THE JOURNAL OF COMPARATIVE NEUROLOGY 245:198-237 (1986)

Optic Tectum of the Eastern Garter Snake, *Thamnophis sirtalis*. II. Morphology of Efferent Cells

DENNIS M. DACEY AND PHILIP S. ULINSKI
Department of Anatomy and Committee on Neurobiology, The University of Chicago, Chicago, Illinois 60637

ABSTRACT

Tectal efferent neurons were retrogradely filled from extracellular injections of horseradish peroxidase (HRP) into pathways efferent from the tectum. *Tectorotundal neurons* have cylindrical dendritic trees, 80–100 μm in diameter, that extend vertically across the central and superficial tectal layers. Apical and basal dendrites are laden with complex appendages. The axon gives rise to an intratectal, collateral arbor that extends horizontally into the stratum griseum centrale beyond the cell's dendritic tree. The parent axon exits the tectum laterally in the tectothalamic tract. *Tectogeniculate neurons* also have narrow, radially oriented, and highly branched apical dendrites, but their basal dendrites are infrequently branched and lack appendages. An intratectal axon collateral forms a small, spherical arbor overlapping the apical dendrites in sublayer c of the stratum fibrosum et griseum superficiale. The parent axon ascends vertically and just below the stratum opticum turns rostrad to follow the optic fibers to the diencephalon. *Tectoisthmi neurons* have small somata and thin, radial dendrites that arborize below the pial surface in the stratum zonale. An intratectal axon collateral forms a spatially restricted arbor ventral to the soma in register with the dendritic tree. *Tectoisthmobulbar neurons* have dendrites that arborize extensively in sublayer a of the stratum fibrosum et griseum superficiale. The axon exits the tectum without collateralizing and joins a small-caliber component of the ventral tectobulbar tract. *Ipsilateral tectobulbar neurons* have stellate dendritic fields, 150–250 μm in diameter, that are restricted to the deep layers of the tectum. Sparsely branched dendrites are appendage-free but bear many short, fine spicules. The axon initially ascends from the soma and recurves into the stratum album centrale without collateralizing before joining a medium-caliber component of the ventral tectobulbar tract. *Crossed tectobulbar neurons* have large, stellate dendritic trees with diameters ranging from 200 to 500 μm. Like ipsilateral tectobulbar neurons, their dendrites are appendage-free but bear spicules. Their thick-caliber axons exit the tectum without collateralizing and course deep in the stratum album centrale to reach the dorsal tectobulbar tract.

Key words: tectobulbar, tectoisthmi, tectothalamic, tectal efferent pathways, intratectal connections, horseradish peroxidase

This is the second in a series of five papers that provide a detailed description of the anatomy of the optic tectum of the eastern garter snake, *Thamnophis sirtalis*, with the overall goal of relating topographic and nontopographic tectal systems to the production of orienting movements. The preceding paper (Dacey and Ulinski, '86a) described the morphology of tectal efferent axons and showed that they consist of six axon types distinguished by their course and terminal morphology in the brainstem. This paper describes the morphology of the dendrites and intratectal axon collaterals of neurons filled from injections of HRP into the tectal efferent pathways. The results show that each of the six efferent pathways can be associated with a

Accepted September 25, 1985.

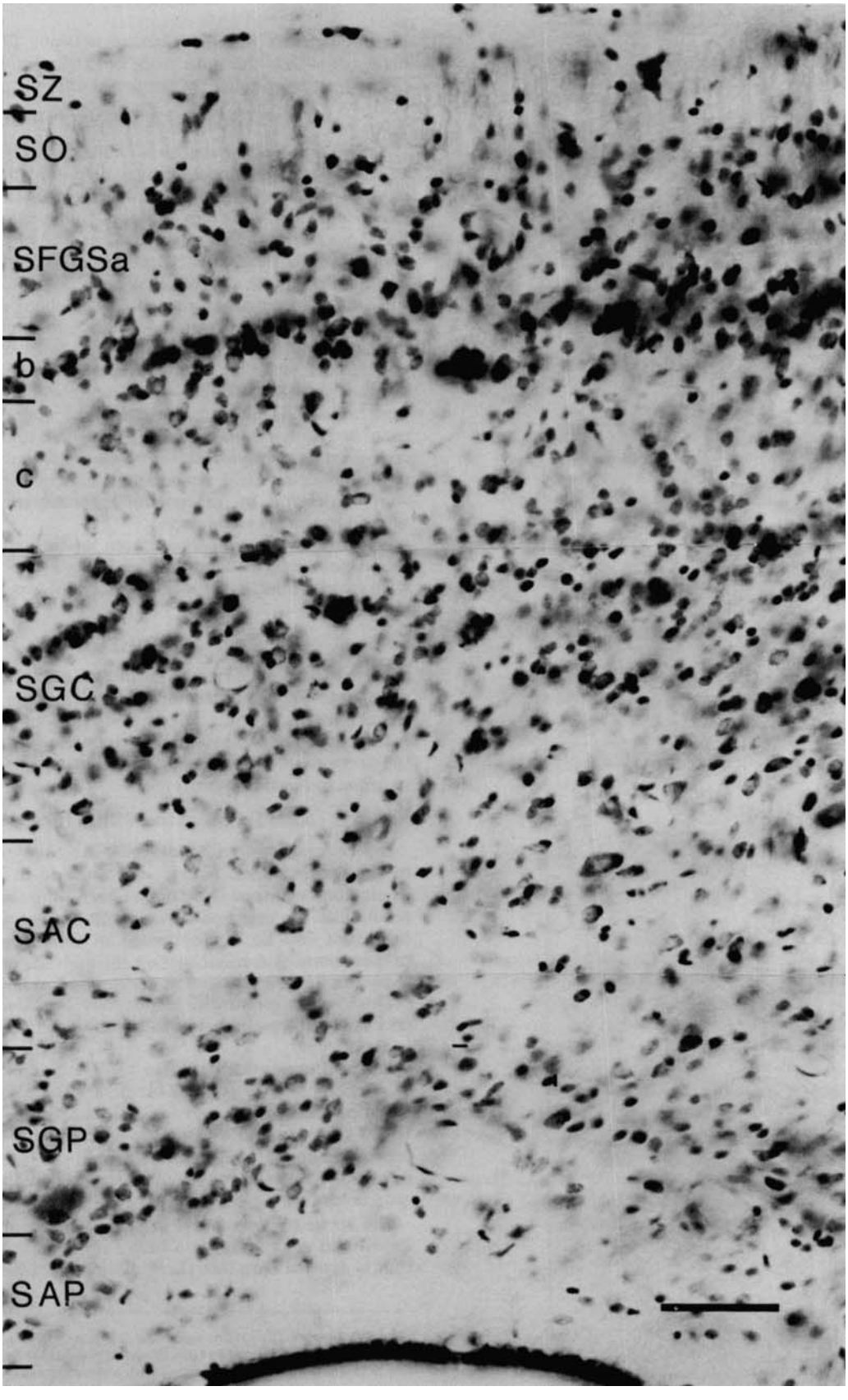
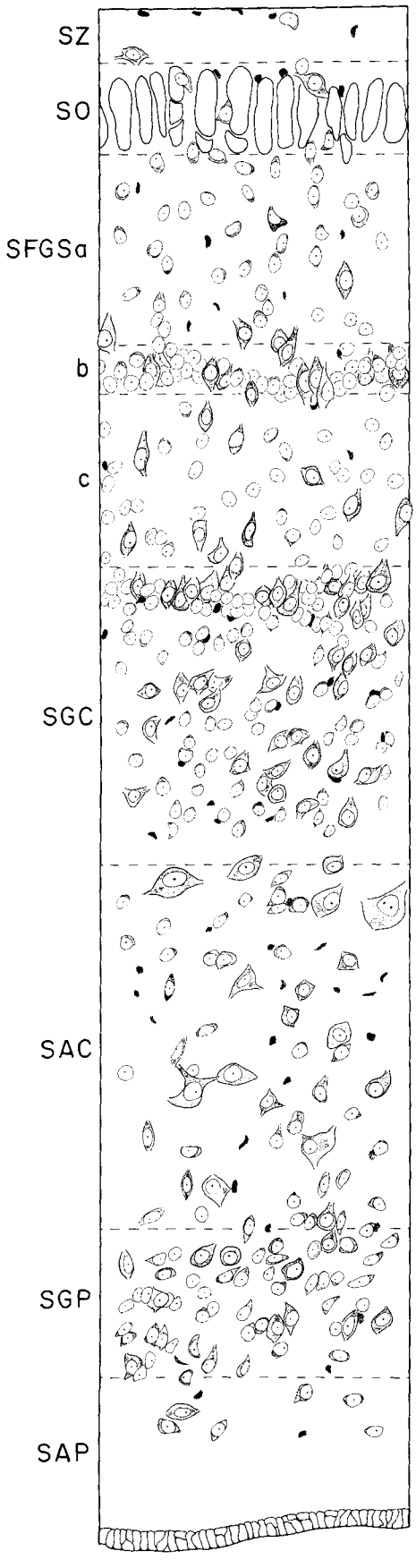


Fig. 1. Nissl-stained coronal section through the middle of the optic tectum in *Thamnophis*. The stratum fibrosum et griseum centrale (SFGS) is divided into three sublayers. A thin, cell-dense sublayer b is interposed between the thicker sublayers a and c of lower cell density. Abbreviations in this and the following figures: SAC, *stratum album centrale;* SAP, *stratum album periventriculare;* SFGS, *stratum fibrosum et griseum superficiale;* SGC, *stratum griseum centrale;* SGP, *stratum griseum periventriculare;* SO, *stratum opticum;* SZ, *stratum zonale.* Scale bar = 50 μm. Cresyl violet stain; 25-μm-thick section.



morphologically distinct class of neuron. The Discussion brings together the data from both papers to summarize the overall morphology of the tectal efferent neurons.

MATERIALS AND METHODS

A description of the methods for surgery, HRP histochemistry, and morphological analysis is provided in a previous paper (Dacey and Ulinski, '86a). The results of the present paper were derived from animals that received iontophoretic injections of HRP in the pontine and medullary brainstem reticular formation (12 snakes), the midbrain nucleus isthmi (9 snakes), or the thalamus (18 snakes). Densely filled cells in cobalt-enhanced diaminobenzidine material were reconstructed through serial 80-μm-thick sections cut in the coronal plane. Sections were lightly counterstained with cresyl violet to permit precise determination of the laminar position of labeled neurons. Camera lucida tracings are not adequate to illustrate the dimensions of neurons in the horizontal plane, but some information was recovered by using estimates of dendritic length to approximate dendritic field shapes and sizes. Dendritic lengths were estimated by using the trigonometric method described in the previous paper.

Nissl material was derived from brains embedded in celloidin, sectioned at 25 μm in the coronal plane, and stained with cresyl violet. Fiber-stained material was also available for study.

RESULTS

The experimental results permit a description of the morphology of the dendrites and intratectal axon collaterals of tectal efferent neurons. However, to present these results it is first necessary to briefly describe the cytoarchitecture of the tectum in *Thamnophis* and the appearance of tectal neurons in Nissl preparations.

Tectal cytoarchitecture

Huber and Crosby ('33) described tectal cytoarchitecture in the water snake, *Natrix sipedon*, and in *Thamnophis*. Their nomenclature is extended here to provide a detailed account of the cell and fiber layers, and of the variety of cells that can be distinguished in *Thamnophis* in Nissl preparations. A coronal section through the optic tectum is shown in Figure 1. Seven major layers can be recognized.

The *stratum zonale* (SZ) is a narrow, 25–30-μm-thick, cell-poor zone interposed between the pial surface and the stratum opticum.

The *stratum opticum* (SO) is 35–45 μm thick and consists of discrete, tightly packed bundles of axons that are oriented parallel to the rostrocaudal axis. Single fascicles are 10–20 μm wide and are separated from each other by cell-poor zones about 5 μm wide. These cell-poor gaps are continuous with the stratum zonale above and the superficial gray below.

The *stratum fibrosum et griseum superficiale* (SFGS), or superficial gray layer, is a broad zone, 180–200 μm thick, that is divided here into three distinct sublayers (SFGSa,b,

Fig. 2. Camera lucida tracing of the cell population in a Nissl-stained coronal section through the tectum. Somata that could be brought into focus over a 15-μm-thick zone were traced with a drawing tube. Nissl substance is represented schematically with fine stippling. The small, irregularly shaped and densely stippled structures are glial cell nuclei. Oval outlines in the stratum opticum are tracings of fascicles of optic fibers. Abbreviations as in Figure 1.

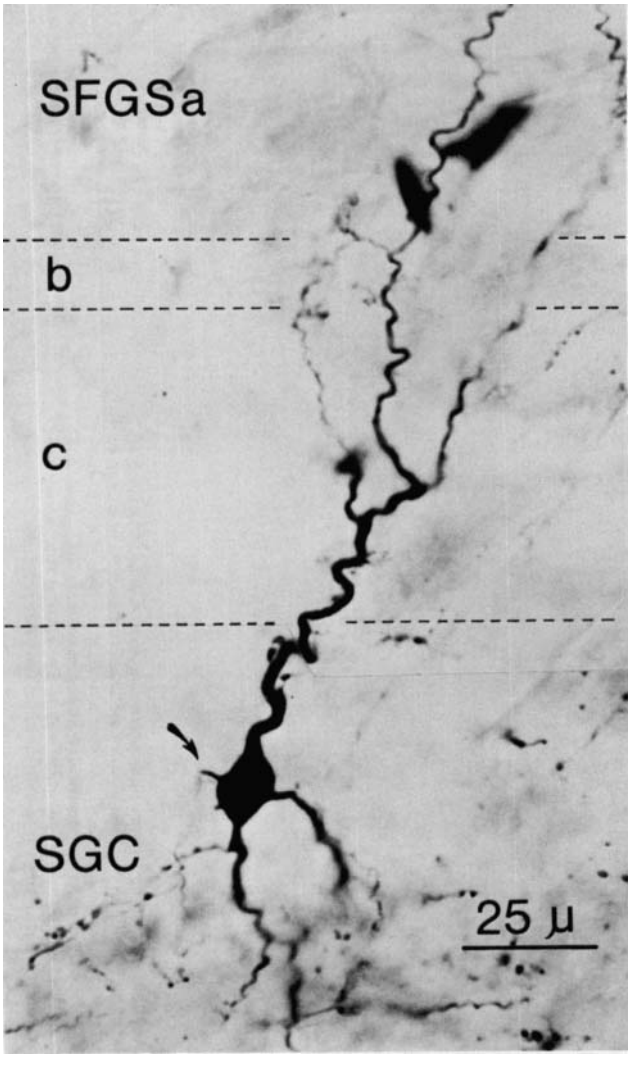


Fig. 3. Tectorotundal cell retrogradely filled from an injection of HRP into the nucleus rotundus. Arrow indicates axon arising from soma. The camera lucida tracing of this cell is illustrated in Figure 4; 80-μm-thick section.

and c). Sublayer b is a narrow, 15–25-μm-thick, cell-dense band that is situated in the center of the SFGS. It separates two thicker sublayers, a and c, that are 60–70 μm thick and contain fewer more scattered cells.

The *stratum griseum centrale* (SGC), or central gray layer, is a broad, 100–150-μm-thick, cellular zone situated just below the SFGS. Its upper border is set off from SFGSc by a region of increased cell density. However, there is no sharp ventral border to this region; the density of cells gradually decreases from superficial to deep in the SGC, forming a transition zone between it and the stratum album centrale.

The *stratum album centrale* (SAC) or central white layer is a 100–150-μm-thick zone of lower cell density. In fiber-stained sections it contains bundles of fine and large-caliber fibers oriented parallel to the tectal surface.

The *stratum griseum periventriculare* (SGP) is a thin zone, 50–60 μm thick, of moderate cell density. It is set off from the SAC above by a distinct cell-poor region 10–20 μm thick. The SGP is continuous ventrally with the periaqueductal gray of the midbrain.

The *stratum album periventriculare* (SAP) is a thin, cell-poor region below the SGP. In fiber-stained sections it appears not as a fiber layer, but as a cell-poor neuropile traversed by a moderate number of obliquely ascending, fine-diameter fibers. The SAP is bordered ventrally by the ventricular ependyma.

The appearance of Nissl-stained tectal neurons is shown in Figure 2. This is a camera lucida tracing of a coronal section through the middle of the tectum. All of the cells that could be brought into focus in a 15-μm section are shown and their cytoplasm is represented schematically with stippling. Several major groups of tectal cells can be distinguished by size, shape, and staining characteristics of the somata.

Small spherical cells, 4–6 μm in diameter, are present in all tectal layers. These cells have little cytoplasmic staining and appear as round, pale-staining nuclei containing darkly stained nucleoli. Cells of this sort are packed at relatively high density in sublayer b of the superficial gray and at the upper border of the central gray, where they participate with cells of other types in clusters of two to five apparently apposed somata.

Spherical and *pear-shaped cells*, 6–10 μm in diameter, are present in the upper half of the central gray and throughout the superficial gray where they are most obvious in sublayers a and c. They are distinguished from the small spherical cells just described by a slightly more abundant cytoplasm that caps the pole of the nucleus, giving it a pear or teardrop shape.

Medium pear-shaped cells, 8–12 μm in diameter, have relatively abundant and lightly staining cytoplasm that completely surrounds the nucleus and often reveals the beginning of a prominent apical dendrite. These are present throughout the superficial and upper central gray but are most prevalent in the band of cells clustered at the upper border of the central gray.

Medium fusiform cells, 12–15 μm in diameter, have plump, cytoplasm-rich somata with thick, vertically elongated upper and lower poles. These cells are also scattered throughout the superficial and central gray, but are most easily observed in the middle of the central gray.

Medium multipolar cells, 10–15 μm in diameter, have spherical, triangular, or vertically fusiform somata. Their abundant cytoplasm often shows slight clumping of Nissl substance. They are present in the lower two-thirds of the central gray and, more rarely, in the central white matter.

Large multipolar cells, 15–30 μm in diameter, are rich in darkly staining cytoplasm. They contain relatively large nuclei, 6–8 μm in diameter, and double nucleoli are sometimes observed. These conspicuous cells appear scattered throughout the central white layer and the upper margin of the periventricular gray layer; they are most prevalent in a narrow zone at the interface of the central gray and white layers.

Horizontally fusiform cells are medium sized, 10–15 μm in diameter, and are found scattered in the stratum zonale, stratum opticum, and upper half of the superficial gray. Although they appear to be a very small population, their size, Nissl-rich cytoplasm, and often multipolar somata stand out vividly in a region containing a relatively low density of small, pale cells.

Tectal efferent neurons

Retrograde filling after injections of HRP at various points along the major efferent pathways indicates that a distinct

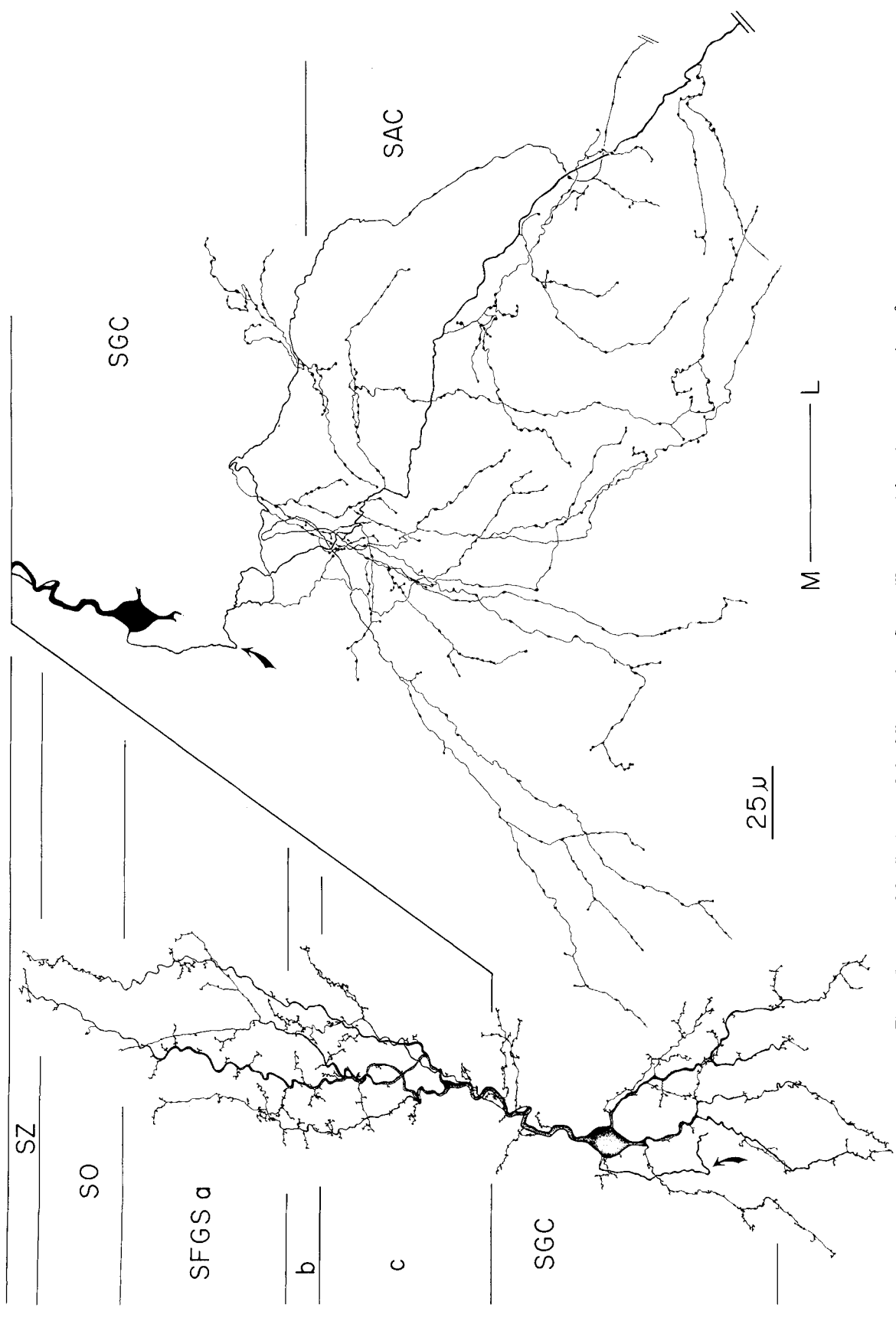


Fig. 4. Tectorotundal cells. This and the following three figures illustrate serial section reconstructions of HRP-filled neurons whose axons could be traced into the tectorotundal pathway. The five shown were chosen to document the pattern and variation in tectorotundal cell morphology. The characteristic features of the tectorotundal cell are a narrow cylindrical dendritic field that spans the superficial (SFGS) and central (SGC) layers and a widespread axon collateral projection into the central gray and white layers. For clarity, the axonal and dendritic arbor of this cell are shown separately; the arrow in each tracing indicates the same point. M-L: medial-lateral.

