JOURNAL OF MORPHOLOGY 247:217–228 (2001)

Cytoarchitectonic Study of the Brain of a Perciform Species, the Sea Bass (*Dicentrarchus labrax*). I. The Telencephalon

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ABSTRACT A cytoarchitectonic analysis of the telencephalon of the sea bass *Dicentrarchus labrax,* based on cresyl violet-stained serial transverse sections, is presented. Rostrally, the brain of the sea bass is occupied by sessile olfactory bulbs coupled to telencephalic hemispheres. The olfactory bulbs comprise an olfactory nerve fiber layer, a glomerular layer, an external cellular layer, a secondary olfactory fiber layer, and an internal cellular layer. Large terminal nerve ganglion cells are evident in the caudomedial olfactory bulbs. We recognized 22 distinct telencephalic nuclei which were classified in two main areas, the ventral telencephalon and the dorsal telencephalon. The ventral telencephalon displays four periventricular cell masses: the dorsal, ventral, supracommissural, and postcommissural nuclei; and four migrated populations: the lateral, central, intermediate, and entopeduncular nuclei. In addition, a periventricular cell population resembling the lateral septal organ reported in birds is observed in the ventral telencephalon of the sea bass. The dorsal telencephalon contains 13 nuclei, which can be organized into five major zones: the medial part, dorsal part, lateral part and its ventral, dorsal, and posterior divisions, the central part, and posterior part. Based on histological criteria, two cell masses are recognized in the ventral division of the lateral part of the dorsal telencephalon. The nucleus taenia is found in the caudal area of the dorsal telencephalon, close to the ventral area. This study represents a useful tool for the precise localization of the neuroendocrine territories and for the tracing of the neuronal systems participating in the regulation of reproduction and metabolism in this species. J. Morphol. 247: 217–228, 2001. © 2001 Wiley-Liss, Inc.

KEY WORDS: telencephalon; cytoarchitecture; neuroanatomy; perciformes; fish; teleost

The forebrain of ray-finned fish and land vertebrates varies considerably as a result of differences in ontogenetic development (Nieuwenhuys, 1963). In tetrapods, the inversion and evagination of the dorsolateral prosencephalic wall commonly produces paired telencephalic hemispheres enclosing lateral ventricles. In ray-finned fish, an eversion of the dorsal half of the lateral walls produces two solid masses bordering a single ventricular cavity (Braford, 1995; Northcutt, 1995). The degree of this eversion varies considerably among actinopteryrians. This fact, together with the differential hypertrophy and thickness of cerebral walls, results in a wide variety of telencephalic organization that reaches the most complex pattern in teleosts (Northcutt and Braford, 1980; Northcutt and Davis, 1983). The telencephalon of ray-finned fish consists of two olfactory bulbs located rostroventrally to paired cerebral hemispheres (Northcutt and Davis, 1983). The cytoarchitecture of the telencephalon has been described in different ray-finned fishes, including teleosts (Nieuwenhuys, 1963; Peter and Gill, 1975; Peter et al., 1975; Northcutt and Braford, 1980; Northcutt and Davis, 1983; Prasada Rao and Finger, 1984; Díez et al., 1987; Marino-Neto and Sabbatini, 1988; Maler et al., 1991; Wullimann et al., 1996; Riedel, 1997; Riedel and Krug, 1997) and tentative homologies between the ventral and dorsal telencephalon with the subpallium and pallium of tetrapods, respectively, have been proposed (Nieuwenhuys, 1963; Northcutt and Braford, 1980; Northcutt and Davis, 1983; Nieuwenhuys and Meek, 1990; Braford, 1995). The ventral telencephalon exhibits a relatively constant pattern of organization in rayfinned fish, although its relative size and the number of cells groups may vary among them (Nieuwenhuys, 1963; Northcutt and Davis, 1983). The dorsal

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Contract grant sponsor: CICYT; Contract grant number: CYTMAR MAR95-1888-C03-02; Contract grant sponsor: UE; Contract grant number: FAIR CT97-3785.

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telencephalon, which shows a greater interspecific diversity in shape and size, was initially divided by Nieuwenhuys (1963) into four zones, three longitudinal zones (medial, dorsal, and lateral zones) and a central zone. Later, Northcutt and Braford (1980) added a fifth caudal zone (posterior zone) characterized by receiving a large number of the secondary olfactory fibers.

Perciformes are representative of the most successful radiation of teleosts and constitute the largest and most diverse order of extant vertebrates (Lauder and Liem, 1983). However, little information is available on their brain organization. To our knowledge, major cell groups comprising the telencephalon have only been reported in the green sunfish, *Lepomis cyanellus* (Northcutt and Davis, 1983), the Siamese fighting fish, *Betta splendens* (Marino-Neto and Sabbatini, 1988), and, more recently, in the gilthead seabream, *Sparus aurata* (Muñoz-Cueto et al., in press). The sea bass (*Dicentrarchus labrax*), a perciform species important for Mediterranean aquaculture, exhibits seasonal spawning coinciding with natural fasting periods (Gutiérrez et al., 1987). Although research on different aspects of sea bass physiology has increased considerably, brain studies have been systematically omitted and only two studies have been directed to elucidate the cerebral distribution of salmon gonadotropin-releasing hormone (Kah et al., 1991) and amines (Batten et al., 1993). Such a situation is probably the consequence of the lack of neuroanatomical information for this species. In this work we present a cytoarchitectonic study of the sea bass telencephalon. This work has been carried out as a basis for the precise localization of neuroendocrine territories and for the tracing of the neuronal systems participating in the regulation of reproduction and metabolism in sea bass.

MATERIALS AND METHODS

Animals

Animals used in this study were adult sea bass (*Dicentrarchus labrax*) specimens (n = 7) obtained from a local fishery (Cupimar, Cádiz, Spain) ranging from 20–30 cm in length.

Histology

Animals were anesthetized in a small tank containing tricaine methasulfonate (MS 222) and perfused transcardially with 0.9% saline solution followed by Bouin's fixative. Brains were removed and postfixed in sublimated Bouin's-Hollande fixative for 24 h, dehydrated, and embedded in paraffin. For cytoarchitectonic analysis, serial sections were cut at 10 μm in the transverse plane on a rotary microtome, mounted in gelatinized slides, stained with cresyl-violet (Gabe, 1968), and analyzed on an Olympus BH-2 photomicroscope. Different cell groups were identified according to the following criteria: 1) characteristic size, shape, and staining intensity of the perikaryon; 2) packing density and distribution pattern of the cell bodies; 3) neuropil surrounding cell groups; and 4) consistency of cell groups in different brains. The brain most symmetrically sectioned was photographed at different magnifications using panchromatic Agfapan APX 25 Films (AGFA). Representative sections were copied onto transparent paper, digitized, and compared to their respective photographs. The section through the anterior commissure was chosen as the transverse zero point. Distances from the zero point are expressed in μm and drawings anterior or posterior to the zero point are indicated as - or +, respectively.

