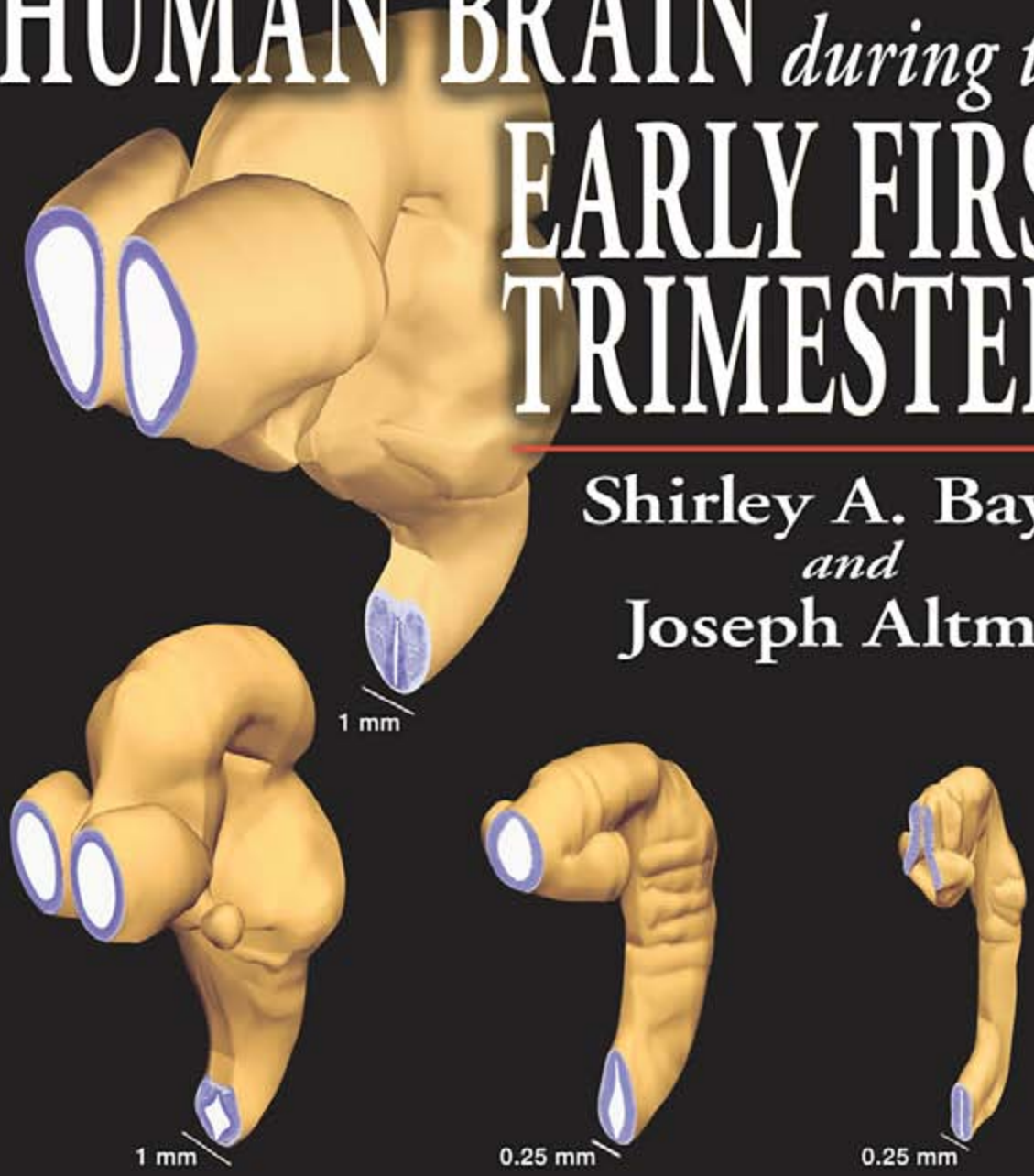
ATLAS OF
HUMAN CENTRAL NERVOUS SYSTEM DEVELOPMENT
VOLUME 5

# *The* HUMAN BRAIN *during the* EARLY FIRST TRIMESTER

Shirley A. Bayer
*and*
Joseph Altman

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# *The* HUMAN BRAIN *during the* EARLY FIRST TRIMESTER

**Shirley A. Bayer *and* Joseph Altman**

CRC Press
Taylor & Francis Group
Boca Raton London New York

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CRC Press
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6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

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10 9 8 7 6 5 4 3 2 1

International Standard Book Number-13: 978-0-8493-1424-7 (Hardcover)

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# DEDICATION

We dedicate this volume to the new generation of neuroscientists: those who use powerful molecular techniques to study the mechanisms of central nervous system (CNS) development, and those who use advanced scanning techniques to monitor the development of the CNS under normal and abnormal conditions.

# ACKNOWLEDGMENTS

We thank Dr. William DeMyer, pediatric neurologist at Indiana University Medical Center, for access to his personal library on human CNS development. We also thank the staff of the National Museum of Health and Medicine at the Armed Forces Institute of Pathology, Walter Reed Hospital, Washington, D.C.: Dr. Adrianne Noe, Director; Archibald J. Fobbs, Curator of the Yakovlev Collection; Elizabeth C. Lockett; and William Discher. We are most grateful to Dr. James M. Petras at the Walter Reed Institute of Research who made his darkroom facilities available so that we could develop all the photomicrographs on location rather than in our laboratory in Indiana. Finally, we thank Barbara Norwitz, Kari Budyk, and Suzanne Lassandro at CRC Press/Taylor & Francis for their personal attention to us and for expert help during production of the manuscript.

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# PART I

# INTRODUCTION

## A. Organization of the Atlas

This is the last volume in the *Atlas of Human Central Nervous System Development* series. It deals with human brain development during the early first trimester from the 3rd through the 7th gestational weeks (GW3-GW7). Volume 1 (Bayer and Altman, 2002) records the development of the spinal cord from GW4 to the 4th postnatal month. Volumes 2 through 5 deal with prenatal brain development. The analysis procedes in reverse (older-to-younger) order: from more recognizable brain structures in the third trimester to progressively less familiar structures in the second trimester to often uncertain or hypothetical structures in the first trimester. Volume 2 (Bayer and Altman, 2004a) records brain development during the third trimester, with specimens ranging in age from GW37 to GW26; its major theme is the *maturation of the brain's settled and enduring neuron populations.* Volume 3 (Bayer and Altman, 2005) deals with brain development during the second trimester, with specimens ranging in age from GW24 to GW13.5; its major theme is the *migration, sojourning, and settling of the brain's diverse neuron populations.* Volume 4 (Bayer and Altman, 2006) presents brain development during the late first trimester, with specimens ranging in age from GW11 to GW7.5; its major theme is the *neuroepithelial mosaics that generate different populations of neurons and glia.* This volume presents brain development during the early first trimester, with specimens ranging in age from GW7.0 to GW3.2, and has four major themes: *(1) growth of the stockbuilding neuroepithelium along the expanding shorelines of the brain's superventricles, (2) early neurogenesis, (3) the onset of brain parenchymal development related to the expansion and decline of the superarachnoid reticulum, and (4) the inductive and signaling interactions between the brain and peripheral structures in the skull.*

The present volume features 14 normal specimens. Approximately two specimens near the same age were selected for analysis, one cut in the transverse (mainly coronal) plane, the other cut in the sagittal plane. For the oldest age group (GW7), there is a third specimen sectioned mainly in the horizontal plane. (Younger horizontally sectioned specimens are not in any of the collections we examined.) Each specimen is presented as a series of grayscale photographs of its Nissl-stained brain sections including the surrounding skull (**Parts II** through **XV**). The photographs are shown from anterior to posterior (coronal specimens), medial to lateral (sagittal specimens), and dorsal to ventral (horizontal GW7 specimen). Portrait orientation is used for the coronal specimens; the dorsal part of each section is toward the top of the page, the ventral part at the bottom, and the midline is in the vertical center of each section. Landscape orientation is used for the horizontal specimen; the anterior part of each section is facing to the left (bottom of page), posterior to the right (top of page), and the midline is in the horizontal center of each section. All coronal and horizontal specimes have computer-aided 3-dimensional reconstructions of their brains showing each section's location. That reconstruction clears up the ambiguity about the exact plane of sectioning through each brain; a problem we addressed in Volume 4. Portrait orientation is used for all sagittal specimens; the anterior part of each section is facing left, posterior right, dorsal top, and ventral bottom. **Parts II** through **XV** contain companion plates, designated as **A** and **B** on facing pages. **Part A** on the left page shows the full contrast photograph with labels of the skull and peripheral neural structures; **part B** on the right page shows low contrast copies of the same photograph with superimposed outlines of the labeled brain parts. The *low magnification plates* show entire sections to identify the large structures and subdivisions of the brain. The *high magnification plates* feature enlarged views of the brain core to identify smaller structures. For ease of interpretation in all plates, the ventricles are labeled in **CAPITALS**, the neuroepithelium and other germinal zones in **Helvetica bold**, transient structures in ***Times bold italic***, and permanent structures in Times Roman or **Times bold**. Fixation artifacts are usually outlined with dashed lines in **part B** of each plate, but few specimens in this volume have artifacts.

Since this is the final volume in the series, a **Concluding Essay (Part XVI)** links major themes of brain development at the cell and tissue level (described in the Atlas Series) with current neuro-developmental studies on gene expression and other molecular markers. **Figure 15** to **Figure 43** in the essay bring together photographs of individual brain structures at various ages so that the sequence of development is immediately apparent. An **Appendix** contains **tables** listing the estimated timespans of neurogenesis for the major populations in the human central ner-

vous system (CNS) based on experimentally determined data in rats. **References** follow the appendix, and the Atlas concludes with an alphabetized **Glossary** that defines the developmental structures labeled in the plates.

## B. Specimens

All specimens are from the collections of human embryos and fetal brains currently kept at the National Museum of Health and Medicine, Armed Forces Institute of Pathology, Washington, D.C. Nine specimens are from the Carnegie Collection and are designated by their respective numbers with the prefix C. The Carnegie Collection was started by Franklin P. Mall (1862-1917) and expanded at the Carnegie Institution of Washington under the direction of George L. Streeter (1873-1948) and George W. Corner (1889-1981). Five specimens are from the Minot Collection and are designated by their respective numbers with the prefix M. The Minot Collection is named after Charles S. Minot (1852-1914), who collected and prepared over 1900 embryos of different animal species, and approximately 100 human embryos, close to a century ago.

## C. Photography and Computer Processing

All specimens were photographed using either an Olympus photomicroscope or a Wild photomakroskop. The magnification varied for each specimen according to the size of the head; the section with the largest area that could be accommodated within the field of view set the magnification for all sections of a particular specimen. All photographs were taken with a green filter to increase the contrast of the black and white film (Kodak technical pan #TP442). The film was developed at 20°C for 6 to 7 min in Kodak HC110 developer (dilution F), followed by Kodak stop bath for 30 s, Kodak fixer for 5 min, Kodak hypo clearing agent for 1 min, running water rinse for 10 min, and a brief rinse in Kodak photoflo before drying.

The negatives were scanned at 2700 dots-per-inch (dpi) with a Nikon Coolscan-1000 35-mm film scanner, which was interfaced to a PowerPC G3 Macintosh computer running Adobe Photoshop with a plug-in Nikon driver. To capture the subtle shades of gray, the negatives were scanned as color positives, inverted, and converted to grayscale. Using the enhancement features built into Adobe Photoshop and the additional features of Extensis Intellihance, adjustments were made to increase contrast and sharpness. When the image resolution was set to 300 dpi, a full-size photographic file printed at approximately 12 to 10 in. Most images are shown at slightly reduced full size on separate pages. Adobe Illustrator was used to superimpose labels and to outline structural details on low contrast copies of the Adobe Photoshop files. The plates were placed into a book-form layout using Adobe InDesign. Finally, camera-ready files were provided to Taylor & Francis in Adobe portable document format (pdf).

The entire brain and upper cervical spinal cord of each transversely cut specimen was three-dimensionally reconstructed in five steps. *First,* photographs of serial sections were made throughout the entire brain; the negatives were scanned and converted to computer files as described in the preceding paragraph. *Second,* all the files of sections selected for the reconstruction were placed into one large Photoshop file that contained a separate photograph in each layer. By altering the visibility and transparency of these layers the sections were aligned to each other as they were before sectioning. Then each layer was saved as a separate file. *Third,* Adobe Illustrator was used to outline the brain surface of each aligned section, and these contours were saved in separate Adobe Illustrator encapsulated postscript (eps) files. *Fourth,* the eps files were imported into 3D space (x, y, and z coordinates) using Cinema 4DXL (C4D, Maxon Computer, Inc.). For each section, points on the contours have unique x-y coordinates and the same z coordinate. By calculating the distance between sections, the entire array of contours was stretched out in the z axis. The C4D loft tool builds a "skin" of the brain as a spline mesh of polygons. The polygons start from the x-y points on the first contour with the most anterior z coordinate, to the x-y points on the next contour behind it, and finish with the x-y points on the last contour with the most posterior z coordinate. The spline meshes of the entire brain surface were rendered at various camera angles as completely opaque using the C4D ray-tracing engine. These reconstructions are shown in **Figure 1** to **Figure 14.** *Fifth,* spline meshes of the brain surface posterior to a specific section (coronal brains) or ventral to a specific section (horizontal brain) were rendered with a copy of the photograph of the particular section texture-mapped as a cap on the model. These reconstructions are shown as **insets in Part A** of each low magnification plate of the coronal and horizontal specimens.

## D. Identification of Transient and Immature Brain Regions

With the exception of the rhombomeres in the pons and medulla that are visible prior to and including GW5.5, the identification of most structures in early first trimester human brain—in particular, the various neuroepithelial (NEP) compartments—have received little attention in the past. Most identifications are based on our previous $^{3}$H-thymidine autoradiographic work with rats. There is a great similarity between the rat brain and human brain in the sequential order of neurogenesis and early neuronal differentiation, especially in the brainstem. Our experimental studies in the rat and the rationale for most of the proven or putative identifications we make are in the following publications.

*Amygdala:* Bayer (1980c).
*Basal Ganglia:* Bayer (1984, 1985b, 1987).
*Cerebellum:* Altman and Bayer (1978a, 1982a, 1985a,

1985b, 1985c, 1997).
*Cerebral Cortex:* Altman and Bayer (1990a, 1990b); Bayer and Altman (1990, 1991a).
*Cranial Nerve Nuclei:* Altman and Bayer (1980a, 1980b, 1980c, 1982b).
*Hippocampus:* Altman (1963); Altman and Das (1965a); Altman and Bayer (1975, 1990c, 1990d, 1990e); Bayer (1980a, 1980b).
*Hypothalamus:* Altman and Bayer (1978c, 1978d, 1978e, 1986).
*Medulla:* Altman and Bayer (1978b, 1980a, 1980b, 1980c, 1982b).
*Midbrain:* Altman and Bayer (1981a, 1981b, 1981c).
*Olfactory Bulb:* Altman (1969); Bayer (1983).
*Pontine Area:* Altman and Bayer (1978b, 1980d, 1987a, 1987b, 1987c, 1987d).
*Precerebellar Nuclei:* Altman and Bayer (1978b, 1987a, 1987b, 1987c, 1987d, 1997).
*Preoptic Area:* Altman and Bayer (1986); Bayer and Altman (1987).
*Rhinencephalon:* Bayer (1985a, 1986a, 1986b); Bayer and Altman (1991b).
*Septal Area:* Bayer (1979a, 1979b).
*Spinal Cord:* Altman and Bayer (1984, 2001).
*Thalamus:* Altman and Bayer (1979a, 1979b, 1979c, 1988a, 1988b, 1988c, 1989a, 1989b, 1989c).

## E. Major Developmental Features of the First Trimester Brain

In **Part XVI**, **Concluding Essay**, we summarize the landmark events that characterize the development of the human CNS during the first trimester. Briefly reviewed, they are the following.

(i) For several weeks after closure of the neural tube (the future spinal cord) and the neural vesicles (the future rhombencephalon, mesencephalon, diencephalon, and telencephalon), the CNS consists of a single proliferative tissue, the *stockbuilding neuroepithelium* (NEP). These NEP cells do not produce neurons and neuroglia but rather the growing stock of pluripotent progenitor cells that will later give rise to the differentiating cells of the CNS.

(ii) The proliferating NEP cells undergo mitosis near the lumen of the ventricles, hence the growth of the stockbuilding NEP matrix is associated with the expansion of the narrow protoventricles to produce the large rhombencephalic, mesencephalic, diencephalic, and telencephalic *superventricles*.

(iii) The rate of stockbuilding cell mitosis varies in different components of the NEP matrix in relation to the sizes of the neuronal populations being generated for different brain structures. This results in a variegated ventricular shoreline (rhombomeres, evaginations, invaginations, eminences). We refer to these distinguishable NEP matrix shorelines as *NEP cell mosaics*.

(iv) When NEP cell proliferation shifts from stockbuilding progenitor cells to unloading postmitotic neurons and neuroglia, these cells migrate outward and accumulate in the brain parenchyma, the space situated between the NEP and the pia. We present evidence that the formation of a hitherto unidentified meningeal structure, the *superarachnoid reticulum*, is related to this parenchymal expansion. The superarachnoid reticulum is a broad, fluid-rich meningeal tissue sandwiched between the early-developing pia and the formative dura. The initial expansion of the superarachnoid reticulum antedates the appearance of the brain parenchyma. While the parenchyma continually expands as more and more neurons migrate into it and differentiate, the superarachnoid reticulum continually shrinks until it is a thin meninx. We postulate that the transient hypertophy of the superarachnoid reticulum serves as a *parenchymal expansion field* for the developing brain.

(v) The shrinkage of the NEP matrix is coupled with *cell migration*. A small complement of migrating cells produce fate-restricted *secondary germinal matrices* away from the ventricle, such as the external germinal layer of the cerebellum and the subgranular zone of the hippocampus. The bulk of migrating cells are young neurons that may sojourn in *transitional fields* but eventually settle in their final locations throughout the parenchyma.

(vi) Peripheral and central inductive and signaling mechanisms play a major role in producing fate-restricted NEP cell mosaics, guiding migrating neurons, and directing axons to grow to their targets. Interactions between the NEP and the cephalic and branchial placodes (peripherocentral signaling) influence the diversification of NEP mosaics. Centro-central signaling between CNS structures is responsible for the coordinated development of different brain regions not directly connected with the periphery.

(vii) An attempt is made to relate the morphological evidence for NEP matrix diversification, cell-fate restriction, neuronal migration, and axonal guidance in the human CNS with the underlying genetic and molecular mechanisms revealed by current research in animals.

# PART II: GW7 CORONAL

This specimen is embryo #2155 in the Minot Collection, designated here as M2155. The crown-rump length (CR) is 17.5 mm estimated to be at gestational week (GW) 7. Most of M2155's brain sections are cut (10 μm) in the coronal plane, but the plane shifts to predominantly horizontal in the posterior medulla. We photographed 71 sections at low magnification from the frontal prominence to the posterior tips of the mesencephalon and cerebellum. Seventeen of these sections are illustrated in **Plates 1AB to 17AB**. All photographs were used to produce computer-aided 3-D reconstructions of the external features of M2155's brain (**Figure 1**), and to show each illustrated section *in situ* (*insets,* **Plates 1A-17A**). A prominent developmental strategy during the early first trimester is that **many developing brain structures interact with primordial structures in the head and neck**. Consequently, each illustrated section shows the brain with all surrounding tissues. Labels in **A Plates** (normal-contrast images) identify non-neural and peripheral neural structures; labels in **B Plates** (low-contrast images) identify central neural structures. **Plates 18-20** show high-magnification views of the cerebral cortex, diencephalon, and mesencephalon. Some high-magnification plates are rotated 90˚ (landscape orientation) to more efficiently use page space. The brain of M2155 has considerable variation in the thickness of the neuroepithelium and in the number of migrating neurons in various parts of the brain parenchyma.

Throughout the telencephalon, the neuroepithelium is the most prominent structure surrounding the enlarging telencephalic superventricle. A cell-sparse primordial plexiform layer is adjacent to the cerebral cortical neuroepithelium. A few pioneer Cajal-Retzius neurons have migrated into this layer, but most cortical neurons have not yet been generated. The cerebral cortical neuroepithelium is growing by adding more neuonal stem cells that will produce neurons during the late first trimester (**Volume 4**, Bayer and Altman, 2006) and early second trimester (**Volume 3**, Bayer and Altman, 2005). In contrast to the cerebral cortical neuroepithelium, the basal ganglionic and basal telencephalic neuroepithelia do have adjacent migrating neurons. In some areas, these neurons appear to migrate together in early (outermost and less dense) to late (innermost and most dense) waves. In accordance with the peripheral interaction theme, there is only the slightest indication of an olfactory bulb evagination in spite of the fact that a fully invaginated olfactory epithelium is in the nasal cavity and olfactory nerve fibers already contact the brain just anterior to the basal telencephalon. We hypothesize that olfactory nerve fibers have the capacity to induce the cortical neuroepithelium to proliferate and evaginate into an olfactory bulb later on. There is an olfactory evagination by GW7.5 (*See* **Volume 4**, Bayer and Altman, 2006, **Plates 188A and B**, pp. 464-465).

The diencephalic neuroepithelium surrounds a slit-like superventricle. It is thinnest in the hypothalamic and subthalamic areas, where it is surrounded by densely packed waves of migrating neurons. It is postulated that these areas of the superventricle have shrinking shorelines as the neuroepithelia "unload" their stock of neuronal precursors. In contrast, the superventricle shoreline is still expanding as the thalamic neuroepithelium continues to add more neuronal precursors than to unload postmitotic neurons. The few neurons outside the thalamic neuroepithelium are postulated to be the oldest neurons in the ventral complex, posterior complex, and the reticular nucleus.

The mesencephalon contains a stockbuilding neuroepithelium in the pretectum and tectum (relatively few adjacent migrating neurons). On the other hand, the tegmental and isthmal neuroepithelia are much thinner because most of their neuronal progeny has migrated out. These cells accumulate as inner dense clumps and outer sparse arrays interspersed among the thick accumulations of subpial fiber bands in the tegmental and isthmal parenchyma.

Both the pons and medulla have neuroepithelia that are shrinking as they have already unloaded their neuronal precursors into an expanding parenchyma. Cells are migrating and settling in longitudinal arrays at the pontine flexure. A few cells are settling in the superior olive complex and many are settling in the reticular formation throughout the pons and medulla. Facial motor neurons are migrating from medial to lateral, leaving behind their axons in the genu of the facial nerve. Migrating cochlear nuclear neurons are outside the neuroepithelium in the anterior part of the lower rhombic lip, while migrating inferior olive neurons are in the posterior intramural migratory stream outside the precerebellar neuroepithelium in the posterior lower rhombic lip; some neurons have already settled in the inferior olive. Many neurons have settled in the solitary nucleus, surrounding a definite solitary tract. The hypoglossal nucleus is also distinguishable in the lower medulla.

