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## Microscopic Structure of the Brain of *Barbus meridionalis* Risso.

### I. Telencephalon.

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With 7 Figures

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**Summary:** The telencephalon of *Barbus meridionalis* is composed of two oval telencephalic lobes separated by a medial ventricle and joined exclusively by the anterior commissure. Histologically, the dorsal and ventral telencephalic areas are well defined, the limiting plane between them being a cell free zone. In the ventral area it is possible to distinguish the following parts: dorsal, supracommissural, postcommissural, lateral, inter-media and the nucleus entopeduncularis. In the dorsal area there are three peripheral longitudinal zones — medialis, dorsalis and lateralis — together with a central zone; caudally situated is a posterior dorsolateral region which is the main receptor site for olfactory fibers and closely associated to this is the nucleus tenia. The olfactory projections to the telencephalon course along two bundles: the medial and the lateral olfactory tracts.

The telencephalon projects to diencephalic regions via three large bundles: the lateral and medial telencephalic bundles and the strio-medullary system.

### Introduction

SHELDON (1912) and HOLMGREN (1922) established the basis upon which the histological knowledge of the telencephalon was later founded. Prior to this, numerous studies had already been carried out (BELLONCI, 1882; RABL-RUCKARD, 1894; CATOIS, 1901; GOLDSTEIN, 1905; ARIENS-KAPPERS, 1906, 1908, 1911, 1928; JOHNSTON, 1911; VAN DER HORST, 1917; HOLMGREN, 1920), some of them, however, based on mistaken interpretations of the telencephalic lobes.

Later studies provided other descriptions which constitute an approximation to the cytoarchitecture and some of the connections of the major telencephalic areas (ARIENS-KAPPERS et al., 1936; MILLER, 1940; NIEUWENHUYNS, 1959, 1960a, b, 1963; DROOGLEVER FORTUYN, 1961; SCHNITZLEIN, 1962, 1964). However, some aspects remain to be fully elucidated, particularly with respect to the connections and the subdivisions of the major telencephalic areas; this is due to species differences and the heterogeneous criteria employed by different authors (HERRICK, 1922; KUHLENBECK, 1929; KALLEN, 1947; NIEUWENHUYNS, 1963; NORTHUTT and DAVIS, 1982).

The telencephalon of Actinopterygii differs considerably from that of other vertebrates as a result of their ontogenetic development. This takes place by the process named by GAGE (1893) as eversion: during embryonic development the lateral walls of the initial tube-shaped structure curve progressive-

ly outwards and become thicker in their dorsal region, while the ventral portions maintain their original position. The lateral walls constitute the neuronal masses of the telencephalon whereas the dorsal part continues to be fine and membranous, forming the tela telencephali or ependymal roof, which spreads laterally and ventrally while the lateral walls continue their process of eversion. The thickness of these walls and the degree of eversion are highly variable, as reflected in the large diversity of telencephalic types in the different subclasses of Actinopterygii.

In the present work we studied the localization of the telencephalic areas and their principal connections of a freshwater Teleost, *Barbus meridionalis*, common in European rivers but concerning which there are few data in the pertinent scientific literature.

### Material and Methods

Fifteen adult specimens of *Barbus meridionalis* Risso, of the Cypriniform order, captured in the river Tormes (Salamanca, Spain) with a weight of  $185 \pm 8$  g and length of  $23.7 \pm 2.7$  cm were used in this study. After anaesthesia with methyl-sulphonate-ethyl-m-aminobenzoate at 0.03% the animals were decapitated and the encephalon rapidly removed.

Regardless of the fixative employed and of the staining technique used for each of them, all pieces were embedded in "Paraplast"; once shaped, the blocks were cut, obtaining 10  $\mu$ m serial sections of the whole telencephalon.

The following techniques were used: A) For the study of general morphology: Hematoxylin-Eosin; B) To determine

the distribution of neuronal bodies: variants of the Nissl technique, using Thionine or Cresyl Violet; C) To demonstrate myelinic organization: the Kulschitzky and Kluver-Barrera methods.

Analysis of the preparations was conducted by comparing equivalent sections (transverse and longitudinal), stained with the different methods, by direct observation under the microscope, by photos obtained with a Zeiss III photomicroscope, and camera lucida drawings (Zeiss).

## Results

The telencephalon of the *Barbus* is situated on the rostralmost part of the encephalon and comprises the olfactory bulbs and the hemispheres or cerebral lobes (Figs. 1a, 1c, 1d). The olfactory bulbs are formed as evaginations from the anterior parts of the cerebral hemispheres to which they are joined by means of two long fibrous tracts (Figs. 1a, 1c), and in their caudal part they present the bulbar ventricles which are a continuation of the telencephalic ventricle.

As is the case of other Actinopterygii, the *Barbus* has an everted telencephalon; because of this, the cerebral hemispheres are two solid masses separated from each other by a T-shaped medial ventricle (Fig. 1b), displaced towards the surface of the telencephalon and delimited by an ependymal membrane which dorsally covers the telencephalic lobes and is joined to them on their lateral part. On its caudal part the ventricle communicates with the diencephalic and mesencephalic ventricular spaces (Fig. 1e).

The ventricular surface of the telencephalon features a series of grooves which are of use in distinguishing the different areas of the hemispheres:

- The sulcus externus or endorhinal fissure (s. ext) (Figs. 3b, 3c, 4a, 4b, 4c, 7b): this marks the limit between the pallium and the basal parts of the telencephalon. Because in the *Barbus* eversion is very pronounced, this sulcus is deeper than other species or in younger specimens of the same species where eversion is incomplete.
- The diencephalic-telencephalic sulcus or sulcus terminalis telencephali (s. term. t) (Fig. 5a): this is the caudal continuation of the former groove. It is situated in the caudal position with respect to the anterior commissure, separating the preterminal nuclei from the mass of diencephalic preoptic cells.
- Sulcus Ypsiliformis (s. yps.) (Figs. 3a, 3b): this is positioned rostrally on the dorsal surface and courses towards the lateral surface in the caudal portion.
- Sulcus lateralis (s. lat) (BANNISTER, 1972) (Fig. 3c): this is situated ventrolaterally in the anterior

part of the telencephalon, passing caudally to a dorsolateral position to join the sulcus ypsiliformis.

- Sulcus limitans telencephali (s. lim. t) (SHELDON, 1912) (Fig. 3b): this forms the dorsal limit between the pallial and basal parts of the telencephalon and courses dorsocaudally.

Cytoarchitecturally, two main regions may be distinguished: the area ventralis telencephali (V) and the area dorsalis telencephali (D) (KALLEN, 1951) situated in the ventromedial and dorsolateral positions, respectively, in the adult telencephalon. Both areas are equivalent, respectively, to the subpallium and pallium of other vertebrates.

One characteristic of the telencephalon of Teleosts is the absence of a clear differentiation in individualized nuclei (BURR, 1928). However, within the two principal areas it is possible to distinguish several

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Fig. 1. Schemes of microscopic views of the encephalon of *B. meridionalis*.

- a) Dorsal view, showing the olfactory bulbs and tracts.
- b) Coronal section showing the ventricular organization.
- c) Ventral view.
- d) Lateral view.
- e) Longitudinal section showing ventricular organization.

Figs. 2—6: The schemes represent a series of transverse sections of the telencephalon. The level of each section is shown in the small drawing in the upper left corner.

2: Rostral section of the telencephalon. This begins with Dc surrounded by Dm and Dl.

Figs. 3—5 see page 258—260

3a, b, c: Transverse sections before the anterior commissure; the olfactory tracts reach the base of the telencephalon; they split into two components: the tom, which intermingles its fibres with Vd cells and caudally with Vv cells; and the tol which shifts laterally and penetrates into the telencephalon at the beginning of the s. ext.; it arches over this, occupying the zone of the Dl adjacent to the meningeal surface.

- 4: a) Transverse section rostral to the anterior commissure: the tom divides into two components, tom-dl and tom-vm. The axons of the ltb descend in separate fascicles to the basal meningeal surface. The Dlp appears, occupying the ventrolateral lobe.
- b) The beginning of mtb, the NT and the NE grouped around a fascicle of the ltb appear at the level of anterior commissure.
- c) Transverse section through the caudal part of the anterior commissure, the preoptic recess reaches the telencephalon, the tractus tenia courses ventral to the NT.

