The Telencephalon of the Western Painted Turtle *(Chrysemys picta belli)*

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CONTENTS

I. INTRODUCTION

Comparative neuroanatomical studies have been conducted for more than a hundred years. Yet few of these studies have been concerned with variation within the classes of lower tetrapods. Workers have tended to view the telencephalon as a conservative structure. This has produced a concept of linear evolutionary morphogenesis whereby the living reptilian brain is viewed as a structure homologous to the ancestral reptilian structure which gave rise to mammals. This belief has lead to the interpretation and construction of reptilian homologies which are viewed as an intermediate level of organization leading to the avian or mammalian condition.

In an earlier work (Northcutt, 1966), the author suggested that this was not the case. The telencephalon was found to vary far more in reptiles than in any other group of living tetrapods. It was suggested that at least two major lines of telencephalic evolution occurred in reptiles. This division was explored in a subsequent work (Northcutt, 1967) in which the author described in detail the histological variations, and reviewed the physiological specializations which have resulted from this evolutionary divergence. The division into sauropsid and theropsid evolutionary lines was based on the histological analysis of the dorsal pallial component in living reptiles following the terminology of Watson (1954) who originally proposed these divisions

based on extensive paleontological evidence. It appears that the cortical organization of these two lines evolved in different functional directions. The sauropsid line, represented by the living reptiles (except turtles) and birds, is characterized by a dorsolateral component of the dorsal cortex which has lost Golgi Type I neurons. The theropsid line, represented by the turtles and living mammals, is characterized by a dorsolateral component of the dorsal cortex which has retained Golgi Type I neurons of motor function. The sauropsid condition has been confirmed by experimental anatomical evidence (Goldby, 1937; Schapiro, 1964; and Northcutt, 1968). This line must be viewed as the product of an evolutionary history leading, not to modern mammals, but to birds. As such, the structure of living reptiles along this line represents a distinct morphological form evolving along functional lines solving the problems of living reptiles. Sauropsid reptiles are far removed from the ancestral reptilian condition (Romer, 1966).

This report describes in detail the telencephalic centers and their connections in the western painted turtle *(Chrysemys picta belli)*. The analysis, based on both normal and experimental material, attempts to determine the structural and functional significance of these members of the theropsid radiation. Specific attention is focused on the pallial and dorsolateral wall neural groups in an attempt to clarify their homologies with the homologies of the sauropsid reptilian line.

II. MATERIALS AND METHODS

The western painted turtle, *Chrysemys picta belli,* was chosen for this study because this species can be obtained in large numbers and kept in captivity over long periods of time. Its position in the chelonian radiation is intermediate; it is neither primitive nor highly advanced (Weaver and Rose, 1967).

The individuals used varied in carapace length from 12.27 to 17.34 cm. They were housed in a large holding pen divided into dry earth and a pool. The photoperiod was controlled (12 hours of light and 12 hours of darkness); mean air temperature was 30.5°C ± S.E. 0.8. Table 1 lists the histological techniques used. Histological methods were employed for both normal and experimental material.

The normal silver impregnation methods of Bodian and Golgi-Cox were employed to stain unmyelinated fibers and cell types. Weil and Klüver series were used to stain myelinated tracts and nuclear relationships. Cresyl violet series were employed to differentiate nuclear groups and their topographical variations.

The experimental degeneration technique of Nauta and Gygax (1951), as modified by Guillery, Shirra, and Webster (1961), was used to determine the direction and termination of telencephalic connections observed by normal histological methods. Operations were performed on twelve specimens under cold narcosis, produced by placing the

TABLE 1

SERIES OF *CHRYSEMYS PICTA BELLI*

Series	Stain	Plane of Section	Thickness (μ)
Cp 1	Cresyl violet	transverse	40
Cp 2	Cresyl violet	transverse	40
Cp 3	Cresyl violet	sagittal	40
Cp 4	Cresyl violet	horizontal	40
Cp 5	Weil	transverse	40
Cp 6	Weil	sagittal	40
Cp 7	Weil	horizontal	40
Cp 8	Golgi-Cox	horizontal	120
Cp 9	Golgi-Cox	sagittal	120
Cp 10	Golgi-Cox	transverse	120
Cp 11	Golgi-Cox	transverse	120
Cp 12	Nauta (7 days)	horizontal	15
Cp 13	Nauta (14 days)	transverse	15
Cp 14	Nauta (21 days)	sagittal (control)	15
Cp 15	Klüver	transverse	15
Cp 16	Bodian	transverse	15
Cp 17	Nauta (14 days)	transverse	15
Cp 18	Nauta (14 days)	transverse	15
Cp 19	Nauta (14 days)	transverse	15
Cp 20	Nauta (14 days)	transverse	15
Cp 21	Nauta (14 days)	transverse	15
Cp 22	Nauta (14 days)	transverse	15
Cp 23	Nauta (30 days)	sagittal	15
Cp 24	Nauta (14 days)	transverse	15
Cp 25	Klüver	sagittal	15
Cp 26	Nauta (14 days)	transverse	15
Cp 27	Nauta (14 days)	transverse	15
Cp 28	Nauta (14 days)	transverse (control)	15
Cp 29	Klüver	horizontal	15

animals in a refrigerator until their body temperature reached 5°C. The skull was trepanned using a 0.5 cm. diameter trepan bit powered by a small electric hand drill. The dura was incised and a lesion produced by vacuum suction. The lesion was then packed with Gelfoam, the bone plug replaced and secured by painting celloidin over the surface of the skull. Two sham operated specimens were used as controls: the skulls were trepanned, the dura incised and the bone plugs replaced. The operations were not performed under aseptic conditions, but no animals died, and subsequent examination of the brains showed no infection or abscess formation. Postoperative survival time (Table 1) ranged from seven to thirty days. All animals

were killed by an overdose of sodium pentobarbital injected intraperitoneally, and perfused with 10 percent neutral formalin. The brains were removed and stored in the fixative from two to twelve weeks. No differences could be detected in the quality of the impregnations with respect to duration of fixation. Similar results were reported by Goldby and Robinson (1962).

Unilateral telencephalic ablations were performed on nine of the experimental animals (Cp 17 through 22, 24, 26, and 27). The extent and position of the ablation is illustrated for each animal in Figures 11 through 13. A transverse section for each ablation is also figured. Each section illustrates the maximal extent of the lesion (indicated by hatched area), and extent of axonic degeneration of passage (stippled area). Terminal degeneration is shown by plus signs. Unilateral olfactory nerve or bulbar ablations were performed on three experimental animals (Cp 12, 13, and 23). These are not illustrated.

The modified Nauta technique demonstrates degenerating fibers as intensely argentophilic granules of irregular shape and size. Normal fibers may stain a light brown or be suppressed entirely, depending on the concentration of pyridine used and the subsequent reduction

TABLE 2

SERIES OF COMPARATIVE REPTILES

Series	Genera	Stain	Plane of Section	Thickness (μ)
A-1	*Alligator mississippiensis*	Cresyl violet	transverse	15
A-2	*Alligator mississippiensis*	Golgi-Cox	transverse	100
A-3	*Alligator mississippiensis*	Golgi-Cox	transverse	100
C-1	*Caretta caretta*	Cresyl violet	transverse	40
C-2	*Caretta caretta*	Golgi-Cox	transverse	120
Cs-1	*Chelydra serpentina*	Golgi-Cox	transverse	120
Cs-2	*Chelydra serpentina*	Klüver	transverse	15
Cv-1	*Crotalus v. helleri*	Klüver	transverse	15
Cv-2	*Crotalus v. helleri*	Golgi-Cox	transverse	120
G-1	*Gopherus agassizi*	Cresyl violet	transverse	15
G-2	*Gopherus agassizi*	Golgi-Cox	transverse	100
Ps-1	*Pseudemys scripta*	Golgi-Cox	transverse	120
Ps-2	*Pseudemys scripta*	Cresyl violet	transverse	15
S-1	*Sphenodon punctatus*	Cresyl violet	transverse	15
S-2	*Sphenodon punctatus*	Klüver	transverse	15
Ts-1	*Trionyx spiniferus*	Golgi-Cox	transverse	120
V-1	*Varanus niloticus*	Cresyl violet	transverse	15

in the ammoniacal silver solution. While complete suppression of normal fibers allows the degenerating debris to be seen clearly, such suppression also decreases the number of argentophilic granules stained (Heimer, 1967).

Fibers were judged to be degenerative if they evinced clear fragmentation and irregularity in their granular arrangement. Pericellular preterminal and terminal degeneration is characterized by a winding of the debris over the cell body to form droplike swellings which are often clustered (Fig. 17B). Terminal degeneration was not considered to have occurred unless it could be demonstrated that the droplike granules were in contact with cell bodies or formed dense fields of droplike granules among the dendritic fields of cellular layers (Figs. 15C and 18A). Terminal structures were not impregnated in the control turtles.

Serial sections of other reptilian brains were employed for comparison with the western painted turtle and for checking earlier work (Table 2).

III. HISTORICAL NOTES

The literature on the forebrain of turtles appears extensive (Table 3), but closer examination reveals that few of these studies are primarily concerned with detailed descriptions of the entire turtle forebrain. The list in Table 3 compiles date, discipline, author, and genera studied. The current scientific name is added parenthetically, but only at the first occurrence in the list.

The earliest studies on the turtle forebrain (Cuvier, 1809; Carus, 1814; and Owen, 1866) concern the external morphology and are largely of historical interest as representing the beginnings of comparative studies. Stieda (1875) and Humphrey (1894) made the first systematic attempts at histological description. Although generalized, these studies lay the framework for more detailed comparative studies.

The works of Gage (1895), Edinger (1896), and Johnston (1915) were the first truly comparative studies. They attempted to establish homologies throughout the vertebrate telencephalon. Johnston's work on *Cistudo carolina (= Terrapene carolina)* laid the foundation for further studies on the telencephalon of turtles. He presented theories which are still of interest to comparative anatomists.

Papez (1935) described the thalamic centers of *"Chelone midas"* and *Pseudemys elegans* and established their mammalian homologies. While these homologies now appear partially incorrect, this work is

TABLE 3

PREVIOUS WORK ON THE FOREBRAIN OF TURTLES

Date	Author	Genus
	Discipline: Descriptive	
1809	Cuvier	unknown
1814	Carus	unknown
1866	Owen	*Chelone*
1875	Stieda	*Testudo graeca* *Emys europaea* (= *E. orbicularis*)
1881	Rabl-Ruckhard	no genus listed
1887	Osborn	*Emys europaea* *Testudo graeca*
1893	Meyer	*Testudo graeca* *Chelone mydas* (= *Chelonia mydas*)
1893a	Herrick, C. L.	*Aspidonectes spinifer* (= *Trionyx spiniferus*)
1893b	Herrick, C. L.	no genus listed
1894	Humphrey	*Chelydra serpentina*
1895	Gage	*Amyda mutica* (= *Trionyx muticus*)
1896	Edinger	*Chelone mydas*
1903	Smith	*Chelone mydas*
1910	Herrick, C. J.	*Cistudo carolina* (= *Terrapene carolina*) *Chrysemys marginata* (= *Pseudemys picta marginata*)
1911	de Lange	*Chelone midas* *Testudo graeca*
1913a	Johnston	*Cistudo carolina*
1913b	Johnston	*Emys lutaria* (= *Emys orbicularis*)
1915	Johnston	*Cistudo carolina*
1916	Bailey	*Chrysemys marginata*
1917	McCotter	*Chrysemys punctata* (= *Emys orbicularis*)
1919	Smith	*Testudo graeca* *Chelone mydas*
1919	Larsell	*Chrysemys marginata*
1923	Johnston	*Cistudo carolina*

TABLE 3 — Continued

Date	Author	Genus
	Discipline: Descriptive	
1923	Rose	*Emys lutaria* *Testudo graeca*
1935	Papez	*Chelone midas* *Pseudemys elegans*
1936	Craigie	*Emydoidea blandingi* *Chrysemys marginata*
1936	Goldby	*Testudo graeca*
1939	Crosby and Humphrey	*Chelydra serpentina* *Chrysemys marginata* *Sternotherus odoratus* *Emys melageris* (= *Emydoidea blandingi*) *Pseudemys elegans* *Graptemys pseudogeographica*
1939	Curwen and Miller	*Pseudemys scripta*
1948	Schepers	*Testudo geometrica*
1953	Allison	*Cistudo*
1963	Filimonoff	*Testudo graeca*
1964	Filimonoff	*Testudo graeca*
1966	Baumann	*Chrysemys picta*
1966	Crosby et al.	no genus listed
1966	Platel	*Clemmys leprosa*
1967	Carey	*Terrapene carolina*
1967	Hewitt	*Testudo graeca*
1967	Kirscle	*Terrapene mexicana*
	Discipline: Embryological	
1916a	Johnston	*Chelydra serpentina*
1925	Holmgren	*Chrysemys marginata*
1939	Krabbe	*Chelydra serpentina*
1951c	Källén	*Chrysemys picta*
	Discipline: Physiological	
1884	Fano	*Emys europaea*
1901	Bickel	unknown

TABLE 3 — Continued

Date	Author	Genus
	Discipline: Physiological	
1905	Sergi	*Testudo graeca*
1916b	Johnston	*Chelydra serpentina* *Cistudo carolina*
1925	Koppanyi and Pearcey	no genus listed
1929	Parschin	*Emys orbicularis*
1930	Poliakoff	*Emys orbicularis*
1933a	Hasratzan	unknown
1933b	Hasratzan and Alexanjan	unknown
1933	Wojtusiak	*Emys orbicularis* *Clemmys caspica*
1934	Tuge and Yazaki	*Clemmys japonica*
1937	ten Cate	*Emys europaea* (= *Emys orbicularis*)
1939	Bremer et al.	*Emys europaea*
1961a	Orrego	*Pseudemys scripta*
1961b	Orrego	*Pseudemys scripta*
1962a	Orrego	*Pseudemys scripta*
1962b	Orrego and Lisenby	*Pseudemys scripta*
1964	Davydova	*Emys orbicularis*
1965	Karamyan	*Emys orbicularis*
1965	Belekhova and Zagorul'ko	*Emys lutaria*
	Discipline: Degeneration	
1956	Gamble	*Testudo graeca*
1967	Kosareva	*Emys orbicularis*

an excellent summary of earlier thought on thalamic relationships, and it is still the only work on thalamic centers in turtles.

The most complete work is the excellent monograph on the telencephalon of *Testudo geometrica* by Schepers (1948). He correlated the terminology of previous workers and codified these terms as they apply to turtles. His work has seldom been cited, probably due to the unfortunate complexity of his terminology.

In 1923, Rose completed the most detailed analysis of the variation within the reptilian telencephalon and attempted to establish valid homologies among the telencephalons of vertebrates. Similar studies were published by Filimonoff in 1963 and 1964. Both of these workers disagree with the homologies established by the American and German schools of comparative neuronanatomy. However, both Rose's and Filimonoff's studies are based only on normal preparations and it is impossible to evaluate their interpretations of structure or those of their critics without experimental anatomical studies. A number of descriptive works have appeared recently (Baumann, 1966; Carey, 1967; and Hewitt, 1967). These workers have again relied on normal preparations. The same limitations of interpretation exist in these works as in earlier works. Only two experimental anatomical studies exist on the forebrain of turtles: Gamble (1956) traced the olfactory projections in *Testudo graeca,* and Kosareva (1967) traced the optic projections in *Emys orbicularis.* However, these studies are not central to the problem of the structure and connections of the nuclei of the telencephalon proper and their homologies in other reptiles.

Conflicting concepts on the significance of neural groups in the forebrain exist in the literature and call for the kind of experimental analysis of the basic structures and connections made here. With this information, an attempt is made to integrate embryological and physiological data with anatomical studies.

IV. CELL GROUPS

The cellular groups making up the telencephalon are described first. This configuration of nuclei and cortices can then be used as a framework for the description of fibers which interconnect these groups. The following criteria are used for the delineation of major cytoarchitectural boundaries: (1) cell free gaps which often mark major changes in type of cell structure and represent points for the entry or exit of fiber bundles; (2) transitional points in which there is a continuous cellular layer but with sudden changes in cell type, e.g., change from Golgi Type I to Type II; (3) a break or shift in the topographical position of cells, e.g., transition from hippocampus, pars dorsomedialis to pars dorsalis (Fig. 1); and (4) a change in the type of fiber system which is afferent or efferent to an area. The use of fiber systems has been in dispute among workers, yet fibers are part of the cells we study. To ignore this fact in establishing boundaries is ill-advised. Likewise, it has been commonly assummed that the afferent projections to an area are of cytoarchitectural significance in that they presumably affect the cellular differentiation seen in any given area. If morphology has any significance, we must assume that cellular differentiation represents specialization of a form-function complex of characters which must take connections into account.

Olfactory Bulb

The olfactory apparatus of the western painted turtle is identical to that described in *Chrysemys punctata* by McCotter (1917). The nasal fossa consists of a principal nasal chamber which communicates anteriorly with the naris and posteriorly with the choana. Whether turtles possess a vomeronasal organ (Jacobson's organ) has long been questioned. Johnston (1915) and Schepers (1948) did not recognize the nerve in their preparations and subsequently did not recognize an accessory olfactory bulb. Seydel (1896) claimed that the ventral half of the nasal cavity was homologous to the vomeronasal organ of other tetrapods. Parsons (1958 and 1959) studied the embryology of this region in turtles and concluded that Seydel was correct.

The vomeronasal nerves arise from the ventral half of the nasal chamber and pass through the nasal canal where they project onto the dorsal half of the olfactory bulb. The olfactory nerves arise from the dorsal half of the nasal chamber and pass through the nasal canal where they project onto the rostral pole and ventral half of the olfactory bulb.

The olfactory bulb is not divided into distinct main and accessory bulbs as in lizards (Armstrong, Gamble, and Goldby, 1953). The dorsal half of the olfactory bulb in the turtle corresponds to the accessory olfactory bulb in lizards, and the rostral pole and ventral half of the bulb correspond to the main olfactory bulb in lizards. Such a division has been recognized by Crosby and Humphrey (1939).

Both dorsal and ventral olfactory regions contain the same layers. The bulb consists of seven neural layers (Fig. 14A) as in all higher vertebrates. The outermost layer (Layer 1, olfactory or vomeronasal fila) consists of fibers from the nasal chamber which end in Layer 2 (glomerular layer). The glomeruli do not form a continuous cap around the bulb but form a dorsal and a ventral division. They are separated by a fiber zone on the medial and lateral bulbar walls. Individual glomeruli are interconnected by intraglomerular neurons whose cell bodies lie between glomeruli.

The dendrites of the intraglomerular neurons may end in one or more glomeruli with their axons projecting to other glomeruli. These neurons, along with tufted cells, form the external granular layer (Layer 3, Fig. 14A). This layer is not as well developed in turtles as in lizards (Northcutt, 1967), although typical tufted cells are found in both orders. The tufted cells are identical to those described by Valverde (1965) in mammals, and are so well known that no description is necessary. The fourth layer, the external molecular or plexiform

layer, consists of the axons of the tufted cells, dendrites of mitral cells, and axons of the internal granular cells.

The fifth layer is composed of mitral cells (Fig. 7A). These cells are triangular in shape and their cell bodies possess two to four main dendrites. Two to three of these processes ascend toward the surface and form part of the glomeruli. The remaining dendrites pass horizontally, branching among the axons of the internal granular cells. The mitral axons are in part myelinated and pass into the internal molecular or plexiform layer (Layer 6, Fig. 14A) where they form the olfactory tracts.

The internal granular layer (Layer 7; Fig. 7B) consists of two types of cells. It is difficult, if not impossible, to delineate dendrites and axons in the classical sense. The cells possess short, highly branched projections on the ventricular side of their cell bodies, if they are located near the ependyma, and a long apical process on the superficial surface of their cell bodies. The apical process which passes to the external granular layer ends on the dendrites of mitral cells. Thus, this process appears to function as an axon. Some of these processes may reach the glomeruli. If the cell bodies of the neurons of the internal granular layer are located farther from the ependyma, they do not possess such a strong apical process. Under these conditions their cell bodies appear fusiform with a series of processes branching from each pole of the cell body.

Olfactory Peduncle

A true peduncle can hardly be said to exist in the western painted turtle. The olfactory bulb does not end sharply as in lizards; rather, its cell masses grade into the telencephalon proper. The dorsal vomeronasal glomerular and internal granular layers extend farther posteriorly than does the ventral main olfactory formation. The glomerular and mitral cell layers end sharply and the internal plexiform layer assumes a superficial position as the ventral posterior border of the olfactory bulb is reached. The ventral internal granular layer transforms into a larger cell type and becomes the olfactory tubercle and the anterior olfactory nucleus. This transition can often be seen on a single transverse section. The lateral division of the internal granular layer becomes less compact in terms of cell density per unit volume, and the cells become larger. The medial division of this formation retains the typical architectonic pattern for the internal granular layer.

Posterior to these cellular transitions, the dorsal bulb undergoes a similar transition. The vomeronasal glomeruli and mitral cells are lost in the lateral surface first. The internal plexiform layer assumes a lateral superficial position and becomes the lateral olfactory tract. The lateral region of the dorsal internal granular layer is replaced by larger neurons of the pyriform cortex. As the pyriform cortex becomes established the dorsomedial vomeronasal glomeruli and mitral cells are lost, and the internal plexiform layer assumes a superficial position and becomes the medial olfactory tract. The internal granular layer is replaced dorsally by cells of the dorsal cortex, and medially by cells of the primordium hippocampi.

The olfactory tracts, while formed by regional segments of the internal plexiform layer, are not segregated according to the location of their mitral cell axons. Ablation of the dorsal mitral cell layer results in degeneration not only in the dorsal half, but throughout the entire internal plexiform layer (Cp 12).

The anterior olfactory nucleus is much larger in turtles than in the green iguana and most other reptiles (Northcutt, 1967). It is bordered dorsally by the floor of the lateral ventricle and forms the entire rostral floor of the telencephalon except for a thin ventral covering of cells, the olfactory tubercle. The anterior olfactory nucleus lies anterior to the paleostriatum, but there is no clearly distinguishable border between the two formations. The anterior olfactory nucleus is not sharply separated from the olfactory tubercle, and the tubercle is not as well differentiated histologically in turtles as in lizards.

Three types of cells are found in the anterior olfactory nucleus. The largest population consists of goblet-shaped neurons with two major dendritic processes. No preferred orientation within the nucleus could be determined. Many of the dendrites extend toward the ventral surface and presumably receive impulses from the olfactory tract. These goblet cells possess long axons which project out of the nucleus. The second type of neuron observed consisted of small polygonal cells located in the interior and possessing two major dendritic processes which project from opposite sides of the cell body. The axon, which normally originates from the cell body at a 90 degree angle from either of the dendrites, is long and appears to leave the nucleus. The third type of cell is intrinsic and appears to interconnect the other elements. Axons of the goblet and polygonal neurons project to the olfactory tubercle and the rostral division of the parolfactory nuclei. In horizontal sections, an "olfactory" component of the anterior commissure can be seen; it is not as well developed as in the green iguana or in most other lizards. This compact commissure could not be traced

to the olfactory bulbs. It is probable that this division of the anterior commissure is composed of fibers which interconnect the anterior olfactory nuclei. It is also probable that anterior olfactory nuclear connections exist with the primordium hippocampi, but the author is not certain of these connections.

Centers of the Hemisphere

The reptilian hemispheres are divided into a dorsal roof or pallium, and a ventral region (basal or subpallial region). The exact boundary on the lateral wall, and the respective derivatives of pallium and subpallium, have long been in dispute. Therefore, the cellular groups of the telencephalon proper are here described without reference to their origin, and this problem is dealt with in the discussion section.

TUBERCULUM OLFACTORIUM

(Figs. 1 and 7C). The olfactory tubercle begins in the peduncle at the same level as the anterior olfactory nucleus. It continues posteriorly where it is capped dorsally by the paleostriatum. It ends just anterior to the anterior commissure where it is followed by the nucleus of the diagonal band of Broca (Fig. 2).

Three cell types were recognized in this formation: pyramidal, polygonal, and fusiform. The pyramidal cells possess a long, unbranched apical dendrite which projects toward the ventral surface and appears to synapse with olfactory fibers. The axons of these cells could not be traced for long distances, but they probably project to other centers.

The polygonal cells (Fig. 7C) are larger than the pyramidal cells. They appear to possess two to three major dendrites which are shorter than the dendrites of the pyramidal cells. The polygonal cells are oriented toward the incoming olfactory fibers, and their axons are long and appear to leave the tubercle. The axons of these polygonal cells possess collaterals which project to the other elements in this formation.

