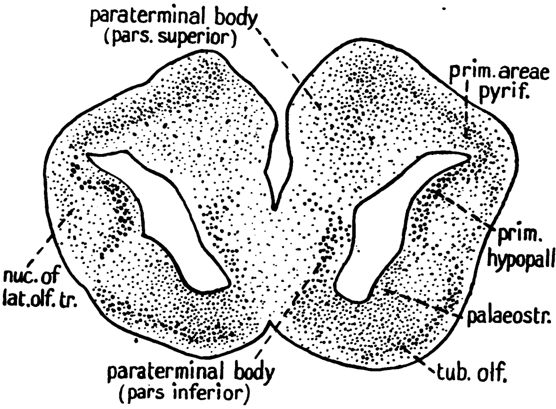

Fig. 6

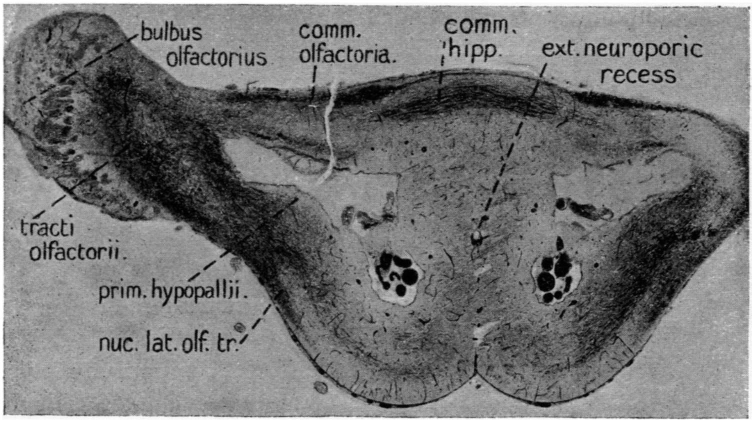

Fig. 7. Actual photograph of a transverse section of cerebrum of *Scyllium* (prepared by the Weigert method) to demonstrate the distribution of the fibre tracts in the region. *comm. olfactoria* = the so-called "corpus callosum" of Johnston.

If the cell masses of the same form are now considered in the light of what has already been shown it is clear from fig. 6 (copy of lantern slide taken from an actual photograph by Elliot Smith) and figs. 8 and 9, which show the distribution of the cell masses in an embryo of *Scyllium*, that the ventral part of the forebrain is a palaeostriatum ensheathed by a definite cortex, which is the tuberculum olfactorium, although the typical "islet" formation is not very characteristically developed, probably owing to its primitive lack of differentiation. Immediately lateral to the limits of this palaeostriatum, as indicated by the ventricular sulcus, there is a bulging in of the ventricle corresponding to a cellular mass continuous dorsally with the pallial formation. But this very definite cell mass lies deep to a cortical differentiation, which is the cellular area serving as the receptive nucleus of the lateral olfactory

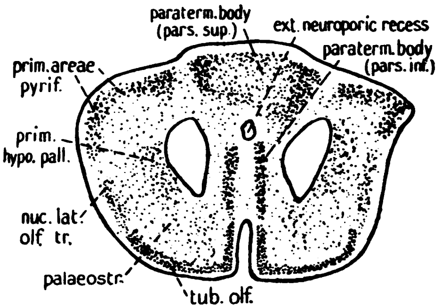

Fig. 8. Transverse section of cerebrum of developing *Scyllium* anterior to third ventricle to illustrate the cell-mass distribution.

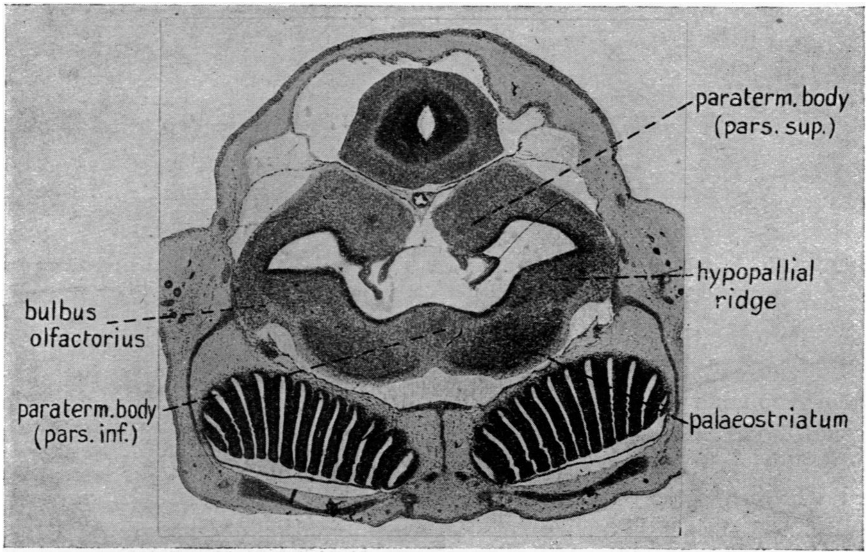

Fig. 9. Photograph of transverse section of developing *Scyllium* in region of attachment of the olfactory bulb. Note nucleus of lateral olfactory tract and the hypopallial ventricular bulging lateral to the palaeostriatum which is covered by the tubercular cortex.

tract as we have already observed. The distinctive nature of the structures referred to is thus shown diagrammatically in the foetal brain (figs. 8 and 9) where the disturbing influence of the developing tracts has not, as yet, reached its full expression. The common point where the primordium hypopallii and the lateral olfactory tract nucleus meet the pallial formation dorsally is to be recognised as the primordium of the pyriform lobe of higher forms. The deduction that we have in *Scyllium* the beginning of that process of a "dragging in" of a cortical structure to form those portions of the striatal complex known as the hypopallium in reptiles is obvious, and we have further an ocular demonstration of the activity of the factors in that process, viz., a superficial set of impulses (lateral olfactory tract) retaining at the surface (on Ăriens Kappers's principle of neurobiotaxis) a cellular layer clearly definable as the nucleus of the lateral olfactory tract, and a deep set of impulses coming in by way of fibres closely associated with the forebrain bundle, which, attracting the deeper cortical cells towards the source of their stimulus, cause the formation of the ventricular bulging, in a way exactly homologous to that shown by Johnston for the turtle ('15).

