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Optic Tectum of the Eastern Garter Snake, *Thamnophis sirtalis*. I. Efferent Pathways

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ABSTRACT

Extracellular, iontophoretic injections of horseradish peroxidase were used to anterogradely fill axons efferent from the optic tectum in garter snakes. The tectal efferent pathways consist of six axon types with distinct projections and terminal morphologies. *Tectogeniculate axons* pass into the diencephalon via the optic tract, bearing collaterals that form spatially restricted, rodlike arbors in the pretectum, the ventral lateral geniculate nucleus, and the ventrolateral nucleus. *Tectoisthmi axons* exit the tectum as a thin-caliber component of the ventral tectobulbar tract. They form spatially restricted, spherical arbors within nucleus isthmi. *Tectoisthmobulbar* axons also give rise to small, spherical arbors within nucleus isthmi, but the parent axons continue caudally into the pontine and medullary reticular formation issuing many short collateral branches. *Tectorotundal axons* reach the diencephalon via the tectothalamic tract and give rise to fine terminal collaterals in the nucleus of the tectothalamic tract ipsilaterally and in nucleus rotundus bilaterally. Single axons form sheetlike terminal fields that span the rostrocaudal extent of nucleus rotundus. *Ipsilateral tectobulbar axons* descend into the midbrain tegmentum where they issue several thick collaterals that terminate widely throughout the nucleus lateralis profundus mesencephali. The parent axon continues caudally giving off several widely spreading collaterals within the pontine and medullary reticular formation. *Crossed tectobulbar axons* enter the dorsal tectobulbar tract and cross the midline to form the predorsal bundle. Single axons give rise to terminal collaterals in the nucleus lateralis profundus mesencephali bilaterally, the contralateral pontine and medullary reticular formation, and the intermediate gray of the cervical spinal cord.

Key words: sensorimotor transformation, tectoreticular, axon morphology, horseradish peroxidase

A major feature of the vertebrate optic tectum is its topographically organized sensory and motor maps. Consequently, the vast majority of anatomical and physiological studies of tectal organization have been devoted to detailed analyses of the precision and pattern of these maps. However, there is growing evidence from this work that the tectum can also represent information in nontopographic or non-point-to-point maps. Horseradish peroxidase (HRP) fills of tectoreticular axons in turtles (Sereno, '85), cats (Grantyn and Grantyn, '82), and frogs (Masino et al., '84) have shown clearly that the projection of the tectum to the brainstem reticular formation is not topographically organized. Similarly, the ascending tectothalamic projection to nucleus rotundus in reptiles and birds lacks topography, with the result that units in rotundus have extremely large visual receptive fields (Revzin, '79; Rainey and Ulinski, '82; Dacey and Ulinski, '83; Berson et al., '84).

It seems certain that its topographic maps provide the tectum with a necessary framework of information about the position of objects in the external world, but the functional role of nontopographic maps is less clear. A potential clue comes from the work of McIlwain, who was the first to direct attention to the very large visual receptive fields in the deep layers of cat superior colliculus and to suggest a model in which the location of a stimulus in the superficial colliculus might be encoded in the spatial pattern of activity of wide field units in the deep layers (McIlwain, '76, '82). Similar conclusions concerning the movement-related dis-

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charges of collicular cells have been reached by Sparks and Mays ('80) in monkeys. Both McIlwain and Sparks and Mays indicate that the coordinates of an orienting movement elicited by tectal stimulation must somehow be derived from this spatial pattern of activity. We (Dacey and Ulinski, '83; Sereno and Ulinski, '85) have recently discussed some of the mechanisms whereby nontopographic projections could account for the types of spatial activity patterns described in cats and monkeys.

Although movements of the eyes and head in cats and monkeys have been intensively studied in recent years, directed, reflex-like movement of the body, head, eyes, ears, or whiskers to an external stimulus is a general and biologically relevant feature of behavior. Further, there is a considerable body of evidence (see Dacey and Ulinski, '86d) implicating the optic tectum (or superior colliculus) in the control of such orienting movements. The way in which topographic and nontopographic tectal projections interact in producing orienting movements is therefore a general unresolved question in neurobiology. An answer to this question will require detailed understanding of intratectal organization and its relation to tectal efferent and afferent systems. Recent use of intracellular and extracellular injections of HRP to characterize the axon and dendritic morphology of tectal neurons has made progress in this direction and has provided the first firm evidence for major, intratectal connections (McCrea and Grobstein, '83; Mooney et al., '84; Sereno, '85) and for a complex set of functionally and morphologically distinct tectal efferent pathways to the brainstem reticular formation (Grantyn and Grantyn, '82; Lazar et al., '83; Hughes et al., '84; May and Hall, '84; Grantyn and Berthoz, '85; Hardy et al., '85; Sereno, '85; Sereno and Ulinski, '85).

The present study continues this type of analysis of tectal organization. It is the first in a series of five papers that examines in detail the morphology of tectal neurons and projection systems in the eastern garter snake, *Thamnophis sirtalis*, emphasizing the possible roles of topographic and nontopographic tectal systems in producing orienting movements. (The remaining papers in the series will appear in the succeeding four issues of this journal.) We were led to undertake this project by our success in using extracellular HRP labeling techniques to fill tectal neurons in *Thamnophis* in other projects (Dacey, '82; Dacey and Ulinski, '83). The brain is relatively small in garter snakes, making it possible to completely fill many of the axon systems that are afferent and efferent to the tectum. We have found that small, focal injections of HRP in the tectum frequently permit the complete reconstruction of individual neurons to an extent that is difficult to achieve in larger animals. At the same time, tectal organization in *Thamnophis* seems to conform to the general vertebrate pattern, so our results in this particular species are likely to have general relevance in understanding vertebrate orienting movements.

This and the second paper (Dacey and Ulinksi, '86a) describe the morphology of tectal efferent neurons. They show that some of these neurons give rise to topographic projections while others form nontopographic projections. The third paper (Dacey and Ulinski, '86b) describes the morphology of tectal neurons whose projections are intrinsic to the tectum. It shows that these neurons can have widespread but highly patterned projections within the tectum. The fourth paper (Dacey and Ulinski, '86c) describes the terminal morphology of retinal afferents to the tectum. It shows that the majority of retinal arbors are approximately the same size and shape. There are significant variations in the diameters of the axons and terminal boutons on retinal afferents, but all variants potentially contact several classes of tectal intrinsic and efferent neurons. The fifth paper (Dacey and Ulinski, '86d) describes the major nonretinal afferents to the tectum and shows that they include both topographically and nontopographically organized projections. It concludes with a general discussion of the function of the tectum and offers an hypothesis for the neural mechanisms that may subserve tectally mediated orienting movements.

MATERIALS AND METHODS

Experimental procedure

Injections of horseradish peroxidase (HRP) were made iontophoretically (Graybiel and Devor, '74) into the optic tecta of 60 garter snakes (*Thamnophis sirtalis*). Animals were packed in ice to induce torpor. Single current pulses of 1–10 μA for 15–60 seconds were used to eject Sigma type VI HRP (in pH 8.6 Tris buffer) from a micropipette with an internal tip diameter of 5–10 μm. Animals were perfused after 2, 3, or 4 days with buffered normal saline followed by a buffered solution of 1% formaldehyde and 3% glutaraldehyde. Brains were infiltrated with a phosphate-buffered 30% sucrose solution for 12 hours, and frozen sections were cut in the coronal plane at 40, 80, 100, or 120 μm. Sections were processed according to the cobalt-enhanced diaminobenzidine (DAB) method of Adams ('77). The pH of the incubating solutions was adjusted to 5.1 and DAB concentration was increased to 0.25% (Malmgren and Olsson, '78). Incubation times in both the cobalt and DAB solutions were 30 minutes. Sections were mounted serially from phosphate buffer, briefly air dried and coated with 1% celloidin, and lightly counterstained with cresyl violet.

Anterograde labeling was determined first in 15 cases sectioned at 40 μm and studied with 40× dry and 100× oil-immersion objectives to distinguish the trajectories and terminal patterns of anterogradely labeled fibers from retrogradely filled tectal afferents (Dacey and Ulinski, '86d). The overall pattern of anterograde filling was then plotted at 62.5×, in several cases sectioned at 80 μm (e.g., Figs., 1–3 were taken from a representative case). The positions of anterogradely labeled axons were charted at 100× magnification and they were then traced at a slightly higher magnification (250×) and redrawn in the plots by eye as accurately as possible.

Reconstructions of single, solid-filled axons were accomplished with the aid of a drawing tube at 1,560× total magnification (100× objective). Axon segments traced through single sections were aligned in the proper orientation with adjacent segments by noting the position of multiple landmarks (blood vessels, other labeled axons and cells) surrounding the identified axon. Segments were drawn in as much detail as possible at low magnification (62.5×) to serve as a precise record of the axon's position. The actual lengths of axons obliquely traversing a section were estimated by determining the hypotenuse of a right-angled triangle formed by the section thickness and the length of the axon traced in two dimensions. The scale bars are therefore useful for indicating axon width or bouton size, but are inaccurate as indicators of axon length.

NOMENCLATURE

The nomenclature used for tectal layers is that of Huber and Crosby ('33). The naming of cells groups and fiber tracts in the diencephalon and midbrain generally followed Warner ('31, '46), with some recent clarifications introduced by Halpern and Frumin ('73), Northcutt and Butler ('74), and Halpern ('80). The identification of the dorsal lateral geniculate nucleus (DGN) in this paper is a suggestion based on the results of autoradiographic studies of retinal projections (du Lac and Dacey, '81). Nomenclature for the brainstem reticular fields follows Newman and Cruce ('82). Identification of other brainstem structures arises from a variety of recent descriptive studies (e.g., Moody and Metzler, '80; Miller, '80; Molenaar, '77; ten Donkelaar and Nieuwenhuys, '79; Molenaar and Fizaan-Oosteveen, '80).

RESULTS

We first describe the tectal efferent pathways shown by anterograde filling after large HRP injections into the tectum. The axons that make up these pathways are then reconstructed in serial sections of single, solid-filled axons. These results show that six axon types, distinct in both location and terminal organization, contribute to the tectum's efferent projections. The problem of determining which tectal neurons give rise to these axons is considered in the next paper (Dacey and Ulinski, '86a).

