

Olfactory Bulb Projections in the Bichir, *Polypterus*¹

MARK R. BRAFORD, JR. AND R. GLENN NORTH CUTT

Department of Zoology, University of Michigan,
Ann Arbor, Michigan 48104

ABSTRACT The central projections of the olfactory bulb were studied in *Polypterus* using the Nauta and Fink-Heimer techniques. Two major target areas were identified in the subpallium: the lateral subpallial nucleus and the dorsal and ventral entopeduncular nuclei. The connections are predominantly, if not exclusively, ipsilateral. In the pallium a massive ipsilateral projection to the superficial third of the medial pallium was demonstrated while the remainder of the pallium was found to be free of degeneration. Thus it appears that the pallium of *Polypterus* is not uniform throughout, as has been suggested in the literature. This contention is also supported by an analysis of the pallial cytoarchitecture. Because the pallium of *Polypterus* is everted, rather than inverted and evaginated, the topographically medial pallium is in topological correspondence with the lateral pallium of tetrapods. On the basis of this topological correspondence and the similarity of afference from the olfactory bulb, it is argued that the "medial" pallium of *Polypterus* is homologous to the pyriform pallium of tetrapods. The findings of this study are compared to those of similar studies in teleosts, which also have an everted pallium. An apparent conflict appears and suggestions for resolving it are offered.

Polypterus and its close relative, *Calamoichthys*, inhabit the fresh waters of tropical Africa. Their taxonomic position has been much debated in the literature, and they have been variously assigned to the chondrosteian actinopterygians, the crossopterygians, and a higher category of their own, the brachiopterygians. They are generally considered today to be the end representatives of an unknown actinopterygian lineage (Schaeffer, '69) and are placed by most workers in the Chondrostei along with the sturgeons and paddlefishes (Romer, '66; Moy-Thomas, '71).

In *Polypterus*, as well as the other actinopterygian fishes, the adult organization of portions of the telencephalon is achieved by an embryological strategy which is fundamentally different from that found in other vertebrates (fig. 1). In most vertebrates the lateral walls of the embryonic telencephalon undergo an inversion, which is followed by an evagination (Holmgren, '22), but in the actinopterygians the telencephalon is everted (Gage, 1893; Studnicka, 1896; Holmgren, '22; Källén, '50, '51; Nieuwenhuys, '62). In *Polypterus*, after a slight and transitory inversion, the

lateral walls begin to protrude into the ventricles and the lines of attachment of the telencephalic roof plate move laterally and then ventrally (Holmgren, '22; Nieuwenhuys et al., '69). A major consequence of this eversion process is the mediolateral reversal of the dorsal portion of the telencephalon of *Polypterus* relative to its orientation in inverted-evaginated forebrains.

Two features of the everted pallium of *Polypterus* make it an especially favorable choice for comparison with inverted forebrains. First, the eversion in *Polypterus* is a relatively simple one, and it proceeds without the thickening of the walls seen in other actinopterygians. Second, relatively few cells in the pallium of *Polypterus* migrate away from the ependyma in contrast to the situation in other actinopterygians. Consequently, their positions in the adult brain are presumably accurate indications of their sites of origin.

In inverted forebrains the dorsal telencephalon is usually divided into three longitudinal zones: a medial or hippocampal pallium, a dorsal or general pallium, and

¹ A preliminary report of this work appeared in abstract form (Braford, '73).

Abbreviations
(figs. 2-11)

AC, anterior commissure
C, cerebellum
CEN, caudal entopeduncular nucleus
DEN, dorsal entopeduncular nucleus
DSN, dorsal subpallial nucleus
ECL, external cellular layer
GL, glomerular layer
ICL, internal cellular layer
LSN, lateral subpallial nucleus
M, medulla
OB, olfactory bulb
ON, olfactory nerve

OT, optic tectum
Pl, "medial" pallial area
PCN, postcommissural nucleus
PPN, periventricular preoptic nucleus
PV, pseudoventricle
RN, retrobulbar nucleus
SCN, supracommissural nucleus
SOF, secondary olfactory fibers
TEL, telencephalon
VEN, ventral entopeduncular nucleus
VSN, ventral subpallial nucleus

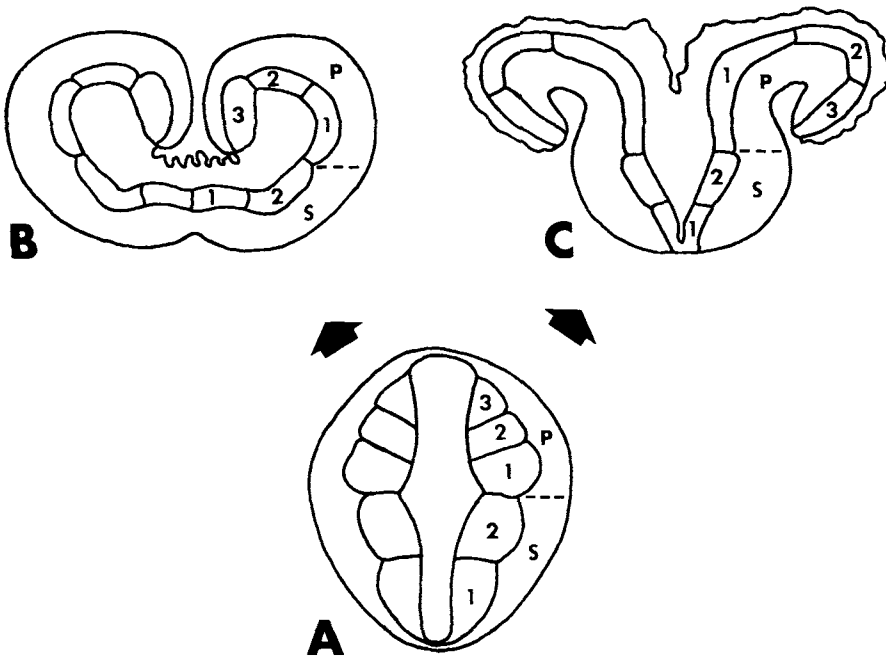


Fig. 1 Schematic representations of the way in which the topology of the fundamental subdivisions of the embryonic telencephalon (A) might be preserved following inversion in land vertebrates (B) and eversion in *Polypterus* (C). S1, septal region; S2, striatum; P1, pyriform pallium; P2, general pallium; P3, hippocampal pallium.

