THE EVOLUTION OF THE CEREBRAL CORTEX¹

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WITH TWENTY FIGURES

In the course of a general treatment of the nervous system of vertebrates, published in 1906, the writer stated briefly the results of personal investigations upon a number of topics. In some cases, it has since appeared, the brief treatment did not present adequately the evidence upon which the conclusions were based. Circumstances have greatly delayed the publication of this evidence in more complete form. Recent papers have treated with some fullness the mesencephalic root of the trigeminus, the origin of taste buds and the question of the boundary between diencephalon and telencephalon. The subject of the present paper is to be taken up in a series of short papers with the purpose of demonstrating the early stages in the phylogenetic history of the cerebral cortex. It is but just to say that the great bulk of the evidence now presented upon these various subjects was in hand before the book referred to was written.

The boundary between diencephalon and telencephalon is marked by the velum transversum above and by the caudal surface of the chiasma-ridge below. The telencephalon consists of a ventral portion occupied by the optic chiasma and other decussating fibers and a dorsal portion comprising the corpus striatum, rhinencephalon, cortex, lamina terminalis, tela chorioidea, etc.

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The ventral portion never enters into the evaginations by which the lateral lobes or "hemispheres" are formed. Of the dorsal portion only a part is evaginated in primitive vertebrates and successively more and more of the wall of the unpaired ventricle turns out to become the wall of the lateral ventricle in the higher classes of vertebrates. For reasons of practical convenience in description the distinction between evaginated and non-evaginated parts of the forebrain will be more often used than the more fundamental distinction between dorsal and ventral portions. It is necessary to have unambiguous terms to express this distinction, especially in view of the changes which take place from one class of vertebrates to another, resulting in the transformation or translocation of non-evaginated area into the evaginated. For the non-evaginated wall of the unpaired ventricle in all classes may be used the term *telencephalon medium*. I have suggested (1909) that the term *hemisphere* be used to include all that belongs to one-half of the telencephalon. If, on the contrary, it is desirable to retain for the hemisphere the boundaries given it in the BNA, namely the walls of the lateral ventricles in man, it should have the same significance in lower vertebrates. If this usage is adopted it must be clearly recognized that in various classes of lower vertebrates the term hemisphere will include little or none of the cortical areas which predominate in the hemisphere of man. While the question of this usage is being settled, the term *lateral lobes* used by the older anatomists may be used for the evaginated portion of the forebrain without ambiguity.

In median sagittal section of the embryonic forebrain (figs. 17-20), the roof begins at the preoptic recess and extends around the convex surface to the velum transversum. The median seam is the telencephalic part of the roof plate of His. About the middle of this is seen in many vertebrates a neuroporic recess, marking the point at which the neural tube remained longest in connection with the ectoderm. That part of the roof plate which lies between this point and the chiasma is known as the lamina terminalis; that part which extends from the recessus neuroporicus to the velum transversum is the lamina supraneuroporica. It should be emphasized that *it is only for reasons of practical convenience that the lam-*

ina terminalis has been distinguished from the remainder of the roof plate, from which it does not differ in any important way. The neural tube does not end forward in a wide opening whose dorso-ventral diameter is measured by the lamina terminalis after the lateral walls are fused together. Rather, as the neural plate rolls

FIG. 1. Schemata to illustrate the two conceptions of the lamina terminalis. In all the sketches the neural tube is viewed from the left and a little in front. In A is represented the common view that the neural tube has a roof plate and a floor plate of equal length. The lamina terminalis is formed by the fusion of the side walls, lettered *Hirnnahrt of His*. The upper boundary of this would be marked by the neuroporic recess, the lower boundary by the optic chiasma. In B, C and D is illustrated the view stated in the text. The closing of the neural tube is retarded by its relation to the olfactory placode. There is fundamentally a single seam of closure, all of which belongs to the roof plate. The part of this seam between the olfactory nerve and the optic chiasma comes to have the appearance of an endplate (lamina terminalis) because of the forebrain flexure, and this is due to the influence of the olfactory nerve and its centers.