The cerebellar neuroepithelium is exceptional in the rhombencephalon because it is the only neuroepithelium still in the stockbuilding phase, mainly adding precursors of Purkinje cells. Many deep nuclear neurons have already been generated and are migrating in the cellular layers of the cerebellar transitional field. The fibrous layers probably contain afferents from the spinal cord and the vestibular ganglion.

# M2155 Computer-aided 3-D Brain Reconstructions

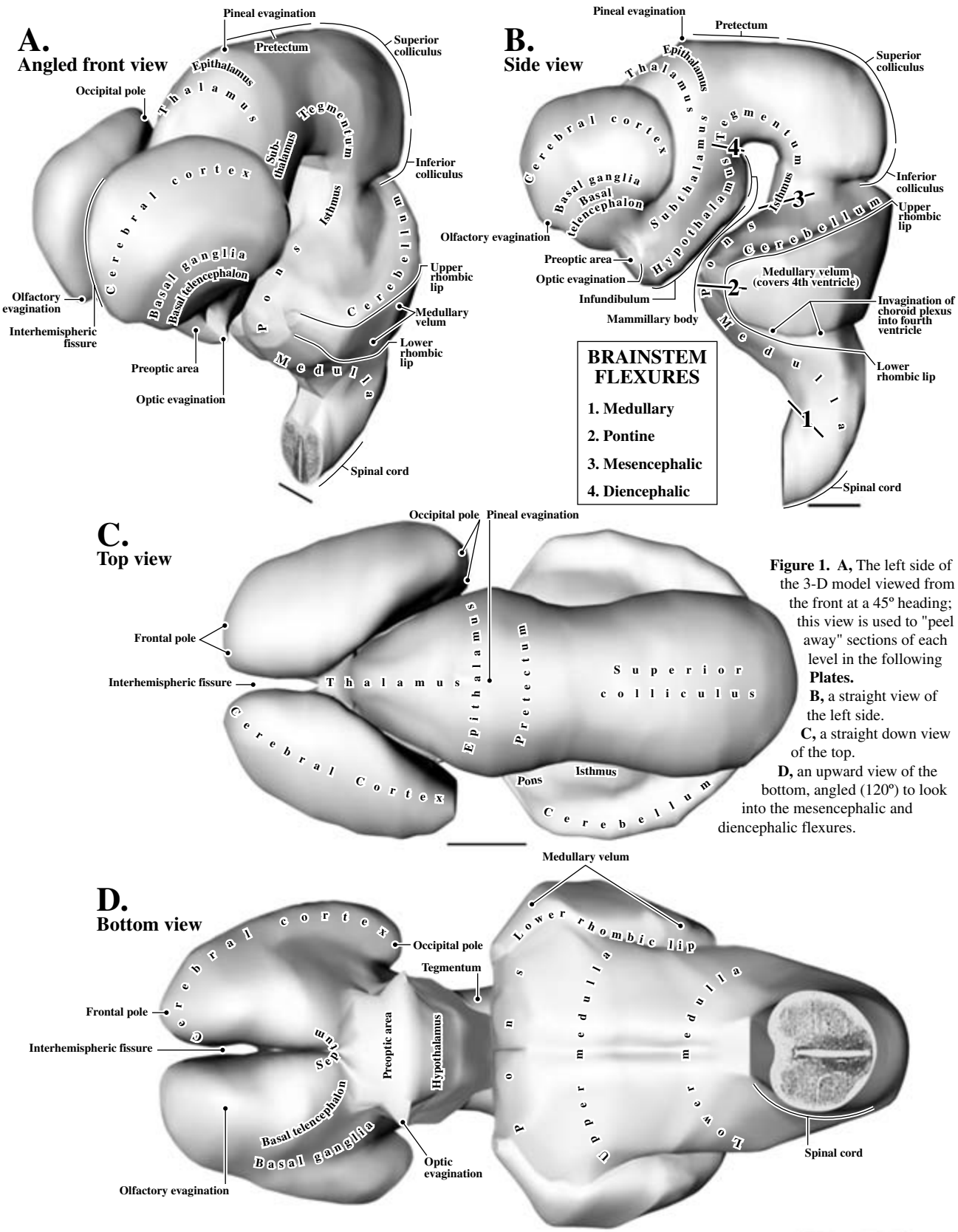



**Figure 1. A,** The left side of the 3-D model viewed from the front at a 45º heading; this view is used to "peel away" sections of each level in the following **Plates.**
**B,** a straight view of the left side.
**C,** a straight down view of the top.
**D,** an upward view of the bottom, angled (120º) to look into the mesencephalic and diencephalic flexures.

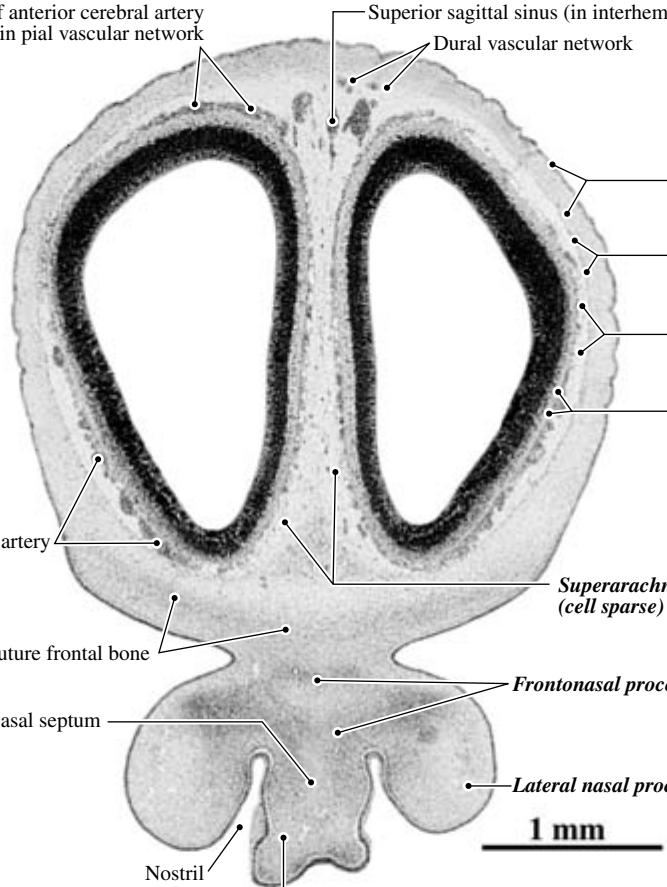
**Scale bars = 1 mm**

# PLATE 1A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 1: Section 50

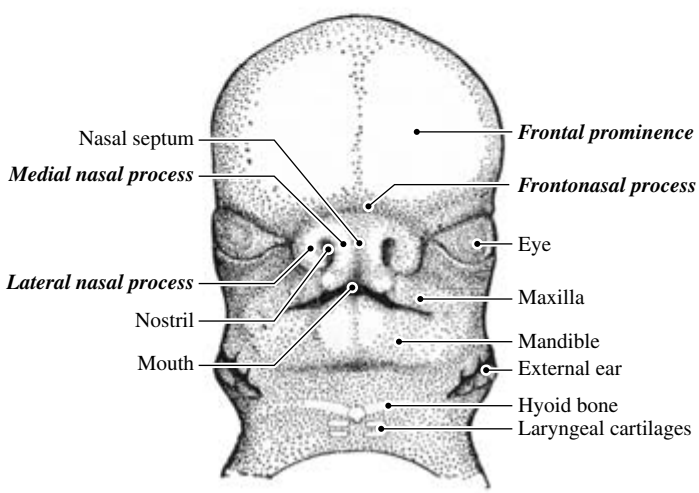
### Non-neural structures labeled

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.




**Level 1: Computer-aided 3-D Brain Reconstruction**

**The GW7 Face and Neck**
**Figure 247E modified (Patten, 1953, p. 429.)**

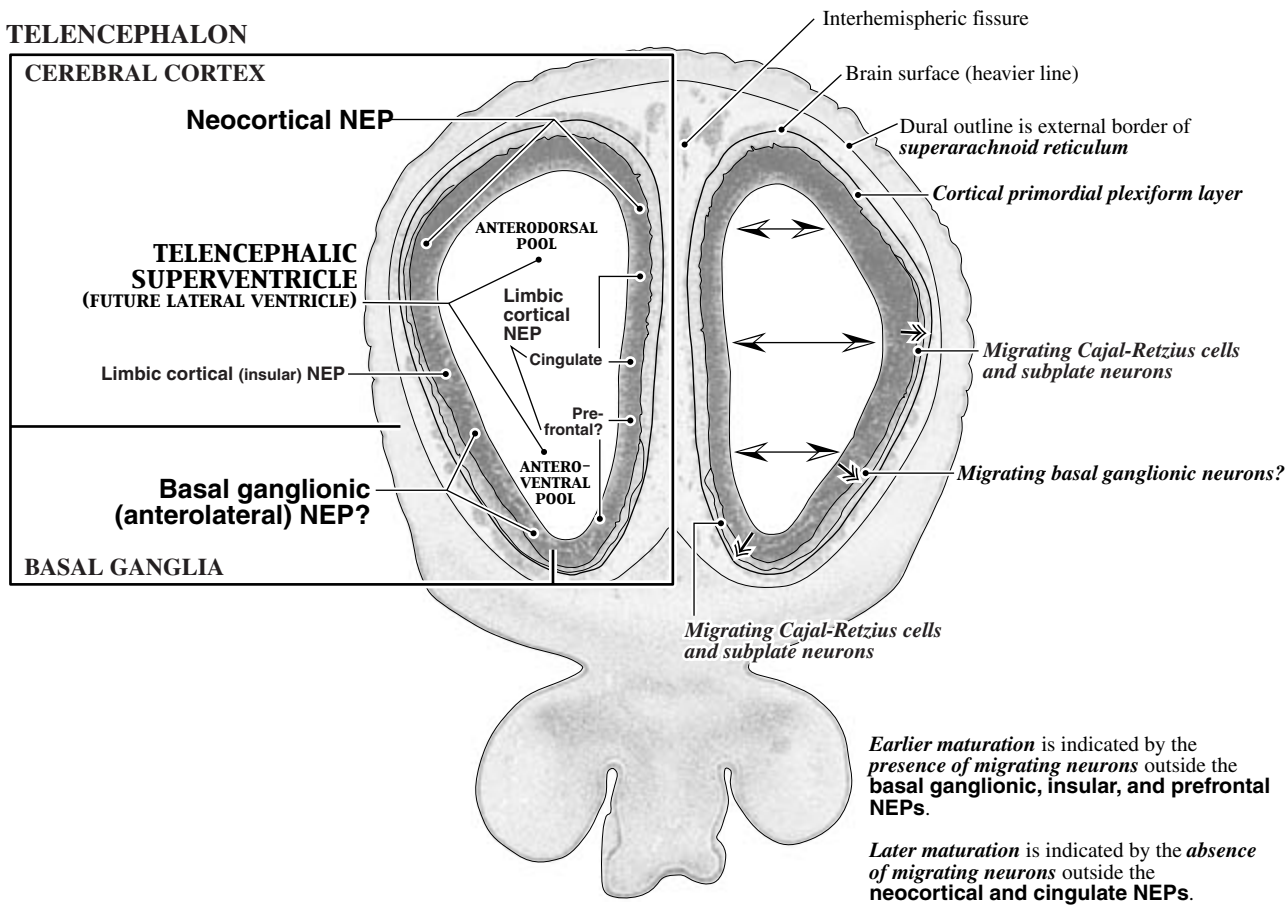


# PLATE 1B

FONT KEY:
VENTRICULAR DIVISIONS – CAPITALS
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**NEP - Neuroepithelium**

## Neural structures labeled

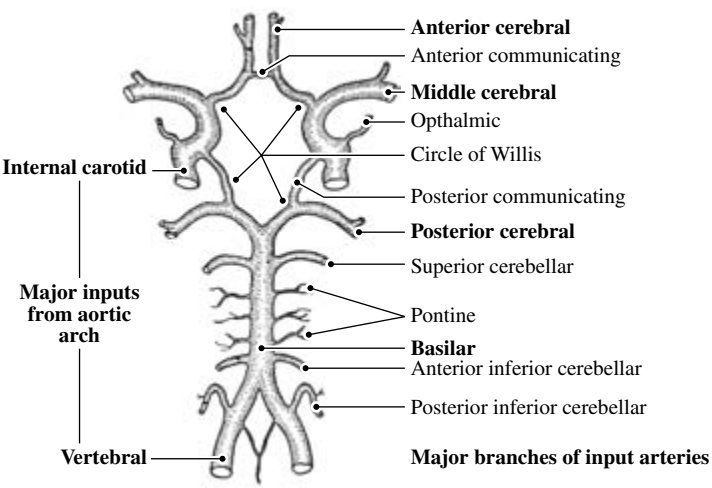



***Earlier maturation*** is indicated by the ***presence of migrating neurons*** outside the **basal ganglionic, insular, and prefrontal NEPs**.

***Later maturation*** is indicated by the ***absence of migrating neurons*** outside the **neocortical and cingulate NEPs**.

## Major Arteries at Base of Brain

**Figure 394D modified (Patten, 1953, p. 625.)**



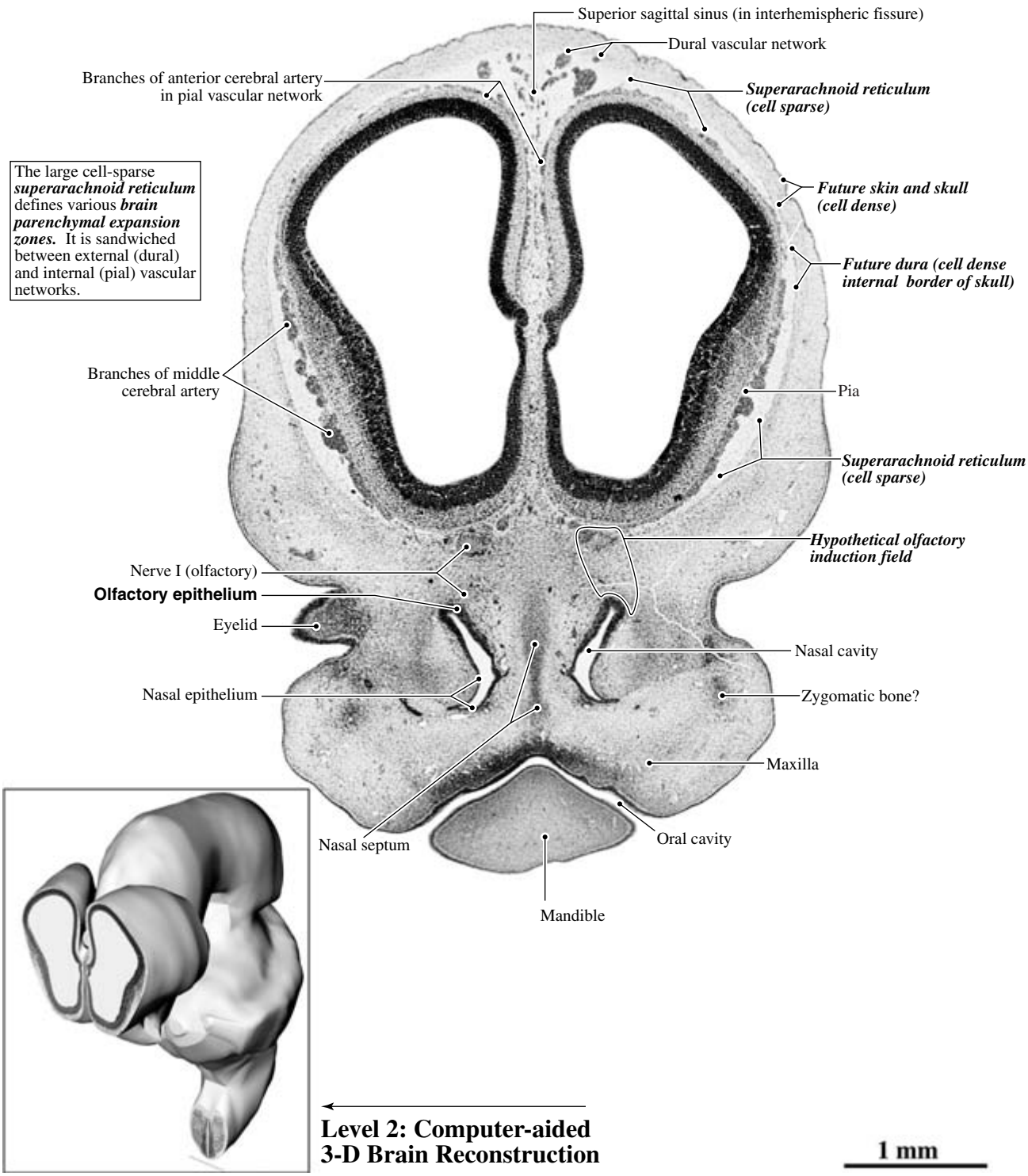

**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

# PLATE 2A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 2: Section 116

### Peripheral neural and non-neural structures labeled

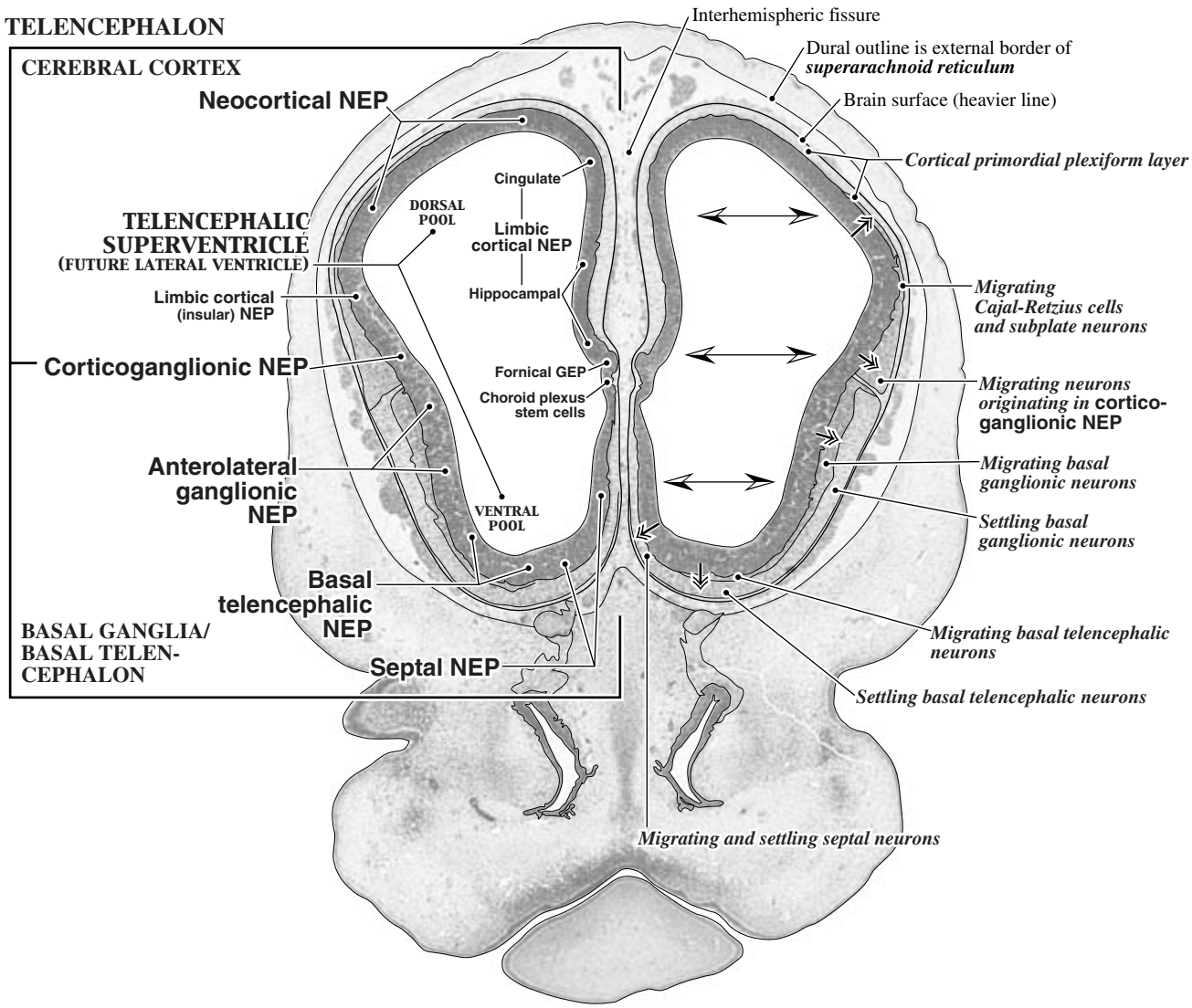


# PLATE 2B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**ABBREVIATIONS:**
**GEP - Glioepithelium**
**NEP - Neuroepithelium**

