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Organization of the Telencephalon in the Channel Catfish, *Ictalurus punctatus*

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ABSTRACT The cytoarchitectonics of the telencephalon of the channel catfish, *Ictalurus punctatus,* are described as a basis for experimental analysis of telencephalic afferents and efferents. The olfactory bulb comprises: (1) an outer layer of olfactory nerve fibers, (2) a glomerular layer, (3) an external cell layer, (4) an inner fiber layer, and (5) an internal cell layer. The telencephalic hemispheres comprise the areas ventralis and dorsalis telencephali. The area ventralis consists of: (1) a precommissural, periventricular zone including nucleus 'nother (Vn), the ventral nucleus (Vv), and the dorsal nucleus (Vd); (2) a precommissural, migrated zone of central (Vc) and lateral (Vl) nuclei; (3) a supracommissural nucleus (Vs); (4) a caudal commissural zone of postcommissural (Vp) and intermediate (Vi) nuclei; and (5) a preoptic area (PP). The area dorsalis comprises: (1) medial (DM), (2) dorsal (Dd), (3) lateral [DL, containing dorsal (DLd), ventral (DLv), and posterior (DLp) regions], (4) posterior (DP), and (5) central (DC-1, -2, -3) areas. Nucleus taeniae (NT) is transitional between areas dorsalis and ventralis.

The embryonic neural tube of all vertebrates consists of paired side plates of presumptive neural tissue, flanked dorsally by a thin roof plate, the lamina supraneuroporica, and ventrally by a somewhat thinner floor plate, the lamina terminalis (Nieuwenhuys, '65). Telencephalic morphogenesis is characterized by (a) an inversion or in-pocketing of the side-plates followed by an evagination, or (b) an eversion of the dorsal roof of the thickened side plates (Källén, '51a; Nieuwenhuys, '62a). Whereas process "a" occurs among lungfish and land vertebrates, process "b" characterizes actinopterygians (ray-finned fishes). The only extant crossopterygian, *Latimeria,* reveals an intermediate condition (Nieuwenhuys, '65).

The eversion process of actinopterygians results in a lateral expansion of the thin roof plate, forming a dorsal tela chorioidea enclosing a median T-shaped ventricle. The underlying side plates form the cerebral hemispheres. Among actinopterygians, the eversion process ranges from slight to extreme. Varying degrees of eversion, as well as differential hypertrophy of the hemispheric walls, produces a wide variety of organizational patterns. Among polypteriforms (bichirs and reedfish), eversion is extreme, while hemispheric thickening is minimal (Holmgren, '22; Nieuwenhuys, '63; Braford and Northcutt, '74). In contrast, eversion is slight among chondrosteans (sturgeons and paddlefish), but these show increased hypertrophy of the telencephalic walls (Johnston, '11; Nieuwenhuys, '63; Northcutt and Braford, '80). Similarly, holosteans show hemispheric hypertrophy, and slight eversion, as do gars (Northcutt and Braford, '80), or moderate eversion, as do bowfins (Nieuwenhuys, '63). The 20–30,000 species of teleosts present a vast diversity of forms. Eversion ranges from slight (salmonids, Nieuwenhuys, '63; Northcutt and Braford, '80) to extreme (osteoglossiforms, Weston, '37; Meader, '39; Nieuwenhuys, '63). Similarly, differentiation of the hemispheric walls ranges from moderate (salmonids) to extreme (osteoglossiforms).

Few experimental studies of the telencephalon of teleosts document the origin or termination of afferents or efferents in the context of detailed cytoarchitectural criteria. The available analyses comprise three degeneration studies of secondary olfactory pathways (Scalia and Ebbesson, '71; Ito, '73; Finger, '75), a degeneration study of telencephalic efferents (Vanegas and Ebbesson, '76), and HRP studies of the origin of telencephalic–tectal and dien-

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cephalic–telencephalic pathways (Ito and Kishida, '77, '78). The studies of Vanegas and Ebbesson ('76) and Ito and Kishida ('78) are not concerned with connections of specific telencephalic regions and do not allow recognition of functional subdivisions of the telencephalon. The remaining studies lack uniformity in nomenclature or in the number of recognized telencephalic subdivisions. Excepting for the study of Scalia and Ebbesson ('71), they lack detailed photographs of Nissl sections through the telencephalon, thus hindering attempts to correlate the location and extent of secondary olfactory targets (Ito, '73; Finger, '75) or HRP-labeled cells (Ito and Kishida, '77) with the telencephalic regions detailed in cytoarchitectonic studies (Sheldon, '12; Nieuwenhuys, '63; Northcutt and Braford, '80).

This study documents the organization of the telencephalon of the channel catfish, *Ictalurus punctatus,* and is the basis for the demonstration of the specific origin and termination of telencephalic pathways (Bass, '80a,b). This analysis facilitates comparisons with other actinopterygians, indeed other vertebrates, and the integration of future experimental data into a recognized cytoarchitectural framework.

MATERIALS AND METHODS

Six adult (28- to 35-cm, snout–tail length) channel catfish, *Ictalurus punctatus,* were collected at Spring Valley Trout Farm, Dexter, Michigan. For cytoarchitectural analysis (nonexperimental material) animals were perfused transcardially with 0.7% saline followed by AFA (90 ml of 80% ethanol, 5 ml of glacial acetic acid, 5 ml of Formalin). Following removal from the skull, all brains were fixed for at least 1 week and were subsequently embedded in paraffin. Brains were sectioned on a rotary microtome at 15 μm in transverse, horizontal, or sagittal planes and were stained with cresyl violet to reveal the cell bodies. One transverse series was prepared according to the Klüvér–Barrera method to reveal both cell bodies and myelinated fibers. The brains of two adults and two juveniles were removed from the skull without prior perfusion and treated with the Golgi–Cox procedure of Ramón–Moliner ('58). The Golgi material was embedded in celloidin and cut in the transverse plane at 50 or 75 μm.

RESULTS

Nomenclature

Here I use the nomenclature of Nieuwenhuys [('63) which see for a table of synonyms for previous terminologies], as modified by Northcutt and Braford ('80), for the following reasons: (1) The nomenclature is based on topographical position of cell groups and infers no homologies to telencephalic subdivisions as recognized in land vertebrates. (2) These studies represent a broad survey of telencephalic organization among a wide range of actinopterygians. (3) This nomenclature forms a foundation for the interpretation of embryological (Nieuwenhuys, '62a,b), histochemical, and degeneration (Northcutt and Braford, '80) studies in a series of actinopterygians.

Overview

Figure 1A is a dorsal view of the brain of *Ictalurus punctatus,* and indicates the levels of the transverse sections illustrated in Figures 3 and 6–10. Figure 2 shows a parasaggital section and illustrates the cell groups along the medial aspect of the telencephalon.

The telencephalon consists of the pedunculated olfactory bulbs, the paired hemispheres, and the telencephalon medium, which contains the anterior commissure and the preoptic area (Figs. 1A, 2). The paired hemispheres flank a median T-shaped ventricular space covered dorsolaterally by the tela chorioidea, which attaches to the telencephalon along the ventrolateral surface (Figs. 6–10). The meninges extend from the tela along the ventral surface of the brain.

Olfactory bulb

In catfish, as in several other teleosts (e.g., Cypriniformes, Osteoglossiformes, Mormyriformes, Anacanthidae), the olfactory bulbs extend away from the telencephalon, thus increasing the length of the olfactory peduncles or tracts. The pedunculated bulbs lie closely apposed to the peripheral olfactory epithelium (Fig. 1). The epithelium's neurosensory cells are connected to the olfactory bulb via short medial and lateral olfactory nerves; both bundles cross repeatedly as they enter the bulb.

In polypterids, holosteans, chondrosteans, and some teleosts (e.g., *Salmo* and *Anguilla*), the olfactory bulb arises as a rostral evagination of the telencephalon and encloses a central ventricle. Among most teleosts the bulb develops as a rostroventral thickening of the hemisphere (Nieuwenhuys, '67). This condition was apparent in several specimens of *Ictalurus* collected for this study. Here the olfactory bulb was sessile, i.e., nonpedunculated and attached to the ipsilateral telencephalon. In four animals the left (two females), right (one female), or both (1 male) bulbs were ses-

