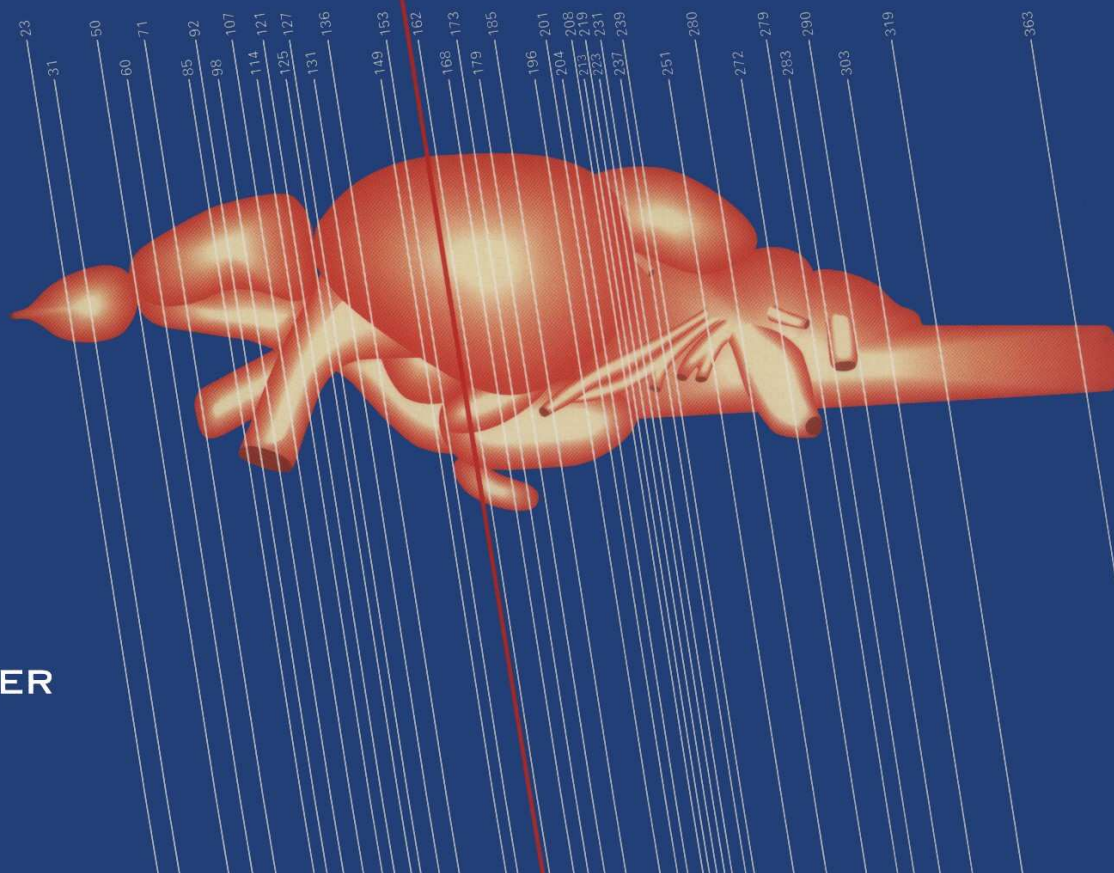
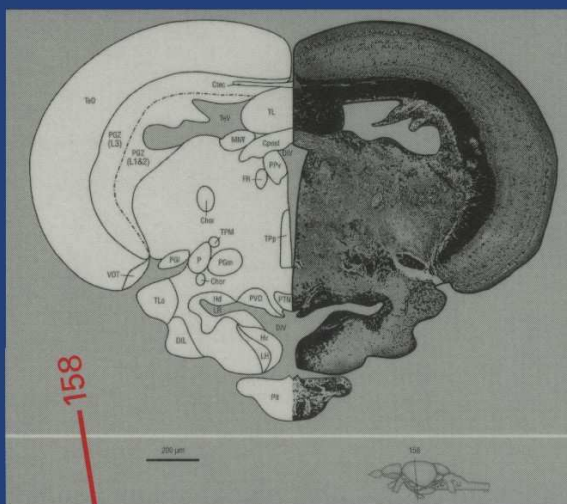


NEUROANATOMY OF THE **Zebrafish** Brain

A TOPOLOGICAL ATLAS

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BIRKHÄUSER



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A Topological Atlas

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1 Introduction: neuroanatomy for a neurogenetic model system

«Zebrafish hit the big time»: This title of a recent commentary in *Science* (Kahn, 1994) reflects the growing importance of a new model organism for developmental research, the zebrafish *Danio rerio* (Fig. 1). Pioneering work using this model began in the laboratories of George Streisinger and Charles Kimmel in the early 1970s, and to date studies of zebrafish have contributed notably to understanding early nervous system development and its genetic regulation in at least three areas:

1. Differentiation of first neurons and their associated tracts and commissures in the embryonic zebrafish brain
2. Neuromeres and expression of regulatory genes in embryonic zebrafish
3. Generation of zebrafish mutants via saturation mutagenesis

In this introduction, we will discuss briefly the relevance of a zebrafish brain atlas to these areas of research. However, rather than review each of these areas in detail, we will focus on how the neuroanatomy of the adult zebrafish brain might be helpful for future research in this model system.

Differentiation of first neurons and their associated tracts and commissures in the embryonic zebrafish brain

The first embryonic neurons in the zebrafish central nervous system (CNS) can be visualized immediately prior to final mitosis during neuromere formation and are found in a serially repeated sequence in the spinal cord (Hanneman and Westerfield, 1989; Bernhardt et al., 1990; Kuwada et al., 1990) and in the brain (Hanneman et al., 1988; Wilson et al., 1990). Soon thereafter, these neurons extend pioneering axons in a highly predictable, stereotyped fashion, and by 24 hours they form an early scaffold of tracts and commissures (Fig. 2; Metcalfe et al., 1986; 1990; Chitnis and Kuwada, 1990; Wilson et al., 1990; Wilson and Easter, 1991; Ross et al., 1992). This early axon scaffold includes eight tracts and four commissures (Fig. 2). At 48 hours, the number of fibers in these early tracts has increased by a hundredfold, and three more tracts and their commissures (intertectal and habenular commissures, commissure of the posterior tuberculum) have formed (Wilson et al., 1990), resulting in a total of eleven tracts and seven commissures. (Since many of the designations for early tracts



Figure 1. Adult zebrafish

and commissures only apply to the embryonic zebrafish brain, they are not listed in the index.)

The fact that many follower axons between 24 and 48 hours of development grow along the few axons constituting the early scaffold indicates that the first (pioneer) axons might provide cues to guide the follower axons (Wilson et al., 1990). However, the pioneer axons themselves and all axons approaching axonal intersections necessarily need additional guidance cues (Chitnis and Kuwada, 1991; Chitnis et al., 1992), indicating that multiple guidance cues may be required generally for orderly axonal outgrowth.

Many early regulatory genes have expression boundaries at positions where the neurons and tracts of the early scaffold are located, and this early morphological patterning can be changed systematically by experimentally altering gene expression (Wilson et al., 1993; Macdonald

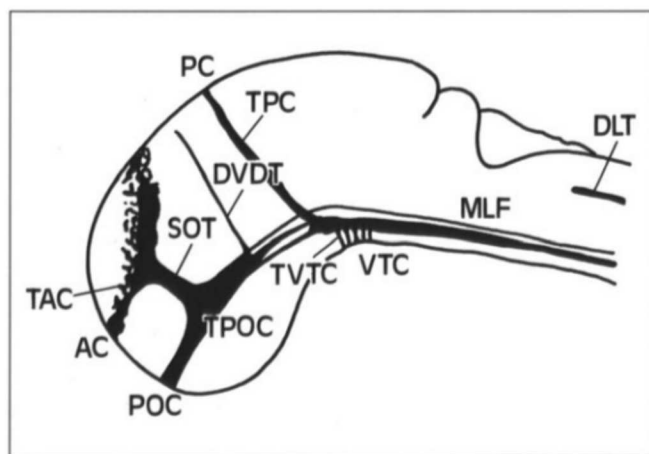


Figure 2.

At day 1 postfertilization, a simple scaffold of eight tracts can be visualized in the zebrafish immunohistochemically (see text). Four tracts are associated with commissures (tract of the anterior commissure (TAC), tract of the postoptic commissure (TPOC), tract of the posterior commissure (TPC), tract of the ventral tegmental commissure (TVTC). The four additional tracts are the supraoptic tract (SOT), the dorsoventral diencephalic tract (DVDT), the medial longitudinal fascicle (MLF), and the dorsal longitudinal tract (DLT). Also present in the telencephalon at day 1 (but not shown) are fibers of the olfactory nerve. Compiled from Metcalfe et al. 1986 & 1990, Chitnis & Kuwada 1990, Wilson et al. 1990, and Ross et al. 1992.

et al., 1994). This indicates that the early scaffold in the brain might reflect early regionalization processes. Thus, another hypothesis, namely, that the early scaffold is a transitory structure during embryogenesis, must also be considered. Documentation of the postembryonic transformation of embryonic CNS structures into their adult configuration in the zebrafish is needed in order to decide whether the early scaffold develops directly into adult nuclei and tracts or, alternatively, represents a transitory embryonic structure.

A striking similarity in the organization of the embryonic and adult zebrafish brain is that each of the seven commissures present at 48 hours corresponds topologically to adult commissures. They bear the same names in both life stages, except for the embryonic ventral tegmental commissure, which is called the ansulate commissure in adult teleosts. However, since we observe 13 adult commissures, the development of 6 commissures remains undocumented at present. The good topological correspondence between embryonic and at least some adult tracts and commissures does seem to suggest that they develop into each other by addition of fibers, though the alternative hypothesis that all embryonic tracts may be transitory must be kept in mind. The fact that all embryonic tracts are in a subpial position, i.e. they are located at the periphery of the CNS, in contrast to most adult tracts, which lie deep in the CNS, lends support to the latter hypothesis. Another way of comparing embryonic and adult zebrafish brains is to look at neuronal connections in both life-history stages. The embryonic neuronal connections constituting the early axon scaffold are shown in Figure 3, and the adult connections are discussed in chapter 6. In the embryonic and the adult zebrafish brain, the medial longitudinal fascicle (MLF) carries descending axons of neurons in the nucleus of the medial longitudinal fascicle (NMLF). Similarly, the embryonic dorsal longitudinal tract (DLT) carries descending primary sensory fibers of trigeminal ganglion cells, as does the adult descending trigeminal root (DV). Such cases support the hypothesis that parts of the early scaffold develop directly into adult structures. Other

embryonic connections clearly are transitory, such as the ascending axons of the spinal Rohon-Beard cells in the DLT (Metcalf et al., 1990) or the tegmental neurons, whose axons ascend in the tract of the postoptic commissure to cross in that commissure (Wilson et al., 1990); both connections are absent in the adult brain.

It is evident that a large gap of knowledge exists between the detailed documentation of neural development in the embryonic zebrafish and its adult neuroanatomy. Thus, the postembryonic development of the zebrafish brain must be studied before we can understand by which mechanisms the developmental transformation from the relatively simple embryonic condition to the complex adult brain occurs. As exemplified above, the atlas of the adult zebrafish brain is a necessary tool for doing so.

Neuromeres and expression of regulatory genes in the embryonic zebrafish

Recently, theories on the neuromeric organization of the vertebrate brain have enjoyed a renaissance. Although classical observations of repeated constrictions along the rostrocaudal axis of the vertebrate hindbrain were long disqualified as artifactual, today, the reality of neuromeres in the vertebrate hindbrain (rhombomeres) is substantiated by various approaches, such as the investigation of primary neurons, early axonal pathfinding processes, glial boundaries, proliferation zones, and, most important, differential gene expression coinciding with neuromere boundaries (Holland and Hogan, 1988; Keynes and Stern, 1988; Lumsden and Keynes, 1989; Murphy et al., 1989; Wilkinson et al., 1989a; 1989b; Lumsden, 1990; Wilkinson and Krumlauf, 1990; Clarke and Lumsden, 1993).

In terms of gene expression, rhombomeres are best characterized by different expression boundaries of homeobox genes of the *hox*-cluster and by the zinc-finger gene *Krox-20* (Holland and Hogan, 1988; Murphy et al., 1989; Wilkinson et al., 1989a; 1989b; Wilkinson and Krumlauf, 1990). In tetrapods, eight rhombomeres are recognized while only seven have been described for the zebrafish

(Kimmel, 1993). Since rhombomeres 3 and 5 express the zinc-finger gene *Krox-20* in tetrapods (Wilkinson et al., 1989a; 1989b) as well as in the zebrafish (Oxtoby and Jowett, 1993), one must conclude that zebrafish lack the most caudal rhombomere. Also similar to tetrapods, the gene expression boundaries at the spinal cord-brain stem junction of two zebrafish *hox* genes (*hox-2.1* and *hox-2.2*) correspond well with those of their mouse orthologs (*Hox-2.1* and *Hox-2.2*), although in zebrafish they clearly extend into the most posterior hindbrain (Njølstad and Fjose,

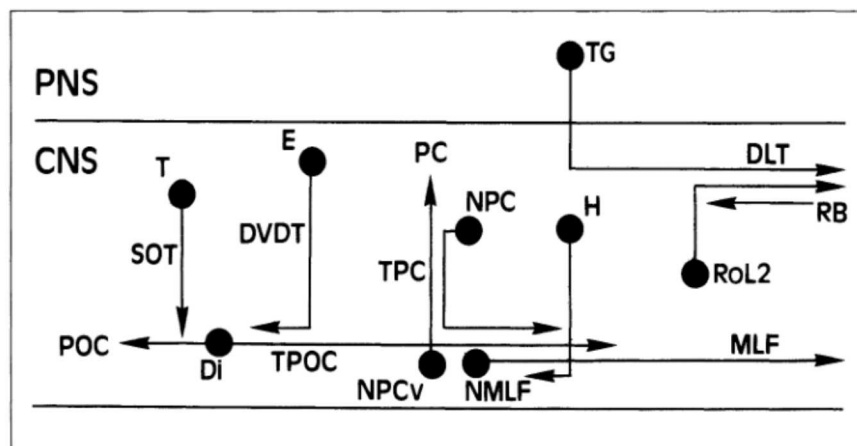


Figure 3.

Neuronal origins and pathfinding of axons that constitute the early scaffold of tracts shown in figure 2. Axons originate from clusters of primary neurons, which are shown here as single cells. Abbreviations: CNS: central nervous system; Di: diencephalon; DLT: dorsal longitudinal fascicle; DVDT: dorsoventral diencephalic tract; E: epiphysis; MLF: medial longitudinal fascicle; NMLF: nucleus of the medial longitudinal fascicle; NPCv: ventral nucleus of the posterior commissure; PC: posterior commissure; PNS: peripheral nervous system; POC: postoptic commissure; RB: Rohon-Beard cells; RoL2: individual cell in the superior reticular formation; SOT: supraoptic tract; T: telencephalon; TG: trigeminal ganglion cells; TPC: tract of the posterior commissure; TPOC: tract of the postoptic commissure. Compiled from Metcalfe et al. 1986 & 1990, Chitnis & Kuwada 1990, Kimmel 1993, and Ross et al. 1992.

1988; Njølstad et al., 1990). Another homeobox gene, the zebrafish *hlx-1* gene, is expressed in the hindbrain, where it reveals various rhombomeric and subrhombomeric boundaries in a temporal sequence in the zebrafish (Fjose et al., 1994).

Several genes of the homeobox-containing *engrailed* (*Eng*) gene family (Njølstad and Fjose, 1988; Hatta et al., 1991; Fjose et al., 1992; Ekker et al., 1992), one paired box-containing gene, *pax[b]* (Krauss et al., 1991a; 1991b; 1992b; Mikkola et al., 1992; Püschel et al., 1992b), and two genes of the *wnt*-family (*wnt-1* and *wnt[d]*; Molven et al., 1991; Krauss et al., 1992a) are expressed at and probably involved in forming the midbrain-hindbrain boundary in zebrafish. Moreover, the *wnt-1* (Molven et al., 1991), *wnt[a]* (Krauss et al., 1992a) and *pax[a]* (Krauss et al., 1991b; Püschel et al., 1992a) genes are involved in specifying the dorsal hindbrain and spinal cord in zebrafish.

The existence of neuromeres in the prospective midbrain and forebrain (diencephalon and telencephalon) of vertebrates is still somewhat controversial. However, evidence for mesomeres (prospective midbrain) and prosomeres (prospective forebrain) has recently been presented (Bulfone et al., 1993; Figdor and Stern, 1993; Puelles and Rubenstein, 1993). Puelles and Rubenstein (1993) present a predictive and testable overall model of vertebrate forebrain segmentation that includes data on descriptive (histology, morphology) and experimental (histochemistry, grafting) embryology as well as on gene expression data. This neuromeric model suggests that in addition to eight hindbrain neuromeres and one neuromere for the mesencephalon (mesomere), the forebrain consists of six more neuromeres (prosomeres). What is traditionally considered the diencephalic vesicle displays two segments, one for the prepectum (synencephalon, P1) and one that includes the adult epithalamus and dorsal thalamus (P2). Rostral to these two segments are four more prosomeres (P3–P6) constituting the secondary prosencephalon. Several points are important to note with respect to this neuromeric model:

1. As in the rhombencephalon, different gene-expression boundaries in the prosencephalon are co-localized with prosomere boundaries in the rostrocaudal axis. In addition, some prosencephalic gene-expression patterns coincide with boundaries in the dorsoventral plane of the brain.
2. Several expression patterns of early regulatory genes rostral to the rhombomeres in the zebrafish correspond well with the neuromeric model of Puelles and Rubenstein (1993). One of the *pax* genes (*pax[a]*) is expressed in alar plate regions of the future diencephalon and telencephalon (Püschel et al., 1992a), as is its mouse ortholog, the *pax-6* gene. Furthermore, the forebrain expression patterns of one homeobox gene of the *distal-less* family, *dlx2* (Akimenko et al., 1994), as well as of the *wnt[a]* gene (Krauss et al., 1992a) in the zebrafish are similar to the expression patterns of their mouse orthologs, the *Dlx2* and the *Wnt-3* genes.
3. The diencephalon is not the derivative of a single prosomere. All of prosomere 2 contributes to the diencephalon, a portion of prosomere 3 contributes the ventral thalamus, and the (diencephalic) posterior tuberculum derives from the ventral portions of prosomeres 1 to 3.
4. Only the dorsal portions of prosomeres 4 to 6 will become the adult telencephalon, while the ventral portions will develop into the hypothalamus.

The zebrafish thus provides an excellent test system for a neuromeric model of brain organization. A case in point is the posterior tuberculum, which is rather small in tetrapods (e.g. the inconspicuous mammalian subthalamic nucleus), but very large in teleosts (see chapter 6). Its large size makes it easier to study in zebrafish, and combined gene expression and grafting experiments are likely to reveal its embryonic origin, especially now that the neuroanatomy has been established.

There is a long way to go before the complex cascade of interactions of genes and their products in early vertebrate development is understood. The fact that various

2 Taxonomic background

gene-expression patterns in the zebrafish correspond well with the neuromeric model of Puelles and Rubenstein (1993) is very encouraging for further research in this model system, which holds the promise of revealing fundamental neurogenetic patterns and mechanisms in vertebrates.

Generation of zebrafish mutants via saturation mutagenesis

The goal of saturation mutagenesis is to identify most – if not all – genes affecting early animal development and to understand their hierarchical, regulative role during development (for reviews, see: Mullins and Nüsslein-Volhard, 1993; Solnica-Krezel et al., 1994). This approach has recently been applied to the zebrafish system, and the results are impressive. Roughly 1300 zebrafish mutants have been described phenotypically by the Nüsslein-Volhard laboratory, and a further 600 were identified by the Driever laboratory (Kahn, 1994). The identification and cloning of mutant genes is now feasible: an initial genome map of the zebrafish has been constructed, and some of the loci identified by mutation have already been mapped out (Postlethwait et al., 1994). These advances in zebrafish research will greatly facilitate the investigation of the hierarchical interactions of regulatory genes during early ontogeny and, ultimately, may lead to an understanding of pattern formation relevant to vertebrate development in general.

Zebrafish mutants include not only abnormal phenotypes in very early development during the formation of germ layers and those showing massive body plan aberrations but also minor defects that become phenotypically only visible in later development. At the level of a detailed screening of CNS mutants, the present atlas may turn out to be useful, since many phenotypic defects in mutants are likely to differ from wild-type organization at the neuroanatomical level. In order to assess such defects, an atlas of the adult zebrafish CNS appears to be indispensable.

The zebrafish belongs to the teleostean family of cyprinids (minnows), which includes other neurobiologically well investigated species such as goldfish (*Carassius auratus*) and carp (e.g. *Cyprinus carpio*).

In a recent taxonomic revision (Barman, 1991), all species of the genus *Brachydanio* were reassigned to the genus *Danio*. Thus, the current species designation of the zebrafish is *Danio* (formerly *Brachydanio*) *rerio* (Hamilton-Buchanan, 1822). As a cyprinid, the zebrafish belongs to the large group of ostariophysan teleosts (6000 species, Lauder and Liem, 1983). Most ostariophysans are characterized by a sophisticated apparatus – the Weberian ossicles – to transmit sound from the swim bladder to the inner ear. The ostariophysans belong to the most derived group of teleosts, the euteleosts (17 000 species), which have three more basic teleostean outgroups, the osteoglossomorphs, elopomorphs, and clupeomorphs (1000–2000 species).

Zebrafish live in large schools and are communal breeders. Their natural habitats are the freshwaters of South and East Asia, i.e. India, Pakistan, Bangladesh, Burma, Sri Lanka, and Nepal (Barman, 1991).

3 Technical details

Histology

Fifty adult specimens of *Danio rerio* were processed in the course of this study. The animals were deeply anesthetized in methane sulfonate salt (Sigma, Deisenhofen, Germany) before being transcardially perfused with cold 0.1 M phosphate buffer (Sörensen; pH 7.4) followed by cold AFA (90 ml: 80% ethanol, 5 ml: 37% formalin, 5 ml: glacial acetic acid). The fish were then decapitated, and the skulls were opened dorsally to expose the brains. After one day in fixative, the brains were removed from the skulls and again postfixed for at least another month prior to further processing. The brains were then dehydrated, embedded in paraffin, and cut at 12 μm into either transverse, sagittal, or horizontal series of sections. To determine gross anatomy, some brains were fixed as described, removed from the skulls, and investigated under a stereomicroscope.

One specimen of *Danio rerio* was processed similarly, but the whole head was fixed for 15 days after perfusion and then decalcified in Titriplex III (Merck, Darmstadt, Germany) for 19 days. Subsequently, the head was put in Na_2SO_4 overnight and then rinsed in tap water, again overnight, before dehydration and embedding in paraffin. This specimen was cut at 10 μm into a transverse whole head series.

All sectioned brains were stained according to the procedure of Bodian, which reveals neurofilaments (see: Romeis, 1989), and counterstained with the Nissl-stain cresyl violet.

Preparation of figures

One series each of the transverse, sagittal, and horizontal histological sections was chosen for photographic documentation. While the numbers given in the atlas figures depicting the transverse plane represent the actual section numbers, the most lateral and dorsal sections shown in the sagittal and horizontal planes start arbitrarily with section number 1. However, the differences between figure numbers in the sagittal and horizontal series also represent the actual distances between sections.

The whole head transverse series served as a reference for structures that are almost always torn apart by removing the brain from the skull. The pituitary shown in transverse sections was photographed in this series and added to the photographed transverse sections with the aid of computer reconstruction. This was not done for the epiphysis, since it is well demonstrated in its full extent in some of the sagittal sections. Atlas photographs and corresponding ink drawings were computerized for further processing. Using computer techniques, artifacts and other undesired structures such as meninges or ventricular contents were removed, and graphics were added (e.g. background shading and lettering).

4 The brain of the zebrafish *Danio rerio*: an overview

The following account outlines the major CNS divisions in the zebrafish and the organization of these divisions into nuclei or laminae, including a description of major tracts and commissures. CNS divisions will be dealt with according to the classical anatomical sequence: telencephalon, diencephalon, mesencephalon, metencephalon (including cerebellum), myelencephalon, and medulla spinalis. Since many tracts and commissures caudal to the diencephalon extend into several brain parts and even into the spinal cord, they are treated in a final separate section. When appropriate, discrepancies between the neuromeric model of Puelles and Rubenstein (1993) outlined above (see: Introduction) and classical brain divisions will be discussed.

The principal terminology applied to nuclei and larger CNS divisions is indicated at the beginning of each major section. For general review articles on fish neuroanatomy, the reader is referred to Nieuwenhuys (1963), Northcutt and Braford (1980), Northcutt and Davis (1983), Nieuwenhuys and Pouwels (1983), and Nieuwenhuys and Meek (1990).

Tract designations often imply a specific origin and target of their axons. The present text includes only nomenclature on tracts that have been confirmed with experimental neuronal tracing. However, this does not imply that the interconnection indicated in the tract designation as the dominant one is the only one running in a specific tract. Unless unambiguous connectional information already exists in the zebrafish or other teleosts, we remained conservative in using tract designations that imply a specific connection, to allow future terminology to develop meaningfully as refinements of connectivity in the zebrafish brain emerge.

The relative proportions of the major brain divisions of the zebrafish (Fig. 4) reveal some features typical of cyprinids, i.e. relatively large vagal and facial lobes, although these are not as pronounced as in other cyprinid species (such as goldfish or carp). Further comments pertaining directly to specific brain variability in teleosts are given in the appropriate paragraphs of the present chap-

ter, which describes the zebrafish brain. A more general discussion of the functional anatomy of the teleostean brain follows in chapter 6.

Telencephalon

The terminology of Nieuwenhuys (1963) as modified by Northcutt and Davis (1983) is applied except where noted. In teleosts, the topology of the telencephalon (Tel) is highly distorted (Nieuwenhuys and Meek, 1990). In all other vertebrate groups, the telencephalic hemispheres develop by paired evagination and thickening of the most rostral embryonic neural tube, and each hemisphere contains a lateral diverticulum of the ventricle centrally. In ray-finned fish, and most pronounced in teleosts (including the zebrafish), the roof plate of the embryonic telencephalon extends laterally with the effect that the paired alar plates forming the hemispheric walls roll out lateroventrally, a process called eversion. Thus, it is very difficult to infer from the adult topology of teleostean telencephalic cell masses alone their homologous structures in other vertebrates, though some advances have been made recently (see chapter 6).

The most rostral telencephalic divisions are the paired olfactory bulbs. The primary olfactory fibers (nervus olfactorius, I) entering the olfactory bulbs are the axons of the olfactory receptors, which are of placodal origin and, by definition, not part of the CNS. The rest of the telencephalon comprises two subdivisions, area dorsalis and area ventralis telencephali.

Olfactory bulbs

The olfactory bulbs (OB) form paired rostroventral protrusions adjacent to the remaining telencephalon and are interconnected with the latter by two tracts carrying secondary olfactory fibers: the lateral and the medial olfactory tracts. The lateral olfactory tract (LOT) enters the dorsal area of the telencephalon more rostrally compared with the more caudal entrance of the medial olfactory

tract (MOT) into the ventral area of the telencephalon. Each olfactory bulb consists of four laminae that are roughly concentrically arranged throughout most of the bulb's extent, starting peripherally with a primary olfactory fiber layer (POF, present only in the rostroventral olfactory bulbs), followed by a glomerular layer (GL), an external cellular layer (ECL, including the efferent large mitral cells whose axons form most of the lateral and medial olfactory tracts), and an internal cellular layer (ICL). A distinct secondary olfactory fiber layer present in many other teleosts rostral to the formation of the lateral and medial olfactory tracts between the internal and external cellular layers is not apparent in the zebrafish.

Area ventralis telencephali

The ventral telencephalic area (V) is divided into periventricularly located nuclei which are in contact with the median ependymal lining of the ventricle, i.e. dorsal, ventral, supracommissural, and postcommissural nuclei (Vd/Vv/Vs/Vp), and nuclei which have migrated away from the ependyma to various degrees, i.e. central and lateral nuclei, dorsal and ventral entopeduncular nuclei (Vc/Vl/ENd/ENv). Periventricularly, a dorsal (Vd) and a ventral (Vv) nucleus lie rostral to the anterior commissure. The dorsal nucleus (Vd) is contiguous caudally with the supracommissural nucleus (Vs), which in turn is contiguous with the postcommissural nucleus (Vp). A periventricular nucleus called Vn (another nucleus of Nieuwenhuys, 1963) in some other teleosts is not present in the area ventralis telencephali of the zebrafish.

In the rostral, precommissural telencephalon, the migrated nuclei of the area ventralis include the central (= commissural) nucleus (Vc) and the lateral nucleus (Vl). While the central nucleus is located immediately lateral to the dorsal nucleus (Vd), the lateral nucleus has migrated to the very periphery of the brain. A cell-sparse neuropilar region is present between Vl and Vd/Vv. A distinct intermediate nucleus of area ventralis, described in some other teleosts as a lateral extension of the postcommissural nucleus, is absent in the zebrafish.

At caudal telencephalic levels, the lateral nucleus of area ventralis is replaced by the entopeduncular cell clusters. These form separate ventral (ENv) and dorsal (ENd) bands of tightly packed cells starting at the level of the anterior commissure. While the dorsal band of entopeduncular cells disappears more rostrally, the ventral band located around the lateral forebrain bundle extends into the telencephalo-diencephalic boundary (= preoptic) region. The dorsal entopeduncular nucleus may be homologous to the intermediate nucleus of the area ventralis of other species, although no close morphological association with the postcommissural nucleus, which is characteristic for other teleosts, is seen in the zebrafish.

Area dorsalis telencephali

Dorsal to the area ventralis telencephali lie the large cell masses of the area dorsalis telencephali (D). Since most of area dorsalis is developmentally everted, the ependymal lining of the unpaired median ventricle (TelV) continues dorsal to Vd into the medial zone of the dorsal telencephalic area (Dm) and becomes located at the apparent periphery of the telencephalon. A thin tela chorioidea covering most of D encloses the paired telencephalic ventricles. However, this tela has been removed in all our preparations.

Through most of the rostrocaudal extent of area dorsalis, four distinct cell masses, the medial (Dm), dorsal (Dd), lateral (Dl), and posterior (Dp) zones, surround a central zone (Dc). The sulcus ypsiloniformis (SY; Nieuwenhuys, 1959) separates Dd from Dm. Nucleus taeniae (NT) is located immediately ventral to Dp. In the most rostral as well as in the most caudal parts of the zebrafish telencephalon, medial and lateral zones of area dorsalis merge without an apparent boundary.

Although medial, central, and lateral zones of area dorsalis in the zebrafish are large cell aggregates extending over most of the telencephalon, we chose to await first connectional and immunohistochemical data in this species before further subdividing these areas, as has been done for *Salmo* and *Lepomis* (Northcutt and Davis, 1983). These

species are only distantly related to the zebrafish, and their telencephalic organization is sufficiently different to make a direct comparison of detailed subdivisions difficult at present.

Telencephalic tracts and commissures

The anterior commissure is divided into a dorsal part (Cantd) lying immediately ventral to the supracommissural nucleus of area ventralis telencephali, and a ventral part (Cantv) which abuts the preoptic region dorsally. In the precommissural telencephalon, several fascicles converge rostrocaudally and eventually fuse to form the lateral forebrain bundle (LFB). This is a compact tract located lateral to the medial forebrain bundle (MFB) and both tracts extend into the diencephalon.

The medial olfactory tract (MOT) enters the area ventralis telencephali ventrally and courses caudally, lateral to the ventral nucleus, to the level of the anterior commissure. The lateral olfactory tract (LOT) enters the area dorsalis telencephali more rostrally and courses laterally to the ventral border of the posterior zone of area dorsalis telencephali.

Diencephalon (including synencephalon and pretectum)

The terminology of Braford and Northcutt (1983), Northcutt and Wullimann (1988), and Wullimann and Meyer (1990) is applied except where noted.

The diencephalon proper has five major divisions which, in the adult brain, appear in a dorsoventral arrangement. They are the epithalamus, dorsal thalamus, ventral thalamus, posterior tuberculum and hypothalamus. The area praeoptica, although often considered part of the hypothalamus, is treated here in its own right because it constitutes an intermediate region between telencephalon and diencephalon. The synencephalon (the intermediate region between the dorsal diencephalon and mesencephalon) and the pretectum will also be treated in this section because these regions are intricately intermingled with diencephalic cell groups. The different meaning of

synencephalon in the neuromeric model of Puelles and Rubenstein (1993) is discussed below.

Area praeoptica

The preoptic area encloses the most rostral diencephalic ventricle (DiV) and can be divided into a ventral series of parvocellular preoptic nuclei and a dorsal series of magnocellular preoptic nuclei. The anterior parvocellular preoptic nucleus (PPa) extends rostrally to become located ventral to the telencephalon. It is replaced in the diencephalon by the posterior parvocellular preoptic nucleus (PPp). The suprachiasmatic nucleus (SC) is found ventrolateral to the latter.

Dorsal to the posterior parvocellular preoptic nucleus a magnocellular preoptic nucleus (PM) emerges, which is followed more caudally by the gigantocellular part of magnocellular preoptic cells (PMg). A parvocellular part of the magnocellular preoptic nucleus, as described in the goldfish (Braford and Northcutt, 1983), is not evident morphologically in the zebrafish.

Epithalamus

The epithalamus consists of the dorsal (Had) and ventral (Hav) nuclei of the habenula, and two dorsal outgrowths, the epiphysis (E = pineal organ) and the saccus dorsalis (SD). The latter is a chorioideal tela, whereas the former is an endocrine and light-sensitive organ.

Dorsal thalamus

The dorsal thalamus (DT) emerges below the caudal portion of the ventral habenular nucleus and consists of an anterior nucleus (A) and two more caudally situated nuclei, the dorsal posterior thalamic (DP) and central posterior thalamic (CP) nuclei.

Ventral thalamus

The rostral part of the ventral thalamus (VT) is located directly below the rostral part of the ventral habenular nucleus since it reaches far more rostrally than the dorsal thalamus does. The ventral thalamus is located ventral to

the dorsal thalamus only in its caudal extent. The ventral thalamus consists of an intermediate nucleus (I) as well as ventromedial (VM) and ventrolateral (VL) nuclei. The rostromedial nucleus (R) of Butler and Saidel (1991) is also present in the zebrafish. It lies somewhat lateral to the ventral thalamic nuclei just described and is likely to belong to these nuclei. However, Anken and Rahmann (1995) recognize it as part of the entopeduncular complex.

Posterior tuberculum

As in other teleosts, the posterior tuberculum is much larger than both the dorsal and the ventral thalamus in the zebrafish. Its periventricular part consists of two nuclei, the periventricular nucleus of the posterior tuberculum (TPp) and the posterior tuberal nucleus (PTN), both of which are located between ventral thalamus and hypothalamus, as well as of the paraventricular organ (PVO). The migrated nuclei of the posterior tuberculum include primarily the preglomerular nuclei, which are – in rostromedial to caudomedial sequence – the anterior, lateral, medial, and caudal preglomerular nuclei (PGa/PGl/PGm/PGc). The (preglomerular) tertiary gustatory nucleus (TGN), which has been misinterpreted as the visual nucleus glomerulosus of other teleosts (see chapter 6), is located ventral to the medial preglomerular nucleus. Ventrolateral to the caudal preglomerular nucleus lies the so-called corpus mamillare (CM), which is also included in the posterior tuberculum here. Additional nuclei which are likely to be part of the posterior tuberculum are the posterior thalamic nucleus (P), the nucleus subglomerulosus (SG), and the torus lateralis (TLa).

Hypothalamus

As in other teleosts, the hypothalamus of the zebrafish is by far the largest diencephalic area and includes ventral, dorsal, and caudal zones. While the ventral and caudal zones form most of the median tuberal portion of the hypothalamus (TH), the dorsal zone is additionally expanded laterally and includes the paired inferior (or lateral)

lobes (IL) of the hypothalamus. These are separated from the tuberal hypothalamus by a deep ventral sulcus. All three hypothalamic zones display primarily periventricular cell masses which are flanked laterally by separate migrated nuclei.

The ventral hypothalamic zone with the periventricular nucleus (Hv) extends farthest rostrally. The anterior tuberal nucleus (ATN) and the lateral hypothalamic nucleus (LH) lie lateral to it. More caudally, the dorsal hypothalamic zone emerges and forms paired laterocaudal ventricular recesses (LR) surrounded by periventricular cell masses (Hd). Presumably migrated from these periventricular cell masses are the small-celled diffuse nucleus (DIL) and the larger-celled central nucleus (CIL) of the inferior lobe. The caudal protrusion of the inferior lobe lies ventral to the tegmentum and includes in its dorso-medial aspect the mammillary body (CM, which more likely belongs to the posterior tuberculum). The caudal hypothalamic zone starts out rostrally as a thick periventricular nucleus (Hv), which lies ventral to the posterior tuberal nucleus of the posterior tuberculum. More caudally, the caudal hypothalamus consists of paired posterior ventricular recesses (PR) surrounded by periventricular nuclei (Hc). The pituitary (Pit) is ventrally attached to the ventral and caudal hypothalamic zones. A saccus vasculosus seen in many other teleosts caudal to the pituitary is absent in the zebrafish.

