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Pierre-Yves Risold

The Human Hippocampus

Functional Anatomy,
Vascularization and
Serial Sections with MRI

Fourth Edition

Drawings and Illustrations by
J.L. Vannson and M. Gaudron

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ISBN 978-3-642-33602-7 ISBN 978-3-642-33603-4 (eBook)
DOI 10.1007/978-3-642-33603-4
Springer Heidelberg New York Dordrecht London

Library of Congress Control Number: 2013941136

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Preface

The previous edition of *The Human Hippocampus* has been enriched of numerous modifications for this fourth edition. Some of them concern the history of the terminology applying to this complex structure and whose origin is still unsure. If the anatomy of the hippocampus seems well defined, our understanding of its functions is evolving quickly. Furthermore, its vascularization is still the object of numerous investigations, especially the architecture of the arterial, venous, and capillary networks in relation to hippocampal functions. Advances in medical imaging have allowed many progresses, and 3T MRI views of coronal, sagittal, and axial sections have been improved in this new edition. Each MRI view is associated with drawings and anatomical preparations which allow a better interpretation and a more precise clinical application. Very precise 9.4 T MRI views have been obtained, thanks to Prof. Th. Naidich. The achievement of this work would not have been possible without the illustrations made by J. L. Vannson and M. Gaudron. We are also grateful to Ms. G. Schroeder, Ms. M. Himberger and Ms. I. Von Behrens (Springer-Verlag Heidelberg) who has been a great help to carry out this fourth edition of *The Human Hippocampus*.

Besançon, France
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The aim of this study is to give a precise description of human hippocampal anatomy in view of neurosurgical progress and the wealth of medical imaging methods available. Two major problems render this study more difficult: (1) the complexity of the hippocampal structure, making it one of the most mysterious regions in the central nervous system and (2) the great confusion which plagues its terminology, a confusion which appeared in the earliest descriptions.

From those who have studied the history of hippocampal terminology (e.g., Vogt and Vogt 1937; Tilney 1939; Benninghoff 1940; Klinger 1948; Clara 1959; Meyer 1971), the views of Lewis (1923) have been chosen to be summarized here.

The first description of the hippocampus is credited to Arantius in 1587 (cited by Lewis 1923) who compared the protrusion on the floor of the temporal horn to a hippocampus, or sea horse (see Fig. 3.2). It should be noted, however, that he hesitated between the terms “sea horse” and “silkworm.” In 1729, J. G. Duvernoy (cited by Lewis 1923) first illustrated the hippocampus, and he, too, hesitated between “hippocampus,” “silkworm,” and even “dolphin.” In 1732, Winslow suggested the term “ram’s horn” (see Winslow 1752). *Hippocampus*, *silkworm*, and *ram’s horn* were thus the terms used at the end of this initial period, all based on the intraventricular appearance of the hippocampus.

During the same period, the term *cornu Ammonis*, cited by de Garengot (1742), could have been first described by members of the Alexandrian School of Medicine (300 BC–300 AD)

(Andersen et al. 2007) (Fig. 3.2). In ancient Egypt, the horns of the ram dedicated to the god Amon (or Ammon) were described as the *cornu Ammonis* (Ammon’s horn) (Fig. 3.2).

The term *pes hippocampi* was introduced next. Although it is not known who added foot to the hippocampus, it may be due to Diemerbroek (1672) (cited by Lewis 1923). The description of *pes hippocampi* is uncertain: In some cases, *pes hippocampi* is for the whole hippocampus (Kopsch 1940); for other authors, it may correspond to the anterior end (or head of the hippocampus), characterized by endoventricular sallies or *digitationes hippocampi* (Gertz et al. 1972; Williams 1995; Amaral and Lavenex 2007).

After these periods of confusion, the terminology that is currently most commonly used needs to be clarified. The name hippocampus applies to the entire ventricular protrusion. Thus, the hippocampus comprises two cortical laminae rolled up one inside the other: the *cornu Ammonis* and the *gyrus dentatus* (Figs. 4.1 and 4.2). The subiculum, or transitional cortex between *cornu Ammonis* and the rest of the temporal lobe, is sometimes viewed as part of the hippocampus, constituting a functional unit (Chronister and White 1975). However, since the hippocampus and subiculum do not form a distinct topographical unit, the subiculum is not included in this study. Anatomically and functionally, the hippocampus is also associated to the entorhinal, perirhinal, and parahippocampal cortices to form the *medial temporal lobe* (MTL) (Suzuki 2009).

Sixty hippocampi were examined, the average age of the brains being 57 years (range, 19–85 years). To simplify this account, the hemisphere studied (right or left) and the sex of the subject it was taken from were omitted; previous studies have shown no differences stemming from the particular techniques used (Mani et al. 1986).

The brains were removed between 5 and 12 h after death and were fixed in a 10 % formalin solution. Most had already received an intravascular injection of India ink. In the following, the specific methods used in each chapter are described.

In Chaps. 3 and 4 on the structure and anatomy of the hippocampus, two methods were used:

1. *Dissection of the hippocampus.* With the help of an operating microscope, the hippocampus was examined after ablation of blood vessels and leptomeninges. The choroid plexuses were removed to inspect the ventricular aspect of the hippocampus.
2. *Bodian's method of silver impregnation.* After fixation in formalin, the hippocampus was cut into sections of 10–20 μm and then impregnated by the silver proteinate method. This method is applicable after intravascular injection, and a correlation can thus be established between the neural architecture and the vascular network. Compared with the usual staining by cresyl violet, Bodian's technique has the advantage of showing not only neuronal somata but also their processes. Conversely, and due to density of impregnation, photographs of large areas show insufficient contrast and are of little use.

In Chap. 5 on the hippocampal vascularization, two methods were applied:

1. *Intravascular injection of India ink.* Once the brain had been removed, 400-cc India ink solution diluted by distilled water to 50 % was injected into the carotid and vertebral arteries. Gelatin (5–10 %) was added to the mixture. In our opinion, this method of total vascular injection of the brain through the main arterial trunks is the best way to obtain a good view not only of the arteries but also of the capillaries and, in particular, the veins. In the literature, the cerebral veins have always been studied by

specific retrograde venous injections. Using this last method, however, it is rarely possible to obtain a good feeling of the venous tree. The method of intravascular India ink injection permits the vascular anatomy to be observed in three different ways:

- (a) *Observation of the superficial (leptomeningeal) vessels.* The superficial vessels were dissected with the help of an operating microscope. Arteries and veins were identified, and the point of penetration of arteries and emergence of veins noted (16 hemispheres were used for this study). The preparations were then photographed while immersed in distilled water to prevent reflection and bubbles.
- (b) *Identification of the deep path of intrahippocampal arteries and veins.* Blocks of 3–4-mm thick were cut and cleared using the Spalteholz technique (a mixture of methyl salicylate and benzyl benzoate). The superficial arteries and veins identified during the preceding step were followed into the hippocampal tissue. By this method, it is possible to recognize the intrahippocampal arteries and veins and follow them along their entire course.
- (c) *Thick sections.* After fixation, the brains were cut into coronal, sagittal, or axial sections in relation to the bicommissural plane linking the middle part of the anterior and posterior commissures. Sections (300- μm thick) were made after dehydration, immersion in toluene, and embedding in paraffin. To obtain thick sections without cracks, the block was heated between each cut. Sections were then mounted on slides in gelatin and dried under pressure. Sections were then cleared using the Spalteholz technique. This method provides a picture of the total cerebral vascular pattern (Chap. 6) and allows the intrahippocampal vascular network to be studied. However, the possible deformation of the nervous tissue due to considerable shrinkage following immersion in alcohols and toluene must be taken into account. Thick sections facilitate the identification of cerebral structures according to

differences in the vascular density. White and gray substances are clearly differentiated. In addition, the gray matter nuclei do not have a vascular network of equal density. This technique has already been used to study the vascularization of circumventricular organs and brain stem, cerebral, cerebellar cortices, and pineal gland (Duvernoy 1972, 1975, 1995, 1999a, b, 2005; Duvernoy and Koritke 1964, 1965; Duvernoy et al. 1969, 1971, 1972, 1981, 1983, 2000).

2. *Intravascular injection with low-viscosity resin (Mercox)*. This technique was used to complete the observation of the vessels carried out by intravascular injection of India ink. After local vascular injection of the brain with the resin (Mercox), the tissues were destroyed, and the cast of the vascular network was examined with a scanning microscope.

Thus, accurate observations of the fine vascular network and its spatial organization became possible.

In Chap. 7 on sectional anatomy, each plate includes several figures:

1. *A three-dimensional section of the hippocampus*. The principle of this method is to gradually erode the hemisphere by sectioning it from anterior to posterior for coronal sections, from medial to lateral for sagittal sections, and from superior to inferior for axial sections. Eroded tissue is discarded, and the newly exposed surface of the hemisphere is observed for the purpose of anatomical analysis.
2. *A head section*.
3. *One or several MRI views of 3T and 9T (Prof. Th. Naidich)*.
The bicommissural plane of Schaltenbrand acted as a reference for all these sections.

3.1 Preliminary Remarks

The general situation of the hippocampus in relation to the hemispheres is indicated in Fig. 3.1. The intraventricular aspect of the hippocampus is shown in Fig. 3.2.

Features of the Limbic Lobe

As the hippocampus is part of the limbic lobe, this latter structure will be described first. The limbic lobe (Fig. 3.4) is situated on the inferomedial aspect of the hemisphere, separated from adjoining cortex by the limbic fissure. This fissure is a discontinuous sulcus composed successively of the cingulate, subparietal, anterior calcarine, collateral, and rhinal sulci. Broca (1878) divided the limbic lobe into the limbic and intralimbic gyri, something which has become an established tradition.

The *limbic gyrus* consists of the subcallosal, cingulated, and parahippocampal gyri (the term parahippocampal will be used here, rather than “hippocampal gyrus,” which can lead to confusion with the hippocampus itself). The retrosplenial cortex and a narrowed lobule, the isthmus, join the cingulate and parahippocampal gyri behind and below the *splenium* of the corpus callosum (Vogt et al. 1993). The parahippocampal gyrus can be divided into two segments: (1) the posterior segment is narrow, and its flat superior surface, the *subiculum*, is separated from the hippocampus by the hippocampal sulcus (see Fig. 3.5); (2) the anterior segment is more voluminous and is called the *piriform lobe*, comprising the *uncus* and the *entorhinal area*. The *uncus* curves posteriorly to rest on the parahippocampal gyrus itself from which it is separated by the uncal sulcus. The *uncus* is functionally divided into anterior and posterior parts. The posterior part which belongs to the hippocampus will be studied later. The anterior part displays two protrusions: the *semilunar gyrus* and the *ambient gyrus* (Figs. 3.4 and 4.8), which are separated by the *semilunar sulcus*, both covering a deep nucleus, the amygdala (see Fig. 3.14). The *entorhinal area* is the lower part of the piriform lobe extending to the posterior segment of the parahippocampal gyrus.

The *intralimbic gyrus* arches within the limbic gyrus (Fig. 3.4). Its anterior segment includes a narrow zone in the subcallosal region, the prehippocampal rudiment, partially belonging to the *paraterminal gyrus* and to the septal region (Brodal 1947); its superior segment, a continuation of the prehippocampal rudiment, is the *indusium griseum*, situated on the superior surface of the corpus callosum. The *indusium griseum* is a neuronal lamina covering the corpus callosum as far as its splenium, itself covered on each side of the midline by two small white fasciculi, the medial and lateral longitudinal striae (see Fig. 4.12). Passing around the splenium, the *indusium griseum* reaches the inferior segment of the intralimbic gyrus, the hippocampus, which is the only part that is well developed.

The hippocampus, separated from the subiculum by the hippocampal sulcus, extends forward to the uncus to occupy its posterior segment. The hippocampus is bordered by the *fimbria* (Figs. 3.4 and 3.5).

In relation to the corpus callosum, the intralimbic gyrus is sometimes divided into three parts (Elliot Smith 1897): (1) the precommissural hippocampus (prehippocampal rudiment), (2) the supracommissural hippocampus (*indusium griseum*), and (3) the retrocommissural hippocampus (the hippocampus proper). This terminology takes into account the migration of the hippocampus during development. The human hippocampus follows the progress of the lateral telencephalic vesicle, which starts from the region of the interventricular foramen and curves up and back and then down and under to form the *temporal lobe*. This development is incomplete in most mammals, as rotation of the primitive telencephalic vesicle ceases before a complete temporal lobe is formed. Thus, in the rat, for instance, the retrocommissural hippocampus remains largely dorsal to the thalamus, whereas the human hippocampus curves beneath the thalamus (Fig. 3.6). It will be noted below that these differences contribute to the complexity and confusion of hippocampal terminology.

The development of conceptions about the anatomy and functions of the limbic lobe was clearly presented by Nieuwenhuys et al. (2008).

Broca (1878) first described and named the limbic lobe. From its comparative anatomy, he attributed olfactory functions to these structures. It was therefore later named the rhinencephalon (Turner 1891).

In a subsequent phase in speculation on the limbic lobe by observers such as Papez (1937) and Brodal (1947), it was suggested that, in humans, this lobe is only partially olfactory and is mainly concerned with emotional behavior. In addition, the amygdala was seen as part of the limbic lobe. Maclean (1970) subsequently included numerous subcortical structures such as the septum, midline thalamus, habenula, and hypothalamus in the limbic lobe, something which was later criticized by LeDoux (1989). Thus, from the single entity of Broca, the limbic lobe became an organization, the so-called limbic system, composed of disparate anatomical units with common functions. Nauta (1958) developed this concept further, insisting on the functional importance of certain regions of the neuraxis, such as the septum, preoptic area, hypothalamus, and mesencephalon, regions closely

related to the hippocampus. The hypothalamus makes a link between the limbic and endocrine system reasonable. The mesencephalon, said to form a “mesolimbic system” through its paramedian structures, could enable visceral information ascending in the brain stem to influence general functioning of the limbic system.

General Feature of Hippocampal Anatomy

The general arrangement of the hippocampus is shown in Fig. 3.2. It bulges into the temporal horn of the lateral ventricle, and its general appearance does indeed resemble a sea horse in shape. It is arched around the mesencephalon (see Figs. 3.2 and 3.3), and the arch can be divided into three segments:

1. A body, or middle segment, which is sagittally oriented
2. A head, or anterior segment, which is transversely oriented and dilated and which shows elevations, the digitations hippocampi
3. A tail, or posterior segment, which is also oriented transversely and which narrows, disappearing beneath the splenium

Fig. 3.1 (a, b) Coronal section of the brain. (a) Head section. Bar, 10 mm. (b) 3T MRI view, T⁻¹-weighted image. 1 right hippocampus, 1' left hippocampus, 2 parahippocampal gyrus, 3 fusiform gyrus, 4 inferior temporal gyrus, 5 middle temporal gyrus, 6 superior temporal gyrus, 7 lateral fissure, 8 postcentral gyrus, 9 central sulcus, 10 precentral gyrus, 11 superior frontal gyrus, 12 cingulate gyrus, 13 corpus

callosum, 14 lateral ventricle, 14' caudate nucleus, 15 thalamus, 16 putamen, 17 temporal (inferior) horn of the lateral ventricle: the hippocampus belongs to the floor of this cavity (see Fig. 3.2a), 18 red nucleus, 19 substantia nigra, 20 pons, 21 tentorium cerebelli, 22 ambient cistern

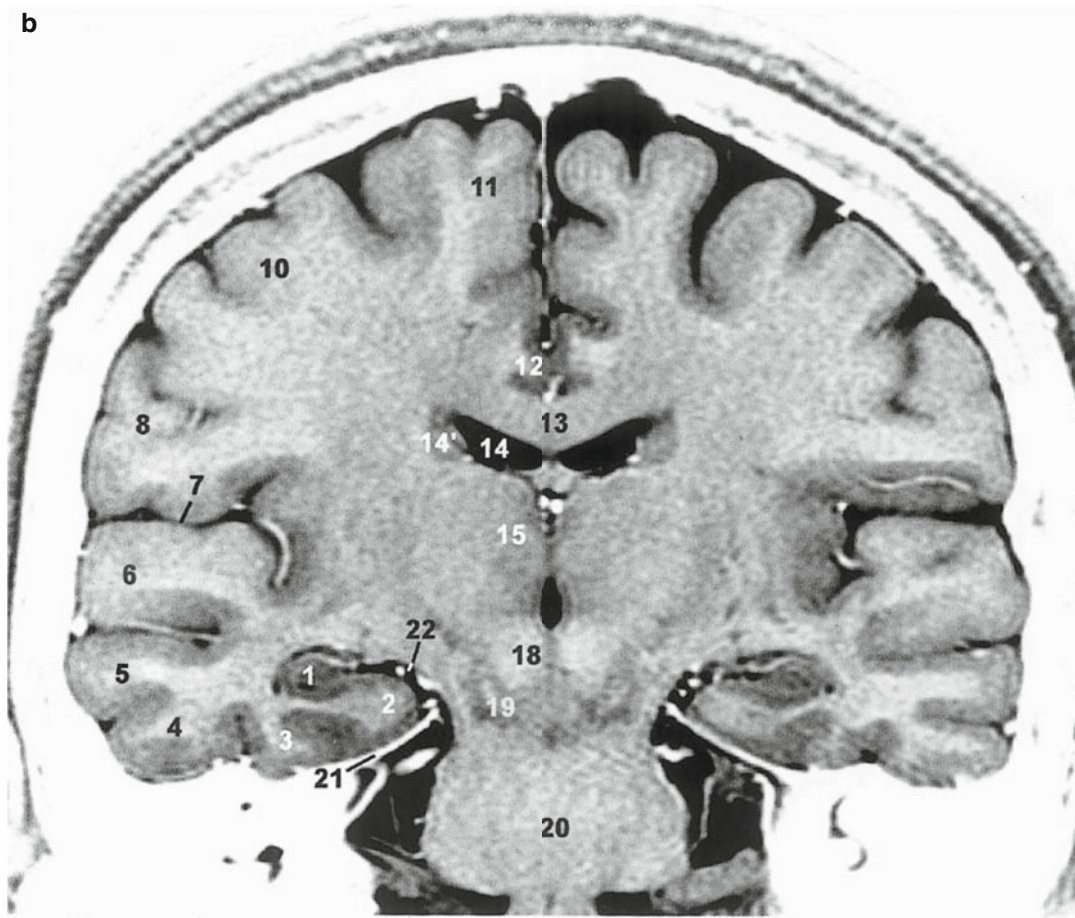
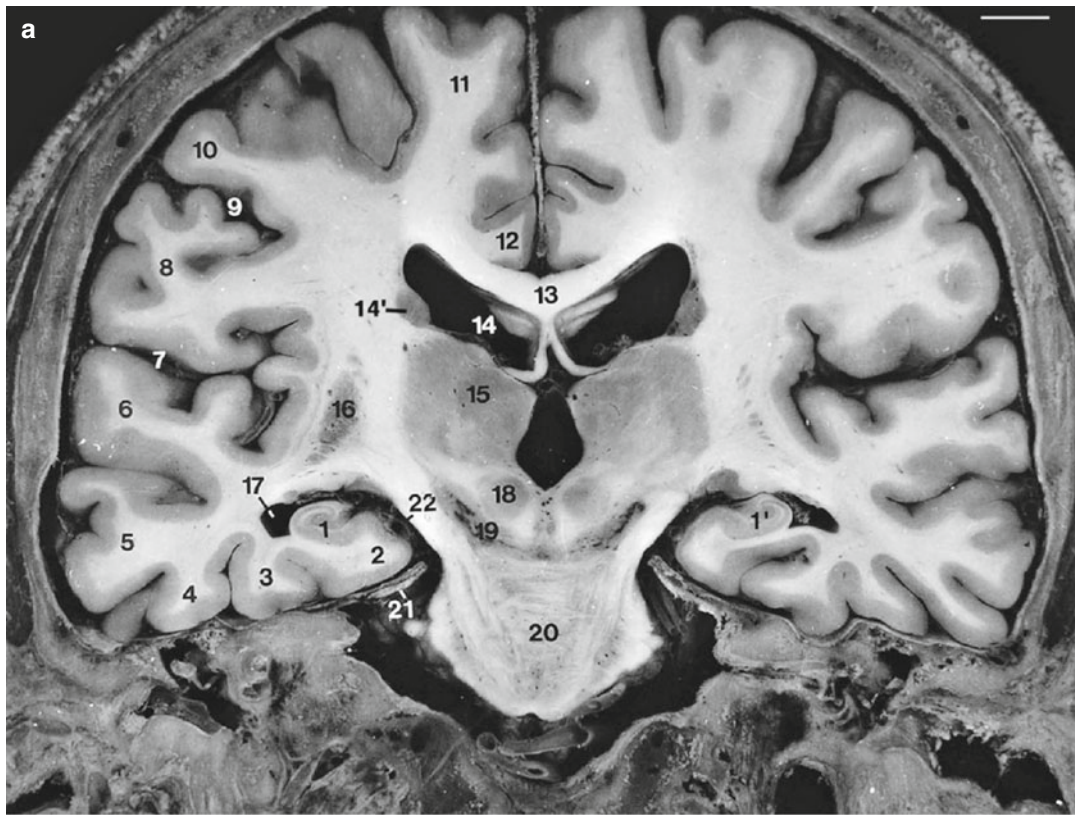




Fig. 3.2 (a) Intraventricular aspect of the right hippocampus. The temporal horn has been opened and the choroid plexuses removed. Bar, 6.5 mm. 1 hippocampal body, 2 head and digitations hippocampi (internal digitations), 3 hippocampal tail, 4 fimbria, 5 crus of fornix, 6 subiculum, 7 splenium of the corpus callosum, 8 calcar avis (hippocampus minor), 9 collateral trigone, 10 collateral eminence, 11 uncus

recess of the temporal horn. Main explanation of the terms of hippocampus: (b) Hippocampus or sea horse. (c) Horn of the ram dedicated to the god Amon (or Ammon): Ammon's horn or cornu Ammon is seen in the temple of Karnak, Louxor, Egypt. However, this description of cornu Ammonis is not admitted by all

Fig. 3.2 (continued)



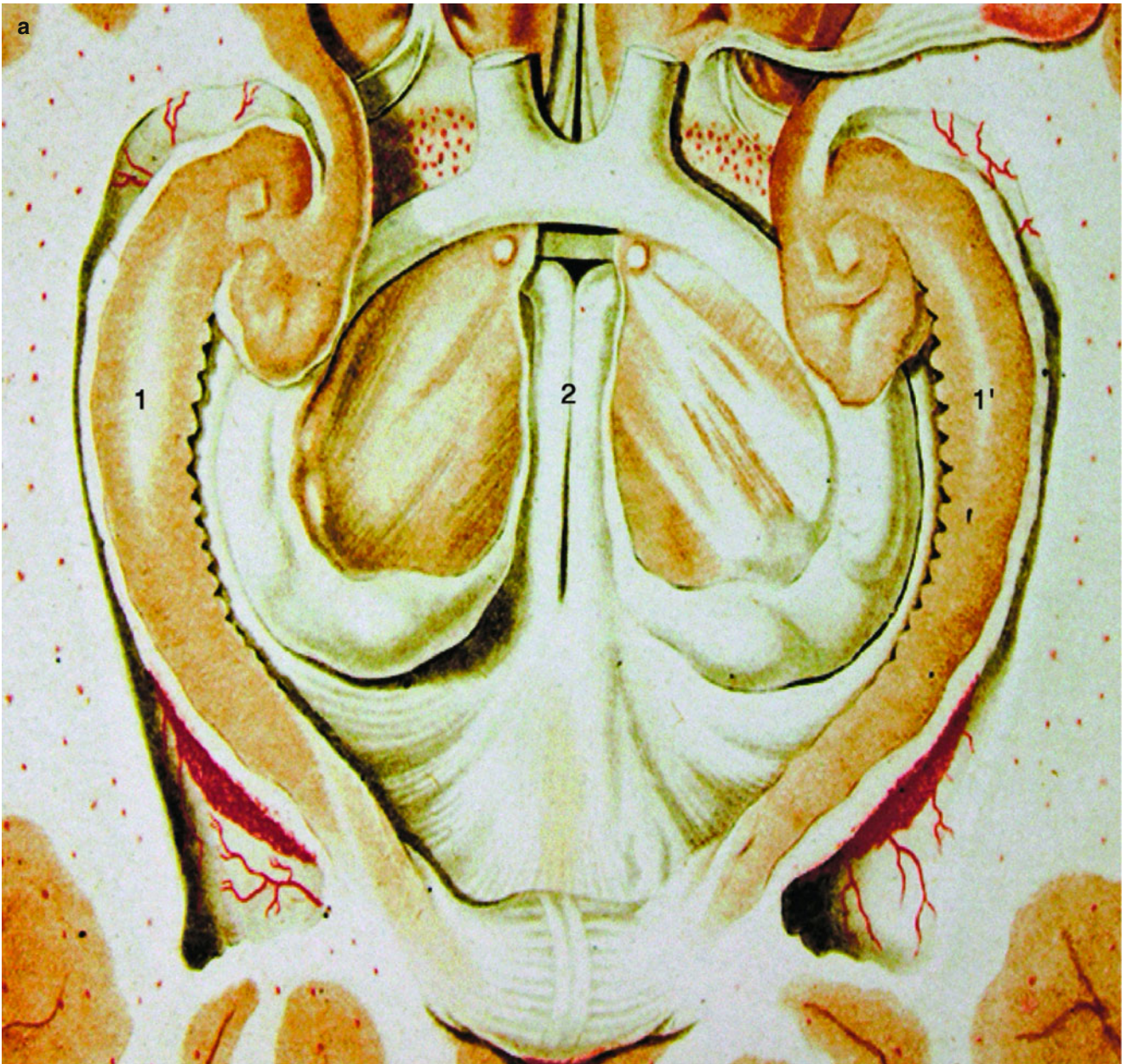
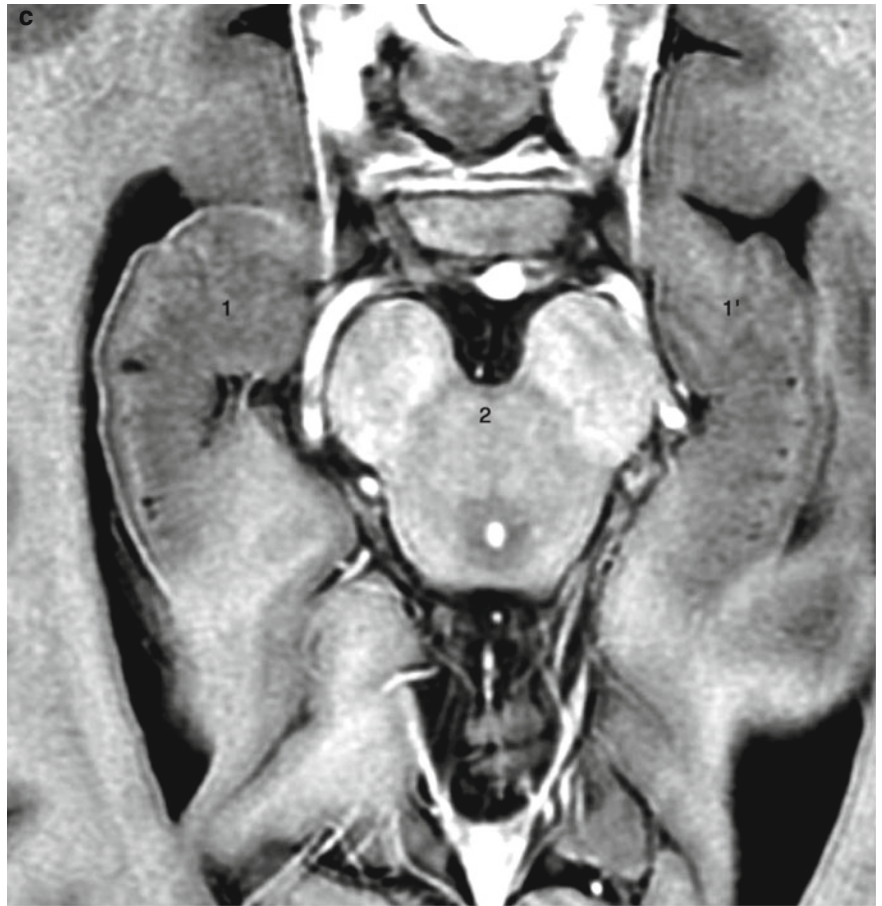


Fig. 3.3 (a) Drawing of the hippocampus by Vicq d'Azyr (1786). The right and left hippocampi (1) encircle (embracing) the median structures (2). (b) Dissection (endoventricular view) of the right and left

hippocampi (1, 1'); 2 mesencephalon. (c) MRI view; 1 hippocampus, 2 mesencephalon

Fig. 3.3 (continued)



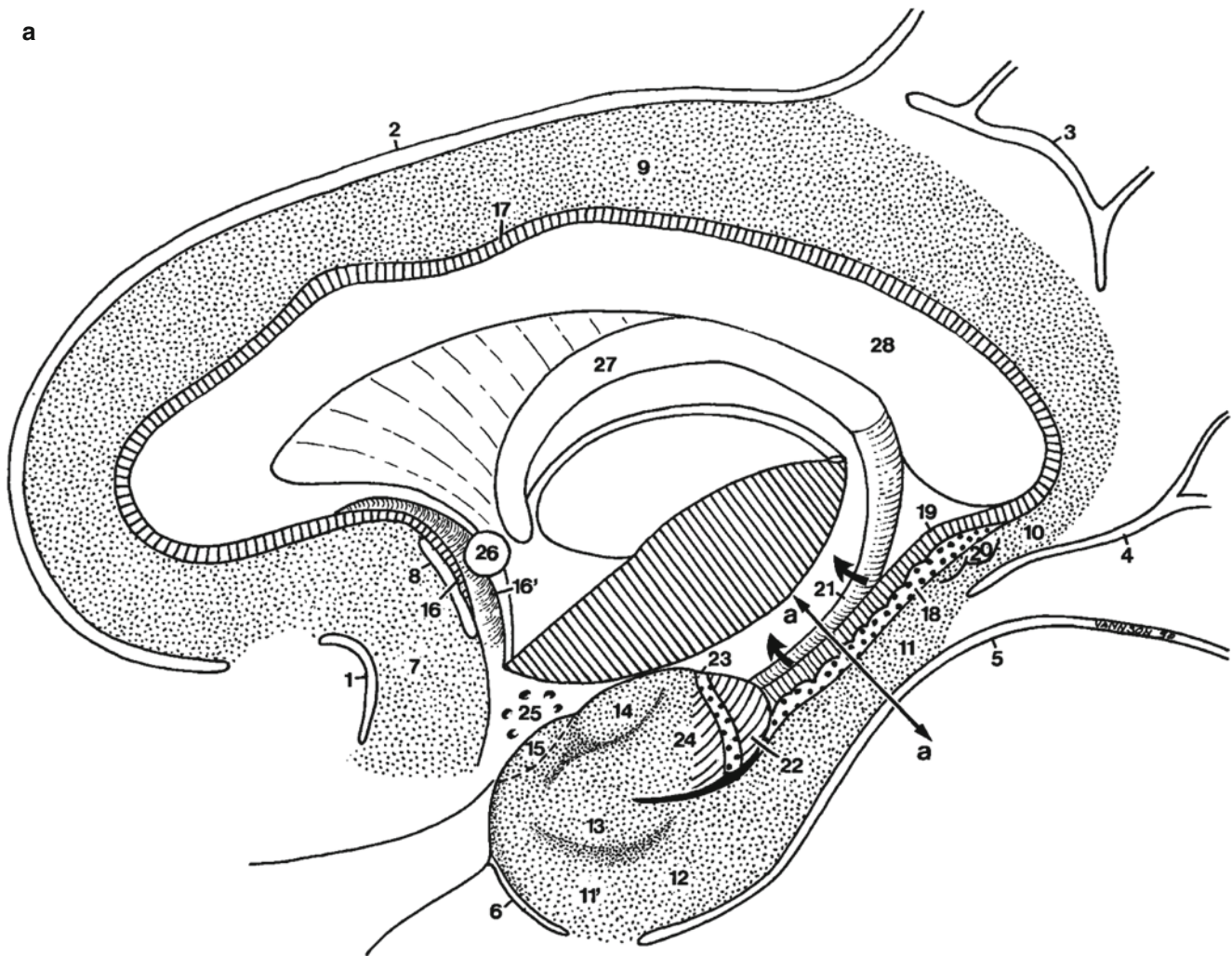


Fig. 3.4 (a) Drawing and (b) dissection showing a sagittal section, right hemisphere. The limbic lobe is separated from the isocortex by the limbic fissure and may be divided into two gyri: the limbic and intralimbic gyri. The line a-a indicates the plane of section on Fig. 3.5. Bar, 7.7 mm. Limbic fissure: 1 anterior paraolfactory sulcus (subcallosal sulcus), 2 cingulate sulcus, 3 subparietal sulcus, 4 anterior calcarine sulcus, 5 collateral sulcus, 6 rhinal sulcus. Limbic gyrus, 7 subcallosal gyrus, 8 posterior paraolfactory sulcus, 9 cingulate gyrus, 10 isthmus, 11 parahippocampal gyrus, posterior part, 11' parahippocampal gyrus,

anterior part (piriform lobe). Piriform lobe: 12 entorhinal area, 13 ambient gyrus, 14 semilunar gyrus (13 and 14 correspond to nuclei of the amygdala), 15 prepiriform cortex. Intralimbic gyrus: 16 prehippocampal rudiment, 16' paraterminal gyrus, 17 indusium griseum. Hippocampus: 18 gyrus dentatus, 19 cornu Ammonis, 20 gyri of Andreas Retzius, 21 fimbria (displaced upward, arrows), 22 uncal apex, 23 band of Giacomini, 24 uncinata gyrus, 25 anterior perforated substance, 26 anterior commissure, 27 fornix, 28 corpus callosum

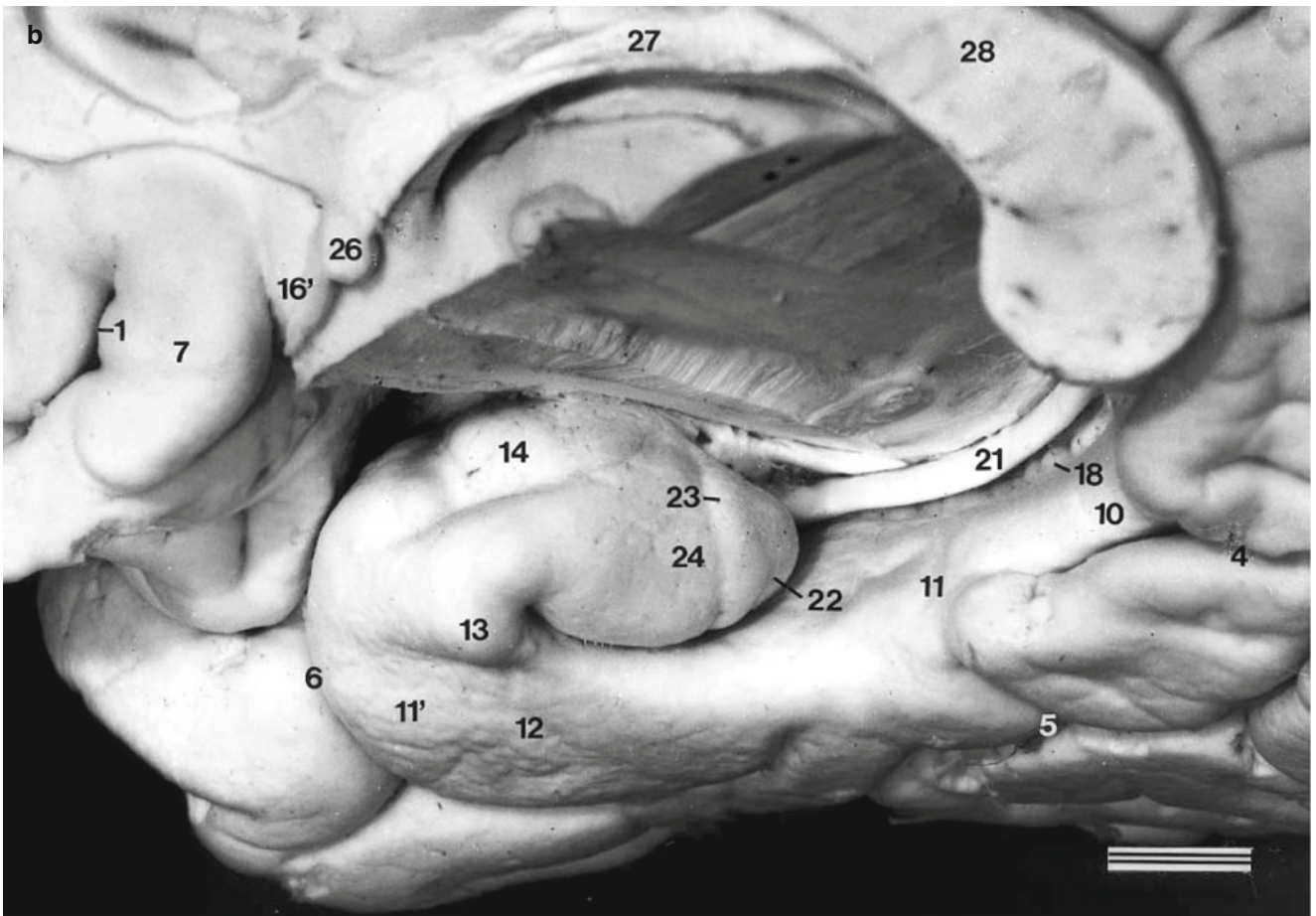


Fig. 3.4 (continued)

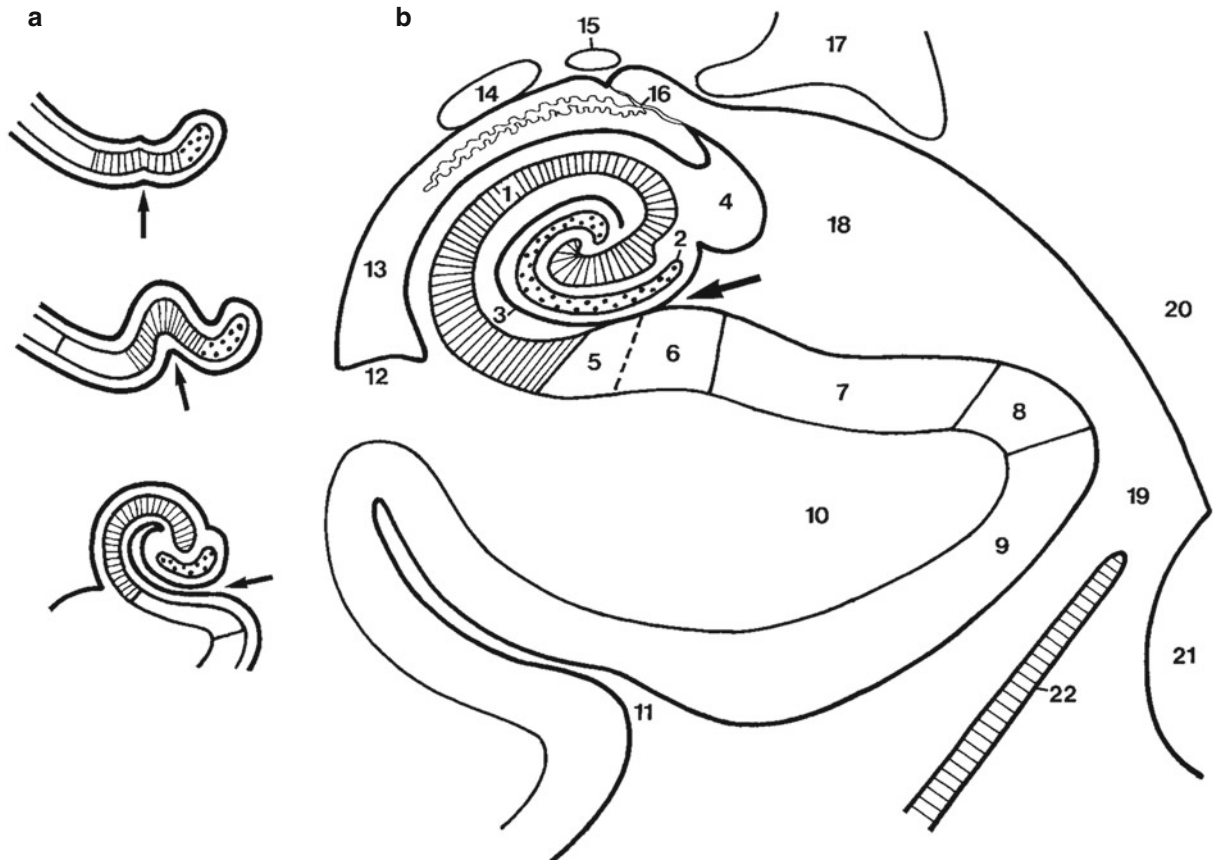


Fig. 3.5 (a) Development of the gyrus dentatus (*dotted area*) and of the cornu Ammonis (*hatched area*) toward (b) their definitive disposition. *Arrows* indicate the hippocampal sulcus (superficial part) (Modified after Williams 1995). 1 cornu Ammonis, 2 gyrus dentatus, 3 hippocampal sulcus (deep or vestigial part), 4 fimbria, 5 prosubiculum, 6 subiculum proper, 7 presubiculum, 8 parasubiculum, 9 entorhinal area,

10 parahippocampal gyrus, 11 collateral sulcus, 12 collateral eminence, 13 temporal (inferior) horn of the lateral ventricle, 14 tail of caudate nucleus, 15 stria terminalis, 16 choroid fissure and choroid plexuses, 17 lateral geniculate body, 18 lateral part of the transverse fissure (wing of ambient cistern), 19 ambient cistern, 20 mesencephalon, 21 pons, 22 tentorium cerebelli

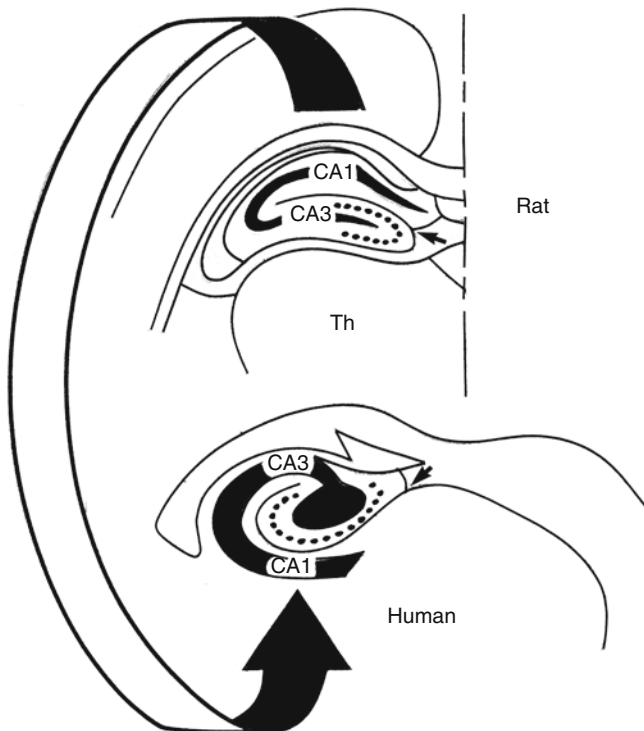


Fig. 3.6 Site of CA1 and CA3 in rats and humans (see p. 16). *Arrowheads* show the hippocampal sulcus. The *arrow* indicates the inversion of arrangements in the hippocampus in these two species. CA1 superior region, CA3 inferior region, Th thalamus

3.2 Structure

The characteristics of hippocampal structures are merely summarized here; for more detailed information, the reader is referred to the fundamental works by the following authors: Ramon y Cajal 1911, 1968; Lorente de No 1934; Vogt and Vogt 1937; and Blackstad 1956, 1958. In addition, the following works may be consulted: Gastaut and Lammers 1961; Isaacson 1974; Angevine 1975; Chronister and White 1975; Tryhubczak 1975; O'Keefe and Nadel 1978; Carpenter and Sutin 1983; Schwerdtfeger 1984; Kahle 1986; Amaral and Insausti 1990; Williams 1995; and Nieuwenhuys et al. 2008.

The hippocampus is bilaminar, consisting of the cornu Ammonis (or hippocampus proper) and the gyrus dentatus (or fascia dentata), with one lamina rolled up inside the other (Figs. 3.7 and 3.8). Elliot Smith (1897) and Williams (1995) looked for an explanation for this during cerebral development. In early development, the two laminae are continuous. For reasons still uncertain, the anlage of the cornu Ammonis bulges into the ventricular cavity to an increasing extent. Formation of the hippocampal sulcus at the cortical surface corresponds to this fold (Fig. 3.5a). The gyrus dentatus becomes concave and seems to slip beneath the medial end of the cornu Ammonis, perhaps due to asymmetry of development between the two structures. A final position is arrived at in which the cornu Ammonis and the gyrus dentatus resemble two interlocking, U-shaped laminae, one fitting into the other (see Fig. 4.1) and separated from each other by the hippocampal sulcus.

The hippocampal sulcus may be divided into deep and superficial parts. The deep part of the hippocampal sulcus soon disappears or remains visible as the *vestigial hippocampal sulcus* (Humphrey 1967), and its superficial part is clearly seen on the temporal lobe surface as the *superficial hippocampal sulcus*.

Two formations are thus studied here: the cornu Ammonis and the gyrus dentatus. Their typical position in the hippocampal body remains in the head and tail, possibly with slight variations (see Fig. 4.1).

The cornu Ammonis and the gyrus dentatus are the simplest part of the cortex, the *allocortex* (or archeocortex), as compared with the more complex *isocortex* (or neocortex) (see p. 17).

3.2.1 Cornu Ammonis (Hippocampus Proper)

From the deepest level to the surface, that is, from the ventricular cavity toward the vestigial hippocampal sulcus, the cornu Ammonis may be divided into six layers: the alveus, stratum oriens, stratum pyramidale, stratum radiatum, stratum lacunosum, and stratum moleculare (Figs. 3.7, 3.8, 3.9, and 3.10).

The *alveus* covers the intraventricular surface and contains axons of the hippocampal and subicular neurons, which are the main efferent pathway of these structures. These fibers then enter the fimbria (see Fig. 3.15). The alveus also contains afferent fibers largely from the septum (see Fig. 3.19).

The limits of the *stratum oriens* are poorly defined because the latter blends with the underlying stratum pyramidale, particularly in humans (Stephan and Manolescu 1980). It is composed of scattered nervous cells (basket cells) and is crossed by the axons of pyramidal neurons as they arrive at the alveus.

The *stratum pyramidale* contains the pyramidal neurons, the main element of the cornu Ammonis. A pyramidal soma is typically triangular, its base facing the alveus and its apex facing toward the vestigial hippocampal sulcus (see Fig. 3.13). From its base, the axon traverses the stratum oriens to the alveus. Such pyramidal neurons mainly project to the septal nucleus, but some are association fibers for the other pyramidal neurons and perhaps cross to the contralateral hippocampus (Gloor et al. 1993). While on course, such axons have Schaffer collaterals (Schaffer 1892), which curve back into the stratum radiatum and reach other pyramidal neurons (see Figs. 3.13 and 3.15). The fundamental role of these collaterals is described p. 28. At the apex of each pyramidal neuron is an apical dendrite, the length of which is remarkable because it traverses the entire thickness of the cornu Ammonis to reach the stratum moleculare near the vestigial hippocampal sulcus. In addition to the apical dendrite, there are basal dendrites from the soma basal angles; some of these arborize in the stratum oriens. Thus, hippocampal pyramidal neurons have sometimes been called “double pyramidal” because of their double dendritic trees (Isaacson 1974). The soma is surrounded by a dense plexus of arborizations from basket cells with somata in the stratum oriens (see Fig. 3.13). Basket-type interneurons and stellate neurons are also scattered throughout the stratum pyramidale itself (Olbrich and Braak 1985), as in other layer of the cornu Ammonis (Braak 1974).

The *stratum radiatum* consists mainly of apical dendrites from pyramidal neurons, the parallel arrangement of which gives this layer a striated appearance. In the stratum radiatum, apical dendrites connect with Schaffer collaterals, fibers from septal nuclei, and commissural fibers.

The *stratum lacunosum* contains mainly numerous axonal fasciculi parallel to the surface of the cornu Ammonis, formed mainly of perforant fibers and Schaffer collaterals.

The *stratum moleculare* adjoins the vestigial hippocampal sulcus. Because of the partial sulcal disappearance during development, the stratum moleculare of the cornu Ammonis blends with that of the gyrus dentatus. The stratum moleculare contains few neurons, and here, too, these are considered as interneurons. It contains the original

arborizations of apical dendrites of pyramidal neurons. Thus, by their prolongation, pyramidal neurons reach all layers of the cornu Ammonis. Their dendrites receive a great deal of information, as summarized in Fig. 3.13.

As the allocortex usually shows only three layers, the six layers of the cornu Ammonis described above are grouped into three layers: the stratum oriens, the stratum pyramidale, and a layer which combines the strata radiatum, lacunosum, and moleculare, that is, the molecular zone (Ramon y Cajal 1911, 1968; Lorente de No 1934).

Regional Variations

In coronal sections, the cornu Ammonis has a heterogenous structure due to different aspects of its pyramidal neurons. The cornu Ammonis has thus been described as having four fields (Fig. 3.7), which Lorente de No (1934) named CA1–CA4.

CA1 continues from the subiculum. Its pyramidal somata are typically triangular (Fig. 3.11) and generally small and scattered (Mouritzen Dam 1979). The stratum pyramidale of human CA1 is large, but it is narrow and dense in rats (Stephan 1983). Two sublayers have been distinguished in the stratum pyramidale of human CA1: a stratum profundum and a stratum superficiale (Braak 1974), the former in contact with the stratum oriens, with few pyramidal neurons, while the latter contains numerous ones.

CA2 is composed of large, ovoid, densely packed somata (Figs. 3.7, 3.8, 3.9, 3.10, and 3.11), making the stratum pyramidale dense and narrow, in sharp contrast to CA1 (Braak 1980). Its presence, a matter of debate in numerous species (Blackstad 1956; Schwerdtfeger 1984), is clear in human and simian hippocampi (Amaral et al. 1984).

CA3 corresponds to the curve, or genu, of the cornu Ammonis, where it enters the concavity of the gyrus dentatus. Its pyramidal somata are like those in CA2, but their density is less pronounced (Figs. 3.7, 3.8, 3.9, 3.10, and 3.11). A typical feature of CA3 is the presence of fine, nonmyelinated fibers, the mossy fibers, which arise from the gyrus dentatus. These fibers surround the pyramidal somata and are also compressed between the strata radiatum and pyramidale, thus forming a supplementary layer, the stratum lucidum that is characteristic of CA3 (see Figs. 3.7, 3.8, and 3.9).

CA4 is situated within the concavity of the gyrus dentatus, which distinguishes it from CA3. Somata in this field are ovoid, large, few in number, and scattered among intertwined large and mossy myelinated fibers characteristic of CA4 (Fig. 3.11). It is now often admitted that CA4 is functionally assimilated to CA3 (Insausti and Amaral 2004).

Other divisions have been suggested, in particular by Rose (1927), who divided the cornu Ammonis into five sectors, H1–H5 (H, hippocampus). H1 corresponds to CA1 but also extends into the adjacent subiculum. H2 and H3 correspond to CA2 and CA3, respectively, whereas H4 and H5 correspond to CA4, slightly overlapping into CA3. Vogt and

Vogt (1937) simplified this terminology by limiting themselves to three fields: H1 for CA1, H2 for CA2 and CA3, and H3 for CA4.

Taking into account the different sensitivity to hypoxia in different fields in the cornu Ammonis, CA1 is said to be a “vulnerable sector,” or Sommer sector (Sommer 1880), whereas CA3 is called a “resistant sector,” or Spielmeyer sector (Spielmeyer 1927), CA4 being a sector of medium vulnerability, or Bratz sector (Bratz 1899) (see p. 30). The rich abundance of terminology concerning the cornu Ammonis is noteworthy.

Terminological confusion is augmented by variations in the position of the hippocampus in different species. Thus, during development, the rat hippocampus, which is involved in an only partial hemispheric rotation, remains dorsal (Powell and Hines 1975; König and Klippel 1963). In this species, a division is often distinguished in the hippocampus or cornu Ammonis, separating it into superior and inferior regions (Ramon y Cajal 1911, 1968; Blackstad 1956; Isaacson 1974; Stephan 1983). The superior region contains CA1 and the inferior region CA3. In humans, however, the rotation is complete (Tilney 1939). The hippocampus is ventral, and the relation of CA1 to CA3 is thus the opposite of that found in rats (Fig. 3.6).

3.2.2 Gyrus Dentatus (Fascia Dentata, Gyrus Involutus)

In coronal sections of the hippocampal body, the gyrus dentatus is a narrow, dorsally concave lamina. Its concavity envelopes the CA4 segment of the cornu Ammonis (Figs. 3.7 and 3.9).

The gyrus dentatus is separated from CA1–CA3 by the hippocampal sulcus, which disappears soon after its development and becomes vestigial. A few residual cavities may persist (Figs. 3.7, 3.10, and 5.20). The cornu Ammonis and the gyrus dentatus are thus fused together, separated only by the vestigial hippocampal sulcus. At the far end of this sulcus, the layers of the gyrus dentatus and the cornu Ammonis are so closely approximated that it becomes impossible to distinguish them, but the residual cavities are important in certain case to separate the cornu Ammonis from the gyrus dentatus.

A narrow segment of gyrus dentatus, the margo denticulatus (Klinger 1948), is visible on the temporal lobe surface. In humans, it has a characteristic toothed appearance (see Fig. 4.3). The margo denticulatus is the border of primitive cortex. It overlaps the subiculum, separated from it by the superficial hippocampal sulcus and from the fimbria by the fimbriodentate sulcus (Fig. 3.7).

In structure, the gyrus dentatus is simpler than the cornu Ammonis. The three layers of the allocortex are plainly visible, that is, the strata molecular and granulosum and

the polymorphic layer (Figs. 3.7 and 3.9). The *stratum granulosum*, the main layer, contains somata of granular neurons, which are small and round but densely packed, making the layer easy to distinguish (Fig. 3.12). Their axons are “mossy” and traverse the polymorphic layer to CA4 and CA3. A single dendrite escapes from the basal pole of each granular soma and extends into the stratum moleculare (Fig. 3.13). The *stratum moleculare* is thick and separated from the stratum moleculare of the cornu Ammonis by the vestigial hippocampal sulcus. Its external two thirds near the hippocampal sulcus receives fibers from the perforant pathway (Fig. 3.13), whereas the inner third, in contact with the stratum granulosum, is occupied by commissural and septal fibers (Lynch and Cotman 1975; Cerbone et al. 1993). The *polymorphic layer* (or plexiform layer) unites granular layer to CA4 and is crossed by axons of granular neurons. In the molecular and polymorphic layers, there are few interneurons.

The gyrus dentatus (fascia dentata) and CA4, which it encloses, constitute an entity that Blackstad (1956) designated the *area dentata* (Fig. 3.9), whereas CA4 alone is sometimes called the end folium, the end blade, or the hilus of fascia dentata.

Figures 3.8 and 3.10 show a transverse section of hippocampus after intravascular injection of India ink; the hippocampal organization is partially revealed by differences in density of the capillary network. The special features of the capillary density of different hippocampal regions will be studied in Chap. 5.

3.2.3 Structures Joined to the Hippocampus

The hippocampus is prolonged by the *subiculum* which, from an anatomical point of view, forms part of the parahippocampal gyrus. The end of the stratum radiatum of CA1 is considered to mark the division between the cornu Ammonis and the subiculum (Figs. 3.7 and 3.8) (Lorente de No 1934; Blackstad 1956; Braak 1980). The subiculum itself is divided into several segments (Fig. 3.5; Powell and Hines 1975; Williams 1995): (1) the *prosubiculum*, which continues CA1 (and whose existence is not accepted by all); (2) the *subiculum proper*, partly hidden by the gyrus dentatus; (3) the *pre-subiculum*, whose small, superficial pyramidal neurons are

packed in clusters, making it characteristically maculate (see Figs. 7.15b and 7.16b; Braak 1980; Amaral et al. 1984); and (4) the *parasubiculum*, which passes around the margin of the parahippocampal gyrus to the entorhinal area on the medial aspect of the gyrus. The *entorhinal area* (Brodmann's area 28) is itself poorly demarcated (Amaral et al. 1987). Although its presence in the uncus and anterior end of the parahippocampal gyrus (Figs. 3.4, 3.16, and 3.18) is generally accepted, its posterior extension along the parahippocampal gyrus is uncertain. This posterior extension is thought to be marked in humans where the entorhinal area is well developed (Jacobs et al. 1979; Braak 1980; Hyman et al. 1986). Its special structure will be described later together with its functions (see p. 27).

The *amygdala*, which belongs to the limbic lobe, is often described together with the hippocampus as far as its function is concerned. Its structure, as described by Braak and Braak (1983) and Amaral et al. (1992), is shown in Fig. 3.14. The cortical and medial nuclei are olfactory centers, whereas the basal, lateral, and central nuclei have limbic functions (Aggleton 1992), which are described on p. 29.

From an anatomical point of view, the limbic lobe may be divided into limbic and intralimbic gyri. According to its structure, however, the limbic lobe is usually divided into the *allocortex*, including the hippocampus (cornu Ammonis and gyrus dentatus), the proximal part of the subiculum, and the indusium griseum (the amygdala is often included in this group), and the *periallocortex*, made up of the transitional cortex between the allocortex and isocortex, including the cingulate and parahippocampal gyri (Schwerdtfeger 1984; Chronister and White 1975; Jacobs et al. 1979; Braak 1980; Van Hoesen 1982; Swanson 1983; Kier et al. 1995).

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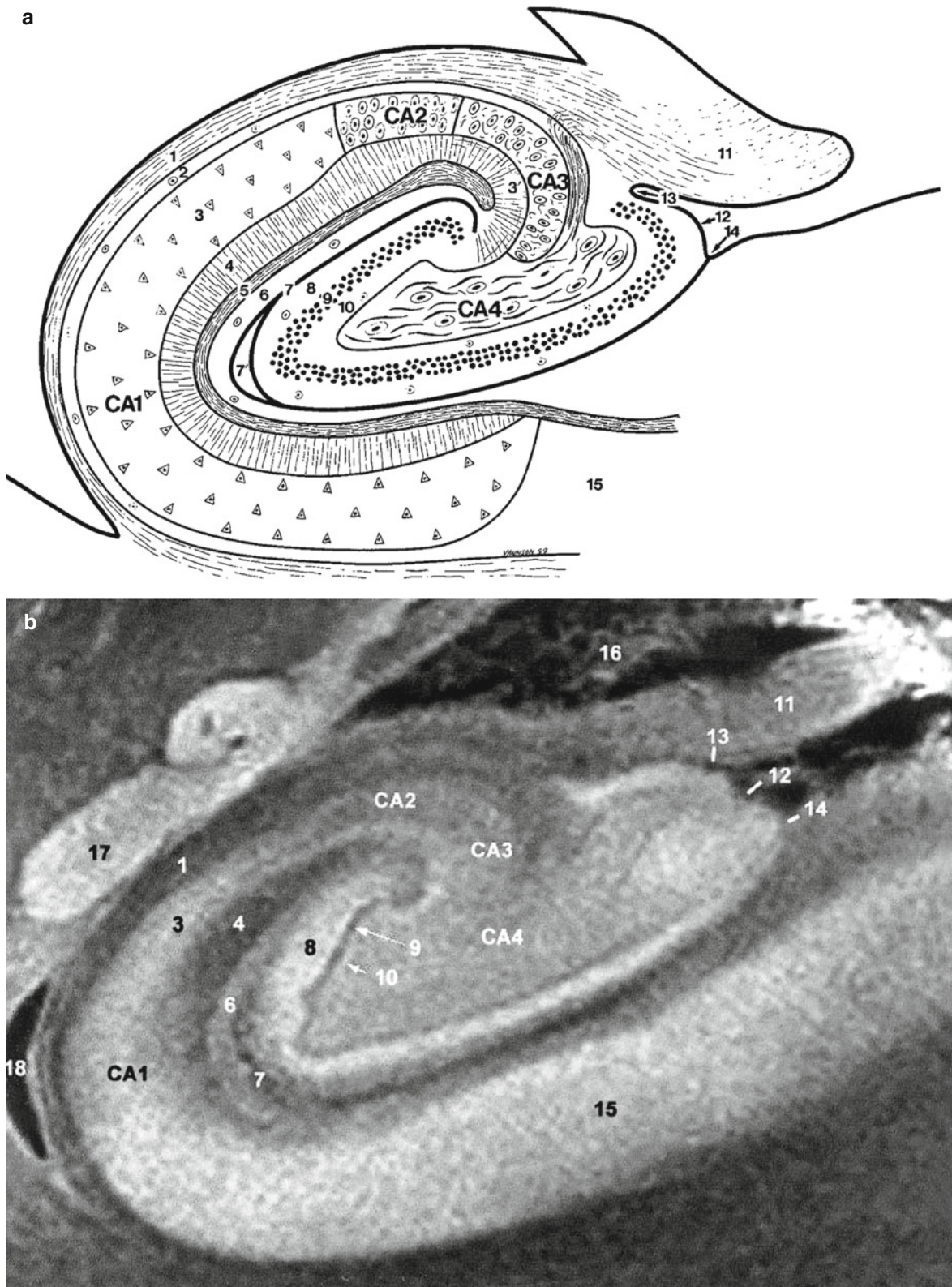


Fig. 3.7 (a, b) Diagram and 9.4T MRI view (From T. Naidich) of the structure of the hippocampus (coronal section) CA1–CA4, fields of the cornu Ammonis. Cornu Ammonis: 1 alveus, 2 stratum oriens, 3 stratum pyramidale, 3' stratum lucidum, 4 stratum radiatum, 5 stratum lacunosum, 6 stratum moleculare, 7 vestigial hippocampal sulcus (note a

residual cavity, 7'). Gyrus dentatus: 8 stratum moleculare, 9 stratum granulosum, 10 polymorphic layer, 11 fimbria, 12 margo denticulatus, 13 fimbriodentate sulcus, 14 superficial hippocampal sulcus, 15 subiculum, 16 choroid plexuses, 17 tail of caudate nucleus, 18 temporal (inferior) horn of the lateral ventricle

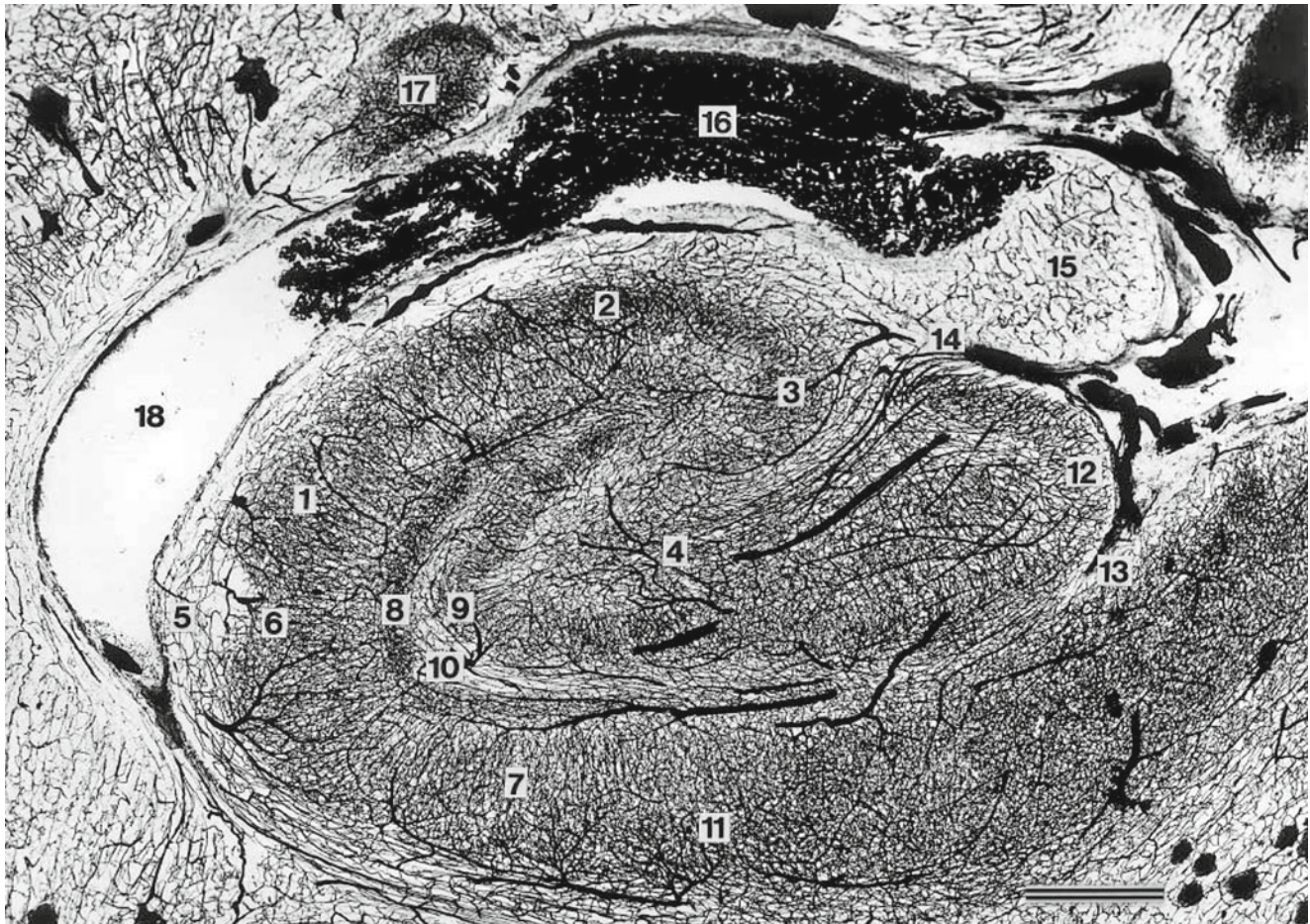


Fig. 3.8 Coronal section of the hippocampal body after intravascular India ink injection. The layers of the hippocampus (see Fig. 3.7) can be distinguished due to differences in their vascular density. The stratum moleculare of the cornu Ammonis (8) and that of the gyrus dentatus (9) are separated by the vestigial hippocampal sulcus (10). Note the high vascular density of the subiculum (11) in comparison to that of the adjacent stratum radiatum of CA1 (7), Bar, 1.5 mm. Cornu Ammonis: 1–4

CA1–CA4 (fields of the cornu Ammonis). Sublayers of CA1: 5 alveus, 6 stratum pyramidale, 7 strata radiatum and lacunosum, 8 stratum moleculare. Gyrus dentatus: 9 stratum moleculare, 10 vestigial hippocampal sulcus, 11 subiculum, 12 margo denticulatus, 13 superficial hippocampal sulcus, 14 fimbriodentate sulcus, 15 fimbria, 16 choroid plexuses, 17 tail of caudate nucleus, 18 temporal (inferior) horn of the lateral ventricle

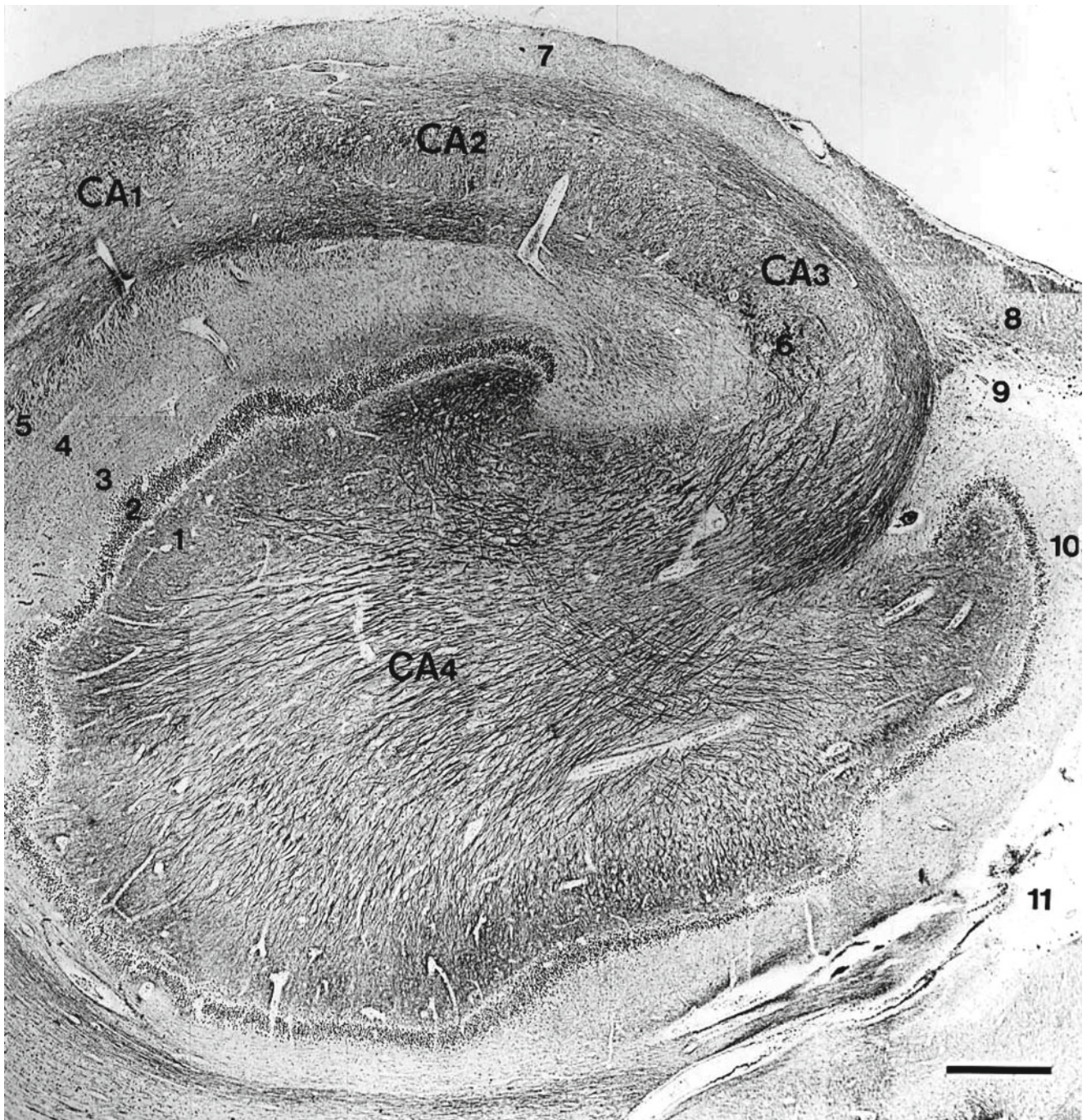


Fig. 3.9 Enlargement of the dentata area. The gyrus dentatus and CA4 together form the area dentata. Silver impregnation, Bodian. Bar, 590 μ m. CA1–CA4, fields of the cornu Ammonis. Gyrus dentatus: 1 polymorphic layer, 2 stratum granulosum, 3 stratum moleculare. Cornu

Ammonis: 4 stratum moleculare, 5 stratum lacunosum, 6 stratum lucidum, 7 alveus, 8 fimbria, 9 fimbriodentate sulcus, 10 margo denticulatus, 11 superficial hippocampal sulcus

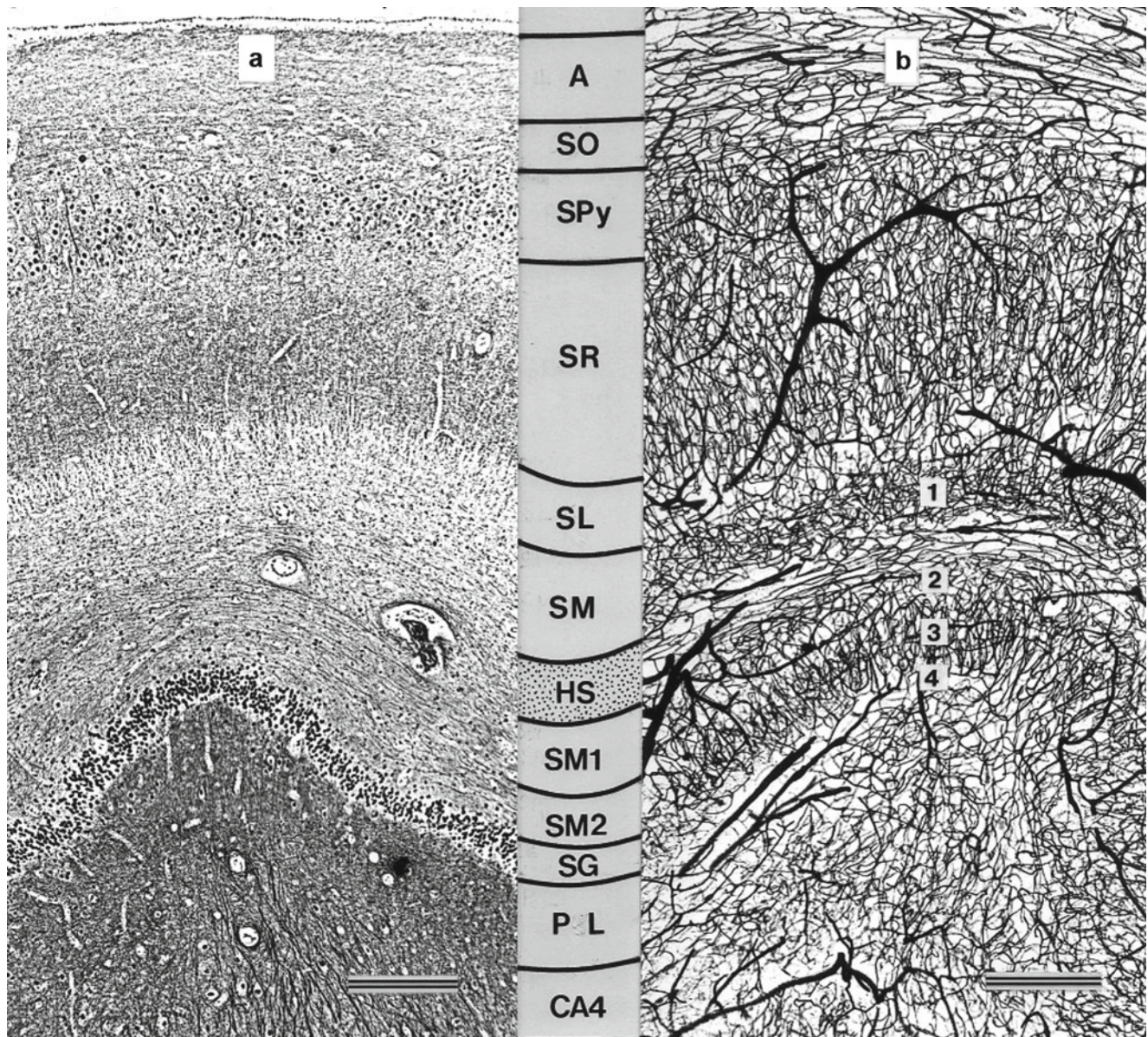


Fig. 3.10 (a, b) Structure of the hippocampus. (a) Silver impregnation (Bodian). (b) Intravascular India ink injection, showing the varying density of the vascular network in different hippocampal layers. Note high vascular density in the stratum moleculare of the cornu Ammonis (1). Bar, 600 μ m. Cornu Ammonis: A alveus, SO stratum oriens, SPy stratum pyramidale, SR stratum radiatum, SL stratum lacunosum, SM

stratum moleculare, HS vestigial hippocampal sulcus. Gyrus dentatus: SM1 stratum moleculare, external two thirds, SM2 stratum moleculare, inner third, SG stratum granulosum, PL polymorphic layer, CA4 field of the cornu Ammonis. 1 Stratum moleculare, 2 external part of stratum moleculare of the gyrus dentatus, 3 inner part, highly vascularized, 4 stratum granulosum, poorly vascularized

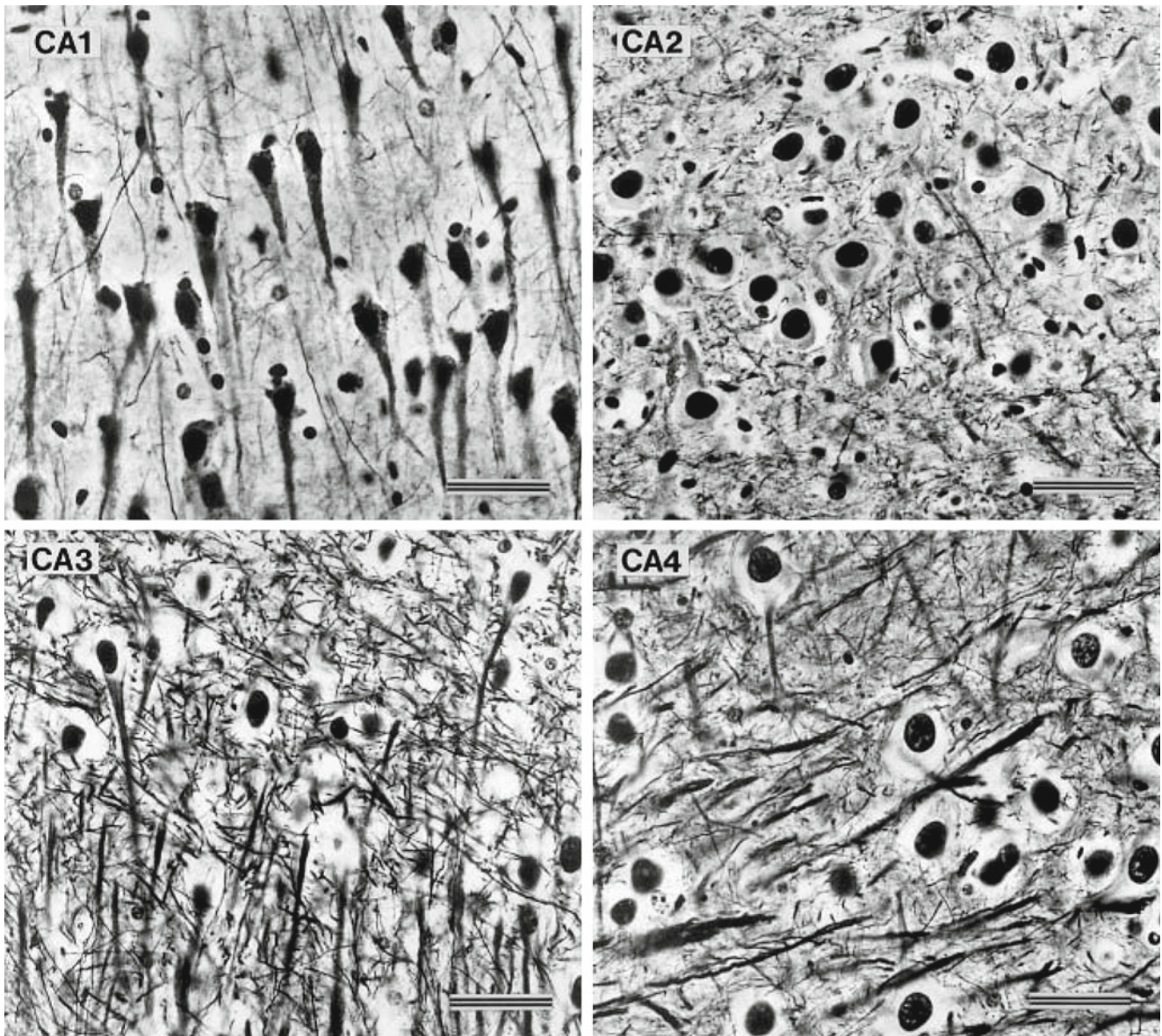


Fig. 3.11 Neuronal types in the cornu Ammonis. Silver impregnation, Bodian. *Bar*, 52 μm . CA1–CA4, fields of the cornu Ammonis

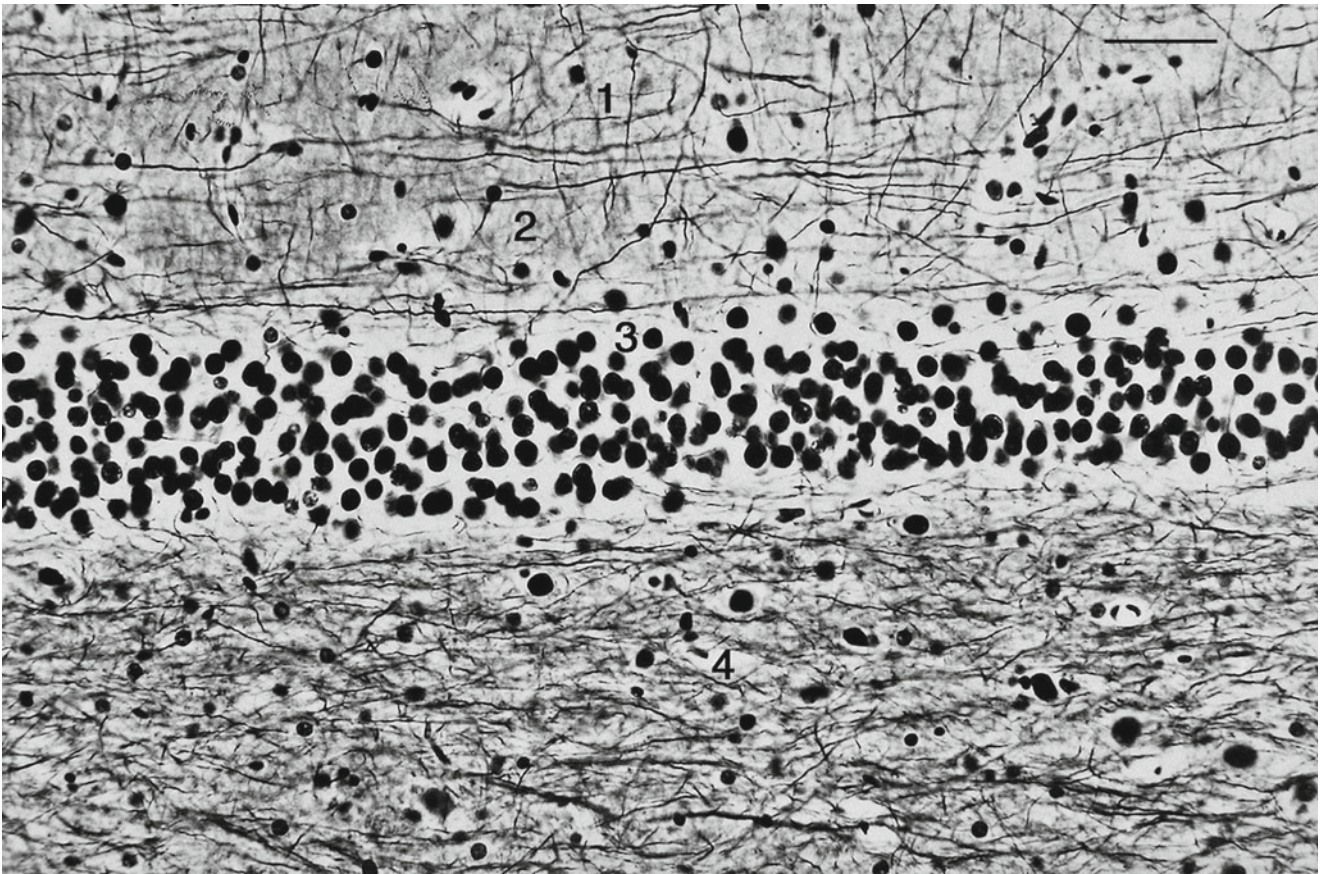


Fig. 3.12 Neuronal types in the gyrus dentatus. Silver impregnation, Bodian. Bar, 85 μ m. 1 stratum moleculare, external part, 2 stratum moleculare, inner part, 3 stratum granulosum, 4 polymorphic layer

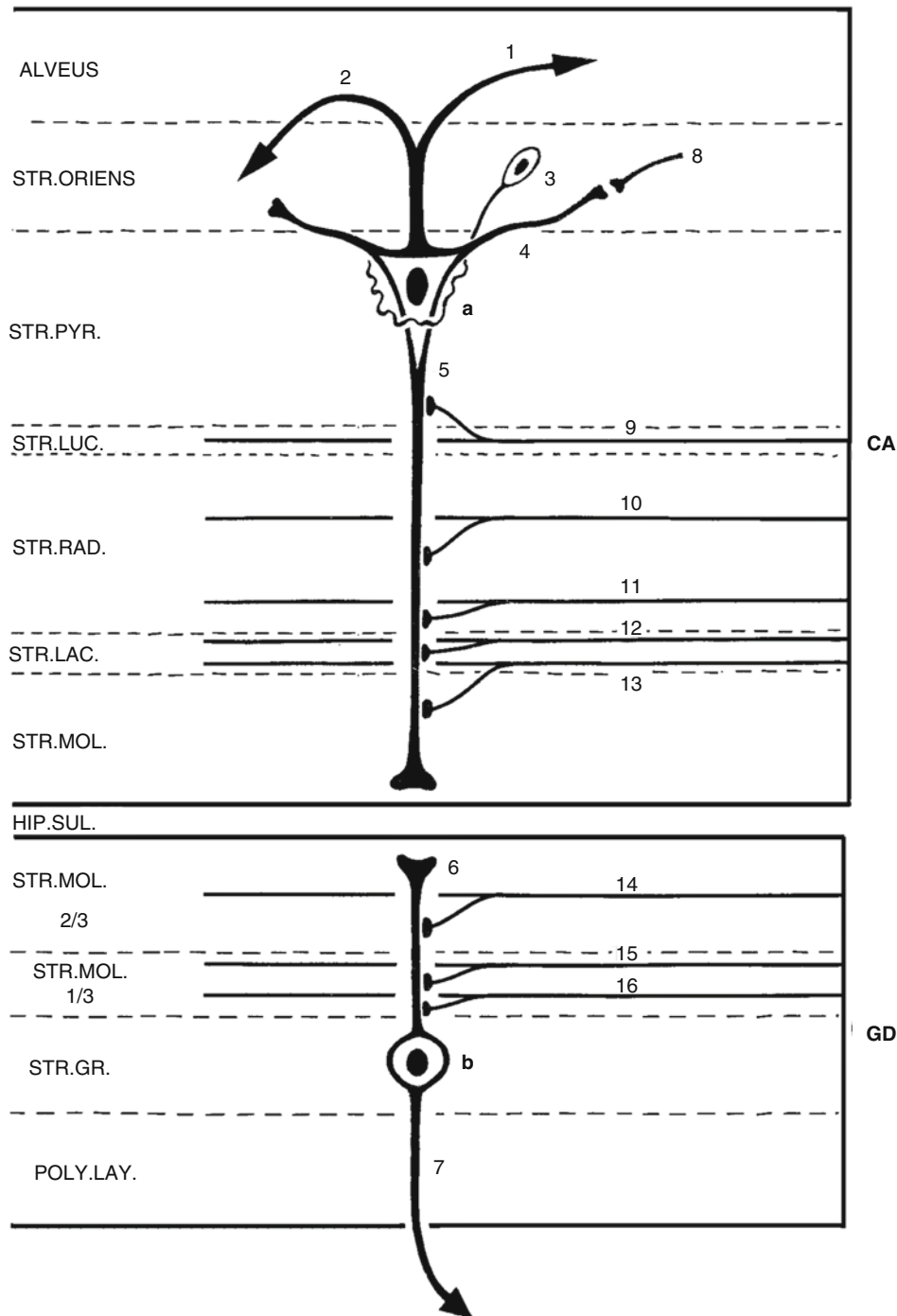


Fig. 3.13 Overview of the principal connections of pyramidal (a) and granular (b) neurons CA cornu Ammonis, GD gyrus dentatus. 1 axon of a pyramidal neuron, 2 Schaffer collateral, 3 basket cell, 4 basal dendrite, 5 apical dendrite, 6 apical dendrite of a granular neuron, 7 axon (mossy fiber) of a granular neuron, 8 connections of a basal dendrite of a pyramidal neuron with other pyramidal neurons and with septal and commissural fibers, 9 mossy fibers (stratum lucidum into CA3), 10 septal and commissural fibers, 11, 12 Schaffer collaterals, 13, 14 perforant

path, 15 commissural fibers, 16 septal fibers. Layers of the cornu Ammonis: alveus, stratum oriens (*STR. ORIENS*), stratum pyramidale (*STR. PYR.*), stratum lucidum (*STR. LUC.*), stratum radiatum (*STR. RAD.*), stratum lacunosum (*STR. LAC.*), stratum moleculare (*STR. MOL.*), vestigial hippocampal sulcus (*HIP. SUL.*). Layers of the gyrus dentatus: stratum moleculare, external two thirds (*STR. MOL. 2/3*), stratum moleculare, inner third (*STR. MOL. 1/3*), stratum granulosum (*STR. GR.*), polymorphic layer (*POLY. LAY.*)

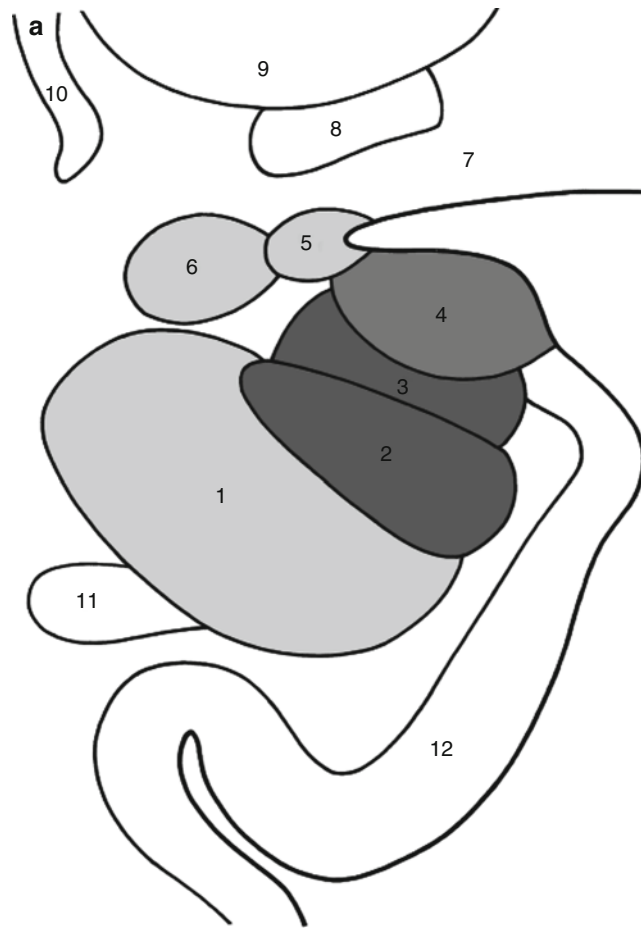


Fig. 3.14 (a, b) Structure of the amygdala. (a) Drawing of a coronal section. (b) Intravascular India ink injection. Bar, 1.8 mm. 1 lateral nucleus, 2 basal nucleus, 3 accessory basal nucleus, 4 cortical nucleus,

5 medial nucleus, 6 central nucleus, 7 anterior perforated substance, 8 anterior commissure, lateral part, 9 putamen, 10 claustrum, 11 uncal recess of the temporal horn, 12 ambient gyrus



Fig. 3.14 (continued)

3.3 Functions and Connections

This section, which goes beyond the author's field of research, is based on an abundant body of work found in the literature, in particular the following: Ramon y Cajal 1911; Lorente de No 1934; Papez 1937; Blackstad 1958; Crosby et al. 1962; Hjorth-Simonsen and Jeune 1972; Andersen 1975; Chronister and White 1975; O'Keefe and Nadel 1978; Walaas 1983; Lopez da Silva et al. 1984; Schwerdtfeger 1984; Crunelli et al. 1985; Teyler and DiScenna 1985; Van Hoesen 1985; Rosene and Van Hoesen 1987; Amaral and Insausti 1990; Squire and Zola-Morgan 1991; MacLean 1992; Eichenbaum et al. 1994; Markowitsch 1995a, b; Williams 1995; Suzuki and Clayton 2000; Amaral and Lavenex 2007; and Nieuwenhuys et al. 2008.

Based on this significant amount of research, only a general survey of the hippocampal functions shall be given here. It should be noted that some of the results presented here are controversial and may thus be subject to discussion. However, it may be helpful for the reader to find an overview of the hippocampal functions, as currently described, even if some of these hypotheses are not considered to be valid ones in the future. The possible functions of the hippocampus are divided into four categories: (1) learning and memory, (2) regulation of emotional behavior, (3) certain aspect of motor control, and (4) regulation of hypothalamic functions.

3.3.1 Learning and Memory

It is generally admitted that the hippocampus has a critical role in learning and memory. Information arising from large isocortical zones converges to the entorhinal area and then to the hippocampus. Thus, newly acquired items cross the hippocampal filter before being fixed in the isocortex. It is possible to distinguish the memory of new or recent items, which depends on the hippocampus (short-term memory), from that of the old ones (long-term memory), which depends on the isocortex. The entorhinal area, despite its small size, is the principal input to the hippocampus. It is composed of the periallocortex and is divided into deep and superficial layers (Hevner and Wong-Riley 1992; Insausti et al. 1995; Solodkin and Van Hoesen 1996). The superficial layers mainly comprise layers II and III (see Figs. 3.15 and 3.17). In layer II, clusters of large pyramidal neurons (Hyman et al. 1986; Green and Mesulam 1988) are visible on the surface of the entorhinal area, which has a granular aspect (verrucae gyri hippocampi; Fig. 4.8). This aspect allows macroscopical delineation of the limits of the entorhinal area, which is situated mainly on the piriform lobe and extends caudally along the subiculum to the parahippocampal gyrus.

The hippocampus is implicated in all aspects of the declarative memory, that is, the *semantic memory*, which

involves memory of facts and concepts; the *episodic memory*, which permits conscious recollection of events and the relations between them; and the *spatial memory*, which involves spatial location recognition (Kopelman 1993; Eichenbaum et al. 1994; Kesner 1994; Markowitsch 1995a, b). Thus, it should be noted that the hippocampal allocortex, composed of only three layers, has very high cognitive functions. Moreover, the hippocampal neurons have remarkable plasticity: repetitive stimulations produce a persistent modification of their physiological state (long-term potentiation; Trillet 1992). Finally, the hippocampus can produce new neurons throughout life (Eriksson et al. 1998).

After passing through the hippocampus, the information to be memorized is stored in the association cortex. The hippocampal projections involve large neocortical areas, including in particular the prefrontal and retrosplenial cortices (Markowitsch 1995a, b), as shown by positron emission tomography (PET) and functional MRI methods. At present, the storage mechanisms are largely unknown; they may be based on persistent changes in the biochemical structure of neurons obtained through a chain of biological modifications. Certain neurotransmitters are involved in these modifications, such as acetylcholine (ACh), arginine vasopressin (AVP), and endorphins.

The hippocampal pathways involved in learning and memory, their control, and a brief survey of clinical implications will be studied below.

3.3.1.1 Hippocampal Pathways Involved in Memory

Based on the course of the intrahippocampal fibers, it is possible to divide the intrahippocampal circuitry into two pathways: the *polysynaptic pathway*, which links all parts of the hippocampus by a long neuronal chain, and the *direct pathway*, which directly reaches the output neurons of the hippocampus. For more information, the reader is referred to the following works: Amaral and Insausti 1990; Maclean 1992; Witter and Groenewegen 1992; Eichenbaum et al. 1994; Leonard et al. 1995; and Markowitsch 1995a, b.

Polysynaptic Intrahippocampal Pathway (Figs. 3.15 and 3.16)

The intrahippocampal circuitry is composed of a long neuronal chain made up of the entorhinal area, the gyrus dentatus, CA3, CA1, and the subiculum. First of all, its organization will be studied, and its cortical projections and functions will then be described.

The origin of the *polysynaptic pathway* is layer II of the *entorhinal cortex* (Amaral and Insausti 1990), from which the perforant path arises. The *perforant path* "perforates" the subiculum to reach the gyrus dentatus. The majority of the fibers making up the perforant path reach the stratum moleculare of the *gyrus dentatus* after traversing the vestigial hippocampal sulcus. In the

external two thirds of the molecular layer, they are in contact with dendrites of granular cells (Cerbone et al. 1993). Thus, the perforant path, composed of glutaminergic fibers, has an excitatory action on the gyrus dentatus.

The next link in the chain is the *gyrus dentatus*, whose axons of granular neurons, the mossy fibers, are glutaminergic and have a large content of zinc (McLardy 1962; Frederikson et al. 1983). These fibers traverse the polymorphic layer and stimulate the dendrites of CA4 and especially those of CA3 (Treves 1995).

The axons of CA3 and CA4 enter the alveus and then the fimbria; however, they first emit the Schaffer collaterals, which reach the apical dendrites of CA1 in the strata radiatum and lacunosum (Fig. 3.13). The CA2 field, which has not yet been discussed here, is in fact quite distinct in human and has an obscure role. Its marked cellular density and its intense vascularization (see Chap. 5) might, however, correspond to a particular function (Veazey et al. 1982).

Since Ramon y Cajal's description (Ramon y Cajal 1911), axons of CA1 have been considered the main output of the hippocampus by way of the *alveus* and then the fimbria. Currently, a supplementary link is considered to be joined to the chain, a link formed by the subiculum. Thus, by entering the alveus, the axons of CA1 produce collaterals which reach the subiculum.

The *subiculum* therefore emits the definitive response, by fibers constituting the major part of the alveus and then the fimbria. The neurons of the subiculum are glutaminergic, as are those of the preceding parts of the polysynaptic chain (Francis et al. 1994).

The *polysynaptic pathway* is thus composed of the following elements: the entorhinal area, the gyrus dentatus, the cornu Ammonis, and the subiculum. For this reason, these structures, with their disparate anatomy, are sometimes grouped together as the "hippocampal formation," a single functional unit (Powell and Hines 1975; Rakic and Nowakowski 1981; Teyler and DiScenna 1984; Amaral and Campbell 1986; Squire 1986).