Abbreviations

ac	anterior commissure
C	cerebellum
cg	commissure of Goldstein
DC-1, 2, 3	parts of the central zone of area dorsalis telencephali (D)
Dd	dorsal zone of D
Dl	lateral zone of D
DLd	dorsal part of lateral zone of D
DLp	posterior part of lateral zone of D
DLv	ventral part of lateral zone of D
DM	medial zone of D
DPr	rostral portion of posterior zone of D
DPc	caudal portion of posterior zone of D
e	external sulcus (after Källén, '47 and Nieuwenhuys, '62b)
Ec	caudal entopeduncular nucleus
Ed	dorsal entopeduncular nucleus
Ev	ventral entopeduncular nucleus
F	facial lobe
GL	glomerular layer of olfactory bulb
HA	anterior hypothalamic nucleus
ICL	internal cell layer of olfactory bulb
IL	inferior lobe
lt	lateral olfactory tract
m	meninges
M	medulla oblongota
MCL	mitral cell layer of the olfactory bulb
mt	medial olfactory tract
mta	ascending component of medial olfactory tract
mtd	descending component of medial olfactory tract
N	nervus terminalis ganglion cells
NT	nucleus taeniae
OB	olfactory bulb
OE	olfactory epithelium
ON	olfactory nerve
OP	olfactory peduncle
OT	optic tract
P	pituitary
PLL	posterior lateral line lobe
PM	magnocellular preoptic nucleus
PP	periventricular preoptic nucleus
PPa	anterior segment of the parvocellular part of PP
PPp	posterior segment of the parvocellular part of PP
pr	preoptic recess
rh	rhinocoele
S	spinal cord
SC	suprachiasmatic nucleus
sl	sulcus limitans (after Källén, '47)
slt	sulcus limitans telencephali (after Nieuwenhuys, '63)
SOF	secondary olfactory fiber layer
sy	sulcus ypsiliformis (after Sheldon, '12)
T	telencephalon
tc	tela chorioidea
TeO	optic tectum
v	ventricle
V	vagal lobe
Vc	central nucleus of area ventralis telencephali (V)
Vd-d	dorsal division of the dorsal nucleus of V
Vd-v	ventral division of the dorsal nucleus of V
Vi	intermediate nucleus of V
Vl	lateral nucleus of V
Vn	'nother nucleus of V
Vp	postcommissural nucleus of V
Vs	supracommissural nucleus of V
Vv	ventral nucleus of V
Vv-d	dorsal division of Vv
Vv-v	ventral division of Vv
x	mitral-like cells of a sessile olfactory bulb
z	sulcus z

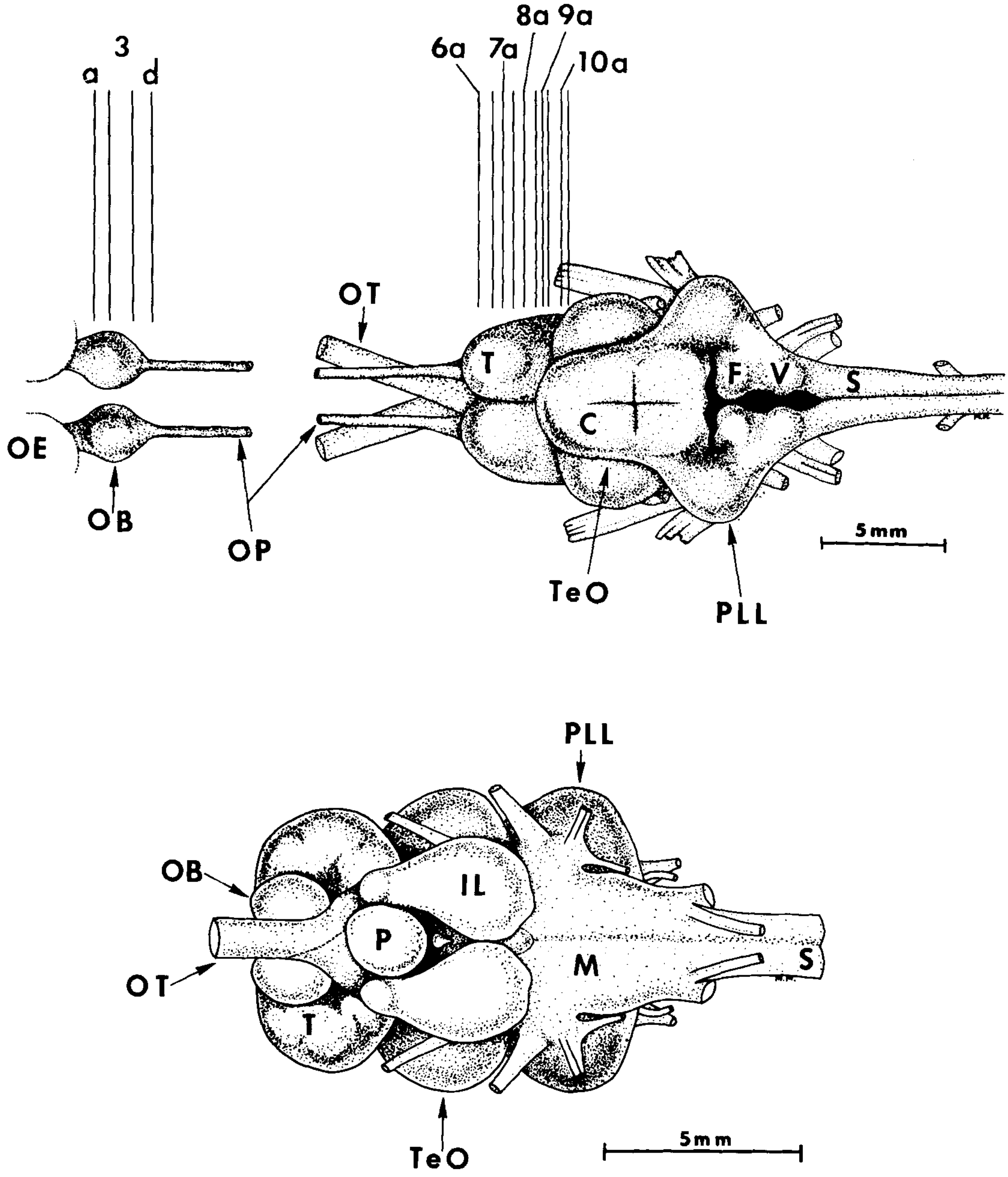

Fig. 1. (A) Dorsal view of the brain of the channel catfish, *Ictalurus punctatus*. Numbered lines indicate the levels of the transverse sections in Figures 3, 6–10. (B) Ventral view of the brain of a specimen of *I. punctatus* with two sessile bulbs.

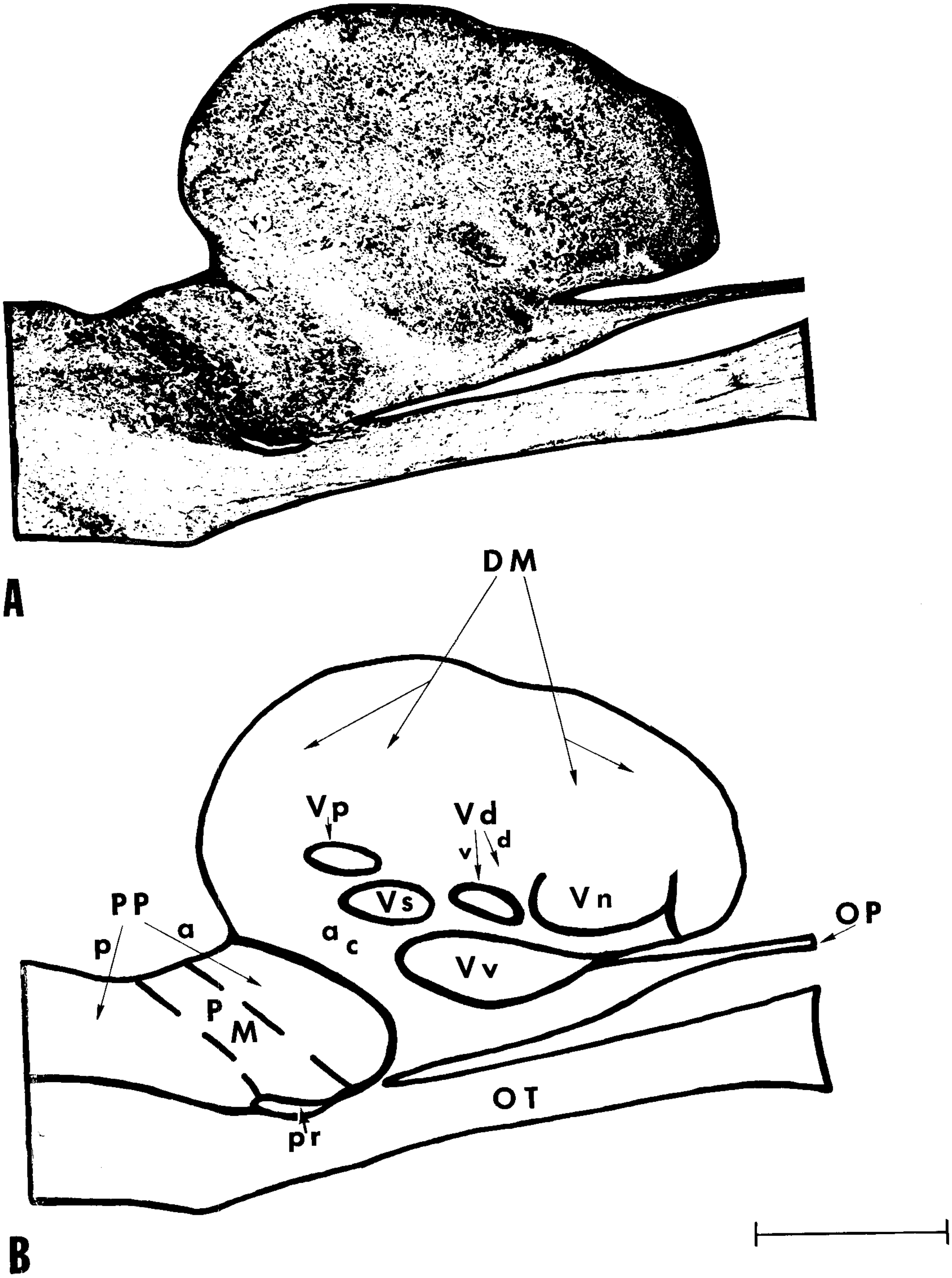

Fig. 2. Parasiggital view of the telencephalon showing the position of telencephalic nuclei. (A) Photomicrograph of a Nissl preparation. (B) Line drawing of the approximate position and extent of nuclei illustrated in A. Bar scale is 1 mm.

sile; as suspected, these nonpedunculated bulbs appear as ventral thickenings of the rostral telencephalon (Fig. 1B). This condition is previously unreported.

