Reprinted from THE JOURNAL OF COMPARATIVE NEUROLOGY
Vol. 169, No. 1, September 1, 1976 

# Retrosplenial Cortex in the Rhesus Monkey: A Cytoarchitectonic and Golgi Study

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*ABSTRACT* The laminar and cellular structure of retrosplenial cortex in the rhesus monkey was studied with Nissl stained and rapid Golgi impregnated tissue and the results were used to evaluate morphological features of a cortical transition zone. The granular layer of retrosplenial granular cortex is composed primarily of small, densely packed, star pyramidal cells. These cells branch within the granular layer itself, while the apical dendrite enters layer I where it branches infrequently or not at all. This cell type is similar to the star pyramid first described by Lorente de Nó except in its areal and laminar distribution.

Cytoarchitectonic observations of retrosplenial agranular cortex show that, although this area is relatively "agranular" in comparison to other cortical areas, it does possess an incipient layer II and layer IV. These layers are composed mainly of small and medium sized pyramidal cells, but many non-pyramidal cell types were found in these and other layers in this area in rapid Golgi preparations. Stellate cells with beaded or smooth, lightly spinous dendrites were found throughout layers I–IV, while fusiform cells with smooth or very lightly spinous dendrites appear in layers III–VI.

Areas surrounding retrosplenial cortex in the posterior cingulate region were also evaluated in Nissl and Golgi preparations including the indusium griseum, subiculum (dorsal to the corpus callosum) and area 23. The laminar and cellular constituents of retrosplenial cortex were then evaluated in the context of cortical architectonic transition. The transition from one cellular layer in the indusium griseum to five cellular layers in area 23 is made by the addition of layers II, III, IV and VI in retrosplenial cortex to the one ganglionic layer of the indusium griseum and subiculum. Besides the addition and subdivision of layers in retrosplenial cortex, two aspects of cell morphology were found to change in this region. First, the structure of pyramidal cells progressively changes from those in the indusium griseum which have predominently round or oval somata and a preponderance of apical and few basal dendrites to those in layer V of retrosplenial cortex and area 23 which have pyramidal shaped somata and a great number of basal dendrites which branch frequently and spread horizontally for hundreds of microns. Second, there is a change in the number and distribution of non-pyramidal cell types. Evidence was not found that the indusium griseum, dorsal subiculum or layer V of retrosplenial granular cortex contain a significant number of stellate or fusiform cells. At the retrosplenial granular/agranular border, though, these cells gradually begin to constitute a greater proportion of the cell population and in area 23 form a major component of layer IV. Since these laminar and cellular changes are similar, in part, to those observed by previous investigators as characteristic of ascending phylogenetic and ontogenetic development, cortical architectonic transition represents another dimension along which the cortex progressively elaborates.

The retrosplenial cortex of primates is located in the posterior cingulate gyrus. The most striking cytoarchitectonic feature of this region is change in the pattern of its lamination. Retrosplenial cortex lies between the bilaminated indusium griseum and the six layered area 23 of Brodmann

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('05) and is, therefore, in an intermediate cytoarchitectonic location. This position suggests that retrosplenial cortex represents a critical step in cortical architectonic transition.

Before the transitional nature of retrosplenial cortex can be adequately evaluated, its cellular as well as laminar composition should be considered. Our knowledge of the cellular constituents of this cortex in the primate is based entirely on the cytoarchitectonic investigations of Rose ('27) in the chimpanzee and human and Economo ('29) in the human, since the only study of retrosplenial cortex in Golgi preparations is Ramón y Cajal's work ('11, '22) in rodents. Due to their reliance on Nissl stained material, though, neither Rose or Economo were able to incorporate the specific characteristics of dendritic or axonal structure into their analyses. As a result, they could not specify what cell types composed various layers except in cases where predominently pyramidal cells were involved. In instances where a layer is composed of cells whose somata are small and densely packed like the granular layer of retrosplenial granular cortex, Rose and Economo were limited to confusing references about "granule cells" while at least five cell types have frequently been described in studies of Golgi preparations which would fulfill these criteria: stellate cells with beaded dendrites, stellate cells with spinous dendrites, granule cells (Valverde, '71), fusiform cells or star pyramidal cells (Lorente de Nó, '49); each of these categories may be further subdivided according to axonal distribution. Furthermore, even when a layer or area is composed predominently of pyramidal cells, this does not mean that non-pyramidal cells are not also present as cytoarchitectonic observations may imply. Since "agranular" motor cortex (area 4 of Brodmann, '05) has a number of non-pyramidal cell types (Ramón y Cajal, '11; Marin-Padilla, '70a,b; Kemper et al., '73), it is likely that the "agranular" division of retrosplenial cortex also contains cells which are not pyramidal types and which have not been previously described in this area in the primate.

Since the present study will consider detailed cell morphology, questions regarding features of cortical transition other than the traditionally recognized aspects of lamination might be considered. The most important of these questions is the following: Once a cytoarchitectonic continuity has been established between a layer of one area and that in another area, do the cells in this layer undergo systematic change in terms of either the density and/or shape of their somata as revealed in Nissl stained material and/or dendritic trees as seen in Golgi preparations? From the study of cyto- and fibroarchitectonics in the adult animal as well as from phylogenetic and ontogenetic perspectives, it is known, for example, that differing cortical cell densities are related to various other cortical structures like dendritic trees, afferent axonal plexuses and cortical folding. Eayrs and Goodhead ('59) observed that the decreasing cell density seen during ontogenetic development of the rat neocortex is associated with an increasing differentiation of the dendritic tree. This relationship may hold for architectonic transition as well, since the dendritic arbor of cells in a layer that is cell dense in one area and less dense in another may undergo increasing elaboration. If these changes do occur, the characterization of cortical architectonic transition can be extended to include changes in cellular morphology as well as the more conventionally recognized changes in laminar characteristics.

The intention of the present study is to survey the areal, laminar and cytological constituents of retrosplenial cortex. The laminar and cell morphology in the three retrosplenial areas will then be assimilated in the context of architectonic transition in the posterior cingulate gyrus. These data may provide a better understanding of the nature of cortical transition as well as a framework for the definition of the anatomical connections and functions of these areas.

## MATERIALS AND METHODS

Seven brains of 2–12-month-old rhesus monkeys (*Macaca mulatta*) from the collection of Dr. P. Rakic at Harvard Medical School were used for this study. Perfusion and fixation of this material has been described previously by Rakic ('71, '72). The Stensaas ('67) modification of the del Rio Hortegas ('28) rapid Golgi was used to stain

tissue blocks which were then embedded in low viscosity nitrocellulose (Hercules Power Company, Boston, Massachusetts). Sections were cut serially in the coronal or horizontal planes in cycles of 75, 100 and 125 microns thick. The 75-micron thick sections were counterstained with toluidine blue. Boundaries of cortical laminae were delineated using the counterstained sections and, where this procedure proved inconclusive, measurements from the pia and from larger cells impregnated in layers IIIc and Va were used as an aid.

Golgi analysis of the cerebral cortex with its great variety of cell types and sizes is facilitated if drawings at two or more magnifications are made. Low magnification (× 500) drawings were made of small groups of cells within a given field in order to evaluate the exact relationships between the dendritic spheres of different cells. The same cells were then drawn at high magnification (× 1,250 with oil immersion) to display details of somal, dendritic and axonal morphology. Camera lucida drawings were made with a Wild drawing tube attached to a Zeiss microscope.

Cytoarchitectonic analysis was done using material from an adult rhesus monkey brain that had been embedded in celloiden, serially sectioned at 20 microns thick in the coronal plane and stained with cresyl violet. Fibroarchitectonics were studied from another rhesus monkey brain which was embedded in egg-albumin, frozen with dry ice, serially sectioned at 26 microns thick in the coronal plane and stained with a reduced silver stain for normal axons (Vogt, '74).

## RESULTS

### I. *Cytoarchitecture*

Immediately dorsal to the corpus callosum is a sheet of cells which have large and densely packed somata and has been termed the indusium griseum (Fish, 1893; Elliot Smith, 1897). External to the indusium griseum (IG in fig. 2) is a cell sparse layer that contains a dense, subpial, myelinated fiber plexus which is the taenia tecta (tt in fig. 3; Elliot Smith, 1897; Rose, '27, '27a). Bordering the indusium griseum laterally is the subiculum (Rose, '27) which has only one cellular layer in this position dorsal to the corpus callosum while in its ventral position the subiculum has three cellular layers (Lorente de Nó, '34). Cells in the dorsal subiculum are surrounded by a dense fiber plexus and have smaller and less densely packed somata than those in the indusium griseum. These two areas together constitute the gyrus fasciolaris and the sulcus which separates the fasciolate and cingulate gyri is called the sulcus corpus callosi (Rose, '27).

Retrosplenial cortex borders the dorsal subiculum on the ventral portion of the cingulate gyrus and has a granular and agranular division which is based on the occurrence of a layer of small, densely packed cells in retrosplenial granular cortex. Economo ('29) designated the granular layer of retrosplenial cortex layer III(IV). This classification will be used in the present study instead of Rose's ('27) designation layer II–IV for three reasons: First, layer II of neocortex is not directly continuous with the granular layer of retrosplenial granular cortex and, as the following Golgi analysis will demonstrate, does not contain the same cell types. Second, the following Golgi analysis will also show that the granular layer contains primarily star pyramidal cells which may be interpreted as a continuation of the pyramidal cells found in layer III of adjacent areas in concurrence with Economo's view that these cells are a "granulization" of layer III cells. Third, since the proportion of cells with spinous dendrites versus those with smooth or beaded dendrites is greater in this layer than is usually the case in neocortical layer IV, it would be incorrect to consider the granular layer of retrosplenial granular cortex equivalent to neocortical layer IV. The brackets around IV in the designation layer III(IV) emphasizes this distinction.

Retrosplenial granular 1 cortex (RSg1) is the most lateral of two subdivisions of retrosplenial granular cortex and has three distinct cellular layers: layer III(IV) which lies below layer I, layer Va which contains large pyramidal cells and layer VI which does not underlie the full extent of RSg1 and contains small, diffusely packed, polymorphic cells. Cell density within layer III(IV) is not constant, since the outer two-thirds of this layer is densely packed with small cells among which appear an occasional larger cell (fig. 6) while the inner one-third of this layer is less cell dense, contains an intermingling of the small cells

of this layer with the larger pyramidal cells of layer Va and a fiber plexus (fig. 3: white arrow). Dense fiber plexuses are found in layers I and Vb.

The medial division of retrosplenial granular cortex (RSg2) differs cytoarchitectonically from RSg1 in that a layer IIIa-b is interposed between layers I and III(IV) which contains medium sized pyramidal cells, the granular layer becomes less dense at its medial extent (toward the midline) and layer Vb contains a number of small cells which are not present in RSg1. The fibroarchitecture of these two areas differs in that the fiber plexus of the inner one-third of layer III(IV) cannot be distinguished in RSg2.

