THE CELL MASSES IN THE FOREBRAIN OF THE TURTLE, CISTUDO CAROLINA¹

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SIXTY FIGURES

In continuation of work upon the forebrain, it is the writer's intention to study the origin, growth and differentiation of the general pallium in the series of vertebrates. In doing this it will be necessary to keep constantly in mind the relations of the general pallium to the hippocampal formation, which has been described in earlier papers. The history of the amygdaloid complex and of the pyriform lobe is also intimately concerned. Finally, the position and arrangement of the fiber tracts connecting the hemispheres with the brain stem bear an important relation to the morphology of the cell masses in the forebrain.

In order to be able to compare given brain structures in lower and higher vertebrates it is necessary to have a description of the brain of some intermediate form in which the more common ichthyopsid characters can be recognized and in which at the same time the hippocampus and general pallium are present. For this purpose the brain of the turtle has been chosen and it serves admirably because of the relationship of the chelonia to the ancestors of mammals. The present paper will be confined almost wholly to description, the review of literature and the discussion of hypotheses being deferred to later papers.

METHODS

The results here presented have been obtained chiefly from the study of cell preparations. The results from the study of fiber tracts, although used in connection with this work, will be reported only briefly. The object has been to define the aggre-

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THE JOURNAL OF COMPARATIVE NEUROLOGY, VOL. 25, NO. 5 OCTOBER, 1915 gations of neurones which there is reason to think are concerned with specific functions and to determine the position, extent and limits of these cell masses. Criteria depended upon are the position, size, form and grouping of the cells, their relation to fiber tracts and their relation to neighboring cell-masses. The more important aggregations of neurones are either separated from neighboring masses by cell-free zones, or they present a sudden transition to other masses whose cells differ markedly in size, position, staining qualities, etc. Sometimes sulci mark the lines of demarcation. Typical sections have been drawn to show the arrangement of cells in various regions and the lines of demarcation between the aggregations of neurones. To gain an understanding of the morphological relations, dissection and modelling have been practiced. After the various cell masses had been studied and their limits determined, a model was made of the right hemisphere together with a small adjacent part of the diencephalon. In making the plates for this model the limits of the several cell-masses were drawn under the projection microscope. The plates were then cut along these limiting lines but the parts not separated from one another. The model was then piled and fastened together as a whole and the several parts separated at last along the lines of the cuts. In this manner it was possible to pile the model accurately in the form of the control brain and since each part was strongly fastened together there was no distortion of the parts.

I am indebted to Dr. Wm. F. Allen for the beautiful photographs of this model.

DESCRIPTION

As is well known, the turtle has fairly large hemispheres whose caudal poles lie at the sides of the mesencephalon. The disposition of the hippocampal formation and the olfactory tubercle in the medial wall have been described in a previous paper. Other features in this wall will be taken up in later sections. The lateral wall shows a broad depression where the hemisphere connects with the brain stem which at once suggests comparison with the insular region in the mammalian brain (fig. 1). The dorsal border of this depression is formed by a low ridge which extends rostrally into the lateral wall of the olfactorý bulb. This ridge is traversed by the lateral olfactory tract and is therefore to be compared with the pyriform lobe of the mammalian brain. Near its rostral end it presents an apparent thickening which causes a decided elevation of the surface (figs. 5, 26). The sulcus which bounds the pyriform lobe dorso-laterally varies in depth in different individuals, but is always well marked in its rostral portion. It is the fissura rhinalis.

The insula-like region is clearly seen in the entire brain to be trasversed by bundles of medullated fibers (fig. 1). Sections show these to be a continuation of the crus cerebri (figs. 32, 49), and therefore comparable to the capsula interna. The absence of a cortical layer covering the internal capsule shows that this does not correspond to the insula. It is the corpus striatum which retains a condition analogous to that seen in the fish brain and is not yet covered in by pallium.

Caudal to the striatum there is a well-developed occipitotemporal pole whose presence adds to the similitude of the turtle's brain to that of a mammal. The pyriform lobe appears to blend with the occipital lobe. Along its lower border is a groove which at the rostral end is the sulcus endorhinalis. Behind the striated area a deep groove continues for some distance toward the caudal pole. This groove will be called the fissura amygdaloidea. A part of the area appearing below it in lateral view is occupied by the amygdaloid complex (fig. 5). The reason for calling this the amygdaloid fissure, however, is that it represents the line of infolding of an important body which becomes in mammals a part of the amygdaloid complex.

Rostral to the striated area appears the smooth lateral surface of the tuberculum olfactorium and adjacent olfactory area, including the lateral portion of the homologue of the anterior perforate space. Between this region and the pyriform lobe rostral to the striatum is the sulcus endorhinalis (figs. 19 to 26).

The vault of the hemisphere is occupied, as we shall see, by the general pallium. It is very evident that if the expansion of the general pallium were to push the pyriform lobe ventro-laterally until it was driven down nearly upon the basal surface and until the migrated general pallium itself had covered over the striatum, there would be produced a fairly exact counterpart of the primitive mammalian brain. This is the condition of the brain of an opossum or rabbit, in both of which the lateral (Sylvian) fissure is little deeper than the analogous striatal depression in the turtle's brain. The further expansion of the frontal and caudal poles produces the opercula bounding the lateral fissure.

On the dorsal surface just behind the olfactory peduncle occurs a slight rounded elevation (figs. 3, 25) which forms a part of the pallial thickening to be described below.

On the medial surface of a brain from which the stem has been cut away and the choroid plexus removed (fig. 3) it is seen that a wide chorioid fissure extends caudad in a simple curve from the interventricular foramen into the temporal pole. On removing the medial wall of the hemisphere there are exposed certain ridges which constitute some of the most characteristic features of the reptilian brain (figs. 4, 10). Three main bodies are to be distinguished: a *dorsal ventricular ridge*, the largest and most prominent; beneath it and extending farther rostrad, the *striatum*; and rostrally in the dorsal wall a smaller *pallial thickening*.

Three longitudinal ventricular grooves are to be distinguished: dorsal, middle and ventral. The dorsal ventricular groove is a very deep groove between the dorsal ridge and the pallium (figs. 4, 11 to 22). The middle groove runs beneath the dorsal ridge from the amygdaloid region forward into the olfactory bulb. A bifurcation of the caudal end of this groove and its significance will be mentioned later. The ventral groove is medial to the striatum. It dips very deep into the olfactory tubercle but is shallow rostral and caudal to this level.

The term epistriatum was first used by Edinger to designate a body in the reptilian forebrain to which C. L. Herrick had traced a large part of the olfactory tract. In the 1904 edition of Edinger's textbook this body is labelled epistriatum in figures 117, Varanus; 122 and 123, Schemata; 125b, lizard. This usage is followed by de Lange in a recent paper on Varanus. In Edinger's figure 121 the term epistriatum is applied to an entirely different body in the turtle, the dorsal ventricular ridge of the present paper. In figure 125a, which also represents the turtle, this ridge is called mesostriatum and the term epistriatum is applied to the pallial thickening. Since the structure to which the term epistriatum was first applied does not appear as a special body or ridge in the turtle brain and since the author of the term uses it for at least three different bodies in the reptilian brain, the term will not be used in the present paper. The use of purely descriptive terms will help to avoid confusion.

In the dissected brain or in the model from which the hippocampal formation has been removed (figs. 4, 10) it is seen that the dorsal ventricular ridge bends down into the temporal pole. Here it enters into close relations with the amygdaloid complex which must be discussed later.

FORMATIO OLFACTORIA

The formatio olfactoria is that portion of the forebrain which receives fila olfactoria and contains mitral cells and glomeruli. It forms the rostral part of the olfactory bulb and extends farther caudally on the dorsal than on the ventral surface. Thus the peduncular constriction is placed obliquely, as is evident in figures 3 and 5. The bulb in its rostral part is nearly triangular in cross section (fig. 30). The olfactory nerve divides into distinct ventral and dorsal roots. The ventral spreads upon the dorsal surface of the bulb and enters the brain farther rostrally than does the dorsal root. The ventral root spreads over somewhat more than the lower half of the medial and lateral walls (fig. 30) and the rostral surface. The dorsal root continues over the bulb as a high ridge and spreads out in the dorsal wall in its caudal part. At its greatest extent, near the peduncle, this root extends half way down on the medial and lateral surfaces. The areas in which bundles of fila olfactoria are evident are shown in figures 28, 29, 30. It is certain, however, that many fila extend either in small bundles or singly some distance beyond these limits before ending in relation with neurones of the formatio olfactoria.

The limits of the formatio olfactoria can be determined more accurately by a study of the form, size and grouping of the cells. Throughout all the area where fila olfactoria are visible, the wall of the bulb consists of a thick layer of granule cells adjacent to the ventricle, and a fiber layer of varying thickness in the midst of which are scattered large and small mitral cells. In the areas not covered by bundles of fila olfactoria the mitral cells are less numerous and sometimes absent (figs. 28, 29, 30).

The deep granule cells are very numerous, closely crowded and sometimes arranged in irregular concentric layers. Golgi sections show that they possess two or more long slender dendrites radially placed and that the dendrites interlace with those of the mitral cells in the glomeruli. These cells are therefore true olfactory receptive cells, comparable to the deep cells of the olfactory formation of fishes (Johnston '01). The granule cells form a dense thick layer surrounding the ventricle throughout the whole extent of the bulb (figs. 28, 29, 30) and constitute the greater part of its volume. The groove or constriction which marks the olfactory peduncle follows accurately the caudal border of this granule cell layer. In the lateral wall the pyriform lobe and the olfactory tubercle push forward somewhat and the peduncular groove presents a V-shaped bend forward (fig. 5), but everywhere the groove faithfully indicates the boundary between primary or bulbar structure and the secondary centers or olfactory lobe.

The layer of mitral cells and of small brush cells is not as extensive as that of granule cells. In the rostral half of the bulb this layer is continuous around the periphery of the section, but the cells are less numerous in the lateral and medial angles where the fila olfactoria are not evident. In the caudal part of the bulb the corresponding areas become quite free from mitral cells for some distance (fig. 29, 31). The distribution of the mitral cells is determined by their relation to the fila olfactoria. Golgi preparations show that the dendrites of mitral cells and of the small brush cells penetrate the bundles of fila and ramify richly, thus transforming the bundles into elongated glomeruli or series of glomeruli. A brush often lies on the surface of one of these

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bundles and its dendrites wrap around and penetrate the bundle. The formation of glomeruli in the course of large bundles of fila is a condition similar to that in Petromyzon described by the writer (1902). In addition to these large glomeruli are numerous smaller ones formed by the dendrites of small brush cells and of granule cells.

The formatio olfactoria consists then of (1) an enormous number of granule cells whose bodies form the dense peri-ventricular layers and whose rather straight dendrites radiate outward to form glomeruli or to mingle with dendrites of other cells in glomeruli; (2) a peripheral layer of mitral cells and small brush cells presenting a great variety of forms, whose dendrites form the large glomeruli by ramifying in the bundles of fila olfactoria; and (3) of the incoming fila olfactoria and the afferent and efferent fibers connecting the bulb with the rest of the brain.

The gross structure known as the olfactory bulb in the turtle consists of formatio olfactoria and nothing else. While the hippocampal formation and the pyriform lobe both push forward into close contact with the olfactory formation, the groove which marks the peduncle corresponds accurately to the line of division in the internal structure. The so-called nucleus olfactorius anterior in this brain is very clearly distinct from the granule cell layer of the olfactory bulb and does not extend forward beyond the peduncular constriction.