The pedunculated bulb of catfish comprises five concentric laminae (Fig. 3): (1) an outer layer of olfactory nerve fibers (ON), (2) a glomerular layer (GL), (3) an external cell layer of mitral cells and various-sized smaller elements (MCL), (4) an inner fiber layer containing bulbar efferents (SOF), and (5) an internal cell layer of medium- and small-sized cells (ICL)—the so-called anterior olfactory nucleus (Sheldon, '12; Nieuwenhuys, '67). The boundaries depicted are not absolute, as elements of the MCL and ICL extend into the adjacent laminae. Also, the cells comprising the ICL and MCL are heterogeneous and comprise no single morphological type.

The mitral cells, which often appear clumped in small groups, are mixed with smaller elements resembling cells of the ICL. These smaller cells grade over into the ICL and obscure the boundaries of the SOF. The ICL often extends far medially or dorsally, merging with the MCL. Caudally, a few ICL cells extend into the medial division of the olfactory peduncle, but the majority of ICL cells form a distinct boundary. A ventricular space, or rhinocoele (rh, Fig. 3D, after Sheldon, '12) bounded by a thin epithelial roof caps the peduncle. The ventricle and roof are extensions of the medial telencephalic ventricle and the tela, respectively.

The organization of the sessile left olfactory bulb of one female specimen is described to aid the interpretation of major telencephalic boundaries (Fig. 4). The typical concentric organization of the bulb is absent. No primary olfactory layer is evident, as no olfactory nerve is associated with the sessile bulb. Cell bodies with diameters similar to mitral cells or pedunculated bulbs are scattered along a ventromedial and dorsolateral zone (x, Fig. 4A,B). There is a well-developed ICL that appears, at rostral levels, to consist of dorsal and ventral divisions. Smaller elements, resembling ICL cells, are mixed with the mitral-like cells, reminiscent of the normal condition. The bulb is enveloped by a dense connective tissue layer, as in pedunculated cases.

Caudally, the ICL merges with the area ventralis telencephali. Some of the smaller cells of the ICL appear to continue dorsal to the central nucleus of area ventralis (Vc, Fig. 4D). A small cluster of deeply staining cells along the dorsomedial aspect of the bulb is continuous with the dorsal component of the pars ventralis of nucleus ventralis telencephali (Vv-d, Fig. 4B–D).

Nervus teminalis ganglion

Small clusters of three to four large (20-μm) deeply staining cells appear along the ventromedial surface of the olfactory nerve (Fig. 5). While the majority of cells appear rostral to the olfactory bulb proper, scattered cells often extend along the periphery of the layer of olfactory nerve fibers. These cells appear to correspond to the nervus terminalis ganglion (N, Fig. 3A) as described by Brookover and Jackson ('11) in catfish, and Sheldon ('09) in carp.

Olfactory tracts

An extended olfactory peduncle (OP, Figs. 1, 2) connects the olfactory bulb to the telencephalon. Each peduncle comprises at least three divisions: the ascending and descending components of the medial olfactory tract (mta, mtd, respectively; Fig. 3D) and the lateral olfactory tract (lt, Fig. 3D). These divisions of the tract contain several components which are discussed in detail in an autoradiographic analysis of the secondary olfactory pathways (Bass, '80a).

Telencephalic hemispheres

Area ventralis telencephali

A cell-free area, the "zona limitans" is often recognized as defining the boundary between the areas ventralis and dorsalis telencephali (Johnston, '11; Holmgren, '22; Källén, '51b). In *Ictalurus punctatus* the position of this zone is unclear. However, specimens having sessile bulbs let one recognize this major boundary. In teleosts with sessile bulbs, the olfactory bulb is replaced caudally by the ventral telencephalic division (Källén, '47; Nieuwenhuys, '63; Northcutt and Braford, '80). Similarly, in specimens of *Ictalurus* with sessile bulbs, the bulb is replaced caudally by five-cell groups of the area ventralis: medially by (1) nucleus ventralis (Vv, Fig. 4B–D), laterally by (2) nucleus centralis (Vc, Fig. 4B–D) and (3) nucleus lateralis (Vl, Fig. 4B–D), and dorsomedially by (4) nucleus "nother" (Vn, Fig. 4B,C) and (5) nucleus dorsalis (Vd, Fig. 4D). As mentioned earlier, Vv clearly extends into the olfactory bulb (Fig. 4B,C), while Vc and Vl arise lateral, and Vn and Vd arise medial to the internal cell layer (ICL, Fig. 4B–D).

In general, the area ventralis contains five major zones: (1) a precommissural, periventri-

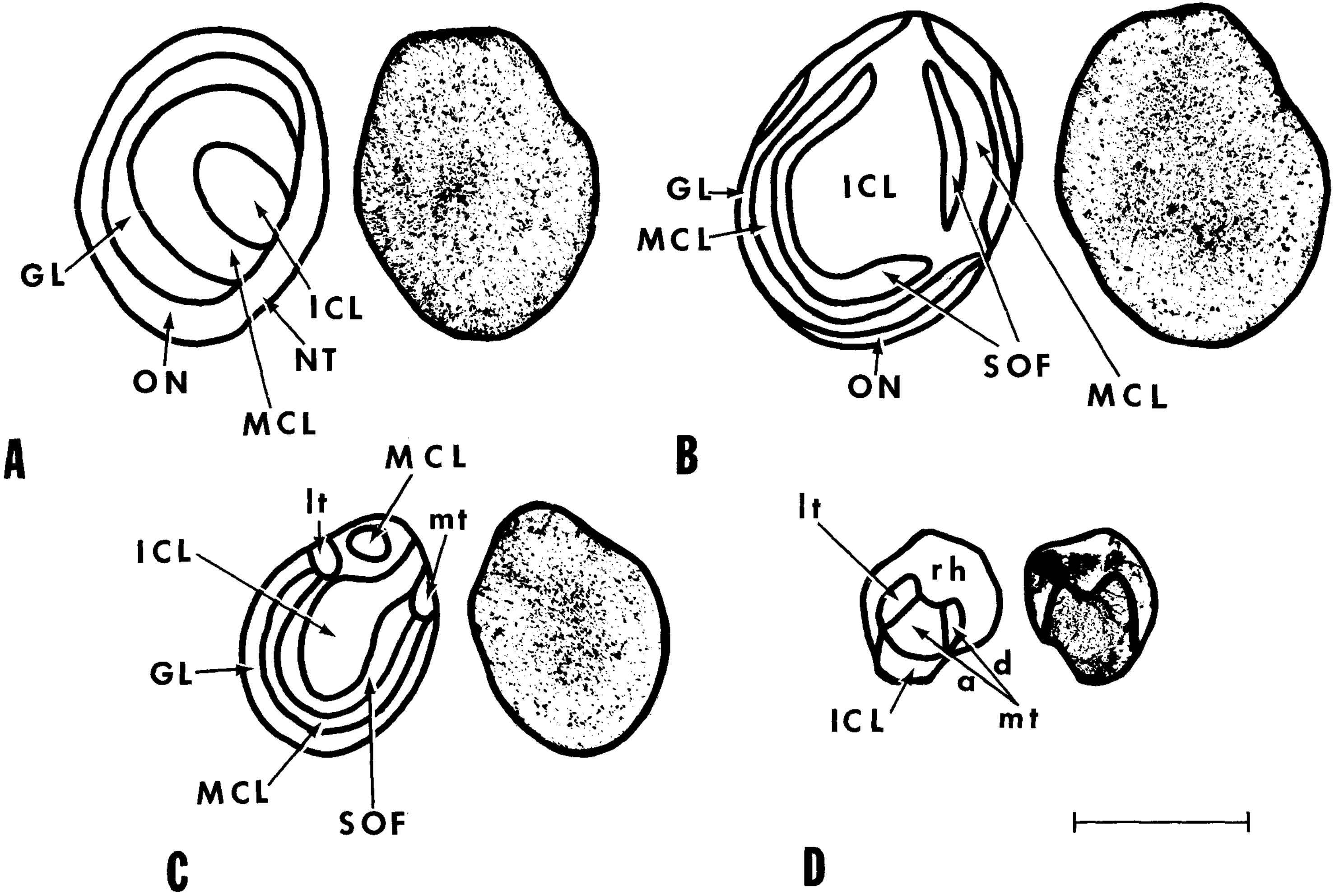

Fig. 3. (A–D) Transverse sections through the olfactory bulb. A Nissl preparation is shown on the right. To the left is a line drawing indicating the position of the laminae and tracts within the olfactory bulb. Bar scale is 1 mm.

