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Differentiation In The Telencephalon Of A Typical Teleost Fish, Galeichthys Felis.

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DIFFERENTIATION IN THE TELENCEPHALON OF A TYPICAL TELEOST FISH, *GALEICHTHYS FELIS*

by

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I. INTRODUCTION

The development of the nervous system has been studied in representatives of all orders of the Class Vertebrata (Edds, 1970). Descriptions of telencephalic development in vertebrates have been given for all levels of the phylogenetic scale from fish (Johnston, 1911; Källen, 1951; and Nieuwenhuys, 1961) to man (e.g., Humphrey, 1966 and 1967; and Windle, 1970). Throughout these and other investigations homologies have been determined in general for the vertebrate telencephalon from amphibians to man, with the notable exception of the Teleostei, or bony fish.

Disagreements over the homologization of the fish telencephalon with that of the higher vertebrates have ensued since Susanna Gage (1893), in morphological studies of Dimectylys viridescens, Amia, and the lamprey, indicated that the teleost telencephalon might represent an everted form of the primitive neural tube. This is in contrast to the supposed inverted form of the telencephalic neural tube in the other vertebrates. This argument was advanced by Dr. Gage and her successors as an explanation for the lack of lateral ventricles in the telencephala of the bony fishes and has subsequently resulted in a confusing array of nomenclature and theories for the definition of the nuclei and fiber systems in the Actinopterygii. Holmgren (1925), for example, concluded that the lateral hemispheric eversion suggested by Gage has reversed the topography of the dorsal hemispheric areas, such that the homologue of the hippocampal formation (which is situated dorsomedially in higher submammalian vertebrates) in fishes is repre-

sented by the lateralmost nucleus of the dorsal hemispheric wall. Ariens Käppers, Huber and Crosby (1936), on the other hand, noted the similarities of hemispheric fiber connections between the bony fish and higher forms, and suggested that they represented homologous systems. Weston continued this theory and suggested that the lateralmost dorsally situated cells in the forebrain of Actinopterygian fishes form a primordial amygdaloid area. Various contemporary authors (Droogleever Fortuyn, 1961; Schnitzlein, 1964; and Singh, 1969) agreed with these conclusions and established homologies for the remainder of the telencephalic nuclei in many representative fishes. Other authors, such as Källen (1951) and Nieuwenhuys (1961, 1962, 1963a and 1963b), have adhered to the initial premise of Gage (1893) and have derived a nomenclature for the nuclei on the basis of topography, rather than homology.

The consequences of these disagreements have obviously been manifested in the behavioral, physiological, and anatomical studies conducted upon the teleost telencephalon. The significance of experimental studies on this structure is greatly reduced if no basis exists for comparing these systems to those of higher forms. Therefore, a series of studies was undertaken by the present author to determine if topographical, cytological, and hodological patterns in the telencephalon of a typical adult teleost fish offered insight into homological relationships to higher vertebrates. The initial investigation utilized the adult marine, or sea catfish, Galeichthys felis (Morgan, 1971). The conclusions of this study substantiated and extended the concept that the nuclei and fiber systems in fish possess homologies in higher vertebrates. However, this research

effort alone failed to provide an adequate explanation for the lack of lateral ventricles in the Teleostei, and, as a consequence, the present investigation ensued.

Basically, the intent of this continuing investigation was 1) to describe the morphological development of the telencephalon of a typical teleost, 2) to determine if the suggested homologues in the Actinopterygian forebrain would agree with homologies determined on a comparative embryological basis, and 3) to determine on the basis of the above information if a plausible theory could be developed to explain the lack of lateral ventricles in the bony fishes.

II. COLLECTION AND LABORATORY REARING OF EMBRYONIC GALEICHTHYS FELIS

A. Collection

The marine catfish, Galeichthys felis, was chosen as the laboratory animal for this investigation for four basic reasons. Firstly, the adult telencephalon in this fish is relatively well differentiated in comparison to the salmonids. Secondly, the eggs and embryos of this species are among the largest known of the teleost fishes. Thirdly, the male marine catfish orally incubates the eggs, i.e., the male (through an unknown phenomenon) obtains and carries the fertilized ova in his oral cavity for a period of 60 to 80 days (Gunther, 1947, and Ward, 1957). Fourthly, the large size of the males (8 to 12 inches fork length) and their estuarine habitat during incubation allow them to be collected readily by the use of an otter trawl.

The adult, juvenile, and embryonic material was collected during the summer of 1971. Previous experience in the localization of the incubating males allowed for the collection of approximately 250 embryonic and juvenile specimens from the Mississippi Sound. These animals ranged from 3 millimeter blastodisc stages to 50+ millimeter juveniles.

Immediately following collection, the eggs and juveniles were removed from the host males and placed in cooled sea water. They were then transported to the Marine Environmental Sciences Consortium, Point Aux Pins Facility, Bayou La Batre, Alabama, where they were

incubated artificially.

B. Laboratory Rearing

Early attempts (1969 and 1970) to rear marine catfish embryos in the laboratory had proven disappointing since a given series could be maintained only approximately two weeks before the death of the majority of the specimens. It was noted that a fungal growth infested the chorionic membrane a few days subsequent to the removal of the eggs from the host male, and that the death of the embryo followed the induced chorionic breakdown. Therefore, a special plexiglass tank was designed prior to the collecting efforts of 1971 in an attempt to correct this problem.

A forty gallon tank forty-eight inches long, fourteen inches high, and twelve inches wide was constructed of 5/8 inch plexiglass. This material was selected in order to eliminate the buildup of harmful deposits which occurs on glass in salt water aquaria.

Cheesecloth was attached to a plexiglass ladder frame which was then suspended approximately one and one half inches below the water level in the tank. The embryos were placed on the cheesecloth and thereby maintained slightly below the water surface. The hatched fish were placed in holders constructed by stretching nylon mesh over a cubic plastic frame. These holders were then placed in the same tank in which the embryos were kept.

In order to mimic the flow of water over the eggs which occurs in the natural environment as a result of the male host's respiration, a paddlewheel apparatus was affixed to one end of the tank. The paddlewheel-induced motion of the water constantly agitated the eggs,

serving both to prevent the accumulation of debris on the chorionic surface as well as to prevent the chorion from remaining constantly pressed against the cheesecloth at any particular point.

The water was treated weekly with a commercially available fungicide, which contained silver nitrate as its active ingredient. Artificial seawater salts and trace elements (Instant Ocean) were used in lieu of natural seawater to further reduce the presence of contaminants. Side filters were placed at either end of the tank and filled with crushed coral. These filtration beds were both seeded from another operating saltwater aquarium for formation of the bacterial colony necessary for the conversion of nitrogenous wastes. Several small fish were maintained in the tank prior to the introduction of the embryonic and juvenile specimens to maintain the bacterial colonies. The acidity of the aquarium was monitored daily by use of a pH meter, but remained stable at approximately 8.0 $\pm$ 0.2 throughout the experiment.

Temperature was regulated by cooling the laboratory to approximately 22° C and then warming the water to 28° C with two thermostatically controlled aquarium heaters. Salinity of the tank was stabilized at 26 °/$_{oo}$ by the addition of distilled water to maintain the volume at a predetermined level. Samples from the aquarium were titrated weekly and compensation made for any salt loss.

Following collection, both embryos and juveniles were acclimated to their new environment over a four-hour period by the gradual addition of artificial seawater to the natural seawater in which they were transported. Transfer to the tank was made via a nylon net to reduce the transfer of contaminants.

These procedures proved quite successful in that some of the specimens were maintained in the laboratory as long as 43 days with no apparent ill effect. Less than 5 percent of any given series died, and this was probably attributable to collection trauma.

III. TECHNICAL PROCEDURES

The embryonic fish were removed from the aquaria prior to fixation and observed under a dissecting microscope to determine viability and condition. All of the material was fixed alive.

Unhatched specimens were fixed by the following procedure. The egg was gripped at its ventral pole with tissue forceps, and an incision was quickly placed in the chorion over the embryo. The living embryo and yolk were then extruded through the incision directly into either alcoholic Bouin's fixative or ammoniacal alcohol made from one part ammonium hydroxide (28% NH_3) and 99 parts ethyl alcohol.

The juveniles (hatched fish) were placed on ice until inactive. The roof of the skull was then removed and the still living specimen was immersed in either Bouin's fixative or ammoniacal alcohol.

Following fixation and alcohol dehydration, all specimens were photographed next to a millimeter scale using a Honeywell Pentax camera and bellows extension unit. Fixed length was determined from the photographs.

All unhatched specimens were fixed for approximately 24 hours (in Bouin's fluid) and then dehydrated in a graded ethyl alcohol series until all traces of the fixative were removed. The embryos were subsequently cleared with xylene and embedded in paraffin. Hatched stages were treated in an analogous manner, with the exception that the brain was removed prior to alcohol dehydration. Two hundred and eleven specimens were preserved.

Of these specimens, four were sectioned transversely at a thickness of 10 u and stained with hematoxylin and eosin. Forty-two specimens were cut transversely into sections 15 u thick, and stained with Windle, Rhines, and Rankins (1943) thionin technique. A series of 10 animals were sectioned sagittally and horizontally and also stained with thionin. A series of 39 embryos was sectioned transversely, 12 sagittally, and 8 horizontally at a thickness of 15 u and impregnated with Protargol (Bodian's technique, 1936). Three specimens which had been fixed in ammoniacal alcohol were impregnated with pyridine silver by Foley's procedure (1938).

Microscopic sections were photographed with a Leitz Orthoplan microscope and camera unit. Drawings were prepared from overhead projections of photographic negatives and completed with the aid of a light microscope.

IV. DESCRIPTION OF THE MATERIAL

A. Introduction

Neuroembryological investigations of other vertebrates have commonly used the description of selected "stages" to demonstrate developmental trends. However, the embryogenesis of the nervous system is marked by the migration of cell populations over proportionately large distances and by the formation of various fiber systems over an extended period of time. Consequently, descriptions of selected stages may fail to convey properly the changing relationships and, therefore, the implied significance of these cellular movements and of the generation of fiber systems as they vary in a temporal sequence. The following description is based upon deduced subdivisions of developmental sequences which are termed "intervals". Essentially, an interval of development is initiated by the appearance of distinct nuclear and/or fiber populations (or sets of populations) which were not present in the preceding interval; it is terminated by the manifestation and/or differentiation of additional structures. Thus, an interval of development, as presented here, may represent a number of stages; it stresses the relationships of the cellular and fiber structures by emphasizing alterations of morphology.

The terminology employed in this study is that determined for the same fish in a previous investigation of adult telencephalic morphology (Morgan, 1971). Certain embryological terms, however, require definition. In this text "pallial anlage" is applied to the

homogeneous, undifferentiated band of cells which ultimately gives rise to the adult hippocampal, general (or dorsal) pallial, and piriform cortical formations. The adjective "primordial" as used in both the previous and present studies emphasizes phylogenetic rather than ontogenetic relationships. Specifically, the modifier "primordial" indicates that the described area in the Actinopterygii represents a very primitive or early form of the more greatly differentiated but homologous structure in the higher vertebrates.

The following description is divided into seven intervals of development, beginning with the relatively undifferentiated prosencephalon of an embryo from 6 to 7 millimeters in length and extending through the attainment of the adult telencephalic configuration in a 45 millimeter juvenile. A single stage is illustrated for each interval and variations in morphology and relationships within an interval are described within the text.

B. Interval I

Gross specimen. During the first interval of development the embryonic sea catfish measures from approximately 6 to 7 millimeters in fixed length. The embryo lies relatively straight on the yolk, and the otic vesicles and lens placodes are prominent. Enlargements of the neural tube at rostral levels represent the tectal and the rhombencephalic anlagen. The prosencephalon in these stages is relatively diminutive (Fig. 1).

Histological. Throughout the neural tube a simple columnar to cuboidal ventricular zone, an intermediate zone, and a marginal

zone are apparent (Boulder Committee, 1970). In the rostral tip of the prosencephalon of this interval no evagination or eversion of the dorsal brain wall has occurred (Fig. 2). The lumen of the neural tube is narrow and slit-like. The lateral marginal zone is only faintly visible and the intermediate zone is filled with small, homotypic cells. No nerve fibers could be detected in the material investigated.

The olfactory placodes in this interval lie lateral to the prosencephalic walls (Fig. 2). Each placode is several cells thick, but no cytodifferentiation has occurred and no olfactory fila have been generated. Mitotic figures are numerous in both the placodes and in the ventricular zone.

C. Interval II

Gross specimen. During Interval II (7 to 8 millimeters total fixed length) the marine catfish embryo exhibits distinct eyes and a marked widening of the rhomboid fissure (Fig. 3). The cerebellar anlage is apparent and the otic vesicles are relatively less dominant. Pectoral fin buds are developing from the more rostral somites and the opercular anlagen can be detected lateral to the otic vesicles.

Histology. The configuration of the telencephalon is altered from that of the preceding interval in that a dorsal, laterally directed evagination coupled with a widening of the ventricle gradually produces a v-shaped lumen (Figs. 4 and 5), in contrast to the slit-like lumen characteristic of Interval I. A marked lateral evagination at the telencephalic-diencephalic junction results in a posterior

proliferative zone (Fig. 6). Nuclear subdivisions can be detected in the intermediate zone as cytodifferentiation is initiated.

The olfactory placodes in this interval maintain their position lateral to the telencephalic wall and caudal to the rostral pole of the hemisphere (Fig. 4). The laminae of these placodes have increased in thickness and contain fusiform neurons. Olfactory fila emerge from the medial aspect of each placode and course first rostrally, then medially as a small, round fiber bundle to ramify over the anterior ventrolateral hemisphere. At the site of entrance of the olfactory fila, a lateral migration of small neuroblasts from the rostral ventricular zone produces a slight bulge on the lateral hemisphere wall. This bulge demarcates the anlage of the olfactory bulb (Figs. 4 and 5). No cytodifferentiation is detectable in this area, and no olfactory tract fibers have as yet been generated.

A column of undifferentiated neuroblasts situated caudal to the developing olfactory bulbs along the ventromedial hemisphere wall represents the presumptive septal area (Fig. 5). These cells merge spinalward with the as yet undifferentiated diencephalon.

Dorsal to the septal area, a proliferation of neuroblasts directed laterally from the intermediate region of the rostral hemisphere has resulted in a dorsal aggregation of relatively large cells which constitutes the striatal anlage (Figs. 4 and 5). Projecting ventrolaterally from this striatal area are fibers which accumulate in the lateral wall, pass caudally, and then dorsocaudally through the diencephalon into the mesencephalon. These axons comprise the ventral peduncle of the lateral forebrain bundle (Figs. 5, 6 and 7).

In the dorsocaudal hemisphere, a mass of homotypic, undifferentiated cells migrates in both a ventrolateral and a rostroventral direction from the dorsal and posterior ventricular zones. Fibers emanating from this aggregation pass caudoventrally through and with the lateral forebrain bundle toward the region of the lamina terminalis and presumptive preoptic and hypothalamic regions. This nuclear area is the anlage of the primordial amygdaloid complex (Fig. 5) and the fiber fascicles represent the homolateral component of the developing stria terminalis (Figs 6 and 7). Neuronal immaturity prevents the subdivision of the striatal and the amygdalar anlagen.

The telencephalon in the second interval is thus characterized by the appearance of the olfactory fila and olfactory bulbs, of the anlagen of the septal, striatal and amygdalar areas, and by the development of the lateral forebrain bundle and stria terminalis.

D. Interval III

Gross Specimen. In comparison with Interval II, the appearance of the embryos in Interval III becomes markedly altered (Fig. 8). The retina and lens of the eye are quite large. Maxillary barbels are prominent and the pectoral fins have developed their characteristic shape. The gross brain is changed primarily in terms of proportion, i.e., the optic tectum is much more pronounced than in Interval II, whereas the relative width of the myelencephalon is somewhat reduced. The cerebellar anlagen remain diminutive and the telencephalon is inclined rostroventrally. Overall length of the embryos increases from approximately 8 to 9 millimeters.

Histological. The overlying telencephalic membrane is unchanged in terms of its dorsolateral attachment to the wall of each hemisphere (Figs. 9, 10 and 11). The habenular anlagen are more prominent and a definite epiphysis is present between them. A thin tela choroidea extends into the midline ventricle. During the course of the third interval the midline ventricle continues to become reduced in its transverse dimension.

The olfactory placodes remain lateral to the telencephalic hemispheres during Interval III, but are more deeply invaginated than those of the preceding intervals (Fig. 10). No new cell types are present. The olfactory fila emerge as before from the medial aspect of the placodes and course rostromedially (Fig. 10) to ramify over the caudolateral aspect of the olfactory bulbs. Neither a vomeronasal nerve nor Jacobsen's organ (Brookover, 1914) was identifiable.

The developing olfactory bulbs in Interval III form more pronounced bulges on the hemisphere wall (Fig. 9). In transverse section each olfactory bulb anlage appears spherical. They occupy the entire area of the anterior intermediate hemisphere wall from the ventricular zone medially to the outer limiting membrane laterally. Histologically, a few glomeruli are present at the periphery of the bulb adjacent to the overlying olfactory fila. Deep to this developing glomerular layer a few cells with more compact Nissl material represent the beginning of the mitral cell layer. Dorsally the olfactory bulbs are bounded by an area of homogeneous, undifferentiated cells which probably represents in part the anterior olfactory nucleus and in

part the cells of the septal anlage, although a definitive determination for this interval was not possible.

Caudally and ventrally the olfactory bulb is replaced by cells of the presumptive septal area (Fig. 10). During the third interval the precommissural septal anlage is delimited caudally by the developing anterior commissure (Figs. 11, 39 and 40). Although no cytodifferentiation was detected in this area during the third interval, those cells which are situated about and intermingled with the fibers of the anterior commissure in these stages represent the bed nucleus of the anterior commissure. The supracommissural septum extends spinalward to merge indistinctly with the rostral diencephalon (Fig. 11).

Dorsal to the septal anlage and ventral to the striatal-amygdalar proliferative zones, cells can be seen migrating from a rather restricted region of the ventricular zone towards the ventrolateral hemisphere wall (Fig. 10). These cells, which represent the forming lateral zone of the tuberculum olfactorium, pass through the fibers of the lateral forebrain bundle and stria terminalis but remain medial to the lateral olfactory tract. This developing nucleus is prominent rostrally but becomes more diffuse caudally at the level of the anterior commissure. Histologically, these neuroblasts are distinctly larger than those of the septal area and exhibit more diffuse Nissl material than do those of the striatum or amygdala.

The developing striatal area, which is situated dorsal to the proliferative ventricular area of the lateral zone of the tuberculum olfactorium and rostral and rostroventral to the primordial amygdaloid

anlage (Figs. 9 and 10), contains a relatively greater number of cells than in the preceding interval. At this stage of development, however, no discernable subdivision of the striatal area is possible. Rostrally, the striatal area is continuous with the olfactory bulbar formation and caudally it overlaps medially and is ultimately replaced by the primordial amygdaloid anlage.

The primordial amygdaloid anlage in this interval continues to occupy the caudal, dorsolateral hemisphere wall (Fig. 11). This area is bounded by the slightly larger-celled striatal area ventromedially and by the migrating cells of the lateral zone of the tuberculum olfactorium ventrolaterally. Caudally the primordial amygdaloid anlage occupies the entire dorsal hemisphere and is indistinctly separated from the diencephalon. A thin, acellular region is present immediately beneath the proliferative areas for both the striatal and the amygdaloid anlage (Figs. 10 and 11).

In Interval II the almost simultaneous appearance of the lateral forebrain bundle and the stria terminalis was noted. During Interval III, however, the lateral olfactory tract appears, and the course of the stria terminalis is extended, the latter by the initiation of the formation of the anterior commissure (Figs. 11, 39 and 40). The lateral olfactory tract passes from the dorsocaudal aspect of the olfactory bulb and the anterior olfactory nucleus along the lateral hemisphere wall adjacent to the developing lateral tubercular and amygdalar regions.

Some of the fascicles which course from the presumptive amygdaloid nucleus medial to the lateral olfactory tract decussate in the

anterior commissure during the third interval. Following decussation, these fibers pass to both the amydaloid areas of the opposite hemisphere and to the presumptive preoptic and anterior hypothalamic regions of the opposite side. These systems thus constitute interamygdalar and stria terminalis components of the anterior commissure, respectively (Figs. 39 and 40). A decussation of the lateral forebrain bundle does not appear to occur in this interval.

In diencephalic levels, a few fibers turn dorsalward from the homolateral, caudally coursing stria terminalis to pass through the thalamus to the habenular anlagen. This pathway probably represents the beginning of the amygdalohabenular tract, but confirmatory experimental evidence will be required for an absolute definition.

Histologically, Interval III is thus characterized by recognizable differentiation in the olfactory bulb and by the delineation of the septal anlagen. The most pronounced change, however, is the decussation of the stria terminalis and interamygdaloid fascicles to initiate the formation of the anterior commissure, and the appearance of the lateral olfactory tract.

E. Interval IV

Gross Specimen. Interval IV is represented by embryos which are from one to six days older than the latest stages of Interval III. In overall appearance little change is apparent (Fig. 12); the neural structures grossly retain approximately the same proportions and the length of the specimens increases only from 9 to 12.5 millimeters.

Histological. In transverse section the position of the overlying telencephalic membrane is not altered in this interval, i.e., it maintains its dorsolateral attachment (Figs. 13, 14, 15 and 16). Histologically, however, Interval IV is characterized by the appearance of the presumptive pallial area, the anterior amydaloid continuation and the corticomedial amygdaloid nucleus. The medial olfactory tract can also be recognized in this interval.

The olfactory placodes in Interval IV continue to enlarge and invaginate, although little folding of the placode occurs. The only identifiable differentiated neurons are the fusiform cells, the axons of which form the olfactory fila. The remaining cellular constituents of the placodes are small, elongate, and densely packed. The olfactory fila, as in Interval III, course rostrally and medially (Fig. 13) to ramify over the caudolateral surface of the bulb.

The position of the olfactory bulbs remains relatively unchanged during the fourth interval in that they extend from the ventricular zone laterally to form increasingly larger bulges on the lateral hemisphere walls (Fig. 13). The region of the ventricular zone from which the olfactory bulb proliferates remains characteristically thicker peripherally with a definite thinning of the ventricular cells centrally (Fig. 13). The migrating neuroblasts follow a semicircular path into the bulb which is demonstrated by the orientation of the cell processes. Cytodifferentiation in the olfactory bulbs becomes much more pronounced in Interval IV. In the preceding stages, the bulb was typified as a relatively undifferentiated sphere of cells with only a few recognizable mitral cells centered around the point

of entrance of the olfactory fila. Although this condition prevails in the initial stages of Interval IV, the older embryos gradually develop a more definitive mitral cell layer. Centrally, smaller neurons form the internal granular cell layer, which is continuous caudally with the cells of the anterior olfactory nucleus. Internal and external plexiform layers could not be established in this interval.

The anterior olfactory nucleus becomes somewhat better delineated in Interval IV as a group of small, homotypic cells which are interposed between the internal granular cell layer of the olfactory bulb and the adjacent nuclear areas of the hemisphere (Fig. 13). Dorsally, a few cells of the developing striatum lie adjacent to this nucleus and dorsolaterally the anterior amygdaloid nucleus is continuous with it. Caudally and ventrocaudally the cells of the anterior olfactory nucleus blend imperceptibly with the septal anlage. All of the foregoing relationships remain relatively constant throughout Interval IV.

The septal (and possibly the medial tubercular) anlage in these stages extends spinalward along the medial hemisphere wall from the anterior olfactory nucleus rostrally to levels caudal to the anterior commissure (Figs. 14 and 15). Dorsally the septal nucleus is delimited by the proliferation of cells of the lateral zone of the tuberculum olfactorium. Caudally, the supracommissural septal cells make an indistinct transition into the diencephalon. As in the previous interval, the anterior commissure is surrounded by its bed nucleus, which is derived from the supracommissural septum (Fig. 15). Ventrally, no medial tubercular cells were detected.

In the preceding intervals a thin, generally acellular region was evident just ventral to the dorsal ventricular cells (Figs. 9 and 10). In Interval IV, however, this space becomes occluded rostrally by small, undifferentiated, homotypic cells which represent the beginning of the pallial anlage, or region from which the primordial hippocampal formation, the primordial general pallium, and the primordial prepiriform and piriform cortices will ultimately be derived. This anlage constitutes a thickened band of cells which is bounded medially by the migrating cells of the lateral zone of the tuberculum olfactorium and extends from this point dorsally and laterally (closely applied to the ventricular zone) to approximately the attachment point of the dorsal telencephalic membrane (Figs. 13 and 14). Rostrally, these pallial cells are contiguous upon the dorsal aspect of the anterior olfactory nucleus, but extend caudally only to mid-hemisphere levels where they are replaced by the developing amygdaloid complex and cell-free space previously described. The cells of the striatal and amygdaloid nuclei continue to migrate through and around the cells of this presumptive pallial area. Primordial hippocampal, general pallial, and piriform cortices could not be established in this interval due to the continued migration of other cells through this region and the lack of adequate cytodifferentiation. However, this does not preclude the presence of at least two of these three areas at this stage of development in undifferentiated form, which could be predicted on the basis of later intervals. Accordingly, the initial pallial anlage probably consists at least of the primordial hippocampal and piriform cortices, which will differentiate during

the subsequent intervals. The primordial general pallium differentiates rather late in development and is present at that time in only the middle one-third of the hemisphere. Thus, general pallial neuroblasts may not be present in these stages. Establishment of precise times of origin and boundaries within this anlage in Interval IV will require autoradiographic analysis.

The lateralmost region of the dorsal ventricular zone in Interval IV becomes the proliferative area for the primordial corticomedial amygdaloid nucleus and the anterior amygdaloid continuation in the middle and rostral segments of the hemisphere, respectively. The latter nucleus consists of a densely packed column of cells (Fig. 13) extending from the dorsolateral aspect of the anterior olfactory nucleus caudad to lie lateral to, and then indistinctly blend with, the cells of the primordial corticomedial amygdaloid nucleus. The corticomedial amygdaloid nucleus is situated more caudally in the hemisphere between the most dorsolateral ventricular zone cells dorsally, fibers of the lateral olfactory and amygdalohabenular tracts laterally, and the remaining strio-amygdaloid complex medially (Fig. 14). The corticomedial amygdaloid nucleus in these stages does not extend caudally beyond the level of the anterior commissure.

The remaining amygdaloid anlage which lies medial to the corticomedial amygdaloid nucleus (in its anterior extent) constitutes the primordial basolateral amygdaloid nucleus. This area lies ventral to the pallial laminae and lateral to the striatum in anterior hemisphere levels (Fig. 15). More caudally, the basolateral amygdaloid complex constitutes the major nuclear mass of the hemisphere (Fig. 16).

It lies in apposition to the ventricular zone dorsally and is dorsal to the lateral forebrain bundle, stria terminalis, and the amygdalohabenular tract.

The striatum, as in the preceding stages, occupies primarily rostral and midhemisphere levels and is replaced caudally by the primordial basolateral amygdaloid complex. Rostrally, the presumptive striatal cells, distinguishable by their larger size, lie adjacent to the dorsocaudal aspect of the anterior olfactory nucleus (Fig. 13). Ventrally the striatal anlage is bounded by, and in part intermingled with, the migrating cells of the lateral zone of the tuberculum olfactorium (Fig. 14). Dorsomedially and medially, the smaller, more closely aggregated cells of the presumptive pallial area intervene between the proliferative ventricular zone and the striatal region (Figs 13 and 14). Consequently, neuroblasts migrating from the dorsal ventricular layer to the presumptive striatum must pass through the dorsomedial pallial anlage. As in Intervals II and III, the absence of a dorsal peduncle of the lateral forebrain bundle and the lack of cytodifferentiation within the striatum preclude the designation of a neostriatum. Ventrally, however, large cells which are derived from the striatal region become interspersed among the fibers of the lateral forebrain bundle and the stria terminalis. These neurons, which maintain this same approximate relationship throughout the remaining developmental stages, constitute the paleostriatum primitivum. Lack of adequate cytodifferentiation does not as yet permit the designation of a hyperstriatum or a paleostriatum augmentatum.

In the later stages of Interval IV the initial fibers of the medial olfactory tract can be detected as they pass from the ventromedial aspect of the olfactory bulb caudally for a short distance along the ventrolateral hemisphere wall in relation to the presumptive septum. Such fascicles (in these stages) are detectable only in approximately the rostral one-third of the hemisphere, and probably do not extend any further caudad. It appears that some of the fibers which comprise this pathway have their cells of origin in the anterior olfactory nucleus. During their course, fibers of the medial olfactory tract turn medially and dorsomedially to enter the precommissural septum. The dorsolateral margin of this fiber system caudal to the olfactory bulb is intermingled with fibers of the lateral olfactory tract. A commissural component from the medial olfactory tract was not present in these stages.

The fibers of the lateral olfactory tract in Interval IV emerge from the dorsocaudal aspect of the olfactory bulb and lie, as in previous stages, along the dorsolateral hemisphere wall. Ventromedially, these fibers accompany the dorsolateral medial olfactory tract. Medially the lateral olfactory tract is apposed to the developing lateral zone of the tuberculum olfactorium and to the corticomedial amygdaloid area, to which it distributes fibers.

The relationships and distribution of the lateral forebrain bundle remain unchanged from those of the previous interval. A dorsal peduncle of the lateral forebrain bundle could not be detected in the available embryonic material in this interval. Fibers originating from the paleostriatum primitivum could not be traced to their

termination as distinct from the other fascicles of the ventral peduncle of the lateral forebrain bundle.

Many of the fascicles of the stria terminalis become much more clearly demarcated in the amygdalar region during Interval IV due to their segregation from the lateral olfactory tract and amygdalohabenular fibers by the developing primordial corticomedial nucleus. As in Interval III, however, many of the fibers of the stria terminalis become intermingled ventromedially with those of the lateral forebrain bundle, while others course ventrally along the ventrolateral hemisphere wall to reach the preoptic and anterior hypothalamic regions of the same side.

At approximately the level of the telencephalic-diencephalic junction, a small number of fascicles which course in part with the lateral olfactory tract turn dorsalward to pass through the rostral diencephalon to the habenula (Fig. 26). Their precise ipsilateral or contralateral termination could not be discerned in the material investigated. Piriform-habenular, preopticohabenular, septohabenular and hippocampohabenular pathways were not detected in these stages.

The anterior commissure (Fig. 15) remains essentially unchanged throughout Interval IV, i.e., it contains interamygdalar fibers and decussating fascicles of the stria terminalis. No contributions from the medial hemisphere or pallial anlage were detected.

The fourth interval of telencephalic development in the Galeichthys felis embryo is distinguished by the appearance and elaboration of the presumptive pallial area, the corticomedial amygdaloid nucleus, the anterior amygdaloid continuation, and the medial olfactory and

amygdalohabenular tracts. Cytologically, no subdivision of the pallial anlage was possible.

F. Interval V

Gross Specimen. The appearance of the embryos in Interval V (12.5 to 14.5 millimeters) is not greatly altered from that of the fourth interval, although growth and differentiation proceed quite rapidly in this phase of development. The ribs are more distinct than in the previous stages and the coiling of the embryo on the yolk is much more pronounced than in Interval IV (Fig. 17).

Grossly, the appearance of the brain is consistent with that of the preceding interval. However, the rather diminutive cerebellar anlage of Interval IV becomes much more pronounced by the final stages of Interval V.