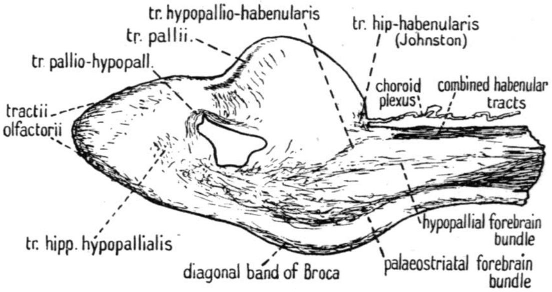

Fig. 10.

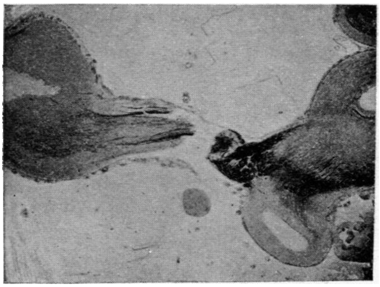

Fig. 10 *a*.

Fig. 10 *a*. Photograph of the section from which fig. 10 was drawn to show the relation of the diencephalon and mesencephalon to the cerebral hemisphere in *Scyllium*.

The probable source of this deep set of fibres associated with such an important modification of the originally simple pattern of the pallium will undoubtedly be discovered by a fuller study of the Selachian brain. My own studies of three series of specimens stained by the Weigert method, (transverse, sagittal and horizontal) controlled by the examination of Bielschowsky series, have convinced me that the forebrain bundle in *Scyllium* has two distinct components; one is the ordinary basal bundle constituents, which has long been recognised, while the other concerns the most dorsal and lateral portion. In both sagittal (fig. 10) and horizontal (fig. 11) series, this element of the forebrain bundle is seen to be quite distinct from the basal portion and its goal has been determined as the region I have described as the hypopallial primordium. I have no doubt (from my series) that it is a dorsal thalamic tract and it seems also to receive accessions direct from the tectum opticum. These accessions correspond with the "strio-tectal" tract found by Franz ('12) in various bony fishes. Johnston has described in the Selachian forebrain a so-called "somatic area," and Judson Herrick accepts this reading, as is shown by his retention of this conception in his *Introduction to Neurology*—though elsewhere ('17) he has recognised the striatal nature of Johnston's "somatic area." I have been unable to find any specialised area corresponding with Johnston's description, and more particularly I cannot admit that the structure defined by him is the special site of termination of the more recent thalamic and tectal tracts that appear in this cerebrum. Undoubtedly the hypopallial formation extends a long way posteriorly; but it can everywhere be distinguished from such unrelated elements as the tractus taeniae, which Johnston also traces to his "somatic area." But this and other divergent results I shall discuss in a future communication. That the recognition of the fallacy of these views is of crucial importance is evident from an examination of the deductions made by Johnston from his data. He has reopened the classical dispute concerning the presence of callosal fibres in the hippocampal commissure, and in support of his thesis has claimed to have discovered a so-called "corpus callosum" in the Selachian forebrain. A study of his diagrams (or better still actual specimens of Selachian brains) will show that the fibres he has termed callosal take their origin in an area including the lateral olfactory tract and the lateral part of the tubercular cortex. I have therefore termed it the *commissura olfactoria* (see fig. 7). Specialised commissural connections of these primitive olfactory regions cannot be homologised with a structure so dissimilar functionally as the corpus callosum. This is derived from the neopallium

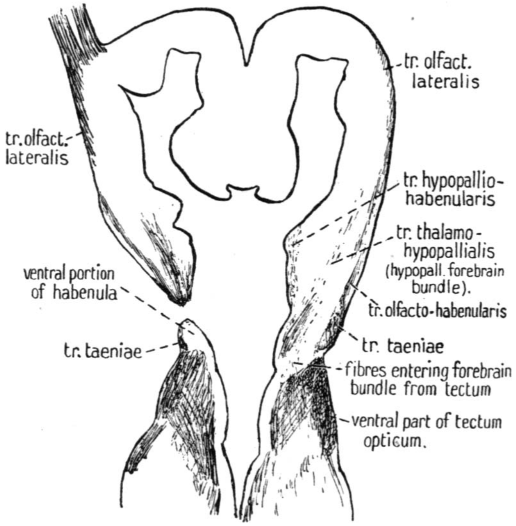

Fig. 11. Diagram of horizontal section of brain of *Scyllium* to illustrate in particular the afferent and efferent paths of the hypopallial primordium.

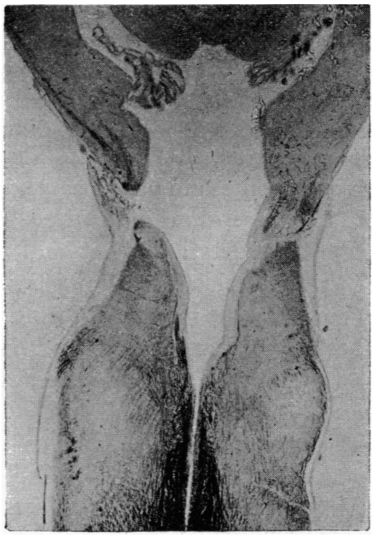

Fig. 11 *a*. Actual photograph of the section from which fig. 11 was drawn.

which is not yet differentiated in fishes. As we now know, the neopallium appears definitely for the first time in the Reptilia and the site of its origin is closely related with the anterior end of the hypopallial region. The appearances in this particular part of the Selachian forebrain are highly interesting and suggestive of a foreshadowing of the neopallium: but their consideration will have to be deferred to my later communication. Meantime it is to be recognised that this anterior extremity of the hypopallium has no relationship whatever to Johnston's fictitious "corpus callosum."