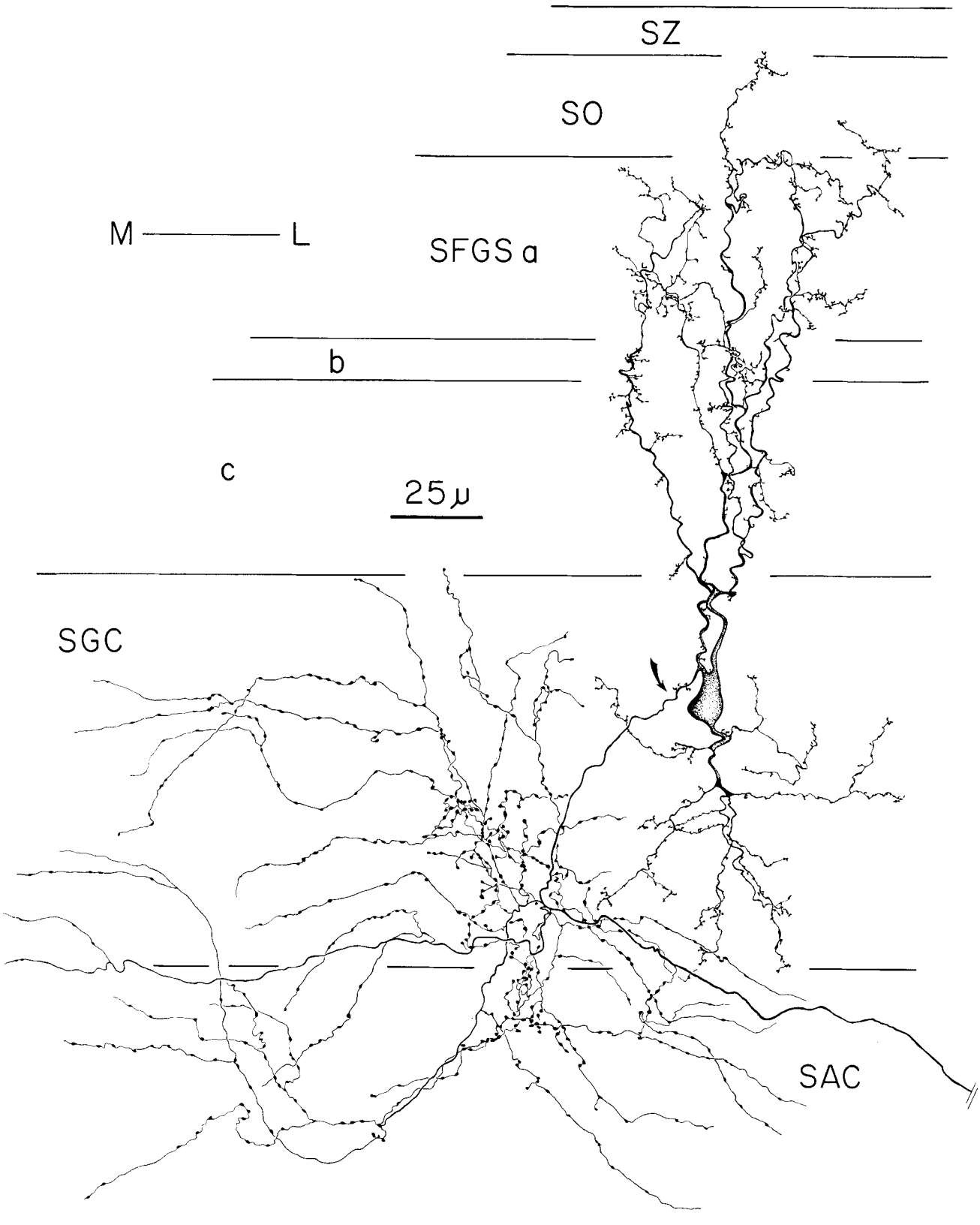


Fig. 5. Tectorotundal cell. This neuron also has its soma positioned in the middle of the stratum griseum centrale. Dendrites bear threadlike, elongate appendages laden with clusters of complexly indented swellings. The axon forms a dense terminal plexus in the vicinity of the cell's lower dendrites, and then gives rise to a large number of terminal collaterals that extend away from the cell's dendritic domain in the horizontal plane. The origin of the axon is indicated by the arrow. M-L: medial-lateral.

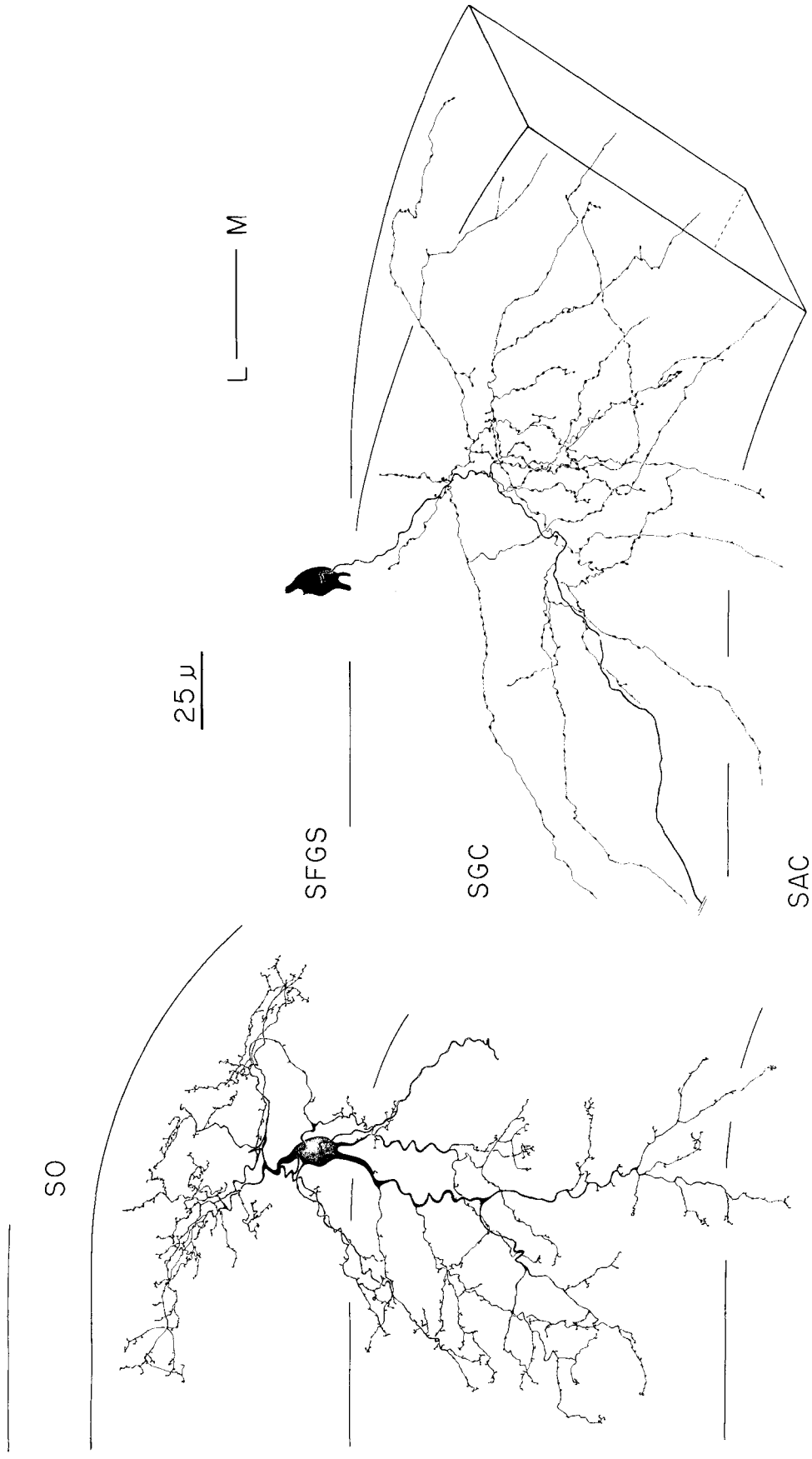


Fig. 6. Tectorotundal cell. The soma of this neuron is located in the stratum fibrosum et griseum superficiale. However, the size and distribution of its dendritic field and its axon collateral system are the same as for the neurons shown in Figures 4 and 5. M-L: medial-lateral.

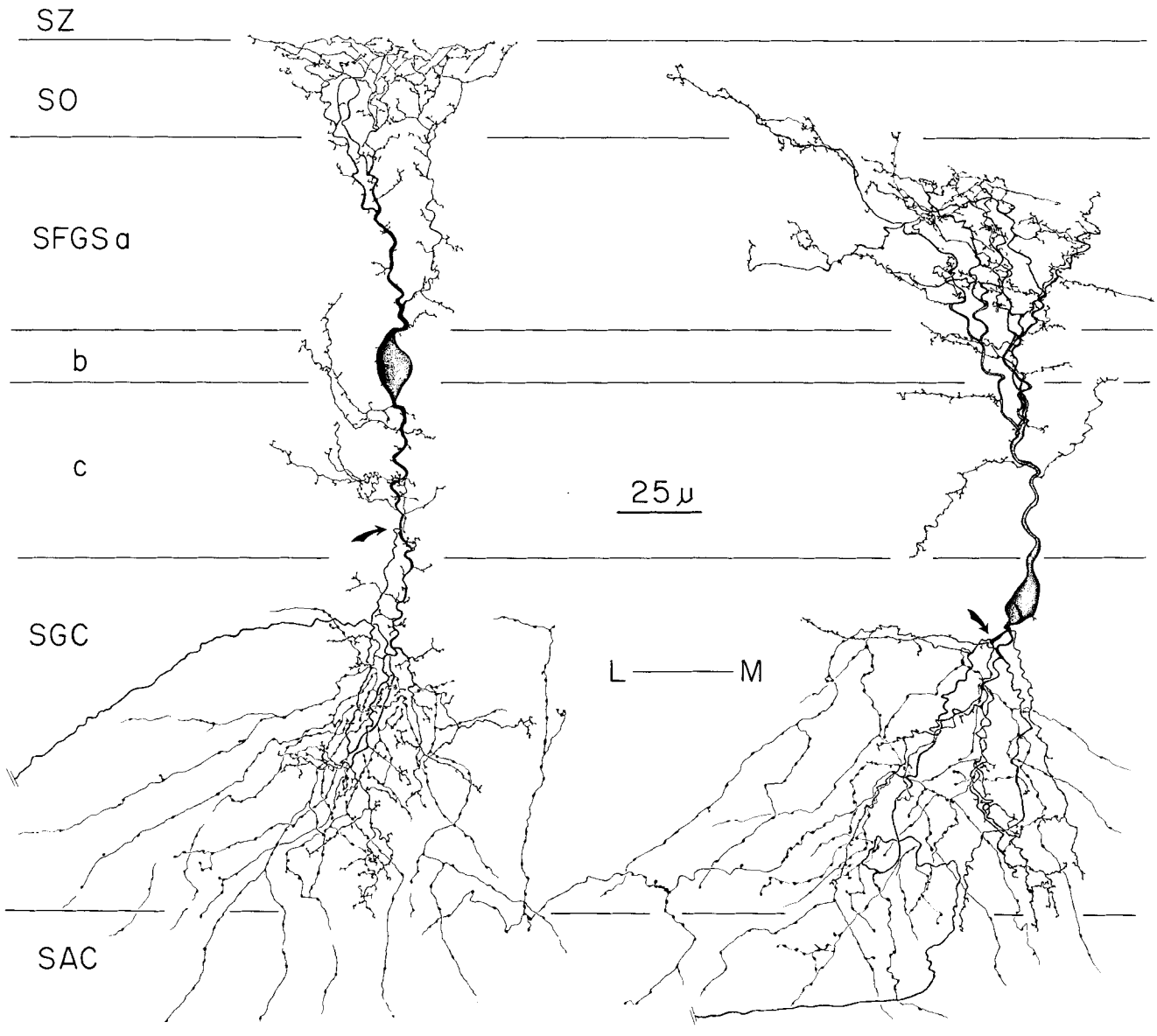


Fig. 7. Tectorotundal cells. Despite variations in the laminar position of their somata, these two neurons also have dendritic fields that span the strata fibrosum et griseum superficiale and griseum centrale. In the more superficially located neuron the descending dendrite is relatively elongate. The axon (arrow) always appears near the border of the superficial with the central gray, regardless of soma position.

class of tectal neurons gives rise to each of six efferent axon types described in a previous paper (Dacey and Ulinski, '86a). The illustrations used below to describe each class were chosen to document the characteristic morphology and distribution of each neuron type, and to show how these patterns vary within each class.

Tectorotundal cells. Injections of HRP into either the tectothalamic tract in the rostral forebrain or directly into nucleus rotundus filled axons within the tectorotundal pathway while leaving the other efferent tracts unlabeled. Retrogradely filled fibers ascend from the tectothalamic tract and course medially in the superficial one-third of the stratum album centrale. Somata containing granular, diffuse or dense HRP reaction product were present throughout the thickness of the strata griseum centrale and fibrosum et griseum superficiale; they showed a slight tendency to concentrate in the middle of the stratum griseum centrale. A photomicrograph of a tectorotundal neuron filled from an injection into nucleus rotundus is shown in Figure 3. A camera lucida reconstruction of this neuron is shown in Figure 4 and other examples are shown in Figures 5–7.

The soma of a tectorotundal cell is oval or vertically fusiform, measuring 12–15 μm along the short axis and 15–20 μm along the long axis. They most likely correspond to the medium-sized fusiform cells of the central gray observed in Nissl preparations.

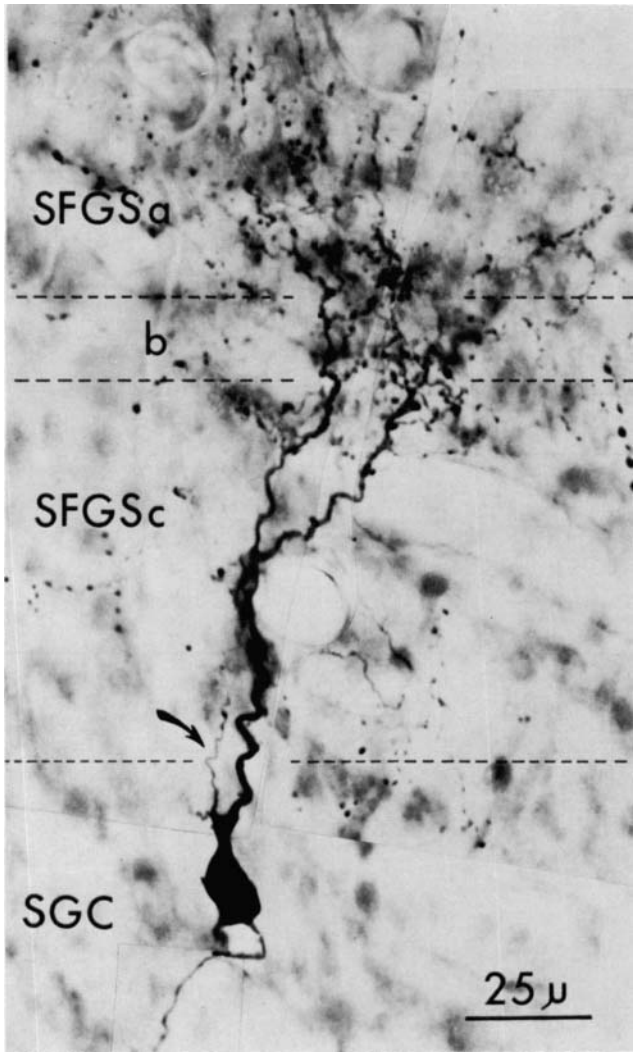


Fig. 8. Tectogeniculate cell retrogradely filled from an injection of HRP into the tectogeniculate pathway at the level of the pretectum. The ascending axon is indicated by the arrow. A camera lucida reconstruction of this cell is shown in Figure 9.

The basic structure, shape, and laminar position of the dendritic trees of tectorotundal neurons is demonstrated clearly in Figures 4 and 5. The upper and lower poles of the somata give rise to one or, less often, two stout primary dendrites. The upper dendrites ascend radially into the superficial layers and reach the ventral border of the stratum zonale. The lower dendrites descend radially through the central gray layer to the upper border of the stratum album centrale. Both upper and lower dendrites branch dichotomously once or twice. Secondary dendrites arise at slightly oblique angles so that the overall dendritic field is hourglass-shaped, with the maximum spread of both upper and lower dendritic trees about 75–100 μm. Thin, terminal branchlets arise from the somata and dendrites. They may be short and extend horizontally from their point of origin, or they may be long and infrequently branched, extending parallel with the neuron's long axis. These slender appendages bear small, oval swellings and globular protrusions that may be complexly indented or lobulated, giving them a gnarled, clawlike appearance. The appendages have a fairly homogeneous distribution on the neuron and appear to provide a major part of its total dendritic surface. The ascending dendrites of tectorotundal neurons positioned superficially in the tectum are shortened and the descending dendrites are long, but the total extent of the neuron—from the stratum opticum to the stratum album centrale—remains constant (Figs. 6,7).

Axons of tectorotundal neurons are thickened and conical (Figs. 4,6) as they arise from a soma. When issuing from a dendrite, however, (Figs. 5,7) they begin as inconspicuous, threadlike filaments blending in with the many thin, dendritic branchlets. In either case, the axon is initially smooth and often makes a brief horizontal excursion before turning ventrally and descending in an oblique path to the lower half of the stratum griseum centrale. There it begins to meander and coil about, issuing many fine, varicose collaterals. A distinct cluster of collaterals and terminal boutons is formed within or just adjacent to the cell's lower dendritic tree. Single beaded filaments arise from this cluster, radiate either downward or horizontally, and arborize mainly in the stratum griseum centrale. The parent axon emerges from this tangle, descends obliquely into the stratum album centrale, and courses laterally into the tectothalamic tract. The complete dimensions of the collaterals of tectorotundal neurons could not be determined unequivocally due to fading of the HRP reaction product in the longest and thinnest collaterals. However, single collaterals were often traced up to 350 μm away from a neuron's dendritic field, and they probably extend farther since tectorotundal neurons situated in the lateral tectum were often retrogradely filled from a distance of 600–700 μm by small injections of HRP into the medial tectum. Because the axons of tectorotundal neurons course laterally, HRP labeling must have resulted via collaterals extending medially over this distance.

Tectogeniculate cells. Injections of HRP into the tectogeniculate pathway at the rostral pole of the tectum or at the level of the ventral lateral geniculate nucleus retrogradely fill axons that course caudally into the tectum in the stratum fibrosum et griseum superficiale just ventral to the stratum opticum. The overall distribution of labeled neurons in the tectum after this kind of injection was similar to that of the tectorotundal system, even though no tectorotundal fibers were filled. Tectogeniculate neurons were present throughout the stratum griseum centrale and the lower half of the stratum fibrosum et griseum superficiale. The largest number of neurons, however, occurs at the border of the stratum griseum centrale with the stratum fibrosum et griseum superficiale, slightly superficial to the region that contains the highest density of tectorotundal neurons. A tectogeniculate neuron backfilled from an injection into the tectogeniculate path in the pretectum is shown at low magnification in Figure 8. This and other tectogeniculate neurons are shown in camera lucida reconstructions in Figures 9–13. The somata are spherical or pear-shaped (8–12 μm in diameter) and slightly smaller than tectorotundal neurons. They probably correspond to the medium pear-shaped somata that are abundant at the interface of the superficial and central gray in Nissl preparations (Figs. 1,2). Each soma is smooth, save for an occasional knoblike protrusion, and gives rise to a single thick dendrite that ascends radially into the superficial gray layers, and to one or two thin basal dendrites that descend into the deeper tectal layers (e.g., Figs. 9–11).

