THE DEVELOPMENT OF THE DORSAL VENTRICULAR RIDGE IN TURTLES¹

J. B. JOHNSTON

University of Minnesota

TWENTY-SEVEN FIGURES

In the adult turtle (Johnston, '15 b) the large ridge projecting into the ventricle from the lateral wall of the hemisphere has strong fiber connections with the cerebral peduncle and has obvious close relations with the cortical layers of the pallium in the caudal pole. Indeed, in its caudal part this ridge appears to be a fold of the whole thickness of the brain wall and is marked externally by the 'amygdaloid fissure.' Here the cell layers of the general pallium turn in to become continuous with the cell masses of the ridge. It is evident from these facts that the relations of the dorsal ventricular ridge are chiefly with the general pallium. Its position lateral and dorsal to both the caudate and lentiform nuclei shows that it does not belong to the corpus striatum. Its independence from other cell masses in its rostral part gives one the impression (from the study of adult material alone), that the ridge has been formed by infolding from the caudal region ('15 b, p. 417).

The origin of this ridge in the embryo should throw light not only on its relations in the turtle but also on its significance in the evolution of the mammalian brain. I am able to give the main outlines of the development on the basis of a series of early embryos of *Chelydra serpentina*, for which I am indebted to Dr. C. E. Johnson of this University; and of sections of 17, 20, and 28 mm. embryos of *Chrysemys*, belonging to the Anatomical Laboratory of Washington University for the loan of which I am indebted to Dr. Edwin A. Baumgartner.

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The material in both cases was beautifully sectioned and stained. The brains of freshwater turtles are so similar that the younger stages of *Chelydra* can be readily compared with the later stages of *Chrysemys* for the rather general purposes of this study.

AREAS OF PROLIFERATION IN THE EARLY EMBRYO IN RELATION
TO CELL MASSES OF THE ADULT BRAIN

Broadly speaking, three periods are to be recognized in the development of cell masses in the telencephalon: a period of evagination of the hemispheres and formation of indifferent cells by mitosis of the germinal cells; a period of form changes and further proliferation of cells in which the successive formation of functionally independent cell masses is noticeable; and a period during which the growth of fiber bundles and other factors bring about the definitive form of the adult cell masses.

In the first period the wall of the telencephalon consists of a deep layer of spongioblasts and dividing germinal cells, a thick layer of indifferent cells and a superficial clear layer or marginal veil of very varying thickness. The thickest part of the marginal veil forms the floor of the groove along the lower border of the hemisphere, at its junction with the brain stem. This is the course of the future lateral forebrain bundle or *crus cerebri*. The indifferent cells form a continuous layer with no indication of individual masses.

The second period begins with the appearance of independent cell masses separated by cell-free zones which show in sections as clear lines or areas. Such cell-free zones in adult brains have been commonly regarded as boundary lines between individual cell masses which are presumed to have different functions; i.e., centers or nuclei. Similar cell-free zones in the brains of lower vertebrates have been used in recent years as landmarks between important morphological regions, as the pallial and basal areas. The writer has pointed out the need of caution in interpreting these zones in this connection ('13 b, p. 382). It is now to be noted that the formation of individual masses of cells is dependent upon the proliferation of cells from different regions of the germinal cell layer and upon the proliferation

of cells at successive periods of development. Thus the proliferation of cells in the dorsal wall gives rise to pallium, that in the basal wall gives rise to various olfactory centers, corpus striatum, etc. Also, certain centers owe their origin to the proliferation of cells in an early stage, other centers to proliferation in later stages. The former come to lie superficial to the latter and the two are separated by cell-free zones. A further factor is the shifting or spreading of cell masses, whether due to cell-migration or to mechanical forces. These several factors must be taken into account in any attempt to use the embryological method in the study of the significance of cell-grouping in the brain.