TRACTUS OLFACTORIUS

At the olfactory peduncle the fibers of the olfactory tract (figs. 55, 56, 57) have the following disposition. The largest bundles lie on the lateral surface and pass caudad into the pyriform lobe. These fibers arise from the greater part of the lateral and from the dorsal surface of the bulb. On the dorsal surface of the peduncle a large bundle, which has its origin in the dorsal part of the medial wall, crosses obliquely from the medial to the lateral surface and joins the bundle last mentioned. These constitute the lateral olfactory tract. Its further course will be described in connection with the pyriform lobe. Fibers arising from the remaining ventral and medial parts of the bulb collect into a broad sheet ventral to the large bundle first mentioned. This sheet constitutes the medial olfactory tract. It is thick where it abuts upon the large lateral tract but spreads as a very thin sheet over the ventral and part of the medial surface. This tract runs caudad over the ventro-lateral surface of the tuberculum, gradually diverges from the lateral tract and gives diffuse fibers to the tuberculum and the parolfactory area. The medial tract borders the striatal area in front and below as the lateral tract borders that area dorsally.

Two compact terminal bundles of the medial tract are of especial importance. One bends up into the medial wall between the tuberculum and the commissures and is distributed to this region (gyrus subcallosus) and to the hippocampal formation. This is obviously the equivalent of the olfactory tract component in the precommissural fornix system of mammals. The second bundle continues along the lateral border of the medial tract and runs directly caudad to the amygdaloid prominence, where it enters the nucleus of small cells hereafter to be described as the nucleus of the lateral olfactory tract. This bundle runs along with the large bundle which connects the amygdaloid complex with the hippocampus through the precommissural system (olfactory radiations of Zuckerkandl or fiber bundle of the diagonal band of Broca).

CORPUS STRIATUM

Under this name will be described the structures which are homologous with the chief parts of the corpus striatum in human and mammalian brains. Attention has been called to the fibers of the crus cerebri which are seen in a depression on the lateral surface of the telencephalon. A section at the rostral border of this region (figs. 21, 34) shows two great bundles of fibers cut in cross section, the lateral forebrain bundle or crus and the medial forebrain bundle. The fibers of the crus rise in fascicles (internal capsule) scattered through the outer part of the thick latero-basal wall to the dorsal ventricular ridge and pallial thickening. These include somatic sensory fibers and probably also fibers descending to the motor centers. The medial bundle

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consists of fibers which connect the olfactory centers with the hypothalamus and lower motor correlation centers. From this bundle fibers rise radially into the dense cell mass forming the floor of the ventricle (figs. 21 to 24, 34).

The whole mass in the latero-basal wall is the corpus striatum. It consists of two portions, a lateral much larger part containing large cells and a medial smaller part containing small cells (figs. 21, 22). The coarser fascicles of the crus rise in a curve through the lateral part into the dorsal ventricular ridge and the general pallium (figs. 32, 33). The finer fascicles of the medial bundle rise in almost straight lines radially in the rostral end of the medial part (fig. 34). In man the condensation of the pallial portion of the crus fibers into a plate-like internal capsule has taken place within a lateral large-celled area, the greater part of which is situated external to the capsule and is known as the lentiform nucleus. The remainder of the large cells together with a dense small celled area next the ventricle constitute the caudate nucleus.

In the turtle the large-celled and small-celled areas are clearly distinct from one another. The small-celled area will be called the caudate nucleus, the large-celled area the lentiform nucleus.

The caudate nucleus presents well marked head and tail portions. Far rostrad (fig. 26) this nucleus forms the floor of the ventricle between the ventral and middle ventricular grooves and occupies almost the entire thickness of the latero-basal wall. At its medial border it is continuous with the lateral parolfactory nucleus. This relation has been described for both reptiles and mammals in a previous paper ('13b, p. 389). Its basal surface is largely covered by the medial forebrain bundle from which fascicles enter the caudate. Followed rostrad in transverse sections the caudate is seen to be covered in by the layers of the olfactory tubercle which are continuous with the parolfactory area medially and the pyriform lobe laterally (fig. 27). In these layers are imbedded the olfactory tract fibers as elsewhere described. Continuing forward, the tuberculum and olfactory nuclei increase in thickness and the caudate grows smaller (fig. 28) until just behind the peduncle the caudate

It is this rostral end of the caudate nucleus that the disappears. writer identifies with the nucleus olfactorius anterior of Edinger and other authors. Following sections caudad, the sheet of olfactory fibers and cells scarcely disappear from the surface of the caudate until large cells appear in the lateral wall (fig. 26). Beneath the anterior end of the dorsal ventricular ridge this largecelled nucleus rapidly grows larger and the caudate smaller (figs. 22, 21) until the caudate is confined to a part of the floor of the ventricle adjacent to the ventral groove (fig. 20). From this point the tail of the caudate extends caudally to the point where the middle ventricular groove bifurcates (fig. 15, 10). Before this point is reached the caudate is in connection medially with the anterior nucleus region of the thalamus over the crus and the stria medullaris (figs. 17, 18). The caudate then grows thicker and merges insensibly with the small-celled mass of the amygdaloid complex (nucleus of the lateral olfactory tract) (figs. 15, 16). The caudate then disappears from the sections, its place being taken by an area of neuropile. Horizontal and sagittal sections show in this position a cell-free zone bounding the caudate behind, which corresponds to the ventral arm of the middle ventricular groove as it bends down into the temporal horn of the ventricle.

The caudate nucleus throughout its whole extent consists of small cells without regular arrangement. In its head portion it receives fibers from the olfactory tract and the medial forebrain bundle and gives fibers to the latter. In its tail portion are imbedded the stria terminalis and the great lateral olfactory projection tract of Cajal (figs. 48, 49).

A peculiar vesicular structure found in the head of the caudate and in the lateral parolfactory nucleus should be described here. The greater number of these structures are found around the depression of the ventricle which extends down into the tuberculum but some are found also in the lateral part of the caudate not far from the middle ventricular groove. At first sight these structures appear to be clusters of small cells arranged radially about a core somewhat like clusters of grapes about the stem. The clusters are elongated sometimes in the plane of transverse sections, sometimes obliquely to it. In the latter case they may extend through as many as twelve sections ten microns in thickness. When the clusters are cut either across the long axis or lengthwise of it, the core is almost always seen to contain a lumen around which the cells are arranged (fig. 35). The lumen is bounded by a strong limiting membrane and contains more or less of lightly staining material, resembling mucus. Occasionally a flattened nucleus is seen in the lumen.

In the caudate and parolfactory nuclei these vesicles are found only near the ventricle except in the area where these two nuclei meet beneath the ventral ventricular groove. Here they are found farther from the ventricle, even in the deeper layer of the tuberculum olfactorium. In this region these vesicles lie adjacent to or intermingled with the islands of Calleja, to be described below. It was at first thought, indeed, that these were islands of a special type. The vesicular arrangement and other characters of the cells, however, differentiate these structures sharply from the islands of Calleja. The cells are typically columnar and radially arranged around the lumen, the nuclei usually placed near the peripheral end of the cells. The cellbodies are often filled with small granules unlike the Nissl-bodies of adjacent nerve cells. The nuclei are small, ovoid and dense, resembling those of ependyma cells rather than those of nerve cells. There are often larger cells, obviously nervous, wedged in among or closely applied to the outer surface of the small cells of the vesicles. Although the fascicles of nerve fibers in the caudate often pass close over the surface of these vesicles and sometimes diffuse fibers appear to run ventrad from a vesicle, I have not found in Cajal or Golgi sections fibers arising from the cells of the vesicles.

I suspect that these vesicles are composed chiefly of ependyma cells and that their lumina represent vestiges of ventricular cavity which have been pinched off during development. This might happen owing to the thickening of the caudate and parolfactory nuclei and consequent encroachment upon the ventral part of the ventricle. The fact that these cell clusters are not penetrated by the neuropile (fig. 35) and the fact that no definite fascicles of nerve fibers are found running to or from them, constitute negative evidence as to their nervous function. At the same time, nerve cells are often found closely related to or imbedded in the ependyma and further study will be necessary to determine the origin, character and significance of these structures.

THE LENTIFORM NUCLEUS

At its rostral end this nucleus appears simply as scattered large cells, outside of the small-celled caudate, among which fascicles rise from the crus to the pallial thickening in the rostral part of the roof. Beneath the rostral end of the dorsal ridge this nucleus has grown to a large body in the lateral wall and has reached the ventricle (figs. 22, 23). From this point caudad a peculiar band of thickened ependyma covers the ventricular surface of this nucleus (figs. 15 to 22, 36). This thick band extends some distance below the middle ventricular groove and bends round that groove into its dorsal wall. While the ependyma elsewhere in the lateral ventricle has from one to three rows of nuclei, this band consists of very tall cells and presents as many as seven to nine rows of nuclei. The peripheral processes of these cells are strong and give a prominent striation to the adjoining nucleus (figs. 36, 37). The curved course taken by these processes which come from the dorsal wall of the middle groove (fig. 37) shows that the groove was formed within the ependymal band and near the border of this nucleus. It also shows how the groove has been formed during the development of the individual by the pushing in of the dorsal ridge which forced this border of the nucleus to be bent over. This thickened ependyma extends right back into the dorsal branch of the middle ventricular groove, where it quickly disappears. Throughout its length this thickened band of ependyma covers a nucleus whose cells are distinctly larger and usually much more numerous than those of the adjoining caudate.

In the striatal area this nucleus makes up the whole thickness of the wall and is traversed by the fascicles of the crus as above noted. Toward the caudal border of the striatal depression

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(figs. 17, 16) the lentiform nucleus becomes covered externally by a layer of small cells which reaches from the pyriform lobe to the amygdaloid complex and will be described below as the nucleus of the lateral olfactory tract. The lentiform nucleus now decreases in volume caudally, contains several dense collections of cells which are closely related to the thickened ependyma of the middle groove (figs. 16, 33), becomes less rich in cells and finally merges with the central core of the dorsal ventricular ridge behind the end of the middle groove (fig.14).

Throughout its whole length the lentiform nucleus is sharply delimited from the pyriform lobe and (except at its caudal end) from the dorsal ventricular ridge, by cell-free zones. It is marked off from the caudate only by a rather sudden change from large to small cells. The thickened ependyma covering its surface is sometimes separated from that covering the caudate by a slight, sharp groove.

Among the fascicles of the internal capsule which come rom the sensory bundle of the crus (see later section on the pallium), are found many cells conspicuously larger than the ordinary cells of the lentiform nucleus. The position of these is indicated in figures 18 and 19. They may prove of importance in further comparisons with the mammalian brain.

TUBERCULUM OLFACTORIUM

The tuberculum consists of a cap of two layers of cells covering the basal surface of the caudate nucleus at its rostral end (fig. 27). The outer layer is sparsely filled with small cells and is closely related at its medial border with the medial parolfactory nucleus and at its lateral border with the pyriform lobe at the sulcus endorhinalis (figs. 26, 27). The inner layer has larger cells and is characterized by the grouping into islands which have been described by Calleja and Cajal. These islands are for the most part clusters of the large cells of the deep layer. They contain from four or five to many cells, which present no regularity of arrangement. The cell bodies are pear-shaped or stellate and are largely filled by vesicular nuclei with prominent nucleoli. In these respects they do not differ materially from the cells scattered between the islands. Some of the cells in the islands take a lighter, more transparent and brilliant stain in neutral red than others.

In addition to the islands of large cells there are a number of dense clusters of small cells which are undoubtedly nerve cells. These clusters do not present a core or lumen and the neuropile does not shrink away leaving a clear space around them as happens in the case of the vesicles described in the caudate nucleus. The true islands are confined to the deeper layer of the tuberculum. It must be noted, however, that the tuberculum extends into the medial wall and merges with the medial parolfactory The distribution of the islands may arbitrarily be taken nucleus. as determining the extent of the tuberculum. The greater number of islands is found near the mediobasal angle and they do not extend far laterally. Caudally the islands disappear from the basal surface where the medial forebrain bundle collects (fig. 24) and are found farther caudad in the medial wall.