RESULTS

Gross Morphology

Figure 1 shows a lateral view of the brain of *Dicentrarchus labrax* and the lines indicate the levels of the transverse sections illustrated in Figure 2. The most rostral part of the brain is occupied by sessile olfactory bulbs coupled to telencephalic hemispheres (Fig. 1). Three main sulci can be distinguished in the surface of the cerebral hemispheres (Fig.2E): 1) the sulcus ipsilyformis, in the dorsal surface of the telencephalon; 2) the sulcus limitans, in the medial zone, which delimits medially the dorsal and ventral telencephalic areas; and 3) the sulcus externus, a pronounced fissure in the basal region that marks the ventrolateral limits between the dorsal and ventral telencephalon. The serial sections revealed two additional sulci: i) a pronounced sulcus that separates Dm2 and Dm3 rostrally, two divisions of the medial part of the dorsal telencephalon (Dm) (Fig. 2E, open arrowhead); and ii) a sulcus associated with the end of the dorsal division of the lateral part of the dorsal area (Dld), which separates it from the onset of the posterior division of the lateral part of the dorsal telencephalon (Dlp) (Fig. 2F,G).

Olfactory Bulbs

The olfactory bulbs of sea bass are sessile. As in other teleosts, histological analysis reveals an arrangement in five concentric laminae in the following centripetal order (Fig. 2A): the primary olfactory fiber layer (OLN); the glomerular layer (GL); the external cell layer (ECL), characterized by the presence of large mitral cells and smaller, rounded neurons; the secondary olfactory fiber layer (SOF); and the internal cell layer (ICL), which is formed by small, densely packed cells. Although a ventricular cavity cannot be distinguished in the olfactory bulbs, a region almost devoid of cells is evident in the center of the internal cell layer (Fig. 2A). Small clusters of a few, large terminal nerve ganglion cells are present in the caudomedial olfactory bulbs (Figs.

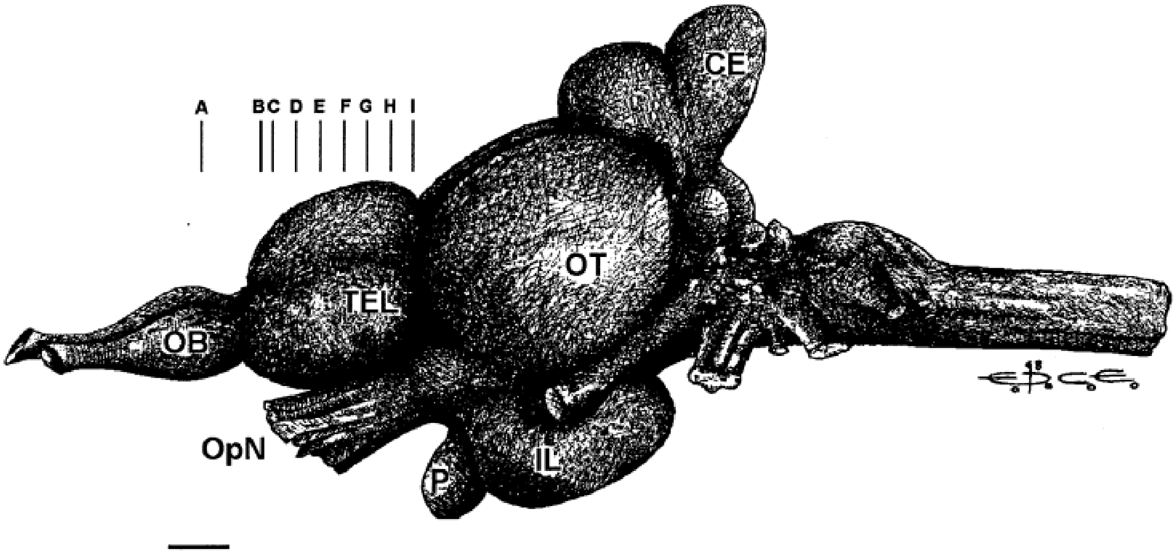


Fig. 1. Lateral view of the brain of the sea bass (*Dicentrarchus labrax*). Lines indicate the levels of the transverse sections in Figure 2. Scale bar is 1 mm. CE, cerebellum; IL, inferior lobe of the hypothalamus; OB, olfactory bulbs; OpN, optic nerve; OT, optic tectum; P, pituitary; TEL, telencephalon.

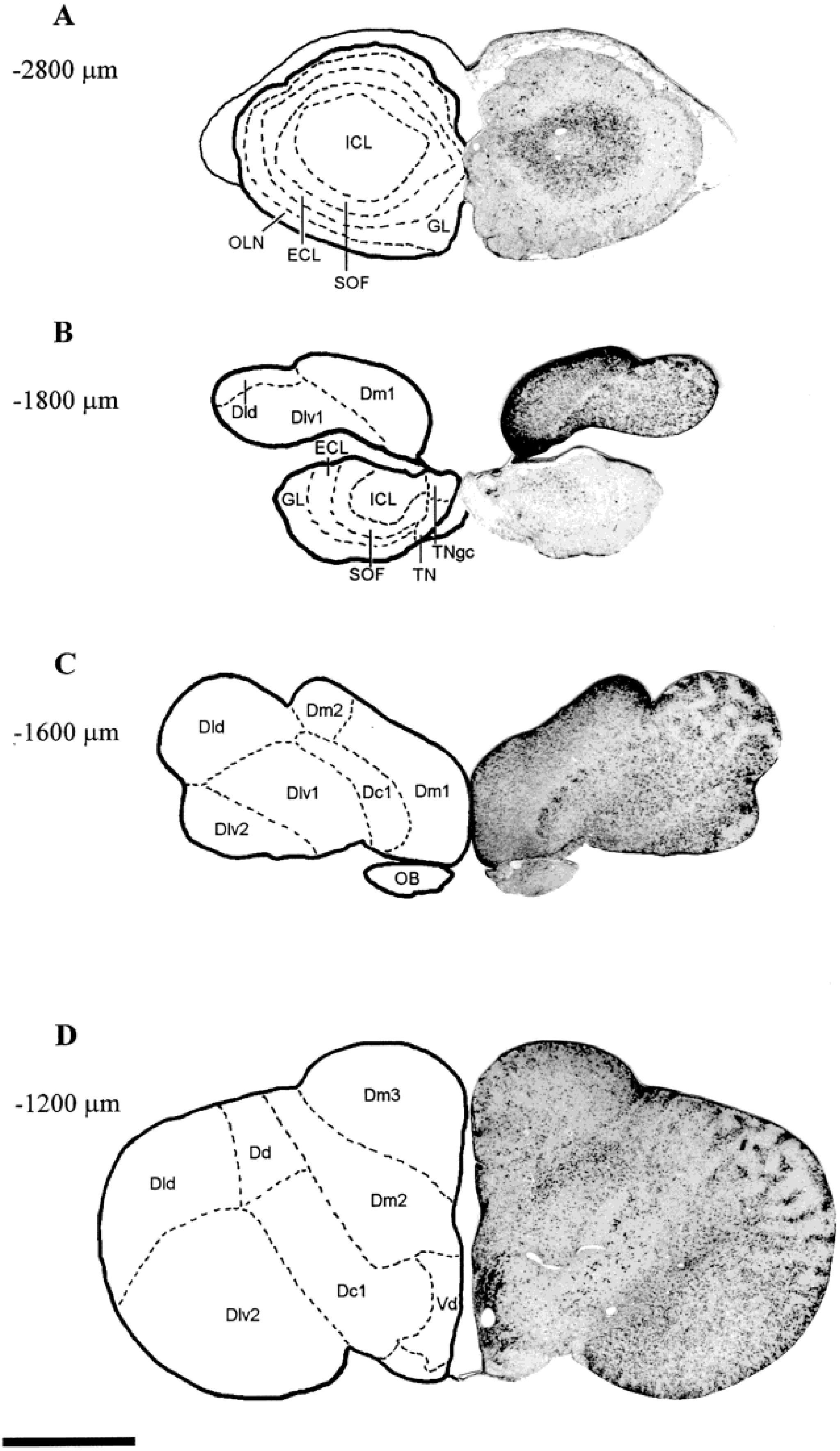
2B, 4A). Caudally, the concentric organization of the bulbs is less evident and the cells of the internal cell layer join the ventral telencephalon.