5a, b, c: These sections correspond to the end of the telencephalon and the beginning of the diencephalon and mesencephalon (optic tectum): the ltb-d, t.olf-H and tohi course caudally through the preoptic region.

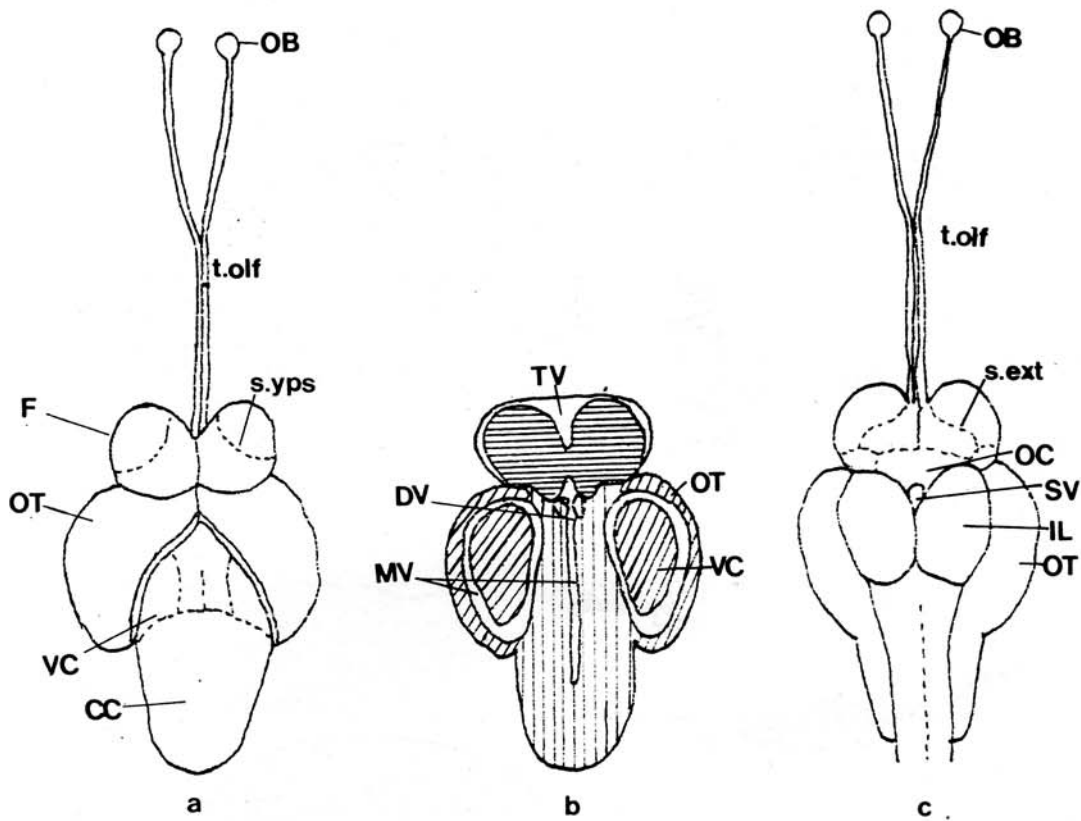


Fig.1

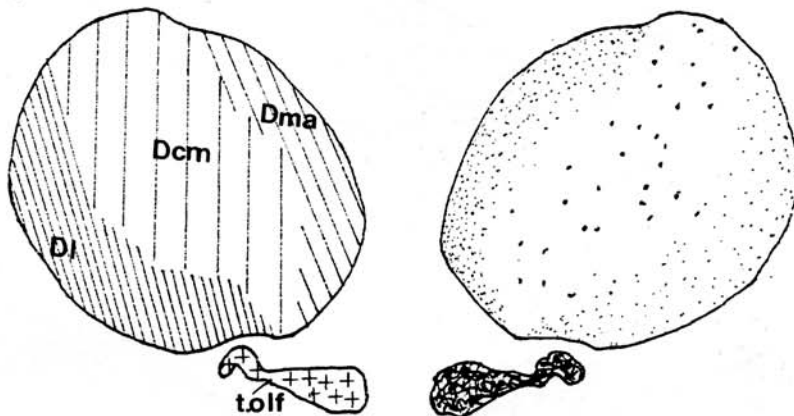
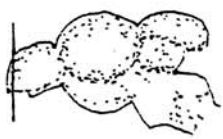
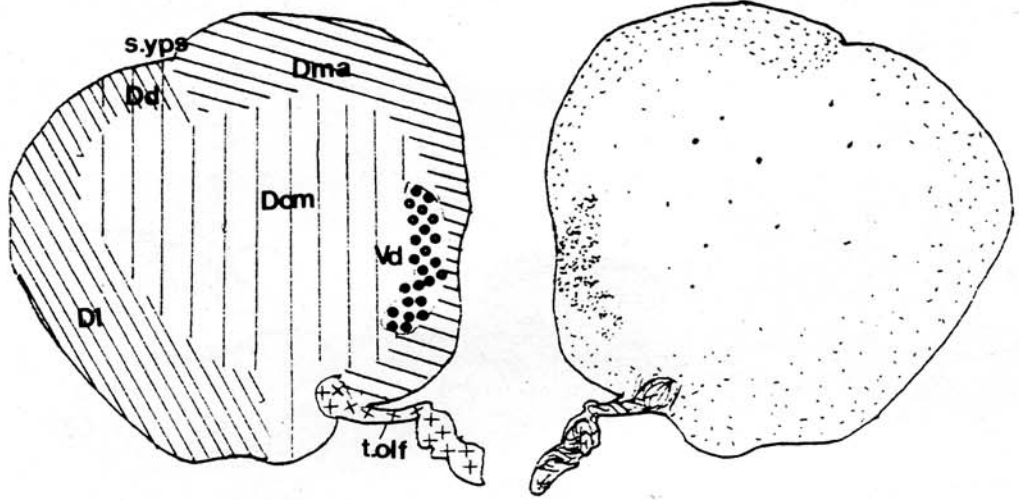
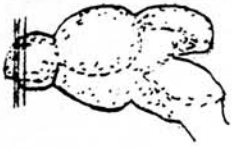
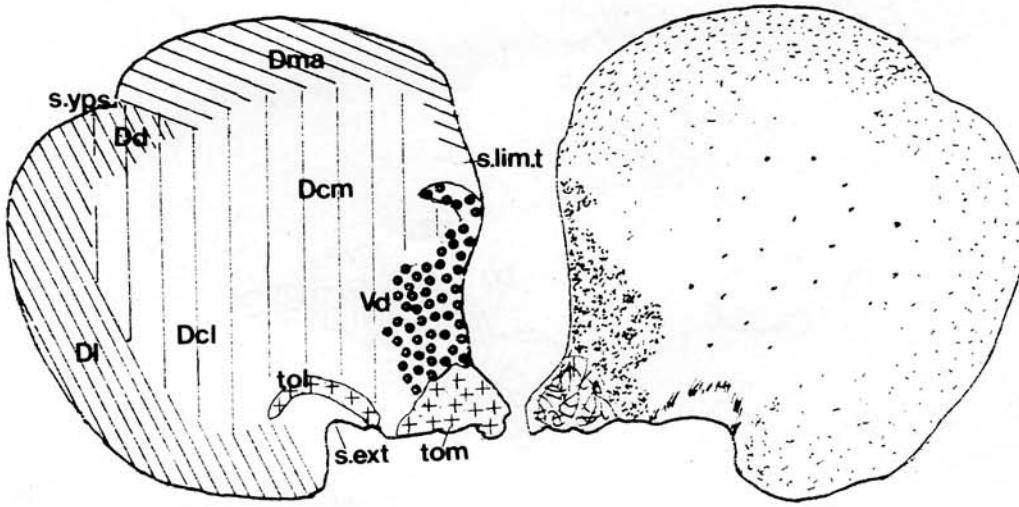