The apical dendritic tree of the tectogeniculate neuron is demonstrated clearly in Figures 9 and 11. It ascends radially and bifurcates into two terminal dendrites before

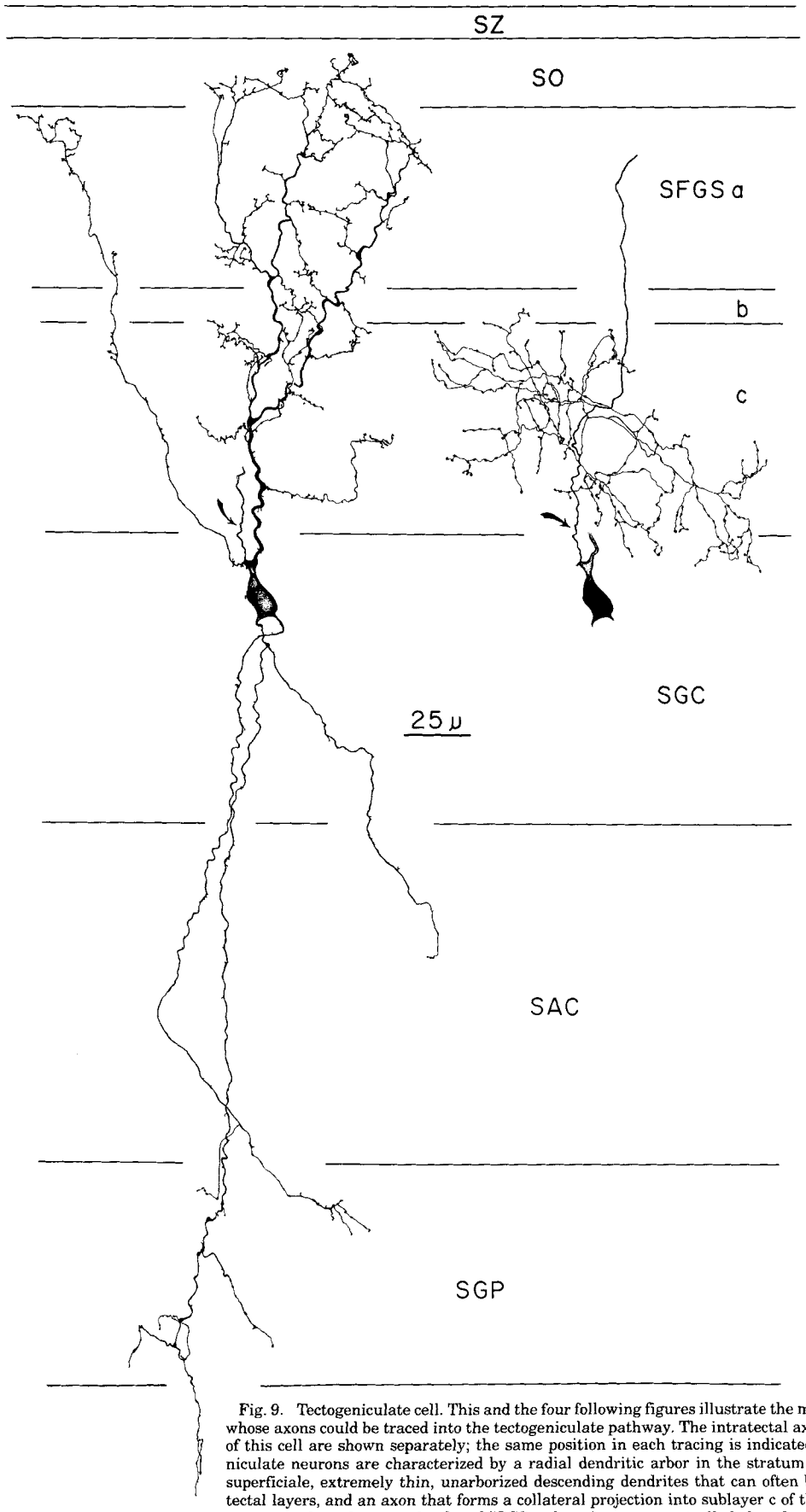


Fig. 9. Tectogeniculate cell. This and the four following figures illustrate the morphology of neurons whose axons could be traced into the tectogeniculate pathway. The intratectal axon and dendritic tree of this cell are shown separately; the same position in each tracing is indicated by arrows. Tectogeniculate neurons are characterized by a radial dendritic arbor in the stratum fibrosum et griseum superficiale, extremely thin, unarborized descending dendrites that can often be traced to the deep tectal layers, and an axon that forms a collateral projection into sublayer c of the SFGC. The parent axon ascends to the upper border of SFGSa where it courses rostrally below the stratum opticum.

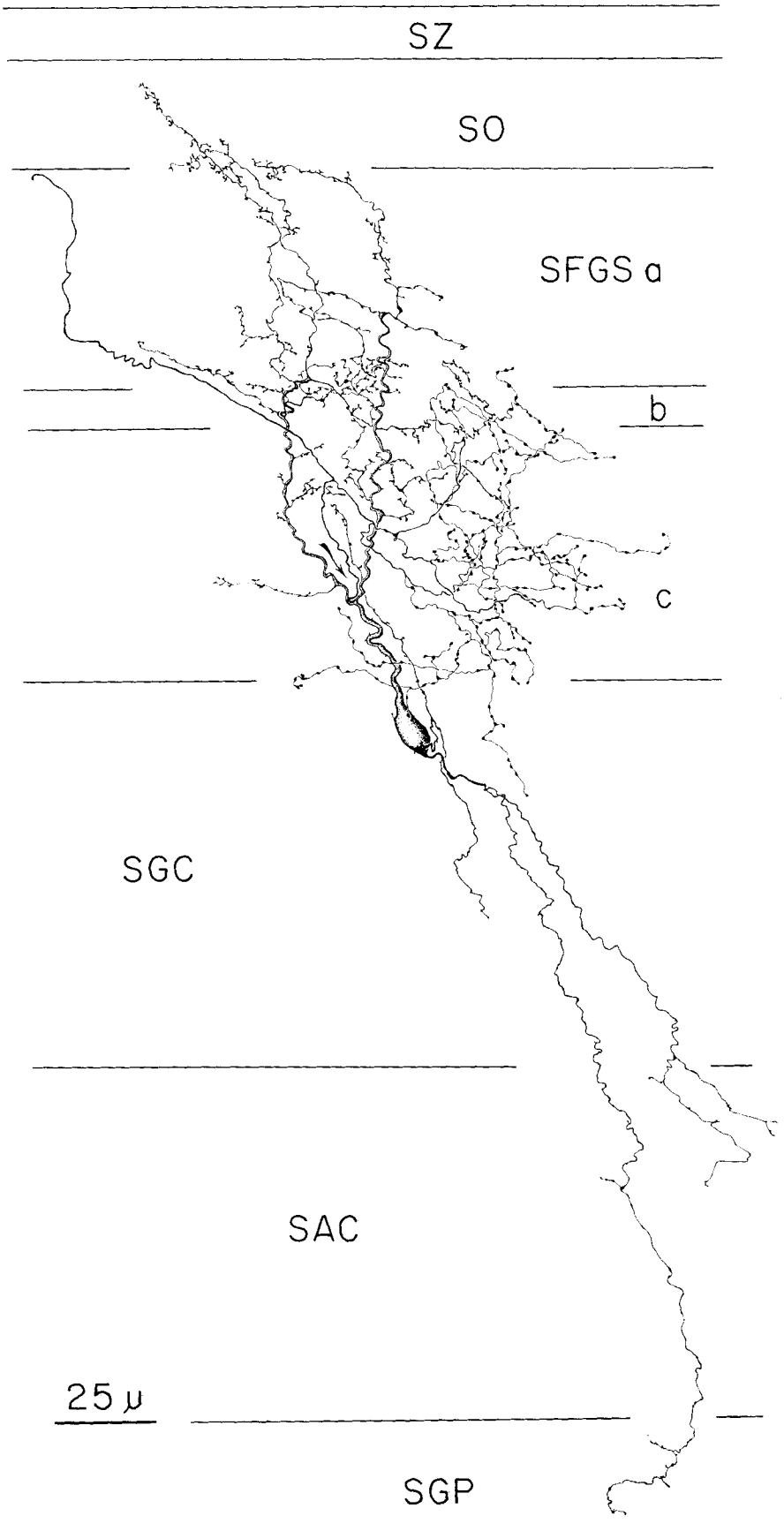


Fig. 10. Tectogeniculate cell. The majority of tectogeniculate neurons have their somata located at the border of the superficial (SFGS) and central gray (SGC) layers. The axon arbor in sublayer c is small and spherical, 50–100 μm in diameter, and usually overlaps the cell's dendritic tree but occasionally, as in this cell, is slightly displaced from the dendritic domain. The origin of the axon from a secondary dendrite is indicated by the arrow.

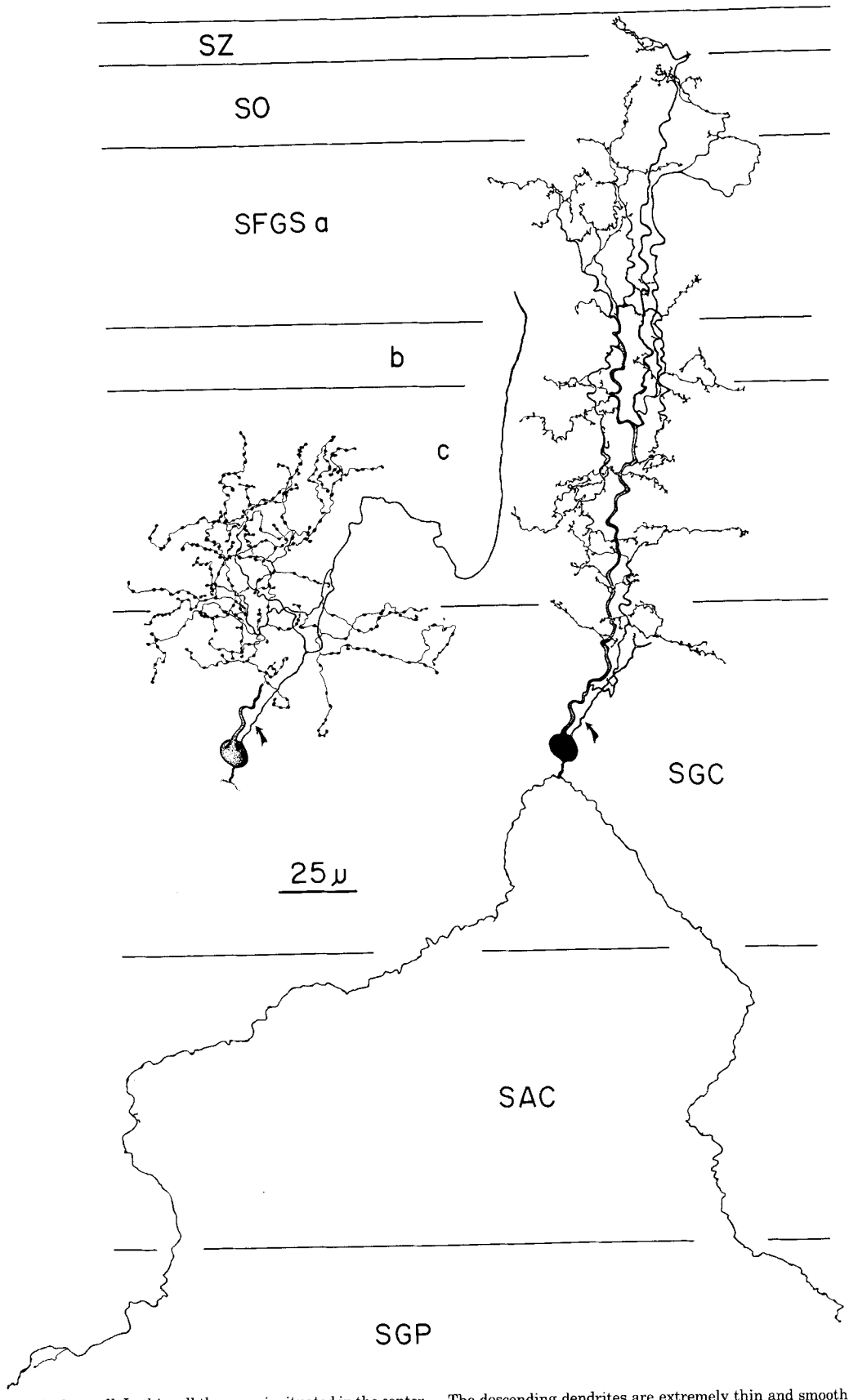


Fig. 11. Tectogeniculate cell. In this cell the soma is situated in the center of the SGC. However, the ascending dendrites of tectogeniculate cells do not begin to arborize until they reach the border between the strata fibrosum et griseum superficiale and griseum centrale, regardless of soma position. The descending dendrites are extremely thin and smooth. They sometimes extend obliquely beyond the cylindrical dendritic domain defined by the superficial arbor. Arrows indicate the same point in the axonal and dendritic tracings.

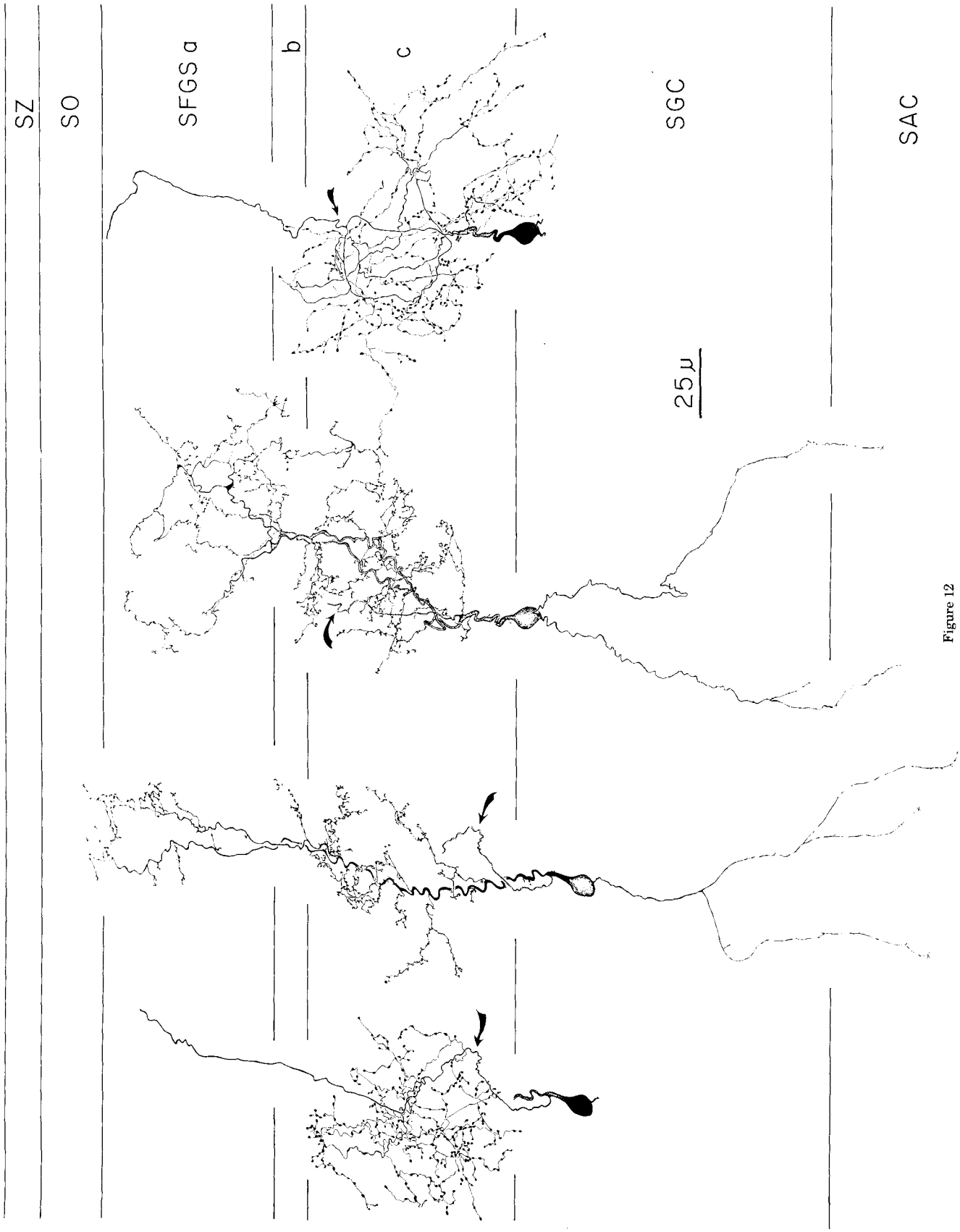


Figure 12

reaching sublayer a. These continue to ascend into sublayer a, occasionally reaching the stratum opticum and the stratum zonale. Unlike the secondary dendrites of the tectorotundal neurons—which give the dendritic tree a distinct conical shape—the secondary dendrites of the tectogeniculate cells often ascend vertically to the tectal surface (e.g., Fig. 11). They occupy a narrow, cylindrical space, 60–80 μm in diameter, extending from the lower edge of the stratum fibrosum et griseum superficiale to the stratum opticum. Many thin, complex branchlets issue from both the primary and secondary ascending dendrites. These threadlike structures, usually less than 1 μm in diameter, either extend horizontally from their origin or course parallel to the dendrites giving off short, horizontally oriented appendages. They are indistinguishable from the branchlets of tectorotundal neurons, forming a variety of irregular shapes that range from simple knoblike protrusions to clusters of lobulated swellings.

One or two extremely thin processes arise from the lower poles of the tectogeniculate somata. These dendrites descend vertically to the deep gray matter of the tectum with little change in diameter or branching pattern. Very short hairlike spicules are occasionally present (e.g., Fig. 10). The dendrites may have irregularly spaced swellings and varicose branchlets near their termination (Figs. 9,10), but most are strikingly smooth (e.g., Fig.11) compared to the appendage-laden upper dendrites. Some dendrites extend obliquely up to 200 μm from the soma in the horizontal plane (Figs. 11,12).

Somata of tectogeniculate neurons situated in the upper half of the stratum fibrosum et griseum superficiale bear dendrites in a modified pattern. The soma in Figure 13 is positioned in sublayer b of the stratum fibrosum et griseum superficiale and, unlike more deeply situated tectogeniculate somata, bears thin terminal branchlets that arborize in the superficial gray. The thin descending dendrite also arborizes heavily within the stratum fibrosum et griseum superficiale but does not enter the stratum griseum centrale. These neurons thus have characteristic cylindrical arbors spanning the superficial layers but lack the threadlike descending dendrites present in the more deeply situated tectogeniculate neurons.

Axons of tectogeniculate neurons are remarkably constant in form. For neurons with somata in the stratum griseum centrale, an axon arises from the soma or the initial part of the apical dendrite and ascends vertically to sublayer c of the stratum fibrosum et griseum superficiale (Figs. 9–12). It bifurcates into branches of unequal thickness about the middle of this sublayer. The thicker branch continues to ascend through the stratum fibrosum et griseum superficiale and turns rostrad as it reaches the lower border of the stratum opticum. The thinner branch remains in sublayer c and gives rise to a collateral arbor that overlaps the neuron's dendritic field. These collaterals are highly branched and varicose. They often turn back upon themselves so that the shape of the arbor is nearly spherical and is densely packed with terminal boutons. They are almost entirely restricted to sublayer c of the stratum fibrosum et griseum superficiale, but collaterals occasionally penetrate the upper portion of the stratum griseum centrale (Figs. 11,13) and sublayer b of the stratum fibrosum et griseum superficiale (Fig. 12). The constant position of these arbors is emphasized by the superficially positioned tectogeniculate neuron shown in Figure 13. Its axon descends from the soma to form the characteristic terminal arbor in sublayer c and then recurves to ascend through the stratum fibrosum et griseum superficiale to enter the tectogeniculate pathway.

Tectoisthmi cells. Injections of HRP into the ventral tectobulbar tract at the level of nucleus isthmi labeled a population of tectal neurons that was never labeled by injections placed caudal to nucleus isthmi. These neurons are the likely source of tectoisthmi axons. A cluster of these tectoisthmi neurons is shown in Figure 14A, and the morphology of tectoisthmi neurons over the complete range of the laminar positions of their somata is illustrated in Figures 15–18. The small somata, 6–10 μm in diameter, are distributed throughout the strata fibrosum et griseum superficiale and griseum centrale. They probably correspond to the spherical or pear-shaped somata scattered throughout these layers in Nissl preparations (Figs. 1,2).

Variation in the laminar position of the somata of tectoisthmi neurons is linked to variation in the morphology of the ascending and descending dendrites of these cells. Tectoisthmi neurons with somata positioned more superficially (Figs. 16,17) have short ascending dendrites that branch closer to the stratum opticum. Neurons with somata at the border of the superficial gray and stratum opticum (Fig. 15) have dendrites that immediately break up into terminal branches spreading horizontally and ascending through the stratum opticum in a candelabra-like pattern. Somata deep in the tectum each bear a single, relatively thick radial dendrite that ascends into the stratum fibrosum et griseum superficiale (Fig. 18). This dendrite may dichotomize into branches of equal thickness and may also issue thinner, secondary branches that extend radially. A small number of short, complex appendages and threadlike branchlets project horizontally from these dendrites. Secondary dendrites and thin, tertiary branches with few appendages ascend through the stratum opticum, often working their way among fascicles of optic fibers before they reach the stratum zonale. Within the stratum zonale, the dendrites branch profusely into nests of horizontally flattened appendages that bear a variety of complex swellings. The appendages are interwoven into a dense plexus that includes dendrites from several tectoisthmi neurons. Regardless of soma position, the dendritic field of a single tectoisthmi cell approximates a cylinder with a diameter of 60–80 μm within the stratum zonale.

Dendrites arising from the lower poles of the tectoisthmi neurons also vary with the laminar position of the soma. The most superficial neurons (Fig. 15) have single, thin dendrites that arborize sparsely in the superficial gray, bearing a modest number of terminal appendages. Neurons with somata situated at successively deeper levels (Figs. 17,18) have short descending dendrites or only a few thin terminal branchlets that arise from the soma and arborize in its vicinity.

Axons of tectoisthmi neurons originate from a thin basal dendrite or directly from the lower pole of the soma (arrows, Figs. 15–18). They often arise from the end of a short basal projection whose identity seems to suddenly change from that of a dendrite to that of an axon. Somata situated most

Fig. 12. Tectogeniculate cells. In contrast to the smooth, thin, descending dendrites, the upper dendrites of tectogeniculate cells bear numerous thin branchlets. These varicose appendages extend horizontally away from or in parallel with the primary dendrites. They arborize in small clusters of gnarled protrusions and lobulated swellings to construct a dense plexus in the SFGS.