Telencephalic Hemispheres

As in other species, the sea bass telencephalic hemispheres can be divided into two main regions, the ventral telencephalon (V) and the dorsal telencephalon (D). Using the histological criteria defined above, we divided the ventral and the dorsal telencephalon into 9 and 13 cell masses, respectively.

Ventral telencephalon. In sea bass, the olfactory bulb is replaced caudally by the ventral telencephalon. The rostralmost cell mass appearing in the ventral telencephalon is the dorsal nucleus (Vd), which lies on the ventral border of the medial ventricle (Figs. 2D, 3A). The dorsal nucleus of the ventral telencephalon is characterized by the presence of medium-sized, rounded, and darkly stained cells (Fig. 3A). The ventral nucleus of the ventral telencephalon (Vv) appears caudal to the dorsal nucleus along the ventromedial periventricular surface, displacing it dorsally (Figs. 2E, 3A). The cells of the ventral nucleus are smaller and more lightly stained than those of the dorsal nucleus. More caudally, the neurons of the ventral nucleus become more loosely distributed and a lamina of intensely stained cells is evident parallel to the ventricular surface (Fig. 3B). In sea bass, an ependymal column of small, densely stained and packed cells line the ventricle and is associated with the most dorsal aspect of ventral nucleus (Fig. 3A,B). This structure resembles the lateral septal organ (LSO) described in birds and we have assigned this nomenclature to it. Slightly rostral to the anterior commissure, the dorsal nucleus is displaced laterally by the supracommissural nucleus of the ventral telencephalon (Vs) (Figs. 2F, 3B). The supracommissural nucleus is clearly differentiated from the dorsal nucleus because their cells are smaller, more lightly stained, and less densely packed. More caudally, the supracommissural nucleus is replaced by the postcommissural nucleus (Vp), which marks the telencephalic–diencephalic transition (Fig. 2G,H). This cell mass is composed of small cells organized in clusters (Fig. 3C).

Two migrated cell masses are observed in the lateral region of the ventral telencephalon at the precommissural level. Rostrally, the lateral nucleus of the ventral telencephalon (Vl) starts as a collection of small and scattered neurons located dorsomedially to the sulcus externus (Figs. 2E,F, 3B). Slightly caudal and dorsolateral to the lateral nucleus appears the central nucleus of the ventral telencephalon (Vc), which contains larger and more intensely stained neurons. At its rostral pole, the cells of the central nucleus are relatively grouped (Figs. 2F, 3B), but caudally they adopt a more diffuse appearance between the fibers of the lateral forebrain bundles (LFB) (Fig. 2G). At the postcommissural level, the entopeduncular nucleus (E) appears, bordering the lateral forebrain bundle ventromedially (Fig. 2H,I). This nucleus is composed of very small, densely packed, and deeply stained neurons (Fig. 3D). In the caudal telencephalon, small cells lying in a dorsomedial position to the lateral forebrain bundle are recognized as the intermediate nucleus of the ventral telencephalon (Vi).


A
-2800 µm
ICL
OLN
ECL
SOF
GL
B
-1800 µm
Dld
Dlv1
Dm1
ECL
GL
ICL
SOF
TN
TNgc
C
-1600 µm
Dld
Dm2
Dlv1
Dc1
Dm1
Dlv2
OB
D
-1200 µm
Dm3
Dd
Dld
Dm2
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Vd
Dlv2

Figure 2.