Fig.2

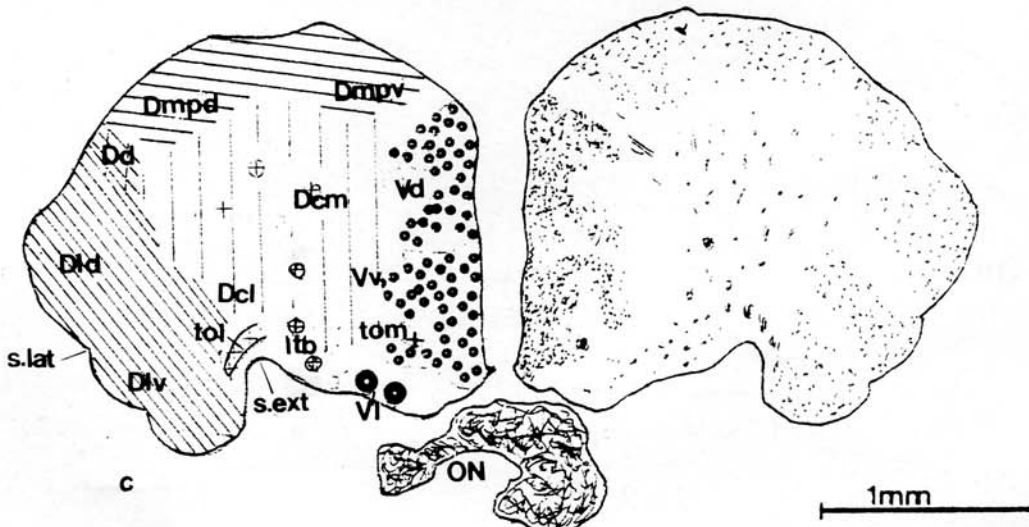
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a

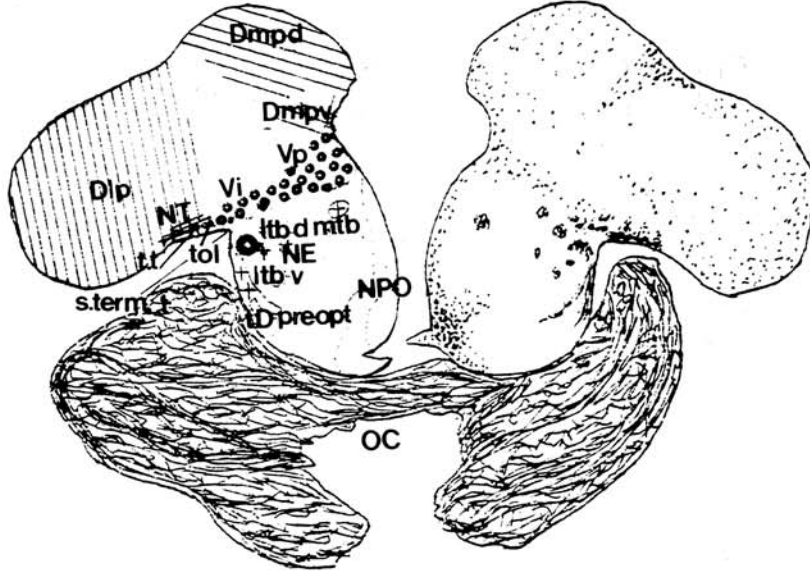
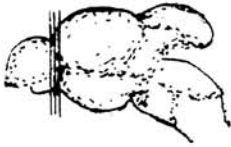