## Central neural structures labeled



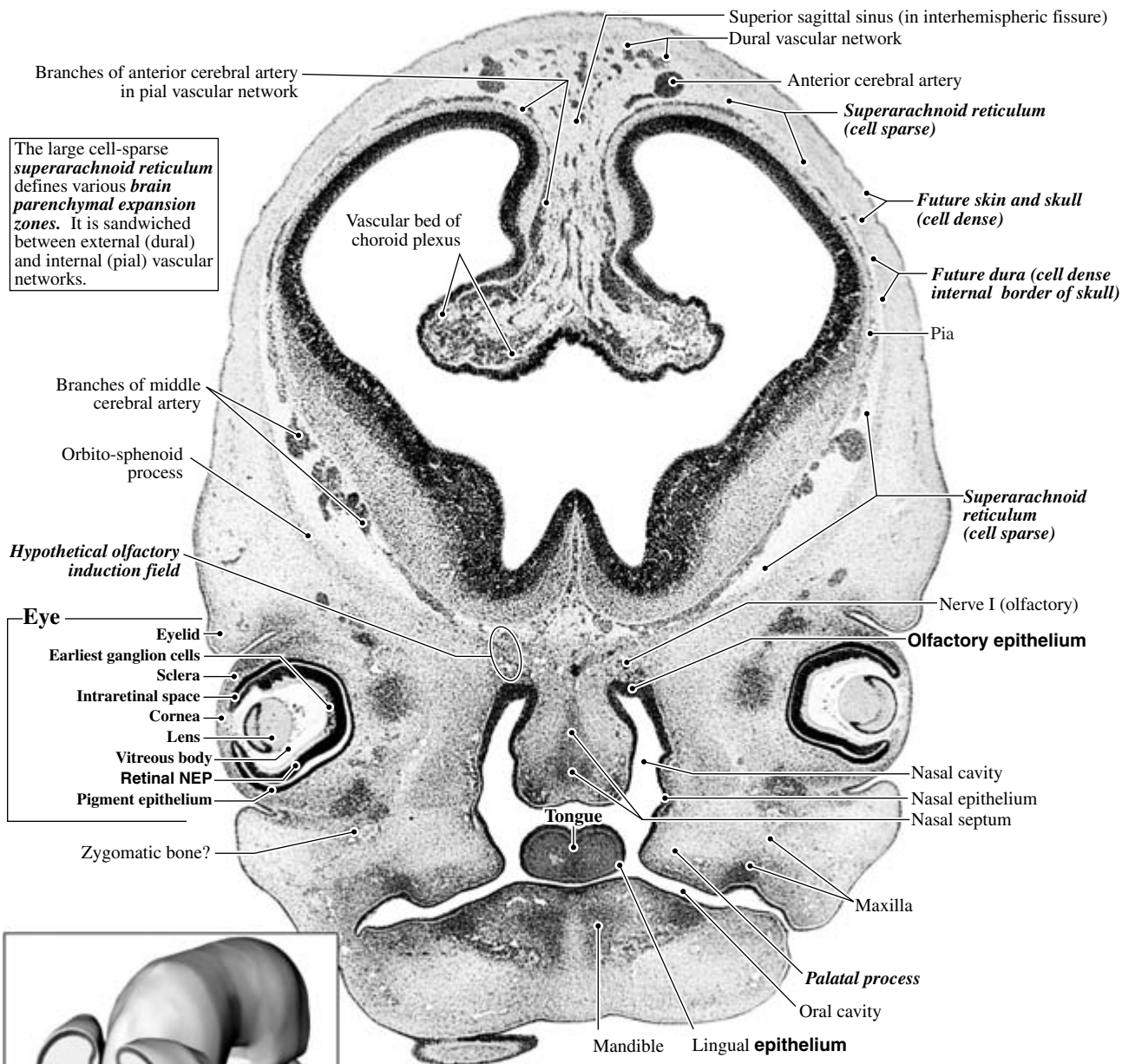

**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

# PLATE 3A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 3:
## Section 164

### Peripheral neural and non-neural structures labeled




The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

**Level 3: Computer-aided 3-D Brain Reconstruction**

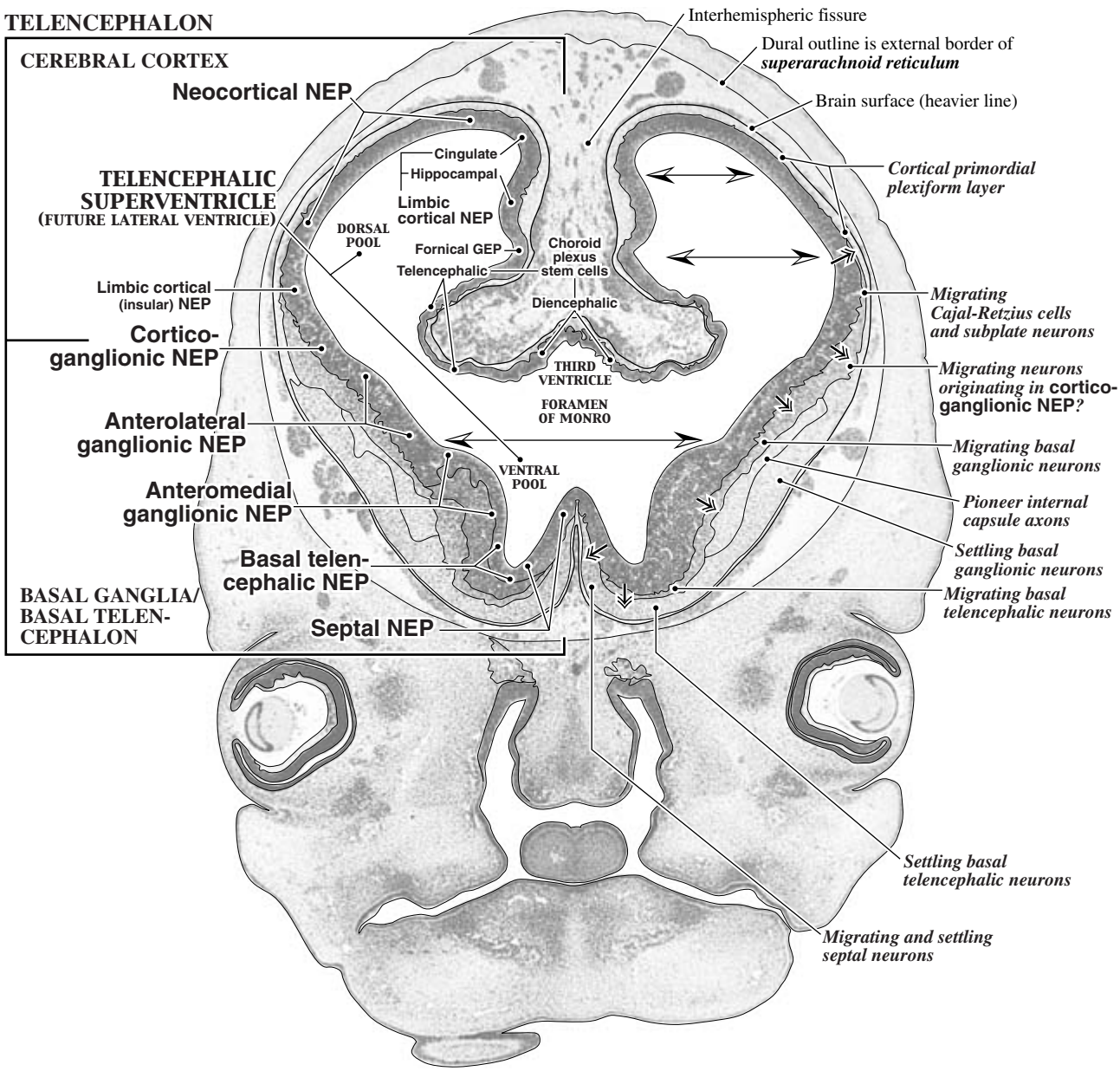
**1 mm**

# PLATE 3B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**ABBREVIATIONS:**
**GEP - Glioepithelium**
**NEP - Neuroepithelium**

## Central neural structures labeled




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

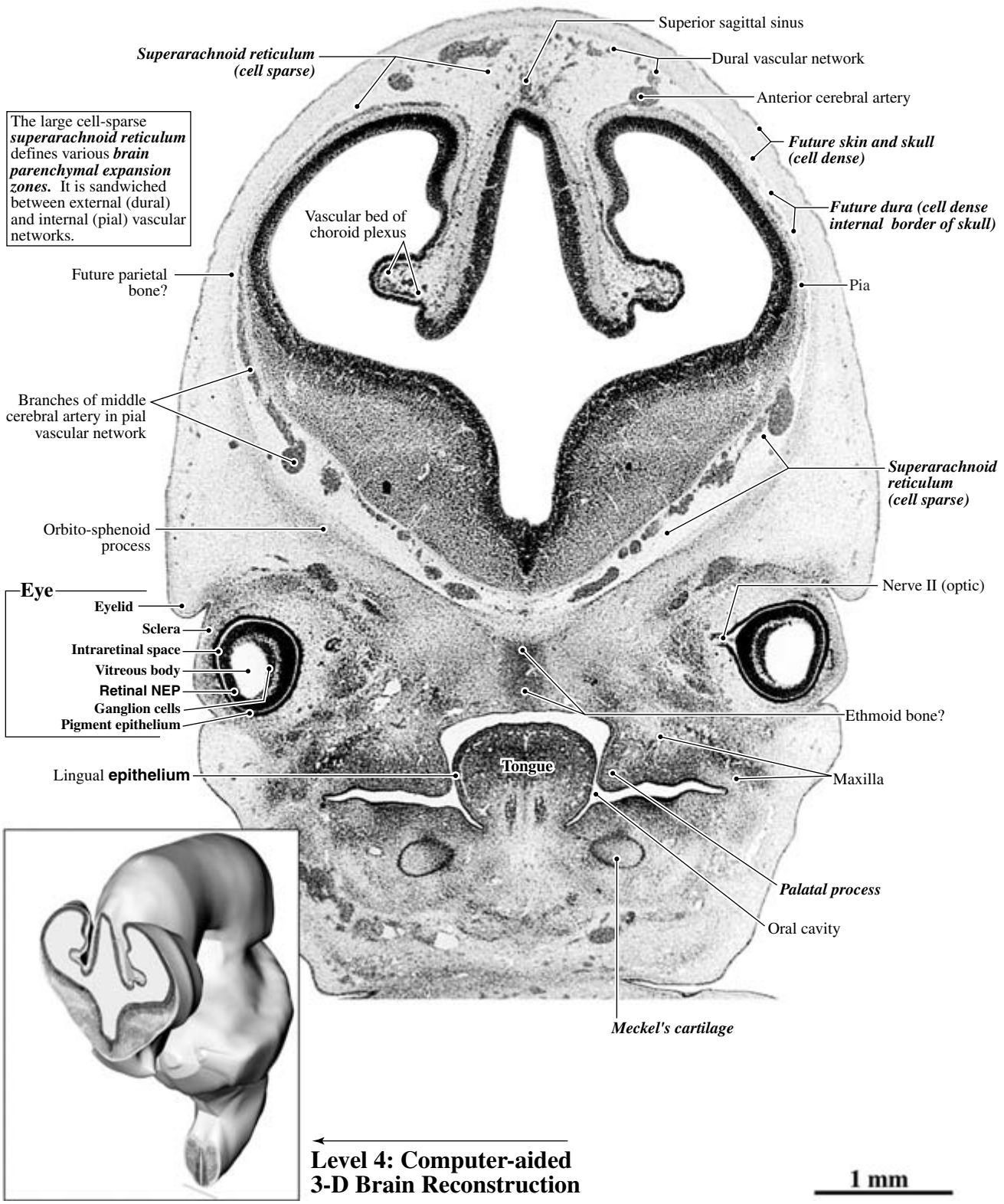
**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

# PLATE 4A

**See a high magnification view of the thalamus and cerebral cortex in Plates 18A and B.**

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 4:
## Section 201

**Peripheral neural and non-neural structures labeled**

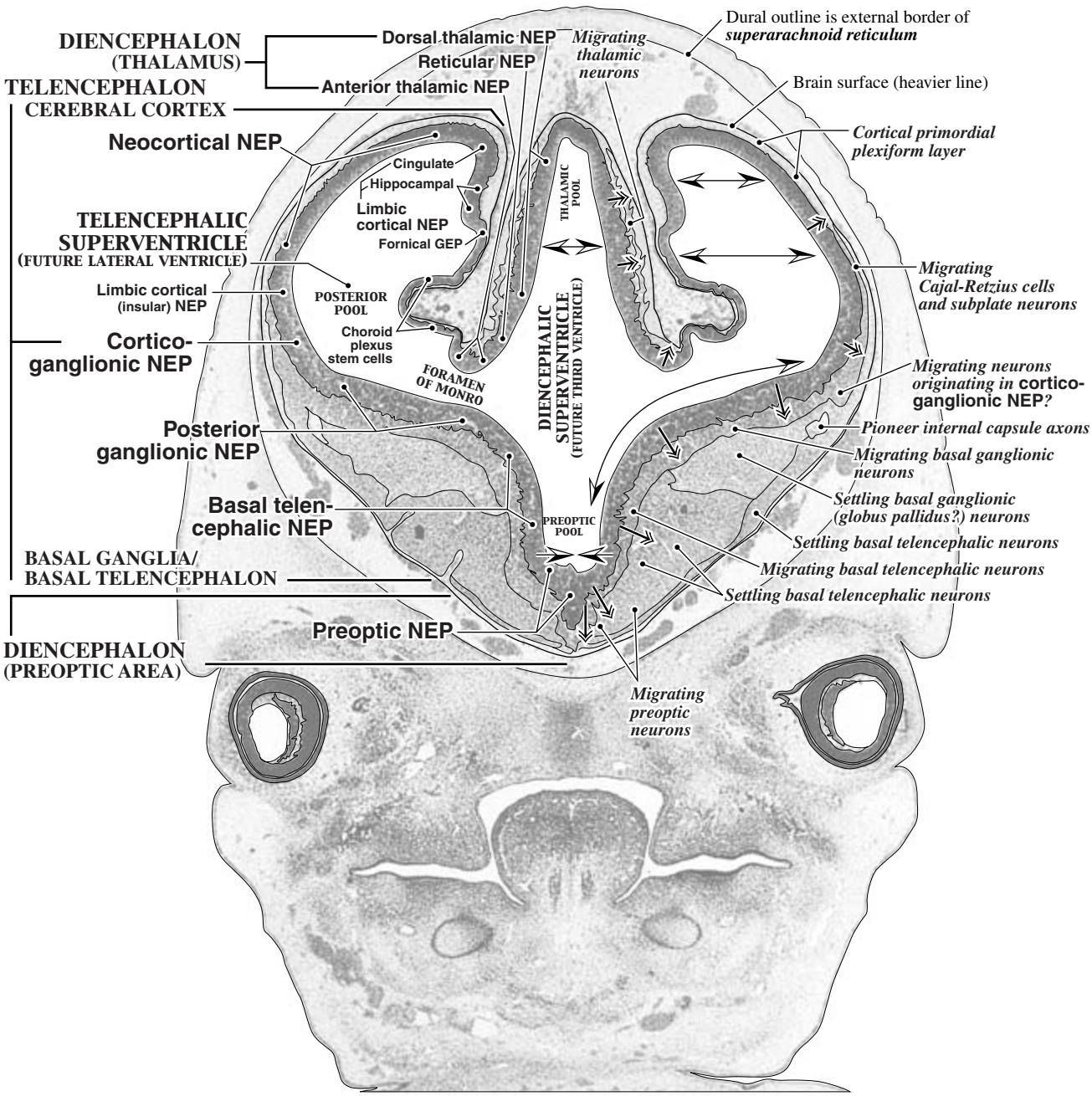


# PLATE 4B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**ABBREVIATIONS:**
**GEP - Glioepithelium**
**NEP - Neuroepithelium**

## Central neural structures labeled




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

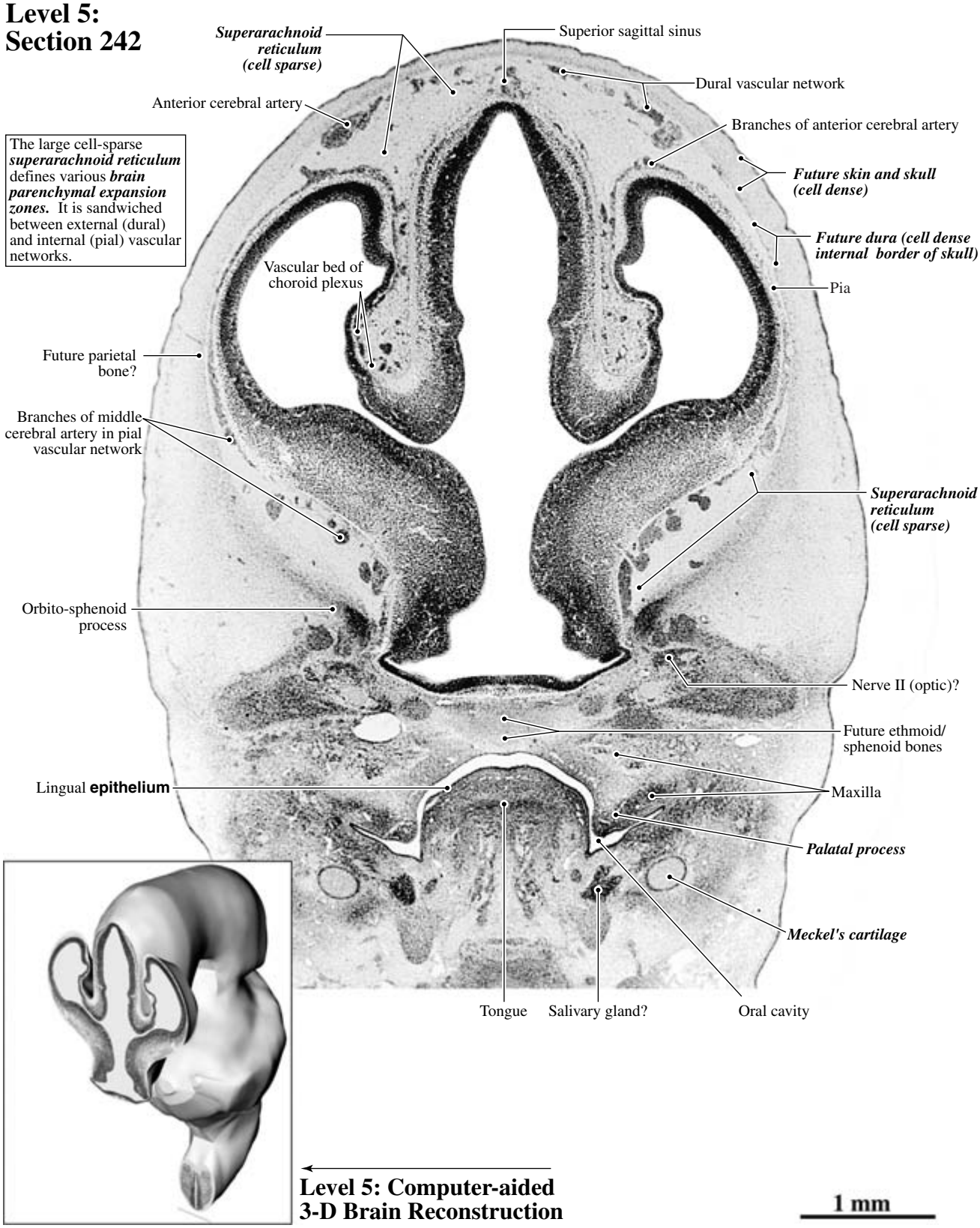
**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 5A

**See a high magnification view of the thalamus and cerebral cortex from Section 236 in Plates 19A and B.**

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 5:
## Section 242

**Peripheral neural and non-neural structures labeled**




The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

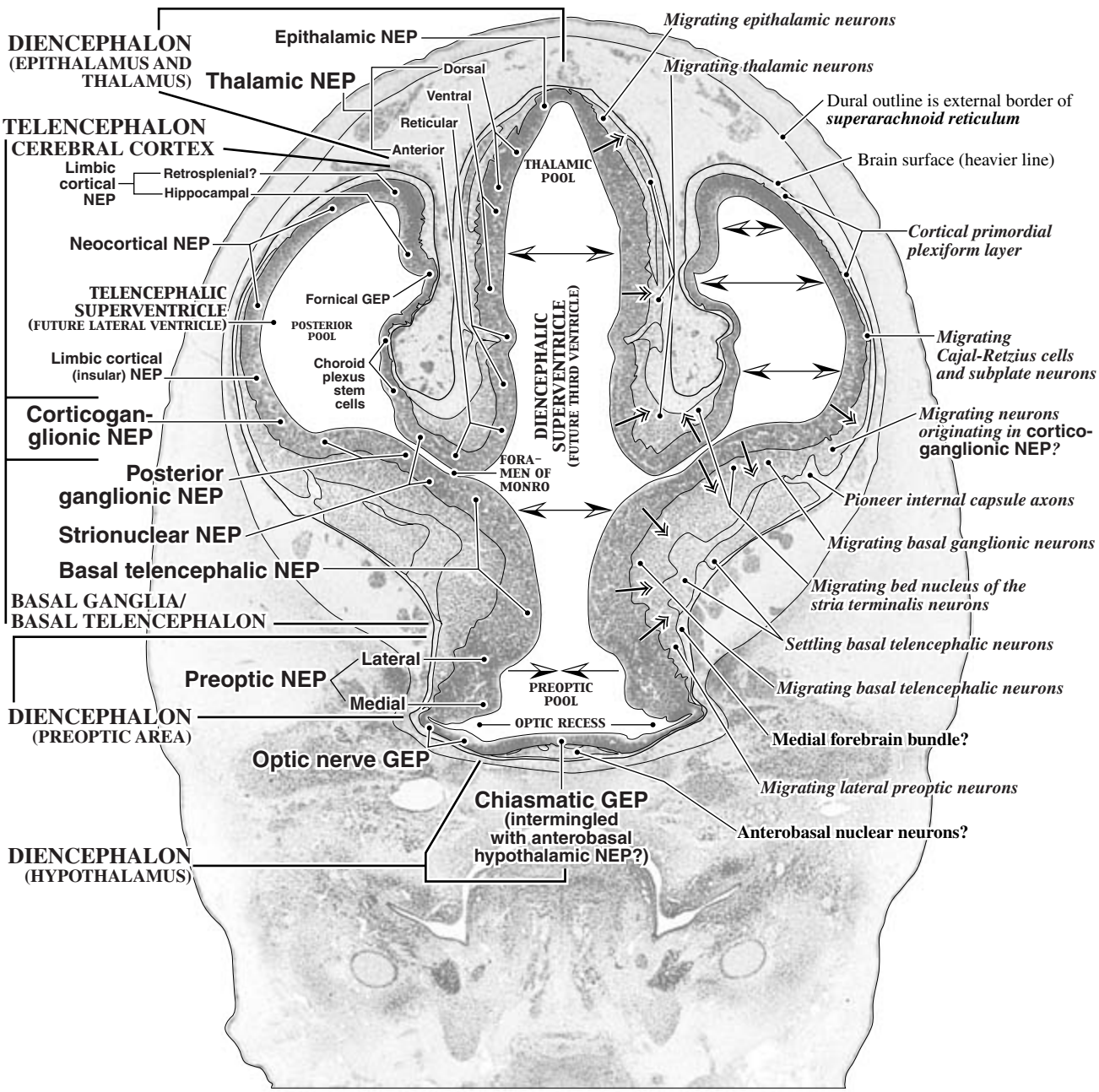
**Level 5: Computer-aided 3-D Brain Reconstruction**

# PLATE 5B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**ABBREVIATIONS:**
**GEP - Glioepithelium**
**NEP - Neuroepithelium**