The caudal extent of RSg is demonstrated in figure 5A which shows the continuity of the granular layer of RSg1 and that of the presubiculum on the ventral surface; a white pointer separates these two areas. Since Filimonov ('49) treated retrosplenial cortex as a subdivision of the presubiculum, while Rose ('27) and Economo ('29) defined a separate retrosplenial area, the issue of the precise nature of the architectural differences, if any, between the presubicular and retrosplenial (RSg1) cortices is raised. Though the cytoarchitecture of the presubiculum varies in both its medial-lateral and rostro-caudal extent, one may discern the following differences when comparing RSg1 with the presubicular cortex: the presubicular granular layer is less cell dense than that in RSg1 and the presubicular layer is also interupted by the perforant path at its medial extremity; two lamina dissecans are accentuated in the presubiculum whereas RSg1 only has an internal lamina dissecans which is termed layer Vb; layer V of the presubiculum is, at points, discontinuous while RSg1 has a clear layer V throughout its entire extent.

The caudal extent of RSg1 and RSg2 is penetrated by the cingulum bundle which displaces a component of this area laterally into the calcarine sulcus as shown by the pointer in figure 5B. Rostrally, retrosplenial cortex can be followed almost the full distance of area 23. Figure 4 demonstrates the topographic distribution of retrosplenial granular and agranular cortex. In summary, a number of components of this region have counterparts on the ventral hippocampal and parahippocampal gyri. The indusium griseum courses around the splenium of the corpus callosum in continuity with the hippocampus, the subiculum is continuous from the dorsal to ventral surfaces, the sulcus corpus callosi is continuous with the hippocampal fissure and retrosplenial granular cortex abuts the presubiculum.

Retrosplenial agranular cortex (RSag of Rose, '27; LD of Economo, '29) lies between RSg2 and area 23 of Brodmann ('05). The laminar composition of RSag is particularly difficult to define because of the lack of complete differentiation of one layer from another. While layers I, IIIa-b, Va, Vb and VI are clearly distinguishable, the nature of layers II, IIIc and IV is not as evident. Delineation of layer IV depends upon the existence of large pyramidal cells at the bottom of layer III. When these layer IIIc pyramidal cells are found, one of two situations results. Either they lie immediately above layer Va pyramidal cells, in which case layer IV cannot be distinguished, or layer IIIc and Va pyramidal cells are found one or two hundred microns apart in which case a layer of smaller, more densely packed cells can be found and considered to be layer IV. That layer IV exists at all in this area suggests that the "agranular" designation for this area should not be taken in the strictest sense of not having a layer IV. When the term "agranular" is used to characterize an area, it may refer to the lack of a well defined layer IV when compared to a number of other cortical areas but does not preclude its existence. With respect to RSag, layer IV is more accurately described as "dysgranular"; a designation made by Roberts and Akert ('63) and Sanides ('70) for a layer IV which is incipient and consists of stellate and small pyramidal cells intermingled with layer IIIc pyramidal cells.

Another difficulty in interpreting the characteristics of the external pyramidal layer of RSag is defining layer II. Layer II is distinguishable when cells immediately adjacent to layer I are more densely packed and slightly smaller than those in layer IIIa-b. There is, though, variance in the lateral-medial extent (toward the midline) of layer II, since it is almost always found at the RSag/area 23 border and less fre-

quently seen at the RSg2/RSag border. Both Rose ('27: Fig. 25) and Economo ('29: Fig. 50) reported that at least the medial extent of RSag has a distinct layer II.

Although there is a degree of variability in the cytoarchitecture of RSag, it may be identified in the following way. The medial border of RSg2 is marked by the discontinuation of layer III(IV). If layer II of RSag can be followed laterally to the RSg2/RSag border, this provides another reference point, since RSg2 does not have a layer II. The medial border of RSag with area 23 can be defined first by the generally higher cell density of layers II and III and second by the differences between layer II in each area. Layer II of RSag is almost always identifiable medially and contains pyramidal cells which have rounded or polygonal somata while those of layer II in area 23 have somata which are reduced in width, lancet shaped and less densely packed. Layer Va pyramidal cells in area 23 are larger than those in layer Va of RSag, providing one more reference point for this border. In fiber stained preparations (fig. 3) a dense band of fibers in layers Va and Vb distinguishes RSag from RSg2 and area 23. This pattern of fibers has been termed "unitostriate" by both Brodmann ('10) and Vogt ('10). The lateral-medial extent of RSag in the rhesus monkey, when defined in this manner, is very similar to that of the human (Rose, '27). Table 1 compares the areal subdivisions of retrosplenial cortex made by previous authors with that used in the present study.

TABLE 1

*Comparison of nomenclature used for the retrosplenial areas*

| Economo ('29) | Rose ('27) | Present study |
|---|---|---|
| LE 2 | RSg$\alpha$ and $\beta$ | RSg1 |
| LE 1 | RSg$\gamma$ | RSg2 |
| LD | RSag | RSag |

## II. *Golgi analysis*

### A. *Retrosplenial granular cortex*

The small cells of layer III(IV) in RSg1 and RSg2 which account for the granular appearance of this layer are mainly star pyramidal cells, many of which have a spindle shaped soma and dendritic tree. A few small cells do not fit into this category and usually are spinous stellate cells. All of these cells have relatively slender dendrites with a light to moderate number of spines (fig. 7). There are two different types of spines. The most common type has a slender pedicel 1–3 microns long, a round or oval head which may range in width from 1–2 microns and fits into the pedunculated category of spines suggested by Jones and Powell ('69) and the thin, Type 3 spine of Peters and Kaiserman-Abramof ('70). The second group of spines is elipsoid in shape and is comparable to the sessile type of Jones and Powell and the stubby, Type 1 spine of Peters and Kaiserman-Abramof. These sessile spines are shorter than the pedunculated variety and there is no apparent pedicel. The top of the spine can be wider, ranging from 1.5–2 microns wide, while it tapers down slightly at the base. The sessile form appears much more infrequently than the pedunculated one and, when they are found, number only one or two per dendritic branch.

Cells without spines are seen only rarely in RSg1, e.g., occasional small stellate cells with beaded dendrites in layer I and a few fusiform cells with smooth dendrites in the deeper layers. These cells probably made up less than 5% of the total cell population in RSg1. This observation is confirmed in overstained rapid Golgi sections, usually found near the face of the tissue block, in which dendritic surfaces with spines overwhelmingly predominate. The number of cells with smooth or beaded dendrites increases in RSg2 and RSag.

Star pyramidal cells have either round or slightly oval somata (fig. 7). The apical dendrite branches 3–5 times within the first 40–60 microns and then usually remains unbranched into layer I, while those cells immediately adjacent to layer I do branch in that layer. Since there are few basal dendrites on these cells, particularly in RSg1, they frequently appear to be asymmetrically distributed like cells a and l in figure 7. The number of basal dendrites is greater in RSg2 and the basal dendritic skirt is correspondingly more symmetrical like those of cells g, i and j. Spindle shaped, star pyramidal cells (fig. 7: cells c, e, f) were found which have somata that are oval and basal dendrites which, rather than emanate in a horizontal direction from the

soma, are more concentrated at the bottom of one side of the soma and project at an oblique angle from the soma.

Although the axons of the star pyramidal cells were always severed within the grey matter by the microtome knife in these preparations, it can be said that the axon emanates from the bottom of the soma as is typically the case for pyramidal cells and that they are usually slender and even beaded. Within the first 100 microns only one or two collateral branches, if any, have been observed.

Also within layer III(IV) larger cells are occasionally found. As the cytoarchitectonic analysis suggested, there is a commingling of layer V cells with cells of the granular layer at two places: at the bottom of layer III(IV) and at the RSg2/RSag border. These large cells of layer V (fig. 1) are pyramidal cells, typical in somal shape and dendritic distribution, with a dense population of spines and an apical dendrite which has terminal branches in layer I. Since the breadth of the basal dendritic skirt is extensive, there is continual overlap of these basal dendritic fields in layer V. Those cells which are nearest to the depths of the sulcus corpus callosi are greatly distorted in dendritic pattern although still recognizable as pyramidal cells.

Layer VI, as well as the pyramidal cells of which it is composed, is very rudimentary in RSg1 but more elaborated in RSg2. Layer VI does not extend the full distance of RSg1 (fig. 2) and the pyramidal cells in it are small, have oval or round somata and poorly spinous apical and basal dendrites. Pyramidal cells in layer VI of RSg2 are larger than those in RSg1 and have more extensively developed basilar dendritic trees (fig. 1).

B. *Retrosplenial agranular cortex*

Layers I, II and IIIa-b

Figures 8 and 9 illustrate the type and depth of cells in layers I and II. Small stellate cells with either radially protruding dendrites (fig. 8: a, b, c, f) or dendrites oriented toward the pia (fig. 8: d, j) predominate at the bottom of layer I and the top of layer II. Although spines are not numerous on the dendrites of these cells, many stellate cells with smooth dendrites have slender, pedunculated spines. Stellate cells with extensively beaded dendrites (fig. 8: f) do not have spinous processes. Besides these small stellate cells there is a population of large stellate cells scattered throughout layer II, particularly in the bottom half of this layer (fig. 8: g, k; fig. 9: c). Dendritic orientation and surface structure of these cells is similar to that of the small stellate cells.

Most of the cells throughout layer II are small to medium sized pyramidal cells (fig. 8: e, h and i perikaryon; fig. 9: a,b). The somata of these cells are not strictly pyramidal shaped but are more polygonal while the specific features of dendritic and axonal morphology are typical of pyramidal cells. In figure 6 it may be observed that pyramidal cells in RSag get progressively larger and the somata more pyramidal shaped in layers II, IIIa-b and IIIc. Cell d in figure 9 is one example of a layer IIIa-b pyramidal cell, a layer which also contains stellate cells (fig. 11: d, e) intermingled with these pyramids.

The axons of stellate and fusiform cells in layers II and IIIa-b (fig. 8: j; fig. 9: c; fig. 11: e) bifurcate, sending beaded collaterals into layer I and into deeper layers as well, while the descending primary axon of other of these cells (fig. 8: d) sends collaterals to layer I. The axon of cell k in figure 8 did not appear to be impregnated but the form of the ending of one of the dendrites is so similar to axonal morphology in terms of thickness, angle of branching and dialation that it may possibly be the beginning of the axon of this cell.

Vogt and Pandya ('76) have found that cortical afferents from area 23 and cortex surrounding the principal sulcus project to layers I and II of RSag. It would, therefore, be possible that horizontal fibers impregnated in Golgi preparations in layers I and II (fig. 9) might frequently be of extrinsic cortical origin, though an intrinsic origin is also possible from the externally directed collaterals of cells in deeper layers of this cortex. Though it has not been possible to distinguish between afferent and intrinsic terminal fibers on the basis of axon morphology, figure 10 (A,B,C) shows the form of some of these axons and the manner in which they may terminate on dendrites in layer I. Afferents and/or axon collaterals entering layers I and II make contact with the apical dendrites of pyramidal cells as well as the dendrites of stel-

late cells (indicated by the pointers in fig. 9).

Layers IIIc and IV

The large pyramidal cells in the lower one-third to one-half of layer III constitute layer IIIc (figs. 6, 11: b, 12). These pyramidal cells have some of the most densely packed spines of any cells in this area and a well developed basilar dendritic skirt which stretches extensively in a horizontal direction and also descends to spread throughout layer IV. Cell b (fig. 11) has basal dendrites which project over 100 microns into layer IV, a distance that is equivalent, at points, to the full thickness of that layer. Dendritic interlocking of cells in layers IIIc and IV is also demonstrated in figure 11, where the dendrites of stellate cell a are interwoven with the basal dendrites of pyramidal cell b.

