THE FOREBRAIN OF ALLIGATOR MISSISSIPPIENSIS

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FORTY-SIX FIGURES

CONTENTS

The olfactory system is highly developed in the reptilian forebrain. Not only are large basal nuclei present, but there is clearly differentiated cortex and all the important olfactory tracts of higher forms are represented. The larger part of the forebrain, then, is concerned in the reception of olfactory impulses and their correlation with incoming diencephalic impulses of various sorts. In fact, the diverse distribution of the incoming diencephalic tracts, each of which has its own characteristic functional significance, has been one of the prime factors in the differentiation of the forebrain into its various cortical and basal centers. Although the greater part of the reptilian forebrain is under the influence of the olfactory fibers, there is a considerable portion which receives a much smaller number of these fibers and is dominated by the ascending fibers from the somatic nuclei of the thalamus. Through these somatic diencephalic fibers, the functional motive for the formation of the corpus striatum and the neopallum has been introduced into the hemispheres and in the alligator forebrain these somatic centers are already beginning to take form and to establish certain characteristic and fundamental relationships which will be discussed later.

The specific distribution of the olfactory and the non-olfactory fibers, the positions and the relations of the various centers and, finally, an analysis of these data in terms of their functional significance, these are all essential to the adequate understanding of the morphology and the evolution of the forebrain. The present report is concerned with a description of these centers in the alligator forebrain and of the fiber tracts which put these centers into relation with each other and with the diencephalon. Finally, an attempt has been made to effect a partial correlation and interpretation of the factual data obtained.

The advice and assistance of Dr. C. Judson Herrick have made possible whatever there may be of value in these notes. For these things and for the opportunities accorded me in his laboratory, I wish to thank him most sincerely. I am indebted to Miss Jeannette B. Obenchain for assistance in technique and to other members of the Department of Anatomy of the University of Chicago who have given helpful suggestions. Mr. Streedain has very kindly made the drawings of the gross material and has lettered the drawings of the microscopic material and otherwise aided in preparing them.

MATERIALS AND METHODS

The animal chosen for study was Alligator mississippiensis. The individuals were small, varying in length from 30 to 55 cm. The drawings of the surface anatomy (figs. 1 and 2) were made from the brain of a 55 cm. alligator.

The silver impregnation methods of Golgi and Cajal and the toluidin blue method were the chief ones employed. Two rather imperfect series, one stained with Ehrlich's haematoxylin and the other by the Leuden van Heumen method, were used to check certain fiber tracts, but the paths described in this paper are almost entirely those brought out by the method of Cajal. These series were further supplemented by a transverse series stained with carmine and a second such series stained with haematoxylin (both the property of Dr. C. J. Herrick). One of the Cajal series was very kindly loaned by Dr. P. S. McKibben.

Several specimens were stained by various modifications of the Weigert method. While the results were very satisfactory for the study of parts of the brain below the thalamus, these preparations contributed little of value in the study of the connections of the cerebral hemisphere because practically none of the fiber tracts in this part of the brain at the ages here investigated have become myelinated.

HISTORICAL NOTES

Rabl-Rückhard ('78) gave an excellent description and some very clear pictures of the gross appearance of the brain of the adult Alligator mississippiensis. A brief description of the external form and some details of the microscopic anatomy of the same species were given by C. L. Herrick ('90), based upon young specimens under 45 cm. long. Figures of the alligator brain are given in Wiedersheim's Comparative Anatomy and other figures and descriptions of the external form are scattered throughout the literature and it is unnecessary to enter into a detailed account of the gross relations, the essential features of which are shown in figures 1 and 2. DeLange ('11) presents a series of photographs of surface views of reptilian brains, among which are those of Alligator sklerops, and in a later paper ('13) the same author publishes a series of twenty sketches of cross sections through the thalamus and the midbrain of this species. Unger ('11) has given a brief account of structure and fiber tracts of the forebrain of young specimens of Alligator lucius and Crocodilus niloticus which is preceded by an excellent summary of previous work on the forebrain of the Crocodilia.

Many workers have indicated the presence of an epiphysis in the alligator brain. The work of Albert Reese ('10) has shown the structure so named is a paraphysis and that no epiphysis is present in the alligator, even in the embryo. In 1908, Reese published an account of the general embryological development of Alligator mississippiensis.

No attempt will be made to review systematically the extensive literature on the brains of reptiles in general, though references to this literature will be made as occasion may arise. Among the classical descriptions of the reptilian brain especial mention should be made of the valuable description and figures of the turtle brain published in 1895 by Mrs. Susanna Phelps Gage, in commemoration of whose important contributions to comparative neurology the current volume of The Journal of Comparative Neurology is dedicated.

CELL STRUCTURES

The positions of the nuclei of the telencephalon, with such details of their cell arrangement and cell structure as have been observed, will first be described, together with some more fragmentary observations on the diencephalic nuclei. Then using these facts for orientation, the courses and connections of the fiber tracts will be considered.

Olfactory Bulb

Johnston ('13) described the presence of a nervus terminalis in the reptiles. The preparations available are not suitable for the identification of this nerve in the alligator.

The cell bodies of the peripheral olfactory neurones lie in the olfactory epithelium of the nasal cavity. Their axones pass back as fibers of the olfactory nerve or 'fila olfactoria.' These fibers are unmyelinated and, after a very short course, enter the olfactory bulb. In its outer portion they break up into terminal arborizations which form synapses with dendrites of the mitral cells (figs. 23 and 24) and with other receptive cells of the olfactory bulb.

These places of synapse are called glomeruli and, scattered among these glomeruli, are a number of small cells which send their dendrites and, probably, their axones (though there is no proof in the material used for this statement), into the various glomeruli and so serve for the correlation of impulses. These are the type that Cajal calls intraglomerular cells.

Mitral cells (figs. 23 and 24). In transverse sections, the mitral cells have a ring-like arrangement around the granule cells as a center (fig. 13). Near the anterior end of the bulb they form a somewhat diffuse mass but soon take on their characteristic arrangements. They are replaced by other cell groups in the olfactory crus.

In the ventro-medial portion of the bulb, near its anterior end, the mitral cells form a curious depression or 'fossa.' This 'fossa' was first described by C. L. Herrick ('90), who said that a separate slip of the olfactory tract arises from it. The 'fossa' is very evident in both the toluidin blue series and those series prepared by the Cajal method. In the latter series, the fibers can be seen passing caudad from it and forming a part of the tractus olfactorius. There is a special thickening of the glomerular layer in that region, which pushes the mitral cells inward and causes the depression. Beyond being a point of entrance for a particularly large number of olfactory fibers, it does not appear to have any special significance.

A study of the toluidin blue preparations shows a considerable variation in the shape and size of the different mitral cells. On the whole, the nuclei tend to be rather large and are usually placed nearer the ventricular border of the cell. An abundance of Nissl substance is present in the cytoplasm.

The variations in size among the mitral cells are brought out most clearly in the Golgi preparations. Some of the different types observed there are illustrated in figures 23 and 24. Round, stellate, and large pyramidal forms are seen. A mitral cell usually has two main dendrites and several smaller dendritic branches. The larger dendrites are thick and thorny and enter into the formation of glomeruli with the incoming olfactory fibers. The smaller dendrites extend as far outward as the glomeruli but have never been observed entering into the formation of a glomerulus. They intermingle with the dendrites of other mitral cells and granule cells and so make one of the important elements of the plexiform layer. This plexiform layer, then, provides an additional mechanism for the increasing and the summating of stimuli.

The axones of the mitral cells arise from their ventricular border. A short distance from the cell body, the axones of the larger cells divide into two main branches of approximately equal size. One branch enters the granule cell layer and comes into synaptic relations with its neurones. The other branch runs caudad in the tractus olfactorius, giving off, at various levels, numerous fine collaterals into both the granule cell and the plexiform layers. The first branch and fine collaterals of the second branch are chiefly (although not entirely) to provide a mechanism for the summation and strengthening of stimuli. The main part of the second branch provides for the conduction of the impulse to the secondary centers. In some of the mitral cells apparently only one of the branches may be present. When this is the case, it is usually the one into the tractus olfactorius which is represented.

Granule cell layer (figs. 13 and 25 to 28). The inner granule cells occupy the inner portion of the bulb about the ventricle, next to its ependymal lining. Extending caudad, at about the beginning of the olfactory crus, this layer is replaced by the cells of the nucleus olfactorius anterior, although the material at hand has not permitted the drawing of so precise a line of demarcation as Johnston ('15) is able to do in Cistudo carolina.

In teleosts, Sheldon ('12) has called the whole mass a part of the nucleus olfactorius anterior and then explained that certain neurones function as granule cells. The conditions found in the alligator represent an advance in differentiation over those described for teleosts; yet even here it does not appear that the granule cell layer is so physiologically distinct from the nucleus olfactorius anterior since, in part, its cells still serve as secondary olfactory neurones.

The granule cell layer shows a wide range of types among its neurones. The following types, based on a study of Golgi preparations, have been distingushed among the granule cells of the bulb.

1. Intrinsic or type II cells. These neurones have small cell bodies, with dendrites that are short, thorny, and branching, and which pass out in every direction from the cell body. No axones can be distinguished. These cells are intrinsic neurones, serving for the correlation of impulses within the layer. Some of the smaller stellate cells appear to serve as intrinsic neurones, at least so far as can be judged from the material studied.

2. Stellate cells (figs. 27, 28). These are similar in appearance to the cells so named by Sheldon in the teleostean olfactory bulb. The cell bodies are angular or somewhat star-shaped as the name indicates. The dendrites are thick and thorny and many branched and extend out towards the periphery of the bulb. In the plexiform layer they interlace with the dendrites of the mitral cells and of the goblet cells. Some of the dendrites extend outward into the glomerular layer but it was not determined whether these dendrites actually entered into the formation of glomeruli, as Sheldon ('12) found to be the case in the teleosts. The axones in many cases form synapses with branches of the mitral cell dendrites. Sometimes they enter the tractus olfactorius, although they have been followed no great distance in it. Some of the smaller stellate cells do not send their dendrites outward beyond the cell bodies of the mitral cells. Furthermore the axones of such cells often end about other cells of the bulb and so serve as intrinsic neurones.

3. Goblet cells (figs. 25 to 27). These are large, oval cells whose dendrites are similar in appearance to those of the stellate cells. Sometimes the dendrites of the goblet cells reach the glomerular layer, and have been seen entering into the formation of a glomerulus. In other cases, the dendrites of the goblet cells do not enter the glomerular layer but are dependent upon the mitral cells for their stimulation. The axones of the goblet cells enter the tractus olfactorius, at least in some cases.

From the standpoint of their types of synaptic connection apparently three functions are served by the neurones of the granule cell layer. The first of these is that of diffusing and summating the incoming olfactory impulses and so strengthening the discharge into the hemispheres. This purpose is served by the type II cells, the stellate cells, and, in part, by the goblet cells (particularly those found in the anterior part of the bulb). All these cells receive their impulses by way of the mitral cells and do not send their axones into the tractus olfactorius.

A second group of these stellate and goblet cells send their dendrites into the glomeruli and their axones into the tractus olfactorius and so, from a functional standpoint, are practically mitral cells.

The third function served by neurones of the granule cell layer is that of acting as the cells of secondary olfactory nuclei. Such cells receive impulses from the mitral cells and send their axones into the tractus olfactorius. The goblet and stellate cells offer examples of this type of neurone.

Judging from what is known of the development and specialization of the centers of the central nervous system, it seems but fair to suppose that, in phylogeny, the centers of the olfactory bulb arose from undifferentiated central gray. Johnston ('98) has shown that in Petromyzon and in Acipenser, neurones of this mitral cell type are found all through the central gray. The same author ('15) has described, in Cistudo carolina, a granule cell layer in which are cells functioning as mitral cells.

Certain cells of the central gray (on the whole those nearer the periphery) will receive a larger number of the incoming olfactory impulses. Under the operation of neurobiotaxis (Kappers, '14) such cells will be drawn toward the periphery and, in this way, a mitral cell layer will be formed. Accompanying such a migration toward the surface and the consequent higher specialization, there will be a differentiation in form and in size to meet the greater demands.

Not all the cells left in the central gray will lose their connection with the fila olfactoria and so certain goblet cells and probably some of the stellate cells (although the proof for this is not absolutely clear) found in the olfactory bulb of the alligator illustrate this condition, for they lie in the granule cell layer—the position of the primitive central gray—yet aid in the formation of the glomeruli and send their axones into the tractus olfactorius. Sheldon ('12) has shown a similar condition in his description of certain stellate and goblet cells in the olfactory bulb of teleosts.

Other stellate cells and many of the larger goblet cells of the reptilian granule cell layer have lost their connection with the fila olfactoria and receive their impulses by way of the axones of the mitral cells. In turn, they send their axones through the tractus olfactorius and, from a functional standpoint, are secondary olfactory neurones. A similar state of affairs has been described by Sheldon ('12) for teleosts.

A smaller number of small stellate cells and goblet cells have lost their connection with the tractus olfactorius and discharge into the plexiform layer, serving apparently the usual correlating and summating function of granule cells. Are these the forerunners of the most highly specialized granule cells of higher forms?

Olfactory crus

The anterior continuation of three of the centers of the hemisphere are to be found in the crus (fig. 14). These are the nucleus olfactorius anterior, the pyriform lobe complex, and the hippocampus. Mitral cells are found in the olfactory bulb back to the point where it passes over into the crus. There they are replaced on the lateral side by cells of the pyriform lobe complex and on the medial side by the anterior continuation of the hippocampus. In the anterior end of the crus, the granule cell layer is replaced by the cells of the nucleus olfactorius anterior, which takes its characteristic ventro-medial position. The position, cell structure, and significance of these centers will be discussed immediately under the head of centers of the hemisphere.

Centers of the hemisphere

Both basal and cortical centers are found in this region in the alligator. The former will be described first. The term olfactory lobe will be used a number of times in the following description. By that term is meant the anterior portion of the hemisphere, including the secondary olfactory nuclei from the posterior end of the crus to the beginning of the primordial general cortex.

Nucleus olfactorius anterior (figs. 3 to 5 and 14). In the crus the nucleus olfactorius anterior occupies a ventro-medial position. It extends back into the hemisphere and runs caudad for some distance. It is gradually pushed away from the surface by the cortical layer of the tuberculum olfactorium and is directly continuous with the non-cortical part of that nucleus. Throughout most of its extent in the hemisphere the boundary between it and the anterior end of the caudate nucleus can not be defined. Johnston ('15) has described this nucleus in the turtle. He considers, however, that it makes up, for the most part, just the head of the caudate nucleus.

So far as has been observed in the preparations made after the Golgi method, the cells of the nucleus olfactorius anterior are round or goblet shaped and are comparable in form and general appearance with the goblet cells of the granule layer of the olfactory bulb. Figure 29 shows a goblet cell of this nucleus.

This nucleus is a secondary olfactory center, receiving impulses by way of the tractus olfactorius and discharging, through the axones of its cells, into the tuberculum olfactorium, the parolfactory region, and the hippocampus.

Area parolfactoria (figs. 7 to 9, 16, 17). The cell groupings found in the ventro-medial wall of the hemisphere in lower vertebrates have caused much discussion. Meyer ('95), Unger ('06), C. J. Herrick ('10), Johnston ('13 and '15), and a number of other observers have mapped out the cell groups in this region. They have not all agreed in regard to the embryological and phylogenetic significance of these cell masses and as a result a somewhat confusing nomenclature has appeared.

In his 1913 paper Johnston has discussed fully the relative positions and extents of the cell masses in this ventro-medial region of the hemisphere in cyclostomes, selachians, reptiles, and monotremes. Among the reptiles, he has described particularly the conditions found in the turtle. In regard to the alligator he says ('13, p. 387), "In Alligator mississippiensis the features described above (that is the relations of the primordium hippocampi and the parolfactory area in the turtle) are repeated so exactly that it is unnecessary to present separate drawings. There are differences in general form, and the area parolfactoria is relatively smaller than in the turtle."

In the turtle Johnston has pointed out the presence of a primordium hippocampi, ventral to the hippocampal formation. A similar primordium is present in the alligator and below this primordium and separated from it by a cell free zone and, in turtles, by a sulcus limitans hippocampi (Johnston, '13) is the area parolfactoria (in part, Herrick's septal area). This parolfactory area is divided into medial and lateral portions which, following Johnston ('15), have been termed in this account the medial and lateral parolfactory nuclei respectively. This area parolfactoria is not the lobus parolfactorius of Edinger.

Medial parolfactory nucleus (figs. 7 to 9, 16, 17). This nucleus consists of cells of the more medial part of the parolfactory area. In the anterior end of the hemisphere it cannot be sharply separated from the lateral part of the area but farther caudad it is separated off by the fibers of the medial forebrain bundle. This nucleus as it is here described is practically the same as the medial parolfactory nucleus described for Cistudo carolina by Johnston ('15). Medialward it is bounded by the nucleus of the diagonal band of Broca.

Lateral parolfactory nucleus (figs. 7 to 9, 16, 17). The lateral parolfactory nucleus bulges out into the ventricle. Ventralward it follows the ventricle and cannot be sharply separated from the nucleus accumbens, so that by some writers the whole cell mass has been called nucleus accumbens septi. Dorsalward this lateral parolfactory nucleus, in the more anterior region of the forebrain, is clearly marked off from the primordium hippocampi by a cell-free zone and, in the turtle, by the sulcus limitans hippocampi. Farther caudad, however, the line of separation between the two becomes indistinct. In the region just anterior to the commissure, if the writer has understood Johnston correctly, the sulcus disappears. Certainly in both the alligator and the turtle (Cistudo carolina) the cell-free zone disappears and there is no line of demarcation, so far as could be determined from the material available, between the primordium hippocampi and the more posterior portion of the nucleus parolfactorius lateralis. A cell mass is thus formed which has cells apparently of the type both of the primordium hippocampi and of the lateral parolfactory nucleus, although the latter type appears to predominate. Consequently, Herrick ('10) after a study of amphibian and reptilian material (including Lacerta, Cistudo carolina, and Alligator mississippiensis) and after an examination of embryonic reptilian brains from the Harvard collection, reached the conclusion that this nucleus was a part of his septal nucleus, consisting of cells of the basal region which had invaded this region, migrating upward along the descending hippocampal fibers.