Histological. The structure and placement of the olfactory placodes in Interval V are similar to those of the preceding interval, although the placodes do become more deeply invaginated. Cytologically, this structure remains essentially unchanged.

The olfactory fila, which in previous intervals coursed rostromedially, pass more directly medialward in Interval V (Fig. 18). In earlier embryos the olfactory fila approached the caudolateral aspect of the olfactory bulb, but in these stages the olfactory fila are positioned ventrolaterally as they contact the bulb.

The olfactory bulbs in Interval V gradually produce more prominent bulges in the lateral hemisphere wall as they begin to become

pedunculated (Fig. 18). The olfactory fila ramify over the exposed surfaces of the bulbs as before but their glomerular junctions are more numerous than in the preceding intervals (Fig. 29). An increase in the number of mitral cells is also apparent but internal and external plexiform layers could not be discerned in the available material. The internal granular cell layer remains continuous with the anterior olfactory nucleus.

The relationships of the anterior olfactory nucleus in Interval V are unchanged from those of Interval IV (Fig. 18). The transition from the internal granular cell layer of the olfactory bulb into the anterior olfactory nucleus is indistinct.

The septal area in Interval V extends, as in Interval IV, along the medial hemisphere wall from levels immediately posterior to the olfactory bulb through planes caudal to the anterior commissure (supracommissural septum), after which it diminishes (Figs. 19 and 20). This region is marked in Interval V by the beginning of detectable cytodifferentiation of the medial and lateral septal nuclei. The cells of the lateral septal nucleus are first distinguishable in the later stages of this interval just rostral to the anterior commissure in the intermediate region of the septal area (Fig. 19). Cytologically the lateral septal nucleus is indicated by darker staining Nissl substance and a slight increase in cell size. The remaining cells of the septal area constitute, for the most part, the pars dorsalis and pars ventralis of the medial septal nucleus. Ventromedially and rostrally a medial zone of the tuberculum olfactorium could not be differentiated from the medial septal nucleus, pars

ventralis, and the existence of this zone in Interval V is doubtful based on its late differentiation in this species (see Interval VI). At commissural levels the cells of the septal area continue caudally to intermingle with the fibers of the anterior commissure forming its bed nucleus, as in the preceding stages (Fig. 20). The remaining more dorsally situated cells of the supracommissural septum constitute, for the most part, the anlage of the bed nucleus of the hippocampal commissure.

In Interval IV the pallial anlage extended from the rostral pole of the telencephalon caudad to approximately mid-hemisphere levels. During Interval V the pallial anlage gradually extends throughout most of the hemisphere adjacent to the dorsal ventricular cell zone (Figs. 18, 19 and 20). Rostral to the anterior commissure, this pallial anlage is bounded medially by the stream of cells which is migrating laterally and ventrally to form the lateral zone of the tuberculum olfactorium (Fig. 19). At commissural and postcommissural levels the supracommissural septum establishes the medial boundary (Fig. 20). Laterally the presumptive pallial area is bounded by the dorsolateral attachment of the overlying telencephalic membrane. The pallial anlage during this period of development becomes more diffuse as cells begin to migrate out from it.

In the early stages of Interval V at the level of the anterior commissure and lamina terminalis the cells which lie ventromedial to the pallial area begin to form a thickened, rounded cluster which constitutes the anlage of the primordial dentate gyrus (Fig. 20). During these stages the cells of the dentate gyrus anlage remain

undifferentiated. As development progresses, this anlage extends rostral to commissural levels and later slightly spinalward from the anterior commissure. This presumptive area is bounded by the supracommissural septum ventrally, the striatum laterally, and the presumptive pallial cells dorsally. No nerve fiber connections (including the fornix) were noted in the specimens investigated.

The cortical pallial cells which lie immediately adjacent to the primordial dentate gyrus anlagen (Fig. 20) probably constitute the undifferentiated cells of the primordial cornu ammonis and primordial subiculum, although cytologically no such subdivision was possible in these stages. Definition of the cortical subdivisions is difficult in Interval IV also because of the continued migration of striatal cells from the overlying ventricular zone through the pallial anlage.

In the more lateral pallial cell region an analogous situation exists in that the lack of adequate cytodifferentiation, fiber connections and the intermingling of cells from the other nuclear areas precludes the establishment of even approximate boundaries between the other cortical anlagen. The characterization of the primordial prepiriform, piriform, and general pallial cortices during this interval will require histochemical and autoradiographic analysis.

The lateralmost region of the dorsal ventricular zone, i.e., that area adjacent to the site of attachment of the overlying telencephalic membrane, continues as a proliferative zone for the corticomedial amygdaloid nucleus and the anterior amygdaloid continuation (Figs. 18 and 19). The relationships of the latter area are similar

to those of the preceding interval, although the rostrocaudal extent is lengthened as a consequence of hemisphere growth. In the latest stages of Interval V, the anterior amygdaloid continuation becomes less compact in the region of the anterior olfactory nucleus. The column of anterior amygdaloid cells is contiguous medially to the presumptive prepirifrom cortex at its proliferative region and to the striatum in its more rostroventral extent.

The corticomedial amygdaloid nucleus (Fig. 19) undergoes little evident alteration in Interval V other than for longitudinal elongation and an increase in cell number. As in Interval IV, the corticomedial amygdaloid nucleus cannot be detected in transverse levels through the rostralmost portion of the hemisphere and is reduced caudally beyond commissural levels.

During the fifth interval of development in Galeichthys felis embryos, proliferation of cells from the dorsointermediate and the posterior ventricular zones continues to contribute to the expansion of the basolateral amygdaloid area (Figs. 19, 20 and 21). These cells in these and subsequent stages migrate ventrally and anteriorly through the layer of undifferentiated pallial cells which in the oldest embryos of Interval V completely intervenes between the ventricular cell zone and the primordial basolateral amygdaloid nucleus. As in Interval IV, no distinction between the pallial cells and the transient amygdalar cells is possible, but a generalized increase in the cell numbers of the basolateral amygdala confirms their continued proliferation and migration. Basal and lateral subdivisions could not be distinguished in the preparations utilized.

The lateral zone of the tuberculum olfactorium in these stages continues to be proliferated from the small ventricular cell zone situated adjacent to the dorsal boundary of the medial septal nucleus, pars dorsalis (Fig. 19). The relationships of this lateral zone remain unchanged, although an increase in the number of cells is apparent. However, the lateral zone of the tuberculum seems less cellular than that of the previous interval due to the presence of more nerve fibers and a probable increase in the number of blood vessels and glia. The medial zone of the tuberculum olfactorium was not recognizable in this interval, although its anlage may be present among the cells of the medial septal nucleus, pars ventralis.

In transverse section caudal to the level of the olfactory bulb in the later stages of Interval V, the striatum is demarcated ventrally by the migrating cells of the lateral zone of the tuberculum olfactorium, laterally by the primordial basolateral amygdaloid nucleus, and dorsally and medially by the presumptive pallial cells. Furthermore, in these embryos at such levels the striatal areas may be subdivided into a hyperstriatum, a common anlage of the neostriatum and paleostriatum augmentatum and, more caudally, into a paleostriatum primitivum. The more medially situated cells represent the anlagen of the neostriatum and paleostriatum augmentatum (Fig. 19). These neuroblasts are slightly smaller and have more diffuse Nissl material than do those of the lateral striatal region. In anterior hemisphere levels, these anlagen are juxtaposed ventromedially to the migrating cells of the lateral zone of the tuberculum olfactorium, but, in levels caudal to the region of this tubercular zone, this area lies

dorsolateral to the developing primordial dentate gyrus anlagen (Fig. 20). Also, in levels beginning slightly rostral to the anterior commissure (at which point no cells of the lateral striatal area are present) and extending caudally, these striatal anlagen are contiguous laterally upon the primordial basolateral amygdala (Fig. 20). Although no cytological distinctions can be made between these two cell populations at this time, their designation as the anlagen of the paleostriatum augmentatum and the neostriatum was made on the basis of later intervals in which the more ventrally situated cells become related medially to the septal area and the more dorsally situated cells project fibers into the dorsal peduncle of the lateral forebrain bundle.

Located lateral to the anlagen of the neostriatum and paleostriatum augmentatum in the anterior third of the hemisphere is the hyperstriatum (Figs. 18 and 19). These cells can be distinguished from the remainder of the striatum on the basis of their slightly larger size and more compact Nissl material. The hyperstriatum is bordered laterally and caudally by the primordial basolateral amygdala and dorsally by the presumptive pallial cells.

The fibers of the medial olfactory tract are continuous laterally with those of the lateral olfactory tract as they project from the dorsocaudal aspect of the olfactory bulb. Initially the medial olfactory tract lies along the ventromedial hemisphere surface (Fig. 19), contributing in course to the anterior olfactory nucleus and the septum. These fibers also appear to contribute to the cells of the pallial anlage which approximate the dorsomedial aspect of the

anterior olfactory nucleus but definitive terminations could not be established in the material investigated. After passing a short distance caudal to the olfactory bulb, the remaining medial olfactory tract fibers turn dorsally into the hemisphere. At this point, a well defined fasciculus separates from the main bundle (in the terminal stages of Interval V) and courses caudalward along the medial aspect of the lateral forebrain bundle to commissural levels, where this fascicle decussates. Fibers of the medial olfactory tract could not be discerned beyond commissural levels in these stages.

The lateral olfactory tract arises from the dorsolateral aspect of the olfactory bulb to pass caudally along the lateral hemisphere surface (Fig. 18). As in the previous intervals, numerous contributions to the anterior amygdaloid, lateral tubercular and corticomedial amygdaloid nuclei are present. The lateral olfactory tract is crossed by many more fascicles of the lateral forebrain bundle and stria terminalis than in earlier embryos and it intermingles caudally with the fibers of the amygdalohabenular tract (Figs. 22, 23, 41 and 42).

During the middle and subsequent stages of the fifth interval fibers extend through the septal area to the preoptic nucleus at commissural levels. These fascicles constitute the septo-preoptic component of the medial forebrain bundle (Morgan, 1971; tractus olfactothalamicus, pars intermedialis of Sheldon, 1912). However, the septo-hypothalamo-mesencephalic bundle (tractus olfacto-hypothalamicus medialis of Sheldon, 1912) which courses dorsal to the commissures in the adult marine catfish (Morgan, 1971) could not be detected in

these stages.

Fascicles from the presumptive neostriatum which contribute to the lateral forebrain bundle could not be traced to or from the dorsal thalamus in these stages. The ventral peduncle is formed primarily by contributions from the paleostriatal nuclei and projects to the ventral thalamus, hypothalamus, and midbrain tegmentum as in the previous interval (Figs. 22 and 23).

The stria terminalis continues in Interval V to form the predominant component of the anterior commissure (Figs. 41 and 42), and, in these stages, distinction between the stria terminalis and the interamygdaloid components (which comprises the more dorsally situated fibers) is apparent. These relationships remain relatively unchanged throughout Interval V.

The lateral corticohabenular tract in the fifth interval is formed by fibers from the primordial basolateral and corticomedial amygdaloid nuclei and possibly contains contributions from the presumptive prepiriform and piriform cortices. These fascicles accumulate laterally between the corticomedial and the basolateral amygdaloid nuclei and pass caudally to the telencephalic-diencephalic junction. At this point the lateral corticohabenular pathway ascends at first directly dorsomedially through the ventral thalamus, then rostrodorsally through the dorsal thalamus to the homolateral habenula (Fig. 26). Many of these fibers decussate in the habenular commissure and appear to synapse in part in the habenular nucleus of the opposite side. Some of the crossed fibers may enter the contralateral stria medullaris. The medial preopticohabenular, septohabenular, tuberculohabenular and hippocampohabenular components of the stria medullaris

(Morgan, 1971) could not be adequately demonstrated in the available material. A small bundle which courses laterally from the preoptic region around the lateral zone of the tuberculum olfactorium in the region of the anterior commissure appears in subsequent intervals to constitute the lateral preopticohabenular tract. In these stages, however, this pathway could not be traced into the region of the diencephalon.

The fifth interval of development in Galeichthys felis is thus distinguished by the differentiation of the medial and lateral septal nuclei, the primordial dentate gyrus, the hyperstriatum and the paleostriatum primitivum. Also, a medial olfactory tract component of the anterior commissure and the septo-preoptic segment of the medial forebrain bundle are established. No evidence of a fornix, hippocampal commissure, or medial corticohabenular pathway was noted.

G. Interval VI

Gross Specimens. The sixth interval of development in the sea catfish is that period in which most of the remaining telencephalic nuclear anlagen differentiate into histologically distinct areas. The embryonic fish in these stages is still confined by the chorion, but increases in size from approximately 14.5 to 20 millimeters in length. Pigmentation of the skin is initiated in these stages and the eyes become increasingly more encapsulated by the skull (Fig. 27). The overlying telencephalic membrane retains the approximate dorsolateral attachment of the preceding interval.

Histological. The olfactory placodes in Interval VI continue to shift rostrally in relation to the anterior pole of the hemisphere so that in the later stages of this interval the placodes are situated ventral and slightly rostral to the olfactory bulbs. The placodes continue to expand until in the late stages of this interval four longitudinally coursing ridges are present. Concomitant with the infolding of the placodes is their encapsulation by a circumferential flap of surface tissue.

The olfactory fila emanate from the core of each of the four placodal ridges as four distinct fasciculi which coalesce at the base of the placode to form a single bundle of fibers. This bundle courses dorsally and medially to ramify over the ventral aspect (future anterior pole) of the olfactory bulb (Fig. 24). The olfactory fila then turn into the substance of the bulb to synapse in the characteristic glomeruli (Fig. 24).

The olfactory bulbs become increasingly pedunculated in Interval VI (Fig. 28). Cytologically, little change is apparent in the olfactory bulb from the preceding interval. The mitral cells remain clustered, the glomeruli are distinct (Fig. 24) and internal and external plexiform layers are not evident. The internal granular cell layer merges dorsomedially with the anterior olfactory nucleus. Continued proliferation into the olfactory bulbs is evidenced by the thickened ventromedial ventricular cell layer and by the migrating columns of cells containing both heavy and diffuse staining Nissl material.

The anterior olfactory nucleus in these embryos is continuous

ventrolaterally with the internal granular cell layer of the olfactory bulb (Fig. 28). In transverse planes slightly posterior to the olfactory bulbs, the more elongated cells of the lateral zone of the tuberculum olfactorium and the much smaller cells of the anterior amygdaloid continuation are contiguous to the anterior olfactory nucleus. Ventrocaudally, in the later stages of Interval VI, the anterior olfactory nucleus impinges upon the differentiating medial zone of the tuberculum olfactorium and is replaced caudally by the cells of the medial septal nucleus, pars ventralis. Dorsomedially, the anterior olfactory nucleus comes into contact with those cells of the pallial anlage which ultimately differentiate into the anterior continuation of the hippocampus. Dorsally and dorsolaterally this nucleus is apposed to the striatal and prepiriform regions.

Proliferation of the septal area continues throughout Interval VI, although a gradual slowing of the proliferative rate is evidenced in the later stages by a thinning of the adjacent ventricular zone. As in the fifth interval, a medial septal nucleus anlage, a lateral septal nucleus (Fig. 29), a bed nucleus of the anterior commissure and a supracommissural septum (Fig. 30) are present. In the sixth interval a bed nucleus of the hippocampal commissure becomes distinguishable as the fibers of that commissure appear and decussate in the later stages. This nucleus is adjacent to and intermingled with the interhippocampal fibers.

No cytological changes occur in the medial septal nucleus during the early and middle stages of Interval VI. As in the preceding intervals, the ventral region of the medial septal area probably

constitutes the anlagen of both the medial septal nucleus, pars ventralis, and the medial zone of the tuberculum olfactorium. In the latest stages of the sixth interval the medial zone of the tuberculum olfactorium differentiates laterally from this region (Fig. 29). The remaining periventricular cells constitute the medial septal nucleus, pars ventralis (Fig. 29). The lateral septal nucleus (Fig. 29) increases in size and becomes intermingled with the fibers of the medial forebrain bundle, the precommissural fornix, the medial olfactory tract, and the medial corticohabenular system as development progresses. In later embryos of this interval, the oval, circumscribed appearance of the lateral septal nucleus is striking in sagittal sections, but in transverse planes the rosette arrangement of its more medial cells persists.

In the preceding interval, the cells of the pallial anlage were described as homotypic and densely packed, except for the regions of the primordial dentate gyrus and the anterior amygdaloid continuation. However, in the first stages of the sixth interval, marked histological change begins to occur in this area.

The cells of the pallial anlage which were proliferated from the rostromedial ventricular zone gradually differentiate in these stages into the anterior continuation of the hippocampus (Fig. 28). This nuclear area lies rostral to the septum, the primordial dentate gyrus and the proliferating lateral zone of the tuberculum olfactorium and is replaced caudally by them. The anterior continuation of the hippocampus merges with the dorsomedial aspect of the anterior olfactory nucleus and is bordered laterally by the presumptive pallium

and the neostriatum. These relationships persist in the adult form.

The position of the primordial dentate gyrus anlage in the dorsomedial hemisphere wall remains unaltered in Interval VI (Figs. 29 and 30). However, as development progresses, the differentiating polymorphic cells of the primordial cornu ammonis form the dorsomedial boundary of the primordial dentate gyrus (Fig. 29). The neostriatum, which is situated lateral to the primordial dentate gyrus and ventral to the developing primordial cornu ammonis in these stages, becomes cytologically differentiable from the paleostriatum augmentatum (Figs. 28 and 29). In the latest stages of Interval VI the fornix intervenes between the primordial dentate gyrus and the neostriatum as it courses ventrolaterally towards the septum. Rostrally, the dentate gyrus is preceded by the anterior continuation of the hippocampus and extends caudally only slightly beyond commissural planes.

The approximate medial third of the pallial area caudal to the anterior continuation of the hippocampus which is bounded by the dentate gyrus ventromedially and laterally by the neostriatum (in the rostral hemisphere) and basolateral amygdala (in the caudal hemisphere) begins to differentiate into larger, more darkly staining cells in the last stages of Interval VI. These cells constitute the recognizable beginning of the primordial cornu ammonis and subicular areas (Figs. 29 and 30), although, as previously noted, their anlagen are probably present in much earlier embryos. The primordial cornu ammonis and subicular areas become related laterally to the differentiating primordial general pallium (Fig. 29) in the middle one-third of the hemisphere and primordial piriform cortex in the caudal one-third.

Subsequently, the primordial hippocampal formation gives rise to the initial fascicles of the fornix system. Continued migration of undifferentiated neostriatal cells through this area may possibly occur in this and the following interval.

In the oldest embryos of the sixth interval an area of pale staining cells which represents the primordial general pallium becomes evident between the primordial basolateral amygdaloid nucleus and the primordial piriform cortex laterally and the neostriatal and hippocampal areas medially (Fig. 29). In the rostral hemisphere this primordial general pallium is continuous ventrally with the hyperstriatum, which consists of slightly larger cells with more concentrated Nissl material. The primordial general pallium in this interval does not extend to the level of the anterior commissure.

The presumptive prepiriform region in Interval V was described as a part of an area of homotypic, lightly staining cells situated in the anterior hemisphere adjacent to the striatum medially, the ventricular cell zone dorsally and the anterior amygdaloid continuation laterally. Caudally, this presumptive prepiriform area was continuous with the primordial corticomedial amygdaloid nucleus and the undifferentiated cells of the lateral pallial anlage. During Interval V these relationships remained constant; however, in the younger embryos of the sixth interval the prepiriform region becomes distinguished caudally from the differentiating cells of the primordial piriform cortex. In later stages, the primordial prepiriform and piriform regions are further circumscribed by the differentiating primordial general pallium dorsomedially, medially by the hyper-

striatum and ventrolaterally by the anterior amygdaloid continuation. These relationships persist into the adult form.

The neurons of the primordial piriform cortex (Fig. 29) in Galeichthys felis embryos become recognizable by their large pale-staining nuclei (evident in Protargol preparations) during the early stages of Interval VI. These cells continue to be elaborated through much later stages. The differentiated neurons of the piriform cortex migrate away from the undifferentiated band of pallial cells, although the piriform cortex of the adult is ultimately apposed to the ventricular ependymal layer. In late stages of Interval VI the piriform region becomes delimited medially by the larger, differentiated cells of the developing primordial general pallium in the middle one-third of the hemisphere. In the caudal one-third of the hemisphere the primordial piriform cortex impinges medially on the lateral aspect of the hippocampal formation. The primordial piriform cortex also overlies the lateral and caudal aspects of the basolateral amygdaloid nucleus in the caudal pole of the telencephalon. The primordial corticomedial amygdaloid nucleus lies deep to the piriform area in the middle one-third of the hemisphere.

In the older stages of the preceding interval, the cells of the anterior amygdaloid continuation which were adjacent to the anterior olfactory nucleus became less tightly aggregated. In the sixth interval this dispersement continues caudally until the most posterior cells of the anterior amygdaloid continuation blend imperceptibly into the corticomedial amygdaloid nucleus. Consequently, this anterior amygdaloid area becomes much less distinct in transverse

sections.

The primordial corticomedial amygdaloid nucleus (Fig. 29) in the sixth interval extends caudad from the anterior amygdaloid nucleus through transverse planes slightly rostral to the anterior commissure, after which it is replaced entirely by the primordial basolateral amygdala. As noted previously, the proliferative areas of the primordial piriform cortex and the primordial corticomedial amygdaloid nucleus occupy the lateralmost ventricular zone. These regions consequently cannot be distinguished from each other in the area adjacent to the ventricle. In the rostral hemisphere the corticomedial amygdaloid nucleus is bordered medially and dorsally by the hyperstriatum, and, to a lesser extent, by the primordial general pallium. More caudally, the primordial corticomedial amygdaloid nucleus is bounded medially and dorsally by the larger-celled basolateral area and ventrally by the lateral olfactory and corticohabenular tracts.

The primordial basolateral amygdaloid nucleus (Figs. 29, 30 and 31) continues as the predominant nuclear area in the caudal one-third of the telencephalon in the embryos of this interval. Furthermore, its relationships become more clearly defined in the course of its development. Rostrally the primordial basolateral amygdaloid nucleus is recognizable, anterior to commissural planes, lateral to the developing primordial general pallial and hyperstriatal areas. In transverse sections caudal to the commissure, the medial boundary is formed by the differentiating hippocampal formation. Basally, the basolateral region is bounded by the corticomedial amygdaloid nucleus through its rostral extent and thereafter by the lateral

corticohabenular tract toward the caudal pole of the hemisphere. Laterally, the primordial piriform cortex overlies the entire basolateral nucleus.

By the time the embryo is approximately 18 millimeters long, the striatal relationships described for the adult (Morgan, 1971) marine catfish are established. These subdivisions include the paleostriatum primitivum, the paleostriatum augmentatum, the hyperstriatum and the neostriatum.

During Interval IV the paleostriatum primitivum was a group of large cells intermingled with the ventral peduncle of the lateral forebrain bundle (see Figure 20). This nucleus was derived from the ventralmost cells of the striatal anlage which were actually proliferated during the preceding intervals. The basic relationships of the paleostriatum primitivum appear to shift more caudally until, in the definitive adult configuration, the rostral limit comes to lie just rostral to the anterior commissure (Fig. 30). Dorsally and rostrally these cells are continuous with the paleostriatum augmentatum, and ventrally are interspersed among the fibers of the lateral forebrain bundle and the stria terminalis. At the level of the anterior commissure the paleostriatum primitivum becomes rapidly reduced in size and merges with the entopeduncular nucleus at the telencephalic-diencephalic junction.

The paleostriatum augmentatum and the neostriatal anlagen cannot be subdivided cytologically in the early stages of Interval VI. Furthermore, the dorsal peduncle of the lateral forebrain bundle could not be identified at thalamic levels in the material investigated,

although contributions to the lateral forebrain bundle from the more dorsal cells of the medial striatal area were observed in the early stages of the previous interval. These dorsomedial striatal cells constitute the neostriatum (Figs. 28 and 29) which in these and later stages is related to the hippocampal formation dorsally and medially and to the hyperstriatum and the primordial general pallium laterally throughout the remainder of development. However, the more ventrally situated cells of the medial striatal region which lie lateral and dorsolateral to the developing lateral zone of the tuberculum olfactorium and medial to the hyperstriatum constitute the paleostriatum augmentatum (Figs. 28 and 29). The paleostriatum augmentatum, which was derived from the same region of the ventricular zone as the neostriatum, in later stages (i.e., following cessation of proliferation of the lateral zone of the tuberculum olfactorium) become related medially in the rostral hemisphere to the lateral septal nucleus, a position corresponding to that of the nucleus accumbens. Caudal to commissural levels the paleostriatum augmentatum diminishes in size. In these more caudal levels the paleostriatum augmentatum comes into relationship ventrally with the paleostriatum primitivum (Fig. 30).

The hyperstriatum forms the predominant striatal nuclear mass rostrally but it diminishes caudally (Figs. 28 and 29). In Interval VI the large, darkly-staining cells of the hyperstriatum are related dorsally to the primordial general pallium, laterally to the prepiriform area in more rostral levels, more caudally to the basolateral amygdaloid nucleus, and medially to the differentiating neostriatum and paleostriatum augmentatum. These relationships persist into the

definitive adult form.

The medial zone of the tuberculum olfactorium begins to differentiate from the cells of the ventral septo-tubercular anlage during the sixth interval (Fig. 29). This tubercular zone is distinguishable in the ventrolateral septo-tubercular area immediately caudal to the olfactory bulb and in apposition dorsally to the medial olfactory tract. It extends only a short distance spinalward from these levels. The cells of the medial zone of the tuberculum olfactorium are characterized by an apical concentration of Nissl material and a slightly greater size than those of the septal area. No cell islands were observed in this interval.

The lateral zone of the tuberculum olfactorium continues to be elaborated throughout the sixth interval (Fig. 29). The proliferative zone for this nucleus remains caudal to the anterior continuation of the hippocampus between the neostriatal proliferative zone dorsally and that of the septal area ventrally. The presumptive lateral tubercular cells lie at first laterally between the striatum dorsally and the lateral septal nucleus ventrally and then continue ventralward into the ventrolateral hemisphere. In their migration these cells pass through and remain in part intermingled with the fibers of the lateral forebrain bundle and the lateral olfactory tract. The lateral tubercular zone in Interval VI is apposed ventromedially to the medial zone of the tuberculum olfactorium and lies, as in the adult, rostral to the anterior commissure.

During Interval VI the septo-preoptic component of the medial forebrain bundle continues to be elaborated. Also, in the later

stages of the sixth interval, fascicles from the medial septal nucleus and the lateral septal nucleus pass spinalward dorsal to the anterior commissure and intermingled with those fibers of the medial olfactory tract which ultimately pass to diencephalic levels (Fig. 25). These fascicles constitute the septo-hypothalamo-mesencephalic component of the medial forebrain bundle described for the adult fish (Morgan, 1971). The precise course and relationships of the postcommissural medial olfactory tract and medial forebrain bundle are difficult to distinguish in the sixth interval because of the appearance of fibers of the postcommissural fornix and probably components of the medial corticohabenular system. These latter two systems become intermingled and course caudally into the diencephalon with the former two bundles.

The fornix system described in the adult marine catfish (Morgan, 1971) is the last major fiber system to form in the embryo. Concomitant with the differentiation of the primordial cornu ammonis and the subicular areas, fibers interrelate the hippocampal formation with the medial septal nucleus, pars dorsalis. These pathways represent the beginning of the precommissural fornix. However, this fiber system is elaborated primarily in stages which succeed those of the sixth interval. The direction of conduction could not be established for the precommissural fornix in these stages and the fascicles may well include septohippocampal fibers.

In the terminal stages of Interval VI, a few fascicles pass from the primordial dentate gyrus and cornu ammonis to intermingle with the fibers of the medial olfactory tract and the medial forebrain bundle as the latter two systems course dorsal to the anterior

commissure into the diencephalon (Fig. 25). These hippocampal components, which constitute the postcommissural fornix of the adult (Morgan, 1971), could be traced as individual fascicles only slightly posterior to commissural levels.

The lateral forebrain bundle remains relatively unaltered in course and relationships from the fifth interval throughout the sixth interval (compare Figures 22 and 23 with Figures 32 and 33). The neostriatum, paleostriatum augmentatum and paleostriatum primitivum contribute to the lateral forebrain bundle. As in the preceding stages, a dorsal peduncle of the lateral forebrain bundle could not be demonstrated. Also in Interval VI, the striato-hypothalamic component of the ventral peduncle becomes relatively larger than the striato-mesencephalic fasciculus which predominated in earlier stages. A commissural component was not recognized in these specimens.

The relationships of the stria terminalis (Figs. 32 and 33) described for Interval V persist throughout the remainder of embryonic development. However, there is an apparent increase in the number of stria terminalis fibers.

In the fifth interval of development the amygdalohabenular component of the lateral corticohabenular tract was identified (see Figure 26). During the sixth interval, fibers from the differentiating prepiriform and piriform cortices can also be detected as they pass ventromedially through and around the amygdaloid formation to intermingle with the fibers of the lateral olfactory tract, amydalohabenular tract, and stria terminalis. These fibers could not be traced to their termination in the normal embryonic material but probably

constitute the piriformhabenular component of the lateral cortico-habenular tract of the adult catfish.

The lateral corticohabenular division of the stria medullaris in the early embryos of the fifth interval coursed spinalward in the lateral hemisphere to approximately the level of the telencephalic-diencephalic junction. The fibers then turned dorsomedially to reach the habenula. During the later stages of Interval V and in the early embryos of Interval VI, these fibers gradually arch more medially and less dorsally. Ultimately, the lateral corticohabenular tract passes almost directly from the lateral region into the medial region of the ventral thalamus where it accumulates immediately dorsal to the medial forebrain bundle. After receiving fascicles which accompany the medial forebrain bundle, the combined system courses rostrodorsally through the ventral and the dorsal parts of the thalamus to the habenulae.

In the adult catfish the medial corticohabenular component of the stria medullaris (Schnitzlein, 1962; and Morgan, 1971) courses with the septo-hypothalamo-mesencephalic division of the medial forebrain bundle, the post-commissural fornix and the diencephalically coursing fibers of the medial olfactory tract. However, in the embryonic marine catfish, these combined pathways could not be distinguished separately in the normal Protargol preparations in telencephalic levels. Consequently, times of origin for the individual systems could not be established. Furthermore, the medial corticohabenular pathway, which can be identified in diencephalic levels during the early stages of Interval VI, could not be subdivided in the

normal embryonic material into the septohabenular, the hippocampohabenular and the medial preopticohabenular systems which were described for the adult fish (Morgan, 1971).

The anterior commissure was composed of interamygdalar, stria terminalis and medial olfactory tract components in Interval V. During the early stages of Interval VI, interseptal and intertubercular fibers are added, and, in the latest stages of the interval, the hippocampal commissure is initiated.

The interamygdaloid component of the anterior commissure in the sixth interval retains its dorsal position, although it becomes somewhat intermingled with the decussating fibers of the medial olfactory tract. The interseptal and intertubercular connections are situated immediately ventral to the above two components (Figs. 43 and 44). The interseptal fibers originate from both the medial and the lateral septal nuclei primarily at the caudal end of the precommissural septum. Some septal connections may possibly have been established in earlier stages, but their presence could not be demonstrated in the material investigated. Crossing ventral to the septal connections are the stria terminalis fibers (Figs. 43 and 44). An interstriatal component could not be detected in these stages. Ariens Käppers, Huber and Crosby (1936) have suggested that the decussating fibers of the stria terminalis may have been considered to be a decussation of the lateral forebrain bundle by other investigators. In the final stages of Interval VI a few fascicles from the hippocampal complex decussate dorsal to the anterior commissure. These fibers represent the initiation of the formation of the hippocampal commissure.