THE FATE OF THE NUCLEUS OF THE LATERAL OLFACTORY TRACT

Reference to figs. 6 and 8 shows how this nucleus bears a very precise relationship to the hypopallial primordium. This is an anatomical arrangement concerning the nature of which I was for a long period greatly exercised, seeing that Elliot Smith had described the continuity of the hypopallium with the pyriform cortex, but had not entered into other problems concerned in the process of evolution of the striatal complex. The study of the tract-distribution has however given the clue, and obviously the study of the cerebrum of *Sphenodon*—in order to understand what had become of this lateral olfactory nucleus—was of considerable moment. Owing to the liberality of Prof. A. Dendy I had the opportunity of studying the development of its striatal complex. This study revealed a continuous series, from the simple form resembling the condition found in the Selachian brain to the fully developed adult described by Elliot Smith. During development (e.g. fig. 12) there is to be recognised a small, though definite rudiment of this nucleus perforated by the lenticulo-striate artery, and even in the adult *Sphenodon* some scattered nuclei, representative of this primitive structure, are to be recognised. In the course of his paper ('20) Elliot Smith corrected his earlier conception and pointed out that the lateral edge of the pyriform primordium is continued into the hypopallium "without any disturbance of the superficial layer of the pallium, which still remains in unbroken continuity with the surface of the palaeostriatum, but without the intervention of any furrow." It will be seen that my interpretation of the facts (as illustrated by this comparative study) is that the infolding of hypopallium is merely the expression of an exuberant

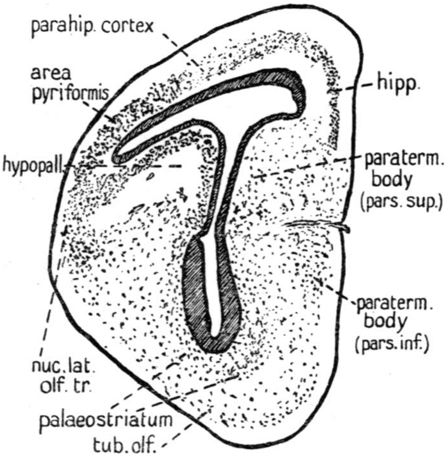

Fig. 12. Transverse section of brain of *Sphenodon* (stage *R*) to show condition of the nucleus of the lateral olfactory tract (*L.O.T.*) at this stage.

growth of the internal layer of the "primordium hypopallii" in the Reptilia, which has caused a bulging inwards of the ventricular wall, while the unbroken contour of the surface is merely the exhibition of the influence of the fibres of the lateral olfactory tract in keeping a small cellular layer at the surface.

It would have been unnecessary to have emphasized this fact were it not that many Reptilia fail to demonstrate the diagrammatic "cortical" continuity of the hypopallium of *Sphenodon*, or of *Lacerta* as figured by De Lange. It is apparent from the study of the turtle (Johnston, '15) and the alligator (Crosby, '17) that there are in these forms certain anomalous conditions of the striatal complex not easily reconciled with that of more archaic forms. The same is true of the striatum in snakes and monitors. What the exact explanation of all the forms of striatum exhibited by these families is we are not yet in a position to say. In some reptiles, such as *Varanus* (e.g. Elliot Smith's paper, '20), there is a very diffuse scattering of the hypopallial cells, in others it does not seem unlikely that there is a spreading out laterally of the palaeostriatum, to separate the hypopallium and the nucleus of the lateral olfactory tract (Johnston, '15); and in these it would seem that the division of the original cortical cell mass and the entrance of the fibres causing the differentiation of the hypopallium, have supplied the path for the spreading referred to. Further, much of the complexity of this interesting site is to be understood, when it is recognised that the adjacent superficial areas (pyriform lobe, superficial layer or nucleus of lateral olfactory tract, and tuberculum olfactorium) are subject to the influence of identical stimuli—hence a tendency to closer grouping of the masses, and homogeneity of structure, with an obscuring of the phylogenetic landmarks. That the embryological history, however, depicts the several stages in the phylogenetic development of these structures has been demonstrated by Elliot Smith even for man.

THE AMYGDALOID COMPLEX

With the historical aspect of this problem I do not intend to deal, for it has been well summarised by Völsch ('06) who has pointed out the conclusions arrived at by Meynert ('67), Mondino ('85), Ganser ('82), Honegger ('90), Ziehen, Kölliker, Cajal and other observers whose researches are for the most part restricted to the mammalian orders. In 1867 Meynert insisted upon the close relationship between the claustrum and the amygdala, but despite our advance in knowledge of the fibre tracts and the means of investigating them, the amygdaloid complex has remained unravelled.

To keep the issues clear, this division of the corpus striatum is considered separately. The first striking observation in regard to this portion of the striatum in *Notoryctes* which confronted me, was that in any typical section of the region (e.g. fig. 13—Section C. 3. 5. of this series) there was very definite evidence of a "cortical" layer of cells covering all parts of the corpus striatum, including the region known as the amygdala. Further the amygdaloid complex has a very definite location between the hippocampus medially and the pyriform lobe laterally, and the transition from subiculum to amygdala is not very apparent. From Johnston and Crosby's descriptions it is obvious that essentially the same relationships hold good for this region in the turtle and the alligator, where the so-called amygdala is treated as a complex of the homologue of the nucleus of the tractus pallii (in fishes) together with the projection tracts of the lateral olfactory nucleus and pyriform lobe. The homology of the tractus pallii with a specific portion of the stria terminalis (olfactory projection tract of Cajal) may be regarded as established. It will therefore be evident, that if the homologues of the various components of the amygdaloid nucleus of higher forms can be isolated in the Selachian forebrain, we are in a position (owing to the definite homologies existing between the reptilian and mammalian forebrain) to explain the mammalian modifications.

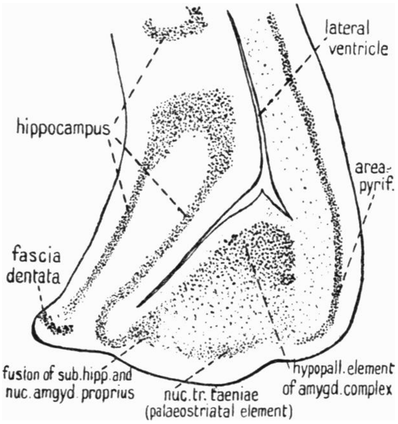

Fig. 13. Ventral half of a transverse section. (C. 3. 5. of this series) of the cerebral hemisphere in *Notoryctes typhlops* to illustrate the components of the amygdaloid complex at this level.