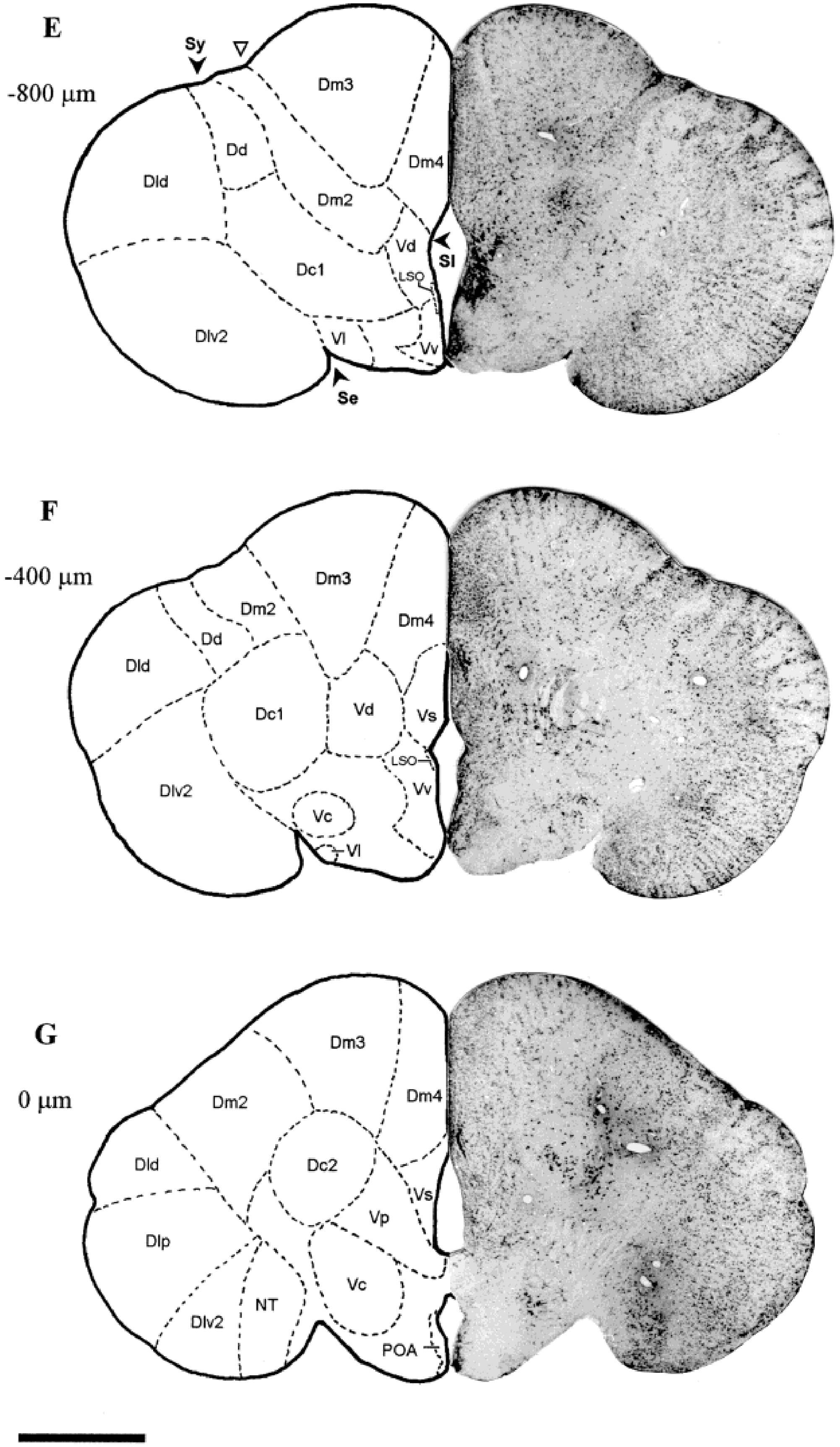


Figure 2. (Continued.)

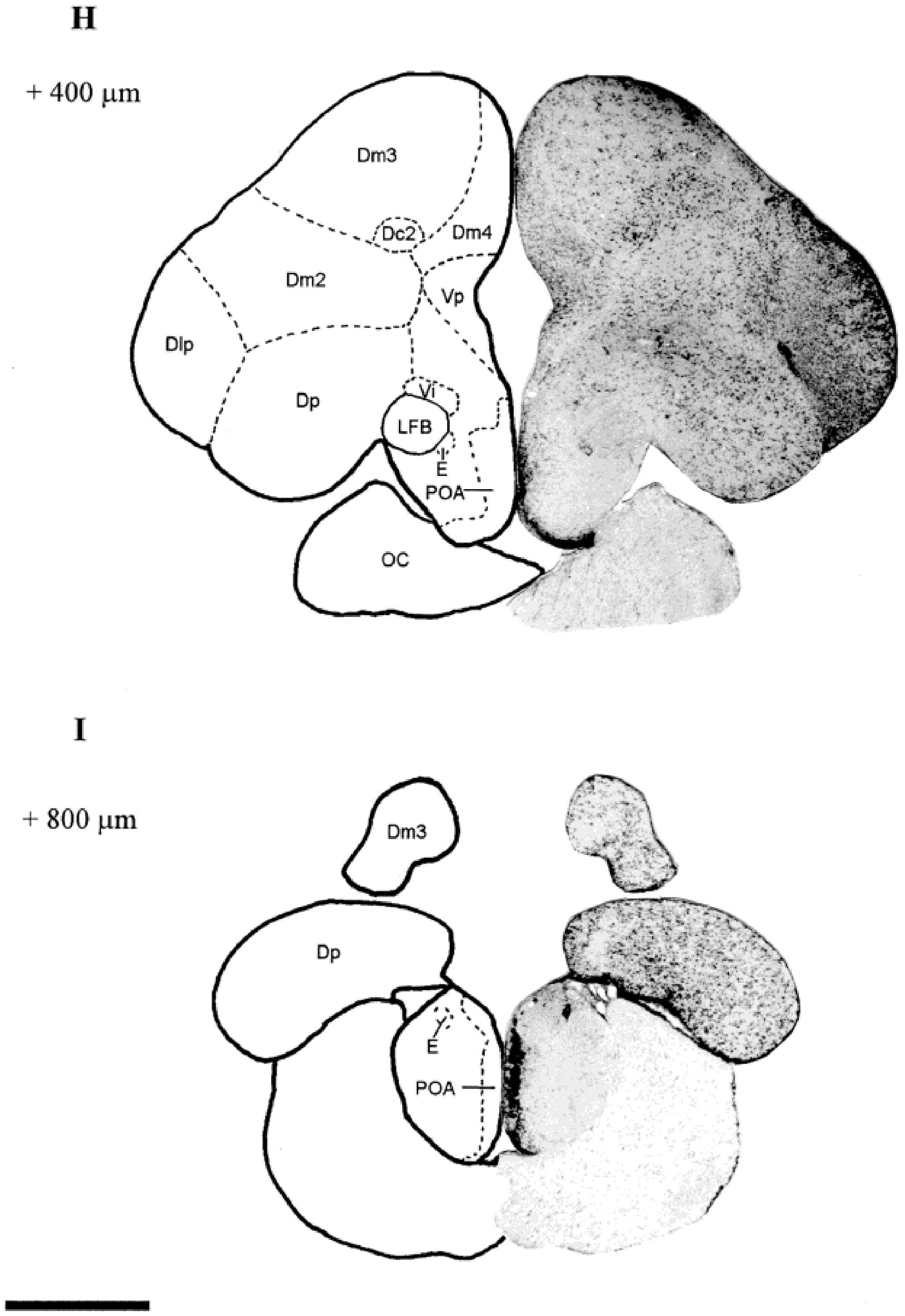


Fig. 2. Sequence of transverse sections from rostral (**A**) to caudal (**I**) level in the telencephalon of the sea bass *Dicentrarchus labrax*. Photomicrographs on the right are stained with cresyl-violet; hemisections drawn on the left show the different regions. Distances from the zero point (anterior commissure) are expressed in µm (−, rostrally; +, caudally). Solid arrowheads in **E** represent the main telencephalic sulci. Open arrowhead in **E** shows a dorsal unnamed telencephalic sulcus. Scale bar is 1 mm. Dc1, central part of the dorsal telencephalon, subdivision 1; Dc2, central part of the dorsal telencephalon, subdivision 2; Dd, dorsal part of the dorsal telencephalon; Dld, dorsal division of the lateral part of the dorsal telencephalon; Dlp, posterior division of the lateral part of the dorsal telencephalon; Dlv1, ventral division of the lateral part of the dorsal telencephalon, subdivision 1; Dlv2, ventral division of the lateral part of the dorsal telencephalon, subdivision 2; Dm1, medial part of the dorsal telencephalon, subdivision 1; Dm2, medial part of the dorsal telencephalon, subdivision 2; Dm3, medial part of the dorsal telencephalon, subdivision 3; Dm4, medial part of the dorsal telencephalon, subdivision 4; Dp, posterior part of the dorsal telencephalon; E, entopeduncular nucleus; ECL, external cellular layer of olfactory bulbs; GL, glomerular layer of olfactory bulbs; ICL, internal cellular layer of olfactory bulbs; LFB, lateral forebrain bundle; LSO, lateral septal organ; NPO, preoptic nucleus; NT, nucleus taenia; OB, olfactory bulb; OC, optic chiasma; OLN, olfactory nerve layer of olfactory bulbs; POA, preoptic area; Se, sulcus externus; Sl, sulcus limitans; SOF, secondary olfactory fiber layer of olfactory bulbs; Sy, sulcus ipsilyformis; TN, terminal nerve; TNgc, terminal nerve ganglion cells; Vc, central nucleus of the ventral telencephalon; Vd, dorsal nucleus of the ventral telencephalon; Vi, intermediate nucleus of the ventral telencephalon; Vl, lateral nucleus of the ventral telencephalon; Vp, postcommissural nucleus of the ventral telencephalon; Vs, supracommissural nucleus of the ventral telencephalon; Vv, ventral nucleus of the ventral telencephalon.