Interval VI is thus characterized by the differentiation of the bed nucleus of the hippocampal commissure, the medial zone of the tuberculum olfactorium, the anterior continuation of the hippocampus and the neostriatum and the paleostriatum augmentatum. All of the derivatives of the pallial anlage are established during Interval VI. A septo-hypothalamo-mesencephalic component is added to the medial forebrain bundle and the fornix system is initiated. The piriformhabenular and medial corticohabenular components of the stria medullaris become recognizable. Interseptal and intertubercular fibers appear in the anterior commissure and the hippocampal commissure begins to form.

H. Interval VII

Gross Specimens. The seventh interval of development proceeds through hatching to the arrest of mitotic activity in the telencephalon at approximately 50 millimeters. The earliest stages of Interval VII thus resemble those of Interval VI whereas the later stages have a typical adult appearance (Fig. 34), i.e., pigmentation is complete and the yolk sac is entirely absorbed, although the abdominal wall in these juveniles is thin and translucent. As growth progresses in this interval, the embryo becomes increasingly more coiled on the yolk prior to hatching and the yolk mass is gradually reduced.

Grossly, the olfactory bulbs become pedunculated and the cerebellum enlarges significantly, although in 50 millimeter juveniles the cerebellum does not overhang the telencephalon as in the adult. The relative proportion of the myelencephalon to the other major

divisions is substantially reduced. The sulci identified in the adult brain become evident only after hatching. The endorhinal fissure appears first medial to the olfactory tract and is followed by the establishment of the sulcus ypsiliformis which grossly delineates the primordial general pallium. The dorsal telencephalic membrane, which in Interval VI was attached dorsolaterally, appears to gradually "descend" in Interval VII along the lateral hemisphere wall until it attains the typical ventrolateral attachment of the adult (Figs. 45 and 46). This descent, however, is more apparent than real in that it is the result of the dorsally directed growth and expansion of the hemispheres into the ventricle (see "Discussion").

Histological. In the earlier stages of Interval VII a small, ventricular evagination appears at the site of proliferation of the olfactory bulb. This evagination is transitional, however, in that it is no longer evident after the bulbs become completely pedunculated. The rhinocoele defined in the adult (Miller, 1940, and Morgan, 1971) is not a continuation of this evagination; it is formed by the olfactory tracts basally and ventromedially but dorsally it is delimited by the overlying telencephalic membrane. The rhinocoeles of the adult are therefore actually extensions of the midline telencephalic ventricle.

The olfactory bulbs during the seventh interval continue to rotate rostrally until, shortly after hatching, the anterior pole assumes its proper adult orientation. Pedunculation is not totally accomplished until the juvenile state is reached. In specimens 45 millimeters long the olfactory bulbs are positioned only a few millimeters rostral to the anterior pole of the hemisphere.

Histologically the olfactory bulbs remain relatively unchanged

from the previous intervals (Fig. 35) although the internal granular cells are gradually separated from the anterior olfactory nucleus by the pedunculation process. A continuation is maintained between these nuclear areas by cells dispersed along the olfactory peduncle.

The anterior olfactory nucleus (Fig. 35) in this interval assumes the relationships characteristic of the adult, i.e., it is related to the anterior continuation of the hippocampus dorsomedially, the paleostriatum dorsally and the prepiriform cortex and anterior amygdaloid continuation dorsolaterally. Caudomedially, the anterior olfactory nucleus is apposed to the medial septal nucleus, pars ventralis and the medial zone of the tuberculum olfactorium.

The relationships of the septal nuclei (Figs. 36 and 37) remain unaltered from the previous interval. The rosette arrangement of the lateral septal nucleus gradually dissipates as the fibers of the medial forebrain bundle, fornix and medial corticohabenular tract continue to invade this nucleus in their course. The bed nucleus of the anterior commissure is better delineated in Interval VII from the supracommissural septum of earlier stages (Fig. 37). The remainder of the supracommissural septum in part forms the bed nucleus of the hippocampal commissure (Fig. 37) and the postcommissural cells are gradually reduced in number. In the precommissural septum proliferation and differentiation continues well past hatching as is evidenced by the thickened adjacent neuroepithelium.

The medial zone of the tuberculum olfactorium continues to differentiate ventrolateral to the medial septal nucleus, pars ventralis until post-hatching stages. The cellularity of the lateral zone of tuberculum olfactorium (Fig. 35) is gradually reduced until

the relatively acellular adult configuration is attained.

The relationships established for the pallial derivatives during Interval VI remain constant throughout the rest of development. The primordial dentate gyrus anlage (Fig. 37), which maintained its spheroid configuration in transverse sections throughout Interval VI, gradually elongates in a ventrolateral direction between the striatum dorsally and laterally and the medial septal nucleus, pars dorsalis, ventrally. The anterior hippocampal continuation, the primordial cornu ammonis, the primordial subiculum, the primordial general pallium, and the primordial prepiriform and piriform cortices continue to differentiate in stages subsequent to hatching, although mitosis is gradually arrested from medial to lateral (Figs. 35, 36, 37 and 38). Thus, the primordial piriform cortex differentiates the earliest and is proliferated longer than the other pallial derivatives.

The pallial regions are further delimited after hatching by the sulcus ypsiliformis which marks the apposition of the primordial general pallium and the primordial piriform cortex. The vertical limb of this sulcus marks grossly the transition between the primordial prepiriform and the piriform cortices.

The relationships of the primordial amygdaloid complex (Figs. 35, 36, 37 and 38) which were established in Intervals V and VI persist as the adult configuration. Whether or not the proliferation of amygdalar neuroblasts continues until mitosis ceases in the dorsolateral ventricular cell layer will require experimental documentation.

The adult striatal configuration was also established in the previous interval, although the paleostriatum augmentatum is more

easily distinguished in Interval VII following cessation of the migration of lateral tubercular neuroblasts through it. Also, the cells of the central striatal nucleus, which persist as a discrete structure in many other teleosts, cannot be identified in the adult catfish.

The fiber systems of the medial wall in Interval VII become much more distinct than in previous stages (Figs. 45 and 46). The fornix system, particularly the postcommissural fornix, is easily identified dorsal to the anterior commissure, where its fibers intermingle with those of the medial olfactory tract, the medial forebrain bundle and the medial corticohabenular system. Separate components of the latter pathway could not be traced through this combined bundle, although their existence in the adult has been demonstrated (Schnitzlein, 1962, and Morgan, 1971).

The lateral wall fiber systems are all established prior to the seventh interval of development. However, a general increase in the number of fibers in the lateral forebrain bundle and the stria terminalis was noted. The number of ascending fascicles incorporated into these systems will require experimental determination.

Development of the telencephalon in Interval VII thus consists primarily of additional differentiation of previously established nuclei, of the addition of fibers to previously established systems, of the establishment of many association fibers and of an increase in the glial population. Also notable in this interval are the alteration of the attachment sites of the overlying telencephalic membrane and the appearance of the hemispheric sulci characteristic of the adult.

V. DISCUSSION

In a previous investigation (Morgan, 1971), the cellular morphology, topography and connections of the various nuclear areas in the telencephalon of the teleost fish, Galeichthys felis, were described and discussed in terms of the available literature. The conclusions of this work were basically in agreement with those of Droogleever Fortuyn (1961), Schnitzlein (1964), Crosby, DeJonge and Schneider (1966), Singh (1969) and others who have agreed that the basic plan of the teleostean forebrain is essentially homologous to that of the higher vertebrates. However, a satisfactory explanation for certain anomalies in the nuclear topography of these forms has not been advanced. Some authors have supposed that a "plastic shift" (Weston, 1937) of the nuclei has occurred while others have conjectured that the extreme bulbar evagination manifest in Ganoids represents the initial formation of the lateral ventricles (Källen, 1951). A third group of investigators denies the suggested homologies, concluding instead that the dorsal hemisphere is an everted structure in the Actinopterygii and consequently is an aberration (Gage, 1893; Nieuwenhuys, 1961, 1962, 1963a and 1963b). A comparison of the ontogeny of the telencephalon with that of the other vertebrates substantiates the homologies previously reported by this author.

Initial insight is provided by the alteration of the configuration of the telencephalic hemispheres during embryonic development. Following neuralation, the forebrain is oval in transverse section with an equidistant hemispheric separation by a single, slit-like

ventricle (Fig. 47), as reported by Gage (1893). Shortly thereafter, however, following the onset of migration of neuroblasts into the intermediate zone, a marked widening of the midline ensues by a "folding out" of the primordial hemispheres, as indicated in Figure 48. The ventricular lumen consequently becomes v-shaped. The future dorsal telencephalic membrane in this stage remains thickened peripherally but it is thinner towards the midline.

As the septal, striatal, and amygdalar anlagen become well established, the hemisphere walls expand into the previously widened ventricle, reducing the interhemispheric distance dorsally and producing a characteristic t-shaped lumen (Fig. 49). This process is continued until the adult configuration is attained (Fig. 50). Specifically, the growth of the hemispheres is directed dorsally into the ventricle, rather than laterally as would be expected if there were the extreme eversion suggested by Gage (1893). The position of the attachment of the dorsal membrane on the dorsolateral margins on the hemispheres remains constant until virtually all of the nuclear areas have been elaborated and differentiated. The ventrolateral position of the membrane hemisphere junction is thus dictated by the dorsally directed growth of the hemisphere and not by extreme eversion, although a slight "eversion", or, more correctly, a "folding out" of the hemispheres occurs very early in development.

The development of the olfactory bulbs in Galeichthys felis embryos is preceded by the elaboration of the olfactory placodes in 5 to 7 millimeter stages. Subsequently, the olfactory fila emerge from the placodes and penetrate the anterior hemisphere medium at

approximately 7.5 to 8.0 millimeter stage lengths. Immediately following the entrance of the olfactory fila, neuroblasts begin to migrate laterally from the area of the ventricular cell zone which is immediately opposite the site of penetration of the fila. As neuroblasts begin to accumulate about this site, a slight bulge appears on the rostral hemisphere wall. Further embryonic growth is characterized by an increased bulging of the bulbar anlagen and a gradual separation from the telencephalon medium. The rhinocoele defined in the adult (Morgan, 1971) is a consequence of these growth processes and the eventual pedunculation of the olfactory bulbs, rather than the consequence of an evaginative process. However, a slight evagination is present on the ventricular surface from which the bulb is proliferated in the juvenile marine catfish. This latter cavity is at no time continuous with that of the so-called adult rhinocoele.

Coupled with these growth processes is the changing orientation of the future anterior poles of the adult olfactory bulbs. Initially, the olfactory fila ramify over the caudolateral aspect of each olfactory bulb anlage (future anterior pole). However, as development progresses the future anterior pole gradually rotates through an arc directed first ventromedially and then dorsally until it assumes its adult, rostral orientation. This is accomplished while the posterior pole is still in continuity with the rest of the telencephalic hemisphere. During this time the dorsomedial part of the bulb forms a part of the rostroventral wall of the median telencephalic ventricle, as described for the adult sunfish (whose bulbs remain

sessile) by Droogleever Fortuyn (1961).

The glomeruli of the olfactory bulb (Miller, 1940, and Morgan, 1971) are first distinguishable at an embryonic stage length of approximately 10 millimeters. These structures form peripherally in the region of the bulb over which the olfactory fila ramify. Concomitantly, differentiation of the mitral cell layer is initiated just deep to the glomerular layer. As development proceeds, these structures gradually increase in number. The internal and external granular cell layers are not well defined until proliferation of the cells of the olfactory bulb is essentially complete, although their earlier differentiation is predictable. The development of the olfactory bulbs in the marine catfish in general follows a pattern similar to that described for the lungfish, Protopterus (Rudebeck, 1945), for the amphibian, Discoglossus (Clairambault, 1962), for the chick (Jones and Levi-Montalcini, 1958) and for the mouse (Hinds, 1968a and 1968b). The autoradiographically determined times of origin of the cytological components of the olfactory bulbs described in the latter study are analogous to the sequence in which development can be followed in the normal catfish material.

The anterior olfactory nucleus in the adult marine catfish exhibits relationships common to those of the homologous structures in other vertebrates (Crosby, DeJonge, and Schneider, 1966, and Morgan, 1971). In many of the early embryonic stages of this animal, however, these relationships are somewhat confused by 1) the rotation of the olfactory bulbs, 2) the proximity of the olfactory bulbs to the septal area and 3) the similarity of the mature neurons of the anterior

olfactory nucleus to those of the internal granular cells of the olfactory bulb and the undifferentiated septal cells. Therefore, this nucleus cannot be adequately defined until the fourth interval of development during which time it is gradually circumscribed by the differentiating striatal and pallial anlagen. The relationships of the anterior olfactory nucleus become much more distinct as development progresses.

In the mature marine catfish the septal area (including the medial zone of the tuberculum olfactorium) occupies the ventromedial hemisphere wall from the level of the anterior commissure rostral to the anterior olfactory nucleus and anterior continuation of the hippocampus. The fully differentiated septum in the adult Galeichthys consists of a medial septal nucleus with dorsal and ventral subdivisions, a lateral septal nucleus, and the bed nuclei of the anterior and the hippocampal commissures. In the embryonic catfish of 7 to 8 millimeters the septal neuroblasts migrate from the ventromedial ventricular zone in a generally lateral direction to form an undifferentiated cell column which extends from posterior bulbar levels caudally to blend with the undifferentiated diencephalon. This septal configuration conforms to that described for the 7.0 millimeter stage of Amia (Johnston, 1911), the 14.5 millimeter stage of Epiceratodus (Rudebeck, 1945) and the "P" stage of Sphenodon punctatum (Hines, 1923). These relationships persist throughout the second interval in Galeichthys, although expansion proceeds in both rostro-caudal and medio-lateral directions as, for example, in Sphenodon (Hines, 1923). By approximately the 11 millimeter stage lengths the medial septal nucleus

begins to differentiate from this presumptive septal area in the more rostral hemisphere levels, while caudally the decussating fibers of the anterior commissure delineate the bed nucleus of the commissure. The lateral septal nucleus of the adult catfish does not differentiate until the fifth interval. These cells remain immediately adjacent to the ventricular cell zone during the earlier stages, thereby dividing the medial septal nucleus into dorsal and ventral parts. The sequence of the differentiation of the septal nuclei conforms to that of Epiceratodus (Rudebeck, 1945), Sphenodon (Hines, 1923), Chrysemys (Holmgren, 1925) and the mouse, Mus (Angevine and Sidman, 1961), in that the differentiation of the medial septal nucleus substantially precedes that of the lateral septal nucleus, further confirming the previously suggested homologies of these nuclei (Crosby, Dejonge, and Schneider, 1966, and Morgan, 1971). In addition, the medial septal nucleus is continuous with the caudomedial aspect of the anterior olfactory nucleus, whereas the lateral septal nucleus is not. Similar relationships were described for the turtle, Chrysemys (Holmgren, 1925).

During the first three intervals of development in Galeichthys embryos a cell-free zone is apparent between the ventricular cell zone dorsally and the striatal and amygdalar neuroblasts which have migrated ventrally. In the fourth interval a dense aggregation of neuroblasts adjacent to the ventricular zone olbiterates this cell-free space and forms a cap of undifferentiated cells which extends initially through the anterior two-thirds of the hemisphere and a short time later throughout the hemisphere. This initial accumulation of neuroblasts next to the dorsal neuroepithelium which has

been described for the Selachii (Bäckstrom, 1924), Dipnoi (Rudebeck, 1945), Amphibia (Burr, 1922, and Piatt, 1951), Reptilia (Holmgren, 1925), Aves (Jones and Levi-Montalcini, 1958) and Mammalia (Humphrey, 1967) constitutes the presumptive pallium of Herrick (1948) from which the primordial hippocampal formation, the primordial general pallium, and the primordial prepiriform and piriform cortices ultimately differentiate. Subsequent to the formation of the cellular condensation, neuroblasts begin to migrate outwards from it and to differentiate into the various pallial subdivisions, as was also described for the aforementioned vertebrates.

The earliest recognizable pallial subdivision in the sea catfish is the primordial dentate gyrus anlage which appears first as a spheroidal aggregation of cells dorsal to the anterior commissure. The formation of this anlage is by the interposition of cells from the medial pallium dorsally and the supracommissural septum ventrally. A similar configuration of the anlagen of the primordial dentate gyrus has been described in a human embryo of 11 weeks (Humphrey, 1966). As development progresses, this anlage elongates in a primarily rostral direction but remains undifferentiated until later stages.

In slightly older stages the more lateral sector of the presumptive pallial area begins to differentiate rostrally into the primordial prepiriform cortex and more caudally into the primordial piriform cortex. Proliferation and differentiation of these latter primordia persist until the ultimate arrest of mitosis in the dorsal ventricular zone of the juvenile. Following the start of differentiation in the primordial piriform cortex is the beginning of differentiation of the

primordial cornu ammonis (and possibly subicular region) in Interval VI. The final pallial derivative to differentiate is the primordial general pallium whose large, darkly staining cells appear between the primordial piriform cortex laterally and the primordial hippocampal cortex medially in the middle one-third of the hemisphere. The location of the primordial general pallium is homologous with that of the turtle, in which the general pallium also appears only in the middle one-third of the hemisphere (Holmgren, 1925).

The derivation of the pallial subdivisions in Galeichthys felis in general conforms to that described for representative higher vertebrates, with certain exceptions. For example, the condensation of pallial neuroblasts adjacent to the ventricular cell zone is reflected in all vertebrate forms, as previously stated. The autoradiographic investigations of Angevine and Sidman (1961 and 1962) indicate that the earliest derived cells of the mammalian cortices remain adjacent to the ventricular region, whereas those which are proliferated later migrate away from the ventricles. Thus, the phylogenetically older neurons would presumably not be found superficially. The majority of the hippocampal, piriform and general pallial cells do subsequently migrate away from the ventricle in the marine catfish, although a laminate pattern is suggested only in the primordial pirifrom cortex and primordial cornu ammonis of the adult catfish (Morgan, 1971).

The sequential differentiation of the pallial subdivisions conforms basically to that of the higher forms in that the primordial piriform cortex differentiates first and is followed in sequence by the primordial cornu ammonis-subiculum, the primordial dentate gyrus,

and finally by the primordial general pallium. This basic sequence has been described in part for the Selachii (Bäckstrom, 1924), Dipnoi (Rudebeck, 1945), Amphibia (Sorderberg, 1922), Reptilia (Holmgren, 1925) and man (Humphrey, 1967). It should be noted, however, that in an investigation of the ontogeny of the ganoid forebrain, Källen (1951) did not discern a presumptive pallial band as has been described for the marine catfish, nor did this investigator recognize the formation of migration layers.

During the second interval of development, an aggregation of neuroblasts proliferated from the dorsal ventricular zone accumulates in the rostrodorsal hemisphere as the presumptive striatum. Shortly thereafter fascicles are generated from this region which pass caudally into diencephalic and mesencephalic levels as the ventral peduncle of the lateral forebrain bundle. In an investigation of early stages in Amblystoma, Burr (1922) noted that in the more caudal hemisphere levels the number of fibers in the lateral forebrain bundle increased. He therefore assumed that many of the fascicles of the early lateral forebrain bundle were ascending from lower levels. Confirmatory experimental evidence must precede a definitive conclusion of a similar occurrence in Galeichthys felis. In the embryonic turtle, Chrysemys, the analogous situation exists in the second stage described by Holmgren (1925), i.e., formation of an aggregation of striatal neuroblasts followed by the establishment of the lateral forebrain bundle. In this stage of the turtle embryo, Holmgren noted the presence of numerous cells situated dorsal to the forming striatum which represented the anlage of the piriform cortex. In Galeichthys

felis embryos the proliferation of the cortical areas occurs subsequent to the initial elaboration of the striatal anlage, and the relationships of the pallial cortex are somewhat altered, although predictably so, by the failure of the teleostean hemisphere to develop lateral ventricles. However, in an autoradiographic analysis of nuclear and cortical origin in the telencephalon of the mouse, Sidman and Angevine (1962) reported that the initiation of the proliferation of the striatal nuclei either precedes the elaboration of the overlying cortex, as in the case of the globus pallidus, or that cortical and striatal neuroblasts may be proliferated in unison, as with the caudate, putamen, and convexal cortex of the mouse. The chronology of the differentiation and proliferation of these areas in the mouse thus is similar to the sequence seen in the sea catfish.

As development proceeds in embryonic Galeichthys, the cells which formed the more ventral segment of the striatum in early stages become intermingled with the fibers of the lateral forebrain bundle and thus are delineated as the paleostriatum primitivum. The more dorsal cells of the striatum remain lateral to the septal area and presumptive hippocampal region where they form the anlagen of the paleostriatum augmentatum and the neostriatum. These latter two nuclear masses are difficult to subdivide in the embryonic marine catfish until the sixth interval of development because of the migration of cells of the lateral zone of the tuberculum olfactorium through the ventral region of these anlagen and because of the rather late establishment of the dorsal peduncle of the lateral forebrain bundle. In general, the more dorsally situated cells in the juvenile constitute

the neostriatum and those which are apposed medially to the septal nuclei constitute the paleostriatum augmentatum. The hyperstriatum, which is also elaborated in Galeichthys during the fifth interval, proliferates and differentiates lateral to the paleostriatal and neostriatal anlagen. These cells are larger and more darkly staining than are those of the other striatal anlagen and become related dorsally to the primordial general pallium as that structure differentiates during the final stages of Interval VI. The sequence of proliferation as well as the topography of the proliferation areas of the striatum in the marine catfish essentially agree with that described for other forms. Hines (1923) reported that in Sphenodon the paleostriatum forms prior to the neostriatum and is situated ventral to that nucleus. It should be noted that the more caudal portion of the dorsal ventricular ridge which is labeled neostriatum in Sphenodon by Hines (1923) probably represents the basolateral amygdaloid area, whereas the more rostral segment probably represents the hyperstriatum as described in the reptile by Carey (1966) and Crosby, DeJonge and Schneider (1966). Nevertheless, the sequence of the appearance of these areas is approximately the same in both species.

Topographically, in all submammalian forms described, the hyperstriatum originates most dorsally and neostriatum and paleostriatum are proliferated from the more ventral areas of the ventricular zone. Galeichthys felis conforms to this pattern. The homologies of these areas are thus further confirmed by their ontogenetic similarities.

The adult amygdalar formation throughout the vertebrate phylo-

genetic scale has been basically subdivided by Schnitzlein, Hoffman, Hamel and Ferrer (1967) into an anterior amygdaloid continuation, a corticomedial amygdaloid nucleus and a basolateral amygdaloid nucleus on the basis of topography, cytology and fiber connections. These subdivisions have subsequently been identified in the adult marine catfish (Morgan, 1971). The embryonic site of origin of the amygdaloid complex as described for the various submammalian forms (under differing terminologies) is essentially situated between (and partially overlapped by) that of the piriform cortex dorsally and the striatal complex rostrally and ventrally. For example, in the turtle, the caudal portion of the dorsal ventricular ridge of Johnston (1916) or the posterior proliferation of the tertiary piriform cortex of Holmgren (1925) which has been identified by Crosby, DeJonge and Schneider (1966) as belonging to the amygdaloid complex of reptiles, originates from a proliferative site which occupies the equivalent position. In the embryonic catfish of approximately 8 millimeters (Interval II) the amygdalar anlage is first recognizable as a homotypic cell mass which is proliferated from the dorsal ventricular cell zone of the caudal telencephalon. Rostrally, the overlapping of the amygdalar anlage by the striatum corresponds to the relationships of these nuclei in Holmgren's Stage 16 of Chrysemys (1925). During the course of development this relationship is maintained but, with the appearance of the presumptive pallial area in the course of the fourth interval, the amygdalar anlage is subsequently overlapped dorsally in part by the anlagen of the prepiriform and piriform cortices. Concomitantly, the anterior amygdaloid continuation, the primordial

corticomedial amygdaloid nucleus, and the primordial basolateral amygdaloid nucleus become differentiable. The extent of overlap of these areas, however, is somewhat ambiguous in that the primordial corticomedial amygdaloid nucleus and the primordial prepiriform and piriform cortices are elaborated in unison from approximately the same sites and no distinct transition could be established among the three. However, the anterior amygdaloid continuation, which is proliferated from approximately the same area as is the corticomedial amygdaloid nucleus, but, more rostrally, is quite distinct as a column of densely packed cells which extends forward to impinge on the anterior olfactory nucleus.

The sequence of development of the primordial amygdaloid nuclei in Galeichthys felis is best reflected by the times of origin described for the homologous structures (Crosby, DeJonge and Schneider, 1966, and Schnitzlein, Hoffman, Hamel and Ferrer, 1967) in the mouse telencephalon by Sidmann and Angevine (1962). In the mouse, the amygdalar anlagen are proliferated either prior to (medial and cortical amygdaloid nuclei) and/or together with neuroblasts of the overlying periamygdalar cortex, as in Galeichthys felis. The primordial amygdaloid complex in Galeichthys felis conforms with the Selachii (Bäckstrom, 1924), Amphibians (Sörderberg, 1922), Reptilia (Johnston, 1916, and Holmgren, 1925) and Mammalia (Holmgren, 1925, and Humphrey, 1968) in terms of the telencephalic sites of origin. Therefore, the amygdalar homologies of Weston (1937); Droogleever Fortuyn (1961); Schnitzlein (1964); and Crosby, DeJonge and Schneider (1966) for teleosts are further documented by the similarity of their embryonic formation to

to that of the other vertebrates.

The tuberculum olfactorium in both submammalian and mammalian forms has been partitioned into various zones and subdivisions (lateral, intermediate and medial zones and rostral, middle and caudal subdivisions) on the basis of cytology (Humphrey, 1967). Functionally, however, the tuberculum may be divided into a medial zone (olfactovisceral) and a lateral zone (olfactosomatic) according to Crosby, DeJonge and Schneider (1966). The ontogenetic derivation of the tuberculum olfactorium identified in the adult marine catfish (Morgan, 1971) indicates that this structure is in fact comprised of cells proliferated from two separate regions of the ventricular neuroepithelium, i.e., the lateral zone originates from a small neuroepithelial area situated between the striatal proliferative zone dorsally and the medial septal proliferative area ventrally, whereas the medial zone is derived from a small neuroepithelial region ventral to the medial septal nucleus, pars ventralis. Of these two tubercular areas, the lateral zone is the more precocious, appearing during the third interval of development. These cells migrate first laterally, then ventrally around the septal area and, in part, through the striatum to attain the typical ventrolateral position characteristic of the adult fish. As differentiation proceeds, the lateral zone becomes increasingly less cellular and more deeply placed in the hemisphere, as described in the lungfish embryo (Rudebeck, 1945) and in other vertebrates. This appearance is probably a consequence of the increasing number of lateral olfactory tract and lateral forebrain bundle fibers which traverse the lateral zone and possibly is also the result of embryonic

cell death.

The medial zone of the tuberculum olfactorium is not recognizable until quite late in development in Galeichthys felis although the presumptive neuroblasts for this area may be proliferated in earlier stages. A cell island resembling those found in other vertebrates has been described in an Adult (Morgan, 1971), but neither primary nor secondary islands (Schnitzlein and Crosby, 1967, and Humphrey, 1967) were detected in this region at any point during development.

The ontogenetic development of the nuclear areas in the telencephalon of Galeichthys felis in many ways reflects the patterns which are found throughout the vertebrate scale. Certain anaomalous situations, such as the supposedly reversed topography of the pallial derivatives based upon the inversion-eversion theory of development of the ventricular system (reviewed by Nieuwenhuys, 1963), are not in agreement with the hodological, cytological and topographical evidence presented (Morgan, 1971). The homologies drawn by Weston (1937), Droogleever Fortuyn (1961), Schnitzlein (1964) and Crosby, DeJonge and Schneider (1966) may be questioned on the basis of the topographical relationships of the piriform cortex to the primordial amygdaloid nuclei and the hippocampal formation to the striatal complex. However, it appears that these conditions are explicable on the basis of the ontogenetic evidence presented by recognizing that the telencephalic hemispheres of the Actinopterygii are non-evaginated, rather than everted structures. Thus by visualizing the effect that an evaginative process, similar to that described for amphibians, might have on the adult configuration of the telencephalic nuclei of this fish, these

differences may be accounted for without supposing that a "plastic shift" (Weston, 1937) of these nuclear areas has occurred.

In the early embryonic stages of the marine catfish (Intervals I to III) the lateral wall amygdalar, striatal, and tubercular nuclei and the medial wall septal anlage are elaborated. A slight "folding out" of the hemispheres occurs, but does not effect the vertical arrangement of the proliferative zones of these nuclei. This early hemispheric topography is illustrated in Figures 51 and 52.

During the fourth interval of development in Galeichthys the pallial anlage appears just deep to the ventricular zone. If, at this point, an evaginative process similar to that described for Amblystoma (Burr, 1922, and Källen, 1951) occurred in the marine catfish, a configuration such as that depicted schematically in Figures 53 and 54 would exist. In Amblystoma (Burr, 1922) the hemispheric evagination is directed first laterally, then rostrally, and finally caudally to produce the characteristic lateral ventricles. Furthermore, as noted by Källen (1951) in Amblystoma "... the caudal lobes of the hemispheres are formed from the primarily developed hemispheres." An analogous conclusion was reached for Epiceratodus by Rudebeck (1945). The lateral part of the primary telencephalic hemispheres in Galeichthys embryos containing the amygdalar, striatal, and lateral tubercular anlagen are comparable to the ventrolateral and caudal walls of an evaginated telencephalon. An evagination beginning at the caudal limit of the pallial anlage would separate it from the nuclei of the lateral wall (Figs. 53 and 54). The pallial derivatives would thus constitute the dorsomedial and dorsal walls of the evaginated

hemisphere. The septal nuclei would remain initially static in the ventromedial quadrant (Fig. 54).

With increasing evagination, as depicted in Figure 55, and the elaboration of the primordial piriform and dentate gyrus areas, the arrangement depticted in Figure 56 would be attained. Specifically, the proliferative neuroepithelium of the hippocampal formation and general pallial area would move caudally along the ventricular surface of the hemisphere to the level of the site of evagination (the interventricular foramen) where these neuroepithelial cells would migrate slightly lateralward, then rostralward to occupy the dorsomedial surface of the embryonic lateral ventricle (Fig. 56). The more laterally situated neuroepithelial cells of the piriform anlagen through a caudoventral, then lateral, then rostrolateral and caudolateral movement (as would be expected in an evaginative process similar to that of Amblystoma) would result in a displacement as illustrated schematically in Figures 55 and 56.

Septal and medial tubercular evagination would be accomplished in a similar manner by a dorsal, then lateral, then rostral, and rostroventral displacement. As a consequence of this septal displacement the olfactory bulb, which normally develops laterally in the fish, would gradually rotate to the typical ventromedial position seen in the higher vertebrates.

Subsequent evagination would proceed in a like manner until the adult hemisphere attained the appearance and configuration depicted in Figures 57 and 58. In Amblystoma, a late, caudally directed evagination also occurs (Källen, 1951) which is not illustrated here

for the hypothetical fish, but would be a perfectly plausible occurrence if the teleost hemisphere did evaginate.