## Central neural structures labeled




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

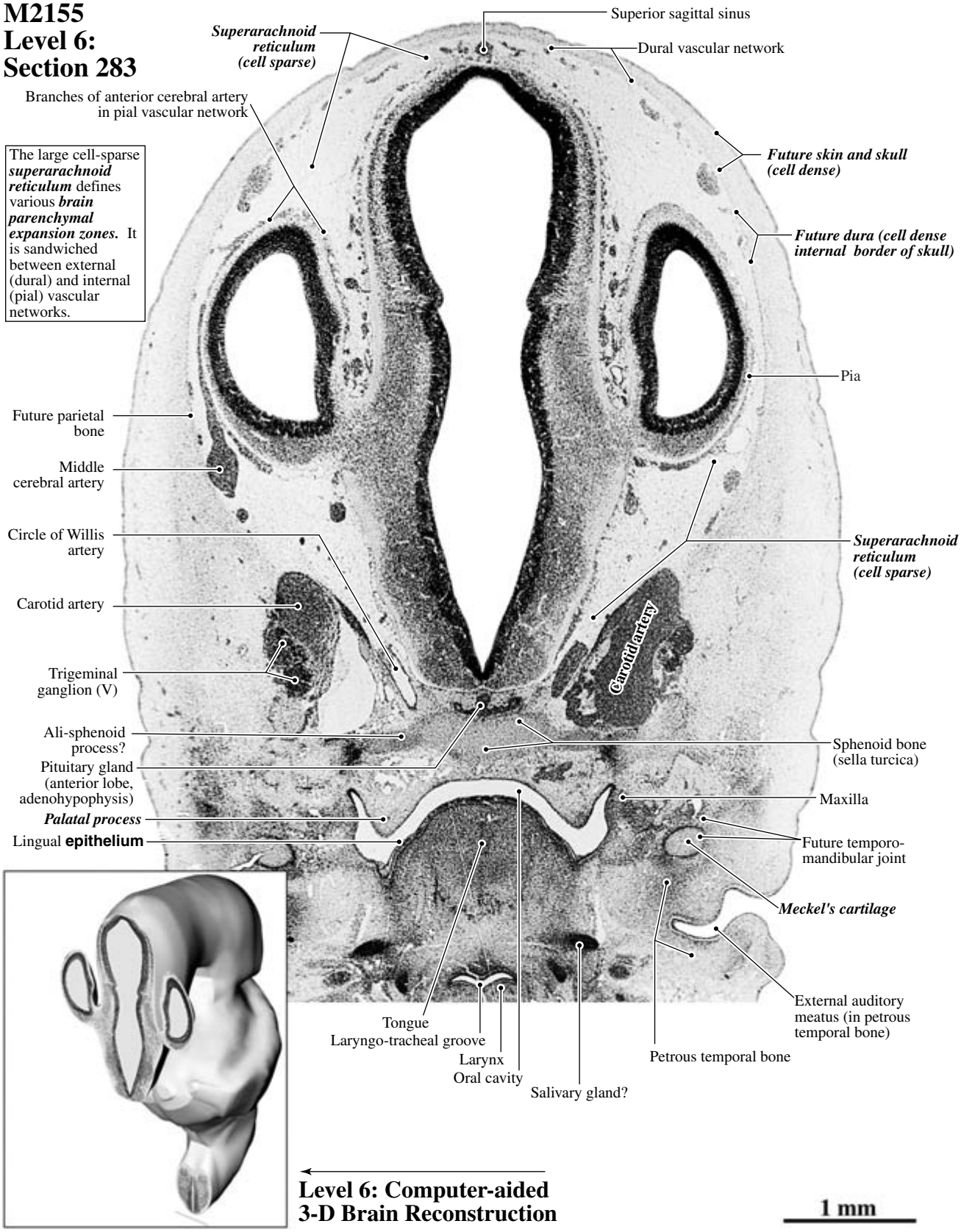
**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 6A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 6:
## Section 283

## Peripheral neural and non-neural structures labeled

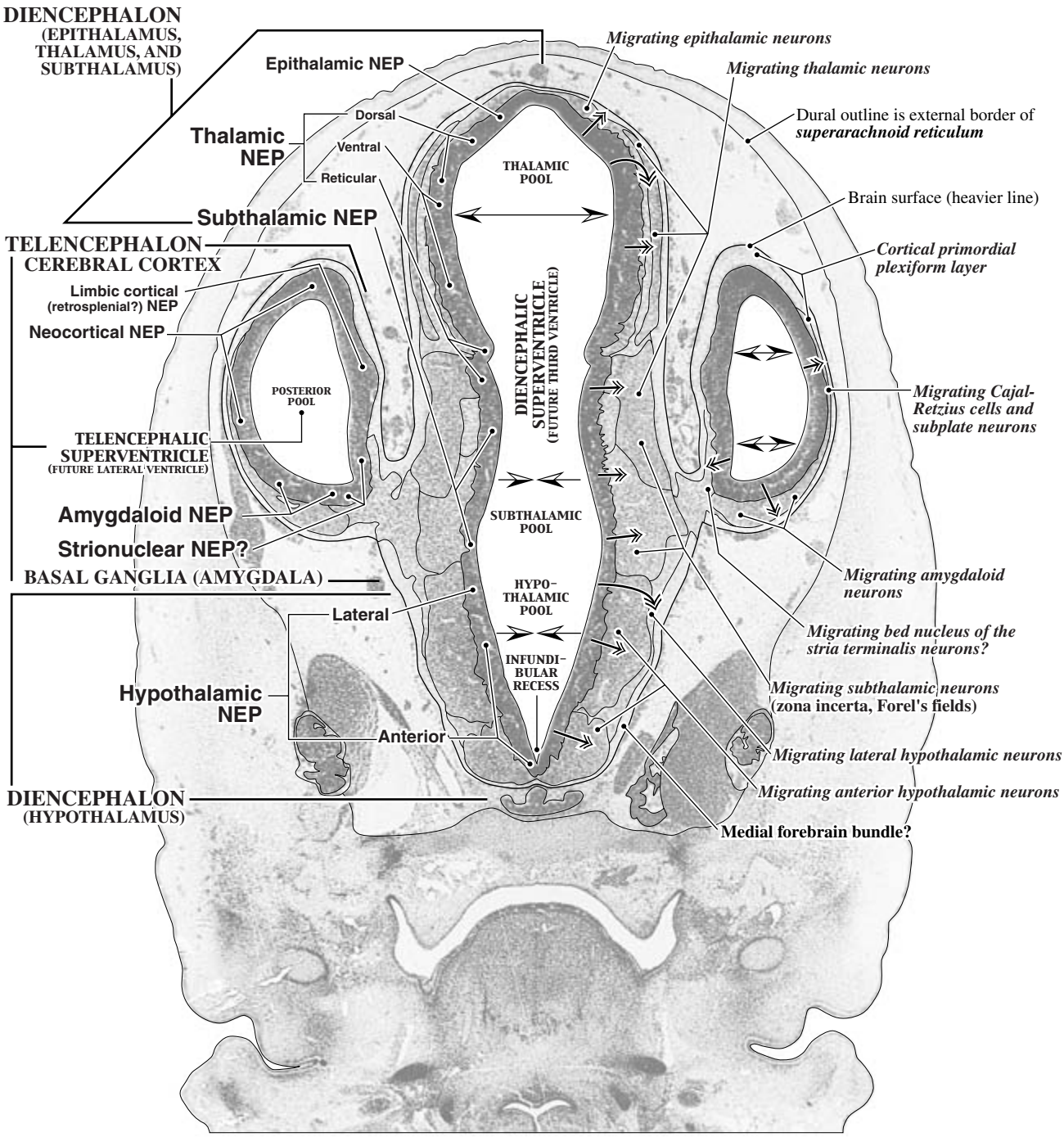


# PLATE 6B

## NEP - Neuroepithelium

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

## Central neural structures labeled




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

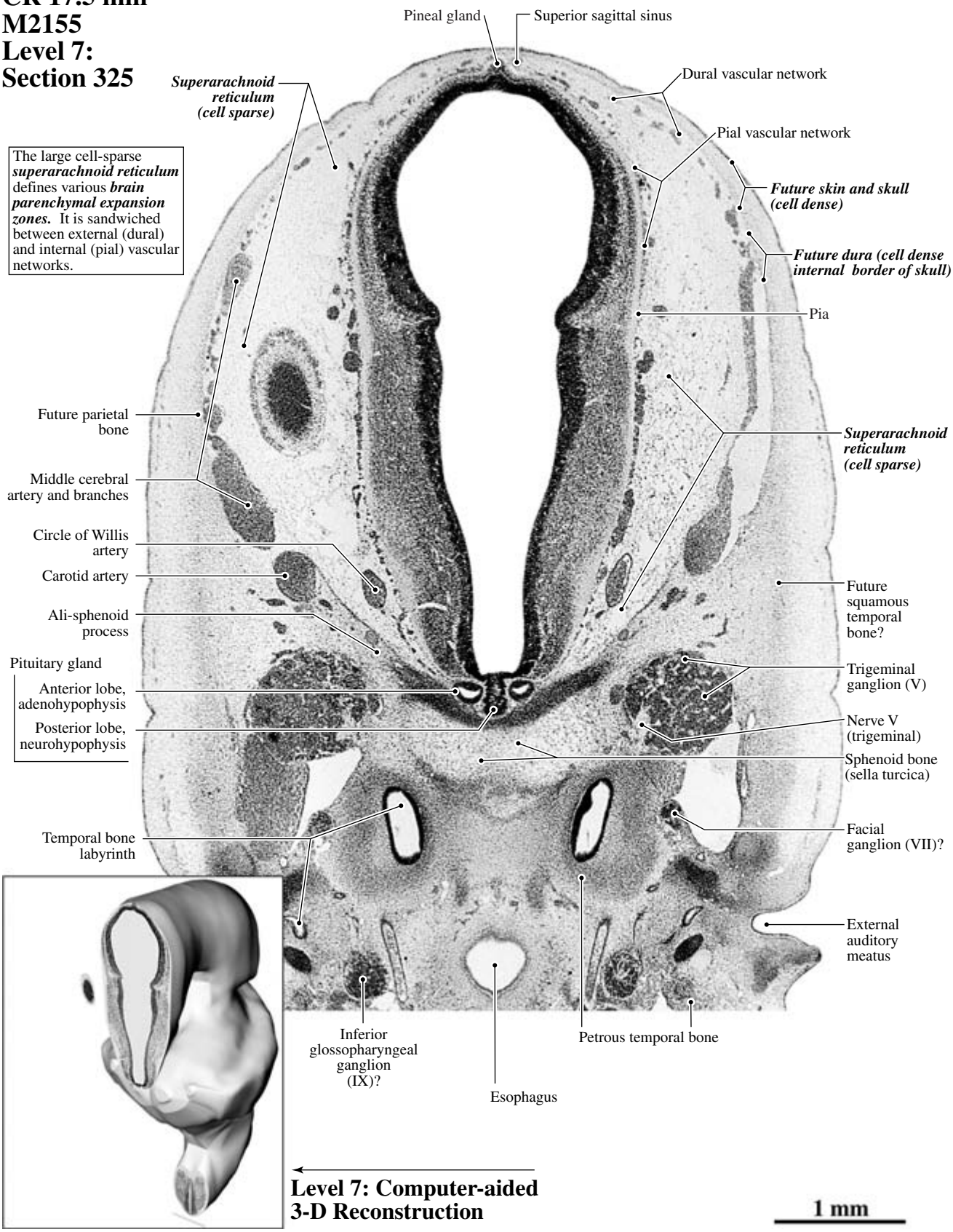
**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 7A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 7:
## Section 325

## Peripheral neural and non-neural structures labeled



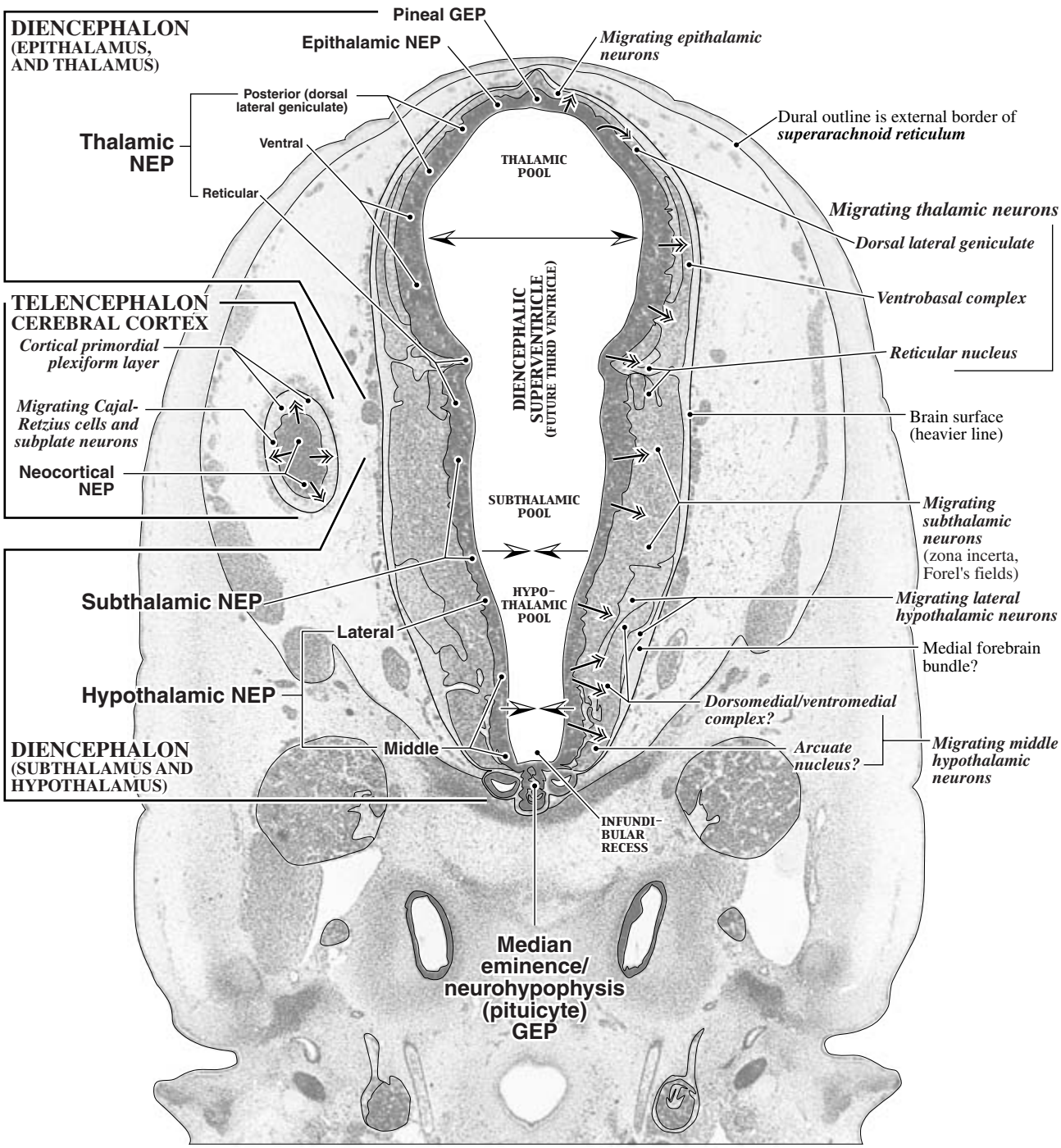

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

# PLATE 7B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**ABBREVIATIONS:**
**GEP - Glioepithelium**
**NEP - Neuroepithelium**

## Central neural structures labeled




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

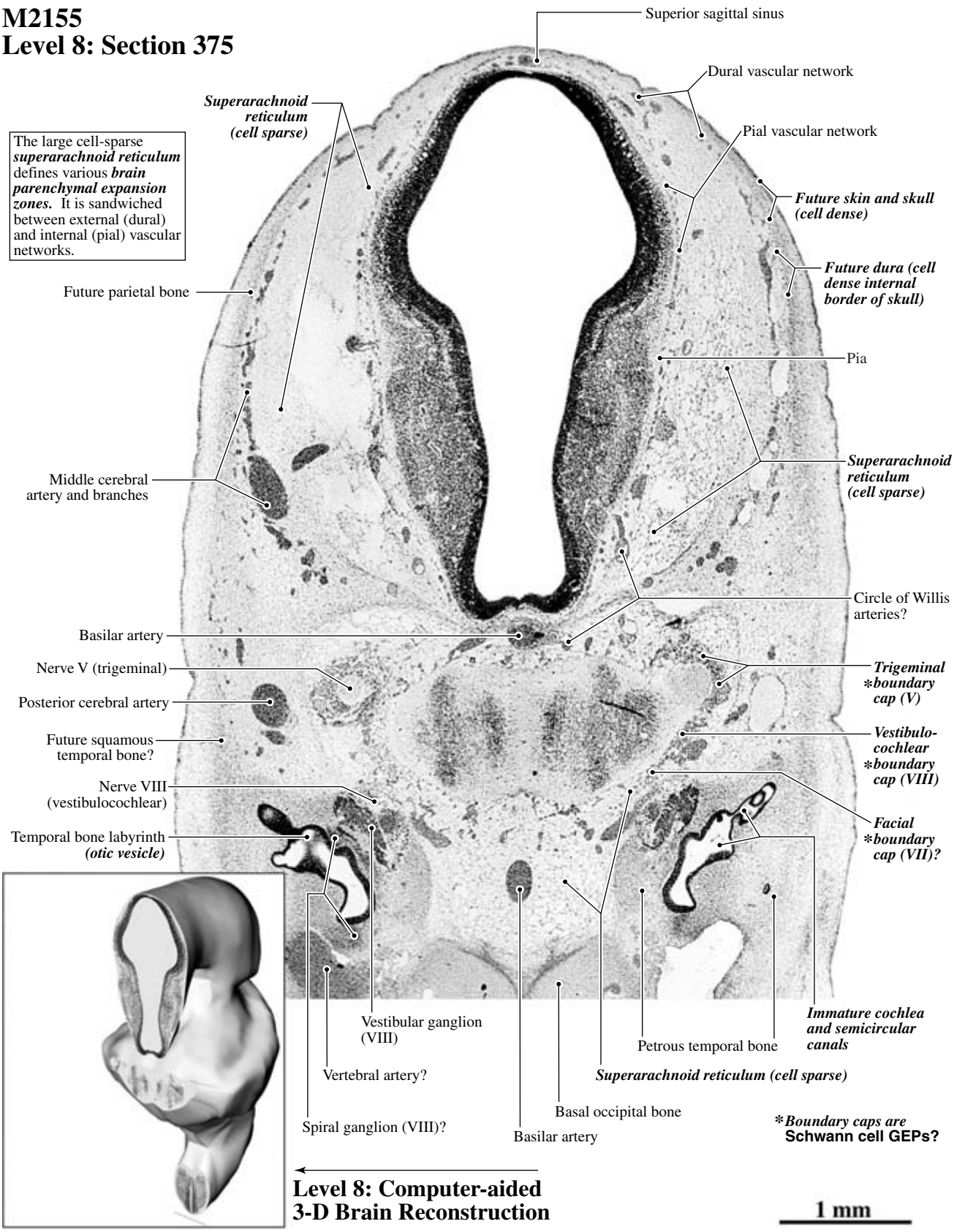
**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 8A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 8: Section 375