a lateral or pyriform² pallium. The everted pallium of *Polypterus* has been interpreted in three different ways in the literature. Holmgren ('22) identified three longitudinal zones and suggested that the medial one corresponded to the lateral or pyriform pallium of inverted forebrains, the dorsal one to the dorsal or general pallium, and the lateral one to the medial or hippocampal pallium. Wright ('67), apparently denying an eversion process in *Polypterus*, called the medial area hippocampal, the dorsal area general, and the

lateral area pyriform and amygdalar. Nieuwenhuys ('60, '63, '67) concluded that the pallium of *Polypterus* was uniform throughout and that the entire pallium was in receipt of fibers from the olfactory bulb. These three divergent views are based on studies of normal embryonic and/or adult material. Experimental studies in a variety of species with inverted

² The lateral part of the pallium is usually termed pyriform in amphibians and reptiles and prepyriform in birds and mammals. In this paper, for simplicity, we will refer to this area as pyriform in all vertebrates.

forebrains have demonstrated the primary pallial target of secondary olfactory fibers to be the lateral or pyriform area.³ Given these results, the possibility arises of identifying the pyriform area in the everted pallium of *Polypterus* by tracing degenerating fibers from lesions of the olfactory bulb. From Holmgren's analysis one would predict that these fibers project to the medial portion of the pallium. Wright's work would indicate that they connect with the lateral pallium, while that of Nieuwenhuys would suggest that they distribute to the entire pallium.

MATERIALS AND METHODS

Five specimens of *Polypterus palmas* Ayres 1850 and two specimens of *Polypterus ornatipinnis* Boulenger 1902 were subjected to unilateral aspiration lesions of the olfactory bulbs under MS-222 anesthesia. Following postoperative survival times ranging from 5 to 29 days at 27°C, the animals were sacrificed under MS-222 anesthesia by transcardial perfusion with 10% formalin. The brains were removed, fixed in 10% formalin for at least one week, and embedded in 25% gelatin. Frozen sections were cut at 25 μ , stored in 2% formalin in the refrigerator, and processed by several modifications of the

Nauta (Ebbesson, '70) and Fink-Heimer (Fink and Heimer, '67) procedures for the demonstration of degenerating axoplasm. Appropriate sections were drawn with the aid of a Bausch and Lomb microprojector, and the degeneration was plotted on these drawings. Cresyl violet and Bodian stained material of *P. palmas* and *Calamoichthys calabaricus* Smith 1865 and Golgi-Cox material of *P. palmas* were used to study the normal anatomy of the olfactory bulbs and telencephalon. Selected sections in a cresyl violet series of *P. palmas* were photographed on Kodalith Ortho film, type 3, with a Leitz large-format camera (figs. 3-9).

RESULTS

Normal anatomy

A dorsal view of the brain of *P. palmas* is shown in figure 2 with arrows indicating the levels of the transverse sections shown in figures 3-9. The nomenclature used in the the following descriptions is taken from Nieuwenhuys and Bodenheimer ('66) and Nieuwenhuys ('67) unless otherwise indicated.

³ For elasmobranchs see Ebbesson and Heimer ('70); for amphibians: Scalia et al. ('68), Royce and Northcutt ('69); for reptiles: Heimer ('69), Scalia et al. ('69), Northcutt ('70), Halpern ('73); for birds: Rieke and Wenzel ('73); for mammals: Scalia's review ('70).

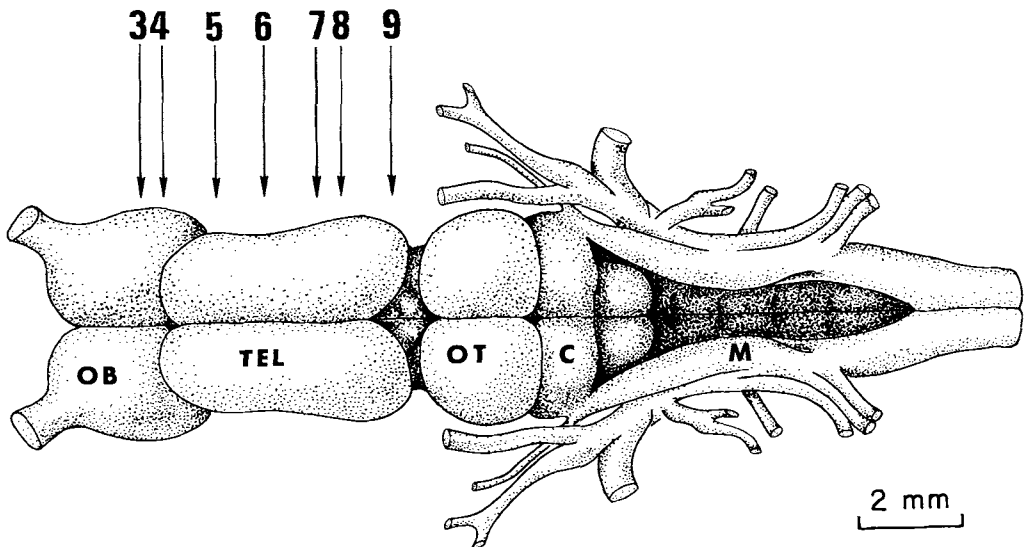


Fig. 2 Dorsal view of the brain of *Polypterus palmas*. Numbered arrows indicate the levels of the transverse sections in figures 3-9.