b

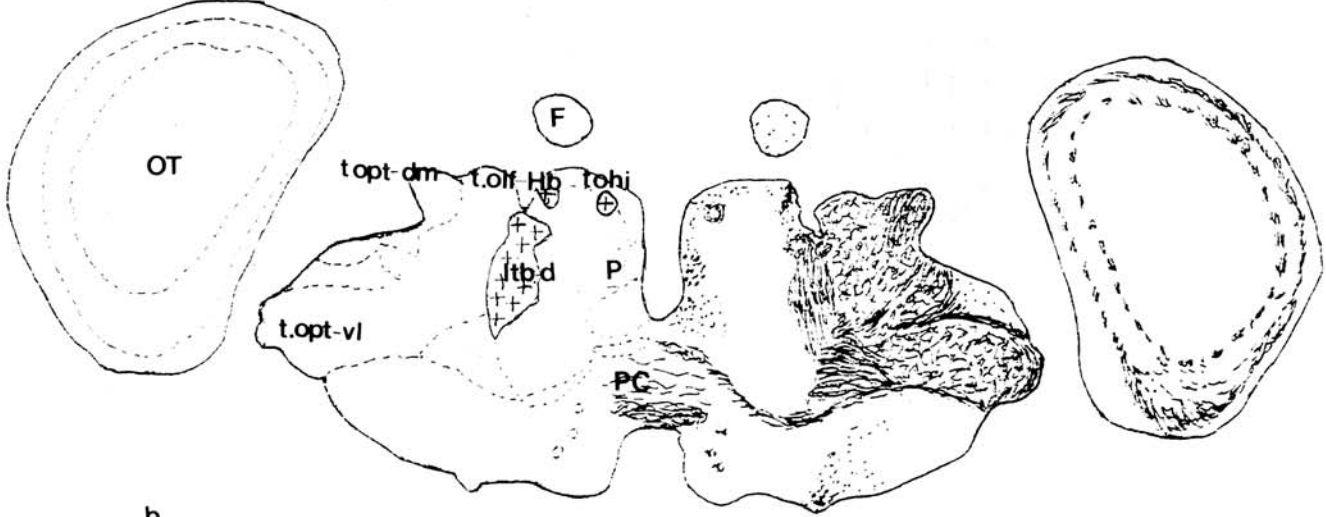


c

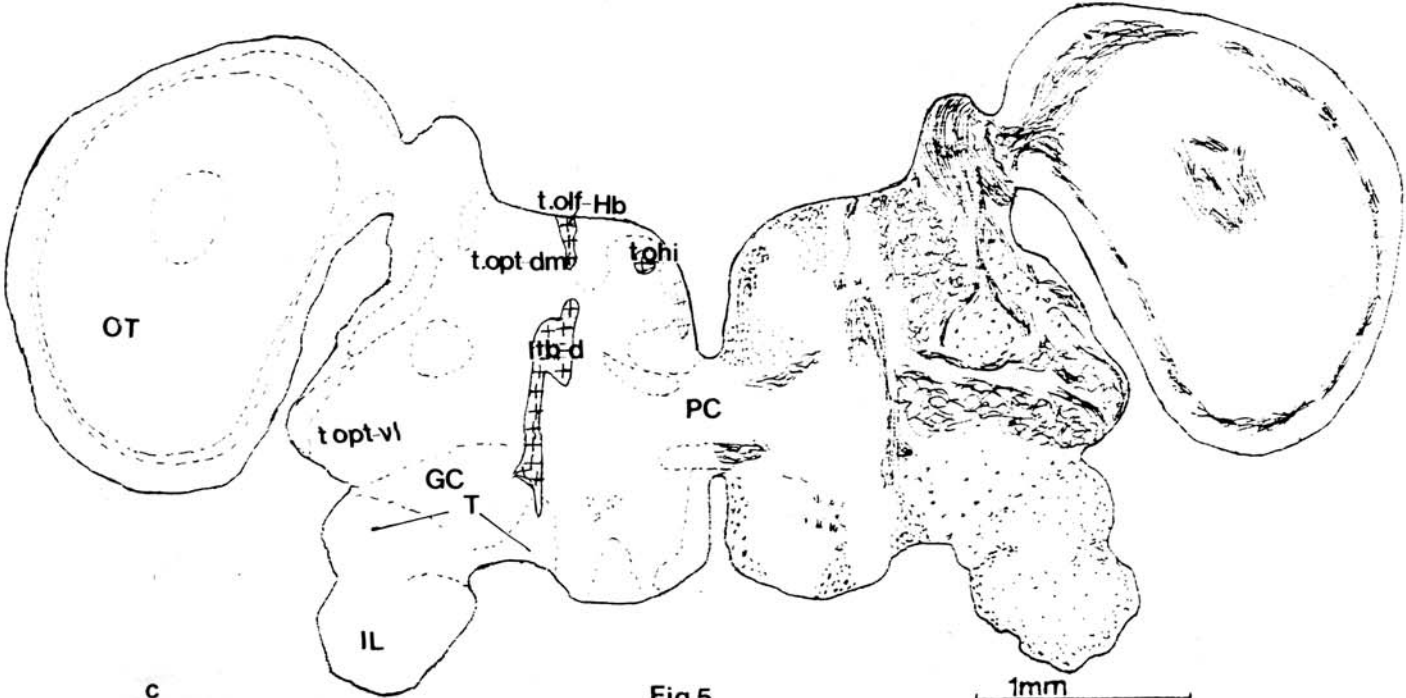
Fig.3



a

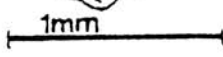


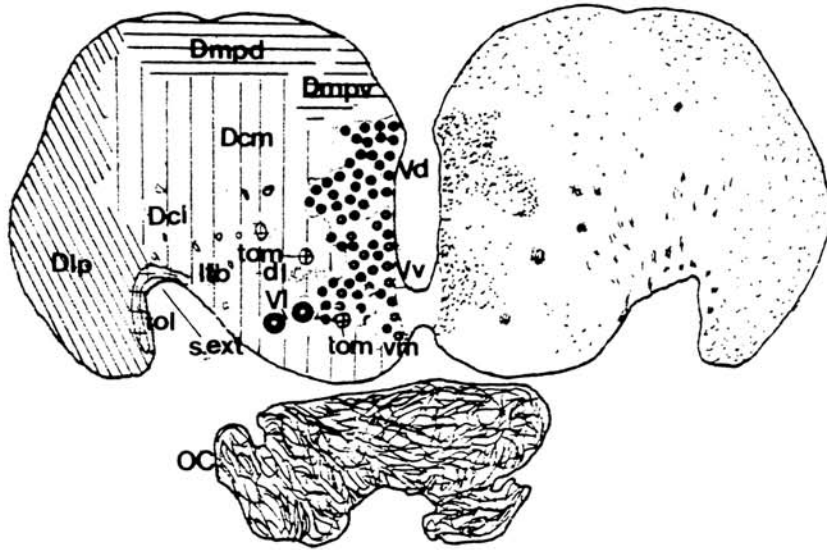
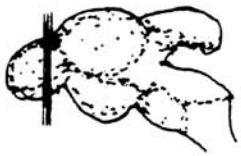
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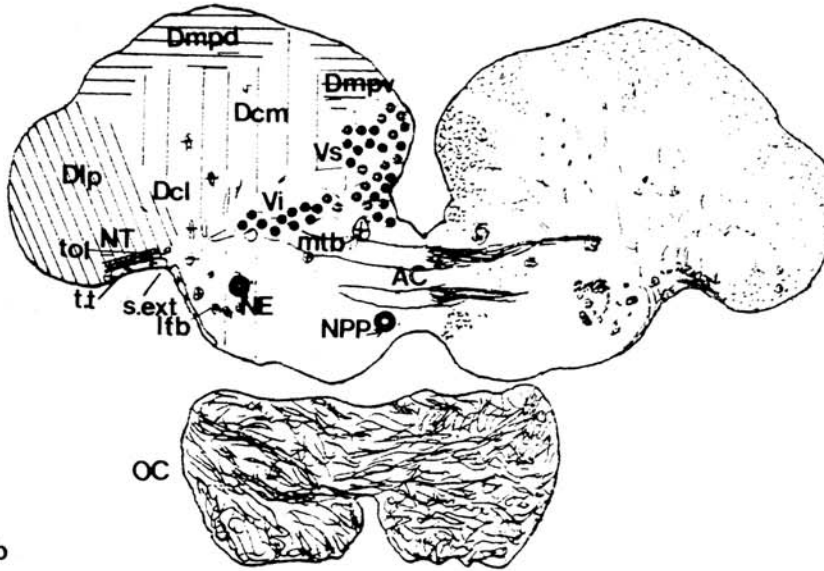
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Fig.5

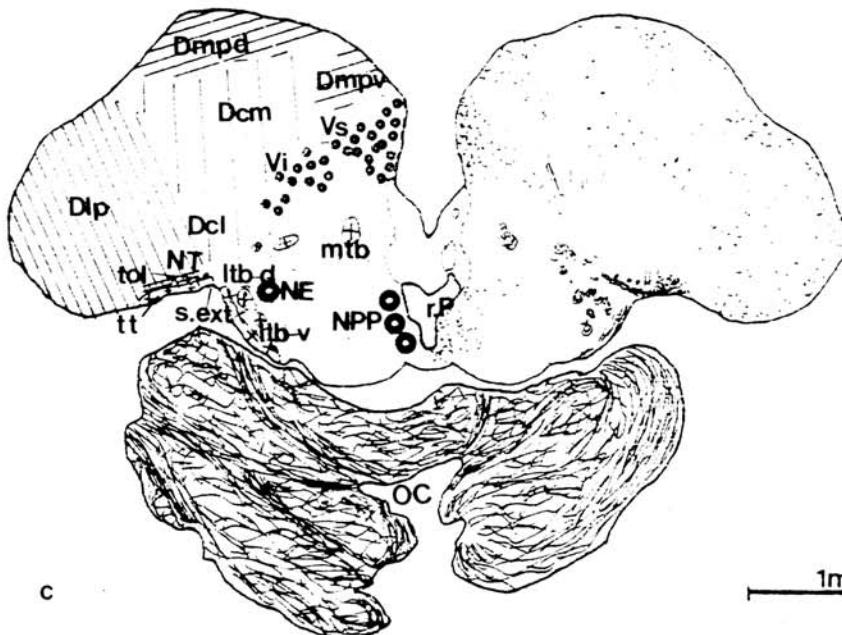




a



b



c

1mm

Fig.4

nuclear masses which can be separated as a function of size, disposition of the cells, neuronal density, fibres and the presence of grooves.

#### *Area ventralis telencephali* (V).

The medial surface of the ventral area is composed of the ependymus of the telencephalic ventricle; its lateral surface is lined by the meningeal tissue. Dorsally, it is joined to the area dorsalis telencephali (D). The separation between these two areas is marked by a cell-free zone.

Inside the V zone it is possible to differentiate the following nuclear masses: the area ventralis telencephali pars dorsalis (Vd), the pars ventralis (Vv), the supracommissuralis (Vs), the pars postcommissuralis (Vp), the pars intermedia (Vi), and the nucleus entopeduncularis (NE).

Areas Vv and Vd are disposed along a longitudinal plane on the border of the medial ventricle. The dorsal part (Vd) is a zone of cells arranged in groups and somewhat larger than those of the Vv. It extends in a dorsal position to the tractus olfactorius medialis. Ventrally it is limited by the Vv and dorsally it is separated from the D zone by a cell-free zone. (Figs. 3b, 3c, 4a, 4b, 4c).

Caudally, Vd continues to run dorsally to the anterior commissure (AC), forming the so-called Vs part (Figs. 4b, 4c), and more caudally it reaches the telencephalic-diencephalic transition zone where it becomes the Vp (Fig. 5a). In the *Barbus*, this latter exhibits a lateral extension, the Vi (Figs. 4b, 4c, 5a), which tends to join up with the posterior part of the lateral zone of D (Dlp) in the caudal portion of the telencephalon.

The VI zone (Figs. 3c, 4a) contains large cells diffusely disposed between the fibres of the lateral telencephalic bundle. It is situated at the extreme end of the ventrolateral region of the telencephalon, anterior to the NE.

The Vv zone (Figs. 3c, 4a) occupies the ventromedial region of the telencephalon, rostral to the anterior commissure; caudally to this commissure, it continues with the hypothalamic nucleus preopticus periventricularis (NPP). The cells comprising it extend over the ventricular surface and are densely packeted, whereas the more lateral cells are more diffuse.

The nucleus entopeduncularis (NE) (Figs. 4b, 4c, 5a) appears behind the anterior commissure, replacing the VI at this point, grouped around a fascicle of the lateral telencephalic bundle exactly at the point where this latter leaves the telencephalon.

#### *Area dorsalis telencephali* (D)

This extends throughout the cerebral hemispheres covering the ventral area (V). The cytoarchitectural

differences between both areas and the presence of an intermediate zone free of cells permit a distinction between them.