**Peripheral neural and non-neural structures labeled**

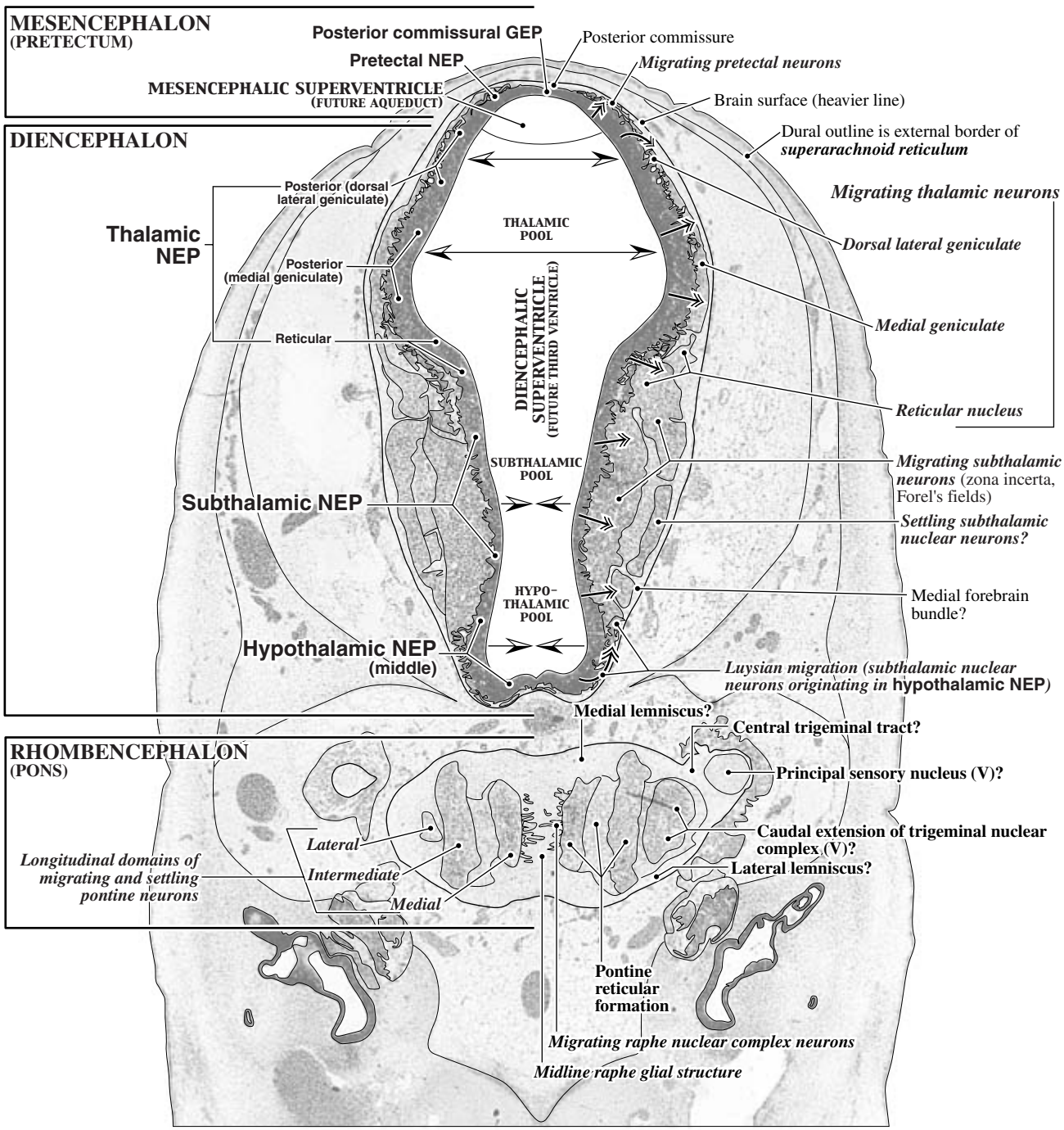


# PLATE 8B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

## Central neural structures labeled

**ABBREVIATIONS:**
**GEP - Glioepithelium**
**NEP - Neuroepithelium**




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

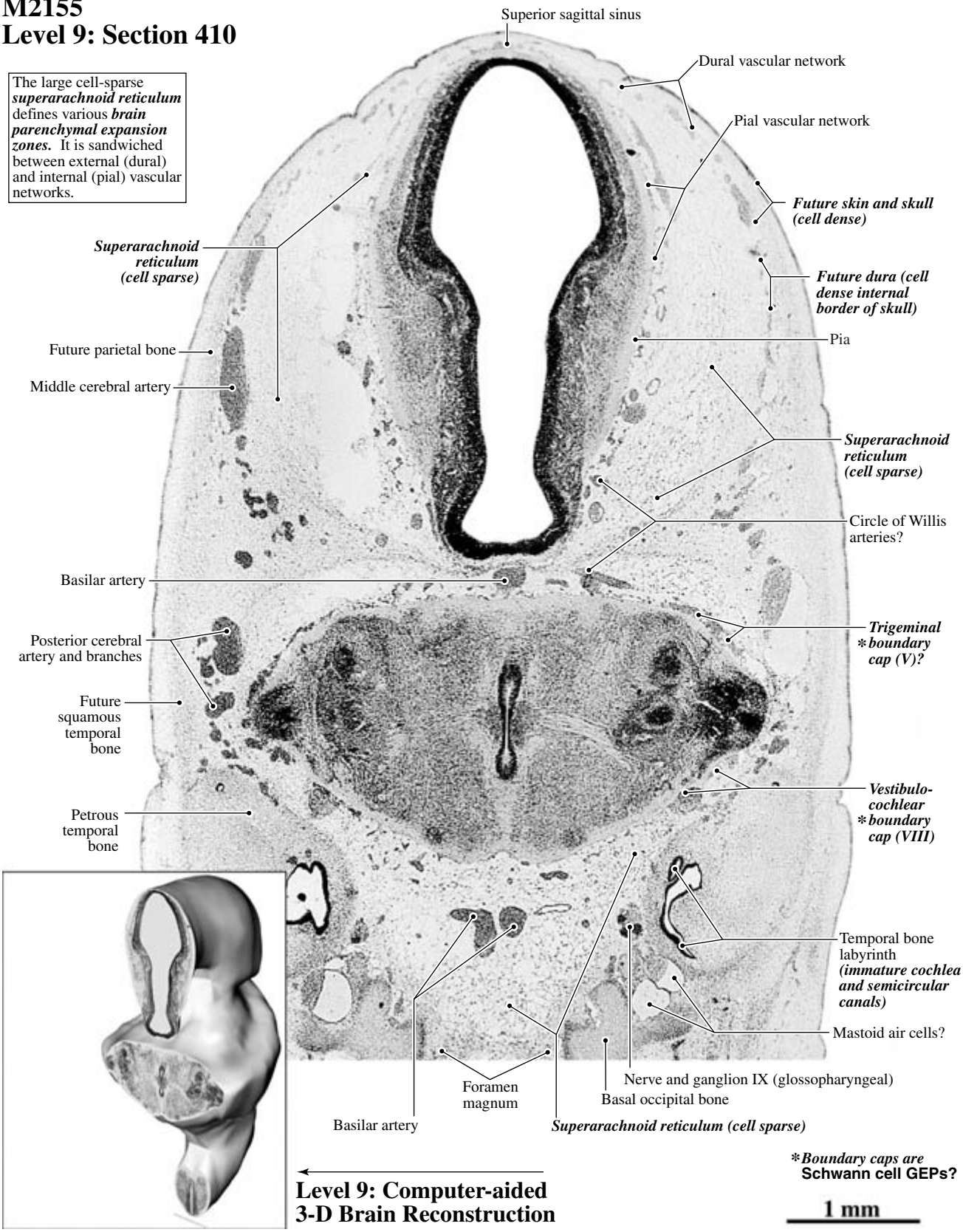
# PLATE 9A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 9: Section 410

**See a high magnification view of the mesencephalon and diencephalon from Section 390 in Plates 20A and B.**

**Peripheral neural and non-neural structures labeled**

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.




**Level 9: Computer-aided 3-D Brain Reconstruction**

***Boundary caps are Schwann cell GEPs?**

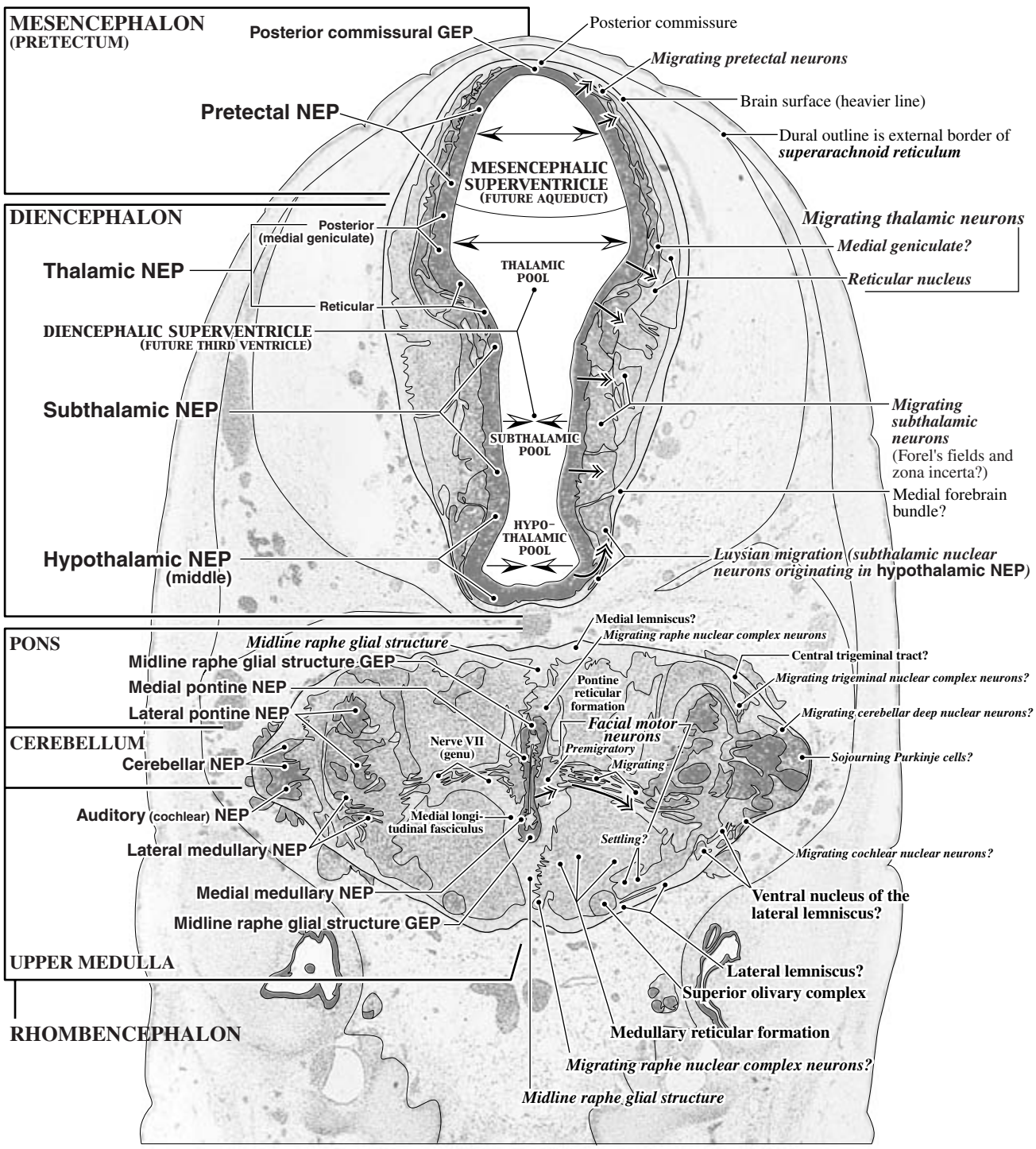
1 mm

# PLATE 9B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**ABBREVIATIONS:**
**GEP - Glioepithelium**
**NEP - Neuroepithelium**

## Central neural structures labeled




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

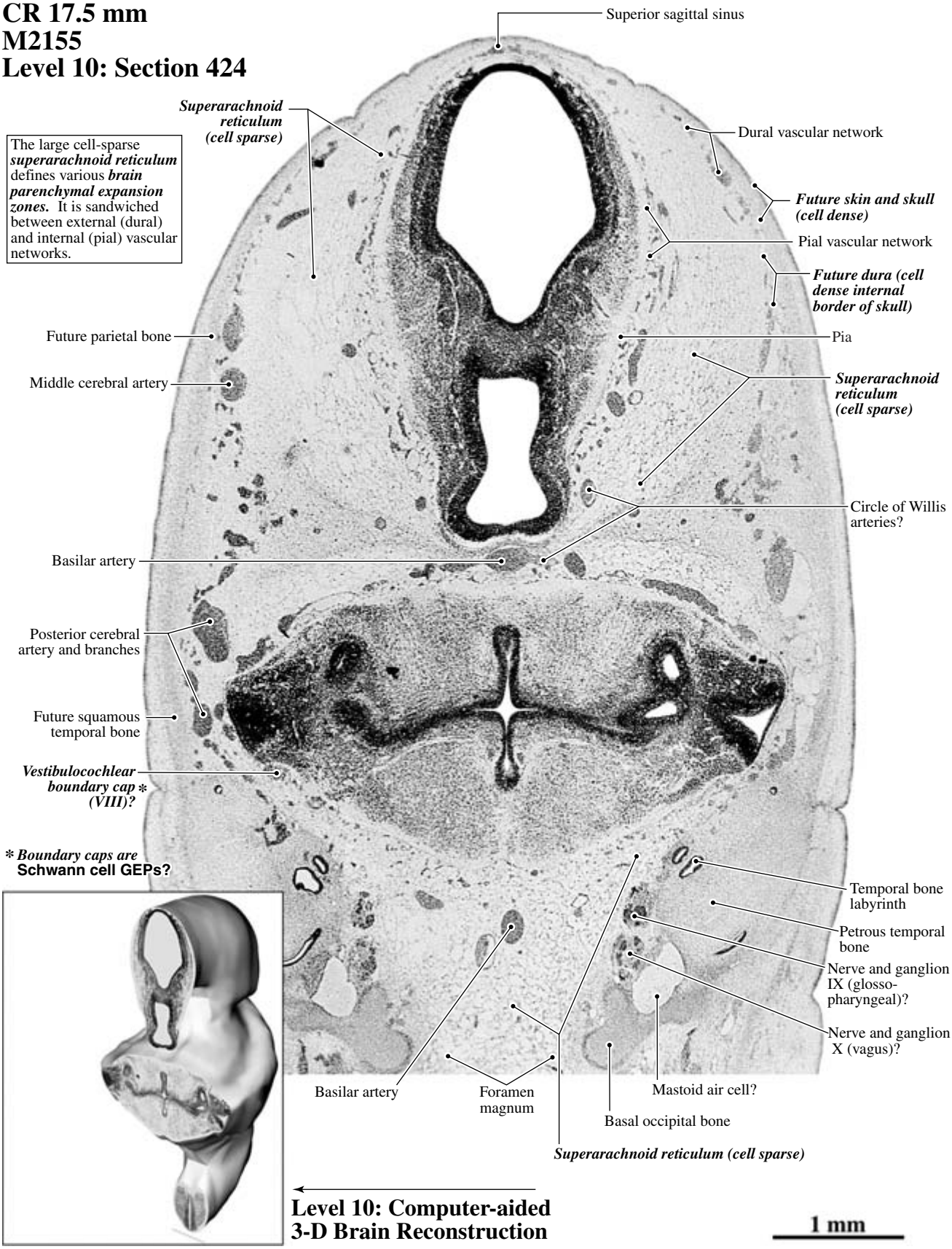
**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 10A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 10: Section 424

**Peripheral neural and non-neural structures labeled**

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.




**Level 10: Computer-aided 3-D Brain Reconstruction**

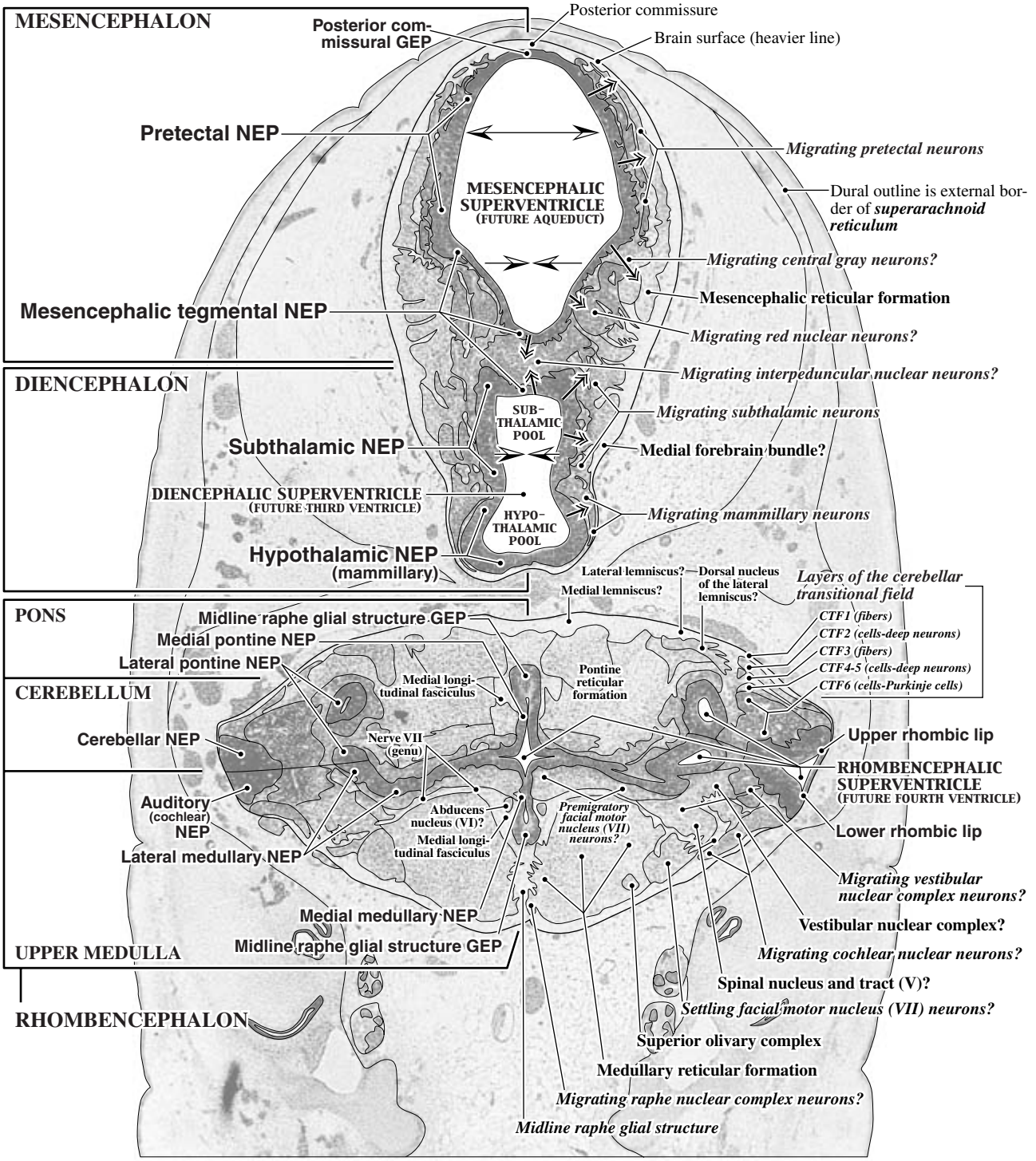
**1 mm**

# PLATE 10B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

## Central neural structures labeled

**ABBREVIATIONS:**
***CTF - Cerebellar transitional field***
**GEP - Glioepithelium**
**NEP - Neuroepithelium**




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

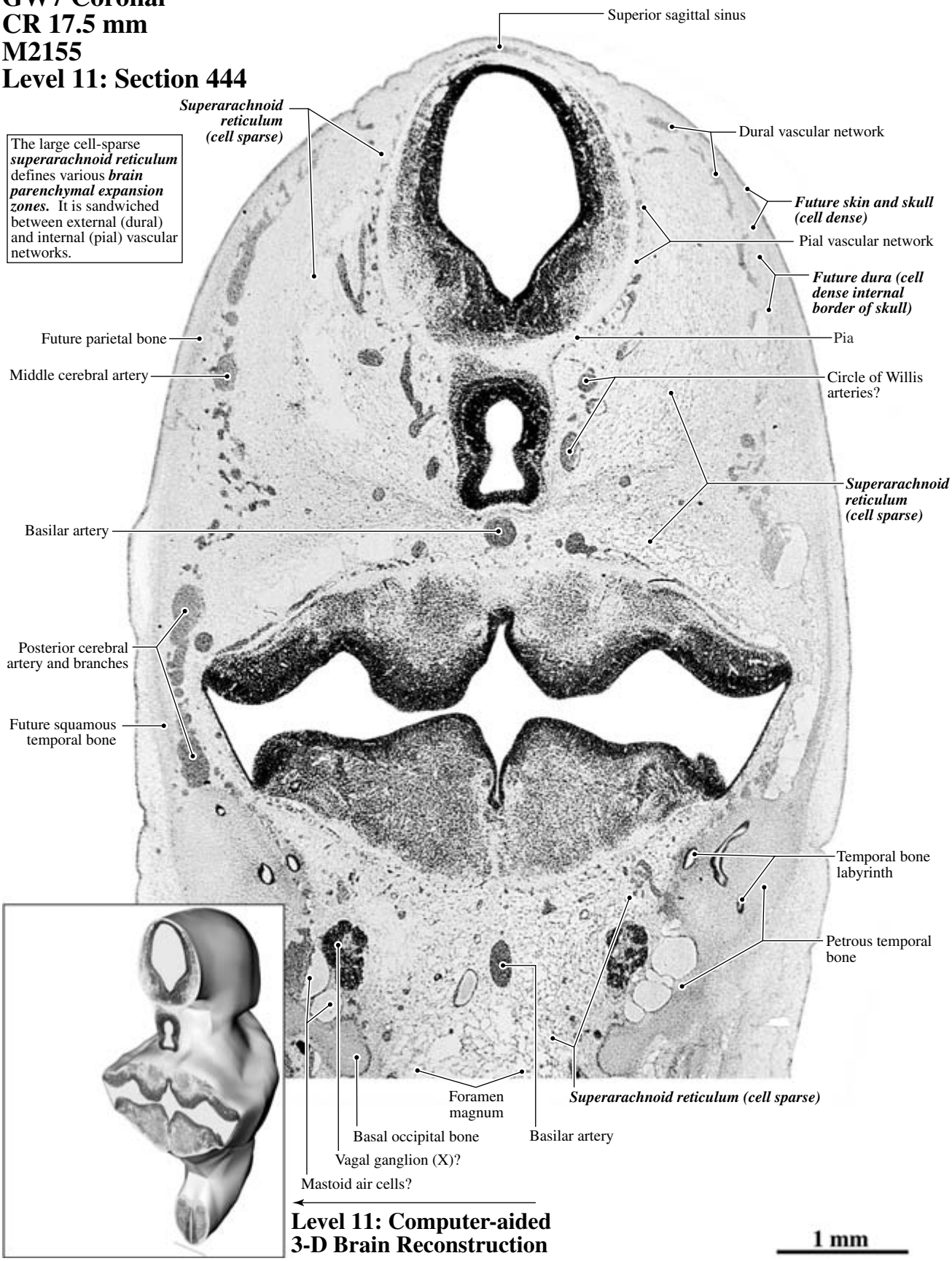
**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 11A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 11: Section 444