The tubercle, in its anterior part, is not sharply separated from the anterior olfactory nucleus. Neither is its posterior part sharply divided from the paleostriatum. Accordingly, the neurons grade from one formation to the other. Most of these cells are fusiform in appearance. The cell bodies have dendrites branching from each pole of the cell body. Often one polar dendritic branch projects into the olfactory

tubercle, whereas the other polar branch projects to a second formation. The axon usually originates from the base of the shorter dendrite and cannot be traced for any considerable distance.

AREA PAROLFACTORIA

(Figs. 2, 7D, and 8A). The ventromedial wall of the turtle telencephalon contains three nuclei: the primordium hippocampi, the nucleus parolfactorius lateralis and the nucleus parolfactorius medialis. The primordium hippocampi (Figs. 1 through 4) is first seen rostrally at the level of the anterior olfactory nucleus and is thus bordered by this structure ventrally. The lateral ventricle and the hippocampal cortex lie at its lateral and dorsal borders respectively. The primordium hippocampi continues posteriorly until it reaches the posterior border of the hippocampal commissure where it ends (Fig. 4).

The parolfactory region is first seen just below the primordium hippocampi in the rostral telencephalon as a bulge in the ventromedial wall of the lateral ventricle. Anteriorly there is a single group of cells, but as this group passes posteriorly it is divided by the fornix and becomes the lateral and medial parolfactory nuclei (Fig. 2). These two nuclei continue posteriorly until the anterior commissure is reached (Fig. 3). The medial parolfactory nucleus stops just anterior to the commissure, and the lateral parolfactory nucleus grades into the area ventralis anterior, just posterior to the commissure (Fig. 3).

Analysis of these three nuclei in Golgi preparations does not reveal sharp or major differences in the three cellular populations that exist in all three nuclei. The first population (Fig. 7D) consists of polygonal or small pyramidal cells. Their dendritic branches are oriented in all directions within the three nuclei, and it is impossible to describe input or output surfaces for these nuclei. The axons of these cells are long and project into the fornix bundle which separates the medial and lateral parolfactory nuclei. Axons can be traced which ascend or descend in this bundle from the primordium hippocampi, and the lateral and medial parolfactory nuclei.

The second population consists of fusiform cells (Fig. 8A). One or two dendrites extend from each pole of the cell body and may stretch completely across the medial wall. Their dendrites are covered with boutons, and these endings can be traced to these dendrites from both lateral and medial parolfactory nuclei, as well as the fornix system. The axons of the fusiform cells originate from either the cell body or the base of one of the dendrites. The axons could not be traced any distance, and it is not known whether or not these cells are intrinsic.

The third population consists of stellate cells which are intrinsic and interconnect the other two cellular populations. Ablation of the dorsal cortex, pars dorsomedialis, and the hippocampal cortex (Cp 17) results in terminal degeneration in all three nuclei of the parolfactory region. Details of this degeneration are covered in the discussion of fibers. However, these results, supported by the Golgi analysis, leave little room for the classical belief that the lateral parolfactory nucleus is a way-station for descending impulses from the hippocampus, and that the medial parolfactory nucleus is a similar area for ascending impulses (Crosby, 1917).

NUCLEUS COMMISSURAE ANTERIORIS

(Fig. 3). Scattered among the fibers of the anterior commissure is a group of fusiform neurons which form the nucleus of this commissure. The nucleus is not well defined and grades into the nucleus commissurae hippocampi and nucleus interstitialis. These fusiform cells give rise to dendrites at each pole of the cell body. Typically one of the dendrites bifurcates almost immediately after leaving the cell body. It is at the base of this dendritic trunk that the axon hillock is normally found. The other polar dendrite does not bifurcate. Both dendrites are extremely long and together they may form a dendritic field whose diameter is 150 to 250μ. The cell bodies are often located just dorsal or ventral to the fibers of the commissure. One dendrite projects into the fiber stream, whereas the other projects into the surrounding nuclei. Fibers of the anterior commissure synapse on the commissural dendrite, and axons of these fusiform cells enter the commissure.

NUCLEUS COMMISSURAE HIPPOCAMPI

(Fig. 3). Like the anterior commissure, the hippocampal commissure also possesses neurons scattered among its fibers. Unlike those of alligators (Crosby, 1917), the neurons in these two commissures are identical in the western painted turtle. Similar conditions exist in the other turtle material examined (Table 2). These fusiform cells form synapses with the cortical commissural fibers, and their axons probably project to the cortical formations and possibly to lower basal centers.

NUCLEUS PERIVENTRICULARIS PREOPTICUS

(Fig. 3). This nucleus lines the wall of the preoptic recess of the

third ventricle, and begins just rostral to the anterior commissure. It is bordered laterally by the interstitial nucleus, and posteriorly by the beginning of the nucleus periventricularis hypothalami with which it is continuous. The cells of this formation form two populations. The first population consists of polygonal cells similar to those observed in the green iguana (Northcutt, 1967). The dendritic pattern is large (100-150μ), and the dendrites synapse with fibers of the stria terminalis and descending fibers of the medial forebrain bundle. It is probable that this last set of fibers was confused with the medial olfactory tract in the green iguana (Northcutt, 1967). Ablation of the olfactory bulb does not result in degeneration in the periventricular preoptic nucleus. However, ablation of the medial and dorsomedial cortical formations does result in degeneration in this nucleus. These connections and the experimental evidence for their existence are reviewed in the fiber section. The axons of these polygonal cells are long and project laterally and posteriorly into the hypothalamic nuclei.

The second population of cells consists of fusiform elements similar to those found in the nuclei of the commissures. However, these cells are smaller, and their axons could not be identified.

NUCLEUS INTERSTITIALIS

(Figs. 3 and 4). This nucleus begins at the level of the anterior commissure (Fig. 3) and ends at the level of the lateral hypothalamic nucleus. Dorsally it is bordered successively more caudal by the nucleus of the anterior commissure, the area ventralis anterior, and the area triangularis. Laterally and ventrally, it is bordered by the basal forebrain bundle (lateral and medial forebrain bundles), and medially by the periventricular cell masses of the third ventricle.

The same two cellular populations, small projection cells and fusiform cells, are recognized in both the western painted turtle and the green iguana. The axons of both cellular populations appear to project into the anterior commissure or more posteriorly to the hypothalamic nuclei.

NUCLEUS OF THE DIAGONAL BAND OF BROCA

(Fig. 2). This formation was first described in turtles by Johnston (1915). It was originally described as a band of tissue connecting the lateral and medial olfactory centers. In 1952, Gamble demonstrated in *Lacerta viridis* that this band contains an olfactory bundle which enters the stria medullaris and crosses to the contralateral hemisphere,

reenters the opposite stria and projects to the parolfactory region. This pathway is also present in *Testudo graeca* (Gamble, 1956). The existence of this pathway in the western painted turtle has been confirmed by degeneration studies and is discussed in the description of the olfactory tracts and stria medullaris.

Golgi analysis of the diagonal band reveals that fibers run diagonally between the parolfactory and amygdaloid areas. In addition, two cellular populations can be identified in the diagonal band. The first population consists of typical fusiform cells. Their dendrites project parallel to the diagonal fibers, and their axons project with these fibers. Axonic collaterals from the adjacent parolfactory and paleostriatal nuclei enter the diagonal band and end on the dendrites of these fusiform cells.

The second population consists of small polygonal and pyramidal cells. The cell bodies are located very near the pia, and their dendrites, usually two in number, project into the parolfactory and paleostriatal nuclei. Their axons project into the dense fibers forming the diagonal bundle and are lost.

CELLULAR GROUPS OF THE LATERAL WALL

(Figs. 1 through 6, 8C and 9C). The division of the lateral wall into nuclei, and the phylogenetic significance of these nuclei have generated the vast majority of studies on the reptilian telencephalon. Two problems confront workers analyzing this region. The first is establishing the roof-floor boundary, which has topographical significance in determining homologies with other tetrapodal classes. The second problem is recognizing corresponding homologies in other reptilian orders.

These nuclei are described and named, insofar as possible, according to the nomenclature of the author's earlier work (Northcutt, 1967). The present analysis indicates that part of the nomenclature is inadequate, and that new nomenclature should be proposed. However, this will not be done at present, since the literature is overflowing with names for the same nuclei, as well as the same name for different nuclei, both within and between classes. Until our knowledge is more complete, the formulation of new nomenclature would inevitably be incomplete and inadequate. The phylogenetic significance of the lateral wall and its proposed homologies is presented in the discussion where the significance of cellular differentiations and fiber connections can be summarized and compared with the earlier literature.

The nuclei of the lateral wall are divided into two major divisions in accordance with the author's earlier work. The first division con-

sists of an anterior group of nuclei: paleostriatum, nucleus accumbens, dorsal ventricular ridge (pars anterior), and core nucleus (Figs. 1 and 2). This division is united by common input via the dorsal peduncle of the lateral forebrain bundle. Its output is via the ventral peduncle of the lateral forebrain bundle. The nucleus accumbens also receives input from the olfactory tract and the medial forebrain bundle, and may contribute efferent fibers to the latter system (Northcutt, 1967).

The second division consists of a posterior group of nuclei: nucleus basalis amygdalae, dorsal ventricular ridge (pars posterior), and nucleus centralis amygdalae (Figs. 4 through 6). This division is united by sensory input, olfactory and visceral, via the lateral olfactory tract and the stria terminalis. Its motor output is via the stria medullaris and the stria terminalis, and it appears to be part of a system for integration and response to visceral stimuli.

The nucleus accumbens is located ventral to the primordium hippocampi and medial to the paleostriatum (Fig. 1). Rostrally, it is first seen as a continuation of the anterior olfactory nucleus, and no clearly defined boundary between it and the paleostriatum exists. Initially, it forms the floor of the lateral ventricle but is rapidly replaced by the parolfactory nuclei (Fig. 2).

The paleostriatum is first seen at the same level as the nucleus accumbens, and is also a continuation of the anterior olfactory nucleus. In its rostral part, it is bordered ventrally in succession by the olfactory tubercle (Fig. 1) and by the nucleus of the band of Broca (Fig. 2). Posteriorly, it is bordered ventrally by the lateral forebrain radiations (Fig. 4), and the basal amygdaloid nucleus (Fig. 5). Dorsomedially, its surface forms the ventrolateral wall of the lateral ventricle. Dorsolaterally, it is bordered by the core nucleus of the dorsal ventricular ridge. It continues posteriorly until it reaches the level of the amygdaloid nuclei (Fig. 5).

The paleostriatal complex (paleostriatum and nucleus accumbens) contains three cellular populations similar to those in lizards: stellate cells, small projection cells, and giant polygonal cells. The stellate cells are intrinsic and appear to interconnect the small projection cells and the giant polygonal cells.

The small projection cells (Fig. 9C) synapse with incoming thalamic fibers from the lateral forebrain bundle; and with descending fibers of the dorsal cortex (pars dorsolateralis), and the dorsal ventricular ridge (pars anterior). Ablation of the dorsal cortex (pars dorsolateralis), (Cp 19, 20, and 22) results in degeneration to the paleostriatum (Fig. 18C). Terminal degeneration was confined to the pars lateralis of the paleostriatum. Ablations involving both the dorsal cortex and

the dorsal ventricular ridge (pars anterior), (Cp 17 and 18) show additional degeneration in the paleostriatum. This degenerating component can be traced as a pathway from the dorsal ventricular ridge to the paleostriatum (pars medialis) where terminal degeneration is observed (Cp 17, Fig. 11).

Small projection cells are located in both the lateral and medial divisions of the paleostriatum. The division is primarily based on the number of fibers of passage, and the functional significance, if any, of this division is not known. The unequal distribution of fibers and the differential termination of the fibers of the dorsal cortex and dorsal ventricular ridge (pars anterior) suggest that there might be functional differences however.

Axons of the small projection cells may pass into the core nucleus of the dorsal ventricular ridge. The Golgi material suggests such connections, and there is not an extremely sharp division between the core nucleus and the paleostriatum. The paleostriatum was searched for signs of retrograde cell degeneration following ablation of the dorsal ventricular ridge, but no signs of such degeneration were observed. Resolution of this problem must await discrete ablation of parts of the paleostriatum.

The giant polygonal cells (Fig. 8C) are located among fibers of the lateral forebrain bundle at the point where these fibers enter and leave the ventrolateral portion of the paleostriatum. These cells have been identified in all reptilian groups except Crocodilia. Their function is not known, but they appear to be Type I cells with widely radiating dendrites which come into contact with large segments of the paleostriatum. Their axons project into the lateral forebrain bundle where they could not be followed. They were noted first by P. Ramon (1896) who illustrated them (Figure 3 of his work, Cells h) but did not comment on them.

The dorsal ventricular ridge (pars anterior) (Figs. 1 through 3) is first seen rostrally as a bulge in the lateral wall of the lateral ventricle. As transverse sections are traced caudally, it rapidly expands in size until it nearly fills the lateral ventricle. It is bordered dorsally and laterally by the dorsal and the pyriform cortices. Ventrally, it is bordered by the paleostriatum, from which it is partially separated by a fiber layer. Posteriorly, it grades into the dorsal ventricular ridge (pars posterior) from which it is distinguishable by a change in the major afferent and efferent connections. This transition from pars anterior to pars posterior corresponds closely to the fusion of the pyriform cortex with the dorsal ventricular ridge (Fig. 4). The level at which this fusion is first established is variable from one specimen

to another, and often this does not occur until a level comparable to Figure 5 is reached.

The dorsal ventricular ridge (pars anterior) can be divided into a surrounding superficial layer and a deep core nucleus (Fig. 2). The superficial layer gives the appearance of a cortical layer surrounding a core of fibers among which are loosely scattered neurons. The superficial layer is not a true cortex however. The author defines a true cortex as a sheet of neurons which possess apical dendritic fields oriented on one side of the sheet while their axons project from the other side. Thus a true cortex possesses superficial and deep white regions sandwiching an intermediate gray layer. The sensory input of such a histological field may be either superficial or deep. The superficial field of the turtle dorsal ventricular ridge is histologically organized in a manner similar to the amphibian periventricular pallial formations (Herrick, 1948).

The superficial layer of the dorsal ventricular ridge (pars anterior) consists of three cellular populations: pyramidal cells, small projection cells, and stellate cells. The pyramidal cells (Fig. 8D) are located primarily along the medial surface of the dorsal ventricular ridge. They possess a long apical dendrite which projects into the core nucleus, and two or more basal dendrites which project ventrolaterally in the superficial layer. Their axons leave the somal surface opposite the apical dendrite, and then curve around the soma and project into the core nucleus.

The largest population of cells consists of small projection cells similar to the projection cells of the paleostriatum. They possess multiple dendrites, some branching into the core nucleus, while others branch laterally in the superficial layer. Their axons normally leave their round cell bodies on the side opposite to the dendritic radiation, and project into the core nucleus or into the dorsolateral division of the dorsal cortex. The small projection cells also pass their axons toward the lateral surface of the superficial layer. After penetrating the cell layer, the axons form a ventricular fiberous layer which caps the dorsal ventricular ridge. These axons appear to interconnect various portions of the dorsal ventricular ridge.

The third population of cells consists of intrinsic stellate cells which appear to interconnect the other two elements.

Ablation of the superficial layer of the dorsal ventricular ridge (pars anterior) (Fig. 11, Cp 17) results in terminal degeneration on cells of the homolateral core nucleus, paleostriatum, and contralateral dorsal ventricular ridge (pars anterior). Degenerating fibers of passage were observed in the anterior commissure and in both lateral

forebrain bundles. Thus it appears that the axons of the pyramidal and small projection cells may either project to the core nucleus or leave the dorsal ventricular ridge and project: (1) to the homolateral, dorsolateral division of the dorsal cortex; (2) to the homolateral paleostriatum; (3) to the contralateral dorsal ventricular ridge (pars anterior) via the anterior commissure; and (4) into the homolateral lateral forebrain bundle.

The degenerating fibers from the dorsal ventricular ridge which pass into the lateral forebrain bundle are located in both peduncles. The fibers of the dorsal peduncle were traced to the nucleus rotundus (Fig. 6) of the dorsal thalamus. The fibers of the ventral peduncle were traced to the level of the mesencephalon. The degeneration may continue, but results from the one experimental animal (Cp 17) which allows analysis of these projections are not clear beyond this point. Ablation of the dorsal cortex (Cp 20) does not result in degeneration of the nucleus rotundus. However, ablation of both the dorsal cortex and dorsal ventricular ridge (Cp 17) does result in degeneration of the nucleus rotundus. The dorsal ventricular ridge (pars anterior) also receives input from the dorsolateral division of the dorstal cortex. Ablation of this pallial division (Cp 20; Fig. 12) results in degenerating fibers of passage to the core nucleus and superficial layer (Fig. 17C). Terminal degeneration can be seen in both the core nucleus (Fig. 17B) and in the superficial layer.

The core nucleus contains both small projection and intrinsic stellate neuronal populations. It appears to serve as a point of synapse for fiber systems entering and leaving the dorsal ventricular ridge. From the ablation experiments, it is clear that both entering and exiting fiber systems do pass through the core nucleus without synapsing, and many of these fibers may only send collaterals into this nucleus. None of the experimental preparations yielded additional information on this nucleus due to the fact that all ablations which involved the core nucleus also involved the superficial layer of the dorsal ventricular ridge.

The posterior group of nuclei which form the lateral wall of the telencephalon are divided into three nuclei: the dorsal ventricular ridge (pars posterior), the central amygdaloid nucleus, and the basal amygdaloid nucleus (Fig. 6).

The rostral border of the dorsal ventricular ridge (pars posterior) begins in cross sections at approximately the level of the anterior commissure (Fig. 3). However, its rostral border is variable from one specimen to another and can be determined only by examination of the connections. It is bordered laterally by the pyriform cortex with

which its superficial layer is continuous (Fig. 6). Ventrally, it is bordered by the paleostriatum anteriorly, and by the basal amygdaloid nucleus posteriorly. Like the anterior division of the dorsal ventricular ridge, the posterior division of the dorsal ventricular ridge can be divided into a core nucleus, here described as the central amygdaloid nucleus, and a surrounding superficial layer.

The topographical relationship of the posterior division of the dorsal ventricular ridge to the dorsal cortex and pyriform cortex is highly variable from one specimen to another in the western painted turtle. The dorsolateral division of the dorsal cortex is not constant in its posterior configuration. In several cases, it does not remain in contact with the dorsal ventricular ridge beyond the level of the anterior commissure (Fig. 2). In two cases (Cp 24 and 26), it continues posteriorly and fuses with the posterior division of the dorsal ventricular ridge. This relationship was also observed in the neonatal material of *Caretta*. The pyriform cortex, in all cases, subsequently fuses with the posterior division of the dorsal ventricular ridge at a more caudal level (Fig. 6).

The basal amygdaloid nucleus (Figs. 5 and 6) is first seen as an oval mass of cells located ventral to the caudal portion of the paleostriatum. The exact boundary between these two nuclei is not distinct however. The basal amygdaloid nucleus rapidly replaces the paleostriatum and occupies the entire caudal subpallial telencephalic pole. It is bordered posteriorly on the medial side by the hippocampal cortex, and on the lateral side by the pyriform cortex.

The posterior division of the dorsal ventricular ridge contains the same three cellular populations observed in the anterior division of the dorsal ventricular ridge: pyramidal, small projection, and stellate neurons. The same internal cellular relationships are seen. Some of the pyramidal neurons are inverted, and their apical dendrites project toward the surface fibrous layer, rather than deep into the central amygdaloid nucleus. The dorsal ventricular ridge (pars posterior) receives input from the pyriform cortex, dorsolateral division of the dorsal cortex, central and basal amygdaloid nuclei, and associative fibers from the contralateral amygdaloid complex via the commissural division of the stria terminalis. The dorsal ventricular ridge (pars posterior) projects to the homolateral central and basal amygdaloid nuclei and to the contralateral posterior division of the dorsal ventricular ridge and amygdaloid complex via the stria terminalis. It also projects to the preoptic division of the stria terminalis, but connections with the stria medullaris do not appear to be present.

The central and basal amygdaloid nuclei also contain three cellular populations: fusiform, small projection, and stellate neurons. The

fusiform neurons are very similar in appearance to those observed in the periventricular preoptic nucleus. Their cell bodies are located primarily in the basal amygdaloid nucleus. One polar dendrite projects into the lateral olfactory tract and the other polar dendrite projects into the central amygdaloid nucleus. Their axons enter the stria medullaris or project into the central amygdaloid nucleus. The small projection and stellate neurons present no relationships different from those described in the dorsal ventricular ridge (pars anterior et posterior).

The central and basal amygdaloid nuclei receive both ipsilateral and contralateral inputs from the pyriform cortex, lateral olfactory tract, and input from the homolateral superficial layer of the posterior division of the dorsal ventricular ridge. Both nuclei appear to project into the stria medullaris and stria terminalis. The exact contralateral amygdaloid distribution, if any, was not possible to determine due to the nature of the ablations made in the present study.

CORTICAL CENTERS

(Figs. 2 through 6, 8B, 9A and B, 10, 15, 17A, 18, and 19). Turtles, like all other tetrapods, possess three main divisions in the roof of the telencephalon. The medial surface forms the hippocampal cortex, the dorsal surface the dorsal cortex, and the lateral surface the pyriform cortex. Rostrally these cortices are separated by cell free regions (Fig. 1). Caudally, however, they can be distinguished only by differences in cell type and connections.

The hippocampal cortex (Fig. 8B) does not extend as far into the rostral pole as the dorsal and pyriform cortices. The hippocampus begins approximately two millimeters behind the dorsal cortex (Fig. 11). It is divisible throughout its length into a pars dorsomedialis and a pars dorsalis. The dorsomedial division forms a more compact cellular layer than the dorsal division (Fig. 1). In the lizards, the dorsomedial division is composed primarily of correlation cells (Northcutt, 1967), and the dorsal division of double pyramid and projection cells. Such a clear-cut division in turtles does not exist. The cell bodies are located more periventricularly in the western painted turtle than in the green iguana. The alveus is not as well developed, and a large number of the axons of these cells course superficially to pass just above the upper limit of the layer of the cell bodies. There is marked variation among genera of turtles in the development of the alveus.

The hippocampus of the western painted turtle contains the same neuronal populations observed in alligators (Crosby, 1917) and the

green iguana (Northcutt, 1967). These are: goblet, correlation, double pyradimal, small projection, and intrinsic neurons. The goblet and correlation cells are confined to the rostral region of the pars dorsomedialis. The double pyramidal cells are few in number and do not form a compact, distinct, dorsomedial division as in the green iguana. The small projection cells are found in both divisions of the hippocampus and their dendrites are heavier and longer than in the green iguana.

The hippocampus continues posteriorly along the entire length of the telencephalon and forms the posteromedial pole of the telencephalon. Ablation of the hippocampus (Cp 17, 18, 21, 24, and 27) resulted in degeneration of the hippocampal commissure, and terminal degeneration in the contralateral hippocampus (Fig. 18D). All of these ablations also included the dorsal cortex however. Ablation of the dorsal cortex in Cp 22 also resulted in degeneration of the hippocampal commissure, and light degeneration in the contralateral medial and dorsal cortices. The difference in the intensity of degeneration between these ablations suggests that the hippocampus, dorsomedial division of the dorsal cortex, and perhaps the dorsolateral division of the dorsal cortex contributes cortical association fibers to the hippocampal commissure. A more definite resolution will require more discrete ablations.

It is possible that the hippocampus distributes fibers to the amygdaloid nuclei in the caudal pole. No experimental material is available to confirm this possibility, but the normal material suggests such connections where the hippocampus is in contact with these nuclei ventroposteriorly.

Unilateral ablation of the olfactory bulb (Cp 13) results in very limited degeneration in the rostral hippocampus. Thus, it appears that whatever olfactory information is transmitted to the hippocampus arrives only after synapsing in other telencephalic centers. A possible exception to this case will be described in reference to the anterior olfacto-habenular tract.

Ablation of the hippocampus and dorsal cortex (Cp 17) results in degenerating fibers of passage which can be traced to the nucleus dorsomedialis anterior thalami and nucleus lateralis thalami (nomenclature of Papez, 1935). Ablation of the dorsal cortex alone (Cp 20 and 26) also shows degeneration within these nuclei. Therefore, it is impossible to decide on this basis, the exact source of degeneration. The hippocampus may be involved, but it will require ablation of this region alone to establish this possibility. The major efferent connections of

the hippocampal cortex are discussed along with the other divisions of the medial forebrain bundle.