Johnston ('13), on the other hand, has considered this intermediate cell group a part of the primordium hippocampi, basing his conclusion partly on the presence of the fornix fibers and the fibers of the hippocampal commissure, and especially on its position, as he believes from a study of embryonic material, above the neuroporic recess in a thickened portion of the lamina supra-neuroporica.

In the more anterior part of the brain, the ventro-lateral, small celled area (Johnston's caudate nucleus) is apparently continued around the corner of the ventricle to the medial surface (figs. 7 to 9, 16, 17). This continuation of the caudate has been termed nucleus accumbens by many observers. Johnston includes this nucleus accumbens in his nucleus parolfactorius lateralis.

It will be seen from the above discussion that the terms lateral septal nucleus (Herrick '10) and lateral parolfactory nucleus (Johnston '13 and '15) are not synonymous. If the writer has understood the authors correctly, the two masses compare as follows. The lateral septal nucleus (Herrick '10) equals the lateral parolfactory nucleus (Johnston '13 and '15) plus a part of the posterior portion of the primordium hippocampi (Johnston '13 and '15) minus the nucleus accumbens (Herrick '10).

Having had no opportunity to study reptilian embryological material, the writer is in no position to decide which nomenclature is the better of the two. A most thorough study of the nuclei in the developing brain will be necessary before anything definite along that line can be determined. For convenience the terminology of Johnston has been adopted except that the name nucleus accumbens has been retained.

The essential point is that in the alligator, in the region of the fornix fibers and other descending hippocampal systems, there is a cell mass which serves as a place of synapse for many of the descending fibers. This cell group has been identified in a number of reptiles besides Alligator mississippiensis. Furthermore, so far as is now known, there are two possible sources of origin for this cell mass. The first theory is that it is a specialization of a portion of the primordium hippocampi as a place of synapse between the hippocampus and the basal centers. The second theory implies that cells, situated in the basal region and serving as places of synapse for descending fibers, moved upward toward their source of stimulation according to the principle of neurobiotaxis (Kappers, '14) and invaded the region of the primordiun hippocampi.

Tuberculum olfactorium (figs. 5, 6, 7, 15). This nucleus begins in the hemisphere a short distance behind the olfactory crus. It is ventro-medial in position and is continuous anteriorly with the nucleus olfactorius anterior, from which it can be distinguished by the cortex-like arrangement of its outer layer of cells. Its inner portion is made up of small groups of cells which show, though not so clearly as in some forms, the arrangement into islands so characteristic of the highly developed tuberculum olfactorium. The cortical and non-cortical layers of the tuberculum olfactorium are shown in the drawings of the toluidin blue sections from this region (figs. 5 to 7).

Laterally the tuberculum olfactorium lies in close relation to the pyriform lobe, although its cortical layer is separated from the latter by an area of scattered cells which belong apparently with the nucleus of the lateral olfactory tract (see discussion of that nucleus). Medially the tuberculum olfactorium is in close relation with the parolfactory region.

The relations described here are in all essential points the same as those described for the tuberculum olfactorium of turtles (Johnston, '15). The differences in the two forms are to be found in the somewhat higher development of the islands of Calleja in the turtle and in the absence in the turtle of so well developed a cortical layer as is found in the alligator. The tuberculum olfactorium does not appear as a clearly defined nucleus in Amphibia. In certain Dipnoi (Lepidosiren) described by Elliot Smith ('08) it appears in an exaggerated form. The Golgi material available does not show the cell forms in this region.

Nucleus commissurae hippocampi (figs. 18 and 19). This nucleus is really only a specialized portion of the primorium hippocampi, consisting of clusters of cells of that primordium which are mingled with the descending hippocampal fibers and which collect particularly about the point of decussation of the fibers of the hippocampal commissure. The cells of this nucleus serve as a place of synapse for commissural fibers and as cells of origin for some of the fibers of the medial cortico-habenular tract. In fact cells of this nucleus accompany this latter tract until it enters the stria medullaris and are probably a remnant of the broad gray connection found in lower forms between the hippocampal and the habenular regions.

Nucleus commissurae anterioris (fig. 18). This name has been given to the cells forming the bed nucleus of the anterior commissure. They resemble in general character the cells of nucleus preopticus but are quite distinct in type from those forming nucleus commissurae hippocampi. The cells of the nucleus commissurae anterioris afford a place of synapse for some of the fibers of the commissural division of the stria terminalis.

Nucleus preopticus (figs. 9, 10, 18 to 21). This term has been applied to the cell mass which appears in the region of the preoptic recess just in front of the level of the commissures and which extends caudad still occupying this position. It passes over into the hypothalamic region with no definite line of separation between the two areas. The nucleus preopticus receives impulses from the stria terminalis, from fibers of the medial olfactory tract which have decussated by way of the anterior commissure, and, at its anterior end, from some few fibers of the tract of the diagonal band of Broca.

Interstitial nucleus (figs. 10, 19, 20). Cajal ('11, vol. 2, p. 723) described this nucleus and figured it in the mouse, calling it "noyau interstiel de la voie de projection de l'écorce temporale." He says further "Malheureusement, il ne nous a pas été possible de déterminer de façon précise les relations qui existent entre la bandelette semi-circulare et ce noyau, et cela à cause de la rareté des bonnes imprégnations. Ajoutans que cet amas de la région sousthalamique pourrait fort bien être encore un ganglion moteur."

Johnston ('15) has described the olfactory projection tract of Cajal for the turtle but has said nothing of the interstitial nucleus. In the alligator the nucleus appears in the preoptic region near the posterior end of the hemisphere as a ridge of cells extending lateralward in close relation with the nucleus ventro-medialis, arching dorso-medialward above the forebrain bundles and extending medialward into relation with the more dorsal part of the mass of the preoptic nucleus. It extends caudad throughout the preoptic region but in the hypothalamic region is gradually replaced by the hypothalamic nuclear ridge.

Part of the fibers of the olfactory projection tract of Cajal arise from the ventro-medial nucleus. Cajal ('11, vol. 2, p. 725, fig. 463) has shown some of the neurones of that nucleus giving rise to these fibers. Many of the fibers having such an origin quite probably send off collaterals among the cells of the interstitial nucleus. Part of the fibers of this olfactory projection tract arises from the interstitial nucleus. The tract passes caudad with the fornix into the ventral part of the hypothalamus.

Nucleus of the diagonal band of Broca (figs. 8, 9, 17). This nucleus was first described for reptilian brains by Johnston ('15) in the turtle, Cistudo carolina. It is present in the alligator in practically the same relations as in the turtle. It appears behind the level of the tuberculum olfactorium as a dense collection of cells arranged in a cortex-like layer in the ventro-medial angle of the hemisphere. It extends dorsalward along the medial surface as a somewhat less dense, cortex-like layer which comes into relation with the medial parolfactory area and cannot be sharply distinguished dorsalward from the cell mass of the primordial hippocampus. It extends from the ventro-medial region lateralward, as scattered clusters of cells, into relationship with the nucleus of the lateral olfactory tract. The nucleus of the diagonal band extends posteriorly just outside of the medial forebrain bundle into the region of the preoptic nucleus. It is accompanied, as in the turtle, by bundles of fibers which serve for connecting the lateral and medial olfactory areas. The writer is particularly indebted to Dr. C. J. Herrick for aid in identifying this nucleus in the alligator.

Basal nuclei of the lateral wall. Students of the reptilian brain have generally recognized two basal centers in the lateral wall of the cerebral hemisphere, the corpus striatum and the epistriatum, and some have recognized a third region distinct from both of these, comparable with the mammalian nucleus amygdalae. According to these observers, the epistriatum is the more dorsal member of the complex and is in continuity with the cortical lamina. The extent of this continuity varies in different reptiles, depending upon the species and the general form relations of the hemisphere, particularly upon the ventro-lateral extent of the ventricle. In Testudo graeca, DeLange ('13a, p. 113, fig. 8.) has shown that the epistriatum is continuous with the lateral or pyriform lobe cortex throughout its whole extent. Kappers and DeLange consider the epistriatum to be striatal in origin and to have acquired secondarily a connection with the cortical lamina. They consider the epistriatum an olfactory nucleus of the second order and the entire epistriatum complex the homologue of the mammalian nucleus amygdalae.

On the other hand, Elliot Smith ('10) has considered the epistriatum to be of cortical origin. He believes that the effecting of olfacto-somatic correlations in the reptilian hemisphere and, particularly, the entrance of tactual fibers into the dorsal part of the hemisphere lead to the disturbance of the morphological relations of the centers of the forebrain. He says "One curious manifestation of these disturbing influences is seen in the ingrowth (toward the lateral ventricle) of part of the overgrowing pallium, forming a structure to which Edinger gave the name 'epistriatum.' The epistriatum is not a part of the striate body but is cortical in nature. Moreover it is not a morphological subdivision of the hemisphere which can be identified in other groups of vertebrates, as many anatomists believe. It is merely a peculiar adaptation of structure to meet the conditions favorable to the reptile;—namely the disturbing influence of the recent admission of tactile impressions into the hemisphere."

In his 1915 paper, Johnston, following Edinger and Kappers (Kappers, '06, p. 9), suggests that the term 'epistriatum' be dropped, basing his suggestion on the facts that "the structure to which the term was first applied, does not appear as a special body or ridge in the turtle brain" and that "the author (Edinger) of the term uses it for at least three different bodies in the reptilian brain." The conditions found in the forebrain of Alligator mississippiensis certainly support Johnston's suggestion.

In the anterior end of the hemisphere of the alligator several large cell masses are found in the basal portion of the lateral wall. 1. There is a dorso-lateral area which includes a part or all of the 'epistriatum' as that term is used by some recent writers on the reptilian brain and is comparable with the dorsal ventricular ridge (Johnston, '15) in turtles, though perhaps not exactly homologous with that area. 2. Below the dorso-lateral area, in a ventro-medial position, are two nuclei which belong to the corpus striatum of Johnston. The more dorsal large celled mass is the ventro-lateral, large celled nucleus of this description, comparable with Johnston's nucleus lentiformis in the turtle. 3. The more ventral small celled mass is the ventro-lateral, small celled area of this description and is comparable with the area termed nucleus caudatus in turtles. 4. Between the dorso-lateral area and the ventro-lateral, large celled area, in the anterior end of the brain, there is an intermedio-lateral area which at first is closely tied up with the anterior part of the nucleus of the lateral olfactory tract, but later becomes continuous with the dorso-lateral area and probably is a part of that area. 5. The nucleus of the lateral olfactory tract is situated in the lateral part of the hemisphere, ventral to the dorso-lateral area and dorso-lateral and lateral to the ventro-lateral areas (the corpus striatum of Johnston's description). It lies in intimate relation with the intermedio-lateral area and is apparently continuous with it. Dorsalward it is at first clearly distinct from the dorso-lateral area but finally merges with it. Behind the level of the tuberculum olfactorium the more ventral part of the nucleus of the lateral olfactory tract becomes continuous with the nucleus of the diagonal band of Broca and then swings farther ventralward until it occupies the greater portion of the ventral region of the hemisphere internal to the cortex of the pyriform lobe and in close relationship with it. The nucleus of the lateral olfactory tract of the alligator, as the name is used in this paper, includes both the nucleus of that name and a small celled, ventral portion of the pyriform lobe as described in turtles. 6. In close relation with the nucleus of the lateral olfactory tract in the ventro-medial angle of the posterior half of the hemisphere is a nucleus to which the name of the ventro-medial nucleus has been given. This nucleus (figs. 18 to 21) gives rise to the projection tract of Cajal, and corresponds to the medial large celled nucleus described in turtles (Johnston, '15). 7. The outer ventro-lateral and ventral portions of this lateral wall are occupied farther cephalad by the cells of the tuberculum olfactorium and behind the level of that cell mass (8) by a part of the nucleus of the diagonal band of Broca. These two centers have been described previously. (For a more complete discussion of the extent, relations, and fiber connections of these nuclei of the lateral wall see the special headings.)

Dorso-lateral area (figs. 7 to 10, 12, 15 to 19). This area forms most of the large eminence which projects from the ventro-lateral wall of the hemisphere into the lateral ventricle and nearly fills that cavity. Its lateral aspect is exposed in the dissection illustrated in figure 2. The anterior end of the dorsal area is marked by the previously mentioned inward fold of the dorso-lateral cortex (figs. 5, 6, 7) which may be considered primordial general pallium. In the turtle, as many writers have shown, there is a pallium-like infolding throughout the whole extent of a somewhat similar area, the dorsal ventricular ridge of Johnston ('15). In all but its most anterior portion, the dorso-lateral area in the alligator is cut off from the pallial areas by the outward and downward growth of the lateral ventricle, so that the infolding can be plainly seen only in the anterior end of the hemisphere. The dorso-lateral area is bounded ventrally by the intermedio-lateral area and then by the ventro-lateral large celled area and ventro-laterally by the anterior end of the nucleus of the lateral olfactory tract (figs. 7, 8). Behind the ventro-lateral areas (the lentiform and caudate nuclei of Johnston) it is bounded ventrally by the posterior portion of the nucleus of the lateral olfactory tract (fig. 12). Olfactory fibers from the lateral olfactory tract distribute to the dorso-lateral area from behind the level of the general cortex infolding to the posterior end of the area. Ascending somatic sensory fibers from the thalamus also distribute throughout practically all parts of this region and, in some parts of the area, these somatic connections alone are present without admixture with olfactory fibers. This purely somatic region includes practically all the dorso-lateral area at the anterior end of the brain. Farther caudad an increasingly large amount of the lateral and dorso-lateral portions of this area receives olfactory fibers and only the dorso-medial portion is relatively pure somatic in type of correlation. The ridge of primordial general cortex implies a very close relation between the somatic dorso-lateral area and the general cortex.

The ventro-lateral areas as they have been termed in this description of the alligator brain are apparently directly comparable with the corpus striatum which Johnston has described in turtles. If that author has been correctly interpretated, the ventro-lateral small celled nucleus of this description is nucleus caudatus, while the ventro-lateral large celled nucleus is the nucleus lentiformis of turtles. The writer has avoided the specific terms employed by Johnston because she does not have sufficient knowledge of the development of the striatum throughout the vertebrate series to be certain of the homologies.

Ventro-lateral small celled area (Johnston's nucleus caudatus). This nucleus (figs 7 to 9) begins a short distance behind the olfactory crus and, increasing in size, extends backward to the level of the anterior nucleus of the thalamus with which its posterio-medial portion lies in close relation. Posteriorly its ventral and lateral portions lie in close relation with the posterior part of the nucleus of the lateral olfactory tract. Anteriorly it cannot be sharply delimited from the nucleus olfactorius anterior. Johnston ('15) in turtles, where the relationships of the caudate nucleus are practically the same as the relationships of this area in the alligator, has considered the nucleus olfactorius anterior and some associated gray as giving rise to the head of the caudate nucleus in mammals. The great increase in the neopallial area in higher forms is accompanied by an increase in the number of fibers (internal capsule fibers) distributing to that cortical area. These fibers are imbedded in the caudate nucleus and more posteriorly are ventral to it and so push this cell mass dorsalward and caudalward as they increase in number during phylogeny. The upward, backward and downward growth of the general cortex and the downward growth of the pyriform lobe have produced the typical curve of the caudate nucleus of higher forms.

The ventro-lateral small celled area is continuous around the ventral border of the ventricle and onto its medial surface and this continuation represents the nucleus accumbens of higher forms. This apparently belongs to the striatum complex, although Johnston ('13, p. 421) has joined it to the nucleus lateralis septi of previous authors under the name of nucleus parolfactorius lateralis (see the discussion of the parolfactory nuclei).

Ventro-lateral large celled area (Johnston's nucleus lentiformis) (figs. 7 to 10, 17 to 19). This nucleus appears as a group of cells just dorsal to the small celled area at the anterior of the hemisphere and laterally close to the nucleus of the lateral olfactory tract. Farther caudad it is partially separated from the ventro-lateral small celled area (Johnston's caudate) by a special fascicle of the lateral forebrain bundle. In the posterior part it forms a heavy ridge of cells over the dorsal and dorsolateral portions of the small celled area. It disappears in front of the posterior end of the latter area at about the level of the foramen of Monro. The larger size of the cells of the ventrolateral large celled area makes it easy to distinguish this nucleus from the ventro-lateral small celled area.

Intermedio-lateral area (figs. 7, 8). This area is found at the level of the posterior part of the infolding of the general cortex and in the region just caudad to that infolding. The intermedio-lateral area is ventral to the dorso-lateral area, dorsal to the ventro-lateral areas and medial to the nucleus of the lateral olfactory tract. It lies in so close relation with this last nucleus especially in its more anterior extent that it is not practicable to attempt to draw any sharp boundary line between them. The intermedio-lateral area is separated from the ventro-lateral areas by a cell free zone in which are fibers which belong in part at least to the lateral forebrain system. A sulcus in the ventricular wall indicates the position of the boundary line between the intermedio-lateral and ventro-lateral area. The anterior portion of the former area is separated from the dorso-lateral area by a cell free zone but the two areas fuse into one, behind the level of the infolding of the general cortex. So far as the evidence goes, the intermedio-lateral area appears to belong with the dorso-lateral area. Possibly it is a representative of some part of the striatum complex of higher forms.