**Peripheral neural and non-neural structures labeled**

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

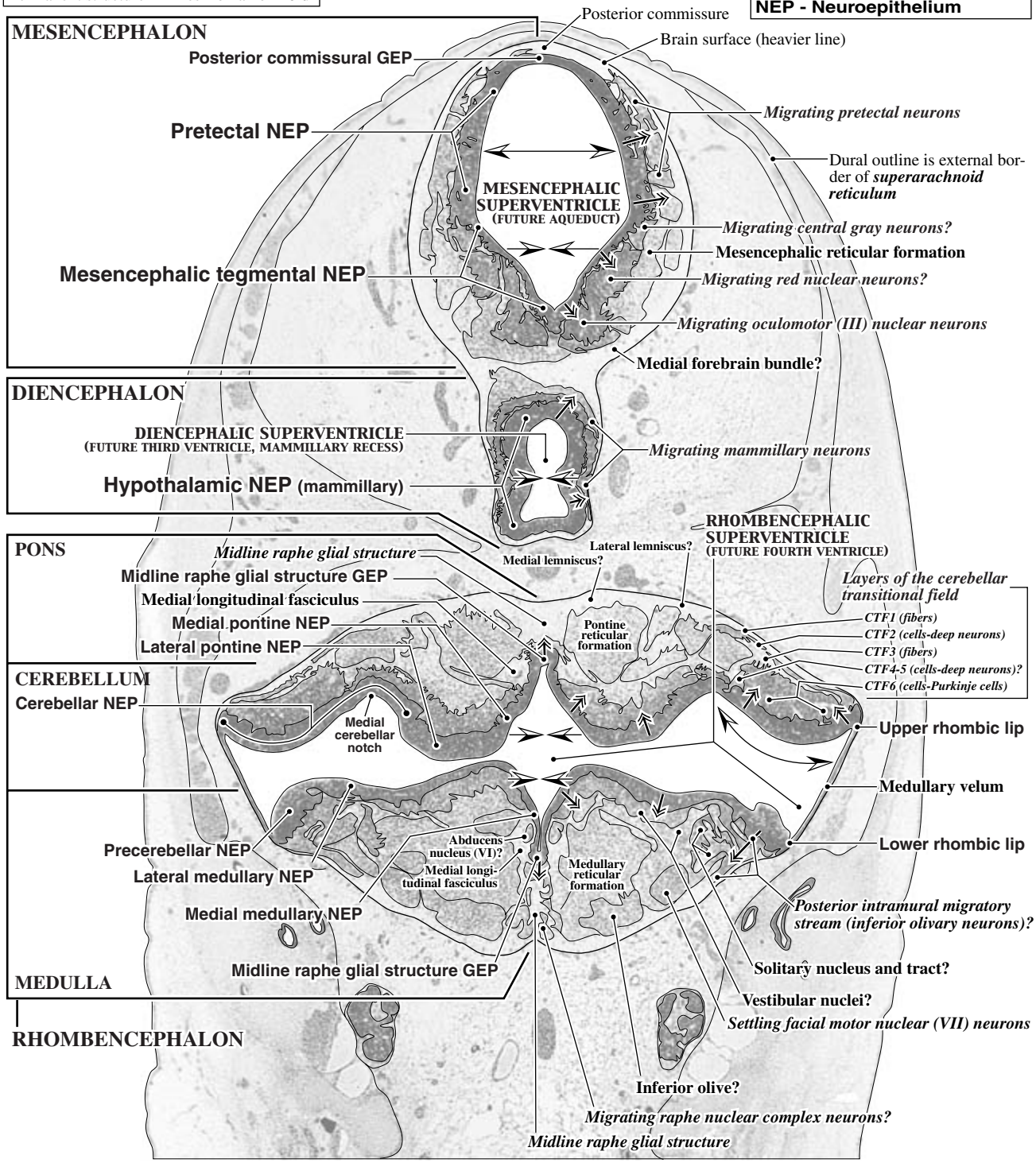


# PLATE 11B

## Central neural structures labeled

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

**ABBREVIATIONS:**
***CTF - Cerebellar transitional field***
**GEP - Glioepithelium**
**NEP - Neuroepithelium**




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

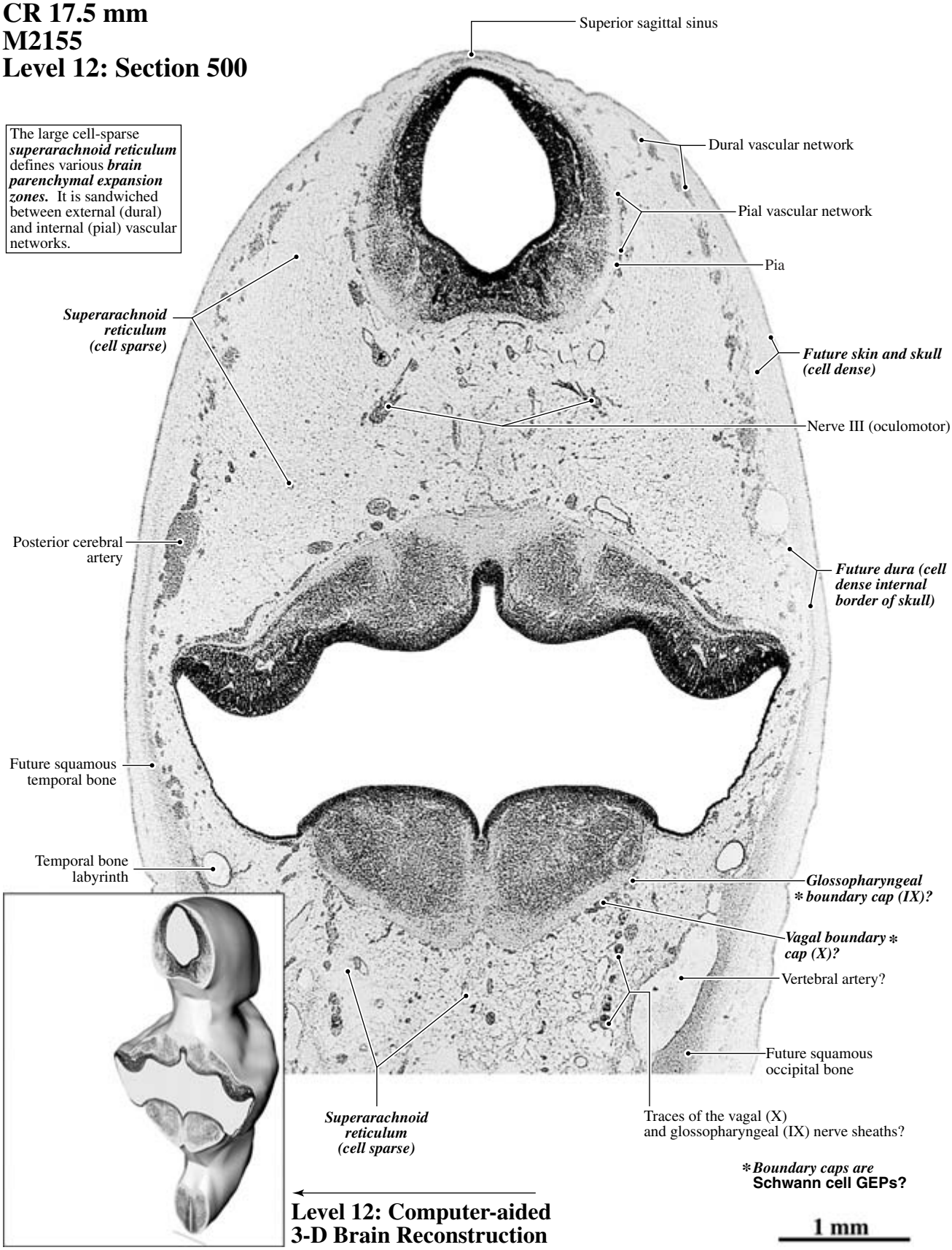
**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 12A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 12: Section 500

**Peripheral neural and non-neural structures labeled**

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.



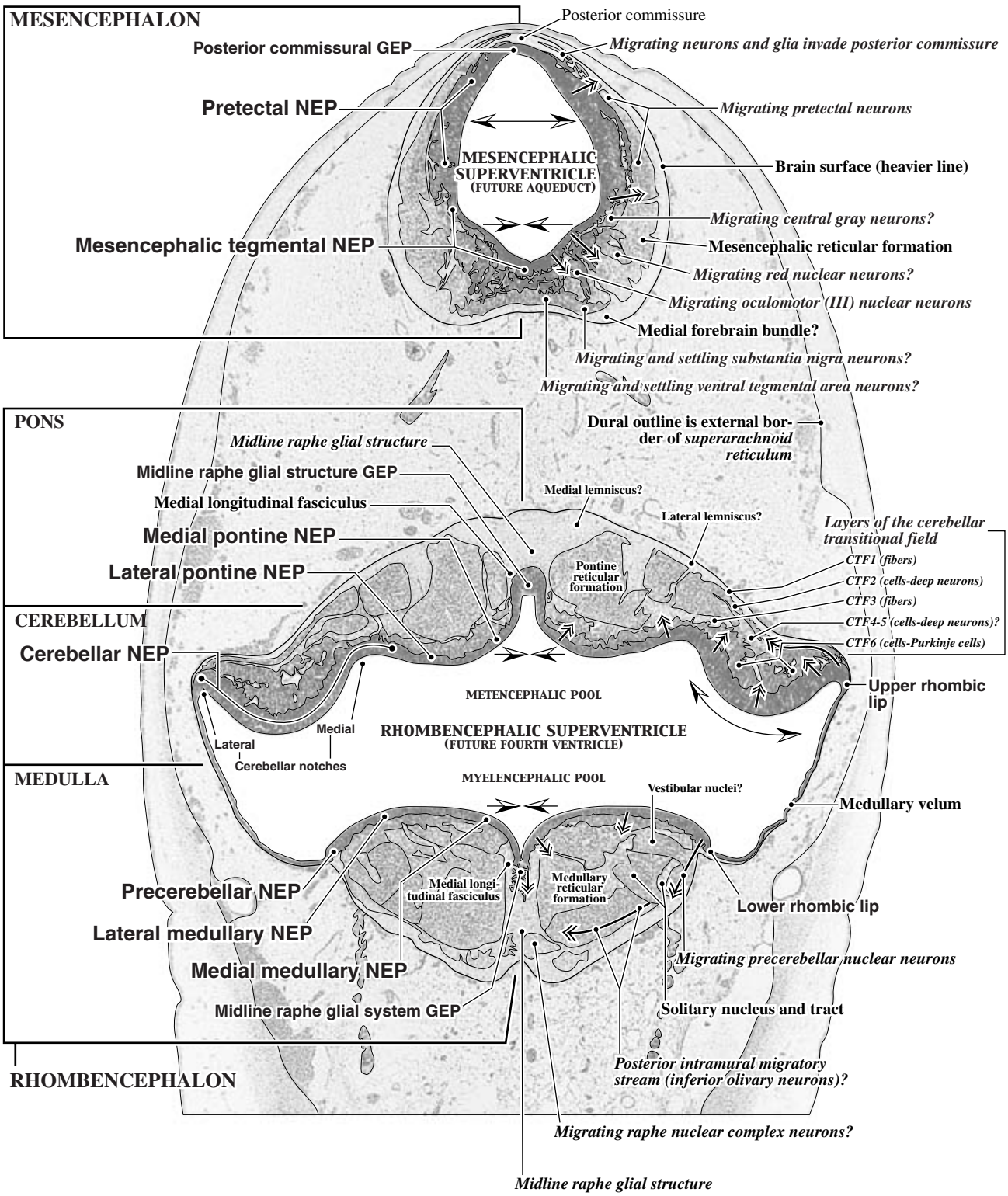

**Level 12: Computer-aided 3-D Brain Reconstruction**

# PLATE 12B

**FONT KEY:**
**VENTRICULAR DIVISIONS – CAPITALS**
**Germinal zone - Helvetica bold**
***Transient structure - Times bold italic***
Permanent structure - Times Roman or **Bold**

## Central neural structures labeled

**ABBREVIATIONS:**
***CTF - Cerebellar transitional field***
**GEP - Glioepithelium**
**NEP - Neuroepithelium**




**Arrows** indicate the presumed ***direction of neuron migration*** from neuroepithelial sources.

**Arrows** indicate the regionally ***expanding shoreline*** of the superventricle with increase in stockbuilding NEP cells.

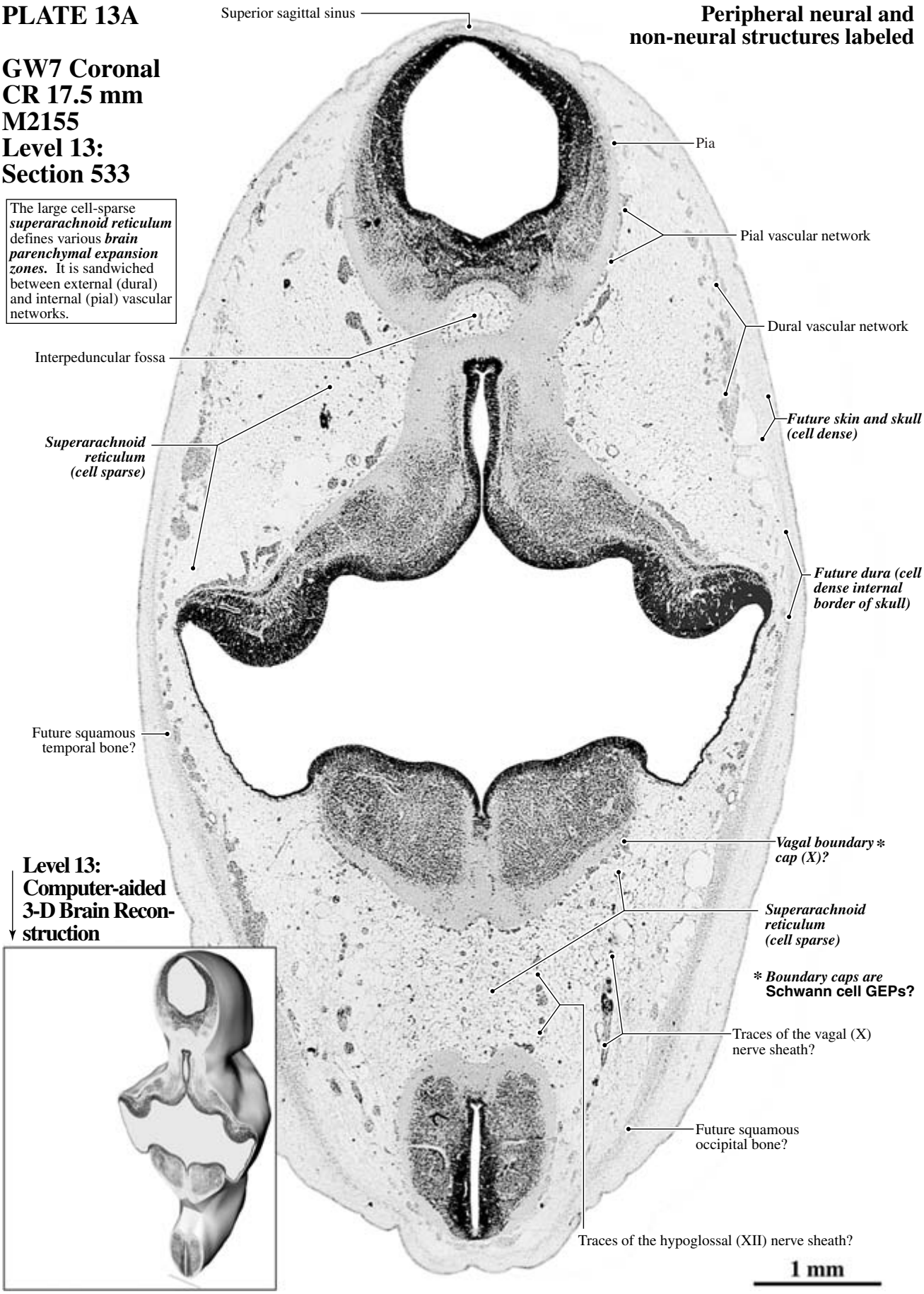
**Arrows** indicate the regionally ***shrinking shoreline*** of the superventricle as NEP cells are depleted while generating neurons.

# PLATE 13A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 13:
## Section 533

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

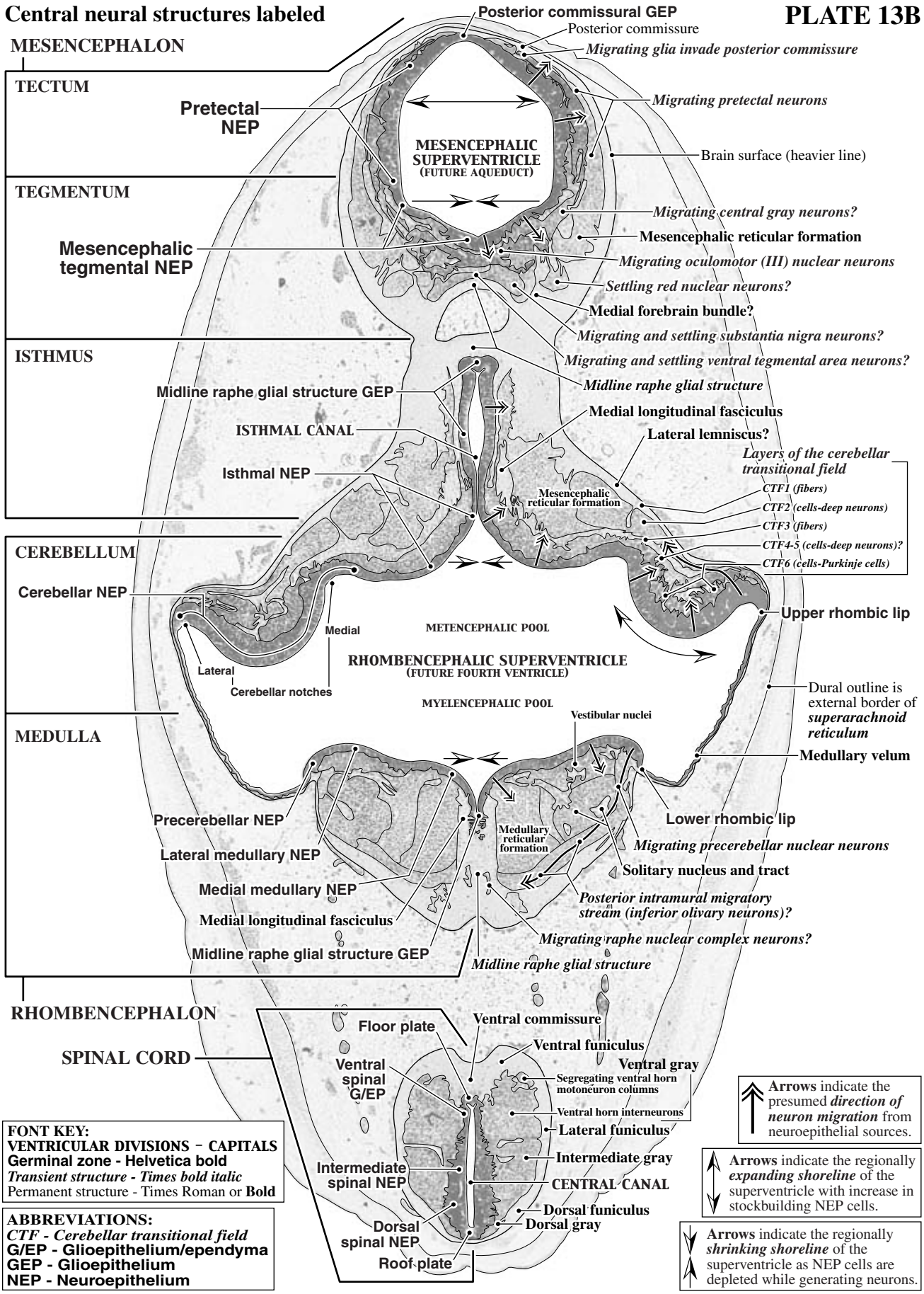
**Peripheral neural and non-neural structures labeled**




**Level 13: Computer-aided 3-D Brain Reconstruction**

# Central neural structures labeled

# PLATE 13B

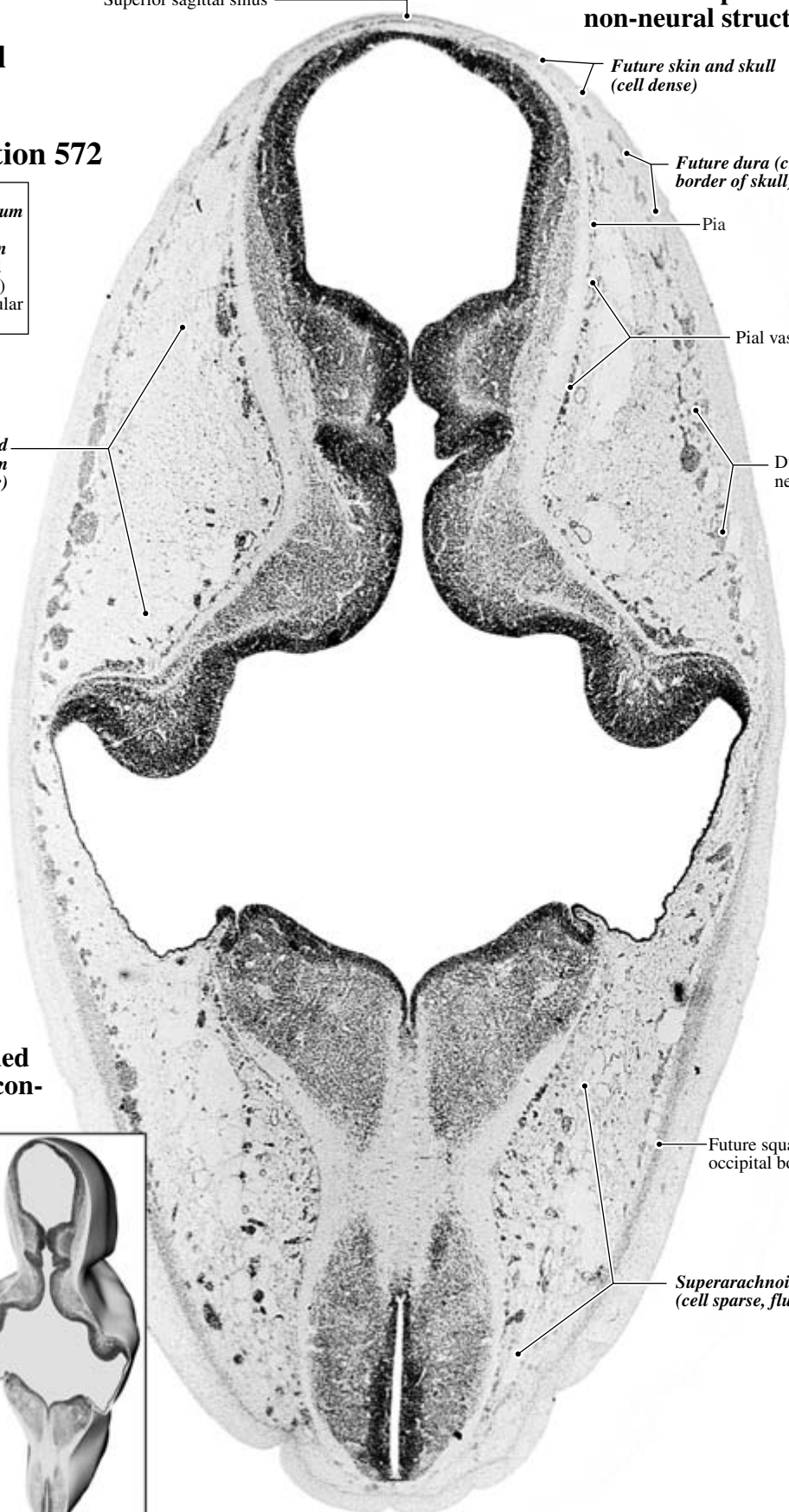


# PLATE 14A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 14: Section 572

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

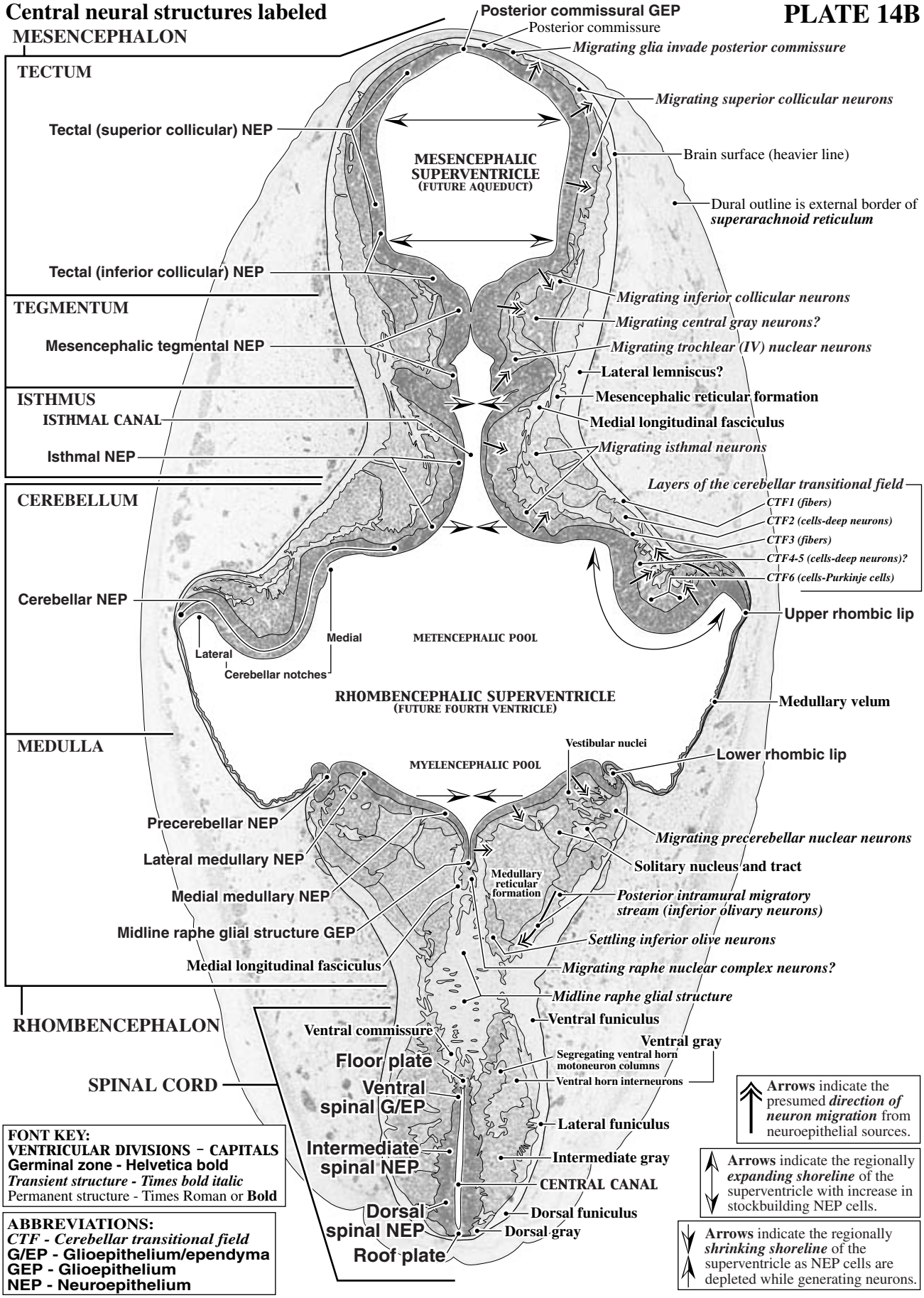
**Peripheral neural and non-neural structures labeled**