ABBREVIATIONS

<i>c.a.</i>	commissura anterior	<i>n.olf.</i>	nervus olfactorius
<i>c.call.</i>	corpus callosum	<i>n.term.</i>	nervus terminalis
<i>ch.</i>	optic chiasma	<i>olf.som.</i>	correlation tract between olfactory nuclei and primordium of soma- tic cortex
<i>c.hipp.</i>	commissura hippocampi	<i>par.</i>	paraphysis
<i>c.pall. ant.</i>	commissura pallii ante- rior	<i>p.c.b.</i>	precommissural body
<i>c.post.</i>	commissura posterior	<i>p.h.</i>	primordium hippocampi
<i>c.sup.</i>	commissura superior	<i>r.n.</i>	recessus neuroporicus
<i>ep.</i>	epiphysis	<i>r.m.ext.</i>	recessus neuroporicus externus
<i>f.bulb.</i>	formatio bulbaris	<i>r.p.</i>	recessus praepoticus
<i>f.i.</i>	foramen interventricu- lare	<i>som. area.</i>	primordial somatic cor- tex
<i>g.hab.</i>	ganglion habenulae	<i>tr.taen.</i>	tractus taeniae
<i>hem.</i>	lateral lobe of forebrain	<i>tr.th-cort.</i>	tractus thalamo-corti- calis (somatic)
<i>inf.</i>	recessus infundibuli	<i>v.tr.</i>	velum transversum
<i>l.s.</i>	lamina supraneuroporica		
<i>l.t.</i>	lamina terminalis		
<i>m.</i>	point of attachment of the membranous tela to the massive lamina supraneuroporica

FIG. 2. Sketch of the right half of the fore part of the brain of the sturgeon as seen from the medial surface. The primordium hippocampi is bounded below by the sulcus Monroi. The velum transversum is attached to the brain wall behind the so-called praethalamus.

up the neural tube tapers to a point in the preoptic recess, and the lamina terminalis is the anterior part of the seam of closure along the mid-dorsal line (fig. 1). The conception of a "frontal Hirn-naht" of His is fundamentally wrong, but its convenience in descriptive anatomy has led to its continued use. The writer has at times inadvertently used or implied it, although he has held for some years the view here expressed. This view has been expressed by other workers also. The two views are incompatible and that of His is inconsistent with the facts of embryology and phylogenesis of the forebrain.

It is necessary to define more exactly how the velum transversum indicates the boundary between the diencephalon and telencephalon. The velum is a transverse in-folding of the tela chorioidea and owing to the arched form of the membranous roof in most vertebrates the lateral borders of the velum may be compared to the pillars of an arch. Where these pillars of the velum meet the lateral nervous walls of the brain in the embryo, these walls are indented by a vertical groove. This groove marks the boundary between the diencephalon and telencephalon. In the adult this boundary is marked by the attachment of the pillars of the velum to the massive lateral walls. In the brains of many fishes the arch of the velum is inclined forward so that the boundary line in question is not marked by the position of the velum in median sagittal section but by the place of attachment of the velum to the lateral wall. Fig. 2 shows what is meant in the case of the brain of the sturgeon, and the relations of the velum will be amply illustrated in the later papers of this series.

The features of the telencephalon in which we are chiefly interested are (1) the degree of evagination of the lateral lobes and the functional areas contained in these in different classes of vertebrates; (2) the area from which the hippocampal formation of higher brains is derived; (3) the area from which the general cortex is derived; and (4) the morphological position and value of the pallial commissures. These features will be reviewed very briefly by the aid of simple schematic figures.

The treatment of the cortex assumes the principle stated in a previous paper (1909, pp. 518-525) that the cortex develops from

centers in primitive vertebrates which serve for the correlation of incoming impulses of different kinds. The cerebral cortex everywhere is nothing else than a complex of correlation centers.

CYCLOSTOMES

In cyclostomes the evagination carries out the formatio bulbaris and the secondary olfactory centers in larger part. Indirectly, owing to crowding from in front, the wall of the telencephalon medium is folded so as to enter into the caudal wall of the lateral lobe. This is a part of the region heretofore named "striatum." It is not a proper part of the evagination and the folding spoken of accounts for the bifurcation of the lateral ventricle (fig. 4). The telencephalon medium includes secondary olfactory centers below and in front of the foramen interventriculare, so-called striatum below and behind the foramen, and primordium hippocampi (heretofore called "epistriatum") above the foramen. (See figs. 3 and

FIG. 3. *Petyromyzon dorsatus*, late ammocetes. Sketch of left half of fore part of brain to show functional areas in the telencephalon. The heavy broken line marks approximately the boundary between the telencephalon and diencephalon.