Nucleus of the lateral olfactory tract (figs. 5 to 10, 12, 16 to 19). This nucleus can be distinguished from the other cell masses in the lateral wall of the hemisphere by the smallness of its cells. It begins as a small cluster of cells scattered along the inner border of the cortex of the pyriform lobe and between that cortex and the cortex-like superficial layer of the tuberculum olfactorium. Close to its anterior end the cells of the upper .or more dorsal portion of the nucleus group themselves more closely together and a clearly defined nucleus is formed which is ventral to the dorsal-lateral area and lateral to the ventro-lateral large celled area. At first this upper portion of the nucleus of the lateral olfactory tract remains distinct from the surrounding cell masses of the hemisphere wall; but as it is followed caudad it gradually comes into close relation with the cell mass of the dorso-lateral area and finally merges with it with no sharp delimiting line between the two, a greater and greater number of large cells appearing among the small cells in that region until apparently the mass has become a part of the dorso-lateral area. The ventral portion of the nucleus, at the anterior end of the brain, consists of diffuse clusters of cells lying in close relation with the pyriform lobe, the cortex of the tuberculum olfactorium, and, farther caudad, the nucleus of the diagonal band of Broca. At approximately the level of the fusion of the anterior dorsal portion of the nucleus of the lateral olfactory tract with the dorso-lateral area, the ventral portion of the former nucleus broadens out and extends to the posterior end of the hemisphere, occupying first a ventro-lateral and then a ventral position.

A part (probably the more ventral portion) of the anterior dorsal portion of this nucleus of the lateral olfactory tract, as it has been described for the alligator, is quite probably comparable with the small celled, ventral part of the pyriform lobe observed by Johnston ('15) in the turtle. In describing this small celled part Johnston says that in the rostral part of the brain of Cistudo carolina it may be sharply distinguished from the large-celled portion both by the difference in cell character between the two regions and by the more ventral position of the small celled portion, which extends below the sulcus endorhinalis and expands behind the posterior part of the striatal area into the nucleus of the lateral olfactory tract. In the alligator the continuance of the pyriform lobe cortex (Johnston's large celled medial portion) farther ventralward, has pushed this small celled portion inward and crowded it somewhat dorsalward so that it lies for the most part, medial to the pyriform lobe cortex instead of ventral to it as in turtles. Furthermore the anterior, dorsal end of the nucleus of the lateral olfactory tract (Johnston's small celled, ventral portion of the pyriform lobe) is much larger in the alligator than in the turtle and this increase in size has probably been another important factor in bringing about the change in the relative positions of the two cell masses.

The more ventral and posterior portions of the nucleus of the lateral olfactory tract as that nucleus has been described for the alligator are comparable to nearly all of the nucleus of that name described for the turtle (Johnston, '15). Here again, however, there is one point of difference, for, while in the turtle the nucleus occupies the outer portion of the hemisphere in the posterior part of the forebrain, in the alligator the cortex of the pyriform lobe extends downward and occupies the outer portion of the ventral wall, the nucleus of the olfactory tract lying internal to it and in close relation with it. (For a further discussion of these relations and their significance see the account of the pyriform lobe.)

To summarize, the nucleus of the lateral olfactory tract as it is present in the alligator is practically the equivalent of the nucleus of that name and the small celled ventral part of the pyriform lobe in turtles, except that the last named area has been greatly elaborated in the alligator and its more anteriodorsal portion may very well have taken on an added significance from its intimate relation with the somatic dorso-lateral, area.

Ventro-medial nucleus (figs. 10, 12, 18, to 21). This nucleus occupies the extreme ventro-medial portion of the hemisphere, extending throughout about the posterior half of the hemisphere. It has broad connections with the habenula by way of the stria medullaris and it gives rise to the great olfactory projection tract of Cajal.

This quite evidently is the medial, large-celled nucleus described by Johnston ('15) for Cistudo carolina, although the cells of this nucleus, in the alligator, resemble in size and in cell characteristics the cells of the nucleus of the lateral olfactory tract, except that they are massed somewhat more closely together.

Functional complexes formed by the basal nuclei of the lateral wall. In the foregoing paragraphs, an account has been given of the relative positions and the extents of the various nuclei found in the lateral wall of the hemisphere, and something has been said of their fiber connections. Two problems then arise, the first regarding the way in which these centers interact in the functioning brain of the alligator; the second regarding their phylogenetic significance as forerunners of centers found in mammalian brains.

Two types of nervous impulses enter the lateral wall of the cerebral hemisphere, (1) descending impulses from the olfactory area, and (2) ascending somatic sensory impulses from the centers of the thalamus. The nuclear pattern of this basal area of the forebrain has been determined in large measure by the distribution and mutual interconnections of the incoming fibers of these two systems.

The first type of nervous impulse includes the secondary and tertiary fibers of the lateral olfactory tract, which, entering from in front, distribute to the nucleus of that tract throughout its entire extent and, turning gradually dorsalward, in the posterior half of the hemisphere distribute to the lateral portions of the dorso-lateral area. The lateral part of this dorso-lateral area, the nucleus of the lateral olfactory tract, and the ventro-medial nucleus all give rise to fibers of the stria medullaris and the first two masses (and in turtles the ventro-medial nucleus also) discharge through the stria terminalis. The ventro-medial nucleus in both the turtle and the alligator discharges into the diencephalon through the great olfactory projection tract of Cajal.

The identification of the amygdaloid complex of higher forms is based on the following features: 1) upon its reception of fibers from the lateral olfactory tract (figs. 16, 18); 2) upon its relation to the pyriform lobe cortex (figs. 7 to 10); 3) upon its giving rise to fibers of the stria terminalis (figs. 19 to 21—in this is included its connection with the opposite side of the brain by way of the anterior commissure); 4) upon its giving rise to fibers of the stria medullaris (figs. 16 to 21). It is evident that the group of centers just discussed, i.e., the nucleus of the lateral olfactory tract, the ventro-medial nucleus, and the more lateral part of the dorso-lateral area, make up such an amygdaloid complex.

The second type of impulse which enters the lateral wall of the hemisphere is somatic, being transmitted by the somatic sensory radiations from the lateral and medial nuclei of the thalamus to the ventro-lateral areas (caudate and lentiform nuclei). These areas, then, are centers for the correlation of somatic sensory impulses in the hemisphere and are, therefore, the forerunners of the mammalian corpus striatum. They discharge into the lower brain centers through the lateral forebrain bundle.

A part of the somatic sensory fibers pass beyond the ventro-lateral large celled area (Johnston's nucleus lentiformis) into the dorsal area, so that at the level of the primordial general cortex (figs. 5, 6, 15), this dorsal area is entered almost exclusively by the somatic correlation fibers and hence is a somatic correlation center of striatal type. This area at its anterior end probably exhibits the highest type of somatic correlation tissue found in the brain of the alligator, and the entrance of association fibers from the adjacent cortical centers into its dorsal part has given the conditions favorable for the differentiation of primordial general cortex (i.e., cortex approaching the neopallial in type).

It will be remembered that behind the level of this thickening representing primordial or transitional general cortex the lateral part of the dorso-lateral area receives olfactory fibers and probably some somatic fibers, and belongs to the amygdaloid complex. Whether this portion becomes a somatic part of the amygdaloid complex of higher forms, as Johnston ('15) believes is the case with the dorsal ventricular ridge in turtles, or whether it is a step toward the enormous striatum complex found in birds, cannot be decided without a much greater knowledge of other vertebrate forms than the writer possesses. In any case, it is very evident that the dorso-lateral area must be regarded as a structure of intermediate or transitional type, containing primordia related to three diverse structures in the mammalian brain, viz., corpus striatum, amygdaloid complex, and the general cortex.

Cortical centers of the hemisphere. Within the pallium three types of cortical centers may be distinguished. One of these, the hippocampus, is concerned primarily with olfacto-visceral correlations. The pyriform lobe cortex is concerned chiefly with olfacto-somatic correlations, with some involvement of the general visceral centers of the hypothalamus. The third type, the general cortex, is largely concerned with somatic correlations, and is differentiating toward true neopallium.

Hippocampus (figs. 3 to 10, 12, 14 to 21). Spitzka was the first to suggest that the dorso-medial wall of the hemisphere was hippocampus, although he still called the hippocampal commissure the corpus callosum. From that time the homology of this medial cortex has been recognized by most observers, including Edinger, Brill, Meyer and Elliot Smith. Very good summaries of the earlier studies on the hippocampus and its commissure are given in Elliot Smith's article ('03) dealing with the morphology of the cerebral commissures in vertebrates and in the Arris and Gale lectures ('10). In this connection it is interesting to note that Johnston ('15) has reopened the question of the presence of true callosal fibers in the dorsal or hippocampal commissure of both marsupials and reptiles. His evidence for their presence is based on experimental work. In regard to reptiles he says, page 404, "in the turtles the lack of medullation in the dorsal commissure has made it impossible thus far to secure positive evidence as to the presence of callosal fibers." He argues that they should be present because of the great number of ascending fibers carrying sensory impulses from the thalamus to the telencephalon in reptiles. Others, as Ramón y Cajal, Unger, and Pedro Ramon, have claimed that various reptiles have true callosal fibers.

Adolf Meyer ('92) was the first person to distinguish between the dorsal and the dorso-medial portions of the hippocampus. The dorso-medial portion arises rostrad in the narrow part of the olfactory crus and there occupies a somewhat dorsal as well as a dorso-medial position (fig. 3). At this level it lies in close relation dorso-lateralward with the cortex of the pyriform lobe. As it extends caudad into the hemisphere, the dorso-medial cortex takes its characteristic position and dorsal to it appears a group of scattered cells of a larger size which, judging from their fiber connections, are strongly under the influence of the dorso-medial portion. This latter group constitutes Adolf Meyer's dorsal portion of the hippocampus and is the 'subiculum' described by Johnston ('15) in turtles. Except at the very anterior end of the hemisphere, the hippocampal formation and the cortex of the pyriform lobe are separated by the general pallium. Ventralward, the dorso-medial portion of the hippocampus is continuous with a diffuse mass of small cells, the primordium hippocampi.

In the more anterior part of this dorso-medial region of the hippocampus, the cells, as seen in Golgi preparations, are goblet-shaped and are comparable with the cells of the secondary olfactory nuclei. They are more nearly related in type to the small projection cells of the hippocampus. The most anterior portion of the hippocampus probably does function to considerable degree at least, as a secondary olfactory nucleus. Other cell types found in the hippocampus are as follows:

1. Correlation cells (fig. 31). The correlation cells of this type are found in the dorsal portion of the dorso-medial area at the anterior part only, so far as is known. They are especially interesting because of their resemblance to the cells of the hippocampal regions in Amphibia (Herrick, '10). These are probably phylogenetically the oldest of the highly specialized cells of the hippocampus.

2. Double pyramid cells (figs. 35, 36). These are the cells which especially give character to the dorso-medial portion of the hippocampal cortex. Their cell bodies are large and more or less pyramidal in form. Thick, thorny, bushy dendrites spread out lateralward and medialward from the cell body but are especially thick on the medial side, where they can often be seen breaking up around the terminal arborizations of the incoming medial olfactory, parolfacto-cortical and tuberculo-cortical tracts. Sometimes the impulse reaches the double pyramid cell through an interpolated neurone. The dendrites which are directed lateralward, receive olfactory impulses from the

pyriform lobe and the nucleus of the lateral olfactory tract. These impulses come by way of the alveus which carries impulses in both directions, as it does in higher forms. The laterally directed dendrites receive short association fibers from the alveus and perhaps impulses from other incoming fibers.

The axones of the double pyramids are slender and run lateralward, dividing in many cases into two branches (fig. 36). One of these branches enters the alveus and can often be traced a long distance, although it has been impossible as yet to follow any single fiber all the way into the pyriform lobe. The second branch, when present, goes to the septum or enters one of the descending diencephalic tracts (the fornix or tractus cortico-habenularis).

3. Small projection cells (figs. 32, 33). Besides the double pyramid cells there are other projection cells in the hippocampus. These are smaller than the ones just described and may be either pyramidal, oval or nearly round in form. They are usually either slightly lateral or slightly medial to the double pyramids and send their dendrites to both lateral and medial surfaces, where they receive the same sorts of impulses as are brought to the double pyramids. The axones, like those of the latter, may divide into two branches (fig. 33), one entering the alveus and the other running ventralward into the septum and presumably, in some cases, entering tracts descending to the diencephalon.

4. Small intrinsic cells (fig. 34). The dendrites of the double pyramid and small projection neurones form a thick feltwork on each side of the more deeply placed cell bodies. Scattered through this feltwork are cells of several types, only one type of which is shown in the figures, which send out relatively short bushy dendrites and receive collaterals from incoming fibers or from axones of the hippocampal projection cells and discharge back into the dendrites of the latter. In this way the whole of the hippocampus is tied up together and correlated and unified responses are made possible. Some of these cells are typical type II neurones, others have longer, less branched processes and short slender axones. Both of these sorts are apparently intrinsic to the hippocampus.

Levi ('04) has described cells of the double pyramid and small projection types in the hippocampus of reptiles. The account given here agrees substantially with the descriptions and figures given in his article. It is interesting to note that the medial side of the dorso-medial cortex, as Levi suggests, appears to be concerned mainly with the reception of incoming stimuli from the lower brain centers, while, on the other hand, the main projection fibers which connect the hippocampus with the pyriform lobe (the alveus) and with the diencephalon (fornix and the tractus cortico-habenularis medialis) leave on the lateral side. In the turtle the hippocampal cortex lies close to the ventricle. Presumably, in that case, many of the efferent fibers leave on the medial side, but so far as is known, there is no literature on that subject. It is certain, however, that the dorso-medial region of the hippocampal cortex of the alligator represents a higher differentiation than the corresponding region in the brain of the turtle and that this differentiation is marked, not only by a more definite cell arrangement and possibly by a more specialized cell form, but also by a new position of the cell mass produced by a biotactic movement of the cell group away from the ventricular wall and in the direction of the incoming impulse.

Meyer ('92) and Levi ('04) claimed that the dorso-medial portion of the reptilian hippocampus was gyrus dentatus. This contention was denied by Ramón y Cajal, who, in an elaborate series of histological studies, showed that from its cell types and manner of connection, it could not be considered pure gyrus dentatus. In the Arris and Gale lectures ('10), Elliot Smith admits the correctness of the Cajal observations but says that the dorso-medial portion is undergoing a differentiation toward the production of gyrus dentatus and that it is the forerunner of that structure. This seems a fair statement of the conditions.

The dorsal portion of the hippocampal cortex does not show the regular arrangement of cell layers found in the dorso-medial portion, and in general, its mass of cells shows a lighter staining reaction to toluidin blue. Figure 31 shows one type of correlation cell found in this dorsal region. This dorsal part appears to be concerned chiefly with the association of impulses rather than as a receptive center, its main incoming impulses, so far as known, coming in through the alveus. As Elliot Smith and Levi have suggested, this is probably the forerunner of the hippocampal cortex as distinguished from the gyrus dentatus. Johnston ('15), however, regards this dorsal cortex as the forerunner of the mammalian subiculum. From the region of the infolding of the primordial general cortex (fig. 6) in the alligator this dorsal part of the hippocampal cortex is continuous with the general cortex.

The presence in the alligator of a primordium hippocampi, such as Johnston ('13 and '15) has described in turtles, has already been mentioned. In the turtle that author has shown the presence, on the medial wall of a fimbrio-dentate sulcus (Elliot Smith's sulcus limitans hippocampi) between the dorso-medial portion of the hippocampus and the primordium hippocampi and a sulcus limitans hippocampi and a cell free zone between the primordium hippocampi and the parolfactory area (Herrick's ('10) septal area) in the anterior part of the brain. On the ventricular side of the medial wall in the turtle are two sulci which correspond to those on the lateral wall and separate the same areas. In the alligator in the material which was studied, no well defined sulci are in evidence on the medial surface of the hemisphere in these regions but the ventricular sulci are present in positions corresponding to those in which they are found in the turtle; and the primordium hippocampi, in the more anterior part of the hemisphere, is separated from the septal or parolfactory area by a cell free zone. An interesting fact, but one whose significance is not clearly understood, is the presence on the ventricular surface of a relatively thin ependymal layer over the dorso-medial portion of the hippocampus and of the primordium hippocampi, which becomes thickened over the septal or parolfactory region. Under the head of the parolfactory area, the relative positions and the relations of the primordium hippocampi and the lateral parolfactory nucleus have been discussed.

Johnston ('13, figs. 23 to 27, pp. 446–447) has shown that the primordium hippocampi extends forward in the hemisphere considerably anterior to the hippocampus proper. In the alligator the dorso-medial cortical area extends forward into the region just posterior to the olfactory crus and the primordium hippocampi, though quite plainly present, is relatively smaller than in the turtle. This means that in the alligator the hippocampus in this region is more highly specialized than in the turtle. The cells making up the primordium hippocampi are small and are arranged in a diffuse mass. They are not impregnated in the Golgi preparations which were studied.

Pyriform lobe (figs. 3 to 10, 12, 14 to 19). The pyriform lobe has important functions both as a secondary olfactory center and as a correlation mechanism of high order. By means of connections with the olfactory bulb and the basal and cortical centers of the hemisphere it receives both correlated and uncorrelated olfactory material. By means of its connection with the tuberculum olfactorium and, also, through short correlation fibers from the somatic centers of the hemisphere, it receives correlated somatic material. It receives impulses from the other cortical centers by way of the alveus. Consequently it serves, in part at least, as an olfacto-somatic correlation center of high order.