The difficulty of locating an incipient layer IV in RSag in Nissl stained material is compounded in Golgi preparations where only a small percentage of the cells are impregnated. When layer IIIc or Va pyramidal cells could be identified (figs. 11, 12), a number of different cell types were found in the adjacent layer IV: stellate (figs. 11: a, 12: b), fusiform (fig. 12: e) and small-medium sized pyramidal cells (fig. 12: a). From the cells impregnated in this Golgi sampling and cytoarchitectonic observations it appears that, although stellate cells are found in layers I–IV and fusiform cells in layers III–VI, layer IV contains a larger number of small to medium sized pyramidal cells. Golgi preparations with more densely impregnated layers III–V would be helpful in further resolution of the proportion of one cell type to another in layer IV.

Layers V and VI

The pyramidal cells of layer Va are as large as those of layer IIIc in terms of somal size and breadth of horizontal spread and frequency of branching of the basal dendrites. The internally spreading basal dendrites of these layer Va cells traverse the full extent of layer Vb (fig. 13: c). Cells in layer Vb are generally smaller than those in layers Va or VI and tend to have fewer spines and a wider variety of dendritic field shapes (fig. 13: a, b, e, f). Cell e of figure 12 is particularly interesting since, although its soma is shaped like a pyramid and the primary segments of the dendrites emanate as in a pyramidal cell, it lacks the usual longer apical dendrite, has only a sparse population of spines and has two axons emanating from above rather than below the soma. One of the axons of this cell contacts an oblique dendrite of the neighboring cell f as indicated in figure 10D.

One striking aspect of pyramidal cell typology in the deeper layers of retrosplenial cortex is that no inverted pyramidal cells were observed. The inverted pyramid is one of two pyramidal cell types described by Globus and Scheibel ('67) which are found in neocortical layers V and VI and have an apical dendrite which is directed internally toward the white matter instead of in the direction of the pia. Although the absence of these cells in the present investigation may be attributed to the selective impregnation of the Golgi procedure, a survey of layers V and VI in Nissl preparations provides a partial confirmation of this observation. The apical dendrites of pyramidal cells in layer Va of RSg1 (fig. 6), for example, are all clearly oriented toward the pia.

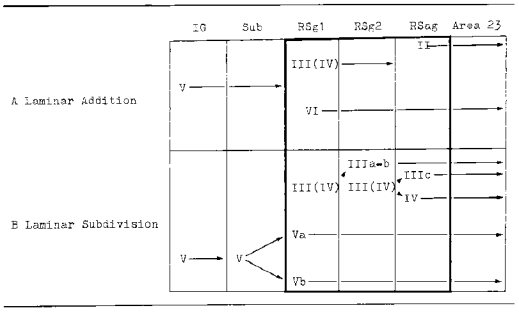
### III. *Laminar structure in the context of transition*

Cortical architectonic transition may be defined as progressive change in any component of the neuropil between two or more cortical areas. Since the indusium griseum has only one cellular layer while area 23 has five, it is obvious that changes in laminar structure do occur in the posterior cingulate gyrus.

Successive changes in the lamination of this region centers around layer V which is the common link between all areas of the posterior fasciolate and cingulate gyri, in that the cellular layer of the indusium griseum is continuous with layer V of retrosplenial cortex and area 23. Also throughout this region, this layer contains the relatively largest cells in each of these areas (fig. 2). Thus, laminar architectonic transition in this region may involve both the addition of layers to this base or common layer as well as changes within it (e.g., sub-division due to changes in cell size and/or density). A number of investigators studying the cytoarchitecture (Brodmann, '09; Lorente de Nó, '34; Filimonov, '49)

TABLE 2

*Laminar architectonic transition: indusium griseum to area 23*




and ontogenesis (Filimonov, '47; Poliakov, '49) of the hippocampal and parahippocampal gyri of primates have made a similar observation where the granular layer of the presubiculum is interpreted as being added to the pyramidal layers of the subiculum and hippocampus.

Table 2A summarizes the areas in which layers are added and table 2B indicates the areas where the layers subdivide. The heavy line around the retrosplenial areas in this table emphasizes that most laminar addition and subdivision in this region occurs within retrosplenial cortex.

Laminar architectonic transition proceeds in the following manner. Cell density first decreases at the border of the indusium griseum and the subiculum. This ganglionic layer then subdivides in RSg1 into layer Va which contains large pyramidal cells and Vb which is a dense fiber plexus. The a and b subdivisions continue in RSg2, RSag, area 23 and throughout neocortex, though not always containing the same elements.

In RSg1 another laminar architectonic change occurs: the granular layer III(IV) is added to layer V. Since layer III(IV) is continuous with layers III and IV and contains predominantly pyramidal cells, the addition of layer III(IV) marks the first appearance of the external pyramidal layer. The subdivision of layer III(IV) in RSg2 and RSag results in layers IIIa-b, IIIc and IV which continue in area 23 and other neocortical areas.

Two other layers are added in retrosplenial cortex, but do not subdivide in this cortex. Layer VI is added in RSg1 and layer II in RSag.

## IV. *Cell structure in the context of transition*

There are two particularly striking aspects of laminar architectonic transition in the fasciolate and cingulate gyri. First, cell density decreases significantly at the border between the indusium griseum and subiculum and in layer III(IV) between RSg1 and RSg2/RSag and second, new layers are added with layers III(IV) and VI first appearing in RSg1 and layer II in RSag. Since the indusium griseum contains primarily one cell type while area 23 contains a full range of pyramidal, stellate and fusiform cell types, it is possible that cell structure is involved in architectonic transition as well as lamination. Just as retrosplenial cortex is the focal point for the addition and subdivision of layers, it may be possible that the proportion of one cell type to another and/or cell structure itself changes progressively.

A sampling of cell types by layer from six areas in the posterior fasciolate and cingulate gyri is presented in figure 1. Where pyramidal cells are the predominent cell type, the largest were chosen from each layer for illustration to facilitate the comparison of similar cells from area to area. Such a scheme, though oversimplified because it excludes many of the small cell types in some layers, serves as a starting point for developing hypotheses regarding progressive changes in cell type and structure. Since the reconstruction of Golgi preparations in figure 1 does not represent cell density, the Nissl stained section in figure 2A may be used in combination with figure 1 when interpreting various aspects of architectonic transition involving both cell type and cell density.

Ramón y Cajal ('11) called cells of the indusium griseum of rodents "atrophic cerebral pyramids." These cells in the monkey are also atypical pyramidal cells (IG in fig. 1), having a preponderance of apical dendrites which ascend through layer I with no or few basal dendrites that emanate from the soma at an oblique angle. All dendrites, except for primary and secondary branches, are heavily covered with sessile spines and the somata of these cells are round or oval shaped.

In contrast to the pyramidal cells in the indusium griseum, those in the dorsal sub-

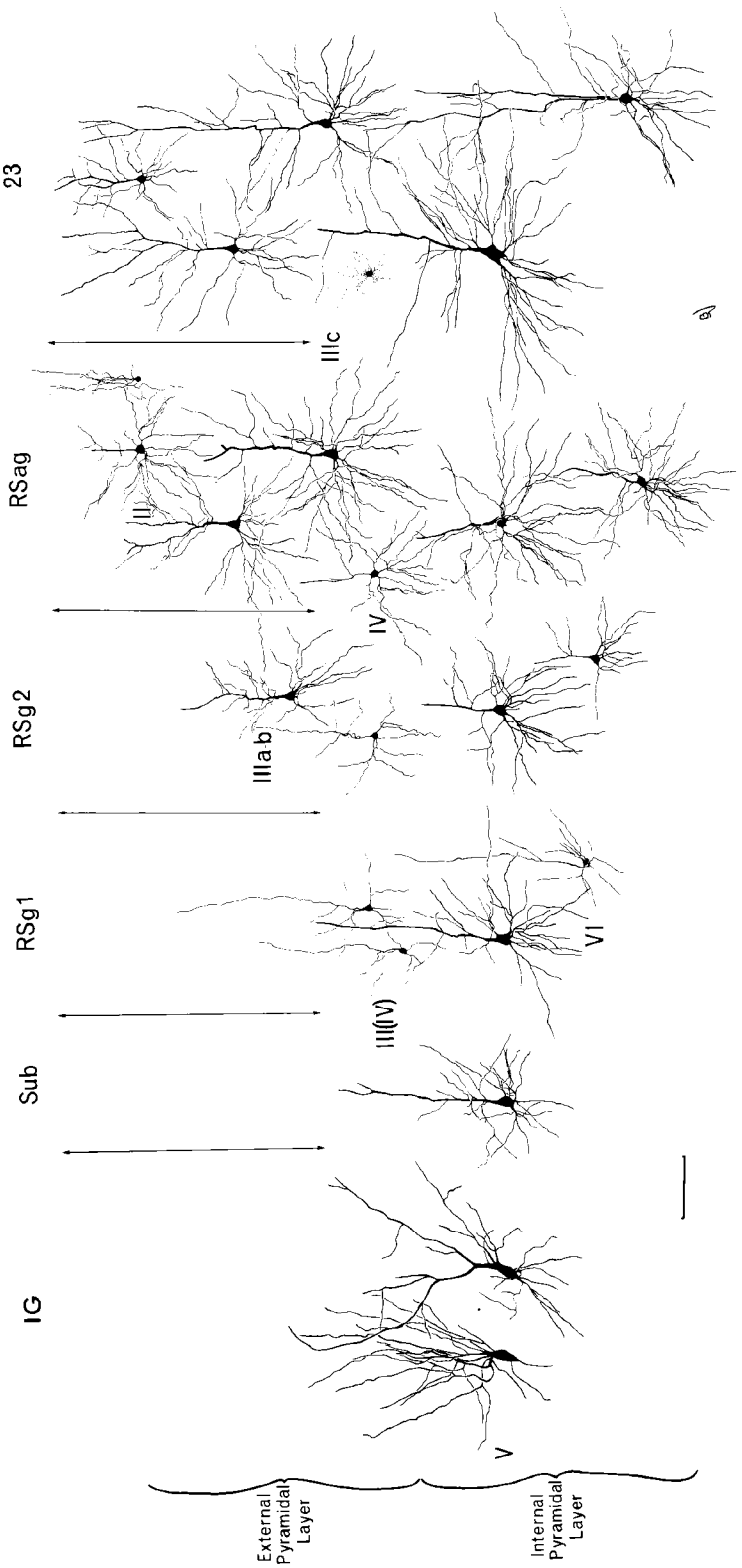



Fig. 1 A sampling of cells from each layer in the posterior fasciolate and cingulate gyri. Where pyramidal cells are the most representative cell type, larger ones were chosen for presentation. IG, indusium griseum; Sub, subiculum. Rapid Golgi, scale, 50 $\mu$.

iculum are typical in shape. These cells have a greater number of basal dendrites which branch more frequently and emanate from the soma in a horizontal rather than an oblique direction. The spines on the dendrites of these cells are predominantly pedunculated in contrast to the sessile spines of cells in the indusium griseum and the somata of subicular cells are more pyramidal shaped.