The dorsal cortex begins at the rostral pole of the telencephalon where it is bordered laterally by the pyriform cortex, which appears a few sections in advance of the dorsal cortex. The dorsal cortex does not reach the caudal pole but stops just short of it where it is replaced medially by the hippocampal cortex, and laterally by the pyriform cortex. Medially, the dorsal cortex is distinguished from the hippocampal cortex by a constriction in the scattering of cells between the dorsal cortex and the hippocampus (Figs. 1 and 2). Although this division is clear in Klüver preparations, no such boundary can be observed in Golgi material, and it is probable that no sharp functional differences occur along this boundary. This view is reinforced in the discussion of the fiber connections between the hippocampus and dorsal cortex.

The lateral border of the dorsal cortex is much clearer. Rostrally, it is located just ventral and medial to the upper border of the pyriform cortex (Figs. 1 and 2). This border is recognized by an abrupt change in cell type between the two formations, and by a fiber bundle passing between the lateral border of the dorsal cortex and the ventral border of the pyriform cortex. Caudally, the lateral border is not so easily observed. It normally occurs somewhat dorsal to the dorsolateral extension of the lateral ventricle (Fig. 5). At this point, the cells of the dorsal cortex are widely scattered across the depth of the roof, and are clustered together in groups of four to seven cells each. In contrast, the pyriform layer is compact, and the cell bodies are packed against each other forming a sharp layer. A similar type of clustering is seen at the rostrolateral border of the dorsal cortex. The clustering appears to be due to the passage of fibers through the cortical layer at each of these points.

The dorsal cortex is divided throughout its length into dorsolateral and dorsomedial divisions. These divisions are based on differences in type of cells present, and the afferent and efferent connections to these divisions. Figure 10 illustrates part of these differences. Figures 10A and 10C are photomicrographs taken from typical regions of the dorsomedial and dorsolateral divisions of the dorsal cortex. Figures 10B and 10D are reconstructions based on the photographs and two sections (240μ in thickness) preceding and following the photographed sections. The line drawings were produced by tracing the actual photographs taken at different focal depths of the described sections.

The dorsomedial division of the dorsal cortex is composed of three neuronal populations: pyriform projection neurons (Type A), double

pyramidal neurons (Type B), and intrinsic or associative neurons (Type C). The largest population consists of pyriform projection neurons. These neurons possess pear-shaped cell bodies with two apical dendrites which are highly branched and extend to the surface of the cortex. Their axons normally arise from the lateral surface of the cell bodies and project toward the center of the cortical depth where they turn medially and join the hippocampus. They receive synaptic input from both the superficial cortical fiber layer and the deep alveus. Some of these cells (Cell D, Fig. 10B) appear to pass their axons into the alveus. They may represent a different class of neurons since they possess basal dendrites which are not observed in the pyriform projection cells.

The second population consists of double pyramidal neurons (Cell B, Fig. 10B). These neurons are always located near the ependymal layer and are larger than the cells of the other populations. They possess multiple dendritic radiations similar to those of the pyriform projection cells, but their axons pass into the alveus rather than into the more dorsal fiber fields.

The third population is scattered throughout the depth of the cortex and appears to be primarily intrinsic or associative in nature. They possess lateral radiating dendrites which normally form synapses with fibers of the superficial and middle layers. Their axons are highly branched and form multiple contacts within the cortex.

Ablation of all of the cortices (hippocampal, dorsal, and pyriform cortices) results in heavy degeneration dorsal to their cellular layers (Fig. 18A). This suggests that the majority of the fibers, both afferent and efferent, course above the cell layers. This is not surprising because of the close proximity of these cellular layers to the ependyma.

None of the ablations were confined to the dorsomedial division of the dorsol cortex. However, comparison of Cp 26 (which involves only the dorsal cortex) with Cp 22 (which primarily involves the dorsolateral division of the dorsal cortex) allows some deductions to be made with caution. Ablation of the dorsomedial cortex results in heavy degeneration along the medial and lateral roof of the cortex (Fig. 15D). This can be traced along the hippocampal surface and into the basal regions of the telencephalon. While degeneration is observed in the ablation which involves the dorsolateral cortex (Cp 22), this degeneration is confined medially, to the dorsomedial division of the dorsal cortex, suggesting that the degenerated axons are of an intrinsic nature. Ablation of the dorsal cortex (Cp 26, Fig. 13) results in degeneration in the anterior dorsomedial and lateral thalamic nuclei. Similar thalamic degeneration was observed in Cp 17 and 22 which involved the

dorsomedial division of the dorsal cortex and the hippocampus, and the dorsolateral division of the dorsal cortex respectively. These three animals (Cp 17, 22, and 26) present a combination of overlap in ablations which suggests that both the dorsolateral and dorsomedial divisions of the dorsal cortex form connections with the two thalamic nuclei named above.

Ablation of the dorsal cortex (Cp 26) results in degeneration in the hippocampal commissure, the contralateral hippocampus, and the contralateral dorsal cortex. If the hippocampus is involved (Cp 17), the entire hippocampal commissure degenerates (Fig. 16A). Thus the dorsomedial division of the dorsal cortex, and the hippocampus possess associative fibers which project to the contralateral cortical regions. From the above listed ablations, it is not possible to exclude the dorsolateral division of the dorsal cortex from association with this system. However, other evidence (Klüver series) suggests that this division of the dorsal cortex may possess associative projections which pass through the anterior commissure rather than the hippocampal commissure. In horizontal sections, a myelinated component can be traced from the dorsolateral division of the dorsal cortex to the anterior commissure. Ablations which involve the dorsal cortex, pars dorsolateralis, (Cp 20, 22, and 26) show degeneration in the anterior commissure. Unfortunately, all of these ablations involve other structures which might also have such connections. Therefore, it can only be suggested on the strength of normal descriptive observations that connections between the two dorsal cortices (pars dorsolateralis) exist. The remaining efferent connections of the dorsal cortex (pars dorsomedialis) are described as part of the medial forebrain bundle.

The dorsolateral division of the dorsal cortex (Fig. 10) is composed of the following cellular populations: small pyramidal neurons (Type A), large pyramidal neurons (Type B), polygonal projection neurons (Type C), intrinsic stellate neurons (Type D), and pyriform projection neurons (Type E). The neurons of the pars dorsolateralis are more compact than those of the pars dorsomedialis. The cells of the dorsolateral division are farther removed from the ependymal layer, and the alveus is more developed. An exception to this statement, however, exists in the lateral rostral region which has been termed the pallial thickening by Johnston (1915). Here the cells are clustered, and an additional cell type is dominant (Fig. 9B). This cell type is a polygonal projection cell similar to Cell-type C in the more medial portion of the pars dorsolateralis of the dorsal cortex.

The large and small pyramidal cells of the pars dorsolateralis (Fig. 10D) are common and appear to be very similar to neocortical pyra-

midal cells observed in mammals. They possess a long apical dendrite along which numerous synapses can be observed. The axo-dendritic endings appear to belong to axons projecting from the superficial fibrous layer. The pyramidal cells possess basal dendrites which are in contact with the alveus, and their axons project into the alveus and appear to sweep laterally toward the core nucleus of the anterior division of the dorsal ventricular ridge.

The polygonal projection cells (Type C, Fig. 10D) possess three to four dendritic trunks which are highly branched. Their axons also project into the alveus. Their dendrites appear to occupy a larger field than the pyramidal neurons, and they are more similar in structure to the neurons of the pars dorsomedialis than to the pyramidal neurons.

The stellate associative neurons (Type D, Fig. 10D) possess multiple dendrites which span larger fields than any of the other cellular elements, and their axons branch extensively among the other cellular elements.

The pyriform projection neurons (Type E, Fig. 10D) appear identical to the pyriform cells of the dorsomedial division of the dorsal cortex. Their axons could not be traced for long distances; presumably they are identical to the pyriform cells of the pars dorsomedialis.

The polygonal projection cells of the rostral thickening of the pars dorsolateralis differ from the other polygonal neurons in their dendritic pattern (Fig. 9B). Two main dendritic trunks branch from opposite sides of their cell bodies. The dendrites are long and project into the superficial fibrous layer of the dorsal cortex where they contact the fibers of an ascending thalamic pathway. The axons of these cells arise from that surface of the cell body nearest the dorsal ventricular ridge and pass into the core nucleus.

As previously noted, ablation of the dorsolateral division of the dorsal cortex results in terminal degeneration in the homolateral core nucleus, anterior division of the dorsal ventricular ridge, and lateral division of the paleostriatum. The path of this degeneration is a complex one. In the rostral half of the telencephalon, a group of fibers can be traced from the dorsal peduncle of the lateral forebrain bundle to the dorsolateral division of the dorsal cortex. This fiber complex arises from the dorsal peduncle and projects laterally and anteriorly until it reaches the rostral pole of the telencephalon. At this point, it turns dorsally and ascends toward the dorsal cortex. It radiates from the dorsolateral border of the paleostriatum and ascends between the medial border of the pyriform cortex and the lateral border of the core nucleus. At this level, it penetrates the cellular layer of the dorsolateral division of the dorsal cortex and turns medially and caudally

to fan out in the superficial fibrous layer of the dorsolateral division of the dorsal cortex. While this fiber complex has been described as an ascending system, it contains descending fibers. Fibers can be traced from the dorsolateral division of the dorsal cortex into this system both in normal and experimental preparations. These fibers either turn and enter the anterior division of the dorsal ventricular ridge or pass to the lateral division of the paleostriatum.

Analysis of this fiber system is further complicated by the fact that projections to and from the anterior division of the dorsal ventricular ridge and the lateral forebrain bundle occur in this region. The core nucleus lies on the medial border of this dorsal cortical pathway and is the focal point of an equally complex radiating fiber system.

A more complete understanding of this rostral telencephalic fiber complex will require detailed experimental work. For this reason, the pathway will not be named since any nomenclature would be premature at this point. However, for purposes of identification this pathway has been called the "internal capsule" in *Cistudo (= Terrapene)* by Johnston (1915), the "anterior division of the dorsal peduncle of the lateral forebrain bundle" in *Terrapene* by Carey (1967), and the "fiber bundle of the pallial thickening" in *Testudo* by Hewitt (1967).

Another fiber bundle is associated with the dorsal and pyriform cortices in the region just posterior to the anterior commissure in several of the specimens examined. This bundle is myelinated and is seen just rostral to the point where the lateral edge of the dorsolateral division of the dorsal cortex loses contact with the dorsal ventricular ridge. This occurs as the inferior horn of the lateral ventricle joins the body of the lateral ventricle. Two types of fibers are observed. The first group of fibers appears to connect the posterior division of the dorsal ventricular ridge with the dorsal cortex. The second group appears to originate in the alveal layer of the dorsal and pyriform cortices. These fibers sweep along the medial edge of the pyriform cortex and enter the stria terminalis. They cannot be followed beyond this point, and it is not known whether they are commissural or preoptic in distribution. Gamble (1956) has recognized a cortical division of the anterior commissure in *Testudo*. The western painted turtle also may possess such a component but the experimental ablations are not sufficiently precise to give a definite answer.

The pyriform cortex in the western painted turtle is the first cortical layer seen in rostral sections. Rostrally, it lies dorsal and lateral to the lateral edge of the dorsal cortex (Figs. 1 and 2). Posteriorly, the pyriform cortex occupies the entire lateral wall of the telencepha-

lon, and is fused at its dorsal edge with the dorsal cortex and at its ventral edge with the posterior division of the dorsal ventricular ridge (Fig. 5). Rostrally, the pyriform cortex is divided into a large-celled dorsal lamina and a small-celled ventral lamina. As the pyriform cortex passes posteriorly, these two laminae fuse and produce a single cortical layer. Gamble (1956) reported that the ventral lamina forms the nucleus of the lateral olfactory tract in *Testudo*. Similar relationships are not seen in *Chrysemys*. In fact, a nucleus of the lateral olfactory tract is not identifiable in the *Chrysemys* material. There are no cell masses in the region where a nucleus of the lateral olfactory tract is normally expected. However, the basal amygdaloid nucleus of *Chrysemys* may contain cells normally recognized as part of the nucleus of the lateral olfactory tract. The connections of the basal amygdaloid nucleus are similar to those of the nucleus of the lateral olfactory tract, and expect for its posterior position, probably either name would be justifiable for this cell mass. The division by all workers of the amygdaloid ridge into nuclei is rather arbitrary as it is based on little information about distribution of fibers and their connections.

The structure and function of the pyriform cortex in reptiles has been largely ignored, and the present work is no exception. No ablations were confined to the pyriform cortex and therefore little can be said about its projections. As is pointed out in the fiber descriptions, olfactory bulb ablations demonstrate that all parts of the pyriform cortex receive secondary olfactory fibers.

Golgi-Cox preparations of the pyriform cortex reveal a highly organized cortex. It possesses at least six cellular populations: fusiform cells, large and small polygonal cells, pyramidal cells, double pyramidal cells, and pyriform cells. The fusiform cells are located throughout the cortex and are oriented at right angles to the dendrites of the other cellular types; they appear to be intrinsic elements. Two types of polygonal cells are observed. The ventral lamina and the dorsal lamina both contain small polygonal cells (Fig. 9A). Large polygonal cells appear in the posterior division of the dorsal lamina. Their cell bodies lie dorsal to the general layer of cell bodies, and show best in horizontal sections. They possess two main dendritic trunks which project at right angles to the dendrites of the other cells and may possess a total dendritic field of 250μ. Their axons could not be followed. The pyramidal and pyriform cells possess the classical features of such cell types and are located throughout the dorsal lamina. They appear to be the main projection elements of the pyriform cortex.

V. FIBER CONNECTIONS

The description of the major fiber systems in the telencephalon of the western painted turtle is summarized using both normal and experimental material. Most of the descriptions are based in part on normal material and as such are speculations as to probable connections.

Tractus Olfactorius

In accordance with earlier work, this system has been divided into three divisions: a medial olfactory tract, an intermediate olfactory tract, and a lateral olfactory tract. The first two tracts are confined to the rostral pole of the telencephalon and are not highly developed. The lateral olfactory tract is extensive and is the major tract of the three in the western painted turtle.

TRACTUS OLFACTORIUS MEDIALIS

Unilateral ablation of the anterior portion of the olfactory bulb (Cp 13) results in degeneration throughout the internal plexiform layer. Degeneration in this layer presumably results from destruction of the mitral and granular cells. In the peduncle, the internal plexiform layer is broken up into three superficial regions of degeneration.

Each of these regions corresponds to an olfactory tract. The medial region lies just superficial to the parolfactory region. This medial degeneration component is very light and appears to distribute to the rostral region of the parolfactory nuclei and hippocampus. Some degenerating fibers could also be traced to the anterior olfactory nucleus along its rostral medial border.

TRACTUS OLFACTORIUS INTERMEDIUS

This tract is represented in experimental material (Cp 13) as the ventral degenerating component lying lateral and ventral to the medial component. It is closely related, topographically, to the third degenerating component, the lateral component, and may actually be a part of it. Degenerating fibers can be traced from the ventral component to the anterior olfactory nucleus (Fig. 14B). Fibers pass through the olfactory tubercle as part of the projection to the anterior olfactory nucleus and appear to terminate in both of these nuclei.

No degeneration was observed in the anterior commissure in any animals with ablations of the olfactory bulb (Cp 12, 13, and 23). Thus there does not appear to be any second order olfactory fibers interconnecting the olfactory bulbs via the anterior commissure. Similar results were reported by Gamble in *Lacerta* (1952) and *Testudo* (1956).

TRACTUS OLFACTORIUS LATERALIS

(Figs. 15A, B, and C). This tract is represented in Cp 13 by the lateral degenerating component. Rostrally, it lies superficial to the ventrolateral edge of the olfactory tubercle and extends laterally and dorsally until it reaches the dorsal edge of the pyriform cortex. Degenerating fibers could be seen to extend throughout the length of the homolateral pyriform cortex. In both the anterior and posterior divisions of the pyriform cortex (Figs. 15A and B), the degenerating fibers are mainly distributed in the superficial fibrous layer of the cortex. However, some degeneration could be observed in the cellular layer of the pyriform cortex (Fig. 15C). More anteriorly, degenerating fibers could be traced to the anterior olfactory nucleus and the olfactory tubercle.

Degenerating fibers in the homolateral lateral olfactory tract could also be traced into the basal and central amygdaloid nuclei but not into the superficial layer of the posterior dorsal ventricular ridge.

The crossed components of the lateral olfactory tract first described

by Gamble (1952) are also obvious. Degenerating fibers could be traced into the stria medullaris and followed through the habenular commissure to the contralateral stria medullaris. Here the degenerating fibers follow two pathways. The first pathway corresponds to the lateral corticohabenular tract which flows over the superficial ventromedial surface of the telencephalon (Fig. 5). Degenerating olfactory fibers could be traced in this pathway to the posterior pyriform cortex, basal amygdaloid nucleus, and the central amygdaloid nucleus. The second group of degenerating fibers follows the anterior olfactohabenular tract. This pathway could be seen as a compact degenerating bundle arising from the posterior ventromedial surface of the telencephalon and projecting dorsally and medially until it assumed a position on the medial telencephalic wall just superficial to the parolfactory and hippocampal formations. This pathway could be traced to the rostral pole of the telencephalon where it distributed fibers to the parolfactory nuclei (Fig. 14C), the rostral hippocampus and the dorsal cortex, and the anterior olfactory nucleus.

Golgi studies suggest that other connections are made with nuclei scattered along the path of the olfactory radiations. It is probable that fibers exist in the olfactory radiations which are tertiary in nature and do not degenerate when the olfactory bulbs are ablated. For example, fibers from the anterior olfactory nucleus to the parolfactory nuclei and hippocampus probably exist.

Tractus Tuberculo-Corticalis

The absence of olfactory fibers throughout the length of the hippocampus, except in its most rostral extent, poses the interesting question of the nature of the sensory input to the hippocampus. In Golgi preparations, fibers can be traced between the tubercle and the hippocampus; the nature and direction of these fibers is not known. Ablation of the hippocampus and dorsomedial division of the dorsal cortex (Cp 17, Fig. 11) results in terminal degeneration among most nuclei of the ventromedial basal wall of the telencephalon. This suggests that part of the fibers in this region are efferent from the dorsomedial pallium to the ventromedial basal nuclei.

Parolfacto-Cortical Tracts

Axons from both parolfactory nuclei ascend in the fornix system and pass to the hippocampus. In the rostral portion of the telencepha-

lon where the precommissural fornix fibers are few, some axons of the parolfactory nuclei can be traced intact into the hippocampal formation. These fibers constitute the tractus parolfacto-corticalis.

Cortico-parolfactory connections also exist; ablation of the dorsal cortex (Cp 20, Fig. 12) results in terminal degeneration in the parolfactory nuclei. Golgi preparations show neurons of the hippocampus that project to the parolfactory nuclei, and ablations of the dorsomedial division of the dorsal cortex and the hippocampus (Cp 17) result in massive terminal degeneration in both parolfactory nuclei. This pathway is termed the tractus cortico-parolfactorius.

Commissures

Turtles possess only two telencephalic commissures rather than three, as do lizards, snakes, and sphenodons. These are the anterior and the hippocampal commissures. The hippocampal commissure has often been termed the anterior pallial commissure in contrast to the posterior pallial commissure or commissura aberrans of Elliot Smith (1903).

ANTERIOR COMMISSURE

(Figs. 3 and 16A and B). The myelinated fibers of this commissure have traditionally been divided into two major components: an olfactory division, and a commissural division of the stria terminalis. A well-developed olfactory division is not seen in the western painted turtle as in lizards. In either group, ablation of the olfactory bulbs does not result in degeneration of the so-called olfactory division, which suggests that this division is not composed of olfactory bulb fibers. Analysis of normal material suggests that this "olfactory" division may be composed of associative fibers betwen the two anterior olfactory nuclei. Confirmation of this point will require experimental ablation of the anterior olfactory nuclei.

The second division of the commissure also appears to bear an inadequate name. Although fibers of the stria terminalis do exist in the anterior commissure, it appears to contain other fiber systems as well. Ablation of the dorsal cortex and pyriform cortex (Cp 19, Fig. 11) results in degeneration in the anterior commissure (Fig. 16B). Earlier reference was made to normal material which suggested that an associative pathway exists between the pyriform cortices and the dorsolateral divisions of the dorsal cortices via the anterior commis-

sure. In addition, ablation of the anterior or posterior division of the dorsal ventricular ridge results in degeneration in the anterior commissure.

COMMISSURA HIPPOCAMPI

(Figs. 3 and 16A and B). Unlike the fibers of the anterior commissure, the fibers of the hippocampal commissure are unmyelinated in the western painted turtle. This commissure contains fibers of association between the hippocampal cortices and the dorsomedial divisions of the dorsal cortex. Projection fibers from the hippocampus and dorsomedial division of the dorsal cortex also cross through the hippocampal commissure to terminate in other nuclei of the contralateral telencephalon. The distribution of these fibers is described in the descriptions of the fornix and medial forebrain bundle.

Tract of the Diagonal Band of Broca

Golgi preparations reveal fibers which run between the parolfactory nuclei and the amygdaloid nuclei in the same hemisphere. No definitive statement on connections can be made, since no lesions were placed specifically in the parolfactory nuclei, and ablations which did involve the subpallial amygdaloid nuclei also involved other regions with fibers in this tract.

Stria Terminalis

This system is divided into a commissural division and a preoptic division. Both divisions of the stria terminalis originate in the posterior ventrolateral telencephalon (Fig. 4). Fibers of the stria terminalis converge and pass through the paleostriatum and turn medially and dorsally to pass dorsal to the lateral forebrain bundle. At this point, the two divisions separate and the commissural division passes rostrally to enter the anterior commissure (Fig. 3). The commissural division contains interhemispheric fibers between the two posterior divisions of the dorsal ventricular ridge and possibly between the basal and central amygdaloid nuclei. This division also appears to contain pyriform interhemispheric fibers which were described in conjunction with the dorsolateral component of the dorsal cortex.

The preoptic division, after reaching the lateral forebrain bundle, turns ventrally and passes into the periventricular preoptic and hypothalamic nuclei. All three nuclei of the posterior lateral wall of the telencephalon contribute fibers to the preoptic division of the stria terminalis. The pyriform cortex may also contribute to this system but this must be confirmed by additional study.

Intrahemispheric Fiber Systems

Three fiber groups are normally found associated with the pallial formations in all higher vertebrates: alveus, fimbria and fibrae tangentiales. These groups, for the most part, do not form homogeneous bundles containing fibers projecting to a single area. Commonly, they are collections of fibers arising from a single area but projecting to several different regions. These fiber groups usually also contain associative elements between two or more of the pallial divisions, and fibers of passage whose only relationship to the fiber group is that they pass through it. In addition, an associative system within the dorsal ventricular ridge will be described.

The alveus is a group of fibers located along the ventral surface of all pallial elements in the western painted turtle. It contains association and projection fibers from all pallial elements. The alveus is poorly developed in turtles as compared to other reptiles. The alveus also contains afferent fibers which project to the pallial regions. For the most part, however, these afferent fibers do not end in the alveal layer but pass through the cellular layer of the cortices and synapse on dendrites in the superficial fiber layer.

The fimbria is a dense layer of fibers located along the ventromedial border of the hippocampus. It occupies a similar position in the green iguana. However, many fibers join this complex from the dorsal superficial fibrous layer rather than from the alveal layer, as in lizards. The fimbria contains fibers from the hippocampus and dorsomedial division of the dorsal cortex. After joining the fimbria, these fibers pass rostrally to join the fornix system, the hippocampal commissure, and perhaps the medial cortico-habenular tract.

The fibrae tangentiales are intrinsic elements which interconnect the cortical fields. These fibers mainly arise from horizontal cells located in the superficial fiber layer. The superficial fiber layer also contains fibers of Type I neurons of the cellular layer, as well as sensory fiber terminals projecting to the cortical regions.

Ablation of the anterior division of the dorsal ventricular ridge (Cp

17, Fig. 11) results in terminal degeneration in the posterior division of the dorsal ventricular ridge (Fig. 17D). While part of this degeneration is probably due to the interruption of afferent fibers passing into the dorsal ventricular ridge, Golgi preparations demonstrate that an intrinsic fiber system interconnecting the two divisions of the dorsal ventricular ridge is located on the ventricular surface of this structure. Thus part of the degeneration involves this intrinsic system.