In the anterior end of the hemisphere, in the region of the olfactory lobe, the pyriform lobe cortex and the hippocampal cortex lie in close relation with each other dorsally. They are soon separated, however, by the general pallium which intervenes between them throughout the remaining extent of the hemisphere. Ventrally the pyriform lobe lies in close relation with the tuberculum olfactorium, separated from it only by some scattered cells of the anterior division of the nucleus of the lateral olfactory tract. Behind the tuberculum olfactorium, the cortex of the pyriform lobe is bounded ventrally by the nucleus of the diagonal band of Broca and by the nucleus of the lateral olfactory tract. Near the posterior end of the hemisphere, this latter nucleus, which there occupies all the ventral surface excepting the portion occupied by the ventro-medial nucleus, acquires a cortex-like arrangement of its superficial cells (fig. 12) which layer is continuous with the cortex of the pyriform lobe and to all intents and purposes is a part of that area since the pyriform lobe cortex itself arose as a differentiation of the neurones of the nucleus of the lateral olfactory tract (see Johnston '15 and the general discussion at the end of this paper).

Medialward the pyriform lobe cortex is bounded by the dorso-lateral area and by the anterior part of the nucleus of the lateral olfactory tract. This anterior division bears about the same relation to the pyriform lobe cortex that the primordial hippocampus bears to the hippocampal cortex proper, i.e., it consists of cells which have practically the same type of connections as do the cells of the pyriform lobe cortex. It represents the general area from which the specialized pyriform lobe cortex has developed. In this paper it has been considered as the anterior part of the complex of the nucleus of the lateral olfactory tract, but it might equally as well be termed primordial pyriform lobe cortex or the small celled portion of the pyriform lobe complex, as Johnston ('15) has called it in turtles. (For a further description of this anterior division of the nucleus of the lateral olfactory tract see the description of that nucleus).

The writer has not been able to identify the sulcus endorhinalis and the sulcus rhinalis is slight but does show in some preparations. The cell type illustrated in figure 39 is found in the anterior end of the pyriform lobe. It resembles the cells found in the secondary olfactory centers, which is not surprising since the anterior end of the pyriform lobe cortex itself probably serves to a considerable degree as such a secondary center. The Golgi material available for study does not show the cell types found in the more posterior part of this cortex.

General cortex (figs. 4 to 10, 12, 16 to 19). As has been stated, the cortex of the pyriform lobe and the hippocampal cortex are separated from each other by the general cortex except at the anterior end of the brain in the region of the olfactory lobe. In many reptiles this cortex forms a definite lamina separated from the other cortical areas by distinct limiting zones but in the alligator, at least in the material studied, no such sharp limiting zones are visible. Medialward as in the turtle, it grades over into the thicker dorso-medial part of the hippocampal cortex (Johnston's subiculum, '15). Lateralward it is continuous with the cortex of the pyriform lobe. The rhinal fissure is demonstrable in some of the material but is relatively slight.

In the anterior end of the dorso-lateral area of the hemisphere there is a ridge of cortex-like cells which has the appearance of being a fold of the general cortex. This has been termed in the present paper, primordial general cortex. Between the primordial portion and the general cortex proper, at the medial border, there is a small space (fig. 6) which permits association fibers of the alveus system to reach the former portion. Johnston ('15) has described in turtles a ridge of cells similar to the primordial general cortex of this description. He calls it the dorsal ventricular ridge but says that it belongs to the general pallial complex (the general cortex of this description). In a later paper ('16) he shows that both the ridge and the general cortex are derived during embryonic development from the dorso-lateral area. Phylogenetically the general cortex complex arose under the influence of at least two types of fibers. 1. The one type consists of fibers carrying impulses from the somatic centers of the diencephalon to the dorso-lateral area of the forebrain by way of the lateral forebrain bundle. 2. Into this dorso-lateral area association fibers from the hippocampal and pyriform lobe complexes also distribute. As these latter areas differentiated a higher type of integrated impulses was brought in and, within the dorso-lateral area, neurones exhibiting a cortex-like type of differentiation appear. In this way within the basal dorso-lateral area, a primordial general cortex is probably formed. What the factors were which caused this primordial cortex to become more superficial in position and to separate from the basal dorso-lateral area to take on a true cortical form, of course is not certainly known. Perhaps one cause lies in the neurobiotatic influence of the association fibers, the neurones migrating out along their dendrites toward the source of their stimulation.

The whole of the general cortex complex is a step toward the differentiation of a neopallial area. To be sure, this complex is still closely linked with cortical olfactory areas, but it has a relatively large somatic component and its connection with the basal somatic areas is intimate. As maintained by Elliot Smith and others, it cannot be regarded as true neopallium, but rather represents a process of differentiation in that direction.

Johnston ('16a) by a series of experiments on the turtle brain has reached the conclusion that there is some degree of cortical localization in the general pallium of that reptile. The writer at present has not sufficient data to determine whether or not there is any localization pattern in Alligator mississippiensis.

Centers of the diencephalon

The diencephalon may be divided into the three usual divisions (1) the epithalamus; (2) the thalmus; (3) the hypothalamus. It is not the purpose of this report to go into the question of nuclear localization in these regions nor to attempt to describe the character of the cell groups. There has not been sufficient work done to justify such an attempt. Only a few of the more outstanding facts of especial interest in connection with the discussion of the forebrain will be mentioned.

At the end of his 1913 paper, DeLange has given a series of outlines of the diencephalon of the alligator in which the positions of the various nuclei and their topographic relations to the various fiber tracts are indicated. These have been of the greatest help.

Epithalamus. The part of the epithalamus which is particularly concerned with the reception of olfactory impulses is the habenula (figs. 11, 12, 21). This nucleus lies at the dorsal surface of the diencephalon and projects into the ventricle. The stria medullaris brings impulses to this nucleus. It consists of three smaller nuclei; a medial one of closely packed cells, a dorsal and more anterior one which apparently receives part of the tractus cortico-habenularis medialis and, lastly, a ventral one of larger cells that, farther caudad, connects with the cell mass of nucleus magnocellularis. The habenulae of the two sides connect with each other by means of the commissura habenularum (fig. 12).

Thalamus. There are really three types of nuclei in the thalamus proper: a medial group which connects chiefly with the visceral centers, a lateral group which is the place of termination for the somatic impulses brought in by the optic and lemniscus systems and, intermediate between these two groups, a third nucleus which receives fibers of both the visceral and somatic type. This nucleus is the nucleus medialis or the nucleus rotundus of some authors.

In the medial group are the nucleus anterior and the nucleus magnocellularis. The nucleus anterior (figs. 10 and 11, 20), as its name implies, lies at the very anterior end of the thalamus. It is dorsal in position and its cells are smaller and more closely packed together than are the cells of the lateral nucleus. It receives fibers from the hypothalamus and is connected with the small celled ventro-medial part of the hemisphere by means of a fiber tract.

The lateral group includes the nucleus lateralis, a special derivative of this nucleus—the pulvinar—and another optic center which most writers have termed the corpus geniculatum laterale. The nucleus lateralis is conspicuous because of the large size of its neurones. The cell bodies of these neurones (figs. 41, 42, 43) are large, goblet or triangular in shape, and have thick thorny dendrites which extend out in every direction from the cell bodies. The axones enter the lateral forebrain bundle. This nucleus is lateral in position, being lateral and somewhat ventro-lateral to the nucleus anterior and lateral to the nucleus medialis (or rotundus). It receives lemniscus fibers and some optic fibers and, with the lateral thalamic optic centers, represents the beginning of the neothalamus (Edinger) of higher forms, i.e., that lateral portion of the thalamus which serves as a place of synapse for nervous impulses passing to the neopallium and which develops parallel with the development of the neopallial cortex. In the more posterior part of the thalamus, a lateral portion has begun to differentiate away from this nucleus and to form a beginning of the pulvinar. This separate nucleus is developed under the direct influence of the incoming optic fibers.

There are other cell masses in the thalamus proper, as for example the nucleus reuniens figured in the alligator brain by

DeLange ('13); but the writer knows too little of their relationships or significance at present to discuss them.

Hypothalamus. The hypothalamus of the alligator is highly developed. An examination of figures 11 and 12 will show that a number of cell groups are present. In his 1913 paper DeLange has named these different groups. No attempt has been made to do so in the present paper because of a lack of knowledge of the fiber connections of the different groups.

FIBER CONNECTIONS

With the foregoing descriptions of the cell groups as a basis, attention can now be turned to the courses and terminations of such of the fiber tracts as have been worked out. Papers published by C. L. Herrick, Edinger, Adolf Meyer, Kappers, Unger, DeLange, and Johnston contain descriptions of the fiber connections of the reptilian brain. These descriptions in almost every case, have been based on adult material, the work being done with Weigert preparations which bring out the myelin sheaths. On the other hand, the work for this paper has been done chiefly with Cajal and Golgi material, which bring out the unmyelinated fibers and, in many cases, the axis cylinders of the myelinated ones. Repeated attempts to prepare a series stained by the Weigert method were not successful so far as the forebrain was concerned. These failures, of course, may have been due to faulty technique, but only extremely young material was available and in such material many of the myelin sheaths may not have become mature. C. J. Herrick ('10) has figured on pages 537, 539, and 541 some cross sections of the forebrain and the thalamus of Alligator mississippiensis showing the fiber tracts and the positions of some of the centers. These drawings were made from Cajal material and were of much help. A series stained with Ehrlich's haematoxylin and an imperfect series prepared by the Leuden van Heumen method were used to check the results obtained by the Cajal method.

Tractus olfactorius

Following the human terminology, the writer has considered this tract to consist of three divisions, a medial, an intermediate, and a lateral, although the first two are very closely associated and have both been considered by many authors under the name of the medial olfactory tract. (For a diagram of the distribution of these tracts see figs. 44 to 46). The data given here have been obtained, partly by the study of sections prepared by the use of Ehrlich's haematoxylin and by the Leuden van Heumen method and partly by work with a Cajal series in which the axis cylinders of any myelinated fibers, as well as the unmyelinated fibers, were brought out. The data in all probability are not complete.

Tractus olfactorius medialis (figs. 13, 14, 44). This tract has been described in reptiles by Edinger ('88), Adolf Meyer ('92), C. L. Herrick ('93), Unger ('06), DeLange ('11), and Johnston ('15). As its name implies, it lies medial to the ventricle of the bulb and arises, in general, from the more medially and ventromedially placed mitral and granule cells. Throughout the bulb, this tract is lateral to the mitral cells. In the crus many of its fibers end in the nucleus olfactorius anterior or send their collaterals to that nucleus. The projection cells of the nucleus, in turn, send axones to join the tract. Thus the medial olfactory tract is made up of fibers from both primary and secondary olfactory centers.

In the anterior end of the hemisphere the tractus olfactorius medialis has come to lie along the medial surface and it occupies this medial position as it passes caudad, discharging at various levels into the dendrites of the intrinsic cells, the double pyramids and the small projection cells of the hippocampus.

Tractus olfactorius intermedius (fig. 14). This fiber tract, arising from mitral and granule cells and not distinguishable from the medial tract until the hemisphere is reached, ends in the nucleus olfactorius anterior and the medial part of the tuberculum olfactorium. Other fibers pass farther caudad and appear to enter the nucleus of the diagonal band of Broca. It is joined by fibers from the nucleus olfactorius anterior to the tuberculum olfactorium. Part of its fibers pass through the anterior commissure to the other side and end there in the nucleus olfactorius anterior and, probably, partly in the tuberculum olfactorium. These connections have been described by nearly all the later workers on the reptilian brain.

Johnston ('15) in the turtle has considered the· medial and intermediate tracts both under the name of the medial olfactory tract. He describes a very interesting bundle of this medial tract which runs caudad with the fiber bundle of the diagonal band of Broca to the nucleus of the lateral olfactory tract. Quite probably this tract is present in the alligator but the material available does not permit of its identification.

Tractus olfactorius lateralis (figs. 13 to 19, 44 to 46). Edinger ('88), Adolf Meyer ('92), C. L. Herrick ('93), Unger ('06), Kappers and Theunissen ('08), DeLange ('11), and Johnston ('15) have described this tract in reptiles. In general it arises from the more laterally placed mitral cells and projection granule cells of the bulb but some of the fibers come from the dorso-medial portion and cross over to join the lateral tract. Like the medial tract, this lateral one at first lies internal to the mitral cell layer. While still in the bulb it begins to swing out to the surface and in the crus and lobe it lies mainly along the lateral border of the hemisphere. Near the anterior end of the hemisphere it divides into an outer and an inner division. The inner division enters the nucleus of the lateral olfactory tract and distributes to it throughout its whole extent. The outer division ends in synaptic relations with cells of the pyriform lobe and sends some fibers to the more lateral portions of the tuberculum olfactorium. The tractus olfactorius lateralis not only sends fibers to the pyriform lobe but, in the crus and the anterior end of the hemisphere, at least, it also receives fibers from it. This tract, then, carries both secondary and tertiary impulses.

Tractus tuberculo-corticalis

From the tuberculum olfactorium a band of fibers runs along the medial border of the hippocampal cortex and discharges into the dendrites of the hippocampal cells. This is the tractus tuberculo-corticalis (figs. 14, 15). Some fibers swing to the lateral side of the hippocampus; these may be cortico-tubercular fibers. Farther cephalad some olfacto-cortical fibers from the nucleus olfactorius anterior join this tract.

Parolfacto-cortical tracts

Tractus parolfacto-corticalis (figs. 16. 17). Fibers swing upward from the medial parolfactory area of the septal region to the dorso-medial cortex of the hippocampus, entering this latter mainly, at least, on the medial side. In view of the fact that the medial surface of the hippocampus is mainly concerned, as far as one can judge from the impregnations of its cells (see discussion of the hippocampal cortex), with the reception of impulses, it seems quite probable that these fibers are concerned chiefly in carrying impulses from the parolfactory area to the cortex, i.e., they are parolfacto-cortical fibers. Since the medial parolfactry nucleus receives fibers from the medial olfactory tract and short fibers from the tuberculum olfactorium and since it is connected by way of the diagonal band of Broca with the lateral olfactory area and with the hypothalamus by way of the medial forebrain bundle, this nucleus probably serves as an olfacto-visceral correlation center and discharges the resultant of this correlation into the hippocampus by way of the parolfacto-cortical tract just described.

Tractus cortico-parolfactorius (fig. 17). Accompanying the lateral border of the fornix longus (see the account of the fornix beyond) as it swings ventralward from the hippocampus, there are relatively numerous fibers which enter the more dorsal portion of the lateral parolfactory nucleus and, spreading out, distribute to approximately all parts of this cell mass. Fibers can be traced from this nucleus passing out medialward and ventralward to join the medial forebrain bundle. Since the lateral side of the dorso-medial part of the hippocampus is concerned mainly with the discharge of nervous impulses (see the discussion of the dorso-medial part of the hippocampal cortex), it is probable that the majority of fibers between the lateral parolfactory nucleus and the hippocampus conduct in the descending direction and that the nucleus functions as a place of synapse between the hippocampal cortex and the lower brain centers.

So far as the present data go they appear to suggest a division of labor between the medial and the lateral parolfactory regions (medial and lateral septal nuclei of some authors) and to suggest a motive for their differentiation, viz., that the medial nucleus is a way-station for ascending impulses going toward the hippocampus and the lateral nucleus is a similar station for descending impulses coming from the hippocampus. The writer is aware that the data are insufficient for a definite conclusion and that experimental researches or even more favorable Golgi material may prove these suggestions erroneous.

Commissures of the forebrain

There are two large commissures in the forebrain, the hippocampal commissure and the anterior commissure.

Commissura hippocampi (figs. 18, 19). The fibers of this commissure arise as axones of the projection cells of the hippocampus, which run ventralward and across the mid-line just above the anterior commissure. After crossing, some of the fibers appear to end in the nucleus commissuralis, but most of them pass dorsalward and end in synaptic relation with the cells of the opposite hippocampus. Thus the hippocampi of the two sides are put into connection with each other and enabled to work in a correlated way.

The commissura hippocampi has been the cause of much dispute among the earlier neurologists. Osborn ('87) identified it as the corpus callosum and for a time this interpretation was generally accepted. Adolf Meyer ('85) showed it to be the commissure of the medial and dorso-medial wall, which regions he identified as hippocampus. Elliot Smith ('03) claimed that in reptiles and monotremes there were no callosal fibers in the dorsal commissure. Johnston ('13a, pp. 402-404) is quite certain from a series of experiments performed on the opossum that in this form there are callosal fibers in the hippocampal commissure. He believes that callosal fibers are present in that commissure in reptiles also, although he does not have the experimental proof for their presence there.

In the alligator, some of the fibers entering into the hippocampal commissure appear to come from the region of the general cortex and so to favor Johnston's conclusions, but of course nothing definite can be settled in this regard until some further degeneration experiments have been carried out. Unger, Kappers, DeLange, and others have described and figured the medullated fibers of the hippocampal commissure.

Commissura anterior (fig. 18). The following components of this commissure have been identified:

a. Stria terminalis fibers. The course of these fibers through the commissure is described under the account of the fiber systems (see account of stria terminalis pars commissuralis).

b. Fibers from the tractus olfactorius intermedius to the tuberculum olfactorium and the nucleus olfactorius anterior of the other side. These are myelinated.

c. Also, short fibers from the nucleus olfactorius anterior and the tuberculum olfactorium of one side to the corresponding centers of the other side.

d. So-called 'commissura epistriata' fibers (DeLange '11). These are included under the description of the stria terminalis fibers. This component consists of true commissural fibers of the stria terminalis, which connect the pyriform lobe and the nucleus of the lateral olfactory tract of the two sides of the brain, and of decussating fibers of other types.

Tract of the diagonal band of Broca

These fibers connect the region of the nucleus of the lateral olfactory tract with the parolfactory region and the nucleus commissurae hippocampi of the same side. These fibers pass ventrally of the basal forebrain bundles close to the surface of the brain. Caudalward many of the fibers end in the ventro-medial nucleus and a few of them enter the anterior end of the nucleus preopticus. This fiber tract has been seen and more fully described by Johnston ('15, p. 407) in the brain of the turtle. Because of the deposit of silver on the outer surface of the Cajal material in this region, it has been impossible to study this fiber tract in the alligator as carefully as would be desirable. Apparently, however, it is made up, in part, of short fibers which form synapses among the cells of the diagonal band (see the description of this nucleus). The significance of this tract lies in the opportunity it gives for a close connection between the lateral and medial olfactory areas of the hemisphere (figs. 16 to 19).