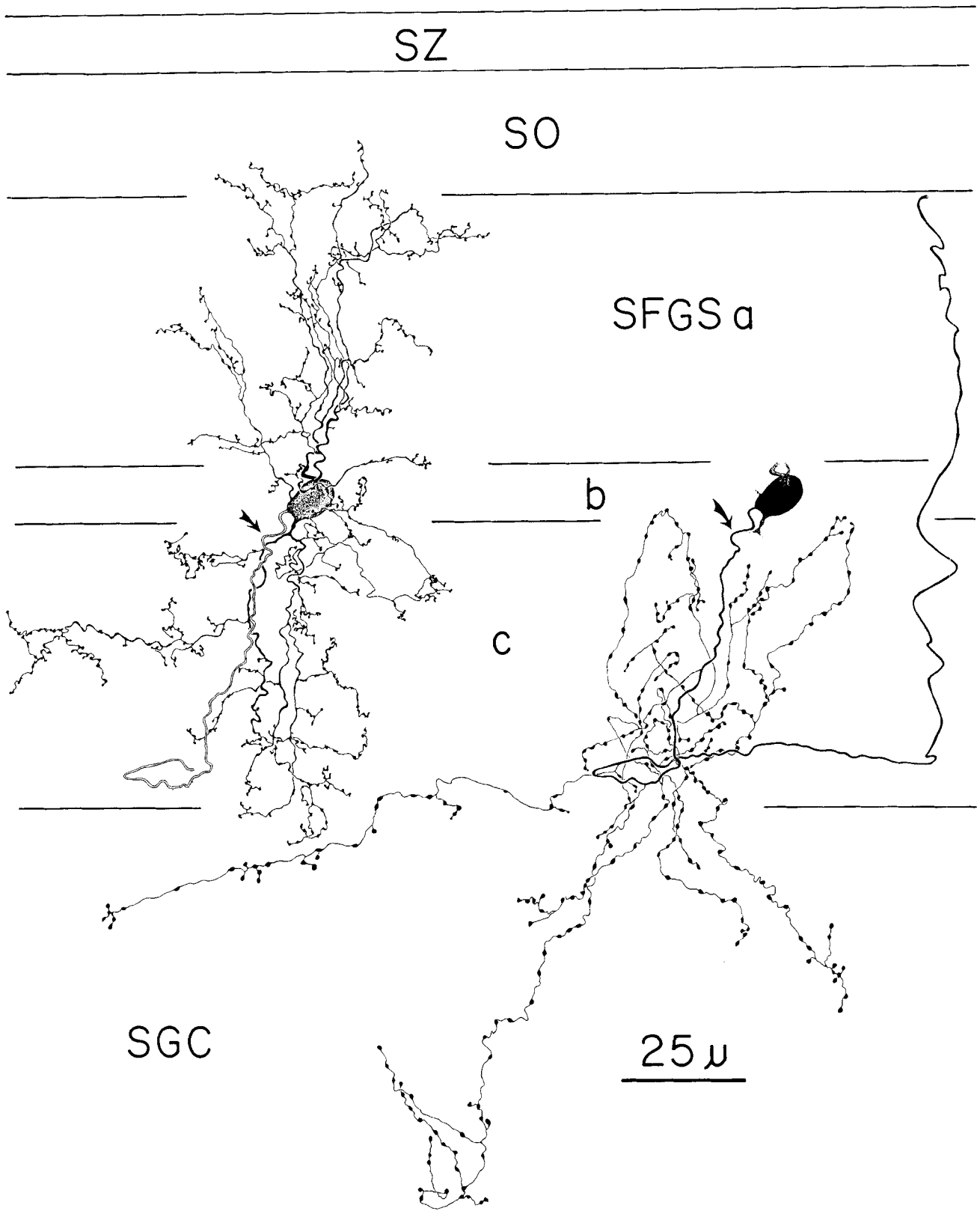


Fig. 13. Tectogeniculate cell. In this neuron the soma is situated in the center of the stratum fibrosum et griseum superficiale and it lacks the thin, descending dendrites observed on more deeply situated neurons. However, it retains a dendritic arbor that spans the stratum fibrosum et griseum centrale. A consequence of the superficial position of the soma is that the axon must initially descend, arborize within sublayer c, and then recurve to ascend and reach the tectogeniculate pathway at the ventral border of the stratum opticum (SO).

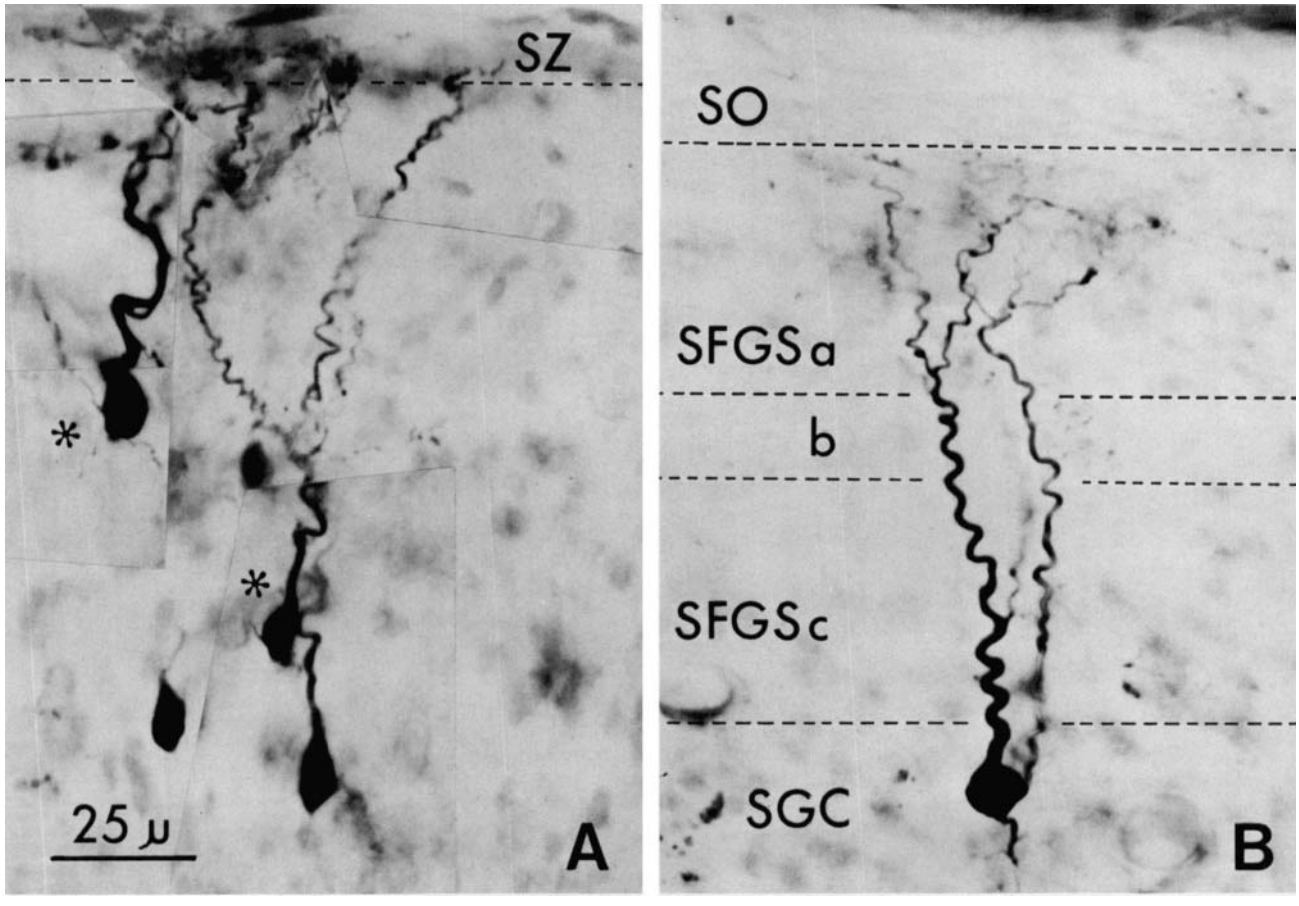


Fig. 14. A. Tectoisthmi neurons in the superficial gray layers. The radial dendrites of these small neurons form a dense arbor in the stratum zonale (SZ). Camera lucida reconstructions of the neurons marked with asterisks (*) are illustrated in Figure 16. B. Tectoisthmobulbar cell. These neurons are similar in morphology to tectoisthmi cells but have a dendritic arbor in sublayer a of the stratum et griseum centrale. The camera lucida reconstruction of this cell is shown in Figure 19.

superficially (Figs. 15,16) have axons that descend vertically from the soma or arise deeper within the stratum fibrosum et griseum superficiale from a basal dendrite. The axon issues thin, varicose collaterals within the lower half of the stratum fibrosum et griseum superficiale; these form small terminal arbors. Neurons situated more deeply in the stratum fibrosum et griseum superficiale (Fig. 17) or in the upper central gray (Fig. 18) have axons that descend vertically, each forming a small collateral arbor in the central gray. Somata situated in the central gray issue axons that descend into the adjacent central white matter without collateralizing.

Tectoisthmobulbar neurons. These neurons were backfilled by injections of HRP into nucleus isthmi or caudal to isthmi in the ventral tectobulbar tract. A photomicrograph of a tectoisthmobulbar neuron is shown in Figure 14B. Camera lucida reconstructions of these neurons are shown in Figures 19–22. The size and shape of their somata and the primary dendrites of these neurons are very similar to those of tectoisthmi neurons, but their somata have a more restricted laminar distribution that ranges from the middle of sublayer c of the stratum fibrosum et griseum superficiale to the middle of the stratum griseum centrale.

The characteristic feature of tectoisthmobulbar neurons is a rich dendritic arbor in sublayer a of the stratum fibrosum et griseum superficiale. A thick, primary dendrite usually arises from the conical upper pole of the soma and ascends without branching through sublayers c and b. Thin secondary and tertiary branches issue fine terminal branchlets and complex appendages that arborize in an interweaving, dense plexus that is neatly restricted to sublayer a. Branches in the lower superficial gray layers invariably bear a reduced complement of terminal branchlets; they often project in isolation horizontally from a radial dendrite (e.g., Figs. 19, 20). Tectoisthmobulbar somata usually lack major descending dendrites, but bear one or more thin, elongated branchlets. Some of these branchlets descend vertically a short distance; others arborize horizontally from their point of origin. The result is the formation in many neurons of a wreathlike arbor around the base of the soma (Fig. 21). The dendritic field is cylindrical and ranges in width from 60 to 100 μm.

Axons of the tectoisthmobulbar neurons originate close to the somata from one of the thin dendrites or, occasionally, as a continuation of a seemingly aborted dendrite (e.g., Fig. 22). Proximal segments of these axons are thin (less than

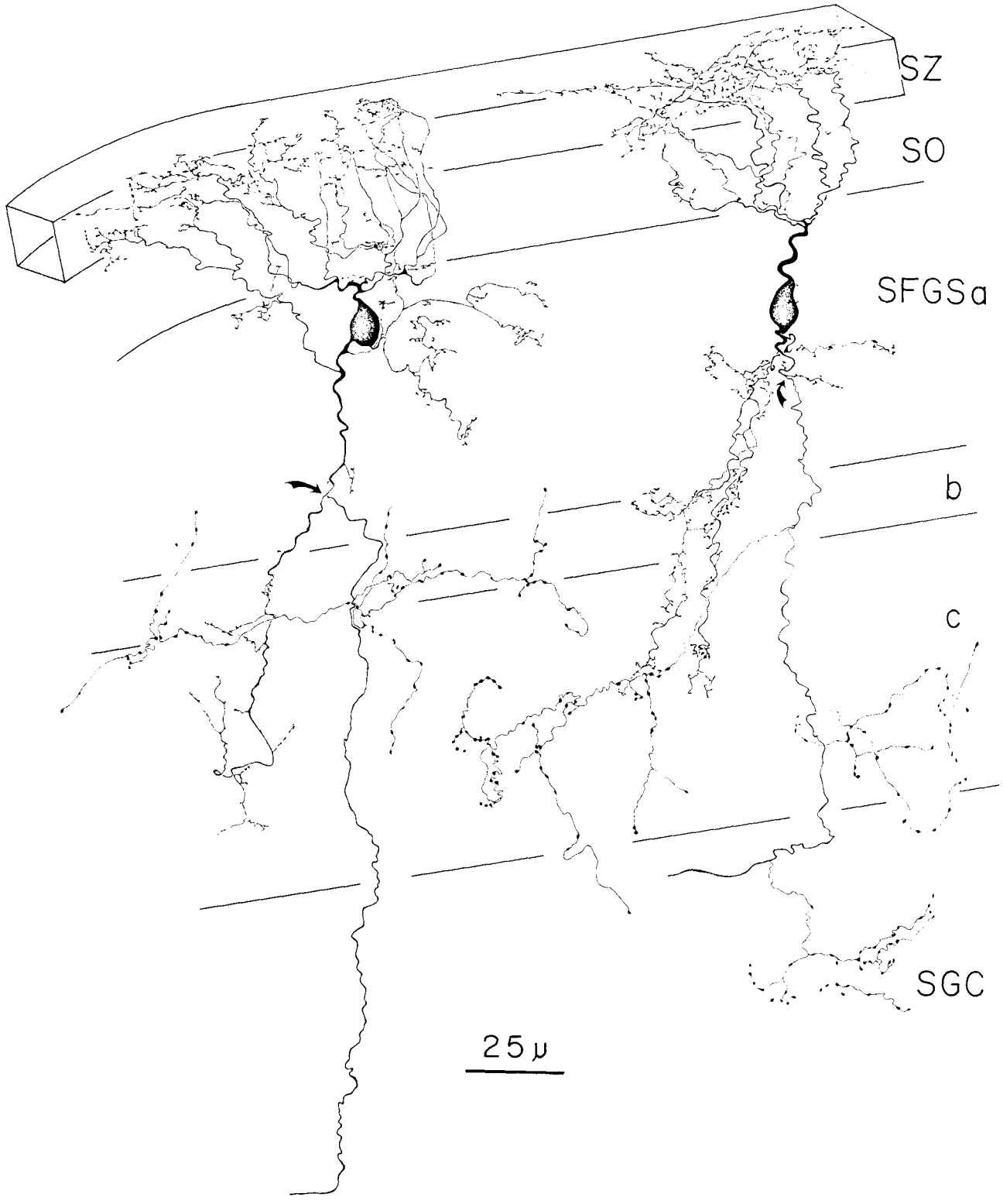


Fig. 15. Tectoisthmi cells. This and the following three figures illustrate the morphology and laminar distribution of cells that were retrogradely filled from injections of HRP into the ventral tectobulbar tract rostral but not caudal to nucleus isthmi. Somata in the upper part of the stratum fibrosum et griseum superficiale have short, radial dendrites that ascend through the optic fascicles in the stratum opticum and arborize in the stratum zonale. Thin descending dendrites extend for a variable distance into the stratum fibrosum et griseum superficiale. The axons (arrows) issue local collaterals in the strata fibrosum et griseum superficiale and griseum centrale.

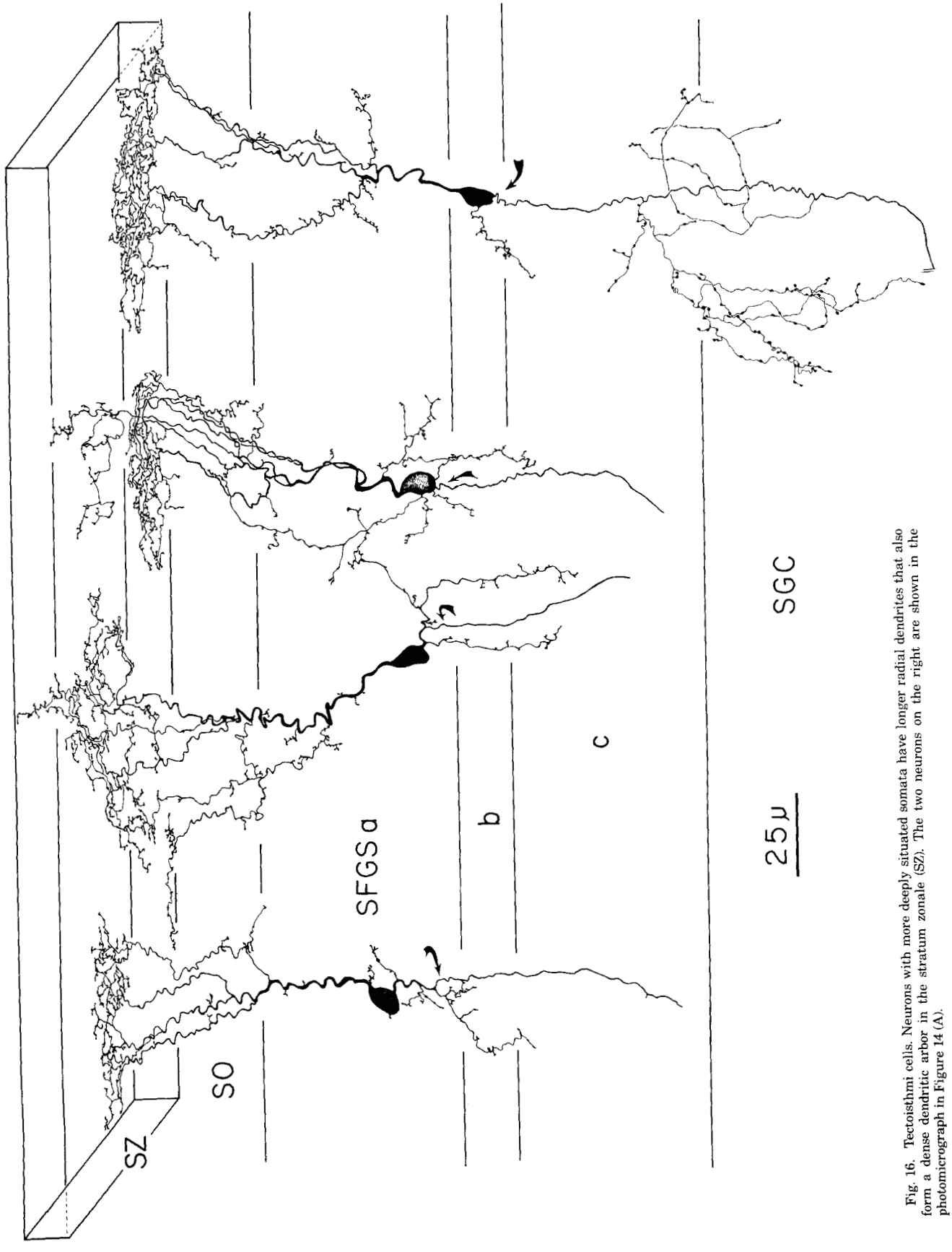


Fig. 16. Tectoisthmi cells. Neurons with more deeply situated somata have longer radial dendrites that also form a dense dendritic arbor in the stratum zonale (SZ). The two neurons on the right are shown in the photomicrograph in Figure 14 (A).

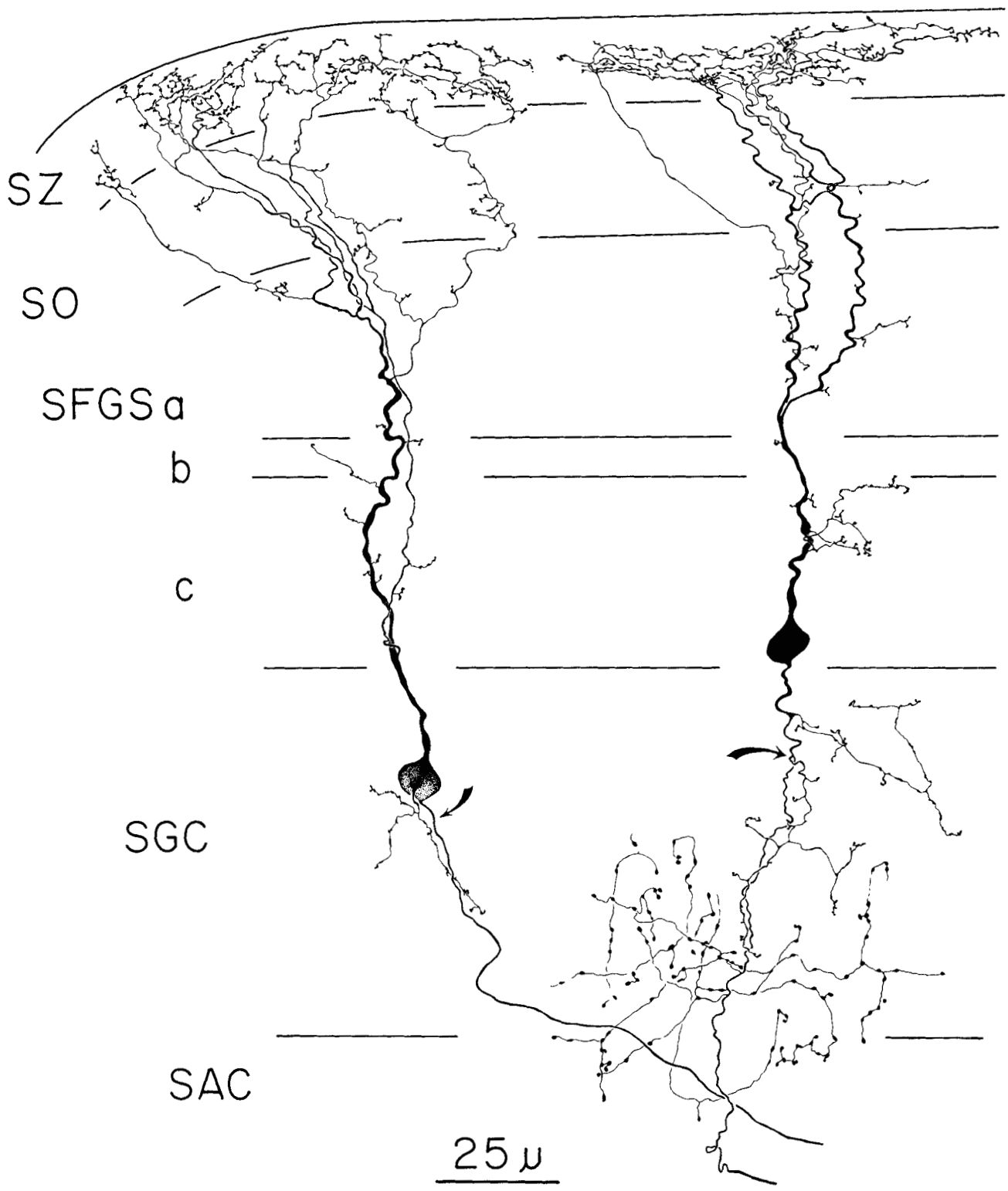


Fig. 17. Tectoisthmi cells. The radial dendrites of tectoisthmi neurons have a low density of dendritic appendages in the strata fibrosum et griseum superficiale, griseum centrale, and opticum. Thin secondary dendrites terminate in the stratum zonale by arborizing profusely as thin, varicose branchlets bearing clusters of clawlike protrusions. Origins of axons are indicated by the arrows.