THE ELEMENT *A*

The destination of the tractus pallii in the Selachian forebrain is the posterior and lateral part of the roof of the forebrain. Its situation is very definite—between Johnston's "primordium hippocampi" medially and the primordium of the pyriform lobe and nucleus of the lateral olfactory tract laterally—in short it corresponds with at least part of the region I have indicated in *Notoryctes*. This cortical area in *Scyllium* (fig. 14) is situated very deeply abutting upon the dorsolateral aspect of the "posterior arm of the ventricle" and is to be distinguished by the shower-like appearance of the fibres of the tractus pallii as they pass in from the superficial tract. It is to be noted that the region is quite separate from and unrelated to the other elements grouped with it in higher forms

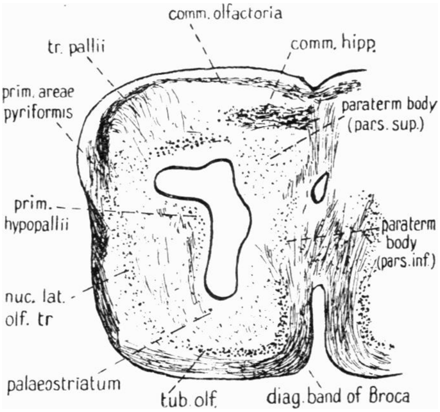

Fig. 14. Transverse section of cerebrum of *Scyllium* (adult) to show the distribution of the tractus pallii and the situation of its nucleus. Drawn from specimen stained by Bielschowsky method.

as the "amygdaloid complex." In this posterior part of the forebrain (cf. fig. 9) the palaeostriatal region is mainly occupied by the forebrain bundle, and is continuous with its fellow of the opposite side through the nucleus preopticus. The hypopallium is relatively small, and is found to be the site of origin of a descending tract. But its cellular layer is continuous laterally with the region into which the tractus pallii discharges. The posterior limits of the pyriform and lateral olfactory tract elements are hard to distinguish, but these with the palaeostriatal cortex of this region (i.e. the nucleus taeniae) are the site of origin of important habenular connections.

Practically the same arrangement is found by Johnston for the turtle, and *Sphenodon* presents a diagrammatic relationship of the constituents in this region (fig. 15) the hypopallium and nucleus tracti pallii (*Sph. I.* 33. 1. 3) still preserving their ventricular position and their relationship to one another and to the hippocampus. The isolated character of "the large-celled medial nucleus" constituent of the complex has been insisted upon by Johnston in his description of the cell masses in the turtle. It may be referred to as the "amygdala proper" (Johnston's medial large-celled nucleus, Crosby's ventro-medial nucleus—though the latter author's failure to separate the subiculum hippocampi from the ventro-medial nucleus, throws some doubt upon the exactitude of her delimitation of this region). At the same time, Johnston's identification of the medial large-celled nucleus in diagrams 15 and 16 in his paper ('15) is incorrect. This region is not a portion of the amygdala proper, but is the palaeostriatal cortex, here quite distinct, and as is evident in fig. 15 of this paper, forms the nucleus tracti taeniae.

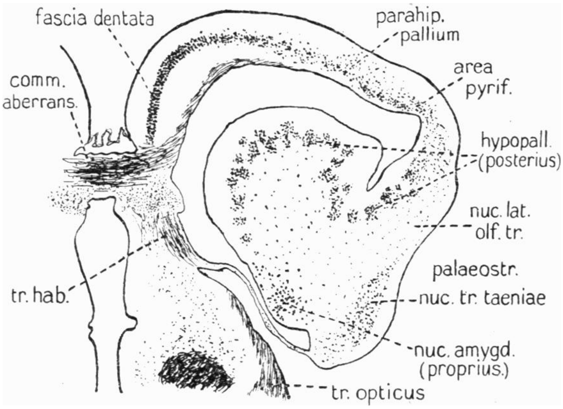

Fig. 15. Lateral section of adult *Sphenodon* to illustrate the morphological relationship of the amygdaloid complex. See text. (Dendy's series *Sph. I.* 33. 1. 3.)

In their *Anatomical Guide to Experimental Researches on the Rabbit's Brain*, Drs Winkler and Potter (fig. xi, reproduced here as fig. 16) have identified three separate cell-masses lying in the space between the pyriform lobe and the tractus opticus, terming them respectively the nucleus amygdalae, subiculum cornu ammonis and zona presubicularis.

This complex has also been the subject of an extensive and painstaking research by Max Völsch ('06 and '10–'11): but, as his investigations were limited to the Mammalia, he found little more than a progressive differentiation in this area when traced through the series. His work has been of significance however in determining that for all mammals the amygdaloid complex can be roughly divided into the three components outlined by Winkler and Potter and insisted upon in this paper.

Accepting then the fundamental division of the complex into three regions, it is the "zona presubicularis" of Winkler and Potter or "basaler Spitzenkern" of Völsch that corresponds with the "large-celled medial nucleus" of Johnston (amygdala proper) and seems to be the homologue of the nucleus of the tractus pallii in fishes.