FIG. 4. *Petromyzon dorsatus*, late ammocoetes. *A*, transverse section of telencephalon; *B*, horizontal section, both through the foramen interventriculare. The broken line beneath *som. area* in *B* marks approximately the boundary between diencephalon and telencephalon. The region labeled somatic area has heretofore been called striatum.

4.) That this primordium hippocampi belongs to the telencephalon and not to the diencephalon as held by Edinger, Sterzi, Tretjakoff and others is shown by the attachment of the velum transversum to the brain wall between this body and the ganglion habenulæ. The primordium hippocampi presents certain definite histological characteristics which are constant in fishes and amphibians. It receives olfactory fibers of the second order by way of a decussation in the lamina supranucroporica and receives ascending fibers from the hypothalamus, the tractus pallii. The hypothalamus is a tertiary visceral and gustatory center in other fishes and amphibians and may be supposed to have similar functions in cyclostomes. The entrance of the tracts mentioned into the primordium hippocampi constitutes it a correlating center for olfactory and visceral impulses. It would thus furnish the starting point for the differentiation of the hippocampus and may possibly contribute to the formation of other structures.

The area called striatum is probably the beginning of the general or somatic cortex, but requires further investigation.

FIG. 5. *Scyllium stellare*, anterior part of the brain seen from above. The medial olfactory nuclei are very large, and the primordium hippocampi and anterior pallial commissure are carried far back. The line *r.n.ext.* marks the dorsal opening to the sagittal fissure. The line *v.tr.* marks the point of attachment of the velum transversum.

FIG. 6. *Scyllium stellare*, sketch of right half of fore part of brain. The telencephalic areas are lettered. The course of the nervus terminalis in *Scyllium* is shown in black. In light outlines the dorsal course of the nerve as seen in *Hexanchus*, *Squalus* and others. In *Scyllium*, instead of a slender external neuroporic canal there is a narrow fissure open both dorsally and ventrally. The somatic area is on the lateral surface. Its outline is projected upon the sagittal plane.

The anterior commissure lies in the lamina terminalis and connects the striatal areas. The commissure differs greatly in size in different species of petromyzontes and its constitution is not well understood.

The hippocampal primordia occupying the dorsal part of the walls of the unpaired ventricle converge forward and meet in a slight thickening of the lamina supraneuroporica (figs. 3 and 4). In this thickening are two kinds of fibers: (1) fibers crossing from the formatio bulbaris of one side to the primordium hippocampi of the other side, and (2) fibers which connect directly the evaginated portion of the so-called striatum. The important thing to notice here is that a decussation and a true commissure are found here in the *pallial position*, that is, above the neuroporic recess.

SELACHIANS

In selachians the evagination of lateral lobes has gone farther than in cyclostomes. Especially, the lateral ventricles are longer, the olfactory bulbs are carried out away from the secondary centers. The primordium hippocampi extends out some distance as the roof of the lateral ventricle, invades the lamina supraneuroporica as a great gray mass in which the pallial commissures lie and extends along the upper border of the wall of the unpaired ventricle (figs. 5, 6 and 7). The wall of the telencephalon medium is largely made up of a somatic correlation area, the beginning of the general cortex. That this area is wrongly assigned to the diencephalon by Edinger and others is indicated by the attachment of the velum just in front of the ganglion habenulæ (figs. 5 and 6).

The primordium hippocampi occupies the massive roof and is separated from the medial olfactory nuclei by the external neuroporic recess and a cell-free zone, the *zona limitans* (fig. 7). It receives from in front fibers of the olfactory tract (secondary) and direct and crossed fibers from both medial and lateral olfactory nuclei (tertiary fibers). The crossed fibers decussate in the lamina supraneuroporica where it is greatly thickened by the primordium hippocampi itself. Also, a large tractus pallii comes up from the hypothalamus to the primordium hippocampi as in cyclostomes. A part of this tract is uncrossed, a part crosses in the

FIG. 7. *Scyllium stellare*, schematic transverse section of the telencephalon through approximately the line *a-a* of Fig. 6. The lateral ventricle is reconstructed from a number of sections before and behind this line.

postoptic decussations. The primordia of the two sides are connected by true commissural fibers in the anterior pallial commissure (fig. 8). Finally, that portion of the primordium which extends along the telencephalon medium is traversed by great numbers of fine fibers which cross in the superior commissure and constitute a true posterior pallial commissure of the hippocampal primordia (fig. 8).