Fornix

The fornix is the major efferent pathway of the hippocampus. It also contains fibers of other origins. Ablation of the dorsal cortex (Cp 17, 18, and 19; Fig. 11) results in degeneration in the fornix, and in terminal degeneration in lower nuclear groups which receive fornix fibers. None of the ablations were confined to the hippocampus, thus a division of fibers from it and the dorsal cortex (pars dorsomedialis) cannot be made. Analysis of Golgi material suggests that these two cortical regions are very similar with regard to direction of their output and that no sharp architectonic division exists between their fields except for minor differences in the compactness of the cellular layer. In lizards and snakes, there is a pronounced cellular discontinuity in the cortical cellular layer between hippocampus and dorsal cortex (pars dorsomedialis). A similar break is not seen in turtles.

Although the fornix is described here as a distinct fiber system, it can also be considered as a subdivision of the medial forebrain bundle. The origin and radiation of the fornix within the cortical regions is distinct from the other divisions of the medial forebrain bundle, but in the basal regions several components of the fornix form connections similar to those of other components of the medial forebrain bundle. Inclusion of the fornix as a pallial contributor to the medial forebrain bundle means that the telencephalon is connected to lower brain centers via two divisions of a fiber system. The lateral basal and lateral pallial regions are connected via the lateral forebrain bundle, and the medial basal and medial pallial regions are connected via the medial forebrain bundle.

The fornix complex is traditionally divided into three components: the commissura fornicis, the columna fornicis, and the fornix longus.

COMMISSURA FORNICIS

This is a component of fibers located in the hippocampal commis-

sure. This component contains fornix fibers which decussate and project to the contralateral cortical areas and other telencephalic centers.

COLUMNA FORNICIS

This component contains fibers which do not decussate but project to homolateral nuclei. Ablation of the dorsal cortex (pars dorsomedialis) and hippocampus results in terminal degeneration in both hemispheres. Homolaterally, degenerating axons were traced to all nuclei of the parolfactory region, the periventricular preoptic nucleus, the anterior hypothalamic nucleus, and the dorsal ventricular ridge (pars posterior). Degenerating axons which terminate in the dorsal ventricular ridge pass from the cortical regions into the fornix. At the level of the hippocampal commissure, these fibers curve laterally and enter the stria terminalis where they project into the central amygdaloid nucleus of the dorsal ventricular ridge.

Ablation of the dorsal cortex (pars dorsomedialis) and the hippocampus results in degeneration in two thalamic nuclei: anterior dorsomedialis nucleus and lateral nucleus. Degenerating fibers from these nuclei pass along the ventral border of the nucleus rotundus where they curve medially and pass just lateral to the periventricular preoptic nucleus. This fiber bundle then enters the medial forebrain bundle. Both of these thalamic nuclei appeared to show terminal degeneration. Therefore, this pathway was interpreted as efferent from the medial pallial regions. However, further studies are needed to confirm this possibility.

FORNIX LONGUS

This component classically includes fibers which decussate in the hippocampal commissure and project to contralateral regions. Two major pathways have been identified and traced in the experimental material. Ablation of the medial cortical areas (dorsomedial division of the dorsal cortex and the hippocampus) results in degenerating fibers which pass rostrally in the fimbria and decussate in the hippocampal commissure. After decussating, one component passes ventrally, terminating in part in the parolfactory region and in part entering the medial forebrain bundle and terminating in the periventricular preoptic nucleus (Fig. 14D). The second component after decussating in the hippocampal commissure, enters the stria terminalis and terminates in the central amygdaloid nucleus. Some of the fornix fibers which

decussate and enter the medial forebrain bundle may project caudally and dorsally to enter the dorsal thalamic nuclei, and two of the preparations show light degeneration in this region. However, the stria medullaris borders both of these thalamic nuclei as a loose bundle of fibers. In every ablation, the stria medullaris demonstrated degenerating fibers complicating interpretation of degeneration in these thalamic nuclei.

Stria Medullaris

The stria medullaris arises from both basal and pallial regions of the telencephalon and projects to the habenular nuclei (Figs. 4 through 6). The exact nature and conductional direction for the components of the stria medullaris is not completely known. Crosby (1917) followed the nomenclature of Herrick (1910) and recognized six components of the stria medullaris: tractus cortico-habenularis medialis, tractus cortico-habenularis lateralis anterior et posterior, tractus olfacto-habenularis medialis, lateralis, et posterior. Kappers, Huber, and Crosby (1936) retained Herrick's nomenclature but recognized a second component of the tractus cortico-habenularis medialis, a tractus cortico-habenularis medialis pars inferior. Goldby (1934) did not follow exactly the nomenclature of these workers but divided the stria medullaris into four groups: lateral and medial cortico-habenular fibers, and lateral and medial olfacto-habenular fibers. In addition, he recognized a new medial component, the anterior olfacto-habenular tract, as a subdivision of the medial olfacto-habenular fibers.

The anterior and posterior divisions of the lateral cortico-habenular tract and the anterior olfacto-habenular tract are now known to consist primarily of crossed olfactory fibers of the lateral olfactory tract (Gamble, 1952 and 1956). Results of ablation of the olfactory bulb in the western painted turtle are in agreement with the description of the contralateral projections of the lateral olfactory tract by Gamble. However, there is disagreement on the extent of the homolateral projections.

Ablation of the hippocampus (Cp 17, Fig. 11) results in degenerating fibers which were traced to the homolateral habenular nucleus. This suggests that the medial cortico-habenular tract does exist and that its connections have been correctly interpreted in the literature as a homolateral tract connecting the hippocampus and habenula.

The remaining tracts are all basal in origin and presumably project to the habenula. No ablations were placed in the preoptic nucleus or

habenula, and therefore nothing is known about their distribution and direction of conduction. These tracts are believed to interconnect the preoptic nucleus and the habenula.

Olfactory Projection Tracts

Two tracts interconnecting the hypothalamic centers with the nuclei of the lateral hemispheric wall have been described in the literature. These are the ventral olfactory projection tract and the olfactory projection tract of Cajal. The ventral olfactory projection tract is thought to arise from cells of the basal amygdaloid nucleus, dorsal ventricular ridge (pars posterior) and the pyriform cortex, and is thought to project to the hypothalamus. This pathway could be recognized in normal material as a ventral division in the collection of fibers which curve around the ventromedial edge of the telencephalon to enter the thalamus. Ablation of the posterior pole of the telencephalon (Cp 24 and 27, Fig. 13) showed heavy degeneration in this collection of fibers. However, the preoptic division of the stria terminalis also passes through this bundle and differences in fiber origin, if any, could not be determined due to the large size of the ablations. Therefore the existence of a ventral olfactory projection tract, separate from the preoptic division of the stria terminalis, has not been established. Yet clearly, basal centers of the amygdaloid complex do project to the hypothalamic centers.

The olfactory projection tract of Cajal is thought to arise from cells of the interstitial nucleus (Fig. 4) and the basal amygdaloid nucleus. This tract is thought to pass dorsal to the medial forebrain bundle and to terminate in the hypothalamus. Experimentally, nothing is known of its connections.

Basal Forebrain Bundle

Two great fiber components constitute the basal forebrain bundle. In normal material, this bundle can be traced with certainty between the telencephalon and the mesencephalon. Within the mesencephalon and the diencephalon, it is divided into dorsal and ventral components, but on entering the telencephalon, the components are divided into lateral and medial divisions. This change in topographical divisions has resulted in diverse nomenclature. The basic divisions of the basal forebrain bundle are considered here as lateral and medial as is most frequently done in the literature (Kappers, Huber, and Crosby, 1936).

LATERAL FOREBRAIN BUNDLE

(Figs. 2 through 6, 8C, 16C and D, 17A, and 18B and C). The lateral forebrain bundle is the major pathway connecting the lateral half of the telencephalon with lower centers. It has been divided into a dorsal and a ventral peduncle (Huber and Crosby, 1926). The dorsal peduncle connects the telencephalon with the dorsal thalamus, and the ventral peduncle connects the telencephalon with the ventral thalamus and mesencephalon. The dorsal peduncle is primarily afferent from the thalamus to the telencephalon, and the ventral peduncle is primarily efferent from the telencephalon to lower centers (Powell and Kruger, 1960).

Throughout the rostral thalamus (Fig. 5) and as it enters the telencephalon (Fig. 4), the dorsal penducle is a compact circular bundle of fibers. Caudally, it spreads over the dorsal thalamic nuclei (Fig. 6). On entering the telencephalon, it forms the more ventral of the two divisions which compose the lateral forebrain bundle (Fig. 4). The dorsal peduncle is divided into four major tracts: anterior, intermedial, medial, and internal. The anterior tract arises from the anterior dorsomedial and lateral thalamic nuclei (Fig. 6). In the western painted turtle, the fibers of this tract appear to encapsulate these nuclei and enter the dorsal peduncle after curving laterally around the dorsal peduncle. The anterior tract, as it enters the telencephalon, is the most ventral and lateral component of the dorsal peduncle. The anterior tract passes rostrally and laterally into the rostral portion of the telencephalon where it turns and fans out dorsal to the paleostriatum. It radiates medially from a compact bundle just medial to the pyriform cortex, and its fibers have been previously described as the "fiber bundle of the pallial thickening." The anterior tract appears to terminate in the core nucleus of the dorsal ventricular ridge and the dorsolateral division of the dorsal cortex.

Ablation of the dorsal cortex (Cp 17, 18, 19, and 20; Figs. 11 and 12) results in degeneration along the anterior tract into the dorsal peduncle. The degenerating fibers could not be traced within the bundle in transverse sections, but could be traced again at the caudal end of the tract where they emerged to end in the thalamic nuclei. Since ablation of the medial cortical regions also results in degeneration in these same nuclei (anterior dorsomedial and lateral), and since none of the ablations are definitely restricted to the dorsolateral cortex, the direction of conduction could not be determined from the ablations. However, the anterior tract could be observed, both in Bodian and in Golgi preparations, to project through the cellular layer of the dorsolateral

division of the dorsal cortex and fan out in the superficial fibrous layer. In Golgi preparations, axons from this bundle are observed to end on the dendrites of cells of the cellular layer.

Rostrally, analysis of the anterior tract is further complicated (Fig. 17A) as it is interwoven with efferent fibers projecting from the cortex to the dorsal ventricular ridge (Fig. 17B) and to the paleostriatum (Figs. 18B and C). In addition, fibers project to the dorsal cortex from the dorsal ventricular ridge via the same pathway. It is possible that efferent fibers from the lateral division of the telencephalon project to the thalamic nuclei via the anterior tract, but ablations which do not involve the dorsomedial division of the dorsal cortex or hippocampus are needed to explore this possibility.

The intermedial tract of the dorsal peduncle of the lateral forebrain bundle arises from the nucleus rotundus as large myelinated fascicles (Fig. 6). The anterior nucleus of Papez (A. vent. ant., Fig. 4) may also give rise to fibers which join this tract. The intermedial tract passes rostrally as a ventromedial component of the lateral forebrain bundle (Fig. 3). It is capped by the fibers of the ventral peduncle of the lateral forebrain bundle and the stria terminalis. As the intermedial tract approaches the rostral half of the telencephalon, it curves dorsally and fans into the lateral paleostriatum (Fig. 2). Some of its fibers may reach the core nucleus of the dorsal ventricular ridge.

Ablations involving the paleostriatum (Cp 18 and 22; Figs. 11 and 12) and dorsal ventricular ridge, pars anterior, show terminal degeneration in the homolateral rotundus (Fig. 16C) but not in the contralateral nucleus rotundus (Fig. 16D). Thus, the intermedial tract may contain efferent fibers from both the paleostriatum and dorsal ventricular ridge to the nucleus rotundus and, perhaps, to the anterior nucleus. However, in one case (Cp 21, Fig. 12), ablation of the paleostriatum resulted in cellular chromatolysis in the nucleus rotundus which suggests that the intermedial tract also contains afferent fibers from the nucleus rotundus to the paleostriatum or dorsal ventricular ridge. Based on the present experimental material it is not possible to decide whether the nucleus rotundus projects and receives projections from both the dorsal ventricular ridge and paleostriatum or only one of these nuclei via the intermedial tract.

The remaining two tracts of the dorsal peduncle of the lateral forebrain bundle (medial and internal tracts) were identified only in the diencephalon. They did not show degeneration following ablation of the telencephalon, which suggests that they may not possess telencephalic connections.

The ventral peduncle of the lateral forebrain bundle is divided into four major tracts or fascicles: dorsal strio-tegmental, ventral strio-tegmental, strio-hypothalamic, and strio-tectal (Huber and Crosby, 1926). The ventral peduncle begins as a fibrous radiation from the paleostriatum and dorsal ventricular ridge areas (Fig. 3). It curves medially and ventrally and becomes more compact as it collects above the more ventral sensory radiations of the dorsal peduncle. As it passes into the diencephalon, it curves around and through the medial edge of the dorsal peduncle and comes to lie directly beneath the dorsal peduncle. Therefore, the ventral peduncle lies ventral to the dorsal peduncle only in the diencephalon. The ventral peduncle (L. f. b. p. v.) remains a fairly compact bundle (Fig. 6) until it reaches the posterior commissure of the diencephalon. It lies medial to the optic tract until it passes into the mesencephalon where it assumes a position on the ventrolateral floor of the tegmentum. In normal preparations, it could be traced just caudal to the exit of the oculomotor nerves where it radiated into the tegmentum.

Ablation of the dorsal cortex (Cp 20 and 26; Figs. 12 and 13) does not result in observed degeneration in the ventral peduncle. However, degenerating fibers are seen just medial to the ventral peduncle and these appear to project to the lateral thalamic nucleus.

Ablation of the dorsal ventricular ridge (Cp 17, Fig. 11) results in degeneration in both homolateral and contralateral ventral peduncles. There is heavy degeneration and even partial loss of fibers in the homolateral ventral peduncle, and light degeneration along the course of the contralateral ventral peduncle.

Ablation of the paleostriatum (Cp 19, 21, 24, and 27; Figs. 11, 12, and 13) results in similar degeneration. Ablation of almost the entire hemisphere (Cp 21, Fig. 12) results in massive loss of fibers in the homolateral ventral peduncle. However, a few normal fibers remain which suggests that the ventral peduncle contains decussating fibers or ascending fibers from other centers.

At present, it is impossible to state which tracts arise from the dorsal ventricular ridge and which from the paleostriatum. However, comparison of the degenerative pattern of Cp 17 with that of Cp 19 suggests that both the dorsal ventricular ridge and the paleostriatum contribute fibers to all four tracts of the peduncle.

The strio-hypothalamic tract is the first of these tracts to terminate. In the rostral diencephalon, degenerating fibers were traced to the anterior, lateral, and periventricular hypothalamic nuclei. Terminal degeneration was seen in all three nuclei in both homolateral and contralateral regions.

Degenerating fibers which curved dorsally, just medial to the optic tract were traced from the lateral surface of the ventral peduncle to the tectal region. These fibers appear to represent the strio-tectal tract. It is not known whether they reach the optic tectum without synapsing since the degenerating fibers were few in number and appeared to interweave among the darker stained optic tract fibers.

The ventral peduncle continues into the tegmentum as a fairly compact bundle until it reaches a level just posterior to the exit of the the oculomotor nerve where it terminates among the cells of the tegmental reticular formation. The author could not distinguish separate dorsal and ventral strio-tegmental tracts as Schapiro (1964) was able to do, but this might be possible in preparations with a lighter background. Impregnation of normal fibers in the tegmental region obscured detailed study and the ventral peduncle could not be traced beyond this level.

MEDIAL FOREBRAIN BUNDLE

(Figs. 4 through 6). This bundle is divided into a cortical and a basal division. The cortical division is represented by the fornix complex already described. All divisions of the fornix appear to be efferent from cortical regions to lower centers. No ablations have been interpreted as supporting the recognition of afferent fibers from diencephalic centers to cortical regions. The use of the term fornix to describe such a complex system of fibers arising from more than a single cortical area is inappropriate as this term has been used previously to describe just the efferent projections of the hippocampus.

The basal medial forebrain bundle is divided into parolfacto-hypothalamic (tractus septo-mesencephalicus of Unger and de Lange) and hypothalamo-parolfactory tracts. Golgi preparations demonstrate that fibers do exist between parolfactory and hypothalamic nuclei. However, no ablations were performed in this region and nothing can be added about the connections of these tracts.

VI. DISCUSSION

The histological organization of the telencephalon of the western painted turtle differs markedly from that of other reptiles. This is correlated with divergent physiological properties.

The olfactory apparatus of turtles is organized differently from that of most other reptiles. Turtles do not possess a distinct Jacobson's organ. Seydel (1896) and Parsons (1959) have shown that the highly developed Jacobson's organ in other reptiles arises from the ventral region of the nasal cavity. It appears that turtles possess this structure in a rudimentary or vestigial condition. As such, the development of a highly organized accessory bulb does not seem probable. Most workers have not recognized a distinct Jacobson's organ or its telencephalic equivalent, the accessory olfactory bulb (Johnston, 1915; McCotter, 1917; Crosby and Humphrey, 1939; and Schepers, 1948). However, Gamble (1956) and Platel (1966) state that a small accessory bulb is located on the dorsal and posterior region of the main bulb in *Testudo* and *Clemmys* respectively. No such division could be recognized in *Chrysemys*.

Ablation of the olfactory bulb in *Chrysemys* results in degeneration of the lateral olfactory tract throughout the length of the homolateral pyriform cortex. However, Gamble (1952 and 1956) reported that similar ablations in *Lacerta* and *Testudo* result in degeneration only

in the anterior region of the pyriform cortex. It is possible that these differences represent generic variation, but Scalia (1968) and Karten (personal communication) have observed degeneration throughout the pyriform cortex in *Alligator* and *Tupinambis* respectively. Alternatively, the difference may result from differences in histological methods.

The anterior olfactory nucleus in *Chrysemys* and other turtles appears larger than in other reptiles. Crosby and Humphrey (1939) recognized a dorsal division of this nucleus located above the olfactory ventricle as it joins the lateral ventricle. Platel (1966) similarly recognizes this dorsal division in *Clemmys*. Platel's accessory olfactory bulb corresponds to this author's caudal limit of the main bulb. Platel's rostral archipallium corresponds to this author's dorsolateral division of the dorsal cortex. Ablation of this area, as was previously demonstrated, reveals connections which do not support interpretation of this region as archipallium (hippocampus). Platel's dorsal division of the anterior olfactory nucleus corresponds to this author's rostral pyriform cortex. Analysis of the cell types and connections in *Chrysemys* demonstrates that this cellular layer should be considered a lateral cortical area.

The exact nature of the telencephalic projections to the dorsal thalamus in *Chrysemys* is difficult to determine based on the experimental material presented. This is primarily due to the small number and the large size of the ablations made. The dorsal cortex definitely projects to the dorsal thalamus. It appears that the dorsal cortex, pars dorsomedialis, and/or the hippocampus projects to the anterior dorsomedial thalamic nucleus via the medial forebrain bundle. The pars dorsolateralis of the dorsal cortex may project to the ventral part of the lateral thalamic nucleus via a division of the anterior tract of the lateral forebrain bundle. However, if it does, it must leave the anterior bundle rostrally in the telencephalon and project just medial and ventral to the ventral peduncle of the lateral forebrain bundle in the diencephalon.

The anterior division of the dorsal ventricular ridge and/or the paleostriatum appears to project to the nucleus rotundus. The marked change seen in rotundus in Cp 18 suggests that the dorsal ventricular ridge does project to nucleus rotundus. The cellular chromatolysis seen in nucleus rotundus following massive ablation of the dorsal ventricular ridge and paleostriatum (Cp 21) might be interpreted as rotundal cells projecting to paleostriatum or the ablation in Cp 18 was not large enough to produce large numbers of chromatolytic cells in the nucleus rotundus as it interrupted only a very small rostral part

of the superficial part of the dorsal ventricular ridge. These interpretations must remain tentative until a more complete study is made.

The major differences between the telencephalon of turtles and that of other reptiles are the cellular composition and connections of the dorsal cortex, and the cellular arrangement of the dorsolateral telencephalic wall. The dorsal cortex in reptiles can be divided into two components, dorsomedial and dorsolateral. The dorsomedial component consists of Golgi Type I and II neurons. The Type I neurons are projection neurons which pass via the medial forebrain bundle to lower medial telencephalic and diencephalic centers. The Type II neurons are intrinsic neurons which do not project from the cortex but are connecting elements within it. The dorsomedial division of the dorsal cortex appears functionally related to the hippocampus. Its histological organization is identical in all reptiles.

The dorsolateral division of the dorsal cortex differs markedly among reptiles. In reptiles, except turtles, this division appears to contain only Type II neurons. Ablation of this division does not result in degeneration of lower lateral telencephalic structures (Schapiro, 1964; and Northcutt, 1968). Similar results were obtained by Goldby (1937) in *Lacerta* following ablation of the rostral cortical areas. Nor does the dorsolateral division of the dorsal cortex appear to receive direct thalamic input. Kruger and Berkowitz (1960), and Powell and Kruger (1960) experimentally demonstrated that direct thalamic connections exist only to the paleostriatum in *Alligator* and *Lacerta*. In each genus, thalamic projections to the dorsal cortex could occur only via the lateral forebrain bundle in the rostral part of the hemisphere. Ablation of this cortical region did not result in thalamic retrograde degeneration. In both *Alligator* and *Lacerta,* retrograde cellular degeneration was accepted as the criterion of thalamic projection. The problem of sustaining collaterals and the possibility of interpretational error associated with this method is well recognized, and thus the possibility of a thalamic input cannot be totally discounted. Schapiro (1964) reported that degenerating fibers were traced to anterior thalamic, lateral thalamic, anterior dorsomedial, anterior dorsolateral, and reuniens and rotundus nuclei following ablation of the dorsal cortical region of the dorsal pallium and portions of the dorsolateral region of the striatum in *Caiman sclerops*. None of Schapiro's ablations were confined to the dorsal cortex, therefore the exact origins of the degenerating fibers were not known.

The only other experimental evidence for thalamic projection to the dorsolateral division of the dorsal cortex in this evolutionary line of reptiles is the work of Karten and Nauta (1968). While this work

is on birds, it is believed that birds stem from a group of thecodont reptiles which are closely represented today by alligators. Evidence of thalamic projections to the cortex of birds would strongly suggest similar connections in alligators.

Karten and Nauta (1968) reported thalamic projection from the dorsal thalamic region to the hyperstriatum accessorium and intercalatus superior in the burrowing owl *(Speotyto conicularia)*. Huber and Crosby (1929), and Durward (1930) suggested that the hyperstriatum accessorium of birds is homologous with a part of the dorsal cortex in reptiles. If this homology is correct, the sauropsid reptilian line possessed thalamic radiations to the dorsal cortex at some period in its history, or these connections appeared *de novo* in living birds. Further experimental work is needed to resolve this problem.

In turtles, the dorsolateral divisions of the dorsal cortex possesses both Golgi Type I and II neurons. The Type I neurons project from the cortex to telencephalic centers via the lateral forebrain bundle. This cortical region appears to receive a direct thalamic projection via the anterior component of the lateral forebrain bundle. In addition, interhemispheric fibers may exist with the contralateral dorsal cortex via a division of the anterior commissure. These conclusions are based on experimental evidence from the histological analysis of *Chrysemys*.

Functional studies on the dorsal cortex of reptiles support the proposed division into two anatomical lines of reptilian evolution. Evoked potential studies on the cortical elements of reptiles have produced two types of results: in the alligator (Kruger and Berkowitz, 1960; and Moore and Tschirgi, 1962) afferent somatic sensory projections and visual projections are not circumscribed and show almost complete overlap. In turtles (Orrego and Lisenby, 1962) afferent sensory projections, and visual and olfactory projections are discrete and well circumscribed. At present, it is not known whether the somatic projections are organized as diffuse or somatotopic systems in either of the two reptilian groups. Kruger and Berkowitz (1960) suggested that a crude rostrocaudal somatotopy with the head represented caudally might exist in the alligator. However, Moore and Tschirgi (1962) found no obvious somatotopic organization in the alligator.

Stimulation experiments do not clearly establish the presence or absence of cortically originating motor systems. Bagley and Richter (1924) were able to produce movements similar to swimming or walking in the alligator by stimulating the dorsal cortex and hippocampus. This activity was abolished by a superficial incision along the medial border of the hippocampus, but not by a similar incision along the lateral border of the dorsal cortex. Schapiro (1964) implanted chronic

electrodes in the dorsal cortex of *Caiman*. Stimulation of the dorsal cortex in unanesthetized and unrestrained animals did not cause overt motor responses. However, his experiments suggested that the dorsal cortex did exert an influence on motor function associated with the head region. Removal of the dorsal cortex resulted in lack of head, eye, and neck movement which had occurred previously on stimulating at the same intensity the dorsolateral region with the dorsal cortex intact.