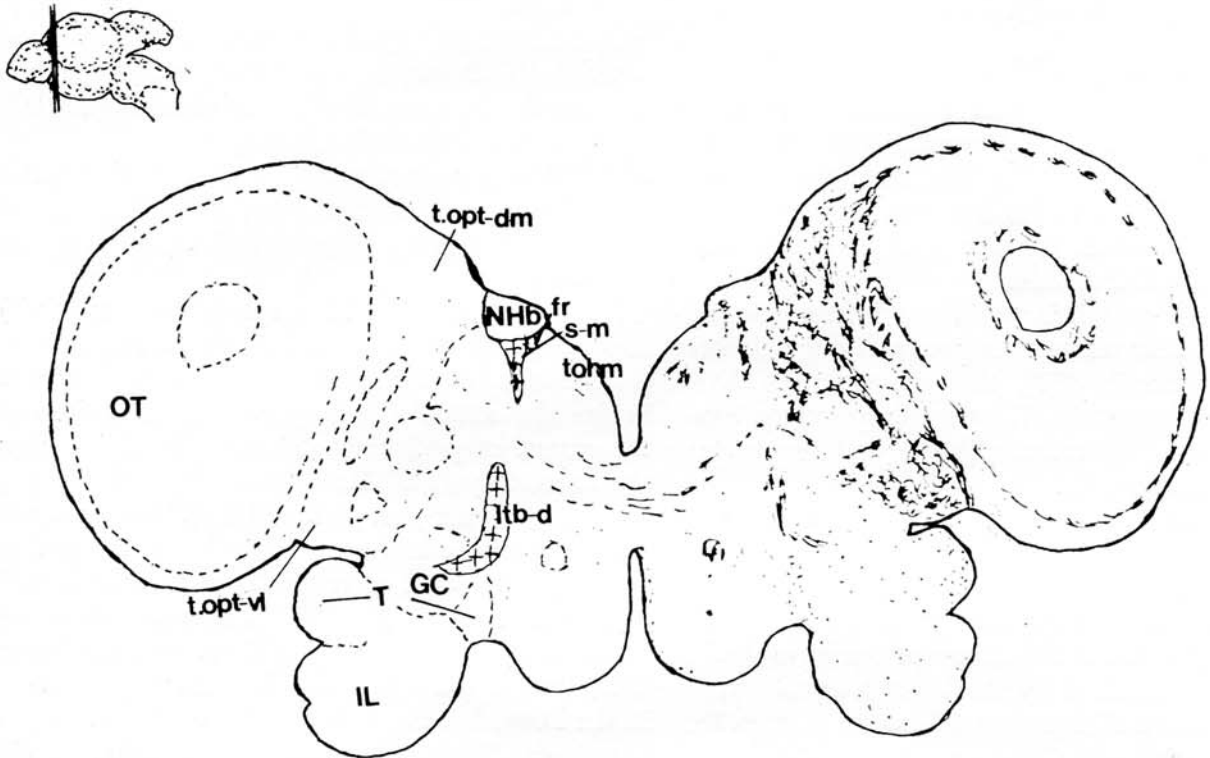
In the *Barbus* it is possible to note three longitudinal zones in the D which extend along the ependymal surface: the dorsomedial (Dm), the dorsodorsal (Dd) and the dorsolateral (Dl) zones, along the s. yps. These three zones surround another more interior zone, the dorsocentral zone (Dc), and within each of these three regions other subdivisions may be observed.

Dm (area dorsalis telencephali pars medialis) arises rostrally and extends into the caudal pole of the hemispheres. Two portions can be distinguished in it, the anterior and posterior, according to the extent of packeting and the size of its cells: the anterior part of Dm (Dma) (Figs. 2, 3a, 3b) and the posterior part of Dm (Dmp). The former is composed of smaller neurons disposed in incomplete layers parallel to the ventricular surface; it is well separated from Vd by a cell-free zone corresponding to the s. lim. t. The second, Dmp, contains larger cells, though the density of these is very reduced; in the Dmp, in turn, it is possible to differentiate a dorsal zone (Dmpd) (Figs. 3c, 4a, 4b, 4c, 5a, 7a, 7b) and a ventral one (Dmpv) (Figs. 3c, 4a, 4b, 4c, 5a) separated by a space with few cells.

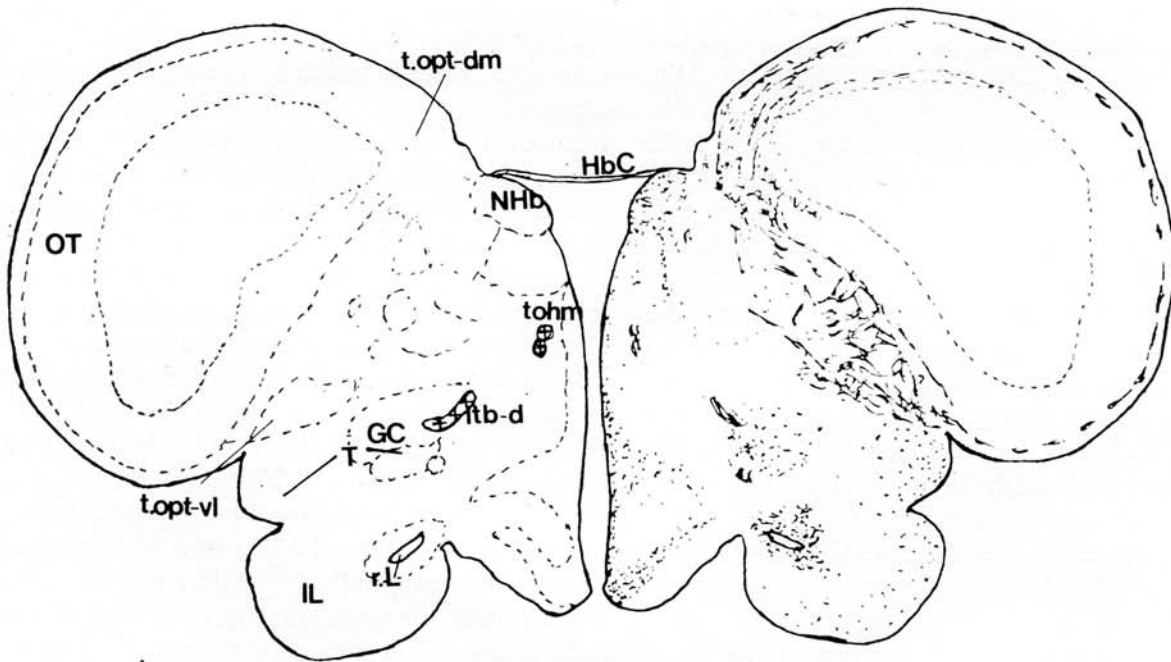
Dd (area dorsalis telencephali pars dorsalis) (Figs. 3a, 3b, 7b) is a poorly-defined zone where Dl and Dc neurons are mixed together. Its extension is limited and its position is soon occupied by Dl.

Dl (area dorsalis telencephali pars lateralis) is a very extensive zone in which it is possible to establish three subdivisions: dorsal (Dld) characterized by medium-sized cells; this is separated from the ventral subdivision (Dlv) (Fig. 3c) by the s. lat and by the presence in this region of a line of greater cell density. The posterior subdivision (Dlp) (Fig. 4a, 4b, 4c, 5a, 7b) occupies a prominent ventrolateral lobe of the telencephalon, posterior to the anterior commissure. Dlv may be distinguished from the areas surrounding it by the small size of its cells which appear in small densely packeted groups (Dlp shares with V the reception of olfactory fibres). Closely associated to Dlp is the nucleus tenia (NT) (Figs. 4b, 4c, 5a, 7b) which is recognizable by its very small neurons which stain intensely with Thionine and are arranged forming rows perpendicular to the surface of the lobe. Their position is ventromedial with respect to Dlp, and juxtaposed to the caudolateral wall of the s. ext. where the membranous roof is attached. At more caudal levels this group of neurons is continuous with Vi and Vp.

Dc (area dorsalis telencephali pars centralis) is easily distinguishable from the surrounding areas



a



b

Fig.6

1mm

6a, b: Sections through the habenular ganglion showing the entry of the s-m, ltb-d and tohm in the thalamus and in the posterior tubercle.