This increase in the relative proportion of basal to apical dendrites between the indusium and subiculum corresponds to the sudden decrease in cell density which also occurs at the border between these two areas (fig. 2A). It is reasonable to presume that cell density would have to decrease in order to accomodate cells that have a more extensive, horizontally spreading basilar dendritic field as well as the fiber plexus which is part of this layer in the subiculum. In layer V of RSg1 pyramidal cells have even more extensive basilar dendritic fields and those in layer V of area 23 have the greatest number of basilar dendrites which extend horizontally the greatest distance. In addition, pyramidal cell somata in RSag and area 23 are the most clearly pyramidal shaped, presumably due to their more elaborate basilar dendritic skirts.

Besides these changes in cell structure and density, there is an actual addition of one or more cell types in retrosplenial cortex. Layer III(IV) in RSg1 contains star and spindle shaped pyramidal cells which are not found in the fasciolate gyrus. It is interesting to note, though, that since cells in the indusium griseum and layer III(IV) of RSg are very densely packed, somal shapes and dendritic orientation are quite similar. The somata in both layers are round or oval shaped and the basal dendrites frequently emanate from the soma at an oblique rather than a horizontal direction. As cell density in layer III(IV) decreases and as it subdivides into layers IIIa-b, IIIc and IV in RSg2 and RSag, the same progressive elaboration of somal shape and basilar dendritic field can be observed as has been described in layer V (fig. 1: external pyramidal layer).

In RSg2 and RSag new cell types are also gradually added. Stellate and fusiform cells are rarely seen in either the indusium, dorsal subiculum or RSg1. The general lack of small cell types in layer Va of RSg1 is particularly noticeable in figure 6. In RSg2 and RSag these cells are encountered frequently with stellate cells dispersed throughout layers I–IV of RSag and fusiform cells in layers III–VI. Thus, the addition of layer II and subdivision of layer III(IV) into layers III and IV in RSag occurs in conjunction with the gradual addition of new cell types to this area and to a lesser extent in RSg2.

In area 23, where layer IV is wider and more cell dense than in RSag, the number of stellate cells with beaded dendrites increases greatly. Though statements regarding cell density are difficult to substantiate in Golgi preparations, figure 13B shows a nest of three stellate cells which were found in layer IV of area 23 that demonstrate the greatest packing density that these cells can attain. This dense arrangement of stellate cells was never observed in layer IV of RSag. The change in the relative proportion of one cell type to another in the same layer of two adjacent areas is another form of the cellular aspect of cortical architectonic transition.

In conclusion, there are a number of strong correlations between the laminar and cellular components of cortical transition. First, somal shape and basilar dendritic field are two components of cell structure which are elaborated as cell density decreases. Second, new cell types are frequently found in areas in which a new layer is also added or an existing one subdivided. Third, as a layer becomes more accentuated cytoarchitectonically from one area to another, the relative proportion of one cell type to another may change as well.

## DISCUSSION

A number of architectural features of retrosplenial cortex in the rhesus monkey have been described. An analysis of Golgi impregnated material showed that the granular layer of retrosplenial granular cortex (layer III(IV)) contains primarily star pyramidal cells which are similar to the star pyramid described by Lorente de Nó ('49). The oblique branches of the apical dendrite of these cells arborizes three to five times within a short distance from the

soma and the apical dendrite enters layer I where it has little or no terminal branching. Though the axons of these cells could not be traced to the white matter in the present study, it is probable that they have an extrinsic trajectory, since Ramón y Cajal ('11, '22) found that the axon of each category of cell contained in the granular layer of the rodent's "interhemispheric cortex" projects into the white matter. Since Lorente de Nó also found that the axons of star pyramids in layer IV of isocortical structures descend into the white matter, the cells of the granular layer in retrosplenial cortex possess most of the characteristics of star pyramidal cells except in their areal and laminar distribution.

Lorente de Nó ('49) observed star pyramids in layer IV of "the whole temporo-parieto-occipital isocortex" and this cell type as well as cells with a similar dendritic configuration have been seen more recently by Valverde ('71) and LeVay ('73) in area 17 and by Jones ('75) in areas 3, 1 and 2. Cytoarchitectonic observations of the present study suggest that the granular layer of retrosplenial cortex is the earliest and least differentiated stage of the external pyramidal layer in the primate cortex, since neither the adjacent indusium griseum nor the dorsal subiculum have more than one ganglionic layer which is itself equivalent to the internal pyramidal layer. That the star pyramidal cell is found in the granular layer of an area as cytoarchitectonically elementary as retrosplenial granular cortex implies that the star pyramid is the earliest form of pyramidal cell to be found in the primate external pyramidal layer.

Comparison of the cells in layer III(IV) of the monkey with those of the homologous granular layer in rodents suggests a species difference in the structure of these cells. Ramón y Cajal ('11, '22) described the apical dendrites of cells in the granular layer of rodents as terminating in tufts in layer I and the basal dendrites branching in the inner plexiform layer. This contrasts with the present report in the monkey where the oblique and basal dendrites of the star pyramidal cell branch primarily within the granular layer itself. This difference may be partially attributed to the generally higher cell density in rodents which could preclude the oblique and basal dendrites from spreading extensively within this layer. It is also possible that cells in the granular layer are more pyramidal shaped in ascending phylogenetic species. The cells described by Ramón y Cajal in this layer of the rodent are not pyramidal shaped but, rather, one type is fusiform shaped and the other quite similar to the star cell seen by Lorente de Nó ('33) in layer II of entorhinal cortex.

Although the conclusions of the present investigation support those of Rose ('27) and Economo ('29) regarding the structure and location of retrosplenial agranular cortex, it was found that two qualifications of the term "agranular" should be made when it is used for this area. First, this cortex is not cytoarchitectonically "agranular" in the strict sense of not having a layer IV. Although this area is relatively "agranular" when compared to other cortical areas, it does have an incipient layer IV that is more accurately described as "dysgranular." Roberts and Akert ('63) and Sanides ('70) have used this term for layer IV when it is intermittent and the cells of this layer are intermingled with layer IIIc pyramidal cells. Second, although no layer in this area is composed mainly of "granular cells," Nissl and Golgi preparations of retrosplenial agranular cortex demonstrate that this area contains a larger number of non-pyramidal cells than do the two granular divisions. In retrosplenial agranular cortex stellate cells with beaded dendrites or with smooth, lightly spinous dendrites are found in layers I–IV, while fusiform cells with smooth dendrites that are occasionally lightly spinous are scattered throughout layers III–VI. Although these cell types have been observed by many previous investigators, their particular significance in this cortical region lies in their differential areal distribution and will be discussed further in relation to cortical transition.

Besides having evaluated the individual characteristics of each area, layer and cell type in retrosplenial cortex, the present investigation has considered these structures in comparison to other areas in the posterior cingulate region. This comparison resulted in a consideration of cortical architectonic transition. The Vogts ('19)

defined transition as the intermingling of two extreme laminar patterns in an intermediate area which shares some but not all of the characteristics of each extreme. Economo ('29) later made a more explicit attempt to characterize transition in terms of change in cell types. In his classification of isocortical areas into five types, there are two extreme types termed heterotypical isocortex (e.g., visual and motor cortex) in which the six layers are not clearly distinguishable. The three intermediate types are called homotypical and have varying degrees of elaboration in each of the six layers. Economo then defined two trends called "granulization" and "pyramidization" depending on whether the areas under consideration contained progressively more "granular cells" like cortex or more pyramidal cells as in motor cortex. These trends were also observed in allocortical structures. Many Golgi studies, though, have shown that the laminar characteristics of granularity which include somal size and packing density do not adequately determine the specific features of cell type which also includes dendritic and axonal features. Two layers which are granular, for example, can contain different cell populations as in layer III(IV) which contains star pyramidal cells and layer IV of area 23 which contains many stellate cells with beaded dendrites as well as star pyramidal cells. Thus, cytoarchitectonic observations alone cannot be relied on to distinguish changes in cell type and structure but must be combined with the use of Golgi preparations.

The definition of cortical architectonic transition suggested in the present study proposes that progressive change in any component of the neuropil between two or more areas constitutes transition. Though this might include changes in the connections, histochemistry, glial cell distribution, fine structure and other components of the neuropil, it has been demonstrated that both laminar and cellular structure are involved in transition in the posterior cingulate region. An evaluation of the transitional features of a cortical area as elementary as retrosplenial cortex provides one basis for homologizing the layers of this area with those found in neocortex. Thus, the granular layer is not a mixture of cells that are equivalent to layers II–IV of neocortex but contains the predecessors of layer III pyramidal cells and layer IV star pyramidal cells.

Ramón y Cajal ('11) recognized that ascending phylogenetic and ontogenetic development involves a progressive elaboration of the basilar dendritic tree of pyramidal cells and he and Lorente de Nó ('49) also observed that ascending phylogenetic development includes an increase in the number of cells with short axons. These same changes have been shown in the present investigation to be characteristic of cortical architectonic transition in the primate. Progressive change in the structural configuration of a series of cortical areas implies that an elaboration of functional capabilities also occurs in the posterior cingulate region. Since little is known regarding the function of these areas, differences in laminar and cellular structure may provide insight for suggesting possible functional relationships.

## ACKNOWLEDGMENTS

I would like to thank Dr. Deepak Pandya for the insight and direction he has provided throughout the course of this research. I would also like to thank Dr. Pasko Rakic from Harvard Medical School for graciously providing me with unlimited access to his exquisitely prepared Golgi material.

The excellent photographic technique of Larry Cherkas made the reproduction of these illustrations possible. This research was supported in part by grants from the National Institutes of Health (NS 06209, 09211 and 11233).

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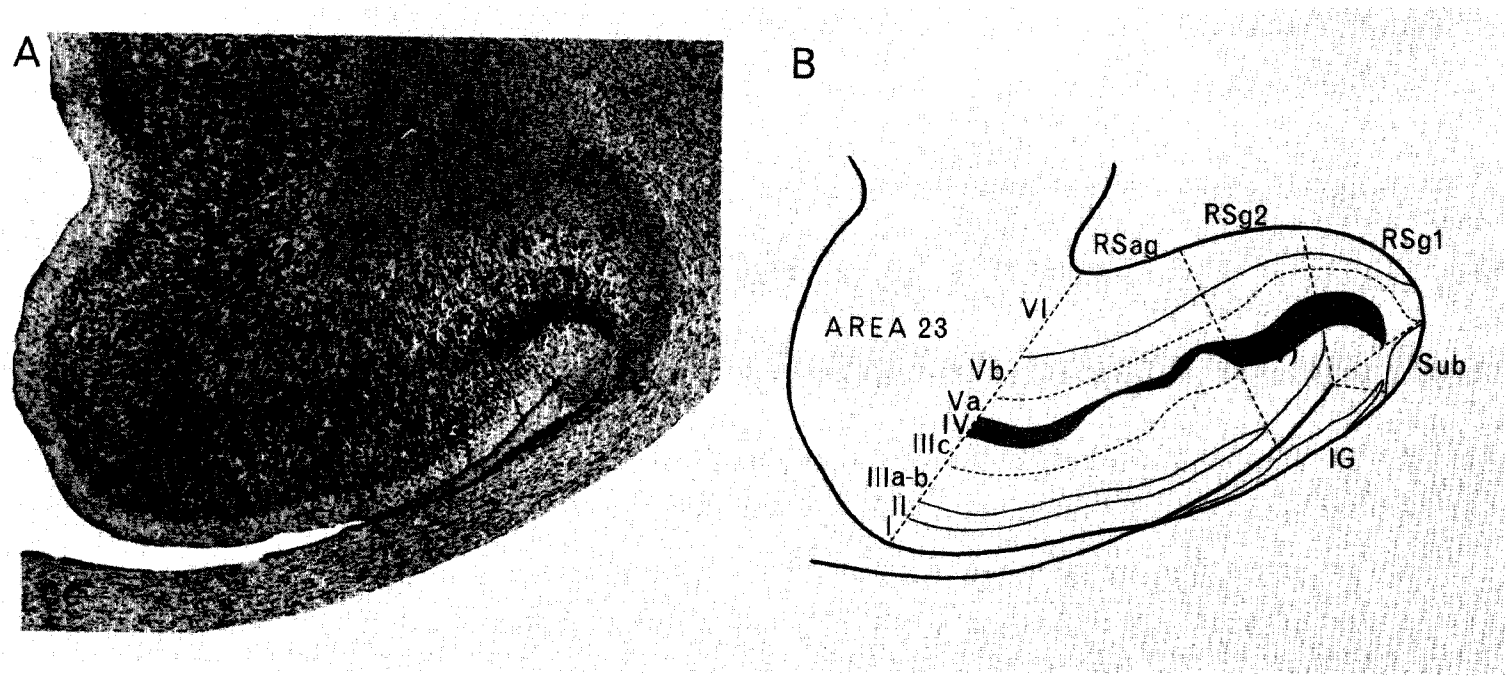
## PLATE 1