From the primordium hippocampi fibers collect forward and descend through the medio-rostral and ventral wall between the lateral ventricles and go to the hypothalamus. They form definite bundles which are undoubtedly homologous with the fornix (fig. 8).

The existence of a somatic correlation center in the telencephalon is indicated by the presence of large numbers of fibers in the basal bundle which connect this area with the centers of the lemniscus and of the optic tracts in the thalamus. A descending path extending from this somatic area to the ventral part of the thalamus and to the motor centers forms part of the basal bundle described many years ago by Edinger. From the somatic area

FIG. 8. Scheme of fiber tracts connected with the primordium hippocampi in selachians, based on *Scyllium*.

arises a large part of the fibers going to the nucleus habenulæ. These fibers may be given the name *tractus tæniæ* and are to be sharply distinguished from the fibers arising from olfactory centers, which should be called *tractus olfacto-habenularis*. Special tracts serving for correlation between somatic and olfactory centers will be described in a later paper. The somatic areas of the two sides are connected by a true commissure which crosses in the lamina supra-neuroporica above (ectal to) the commissura hippocampi (figs. 7 and 9). This commissure has the essential morphological and functional relations of a *corpus callosum*.

FIG. 9. Scheme of fiber tracts of the primordial somatic cortex in selachians, based on *Scyllium*. The ascending and descending fibers between thalamus and somatic cortical area occupy the middle of the figure and are not lettered.

The *nervus terminalis* enters the forebrain in selachians at a point immediately below and lateral to the neuroporic recess, and its fibers are directed toward the somatic area. This is the true or internal origin of the nerve as far as now understood. In some forms the nerve reaches this point by entering the dorsal surface and running down in the walls of the external neuroporic recess. In other forms it enters below and runs up to the same point. This difference is due to the secondary fusion of the medial olfactory regions which, apparently, has in some cases proceeded from below upward and pushed the nerve to the upper surface, in other cases proceeded from above downward and pushed the nerve to the lower surface (fig. 6).

FIG. 10. *Amia calva*, schematic transverse section through the anterior commissure. The crossed olfacto-cortical tracts are shown above, the true commissural fibers of the primordium hippocampi below. The letters *f.i.* mark the sulcus (Monroi) which indicates the line of evagination and the position of the foramen in typical evaginated brains.

GANOIDS AND TELEOSTS

In these forms the evagination of lateral lobes has proceeded only so far as to form the olfactory bulbs which enclose lateral ventricles. All the rest of the forebrain constitutes a telencephalon medium whose walls are more or less everted as has been well described by Mrs. Gage and by several later writers (fig. 10). In the ventricular surface of each wall can usually be seen a sulcus Monroi which leads forward to the lateral ventricle (figs. 2, 10 and 11).

This sulcus marks the line of evagination and the position of the foramen interventriculare in those forms whose forebrains are evaginated.

Above this sulcus the ventricular surface of the lateral wall is covered to a variable depth by the peculiar tissue which constitutes the primordium hippocampi. Laterally this body is separated from the somatic correlation area by a sulcus somewhat below the line of the tænia (fig. 10).

FIG. 11. Sketches for comparison of everted and evaginated types of forebrain. A, transverse section of forebrain of young *Amia* (25 mm.); B, diagram to show the translocation of parts that would take place in the evagination of such a brain. The course of the commissure is indicated by continuous lines. In B, the broken lines show the actual course of the "commissura hippocampi" behind the lateral ventricle in amphibians.

From in front the primordium hippocampi receives olfactory fibers of the second and third orders, many of which decussate in the anterior commissure complex. From behind, the large tractus pallii comes up from the hypothalamus, partly decussating in the anterior commissure (fig. 12). The hippocampal primordium although very different in form, has essentially the same relations as in cyclostomes and selachians.

The somatic area receives fibers from the lemniscus center in the thalamus, and probably from the tectum mesencephali (fig.

12). Fibers ascending from the lateral geniculate bodies have not yet been seen. In these forms also there is a clear distinction between the tractus tæniæ and the tractus olfacto-habenularis.

Ganoids and teleosts possess no true anterior pallial commissure. The fibers connecting both the hippocampal and the somatic cortical primordia pass by way of the anterior commissure complex. A detailed discussion of this fact and its connection must be

FIG. 12. Scheme of fiber tracts connected with the primordial cortex of the sturgeon.

postponed, but it should be held in mind that the commissures of the cortical areas cross beneath the unpaired ventricle, then pass lateral, external and caudal to the foramina and lateral ventricles and so into the everted areas which correspond more or less completely to the roof of brains of the evaginated type (figs. 10 and 11).