CHELYDRA SERPENTINA

In the oldest Chelydra embryo studied, it is possible to recognize several of the important cell masses and fiber bundles of the telencephalon and in part the boundary lines between pallial and basal areas. Examination of the model (figs. 1, 2) and of sections (figs. 6 to 14) shows that the telencephalon and dien-cephalon are narrow from side to side and high dorso-ventrally. The hemisphere is a simple sac which projects much farther rostrad than caudad. The interventricular foramen is still very large. Behind it, the thin wall which represents the choroid plexus extends nearly half way to the caudal pole. This stage illustrates very clearly, both in its general form and its internal structure, how much the rostral pole of the hemisphere precedes the caudal pole in development. The outer surface of the brain shows few of the landmarks which are seen in later embryos and adults. The stem-hemisphere sulcus is of course the most prominent. The olfactory peduncle is not yet formed, but the broad depression on the lateral surface may represent the beginning of constriction. The fissura prima and diagonal band are recognizable at the medio-basal angle in front of the preoptic recess. There is a shallow furrow over the rostral part of the foramen which may be the beginning of the sulcus fimbrio-dentatus.

The ventricle shows a very sharp ventral groove leading forward from the foramen and much deepened in the region of the future tuberculum olfactorium. The middle ventricular groove is clearly marked in the region rostral to the foramen, while the dorsal groove has not yet appeared.

In spite of the simple form of this brain, the internal structure shows considerable advance in differentiation.

The sections illustrated in figures 6 to 14 can be understood best by beginning with that which passes through the rostral border of the foramen interventriculare (fig. 9). In the medial wall above the foramen are recognized the primordium hippocampi and the fimbria, one of the early fiber tracts to be formed in the embryo. The dorsal wall is occupied by pallium, the medial portion by hippocampal, the lateral portion by general pallium. In the lateral wall the pallium seems to be limited by a ventricular groove and by a cell-free space. This boundary line strongly reminds one of the lateral zona limitans of the selachian and frog brains (Johnston, '11 a). The later embryos show this groove to be the middle ventricular groove of the adult brain and the clear area becomes the cell-free zone separating the dorsal ventricular ridge and the nucleus lentiformis in the adult. In the lower half of the lateral wall the following structures are seen in the figure: an active proliferation which gives rise to the nucleus lentiformis, the nucleus caudatus, the lateral and medial forebrain bundles, the anterior commissure bundle, the fiber layer of the diagonal band, and the lateral olfactory area. Although I have not sufficient stages to enable me to follow the history of these structures, there is evidence that the superficial cell layer which represents the lateral olfactory nucleus has been derived from the layers of indifferent cells in the early embryo and that the mass of the caudate nucleus represents a later proliferation. The embryo shows clearly that the lentiform nucleus is beginning to form when the caudate is already completely formed or nearly so. As the other sections are studied it will become evident that the lentiform nucleus is formed by a proliferation distinctly dorsal to the caudate and that the changes in later development bring

it into a position lateral to the caudate. There is some indication of the superficial layer of the olfactory area spreading upward beyond the middle ventricular groove (at the point marked *l.pyr*).

Passing caudad from this level, in the next section drawn (fig. 8) the same structures are to be seen in the lateral wall. The middle ventricular groove has almost disappeared, however, and the proliferating area for the lentiform nucleus is much smaller. The next section drawn (fig. 7) is the last one in which the lentiform proliferation can be recognized and with it the locus of the pallial border. In the lower part of the hemisphere the lateral olfactory area is represented by a large collection of cells closely related to the caudate nucleus and the diagonal band. This is the nucleus of the lateral olfactory tract and the next section shows the close relation of both this and the diagonal band to the stria medullaris. Caudal to this the nucleus of the lateral olfactory tract soon disappears and the hemisphere wall presents the appearance of an undifferentiated pallium, except for the fimbria and the thin choroidal area in the medial wall.

The next section rostrad from the one first described passes through the anterior commissure (fig. 10). The lentiform proliferation appears larger, the diagonal band fibers approach those of the olfacto-hypothalamic system. In figures 9, 10, and those of sections farther rostrad, one of the most noteworthy features is the mass of cells proliferating from the deep layers of the pallium. The medial border of the pallium does not show active proliferation but in the lateral three-fourths many new cells are forming and these appear to be streaming laterad into the thick wall just dorsal to the middle ventricular groove. Indeed the proliferation and streaming of these cells is the active cause for the thickening of this part of the wall and the formation of the middle ventricular groove. Further thickening of this part of the wall deepens this groove and produces the dorsal ventricular groove at the point indicated in figure 9.