### EXPLANATION OF FIGURES

2 A Nissl stained, celloiden section of the posterior cingulate region. CC, corpus callosum.

B Line drawing of figure 2A in which the lamination of the retrosplenial areas has been demarcated. IG, indusium griseum; Sub, subiculum.


A
B
RSag
RSg2
RSg1
AREA 23
VI
Vb
Va
IV
IIIc
IIIa-b
II
I
Sub
IG

## PLATE 2

### EXPLANATION OF FIGURES

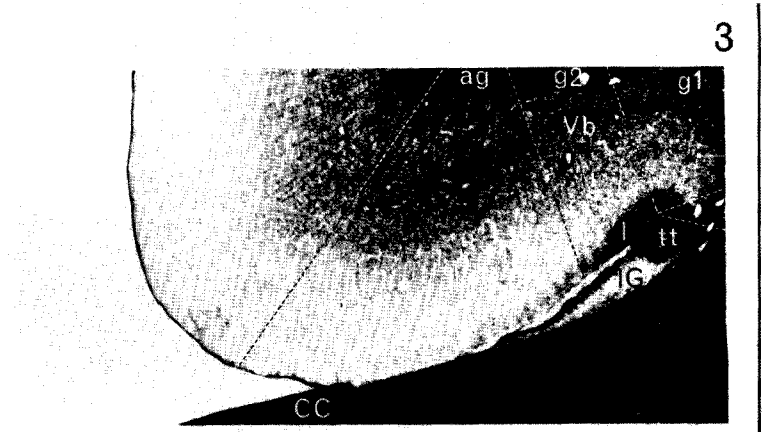
3 A reduced silver stain for normal axons in the posterior cingulate region. The white arrow points to a fiber plexus in layer III(IV). IG, indusium griseum; tt, taenia tecta; CC, corpus callosum.

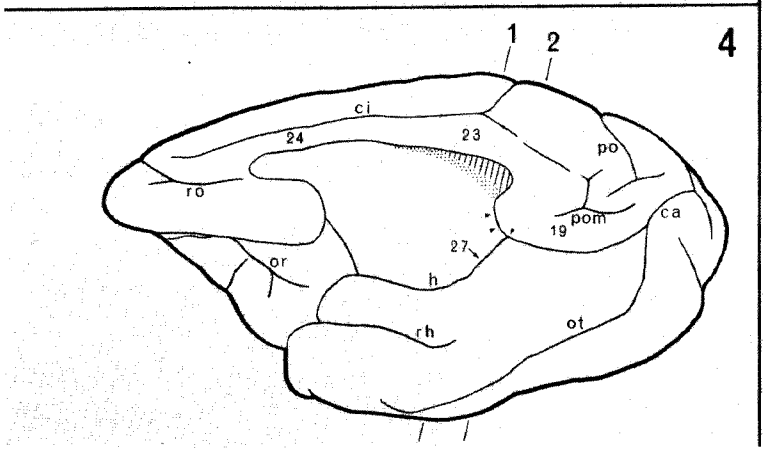
4 Topographic distribution of retrosplenial granular cortex (dots) and retrosplenial agranular cortex (lines). The corpus callosum has been removed so that the ventral border of the cingulate gyrus can be observed. Retrosplenial granular cortex continues in the callosal and calcarine sulci as indicated by the pointers. Level 1 corresponds to that of figure 2 and 3 while level 2 is equivalent to that of figure 5. Sulci: ca, calcarine; ci, cingulate; h, hippocampal; or, orbital; ot, occipitotemporal; po, parieto-occipital; pom, medial parieto-occipital; rh, rhinal; ro, rostral. Areas 19, 23, 24 and 27 are those of Brodmann ('05).

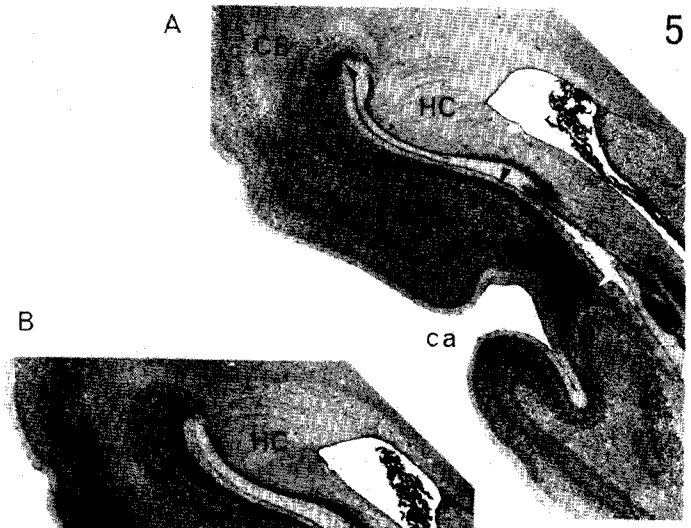
5 Nissl stained, celloiden embedded sections demonstrating the continuity between retrosplenial granular cortex and the presubiculum. HC, hippocampal commissure; CB, cingulum bundle; ca, calcarine sulcus.

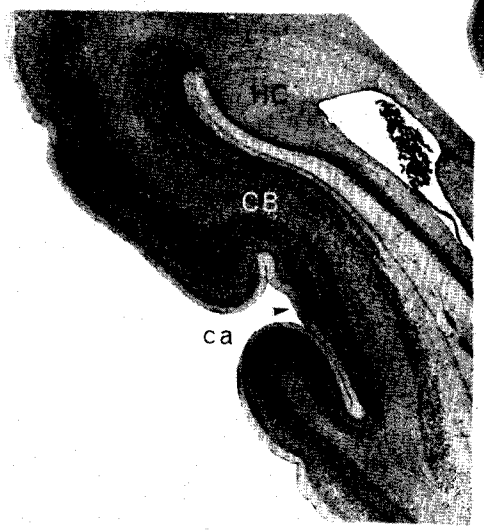
A White pointer delineates RSg from the presubiculum. Black pointers signify layer III(IV) of RSg.

B Black pointer in the calcarine sulcus indicates the calcarine component of retrosplenial granular cortex.


3
ag
g2
g1
Vb
l
tt
IG
CC


4
1
2
ci
24
23
po
ro
pom
19
ca
27
or
h
rh
ot

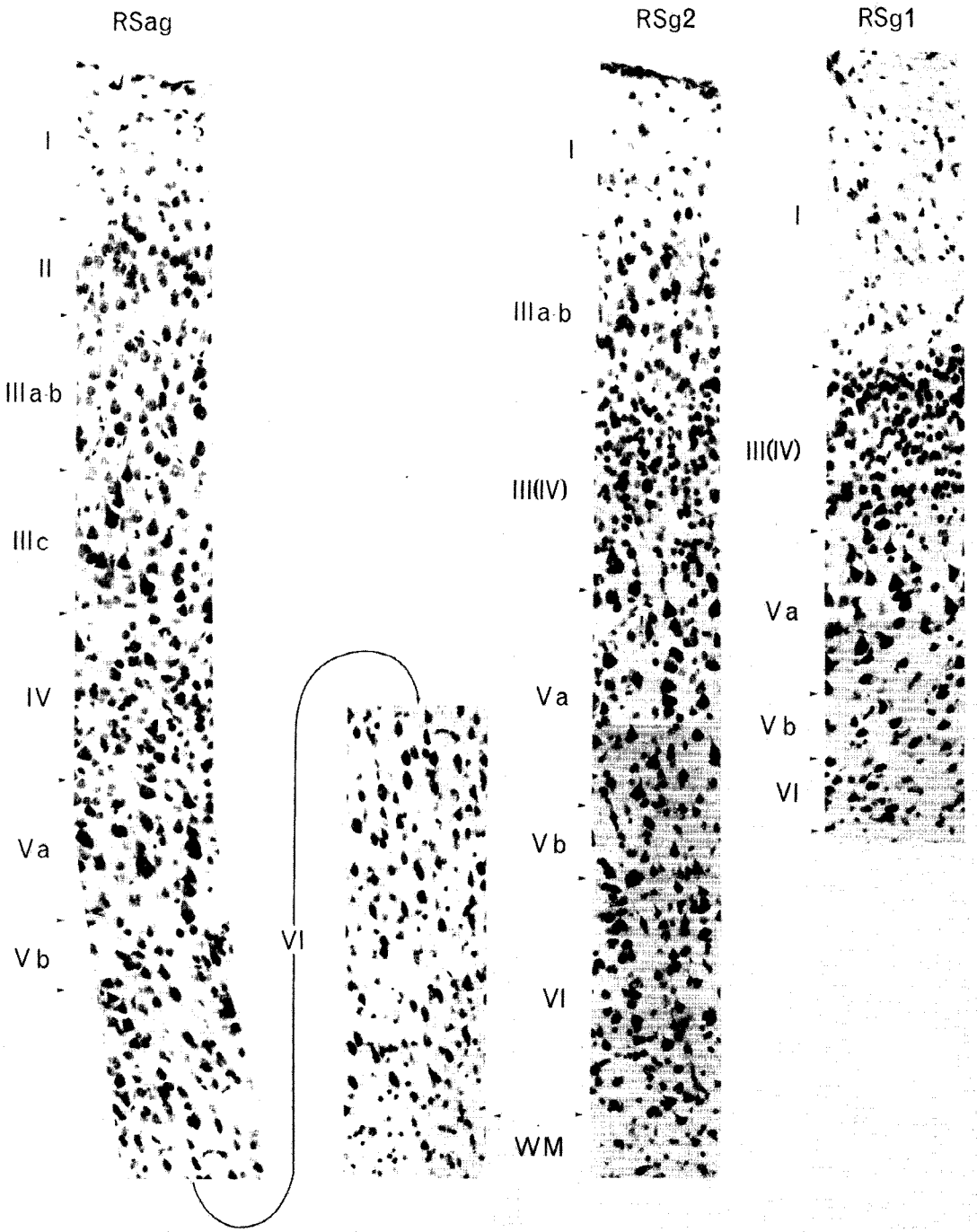

A
5
CB
HC
ca


B
HC
CB
ca

## PLATE 3

### EXPLANATION OF FIGURE

6 Higher magnification cytoarchitecture of retrosplenial cortex. Same celloiden embedded section as used for figure 2A. WM, white matter.