Since the studies carried out by Blackstad et al. (1970), Andersen et al. (1971), Hjorth-Simonsen and Jeune (1972), and Andersen (1975), precise arrangements have been attributed to the hippocampal pathways; the hippocampus may hence contain many lamellae arranged transverse to the hippocampus axis. Each lamella is a functional unit, with a narrow strip of gyrus dentatus linked to a narrow strip of CA3 and then CA1. Likewise, neurons in the entorhinal area may be precisely arranged in relation to each lamella. Finally, all lamellae may be associated by longitudinal fibers, as described by Schaffer (1892), Ramon y Cajal (1911, 1968), and Lorente de No (1934). This lamellar arrangement, which appears to be restricted to the mossy fibers, has been recently discussed (Amaral and Witter 1989; Witter and Groenewegen 1992; Amaral and Insausti 1990).

Hippocampal Output to the Cortex (Fig. 3.16)

The principal outputs of the polysynaptic pathway to the cortex follow the fimbria, the crus and body of the fornix, and the columns of the fornix, also known as the postcommissural fornix (behind the anterior commissure). The nervous impulses then reach the anterior thalamic nucleus, either directly (Devinsky and Luciano 1993) or via the mammillary bodies, extending from there into the mammillothalamic tract. Other thalamic nuclei, such as the intralaminar nuclei, and the hypothalamus may possibly be reached (O'Keefe and Nadel 1978; Teyler and DiScenna 1984; Bentivoglio et al. 1993).

From the thalamus, impulses reach the posterior cingulate cortex (area 23) and the retrosplenial cortex (areas 29 and 30). Some projections reaching the anterior cingulate cortex (area 24) will be discussed later.

Input from the Cortex (Fig. 3.16)

The fibers originate in a large cortical area which include many sites where the sensory informations converge such as posterior parietal association cortex (area 7) and the neighboring temporal and occipital cortices (areas 40, 39 and 22) (Swanson 1983; Braak et al. 1996 and Nieuwenhuys 2008). In the monkey, this cortex is restricted to the sides of the superior temporal sulcus, that is, the middle temporal (MT) and medial superior temporal cortices (MST). The posterior parietal association cortex sends fibers to the entorhinal area through the parahippocampal gyrus. The main function attributed to the posterior parietal association cortex, related to the superior visual system, is perception of the position of an object in space (Andersen et al. 1990; Mountcastle 1995; (Where) Suzuki and Amaral 2004). This spatial perception is thought to then be memorized through the polysynaptic pathway, and the episodic memory and the memory of facts in relation to each other apparently also depend on this system. The polysynaptic pathway and its cortical projections are often referred to as the *medial limbic system of Papez* (Papez 1937) or the *Delay and Brion system* (Delay and Brion 1969; Suzuki 2009).

Direct Intrahippocampal Pathway (Figs. 3.17 and 3.18)

The direct intrahippocampal pathway is referred to as being direct because the fibers reach CA1 and the hippocampal outputs directly without following the polysynaptic chain.

The origin of the direct pathway is found in layer III of the entorhinal cortex (Fig. 3.17). From this layer, fibers directly reach the pyramidal neurons of CA1 by a different pathway from that of the perforant path (Du et al. 1993). The CA1 neurons project onto the subiculum, the axons of which return to the deep layers of the entorhinal area (MacLean 1992).

Hippocampal Output to the Cortex

The output of the direct pathway to the cortex is believed to reach the inferior temporal association cortex, the temporal pole, and the prefrontal cortex (Fig. 3.18).

Input from the Cortex

The main input from the cortex (Fig. 3.18) is the inferior temporal association cortex (areas 37, 20), which reaches the entorhinal area through the perirhinal cortex (areas 35, 36). The functions of this cortex, which is connected to the inferior visual system, are the recognition and description of objects (*What* – Suzuki and Amaral 2004), the memorization of which may depend on the direct pathway. More generally, the semantic memory is believed to involve this system.

In conclusion, the fundamental function of hippocampus and entorhinal cortex in the memorization process is generally accepted. It depends on two systems, each with specific functions (Squire et al. 1994): the *polysynaptic pathway*, the most primitive one, is mainly involved in episodic and spatial memory, whereas the *direct pathway*, the most important in humans, is mainly involved in semantic memory. Before converging on the entorhinal cortex, the cortical fibers related to the polysynaptic pathway relay to the parahippocampal gyrus, whereas those connected to the direct pathway reach the hippocampus through the perirhinal cortex (Suzuki 1994; Suzuki and Amaral 1993, 1994, 2004; Leonard et al. 1995; Williams 1995). In both pathways, the entorhinal area has a crucial role. It is the sole input to the hippocampus, with the subiculum as its main output. It seems that the entorhinal area and subiculum are divided into specific functional zones (Amaral et al. 1987; Witter and Groenewegen 1992). In the medial temporal lobe, memory systems (MTLMS; Squire and Zola-Morgan 1991; Suzuki and Amaral 2004; Suzuki 2009) include the hippocampus, entorhinal, perirhinal, and parahippocampal cortices. The last two areas play important roles and, in some cases, may stand in for the hippocampus. In particular, the perirhinal cortex detects and recognizes previously perceived stimuli (recognition memory, Suzuki and Clayton 2000). The right hippocampus seems particularly involved in memory for locations, and the left is more involved in episodic memory (Burgess et al. 2002). In a general way, it seems that the right hippocampus is often larger than the left hippocampus. It is also reported that the hippocampus is larger in women than men (Agartz et al. 1999).

The role of the amygdala in memorization is controversial. It may act in parallel with the hippocampal pathways (Aggleton 1986; Devinsky and Luciano 1993; Markowitsch 1995a, b). From the basal and lateral nuclei of the amygdala (see Figs. 3.14 and 3.20b), the ventral amygdalofugal tract reaches the dorsomedial thalamic nucleus, whose function in memory are well known (Squire and Zola-Morgan 1988). However, the involvement of the amygdala in memory is a matter of debate and is even denied by some (Zola-Morgan et al. 1989; Nieuwenhuys et al. 2008).

3.3.1.2 Regulatory Circuits

Numerous circuits may regulate the main principal pathways and can thus be described as internal regulatory circuits,

entirely within the hippocampus, and external regulatory circuits, which involve extrahippocampal structures.

Internal Regulatory Circuits

Basket Neurons. The basic elements in these circuits are the interneurons, so-called basket neurons, described by Ramon y Cajal (1911, 1968), which occur in the cornu Ammonis and gyrus dentatus. In the cornu Ammonis, they are largely situated in the stratum oriens but are also scattered in other layers. They receive impulses from pyramidal neurons, and their axons return to numerous such neurons, forming basket arborization around their cell bodies (Fig. 3.13). Through their GABA-containing fibers, basket neurons powerfully inhibit pyramidal neurons (Haefely and Polc 1986; Nunzi et al. 1986). In the gyrus dentatus (Amaral and Campbell 1986), basket neurons situated in the molecular and polymorphic layers may influence granular neurons, just as basket neurons in the cornu Ammonis influence pyramidal neurons. In other words, basket neurons, stimulated at first by collaterals of mossy fibers, go on to inhibit granular neurons by retroaction. Thus, the GABAergic interneurons modulate the hippocampal functions (Buckmaster and Soltesz 1996).

Neurotransmitters. Interneurons producing neurotransmitters other than GABA have been described in the hippocampus. The cornu Ammonis and gyrus dentatus do in fact contain neurons producing substance P, vasoactive intestinal polypeptide (VIP), cholecystokinin (CCK), somatostatin, corticotrophin-releasing factor (CRF), and neuropeptide Y. All such neurons intervene in local inhibitory or excitatory circuits (Amaral and Campbell 1986; Köhler et al. 1986; Nunzi et al. 1986; Chan Palay 1987). In addition, granular neurons from the gyrus dentatus may produce enkephalins and dynorphins, which may reach the cornu Ammonis through mossy fibers (Siggins et al. 1986). However, some investigators believe that enkephalin-containing neurons are present in only very small numbers in humans, and thus, distribution of neuropeptides could be very variable according to species (Sakamoto et al. 1987).

Pyramidal Neurons. Finally, it seems possible that the pyramidal neurons might influence each other. In fact, collaterals of their axons connect with basal dendrites of other pyramidal neurons (Fig. 3.13).

External Regulatory Circuits

The external regulatory circuits involve the septal nuclei, the contralateral hippocampus by commissural fibers, neuromediators of extrahippocampal origin, and certain areas of cerebral cortex.

Septal Nuclei. Chief circuits uniting septal nuclei and the hippocampus (Fig. 3.19) have been known since the studies performed by Green and Arduini (1954) and later by Petsche et al. (1962), Lynch et al. (1978), and Swanson (1978).

Axons of hippocampal subicular pyramidal neurons are the origin of these circuits (Fig. 3.15). Via the fimbria and

then the precommissural fornix (in relation to the anterior commissure), such fibers reach the lateral septal nucleus, from which impulses reach the medial septal nucleus and the nucleus of the vertical limb of the diagonal band (Fig. 3.20a). These two nuclei are important cholinergic centers: Ch1 for the medial septal nucleus and Ch2 for the nucleus of the vertical limb. From these nuclei, cholinergic and GABAergic fibers project back to the hippocampus by the same route, that is, the precommissural fornix and fimbria (Fig. 3.19).

Septal fibers end on granular neurons in the gyrus dentatus and pyramidal neurons in the cornu Ammonis (Fig. 3.13). The septal cholinergic fibers are excitatory, acting on pyramidal and granular neurons (Bilkey and Goddard 1985) either directly or indirectly by inhibiting the inhibitory action of hippocampal interneurons. They enhance the capacity for memorization, especially for spatial memory and learning (Stackman and Walsh 1995; Alonso et al. 1996).

Through these projections, the septum may control a special hippocampal activity, the rhythmic slow wave activity or theta rhythm. The septum itself may be controlled by excitatory or inhibitory influences from the brain stem's reticular formation (Vanderwolf et al. 1985). Rhythmic slow wave activity, controlled by the septum, is thought to be localized in the gyrus dentatus and CA1. Unlike the fast and continuously desynchronized rhythm of wakefulness, the theta rhythm is slow and only present during specific types of behavior, such as exploration of an unknown environment (O'Keefe and Nadel 1978; Vertes 1985). It has also been implicated in learning (Schwerdtfeger 1984). It should be noted, however, that the hippocampal theta rhythm has not been clearly detected in humans or other primates. Finally, the septum may have a modulatory role (as a pacemaker) on information arriving in the hippocampus from the entorhinal cortex (Lynch et al. 1978; O'Keefe and Nadel 1978; Lopez da Silva et al. 1984, 1985; Bland 1986; Ridley et al. 1996).

Commissural Fibers. The two hippocampi are joined via the fornix by commissural fibers. In rodents, all hippocampal regions are connected to the corresponding contralateral regions. In primates, however, commissural fibers are debated (Amaral et al. 1984). The work of Gloor et al. (1993) shows a dorsal hippocampal commissure *in humans*, connecting mesiotemporal and particularly left and right entorhinal areas. This dorsal hippocampal commissure is attached to the ventral surface of the splenium and corresponds to the previously described psalterion. In humans, a ventral hippocampal commissure located near the anterior commissure is uncertain.

Neuromediators. Numerous endings of nerve fibers of extrahippocampal origin which liberate neuromediators have been described in the hippocampus, where they certainly play a regulatory role.

In addition to cholinergic septal fibers, terminals of monoaminergic pathways have been described in the hippocampus (Moore 1975). Thus, noradrenergic fibers arising from the

locus coeruleus and belonging to the dorsal noradrenergic bundle (Davis et al. 1989) may reach the hippocampus via the fornix but also via the longitudinal striae (Nieuwenhuys 1985). Serotonergic fibers from the nuclei of the raphe may also reach the hippocampus via the longitudinal striae, perhaps with an inhibitory role (O'Keefe and Nadel 1978). The presence of dopamine is more doubtful, although in rodents only a limited number of fibers have been described coming from the substantia nigra (A9) and ventral tegmental area (A10) (Bischoff 1986). In humans, the dopaminergic projections seem to be more abundant (Samson et al. 1990).

Many neuropeptidergic terminals have been found in the hippocampus, such as vasopressin, somatostatin, substance P, neuropeptide Y, and α -melanocyte-stimulating hormone (α -MSH), although their functions have not been explained (Nieuwenhuys 1985).

Cortical Regulation. Direct connections seem to exist between the neocortex and the hippocampus (Schwerdtfeger 1979). Thus, the cingulate gyrus projects directly to hippocampus. Direct afferents from temporal and prefrontal lobes have also been described.

3.3.1.3 Clinical Implications

Clinical observations after surgical ablation and in neurological diseases show that, in humans, the deficits brought about by hippocampal damage mainly produce disorders of memory, particularly short-term memory (Vanderwolf et al. 1985). Marked defects in remembering events that occur after appearance of the lesion (producing anterograde amnesia) can be observed, but most frequent defects are in spatial memory.

The etiology of many hippocampal disorders has been the root of much controversy, particularly in explaining lesions that cause temporal lobe epilepsy. It has long been observed that the CA1 field (and adjacent subiculum) has a specific sensitivity to anoxia. CA1 is therefore known as the vulnerable sector or Sommer sector (Sommer 1880). In contrast, CA3 remains healthy and is known as the resistant Spielmeyer sector (Spielmeyer 1927). CA4 (end folium) is only partially affected (Bratz sector; Bratz 1899). The sensitivity of CA2 to anoxia is controversial; for some researchers, it belongs to the resistant sector (Rutecki et al. 1989; Kotapka et al. 1994) and, for others, to the vulnerable sector (Zola-Morgan et al. 1992; Kartsounis et al. 1995). Lesions of CA1, and to a lesser degree of CA4, constitute the classic sclerosis of the cornu Ammonis, or mesial temporal sclerosis, and frequently produce memory impairment (Zola-Morgan et al. 1986). A loss of digitations in the hippocampal head is a sign of mesial temporal sclerosis (Oppenheim et al. 1998).

The selective vulnerability of certain hippocampal regions to anoxia has not yet been fully explained (Margerison and Corsellis 1966). It was first proposed that vascular arrangements might be the cause of this selective vulnerability (vascular theory; Scharrer 1940; Gastaut and Lammers 1961).

The studies by Uchimura (1928) showed that the vulnerable sector (CA1) was supplied by *long arteries*, which are more sensitive to variations in blood pressure than those of the resistant sector supplied by *short arteries* (see Chap. 5). Spielmeier (1927) believed that epileptic seizure produces vascular spasms causing secondary damage to this vulnerable sector, but Penfield and Jasper (1954) were of the opinion that a primary vascular disorder produces the lesion, perhaps due to trauma at birth leading to herniation of the temporal lobe through the *tentorial incisure* and compression of vessels supplying the hippocampus; Gastaut and Lammers (1961) extended this idea of vascular damage to any cause of temporal herniation, such as cranial trauma or cerebral infarct. The hippocampal lesion produced by this mechanism was called *incisural sclerosis* (Earle et al. 1953).

The specific arrangements of the CA1 arteries (Chap. 5) resemble those of arteries supplying Purkinje neurons in the cerebellum (Duvernoy et al. 1983). However, selective ischemic lesions of CA1 have the same appearance as those found in the region of Purkinje neurons (Spielmeier 1930; Scharrer 1944; Corsellis and Meldrum 1976; Corsellis and Bruton 1983).

However, despite the specific arrangement of the vessels, the vascular theory explaining the selective vulnerability of the hippocampus to anoxia was criticized by Vogt and Vogt as early as 1937 and has now been abandoned (Nilges 1944; Fleischhauer 1959; Friede 1966; De Reuck et al. 1979), yielding to a theory based on metabolic characteristics of neurons or on features of synapses and, more particularly, of receptors on pyramidal neurons.

A sudden and transient experimental cerebral ischemia in rats produces delayed and irreversible cell damage in the CA1 field of the hippocampus. The lesion does not appear until after an interval of about 4 days, whereas a lesion in CA4 is rapid but reversible (Kirino 1982; Kirino et al. 1986). *The delayed neuronal death* appearing in CA1 can be avoided experimentally by the previous destruction of CA3, the current explanation for which is that glutaminergic synapses of Schaffer collaterals originating in CA3 may have a toxic effect on CA1 during anoxia (Onodera et al. 1986). Thus, blockage of synaptic terminals on a neuron might protect it from the consequences of anoxia (Johansen et al. 1984; Rothman 1984). The toxic excitatory action of glutaminergic neurons of CA3 on CA1 may be due to lesion of GABAergic interneurons (Khazipov et al. 1993). At present, the oversecretion of glutamate by CA3 is criticized (Schmidt-Kastner and Freund 1991), and the selective vulnerability of CA1 seems to be due to an overactivity of glutamate receptors (*N*-methyl-D-aspartate receptors, NMDA; Du et al. 1993), which are especially numerous on CA1 neurons, and to an increased intracellular concentration of Ca^{2+} , which are especially numerous on CA1 neurons, and to an increased intracellular concentration of Ca^{2+} , which produces degenerative processes in these neurons (Kudo et al. 1990; Olney et al.

1993; Kotapka et al. 1994; Ikonovic et al. 1995; Schreiber and Baudry 1995). The origin of the selective vulnerability of specific hippocampal neurons to anoxia remains unclear.

Selective damage also occurs in certain hippocampal regions from causes other than anoxia (Pinard et al. 1984). Kainic acid produces selective lesions in CA3, which might be due to a dysfunction of synapses between terminals of mossy fibers and pyramidal neurons in this field (Collins 1986). Damage in the gyrus dentatus has also been observed in hypoglycemia (Collins 1986).

Hippocampal neuronal loss in aging and Alzheimer's disease seems to be different, although some discrepancies exist between the findings of different researchers, perhaps due to interindividual variations; in *aging*, the main site of neuronal loss is described as being either in CA1 and CA4 (Mani et al. 1986; West 1993) or restricted to CA1 and the subiculum (Simic et al. 1997). In *Alzheimer's disease*, although a lesion of the subiculum is always found, the occurrence of such damage in either CA1 (Bell and Ball 1981; Haigler et al. 1985; Doebler et al. 1987; West 1993) or the gyrus dentatus (Simic et al. 1997) is debated. Only the CA2 field seems to escape damage.

Obviously, all these observations cannot be explained by the peculiar arrangement of vessels, but they do support the idea of a cell-specific structure of the different hippocampal fields (Babb et al. 1984; Haigler et al. 1985; Mani et al. 1986). The lesions specific to each of these different fields suggest that each has specific functions (Lopes da Silva and Arnolds 1978). This fine specialization is a remarkable feature of the hippocampal allocortex (For more information concerning the implication of the hippocampus in human disease, see Walker et al. 2007).

3.3.2 Emotional Behavior

Since the studies carried out by Papez (1937), regulation of emotional behavior has been considered the chief function of the hippocampus. At present, this function is mainly ascribed to the amygdala (LeDoux 1993; Gallagher and Holland 1994). Fibers arising from the basolateral amygdalar nucleus, which project to the dorsomedial thalamic nucleus and then to the prefrontal cortex, are thought to regulate an individual's behavior. Moreover, the central nucleus of the amygdala is believed to modulate the autonomic reactions produced by emotions (Martin et al. 1991). It is, however, accepted that the hippocampus may intervene in the regulation of some emotional behavior, especially that produced by pain; projections from the polysynaptic hippocampal pathway converge on the anterior cingulate cortex (area 24; Fig. 3.16), where end the spinoreticulothalamocortical pathways involved in the perception of some aspect of pain (Maclean 1992; Vogt et al. 1993; Graybiel et al. 1994; Adolphs et al. 1995; Ono et al. 1995; Williams 1995).

3.3.3 Motor Control

The hippocampus is believed to participate in the control of the *ventral striatal loop* (or limbic loop) belonging to the limbic system (Groenewegen et al. 1991; Witter and Groenewegen 1992; Maclean 1992). The ventral striatal loop (Fig. 3.20) is organized like the well-known dorsal striatal loop but involves different structures. The main center of this loop is the ventral striatum or nucleus accumbens (Fig. 3.20a), which receives projections from the prefrontal cortex and control the ventral pallidum. The ventral pallidum, which is of ill-defined location in humans (Fig. 3.20b), projects to the dorsomedial thalamic nucleus, although this projection is controversial in primates (Haber et al. 1993). From the dorsomedial nucleus, fibers return to the prefrontal cortex. The ventral striatum (nucleus accumbens) is itself controlled by dopaminergic fibers arising from the ventral tegmental area (cell group A10) and belonging to the dopaminergic mesolimbic system, as well as by the amygdala and the hippocampus. Fibers from the hippocampus reach the ventral striatum by way of the precommissural fornix (Lavin and Grace 1994). The ventral striatal loop may play a role in the control of motor behavior (e.g., motor reaction of emotion) and are thought to be involved in the mechanism of drug addiction (Williams 1995).

3.3.4 Hypothalamus

The hippocampus is involved in the regulation of the hypothalamo-hypophysial axis. Through its projections to the

paraventricular hypothalamic nucleus, it may inhibit the hypophysial secretion of adrenocorticotrophic hormone (ACTH) (Jacobs et al. 1979; Teyler et al. 1980; Herman et al. 1989; Diamond et al. 1996).

3.3.5 Comparative Studies

This survey of the main hippocampal functions is of course incomplete, and some of these functions are controversial. Comparative studies do not shed much light on hippocampal functions. The size of the hippocampus generally increases in higher species (O'Keefe and Nadel 1978; Stephan 1983; West and Schwerdtfeger 1985). The very large size of the primate hippocampus, in contrast to that in insectivores, might be correlated with improved learning and memory. However, some highly evolved species, such as dolphins (Addison 1915; Jacobs et al. 1979) and whales (Stephan and Manolescu 1980; Schwerdtfeger 1984), have a small hippocampus. Moreover, hippocampal functions may differ among species (Howe and Courage 1993; Markowitsch 1995a). Notable support for this hypothesis is provided by the following: the particular development of certain zones, such as CA1 and the gyrus dentatus in humans and monkeys (Tilney 1939; Stephan and Manolescu 1980; Amaral and Campbell 1986; Schwerdtfeger 1986); divergence in commissural projections in humans and rodents (Wilson et al. 1987; Gloor et al. 1993); and the great variations in the distribution of neuropeptides according to species (Sakamoto et al. 1987).

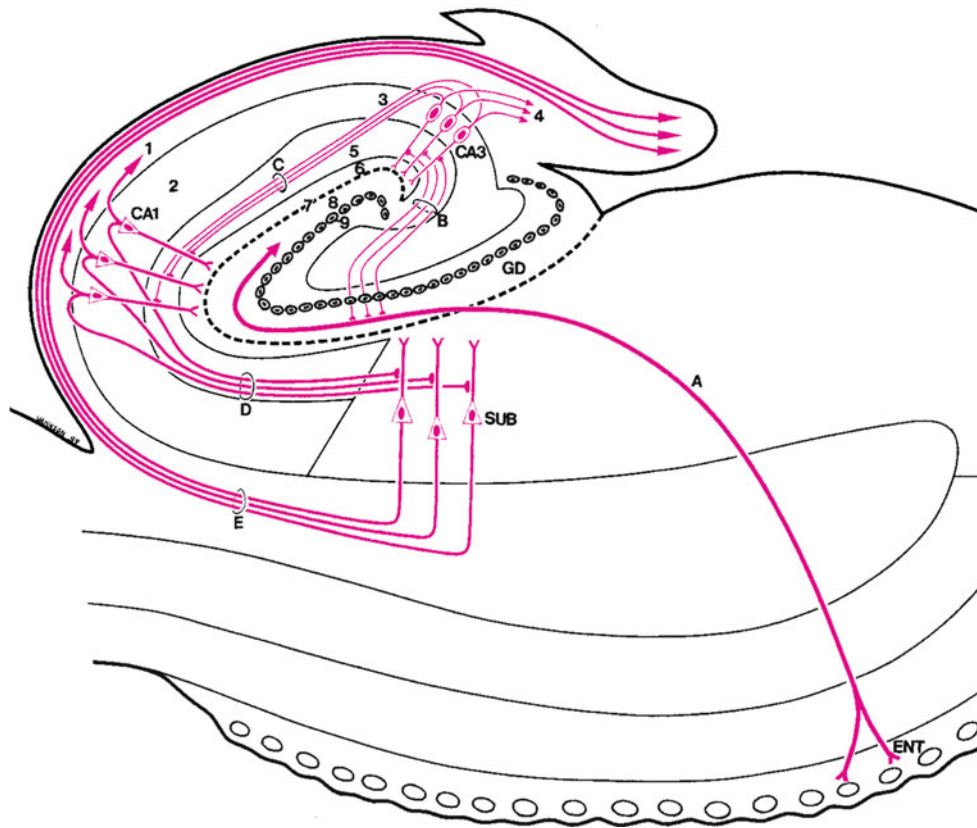


Fig. 3.15 Polysynaptic intrahippocampal pathway. A–E are parts of the neural chain forming the polysynaptic intrahippocampal pathway (see p. 27). Cornu Ammonis: 1 alveus, 2 stratum pyramidale, 3 Schaffer collaterals, 4 axons of pyramidal neurons (mainly to septal nuclei), 5 strata lacunosum and radiatum, 6 stratum moleculare,

7 vestigial hippocampal sulcus. Gyrus dentatus (GD): 8 stratum moleculare, 9 stratum granulosum. CA1, CA3 fields of the cornu Ammonis, SUB subiculum. ENT (Layer II of the entorhinal area) is the origin of this chain; its large pyramidal neurons are grouped in clusters, giving a granular aspect at the entorhinal surface

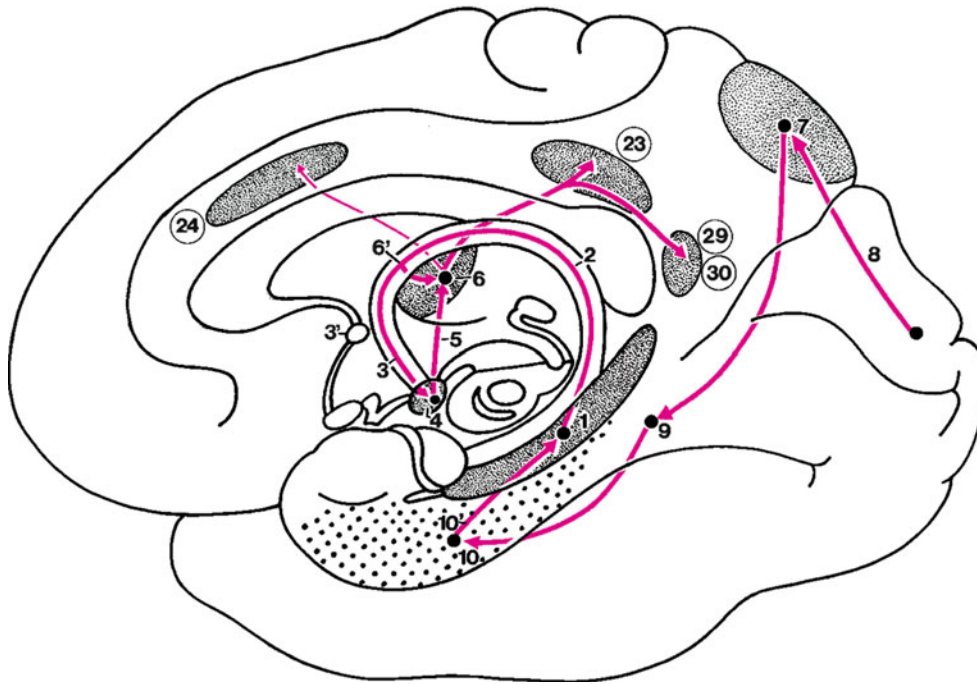


Fig. 3.16 Cortical connections of the polysynaptic intrahippocampal pathway. Hippocampal outputs fibers to the cortex: arising from the hippocampus (1), fibers successively reach the body (2) and column (3) of fornix (3', anterior commissure), the mamillary body (4), and then, via the mammillothalamic tract (5), the anterior thalamic nucleus (6); some fibers reach this nucleus directly (6'); from the anterior thalamic

nucleus, the main cortical projections are the posterior cingulate (area 23) and retrosplenial (areas 29, 30) cortices; some fibers may project to the anterior cingulate cortex (area 24) (see p. 31). Input fibers from the cortex to hippocampus: the posterior parietal association cortex (7) in relation to the superior visual system (8) projects via the parahippocampal gyrus (9) to the entorhinal area (10); 10' perforant fibers

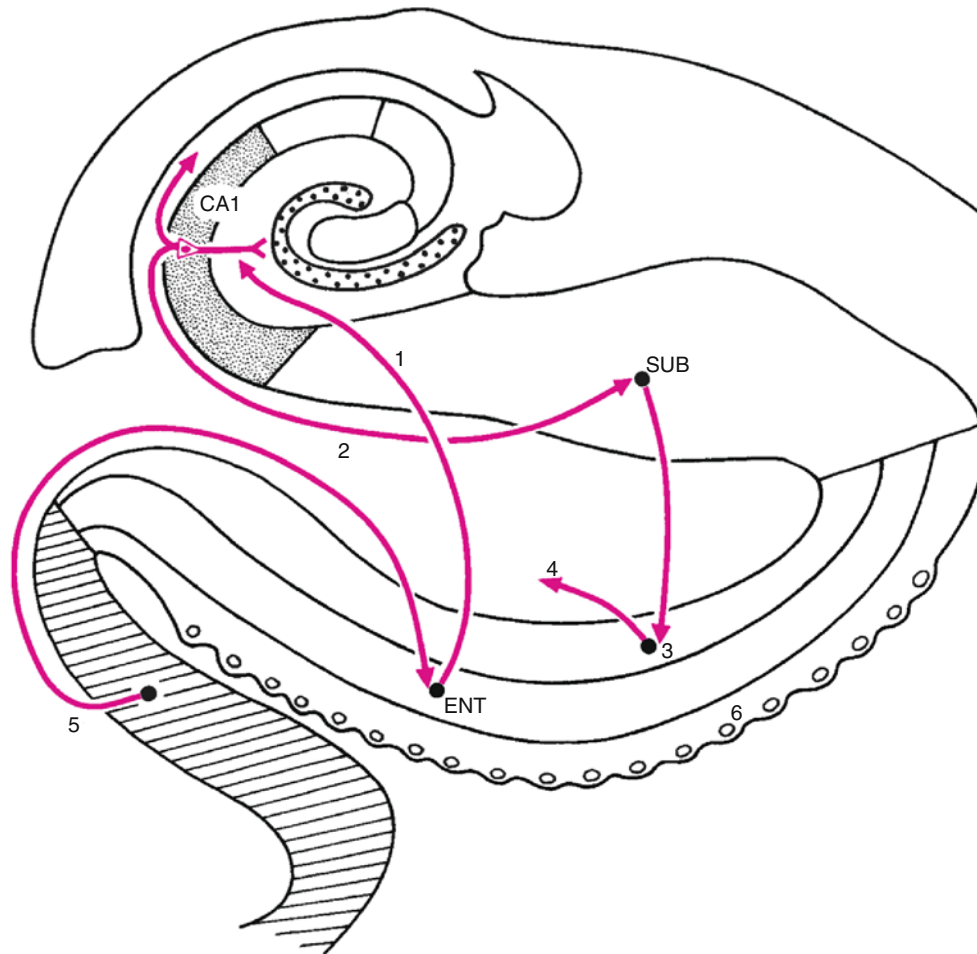


Fig. 3.17 Direct intrahippocampal pathway. The entorhinal area (*ENT*) (layer III) projects directly (*1*) onto CA1 pyramidal neurons, which innervate (*2*) the subiculum (*SUB*). Subicular axons project back to the deep layers of the entorhinal cortex (*3*). The neurons of these layers

send axons to the association cortex (*4*) (see Fig. 3.18). The direct pathway receives inputs through the perirhinal cortex (*5*) (see Fig. 3.18). *6* layer II of the entorhinal cortex

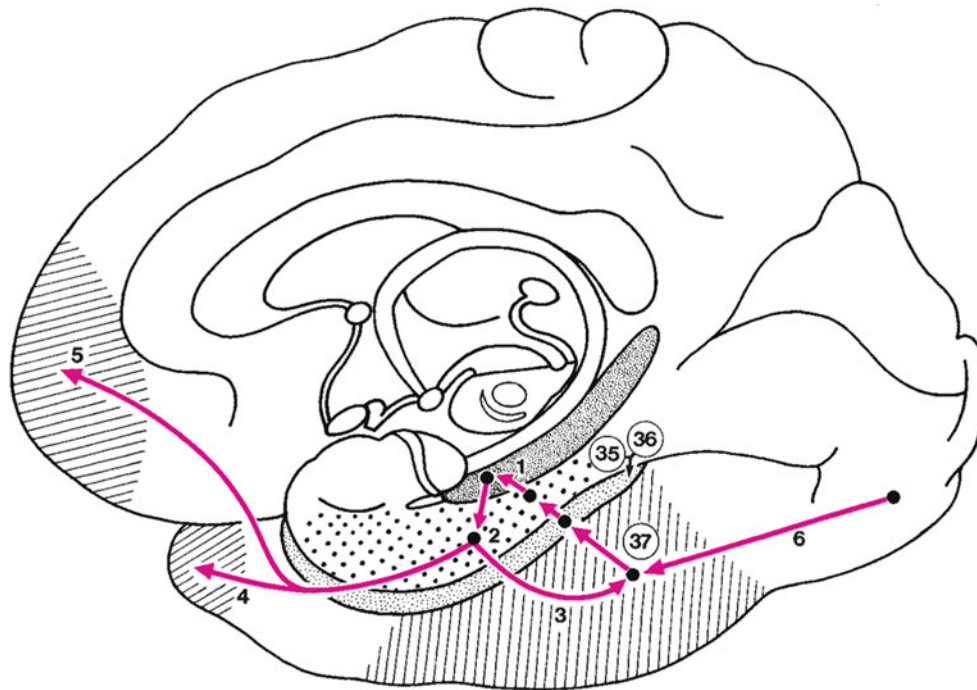


Fig. 3.18 Cortical connections of the direct intrahippocampal pathway. 1 intrahippocampal circuitry (see Fig. 3.17). Hippocampal outputs fibers to the cortex: from the deep layers of the entorhinal cortex (2), fibers reach the inferior temporal association cortex (3), the temporal pole (4),

and the prefrontal cortex (5). Inputs fibers from the cortex to hippocampus: the main origin of these fibers is the inferior temporal association cortex (area 37) in relation to the inferior visual system (6), reaching the entorhinal cortex through the perirhinal cortex (areas 35, 36)

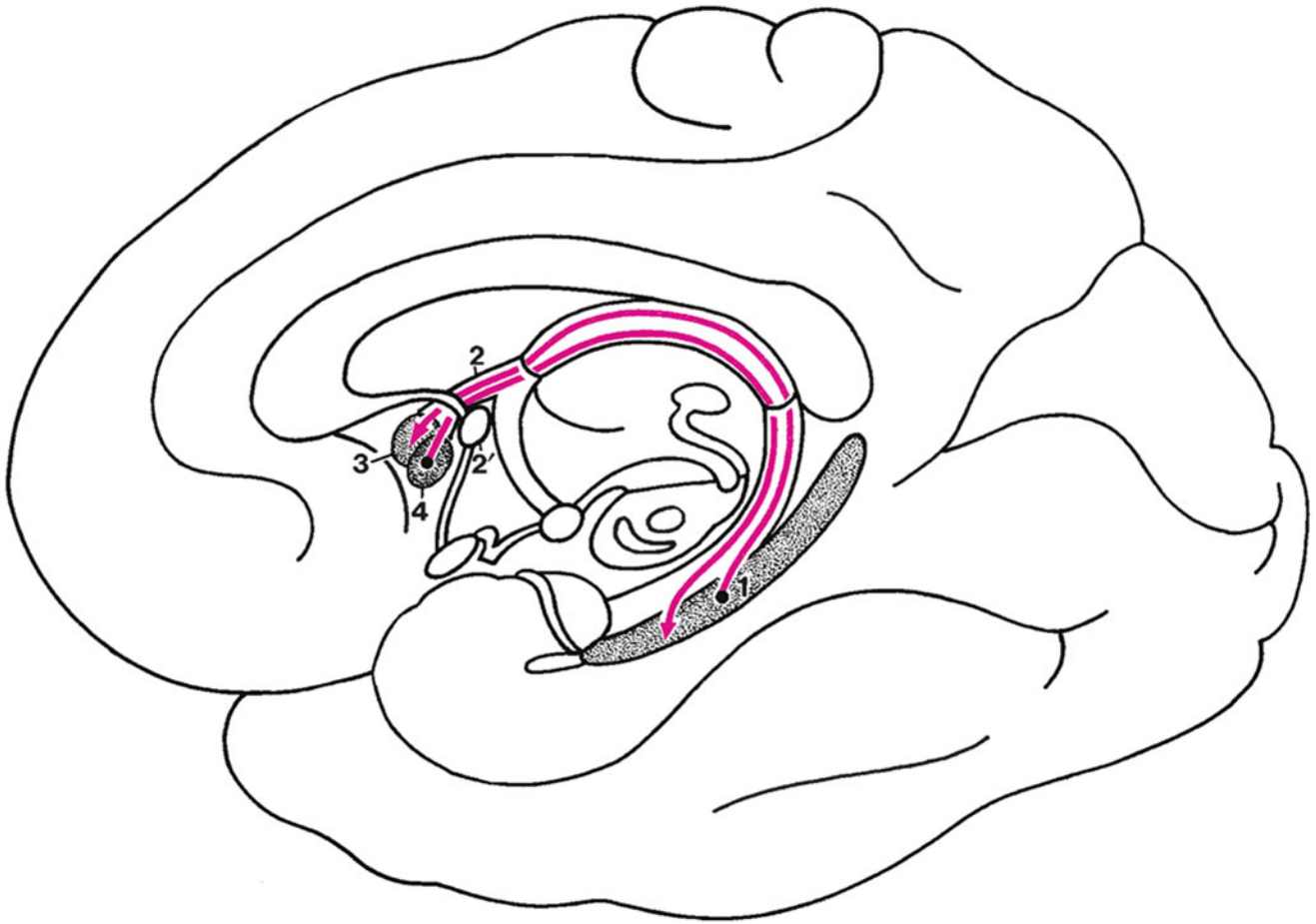


Fig. 3.19 Septal connections of the hippocampus. Axons of the cornu Ammonis (1) (see Fig. 3.15), via the precommissural fornix (2), reach the lateral septal nucleus (3). The fibers from the medial septal nucleus (4) go back to the hippocampus by the same way. 2' anterior commissure

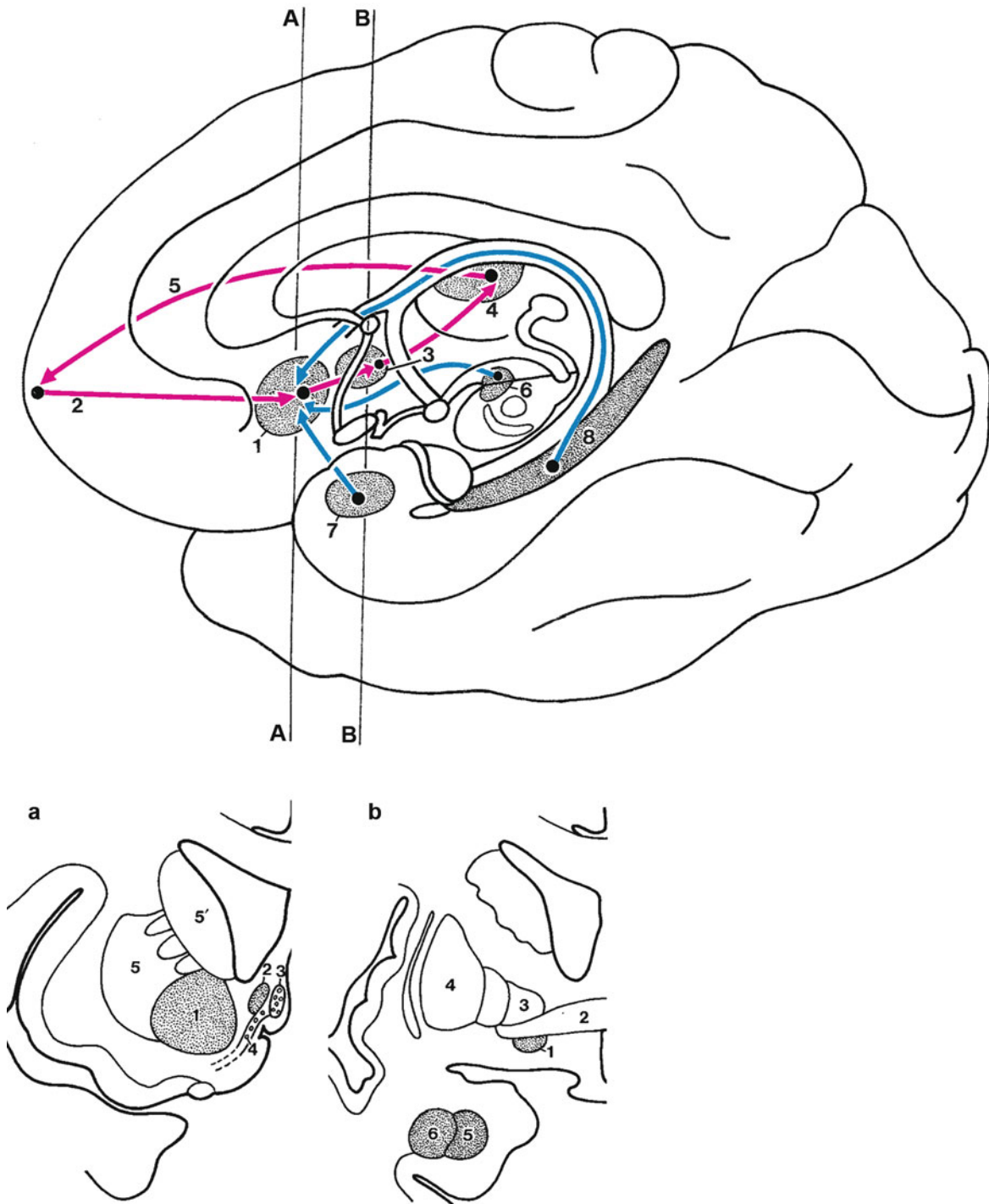


Fig. 3.20 *Top*, ventral (limbic) striatal loop. The ventral striatum (nucleus accumbens) (1) receives fibers from the prefrontal cortex (2) and controls the ventral pallidum (3). The ventral pallidum projects to the dorsomedial thalamic nucleus (4), whose fibers return to the prefrontal cortex (5). The ventral tegmental area (6) (dopaminergic mesolimbic system A10), the amygdala (7), and the hippocampus (8) control the ventral striatal loop. *Bottom*, planes of subjacent coronal sections corresponding to A and B in the top panel. (a) Coronal section

showing the situation of the ventral striatum (n. accumbens) (1), lateral septal nucleus (2), medial septal nucleus (3), nucleus of the vertical limb of the diagonal band (4), putamen (5), and caudate nucleus (5') (5 and 5': dorsal striatum). (b) Coronal section showing the situation of the ventral pallidum (1), anterior commissure (2), globus pallidus (dorsal pallidum, 3), putamen (4; dorsal striatum), amygdala, basal nucleus (5), and amygdala, lateral nucleus (6)

4.1 Preliminary Remarks

Hippocampal anatomy is so complex that its description can only be understood with the aid of the figures grouped at the end of this chapter (Figs. 4.1, 4.2, 4.3, 4.4, 4.5, 4.6, 4.7, 4.8, 4.9, 4.10, 4.11, 4.12, 4.13, 4.14, 4.15, 4.16, 4.17, 4.18, 4.19, 4.20, 4.21, 4.22, 4.23, 4.24, and 4.25).

The hippocampus forms an arc whose anterior extremity is enlarged and whose posterior extremity narrows like a comma (Fig. 3.2). As with some other hemispheric structures, for example, the caudate nucleus, the hippocampus can be divided into three parts: (1) an anterior part, or *head*; (2) a middle part, or *body*; and (3) a posterior part, or *tail*. It has a total length of between 4 and 4.5 cm; the body is on average 1 cm wide, and the head is 1.5–2 cm wide (Poirier and Charpy 1921; Testut and Latarjet 1948; Dejerine 1980). Although not particularly studied in this work, no important macroscopical differences have been observed between the right and left hippocampi or between hippocampi taken from male and female individuals.

Figure 4.1 shows the general position of the two components of the hippocampus. The cornu Ammonis and the gyrus dentatus form two interlocking U-shaped laminae. As shown by Giacomini (1884) and later by Mutel (1923), the position of these two cortical laminae is the same in all three parts of the hippocampus. Thus, because of the curvature of the hippocampus, the gyrus dentatus and the cornu Ammonis have the same reciprocal position in a coronal section of the body as in a sagittal section of the head or of the tail (Figs. 7.3 and 7.13).

Figure 4.2 shows the general form of the gyrus dentatus. It is folded, perhaps because of some obstacle during development; folding is especially marked in higher mammals. On the surface, these folds form the well-known “teeth” or *dentes* of the gyrus, whose deep part has extensions into the hippocampal body, head, and tail. Note that its anterior end (in the uncus) and posterior end (in contact with splenium) have a similar appearance, like a narrow and concave lamina devoid of *dentes*.

Having presented this global aspect of hippocampal morphology, the body, head, and tail will now be studied in succession.

4.2 Hippocampal Body

Two aspects of the hippocampal body will be considered: the intraventricular, or deep part, and the extraventricular, or superficial part.

4.2.1 Intraventricular Part (Figs. 3.3 and 4.3)

The intraventricular part is an element of the floor in the lateral ventricle (temporal or inferior horn). It is a strongly convex protrusion, smooth and padded with ependyma covering the alveus. Numerous subependymal veins radiate on its surface (Fig. 5.9; Wolf and Huang 1964; see p. 72). In depth, the intraventricular part corresponds to the CA1–CA3 fields of the cornu Ammonis (Fig. 3.7). The hippocampal body is bordered medially by the fimbria and laterally by the narrow collateral eminence, which marks the intraventricular protrusion of cortex covering the collateral sulcus (Figs. 3.2, 3.5, and 4.3). The roof of the temporal horn overhangs the intraventricular part of the hippocampal body; it is composed of the temporal stem, the tail of the caudate nucleus, and the stria terminalis (Figs. 3.5 and 3.8). The temporal stem is a narrow lamina of white matter between the ventricular cavity and the fundus of the superior temporal sulcus (Figs. 7.4d, 7.5d, 7.6d, 7.7d, and 7.8d).

Note that the intraventricular hippocampal surface is almost entirely hidden by voluminous choroid plexuses; only the hippocampal head is devoid of these plexuses (Figs. 4.18 and 5.8). The choroid plexuses in the temporal horn are the inferior extremity of a unique formation, the choroid plexuses of the prosencephalon, which are all visible in Fig. 4.17. Choroid plexuses of the temporal horn are attached to a double

layer, formed of ependyma and pia, which together make up the tela choroidea of the temporal horn (Fig. 4.16a).

Precise definition of the prosencephalic tela choroidea is controversial and needs to be discussed here. Most classic texts refer to the tela choroidea of prosencephalon as *two pial layers* trapped in the median part of the transverse fissure during development of the commissures and telencephalic vesicles (Villiger and Ludwig 1946; Testut and Latarjet 1948; Clara 1959; Kahle 1986; Yasargil 1987; Williams 1995). One layer covers the inferior surfaces of fornix and splenium, while the other covers the third ventricle and thalamus. Lateral extensions of the tela form the choroid plexuses in the bodies of lateral ventricles. The two pial layers delimit a space between them, the velum interpositum, which contains the internal cerebral veins. Curiously, however, this definition of the tela has not been extended to the temporal horns and lateral parts of the transverse fissure. Consequently, there is a lack of nomenclature here. For this reason, another description, used by several authorities, particularly Crosby et al. (1962), Bargmann (1964), and Carpenter and Sutin (1983), has been followed here.

The tela choroidea is thus the juxtaposition of *one ependymal layer* and *one pial layer* (Fig. 4.16a). The tela choroidea of the lateral ventricle closes the choroid fissure and fixes the choroid plexuses. The tela is attached to a thickening of the ventricular wall, the taenia of the tela choroidea. This description has the advantage of setting clear limits to the tela choroidea and of being applicable to the different ventricles.

The tela choroidea in the temporal horn is stretched between two taeniae, the taenia of the stria terminalis and that of the fimbria. Whereas the former is only slightly visible, the latter can often be clearly seen (Fig. 4.16a).

At the junction of hippocampal body and head, when the uncus appears, the taeniae of the fimbria and stria terminalis unite. This union is the velum terminale of Aeby (1871) or inferior choroidal point (Nagata et al. 1988), a triangular lamella attached to superior surface of the uncus and of variable development (Fig. 4.9).

4.2.2 Extraventricular or Superficial Part

The extraventricular part of the hippocampus, visible on the medial surface of the temporal lobe, is reduced in size. It is limited to the gyrus dentatus, fimbria, and superficial hippocampal sulcus (Figs. 3.4a and 4.3).

The superficial part of the gyrus dentatus is the *margo denticulatus*, composed of rounded protrusions which form the dentes of the gyrus. There are usually about 15 dentes (Poirier and Charpy 1921; Stephan 1975), those in the middle being the largest. They diminish in size caudally and cranially. Numerous vessels penetrate the sulci between them and thus supply the hippocampus (see Chap. 5). The dentes of the margo denticulatus are surface manifestations of

general folding in the gyrus dentatus (Fig. 4.2). The occurrence of dentes on the margo denticulatus is specific to humans and higher primates (Tilney 1939).

The fimbria is a narrow, white strip (Figs. 3.2 and 4.3) which more or less hides the margo denticulatus, having individual variations. A deep fimbriodentate sulcus separates these two structures (Fig. 3.7).

The margo denticulatus is bordered inferiorly by the *superficial hippocampal sulcus*, which separates it from subadjacent subiculum (Figs. 3.5, 3.7, and 4.3).

4.2.3 Relations with Adjacent Structures

The extraventricular, superficial part of the hippocampus and the tela choroidea of the temporal horn together form the fundus of a deep fissure, the *lateral part of the transverse fissure* (Figs. 3.5 and 7.9d). The roof of the latter is formed by the lateral geniculate body rostrally and the pulvinar caudally (Figs. 7.8d and 7.9d). Its floor is the flattened surface of the subiculum in its pre- and parasubicular segments. Since Liliequist (1959), the subarachnoid space in the transverse fissure has often been called the wing of the ambient cistern. In fact, this subarachnoid space communicates medially with the ambient cistern, situated between the temporal lobe and lateral mesencephalic surface (Figs. 3.5, 7.8d and 7.9d).

The transverse fissure contains vessels running toward the subiculum, the hippocampus (see Chap. 5), and the geniculate bodies. The posterior cerebral artery, usually in the ambient cistern (Fig. 7.6b, d), sometimes curves into the transverse fissure (Fig. 5.5; Lecaque et al. 1978; Yasargil 1984).

The ambient cistern contains numerous vessels which curve round the mesencephalon. These are, in descending order, the posterior cerebral artery (P2 segment), with the adjacent basal vein, and the posteromedial choroidal, collicular, and superior cerebellar arteries (Khan 1969; Duvernoy 1999a, b; Lang 1981). The free edge of the tentorium cerebelli is far from the hippocampal body, since it usually follows the inferior surface of the parahippocampal gyrus (Fig. 4.25). Finally, the cerebellum limits the ambient cistern below via the tentorial opening (Fig. 7.9d).

4.3 Hippocampal Head

The hippocampal head includes an intraventricular part, the *digitationes hippocampi*, and an extraventricular or uncal part.

4.3.1 Intraventricular Part

The intraventricular part is the anterior part of the arc of the hippocampus. It features the *digitationes hippocampi* or

internal digitations (Figs. 3.2 and 4.4). There are usually three or four digitations, sagittally oriented and separated by small but definite sulci (Klinger 1948). A *vertical digitation* sometimes joins them, corresponding to the intraventricular part of the medial surface of the uncus (Figs. 4.1 and 7.6b, c). There are two opposing theories on the origin of digitations. Some consider them due to a cortical atrophy (Zuckerkanndl 1887), whereas others (Giacomini 1884; Testut and Latarjet 1948) believe that their characteristic folding is due to some obstacle to forward development of the hippocampus, which is the more likely theory.

In frontal sections, the digitations are seen to be transverse foldings of the cornu Ammonis (Figs. 4.6 and 5.23). The folding is also visible on the extraventricular surface of the head, as will be seen later; for this reason, Retzius (1896) referred to the intraventricular digitations as *internal digitations* and to the extraventricular ones as *external digitations*. Each digitation is cored by a digital extension of the gyrus dentatus (Fig. 4.2).

When the hippocampal digitations appear at the junction of the body and head, the fimbria gives way to a thick alveus which covers them. The taeniae of the fimbria and stria terminalis unite, forming the velum terminale (see p. 40; Fig. 4.9). As the tela choroidea is absent from anterior part of the temporal horn, the hippocampal head is free of choroid plexuses and is visible in intraventricular views (38, 53). Anterior to the hippocampus, the ventricular cavity is often prolonged into the deep part of the uncus, as the *uncal recess* of the temporal horn (Figs. 3.2 and 7.18b; Klinger 1948). The intraventricular surface of the amygdala, composed of basal and lateral nuclei, overhangs the hippocampal head along almost its entire surface (Figs. 7.15, 7.16, 7.17, and 7.18). The hippocampal digitations and amygdala are often joined together across the ventricular cavity (Fig. 4.4).

4.3.2 Extraventricular or Uncal Part

Understanding this complex region requires a general description of the uncus, based on the observations made by Retzius (1896).

The uncus, or anterior segment of the parahippocampal gyrus, curls posteriorly to rest on the parahippocampal gyrus itself, separated from the latter by the uncal sulcus (Figs. 4.7 and 4.8). This posterior curving of the uncus may be due to obstruction by the amygdala to anterior development of the parahippocampal gyrus (Stephan and Manolescu 1980). Others consider that the fimbria, fixed to the uncal apex (Figs. 4.7 and 4.8), holds the uncus back during anterior development of the parahippocampal gyrus (Giacomini 1884; Mutel 1923; Anthony 1947; Grassé 1972). Note that the uncus is especially well developed in humans and primates (Tilney 1939).

The uncus is structurally divided into an anterior segment, belonging to the piriform lobe (see p. 5), and a posterior segment, belonging to the hippocampus (Giacomini 1884; Mutel 1923).

Anterior Segment

Two distinct protrusions can be discerned in the anterior segment, the semilunar gyrus and the ambient gyrus, separated by the semilunar or amygdaloid sulcus (Figs. 4.8 and 4.9; Turner 1981). The *semilunar gyrus* covers the cortical nucleus of the amygdala (Fig. 3.14) and is separated from the anterior perforated substance by a deep fold, the endorhinal sulcus (Figs. 4.9 and 4.11). The *ambient gyrus* shows a marked uncal notch, produced by the free edge of the tentorium cerebelli (Figs. 4.8 and 4.25). The ambient gyrus continues into the anterior extremity of the parahippocampal gyrus, which is limited by the rhinal sulcus (Fig. 3.4). The anterior part of the parahippocampal gyrus has an irregular surface formed of small protrusions named by Retzius (1896) and Klinger (1948) as the *verrucae gyri hippocampi* (Fig. 4.8); the significance of these protrusions is explained on p. 27.

Posterior Segment

The posterior segment is part of the hippocampus and the subiculum and is separated from the parahippocampal gyrus by the uncal sulcus. It has an inferior surface, hidden in the uncal sulcus, and a medial surface, exposed on the medial aspect of the temporal lobe.

Inferior Surface

This surface, visible only after ablation of the subjacent parahippocampal gyrus, is divided into the band of Giacomini, the external digitations, and the inferior surface of the uncal apex (Figs. 4.5 and 5.12).

In the hippocampal body (Fig. 4.2), the gyrus dentatus is a medially concave cellular layer whose superficial, visible segment forms the margo denticulatus, which is flanked by the superficial hippocampal sulcus. In the hippocampal head, the gyrus dentatus has the same appearance, but the cellular layer is caudally concave (Figs. 4.2 and 4.7). The segment of the gyrus dentatus visible here is the *band of Giacomini*, and it is also flanked by the superficial hippocampal sulcus. This change in terminology complicates the description, for the visible segment of the gyrus dentatus, both in the body and in the head of the hippocampus.

On the inferior uncal surface (Fig. 4.5), the margo denticulatus turns into the band of Giacomini at a right angle. The band crosses the inferior uncal surface to appear on its medial surface (Figs. 4.7 and 4.8). The flattened surface of the band often makes it difficult to identify. Rostrally, it is well defined by the superficial hippocampal sulcus, which can always be distinguished.

The *external digitations*, anterior to the band of Giacomini, form two or three small, convex lobules separated by sagittal

sulci (Fig. 4.5). These digitations are inverse images of the internal digitations (digitationes hippocampi), visible on the intraventricular aspect of the hippocampal head (Figs. 4.6, 5.23, and 7.6b). The external and internal digitations are due to folding of the cornu Ammonis. These folds vary in thickness, as is frequent in cortical gyri in general. The cortex of the cornu Ammonis is thick in the external and thin in the internal digitations. Digitations are principally formed by the CA1 field of the cornu Ammonis.

The *inferior surface of the uncal apex* (Fig. 4.5) is posterior to the band of Giacomini (the term “uncal apex” is preferred to “intralimbic gyrus,” which is sometimes used, as the latter may be confused with the intralimbic gyrus proper). The uncal apex is the caudal end of the uncus; the fimbria is attached to its extremity. Its inferior surface is like a cone, and its base is separated from the band of Giacomini by a discrete sulcus. Retzius (1896) likened this surface to a helmet, with the band of Giacomini forming its edge. The uncal apex is made up of CA3 and CA4 covered by alveus (Fig. 4.7). In the hippocampal body, all these structures are deep and hidden by the fimbria (Fig. 3.7). In the uncus, the fimbria has disappeared, and CA3 and CA4, covered by alveus, appear on the surface as the uncal apex. Because of this inversion, Elliot Smith (1896) named the uncal apex the hippocampus inversus, a term later used by numerous workers (Gastaut and Lammers 1961).

Medial Surface

This surface, visible on the medial aspect of the temporal lobe (Figs. 3.4, 4.7, 4.8, and 4.9) is divided into the terminal segment of the band of Giacomini, the medial surface of the uncal apex, and the uncinete gyrus.

The *terminal segment of the band of Giacomini* appears on the upper lip of the uncal sulcus; it follows a vertical route on the medial surface of the uncus and is flanked by the terminal segment of the superficial hippocampal sulcus. In toto, the band has an initial, hidden segment on the inferior uncal surface (pars occulta, Fig. 4.5) and a visible terminal segment on the medial uncal surface (pars aperta, Fig. 4.8) (Villiger and Ludwig 1946; Klinger 1948). As described earlier, the band is the equivalent of the margo denticulatus, that is, the superficial segment of the gyrus dentatus. The deep segment of the gyrus dentatus is a vertical and caudally concave cellular layer of the uncal apex (Figs. 4.2 and 4.7). The band of Giacomini and the gyrus dentatus diminish superiorly and disappear at the superior edge of the uncus.

The *medial surface of the uncal apex* resembles the inferior surface described above. It is also composed of CA4 and CA3, is covered by alveus, and forms the hippocampus inversus (Fig. 4.7). The junction of the fimbria to the apex of the uncus is clearly distinguishable.

The *uncinate gyrus*, anterior to the band of Giacomini, joins up with the ambient gyrus. Its structure is uncertain, but

it seems to be composed of a strip of the CA1 field, overflowing from the hippocampal sulcus, and of the subiculum as far as the ambient gyrus (Figs. 4.7, 7.24, and 7.25; Vogt and Vogt 1937; Braak 1980).

4.3.3 Relations of the Uncus with Adjacent Structures

The anterior and posterior uncal segments have different relations. The *anterior segment* is the lateral limit of the anterior perforated substance, the interpeduncular region, and the chiasmatic and interpeduncular cisterns. It is related to the oculomotor nerve, the first segment of the middle cerebral artery, the posterior communicating artery, the tuber, and the hypophysial stalk (Figs. 4.10, 4.11, and 4.20). The *posterior segment* is situated near the crus cerebri but is separated from it by the narrow crural cistern (Figs. 4.10, 4.11, 4.21, 7.24d, and 7.25d).

Numerous vessels cross the uncal surface (Yasargil 1984). On the superior uncal surface, the anterior choroidal artery follows the semilunar sulcus, separating the semilunar gyrus from the ambient gyrus (Figs. 4.24 and 5.14). The anterior choroidal artery reaches the uncal apex and choroid plexuses of the temporal horn; here, it supplies an uncal branch (Carpenter et al. 1954), which descends with the band of Giacomini and reaches the uncal sulcus (Fig. 5.11).

The posterior cerebral artery (P2 segment) runs along the medial uncal surface, hiding the uncal sulcus (Fig. 4.24). It is often accompanied by the basal vein (Fig. 4.23). At the uncal apex, the basal vein receives an important collateral, the inferior ventricular vein (vein of the temporal horn). Below the posterior cerebral artery, the free edge of the tentorium cerebelli is situated, with which the trochlear nerve is associated (Fig. 4.24).

Relations between the tentorial edge and uncus have been studied by Yates (1976) and Noël et al. (1977), among others. These relations depend on the size of the tentorial opening (Fig. 4.22), which greatly varies (Corsellis 1958). Often, however, the tentorial edge is close to the uncus, where it frequently marks the ambient gyrus (uncal notch) (Lang 1985; Fig. 4.8). In herniation of the temporal lobe, the uncus may slip between the tentorial edge and the crus cerebri. In addition to lesions due to compression of the mesencephalon, uncal herniation may also compress the P2 segment of the cerebral artery against the tentorial edge, causing marked hemodynamic disturbances (incisural sclerosis, see p. 31).

Crossing the uncus is not the only critical point in passage of the posterior cerebral artery. At the posterior extremity of the parahippocampal gyrus, the beginning of the P3 segment of the artery has to cross a narrow cleft between the parahippocampal gyrus and tentorial edge. It is likely that temporal herniation may compress the artery here (Fig. 4.20).

4.4 Hippocampal Tail

The tail is the posterior part of hippocampal arc (Fig. 3.2). As with the body and the head, the tail can be divided into intraventricular and extraventricular parts.

4.4.1 Intraventricular Part

The intraventricular part is a transverse bulge, oriented like the intraventricular part of the head but smaller. Although digitations do not appear on the surface of the tail, its internal structure is similar to that of the head and is composed of a vast layer of the cornu Ammonis centered by digital extensions of the gyrus dentatus (Figs. 4.2 and 7.10). The intraventricular surface of the tail is thickly covered by the alveus and subependymal veins. The intraventricular part is flanked medially by the fimbria and laterally by the collateral trigone; the flat surface of the collateral trigone and the intraventricular part of the tail together form the floor of the atrium (Fig. 3.2). Caudally, the convexity of the hippocampus reaches a marked protrusion, the calcar avis (Figs. 3.2, 4.19, and 4.22). The atrial roof overhanging the tail is composed of the caudate nucleus with the stria terminalis alongside. A strip of white matter, chiefly visual (optic radiations), separates the cerebral cortex from the ventricular cavity (Fig. 7.22d). The choroid plexuses here are even more voluminous than near the hippocampal body, forming the *choroid glomus*, which hides the ventricular floor completely (Figs. 4.17 and 5.8).

4.4.2 Extraventricular Part

Full discussion of the controversy in studies of this region will be avoided here, since this would only further complicate the problems; the description will thus be simplified to correlate the hippocampal surface with its internal structure.

The extraventricular part of the hippocampal tail may be divided into an initial segment (a continuation of the body), a middle segment, and a terminal segment inferior to the splenium (Fig. 4.12).

The *initial segment* of the tail resembles the body. The margo denticulatus is divided into dentes which successively decrease in size (Fig. 4.3). In its deep part, the gyrus dentatus has many extensions penetrating deeply into the hippocampus (Fig. 4.2). The margo denticulatus is partly hidden by the fimbria and is separated from the subiculum by the superficial hippocampal sulcus.

In the *middle segment*, three modifications appear (Fig. 4.12):

1. The *margo denticulatus* becomes smooth and narrow, forming the fasciola cinerea, which is limited below by the superficial hippocampal sulcus. The *fasciola cinerea* thus prolongs the margo denticulatus and, like it, forms

the visible part of the gyrus dentatus (Giacomini 1884; Klinger 1948).

2. The *fimbria*, which in the initial segment hides the margo denticulatus, separates from it, ascending to join the crus of fornix. Thus, the fimbriodentate sulcus widens progressively. Hence, a whitish band appears, the *gyrus fasciolaris*, which is composed of CA3 and covered by a thin layer of alveus (Fig. 4.12). The CA3 field of the cornu Ammonis is deep and hidden in the hippocampal body, but in this segment, it is superficial. Hence, the gyrus fasciolaris is referred to as the hippocampus inversus, as is the uncus apex (Elliot Smith 1898; Gastaut and Lammers 1961). Sometimes, a hippocampus inversus is prolonged anteriorly in the hippocampal body, in which case the fimbria and the margo denticulatus remain separate (Fig. 4.15). This arrangement is rare in humans but is frequent in many macrosmatic mammals. The gyrus fasciolaris is separated from the fasciola cinerea by the sulcus dentatofasciolaris (Retzius 1896; Fig. 4.12).
3. CA1 is deep in the hippocampal body and hidden by the subiculum. In the tail, on the other hand, CA1 appears progressively at the surface of the parahippocampal gyrus (Fig. 4.12). The CA1 layer, which is here heavily folded, sometimes raises the surface of the parahippocampal gyrus, producing rounded bulges, the so-called gyri of Andreas Retzius (Retzius 1896; Fig. 6.10). The terms “gyri retrospleniales” (Riley 1960; Naidich et al. 1987) or “*eminentiae subcallosae*” (Zuckerkanndl 1887) can lead to confusion with other cortical regions.

The gyri of Andreas Retzius are separated from the fasciola cinerea by the superficial hippocampal sulcus; Figs. 4.12 and 4.13 show well-developed gyri of Andreas Retzius, whereas they are absent in Fig. 4.3.

In summary, the middle segment of the hippocampal tail consists, in descending order, of the gyrus fasciolaris, the fasciola cinerea, and the gyri of Andreas Retzius.

The *terminal segment of the hippocampal tail* (see Figs. 4.12 and 6.11) covers the inferior splenial surface and, alone, merits the name subsplenial gyrus (Riley 1960; Gastaut and Lammers 1961), a term sometimes applied to the entire tail.

The results of this study provide support for the view (Elliot Smith 1898; Macchi 1951; Stephan 1975) that the fasciola cinerea, which is an extension of the gyrus dentatus, has disappeared in the terminal segment of the hippocampal tail, although some (Giacomini 1884; Ariens Kappers et al. 1967) regard it as extending to dorsal surface of the corpus callosum. The subsplenial gyrus, which prolongs the gyrus fasciolaris, is thus a thin layer of cornu Ammonis that surrounds the splenium and is continued by the indusium griseum on the dorsum of the corpus callosum (Klinger 1948; Tryhubczak 1975). It appears that the CA3 neuronal type forms the medial edge, while most of the subsplenial gyrus

consists of CA1 (Schwerdtfeger 1984), although identification of neuronal types is difficult in this region (Ramon y Cajal 1911, 1968; Klinger 1948). In the callosal sulcus, the lateral edge of the subsplenial gyrus joins with the cortex of the isthmus of the cingulate gyrus (Fig. 7.9; Jacobs et al. 1979).

The origin and structure of longitudinal striae could not be elucidated by the methods used in this study. The medial and lateral longitudinal striae are currently considered to be aberrant fibers of the fornix which, on leaving the fimbria, reach the dorsum of the corpus callosum on the indusium griseum to join the fornix again rostrally (Williams 1995; Nieuwenhuys et al. 1988). The origin of these small fascicle in the hippocampus (Fig. 4.12) is uncertain. The medial stria may stem from the fasciola cinerea and the lateral stria from the gyrus fasciolaris (Giacomini 1884; Elliot Smith 1897; Ramon y Cajal 1911, 1968; Dejerine 1980), but Duval (1881) and Macchi (1951) deny any connection between the indusium griseum and longitudinal striae on the one hand and the hippocampus on the other.

4.4.3 Relations with Adjacent Structures

The extraventricular, superficial part of the hippocampal tail has relations similar to those of the body. The tail forms the depths of the lateral part of the transverse fissure (Fig. 7.21b). Among the vessels in this fissure, the trunk of the medial atrial vein is noteworthy (Salamon and Huang 1976; Lang 1981). As shown in Fig. 4.13, the trunk of the medial atrial vein is the junction of subependymal branches which cross the calcar avis and then perforate the fimbria. The longitudinal hippocampal veins join these branches (see p. 71). The trunk of the medial atrial vein is situated in a triangular zone, the subcallosal trigone, formed by the separation between the crus of fornix and the hippocampal tail (Fig. 4.12).

The transverse fissure leads into the ambient cistern medially (Figs. 3.5 and 7.9d) and, more caudally, the quadrigeminal cistern (Fig. 7.10d). The latter is situated beneath the splenium and adjoined by the pineal gland, colliculi, and cerebellum through the tentorial opening. The quadrigeminal cistern contains numerous vessels, that is, posterior cerebral and posteromedial choroidal arteries, terminal branches of collicular arteries, and terminal segments of basal and internal cerebral veins flowing into the vein of Galen (Duvernoy 1975; Wolfram-Gabel 1983).

4.5 General Features

At the end of this study of a particularly complex region, several practical points should be noted:

- The structure of the hippocampus is the same in its different segments, as Giacomini (1884) and Mutel (1923) have shown. The cornu Ammonis has in fact an analogous structure in the head, body, and tail of the hippocampus (Fig. 4.1), as does the gyrus dentatus, which forms a continuous U-shaped lamina into which the cornu Ammonis penetrates. The visible segment of the gyrus dentatus is known as the margo denticulatus in the body, the band of Giacomini in the uncus, and the fasciola cinerea in the tail. However, it is in fact the same structure, and the same term could be used for its whole length. Note that the visible part of the gyrus dentatus is bordered by the superficial hippocampal sulcus along its entire length.
- Because of the arched form of the hippocampus, coronal sections of the body and sagittal sections of the head and tail have similar appearances, which may lead to confusion (Figs. 7.3 and 7.13).
- Also because of the hippocampal curve, coronal sections are often difficult to interpret. Whereas coronal sections of the hippocampal body correspond to classic views of the hippocampus (Fig. 7.8), coronal sections of the hippocampal head (Figs. 7.5, 7.6, and 7.7) and of the hippocampal tail (Figs. 7.9 and 7.10) cut through these formations tangentially. In particular, a section of the body and a section of the uncus can be found in the same figure (Fig. 7.7).

The anatomical study presented here is designed to make it easier to understand sections of the hippocampus in different planes, which are becoming increasingly clear in medical and academic imaging (see Chap. 7).

Figures 4.17, 4.18, 4.19, 4.20, 4.21, and 4.22 are dissections at descending levels in the diencephalon and brain stem showing the relation of these median structures to the hippocampus.

Figures 4.23, 4.24, and 4.25 show sagittal sections in which cerebellum and brain stem have been removed. These sections show in succession the relationships of the uncus and parahippocampal gyrus with the basal vein and posterior cerebral artery (Fig. 4.23), the posterior cerebral artery only (Fig. 4.24), and the free edge of the tentorium cerebelli (Fig. 4.25).

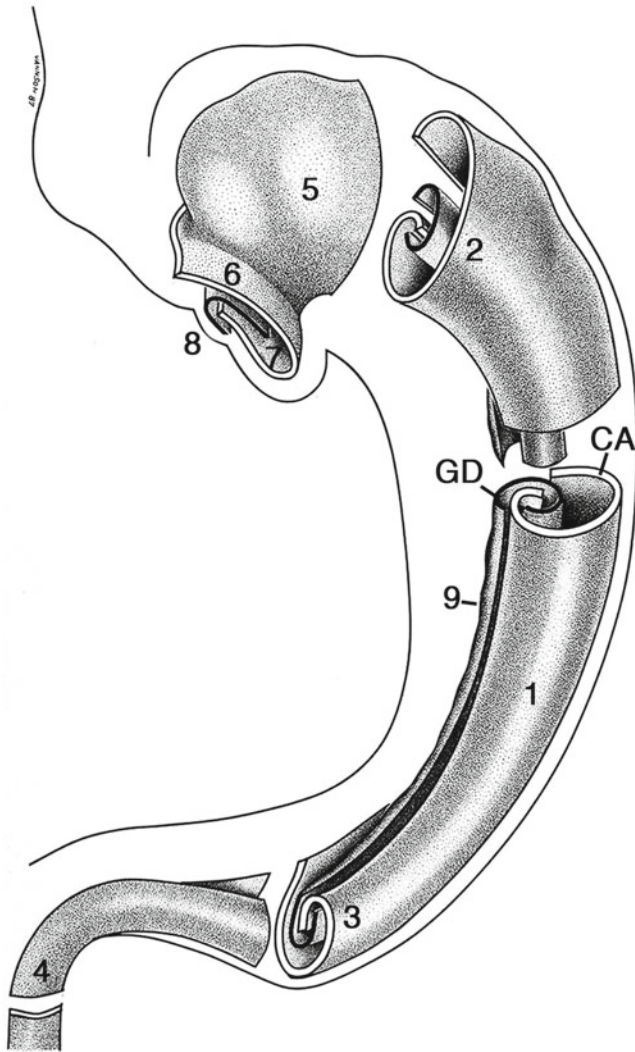


Fig. 4.1 General view of the internal structure of the hippocampus. The cornu Ammonis (CA) and gyrus dentatus (GD) form two interlocking U-shaped laminae. 1 hippocampal body, 2 hippocampal head, 3 hippocampal tail, 4 terminal segment of the tail, 5 digitationes hippocampi, 6 vertical digitation, 7 cornu Ammonis and gyrus dentatus in the medial surface of the uncus, 8 band of Giacomini, 9 margo denticulatus

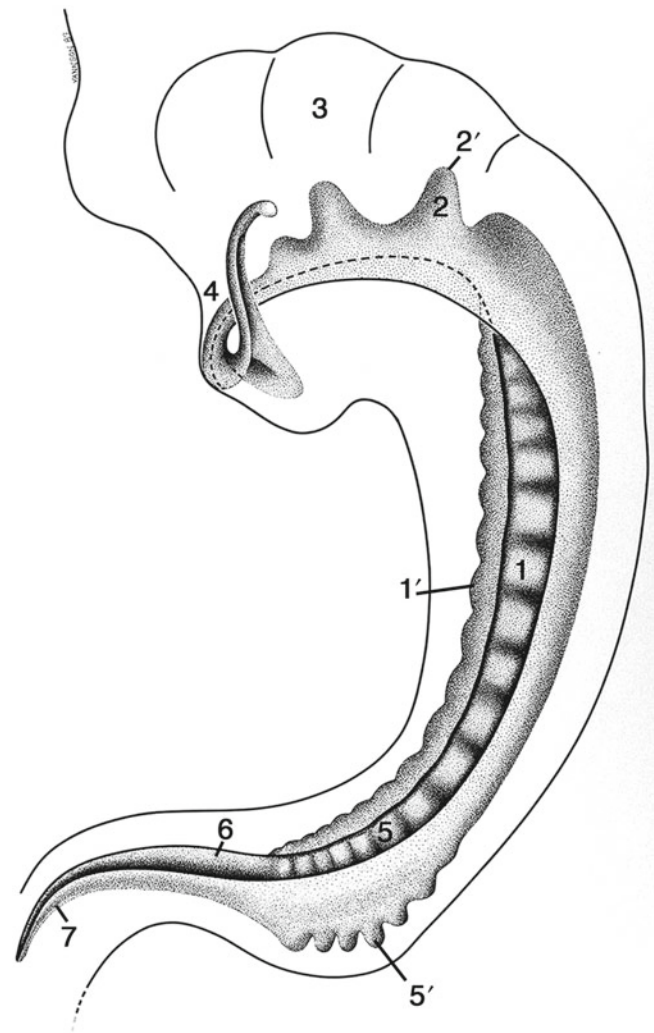


Fig. 4.2 Gyrus dentatus seen through the hippocampus (transparent). 1 gyrus dentatus in the hippocampal body, 1' margo denticulatus, 2 gyrus dentatus in the hippocampal head, 2' digital extensions of the gyrus dentatus, 3 digitationes hippocampi, 4 band of Giacomini and terminal part of gyrus dentatus in the medial surface of the uncus, 5 gyrus dentatus in the hippocampal tail, 5' digital extensions of the gyrus dentatus, 6 fasciola cinerea, 7 terminal part of the fasciola cinerea

Fig. 4.3 Aspect of hippocampus after opening of the temporal horn of the lateral ventricle. *Bar*, 3.6 mm. 1 intraventricular aspect of hippocampal body, 2 fimbria, 3 taenia fimbriae (*right arrow*), 4 dentes of margo denticulatus, 5 superficial hippocampal sulcus, 6 subiculum and parahippocampal gyrus, 7 hippocampal tail, 8 calcar avis, 9 collateral trigone, 10 collateral eminence

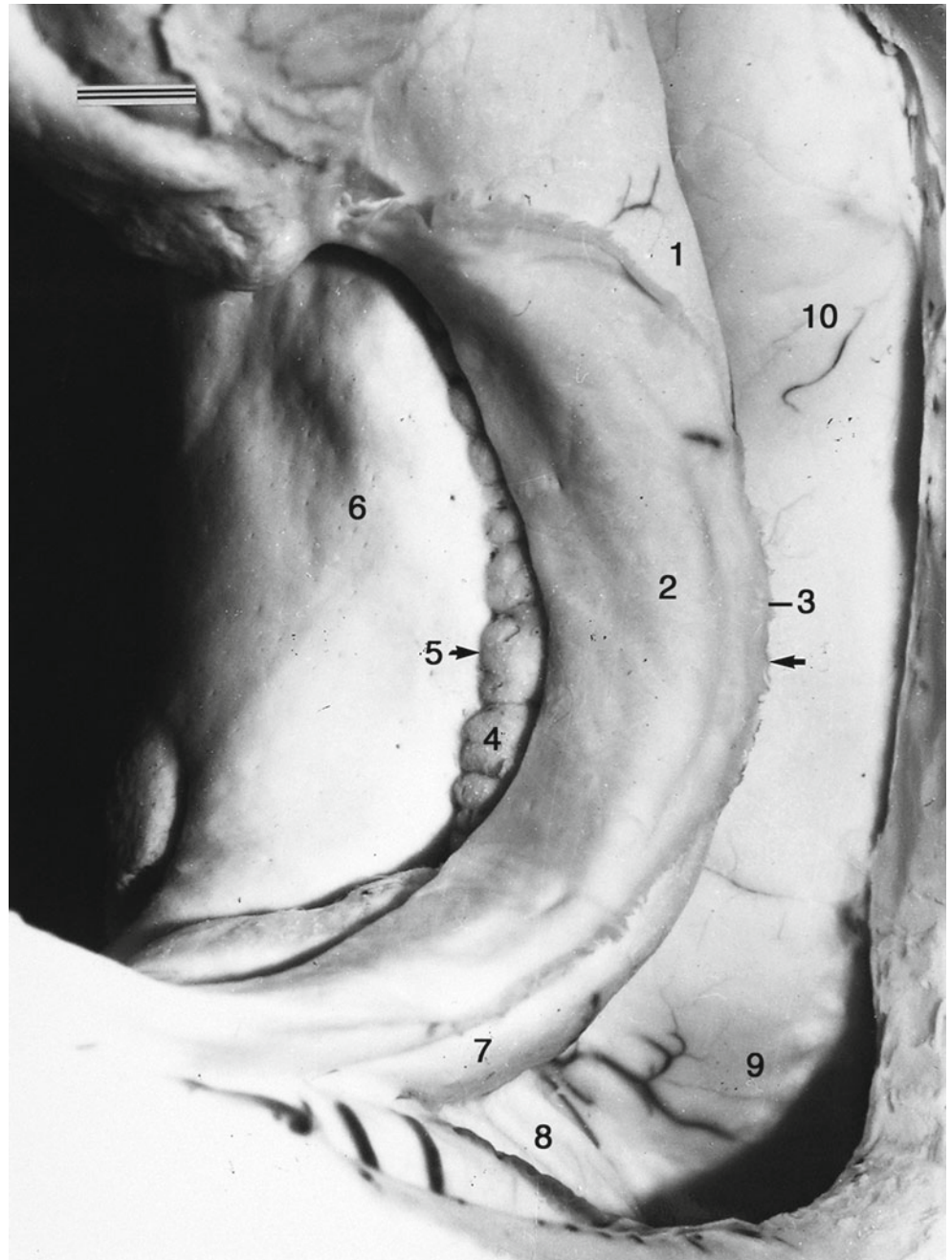


Fig. 4.4 Intraventricular aspect of the hippocampal head (seen from the direction of *arrow A* in Fig. 4.6). *a-b*, plane of the section in Fig. 4.6. *Bar*, 6.6 mm. 1, 2 digitationes hippocampi (internal digitations), 3 vertical digitation, 4 cut section of the adhesion between digitationes hippocampi and amygdala through the ventricular cavity

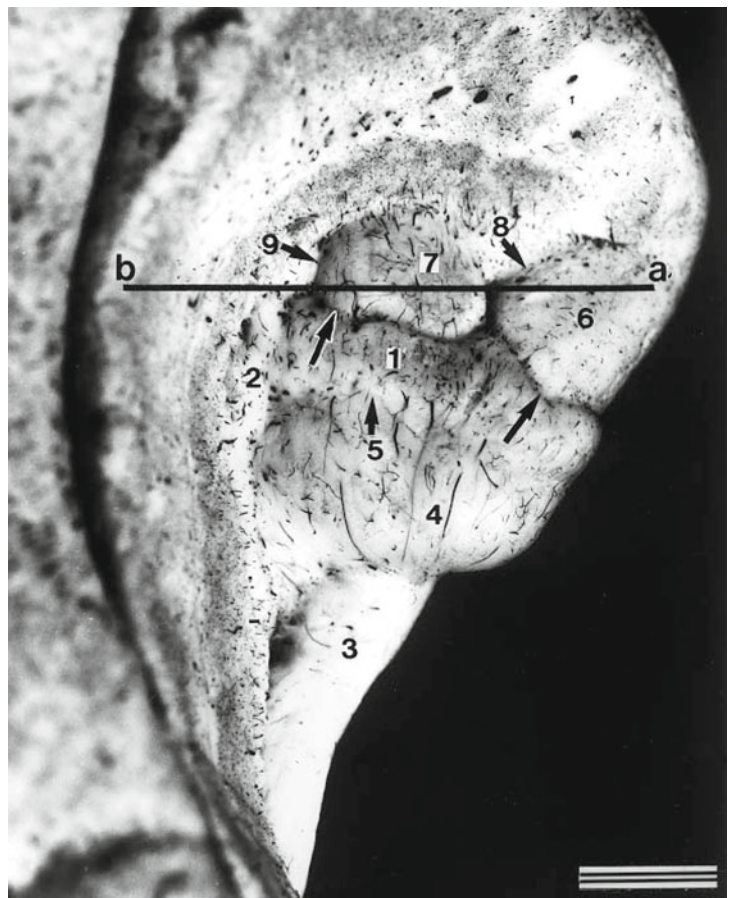
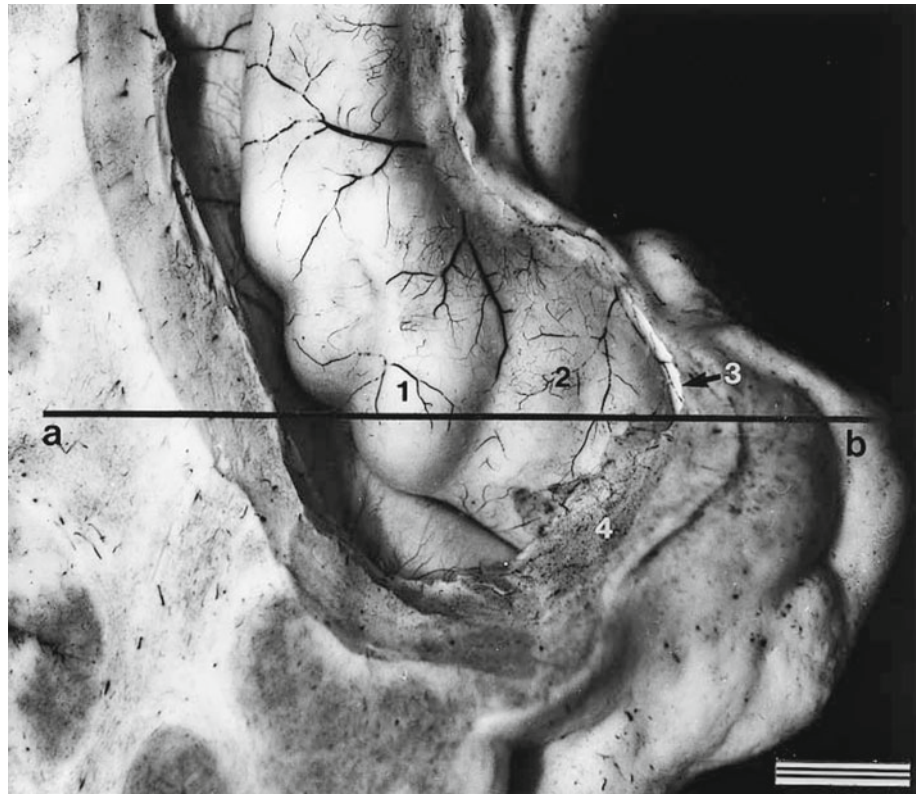


Fig. 4.5 Inferior aspect of the hippocampal head (seen from the direction of *arrow B* in Fig. 4.6). The parahippocampal gyrus has been removed. *a-b*, plane of section in Fig. 4.6. *Arrows* indicate the superficial hippocampal sulcus. *Bar*, 5 mm. 1 band of Giacomini, 2 margo denticulatus, 3 insertion of the fimbria on the uncus, 4 inferior surface of the uncus covered with alveus (hippocampus inversus), 5 prelimbic sulcus, 6, 7 external digitations, 8, 9 sulci between the external digitations

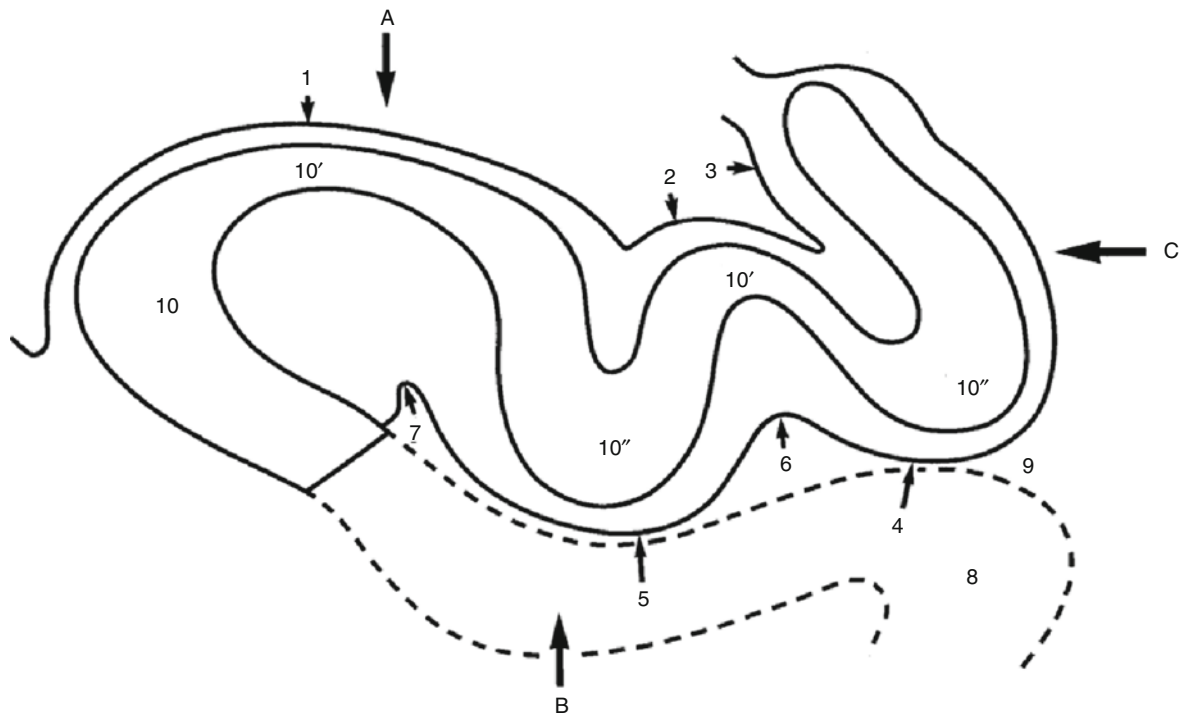


Fig. 4.6 Transverse section of the hippocampal head; *A* intraventricular aspect of hippocampal head, *B* inferior aspect of the hippocampal head, *C* medial aspect of uncus (see Fig. 4.8). 1, 2 internal digitations (digitationes hippocampi), 3 vertical digitation, 4, 5 external digitations,

6, 7 sulci between the external digitations, 8 the parahippocampal gyrus has been removed, 9 uncus sulcus, 10 cornu Ammonis, thin in the internal digitations (10') but thick in the external digitations (10'')

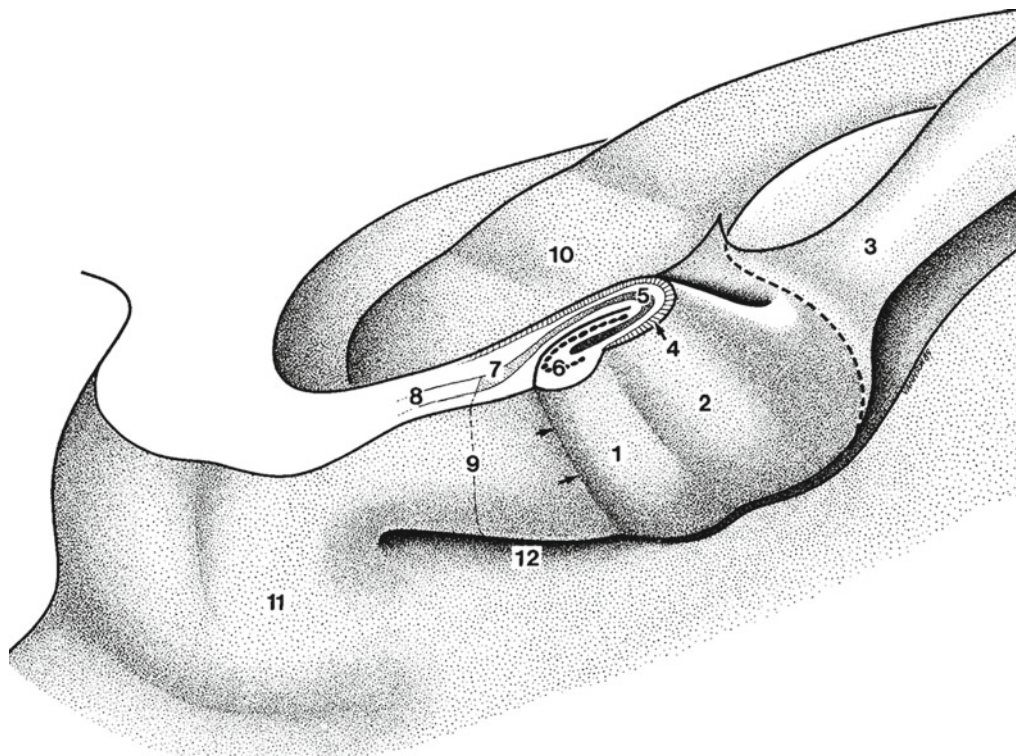


Fig. 4.7 Possible structure of the posterior uncal segment 1 band of Giacomini (arrows along the superficial hippocampal sulcus), 2 uncal apex, 3 fimbria. Structure of posterior uncal segment: 4 alveus covering the uncal apex (hippocampus inversus), 5 CA3 field, 6 gyrus dentatus,

7 CA1 field, 8 subiculum, 9 uncinatus gyrus, 10 intraventricular aspect of hippocampal head after opening of the ventricular cavity, 11 ambient gyrus, 12 uncal sulcus



Fig. 4.8 Medial aspect of the uncus (see *arrow C* in Fig. 4.6). *Bar*, 4 mm. Posterior segment of medial uncal surface belonging to the hippocampus: *1* band of Giacomini (*arrows* along the superficial hippocampal sulcus), *2* medial surface of uncal apex, *3* fimbria, *4* choroid fissure (the choroid plexuses have been removed), *5* uncinata gyrus, *6* uncal

sulcus. Anterior segment of medial uncal surface belonging to the piriform lobe; *7* entorhinal sulcus, *8* semilunar gyrus, *9* semianular sulcus, *10* ambient gyrus, *11* uncal notch produced by the free edge of the tentorium cerebelli, *12* entorhinal area and verrucae gyri hippocampi, *13* rhinal sulcus, *14* parahippocampal gyrus

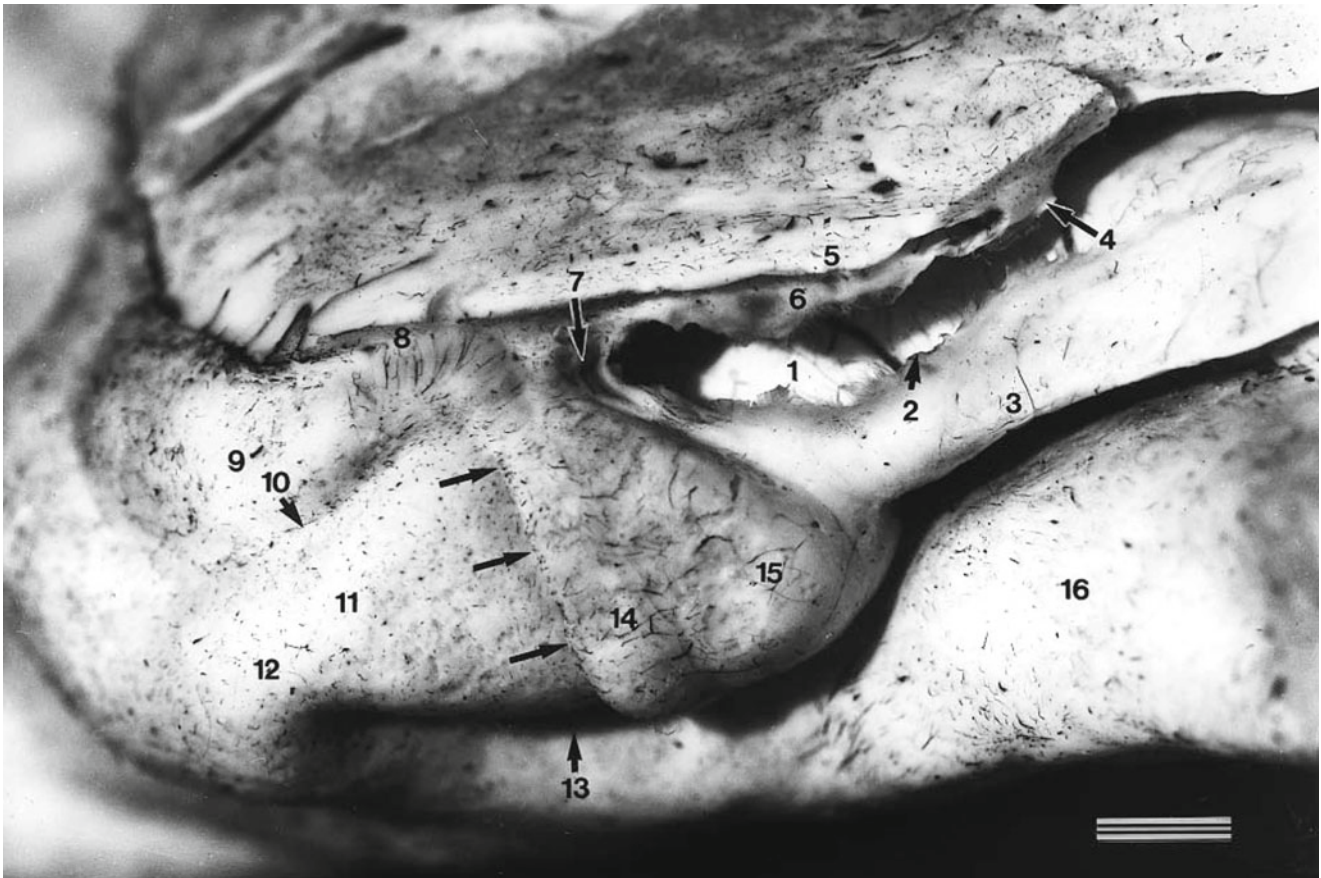


Fig. 4.9 Superior aspect of the uncus. *Arrows* indicate the superficial hippocampal sulcus. *Bar*: 3.8 mm. *1* choroid fissure (the choroid plexuses have been removed), *2* taenia fimbriae, *3* fimbria, *4* stria terminalis, *5* optic tract, *6* taenia of stria terminalis, *7* velum terminale (Aeby) or

inferior choroidal point, *8* endorhinal sulcus, *9* semilunar gyrus, *10* semianular sulcus, *11* uncinete gyrus, *12* ambient gyrus, *13* uncal sulcus, *14* band of Giacomini, *15* uncal apex covered with alveus (hippocampus inversus), *16* parahippocampal gyrus