Tectal efferent pathways

Tectal efferents course in the tectogeniculate path, the tectorotundal path, and in the crossed and uncrossed tectoreticular paths. The organization of these pathways is described in the following sections. To save space, we present chartings (Figs. 1–3) of spaced serial sections from only a single experiment in which a large injection of HRP was made into one lobe of the optic tectum. However, the results in this case are representative of those obtained in other cases.

Tectogeniculate pathway (Fig. 1). Injections of HRP into the superficial layers of the tectum fill a large population of fibers in the stratum fibrosum et griseum superficiale (SFGS) just ventral to the stratum opticum (SO). Filled axons run to the rostral pole of the tectum where those constituting the tectogeniculate pathway (TG, Fig. 1) turn ventrally and enter the pretectum. The charting in Figure 1 shows these fibers in three serial sections (e–g) as they pass ventrally and laterally through the pretectum. Labeling of terminals is dense in the pretectal nucleus (Pt), mesencephalic lentiform nucleus (LM), and the geniculate pretectal nucleus (GP). Fibers continue to course ventrorostrally into the thalamus, lateral to nucleus rotundus and medial to the retinal terminal zone of the lateral thalamus, where they occupy a wedge-shaped region that includes the ventrolateral nucleus (VL) and is bordered by the medial cell plate of the ventral geniculate nucleus (VGNcp). Vari-

Abbreviations

Bi	Bishoff's nucleus
Cer	cerebellum
CG	central gray
Co	cochlear nucleus
DF	dorsal funiculus
DGN	dorsal geniculate nucleus
DH	dorsal horn
DM	dorsal medial nucleus
DTB	dorsal tectobulbar tract
GP	geniculate pretectal nucleus
HC	habenular commissure
HP	habenulopeduncular tract (fasciculus retroflexus)
IP	interpeduncular nucleus
Ist	nucleus isthmi
LC	locus coeruleus
LF	lateral funiculus
LFB	lateral forebrain bundle
LH	lateral habenula
LL	lateral lemniscus
LM	lentiform mesencephalic nucleus
LPM	lateralis profundus mesencephali nucleus
LT	lentiform thalamic nucleus
Mes V	mesencephalic nucleus of the trigeminal
MH	medial habenula
ML	medial lemniscus
MLF	medial longitudinal fasciculus
Mot V	motor nucleus of the trigeminal
MTTh	medial tectothalamic tract
NDF	nucleus of the dorsal funiculus
NLL	nucleus of the lateral lemnicus
NSM	nucleus of the stria medullaris
NTTh	nucleus of the tectothalamic tract
NVSo	nucleus of the ventral supraoptic decussation
OT	optic tract
Ote	optic tectum
Ov	nucleus ovalis
Pag	periaqueductal gray
PB	predorsal bundle
PC	posterior colliculus
PCo	posterior commissure
Pd	predorsal bundle
Pdo	posterodorsal nucleus
Pr V	principal nucleus of the trigeminal
Pt	pretectal nucleus
RI	inferior raphe
RID	reticularis inferioris pars dorsalis
RIV	reticularis inferioris pars ventralis
RM	reticularis medialis
Ro	nucleus rotundus
RSL	reticularis superioris pars lateralis
RSM	reticularis superioris pars medialis
RVL	reticularis ventralis pars lateralis
Sp	suprapeduncular nucleus
Sp V	spinal nucleus of the trigeminal
SR	superior raphe
TG	tectogeniculate pathway
TTh	tectothalamic tract
TThx	tectothalamic tract, crossed
VeVl	ventrolateral vestibular nucleus
VeVm	ventromedial vestibular nucleus
VGNcp	ventral geniculate nucleus, cell plate
VGNnp	ventral geniculate nucleus, neuropile
VH	ventral hypothalamus
VL	ventrolateral nucleus
vm	ventromedial sector of nucleus rotundus
Vr	motor root of the trigeminal
VSoD	ventral supraoptic decussation
VTB	ventral tectobulbar tract
III	oculomotor nucleus
IIIr	root of the third cranial nerve
X	motor nucleus of the vagus
XII	hypoglossal nucleus

Layers of the optic tectum

SAC	stratum album centrale
SAP	stratum album periventriculare
SFGS a,b,c	stratum fibrosum et griseum superficiale, sublayers a, b, and c
SGC	stratum griseum centrale
SGP	stratum griseum periventriculare
SO	stratum opticum

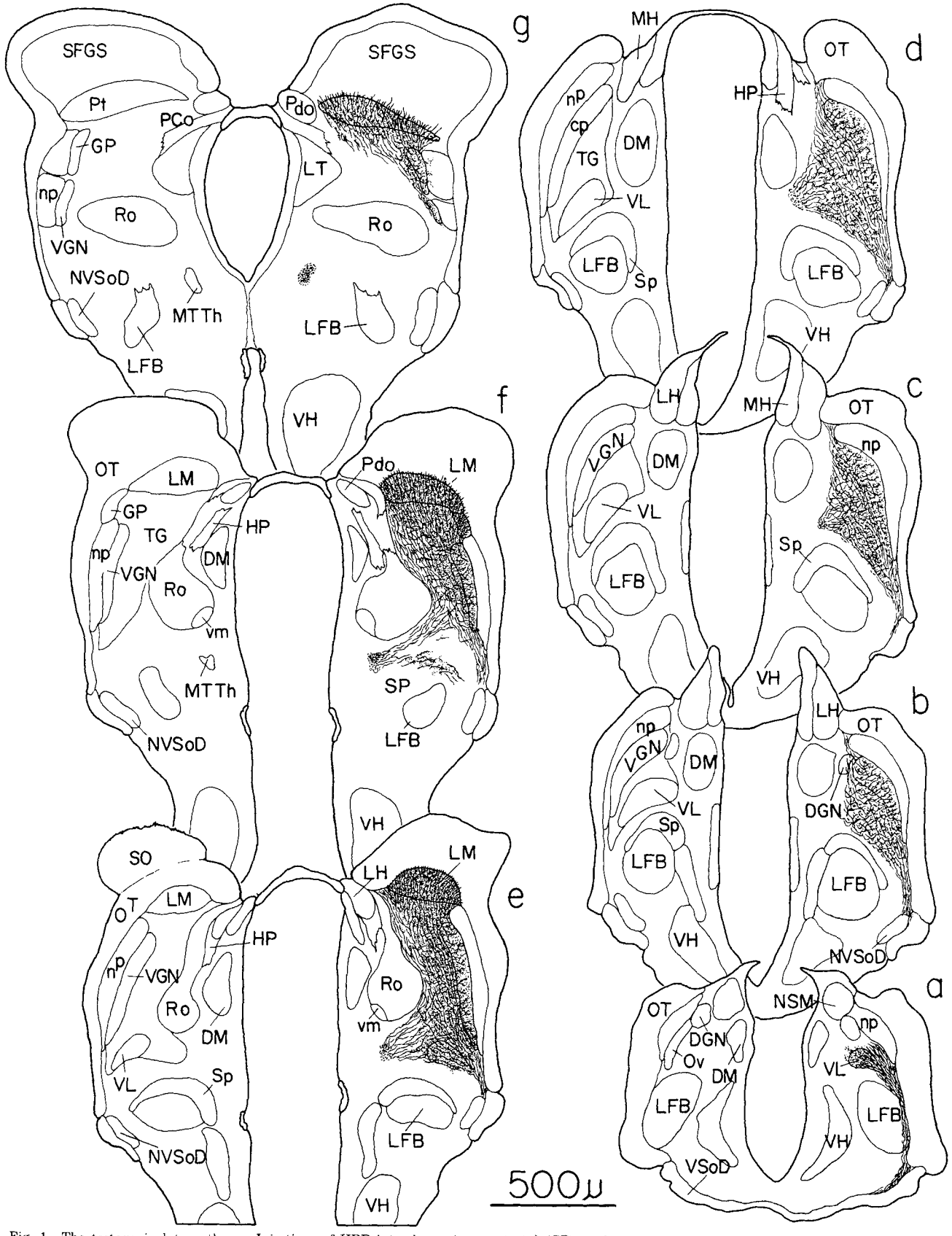


Fig. 1. The tectogeniculate pathway. Injections of HRP into the optic tectum (indicated by the heavy stippling in Figs. 2, 3) anterogradely fill a massive fiber system that courses rostrally in the stratum fibrosum et griseum superficiale (SFGS) and descends into the rostral pretectum and lateral thalamus at the rostral pole of the tectum. The terminal field occupies the mesencephalic lentiform (LM), pretectal (Pt), and geniculate pretectal (GP) nuclei, the cell plate of the ventral geniculate nucleus (VGNcp), and the ventrolateral thalamic nucleus (VL). A small contingent of fibers enters the tectogeniculate pathway via the medial tectothalamic tract (MTTh). Tectogeniculate fibers do not enter nucleus rotundus (Ro) medially or the retinorecipient neuropile (np) laterally. Axons (wavy lines) and terminals (stippling) were drawn by eye from the camera lucida tracings.

cosities are present throughout the entire rostrocaudal extent of these two regions as well as in the fiber pathway itself. A small contingent of fibers courses ventrolaterally below the retinorecipient neuropile to enter the ventral supraoptic decussation (VSoD) in the rostral diencephalon (Fig. 1a). They could be traced in some cases to the contralateral ventrolateral thalamic nucleus (not shown in Fig. 1). The fibers and their terminal fields do not encroach upon nucleus rotundus (Ro) medially or the retinal terminal zone laterally. Another relatively small contingent of fibers enters this terminal field via the medial tectothalamic tract (Fig. 1, MTTh). These fibers descend from the tectal gray in the dorsal tectobulbar tract (Fig. 3, DTB) and turn rostrally in a ventromedial position adjacent to the periaqueductal gray and medial longitudinal fasciculus. They course laterally at mid-diencephalic levels, ventral to nucleus rotundus, and enter the tectogeniculate pathway. In some cases, a few fibers from the medial tectobulbar pathway do not join the tectogeniculate pathway. They split off ventrolaterally and terminate in the suprapeduncular nucleus (Fig. 1f).