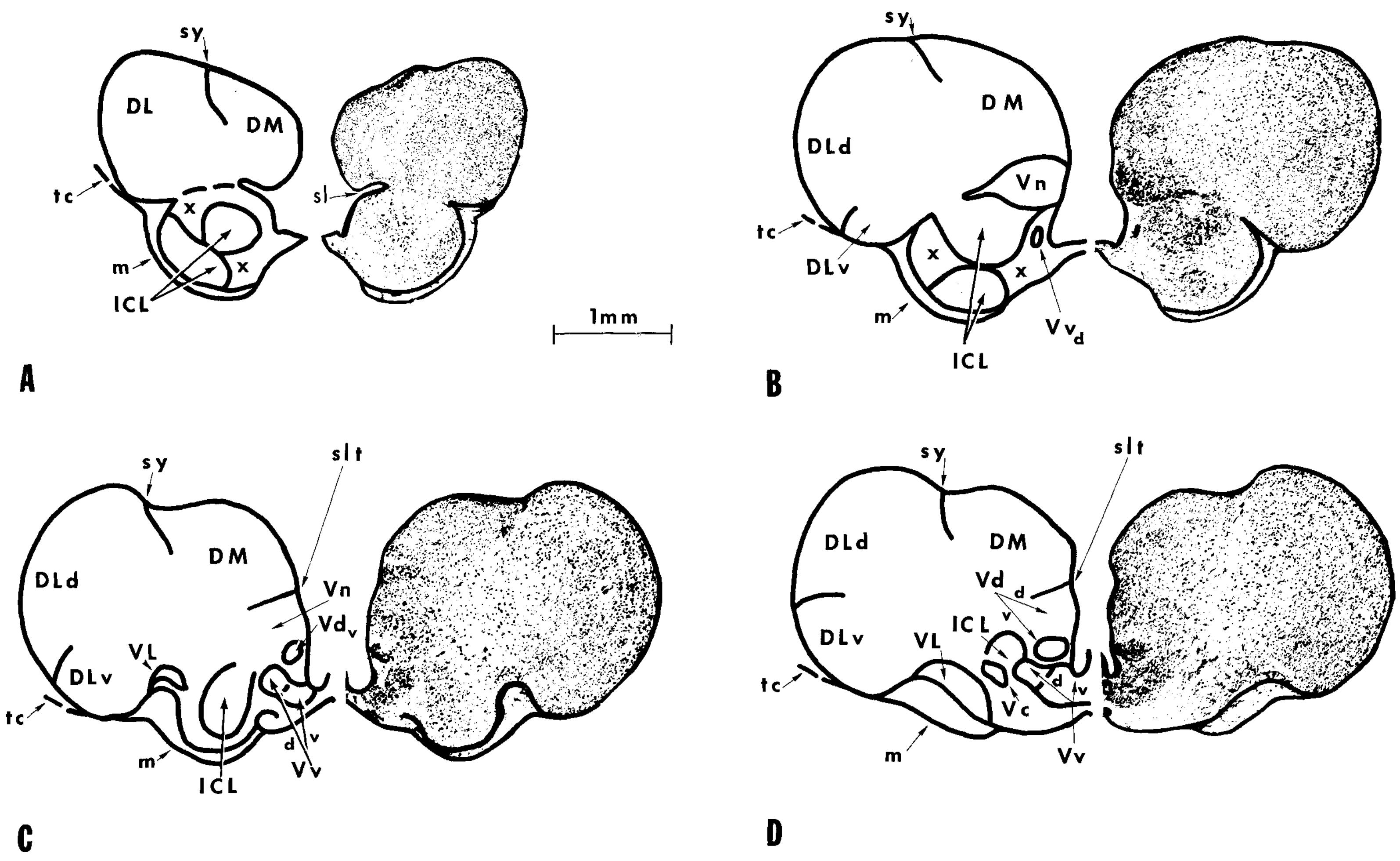

Fig. 4. (A–D) Transverse sections through the telencephalon of a specimen with a sessile olfactory bulb. A Nissl preparation appears to the right. To the left is a line drawing of the olfactory bulb and telencephalon. Bar scale is 1 mm.

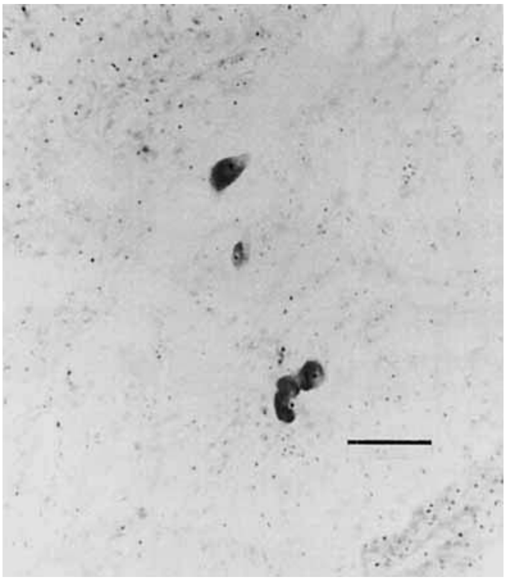

Fig. 5. Photomicrograph of a section through the rostromedial olfactory bulb illustrating cells of the nervus terminalis ganglion that lie embedded within the olfactory nerve. Bar scale represents 50 μm.

cular zone including Vn, Vv, and Vd; (2) a precommissural, migrated zone including Vc and Vl; (3) a supracommissural division—Vs; (4) a caudal commissural zone including a postcommissural nucleus, Vp and a migrated intermediate nucleus, Vi; and (5) a preoptic area that is a continuation of area ventralis ventral to the anterior commissure (Fig. 2).

Rostral to the anterior commissure, Vn, Vv, and Vd dominate the medial ventricular surface of the telencephalon. Vn is the most rostroventral cell group of area ventralis, arising as a dense cluster of deeply staining cells (Figs. 2, 4B, 6B). Caudally, Vn is dispersed into smaller cell clusters assuming a laminar appearance (Figs. 4C, 7A).

As the medial ventricular surface expands, displacing Vn dorsally, Vv appears along the ventromedial periventricular surface (Figs. 2; 4B–D; 7A). Vv comprises a wedge-shaped cluster of deeply staining neurons associated with a thickened ependymal zone of pseudostratified epithelium. Caudally, Vv is divided into ventromedial and dorsolateral components (Vv-v and Vv-d, respectively, Figs. 4C–D; 7B), merging into a diffuse mass at rostral commissural levels (Fig. 8A). Vv is finally replaced by a recognizable supracommissural zone, Vs (Fig. 8B), which forms an ill-defined zone of scattered elements as fibers of the medial and lateral olfactory tracts collect to cross within the caudal anterior commissure (Fig. 9A; see also Bass '80a).

The most expansive precommissural portion of area ventralis is Vd, comprising two distinct components (Figs. 2; 4C,D; 7A): (1) a dorsal component, Vd-d, replaces Vn caudally and similarly contains small cell laminar clusters and (2) a ventral cigar-shaped component, Vd-v, that arises separately on the medial ventricular surface (Fig. 11A). Previously, Vd-v is described solely as Vd (Bass, '78, '79a). Scattered elements form a diffuse boundary between Vd-v and Vd-d. A prominent sulcus, the sulcus limitans telencephali (slt, Figs. 4C,D; 7B; 8A; after Nieuwenhuys, '63), marks the dorsal boundary of Vd to rostral commissural levels, as Vd is replaced by an expanding area dorsalis (DM, Fig. 8B; see below).

Two migrated cell groups, Vc and Vl, appear at precommissural levels. Vc (Fig. 6B) arises at far rostral levels as a small cluster of cells interposed between the medial and lateral divisions of the olfactory tract (see Bass, '80a). Caudally, Vc assumes a diffuse appearance and continues to occupy a centromedial position lateral to Vv (Figs. 4D; 7A,B; 8A). As the commissural ridge expands (Fig. 8B), Vc is dispersed by the lateral forebrain bundles and no longer forms a well-defined cluster.

Occupying a more superficial, submeningeal position is Vl, a crescent-shaped group of lightly staining neurons that appear dorsomedial to the sulcus externus (e, Figs. 6–9) of Källén ('47) and Nieuwenhuys ('62b). Vl, as Vc, is dispersed by the lateral forebrain bundles, remnants of these nuclei continuing amid these fibers to caudal commissural levels (Figs. 8B; 9A). These cells are replaced at postcommissural levels by a well-defined entopeduncular complex containing small, densely packed, deeply staining, cells (Ed, Ev, Ec; Figs. 9B; 10A,B).

At postcommissural levels, a small group of cells emerges on the medial ventricular surface (Fig. 9A), the majority of them migrating laterally to form a recognizable nucleus Vp (Fig. 9B).

The most caudal cell group of area ventralis is Vi, arising as a compact group of lightly staining cells continuous ventromedially with the preoptic area (Fig. 10A,B). While Nieuwenhuys ('63) defines Vi as a lateral extension of Vp, the continuity between these nuclei is obscure in *Ictalurus*. While Vi lies near a caudal portion of the area dorsalis (DM, Fig. 10A,B), it is never continuous with this zone, separated by a cell-free region.