Olfactory bulbs. As is typical for vertebrates, the olfactory bulbs are formed by evaginations of the telencephalic walls. The bulbs display a pattern of concentric laminae in the following centripetal order: (1) olfactory nerve fibers, (2) glomerular layer, (3) external cellular layer, (4) layer of secondary olfactory fibers, (5) internal cellular layer, and (6) ependyma (figs. 3-5). The large mitral cells are scattered in the inner portion of the external cellular layer and the outer portion of the sec-

ondary olfactory fiber layer. As Nieuwenhuys ('63) has pointed out, the extreme mediocaudal portion of the evaginated part of the telencephalon is devoid of glomeruli and thus should not be considered a part of the olfactory bulb. Holmgren and Nieuwenhuys have both regarded this area as part of the septum and have variously designated a cell mass in this region as nucleus olfactorius anterior pars precommissuralis (Holmgren, '22) or nucleus septi (Nieuwenhuys et al., '69). We

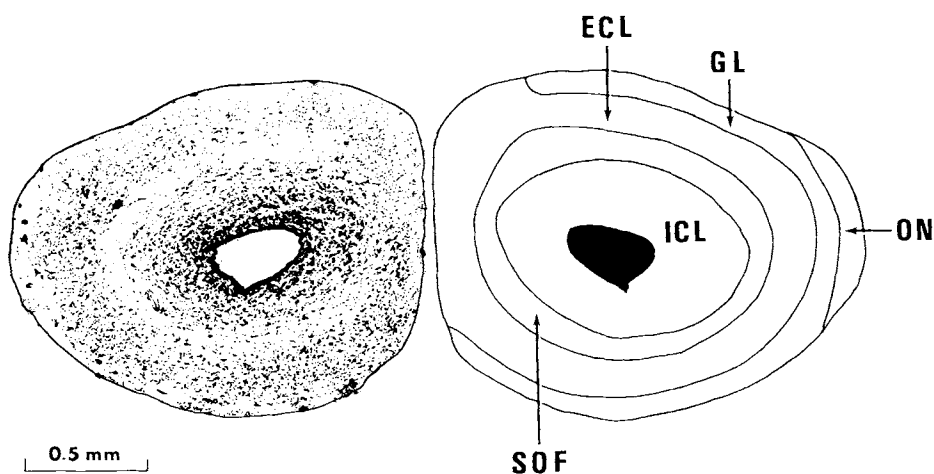


Fig. 3 Transverse section through the olfactory bulb. In this and the following six figures the left side is a high contrast photograph of a section stained with cresyl violet. On the right the major cell groups are indicated and the distribution of degenerating particles following olfactory bulb removal is shown with stippling.

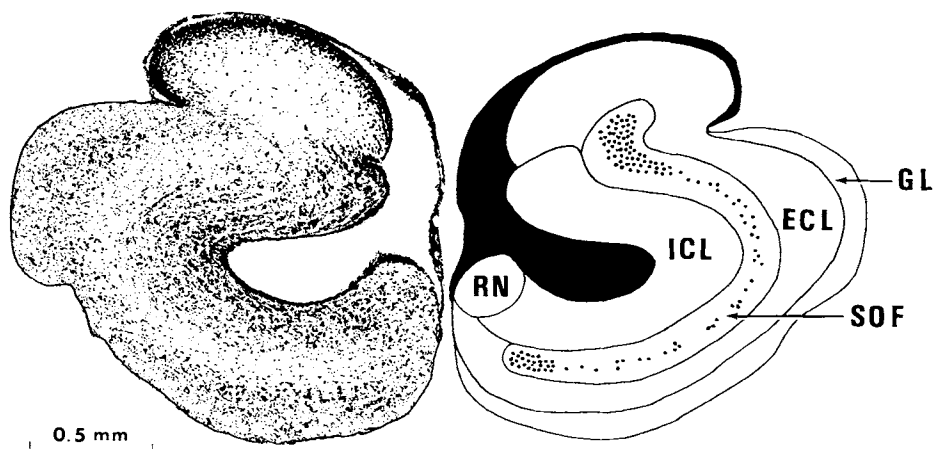


Fig. 4 Transverse section through the caudal part of the olfactory bulb formation and the rostral part of the telencephalon.

have identified the same group of cells (fig. 4) but for the present prefer the neutral name, retrobulbar nucleus.

Subpallium. On the basis of cytoarchitectural observations in embryonic and adult material, the telencephalon proper can be divided into a dorsal pallium and a ventral subpallium (Holmgren, '22; Nieuwenhuys et al., '69).

At rostral levels of the subpallium three cell groups are present: the dorsal and ventral subpallial nuclei in a periventricular position and the lateral subpallial nucleus in a migrated position (figs. 5, 6). The dorsal subpallial nucleus is subjacent to the pallium and forms a crescent of deeply-staining cell clusters. Caudally, its dorsolateral aspect is differentially characterized by the presence of transversely oriented fibers. At the level of the anterior commissure, the dorsal subpallial nucleus appears to be caudally continuous with the supracommissural nucleus (fig. 7), which, in turn, grades into the postcommissural nucleus farther caudally (figs. 8, 9). The ventral subpallial nucleus lies beneath the dorsal nucleus and extends from the retrobulbar nucleus rostrally to the anterior commissure caudally. The lateral subpal-

lial nucleus appears slightly behind the caudalmost part of the olfactory bulb formation as a cigar-shaped group on the lateral surface of the brain. As it is followed caudally, its shape becomes more elliptical and its cells more scattered (fig. 7). It disappears at about the level of the anterior commissure. At levels caudal to this commissure the preoptic recess of the third ventricle appears ventrally in the midline and is surrounded by cells of nucleus preopticus periventricularis (figs. 7-9). This nucleus adjoins the postcommissural nucleus dorsally, forming a continuous periventricular band of cells. In a migrated position in the caudal subpallium a complex of three "entopeduncular" nuclei are seen (figs. 8-9). The dorsal and ventral entopeduncular nuclei are cytologically similar and are composed of small cells. The caudal entopeduncular nucleus contains somewhat larger cells and extends into the thalamus.

Pallium. The eversion of the dorsal telencephalon results in a large ependymal surface which is overlain by a greatly expanded telachoroidea. The caudal pallium has undergone an invagination (Nieuwenhuys et al., '69), producing an extracere-