There is a very close resemblance between the tuberculum olfactorium in the turtle and the 'superficial basal area' described by the writer in selachians (1911). The writer was unwilling at that time to give the name tuberculum olfactorium to this area because it seemed to include parts of the medial and lateral olfactory nuclei and the region corresponding to the anterior perforate space. The close relation of the tuberculum to medial and lateral olfactory nuclei is common throughout vertebrates and I shall present evidence at another time that the tuberculum and anterior perforate space are by no means wholly independent.

ANTERIOR PERFORATE SPACE

The area corresponding to the anterior perforate space of mammals is not sharply marked off in the turtle. It occupies the caudal part of the basal surface of the large rounded prominence rostral to the optic chiasma. The rostral half of this surface shows the characteristics of the olfactory tubercle. The caudal half lacks these peculiarities and is largely filled by the medial forebrain bundle.

DIAGONAL BAND OF BROCA AND GYRUS SUBCALLOSUS

The large basal mass which includes the head of the caudate, the parolfactory nuclei, the tuberculum olfactorium and the anterior perforate space appears on the medial surface as a rounded area (figs. 3, 6) bounded dorsally and caudally by a groove which descends to the basal surface, bends transversely, and disappears. This groove, as the further description will make clear, is the homologue of the fissura prima of His.

The area dorsal to the horizontal limb of this fissure is the primordium hippocampi (Johnston '13 b). The area between the fissure and the lamina terminalis (fig. 6, g.s.) is occupied by a cell mass and a fiber bundle both of which are characteristic of this region in all mammals and perhaps in all vertebrates. In a previous paper ('13 b) this cell mass has been included in the description of the medial nucleus parolfactorius in both the turtle and mammals. This was an error. Since this cell mass lies caudal to the fissura prima in mammals, it is outside the limits of the parolfactory area. It may be spoken of as the nucleus of the diagonal band. In mammals this consists of a thin plate of closely packed cells which extends from a point rostral to the anterior commissure down in front of the optic chiasma and caudad on the latero-basal surface to the amygda-It is very sharply marked in the rabbit and has loid complex. been figured in the opossum and bat ('13 b, figs. 28, 42). The distinction between this nucleus and the medial parolfactory nucleus is shown in figure 46 of the paper referred to, where this nucleus consists of small cells rostral to the anterior commissure and is not separately labelled. The cell-free zone between this and the medial parolfactory nucleus corresponds to the fissura prima.

In the turtle the same plate of cells is found (figs. 20, 21) occupying the medial surface rostral to the anterior commissure and extending down close in front of the preoptic recess, near the large-celled supraoptic nucleus (fig. 19), and continuing laterally and caudally ectal to the medial forebrain bundle (fig. 18) until it expands into the large anterior nucleus of the amygdaloid complex from which arises the great olfactory projection tract (fig. 17). The relations to the amygdaloid will be further described in the next section. The extreme rostral and upper end of this nucleus is the very dense collection of cells seen near the recessus superior in figures 19 and 39. There is no break in the continuity of the nucleus described but on the basal surface in front of the optic chiasma and lateral to the optic tract, the number of cells is much less than in the medial wall. Throughout the length of the nucleus its cells are small and are somewhat elongated in the direction of the densely packed bundle of fine fibers among which they lie.

The fibers in question enter into the precommissural bundles of the fornix system in the medial wall. They are the olfactory radiations of Zuckerkandl and constitute the chief pathway from the amygdaloid region to the hippocampus. Compare '13 b, p. 410. From the amygdaloid forward along the basal surface these fibers form a low ridge parallel with the optic tract (figs. 1, 8, 19) and in this position the bundle is clearly visible in the entire brain (fig. 2). The bundle is clearly distinct from the medial forebrain bundle which lies ental to this. In front of the optic chiasma the bundle is seen to be composed of two parts, one of which is derived from the medial olfactory tract as above described, while the other bends up into the medial wall. spreads out in the area between the fissura prima and the commissures, and enters the hippocampus (figs. 56, 57). The triangular area between the fissura prima and the commissures in which this bundle spreads out like a fan is the equivalent of the mammalian gyrus subcallosus. Lateral to the optic chiasma this bundle passes close to the supra-optic nucleus and there seems to be a connection between the two which has not vet been carefully studied.

The homology of the area described in this section with the gyrus subcallosus and the diagonal band of the mammalian brain is obvious. Its chief morphological significance is that it represents the persistence of the preoptic and precommissural connection between the medial olfactory area and hippocampus on the one hand and the lateral olfactory area and amygdaloid complex on the other hand. In the ichthyopsid brain where the temporal pole has not yet been formed, the continuity of the corresponding regions is broad and direct. The size and functional importance of this connection in reptiles and mammals is of great significance for the explanation of the evolution of the temporal pole and the general pallium.

LOBUS PYRIFORMIS

As already indicated the pyriform lobe forms a somewhat prominent ridge along the dorso-lateral surface of the hemisphere, extending from the olfactory peduncle into the caudal pole. It is separated from the general pallium dorsally by the fissura rhinalis. Rostrad this fissure runs obliquely mesad and joins the peduncular groove or constriction as it bends down into the medial wall. Caudally the fissura rhinalis presents considerable individual variation in its depth and length. Usually it fades away at about the middle of the hemisphere (fig. 1) so that there is no gross boundary line between the caudal part of the pyriform lobe and the general pallium. In the rostral part of the hemisphere a slight sulcus endorhinalis approximately marks the boundary between the pyriform lobe and the area occupied by the tuberculum and corpus striatum (figs. 22 to 26). The caudal continuation of this sulcus becomes much deeper between the pyriform lobe and the striatal area (fig. 1) and bends down between the striatal area and the amygdaloid prominence. At the point of bending is the deepest part of this groove and from this point the amygdaloid fissure extends caudad as above described.

The pyriform lobe consists of the lateral olfactory tract and the special gray matter accompanying the tract. Sections through the middle or rostral part of the lobe (figs. 19, 25) show that it consists of a superficial fiber layer and a deeper plate of cells and that it is everywhere very clearly and sharply separated from the border of the pallium, the dorsal ventricular ridge and the lenticular nucleus by a cell-free zone. This cell-free zone is more sharply marked than any other in the brain.

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The outer surface of the lobe is covered by a continuous sheet of fibers of the lateral olfactory tract. These arise in larger part from the lateral wall of the olfactory bulb and in smaller part from the dorsal and medial wall. The former fibers enter the extreme rostral end of the pyriform lobe on the lateral surface of the peduncle; the latter cross from the medial to the lateral side in the peduncular groove on the dorsal surface and join the former fibers to make up the common tract (figs. 55, 56).

Just behind the peduncular constriction the pyriform lobe appears to thicken rapidly. This thickening forms a conspicuous rounded prominence on the dorso-lateral surface of the hemisphere (figs. 26, 5). The arrangement and relations of the cell masses in this prominence show at once that it is made up of two parts. The surface layer of cells belongs to the pyriform lobe and is no thicker here than elsewhere. The elevation here is due to the deep layer of cells which is the thickened lateral border of the general pallium (figs. 24, 25, 26). This is indeed a lateral extension of the dorsal pallial thickening, which lies beneath the pyriform lobe as the lateral border of the pallium does throughout the rostral two-thirds of the lobe. The pyriform lobe, then, is not actually thickened but is merely bulged out by the thickening of a pallial formation beneath.

The majority of cells in the pyriform lobe are large multipolar cells with large dendrites. In regard to this a comparison of the pyriform lobe with other parts of the forebrain reminds one of the comparison between Deiters' nucleus and adjacent nuclei in the medulla oblongata. The cells are noticeably larger in the rostral half of the lobe than in the caudal, the largest cells and the greatest proportion of large cells being found just behind the prominence above mentioned. In the caudal part the cells become distinctly smaller and where the lobe broadens out to form the lateral wall of the ventricle, the cells take on pyramidal forms much like the cells of the general pallium or the hippocampus.

Throughout the rostral half of the pyriform lobe small cells are almost wholly confined to its ventral portion (figs. 19, 25, 40). These small cells extend somewhat below the sulcus endorhinalis, and the cell-free zone, which accurately marks the boundary of the lobe, meets the surface ventral to the sulcus endorhinalis. This sulcus is therefore actually within the area of the pyriform lobe. At the caudal border of the striatal area the band of small cells along the ventral border of the pyriform lobe spreads ventrad in a broad sheet across the base of the amygdaloid fissure (fig. 5) and expands into a large nucleus of small cells occupying the lateral and rostral part of the amygdaloid prominence (figs. 17, 16). This sheet of small cells is accompanied by a large bundle of fibers from the lateral olfactory tract which ends in this nucleus. This is the nucleus of the lateral olfactory tract (figs. 5, 17).

A further examination of the relations of the small cells in the pyriform lobe shows that essentially two nuclei or two cell groups are to be distinguished. The small cells in the region of the amygdaloid fissure are very clearly separated from the largecelled part of the lobe by a space or cell-free zone (figs. 15, 16, 17). Farther forward although there is no space separating them, the small cells do not mingle with the large cells and the smallcelled band becomes continuous with the superficial layer of the tuberculum and through that with the medial olfactory nucleus (fig. 26). The large-celled nucleus, on the other hand, maintains its identity rostrad to the peduncle as already described Moreover, the location of the small cells below the (fig. 28). endorhinal sulcus gains significance from the fact that at the level of the tuberculum the small-celled band spreads ventrally to become continuous with the superficial layer of the tuberculum. The cell-free zone which limits the pyriform lobe internally now becomes continuous with the limiting zone which appears between the caudate sulcus and the layers of the tuberculum (figs. 26, 27).

These relations when summed up with the description that has gone before show that there is a continuous area of small-celled olfactory nuclei comprising the medial parolfactory nucleus, the superficial layer of the tuberculum, the small-celled band of the pyriform lobe, the small-celled nucleus of the amygdaloid complex and the nucleus of the diagonal band. These together constitute a continuous ring which surrounds the crucial-striatal area. The whole of this ring receives fibers from either the lateral or medial olfactory tract. This continuous complex of smallcelled nuclei seems to serve as an intermediate selecting and distributing station through which olfactory impulses are forwarded to the cortical center for sensation, the hippocampus; or to one of the motor correlation centers in the diencephalon, or to centers lower down the brain stem (compare Johnston '15 a). The greater part of the pyriform lobe made up of large cells is probably concerned with olfacto-somatic correlation. Other places for correlation of olfactory and somatic impressions are probably found in the amygdaloid complex and in the hippocampus (subiculum). The distribution of large cells in the pyriform lobe probably gains significance from their relation to the pallial thickening.

The boundary line between the pyriform lobe and the general pallium is less distinct in the caudal part than elsewhere. -Asthe pyriform lobe is followed caudad in sections to the point where it forms the whole thickness of a part of the wall of the ventricle (figs. 13 to 15) the cell-free zone at first continues as a very clear oblique dividing line in this wall (fig. 14). This overlapping of the general pallium by the border of the pyriform lobe is very characteristic. This dorsal border of the lobe rises dorsally in its caudal portion as the model clearly shows (fig. 5). In transverse sections through the region in which the small-celled portion of the pyriform lobe spreads ventrad to merge with the nucleus of the lateral olfactory tract, the cell masses of the dorsal ventricular ridge begin to be connected by a thick curved layer of cells with what appears to be the cell layer of the pyriform lobe in the lateral wall (fig. 15). When this relation is studied in sections farther caudad (figs. 11, 12) it is clearly seen that it is the general pallium which thus enters into continuity with the ventricular ridge. In transverse sections there is no sharp boundary between pyriform lobe and general pallium. It is noticed, however, that there is a narrow portion of the wall adjacent to the dorsal boundary of the lobe in which the cells are placed close to the ventricular surface (fig. 12). The oblique line bounding the lobe dorsally at length gives way to a narrow area in which the cells of the lobe meet those of the pallium above in a confused mass. The ventro-caudal margin is not clear. Sections give the impression that the pyriform lobe merges insensibly with the general pallium in this region. In the model this boundary has been fixed arbitrarily.