Tectorotundal pathway (Fig. 2). The course and termination of the tectorotundal pathway has already been described in detail (Dacey and Ulinski, '83) and will only be outlined here. Tectal injections encroaching on the central layers of the tectum fill a group of fibers that course laterally below the stratum griseum centrale (SGC) to the ventrolateral margin of the tectum. These fibers travel rostrally in this position, gathering into the tectothalamic tract, which forms a conspicuous bulge on the lateral surface of the midbrain (Fig. 2f, TTh). Fibers in this pathway give rise to a heavy terminal field at rostral midbrain levels, where they are embedded in a group of large cells called the nucleus of the tectothalamic tract (Fig. 2e, NTTh). The fibers stream medially and then rostrally at pretectal levels, encompassing the cytoarchitectonic boundaries of nucleus rotundus (Ro). Tectorotundal fibers course dorsomedially through the nucleus giving rise to thin collaterals. Some fibers give rise to a crossed projection by ascending dorsomedially from the rostral pole of rotundus, crossing the midline in the habenular commissure, and then descending into the rostral pole of the contralateral nucleus. Other fibers descend along the brainstem surface below the optic tract, cross the midline in the ventral supraoptic decussation, and reach the caudal pole of rotundus via the tectothalamic tract.

Ipsilateral tectoreticular pathways (Fig. 3). A complex pattern of axonal and terminal filling occurs bilaterally in brainstem structures from midbrain to spinal cord after large HRP injections in the tectum. Two distinct fiber groups descend from the stratum album centrale (SAC) into the ipsilateral midbrain tegmentum. The first contains very fine-caliber fibers that course just medial and ventral to the ipsilateral tectothalamic tract as the ventral tectobulbar tract (VTB, Fig. 3). These axons travel ventrocaudally at midtectal levels into a densely packed group of small, spherical neurons, identified as nucleus isthmi (Dacey and Ulinski, '86d). They generate a dense mass of fine-caliber collaterals and terminal boutons in the nucleus (Fig. 3a,b). Many fibers continue ventrocaudally close to the surface of the brainstem, run along the ventrolateral surface of the brainstem, and descend to caudal medullary levels in a thin ribbon (Fig. 3c–f). Very fine collaterals arise from this pathway at all levels; they are short and produce a sheetlike terminal zone that is embedded in the pathway. This component of the ventral tectobulbar pathway and its bed terminal field decrease in size as it progresses caudally to the medulla–spinal cord junction. Some of this reduction is due to fading of HRP in some fibers as they extend caudally. However, the pathway terminates before reaching the spinal cord even in cases with densely filled axons.

A second contingent of ipsilateral fibers descends into the midbrain tegmentum just medial to the fine-caliber component at the lateral margin of nucleus lateralis profundus mesencephali (LPM). These are medium-caliber fibers (1–2 μm in diameter). They contribute thick collaterals to a massive terminal field in lateralis profundus mesencephali and proceed into the ventrolateral midbrain tegmentum (Fig. 3). Small, somewhat scattered fascicles of these axons take up a position slightly dorsal and lateral to the fine-caliber tectobulbar axons and course caudally as a component of the ventral tectobulbar tract. Some collaterals emanating from this pathway course medially and cross the midline ventral to the predorsal bundle at midbrain (Fig. 3a,b) and pontine levels. Other collaterals ascend into the dorsolateral reticular fields—reticularis superioris pars lateralis, reticularis medialis, and reticularis inferioris pars ventralis and dorsalis (Fig. 3c–f). Some pass through these regions to contribute terminal collaterals to the principal and spinal trigeminal nuclei (Fig. 3d,e), the locus coeruleus and nucleus of the lateral lemniscus (Fig. 3c). In general, the total terminal zone arising from this pathway forms a continuous, rostrocaudally aligned column in the lateral reticular fields of the midbrain, pontine, and medullary tegmentum. None of the fibers could be traced beyond the caudal medulla. A small number of very large-caliber fibers (3 μm in diameter) occupy this position at the medulla–spinal cord junction (Fig. 3g), but they apparently arise from a retrogradely labeled tectal afferent source and will be considered in a subsequent paper (Dacey and Ulinski, '86d).

Contralateral tectoreticular pathway. A third tectobulbar pathway emanates from the ventromedial margin of the stratum album centrale and forms a distinct bundle at the lateral margin of the periaqueductal gray (Pag) medially and the nucleus lateralis profundus mesencephali (LPM) laterally. These axons turn ventromedially at midtectal levels and pass through the oculomotor fibers, cross the midline ventral to the medial longitudinal fasciculus, and course caudally as the predorsal bundle (Pd, Fig. 3). Solid-filled fibers were traced to the cervical cord. Primary collaterals arise from this bundle throughout its extent. They radiate dorsolaterally at caudal tectal levels (Fig. 3a,b) and arborize in reticularis superioris pars lateralis and nucleus lateralis profundus mesencephali. Collaterals in the pontine and medullary reticular core radiate laterally about 200–300 μm and form a massive terminal zone within reticularis medialis and reticularis inferioris pars dorsalis. A few extend dorsolaterally and arborize in the spinal trigeminal nucleus. Most of the terminals occupy a continuous, rostrocaudally aligned column ventral to the medial longitudinal fasciculus and medial to the terminal distribution of the ventral tectobulbar pathways. At the ventral pole of the spinal cord predorsal fibers occupy a position close to the midline at the ventral surface of the brain. Primary collaterals ascend vertically from this point and arborize in the spinal gray dorsomedial to the motoneurons in the ventral horn (Fig. 3). The bouton distribution within the predorsal terminal zones is clustered and patchy, like that described for the ventral pathway.

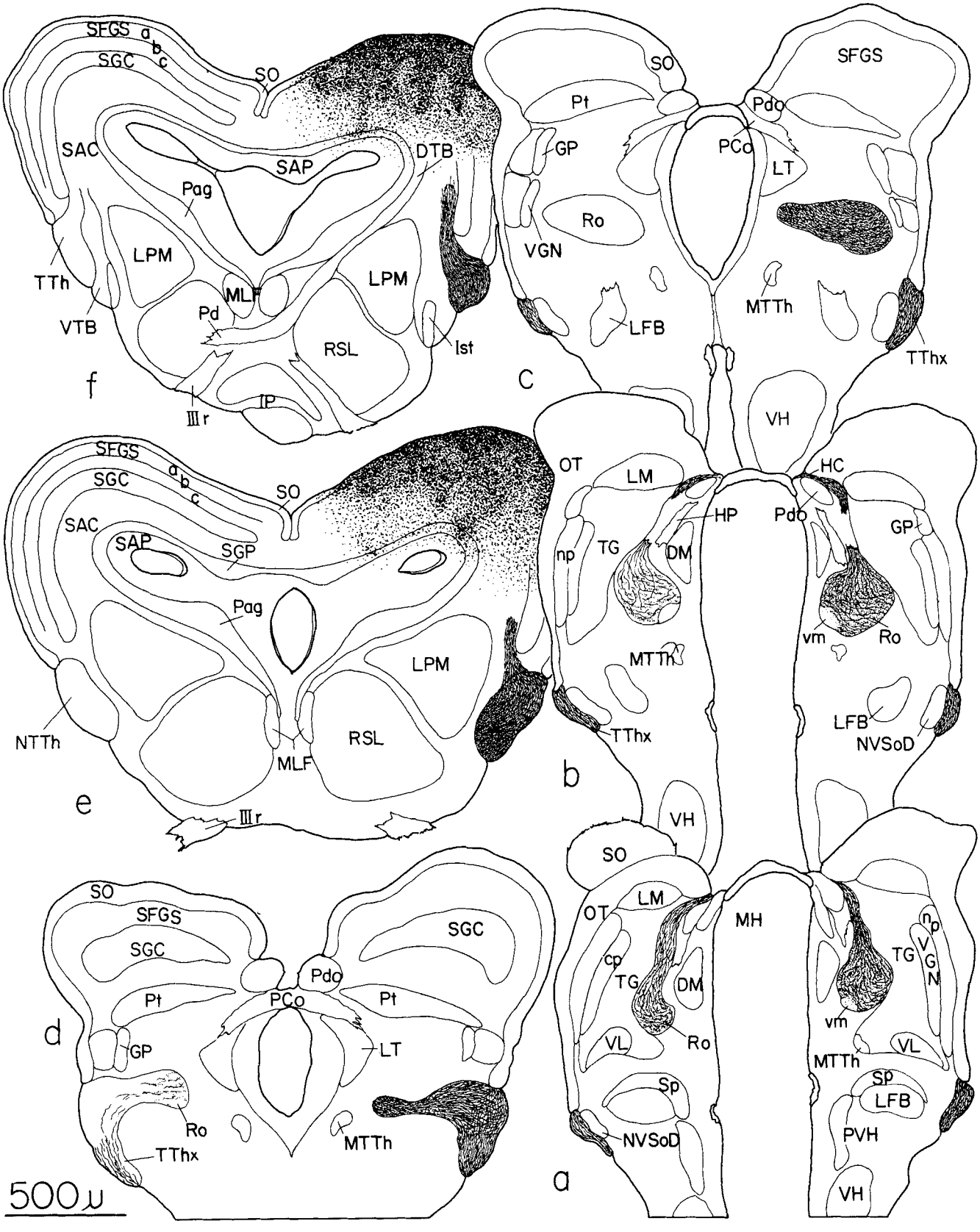


Fig. 2. Tectorotundal pathway. This pathway arises from the stratum album centrale (SAC) and ascends to the diencephalon at the lateral margin of the tectal roof in the tectothalamic tract (TTh). It turns medially to enter the nucleus rotundus (Ro) at the caudal border of the diencephalon. Terminals are present in the nucleus of the tectothalamic tract (NTTh) ipsilaterally and rotundus bilaterally. Tectorotundal fibers cross in the habenular commissure (HC) and the ventral supraoptic decussation (VSoD).