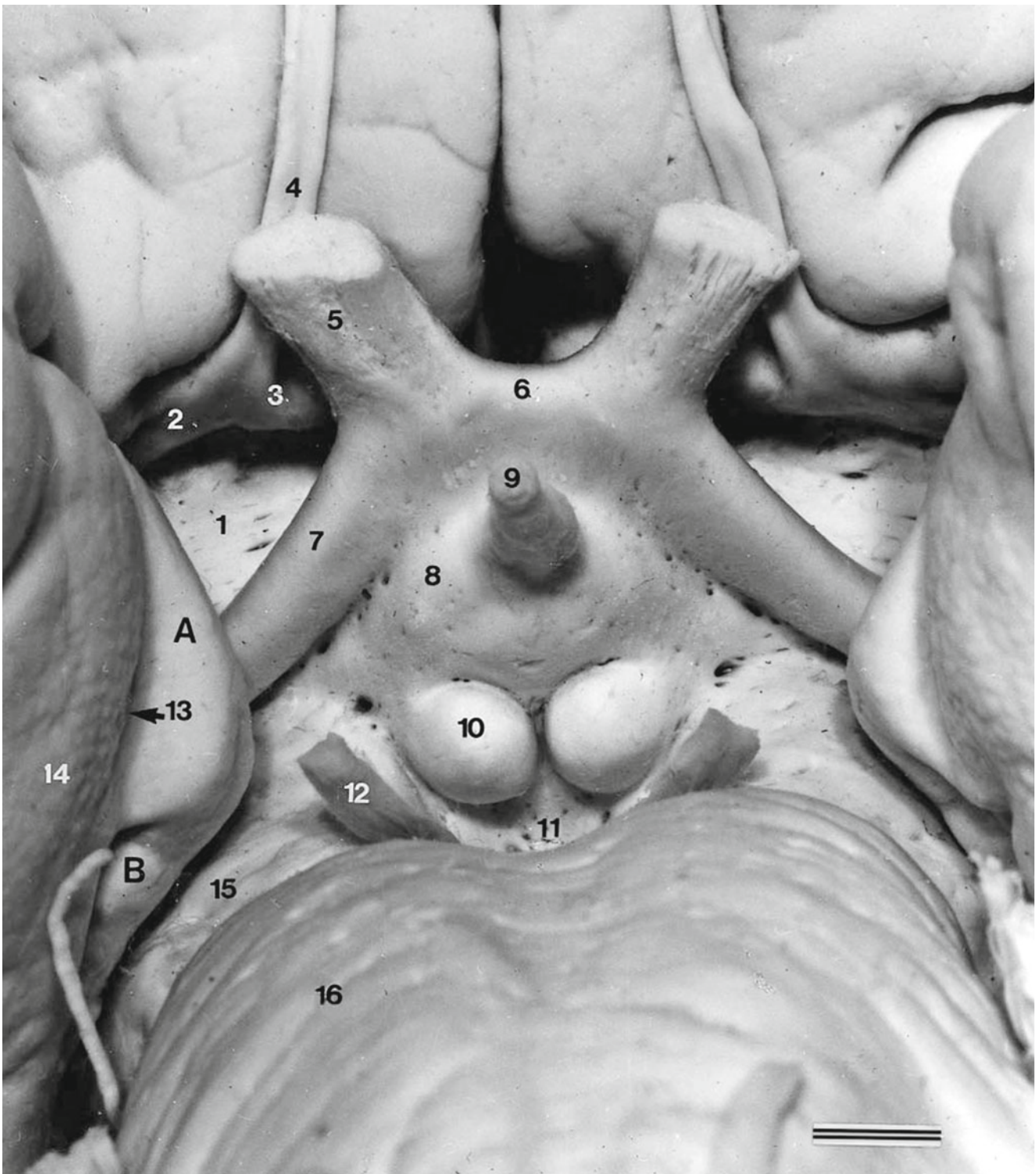


Fig. 4.10 Inferior cerebral aspect to show relation of the uncus to adjacent structures. Note the small protrusions of the entorhinal area (*14*), the verrucae gyri hippocampi, due to neuronal clusters in the entorhinal cortex (see Fig. 3.15). *Bar*, 4.8 mm. *A* Relation of the anterior segment of the uncus: *1* anterior perforated substance, *2* lateral olfactory stria, *3* medial

olfactory stria, *4* olfactory tract, *5* optic nerve, *6* optic chiasma, *7* optic tract, *8* tuber, *9* cut surface of the hypophysial stalk, *10* mamillary body, *11* interpeduncular fossa, *12* oculomotor nerve, *13* uncus notch produced by the free edge of the tentorium cerebelli, *14* entorhinal area. *B* Relation of the posterior segment of the uncus: *15* crus cerebri, *16* pons

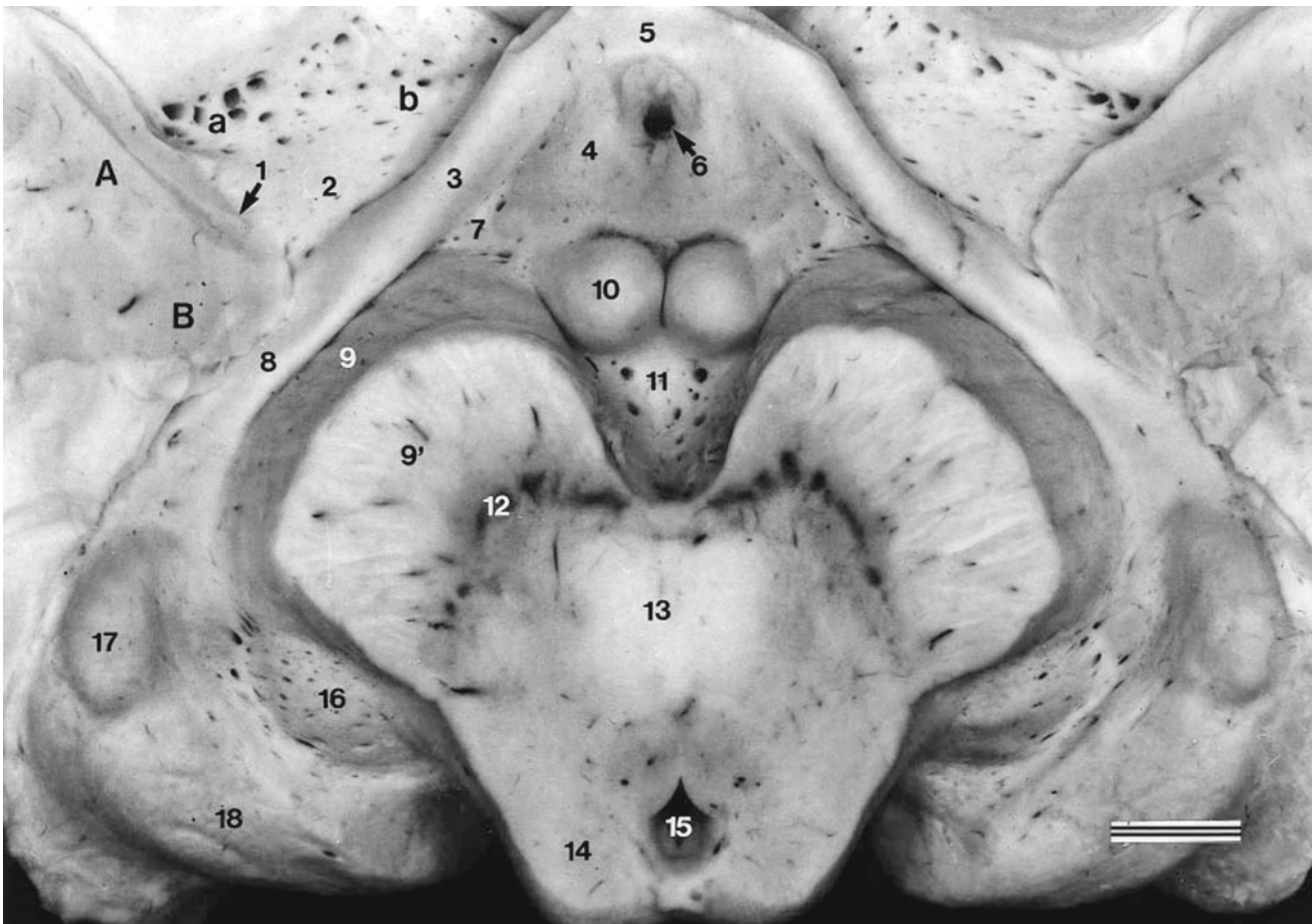


Fig. 4.11 Inferior cerebral aspect to show relation of the uncus to basal structures. The uncus and the mesencephalon have been partly cut off. *Bar*, 5.5 mm. *A* Relation of the anterior segment of the uncus: 1 endorhinal sulcus, 2 anterior perforated substance (*a* penetration point of lateral lenticulostriate arteries, *b* penetration point of medial lenticulostriate arteries), 3 optic tract, 4 lateral tuber, 5 optic chiasma, 6 infundibulum of the third ventricle (opened), 7 lateral perforated substance. *B* Relation

to the posterior segment of the uncus: 8 optic tract, 9 crus cerebri, 9' cut surface of the crus cerebri, 10 mamillary body, 11 posterior perforated substance and penetration point of thalamoperforating arteries, 12 substantia nigra, 13 brachium conjunctivum, 14 inferior colliculus, 15 cerebral aqueduct, 16 medial geniculate body and penetration point of thalamogeniculate arteries, 17 lateral geniculate body, 18 pulvinar

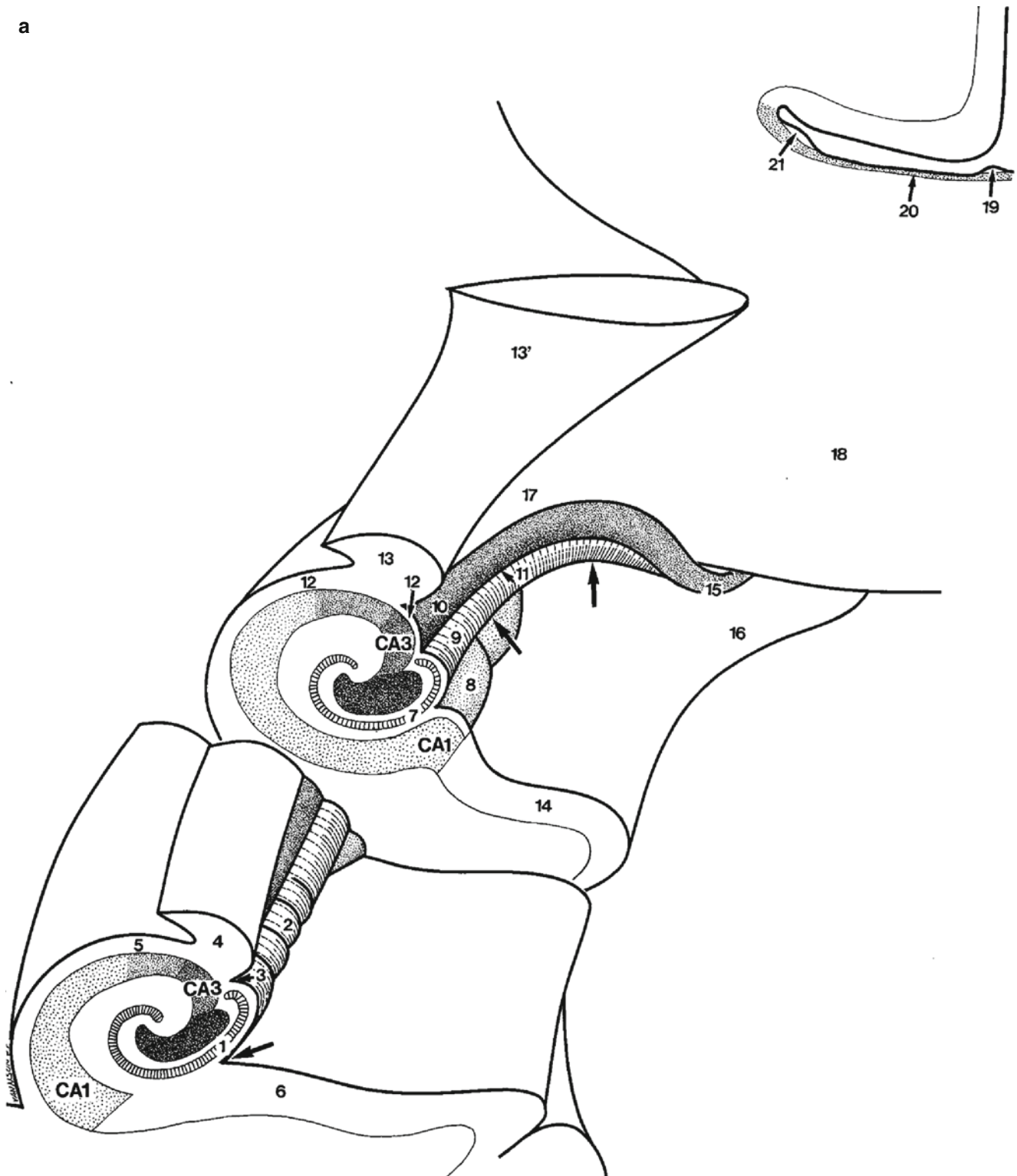


Fig. 4.12 (a) Drawing and (b) dissection showing the structure of the three segments of the extraventricular part of hippocampal tail (the fimbria is partly removed). *Arrows* indicate the superficial hippocampal sulcus. Note the whitish appearance of the hippocampus inversus in (b) (10). *Bar*, 4.4 mm. Initial segment of the tail: CA1, CA3 fields of cornu Ammonis, 1 gyrus dentatus, 2 last dentes of margo denticulatus, 3 fimbriodentate sulcus, 4 fimbria, 5 alveus, 6 subiculum. Middle segment of the tail: 7 gyrus dentatus, 8 gyri of Andreas Retzius composed of

CA1, 9 the fasciola cinerea, an extension of the margo denticulatus, 10 gyrus fasciolaris composed of CA3 covered with alveus (hippocampus inversus), 11 sulcus dentatofasciolaris, 12 alveus, 13 fimbria, 13' crus of fornix, 14 subiculum. Terminal segment of the tail: 15 the subsplenial gyrus, an extension of the gyrus fasciolaris, 16 isthmus, 17 subcallosal trigone, 18 splenium, 19 medial longitudinal stria, 20 indusium griseum, 21 lateral longitudinal stria



Fig. 4.12 (continued)

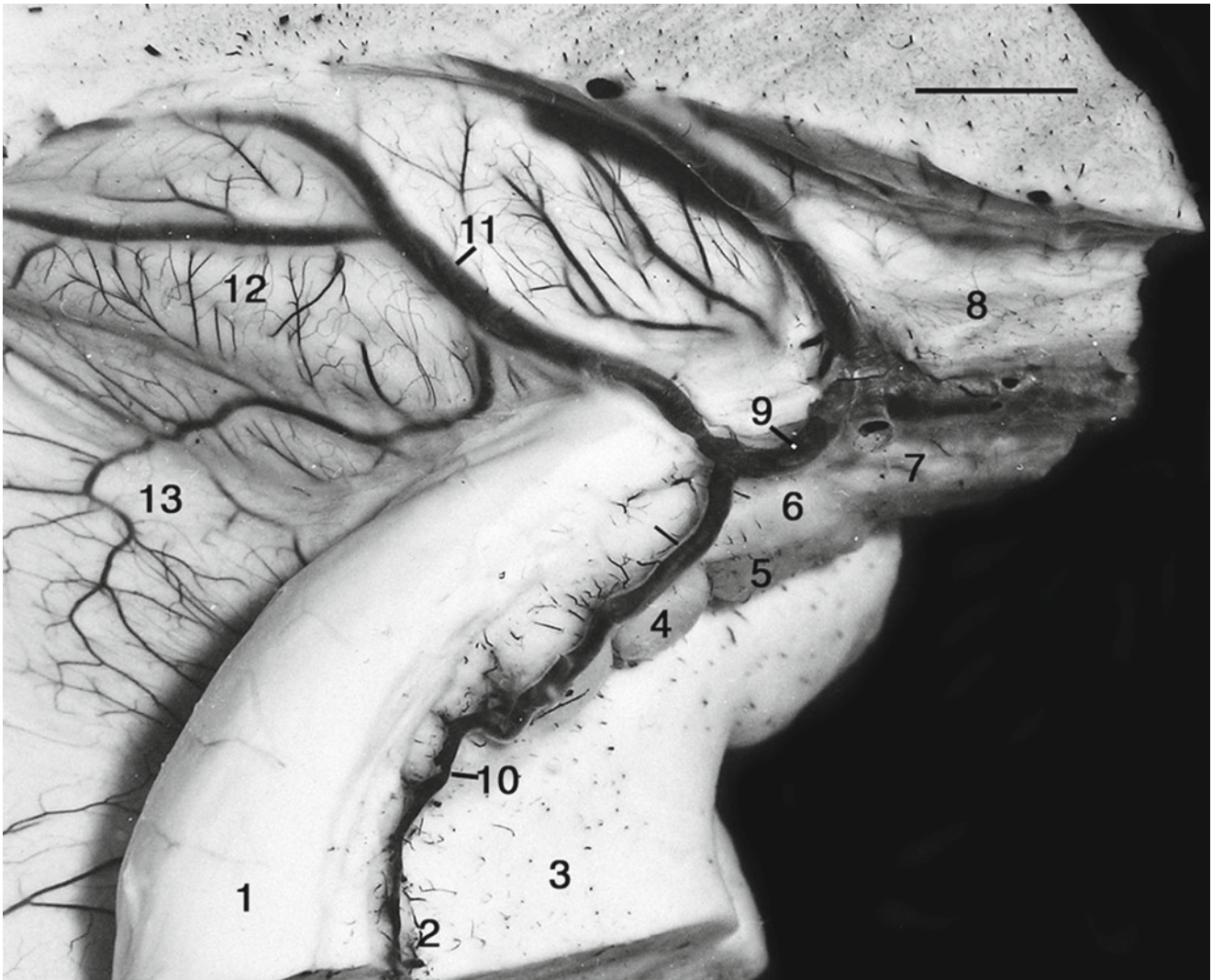


Fig. 4.13 Hippocampal tail. *Bar*, 3.7 mm. *1* ventricular cavity opened and fimbria partly removed, *2* margo denticulatus, *3* subiculum, *4* gyri of Andreas Retzius, *5* fasciola cinerea, *6* gyrus fasciolaris, *7* splenium of the corpus callosum, *8* corpus callosum, *9* trunk of the medial atrial

vein situated in the subcallosal trigone, *10* venous arch of the fimbriodentate sulcus draining into the medial atrial vein, *11* subependymal atrial veins passing through the crus of fornix to reach the trunk of the medial atrial vein, *12* calcar avis, *13* collateral trigone



Fig. 4.14 Posterior aspect of a cerebral section. *Bar*, 4.6 mm. 1 corpus callosum, 2 splenium, 3 crus of fornix, 4 subcallosal trigone, 5 gyrus fasciolaris, 6 fasciola cinerea, 7 the subsplenic gyrus, an extension of the gyrus fasciolaris, 8 isthmus, 9 parahippocampal gyrus

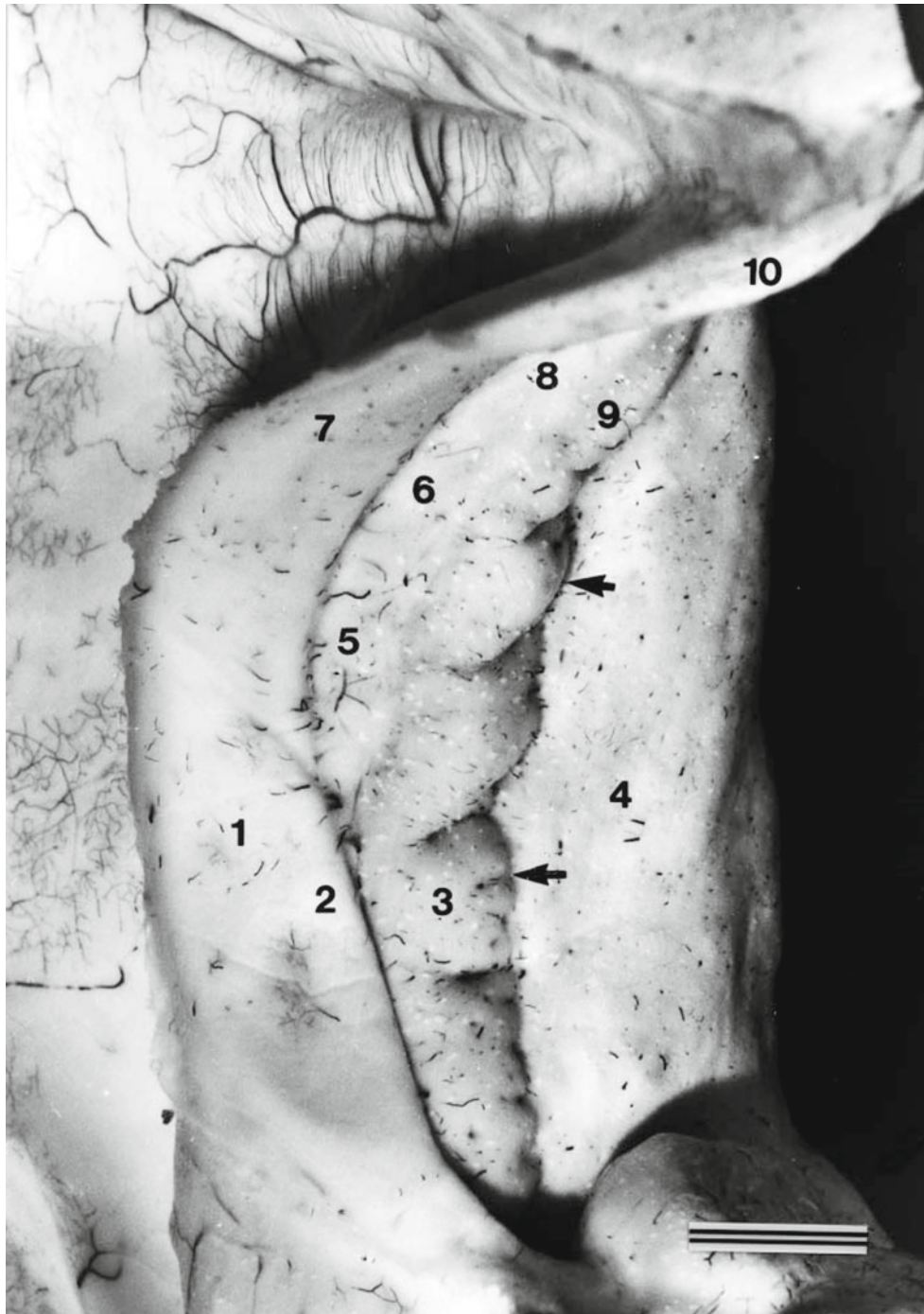


Fig. 4.15 Extraventricular part of hippocampal body and tail. In this case, the fimbriodentate sulcus is large and hence CA3, covered with alveus, is visible, forming the hippocampus inversus (6). *Arrows* indicate the superficial hippocampal sulcus. *Bar*, 4.6 mm. 1 hippocampal

body, 2 fimbria, 3 margo denticulatus, 4 parahippocampal gyrus, 5 fimbriodentate sulcus, 6 hippocampus inversus, 7 hippocampal tail, 8 gyrus fasciolaris, 9 fasciola cinerea, 10 crus of fornix

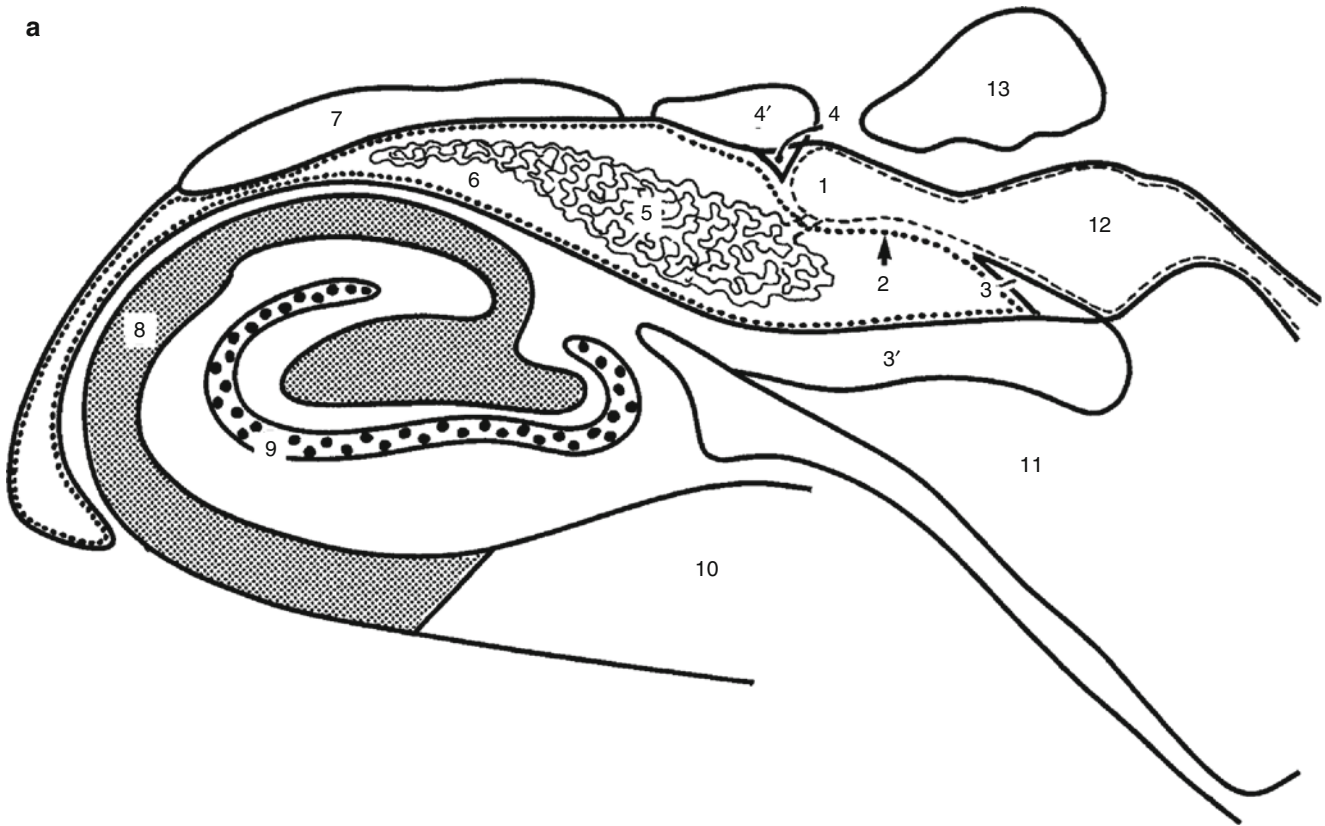


Fig. 4.16 (a, b) Coronal section of hippocampus and temporal horn of lateral ventricle. (a) Explanatory diagram. (b) Intravascular India ink injection. The tela choroidea (2) is composed of an ependymal layer (*large dots*) and a pial layer (*small dots*), as described on p. 40. Bar, 1.4 mm. 1 choroid fissure, 2 tela choroidea, 3 taenia of fimbria,

3' fimbria, 4 taenia of stria terminalis, 4' stria terminalis, 5 choroid plexuses, 6 ventricular cavity of the temporal (inferior) horn, 7 caudate nucleus, 8 cornu Ammonis, 9 gyrus dentatus, 10 subiculum, 11 uncus apex (see Fig. 7.7), 12 lateral part of the transverse fissure (wing of ambient cistern), 13 lateral geniculate body



Fig. 4.16 (continued)



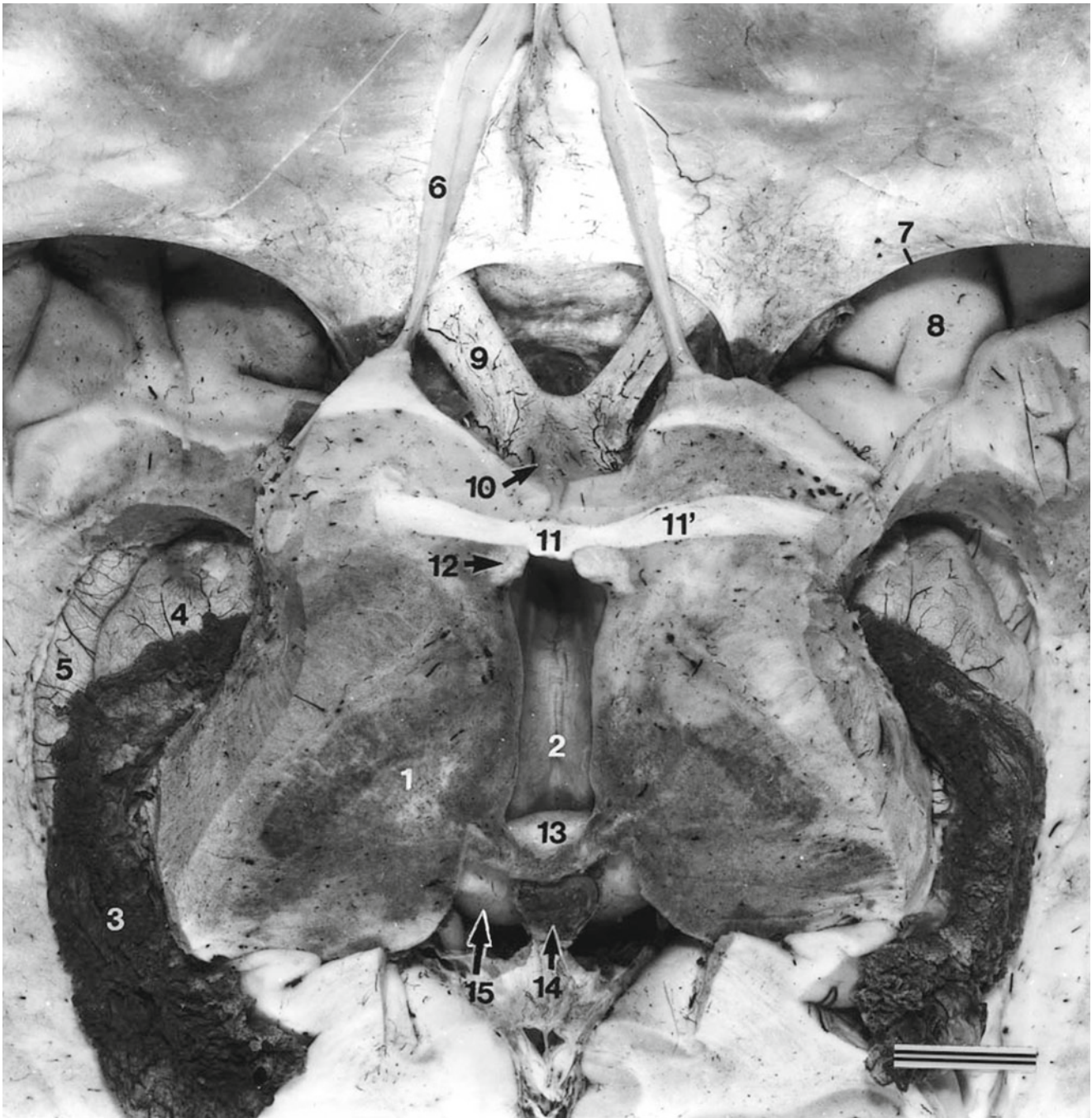


Fig. 4.18 Horizontal section of thalamus and third ventricle. The choroid plexuses of the temporal horn hide the hippocampal body and tail, but the head (digitationes hippocampi) is free of choroid plexuses and is visible. *Bar*, 11 mm. 1 thalamus, 2 third ventricle, 3 choroid plexuses of temporal horn, 4 head (digitationes hippocampi), 5 collat-

eral eminence, 6 olfactory tract, 7 lesser wing of sphenoid, 8 temporal pole, 9 optic nerve, 10 lamina terminalis, 11 anterior commissure, median part, 11' anterior commissure, lateral part, 12 column of fornix, 13 posterior commissure, 14 pineal gland, 15 superior colliculus

Fig. 4.17 The superior cerebral structures (frontal and parietal lobes, corpus callosum, and fornix) have been removed to show the superior aspect of the thalamus and caudate nucleus. The choroid plexuses of the prosencephalon are seen along their whole length in 3–6. *Arrow*, inter-ventricular foramen. *Bar*, 11.8 mm. 1 thalamus, 2 caudate nucleus, 3

roof of the third ventricle, 4 body of the lateral ventricle, 5 atrium, 5' choroid glomus, 6 temporal or ventricular horn, 7 hippocampal head (free of choroid plexuses), 8 occipital horn, 9 superior colliculus, 10 pineal gland, 11 anterior calcarine sulcus, 11' calcar avis, 12 olfactory tract, 13 olfactory bulb, 14 lesser wing of sphenoid, 15 temporal pole

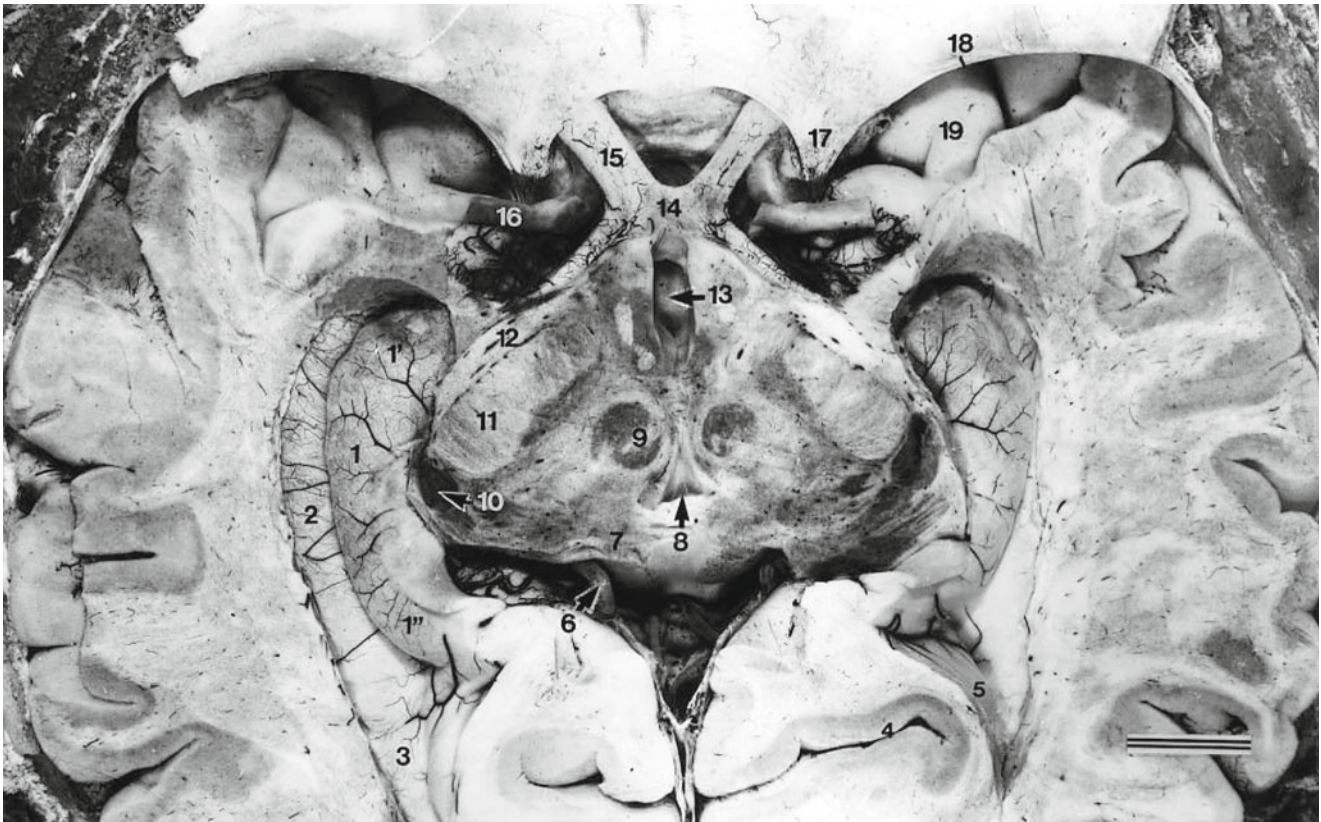


Fig. 4.19 Horizontal section at the junction of diencephalon and mesencephalon. The temporal horns have been opened and the choroid plexuses removed. *Bar*, 13.8 mm. 1 hippocampal body, 1' hippocampal head, 1'' hippocampal tail, 2 collateral eminence, 3 occipital horn, 4 anterior calcarine sulcus, 5 calcar avis, 6 P3 segment of the posterior

cerebral artery, 7 superior colliculus, 8 cerebral aqueduct, 9 red nucleus, 10 lateral geniculate body, 11 crus cerebri, 12 optic tract, 13 floor of the third ventricle, 14 optic chiasma, 15 optic nerve, 16 middle cerebral artery, 17 anterior clinoid process, 18 lesser wing of sphenoid, 19 temporal pole



Fig. 4.20 Horizontal section of upper mesencephalon. The temporal horns have been opened and the choroid plexuses removed. Note the radial disposition of subependymal veins. The right and left hippocampi encircle the mesencephalon. The posterior cerebral artery may be divided into three segments (P1, P2, and P3): P1 segment in the interpeduncular fossa (*a*); the P2 segment may be subdivided into two parts, the first (*b*) in close relationship to the uncus in the crural cistern and the second (*c*) lining the margin of the parahippocampal gyrus in the ambient cistern; beginning of P3 segment (*d*) reaching the occipital lobe through a narrow cleft between posterior part of parahippocampal gyrus and free edge of tentorium cerebelli. *Bar*, 8.7 mm. *1* hippocampal body,

1' hippocampal head, *1''* hippocampal tail, *2* fimbria, *3* crus of fornix, *4* collateral eminence, *5* superior colliculus, *6* medial geniculate body, *7* cerebral aqueduct, *8* oculomotor nucleus, *9* red nucleus, *10* substantia nigra, *11* crus cerebri, *12* posterior segment of uncus in close relationship with the crus cerebri, *13* semilunar gyrus, *14* ambient gyrus, *15* anterior choroidal artery in the semilunar sulcus, *16* oculomotor nerve, *17* pons, *18* basilar artery, *19* posterior communicating artery, *20* internal carotid artery, *21* hypophysial stalk, *22* optic nerve, *23* anterior clinoid process, *24* lesser wing of sphenoid, *25* temporal pole, *26* parahippocampal gyrus, *27* tentorium cerebelli

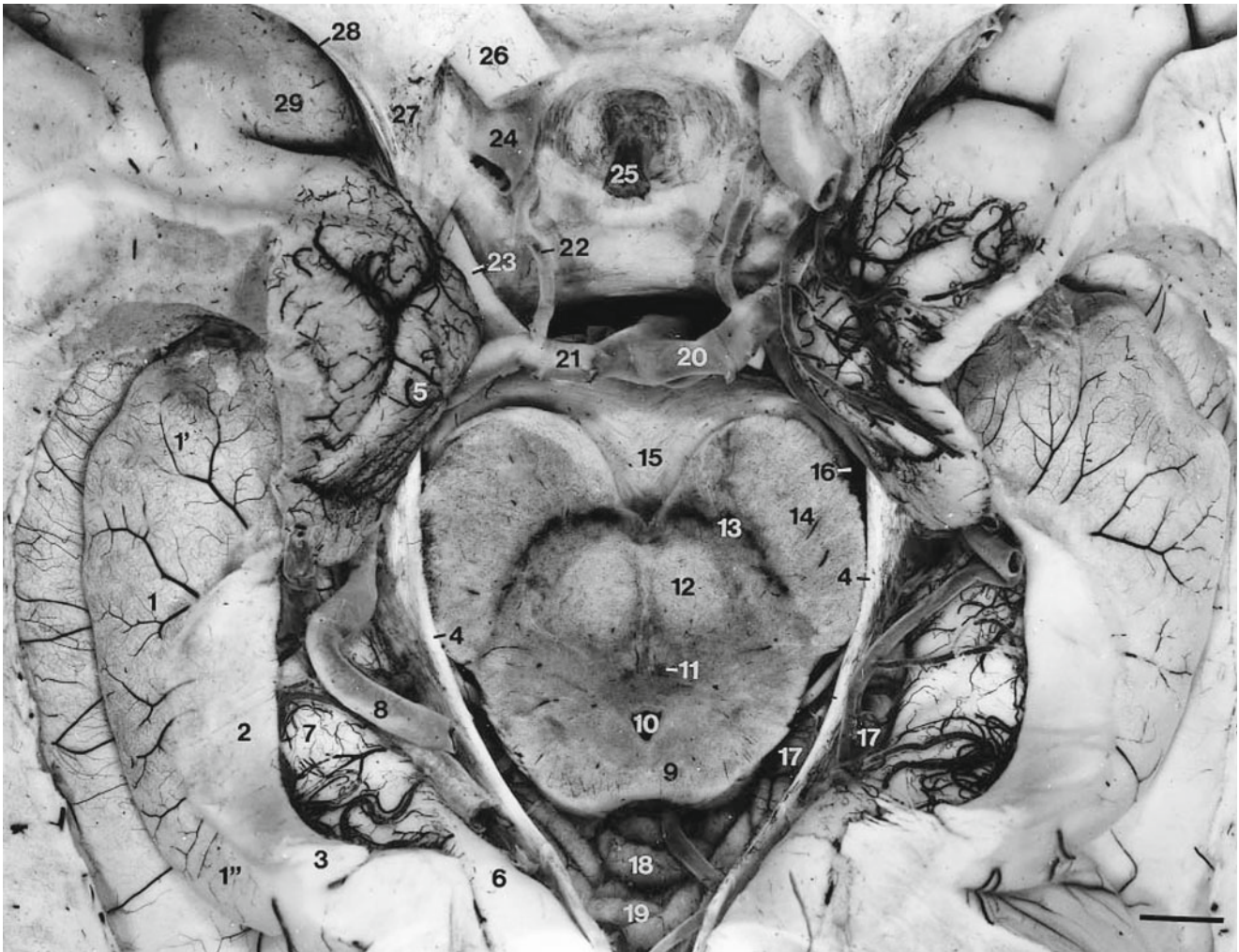


Fig. 4.21 Horizontal section of lower mesencephalon. This preparation shows the cisterns around the mesencephalon. The tentorium cerebelli (4) is in contact with the anterior (uncus, ambient gyrus, 5) and posterior parts (isthmus, 6) of the parahippocampal gyrus, whose middle part (subiculum, 7) is far from the free edge. *Bar.* 10.5 mm. 1, hippocampal body; 1', hippocampal head; 1'', hippocampal tail; 2, fimbria; 3, crus of fornix; 4, free edge and opening of the tentorium cerebelli; 5, uncus, ambient gyrus; 6, isthmus; 7, subiculum; 8, P2 segment of the posterior cerebral artery, following a curved path on the superior sur-

face of the subiculum; 9, inferior colliculus; 10, cerebral aqueduct; 11, trochlear nucleus; 12, brachium conjunctivum (superior cerebellar peduncle); 13, substantia nigra; 14, crus cerebri; 15, interpeduncular (intercrural) cistern; 16, crural cistern; 17, ambient cistern (over and below the free edge); 18, quadrigeminal cistern; 19, superior vermis of cerebellum; 20, basilar artery; 21, P1 segment of the posterior cerebral artery; 22, posterior communicating artery; 23, oculomotor nerve; 24, internal carotid artery; 25, hypophysial stalk; 26, optic nerve; 27, anterior clinoid process; 28, lesser wing of sphenoid; 29, temporal pole

Fig. 4.22 Horizontal section at the junction of mesencephalon with pons. *Right*, the temporal lobe has been removed to show the tentorium cerebelli and the free edge (*arrows*) of the tentorial opening. *Left*, the parahippocampal gyrus and the hippocampus have been left intact. *Bar.* 9.2 mm. 1 junction between pons and mesencephalon, 2 tentorium cerebelli, 3 anterior clinoid process, 4 optic nerve, 5 hypophysial stalk, 6 internal carotid artery, 7 posterior communicating artery, 8 oculomotor

nerve, 9 superior vermis, 10 hippocampal body, 10' hippocampal head, 10'' hippocampal tail, 11 calcar avis, 12 collateral eminence, 13 uncal recess of the temporal horn, 14 cut surface of amygdala, 15 margo denticulatus, 16 the subiculum (parahippocampal gyrus) forming the floor of the transverse fissure, 17 posterior cerebral artery in the ambient cistern (P2 segment), *arrowheads* show its branches to the hippocampus (see p. 70), 18 uncus





Fig. 4.23 Sagittal section (cerebellum and brain stem removed). The lower part of the medial surface of the uncus is hidden by the oculomotor nerve (2), the posterior cerebral artery (3), and the basal vein (4). Bar, 7 mm. 1 medial surface of the uncus, 2 oculomotor nerve, 3 poste-

rior cerebral artery (P2 segment), 4 basal vein, 5 inferior ventricular vein (vein of temporal horn), 6 free edge of tentorium cerebelli, 7 trochlear nerve, 8 ambient gyrus, 9 trigeminal nerve, 10 posterior cranial fossa, 11 internal acoustic meatus and vestibulocochlear nerve

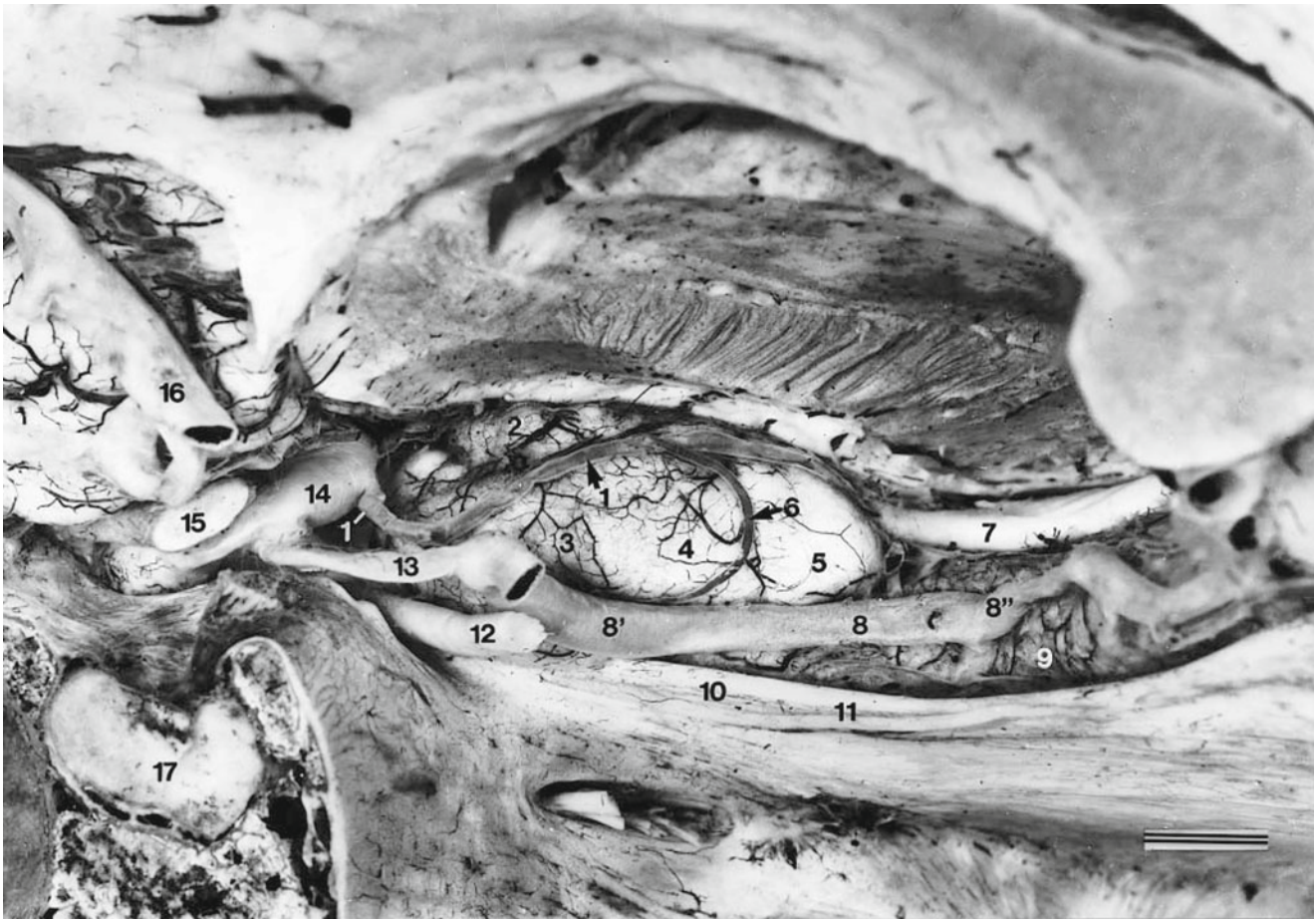


Fig. 4.24 Sagittal section (cerebellum and brain stem removed). The anterior choroidal artery (1) is situated in the semilunar sulcus, which separates the semilunar gyrus (2) and the ambient gyrus 3. Note that P2 segment of the posterior cerebral artery (8) is divided into two parts, the first (8') along the uncus in the crural cistern and the second (8'') along the parahippocampal gyrus in the ambient cistern. *Bar*, 6.5 mm. 1 anterior choroidal artery, 2 semilunar gyrus, 3 ambient gyrus, 4 uncinat

gyrus, 5 uncus apex, 6 uncal branch of the anterior choroidal artery crossing the medial surface of the uncus (see Figs. 5.13 and 5.14); 7 fimbria, 8 P2 segment of the posterior cerebral artery, 9 parahippocampal gyrus, 10 free edge of tentorium cerebelli, 11, trochlear nerve, 12 oculomotor nerve, 13 posterior communicating artery, 14 middle cerebral artery, 15 optic nerve, 16 anterior cerebral artery, 17 hypophysis

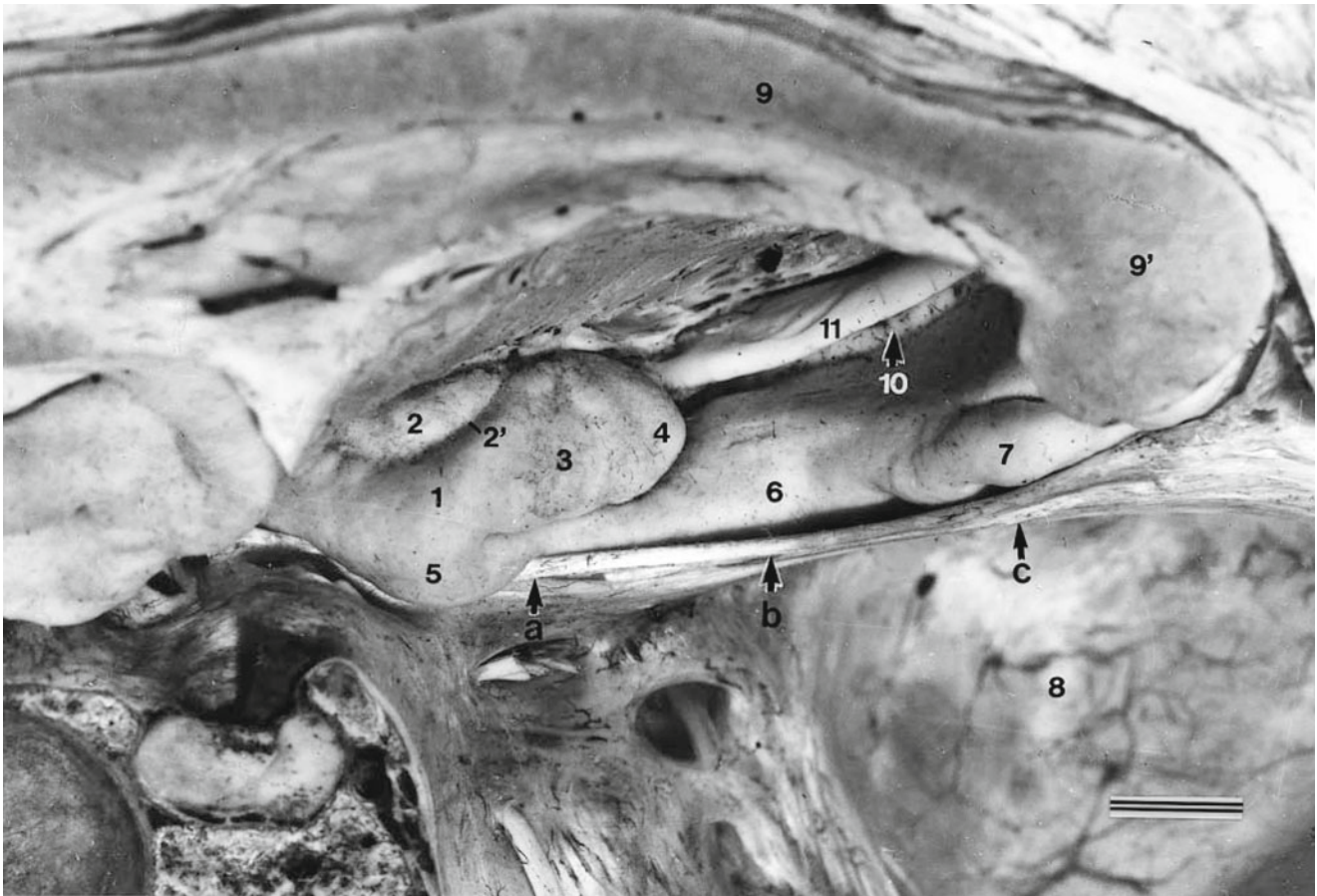


Fig. 4.25 Sagittal section (cerebellum and brain stem removed). Bar, 7 mm. 1 medial surface of uncus, 2 semilunar gyrus, 2' semianular sulcus, 3 uncinete gyrus, 4 uncal apex, 5 ambient gyrus overlying the free edge of the tentorium cerebelli (*arrow a*), 6 middle part of the

parahippocampal gyrus far from the free edge (*arrow b*), 7 posterior part of the parahippocampal gyrus (isthmus) in close contact with the free edge (*arrow c*), 8 posterior cranial fossa, 9 corpus callosum, 9' splenium, 10 margo denticulatus, 11 fimbria

Two steps have characterized the study of the hippocampal vessels during the last few decades. In a first step, the special aspect of blood vessels was used to explain the particular vulnerability of the hippocampus to anoxia (Uchimura 1928; Scharrer 1940). In a second step, the knowledge of the vascular anatomy paralleled new progress in surgery of the hippocampus (Wieser and Yasargil 1982; Olivier 1996).

The superficial (leptomeningeal) vessels and the intrahippocampal (deep) vessels will be successively studied (Figs. 5.1, 5.2, 5.3, 5.4, 5.5, 5.6, 5.7, 5.8, 5.9, 5.10, 5.11, 5.12, 5.13, 5.14, 5.15, 5.16, 5.17, 5.18, 5.19, 5.20, 5.21, 5.22, 5.23, 5.24, 5.25, 5.26, 5.27, 5.28, 5.29, 5.30, 5.31, 5.32, 5.33, and 5.34).

5.1 Superficial (Leptomeningeal) Blood Vessels

5.1.1 Superficial Hippocampal Arteries

5.1.1.1 General Remarks

The hippocampal arteries arise mainly from the posterior cerebral artery and to a lesser degree from the anterior choroidal artery (Stephens and Stilwell 1969).

The *posterior cerebral artery* can be divided, during its perimesencephalic path, into two segments: P1 segment, which is located in the intercrustral (or interpeduncular) cistern, and P2 segment, which is situated in the crural (along the uncus) and ambient cisterns (Fig. 4.20). In the ambient cistern, the posterior cerebral artery is usually situated along the margin of the parahippocampal gyrus (Figs. 5.1 and 5.3) but may cover the subiculum by occasional loops (Fig. 5.5) in the wing of the ambient cistern (laterally closed by the choroid fissure). In its P2 segment, the posterior cerebral artery gives rise to numerous important branches, which render the surgical approach to the medial temporal lobe particularly difficult (Gaffan and Lim 1991). These branches are the inferior temporal arteries (Fig. 5.15), which are usually divided into the anterior, middle, and posterior inferior temporal arteries; the posterolateral choroidal artery (Fig. 5.8) and the splenic artery (Figs. 5.2, 5.3,

and 5.4) (Stephens and Stilwell 1969; Margolis et al. 1974; Lecaque et al. 1978; Milisavljevic et al. 1986).

The anterior choroidal artery, a branch of the internal carotid artery, reaches the choroid fissure and the choroid plexuses of the temporal (or inferior) horn. During its course in the semianular sulcus of the uncus (Figs. 4.24, 5.13, and 5.14), the anterior choroidal artery give rise to an uncal branch, which crosses by a descending path the medial surface of the uncus and disappears into the uncal sulcus (Fig. 5.11; Carpenter et al. 1954; Stephens and Stilwell 1969; Goldberg 1974; Rhoton et al. 1979; Fujii et al. 1980; Hussein et al. 1988; Morandi et al. 1996).

5.1.1.2 Origin (Figs. 5.1, 5.2, 5.3, 5.4, 5.5, 5.6, 5.7, and 5.11)

General Arrangement

Three arteries (or group of arteries) usually vascularize the hippocampus: the anterior, middle, and posterior hippocampal arteries. The anterior and middle arteries arise either from the trunk of the posterior cerebral artery or from its inferior temporal branches, whereas the posterior hippocampal artery frequently arises from the splenic artery, a branch of the posterior cerebral artery.

Variations

Numerous variations have been described concerning the origin of the hippocampal arteries (this is true of the whole superficial arterial network of the brain). As the number of hemispheres observed in this study concerning the superficial vessels was insufficient ($n=16$), the reader is referred to the work of Lang (1981) and Marinkovic et al. (1992) and to the more recent, exhaustive studies carried out by Erdem et al. (1993). In these later studies, the origins of the hippocampal arteries were divided into five groups of decreasing frequency:

Group A. This is most frequent type (57 %) and is characterized by mixed origins of the hippocampal arteries; it corresponds to the type of description presented here (Figs. 5.1 and 5.5). Origins from the anterior and posterolateral choroidal arteries may be included in this group.

Group B. In this group, the hippocampal arteries mainly arise from all the inferior temporal arteries (27 %).

Group C. In this group, the hippocampal arteries only arise from the anterior inferior temporal artery (10 %).

Group D. The trunk of the posterior cerebral artery was the principal supply of the hippocampal arteries (3 %) in this group. Uchimura's artery may belong to group D.

Group E. The anterior choroidal artery was the main supply to the hippocampus (3 %) in this group.

Course and Branches

The hippocampal arteries can be divided into two groups according to their territories: the middle and posterior hippocampal arteries supply the hippocampal body and tail, whereas the anterior hippocampal artery vascularizes the hippocampal head and uncus.

5.1.1.3 Middle and Posterior Hippocampal Arteries

(Figs. 5.1, 5.2, 5.3, 5.4, 5.5, 5.6, and 5.7)

The middle (the largest) and the posterior hippocampal arteries have a straight or slightly curved path on the flat surface of the subiculum, supplying this structure by small and scattered branches. When they reach the hippocampus, the hippocampal arteries curve to follow a sinuous, longitudinal course parallel to the superficial hippocampal sulcus and the margo denticulatus (Muller and Shaw 1965; Sasaki et al. 1993). Along their *longitudinal terminal segment*, the hippocampal arteries give rise to numerous branches, which can be divided into large and small branches (their intrahippocampal path is described on p. 71). The large branches directly penetrate the hippocampus in the deep sulci between the dentes of the margo denticulatus (Figs. 5.6 and 5.7). These dentes, which are only present in primates, have an unknown origin. It is possible that the penetration of the large arteries at a right angle, which produces depressions on the surface of the margo denticulatus, may contribute to the formation of the dentes. The small arteries penetrate the whole surface of the margo denticulatus. Some small, parallel arteries have a rectilinear course on the margo denticulatus and penetrate the hippocampus in the fimbriodentate sulcus (Figs. 5.1 and 5.6). Because of their appearance, they may be called "straight arteries." It should be noted that, contrary to the observations made by Marinkovic et al. (1992), the straight arteries are not important in size or number and have a reduced intrahippocampal territory (see p. 71). Moreover, it appears that this aspect is not specific to the fimbriodentate sulcus but may be found in other encephalic sulci, for example, in the bottom of cerebellar sulci (Duvernoy et al. 1983).

The middle and posterior hippocampal arteries are richly anastomosed (Fig. 5.1). In some cases, anastomoses between their longitudinal terminal segments form a continuous arterial arcade along the superficial hippocampal sulcus. According to observations by Scharrer (1940), a continuous

arcade and its branches arising at right angles in a rake-like appearance may explain the particular vulnerability of hippocampal tissue to anoxia due to a sudden fall in blood pressure. In fact, this continuous arcade, previously described by Heiman (1938), Nilges (1944), and Lindenberg (1957), is rarely found in humans (Muller and Shaw 1965).

5.1.1.4 Anterior Hippocampal Artery

(Figs. 5.11 and 5.12)

The anterior hippocampal artery contributes to the dense hippocampo-parahippocampal arterial complex (Fig. 5.16), together with ramifications of the anterior inferior temporal artery (Marinkovic et al. 1992). This complex, in relation to the uncus apex, is partly hidden by the voluminous trunks of the posterior cerebral artery and basal vein in a medial view. The anterior hippocampal artery usually arises from the anterior inferior temporal artery (Muller and Shaw 1965). It disappears into the uncus sulcus and often reappears on the surface of the piriform lobe, participating in the vascularization of the subjacent entorhinal area (Fig. 5.17). During its hidden course in the uncus sulcus, it gives rise to branches which mainly penetrate the longitudinal sulci between the external digitations and vascularize the hippocampal head (Figs. 5.12 and 5.23). The uncus branch of the anterior choroidal artery (Figs. 5.11, 5.13, and 5.14) is frequently anastomosed with the anterior hippocampal artery within the uncus sulcus (Fig. 5.12). The contribution of the anterior choroidal artery to the vascular supply of the hippocampal head is highly variable and may be preponderant in some cases (Gastaut and Lammers 1961).

5.1.2 Superficial Hippocampal Veins

The hippocampal veins are branches of the basal vein (Huang and Wolf 1974). The origin of the *basal vein* is situated on the anterior perforated substance. Its first ventral segment extends until it receives the inferior ventricular vein (vein of the temporal horn). During its course, the basal vein is in close contact with the medial surface of the uncus and hides the uncus sulcus together with the posterior cerebral artery (Fig. 4.23). Its second laterodorsal segment crosses the mid-brain lateral surface to reach the vein of Galen (Duvernoy 1975). During its laterodorsal segment in the ambient cistern, the basal vein is situated just above the P2 segment of the posterior cerebral artery (Fig. 5.1b) and receives the venous drainage of the hippocampus.

The superficial hippocampal veins have a simpler, more typical aspect than the arteries. They form two longitudinal superficial venous arches covering the fimbriodentate and the superficial hippocampal sulci (as a general rule, the superficial cerebral veins often follow the sulci on the nervous tissue surface). On account of their position, these two

arches may be called the venous arch of fimbriodentate sulcus and the venous arch of superficial hippocampal sulcus.

The *venous arch of the fimbriodentate sulcus* (Figs. 5.1, 5.2, and 5.8) is often hidden by the fimbria (Fig. 5.3). This continuous arcade receives the subependymal intrahippocampal veins at a right angle, and these are visible on the intraventricular aspect of the hippocampus.

The *venous arch of the superficial hippocampal sulcus* (Figs. 5.1, 5.3, and 5.8) is often discontinuous. It receives the deep or sulcal intrahippocampal veins (see p. 72) emerging either from the hippocampal sulcus or from the sulci between the dentes of the margo denticulatus. These two arches join together at their anterior and posterior extremities. The anterior extremity of these arches flows into the inferior ventricular vein (often called the vein of the temporal horn), and the posterior extremity reaches the medial atrial vein. Both the inferior ventricular and the medial atrial veins are tributaries of the basal vein: the inferior ventricular vein (vein of the temporal horn) reaches the basal vein near the uncus apex (Fig. 5.1), and the medial atrial vein crosses the subcallosal trigone to join the basal vein (Figs. 4.13 and 5.1).

5.2 Intrahippocampal (Deep) Blood Vessels

In the following, the intrahippocampal arteries and veins and the hippocampal capillary network will be studied. Our description represents the results of observations of blocks several millimeters thick that were cleared using the Spalteholz technique (see p. 3). In these blocks, it is possible to follow arteries and veins along their whole course.

5.2.1 Intrahippocampal Arteries

As described on p. 70, the branches of the longitudinal terminal segment of superficial hippocampal arteries are divided into large and small arteries. According to their intrahippocampal aspect and situation, these two groups may be subdivided into large ventral, large dorsal, small ventral, and small dorsal intrahippocampal arteries. This description correlates well with the observations made by Marinkovic et al. (1992). The intrahippocampal arteries are characterized by their curved path following the rolling up of the cornu Ammonis and the gyrus dentatus.

Large Ventral Intrahippocampal Arteries (Fig. 5.18)

The large ventral intrahippocampal arteries penetrate the hippocampus between the dentes of the margo denticulatus. They cross the proximal part of the gyrus dentatus, briefly follow the vestigial hippocampal sulcus, and course in the stratum lacunosum and sometimes in the stratum pyramidale of CA1 (Altschul 1939; Hens and Van den Bergh 1977;

Sasaki et al. 1993). The large ventral arteries vascularize CA1 (the *Sektorgefasse* of Uchimura 1928) and, by their terminal ramifications, CA2. Arterial branches arising from the large ventral arteries often have a long and oblique course through CA1. The collaterals of these branches often arise in a curiously recurrent aspect (Fig. 5.26). These long branches of the large ventral arteries, specific to CA1, vascularize the pyramidal neurons, whereas the short branches reach the molecular layer of the cornu Ammonis (Fig. 5.18).

5.2.1.1 Large Dorsal Intrahippocampal Arteries

(Figs. 5.18, 5.20, and 5.24)

The large dorsal intrahippocampal arteries have a shorter, curved route in comparison to the large ventral arteries. They penetrate between the dentes of the gyrus dentatus and are then situated inside CA4 along the gyrus dentatus. Their terminal segment reaches CA3 and sometimes CA2, via a sharp curve. Along their route, the large dorsal arteries also vascularize CA4 and the distal part of the gyrus dentatus. The branches to the gyrus dentatus have a long, typically rectilinear course. Fine ramifications arise at right angles from these branches and reach the molecular layer of the gyrus dentatus across its granular layer (Figs. 5.18, 5.28, and 5.29). Some branches supplying the terminal curved part of the gyrus dentatus have a brushlike appearance (Figs. 5.18 and 5.30).

5.2.1.2 Small Ventral Intrahippocampal Arteries

(Fig. 5.18)

The small ventral intrahippocampal arteries penetrate the surface of the margo denticulatus. They vascularize the proximal part of the gyrus dentatus (Uchimura 1928) with the same rectilinear course as those previously described in its distal part.

5.2.1.3 Small Dorsal Intrahippocampal Arteries

(Figs. 5.18 and 5.21)

The small dorsal intrahippocampal arteries cross the surface of the margo denticulatus and reach the fimbriodentate sulcus. On account of their rectilinear and parallel superficial path (see p. 70), they are often referred to as “straight arteries.” This denomination may thus be restricted to the small dorsal arteries (although, in the description by Marinkovic et al. (1992), all the intrahippocampal arteries were called straight arteries). The few, fine straight arteries have a small intrahippocampal territory limited to CA3 and the adjacent part of CA4.

5.2.1.4 Variations

The intrahippocampal territories of these four arterial groups are the subject of variations. For example, an artery belonging to the large ventral or the large dorsal (Fig. 5.21) group may have a territory extending to almost the whole hippocampal tissue visible on a section. In most cases, however

(Fig. 5.18), CA1 is only vascularized by the large ventral arteries, whereas CA2 and CA4 and the gyrus dentatus have several supplies coming from different arterial groups (Uchimura 1928; Scharrer 1940). This specific arterial supply of CA1 and the long course of its arterial branches have been the support to the vascular theory explaining the selective vulnerability of CA1 to anoxia. However, the vascular theory has now been abandoned, as described on p. 31. Against this explanation, it may be noted that the gyrus dentatus, like CA1, is vascularized by long, fine arteries, whereas it is generally considered as a sector resistant to anoxia.

5.2.2 Intrahippocampal Veins (Fig. 5.19)

The intrahippocampal veins have been poorly studied, probably due to technical difficulties (see p. 3). In the hippocampus, two types of veins may be distinguished: the sulcal and subependymal intrahippocampal veins.

5.2.2.1 Sulcal Intrahippocampal Veins (Figs. 5.19 and 5.20)

The sulcal intrahippocampal veins have their whole course in the vestigial hippocampal sulcus and are thus situated between the strata molecularia of the cornu Ammonis and the gyrus dentatus. Originating from the distal part of CA1 and from the adjacent CA2 field, they follow a curved path and reach the venous arch of the superficial hippocampal sulcus. On their concave side, the sulcal veins receive fine branches from the stratum moleculare of the gyrus dentatus (Figs. 5.19 and 5.31). Their convex side receives branches from the stratum moleculare of the cornu Ammonis and large venous branches draining CA1 and the adjacent subiculum (Fig. 5.19).

5.2.2.2 Subependymal Intrahippocampal Veins (Figs. 5.9, 5.10, and 5.19)

The subependymal intrahippocampal veins have a long, arched path that can be observed in endoventricular views of the hippocampus (Wolf and Huang 1964; Lazorthes et al. 1976). They have a regular and radial aspect and reach the venous arch of the fimbriodentate sulcus through the fimbria. The subependymal intrahippocampal veins drain the blood of the deep layers (Fig. 5.27) of CA2, CA1, and the adjacent subiculum. In addition to the sulcal and subependymal veins, small intrahippocampal veins may partially drain CA2, CA3, and CA4 directly into the vein of the fimbriodentate sulcus (Fig. 5.19).

5.2.3 Hippocampal Head

The above description of the intrahippocampal arteries and veins concerns the body and tail of the hippocampus. The hippocampal head is vascularized by arterial and venous axes

situated within each digitation (Fig. 5.23). These vascular axes stem from the superficial network situated in the sulci between the external digitations observed in the uncal sulcus (Fig. 5.12).

5.2.4 Vascular Network

In the hippocampus, it is possible to recognize the layers of the cornu Ammonis and the gyrus dentatus according to their different vascular densities (Figs. 5.20, 5.21, 5.22, and 5.24); in the cornu Ammonis, the strata pyramidale and oriens have a marked vascular density (Cobb 1929). Vessels in the stratum radiatum are arranged in parallel, like the apical dendrites of its pyramidal neurons. The vascular network of the stratum radiatum is generally poor and appears in sections as a light band whose end indicates the limit of the hippocampus and the beginning of the subiculum (Figs. 3.8, 5.20, and 6.6b; Uchimura 1928). The stratum lacunosum is the least vascularized layer of the cornu Ammonis. Among the fields in the stratum pyramidale, the remarkable vascular density of CA2 is notable (Fig. 5.20), followed in intensity by CA3, whereas CA1 is poorly vascularized; however, the most intense vascular density in the cornu Ammonis is in the stratum moleculare (Figs. 5.20, 5.21, and 5.22). In the gyrus dentatus, it is also the stratum moleculare that is the most densely vascularized (Figs. 5.21, 5.22, and 5.24), whereas the stratum granulosum is almost devoid of capillaries (Figs. 3.10 and 5.28). Thus the vascular networks of the strata molecularia of the cornu Ammonis and the gyrus dentatus are especially dense and separated by a clear lamina without capillaries, the vestigial hippocampal sulcus.

Numerous researchers have studied the differences in density of capillary networks in many regions of the gray matter. A relation generally exists between the density of neuronal somata and capillary networks, but many exceptions have been recorded. In the hippocampus, for example, the stratum granulosum, although extremely rich in neurons, is only poorly vascularized, while the strata molecularia of the cornu Ammonis and the gyrus dentatus, both poor in neurons, show the highest vascular density in the hippocampus. The intensity of capillary networks may thus be due more to the density of synapses than to the number of neuronal somata (Lorente de No 1928; Dunning and Wolff 1937; Wolff 1938; Craigie 1945; Duvernoy et al. 1981).

The intrahippocampal vascularization, like that of the isocortex, is of a network vascular type, composed of a continuous capillary network (a loop vascular type composed of independent vascular trees is found in some mammals, e.g., opossums; Scharrer 1944). Despite this continuous capillary network, the capillary anastomoses are inefficient to correct a local insufficiency in blood supply (Klosovskii 1963).

In the hippocampus, as in the isocortex (Ravens 1974), large arterial, venous, or arteriovenous anastomoses have never been found. However, precapillary arterial and arteriovenous shunts may be present in the vascular network of the hippocampus resembling those described in the isocortex (Hasegava et al. 1967; Kennady and Taplin 1967; Duvernoy 1999a; Duvernoy et al. 1981).

The presence of vascular units, each with a vein at the center and surrounded by an arterial ring, has been described in the isocortex (Wolff 1976; Bär 1980; Duvernoy et al. 1981). The folded aspect of the hippocampal allocortex makes this research difficult. However, some features suggest that such vascular units may exist; the succession of penetrations or emergences of the hippocampal arteries and veins between the dentes of the margo denticulatus (Figs. 5.6 and 5.7; Nilges 1944; Lierse 1963), the position of the subependymal intrahippocampal veins at regular intervals, and the bush-like aspect of the hippocampal capillary network are particularly noteworthy (Figs. 5.9 and 5.25).

The vascular network of the hippocampus does in fact have some features in common with that of the isocortex. For example, as in the isocortex (Pfeifer 1930; Saunders and Bell 1971; Duvernoy et al. 1981), each arterial branch is surrounded by a circular zone of nervous tissue devoid of capillaries (Fig. 5.26). The significance of this capillary-free space

is unknown. However, it is possible that the nervous tissue in the capillary-free space may be supplied by the arterial branch itself, whose wall characteristics allow an exchange with the adjacent tissue (Cervos-Navarro and Rozas 1978).

As in the vascular isocortical network, arterial coilings and capillary deformations are often found in the hippocampus, especially in the pyramidal layer of CA2. These special features (visible in Figs. 5.32, 5.33, and 5.34) have not yet been explained (Hassler 1967; Saunders and Bell 1971; Duvernoy et al. 1981).

However, the vascular hippocampal network differs in many points from that of the isocortex. For example, the long tangential course of arteries and veins (Figs. 5.18 and 5.19) contrasts with the isocortical blood vessels, whose course is perpendicular to the surface with a palisade aspect. Curiously, the vascular organization of the allocortical hippocampus is in many points similar to that of the cerebellar cortex (Spielmeyer 1930; Duvernoy et al. 1983).

This study of the hippocampal vessels completes previous research on the vascularization of the isocortex, cerebellar cortex, brain stem, and circumventricular organs, which together offer a general view of the vascular architecture of the brain (Duvernoy 1972, 1995, 1999a, b; Duvernoy and Koritke 1964, 1965; Duvernoy et al. 1969, 1971, 1972, 1981, 1983, 2000; Duvernoy and Risold 2007).

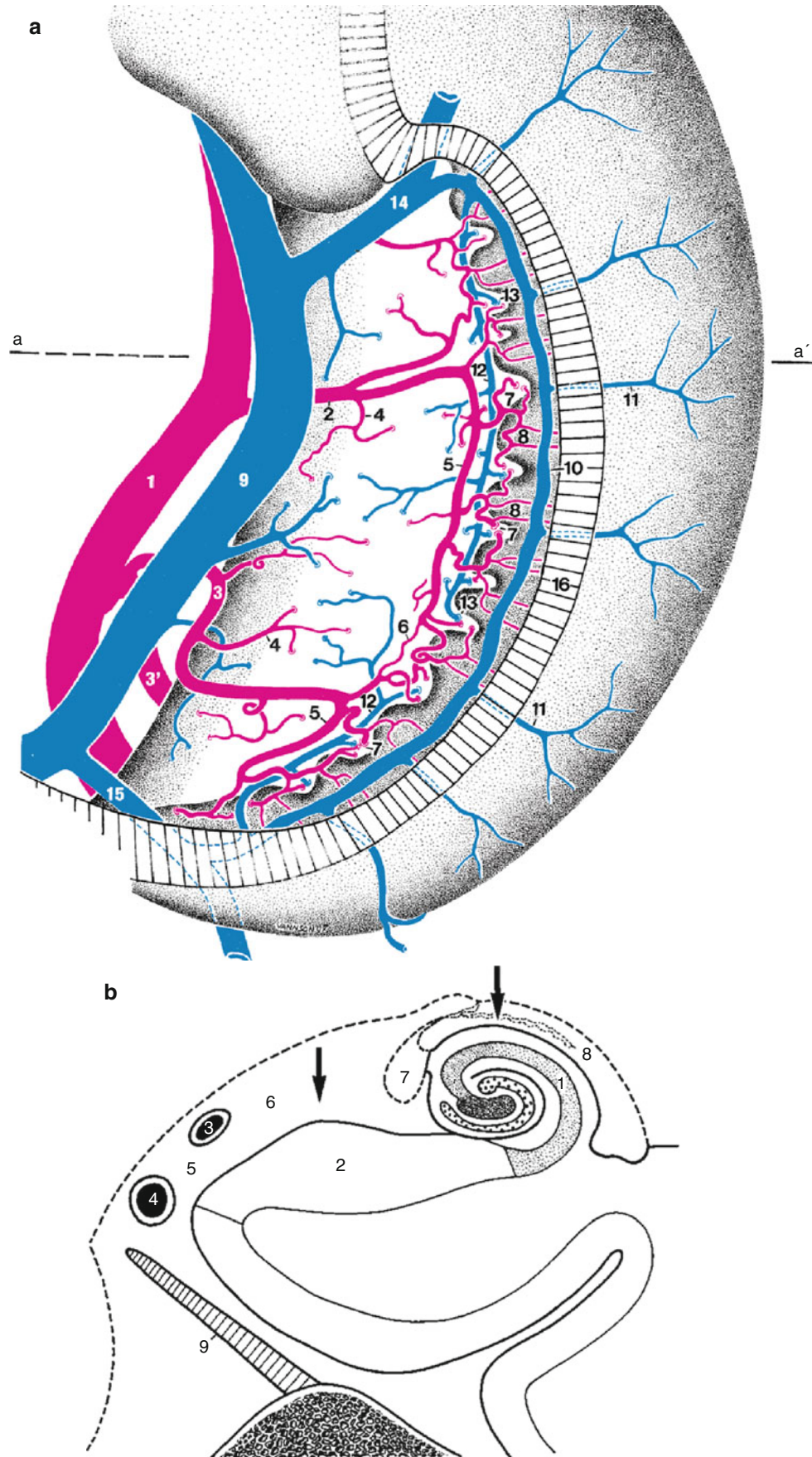


Fig. 5.2 Intravascular India ink injection. Bar, 2.8 mm 1 superior surface of subiculum, 2 margo denticulatus, 3 fimbria (removed), 4 middle hippocampal arteries, 5 posterior hippocampal artery arising from a splenic artery (5'), 6 longitudinal terminal segments of the hippocampal arteries, 7 arterial branches to the subiculum, 8 large arterial branches penetrating the hippocampus between the dentes (9) of margo denticulatus, 10 venous arch of the fimbriodentate sulcus receiving the subependymal intrahippocampal veins (11), 12 venous arch of the superficial hippocampal sulcus, 13 superficial hippocampal sulcus



Fig. 5.1 (a) Superficial arteries and veins of hippocampal body and tail. The temporal horn has been opened and the fimbria removed, as seen in (b) superficial arteries: 1 posterior cerebral artery, 2 middle hippocampal artery arising from the trunk of the posterior cerebral artery, 3 posterior hippocampal artery arising from an inferior temporal artery (3'), 4 arterial branches to the subiculum, 5 longitudinal terminal segment of the hippocampal arteries running along the superficial hippocampal sulcus, 6 anastomosis between the longitudinal terminal segments of hippocampal arteries, 7 large arterial branches penetrating in the sulci between the dentes of the margo denticulatus, 8 small arterial branches (straight arteries). Superficial veins: 9 basal vein. The longitudinal hippocampal veins may be divided into two venous arches: 10 venous arch of the

fimbriodentate sulcus receiving the subependymal intrahippocampal veins (11), visible in an endoventricular view, 12 venous arch of the superficial hippocampal sulcus receiving the sulcal intrahippocampal veins (13) emerging between the dentes of margo denticulatus. These two arches are drained into the basal vein by the inferior ventricular vein (vein of the temporal horn, 14) and by the medial atrial vein (15). 16 cut surface of fimbria. (b) Transverse section of the hippocampus according to the plane *a-a'* shown in (a), showing the superior aspects of subiculum and hippocampus (arrows) after removal of central structures (dotted lines) 1 cornu Ammonis, 2 subiculum, 3 basal vein, 4 posterior cerebral artery, 5 ambient cistern, 6 wing of ambient cistern, 7 fimbria (removed), 8 choroid plexuses (removed)

Fig. 5.3 Same preparation as in Fig. 5.2 (the fimbria is left intact). The temporal (inferior) horn has been opened and the choroid plexuses removed. Note on the surface of the fimbria (1) the imprints left by branches of choroidal arteries (*arrowheads*). *Bar*, 3 mm. 1 fimbria, 2 margo denticulatus (partly hidden by the fimbria), 3 posterior cerebral artery lining the margin of the parahippocampal gyrus (4), 5 middle hippocampal arteries, 6 splenial artery, 7 venous arch of the superficial hippocampal sulcus (the venous arch of the fimbriodentate sulcus is hidden by the fimbria), 8 endoventricular view of the hippocampus



Fig. 5.4 Intravascular India ink injection. *Bar*, 2.6 mm *f* fimbria, 2 margo denticulatus (largely hidden by the fimbria), 3 subiculum, 4 posterior cerebral artery, 5 middle hippocampal arteries arising from the posterior cerebral artery, 6 group of posterior hippocampal arteries arising from a curved splenial artery (7), which is a branch of the posterior cerebral artery, 8 large arterial branches penetrating the hippocampus between the dentes of the margo denticulatus (9)



Fig. 5.5 Vascular India ink injection. The fimbria has been removed (1) to show the margo denticulatus (2). This preparation shows several superficial hippocampal arteries with various origins. Bar, 2.9 mm. 1 fimbria (removed), 2 margo denticulatus, 3 middle hippocampal artery arising from a posterolateral choroidal artery (3'), whose course toward the temporal horn has been cut off (arrow), 4 middle hippocampal artery arising directly from the posterior cerebral artery (5), which curves on the subicular surface (6), 7 posterior hippocampal artery arising from a small inferior temporal artery (7'), 8 posterior hippocampal artery arising from the splenic artery (8'), 9 longitudinal terminal segment of the hippocampal arteries situated along the superficial hippocampal sulcus (10). 11 small "straight" arteries, 12 large arterial branches penetrating between the dentes of margo denticulatus, 13 endoventricular aspect of the hippocampal tail

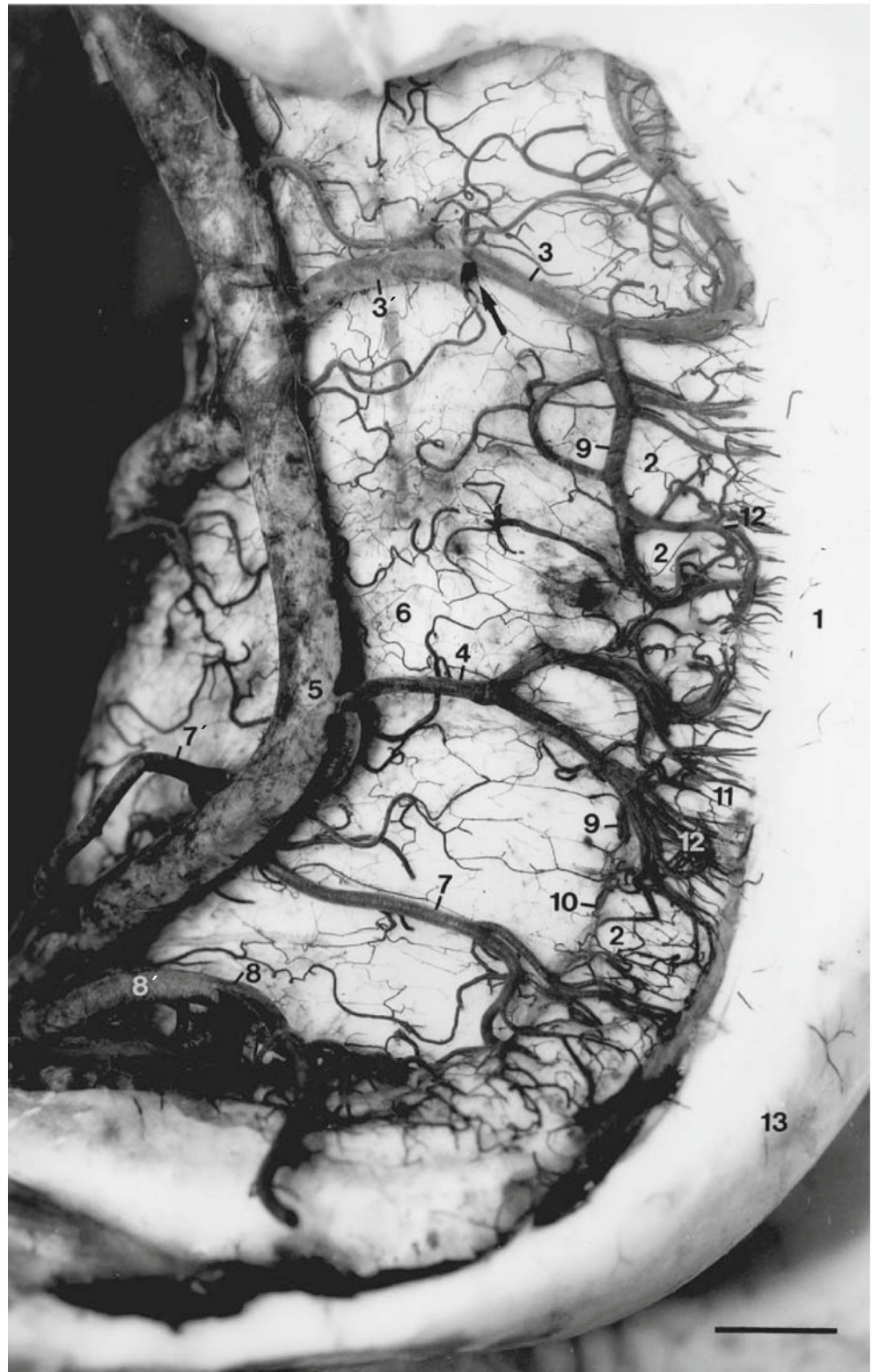


Fig. 5.6 Enlargement of Fig. 5.5 to show with more details the large arterial branches (1) penetrating in the sulci between the dentes of margo denticulatus (2). 3 straight arteries, 4 subiculum. The temporal horn has been opened, and the choroid plexuses were removed to show the endoventricular aspect of hippocampus (5). Bar, 1.6 mm



Fig. 5.7 Intravascular India ink injection. On this preparation, the middle group of hippocampal arteries (*1*), arising from an inferior temporal artery (*1'*), is the main arterial supply to the hippocampal body. *Bar*, 2.5 mm. *1* middle group of hippocampal arteries, *1'* inferior temporal artery, *2* the posterior hippocampal artery with a territory restricted to the terminal segment of the tail, *3* large arterial branches penetrating in the sulci between the dentes of margo denticulatus (*4*), *5* venous arch of the fimbriodentate sulcus, *6* subiculum, *7* posterior cerebral artery

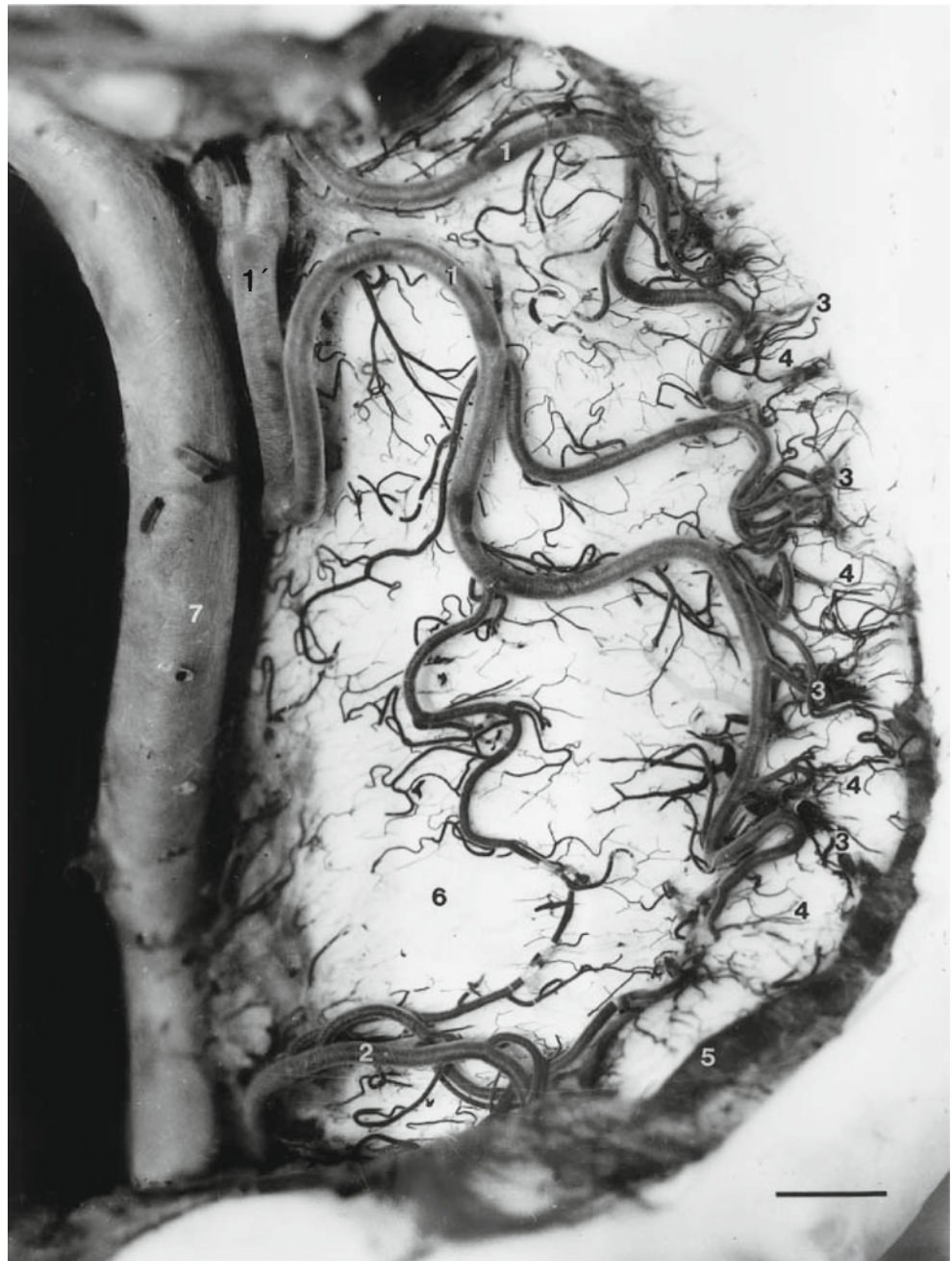


Fig. 5.8 Intravascular India ink injection. The temporal (inferior) horn of the lateral ventricle has been opened. *Bar*, 5.3 mm. 1 choroid plexuses of the temporal horn covering and hiding the hippocampal body and tail, 2 the hippocampal head, devoid of choroid plexuses, is clearly visible, 3 choroid glomus, 4 anterior choroidal artery, 5 posterolateral choroidal artery arising from the posterior cerebral artery (6), 7 fimbria, 8 the margo denticulatus, large in this preparation, is free from the fimbria, 9 venous arch of the fimbriodentate sulcus, 10 venous arch of the hippocampal sulcus, 11 subiculum, 12 crus of fornix

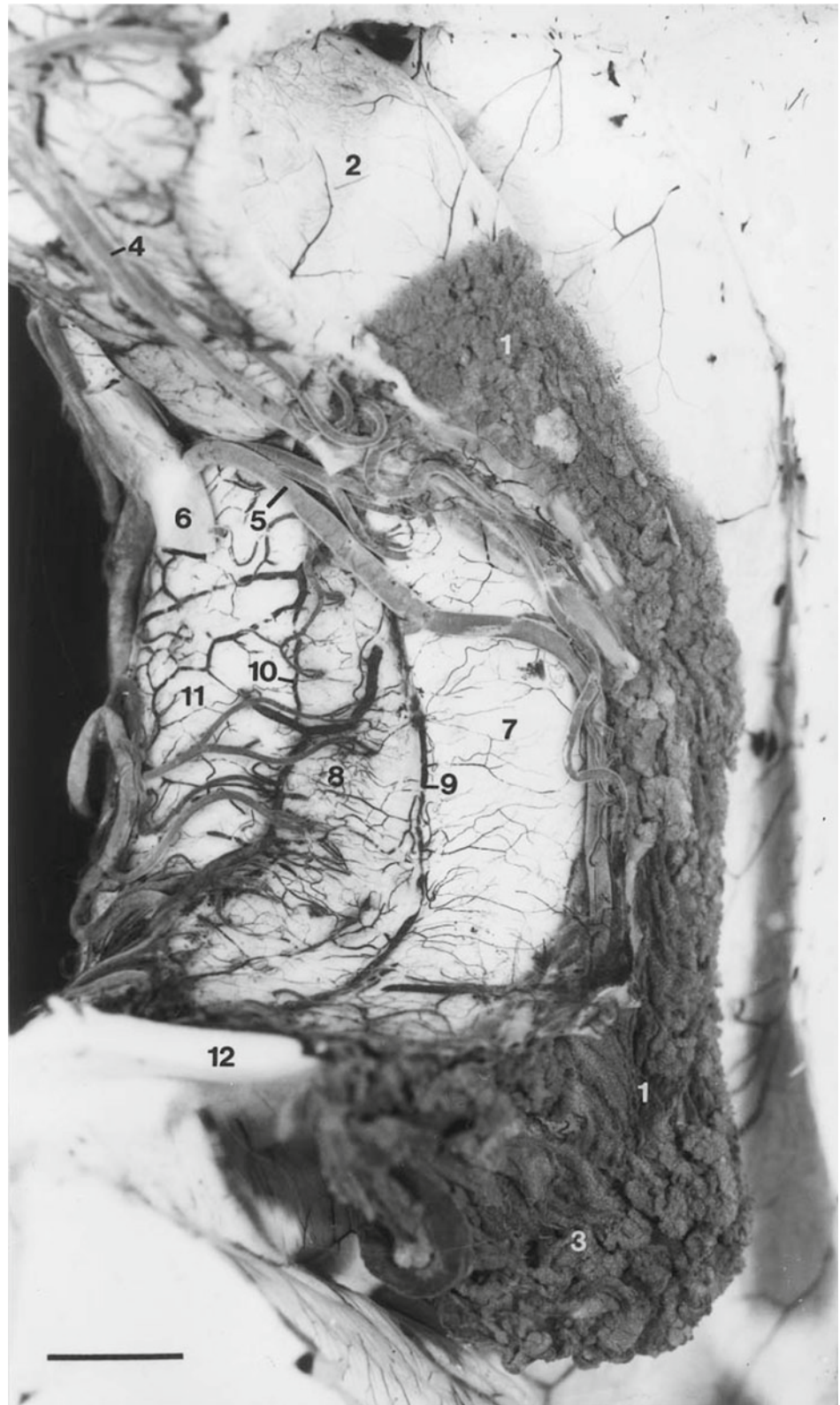


Fig. 5.9 Intravascular India ink injection. The temporal (inferior) horn of the lateral ventricle has been opened, and the choroid plexuses were removed. *Bar*, 5.2 mm
 1 hippocampal head and digitationes hippocampi, 2 hippocampal body, 3 hippocampal tail, 4 fimbria, 5 collateral eminence, 6 collateral trigone, 7 calcar avis, 8 occipital horn, 9 subependymal intrahippocampal veins (note the regular and radial arrangement), 10 subiculum



Fig. 5.10 Intravascular India ink injection. The temporal (inferior) horn of the lateral ventricle has been opened, and the choroid plexuses were removed. *Bar*, 2.8 mm. 1 hippocampal head, 2 hippocampal body, 3 fimbria, 4 subependymal intrahippocampal veins (note the fine arborizations)



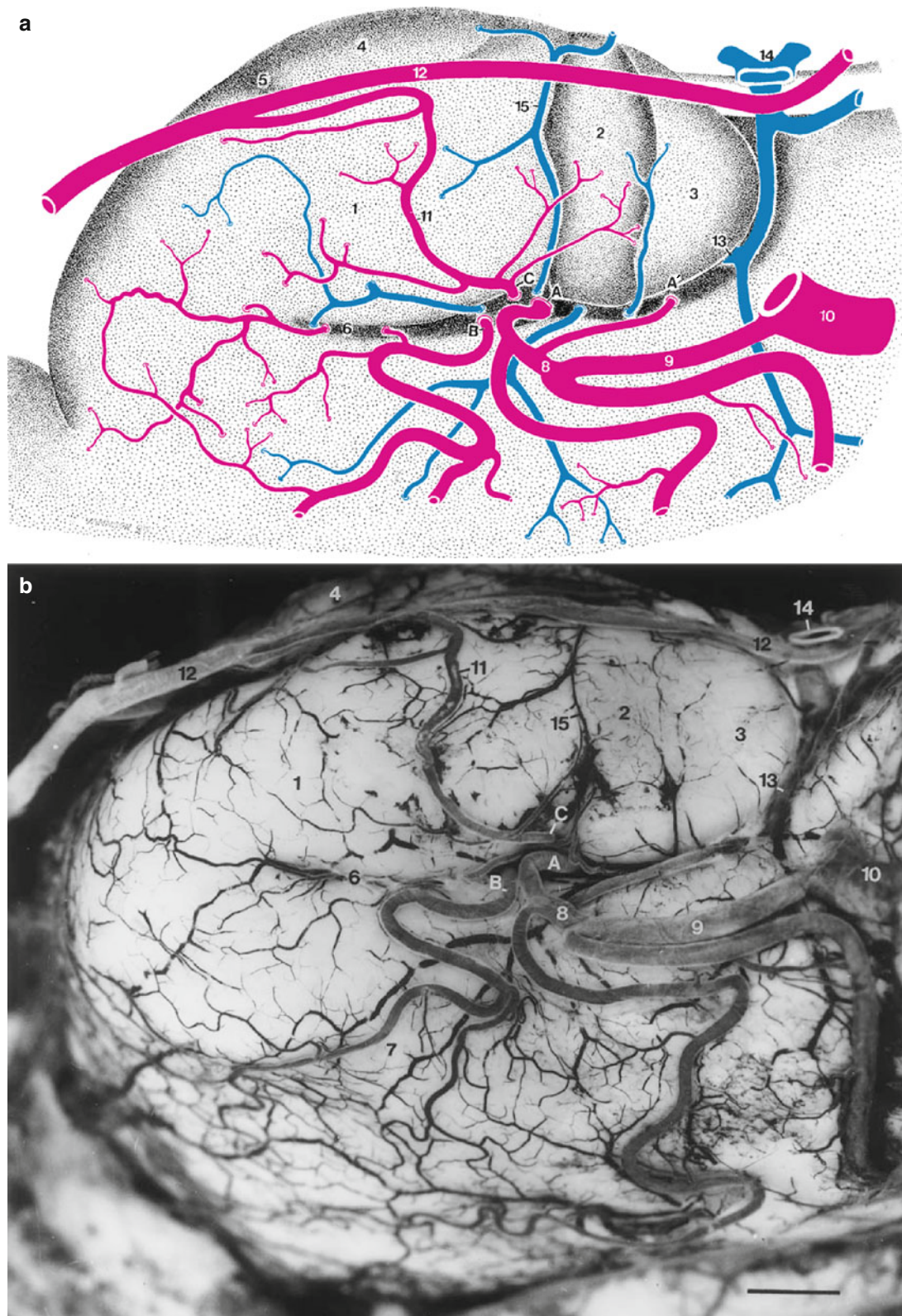


Fig. 5.11 (a, b) Medial aspect of the piriform lobe (uncus and entorhinal area). (a) Drawing. (b) India ink injection. The anterior hippocampal artery (8) penetrates (A) into the uncus sulcus (see Fig. 5.12a) and often reappears (B) to vascularize the entorhinal area (7). The uncus branch of the anterior choroidal artery (11) penetrates into the uncus sulcus (C). A' Collateral branch of the anterior hippocampal artery. The venous network of the hippocampal head emerging from the uncus sulcus (13) is drained toward the inferior ventricular vein (14). Bar,