Synencephalon

According to Braford and Northcutt (1983), the synencephalon designates a series of structures which are intermediate between the dorsal diencephalon and mesencephalon. These structures are located in the vicinity of the posterior commissure and include the nucleus of the medial longitudinal fascicle (NMLF), the periventricular pre-tectum (PPd/PPv), the paracommissural nucleus (PCN), and the subcommissural organ (SCO). Note, however, that in the neuromeric model of Puelles and Rubenstein (1993), the synencephalon is the most caudal prosomere (P1) and gives rise to all pretectal nuclei.

Pretectum

The pretectum is one of the most variable brain regions in teleosts (Northcutt and Wullimann, 1988; Wullimann and Meyer, 1990; Butler et al., 1991; Wullimann et al., 1991b). Following Braford and Northcutt (1983), we recognize a periventricular pretectum (see this chapter: Synencephalon), a central, and a superficial pretectum. The number and morphology of superficial and central pretectal nuclei in the zebrafish clearly represent the reduced pattern of pretectal organization in teleosts, in which nucleus corticalis as well as nucleus glomerulosus are absent (see chapter 6). The superficial pretectum is embedded in the optic tract and includes a parvocellular (PSP) and a magnocellular (PSM) nucleus. The PSM is caudally contiguous with the posterior pretectal nucleus (PO), whose cells appear to be slightly less large and less orderly arranged around a central neuropil compared with the magnocellular superficial pretectal nucleus. The central pretectal nucleus (CPN) is found dorsal to PSM and PO. The accessory pretectal nucleus (APN) lies dorsolateral to the posterior pretectal nucleus. Two additional nuclei are sometimes considered part of the pretectum: the dorsal accessory optic nucleus (DAO), which is ventrally adjacent to PSM and PO, and the ventral accessory optic nucleus (VAO), which lies more ventromedially. The VAO is very large in zebrafish compared with other cyprinids.

As mentioned already, all pretectal nuclei discussed here may derive from prosomere 1 and form the larger synencephalon of Puelles and Rubenstein (1993). Another hypothesis of interest here is that the superficial pretectal nuclei (PSP/PSM) may be homologous to the griseum tectale of birds (Marin and Puelles, 1994), in which case the superficial pretectal nuclei would be a derivative of the mesencephalic vesicle (mesomere) and not of prosomere 1 (L. Puelles, personal communication).

Diencephalic tracts and commissures

Starting in the telencephalon, both lateral and medial forebrain bundles (LFB/MFB) extend as distinct tracts

into the diencephalon, the lateral one dorsal to the preglomerular area and the medial one approaching the posterior tuberal nucleus.

Ventral to the anterior preoptic region, the optic nerves (nervus opticus, ON, II) interdigitate in the optic chiasm (CO) and reach the contralateral side of the brain. Beyond the chiasm, the optic fibers are conventionally called the optic tract (OT), which is composed of a dorso-medial (DOT) and a ventrolateral (VOT) optic tract. The DOT runs dorsally along the lateral surface of the posterior preoptic and thalamic regions towards the optic tectum, while the VOT courses caudally along the ventral boundary of the optic tectum.

The pretecto-mammillary tract (TPM) originates in the magnocellular superficial pretectal nucleus and runs through the posterior pretectal nucleus to terminate in the mammillary body. The habenular nuclei project via the fasciculus retroflexus (FR; = tractus habenulo-interpeduncularis) to the interpeduncular nucleus (NIn; Villani et al., 1994).

The habenular commissure (Chab) runs between the two dorsal habenular nuclei.

Immediately caudal to the optic chiasm lies the large postoptic commissure (Cpop; = supraoptic commissure). The minor and transverse commissures are included here in the postoptic commissure, since they were not as clearly separable as in other species. Ventral to the postoptic commissure, the horizontal commissure (Chor) crosses the midline within the ventral hypothalamic zone. The tracts forming the horizontal commissure run caudally on each brain side, ventral to the preglomerular area, beyond which they turn first dorsally and then rostrally again towards the anterior tip of the optic tectum. All along their course, these tracts are also referred to as the horizontal commissure. A third diencephalic commissure lies caudal to the posterior tuberal nucleus. This is the commissure of the posterior tuberculum (Ctub; Herrick, 1948).

The posterior commissure (Cpost) is located in the region treated earlier as synencephalon.

Mesencephalon

The terminology of Nieuwenhuys and Pouwels (1983) is applied except where noted.

The mesencephalon includes, dorsally, the (multisensory) optic tectum and, ventrally, the torus semicircularis and the tegmentum.

Tectum opticum

The optic tectum (TeO) is the most complex layered structure in the zebrafish brain. It consists of four zones (periventricular grey zone, deep white zone, central zone, and superficial grey and white zone), which can be further subdivided into 15 layers (Northcutt, 1983). Different from all other vertebrates, the most superficial tectal layer in teleosts does not consist of retinal fibers (see chapter 6: Vision). This marginal layer consists of axons whose perikarya are in the torus longitudinalis (TL). The latter is a paired, longitudinal eminence of granular cells attached to the tectum. It is located in the medial tectal ventricle (TeV) and only occurs in ray-finned fish (for a review, see: Wullimann, 1994). The intertectal commissure (Ctec) runs between the tectal hemispheres.

Torus semicircularis

The sensory torus semicircularis (TS) is the mesencephalic target of ascending octavolateralis systems and lies on top of the lateral tegmentum from where it bulges out into the tectal ventricle. In cyprinids, the central nucleus (TSc) is related to audition and the ventrolateral nucleus (TSvl) is related to mechanoreception (Echteler, 1984; McCormick and Hernandez, 1996).

Tegmentum

The term tegmentum is used ambiguously in the literature. In mammals, the roof of the mesencephalon consists of the superior colliculus (tectum opticum of other vertebrates, which is part of the visual system) and the inferior colliculus (torus semicircularis of other vertebrates, which is part of the auditory system). The ventral mesencephalon is sep-

arated from this roof by the ventricle and forms the tegmentum, which has a dominant role in motor functions. The tegmentum arises embryonically from the basal plate, in contrast to the alar plate-derived, sensory-related tectum opticum and torus semicircularis.

The tegmentum includes many motor structures, such as the oculomotor (NIII) and trochlear (NIV) nerve nuclei, the parasympathetic Edinger-Westphal nucleus (EW), the nucleus ruber (NR), and the most rostral portion of the superior reticular formation (SRF). It also harbors the dorsal and rostral tegmental nuclei (DTN/RT), the perilemniscal nucleus (PL), the nucleus of the lateral lemniscus (NLL), and the interpeduncular nucleus (NIn). The rostral tegmental nucleus as defined by Grover and Sharma (1981) is homologous to the lateral thalamic nucleus defined by Braford and Northcutt (1983). However, we prefer Grover and Sharma's term here since they were the first to show that in cyprinids a projection to the optic tectum originates in the rostral tegmental nucleus. The nucleus of the lateral lemniscus is defined according to Prasada Rao et al. (1987), who showed that this nucleus projects to the spinal cord in goldfish. Recently, Becker et al. (1995) have confirmed this for zebrafish.

Whereas the axons of the oculomotor nerve (nervus oculomotorius, III) exit the brain ventrally between tegmentum and inferior lobe, the trochlear motor nucleus sends its axons dorsally, where they decussate (DIV) in the valvula cerebelli, turn caudolaterally, and exit the brain as the trochlear nerve (nervus trochlearis, IV) between torus semicircularis and rhombencephalon.

The tegmentum is bordered rostrally by the synencephalon, the dorsal thalamus, and the posterior tuberculum; ventrally by the hypothalamus; and dorsolaterally by the torus semicircularis. Caudally, the tegmentum is contiguous with the medulla oblongata without a clearcut morphological boundary. The interpeduncular nucleus and the trochlear nucleus are often considered to be the most caudal tegmental nuclei. However, the rhombencephalic griseum centrale as well as the superior reticular formation extend rostrally up to this level. A final deci-

sion on tegmental boundaries may result from homeotic gene expression data and grafting experiments. Recently, Marin and Puelles (1994) have demonstrated an embryonic polarizing gradient from the (rhombencephalic) isthmus region acting on the differentiation of mesencephalic structures in the avian brain. Their experiments indicate a mesencephalic-rhombencephalic boundary lying somewhat more rostral, i.e. between the oculomotor and trochlear motor nuclei and rostral to the interpeduncular nucleus.

Rhombencephalon (metencephalon and myelencephalon)

The terminology of Nieuwenhuys and Pouwels (1983) is applied except where noted.

The rhombencephalon (hindbrain) is often divided into a rostral metencephalon and a caudal myelencephalon. With the exception of the cerebellum, the ventral (medullary) remainder of the metencephalon can be separated only arbitrarily from the more caudal myelencephalic portion of the medulla oblongata. Thus, we treat cerebellum and medulla oblongata as entities here. Medulla oblongata and tegmentum are collectively referred to as brain stem.

The terms metencephalon and myelencephalon are only meaningful in mammals and birds. In those derived vertebrates, the metencephalon appears to be clearly separable from the myelencephalon as it exhibits a large dorsal cerebellum and ventral pons, which consists of relay neurons for cortical fibers to the cerebellum.

Cerebellum

As in all teleosts, the cerebellum (Ce) of the zebrafish has three parts: the vestibulolateralis lobe (including the medial caudal lobe, LCa, and the paired lateral eminentiae granulares, EG), the corpus cerebelli (CCe), and the valvula cerebelli, which has medial and lateral subdivisions (Vam/Val). The cerebellar commissure (Ccer) is located

within the ventral boundary zone between valvula and corpus cerebelli.

Although the valvula extends into the tectal ventricle, its histology (presence of a granular and a molecular layer, plus aggregations of large Purkinje- and eurydendroid cells) and its caudal attachment to the rostral medulla oblongata leave no doubt about it being part of the cerebellum. While both the vestibulolateralis lobe and the corpus cerebelli have homologues in other vertebrates, the valvula cerebelli is uniquely present in ray-finned fishes (Nieuwenhuys, 1967; Wullimann and Northcutt, 1988; 1989).

Medulla oblongata

Primary sensory and motor nuclei

The medulla oblongata (MO) contains the sensory and motor nuclei of the trigeminal (nervus trigeminus, **V**), abducens (nervus abducens, **VI**), facial (nervus facialis, **VII**), octaval (nervus octavus, **VIII**), glossopharyngeal (nervus glossopharyngeus, **IX**) and vagal (nervus vagus, **X**) nerves. The anterior and posterior lateral line nerves (ALLN/ PLLN) are separate from the other cranial nerves. In terms of the number of ganglia and peripheral innervation of neuromasts, both the anterior and posterior lateral line nerve roots include more than one nerve (Northcutt, 1989). However, these nerves are included here in the anterior and posterior lateral line nerve roots shown for the zebrafish (Fig. 4).

There are two separate trigeminal motor nuclei, one located dorsally to the lateral longitudinal fascicle (NVmd), and one situated at the ventrolateral edge of this fascicle (NVmv). Both motor nuclei extend more caudally where the lateral longitudinal fascicle runs more medially. Four trigeminal sensory nuclei (Puzdrowski, 1988) are described here. The most rostral, the isthmus primary sensory trigeminal nucleus (NVs), lies immediately caudal to the secondary gustatory nucleus. More caudally, at the medio-dorsal edge of the descending trigeminal root (DV), lies the less clearly delineated (sensory) nucleus of the descending trigeminal root (NDV). It can best be recognized at the

level of the caudal octavolateralis region. A third trigeminal sensory nucleus, the medial funicular nucleus (MFN), emerges at the very end of the medulla oblongata. The large pyriform neurons of the mesencephalic nucleus of the trigeminal nerve (MNV; located at the tectal ventricle near the synencephalon and optic tectum) have sensory fibers running peripherally in the trigeminal nerve (see chapter 6: Motor nuclei of cranial nerves).

The abducens nerve has two separate populations of motor neurons. The rostral motor nucleus and its root (VIr) are located at the level of the superior reticular formation, and the caudal motor nucleus (NVlc) and its root (Vlc) are at the level of the intermediate reticular formation. Once outside the brain stem, the roots fuse and course rostrally.

The sensory root of the facial nerve (VII_s) enters the brain stem together with the anterior lateral line nerves. The sensory facial root first courses towards the midline of the brain stem, where it turns caudally and finally terminates in the facial lobe (LVII). Ventral to the facial sensory root and dorsal to the ventral rhombencephalic commissure and intermediate reticular formation lies the facial motor nucleus (NVII_m).

The octaval nerve (VIII) enters the zebrafish brain in an extended rostro-caudal region. Five primary sensory nuclei receive its projections: the anterior, magnocellular, descending, and posterior octaval nuclei, plus the tangential nucleus. It is difficult to subdivide the octaval area in teleosts. Subdivisions of this area in the zebrafish were carried out in close comparison with a detailed connective study in the goldfish (McCormick and Hernandez, 1996).

The large neurons of the tangential nucleus (T) are located at the periphery of the brain stem, immediately ventral to the entrance of the anterior portion of the octaval nerve. These darkly staining neurons have a very distinctive large nucleus and nucleolus, and are distributed over a distance of only about 100µm. The slightly smaller neurons located more caudally are part of the descending octaval nucleus (DON), which is by far the

largest octaval system. It not only extends ventrally and dorsally around the octaval root but also reaches far medially. Its most caudal part at the level of the vagal root is referred to as the posterior octaval nucleus (PON). The magnocellular octaval nucleus (MaON) is located between the tangential nucleus and the transversely coursing portion of the sensory facial root. Rostral to the magnocellular octaval nucleus, the anterior octaval nucleus (AON) arches dorsally around the descending trigeminal root. Dorsal to the inner arcuate fibers, another octaval-related nucleus (although not a primary sensory nucleus) is present, referred to as the secondary octaval population (SO).

The root of the glossopharyngeal nerve (IX) which is peripherally related to the first gill arch, enters the brain ventral to the secondary gustatory tract. While its sensory nucleus forms a cell aggregation (LIX) located intermediate between facial and vagal lobes, its motor neurons do not form a separate nucleus. Rather, they are contained in the visceromotor column together with the motor neurons of the vagal nerve (NX_m). The vagal nerve innervates the remaining gill arches and is, therefore, of much larger diameter. It carries gustatory information which is processed in the vagal lobe (LX), a large, paired brain stem structure flanking the unpaired facial lobe laterally. While some degree of histological segregation is apparent within the vagal lobe, a clear lamination, as seen in goldfish or carp, is absent. Also, from histology alone it cannot be decided whether motor neurons are included in the vagal lobe or not. The viscerosensory commissural nucleus of Cajal (NC) lies caudal to the vagal lobe.

There are two sensory nuclei related to the lateral line nerves in the zebrafish: the medial and caudal octavolateralis nuclei. The extensive medial octavolateralis nucleus (MON) is located in the most dorsal brain stem above the octaval nuclei; it is covered by a molecular layer called the cerebellar crest (CC). The latter is conventionally considered part of the medulla oblongata and not of the cerebellum, although the granular eminence cells extend parallel fibers into the cerebellar crest. The caudal

octavolateralis nucleus (CON) is smaller and lies lateral to the facial and vagal lobes.

Reticular formation

The rhombencephalic reticular formation can be divided into midline, medial, and lateral columns (Nieuwenhuys and Pouwels, 1983). Immediately caudal to the interpeduncular nucleus, the midline column includes the superior raphe nucleus (SR). Its large neuronal perikarya are surrounded by a distinct neuropil. This is not the case for the more irregularly spaced neurons of the inferior raphe nucleus (IR), which lie in the ventral midline of the brain stem at the level of the facial and vagal lobes. The medial column of the reticular formation includes the superior, intermediate, and inferior nuclei of the reticular formation, called here for convenience superior, intermediate, and inferior reticular formation (SRF/IMRF/IRF). The superior reticular formation extends rostrally into the mesencephalon. The lateral column of the reticular formation includes the cerebellar-projecting lateral reticular nucleus (LRN).

Additional medullary nuclei

The griseum centrale (GC) is a longitudinally oriented nucleus situated along the ventral lining of the rhombencephalic ventricle. It extends partially into the mesencephalon.

The locus coeruleus (LC) consists of a few conspicuously shaped, large neurons dorsal to the superior reticular formation. Their widespread noradrenergic projections have recently been documented in the zebrafish (Ma, 1994a; 1994b).

The nucleus lateralis valvulae (NLV) is a large collection of granular cells at the ventral border of the cerebellum and brain stem. The dorsal tegmental nucleus (DTN) is sometimes considered part of the NLV. However, its cells are more densely packed than are those of the NLV and extend rostrally into the mesencephalon.

Two higher-order sensory nuclei are clearly delineable in the rostral brain stem. The visually related nucleus isthmi

(NI) and the secondary gustatory nucleus (SGN). The large Mauthner cell (MAC) lies in the rostral octavolateralis region, between the anterior octaval nucleus and the ventral rhombencephalic commissure. It has two large dendrites, a lateral one extending towards the anterior/magnocellular octaval nuclei and a ventral one extending into the intermediate reticular formation. The Mauthner axon (MA) crosses the midline within the dorsal part of the medial longitudinal fascicle (MLF), and this heavily myelinated axon then descends in the MLF into the spinal cord.

The inferior olive (IO) is a large nucleus at the ventral periphery of the caudal brain stem. It is the source of climbing fibers reaching the cerebellum in teleosts (Finger, 1983; Wullimann and Northcutt, 1988; 1989).

Medulla spinalis

The terminology of Nieuwenhuys and Pouwels (1983) is applied except where noted. Only the rostral spinal cord at the level of the entrance of the second dorsal root (DR) is characterized here. The second dorsal root is treated here, because the first dorsal root is minute. (Note, however, that the corresponding first ventral root is huge and likely innervates hypaxial (somatic) musculature in the lower jaw.) First dorsal and ventral spinal roots are located approximately 100–150 μm caudal to the commissura infima of Haller. The second dorsal root, shown in this atlas, lies about 500–800 μm caudal to that commissure.

At the level of the second dorsal root, dorsal and ventral horns (DH/VH) of the grey matter are clearly visible surrounding the central canal (C). The longitudinally running tracts have been rearranged dramatically compared to their position and composition in the brain stem. They lie in the peripherally located white matter. The white matter of the spinal cord can be subdivided here into dorsal, lateral (which consists of a dorsal and a ventral part),

and ventral funiculi (Fd/Fld/Flv/Fv), as in mammalian neuroanatomy (Nieuwenhuys et al., 1988).

Brain stem/spinal tracts and commissures

The terminology is according to Nieuwenhuys and Pouwels (1983) unless otherwise indicated.

Approximately at midtectal levels, the descending fibers of the optic tectum form the massive tecto-bulbar tract (TTB) running ventromedially along the surface of the torus semicircularis and the tegmentum. Many fibers in the tecto-bulbar tract cross the midline in the ansulate commissure (Cans), which is located immediately rostral to the interpeduncular nucleus. Lateral to this nucleus, the crossed tecto-bulbar tract (TTBc) then continues its caudal course into the ventromedial brain stem. A portion of the uncrossed tecto-bulbar tract (= tractus tectobulbaris rectus, TTBr) detaches very rostrally from the main tecto-bulbar fiber masses and runs caudally, separate from the more laterally located main portion of the uncrossed tecto-bulbar tract. At the level of the inferior reticular formation, both TTBc and TTBr are no longer visible.

Because of its large size, the medial longitudinal fascicle (MLF) is often considered to be the major descending fiber system in the brain of anamniotes. It begins within the nucleus of the MLF and runs – immediately ventral to the rhombencephalic ventricle (RV) – towards the caudal end of the medulla oblongata. Whereas the dorsal part of the MLF (including the Mauthner axon) continues to course into the spinal cord, the ventral portion of the MLF associates with other fiber systems in the funiculus ventralis prior to reaching the spinal cord. Throughout most of its rhombencephalic extent, the MLF is intersected by the ventral rhombencephalic commissure (Cven). A smaller commissure, the octavolateralis-related inner arcuate fibers (IAF), also crosses via the MLF.

The ascending lateral longitudinal fascicle (LLF) is the homologue of the mammalian lateral lemniscus. The LLF contains fibers of the auditory and mechanosensory sys-

tems which originate in the primary sensory brainstem nuclei and terminate in the torus semicircularis. Caudally, the LLF lies dorsal to the superior reticular formation, adjacent to the ventral rhombencephalic commissure. It becomes displaced more laterally as it approaches the torus semicircularis.

The anterior mesencephalo-cerebellar tract (TMCa) carries mostly cerebellar afferents from the pretectum (Wullimann and Northcutt, 1988; 1989). The TMCa runs medial to the lateral longitudinal fascicle for some distance before turning dorsally to traverse the nucleus lateralis valvulae. Upon entering the cerebellum, part of the TMCa fuses with the posterior mesencephalo-cerebellar tract (TMCp), which contains the axons of the dorsal tegmental nucleus and nucleus lateralis valvulae. The TMCa and TMCp together form the anterior cerebellar tract (AC). A posterior cerebellar tract (PC) carrying cerebellar afferents from many brain stem nuclei (Wullimann and Northcutt, 1988; 1989) enters the cerebellar corpus at the level of the granular eminence. Many efferent cerebellar fibers decussate in the brachium conjunctivum and terminate, for example, in the nucleus ruber (Wullimann and Northcutt, 1988). In the zebrafish we could not identify the brachium conjunctivum neuroanatomically.

On entering the brain stem, the sensory root of the trigeminal nerve (Vs) bifurcates. Besides giving off fibers to the isthmus primary sensory trigeminal nucleus (NVs; Puzdrowski, 1988), the sensory trigeminal root turns caudally and becomes the descending trigeminal root (DV). Located ventral to the octavolateralis area, the DV descends towards the caudal tip of the medulla oblongata. Here, the DV is located lateral to the medial funicular nucleus, which receives a considerable trigeminal input. Those fibers which eventually project further caudally into the spinal cord become located within the dorsal part of the lateral funiculus.

Throughout most of its course, the descending trigeminal root is accompanied ventromedially by the ascending secondary gustatory tract (SGT), which runs from the primary gustatory centers to the secondary gustatory nucleus.

The bulbo-spinal tract (TBS) emerges medial to the caudal intermediate reticular formation and runs caudally, constantly growing in size, along the medial edge of the inferior reticular formation. Immediately prior to reaching the spinal cord, the bulbo-spinal tract is displaced laterally and associates with other tracts in the dorsal part of the funiculus lateralis.

The vestibulo-spinal tract (TVS) forms at the rostral level of the inferior reticular formation where it lies dorsal to

the inferior olive. It associates more caudally with other tracts in the ventral part of the funiculus lateralis. Both the TVS and the TBS carry descending spinal projections. Two additional commissures are present in the medulla oblongata. The commissure of the secondary gustatory nuclei (Cgus; Herrick, 1905) runs between these large, paired sensory nuclei. The commissura infima of Haller (Cinf) is located dorsal to the commissural nucleus of Cajal.

5 The brain of the zebrafish *Danio rerio*: a neuroanatomical atlas

External view

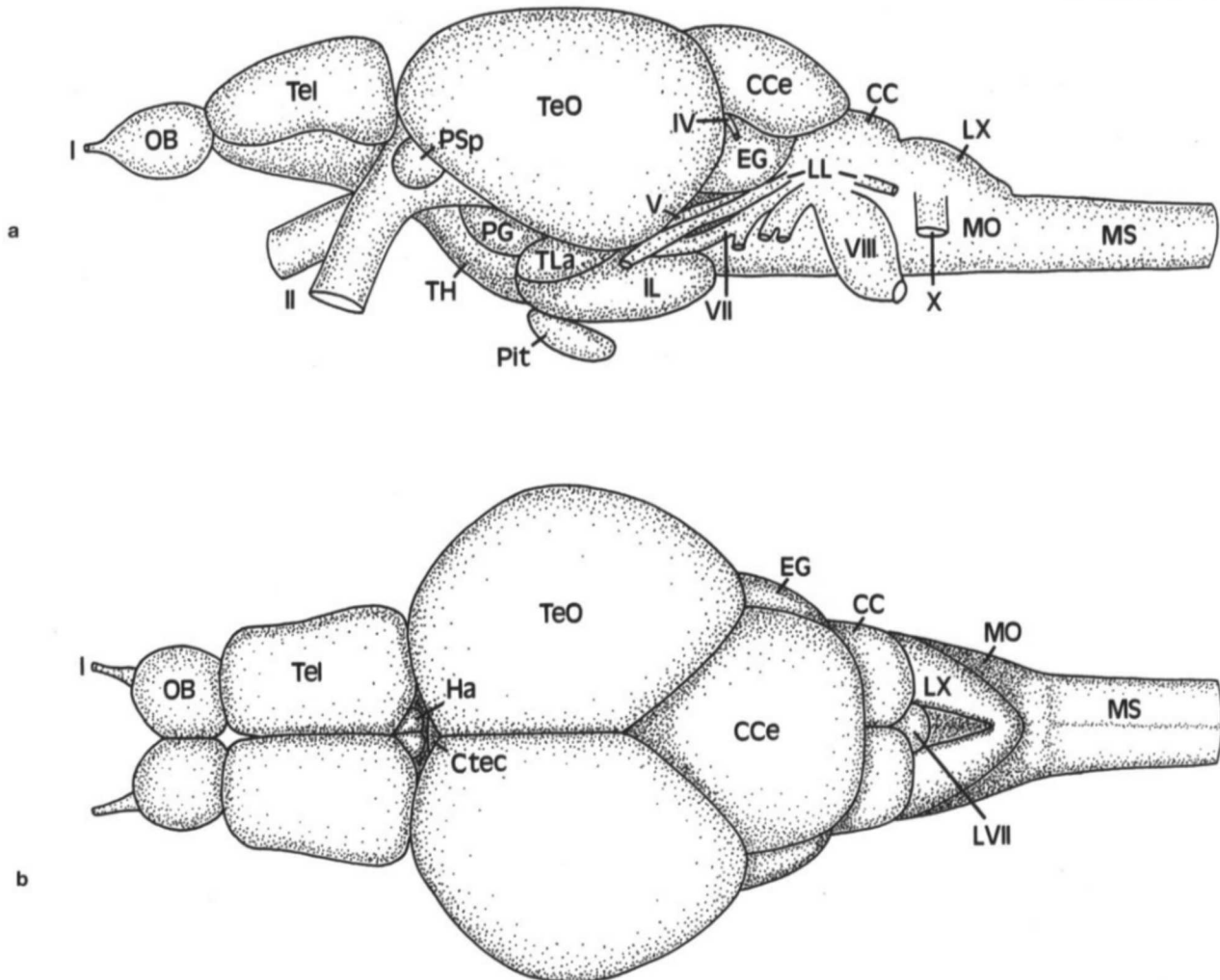


Figure 4.

Lateral (a) and dorsal (b) views of the adult zebrafish brain. The telencephalon comprises a dorsal and a ventral telencephalic area as well as an olfactory bulb, which is entered rostrally by the olfactory nerve. The diencephalon is located rostroventral to the midbrain and is largely covered by the optic tectum. Externally visible portions of the diencephalon include the optic nerve, the preglomerular area, the torus lateralis, the habenula, and the hypothalamus. The hypothalamus can be separated into a rostromedial tuberal hypothalamus and paired lateral lobes. Saccus dorsalis and epiphysis were removed during preparation and are not shown. The brainstem, which harbors most cranial nerve roots except for the optic and olfactory nerves, is covered rostrally by the cerebellum (i.e. the corpus cerebelli and the granular eminence), and includes more caudally the crista cerebellaris, the prominent paired vagal lobes, and the unpaired facial lobe. Finally, the medulla oblongata grades into the spinal cord (medulla spinalis).

CC crista cerebellaris
CCe corpus cerebelli
Ctec commissura tecti
EG eminentia granularis
Ha habenula
IL inferior lobe of hypothalamus
LL lateral line nerves
LVII facial lobe
LX vagal lobe
MO medulla oblongata
MS medulla spinalis
OB olfactory bulb
PG preglomerular area
Pit pituitary

PSp parvocellular superficial pretectal nucleus
Tel telencephalon
TeO tectum opticum
TH tuberal hypothalamus
TLa torus lateralis
I olfactory nerve
II optic nerve
IV trochlear nerve
V trigeminal nerve
VII facial nerve
VIII octaval nerve
X vagal nerve

Cross Sections

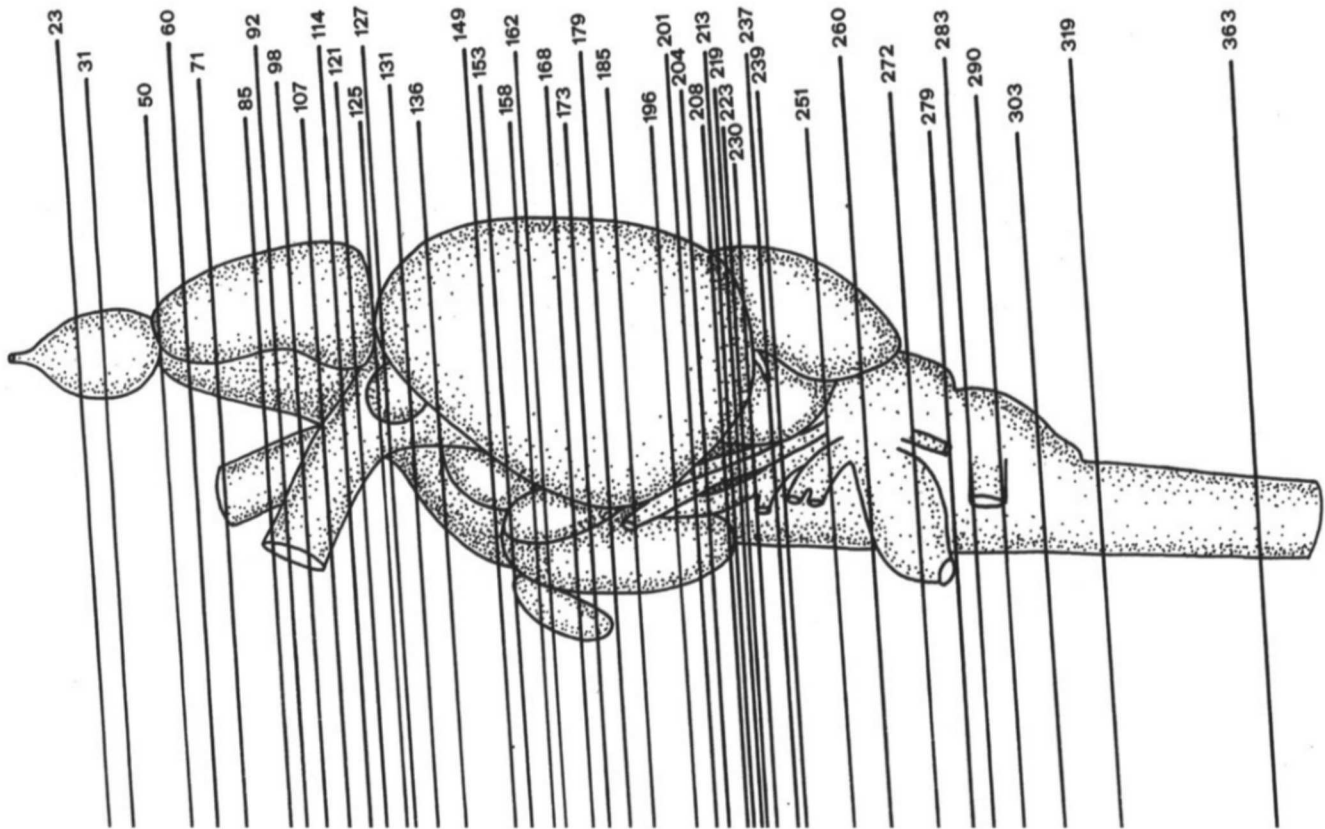


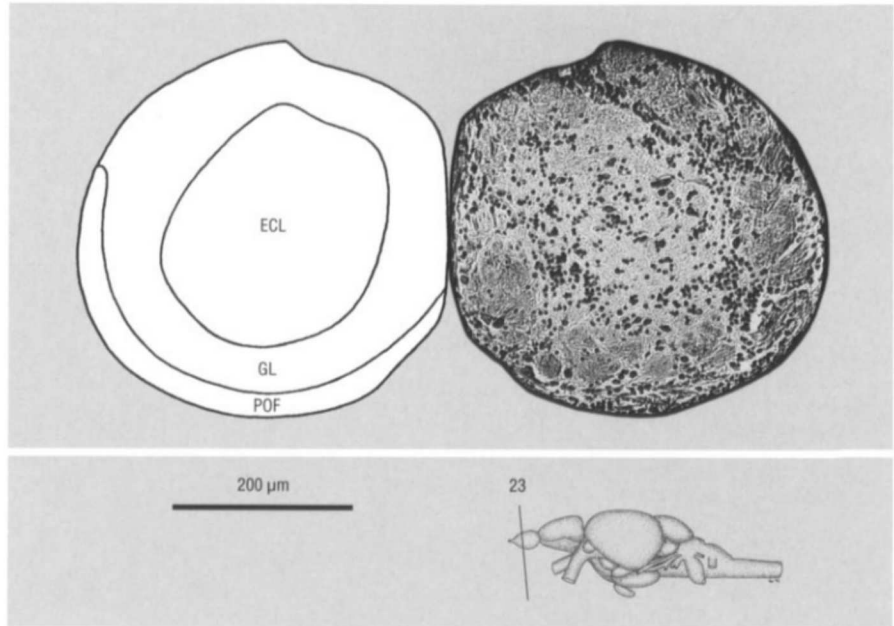
Figure 5.

Lateral view of the adult zebrafish brain indicating the position of levels illustrated in the following series of cross sections. This series gives a detailed overview of the neuroanatomy of the adult zebrafish brain. Individual sections were not taken at equal intervals but were chosen according to the appearance of novel anatomical structures, beginning

from the rostralmost extension of the olfactory bulb and proceeding through the entire brain up to the rostral spinal cord. The section plane of this series is bent slightly rostroventrally rather than corresponding to the ideal vertical axis.