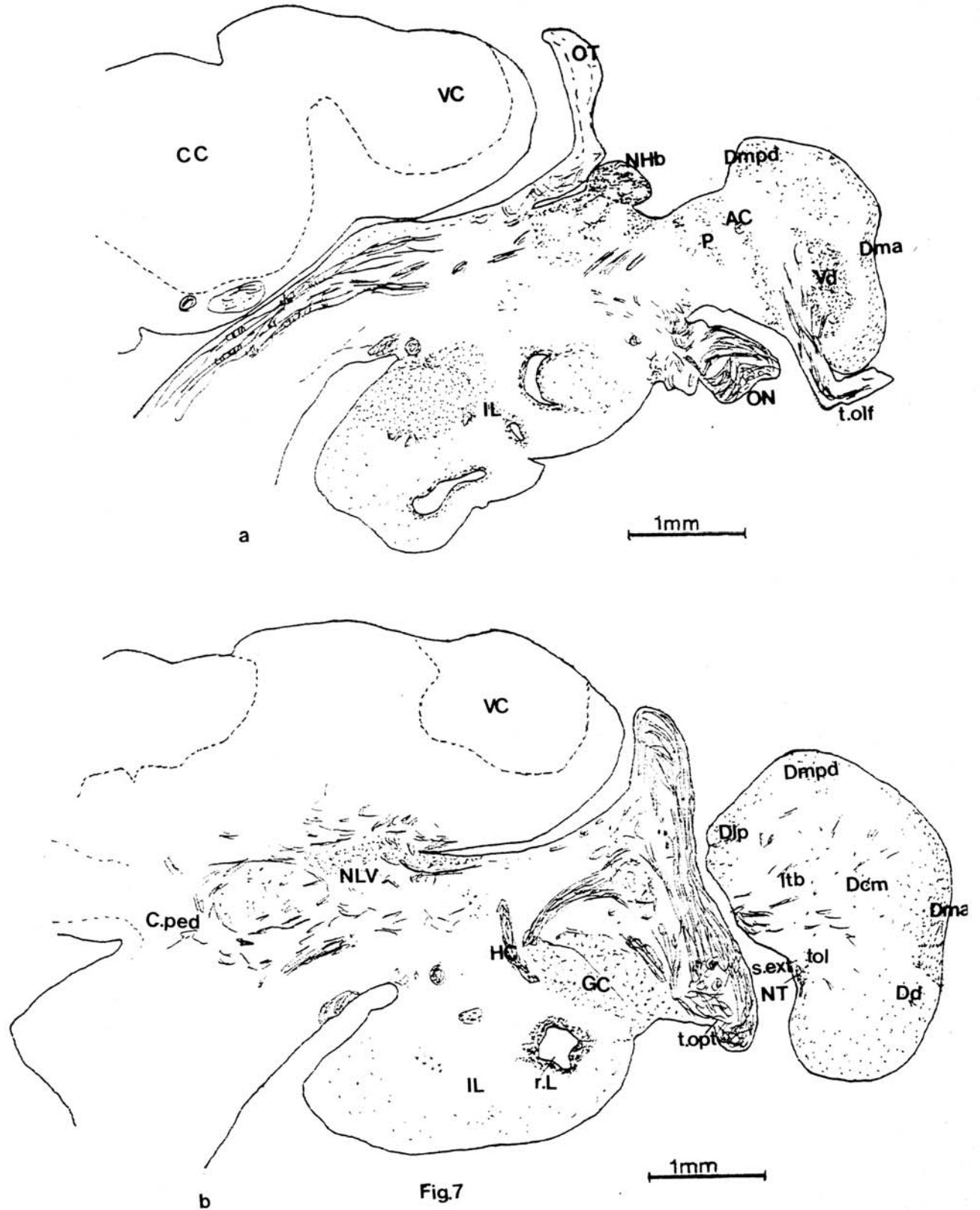
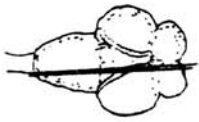


Fig. 7: Longitudinal sections of the encephalon: a) through the habenular ganglia. b) Section parallel and external to a.

because it is composed of large and very diverse neurons. In the more rostral levels it occupies the whole of the central portion of the telencephalic lobes, surrounded medially by Dm and laterally by Dl. In the *Barbus*, several subdivisions may be established in the Dc: medial (Dcm), lateral (Dcl) and dorsal (Dcd). The medial subdivision (Figs. 2, 3a, 3b, 3c, 4a, 4b, 4c) is composed of larger neurons and is separated from Dcl by a small cell-free zone; the lateral subdivision (Figs. 3b, 3c, 4a, 4b, 4c) is composed of smaller neurons and Dcd is somewhat undifferentiated. More caudally, the larger Dcm neurons acquire a more dorsal position, whereas those of Dcl appear intermingled with those of Dlp just above the NT.

Regarding fibroarchitecture, we shall first deal with the fibers originating in the olfactory bulbs (olfactory tracts), then with those relating the telencephalon to ventral hypothalamic portions and other diencephalic nuclei (medial and lateral telencephalic bundles and the strio-medullary system).

#### *Tractus olfactorius (t. olf)*

The axons of the mitral cells of the olfactory bulbs are united in two long tracts until they reach the base of the telencephalon. At this point, the olfactory tract splits into two components: the tractus olfactorius medialis (tom) and the tractus olfactorius lateralis (tol).

The tom is originally a strongly myelinated bundle which enters the ipsilateral telencephalic lobe through its ventromedial vertex (Fig. 3b) intermingling its fibers with the Vv cells. It courses in a caudal direction laterally to Vv, (Fig. 3c), until the beginning of the anterior commissure (AC) (Fig. 4a) where it divides into two components with a rather amyelinic appearance: dorsolateral and ventromedial. The former (tom-dl) is situated in lateral position with respect to the Vd, whereas the latter (tom-vm) is located between the Vv and Vl. In the dorsal part of the AC appears an amyelinic bundle, which is distributed laterally over Vi and courses towards Dlp, intermingling with the fibers of the lateral telencephalic bundle, and possibly with those of the tol (Figs. 4b, 4c). More caudally, there are vertically arranged fibers which are dispersed over the NT, the tractus tenia (t. t.) or tractus olfacto-habenularis (t. olf-Hb) and the end part of the tol (Figs. 4c, 5a); this could be the end point of the tom, where it would mix with the fibers of the abovementioned tracts.

The tol is a bundle of myelinic fibers (Fig. 7b) which, from its position in the olfactory tracts, shifts laterally and penetrates into the telencephalon at the beginning of the s. ext. (Fig. 3a); it then arches

over this in a more caudal level (Fig. 3b), occupying the zone of the Dl adjacent to the meningeal surface and then of the Dlv and Dlp (Figs. 3c, 4a). Its medial part reaches the Vl, extending along the medial part of the s. ext. (Figs. 4a). At AC level and in later sections, this tract is considerably reduced, intermingling with the t. t. and the tom (Figs. 4c, 5a). Accordingly, some fibers of the tol might reach the habenular region and decussate in the habenular commissure (HbC) to pass into the contralateral hemisphere.

On the telencephalic commissural plane (Fig. 4b) it is possible to distinguish at least three bands of amyelinic longitudinal fibers: the dorsal most band corresponds to those which decussate from the tom; the nature of the others, however, remains unknown though they could be commissural fibers of association between symmetric regions of the D, or interbulbar connections, or perhaps some fascicle of the lateral telencephalic bundle which decussates at this point.

#### *The medial telencephalic bundle (mtb)*

This connects masses of cells of the border of the ventricle, cells belonging to the V, with the preoptic nucleus and the hypothalamus. It is an amyelinic bundle which appears in the Vs and continues in the Vp after which it follows a caudal course close to the ventricular surface (Figs. 4b, 4c, 5a). It constitutes a complex system whose principal components are the tractus olfacto-hypothalamicus medialis (tohm) and the tractus olfacto-hypothalamicus intermedia (tohi). The former (tohm) (Figs. 6a, 6b) comprises fibers which pass from the Vs, where the complete bundle is originated, to the region of the nucleus posterior tubercis in the zone of the posterior tubercle; accordingly, it has a very long trajectory, always close to the diencephalic ventricle, and in ventromedial position with respect to the fasciculus retroflexus (fr) (Fig. 6a) which is originated in the diencephalic habenular ganglia. The second fascicle (tohi) connects the septal regions with the preoptic nuclei, apparently intermingled with its cells (Figs. 5a, 5b).

#### *The lateral telencephalic bundle (ltb)*

This is the largest system of fibers in the telencephalon of the *Barbus*. The axons which comprise it appear throughout the D except in Dlp, Dm, and NT, and descend in separate fascicles to the basal meningeal surface of the telencephalon (Figs. 3c, 4a, 4b, 7b).

This bundle comprises two parts: the dorsal, composed of myelinic and amyelinic fibres, which courses in a caudal direction and connects with the diencephalic glomerular complex (GC) (Fig. 4c, 5b, 5c, 6a, 6b) and the ventral part, formed exclusively of

thin amyelinic fibres, which connects with the hypothalamus (Figs. 4c, 5a).