2.5 mm. 1 medial aspect of the uncus, 2 band of Giacomini, 3 uncus apex, 4 semilunar gyrus, 5 semiannular sulcus, 6 uncus sulcus, 7 entorhinal area, 8 anterior hippocampal artery arising from an anterior inferior temporal artery (9), 10 posterior cerebral artery, 11 uncus branch of the anterior choroidal artery, 12 anterior choroidal artery, 13 venous drainage of the hippocampal head, 14 vein of the temporal horn (inferior ventricular vein), 15 vein of the superficial hippocampal sulcus bordering the band of Giacomini

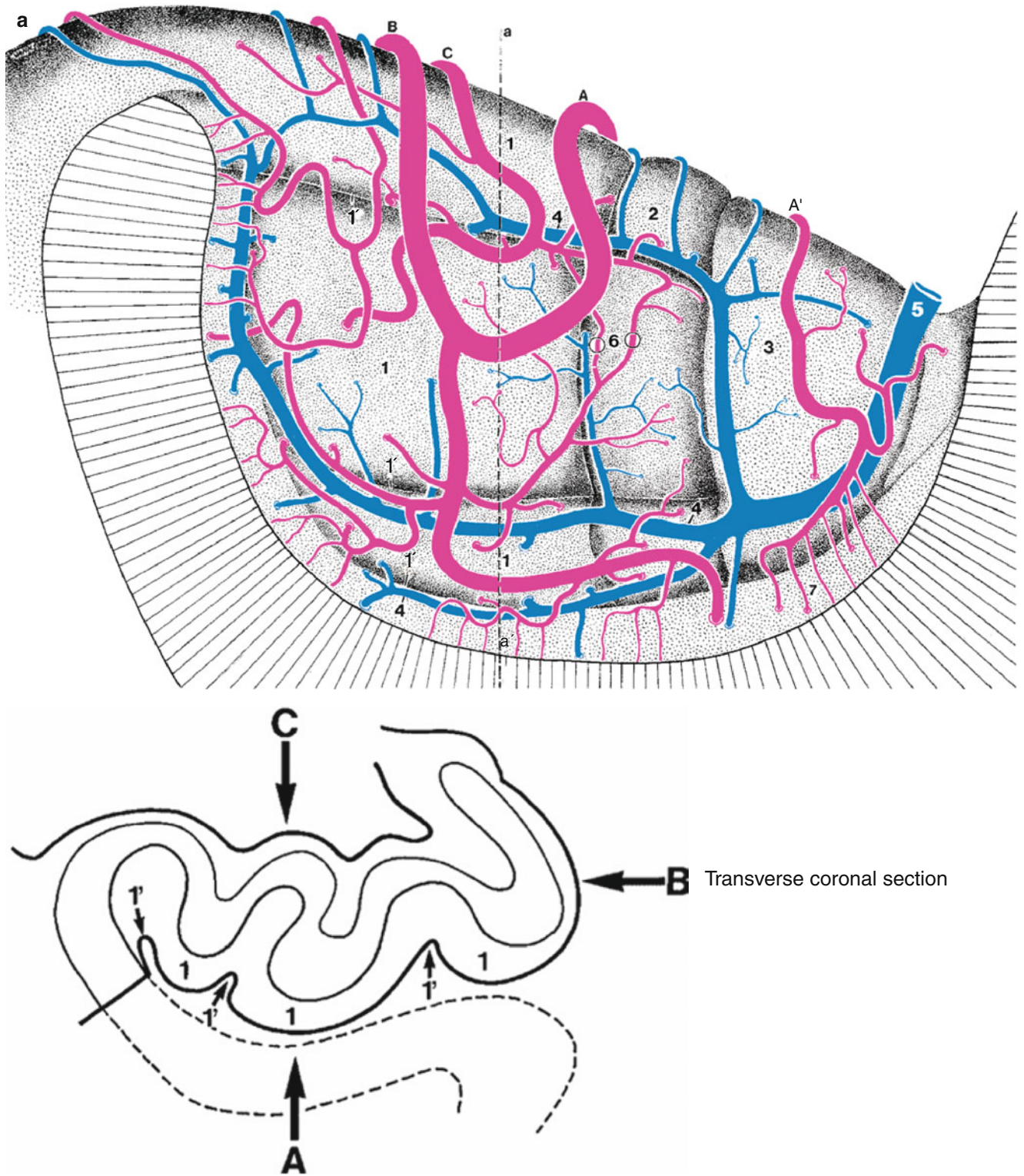


Fig. 5.12 (a) Drawing and (b) intravascular injection showing the superior side of the uncus after ablation of its inferior side, as shown in C. By this method, the inferior surface of the hippocampal head may be seen. Bar, 2.2 mm. 1 external digitations, 1' sulci between these digitations. The parts of the band of Giacomini (2) and of the uncus apex (3) normally hidden in the uncus sulcus are visible by this dissection. The arterial branches vascularizing the hippocampal head mainly penetrate into the sulci between the external digitations. The venous network is also mainly situated in these sulci (4). 5 venous drainage toward the inferior ventricular vein (corresponds to 13 in Fig. 5.11), 6 arterial anastomoses between branches of anterior

hippocampal and anterior choroidal arteries, 7 straight arteries. A anterior hippocampal artery penetrating into the uncus sulcus and emerging from it (B), C uncus branch of the anterior choroidal artery penetrating into the uncus sulcus (see corresponding lettering in Fig. 5.11), A' collateral of anterior hippocampal artery. Transverse coronal section of the hippocampus according to the plane a-a' shown in Fig. 5.12a. The inferior side of the uncus sulcus has been removed (dotted line) A inferior aspect of the uncus, B medial aspect of the uncus, C superior (endoventricular) aspect of the uncus: internal digitations (digitationes hippocampi) in relation to the temporal horn of the lateral ventricle. 1 external digitations, 1' sulci between external digitations

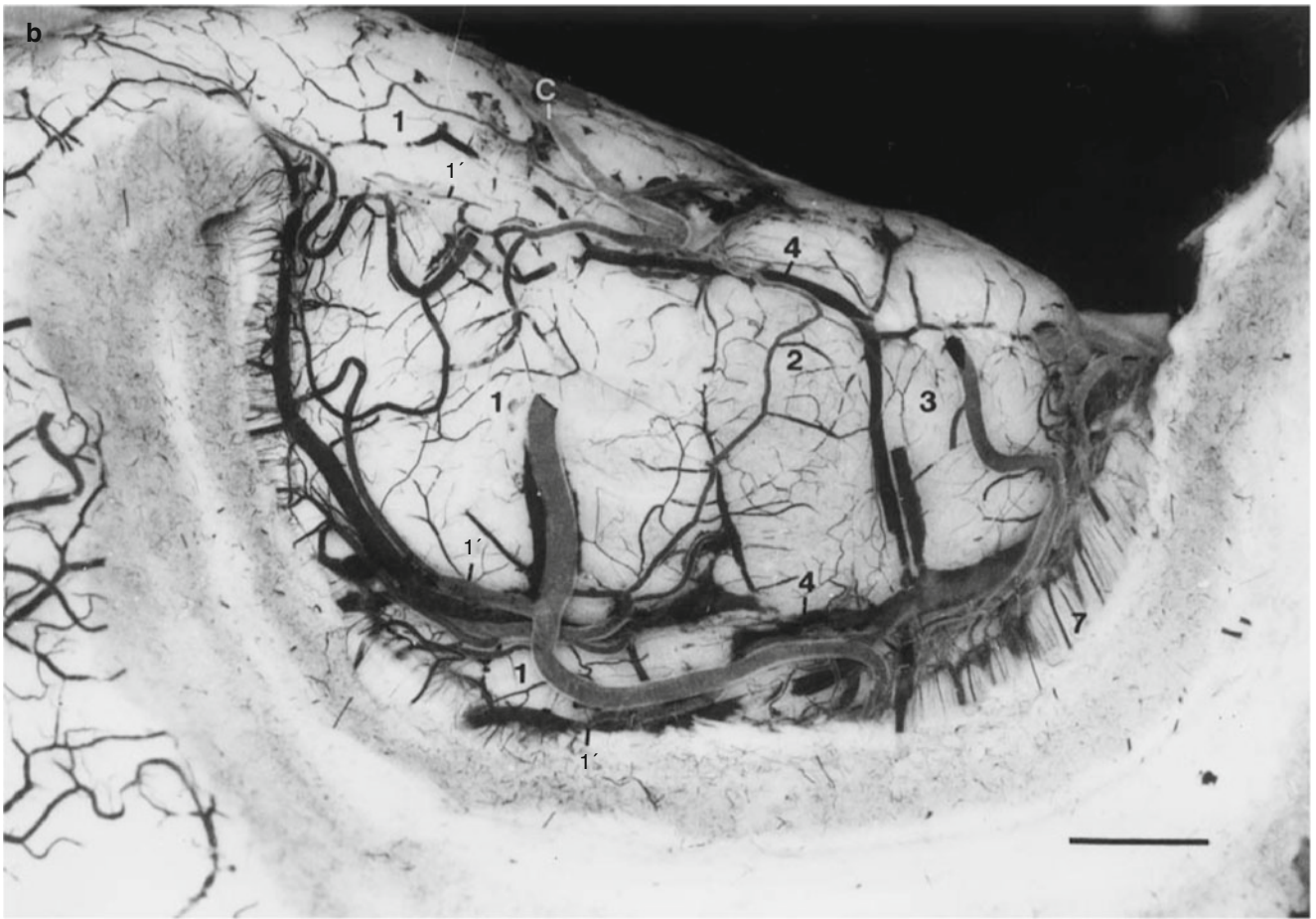


Fig. 5.12 (continued)

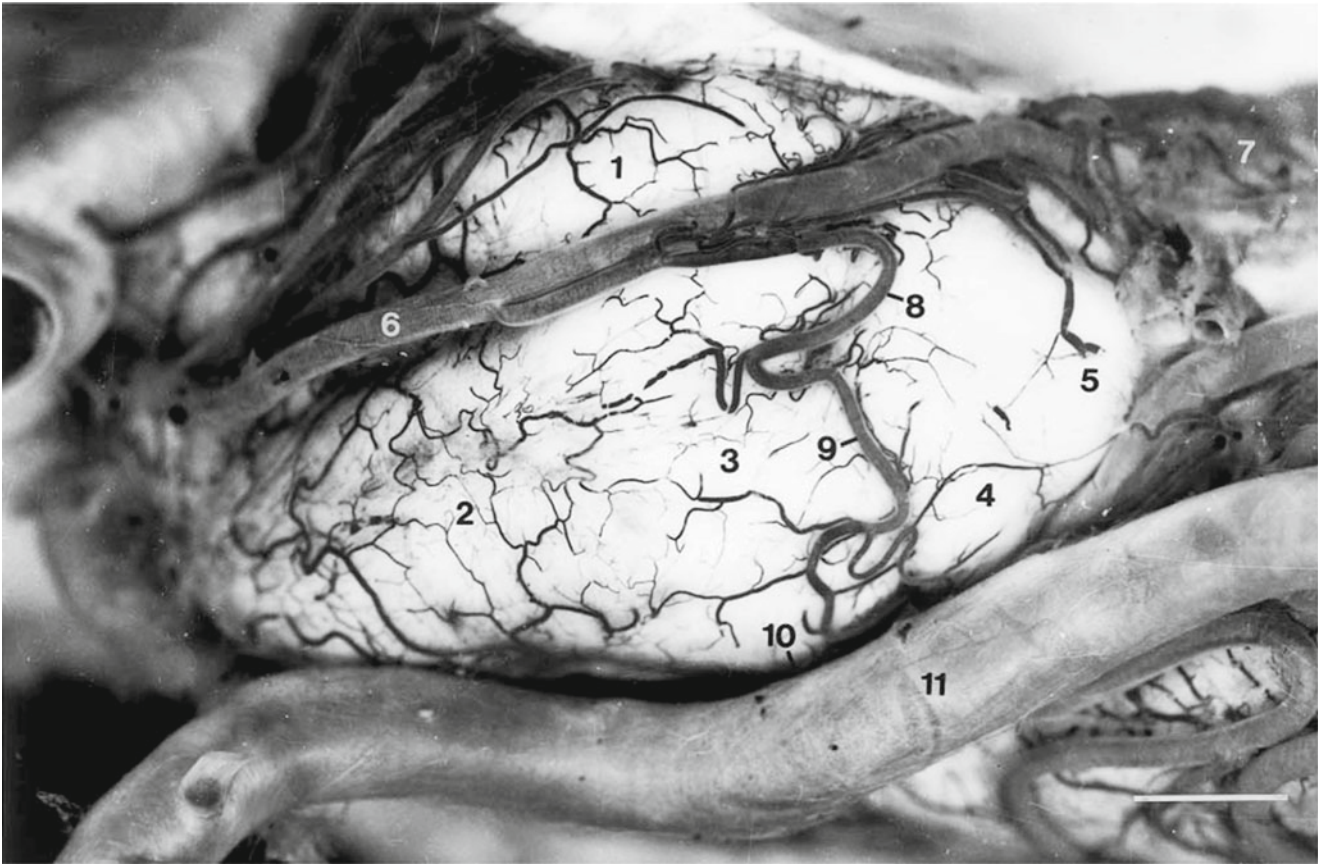


Fig. 5.13 Superior aspect of the uncus. Intravascular India ink injection. *Bar* 2.7 mm. 1 semilunar gyrus, 2 ambient gyrus, 3 uncinuate gyrus, 4 band of Giacomini, 5 uncal apex, 6 the anterior choroidal artery courses in the semiannular sulcus to reach the choroid plexuses of the

temporal horn (7), 8 uncal branch of the anterior choroidal artery running along the uncal part of the superficial hippocampal sulcus (9) to reach the uncal sulcus (10) 11 posterior cerebral artery

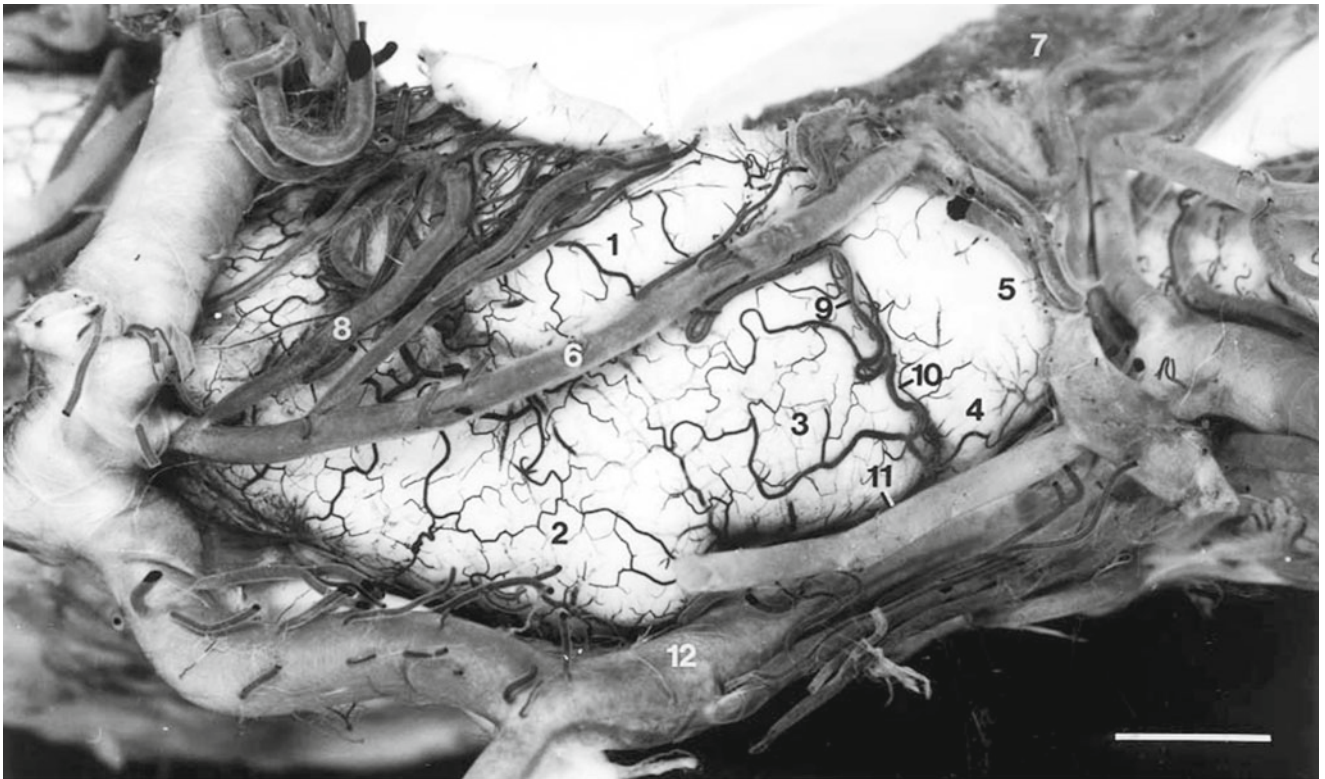


Fig. 5.14 Superior aspect of the uncus. Intravascular India ink injection. Bar, 3.3 mm. 1 semilunar gyrus, 2 ambient gyrus, 3 uncinete gyrus, 4 band of Giacomini, 5 uncal apex, 6 anterior choroidal artery situated in the semiannular sulcus and reaching the choroid plexuses of

the temporal horn (7), 8 deep perforating branches of the anterior choroidal artery, 9 the uncal branch of the anterior choroidal artery courses along the superficial hippocampal sulcus (10) to reach the uncal sulcus (11), 12 posterior cerebral artery

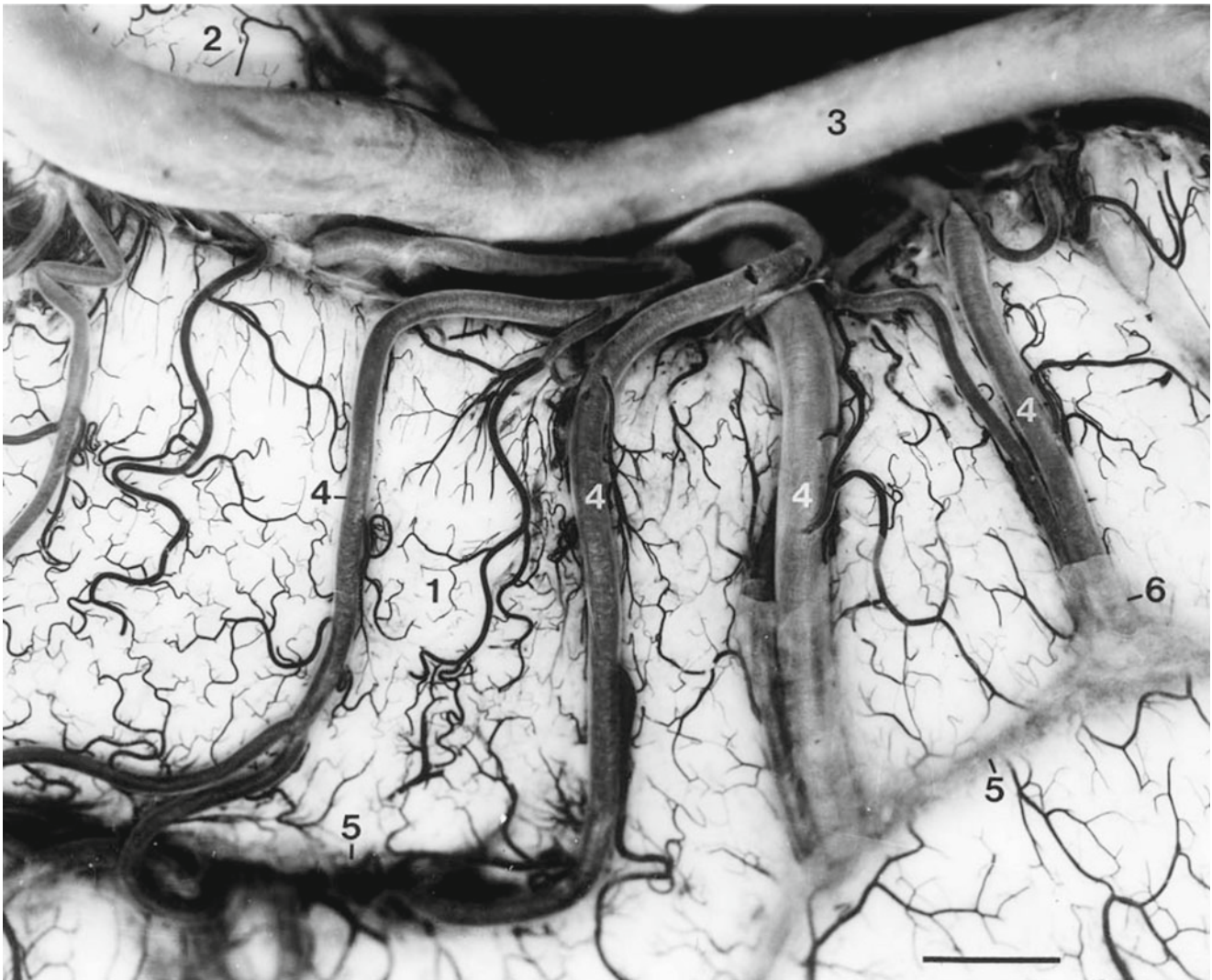


Fig. 5.15 Inferior view of the temporal lobe. Intravascular India ink injection. *Bar* 2.5 mm. 1 parahippocampal gyrus, 2 uncal apex, 3 posterior cerebral artery (P2 segment) located along the margin of the para-

hippocampal gyrus, 4 group of inferior temporal arteries crossing the parahippocampal gyrus to reach the collateral sulcus (5), 6 the arachnoid has been left partly intact

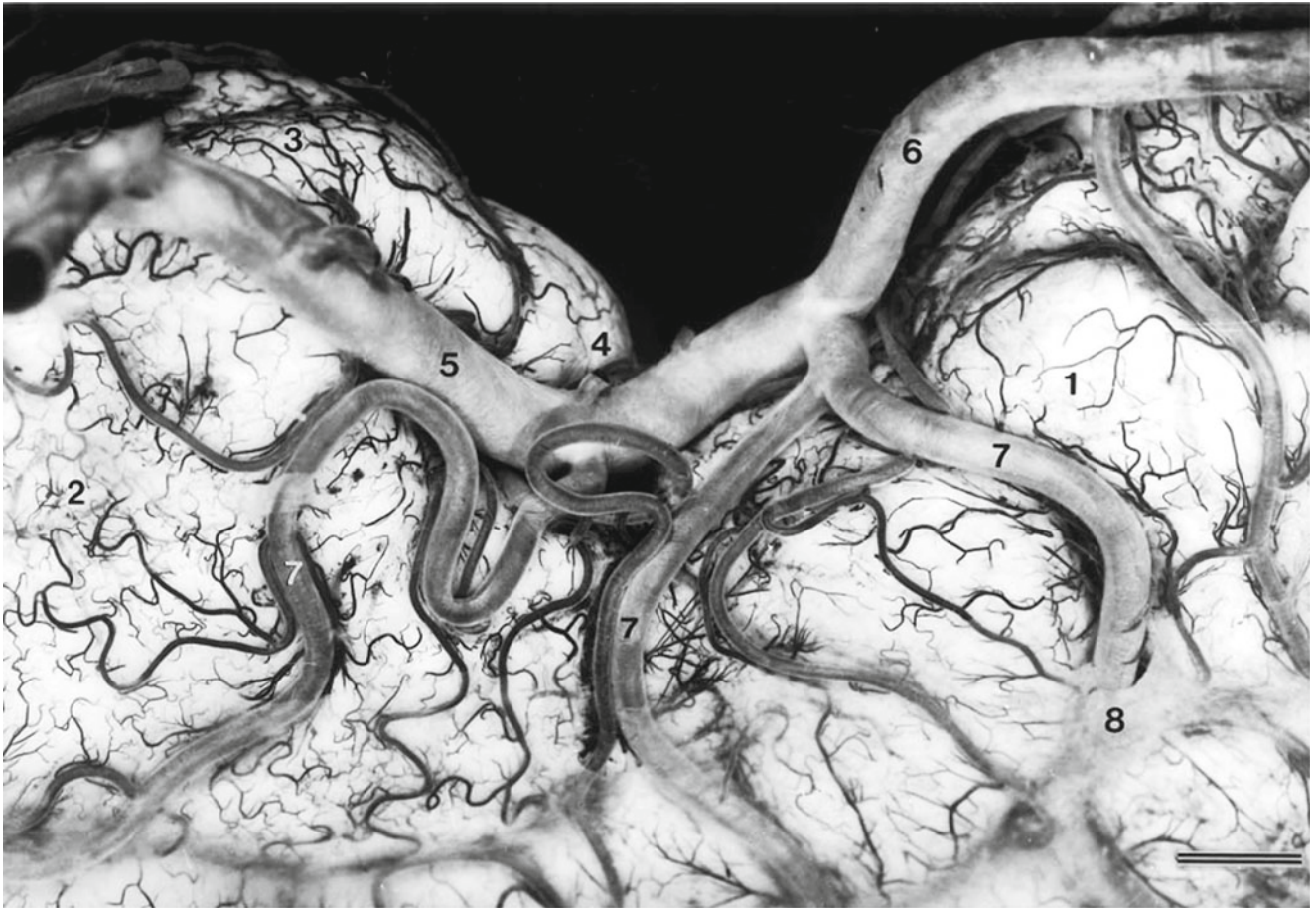


Fig. 5.16 Inferior view of the temporal lobe. Intravascular India ink injection. *Bar*, 4 mm. 1 parahippocampal gyrus, 2 entorhinal area, 3 uncus, ambient gyrus, 4 uncal apex. The P2 segment of the posterior cerebral artery may be divided into two parts: the first part (5) crosses the uncus and hides the uncal sulcus, and the second part (6) follows the

margin of the parahippocampal gyrus. Note the high density of the hippocampal parahippocampal arterial complex situated at the level of the uncal apex and composed of the trunk of the posterior cerebral artery and its numerous collaterals, in particular the group of anterior inferior temporal arteries (7), 8 the arachnoid has been left partly intact

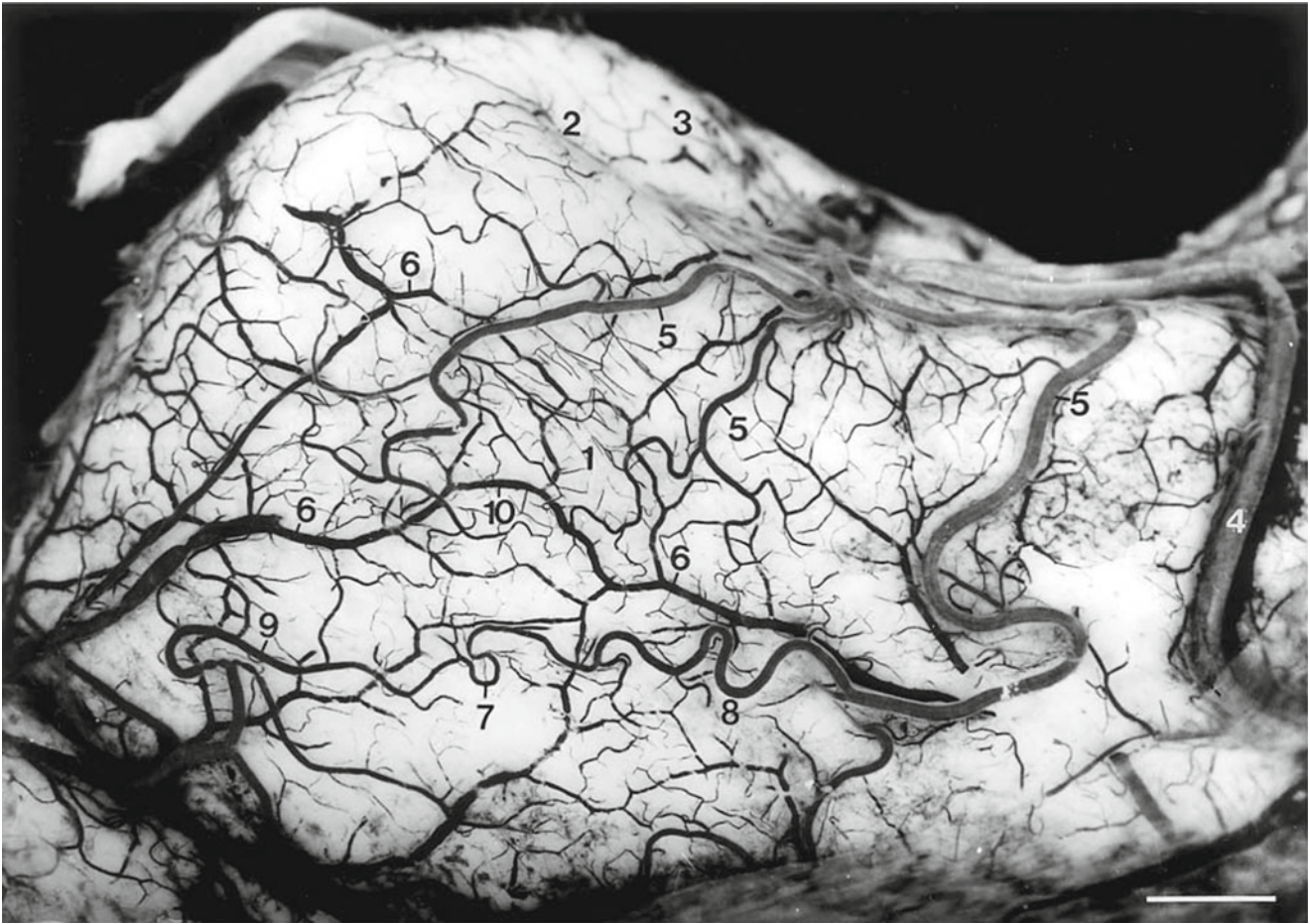


Fig. 5.17 Inferior aspect of the piriform lobe whose medial aspect is seen in Fig. 5.11b. Note the dense arterial and venous networks covering the entorhinal area. *Bar*, 5 mm. 1 entorhinal area, 2 uncal sulcus, 3 uncus, 4 anterior inferior temporal artery, 5 branches of the anterior hippocampal

artery supplying the entorhinal area; 6 arterial and venous networks, 7 arterial anastomosis between a branch of the anterior hippocampal artery (8) and a branch of the middle cerebral artery (9), 10 venous anastomoses

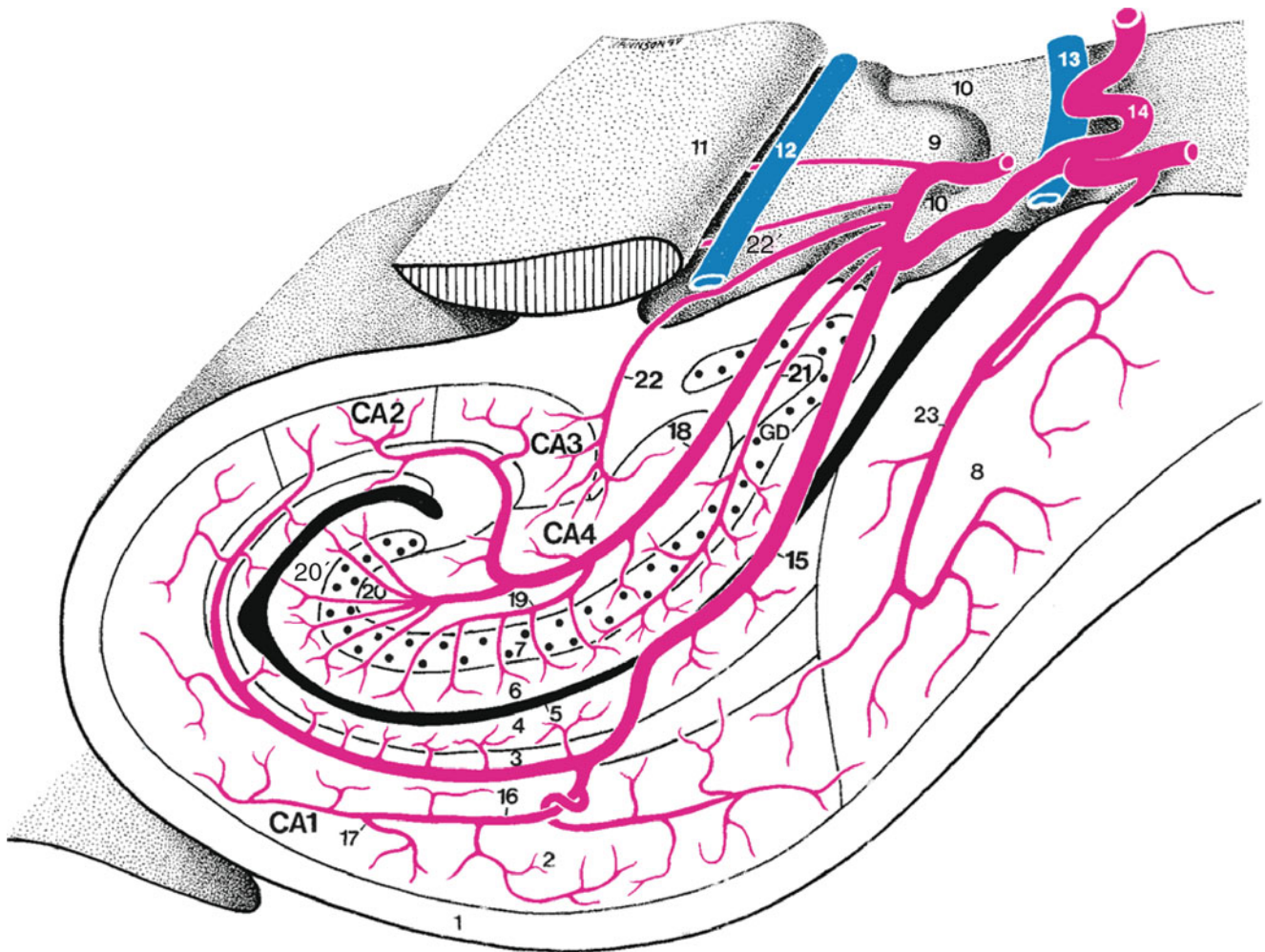


Fig. 5.18 Coronal section showing the arterial supply of the hippocampal body. Cornu Ammonis: CA1–CA4 fields of the cornu Ammonis. 1 alveus, 2 stratum pyramidale and stratum radiatum, 3 stratum lacunosum, 4 stratum moleculare, 5 vestigial hippocampal sulcus. Gyru dentatus (GD): 6 stratum moleculare, 7 stratum granulosum, 8 subiculum, 9 dentes of margo denticulatus, 10 sulci between dentes, 11 fimbria 12 venous arch of the fimbriodentate sulcus, 13 venous arch of the superficial hippocampal sulcus, 14 longitudinal terminal segment of the superficial hippocampal arteries. The intrahippocampal arteries may be divided into the large dorsal, large ventral, small ventral, and small dorsal group: 15 large ventral intrahippocampal arteries, with a long course in CA1 reaching CA2, 16

collaterals with a long path in the pyramidal layer of CA1, 17 note their branches often stemming in a counterflow way, 18 large dorsal intrahippocampal arteries situated in CA4 along the gyru dentatus and reaching CA3 and CA2, 19 branches with a rectilinear path supplying the molecular layer of the gyru dentatus, 20 branches with a brushlike appearance supplying the genu of the gyru dentatus (20'), 21 small ventral intrahippocampal arteries reaching the proximal part of the gyru dentatus with a rectilinear course, 22 small dorsal intrahippocampal arteries (straight arteries, 22') with a territory restricted to part of CA3 and CA4; 23 the arteries of the subiculum have a long course similar to that of CA1

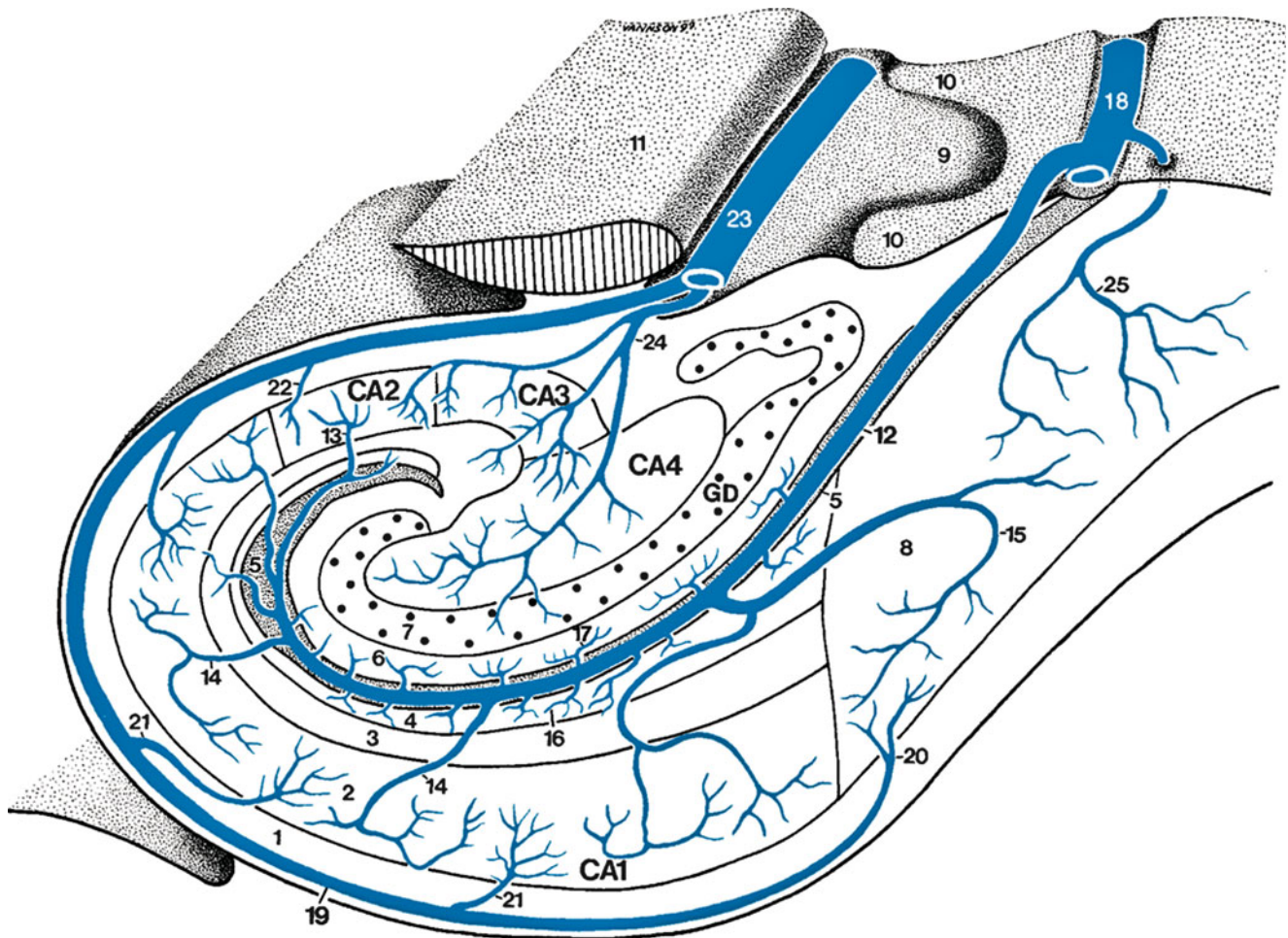


Fig. 5.19 Coronal section showing the venous supply of the hippocampal body. Cornu Ammonis: CA1–CA4 fields of the cornu Ammonis. 1 alveus, 2 stratum pyramidale and stratum radiatum, 3 stratum lacunosum, 4 stratum moleculare, 5 vestigial hippocampal sulcus. Gyrus dentatus (GD): 6 stratum moleculare, 7 stratum granulosum, 8 subiculum, 9 dentes of margo denticulatus, 10 sulci between dentes, 11 fimbria. The main venous drainage of the hippocampus depends on two groups of intrahippocampal veins: the sulcal intrahippocampal veins (12) and the subependymal intrahippocampal veins (19). 12 The whole course of the sulcal intrahippocampal veins is

situated in the vestigial hippocampal sulcus (5); they drain by long branches parts of CA2 (13), CA1 (14), and the subiculum (15) and by small branches of the molecular layers of the cornu Ammonis (16) and the gyrus dentatus (17); the sulcal veins flow into the venous arch of the superficial hippocampal sulcus (18), 19 the subependymal intrahippocampal veins have a long course in the alveus draining parts of the subiculum (20), CA1 (21), and CA2 (22); they flow into the vein of the fimbriodentate sulcus (23); some small veins (24) draining parts of CA3 and CA4 may directly reach the vein of the fimbriodentate sulcus, 25 veins of the subiculum

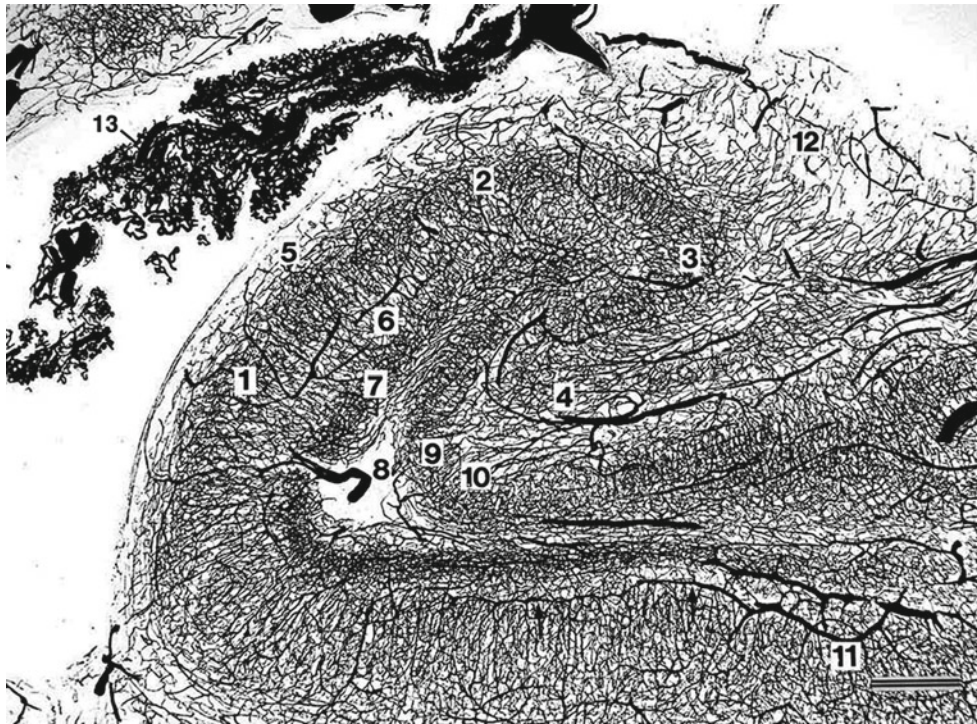


Fig. 5.20 Coronal section of the hippocampal body, intravascular India ink injection. Bar 1 mm. Cornu Ammonis: 1, 2, 3, 4 CA1, CA2, CA3, CA4, 5 alveus, 6 clear aspect of the stratum radiatum of CA1, 7 high vascular density of the stratum moleculare of CA1, 8 vestigial

hippocampal sulcus with intrahippocampal veins, 9 high vascular density of the stratum moleculare of the gyrus dentatus, 10 polymorphic layer, 11 (with arrows) long arterial branches in the stratum lucidum of the cornu Ammonis, 12 fimbria, 13 choroid plexus



Fig. 5.21 Coronal section of the hippocampal body. Intravascular India ink injection. *Bar* : 1 mm. *1* CA1, *2* CA2, *3* CA3, *4* CA4 fields of the cornu Ammonis, *5* gyrus dentatus, Note the high capillary density in the strata molecularia of the cornu Ammonis (*7*) and the gyrus den-

tatus (*6*) separated by the vestigial hippocampal sulcus (*8*), *9* large dorsal intrahippocampal artery with a preponderant territory, *10* small dorsal intrahippocampal arteries (*straight arteries*), *11* temporal horn of the lateral ventricle, *12* choroid plexus, *13* fimbria



Fig. 5.22 Coronal section of the hippocampal body. Intravascular India ink injection. Bar, 770 μm . 1 CA1, 2 CA2, 3 CA3, 4 CA4 : fields of the cornu Ammonis. The pyramidal layer of CA1 is poorly vascularized, whereas that of CA2, CA3, and CA4 are highly vascularized. 5 gyrus dentatus, 6 stratum granulosum, 7 stratum moleculare of the highly vascularized gyrus dentatus, 8 stratum moleculare of CA1 highly

vascularized, 9 the arterial branches supplying the genu of the gyrus dentatus have a brushlike appearance, 10 vestigial intrahippocampal sulcus, 11 stratum radiatum of CA1 poorly vascularized, 12 small dorsal intrahippocampal arteries (*straight arteries*), 13 small ventral intrahippocampal arteries, 14 sulcal intrahippocampal veins

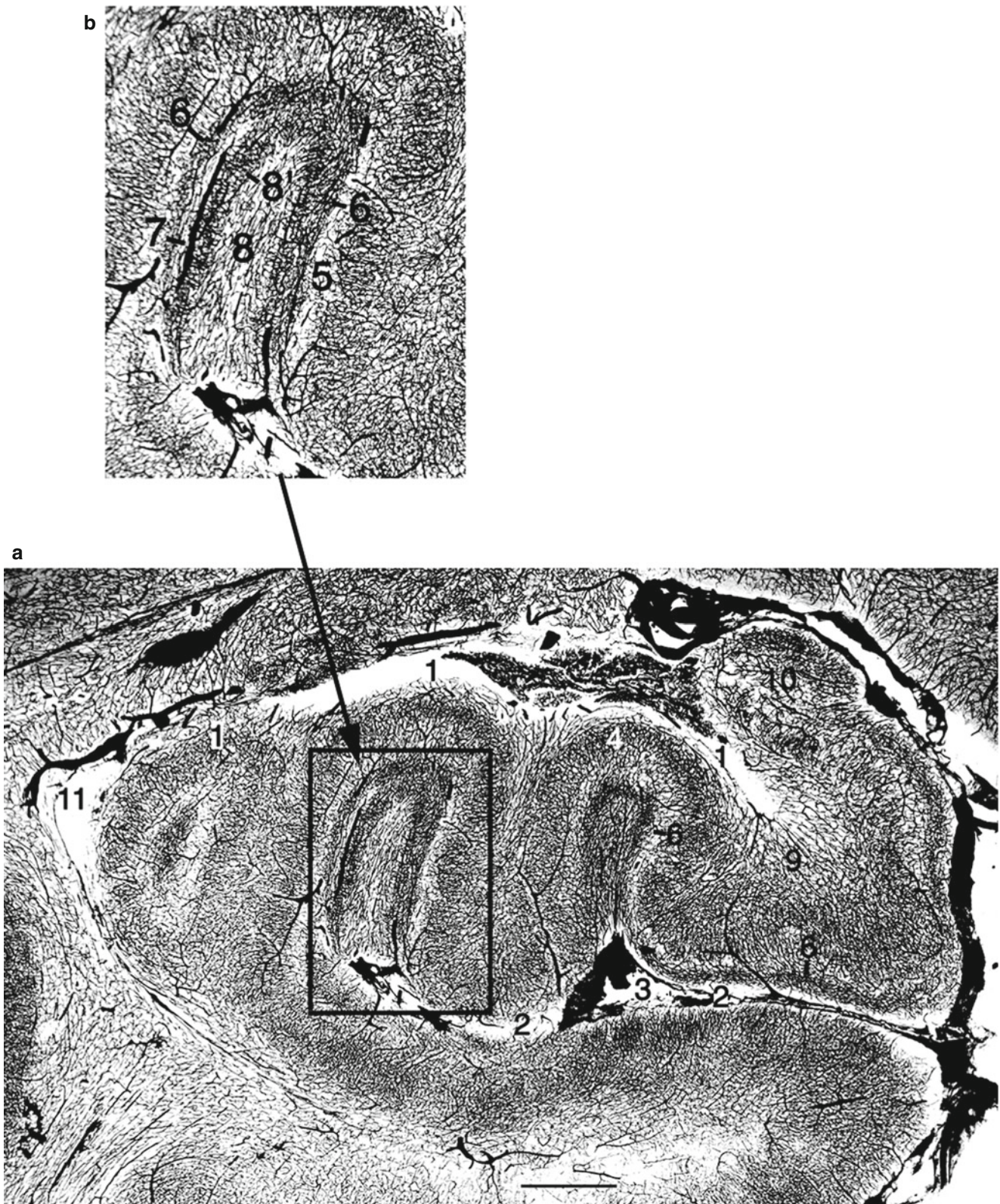


Fig. 5.23 (a) Coronal section of the hippocampal head. Intravascular India ink injection. *Bar* : 2.35 mm. (b) enlargement of a hippocampal digitation 1 digitationes hippocampi (internal digitations), 2 external digitation, 3 uncal sulcus, 4 stratum pyramidale of the cornu Ammonis,

5 stratum radiatum, 6 stratum moleculare of the cornu Ammonis highly vascularized, 7 vestigial hippocampal sulcus and sulcal veins, 8 gyrus dentatus, 8' stratum moleculare of the gyrus dentatus, 9 uncus, 10 band of Giacomini, 11 temporal horn of the lateral ventricle

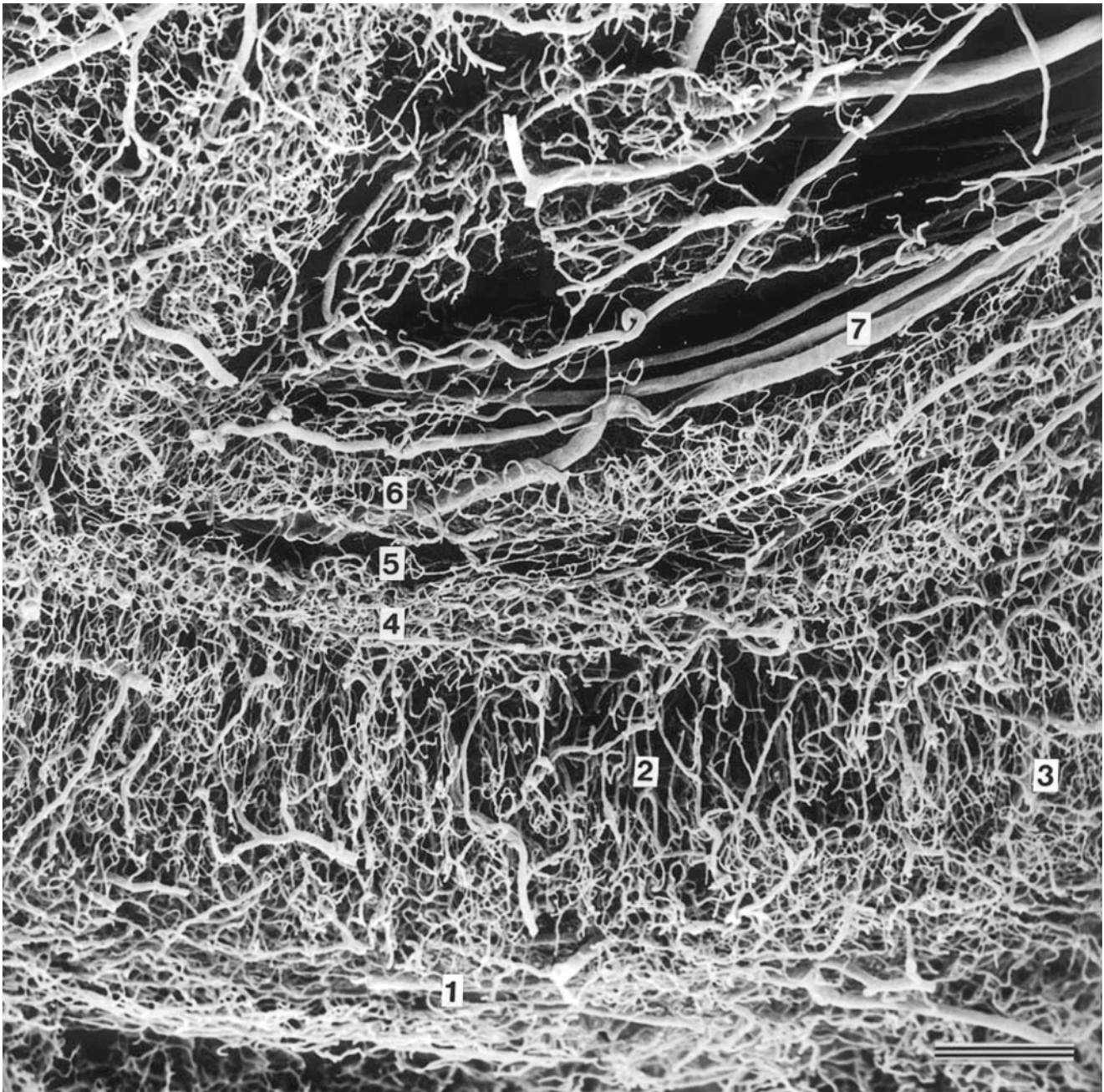


Fig. 5.24 Coronal section of the hippocampal body. Intravascular resin injection (Mercox) and scanning electron microscope view after corrosion. The layers of the cornu Ammonis and the gyrus dentatus can be distinguished according to their specific capillary network densities. The poor vascular network of the strata radiatum and lacunosum (2), in

comparison to that of the adjacent subiculum (3), permits the hippocampal boundary to be delineated. *Bar*, 500 μ m 1 stratum pyramidale of CA1, 2 strata radiatum and lacunosum, 3 subiculum, 4 stratum moleculare of CA1, 5 vestigial hippocampal sulcus, 6 stratum moleculare of the gyrus dentatus, 7 large dorsal intrahippocampal arteries

Fig. 5.25 Dorsal view of the hippocampus after intravascular resin injection (Mercox) and corrosion of the hippocampal tissue. This overall view of the intrahippocampal vascularization shows the bush-like aspect of the capillary network (*arrows*) and its possible division into vascular units. Note the dense ramifications of the middle and posterior superficial hippocampal arteries (2, 3) at the hippocampal sulcus level

(4). Note also the regular intervals between the subependymal intrahippocampal veins (6). *Bar*, 3 mm. 1 posterior cerebral artery, 2 middle superficial hippocampal artery, 3 posterior superficial hippocampal artery, 4 hippocampal sulcus, 5 vein of the fimbriodentate sulcus, 6 subependymal intrahippocampal veins





Fig. 5.26 Intravascular India ink injection. Typical aspect of an arterial branch (1) in CA1 (see its position in Fig. 5.20). Note its long oblique path, the important periarterial capillary-free space (2), and the frequent recurrent branching of their collaterals (3) (arrows indicate the direction of the bloodstream). Bar, 600 μm



Fig. 5.27 Intravascular India ink injection. The capillary network of the stratum pyramidale (1) is supplied by deep arteries (2) and drained toward subependymal intrahippocampal veins (3). Bar 160 μm



Fig. 5.28 Intravascular India ink injection. Vascularization of the gyrus dentatus. Fine arterial branches (1) reach the dense vascular network of the stratum moleculare (2) through the poorly vascularized stratum granulosum (3). Note the rectilinear aspect of some arteries (4) in the gyrus dentatus. 5 vestigial hippocampal sulcus. *Bar*, 200 μ m

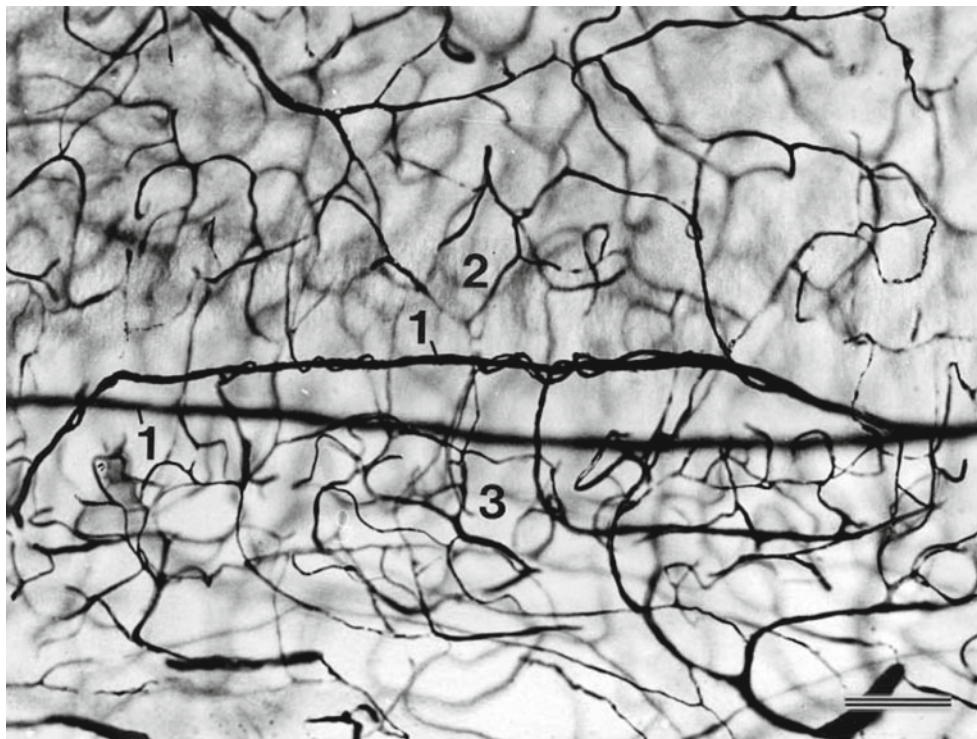


Fig. 5.29 Intravascular India ink injection. The arteries of the gyrus dentatus frequently have a rectilinear aspect. *Bar* 200 μ m. 1 arteries of the gyrus dentatus, 2 stratum granulosum, 3 stratum moleculare

Fig. 5.30 Intravascular India ink injection. The arterial branches (*arrows*) supplying the genu of the gyrus dentatus have a brushlike appearance. *Bar* 160 μm . 1 stratum granulosum; 2 stratum moleculare of the gyrus dentatus

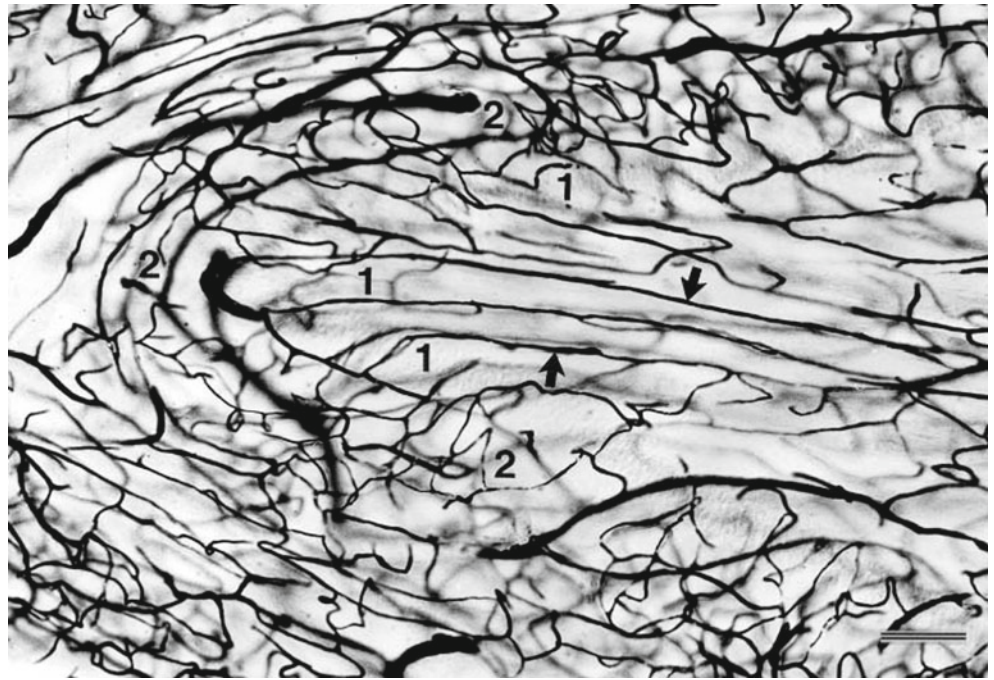


Fig. 5.31 Intravascular India ink injection. *Bar*, 240 μm . 1 arterial supply of the stratum moleculare of the gyrus dentatus, 2 venous drainage toward the sulcal intrahippocampal veins (3) situated in the vestigial hippocampal sulcus, 4 venous drainage of the stratum moleculare of the cornu Ammonis (5)

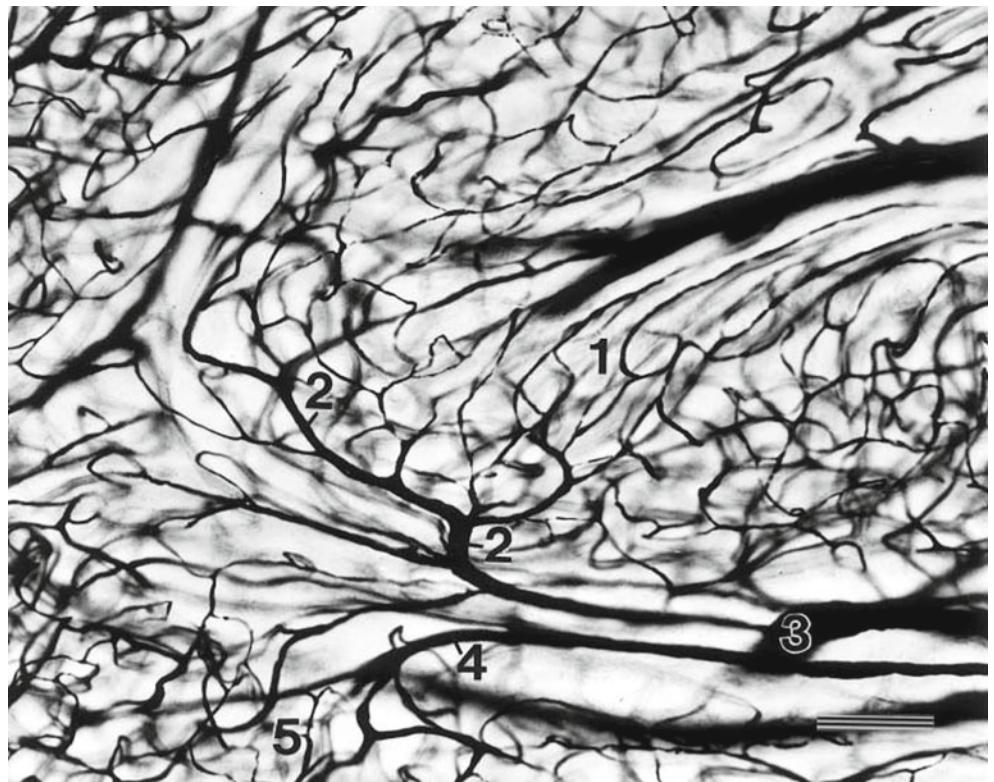


Fig. 5.32 Intravascular India ink injection. Note numerous arterial and capillary deformations (1) within the stratum pyramidale of CA2. Bar, 135 μ m

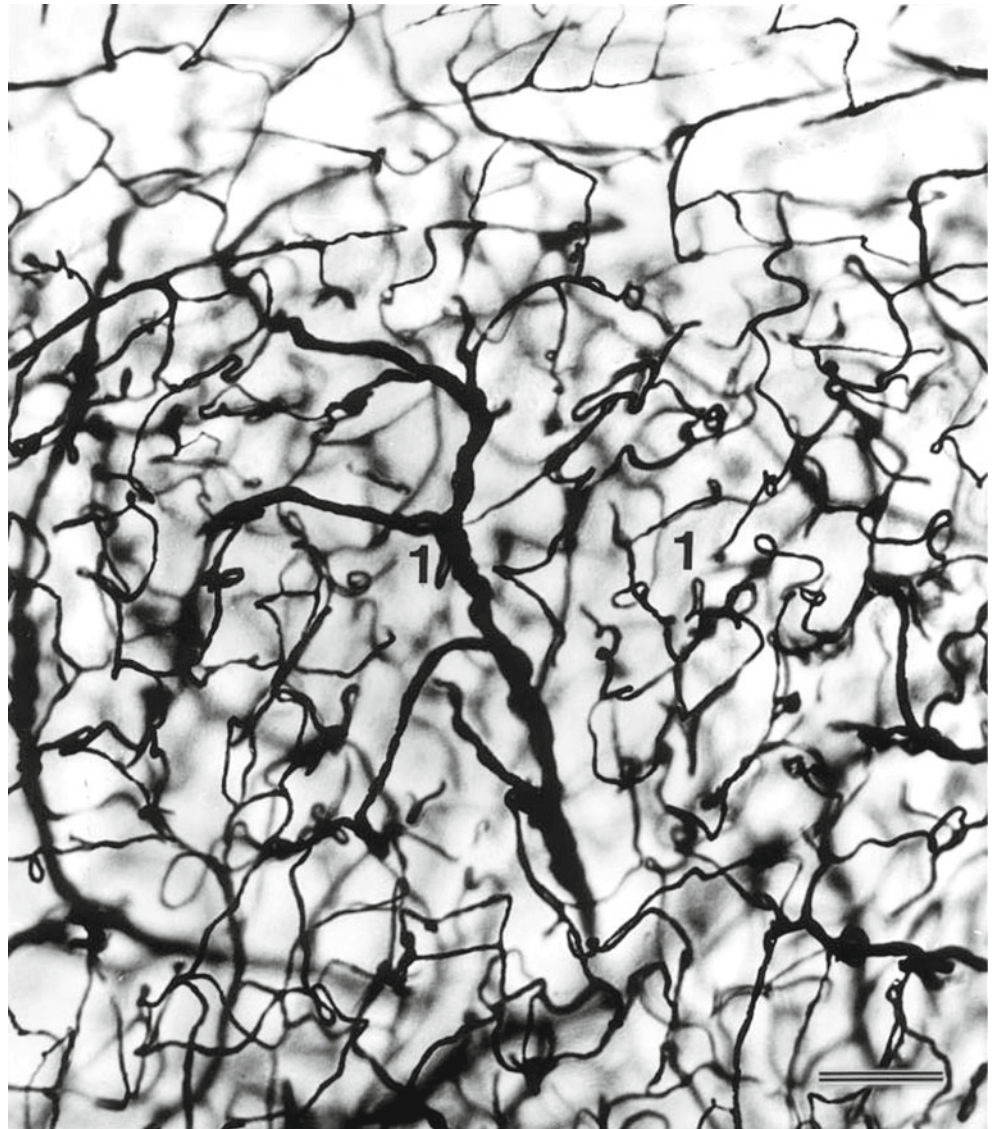
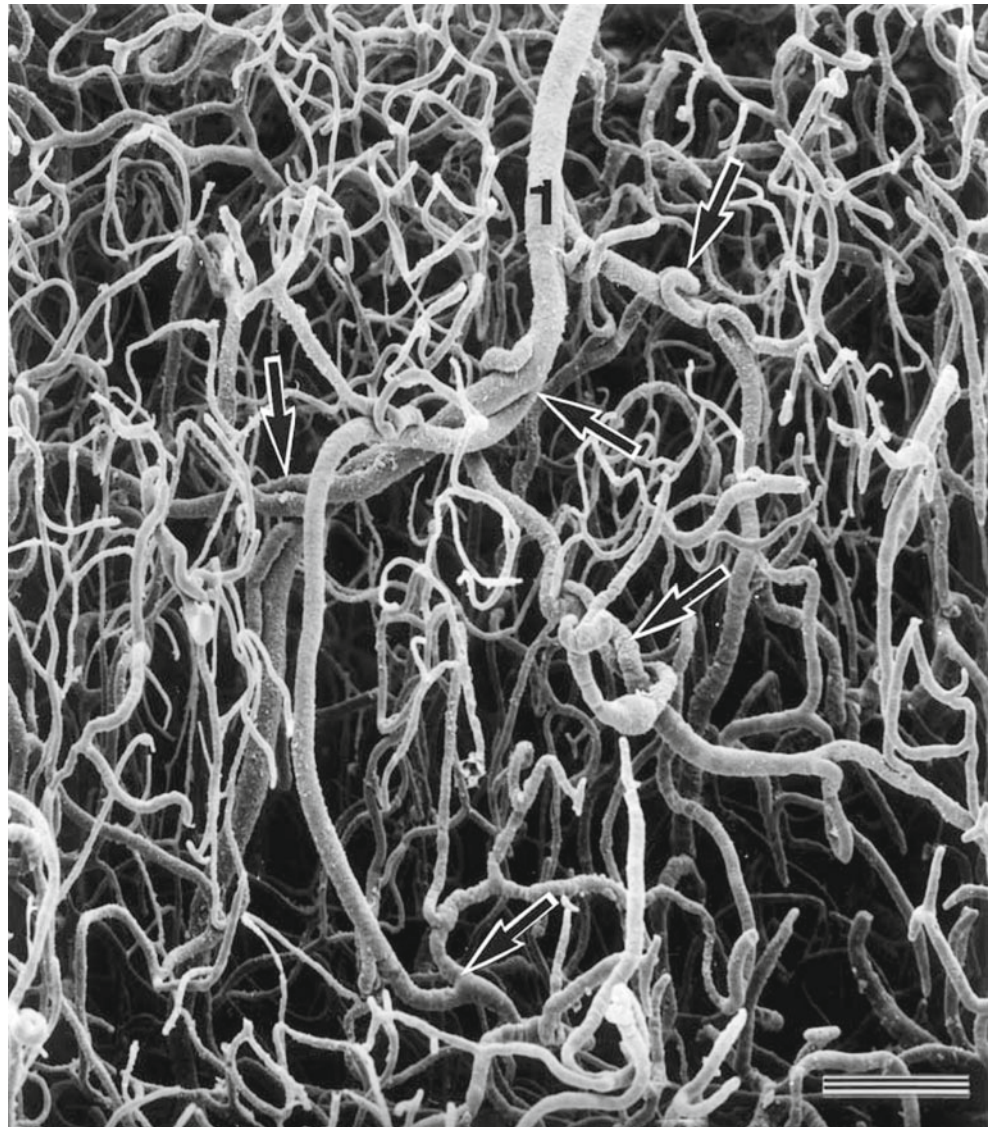


Fig. 5.33 Intravascular resin injection (Mercox) and scanning electron microscope view after corrosion. Note the tortuous aspect (*arrows*) of branches of an artery (*1*) in the stratum radiatum of CA1. *Bar*, 100 μ m



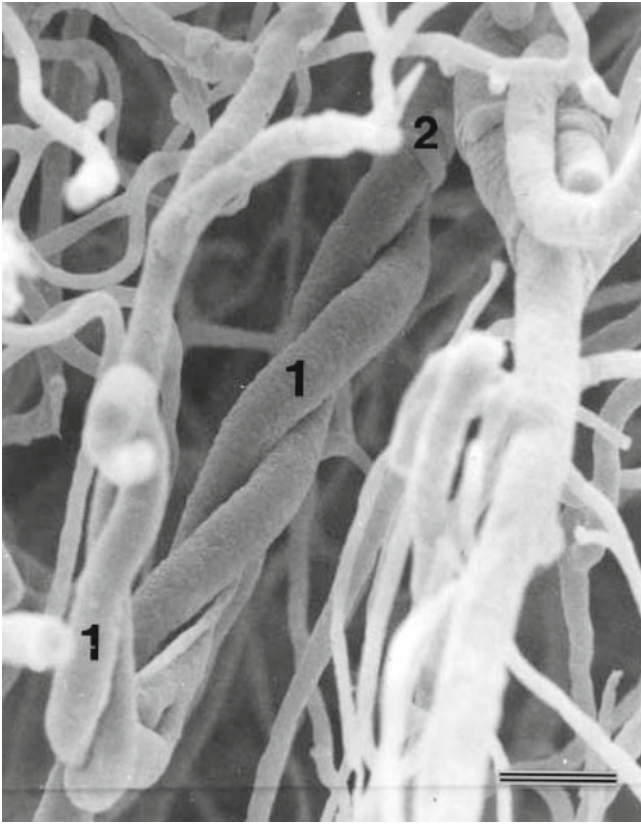


Fig. 5.34 Intravascular resin injection (Mercox) and scanning electron microscope view after corrosion. Coiling of branches (*1*) of an intrahippocampal artery (*2*). Bar, 38 μm

Coronal, Sagittal, and Axial Sections of the Hippocampus Showing Their Relationships with the Surrounding Structures

6

(After intravascular India ink injection)

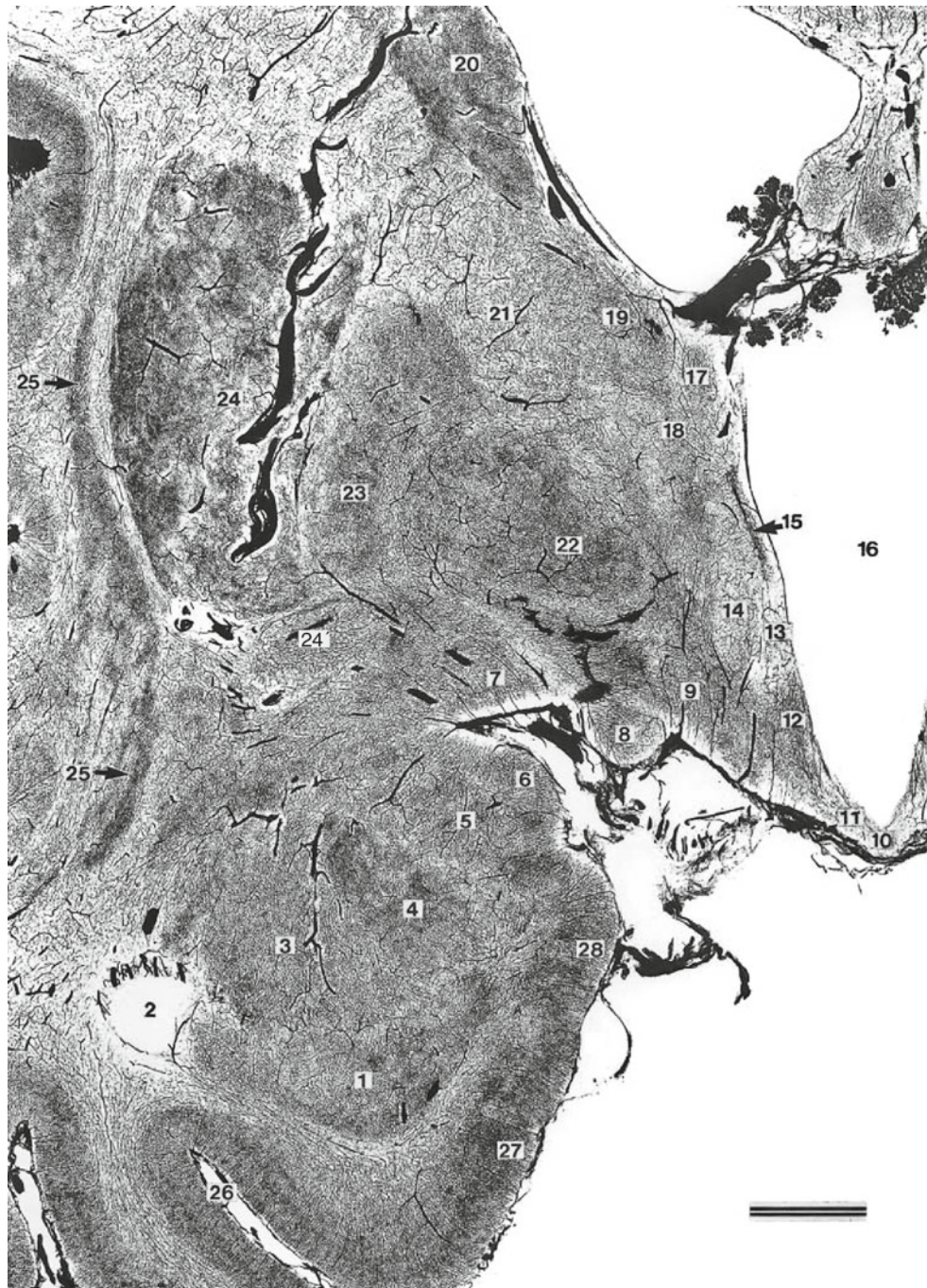


Fig. 6.1 Coronal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 4.3 mm. See Fig. 7.4 for precise description of the hippocampus and MRI. 1 hippocampal head, 2 temporal horn; amygdala: 3 lateral nucleus, 4 basal nucleus, 5 accessory basal nucleus, 6 cortical nucleus, 7 anterior perforated substance, 8 optic tract, 9 lateral hypothalamus, 10 posterior tuber, 11 arcuate hypothalamic nucleus, 12 ventromedial hypothalamic nucleus, 13 dorsomedial hypothalamic

nucleus, 14 column of fornix, 15 paraventricular hypothalamic nucleus, 16 third ventricle, 17 anterior thalamic nucleus, 18 ventral anterior thalamic nucleus, 19 thalamic reticular nucleus, 20 caudate nucleus, 21 genu of internal capsule, 22 globus pallidus, medial part, 23 globus pallidus lateral part, 24 putamen, 24' anterior commissure, 25 claustrum, 26 col-lateral sulcus, 27 parahippocampal gyrus, 28 ambient gyrus

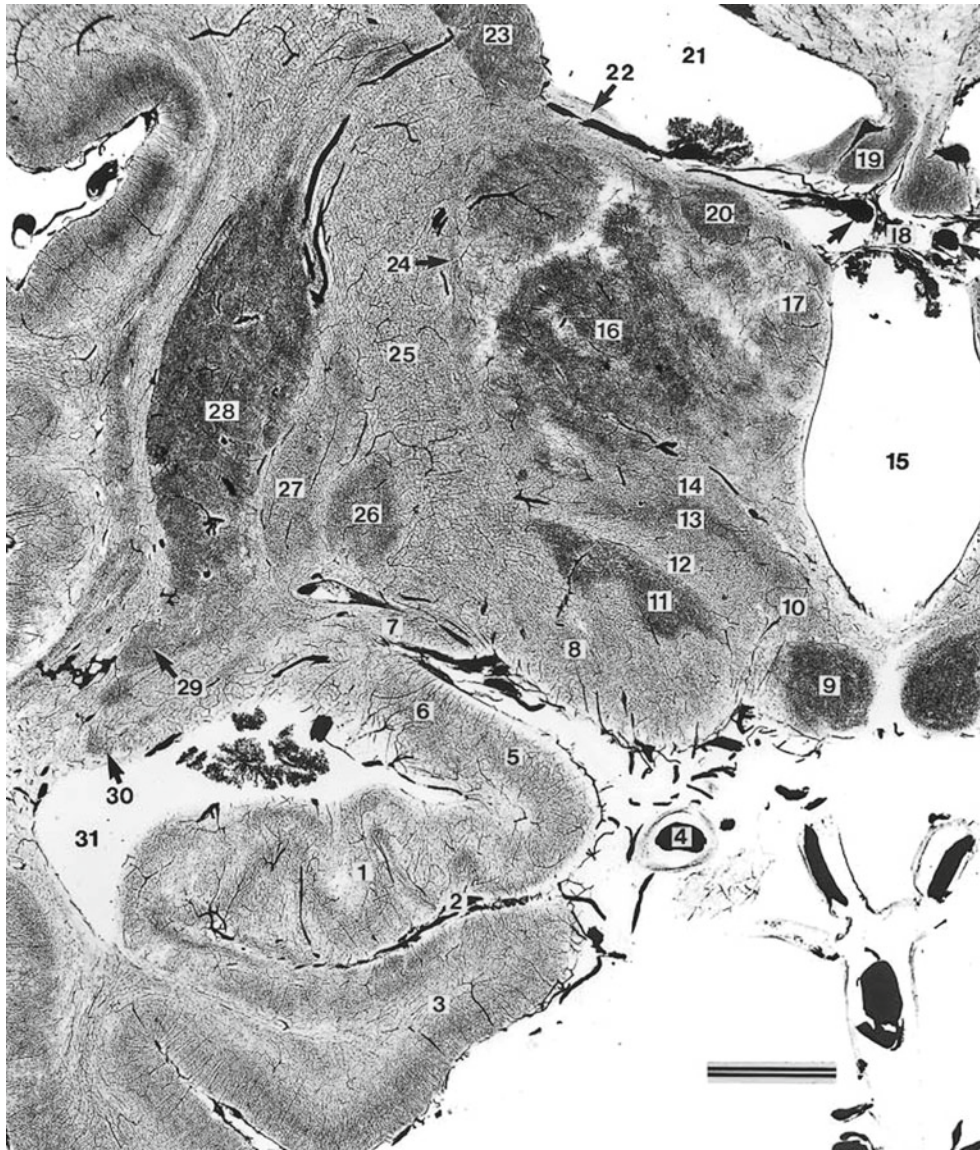


Fig. 6.2 Coronal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 5.2 mm. See Fig. 7.5 for precise description of the hippocampus and MRI. 1 hippocampal head (digitationes hippocampi), 2 uncal sulcus, 3 parahippocampal gyrus, 4 posterior cerebral artery, 5 uncinata gyrus, 6 amygdala (cortical nucleus), 7 optic tract, 8 crus cerebri, 9 mamillary body, 10 posterior hypothalamus, 11 substantia nigra, 12 H2 field of Forel, 13 zona incerta, 14 H1 field of Forel, 15 third ventricle, 16 ventral lateral thalamic nucleus, 17 dorso-

medial thalamic nucleus, 18 median part of the transverse fissure (velum interpositum) arrows indicate the internal cerebral veins, 19 fornix, 20 anterior thalamic nucleus, 21 body of lateral ventricle, 22 lamina affixa, 23 caudate nucleus, 24 thalamic reticular nucleus, 25 posterior limb of internal capsule, 26 globus pallidus, medial part, 27 globus pallidus, lateral part, 28 putamen, 29 peduncle of lentiform nucleus, 30 tail of caudate nucleus, 31 temporal horn of lateral ventricle

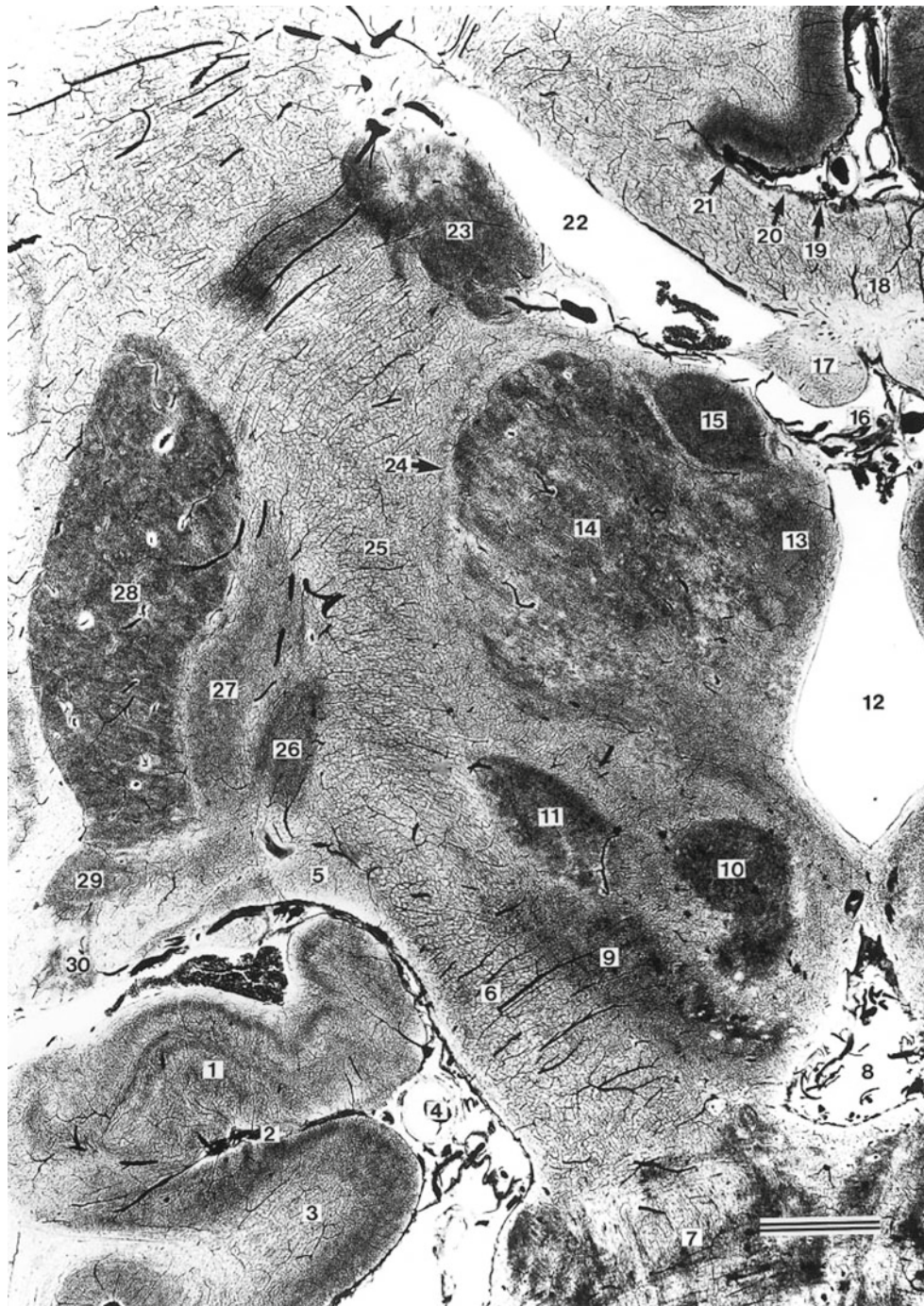


Fig. 6.3 Coronal section of the brain. Vascular injection. Tentorium cerebelli removed. Bar, 4.6 mm. See Fig. 7.6 for precise description of the hippocampus and MRI. 1 hippocampal head (digitationes hippocampi), 2 uncal sulcus, 3 parahippocampal gyrus, 4 ambient cistern, 5 optic tract, 6 crus cerebri, 7 ventral part of pons, 8 interpeduncular fossa (interpeduncular cistern), 9 substantia nigra, 10 red nucleus, 11 subthalamic nucleus, 12 third ventricle, 13 dorsomedial thalamic nucleus,

14 ventral lateral thalamic nucleus, 15 anterior thalamic nucleus, 16 median part of the transverse fissure (velum interpositum), 17 fornix, 18 corpus callosum, 19 medial longitudinal stria, 20 indusium griseum, 21 lateral longitudinal stria, 22 lateral ventricle, 23 caudate nucleus, 24 thalamic reticular nucleus, 25 posterior limb of internal capsule, 26 globus pallidus, medial part, 27 globus pallidus, lateral part, 28 putamen, 29 peduncle of lentiform nucleus, 30 tail of caudate nucleus

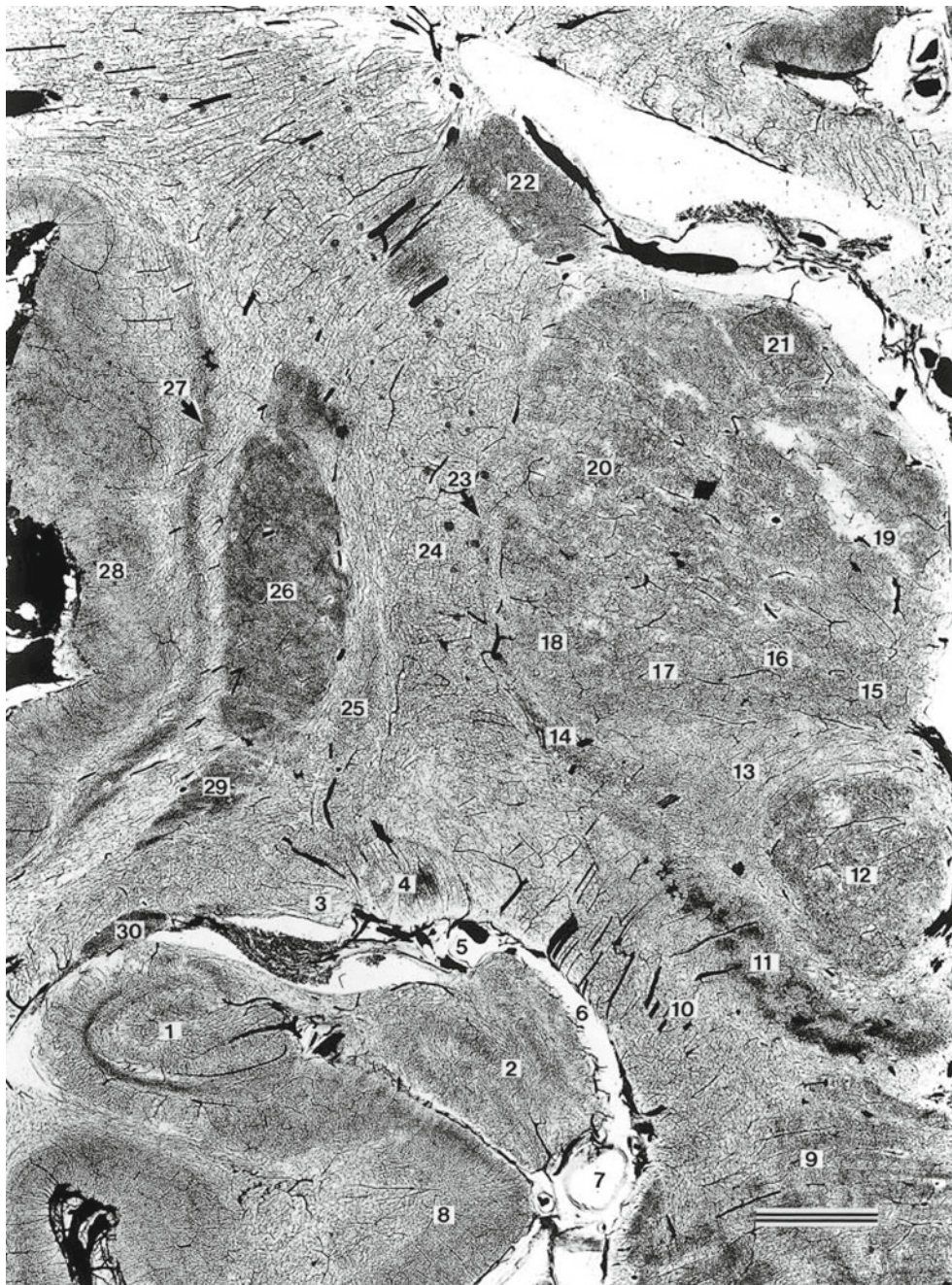


Fig. 6.4 Coronal section of the brain. Vascular injection. Tentorium cerebelli removed. Bar, 4.8 mm. See Fig. 7.7 for precise description of the hippocampus and MRI. 1 hippocampal body, 2 uncus apex, 3 stria terminalis, 4 lateral geniculate body, 5 transverse fissure, 6 crural cistern, 7 posterior cerebral artery, 8 parahippocampal gyrus, 9 ventral part of pons, 10 crus cerebri, 11 substantia nigra, 12 red nucleus, 13 medial lemniscus, 14 zona incerta, 15 Parafascicular nucleus, 16 centromedian

thalamic nucleus, 17 ventral posteromedial thalamic nucleus, 18 ventral posterolateral thalamic nucleus, 19 dorsomedial thalamic nucleus, 20 ventral lateral thalamic nucleus, 21 lateral dorsal thalamic nucleus, 22 caudate nucleus, 23 thalamic reticular nucleus, 24 posterior limb of internal capsule, 25 globus pallidus, lateral part, 26 putamen, 27 claustrum, 28 insula, 29 peduncle of lentiform nucleus, 30 tail of caudate nucleus

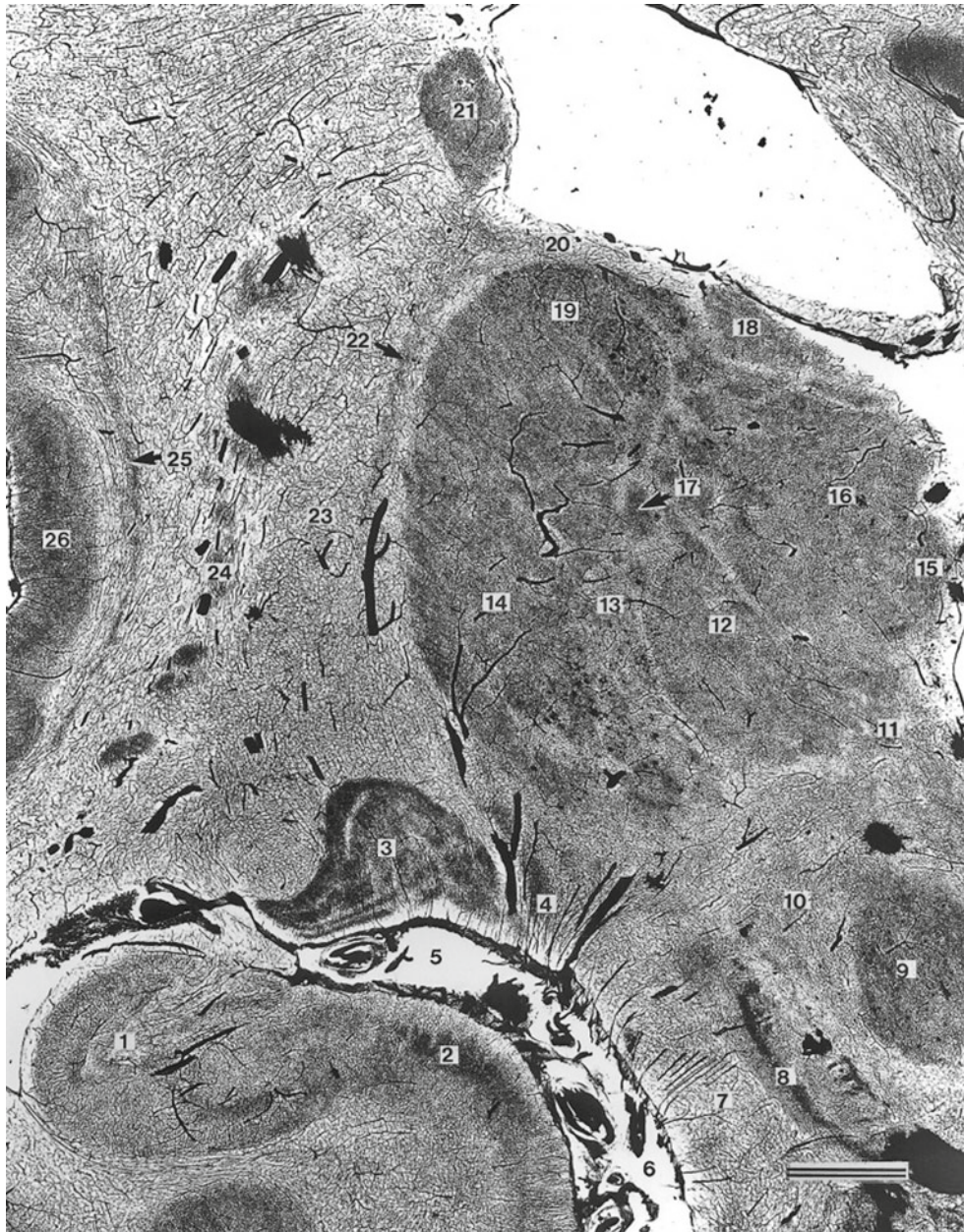


Fig. 6.5 Coronal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 3.8 mm. See Fig. 7.8 for precise description of the hippocampus and MRI. 1 hippocampal body, 2 parahippocampal gyrus (subiculum), 3 lateral geniculate body, 4 medial geniculate body, 5 transverse fissure (lateral part), 6 ambient cistern, 7 crus cerebri, 8 substantia nigra, 9 red nucleus, 10 medial lemniscus, 11 parafascicular nucleus, 12 centromedian thalamic nucleus, 13 ventral posteromedial

thalamic nucleus, 14 ventral posterolateral thalamic nucleus, 15 habenular nucleus, 16 dorsomedial thalamic nucleus, 17 intralaminar thalamic nuclei, 18 lateral dorsal thalamic nucleus, 19 lateral posterior thalamic nucleus, 20 lamina affixa, 21 caudate nucleus, 22 thalamic reticular nucleus, 23 posterior limb of internal capsule, 24 pontes grisei caudolenticulares, 25 claustrum, 26 insula