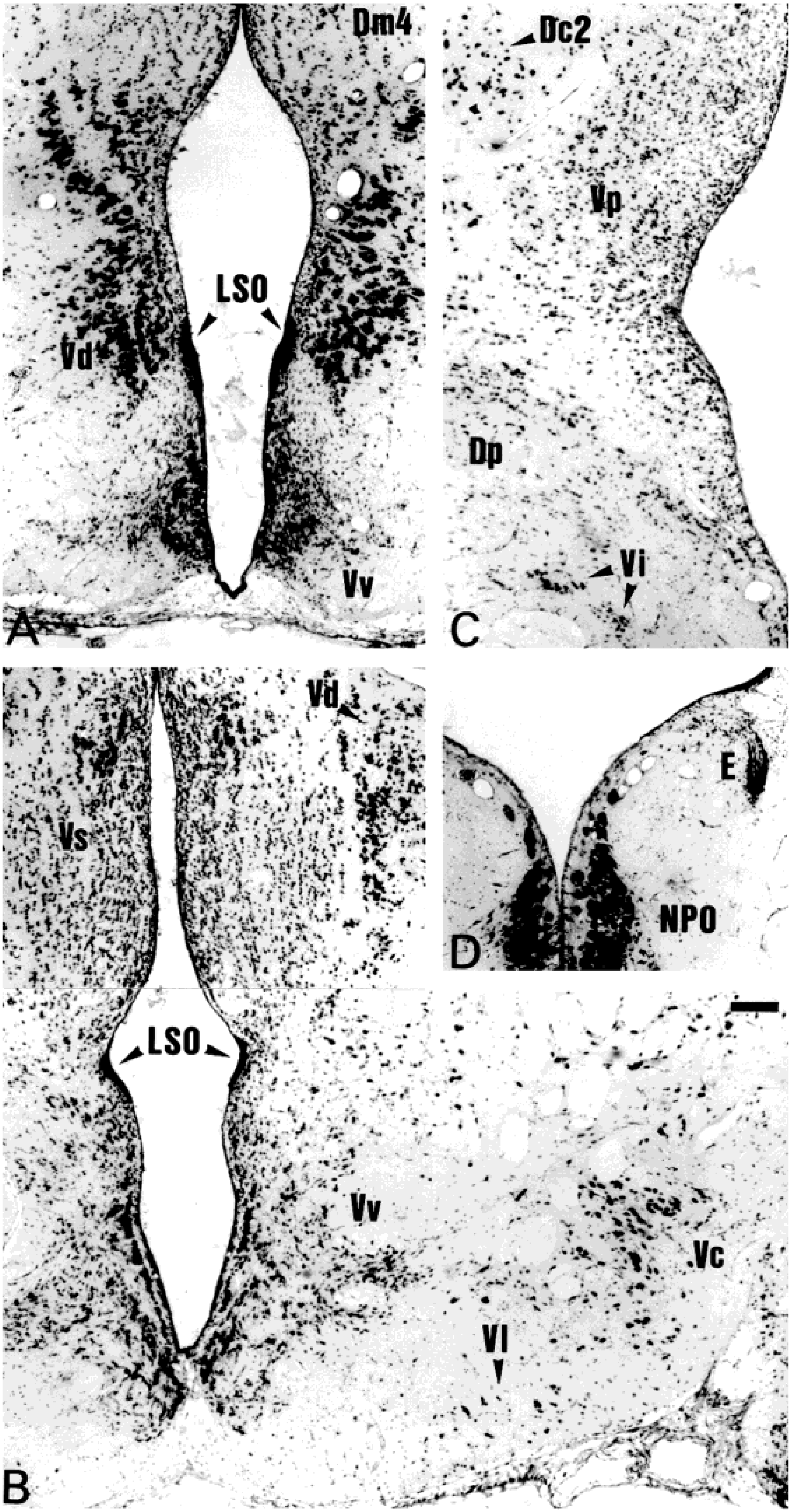


Figure 3.

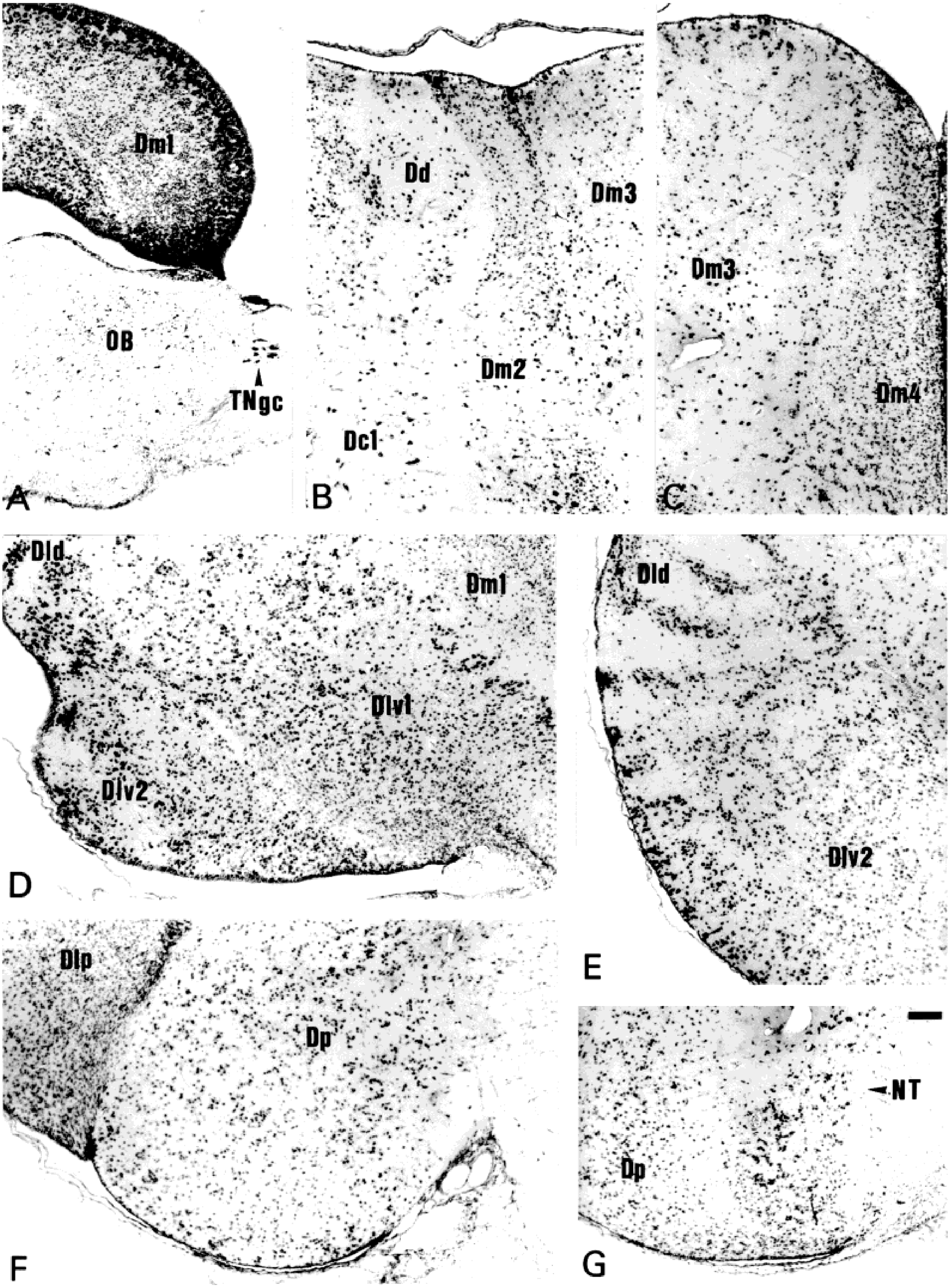
Dorsal telencephalon. The dorsal telencephalon (D) extends throughout the cerebral hemispheres, covering the ventral area. Cell masses in the dorsal telencephalon are organized on five main zones: 1) the medial part (Dm), 2) the dorsal part (Dd), 3) the lateral part (Dl), 4) the central part (Dc), and 5) the posterior part (Dp).