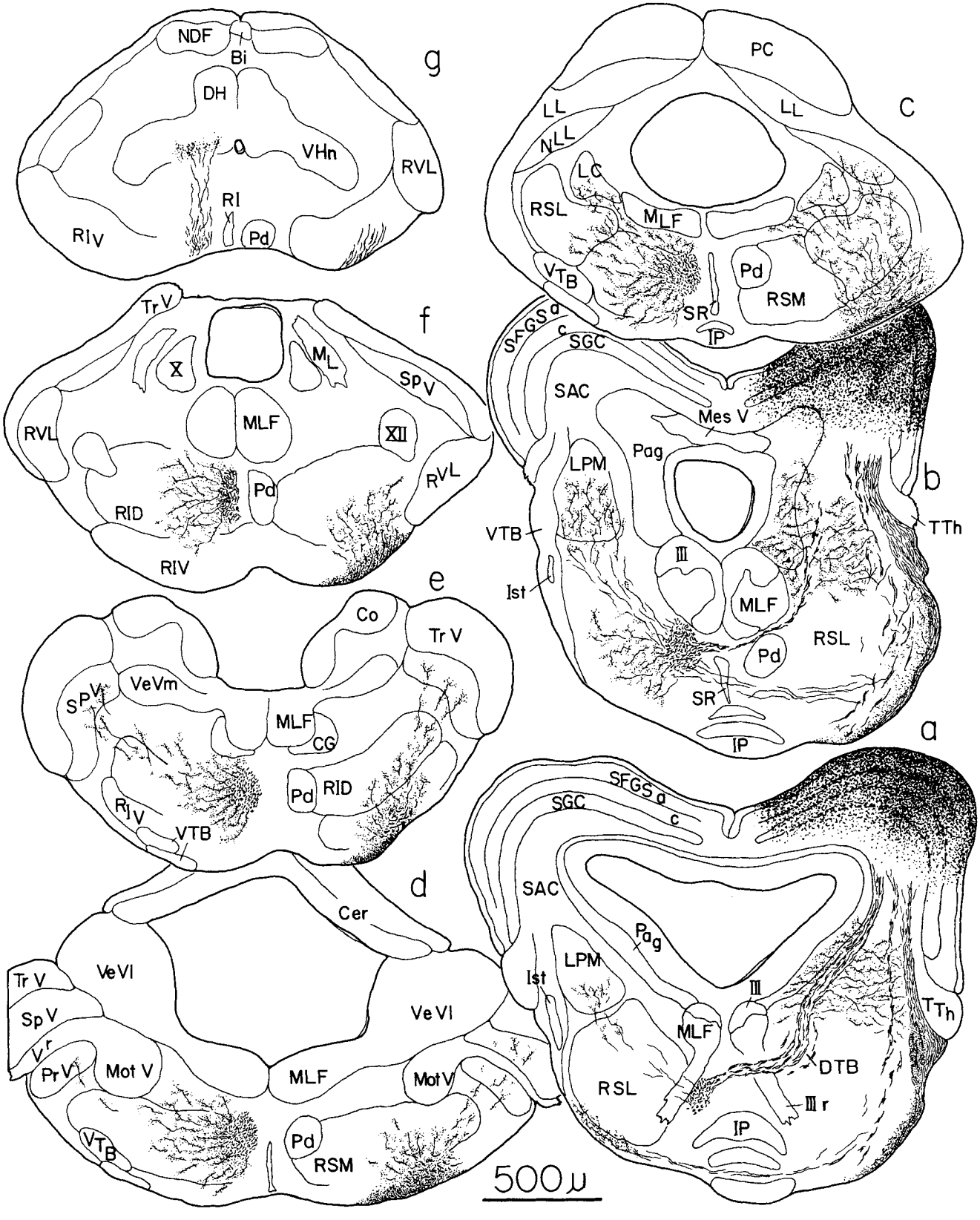


Fig. 3. Tectobulbar pathways. Three fiber groups contribute to the descending tectal pathways. Fine-caliber fibers descend ipsilaterally along the ventrolateral margin of the brainstem in the ventral tectobulbar tract (VTB) issuing terminals to the nucleus isthmi (Ist) and to the ventrolateral margin of the pontine and medullary reticular formation. Medium-caliber fibers descend ipsilaterally just medial to the fine-caliber component. These axons descend medial to nucleus isthmi and course caudally in the ventral tectobulbar tract at its dorsolateral margin. Larger-caliber axons descend through the midbrain tegmentum in the dorsal tectobulbar tract (DTB), cross the midline at the level of the root of the third cranial nerve, and descend to spinal levels close to the midline as the predorsal bundle (Pd).

Morphology of axons in tectal efferent pathways

The large injections just described filled many efferent axons and permit a general description of the course and distribution of the tectal efferent pathways. By contrast, small tectal injections (extending 200–400 μm in the horizontal plane) filled only a few efferent fibers. These axons were isolated and could be followed through serial sections. In this way, the morphology of single tectal efferent axons could be reconstructed and the nature of their contribution to tectal efferent paths and terminal zones determined. Six different axon systems in the tectal efferent paths could be defined on the basis of their course and terminal distribution. At least one axon reconstruction from serial sections is presented for each of the six pathways. These reconstructions portray representative examples from observations of a large number of partially and relatively completely filled axons. Single axons in a given class did show variation in a number of morphological features such as bouton density in a given terminal field, axon caliber, and presence or absence of a particular collateral projection. However, the present results provide only an overview and initial classification of the morphology of tectal efferent axons; variation within a given broad class is not considered in detail.

Tectorotundal axons. These axons contribute terminals to the tectothalamic tract and to nucleus rotundus bilaterally. Part of a reconstructed tectorotundal axon is shown in Figure 4. Four other examples have been described in a previous paper (Dacey and Ulinski, '83). The axon in Figure 4 was followed from the superficial border of the stratum album centrale (SAC) into the tectothalamic tract (Fig. 4, arrow). It was then followed through six 80-μm sections through the diencephalon. The parent axon is approximately 1 μm in diameter and gives rise to a series of irregularly spaced, fine-diameter collaterals bearing terminal boutons. Initial collaterals are given off at pretectal levels within the nucleus of the tectothalamic tract; one is shown in Figure 4, section A. These are usually short and sparsely branched, remaining in the vicinity of the parent axon. Single axons thus contribute relatively small, spatially restricted terminal clusters within a much larger terminal zone in this bed nucleus. The parent axon turns medially to enter the caudolateral pole of rotundus and courses in a straight line dorsoventrally through the nucleus, giving rise to a second series of terminal collaterals. These emerge at irregular intervals, distributing strings of terminal boutons that extend 50–200 μm in the horizontal plane of the parent axon, often reaching the borders of the nucleus, but are restricted in the sagittal plane (10–50 μm). This pattern is difficult to fully appreciate in the axon in Figure 4 because many collaterals are foreshortened; they actually extend some distance away from the axon in the horizontal plane. The shape of the terminal field of a single axon is a sheet flattened in the mediolateral axis and passing through the entire extent of the nucleus.

In some cases the parent tectorotundal axon does not enter the ipsilateral rotundus, but continues rostromedially in the crossed tectothalamic tract, crossing the midline in the ventral supraoptic decussation to reach the contralateral rotundus via the tectothalamic tract. In these cases, the parent axon issues a single collateral in ipsilateral rotundus that shows a trajectory and terminal pattern like that of larger-caliber tectorotundal axons. All the primary tectorotundal axons crossed the midline via this route or via the habenular commissure, accounting for the heavy, if not completely bilateral projection.

Tectogeniculate axons. Small HRP injections into the superficial gray layers of the tectum densely fill single axons that course rostrally in the stratum fibrosum et griseum superficiale at its border with the stratum opticum. An example of the course and morphology of such an axon is shown in Figure 5. This axon was reconstructed through seven serial sections, but only those portions of the axon bearing terminal arbors are shown (A, B, F, and G). As the tectogeniculate axon passes ventrorostrally into the pretectal nucleus it issues two collaterals that extend through the lateral half of the nucleus. One collateral reaches the geniculate pretectal nucleus where it terminates in a small cylindrical arbor. The terminal zones in both the pretectal and geniculate pretectal nuclei appear to represent part of a retinotopically organized projection to the pretectum, overlapping the direct retinal input to these areas (personal observations; Halpern and Frumin, '73). The parent axon descends through the pretectum into a region of low cell density designated here as the tectogeniculate pathway. It courses medial to the cell plate of the ventral geniculate nucleus (Fig. 5D–F). A collateral extends laterally into the cell plate (Fig. 5F) from this position. It is highly branched, shaped like a flattened cylinder, with a diameter of 50–70 μm. Its long axis extends the width of the cell plate. Two other tectogeniculate arbors are shown in Figure 6. Their terminal zones extend across the tectogeniculate path and cell plate. One axon (Fig. 6B) descends from the pretectum in an atypical position directly through the lateral side of the cell plate, but its arbor extends medially to occupy the same terminal zone. Some tectogeniculate axons extend only as far as the geniculate (Fig. 6A), but the parent axon in Figure 5 continues ventrolaterally beyond its collateral arbor in the geniculate and forms a small, spherical arbor in the ventrolateral nucleus. This arbor has a branching pattern similar to that of its sister axon in the geniculate, but is only about one-third the size. Other axons extend beyond the ventrolateral nucleus to enter the crossed tectothalamic pathway (Fig. 6B), cross the midline in the ventral supraoptic decussation, and reach the contralateral ventrolateral nucleus. Both the tectogeniculate and ventrolateral arbors are topographically organized (du Lac and Dacey, '81).

Tectoisthmi axons. Small injections of HRP into the tectum show that the fine-caliber component of the tectobulbar pathway gives rise to a topographically organized projection to a plate of small spherical cells situated at the ventrolateral border of the tectal cortex. The position of this cell group, the nature of its connections with the tectum, and its neuronal organization (Dacey and Ulinski, '86d) indicate that it is equivalent to the nucleus isthmi (or parabigeminal nucleus) described in a variety of other vertebrates. The morphology of tectoisthmi axons is shown in Figure 7. Fine-caliber (approximately 0.5 μm in diameter) fibers descend vertically into the isthmi cell plate and terminate without branching in single arbors (Fig. 7A). These arbors are spherical or oval and extremely small (10–30 μm in diameter). Collaterals arising from the parent axons often recurve, establishing a dense and sharply demarcated nest of terminal boutons. Some tectoisthmi arbors arise as collaterals from stem axons passing through nucleus isthmi.