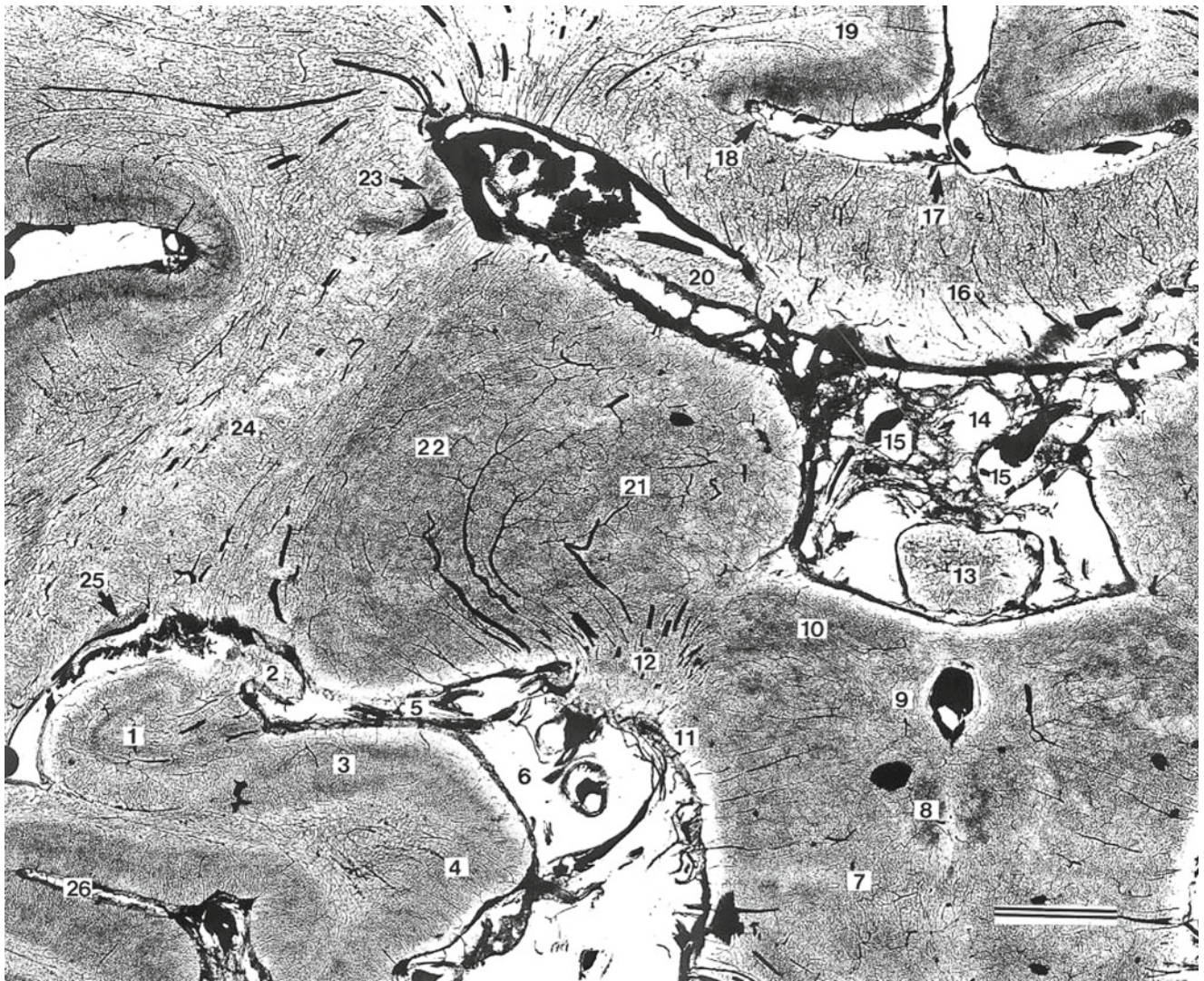


Fig. 6.6 Coronal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 4.4 mm. See Fig. 7.9 for precise description of the hippocampus and MRI. 1 hippocampal body, 2 fimbria, 3 subiculum, 4 parahippocampal gyrus, 5 transverse fissure (lateral part), 6 ambient cistern, 7 brachium conjunctivum, 8 oculomotor nucleus, 9 periaqueductal gray matter, 10 superior colliculus and pretectal area, 11

inferior collicular brachium, 12 superior collicular brachium, 13 pineal gland, 14 quadrigeminal cistern, 15 internal cerebral veins, 16 splenium, 17 medial longitudinal stria, 18 lateral longitudinal stria, 19 cingulate gyrus, 20 fornix, 21 medial pulvinar, 22 lateral pulvinar, 23 caudate nucleus, 24 retrolentiform part of internal capsule, 25 tail of caudate nucleus, 26 collateral sulcus



Fig. 6.7 Coronal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 5.7 mm. See Fig. 7.10 for precise description of the hippocampus and MRI. 1 hippocampal tail, 2 isthmus, 3 anterior calcarine sulcus, 4 parahippocampal gyrus (posterior part), 5 cerebellar hemisphere, 6 locus coeruleus, 7 brachium conjunctivum, 8 inferior

colliculus, 9 quadrigeminal cistern, 10 internal cerebral veins, 11 splenium, 12 medial longitudinal stria, 13 indusium griseum, 14 lateral longitudinal stria, 15 cingulate gyrus, 16 atrium of lateral ventricle, 17 optic radiations, 18 caudate nucleus

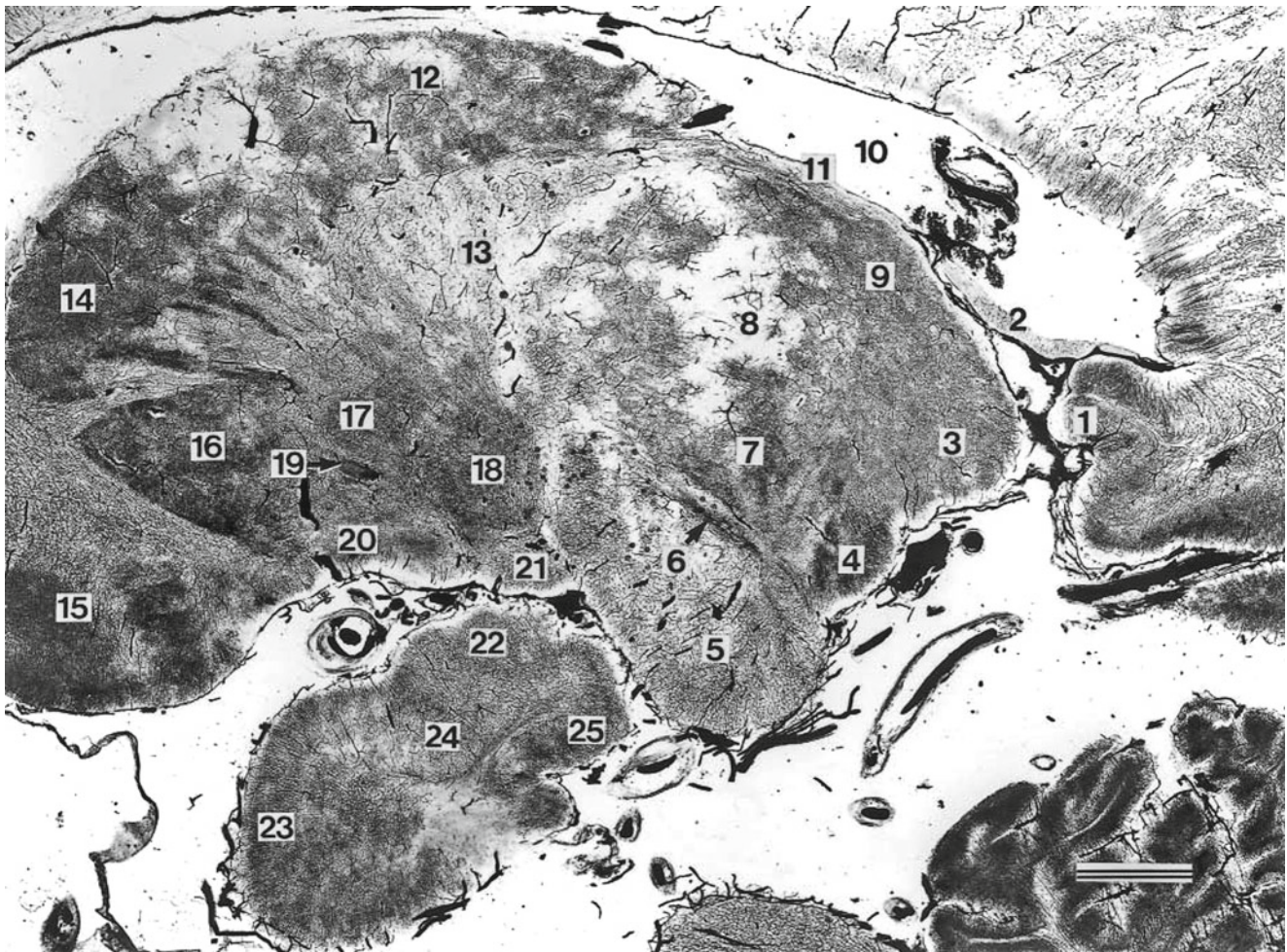


Fig. 6.8 Sagittal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 4.8 mm. See Fig. 7.14 for precise description of the hippocampus and MRI. 1 hippocampal tail, 2 crus of fornix, 3 pulvinar, 4 medial geniculate body, 5 crus cerebri, 6 zona incerta, 7 ventral posterolateral thalamic nucleus, 8 ventral lateral thalamic nucleus, 9 lateral posterior thalamic nucleus, 10 lateral ventricle, 11 lamina affixa, 12 caudate

nucleus, 13 internal capsule, 14 head of caudate nucleus, 15 medial orbital gyrus, 16 putamen, 17 globus pallidus, lateral part, 18 globus pallidus, medial part, 19 anterior commissure, 20 anterior perforated substance, 21 optic tract, 22 cortical nucleus of amygdala, 23 ambient gyrus, 24 accessory basal nucleus of amygdala, 25 uncinete gyrus (head of hippocampus)

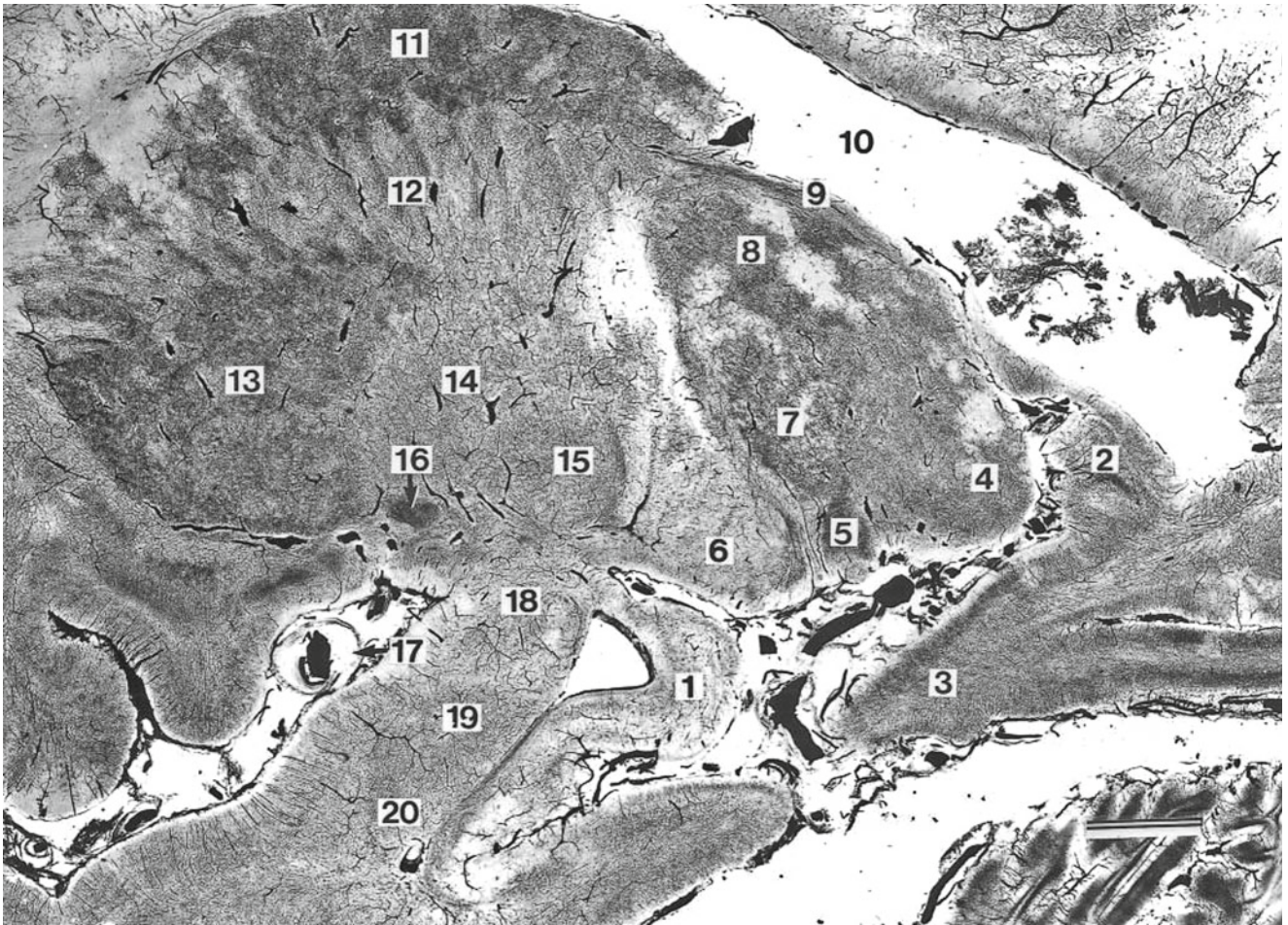


Fig. 6.9 Sagittal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 4.8 mm. See Fig. 7.15 for precise description of the hippocampus and MRI. 1 hippocampal head, 2 hippocampal tail, 3 parahippocampal gyrus, 4 pulvinar, 5 medial geniculate body, 6 crus cerebri, 7 ventral posterolateral thalamic nucleus, 8 lateral posterior

thalamic nucleus, 9 lamina affixa, 10 lateral ventricle, 11 caudate nucleus, 12 anterior limb of internal capsule, 13 putamen, 14 globus pallidus, lateral part, 15 globus pallidus, medial part, 16 anterior commissure, 17 middle cerebral artery, 18 medial nucleus of amygdala, 19 accessory basal nucleus of amygdala, 20 basal nucleus of amygdala

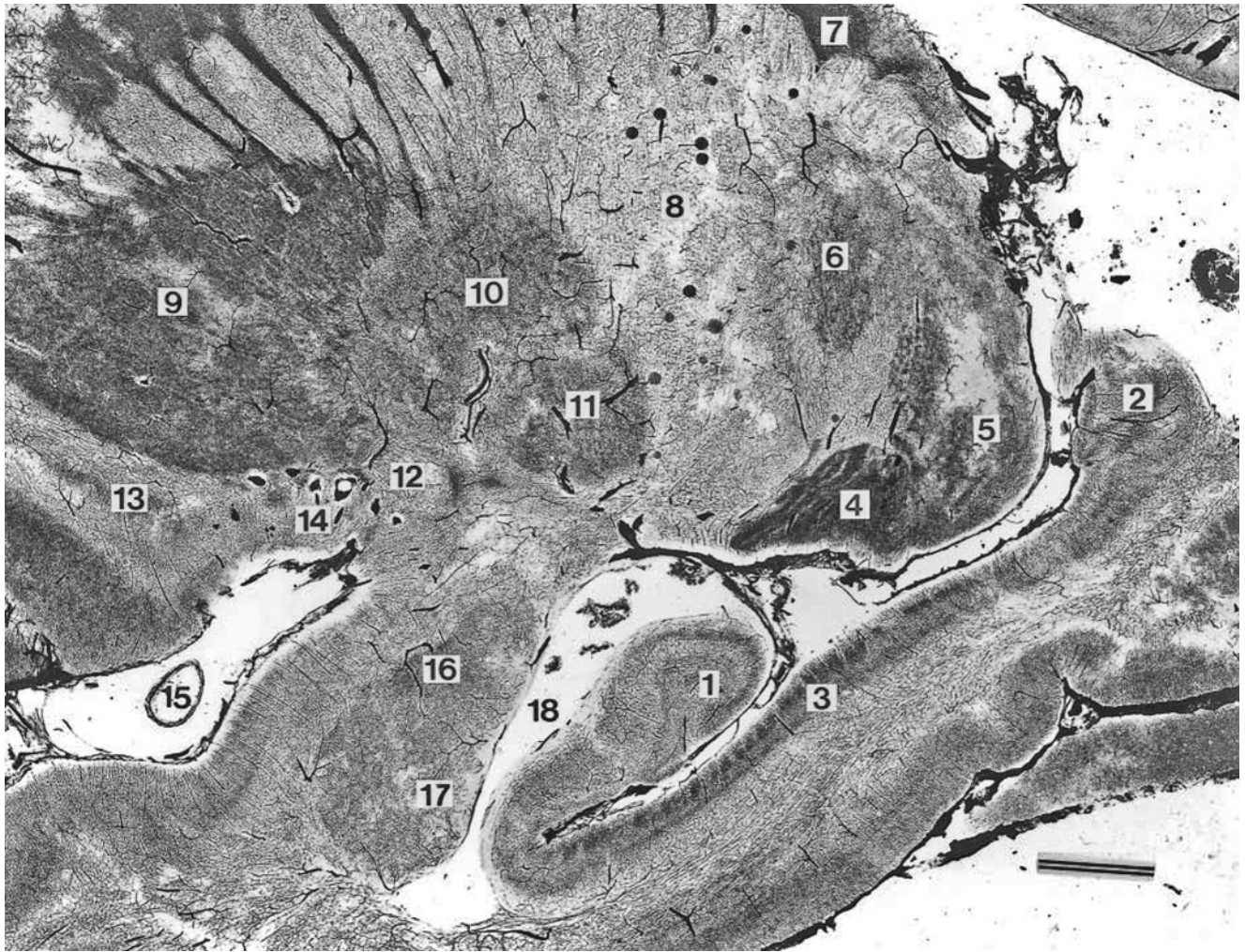


Fig. 6.10 Sagittal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 4.8 mm. See Fig. 7.16 for precise description of the hippocampus and MRI. 1 hippocampal head, 2 hippocampal tail, 3 presubiculum (note the maculate aspect of the capillary network), 4 lateral cerebral artery, 5 pulvinar, 6 lateral posterior thalamic nucleus, 7

caudate nucleus, 8 posterior limb of internal capsule, 9 putamen, 10 globus pallidus, lateral part, 11 globus pallidus, medial part, 12 anterior commissure, 13 claustrum, 14 anterior perforated substance, 15 middle cerebral artery, 16 basal nucleus of amygdala, 17 lateral nucleus of amygdala, 18 temporal horn of lateral ventricle

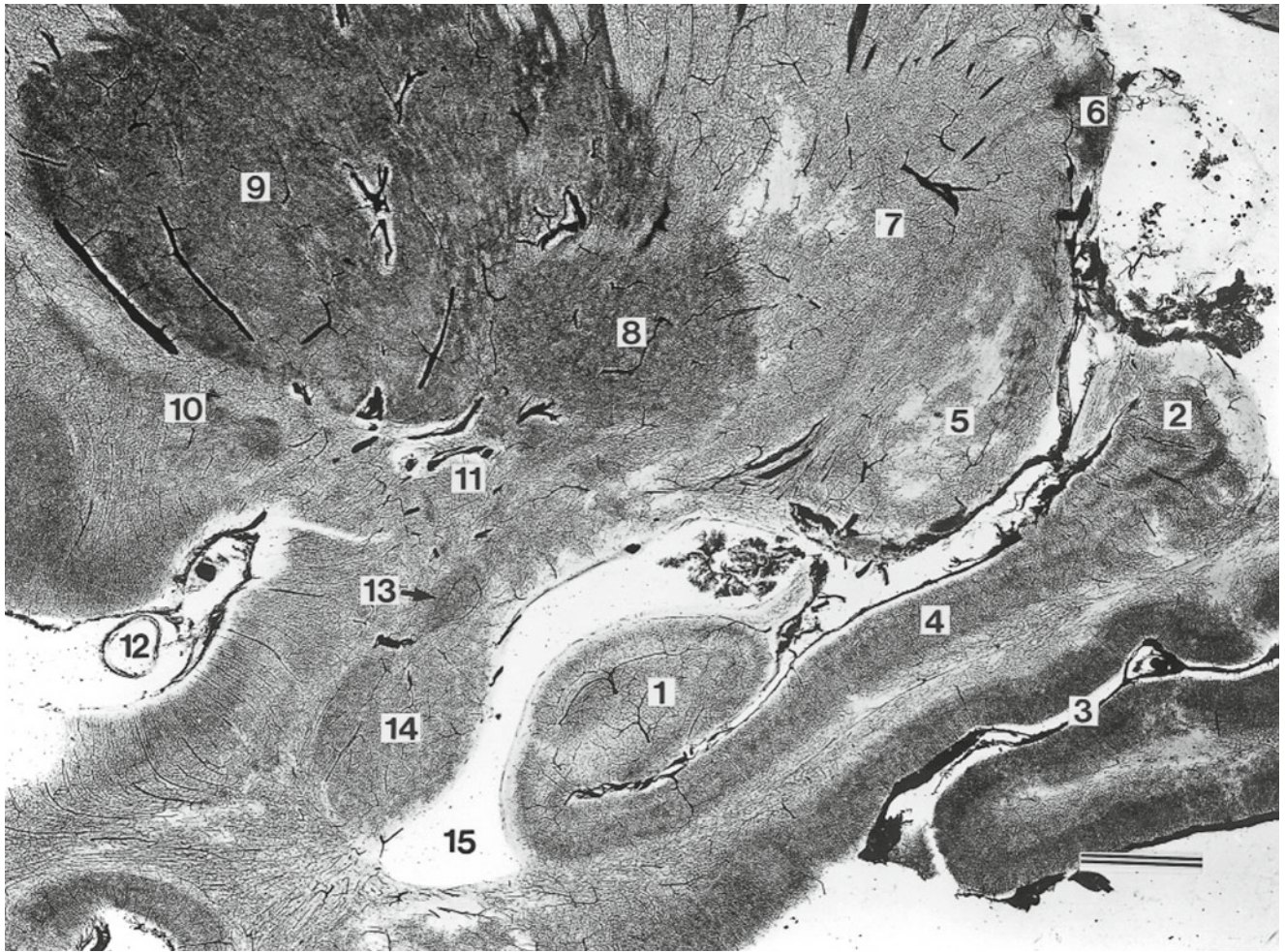


Fig. 6.11 Sagittal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 5 mm. See Fig. 7.17 for precise description of the hippocampus and MRI. *1* hippocampal head, *2* hippocampal tail, *3* collateral sulcus, *4* subiculum, *5* pulvinar, *6* caudate nucleus, *7* retrolen-

tiform part of internal capsule, *8* globus pallidus, lateral part, *9* putamen, *10* claustrum, *11* anterior commissure, *12* middle cerebral artery, *13* basal nucleus of amygdala, *14* lateral nucleus of amygdala, *15* temporal horn of lateral ventricle (uncal recess)

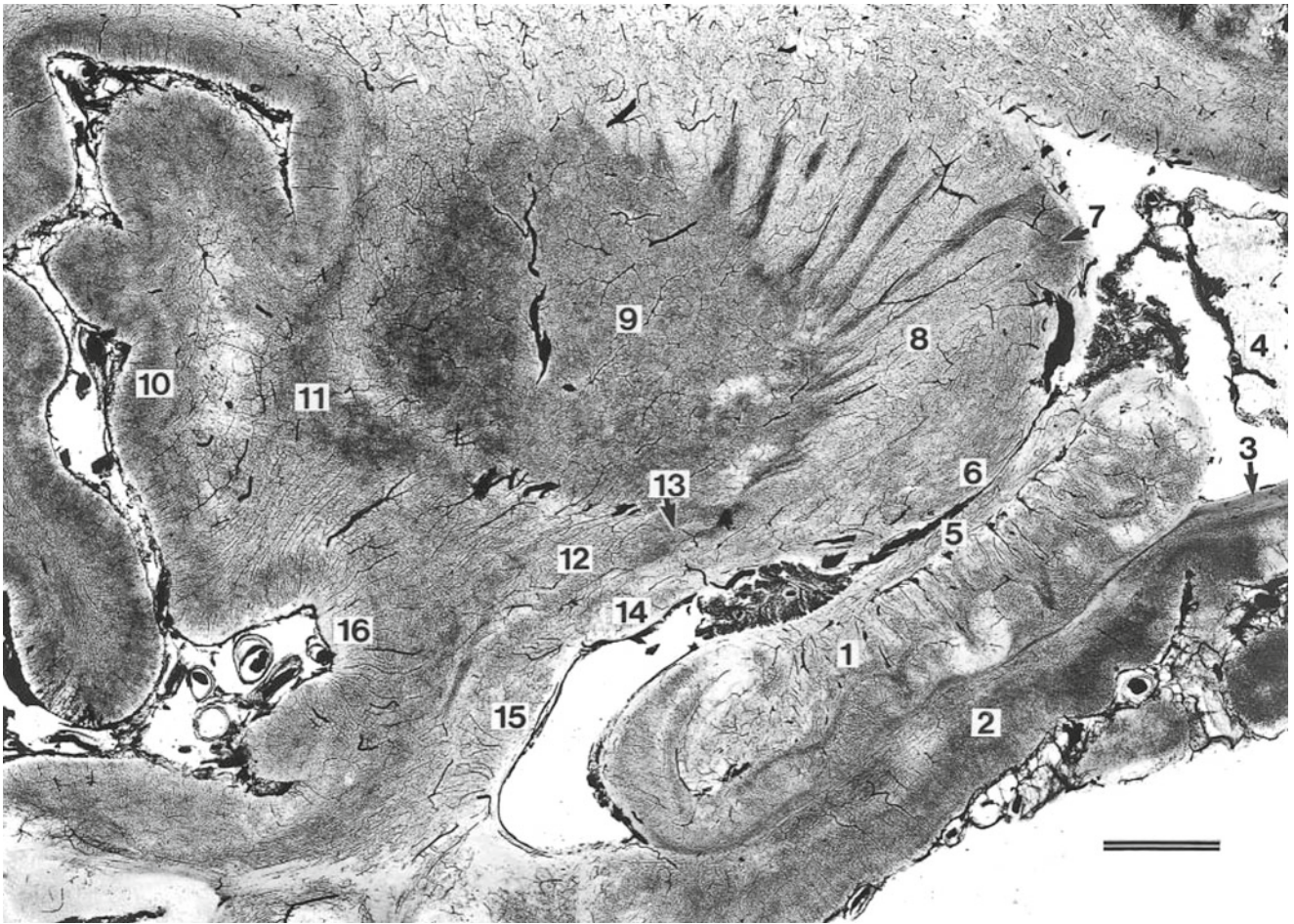


Fig. 6.12 Sagittal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 5 mm. See Fig. 7.18 for precise description of the hippocampus and MRI. 1 hippocampus, 2 parahippocampal gyrus, 3 collateral trigone, 4 atrium, 5 fimbria, 6 stria terminalis, 7 caudate nucleus, 8 retrolentiform part of internal capsule, 9 putamen, 10 insula, 11 claustrum, 12 anterior commissure, 13 peduncle of lentiform nucleus, 14 tail of caudate nucleus, 15 lateral nucleus of amygdala, 16 limen insulae

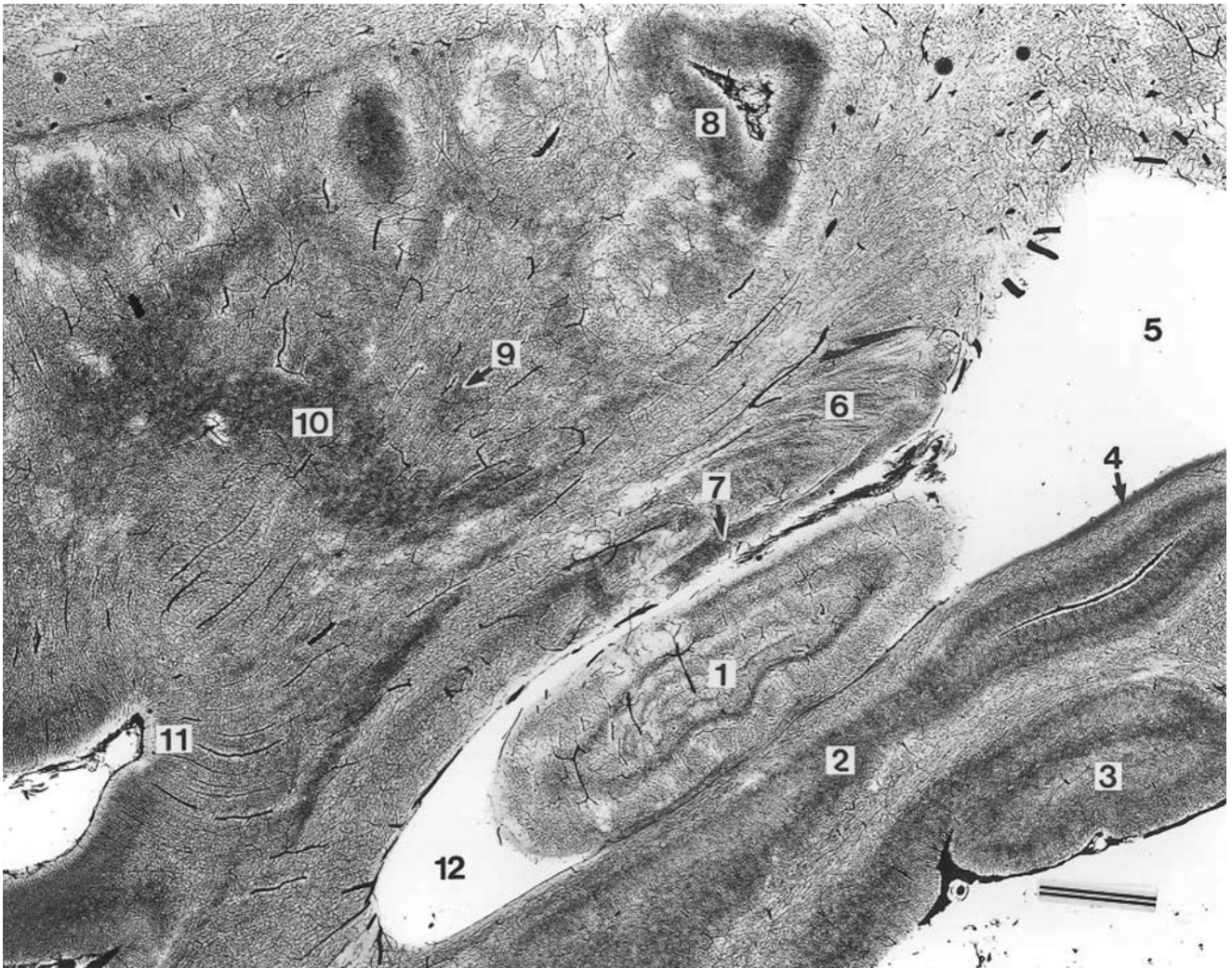


Fig. 6.13 Sagittal section of the brain. Vascular injection. Tentorium cerebelli removed. *Bar*, 4.3 mm. See Fig. 7.19 for precise description of the hippocampus and MRI. 1 hippocampal body, 2 parahippocampal gyrus, 3 fusiform gyrus, 4 collateral trigone, 5 atrium, 6 optic radiations, 7 caudate nucleus, 8 insula, 9 putamen, 10 claustrum, 11 limen insulae, 12 temporal horn of the lateral ventricle

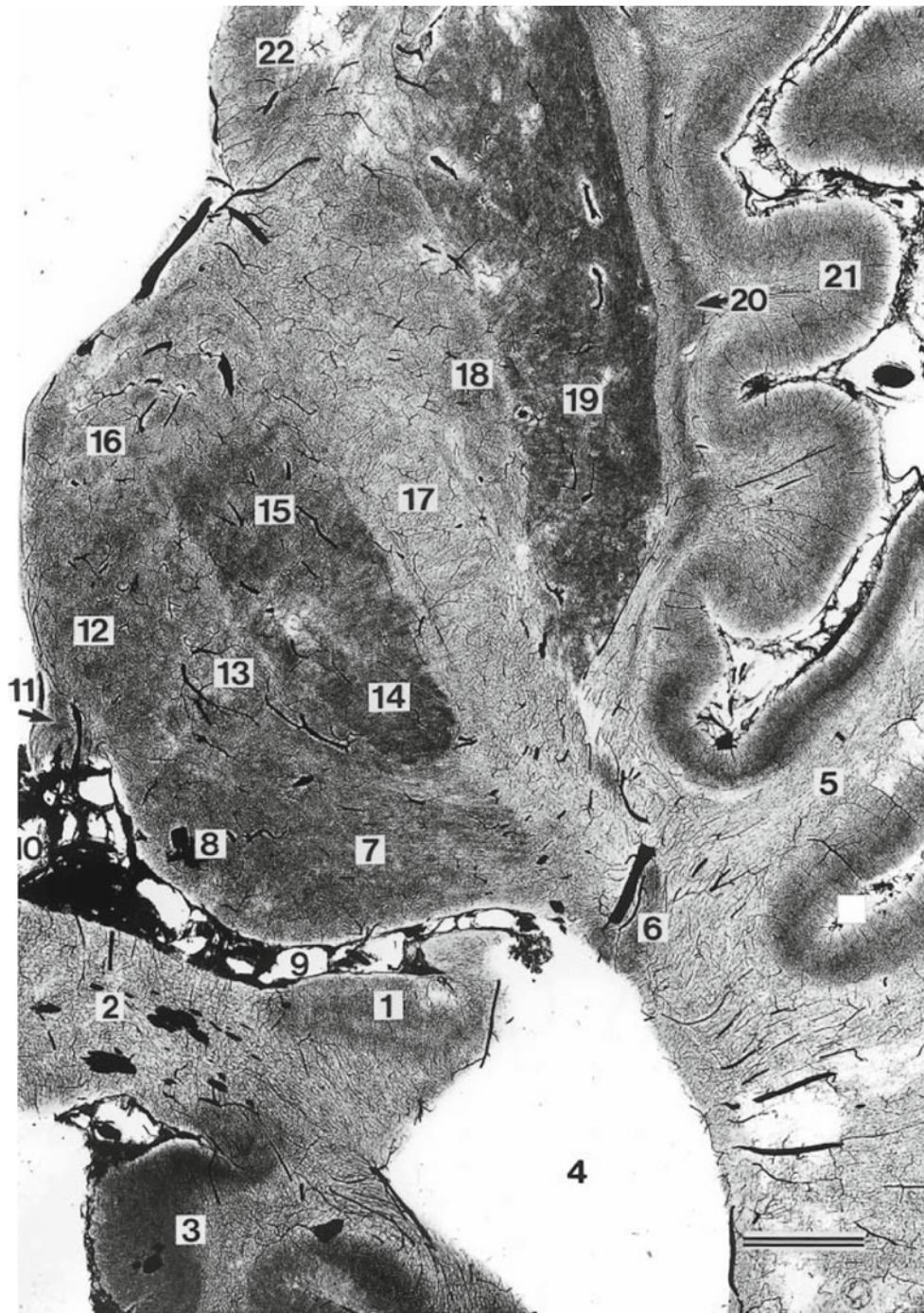


Fig. 6.14 Axial section of the brain. Vascular injection. Bar, 4.6 mm. See Fig. 7.21 for precise description of the hippocampus and MRI. 1 hippocampal tail, 2 splenium, 3 cingulate gyrus, 4 occipital horn of lateral ventricle, 5 superior temporal gyrus, 5' superior temporal sulcus, 6 tail of caudate nucleus, 7 lateral pulvinar, 8 medial pulvinar, 9 transverse fissure, lateral part, 10 quadrigeminal cistern, 11 habenular

nucleus, 12 dorsomedial thalamic nucleus, 13 centromedian thalamic nucleus, 14 ventral posterolateral thalamic nucleus, 15 ventral lateral thalamic nucleus, 16 anterior thalamic nucleus, 17 internal capsule, posterior limb, 18 globus pallidus, lateral part, 19 putamen, 20 claustrum, 21 insula, 22 head of the caudate nucleus

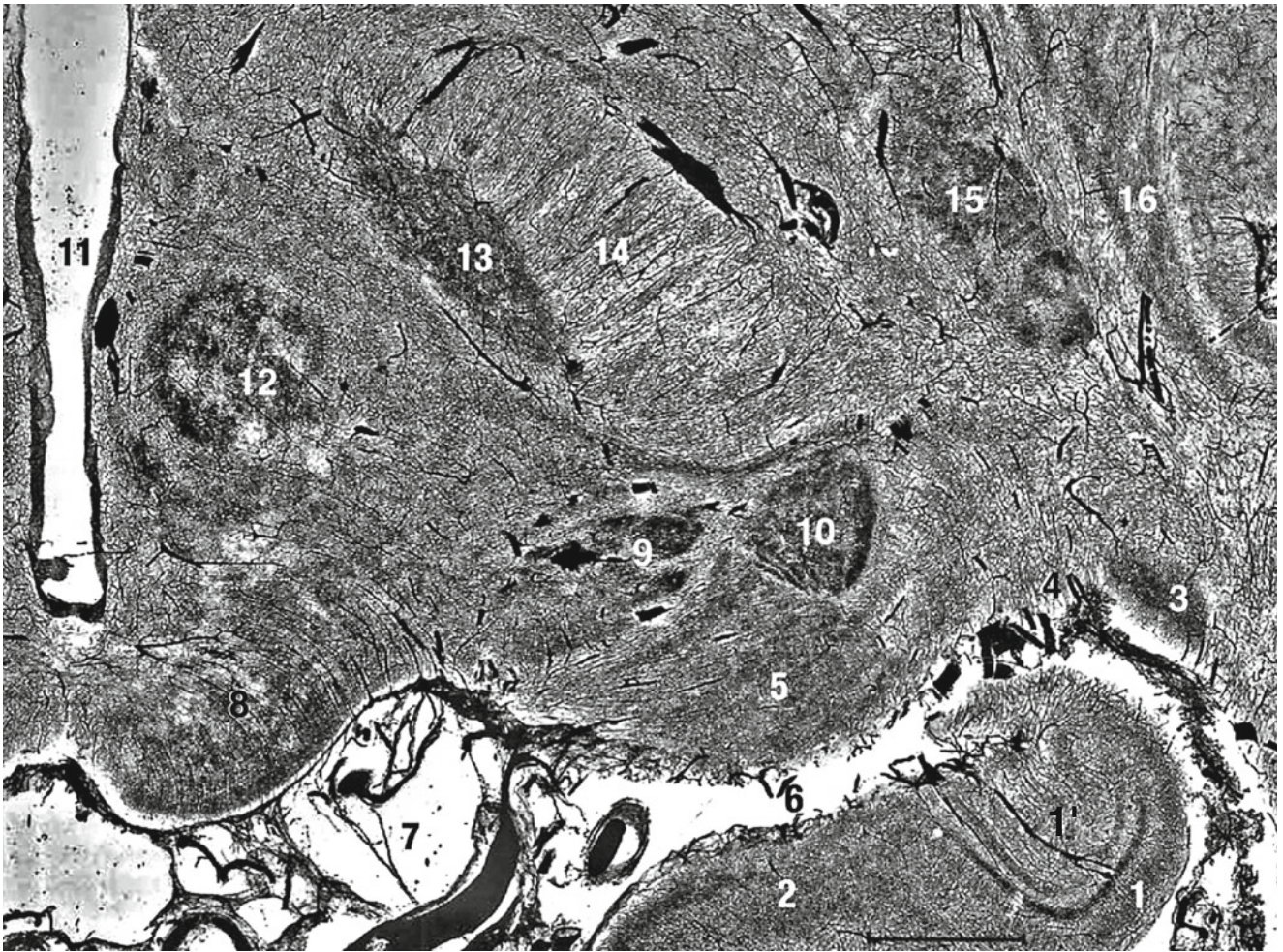


Fig. 6.15 Axial section of the brain. Vascular injection. Bar, 4.7 mm. See Fig. 7.22 for precise description of hippocampus and MRI. 1 hippocampal body, cornu Ammonis, 1' hippocampal body, gyrus dentatus, 2 parahippocampal gyrus, 3 tail of caudate nucleus, 4 stria terminalis,

5 pulvinar, 6 transverse fissure, lateral part, 7 quadrigeminal cistern, 8 superior colliculus, 9 medial geniculate body, 10 lateral geniculate body, 11 third ventricle, 12 red nucleus, 13 subthalamic nucleus, 14 internal capsule, posterior limb, 15 putamen, 16 claustrum



Fig. 6.16 Axial section of the brain. Vascular injection. Bar, 4.8 mm. See Fig. 7.23 for precise description of hippocampus and MRI. 1 hippocampal body, 2 temporal horn of lateral ventricle, 3 tail of caudate nucleus, 4 stria terminalis, 5 lateral geniculate body, 6 parahippocampal gyrus, 7 medial geniculate body, 8 ambient cistern, 9 lemniscal trigone, 10 superior colliculus, 11 cerebral aqueduct, 12 periaqueductal gray matter, 13 oculomotor

nucleus, 14 red nucleus, 15 medial lemniscus, 16 substantia nigra, pars compacta, 16' substantia nigra, pars reticulata, 17 crus cerebri, 18 putamen, 19 external capsule, 20 insula, 21 claustrum, 22 central nucleus of amygdala, 23 semilunar gyrus, 24 optic tract, 25 lamina terminalis, 26 suprachiasmatic recess, 27 tuber, 28 third ventricle, 29 mamillary body, 30 interpeduncular cistern

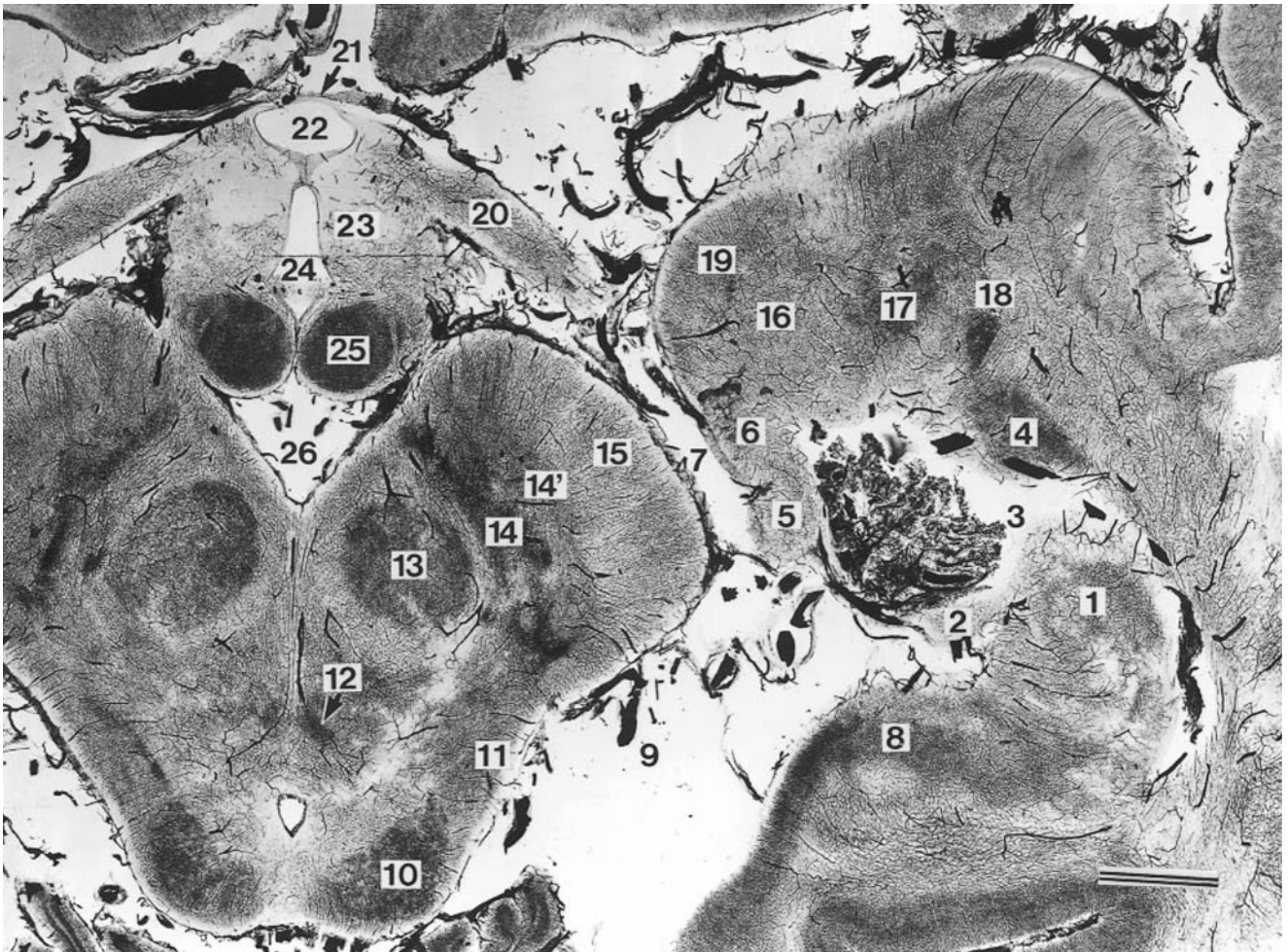


Fig. 6.17 Axial section of the brain. Vascular injection. Bar, 5 mm. See Fig. 7.24 for precise description of hippocampus and MRI. 1 hippocampal body and head (digitationes hippocampi), 2 fimbria, 3 temporal horn, 4 tail of caudate nucleus, 5 uncus apex, 6 uncinatus gyrus, 7 crural cistern (artificially enlarged), 8 parahippocampal gyrus, 9 ambient cistern, 10 superior colliculus, 11 lemniscal trigone, 12 oculomotor nucleus, 13 red

nucleus, 14 substantia nigra, pars compacta, 14' substantia nigra, pars reticulata, 15 crus cerebri, 16 accessory basal nucleus of amygdala, 17 basal nucleus of amygdala, 18 lateral nucleus of amygdala, 19 cortical nucleus of amygdala, 20 optic tract, 21 lamina terminalis, 22 suprachiasmatic recess, 23 tuber, 24 third ventricle, 25 mamillary body, 26 interpeduncular cistern

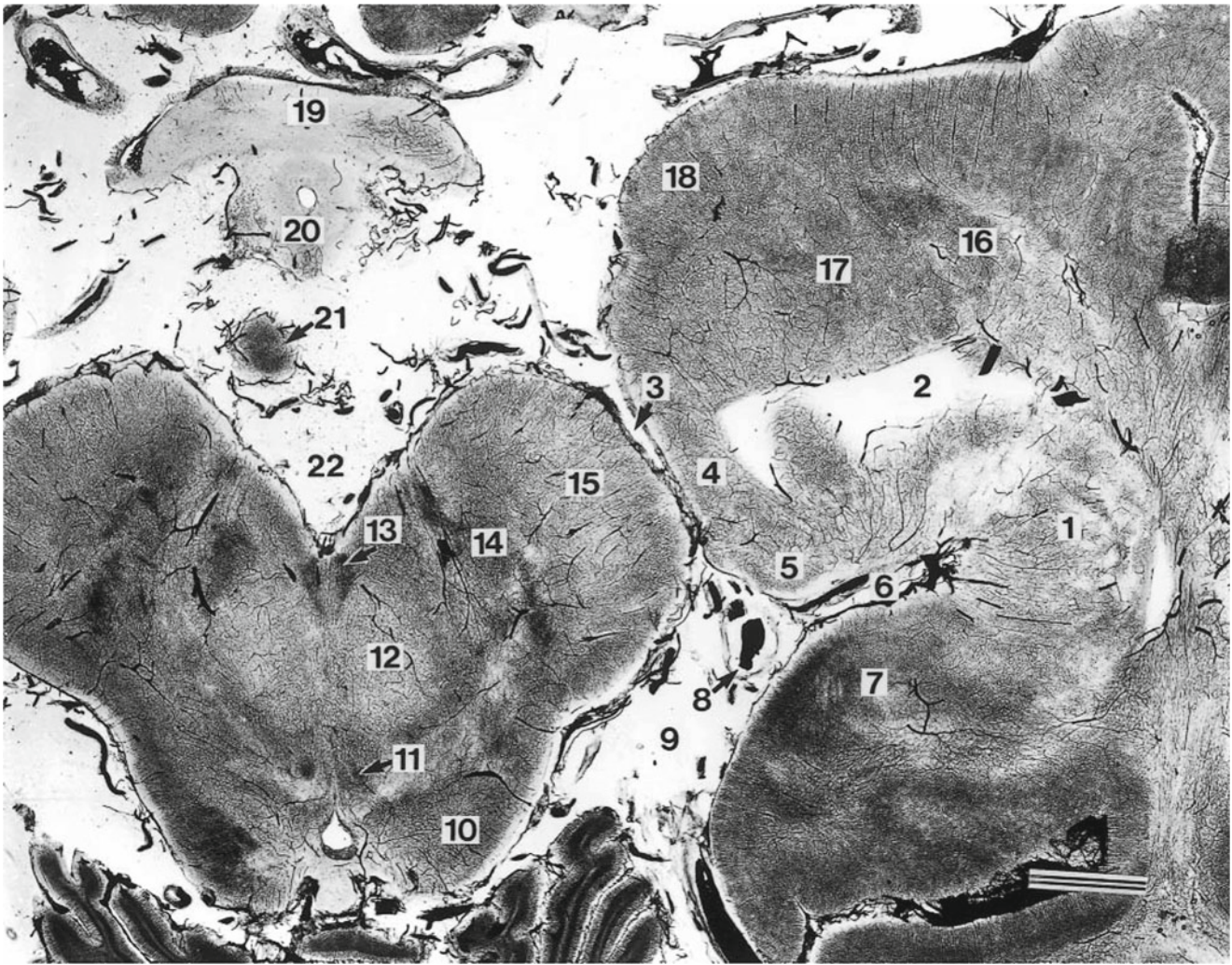


Fig. 6.18 Axial section of the brain. Vascular injection. *Bar*, 4.7 mm. See Fig. 7.25 for precise description of hippocampus and MRI. 1 hippocampal head (digitationes hippocampi), 2 temporal horn (uncal recess), 3 crural cistern, 4 uncinate gyrus, 5 uncal apex, 6 uncal sulcus, 7 parahippocampal gyrus, 8 posterior cerebral artery, 9 ambient cistern,

10 inferior colliculus, 11 trochlear nucleus, 12 brachium conjunctivum, 13 interpeduncular nucleus, 14 substantia nigra, 15 crus cerebri, 16 lateral nucleus of amygdala, 17 basal nucleus of amygdala, 18 ambient gyrus, 19 optic chiasma, 20 infundibulum, 21 mamillary body, 22 interpeduncular cistern

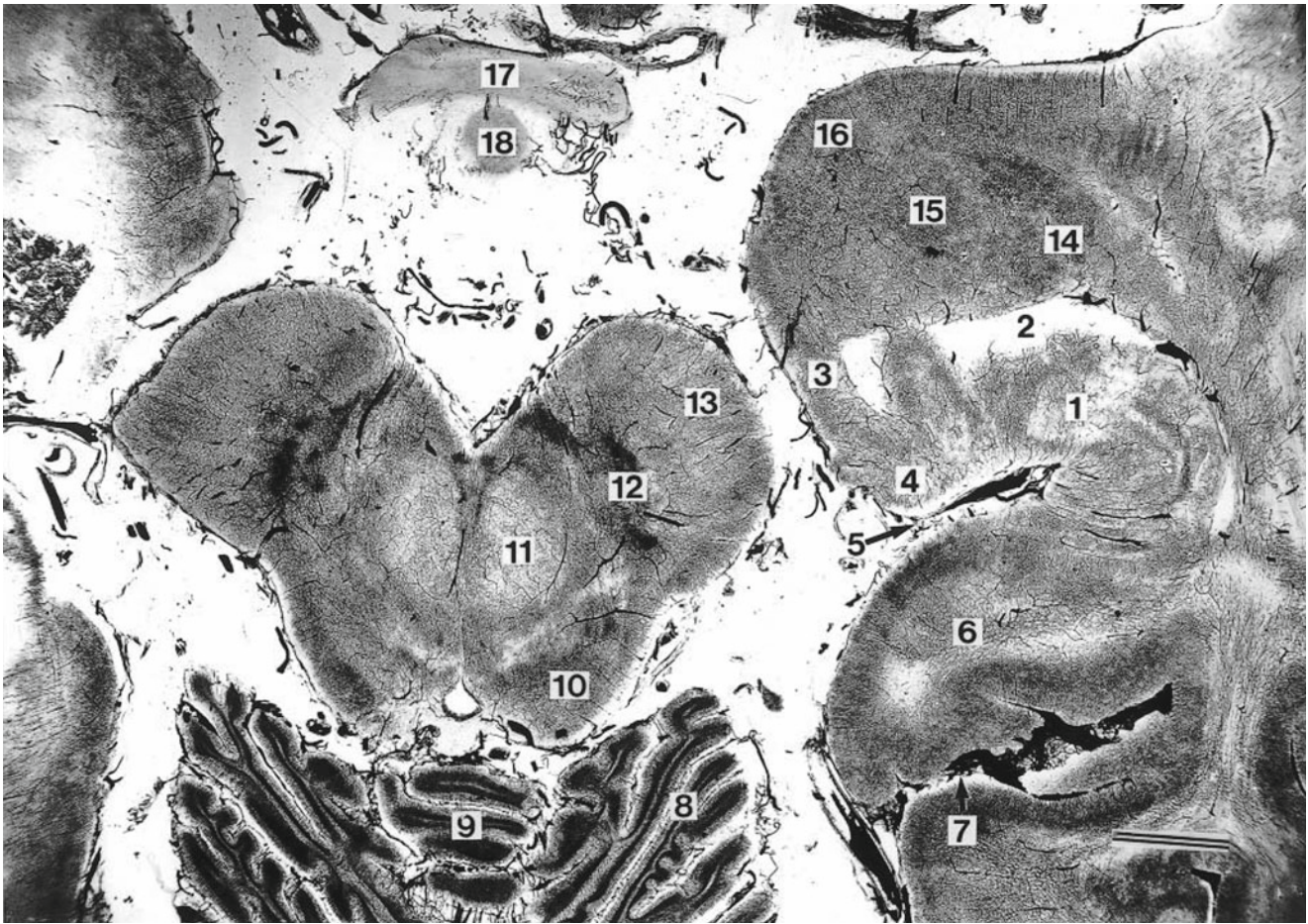


Fig. 6.19 Axial section of the brain. Vascular injection. *Bar*, 5.6 mm. See Fig. 7.26 for precise description of hippocampus and MRI. *1* hippocampal head (digitationes hippocampi), *2* temporal horn of the lateral ventricle (uncal recess), *3* uncinat gyrus, *4* uncal apex, *5* uncal sulcus, *6* parahippocampal gyrus, *7* collateral sulcus, *8* cerebellar hemisphere,

9 vermis, *10* inferior colliculus, *11* brachium conjunctivum, *12* substantia nigra, *13* crus cerebri, *14* lateral nucleus of amygdala, *15* basal nucleus of amygdala, *16* ambient gyrus, *17* optic chiasma, *18* infundibulum

Coronal, sagittal, and axial sections according to the bicommissural plane will be successively studied in 20 plates each composed of 4 pages, showing the plane of the section, details about structures, MRI views, and head section.

The following publications have aided identification of structures visible in the section: Sheps 1945; Olszewski 1952; Kuhlenbeck 1954; Riley 1960, Singer and Yakovlev 1964; Talairach and Szikla 1967; Andrew and Watkins 1969; Roberts and Hanaway 1970; Van Buren and Borke 1972; De Armond et al. 1974; Miller and Burack 1977; Duvernoy 1995, 1999a, b; Dejerine 1980; Gluhbegovic and Williams

1980; Salamon and Huang 1980; Koritké and Sick 1982; Unsöld et al. 1982; Braak and Braak 1983; Haines 1987; Naidich et al. 1987; Talairach and Tournoux 1988; Mark et al. 1993; Jack et al. 2003; Maguire et al. 2003; Theysohn et al. 2009; Thomas et al. 2008; Naidich et al. 2009.

7.1 Coronal Sections

Figures 7.4, 7.5, 7.6, 7.7, 7.8, 7.9, 7.10, and 7.11 show sections of the hippocampus from anterior to posterior levels.

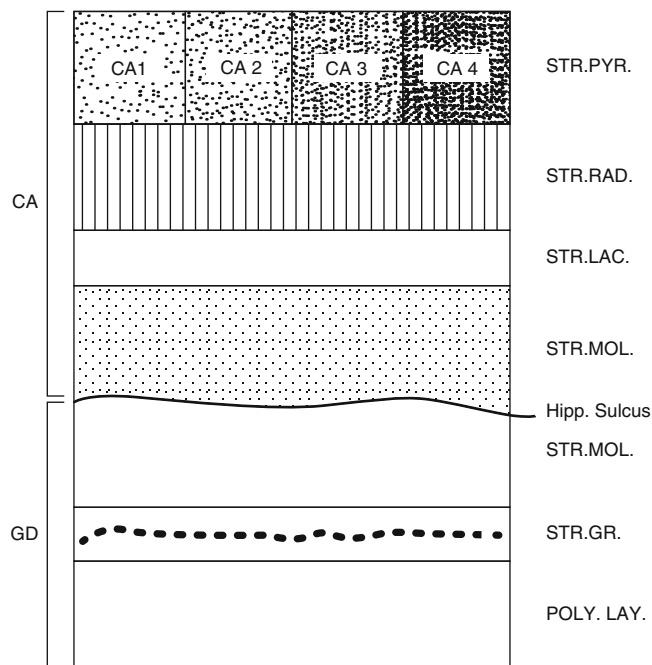


Fig. 7.1 Structure of the hippocampus CA cornu Ammonis, STR. PYR. stratum pyramidale, STR. RAD. stratum radiatum, STR. LAC. stratum lacunosum, STR. MOL. stratum moleculare, Hipp. Sulcus vestigial intrahippocampal sulcus, GD gyrus dentatus, STR. MOL. stratum moleculare, STR. GR. stratum granulosum, POLY. LAY. polymorphic layer

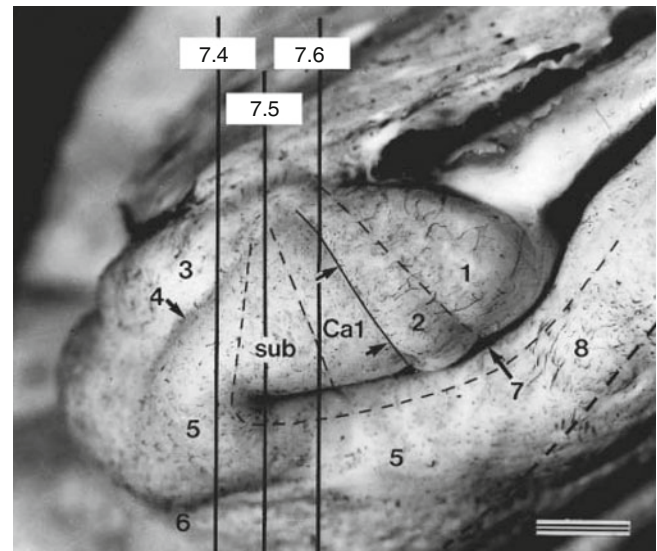


Fig. 7.2 Medial surface of the uncus. This preparation is an indication of the position of CA1 and the subiculum (sub), visible in Figs. 7.4b, 7.5b, and 7.6b. Arrows show the superficial hippocampal sulcus. Bar, 4.4 mm. 1 uncal apex, 2 band of Giacomini, 3 semilunar gyrus, 4 semiangular sulcus, 5 possible situation of the entorhinal area, 6 uncal notch, 7 uncal sulcus, 8 parahippocampal gyrus

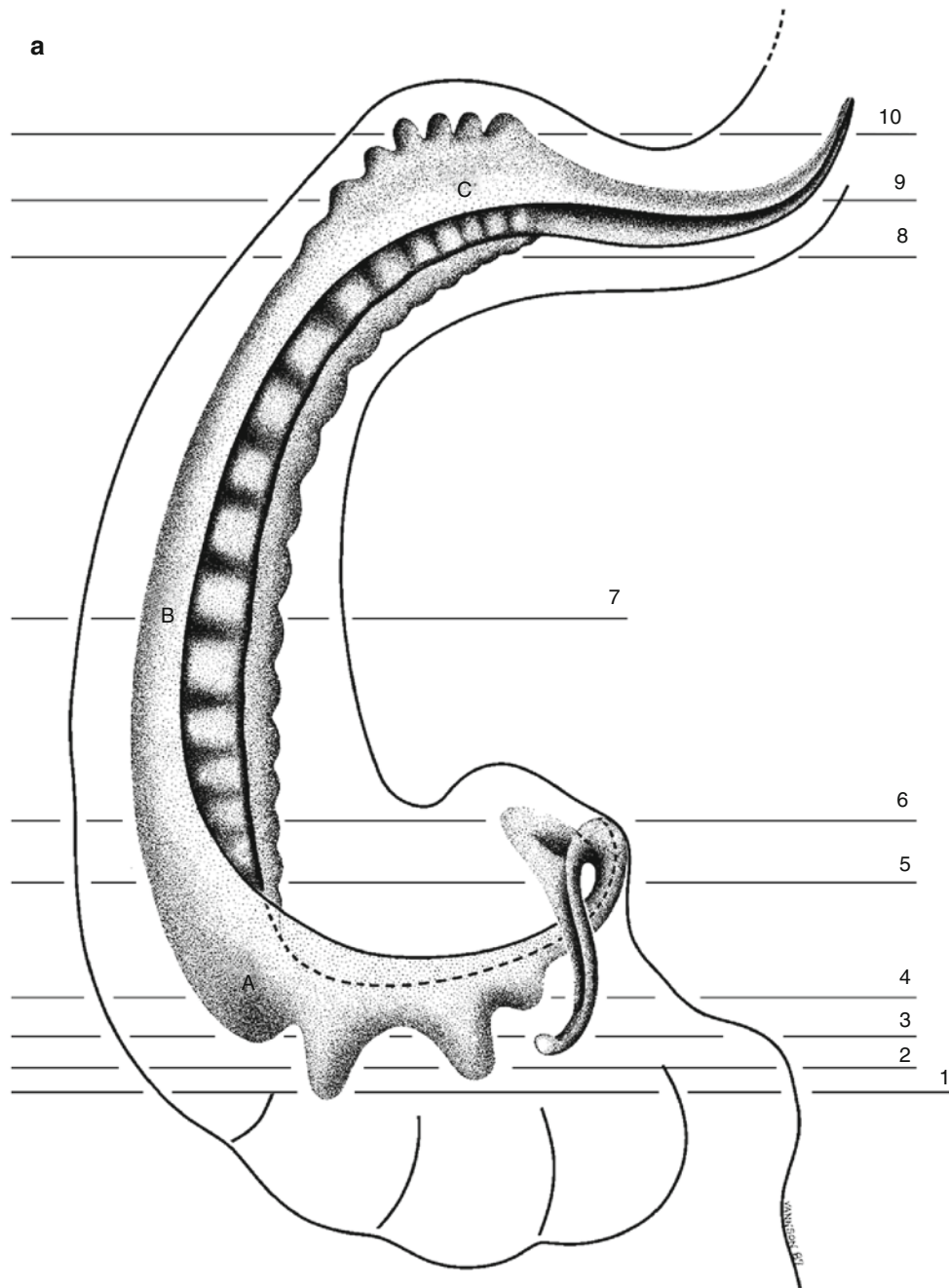


Fig. 7.3 (a, b) General position of the gyrus dentatus in the head (A), body (B), and tail (C) of the hippocampus 1–10. Successive planes of coronal sections are shown in (b)

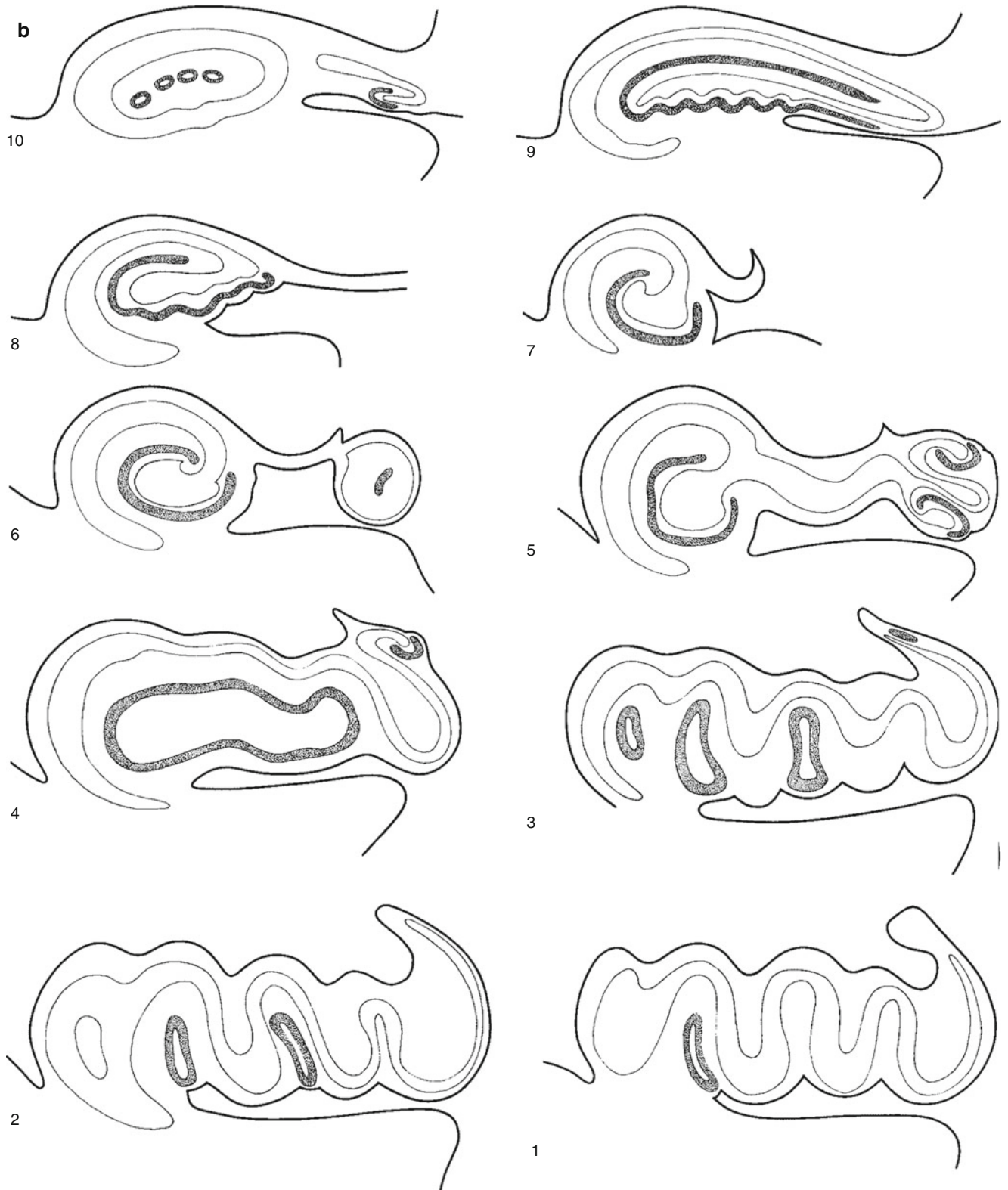


Fig. 7.3 (continued)

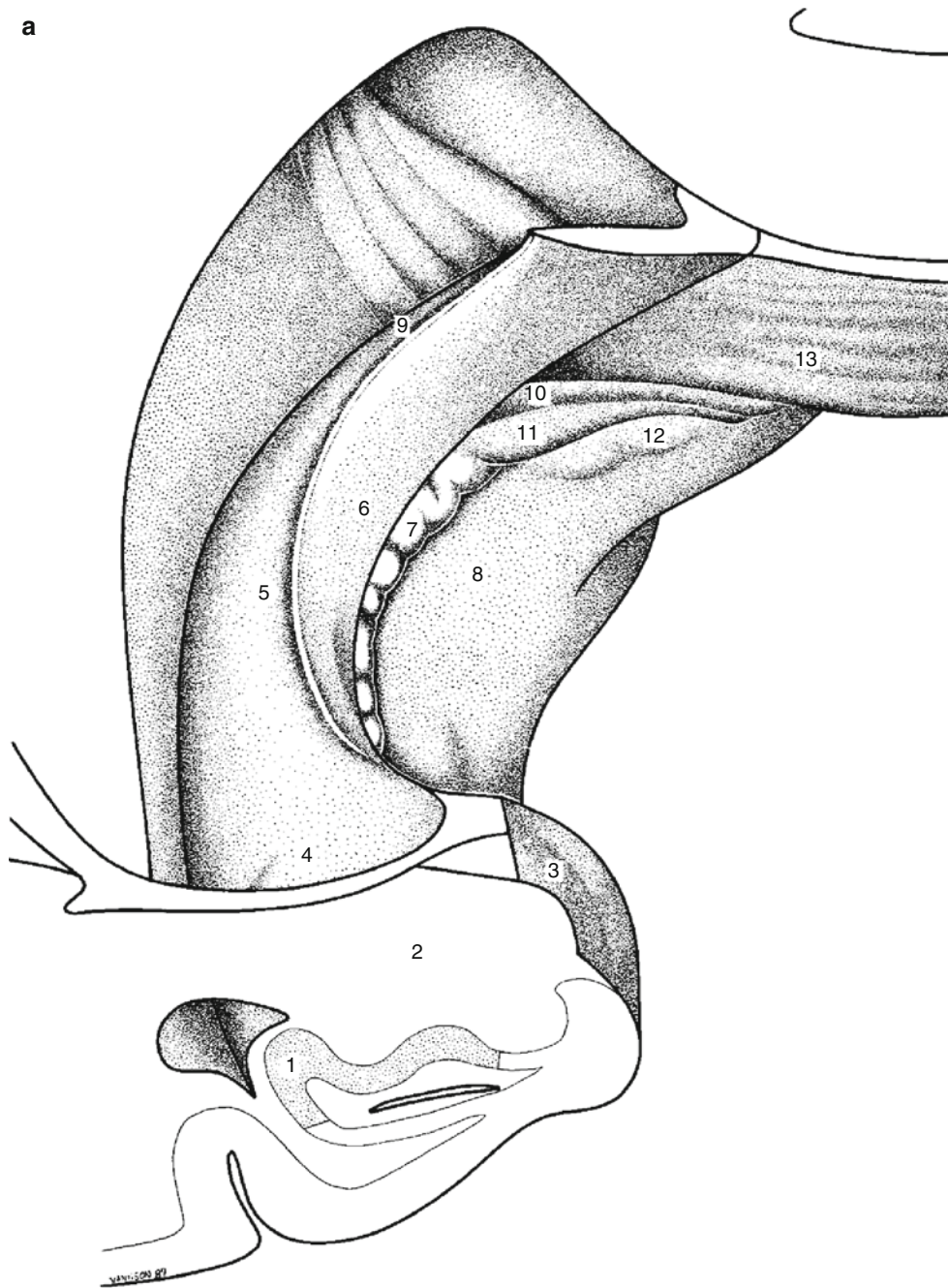


Fig. 7.4 (a) Coronal section of hippocampal head, showing plane of section. 1 *cornu* Ammonis, 2 amygdala, 3 semilunar gyrus, 4 hippocampal head, 5 hippocampal body, 6 fimbria, 7 margo denticulatus, 8 subiculum, 9 hippocampal tail, 10 gyrus fasciolaris, 11 fasciola cinerea, 12 gyri of Andreas Retzius, 13 Splenium (b) explanatory diagram (b') intravascular India ink injection (b'') 9.4T MRI view. 1 *cornu* Ammonis (CA1), 2 subiculum, 3 uncus sulcus, 4 parahippocampal gyrus, 5 uncus notch, 6 ambient gyrus and entorhinal area (see Fig. 7.2), 7 cortical nucleus of amygdala, 7' semilunar gyrus, 7'' semilunar sulcus, 8 entorhinal sulcus, 9 medial nucleus of amygdala, 10 central nucleus amygdala, 11 accessory basal nucleus amygdala, 12 basal nucleus of amygdala, 13 lateral nucleus amygdala, 14 temporal horn of lateral ventricle (c) 3T MRI view. 1 hippocampal head, 1' uncus sulcus, 1'' subiculum, 2 temporal (inferior) horn of the lateral ventricle, 3 lateral nucleus of amygdala, 4 basal nucleus of amygdala,

5 cortical nucleus of amygdala, 6 ambient gyrus, 7 parahippocampal gyrus, 8 collateral sulcus, 9 fusiform gyrus, 10 inferior temporal gyrus, 11 middle temporal gyrus, 11' inferior temporal sulcus, 12 superior temporal gyrus, 12' superior temporal sulcus, 13 temporal stem, 14 lateral fissure, 15 insula, 16 precentral gyrus, 17 middle frontal gyrus, 18 superior frontal gyrus, 19 cingulate sulcus, 20 cingulate gyrus, 21 corpus callosum, 22 fornix, 23 anterior commissure, median part, 24 frontal horn of the lateral ventricle, 25 caudate nucleus, 26 internal capsule, genu, 27 claustrum, 28 putamen, 29 globus pallidus, lateral part, 30 globus pallidus, medial part, 31 anterior commissure, lateral part, 32 optic tract, 33 column of fornix, 34 third ventricle, 35 internal carotid artery, 36 articular disc of the temporomandibular joint, 37 mandibular condyle, 38 basilar artery, 39 posterior cerebral artery, 40 tentorium cerebelli. (d) Coronal head section (posterior view of the section). Bar, 10 mm

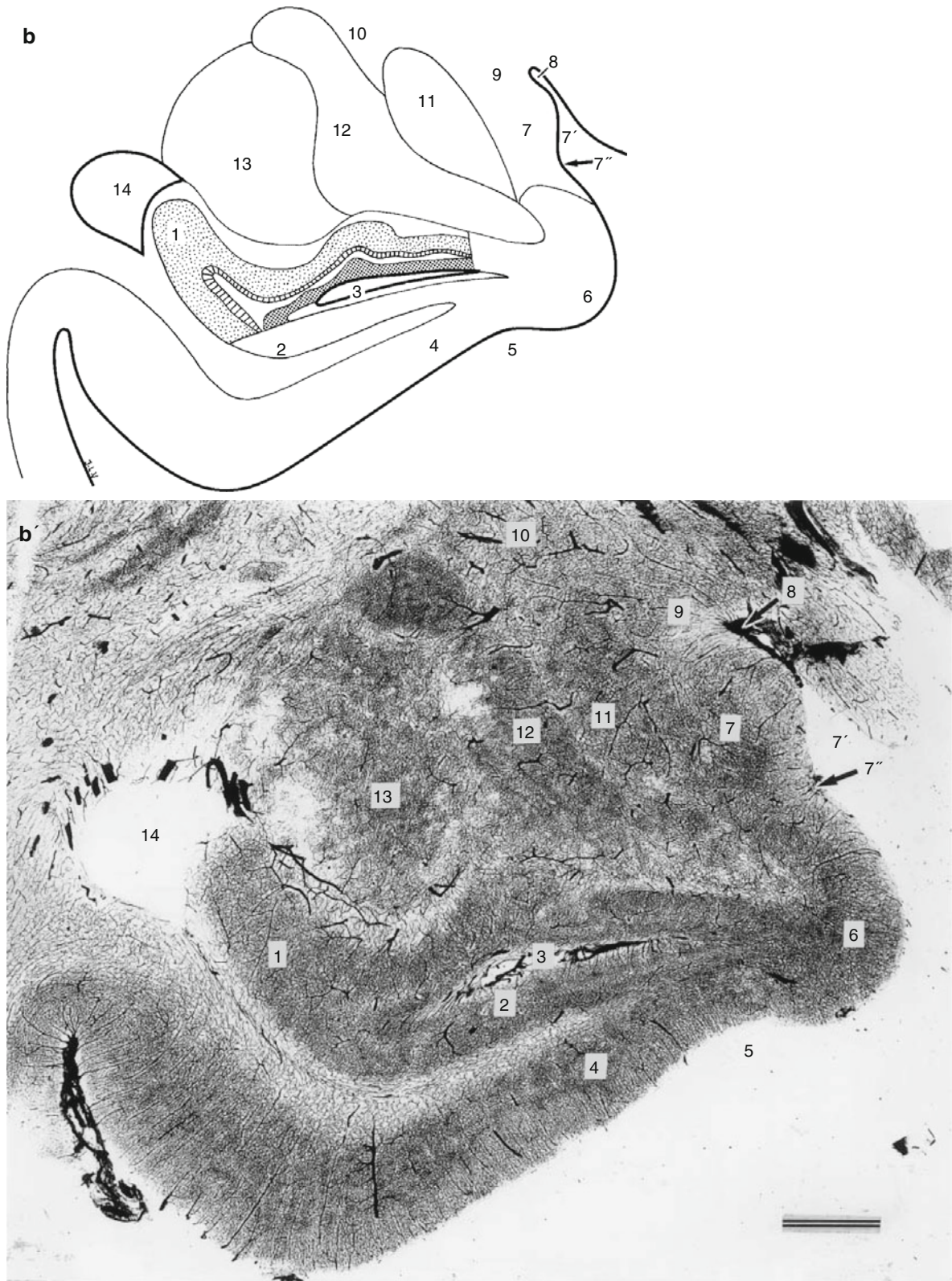


Fig. 7.4 (continued)

Fig. 7.4 (continued)

Fig. 7.4 (continued)

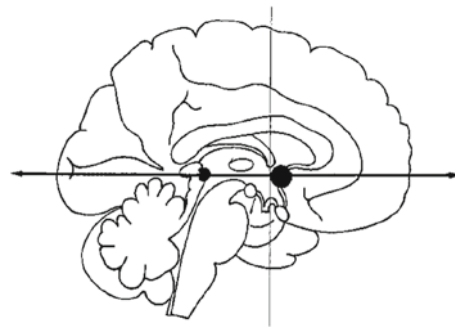
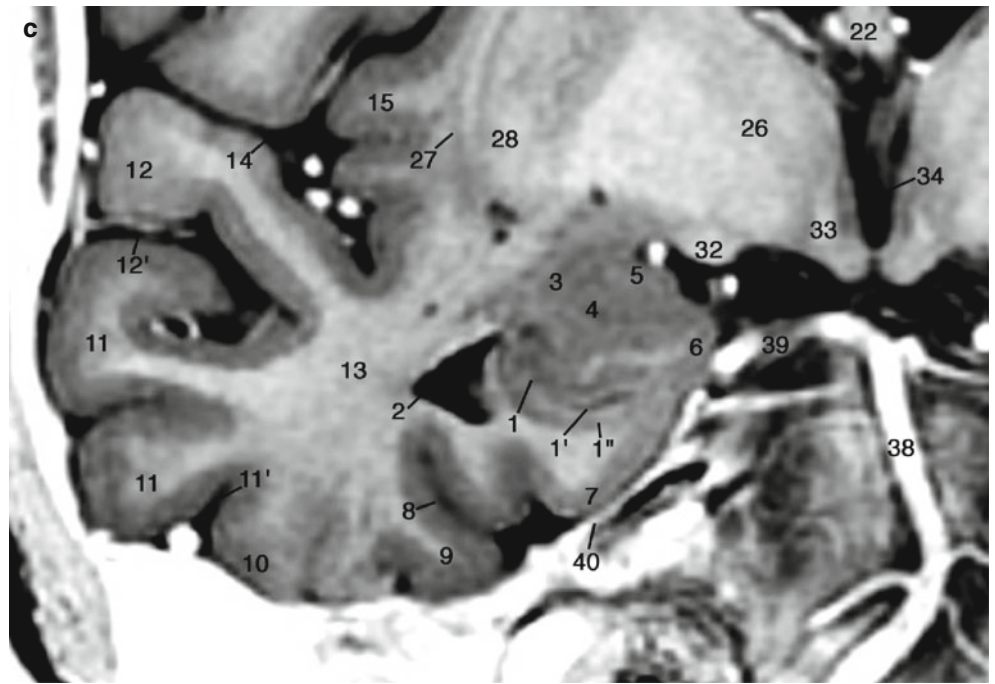
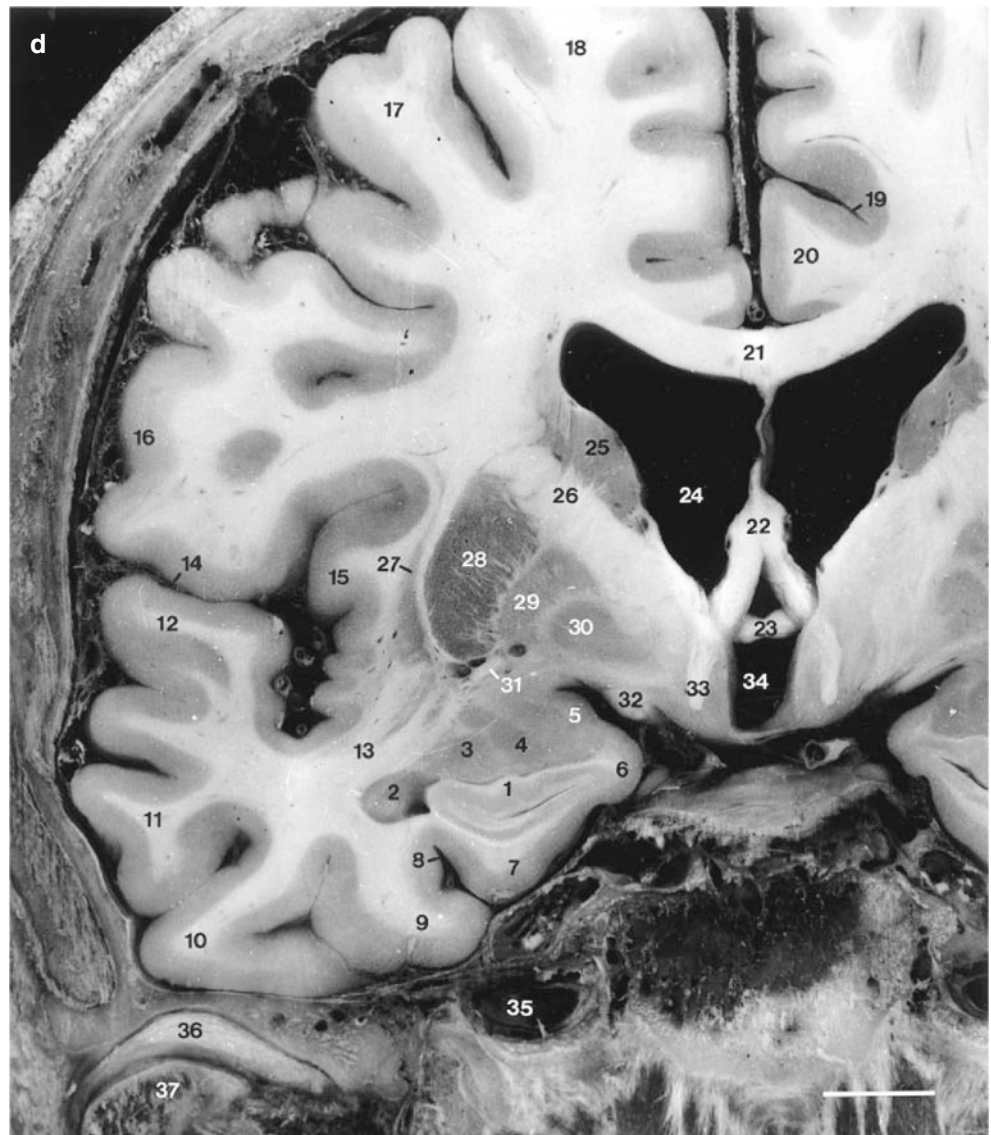


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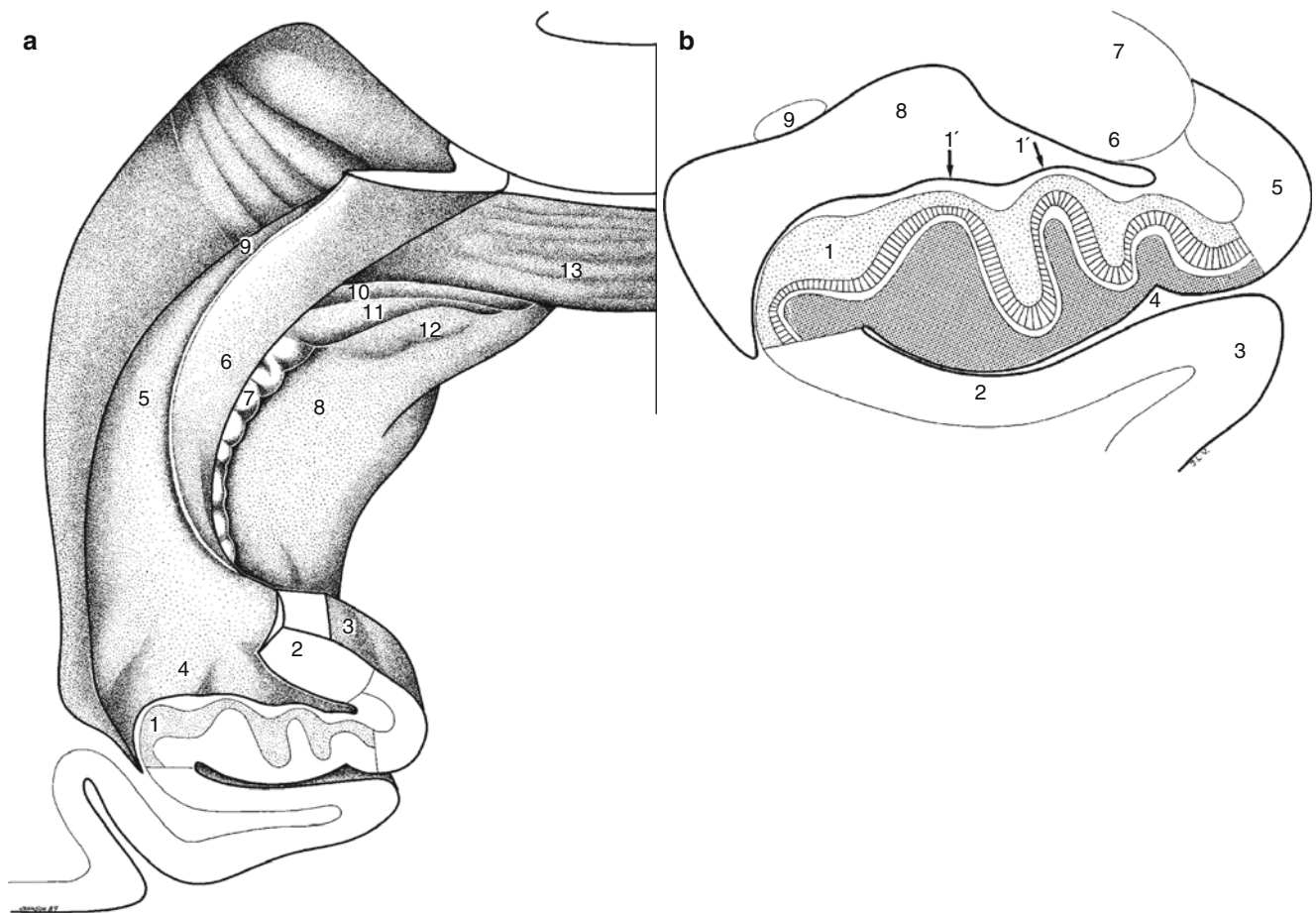


Fig. 7.5 (a) Coronal section of hippocampal head, showing plane of section. 1 cornu Ammonis, 2 amygdala, 3 semilunar gyrus, 4 hippocampal head, 5 hippocampal body, 6 fimbria, 7 margo denticulatus, 8 parahippocampal gyrus, 9 hippocampal tail, 10 gyrus fasciolaris, 11 fasciola cinerea, 12 gyri of Andreas Retzius, 13 splenium. Coronal section of hippocampal head (b) explanatory diagram (b') intravascular India ink injection (b'') 9.4T MRI view 1 cornu Ammonis (CA1), 1' internal digitations (digitationes hippocampi), 2 subiculum, 3 parahippocampal gyrus, 4 uncal sulcus, 5 subiculum in uncinale gyrus (see Fig. 7.2), 6 accessory basal nucleus of amygdala, 7 cortical nucleus of amygdala, 8 temporal horn, 9 tail of caudate nucleus, 10 lateral nucleus of amygdala, 11 basal nucleus of amygdala, 12 cortical nucleus of amygdala. (b') Bar, 2 mm. (b'') 9.4T MRI view. (c) 3T MRI view. 1 hippocampal head, cornu Ammonis, 1' internal digitations (digitationes hippocampi), 2 temporal (inferior) horn of the lateral ventricle, 3 amygdala, 4 uncal

sulcus, 4' uncinale gyrus, 5 parahippocampal gyrus, 6 collateral sulcus, 7 fusiform gyrus, 8 inferior temporal gyrus, 9 middle temporal gyrus, 10 superior temporal sulcus, 11 superior temporal gyrus, 12 temporal stem, 13 lateral fissure, 14 insula, 15 postcentral gyrus, 16 precentral gyrus, 17 middle frontal gyrus, 18 superior frontal gyrus, 19 cingulate sulcus, 20 cingulate gyrus, 21 corpus callosum, 22 fornix, 23 lateral ventricle, 24 caudate nucleus, 25 claustrum, 26 tail of caudate nucleus, 27 putamen, 28 globus pallidus, lateral part, 29 globus pallidus, medial part, 29' striate vessels, 30 internal capsule, posterior limb, 31 ventral anterior thalamic nucleus, 32 third ventricle, 33 optic tract, 34 mammillary body, 35 basilar artery, 36 pons, 37 internal carotid artery, 38 temporomandibular joint, 39 posterior cerebral artery, 40 tentorium cerebelli. (d) Coronal head section. Anterior view of the section. Bar, 10 mm

Fig. 7.5 (continued)

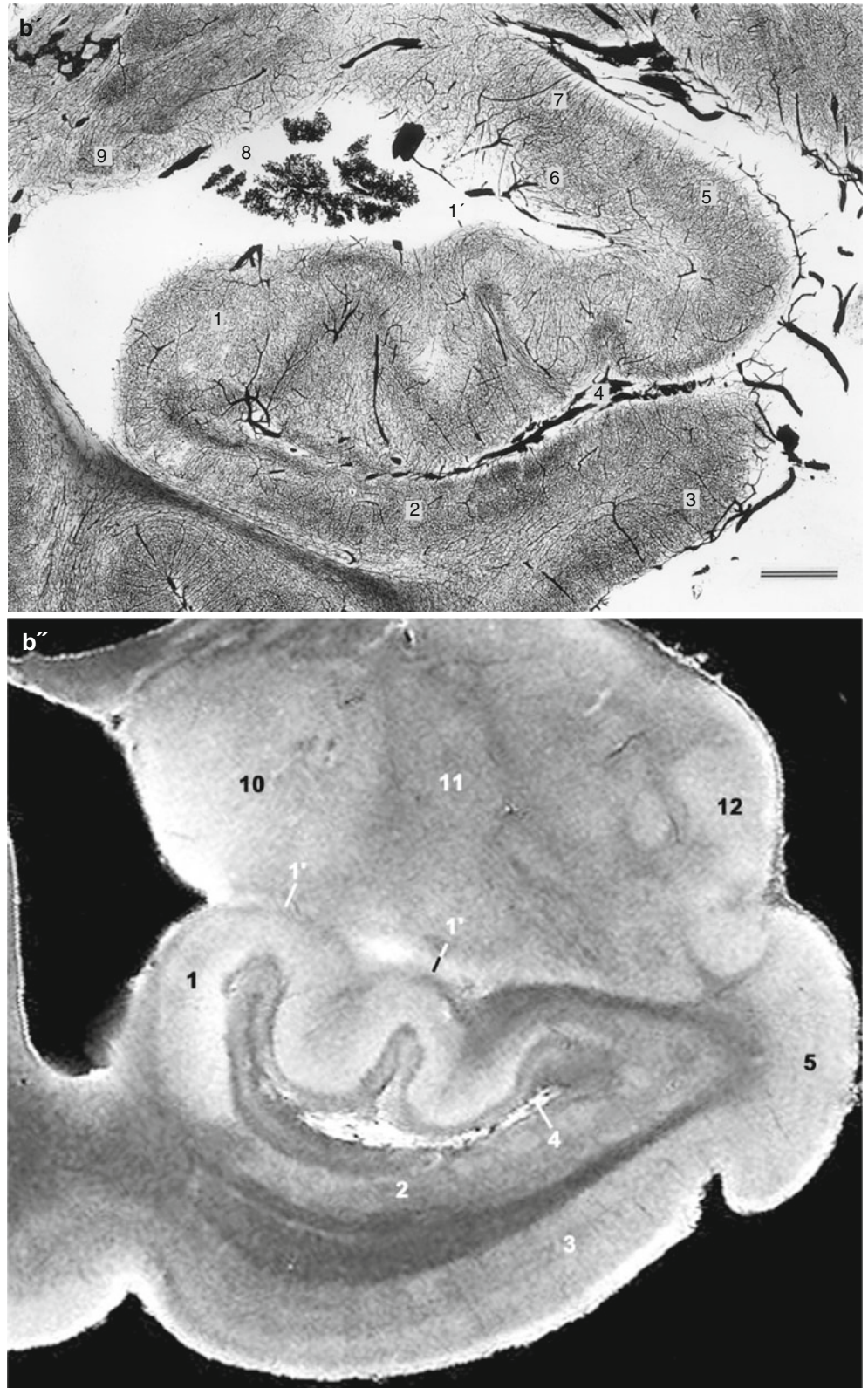


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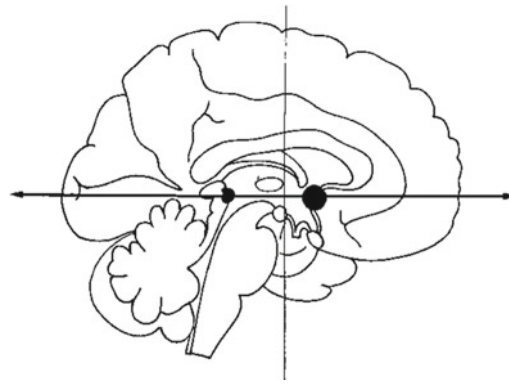
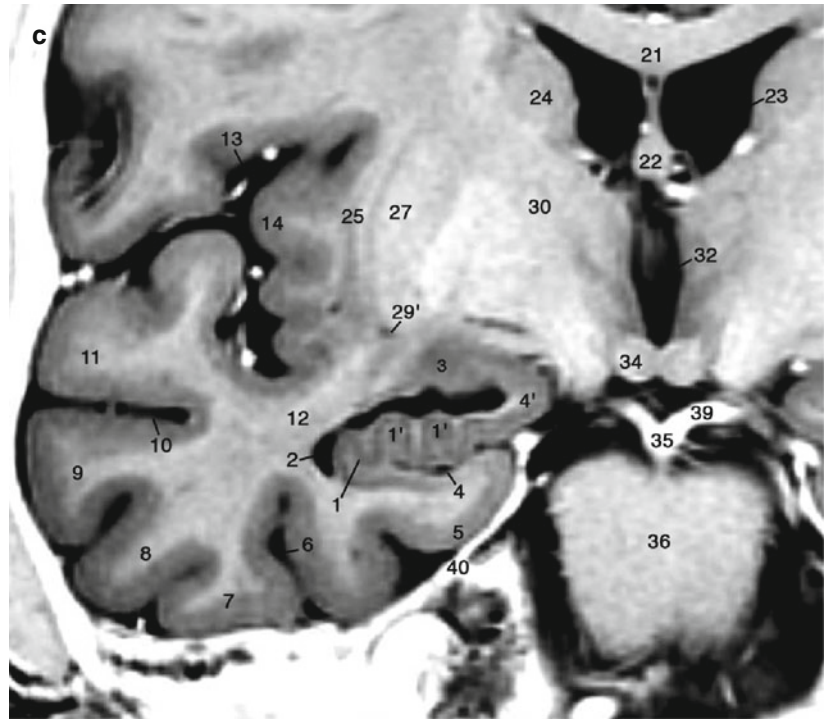
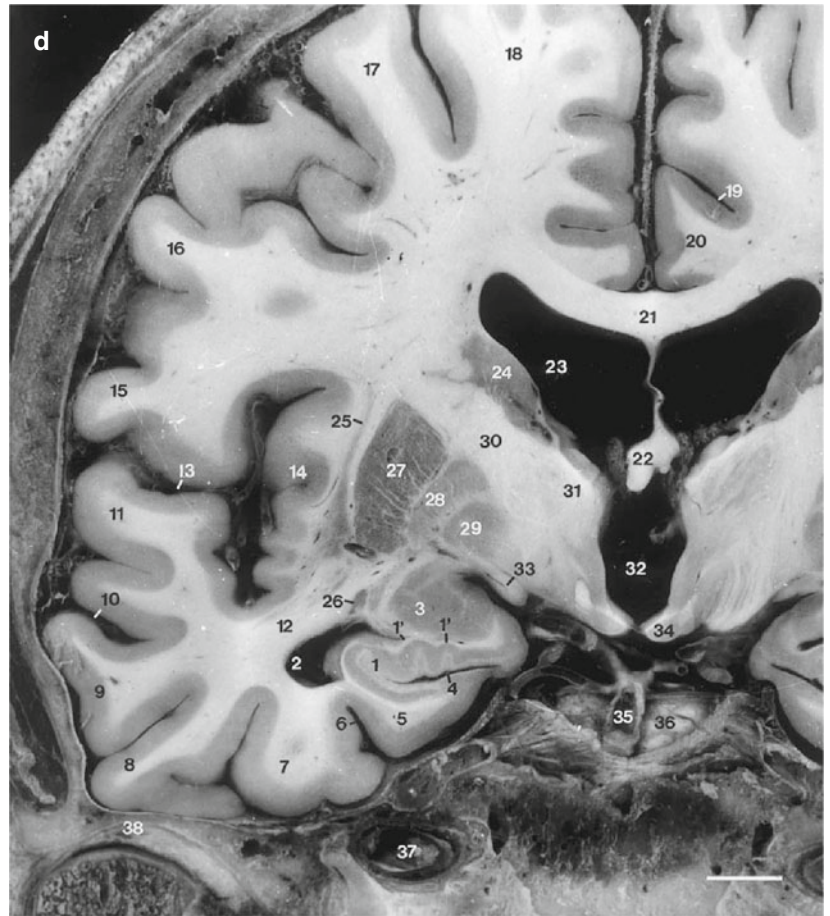