Also inherent in the evagination of the hypothetical hemisphere would be an alteration of the position of the attachment of the dorsal telencephalic membrane. Specifically, the rostral and lateral attachment lines of the ependymal membrane are defined by the peripheral limits of the proliferative neuroepithelium of the hemisphere. During an evagination these attachment sites would gradually move towards the interventricular foramen so that the ultimate alignment would be as depicted in Figure 57, and thereby conform to the positioning of the homologous structures in the other vertebrates.

The reason the Actinopterygian fishes do not develop lateral ventricles is currently unknown. Aronson and Kaplan (1968) have speculated that the unusual conformation of the teleost telencephalon is an adaptation which allows the maximum possible streamlining of the cranium in juveniles where "... cranial space is at a premium." This hypothesis might further account for the failure of the lateral ventricles to develop ontogenetically, although both points must remain at present purely conjectural. Nonetheless, the point remains that the forebrain of the teleostean fishes exhibits in ontogeny the potential to form hemispheres with an overall configuration similar to that of the other vertebrates simply by evolving an evagination process identical to that manifest in the amphibians.

The major telencephalic fiber systems of many of the Actinopterygian fishes have been described in the literature and were reviewed in an earlier paper (Morgan, 1971). A fundamental pattern

of fiber pathways has been illustrated in many of the teleosts (Schnitzlein, 1964; Crosby, Dejonge and Schneider, 1966; and Morgan, 1971) which is essentially homologous to those of the vertebrates. Källen (1954) compared the sequence of development of the telencephalic fiber systems in the mouse with the adult forebrain fiber patterns in the submammalian vertebrates and concluded that the previous suggestion of Shaner (1936) that phylogenetic homologies might be reflected ontogenetically in the higher forms was unfounded. A re-examination of this conclusion seems necessary.

The initial stages of telencephalic development in the marine catfish, as in many of the other described vertebrates (Burr, 1922; Sörderberg, 1922; Holmgren, 1925; Rudebeck, 1945; and Källen, 1951), is characterized by the absence of nerve fascicles. In these species the early hemispheres consist primarily of neuroepithelium, neuroblasts and glia.

With the embryonic onset of differentiation the major fiber systems in Galeichthys felis begin to develop sequentially. The first of these systems that can be recognized in the embryonic marine catfish are the lateral forebrain bundle and the stria terminalis, which appear at approximately the same time (Interval II). These pathways are followed in rapid succession by the development of the lateral olfactory tract and the amygdalohabenular component of the stria medullaris. The lateral forebrain bundle is also apparent first in Amblystoma (Burr, 1922) and Chrysemys (Holmgren, 1925). In Mus musculus the stria terminalis begins to form in Stage 1 (Källen, 1954) and is quickly followed by the development of the lateral olfactory

tract, the ansa lenticularis and a fiber bundle connecting the stria terminalis with the stria medullaris. The ansa lenticularis in the mouse is homologous with the ventral peduncle of the lateral forebrain bundle of Galeichthys (Crosby, DeJonge and Schneider, 1966) and the interconnection of the stria terminalis with the stria medullaris described by Källen probably is the homologue of the amygdalohabenular tract in the catfish. Consequently, the sequence of early development of the fiber systems in the marine catfish parallels very closely that of Mus.

In the later development of Galeichthys felis the similarities become even more pronounced. Fibers of the stria terminalis initiate the formation of the anterior commissure in Stage 3 of Mus. This corresponds to the formation of the anterior commissure in the third interval of development of the marine catfish by the contralateral stria terminalis and interamygdalar fibers. In addition, the medial olfactory tract is initiated in approximately the same sequence in both species.

As development proceeds in both the mouse and Galeichthys the parallelisms continue. In Källen's Stage 4 (1954) the interseptal component of the anterior commissure, the septotubercular and possibly early fornix fascicles were detected. This configuration then remains essentially constant until Stage 7, when the medial forebrain bundle, the interbulbar components of the anterior commissure and the fornix and hippocampal commissure can be identified. By comparison, in the fifth interval of development in Galeichthys, the septo-preoptic component of the medial forebrain bundle, possible septo-tubercular

interconnections, and the commissural component of the medial olfactory tract (probable interbulbar) develop. Subsequently, during Interval VI, the septo-hypothalamo-mesencephalic fascicles of the medial forebrain bundle (whose fibers decussate in part in the anterior commissure), the medial corticohabenular tract of the stria medullaris system (not described for the mouse by Källen) and finally the fornix and hippocampal commissures were established. The sequence of the development of the major fiber systems in the later stages thus follows closely that which occurs in later intervals of development in Galeichthys felis.

This evidence further substantiates the homologies of the fiber systems suggested by Crosby, DeJonge and Schneider (1966) for the Actinopterygian telencephalon. The suggestion, however, that the ontogeny of the fiber systems recapitulates their phylogeny (Shaner, 1936) may not be entirely correct for comparisons throughout the phylogenetic scale. For example, Windle (1970) suggested a sequence of the development of the telencephalic neuronal pathways in man which does not correspond to the sequences described above. Windle noted, however, that the early pathways may not be identified with certainty. A conclusion to this question therefore should not be drawn before more complete data are available on the embryogenesis of the fiber systems throughout the vertebrate scale.

The ontogeny of the telencephalon in Galeichthys felis provides new evidence for a solution to the prevailing disagreement over the relationships of the Actinopterygian forebrain to its counterparts in the other vertebrate orders. Specifically, the everted appearance

of the adult telencephalon is imparted as a consequence of the initial "folding out" of the hemispheres at an early age followed by a dorsomedially directed growth of the hemispheres into the midline telencephalic ventricle. Also, the configuration of the primordial pallial areas, rather than being reversed by an eversion phenomenon, are elaborated in a topographical pattern which would place them in the same classical relationships seen in the other vertebrates, provided an evagination of the telencephalon did occur in the bony fishes. In addition, the sequence of development of both the fiber systems and the nuclear areas in Galeichthys felis parallels rather strikingly the sequence demonstrated in other animals, such as the mouse.

In conclusion, it would appear that the teleost telencephalon, rather than being a grossly everted structure with a resultant nuclear displacement, represents instead primordial, unevaginated hemispheres which are closely homologous to those of the other vertebrates.

VI. SUMMARY

The ontogeny of the telencephalon in a representative teleostean fish, Galeichthys felis, has been studied. A detailed morphological description (which is currently unavailable in the literature) has been given. The development of the marine catfish telencephalon has been divided into seven "intervals" which are phases of development initiated by the appearance of a previously unrepresented nucleus (or nuclei) and/or fiber system and are terminated by the elaboration of additional populations not present during the interval.

In the first interval of development (6 to 7 millimeters total length) the prosencephalon exhibits ventricular, intermediate and marginal zones which are characteristic of the rostral neural tube in other vertebrates. An olfactory placode is present, but no nuclear areas or nerve fibers have differentiated.

During Interval II (7 to 8 millimeters total length) the olfactory fila and the olfactory bulbs begin to differentiate. The septal, striatal and amygdalar anlagen are present and the ventral peduncle of the lateral forebrain bundle and stria terminalis begin to form.

The third interval of development in Galeichthys (8 to 9 millimeters total length) is typified by the beginning of differentiation in the olfactory bulbs and by the generation of the lateral olfactory tracts. Decussation of the contralateral stria terminalis and the interamygdalar fascicles form the early anterior commissure. The initiation of the amygdalohabenular tract was suggested, but will require experimental confirmation.

Interval IV (9 to 12.5 millimeters) includes the early proliferation of the pallial anlage, the corticomedial amygdaloid nucleus and the anterior amygdaloid continuation. The amygdalohabenular pathway is definitely recognizable in this interval and the medial olfactory tract appears.

At the conclusion of Interval V (12.5 to 14.5 millimeters) the medial and lateral septal nuclei, the dentate gyrus anlage, the hyperstriatum and the paleostriatum augmentatum are present in the embryonic telencephalon. The medial olfactory tract component of the anterior commissure and the septo-preoptic component of the medial forebrain bundle are also added in the fifth interval.

In Interval VI (14.5 to approximately 20 millimeter stage lengths) the bed nucleus of the hippocampal commissure, the medial zone of the tuberculum olfactorium, the anterior continuation of the hippocampus, the neostriatum and the paleostriatum augmentatum differentiate. The primordial cornu ammonis and subicular areas of the hippocampus, the primordial general pallium, and the primordial prepiriform and piriform cortices also are apparent. The early fascicles of the fornix system and the piriformhabenular and medial corticocomponents of the stria medullaris are established. The anterior commissure includes the interseptal and intertubercular components, and the hippocampal commissure is initiated.

The final phase of development, Interval VII (20 to 50+ millimeters) consists essentially of maturational changes. The sulci characteristic of the adult hemisphere are formed, cytodifferentiation continues in previously established nuclei, associative interconnections

are added and the glial population is expanded.

The ontogeny of the telencephalon of the marine catfish has been compared with that of the other vertebrates available in the literature. In general, times of origin of nuclear structures and fiber systems are consistent with those described for other forms. An hypothesis, based on ontogeny, is advanced to explain the positions of the nuclear areas in the solid teleostean hemisphere and to compare these nuclei with their homologues in the evaginated hemispheres of the other vertebrates.

VII. LIST OF REFERENCES

Angevine, J.B. Jr., and R.L. Sidman 1961 Autoradiographic study of cell migration during histogenesis of cerebral cortex in the mouse. Nature (London) 192: 766-768.

Ariens Käppers, C.U., C.G. Huber, and E.C. Crosby 1936 The Comparative Anatomy of the Nervous System of Vertebrates, Including Man. Hafner Publishing Co., New York: 1268-1293.

Aronson, L.R. and H. Kaplan 1968 Function of the teleost forebrain. The Central Nervous System and Fish Behaviour. Ed. by D. Ingle. Univ. of Chicago Press, Chicago: 107-125.

Bäckstrom, K. 1924 Contributions to the forebrain morphology in selachians. Acta Zool. 5: 123-240.

Bodian, D. 1936 A new method for staining nerve fibers and nerve endings in mounted paraffin sections. Anat. Rec. 65: 89-97.

Boulder Committee 1970 Embryonic vertebrate CNS: revised terminology. Anat. Rec. 166: 257-262.

Brookover, C. 1914 The development of the olfactory nerve and its associated ganglion in Lepidosteus. Jour. Comp. Neur. 24: 113-130.

Burr, H.S. 1922 Early development of the cerebral hemispheres in Amblystoma. Jour. Comp. Neur. 34: 277-301.

Carey, J.H. 1966 The nuclear pattern of the telencephalon of the blacksnake, Coluber constrictor constrictor. Evolution of the forebrain. Ed. by R. Hassler and H. Stephan. Georg Thieme Verlag, Stuttgart: 73-80.

Clairambault, P. 1963 Le télencephale de Discoglossus pictus (Oth.). Etude anatomique chez le têtard et l'adulte. J. Hirnforsh., 6: 87-121.

Crosby, E.C., B.R. DeJonge and R.C. Schneider 1966 Evidence for some trends in the development of the vertebrate telencephalon. Evolution of the Forebrain. Ed. by R. Hassler and H. Stephan. George Thieme Verlag, Stuttgart: 117-135.

Droogleever Fortuyn, J. 1961 Topographical relations in the telencephalon of the sunfish, Eupomotus gibbosus. Jour. Comp. Neur. 116: 249-263.

Edds, Jr., M.V. 1970 Prefatory comments on the development of the nervous system. The Neurosciences: Second Study Program. Ed. by F.O. Schmitt. Rockefeller Univ. Press, New York: 51-52.

Foley, J.O. 1938 A differential counterstain for toned sections of the peripheral nerves. Anat. Rec., 71: 133-139.

Gage, S. 1893 The brain of Diemyctylus viridescens from larval to adult life and comparisons with the brains of Amia and Petromyzon. Wilder Quarter Century Book, Ithaca, New York: 259-314.

Gunter, G. 1947 Observations on breeding of the Marine Catfish, Galeichthys felis. Copeia 4: 217-223.

Herrick, C.J. 1948 The Brain of the Tiger Salamander. Univ. of Chicago Press, Chicago: 91-122.

Hinds, J.W. 1968a Autoradiographic study of histogenesis in the mouse olfactory bulb. I. Time of origin of neurons and neuroglia. Jour. Comp. Neur. 134: 287-304.

_____ 1968b Autoradiographic study of histogenesis in the mouse olfactory bulb. II. Cell proliferation and migration. Jour. Comp. Neur. 134: 305-321.

Hines, M. 1923 The development of the telencephalon in Sphenodon punctatum. Jour. Comp. Neur. 35: 483-537.

Holmgren, N. 1925 Points of view concerning forebrain morphology in higher vertebrates. Acta Zool. 6: 413-477.

Humphrey, T. 1966 The development of the human hippocampal formation correlated with some aspects of its phylogenetic history. Evolution of the Forebrain. Ed. by R. Hassler and H. Stephan. Georg Thieme Verlag, Stuttgart, 104-116.

_____ 1967 The development of the human tuberculum olfactorium during the first three months of embryonic life. J. Hirnforsch. 9: 437-469.

_____ 1968 The development of the human amygdala during early embryonic life. Jour. Comp. Neur. 132: 135-166.

Johnston, J.B. 1911 The telencephalon of ganoids and teleosts. Jour. Comp. Neur. 21: 489-591.

_____ 1916 The development of the dorsal ventricular ridge in turtles. Jour. Comp. Neur. 26: 481-505.

Jones, A.W. and R. Levi-Montalcini 1958 Patterns of differentiation of the nerve centers and fiber tracts in the avian cerebral hemispheres. Arch. Ital. Biol. 96: 231-284.

Källen, B. 1951 Some remarks on the ontogeny of the telencephalon in lower vertebrates. Acta Anat. 11: 537-548.

_____ 1954 The embryology of the telencephalic fiber systems in the mouse. J. Embryol. and Exp. Morph. 2: 87-101.

_____ 1962 Embryological studies on the nuclei and their homologization in the vertebrate forbrain. Kungl. Fysio. Salls. Hand. 62: 1-35.

Miller, R.N. 1940 The telencephalic zonal system of the teleost, Corydora paliatus. Jour. Comp. Neur. 72: 149-176.

Morgan, G.C. Jr. 1971 The telencephalon of the marine catfish, Galeichthys felis. A master's thesis in the University of Alabama in Birmingham, Birmingham, Ala.

Nieuwenhuys, R. 1961 The morphogenesis and the general structure of the Actinopterygian forebrain. Acta. Morph. Neer.-Scand. 5: 65-78.

_____ 1962 Trends in the evolution of the Actinopterygian forebrain. J. Morph. III: 69-88.

_____ 1963a Further studies on the general structure of the Actinopterygian forebrain. Acta Morph. Neer.-Scand. 6: 65-79.

_____ 1963b The comparative anatomy of the Actinopterygian forebrain. J. Hirnforsch. 6: 171-192.

Piatt, J. 1951 An experimental approach to the problem of pallial differentiation. Jour. Comp. Neur. 94: 105-122.

Rudebeck, B. 1945 Contributions to the forebrain morphology in Dipnoi. Acta Zool. 26: 9-156.

Schnitzlein, H.N. 1962 The habenula and the dorsal thalamus of some teleosts. Jour. Comp. Neur. 118: 225-268.

_____ 1964 Correlation of habit and structure in the fish brain. Amer. Zool. 4: 21-32.

Schnitzlein, H.N. and E.C. Crosby 1967 Telencephalon of the African Lungfish, Protopterus. J. Hirnforsch. 9: 105-149.

Schnitzlein, H.N., H.H. Hoffman, E.C. Hamel, Jr., and N.C. Ferrer 1967 Parallelisms in fiber relations and variations in nuclear patterns in the phylogeny of the amygdala. Arch. Mex. de Anat. 26: 3-40.

Shaner, R.F. 1936 Development of the finer structure and fiber connections of the globus pallidus, corpus of Luys and substantia nigra in the pig. Jour. Comp. Neur. 64:213-233.

Sheldon, R.E. 1912 The olfactory tracts and centers in teleosts. Jour. Comp. Neur. 22: 177-340.

Sidman, R.L. and J.B. Angevine, Jr. 1962 Autoradiographic analysis of time of origin of nuclear versus cortical components of the mouse telencephalon (Abstract). Anat. Rec. 142: 326-327.

Singh, H.R. 1969 Telencephalic nuclear areas in three Indian teleosts. Acta. Anat. 73: 463-480.

Sörderberg, G. 1922 Contributions to the forebrain morphology in amphibians. Acta Zool. III: 1-121.

Ward, J.W. 1957 The reproduction and early development of the Sea Catfish, Galeichthys felis, in the Biloxi (Mississippi) Bay. Copeia 4: 295-298.

Weston, J.K. 1937 Notes on the telencephalon of Morymurus and Gnathonemus. Proc. Kon. Ned. Acad. Wet. Amst. 28: 735-746.

Windle, W.F. 1970 Development of neural elements in human embryos of four to seven weeks gestation. Exp. Neur. 5: 44-83.

Windle, W.F., R. Rhines, and J. Rankins 1943 Thionin method. Stain Tech. 18: 77-86.

VIII. ILLUSTRATIONS

PLATE 1

Explanation of Figure

Fig. 1. Gross photograph of a 7 millimeter Galeichthys felis embryo representative of Interval I. The prosencephalon (prosen.) is comparatively small and the otic vesicles (ves. otic) are prominent. The large rhombencephalon (rhomben.) and the diminutive optic tectal anlage (tect. op. anlage) are recognizable. Numerous small somites are present.

①

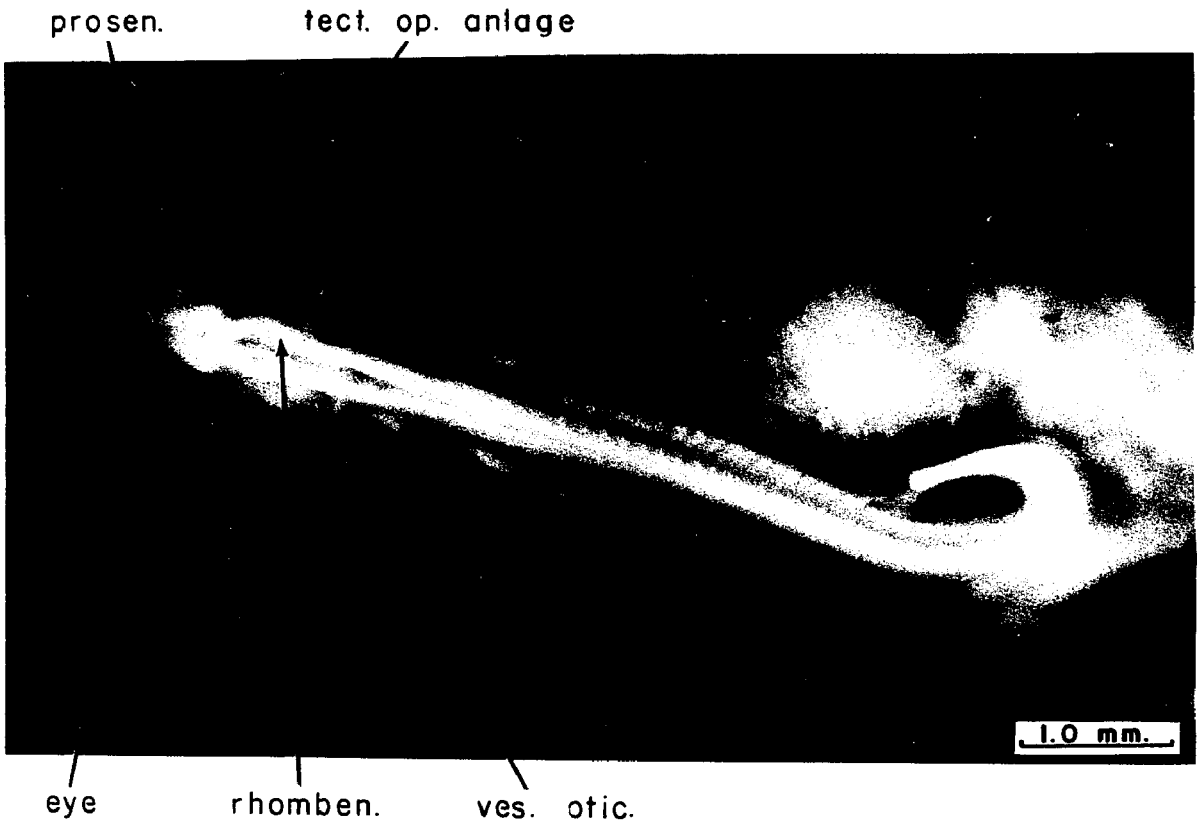


PLATE 2

Explanation of Figure

Fig. 2. Photomicrograph of a transverse section through the head of a 6.5 millimeter embryo typical of Interval I. The three characteristic layers of the embryonic neural tube are defined in the prosencephalon (prosen.). Neither nuclear areas nor nerve fibers are as yet present. The single midline ventricle (vent. med.) is slit-like and the olfactory placodes (plac. olf.) lie directly lateral to the prosencephalon (prosen.).

(Hematoxylin and eosin stain).

(z. vent: ventricular zone; z. intermed.: intermediate zone; z. marg.: marginal zone)

(2)

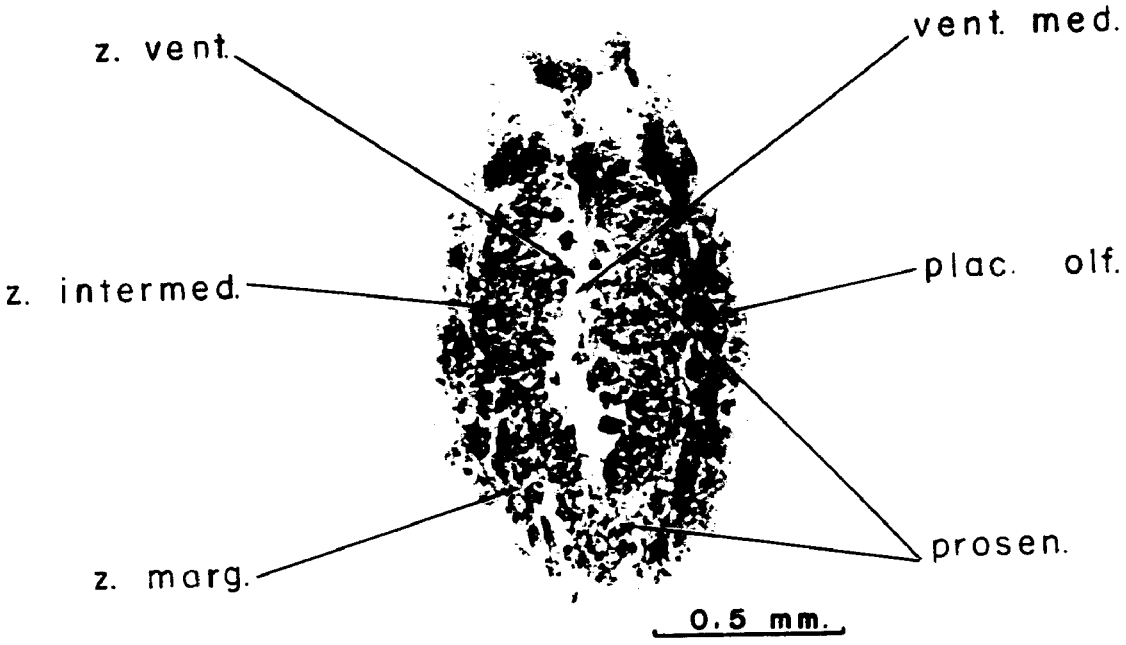


PLATE 3

Explanation of Figure

Fig. 3. Gross photograph of a 7.5 millimeter marine catfish embryo typical of Interval II. The eyes are greatly enlarged in comparison to Interval I (compare with Figure 2). The enlarged rostral somites demarcate the developing pectoral fins (pect. fin bud). The optic tectal anlagen (tect. op. anlage.) are apparent and the rhombencephalon (rhomben.) forms the largest brain division. The telencephalon (tel.) lies in the rostral extreme of the cranial cavity.

3

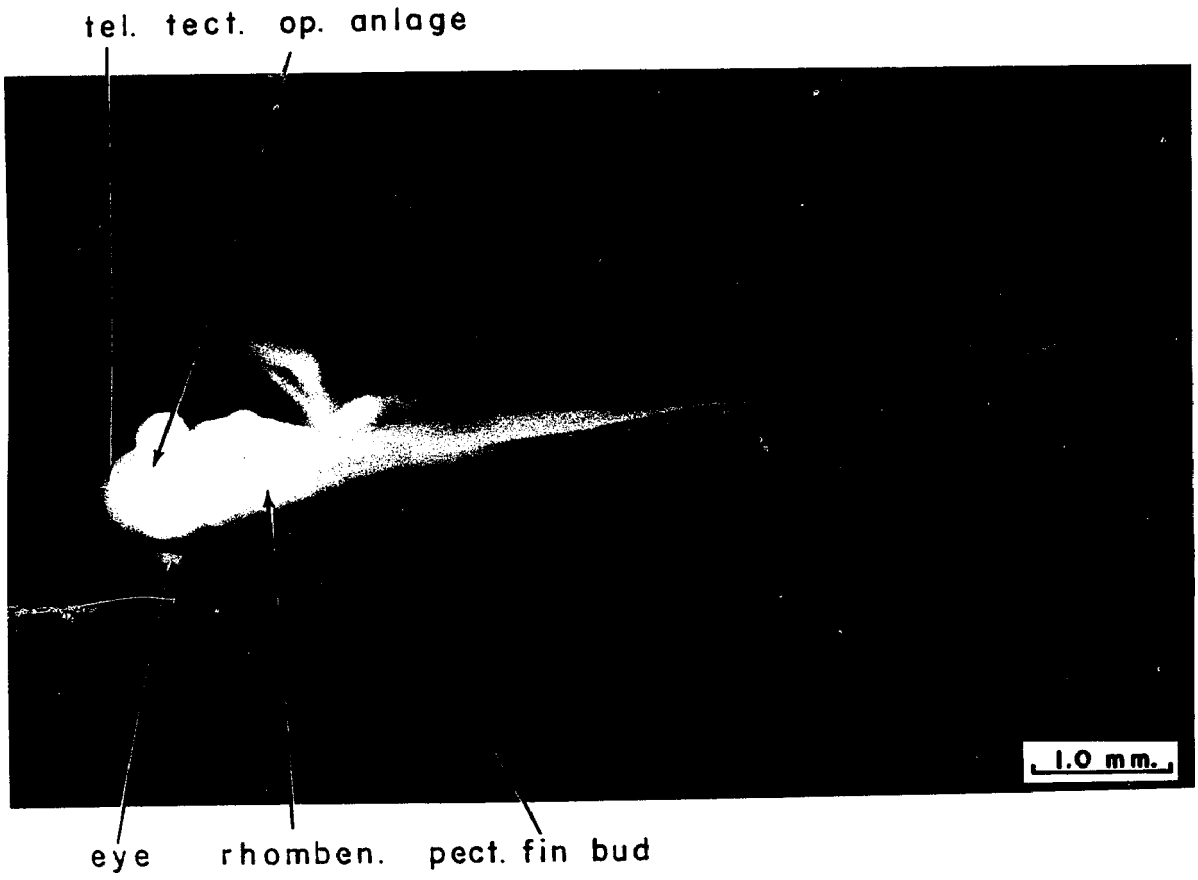


PLATE 4

Explanation of Figures

Fig. 4. Photomicrograph of a transverse section through the rostral tip of the head of an 8 millimeter Galeichthys felis embryo characteristic of Interval II. The large-celled striatal anlage (striat. anlage) lies dorsal to the undifferentiated cells of the developing olfactory bulb (bulb. olf.). The telencephalic membrane (tel. mem.) is thicker than that of the preceding interval. The olfactory placode (plac. olf.) is situated lateral to the hemisphere. The midline ventricle is v-shaped.
(Protargol impregnation)

Fig. 5. Photomicrograph of a transverse section through the head of the same specimen illustrated in Figure 4, but approximately 30 microns spinalward. The primordial amygdaloid anlage (prim. amyg. anlage) is apparent dorsolateral to the striatal anlage (striat. anlage). The presumptive septal (sept. anlage) and bulbar (bulb olf.) areas comprise the ventral hemisphere wall. The ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.) courses through the lateral hemisphere wall.
(Protargol impregnation)

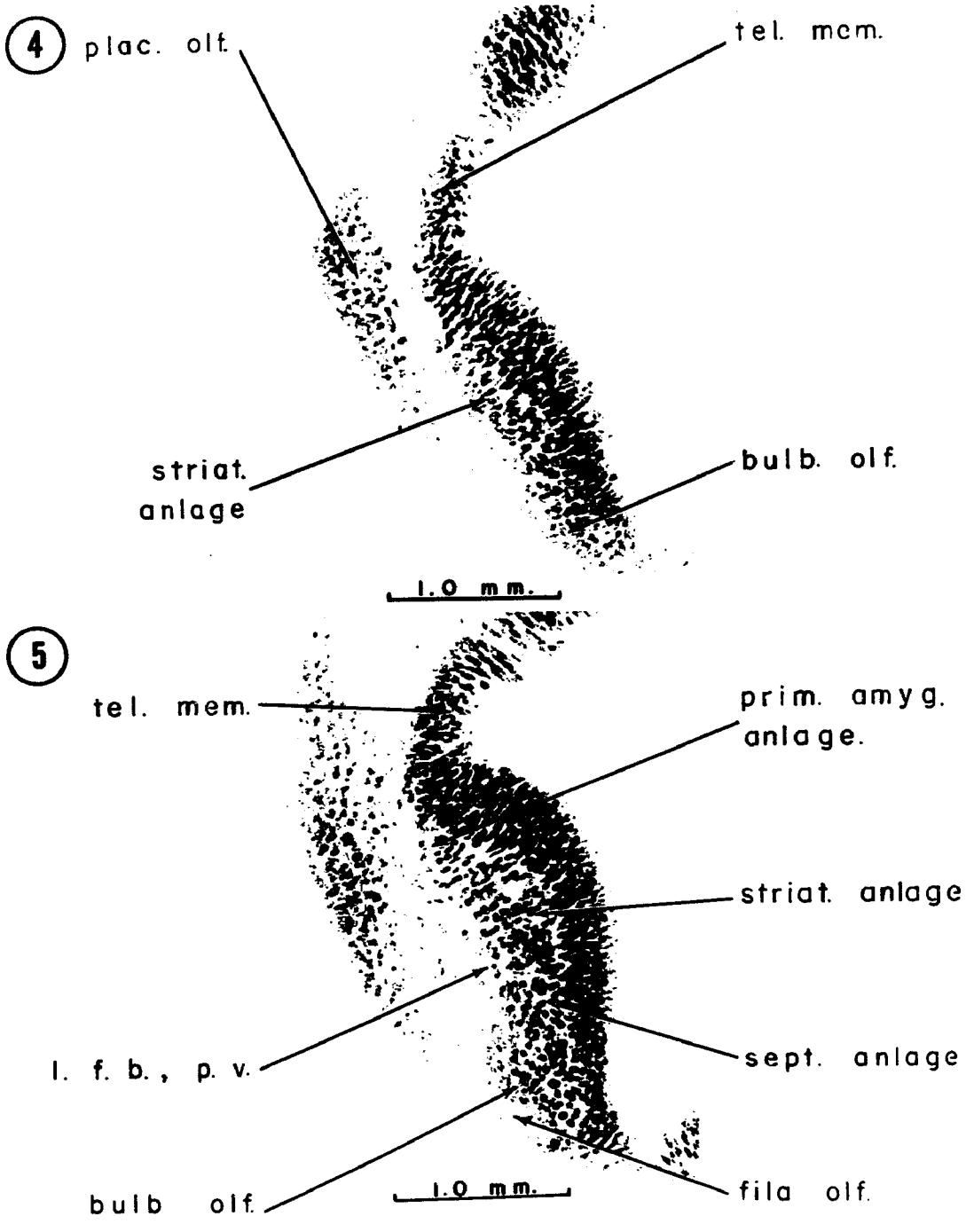

4
plac. olf.
tel. mem.
striat. anlage
bulb. olf.
1.0 mm.
5
tel. mem.
prim. amyg. anlage.
striat. anlage
l. f. b., p. v.
sept. anlage
bulb olf.
1.0 mm.
fila olf.