Tectoisthmobulbar axons. These axons are also of fine caliber and travel in the ventral tectobulbar tract with the tectoisthmi axons. One to three collaterals arise as the axons descend through nucleus isthmi (Fig. 7B). They are spaced within 20 μm of each other, are contained within a

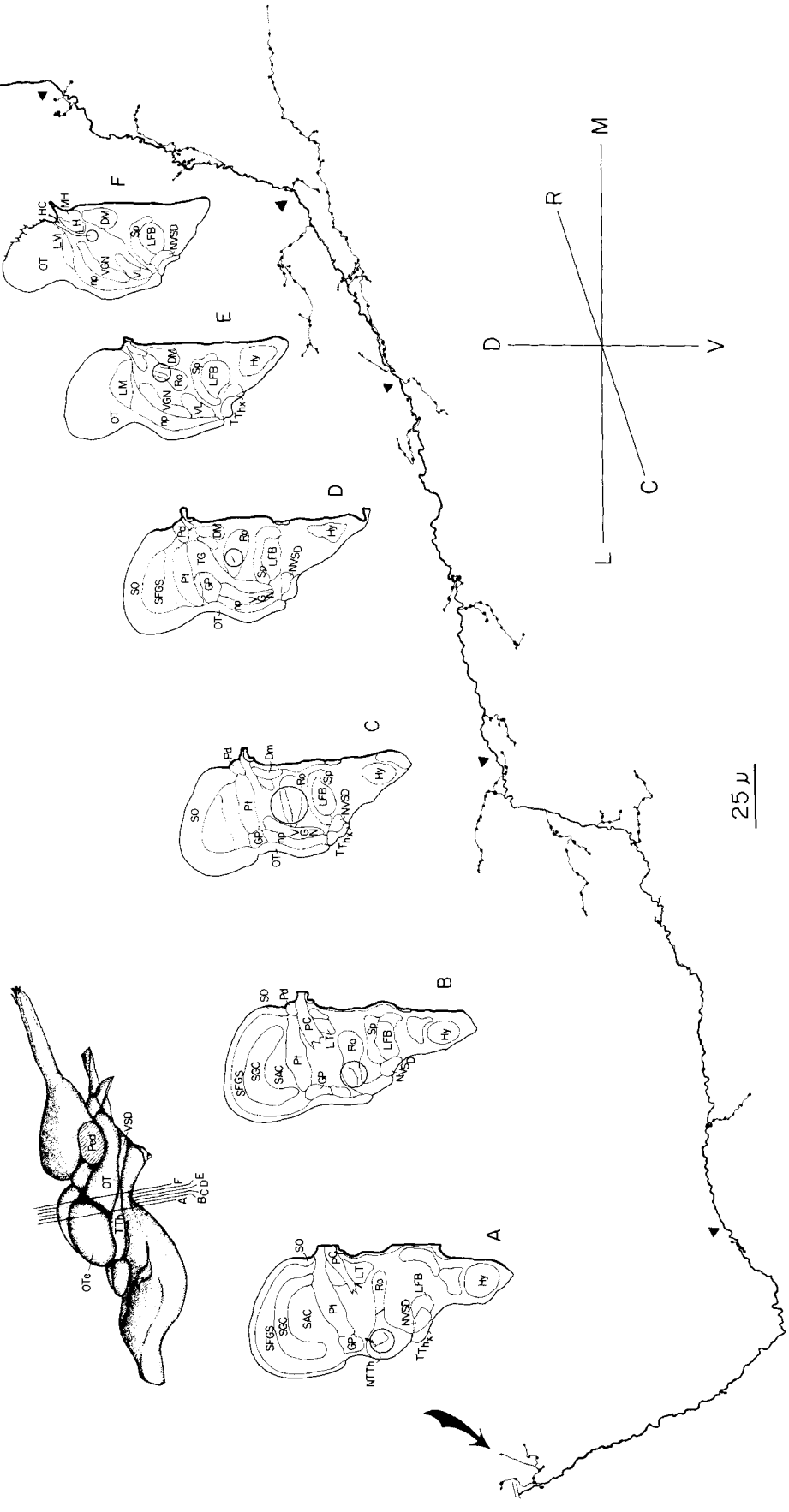


Fig. 4. Tectorotundal axon. This axon was reconstructed through six serial sections from the nucleus of the tectothalamic tract (A) to the rostral pole of rotundus (F). After issuing small terminals caudolateral to the dorsal pole of rotundus, the axon gives rise to several fine-caliber collaterals, constructing a sheetlike terminal field that extends mediolaterally across the nucleus but is flattened in the dorsomedial axis. The arrow at left indicates the beginning of the tracing in section A. The arrowheads along the course of the axon indicate where it was cut for each section.

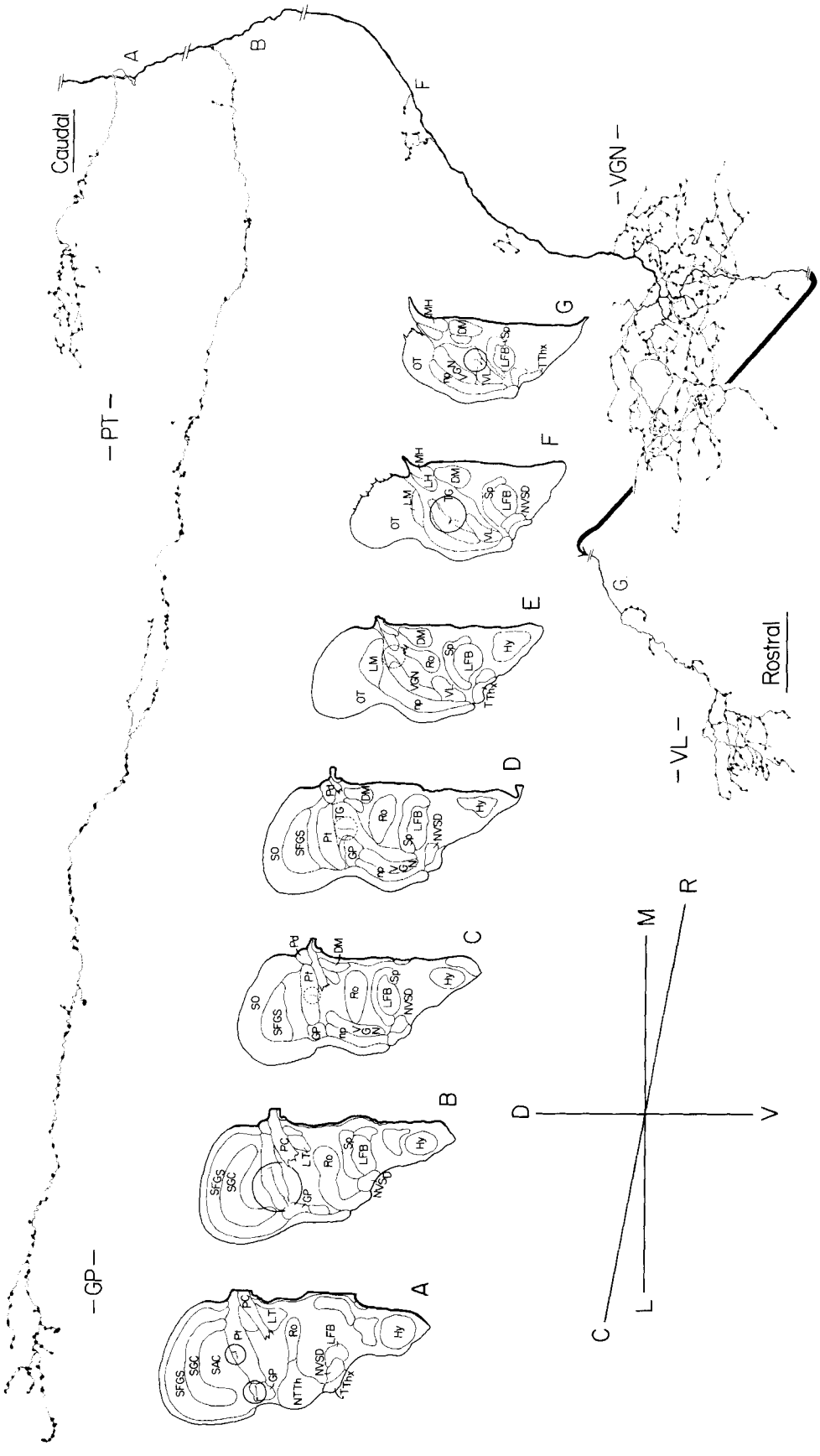


Fig. 5. Tectogeniculate axon. This axon was reconstructed from the same case used for the tectorotundal axon shown in Figure 4. The axon was followed through seven serial sections (circled areas in A–G). Only the parts of the axon bearing collaterals (solid circles A, B, F, and G) are illustrated at higher magnification. Single, topographically organized terminal arbors are formed in the geniculate pretectal nucleus (GP), and the ventrolateral nucleus of the thalamus (VL). The geniculate pretectal, the pretectal, and the ventral geniculate nuclei all receive a topographic retinal input.