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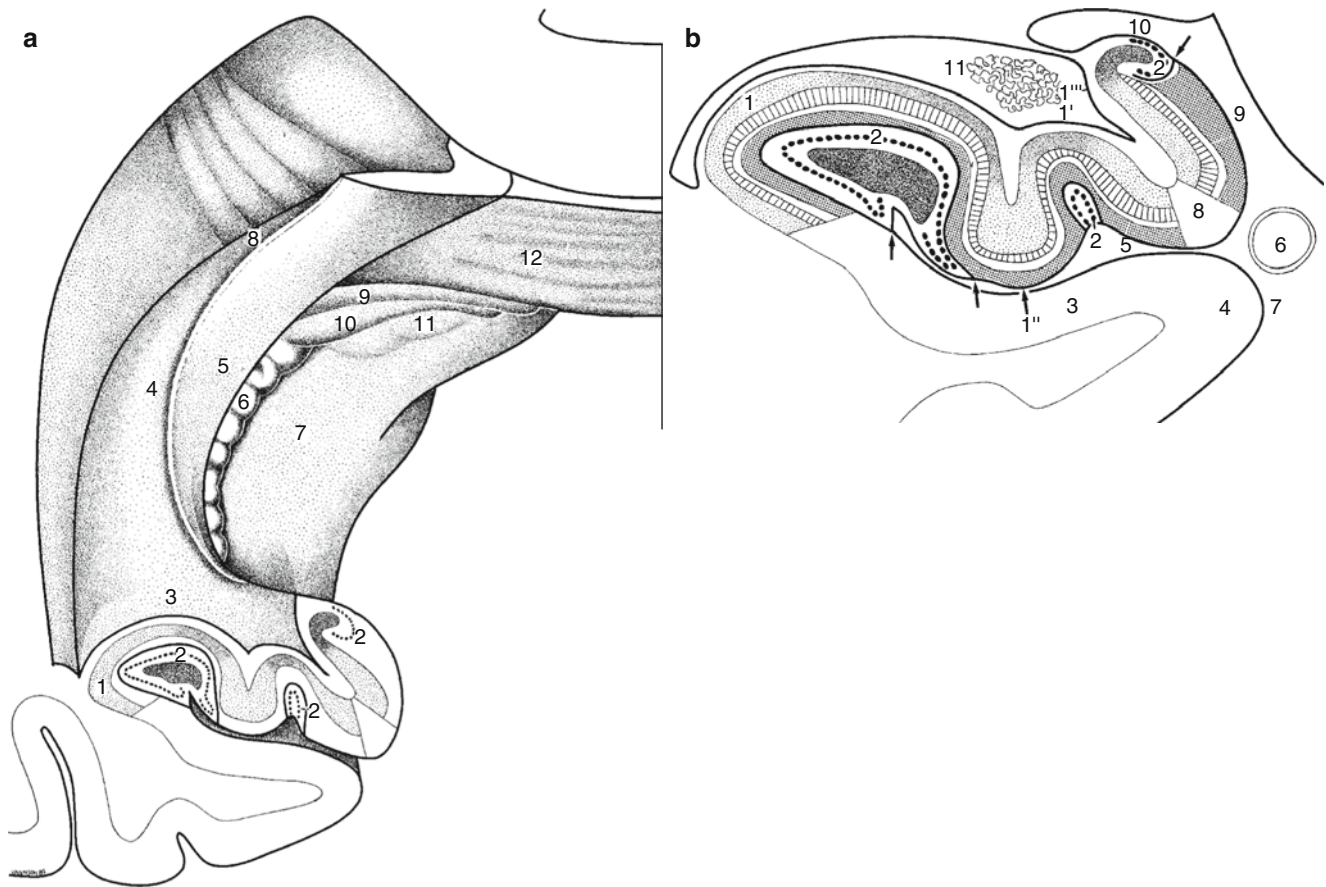


Fig. 7.6 (a) Coronal section of hippocampal head (b) explanatory diagram (b') intravascular India ink injection (b'') 9.4T MRI view. Note the end of stratum radiatum (*asterisk*) and the beginning of subiculum. *Arrows* indicate the superficial hippocampal sulcus. (a) Coronal section of hippocampal head, showing plane of section 1 cornu Ammonis, 2 gyrus dentatus, 3 hippocampal head, 4 hippocampal body, 5 fimbria, 6 margo denticulatus, 7 parahippocampal gyrus, 8 hippocampal tail, 9 gyrus fasciolaris, 10 fasciola cinerea, 11 gyri of Andreas Retzius, 12 splenium. (b) 1 cornu Ammonis 1 cornu Ammonis (CA1–CA4), 1' internal digitations (digitationes hippocampi), 1'' external digitations, 1''' vertical digitation, 2 gyrus dentatus, 3 subiculum, 4 parahippocampal gyrus, 5 uncal sulcus, 6 posterior cerebral artery (P2 segment), 7 crural cistern, 8 subiculum in the medial surface of uncus (see Fig. 7.2), 9 transverse fissure (lateral part), 10 band of Giacomini, 11 temporal horn of the lateral ventricle, 12 lateral nucleus of amygdala, 13 basal nucleus of amygdala, 14 cortical nucleus of amygdala. (b') Bar 2 mm. (b'') 9.4T MRI view. (c) 3T MRI view. 1 hippocampal head, cornu Ammonis, 1' internal digitations (digitationes hippocampi), 1'' external

digitations, 1''' vertical digitation, 2 hippocampal head, gyrus dentatus, 3 subiculum, 4 uncal sulcus, 5 parahippocampal gyrus, 5' collateral sulcus, 6 temporal (inferior) horn of the lateral ventricle, 7 fusiform gyrus, 8 inferior temporal gyrus, 9 middle temporal gyrus, 10 superior temporal sulcus, 11 superior temporal gyrus, 12 temporal stem, 13 lateral fissure, 14 insula, 15 postcentral gyrus, 16 central sulcus, 17 precentral gyrus, 18 middle frontal gyrus, 19 superior frontal gyrus, 20 cingulate sulcus, 21 cingulate gyrus, 22 corpus callosum, 23 fornix, 24 lateral ventricle, 25 caudate nucleus, 26 claustrum, 27 tail of caudate nucleus, 28 putamen, 29 globus pallidus, lateral part, 30 globus pallidus, medial part, 31 internal capsule, posterior limb, 32 optic tract, 33 anterior thalamic nucleus, 34 ventral lateral thalamic nucleus, 35 dorsomedial thalamic nucleus, 36 mamillothalamic tract, 37 subthalamic nucleus, 38 substantia nigra, 39 crus cerebri, 40 third ventricle, 41 mamillary body, 42 posterior cerebral artery, 43 pons, 44 tentorium cerebelli, 45 internal carotid artery, 46 temporomandibular joint. (d) Coronal head section. Anterior view of the section. Bar, 10 mm

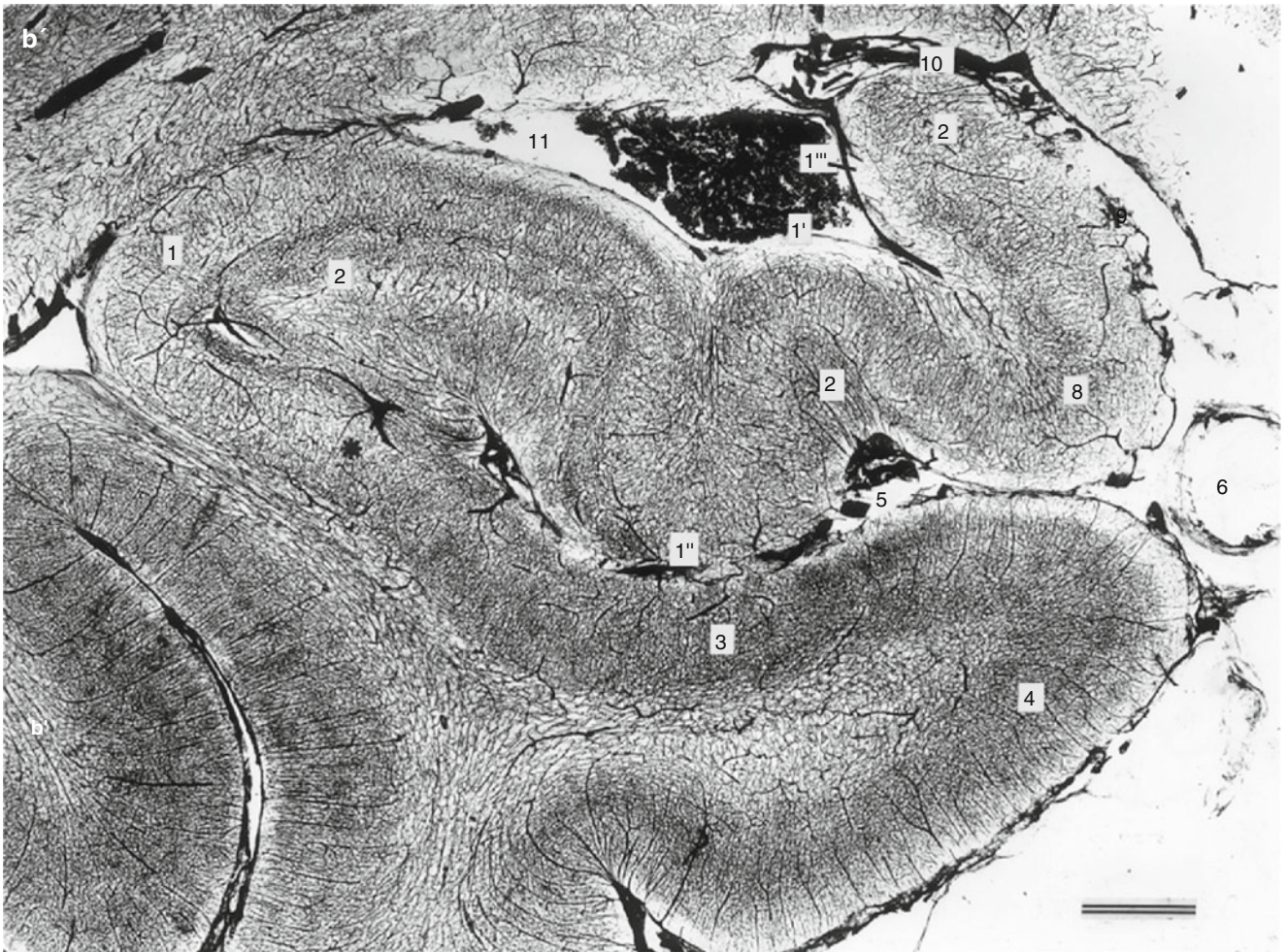


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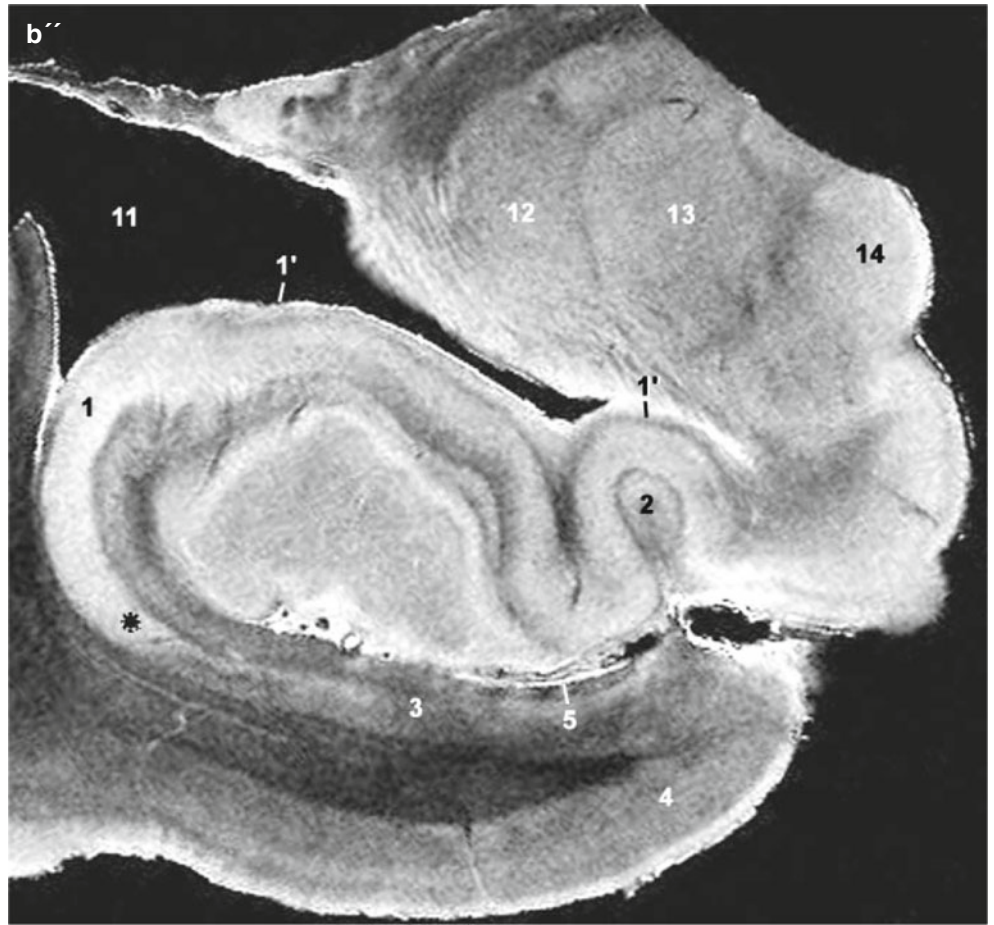


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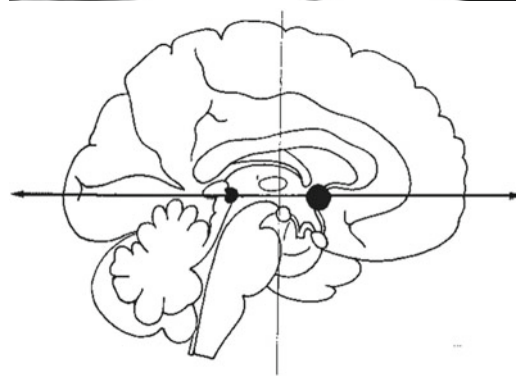
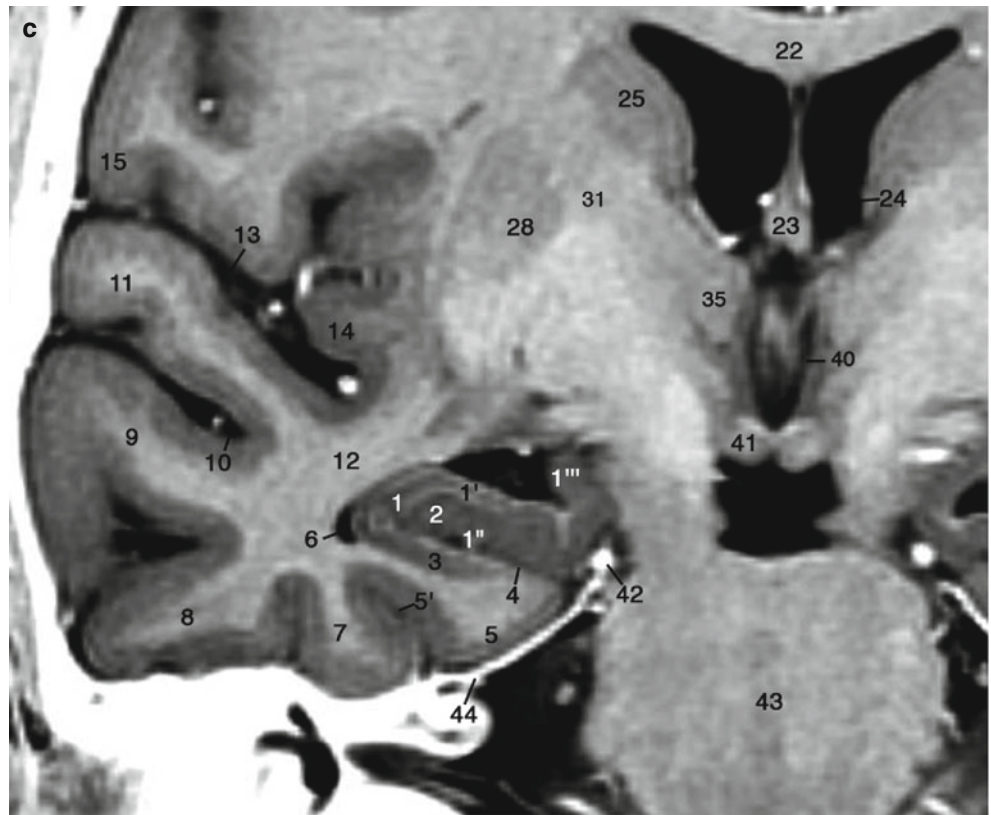
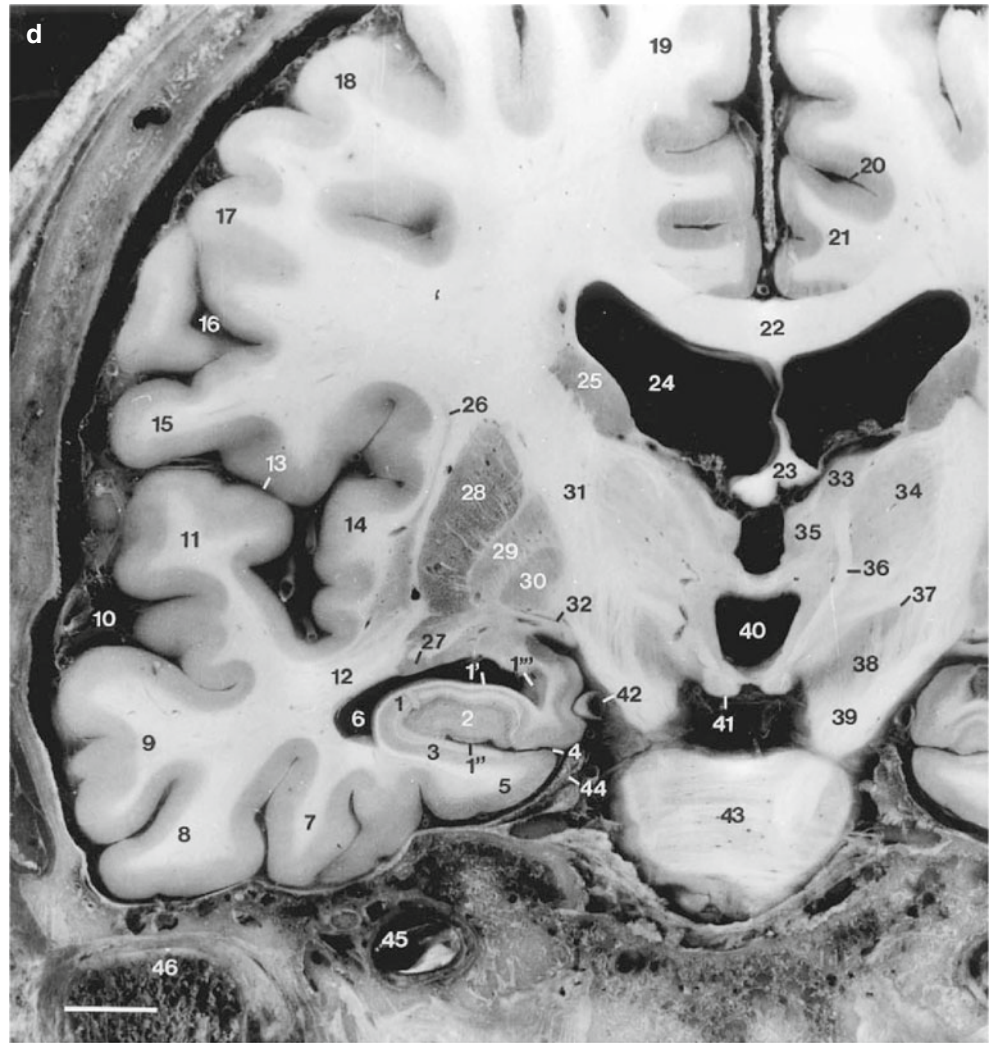


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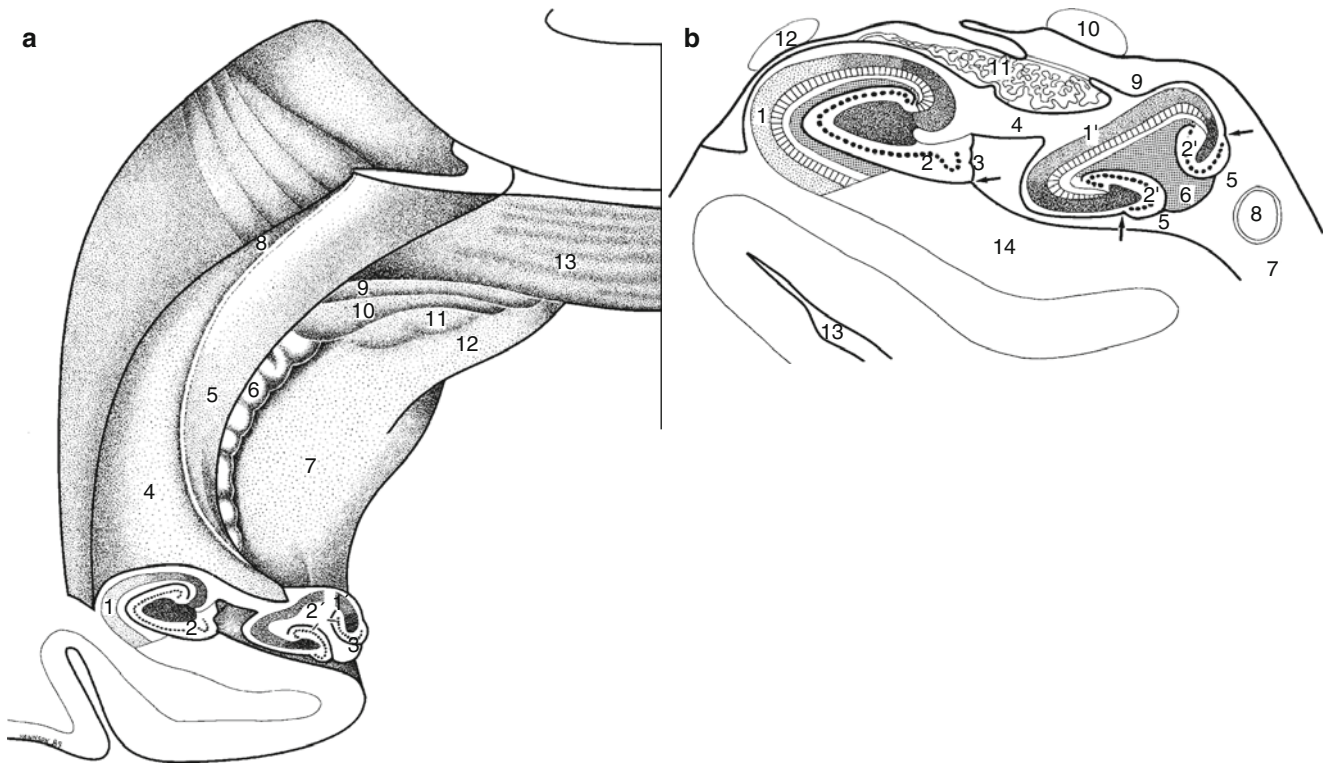


Fig. 7.7 (a) Coronal section of hippocampal body and head (uncal apex), showing plane of section. 1 cornu Ammonis in hippocampal body, 1' cornu Ammonis in hippocampal head, 2 gyrus dentatus in hippocampal body, 2' gyrus dentatus in hippocampal head (uncal apex), 3 uncal apex, 4 hippocampal body, 5 fimbria, 6 margo denticulatus, 7 parahippocampal gyrus, 8 hippocampal tail, 9 gyrus fasciolaris, 10 fasciola cinerea, 11 gyri of Andreas Retzius, 12 isthmus, 13 splenium. (b) Coronal section of hippocampal body and head (b') explanatory diagram (b'') intravascular India ink injection (b'') 9.4T MRI view. Arrows indicate the superficial hippocampal sulcus. 1 cornu Ammonis (CA1–CA4) in hippocampal body, 1' cornu Ammonis (CA3, CA4) in hippocampal head, 2 gyrus dentatus in hippocampal body, 2' gyrus dentatus in hippocampal head, 3 margo denticulatus, 4 fimbria, 5 band of Giacomini, 6 uncal apex, 7 crural cistern, 8 posterior cerebral artery, 9 transverse fissure (lateral part), 10 optic tract and lateral geniculate body, 11 choroid plexuses and temporal horn, 12 caudate nucleus, 13 collateral sulcus, 14 subiculum. (b') Bar 2 mm. (b'') 9.4T MRI view. (c) 3TMRI view.

1 hippocampal body, cornu Ammonis, 2 hippocampal body, gyrus dentatus, 3 fimbria, 4 hippocampal head, uncal apex, 5 uncal sulcus, 6 subiculum, 7 parahippocampal gyrus, 8 collateral sulcus, 9 temporal (inferior) horn of the lateral ventricle, 10 fusiform gyrus, 11 inferior temporal gyrus, 12 middle temporal gyrus, 13 superior temporal sulcus, 14 temporal stem, 15 superior temporal gyrus, 16 lateral fissure, 17 insula, 18 postcentral gyrus, 19 central sulcus, 20 precentral gyrus, 21 centrum ovale, 22 cingulate sulcus, 23 cingulate gyrus, 24 corpus callosum, 25 fornix, 26 lateral ventricle, 27 caudate nucleus, 28 internal capsule, posterior limb, 29 putamen, 30 claustrum, 31 tail of caudate nucleus, 32 optic tract, 33 globus pallidus, lateral part, 34 globus pallidus, medial part, 35 ventral lateral thalamic nucleus, 36 anterior thalamic nucleus, 37 dorsomedial thalamic nucleus, 38 third ventricle, 39 red nucleus, 40 subthalamic nucleus, 41 substantia nigra, 42 crus cerebri, 43 pons, 44 tentorium cerebelli, 45 internal carotid artery, * vestigial hippocampal sulcus. (d) Head section, anterior view of the section. Bar, 10 mm

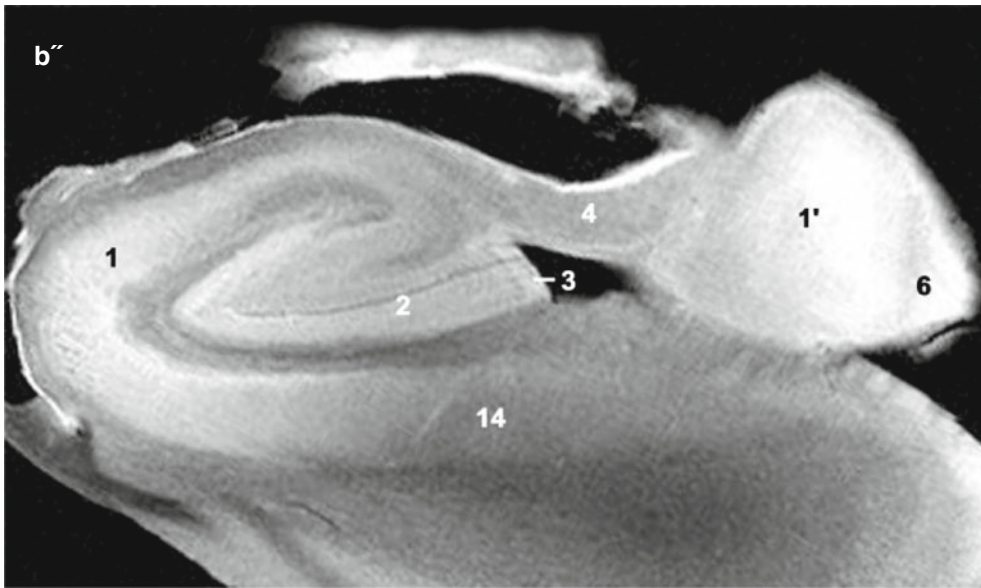


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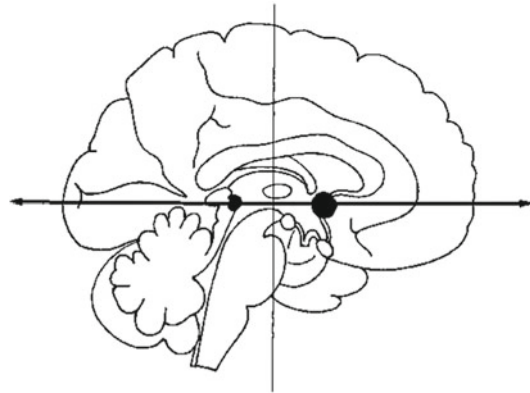
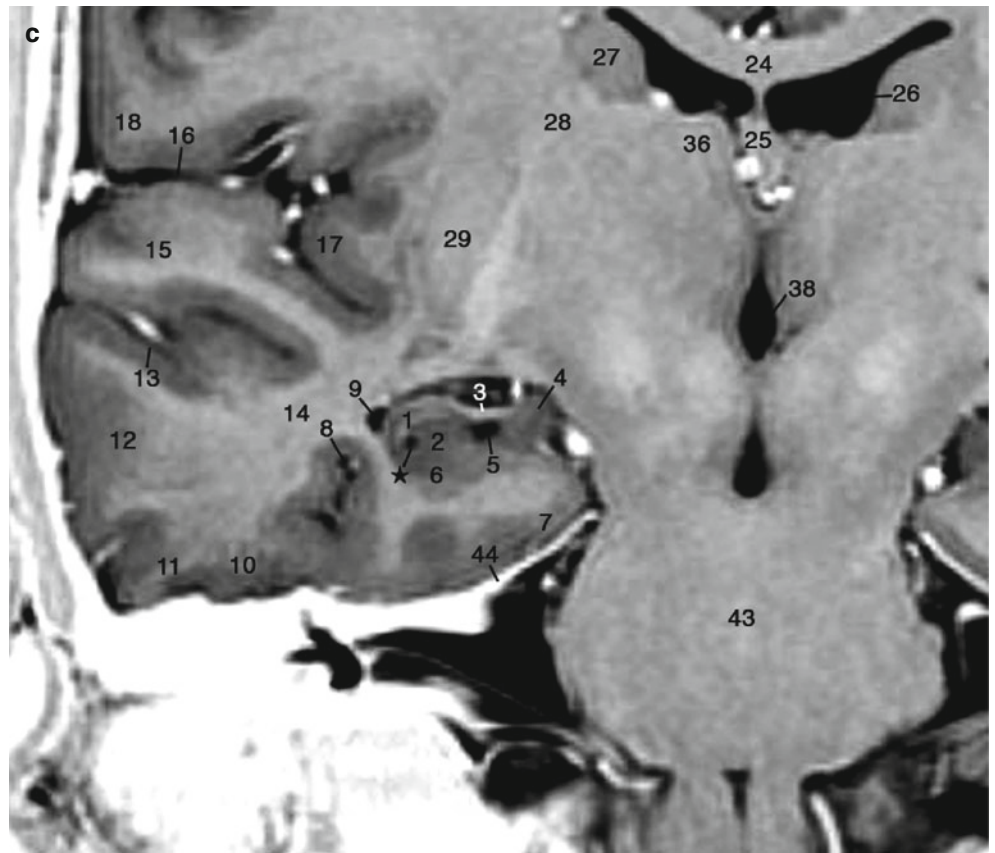
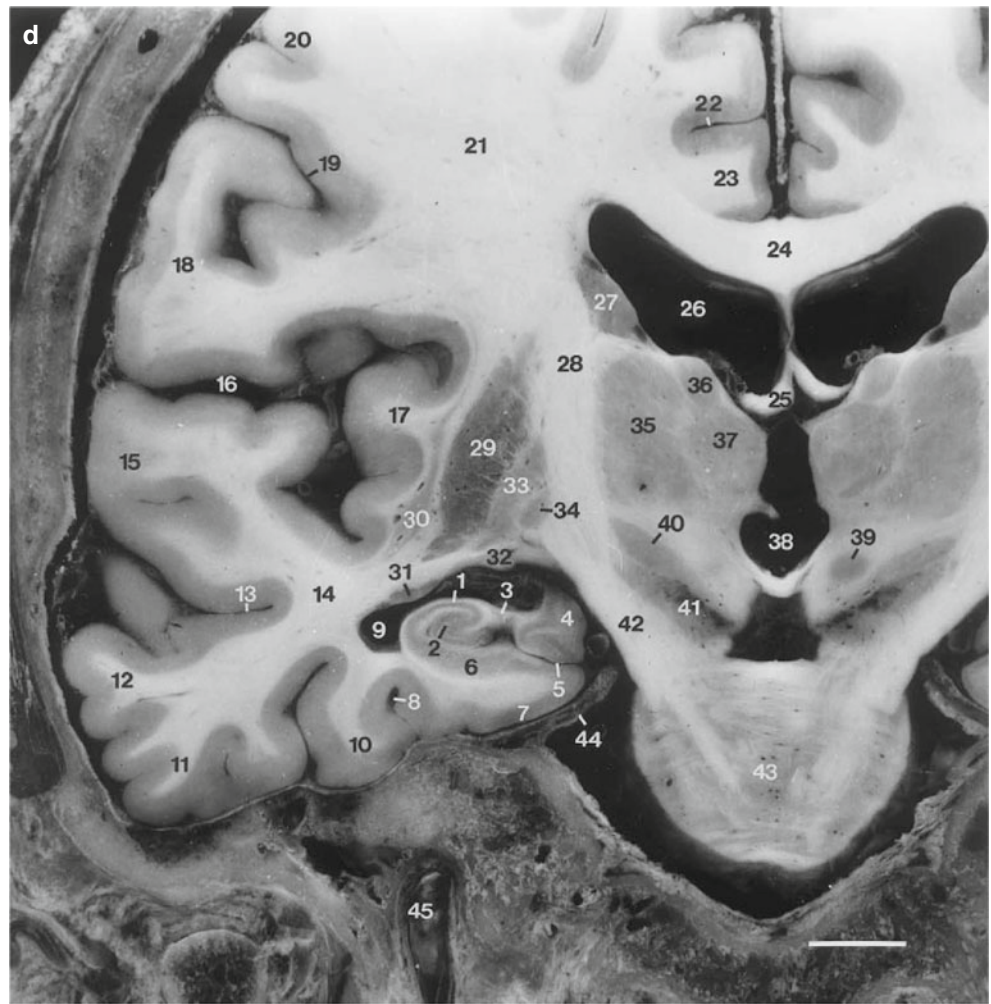


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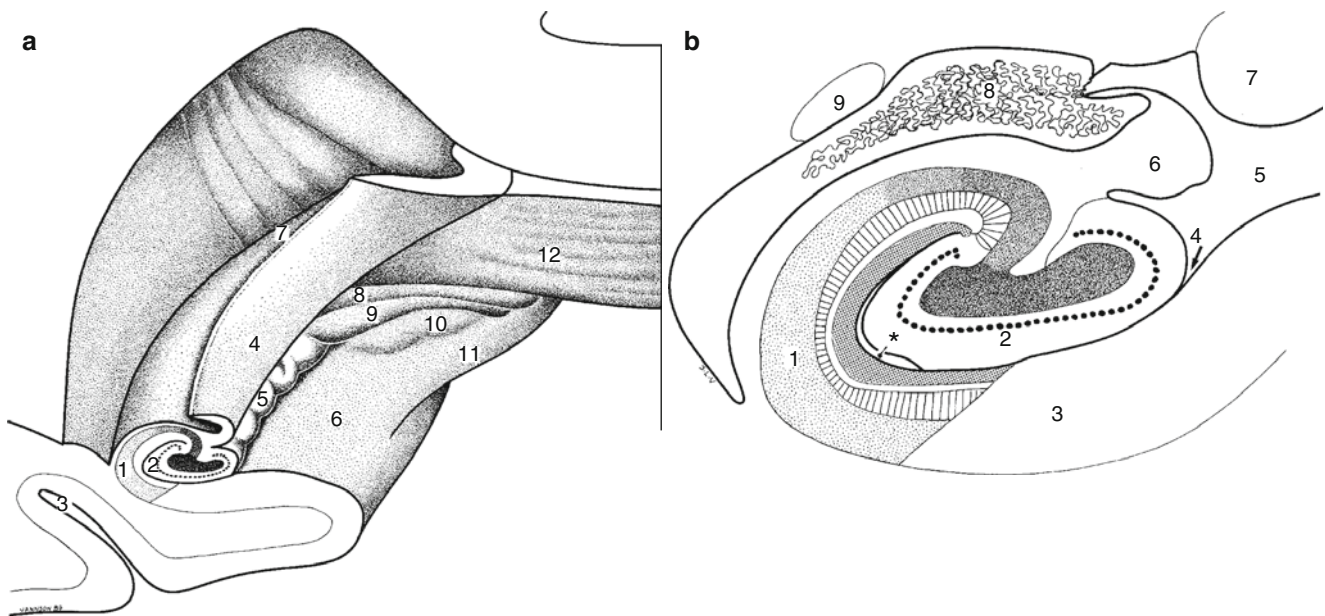


Fig. 7.8 (a) Coronal section of hippocampal body, showing plane of section. 1 cornu Ammonis, 2 gyrus dentatus, 3 collateral sulcus, 4 fimbria, 5 margo denticulatus, 6 parahippocampal gyrus, 7 hippocampal tail, 8 gyrus fasciolaris, 9 fasciola cinerea, 10 gyri of Andreas Retzius, 11 isthmus, 12 splenium. Coronal section of the hippocampal body. (b) Explanatory diagram, (b') intravascular India ink injection, (b'') 9.4T MRI view. *Arrow* indicates the superficial hippocampal sulcus, and *asterisk* shows a residual cavity in the vestigial hippocampal sulcus. 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, 3 subiculum, 4 margo denticulatus, 5 lateral part of the transverse fissure, 6 fimbria, 7 lateral geniculate body, 8 choroid plexuses and temporal horn of lateral ventricle, 9 caudate nucleus. (b') Bar 1.2 mm. (b'') 9.4T MRI view. (c) 3T MRI view. 1 hippocampal body, cornu Ammonis: 1' CA1, 1'' CA2, 1''' CA3, 2 hippocampal body, gyrus dentatus, and CA4, 2' fimbria, 2'' choroid plexuses, 3 subiculum, 4 parahippocampal gyrus, 5 temporal (inferior) horn of the lateral ventricle, 5' alveus, 6 collateral sulcus, 7 fusiform gyrus, 7' lateral occipitotemporal sulcus, 8 inferior

temporal gyrus, 9 middle temporal gyrus, 10 superior temporal sulcus, 11 superior temporal gyrus, 12 transverse temporal gyrus, 13 temporal stem, 14 insula, 15 lateral fissure, 16 postcentral gyrus, 17 central sulcus, 18 precentral gyrus, 19 superior frontal gyrus, 20 cingulate sulcus, 21 cingulate gyrus, 22 corpus callosum, 23 fornix, 24 lateral ventricle, 25 caudate nucleus, 26 pontes grisei caudatolenticulares, 27 tail of caudate nucleus, 28 internal capsule, retrolentiform part, 29 lateral posterior thalamic nucleus, 30 lateral dorsal thalamic nucleus, 31 dorsomedial thalamic nucleus, 32 centromedian thalamic nucleus, 33 ventral posterolateral thalamic nucleus, 34 lateral geniculate body, 35 third ventricle, 36 decussation of superior cerebellar peduncles, 37 substantia nigra, 38 crus cerebri, 39 ambient cistern and posterior cerebral artery, 40 tentorium cerebelli, 41 cerebellum, 42 pons, 43 medulla, pyramid, 44 internal ear, 45 middle ear, 46 external acoustic meatus, * vestigial hippocampal sulcus. (d) Head section, posterior view of the section. Bar, 10 mm

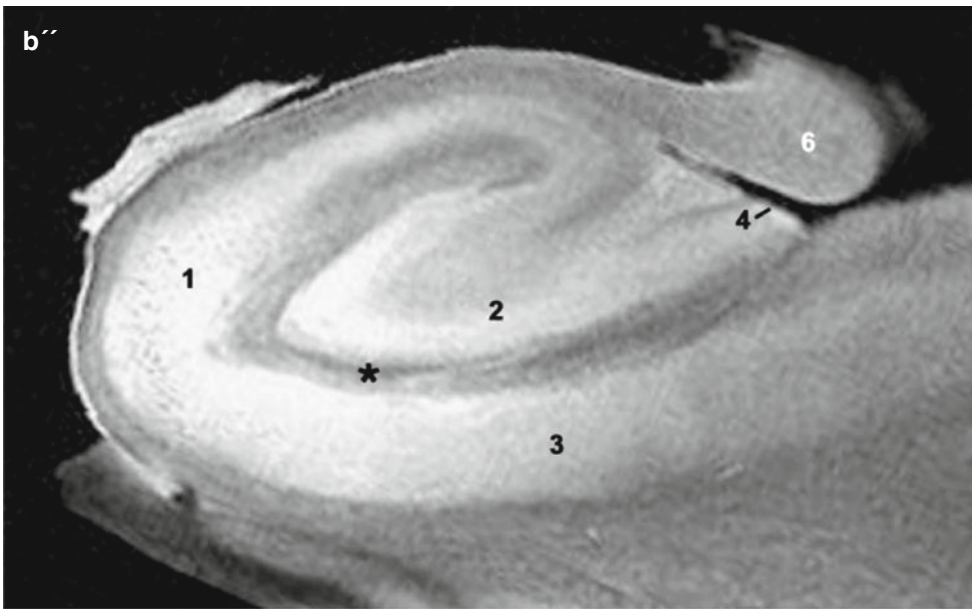


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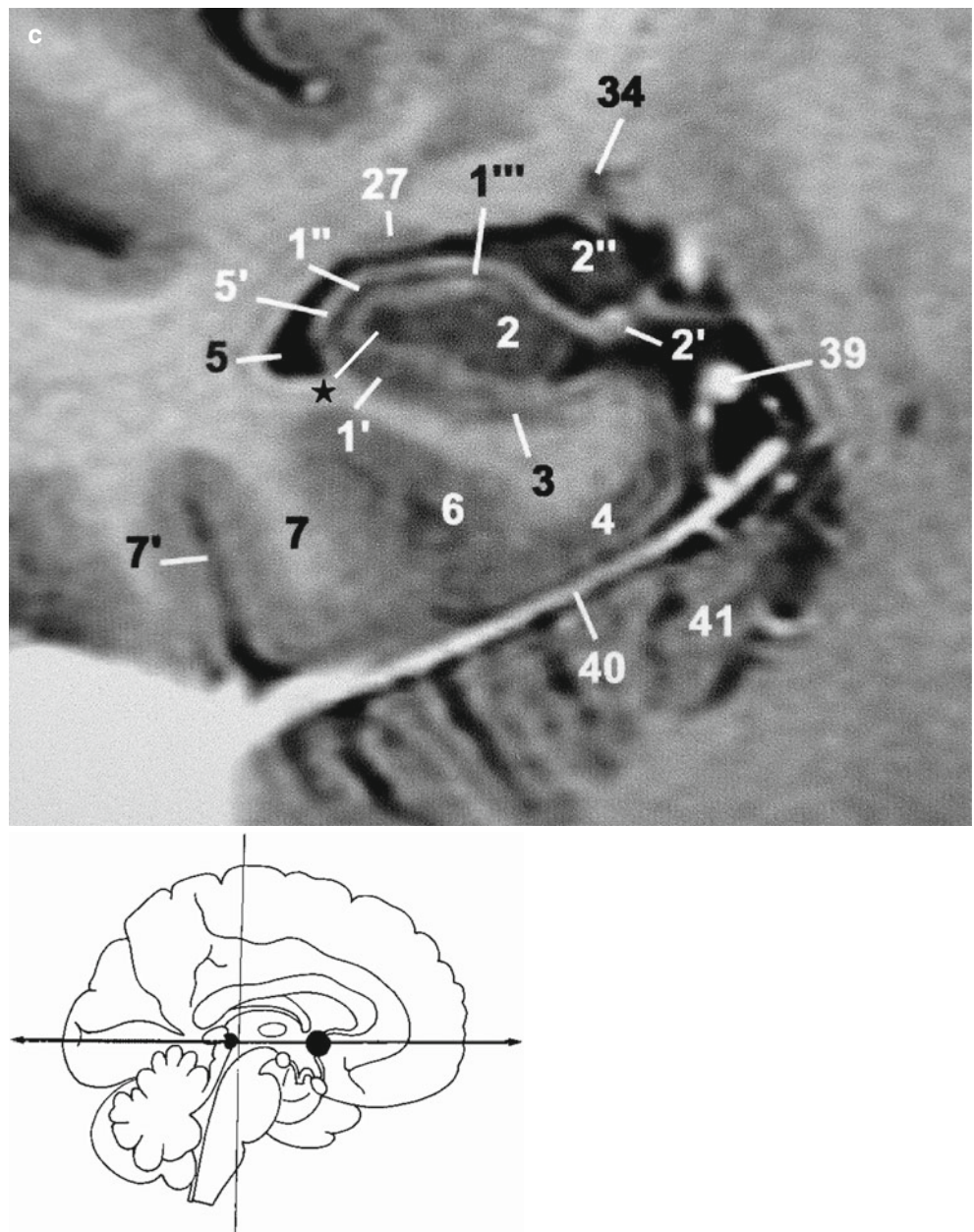
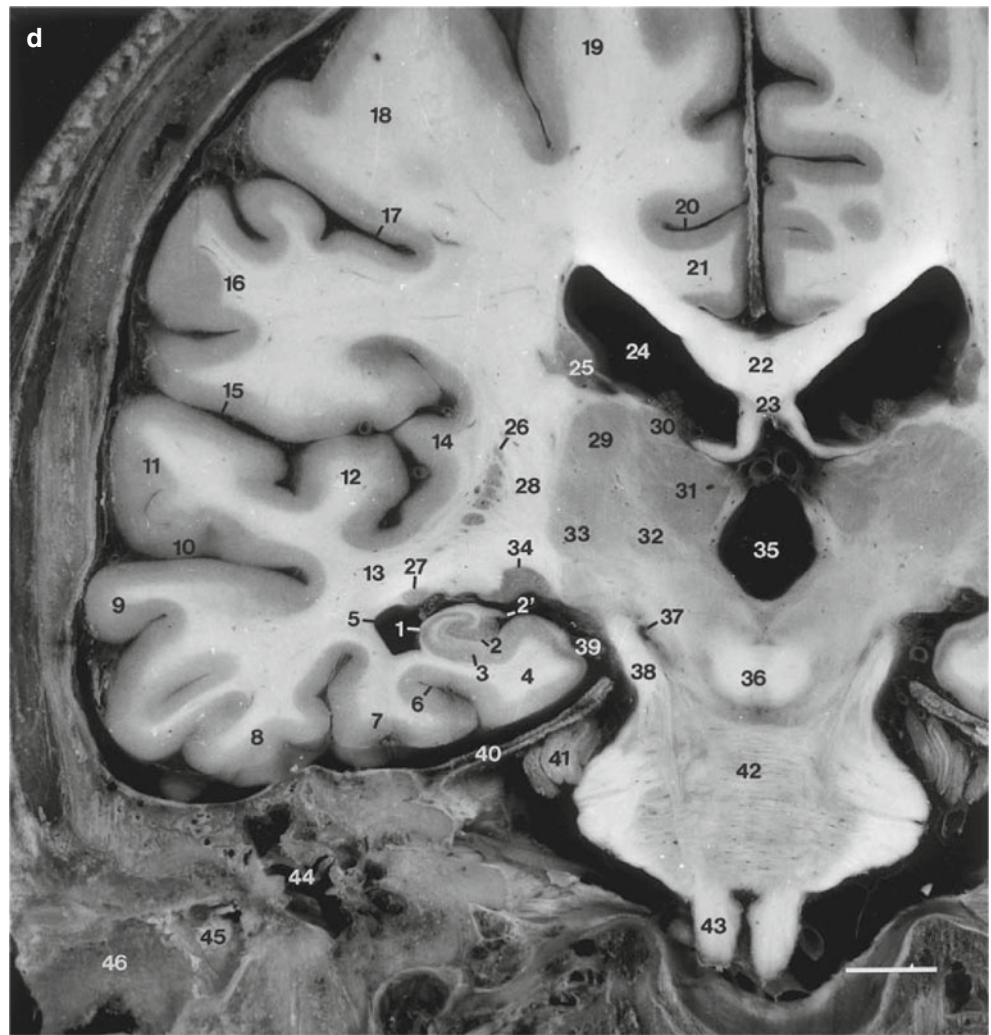


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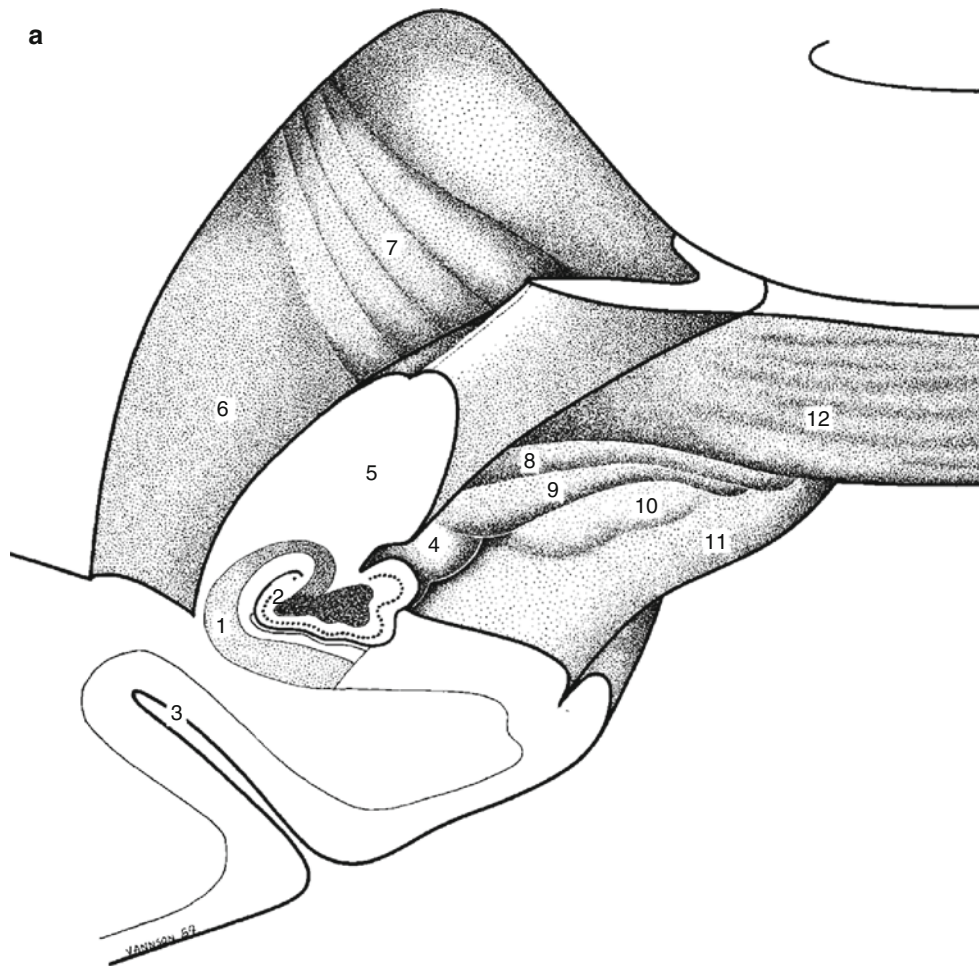


Fig. 7.9 (a) Coronal section of initial segment of the hippocampal tail, showing plane of section. 1 cornu Ammonis, 2 gyrus dentatus, 3 collateral sulcus, 4 margo denticulatus, 5 crus of fornix, 6 collateral trigone, 7 calcar avis, 8 gyrus fasciolaris, 9 fasciola cinerea, 10 gyrus of Andreas Retzius, 11 isthmus, 12 splenium. (b) Coronal section of the hippocampal tail. Intravascular India ink injection with explanatory diagram. Arrow indicates the superficial hippocampal sulcus. Bar, 1.3 mm. 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, stratum moleculare, 3 vestigial hippocampal sulcus, 4 subiculum, 5 lateral part of the transverse fissure, 6 margo denticulatus, 7 crus of fornix, 8 temporal horn of lateral ventricle. (c) 3T MRI view. 1 hippocampal tail, cornu Ammonis, 1' alveus, 2 hippocampal tail, gyrus dentatus, 3 fimbria, 3' margo denticulatus, 4 gyrus of Andreas Retzius, 5 subiculum, 6 parahippocampal gyrus, 7 collateral sulcus, 8 temporal (inferior) horn of the lateral ventricle, 9 fusiform gyrus,

10 inferior temporal gyrus, 10' lateral occipitotemporal sulcus, 11 middle temporal gyrus, 12 superior temporal sulcus, 13 superior temporal gyrus, 13' transverse temporal gyrus, 14 lateral fissure, 15 supramarginal gyrus, 16 postcentral gyrus, 17 central sulcus, 18 precentral gyrus, 19 superior frontal gyrus, 20 cingulate sulcus, 21 cingulate gyrus, 22 splenium of corpus callosum, 23 lateral ventricle, 24 caudate nucleus, 25 crus of fornix, 26 pulvinar, 27 tail of caudate nucleus, 28 wing of ambient cistern (lateral part of the transverse fissure), 29 ambient cistern, 30 pineal gland and quadrigeminal cistern, 31 superior colliculus, 32 inferior colliculus, 33 cerebral aqueduct, 34 brachium conjunctivum (superior cerebellar peduncle), 35 brachium pontis, 36 quadrangular lobule, 37 tentorium cerebelli, 38 flocculus, 39 medulla, 40 vertebral artery, 41 sigmoid sinus, 42 mastoid process, 43 mastoid air cells, * vestigial hippocampal sulcus. (d) Head section, posterior view of the section. Bar, 10 mm

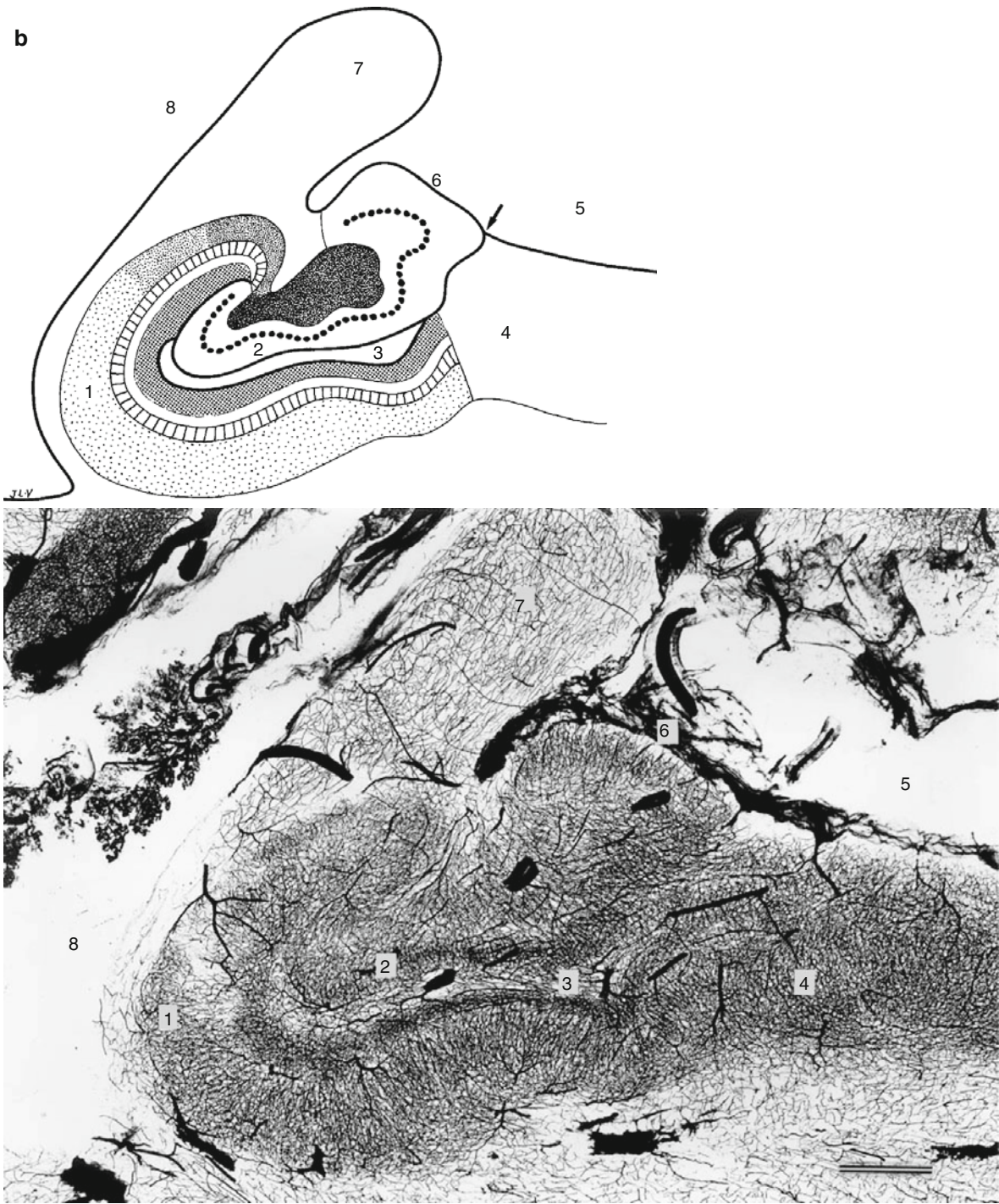


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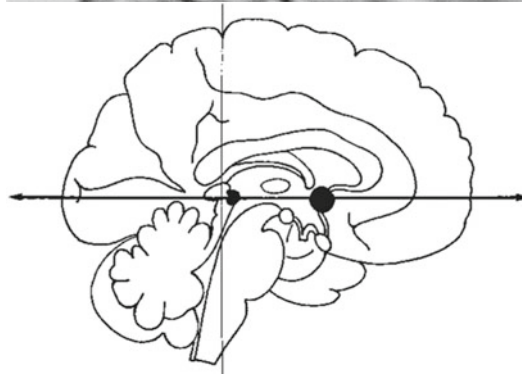
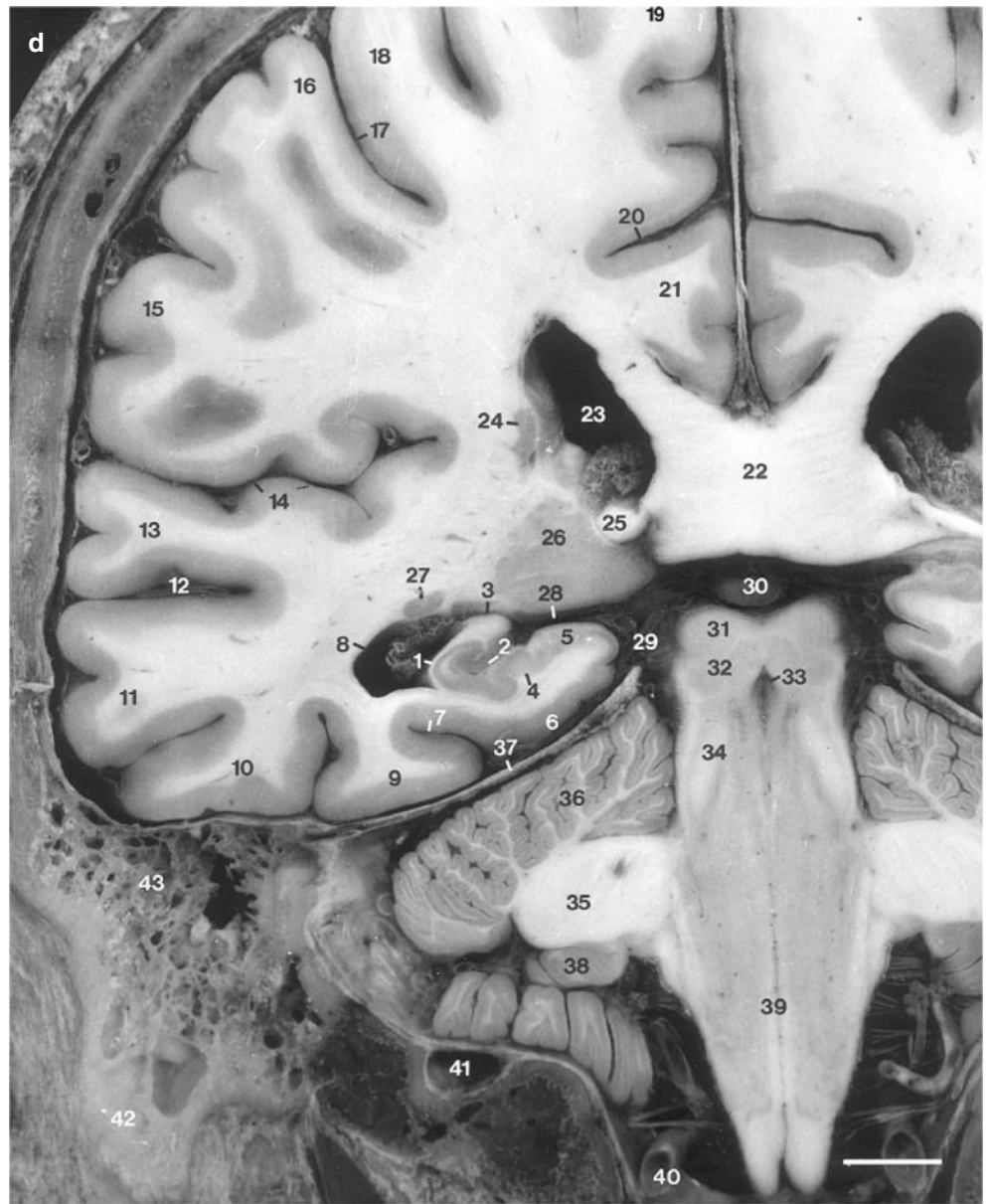


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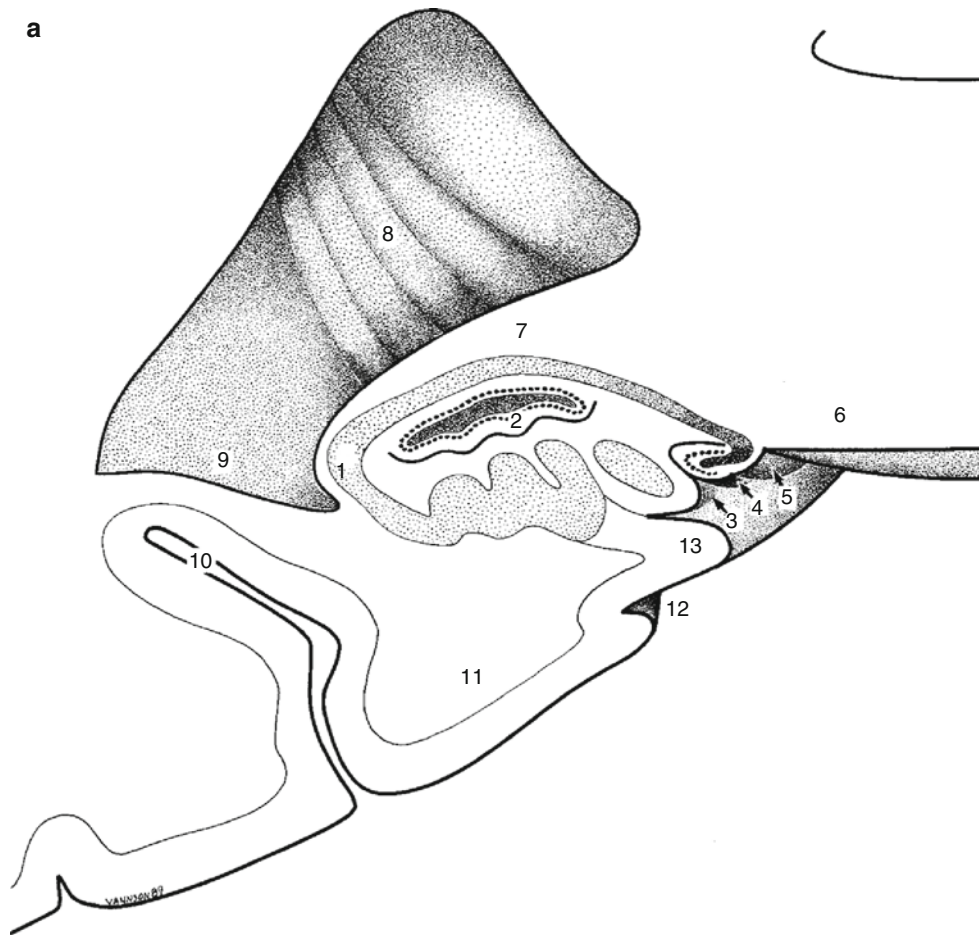


Fig. 7.10 (a) Coronal section of middle segment of the hippocampal tail, showing plane of section. 1 cornu Ammonis, 2 gyrus dentatus, 3 gyrus of Andreas Retzius, 4 fasciola cinerea, 5 gyrus fasciolaris, 6 splenium, 7 crus of fornix, 8 calcar avis, 9 collateral trigone, 10 collateral sulcus, 11 parahippocampal gyrus, 12 anterior calcarine sulcus, 13 isthmus. (b) Coronal section of the hippocampal tail. Intravascular India ink injection with explanatory diagram. Bar, 2.2 mm. 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, 3 gyri of Andreas Retzius, 4 fasciola cinerea, 5 gyrus fasciolaris, 6 splenium, 7 crus of fornix, 8 anterior calcarine sulcus, 9 isthmus. (c) 3T MRI view. 1 hippocampal tail, cornu Ammonis, 1' inferior part of CA1 with a folded aspect, 2 hippocampal tail, gyrus dentatus, 3 crus of fornix, 4 atrium of the lateral ventricle, 5 isthmus, 5' gyrus fasciolaris, 6 anterior calcarine sulcus, 7 parahippocampal gyrus, 8 collateral sulcus, 9 collateral trigone, 10 fusiform gyrus, 11 inferior temporal gyrus, 12 middle temporal gyrus, 13 superior temporal sulcus, 14 superior temporal gyrus, 15 supramarginal gyrus, 16 lateral fissure, posterior ascending segment, 16' caudate nucleus, 17 intraparietal sulcus, 18 postcentral gyrus, 19 central sulcus, 20 precentral gyrus, 21 superior frontal gyrus, 22 cingulate sulcus, 23 cingulate gyrus, 24 splenium, 25 optic radiations, 26 pineal gland and quadrigeminal cistern, 27 superior colliculus, 28 cerebral aqueduct, 29 brachium conjunctivum, 30 quadrangular lobule, 31 tentorium cerebelli, 32 brachium pontis, 33 flocculus, 34 medulla, 35 vertebral artery, 36 sigmoid sinus, 37 mastoid air cells, 38 mastoid process. (d) Head section, posterior view of the section. Bar, 10 mm

pocampal gyrus, 8 collateral sulcus, 9 collateral trigone, 10 fusiform gyrus, 11 inferior temporal gyrus, 12 middle temporal gyrus, 13 superior temporal sulcus, 14 superior temporal gyrus, 15 supramarginal gyrus, 16 lateral fissure, posterior ascending segment, 16' caudate nucleus, 17 intraparietal sulcus, 18 postcentral gyrus, 19 central sulcus, 20 precentral gyrus, 21 superior frontal gyrus, 22 cingulate sulcus, 23 cingulate gyrus, 24 splenium, 25 optic radiations, 26 pineal gland and quadrigeminal cistern, 27 superior colliculus, 28 cerebral aqueduct, 29 brachium conjunctivum, 30 quadrangular lobule, 31 tentorium cerebelli, 32 brachium pontis, 33 flocculus, 34 medulla, 35 vertebral artery, 36 sigmoid sinus, 37 mastoid air cells, 38 mastoid process. (d) Head section, posterior view of the section. Bar, 10 mm

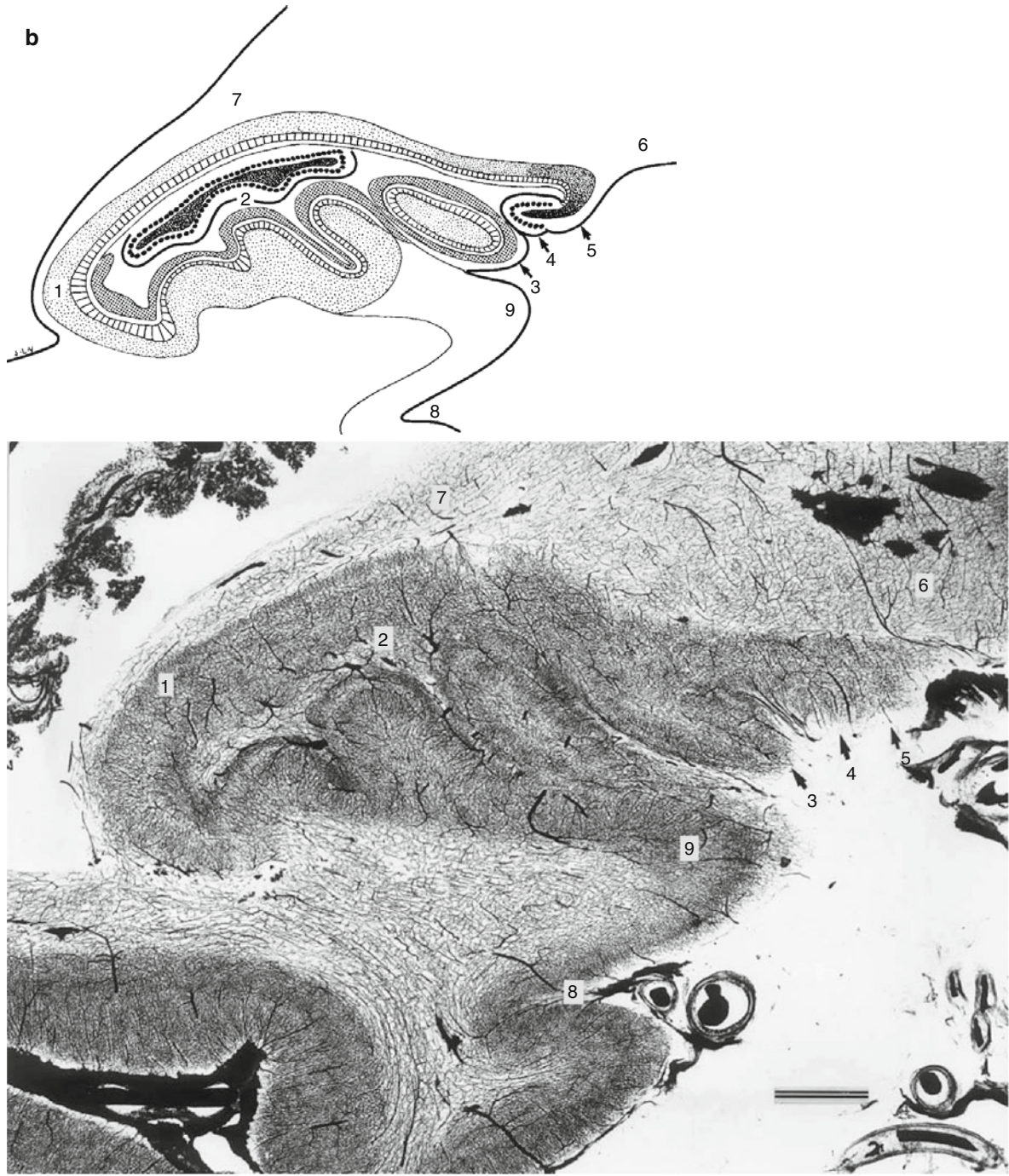


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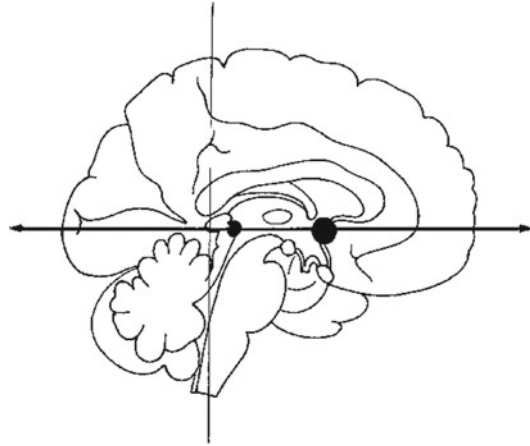
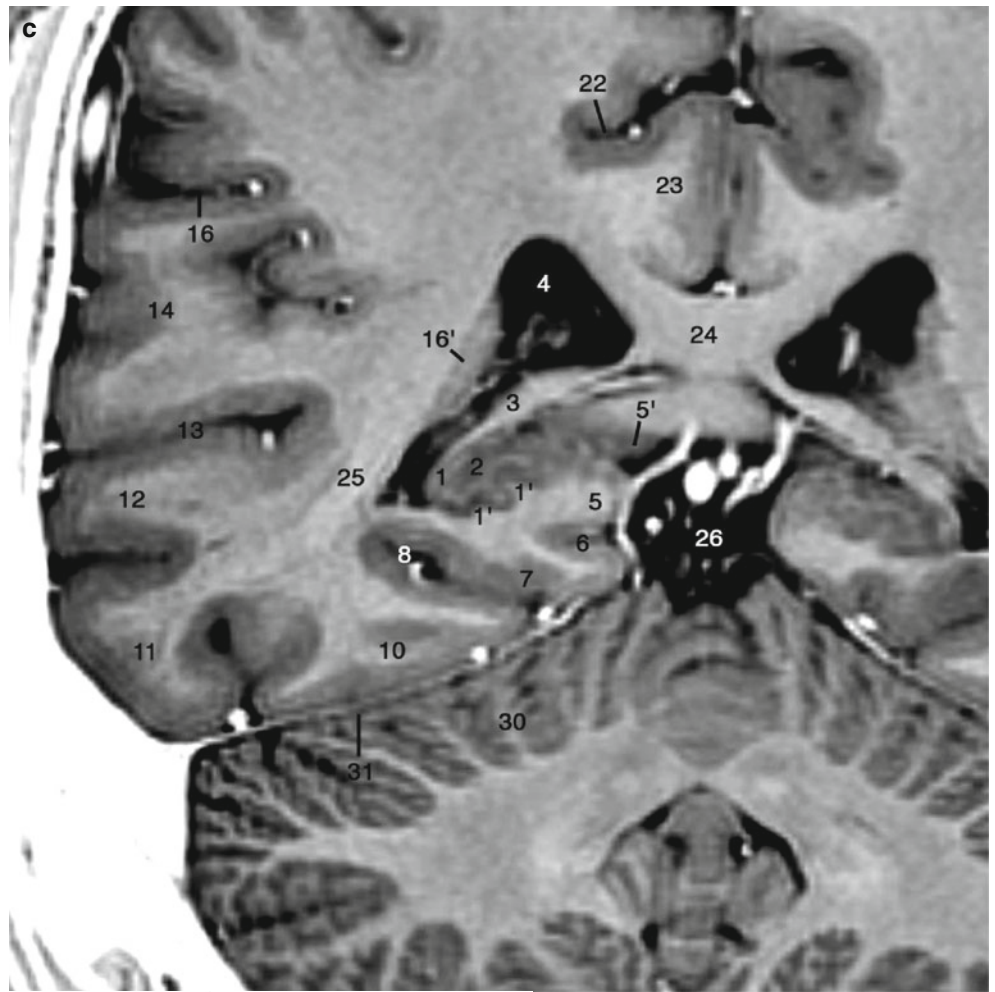
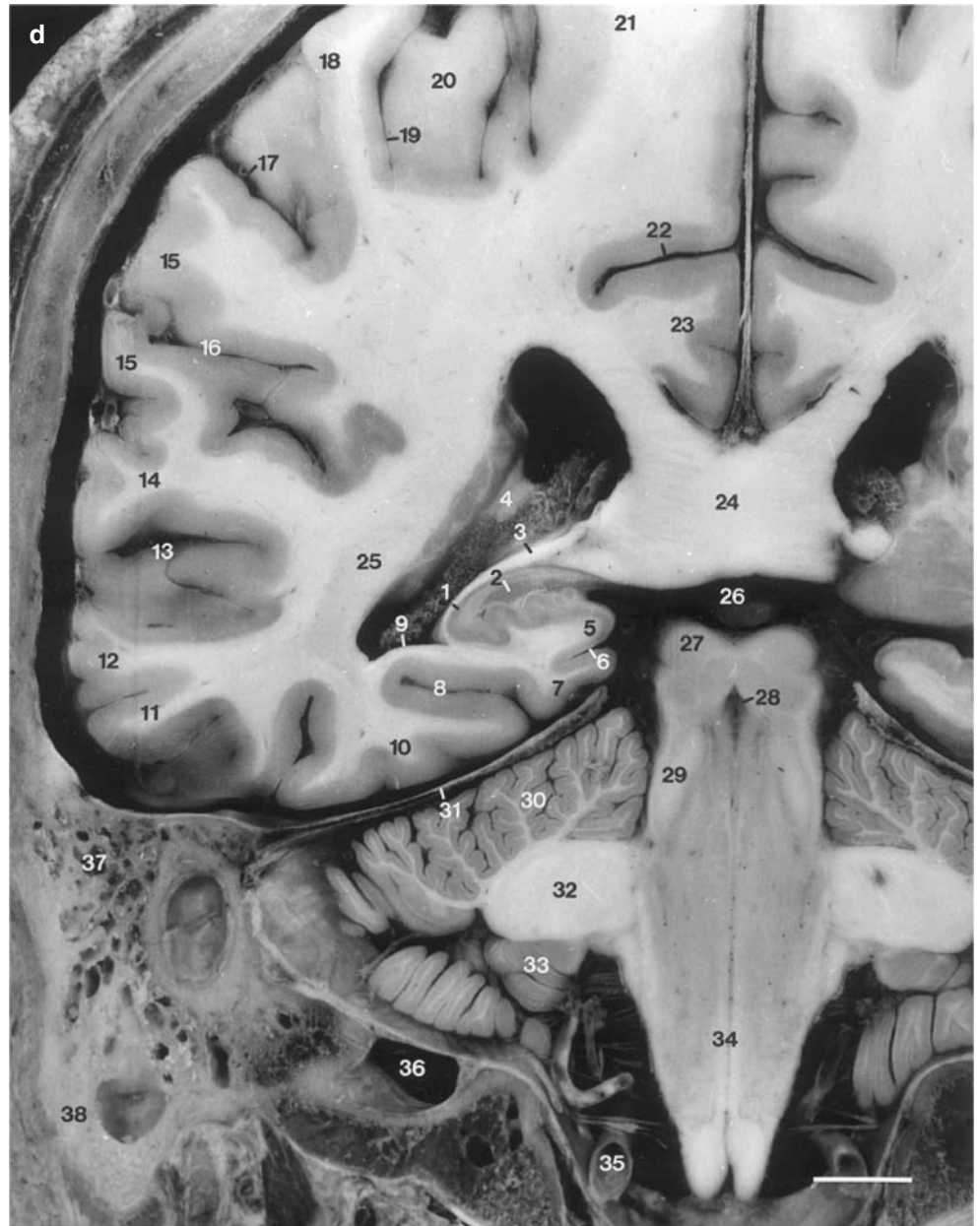


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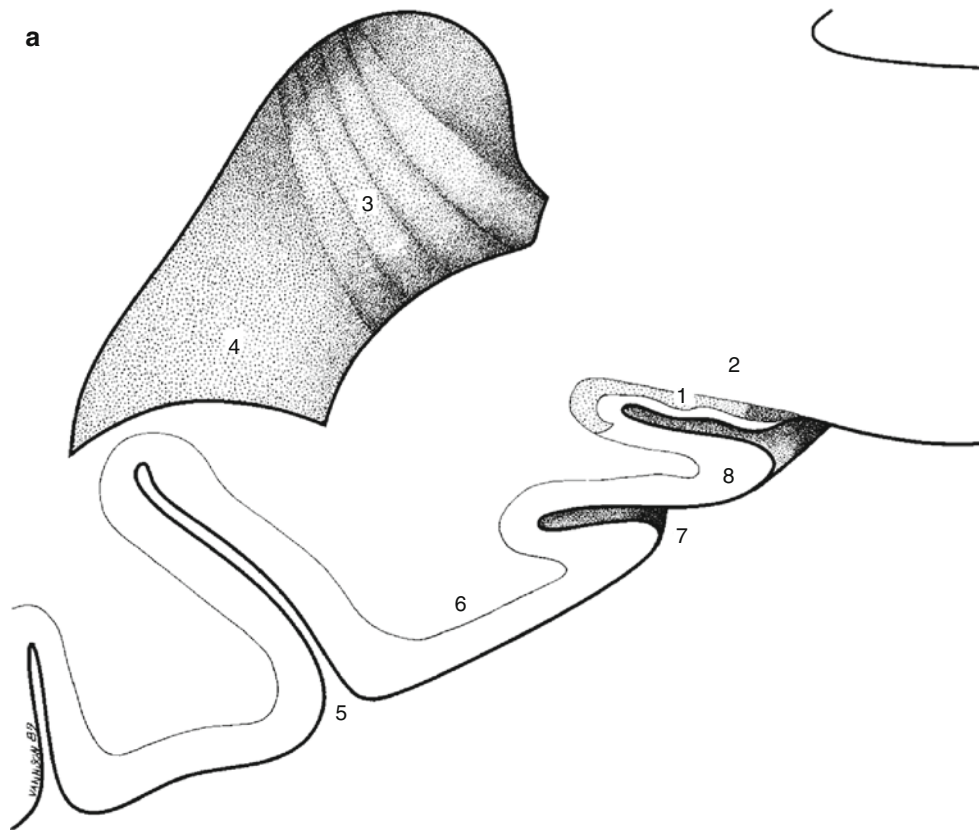


Fig. 7.11 (a) Coronal section of terminal segment of the hippocampal tail, showing plane of section. 1 cornu Ammonis (subsplenial gyrus), 2 splenium, 3 calcar avis, 4 collateral trigone, 5 collateral sulcus, 6 parahippocampal gyrus (posterior part), 7 anterior calcarine sulcus, 8 isthmus. (b) Coronal section of the hippocampal tail. Intravascular India ink injection with explanatory diagram. Bar, 1 mm. 1 cornu Ammonis (subsplenial gyrus, CA1, CA3), 2 longitudinal striae, 3 splenium, 4 subiculum, 5 isthmus. (c) 3T MRI view. 1 cornu Ammonis (subsplenial gyrus), 2 splenium, 3 atrium of the lateral ventricle, 4 isthmus, 5 anterior calcarine sulcus, 6 parahippocampal gyrus, 7 collateral sulcus, 8

collateral trigone, 9 fusiform gyrus, 10 inferior temporal gyrus, 10' inferior temporal sulcus, 11 middle temporal gyrus, 12 superior temporal sulcus, 13 optic radiations, 14 superior temporal gyrus, 15 supramarginal gyrus, 15' lateral fissure, posterior ascending segment, 16 intraparietal sulcus, 17 postcentral gyrus, 18 central sulcus, 19 precentral gyrus, 20 cingulate sulcus, 21 cingulate gyrus, 22 central lobule, 23 tentorium cerebelli, 24 quadrangular lobule, 25 superior semilunar lobule, 26 brachium pontis, 27 fourth ventricle, 28 biventer lobule, 29 transverse sinus. (d) Head section, posterior view of the section Bar, 10 mm

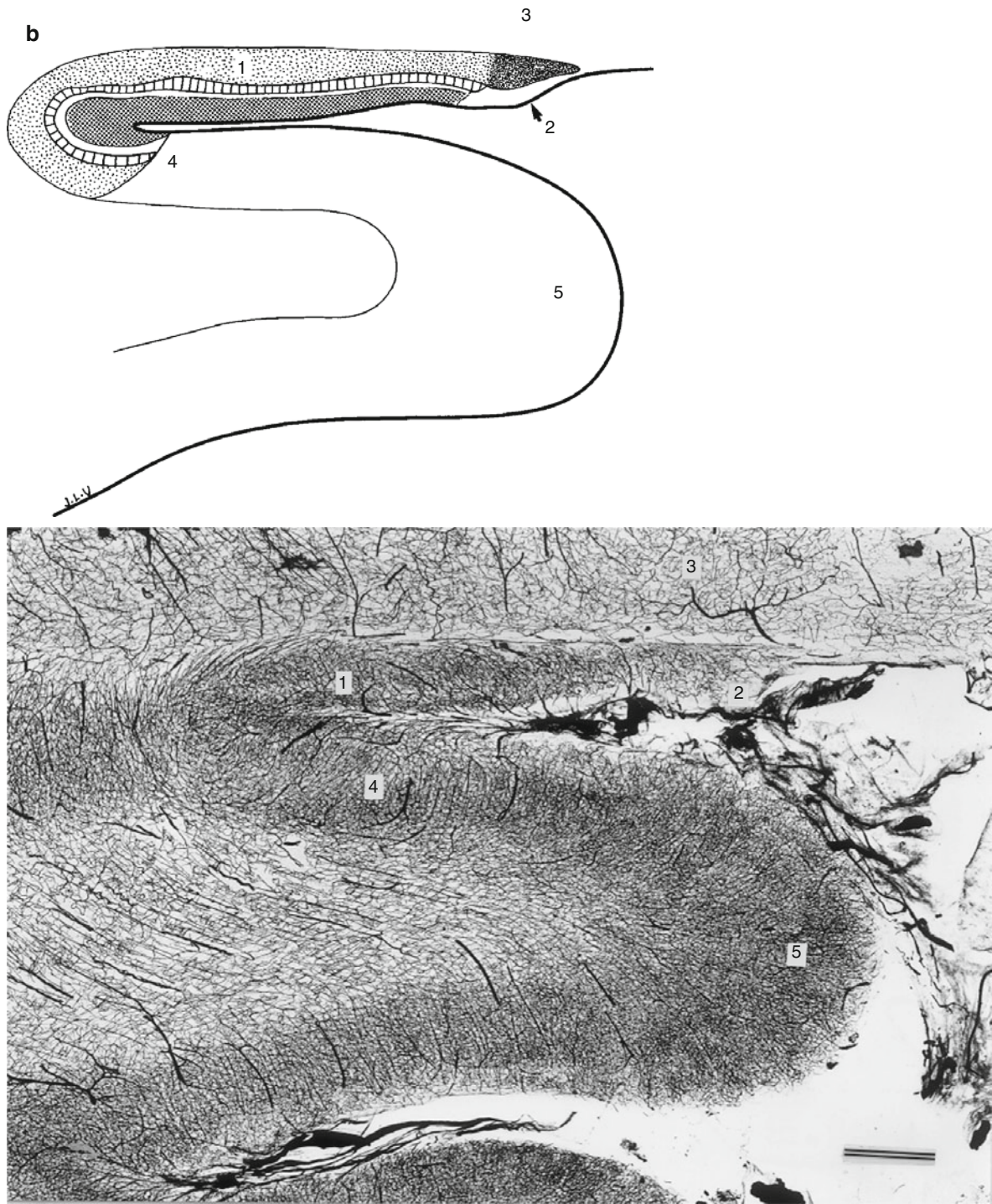


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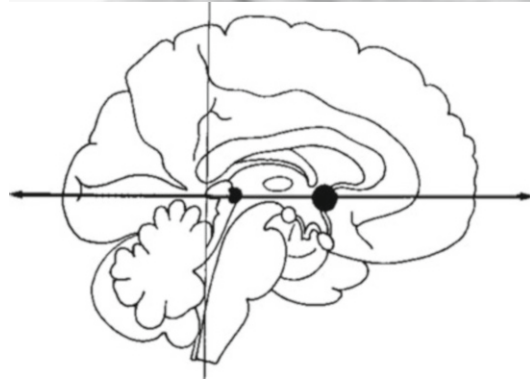
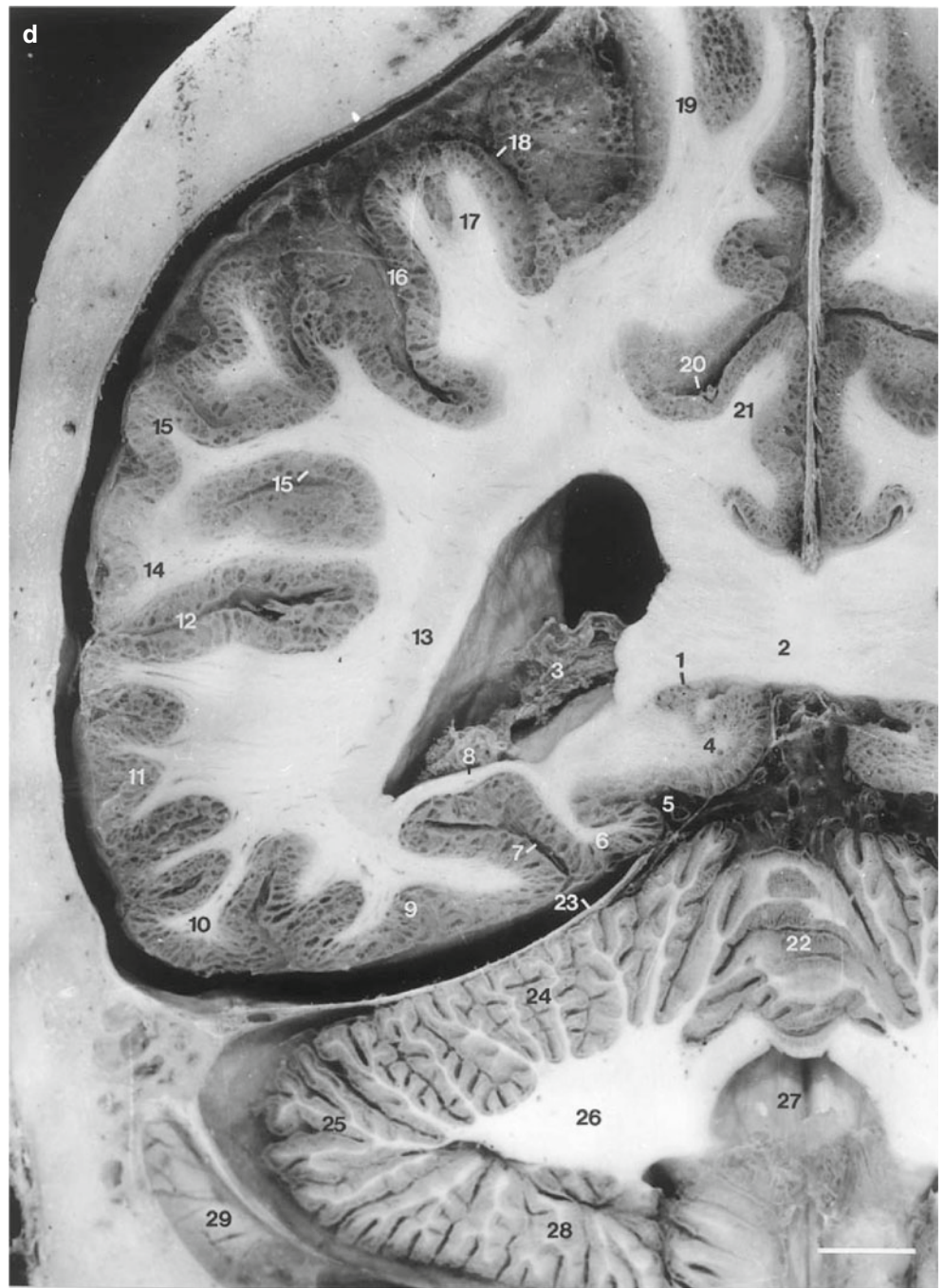
Fig. 7.11 (continued)

Fig. 7.11 (continued)



7.2 Sagittal Sections

Figures 7.14, 7.15, 7.16, 7.17, 7.18, and 7.19 show sagittal sections of the hippocampus from medial to lateral levels.