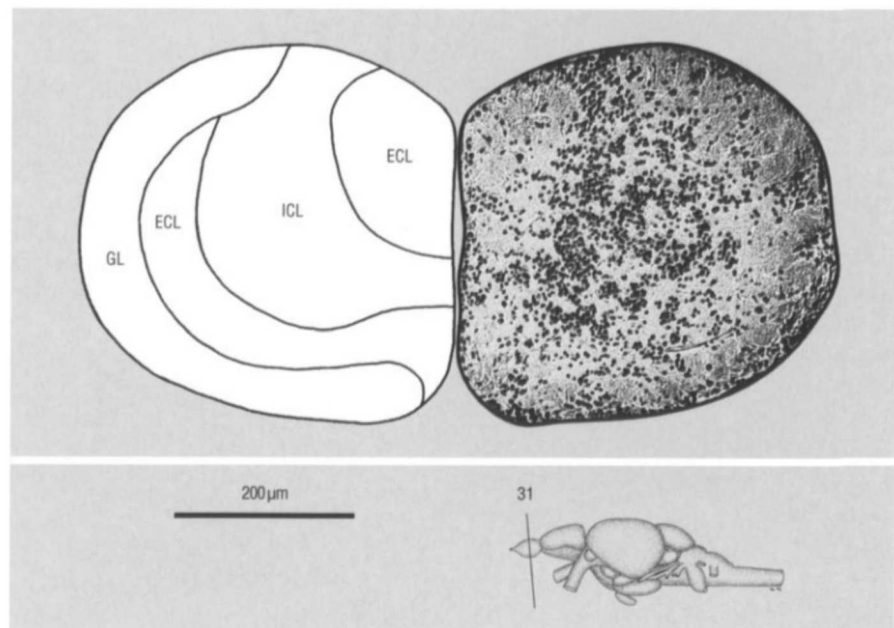
Cross Section 23

ECL external cellular layer of olfactory bulb including mitral cells
 GL glomerular layer of olfactory bulb
 POF primary olfactory fiber layer

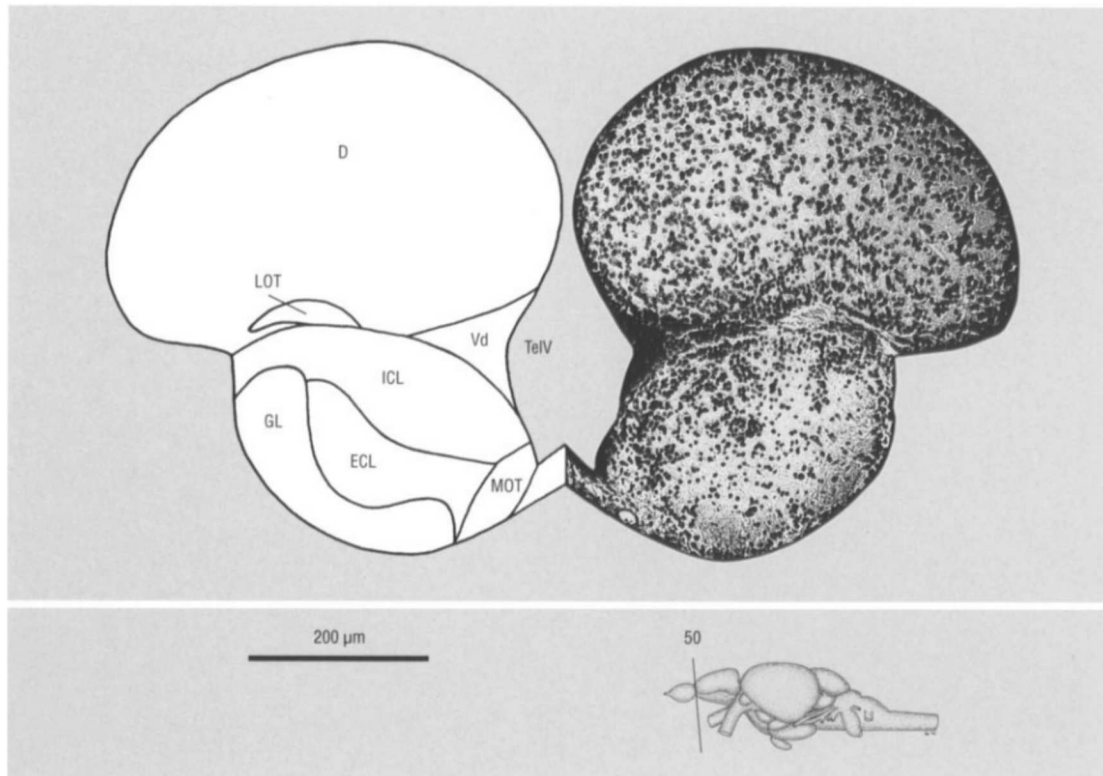


Cross Section 31

ECL external cellular layer of olfactory bulb including mitral cells
 GL glomerular layer of olfactory bulb
 ICL internal cellular layer of olfactory bulb

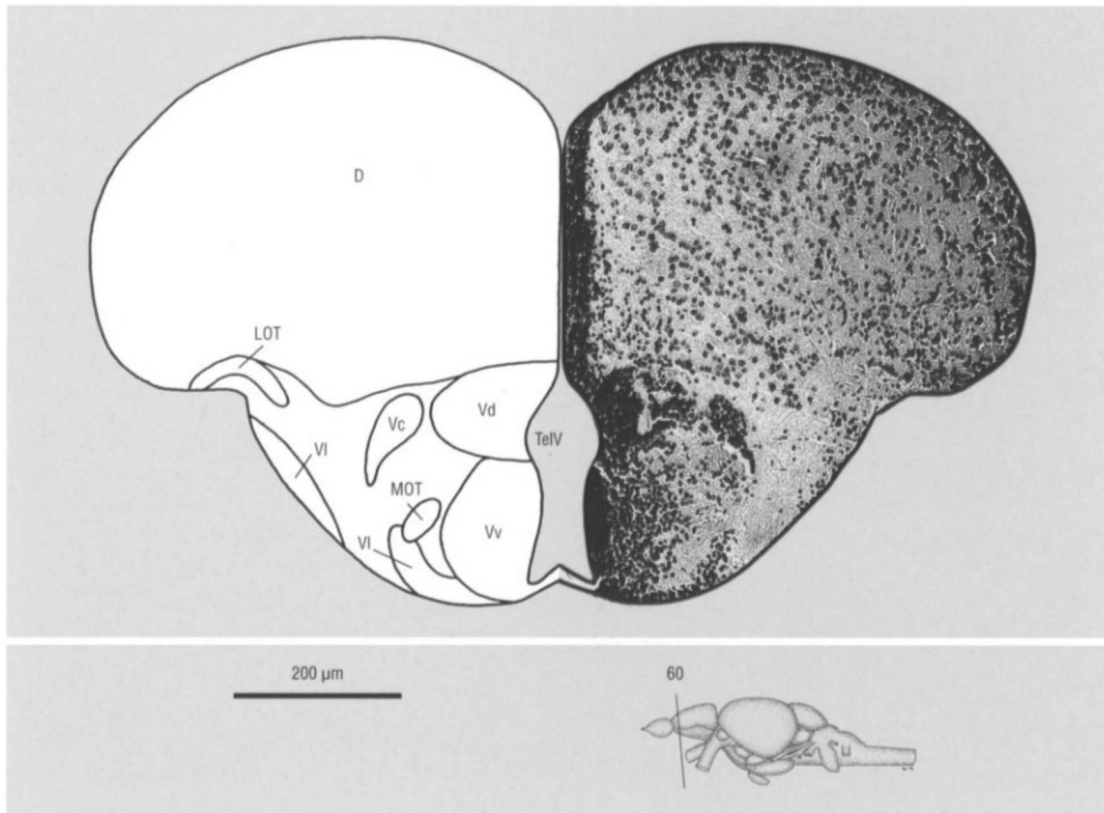


Cross Section 50



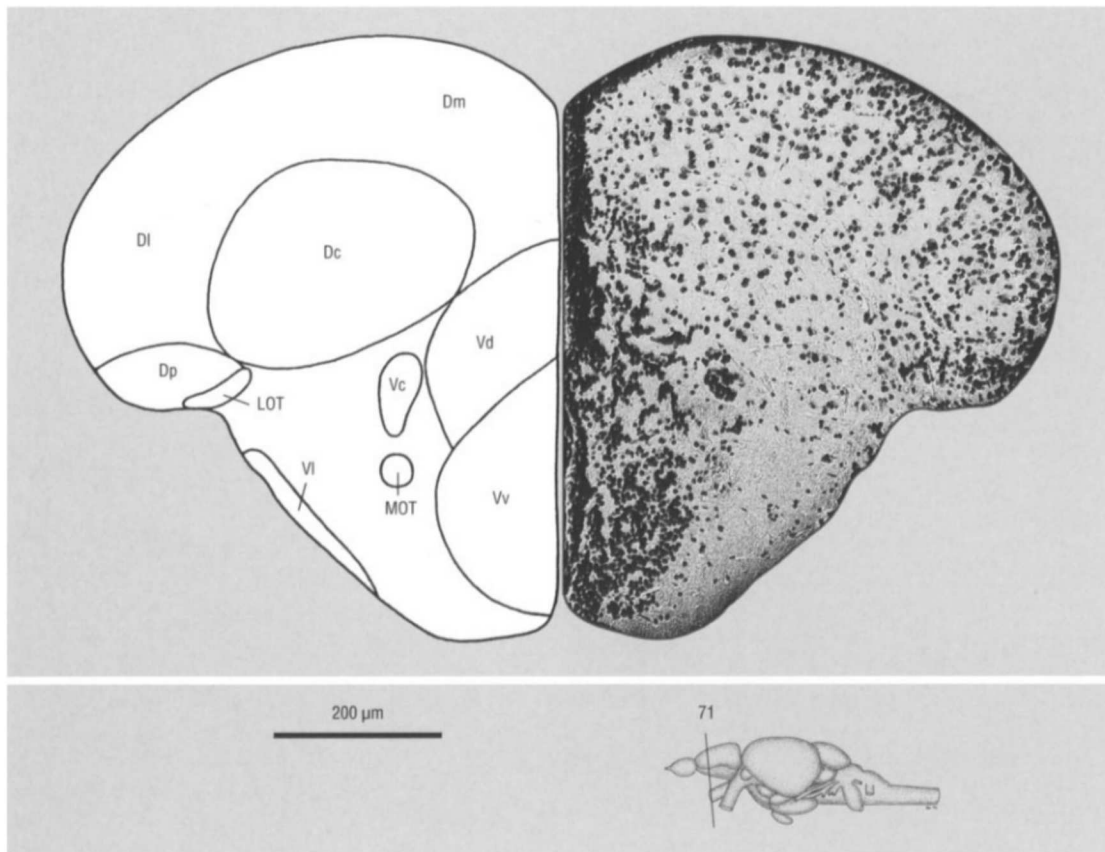
D	dorsal telencephalic area
ECL	external cellular layer of olfactory bulb including mitral cells
GL	glomerular layer of olfactory bulb
ICL	internal cellular layer of olfactory bulb
LOT	lateral olfactory tract
MOT	medial olfactory tract
TelV	telencephalic ventricle
V	ventral telencephalic area
Vd	dorsal nucleus of V

Cross Section 60



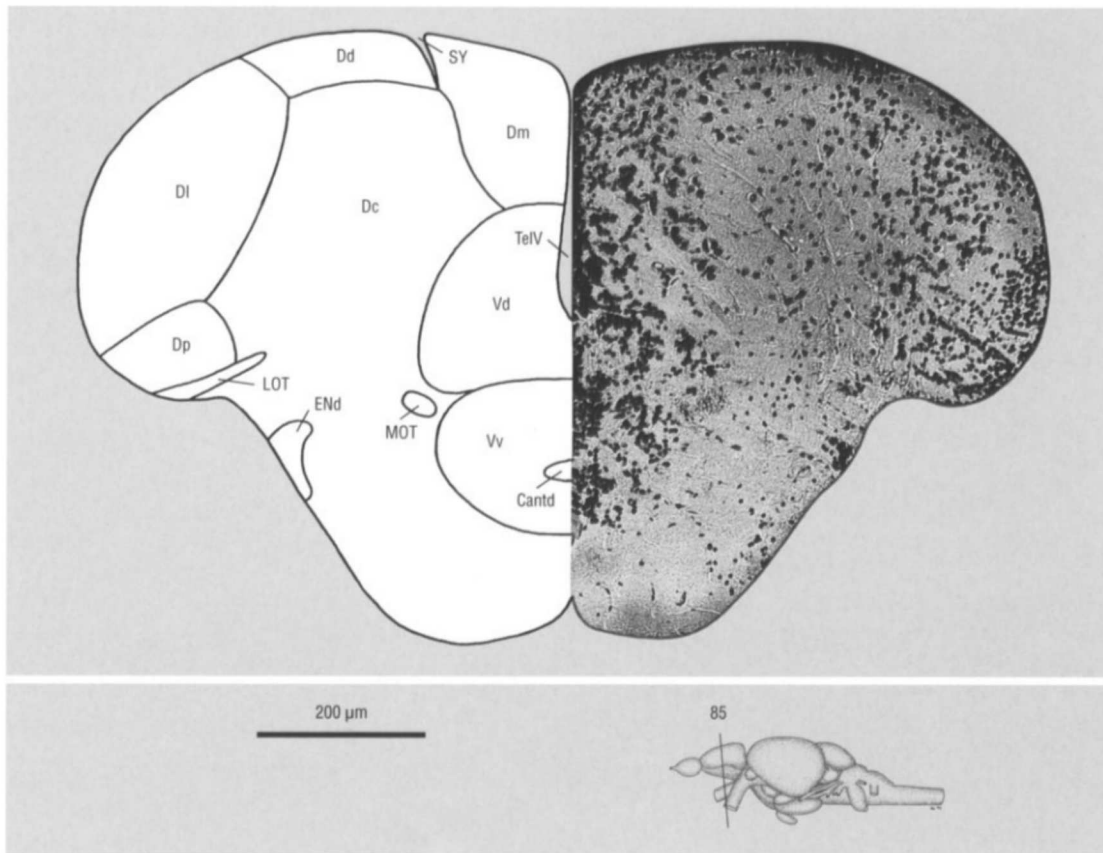
- D dorsal telencephalic area
- LOT lateral olfactory tract
- MOT medial olfactory tract
- TelV telencephalic ventricle
- V ventral telencephalic area
- Vc central nucleus of V
- Vd dorsal nucleus of V
- VI lateral nucleus of V
- Vv ventral nucleus of V

Cross Section 71



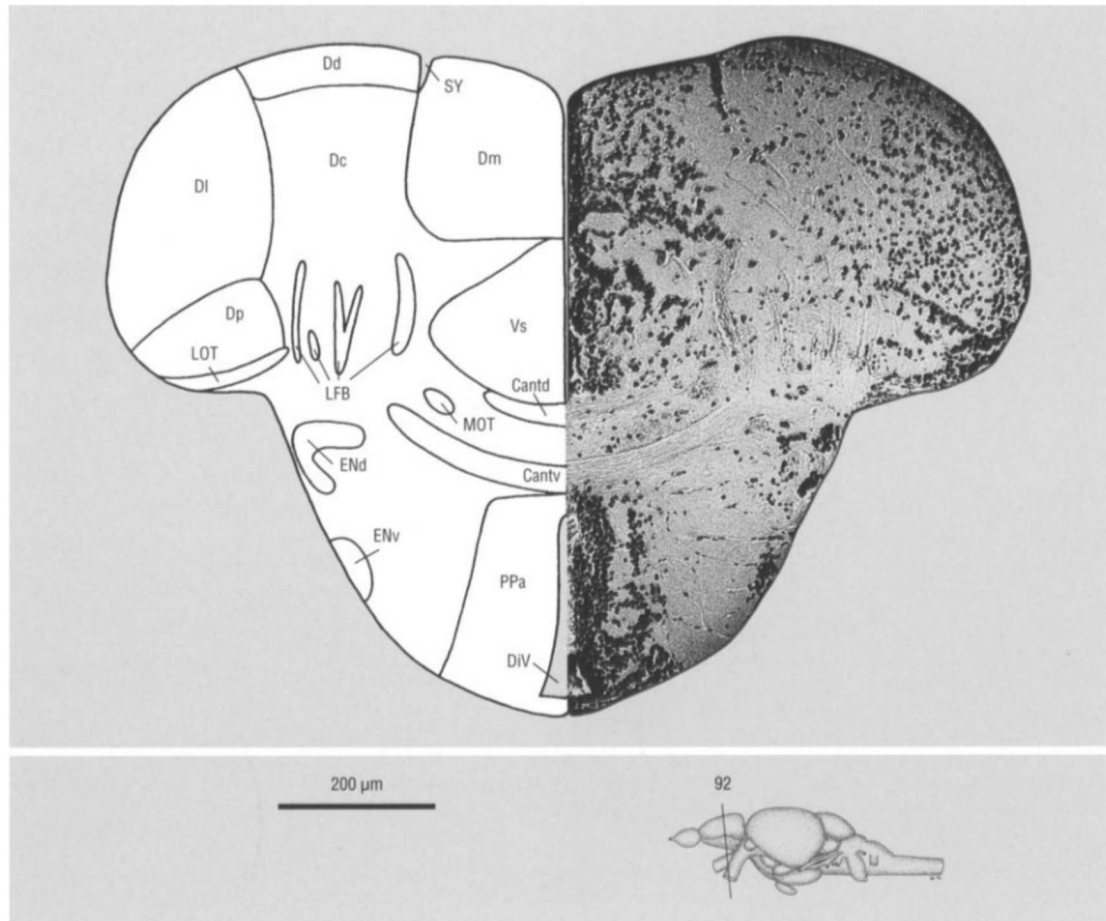
D	dorsal telencephalic area
Dc	central zone of D
Dl	lateral zone of D
Dm	medial zone of D
Dp	posterior zone of D
LOT	lateral olfactory tract
MOT	medial olfactory tract
V	ventral telencephalic area
Vc	central nucleus of V
Vd	dorsal nucleus of V
Vi	lateral nucleus of V
Vv	ventral nucleus of V

Cross Section 85



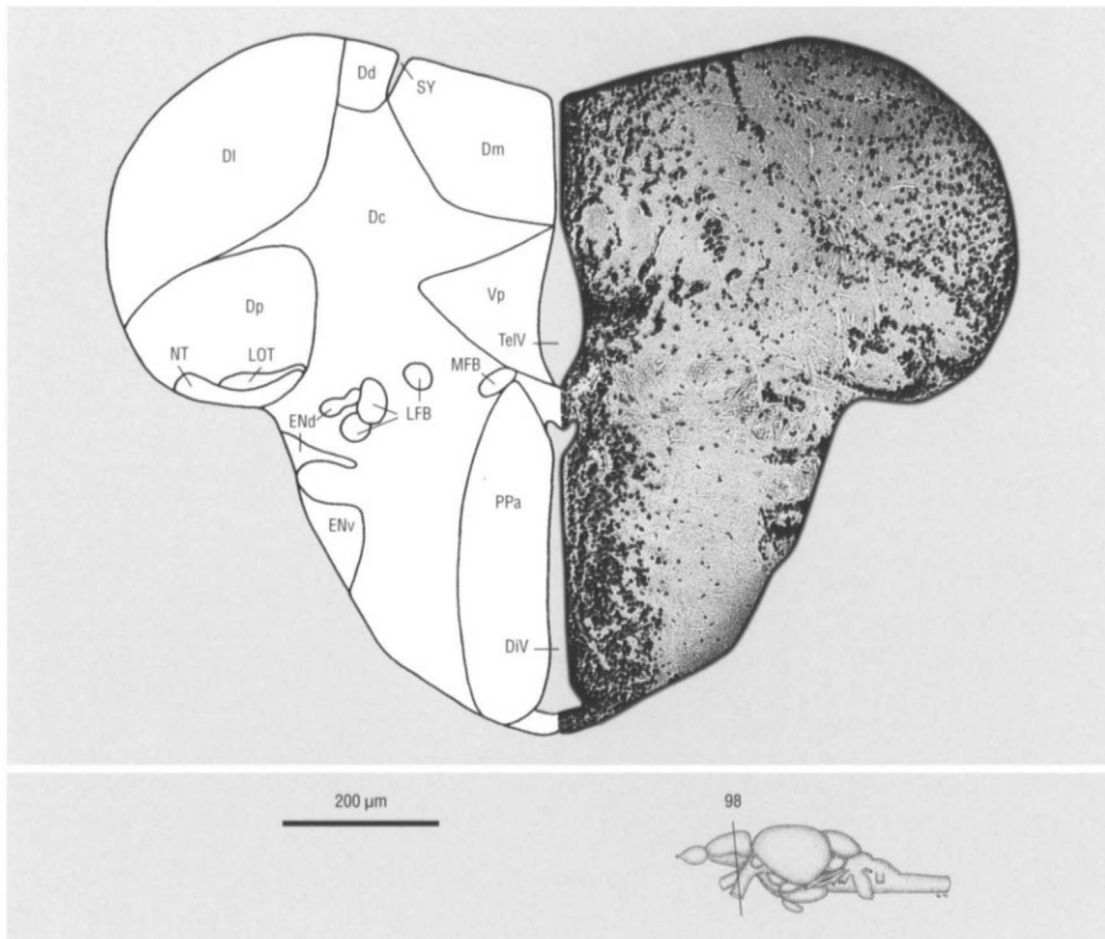
Cantd	commissura anterior, pars dorsalis
D	dorsal telencephalic area
Dc	central zone of D
Dd	dorsal zone of D
Dl	lateral zone of D
Dm	medial zone of D
Dp	posterior zone of D
ENd	entopeduncular nucleus, dorsal part
LOT	lateral olfactory tract
MOT	medial olfactory tract
SY	sulcus ypsilonformis
TelV	telencephalic ventricle
V	ventral telencephalic area
Vd	dorsal nucleus of V
Vv	ventral nucleus of V

Cross Section 92



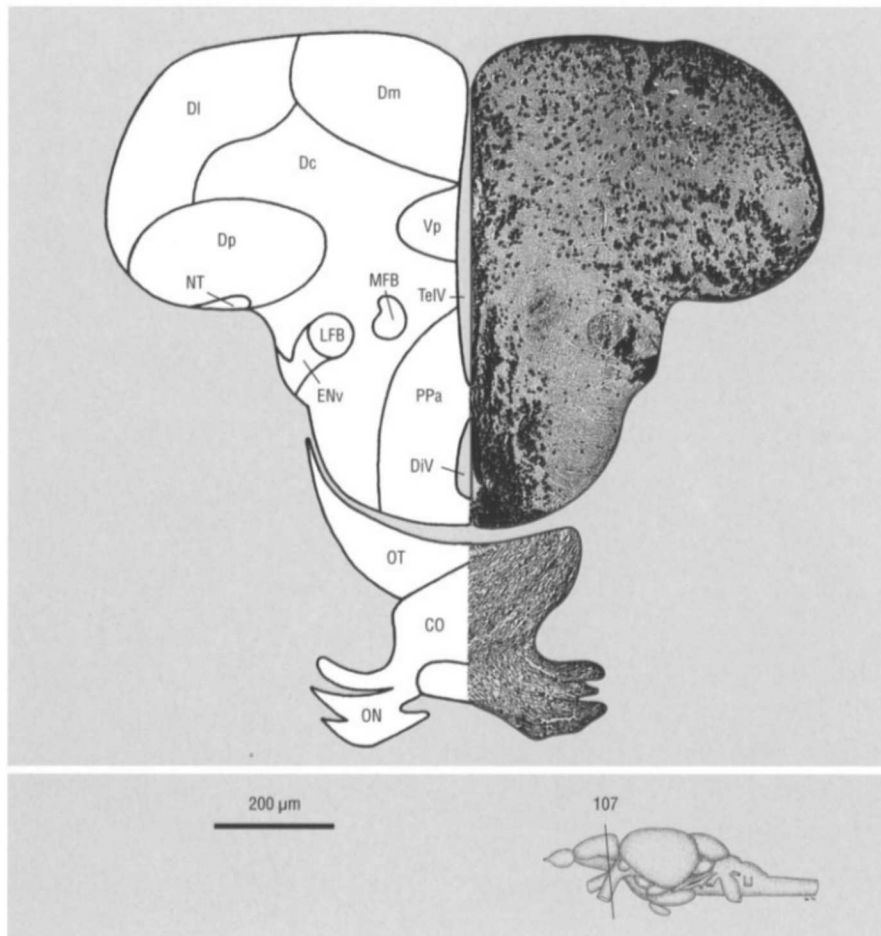
Cantd	commissura anterior, pars dorsalis
Cantv	commissura anterior, pars ventralis
D	dorsal telencephalic area
Dc	central zone of D
Dd	dorsal zone of D
DiV	diencephalic ventricle
DI	lateral zone of D
Dm	medial zone of D
Dp	posterior zone of D
ENd	entopeduncular nucleus, dorsal part
ENv	entopeduncular nucleus, ventral part
LFB	lateral forebrain bundle
LOT	lateral olfactory tract
MOT	medial olfactory tract
PPa	parvocellular preoptic nucleus, anterior part
SY	sulcus ypsilonformis
V	ventral telencephalic area
Vs	supracommissural nucleus of V

Cross Section 98



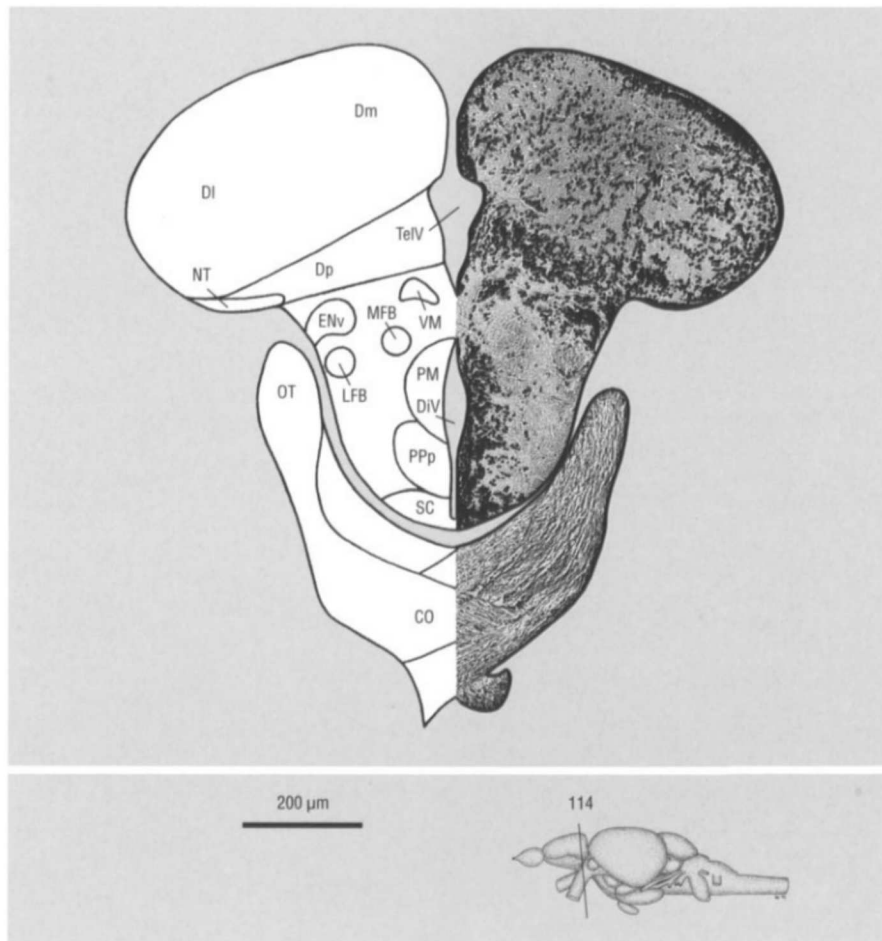
D	dorsal telencephalic area
Dc	central zone of D
Dd	dorsal zone of D
DiV	diencephalic ventricle
DI	lateral zone of D
Dm	medial zone of D
Dp	posterior zone of D
ENd	entopeduncular nucleus, dorsal part
ENv	entopeduncular nucleus, ventral part
LFB	lateral forebrain bundle
LOT	lateral olfactory tract
MFB	medial forebrain bundle
NT	nucleus taeniae
PPa	parvocellular preoptic nucleus, anterior part
SY	sulcus ypsilonformis
TelV	telencephalic ventricle
V	ventral telencephalic area
Vp	postcommissural nucleus of V

Cross Section 107



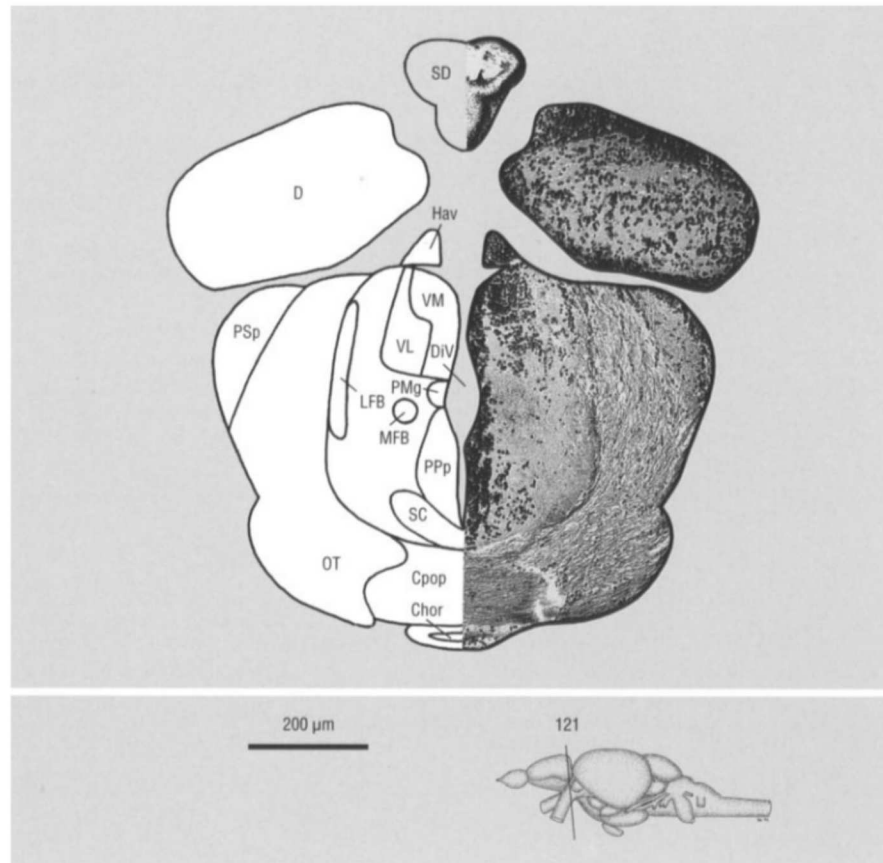
CO	chiasma opticum
D	dorsal telencephalic area
Dc	central zone of D
DiV	diencephalic ventricle
DI	lateral zone of D
Dm	medial zone of D
Dp	posterior zone of D
ENv	entopeduncular nucleus, ventral part
LFB	lateral forebrain bundle
MFB	medial forebrain bundle
NT	nucleus taeniae
ON	optic nerve
OT	optic tract
PPa	parvocellular preoptic nucleus, anterior part
TelV	telencephalic ventricle
V	ventral telencephalic area
Vp	postcommissural nucleus of V

Cross Section 114



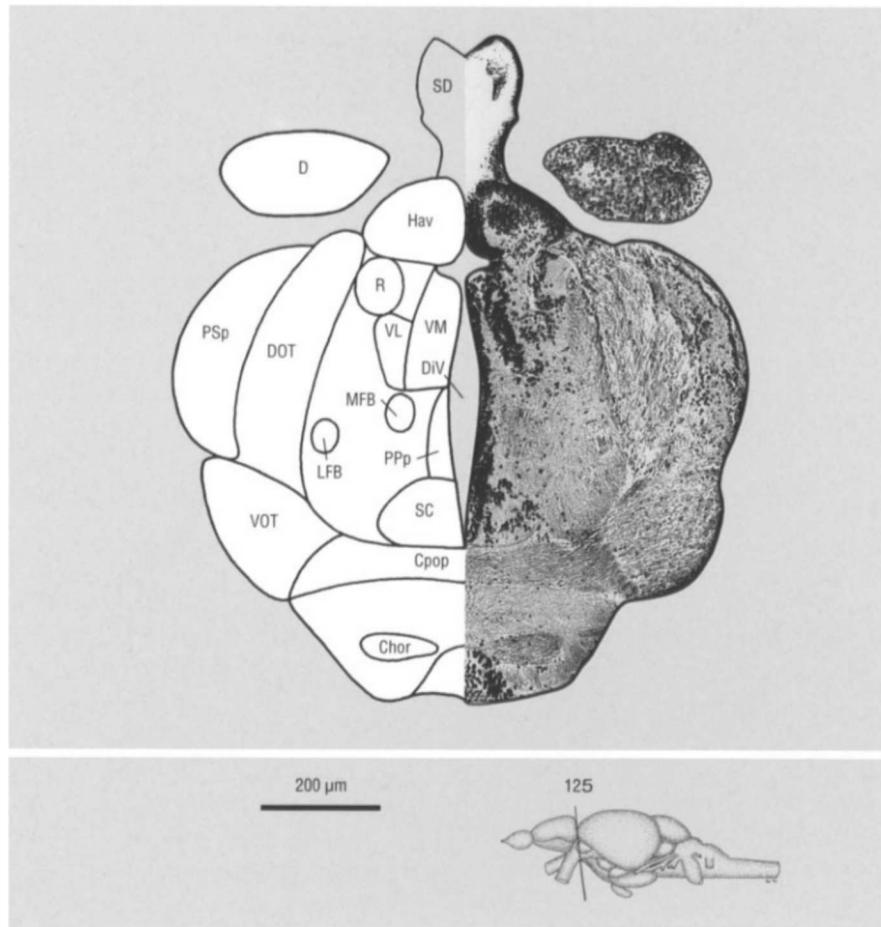
CO	chiasma opticum
D	dorsal telencephalic area
DiV	diencephalic ventricle
DI	lateral zone of D
Dm	medial zone of D
Dp	posterior zone of D
ENv	entopeduncular nucleus, ventral part
LFB	lateral forebrain bundle
MFB	medial forebrain bundle
NT	nucleus taeniae
OT	optic tract
PM	magnocellular preoptic nucleus
PPp	parvocellular preoptic nucleus, posterior part
SC	suprachiasmatic nucleus
TelV	telencephalic ventricle
VM	ventromedial thalamic nucleus

Cross Section 121



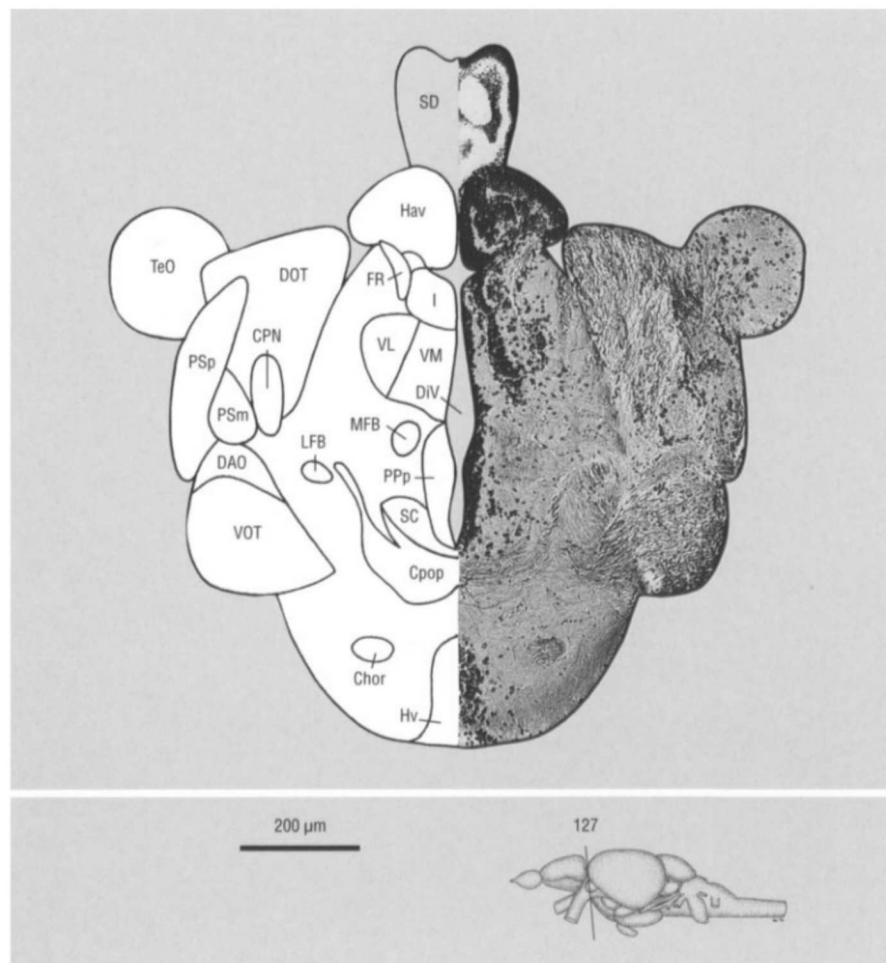
Chor	commissura horizontalis
Cpop	commissura postoptica
D	dorsal telencephalic area
DiV	diencephalic ventricle
Hav	ventral habenular nucleus
LFB	lateral forebrain bundle
MFB	medial forebrain bundle
OT	optic tract
PMg	gigantocellular part of magnocellular preoptic nucleus
PPp	parvocellular preoptic nucleus, posterior part
PSp	parvocellular superficial pretectal nucleus
SC	suprachiasmatic nucleus
SD	saccus dorsalis
VL	ventrolateral thalamic nucleus
VM	ventromedial thalamic nucleus

Cross Section 125



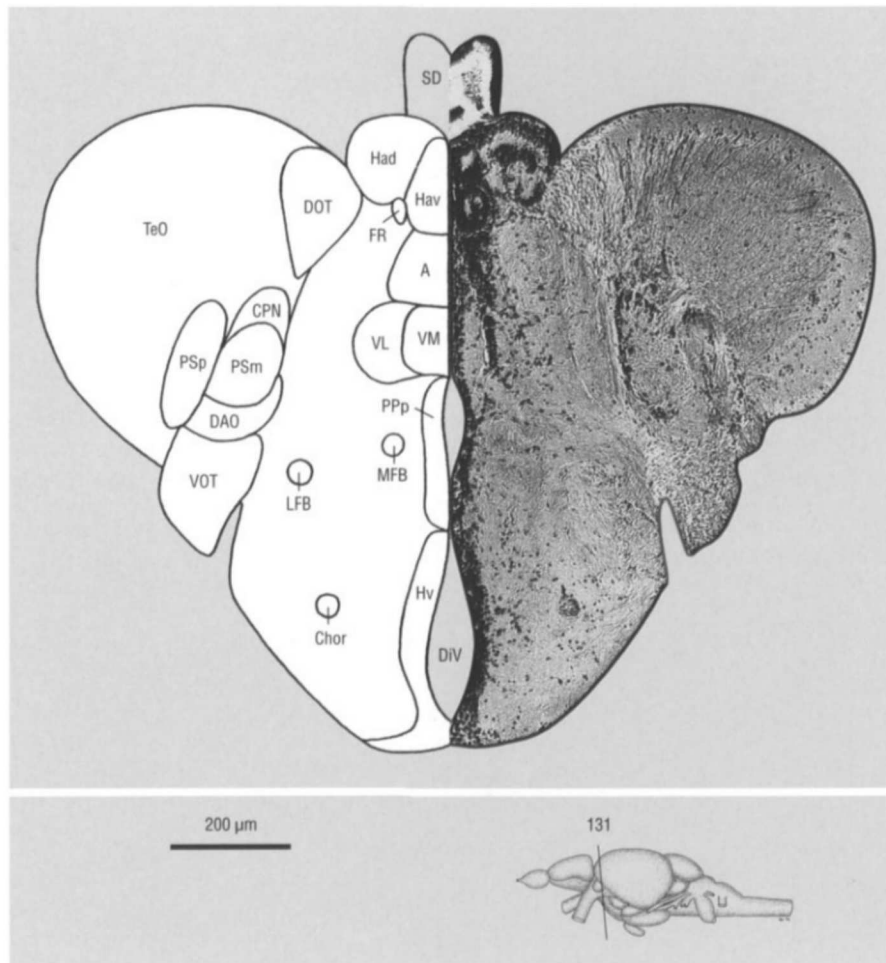
Chor	commissura horizontalis
Cpop	commissura postoptica
D	dorsal telencephalic area
Div	diencephalic ventricle
DOT	dorsomedial optic tract
Hav	ventral habenular nucleus
LFB	lateral forebrain bundle
MFB	medial forebrain bundle
PPp	parvocellular preoptic nucleus, posterior part
PSp	parvocellular superficial preoptic nucleus
R	rostromedial nucleus (of Butler & Saidel 91)
SC	suprachiasmatic nucleus
SD	saccus dorsalis
VL	ventrolateral thalamic nucleus
VM	ventromedial thalamic nucleus
VOT	ventrolateral optic tract