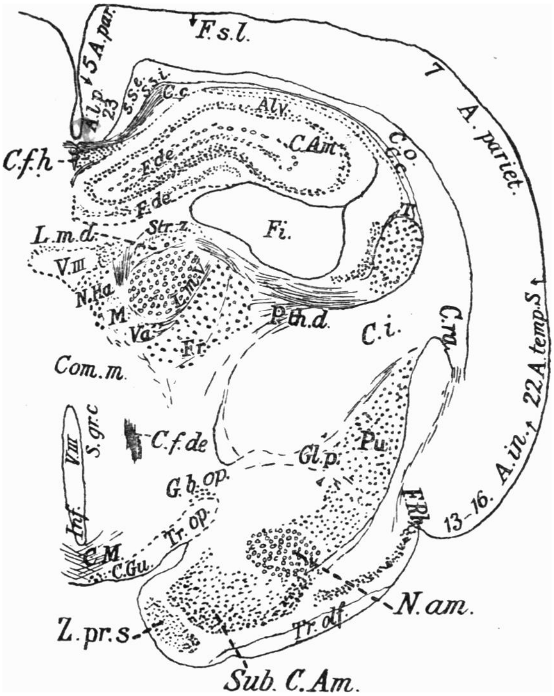

Fig. 16

It is well to recollect that Cajal (p. 723) states for mammals that: "Le noyau amygdalien (the amygdala proper) émet très certainement des fibres qui vont au taenia (semicircularis) mais jusqu'à présent il nous a été *impossible de constater le fait* de visu." Further, although Kölliker ('96) regarded the tract of the so-called taenia semicircularis as arising from the pyriform lobe, lenticular nucleus and amygdaloid nucleus, he nevertheless considered it as an annex of the striatal region, and not an olfactory tract of the third order as did Déjerine. Kölliker's interpretation agrees with Cajal's. Two points concerning Cajal's observations are of the highest importance in the present discussion. First, that direct olfactory tracts never enter the amygdaloid nucleus proper, and second, that he was unable at any time to find a portion of the taenia semicircularis fibres *arising* from its cells, although he carefully searched for such a constituent. He did however believe that some fibres arose from the "cortical" part of the amygdala proper and entered the taenia.

There is no doubt that the one and only area conforming to such a criterion in the Selachian forebrain is this area of distribution of the tractus pallii. The tractus pallii takes origin in the hypothalamus in the cells lining the walls of the large tuber cinereum of these forms, and after extensively decussating just behind the optic chiasma travels partly superficially to, and also amongst, the optic tract fibres to take up a position laterally in the telencephalon medium, until it is distributed (in the manner described above) to the dorsolateral part of the posterior portion of the telencephalic wall and roof.

Kappers and Theunissen ('07) and Kappers and Carpenter ('08) have confirmed the important finding of Wallenberg by a study of degeneration experiments, that "there is one ascending hypothalamic bundle, and one only to the forebrain of animals with a normal forebrain."

Johnston indeed ('09) states that the "tractus lobo-epistriaticus in fishes is believed to carry up gustatory impulses to the epistriatum from the tertiary gustatory centres in the hypothalamus," and has therefore concluded "that the 'epistriatum' must be regarded as a correlating centre for smell and taste and so be a forerunner of the smell-taste cortex." This use of the unfortunate term "epistriatum" can only be deplored, for by the "tractus lobo-epistriaticus" Johnston undoubtedly refers to the one definite tract associating the hypothalamus with the cortex, and this in fishes is the tractus pallii. In Reptilia and Mammalia it is a very definite constituent of the taenia semicircularis which goes to a restricted portion of the so-called "amygdaloid complex"—it is the nucleus amygdalae proper.

There must be some fibre tract which carries into the vertebrate forebrain those impulses, which, when transmitted upwards from their receptive nucleus in the medulla oblongata, are interpreted as sensations of taste. Such a component in the forebrain of fishes would necessarily be large, as taste is one of their dominant senses. Seeing that the tractus pallii is the only ascending tract from the hypothalamus to which Herrick has traced relays from the primary gustatory end nuclei in the medulla, the inference is justifiable that the primary importance of this tract in fishes and the persistence of its homologue throughout the vertebrate series, is due to this function which it subserves. In the Selachian, there is a large correlation bundle connecting the area of distribution of the tract possibly with the hippocampus and certainly with the anterior end of the hypopallial formation. It may be that this latter region is the primary seat of those disturbances which presaged the birth of the neopallial primordium.

Landau ('19) has pointed out that even in the human brain the cells of the nucleus amygdalae are continuous with those of the hippocampus. This is certainly true in Selachians and the reptiles and hence there is a further link here in the chain of phylogenetic evidence. He states that there is a tract connecting the two, and though this may be the case in the Selachian brain, the most apparent connection of the amygdala (nucleus tracti pallii) anteriorly is with the anterior end of the hypopallium (see fig. 10, tractus pallio-hypopallialis).

If the tractus pallii is the bearer of those impulses which are interpreted as sensations of taste in the cerebrum, we are justified in interpreting the amygdaloid nucleus proper and the amygdaloid tubercle associated with it (first named by Kölliker in the rabbit), as the site where these afferent impulses terminate in the mammalian brain.

The superficial position of this element of the complex, which the work of Völsch has shown to have little or no relation to the ventricle in most mammals, calls for some explanation. Indeed he has named it the "basaler Spitzenkern." Apart from those stresses operating in this region, to which I shall be later drawing attention, two facts are to be noted; first, that the nucleus is under the neurobiotactic influence of a superficially placed tract (tractus pallii), second, that Völsch himself has shown how pure mechanical factors of growth can result in the movement of large areas (his nuclei *M* and *T*) from a ventricular situation. It is of some significance that Völsch was unable to confirm the statement of Ganser "that there is a contribution from this nucleus to the anterior commissure," and further that he, too, could not determine whether it was an efferent nucleus. Such then is the status of the element *A*, which may also be termed the "pallial element" of the amygdaloid complex.

In putting forward this hypothesis I am not unaware of the contentions of the American School of neurologists. Far from being deterred by the "epistriatal" hypothesis (of '09) to which I have already referred, they have insisted that taste impulses are carried to the forebrain in the medial forebrain bundle by a tract as yet undiscovered, that this tract discharges into the hippocampal formation, and therefore the hippocampus, being connected by relays of neurones with so-called "visceral" centres in the lower parts of the brain, is an olfacto-visceral correlation centre. Smell is claimed to be a "visceral" sense; and so, in contradistinction to a so-called "somatic" cortex, the American neurologists refer to a "visceral" representation in the cerebrum. These series of gratuitous assumptions are so utterly devoid of any justification that it hardly seems worth while to embark upon an exposure of their fallacy. By the method of argument adopted by Johnston—classifying any mass connected by a fibre tract directly or indirectly with a visceral or somatic nucleus—it would be possible to present a case for the view that any part of the central nervous system whatsoever was either visceral or somatic, as it suited the predilection of the arguer at the moment. In many fishes the taste buds are ectodermal, and satisfy all the requirements of an exteroceptive sense. At most, a taste-organ is a borderland mechanism which, although the balance of evidence may be in favour of such a conclusion, cannot be definitely accepted in the present state of our knowledge as visceral. Finally if the reasoning adopted leads not only to this assumption and those already mentioned, but also, when we have traced our "visceral" relays into the cerebrum, exercises its magic to such a degree as to make us interpret a thorough-going somatic, ectodermal and exteroceptive sense (viz., smell) as a specialised visceral sense, the limit of paradox is undoubtedly reached.