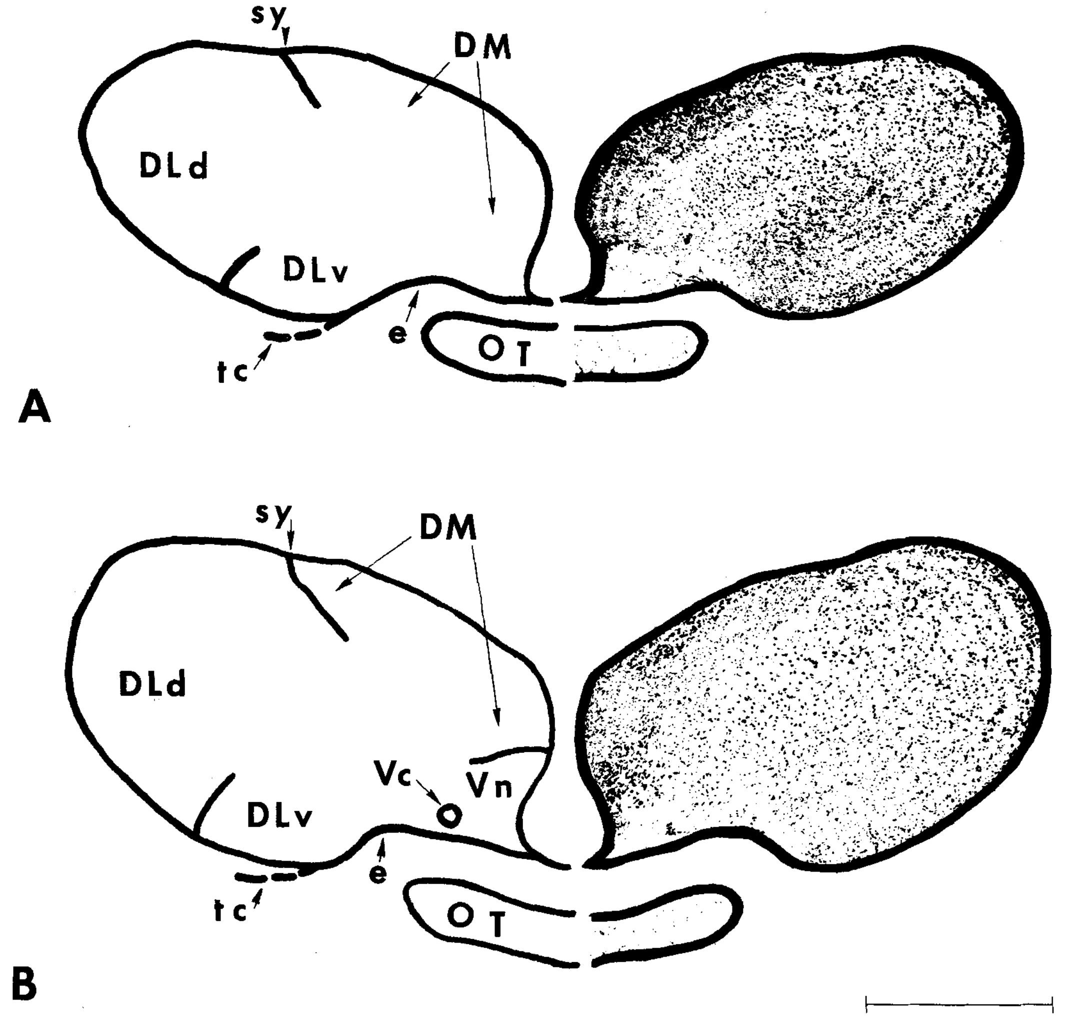

Fig. 6. (A) Transverse section through the rostral telencephalon. In this and Figures 7–10, a Nissl photomicrograph appears on the right. To the left is a line drawing indicating the position of telecephalic nuclei. (B) Transverse section through the rostral pole of nucleus 'nother (Vn) of area ventralis. Bar scale is 1 mm.

Area dorsalis telencephali

The area dorsalis extends the entire length of the telencephalic hemisphere, capping the area ventralis (Fig. 2). Five major zones are recognized: (1) a dorsomedial zone, DM, (2) a dorsal zone, Dd, (3) a dorsolateral zone, Dl, (4) a dorsal posterior zone, DP, and (5) a dorsal central zone, DC. DL and DM extend from rostral to caudal levels (Figs. 6–10), while DC, Dd, and DP appear at midrostral levels, (Figs. 7, 8) and Dd disappears caudal to the anterior commissure (Fig. 10). A cell-free area, the sulcus ypsiliformis (sy, Figs. 4, 6–9; after Goldstein, '05) separates DM from DL and Dd. At caudal levels, DM expands laterally, replacing Dd, and is separated from the expanding posterior division of DL (DLp) by a second cell-free zone (z, Figs. 9B; 10A,B), which is a centrolateral extension of the sulcus ypsiliformis. No cell-free boundary occurs between DM and area ventralis, Dd, and DL (except at caudal levels, Fig. 9B), or DC and the peripheral zones.

DM is characterized by multiple subdivisions of dense clusters of deeply staining cells extending from the ependymal surface, the cell

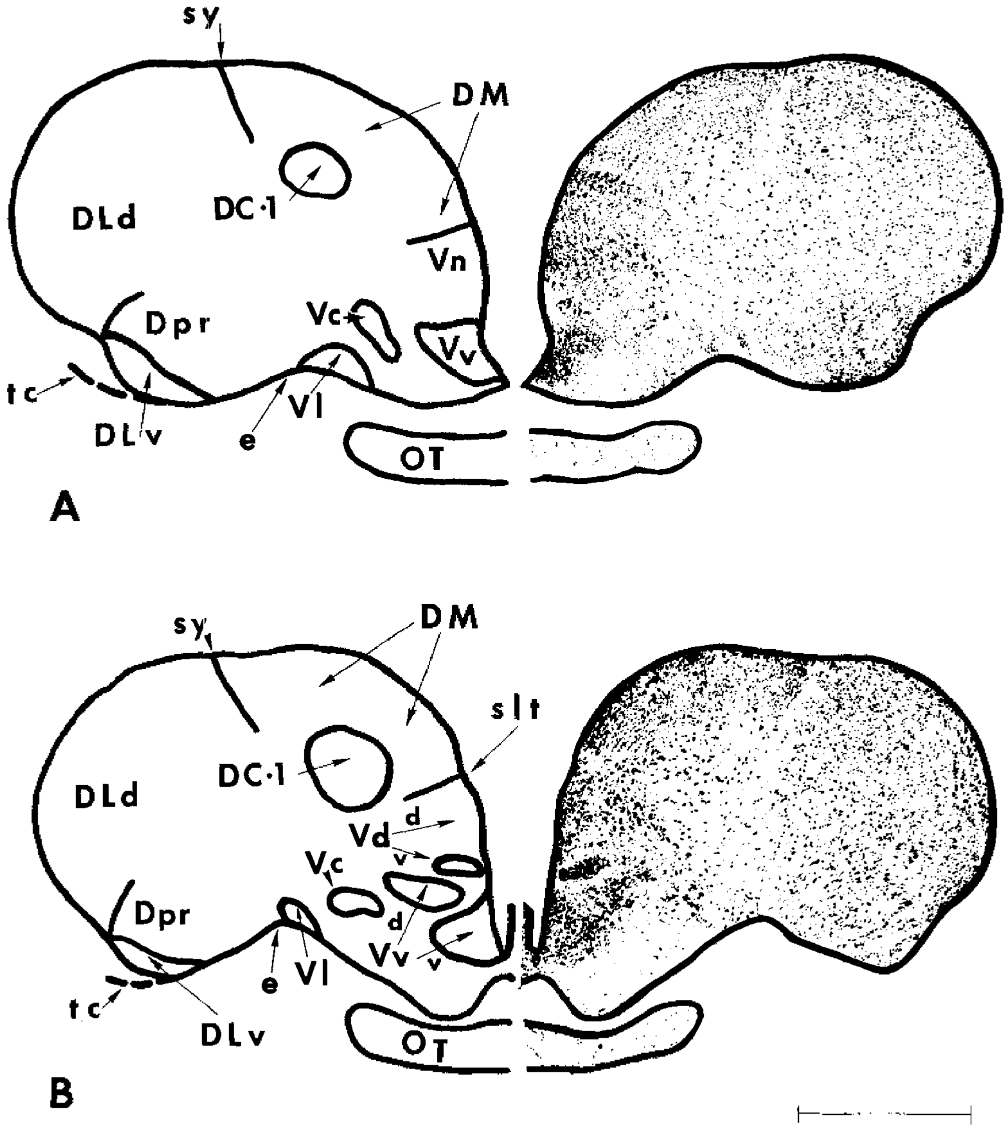

Fig. 7. (A) Transverse section through the caudal pole of Vn as the ventral nucleus (Vv) of area ventralis appears along the median periventricular surface. (B) Transverse section through the rostral pole of the dorsal nucleus (Vd-v, d) of area ventralis. Bar scale is 1 mm.

density decreasing toward the central zone. Northcutt and Braford ('80) separate DM in teleosts into four major divisions on the basis of histochemical data. Until comparable data is available for *Ictalurus*, DM remains undivided.