Cross Section 127



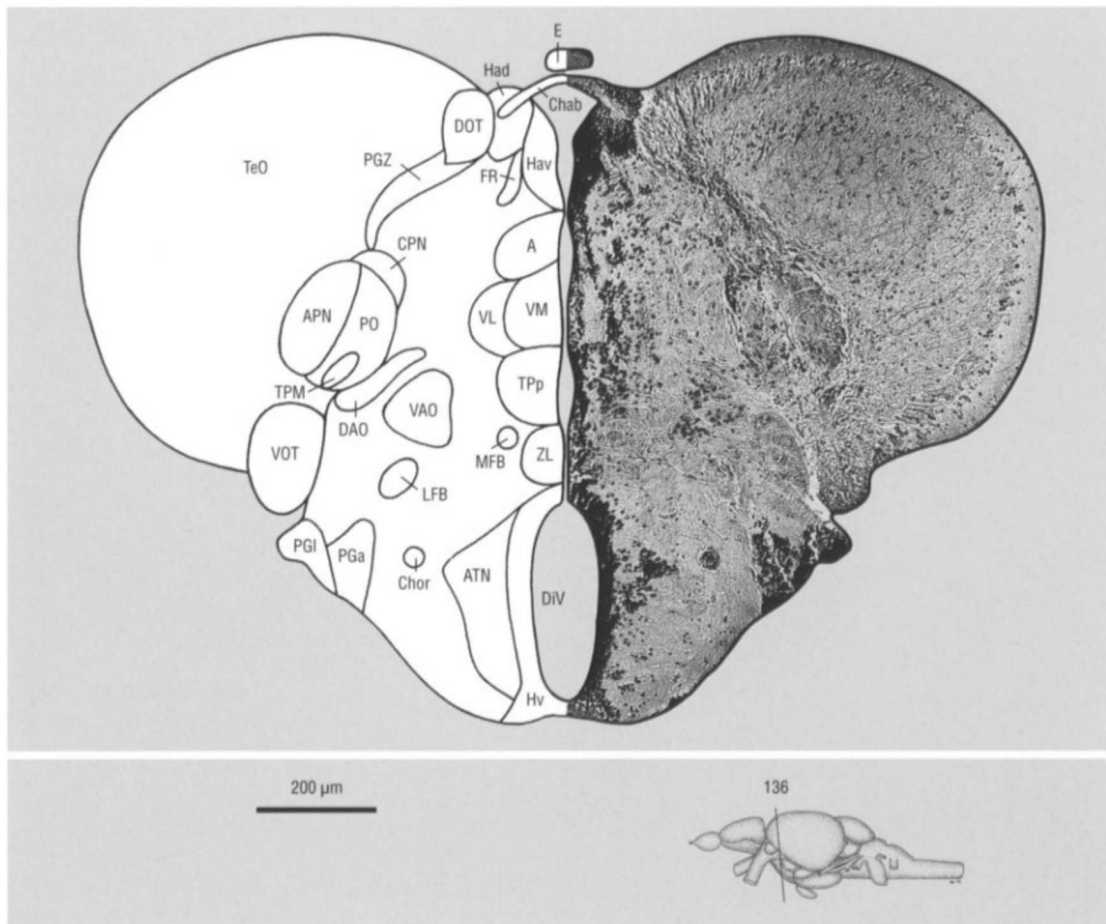
Chor	commissura horizontalis
CPN	central pretectal nucleus
Cpop	commissura postoptica
DAO	dorsal accessory optic nucleus
DIV	diencephalic ventricle
DOT	dorsomedial optic tract
FR	fasciculus retroflexus
Hav	ventral habenular nucleus
Hv	ventral zone of periventricular hypothalamus
I	intermediate thalamic nucleus
LFB	lateral forebrain bundle
MFB	medial forebrain bundle
PPp	parvocellular preoptic nucleus, posterior part
PSm	magnocellular superficial pretectal nucleus
PSp	parvocellular superficial pretectal nucleus
SC	suprachiasmatic nucleus
SD	saccus dorsalis
TeO	tectum opticum
VL	ventrolateral thalamic nucleus
VM	ventromedial thalamic nucleus
VOT	ventrolateral optic tract

Cross Section 131



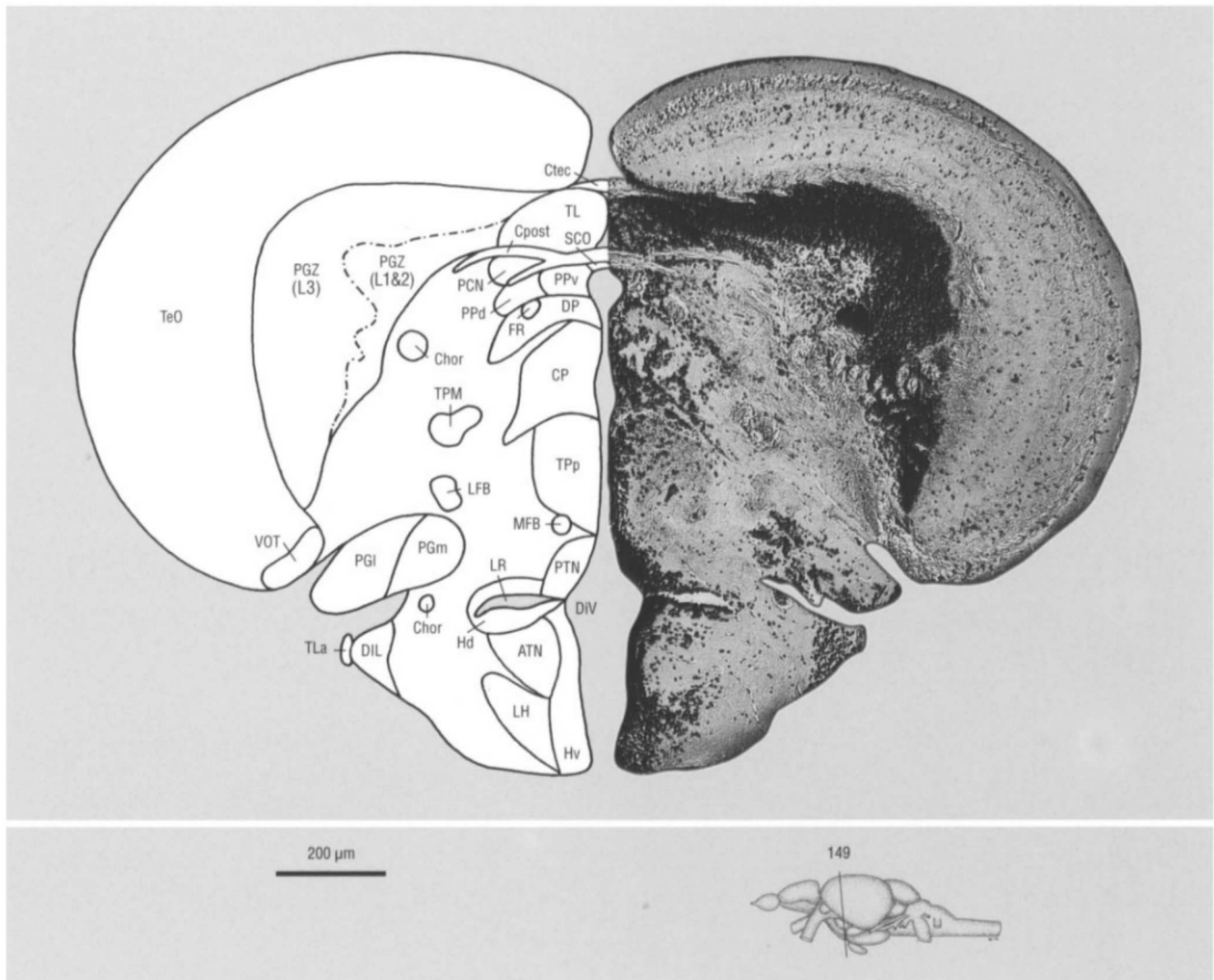
A	anterior thalamic nucleus
Chor	commissura horizontalis
CPN	central pretectal nucleus
DAO	dorsal accessory optic nucleus
Div	diencephalic ventricle
DOT	dorsomedial optic tract
FR	fasciculus retroflexus
Had	dorsal habenular nucleus
Hav	ventral habenular nucleus
Hv	ventral zone of periventricular hypothalamus
LFB	lateral forebrain bundle
MFB	medial forebrain bundle
PPp	parvocellular preoptic nucleus, posterior part
PSm	magnocellular superficial pretectal nucleus
PSp	parvocellular superficial pretectal nucleus
SD	saccus dorsalis
TeO	tectum opticum
VL	ventrolateral thalamic nucleus
VM	ventromedial thalamic nucleus
VOT	ventrolateral optic tract

Cross Section 136



A	anterior thalamic nucleus	LFB	lateral forebrain bundle
APN	accessory pretectal nucleus (of Wullimann & Meyer 90)	MFB	medial forebrain bundle
ATN	anterior tuberal nucleus	PGa	anterior preglomerular nucleus
Chab	commissura habenularum	PGl	lateral preglomerular nucleus
Chor	commissura horizontalis	PGZ	periventricular gray zone of optic tectum
CPN	central pretectal nucleus	PO	posterior pretectal nucleus (of Wullimann & Meyer 90)
DAO	dorsal accessory optic nucleus	TeO	tectum opticum
DiV	diencephalic ventricle	TPM	tractus pretectomamillaris
DOT	dorsomedial optic tract	TPp	periventricular nucleus of posterior tuberculum
E	epiphysis	VAO	ventral accessory optic nucleus
FR	fasciculus retroflexus	VL	ventrolateral thalamic nucleus
Had	dorsal habenular nucleus	VM	ventromedial thalamic nucleus
Hav	ventral habenular nucleus	VOT	ventrolateral optic tract
Hv	ventral zone of periventricular hypothalamus	ZL	zona limitans

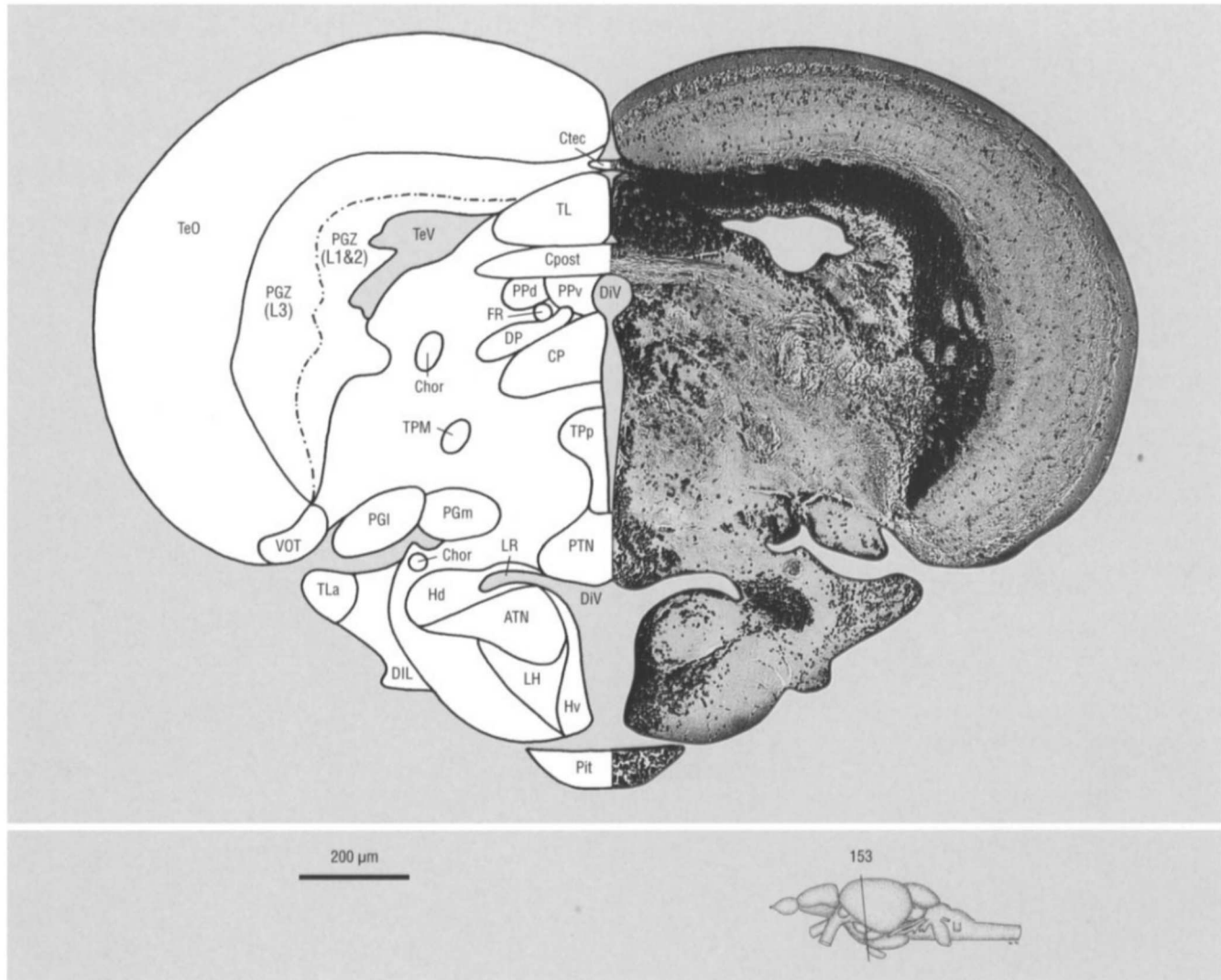
Cross Section 149



ATN anterior tuberal nucleus
 Chor commissura horizontalis
 CP central posterior thalamic nucleus
 Cpost commissura posterior
 Ctec commissura tecti
 DIL diffuse nucleus of the inferior lobe
 DIV diencephalic ventricle
 DP dorsal posterior thalamic nucleus
 FR fasciculus retroflexus
 Hd dorsal zone of periventricular hypothalamus
 Hv ventral zone of periventricular hypothalamus
 LFB lateral forebrain bundle
 LH lateral hypothalamic nucleus
 LR lateral recess of diencephalic ventricle
 MFB medial forebrain bundle

PCN paracommissural nucleus
 PGI lateral preglomerular nucleus
 PGm medial preglomerular nucleus
 PGZ periventricular gray zone of optic tectum
 PPd periventricular pretectal nucleus, dorsal part
 PPv periventricular pretectal nucleus, ventral part
 PTN posterior tuberal nucleus
 SCO subcommissural organ
 TeO tectum opticum
 TL torus longitudinalis
 TLa torus lateralis
 TPM tractus pretectomamillaris
 Tpp periventricular nucleus of posterior tuberculum
 VOT ventrolateral optic tract

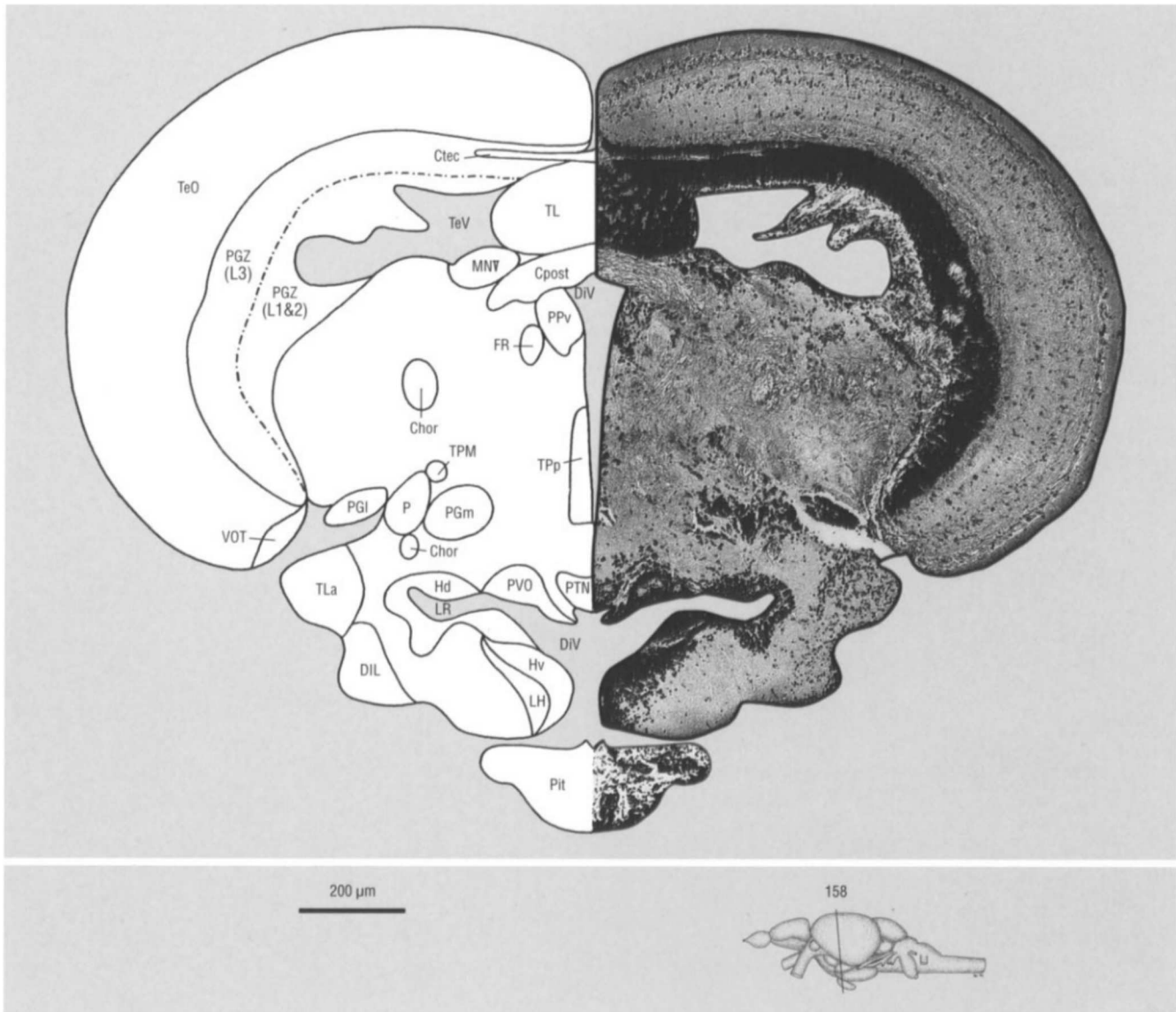
Cross Section 153



ATN	anterior tuberal nucleus
Chor	commissura horizontalis
CP	central posterior thalamic nucleus
Cpost	commissura posterior
Ctec	commissura tecti
DIL	diffuse nucleus of the inferior lobe
DiV	diencephalic ventricle
DP	dorsal posterior thalamic nucleus
FR	fasciculus retroflexus
Hd	dorsal zone of periventricular hypothalamus
Hv	ventral zone of periventricular hypothalamus
LH	lateral hypothalamic nucleus
LR	lateral recess of diencephalic ventricle
PGI	lateral preglomerular nucleus

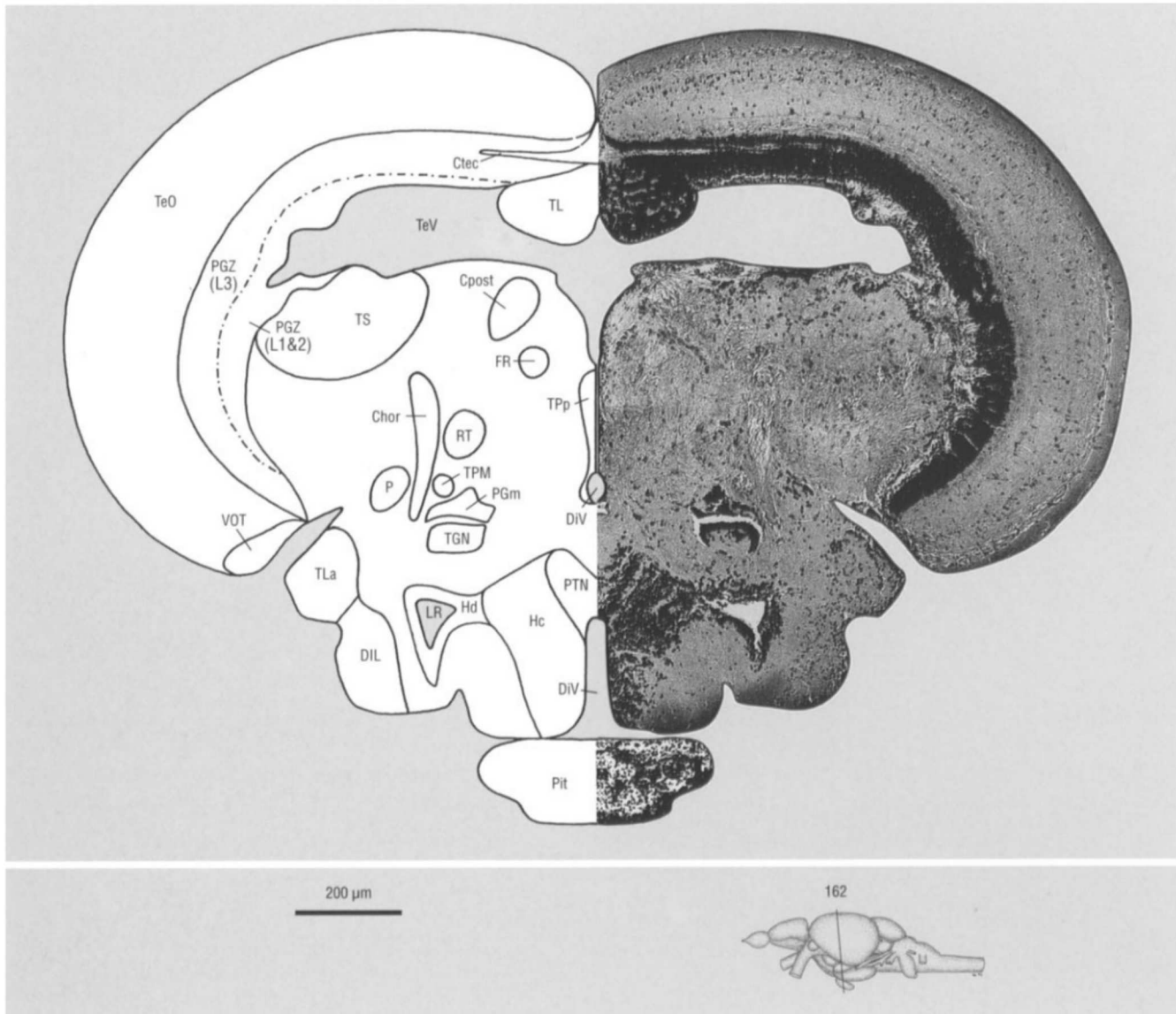
PGm	medial preglomerular nucleus
PGZ	periventricular gray zone of optic tectum
Pit	pituitary
PPd	periventricular pretectal nucleus, dorsal part
PPv	periventricular pretectal nucleus, ventral part
PTN	posterior tuberal nucleus
TeO	tectum opticum
TeV	tectal ventricle
TL	torus longitudinalis
TLa	torus lateralis
TPM	tractus pretectomamillaris
TPp	periventricular nucleus of posterior tuberculum
VOT	ventrolateral optic tract

Cross Section 158



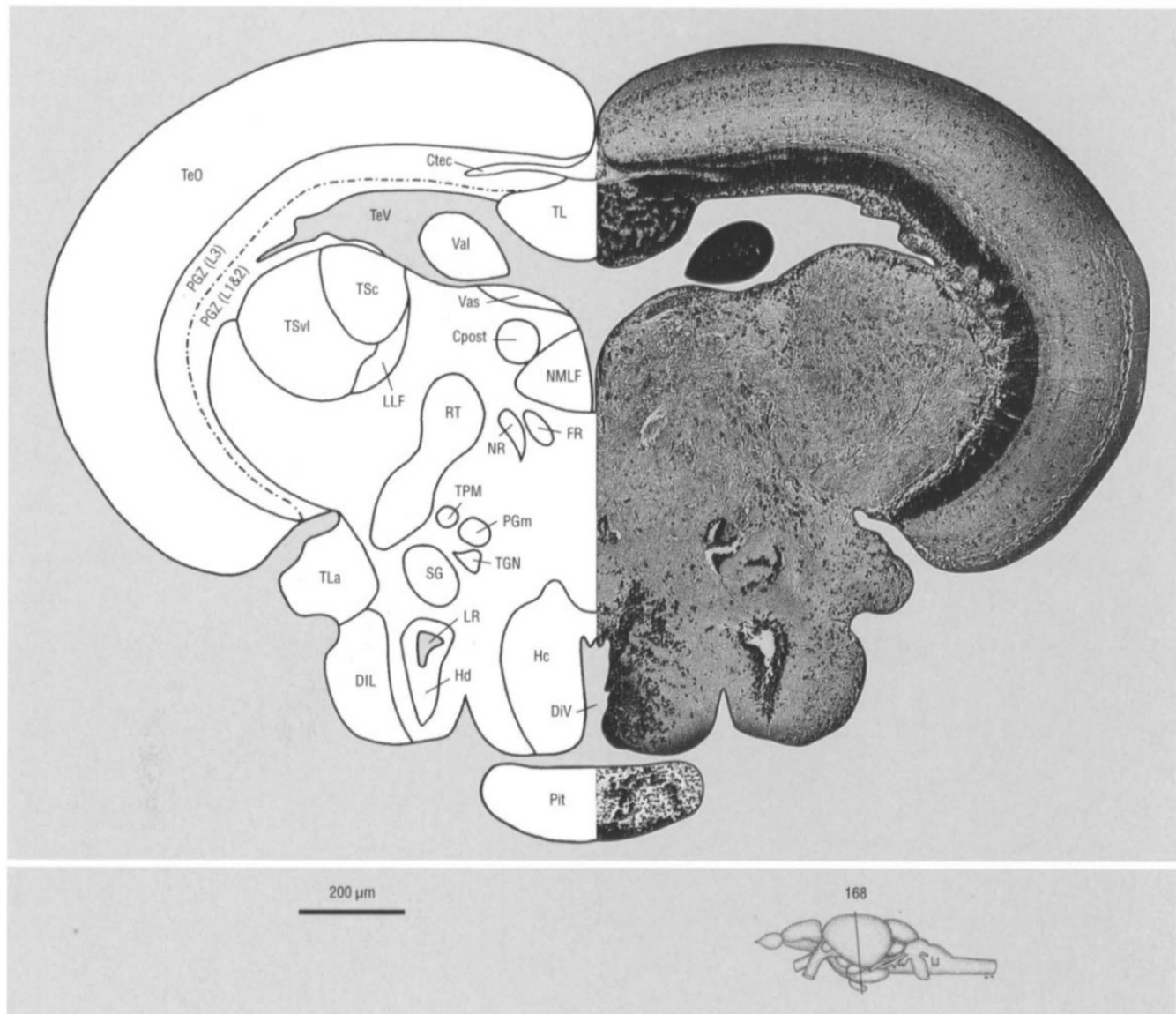
Chor	commissura horizontalis	PGm	medial preglomerular nucleus
Cpost	commissura posterior	PGZ	periventricular gray zone of optic tectum
Ctec	commissura tecti	Pit	pituitary
DIL	diffuse nucleus of the inferior lobe	PPv	periventricular pretecal nucleus, ventral part
DIV	diencephalic ventricle	PTN	posterior tuberal nucleus
FR	fasciculus retroflexus	PVO	paraventricular organ
Hd	dorsal zone of periventricular hypothalamus	TeO	tectum opticum
Hv	ventral zone of periventricular hypothalamus	TeV	tectal ventricle
LH	lateral hypothalamic nucleus	TL	torus longitudinalis
LR	lateral recess of diencephalic ventricle	TLa	torus lateralis
MNV	mesencephalic nucleus of trigeminal nerve	TPM	tractus pretectomamillaris
P	posterior thalamic nucleus	TPp	periventricular nucleus of posterior tuberculum
PGI	lateral preglomerular nucleus	VOT	ventrolateral optic tract

Cross Section 162



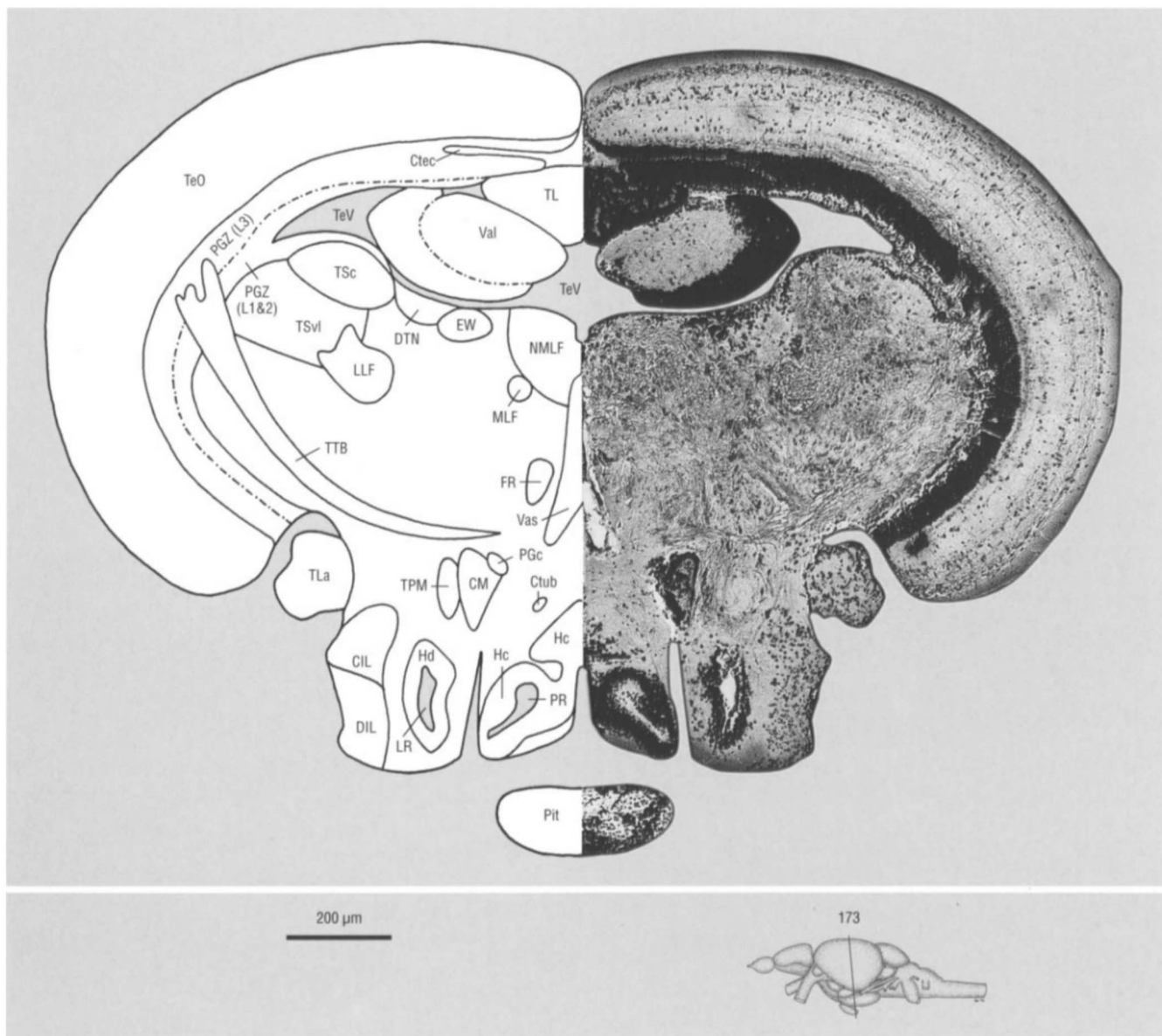
Chor	commissura horizontalis	Pit	pituitary
Cpost	commissura posterior	PTN	posterior tuberal nucleus
Ctec	commissura tecti	RT	rostral tegmental nucleus (of Grover & Sharma 81)
DIL	diffuse nucleus of the inferior lobe	TeO	tectum opticum
DiV	diencephalic ventricle	TeV	tectal ventricle
FR	fasciculus retroflexus	TGN	tertiary gustatory nucleus (of Wullimann 88)
Hc	caudal zone of periventricular hypothalamus	TL	torus longitudinalis
Hd	dorsal zone of periventricular hypothalamus	TLa	torus lateralis
LR	lateral recess of diencephalic ventricle	TPM	tractus pretectomamillaris
P	posterior thalamic nucleus	TPp	periventricular nucleus of posterior tuberculum
PGm	medial preglomerular nucleus	TS	torus semicircularis
PGZ	periventricular gray zone of optic tectum	VOT	ventrolateral optic tract

Cross Section 168



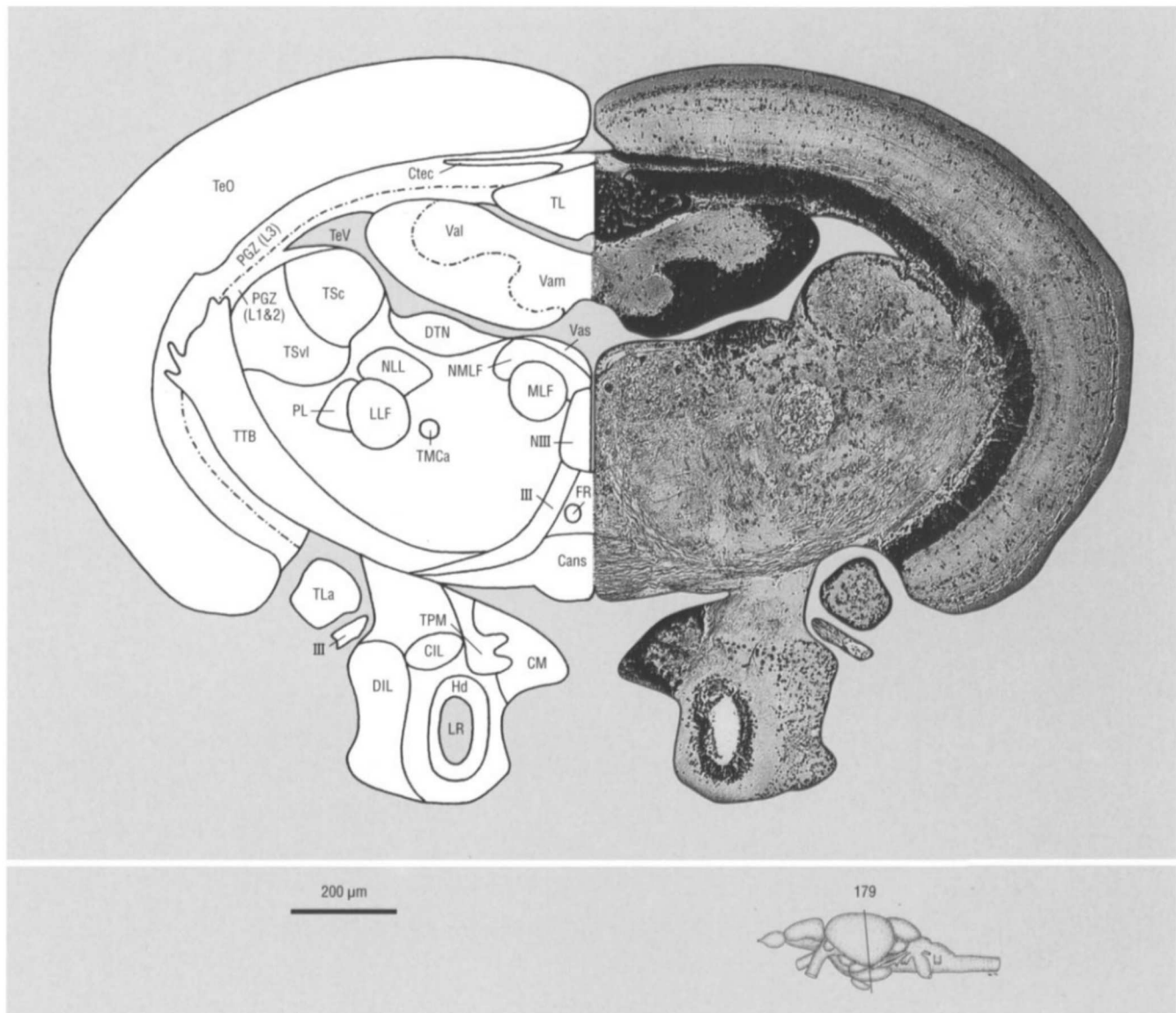
Cpost	commissura posterior	Pit	pituitary
Ctec	commissura tecti	RT	rostral tegmental nucleus (of Grover & Sharma 81)
DIL	diffuse nucleus of the inferior lobe	SG	subglomerular nucleus
DIV	diencephalic ventricle	TeO	tectum opticum
FR	fasciculus retroflexus	TeV	tectal ventricle
Hc	caudal zone of periventricular hypothalamus	TGN	tertiary gustatory nucleus (of Wullimann 88)
Hd	dorsal zone of periventricular hypothalamus	TL	torus longitudinalis
LLF	lateral longitudinal fascicle	TLa	torus lateralis
LR	lateral recess of diencephalic ventricle	TPM	tractus pretectomamillaris
NMLF	nucleus of MLF	TSc	central nucleus of torus semicircularis
NR	nucleus ruber	TSvl	ventrolateral nucleus of torus semicircularis
PGm	medial preglomerular nucleus	Val	lateral division of valvula cerebelli
PGZ	periventricular gray zone of optic tectum	Vas	vascular lacuna of area postrema