In figures 9 to 12 appear important relations of the dorsal border of the olfactory area to the pallium. Here it is quite

clear that the superficial layer of cells of the olfactory area extends up on the outer surface of the pallium and that it is accompanied by a special bundle of fibers. The crowding of cells in this stage is such that it is impossible to determine whether the pyriform lobe cells have spread or migrated up from the lateral surface in the basal region or have been formed here by the proliferation which at this stage is giving rise to the pallium. Farther caudad and in later stages the relations are such as to make the former appear more probable. The cells of the pyriform lobe probably all come from the layer of indifferent cells seen in earlier stages and formed by proliferation in the lateral and basal region before the pallial proliferation seen in this stage began. Pallium and pyriform lobe are still visible in a section (fig. 14) through the peduncle in which the olfactory formation appears in the dorsal wall. The olfactory formation extends far back on the dorsal surface, as is already well known.

CHRYSEMYS

Models were made of the 17 mm. and 28 mm. stages. Most of the chief landmarks of the adult brain are already visible in the 17 mm. embryo (figs. 3, 4, 15, 16, 17). The caudal pole still lags behind the rostral portion in development. The caudal pole projects much farther back than in the oldest *Chelydra* embryo and in the 28 mm. stage the olfactory area (lobus pyriformis) extends relatively farther back than in the 17 mm. stage. The tuberculum olfactorium is well developed and the ventral groove of the ventricle dips deep into it. The middle ventricular groove (fig. 4 and sections) is very sharp and deep in the middle part of the brain and stops abruptly just caudal to the level of the foramen interventriculare. The dorsal ventricular groove appears in the 17 mm. embryo (figs. 4, 17) as a slight groove in the lateral wall some distance from the medio-dorsal angle of the ventricle.

Three sections caudal to the foramen are drawn from the 17 mm. embryo and nine sections from various levels of the 28 mm. embryo. The internal differentiation has already progressed so far in the 17 mm. embryo that it will be unnecessary

to speak of it separately. In both stages many features of the sections can readily be compared with the structures seen in corresponding sections of the adult brain. For this purpose the reader should consult the description of the cell masses in the brain of *Cistudo* in this Journal for October, 1915. The necessary description of individual sections is given in connection with the figures. Here I shall take up the relationships of the lateral margin of the pallium and the dorsal ventricular ridge.

Corpus striatum and lateral olfactory area. In the younger embryos the loosely arranged cells of the lateral olfactory centers cover the outer surface of the caudate and lentiform nuclei and form a continuous layer over the lateral surface of the hemisphere (except dorso-caudally). This is shown in figures 7 to 12, and this interpretation is given to the models. In the 28 mm. embryo there is a small area opposite the foramen in which the striatum and the crus bundle contained in it come to the surface (fig. 21) and the olfactory centers form the pyriform lobe above and the diagonal band below. This small area is painted blue in the model and appears white in figure 5. Sections show that it is the elbow of the crus, with certain large cells contained in it ('15 b, p. 405), which comes to the surface here. This is presumably due to the rapid growth of both ascending and descending fibers in the crus. The crowding thus produced leads to the shifting of the cells of the olfactory center upward and downward. This process must go much further in later development until the large striatal area is left exposed in the adult. The embryonic history thus seems to support very clearly the hypothesis ('15 b, p. 428, 429) that the exposed striatal area in the turtle had been covered at an earlier stage of evolution by the lateral olfactory area.

Relations of pyriform lobe and pallial margin. In the caudal half of the hemisphere the pyriform lobe forms a layer external to the corpus striatum and extends up to a thin edge superficial to the dorsal ventricular ridge and the margin of the pallium. This overlapping of the pallial margin by the pyriform lobe persists in the adult. At about the level of the interventricular

foramen the pyriform lobe begins to extend higher on the lateral surface. At the same time thickening of the lateral border of the pallium moves dorsally, becomes crowded and folded on itself and sinks in, forming a projection into the ventricle (figs. 22 to 25). These changes take place rapidly from behind forward so that in thirty or forty sections of 10 microns the place occupied by the thick border of the pallium comes to be taken by the pyriform lobe. From this point forward the pyriform lobe forms a characteristic ridge filled with a dense layer of cells, very much as in the adult.