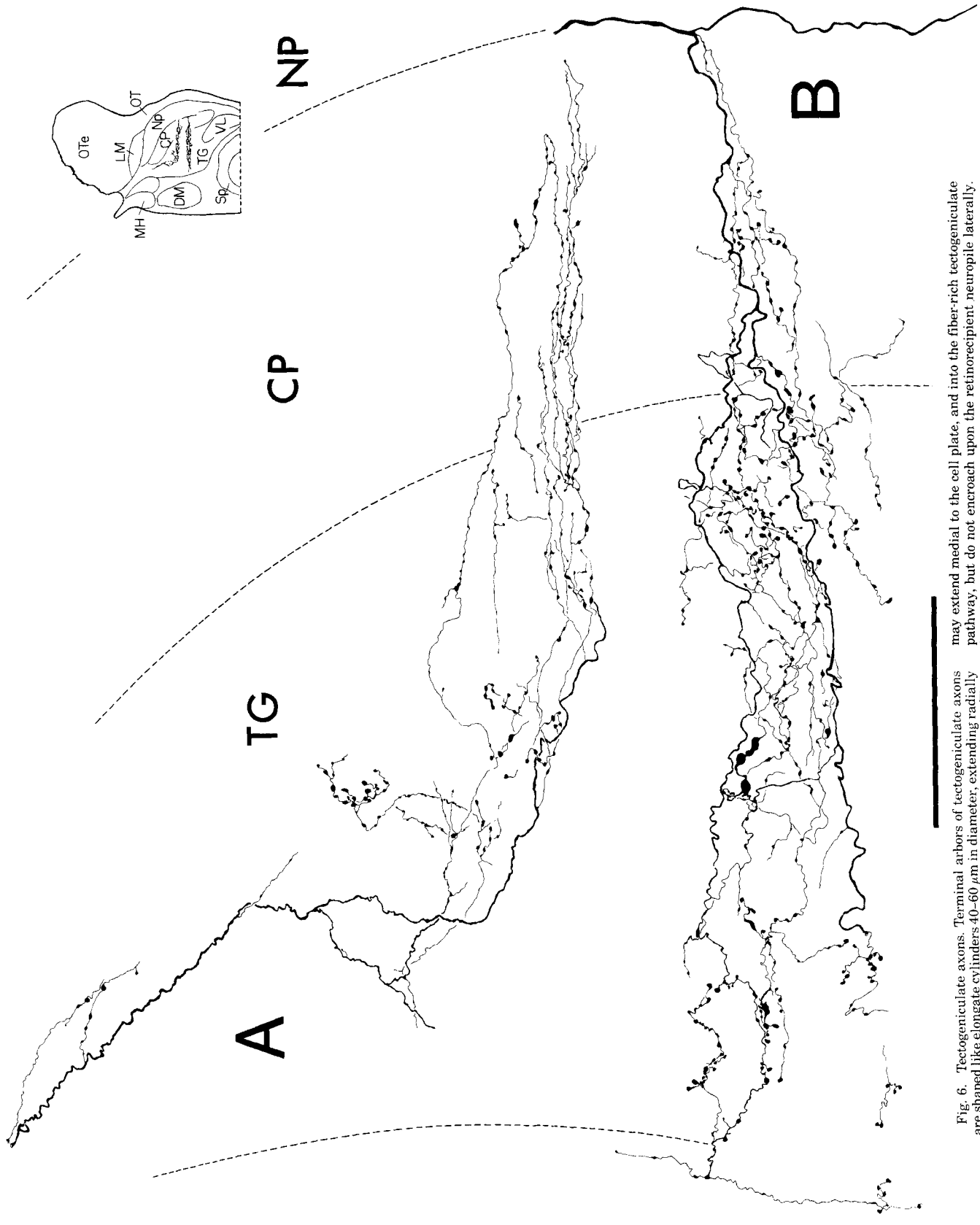


Fig. 6. Tectogeniculate axons. Terminal arbors of tectogeniculate axons are shaped like elongate cylinders 40–60 μm in diameter, extending radially across the cell plate of the ventral lateral geniculate nucleus (VGNcp). They may extend medial to the cell plate, and into the fiber-rich tectogeniculate pathway, but do not encroach upon the retinorecipient neuropile laterally. Scale bar = 50 μm.

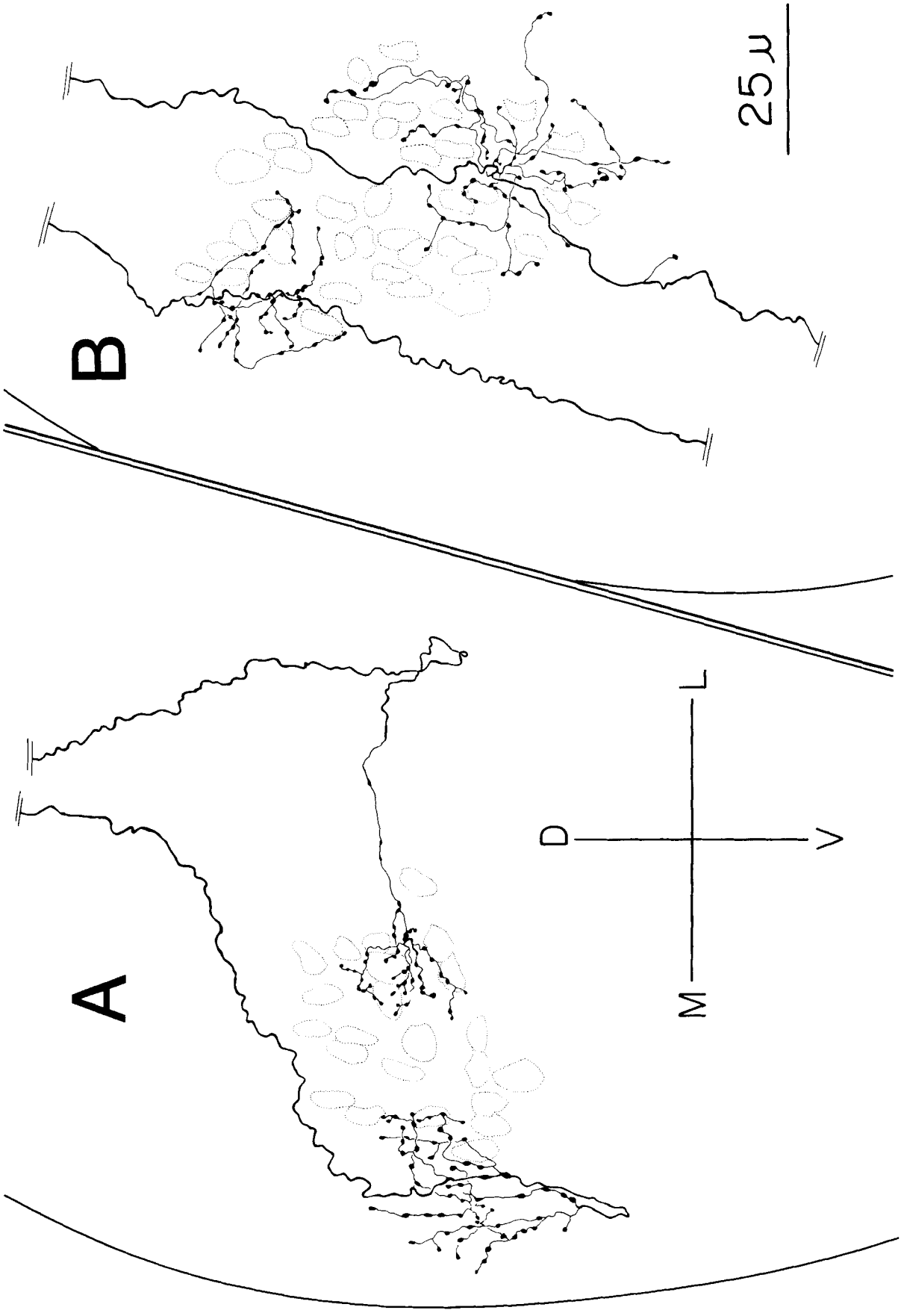


Fig. 7. Tectoisthmi axons. Fine-caliber axons descend vertically into the nucleus isthmi and terminate in extremely small, spherical arbors 10–30 μm in diameter (A) or course through the nucleus giving rise to a similarly shaped arbor (B). The somata of a few counterstained isthmi cells are outlined by the dotted lines.

single oval zone, and are similar in size, shape, and branching pattern to those formed by tectoisthmi axons (compare Fig. 7A,B). A reconstructed tectoisthmobulbar axon is shown in Figure 8. Three primary collaterals arise in nucleus isthmi to form an oval arbor approximately 25 μm in diameter (Fig. 8b). The parent axon descends ventrolaterally close to the surface of the brainstem within the fine-caliber component of the ventral tectothalamic tract (Fig. 8d–i). Single thin collaterals arise from the axon at regular intervals of 20–100 μm. These collaterals are infrequently branched and bear few terminal boutons. They may be short, extending as little as 10–30 μm from the parent axon, or longer (100–200 μm), travelling rostrally or caudally, parallel and close to the parent axon. The terminal zone occupied by a single axon forms a narrow, ventrocaudally aligned strip that remains within 30 μm of the parent axon. Boutons are sparsely distributed within this zone. Thus, terminals of a single tectoisthmobulbar axon occupy only a minute fraction of the total terminal field of the fine-caliber ventral tectobulbar path (Fig. 3), but small injections disclosed no topographic arrangement of these axons: each injection labeled a small number of axons and terminals throughout the pathway.

Ipsilateral tectobulbar axons. These axons make up the dorsal, medium-caliber component of the ventral tectobulbar pathway. An example of a single reconstructed tectobulbar axon is shown in Figure 9A–C. The parent axon (approximately 2.5 μm in diameter) emerges from a small HRP injection site located at a midtectal level in the central layers. The axon courses laterally in the deep half of the stratum album centrale and turns medially to descend into the midbrain tegmentum (Fig. 9A, a). A series of thick collaterals is given off as the axon courses ventromedially and caudally through the nucleus lateralis profundus mesencephali. These collaterals arise at intervals of 60–100 μm and fan out into the nucleus, bifurcating into secondary collaterals that give off fine, tertiary collaterals with terminal boutons. The terminal collaterals branch in all directions within the nucleus and bear short branchlets and few boutons along their lengths. The overall effect is a widespread but patchy distribution of a large number of boutons throughout the nucleus. The terminal pattern displayed by a single axon thus matches that for the terminal field as a whole, but is less dense.

As the axon continues caudally (Fig. 9B, arrow in section e), a collateral arises, bifurcates, and recurves to ascend back into the profundus terminal zone (Fig. 9B, c,d). Other axons contribute terminal collaterals to the reticularis superioris pars lateralis. Their morphology is similar to that of their sister collaterals in the midbrain, but their spatial organization differs. As the parent axon courses caudally through the pontine and medullary tegmentum (Fig. 9B,C, sections g–m) it gives off single fine-caliber collaterals at intervals of 40–200 μm. These branch infrequently and bear a sparse, patchy distribution of boutons. The boutons appear in small clusters along terminal collaterals. Most of the tectobulbar collaterals remain within 100–150 μm of the parent axon, so terminals from a single axon in the pons and medulla occupy a rostrocaudally aligned cylinder within the total terminal field.