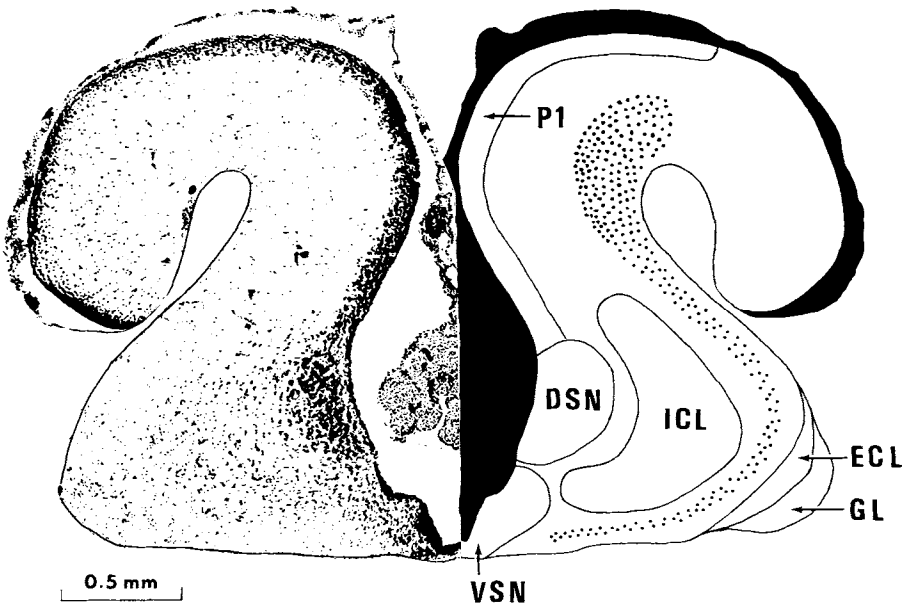


Fig. 5 Transverse section through the caudal extreme of the olfactory bulb formation and the rostral third of the telencephalon.

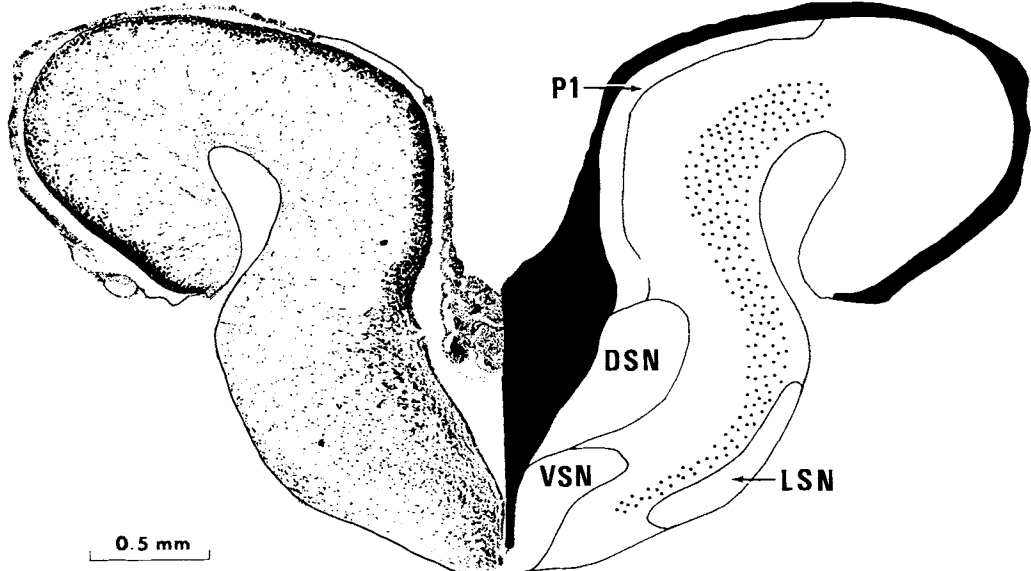


Fig. 6 Transverse section through the mid-telencephalon.

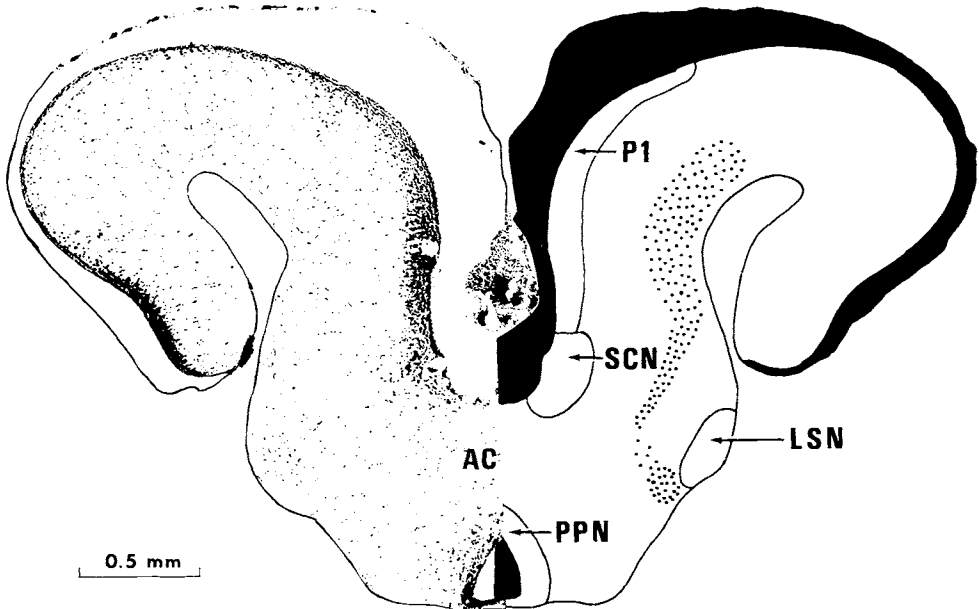


Fig. 7 Transverse section through the level of the anterior commissure.

bral space partially surrounded by brain tissue, which has been termed a pseudo-ventricle (fig. 9).
In the pallium the vast majority of cell bodies are unmigrated and form a thin

sheet against the ependyma. Certain regional differences in the staining properties and the thickness of this pallial sheet are apparent (fig. 10). In Bodian preparations counterstained with cresyl violet the