Accordingly, the area dorsalis telencephalic (D) is related to hypothalamic areas and to some thalamic areas by means of the ltb, while the area ventralis telencephali (V) is connected with hypothalamic and thalamic areas by means of the mtb.

#### *The strio-medullary system (s-m)*

This is the third route of caudal communication of the telencephalon, connecting it with the habenular nuclei. Its main component, t. t. or t. olf-Hb, arises in the NT and might include olfactory fibres of the tol and of the tom. These fibres, which are myelinic, pass through the dorsal portion of the telencephalic peduncle and extend to the habenules (Fig. 6a).

Finally, the presence should be noted of an amyelinic bundle which passes laterally to the ltb; it then arches in its ventral part and adopts a medial position in its course towards the nucleus preopticus (NPO). It corresponds to the tractus dorso-preopticus (t.D-preopt) (Fig. 5a) described by BANNISTER (1972).

#### Discussion

In the first works by RABL-RUCKARD (1882, 1883, 1894) the telencephalic lobes of Teleosts are considered to be equivalent to the basal ganglion or striated body of the other vertebrates, and the ependymal membrane covering the lobes dorsally would be equivalent to the pallium; this interpretation was also adopted by EDINGER (1888), BURCKART (1894) and GOLDSTEIN (1905). However, HERRICK (1891), GAGE (1893) and STUDNICKA (1894, 1895, 1896), among others, concluded that the telencephalon of Teleosts includes pallial components of the telencephalon of other vertebrates and that the so-called membranous pallium is no more than the ependymal roof. Later studies (HOLMGREN, 1920, 1922; KUHLENBECK, 1924, 1929; MILLER, 1940; NIEUWENHUYS, 1960a, b, 1963, 1966; SCHÖBER, 1966) recognised the eversion of the telencephalon which has a pallial portion and another subpallial or basal one. Accordingly, the telencephalon of Teleosts comprises two solid lobes separated from each other by a medial ventricle, and each contains a series of welldefined nuclear masses, many of which could be equivalent to those found in other vertebrates.

Regarding terminology and the subdivisions of the telencephalic nuclei, controversy exists between the different workers addressing the problem (SHELDON, 1912; VAN DER HORST, 1917; HERRICK, 1922; KALLEN, 1947, 1951; DROOGLEVER FORTUYN, 1961; SCHNITZLEIN, 1962, 1964). We have followed that of

NIEUWENHUYS (1963) also employed by BANNISTER (1972), FINGER (1975), PETER and GILL (1975), NORTHCUTT and DAVIS (1982) and MURAKAMI et al. (1983), because it seems to be clearest for an understanding of the topographic organization of the telencephalon.

The nuclear subdivisions of each of the telencephalic areas vary from species to species, above all in the dorsal area; by contrast, the ventral area exhibits a position and a histological structure which are constant in all the subclasses, although its relative size may vary considerably according to the size of the olfactory bulb (NIEUWENHUYS, 1963).

Regarding the area ventralis telencephali (V), in the *Barbus* it is possible to distinguish the nuclei Vv, Vd, Vs, Vp, Vl, Vi and the cell-free zone in the dorsal part of Vd which some authors have called Vn (NIEUWENHUYS, 1963; BASS, 1981b; NORTHCUTT and DAVIS, 1982). The Vn zone is highly variable and whereas in *Salmo* it is absent in *Lepisosteus* it is extremely well-developed and is continuous with the Vl. This suggests that both areas (Vl and Vn) comprise a single functional unit and that the presence and size of the Vn must vary with the extension of the Vl.

In some Teleosts such as *Ictalurus* (BASS, 1981a) and *Salmo* (NORTHCUTT and DAVIS, 1982) a rostral group of large cells has been found known as the central nucleus of the ventral area; this has not been observed by us in the *Barbus*.

Some authors consider the entopeduncular nucleus to be a complex of two cellular aggregates closely associated to the dorsal and ventral telencephalic bundles and which are replaced more caudally by the caudal entopeduncular nucleus which extends inside the diencephalon (BASS, 1981b). On the other hand, NORTHCUTT and BRAFORD (1980) describe in the entopeduncular complex of *Polypterus* three distinct parts: dorsal, caudal and ventral, whereas in *Lepomis* and *Salmo* there is only one nucleus made up of small cells, in agreement with the results of PETER and GILL (1975) in *Carassius auratus* and *Fundulus heteroclitus* and with our own findings in *Barbus meridionalis*.

The caudal portion of the ventral area of the *Barbus* is characterized by the presence of a group of cells disposed on the medial border of the NT constituting a lateral extension of the Vp called the Vi. This has also been identified in *Ictalurus* (BASS, 1981 a, b) and in *Salmo* (NORTHCUTT and DAVIS, 1982) whereas according to NIEUWENHUYS (1963) it only appears in some Teleosts.

In conclusion, the ventral area (V) of Actinopterygii comprises certain constant nuclei: Vd, Vv, and Vl, while the presence of Vc, Vi and Vn is variable.

Likewise, the number of subdivisions of the NE is greater in non-Teleosts species.

The dorsal telencephalic area (D) exhibits a great diversity in shape and size, since the eversion and consequent curvature of the telencephalic walls takes place mainly in the region from which this area is developed and, moreover, the degree of eversion is different between the different groups of Actinopterygii. In most of them it is possible to observe three longitudinal zones: Dm, Dd, and Dl, which are situated along the ependymal surface and surround the Dc. Most authors recognize these four zones though some also describe certain subdivisions and delimit a fifth zone called the Dp (this corresponds to the Dlp zone of NIEUWENHUYS, 1963) also reported by us in the *Barbus*.

Regarding the Dc, BANNISTER (1972) working with *Phoxinus* and PETER and GILL (1975) with *Carassius* and with *Fundulus* described this area as a single zone; by contrast, BASS (1981 a, b) in *Ictalurus* describes three zones which are equivalent to those described by us in *Barbus* as Dcm, Dcd, and Dcl. MURAKAMI et al. (1983) in *Sebasticus marmoratus* also describe several zones in the Dc but consider them as a single nuclear mass in view of the difficulty in studying their connections separately. The reasons for the variability of this structure could be the tendency towards a local concentration of neurons in this area and the tendency towards a segregation into different cell groups (NIEUWENHUYS, 1963).

Different subdivisions have also been described in the Dm zone; BANNISTER's cytoarchitectural findings (1972) distinguish an anterior Dm and another posterior Dm; BRAFORD and NORTHCUTT (1974) and NORTHCUTT and BRAFORD (1980) report the existence of three zones in *Polypterus* and in *Salmo* they recognize four — two anterior parts and two posterior ones — and suggest that the two caudal subdivisions probably represent a single functional entity in view of the high content in catecholamines and acetylcholinesterase which differentiates them from the two more rostral subdivisions. MURAKAMI et al. (1983) believe that these four subdivisions of the Dm can be made taking into account the neuronal distribution, though they only consider two — Dmd and Dmv — because they found no differences in the connections between the rostral and caudal parts. In the *Barbus*, we were able to distinguish a Dma composed of small neurons arranged in layers, and a Dmp, subdivided into Dmpd and Dmpv, formed of large somata.

The Dd zone, adjacent to the sulcus ypsiliformis, has been recognized by most workers, though BANNISTER (1972) includes it within a group that he calls Dd + l.

The Dl zone described by us in the *Barbus* is

distinguishable in all Teleosts and at least three subdivisions can be made in it: Dld, Dlv and Dlp (SHELDON, 1912; WESTON, 1937; NORTHCUTT and BRAFORD, 1980; BASS, 1981a). BANNISTER (1972), however, considers Dl and Dd to be joined and separates Dp in which he includes the NT, and BASS (1981b) separates three zones, but also distinguishes the caudal portion of the Dp, which he also includes the NT. Regarding this latter nucleus, its position varies in Teleosts according to the degree of eversion, though it generally occupies a caudal position, closely associated to the Dp.

The secondary olfactory fibres appear in two well-defined bundles: the tol and the tom, concerning the course and distribution of which there are numerous interpretations.