The greatest mass of the area dorsalis lies lateral to the sulcus ypsiliformis as Dd, DL, and DP. Dd is a compact, small-celled group continuous laterally with DL (Figs. 8, 9). The boundary between these two groups is particularly ill-defined at rostral levels (Fig. 8A,B). At caudal commissural levels Dd expands ventrolaterally, forming a dorsal hillock of scattered cells separated from a more ventral triangular-shaped base of compact cells (Fig. 9B). Dd disappears caudally as DM and DLp expand (Fig. 10A).

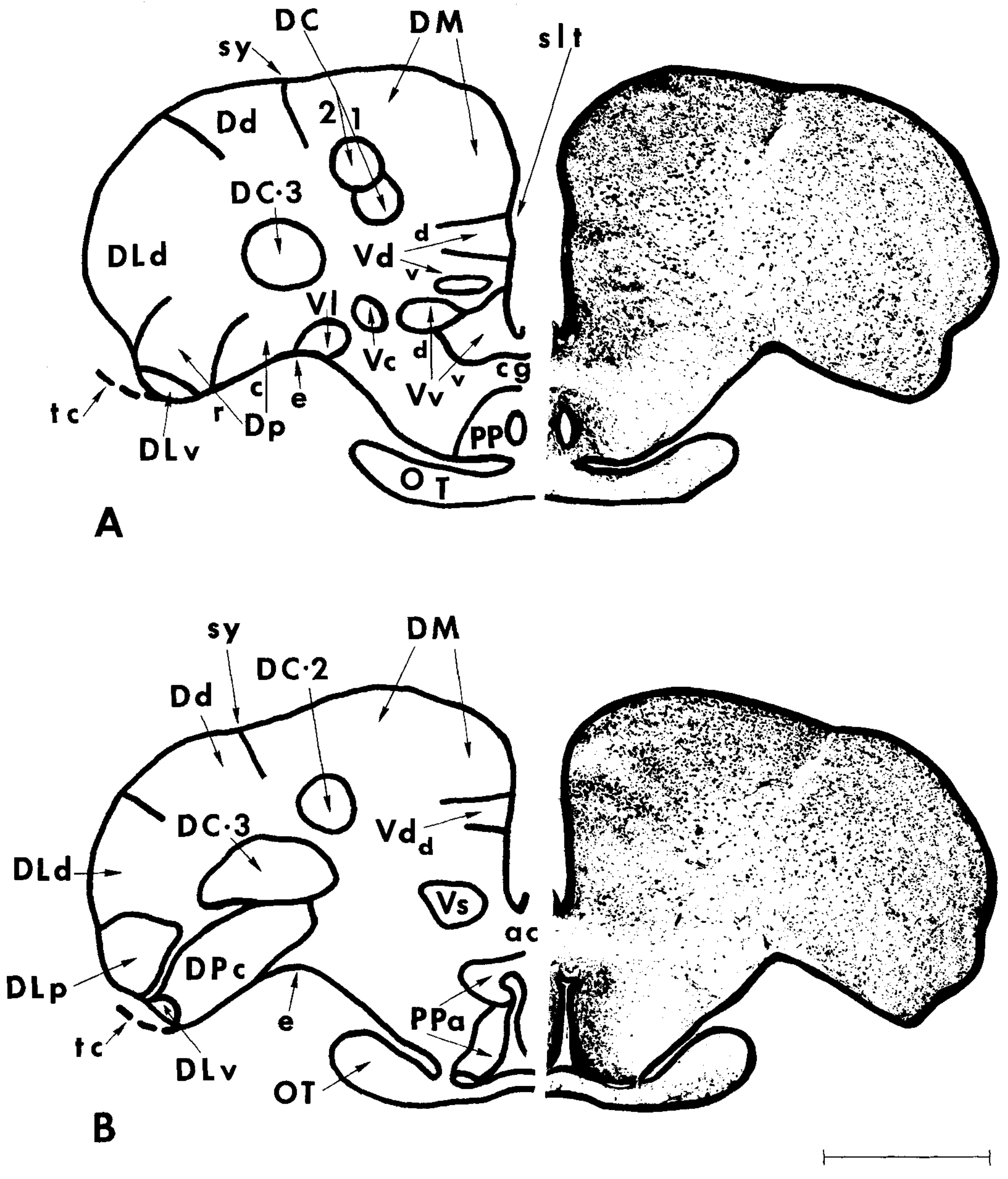

Fig. 8. (A) Transverse section through the rostral commissural ridge at the level of the commissure of Goldstein (cg). (B) Transverse section through the anterior commissure as the caudal segment of the posterior zone of area dorsalis (DPc) expands along the ventrolateral surface of the telencephalon. Bar scale is 1 mm.

The dorsolateral zone makes up the largest component of the area dorsalis and consists of three major divisions: (1) a dorsal division (DLd), (2) a rostral ventral division (DLv), and (3) a posterior division (DLp). DLd is characterized by a narrow periventricular zone and an expansive migrated zone that assumes a laminar-like organization (Figs. 4, 6–11B), while DLv appears as a compact zone (Figs. 4, 6). DLd extends to caudal telencephalic levels and is replaced by a posterior laminar zone, DLp (Figs. 8B; 9A,B). DLv is replaced at rostral

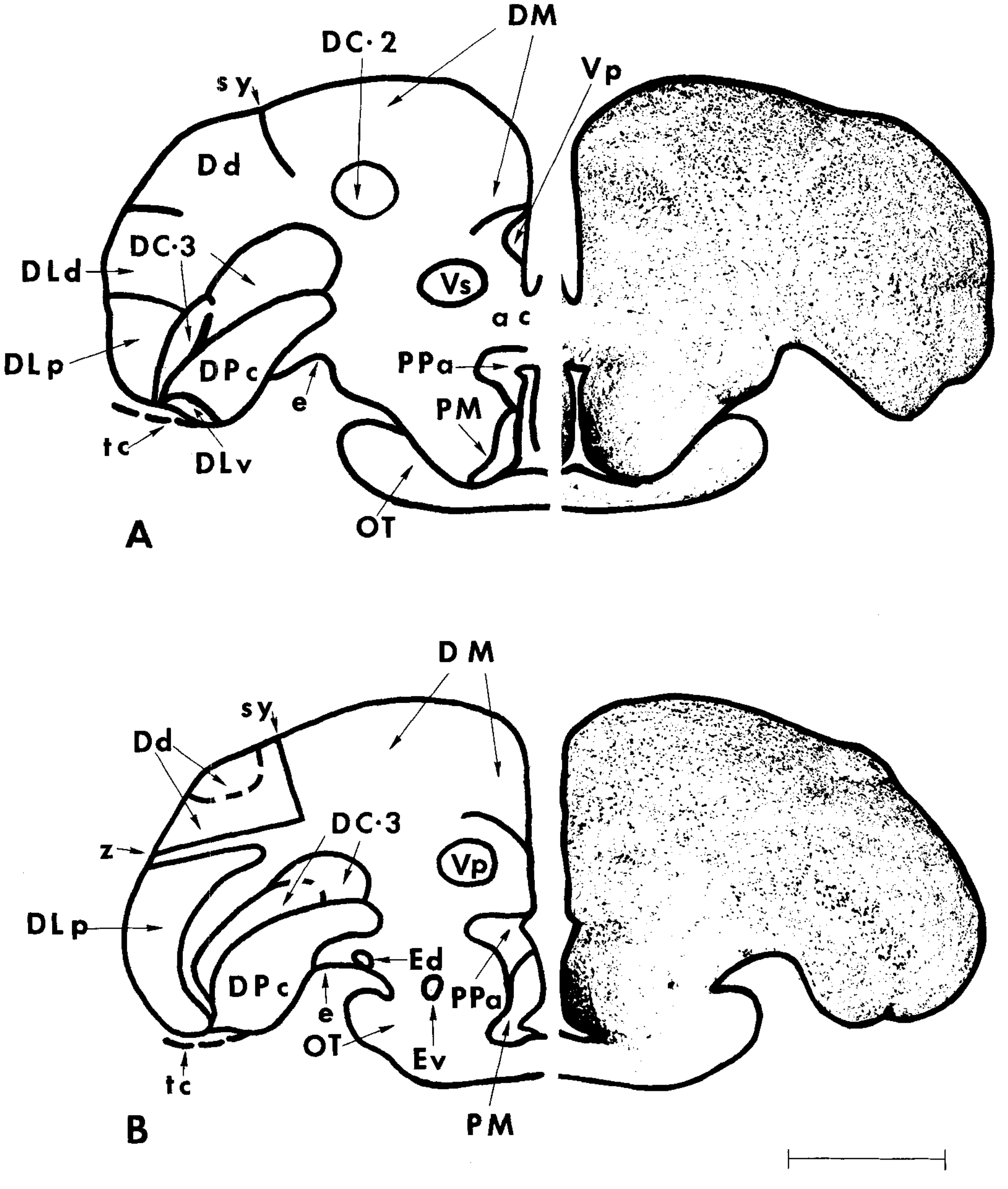

Fig. 9. (A) Transverse section through the caudal pole of the anterior commissure as the postcommissural nucleus (Vp) of area ventralis appears along the median ventricular surface. (B) Transverse section through the caudal pole of the dorsal central zone (DC-3) overlying DPc. Bar scale is 1 mm.

levels by DP (Fig. 7A). A small portion of DLv continues ventrally, to commissural levels, lateral to the attachment of the tela (Figs. 7–9A).