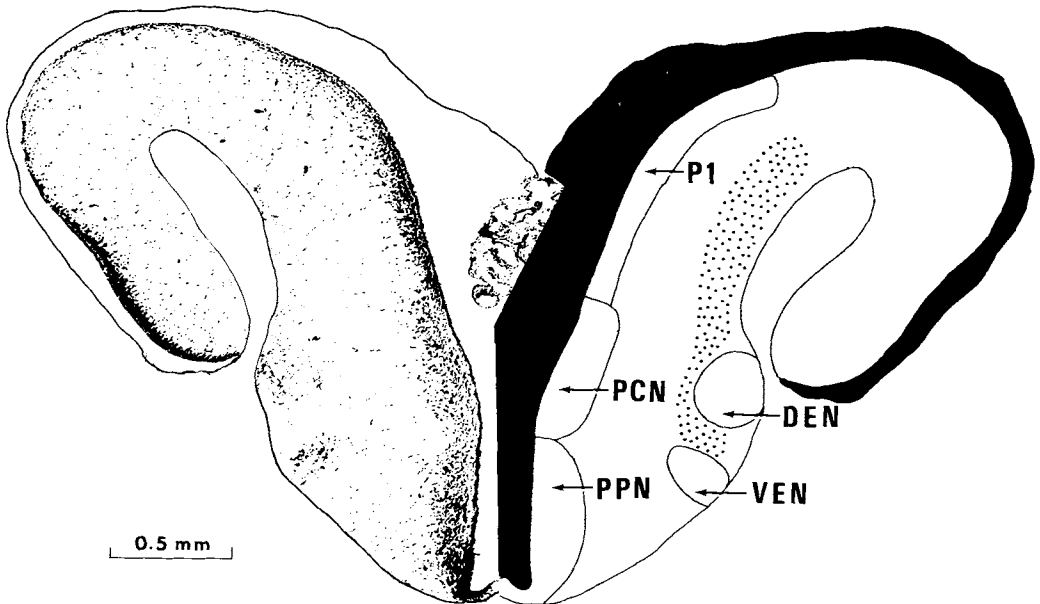


Fig. 8 Transverse section through the caudal telencephalon.

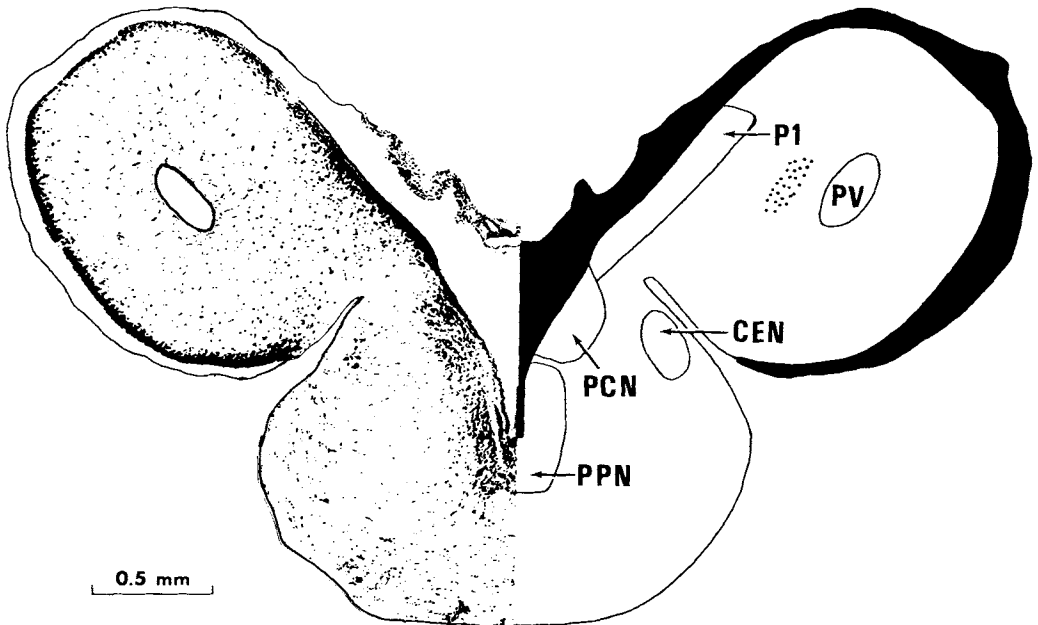


Fig. 9 Transverse section through the caudal pole of the telencephalon at the level of the pseudoventricle.

cells of the medial and lateral portions of the pallium are more intensely stained than those of the intercalated dorsal portion. Furthermore, in the medial and lat-

eral areas the sheet is four to five cells thick, while in the dorsal area it is one or two cells thick (fig. 10A-C). The transitions between these longitudinal zones