The medial part (Dm) exhibits four major subdivisions, Dm1, Dm2, Dm3, and Dm4, and occupies a large rostro-caudal extent, reaching the most caudal portions of the dorsal telencephalon. The medial subdivision 1 (Dm1) is bounded dorsally by the second subdivision of the medial part and laterally by Dc1, the first subdivision of the central part of the dorsal telencephalon (Fig. 2C), and consists of small, rounded, intensely stained cells (Fig. 4A). In addition, a subpopulation of larger cells appears firmly packed near the ventricle (Fig. 4A). At a more caudal level, the cells in Dm1 adopt a laminar disposition in parallel to the ventricular surface, as this nucleus is progressively replaced by the dorsal nuclei of the ventral telencephalon. The subdivision 2 of the medial part (Dm2) starts slightly caudal to Dm1 (Fig. 2C). At rostral levels, Dm2 is bounded laterally by the dorsal part (Dd) and the subdivision 1 of the central part (Dc1) of the dorsal telencephalon and is characterized by the presence of medium-sized and loosely scattered cells (Fig. 4B). More caudally, Dm2 becomes larger in size and exhibits smaller and more intensely stained cells, which are occasionally arranged in clusters (Fig. 2D,E). As the subdivision 3 of the medial part (Dm3) begins, in the dorsomedial pole of the telencephalon (Fig. 2D), the Dm2 shifts laterally, losing its medial position (Fig. 2E–H). Cell-free laminae clearly delimit the Dm2 from both the Dm3 and the dorsal part of the dorsal telencephalon (Fig. 4B). The subdivision 3 (Dm3) is the largest subdivision of the medial part and is composed of medium-sized scattered cells organized in small clusters (Fig. 4B,C). This subdivision adopts the shape of an inverted triangle (Fig. 2E–G) and exhibits larger and more intensely stained cells in its ventral pole. The caudal subdivision of the medial part of the dorsal telencephalon, Dm4, starts in a medial position, displacing Dm2 and Dm3 laterally (Fig. 2E–H). The Dm4 is rostroventrally bounded by the dorsal nuclei of the ventral telencephalon (Figs. 2E, 3A) and appears laterally separated from Dm3 by a space devoid of cells (Figs. 2E, 4C). Caudally, two cell masses of the ventral telencephalon, the supracommissural (Vs) and postcommissural (Vp) nuclei, delimit the ventral border of Dm4 (Fig. 2G,H). The cells of Dm4 are small, rounded, and appear intensely stained with cresyl-violet (Fig. 4C). They are organized in clusters that adopt a laminar arrangement in parallel with the medial ventricle.

The dorsal part of the dorsal telencephalon (Dd) appears associated with the sulcus ipsilyformis in the dorsal surface of the telencephalon (Fig. 2D–F). This nucleus is bounded medially by Dm2 and laterally by the dorsal division of the lateral part of the dorsal telencephalon (Dld). The boundaries between the dorsal part of the dorsal telencephalon and Dm2 are clearly defined, but the limits between the former and the dorsal division of the lateral part of the dorsal telencephalon are less evident, especially at the caudal level (Fig. 4B). Rostrally, the dorsal part of the dorsal telencephalon is formed by a narrow lamina of small cells, which become larger and more intensely stained in the central zone (Fig. 4B). This nucleus moves slightly lateral as the medial part of the dorsal telencephalon increases in size, and it finally seems to merge with the Dm2 and the dorsal division of the lateral part of the dorsal telencephalon (Fig. 2F,G).

The lateral zone of the dorsal telencephalon (Dl) is one of the most extensive components of the telencephalon in the sea bass, extending throughout the complete rostro-caudal course in the dorsolateral and ventrolateral regions of the cerebral hemispheres (Fig. 2B–H). Three major divisions are found in the lateral zone: 1) the ventral division (Dlv), 2) the dorsal division (Dld), and 3) the posterior division (Dlp). In turn, the ventral division can be divided into two cell populations. The lateral–ventral subdivision 1 (Dlv1) emerges more rostrally and is bounded medially by the central subdivision 1 (Dc1) and caudolaterally by lateral–ventral subdivision 2 (Dlv2) (Figs. 2B,C, 4D). The Dlv1 contains small cells that appear densely packed against the ventromedial surface of the telencephalon and move to a more central position coinciding with the rise of the Dlv2. The cells in the Dlv2 are slightly larger and organized in tight columns oriented perpendicularly to the ependymal surface (Figs. 2E,F, 4E). The dorsal division of the lateral part of the dorsal telencephalon (Dld) is clearly differentiated from the Dlv2 because the cells are larger and the neuropil between cell laminae is more evident in the former (Figs. 2D–F, 4E). Caudally, the dorsal division of the lateral part of the dorsal telencephalon is replaced by the posterior division of the lateral part (Dlp), in

Fig. 3. Photomicrographs of transverse sections of *Dicentrarchus labrax* brain stained with cresyl-violet showing at higher magnification the different nuclei of the ventral telencephalon. **A**: Section at the level of Figure 2E. **B**: Section at the level of Figure 2F. **C**: Section at the level of Figure 2H. The Dc2 is also evident at the top left. **D**: Section at the level of Figure 2I. The scale bar in **B** represents 100 μm and is the same for **A**, **C**, and **D**. Dc2, central part of the dorsal telencephalon, subdivision 2; Dm4, medial part of the dorsal telencephalon, subdivision 4; Dp, posterior part of the dorsal telencephalon; E, entopeduncular nucleus; LSO, lateral septal organ; NPO, preoptic nucleus; Vc, central nucleus of the ventral telencephalon; Vd, dorsal nucleus of the ventral telencephalon; Vi, intermediate nucleus of the ventral telencephalon; Vl, lateral nucleus of the ventral telencephalon; Vp, postcommissural nucleus of the ventral telencephalon; Vs, supracommissural nucleus of the ventral telencephalon; Vv, ventral nucleus of the ventral telencephalon.