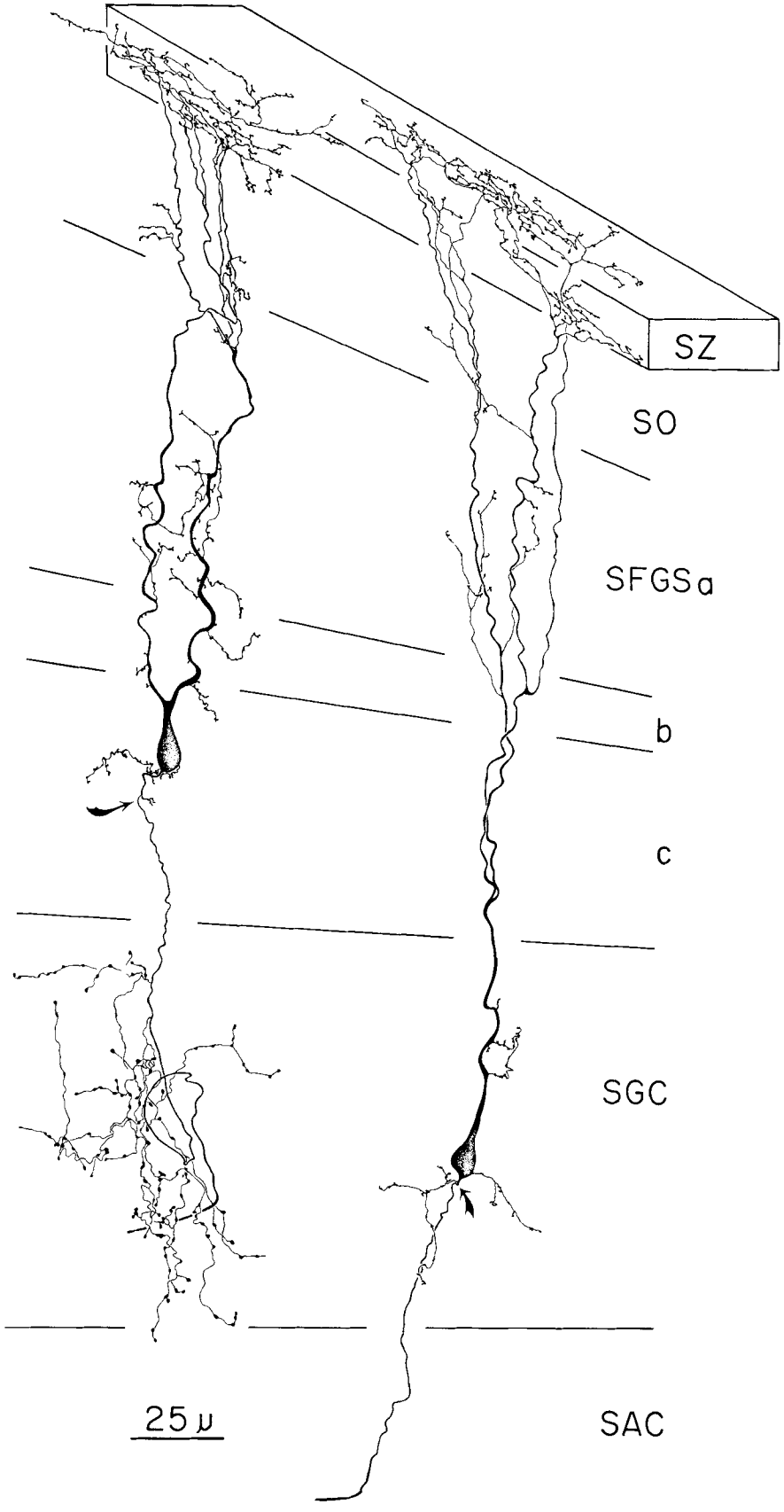


Fig. 18. Tectoisthmi cells. The axons of neurons in the stratum fibrosum et griseum superficiale often form small, collateral arbors in the central gray. However, the axons of cells in the stratum griseum centrale may descend directly into the stratum album centrale without collateralizing. Origins of axons are indicated by the arrows.

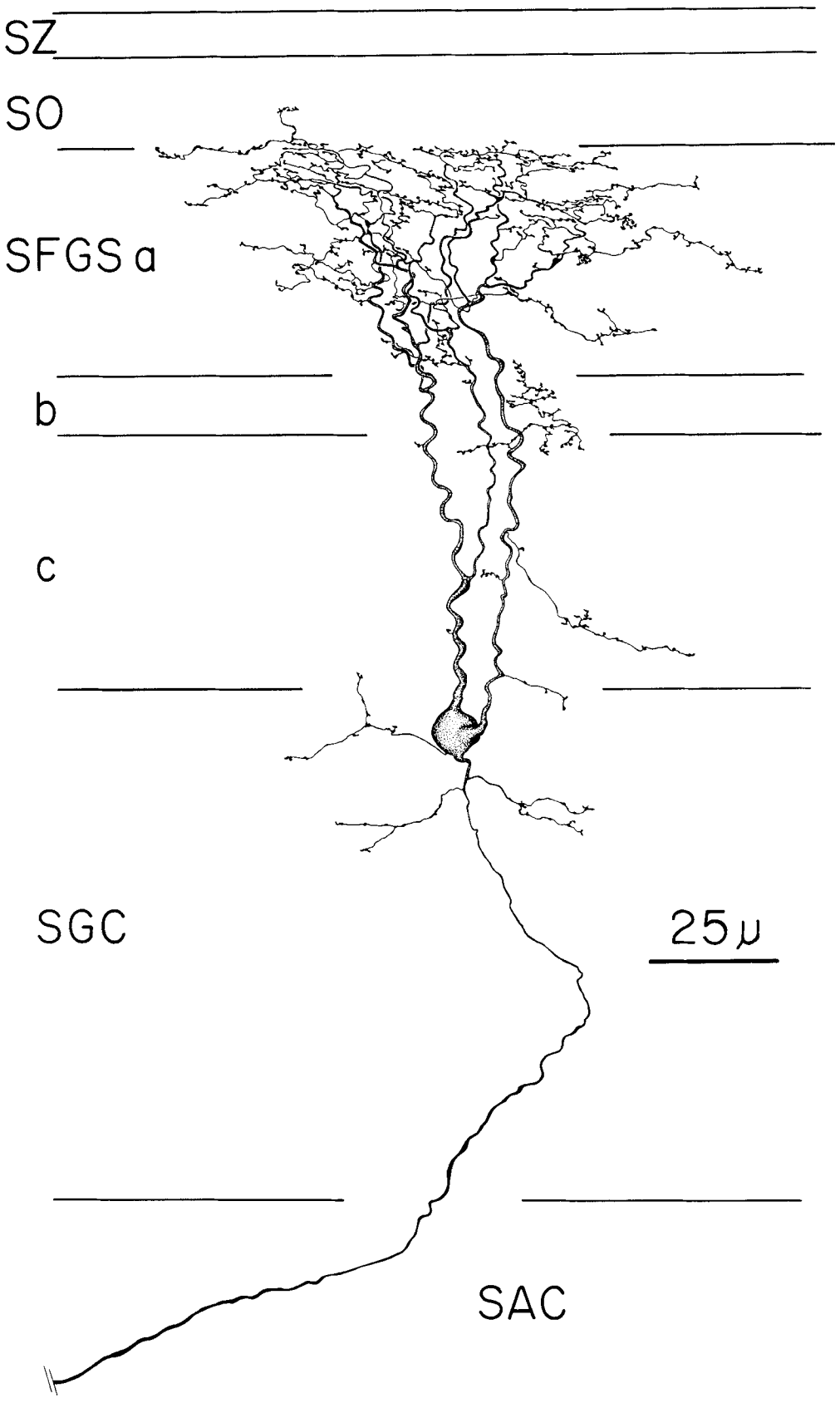


Fig. 19. Tectoisthmobulbar cell. This and the following three figures show the morphology and laminar distribution of neurons labeled from injections into nucleus isthmi and caudal to nucleus isthmi in the ventral tectobulbar tract. All tectoisthmobulbar neurons are characterized by dense terminal dendritic plexuses in sublayer a of the stratum fibrosum et griseum superficiale and a thin axon that does not collateralize within the tectum. In this cell the axon arises as a continuation of a thin basal dendrite.

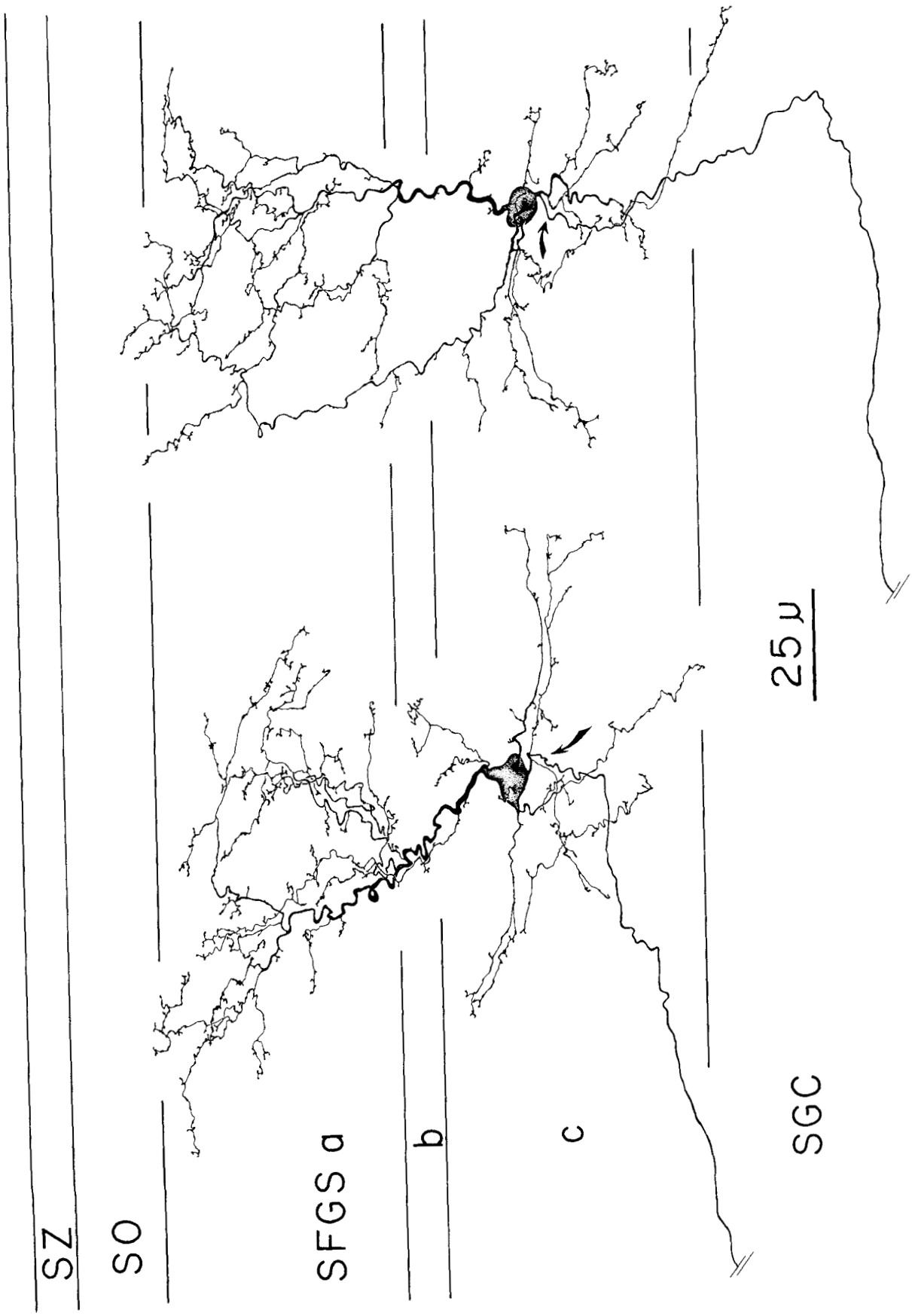


Fig. 20. Tectoisthmobulbar cells. The majority of tectoisthmobulbar cells are located in sublayer c of the stratum fibrosum et griseum superficiale. The basal dendrite of these cells often forms a wreathlike array around the base of the soma. Origins of the axons are indicated by the arrows.

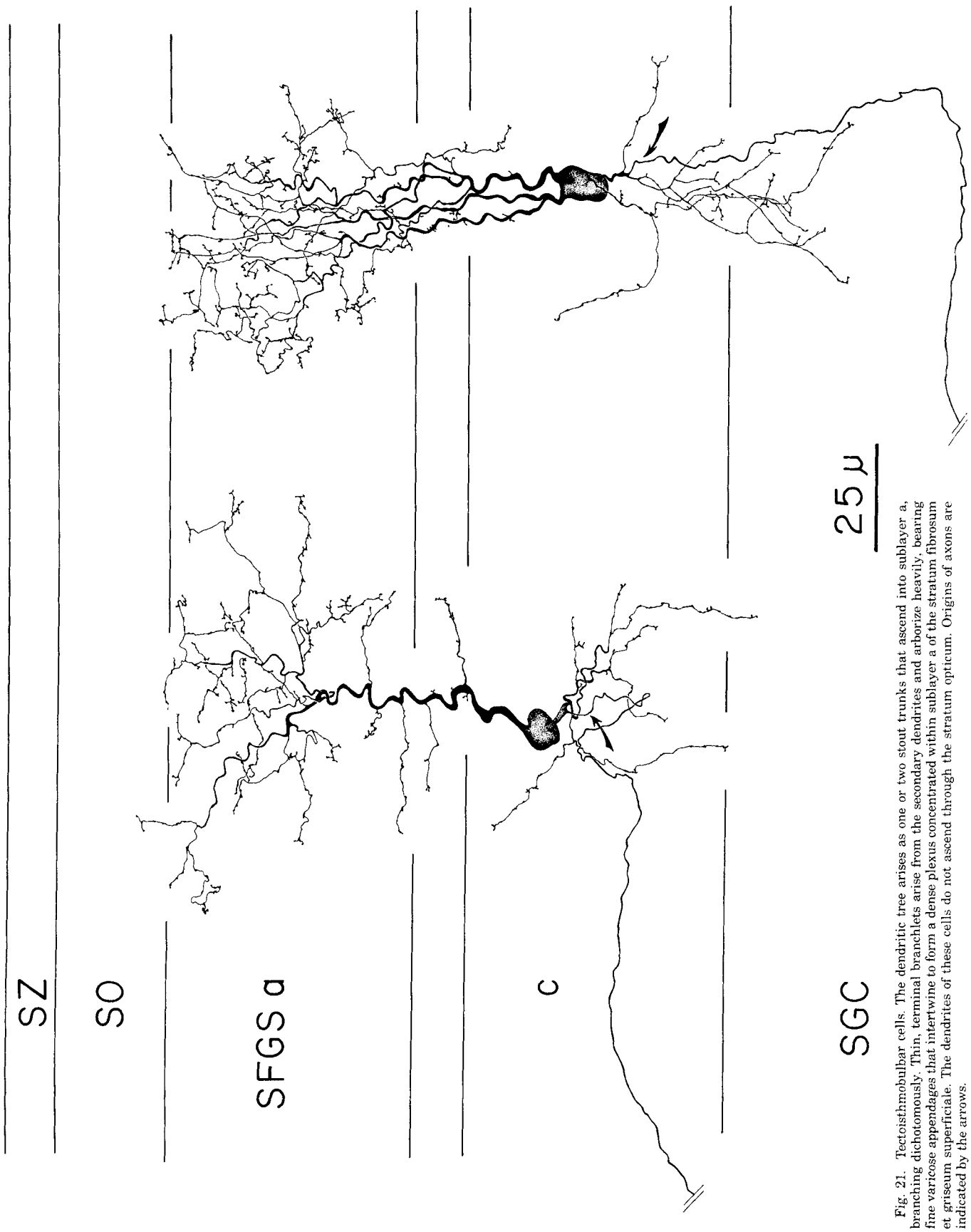


Fig. 21. Tectoisthmobulbar cells. The dendritic tree arises as one or two stout trunks that ascend into sublayer a, branching dichotomously. Thin, terminal branchlets arise from the secondary dendrites and arborize heavily, bearing fine varicose appendages that intertwine to form a dense plexus concentrated within sublayer a of the stratum fibrosum et griseum superficiale. The dendrites of these cells do not ascend through the stratum opticum. Origins of axons are indicated by the arrows.

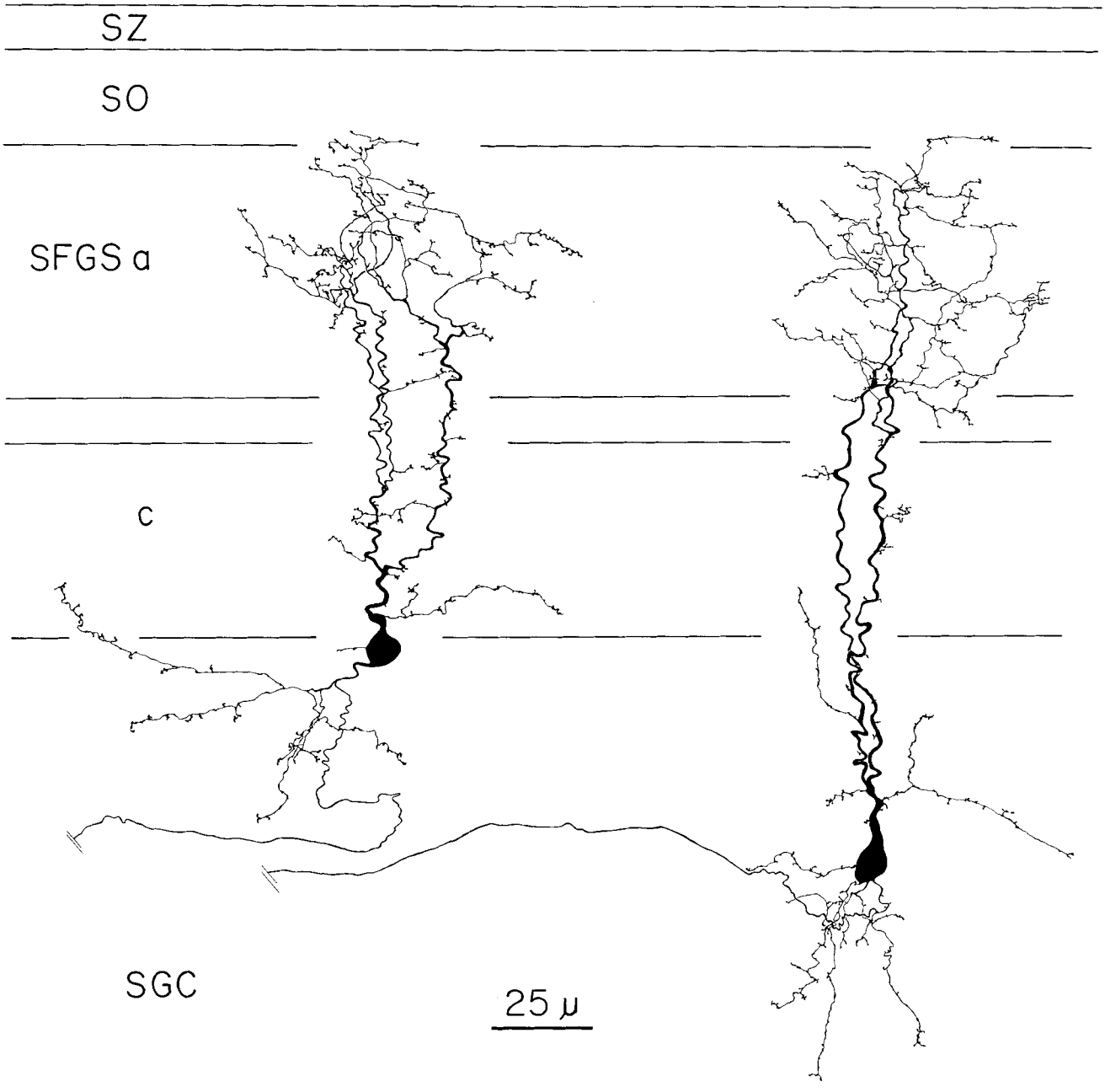


Fig. 22. Tectoisthmobulbar cells. The most deeply situated tectoisthmobulbar cells bear elongate radial dendrites that, like all neurons of this class, bear a sparse distribution of dendritic appendages until they reach sublayer a of the stratum fibrosum et griseum superficiale where they terminate in a dense plexus.

0.5 μm), but they sometimes thicken and reach a diameter of about 1 μm as they descend radially or obliquely in the central gray without branching or issuing collaterals. The axons then turn laterally in the central gray and continue obliquely into the stratum album centrale.

Ipsilateral tectobulbar cells. Injections of HRP into the ventrolateral pontine or medullary reticular formation retrogradely filled the medium-caliber component of the ventral tectobulbar tract. Retrogradely filled axons could be traced from the pontine and midbrain tegmentum to their neurons of origin in the ipsilateral tectum. Labeled somata contributing to this pathway are present throughout the lower half of the central gray and the upper part of the stratum album centrale. There is a tendency for the number of labeled cells to be greatest in the lower third of the stratum griseum centrale. A photomicrograph of a retrogradely filled tectobulbar cell in the lower stratum griseum centrale is shown in Figure 23, and camera lucida recon-

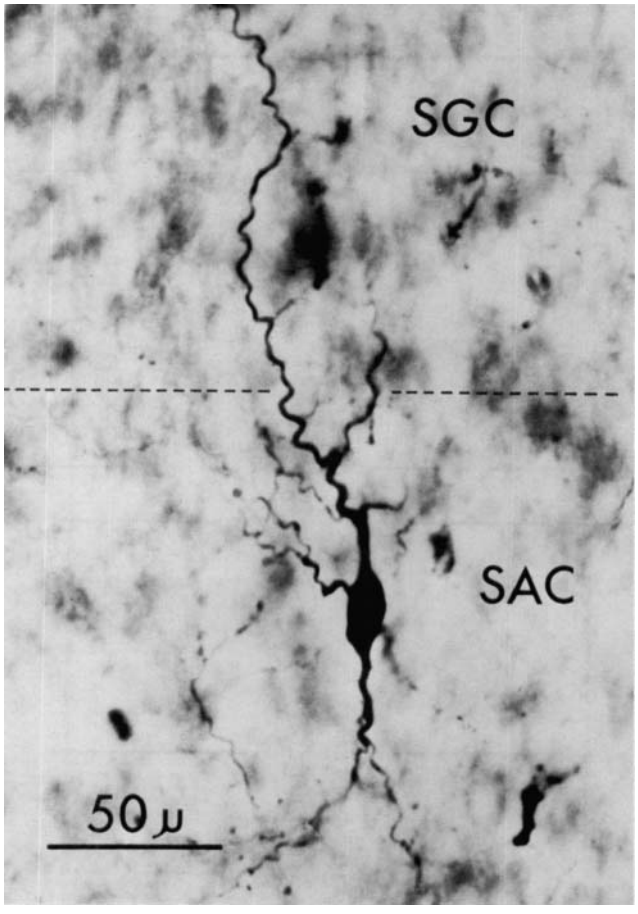


Fig. 23. Ipsilateral tectobulbar neuron retrogradely filled from an injection of HRP into the ipsilateral medullary reticular formation. The axon of this cell was of medium caliber and could be traced into the dorsal component of the ventral tectobulbar tract.

structions illustrate the morphology of these neurons in Figures 24–26. Somata of the tectobulbar neurons are vertically fusiform (10–15 μm along the short axis and 12–20 μm along the long axis) and are dominated by stout primary dendrites arising from their poles. Frequently, however, one to three dendrites emerge from other parts of a soma that is best described as multipolar. They probably correspond to the medium-sized multipolar neurons of the lower stratum griseum centrale (Figs. 1,2).