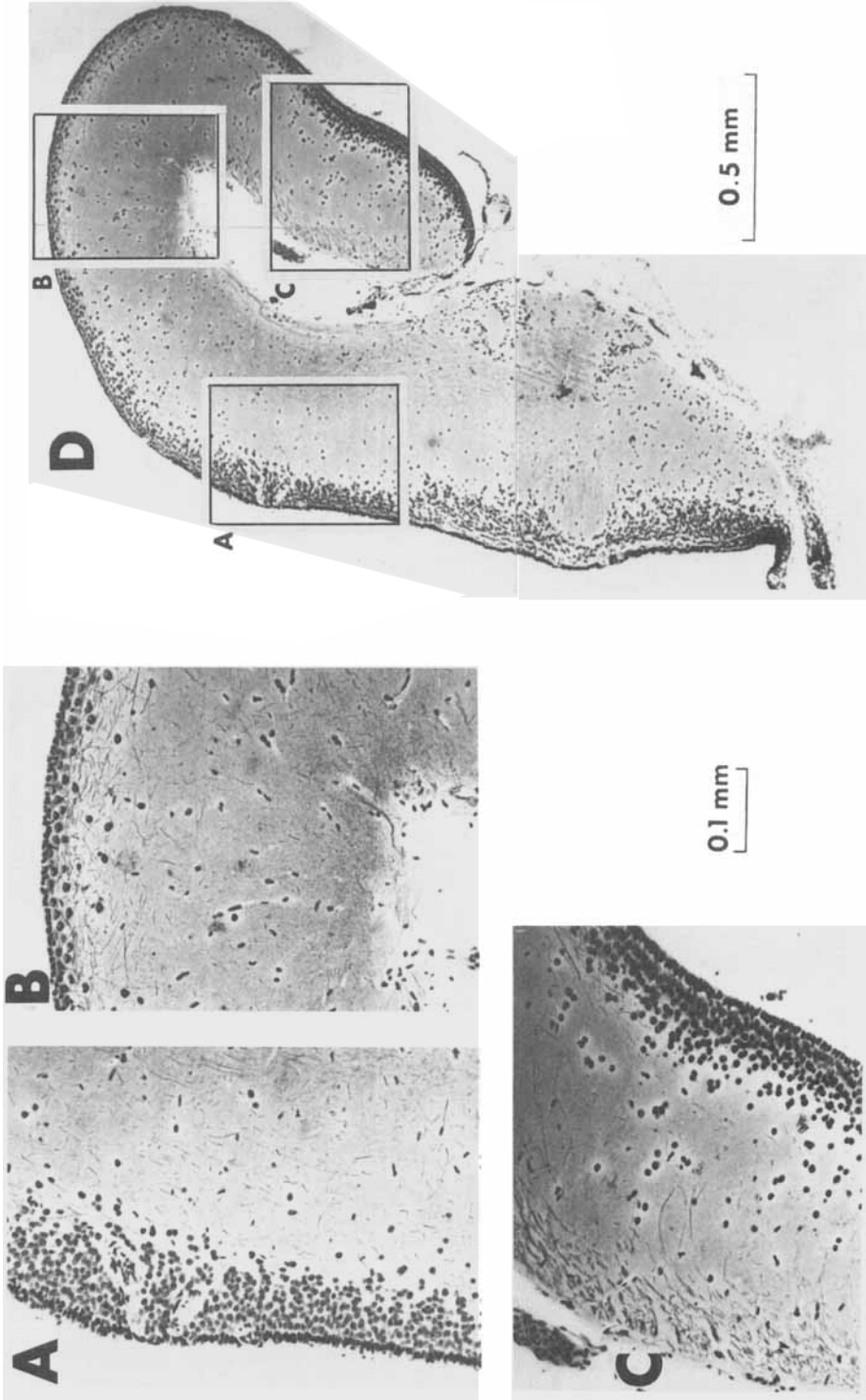


Fig. 10 Photomicrographs of a transverse section at the level of figure 8 showing differential thickness of the pallial sheet in three areas. Bodian material counterstained with cresyl violet.

are usually gradual rather than sharp, and they are more apparent at some rostro-caudal levels than at others. Divisions are especially difficult to make in the rostral pole of the pallium where no thinner area is present dorsally. Golgi-Cox preparations indicate that the cells in the pallial sheet are characterized by multiple apical dendrites which radiate toward the meningeal surface and axons which usually issue from the cell bodies. In addition to the cells which form the pallial sheet against the ependyma, a small number of migrated cells are present. These are more numerous in the lateral area than elsewhere in the pallium.

Experimental results

In the animal with the shortest survival time, five days, there was little evidence of degeneration. At survival times of 10 and 15 days the argyrophilia of the degenerating axoplasm was maximal, decreasing progressively with longer times. The degeneration appeared as very fine particles. The sort of argyrophilic pattern which is usually interpreted as degenerating fibers was not generally apparent, even after a survival time of 29 days. Although two species of *Polypterus* were used in this study, no differences between them were noted at our level of analysis. The following description of the experimental results is based on case PP-OB-2. This specimen of *P. palmas* sustained a pure, unilateral lesion of the olfactory bulb which spared only its most caudal portion. This animal survived 16 days postoperatively and displayed what appears to be the total projection pattern of the olfactory bulb.

In the caudal bulb degenerating fibers are seen collecting at the dorsal and ventromedial extremes of the secondary olfactory fiber layer (fig. 4). These fibers leave the bulb to form the lateral and medial olfactory tracts, respectively. These names do not necessarily imply a homology with the various lateral and medial olfactory tracts of other vertebrates. A clear separation of the two tracts is difficult to make at mid-telencephalic levels, and ours is a somewhat arbitrary one made in order to simplify the description of the results.

The medial olfactory tract lies in a

superficial position in the ventrolateral subpallium. Rostrally it approaches but does not reach the ventral subpallial nucleus (fig. 5). At more caudal levels it is medially adjacent to the lateral subpallial nucleus (figs. 6, 11A). Degeneration is found ventromedial to this nucleus at the level of the anterior commissure (fig. 7). The retrobulbar nucleus and its immediate vicinity are free of degeneration.

The lateral olfactory tract projects to a region between the dorsal and ventral entopenduncular nuclei and to a region medial to the dorsal entopenduncular nucleus in the caudal subpallium (figs. 8, 11B). Its major projection, however, is a massive one to a restricted portion of the pallium. Rostrally, the degeneration occupies the superficial third of the medial pallium, sparing a thin submeningeal strip occupied by tractus pallii. Caudally, the band of degeneration narrows slightly (figs. 8, 11C,D) and diminishes both in density and dorsoventral extent as the caudal pole of the pallium is approached (fig. 9). This area of the medial pallium which receives the olfactory projection corresponds remarkably well with the medial area identified on the basis of cytoarchitectural observations (fig. 11C). The absence of the thinner dorsal portion of the pallial sheet at more rostral levels makes the correspondence there more difficult to determine.

The degeneration patterns described above are all ipsilateral to the lesion in the olfactory bulb. A sparse but consistently present patch of argyrophilic material was found between the dorsal and ventral entopenduncular nuclei on the contralateral side. However, no degenerating fibers were seen crossing the midline in either the anterior or habenular commissures, nor were degenerating fibers observed to the contralateral olfactory bulb. There was a consistently present fine-grain deposit in the glomerular layer of the contralateral olfactory bulb and the intact portions of the ipsilateral bulb. This was interpreted as artefact (Heimer, '70). No degenerating particles were seen pericellularly or within the boundaries of any nuclear group as defined on the basis of the distribution of cell bodies in cresyl violet material.