RSag
I
II
IIIa-b
IIIc
IV
Va
Vb
VI
RSg2
I
IIIa-b
III(IV)
Va
Vb
VI
WM
RSg1
I
III(IV)
Va
Vb
VI

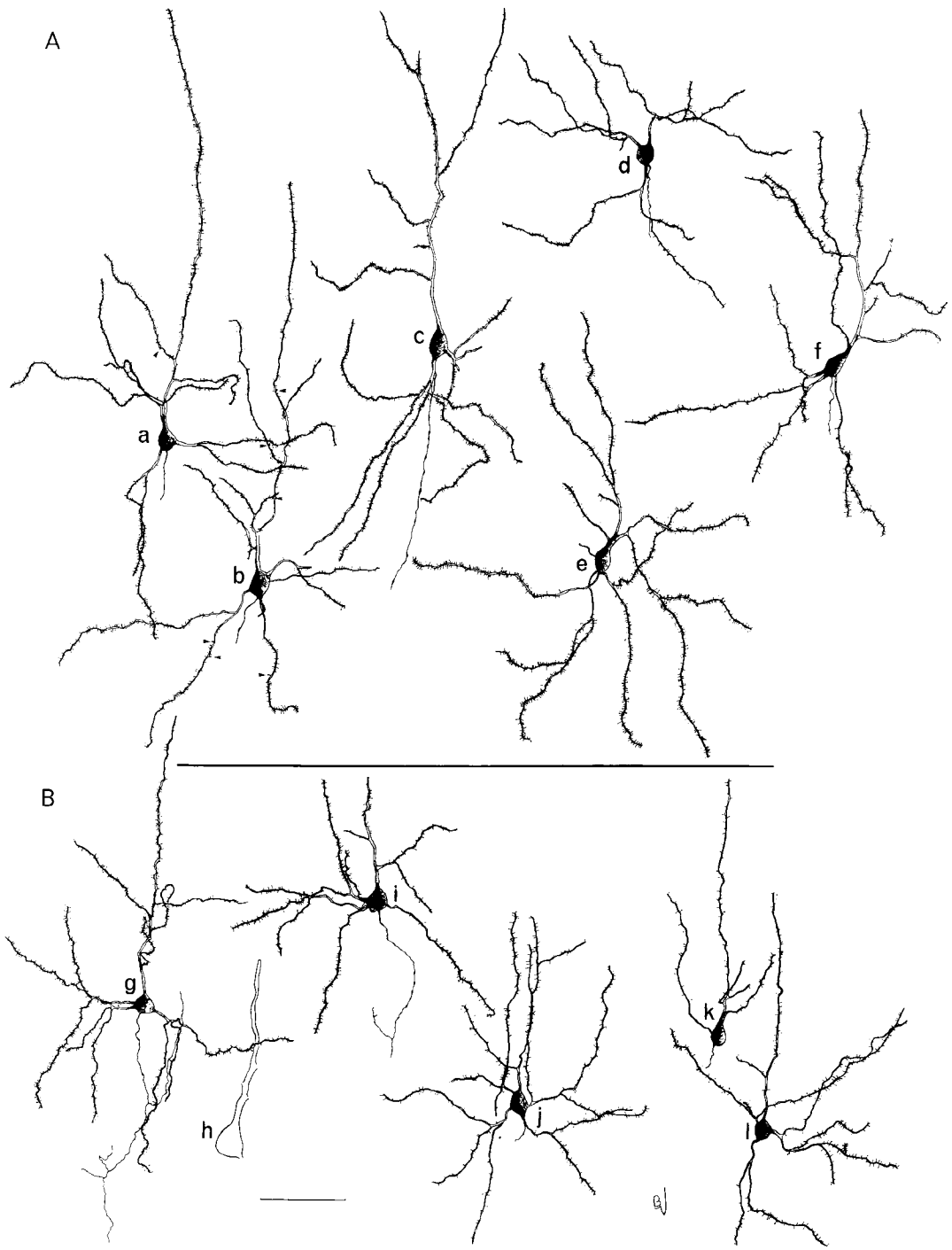
## PLATE 4

### EXPLANATION OF FIGURES

7 A sampling of cells from layer III(IV) which are oriented toward but do not represent actual depths from the pia.

A RSg1, pointers on cells a and b indicate sessile spines.

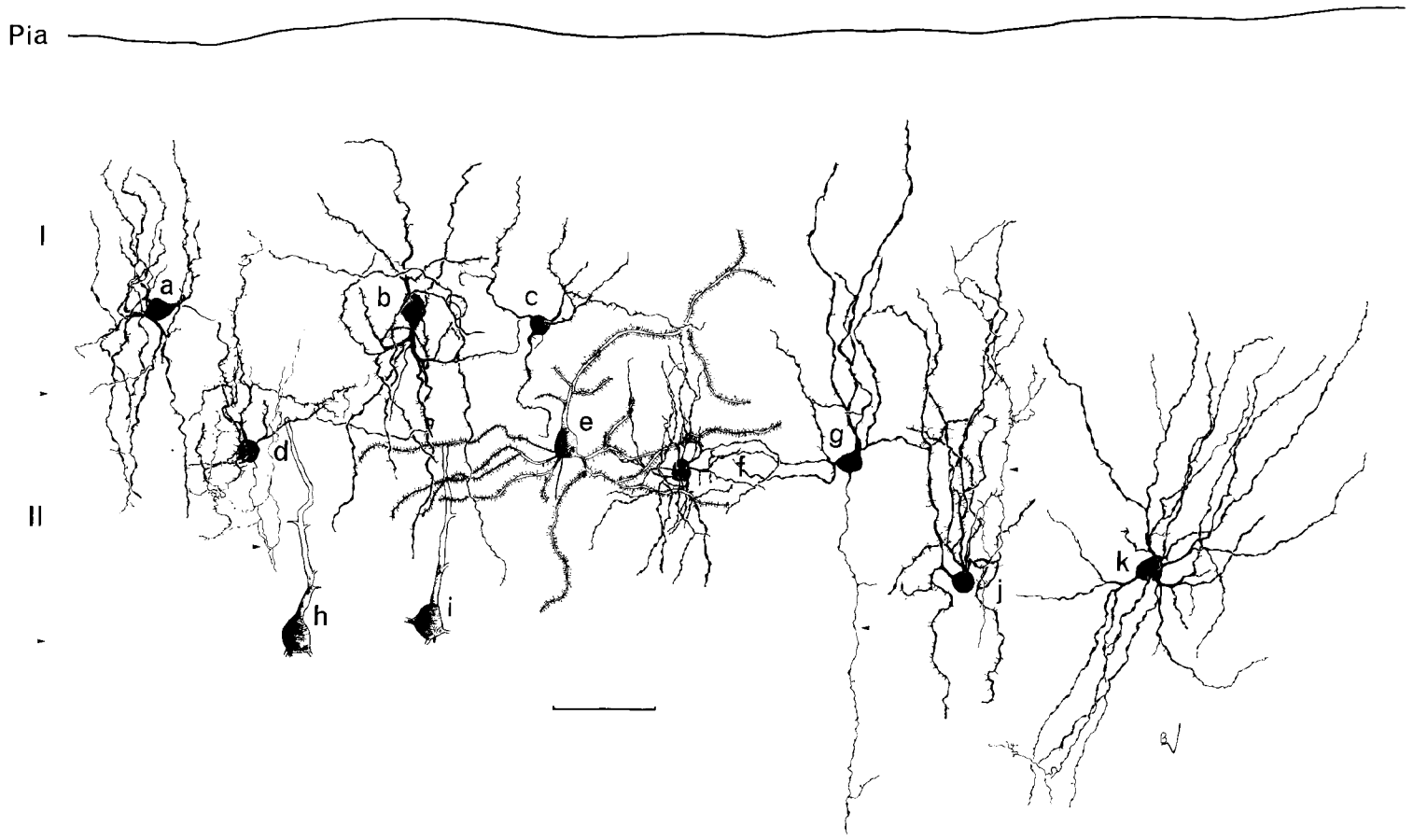
B RSg2, cell h is a layer Va pyramidal cell perikaryon drawn for size reference.


A
a
b
c
d
e
f
B
g
h
i
j
k
l

## PLATE 5

### EXPLANATION OF FIGURE

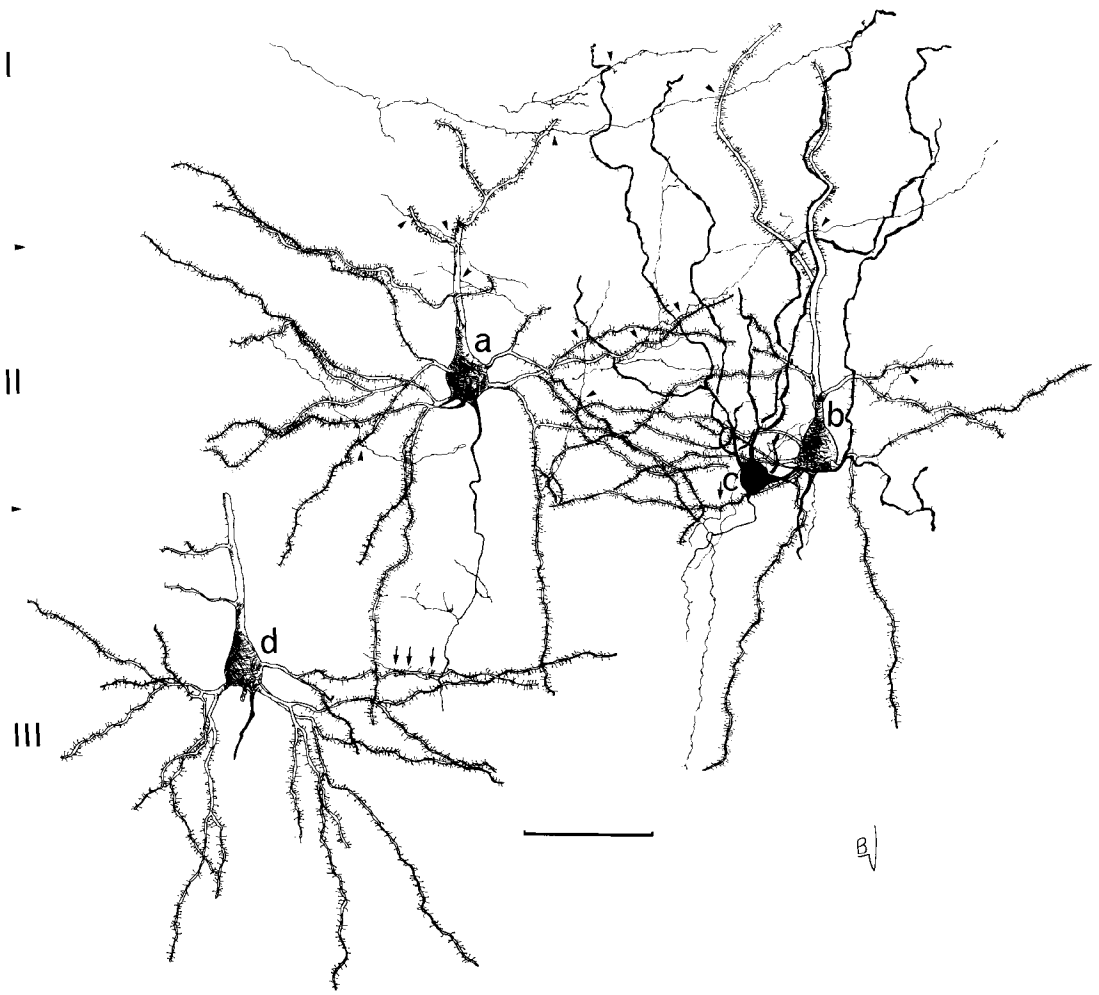
8 Cells from layers I–II of RSag. Pointers indicate axons. Rapid Golgi, scale, 50 $\mu$.