Each primary dendrite issues several thin branches close to the soma that arise at right angles or recurve. Secondary branches may ascend or descend radially, extend horizontally, or curve gently from their point of origin. They maintain a uniform thin diameter of about 1.5 μm and usually show a single bifurcation near their ends. These dendrites vary in length, ranging from 50 to 150 μm. Those that ascend through the stratum griseum centrale terminate abruptly at the interface of the stratum griseum centrale and the stratum fibrosum et griseum superficiale. Dendrites that descend into the stratum album centrale often show a meandering, wavy course and terminate at a variety of depths in this fiber-rich layer. The shapes of the dendritic fields are elliptical (see insets in Figs. 24–26) with their long axes oriented in the coronal plane and ranging from about 150 to 250 μm.

Dendrites of tectobulbar neurons bear a moderate density of short spicules or hairlike protrusions that are short (about 1 μm. in length) and tend to arise in pairs separated by gaps of about 1 μm. Dendrites occasionally give rise to short appendages bearing irregularly shaped varicosities and protrusions like those described for other neuron types. The end of each dendrite is marked by a thickening and one to several bulbous swellings that bear thin, spinelike projections.

Axons of tectobulbar neurons originate from the upper poles of somata or from upper dendrites and ascend vertically in the stratum griseum centrale for 20–100 μm, often reaching the top of this layer. They then make a final short horizontal excursion before recurving and descending laterally and obliquely into the stratum album centrale.

Crossed tectobulbar cells. Injections of HRP into the base of the pontine or medullary reticular formation, close to the midline, retrogradely fill large- and medium-caliber axons in the predorsal bundle. Some of these axons can be traced across the midline into the dorsal tectobulbar tract and to their neurons of origin in the tectum. Labeled somata are distributed from the lower third of the stratum griseum centrale to the upper margin of the periventricular gray layer. However, there is a distinct increase in the density of labeled neurons at the border of the stratum griseum centrale with the stratum fibrosum centrale. A photomicrograph of 2 crossed tectobulbar neurons is shown in Figure 27, and nine camera lucida reconstructions are illustrated in Figures 28–34. These neurons have multipolar bodies that range in diameter from 12 to 30 μm and therefore include the largest neurons in the tectum. They undoubtedly correspond to the large multipolar neurons of the stratum album centrale (Figs. 1,2).

The crossed tectobulbar cells have the largest dendritic fields of the tectal efferent neurons. Four to six thick dendritic trunks issue from each soma in a stellate pattern. They branch dichotomously at acute angles close to the soma. Secondary dendrites may branch once again or extend unbranched in a straight course. Like the ipsilateral tectobulbar neurons, ascending dendrites of crossed tectobulbar neurons do not cross the upper border of the stratum griseum centrale. The pattern of the descending dendrites varies with soma position. When a soma is located in the stratum griseum centrale (Figs. 28,29), a modest complement of dendrites courses downward through the stratum album centrale. When a soma is positioned more deeply (Figs. 33,34), the lower dendrites extend horizontally, skirt the upper border of the periventricular gray layer and turn upward into the strata album centrale and griseum centrale. Regardless of soma position, the dendritic fields are elliptical with long axes oriented in the coronal plane (see insets in Figs. 28–34) and ranging from 250 to 400 μm along the long axis and 80 to 250 μm along the short axis. Fine spicules are distributed evenly along the secondary dendrites and, as for the ipsilateral tectobulbar neurons, often appear in pairs, separated by 1-μm gaps. Terminal boutons anterogradely filled from the HRP injection occasionally nestle in these gaps, creating slight indentations in the dendrite (asterisk, Fig. 29). Each dendrite ends in a prominent cluster of large, clublike swellings and an increased density of spicules.

Axons arise from the somata or from primary dendrites close to a soma and descend vertically through the stratum album centrale, thickening in their course and reaching a

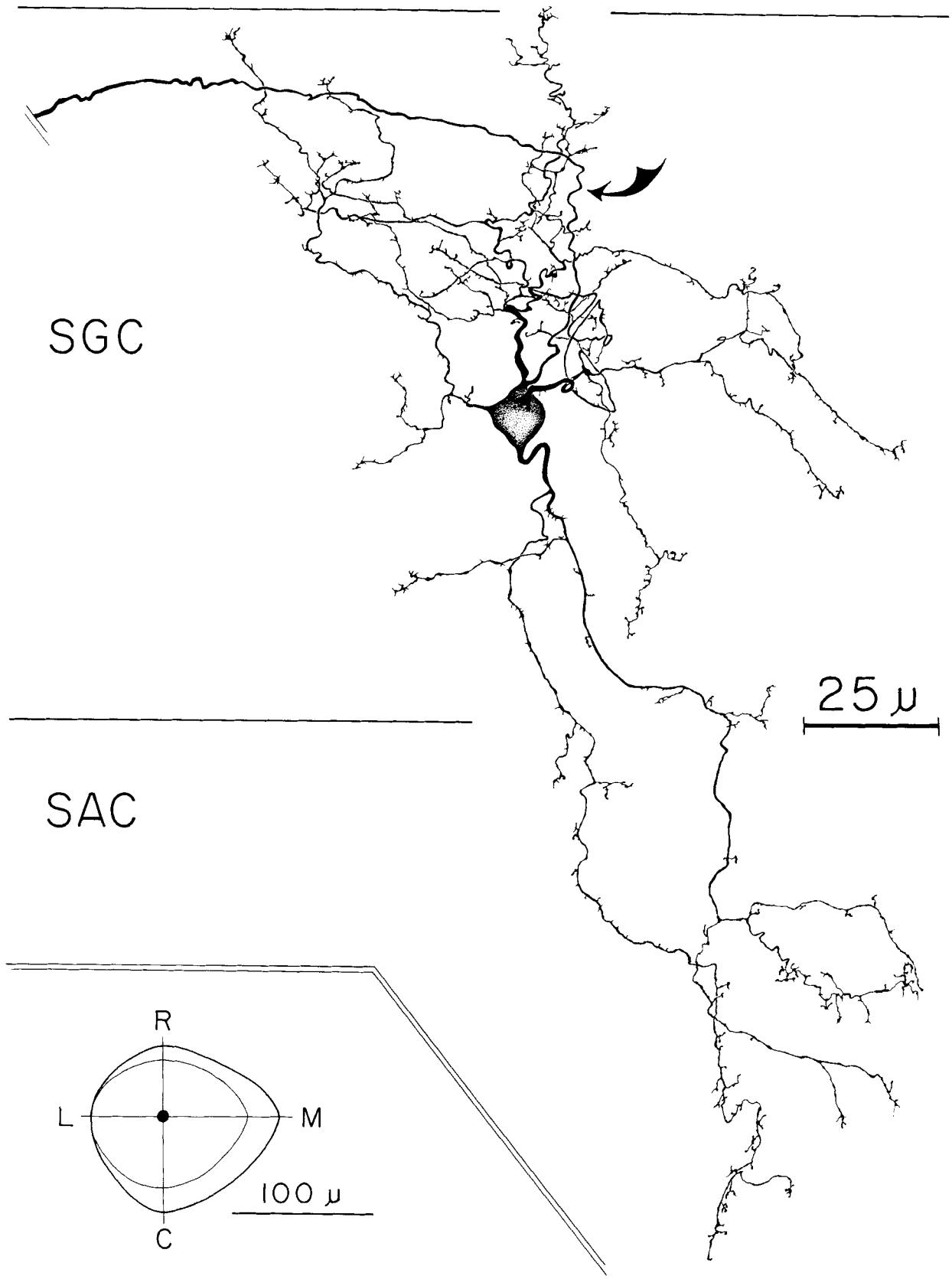


Fig. 24. Ipsilateral tectobulbar cell. This and the following two figures illustrate the morphology and laminar distribution of neurons whose axons could be traced into the ipsilateral reticular formation as the dorsal, medium-caliber component of the ventral tectobulbar tract. Tectobulbar neurons are multipolar, but vertically elongate. The dendritic field occupies the stratum griseum centrale, extends into the stratum album centrale, but never enters the stratum fibrosum et griseum superficiale. The arrow indicates the axon. The insets at the bottom of this and the following figures are approximate projections of the cells' dendritic field spread in the horizontal plane. The black dot represents the position of the soma. The inner circular profile represents a primary dendritic zone, encompassing the bulk of the dendritic arborization, while the outer circle outlines the extension of this primary zone by a few tertiary dendrites.

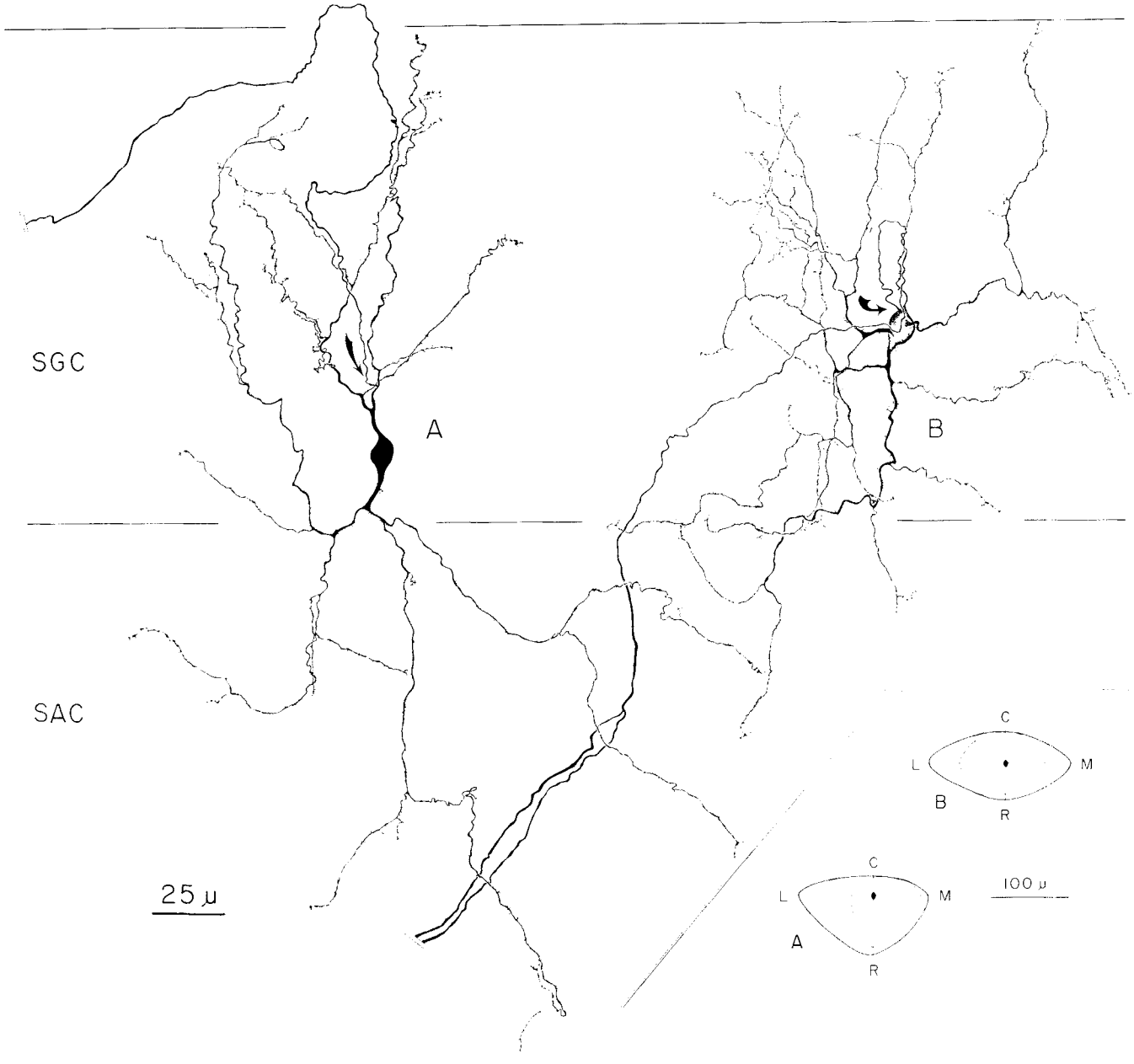


Fig. 25. Ipsilateral tectobulbar cells. A feature of all tectobulbar neurons is an axon that ascends for a variable distance in the central gray before recurving and descending into the central white matter. These axons bear no collaterals in the tectum. Although the axon of the neuron labeled B bifurcates in the tectum, both branches were traced into the ventral tectobulbar pathway. Arrows indicate origins of axons.

diameter of 2.5–3.0 μm in the largest cells. Each axon makes a sharp lateral turn at the ventral border of the stratum album centrale and courses into the dorsal tectobulbar tract at the ventromedial border of the central white layer. Crossed tectobulbar axons do not give rise to collaterals within the tectum.

DISCUSSION

The present results conclude a description of the efferent neurons in *Thamnophis* begun in a preceding paper (Dacey and Ulinski, '86a). It is now possible to summarize the morphology of each of the six types of tectal efferent neuron. For comparison, a single example of each major cell type is shown to the same scale in Figure 35.

Tectorotundal neurons (TRo) in *Thamnophis* have cylindrical dendritic fields that extend radially through the strata fibrosum et griseum superficiale and griseum centrale. They are probably postsynaptic to retinal terminals in the stratum fibrosum et griseum superficiale on their upper dendrites (Repérant et al., '81) and to other topographically organized sensory inputs to the stratum gri-

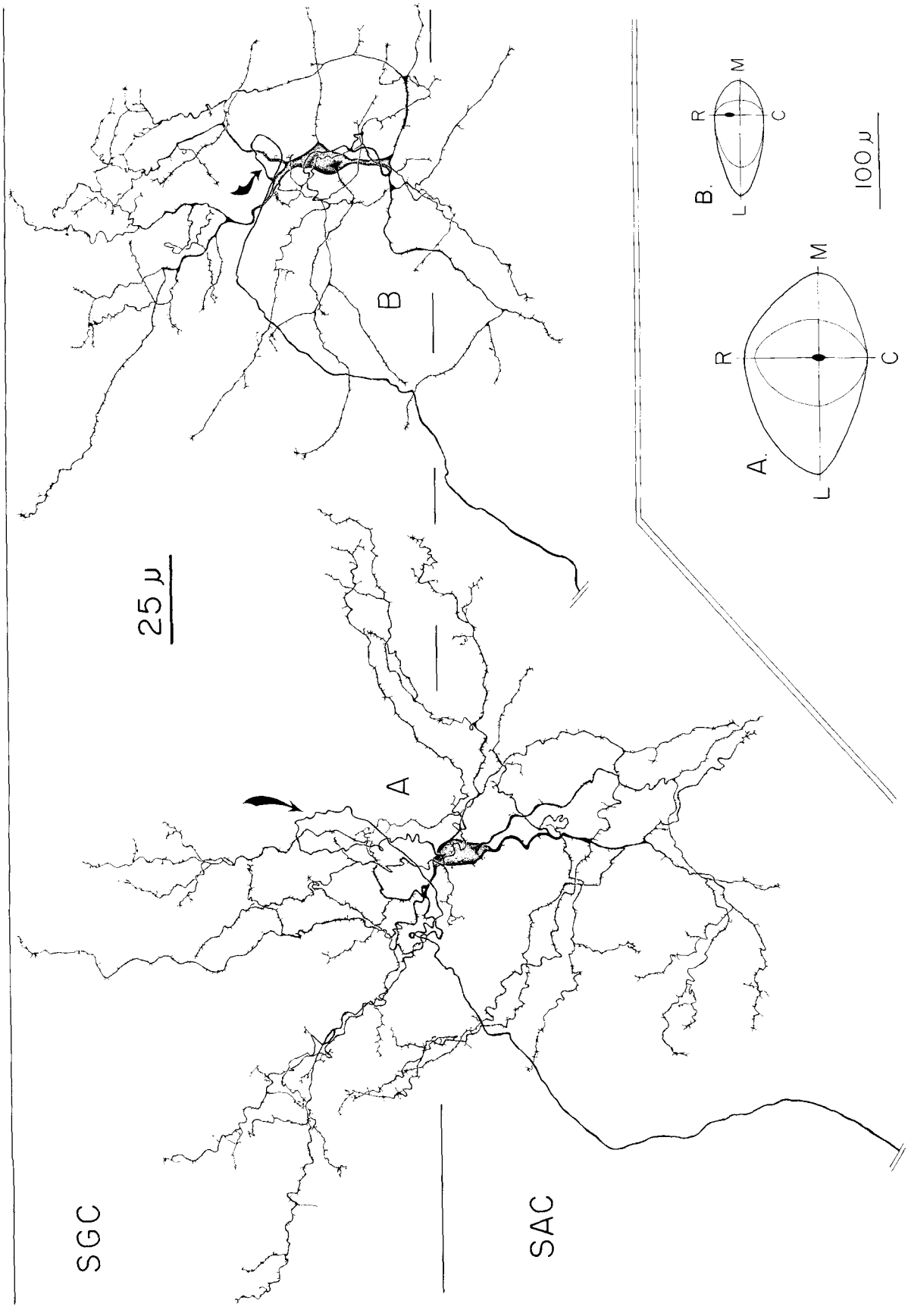


Fig. 26. Ipsilateral tectobulbar cells. Another feature of these neurons is the presence of short, hairlike spicules distributed along the secondary and tertiary dendrites. These spicules most often appear in pairs separated by a gap of about 1 μm. The end of each dendrite expands into a small, clublike swelling bearing numerous spokelike projections. Arrows indicate axons.

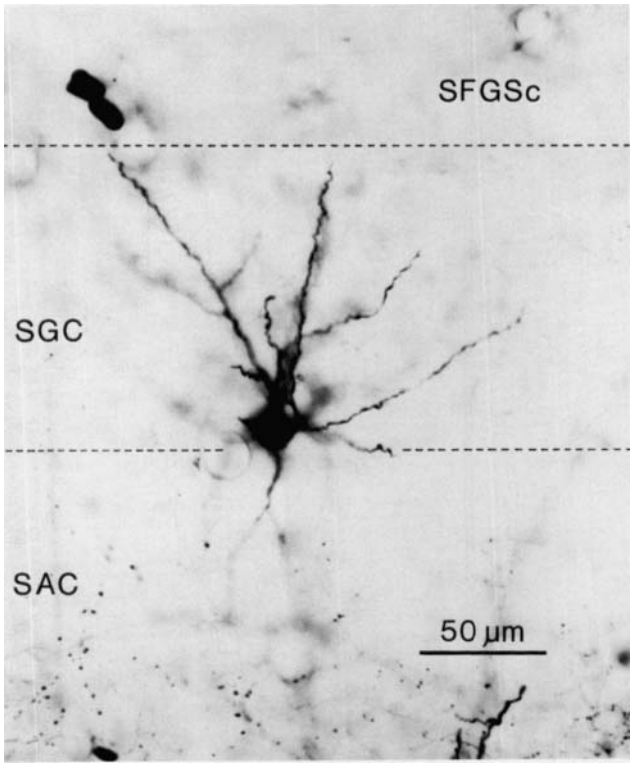


Fig. 27. Crossed tectobulbar neuron retrogradely filled by an injection of HRP into the predorsal bundle in the pontine reticular formation. This cell is viewed in a coronal section through the central tectum; its camera lucida reconstruction is shown in Figure 30.

seum centrale on their lower dendrites (Hartline et al., '78; Kass et al., '78). The receptive field properties of identified tectorotundal neurons have not been studied in any reptilian or avian species, but their laminar position and narrow dendritic field size suggest that they correspond to the bimodal neuron described recently in the rattlesnake tectum (Newman and Hartline, '81).

A partial description of tectorotundal axons is available for the turtle *Pseudemys* (Rainey and Ulinski, '82), but the more complete material available in *Thamnophis* indicates that tectorotundal axons have three components. The first is a dense terminal plexus close to the cell's lower dendritic field in the stratum griseum centrale. The second component is a widespread plexus of terminal collaterals that extends horizontally away from the dendritic field in the stratum griseum centrale. The third component leaves the tectum via the tectothalamic tract to reach the nucleus of the tectothalamic tract and nucleus rotundus. Small injections of HRP in the tectum label fibers scattered throughout the tectothalamic tract regardless of injection site. Tectorotundal axons, therefore, ascend to the diencephalon without maintaining a topographic order. The terminal fields of single axons form flattened, sheetlike domains that extend through the rostrocaudal and mediolateral extent of nucleus rotundus. The projection thus has a spatial order, but it is not topographically organized. Some ideas about the significance of this projecton have been discussed elsewhere (Dacey and Ulinski, '83).