Roughly outlined, this is the obscurantist aspect of the above hypothesis, which has led to the search for a somatic cortex where it did not exist and has created difficulties that have prevented the appreciation of the full significance of the neopallial primordium. The names "visceral" and "somatic" reduce forebrain terminology to an absurdity, and should be completely discarded if the issues are to remain unclouded.

THE ELEMENT *B*

The second element in the constitution of the so-called amygdaloid complex is a cortical layer of cells which includes the nucleus of the diagonal tract of Broca, which in Selachians and even in *Ornithorhynchus* seems inseparable from the cortex I have termed tubercular (Johnston's area superficialis basalis). This tract travels antero-medially to be distributed to the paraterminal region. The remaining constituents of this element are the areas of origin of efferent tracts such as the cortico-habenular tracts (which are represented in *Scyllium* by efferent tracts first from the posterior part of the "primordium hippocampi" of Johnston, second from the nucleus of the lateral olfactory tract, and third the tractus taeniae, which, arising from a specialised part of the postero-lateral portion of the tubercular cortex adjacent to the optic chiasma, passes dorso-posteriorly (the most lateral structure in this region of the telencephalon medium) and runs to the habenula. It is to be recognised that the anterior commissure is a scattered structure in *Scyllium* and that the stria terminalis as a distinctive structure is not observable therein, though it is probably represented by some few fibres, as also is the poorly developed "fornix" system. The characteristic line of olfactory discharge is ostensibly through the habenular system. There may also be a small efferent system in the tractus pallii itself, but of this nothing certain is known. At any rate it must be clearly understood that these efferent paths adjacent to the pallial tract (amygdaloid) cortex only secondarily enter into the constitution of the so-called amygdaloid complex. The nucleus of the diagonal band of Broca (when distinct from the tuberculum olfactorium) and the nucleus taeniae (site of origin of the tractus taeniae) are definite cortical areas.

In Selachians the site of origin of the tractus taeniae (somatic area of Johnston) is so clearly cortical as to have misled Johnston. It covers the palaeostriatum. Throughout phylogenesis this relationship of the nucleus of the tractus taeniae is preserved. Fig. 15 illustrates that this is true for *Sphenodon* and this "Rindenabtheil" of the amygdaloid complex of Völsch is the area which in the turtle Johnston has failed to distinguish from his "large-celled medial nucleus." The habenular tract arising in this nucleus (a true cortex in Selachians) overlying the palaeostriatum is to be regarded probably as the most primitive efferent path through the habenula. When a true olfactory cortex in the shape of a pyriform and a nucleus of the lateral olfactory tract appeared lateral to the palaeostriatum, its posterior efferent fibres utilised the path laid down by the tractus taeniae. These areas lying adjacent to one another and subserving similar functions are to be recognised in the Reptilia but not as clearly as in Selachians. In the Reptilia too, the problem is complicated by the fact that many of these efferent fibres utilise the more direct path to the hypothalamic region, omitting the synapse in the habenula. They appear to have found the path to the hypothalamus along the line of the tractus pallii which they accompany and would undoubtedly utilise the path of the efferent portion of this tract if such exists. This would explain how the more primitive habenular efferent system characteristic of Selachians may give rise to the taenia semicircularis and stria terminalis systems which are found from the Reptilia onwards.

What natural tendency there is for these similarly-functioning areas to come closer together is heightened in the Reptilia by two factors; first, actual stretching of their axones in the so-called "olfactory projection tract of Cajal" to form the characteristic taenia semicircularis; and second, the expansion of the cortex represented now by a definitely developed hippocampal formation, a true pyriform and a nucleus of the olfactory tract, a huge parahippocampal cortex and lastly the primordium neopallii.

The net result of all these factors of a mechanical nature and undoubtedly also active neurobiotactic influence is to heap the primitive palaeostriatal cortex into a nuclear mass: but even in the specialised mammalian classes it will be recollected that Cajal found fibres arising from that region called by him "cortical part of the amygdala". An examination of his text and figures (*op. cit.*) shows that this region corresponds with that termed subiculum hippocampi by Drs Winkler and Potter. It is indeed continuous in Mammalia (owing to the "extrusion" of the "nucleus amygdalae proprius" from its ventricular position as the nucleus tracti pallii in the Selachian forebrain) with the subiculum on the medial aspect and the pyriform laterally. This region discharging into the same areas as the posterior part of the pyriform lobe and lateral olfactory tract is homologous with the nucleus tracti taeniae. Like that region—so clearly differentiated in Dipnoi and other fishes—it is continuous anteriorly with the cortex of the tuberculum olfactorium and nucleus of the diagonal band of Broca, and is the relic of probably the most primitive lines of discharge of correlated olfactory impulses through the habenula, and in higher forms through the hypothalamus also. It may be regarded as the most posterior portion of the "palaeostriatal cortex."

The work of Völsch has shown that this mass is a "Rindenabtheil." This area he has copiously described and figured and we can unhesitatingly regard it as the structure termed the "subiculum cornu Ammonis" by Drs Winkler and Potter, the element *B* of both this paper and that of Völsch, or what may be far better designated as the "palaeostriatal element" of the amygdaloid complex.

That this association of fundamentally differing parts has not been clearly conceived is shown by the fact that it is dealt with "en bloc" by certain writers (e.g. Kappers, '08, in stating that the "secondary epistriatum which is closely related with the tertiary smell-cortex comes to take a wholly caudal and basal situation as the nucleus amygdalae"). This "secondary epistriatum" of birds is probably a far more highly differentiated area than, but is entirely homologous with, the "hypopallium posterius" of this article. Its relationships are most distinct, and will receive immediate attention.