Pia
I
II
a
b
c
d
e
f
g
h
i
j
k

## PLATE 6

### EXPLANATION OF FIGURE

9 A small group of cells in layers I–IIIa-b of RSag. Pointers indicate possible points of afferent or intrinsic termination, while arrows designate points of collateral termination. Rapid Golgi, scale, 50 $\mu$.


I
II
III
a
b
c
d
BV

## PLATE 7

### EXPLANATION OF FIGURES

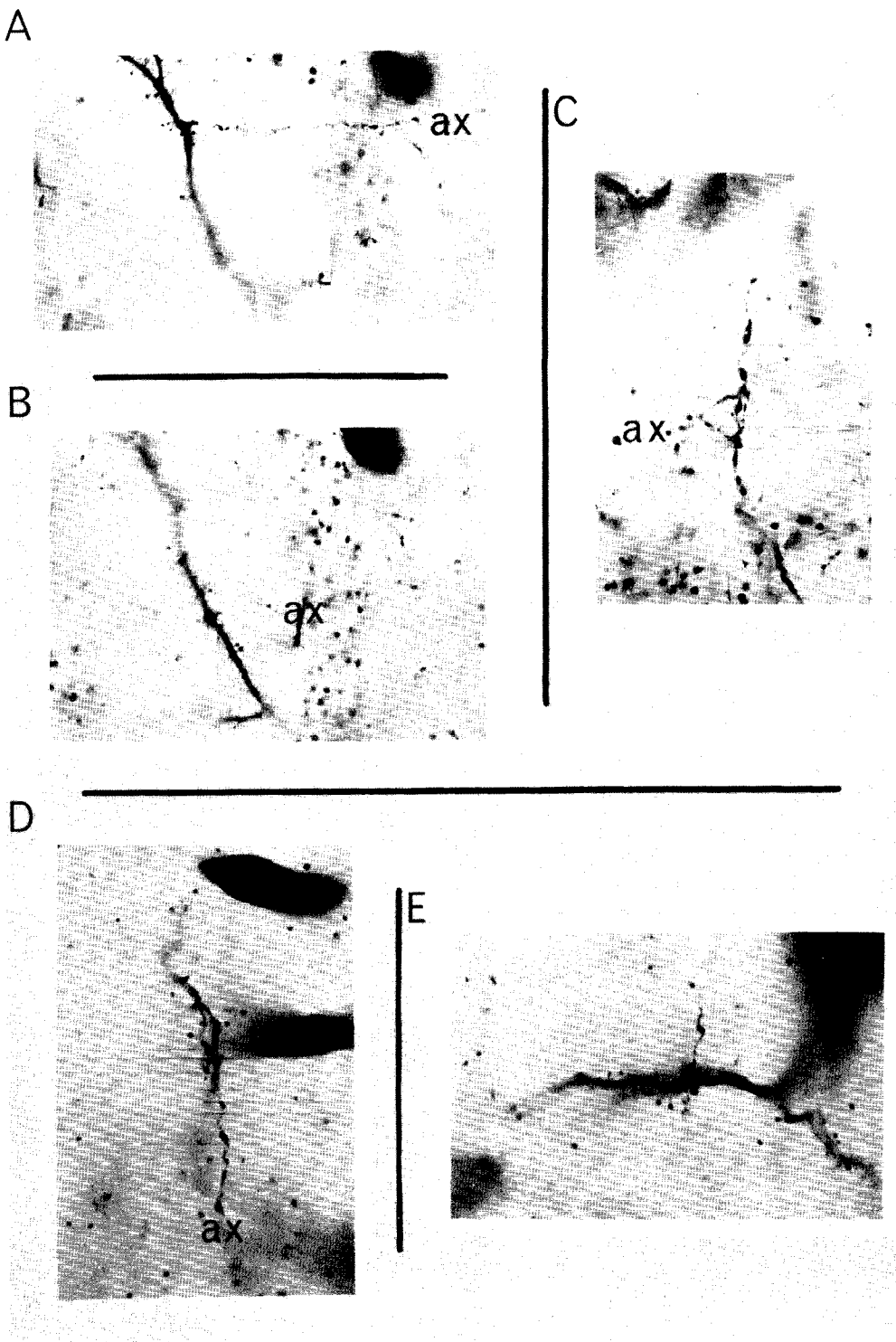
10 Details of RSag morphology. Rapid Golgi, ax, axon.

A,B Afferent or intrinsic axons which appear to terminate on the apical dendrite of a layer IIIa-b pyramidal cell in layer I.

C An afferent or intrinsic axon terminating on the beaded dendrite of a layer I–II stellate cell.

D A possible connection between cells e and f at the pointer in the insert of figure 12.

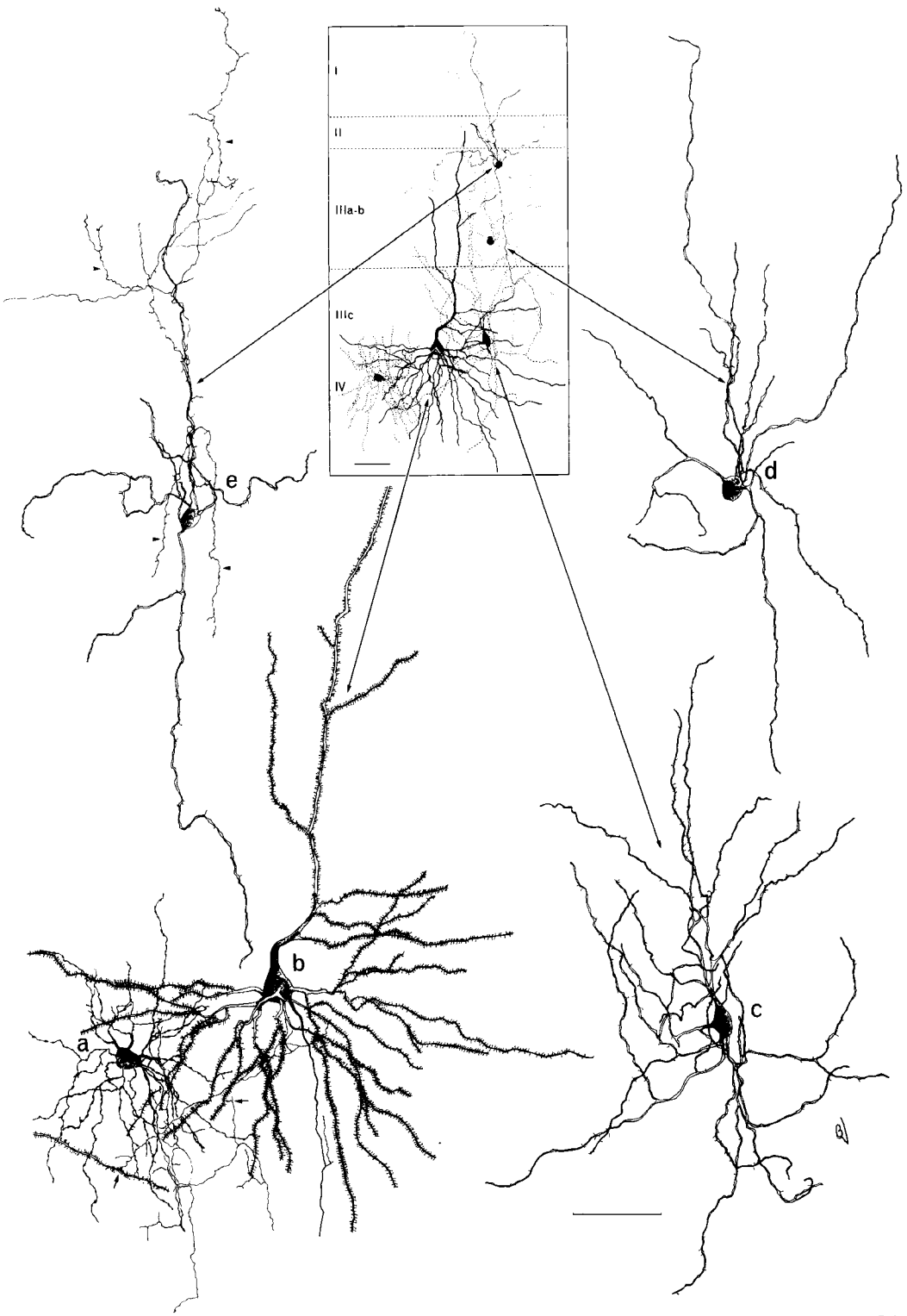
E Variously sized and shaped pedunculated spines on cell d of layer VI at the pointer in figure 13.