Cross Section 173



CIL central nucleus of the inferior lobe
 CM corpus mamillare
 Ctec commissura tecti
 Ctub commissure of the posterior tuberculum
 DIL diffuse nucleus of the inferior lobe
 DTN dorsal tegmental nucleus
 EW Edinger-Westphal nucleus
 FR fasciculus retroflexus
 Hc caudal zone of periventricular hypothalamus
 Hd dorsal zone of periventricular hypothalamus
 LLF lateral longitudinal fascicle
 LR lateral recess of diencephalic ventricle
 MLF medial longitudinal fascicle
 NMLF nucleus of MLF

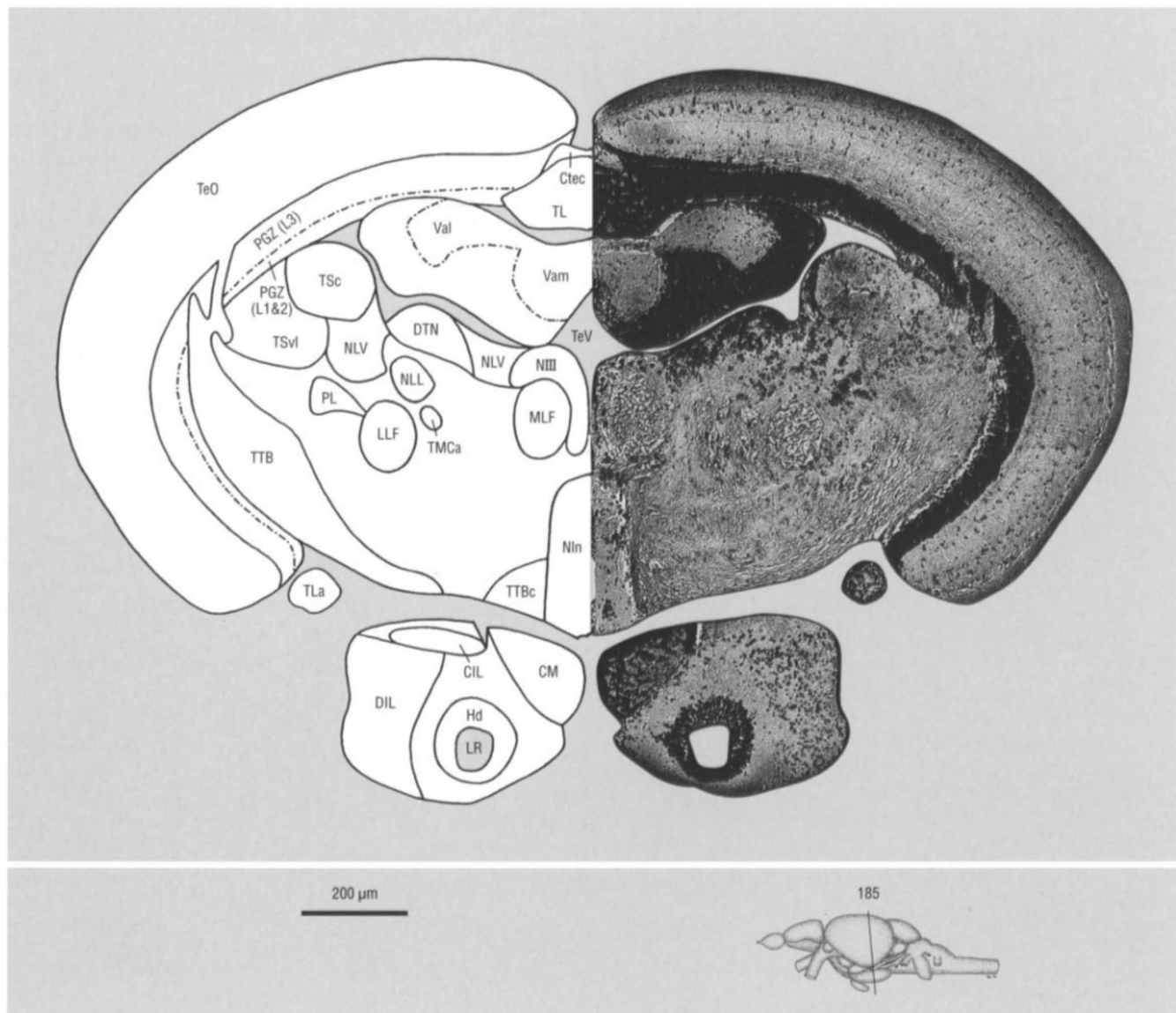
PGc caudal preglomerular nucleus
 PGZ periventricular gray zone of optic tectum
 Pit pituitary
 PR posterior recess of diencephalic ventricle
 TeO tectum opticum
 TeV tectal ventricle
 TL torus longitudinalis
 TLa torus lateralis
 TPM tractus pretectomamillaris
 TSc central nucleus of torus semicircularis
 TSvl ventrolateral nucleus of torus semicircularis
 TTB tractus tectobulbaris
 Val lateral division of valvula cerebelli
 Vas vascular lacuna of area postrema



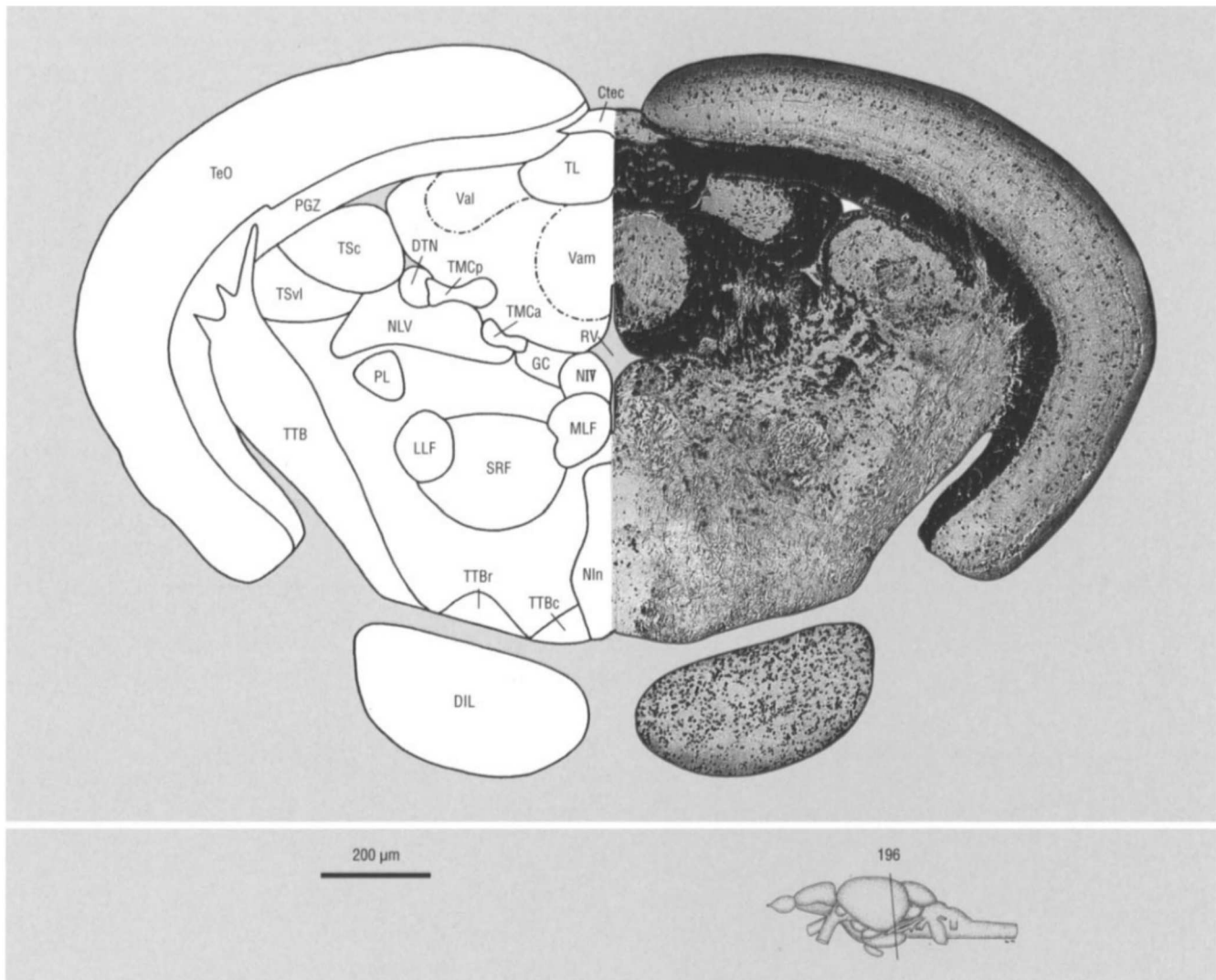
Cans commissura ansulata
 CIL central nucleus of the inferior lobe
 CM corpus mamillare
 Ctec commissura tecti
 DIL diffuse nucleus of the inferior lobe
 DTN dorsal tegmental nucleus
 FR fasciculus retroflexus
 Hd dorsal zone of periventricular hypothalamus
 LLF lateral longitudinal fascicle
 LR lateral recess of diencephalic ventricle
 MLF medial longitudinal fascicle
 NLL nucleus of the lateral lemniscus (of Prasada Rao et al. 87)
 NMLF nucleus of MLF
 NIII oculomotor nucleus
 PGZ periventricular gray zone of optic tectum

PL perilemniscal nucleus
 TeO tectum opticum
 TeV tectal ventricle
 TL torus longitudinalis
 TLa torus lateralis
 TMCa tractus mesencephalocerebellaris anterior
 TPM tractus pretectomamillaris
 TSc central nucleus of torus semicircularis
 TSVI ventrolateral nucleus of torus semicircularis
 TTB tractus tectobulbaris
 Val lateral division of valvula cerebelli
 Vam medial division of valvula cerebelli
 Vas vascular lacuna of area postrema
 III oculomotor nerve

Cross Section 185



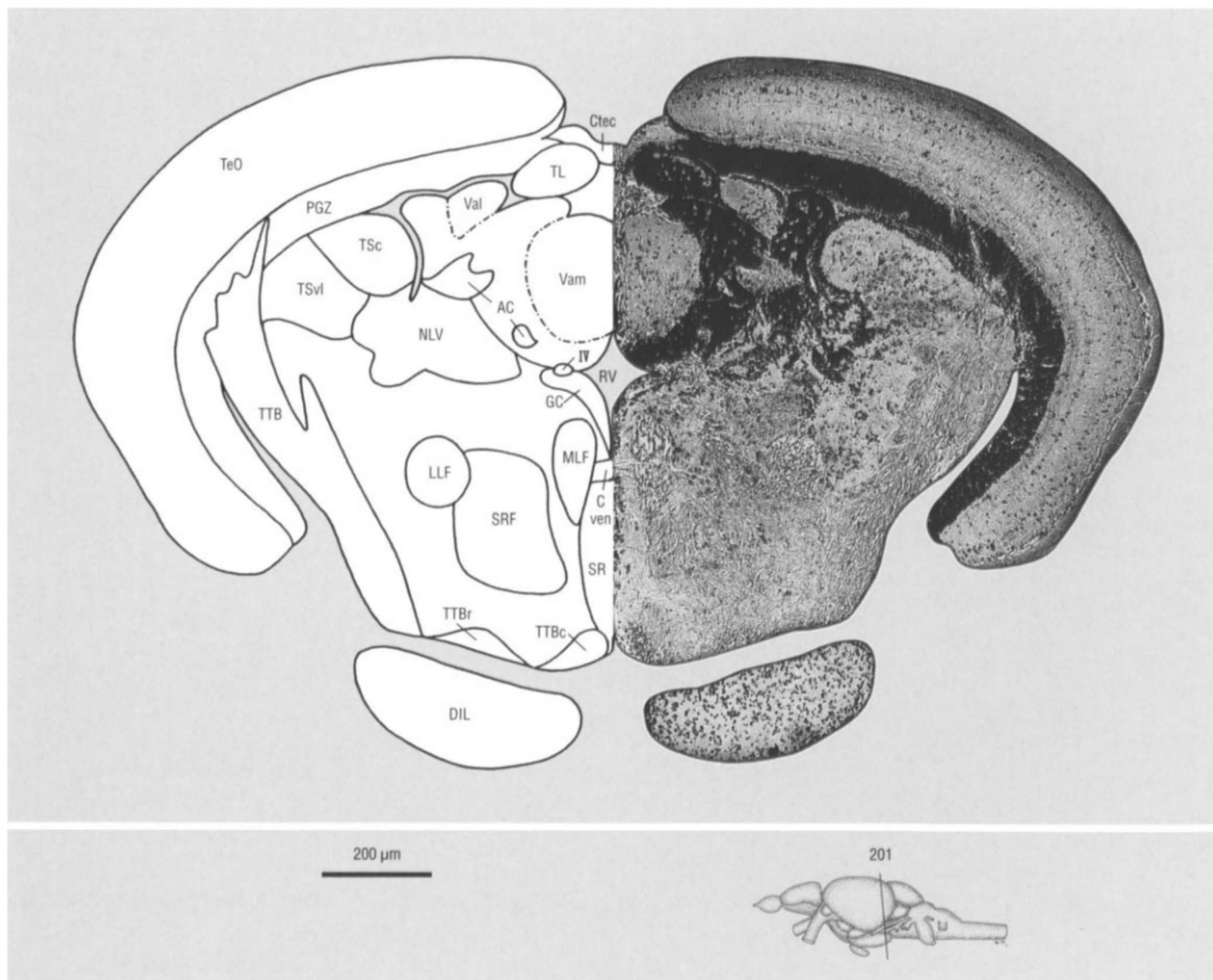
CIL	central nucleus of the inferior lobe	PGZ	periventricular gray zone of optic tectum
CM	corpus mamillare	PL	perilemniscal nucleus
Ctec	commissura tecti	TeO	tectum opticum
DIL	diffuse nucleus of the inferior lobe	TeV	tectal ventricle
DTN	dorsal tegmental nucleus	TL	torus longitudinalis
Hd	dorsal zone of periventricular hypothalamus	TLa	torus lateralis
LLF	lateral longitudinal fascicle	TMCa	tractus mesencephalocerebellaris anterior
LR	lateral recess of diencephalic ventricle	TSc	central nucleus of torus semicircularis
MLF	medial longitudinal fascicle	TSvl	ventrolateral nucleus of torus semicircularis
NIn	nucleus interpeduncularis	TTB	tractus tectobulbaris
NLL	nucleus of the lateral lemniscus (of Prasada Rao et al. 87)	TTbC	tractus tectobulbaris cruciatus
NLV	nucleus lateralis valvulae	Val	lateral division of valvula cerebelli
NIII	oculomotor nucleus	Vam	medial division of valvula cerebelli



Ctec commissura tecti
 DIL diffuse nucleus of the inferior lobe
 DTN dorsal tegmental nucleus
 GC griseum centrale
 LLF lateral longitudinal fascicle
 MLF medial longitudinal fascicle
 NIn nucleus interpeduncularis
 NLV nucleus lateralis valvulae
 NIV trochlear nucleus
 PGZ periventricular gray zone of optic tectum
 PL perilemniscal nucleus
 RV rhombencephalic ventricle
 SRF superior reticular formation

TeO tectum opticum
 TeV tectal ventricle
 TL torus longitudinalis
 TMCa tractus mesencephalocerebellaris anterior
 TMCp tractus mesencephalocerebellaris posterior
 TSc central nucleus of torus semicircularis
 TSVI ventrolateral nucleus of torus semicircularis
 TTB tractus tectobulbaris
 TTBC tractus tectobulbaris cruciatus
 TTBr tractus tectobulbaris rectus
 Val lateral division of valvula cerebelli
 Vam medial division of valvula cerebelli

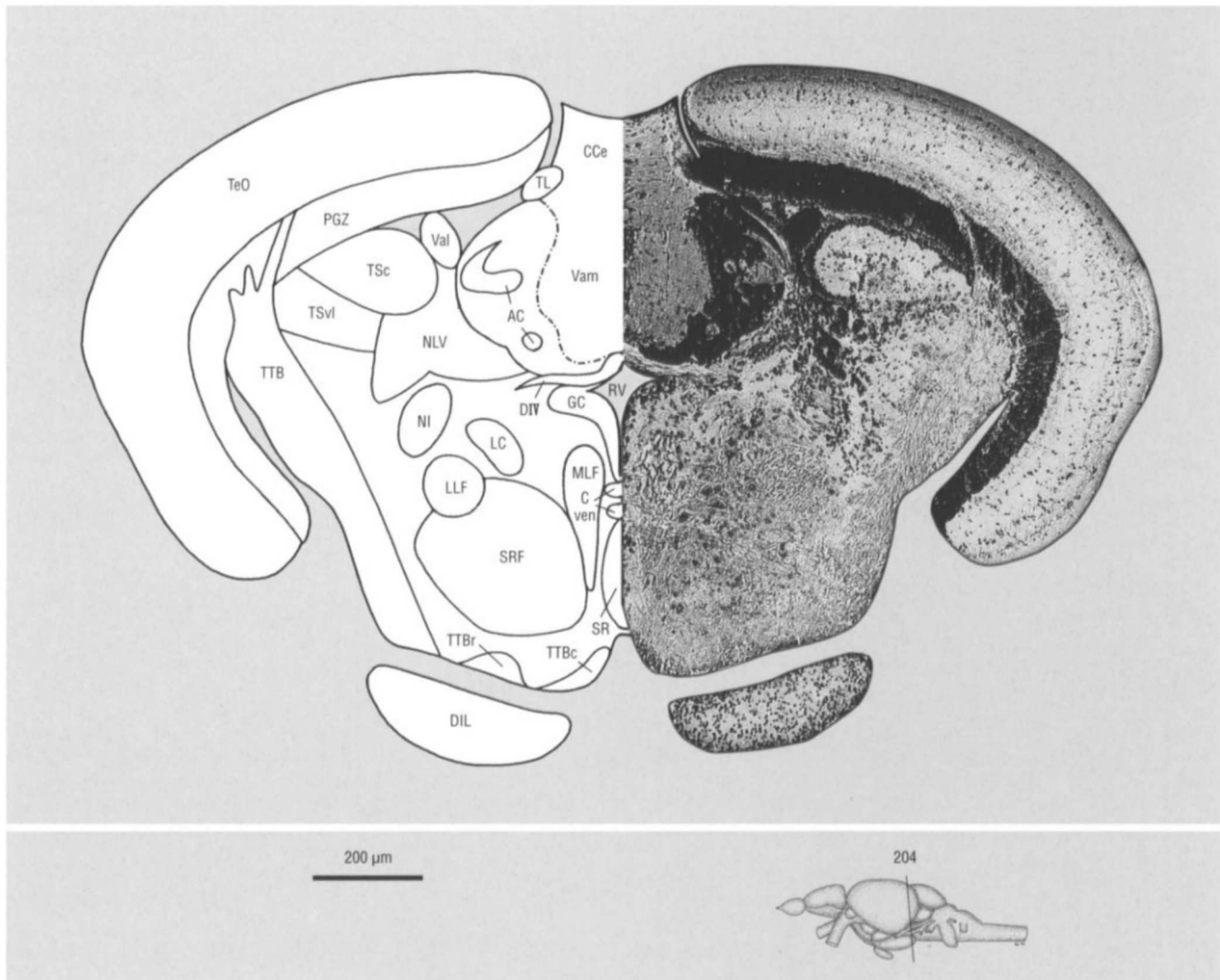
Cross Section 201



AC	anterior cerebellar tract
Ctec	commissura tecti
Cven	commissura ventralis rhombencephali
DIL	diffuse nucleus of the inferior lobe
GC	griseum centrale
LLF	lateral longitudinal fascicle
MLF	medial longitudinal fascicle
NLV	nucleus lateralis valvulae
PGZ	periventricular gray zone of optic tectum
RV	rhombencephalic ventricle
SR	superior raphe

SRF	superior reticular formation
TeO	tectum opticum
TL	torus longitudinalis
TSc	central nucleus of torus semicircularis
TSvl	ventrolateral nucleus of torus semicircularis
TTB	tractus tectobulbaris
TTBc	tractus tectobulbaris cruciatus
TTBr	tractus tectobulbaris rectus
Val	lateral division of valvula cerebelli
Vam	medial division of valvula cerebelli
IV	trochlear nerve

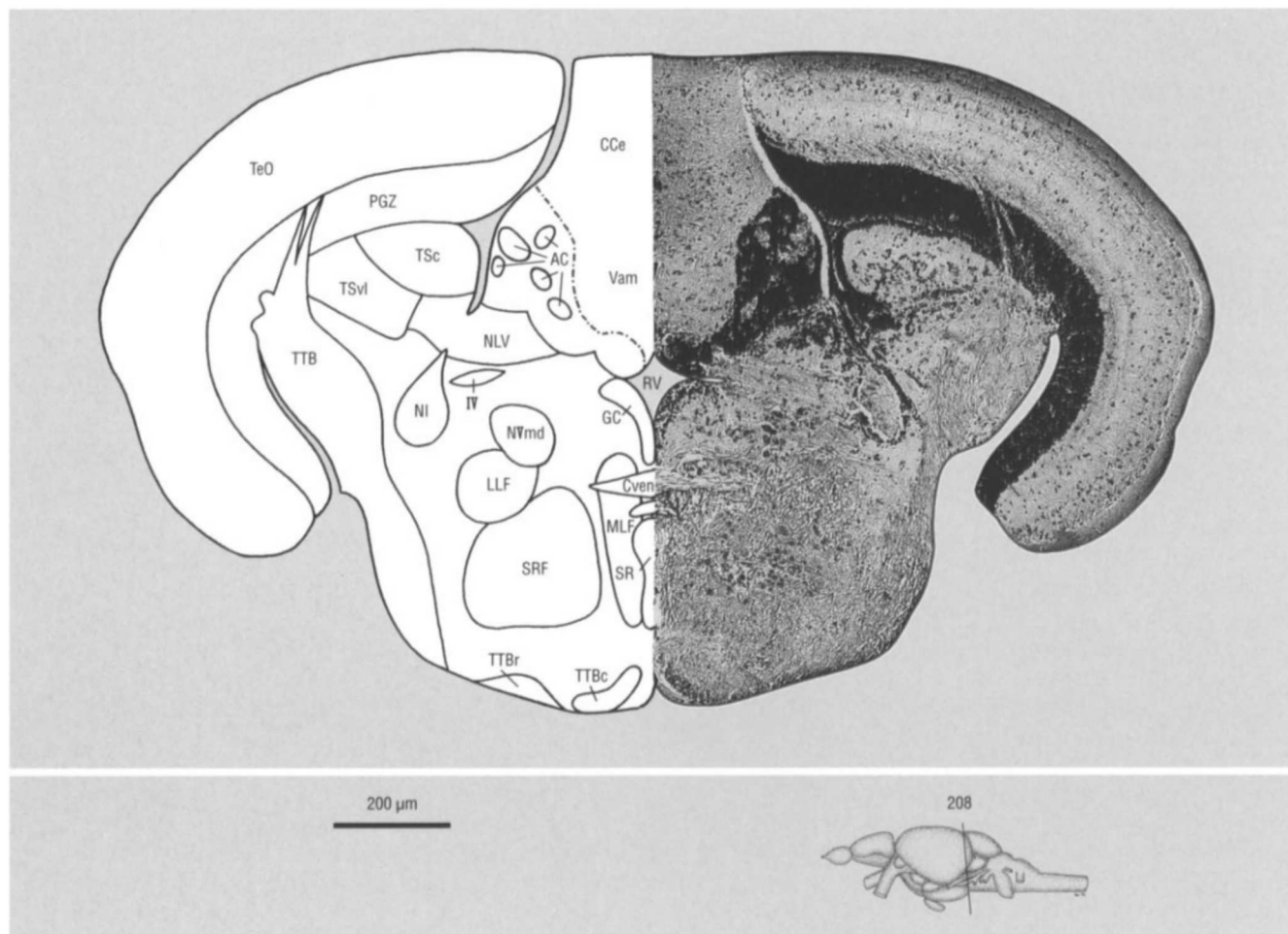
Cross Section 204



AC anterior cerebellar tract
 CCe corpus cerebelli
 Cven commissura ventralis rhombencephali
 DIL diffuse nucleus of the inferior lobe
 DIV trochlear decussation
 GC griseum centrale
 LC locus coeruleus
 LLF lateral longitudinal fascicle
 MLF medial longitudinal fascicle
 NI nucleus isthmi
 NLV nucleus lateralis valvulae
 PGZ periventricular gray zone of optic tectum

RV rhombencephalic ventricle
 SR superior raphe
 SRF superior reticular formation
 TeO tectum opticum
 TL torus longitudinalis
 TSc central nucleus of torus semicircularis
 TSvl ventrolateral nucleus of torus semicircularis
 TTb tractus tectobulbaris
 TTbC tractus tectobulbaris cruciatus
 TTBr tractus tectobulbaris rectus
 Val lateral division of valvula cerebelli
 Vam medial division of valvula cerebelli

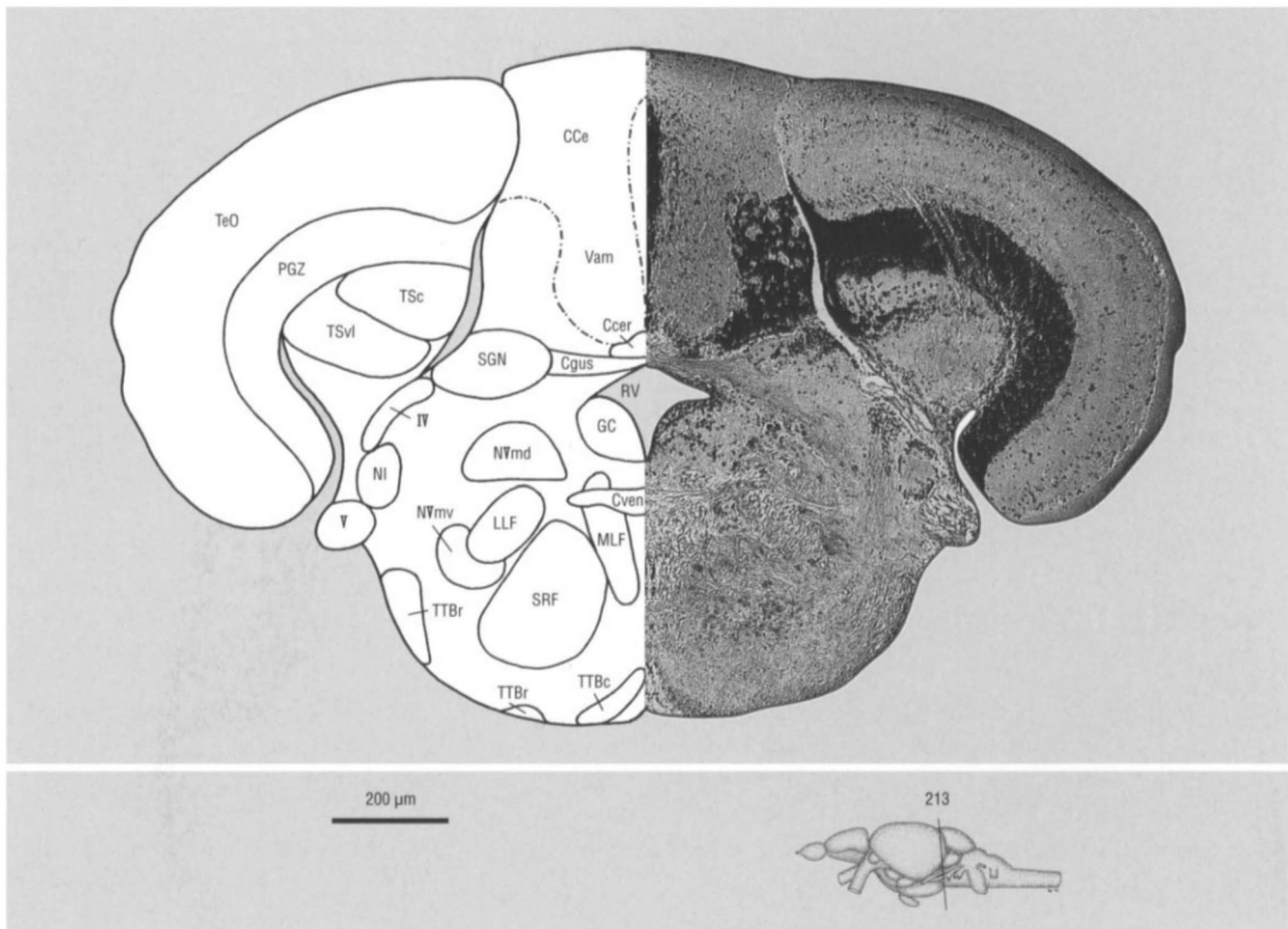
Cross Section 208



AC	anterior cerebellar tract
CCe	corpus cerebelli
Cven	commissura ventralis rhombencephali
GC	griseum centrale
LLF	lateral longitudinal fascicle
MLF	medial longitudinal fascicle
NI	nucleus isthmi
NLV	nucleus lateralis valvulae
NVmd	trigeminal motor nucleus, dorsal part
PGZ	periventricular gray zone of optic tectum
RV	rhombencephalic ventricle

SR	superior raphe
SRF	superior reticular formation
TeO	tectum opticum
TSc	central nucleus of torus semicircularis
TSvl	ventrolateral nucleus of torus semicircularis
TTB	tractus tectobulbaris
TTBc	tractus tectobulbaris cruciatus
TTBr	tractus tectobulbaris rectus
Vam	medial division of valvula cerebelli
IV	trochlear nerve

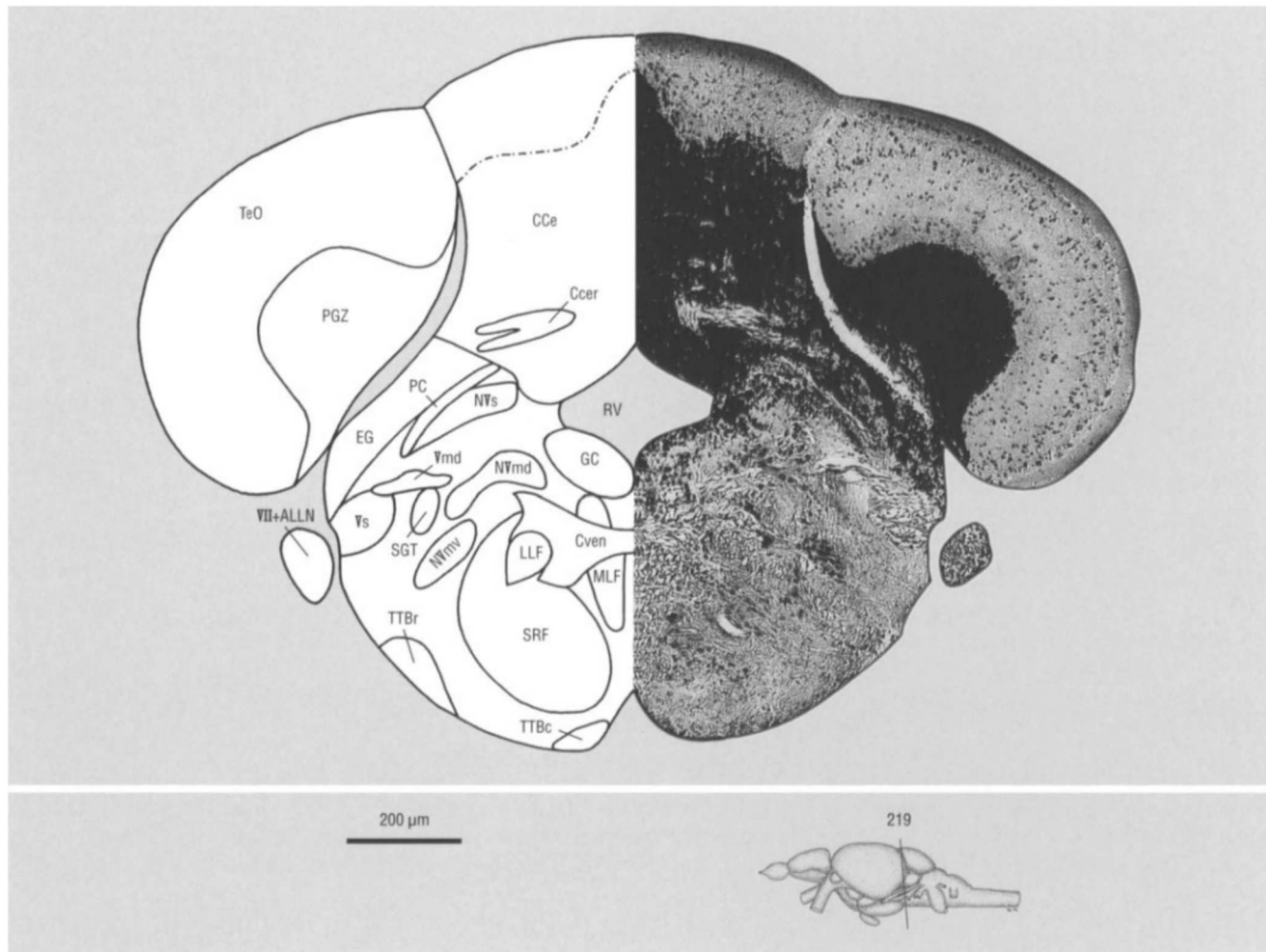
Cross Section 213



CCe	corpus cerebelli
Ccer	commissura cerebelli
Cgus	commissure of the secondary gustatory nuclei
Cven	commissura ventralis rhombencephali
GC	griseum centrale
LLF	lateral longitudinal fascicle
MLF	medial longitudinal fascicle
NI	nucleus isthmi
NVmd	trigeminal motor nucleus, dorsal part
NVmv	trigeminal motor nucleus, ventral part
PGZ	periventricular gray zone of optic tectum
RV	rhombencephalic ventricle

SGN	secondary gustatory nucleus
SRF	superior reticular formation
TeO	tectum opticum
TSc	central nucleus of torus semicircularis
TSvl	ventrolateral nucleus of torus semicircularis
TTBc	tractus tectobulbaris cruciatus
TTBr	tractus tectobulbaris rectus
Vam	medial division of valvula cerebelli
IV	trochlear nerve
V	trigeminal nerve