Tectogeniculate (TG) and *tectoisthmi* (TI) cells also have cylindrical dendritic fields that probably receive retinal input in the superficial gray. Their axons are involved in topographic projections. The tectogeniculate axons form small, spherical collateral arbors within the dendritic fields of their parent neurons and give rise to a retinotopically organized projection to pretectal and thalamic nuclei. The terminal arbors are positioned so that visual projections derived from the tectum and retina are in register in these structures (duLac and Dacey, '81). Anatomical studies in chickens and pigeons have shown similar patterns of tectogeniculate organization (Crossland and Uchwat, '79; Hunt and Kunzle, '76). Similarly, the tectoisthmi axons form small, vertically organized collateral plexuses below their somata and then project directly to nucleus isthmi where they terminate in small spherical arbors. This projection appears to be retinotopically organized, consistent with physiological and anatomical studies in a variety of animals (Hunt et al., '77; Grobstein et al., '78; Gruberg and Udin, '78; Sherk, '79; Mendez-Otero et al., '80; Ito et al., '81). Thus, the morphology of the dendrites and axons of both tectogeniculate and tectoisthmi neurons permit a preservation of retinotopy in their projections.

By contrast, *tectoisthmobulbar neurons* (TIB) show another type of organization. Their dendritic trees are characterized by a small, dense arbor in sublayer a of the stratum fibrosum et griseum superficiale. They are the fourth population of efferent neurons that are likely recipients of retinal input. Their axons leave the tectum without collateralizing, and form small terminal arbors in nucleus isthmi. These arbors resemble the tectoisthmi terminals in size and shape and appear to be in topographic register with them. The parent axons of the tectoisthmobulbar neurons continue caudally without maintaining a relative spatial order and issue a series of fine-caliber collaterals throughout their descent through the ventrolateral pontine and medullary reticular fields. Thus, the axons of the tectoisthmobulbar neurons can preserve retinotopic order in nucleus isthmi, but their descending segments show an extensive distribution in the reticular formation that is spatially organized but without topographic order.

The *crossed* (TBc) and *ipsilateral tectobulbar neurons* (TBi) share several major structural features that distinguish them from the other tectal efferent neurons considered so far. First, their dendritic arbors are restricted to the central and deep layers of the tectum and thus are not direct retinal targets. Second, they have large dendritic fields, ranging from 80 to 400 μm in maximum horizontal spread. Third, their dendritic fields are stellate, rather than vertically elongate, and their dendrites bear short hairlike spicules rather than complex appendages. These neurons resemble some of the tectoreticular neurons that have been shown

Fig. 28. Crossed tectobulbar cell. This and the following seven figures illustrate the morphology and laminar distribution of neurons labeled from injections of HRP into the predorsal bundle and whose axons could be traced into the dorsal tectobulbar tract. The dendrites of these neurons occupy the stata griseum and album centrale but do not extend into the stratum fibrosum et griseum superficiale. The inset at the bottom of the figure shows the cell's dendritic tree projected in the horizontal plane. The core of the dendritic tree (inner profile) is approximately circular with the soma as its center. Distal dendrites tend to extend more in the mediolateral axis than in the rostrocaudal axis, giving the overall dendritic field an ellipsoidal shape.

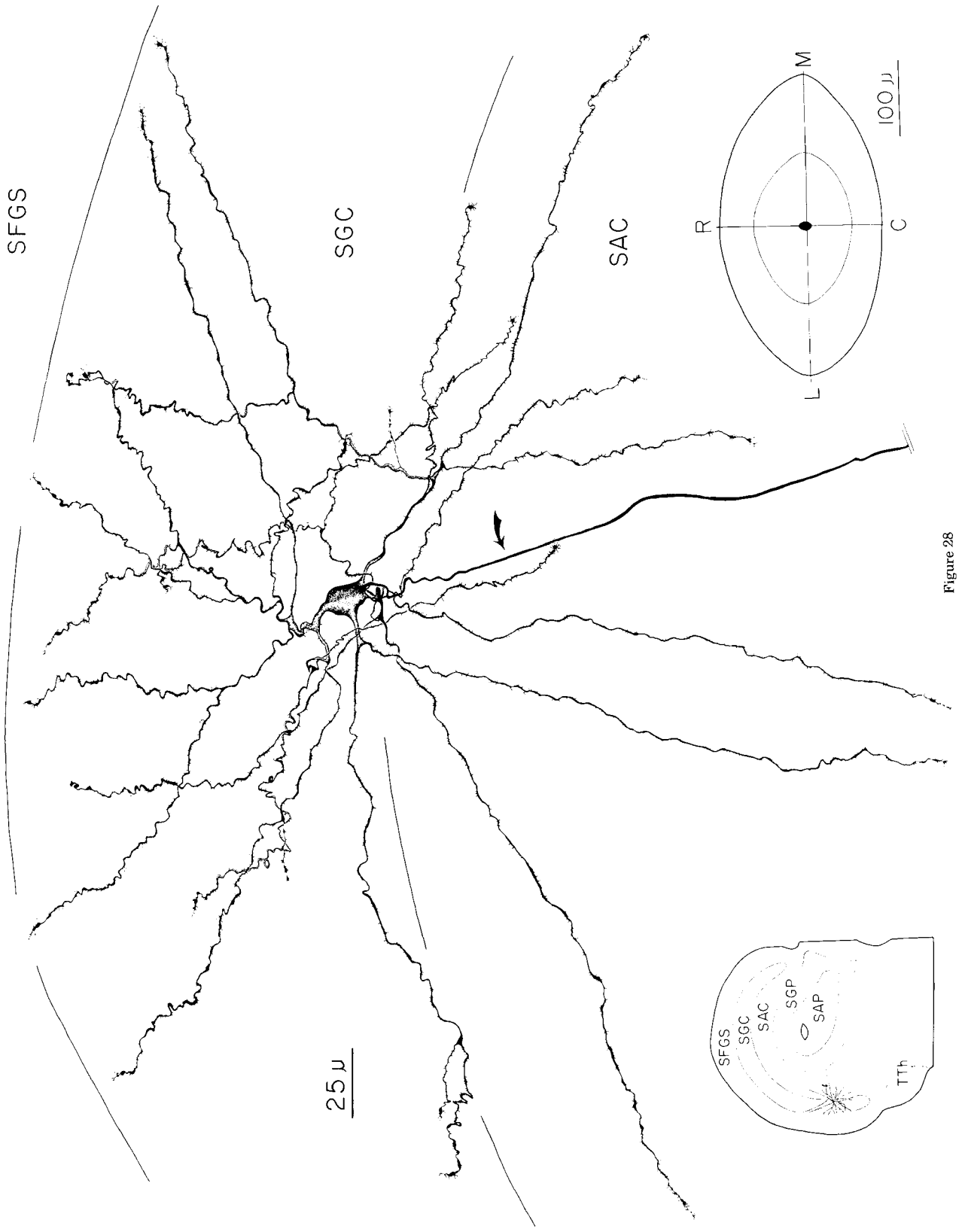


Figure 28

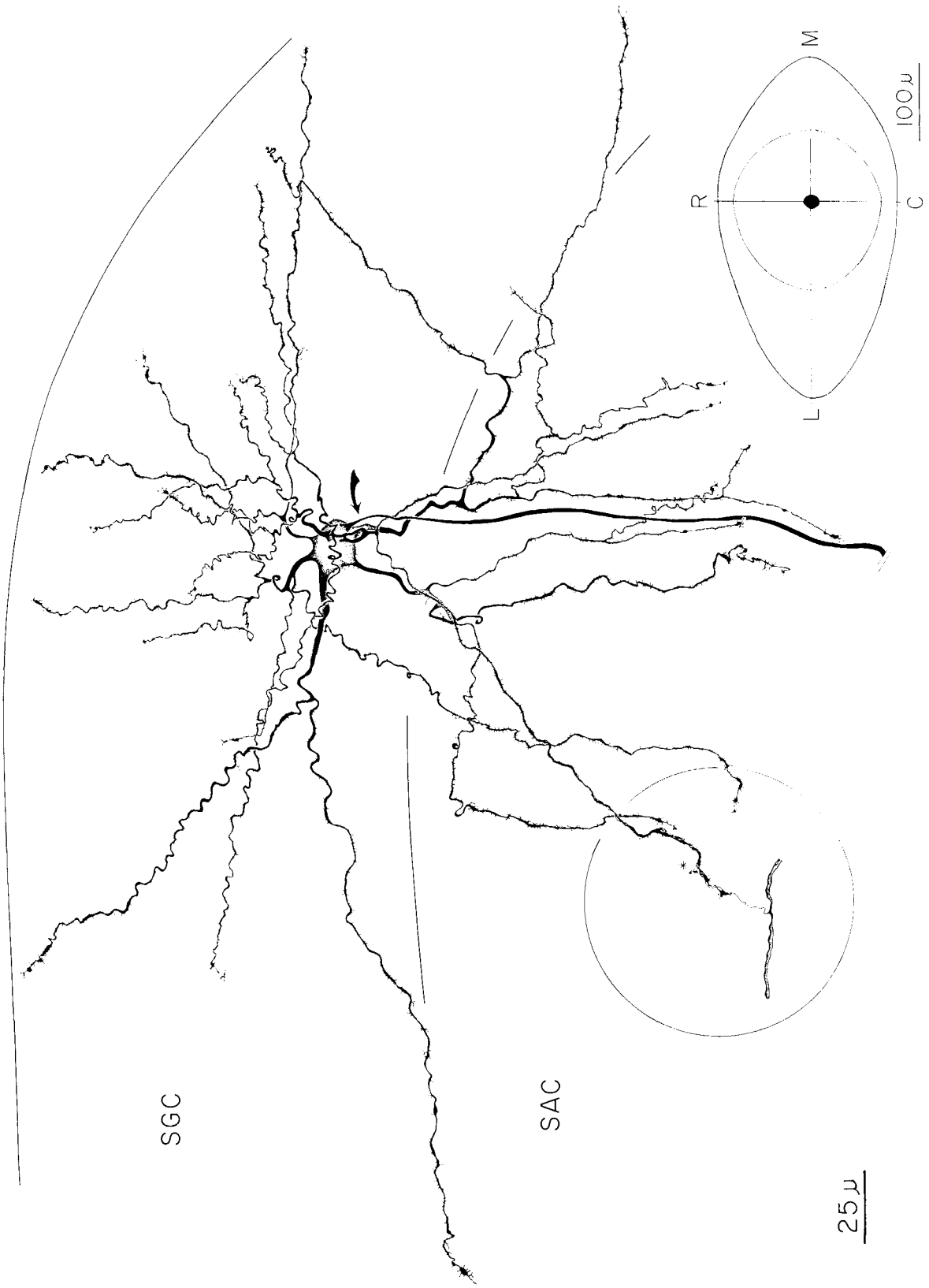


Fig. 29. Crossed tectobulbar cell. Somata situated in the stratum griseum centrale have relatively short unbranched dendrites that terminate abruptly at the border of the strata griseum centrale and fibrosum et griseum superficiale. The descending dendrites radiate into the central white layer for a variable distance. Dendrites bear fine, hairlike spicules that tend to appear in pairs separated by 1-μm gaps. Terminal boutons from tectal afferents of brainstem origin that were anterogradely filled are sometimes observed to occupy these gaps (circled area at lower left; boutons are stippled lightly and indicated by the asterisk). Soma position of this cell is deep in the stratum griseum centrale; dendritic field spread = 430 × 230 μm.

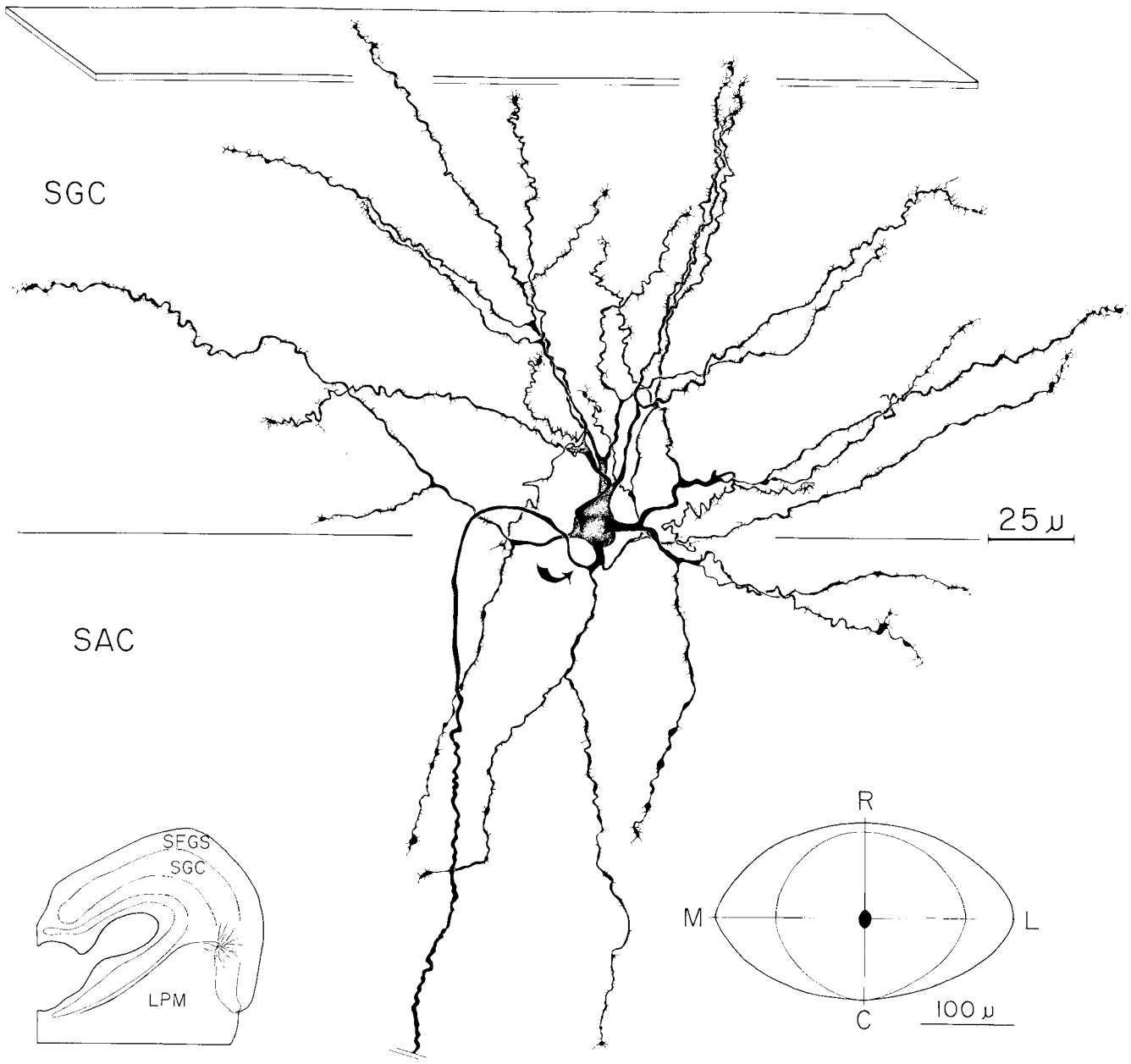


Fig. 30. Crossed tectobulbar cell. The axon (arrow) descends vertically through the stratum album centrale without branching or collateralizing and turns laterally at the border of the central white with the periventricular gray. The position of this cell and its axon in the tectum is shown in the inset at the lower left. The soma is situated at the border of the strata griseum and album centrale. The dendritic field spread = 320 × 180 μm.

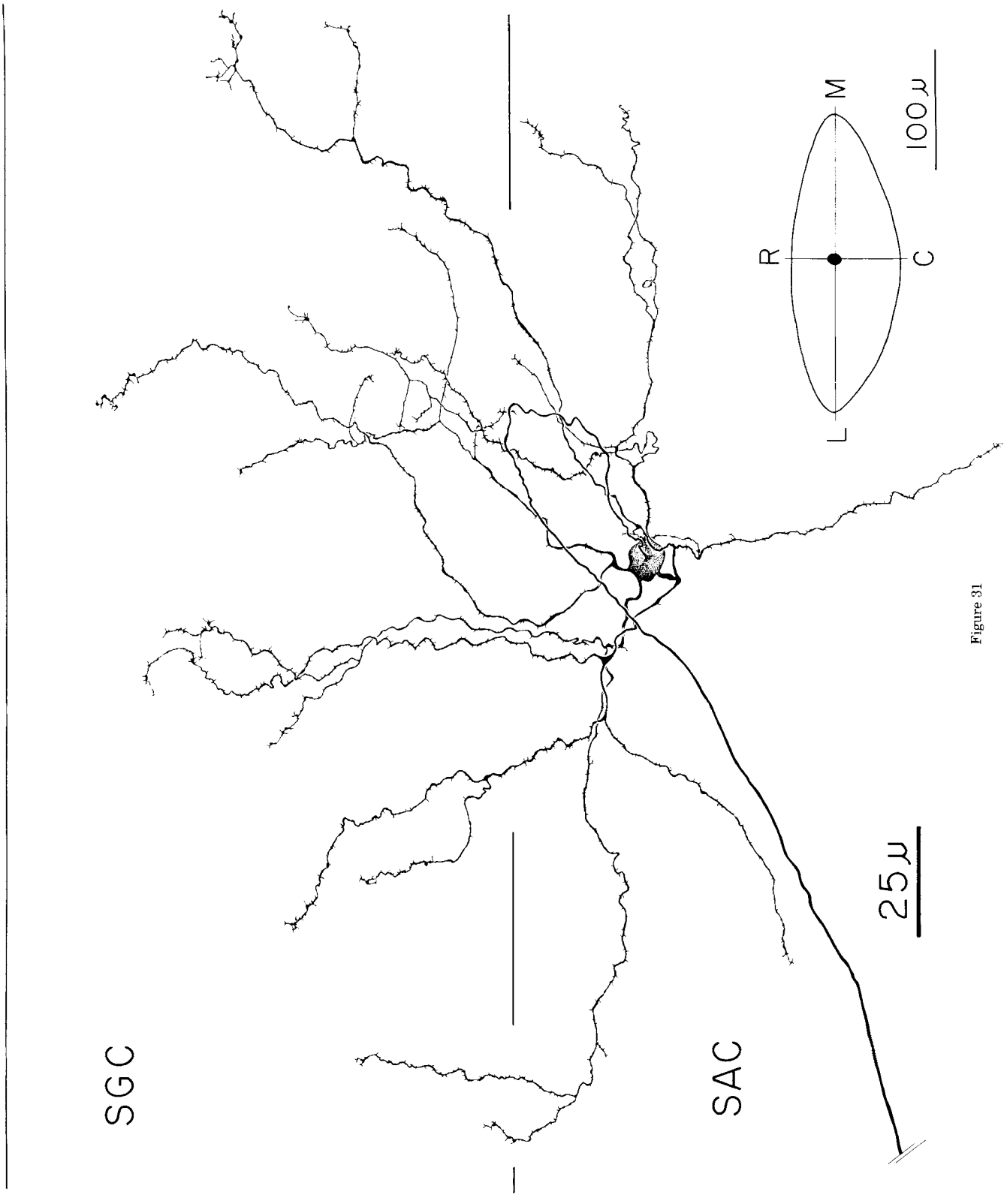


Figure 31

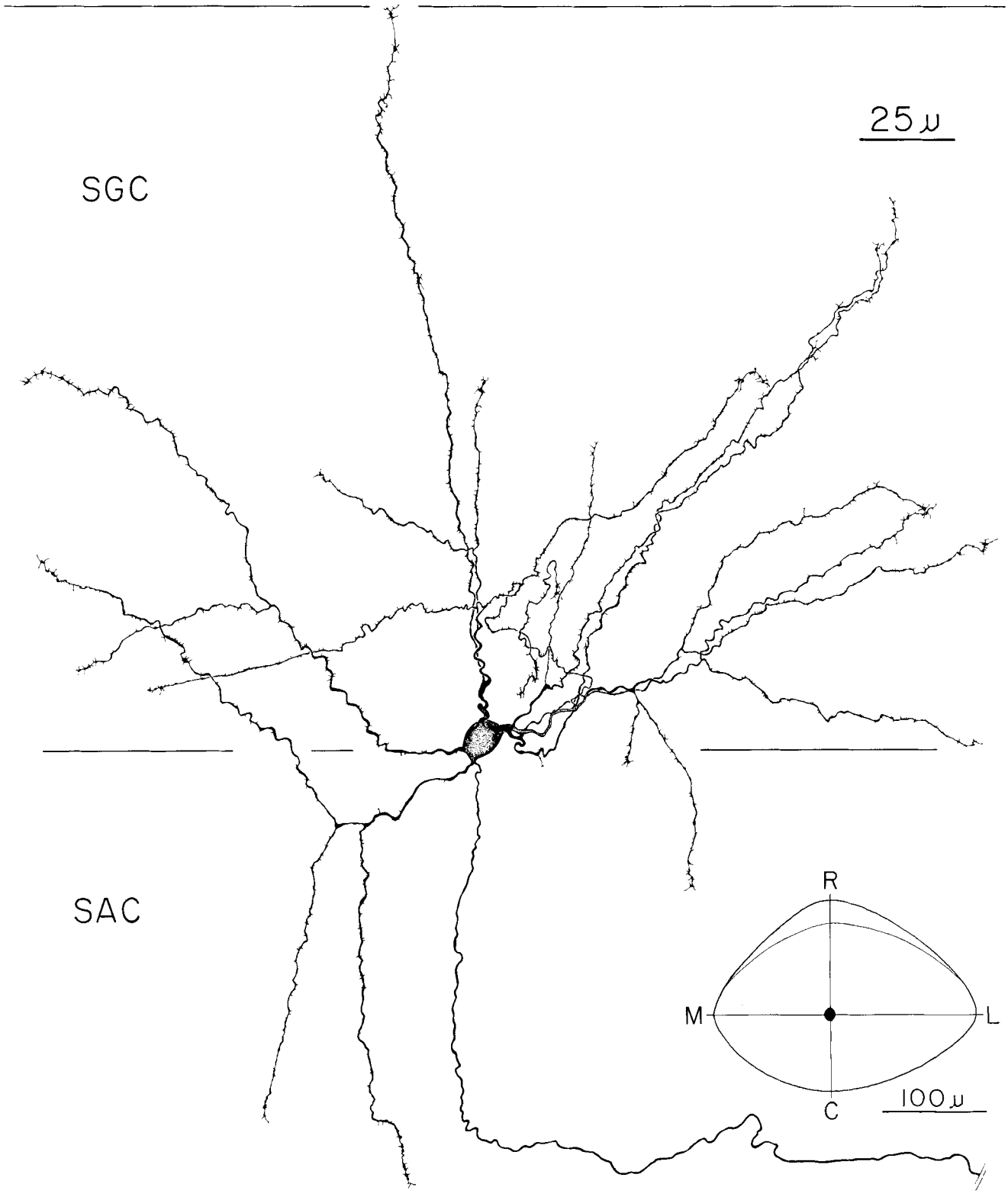


Fig. 31. Crossed tectobulbar cells. These neurons have smaller somata (10 μm in diameter) and smaller dendritic field spreads (250 × 90 μm and 230 × 200 μm, respectively). However, their dendritic structure and laminar spread are identical to the larger crossed tectobulbar cells.