In a few axons, a collateral ascends dorsolaterally to the spinal trigeminal nucleus forming a spatially restricted arbor (Fig. 3 d,e). Some collaterals from tectobulbar axons extend laterally across the tegmentum and cross the midline below the predorsal bundle (Fig. 3b).

Crossed tectobulbar axons. These axons show a terminal organization similar to that of the ipsilateral tectobulbar axons. They include the largest-caliber efferent axons (2.5–3.4 μm in diameter) and have the most widespread distribution in the brainstem. An example of a reconstructed large-caliber crossed tectobulbar axon is shown in Figure 10A–G. The parent axon emerges from a injection site in the stratum album centrale and courses ventromedially along the periaqueductal gray in the dorsal tectobulbar tract. Three thick collaterals radiate laterally into the nucleus lateralis profundus mesencephali, overlapping the terminal zone of the ipsilateral tectobulbar axons (Fig. 10A, a–c). Like ipsilateral collaterals, crossed collaterals have a widespread distribution in nucleus lateralis profundus. Secondary and tertiary collaterals form patchy bouton clusters in the terminal zone. The terminal zone of this axon does not have as great a rostrocaudal extent as does the tectobulbar axon shown in Figure 9 (being restricted to a 200-μm-wide slab), but other axons had more widespread distributions in profundus. Thus, the projection from crossed tectobulbar axons to ipsilateral profundus converges with that from the ipsilateral axons and has a similar spatial organization.

As a parent axon continues ventrocaudally it gives off two collaterals in the vicinity of the ipsilateral oculomotor nucleus (Fig. 10B, d) before turning medially and crossing the midline. These collaterals do not enter the motor nucleus but terminate in sparsely branched arbors around the nucleus within the medial longitudinal fasciculus. At the point where the axon crosses the midline and enters the predorsal bundle it begins to issue a series of collaterals that radiate laterally into the deep midbrain and pontine tegmentum (Fig. 10c–g). These collaterals appear to become myelinated shortly after arising from the parent axon and may course over 500 μm laterally into the tegmentum. They give rise to short secondary branches that generate small clusters of boutons. The collaterals are closely spaced along the parent axon (40–100 μm) so that terminals are present in every 80-μm serial section and there are no terminal-free gaps along the rostrocaudal axis of the tegmentum. The terminal zone occupied by the predorsal segment of a crossed tectobulbar axon thus matches the terminal field established by the entire predorsal projection. This zone is a rostrocaudally aligned cylinder that extends from the midbrain to the medullary tegmentum. Terminal boutons on a single axon are distributed throughout the entire extent of this field, but there are no major concentrations or gaps of boutons in the terminal field even though the bouton distribution is locally very sparse and patchy. The number of boutons contributed by a single axon is a small fraction of the total projection.

The crossed tectobulbar axon illustrated in Figure 10 was not traced beyond the caudal medulla. However, several other crossed tectobulbar axons could be traced to a terminal field in the cervical spinal cord. An example of such an axon is shown in Figure 11. The parent axon ascends from the predorsal bundle and forms a small terminal arbor in the intermediate gray of the spinal cord. The arbor shows a relatively dense cluster of boutons in a horizontally elongate patch just dorsal to the motoneurons.

DISCUSSION

Studies in representatives of each vertebrate class show that all vertebrates possess the same general sets of ascending tectothalamic and descending tectoreticular pathways

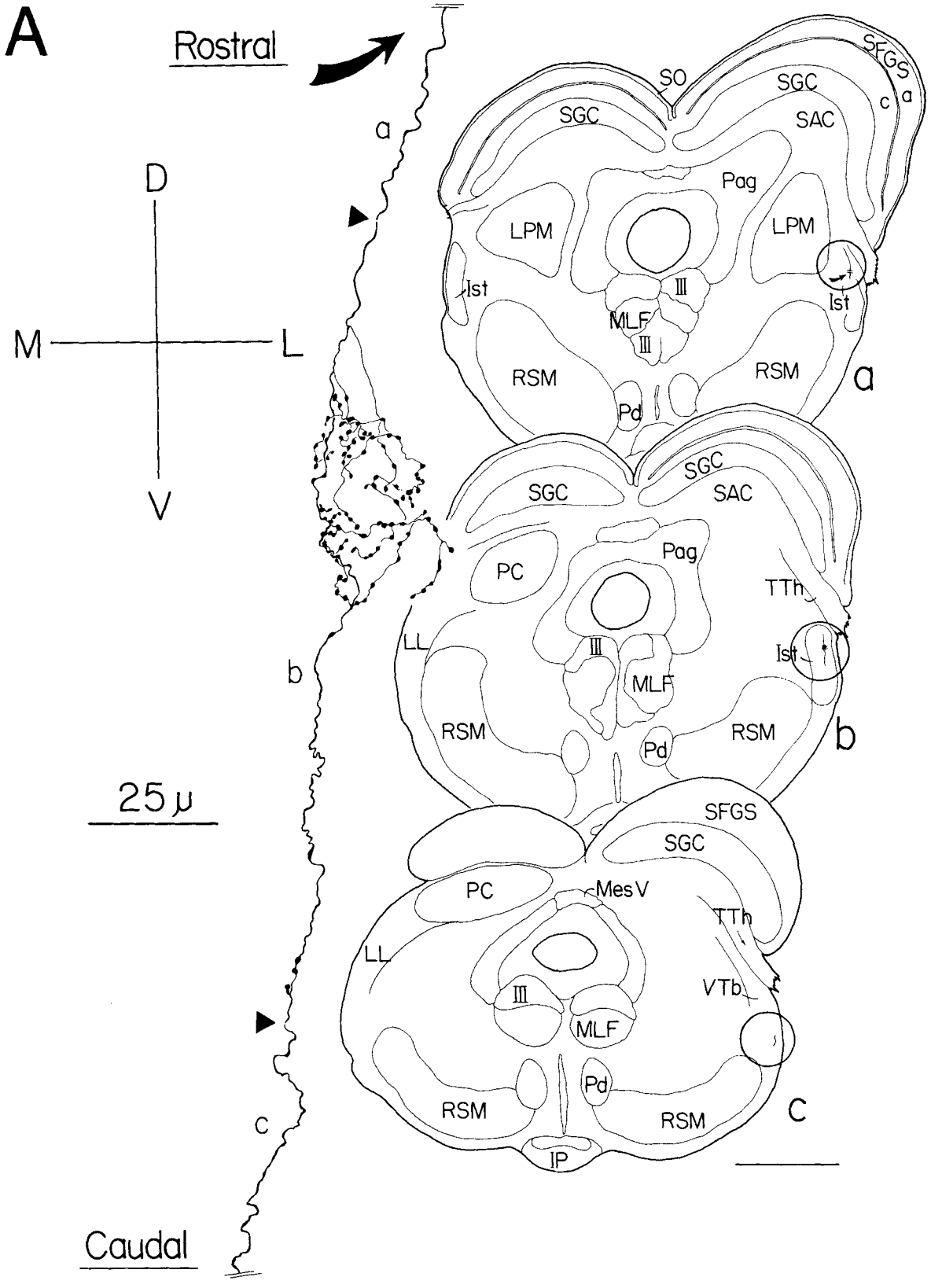
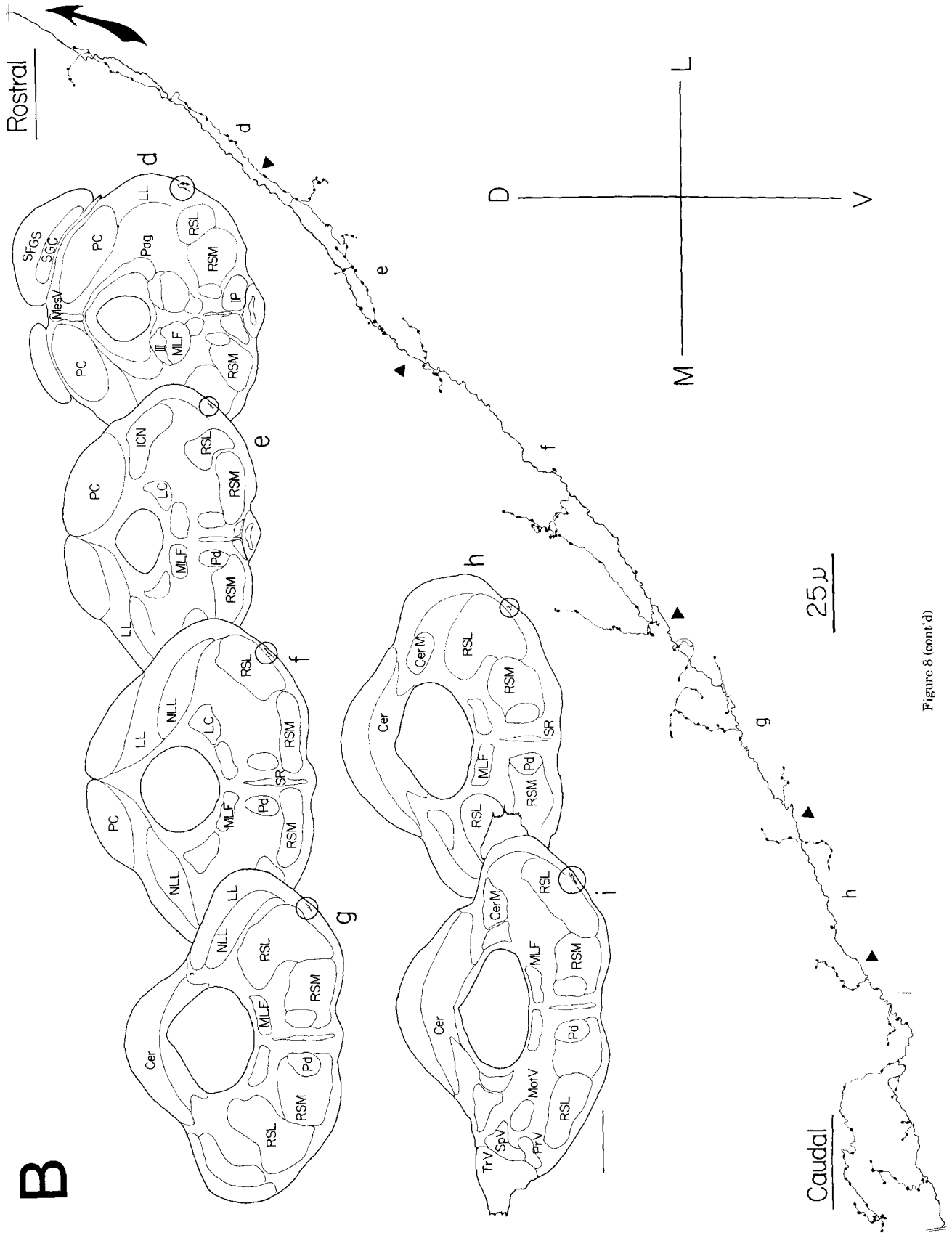