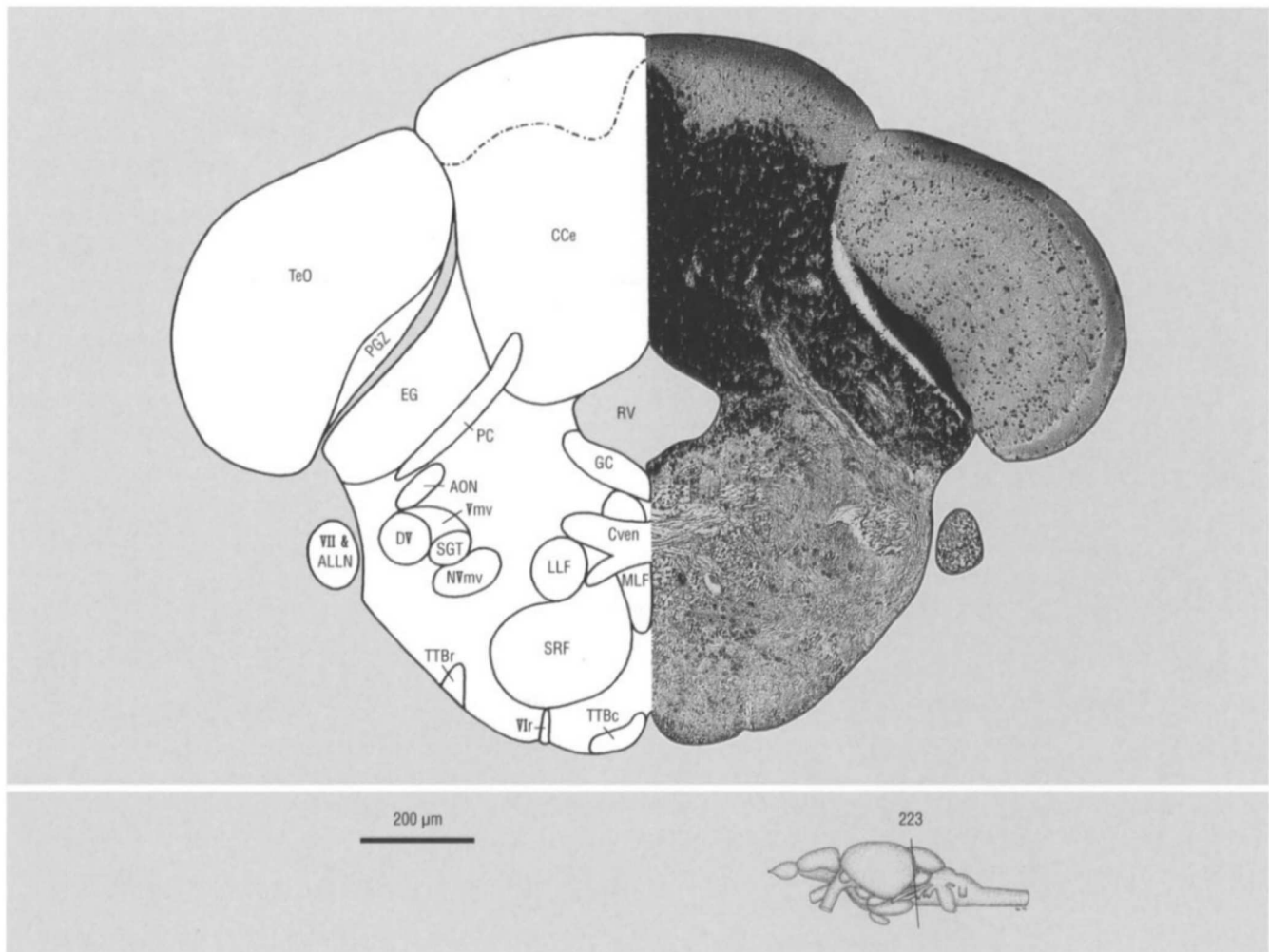
Cross Section 219



ALLN anterior lateral line nerves
 CCe corpus cerebelli
 Ccer commissura cerebelli
 Cven commissura ventralis rhombencephali
 EG eminentia granularis
 GC griseum centrale
 LLF lateral longitudinal fascicle
 MLF medial longitudinal fascicle
 NVmd trigeminal motor nucleus, dorsal part
 NVmv trigeminal motor nucleus, ventral part
 NVs primary sensory trigeminal nucleus

PC posterior cerebellar tract
 PGZ periventricular gray zone of optic tectum
 RV rhombencephalic ventricle
 SGT secondary gustatory tract
 SRF superior reticular formation
 TeO tectum opticum
 TTbc tractus tectobulbaris cruciatus
 TTBr tractus tectobulbaris rectus
 Vmd dorsal motor root of the trigeminal nerve
 Vs sensory root of the trigeminal nerve
 VII facial nerve

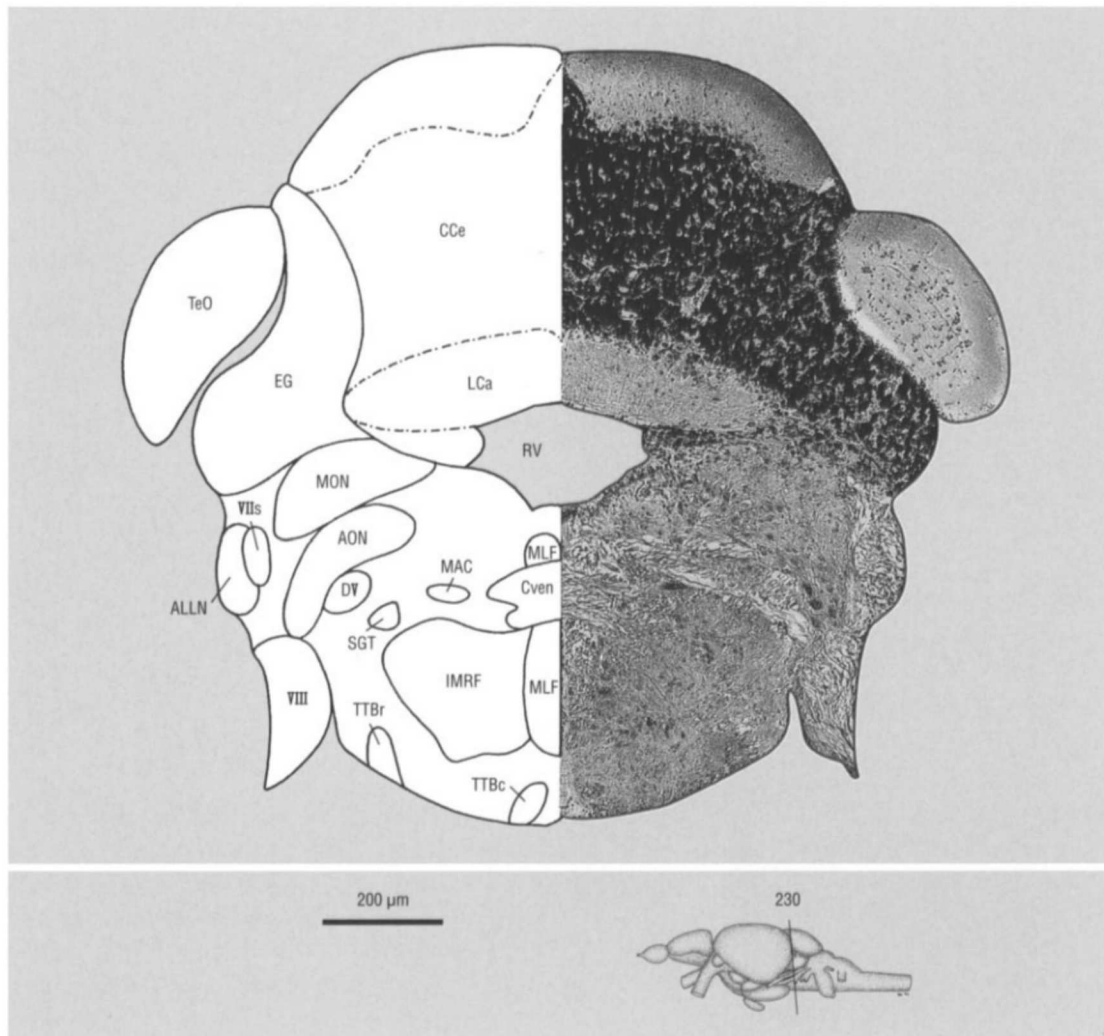
Cross Section 223



ALLN anterior lateral line nerves
 AON anterior octaval nucleus
 CCe corpus cerebelli
 Cven commissura ventralis rhombencephali
 DV descending trigeminal root
 EG eminentia granularis
 GC griseum centrale
 LLF lateral longitudinal fascicle
 MLF medial longitudinal fascicle
 NVmv trigeminal motor nucleus, ventral part
 PC posterior cerebellar tract

PGZ periventricular gray zone of optic tectum
 RV rhombencephalic ventricle
 SGT secondary gustatory tract
 SRF superior reticular formation
 TeO tectum opticum
 TTBr tractus tectobulbaris cruciatus
 TTBr tractus tectobulbaris rectus
 Vmv ventral motor root of the trigeminal nerve
 Vlr rostral root of the abducens nerve
 VII facial nerve

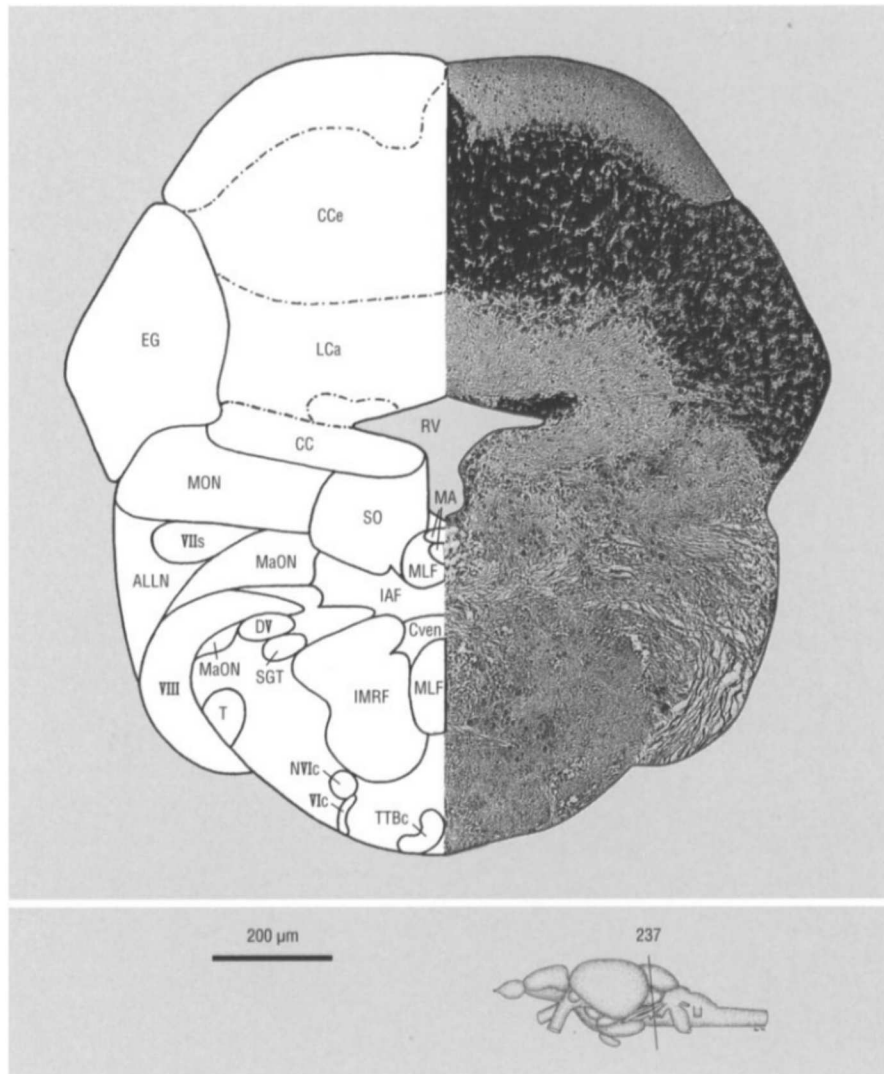
Cross Section 230



ALLN anterior lateral line nerves
 AON anterior octaval nucleus
 CCe corpus cerebelli
 Cven commissura ventralis rhombencephali
 DV descending trigeminal root
 EG eminentia granularis
 IMRF intermediate reticular formation
 LCa lobus caudalis cerebelli
 MAC Mauthner cell
 MLF medial longitudinal fascicle

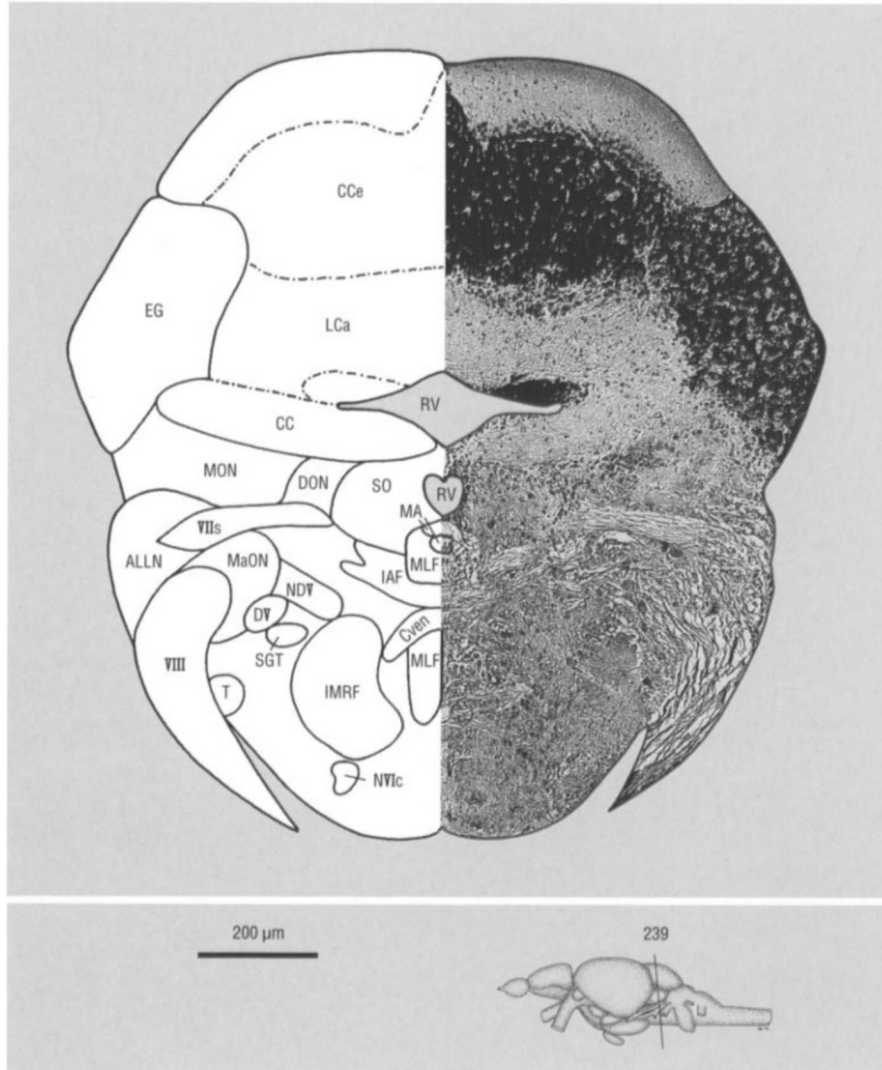
MON medial octavolateralis nucleus
 RV rhombencephalic ventricle
 SGT secondary gustatory tract
 TeO tectum opticum
 TTbC tractus tectobulbaris cruciatus
 TTBr tractus tectobulbaris rectus
 VIIs sensory root of the facial nerve
 VIII octaval nerve

Cross Section 237



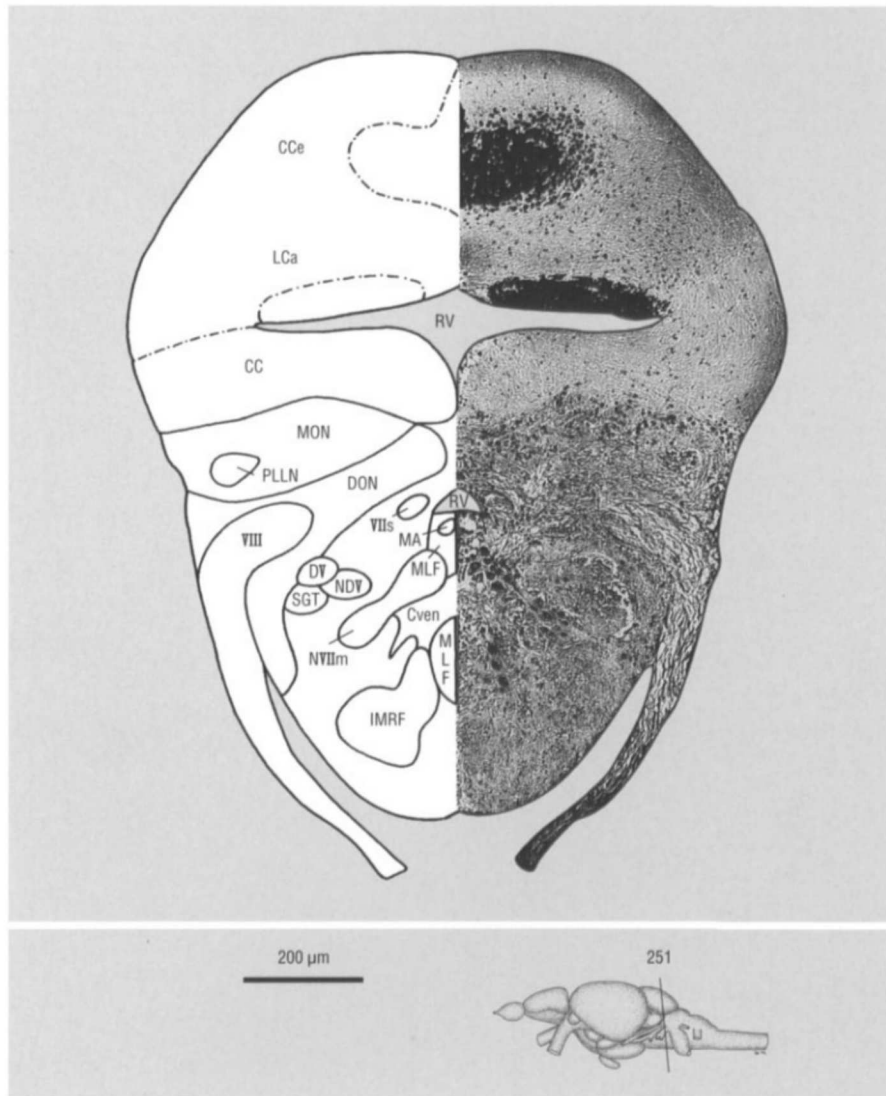
ALLN	anterior lateral line nerves	MON	medial octavolateralis nucleus
CC	crista cerebellaris	NVIc	abducens nucleus, caudal part
CCe	corpus cerebelli	RV	rhombencephalic ventricle
Cven	commissura ventralis rhombencephali	SGT	secondary gustatory tract
DV	descending trigeminal root	SO	secondary octaval population (of McCormick & Hernandez 95)
EG	eminencia granularis	T	tangential nucleus
IAF	inner arcuate fibers	TTBc	tractus tectobulbaris cruciatus
IMRF	intermediate reticular formation		
LCa	lobus caudalis cerebelli		
MA	Mauthner axon	VIIc	caudal root of the abducens nerve
MaON	magnocellular octaval nucleus	VIIIs	sensory root of the facial nerve
MLF	medial longitudinal fascicle	VIII	octaval nerve

Cross Section 239



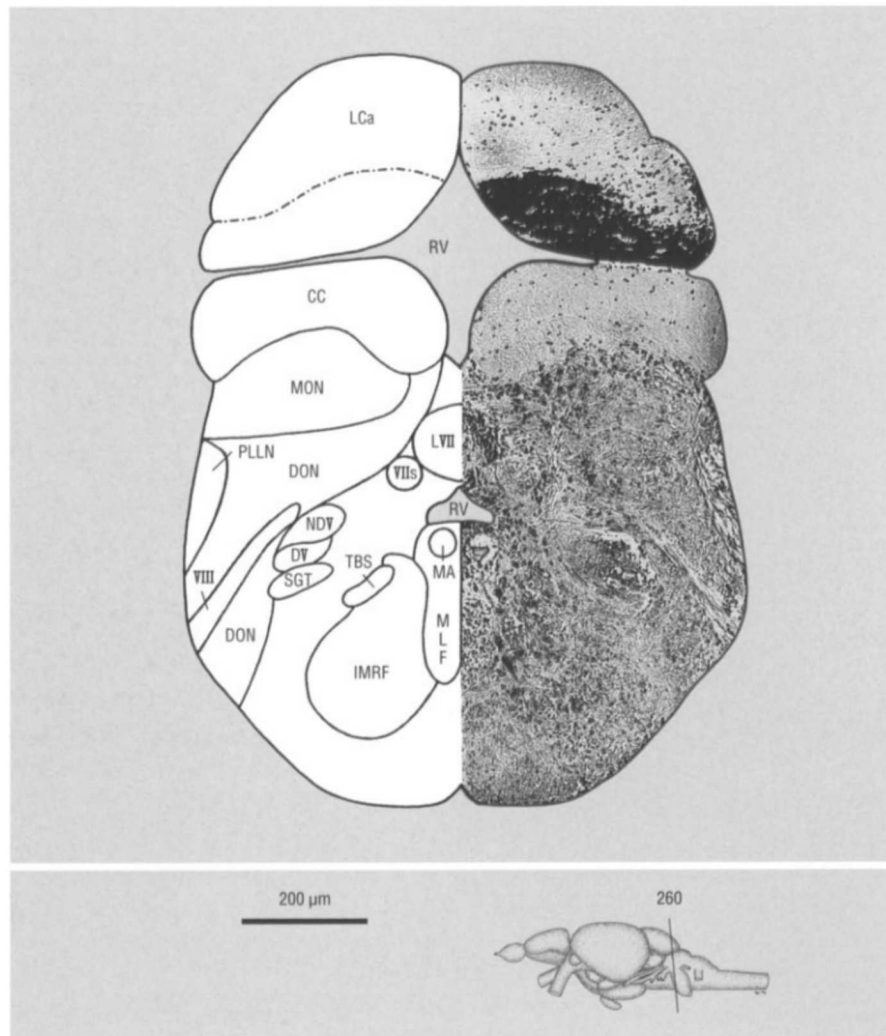
ALLN	anterior lateral line nerves	MLF	medial longitudinal fascicle
CC	crista cerebellaris	MON	medial octavolateralis nucleus
CCe	corpus cerebelli	NDV	nucleus of the descending trigeminal root
Cven	commissura ventralis rhombencephali	NVlc	abducens nucleus, caudal part
DON	descending octaval nucleus	RV	rhombencephalic ventricle
DV	descending trigeminal root	SGT	secondary gustatory tract
EG	eminencia granularis	SO	secondary octaval population (of McCormick & Hernandez 95)
IAF	inner arcuate fibers	T	tangential nucleus
IMRF	intermediate reticular formation	VII _s	sensory root of the facial nerve
LCa	lobus caudalis cerebelli	VIII	octaval nerve
MA	Mauthner axon		
MaON	magnocellular octaval nucleus		

Cross Section 251



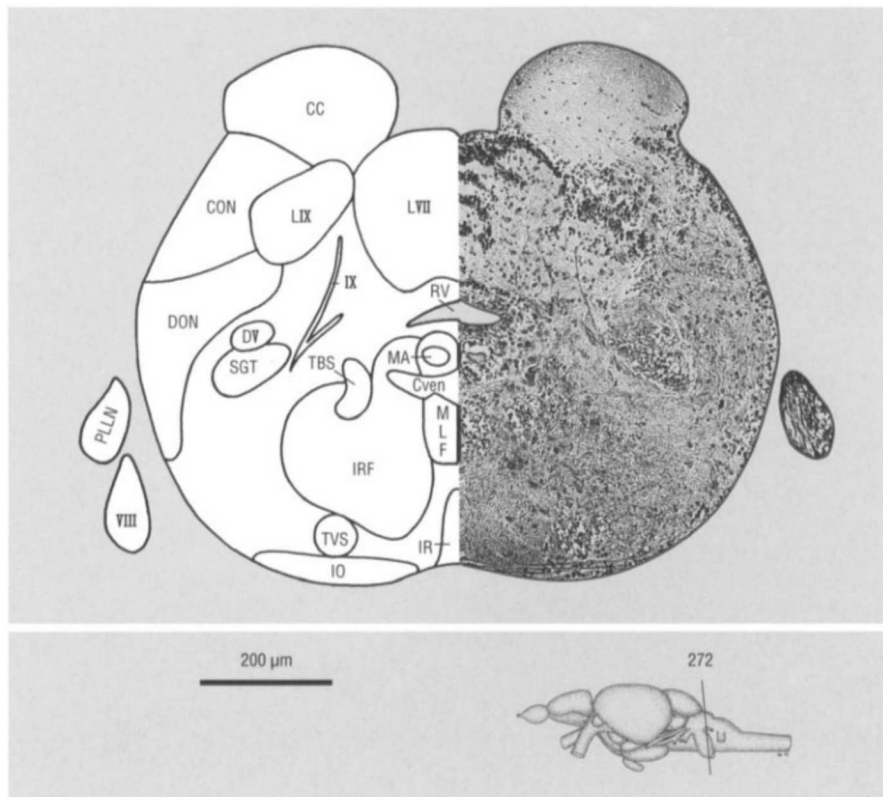
CC	crista cerebellaris	NDV	nucleus of the descending trigeminal root
CCe	corpus cerebelli	NVIIIm	facial motor nucleus
Cven	commissura ventralis rhombencephali	PLLN	posterior lateral line nerve
DON	descending octaval nucleus	RV	rhombencephalic ventricle
DV	descending trigeminal root	SGT	secondary gustatory tract
IMRF	intermediate reticular formation		
LCa	lobus caudalis cerebelli		
MA	Mauthner axon	VIIIs	sensory root of the facial nerve
MLF	medial longitudinal fascicle	VIII	octaval nerve
MON	medial octavolateralis nucleus		

Cross Section 260



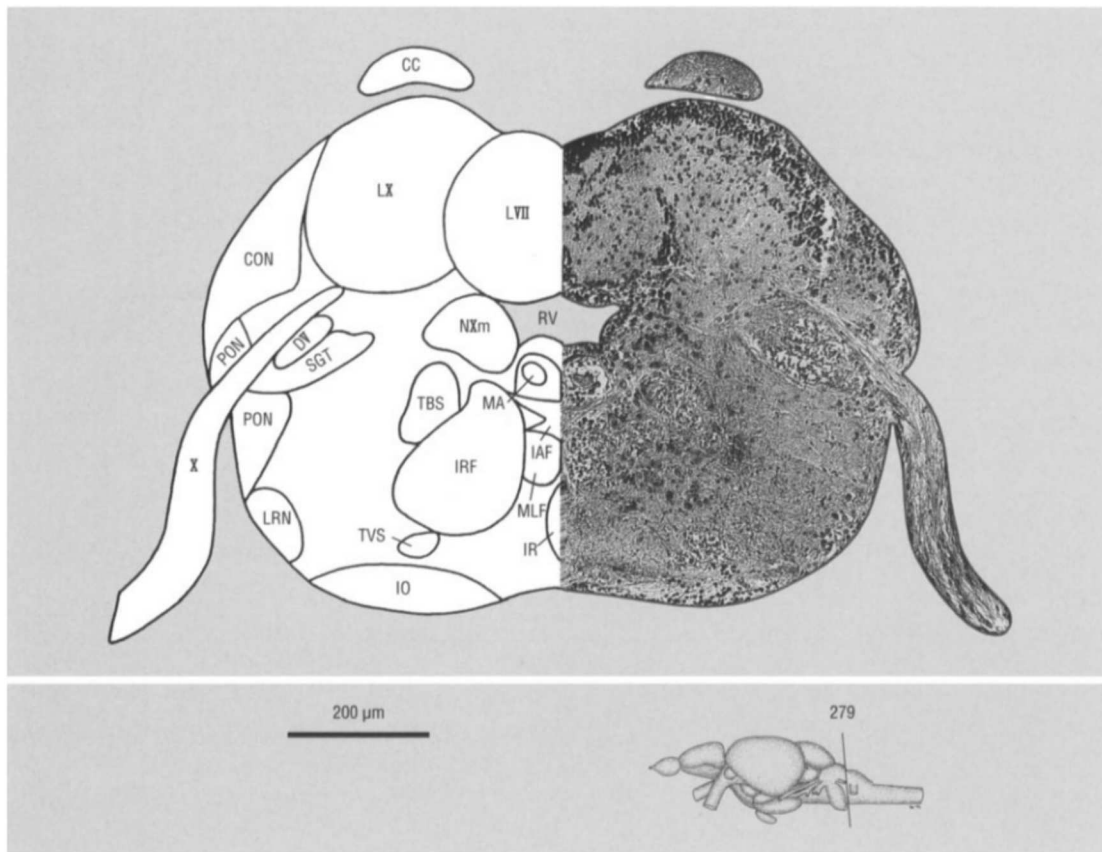
CC	crista cerebellaris
DON	descending octaval nucleus
DV	descending trigeminal root
IMRF	intermediate reticular formation
LCa	lobus caudalis cerebelli
LVII	lobus facialis
MA	Mauthner axon
MLF	medial longitudinal fascicle
MON	medial octavolateralis nucleus
NDV	nucleus of the descending trigeminal root
PLLN	posterior lateral line nerve
RV	rhombencephalic ventricle
SGT	secondary gustatory tract
TBS	tractus bulbospinalis
VII _s	sensory root of the facial nerve
VIII	octaval nerve

Cross Section 272



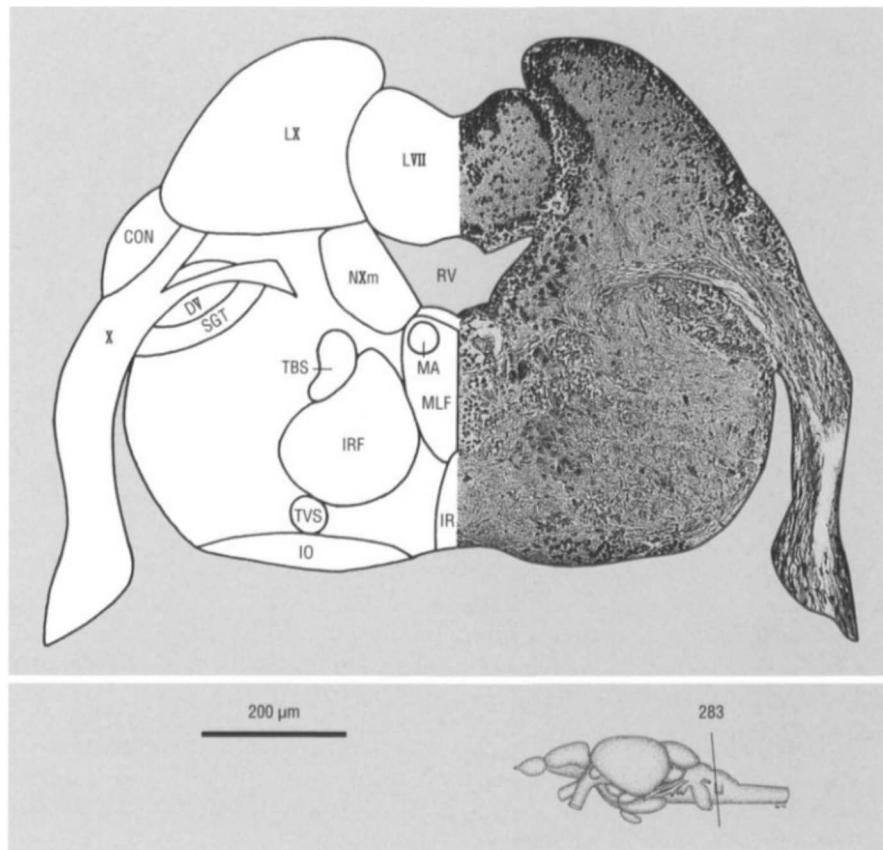
CC	crista cerebellaris
CON	caudal octavolateralis nucleus
Cven	commissura ventralis rhombencephali
DON	descending octaval nucleus
DV	descending trigeminal root
IO	oliva inferior
IR	interior raphe
IRF	inferior reticular formation
LVII	lobus facialis
LIX	lobus glossopharyngeus
MA	Mauthner axon
MLF	medial longitudinal fascicle
PLLN	posterior lateral line nerve
RV	rhombencephalic ventricle
SGT	secondary gustatory tract
TBS	tractus bulbospinalis
TVS	tractus vestibulospinalis
VIII	octaval nerve
IX	glossopharyngeal nerve

Cross Section 279



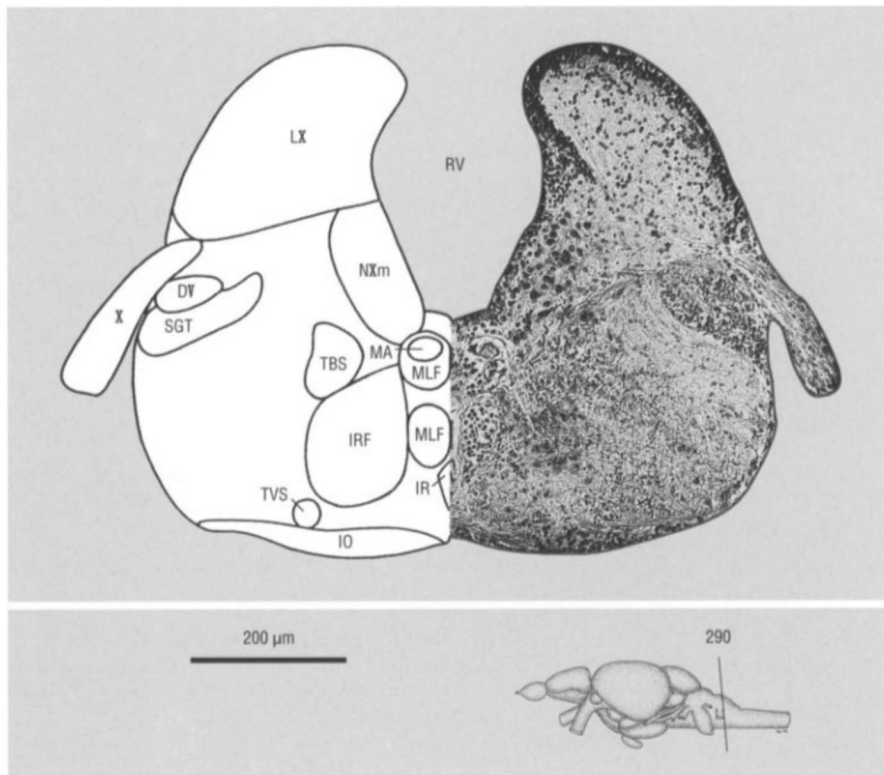
CC	crista cerebellaris
CON	caudal octavolateralis nucleus
DV	descending trigeminal root
IAF	inner arcuate fibers
IO	oliva inferior
IR	inferior raphe
IRF	inferior reticular formation
LRN	lateral reticular nucleus
LVII	lobus facialis
LX	lobus vagus
MA	Mauthner axon
MLF	medial longitudinal fascicle
NXm	vagal motor nucleus
PON	posterior octaval nucleus
RV	rhombencephalic ventricle
SGT	secondary gustatory tract
TBS	tractus bulbospinalis
TVS	tractus vestibulospinalis
X	vagal nerve

Cross Section 283



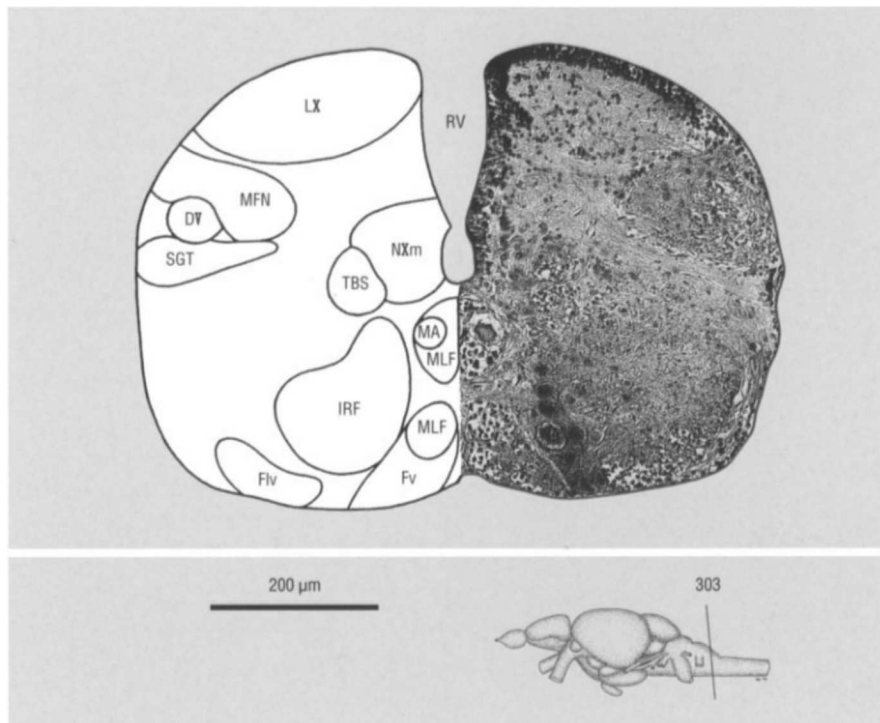
CON	caudal octavolateralis nucleus
DV	descending trigeminal root
IO	inferior olive
IR	inferior raphe
IRF	inferior reticular formation
LVII	lobus facialis
LX	lobus vagus
MA	Mauthner axon
MLF	medial longitudinal fascicle
NXm	vagal motor nucleus
RV	rhombencephalic ventricle
SGT	secondary gustatory tract
TBS	tractus bulbospinalis
TVS	tractus vestibulospinalis
X	vagal nerve