AMPHIBIANS

The evagination of the lateral lobes has gone much farther and is almost complete. The elongation of the forebrain has taken place not at the olfactory peduncle as in many selachians and teleosts, nor at the telencephalon medium as in some selachians and especially in *Chimæra*, but in the region between the foramen interventriculare and the olfactory peduncle. The primordium hippocampi has been nearly all evaginated and forms the upper part of the medial wall of the vesicular lateral lobe, together with an undetermined part of the dorsal wall. In urodeles a small part of it remains in the dorsal part of the wall of the un-

FIG. 13. *Necturus maculatus*, transverse section through the foramen interventriculare. The section is seen from the caudal surface and the commissure related to the hippocampus is represented as passing up lateral to the foramen interventriculare and caudal to the lateral ventricle to reach the hippocampus.

paired ventricle as in cyclostomes. A zona limitans separates the hippocampal area from the medial olfactory area, which occupies the lower part of the medial wall ("septum") and extends into the floor of the unpaired ventricle where it forms the "precommissural body" of Elliot Smith (fig. 14).

The evagination has involved a greater or less part of the somatic area and has been prolonged backward to form a posterior pole. The relations of the hippocampal and somatic areas in this pole are still in doubt.

A partial study of the fiber tracts in several amphibians has shown in connection with the primordium hippocampi fibers from the olfactory centers, an ascending tractus pallii from the hypothalamus and a fornix descending to the hypothalamus as in selachians. The lateral forebrain bundle contains many ascending somatic sensory fibers which end in the lateral parts of the hemisphere. According to Herrick there are present in the frog fibers from the lemniscus centers in the thalamus, optic radiations and auditory radiations. The amphibian brain seems to the writer to present a high degree of complexity and specialization of

FIG. 14. *Necturus*, sketch of right half of forebrain seen from the medial surface. The medial olfactory nucleus, precommissural body and bed of the commissures are shaded by short oblique lines. A part of the precommissural body extends up over the foramen interventriculare. The commissure of the primordium hippocampi runs up behind the foramen interventriculare (compare fig. 15).

structure based upon an apparently simple and primitive arrangement of the neurone-bodies in a central gray. More detailed studies of the fiber connections are necessary to enable us to determine the extent and boundaries of the several functional areas, especially the hippocampal and somatic cortical areas and the pyriform lobe.

The forebrain commissures of amphibians closely resemble those of ganoids and teleosts. In the lamina terminalis are found an anterior commissure chiefly related to the lateral basal bundle and the somatic correlation areas, and a so-called hippocampal commissure (fig. 13). The latter crosses beneath the unpaired ven-

tricle, rises lateral and caudal to the interventricular foramen and bends forward over the proximal part of the lateral ventricle to enter the medio-dorsal or hippocampal area. The disposition of this commissure stands in sharp contrast with that of selachians and of reptiles and mammals and agrees in all essentials with that of ganoids and teleosts. When Osborn ('88) interpreted this commissure as the corpus callosum he recognized the great difficulty presented by its position. The writer has pointed out ('02, '06) that this commissure can not be compared morphologically with the psalterium of mammals. The neglect of this by all recent students of the amphibian brain, and especially the failure to observe the difference in position of the commissures in amphibians and reptiles must lead to confused ideas of forebrain morphology. Compare figs. 14 and 15.

From the posterior pole of the hemisphere a large posterior pallial commissure accompanies the tractus tæniæ to cross in the superior commissure as in selachians.

REPTILES AND MAMMALS

From the work of Elliot Smith, His, Ziehen, Zuckerkandl and others the general relations in the reptilian and mammalian brain are well understood. The hippocampal area occupies the medio-dorsal region of the hemisphere in reptiles and in the series of mammals is modified, owing to the growth of the general cortex and corpus callosum, until in man the only well developed hippocampal formation lies between the splenium of the corpus callosum and the tip of the temporal lobe (uncus). From the somatic area of fishes and amphibians the general cortex has developed between the hippocampus dorso-medially and the pyriform lobe laterally. A part of the somatic area surrounding the lateral basal bundle has differentiated into the corpus striatum through which the enlarged lateral basal bundle runs as the internal capsule.