THE AMYGDALOID COMPLEX

When the hemisphere of the turtle brain is viewed from the lateral and basal aspects (figs. 1, 2, 5, 6) the region which is occupied in part by the amygdaloid complex appears as a basal prominence similar to the temporal pole of the mammalian brain. It is bounded rostrally by the crucial-striatal area, medially by the optic tract and thalamus and laterally by the amygdaloid fissure. Caudally this prominence passes insensibly into the rounded caudal pole.

Nucleus of the lateral olfactory tract. As above described, a part of the lateral olfactory tract bends down across the amygdaloid fissure just caudal to the striatal area and ends in the lateral border and rostral tip of the amygdaloid prominence (fig. 8). This region is therefore clearly homologous with the nucleus of the lateral olfactory tract in the mammalian brain. This nucleus is composed of small cells which occupy the tip and lateral part of the amygdaloid prominence and extend in a thin layer across the amygdaloid fissure to meet in a thickened border the large-celled nucleus of the pyriform lobe (figs. 16, 17). The two nuclei are separated by a cell-free zone and this condition continues back to the end of the nucleus (fig. 13). At the caudal border of the striatal area the thin layer of small cells is traversed by the fibers of the lateral olfactory tract which bend down into this nucleus, and by numerous fibers from the pyriform lobe which pass over the surface of the nucleus to join the stria medullaris (fig. 56). From the tip of the amygdaloid prominence the fibers of the diagonal band go forward as above described. These are also mingled with the stria medullaris. At the same time the small cells of the diagonal band merge with the small-celled nucleus of the lateral olfactory tract (fig. 17). Where the thin layer of small cells forms the boundary of the striatal area it covers in the large-celled lateral nucleus of the corpus striatum (nucleus lentiformis) (fig. 16). In transverse sections the nucleus lentiformis is followed caudad for some distance beyond this, always traversed by bundles of crucial fibers which are bending up into the pallium and the dorsal ventricular ridge. The nucleus lentiformis gradually grows smaller and is replaced by the small-celled nucleus which grows thicker caudally and enters into close relations with the caudate nucleus. Indeed, in its rostral portion the entire amygdaloid eminence is filled with small cells, the ventricular portion being the caudate nucleus, the superficial portion being the enlarged continuation of the nucleus of the lateral olfactory tract (fig. 17).

Relations of the caudate nucleus. It has been stated that the caudate ends about opposite the end of the middle ventricular groove and is bounded by the branch of that groove which bends down into the temporal horn of the ventricle. Here the caudate merges with the nucleus of the lateral olfactory tract in a small-celled mass which constitutes the chief part of the amygdaloid complex. In the lizards this mass, or the caudate part of it, is greatly enlarged and forms a prominent lobe or ridge in the ventricle. C. L. Herrick showed that this was an important olfactory center and it is this lobe which was first called epistriatum by Edinger. It was this body whose relations very naturally suggested to Kappers ('08) that the epistriatum of lower vertebrates formed or entered into the amygdaloid complex of In the turtle this body is simply a part of the amygmammals. daloid complex without hypertrophy. However, if all the other structures to which the term epistriatum has been applied were to be gathered into it, the amygdaloid complex would be a veritable museum!

The caudate nucleus at its rostral end is closely related to the olfactory tubercle and parolfactory area and receives fibers from the medial olfactory tract. At its caudal end it enters into close relations with the nucleus of the lateral olfactory tract and helps to form the olfactory part of the amygdaloid complex.

Medial large-celled nucleus. In sections through the rostral part of the amygdaloid complex the small-celled mass is covered basally by a rounded cap consisting almost wholly of neuropile (figs. 16, 42), only a few medium sized cells being imbedded in it. This neuropile is formed by the interlacing stria medullaris. lateral olfactory tract and olfactory radiations as above described. As the sections are followed caudally the cells in this neuropile increase in number and size until a conspicuous nucleus forms the basal portion of the complex (figs. 15, 43). This is the condition in sections which pass through the caudal border of the stria medullaris. Just caudal to this (figs. 14, 44) the temporal horn of the ventricle penetrates this nucleus. Farther caudally the large cells are all found in the lateral or amygdaloid wall of the ventricle while the hippocampal formation and fimbria appear in the medial wall. The large-celled nucleus lies ventral to the tail of the caudate nucleus. This is the region in which the tail of the caudate merges with the small-celled nucleus of the lateral olfactory tract. Following the sections caudad, the caudate rapidly diminishes and the large-celled nucleus spreads farther dorsad in the large ventricular ridge (figs. 13, 45). At the same time the nucleus of the lateral olfactory tract grows smaller and appears as a rather dense mass of cells near the amygdaloid fissure. Now there appears in the ventral wall between this and the hippocampus an area of scattered cells which on being followed further caudad is found to belong to the general pallium (which see). By the time this condition is reached the caudate has entirely disappeared from the sections and the large-celled nucleus has spread dorsad to the level of the dorsal branch of the middle ventricular groove. Here this nucleus constitutes a ventricular layer of large cells rather closely packed but not arranged in clusters as are the cells of the dorsal part of the dorsal ventricular ridge. Further from the ventricle the lower part of the ridge is filled by the same irregularly placed cells as are found in the dorsal part. Both these and the ventricular layer of large cells merge with the general pallium in the ventral wall. The ventricular layer representing the largecelled nucleus continues over the medial surface of the basal lobe of the ridge to its caudal end.

Further evidence as to the individuality of this nucleus is found in its fiber connections. Only the general disposition of its chief tract will be described here. In the extreme tip of the temporal horn of the ventricle (figs. 10, 13, 14) is seen a small ridge which follows the ventro-rostral border of this nucleus. It is clearly seen in the model and in sections in all planes. This ridge is composed chiefly of fibers which run caudad over the medial surface of this nucleus. In addition to the bundle which forms the ridge there is a thin sheet of fibers in small fascicles covering the whole medial face of this nucleus. All of these fibers gradually disappear as they are traced caudad over this nucleus. in which they have either their origin or ending. Traced rostrad all these fibers pass through the tail of the caudate as a thick bundle. Here the bundle is just lateral (internal) to the stria medullaris as that bundle rises from the nucleus of the lateral olfactory tract to enter the thalamus. The bundle here described now forms the most compact part of the stria terminalis and in addition a large part of its fibers go forward diffusely in the substance of the caudate nucleus. A further discussion of the relations of this bundle will be reserved for a later study of the stria terminalis system. It is evident, however, from the facts given, that what is here described as the medial large-celled nucleus belongs to the amvgdaloid complex and the distribution of the stria terminalis bundle confirms the observations as to its extent, based upon the character and grouping of cells.

Dorsal ventricular ridge. Farther caudally in transverse sections the ventricle pushes around both laterally and ventrally until the whole ventricular ridge is seen attached to a pallial wall and no longer to the brain stem (figs. 11, 12). In this pallial wall the extent of the general pallium and hippocampal formation can be made out, at least roughly, as represented in the model. The dense, deep layer of cells of the pallium turns into the ventricular ridge where it is continued by layers of cells lying adjacent to the ventricle. The sparsely scattered cells in the outer part of the pallial wall are continued into the

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core of the ventricular ridge where they are somewhat more compactly arranged than in the pallium. The section passes through the caudal part of the amvgdaloid fissure. It is readily seen that the ventricular ridge corresponds to the external groove and that the fissure is a true fold of the brain wall. Examination of the relations of all parts of the dorsal ridge gives the impression that the ridge is an infolding of the brain wall from this region and that it has pushed forward well toward the rostral end of the hemisphere. Its cell layers come into continuity with those of the pallium here in the amygdaloid fissure and with no other nucleus whatever. They are sharply distinguished from those of the caudate and lenticular nuclei and from the pyriform lobe and are usually separated from these by cell-free zones (figs. 11 to 22). In its rostral part the ridge is sharply separated from all other cell masses and projects freely into the ventricle.

In a transverse section taken at the level of the stria medullaris the cells in this ridge present the arrangement seen in figure 16. All around the ventricular surface are a great number of large and small clusters of cells. Some of these clusters are large, rounded and have a definite outline. Others are very irregular and their outlying cells mingle with the scattered cells between the clusters. The individual cells of the clusters do not differ materially in size from those of the adjacent general pallium but are conspicuously larger than those in any other part of the same section. In the lower part of the ridge, adjacent to the middle ventricular groove, there is a tendency for the cells to be closely aggregated in a large area without special clusters.

The core or central part of the ridge is largely filled by fibers among which are scattered cells. These cells are smaller than those of the clusters. The ventral part of this area is encroached upon by the lentiform nucleus and by the main body of fibers entering or leaving the ridge (figs. 15 to 22). The dorsal part of the central area of the ridge contains a larger number of cells almost evenly scattered. Many of these cells approach in size those of the clusters. This part has almost the appearance of an independent cell-mass and for convenience may be called the core-nucleus. It extends through nearly the whole length of the ridge as a large, somewhat quadrilateral area bounded laterally by the pyriform lobe and centrally by the cell clusters of the ventricular layer Dorsally it is separated from the thickened border of the general pallium by a cell-free zone of fibers and ventrally it is bounded by the chief fiber mass in the center of the ridge. Toward the rostral end of the ridge this body of cells becomes separated into two masses in the transverse section, owing to the general pallium and lentiform nucleus pressing into it from above and below respectively (fig. 22). Caudally this mass of cells becomes less distinct and merges with the superficial cells of the general cortex as noted at first. Throughout the greater part of its length this core-nucleus is penetrated by numerous fibers which pass up from the internal capsule to the thickened lateral border of the general pallium. Although only a few such fibers are seen in Weigert sections, a great number of non-medullated fibers take this course and they are very conspicuous in Cajal preparations.

Comparison of the turtle brain with that of some lower mammals leads to the suggestion that the dorsal ventricular ridge is the homologue of one of the cell masses which constitute the amygdaloid complex in mammals. This is entirely independent of the homology of the 'epistriatum' with the amygdaloid body suggested by Kappers and others. This ventricular ridge is a wholly different structure from the 'epistriatum' of Kappers. This matter will be discussed in a later paper dealing with the amygdaloid complex in the opossum and some mammals. To follow the comparison here would lead beyond the limits of this paper.

The amygdaloid complex in the turtle includes the following structures: the nucleus of the lateral olfactory tract, the tail of the caudate nucleus, the medial large-celled nucleus and probably the dorsal ventricular ridge. The amygdaloid eminence in the temporal pole is encroached upon by both the hippocampus and the general pallium. The amygdaloid complex has related to it the lateral olfactory tract, a bundle of the medial olfactory tract, the bundle of the diagonal band, the stria medullaris, the stria terminalis, fibers of the sensory radiations from the thalamus, an olfacto-hypothalamic projection tract, and an anterior commissure bundle.

The simple enumeration of these tracts shows that while the amygdaloid complex in mammals is a compact collection of cell masses occupying a restricted area in the temporal pole, it is a complex of very diverse elements which have been brought together by mechanical forces and have no primary functional unity.