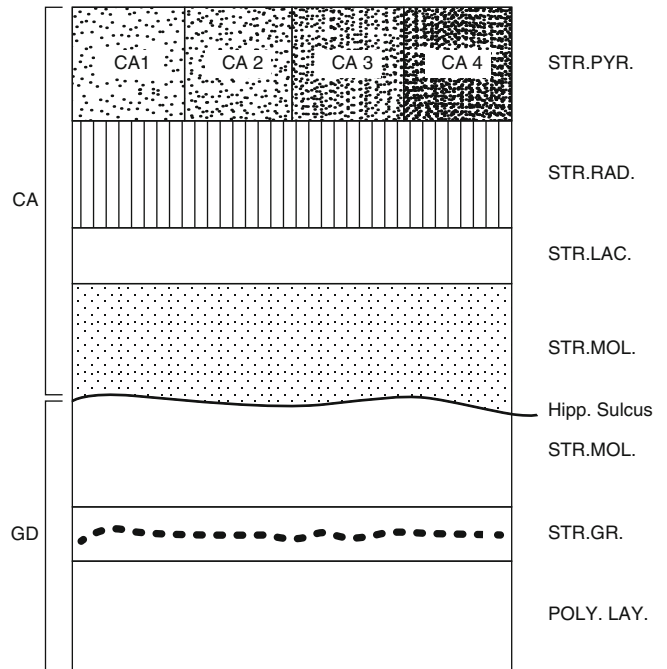


Fig. 7.12 Structure of the hippocampus *CA* cornu Ammonis, *STR. PYR.* stratum pyramidale, *STR. RAD.* stratum radiatum, *STR. LAC.* stratum lacunosum, *STR. MOL.* stratum moleculare, Hipp. Sulcus, vestigial hippocampal sulcus, *GD* gyrus dentatus, *STR. MOL.* stratum moleculare, *STR. GR.* stratum granulosum, *POLY.LAY.* polymorphic layer

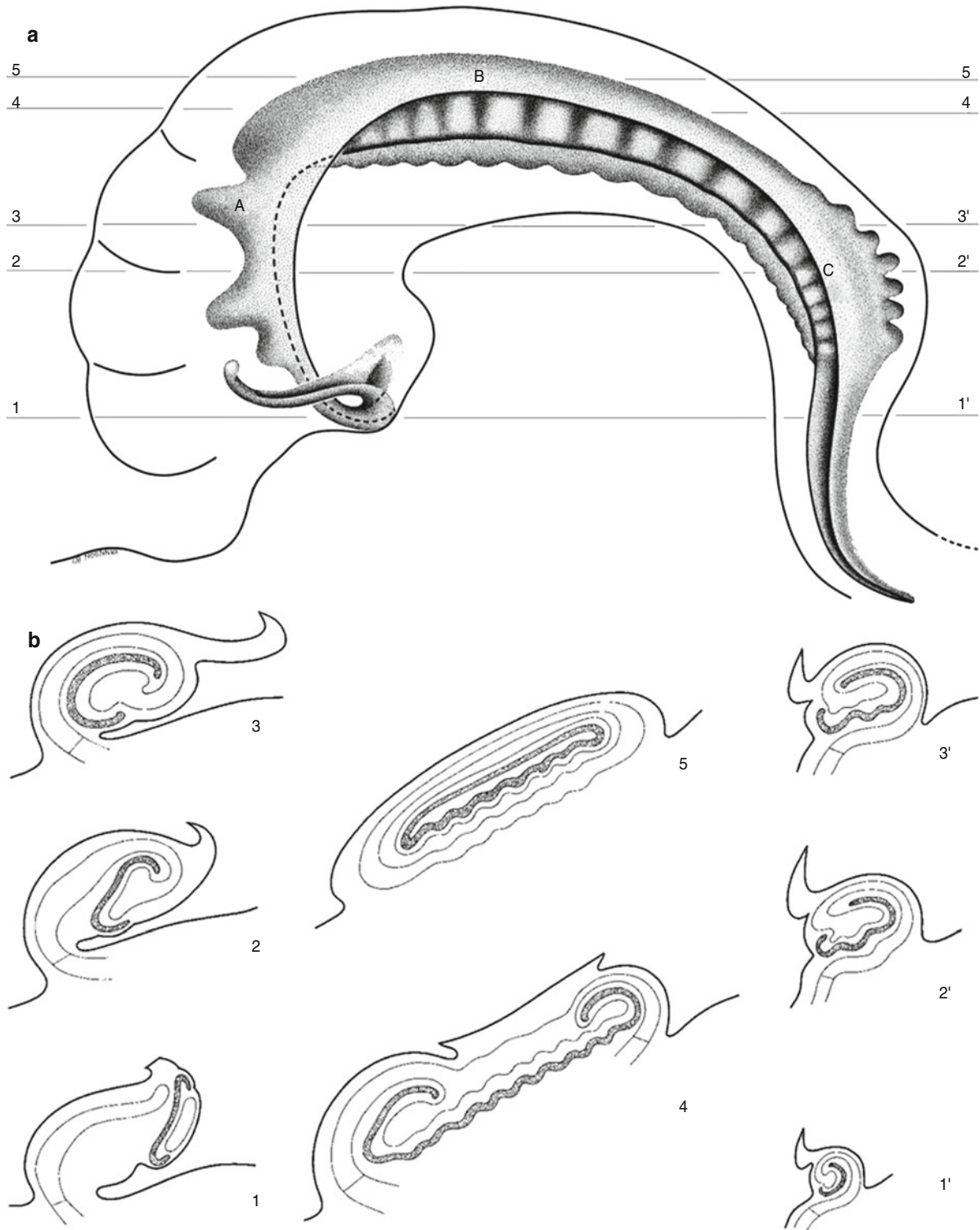


Fig. 7.13 (a, b) General position of the gyrus dentatus in the head (A), body (B), and tail (C) of the hippocampus. One to five, successive planes of sections shown in Fig. 7.13b

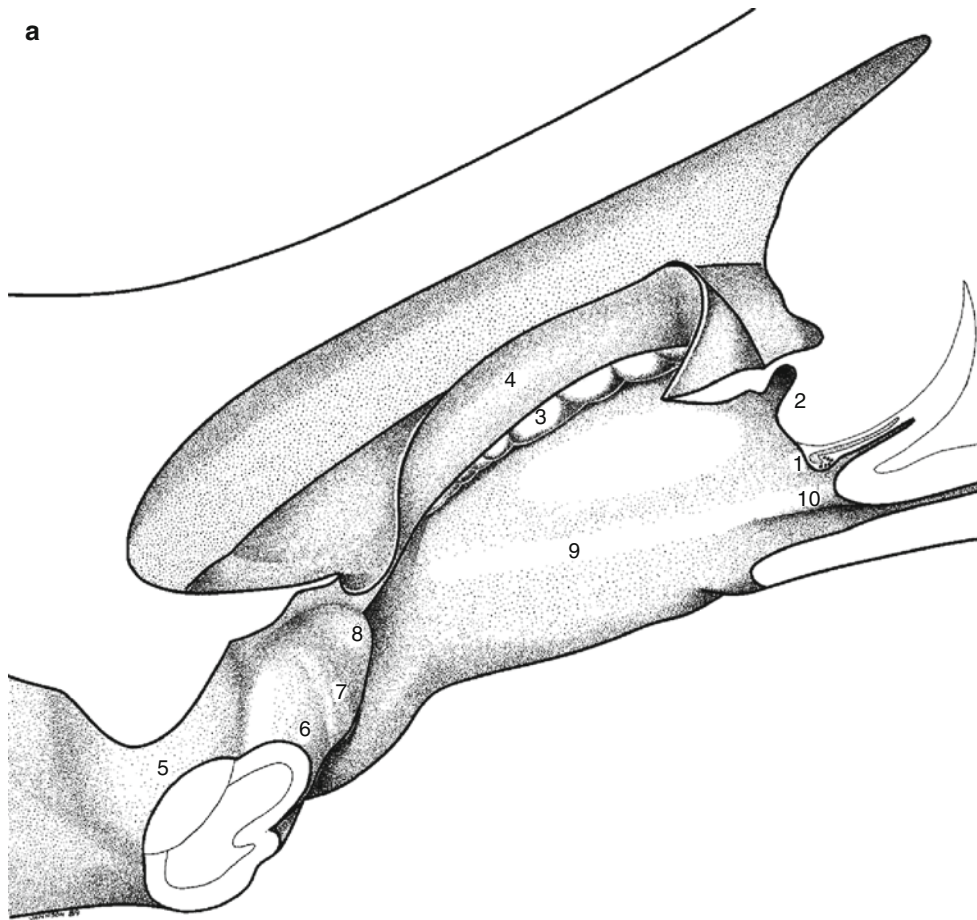


Fig. 7.14 (a) Sagittal section of hippocampus, showing plane of section. 1 hippocampal tail, 2 splenium, 3 margo denticulatus, 4 fimbria, 5 semilunar gyrus, 6 uncinatus gyrus, 7 band of Giacomini, 8 uncus apex, 9 parahippocampal gyrus, 10 isthmus. (b) Sagittal section of uncus. Intravascular India ink injection with explanatory diagram. Bar, 2 mm. 1 uncinatus gyrus, 2 anterior choroidal artery, 3 optic tract, 4 cortical nucleus of amygdala, 5 accessory basal nucleus of amygdala, 6 middle cerebral artery, 7 ambient gyrus, 8 parahippocampal gyrus. (c) Sagittal section of hippocampal tail. Intravascular India ink injection with explanatory diagram. Bar, 2 mm. 1 gyrus fasciolaris, 2 fasciola cinerea, 3 splenium, 4 fornix, 5 pulvinar, 6 isthmus. (d) 3T MRI view. 1 uncinatus gyrus (head of hippocampus), 1' hippocampal tail, 1'' uncal recess of the

temporal horn, 2 amygdala, 3 ambient gyrus, 4 middle cerebral artery, 5 optic tract, 6 putamen, 7 anterior commissure, lateral part, 8 globus pallidus, lateral part, 9 globus pallidus, medial part, 10 caudate nucleus, 11 internal capsule, posterior limb, 12 lateral posterior thalamic nucleus, 13 medial geniculate body, 14 pulvinar, 15 crus of fornix, 16 lateral ventricle, 17 corpus callosum, 18 parieto-occipital fissure, 19 cuneus, 20 calcarine sulcus and striate cortex, 21 lingual gyrus, 22 isthmus, 23 parahippocampal gyrus, 24 tentorium cerebelli, 25 quadrangular lobule, 26 simple lobule, 27 superior semilunar lobule, 28 horizontal fissure, 29 inferior semilunar lobule, 30 biventer lobule, 31 flocculus, 32 trigeminal nerve, 33 trigeminal cave, 34 temporal, petrous part, 35 internal carotid artery, 36 dentate nucleus. (e) Head section. Bar, 10 mm

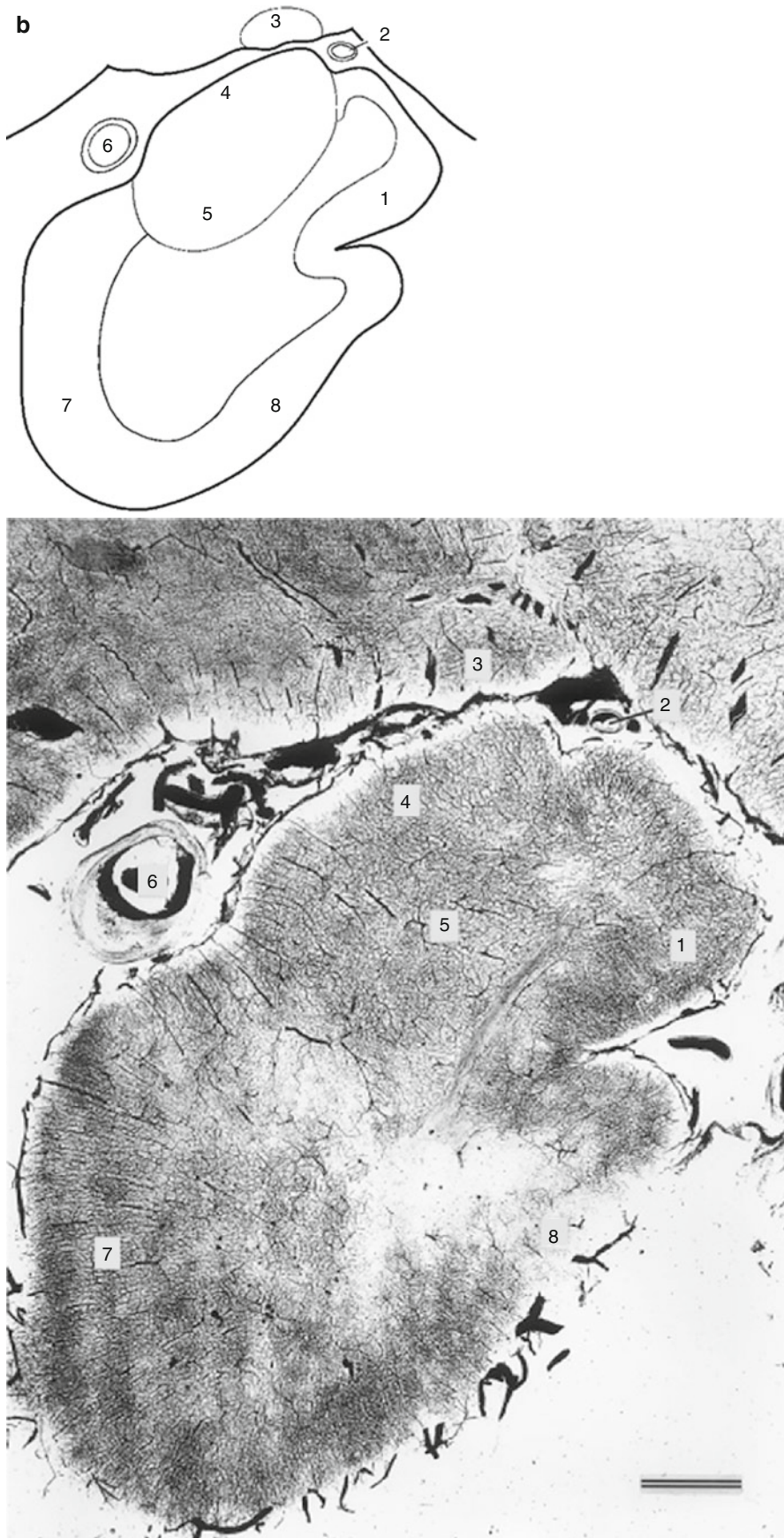


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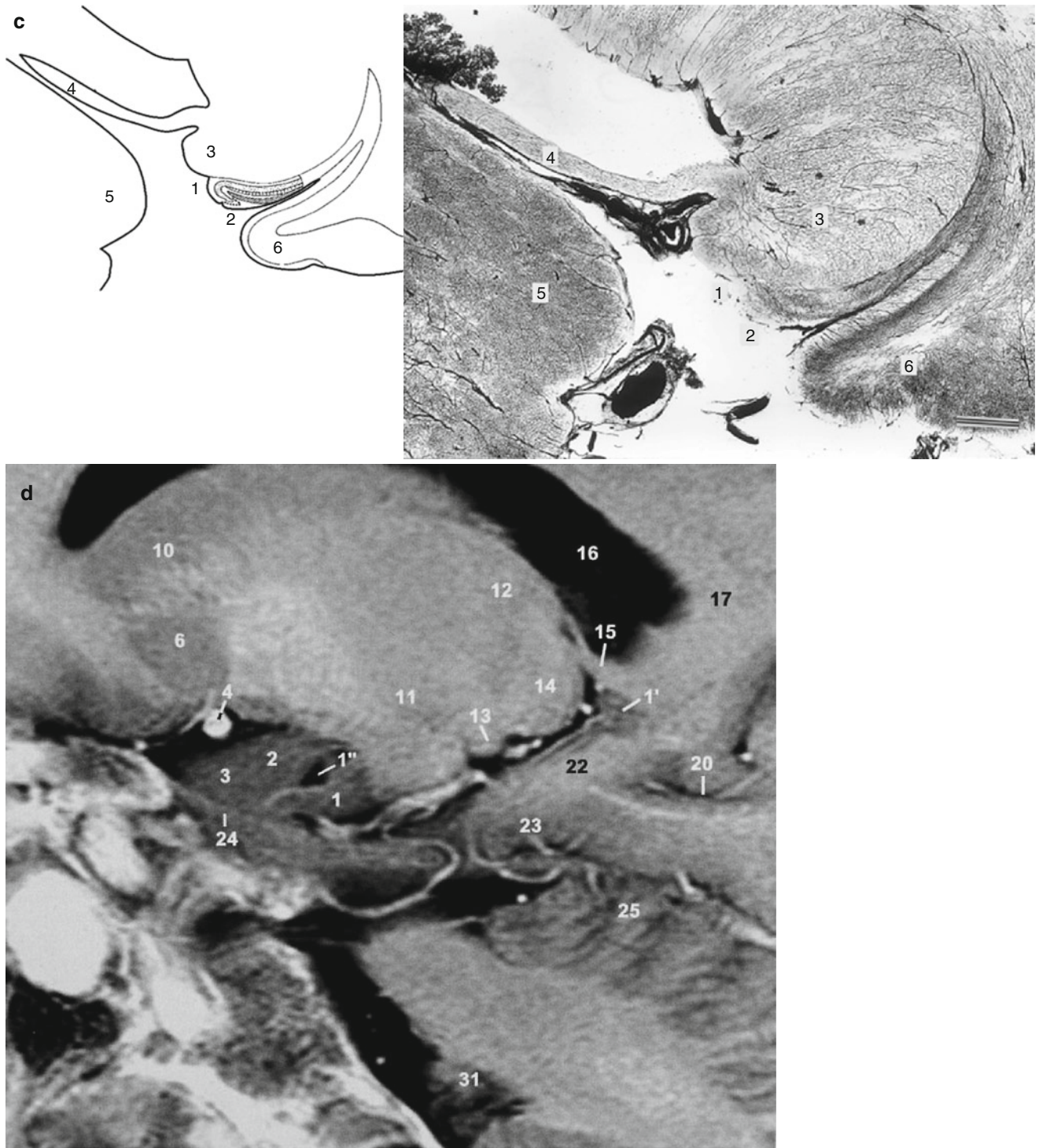


Fig. 7.14 (continued)

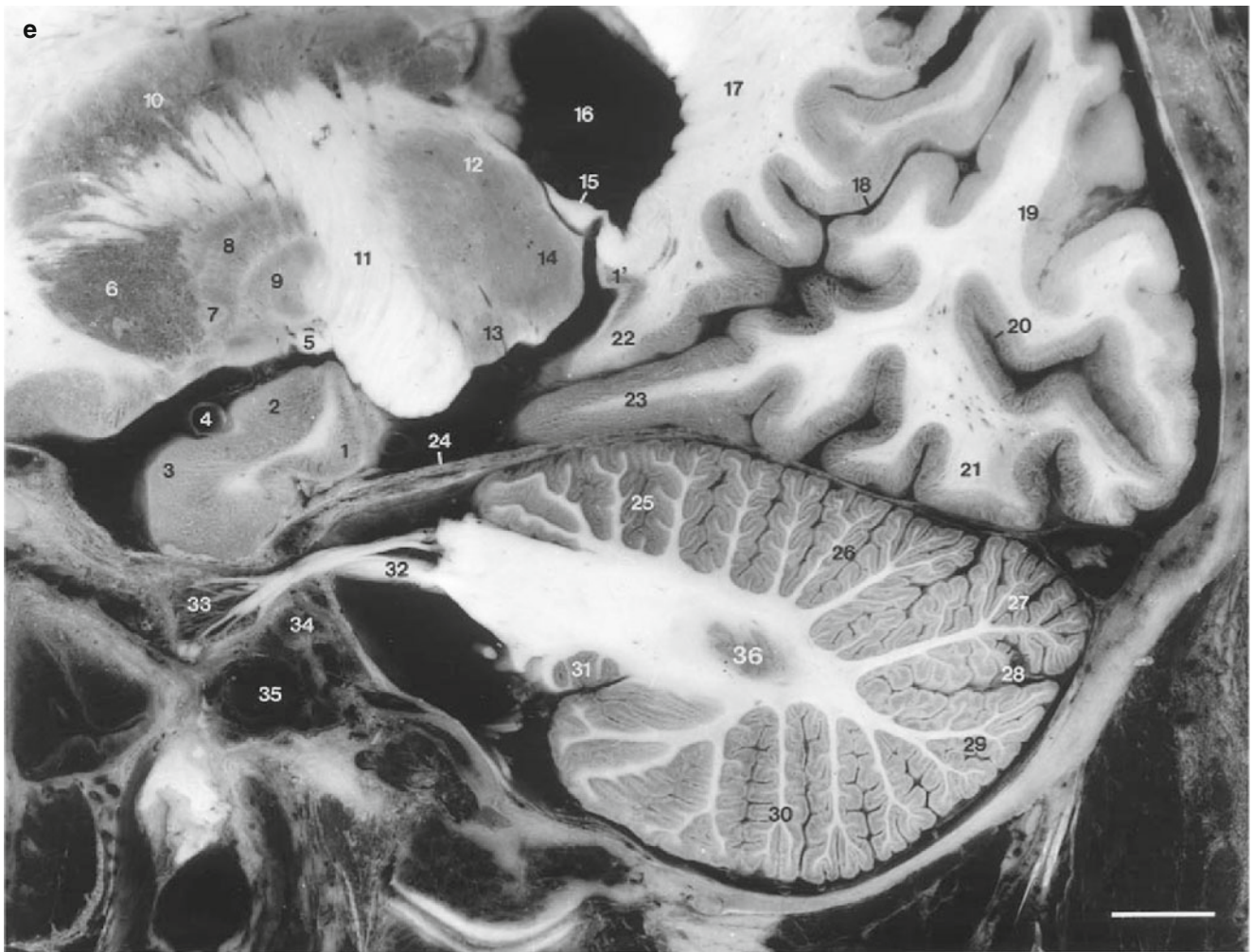


Fig. 7.14 (continued)

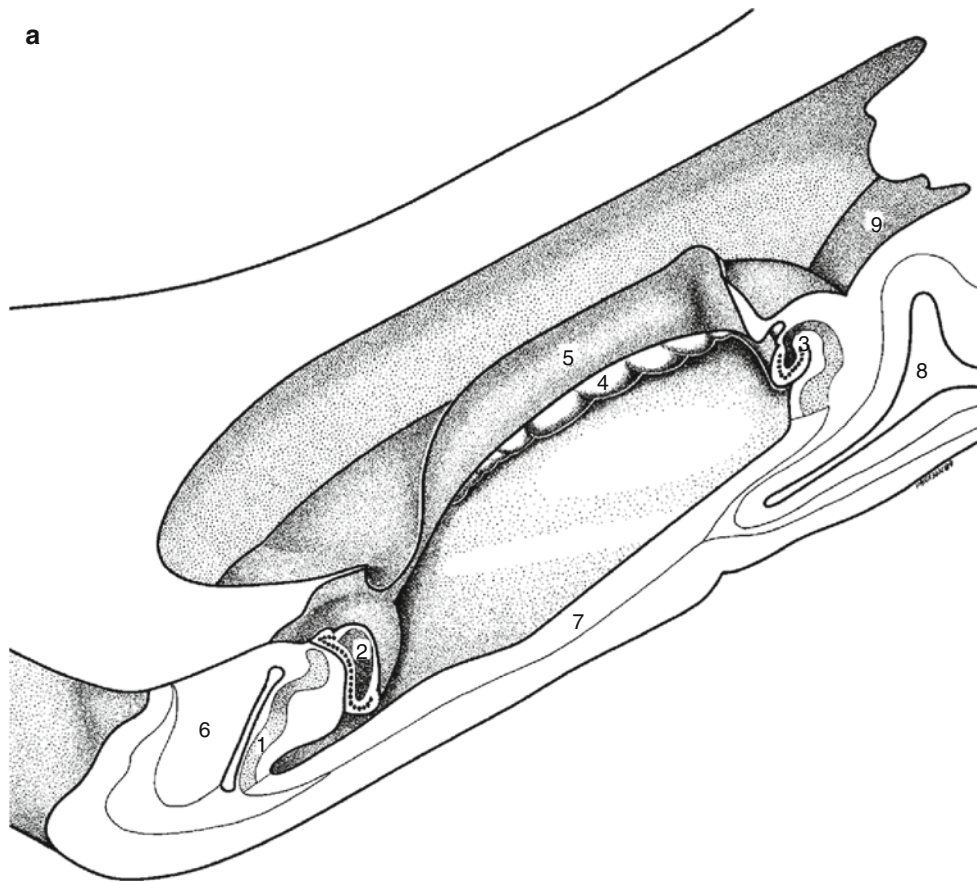


Fig. 7.15 (a) Sagittal section of hippocampus, showing plane of section. 1 hippocampal head, 2 uncus apex, 3 hippocampal tail, 4 margo denticulatus, 5 fimbria, 6 amygdala, 7 parahippocampal gyrus, 8 anterior calcarine sulcus, 9 calcar avis. (b) Sagittal section of hippocampal head. Intravascular India ink injection with explanatory diagram. Note the maculate aspect of the vascular network of the presubiculum (13) in relation to its nervous structure (see p. 17). The *arrow* indicates the superficial hippocampal sulcus. *Bar*, 2.4 mm. 1 cornu Ammonis (CA1, CA2), 2 gyrus dentatus, 3 uncus apex (CA3, CA4), 4 band of Giacomini, 5 cortical nucleus of amygdala, 6 endorhinal sulcus, 7 medial nucleus of amygdala, 8 temporal horn of the lateral ventricle, 9 accessory basal nucleus of amygdala, 10 basal nucleus of amygdala, 11 ambient gyrus, 12 uncus sulcus, 13 presubiculum. (c) Sagittal section of hippocampal tail (middle segment). Vascular India ink injection with explanatory diagram. The *arrow* indicates the superficial hippocampal sulcus. *Bar*, 2.3 mm. 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, 3 fimbria, 4 pulvinar, 5 gyrus fasciolaris,

6 fasciola cinerea, 7 gyri of Andreas Retzius, 8 subiculum, 9 anterior calcarine sulcus, 10 calcar avis, 11 lateral geniculate body. (d) 3T MRI view. 1 hippocampal head, cornu Ammonis, 1' uncus sulcus, 2 hippocampal head, uncus apex, 3 temporal (inferior) horn of the lateral ventricle, 4 amygdala, 4' ambient gyrus, 5 middle cerebral artery, 6 hippocampal tail, cornu Ammonis, 7 hippocampal tail, gyrus dentatus, 8 fimbria, 9 gyri of Andreas Retzius, 10 subiculum, 11 parahippocampal gyrus, 12 putamen, 13 anterior commissure, lateral part, 14 globus pallidus, lateral part, 15 globus pallidus, medial part, 16 caudate nucleus, 17 internal capsule, posterior limb, 18 pulvinar, 19 lateral geniculate body, 19' medial geniculate body, 20 lateral ventricle, 21 superior occipital gyrus, 22 lingual gyrus, 22' calcarine sulcus, 23 quadrangular lobule, 24 simple lobule, 25 superior semilunar gyrus, 26 horizontal fissure, 27 inferior semilunar gyrus, 28 biventer lobule, 29 flocculus, 30 brachium pontis, 31 tentorium cerebelli, 32 trigeminal nerve, 33 trigeminal cave, 34 temporal, petrous part, 35 internal cerebral artery. (e) Head section. *Bar*, 10 mm

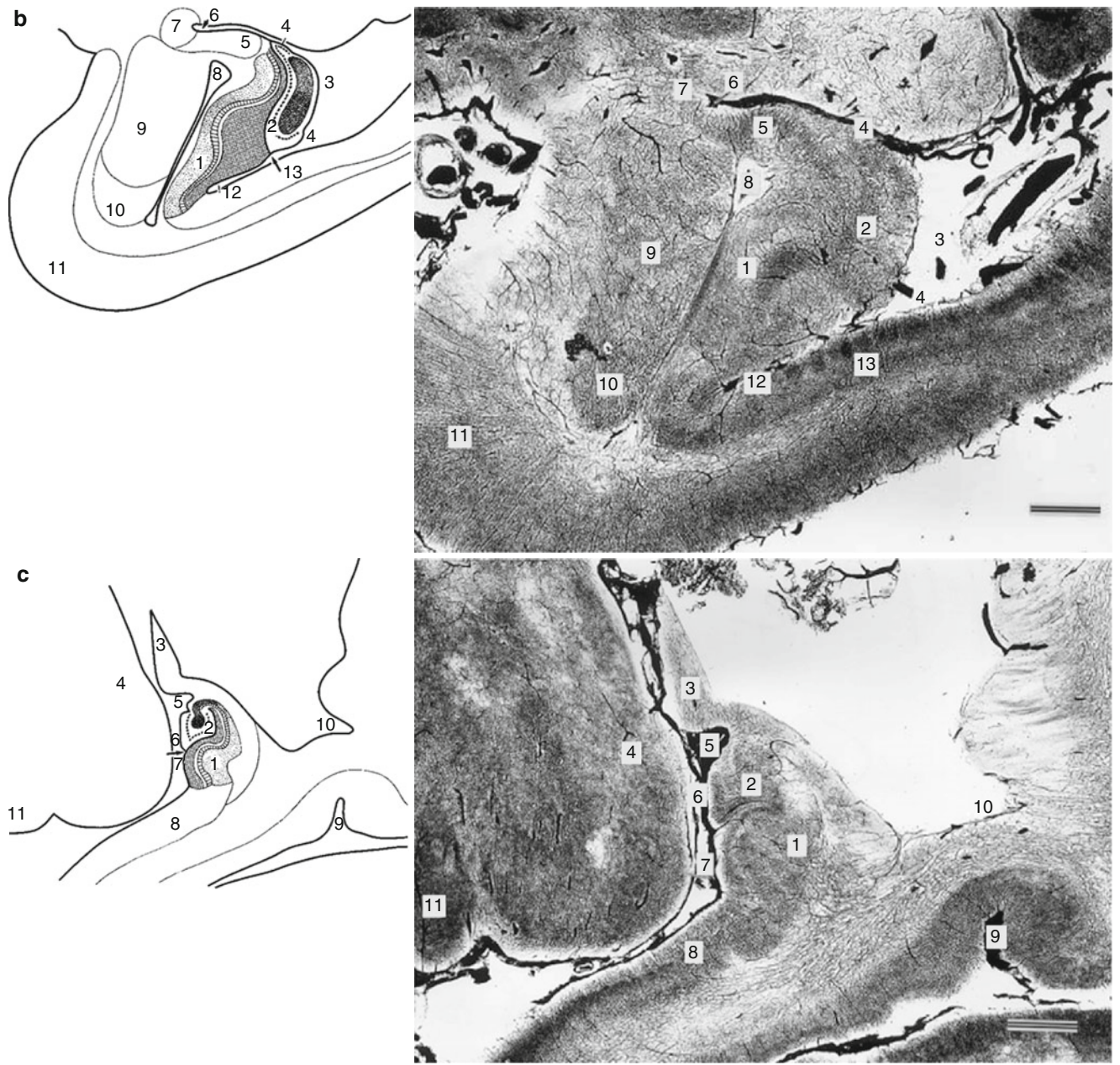
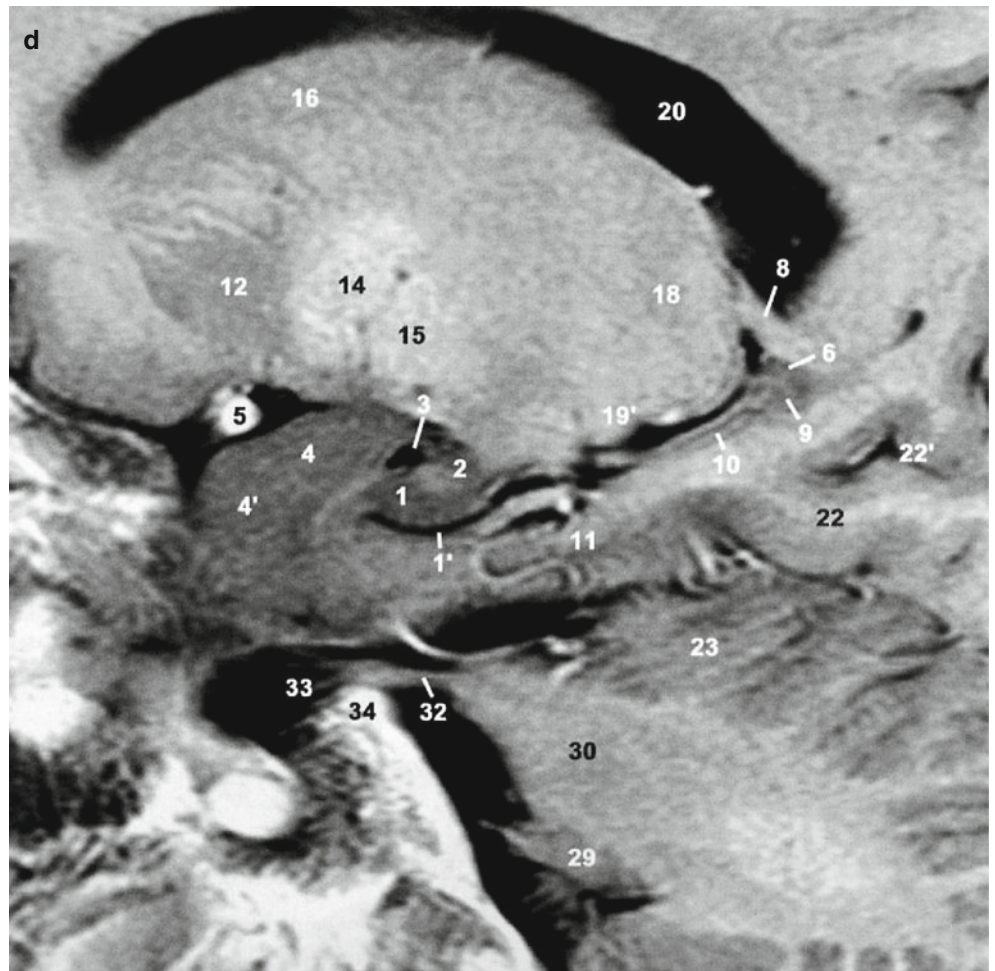


Fig. 7.15 (continued)

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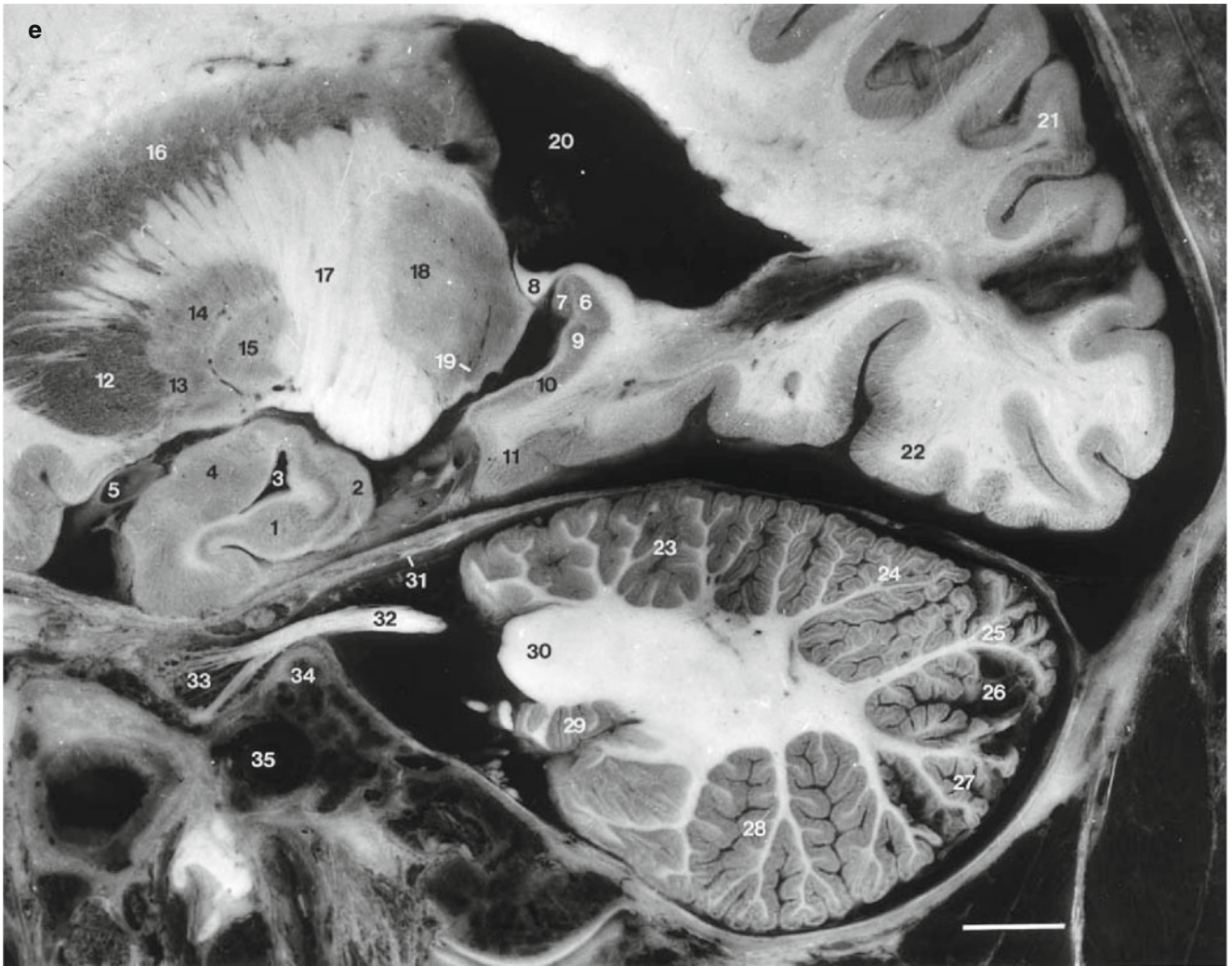


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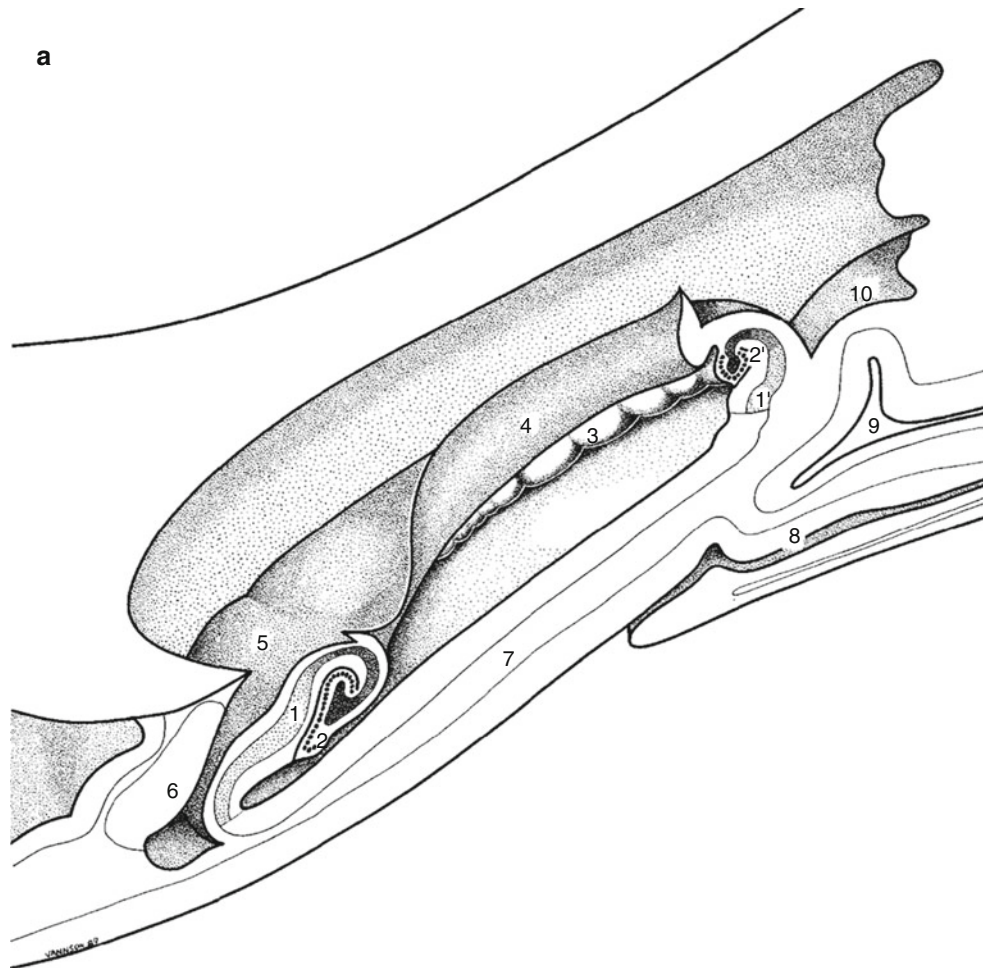


Fig. 7.16 (a) Sagittal section of hippocampus, showing plane of section. 1 cornu Ammonis in the head, 1' cornu Ammonis in the tail, 2 gyrus dentatus in the head, 2' gyrus dentatus in the tail, 3 margo denticulatus, 4 fimbria, 5 digitationes hippocampi, 6 amygdala, 7 parahippocampal gyrus, 8 collateral sulcus, 9 anterior calcarine sulcus, 10 calcar avis. (b) Sagittal section of hippocampal head. Intravascular India ink injection with explanatory diagram. The arrow indicates the superficial hippocampal sulcus. Note the maculate aspect of the capillary network in relation to the structure of the presubiculum (11) (see p. 17). Bar, 2.2 mm. 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, 3 band of Giacomini, 4 uncal apex, 5 fimbria, 6 lateral geniculate body, 7 temporal horn of lateral ventricle, 8 basal nucleus of amygdala, 9 lateral nucleus of amygdala, 10 uncal sulcus, 11 presubiculum. (c) Sagittal section of hippocampal tail (middle segment). Intravascular India ink injection with explanatory diagram. The arrow indicates the superficial hippocampal sulcus. Bar, 2 mm. 1 cornu Ammonis (CA1–CA4),

2 gyrus dentatus, 3 fimbria, 4 pulvinar, 5 fasciola cinerea, 6 gyri of Andreas Retzius, 7 subiculum, 8 calcar avis, 9 atrium. (d) 3T MRI view. 1 hippocampal head, cornu Ammonis, 2 hippocampal head, gyrus dentatus, 2' fimbria, 3 uncal apex, 4 temporal (inferior) horn of the lateral ventricle, 5 amygdala, 6 subiculum, 7 uncal sulcus, 8 hippocampal tail, cornu Ammonis, 9 hippocampal tail, gyrus dentatus, 10 fimbria, 11 middle cerebral artery, 12 anterior commissure, lateral part, 13 putamen, 14 caudate nucleus, 15 globus pallidus, lateral part, 16 globus pallidus, medial part, 17 internal capsule, posterior limb, 18 pulvinar, 19 lateral geniculate body, 20 lateral ventricle, 21 superior occipital gyrus, 22 lingual gyrus, 23 transverse sinus, 24 quadrangular lobule, 25 simple lobule, 26 superior semilunar lobule, 27 horizontal fissure, 28 inferior semilunar lobule, 29 biventer lobule, 30 flocculus, 31 tentorium cerebelli, 32 trigeminal nerve, 33 temporal, petrous part, 34 trigeminal cave, 35 internal carotid artery. (e) Head section. Bar, 10 mm

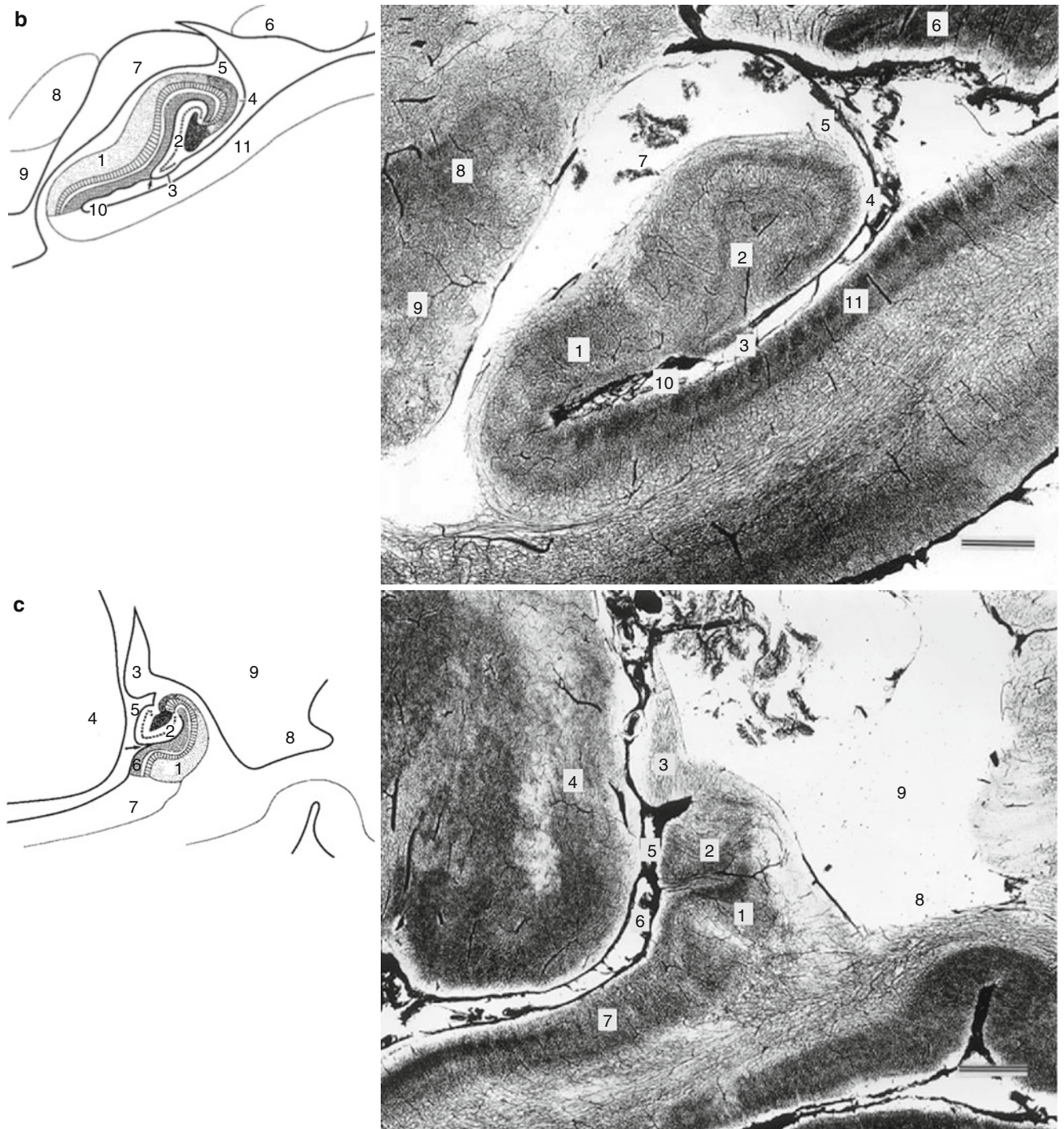
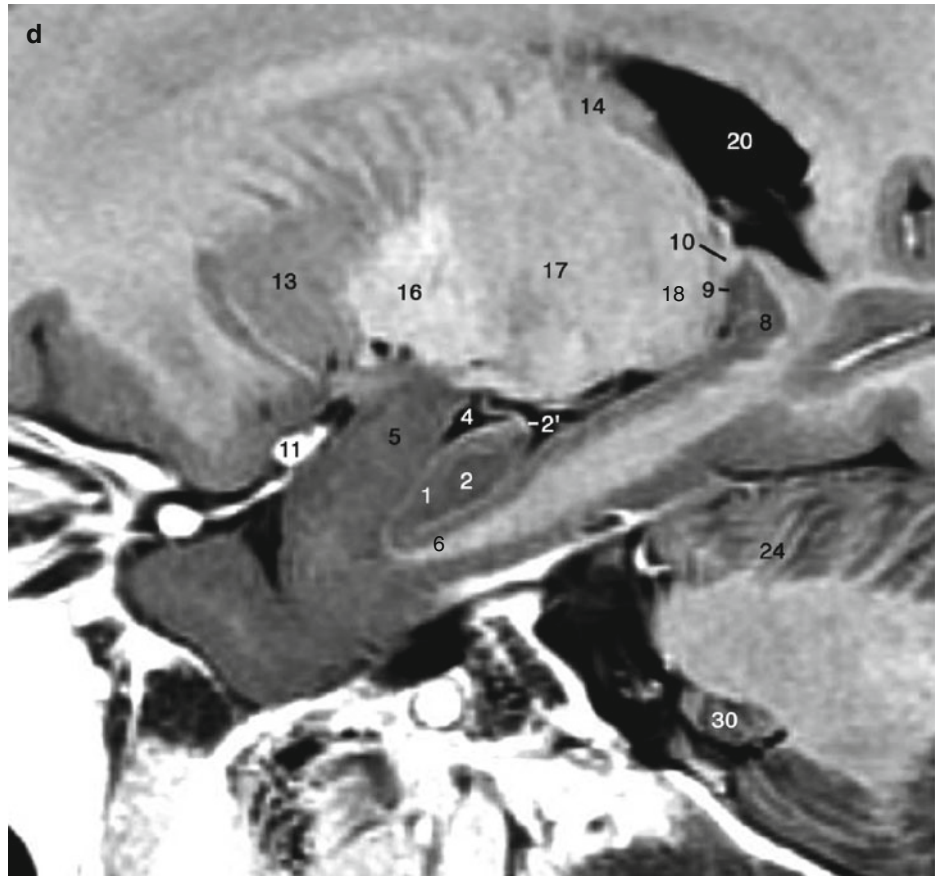


Fig. 7.16 (continued)

Fig. 7.16 (continued)



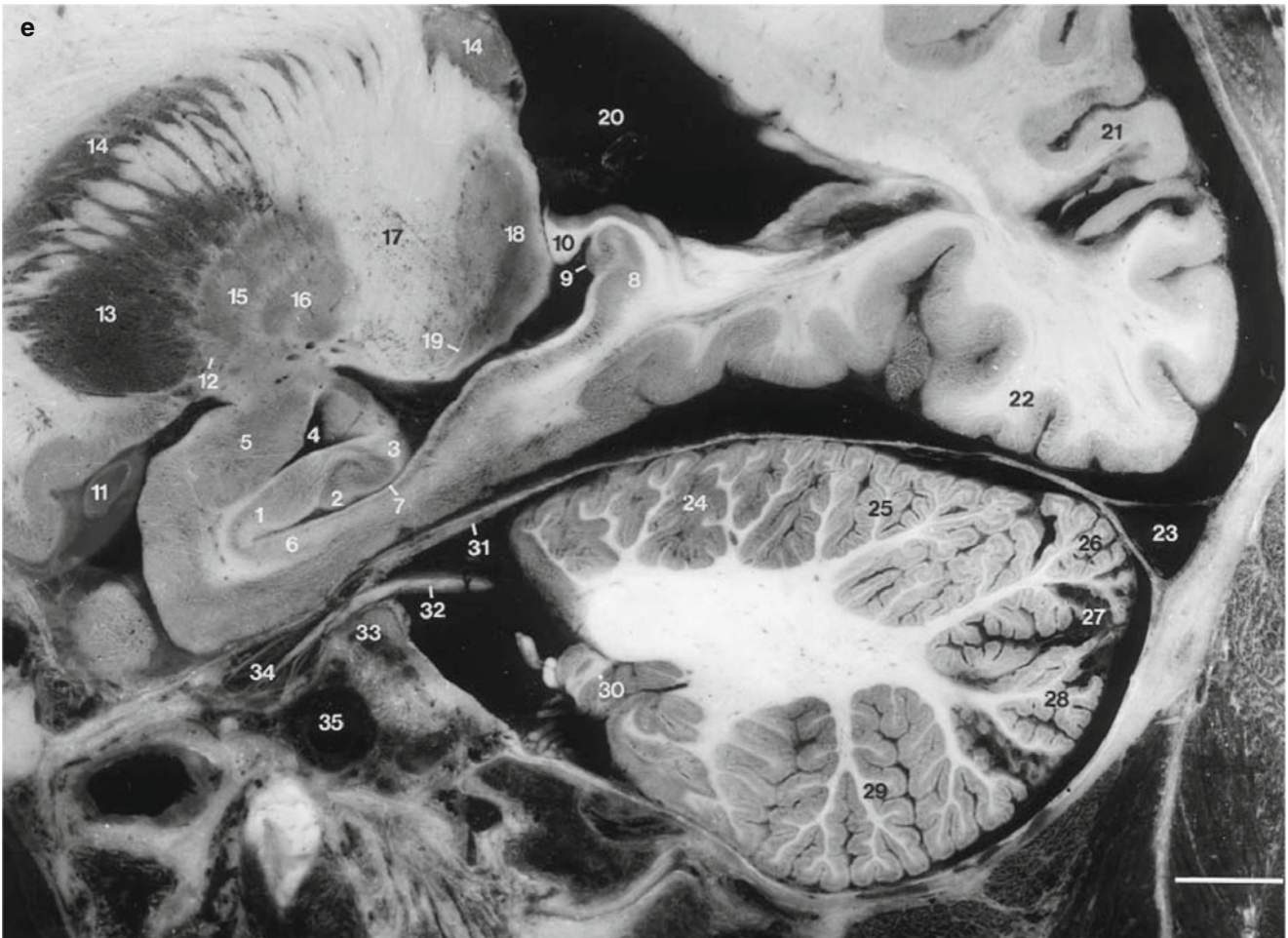


Fig. 7.16 (continued)

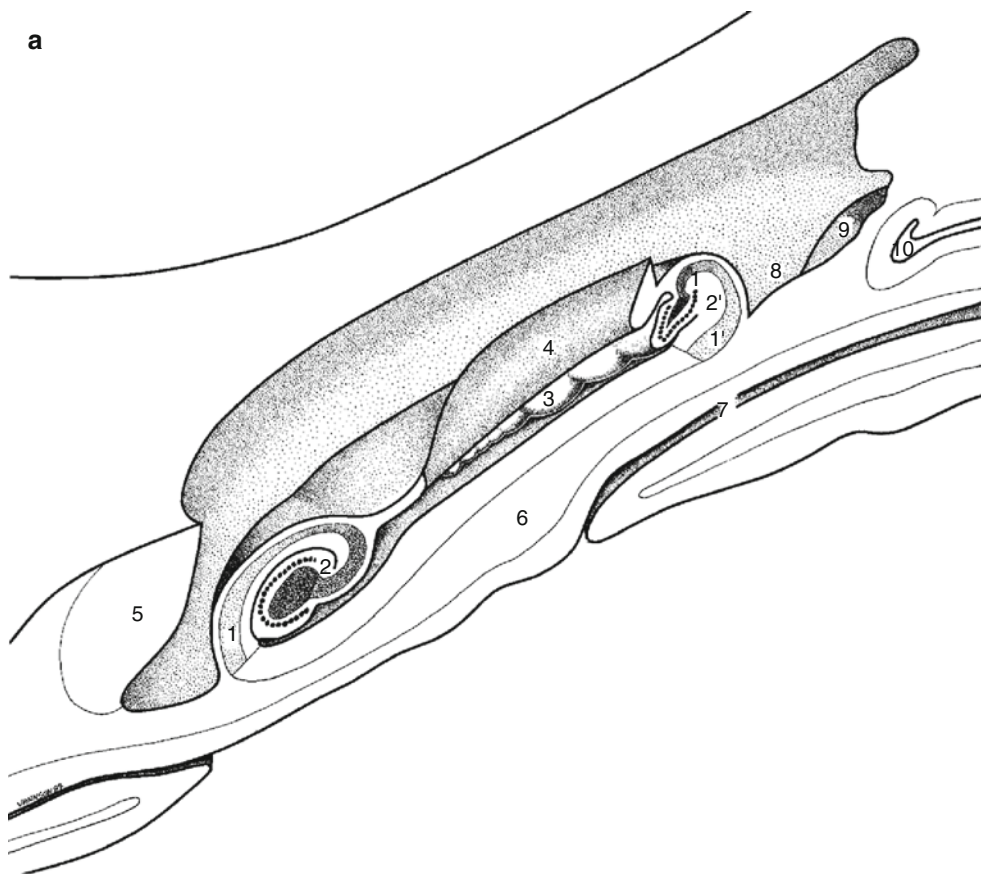


Fig. 7.17 (a) Sagittal section of hippocampus, showing plane of section. 1 cornu Ammonis in the head, 1' cornu Ammonis in the tail, 2 gyrus dentatus in the head, 2' gyrus dentatus in the tail, 3 margo denticulatus, 4 fimbria, 5 amygdala, 6 parahippocampal gyrus, 7 collateral sulcus, 8 collateral trigone, 9 calcar avis, 10 calcarine sulcus. (b) Sagittal section of hippocampal head. Intravascular India ink injection with explanatory diagram. Arrow indicates the superficial hippocampal sulcus. Bar, 2 mm, 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, 2' band of Giacomini, 3 fimbria, 4 stria terminalis, 5 tail of caudate nucleus, 6 basal nucleus of amygdala, 7 lateral nucleus of amygdala, 8 temporal horn of lateral ventricle (uncal recess), 9 uncal sulcus, 10 subiculum, 11 lateral geniculate body. (c) Sagittal section of hippocampal tail (initial segment following the hippocampal body). Vascular injection with explanatory diagram. Arrow indicates the superficial hippocampal sulcus. Bar, 2.5 mm 1 cornu Ammonis (CA1–CA4), 2 gyrus

dentatus, 3 fimbria, 4 margo denticulatus, 5 pulvinar, 6 lateral geniculate body, 7 subiculum, 8 atrium. (d) 3T MRI view. 1 hippocampal head cornu Ammonis, 2 hippocampal head, gyrus dentatus, 3 fimbria, 4 temporal (inferior) horn of the lateral ventricle, 5 amygdala, 6 subiculum, 7 uncal sulcus, 8 hippocampal tail, cornu Ammonis, 8' gyri of Andreas Retzius, 9 hippocampal tail, gyrus dentatus, 10 fimbria, 10' alveus, 11 middle cerebral artery, 12 anterior commissure, lateral part, 13 putamen, 14 globus pallidus, lateral part, 15 globus pallidus, medial part, 16 caudate nucleus, 17 pulvinar, 18 lateral ventricle, 19 middle occipital gyrus, 20 inferior occipital gyrus, 21 fusiform gyrus, 22 collateral sulcus, 23 parahippocampal gyrus, 24 quadrangular lobule, 25 simple lobule, 26 superior semilunar lobule, 27 transverse sinus, 28 horizontal fissure, 29 inferior semilunar lobule, 30 biventer lobule, 31 flocculus, 32 tentorium cerebelli, 33 temporal, petrous part, 34 internal carotid artery, 35 auditory tube. (e) Head section. Bar, 10 mm

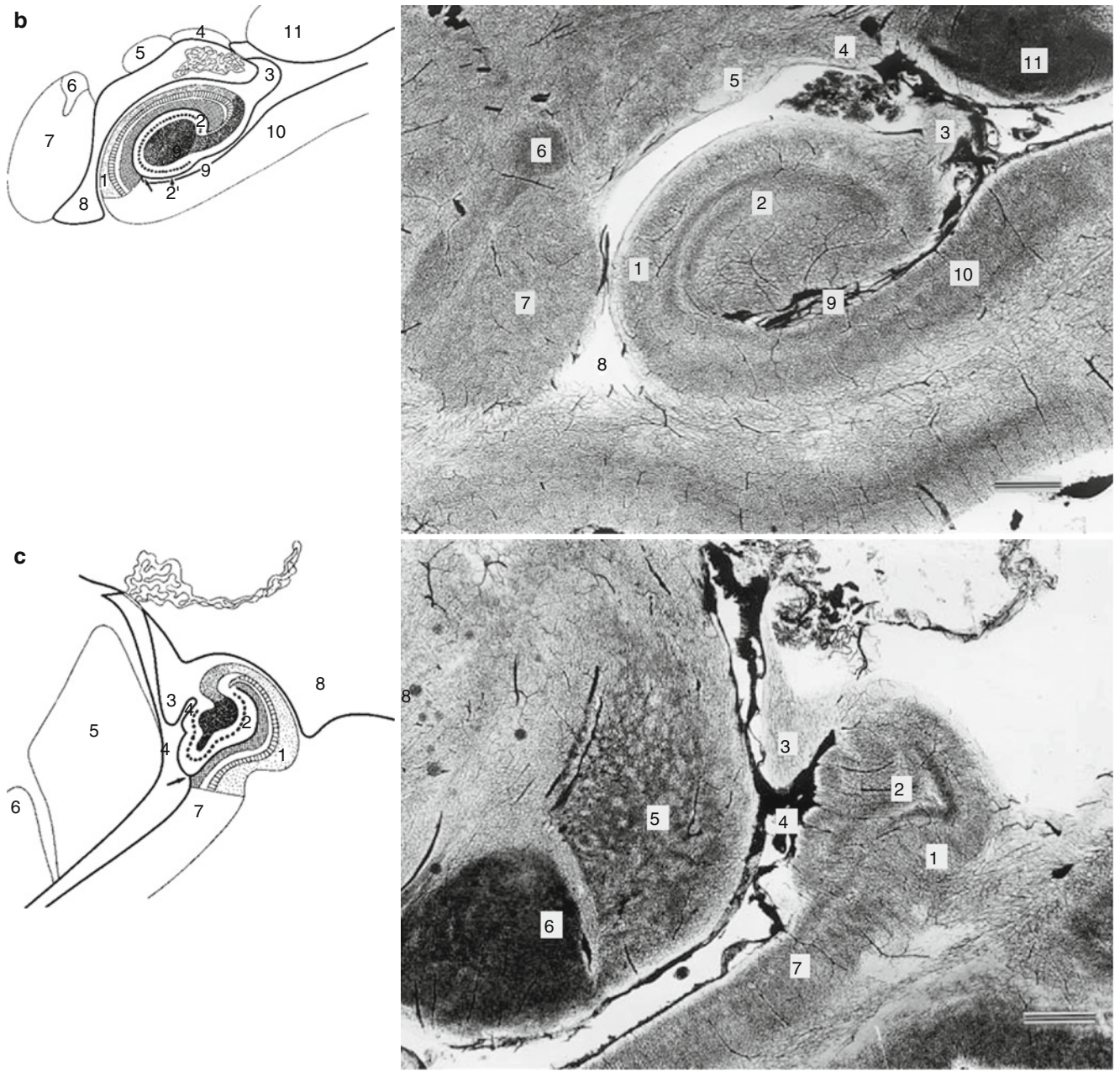
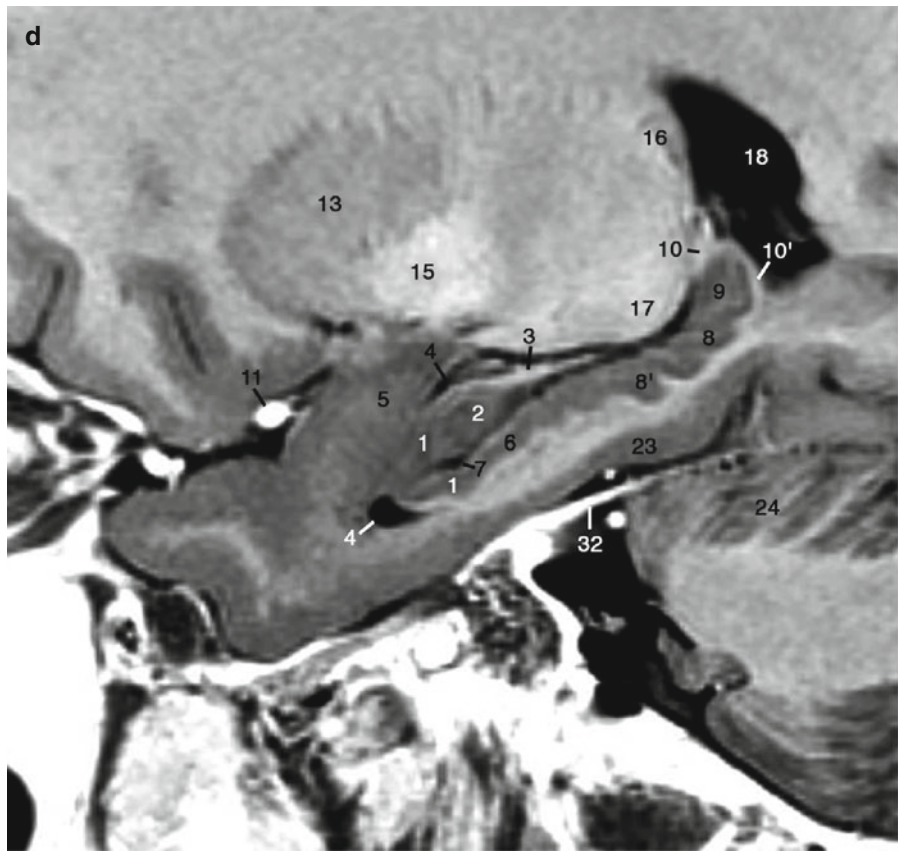


Fig. 7.17 (continued)

Fig. 7.17 (continued)



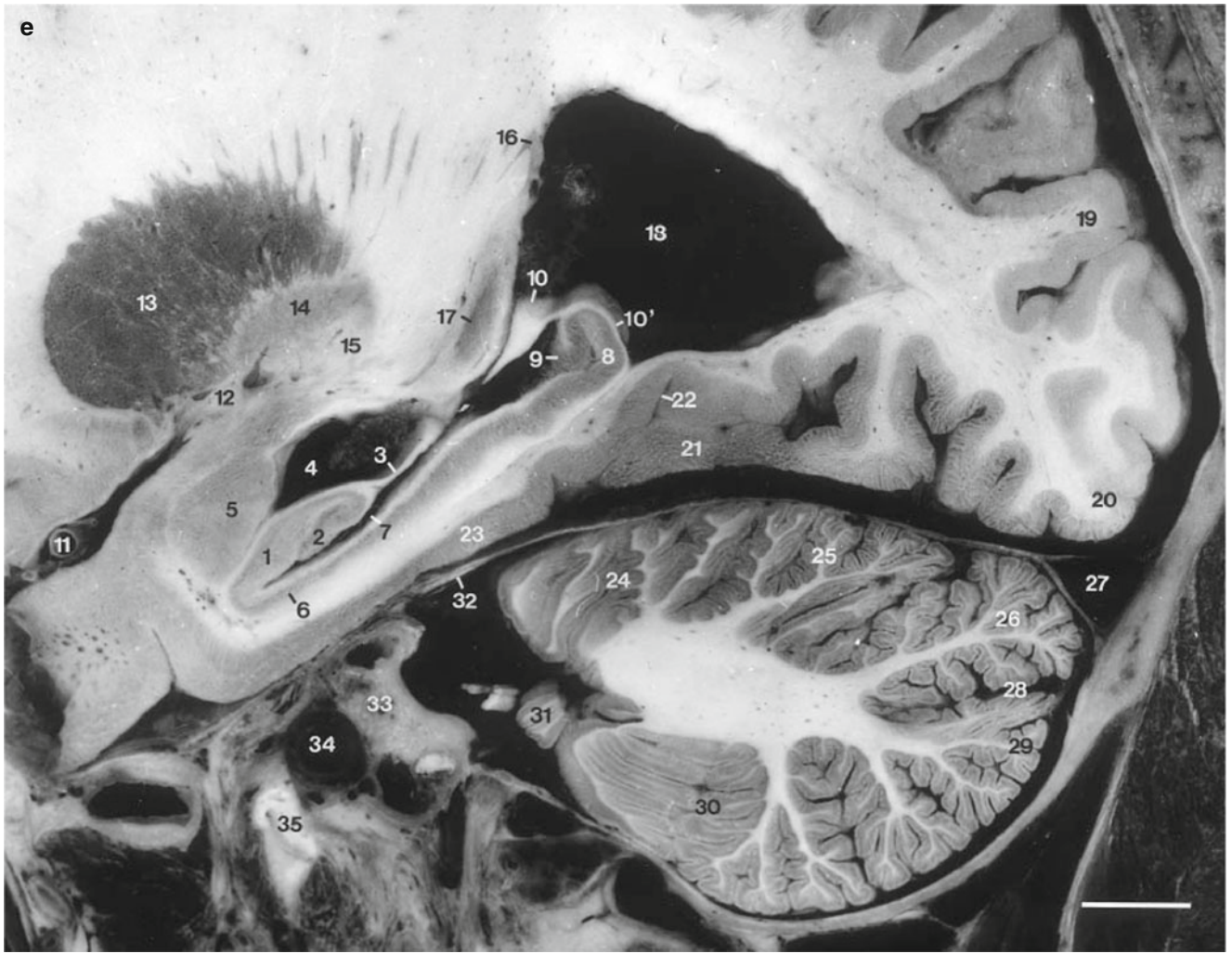


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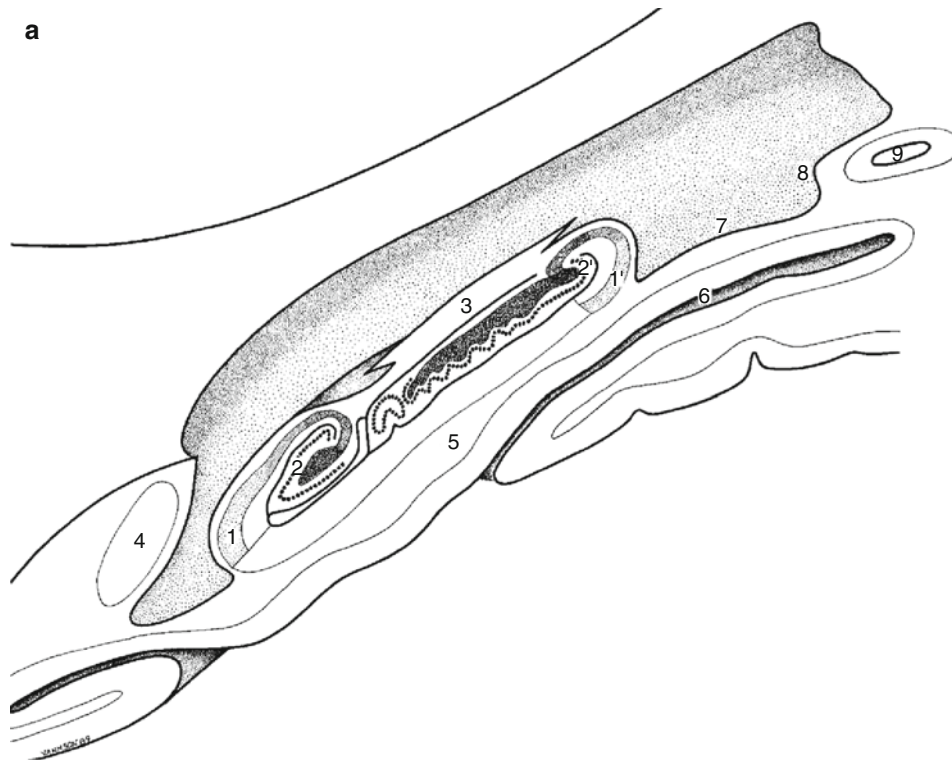


Fig. 7.18 (a) Sagittal section of hippocampus, showing plane of section. 1 cornu Ammonis in the head, 1' cornu Ammonis in the body, 2 gyrus dentatus in the head, 2' gyrus dentatus in the body, 3 fimbria, 4 amygdala, 5 parahippocampal gyrus, 6 collateral sulcus, 7 collateral trigone, 8 calcar avis, 9 calcarine sulcus. (b) Sagittal section of hippocampus. Intravascular India ink injection with explanatory diagram. Arrows indicate the superficial hippocampal sulcus. Bar, 3 mm 1 cornu Ammonis in the head (CA1–CA4), 1' cornu Ammonis in the body (CA1–CA4), 2 gyrus dentatus in the head, 2' gyrus dentatus in the body, 3 fimbria, 4 stria terminalis, 5 caudate nucleus, 6 lateral nucleus of amygdala, 7 temporal horn of lateral ventricle (uncal recess), 8 subiculum, 9 parahippocampal gyrus, 10 collateral trigone, * vestigial hippocampal sulcus. (c) 3T MRI view. 1 hippocampal head, cornu Ammonis, 1' inferior part of CA1 with a folded aspect, 2 hippocampal head, gyrus dentatus, 3 fimbria, 4 temporal (inferior) horn of the lateral ventricle, 5 Amygdala, 8 putamen, 8' striate vessels,

10 atrium of the lateral ventricle, 15 collateral sulcus, 15' collateral trigone, 16 fusiform gyrus, 17 parahippocampal gyrus, 18 quadrangular lobule, 24 tentorium cerebelli, * vestigial hippocampal sulcus. (d) Head section. Bar, 10 mm. 1 hippocampal head, cornu Ammonis, 2 hippocampal head, gyrus dentatus, 3 temporal (inferior horn) of the lateral ventricle, 4 amygdala, 5 hippocampal body, cornu Ammonis, 5' inferior part of the cornu Ammonis with a folded aspect, 6 fimbria, 6' alveus, 7 gyrus dentatus (margo denticulatus), 8 subiculum, 9 parahippocampal gyrus, 10 middle cerebral artery, 11 anterior commissure, lateral part, 12 putamen, 13 globus pallidus, lateral part, 14 caudate nucleus, 15 pulvinar, 16 atrium of the lateral ventricle, 17 middle occipital gyrus, 18 inferior occipital gyrus, 19 transverse sinus, 20 fusiform gyrus, 21 collateral sulcus, 22 quadrangular lobule, 23 simple lobule, 24 superior semilunar lobule, 25 horizontal fissure, 26 inferior semilunar lobule, 27 biventer lobule, 28 tentorium cerebelli, 29 temporal, petrous part, 30 internal carotid artery, 31 auditory tube



Fig. 7.18 (continued)

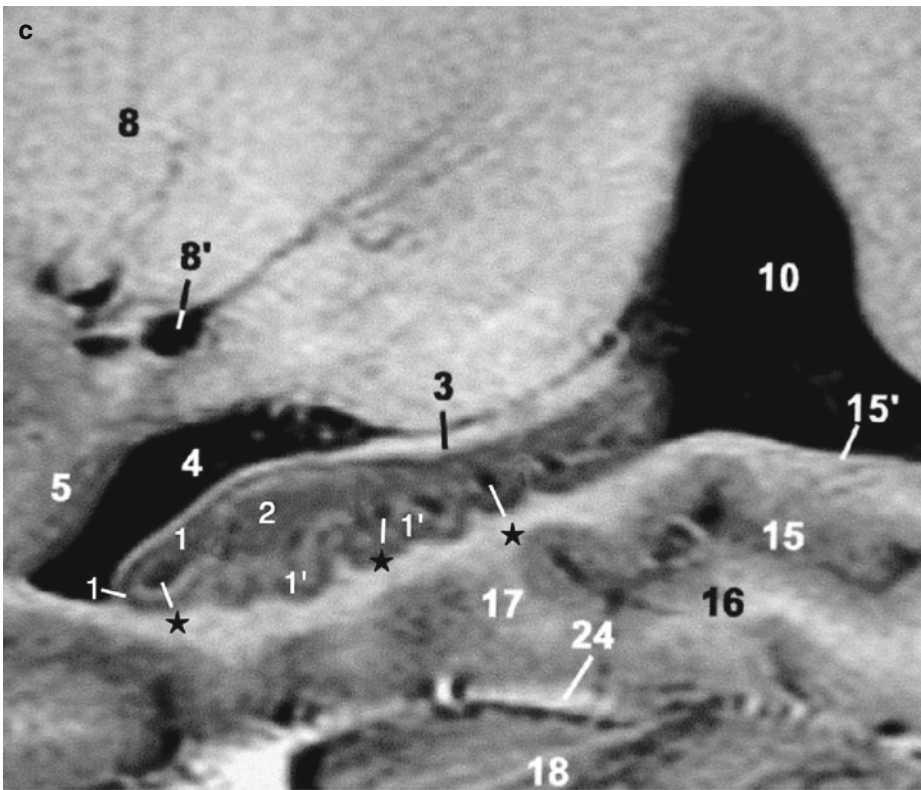


Fig. 7.18 (continued)

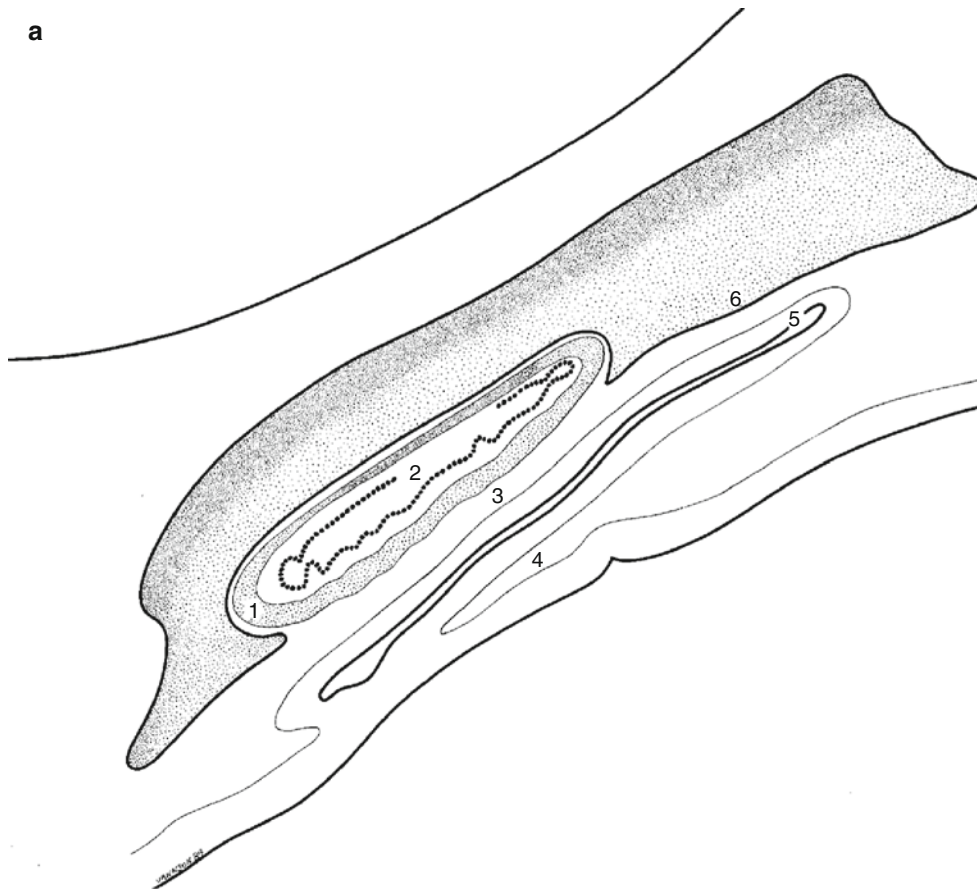


Fig. 7.19 (a) Sagittal section of hippocampus, showing plane of section. 1 cornu Ammonis in the body, 2 gyrus dentatus, 3 parahippocampal gyrus, 4 fusiform gyrus, 5 collateral sulcus, 6 collateral trigone. (b) Sagittal section of hippocampus. Intravascular India ink injection with explanatory diagram. Bar, 3 mm 1 cornu Ammonis (CA1, CA2), 1' cornu Ammonis (CA4), 1'' alveus, 2 gyrus dentatus, 3 collateral trigone, 4 atrium, 5 caudate nucleus, 6 optic radiations, 7 temporal horn, 8 parahippocampal gyrus, 9 fusiform gyrus, * vestigial hippocampal sulcus. (c) 3T MRI view. 1 cornu Ammonis, 1' inferior part of CA with a folded aspect, 2 gyrus dentatus, 3 fimbria, 4 temporal (inferior) horn of the

lateral ventricle, 5 amygdala, 6 claustrum, 7 insula, 8 putamen, 8' striate vessels, 9 caudate nucleus, 10 atrium of the lateral ventricle, 11 superior occipital gyrus, 12 middle occipital gyrus, 13 inferior occipital gyrus, 14 fourth occipital gyrus, 15 collateral sulcus, 15' collateral trigone, 16 fusiform gyrus, 17 parahippocampal gyrus, 18 simple lobule, 19 superior semilunar lobule, 20 transverse sinus, 21 horizontal fissure, 22 inferior semilunar lobule, 23 biventer lobule, 24 tentorium cerebelli, 25 temporal, petrous part, * vestigial hippocampal sulcus. (d) Head section. Bar, 10 mm

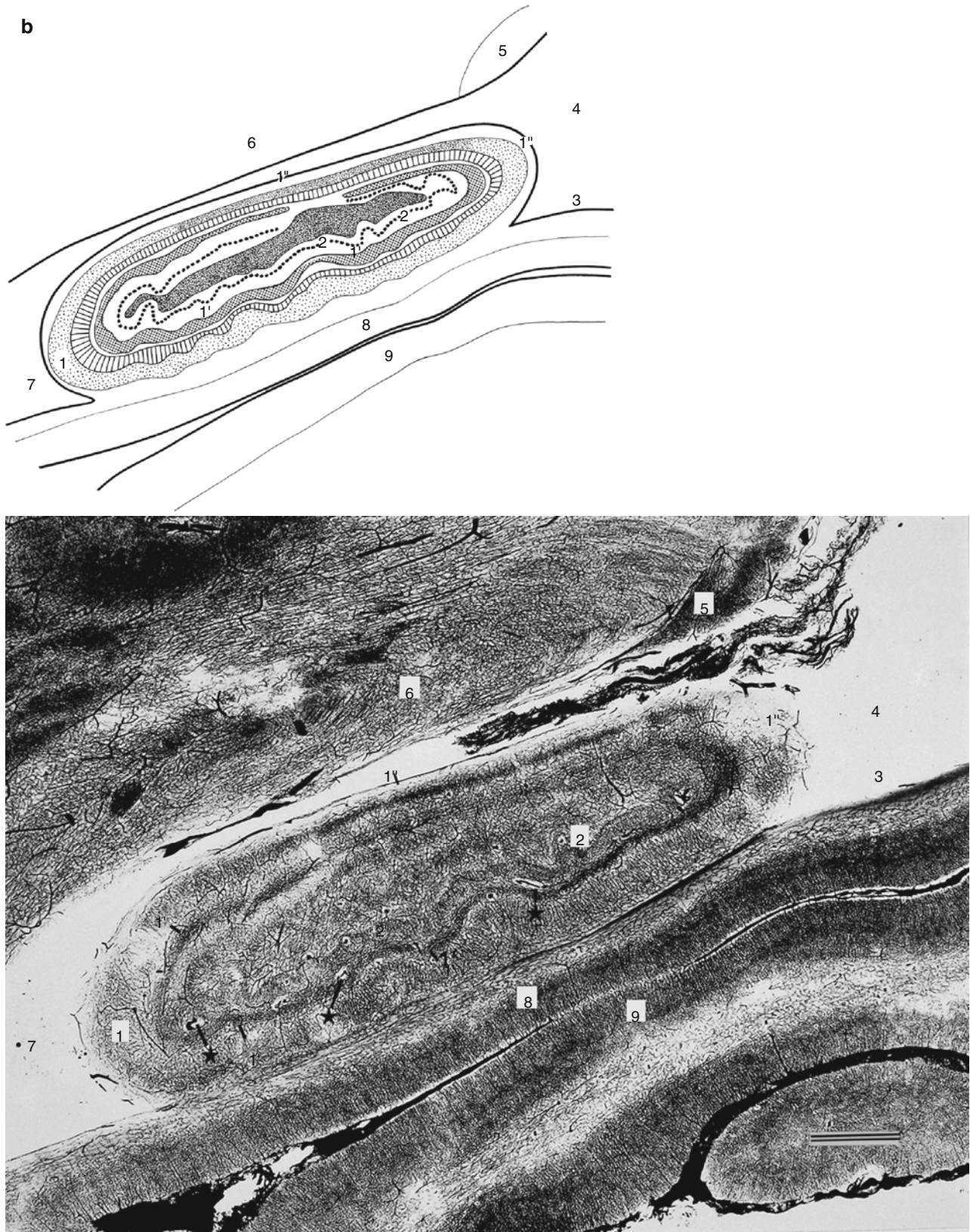


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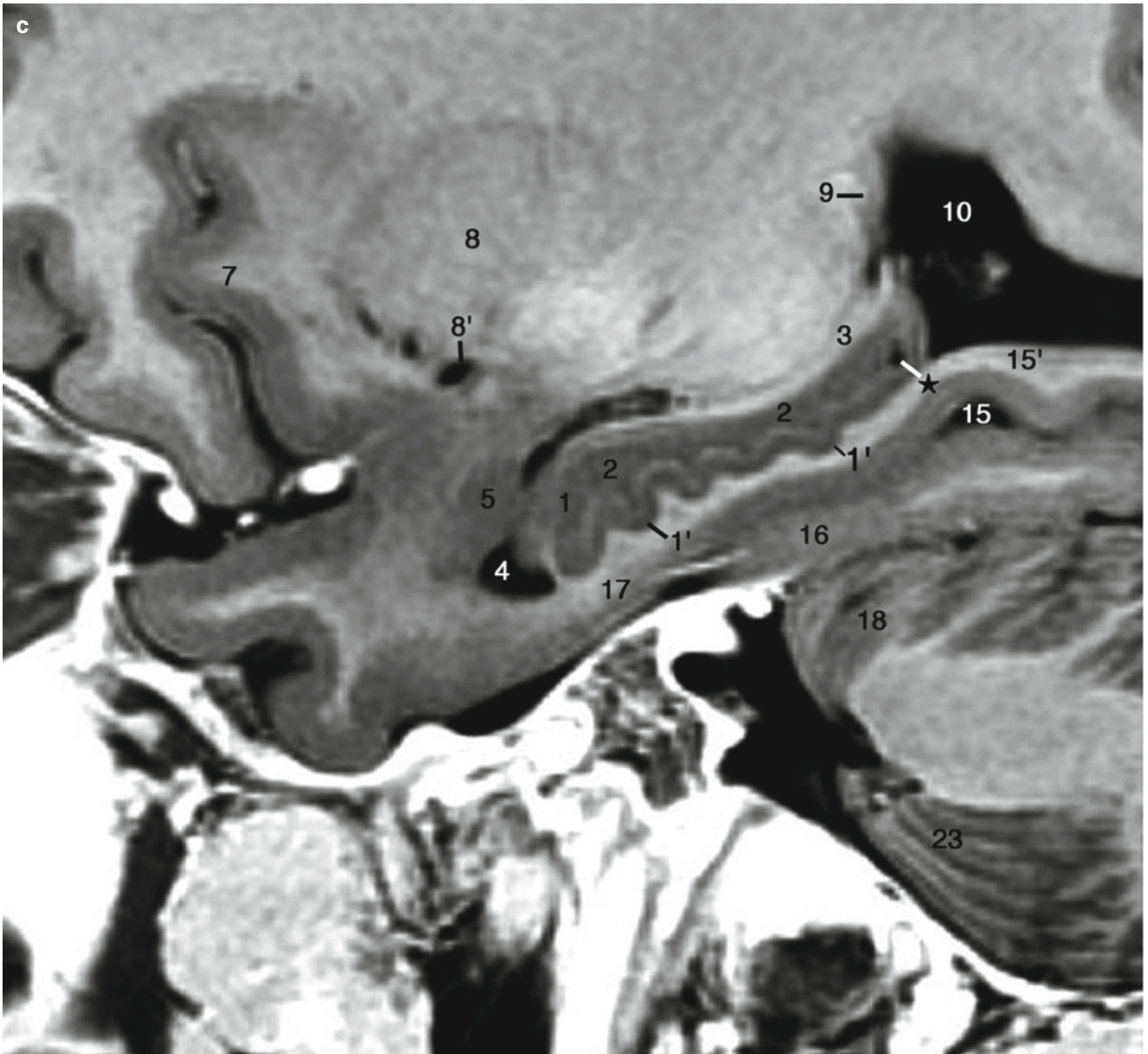


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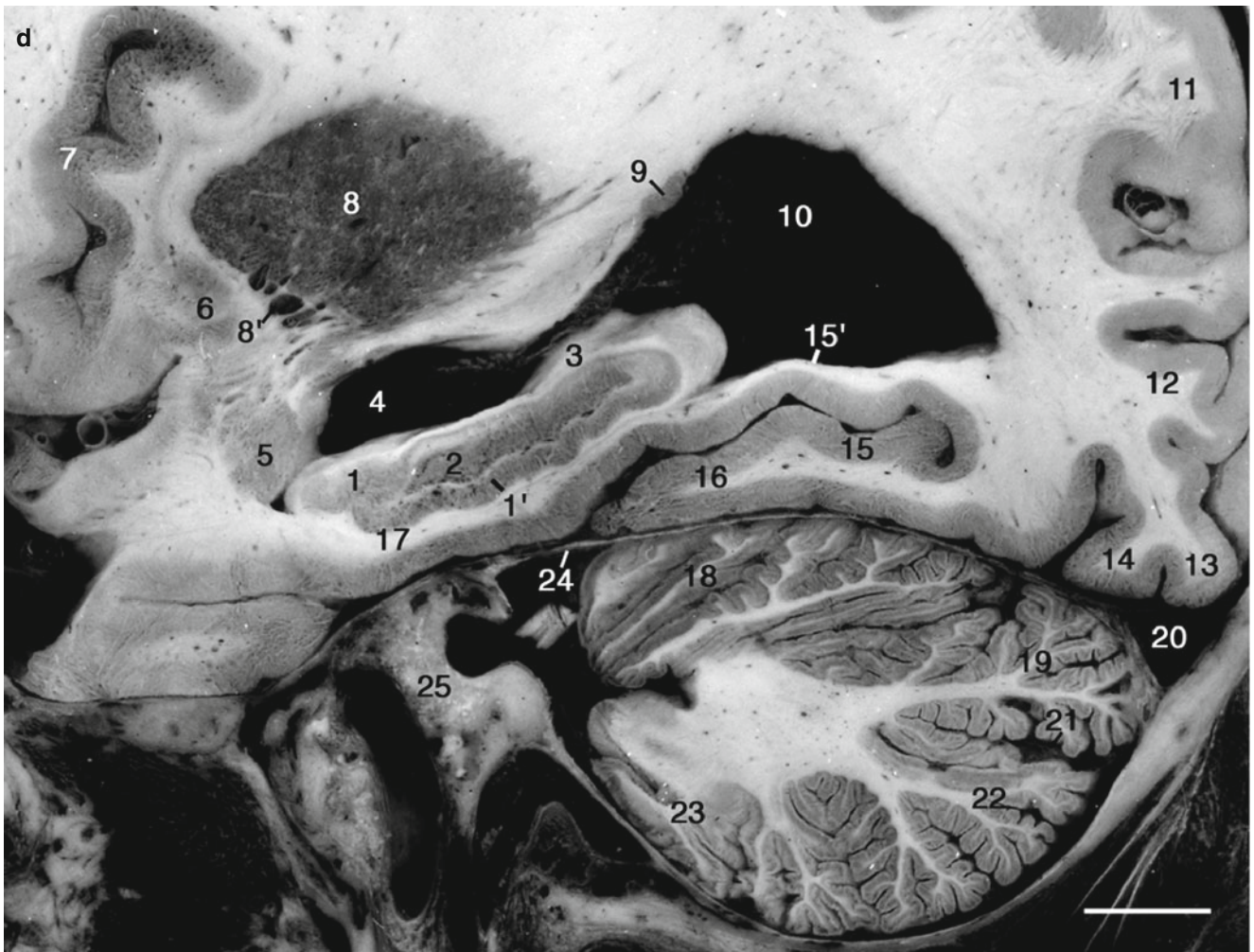


Fig. 7.19 (continued)

7.3 Axial Sections

Figures 7.21, 7.22, 7.23, 7.24, 7.25, and 7.26 show serial axial sections of the hippocampus from upper to lower levels.