Stria terminalis

This stria consists of two divisions.

The commissural portion (*St. term. p. com.*, fig. 18). Slightly anterior to the level of the anterior commissure fibers may be seen passing from the region of the pyriform lobe, the nucleus of the lateral olfactory tract (particularly its dorsal portion), and the extreme ventro-lateral portion of the dorso-lateral area, directly medialward over the dorsal surface of the medial forebrain bundle (*M. F. B.*). Most of these fibers cross to the opposite side through the anterior commissure and distribute to the corresponding regions of the other half of the brain. Some of the fibers end in the bed nucleus of the anterior commissure of the same and the opposite side.

The preoptic portion (*St. term. p. preop.*, figs. 19 to 21). This part is formed by fibers which distribute to the region of the pyriform lobe, the ventro-lateral part of the dorso-lateral area and the nucleus of the lateral olfactory tract from the posterior end of the region reached by the commissural portion of the stria terminalis to the caudal end of the basal portion of the hemisphere. This preoptic division turns medialward and caudalward, lying ventral to the posterior division of the lateral cortico-habenular tract and dorso-lateral and dorsal and in close relation with the olfactory projection tract of Cajal and its accompanying cell band—the interstitial nucleus. This preoptic portion of stria terminalis does not cross in the anterior commissure but passes caudad of it and distributes to the preoptic region of the same side.

Alveus

A large number of the alveus fibers arise as axones of the double pyramid and small projection cells of the hippocampus and run dorsalward then lateralward and then ventro-lateralward around the outer border of the ventricle to the pyriform lobe (figs. 15 to 21). They distribute during their course to the general cortex, the cortex of the pyriform lobe and at least to the anterior end of the nucleus of the lateral olfactory tract (the part which is a derivative of Johnston's small celled portion of the pyriform lobe). From the pyriform lobe and quite possible from these other regions, axones enter the alveus. Probably they distribute to the general pallium and hippocampal cortex.

A small number of alveus fibers at the anterior end of the forebrain swing outward between the hippocampus and the primordial neopallium and distribute along the outer surface of the latter. These association fibers between the two cortical areas have been very significant in determining the evolution of the primitive neopallium.

Fimbria

This is a term applied to the fibers which border the hippocampal cortex along its ventro-medial boundary (figs. 18 to 21). Behind the foramen of Monro these fibers also border the place of attachment of the choroid plexus. In the alligator fibers to the fornix, to the tractus cortico-habenularis medialis, and association fibers between the cortex of the pyriform lobe and the hippocampus are found in the fimbria.

Fibrae tangentiales

These are short association fibers which tie up the medial and the dorso-medial portions of the hippocampus (figs. 15 to 21). They are on the superficial or pial side of the layer of cortical cells. Near the anterior end of the hemisphere short association fibers pass between the dorso-medial portion of the hippocampus and the general cortex.

These short superficial association fibers convey the nervous impulses which probably have operated in the course of the phylogeny to draw the cells of the primordial neopallium from the ventricular to the superficial position (neurobiotaxis; cf. the preceding discussion of the general cortex).

Fornix

In the fornix system of the alligator three parts have been distinguished. The first of these is the commissura hippocampi (commissura fornicis), which has already been described. The other parts are the columna fornicis and the fornix longus.

Columna fornicis (figs. 18 to 21, *F*). The fibers making up this division of the fornix are mainly axones of the double pyramid cells and small projection cells of the hippocampus. As has been said before, the fornix fibers join the hippocampal commissure and the tractus cortico-habenularis medialis. They swing first slightly lateralward and then medio-ventralward. Below the foramen of Monro the columna fornicis fibers separate trom those of the hippocampal commissure and, running caudad, enter the hypothalamus. They are accompanied by the fibers of the olfactory projection tract of Cajal (figs. 19 to 21).

The description here given agrees with the relations brought out by C. J. Herrick ('10). The myelinated fibers of the fornix have been described again and again by workers on the reptilian brain, among the number being Rabl-Rückhard ('81), Edinger ('88 and '96), C. L. Herrick ('93), Adolf Meyer ('92), Unger ('06), and DeLange ('11).

Fornix longus (figs. 16, 17, *F.L.*). This term is applied in mammals to a diffuse collection of fibers of mixed character passing in the medial wall of the hemisphere between the precommissural hippocampus (and adjacent parts of the cortex) and the basal centers of the septum and hypothalamus. In the alligator there is a broad connection between the medial forebrain bundle near its anterior end and the overlying hippocampus which is probably in a general way comparable with the mammalian fornix longus. Since these fibers connect chiefly with the lateral or ventricular side of the layer of cortical cells, they probably are mainly descending projection fibers for the septum and hypothalamus.

Stria medullaris

The stria medullaris is made up of a number of fiber tracts running from secondary and tertiary olfactory centers to the habenula (figs. 11, 20, 21). The terminology here used follows Herrick ('10). The following components were identified and traced out:

1. *Tractus cortico-habenularis medialis* (figs. 18 to 20). This tract arises for the most part from the axones of the double pyramids and small projection cells of the hippocampus. Its fibers leave the hippocampus at the same level as those for the columna fornicis and the commissura hippocampi. All three bundles run ventralward together, the more lateral belonging to the tractus cortico-habenularis medialis, the intermediate ones to the columna fornicis, and the medial ones to the commissura hippocampi. After a time the commissural fibers run more toward the mid-line and become separated from the general fiber mass, while the cortico-habenular fibers turn dorso-lateralward, and, passing caudad into the diencephalon, enter the stria medullaris.

Part of the fibers of this medial cortico-habenular tract arise among the cells of the nucleus commissurae hippocampi. Scattered cells of this nucleus accompany the tract through the greater part of its course. Accordingly the tractus cortico-habenularis medialis receives impulses from the hippocampus of the same and the opposite side, impulses coming from the latter by way of the commissura hippocampi and its nucleus.

2. *Tractus cortico-habenularis lateralis anterior* (figs. 16 to 21). The fibers of the anterior division of the lateral cortico-haben-

ular tract arise from the more anterior part of the nucleus of the lateral olfactory tract, from the cortex of the pyriform lobe in that region, and possibly from the nucleus of the diagonal band of Broca. The fibers run medialward in the ventral part of the forebrain, mingling in part with the fibers of the diagonal band of Broca, which lie on the ventral surface of the brain just external to them. Near the medial border of the hemisphere the anterior cortico-habenular tract turns dorsalward over the ventro-medial nucleus and occupies a position in the angle between that nucleus and the lateral forebrain bundle (figs. 20, 21). In this angle it is joined by a fiber band which extends along the medial surface to the caudal portion of the nucleus ventromedialis among the cells of which nucleus a part of the fibers can be traced (fig. 20). These two components of the tract are joined on their medial surface, at this angle between the ventro-medial nucleus and the lateral forebrain bundle, by the lateral olfacto-habenular tract and the tracts run dorsalward together and enter the stria medullaris and so reach the habenula..

Accompanying the fibers of the anterior division of the lateral cortico-habenular tract from the nucleus of the lateral olfactory tract and the pyriform lobe is a small bundle of fibers arising from the same regions, passing dorsal to the ventro-medial nucleus. Instead of entering the angle, however, between that nucleus and the lateral forebrain bundle, this band of fibers runs farther medialward and joins the medial forebrain bundle (figs. 20, 21). It runs caudalward in this bundle. Its posterior distribution is not certainly known as its fibers cannot be distinguished from others of the medial forebrain tract. Unless it changes its relative position, however, it probably ends in the hypothalamus, but nothing definite is known of its ending. In its connections within the hemisphere and in its relative position in respect to the forebrain bundles, this fiber tract from the pyriform lobe region shows several points in common with the tractus pallii of lower forms (Herrick, '10). It is possible that it and the olfactory projection tract of Cajal may be the representatives of that tract in reptiles. It has been termed in this account, the ventral olfactory projection tract.

The portion of this tract which arises from the pyriform lobe and associated regions is evidently the same tract as that described by Kappers and Theunissen ('08, p. 225) for the lizard, Iguana, under the name tractus olfacto-habenularis (see figures 21 and 22 of their paper). Farther forward these authors describe it as turning lateralward to connect with the 'lateralen Lobusrinde' (fig. 20), which is apparently the pyriform lobe region of the present account.

There are probably other components of this fiber complex which have not been impregnated in the preparations studied.

3. *Tractus cortico-habenularis lateralis posterior* (figs. 20, 21). This large system of fibers arises from the nucleus of the lateral olfactory tract and the ventro-lateral part of the dorso-lateral area. Some of its fibers may arise from the overlying cortex of the pyriform lobe. These fibers pass medialward, at the same time sweeping dorsalward to avoid the area of distribution of the stria terminalis. At the lateral border of the thalamus they run parallel with and dorsally of the stria terminalis fibers (figs. 20, 21) and here they turn abruptly dorsalward to enter the stria medullaris thalami.

4. *Tractus olfacto-habenularis medialis* (figs. 20, 21). This tract arises from the more posterior portion of the nucleus preopticus, runs dorsalward medial to the medial forebrain bundle and turns forward and forms the most anterior part of the stria medullaris.

5. *Tractus olfacto-habenularis lateralis* (figs. 20, 21). This tract has its origin from the more anterior portion of the nucleus preopticus. It runs first lateralward on the extreme ventral surface of the brain ventrally of the basal forebrain bundles, then backward and dorsalward, joining the tractus cortico-habenularis lateralis anterior in the angle between the ventro-medial nucleus and the lateral forebrain bundle and passes dorsalward with it to enter the stria medullaris. (See description of tractus cortico-habenularis lateralis anterior for a further account of the relations.)

6. *Tractus olfacto-habenularis posterior.* This tract arises near the posterior end of the hemisphere from the nucleus of the lateral olfactory tract and the ventro-medial nucleus in the region illustrated in figure 12. It passes directly dorsalward into the stria medullaris.

Olfactory projection tracts

The entire secondary olfactory area is broadly connected with the hypothalamus by way of the medial forebrain bundle. Descending impulses are carried from the medial (septal) wall of the hemisphere through the tractus parolfacto-hypothalamicus (tr. septo-hypothalamicus of some other authors), as described beyond in the account of the medial forebrain bundle. The connections between the olfactory centers in the lateral wall of the hemisphere and the hypothalamus may in the aggregate be termed the olfactory projection tracts, following the usage of Ramón y Cajal. The application of the term projection tracts to these fibers finds its justification in the intimate relation between the secondary or basal olfactory centers and the olfactory cortex of the pyriform lobe in the lateral wall.

There are two of these tracts which enter respectively the ventral and the dorsal sides of the medial forebrain bundle (figs. 19 and 20), which together probably correspond approximately with the so-called tractus pallii of fishes and amphibians.

Ventral olfactory projection tract (figs. 16 to 19). This tract has already been mentioned in our account of the anterior division of the lateral cortico-habenular tract. It arises from cells of the pyriform lobe and the nucleus of the lateral olfactory tract. It runs with the anterior division of the lateral cortico-habenular tract until it reaches the ventral part of the medial forebrain bundle, which latter it accompanies caudad. It probably ends in the hypothalamus.

Olfactory projection tract of Cajal (figs. 19 to 21). The fibers of this olfactory projection tract pass directly dorsalward from the ventro-medial nucleus, then curve medialward and pass caudad lying dorsally of the forebrain bundles and between them and the preoptic portion of the stria terminalis. Some of the fibers arise probably from cells of the interstitial nucleus and fibers from cells of the ventro-medial nucleus probably send collaterals into the interstitial nucleus. The fibers of this great olfactory projection tract as they swing medialward come into relation with the descending fibers of the columna fornicis and there turn sharply caudad and run with the latter bundle backward, medialward and ventralward to the mammillary body (figs. 20, 21). (Dr. C. J. Herrick first called the writer's attention to the fact that fibers of this olfactory projection tract join the fornix fibers and accompany them ventralward).

Ramón y Cajal ('11, vol. 2, pp. 722–723, fig. 462) has described and figured this tract and its associated nucleus in the mouse. Johnston ('15) described the tract in the turtle. He considers it to be the characteristic connection of his medial large celled nucleus of the amygdaloid complex (the ventro-medial nucleus of this description), but does not mention the interstitial nucleus which accompanies it.

Basal forebrain bundles

Medial forebrain bundle (figs. 9, 16, to 21, *M.F.B.*). This is the tractus septo-mesencephalicus of Unger and DeLange. It arises from the parolfactory (septal) nuclei and runs, accompanied by fibers of the fornix longus, medialward and ventralward until it meets the lateral forebrain bundle, which lies farther laterally. The two bundles can be distinguished from each other for a long distance because of a difference in the angles at which the fibers are running. Finally the two become closely mingled and it requires careful study to distinguish them, although such a differentiation is quite practicable. According to DeLange ('13) and Unger ('11) the medial forebrain bundle runs to the midbrain. In the alligator in material prepared by the Cajal method a part of the fibers appear to end in the hypothalamus (tractus olfacto-hypothalamicus of the literature), while others pass caudad to the midbrain (tractus olfacto-peduncularis).

There is no direct evidence in the material studied regarding the direction of conduction, but the probability is that impulses pass in both directions. It serves, then, partly as a discharge path from the parolfactory areas (tractus parolfacto-hypothalamicus and tr. olfacto-peduncularis) and perhaps also from the tuberculum olfactorium, and partly as a pathway by which visceral impulses from the hypothalamic region may reach the medial parolfactory area (tractus hypothalamo-parolfactorius) and, either with or without a synapse there, the hippocampus. Fibers connecting the parolfactory areas and the hippocampus run on the medial and lateral borders of the medial forebrain bundle.

Lateral forebrain bundle (figs. 9, 16, to 21, 37, 45, 46, *L. F. B.*). This bundle is made up in part of axones arising from the projection cells of the striatum. It runs ventro-medialward, joins the medial forebrain bundle on its lateral side, and then passes caudad into the diencephalon. This is the tractus strio-thalamicus of DeLange and Unger.

Besides these components of the lateral forebrain bundle which carry impulses from the striatal region, there are fibers from the lateral and medial nuclei of the thalamus which run ventralward and join the other fibers of this bundle and then go forward to the striatum. These facts are known because axones or the cell bodies of the lateral nucleus and nucleus rotundus have been seen to join this bundle (tractus thalamo-striaticus, or thalamic projection tracts).

There is a second thalamo-striatal path which runs from the anterior nucleus of the thalamus to the ventro-lateral small celled part of the hemisphere (that part which is Johnston's nucleus caudatus). This has been described by Johnston, DeLange, and others.

GENERAL DISCUSSION

The problems of forebrain morphology and especially those dealing with the evolution of the cortical areas have always had a peculiar fascination for the comparative neurologist. The broad lines and many of the details of forebrain development throughout the vertebrate series have been brought out by such observers as Edinger, Elliot Smith, Johnston, Herrick, and Kappers.

It is with considerable hesitation that the writer has undertaken the analysis of the anatomical data given on the preceding pages. Insufficient time and knowledge and the lack of experience have been very clearly realized and the following statements are offered merely as suggestions or as possible interpretations of some of the changes occurring and the factors operating during forebrain evolution.

Following the type of interpretation of Edinger, Herrick, Kappers, and Johnston, centers of the alligator hemisphere may be classified under two general heads which may be subdivided as follows:

I. Centers dominated by olfactory impulses
  A. Basal centers
    1. Medial olfactory area
      Nucleus olfactorius anterior (in part)
      Nuclei of the septum (in part), or parolfactory nuclei
    2. Lateral olfactory area
      Pyriform lobe complex (in part)
      Amygdaloid complex (in part)
    3. Intermediate olfactory area
      Tuberculum olfactorium
      Nucleus olfactorius anterior (in part)
      Nucleus of the diagonal band
    4. Correlation centers between telencephalic and diencephalic regions
      Tuberculum olfactorium (in part)
      Parolfactory nuclei (in part)
      Nucleus commissuralis hippocampi
      Bed nucleus of the anterior commissure
      Nucleus preopticus
      Interstitial nucleus of Cajal
      Amygdaloid complex (in part)
  B. Cortical centers (archipallium of Edinger)
    1. Hippocampal formation
      Small celled non-laminated part of hippocampus (the primordium hippocampi of Johnston, '13 and '15)
      Dorso-medial cortex (primordial gyrus dentatus, Elliot Smith, '96, Meyer, '92, Levi, '04)
      Dorsal cortex (hippocampal cortex, subiculum of Johnston '13)
    2. Lateral cortex (pyriform lobe)
    3. General cortex (to some slight degree)
II. Centers dominated by ascending somatic impulses from the thalamus
  C. Basal centers
    1. Dorso-lateral area
    2. Intermedio-lateral area
    3. Ventro-lateral areas (comparable to corpus striatum of Johnston '15)

D. Cortical centers
  1. General cortex (in part)
    Primordial general cortex (a special portion of this area in close relation with the dorso-lateral area)

The basal olfactory centers of the telencephalon will be seen to be separated into two broad groups. In the first group are those of the medial, intermediate and lateral areas which serve primarily as secondary olfactory centers. These are old in type, having their representatives in the hemisphere from cyclostomes (Johnston, '12, Herrick and Obenchain '13) up through the vertebrate series to man. They were originally simply a place of synapse and consequent redistribution of incoming olfactory impulses.