The extent of the hippocampal formation. The morphological relations of the hippocampal formation have been treated with some fulness in a previous paper ('13 b). There is now to be noticed the boundary between hippocampus and general pallium and the relation of the hippocampal formation to the amygdaloid complex. In the rostral part of the hemisphere the characters shown in figure 47 enable us to fix the boundary of the hippocampus with some degree of accuracy on the basis of cell arrangement. Above the fimbrio-dentate sulcus, which separates the homologue of the fascia dentata from the primordium hippocampi and fimbria, there are first pyramidal cells compactly arranged in a ventricular layer with few peripheral cells. cells are smaller than the cells in most parts of the general pallium but are neither so small nor so closely crowded as the cells in the deep layers in the middle part of the dorsal pallium in this region. This is the portion which is now generally accepted as the homologue of the fascia dentata of mammals. There is no clear separation or distinction between fascia dentata and hippocampus in this turtle's brain.

Dorsal to this, the cells in the medial wall are less closely arranged, appear larger and are less deeply stained. Many cells here are placed far from the ventricle, even lying in the outer half of the wall. Many cells adjacent to the ventricle are distinctly pyramidal in form and have large, dominating apical dendrites. This loose arrangement of cells rather suddenly gives way to a compact arrangement near the dorso-medial angle of the hemisphere. The dorsal area of compact cells will

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be described as part of the general pallium. The area of loose cells probably belongs to the hippocampal formation and the transitional region called the subiculum.

As transverse sections are followed caudad the area which is here assigned to hippocampal formation and subiculum grows rapidly wider. There is nowhere a sharp line of demarcation between hippocampus and general pallium, and none is to be expected. There is everywhere noticeable the point at which the deep cell layer becomes abruptly more compact. This point has been taken as the medial boundary of the general pallium in making the model so that what is there shown as hippocampal formation probably includes the equivalent of the subiculum as well (see fig. 6).

As the sections are traced caudad there is a gradual change in the size of the cells. The cells of the hippocampal formation become smaller, those of the dorsal general pallium somewhat larger, until the difference is at first noticeable, then conspicuous. From the level of the commissures caudad the cells of the hippocampus are much smaller than those of the general cortex.

In the occipital and temporal poles of the hemisphere essentially the same characters are found. Near the fimbria border is an area of dense cells in a deep layer. Next to it is an area with cells loosely arranged and many of them near the periphery (fig. 45). In the temporal region this area of loose cells is narrow and is accompanied by an internal sulcus which serves as an additional landmark. The boundary shown in the model made from transverse sections has been carefully checked up by means of horizontal sections and found to be essentially correct.

The fimbria passes over the interventricular foramen and continues back along the border of the hippocampal formation to which the choroid plexus is attached (fig. 57). The bundle decreases in size as it proceeds but is still fairly large at the caudal end of the choroid fissure. Here the fimbria bends around the end of the fissure and spreads in the medial wall of the ventricle medial to the position of the large-celled amygdaloid nucleus. This is sufficient evidence that the hippocampal formation extends around the end of the choroid fissure into the

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medial wall of the temporal pole and confirms the conclusion based on the study of the cells.

In the temporal pole the hippocampus comes into contact with the general pallium and the large-celled amygdaloid nucleus only, not at all with the nucleus of the lateral olfactory tract or any of the small-celled portion of the amygdaloid complex (fig. 8). The hippocampal formation is intimately related in front with the olfactory bulb and secondary olfactory centers. Caudally it forms the border of the pallium adjacent to the choroid fissure and is bounded on the other side by general pallium. There is no continuity of cell masses between the caudal end of the hippocampus and the caudal part of the secondary olfactory centers. The olfactory apparatus taken as a whole does not form a complete ring following the line of junction of the hemisphere with the brain stem ('limbic lobe'). An opening in this supposed ring occurs between the nucleus of the lateral olfactory tract and the hippocampus.

THE GENERAL PALLIUM

The general pallium occupies the dorsal and caudal walls of the hemisphere and reaches well into the temporal pole. Throughout its whole extent it is interposed between the hippocampus on the one hand and the pyriform lobe and nucleus of the lateral olfactory tract on the other. The pyriform lobe and hippocampus meet one another in front of the rostral end of the general pallium near the olfactory peduncle (fig. 7). The general pallium extends forward slightly further than is shown in the model. The presence of a subiculum between the hippocampus and general pallium and of a definite boundary line between the dorsal border of the pyriform lobe and the general pallium has been described above.

Only the most general features in the structure of the pallium can be described in this paper. By far the greater part of the cell bodies are collected in a dense layer near the ventricle. At the dorso-medial border the cells are mostly pyramidal and there are a few cells scattered in the outer part of the pallium. There are many more of the peripheral cells in the adjacent subiculum. Farther laterally the layer is more compact and the pyramidal form of the cells less evident.

The lateral border of the pallium presents marked characteristics in the rostral half of the hemisphere. In transverse sections the cell layer has a curve near the lateral border which is slight in the caudal part of the hemisphere (fig. 15), becomes more marked rostrally (fig. 17), and near the rostral end is strongly S-shaped (figs. 18, 19). This, together with the slightly larger size of the cells and their arrangement in a very compact layer. suggests rapid growth and mechanical crumpling of the cell This is the border along which internal capsule fibers laver. enter and leave the pallium and there is doubtless a difference of function between this border and the dorsal or medio-dorsal parts of the general pallium. This lateral border becomes gradually thicker as it is followed rostrad and dips down and becomes more and more overlapped by the pyriform lobe. Here the compact plate of cells becomes a thicker mass which in some sections is broken into several masses (figs. 23, 24). At the rostral end this thickened lateral border produces the pallial thickening mentioned in an earlier section.

Toward the rostral end of the pallium the cell layer becomes much less compact except in the lateral thickened border. The pyramidal cells with prominent apical dendrites are mostly confined to the deep layer and outside of these are many cells of stellate or ovoid form. These cells are present in the whole width of the pallium including the subiculum and the lateral thickening. In some sections these cells seem to constitute an incompletely separate layer. When the pallial thickening begins to form a ridge projecting into the ventricle it is noticed that these cells are more numerous in this part of the pallium than elsewhere (figs. 21, 22) and from this point on rostrad they form a conspicuous outer layer of cells in the pallial thickening (figs. 23, 24, 25, 40).

Near its rostral end the total number of cells in the pallium is greatly increased, the deep layer is much thickened and very dense and the outer layer extends well toward the medial border. Indeed, nearly the whole width of the pallium at its rostral end

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bears the characteristics of the lateral thick border. In other words, it may be stated that the body recognized in the gross brain as a pallial thickening occupies the rostral end of the general pallial area and extends caudad as a gradually diminishing lateral thick border. The pallial thickening is characterized by the presence of a well-developed peripheral layer of cells and this suggests a special functional significance for this body.

The pallial thickening last described is the most highly specialized part of the general pallium and is farthest removed from the brain stem. The temporal portion of the pallium, adjacent to the amygdaloid fissure, is the most primitive and simple in structure. In the caudal part of the basal surface of the hemisphere, where the temporal and occipital poles may be said to meet, the general pallium presents a somewhat more open arrangement than in most of the pallium (fig. 46). A larger number of cells are placed near the outer surface. From this point rostrad, toward the amygdaloid eminence, there is the line of transition between pallium and hippocampus and an area of pallium in which the cells become more and more irregularly scattered as one follows the sections forward (figs. 45, 44). At its lateral border this pallial area bends inward to become continuous with the cell masses in the dorsal ventricular ridge (figs. 11, 12). As the sections are followed forward it becomes evident that this part of the pallium is related to that basal and caudal part of the ventricular ridge whose ventricular surface is covered by the large-celled nucleus of the amygdaloid complex (fig. 44).

In sections which pass through the caudal part of the pyriform lobe and the deeper and broader part of the amygdaloid fissure (fig. 13), the caudo-lateral prolongation of the nucleus of the lateral olfactory tract appears in the depth of the fissure. Now the general pallial area on the basal surface is bounded by the hippocampus medially and by the nucleus of the lateral olfactory tract laterally. Internally the pallial cells merge with those of the basal lobe of the ventricular ridge. As the sections are followed forward the nucleus of the lateral olfactory tract increases in size while the hippocampal formation disappears from the sections before the tip of the temporal horn of the ventricle is reached (figs. 45, 44). At the same time the tail of the caudate nucleus appears between the dorsal and basal lobes of the ventricular ridge. The large-celled nucleus now surrounds the temporal horn of the ventricle and occupies the pallial surface medial to the nucleus of the lateral olfactory tract. Now the large bundle of the stria terminalis goes upward and forward from the large-celled nucleus, as above described. Finally the large-celled nucleus disappears from the sections at the level of the stria medullaris.

Thus the general pallium extends forward in the basal wall to the tip of the temporal pole. Its cells in this region are of various forms and are irregularly scattered and there is an intimate merging of the pallium with the large-celled nucleus of the amygdaloid complex. There is no area or avenue of continuity of the cell masses of the pallium with those of the brain stem. There is, however, continuity of the pallium, the large-celled amygdaloid nucleus and the lentiform nucleus of the corpus striatum. The lentiform nucleus imbeds the lateral forebrain bundle and is therefore comparable with the somatic area in the lateral wall of the selachian forebrain. In the turtle there is continuity throughout the cell masses related to the afferent and efferent fibers primarily somatic in function in the lateral bundle, or crus. In the fishes the somatic area is continuous with the sensory centers of the thalamus. That this connection has been lost in the turtle may be attributed to the greater development of the hemisphere which has elongated the crus and drawn the lentiform nucleus away from the thalamus.

The general pallial portion of the hemisphere consists therefore of (1) a broad, rather thin wall forming the roof and caudal pole of the hemisphere; (2) bounding this laterally and anteriorly, a pallial thickening which has a peculiar structure; and (3) a temporal area of simpler structure which is intimately connected with the dorsal ventricular ridge. This ventricular ridge might, indeed, logically be listed as a fourth part of the general pallium.

That these four regions are intimately related and constitute one complex area in the forebrain, comparable to the olfactory area with its several nuclei, is attested at once by the distribution of the fibers of the cerebral peduncle or internal capsule. This great bundle, where it is about to pass from the brain stem to the hemisphere (fig. 33), is bounded laterally by the optic tract and dorsally by the stria medullaris and stria terminalis. Medial and medio-ventral to this bundle is a large area of fibers which contains (1) the olfactory projection tract of Cajal ('04, fig. 778) descending from the olfactory portion of the amygdaloid complex, and (2) the medial forebrain bundle which follows the crus into the hemisphere and runs forward in relation to the tuberculum, caudate and other olfactory nuclei.

The great lateral forebrain bundle or crus is composed of two parts, dorsal and ventral. The dorsal part is coarse-fibered and well medullated. It comes from the nucleus rotundus and adjacent cell masses in the dorsal part of the thalamus which correspond to the thalamic sensory nuclei in mammals. The ventral part consists of finer fibers which are well medullated at least in their course through the thalamus and corpus striatum. This bundle bends somewhat ventrad and runs caudad on the ventro-lateral surface of the thalamus and mid-brain until some distance behind the third nerve where it becomes more diffuse and seems to end at least in large part before the isthmus is reached. Without going further into descriptive details it is evident that the dorsal bundle contains the sensory radiations from the thalamus to the hemisphere and that the ventral bundle corresponds at least roughly to the efferent tracts from the hemisphere as we know them in manmals.

These two bundles behave differently in the hemisphere. The dorsal deeper bundle bends up rapidly in larger and smaller fascicles through the lateral part of the striatum and enters the core of the dorsal ventricular ridge. The fascicles spread rather wide apart as they pass through the striatum but are all deep beneath the surface of the brain. Upon reaching the ventricular ridge the fibers enter into the formation of a uniform lace-work in the meshes of which the cells of the core-nucleus are evenly scattered. From this lace-work many fibers proceed into the dorsal pallium. This is the appearance seen in Cajal prep-

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arations. In Weigert sections the fibers appear to lose their myelin as they enter the dorsal ridge but a small number of medullated fibers are seen running right through the ridge into the pallium (fig. 32). There is at present insufficient evidence to show what proportion of the non-medullated fibers of the sensory bundle reach the pallium but it is clear that a large part of them do so. When transverse sections are followed from behind forward it is seen that the coarse-fibered sensory bundle all rises to the pallium or the ventricular ridge and disappears from the sections before the rostral end of the ridge is reached. The distribution of fibers to the caudal pole of the pallium is partly through the base of the ventricular ridge and partly by way of the fiber-layer of the pallium itself. Very few medullated fibers reach the caudal pole.