Tuge and Yazaki (1934) located three cortical regions in the turtle which, when stimulated, resulted in movement of the head and neck. They were not sure these responses were cortical in origin and did not interpret their results. Bremer, Dow, and Moruzzi (1939) stimulated the cortex of *Emys orbicularis* evoking movement of the neck, jaw, and feet. However, these movements persisted after application of cocaine to the cortex, and they concluded that the movements were related to the spread of current to lower centers.

The results of the evoked potential studies on reptiles suggest that the dorsal cortex of both groups receives thalamic input, and that the organization of this sensory input differs in alligators and turtles. However, these studies reveal little about the nature of the thalamic connections. The results of the stimulation experiments in alligators suggest that some type of motor influence is exerted by the dorsal cortex via the medial forebrain bundle. The presence or absence of any motor influence of the dorsal cortex in turtles is not established. Ablation of the dorsal cortex (pars dorsolateralis) in *Chrysemys* reveals that efferent fibers do exist, but the nature of these fibers must be explored neurophysiologically before their role can be understood. Any statement on their function at this time would be purely conjectural.

The nuclear groups forming the dorsolateral telencephalic wall of turtles differ strikingly from those of other reptiles. In most reptiles (crocodiles, lizards, and snakes) the lateral wall is formed by three major masses: a ventral nucleus (ventrolateral area of Crosby, 1917; or paleostriatum of Northcutt, 1967), and intermediate nucleus (intermediolateral area of Crosby, 1917; or neostriatum of Northcutt, 1967), and a dorsal nucleus (dorsolateral area of Crosby, 1917; or hyperstriatum of Northcutt, 1967). Similarly, three nuclei can be identified in turtles: a ventral mass, an intermediate mass (core nucleus of Johnston, 1915), and a dorsal mass (dorsal ventricular ridge of Johnston, 1915).

The ventral area is similar in all reptiles although its relative volume may vary among groups. The core nucleus of turtles appears

topographically identical with that of the intermediate area in other reptiles. However, its connections with the dorsal area of the lateral wall and dorsal cortex are very different. In turtles, the core nucleus is so intimately related to the superficial layer of the dorsal ventricular ridge that it cannot be separated from this layer on the basis of a distinct cellular boundary. Its connections with the superficial layer of the dorsal ventricular ridge and the dorsal cortex suggest that a division of the dorsal mass in turtles may not exist.

The dorsal ventricular ridge also differs markedly from the dorsal area of other reptiles. The cells of the dorsal ventricular ridge in turtles lie in a C-shaped layer surrounding a core nucleus and a fibrous core. This layer is not a true cortex but suggests an invagination of the telencephalic wall. However, all embryological evidence suggests that this layer forms *in situ* (Johnston, 1916; Holmgren, 1925; and Källén, 1951c). The rostral dorsolateral area in most other reptiles lacks such a layer, although it is common in the caudal dorsolateral area of lizards and snakes as well as turtles. The development of a rostral layer in turtles suggests that its connections may be different from those of other reptiles or that its function may be different.

Little experimental information exists on the connections of this region in reptiles. Powell and Kruger (1960) concluded that thalamic projection to the telencephalon in *Lacerta* was restricted to the lateral division of the paleostriatum. Similar results for the alligator were reported by Kruger and Berkowitz (1960). However, Schapiro (1964) presented evidence for thalamo-striatal and thalamo-cortical connections in *Caiman.* He stated that the lateral division of the dorsolateral area may be a specialized area associated with ascending pathways and afferent information.

In *Chrysemys,* ablations of the dorsal ventricular ridge (pars anterior) suggest that afferent connections from the thalamus via the intermediate tract and, perhaps, the anterior tract of the lateral forebrain bundle may exist. However, it is impossible to state that differences in thalamic input do exist between turtles and other reptiles. There are definitely differences in the connections of the dorsal cortex with the dorsal "striatal" mass in turtles and other reptiles. The dorsal cortex does project to the dorsal component in turtles as demonstrated by ablations in *Chrysemys,* but not in lizards and alligators (Goldby, 1937; Schapiro, 1964; and Northcutt, 1968). Projections from the dorsal component to the dorsal cortex probably exist in both groups. To date, only one experimental study exists on the projections from the dorsal component to lower centers in reptiles (Schapiro, 1964). Schapiro's results in the *Caiman* and the present results in *Chrysemys*

demonstrate no major differences in these lower efferent connections. Thus the only connectional differences appear to be with the dorsolateral division of the dorsal cortex.

The tuatara, *Sphenodon,* also possesses a rostral cellular layer in the dorsal component. The telencephalon of this genus is remarkably similar to that of turtles. The superficial layer of the dorsal area is more clearly separated from the deeper nuclei, and a core nucleus does not appear to exist. The paleostriatum, or an area comparable to it, extends as a single area toward the center of the dorsal component. In *Sphenodon,* a core nucleus, if one exists, appears on a cellular basis to be intimately associated with the basal mass. Durward (1930) reported that the lateral wall in *Sphenodon* was not as clearly divisible into separate cellular masses as other reptiles.

Clearly no agreement exists in the literature on the number of cellular groups composing the lateral telencephalic wall in reptiles. Nor have workers agreed on the homologies within reptiles. Consequently, there is no agreement on the homologies of these various nuclear groups with higher vertebrates. Most workers have relied solely on topographic relationships in establishing homologies. The rostral component of the lateral telencephalic wall in reptiles has been said to be homologous in mammals to the following regions: amygdaloid complex (Johnston, 1915; and Carey, 1967), caudate nucleus (Johnston, 1923; and Hewitt, 1967), caudate and putamen nuclei (Elliot Smith, 1919; Dart, 1920; Kappers, Huber, and Crosby, 1935; and Schepers, 1948), part of the neocortex (Källén, 1962), and the claustrum (Filimonoff, 1964). Obviously, reliance on topographic or topological resemblance is not adequate as a single criterion for determining homologous structures in the telencephalon.

A survey of the major nuclear groups of the lateral telencephalic wall in vertebrates demonstrates great variation in shape and number of nuclei. What are the relationships of these nuclei and what criteria can we use to recognize homologies where they exist? To answer these questions, it is necessary to review the concepts of homology and to define applicable criteria for the telencephalon.

Homology is an interpretative concept. It is based upon educated comparisons within and between organisms. The concept of homology was formulated by Goethe, Oken, and Owen who were leaders of the *Naturphilosophie* school. These workers viewed organisms as specially created and immutable. Observed variation of structures among organisms was interpreted as being of no major significance. What was important was similarity. Groups of organisms were thought to have been created on a divine pattern which was called the archetype.

Owen (1866) classified these similarities into three categories: general homology, special homology, and serial homology. General homology is the similarity between the structure of an actual organism and the archetype. Special homology is the similarity between a structure in one organism and a second structure in another organism. Serial homology is the similarity among repetitive or serial structures within a single organism.

After the publication of Darwin's *The Origin of Species* in 1859, morphologists realized that species do change and that observed variation is the clue to these changes. The concept of homology was redefined and brought within the framework of evolutionary theory in a series of papers by Haas and Simpson (1946), Simpson (1959 and 1961), and Bock (1963). Homology was redefined as follows: "Homologous features (or conditions of the features) in two or more organisms are ones that can be traced back to the same feature (or condition) in the common ancestor of these organisms," Bock (1963, p. 268).

Within the present concept of evolutionary theory at least five types of homologies can be recognized according to Smith (1967). Serial homology is recognized as involving different structures within one individual organism. While this type of homology is important in the nervous system, it obviously does not concern the problem of recognizing homologous structures between organisms. Field homology is recognized as the common ancestry of structures, often recognized as a developmental field, in different individuals. Discrete homology is recognized as common ancestry of structures which can be compared individually rather than depending on a common embryonic source. For example, the primate lung is discretely homologous to the avian lung. But the inferior lobe of the primate left lung is homologous to a similar lobe of the avian lung only as a field homology. Patristic homology is recognized as homology of a structure between two organisms or groups of organisms in which one is directly ancestral to the other. Cladistic homology is recognized as homology of a structure between two organisms or groups of organisms which represent divergent ancestral lines. Thus it is possible to recognize patristic or cladistic discrete homologies as well as patristic or cladistic field homologies. Obviously, serial homologies cannot be so recognized. Unless we are dealing with a fairly complete fossil record it is not possible to recognize patristic homology, and this is certainly the case with regard to the nervous system.

In the case of the vertebrate telencephalon, we are dealing with a discrete homology if we compare the telencephalon of any one ver-

tebrate to the telencephalon of other vertebrates. However in comparing individual cellular groups, it becomes obvious that we are dealing with field homologies. The division of the telencephalon into a pallium and a subpallium among different vertebrates can be recognized as a discrete homology, but within these divisions cellular groups arise both phylogenetically and ontogenetically by subsequent cellular proliferations and migrations (Kuhlenbeck, 1929 and 1938; Källén, 1951a, 1951b, 1951c, 1951d, and 1962; and Jones and Levi-Montalcini, 1958). Recognition and comparison of nuclear groups must be based on comparison of the cellular fields which give rise to these structures. Homologies of nuclei are defined by recognition of common origin from cellular fields in a common ancestor.

Theoretically, all types of homology are based on recognition of common ancestry. However, with most organ systems including the nervous system, a fossil record does not exist in enough detail to ascertain common ancestry. How then can an approximation of common ancestry be obtained? The working method of determining common ancestry and thereby recognizing structures with a common ancestry is recognition of common characters between two or more structures in two or more animals. Recognition of common characters is based on two criteria: the minuteness of resemblance between two structures, and the multiplicity of similarities (Simpson, 1961).

Can homologous cellular fields be recognized in living vertebrates? In the past, three criteria have been used in attempts to recognize such fields: (1) similar fields are limited by similar ventricular sulci, (2) similar fields possess similar cell types and similar topographical relationships, and (3) similar fields possess similar fiber connections.

In 1929, Kuhlenbeck analyzed the telencephalic ventricular sulci and divided the telencephalon into a number of *Grundbestandteile* or basic regions common in all vertebrates. According to Kuhlenbeck, all vertebrates are based on a common structural plan. Nuclear groups in different brains are homologous if they occupy the same topological position. Variation in cellular types and connections were secondary and were of no significance in recognizing homologies.

In 1932, Bergquist studied the early embryology of the diencephalon and reported that areas of cellular proliferation occurred but were not bordered by sulci. Instead, an individual sulcus was found in the center of a proliferating area. Källén (1951a) observed proliferating regions in the telencephalon similar to Bergquist's diencephalic regions. In addition, Källén proposed the concept of migration areas. These areas are regions where the first cellular migrations begin. Källén's migration areas correspond approximately to the proliferation areas

(Grundgebiete) of Bergquist. Both Bergquist and Källén determined homologous areas as common origin of cytoarchitectonic regions without regard to sulci or fiber connections.

No worker, to the author's knowledge, has relied solely on fiber connections in attempting to recognize homologies. However, Nieuwenhuys and Bodenheimer (1966) have evaluated this criterion in relationship to the other two criteria in the diencephalon of *Polypterus.* This work is an excellent critique on present methodology.

All three of these criteria have weaknesses. Nieuwenhuys and Bodenheimer noted that ventricular sulci are variable in lower vertebrates, and that they are obviously useless when nuclear groups have migrated away from the ventricle. However, Källén (1951b) has stated that the ventricular sulci are related to the proliferation process, but he believes them to be of less importance for the study of cell migration. Herrick (1948) also noted that in *Ambystoma* the ventricular sulci do appear to represent boundaries between different morphological and functional regions. Thus, sulci may be of use in comparing regions where migration has not occurred, but obviously they can not be used as a sole criterion.

The use of cytoarchitectonic differences and similarities in establishing homologies is a powerful tool, especially when ontogenetic information is also available. However, several limitations must be noted. As Goldby and Gamble (1957) noted, the proliferating regions in ontogeny are often ill-defined masses or layers, and all studies to date have not utilized specialized neurological staining methods to obtain information on differentiation of individual neurons and fibers. Secondly, as Lashly and Clark (1946) and Clark (1962) have pointed out, studies of cytoarchitectonics can be judged only on the extent to which the criteria used as differentiators have been validated. At present, most criteria used to distinguish cellular masses in lower vertebrates lack validation.

Ontogenetic studies based on cytoarchitectonic differences, when used to establish homologies, can often produce conflicting results if the ontogenetic information is used exclusively. Structures derived from a common embryological field are almost certainly homologous, but derivation from different embryological fields does not necessarily exclude homology. This fact has been documented by de Beer (1951). For example, the thymus can develop from any combination of the three germ layers. And again in *Rana,* the lens of the eye in one species is determined *in situ,* while in the other species it is induced by the optic cup. Also, the trigeminal nerve contains general cutaneous neurons which arise from the neural crest in most vertebrates. But

in the frog, they arise from the epidermal placode. In each case, the homologies are unquestioned even though the organs arise from different fields.

In addition, Smith (1956 and 1960) has pointed out that developmental patterns often change in evolution. These changes involve acceleration of actual rate of passage through developmental sequences, abbreviation of sequences, and extinction of specific sequences. These changes are particularly apt to occur during the later stages of development. Therefore, we should not ask ontogenetic development to give us an exact review of phylogenetic history. At best, it can only give us a sense of developmental relationships. These relationships may mirror the phylogenetic history of an organ or they may present clues to a developmental adaptation solely of significance to a developing organism in relation to a specific environment. Ontogenetic studies cannot give us a simple answer to homologies. Most certainly the information produced by these studies must be used, but with extreme caution.

Fiber tracts have not been used extensively as a criterion for establishing homologies. This is primarily because no reliable methods existed for determining the origin and termination of most fiber systems until recently. In part, this has been responsible for our almost total ignorance about the phylogenetic stability of these systems. We know almost nothing about the mechanics of how fiber systems arise and shift connections. Further, whether such shifts even occur has not been well documented. Nieuwenhuys and Bodenheimer (1966) point out that fiber systems are defined and named by their origin and termination in nuclear masses. If we in turn homologize nuclear masses on the basis of the fiber systems, our logic is circular. But, the same point can be made with regard to the use of nuclear groups in topography. A cell-free boundary occupies the same position in a syllogistic premise as does the fiber system.

There is, at present, no reason to assume that fiber systems are more variable than nuclear masses, since at least half of all fiber systems (efferent systems) are extensions of the neurons of any given nuclear mass. It is the author's opinion that fiber systems are valid as a criterion in establishing homologies, and that their use will become more common as our knowledge of them increases.

Examination of the criteria used by past workers demonstrates that each of the methods has value in establishing homologies. However each of the methods has disadvantages and can lead to erroneous conclusions. The strongest base for the establishment of homologies is through a combination of methods. Such combinations may produce

conflicting evidence. When this occurs the worker should accept the evidence which in his judgment is most reliable and in accord with the coexisting body of knowledge.

Ontogenetic studies of the reptilian telencephalon have produced information on the presumed phylogenetic cellular fields which gave rise to the nuclear masses seen in living reptiles. Kuhlenbeck (1929 and 1967) divided the reptilian telencephalon into longitudinal dorsal (pallial) and basal divisions. Within these divisions, he recognized three dorsal or pallial components and four basal components. The most medial pallial component (D_3) is recognized as medial cortex or hippocampus. The dorsal pallial component (D_2) is further divided into three regions. A medial region called parahippocampus, a dorsal region called primordium neopallii, and a lateral region called regio insularis. This last region does not appear to be recognized in the later work of Kuhlenbeck (1967). If the author interprets him correctly, this component is now considered part of the pyriform cortex. The lateral pallial component (D_1) is recognized as nucleus epibasalis and centralis. The first basal component (B_1) along with the second basal component (B_2) is recognized as the nucleus basalis. The third basal component (B_3) is recognized as nucleus basalis accumbens. The fourth basal component (B_4) is recognized as olfactory cortex. While his analysis is confined to *Lacerta* and *Terrapene*, it would apply to all other reptiles according to Kuhlenbeck.

Holmgren (1925) studied the development of the telencephalon of *Chrysemys marginata* and recognized a pallial and a basal division. He concluded that the pallium was formed by a fusion of two successive cellular proliferations and that later (his Stage 12), the dorsal ventricular ridge formed as a third proliferation. He concluded that the basal region was formed by three columns: a dorsal column forming the caudate, putamen, and pars dorsalis of the lateral olfactory nucleus; a middle column forming the bed of the stria terminalis, the globus pallidus, and the pars ventralis of the lateral olfactory nucleus; and a ventral column forming subtubercular cells, olfactory tubercle, nucleus basalis, nucleus preopticus, and nucleus of the diagonal band.

The most comprehensive study on the comparative ontogeny of the reptilian telencephalon is the work of Källén (1951c). Källén divides the telencephalon into a roof and a floor area. The roof area is composed of at least three migration layers. The first and second migration layers (d^{I} and d^{II}) fuse to form the true cortex. A third migration layer (d^{III}) forms the hypopallium (dorsal ventricular ridge). The division of the dorsal ventricular ridge into an anterior and a posterior division is a secondary process which Källén believes is of minor

morphological significance. The floor area is composed of three migration areas. A dorsal column (c) gives rise to the "striatum" (the intermediolateral and the ventrolateral areas of Crosby), the nucleus of the lateral olfactory tract, and the nucleus centralis (basal amygdaloid nucleus in *Chrysemys* of the present work). A middle column (b) gives rise to the nucleus accumbens, olfactory tubercle, lateral parolfactory nucleus, and the nuclei basalis and interstitialis. A ventral column (a) gives rise to the medial parolfactory nucleus and the nucleus of the diagonal band of Broca.

The divisions of Kuhlenbeck are fundamentally different from those of Holmgren and Källén. Kuhlenbeck's divisions are based on sulci which appear after cellular proliferations, whereas Holmgren's and Källén's divisions are based on embryonic migration areas. However, both groups of workers divide the reptilian telencephalon into approximately the same number of cellular zones or masses and, with minor exceptions, derive the same adult structures from these masses. Although these cellular masses are not similarly named, they do bear similar topological relationships to their counterparts.

It is here proposed that the reptilian telencephalon consists of six longitudinal phylogenetic columns (prototypic columns). This conclusion is based on the ontogenetic evidence of other workers and the architectonic analysis of adult nuclear groups presented in this and previous papers (Northcutt, 1966 and 1967). Similarity between the proposed prototypic columns and the ontogenetic columns of other workers does not mean that they are identical. The ontogenetic columns are used as one line of evidence for the reconstruction of the ancestral condition. This does not imply that the prototypic columns arose in phylogeny or were modified in a manner similar to the existing ontogenetic columns.

It is proposed that both the pallium and the basal region of the reptilian telencephalon are composed of three longitudinal columns (Fig. 19). The pallium consists of a medial PI column, a dorsal PII column, and a lateral PIII column. In living reptiles the PI column is recognized as the hippocampus or medial cortex. The PII column is recognized as forming two components: a PIIa component (dorsomedial division of the dorsal cortex) and a PIIb component (dorsolateral division of the dorsal cortex). The PIII column is recognized as forming two components: a PIIIa component (the dorsal ventricular ridge) and a PIIIb component (the pyriform cortex).

The basal region consists of a dorsolateral BI column, a ventral BII column, and a ventromedial BIII column (Fig. 19). The BI column is recognized as forming the ventrolateral area of Crosby

(paleostriatum of *Iguana* and *Chrysemys*); the intermediolateral area of Crosby (neostriatum of *Iguana,* part of the paleostriatum of *Chrysemys*); nucleus of the lateral olfactory tract of Crosby (same named nucleus in *Iguana;* part of the basal amygdaloid nucleus of *Chrysemys*), and the basal amygdaloid nucleus of *Chrysemys.* The BII column is recognized as forming the nucleus accumbens, the olfactory tubercle, and the interstitial nucleus. The BIII column is recognized as forming the parolfactory region.

The core nucleus and the central amygdaloid nucleus in *Chrysemys* are considered divisions of the PIIIa column rather than divisions of the BI column. Therefore they are not homologous to the intermediolateral area in the alligator or the neostriatum in the green iguana. The core nucleus and the central amygdaloid nucleus are therefore not recognizable as separate cellular masses in alligators or lizards. They must, however, be considered homologous to cellular populations composing part of the dorsolateral area in the alligator and the hyperstriatum anterius in the green iguana. The decision to include the core nucleus and the central amygdaloid nucleus as divisions of the PIIIa column is based on ontogenetic studies and fiber connections which have been described in detail earlier in this work.

The intermediolateral area in the alligator and the neostriatum in the green iguana are homologous structures. They are not seen in turtles as a separate structure but are represented by cellular populations found in the paleostriatum of *Chrysemys.* This is also probably the case in *Sphenodon,* as our material does not show a separate mass between the paleostriatum and the hypopallium.

The PIIIa component (dorsal ventricular ridge) is considered a dorsal division of the lateral pallium in all reptiles. It is considered a fundamental division of the roof, with the pyriform cortex originating as a PIIIb component ventral to it. These conclusions are based on several lines of evidence. All ontogenetic studies clearly have shown it to be of pallial origin (Kuhlenbeck, 1929; Holmgren, 1925; and Källén, 1951c). It does not form as an invagination of the dorsal cortex or pyriform cortex as Johnston (1915) first suggested, but is a proliferation *in situ.* In *Caretta,* the dorsal cortex continues without breaking or clustering beneath the pyriform cortex, and it is continuous with the dorsal ventricular ridge. In several cases, similar relationships were observed in the *Chrysemys* material. This suggests that phylogenetically the dorsal ventricular ridge was originally a component bordered dorsally by the dorsal pallium and ventrally by the pyriform pallium. It is interesting to note that Herrick (1948, pp. 96 and 104) describes such a region in the rostral portion of the telencephalon

of *Ambystoma*. Herrick notes that his rostral pyriform area and dorsolateral sector of the anterior olfactory nucleus contain efferent fibers which project to the striatal nuclei or pass into the lateral forebrain bundle. Clearly these are very odd connections for pyriform cortex. If these connections exist, the amphibian telencephalon is composed of the same prototypic columns believed to form the reptilian brain.

Herrick demonstrated that the dorsal pallium in *Ambystoma* contains Golgi Type I neurons throughout its extent. The medial zone of the dorsal pallium projects to the hippocampus and septum whereas the lateral zone of the dorsal pallium projects to the pyriform pallium and striatum. This suggests that PIIa and PIIb components do exist at the amphibian level. As has already been pointed out, the lateral pallium can also be divided into PIIIa and PIIIb components based on Herrick's descriptions. Herrick (1948) also recognized a dorsal and a ventral striatal region which would follow the lines of the basal divisions proposed by myself in *Chrysemys* and recorded in the ontogenetic literature.

Thus the evolution of the reptilian telencephalon from the amphibian telencephalon can be viewed as the result of changes in the connections of the PIIb component, and changes in the mass and cytoarchitectonics of the PIIIa component. This evolution is believed to have proceeded along two major lines. In the line giving rise to all living reptiles except turtles, the PIIIa component proliferated into the ventricle to produce an area referred to as the dorsolateral area in alligators, or the hyperstriatum or hypopallium in lizards and snakes. This region formed a cellular mass whose histology is recognized as a nucleus. Along this same evolutionary line, the PIIb component lost the Type I neurons and became reorganized as a nucleus. This evolutionary line has been referred to as the sauropsid line in accordance with the work of Watson (1954) and Vaughn (1960).

A second evolutionary line, theropsid line, represented by those reptiles leading to mammals, and probably turtles, is proposed. In this line, the PIIIa component also proliferated into the ventricle but was organized along different histological lines. The PIIIa component did not become a nucleus but developed as a corticoid structure divided into a deep core nucleus and a more superficial layer of cells. The PIIb component retained the Type I neurons and has developed as a true cortex homologous, in part, to the neocortex in mammals.

The telencephalon of *Sphenodon* appears similar to the telencephalon of turtles. On a neuroanatomical basis, it is possible to group it with turtles. The paleontological record of rhynchocephalians, of which *Sphenodon* is a member, is fragmentary. Both lizards and rhynchoce-

phalians arise at approximately the same period in the geological record and are presumed to have evolved from eosuchians (Romer, 1966). However, the evidence for such an origin is not strong. At present, the organization of the rhynchocephalian telencephalon can be viewed either as a case of evolutionary convergence or of parallelism.