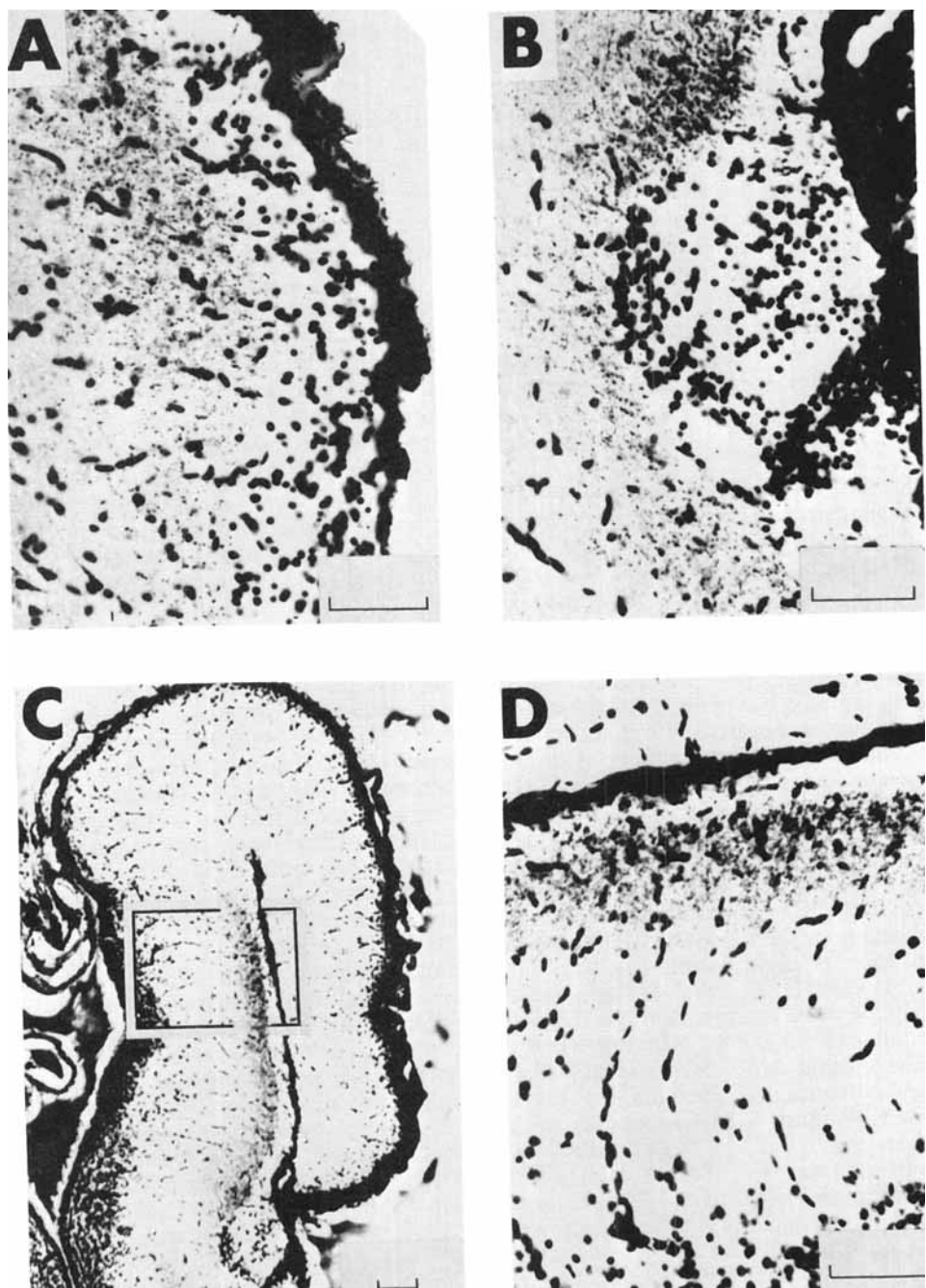


Fig. 11 Photomicrographs showing some details of the distribution of degenerating particles following olfactory bulb removal. A: lateral subpallial nucleus; B: dorsal entopeduncular nucleus; C: pallium, showing the correspondence between the extent of the olfactory projection and the extent of area P1; D: higher power view of part of pallial degeneration in C. Dorsal is to the left in this photograph. Bar scales: 0.1 mm.

DISCUSSION

Limitations

Several factors limit the precision with which we can identify the subpallial targets of the secondary olfactory fibers. First, the uniformly fine nature of the degenerating particles makes it difficult to clearly distinguish between degenerating fibers and terminals. In addition, no degeneration appears within the confines of a nuclear group, suggesting that terminations are axo-dendritic, or possibly axo-axonic, but not axo-somatic. The interpretation of this neuropil is further complicated by observations of Golgi-Cox material which indicate that dendrites of cells in several of the subpallial nuclei extend into the path of the degenerating olfactory bulb efferents. The interpretations we make below as to probable subpallial targets are based on the density and proximity of degenerating particles in relation to various cell groups. Electron microscopy may be useful in further elucidating these relationships.

Subpallium

Two areas in the subpallium which are most probably in receipt of secondary olfactory fibers are the lateral subpallial nucleus and the dorsal and ventral entopeduncular nuclei. Dense concentrations of degenerating particles are seen adjacent to the medial boundary of the lateral subpallial nucleus and in the space between the dorsal and ventral entopeduncular nuclei (fig. 11A,B). In addition, the ventral subpallial nucleus is approached by the medial olfactory tract and the degeneration here is coincident with portions of the dendritic ramifications of cells in this nucleus.

In the developing brain of *Polypterus* the lateral subpallial nucleus migrates from the matrix layer of the subpallium to a superficial position lateral to the dorsal and ventral subpallial nuclei (Nieuwenhuys et al., '69). On the basis of their topological positions alone, the dorsal and ventral subpallial nuclei may be provisionally interpreted as striatum and lateral septum, respectively. The lateral subpallial nucleus has been variously interpreted in the literature as part of nucleus

olfactorius lateralis (Holmgren, '22) and as the olfactory tubercle (Wright, '67). Nieuwenhuys ('67, '69) noted that it corresponds in topological position to the cortex tuberculi olfactorii of Chondrichthyes and suggested that, in addition, it may comprise the homolog of nucleus medialis septi. In terms of its migrated position and its olfactory afference the lateral subpallial nucleus might reasonably be compared to the medial septum and/or the olfactory tubercle.

The dorsal and ventral entopeduncular nuclei originate embryologically from the most dorsal part of the caudal subpallium and attain their final position by a rostro-ventral migration (Nieuwenhuys et al., '69). These cells have been termed nucleus taeniae (Holmgren, '22), part of the lateral preoptic area (Wright, '67), and the equivalent of the entopeduncular nucleus of Frontera in *Rana* (Nieuwenhuys, '66). Another possible interpretation, in view of their olfactory input, is that they represent part of the amygdalar complex.

The ventral subpallial nucleus has been interpreted as equivalent to the lateral septal nucleus by both Holmgren and Nieuwenhuys and as part of the medial septum by Wright. On the basis of information available at present even we are reluctant to speculate further about the nature of this cell group.