PLATE 5

Explanation of Figures

Fig. 6. Photomicrograph of a parasagittal section through the forebrain of an 8 millimeter Galeichthys felis embryo typical of Interval II. The entire specimen was sectioned and impregnated with Protargol.

The ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.) and the stria terminalis (stria. term). fibers are the only telencephalic (tel.) pathways in these stages, and are intermingled throughout their course. The stria terminalis fibers terminate in the rostral levels of the hypothalamus (hypothal.). The lateral forebrain bundle passes to the ventral thalamus, hypothalamus and midbrain tegmentum. The large black arrow points to the posterior proliferative zone of the telencephalon.

Fig. 7. A semi-diagrammatic drawing of the same microscopic section illustrated in Figure 6 to elucidate the described pathways.

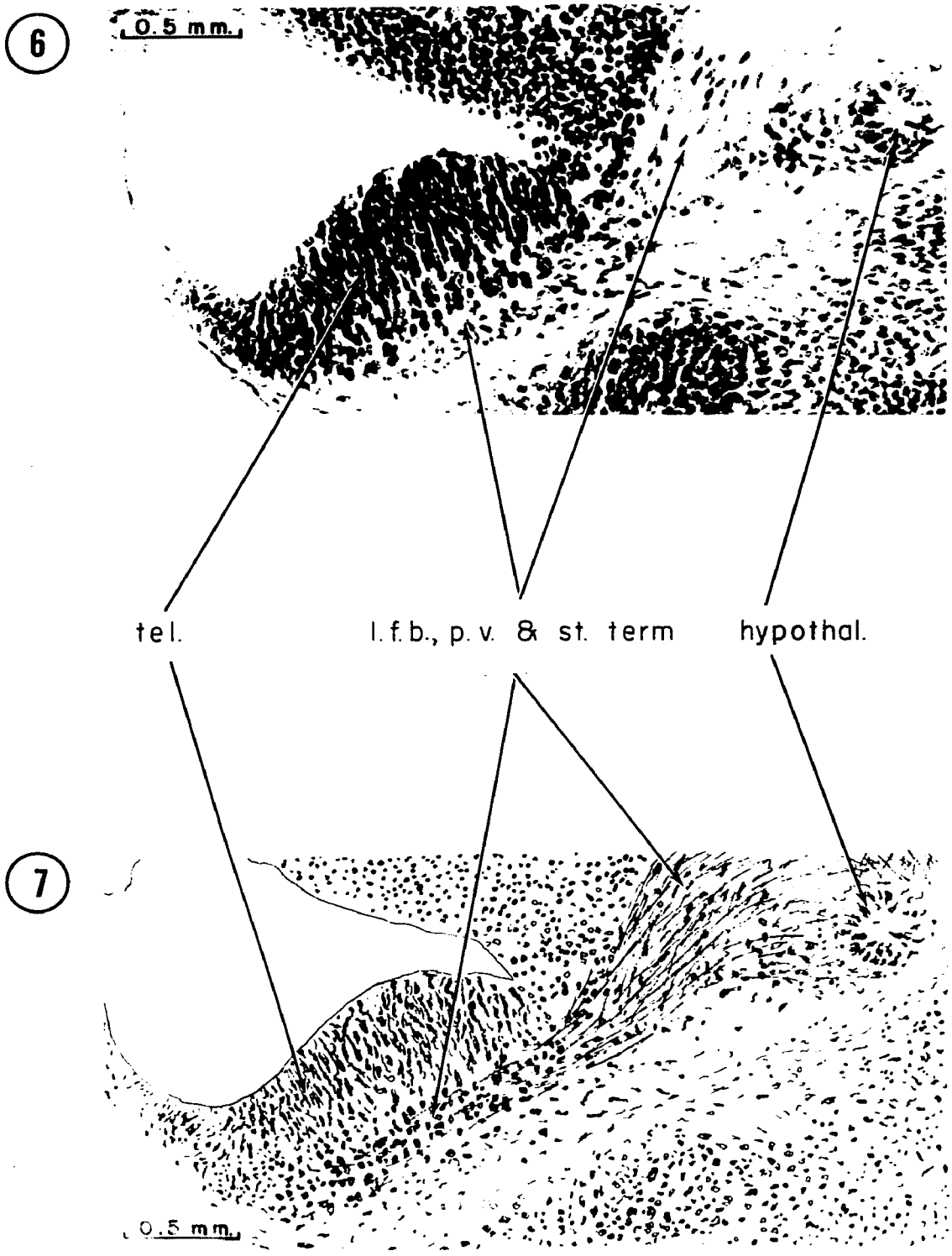

6
0.5 mm.
tel.
l.f.b., p.v. & st. term
hypothal.
7
0.5 mm.

PLATE 6

Explanation of Figure

Fig. 8. Gross photograph of an 8.5 millimeter marine catfish embryo. The telencephalon (tel.) can now be distinguished grossly and the optic tectal anlage (tect. op. anlage.) are quite large. The pigmented retina, operculum (operc.), myelencephalon (myel.) and wing-like pectoral fin (fin. pect.) are readily apparent. This embryo is representative of Interval III.

8

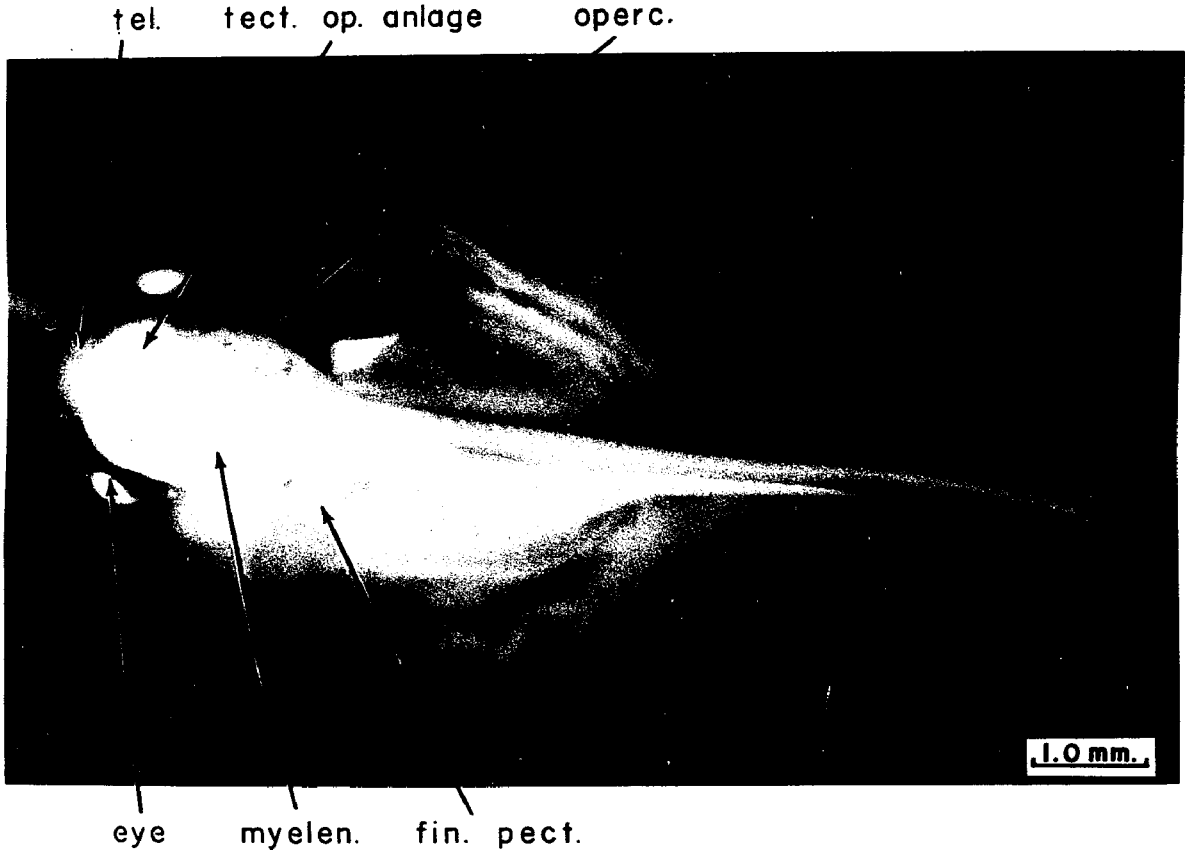


PLATE 7

Explanation of Figures

Fig. 9. Photomicrograph of a thionin-stained transverse section through the rostral end of the telencephalon of an 8.5 millimeter Galeichthys felis embryo characteristic of Interval III. The large-celled striatal anlage (striat. anlage) lies dorsal to the spherical, but undifferentiated olfactory bulb anlage (bulb. olf.).

Fig. 10. Photomicrograph of a precommissural, transverse section through the head (telencephalon) of the same fish illustrated in Figure 9. The striatal anlage (striat. anlage) maintains its dorsal position and is delimited ventrally by the migrating cells of the lateral zone of the tuberculum olfactorium (tub. olf., z. lat.). Ventrally, the undifferentiated septal area (sept. anlage) has replaced the olfactory bulb (bulb. olf.) caudally. The olfactory placode (plac. olf.) has begun to invaginate and the olfactory fila (fila olf.) are present as a distinct fascicle.

Fig. 11. Photomicrograph of a transverse, thionin-stained section through the telencephalon at the level of the anterior commissure from the same specimen illustrated in Figures 9 and 10. The developing amygdalar anlage (prim. amyg.

PLATE 7

Explanation of Figures (continued)

Fig. 11. anlage) has replaced the striatal anlage caudally, and is delimited ventrally by the supracommissural septum (sept. supracomm. anlage). The anterior commissure (comm. ant.) is situated in the ventral hemisphere wall and interdigitates laterally with the fascicles of the lateral forebrain bundle (l.f.b., p.v.) and stria terminalis (stria term.). The large cells of the developing preoptic nucleus (nuc. preop.) are scattered among the fibers of the anterior commissure (com. ant.) but the preoptic recess is not yet present.

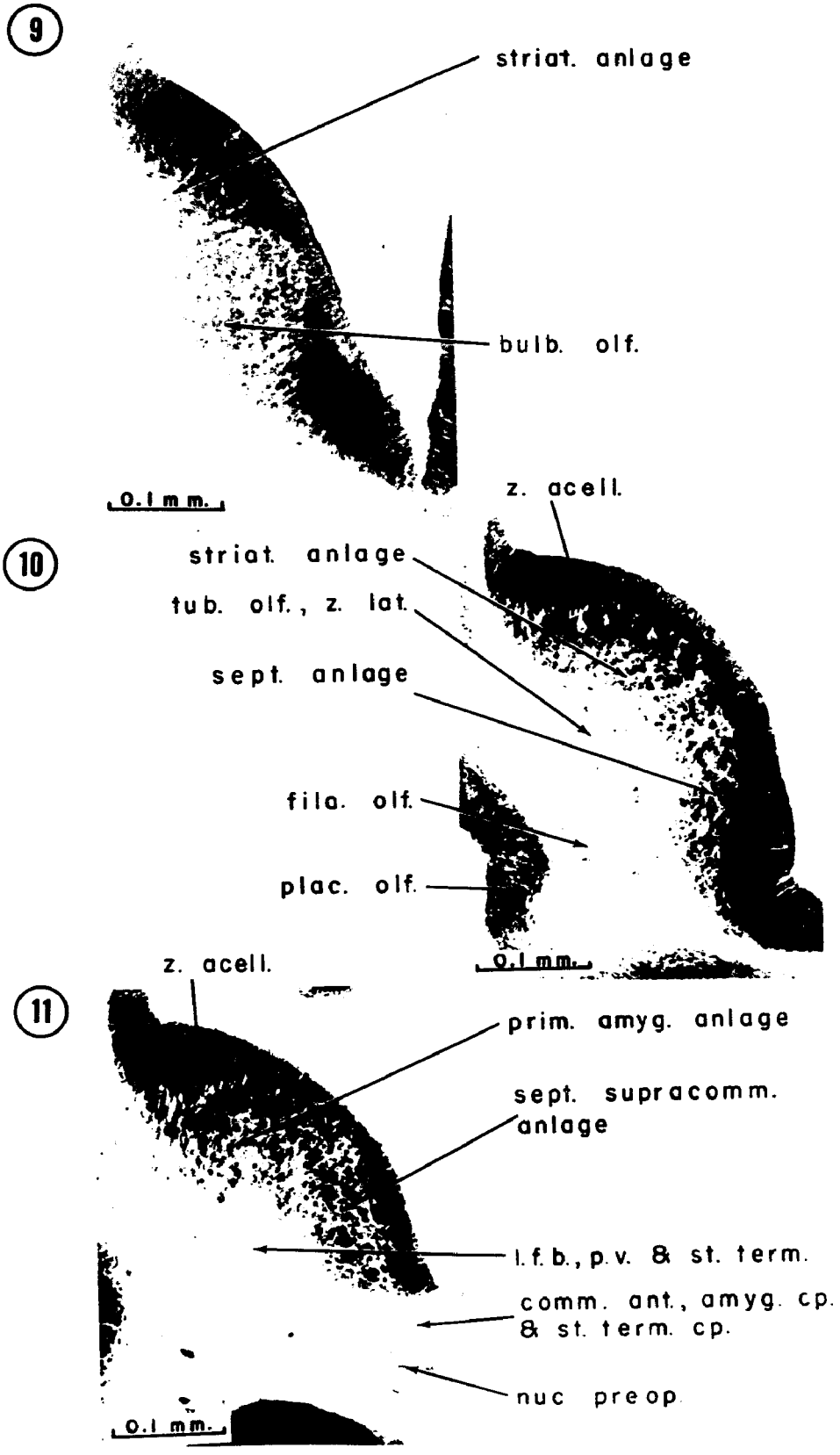

9
striat. anlage
bulb. olf.
0.1 mm.
10
z. acell.
striat. anlage
tub. olf., z. lat.
sept. anlage
fila. olf.
plac. olf.
0.1 mm.
11
z. acell.
prim. amyg. anlage
sept. supracomm. anlage
l.f.b., p.v. & st. term.
comm. ant., amyg. cp. & st. term. cp.
nuc preop
0.1 mm.

PLATE 8

Explanation of Figure

Fig. 12. Gross photograph of a 12 millimeter embryo representative of Interval IV. The telencephalon (tel.) remains diminutive in proportion to the large optic tectal anlage (tect. op. anlage). The metencephalic cerebellar anlage (cereb.) is apparent and the rhomboid fossa is reduced in relative size in comparison to that of Interval III.

(operc.: operculum)

(12)

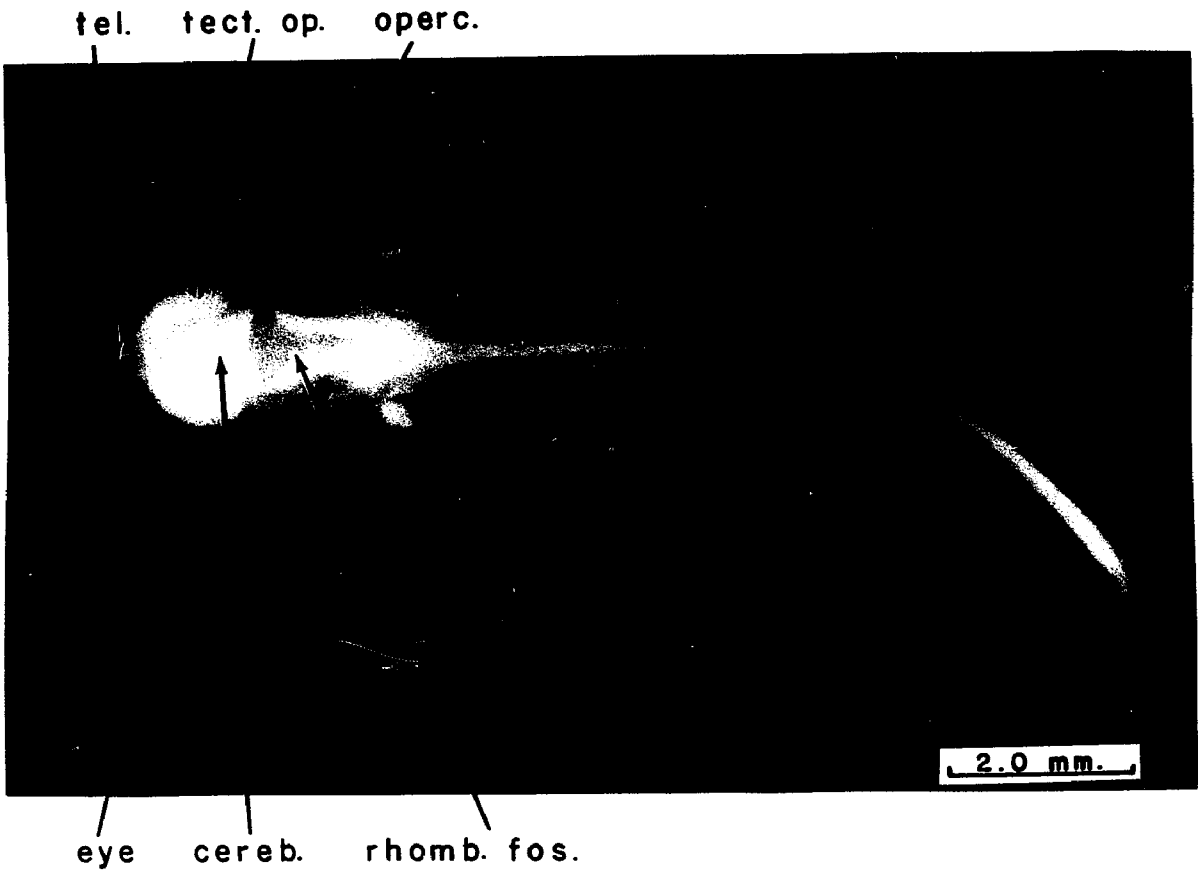


PLATE 9

Explanation of Figures

Fig. 13. Photomicrograph of a transverse section through a whole head mount of a marine catfish embryo 11 millimeters in length. The specimen was stained with thionin, and is representative of Interval IV.

The anterior amygdaloid continuation (amyg. ant.) is situated dorsolaterally adjacent to the dorsomedial pallial anlage (pall. anlage) and the more central striatal area (striat. anlage). The anterior olfactory nucleus (nuc. olf. ant.) intervenes between the pallial anlage (pall. anlage) dorsally and the developing olfactory bulb (bulb. olf.) ventrally. The presumptive septal area (sept. anlage) is situated ventral and caudal to the olfactory bulb (bulb. olf.). Laterally, the olfactory fila (fila olf.) form a distinct fascicle.

Fig. 14. Photomicrograph of a transverse section through the telencephalon (whole head mount) of the same embryo depicted in Figure 13. The primordial corticomedial amygdaloid nucleus (prim. amyg. corticomed.) has replaced the anterior amygdaloid continuation dorsolaterally and is juxtaposed to the pallial anlage (pall. anlage) medially. The striatal anlage (striat. anlage) is situated ventrolateral to the pallial anlage, but lies

PLATE 9

Explanation of Figures (continued)

Fig. 14. dorsal to the proliferating lateral zone of the tuberculum olfactorium (tub. olf., z. lat.). These latter cells delimit the presumptive septal area (sept. anlage) dorsally.

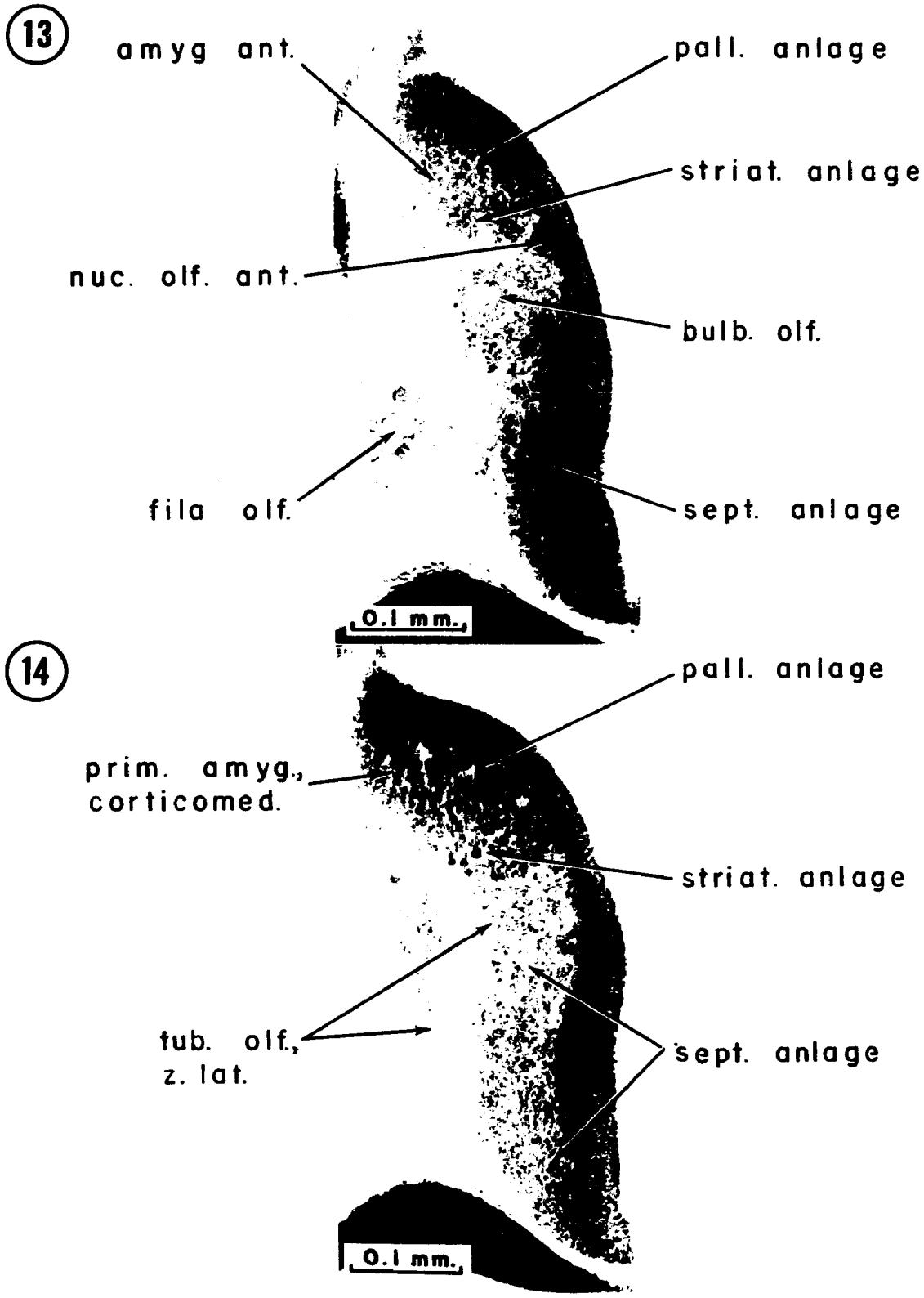

13
amyg ant.
pall. anlage
striat. anlage
nuc. olf. ant.
bulb. olf.
fila olf.
sept. anlage
0.1 mm.
14
pall. anlage
prim. amyg.,
corticomed.
striat. anlage
tub. olf.,
z. lat.
sept. anlage
0.1 mm.

PLATE 10

Explanation of Figures

Fig. 15. Photomicrograph of a transverse, thionin-stained section through the level of the anterior commissure. The specimen is the same as that illustrated in Figures 13 and 14. Dorsally the primordial basolateral amygdaloid nucleus (prim. amyg. basolat.) has replaced the corticomedial amygdaloid nucleus and, in part, the striatal anlage (striat. anlage). The lowermost cells of the striatal anlage probably constitute the paleostriatum primitivum. The more ventral cells of the supracommissural septum (sept. supracomm. anlage) constitute the bed nucleus of the anterior commissure (bed nuc., comm. ant.). The preoptic recess (rec. preop.) and large-celled preoptic area (nuc. preop.) are distinguishable. The anterior commissure (comm. ant.) consists of a stria terminalis component (st. term. cp.) and an interamygdalar component (amyg. cp.).

Fig. 16. Photomicrograph of a transverse section through the telencephalic-diencephalic junction in the same embryo illustrated in Figures 13, 14 and 15 (thionin preparation). The primordial basolateral amygdala (prim. amyg. basolat.), which represents the only telencephalic nuclear area at this level in Interval IV, lies dorsal to the differ-

PLATE 10

Explanation of Figures

Fig. 16. entiating ventral thalamus (thal. vent.) and hypothalamus (hypothal.).
(l.f.b., p.v.: ventral peduncle of the lateral forebrain bundle; st. term.: stria terminalis)

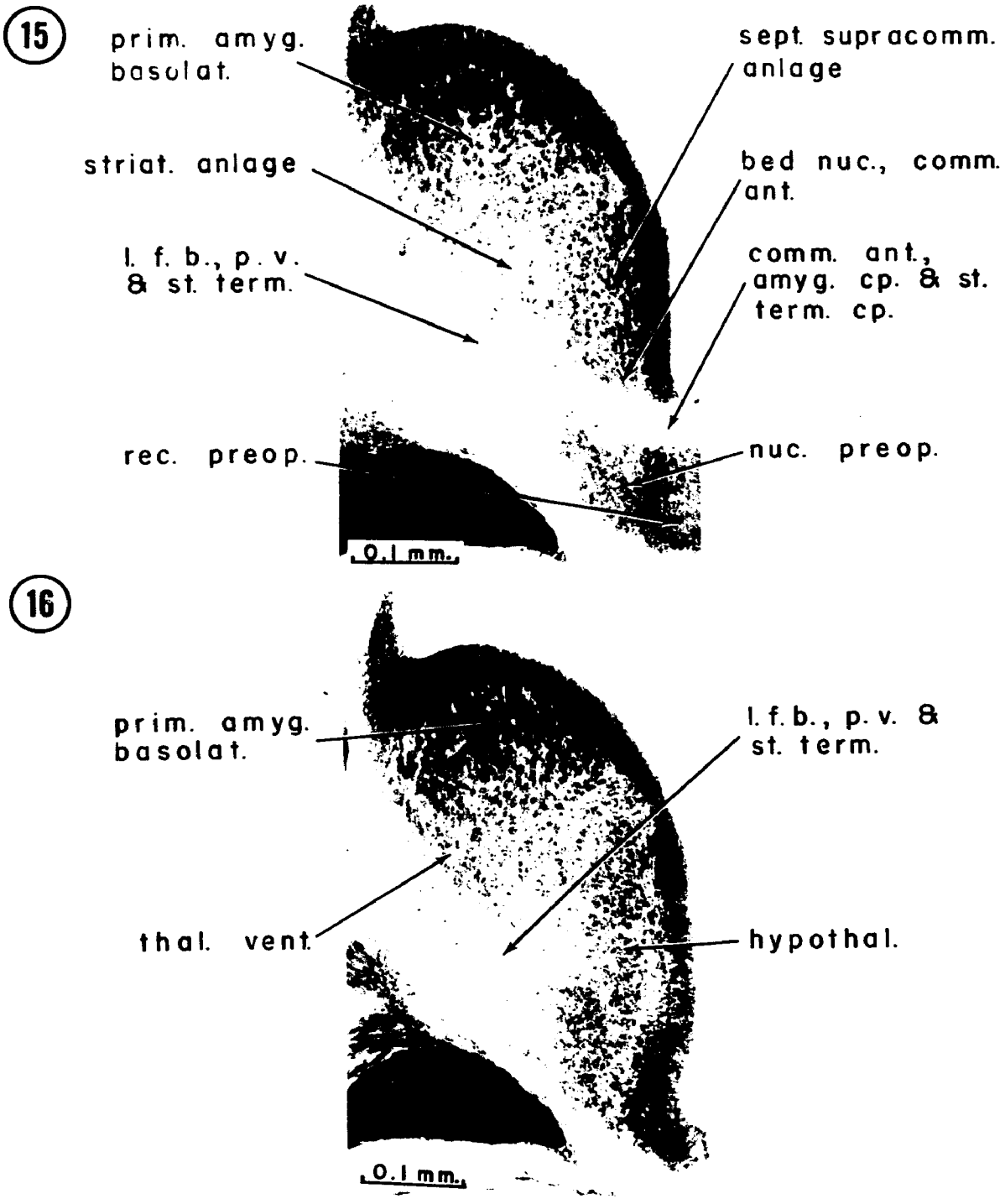

15
prim. amyg. basolat.
striat. anlage
l. f. b., p. v. & st. term.
sept. supracomm. anlage
bed nuc., comm. ant.
comm. ant., amyg. cp. & st. term. cp.
rec. preop.
nuc. preop.
0.1 mm.
16
prim. amyg. basolat.
thal. vent.
l. f. b., p. v. & st. term.
hypothal.
0.1 mm.

PLATE 11

Explanation of Figure

Fig. 17. Gross photograph of a Galeichthys felis embryo 14.5 millimeters in length which is typical of Interval V. The embryo has begun to coil on the yolk sac and the pectoral fins (pect. fin) are more distinct than in the previous stages. The optic tectal (tect. op.) and cerebellar (cereb.) anlagen continue to enlarge and the fourth ventricle (v. IV) is reduced in proportionate size. The abdominal walls reveal the forming ribs.