Analysis of the PIIIa component in reptiles suggests that the homologies which the author has previously suggested with the nuclear groups of the dorsolateral wall in higher vertebrates are not correct (Northcutt, 1967). This problem and its reinterpretation will be dealt with in a subsequent paper. The author now believes the dorsal ventricular ridge (PIIIa) to be of pallial origin and suspects it to be homologous to part of the neocortical formations in mammals.

VII. SUMMARY

The histological organization of the telencephalon of the western painted turtle, *Chrysemys picta belli,* was studied. This analysis employed Bodian, Cresyl violet, Golgi-Cox, Klüver, and Weil methods to stain neural groups and their connections in normal material. A modified Nauta technique was used to confirm the direction and termination of telencephalic connections observed by normal histological methods. The experimental results were determined from the analysis of nine animals with unilateral telencephalic ablations and three animals with unilateral olfactory bulbs or olfactory nerve ablations.

The olfactory apparatus of the western painted turtle does not possess a vomeronasal organ or an accessory olfactory bulb. However, the ventral half of the nasal chamber in the western painted turtle is homologous to a vomeronasal organ in other reptiles. Likewise, the dorsal half of the olfactory bulb in the western painted turtle is homologous to the accessory bulb in other reptiles.

The olfactory bulb contains seven neural layers, as is common to most vertebrates, and gives rise to three olfactory tracts. The medial olfactory tract is homolateral in distribution and terminates in the rostral parolfactory nuclei and hippocampus. The intermedial olfactory tract is also homolateral, and it terminates in the anterior olfactory nucleus and olfactory tubercle. The lateral olfactory tract

distributes fibers both contralaterally and homolaterally. Homolaterally, it terminates in the anterior olfactory nucleus, olfactory tubercle, basal and central amygdaloid nuclei, and in both anterior and posterior divisions of the pyriform cortex. The contralateral lateral olfactory tract passes into the stria medullaris and projects as two systems in the contralateral hemisphere. A rostral system (anterior olfacto-habenular tract) projects to the parolfactory nuclei, anterior olfactory nucleus, rostral dorsal cortex, and rostral hippocampus. The second system (lateral cortico-habenular tract) projects to the posterior pyriform cortex and the basal and central amygdaloid nuclei.

The histological organization of the neural groups of the roof and lateral wall of the telencephalon proper were analyzed in detail. The roof consists of three cortical regions: lateral, dorsal, and medial. The lateral or pyriform cortex receives olfactory projections throughout its entire length and projects to the posterior division of the lateral wall (posterior division of the dorsal ventricular ridge). The pyriform cortex also appears to possess interhemispheric fibers with the contralateral pyriform cortex. These connections occur via the anterior commissure. The dorsal cortex is divided into dorsolateral and dorsomedial components. The dorsolateral component may receive fibers from the anterior dorsomedial and/or lateral thalamic nuclei as well as the anterior division of the dorsal ventricular ridge. These projections occur via the anterior tract of the dorsal peduncle of the lateral forebrain bundle. At present it is only possible to suggest that these pathways end in the dorsal cortex based on the knowledge that the dorsal cortex projects to these thalamic nuclei and that the radiations of these thalamic nuclei project into the superficial layer of the dorsal cortex. The dorsolateral component of the dorsal cortex possesses Golgi Type I motor neurons which project to the homolateral dorsal ventricular ridge (pars anterior), the homolateral paleostriatum, and possibly to the homolateral ventral part of the nucleus lateralis of the thalamus. The dorsolateral component of the dorsal cortex also appears to possess associative fibers with the contralateral dorsal cortex (pars dorsolateralis) via the anterior commissure. The dorsomedial division of the dorsal cortex may receive projections from the anterior dorsomedial thalamic nucleus and it in turn appears to project to the anterior dorsomedial thalamic nucleus via the medial forebrain bundle. Associative fibers also project to the contralateral dorsal cortex (pars dorsomedialis) via the hippocampal commissure.

The medial, or hippocampal cortex is not sharply divided as in lizards or snakes. No major afferent tracts to the hippocampus were recognized but it is possible that the anterior dorsomedial thalamic

nucleus may project to both the dorsal cortex (pars dorsomedialis) and the hippocampus. The efferent tracts from the hippocampus are both crossed and uncrossed. The hippocampal fibers project homolaterally to the parolfactory nuclei, the hypothalamic nuclei, and the central amygdaloid nucleus. Contralaterally, fibers project to the same nuclei after decussating in the hippocampal commissure. The hippocampus also contains associative fibers with the contralateral hippocampus via the hippocampal commissure. The dorsomedial division of the dorsal cortex may also possess similar fiber systems, since no distinction was made between the projection systems of the dorsal cortex (pars dorsomedialis) and the hippocampus.

Three major nuclei compose the lateral wall of the telencephalon of the western painted turtle: the paleostriatum, the dorsal ventricular ridge, and the basal amygdaloid nucleus. The paleostriatum receives fibers from the nucleus rotundus via the intermediate tract of the dorsal peduncle of the lateral forebrain bundle, and from the dorsal ventricular ridge (pars anterior) and the dorsal cortex (pars dorsolateralis). The paleostriatum projects contralaterally and homolaterally to the nucleus rotundus, hypothalamic nuclei, and tegmentum.

The dorsal ventricular ridge is divided into an anterior and a posterior division. The anterior division consists of a superficial cellular layer surrounding a core nucleus. The anterior division of the dorsal ventricular ridge receives thalamic input from the nucleus rotundus and perhaps the anterior dorsomedial and lateral thalamic nuclei. It also receives input via the dorsal cortex (pars dorsolateralis). Its efferent connections are with the paleostriatum, the nucleus rotundus, the hypothalamic and tegmental nuclei, and perhaps the pretectum via the ventral peduncle of the lateral forebrain bundle. It also possesses interhemispheric fibers with the contralateral dorsal ventricular ridge (pars anterior) via the anterior commissure.

The posterior division of the dorsal ventricular ridge is also divided into a superficial cellular layer and a deep nucleus, the central amygdaloid nucleus. These two neural masses, along with the basal amygdaloid nucleus, form the amygdaloid complex of the western painted turtle. The amygdaloid complex receives projections from the lateral olfactory tract, from the pyriform and hippocampal cortices and probably from the dorsal cortex (pars dorsomedialis). It is associated with the contralateral amygdaloid complex via the commissural division of the stria terminalis. Its major efferent pathways are the preoptic division of the stria terminalis, and the stria medullaris.

The organization of the telencephalon of the western painted turtle has been compared with the organization of the telencephalons of other

reptiles. An attempt has been made to establish homologies with the telencephalons of other reptiles after reviewing and evaluating criteria used for recognizing homologies.

The evolution of the reptilian telencephalon from the amphibian telencephalon is viewed as having occurred along two distinct lines. Both the amphibian and the reptilian telencephalon are constructed of three longitudinal pallial and subpallial (basal) columns. However, two components of two of the pallial columns have had very different evolutionary histories in reptiles.

The dorsal pallial column (PII) in amphibians consists of two components, a dorsolateral PIIb and a dorsomedial PIIa. Both components contain Golgi Type I motor neurons. The dorsolateral component projects via the lateral forebrain bundle, and the dorsomedial component projects via the medial forebrain bundle. The lateral pallial column (PIII) in amphibians also consists of two components, a dorsal PIIIa component and a ventral PIIIb. The PIIIa component receives thalamic input and projects via the lateral forebrain bundle. The ventral component receives olfactory input and projects to the basal amygdaloid complex.

In the sauropsid reptilian line, the Golgi Type I neurons were lost in the PIIb component, and the PIIIa component proliferated into the ventricle forming a large nuclear mass. The PIIb component is organized as a nucleus and did not form a true cortex. This line is represented by all living reptiles except turtles.

In the theropsid reptilian line, the Golgi Type I neurons were retained in the PIIb component, and the although the PIIIa component proliferated into the ventricle, it did retain the pallial organization of the amphibian pallium. Thus the PIIb component is organized as a true cortex, and the PIIIa component is organized histologically in a very different manner from the PIIIa component in sauropsid reptiles. The line is represented by turtles and probably the extinct theropsid reptiles.

At present, it is impossible to interpret the position of the tuatara. It may be a primitive sauropsid which has retained the amphibian connections in its PIIb component.

NOTE ADDED IN PROOF

Since this work went to press, a number of points have come to light based on several new publications and continued work in the author's laboratory on the forebrain of *Chrysemys*. W. C. Hall and F. F. Ebner

(Anat. Rec., 1969, 163:193) have published the first report on the thalamotelencephalic projections in *Pseudemys* which is closely related to *Chrysemys*. These authors demonstrate that following unilateral thalamectomies, degenerating fibers were traced to the homolateral paleostriatum, core nucleus of the rostral dorsal ventricular ridge, and rostral dorsal cortex. While they note that degenerating fibers passed through the pallial thickening of Johnston (dorsal cortex, pars dorsolateralis in *Chrysemys*) they believe that few, if any, terminations occur in this region following thalamic ablation. Work by I. T. Diamond and W. C. Hall (Science, 1969, 164:251-261) and G. E. Schneider (Science, 1969, 163:895-901) on the visual system in mammals and its probable evolution raises the interesting question whether or not similar systems exist in reptiles. It is possible that the main if not sole projections of nucleus rotundus in the western painted turtle project to the dorsal ventricular ridge (pars anterior) and that the tecto-rotundo-dorsal ventricular ridge complex in turtles is homologous to the superior collicular-postereolateral-peristriate complex in mammals.

As was pointed out in the discussion, Orrego demonstrated that turtles possess separate visual and somatic cortical areas similar to mammals. This raises a second question as to the nature of the dorsal cortical visual area in *Chrysemys*. It is possible that this cortical region may be homologous to Brodmann Area 17 in mammals. In order to meet the criteria of such a homology, a cortical area should possess the following connections: (1) direct projection of a visual thalamic nucleus homologous to pars dorsalis of the mammalian lateral geniculate nucleus; (2) project to the homologue of peristriate cortex (Brodmann Areas 18 and 19); and (3) project back to the visual thalamic nucleus from which it receives its afferent input and to the pretectum and tegmental gray.

If the analysis of the ablations presented here regarding *Chrysemys* is correct, the pars dorsomedialis of the dorsal cortex should be removed from consideration as the homologue of visual cortex in mammals as its projections appear to place it with the hippocampal cortex as part of a limbic system rather than neocortex. The pars dorsolateralis of the dorsal cortex may possess some of the suggested criteria. It appears to project to the ventral part of the lateral thalamic nucleus which because of its position could receive optic input. The pars dorsolateralis also projects to the dorsal ventricular ridge which could be considered the homologue of peristriate cortex. Based on experimental ablations presented in the present work, the author be-

lieves that either dorsal cortex or the dorsal ventricular ridge also projects to the pretectal and tegmental areas. At present it is only possible to suggest that pars dorsolateralis of the dorsal cortex or part of the dorsal ventricular ridge may be homologous to striate cortex in mammals.

The ablations presented in this work could not by their nature give clear and precise results on the telencephalic projections. Rather an attempt was made to survey the entire telencephalon and to suggest possible relationships. The author hopes to stimulate interest in the nature of the chelonian telencephalon rather than to present a definitive answer to its phylogenetic position and its functional nature.

List of Abbreviations

A. triang.	area triangularis
A. vent. ant.	area ventralis anterior
C. ant.	commissura anterior
C. geni. lat.	corpus geniculatum laterale
C. hip.	commissura hippocampi
C. n.	core nucleus
Cx. dor.	cortex dorsalis
Cx. dor. p. dl.	cortex dorsalis, pars dorsolateralis
Cx. dor. p. dm.	cortex dorsalis, pars dorsomedialis
Cx. pyr.	cortex pyriformis
D. v. r. ant.	dorsal ventricular ridge, pars anterior
H. p. d.	hippocampus, pars dorsalis
H. p. dm.	hippocampus, pars dorsomedialis
Hab.	habenula
L. f. b. p. d.	lateral forebrain bundle, dorsal peduncle
L. f. b. p. v.	lateral forebrain bundle, ventral peduncle
M. f. b.	medial forebrain bundle
N. acc.	nucleus accumbens
N. ant. hypo.	nucleus anterior hypothalami
N. bas. amyg.	nucleus basalis amygdalae
N. cent. amyg.	nucleus centralis amygdalae
N. d. b.	nucleus of the diagonal band of Broca
N. dor. med. a.	nucleus dorsomedialis anterior thalami
N. interst.	nucleus interstitialis
N. lat. hypo.	nucleus lateralis hypothalami
N. lat. thal.	nucleus lateralis thalami
N. parolf. lat.	nucleus parolfactorius lateralis

N. parolf. med.	nucleus parolfactorius medialis
N. peri. hypo.	nucleus periventricularis hypothalami
N. peri. preop.	nucleus periventricularis preopticus
N. rot.	nucleus rotundus
N. vent. hypo.	nucleus ventralis hypothalami
N. vent. thal.	nucleus ventralis thalami
Olf. proj. tr.	olfactory projection tract of Cajal
Op. ch.	optic chiasma
Op. tr.	optic tract
Palst.	paleostriatum
Palst. p. l.	paleostriatum, pars lateralis
Palst. p. m.	paleostriatum, pars medialis
Prim. h.	primordium hippocampi
S. c. l.	superficial cellular layer of dorsal ventricular ridge
St. med.	stria medullaris
St. term.	stria terminalis
T. olf.	tuberculum olfactorium
Tr. cort.-hab. lat.	tractus cortico-habenularis lateralis

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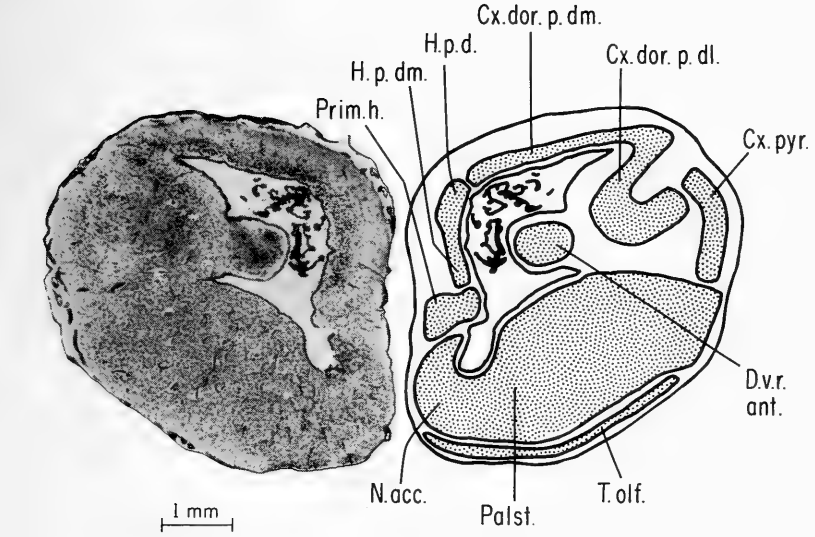


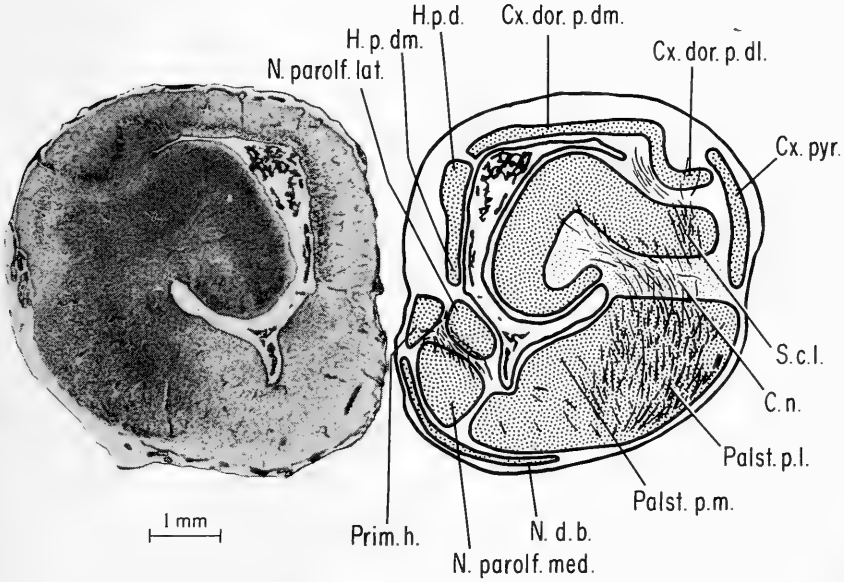
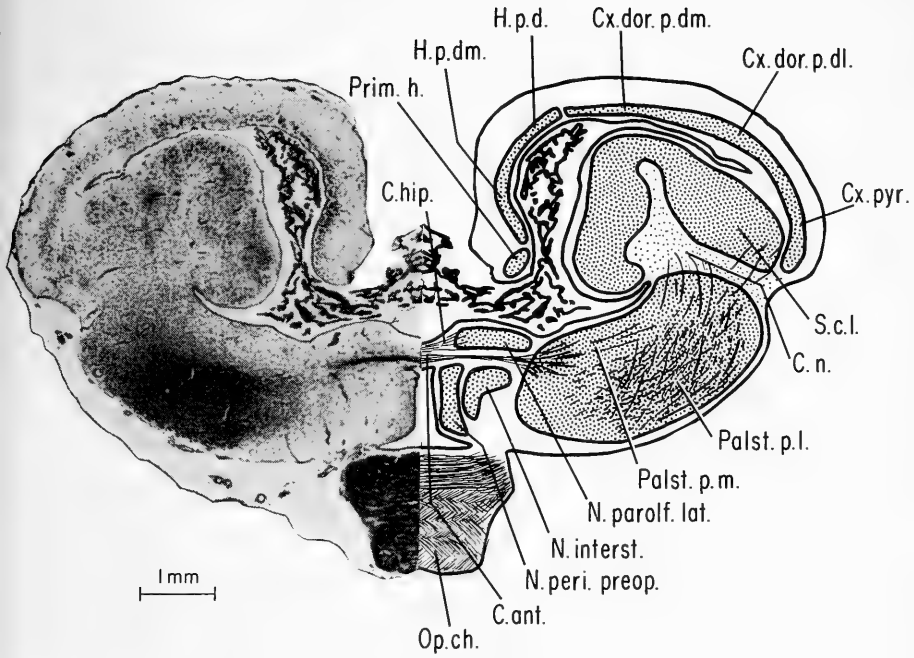


Figure 1. Photomicrograph of a transverse section through the rostral region of the telencephalon of the western painted turtle. Klüver preparation (15μ). Dotted areas denote cortical and nuclear groups.

Figure 2. Photomicrograph of a transverse section through the region of the dorsal ventricular ridge (pars anterior) in the telencephalon of the western painted turtle. Klüver preparation (15μ).

Figure 3. Photomicrograph of a transverse section through the region of the anterior commissure in the telencephalon of the western painted turtle. Klüver preparation (15μ).

Figure 4. Photomicrograph of a transverse section through the dorsal ventricular ridge (pars posterior) in the telencephalon of the western painted turtle. Klüver preparation (15μ).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N.interst.
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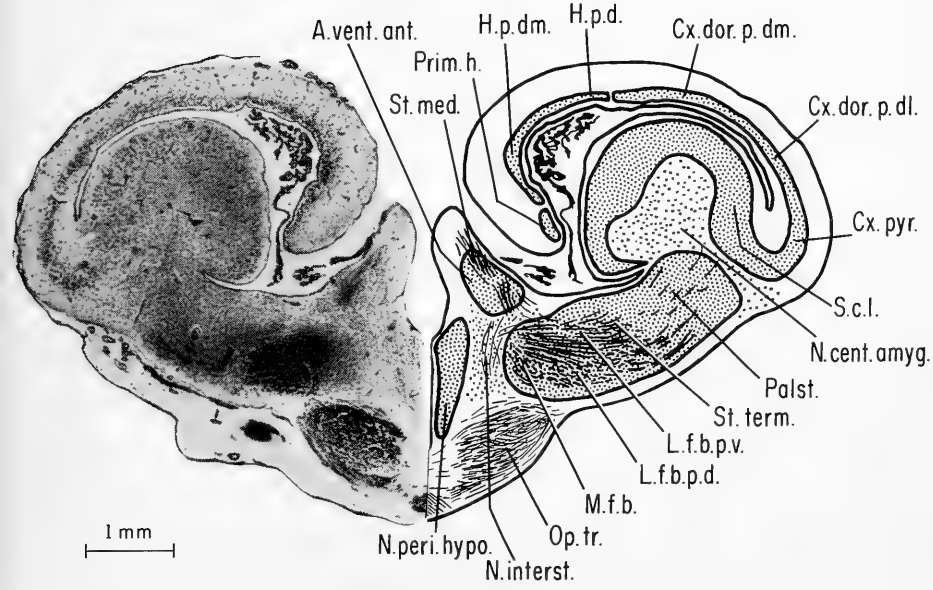
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N.cent.amyg.
Palst.
St.term.
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M.f.b.
Op.tr.
N.peri.hypo.
N.interst.
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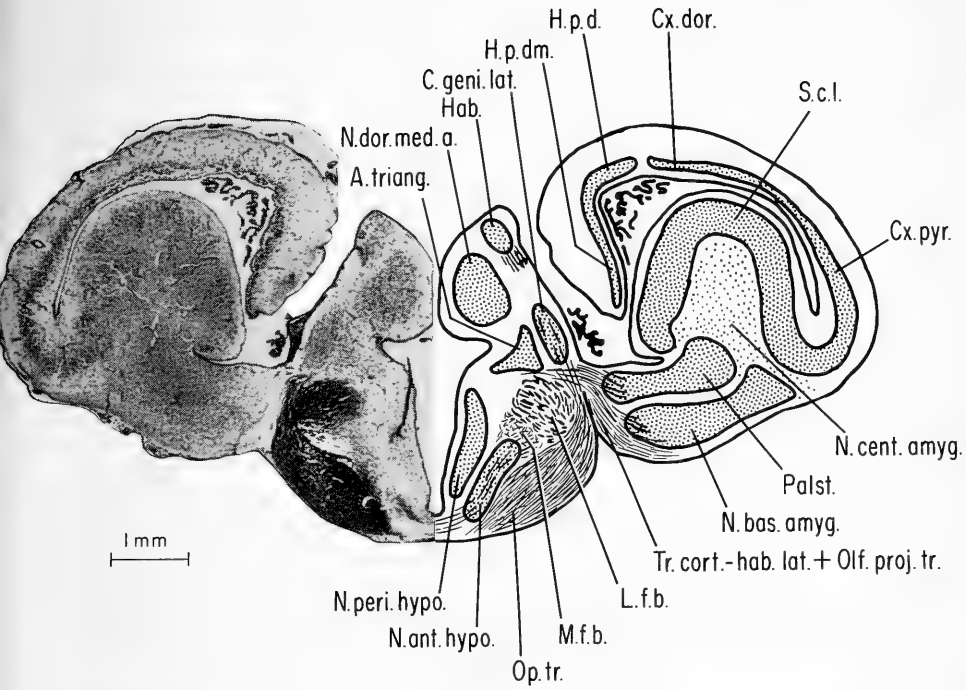
Figure 5. Photomicrograph of a transverse section through the rostral diencephalon of the western painted turtle. Klüver preparation (15μ).