Origin of dorsal ventricular ridge. In the *Chelydra* embryo above described the dorsal part of the lateral wall is thickened by cells coming from a proliferating area in the dorso-lateral wall. The groove which bounds this thickening was identified with the middle ventricular groove of the adult. In the older embryos of *Chysemys* the groove is readily identified but has been very greatly deepened by further thickening of the mass just above it. Likewise the thickening of this mass has produced a groove above it, the dorsal ventricular groove. The thick mass, then, is the dorsal ventricular ridge and in earlier stages it is indistinguishable from the dorsal pallium. In the caudal part of the hemisphere of the older embryos the relations of the dorsal ventricular ridge are not essentially changed from those seen in the *Chelydra* embryo. Caudal to the level of the stria medullaris (figs. 18, 19) this ridge bulges into the ventricle and is covered outside and below by the thick mass of the nucleus of the lateral olfactory tract. In the caudal pole the ridge merges gradually with the general pallium caudal to the level at which the pyriform lobe ends. In the rostral part of the hemisphere (figs. 22, 23) the dorsal ridge has become practically independent of the pallial thickening, very much as it is in the adult. From these embryos it is quite clear that the dorsal ventricular ridge arises as a thickening of the lateral border of the pallium and that its continued growth causes it to project into the ventricle and produces the middle and dorsal ventricular grooves. In the 28 mm. embryo the mass of cells which in the adult was called the core-nucleus of the ridge

is clearly recognizable in the rostral part, back to the level of the caudal border of the foramen interventriculare.

Between the pallial thickening and the cells of the dorsal ventricular ridge appears in the sections a clear space filled by fibers. In the caudal part of the hemisphere, where the dorsal ventricular groove is already formed, this bundle of fibers is seen to hold the same position as an important bundle in the adult. In the adult many fibers from the crus enter this bundle or, more probably, pass through it on their way to the pallium. Here in the embryo the crus is not yet sufficiently developed to enable one to trace it up through the striatum to this level. The strong development at this stage of the bundle here mentioned indicates that it is composed chiefly of fibers connecting parts of the hemisphere; an association bundle, in other words.

Relations of dorsal ventricular ridge to basal structures. In the rostral part of the hemisphere the ridge is from the first clearly marked off from the striatum below by the middle groove and by a prominent cell-free zone. In later embryos this cell-free zone becomes compressed into a narrower line as seen in section and scattering cells are found in it. There is, however, always a clear boundary between the ridge and the developing lentiform nucleus. In section the cell-free zone inclines dorsad toward the lateral surface and passes above the lateral olfactory area. In the rostral part, where the pyriform lobe crowds far dorsal this limiting zone is bent into a semicircular or U-shaped line (figs. 23 to 27). When the writer first studied the adult turtle brain he found it impossible to establish a direct comparison between the lateral zona limitans of the selachian, frog and other simpler vertebrates, and either of the cell-free zones seen in the lateral wall of the turtle brain. It is now evident that the clear zone which in the adult brain passes from a point near the middle ventricular groove toward the lateral surface and then bends dorsad to reach the surface in the sulcus rhinalis above the lobus pyriformis, is the zona limitans of the embryo and corresponds to the zona limitans lateralis in the selachian and frog. (See Johnston, '15 b, figs. 19 to 22 and compare with '11 a, fig. 75). Since the relations of the pyri-

form lobe, corpus striatum and pallium in the turtle are readily comparable with those in the mammal, the identification of the lateral zona limitans in the turtle completes the history of this important landmark throughout the series of vertebrates. The boundary lines between the pallial and basal portions of the hemisphere are now clear in both medial and lateral walls in fishes, amphibians, reptiles and mammals (Johnston, '11 a, '13 b, '15 b).