(17)

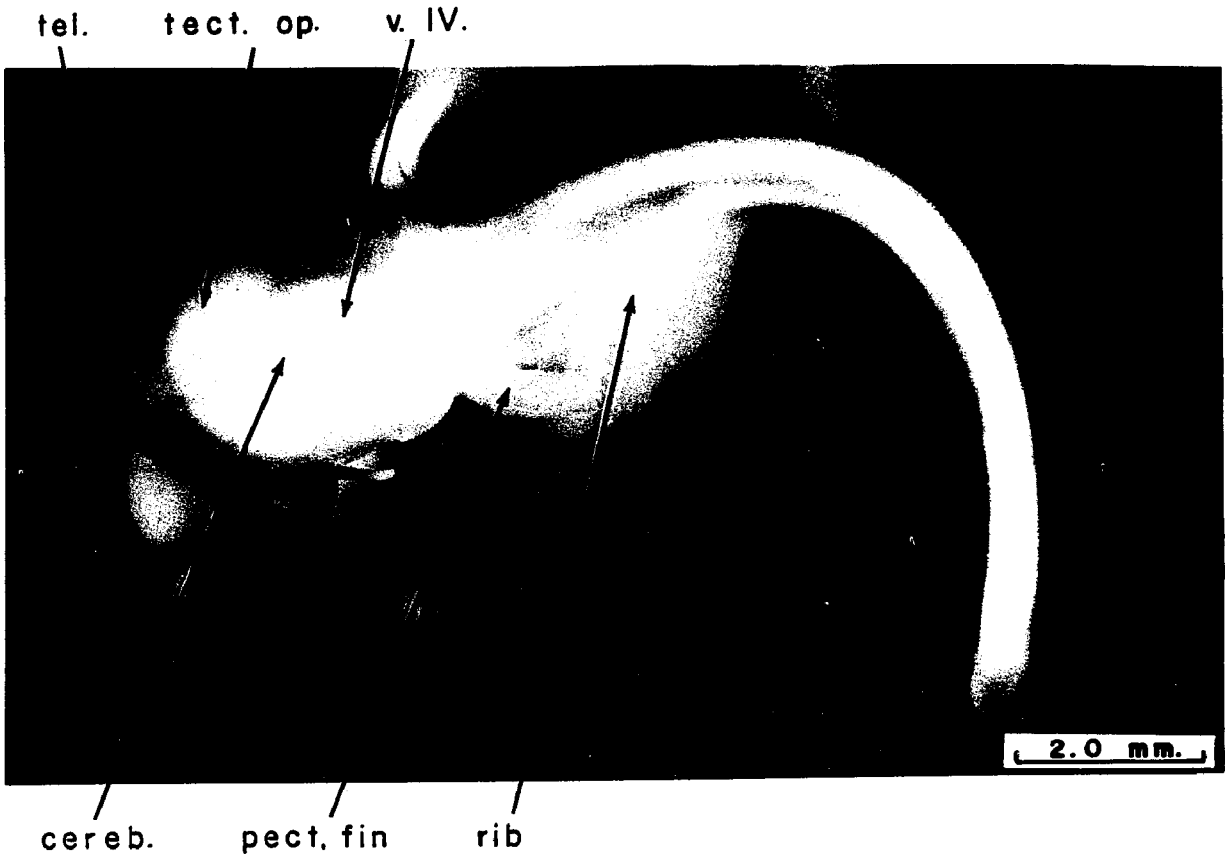


PLATE 12

Explanation of Figures

Fig. 18. Photomicrograph of an obliquely transverse section through the level of the olfactory bulb in a 12.5 millimeter marine catfish embryo. This stage is representative of Interval V. The anterior amygdaloid continuation (amyg. ant.) is situated dorsolaterally in the hemisphere wall and is bounded medially by the pallial anlage (pall. anlage). The pallial anlage (pall. anlage) consists of a thickened band of cells which extends medialward just deep to the ventricular zone to the anterior olfactory nucleus (nuc. olf. ant.). The olfactory bulb (bulb. olf.) in this stage demonstrates definitive mitral cell (l. mit.) and internal granular cell (l. gran. int.) layers. The hyperstriatum (hyperstriat.) is situated centrally. The olfactory fila (fila. olf.) are present ventrolateral to the bulb. The position of the medial (tr. olf. med.) and lateral (tr. olf. lat.) olfactory tracts are marked.

Fig. 19. Photomicrograph of a thionin-stained, transverse section through the telencephalic hemisphere caudal to the level of Figure 18. The pallial anlage (pall. anlage) is situated immediately ventral to the ventricular zone in the dorsal hemisphere and is bounded by the primordial cortico-medial amygdaloid nucleus (prim. amyg. corticomed.)

PLATE 12

Explanation of Figures (continued)

Fig. 19. laterally and the migrating cells of the lateral zone of the tuberculum olfactorium (tub. olf., z. lat.) medially. Juxtaposed to the pallial anlage (pall. anlage) ventrally are the primordial basolateral amygdaloid nucleus (prim. amyg. basolat.) and the striatal area. The hyperstriatum (hyperstriat.) consists of large, darkly-staining neurons. The anlagen of the neostriatum (neostriat.) and paleostriatum augmentatum (paleostriat. aug.), which are situated immediately ventromedial to the hyperstriatum (hyperstriat.), cannot be subdivided in this interval due to the lack of adequate cytodifferentiation. The large-celled lateral septal nucleus (nuc. sept. lat.) is distinguishable from the smaller-celled medial septal nucleus (nuc. sept. med.). The septal area is bounded dorsally and dorsolaterally by the migrating cells of the lateral zone of the tuberculum olfactorium (tub. olf., z. lat.).

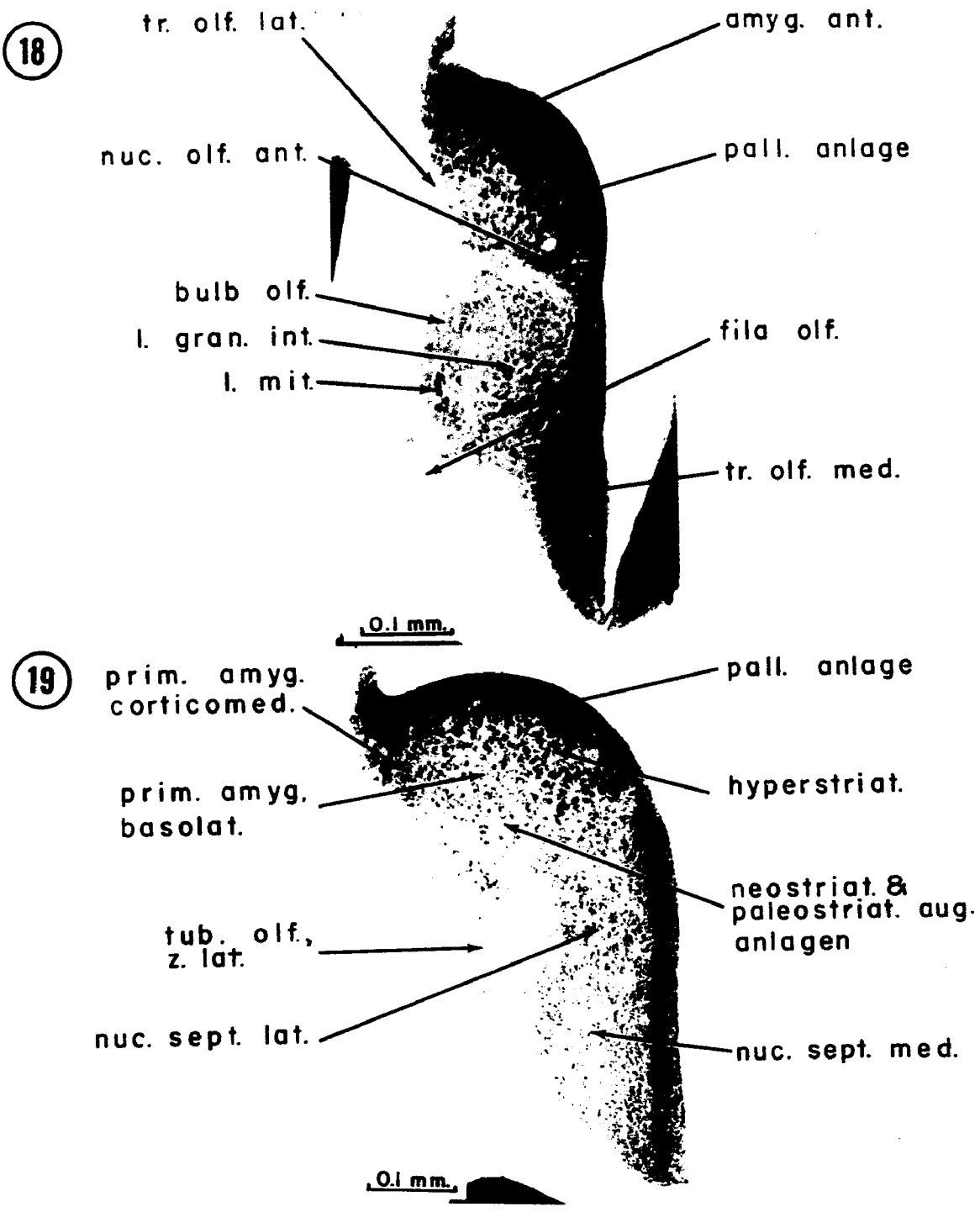

18
tr. olf. lat.
amyg. ant.
nuc. olf. ant.
pall. anlage
bulb olf.
l. gran. int.
l. mit.
fila olf.
tr. olf. med.
0.1 mm.
19
prim. amyg. corticomed.
pall. anlage
prim. amyg. basolat.
hyperstriat.
neostriat. & paleostriat. aug. anlagen
tub. olf., z. lat.
nuc. sept. lat.
nuc. sept. med.
0.1 mm.

PLATE 13

Explanation of Figures

Fig. 20. Photomicrograph of a thionin-stained transverse section through the head of a 12.5 millimeter marine catfish embryo at the level of the anterior commissure (comm. ant.). This microscopic section is from the same brain illustrated in Figures 18 and 19 and is representative of Interval V. Dorsally, the pallial anlage (pall. anlage) is present as a discrete lamina of undifferentiated cells immediately ventral to the dorsal ventricular zone. Medially at this level the differentiating primordial dentate gyrus anlage (prim. gyr. den. anlage) delimits the pallial anlage ventromedially and is itself bounded ventrally by the supracommissural septum (sept. supra-comm.). The remainder of the dorsolateral hemisphere consists of the primordial basolateral amygdalar anlage (prim. amyg. basolat.). The striatal area is more diminutive at this level than at that illustrated in Figure 19. The large cells of the paleostriatum primitivum (paleostriat. prim.) lie ventral to the neostriatal (neostriat.) and paleostriatum augmentatum (paleostriat. aug.) anlagen, intermingled with the fibers of the lateral forebrain bundle and stria terminalis.

PLATE 13

Explanation of Figures (continued)

Fig. 21. Photomicrograph of a transverse section approximately 30 u caudal to that depicted in Figure 20. The primordial basolateral amygdaloid area (prim. amyg. basolat.) comprises the caudal pole of the telencephalon and is delimited ventrally by fibers of the lateral corticohabenular tract (tr. cort. hab. lat.). Ventrally, the combined fibers of the ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.) and the stria terminalis (st. term.) course through the hypothalamus (hypothal.).
(thal. vent.: ventral thalamus)

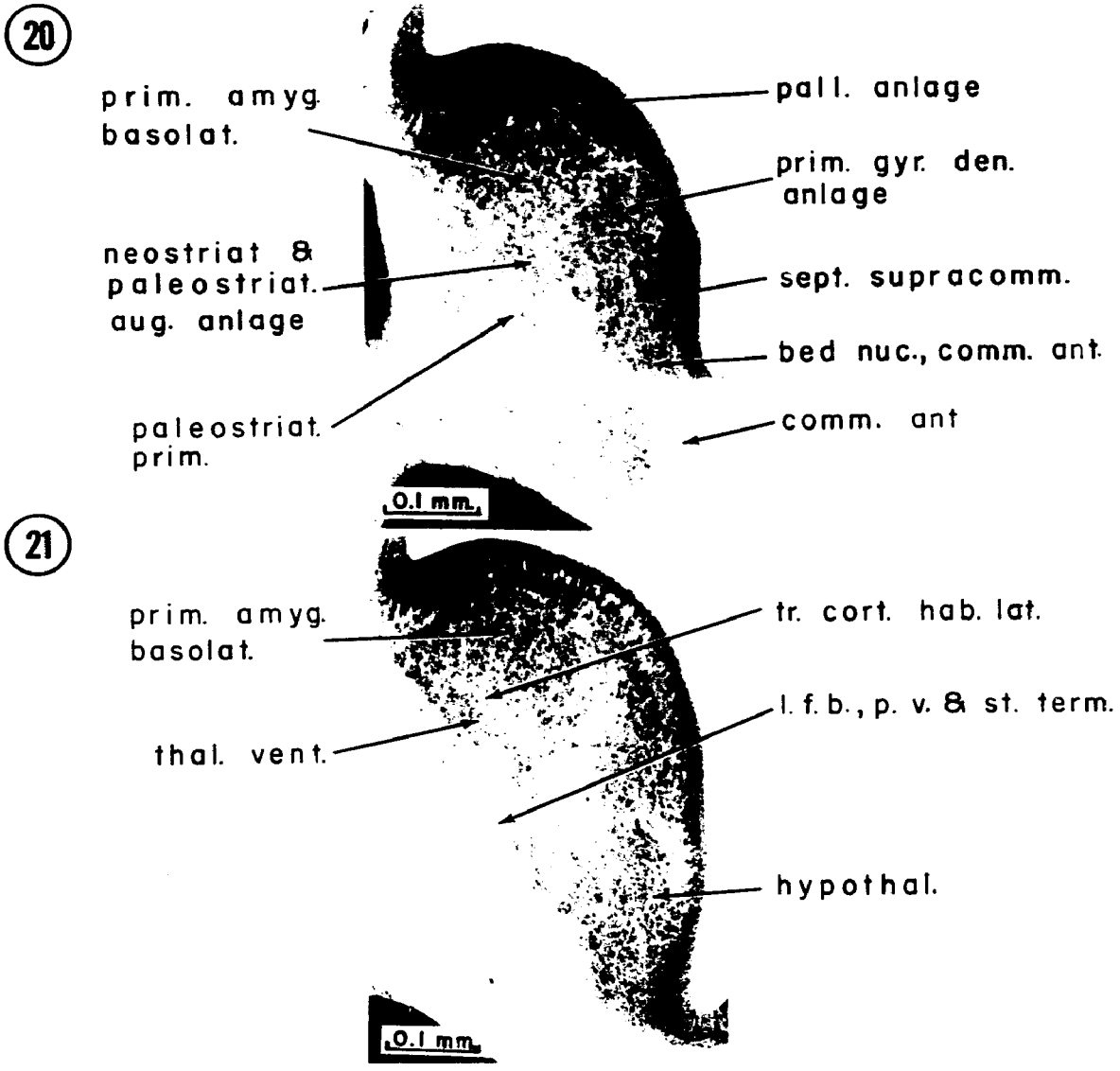

20
prim. amyg. basolat.
pall. anlage
prim. gyr. den. anlage
neostriat & paleostriat. aug. anlage
sept. supracomm.
bed nuc., comm. ant.
paleostriat. prim.
comm. ant
0.1 mm.
21
prim. amyg. basolat.
tr. cort. hab. lat.
l. f. b., p. v. & st. term.
thal. vent.
hypothal.
0.1 mm.

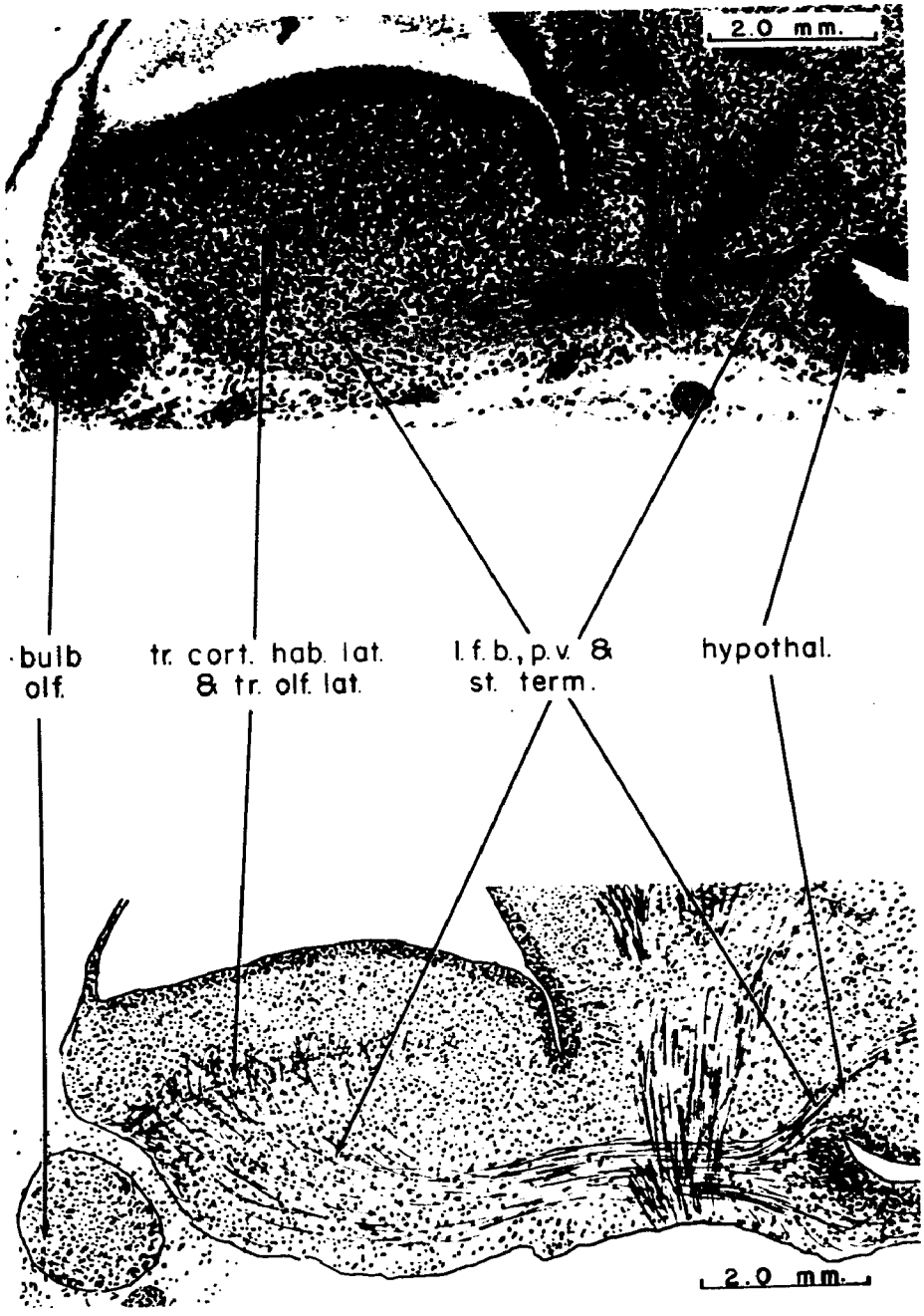
PLATE 14

Explanation of Figures

Fig. 22. Photomicrograph of a parasagittal section through the telencephalon, diencephalon, and part of the mesencephalon of a 13.5 millimeter marine catfish embryo. This specimen, which is included in the fifth interval, was impregnated with Protargol. The plane of the section passes primarily through the course of the lateral forebrain bundle and, in part, the stria terminalis (st. term.). These fiber systems are intermingled in telencephalic levels. In Interval V, only the ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.) is present. These fascicles course through the ascending and commissural optic pathways in the diencephalic levels. The lateral corticohabenular component (tr. cort. hab. lat.) of the stria medullaris and the lateral olfactory tract (tr. olf. lat.) course together in a longitudinal direction in the rostral hemisphere. Contributory fascicles to the lateral forebrain bundle (l.f.b., p.v.) and stria terminalis (st. term.) pass vertically through the lateral corticohabenular (tr. cort. hab. lat.) and lateral olfactory (tr. olf. lat.) tracts.

Fig. 23. Semi-diagrammatic drawing of the same microscopic section illustrated in Figure 22 for elucidation of the fiber systems.

22


2.0 mm.
bulb olf.
tr. cort. hab. lat. & tr. olf. lat.
l.f.b., p.v. & st. term.
hypothal.
2.0 mm.

23

PLATE 15

Explanation of Figures

Fig. 24. Photomicrograph of a section through the olfactory bulb in a 15 millimeter marine catfish embryo typical of the sixth interval The olfactory fila (fila olf.) are present ventrolaterally. The characteristic glomerular (l. glom.), mitral cell (l. mit.) and internal granular cell (l. gran. int.) can be recognized. The lateral olfactory tract (tr. olf. lat.) passes dorsolaterally and caudally along the lateral hemisphere wall. (Protargol impregnation)

Fig. 25. Photomicrograph of the area through which the medial forebrain bundle (m.f.b), postcommissural fornix (fornix) and medial corticohabenular tract (tr. cort. hab. med.) pass at the level of the anterior commissure in a 19 millimeter marine catfish embryo. (Protargol impregnation)

Fig. 26. Photomicrograph of a parasagittal section through the lateral hemisphere wall of a 13.5 millimeter Galeichthys felis embryo typical of Interval V. The lateral recess of the midline ventricle (v. mid.) is present dorsally and is limited caudally by the habenular anlagen (hab. anlage). The primordial basolateral amygdala (prim. amyg. basolat.)

PLATE 15

Explation of Figures (continued)

Fig. 26. comprises the caudolateral pole of the telencephalon and, in this stage, overlaps the ventral thalamus (thal. vent.) ventrally. The lateral olfactory tract (tr. olf. lat.) fibers turn dorsocaudally to enter the lateral hemisphere nuclei. The lateral corticohabenular tract (tr. cort. hab. lat.) courses spinalward through the telencephalon to the ventral thalamus (thal. vent.) then turns dorsally to join the other stria medullaris (stria med.) fascicles in the dorsal thalamus (thal. dors.) to pass to the habenular anlage (hab. anlage).

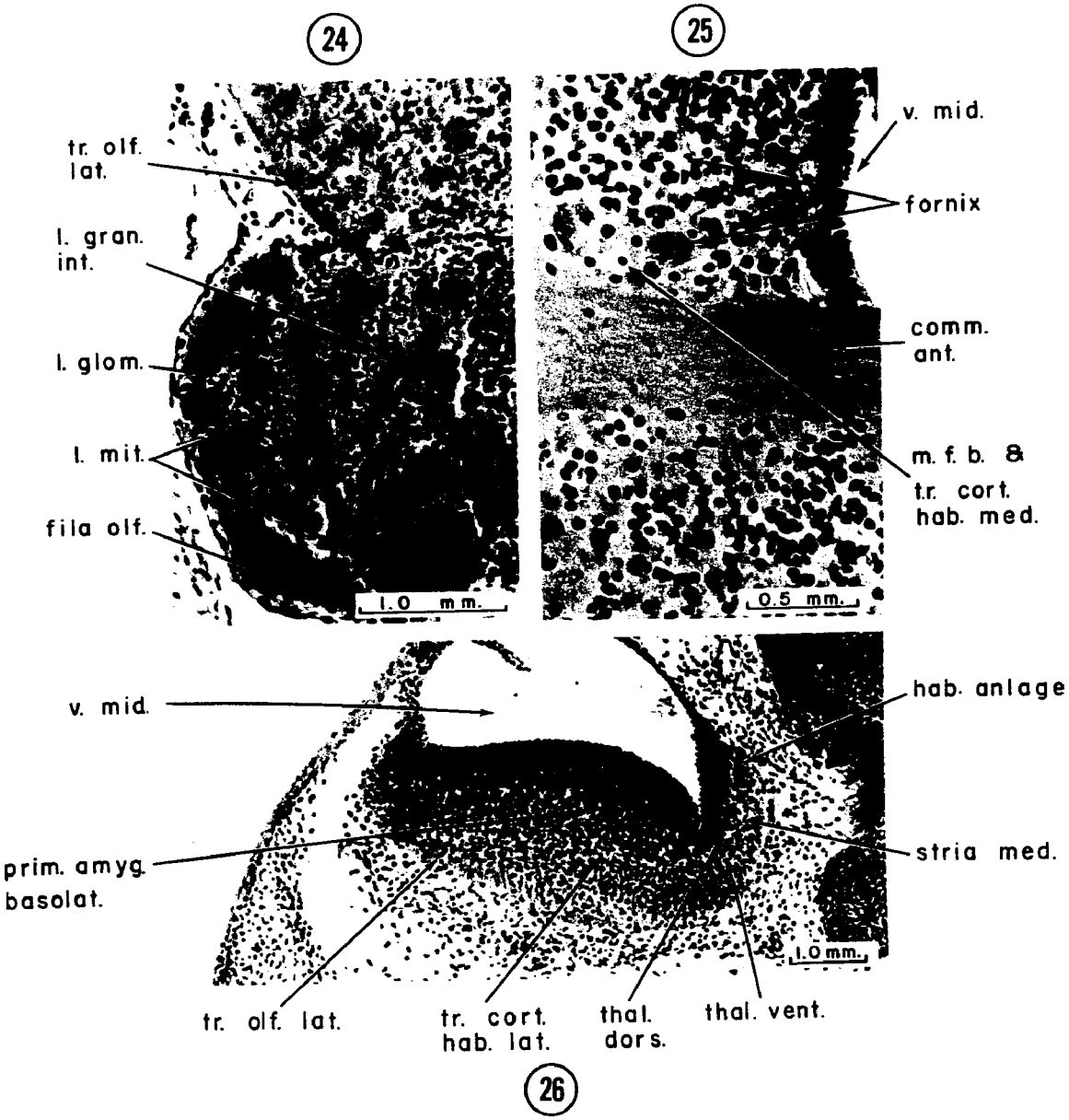

24
25
tr. olf. lat.
l. gran. int.
l. glom.
l. mit.
fila olf.
1.0 mm.
v. mid.
fornix
comm. ant.
m. f. b. &
t.r. cort. hab. med.
0.5 mm.
v. mid.
hab. anlage
stria med.
prim. amyg. basolat.
1.0 mm.
tr. olf. lat.
tr. cort. hab. lat.
thal. dors.
thal. vent.
26

PLATE 16

Explanation of Figure

Fig. 27. Gross photograph of a 17 millimeter Galeichthys felis embryo representative of Interval VI. The eyes are much more encapsulated by the skull than in previous intervals. Pigmentation of the skin has been initiated and pectoral, dorsal, and caudal fins are well formed. The olfactory placodes (plac. olf.) are apparent lateral to the telencephalon (tel.). The optic tectum (tect. op.) and the cerebellum (cereb.) continue to enlarge in relation to the fourth ventricle (v. IV).

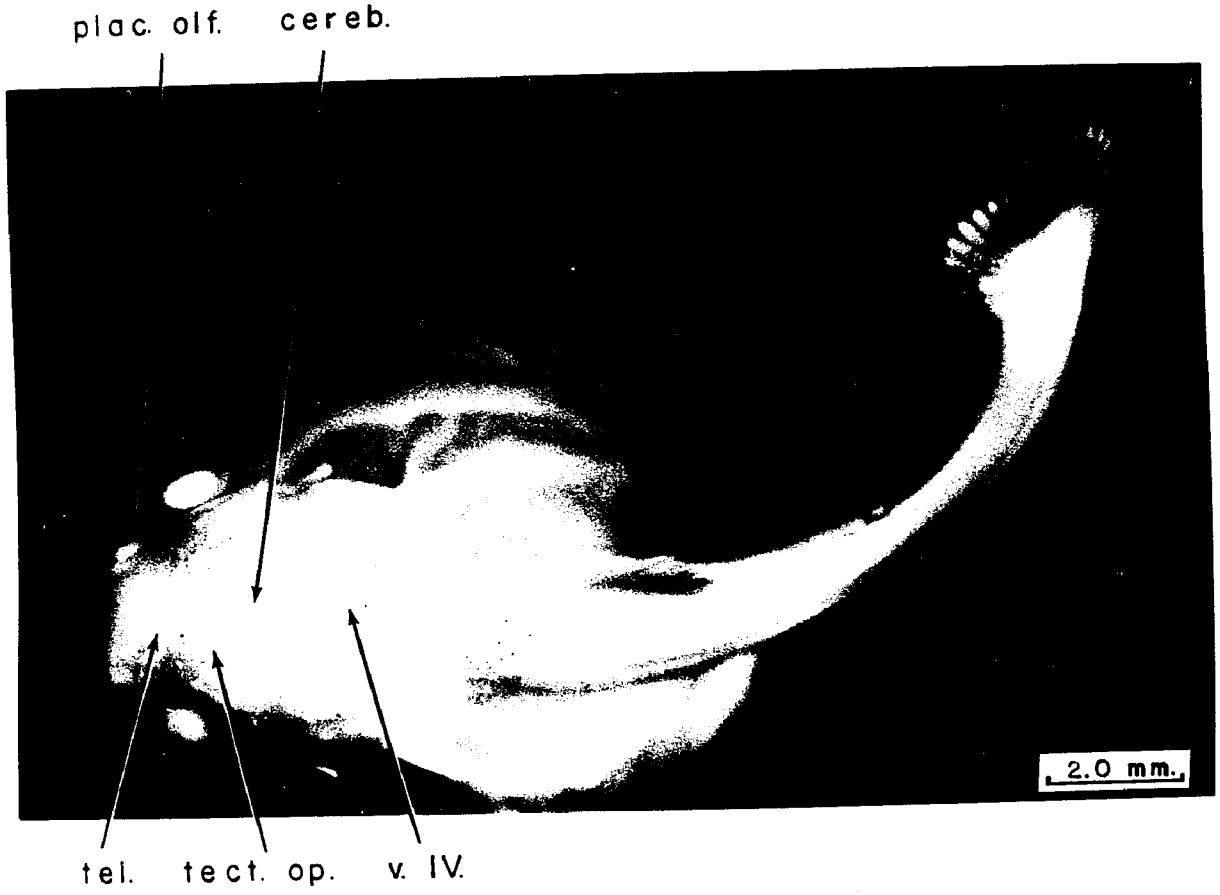

plac. olf.
cereb.
2.0 mm.
tel.
tect. op.
v. IV.

PLATE 17

Explanation of Figures

Fig. 28. Photomicrograph of a transverse section through the head of a 17 millimeter embryo representative of Interval VI. This section through the olfactory bulb was stained with thionin. Dorsally, the pallial anlage (pall. anlage) has differentiated medially into the anterior continuation of the hippocampus (hip. ant.). The primordial general pallial (prim. pall. gen.) and the primordial prepiriform (prim. prepir.) anlagen occupy the dorsal and dorsolateral hemisphere. Ventrolaterally, the anterior amygdaloid continuation (amyg. ant.) is present but more diffuse than in previous intervals. Centrally, the hyperstriatum (hyperstriat.), neostriatum (neostriat.) and paleostriatum augmentatum (paleostriat. aug.) can be distinguished cytologically. The small-celled anterior olfactory nucleus (nuc. olf. ant.) is continuous with the internal granular cell layer of the relatively well differentiated olfactory bulb (bulb. olf.).

Fig. 29. Photomicrograph of a transverse section from the same marine catfish embryo illustrated in Figure 28. The plane of the section is rostral to the anterior commissure and caudal to the olfactory bulb. The primordial dentate gyrus (prim. gyr. den.), primordial cornu ammonis (prim. cornu

PLATE 17

Explanation of Figures (continued)

Fig. 29. am.) and primordial subiculum (prim. subic.) occupy the dorsomedial hemisphere wall, and the primordial general pallium (prim. pall. gen.) is situated dorsally. Laterally, the primordial piriform cortex (prim. pir.) overlies the primordial basolateral amygdala (prim. amyg. basolat.) and, in part, the primordial corticomedial amygdaloid nucleus (prim. amyg. corticomed.). The primordial dentate gyrus has extended nasalward from its commissural position in Interval V, as illustrated in Figure 20. Centrally the hyperstriatum (hyperstriat.), neostriatum (neostriat.) and paleostriatum augmentatum (paleostriat. aug.) retain the relationships of Interval V. The septal area consists of a medial septal nucleus, pars dorsalis (nuc. sept. med., p. d.), a medial septal nucleus, pars ventralis (nuc. sept. med., p. v.) and a lateral septal nucleus (nuc. sept. lat.) and is delimited dorsally by the migrating cells of the lateral zone of the tuberculum olfactorium (tub. olf., z. lat.). Ventrally, a few cells of the medial zone of the tuberculum olfactorium (tub. olf., z. med.) are present.