Figure 6. Photomicrograph of a transverse section through the caudal pole of the telencephalon of the western painted turtle. Klüver preparation (15μ).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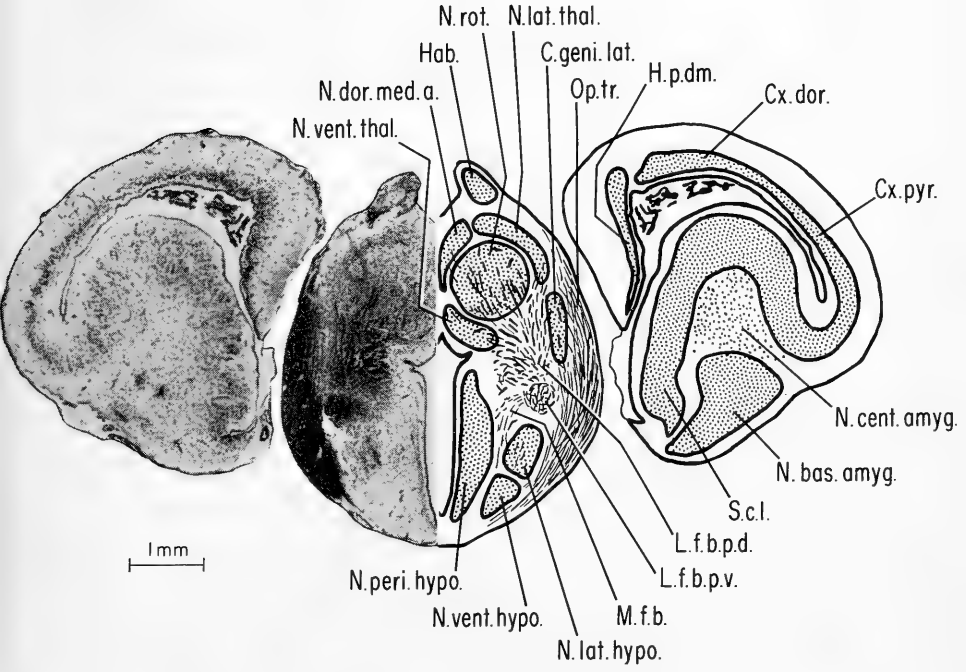
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N.bas.amyg.
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1mm
L.f.b.p.v.
N.peri.hypo.
N.vent.hypo.
M.f.b.
N.lat.hypo.

Figure 7. Photomicrographs of neurons in the olfactory bulb and basal regions of the telencephalon of the western painted turtle. Golgi-Cox preparations.

A. Mitral neurons of the olfactory bulb. Bar scale indicates 100μ. Horizontal section. Rostral is toward top of photograph. Lateral toward right of photograph.

B. Neurons of the internal granular layer of the olfactory bulb. Bar scale indicates 100μ. Orientation same as in 7A.

C. Polygonal cells of the tuberculum olfactorium. Bar scale indicates 100μ. Arrow denotes cell soma. Dorsal is toward top of photograph. Lateral surface is toward left of photograph.

D. Small pyramidal cell of the area parolfactoria. Bar scale indicates 100μ. Arrow denotes cell soma. Orientation same as in 7C.

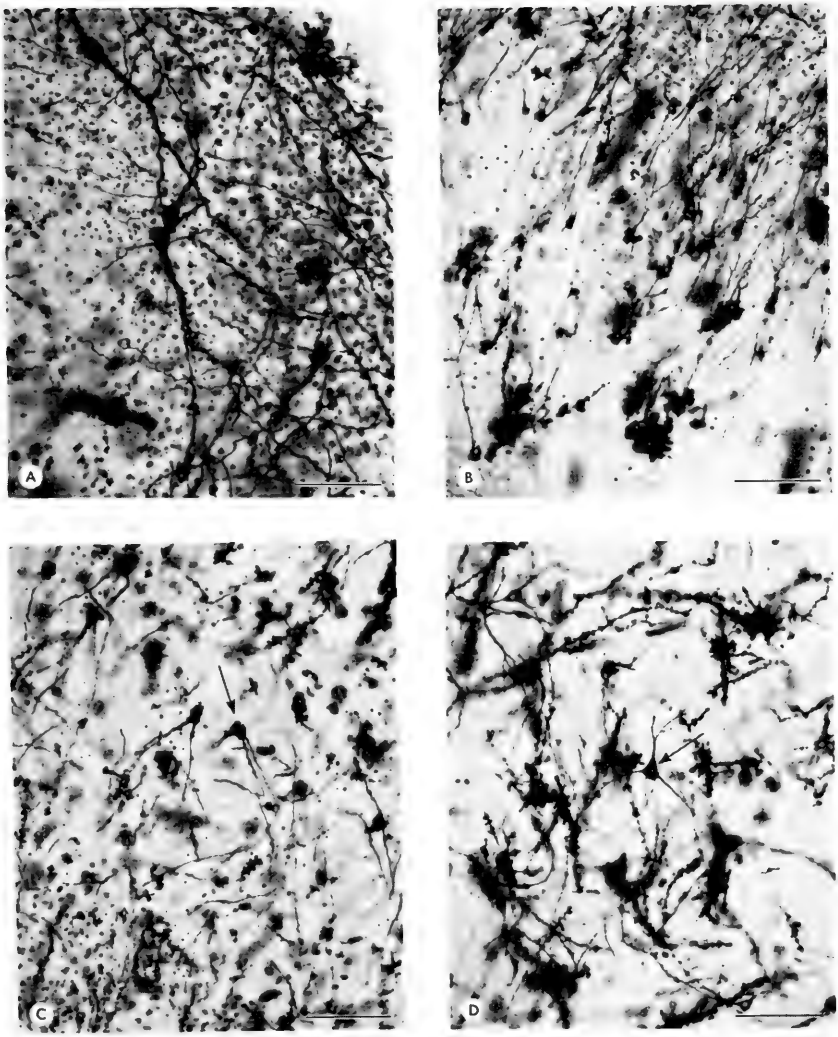
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Figure 8. Photomicrographs of neurons in the area parolfactoria, hippocampus, and lateral wall of the telencephalon of the western painted turtle. Golgi-Cox preparations.

A. Fusiform neuron of the area parolfactoria. Bar scale indicates 100μ. Arrow denotes cell soma. Dorsal is toward top of photograph. Lateral surface is toward left of photograph.

B. Neurons of the hippocampus, pars dorsalis. Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Medial surface toward the right of photograph.

C. Giant polygonal neuron of the paleostriatum. Bar scale indicates 100μ. Arrow denotes cell soma. Dorsal surface is toward top of photograph. Medial surface is toward left of photograph.

D. Pyramidal neuron of the superficial cellular layer of the dorsal ventricular ridge (pars anterior). Bar scale indicates 100μ. Arrow denotes cell soma. Dorsal surface is toward top of photograph. Lateral surface is toward left of photograph.

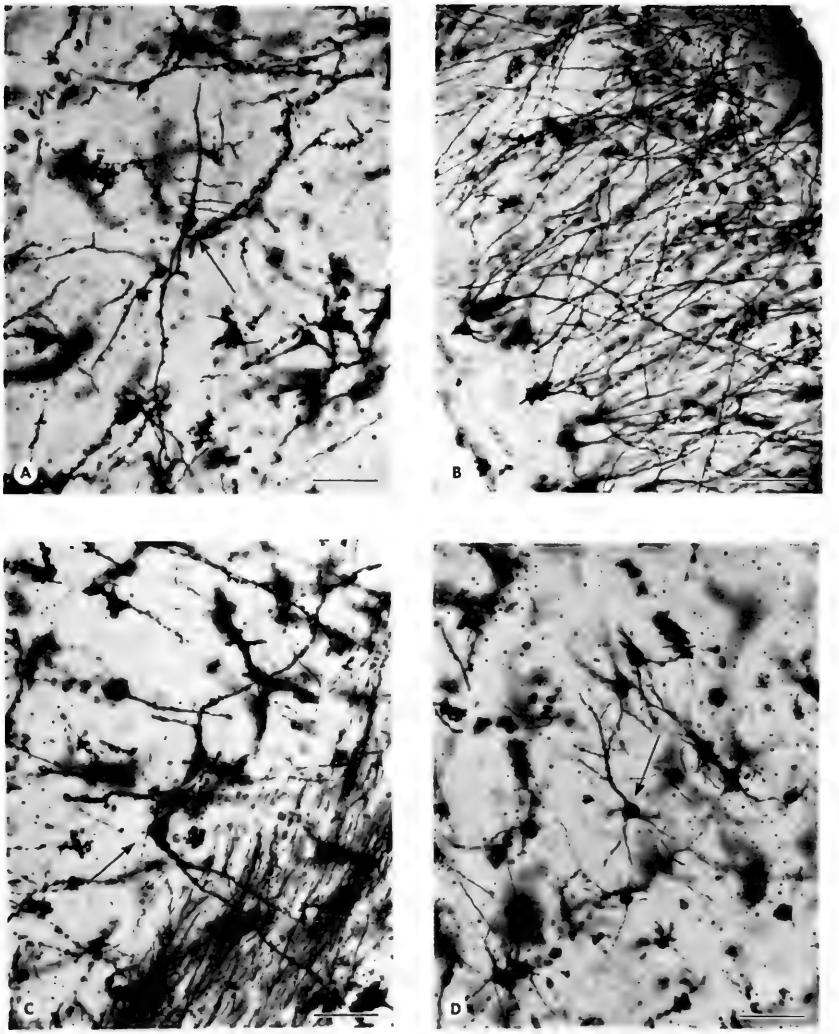
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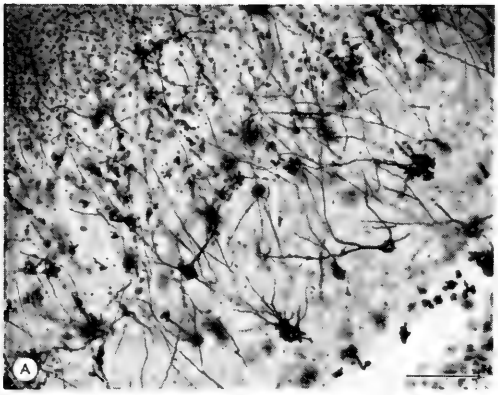
Figure 9. Photomicrographs of neurons in the pyriform cortex, dorsal cortex, and paleostriatum of the telencephalon of the western painted turtle. Golgi-Cox preparations.

A. Neurons of the pyriform cortex. Bar scale indicates 100μ. Dorsal surface is toward upper right corner of photograph. Lateral surface is toward upper left corner of photograph.

B. Polygonal projection neurons of the dorsal cortex (pars dorsolateralis). Bar scale indicates 100μ. Arrow denotes cell soma. Dorsal surface is toward top of photograph. Lateral surface is toward left of photograph.

C. Small projection neurons of the paleostriatum. Bar scale indicates 100μ. Arrow denotes cell soma. Orientation same as in 9B.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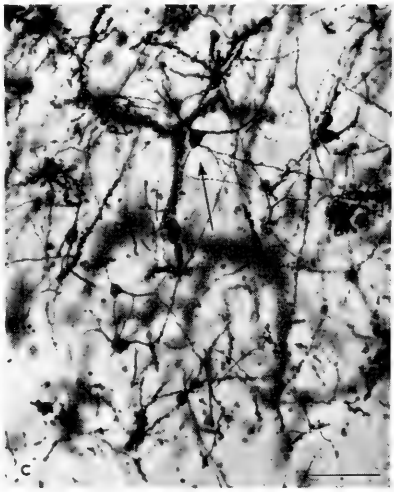
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Figure 10. Photomicrographs and drawings of neurons in the dorsal cortex of the telencephalon of the western painted turtle. Golgi-Cox preparations. Dorsal surface is toward top of photographs. Medial surface is toward left of photographs.

A. Neurons of the dorsal cortex (pars dorsomedialis). Bar scale indicates 100μ.

B. Cellular populations of the dorsal cortex (pars dorsomedialis). Bar scale indicates 100μ. A. pyriform projection neurons; B. pyramidal neurons; C. intrinsic neurons; and D. pyriform projection neurons with basal dendrites.

C. Neurons of the dorsal cortex (pars dorsolateralis). Bar scale indicates 100μ.

D. Cellular populations of the dorsal cortex (pars dorsolateralis). Bar scale indicates 100μ. A. small pyramidal neurons; B. large pyramidal neurons; C. polygonal projection neurons; D. stellate neurons; and E. pyriform projection neurons.


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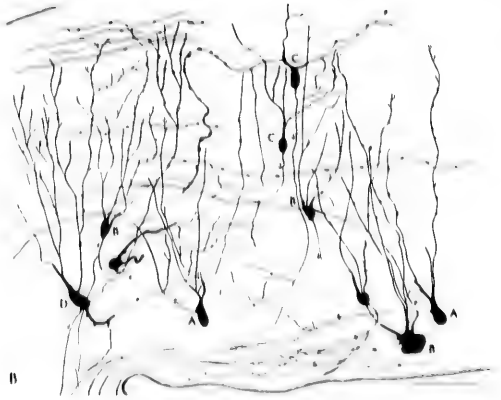
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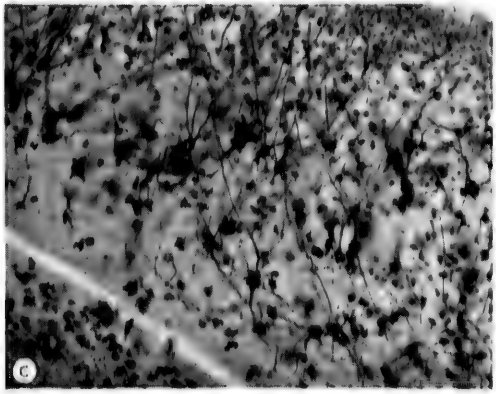
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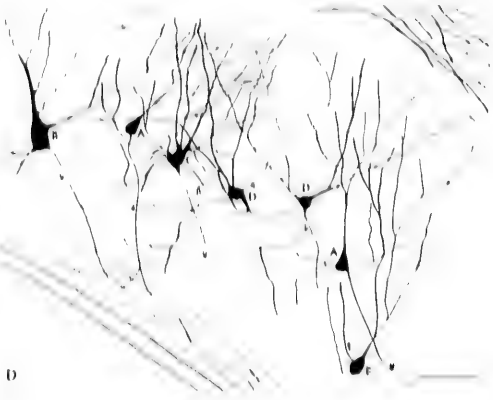
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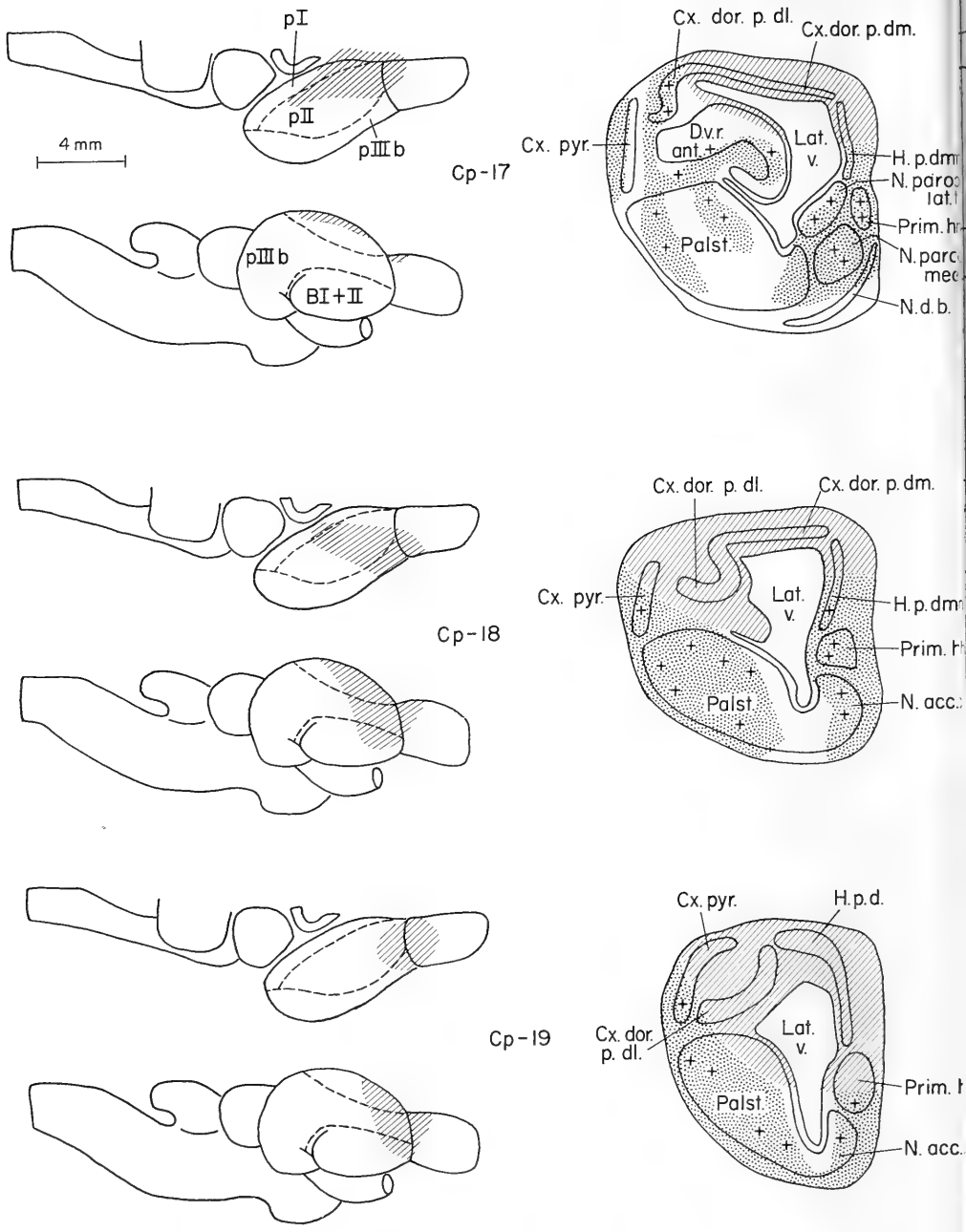


Figure 11. Position and extent of unilateral ablations in the telencephalon of the western painted turtle (Cp 17, 18, and 19). Hatched area on dorsal and lateral views of the entire brain mark external position and extent of ablation. Transverse section for each brain indicates extent of ablation (hatched area), degenerating fibers of passage (stippled area), terminal degeneration (plus signs), and probable terminal degeneration (question marks). PI, medial pallium; PII, dorsal pallium; PIIIb, lateral pallium; and BI + II, basal areas.

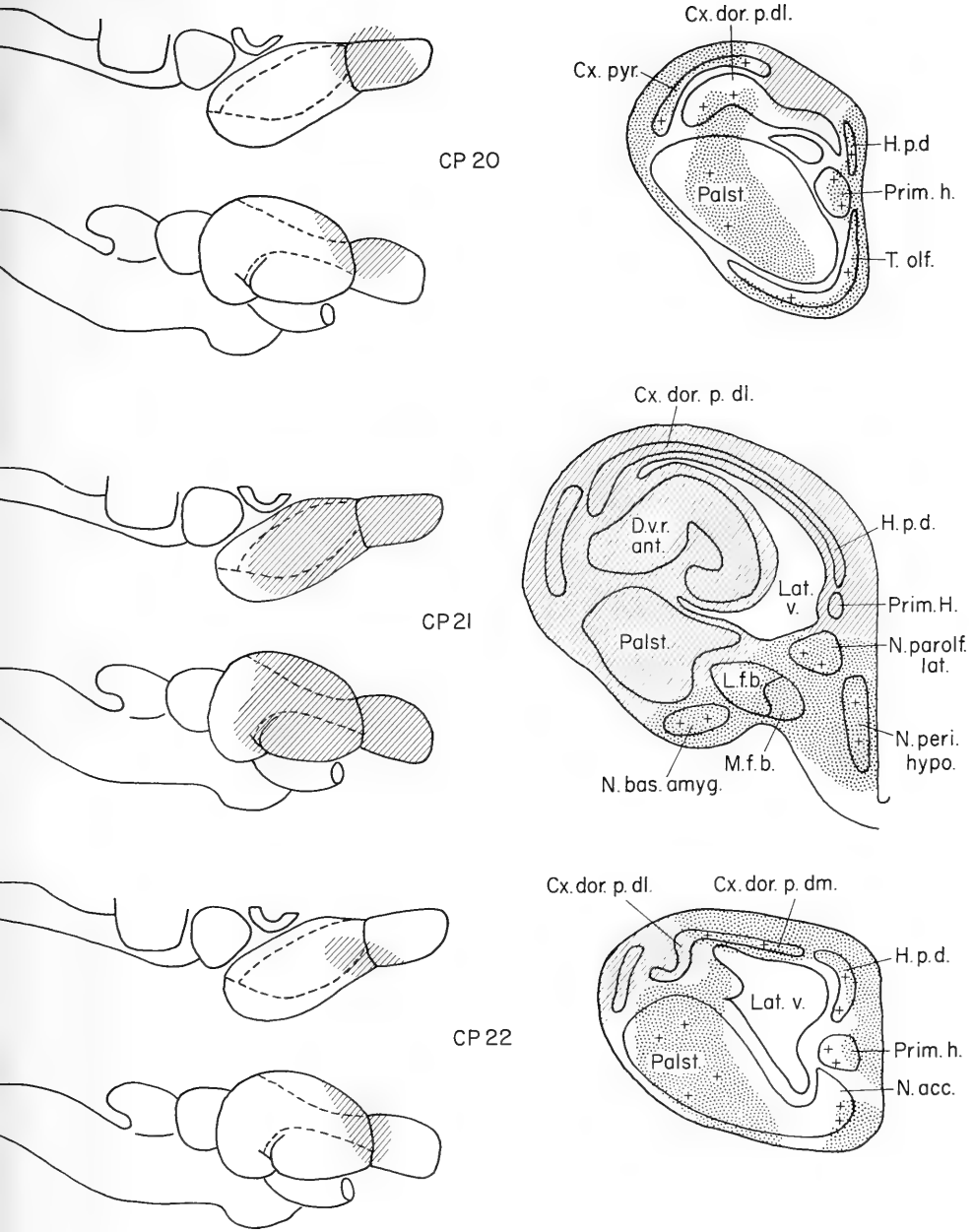
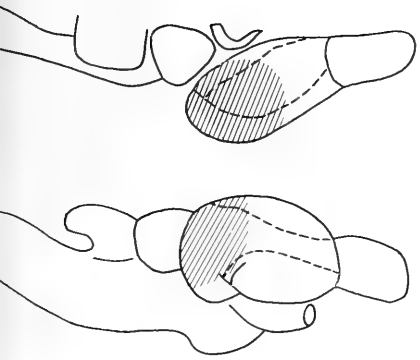
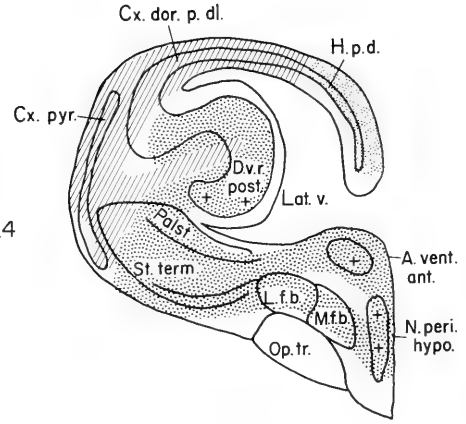


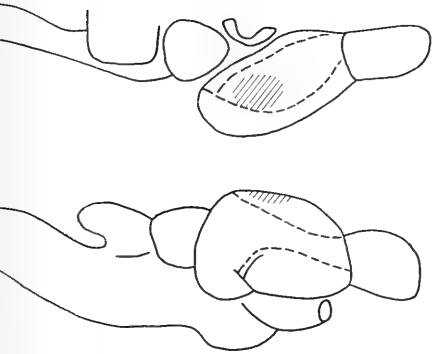
Figure 12. Position and extent of unilateral ablations in the telencephalon of the western painted turtle (Cp 20, 21, and 22). Hatched area on dorsal and lateral views of the entire brain mark external position and extent of ablation. Transverse section for each brain indicates extent of ablation (hatched area), degenerating fibers of passage (stippled area), and terminal degeneration (plus signs).

Figure 13. Position and extent of unilateral ablations in the telencephalon of the western painted turtle (Cp 24, 26, and 27). Hatched area on dorsal and lateral views of the entire brain mark external position and extent of ablation. Transverse section for each brain indicates extent of ablation (hatched area), degenerating fibers of passage (stippled area), terminal degeneration (plus signs), and probable terminal degeneration (question marks).