THE ELEMENT *C*

There is a conspicuous element in this morphologically posterior part of the forebrain which, as far as my knowledge goes, has either been unrecognised or wrongly interpreted by previous investigators. If horizontal sections of the brain of *Scyllium* (fig. 11) be examined in series it will be discovered that in a region, corresponding in situation with the hypopallial rudiment posteriorly, a tract takes origin. It is difficult to distinguish in specimens prepared by the method of Weigert exactly where the posterior limit of the afferent tracts to, and the anterior limit of the efferent tracts from, this longitudinally differentiating hypopallial rudiment, are to be set. In short the most anterior region is mainly an afferent nucleus while the posterior is mainly efferent. In *Scyllium* this posterior efferent part of the hypopallium gives rise to fibres which become bunched together forming the most medial fibre constituent of the region. It later meets the other efferent tracts with which it ascends to the habenula. It appears to be the main discharge mechanism for the newly differentiating hypopallial region.

Sphenodon provides us with a remarkable confirmation of this tentative explanation. The hypopallium in *Sphenodon* has a very definite double constitution for while the anterior part is solid in cell formation the posterior part has a scattered arrangement—a thing which is most conspicuous in longitudinal sections. Here we find also (figs. 17 and 17 *a*) that there has been a crumpling at the line of differentiation between the two portions of hypopallium. The study of the fibre tracts shows that while the anterior portion (figs. 17 and 17 *a*) is the goal of the afferent system from the thalamus, the posterior region discharges by a tract which runs at any rate for the most part to the habenula. It may also discharge in part to the hypothalamus in Reptilia. This hypopallio-habenular constituent, then, is clearly marked in fishes and in reptiles, and evidently must have its homologue in Mammalia.

The habenula gradually decreases in relative importance in phylogenesis and as has been pointed out an increasingly large portion of the efferent system utilises the more convenient passage through the hypothalamic region.

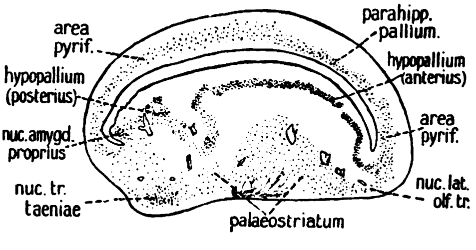

Fig. 17.

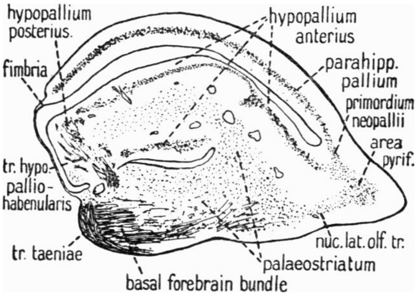

Fig. 17 *a*.

In the diagram reproduced (fig. 16) from the work of Winkler and Potter I have not discussed that element of the amygdaloid complex termed by them the "nucleus amygdalae." From what has been written it is clear that this portion of the complex corresponds in every detail with that posterior region of the hypopallium which discharges (in Selachii and Reptilia) through the habenula for the main part. It only becomes related secondarily to that portion of the palaeostriatal cortex which we have identified as the nucleus tracti taeniae and is very distinct in Selachians, being continuous with the hypopallial bulging into the ventricle. It has apparently been compressed during phylogeny owing to the mechanical changes affecting the expanding cortex and corpus striatum but must be recognised as originally a hypopallial and not a palaeostriatal constituent. It has therefore been designated as such in fig. 18, taken from the *Notoryctes* series, somewhat anterior to fig. 13.

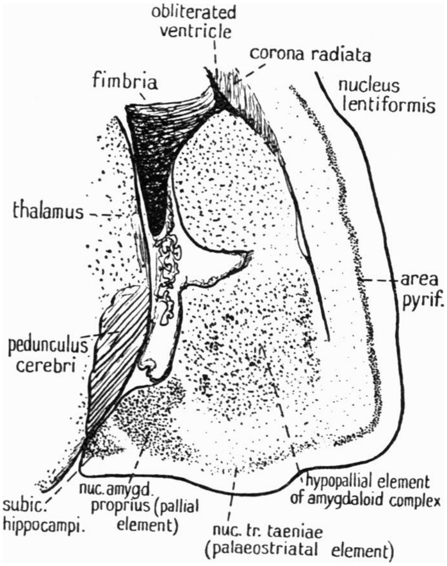

Fig. 18. Ventral half of transverse section of brain of *Notoryctes* some sections anterior to that represented in fig. 13 of this paper. Note the relationships of the three elements of the amygdaloid complex.

In his painstaking monograph Völsch has closely observed this region: "the nucleus amygdalae of Ganser," which he himself has termed the "Areas *M* and *T*." He has shown how in certain classes of Mammalia this mass in ontogeny is forced away from its ventricular position "by the development of the stria and the corpus striatum," and further, that its identity is rendered distinct by a kind of capsular formation, presumably of fibrils. Such a separate element of the amygdaloid complex is certainly the "nucleus amygdalae of Winkler and Potter," which has been regarded (as Völsch has shown) by some as portion of the lentiform nucleus, but by cytological structure and fibre connections it is an element of the amygdaloid complex. It is as clearly too the homologue of the hypopallium posterius (mihi) in Reptilia and forms the element *C* or more suitably the "hypopallial element" of the amygdaloid complex.

It is not part of my scheme here to criticise the work of Völsch. That it shows obvious fallacies has been recently exposed by Landau ('19) and as Elliot Smith has himself shown ('19) the claustrum is cortical; and so the views of Meynert ('67) to-day find confirmation. He (Völsch) thinks that the amygdaloid complex arises by a "sinking in" of what he has called the "intermediate area" of the pyriform lobe, and insists on the corroborative evidence of the two sulci to be found in this region. Such a view would rather naturally follow (see figs. 13 and 18) from researches which, as I have already stated, are confined to the Mammalia. It was the recognition of this that drove me from the study of *Notoryctes* to that of *Scyllium.* The phylogenetic history of this site of early transformations is to be sought in the lowliest and not the more highly organised Vertebrata. His insistence upon the finer cytology of the three constituent elements of the complex which he himself has discovered to be fundamental may have some justification when we are more fully acquainted with the causal factors in the production of its more intimate fibre connections. In the solution of this problem, the Reptilia may afford valuable evidence: for the hypopallium anterius of Reptilia is not a uniform structure. It shows a degree of differentiation which it should be possible to correlate with the different types of stimulus reaching it from the thalamus and it is to be expected that the hypopallium posterius is correspondingly complex. Here lies the key not only to the proper appreciation of the differentiation of cell structure within the three groups found in the mammalian amygdaloid complex by Max Völsch, but also to the understanding of the curious development of the striatal regions in Aves.