**Level 14: Computer-aided 3-D Brain Reconstruction**

# Central neural structures labeled

# PLATE 14B

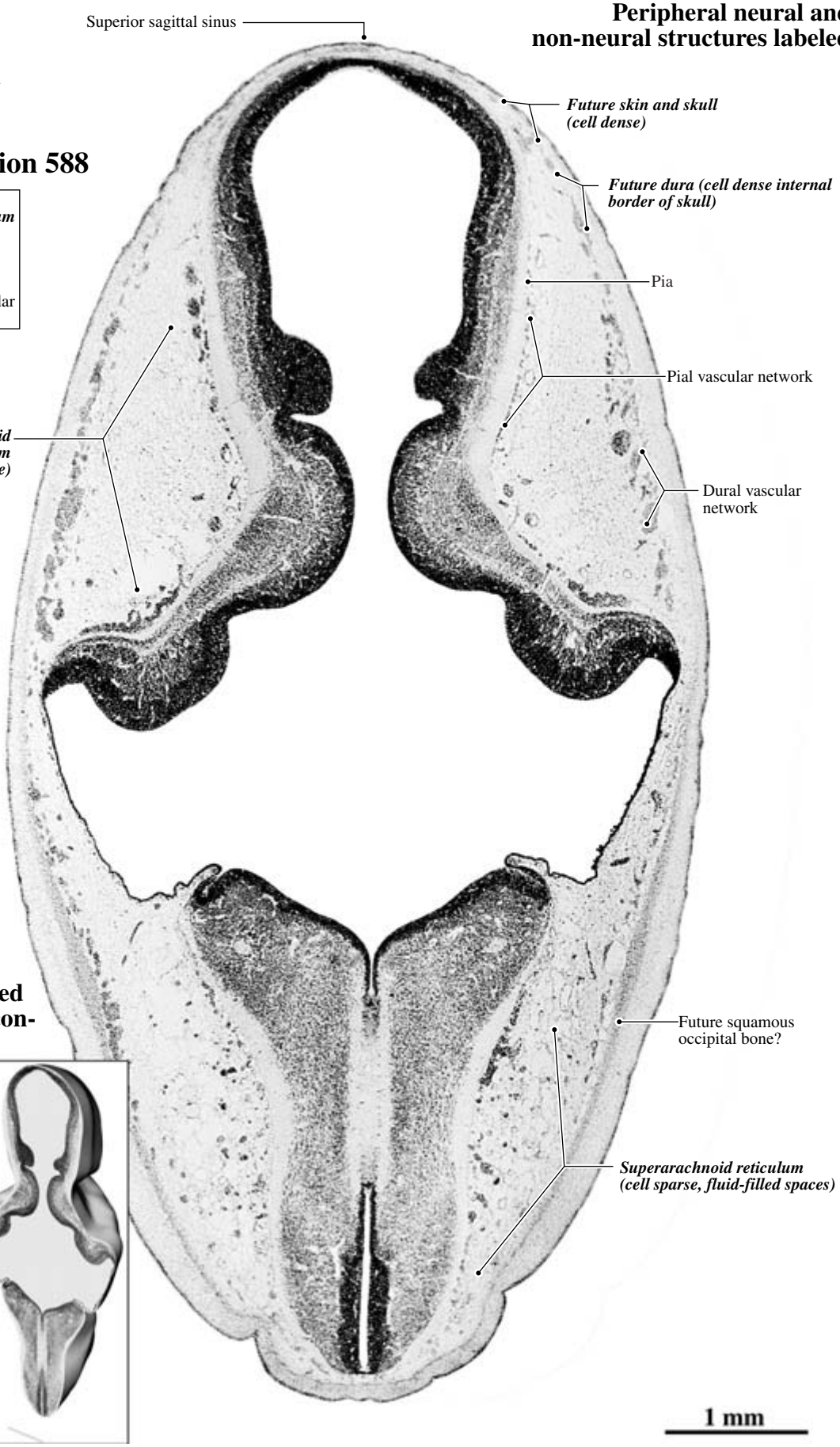


# PLATE 15A

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 15: Section 588

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

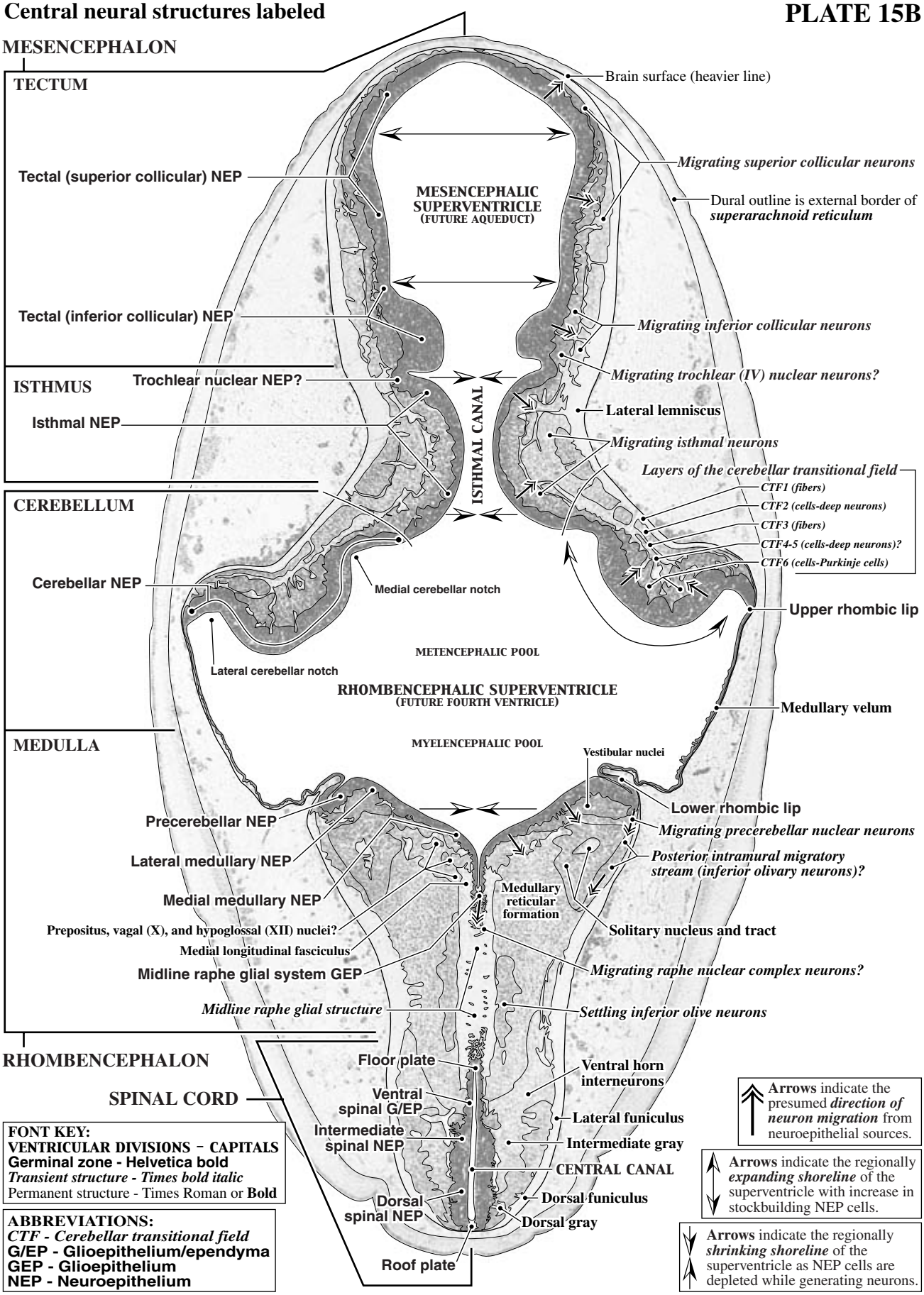
**Peripheral neural and non-neural structures labeled**




**Level 15: Computer-aided 3-D Brain Reconstruction**

## Central neural structures labeled

## PLATE 15B

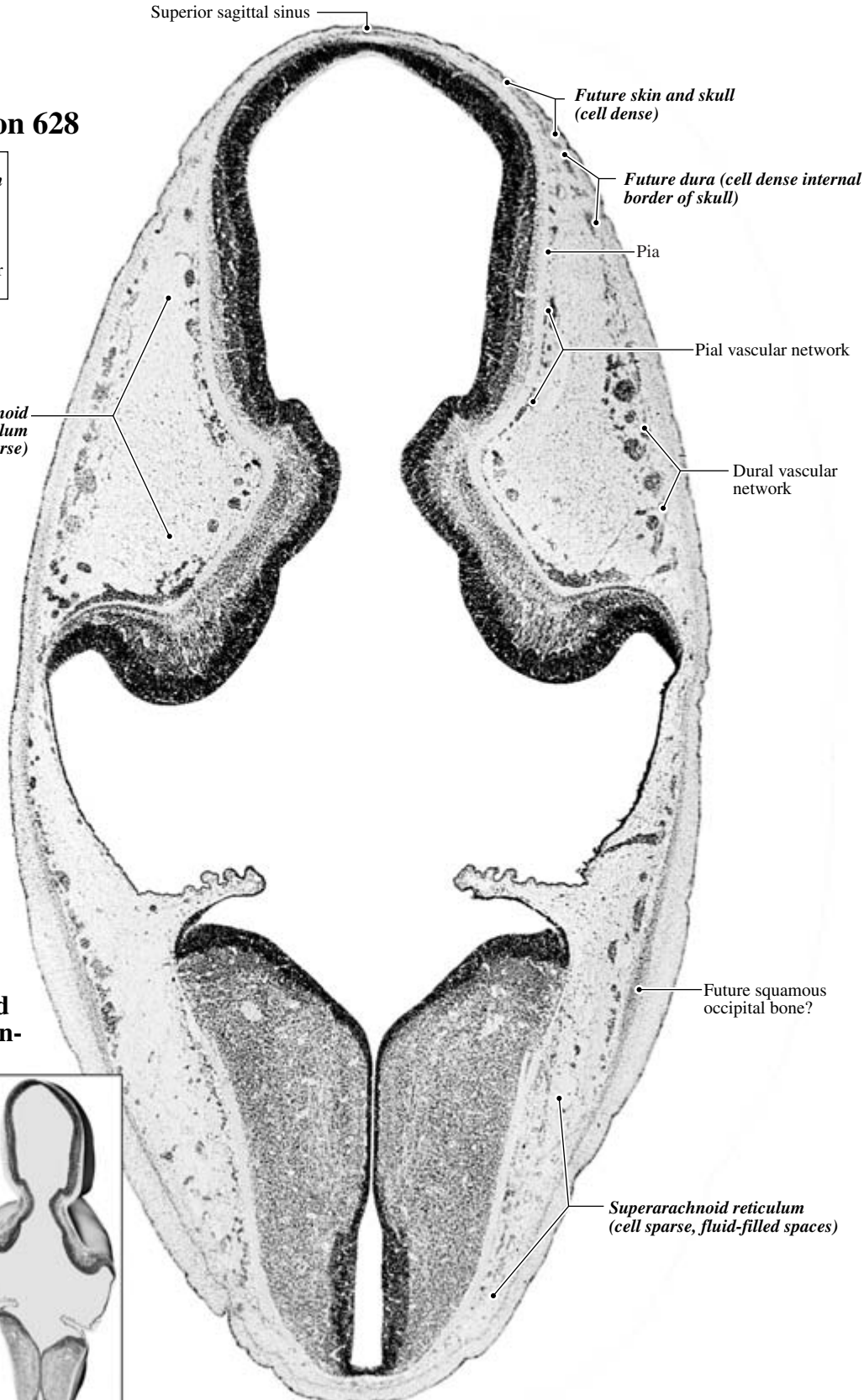


# PLATE 16A

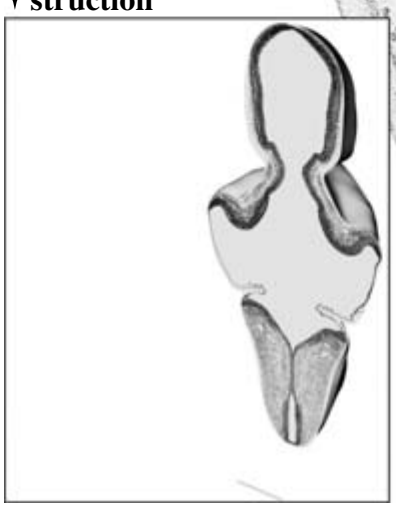
## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 16: Section 628

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.

**Peripheral neural and non-neural structures labeled**

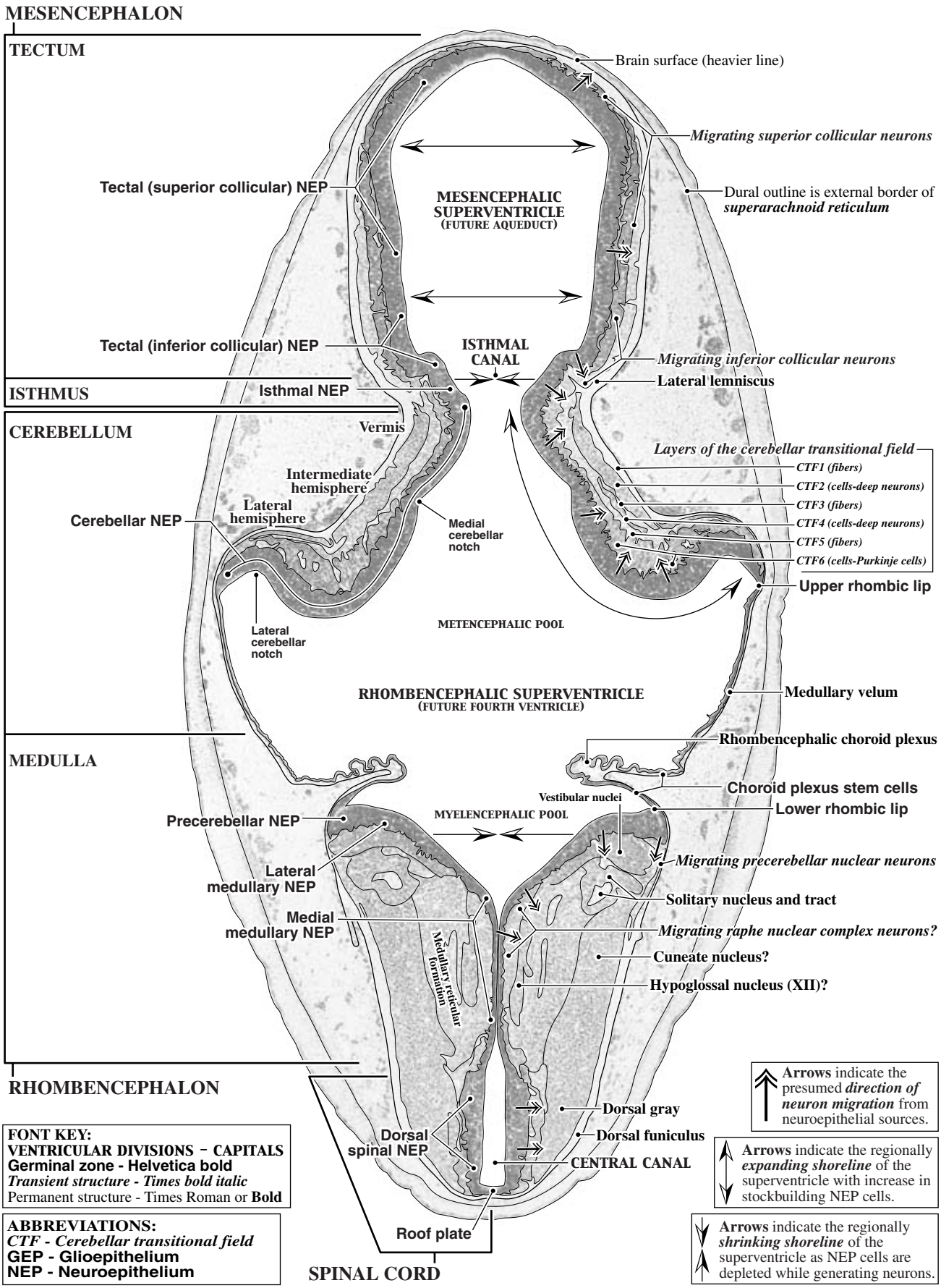



**Level 16: Computer-aided 3-D Brain Reconstruction**



## Central neural structures labeled

# PLATE 16B

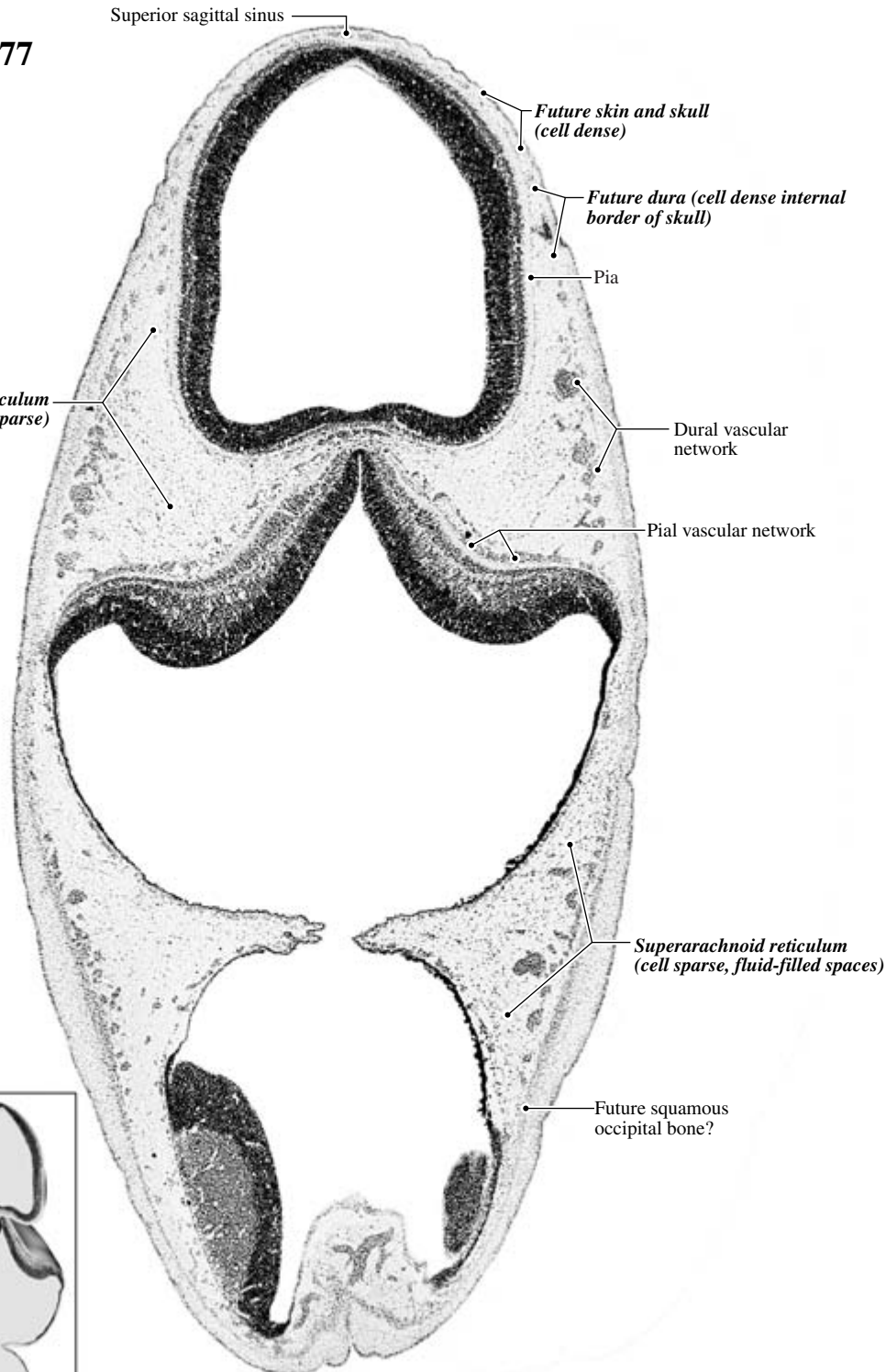


# PLATE 17A

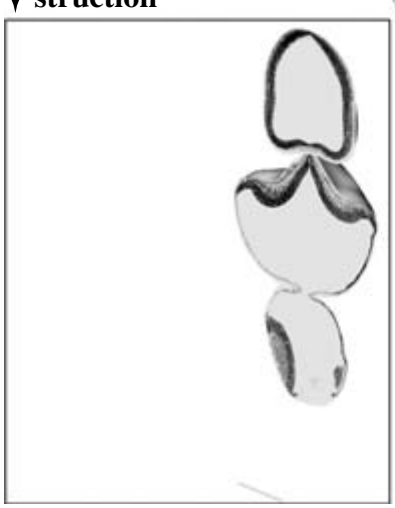
**Peripheral neural and non-neural structures labeled**

## GW7 Coronal
## CR 17.5 mm
## M2155
## Level 17: Section 677

The large cell-sparse ***superarachnoid reticulum*** defines various ***brain parenchymal expansion zones.*** It is sandwiched between external (dural) and internal (pial) vascular networks.