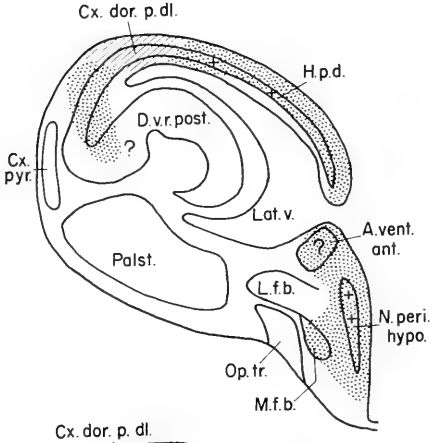


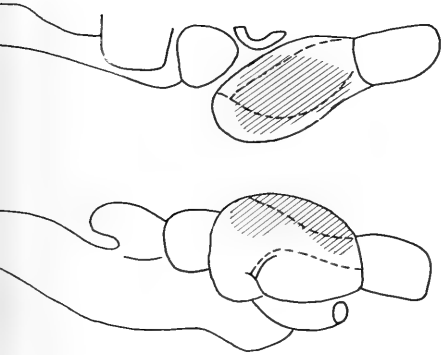
Cp-24





Cp-26





Cp-27

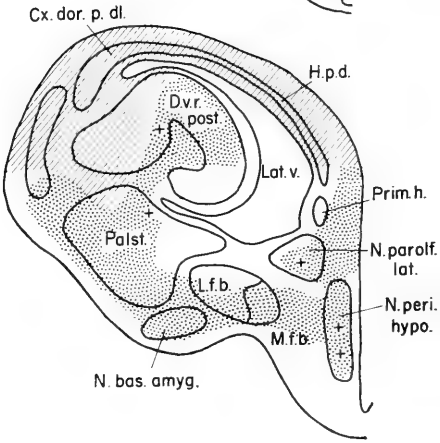


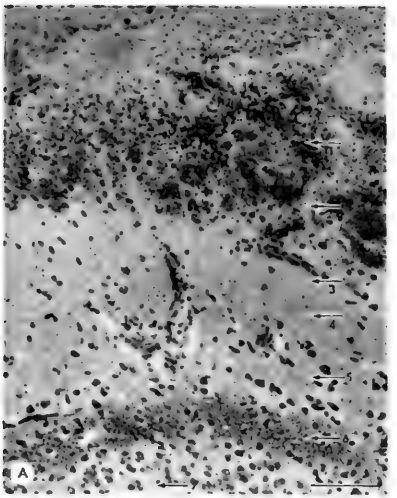
Figure 14. Photomicrographs of degenerating fibers in the telencephalon of the western painted turtle (Cp 13 and 17). Nauta method.

A. Degenerating fibers of passage and terminal degeneration in the olfactory bulb following partial ablation of same (Cp 13). Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Lateral surface is toward left side of photograph. 1, olfactory fila; 2, glomerular layer; 3, external granular layer; 4, external plexiform layer; 5, mitral layer; 6, internal plexiform layer; and 7, internal granular layer. Numbers are placed in center of layers.

B. Terminal degeneration in homolateral anterior olfactory nucleus following ablation of the olfactory bulb (Cp 13). Bar scale indicates 50μ. Orientation is the same as for 14A.

C. Terminal degeneration in contralateral parolfactory region following ablation of the olfactory bulb (Cp 13). Bar scale indicates 50μ. Dorsal surface is toward top of photograph. Lateral surface is toward right side of photograph.

D. Terminal degeneration in homolateral periventricular preoptic nucleus following ablation of dorsal and medial cortices (Cp 17). Bar scale indicates 50μ. Orientation is the same as in 14A.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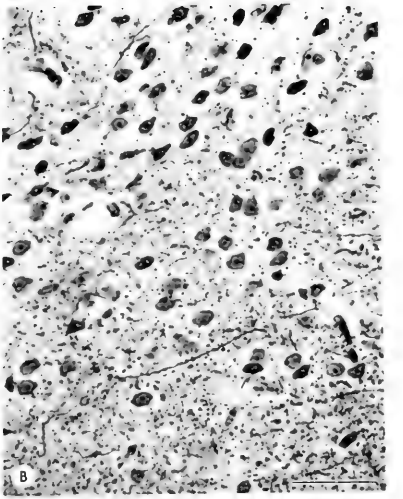
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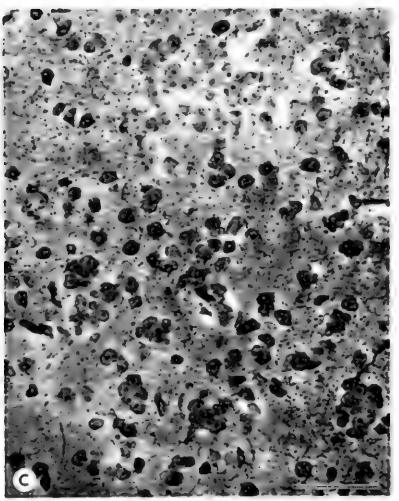
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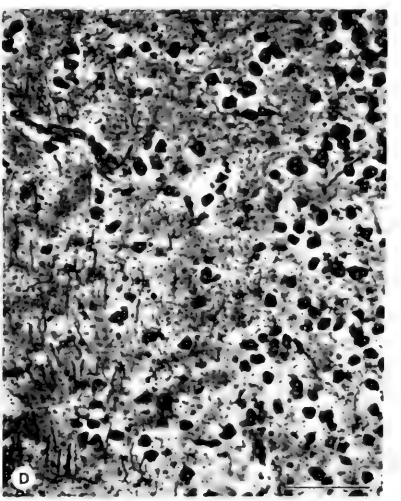
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Figure 15. Photomicrographs of degenerating fibers in the telencephalon of the western painted turtle (Cp 13 and 26). Nauta method.

A. Degenerating fibers in the homolateral pyriform cortex (anterior division) following ablation of olfactory bulb (Cp 13). Bar scale indicates 100μ. Dorsal surface toward top of photograph. Lateral surface toward right side of photograph.

B. Degenerating fibers in the homolateral pyriform cortex (posterior division) following ablation of olfactory bulb (Cp 13). Bar scale indicates 100μ. Orientation same as 15A.

C. Terminal degeneration in homolateral pyriform cortex (posterior division) following olfactory bulb ablation (Cp 13). Bar scale indicates 50μ. Dorsal surface is toward left side of photograph. Lateral surface is toward bottom of photograph.

D. Degenerating fibers of passage and terminal degeneration in homolateral hippocampus following ablation of dorsal cortex (pars dorsomedialis) in Cp 26. Bar scale indicates 100μ. Orientation same as in 15A.

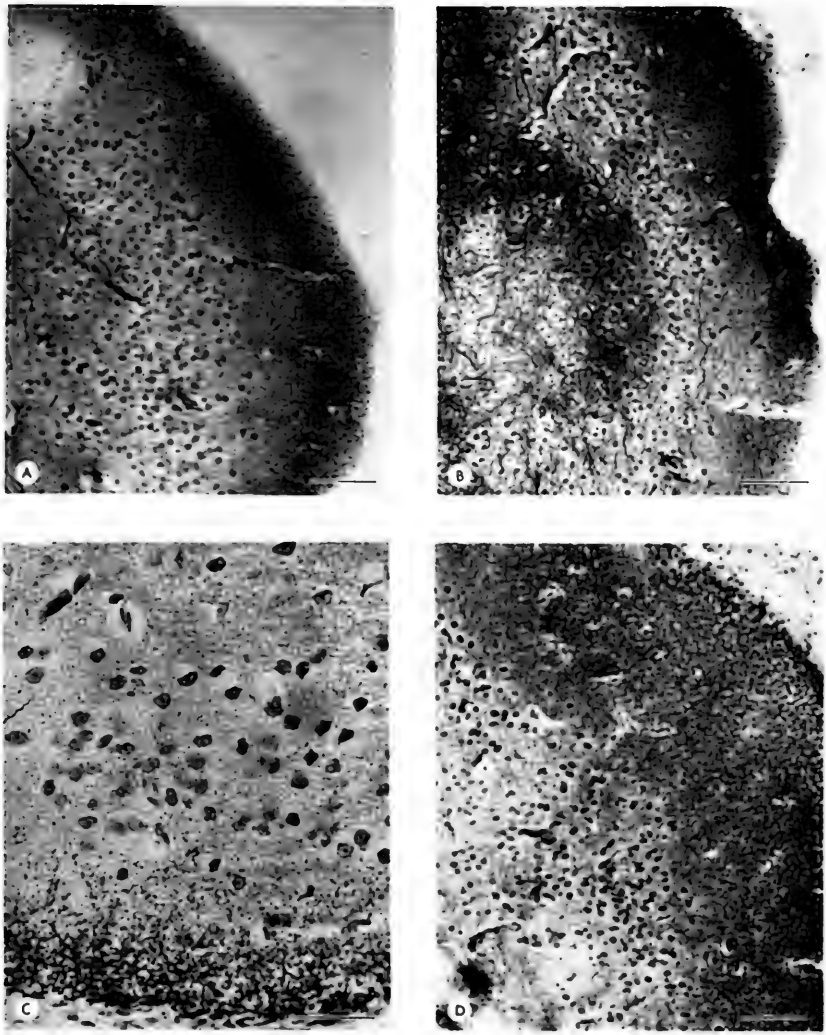
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Figure 16. Photomicrographs of degenerating fibers in the forebrain of the western painted turtle (Cp 17, 18, and 19). Nauta method.

A. Degenerating fibers of the hippocampal commissure (Cp 17). Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Arrow 1 indicates hippocampal commissure. Arrow 2 indicates anterior commissure.

B. Degenerating fibers of the anterior commissure and hippocampal commissure (Cp 19). Bar scale indicates 50μ. Orientation and arrows same as in 16A.

C. Degenerating fibers and terminal degeneration in the homolateral nucleus rotundus (Cp 18). Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Lateral surface is toward left side of photograph.

D. Contralateral nucleus rotundus in Cp 18 showing no degeneration. Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Lateral surface is toward right side of photograph.

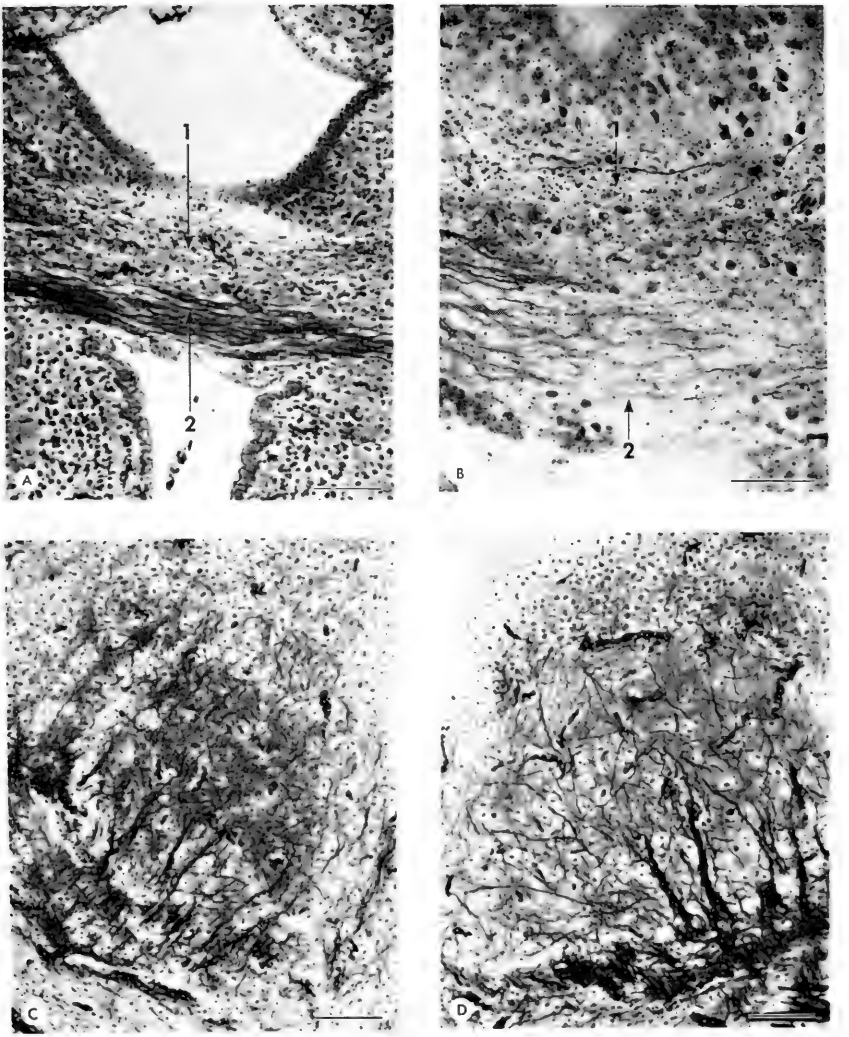
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Figure 17. Photomicrographs of degenerating fibers in the telencephalon of the western painted turtle (Cp 17 and 20). Nauta method.

A. Degenerating fibers in the homolateral core nucleus and paleostriatum following ablation of the dorsal cortex (pars dorsolateralis) in Cp 17. Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Lateral surface is toward left side of photograph.

B. Terminal degeneration in the homolateral core nucleus following ablation of the dorsal cortex (pars dorsolateralis) in Cp 20. Bar scale indicates 50μ. Dorsal surface is toward top of photograph. Lateral surface is toward left of photograph. Arrow indicates preterminal axon and boutons ending on soma of neuron.

C. Degenerating fibers and terminal degeneration in the dorsal ventricular ridge (pars anterior) in Cp 20. Bar scale indicates 50μ. Dorsal surface is toward left side of photograph. Lateral surface is toward bottom of photograph.

D. Terminal degeneration in the homolateral dorsal ventricular ridge (pars posterior) following ablation of the dorsal cortex and part of the dorsal ventricular ridge (pars anterior). Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Lateral surface is toward left side of photograph.

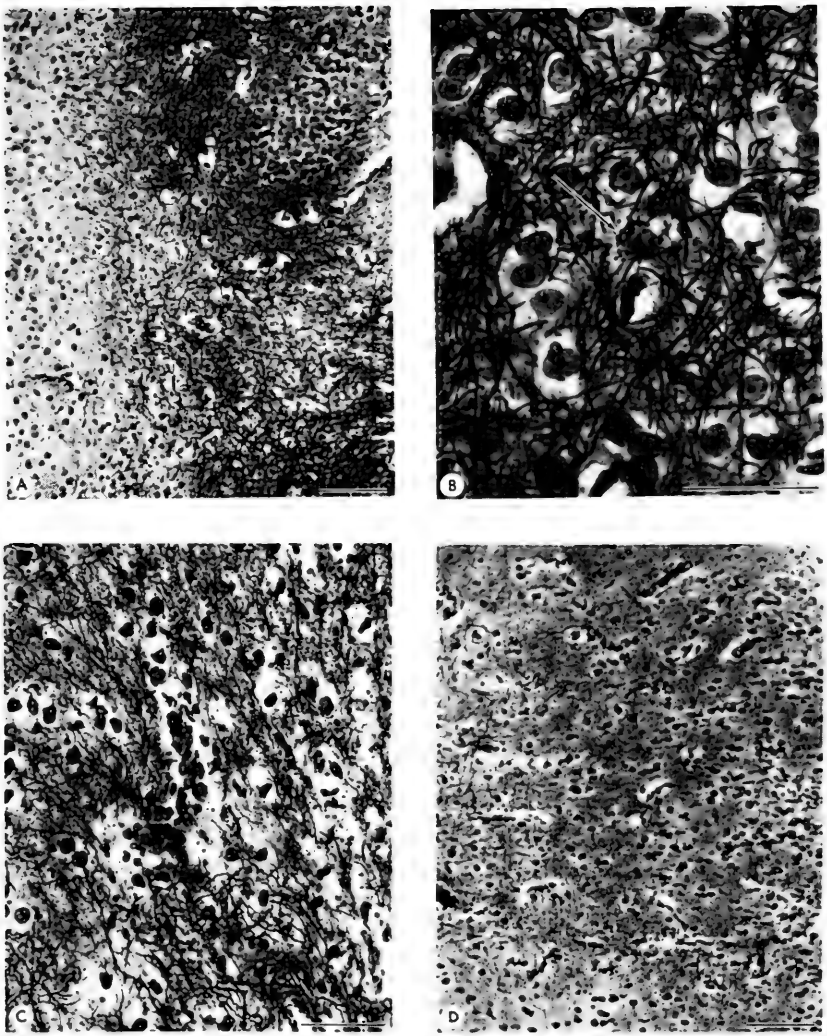

A
B
C
D

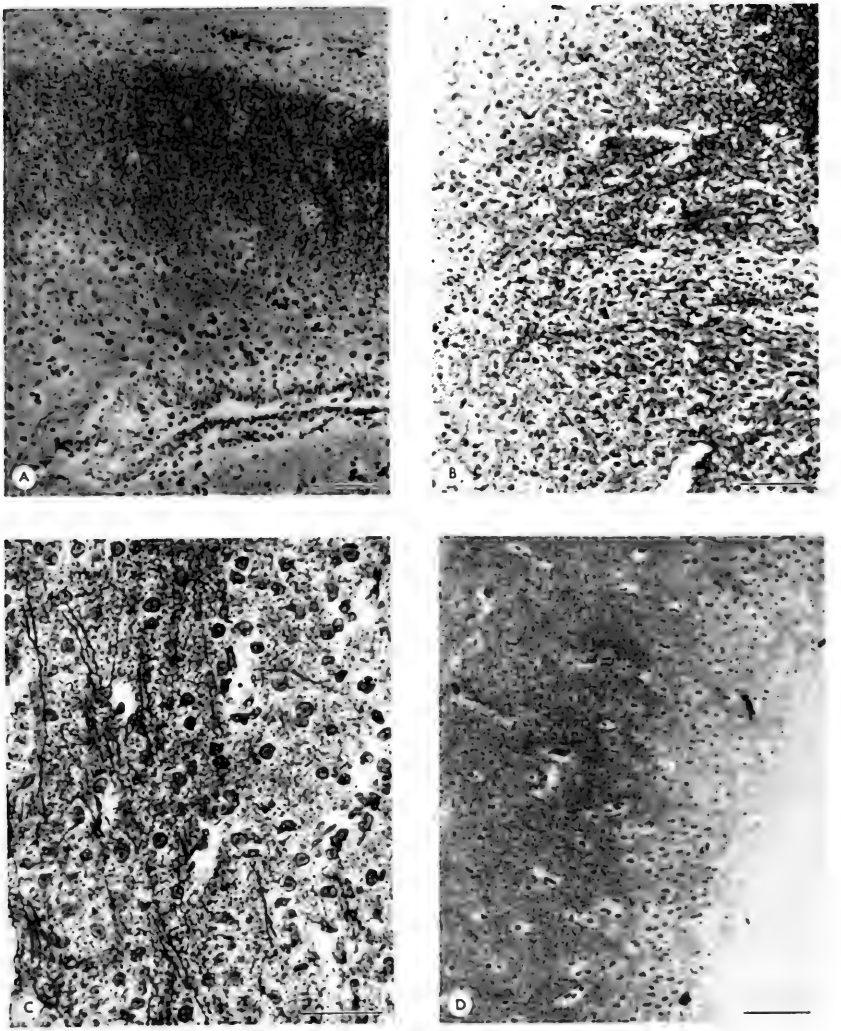
Figure 18. Photomicrographs of degenerating fibers in the telencephalon of the western painted turtle (Cp 17 and 22). Nauta method.

A. Degenerating fibers and terminal degeneration in the homolateral dorsal cortex (pars dorsolateralis) following ablation of the hippocampus and dorsal cortex (Cp 17). Bar scale indicates 100μ. Dorsal surface is toward top of photograph. Lateral surface is toward left side of photograph.

B. Degenerating fibers to homolateral paleostriatum from dorsal cortex (pars dorsolateralis) following ablation of part of the pars dorsolateralis (Cp 17). Bar scale indicates 100μ. Orientation same as in 18A.

C. Terminal degeneration in homolateral paleostriatum following ablation of dorsal cortex (pars dorsolateralis) Cp 22. Bar scale indicates 50μ. Orientation same as in 18A.

D. Terminal degeneration in contralateral hippocampus following ablation of hippocampal cortex (Cp 17). Bar scale indicates 100μ. Dorsal surface toward top of photograph. Lateral surface toward right side of photograph.


A
B
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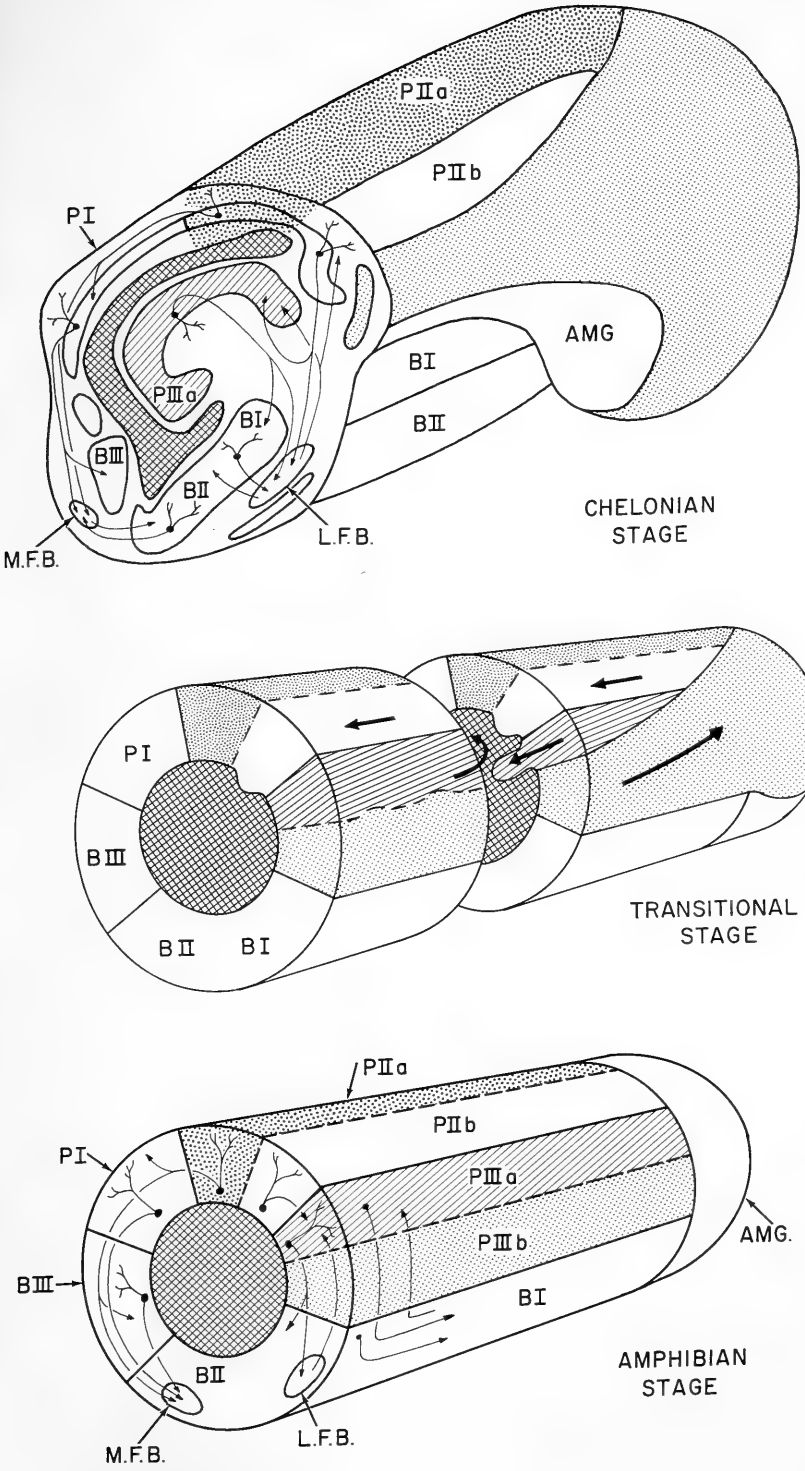
D

Figure 19. Schematic representation of the left telencephalic hemispheres of supposed ancestral amphibian stage leading to modern turtles (Chelonian stage). PI, medial pallial column or field; PIIa, dorsomedial component of dorsal pallial column; PIIb, dorsolateral component of dorsal pallial column; PIIIa, dorsal component of lateral pallial column (dorsal ventricuar ridge); PIIIb, ventral component of lateral pallial column; BI, lateral basal column; BII, ventral basal column; BIII, medial basal column; L. F. B., lateral forebrain bundle; and M. F. B., medial forebrain bundle.


PIIa
PIIb
PI
AMG
BI
BII
PIIIa
BI
BIII
BII
M.F.B.
L.F.B.
CHELONIAN STAGE
PI
BIII
BII
BI
TRANSITIONAL STAGE
PIIa
PIIb
PI
PIIIa
AMG.
BIII
PIIIb
BI
BII
M.F.B.
L.F.B.
AMPHIBIAN STAGE

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Numbers in italics refer to the figures.

A Note on the Author

R. Glenn Northcutt is assistant professor of anatomy at Case Western Reserve University. He received his B.A. from Millikin University in 1963, and his Ph.D. from the University of Illinois in 1968. His other book, *Atlas of the Sheep Brain,* was published in 1966.

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