Cross Section 290



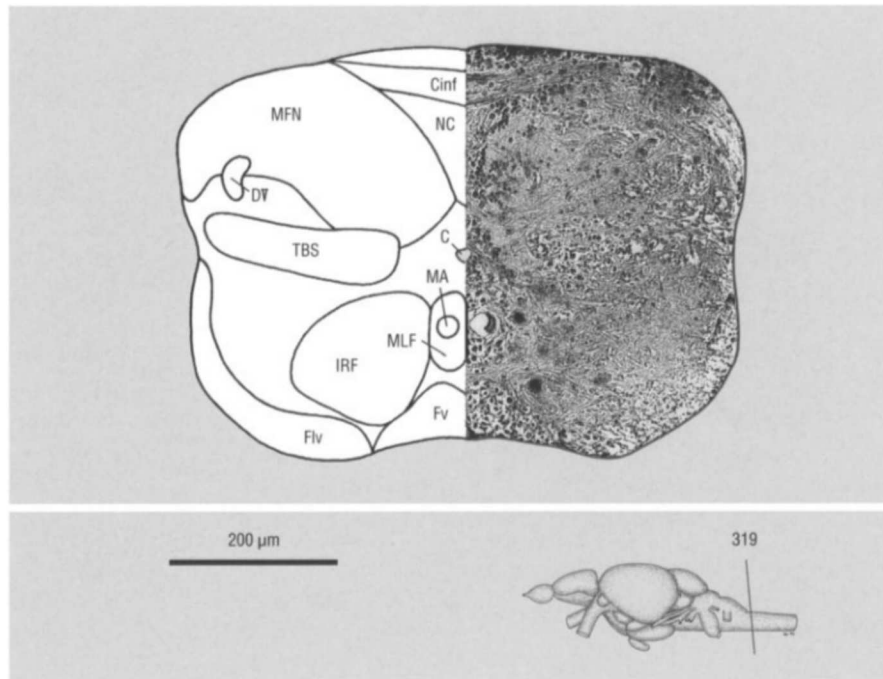
DV	descending trigeminal root
IO	inferior olive
IR	inferior raphe
IRF	inferior reticular formation
LX	lobus vagus
MA	Mauthner axon
MLF	medial longitudinal fascicle
NXm	vagal motor nucleus
RV	rhombencephalic ventricle
SGT	secondary gustatory tract
TBS	tractus bulbospinalis
TVS	tractus vestibulospinalis
X	vagal nerve

Cross Section 303



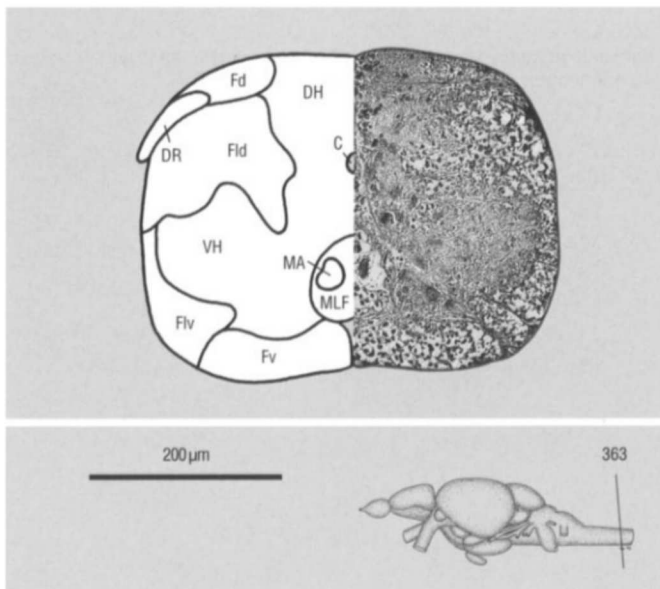
DV	descending trigeminal root
Flv	funiculus lateralis pars ventralis
Fv	funiculus ventralis
IRF	inferior reticular formation
LX	lobus vagus
MA	Mauthner axon
MFN	medial funicular nucleus
MLF	medial longitudinal fascicle
NXm	vagal motor nucleus
RV	rhombencephalic ventricle
SGT	secondary gustatory tract
TBS	tractus bulbospinalis

Cross Section 319



C	central canal
Cinf	commissura infima of Haller
DV	descending trigeminal root
Flv	funiculus lateralis pars ventralis
Fv	funiculus ventralis
IRF	inferior reticular formation
MA	Mauthner axon
MFN	medial funicular nucleus
MLF	medial longitudinal fascicle
NC	commissural nucleus of Cajal
TBS	tractus bulbospinalis

Cross Section 363



C	central canal
DH	dorsal horn
DR	dorsal root
Fd	funiculus dorsalis
Fld	funiculus lateralis pars dorsalis (including TBS)
Flv	funiculus lateralis pars ventralis
Fv	funiculus ventralis (including part of MLF)
MA	Mauthner axon
MLF	medial longitudinal fascicle
VH	ventral horn

Sagittal sections

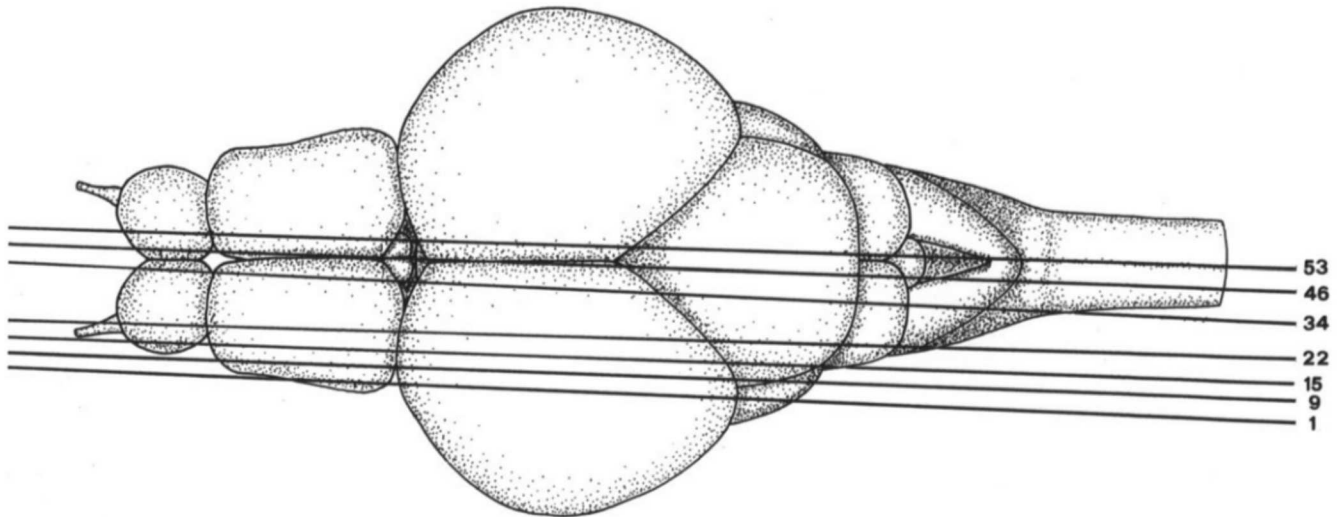
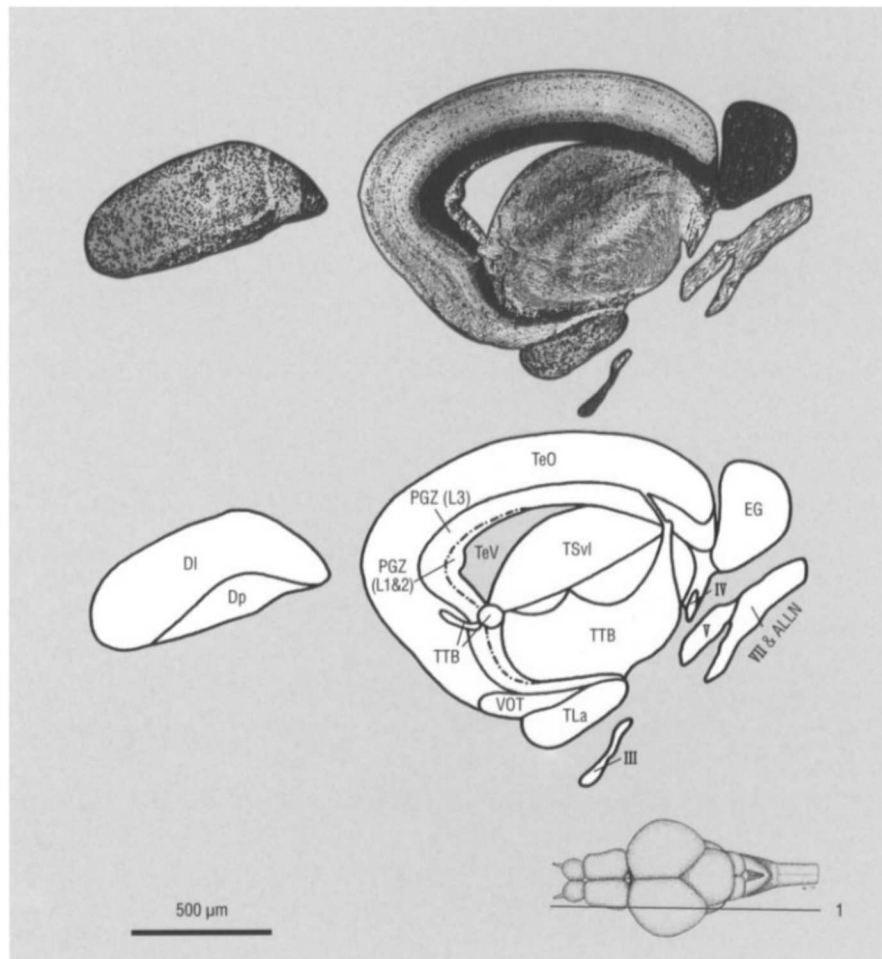


Figure 6.

Dorsal view of the adult zebrafish brain illustrating the position of levels shown in the series of sagittal sections. The series of sagittal sections shown on the following pages proceeds at irregular intervals from lateral to medial, giving an overview of the topological organization of the

left half of the adult zebrafish brain. However, as the section plane does not correspond to the ideal longitudinal axis but deviates to the right side at rostral levels and to the left at caudal levels, neither section 46 nor section 53 represents a perfect midsagittal section.

Sagittal Section 1

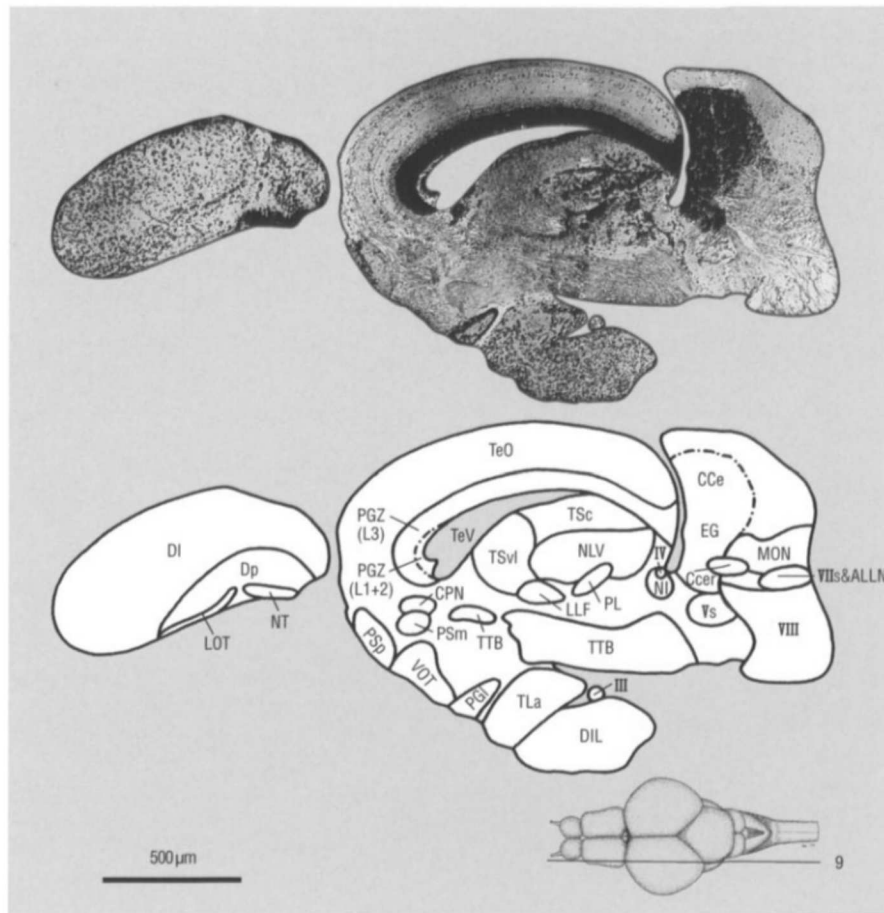


ALLN	anterior lateral line nerves
D	dorsal telencephalic area
DI	lateral zone of D
Dp	posterior zone of D
EG	eminencia granularis
PGZ	periventricular gray zone of optic tectum
TeO	tectum opticum
TeV	tectal ventricle
TLa	torus lateralis
TSvl	ventrolateral nucleus of torus semicircularis
TTB	tractus tectobulbaris
VOT	ventrolateral optic tract
III	oculomotor nerve
IV	trochlear nerve
V	trigeminal nerve
VII	facial nerve

Sagittal Section 9

ALLN	anterior lateral line nerves	PSm	magnocellular superficial pretectal nucleus
CCe	corpus cerebelli	PSp	parvocellular superficial pretectal nucleus
Ccer	commissura cerebelli	TeO	tectum opticum
CPN	central pretectal nucleus	TeV	tectal ventricle
D	dorsal telencephalic area	TLa	torus lateralis
DIL	diffuse nucleus of the inferior lobe	TSc	central nucleus of torus semicircularis
DI	lateral zone of D	TSvl	ventrolateral nucleus of torus semicircularis
Dp	posterior zone of D		
EG	eminencia granularis	TTB	tractus tectobulbaris
LLF	lateral longitudinal fascicle	VOT	ventrolateral optic tract
LOT	lateral olfactory tract		
MON	medial octavolateralis nucleus		
NI	nucleus isthmi	III	oculomotor nerve
NLV	nucleus lateralis valvulae	IV	trochlear nerve
NT	nucleus taeniae	Vs	sensory root of the trigeminal nerve
PGI	lateral preglomerular nucleus	VIIIs	sensory root of the facial nerve
PGZ	periventricular gray zone of optic tectum	VIII	octaval nerve
PL	perilemniscal nucleus		

Sagittal Section 9



Sagittal Section 15

ALLN anterior lateral line nerves
 AON anterior octaval nucleus
 CC crista cerebellaris
 CCE corpus cerebelli
 Ccer commissura cerebelli
 Chor commissura horizontalis
 CIL central nucleus of the inferior lobe
 CPN central pretectal nucleus
 D dorsal telencephalic area
 DAO dorsal accessory optic nucleus
 Dc central zone of D
 DIL diffuse nucleus of the inferior lobe
 DI lateral zone of D
 Dp posterior zone of D
 DTN dorsal tegmental nucleus
 EG eminentia granularis
 GL glomerular layer of olfactory bulb

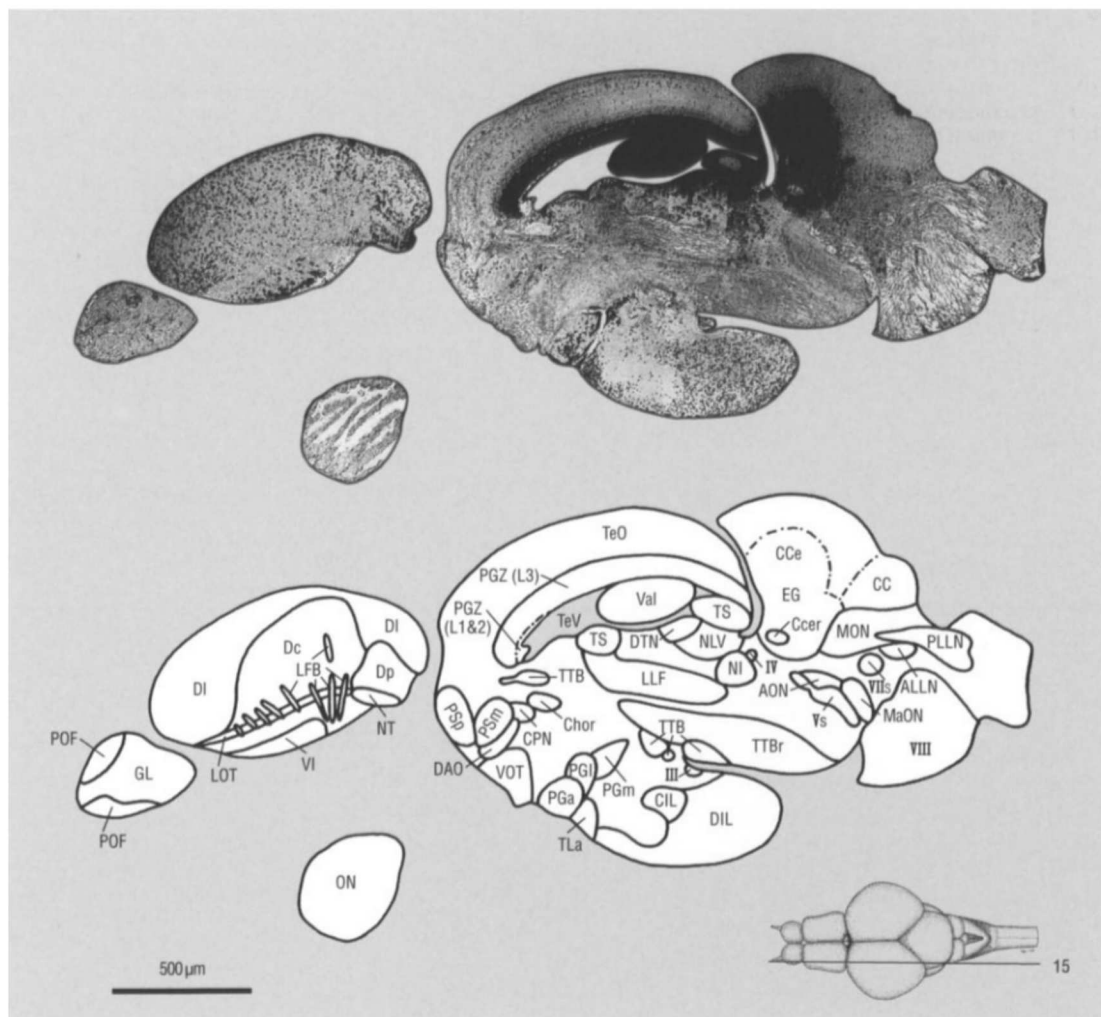
LFB lateral forebrain bundle
 LLF lateral longitudinal fascicle
 LOT lateral olfactory tract
 MaON magnocellular octaval nucleus
 MON medial octavolateralis nucleus
 NI nucleus isthmi
 NLV nucleus lateralis valvulae
 NT nucleus taeniae

ON optic nerve
 PGa anterior pregglomerular nucleus
 PGI lateral pregglomerular nucleus
 PGm medial pregglomerular nucleus
 PGZ periventricular gray zone of optic tectum
 PLLN posterior lateral line nerve
 POF primary olfactory fiber layer
 PSm magnocellular superficial pretectal nucleus

PSp parvocellular superficial pretectal nucleus
 TeO tectum opticum
 TeV tectal ventricle
 TLa torus lateralis
 TS torus semicircularis
 TTB tractus tectobulbaris
 TTBr tractus tectobulbaris rectus
 V ventral telencephalic area
 Val lateral division of valvula cerebelli
 VI lateral nucleus of V
 VOT ventrolateral optic tract

III oculomotor nerve
 IV trochlear nerve
 Vs sensory root of the trigeminal nerve
 VIIs sensory root of the facial nerve
 VIII octaval nerve

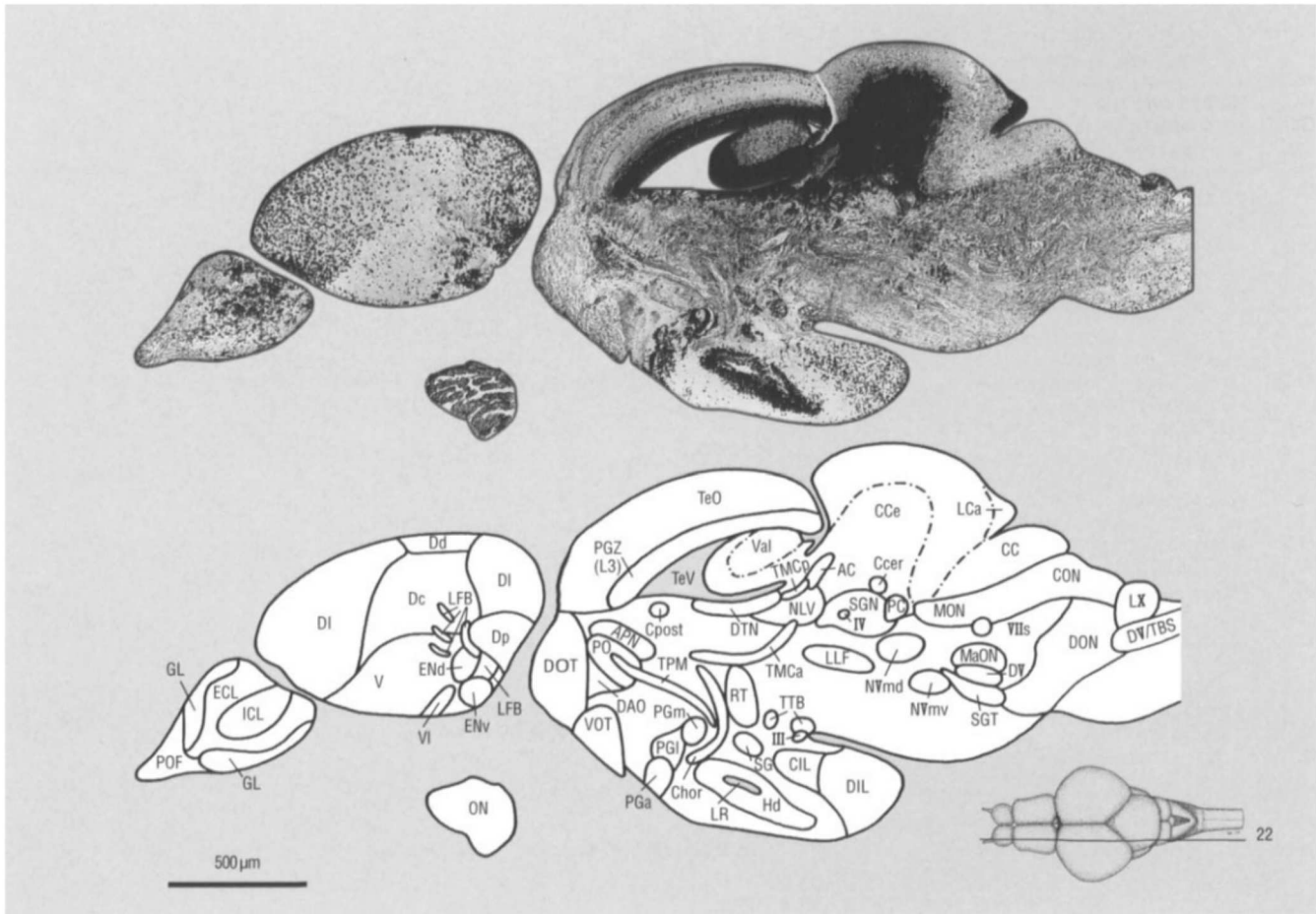
Sagittal Section 15



Sagittal Section 22

AC	anterior cerebellar tract	MaON	magnocellular octaval nucleus
APN	accessory pretectal nucleus (of Wullimann & Meyer 90)	MON	medial octavolateralis nucleus
CC	crista cerebellaris	NLV	nucleus lateralis valvulae
CCe	corpus cerebelli	NVmd	trigeminal motor nucleus, dorsal part
Ccer	commissura cerebelli	NVmv	trigeminal motor nucleus, ventral part
Chor	commissura horizontalis	ON	optic nerve
CIL	central nucleus of the inferior lobe	PC	posterior cerebellar tract
CON	caudal octavolateralis nucleus	PGa	anterior pregglomerular nucleus
Cpost	commissura posterior	PGL	lateral pregglomerular nucleus
D	dorsal telencephalic area	PGm	medial pregglomerular nucleus
DAO	dorsal accessory optic nucleus	PGZ	periventricular grey zone of optic tectum
Dc	central zone of D	PO	posterior pretectal nucleus (of Wullimann & Meyer 90)
Dd	dorsal zone of D	POF	primary olfactory fiber layer
DIL	diffuse nucleus of the inferior lobe	RT	rostral tegmental nucleus (of Grover & Sharma 81)
DI	lateral zone of D	SG	subglomerular nucleus
DON	descending octaval nucleus	SGN	secondary gustatory nucleus
DOT	dorsomedial optic tract	SGT	secondary gustatory tract
Dp	posterior zone of D	TBS	tractus bulbospinalis
DTN	dorsal tegmental nucleus	TeO	tectum opticum
DV	descending trigeminal root	TeV	tectal ventricle
ECL	external cellular layer of olfactory bulb including mitral cells	TMCa	tractus mesencephalocerebellaris anterior
END	entopeduncular nucleus, dorsal part	TMCp	tractus mesencephalocerebellaris posterior
ENV	entopeduncular nucleus, ventral part	TPM	tractus pretectomamillaris
GL	glomerular layer of olfactory bulb	TTB	tractus tectobulbaris
Hd	dorsal zone of periventricular hypothalamus	V	ventral telencephalic area
ICL	internal cellular layer of olfactory bulb	Val	lateral division of valvula cerebelli
LCa	lobus caudalis cerebelli	VI	lateral nucleus of V
LFB	lateral forebrain bundle	VOT	ventrolateral optic tract
LLF	lateral longitudinal fascicle		
LR	lateral recess of diencephalic ventricle	III	oculomotor nerve
LX	vagal lobe	IV	trochlear nerve
		VII	sensory root of the facial nerve

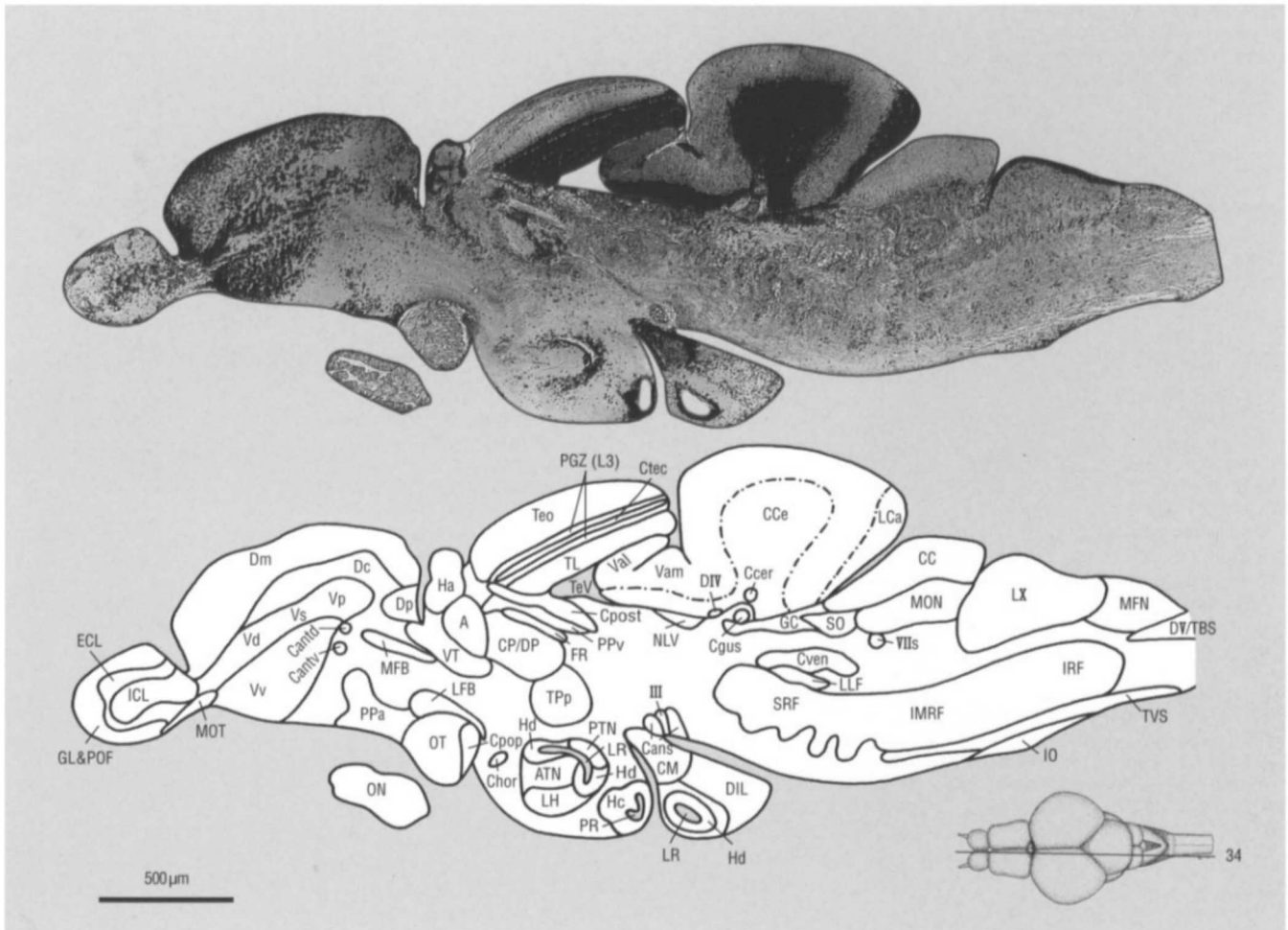
Sagittal Section 22



Sagittal Section 34

A	anterior thalamic nucleus	LH	lateral hypothalamic nucleus
ATN	anterior tuberal nucleus	LLF	lateral longitudinal fascicle
Cans	commissura ansulata	LR	lateral recess of diencephalic ventricle
Cantd	commissura anterior, pars dorsalis	LX	vagal lobe
Cantv	commissura anterior, pars ventralis	MFB	medial forebrain bundle
CC	crista cerebellaris	MFN	medial funicular nucleus
CCe	corpus cerebelli	MON	medial octavolateralis nucleus
Ccer	commissura cerebelli	MOT	medial olfactory tract
Cgus	commissure of the secondary gustatory nuclei	NLV	nucleus lateralis valvulae
Chor	commissura horizontalis	ON	optic nerve
CM	corpus mamillare	OT	optic tract
CP	central posterior thalamic nucleus	PGZ	periventricular gray zone of optic tectum
Cpop	commissura postoptica	POF	primary olfactory fiber layer
Cpost	commissura posterior	PPa	parvocellular preoptic nucleus, anterior part
Ctec	commissura tecti	PPv	periventricular pretectal nucleus, ventral part
Cven	commissura ventralis rhombencephali	PR	posterior recess of diencephalic ventricle
D	dorsal telencephalic area	PTN	posterior tuberal nucleus
Dc	central zone of D	SO	secondary octaval population (of McCormick & Hernandez 95)
DIL	diffuse nucleus of the inferior lobe	SRF	superior reticular formation
Dm	medial zone of D	TBS	tractus bulbospinalis
Dp	posterior zone of D	TeO	tectum opticum
DP	dorsal posterior thalamic nucleus	TeV	tectal ventricle
DIV	trochlear decussation	TL	torus longitudinalis
DV	descending trigeminal root	TPp	periventricular nucleus of posterior tuberculum
ECL	external cellular layer of olfactory bulb including mitral cells	TVS	tractus vestibulospinalis
FR	fasciculus retroflexus	V	ventral telencephalic area
GC	griseum centrale	Val	lateral division of valvula cerebelli
GL	glomerular layer of olfactory bulb	Vam	medial division of valvula cerebelli
Ha	habenula	Vd	dorsal nucleus of V
Hc	caudal zone of periventricular hypothalamus	Vp	postcommissural nucleus of V
Hd	dorsal zone of periventricular hypothalamus	Vs	supracommissural nucleus of V
ICL	internal cellular layer of olfactory bulb	VT	ventral thalamus
IMRF	intermediate reticular formation	Vv	ventral nucleus of V
IO	oliva inferior		
IRF	inferior reticular formation	III	oculomotor nerve
LCa	lobus caudalis cerebelli	VIIIs	sensory root of the facial nerve
LFB	lateral forebrain bundle		

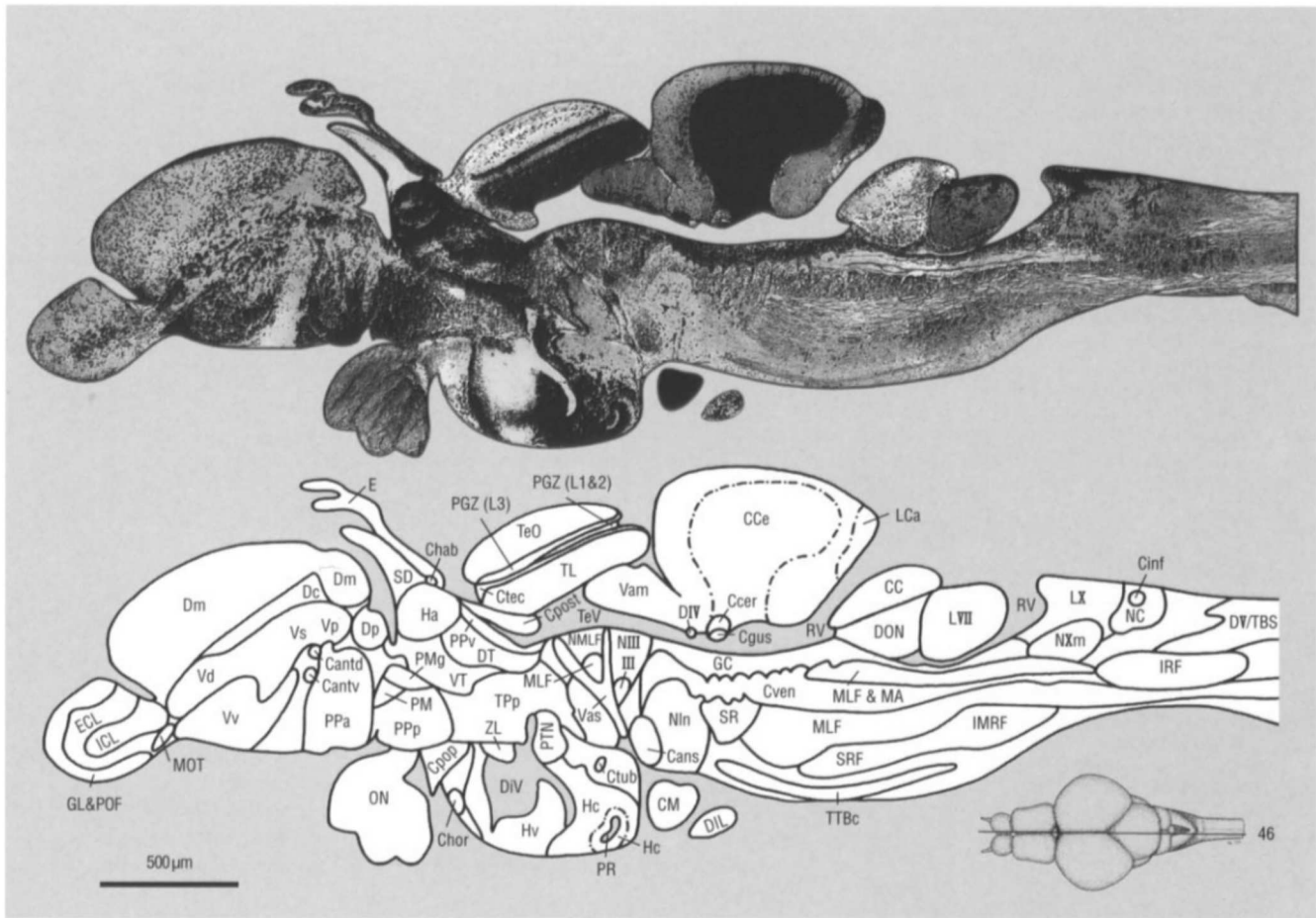
Sagittal Section 34



Sagittal Section 46

Cans	commissura ansulata	MA	Mauthner axon
Cantd	commissura anterior, pars dorsalis	MLF	medial longitudinal fascicle
Cantv	commissura anterior, pars ventralis	MOT	medial olfactory tract
CC	crista cerebellaris	NC	commissural nucleus of Cajal
CCe	corpus cerebelli	NIn	nucleus interpeduncularis
Ccer	commissura cerebelli	NMLF	nucleus of the MLF
Cgus	commissure of the secondary gustatory nuclei	NIII	oculomotor nucleus
Chab	commissura habenularum	NXm	vagal motor nucleus
Chor	commissura horizontalis	ON	optic nerve
Cinf	commissura infima of Haller	PGZ	periventricular gray zone of optic tectum
CM	corpus mamillare	PM	magnocellular preoptic nucleus
Cpop	commissura postoptica	PMg	gigantocellular part of magnocellular preoptic nucleus
Cpost	commissura posterior	POF	primary olfactory fiber layer
Ctec	commissura tecti	PPa	parvocellular preoptic nucleus, anterior part
Ctub	commissure of the posterior tuberculum	PPp	parvocellular preoptic nucleus, posterior part
Cven	commissura ventralis rhombencephali	PPv	periventricular pretectal nucleus, ventral part
D	dorsal telencephalic area	PR	posterior recess of diencephalic ventricle
Dc	central zone of D	PTN	posterior tuberal nucleus
DIL	diffuse nucleus of the inferior lobe	RV	rhombencephalic ventricle
DiV	diencephalic ventricle	SD	saccus dorsalis
Dm	medial zone of D	SR	superior raphe
DON	descending octaval nucleus	SRF	superior reticular formation
Dp	posterior zone of D	TBS	tractus bulbospinalis
DT	dorsal thalamus	TeO	tectum opticum
DIv	trochlear decussation	TeV	tectal ventricle
DV	descending trigeminal root	TL	torus longitudinalis
E	epiphysis	TPp	periventricular nucleus of posterior tuberculum
ECL	external cellular layer of olfactory bulb including mitral cells	TTBc	tractus tectobulbaris cruciatus
GC	griseum centrale	V	ventral telencephalic area
GL	glomerular layer of olfactory bulb	Vam	medial division of valvula cerebelli
Ha	habenula	Vas	vascular lacuna of area postrema
Hc	caudal zone of periventricular hypothalamus	Vd	dorsal nucleus of V
Hv	ventral zone of periventricular hypothalamus	Vp	postcommissural nucleus of V
ICL	internal cellular layer of olfactory bulb	Vs	supracommissural nucleus of V
IMRF	intermediate reticular formation	VT	ventral thalamus
IRF	inferior reticular formation	Vv	ventral nucleus of V
LCa	lobus caudalis cerebelli	ZL	zona limitans
LVI	facial lobe		
LX	vagal lobe	III	oculomotor nerve