The relation of the dorsal ventricular ridge to the amygdaloid complex requires further comparative study. In the adult, it will be remembered, the caudal part of this ridge is separated from the rest by a broad shallow groove which continues in the general direction of the deep middle ventricular groove ('15 b, figs. 4 and 10). This caudal portion of the ridge is made up of the medial amygdaloid nucleus and of an apparent infolding of the general pallium. Even in the oldest of these embryos the dorsal ventricular ridge extends into the tip of the caudal pole as a simple thickening of the general pallium. It seems probable, although the evidence is not sufficient for a definite conclusion, that the caudal portion of the ridge including the large-celled medial amygdaloid nucleus is formed from this thickening of general pallium.

For the photographs of the models I am indebted to Dr. W. F. Allen of the University of Oregon.

LITERATURE CITED

- JOHNSTON, J. B. 1911 a The telencephalon of selachians. *Jour. Comp. Neur.*, vol. 21.
1913 b The morphology of the septum, hippocampus, and pallial commissures in reptiles and mammals. *Jour. Comp. Neur.*, vol. 23.
1915 b The cell masses in the forebrain of the turtle, *Cistudo carolina*. *Jour. Comp. Neur.*, vol. 25.

FIGURES

ABBREVIATIONS

<i>a.p.</i> , area parolfactoria	<i>n.c.</i> , nucleus caudatus
<i>b.o.</i> , bulbus olfactorius	<i>n.d.b.</i> , nucleus of the diagonal band
<i>c.a.</i> , commissura anterior	<i>n.l.</i> , nucleus lentiformis
<i>c.h.</i> , commissura hippocampi	<i>n.o.</i> , nervus olfactorius
<i>ch. op.</i> , chiasma opticum	<i>n.rot.</i> , nucleus rotundus
<i>c.p.a.</i> , commissura pallii anterior	<i>n.tr.olf.lat.</i> , nucleus of the lateral ol-
<i>crus</i> , crus cerebri or lateral forebrain bundle	factory tract
<i>c.st.</i> , corpus striatum	<i>pa.</i> , pallium
<i>d.b.</i> , diagonal band of Broca	<i>pa.th.</i> , pallial thickening
<i>d.v.r.</i> , dorsal ventricular ridge	<i>p.h.</i> , primordium hippocampi
<i>fi.</i> , fimbria	<i>p.o.</i> , pedunculus olfactorius
<i>f.o.</i> , formatio olfactoria	<i>r.p.</i> , recessus praeopticus
<i>f.p.</i> , fissura prima	<i>r.s.</i> , recessus superior
<i>for.i.</i> , foramen interventriculare	<i>s.f-d.</i> , sulcus fimbrio-dentatus
<i>f.rh.</i> , fissura rhinalis	<i>s.m.</i> , stria medullaris
<i>g.p.</i> , general pallium	<i>s.v.d.</i> , dorsal ventricular sulcus
<i>g.s.</i> , gyrus subcallosus	<i>s.v.m.</i> , middle ventricular sulcus
<i>h.</i> , hippocampus	<i>s.v.v.</i> , ventral ventricular sulcus
<i>hy.</i> , hypothalamus	<i>thal.</i> , thalamus
<i>l. pyr.</i> , lobus pyriformis	<i>t.o.</i> , tuberculum olfactorium
<i>l.t.</i> , lamina terminalis	<i>tr.olf-hy.</i> , tractus olfacto-hypothalam-
<i>m.fb.bdl.</i> , medial forebrain bundle	icus
	<i>tr.op.</i> , tractus opticus

Fig. 1. *Chelydra serpentina*. The size of this embryo is indicated by the owner by the words '8.5 mm. carapace.' Lateral view of a model of the right hemisphere. Description in the text.

This and the following models have been merely rubbed with a blunt instrument to smooth the surface. The external surface has been painted so that the olfactory centers and hippocampus appear dark and the general pallium light. The diencephalon has been left with the gray color of the modelling paper and the ventricular surface of the hemisphere has had no treatment whatever. The lamina terminalis and line of attachment of the choroid plexus have been painted white. All the models were made at a magnification of 50 diameters and are reduced one-third in reproduction.