The ventral, fine-fibered bundle spreads laterally in the superficial part of the striatum (nucleus lentiformis) and rises toward the lateral border of the pallium. The fascicles, however, slant forward more as they run dorsally and the whole bundle extends much farther forward than the deeper coarse-fibered bundle. The fascicles break up into diffuse fibers before the pallium is reached and many of the fibers may arise from the lentiform nucleus itself. It is clear, however, that the greater part of these fibers enter into the fiber-layer in which the lateral thickened border of the pallial cell-layer is imbedded. Moreover, the greater part of this bundle is related to the pallial thickening.

In sagittal sections (fig. 51) fascicles from the superficial bundle are traced directly up to the pallial thickening through the rostral part of the striatum, and also around the rostral end of the striatum through the cell-free zone between the striatum and the pyriform lobe. It is interesting to note in sagittal sections that medullated fibers enter the pallium and the ventricular ridge only in the rostral part (half or more) of each. The bundles which rise from the crus into the core of the ventricular ridge lose their myelin or disperse so that they can not be traced farther as fascicles.

In Chrysemys marginata the ventricular ridge is smaller than in Cistudo and does not extend as far forward. The pallila thickening on the other hand is relatively more extensive. In this form the direct course of the superficial fibers of the crus up to the pallial thickening is much more clear than in Cistudo.

It is hoped to test the disposition of these fibers experimentally. If the above conclusions drawn from the study of sections prove to be correct, it is evident that the pallial thickening must be regarded as the chief source of the fibers descending from the pallium to the brain stem. It should be noted that the pallial thickening occupies the same position in the hemisphere as that occupied by the motor area in the lower mammals, except that there is no appreciable frontal association area seen in front Also, the descending fibers lie in front of the sensory radiof it. ations as they do in the mammalian internal capsule. It seems probable that the pallial thickening is chiefly motor (efferent) in function and that the ventricular ridge and a large part of the general pallium are sensory and associational. However, it is probable from my present results that the sensory and motor areas are not wholly independent. Also the whole subject of localization within the sensory field is untouched in the present paper.

SUMMARY AND COMMENTS

The advantage offered by the turtle brain for the study of the evolution of the mammalian cerebral hemisphere is that the turtle occupies such an intermediate position between fishes and mammals that it is possible from the standpoint of the turtle brain to recognize the homologous structures in all three groups and to explain the changes which have taken place from the brain of the fish to that of the turtle and from the brain of the turtle to that of the marsupials and mammals. This is due to the fact that among living reptiles the turtles are most nearly related to the ancestors of mammals and still possess a relatively simple and slightly specialized brain. In some points there would be great advantage from the study of the dipnoan brain, to bridge the gap between the fishes and reptiles. This gap is much wider than that between the reptiles and mammals, since neither the specialized fishes nor the amphibians stand in the line of

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descent of reptiles and mammals. The dipnoans, or some of them, do stand in this line of descent and the evolution of the brain must be traced from the selachians, through the dipnoans, reptiles and marsupials to the mammals.

The main purpose of the present paper is merely to define the morphological relations of the chief cell masses in the brain of the turtle in order that these may be used in future studies as points of reference in comparing ichthyopsid, reptilian and mammalian brains. This is done in the belief that a satisfactory account of the mammalian and human brain must eventually include an account of the origin and evolution of the several structures together with an explanation of existing structural relationships and the course of their evolution on the basis of environment, habits of life and the function of the several parts.

The olfactory area

Upon comparing the secondary olfactory centers of the hinge turtle with those of fishes, the only very noteworthy fact is the appearance in the turtle of a nucleus of the lateral olfactory tract behind the area occupied by the lateral forebrain bundle. This is a distinctly mammalian character. In the selachian (Johnston '11 a) the lateral forebrain bundle is imbedded in the somatic area in the lateral wall of the slender portion of the forebrain known to many authors until recently as the 'praethalamus,' and the lateral olfactory area lies wholly in front of this. The relations are shown in figure 59, in which are roughly indicated the areas from which alone the pyriform lobe and the nucleus of the lateral olfactory tract may have been developed. In the turtle these areas have moved far backward on the lateral surface and the mass which imbeds the lateral forebrain bundle appears as an island surrounded by olfactory nuclei,—the striatal area surrounded by the pyriform lobe, nucleus of the lateral olfactory tract, the diagonal band, the parolfactory nuclei and the tuberculum. This condition, which is so suggestive of, but not wholly similar to, the mammalian condition, has come about by a spreading and migration caudad of the lateral olfactory area,

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chiefly brought about by the great expansion of the dorsal pallium. The expansion of the pallium was accompanied by a great thickening of the lateral bundle and of the cell mass in which it The stretching of the lateral olfactory area was imbedded. accompanying the expansion of the pallium was followed by a collecting together of the olfactory centers into a ring around the striatal area. The striatum then, thickening and bulging outward, came to have its surface freed from the olfactory layer. That a complete ring of olfactory centers was formed around the striatal area was due to the connection which the medial olfactory tract retained with the nucleus of the lateral olfactory tract (fig. 56). This connection of the lateral olfactory nucleus with the medial tract and diagonal band has produced the characteristic bending of a part of the lateral olfactory tract to reach its nucleus in the amygdaloid region (fig. 60).

We have now to note how this condition in the turtle differs from that in the mammal. Although the gross appearance is much the same there is one essential difference, namely, that the striatal area has received a covering of general pallium, converting it into the insula. This has come about by the further expansion of the pallium which has pushed the pyriform lobe down over the striatal area so that in mammals it runs along the ventral border of the insula. Now a part of the lateral olfactory tract sweeps round in a curve to reach its nucleus in the tip of the temporal pole just as in the turtle. There is this difference, however, that the concavity of that sweeping curve is filled not by the striatal area but only by the tuberculum and the anterior perforate space.

The striatal area has thus been the scene of two important migrations of brain substance in the history of vertebrates. Between the fishes and reptiles the olfactory area has spread over the striatum and left its surface free again in the turtle. Between the turtle and mammals the general pallium has spread down over the striatum and left it covered by the insular cortex.

The hippocampal formation

With the expansion of the lateral brain vesicle and the formation of a caudal pole the massive hippocampal primordium in the roof of the selachian forebrain becomes spread out into a thin medial wall of the expanding vesicle. At the same time a part of the choroid roof of the median ventricle is carried out in the medial wall of the lateral ventricle and forms the choroid plexus extending from the interventricular foramen to the temporal pole. The relations of the hippocampus to the secondary olfactory centers in the medial wall have been fully discussed in previous papers and the history of the hippocampus above the reptiles is well known from the work of Elliot Smith and others.

The general pallium

The force which has brought about the changes in the olfactory centers mentioned above is the expansion of the general pallium. This is derived from the anterior end of the somatic sensory column (Johnston '10 c and '11 a) which early in vertebrate evolution extended up into the roof of the forebrain between the lateral olfactory area and the hippocampal primordium. This mass of cells received ascending fibers from the sensory centers in the thalamus and rapidly developed into an important collection of sensory and correlating centers for somatic relations. These centers proved of incomparable value to those vertebrates in which they were the more highly developed, through enabling them to extend the range of environment to which they could adapt themselves.

This expanding general pallium was located between the olfactory area and the hippocampus and was connected with its fellow of the opposite hemisphere by a commissure (corpus callosum) running through the substance of the hippocampus and in close relation to the hippocampal commissure. Under these conditions the expansion of the general pallium brought about great changes in the adjacent structures, as already noted. The first effect was an expansion distinctly in the dorsal or pallial portion of such a lateral forebrain vesicle as exists in the simpler selachian brains. This tended to produce a caudal pole pushing back over the stem or 'prethalamic' portion. To understand the formation of the caudal pole it is essential to see that the expansion began in this dorsal region and proceeded in the direction eventually assumed by the choroid fissure and the hippocampus. From such a beginning the stretching of the hippocampus and pyriform lobe and the migration of the olfactory area over the striatum all are readily understood. The further expansion of the pallium and the differentiation of special centers in it must be the subject of future work for which the present is preparatory.

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REFERENCE LETTERS

a.p., area parolfactoria a.p.a., area perforata anterior b.o., bulbus olfactorius c.a., commissura anterior c.h., commissura hippocampi c.i., capsula interna ch.op., chiasma opticum c.post., commissura posterior c.p.a., commissura pallii anterior crus, crus cerebri or lateral forebrain bundle c.st., corpus striatum d.b., diagonal band of Broca dec.po., decussatio postoptica d.v.r., dorsal ventricular ridge f.am., fissura amygdaloidea fasc.m., fasciculus marginalis f.chor., fissura chorioidea fi., fimbria f.pc., fasciculus praecommissuralis f.o., formatio olfactoria f.p., fissura prima for.i., foramen interventriculare f.rh., fissura rhinalis gl., olfactory glomerulus g.p., general pallium gr., granule cells and laver g.s., gyrus subcallosus $h_{..}$ hippocampus hy., hypothalamus i.C., islands of Calleja l.pyr., lobus pyriformis *l.t.*, lamina terminalis m.fb.bdl., medial forebrain bundle mi., mitral cells and layer n.c., nucleus caudatus n.d.b., nucleus of the diagonal band n.l., nucleus lentiformis n.med.a., large-celled medial nucleus of the amygdaloid complex

n.o., nervus olfactorius n.o.a., nucleus olfactorius anterior n.p.l., nucleus parolfactorius lateralis n.p.m., nucleus parolfactorius medialis *n.rot.*, nucleus rotundus n.sup., nucleus supraopticus n.tr.olf.lat., nucleus of the lateral olfactory tract olf.proj., olfactory projection tract pa., pallium pa.th., pallial thickening p.c., layer of peripheral cells in the pallium p.h., primordium hippocampi p.o. pedunculus olfactorius r.p., recessus praeopticus r.n., recessus neuroporicus r.s., recessus superior s.en., sulcus endorhinalis s.f-d., sulcus fimbrio-dentatus s.l., sulcus limitans hippocampi s.m., stria medullaris s.p.a., substantia perforata anterior s.t., stria terminalis sub., subiculum cornu ammonis s.v.d., dorsal ventricular sulcus s.v.m., middle ventricular sulcus s.v.v., ventral ventricular sulcus thal., thalamus t.o., tuberculum olfactorium t.p., temporal pole t., tectum mesencephali tr.d.b., tract of the diagonal band tr.olf.lat., lateral olfactory tract tr.olf., tractus olfactorius tr.olf.med., medial olfactory tract tr.op., tractus opticus v.III., third ventricle v.l., ventriculus lateralis

Fig. 1 Lateral surface of forebrain. Chief features described in text. The fibers in the striatal area are readily seen both in the fresh brain and in brains prepared in bichromate. These fibers are equivalent to the mammalian internal capsule, but the cortical covering of the insula is wanting. The pyriform lobe shows some cross ridges which probably correspond to bundles of internal capsule fibers and thickenings of the lateral border of the pallium. The amygdaloid fissure was especially well developed in this brain. The whole brain never shows the rostral end of the sulcus endorhinalis as well as sections do.



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Fig. 2 A ventral view of the same brain as in figure 1. The diagonal band and the fibers imbedded in it are readily visible in the entire brain, although the fiber-bundles are much more delicate than those of the internal capsule.