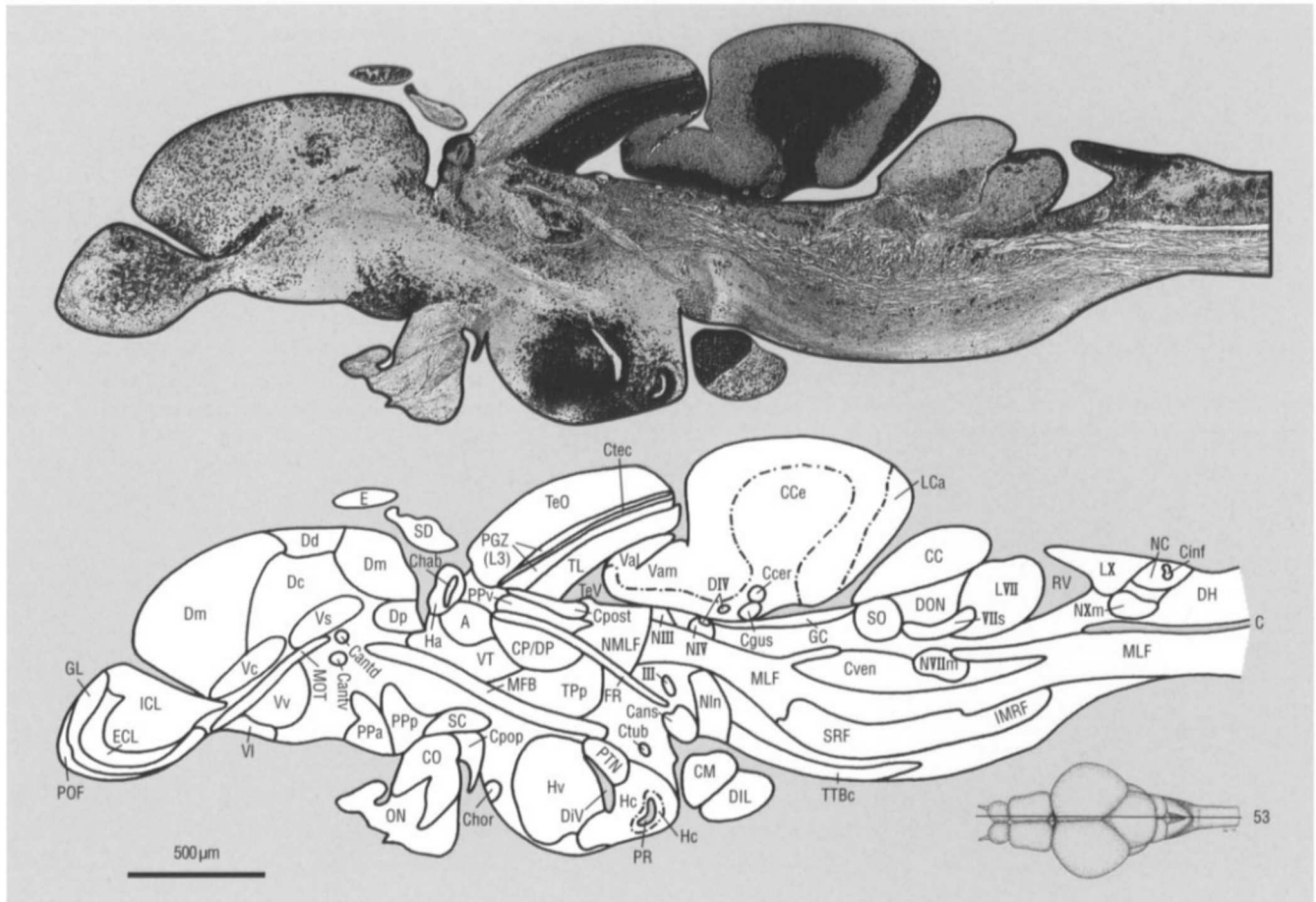
Sagittal Section 46



Sagittal Section 53

A	anterior thalamic nucleus	LVII	facial lobe
C	central canal	LX	vagal lobe
Cans	commissura ansulata	MFB	medial forebrain bundle
Cantd	commissura anterior, pars dorsalis	MLF	medial longitudinal fascicle
Cantv	commissura anterior, pars ventralis	MOT	medial olfactory tract
CC	crista cerebellaris	NC	commissural nucleus of Cajal
CCe	corpus cerebelli	NIn	nucleus interpeduncularis
Ccer	commissura cerebelli	NMLF	nucleus of the MLF
Cgus	commissure of the secondary gustatory nuclei	NIII	oculomotor nucleus
Chab	commissura habenularum	NIV	trochlear nucleus
Chor	commissura horizontalis	NVIIIm	facial motor nucleus
Cinf	commissura infima of Haller	NXm	vagal motor nucleus
CM	corpus mamillare	ON	optic nerve
CO	chiasma opticum	PGZ	periventricular gray zone of optic tectum
CP	central posterior thalamic nucleus	POF	primary olfactory fiber layer
Cpop	commissura postoptica	PPa	parvocellular preoptic nucleus, anterior part
Cpost	commissura posterior	PPp	parvocellular preoptic nucleus, posterior part
Ctec	commissura tecti	PPv	periventricular pretectal nucleus, ventral part
Ctub	commissure of the posterior tuberculum	PR	posterior recess of diencephalic ventricle
Cven	commissura ventralis rhombencephali	PTN	posterior tuberal nucleus
D	dorsal telencephalic area	RV	rhombencephalic ventricle
Dc	central zone of D	SC	suprachiasmatic nucleus
Dd	dorsal zone of D	SD	saccus dorsalis
DH	dorsal horn	SO	secondary octaval population (of McCormick & Hernandez 95)
DIL	diffuse nucleus of the inferior lobe	SRF	superior reticular formation
DiV	diencephalic ventricle	TeO	tectum opticum
Dm	medial zone of D	TeV	telencephalic ventricle
DON	descending octaval nucleus	TL	torus longitudinalis
Dp	posterior zone of D	TPp	periventricular nucleus of posterior tuberculum
DP	dorsal posterior thalamic nucleus	TTBc	tractus tectobulbaris cruciatus
DIIV	trochlear decussation	V	ventral telencephalic area
E	epiphysis	Val	lateral division of valvula cerebelli
ECL	external cellular layer of olfactory bulb including mitral cells	Vam	medial division of valvula cerebelli
FR	fasciculus retroflexus	Vc	central nucleus of V
GC	griseum centrale	VI	lateral nucleus of V
GL	glomerular layer of olfactory bulb	Vs	supracommissural nucleus of V
Ha	habenula	VT	ventral thalamus
Hc	caudal zone of periventricular hypothalamus	Vv	ventral nucleus of V
Hv	ventral zone of periventricular hypothalamus		
ICL	internal cellular layer of olfactory bulb		
IMRF	intermediate reticular formation	III	oculomotor nerve
LCa	lobus caudalis cerebelli	VIIIs	sensory root of the facial nerve

Sagittal Section 53



Horizontal sections

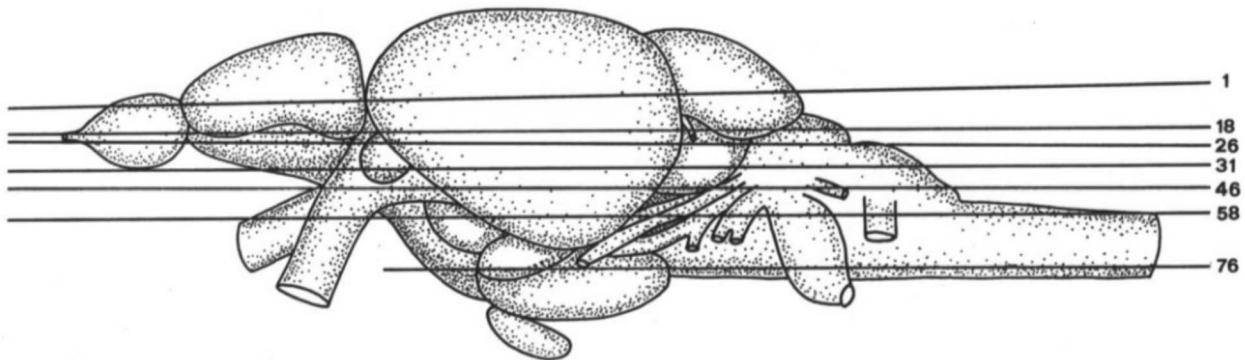
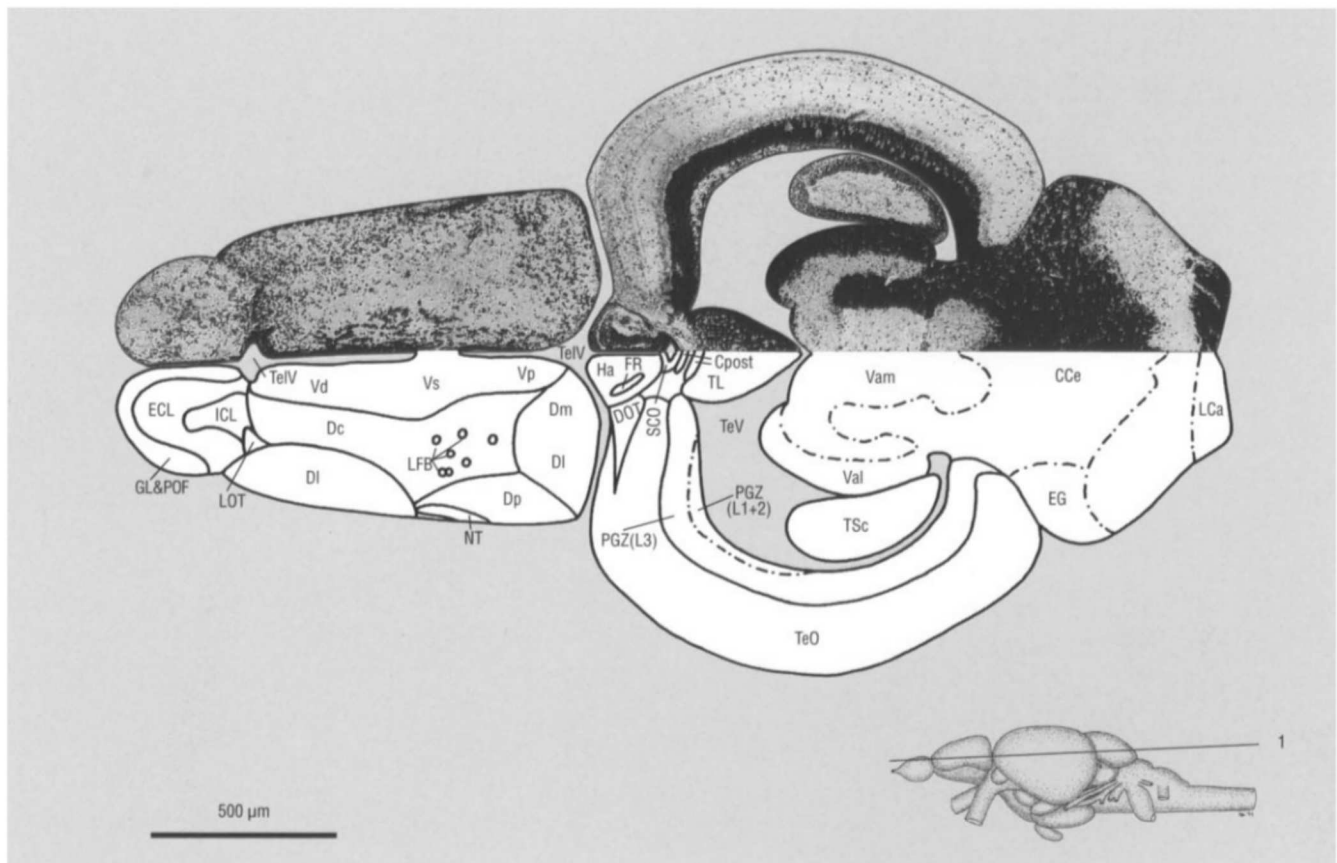


Figure 7.

Lateral view of the adult zebrafish brain demonstrating the position of levels shown in the series of horizontal sections. The selection of horizontal sections shown on the following pages does not include

the most dorsal and ventral aspects of the brain. With regard to the spinal cord, the section plane of this series almost corresponds to the ideal horizontal axis.

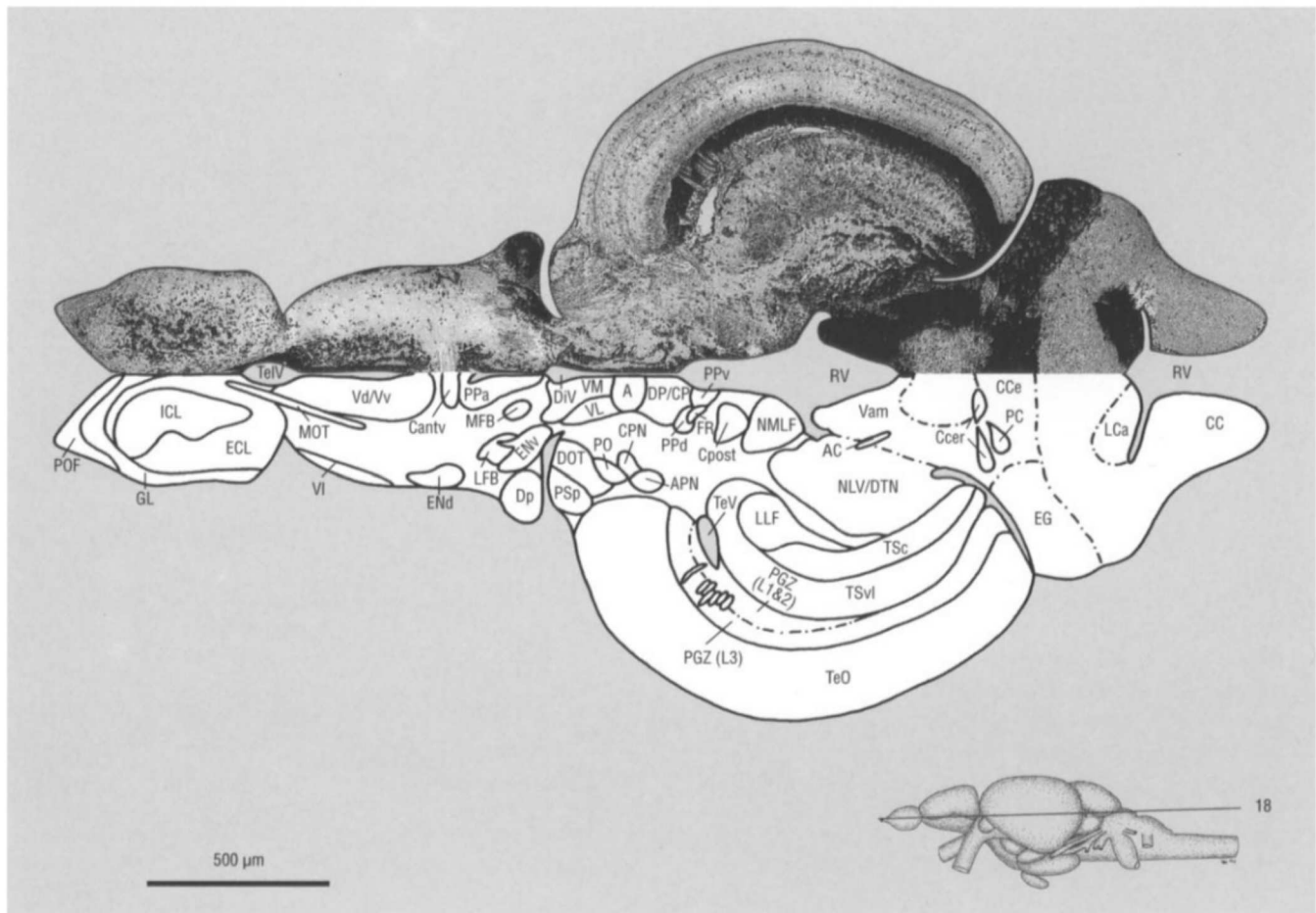
Horizontal Section 1



CCe	corpus cerebelli
Cpost	commissura posterior
D	dorsal telencephalic area
Dc	central zone of D
DI	lateral zone of D
Dm	medial zone of D
DOT	dorsomedial optic tract
Dp	posterior zone of D
ECL	external cellular layer of olfactory bulb including mitral cells
EG	eminentia granularis
FR	fasciculus retroflexus
GL	glomerular layer of olfactory bulb
Ha	habenula
ICL	internal cellular layer of olfactory bulb
LCa	lobus caudalis cerebelli
LFB	lateral forebrain bundle
LOT	lateral olfactory tract
NT	nucleus taeniae

PGZ	periventricular gray zone of optic tectum
POF	primary olfactory fiber layer
SCO	subcommissural organ
TeIV	telencephalic ventricles
TeO	tectum opticum
TeV	tectal ventricle
TL	torus longitudinalis
TSc	central nucleus of torus semicircularis
V	ventral telencephalic area
Val	lateral division of valvula cerebelli
Vam	medial division of valvula cerebelli
Vd	dorsal nucleus of V
Vp	postcommissural nucleus of V
Vs	supracommissural nucleus of V

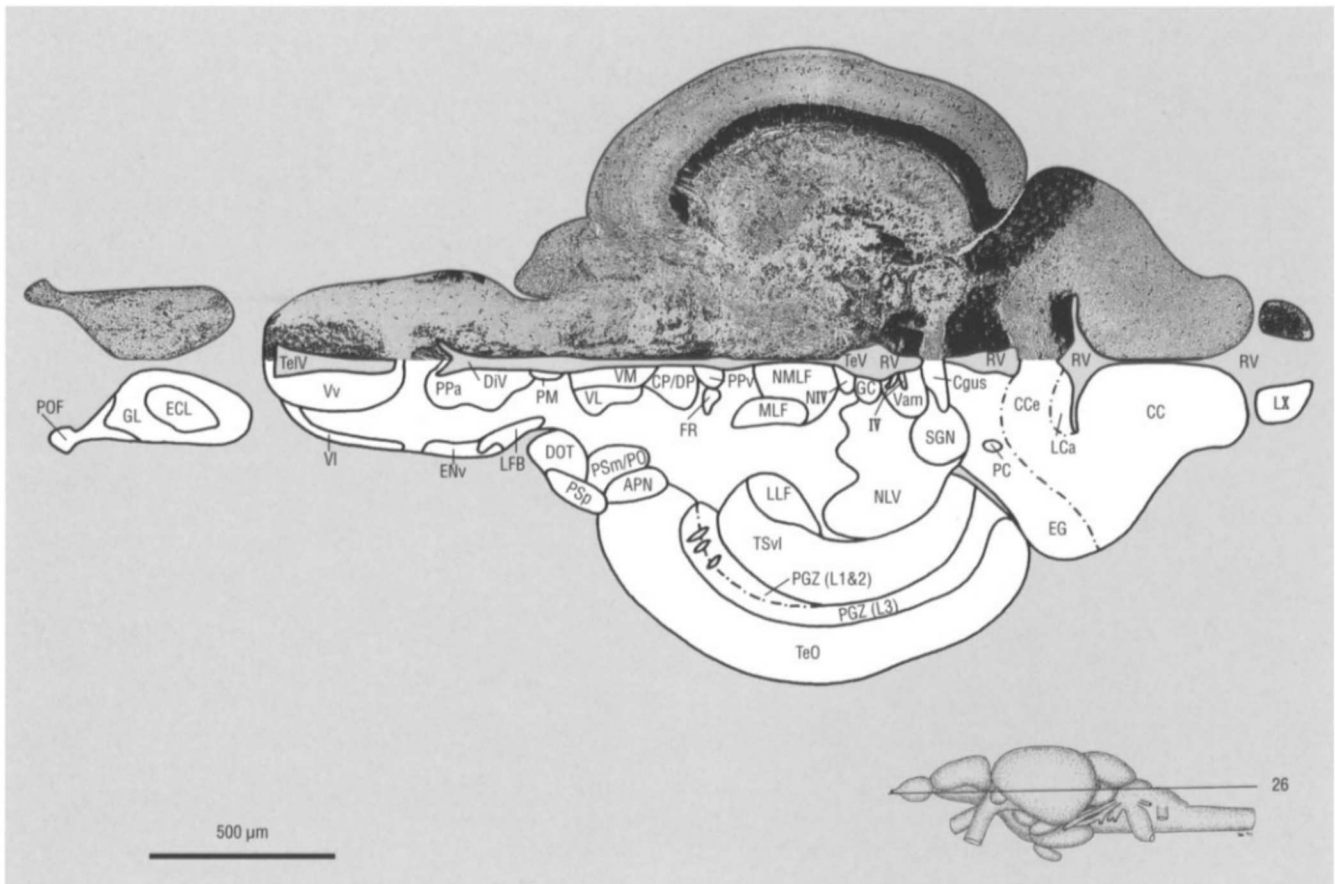
Horizontal Section 18



A	anterior thalamic nucleus
AC	anterior cerebellar tract
APN	accessory pretectal nucleus (of Wullimann & Meyer 90)
Cantv	commissura anterior, ventral part
CC	crista cerebellaris
CCe	corpus cerebelli
Ccer	commissura cerebelli
CP	central posterior thalamic nucleus
CPN	central pretectal nucleus
Cpost	commissura posterior
D	dorsal telencephalic area
Div	diencephalic ventricle
DOT	dorsomedial optic tract
Dp	posterior zone of D
DP	dorsal posterior thalamic nucleus
DTN	dorsal tegmental nucleus
ECL	external cellular layer of olfactory bulb including mitral cells
EG	eminentia granularis
End	entopeduncular nucleus, dorsal part
Env	entopeduncular nucleus, ventral part
FR	fasciculus retroflexus
GL	glomerular layer of olfactory bulb
ICL	internal cellular layer of olfactory bulb
LCa	lobus caudalis cerebelli
LFB	lateral forebrain bundle

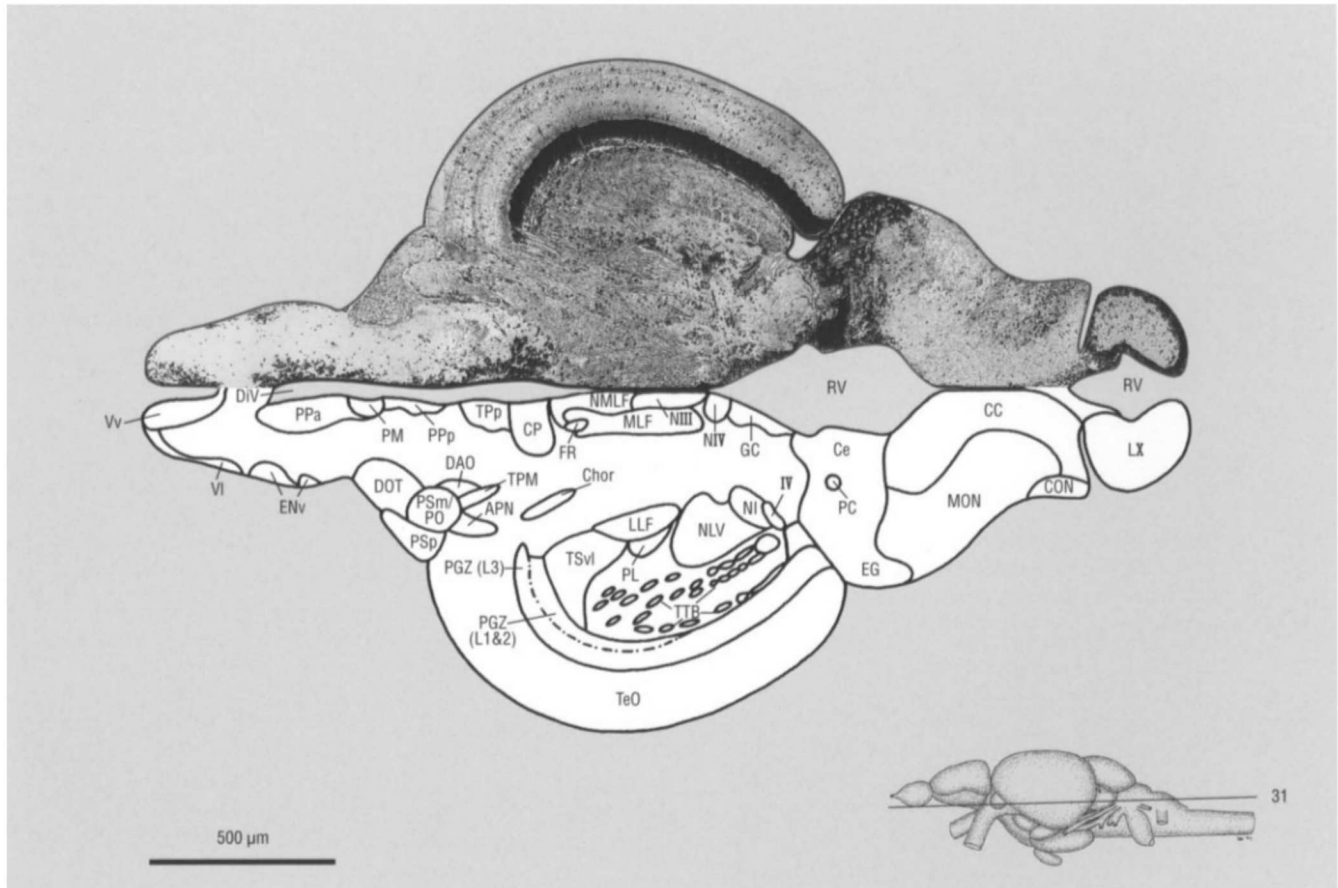
LLF	lateral longitudinal fascicle
MFB	medial forebrain bundle
MOT	medial olfactory tract
NLV	nucleus lateralis valvulae
NMLF	nucleus of the medial longitudinal fascicle
PC	posterior cerebellar tract
PGZ	periventricular gray zone of optic tectum
PO	posterior pretectal nucleus (of Wullimann & Meyer 90)
POF	primary olfactory fiber layer
PPa	parvocellular preoptic nucleus, anterior part
PPd	parvocellular pretectal nucleus, dorsal part
PPv	parvocellular pretectal nucleus, ventral part
PSP	parvocellular superficial pretectal nucleus
RV	rhombencephalic ventricle
TeV	telencephalic ventricles
TeO	tectum opticum
TeV	tectal ventricle
TSc	central nucleus of torus semicircularis
TSvl	ventrolateral nucleus of torus semicircularis
V	ventral telencephalic area
Vam	medial division of valvula cerebelli
Vd	dorsal nucleus of V
VI	lateral nucleus of V
VL	ventrolateral thalamic nucleus
VM	ventromedial thalamic nucleus
Vv	ventral nucleus of V

Horizontal Section 26



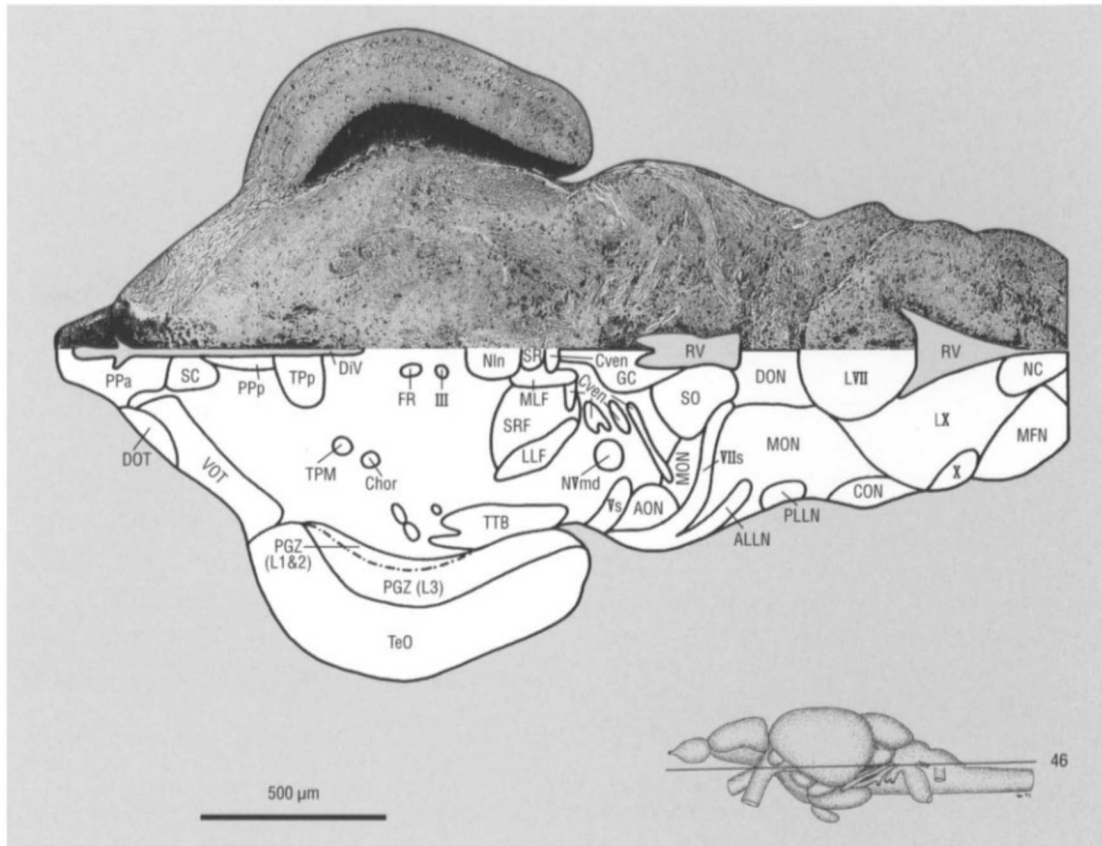
APN	accessory pretectal nucleus (of Wullimann & Meyer 90)	PGZ	periventricular gray zone of optic tectum
CC	crista cerebellaris	PM	magnocellular preoptic nucleus
CCe	corpus cerebelli	PO	posterior pretectal nucleus (of Wullimann & Meyer 90)
Cgus	commissure of the secondary gustatory nuclei	POF	primary olfactory fiber layer
CP	central posterior thalamic nucleus	PPa	parvocellular preoptic nucleus, anterior part
DIV	diencephalic ventricle	PPv	parvocellular preoptic nucleus, ventral part
DOT	dorsomedial optic tract	PSm	magnocellular superficial pretectal nucleus
DP	dorsal posterior thalamic nucleus	PSp	parvocellular superficial pretectal nucleus
ECL	external cellular layer of olfactory bulb including mitral cells	RV	rhombencephalic ventricle
EG	eminencia granularis	SGN	secondary gustatory nucleus
Env	entopeduncular nucleus, ventral part	TelV	telencephalic ventricles
FR	fasciculus retroflexus	TeO	tectum opticum
GC	griseum centrale	TeV	tectal ventricle
GL	glomerular layer of olfactory bulb	TSvl	ventrolateral nucleus of torus semicircularis
LCa	lobus caudalis cerebelli	V	ventral telencephalic area
LFB	lateral forebrain bundle	Vam	medial division of valvula cerebelli
LLF	lateral longitudinal fascicle	VI	lateral nucleus of V
LX	vagal lobe	VL	ventrolateral thalamic nucleus
MLF	medial longitudinal fascicle	VM	ventromedial thalamic nucleus
NLV	nucleus lateralis valvulae	Vv	ventral nucleus of V
NMLF	nucleus of the medial longitudinal fascicle		
NIV	trochlear nucleus	IV	trochlear nerve
PC	posterior cerebellar tract		

Horizontal Section 31



APN	accessory pretectal nucleus (of Wullimann & Meyer 90)	NIV	trochlear nucleus
CC	crista cerebellaris	PC	posterior cerebellar tract
Ce	cerebellum	PGZ	periventricular gray zone of optic tectum
Chor	commissura horizontalis	PL	perilemniscal nucleus
CON	caudal octavolateralis nucleus	PM	magnocellular preoptic nucleus
CP	central posterior thalamic nucleus	PO	posterior pretectal nucleus (of Wullimann & Meyer 90)
DAO	dorsal accessory optic nucleus	PPa	parvocellular preoptic nucleus, anterior part
DIV	diencephalic ventricle	PPp	parvocellular preoptic nucleus, posterior part
DOT	dorsomedial optic tract	PSm	magnocellular superficial pretectal nucleus
EG	eminencia granularis	PSp	parvocellular superficial pretectal nucleus
ENv	entopeduncular nucleus, ventral part	RV	rhombencephalic ventricle
FR	fasciculus retroflexus	TeO	tectum opticum
GC	griseum centrale	TPM	tractus pretectomamillaris
LLF	lateral longitudinal fascicle	TPp	periventricular nucleus of posterior tuberculum
LX	vagal lobe	TSVI	nucleus ventrolateralis of torus semicircularis
MLF	medial longitudinal fascicle	TTB	tractus tectobulbaris
MON	medial octavolateralis nucleus	V	ventral telencephalic area
NI	nucleus isthmi	VI	lateral nucleus of V
NLV	nucleus lateralis valvulae	Vv	ventral nucleus of V
NMLF	nucleus of the medial longitudinal fascicle		
NIII	oculomotor nucleus	IV	trochlear nerve

Horizontal Section 46



ALLN	anterior lateral line nerves	PLLN	posterior lateral line nerve
AON	anterior octaval nucleus	PPa	parvocellular preoptic nucleus, anterior part
Chor	commissura horizontalis	PPp	parvocellular preoptic nucleus, posterior part
CON	caudal octavolateralis nucleus	RV	rhombencephalic ventricle
Cven	commissura ventralis rhombencephali	SC	suprachiasmatic nucleus
DIV	diencephalic ventricle	SO	secondary octaval population (of McCormick & Hernandez 95)
DON	descending octaval nucleus	SR	superior raphe
DOT	dorsomedial optic tract	SRF	superior reticular formation
FR	fasciculus retroflexus	TeO	tectum opticum
GC	griseum centrale	TPM	tractus prepectomamillaris
LLF	lateral longitudinal fascicle	TPp	periventricular nucleus of posterior tuberculum
LVII	facial lobe	TTB	tractus tectobulbaris
LX	vagal lobe	VOT	ventrolateral optic tract
MFN	medial funicular nucleus		
MLF	medial longitudinal fascicle		
MON	medial octavolateralis nucleus		
NC	commissural nucleus of Cajal		
NIn	nucleus interpeduncularis	III	oculomotor nerve
NVmd	trigeminal motor nucleus, dorsal part	Vs	sensory root of the trigeminal nerve
PGZ	periventricular gray zone of optic tectum	VIIIs	sensory root of the facial nerve
		X	vagal nerve