Dm1
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Dlv2
D
Dld
Dlv2
E
Dlp
Dp
F
NT
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G

Figure 4.

which the cells appear more densely packed and organized in clusters (Figs. 2G,H, 4F). The nucleus taenia (NT) lies in the caudal telencephalon, lateral to the sulcus externus (Fig. 2G) and is characterized by its intensely stained neuropil and the presence of darkly stained and densely packed cells. At this level, the Dlv2 ends and its place is occupied by the posterior part of the dorsal telencephalon (Dp), which exhibits small and medium-sized cells organized in horizontal columns (Figs. 2H,I, 4F,G).

The central part (Dc) fills the central region of the dorsal telencephalon, between the medial, dorsal, and lateral parts. Two divisions have been recognized in the central part of sea bass, Dc1 and Dc2. Rostrally, Dc1 has an elongated shape and its major axis is oriented in a ventromedial to dorsolateral direction (Fig. 2C–E). This nucleus contains large, fusiform, and intensely stained cells, which are widely scattered in the neuropil and sometimes appear grouped in pairs or triplets (Fig. 4B). Medially, cells in the Dc1 are slightly smaller and less intensely stained than the lateral ones (Fig. 2D,E). Progressively, the Dc1 adopts a more circular shape and cells become even more widely spaced (Fig. 2F). At postcommissural levels, Dc2 replaces Dc1. It adopts a more dorsal position and is composed of slightly smaller and more intensely stained cells (Figs. 2G,H, 3C).

DISCUSSION

Although topography and number of telencephalic cell masses may vary from species to species, the general organizational pattern of the sea bass telencephalon is similar to that described for other teleosts (Northcutt and Davis, 1983). The rostral extreme of the sea bass brain is occupied by nonpedunculated olfactory bulbs coupled to paired cerebral hemispheres. Twenty-two distinct telencephalic cell groups were recognized, which were classified in two main areas, ventral and dorsal telencephalon.

The histological pattern of the ventral area seems to be more constant among actinopteryrian fishes (Nieuwenhuys, 1963; Northcutt, 1995). However, it should be noted that teleosts exhibit the largest number of cell groups. We recognized in the ventral telencephalon of sea bass the same subdivisions found in other perciform species, e.g., green sunfish (Northcutt and Braford, 1980; Northcutt and Davis, 1983), Siamese fighting fish (Marino-Neto and Sabbatini, 1988), or gilthead seabream (Muñoz-Cueto et al., in press). The ventral telencephalon has also been occasionally divided into pre- and postcommissural aspects (Northcutt and Braford, 1980; Riedel, 1997). In sea bass, the dorsal (Vd), ventral (Vv), and lateral (Vl) nuclei of the ventral telencephalon represent the main precommissural nuclei, the central (Vc) and supracommissural (Vs) nuclei lie at the commissural level, and the postcommissural (Vp), intermediate (Vi), and entopeduncular (E) nuclei are found at the postcommissural position. Topological, immunohistochemical, and connectivity studies were attempted to establish presumptive homologies between subpallial nuclei of tetrapods and the nuclei of the ventral telencephalon of the ray-finned fish (Northcutt, 1995). Thus, the ventral nucleus has been homologized with the lateral septal nucleus of other gnathostomes, but a homology with the nucleus accumbens and other ventral telencephalic nuclei cannot be discarded. As in seabream (Muñoz-Cueto et al., in press), we found a ventricular structure in sea bass that is associated with the dorsal aspect of the ventral nucleus and resembles the lateral septal organ described in avian (Baylé et al., 1974; Kuenzel and Masson, 1988). In birds, the lateral septal organ is composed of cerebrospinal fluid-contacting cells located in the ependymal layer of the telencephalic lateral ventricles. The putative homology between this teleost structure and the avian lateral septal organ would further support the consideration that the ventral nucleus of the ventral telencephalon of ray-finned fish might represent a septal nucleus. In turn, the dorsal nucleus has been thought to correlate with the corpus striatum, the lateral nucleus with the medial septal nucleus and olfactory tubercle, the supracommissural nucleus with the bed nucleus of stria terminalis, and the postcommissural nucleus with the basal amygdala (Northcutt, 1995). The intermediate nucleus of the ventral telencephalon is also evident in the caudal telencephalon of sea bass. This migrated nucleus has been recognized in holosteans and some teleosts (Bass, 1981; Northcutt and Davis, 1983) but not in other teleosts (Riedel, 1997). The entopeduncular nucleus is perhaps the most variable structure of the ventral telencephalon in ray-finned fish. Three different cell groups (dorsal, ventral, and caudal) have been described in *Polypterus,* while a single-cell group was detected in teleosts, e.g., *Salmo,* green

Fig. 4. Photomicrographs of transverse sections of *Dicentrarchus labrax* brain stained with cresyl-violet showing at higher magnification the different nuclei of the dorsal telencephalon. **A**: Section at the level of Figure 2B. **B**, **C**: Sections at the level of Figure 2E. **D**: Section at the level of Figure 2C. **E**: Section at the level of Figure 2D. **F**: Section at the level of Figure 2H. **G**: Section slightly rostral to the level of Figure 2H. The scale bar in G represents 100 μm and is the same for **A** to **F**. Dc1, central part of the dorsal telencephalon, subdivision 1; Dd, dorsal part of the dorsal telencephalon; Dld, dorsal division of the lateral part of the dorsal telencephalon; Dlp, posterior division of the lateral part of the dorsal telencephalon; Dlv1, ventral division of the lateral part of the dorsal telencephalon, subdivision 1; Dlv2, ventral division of the lateral part of the dorsal telencephalon, subdivision 2; Dm1, medial part of the dorsal telencephalon, subdivision 1; Dm2, medial part of the dorsal telencephalon, subdivision 2; Dm3, medial part of the dorsal telencephalon, subdivision 3; Dm4, medial part of the dorsal telencephalon, subdivision 4; Dp, posterior part of the dorsal telencephalon; NT, nucleus taenia; OB, olfactory bulb; TNgc, terminal nerve ganglion cells.

sunfish (Northcutt and Davis, 1983), *Barbus* (Diez et al., 1987), Siamese fighting fish (Marino-Neto and Sabbatini, 1988), or gilthead seabream (Muñoz-Cueto et al., in press). According to the teleost pattern, the entopeduncular nucleus of sea bass is represented by a single-cell population composed of very small and densely packed cells.

As a consequence of differences in the eversion processes of the telencephalic walls, the dorsal telencephalon of ray-finned fish shows much more interspecific variations than the ventral telencephalon. In sea bass, as in other teleosts, the dorsal telencephalon has been divided into five main cell populations: the medial part (Dm), dorsal part (Dd), central part (Dc), lateral part (Dl), and posterior part (Dp) (Northcutt and Davis, 1983).