The second group of basal olfactory centers includes those which have developed within the hemisphere later in the phylogenetic history as a place of correlation between olfactory and non-olfactory impulses. It is significant that some of the centers (as for example the tuberculum olfactorium), judging from their fiber connections, are both secondary olfactory nuclei and correlations centers for olfactory and non-olfactory impulses. It is the forward growth, then, of non-olfactory fibers from the diencephalon into the secondary and tertiary olfactory centers of the hemisphere which has given the impulse toward differentiation to the telencephalon. These nuclei of the hemisphere, which serve as correlation centers for the olfactory and non-olfactory impulses, represent the beginning of that higher differentiation. Yet these basal centers do not form true cortex. In the Amphibia (Herrick, '10) in the ventro-medial part of the hemisphere, centers showing such type of correlation are present and the medial forebrain bundle, which opens the possibility of connection between the olfactory centers and the visceral centers in the hypothalamus, is well developed. In the dorso-medial part of the hemisphere of Amphibia the material, which is the primordium of the hippocampus, is present; it is under the influence of olfactory fibers and, to some extent, of fibers of the ventro-medial area of mixed function as just indicated. But here no clearly developed cortex is found and it is not until the basal olfactory and non-olfactory correlation areas are well developed, as in reptiles, that true hippocampal cortex begins to appear.

Johnston has emphasized the fact that the hippocampus is an olfacto-visceral center, although in a later paper ('15, p. 412) he has said that there are olfacto-visceral correlations in the subiculum as well. It is well to notice that these types of nervous impulses are not first assembled in the hippocampus. On the other hand, this cortex simply brings together material already correlated, partly in the hypothalamus and more completely within the basal telencephalic centers. Three types of centers concerned with olfactory impulses are represented then within the hemisphere.

1. Those basal centers concerned with the distribution of olfactory impulses and their summation and correlation among themselves.
2. Those basal centers concerned with the correlation of olfactory and non-olfactory impulses.
3. Those centers which receive impulses from correlation centers of the second type or from similar non-olfactory correlation centers and integrate these impulses. This integration of material already correlated is characteristic of the reptilian cortex. Into the hippocampus come impulses from the parolfactory area and the tuberculum olfactorium on the one hand, and from the pyriform lobe cortex by way of the alveus on the other hand.

In Amphibia (Herrick, '10) the primordium hippocampi occupies the dorso-medial portion of the medial wall of the hemisphere. This region has all the characteristic fiber tracts of the hippocampus (cf. Herrick, '10, p. 480) but there is no differentiated cortex in this region except possibly to a small degree in Anura, where there is a row of cells close to the surface of the ventro-medial wall which send out wide spreading dendritic processes among the incoming fibers and which resemble in cell characteristics those cells found in the alligator at the anterior end of the hippocampal formation.

In lower reptiles the dorso-medial area begins to form true hippocampal cortex. In the turtle, although, as has already been pointed out (see discussion of hippocampus), there is a clearly defined arrangement of a considerable part of the hippocampal formation into definite cortex-like layers, these layers have not moved out from the ventricle as in higher forms, but still form a ventricular mass.

The hippocampal cortex of the alligator represents another step in advance in differentiation, for here the cortex has moved away from the ventricle and accompanying this differentiation has been the specialization, at least to a considerable extent, of its medial aspect to serve as the afferent side of the cortex and its lateral aspect to serve as the efferent side. One of the causes at least, for the outward migration of cells of the dorso-medial area to form the hippocampal cortex is probably to be found in the operation of the law of neurobiotaxis (Kappers, '14). According to this law, cell bodies tend to migrate along their dendrites toward their source of stimulation. The medial olfactory tracts and other tracts bearing afferent impulses to the hippocampus are on the medial surface of the hemisphere and the cells of the developing cortical layers move out toward the surface of the hemisphere in order that they may come into closer relationship with the incoming impulses.

To recapitulate, the following steps appear to have lead from the primordial hippocampal type to the relatively simple type of cortex found in part of the hippocampal area in the alligator. In Amphibia (Herrick, '10) the afferent and efferent fibers spread out all through the dorso-medial area. Following a higher differentiation of the diencephalic and telencephalic subcortical correlation centers, there is a higher differentiation in the dorso-medial area so that the arrangement of the cells into cortex-like layers, such as we find in the turtle, occurs. This second step is followed in other reptiles by a further specialization of a part of the hippocampal cortex, so that it has an afferent medial side and an efferent lateral one.

The non-olfactory diencephalic fibers, which enter the telencephalon for the purpose of forming correlations with the incoming olfactory impulses, are partly visceral and partly somatic in type. Those ascending from the hypothalamus by way of the medial forebrain bundle to reach the medial wall of the hemisphere carry mainly visceral impulses and the dominant, although not the only, type of correlation in this wall is probably olfacto-visceral.

Impulses of a like kind reach the pyriform lobe region from the hypothalamus by way of the ventral olfactory projection tract (figs. 16 to 19). Thus, this series of steps which seems to have lead to the development of the hippocampus, can no doubt be duplicated in the development of the cortex of the pyriform lobe through the interrelation existing between the hippocampal cortex and the pyriform lobe cortex on the one hand and the interrelation between that latter cortex and the amygdaloid complex on the other, although the details are not very well known. In Amphibia (Herrick, '10) the dorso-lateral area of the hemisphere receives lateral olfactory tract fibers and presumably is the primordial material for the formation of pyriform lobe cortex and perhaps for part of the amygdaloid complex. Moreover, in Amphibia, the somatic area is ventro-lateral in position and receives and sends out fibers through the lateral forebrain bundle. In reptiles, this somatic area has increased in size because of the greater number of somatic fibers that it receives; for accompanying the telencephalic changes there has been an increased growth and differentiation of the thalamic regions, particularly of the lateral portions which receive the fibers of the incoming optic and lemniscus systems. This differentiation of the lateral part of the thalamus (the neothalamus of Edinger) is correlated with an increase in the number of fibers sent forward into the hemisphere from this region. This increase in the incoming fibers has lead to a change in the nuclear pattern among reptiles as compared with the pattern found among Amphibia. Some of the forward extending somatic fibers have begun to pass dorsalward of the old limits of the striatum and in the turtle (Johnston, 15) and in the alligator, perhaps in other reptiles also, the dorsal part of the lateral wall is chiefly a somatic correlation center. The lateral and ventro-lateral portion of this dorsal wall, however, is occupied by the cortex of the pyriform lobe and the anterior part of the nucleus of the lateral olfactory tract. The main part of the latter nucleus is found on the outer surface of the ventral part of the lateral wall external to the striatum complex.

What the factors were which produced these changes in form relation between these amphibian and reptilian brains it is quite impossible at present to say. The following account is offered as a possible suggestion of some of the ways in which these changes were brought about. Even in Amphibia one would expect the lateral part of the dorso-lateral area to be particularly closely tied up with the olfactory tract, for there the dorsal division of the lateral olfactory tract ends (Herrick, '10, p. 523, fig. 40, *tr. olf. d. lat.*). In more highly differentiated forms the same process probably occurred which is known to have happened in other parts of the brain, namely, that part of the cells will migrate outward, away from the general cell mass, in order to form a special receptive center for the incoming olfactory fibers (a nucleus of the lateral olfactory tract) while the remainder will come less directly under their influence. In Amphibia (Herrick, '10) some thalamic somatic fibers reach the dorso-lateral area, although they are few in number compared with the olfactory fibers reaching that region. As one passes from amphibians to reptiles, there is a great increase in differentiation of the somatic thalamic regions, as has been said before, and this differentiation is accompanied by an increase in the number of somatic fibers sent forward into the hemisphere by way of the lateral forebrain bundle. Some of the somatic fibers, passing dorsalward of the old limits of the striatum come into synaptic relation with the neurones corresponding with the old amphibian dorso-lateral area. Part of such fibers will form synapses with olfactory fibers and so a somatic-olfactory center, whose later representatives are the amygdaloid complex and the pyriform lobe cortex, will be formed. Others of these somatic fibers come into synaptic relations with the more medially placed neurones of this dorso-lateral area (i.e., those neurones less directly under the influence of the olfactory fibers). The entrance of this new mass of somatic fibers and the resultant somatic correlation will lead to an increase in both the cell number and cell dfferentiation and in this way a non-olfactory somatic correlation center can well grow up within areas primarily olfactory in type. With the entrance of a larger and larger number of somatic fibers within the area and the corresponding increase in the number and size of the cells, two changes in form relations occur in the lateral hemisphere wall. One change is the pushing outward and downward of the cell masses associated with the lateral olfactory tract so that they come to occupy secondarily a position superficial to the striatal region (the area occupied in the figures by the pyriform lobe and the nucleus of the lateral olfactory tract). The other change is the bulge medialward into the ventricle of the dorso-lateral somatic area which is so characteristic of the forebrains of the turtle and alligator.

The cortex of the pyriform lobe has arisen as a differentiation from the general cell mass of the forebrain which serves as a nucleus for the lateral olfactory tract. In the lower reptiles this cortex has appeared, although it is less differentiated than the olfactory cortex of the medial wall. Johnston ('16) has given very briefly some of the main features of the embryonic development of the lateral olfactory area and the cortex of the pyriform lobe in turtles. He finds the olfactory areas differentiating in the ventro-lateral part of the hemisphere and believes that the pyriform lobe cortex arises from cells of this region which have proliferated and perhaps migrated dorsalward, so that they came to lie external to the dorsal ventricular ridge. He is not certain, however, that they have not developed in situ. So far as the writer is aware, the history of the embryonic development of the pyriform lobe cortex in the alligator is unknown, but in all probability it is very similar to that of the development in the turtle. Of course, the question at once arises as to the factors operating to produce the specialized pyriform cortex from the general nucleus of the lateral olfactory tract and the reason for its new migration dorsalward (if that occurs as Johnston believes). In attempting to find a solution for the question one must look for the entrance into this region of fibers carrying a different type of impulse, for differentiation within an area is not dependent upon an increase in the number of fibers bearing the same sort of impulse but upon the introduction into the region of fibers bearing a new type. Such a new type is introduced into the primordial pyriform lobe by the alveus, which carries the association fibers from the other developing cortical areas, particularly from the hippocampus. These impulses brought by the alveus are the resultants of a relatively high type of progressively advancing integration and give the physiological conditions which the writer has conceived of as being important in the development.

Attention has already been called to the presence of a large basal somatic area in the dorso-lateral region of the forebrain in at least some of the reptiles. This region has been named the dorso-lateral area (figs. 2, 7 to 10, 12, 16 to 19, 44 to 46, *Dl.A.*, in this paper. A similar if not entirely homologous area has been termed the dorsal ventricular ridge by Johnston ('15) who in a recent paper ('16) has given an account of its embryological development. He finds that the dorsal portion of the embryonic brain in the turtle first gives rise by a process of cell proliferation to the general pallial cortex which then occupies a more superficial position. By a secondary proliferation from cells of the dorsal area, if the writer has understood Johnston ('16) correctly, the dorsal ventricular ridge is formed. The lateral portions are in relationship with the general pallial cortex and have the appearance of being an infolding of that area in adult material. In the adult turtle, the dorsal ventricular ridge extends to the caudal end of the hemisphere, showing throughout its extent this relationship with the general pallium. In the alligator the ridge of cells (termed here primordial general cortex) is found only in the anterior end of the hemisphere where it has practically the same relationships as in the turtle. Farther caudad the dorso-lateral area, of which the general cortex is a differentiation, is cut off from the latter region by the outward and downward growth of the ventricle. The dorsal and dorso-medial portions of this dorso-lateral area, however, receive somatic fibers throughout practically their whole extent as far as the caudal end of the area. Association fibers from the hippocampus and the pyriform lobe distribute not only to the general cortex but also to the primordial general cortex in the anterior end of the dorso-lateral area. These superficial tangential association fibers have probably been responsible for the migration of the cells of the general pallium from their original ventricular position to form a more superficial cortical lamina, for their neurobiotactic influence (Kappers) would have this tendency.

SUMMARY

To recapitulate, it appears to us that the following factors are involved in giving the morphological form and typical functional activity of the alligator forebrain:

1. This forebrain is very largely under the dominance of the olfactory system.
2. Its differentiation into basal and cortical centers is due, directly or indirectly, to the entrance of non-olfactory diencephalic impulses.
3. These diencephalic fibers are partly for synaptic relations with the olfactory fibers; and consequently basal centers for the correlation of olfactory and non-olfactory impulses are present. A variety in the type of the incoming diencephalic impulses has lead to the differentiation of a number of different basal nuclei, for it has not been the number of synapses through which an impulse has passed, nor the number of fibers coming into a nucleus, but the variety in the types of stimulation received which has lead to the differentiation of the telencephalic centers.
4. In the lateral wall of the hemisphere the primordial striatum is present, which is practically free from olfactory influence and is under the influence of somatic fibers from the thalamus. The somatic area is larger than in lower forms and correlated with this increase in size is an increase in size and differentiation of the lateral part of the thalamus.
5. There are three primordial cortical areas represented and they all have certain characteristics in common. All of these are primarily for the integration of impulses already correlated in the basal centers or transmitted to them by way of association fibers from the other cortical centers. A certain proportion of comparatively pure olfactory impulses enters the hippocampus and the pyriform lobe; but, as has already been discussed, these

are primitive and, in themselves, insufficient for the formation of cortex.

Again, all the correlated material brought to each of these cortical areas contains olfactory and non-olfactory elements, the latter including visceral and somatic types. The differences in significance of the areas are due to a preponderance of a given type of correlation in each case. In the hippocampus the olfacto-visceral elements are very large and dominate the situation; in the pyriform lobe there is a considerable amount of correlation of the olfacto-visceral type, but there is a sufficient proportion of somatic impulses to give this lateral cortex a different physiological importance from that of the hippocampus. The olfacto-visceral types of correlation are small in the general cortex and the somatic types predominate.

The great significance of this general cortex in the alligator is the appearance of a somatic center having a high cortical type of integration. Nevertheless, since the general cortex is under tolerably direct olfactory influence from the adjacent hippocampal and pyriform cortex (and possibly from other sources), it cannot be regarded as fully differentiated neopallium, though it is undoubtedly the immediate precursor of that type of cortex.

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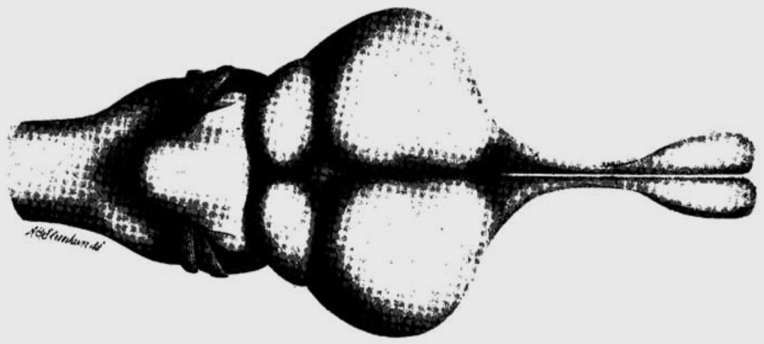
ABBREVIATIONS

A., alveus
ax., axone
C.A., commissura anterior
C.H., commissura hippocampi
C.Hab., commissura habenularum
Cor.C., correlation cell
D.B., diagonal band of Broca
Dl.A., dorso-lateral area
D.pyr.C., double pyramid cell of hippocampus
F., fornix
F.B., forebrain bundles
Fib.tang., fibrae tangentales
Fim., fimbria
F.L., fornix longus
G.C., general cortex
glom., glomerulus
Glom.L., glomerular layer
Gran.L., granular layer
H., hippocampus
Hab., habenula
Hem., hemisphere
H.p.d., hippocampus, pars dorsalis
H.p.dm., hippocampus, pars dorsomedialis
Hypth., hypothalamus
I.Gran.L., inner granule layer
Interm.l.A., intermedio-lateral area
Inters.n., interstitial nucleus
Intr.C., intrinsic cell
L.F.B., lateral forebrain bundle
L.Gob.C., large goblet cell

L.P., lobus piriformis
M.C., mitral cell
M.C.L., mitral cell layer
M.F.B., medial forebrain bundle
N.acc., nucleus accumbens
N.ant.thal., nucleus anterior thalami
N.c.a., nucleus commissurae anterioris
N.c.h., nucleus commissurae hippocampi
N.d.b., nucleus of the diagonal band of Broca
N.lat.thal., nucleus lateralis thalami
N.olf.ant., nucleus olfactorius anterior
N.parolf.lat., nucleus parolfactorius lateralis
N.parolf.med., nucleus parolfactorius medialis
N.preop., nucleus preopticus
N.tr.olf.lat., nucleus tractus olfactorius lateralis
N.vent.med., ventro-medial nucleus
O.Gran.C., outer granule cell
O.Gran.L., outer granule layer
Olf.B., olfactory bulb
Olf.C., olfactory crus
Olf.proj.tr.(Cajal), olfactory projection tract of Cajal
Op.ch., optic chiasma
Op.tr., optic tract
P., pulvinar
Plex.L., plexiform layer
Prim.G.C., primordial general cortex
Prim.h., primordial hippocampus
Proj.C., projection cell of the ventro-lateral area
S.Gob.C., small goblet cell
S.proj.C., small projection cell
St.C., stellate cell
St.med., stria medullaris
St.term.p.com., stria terminalis pars commissuralis
St.term.p.preop., stria terminalis pars preopticus
Taen.c., taenia chorioidea
Taen.f., taenia fornicis
T.olf., tuberculum olfactorium
Tr.cort.hab.lat.ant., tractus cortico-habenularis lateralis anterior
Tr.cort.hab.lat.post., tractus cortico-habenularis lateralis posterior
Tr.cort.hab.med., tractus cortico-habenularis medialis
Tr.cort.parolf., tractus cortico-parolfactorius
Tr.olf., tractus olfactorius
Tr.olf.cort., tractus olfacto-corticalis
Tr.olf.hab.lat., tractus olfacto-habenularis lateralis
Tr.olf.hab.med., tractus olfacto-habenularis medialis
Tr.olf.hab.post., tractus olfacto-habenularis posterior
Tr.olf.interm., tractus olfactorius intermedius
Tr.olf.lat., tractus olfactorius lateralis
Tr.olf.med., tractus olfactorius medialis
Tr.parolf.cort., tractus parolfacto-corticalis
Tr.tub.cort., tractus tuberculo-corticalis
Vent.olf.proj.tr., ventral olfactory projection tract
Vl.A.(l.c.), ventro-lateral large celled area
Vl.A.(s.c.), ventro-lateral small celled area



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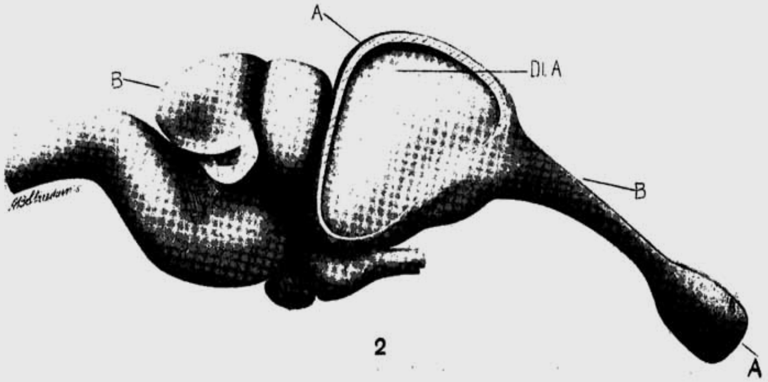

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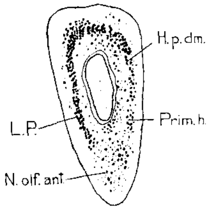
Fig. 1 The brain of Alligator mississippiensis, as seen from the dorsal surface. Drawn from a specimen 55 cm. long. × 3.