As mentioned above, DLv is replaced by DP, a second ventral zone that continues to caudal levels. DP arises lateral to the external sulcus and is separated by DLv from the lateral ventricular surface (Fig. 7A). A rostral division (DPr) consists laterally of clumps of deeply staining cells and medially of smaller lightly staining elements (Fig. 7A,B). The latter gives rise to a caudal DP division (DPc) comprising

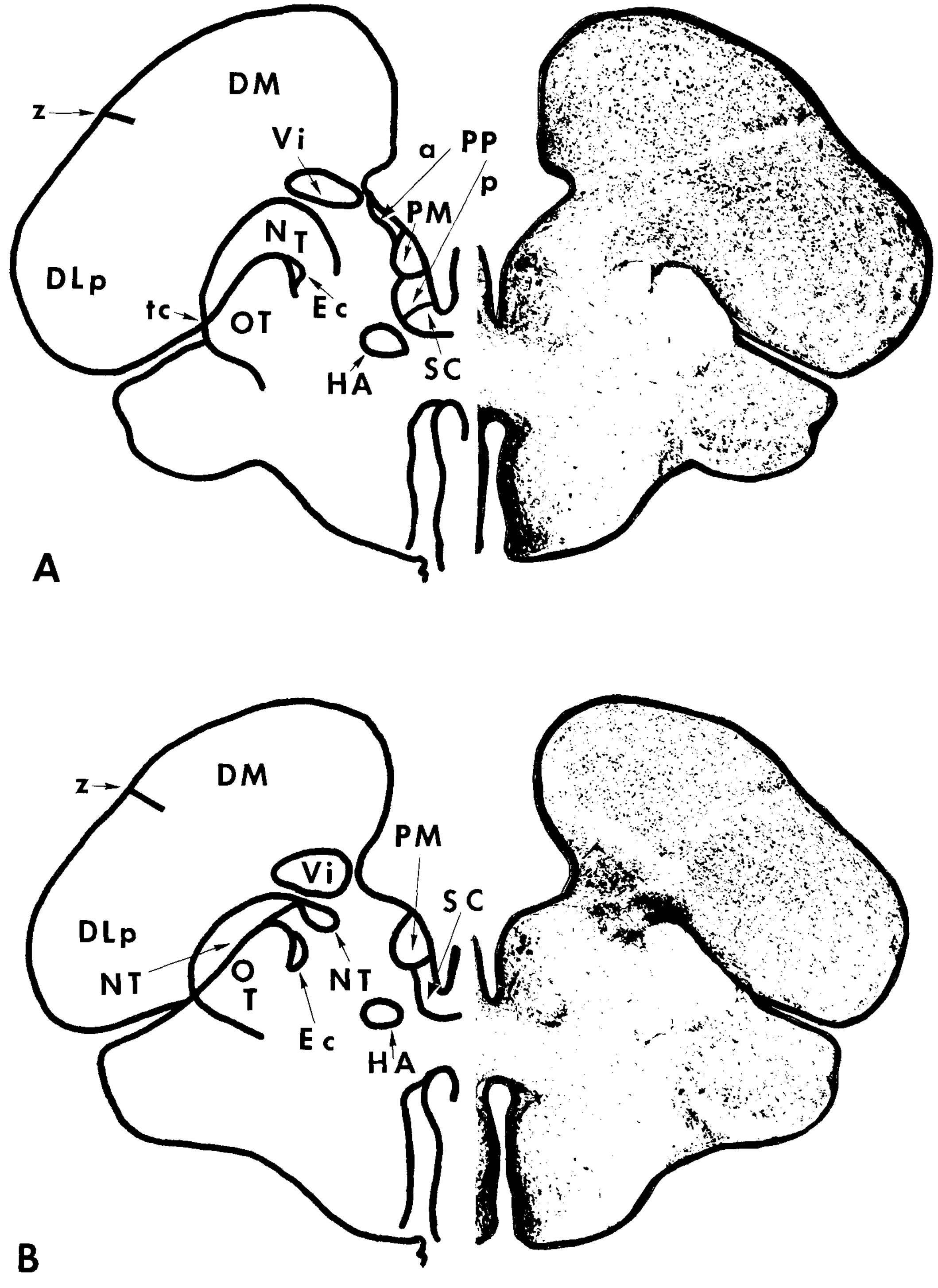

Fig. 10. (A) Transverse section through nucleus taeniae (NT) at a caudal preoptic level (PPA, p; PM). (B) Transverse section through the caudal pole of the telencephalon as the intermediate nucleus (Vi) of area ventralis and NT merge with the lateral preoptic area. Bar scale is 1 mm.

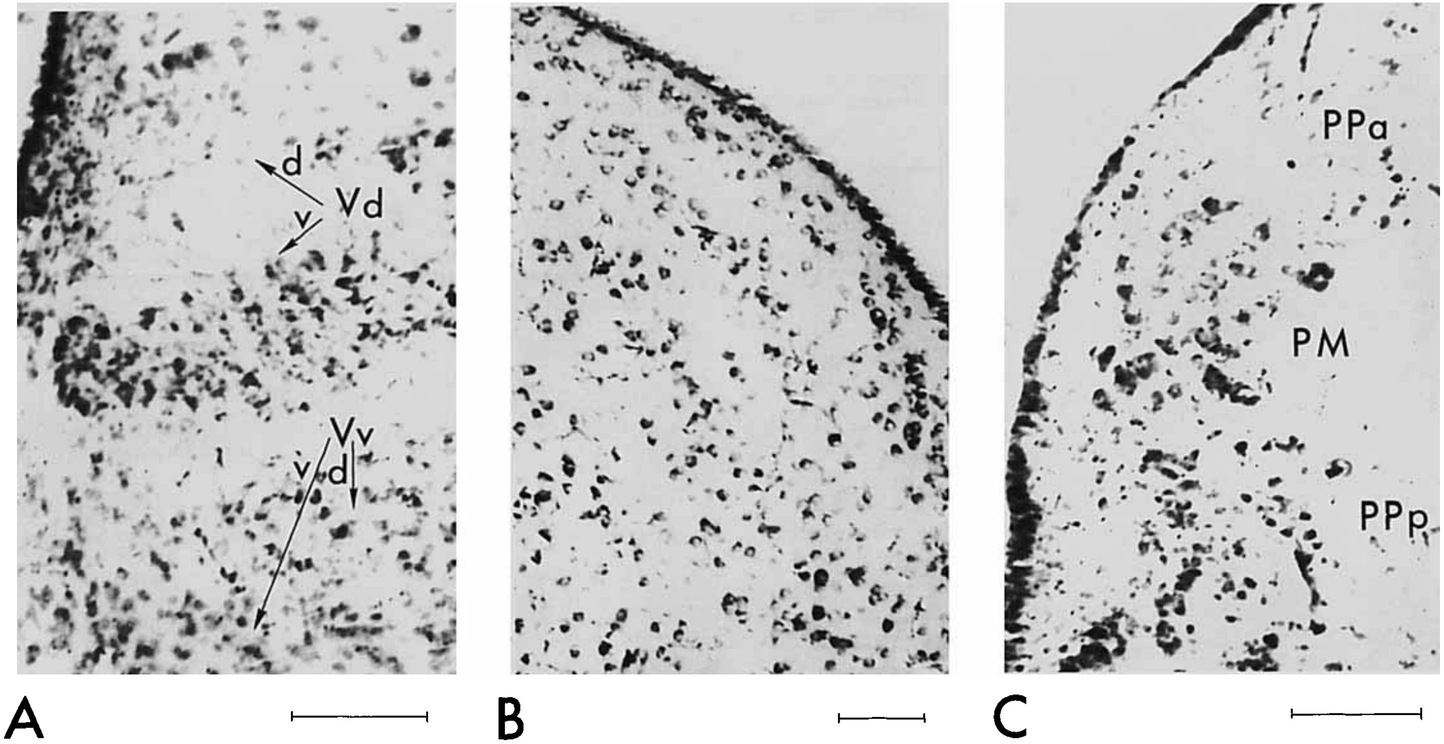

Fig. 11. Photomicrographs of transverse sections of Nissl stained material. (A) Area ventralis telencephali at the level of the ventral division of the dorsal (Vd-v) and ventral (Vv-v) nuclei, and the dorsal division of the dorsal (Vd-d) and ventral (Vv-d) nuclei. (B) The dorsal division of area dorsolateralis (DLd). (C) The caudal preoptic area at the level of the magnocellular nucleus (PM) and anterior (PPa) and posterior (PPp) segments of the parvocellular nucleus. Bar scales for A, B, and C represent 0.1 mm.