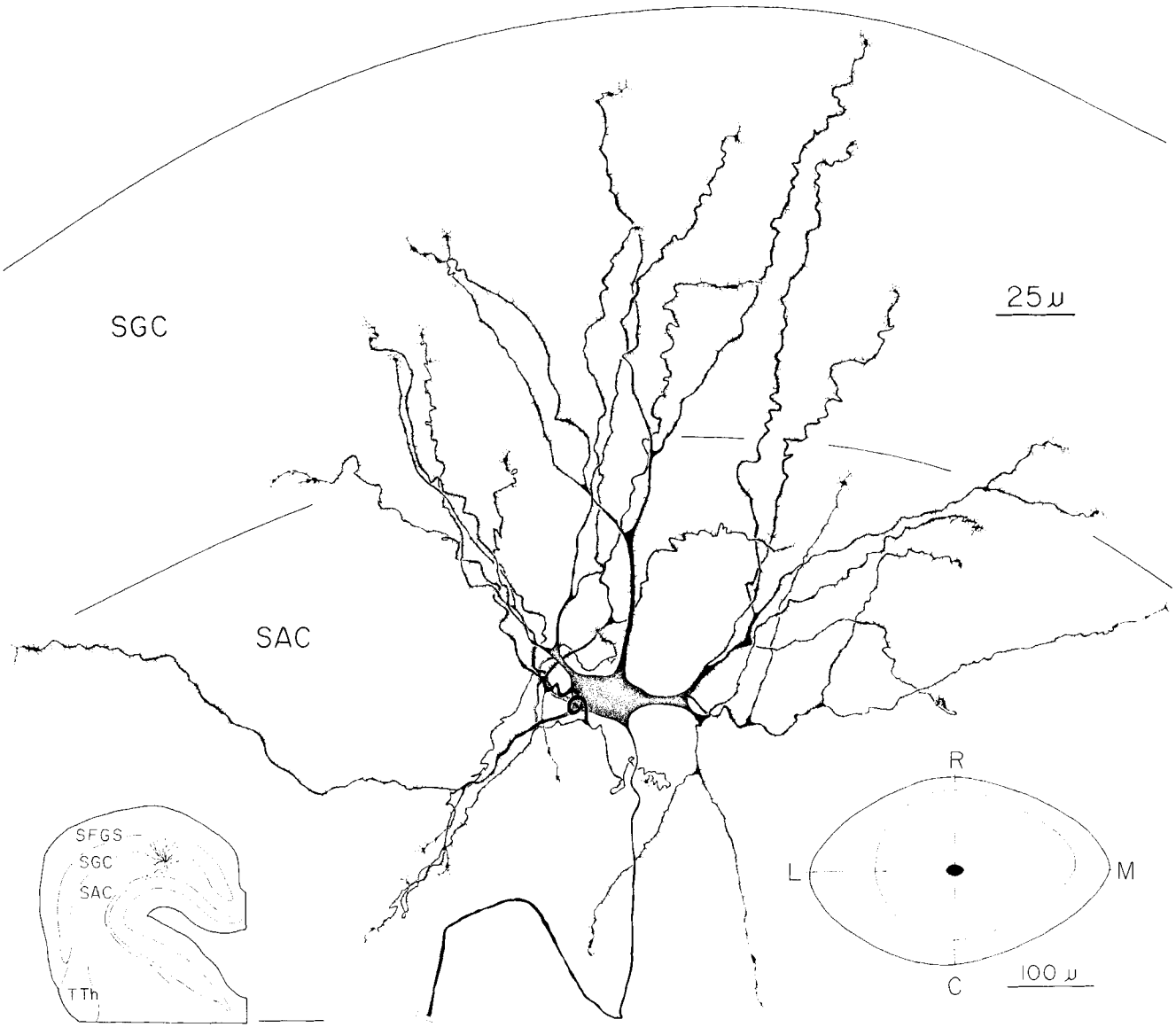


Fig. 32. Crossed tectobulbar cell. In the more deeply situated tectobulbar neurons the majority of dendrites ascend through the stratum album centrale and into the stratum griseum centrale. Inset at lower left shows position of cell and axon in tectum. The soma of this cell is positioned in the upper third of the stratum album centrale. The dendritic field spread = 350 × 210 μm.

with HRP filling in turtle (Sereno and Ulinski, '85) and cats (Grantyn and Grantyn, '82). Based on the estimates of tectal magnification factors obtained by Hartline et al. ('78) in *Crotalus*, the dendritic field sizes of tectobulbar neurons correspond to an angle of approximately 15–30° of visual arc in the central region of the visual field. These neurons probably correspond to "wide field" units present in the central and deep layers in all vertebrates (e.g., McIlwain and Buser, '68; Jassik-Gerschenfeld and Guichard, '72; Cotter, '76; Albano et al., '78; Guthrie and Banks, '78; Niida et al., '80; Graham et al., '81; Stein and Gaither, '81). Axons of tectobulbar neurons leave the tectum without collateralizing and descend through the brainstem issuing collaterals in the midbrain, pontine, and medullary reticular fields.

These observations bear on several general aspects of tectal organization. First, retrograde tracing studies have suggested a laminar distribution of tectal efferent neurons (e.g. Ito et al., '81; Reiner and Karten, '82; Harting and Huerta, '84), there being some tendency for neurons with axons that ascend in the brainstem to have somata positioned more superficially in the tectum than those whose axons descend in the brainstem. In general this is true for *Thamnophis* as well. Thus, the majority of tectorotundal and tectogeniculate neurons have their somata positioned more superficially than the tectobulbar cells. However, in *Thamnophis* it appears that the trend toward laminar seg-

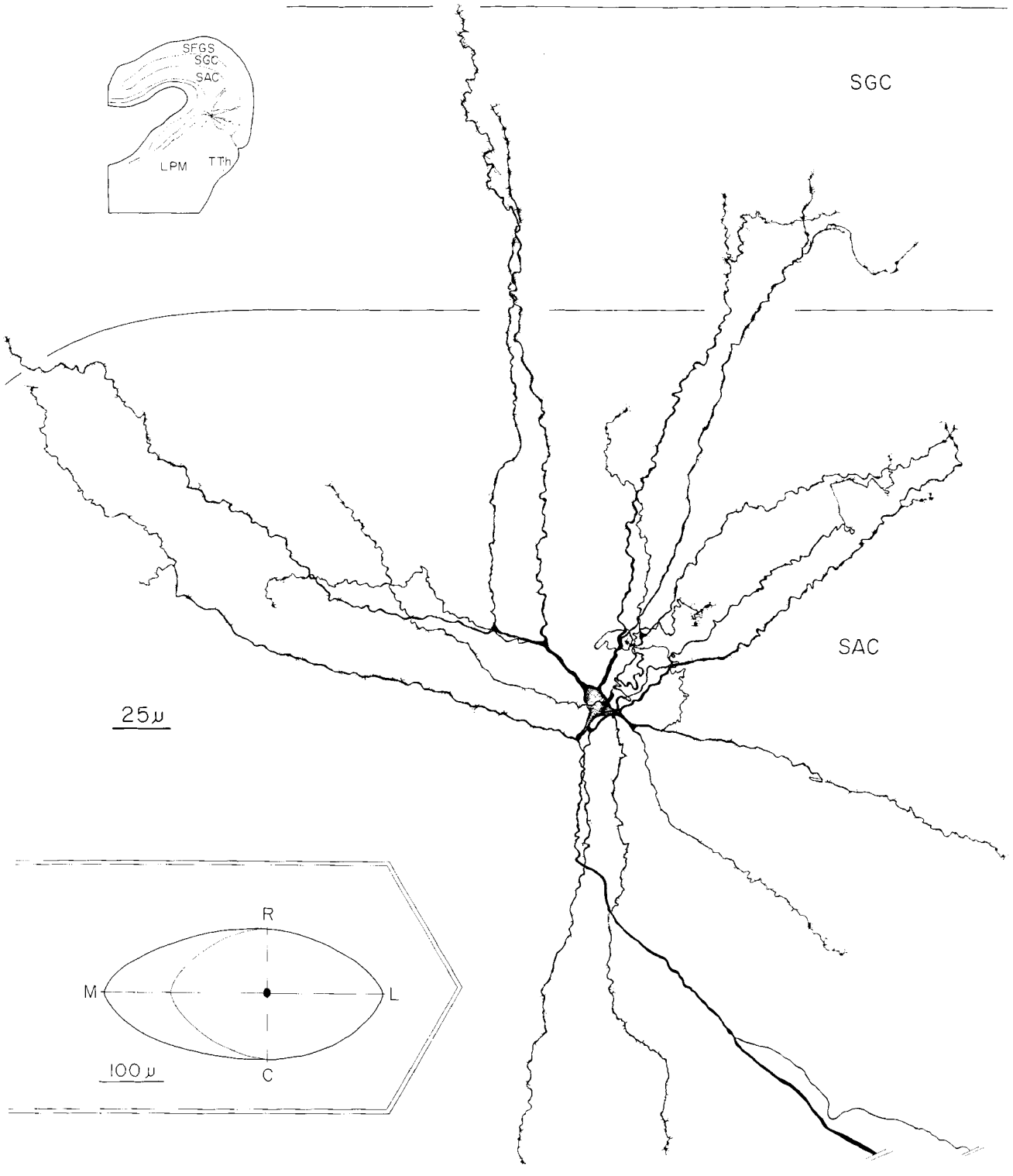


Fig. 33. Crossed tectobulbar cell. This cell has a soma diameter of only 12 μm but shows a large dendritic field spread, 450 × 200 μm. The collateral shown arising from the parent axon projects into the midbrain tegmentum. Inset at the upper left shows the position of the cell and its axon in the tectum. The soma of this cell is positioned in the lower third of the stratum album centrale.

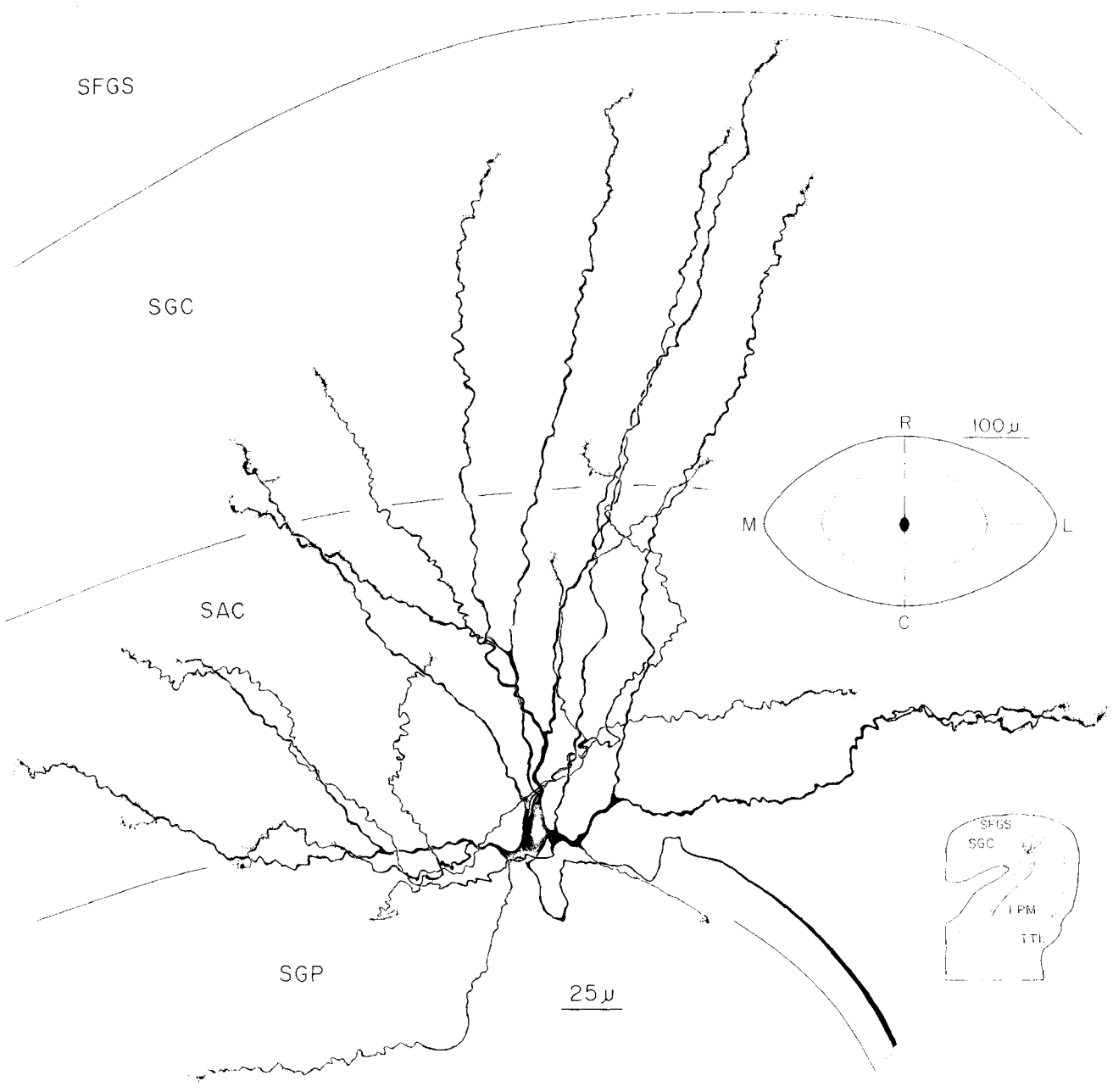


Fig. 34. Crossed tectobulbar cell. Dendrites of the most deeply situated neurons do not extend into the stratum griseum periventriculare (SGP). Inset at lower right shows the position of the cell and its axon in the tectum. The soma of this cell is positioned at the border of the stratum centrale and stratum griseum periventriculare. The dendritic field spread = 450 × 260 μm.

Fig. 35. Summary of tectal efferent neurons. This figure provides an overall summary of the classes of tectal neurons described in this study. Neurons are all drawn to about the same scale to facilitate comparison. The upper figure shows the morphology of the somata, dendrites, and the principal efferent branch of the axon. Tectogeniculate (TG), tectoisthmi (TI), tectoisthmobulbar (TIB), tectorotundal (TRo), ipsilateral tectobulbar (TBi), and contralateral tectobulbar (TBc) neurons are shown. The layers of the tectum are indicated by horizontal lines. The lower figure shows the somata of the tectogeniculate, tectoisthmi, and tectorotundal neurons with their intrinsic axon collaterals drawn in. The origins of the axons are indicated by the arrows.

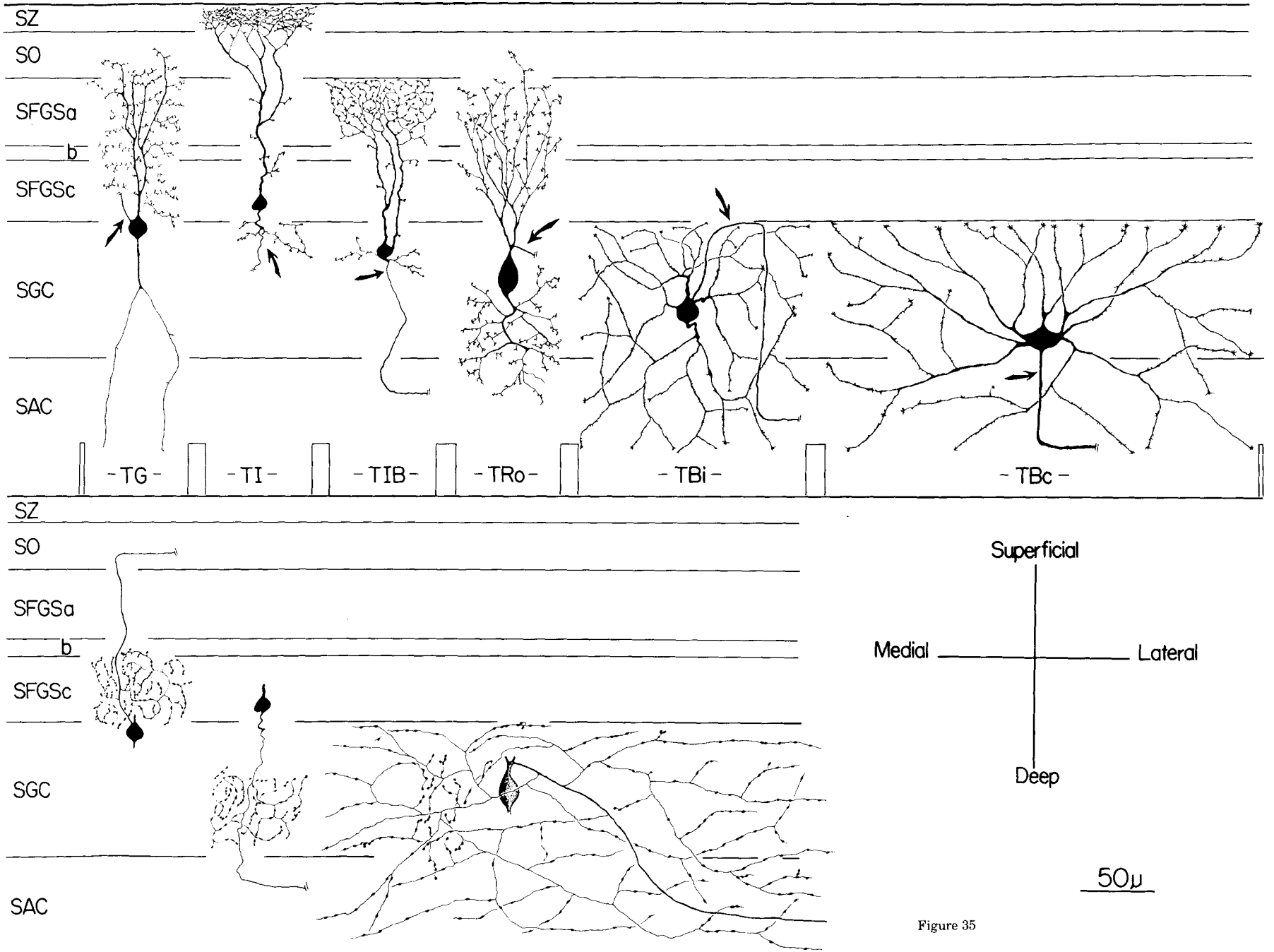

SZ
SO
SFGSa
b
SFGSc
SGC
SAC
- TG -
- TI -
- TIB -
- TRo -
- TBi -
- TBc -
SZ
SO
SFGSa
b
SFGSc
SGC
SAC
Superficial
Medial
Lateral
Deep
50μ

Figure 35

regation of somata is a weak indicator of the much more sharply defined laminar distribution of dendritic arbors. The tectorotundal, tectogeniculate, and tectoisthmi cell bodies, for example, may range from the middle of the central gray to the upper superficial gray. By contrast, the HRP-filled dendritic trees of these cells show highly specific laminar distributions. For example, the hourglass-shaped dendritic tree of the tectorotundal cell spans the central and superficial gray regardless of soma position.

Second, Golgi studies have emphasized the diverse neuron morphology in the vertebrate tectum (e.g., Ramón y Cajal, '11; Sterling, '71; Valverde, '73; Langer and Lund, '74; Quiroga, '78). The results of the present study and other recent studies that have used intra- and extracellular HRP methods to determine the morphology of tectal neurons have shown that even relatively subtle differences in dendritic and axon structure can be linked to a unique set of efferent connections (Mooney et al., '84; Sereno, '85; Sereno and Ulinski, '85). In *Thamnophis*, tectogeniculate, -rotundal, -isthmi, and -isthmobulbar cell types all have radially oriented dendritic trees that may extend into the superficial and deep tectal layers, and all bear complex dendritic appendages of a similar structure. However, the dendritic trees of these cells can all be readily distinguished. For example, the tectorotundal cell differs from the tectogeniculate cell in the structure of its basal dendrites. The tectoisthmi and isthmobulbar cells can each be distinguished by characteristic dendritic plexuses in the stratum zonale and sublayer a of the superficial gray, respectively. In addition, many of the tectal cells that can be defined by their efferent connections also show a characteristic pattern of intratectal connections. The tectorotundal cell, for example, gives rise to a widespread intrinsic projection in the central gray whereas the tectogeniculate cell has a spatially restricted projection to sublayer c of the superficial gray. Thus, a conclusion to be drawn from these overall results is that subtle differences in the structure of a cell's dendrites and axon (that have not been previously observed with the Golgi method) define multiple, distinct cell classes that make parallel sets of efferent connections. These features may be important for determining the synaptic basis of the characteristic response properties of each class of efferent neuron.

Third, previous physiological and connectional studies have argued that intrinsic connections (either via axons or long, radial dendrites) that could link the superficial (retinal receiving) and deep (motor related) layers of the tectum are absent in mammals (reviews: Edwards, '80; Wurtz and Albano, '80; Hall and May, '84) and that this feature may distinguish mammalian from nonmammalian tectal organization in which long, radial dendrites characteristically span the deep and superficial layers. However, more recent use of the intracellular-HRP method reveals widespread intrinsic axon projections and long dendrites that span the full width of the tectum in hamsters (Mooney et al., '84, '85). In *Thamnophis*, major intratectal connections arise from four of the efferent neuron classes and, as will be shown in the next paper in this series, from putative intrinsic neurons as well (Dacey and Ulinski, '86b).

ACKNOWLEDGMENTS

This work was supported by PHS grant NS 12518. Debra Hawkins typed the manuscript. Shirley Aumiller and Maryellen Kurek provided photographic assistance.

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