Pallium

A major finding of this study is a massive projection from the olfactory bulb to a restricted portion of the pallium. We have previously outlined three interpretations of the pallium of *Polypterus* from the literature. Our results are in agreement with Holmgren's analysis. Although Nieuwenhuys ('63) noted that the dorsal part of the pallial sheet is somewhat thinner than the lateral and medial parts, he considered this to be a purely mechanical effect of the local recurvature of the wall and was thus unable to support Holmgren's interpretation. Without denying that the differential thickness may be produced in this way, we suggest that these differences have additional significance as form-function relations. Of particular significance is the correspondence between the thicker medial pallial area and the pal-

lial projection from the olfactory bulb (fig. 11C). That the olfactory projection is confined to one portion of the pallium clearly demonstrates that the pallium of *Polypterus* is not uniform throughout. On the basis of these findings we have designated the medial, olfactory pallium of *Polypterus* as pallial area 1 (P1). Cytoarchitectonic observations suggest that the remainder of the pallium contains at least two cell populations. Additional experimental studies will be required to characterize these pallial areas.

Comparison with inverted forebrains

Although some investigators have reported olfactory bulb projections to the rostral part of the dorsal and/or medial pallia, the major pallial target of secondary olfactory fibers in all inverted forebrains is the lateral or pyriform pallium. It is apparent from the studies of Holmgren ('22) and Nieuwenhuys et al. ('69) that the position of area P1 in the everted pallium of *Polypterus* is topologically equivalent to that of the lateral or pyriform pallium of inverted forebrains (fig. 1). The massive olfactory projection to area P1, taken together with this topological correspondence, constitutes strong evidence that area P1 and the pyriform pallium of tetrapods are homologous. The determination of homologies in the nervous system, as elsewhere, must be based on the minuteness of the resemblance and the multiplicity of the similarities (Simpson, '61). Thus information on the efferent connections and the histochemical properties of area P1 will be important in evaluating the validity of the suggested homology.

Comparison with teleost forebrains

The only previously published experimental study of olfactory bulb projections in an actinopterygian is that of Scalia and Ebbesson ('71) in the moray eel, *Gymnothorax funebris* — a teleost. These workers reported bilateral projections to three areas in the telencephalon: the ventral precommissural part of the ventromedial area, a portion of the posterior lobe, and the ventrolateral pallium. In addition, they found a connection to the contralateral olfactory bulb. All of the decussating fibers crossed in the anterior commissure. Finger (un-

published thesis, '73) has found similar, but not identical, results in an experimental study of the olfactory bulb projections in another teleost, the bullhead catfish, *Ictalurus nebulosus*. In addition to the connections reported by Scalia and Ebbesson, he identified a terminal field in the hypothalamus. Also, in *Ictalurus* the decussating fibers were seen to cross via the interbulbar commissure of Goldstein, the habenular commissure, and the anterior commissure. In *Polypterus* only questionable contralateral degeneration was seen and a pathway of decussation was not apparent in our material.

Scalia and Ebbesson tentatively suggested that the terminal fields in the ventromedial area, the posterior lobe, and the ventrolateral pallium might correspond, respectively, to the olfactory tubercle, the amygdala, and the pyriform cortex of tetrapods. They may also correspond, respectively, to the lateral subpallial nucleus, the dorsal and ventral entopenduncular nuclei, and area P1 of *Polypterus*. In view of the tentative nature of our determination of subpallial olfactory targets in *Polypterus*, these comparisons remain very speculative. The reports of a projection to the ventrolateral part of the teleost pallium in contrast to our finding of a projection to the dorsomedial part of the pallium of *Polypterus* require further comment.

If the teleost telencephalon were formed by a simple eversion process, the following sequence of areas might be expected along the ependymal surface: subpallium, pyriform pallium, dorsal pallium, hippocampal pallium (fig. 1). In *Gymnothorax* and *Ictalurus* the olfactory bulb would appear then to project to the hippocampal rather than the pyriform pallium. Scalia and Ebbesson suggested that the ventrobasal position of the olfactory pallium in both teleosts with everted forebrains and other vertebrates with inverted forebrains is dependent on the specification of developing olfactory areas in vertebrates by reference to extracerebral structures. However, in *Polypterus* the olfactory pallium is not ventrobasal in position. Therefore, we offer some alternatives to Scalia and Ebbesson's suggestion, which do not invoke extracerebral features as determi-

nants of olfactory connections and which at the same time may reconcile the apparent conflict within the actinopterygians.

While it is clear that the olfactory tract in teleosts projects to the *topographically* ventrolateral part of the pallium, it is not clear that this part of the pallium is *topologically* ventrolateral. The apparently aberrant projection of the olfactory bulb to the hippocampal pallium in teleosts may not be aberrant at all, for that pallium may not be hippocampal. With the assumption that the major efferent connection of the olfactory bulb has not changed its pallial target within the actinopterygian radiation, we are led to one or more of the following conclusions: (1) the eversion of the pallium in teleosts is not a simple one and is accompanied by more complicated morphogenetic movements; (2) the migrations of cell populations within the developing teleost pallium obscure their sites of origin from the germinal matrix; and (3) during later stages of development differential proliferations of certain cell populations result in changes in their relative topographical positions. The three processes are not mutually exclusive and may all contribute to the formation of the pallium in teleosts.

In his attempts to compare the telencephala of *Cyprinus carpio* and other teleosts with those of amphibians and reptiles, Sheldon ('12) seems to have come to a similar conclusion. He stated that the eversion of the telencephalon of teleosts is not "a simple bending of the whole wall. . . , but rather a gradual plastic movement of material." His schematic diagrams of transverse sections through the developing brain of *Ictalurus* (= *Ameiurus*) clearly shows changes in the relative topographical positions of certain cell populations.

Several lines of further investigation can be expected to shed light on this problem. First, more information is needed on the development of the telencephalon of teleosts with particular reference to the pattern of cell migrations and subsequent proliferations. Further insight may be gained through comparative chemoarchitectonic studies of the actinopterygian telencephalon, experimental studies of other fiber systems in the actinopterygian fore-

brain, and experimentally determined olfactory connections in other chondrosteans and holosteans, which are in some ways intermediate between *Polypterus* and the teleosts.

ACKNOWLEDGMENTS

We thank Dr. Ann B. Butler for her helpful criticisms of the manuscript and Mr. Louis Martonyi for his expert assistance with the photography. This work was supported by NIH Fellowship (7 F11 NS 2560) to MRB and NIH (5 RO1 NS 11006) and NSF (GB-40134) Research grants to RGN.

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