Fig. 2 A lateral view of the same specimen as in figure 1. A part of the lateral wall has been removed so as to expose the lateral ventricular surface of the dorso-lateral area. × 3. The line *A–A* represents the plane of section of figure 44; the line *B–B* that of figure 45.



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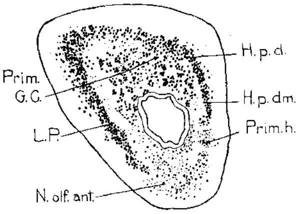

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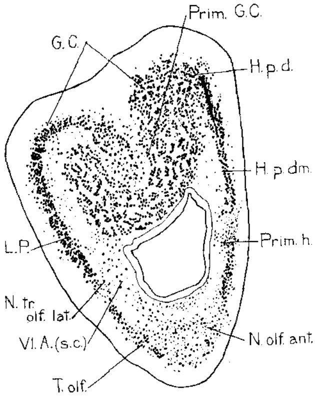

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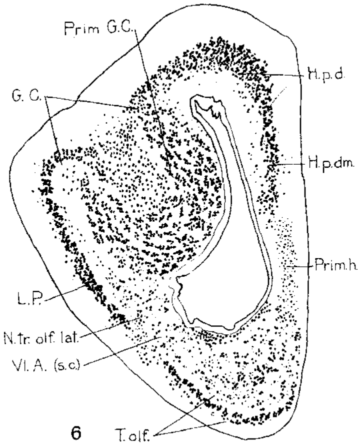

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Figs. 3–12 A series of transverse sections through the hemisphere of Alligator mississippiensis. Toluidin blue. × 19. The serial numbers of the sections figured are appended to the descriptions.

Fig. 3 Section through the posterior part of the olfactory crus showing the anterior part of the pyriform lobe and the hippocampus (14 : 286)

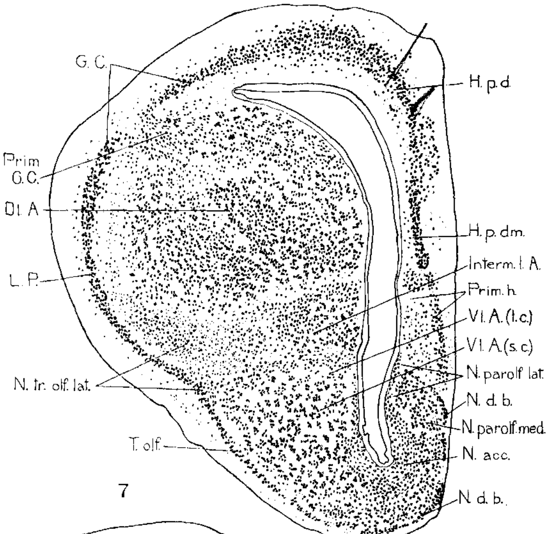
Fig. 4 Section slightly caudad to the preceding, showing the primordium of the general cortex (16 : 318).

Fig. 5 Section illustrating the characteristic appearance of the general cortex (18 : 353).

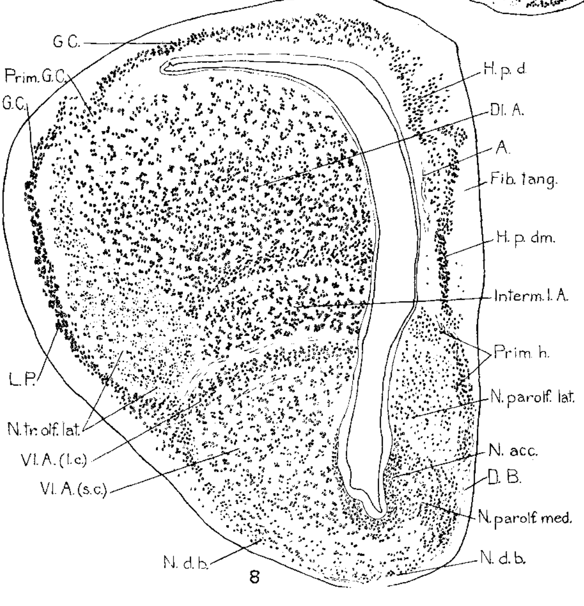
Fig. 6 Section somewhat caudad to the preceding (19 : 370).

Fig. 7 Section through the posterior part of the primordium of the general cortex, showing the basal nuclei of the lateral and medial walls in that region (22 : 416).

Fig. 8 Section slightly caudad to figure 7 (23 : 436).


G. C.
Prim G.C.
Dl. A
L. P.
N. tr. olf. lat.
T. olf.
H. p.d.
H. p. dm.
Interm. l. A.
Prim. h.
Vl. A. (l.c.)
Vl. A. (s. c.)
N. parolf. lat.
N. d. b.
N. parolf. med.
N. acc.
N. d. b.

7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Prim. G.C.
G.C.
L.P.
N. tr. olf. lat.
Vl. A. (l.c.)
Vl. A. (s.c.)
N. d. b.
H. p. d.
Dl. A.
A.
Fib. tang.
H. p. dm.
Interm. l. A.
Prim. h.
N. parolf. lat.
N. acc.
D. B.
N. parolf. med.
N. d. b.

8

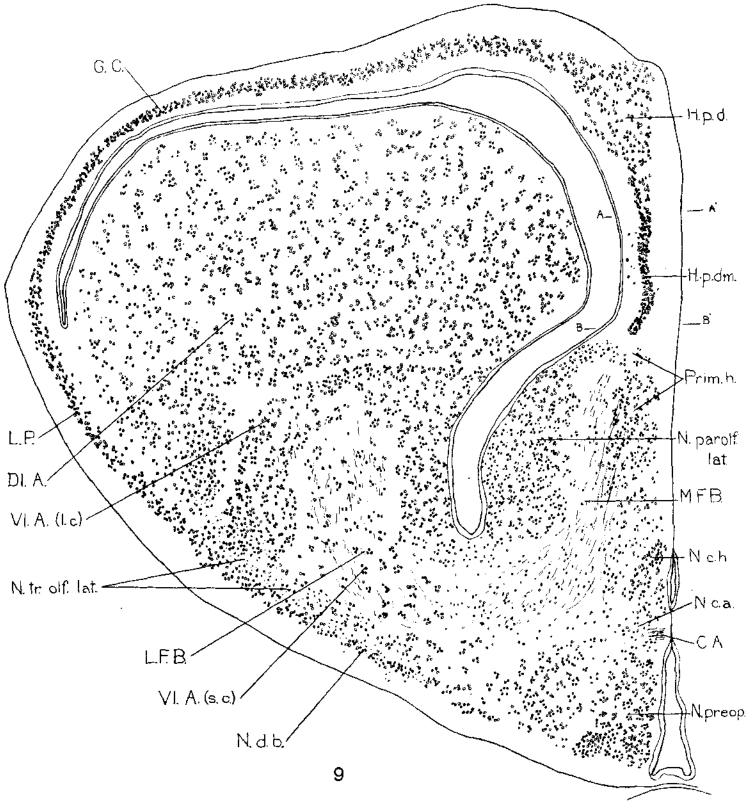

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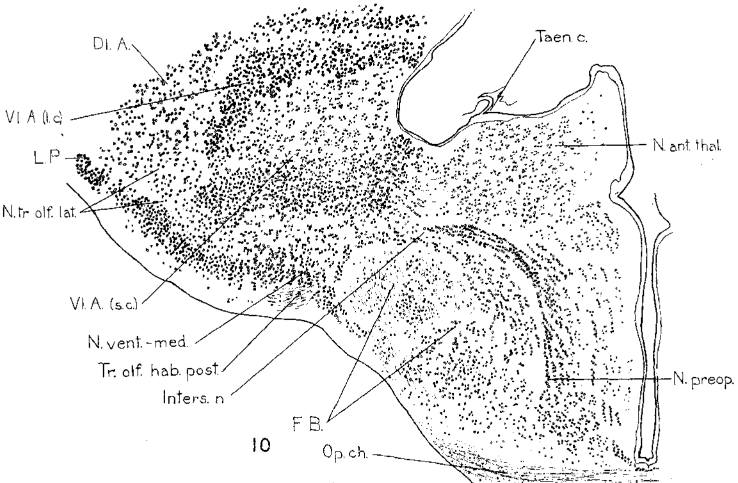
Fig. 9 Section through the level of the diagonal band of Broca, showing the relations of the parolfactory nucleus and primordium hippocampi (27 : 1, 4). (*A–A'* and *B–B'* show the orientation of figure 30.)

Fig. 10 Section through the anterior end of the thalamus. Note the relative positions of the ventro-lateral, small-celled area and the nucleus anterior thalami (29 : 3, 1).

Fig. 11 Section through the nucleus lateralis thalami. Note the large size of the cells (31 : 2, 3).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Taen. c.
Vl. A (l.c)
L.P
N. ant. thal.
N. tr. olf. lat.
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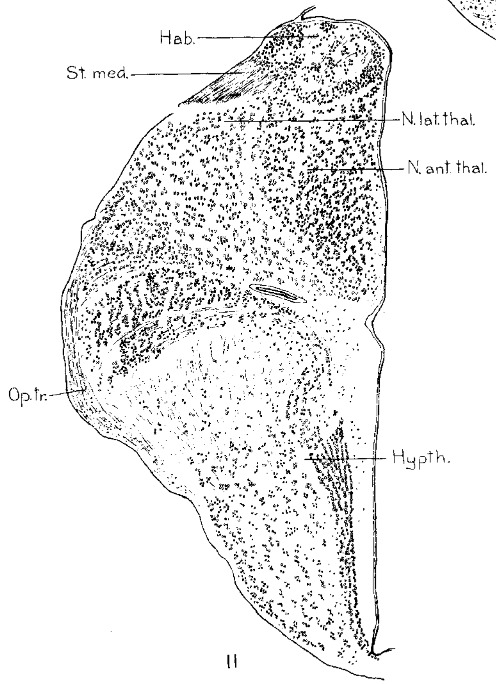
N. vent.-med.
Tr. olf. hab. post.
Inters. n
N. preop.
F.B.
Op. ch.

10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St. med.
N. lat. thal.
N. ant. thal.
Op. tr.
Hypth.

11

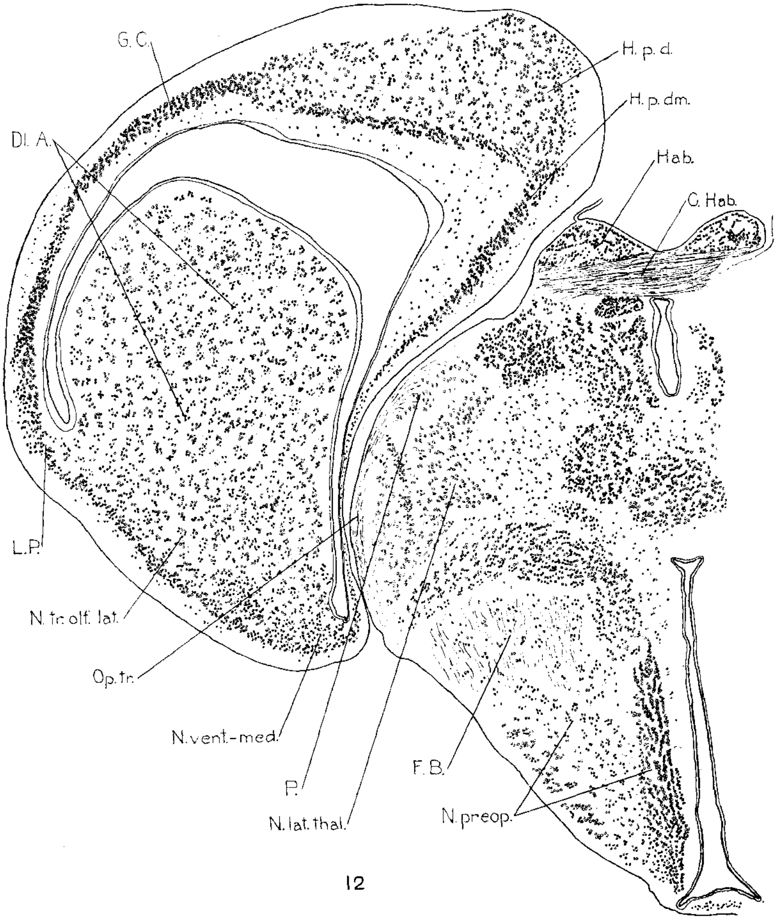

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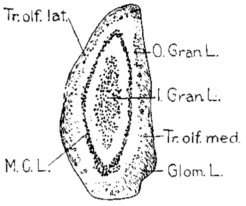
Fig. 12 Section through the habenular commissure. (32 : 3, 3).

Figs. 13–21 Transverse sections prepared by the Cajal method. Sections from two different series were used in preparing this series of drawings. ×13.

Fig. 13 Cross section through the left olfactory bulb anterior to the olfactory ventricle. The characteristic groupings of the internal and external granule cells and the ring-like arrangement of the mitral cells are clearly shown. The incoming fila olfactoria and the glomeruli are shown in the figure (3 : 3, 2).



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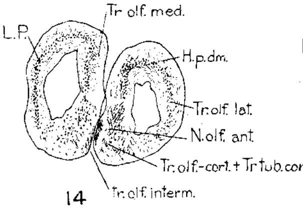

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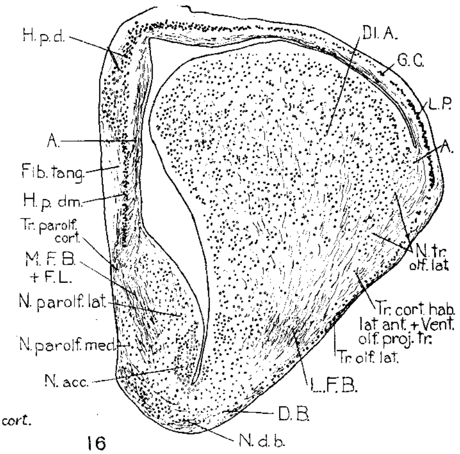

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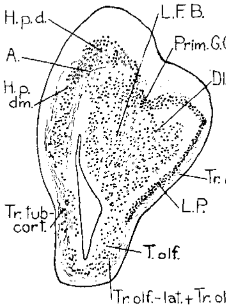

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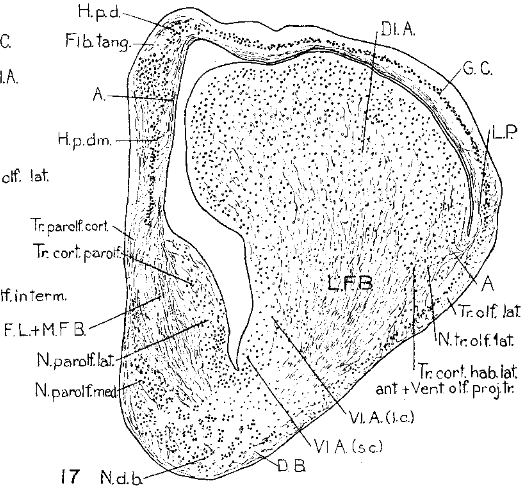

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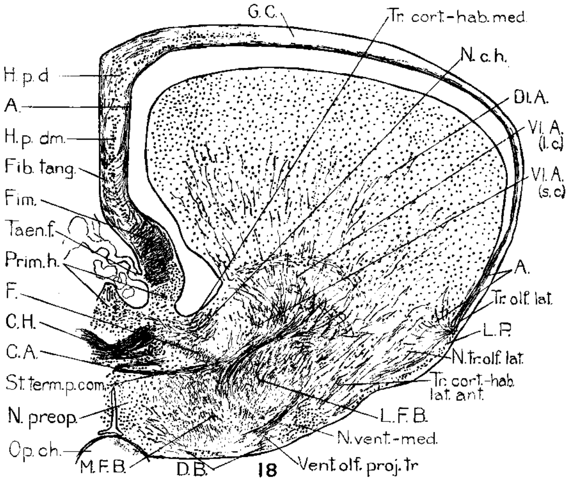
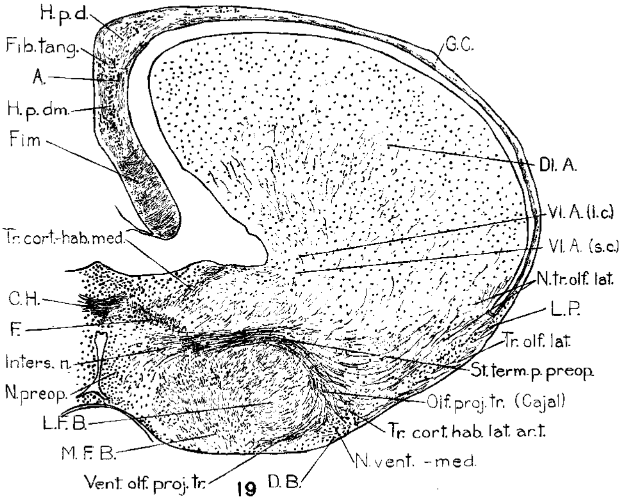
Fig. 14 A transverse section through the posterior part of the olfactory crus where it is broadening out into the hemisphere (3 : 254).