A
ax
B
ax
C
ax
D
ax
E

## PLATE 8

### EXPLANATION OF FIGURE

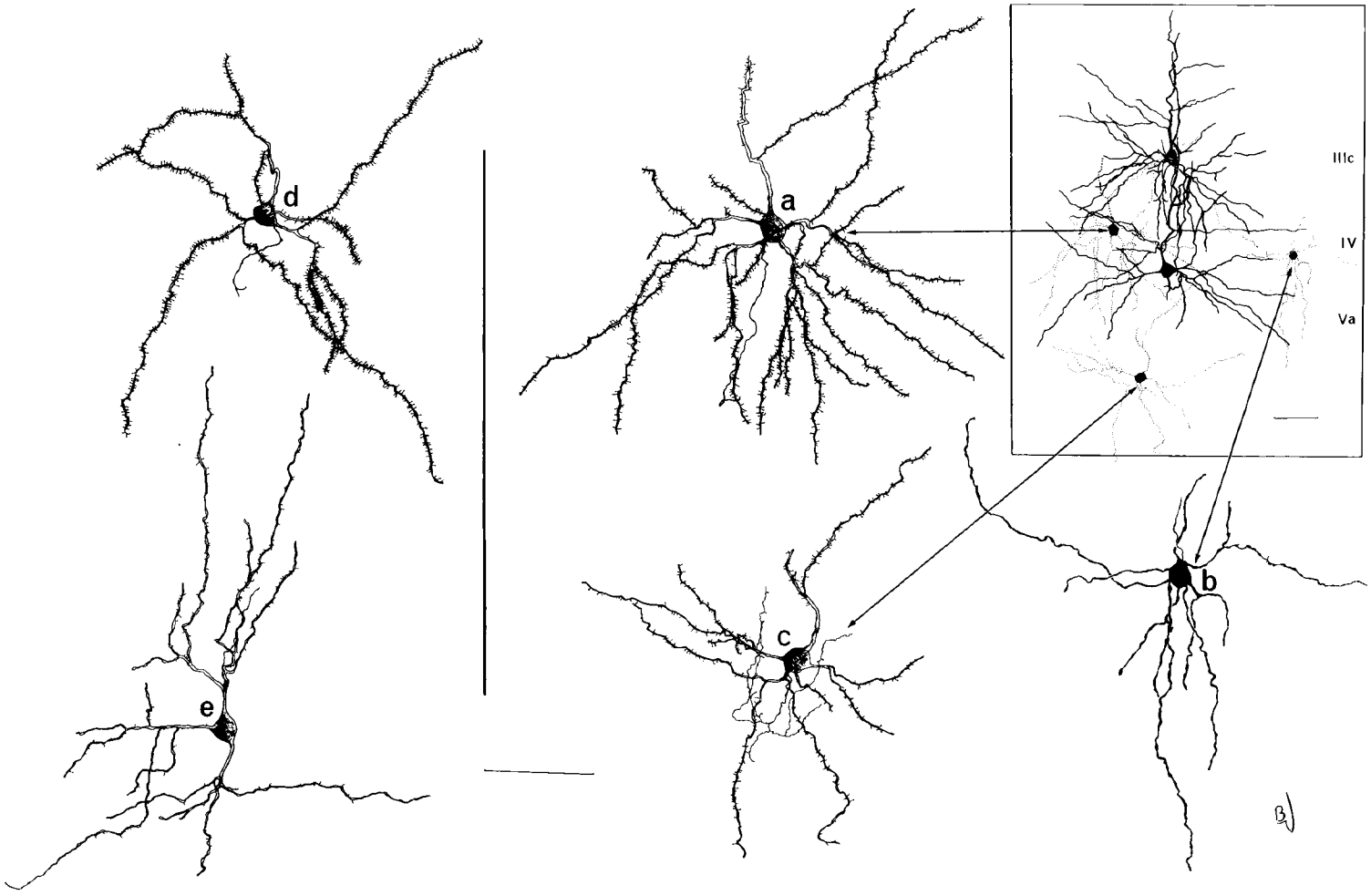
11 Small group of cells from layers IIIa-b–IV of RSag. Pointers on cell e reference its axon, while the small arrows on cell a indicate potential points of collateral termination for that cell. Rapid Golgi, scales, 50 $\mu$.


I
II
IIIa-b
IIIc
IV
a
b
c
d
e

## PLATE 9

### EXPLANATION OF FIGURE

12 Small group of cells from layers III–V of RSag, cells d and e were taken from layer IV in other sections. Rapid Golgi, scales, 50 $\mu$.

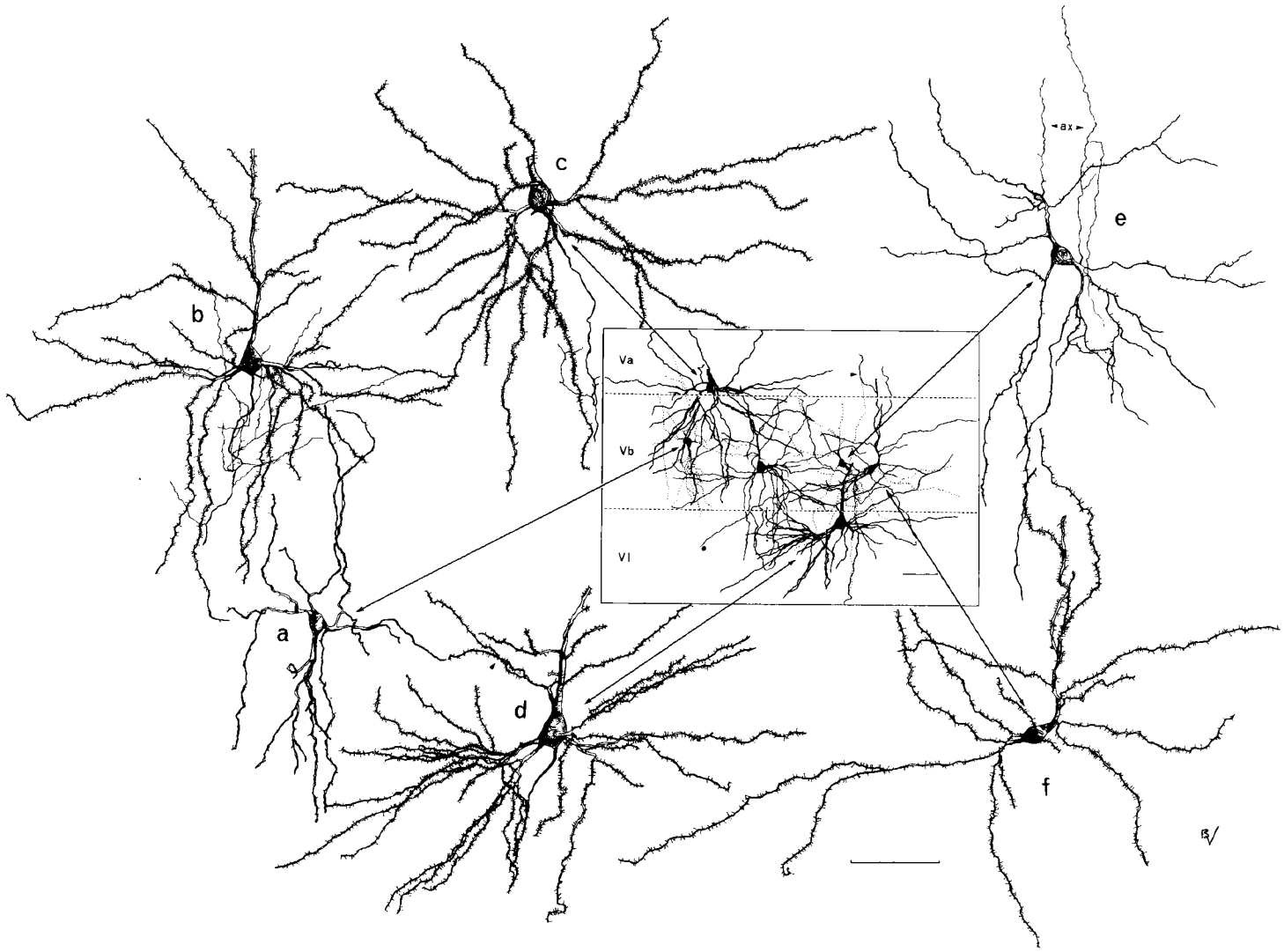

d
a
IIIc
IV
Va
e
c
b

## PLATE 10

### EXPLANATION OF FIGURES

13 Small group of cells from layers Va–VI of RSag. Rapid Golgi, Scales, 50 $\mu$.

Insert: Pointer indicates where cells e and f are in contact, see figure 10. Asterisk indicates the longest basal dendrite of cell f. Higher magnification: Pointer on cell d is the position from which spines were photographed in figure 10. ax, axon.


a
b
c
d
e
f
ax
Va
Vb
VI

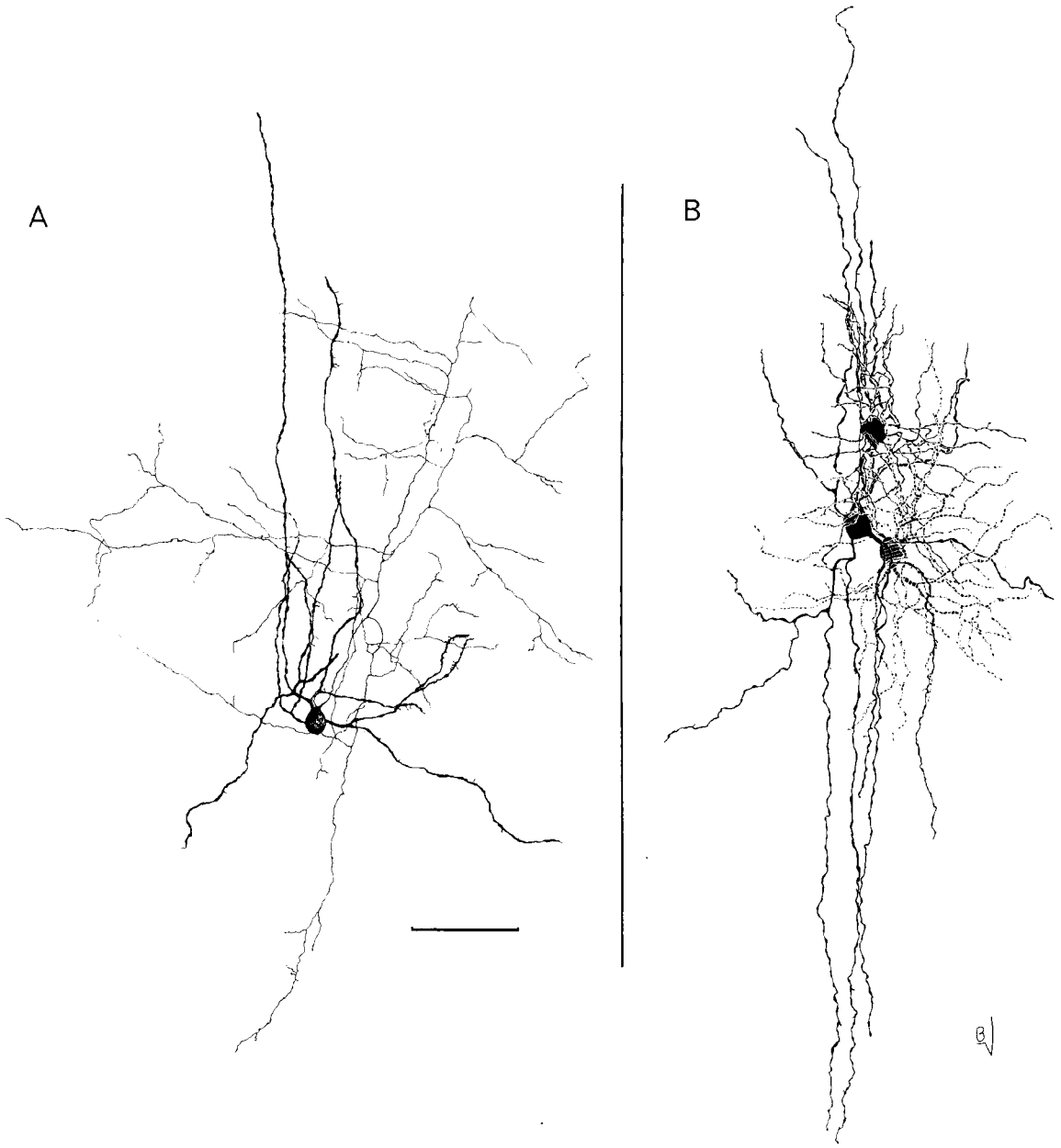
## PLATE 11

### EXPLANATION OF FIGURES

14 Stellate cells from layer IV of area 23. Rapid Golgi, scale, 50 $\mu$.

A Dendritic and axonal arbor of a layer IV stellate cell.

B Nest of three stellate cells with beaded dendrites.


A
B