It must further be remembered that in the amygdaloid region deep to the "Rindenabtheil" (cortical part of the palaeostriatum) there are scattered cells of the palaeostriatum itself filling up the space between the three elements but not obscuring their identity.

A RETROSPECT

(the terms basal and cortical)

For the last quarter of a century and more, the attention of morphologists has been directed to the elucidation of the so-called basal regions of the forebrain. Nothing has done more towards a correct evaluation of the components in this district than the researches of Elliot Smith upon the nature of the "paraterminal body" and "commissure bed," which cleared the way for the appreciation of the hippocampus throughout the vertebrate series. His differentiation between a rhinencephalon and neopallium has been an illuminating conception for the whole of neurological phylogeny. But within the rhinencephalon itself there had been transformations of an exceedingly intricate character long before a neopallium emerged. And these were the changes concerned in the evolution firstly of the palaeostriatum and later of the hypopallium. What was the character of those impulses that first impinged upon the original simple olfactory reception centre, which later grew to be the dominant mechanism of the body, is difficult to say with certainty. They were probably imperfectly differentiated impressions coming up from the massively-responding thalamus of the primitive vertebrate. These newly entering impulses stimulated cell formation in the deeper part of the primitive cortex. The cells by neurobiotactic influence naturally tended to aggregate in the ventral and juxta-thalamic region, while the dorsum of the primitive vesicle remaining freer from disturbing influences became the seat of the formation of a true pallium (cortex).

The nature of the disturbances in a primitive olfactory mechanism caused by this early entrant tract is well illustrated in a diagram (fig. 19) taken from Kappers (*Anat. Anz.* Bd. XXXIII. 1908): but in that figure the more salient example of his neurobiotactic principle is exemplified, not by those cells migrating towards the source of stimulus in the olfactory bulb, but rather by those heaped up round the newly entering tract from below. Such a degenerate Amphibian forebrain shows practically no palaeostriatal differentiation, but in the more clearly differentiated brain of the Selachian the pallium in the region of the palaeostriatum is represented by a cortical formation which rapidly became variously modified for particular purposes. The process of differentiation of this "palaeostriatal cortex" has advanced to the degree recognised in its various elements as we know them, though all the steps in their history are still far from clear. It is probably, broadly-speaking, true that the tuberculum olfactorium proper is a receptive centre for olfactory impulses, that the diagonal tract of Broca is a correlation mechanism between the various olfactory cortices and that the tractus taeniae is an olfactory efferent tract, but there is just as probably much more. The Selachian forebrain also shows us how these earlier cortices developed out of an apparently homogeneous formation lying over the palaeostriatum. But it shows us more, for already we discover an additional disturbing element in the mechanism

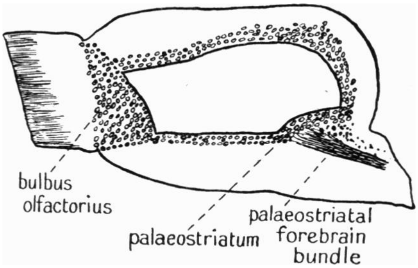

Fig. 19. Taken from Kappers (*op. cit.* '08) to illustrate the possible nature of the conditions arising by the entry of the first "thalamic" impulses leading to the differentiation of a palaeostriatum in the primitive olfactory receptor. Sagittal section of forebrain of *Axolotl.*

which we are now in a position to term a forebrain. It is the only ascending tract we know from the hypothalamus; and in Selachians it has reached a portion of the primitive pallium by a course through, and lateral to, the optic chiasma. It is the tractus pallii the relationships of which have already been discussed. It is possibly the bearer of impulses interpreted by this primitive forebrain as taste and it has its homologue throughout the vertebrate series as the "nucleus amygdalae proprius."

But by far the most significant event in the history of the vertebrate phylum is the entrance for the first time into the forebrain of the Selachian of that dorsal thalamic and presumably also tectal group of fibres, which, passing through the palaeostriatum, invade the pallial formation beyond it and lead to its differentiation into two definite regions, which we have recognised as the hypopallium and nucleus of the lateral olfactory tract respectively. Concerning the impulses borne by this fibre tract we are still ignorant, but it is probable that they are concerned with some degree of tactual discrimination, and the coarser appreciation of sight and sound. And significant is the fact that, together with the changes accompanying the entrance of this tract, there is a specialisation for the discharge by a particular path of the correlated response. This is conceivably by way of the tract here described as the hypopallio-habenular and its homologues.

The origin of the neopallial primordium is a further advance which affects the anterior portion of the hypopallium. It is apparently foreshadowed in the Selachian but it is very clearly present in reptiles, as has been shown by Crosby, Elliot Smith, and Woollard (in a paper read before the Cambridge meeting of the Anatomical Society), and, as I have personally observed, even in the archaic *Sphenodon.* It is a striking fact that these successive modifications of the original olfactory mechanism have affected successively more and more anteriorly lying portions of the forebrain, and that then, the expansion of the region invaded has led to large alterations in shape and relationship of the various areas.

It is clear from these remarks that the usage of the terms "basal" and "cortical" will need definition if they are to remain intelligible expressions of neurological terminology.

Throughout the whole vertebrate series known to us there is no such thing as a pure rhinencephalon; in that primitive vertebrate which possessed a palaeostriatum only, this structure was an addition, a well-defined correlation mechanism composed of gross afferent and efferent elements. Even some term such as "archipallium" which was introduced by Edinger is quite inadequate without definition. There are four definite stages (and perhaps five—if we regard the entrance of the tractus pallii as a stage) in the development of the forebrain—an original olfactory receptor, or placodal stage, a palaeostriatal stage, a pallial stage, a hypopallial stage and a neopallial stage, and the terminology of the forebrain can only be rational when based upon this wide phylogenetic survey.

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