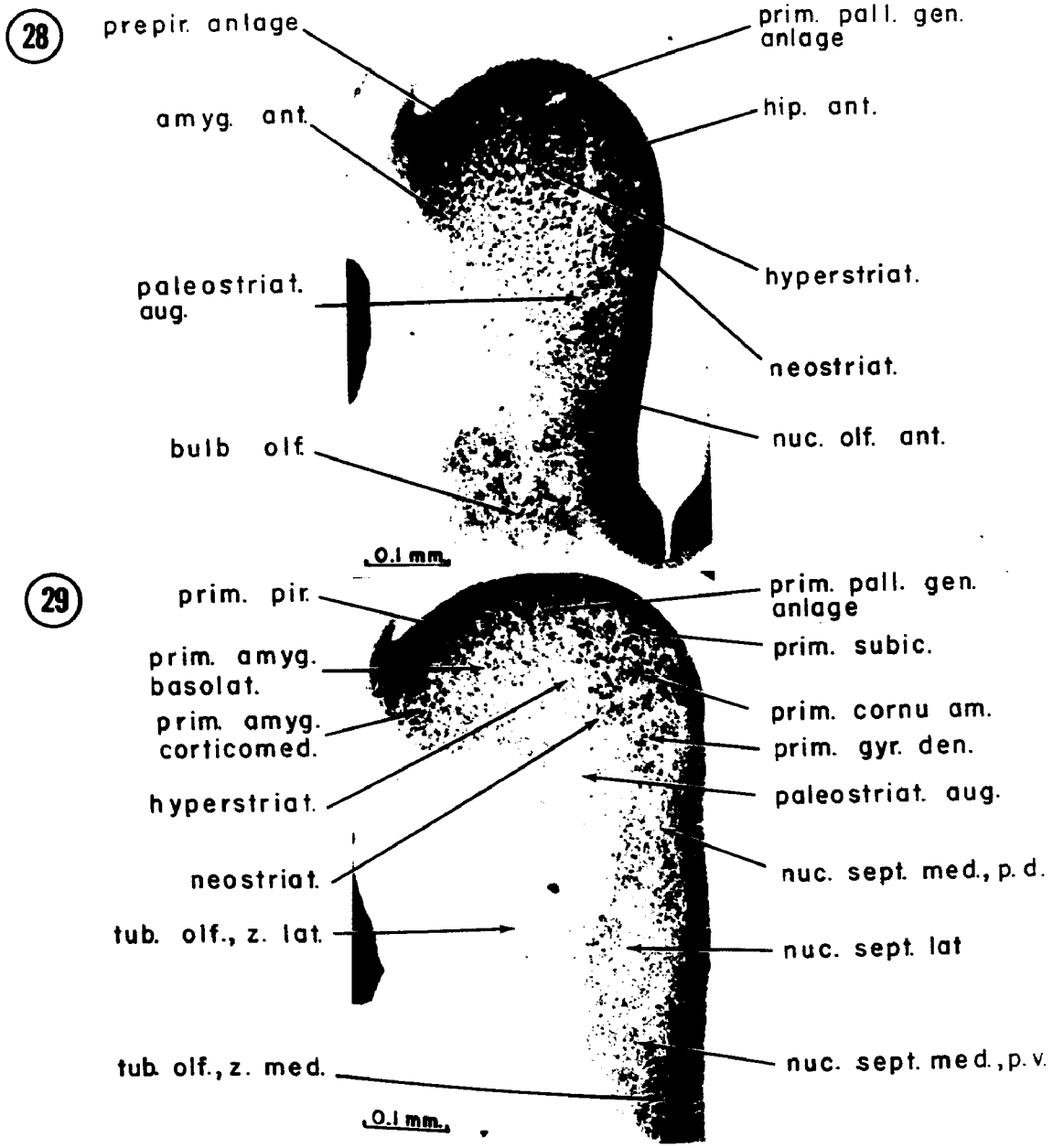

28
prepir. anlage
prim. pall. gen. anlage
amyg. ant.
hip. ant.
hyperstriat.
paleostriat. aug.
neostriat.
nuc. olf. ant.
bulb olf.
0.1 mm.
29
prim. pir.
prim. pall. gen. anlage
prim. subic.
prim. amyg. basolat.
prim. cornu am.
prim. amyg. corticomed.
prim. gyr. den.
hyperstriat.
paleostriat. aug.
neostriat.
nuc. sept. med., p. d.
tub. olf., z. lat.
nuc. sept. lat
tub. olf., z. med.
nuc. sept. med., p. v.
0.1 mm.

PLATE 18

Explanation of Figures

Fig. 30. Photomicrograph of a transverse section through the anterior commissure from the same Galeichthys felis embryo demonstrated in Figures 28 and 29. This section, through the whole head, was stained with thionin. Dorsally, the primordial cornu ammonis (prim. cornu am.) and subicular (prim. subic.) areas of the hippocampal formation are not differentiated. The primordial general pallial cortex is not present in the plane of this section. The primordial piriform cortex (prim. pir.) anlagen overlies and is indistinguishable in thionin stained sections from the primordial basolateral amygdaloid nucleus (prim. amyg. basolat.). In these stages the ventral thalamus intrudes ventral to the lateral corticohabenular tract, but in later stages is separated from the basolateral area by a fissure. Centrally, the paleostriatum augmentatum (paleostriat. aug.), possible neostriatal cells, and the paleostriatum primitivum (paleostriat. prim.) are present. Medially, the primordial dentate gyrus (prim. gyr. den.) and the bed nucleus of the anterior commissure (bed. nuc., com. ant.) are dorsal to the anterior commissure, and the preoptic area (nuc. preop.) is lateral to the preoptic recess.

PLATE 18

Explanation of Figures (continued)

Fig. 31. Photomicrograph of a transverse section taken caudal to the anterior commissure from the same embryo depicted in Figure 30. This thionin stained section is through the telencephalic-diencephalic junction. The primordial piriform cortex (prim. pir.) and the basolateral amygdaloid nucleus (prim. amyg. basolat.) are dorsal to the ventral thalamus (thal. vent.) and the hypothalamus (hypothal.).

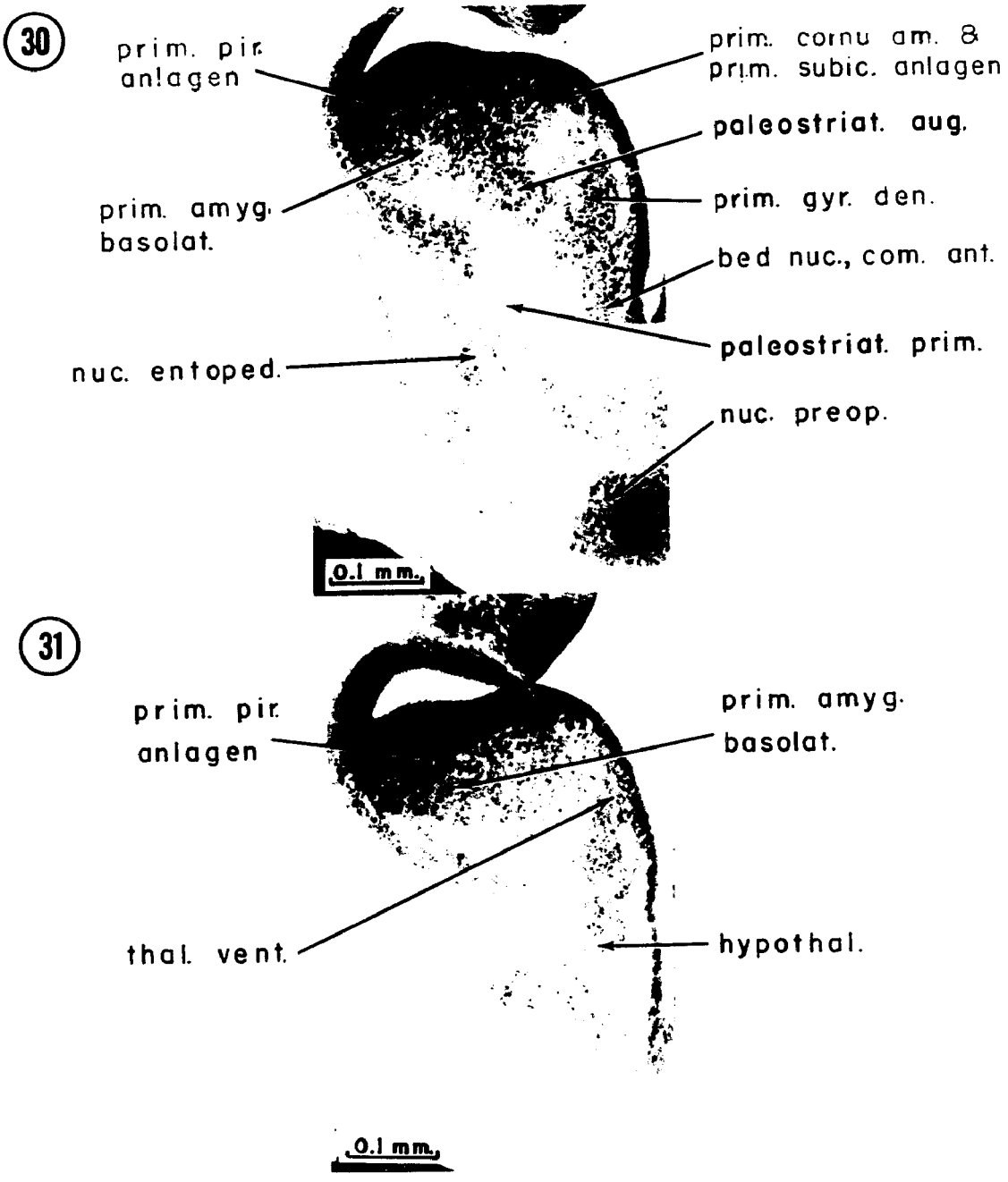

30
prim. pir. anlagen
prim. cornu am. & prim. subic. anlagen
paleostriat. aug.
prim. amyg. basolat.
prim. gyr. den.
bed nuc., com. ant.
paleostriat. prim.
nuc. entoped.
nuc. preop.
0.1 mm.
31
prim. pir. anlagen
prim. amyg. basolat.
thal. vent.
hypothal.
0.1 mm.

PLATE 19

Explanation of Figures

Fig. 32. Photomicrograph of a parasagittal section through the telencephalon, diencephalon, and, in part, mesencephalon of a 17 millimeter catfish embryo. The combined, spinalward coursing fibers of the lateral olfactory tract (tr. olf. lat.) and the lateral corticohabenular tract (tr. cort. hab. lat.) are present. The stria medullaris (st. med.) is apparent in the dorsal thalamus. The ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.) and the stria terminalis (st. term.) course concommitantly in the diencephalon. The dorsal and ventral components of the ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.) are well defined in this stage.

Fig. 33. Semi-diagrammatic drawing of the same microscopic section illustrated in Figure 32 for elucidation of the fiber pathways.

32

tr. olf. lat. &
tr. cort. hab. lat.

st. med.

l. f. b., p. v. &
st. term.

hypothal.

33

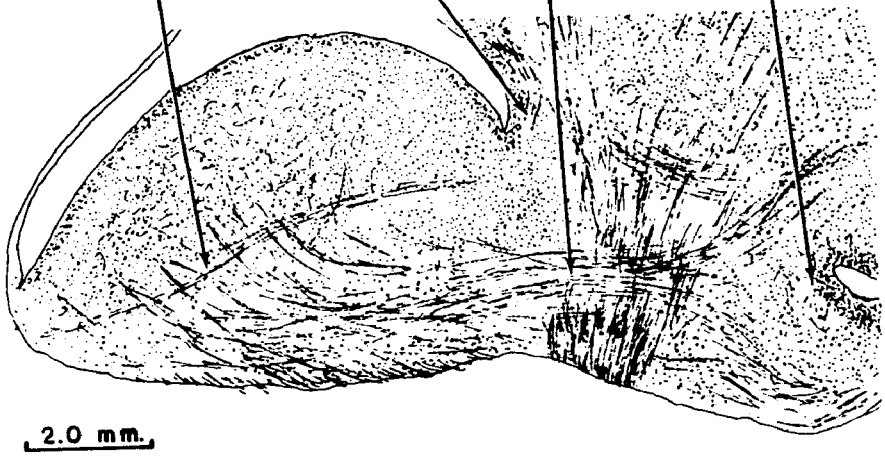


PLATE 20

Explanation of Figure

Fig. 34. Gross photograph of a 44 millimeter juvenile marine catfish typical of Interval VII. The pigmentation is much more advanced than in Interval VI, and the yolk sac has not been completely absorbed. The roof of the skull has been removed. The exposed brain has attained a characteristically adult configuration, with certain exceptions. Specifically, the cerebellum (cereb.) is not so large as that of the adult and does not overhang the caudal poles of the telencephalic hemispheres (tel.). The optic tectum (tect. op.) is proportionately larger than in the adult, and the fourth ventricle (v. IV) is quite reduced.

34

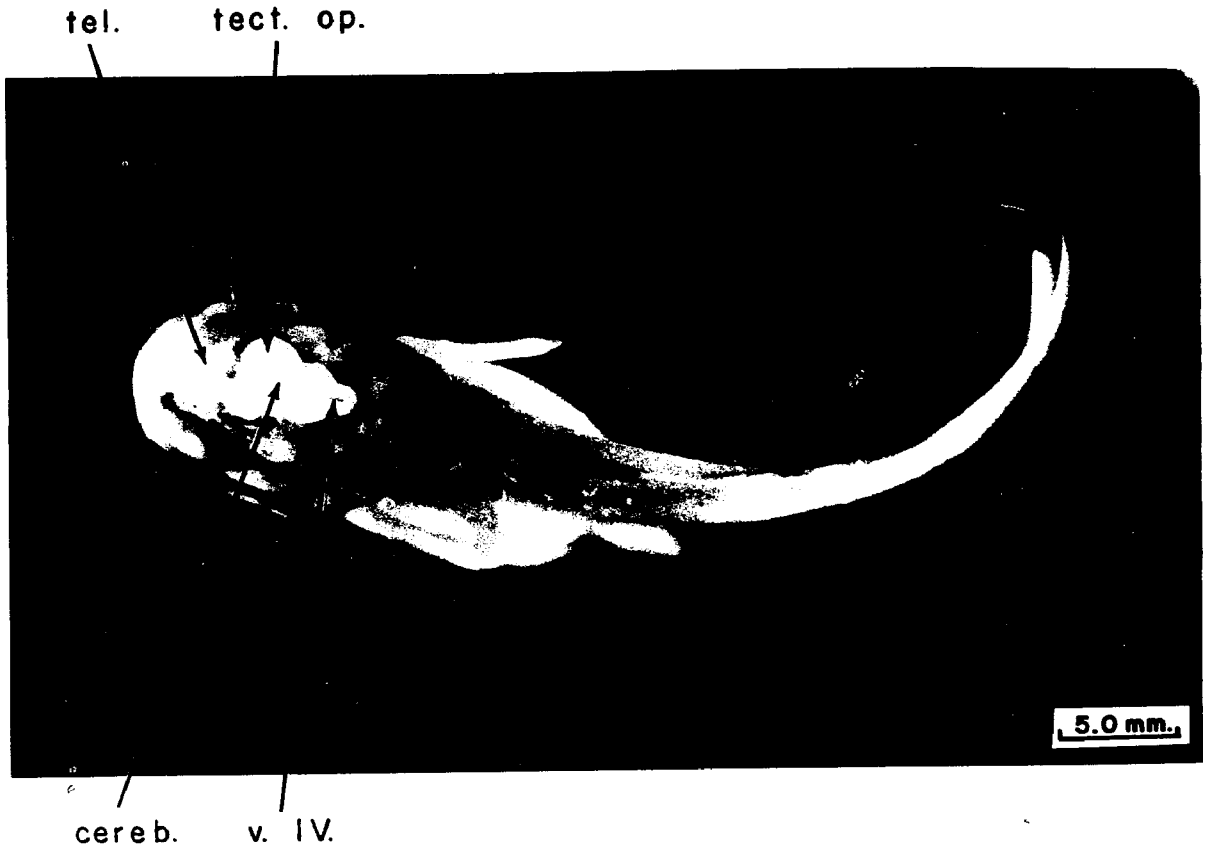


PLATE 21

Explanation of Figures

Fig. 35. Photomicrograph of a transverse section through the rostral pole of the telencephalon of a Galeichthys felis juvenile typical of Interval VII (40 mm.). The plane of the section passes through the olfactory bulb (thionin stain). Immediately below the dorsal ventricular cell layer (from medial to lateral) the anterior continuation of the hippocampus (hip. ant.) and the primordial prepiriform cortex (prim. prepir.) are distinguishable but the primordial general pallial area is not. The anterior amygdaloid continuation (amyg. ant.) is less discrete than in the previous intervals. The hyperstriatum (hyperstriat.) and more ventromedially placed neostriatum (neostriat.) are present centrally. The anterior olfactory nucleus (nuc. olf. ant.) intervenes between the olfactory bulb (bulb. olf.) and the remainder of the hemisphere. The olfactory bulb exhibits the typical adult mitral cell (l. mit.) and internal granular cell (l. gran. int.) layers.

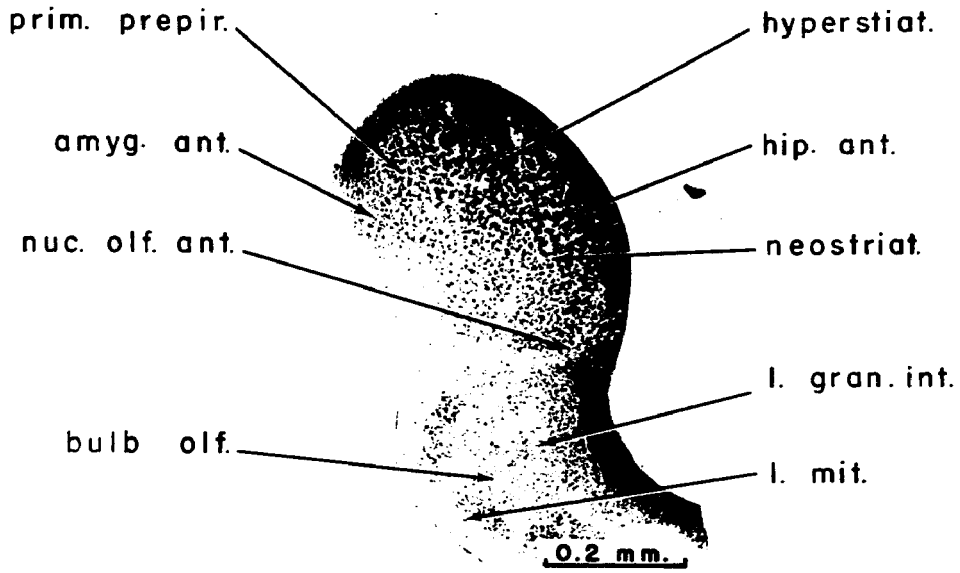
Fig. 36. Photomicrograph of a transverse section through a plane caudal to that depicted in Fig. 35, but from the same specimen. The plane of this section is rostral to the anterior commissure (thionin stain). Dorsally, the

PLATE 21

Explanation of Figures (continued)

Fig. 36. primordial general pallium (prim. pall. gen.) is situated between the primordial hippocampal formation medially and the primordial piriform cortex (prim. pir.) laterally. Ventrolaterally, the primordial corticomedial amygdaloid nucleus (prim. amyg. corticomed.) and the primordial basolateral amygdaloid nucleus (prim. amyg. basolat.) have attained their typical adult relationships. The striatal subdivisions remain centrally placed in the hemisphere. The medial (nuc. sept. med.) and the lateral (nuc. sept. lat.) septal nuclei, and the lateral zone of the tuberculum olfactorium (tub. olf., z. lat.) appear as in the adult.

35


prim. prepir.
amyg. ant.
nuc. olf. ant.
bulb olf.
hyperstiat.
hip. ant.
neostriat.
l. gran. int.
l. mit.
0.2 mm.

36

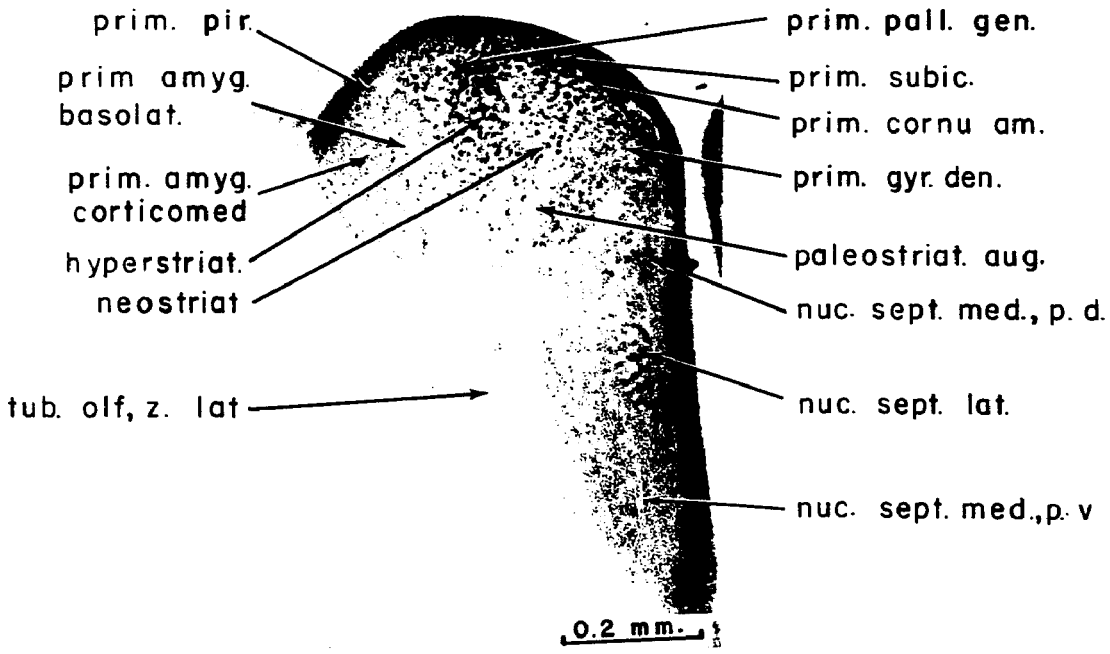

prim. pir.
prim amyg. basolat.
prim. amyg. corticomed
hyperstriat.
neostriat
tub. olf, z. lat
prim. pall. gen.
prim. subic.
prim. cornu am.
prim. gyr. den.
paleostriat. aug.
nuc. sept. med., p. d.
nuc. sept. lat.
nuc. sept. med., p. v
0.2 mm.

PLATE 22

Explanation of Figures

Fig. 37. Photomicrograph of a transverse section through the telencephalon of the same specimen illustrated in Figures 35 and 36. The plane of the section traverses the anterior commissure (thionin stain). The pallial derivatives retain the same configuration as in Fig. 36, as does the primordial amygdaloid area. In the central part of the hemisphere, the hyperstriatum (hyperstriat.) has been replaced caudally by the neostriatum (neostriat.). The paleostriatum augmentatum (paleostriat. aug.) is continuous ventrally with the paleostriatum primitivum (paleostriat. prim.). The supracommissural septum of earlier stages has differentiated into the bed nuclei of the anterior and the hippocampal commissures (bed. nuc., com. ant. and com. hip.). The preoptic nucleus (nuc. preop.) and recess are distinct in the ventral hemisphere.
(prim. gyr. den.: primordial dentate gyrus; prim. cornu am.: primordial cornu ammonis; prim. subic.: primordial subiculum; prim. pall. gen.: primordial general pallium; prim. pir.: primordial piriform cortex; prim. amyg. baso-lat: primordial basolateral amygdala; prim. amyg. corti-comed.: primordial corticomedial amygdala)

PLATE 22

Explanation of Figures (continued)

Fig. 38. Photomicrograph of a transverse section through the telencephalic-diencephalic junction of the same juvenile illustrated in Figures 35, 36 and 37. The primordial piriform cortex (prim. pir.) overlies the primordial basolateral amygdaloid nucleus (prim. amyg. basolat.) dorsally. The nucleus entopeduncularis (nuc. entoped.) is encapsulated and traversed by fibers of the lateral forebrain bundle and the stria terminalis. The ventral thalamus (thal. vent.) and the hypothalamus (hypothal.) form the medial wall.

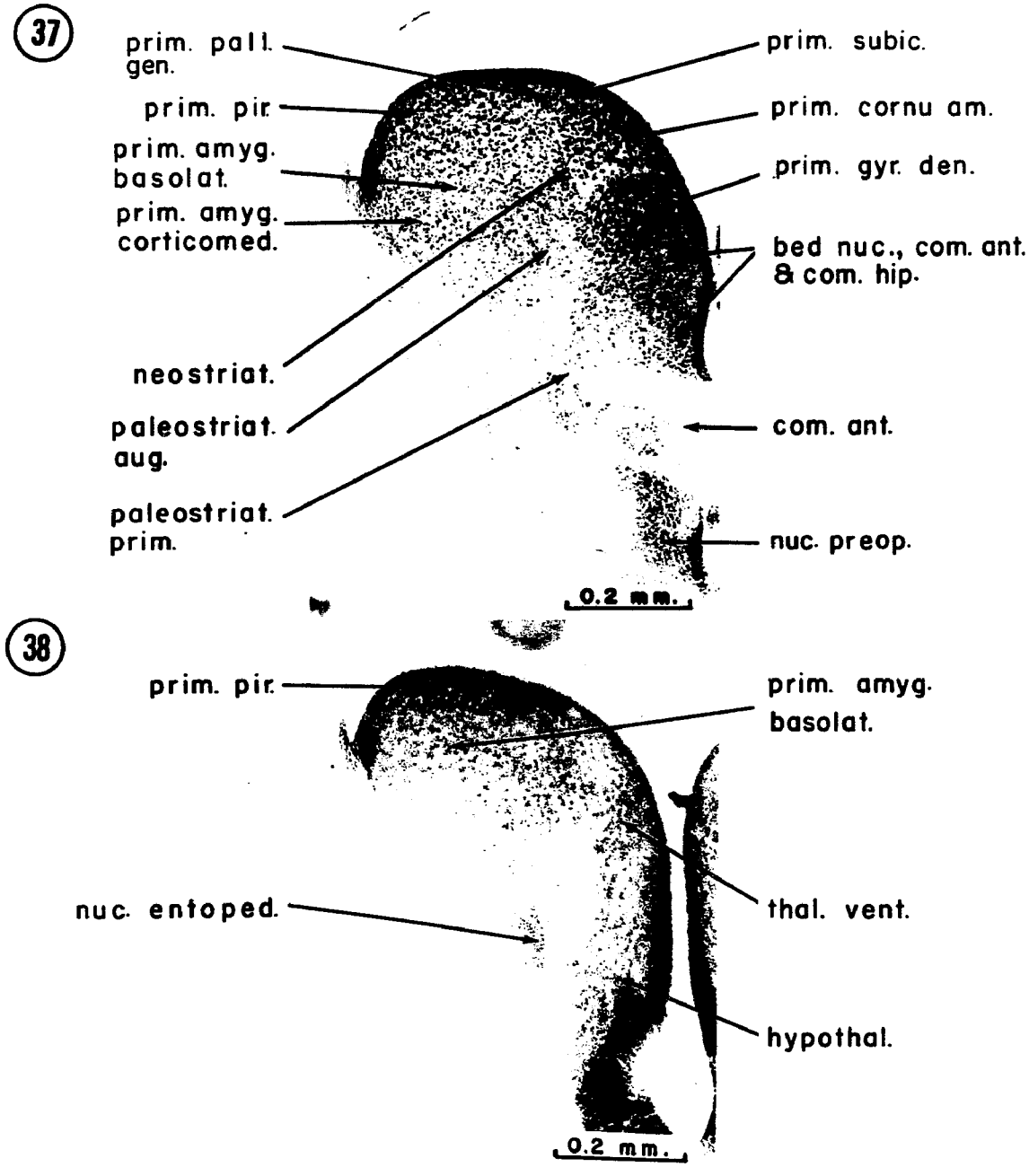

37
prim. pall. gen.
prim. pir.
prim. amyg. basolat.
prim. amyg. corticomed.
neostriat.
paleostriat. aug.
paleostriat. prim.
prim. subic.
prim. cornu am.
prim. gyr. den.
bed nuc., com. ant. & com. hip.
com. ant.
nuc. preop.
0.2 mm.
38
prim. pir.
prim. amyg. basolat.
nuc. entoped.
thal. vent.
hypothal.
0.2 mm.

PLATE 23

Explanation of Figures

Fig. 39 Photomicrograph of a transverse section through the telencephalon of an 8.5 millimeter embryo at the level of the anterior commissure (com. ant.). In this early stage only stria terminalis (st. term. cp.) and interamygdalar (amyg. cp.) components of the anterior commissure are present.
(l.f.b., p.v.: ventral peduncle of the lateral forebrain bundle; st. term.: stria terminalis, ipsilateral component).

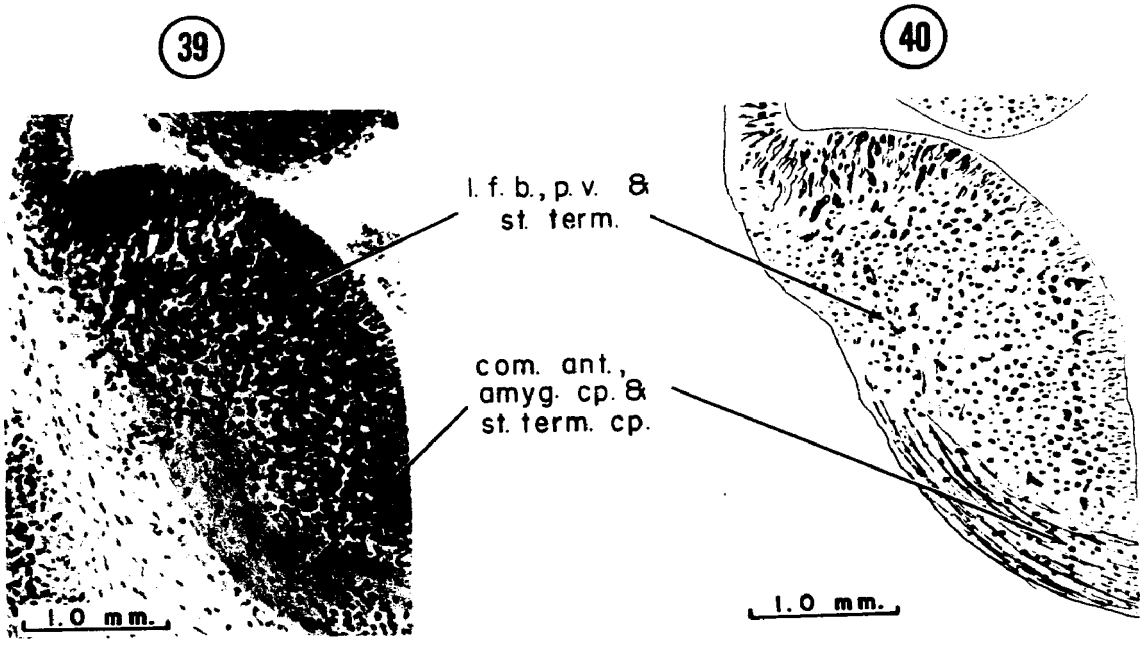
Fig. 40. Semi-diagrammatic outline drawing of the same section as in Figure 39 to elucidate the fiber pathways.