On the basis of histochemical and histological analysis, different subdivisions have been found in the medial part of the dorsal telencephalon of teleosts. While Bass (1981) contemplated a single dorsal–medial zone in *Ictalurus punctatus*, two subdivisions were observed in *Sebastiscus marmoratus* (Murakami et al., 1983) and *Barbus meridionalis* (Díez et al., 1987) and three subdivisions were considered in *Betta splendens* (Marino-Neto and Sabbatini, 1988). According to that described in *Salmo* (Northcutt and Braford, 1980), green sunfish (Northcutt and Davis, 1983), blind cave fish (*Astyanax hubbsi*) (Riedel, 1997), and gilthead seabream (Muñoz-Cueto et al., in press), four major divisions were observed in the medial part of the dorsal telencephalon of sea bass. Northcutt and Braford (1980) and Northcutt and Davis (1983) reported that Dm3 and Dm4 probably constitute a single functional unit, since high concentrations of acetylcholinesterase and catecholamines distinguish them from the more rostral divisions of the medial part. The homologies of the medial part with cell groups in the telencephalon of tetrapods are uncertain. Reiner and Northcutt (1992), based on immunohistochemical studies, suggested that the medial part of the dorsal telencephalon arose evolutionarily in the most advanced ray-finned fishes, and that no comparable structure is found in tetrapods. However, a homology of the medial part with the pallial amygdala has been suggested on the basis of topological, behavioral, and electrophysiological data (Braford, 1995).

As in other teleosts (Singh, 1969; Muñoz-Cueto et al., in press), the central part of the dorsal telencephalon of sea bass has been divided into two cell groups, a rostral Dc1 and a caudal Dc2. Four subnuclei were observed in the central part of two perciforms, *Lepomis cyanellus* (Northcutt and Davis, 1983) and *Betta splendens* (Marino-Neto and Sabbatini, 1988). The Dc1 and Dc2 of sea bass seem to correlate well, both in position and shape, with Dc1 and Dc4 of green sunfish, respectively (Northcutt and Davis, 1983). However, we cannot identify Dc2 and Dc3 described in the green sunfish. Braford (1995) proposed that the cells of the dorsocentral zone represent migrated neurons of periventricular zones and that each should be considered as a unit with its periventricular neighbor. In fact, it seems that our Dc1 represents a central cells mass of the lateroventral zone of the dorsal telencephalon (Dlv), while Dc2 may represent a migrated cell population of the medial part of the dorsal telencephalon. The ventromedial extent of Dc1 could also represent a migrated cell mass of the ventral telencephalon. It is possible that we cannot distinguish Dc2 and Dc3 described in green sunfish because these cell populations might be less differentiated in sea bass and we have incorporated them within their respective peripheral nuclei (dorsal, lateral–dorsal, and medial parts of the dorsal telencephalon).

The dorsal part of the dorsal telencephalon (Dd) of sea bass is a characteristic cell group that lies in the proximity of the sulcus ipsilyformis. In most teleosts, this zone is characterized by the presence of small and densely packed cells (Northcutt and Davis, 1983). However, Riedel (1997) described in the blind cave fish a dorsal part formed by large cells very similar to those of the lateral part of the dorsal telencephalon. In sea bass, the dorsal part of the dorsal telencephalon is a nucleus composed of small and medium-sized lightly stained cells, which resemble those described in other perciform fishes in position and evolution (Northcutt and Davis, 1983; Marino-Neto and Sabbatini, 1988).

The lateral zone of the dorsal telencephalon (Dl) of sea bass can be rostrally divided into ventral (Dlv) and dorsal (Dld) aspects, which are clearly differentiated based on perikaryal size and cell density. These divisions have been described in most teleost fish studied up to now (Bass, 1981; Northcutt and Davis, 1983; Díez et al., 1987; Riedel, 1997). In *Sebastiscus marmoratus*, histochemistry of zinc and fiber connection studies also allow subdivision of the lateral part of the dorsal telencephalon into a dorsal and a ventral zone (Yamane et al., 1996). Based on cell size and packing density of cells, we further subdivided the ventral zone of the lateral part of the dorsal telencephalon (Dlv) into two cell masses, Dlv1 and Dlv2, Dlv1 being rostral with respect to Dlv2. Three subdivisions of Dlv were observed in gilthead seabream (Muñoz-Cueto et al., in press), but neuronal subpopulations of Dlv have never been described in other teleosts. Our tentative subdivision of the Dlv is based on histological criteria. Additional immunocytochemical and fiber connectivity studies are required in order to further support this subdivision. The dorsal zone of the lateral part (Dld) is replaced caudally by the posterior zone of the lateral part of the dorsal telencephalon (Dlp) that is characterized by having clustered cells. A nucleus with similar characteristics has also been described in other teleost fishes, e.g., the Siamese fighting fish (Marino-Neto and Sabbatini, 1988), green sunfish (Northcutt and Davis, 1983), gilthead seabream (Muñoz-Cueto et al., in press), *Salmo* (Northcutt and Davis, 1983), winter flounder (*Pseudopleuronectes americanus*) (Prasada Rao and Finger, 1984), and *Barbus meridionalis* (Díez et al., 1987). The relative position of the nucleus taenia (NT) varies among teleosts but it generally occupies the posterior telencephalic wall, where the tela choroidea arises (Northcutt and Davis, 1983). In sea bass, the NT appears associated with the posterior end of Dlv2, in the caudal aspect of the dorsal telencephalon. The posterior part of the dorsal telencephalon (Dp) was not initially recognized by Nieuwenhuys (1963) but it was later reported as the principal target of the secondary olfactory fibers (Northcutt and Braford, 1980). In sea bass, as in other teleosts, this posterior part appears at the caudal level of dorsal telencephalon, where it replaces the Dlv2, and is medially limited by the NT. Based on its topological position as well as the connectivity pattern, the posterior part of the dorsal telencephalon has been tentatively compared to the primary olfactory cortex of tetrapods (Braford, 1995).

In summary, we report in this article the telencephalic cytoarchitecture of the sea bass as defined using histological techniques. We have characterized 22 distinct telencephalic cell groups that were classified in two main areas: the ventral telencephalon and the dorsal telencephalon. Similar to the cytoarchitectonic pattern of other ray-finned fishes, the dorsal telencephalon is more variable than the ventral telencephalon. In addition, a structure that resembles the tetrapod lateral septal organ has been described in the ventral telencephalon. This study enlarges the information on telencephalic anatomy in teleosts that is available for comparative purposes. Furthermore, this work will represent a useful neuroanatomical tool for future morphological and functional studies to be done in the brain of sea bass and other related perciform species.

ACKNOWLEDGMENTS

The authors thank Dr. C. Sarasquete and F.J. Rodríguez-Gómez for help during the research and preparation of the manuscript. We thank D. Cuenca for the drawing of the sea bass brain. We thank Dr. C. Piñuela for critical reading of the manuscript. J.M.C-R was recipient of a fellowship from the Balaguer-Gonel Foundation.

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