Fig. 2 Medial view of the model shown in figure 1. Description in the text.

Fig. 3 *Chrysemys* embryo of 17 mm. Medial view of a model of the right hemisphere. The narrowing of the interventricular foramen seems to have taken place from above downward on account of the expansion of the hippocampus and general pallium. The white area labelled *c.h.*, is the cut surface of the primordium hippocampi in the median plane. The thin portion of the medial hemisphere wall which will form the choroid fissure and plexus is bounded by a white line.

Fig. 4 Same model as figure 3, with the thalamus, hippocampus and primordium hippocampi removed. The lateral wall of the ventricle shows the dorsal ridge bounded below by the deep middle ventricular groove as described in the text. The dorsal groove is shallow. There is no evident boundary between the dorsal ridge and the pallial thickening at the rostral end.

Fig. 5 *Chrysemys*, 28 mm. Lateral view of a model of the right hemisphere. Note the great elongation of the pyriform lobe in the caudal pole as compared with the condition in figure 1. With regard to the exposure of the corpus striatum on the lateral surface, compare figures 1 and 5 with the figures in '15 b.

Figs. 6 to 14 Transverse sections through the right hemisphere of the *Chelydra* embryo illustrated in figures 1 and 2.

Fig. 6 Section just caudal to the foramen interventriculare. This is the most caudal section in which the nucleus caudatus can be recognized and here it practically fuses with the nucleus of the lateral olfactory tract. Both are undoubtedly parts of the primitive basal olfactory centers which have been carried out into the caudal pole of the hemisphere evagination. There is in this section no apparent boundary between these nuclei which enter into the amygdaloid complex and the general pallium.

Fig. 7 Section through the caudal part of the foramen, 120 microns rostral to figure 6. The nucleus caudatus is much more distinct and the proliferation of cells for the nucleus lentiformis begins to appear. There is now a slight indication of the lateral boundary of the pallium. The letters *s.v.m.* in this and figure 8 indicate the position in which the middle ventricular sulcus is to be formed, although it is not actually present in these sections.

Fig. 8 Section through rostral part of the foramen, 100 microns rostral to figure 7. The lateral olfactory area is represented chiefly by cell masses adjacent to the diagonal band. The nucleus caudatus begins to be separated from this area by the crus entering the hemisphere. The lentiform proliferation is larger and the clear space just above it, which corresponds to the zona limitans lateralis in lower vertebrates, is present from this level forward.

Fig. 9 Section through the rostral wall of the foramen. The position of the foramen is represented by the light space at the medio-ventral angle of the ventricle. The crus has now separated the nucleus caudatus from the nucleus of the diagonal band and both are somewhat removed from the larger mass of the lateral olfactory area which is here labeled *l.pyr.* The middle ventricular sulcus which is present in this section extends farther caudally in older embryos and adult.

Fig. 10 Section through the anterior commissure. Although the lateral olfactory area is continuous in these sections and even the nucleus caudatus is nowhere wholly separated from it, one can clearly see the beginnings of the segregation of the pyriform lobe, diagonal band and caudate nucleus by reason of the enlargement of the lateral forebrain bundle (*crus*). This process will be completed in later stages by the development of the lentiform nucleus and the further enlargement of the *crus*.

Fig. 11 Section just rostral to the preoptic recess where the diagonal band turns up in the medial wall. The dark mass on the medial surface of the area parolfactoria represents the beginning of the nucleus of the diagonal band, which corresponds to the gyrus subcallosus of the mammalian brain. The nucleus caudatus is connected beneath the ventricle with the area parolfactoria. From this level rostrad the olfactory area or lobe is quite continuous from its lateral border at *l.pyr.* to its medial border near *fi*.

Fig. 12 Section 60 microns rostral to figure 11, where the diagonal band fibers rise up in the medial wall to join the fimbria. Although the cells of the pyriform lobe and pallium lie immediately in contact, there appears in many sections a very sharp line as if it were caused by a delicate septum running dorsad from the small fiber bundle beneath *l.pyr.*

Fig. 13 Section through the tuberculum olfactorium. Note that the ventral ventricular sulcus here descends nearer to the surface than elsewhere so that the somewhat bulging tuberculum contains a large pouch of the ventricle.