Fig. 41. Photomicrograph of a transverse section through the telencephalon of an 11 millimeter marine catfish embryo. The anterior commissure consists only of interamygdalar (amyg. cp.) and stria terminalis (st. term. cp.) components, as in Figure 39, but the preoptic recess has formed. The longitudinally coursing amygdalohabenular (tr. amyg. hab.) and lateral olfactory (tr. olf. lat.) tracts lie dorsal to the homolateral stria terminalis (st. term.) and the ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.).

PLATE 23

Explanation of Figures (continued)

Fig. 42. Semi-diagrammatic outline drawing of the same microscopic section photographed for Figure 41 to elucidate the fiber pathways.


39
40
l. f. b., p. v. & st. term.
com. ant., amyg. cp. & st. term. cp.
1.0 mm.
1.0 mm.

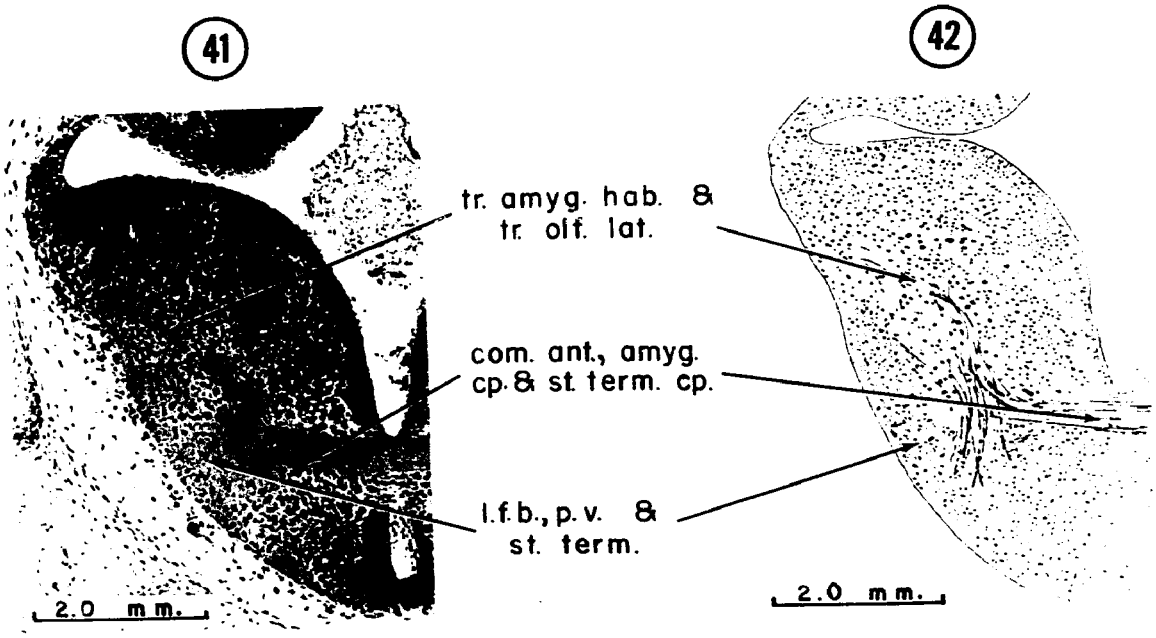

41
42
tr. amyg. hab. & tr. olf. lat.
com. ant., amyg. cp. & st. term. cp.
l. f. b., p. v. & st. term.
2.0 mm.
2.0 mm.

PLATE 24

Explanation of Figures

Fig. 43. Photomicrograph of a transverse section through the telencephalon of a 17 millimeter Galeichthys felis embryo. The anterior commissure is typical of that in the later stages of Interval V and the early stages of the sixth interval. Interseptal (sept. cp.) and intertubercular (tub. cp.) fibers are present in addition to the stria terminalis (com. ant., st. term. cp.) and interamygdalar (com. ant., amyg. cp.) components. Contributory fascicles to the ventral peduncle of the lateral forebrain bundle (l.f.b., p.v.), the homolateral stria terminalis (st. term.), and the longitudinally coursing lateral olfactory (tr. olf. lat.) and lateral corticohabenular (tr. cort. hab. lat.) tracts are crossed by many of the commissural fibers. (Protargol impregnation)

Fig. 44. Semi-diagrammatic drawing of the same transverse section photographed for Figure 43 for clarification of the fiber systems.

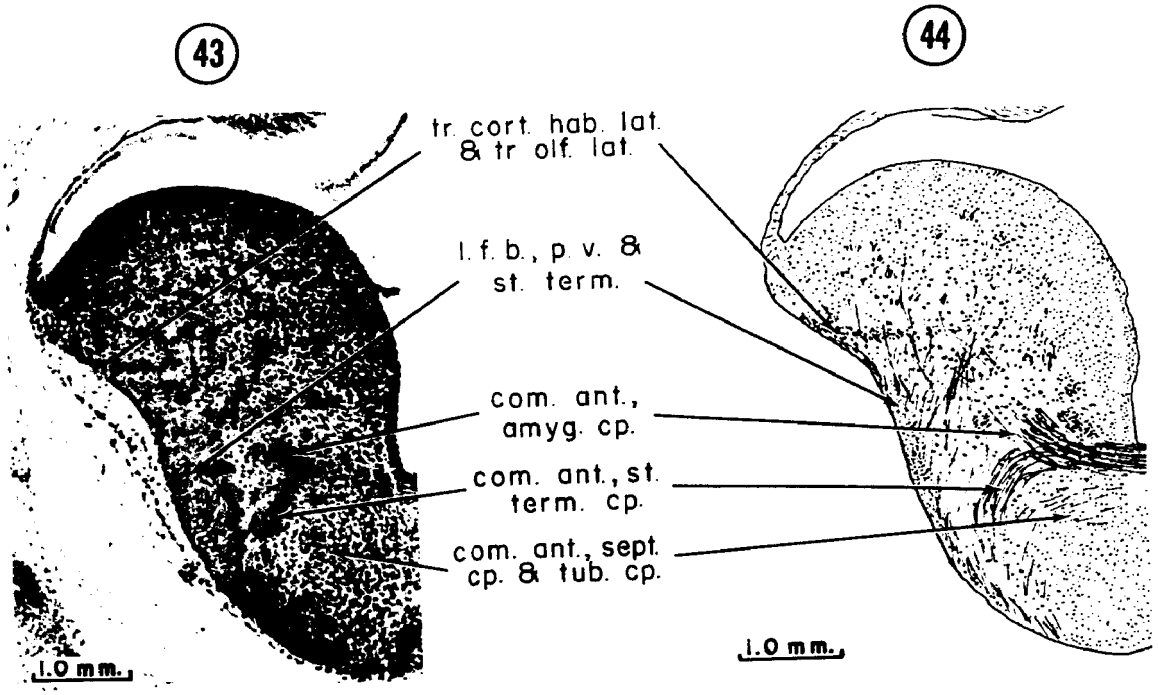
Fig. 45. Photomicrograph of a transverse section at the level of the anterior commissure in a 39 millimeter marine catfish embryo. The plane of the section traverses the caudal region of the anterior commissure, in which the stria termin-

PLATE 24

Explanation of Figures (continued)

Fig. 45. alis (st. term. cp.) and interamygdalar (amyg. cp.) fibers can be demonstrated. The medial olfactory tract and interseptal and intertubercular components cross more rostrally. Fascicles of the hippocampal commissure (com. hip.) are situated dorsal to the anterior commissure. The medial forebrain bundle (m.f.b.), fornix (fornix), and medial corticohabenular tract (tr. cort. hab. med.) pass dorsal to the commissural fibers.
(tr. cort. hab. lat.: corticohabenular tract.; tr. olf. lat.: lateral olfactory tract; l.f.b.: lateral forebrain bundle).

Fig. 46. Semi-diagrammatic drawing of the same section illustrated in Figure 45 included for elucidation of the fiber tracts.


43
44
tr. cort. hab. lat. & tr olf. lat.
l. f. b., p. v. & st. term.
com. ant., amyg. cp.
com. ant., st. term. cp.
com. ant., sept. cp. & tub. cp.
1.0 mm.
1.0 mm.

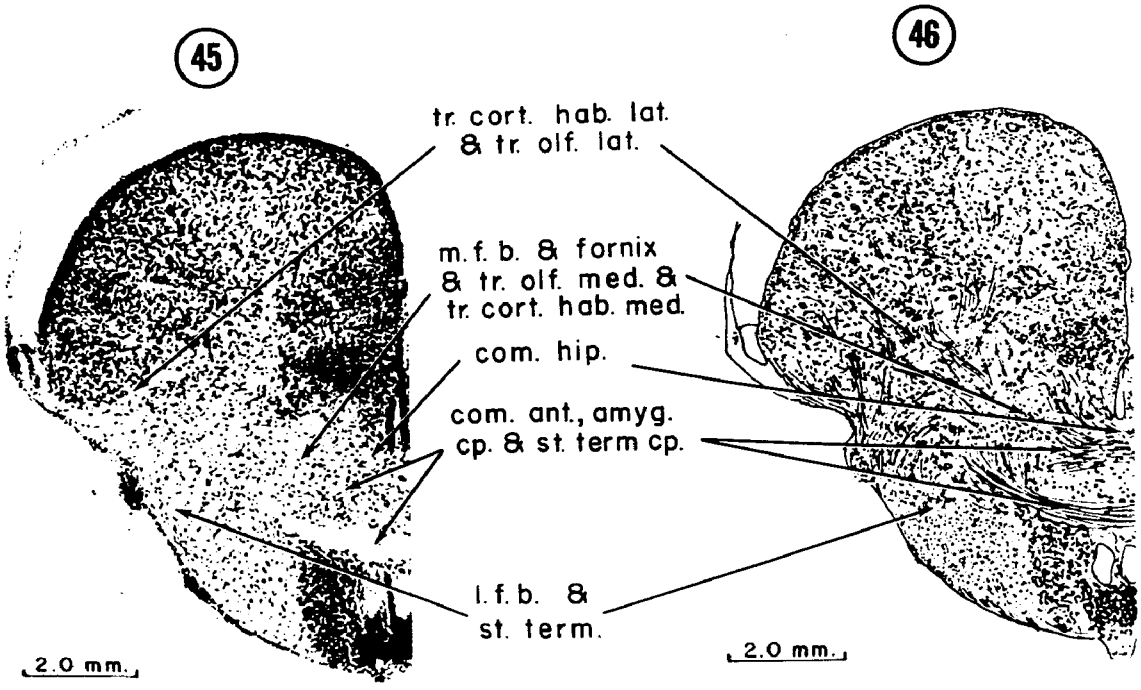

45
46
tr. cort. hab. lat. & tr. olf. lat.
m. f. b. & fornix & tr. olf. med. & tr. cort. hab. med.
com. hip.
com. ant., amyg. cp. & st. term cp.
l. f. b. & st. term.
2.0 mm.
2.0 mm.

PLATE 25

Explanation of Figures

Fig. 47. Outline drawing of a transverse section through the prosencephalon of a 7 millimeter Galeichthys felis embryo to illustrate the conformation of the early hemispheres.

Fig. 48. Outline drawing of a transverse section through the telencephalon of an 8 millimeter embryo. This illustrates the "folding out" of the hemispheres which occurs during Interval II.

Fig. 49. Outline drawing of a representative transverse section through the telencephalon of a 12.5 millimeter marine catfish embryo. This illustrates the position of the attachment sites of the dorsal telencephalic membrane typical of Intervals III through VI.

Fig. 50. Outline drawing of a transverse section through the telencephalon of a 41 millimeter juvenile marine catfish. This demonstrates the typical adult conformation of the dorsal membrane attachment sites.

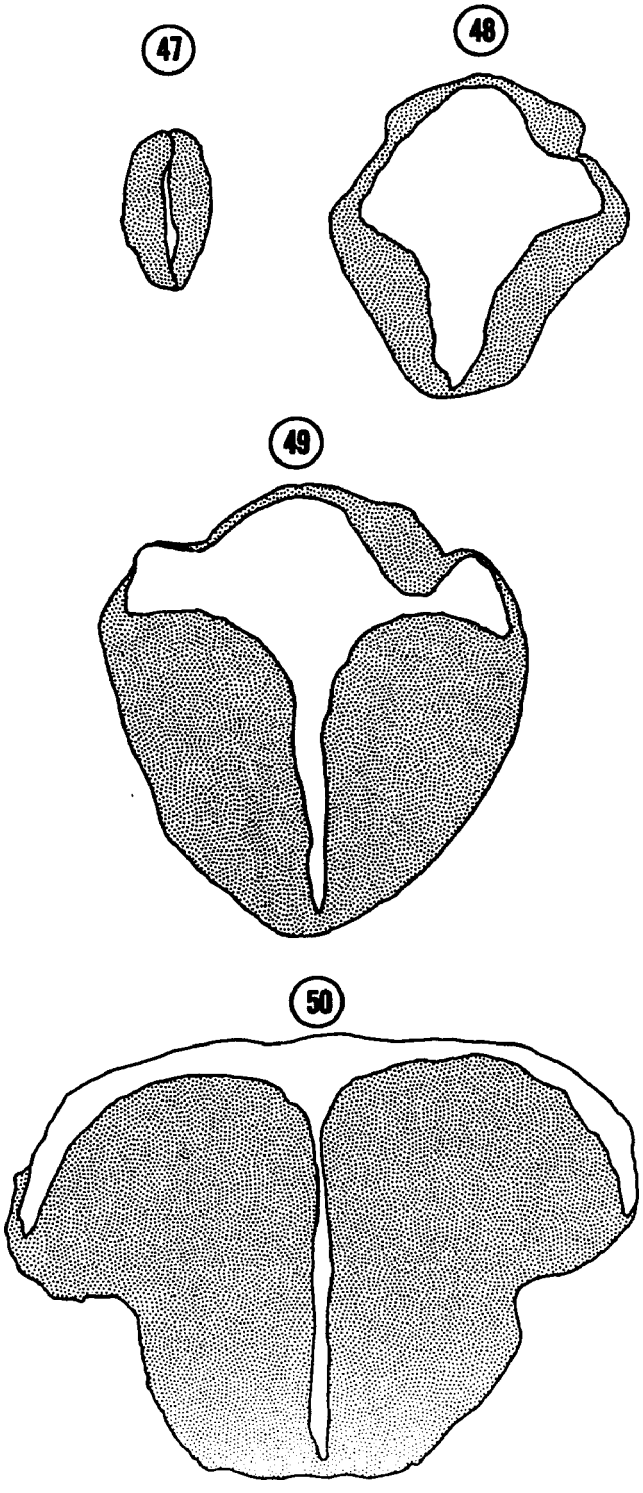

47
48
49
50

PLATE 26

Explanation of Figures

Fig. 51. Drawing of a hypothetical hemisphere (medial surface) demonstrating the position of the proliferation sites for the nuclear groups which are elaborated initially in the marine catfish embryo. The striatum (corpus striatum) and lateral tubercular zone (tub. olf., z. lat.) proliferative sites occupy the rostrodorsal hemisphere and are replaced caudally by the primordial basolateral (prim. amyg. basolat.) and primordial corticomedial (prim. amyg. corticomed.) amygdaloid nuclei. The medial septal nucleus (nuc. sept. med.) occupies the rostroventral quadrant.

Fig. 52. Drawing of a cross-section through the hypothetical hemisphere illustrated in Figure 51 to demonstrate the dorsal to ventral arrangement in the mid hemisphere level of the primordial corticomedial (prim. amyg. corticomed.) and basolateral (prim. amyg. basolat.) amygdaloid nuclei, the striatum (corpus striatum), the lateral zone of the olfactory tubercle (tub. olf., z. lat.) and the medial septal nucleus (nuc. sept. med.). The arrows represent the attachment sites of the dorsal telencephalic membrane dorsally and the interhemispheric floor membrane ventrally.

PLATE 26

Explanation of Figures (continued)

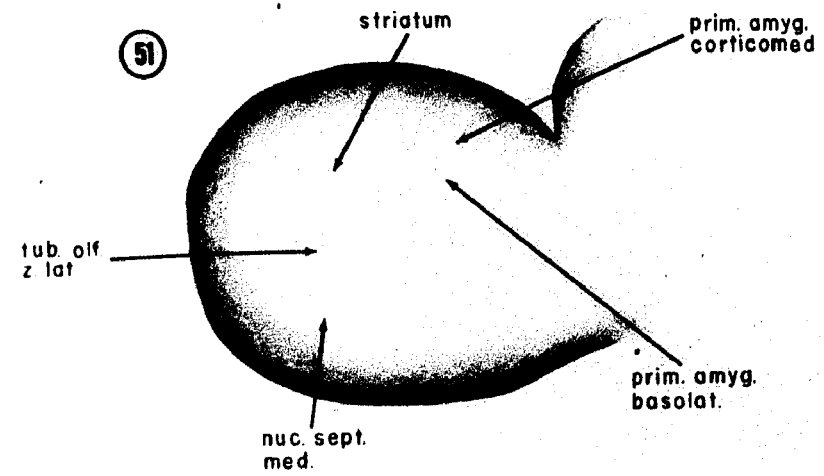
Fig. 53. Drawing of a medial veiw of a hypothetical teleost telencephalon depicting the arrangement of the nuclear proliferation site corresponding to those of Galeichthys during the fourth interval of development. If an evagination process occurred, its approximate initial position would probably lie just caudal to the pallial anlage (pall. anlage). The other nuclear areas would retain the earlier positions depicted in Figure 51.
(prim. amyg. corticomed: primordial corticomedial amygdaloid nucleus; prim. amyg. basolat.: primordial basolateral amygdaloid nucleus; tub. olf., z. lat.: lateral zone of the tuberculum olfactorium; nuc. sept. med.: medial septal nucleus).

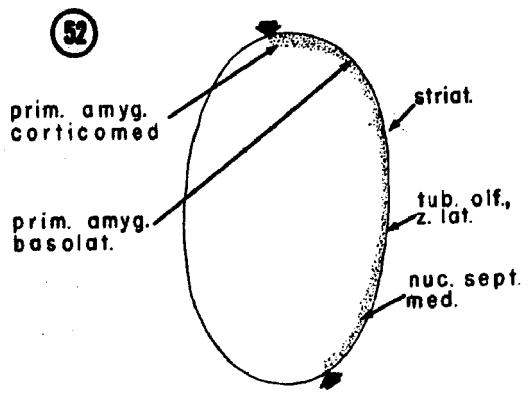
Fig. 54. Drawing of a cross section through the hypothetical evaginating fish telencephalon illustrated in Figure 53. The plane of the section passes just rostral to the evagination site. The proliferative epithelium of the pallial anlage would be displaced into the medial wall of the lateral ventricle by a rostrally directed evagination. The arrangement of the remaining proliferative regions would be unchanged.
(prim. amyg. corticomed: primordial corticomedial amygda-

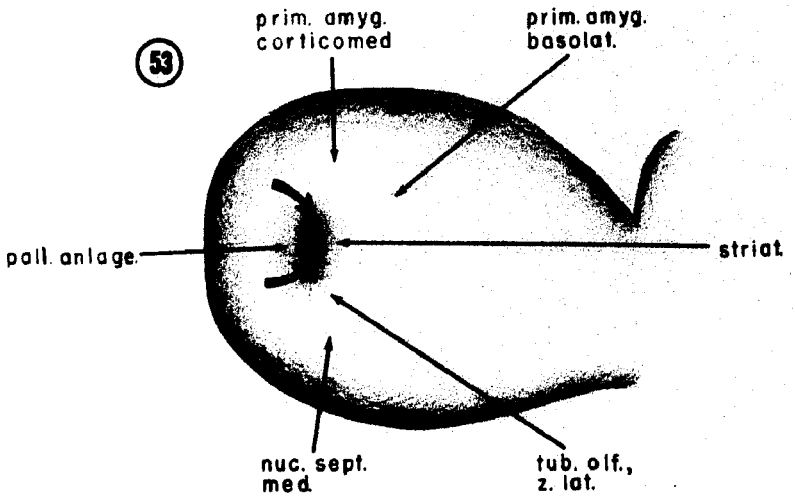
PLATE 26

Explanation of Figures (continued)

Fig. 54. loid nucleus; prim. amyg. basolat.: primordial basolateral amygdaloid nucleus; tub. olf., z. lat.: lateral zone of the tuberculum olfactorium; nuc. sept. med.: medial septal nucleus).


51
striatum
prim. amyg.
corticomed
tub. olf
z. lat
prim. amyg.
basolat.
nuc. sept.
med.


52
prim. amyg.
corticomed
striat.
prim. amyg.
basolat.
tub. olf.,
z. lat.
nuc. sept.
med.


53
prim. amyg.
corticomed
prim. amyg.
basolat.
pall. anlage
striat
nuc. sept.
med.
tub. olf.,
z. lat.

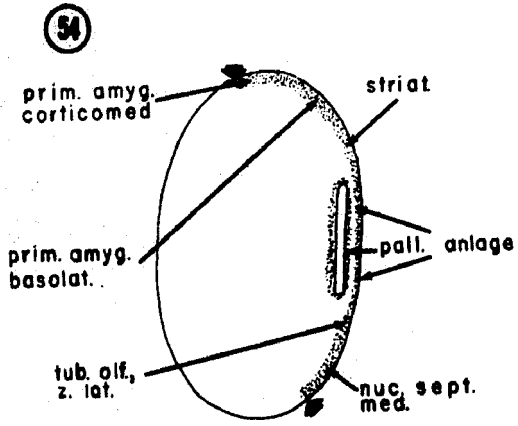

54
prim. amyg.
corticomed
striat
prim. amyg.
basolat.
pall. anlage
tub. olf.,
z. lat.
nuc. sept.
med.

PLATE 27

Explanation of Figures

Fig. 55. Drawing of a medial veiw of a hypothetical teleost telencephalon during the later stages of an evaginative process. The arrows represent the direction of movement of the epithelium into the lateral ventricle. The primordial piriform (prim. pir.) neuroepithelium would migrate ventrocaudally, then rostrodorsally into the ventricle. The primordial general pallial (prim. pall. gen.) and the primordial hippocampal (prim. hi.) and the primordial dentate gyrus (prim. gyr. den.) proliferative sites would migrate caudally, then slightly laterally, and back rostrally into the ventricle. The septal and medial tubercular (septo-tub. anlage) anlage would migrate dorsocaudally, then rostroventrally into the developing lateral ventricle. The remaining proliferative sites, which are established early in development, would continue to form the lateral wall.
(prim. amyg. corticomed: primordial corticomedial amygdaloid nucleus; prim. amyg. basolat: primordial basolateral amygdala; hyperstriat.: hyperstriatum; neostriat: neostriatum; paleostriat. aug.: paleostriatum augmentatum).

Fig. 56. Drawing of a transverse section through the hypothetical evaginating teleost hemisphere illustrated in Figure 55.

PLATE 27

Explanation of Figures (continued)

Fig. 56. The level of the section is just caudal to the interventricular foramen. The lateral wall nuclear sites, i.e., the primordial corticomedial (prim. amyg. corticomed.) and basolateral (prim. amyg. basolat.) amygdaloid nuclei, the hyperstriatum (hyperstriat.), neostriatum (neostriat.), paleostriatum (paleostriat.) and the tuberculum olfactorium (tub. olf., z. lat.), would remain static. The pallial derivatives would continue to migrate into the lateral ventricle to form the dorsomedial, dorsal, and dorsolateral ventricular surfaces. The medial (nuc. sept. med.) and lateral (nuc. sept. lat.) septal nuclei would surface the ventromedial ventricular wall, and the medial tubercular zone (tub. olf., z. med.) would also lie outside of the ventricle at the attachment points of the overlying telencephalic membrane ventrally.

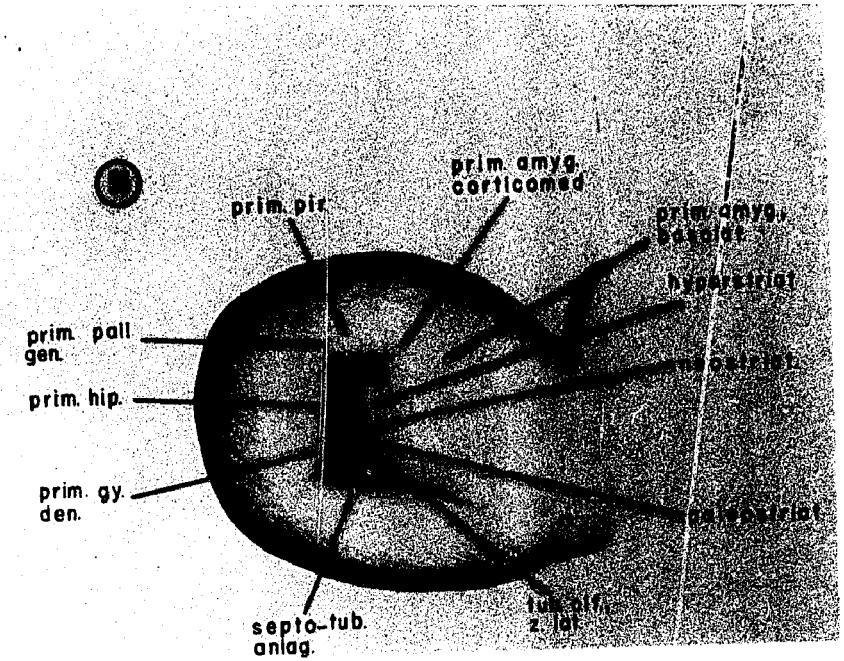
Fig. 57. Drawing of a hypothetical evaginated teleost telencephalic hemisphere after the evaginative process is essentially complete. The medial wall proliferative sites would now all lie on the medial surface of the lateral ventricle (see Figure 58). Only the primordial basolateral amygdala (prim. amyg. basolat.) and the paleostriatum (paleostriat.) would be present in the caudal hemisphere.

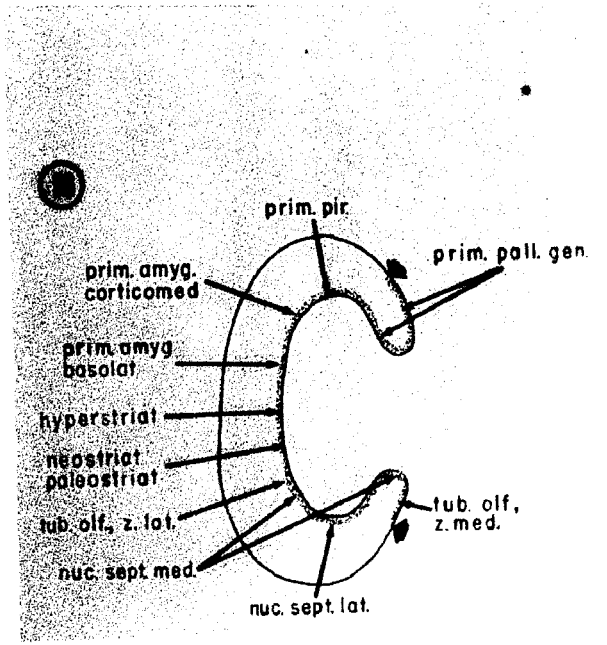
PLATE 27

Explanation of Figures (continued)

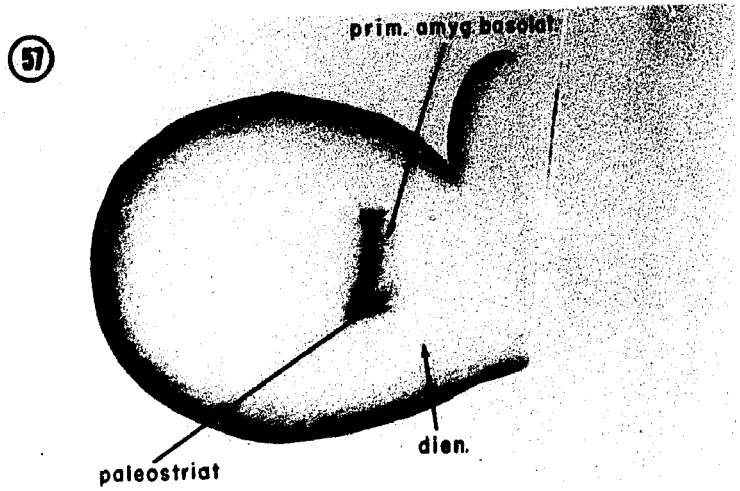
Fig. 57. (dien.: diencephalon)

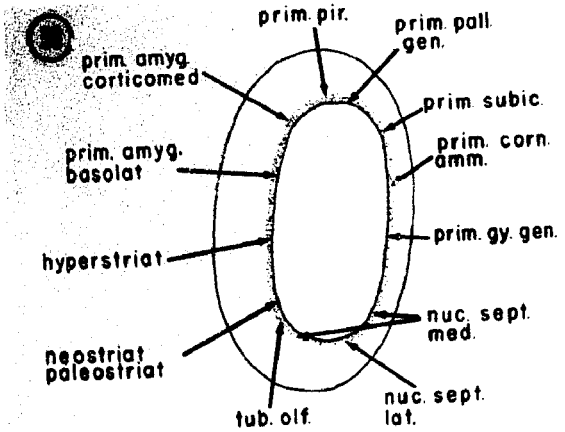
Fig. 58. Drawing of a transverse section through the hypothetical hemisphere depicted in Figure 57. The arrangement of the nuclear areas corresponds to the typical vertebrate configuration described by Crosby, DeJonge and Schneider (1966). The hippocampal formation is situated in the dorsomedial hemisphere, the septal area in the ventromedial part of the hemisphere. The primordial general pallium (prim. pall. gen.) and the primordial piriform cortex (prim. pir.) occupy the dorsal and dorsolateral region of the hemisphere. The primordial corticomedial amygdaloid nucleus (prim. amyg. corticomed.) and the primordial basolateral amygdaloid nucleus (prim. amyg. basolat.) are situated laterally. The hyperstriatum, (hyperstriat.), neostriatum (neostriat.) and paleostriatum (paleostriat.) comprise the remainder of the hemisphere.
(prim. gyr. den.: primordial dentate gyrus; prim. cornu am.: primordial cornu ammonis; prim. subic.: primordial subiculum).


prim. amyg. corticomed
prim. pir.
prim. amyg. basolat.
hyperstriat
prim. pall. gen.
neostriat.
prim. hip.
prim. gy. den.
paleostriat
septo-tub. anlag.
tub. olf. z. lat.


prim. pir.
prim. pall. gen.
prim. amyg. corticomed
prim. amyg. basolat
hyperstriat
neostriat. paleostriat
tub. olf, z. med.
tub. olf., z. lat.
nuc. sept. med.
nuc. sept. lat.

57


prim. amyg. basolat.
paleostriat
dien.


prim. pir.
prim. pall. gen.
prim. amyg. corticomed
prim. subic.
prim. amyg. basolat
prim. corn. amm.
prim. gy. gen.
hyperstriat
nuc. sept. med.
neostriat paleostriat
nuc. sept. lat.
tub. olf.

GRADUATE SCHOOL
UNIVERSITY OF ALABAMA IN BIRMINGHAM
DISSERTATION APPROVAL FORM

Name of Candidate George Cadogan Morgan, Jr.

Major Subject Anatomy

Title of Dissertation

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Dissertation Committee:

W. W. Schnitzlein Chairman

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Date March 2, 1973
25 May 1973