TABLE 1. Summary of Nomenclature of Telencephalic Nuclei in Catfish

Ictalurus punctatus (Present nomenclature)	*Corydora palliatus* (Miller, 1940)	*Galeichthys felis* (Morgan, 1975)	*Ictalurus nebulosus* (Finger, 1975)
Vv-v (ventral division of ventral nucleus of area ventralis)	nucleus praecommissuralis pars inferior	medial septal nucleus pars ventralis	
Vv-d (dorsal division of ventral nucleus of area ventralis)	nucleus praecommissuralis pars inferior	medial septal nucleus pars ventralis	nucleus praecommissuralis pars magnocellularis
Vd-v (ventral division of dorsal nucleus of area ventralis)	nucleus olfactorius anterior pars praecommissuralis	lateral septal nucleus	
Vd-d (dorsal division of dorsal nucleus of area ventralis)	nucleus praecommissuralis pars superior	medial septal nucleus pars dorsalis	
Vn ('nother nucleus of area ventralis)			
Vc (central nucleus of area ventralis); VI (lateral nucleus of area ventralis)	somatic area	lateral zone of olfactory tubercle (in part)	
Vs (supracommissural nucleus of area ventralis)	nucleus commissuralis anterior	bed nucleus of anterior commissure	
VI (intermediate nucleus of area ventralis)		paleostriatum augmentatum (in part)	
VP (postcommissural nucleus of area ventralis)		paleostriatum augmentatum (in part)	
PPa, p (parvocellular preoptic area)	preoptic nucleus	preoptic nucleus	nucleus preopticus pars parvocellularis

DLd (dorsal division of dorsolateral area)	D_1	primordial piriform cortex, primordial basolateral amygdaloid nucleus, primordial general pallium (*rostral*)	area lateralis, area lateralis centralis
DLv (ventral division of dorsolateral area)	D_2	primordial anterior amygdaloid nucleus	area posterior
DLp (posterior division of dorsolateral area)	D_2	primordial piriform cortex, primordial basolateral amygdaloid nucleus	area posterior
DPr (rostral part of posterior dorsal zone)	D_3	primordial corticomedial amygdaloid nucleus	area posterior
DPc (caudal part of posterior dorsal zone)	mediocaudal nucleus	primordial corticomedial amygdaloid nucleus	nucleus teniae
Nucleus taeniae	nucleus taeniae, nucleus entopeduncularis	primordial corticomedial amygdaloid nucleus, paleostriatum augmentatum (caudal)	
Dd (dorsal division of dorsal zone)	Bldp	primordial general pallium	area posterior
DM (dorsomedial zone)	B2, 3; Bld; Blda	anterior continuation of the hippocampus, *primordial subicular* area, primordial cornu ammonis, primordial dentate gyrus	area dorsalis
DC-1, 2 (dorsal central zones lateral to DM)	Blc	neostriatum, paleostriatum	area dorsalis centralis
DC-3 (dorsal central zone associated with DP)	D2C, D3c	primordial basolateral amygdaloid nucleus	area posterior

a homogeneous zone of widely spaced neurons (Figs. 8A,B; 9A,B). A string of deeply staining cells lies along the ventral boundary of DPc medial to the point of attachment of the tela.

The most caudal cell group within area dorsalis is nucleus taeniae (NT, Figs. 10A,B). NT arises dorsal to the external sulcus as the tela is swept medially by the contracted surface of the caudal telencephalon (Fig. 10A). The medium and deeply staining cells of NT form a compact zone as they merge with the lateral preoptic area (Fig. 10B).

The central zone of the area dorsalis (DC) consists of large, widely scattered cells that are divisible into local populations associated with an overlying peripheral zone. The subdivisions presented here are based in part on experimental studies of telencephalic efferents (Bass '80b). In general, DC is divisible into medial (DC-1, DC-2) and lateral (DC-3) subdivisions. DC-1 contains large, widely spaced cells lateral to rostral DM (Fig. 7A,B). A group of smaller, lighter-staining cells, DC-2, extends from the lateral border of DM (near the sulcus ypsiliformis), encroaching on the caudolateral aspect of DC-1 (Figs. 8A,B; 9A). At rostral commissural levels, a medial component of DC-3 comprises large, widely spaced neurons, lying dorsal to DP (Fig. 8A,B). Caudally, DC-3 merges into a lateral crescent-shaped extension of deeply staining neurons (Fig. 9A,B).

The telencephalon medium

The telencephalon medium (after Johnston, '11) consists of the components of the anterior commissure and the preoptic area. The former will be treated in subsequent experimental analyses.

The preoptic area arises ventral to the anterior commissure and contains three major zones (Figs. 2, 8–10, 11C): (1) an anterior parvocellular divsion (PPa, Figs. 8–10), (2) a magnocellular division (PM, Figs. 9–10), and (3) a posterior parvocellular division (PPp, Fig. 10a). A ventromedial segment of PPp is distinguished as a retinal-recipient (unpublished data) suprachiasmatic nucleus (SC, Fig. 10A,B). Scattered elements lying lateral to PPa and PM might comprise a separate pars lateralis division (see Sheldon, '12). At caudal preoptic levels a distinct circular group appears ventrolateral to SC. This group is identified as an anterior hypothalamic nucleus (HA, Fig. 10A,B) and appears to correspond to a similarly named monoamine-containing nucleus identified in *Anguilla* (Fremberg and Van Veen, '77).

DISCUSSION

Present study

Three major phenomena characterize the telencephalon of teleosts (after Nieuwenhuys, '62a,b): (1) eversion of area dorsalis, (2) hypertrophy of ventricular cell masses with concomitant subdivision into multiple zones, and (3) cell migration from the ventricular zones toward the center of the telencephalon. These characters describe the telencephalon of channel catfish: (1) There is a marked eversion as evidenced by the ventrolateral attachment of the tela chorioidea and the depth of the external sulcus (see Figs. 6–9). (2) Dense periventricular cell clusters with multiple subdivisions characterize areas ventralis (V) and dorsomedialis (DM). (3) A sparse periventricular zone, coupled with a large population of centrally migrated cells characterizes dorsolateral (DL) and dorsal posterior (DP) zones. A separate central zone contains subdivisions associated with overlying medial (DM) and lateral (DL, DP) zones.

Nieuwenhuys ('62b) emphasizes that for everted pallia, "further evolutionary development" is associated with the periventricular zone, noting its hypertrophy within DM, Dd, and DL of Osteoglossiformes. In channel catfish, periventricular hypertrophy characterizes DM, while DL, caudal Dd, and DP portray a trend recognized for evaginated pallia of land vertebrates (Nieuwenhuys, '62b): cell migration toward "superficial positions" (topologically equivalent to the central zone of everted pallia; see Northcutt and Braford, '80), with a reduction of the periventricular zone. In land vertebrates, such superficial migrations give rise to a laminar cortex. While no homology is inferred, similar architectural phenomena may characterize the morphology of everted and evaginated pallia. It remains to be elucidated whether these similar designs are adapted to similar functions (see Bass, '79b).

Comparison with earlier catfish studies

The multiplicity of cytoarchitectonic subdivisions revealed here for the channel catfish corresponds closely to that documented for the South American catfish, *Corydora palliatus* (Miller, '40) and the sea catfish, *Galeichthys felis* (Morgan, '75). Miller utilized a nomenclature adapted from Sheldon ('12) and Kuhlenbeck ('24) and recognized an eversion process. She identified a series of longitudinal cell columns in the telencephalon of *Corydora* and, through a series of simple topological transformations (cf. Braford and Northcutt, '74; Northcutt and Braford, '80), inferred direct comparisons with longitudinal zones in amphibians (as described by Kuhlenbeck, '29).

Morgan denied an eversion process, comparing the telencephalon to "primordial, unevaginated hemispheres." Morgan utilized a nomenclature that applies to telencephalic subdivisions in mammals, suggesting direct homologies. Neither of the proposed homologies of Miller or Morgan are supported by recent experimental data (cf. Northcutt and Braford, '80). As Miller and Morgan included detailed drawings of telencephalic cell groups, it is possible to correlate their terminology with the present study (Table 1).

A previous experimental degeneration study of the secondary olfactory pathway in the bullhead catfish, *Ictalurus nebulosus,* lacks a detailed cytoarchitectonic analysis of the telencephalon (Finger, '75). A photograph of a Nissl-stained section through the rostral telencephalon is divided into six major regions which are compared to the recognized cytoarchitectonic zones in previous studies (but not that of Miller's of the South American catfish, *Corydora*). Dorsal, lateral, posterior, and ventromedial areas of the telencephalon are recognized but not included in the table of comparisons. Consequently, this impedes accurate interpretation of the data in the context of detailed cytoarchitectonic studies of the telencephalon of catfish (Miller, '40; Morgan, '75; this report) or any other teleost (Nieuwenhuys, '63; Northcutt and Braford, '80). Table 1 presents an approximate synonomy between Finger's ('75) nomenclature and that employed in the present study.

Functional significance

Earlier nonexperimental studies relate telencephalic differentiation in actinopterygians to the development of olfactory correlation centers, which have connections with the diencephalon (Johnston, '11; Sheldon, '12; Herrick, '21; Meader, '39; Ariens-Kappers et al., '60). Nieuwenhuys ('63) recognizes the appearance of nonolfactory regions within the area dorsalis telencephali of holosteans and teleosts.

Recent experimental degeneration analyses demonstrate a circumscribed olfactory input to the telencephalon in holosteans (Northcutt and Braford, '80) and teleosts (Scalia and Ebbesson, '71; Ito, '73; Finger, '75), as well as polypteriforms (Braford and Northcutt, '74) and chondrosteans (Northcutt and Braford, '80). These studies distinguish substantial nonolfactory recipient tissue in the telencephalon of a representative member of each actinopterygian grade. Subsequent experimental analyses in channel catfish detail the relationship between telencephalic organization and the differentiation of both olfactory and nonolfactory regions (Bass, '80a,b).

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