**Level 17: Computer-aided 3-D Brain Reconstruction**



## Central neural structures labeled

# PLATE 17B

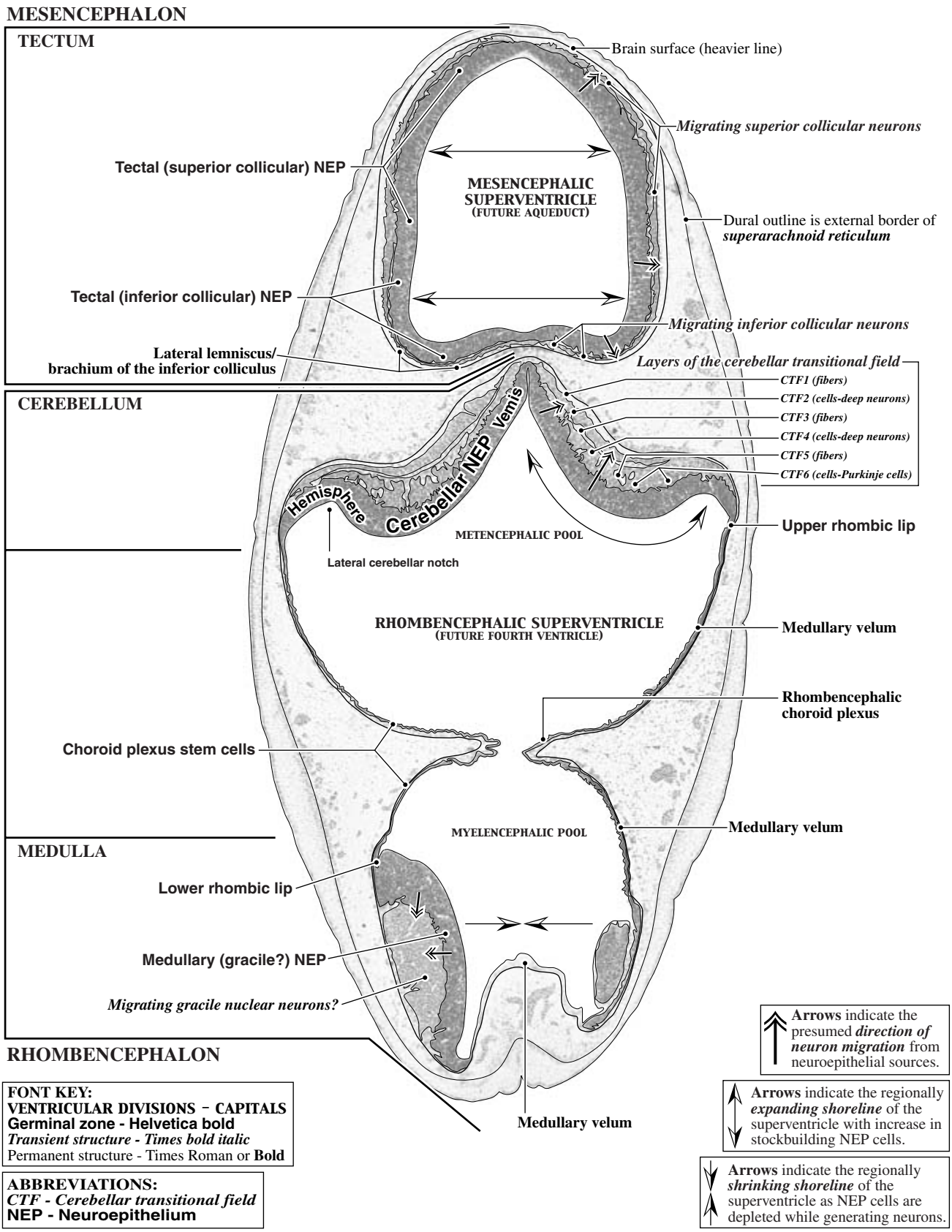
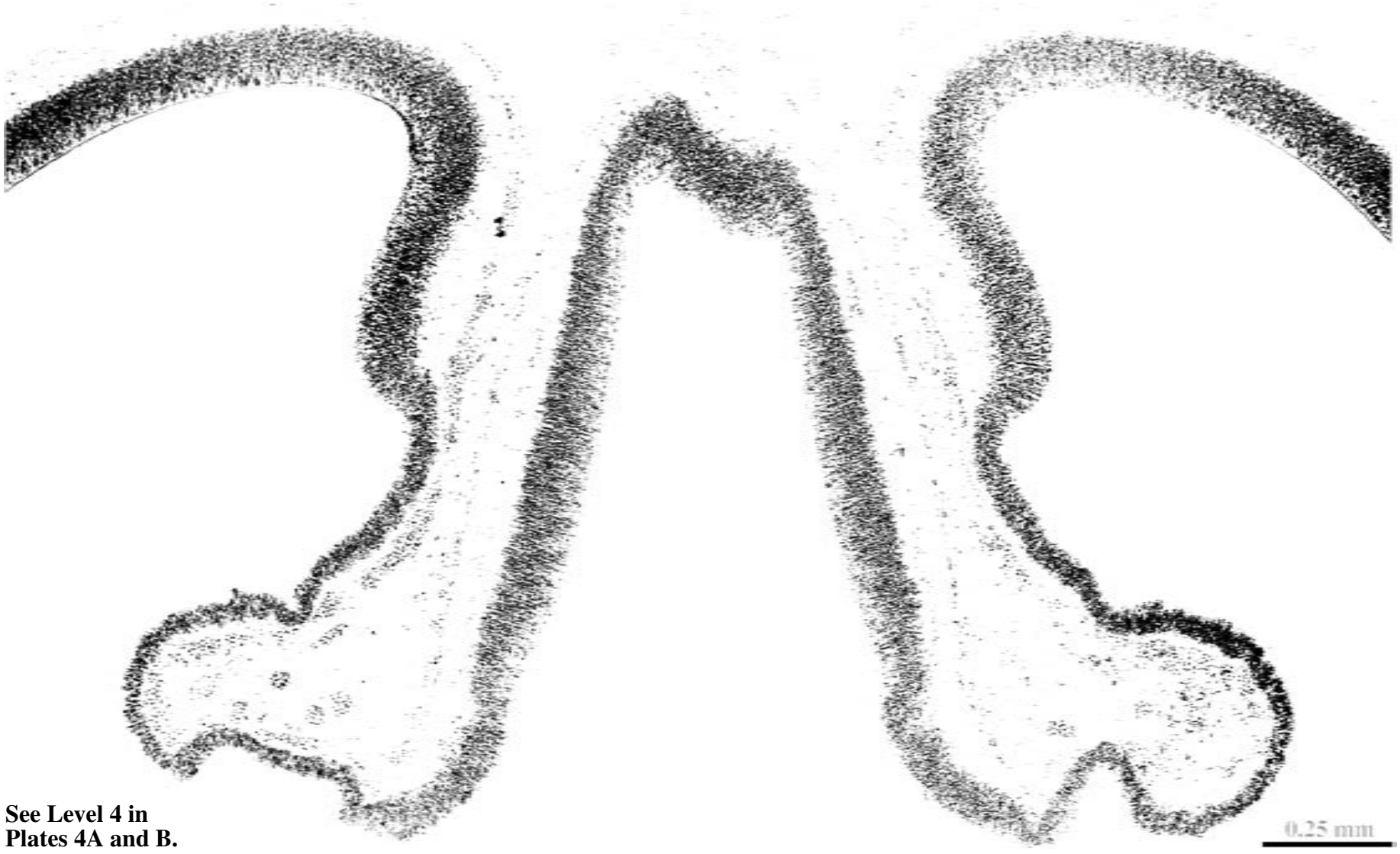


**PLATE 18A**



**GW7 Coronal, CR 17.5 mm, M2155**
**Near Level 4: Section 203**




**See Level 4 in**
**Plates 4A and B.**

# PLATE 18B

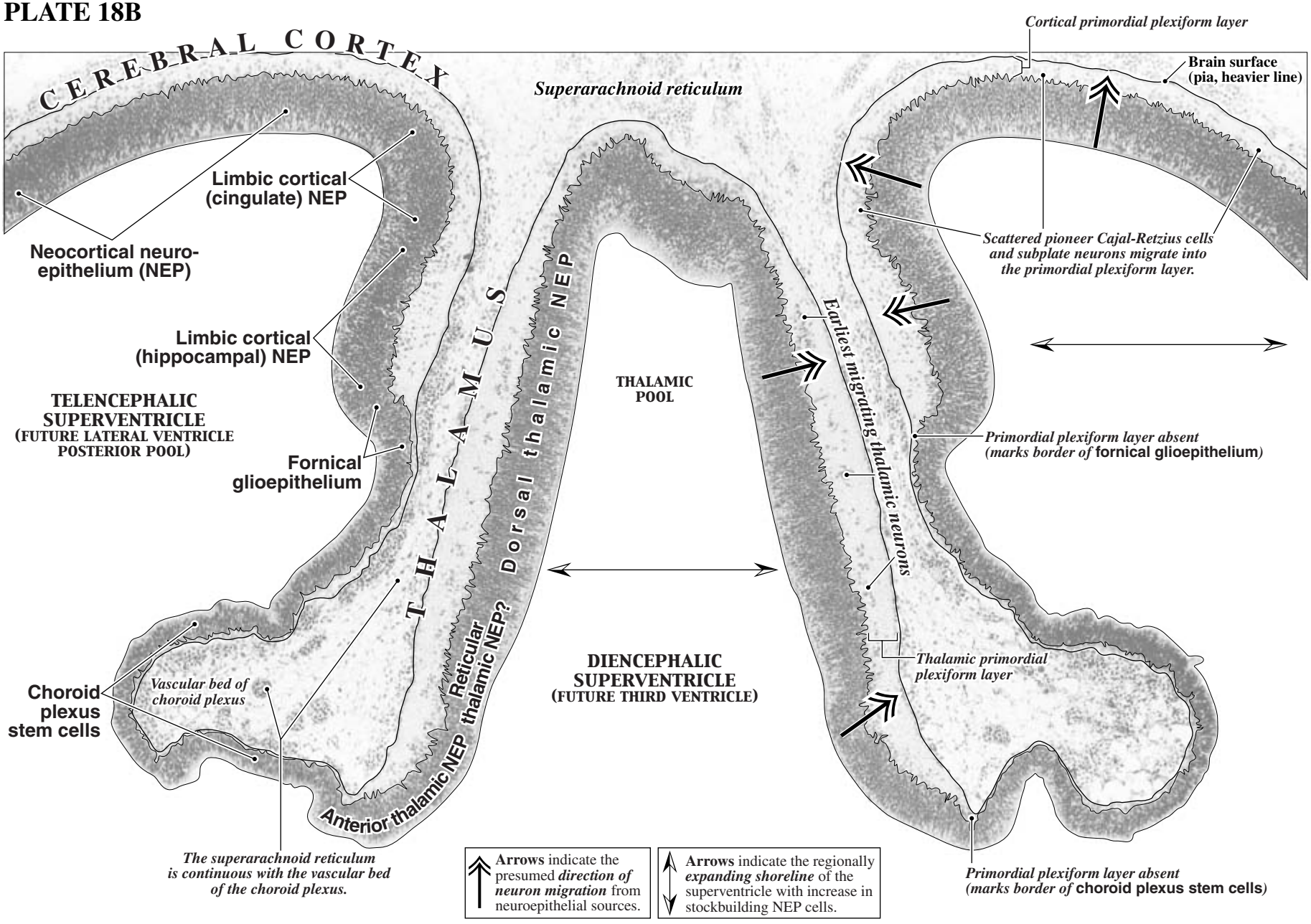
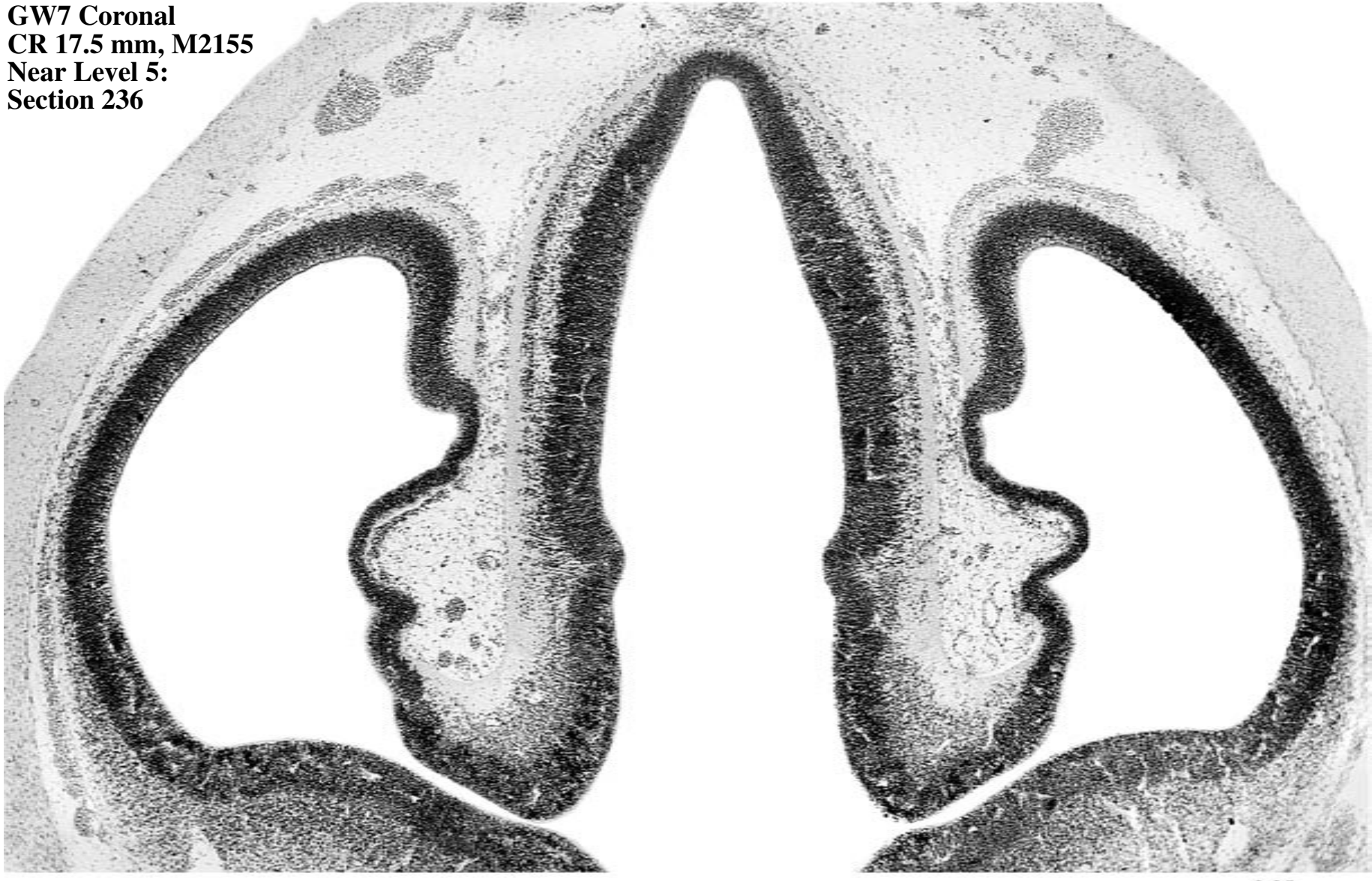

CEREBRAL CORTEX
Superarachnoid reticulum
Cortical primordial plexiform layer
Brain surface (pia, heavier line)
Limbic cortical (cingulate) NEP
Neocortical neuro-epithelium (NEP)
Scattered pioneer Cajal-Retzius cells and subplate neurons migrate into the primordial plexiform layer.
Limbic cortical (hippocampal) NEP
TELENCEPHALIC SUPERVENTRICLE (FUTURE LATERAL VENTRICLE POSTERIOR POOL)
Fornical glioepithelium
THALAMUS
Dorsal thalamic NEP
THALAMIC POOL
Earliest migrating thalamic neurons
Primordial plexiform layer absent (marks border of fornical glioepithelium)
Reticular thalamic NEP?
Anterior thalamic NEP
DIENCEPHALIC SUPERVENTRICLE (FUTURE THIRD VENTRICLE)
Thalamic primordial plexiform layer
Choroid plexus stem cells
Vascular bed of choroid plexus
The superarachnoid reticulum is continuous with the vascular bed of the choroid plexus.
Arrows indicate the presumed direction of neuron migration from neuroepithelial sources.
Arrows indicate the regionally expanding shoreline of the superventricle with increase in stockbuilding NEP cells.
Primordial plexiform layer absent (marks border of choroid plexus stem cells)

**PLATE 19A**

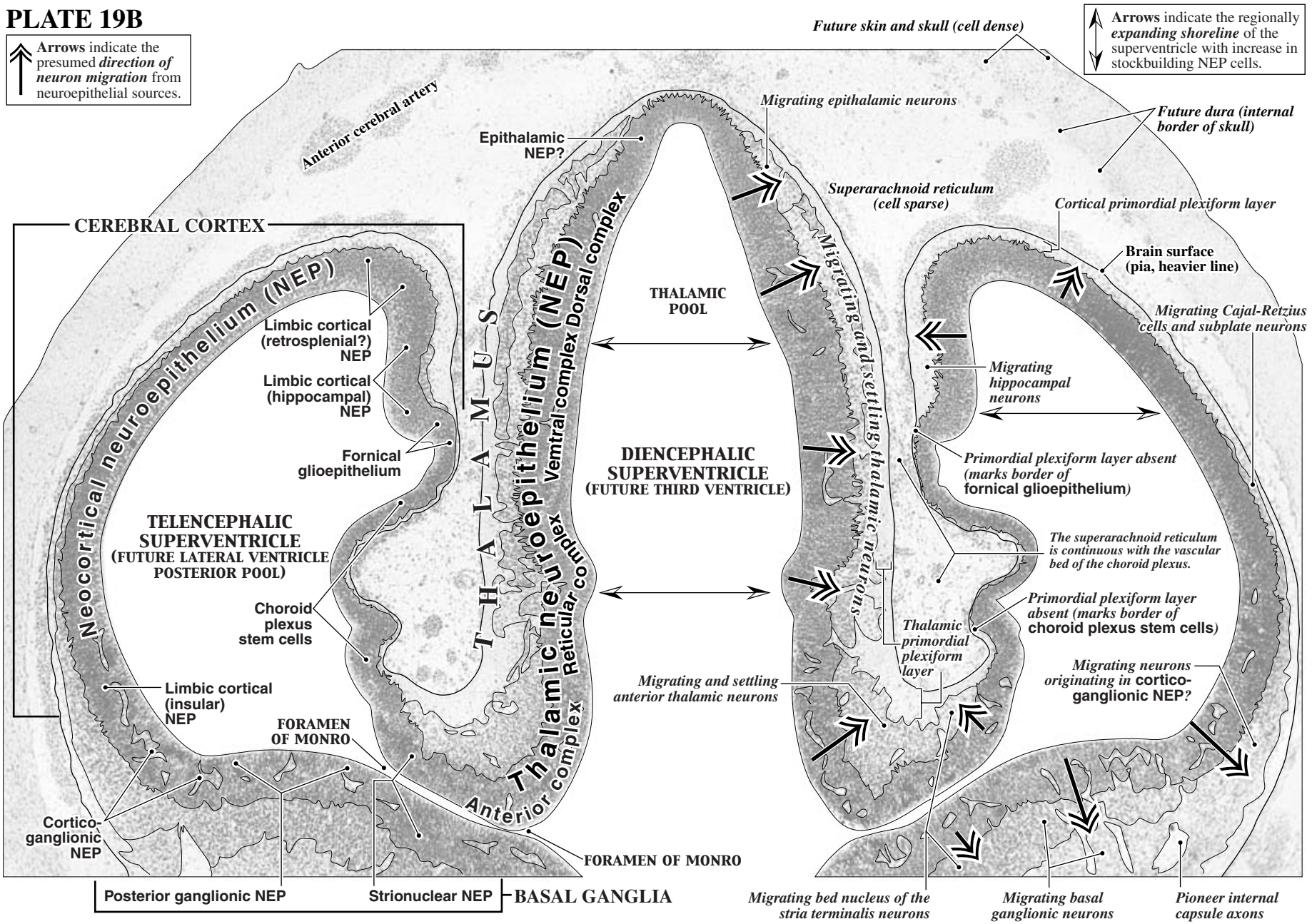


**GW7 Coronal**
**CR 17.5 mm, M2155**
**Near Level 5:**
**Section 236**




**See Level 5 in Plates 5A and B.**

# PLATE 19B


Arrows indicate the presumed direction of neuron migration from neuroepithelial sources.
Arrows indicate the regionally expanding shoreline of the superventricle with increase in stockbuilding NEP cells.
Future skin and skull (cell dense)
Anterior cerebral artery
Epithalamic NEP?
Migrating epithalamic neurons
Future dura (internal border of skull)
Superarachnoid reticulum (cell sparse)
Cortical primordial plexiform layer
CEREBRAL CORTEX
Neocortical neuroepithelium (NEP)
Limbic cortical (retrosplenial?) NEP
Limbic cortical (hippocampal) NEP
Fornical glioepithelium
TELENCEPHALIC SUPERVENTRICLE (FUTURE LATERAL VENTRICLE POSTERIOR POOL)
Choroid plexus stem cells
Limbic cortical (insular) NEP
FORAMEN OF MONRO
Cortico-ganglionic NEP
Posterior ganglionic NEP
Strionuclear NEP
BASAL GANGLIA
THALAMUS
Thalamic neuroepithelium (NEP)
Ventral complex
Dorsal complex
Reticular complex
Anterior complex
THALAMIC POOL
DIENCEPHALIC SUPERVENTRICLE (FUTURE THIRD VENTRICLE)
FORAMEN OF MONRO
Migrating and settling thalamic neurons
Migrating and settling anterior thalamic neurons
Thalamic primordial plexiform layer
Brain surface (pia, heavier line)
Migrating Cajal-Retzius cells and subplate neurons
Migrating hippocampal neurons
Primordial plexiform layer absent (marks border of fornical glioepithelium)
The superarachnoid reticulum is continuous with the vascular bed of the choroid plexus.
Primordial plexiform layer absent (marks border of choroid plexus stem cells)
Migrating neurons originating in cortico-ganglionic NEP?
Migrating bed nucleus of the stria terminalis neurons
Migrating basal ganglionic neurons
Pioneer internal capsule axons