Fig. 15 A transverse section through the right hemisphere at the anterior end of the neopallial primordium (8 : 3, 3).

Fig. 16 A section near the anterior end of the medial forebrain bundle, *M. F. B.* (12 : 4, 1).

Fig. 17 A section a short distance anterior to the hippocampal commissure (14 : 2, 3).

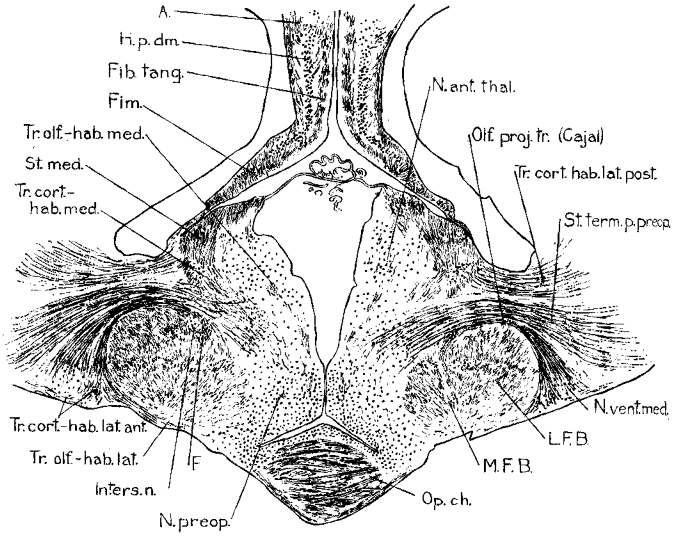




Figs. 18–21 These figures were drawn from a transverse series prepared after the Cajal method and loaned by Dr. P. S. McKibben. × 13.

Fig. 18 A section through the anterior part of the hippocampal commissure (11 : 780).

Fig. 19 A section through the posterior part of the hippocampal commissure and the beginning of the stria medullaris (11 : 788).



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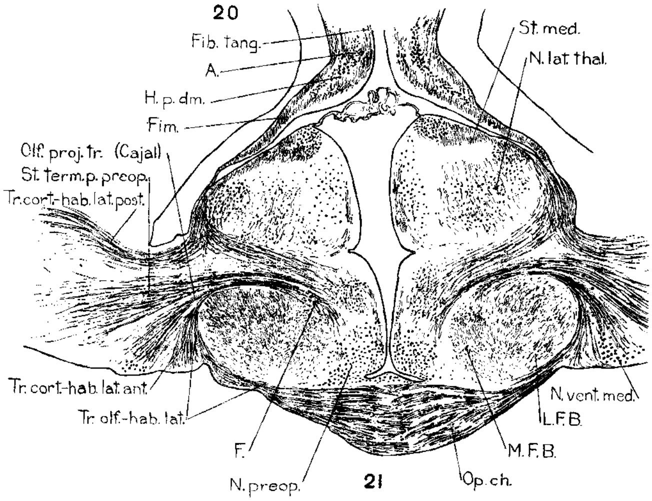

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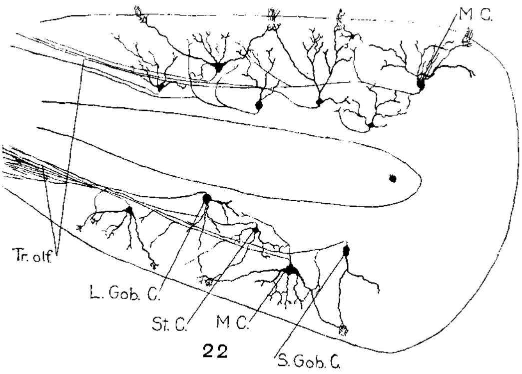
Fig. 20 Section through the anterior part of the thalamus, showing the relations of the fiber tracts (12 : 805).

Fig. 21 Section through the anterior part of the habenula (12 : 823).



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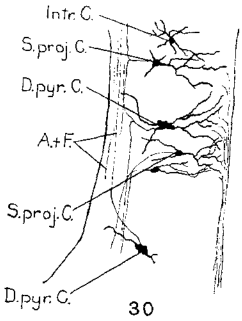

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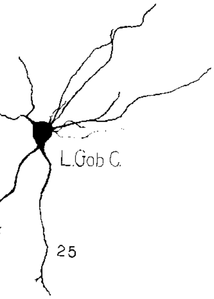

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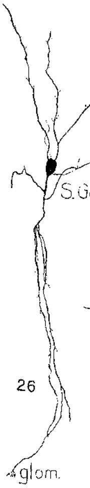

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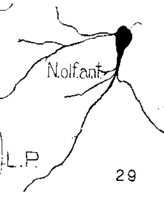

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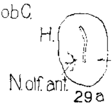

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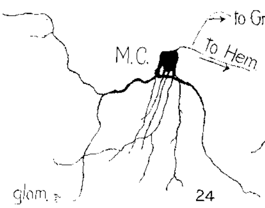

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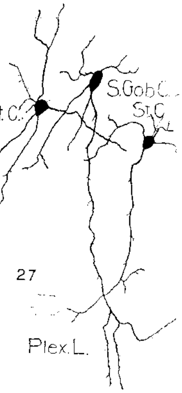

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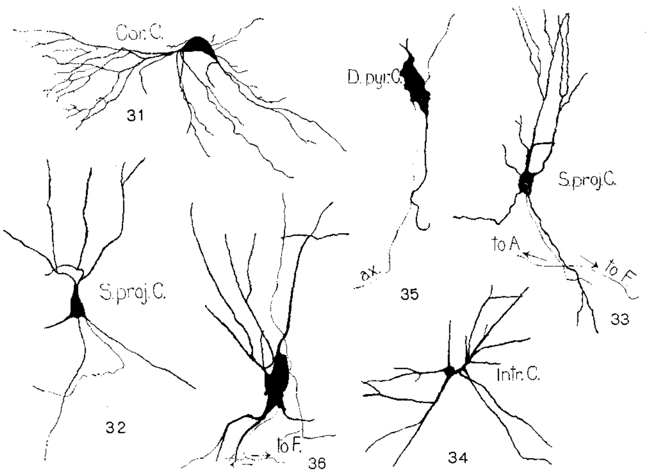


Figs. 22–43 Characteristic cells from various parts of the forebrain and thalamus of Alligator mississippiensis as seen in Golgi preparations. ×90.

Fig. 22 A diagramatic sketch of the positions and relations of the various cell types found in the olfactory bulb.

Fig. 23 Small mitral cells of the olfactory bulb (Gl : 60).

Fig. 24 Large mitral cell of the olfactory bulb (Gl : 73).

Fig. 25 Large goblet cell of the olfactory bulb (Gl : 64).

Fig. 26 Small goblet cell of the olfactory bulb (Gl : 55).

Fig. 27 Group of internal granule cells of the olfactory bulb. Note that one of the stellate cells sends its dendrites down into the plexiform layer and into the region, at least, of the glomeruli. The other does not send its dendrites outward beyond the mitral cells (Gl : 55).

Fig. 28 A small stellate cell of the olfactory bulb (Gl : 96).

Fig. 29 A goblet cell of nucleus olfactorius anterior (Gl : 103).

Fig. 29a A diagram showing the orientation of figure 29.

Fig. 30 A diagram showing the orientation of the hippocampal cells. The positions of the hippocampal cells figured (figs. 31–36) are shown here.

Fig. 31 Correlation cell found in the dorsal part of the hippocampus at the anterior end of the hemisphere (Gl : 104).

Figs. 32 and 33 Small projection cells of the dorso-medial part of the hippocampus (Gl : 139; Gl : 140).

Fig. 34 Intrinsic cell of the hippocampus (Gl : 140).

Figs. 35 and 36 Double pyramid cells. These are the specialized derivatives of projection cells of the dorso-medial portion of the hippocampus. The cells figured are probably imperfectly impregnated (Gl : 140; Gl : 139).

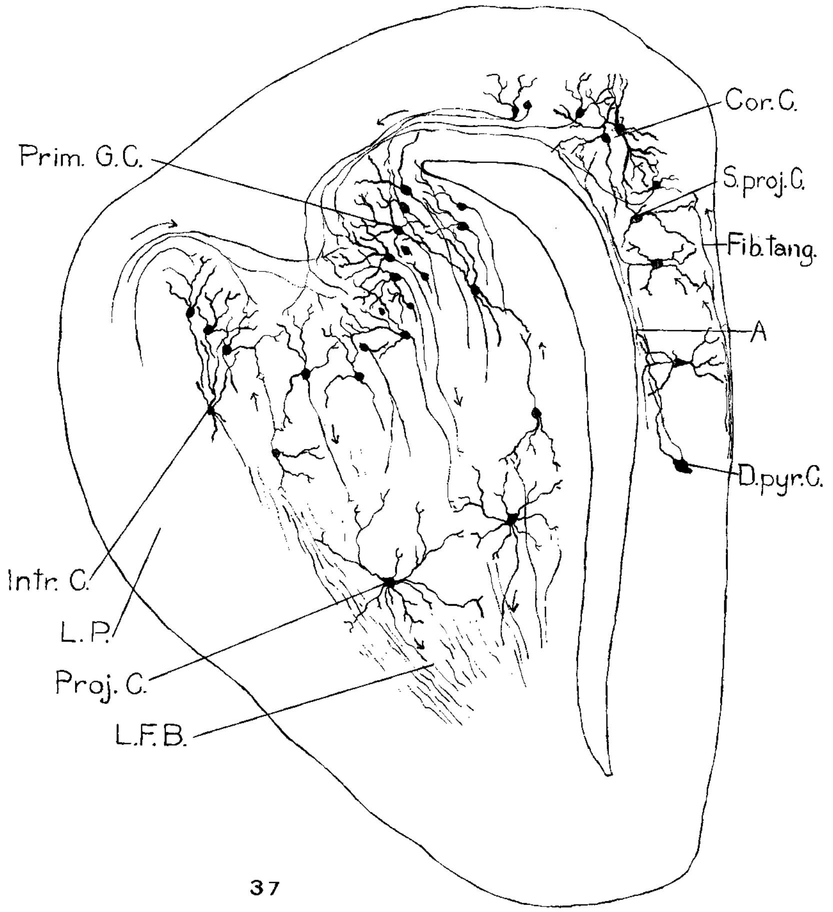


Fig. 37 This is a diagram of a transverse section through the hemisphere at the level of the primordial infolding. The cells of this primordial general cortex are round or goblet shaped (fig. 40) and have their dendrites directed outward and their axones inward and downward into the striatum. The axones come into relationship with the projection cells of the striatum, and, after a synapse, the impulse is carried by the axones of these projection cells through the lateral forebrain bundle to the lower centers. Impulses reach the primordial general cortex from the hippocampus, the pyriform lobe and the thalamus (by way of the lateral forebrain bundle). The interpolated neurone (*Intr.C.*) pictured in the diagram was not brought out very clearly in the Golgi sections, for, although neurones of that type were seen in the sections, they were never clear enough for high power drawings. Several types of neurones can be distinguished in the toluidin blue sections and the cell labeled 'intrinsic cell' is a guess at one of their probable functions.

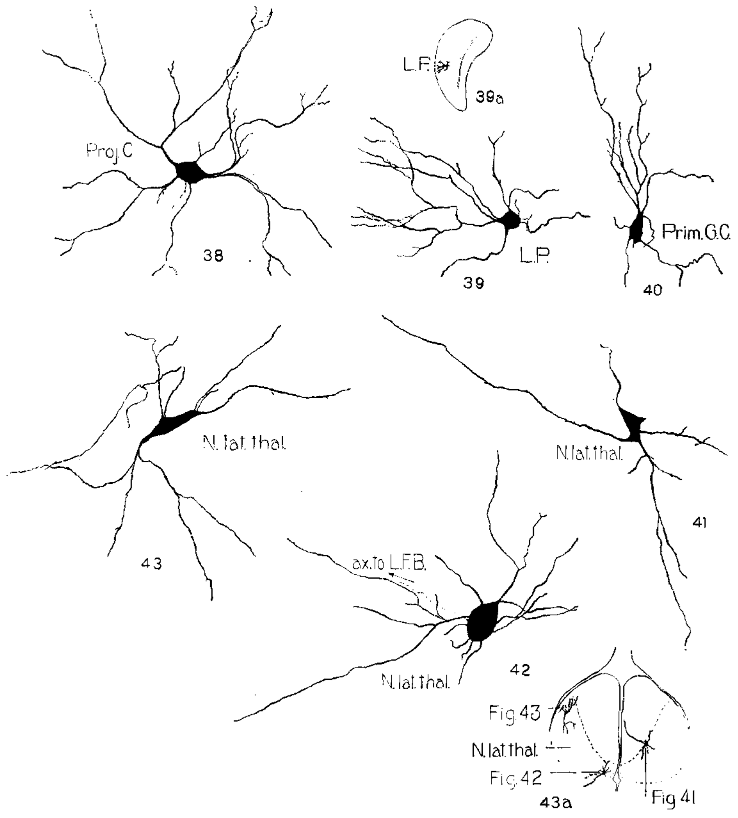


Fig. 38 Projection cell of the ventro-lateral area. For orientation see figure 37 (Gl : 126).

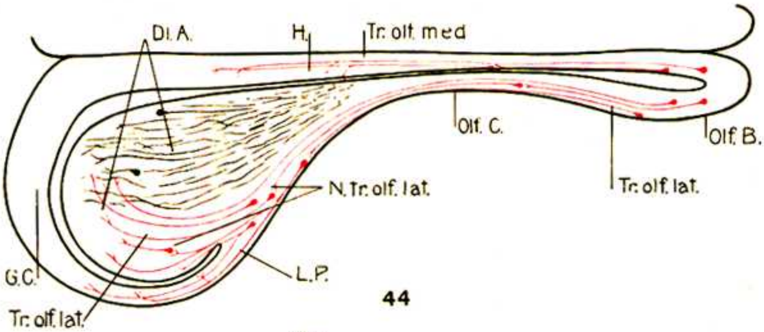
Fig. 39 Cell from the anterior part of the pyriform lobe (Gl : 99).

Fig. 39a Diagram for the orientation of figure 39.

Fig. 40 Cell from the primordial general cortex (Gl : 105). For orientation see figure 37.

Figs. 41–43 Cells of the nucleus lateralis thalami (Gl : L60; Gl : 159; Gl : 159).

Fig. 43a Diagram for the orientation of figures 41–43.



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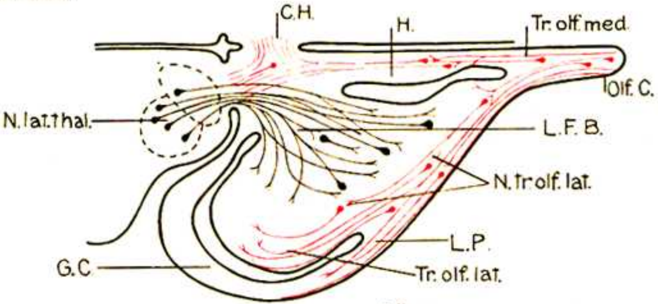

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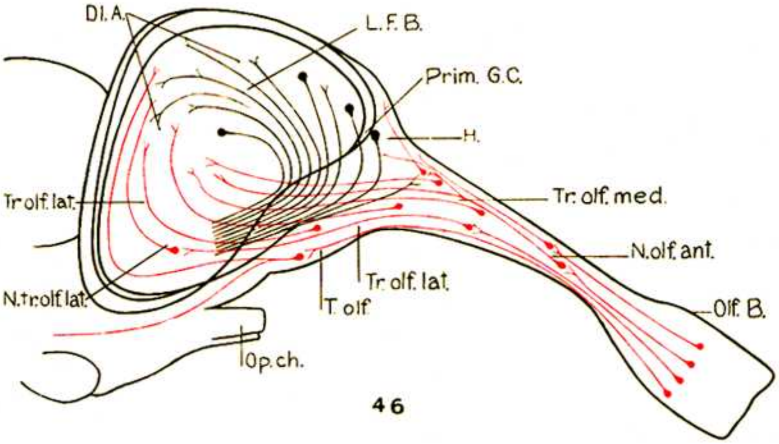

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Fig. 44 A diagram of the connections of the olfactory tracts and the lateral forebrain bundle of the alligator, based on a longitudinal section of the hemisphere in the plane indicated by the line *A-A′* of figure 2. The olfactory tracts are printed in red, the lateral forebrain bundle in black.

Fig. 45 A diagram similar to figure 44, but taken farther ventral and in a somewhat different plane, passing through the level of the hippocampal commissure as indicated by the line *B-B′* of figure 2.

Fig. 46 A diagram of a longitudinal section through the forebrain of the alligator taken in a parasagittal plane, to illustrate the relations of the olfactory and somatic centers. Olfactory fibers red, somatic fibers black.