The disposition of the commissures is of great importance for an understanding of the comparative morphology of the telencephalon. The anterior commissure serves to connect the olfactory

areas and probably contains somatic elements in addition. In mammals two pallial commissures are present, the commissura hippocampi and the corpus callosum; in reptiles the corpus callosum is not yet certainly known. A posterior pallial commissure is present in some reptiles but is unknown in mammals.

In reptiles the hippocampal commissure crosses rostral to the unpaired ventricle. Its arms rise up in front of the interventricular foramina in the medial walls of the lateral ventricles, to enter the hippocampal area directly (fig. 15). In lower mammals the hippocampal commissure has the same position as in reptiles and in higher mammals is carried up over the third ventricle by the upward and backward growth of the hemispheres.

FIG. 15. Sketch of the right half of the forebrain of a reptile to show the relations of the hippocampus and of its commissure. The commissure goes up in the medial wall in front of the foramen interventriculare.

An interesting question arises concerning the position of this commissure with reference to the neuroporic recess. This question does not involve the main facts regarding the history of the hippocampus and its commissure in mammals as set forth by Elliot Smith and others, nor does it affect the question at issue between Smith and His as to the primary or secondary character of the fusion which constitutes the "commissure bed." The question is whether the commissure lies in the lamina terminalis (*below* the neuroporic recess) or in the lamina supraneuroporica (*above* the

neuroporic recess). In reptiles the hippocampal commissure lies more or less close to the anterior commissure so that in late embryos and adults the relations of the neuroporic recess are obscured. In lizards it is probably represented by the recessus inferior of Elliot Smith (fig. 16). The early development shows that the neuroporic recess is situated close in front of the anterior commissure, that above the recess is a thickened part of the lamina supraneuroporica related to the hemispheres; the remainder of this lamina is a membranous tela in which appears the paraphysis just in front of the velum transversum (fig. 17). As the hemispheres

FIG. 16. A portion of a transverse section through the brain of a monitor (*Hydrosaurus*). From G. Elliot Smith. In the figure to the left the line *x-y* shows the plane of the section. *alv.*, alveus; *c.f.*, columna fornicis; *fasc.*, fasciculus marginalis; *hip.*, hippocampus; *para.*, paraterminal body; *rec. i.*, recessus inferior; *rec. s.*, recessus superior; *c. d.*, hippocampal commissure; *c. v.*, anterior commissure.

develop the recessus neuroporicus is reduced or obliterated and the hippocampal commissure comes to lie close to the anterior commissure.

In mammals the neuroporic recess is a prominent pit in front of the anterior commissure in early stages, but the growth of the hemispheres and commissure-bed reduces it to a shallow pit in the same position (figs. 18 and 19). The thickened lamina which constitutes or contains the bed of the hippocampal commissure is the lamina supraneuroporica and extends laterally into the hemispheres as in reptiles. When the hippocampal commissure ap-

pears it is widely enough separated from the anterior commissure so that there can be no doubt that it lies above the neuroporic recess in the lamina supraneuroporica (figs. 18 and 19).

In reptiles and mammals the commissura hippocampi and corpus callosum are said to be embedded in the precommissural body (Elliot Smith and others). This precommissural body is formed by the invasion of the lamina terminalis by the medial olfactory nuclei or by the secondary fusion of these nuclei. Such a fusion is most extensive in selachians where the nuclei are very volumi-

FIG. 17. Median sagittal section of the brain of a turtle embryo at the time of formation of the paraphysis. The broken line marks the di-telencephalic boundary. At *m* is the caudal margin of the nervous part of the lamina supraneuroporica. The tela behind this is not only thin but differs histologically from the lamina supraneuroporica. The neuroporic recess has been traced in earlier stages and undoubtedly lies between the parts identified in this figure as the anterior commissure and the lamina supraneuroporica.

nous. In some mammals also this fused body is very large. So far as my observations go the corpus callosum in mammals is situated along the line of the zona limitans, while the hippocampal commissure is involved or enwrapped to a variable extent in the precommissural body. I can harmonize this with the condition in selachians and with the facts of development in mammals above cited only on the supposition that the precommissural body has secondarily pushed up into the region of the lamina supraneuroporica, probably following along the system of olfacto-hippocampal fibers.