With respect to the tom, some authors have considered this as a single bundle; others distinguish in it two fascicles (SHELDON, 1912; BANNISTER, 1972; MURAKAMI et al., 1983); and FINGER (1975) divides it into three branches, SHELDON (1912) referring to end points, mentions the contralateral Dm and Dl regions, the upper precommissural nucleus (Vd) and the supracommissural nucleus (Vs), but fails to consider the possibility that some of the olfactory fibres might course towards diencephalic regions, such as the olfactory-hypothalamic bundle of ARIENS-KAPPERS (1906). NIEUWENHUYS (1963) also describes the distribution of the fibres of the tom by Vv, Vd and probably by Vs, Vl and the preoptic area; its end point would be in the contralateral Dlp. BANNISTER (1972), however, observes that the tom sends fibres to all the parts of V and that it ends in Dp and Dm both ipsilaterally and contralaterally; moreover, he refers to an interbulbar part of the tom which decussates in AC after which it returns to the contralateral olfactory bulb. FINGER (1975) also traces a branch whose fibres are a mixture of the tol and the tom and which, after decussating in AC, passes through the NPO and finally spreads through the dorsal hypothalamus through the contralateral nucleus posterior tuberis. We also noted in the *Barbus* fibres of the mtb on their way to the nucleus posterior tuberis, in agreement with the findings of MURAKAMI et al. (1983).

The distribution of the fibres of the tol varies considerably according to the interpretations of the different authors: for JOHNSTON (1911), SHELDON (1912), ARIENS-KAPPERS et al. (1936) and MEADER (1939), the whole of the dorsal olfactory area (Dd, Dl and Dc) is under the influence of the olfactory system; KUHLENBECK (1977), in agreement with the previous authors, traces the tol mainly through the pallial region (zone D in this nomenclature). By contrast, NIEUWENHUYS (1963, 1966) traces the tol

mainly through the caudoventral region of the pallium, which he calls Dlp, and holds that most of the dorsal area of Teleost is free from secondary olfactory connections. Like BANNISTER (1972), he ascribes the caudoventral portion (Dlp) as the end point, though this latter author adds that some of its fibres would extend to the habenula, decussating in the habenular commissure to later terminate in the contralateral Dp.

FINGER (1975) working with *Ictalurus* and NORTHCUTT and DAVIS (1982) in *Salmo* and *Lepomis* propose another decussatio of some of the fibres in AC and report the existence of terminations in Dlv and Dc-1 (lateral Dc). MURAKAMI et al. (1983) describe a similar distribution, though in their case through the tom.

Finally, SCALIA and EBBESSON (1971), studying the projections of the olfactory bulb, only found degenerated terminals in the ventrolateral pallium, in the posterior lobe and in the ventromedial area whereas they did not detect projections to the preoptic area nor to the habenular ganglia.

Through the ltb the telencephalon is projected to hypothalamic areas, the dorsal thalamus and the pretectal area, though the principal fascicle of the bundle divides in two: one part of which terminates in the nuclei glomerulosus and preglomerulosus of the posterior tuberculum and the other in the inferior lobes (ARIENS-KAPPERS et al., 1936; SCHNITZLEIN, 1962). The main problem is the course of this bundle: GOLDSTEIN (1905), SHELDON (1912), HOLMGREN (1920) and NIEUWENHUYS (1963) conclude that a large part of this bundle decussates in the AC (in the ventral orientation to the decussatio of the tom), though other authors, such as SCHNITZLEIN (1962) and BANNISTER (1972) do not report any fibres of this bundle decussating in the AC.

Likewise, septal and precommissural regions of the telencephalon (Vs, Vd, and Vv) are connected with the preoptic and hypothalamic regions by a diffuse system of fibres: the mtb (ARIENS-KAPPERS et al. 1936; NIEUWENHUYS 1963; KUHLENBECK, 1977).

EBBESSON and VANEGAS (1976), VANEGAS and EBBESSON (1980) and NORTHCUTT (1981) also describe projections from the mtb and ltb to the thalamus, the hypothalamus, pretectum, optic tectum, and mesencephalic tegment and, furthermore, ITO et al., (1982) and LEE (1984) trace projections from these bundles to the cerebellum.

Finally, the telencephalon receives afferences from diencephalic centres through ascending fibres which course through the ltb and originate in the thalamus, the anterior nucleus preglomerulosus, the nucleus cerebellosus hypothalami (SHELDON, 1912); in the prethalamus nucleus of MEADER (1934)

which is equivalent to the nucleus rotundus or the central optic nucleus of EBBESSON (1972) (ITO et al., 1980; MURAKAMI et al., 1983) and in the glomerulosus complex (ITO and KISHIDA, 1978).

Ascending fibres have also been described in the mtb, originating in the nucleus posterior tuberis (MURAKAMI et al., 1983). Accordingly, the telencephalon would receive not only olfactory impulses but also optic signals.

#### Abbreviations

|           |   |
|-----------|---|
| AC        | anterior commissure                       |
| CC        | corpus cerebelli                          |
| C.ped     | cerebellar peduncles                      |
| D         | area dorsalis telencephali                |
| Dc        | area dorsalis telencephali pars centralis |
| Dcd       | dorsal part of Dc                         |
| Dcl       | lateral part of Dc                        |
| Dcm       | medial part of Dc                         |
| Dd        | area dorsalis telencephali pars dorsalis  |
| DI        | area dosalis telencephali pars lateralis  |
| Dld       | dorsal part of DI                         |
| Dlp       | posterior part of DI                      |
| Dlv       | ventral part of DI                        |
| Dm        | area dorsalis telencephali pars medialis  |
| Dma       | anterior part of Dm                       |
| Dmp       | posterior part of Dm                      |
| Dmpd      | dorsal zone of Dmp                        |
| Dmpv      | ventral zone of Dmp                       |
| DV        | diencephalic ventricle                    |
| F         | Forebrain                                 |
| fr        | fasciculus retroflexus                    |
| GC        | glomerular complex                        |
| HbC       | habenular commissure                      |
| HC        | horizontal commissure                     |
| IL        | inferior lobe of hypothalamus             |
| ltb       | lateral telencephalic bundle              |
| ltb-d     | dorsal part of ltb                        |
| ltb-v     | ventral part of ltb                       |
| mtb       | medial telencephalic bundle               |
| MV        | mesencephalic ventricle                   |
| NE        | nucleus entopenduncularis                 |
| NHb       | nucleus habenularis                       |
| NLV       | nucleus lateralis valvulae                |
| NPO       | nucleus preopticus                        |
| NPP       | nucleus preopticus periventricularis      |
| NT        | nucleus tenia                             |
| OB        | olfactory bulb                            |
| OC        | optic chiasm                              |
| ON        | optic nerve                               |
| OT        | optic tectum                              |
| P         | preoptic area                             |
| PC        | postoptic commissures                     |
| rL        | recessus lateralis                        |
| rP        | recessus preopticus                       |
| s.ext     | sulcus externus                           |
| s.lat     | sulcus lateralis                          |
| s.lim.t.  | sulcus limitans telencephali              |
| s-m       | strio-medullary system                    |
| s.term.t. | sulcus terminalis telencephali            |
| SV        | saccus vasculosus                         |
| s.yps     | sulcus ypsiliformis                       |
| T         | posterior tuberculum                      |

|            |   |
|------------|---|
| t.D-preopt | tractus dorso-preopticus                            |
| tohi       | tractus olfacto-hypothalamicus intermedia           |
| tohm       | tractus olfacto-hypothalamicus medialis             |
| tol        | tractus olfactorius lateralis                       |
| t.olf-Hb   | tractus olfacto-habenularis                         |
| tom        | tractus olfactorius medialis                        |
| tom-dl     | tractus olfactorius medialis pars dorsolateralis    |
| tom-vm     | tractus olfactorius medialis pars ventromedialis    |
| t.opt.     | tractus opticus                                     |
| t.opt-dm   | tractus opticus dorsomedialis                       |
| t.opt-vl   | tractus opticus ventrolateralis                     |
| t.t.       | tractus tenia                                       |
| TV         | telencephalic ventricle                             |
| V          | area ventralis telencephali                         |
| VC         | valvula cerebelli                                   |
| Vd         | area ventralis telencephali pars dorsalis           |
| Vi         | area ventralis telencephali pars intermedia         |
| Vl         | area ventralis telencephali pars lateralis          |
| Vp         | area ventralis telencephali pars postcommissuralis  |
| Vs         | area ventralis telencephali pars supracommissuralis |
| Vv         | area ventralis telencephali pars ventralis          |

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