Fig. 14 Section through the olfactory peduncle. The ventral part of the section cuts the rostral wall of the tuberculum while its dorsal part cuts the olfactory formation.

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Figs. 15, 16, 17 Three transverse sections of the right hemisphere of the 17 mm. *Chrysemys*. Figure 17 falls in the caudal part of the foramen and figure 15 represents next to the last section in which the connection of the hemisphere with the thalamus is seen. Figure 16 is between these two.

In this embryo the mass formed by the pallial proliferation of the earlier stage has become divided into a general pallium and the dorsal ventricular ridge. The ridge projects into the ventricle forming a deep middle ventricular sulcus and a shallow dorsal sulcus. Note that the dorsal sulcus is quite independent of the dorso-medial angle of the ventricle. The dorsal ventricular ridge therefore is clearly a thickening of the lateral wall above the lateral zona limitans. This zona limitans is the light streak in the drawings running diagonally between *d.v.r.* above and *n.l.* and *l.pyr.* below. The nucleus of the diagonal band is very large and definite in figure 17, while in figure 15 and 16 its substance is fused with the nucleus of the lateral olfactory tract. The lentiform proliferation is still in progress, especially from the dorsal lip of the middle sulcus. The peculiar arrangement of ependyma cells seen at this point in the adult already begins to be apparent here.

Figs. 18 to 27 Transverse sections of the right hemisphere of the 28 mm. embryo of *Chrysemys*.

Fig. 18 Section at about the point where the fimbria curves down behind the choroid area. Caudal to this the nucleus of the lateral olfactory tract soon disappears and the dorsal ridge continues on into the caudal pole as a simple thickening of the lateral walls. At *g.p.?* is a partly segregated mass of cells which probably represents general pallium extending from the caudal pole forward to this point in the basal wall as it does in the adult.

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Fig. 19 Section 120 microns rostral to figure 18. In both these sections the connection of the dorsal ridge with the pallium is clear and they illustrate the more embryonic conditions which prevail in the caudal pole than in the rostral part of the hemisphere.

Fig. 20 Section at the point of connection of the hemisphere with the thalamus where the stria medullaris passes into the thalamus. In this and the next two figures the lateral zona limitans appears as a diagonal light line running dorsolaterally from *s.v.m.* to the outer surface.

Fig. 21 Section through the foramen interventriculare. The lentiform and caudate nuclei, neither of which was distinguishable in figure 20, are here quite distinct. The crus in this figure separates the caudate from the nucleus of the diagonal band. From this point rostral for thirty to forty sections the crus lies practically exposed on the lateral surface. This condition is represented by a small striatal area in the model of this brain (fig. 5).

Fig. 22 Section through the anterior commissure. Here the general pallium begins to be decidedly thickened. The motor area of the adult includes this region and extends farther caudad. Forward from this level the olfactory area is again continuous on the lateral, basal and medial surfaces.

Fig. 23 Section through the rostral wall of the preoptic recess and the nucleus of the diagonal band (gyrus subcallosus). Between the level of figure 22 and this the pyriform lobe has rapidly pushed up over the outer surface of the pallial thickening as described in the text. The dorsal ridge is decreasing in size and the arrangement of its cells in this and in figure 22 suggests the core-nucleus of the adult. The dorsal ridge and the pallial thickening form a common large ridge, while in the adult they are separated by a groove (see '15 b, fig. 10).

Fig. 24 Section through the rostral end of the dorsal ridge and through the fissura prima, in which the fibers of the diagonal band are turning up into the medial wall. Both pallial thickening and pyriform lobe are massive.

Figs. 25, 26 and 27 Sections through the anterior part or motor area of the general pallium. The whole of what is called general pallium here becomes more massive in the adult and is included in the pallial thickening. An important feature of these sections is that the general pallium especially at the dorso-medial angle is composed of conspicuously large cells. If the results of experiments reported elsewhere in this journal are to be credited, this is certainly a part of the motor area and probably is concerned with the control of the limbs. The presence of the large cells is readily understood if this is true.