Fig. 3 A medial view of another specimen. (From Johnston '13 b, fig. 20.) The fissura prima curves forward over the parolfactory area. The fimbrio-dentate sulcus runs longitudinally above it. The body between is the primordium hippocampi. Between the fissura prima and the lamina terminalis the diagonal band rises apparently to join the hippocampal primordium directly. The broken line indicates the boundary of the primordium as determined by internal structure. The portion of the diagonal band seen on this surface of the brain is the homologue of the gyrus subcallosus. This figure shows the prominence of the rostral end of the pallium due to the pallial thickening.



Fig. 4 A forebrain from which the entire medial wall of the pallium has been cut away, seen from the medial direction. The large dorsal ventricular ridge is divided into a chief lobe and a basal lobe by a shallow groove. The bifurcation of the middle ventricular groove is not well shown. One branch descends into the temporal horn of the ventricle; the other runs for a short distance in the bottom of the shallow groove on the dorsal ridge. Compare figure 10. This brain shows an unusual prolongation of the basal part of the dorsal ridge into the caudal pole. The part of the striatum seen here is the head and tail of the caudate nucleus.

Figs. 5 to 10 These are photographs of a model of the right half of the forebrain made by the method of plate reconstruction. The method of building up and dissecting the model is explained in the text. Before photographing, the outer surface of the model was lightly smoothed and then painted in two colors. All the olfactory centers including the hippocampus were painted a light yellowgreen. The somatic structures, striatum and general pallium, were painted light blue. In the photographs all the olfactory centers have a dark tone. The ventricular surfaces and the cut surfaces have received no treatment whatever. The hypothalmic region was not completed.

Fig. 5 Lateral surface of the model. The dorsal border of the pyriform lobe is sharply marked through its whole length. The caudal border is only arbitrarily fixed. A broken line marks the limit between the large-celled and small-celled parts of the pyriform lobe. The olfactory part of the amygdaloid eminence appears depressed owing to its color and to its being in shadow. Compare figure 8. The structures surrounding the striatal area constitute a continuous ring of small-celled olfactory nuclei.

Fig. 6 Medial view of the model. The lip of the choroid fissure and the lamina terminalis are painted white. The model is cut between the hippocampal commissure and the anterior commissure, so that the commissure may be removed with the whole hippocampal formation. A broken line indicates roughly the boundary between the hippocampus proper and the subiculum. Probably too large an area is included in the subiculum at the anterior end. The somatic pallium should have been carried farther forward here in constructing the model. Note the oblique position of the peduncular constriction. Note also the fissura prima, the fimbrio-dentate sulcus and the moulding of the caudal pole around the thalamus and midbrain.





Fig. 7 Dorsal view of the model. This requires no comment except to point out that the general pallium should have been continued somewhat farther forward at the expense of the subiculum cornu ammonis.



Fig. 8 Ventral view of the model. This view shows well how the striatal area is completely surrounded by olfactory centers. It also shows that the general pallium extends into the amygdaloid prominence of the temporal pole so as to intervene between the hippocampus and the secondary olfactory nuclei. The temporal pole of the hippocampal formation has no direct relation with the secondary olfactory nuclei on the basal aspect of the brain.



Fig. 9 Lateral view of the model with the pyriform lobe removed. At both its rostral and caudal ends the pyriform lobe forms the whole thickness of the wall over small areas, so that the ventricle is opened in this photograph. Through the greater part of its length the pyriform lobe overlies the thickened lateral border of the pallium and the dorsal ventricular ridge. A broken line marks the boundary between the pallium and this ridge. Along this line a cell-free zone separates the pallium from the ridge but the two can not be dissected apart owing to the continuity of their cell masses in the region of the amygdaloid fissure. The thickening of the lateral border of the pallium which causes the bulging out of the pyriform lobe near its rostral end is clearly seen in this photograph.



Fig. 10 Medial view of the model with the hippocampus removed. The pallial thickening is perhaps better seen here than in the dissected brain (fig. 4). That part of the thalamus which appears behind the anterior commissure is continuous laterally with the tail of the caudate. The ventricular ridge and general pallium are separated from the striatum by a cut which follows the middle ventricular groove to the end of its dorsal branch, and by a cut which runs diagonally downward and forward from the end of the first one and disappears behind the hypothalamus in this view. The bifurcation of the middle ventricular groove is seen just behind the upper angle of the thalamus. From this point the temporal branch descends into the temporal horn of the ventricle. Its course forms a letter X with the second cut above described. Following the course of this groove is the small ridge described in the text as imbedding part of the stria terminalis related to the basal lobe of the ventricular ridge. From this ridge the bundle goes forward in the caudate. The tail of the caudate barely appears in this figure behind the thalamus (n. c.) and bounded by the temporal branch of the middle groove. The thickening and fusion of the caudate with the nucleus of the lateral olfactory tract in the amygdaloid complex lies just lateral to this point. It is in this region that a great hypertrophy of the common caudate-amygdaloid mass produces the 'epistriatum' in the lizards. The triangular area between the two cuts above described belongs to the lentiform nucleus. Note that the general pallium is continuous with the lentiform nucleus through the basal lobe of the ventricular ridge (medial nucleus of amygdaloid complex).

Figs. 11 to 30 Transverse sections of the right hemisphere drawn from sections stained to demonstrate the size and grouping of the cell bodies. The contrasts and lines of separation are not exaggerated. Magnification, 17.5 diameters. The position of each of these sections is indicated in figure 58.

Fig. 11 Section through the base of the dorsal ridge. The dense layer in the medial wall of the pallium is in part hippocampus. The rest of the section belongs to general pallium, with which the ridge is in connection.

Fig. 12 Section a short distance behind the choroid fissure. The dense pallium in the medial wall is hippocampal. The dorsal ridge appears as an infolding of the general pallium. The pyriform lobe presents a confused arrangement of its cells.

Fig. 13 Section at the caudal border of the choroid fissure and the base of the amygdaloid fissure. Hippocampal formation appears both above and below the choroid fissure. The large-celled nucleus appears on the ventricular surface of the basal lobe of the great ventricular ridge. The nucleus of the lateral olfactory tract appears near the base of the amygdaloid fissure. Between them the general pallium is continuous with the central core of the ventricular ridge. Note the small ridge below, which contains the stria terminalis bundle. From this level forward the subiculum cornu ammonis is a conspicuous feature.

Fig. 14 Section through the extreme rostral end of the temporal horn of the ventricle. Hippocampal formation has disappeared below the choroid fissure. The large-celled nucleus surrounds this part of the ventricle. The nucleus of the lateral olfactory tract has grown larger and the caudate nucleus appears and is fused with it. The nucleus lentiformis begins to take shape.



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Fig. 15 Section at the base of the amygdaloid fissure. The general pallium still makes connection with the ventricular ridge and intervenes between the pyriform lobe and the nucleus of the lateral olfactory tract. This last is now larger and merges broadly with the caudate. The lentiform nucleus shows some dense collections of cells.

Fig. 16 Section through the stria medullaris. This is about the largest and densest part of the small-celled area of the amygdaloid complex, consisting of the caudate and nucleus of the lateral olfactory tract. The great enlargement of this body produces the 'epistriatum' in lizards. The olfactory projection tract and part of the stria terminalis are related to this (compare fig. 49) while the stria medullaris enters the neuropile surrounding the rostral end of the medial nucleus. Note the rapid thickening of the lateral border of the dorsal pallium in figures 15 and 16. An angle of the general pallium connected with the ventricular ridge still intervenes between the pyriform lobe and the nucleus of the lateral olfactory tract.

Fig. 17 Section through the extreme tip of the temporal pole or amygdaloid prominence and through the caudal part of the junction of thalamus and striatum. The nucleus lentiformis is larger and the nucleus of the lateral olfactory tract appears divided. The upper portion will in the next figure join the pyriform lobe. The core-nucleus of the ventricular ridge is now well defined. Note the olfactory projection tract curving over the crus.

Fig. 18 Section through the commissures just rostral to the inter-ventricular foramen. The crus bends laterad into the lentiform nucleus. It separates the caudate from the nucleus of the diagonal band which is a continuation of the nucleus of the lateral olfactory tract. Note the continuity of the caudate with the nucleus anterior region of the thalamus in figures 17 and 18. Note also the rapid enlargement of the primordium hippocampi in these figures as it approaches the level of the commissure. For the disposition of the commissures compare figures 32, 48 and 52.



Fig. 19 Section in front of the commissures and behind the optic chiasma. The lentiform nucleus is large; the crus occupies the clear space below it and sends fascicles up through it (internal capsule). The nucleus of the diagonal band forms a thin cell layer between the fiber layer of that band and the medial forebrain bundle. The caudate is small. The upper end of the nucleus of the diagonal band appears here in the gyrus subcallosus adjacent to the hippocampal primordium and the recessus superior. Note the distinct large- and small-celled portions of the pyriform lobe. Also the general increase in thickness and more open formation of the cell layer of the dorsal pallium.

Fig. 20 Section through the optic chiasma. The ventricular ridge grows smaller and the definite pallial thickening begins. The hippocampus proper grows narrow. The hippocampal primordium is only apparently fused with the parolfactory nuclei, as explained in the previous paper. The diagonal band and its nucleus move to the angle between the basal and medial walls. The sulcus endorhinalis separates the small-celled from the large-celled part of the pyriform lobe. The lentiform nucleus is quite superficial in this and several following figures. The clear zones above and below the core-nucleus of the ventricular ridge and between that and the pyriform lobe are the spaces through which internal capsule fibers run to the ridge and the general pallium.

Fig. 21 Section at the level of the gyrus subcallosus. The changes noted in the last section have been carried farther. The lentiform nucleus shows rows of cells due to the arrangement of bundles of internal capsule. In this and figure 22 the diagonal band nucleus merges with the superficial layer of the anterior perforate space and tuberculum olfactorium.

Fig. 22 Section through the anterior end of the dorsal ventricular ridge. The core-nucleus is here divided into two areas by pressure from the pallial thickening. This thickening is the most conspicuous feature of the section. Note the development of a layer of peripheral cells in figures 20, 21 and 22. Compare figure 40. The caudate begins to enlarge and the lentiform to decrease.





Fig. 23 Section through the pallial thickening in front of the ventricular ridge. In this and the next three figures the pyriform lobe is bulged out by the pallial thickening. Although the lentiform nucleus still meets the ventricle, the caudate is greatly enlarged. From here forward the hippocampus is scarcely if at all recognizable. The subiculum continues between the general pallium and the hippocampal primordium. The dividing line between primordium hippocampi and parolfactory area is again clear. In this section the ventral ventricular groove reaches its greatest depth and width. Forward from this the thickening of caudate, parolfactory nucleus and tuberculum nearly obliterate it.

Fig. 24 Section through the middle of the pallial thickening. Islands of Calleja begin to appear in the medial wall. The lentiform nucleus is pushed toward the surface by the caudate. For a detail of the pyriform lobe and part of the pallial thickening compare figure 40.

Fig. 25 Section through the caudal part of the tuberculum olfactorium and the head of the caudate. Note the high dorsal prominence caused by the pallial thickening. This scarcely shows satisfactorily in the figures of the whole brain or model. A part of the apparent thickness of the cell layer is due to the section being slightly oblique to the curvature of the dorsal pallium but the appearance of a distinct peripheral layer of cells is not due to this. Islands of Calleja are grouped in the medio-basal angle. Dark masses farther laterad are merely clumps of large cells in the lentiform nucleus.



Fig. 26 Section a short distance in front of the last. It shows the rostral end of the lentiform nucleus and the spreading of the small-celled part of the pyriform lobe over the striatum as the superficial layer of the tuberculum. The whole width of pallium in figs. 25, 26 has the characters of the thickening.