The bearing of these facts upon the phylogeny of the cortex and its commissures is seen when the brain of the mammalian embryo is compared with the selachian brain (fig. 20). The pallial areas in selachians, reptiles and mammals meet in the lamina supraneuroporica which is thickened by invading gray matter and serves for the passage of the hippocampal commissure and corpus callosum. The cyclostomes present the same condition, but with simpler commissures. The ganoids, teleosts and amphibians present a very

FIG. 18. Median sagittal sections of the forebrain in cat embryos to show the relations of the commissures to the recessus neuroporicus. To the left a 12 mm. embryo (Minot collection No. 400, slide F., sec. 3/6); to the right, a 31 mm. embryo (Minot collection No. 527, slide Bk, sec. 1/3). The section of the 12 mm. stage is slightly oblique. The paraphysis is drawn in dotted outline as it appears in adjacent sections. The slight thickening at *l. s.*, shows that the lamina supraneuroporica is passing over into the medial wall of the hemisphere. The point *m* corresponds to the point so lettered in the turtle embryo. This is about the point at which the recesses neuroporicus has been placed by previous authors. The nearness of this to the paraphysis is sufficient evidence that the lamina terminalis does not extend up to this point. The figures are from free-hand sketches but the relations are essentially correct.

different condition, in which the fibers analogous to the hippocampal commissure and corpus callosum, so far as such fibers exist, run with the anterior commissure in the lamina terminalis. It seems probable that the pallial commissures maintain a true pallial position in cyclostomes, selachians, reptiles, birds and mammals (and possibly dipnoans), while in ganoids, teleosts and

amphibians they have a peculiar disposition the origin of which requires to be explained.

The features in the author's account of the evolution of the cerebral cortex which are distinctive are the following:

1. The telencephalon possesses an unpaired ventricle whose walls constitute a very important part of the forebrain (telencephalon medium).
2. The telencephalon of primitive vertebrates possesses visceral and somatic correlating centers which are the primordia of the hippocampal formation and general cortex respectively.

FIG. 19. Sagittal sections of the forebrain in rabbit embryos to show the relations of the commissures. To the left an embryo of 14 days, 10.5 mm. (Minot collection No. 156); to the right an embryo of 20 days, 29 mm. (Minot collection no. 171.) Drawn as fig. 18.

These correlating centers are equally old (unless the somatic be the older) and the terms archipallium and neopallium are inappropriate. In their stead should be used some such terms as visceral pallium and somatic pallium.

3. These cortical primordia are at first not involved in the evagination of lateral lobes, but lie in the wall of the unpaired ventricle. They are gradually evaginated into the lateral lobes in selachians, dipnoans, amphibians and reptiles.

4. The primordium of the visceral cortex is defined by (1) the entrance of olfactory fibers of the second and third orders, (2) the

entrance of an ascending tract from the hypothalamus of general visceral or gustatory function or both, (3) the possession of a true commissure in the lamina supraneuroporica and another in the superior commissure (anterior and posterior pallial commissures), (4) the presence of true fornix, and by (5) peculiar histological structure. With regard to the commissures, the cyclostomes require further investigation, the ganoids, teleosts and amphibians present a peculiar modification of the anterior pallial commissure and the mammals apparently lack a posterior pallial commissure.

FIG. 20. Sketches for comparison of the human embryonic forebrain with that of the selachian. On the left a sagittal section of the forebrain of *Squalus acanthias* of about 70 mm., from a preparation in the Minot collection. On the right a median sagittal section of the forebrain of a human embryo (Minot collection no. 181, slide A1. sec. 1/3). Drawn as fig. 18.

5. The primordium of the somatic cortex is defined by (1) the entrance of ascending fibers from the thalamus (and tectum mesencephali) chiefly carrying cutaneous, visual and muscle-sense impulses (exteroceptive and proprioceptive centers), (2) giving origin to descending fibers to the thalamus and probably medulla oblongata and spinal cord (Van Gehuchten and others), and (3) the possession of a true pallial commissure (corpus callosum) in the lamina supraneuroporica except ganoids, teleosts, and amphibians. The writer does not accept Edinger's hypothesis that the oral sense

centers in the telencephalon play the chief rôle in the origin of the cerebral cortex. The area recognized by the writer as the primordium of the somatic cortex has been assigned by all recent authors to the diencephalon and is wholly distinct from any center which Edinger has suggested for his oral sense. A cutaneous nerve of the first head segment (*nervus terminalis*) probably entered the primordium of the general cortex, but this is not an *essential* part of the account here given.

I wish to express my best thanks to Dr. C. S. Minot for the opportunity to study his valuable collection of mammalian embryos.