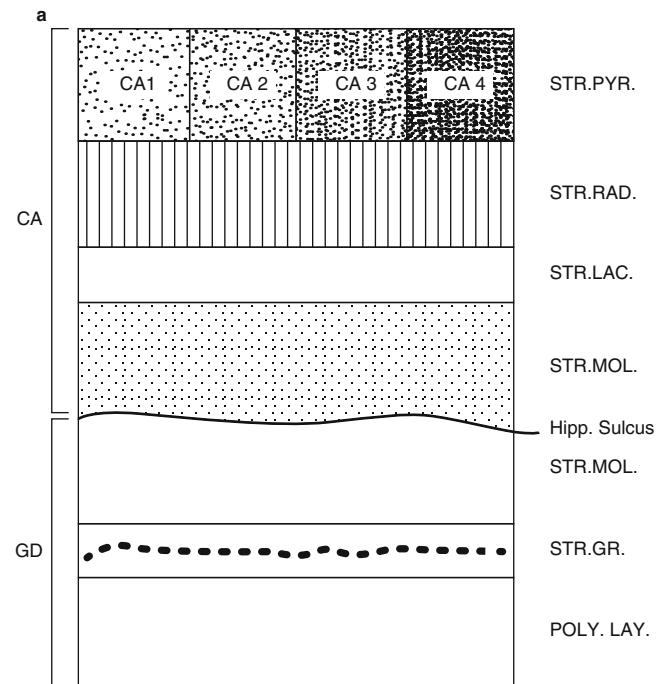


Fig. 7.20 Structure of the hippocampus *CA* cornu Ammonis, *STR. PYR.* stratum pyramidale, *STR. RAD.* stratum radiatum, *STR. LAC.* stratum lacunosum, *STR. MOL.* stratum moleculare, *Hipp. Sulcus* vestigial hippocampal sulcus, *GD* gyrus dentatus, *STR. GR.* stratum granulosum, *POLY. LAY.* polymorphic layer

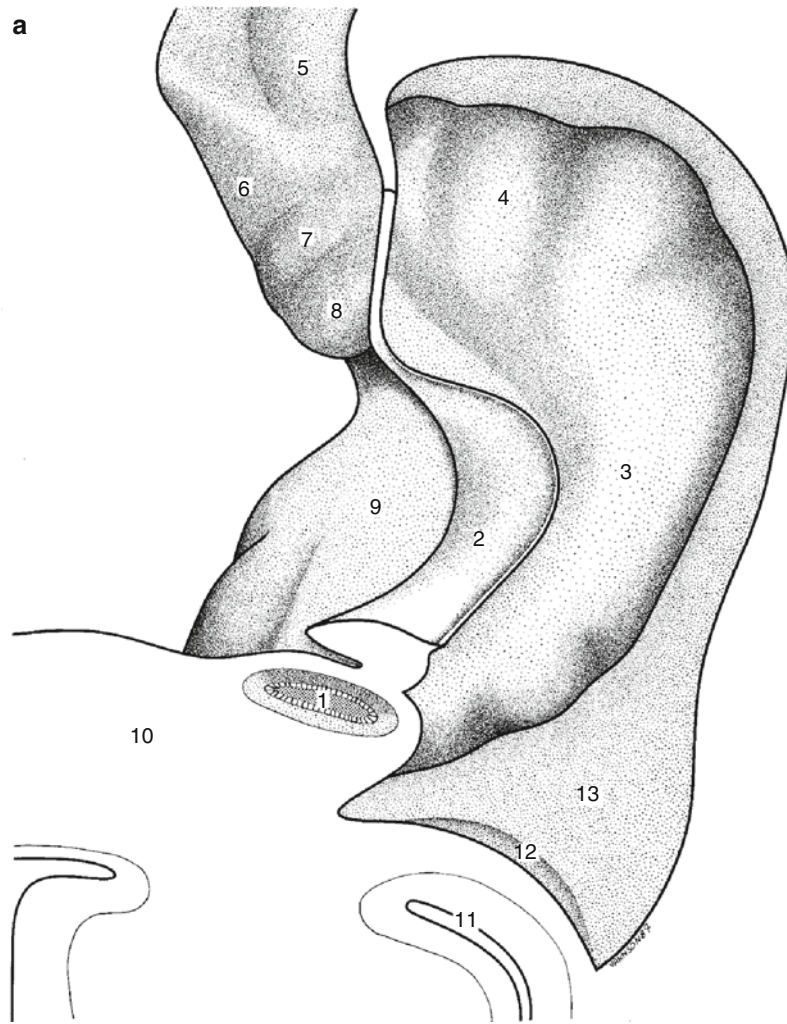


Fig. 7.21 (a) Axial section of hippocampal tail, showing plane of section and structure 1 hippocampal tail, cornu Ammonis (CA1, CA3), 2 fimbria, 3 hippocampal body, 4 hippocampal head (digitationes hippocampi), 5 semilunar gyrus, 6 uncinata gyrus, 7 band of Giacomini, 8 uncal apex, 9 parahippocampal gyrus, 10 splenium, 11 anterior calcarine sulcus, 12 calcar avis, 13 collateral trigone. (b) Axial section of hippocampal tail. Intravascular India ink injection. Bar, 2.3 mm 1 cornu Ammonis, 2 fimbria, 3 atrium of the lateral ventricle, 4 caudate nucleus, 5 pulvinar, 6 transverse fissure, lateral part, 7 splenium. (c) 3T MRI view. 1 hippocampal tail, cornu Ammonis, 2 fimbria, 3 tail of caudate nucleus, 4 atrium of the lateral ventricle, 5 splenium of corpus callosum,

6 pulvinar, 7 stria medullaris, 7' internal cerebral veins, 8 third ventricle, 9 dorsomedial thalamic nucleus, 10 lateral posterior thalamic nucleus, 11 ventral lateral thalamic nucleus, 12 anterior thalamic nucleus, 13 fornix, 14 frontal (anterior) horn of the lateral ventricle, 15 genu of corpus callosum, 16 head of caudate nucleus, 17 internal capsule, anterior limb, 18 internal capsule, genu, 19 internal capsule, posterior limb, 20 putamen, 21 claustrum, 22 insula, 23 precentral gyrus, 24 central sulcus, 25 postcentral gyrus, 26 superior temporal gyrus, 27 superior temporal sulcus, 28 middle temporal gyrus, 29 calcarine sulcus and striate cortex, 30 parieto-occipital fissure, 31 cingulate gyrus. (d) Head section. Bar, 10 mm



Fig. 7.21 (continued)

Fig. 7.21 (continued)

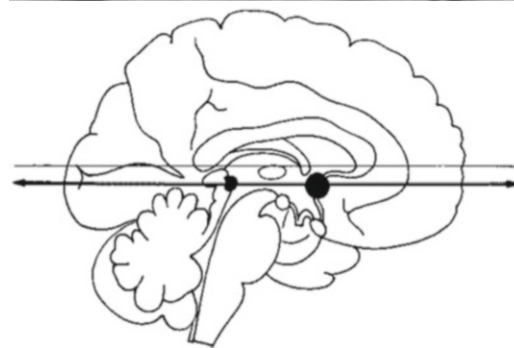




Fig. 7.21 (continued)

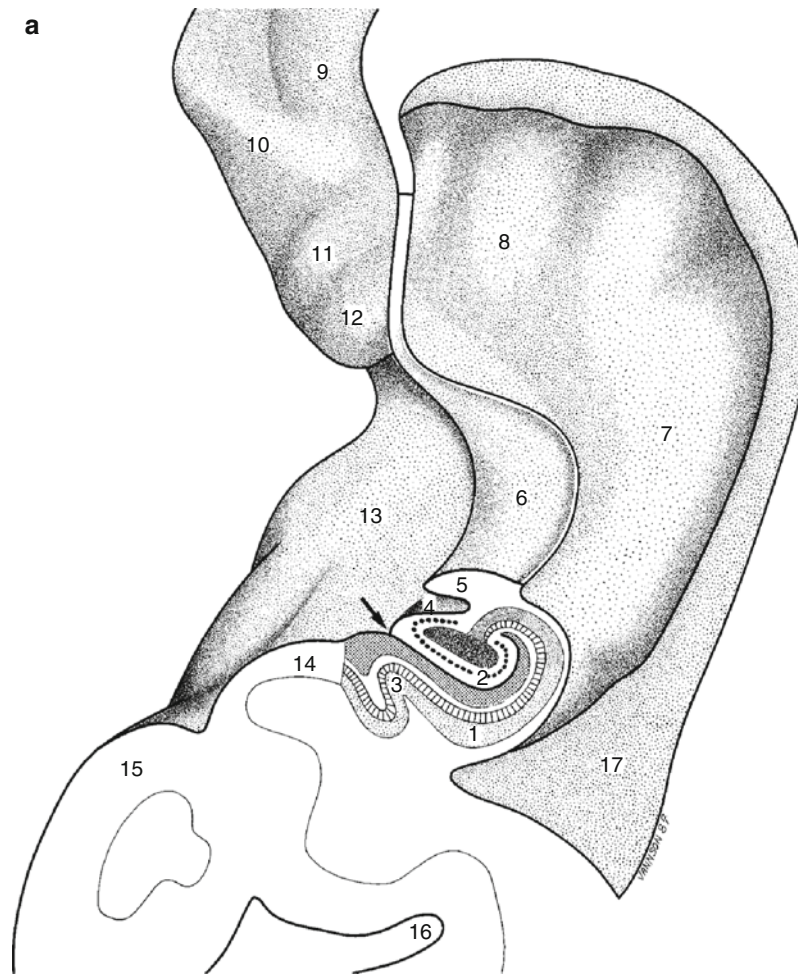


Fig. 7.22 (a) Axial section of hippocampal tail, showing plane of section and structure. *Arrow* indicates the superficial hippocampal sulcus 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, 3 fold of CA1 and gyri of Andreas Retzius (not clearly visible at the surface here), 4 margo denticulatus, 5 cut surface of the fimbria, 6 fimbria, 7 hippocampal body, 8 hippocampal head (digitationes hippocampi), 9 semilunar gyrus, 10 uncinata gyrus, 11 band of Giacomini, 12 uncal apex, 13 parahippocampal gyrus, 14 subiculum, 15 isthmus, 16 anterior calcarine sulcus, 17 collateral eminence. (b) Axial section of hippocampal tail. Intravascular India ink injection. *Bar*, 2 mm 1 cornu Ammonis, 2 gyrus dentatus, 3 fold of CA1 and gyri of Andreas Retzius (not clearly visible at the surface here), 4 margo denticulatus, 5 fimbria, 6 tail of caudate nucleus, 7 stria terminalis, 8 pulvinar, 9 transverse fissure, lateral part, 10 subiculum, 11 temporal horn of the lateral ventricle. (c) 3T MRI view. 1 hippocampal

tail, cornu Ammonis, 2 hippocampal tail, gyrus dentatus, 3 gyrus of Andreas Retzius, 4 fimbria, 5 tail of caudate nucleus, 6 pulvinar, 7 ventral posterolateral thalamic nucleus, 8 superior colliculus, 9 pineal gland, 10 posterior commissure, 11 third ventricle, 12 dorsomedial thalamic nucleus, 13 ventral lateral thalamic nucleus, 14 mamillothalamic tract, 15 interthalamic adhesion, 16 column of fornix, 16' anterior commissure, lateral part, 17 lateral ventricle, frontal horn, 18 head of caudate nucleus, 19 internal capsule, anterior limb, 20 claustrum, 21 insula, 22 putamen, 23 globus pallidus, lateral part, 24 globus pallidus, medial part, 25 internal capsule, posterior limb, 26 lateral fissure, 27 superior temporal gyrus, 28 superior temporal sulcus, 29 middle temporal gyrus, 30 optic radiations, 31 occipital horn of the lateral ventricle, 32 isthmus, 33 anterior calcarine sulcus, 34 lingual gyrus, 35 culmen, 36 tentorium cerebelli, 37 quadrigeminal cistern. (d) Head section. *Bar*, 10 mm

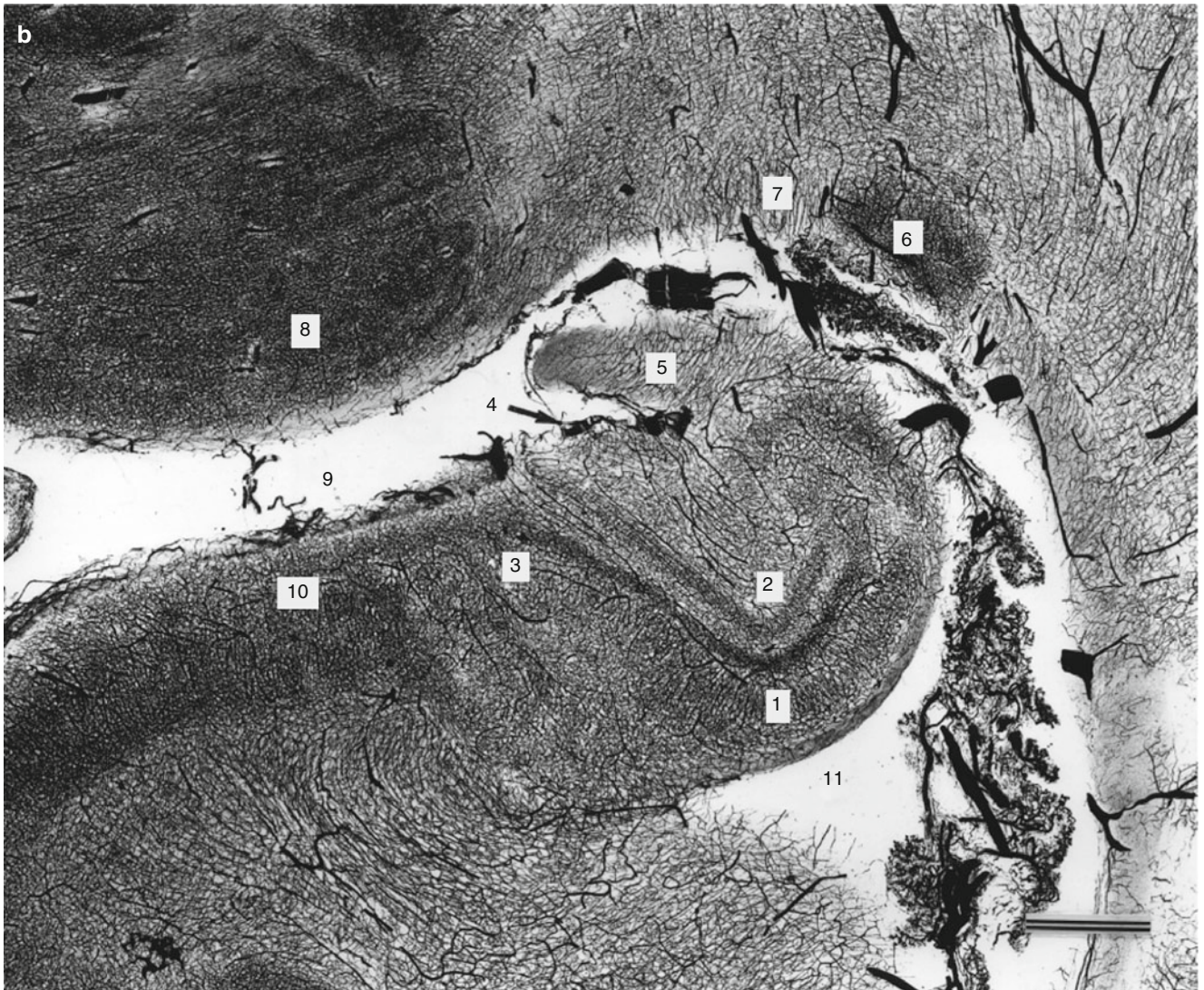
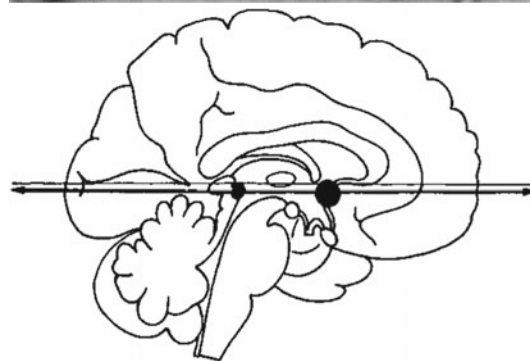
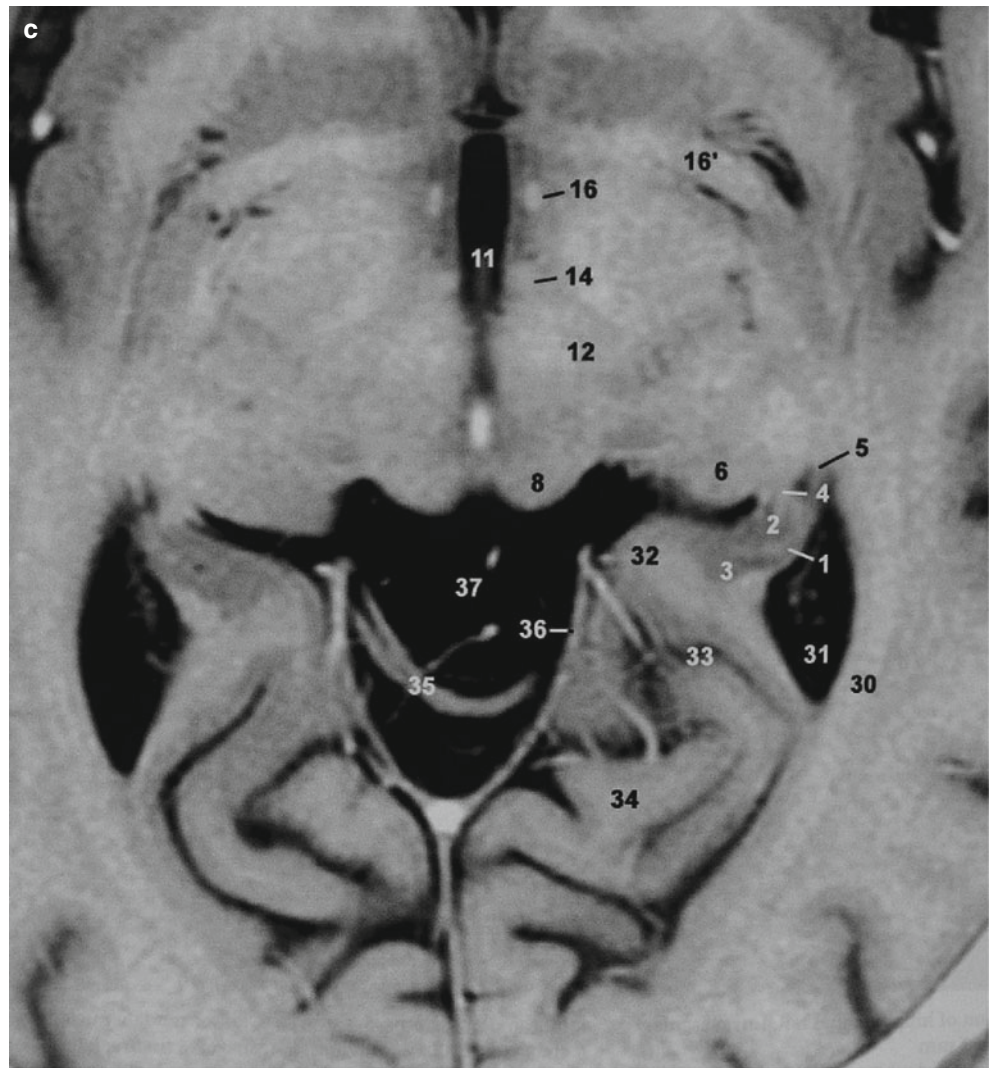


Fig. 7.22 (continued)

Fig. 7.22 (continued)



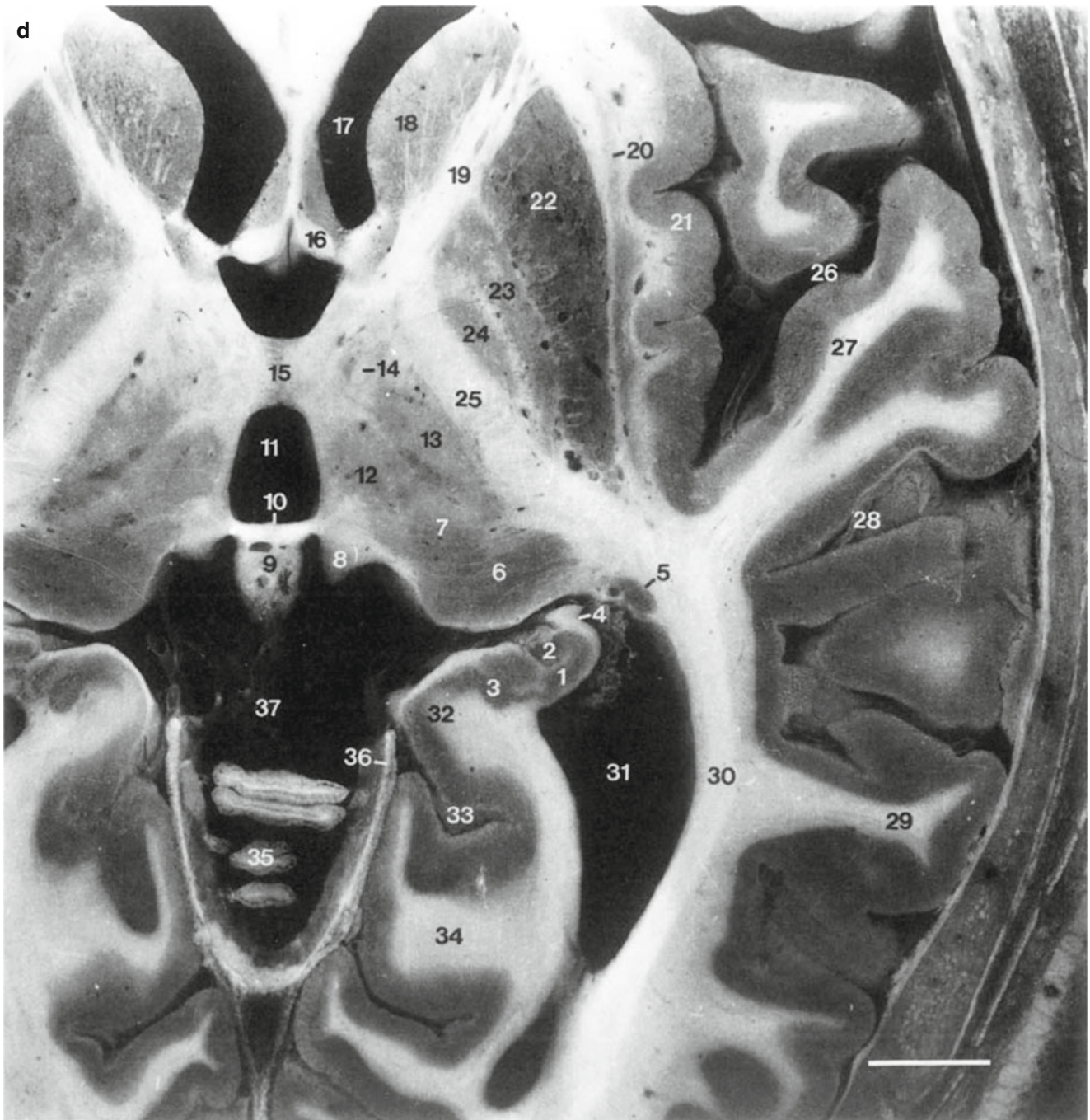


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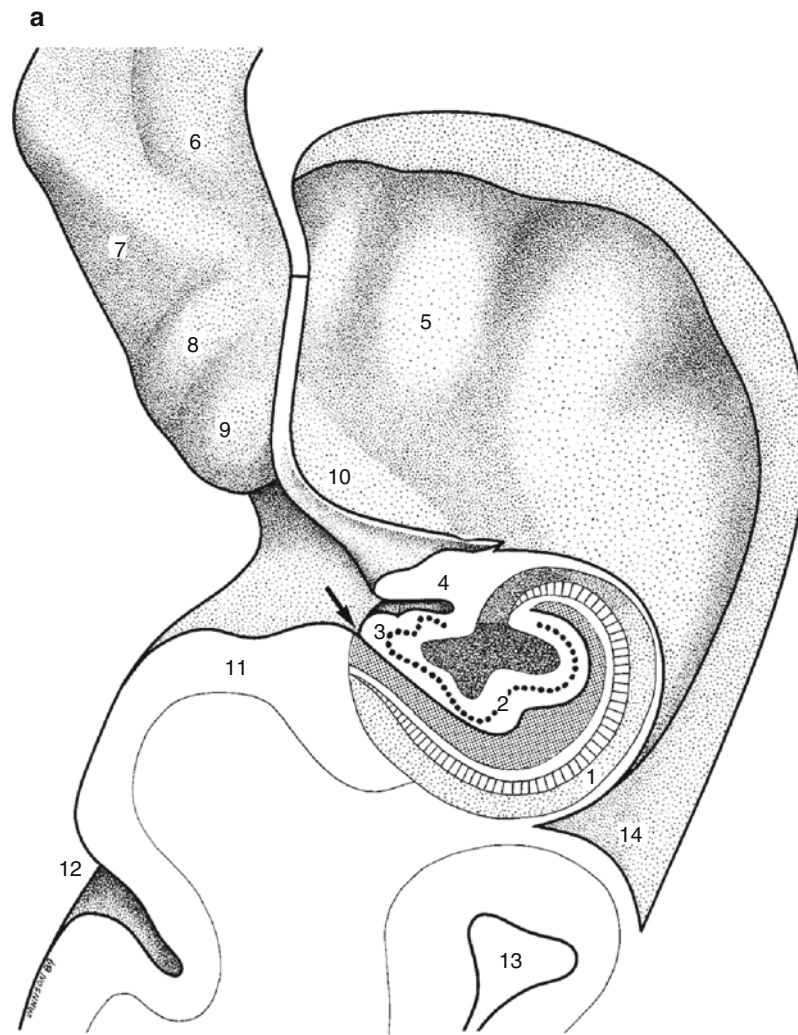


Fig. 7.23 (a) Axial section of hippocampal body, showing plane of section and structure. Arrow indicates the superficial hippocampal sulcus. 1 cornu Ammonis (CA1–CA4), 2 gyrus dentatus, 3 margo denticulatus, 4 cut surface of fimbria, 5 hippocampal head (digitations hippocampi), 6 semilunar gyrus, 7 uncinatus gyrus, 8 band of Giacomini, 9 uncus apex, 10 fimbria, 11 subiculum, 12 anterior calcarine sulcus, 13 collateral sulcus, 14 collateral eminence. (b) Axial section of hippocampal body. Intravascular India ink injection. Bar, 2.3 mm 1 cornu Ammonis, 2 gyrus dentatus, 3 margo denticulatus, 4 fimbria, 5 tail of caudate nucleus, 6 stria terminalis, 7 lateral geniculate body, 8 pulvinar, 9 medial geniculate body, 10 subiculum, 11 anterior calcarine sulcus, 12 collateral sulcus, 13 collateral eminence, 14 temporal horn of the lateral ventricle. (c) 3T MRI view. 1 hippocampal body, cornu Ammonis, 2 hippocampal body, gyrus dentatus, 3 fimbria, 4

subiculum, 5 collateral eminence, 6 temporal (inferior) horn of the lateral ventricle, 7 pulvinar, 8 lateral geniculate body, 9 medial geniculate body, 10 superior colliculus, 11 cerebral aqueduct, 11' periaqueductal gray matter, 12 red nucleus, 13 substantia nigra, 14 mamillothalamic tract, 15 third ventricle, 16 column of fornix, 17 anterior commissure, medial part, 17' anterior commissure, lateral part, 18 caudate nucleus, 19 claustrum, 20 insula, 21 putamen, 22 globus pallidus, lateral part, 23 globus pallidus, medial part, 24 internal capsule, posterior limb, 25 lateral fissure, 26 superior temporal gyrus, 27 superior temporal sulcus, 28 middle temporal gyrus, 29 collateral sulcus, 29' lingual sulcus, 30 lingual gyrus, 31 tentorium cerebelli, 32 parahippocampal gyrus, 32' anterior calcarine sulcus, 33 quadrigeminal cistern, 34 ambient cistern, 35 wing of ambient cistern, 36 culmen. (d) Head section. Bar, 10 mm

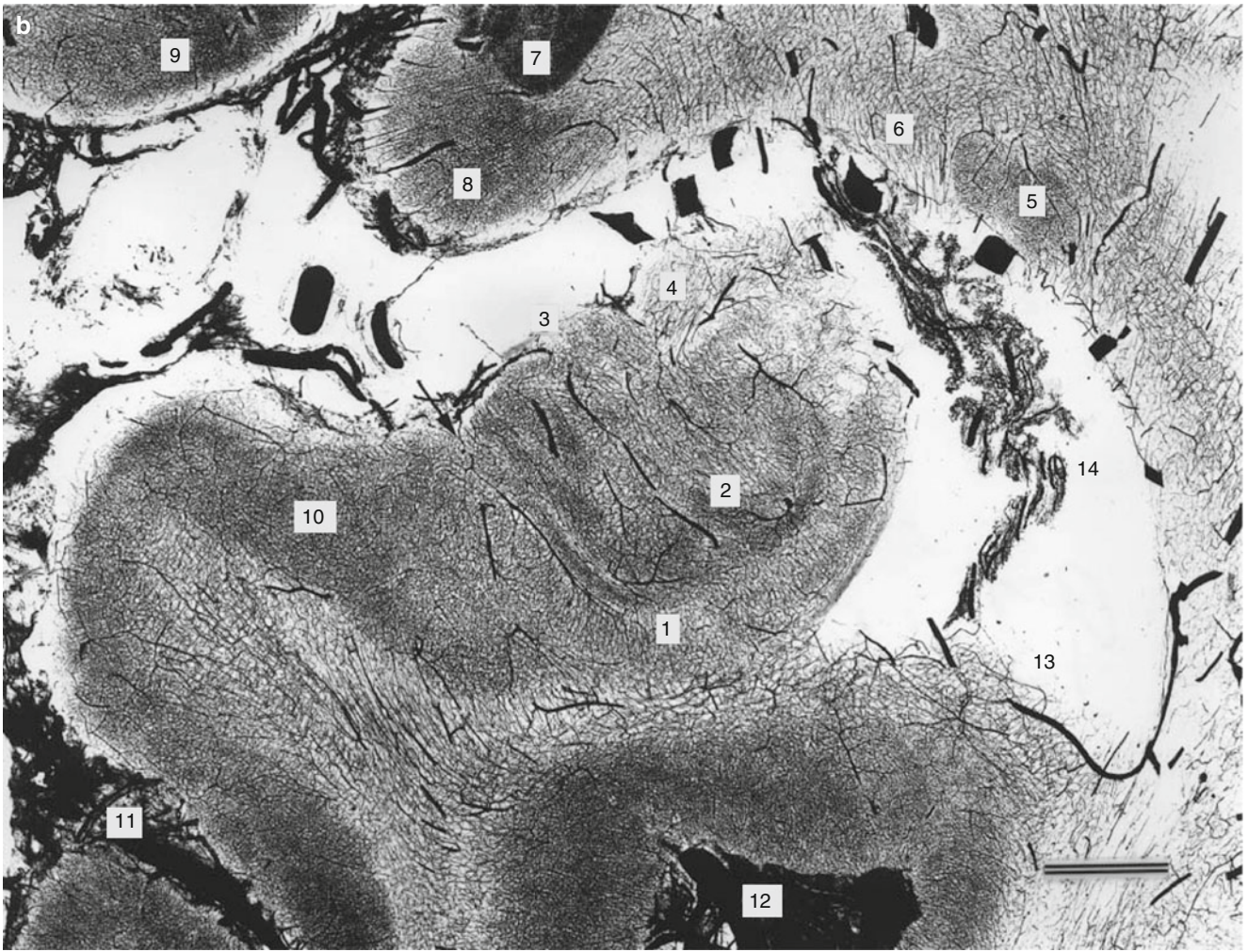
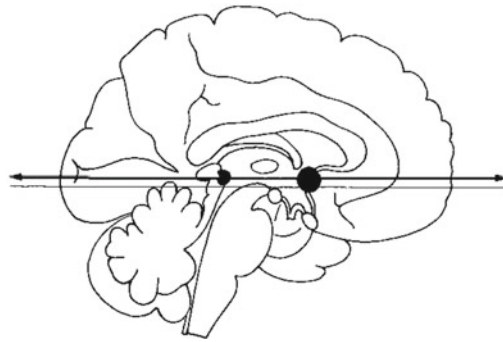
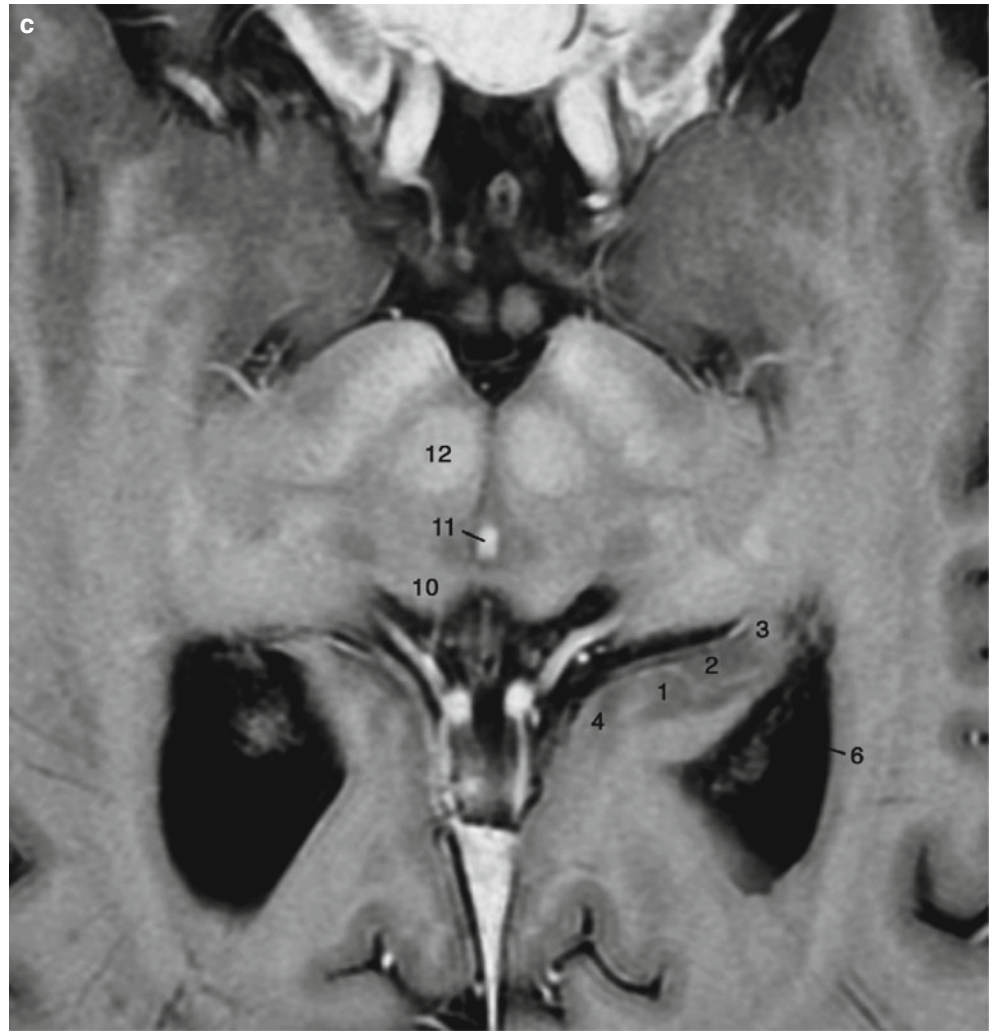


Fig. 7.23 (continued)

Fig. 7.23 (continued)



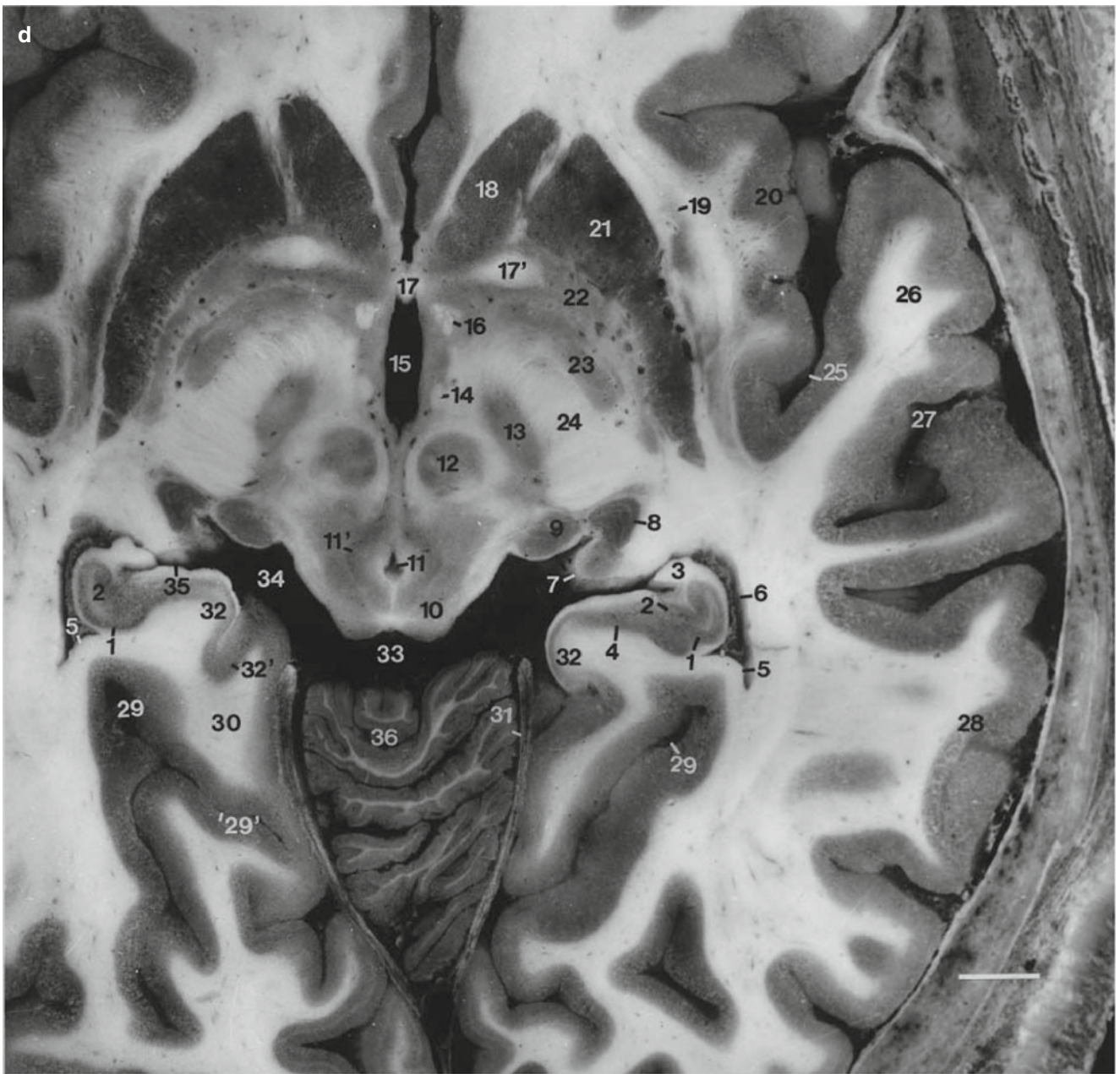


Fig. 7.23 (continued)

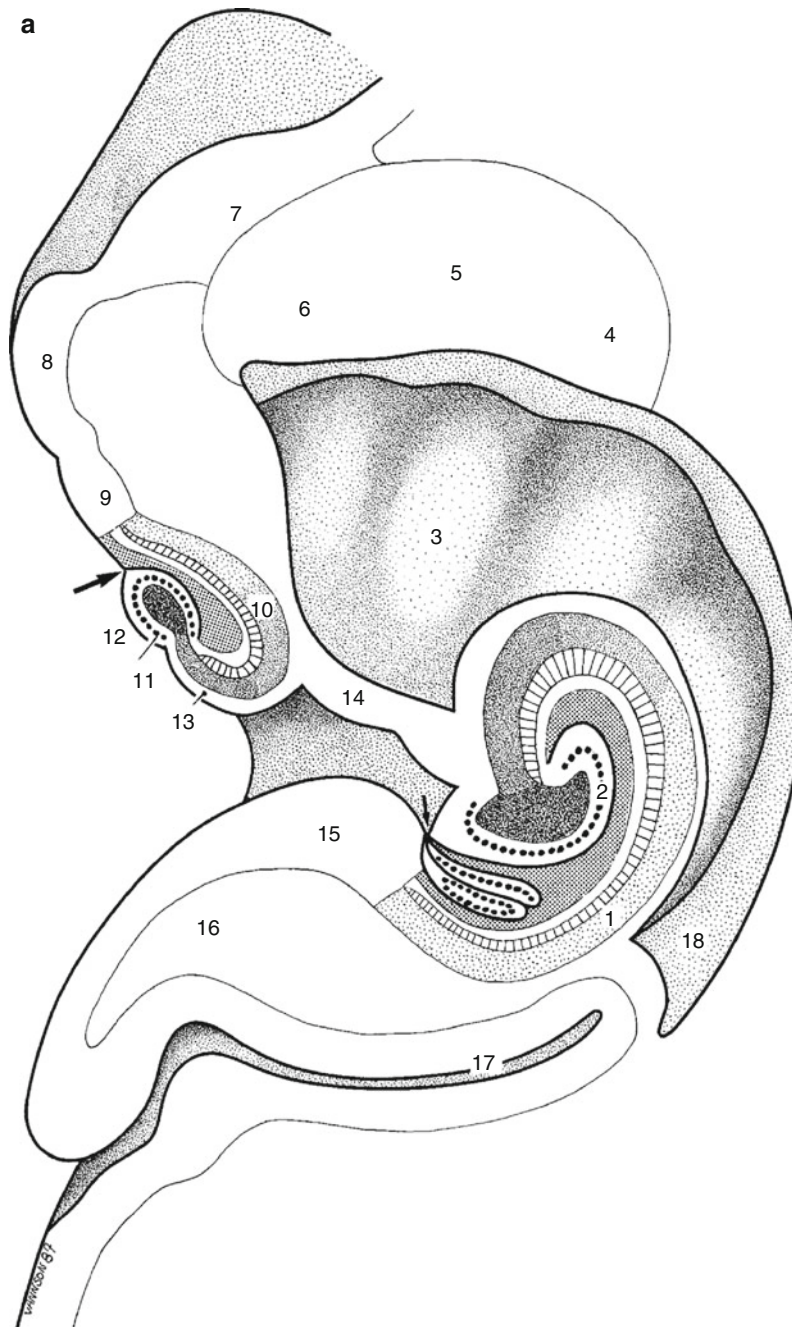


Fig. 7.24 (a) Axial section of the hippocampal body and head, showing plane of section and structure. *Arrows* indicate the superficial hippocampal sulcus. 1 cornu Ammonis in the body (CA1–CA4), 2 gyrus dentatus in the body, 3 hippocampal head (digitationes hippocampi), 4 lateral nucleus of amygdala, 5 basal nucleus of amygdala, 6 accessory basal nucleus of amygdala, 7 cortical nucleus of amygdala, 8 uncinatus gyrus, 9 subiculum, 10 cornu Ammonis in the uncus (CA1–CA4), 11 gyrus dentatus in the uncus, 12 band of Giacomini, 13 uncal apex covered with alveus, 14 fimbria, 15 subiculum, 16 parahippocampal gyrus, 17 collateral sulcus, 18 collateral eminence. (b) Axial section of the hippocampal body and head. Intravascular India ink injection. *Bar*, 2.6 mm 1 cornu Ammonis in the body, 2 gyrus dentatus in the body, 3 tail of caudate nucleus, 4 lateral nucleus of amygdala, 5 basal nucleus of amygdala, 6 accessory basal nucleus of amygdala, 7 cortical nucleus of amygdala, 8 uncinatus gyrus, 9 subiculum in the uncinatus gyrus, 10 cornu Ammonis in

the uncus, 11 gyrus dentatus in the uncus, 12 band of Giacomini, 13 uncal apex, 14 fimbria, 15 temporal horn of the lateral ventricle and choroid plexuses, 16 subiculum. (c) 3T MRI view. 1 hippocampal body, cornu Ammonis, 1' digitationes hippocampi, 2 hippocampal body, gyrus dentatus, 3 subiculum, 4 temporal (inferior) horn of the lateral ventricle, 5 hippocampal head, uncal apex, 6 amygdala, lateral nucleus, 7 amygdala, basal nucleus, 8 amygdala, cortical nucleus, 9 optic tract, 9' optic chiasma, 10 mamillary body, 11 tuber, 12 third ventricle, 13 anterior perforated substance, 14 nucleus accumbens, 15 claustrum, 16 insula, 17 lateral fissure, 18 superior temporal gyrus, 19 superior temporal sulcus, 20 middle temporal gyrus, 21 collateral sulcus, 22 lingual gyrus, 23 parahippocampal gyrus, 24 tentorium cerebelli, 25 culmen, 26 quadrigeminal cistern, 27 cerebral aqueduct, 27' periaqueductal gray matter, 28 brachium conjunctivum, 29 red nucleus, 30 substantia nigra, 31 crus cerebri, 32 crural cistern, 33 ambient cistern. (d) Head section. *Bar*, 10 mm

Fig. 7.24 (continued)

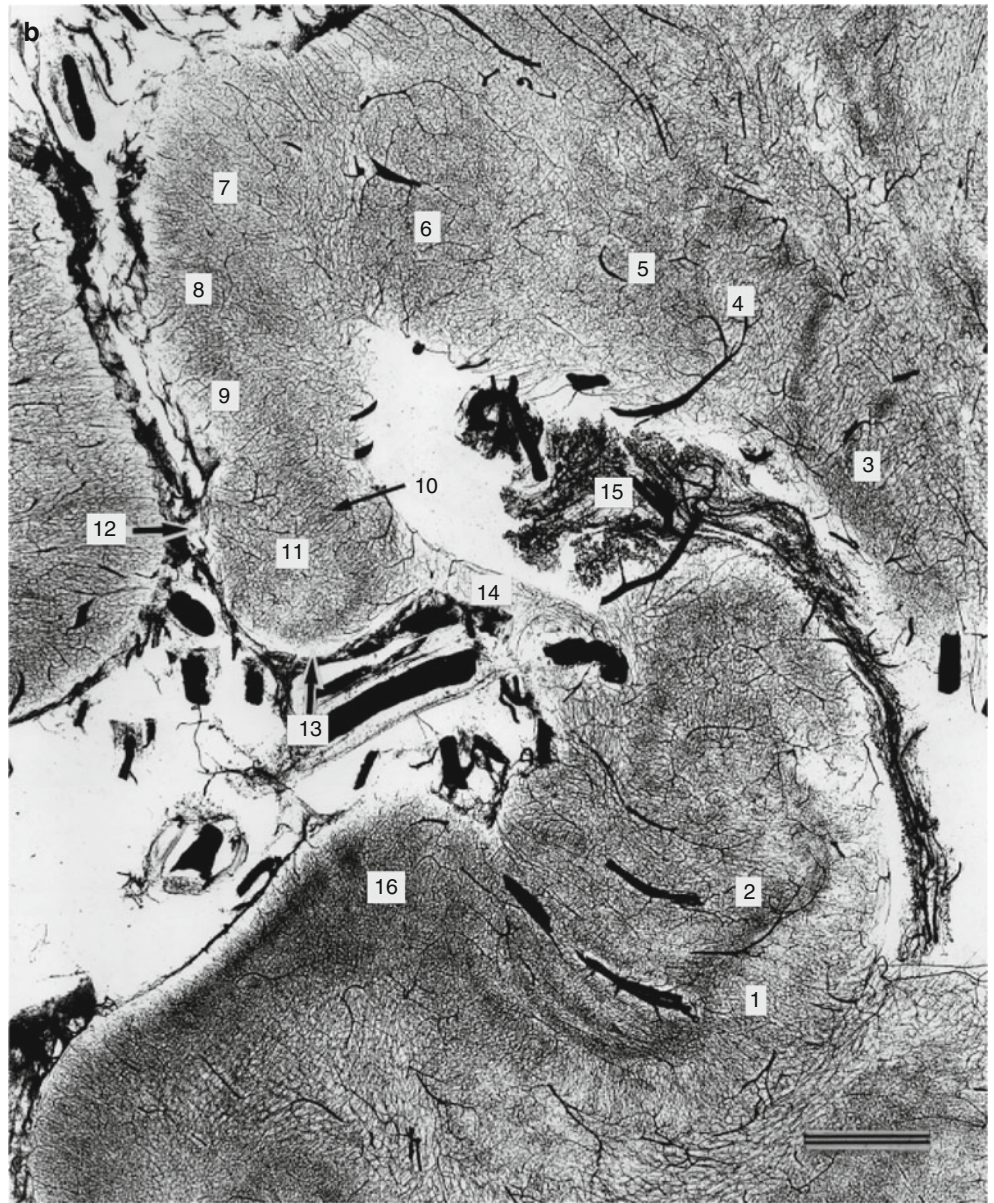


Fig. 7.24 (continued)

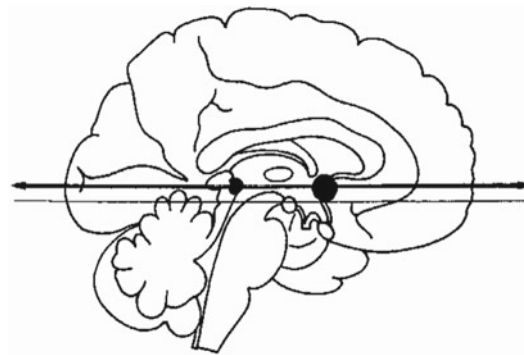
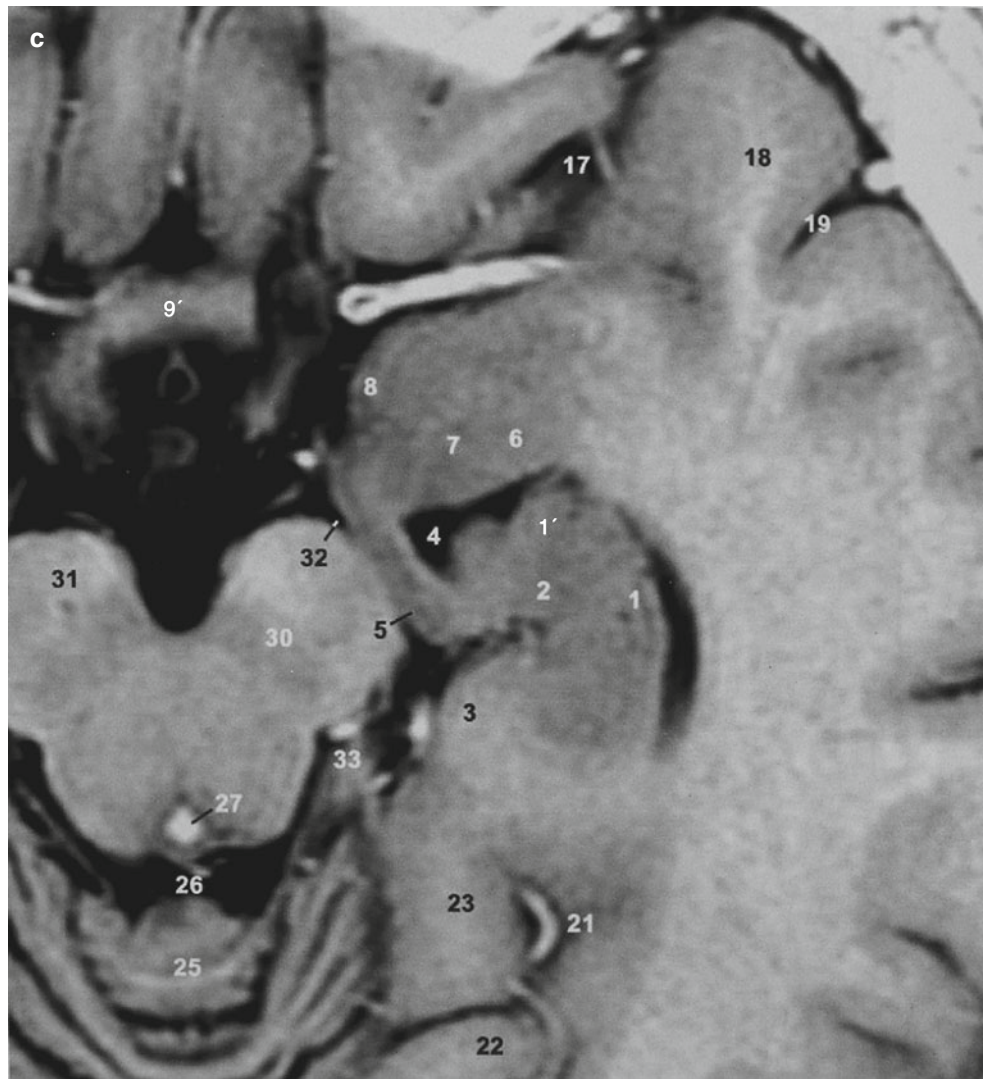




Fig. 7.24 (continued)

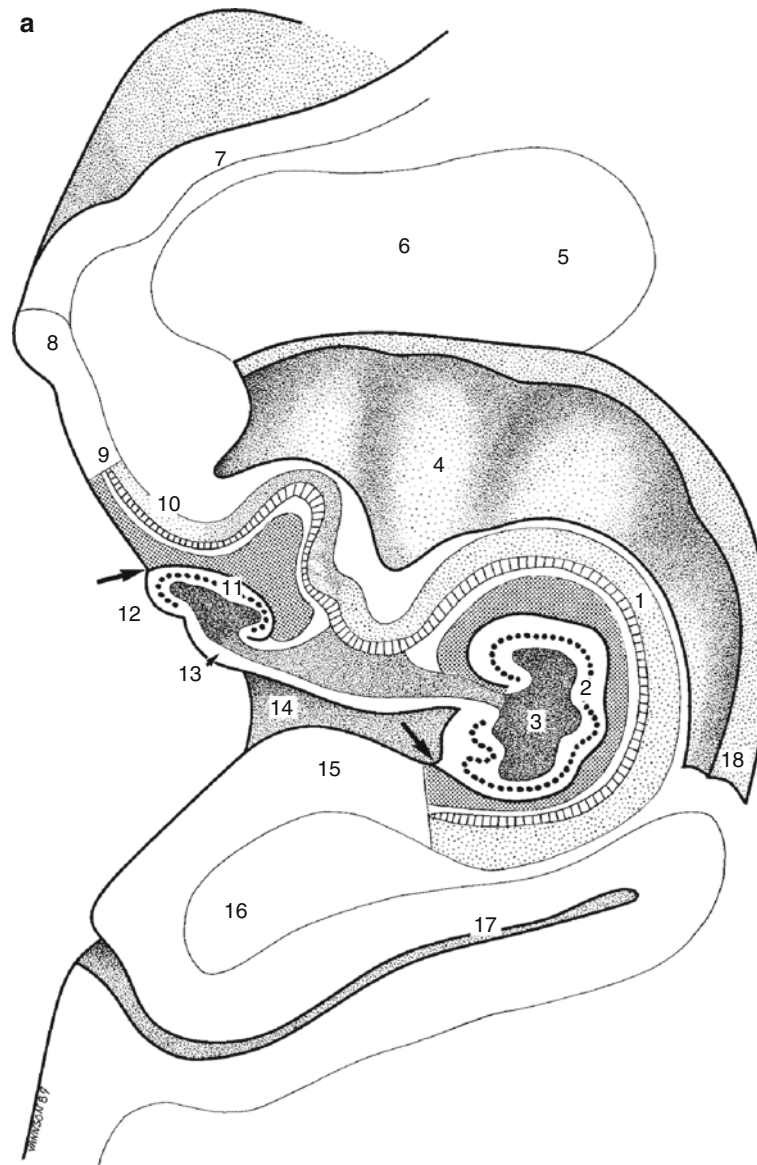


Fig. 7.25 (a) Axial section of hippocampal head, showing plane of section and structure. *Arrows* indicate the superficial hippocampal sulcus 1 cornu Ammonis (CA1) in digitationes hippocampi (internal digitations), 2 gyrus dentatus, 3 CA4 field of cornu Ammonis, 4 digitationes hippocampi (internal digitations), 5 lateral nucleus of amygdala, 6 basal nucleus of amygdala, 7 ambient gyrus, 8 uncinata gyrus, 9 subiculum in the uncinata gyrus, 10 cornu Ammonis in the uncinata gyrus (CA1), 11 gyrus dentatus in the uncal apex, 12 band of Giacomini, 13 uncal apex covered with alveus, 14 uncal sulcus, 15 subiculum, 16 parahippocampal gyrus, 17 collateral sulcus, 18 collateral eminence. (b) Axial section of hippocampal head. Intravascular India ink injection. *Bar*, 2.6 mm 1 cornu Ammonis, 2 gyrus dentatus, 3 CA4 field, 4 digitationes hippocampi (internal digitations), 5 lateral nucleus of amygdala, 6 basal nucleus of amygdala, 7 ambient gyrus, 8 uncinata gyrus, 9 subiculum in the uncinata gyrus, 10 cornu Ammonis in the uncinata gyrus, 11 gyrus dentatus, 12 band of Giacomini, 13 uncal apex covered with alveus, 14 uncal sulcus, 15 subiculum, 16 posterior

cerebral artery, 17 parahippocampal gyrus, 18 collateral sulcus, 19 collateral eminence, 20 temporal horn of the lateral ventricle. (c) 3T MRI view. 1 hippocampal head, cornu Ammonis, 2 hippocampal head, gyrus dentatus, 3 temporal (inferior) horn of the lateral ventricle, 4 digitationes hippocampi (internal digitations), 5 uncal apex, 6 amygdala, lateral nucleus, 7 amygdala, basal nucleus, 8 optic tract, 8' optic chiasma, 9 nucleus accumbens, 10 insula, 10' lateral fissure and middle cerebral artery, 11 superior temporal gyrus, 12 superior temporal sulcus, 13 middle temporal gyrus, 14 lingual gyrus, 15 tentorium cerebelli, 16 collateral sulcus, 17 parahippocampal gyrus, 18 culmen, 19 quadrigeminal cistern, 20 ambient cistern, 21 wing of ambient cistern, 22 superior colliculus, 23 cerebral aqueduct, 24 brachium conjunctivum (superior cerebellar peduncle), 25 substantia nigra, 26 crus cerebri, 27 crural cistern, 28 intercrural (interpeduncular) cistern, 29 mammillary body, 30 tuber, 31 third ventricle, 32 lamina terminalis, * vestigial hippocampal sulcus. (d) Head section. *Bar*, 10 mm

Fig. 7.25 (continued)

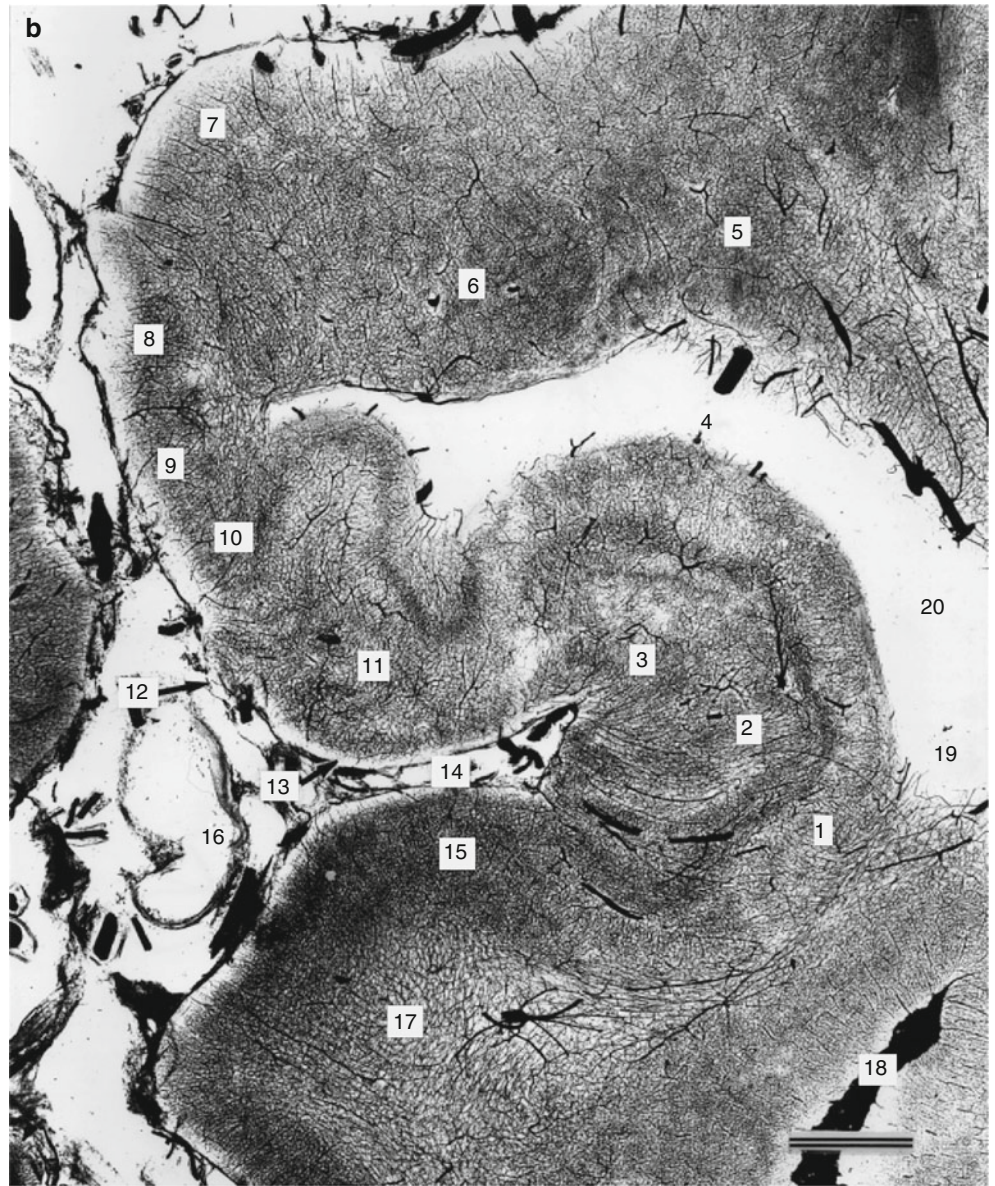


Fig. 7.25 (continued)

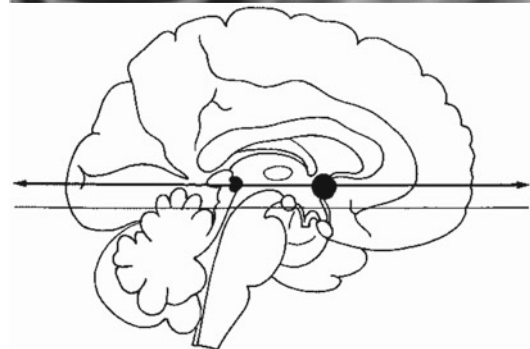
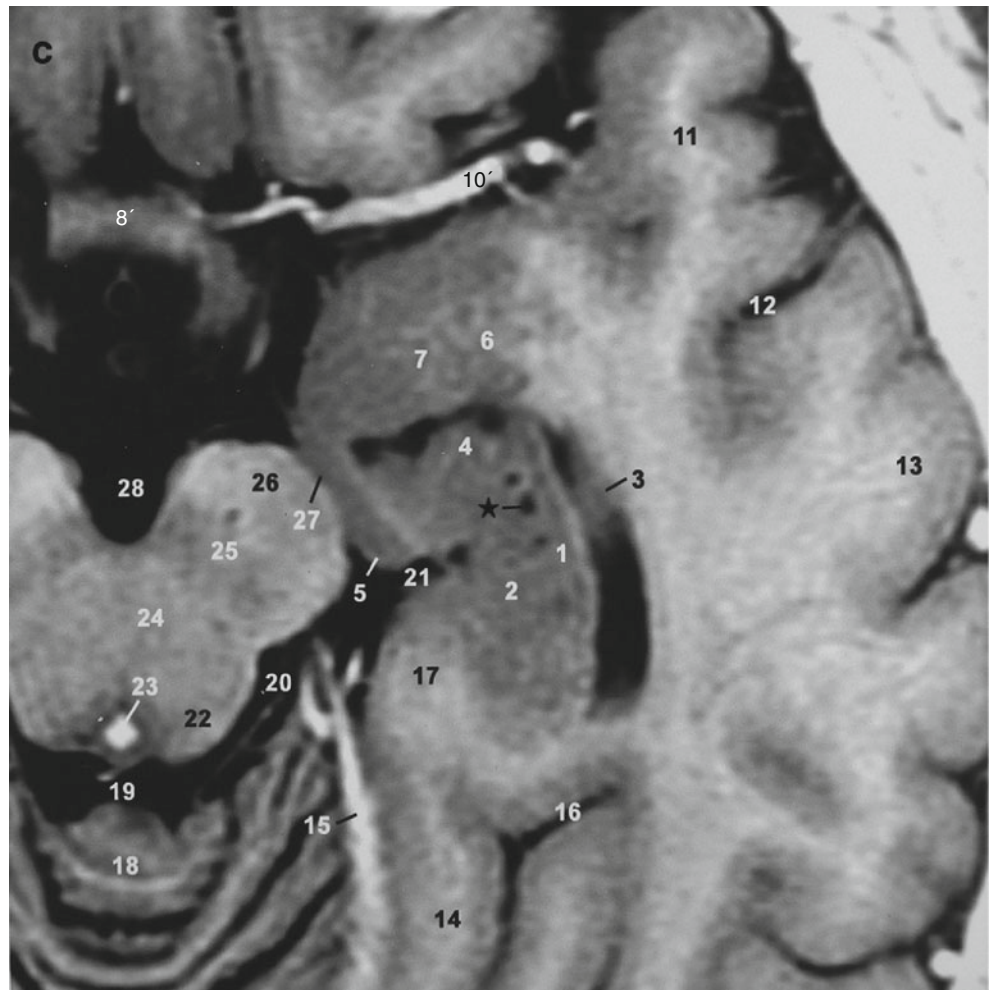




Fig. 7.25 (continued)

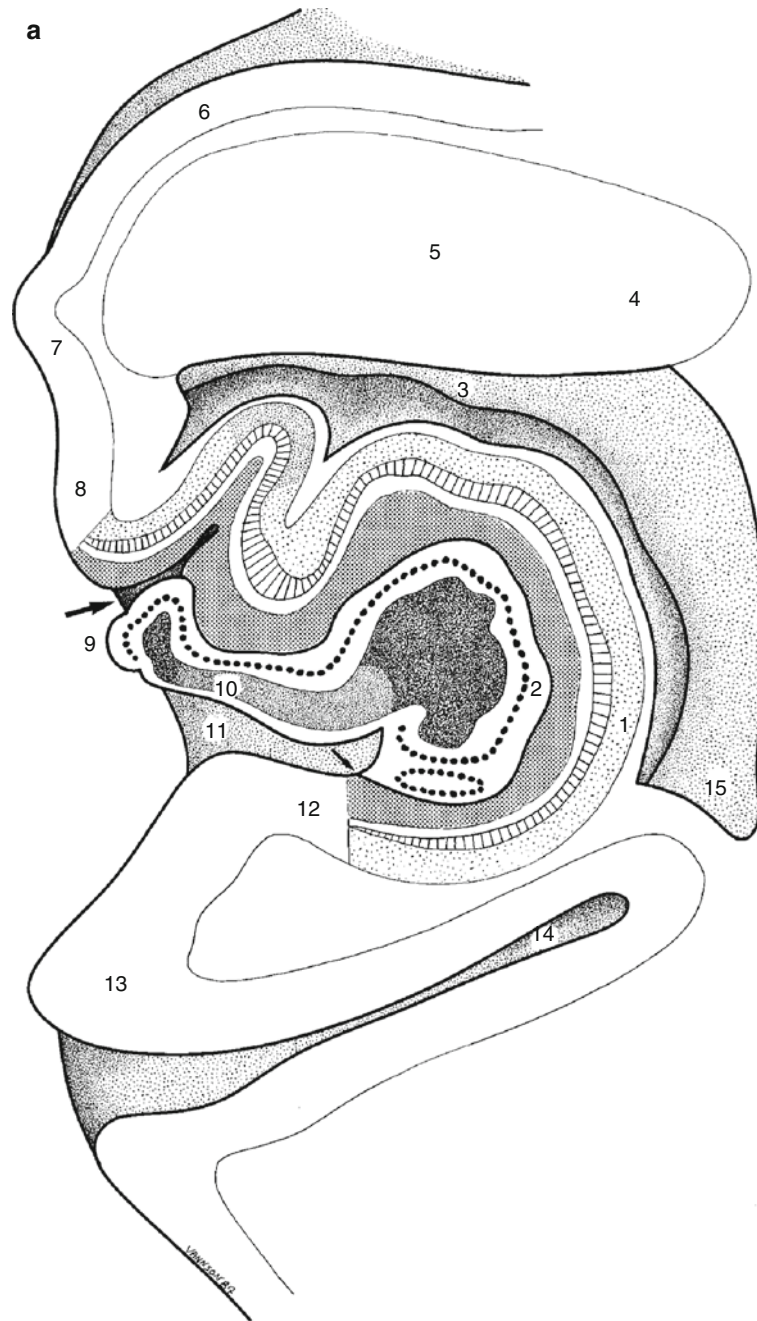


Fig. 7.26 (a) Axial section of hippocampal head, showing plane of section and structure. *Arrows* indicate the superficial hippocampal sulcus 1 cornu Ammonis (CA1) in digitationes hippocampi, 2 gyrus dentatus, 3 uncal recess of temporal horn, 4 lateral nucleus of amygdala, 5 basal nucleus of amygdala, 6 ambient gyrus, 7 uncinata gyrus, 8 subiculum in the uncinata gyrus, 9 band of Giacomini, 10 uncal apex, 11 uncal sulcus, 12 subiculum, 13 parahippocampal gyrus, 14 collateral sulcus, 15 collateral eminence. (b) Axial section of hippocampal head. Intravascular India ink injection. *Bar*, 2.4 mm 1 hippocampal head, cornu Ammonis, 2 hippocampal head, gyrus dentatus, 3 temporal horn (uncal recess), 4 lateral nucleus of amygdala, 5 basal nucleus of amygdala, 6 ambient gyrus, 7 uncinata gyrus, 8 subiculum in the uncinata gyrus, 9 band of Giacomini, 10 uncal apex, 11 uncal sulcus, 12 subiculum, 13 parahippocampal gyrus, 14 collateral eminence. (c) 3T

MRI view. 1 hippocampal head, digitationes hippocampi, 1' hippocampal head, digitationes hippocampi, 2 hippocampal head, gyrus dentatus, 3 uncal apex, 4 temporal (inferior) horn of the lateral ventricle, 5 amygdala, lateral nucleus, 6 amygdala, basal nucleus, 7 ambient gyrus, 8 crural cistern and posterior cerebral artery, 9 brachium conjunctivum, 10 pons, upper part, 10' crus cerebri, 11 intercrural (interpeduncular) cistern and basilar artery, 11' internal carotid artery, 12 oculomotor nerve, 13 hypophysial stalk, 14 optic chiasma, 15 gyrus rectus, 16 posterior orbital gyrus, 17 lateral fissure, basal part and middle cerebral artery, 18 superior temporal gyrus, 19 middle temporal gyrus, 20 inferior temporal gyrus, 21 collateral sulcus, 22 parahippocampal gyrus, 23 tentorium cerebelli, 24 culmen, 25 central lobule, * vestigial hippocampal sulcus. (d) Head section. *Bar*, 10 mm

Fig. 7.26 (continued)

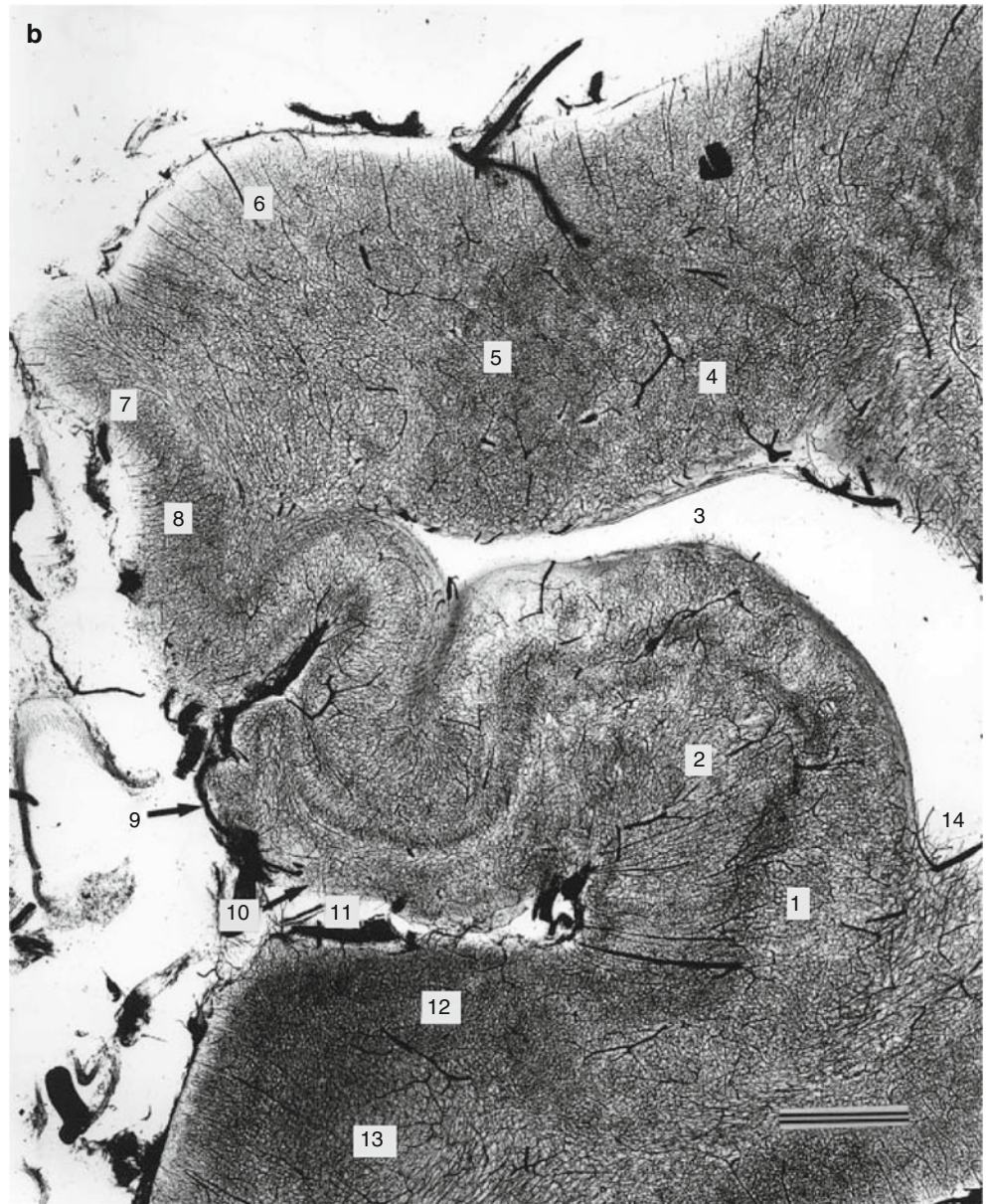


Fig. 7.26 (continued)

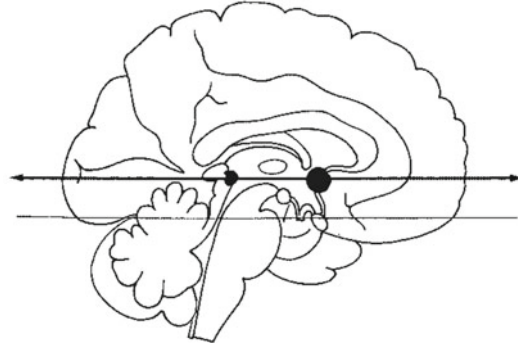




Fig. 7.26 (continued)

Fig. 8.1 Mesial temporal sclerosis. Complex partial seizures. Coronal T2-weighted image at 3.0T. Atrophy and hypersignal of the left hippocampus. Poor visualization of the hippocampal internal structure. The temporal horn is slightly enlarged

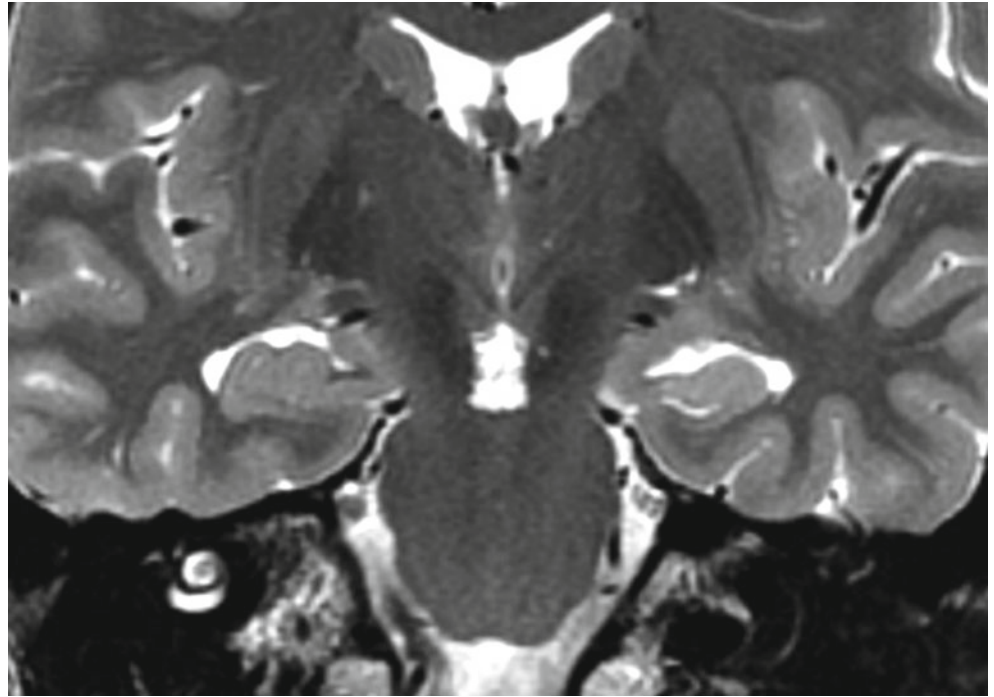


Fig. 8.2 Mesial temporal sclerosis. Long history of complex partial epilepsy. Left temporal mesial sclerosis. Coronal T2-weighted image (a) demonstrates a global atrophy of the left hippocampus and an enlargement of the temporal horn (*short arrow*). All the internal structures are markedly hyperintense (*arrow*). Same image with contrast inversion (b). The internal structures of the left hippocampus appear darker than contralaterally. See Fig. 7.7 for localizing the lesion

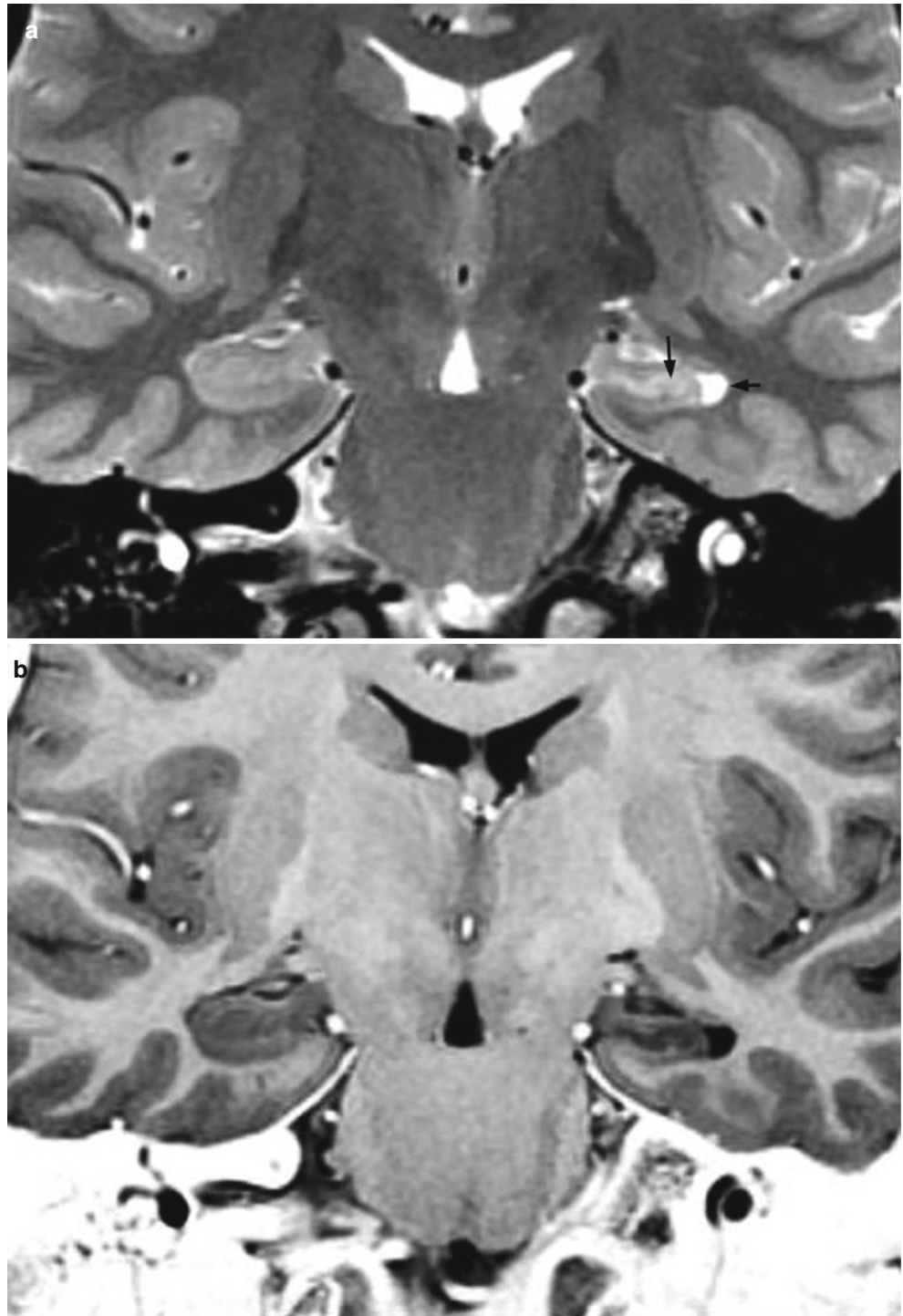


Fig. 8.3 Mesial temporal sclerosis. Medically intractable complex partial seizures. Right mesial temporal sclerosis. Coronal T2-weighted images through the hippocampal head (a) and through the hippocampal body (b) demonstrate loss of hippocampal volume, loss of digitations of the hippocampal head, darkening of the area dentata (*arrow*) and atrophy of the homolateral mamillary body (*white arrow*). See Figs. 7.6 and 7.7 for localizing the lesion

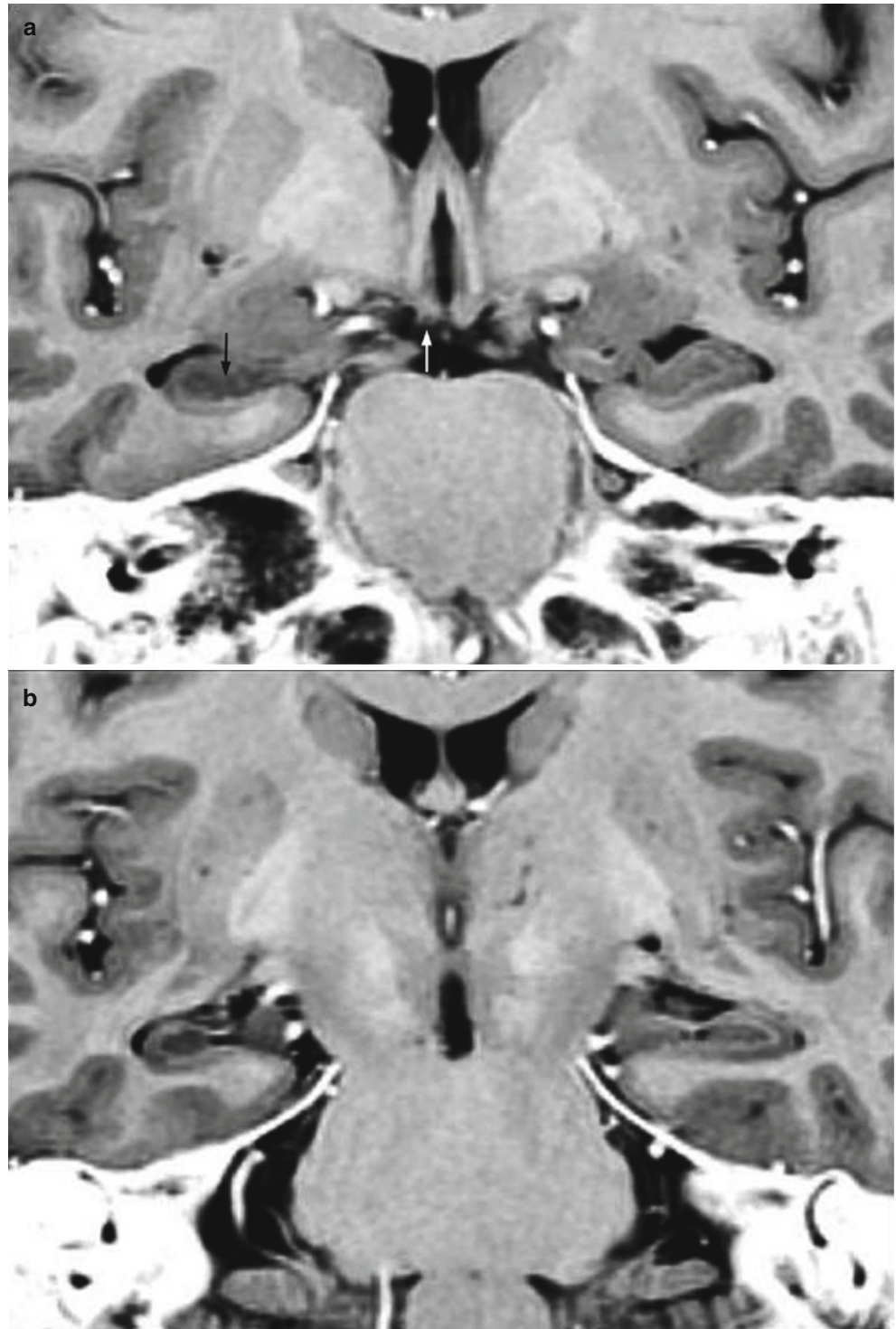


Fig. 8.4 Mesial temporal sclerosis. Complex partial seizures. Coronal T2-weighted images through the hippocampal head (a) and through the hippocampal body (b). On the right side, enlargement of the temporal horn, darkening of all the internal structures of the hippocampus and atrophy of the hippocampal body are demonstrated. There is no atrophy of the hippocampal head. See also the right mamillary body atrophy (*white arrow*). See Figs. 7.6 and 7.7

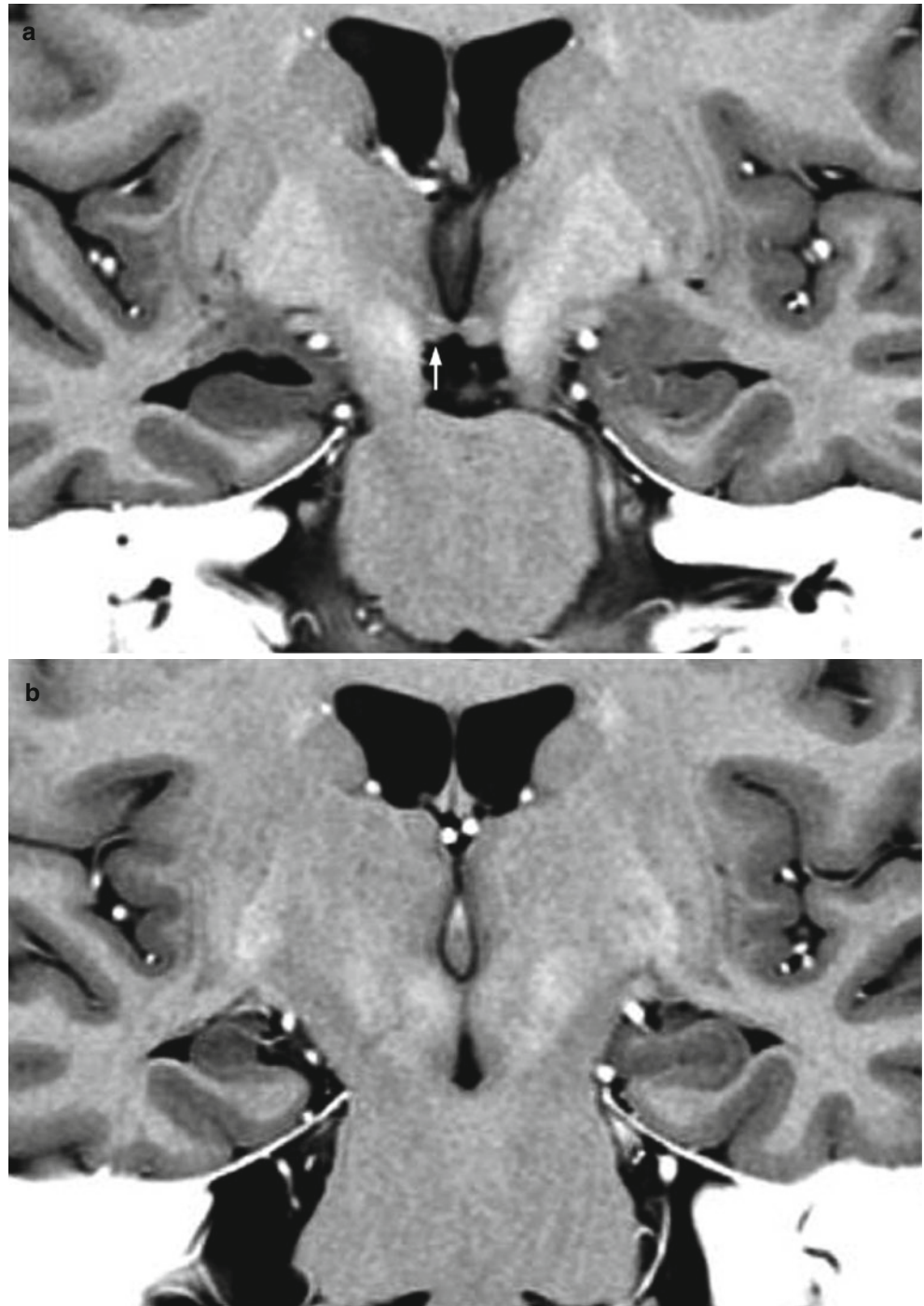


Fig. 8.5 Status epilepticus. T2-weighted coronal images through the hippocampal head (a) and through the hippocampal body (b). On the right side, swelling of the hippocampus and dark area dentata (*arrow*) are observed. See Figs. 7.6 and 7.8

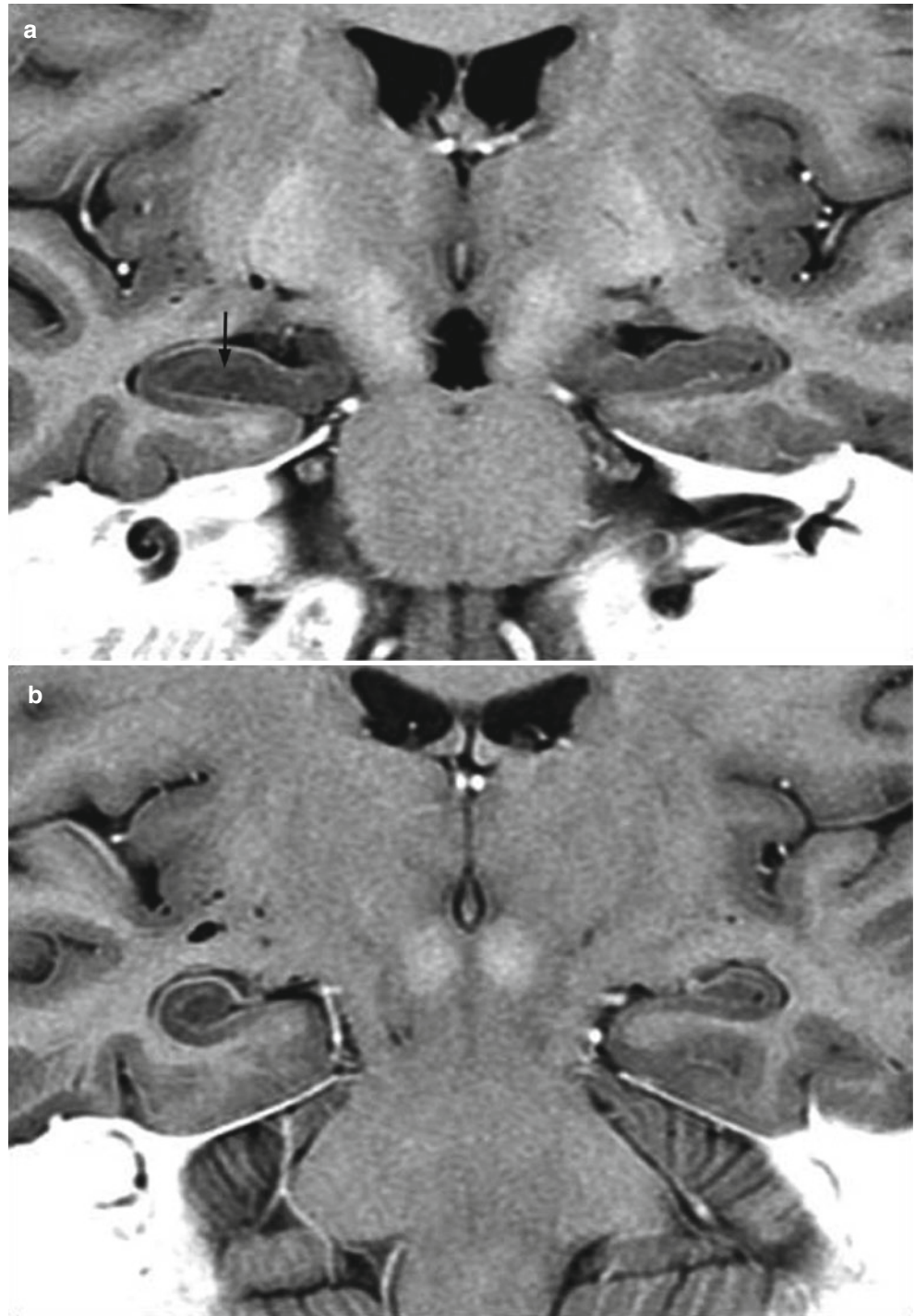


Fig. 8.6 Hypoxemia and hypothermia due to acute barbiturates intoxication. Coronal T2-weighted images through the hippocampal head (a) and through the hippocampal tail (b). On both sides, the hippocampal head is entirely involved. At the level of hippocampal tail, abnormal signal is only seen in CA1 (arrows). See Figs. 7.5 and 7.9

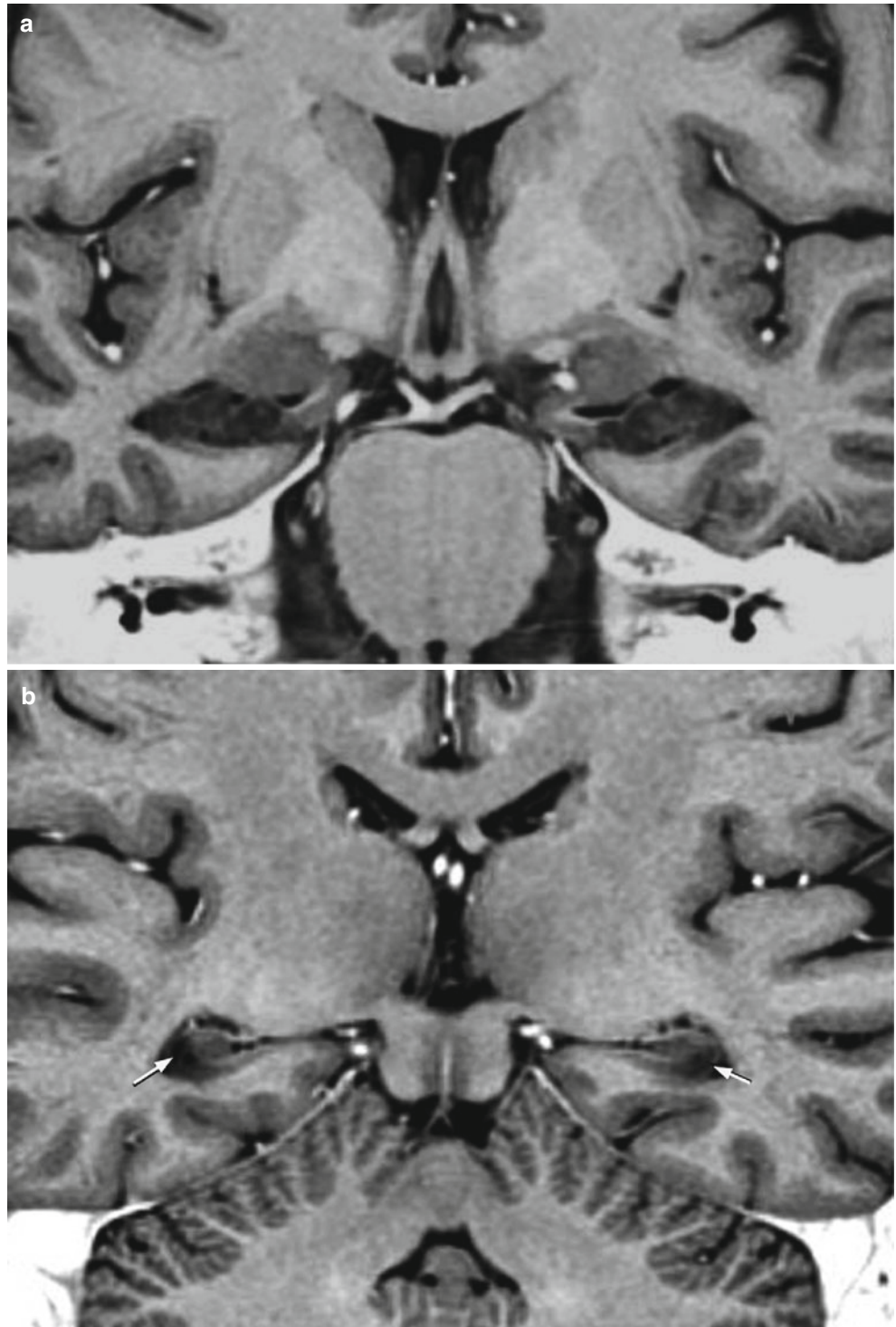


Fig. 8.7 Cocaine and methamphetamine-induced acute cerebral vasospasm responsible for multiple infarcts. Coronal T2-weighted image through the hippocampal head (**a**) demonstrates abnormal signal of CA1 and area dentata on the right side while the left hippocampal head is spared. At the level of hippocampal body (**b**), CA1 is involved in both sides (*arrows*). See Figs. 7.5 and 7.8

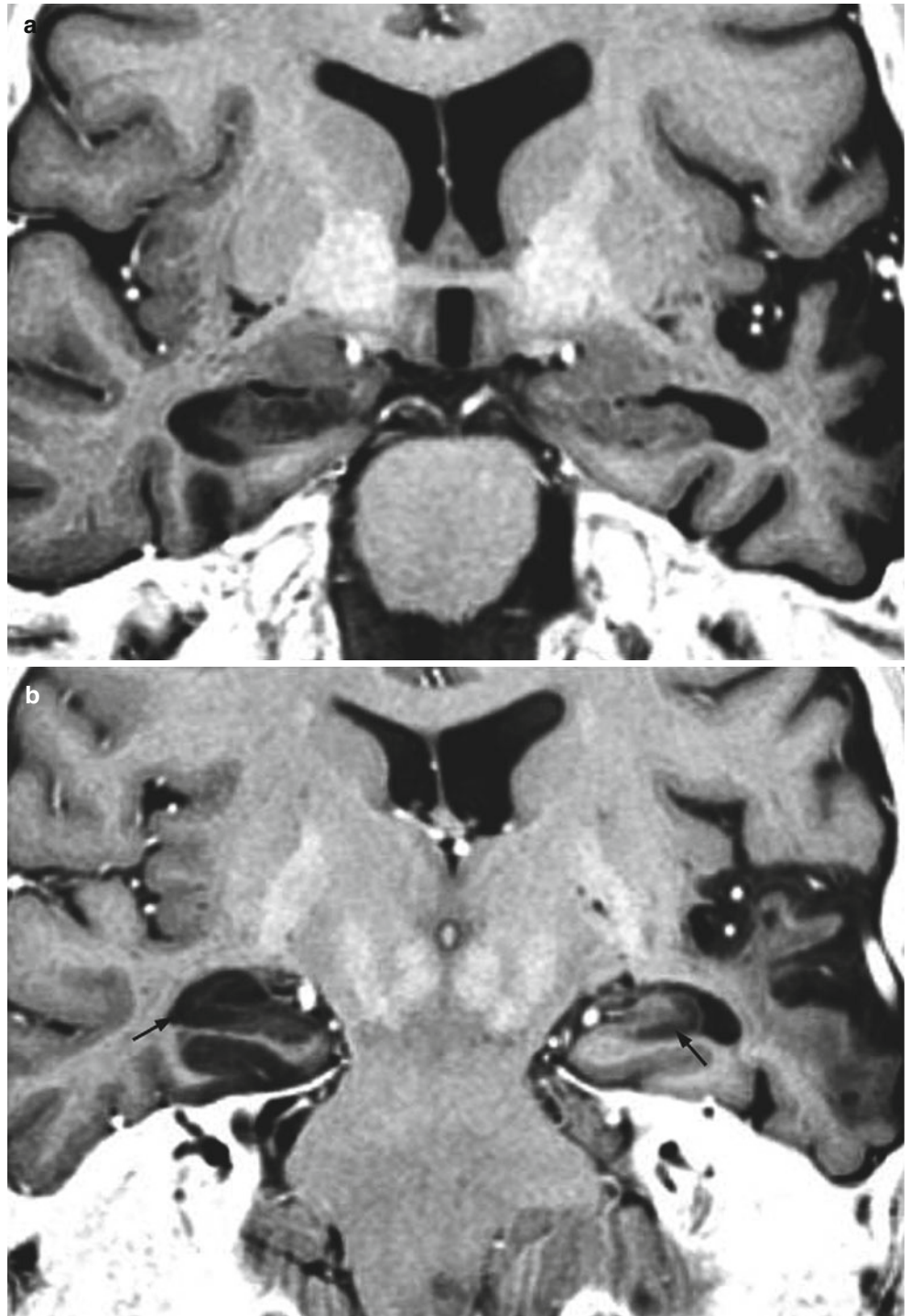


Fig. 8.8 Hippocampal malformation. 5-year-old-male with mental retardation and myoclonic epilepsy. Coronal T2-weighted images through the hippocampal head (a) and through the hippocampal body (b) show a poor delineation of the internal hippocampal structure in both sides and a globular shape of the left hippocampus. Verticalization of the collateral sulcus is observed in both sides (*arrows*). See Figs. 7.5 and 7.8

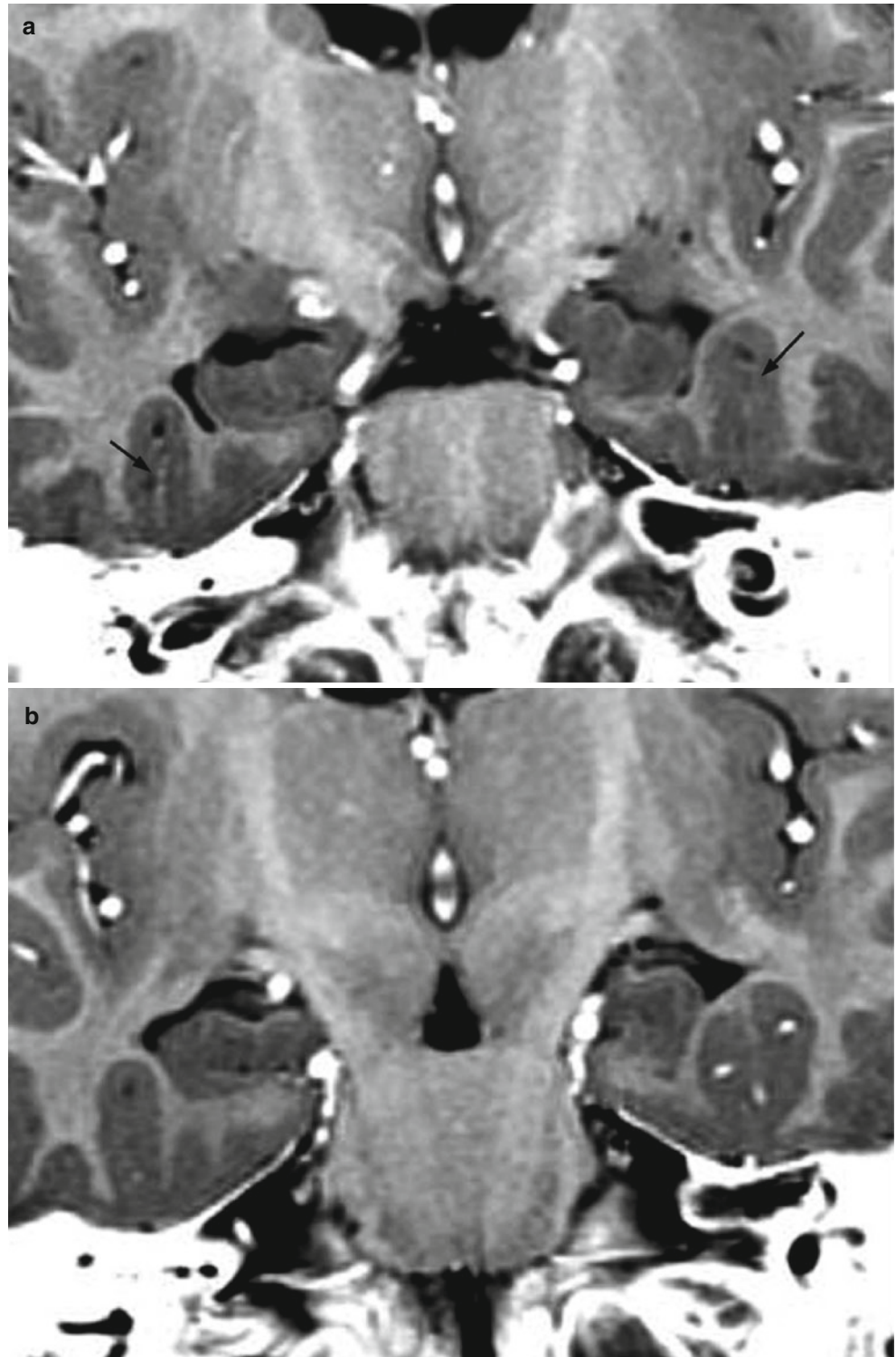
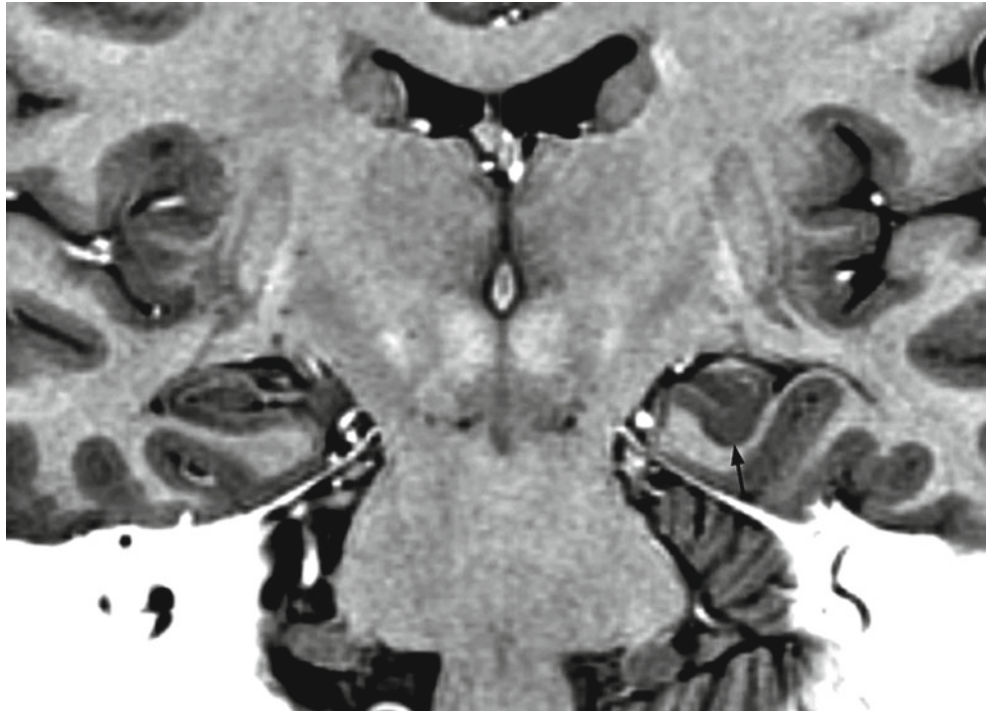


Fig. 8.9 Anatomical variant. 25-year-old-male without history of epilepsy. Coronal T2-weighted image. On the left side, there is evidence of thickening of CA1 and subiculum (*arrow*) which can be considered as an anatomical variant. See Fig. 7.7



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