Fig. 27 Section through the rostral part of the tuberculum. The section passes just behind the peduncular constriction dorsally. Olfactory formation begins to appear 225 microns farther forward. The head of the caudate together with the deep or lateral parolfactory nucleus form one rounded mass covered externally by tuberculum. This is the nucleus olfactorius anterior of authors. Islands of Calleja are in the deep layer of the tuberculum. The tuberculum is continuous with the medial parolfactory nucleus and with the pyriform lobe. The pyriform lobe spreads medially in dorsal wall. General pallium is still present toward medial border and in some clusters of cells beneath pyriform lobe.

Fig. 28 Section through the olfactory peduncle. Both sides are shown, the left side being sectioned near the rostral end of the oblique peduncle, the right side near the caudal end of the peduncle. On the right side fully developed olfactory formation appears in the roof; in the lateral wall the pyriform lobe; below, the end of the nucleus olfactorius anterior and the tuberculum.

Fig. 29 Section through the caudal part of the olfactory bulb. Note the elliptical form of section on the right, the greater number of cells where olfactory glomeruli are present and the distribution of mitral cells with reference to the glomeruli. a, b, regions of this section which are drawn in figure 31.

Fig. 30 Section through the anterior part of the right bulb. Note the triangular form of section and the fact that the dorsal root of the olfactory nerve is just entering the bulb. The bulb is nearly surrounded by glomeruli and the mitral cell layer is continuous except for a short space on the lateral surface where glomeruli are absent.



Fig. 31 Two portions from the section drawn in figure 29 to show the modification of the structure of the olfactory formation due to the presence of glomeruli. The part of the section drawn in a and b respectively is indicated by the same letter in figure 29. Where glomeruli are present the granule cell layer is considerably thicker and more dense and the layer of large mitral cells is added. Magnification 110 diameters.

Fig. 32 Transverse section at the level of the commissures. From Johnston '13b, fig. 17. The right side of the drawing was taken from a section adjacent to that from which figure 18 of the present paper was drawn. The left side was drawn from a Weigert series. The crus shows the two chief bundles described in the text. To what extent the fascicles of the two bundles intermingle as they are distributed to the pallium and the ventricular lobe it is impossible to say from sections of normal brains. The relation of the anterior commissure to the internal capsule is better shown in figure 48. Medial to the crus appear two other bundles. The darker one is the medial forebrain bundle, the lighter is the olfactory projection tract.

Fig. 33 A section similar to the last, taken at the level of the stria medullaris. From Johnston '13b, fig. 18. The two bundles of the crus are separated by a notch medially. The medial forebrain bundle is ventral to the olfactory projection tract and in contact with the postoptic decussation. The lower part of the fiber area beneath the letters c.i., belongs to the olfactory projection tract. The stria medullaris is more superficial.











Fig. 34 A section similar to the last, taken near the rostral end of the ventricular ridge. The internal capsule fibers are related largely to the pallial thickening (c.l.). The medial part of the fiber bundles below belongs to the medial forebrain bundle. Its fibers are related only to the caudate and olfactory nuclei.

Fig. 35 Vesicular structures in the caudate nucleus. a, outline of a transverse section to indicate the position in which such vesicles are found. This is nearly at the same level as figure 25. Vesicles are found both rostral and caudal to this level. b, an oblique section of a vesicle the lumen of which contains a flattened nucleus of unknown character. Two blood corpuscles are seen. Vesicles often have capillaries closely connected with them. c, a transverse section of a vesicle with very sharply defined lumen. Note the granular contents of the inner ends of the cells. There are also faintly stained granules in the lumen. The isolated nuclei in b and c are nuclei of nerve cells lying near the vesicles. Magnification in b and c, 625 diameters.

Fig. 36 Section of the thickened ependyma surrounding the middle ventricular groove including a part of the lentiform nucleus. The nerve cells are drawn in outlines, the nuclei of the ependyma cells in black. The lines represent the peripheral processes of the ependyma cells. From the same section as figure 16. Magnification 112 diameters.



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e d 38

Fig. 37 Same region as figure 36 but on the left side of the brain. A drawing from a Golgi section to show the ependyma cells in the dorsal lip of the middle ventricular groove, and their curved processes.

Fig. 38 Transverse section through the tuberculum olfactorium to show the grouping of cells in the islands of Calleja. From a section adjacent to that shown in figure 24. Magnification 110 diameters. The medio-basal angle of the left side and a small part of that of the right side are included. a, b, c, d, typical islands. e, an island in which larger and small cells are mingled. In some islands similar to this the small cells definitely show the vesicular arrangement with lumina. f, a vesicle similar to those shown in figure 35. Only the nuclei are drawn.



Fig. 39 Transverse section through the upper end of the gyrus subcallosus, showing the dense nucleus of the diagonal band close to the recessus superior. From the same section as figure 19. The position of the hippocampal commissure shows that this nucleus pushes up near the medial surface above the level of the commissure. This is shown in the model, but the ventral border of the hippocampal primordium in front of the commissure curves dorsally still more than is shown in the model (fig. 6). Note how much smaller these cells are than those of the adjacent hippocampal primordium. Indeed these are among the smallest cells in the forebrain. Magnification 110 diameters.



Fig. 40 Transverse section through the pyriform lobe and the pallial thickening to show the form and grouping of the cells. From the same section as figure 24. Magnification 70 diameters. In the upper part of the figure enough of the pallium is drawn to show the importance of the peripheral layer of cells. The deeper cells are smaller and so closely crowded that their processes seldom show at this magnification. The thick dendrites of the larger cells in the pyriform lobe, however, are clearly seen. It is evident that the large cell clusters belong to the pallium and not to the pyriform lobe.



Fig. 41 Transverse section of the caudal part of the pyriform lobe. From the same section as figure 13. Magnification 70 diameters. In the upper part of the figure is seen the sharp dividing line between pyriform lobe and general pallium. No well-marked line of division is seen below.

Figs. 42 to 45 Four transverse sections through the region of the medial nucleus of the amygdaloid complex. From the same sections as 16, 15, 14, 13 respectively. Magnification 70 diameters.





Fig. 42 In this is seen the common mass of small cells formed by the caudate and the nucleus of the lateral olfactory tract. Below it is a mass of neuropile in which appear a considerable number of larger cells belonging to the medial nucleus. The stria medullaris enters into this neuropile while the olfactory projection tract and stria terminalis in part are related to the small-celled nucleus (compare fig. 49).

Fig. 43 Only a little of the small-celled mass is shown. The medial nucleus is larger and more dense and has shifted toward the medial wall.

Fig. 44 The medial nucleus is still larger and surrounds the temporal horn of the ventricle, the rostral end of which is cut by the section. Immediately caudal to this the medial wall of the ventricle is occupied by hippocampal formation.



Fig. 45 In this section the medial nucleus occupies the ventricular surface of the basal lobe of the great ventricular ridge. Ventrally this mass of cells merges with the general pallium. The dense lamina in the medial wall belongs wholly or in part to the hippocampal formation. The small ridge in the lower angle of the ventricle lodges part of the stria terminalis bundle which spreads over the ventricular surface of the medial nucleus.



Fig. 46 Transverse section through the base of the ventricular ridge near its caudal end. From the same section as figure 11. Magnification 70 diameters. The relations are described in the text. The figure shows typical pallial walls laterally and ventrally which appear to be involuted to form the ventricular ridge.

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Fig. 47 A drawing of the subiculum region from the same section as figure 17. Magnification 70 diameters. The figure shows very inadequately the relatively dense layer of the hippocampus below, the more open arrangement of the cells in the subiculum and the abrupt medial border of the general pallium above. This border is marked by the arrow.

Fig. 48 Horizontal section from a Weigert series to show the anterior commissure and stria terminalis. The section is taken just at the level of the most dorsal part of the stria terminalis where it curves over the internal capsule. At this point the anterior commissure meets the stria (compare fig. 32) and continues with it into the small-celled nucleus of the amygdaloid complex.

Fig. 49 Horizontal section somewhat ventral to the level of that drawn in figure 48. This is from another series. The section passes through the lower or ventral part of the stria terminalis where it lies close upon and a little intermingled with the internal capsule. The section is drawn to show that the stria terminalis and the olfactory projection tract are divisions of a common broad bundle arising from the small-celled part of the amygdaloid complex. The bundle which enters the stria terminalis from the basal lobe of the ventricular ridge is drawn although it is almost wholly non-medullated. It can not be traced farther forward in these sections.



Fig. 50 Horizontal section through the temporal pole and thalamus. Same series as figure 49. This section shows the fiber bundle of the diagonal band where it crosses the basal surface of the crus and medial forebrain bundle.

Fig. 51 Parasagittal section close to the right lateral surface. Weigert stain. The cell masses of the pyriform lobe and pallial thickening are outlined in broken lines; also the line of division between the striatum and the amygdaloid complex. The figure shows especially the fibers of the internal capsule entering the pallial thickening.

Fig. 52 Section from the same series as the last. Near the median plane. The section shows the hippocampal commissure rising in the hippocampal primordium to join the fimbria system. There are shown also the relations of the sensory bundle of the crus, the olfactory projection tract and the medial forebrain bundle.



Fig. 53 A section from the same series as the last. It is taken from the left side of the brain. Owing to the oblique plane of the sections this is near the median plane at the level of the third nerve, but farther from the middle in the forebrain than in figure 52.



Fig. 54 A section from the same series, farther laterad than the last. This section shows a part of the sensory and the motor bundle of the crus, the olfactory projection tract and the median forebrain bundle. It is especially interesting to note from these sections that both the olfactory projection tract and the median forebrain bundle run almost wholly to the tegmental region or farther caudad, whereas it has been supposed that they both end for the most part in the hypothalamus.

Fig. 55 A diagram of the lateral olfactory tract together with a part of the medial olfactory tract and of the bundle of the diagonal band. Outline taken from figure 5. The figure shows the bundle which bends down behind the striatal area to end in the nucleus of the lateral olfactory tract in the amygdaloid eminence. At a is seen the bundle which comes from the medial wall of the olfactory bulb, crosses over the dorsal surface in the peduncular groove and joins the lateral tract. The whole course of the diagonal band can not be seen in this lateral view.

Fig. 56 A diagram of the olfactory tract in ventral view. Outline taken from figure 8. The medial and lateral bundles of the olfactory tract are separated by the striatal area containing the fibers of the crus. A bundle of the lateral tract curves around lateral and caudal to this area to reach the nucleus of the lateral olfactory tract, while a bundle of the medial tract passes along the ventral border of the striatal area to reach the same nucleus. From this nucleus, then, fibers enter the stria medullaris and the bundle of the diagonal band. The latter go to the hippocampus by way of the precommissural fornix system.

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Fig. 57 A diagram of tracts in the medial wall. Outline from figure 6. This shows especially how the fimbria system is made up of several components: olfactory tract fibers, precommissural fibers from the diagonal band, hippocampal commissure, and fornix (not drawn).

Fig. 58 Sketch of the right hemisphere after figure 10 with lines to show the position of the sections drawn in figures 11 to 30.



Fig. 59 Schema of the selachian forebrain viewed from the left side. The outline corresponds to that of the forebrain in Scymnus or Heptanehus. The lateral olfactory area is shaded with oblique lines, the corpus striatum with vertical lines. The expansion of the somatic centers in the roof as general pallium is indicated by arrows and the direction of the chief expansion of the hemisphere is indicated by a large arrow. The equivalent of the pyriform lobe and the nucleus of the pallium has been accompanied by a great elongation of this olfactory area.



Fig. 60 Schema. of the forebrain of the turtle viewed from the left side, for comparison with figure 59. The olfactory area has been stretched over and beyond the corpus striatum but does not now form a covering of the striatum. The present condition in the turtle is such as would have been produced if the striatum had been covered by an olfactory layer and then the cells of that layer had withdrawn to the borders of the striatum so as to form a ring of olfactory centers around it.