Fig. 8. Tectoisthmobulbar axon. The axon shown in A and B was reconstructed through nine 80-μm-thick serial sections from the level of nucleus isthmi (Ist) to the caudal pons. The axon segments are marked by the small triangles and the letters for each segment correspond to the letters on the sections. The circled areas mark the position of the axon. The arrows indicate the appearance of the axon in section a and section d. A. It forms a single collateral terminal arbor in the nucleus isthmi (b; see also B in Fig. 7). B. It then courses caudally through the pontine tegmentum along the ventrolateral surface of the brainstem in the fine-caliber component of the ventral tectobulbar pathway (VTB, Fig. 3) issuing a series of short, infrequently branched terminal collaterals that remain in the vicinity of the parent axon. Scale bars for lowercase-lettered sections = 500 μm.



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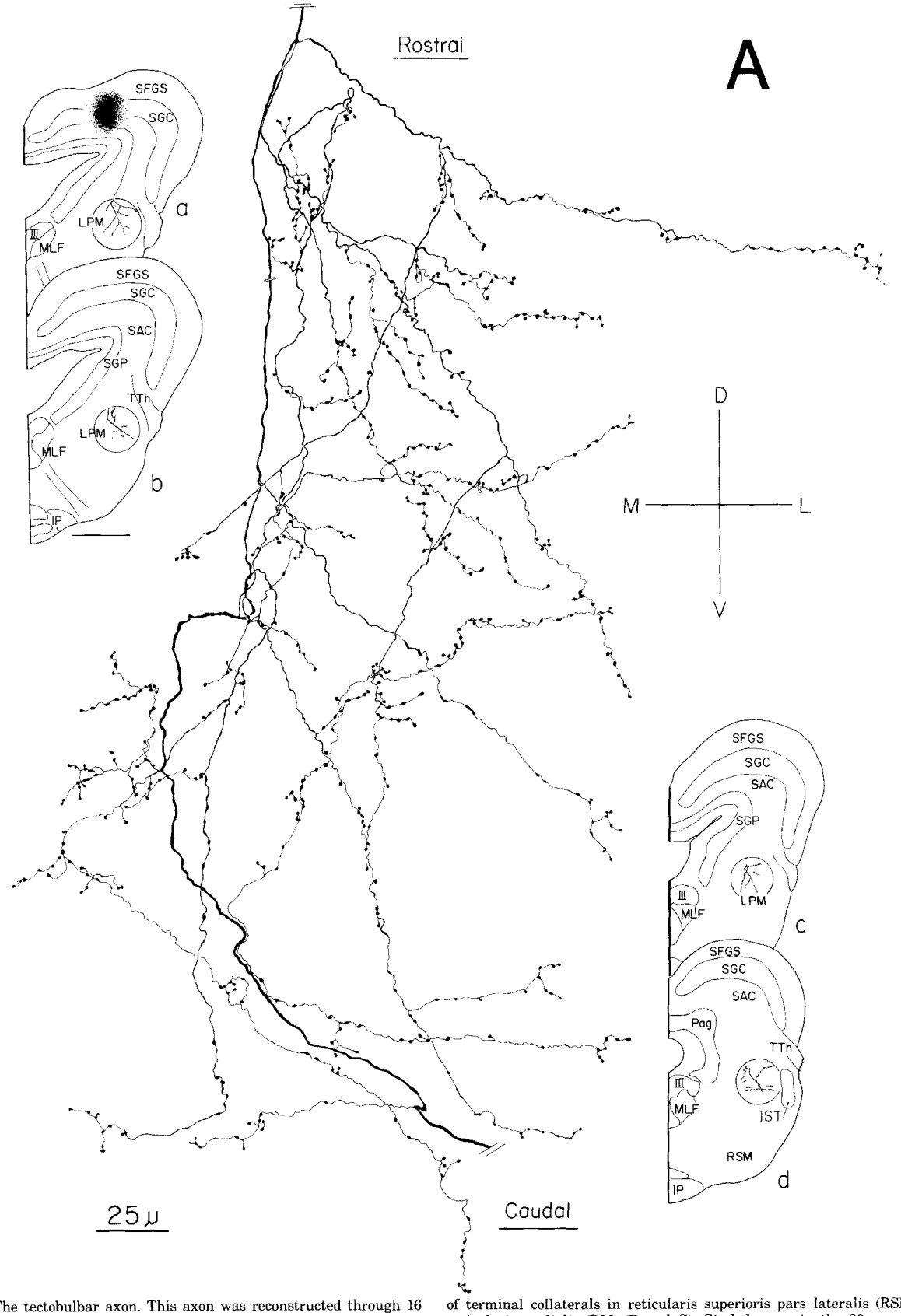
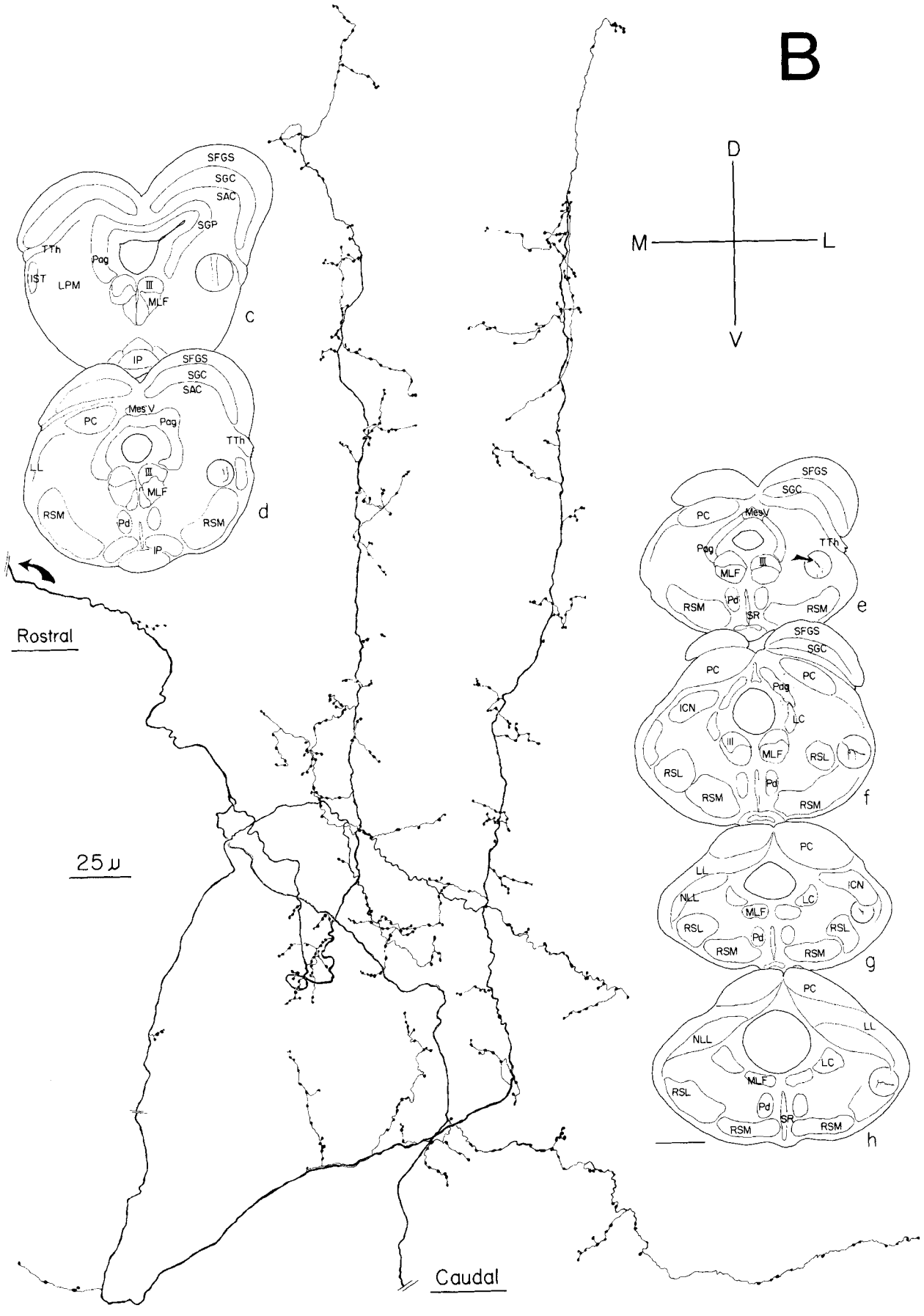


Fig. 9. The tectobulbar axon. This axon was reconstructed through 16 serial sections from the HRP injection site in the tectum (a) to the middle of the medulla (m). It issues several thick primary collaterals in nucleus lateralis profundus mesencephali (A). Terminal arbors radiate through much of the mediolateral and rostrocaudal extent of the nucleus. The axon descends through the pontine and medullary reticular fields issuing a series of terminal collaterals in reticularis superioris pars lateralis (RSL) and reticularis medialis (RM) (B and C). Circled areas in the 80-μm coronal sections show the portion of the axon as it descends through the brainstem. The arrows in B and C indicate the location of the axon in sections e and i respectively. Scale bars for lowercase-lettered sections = 500 μm.



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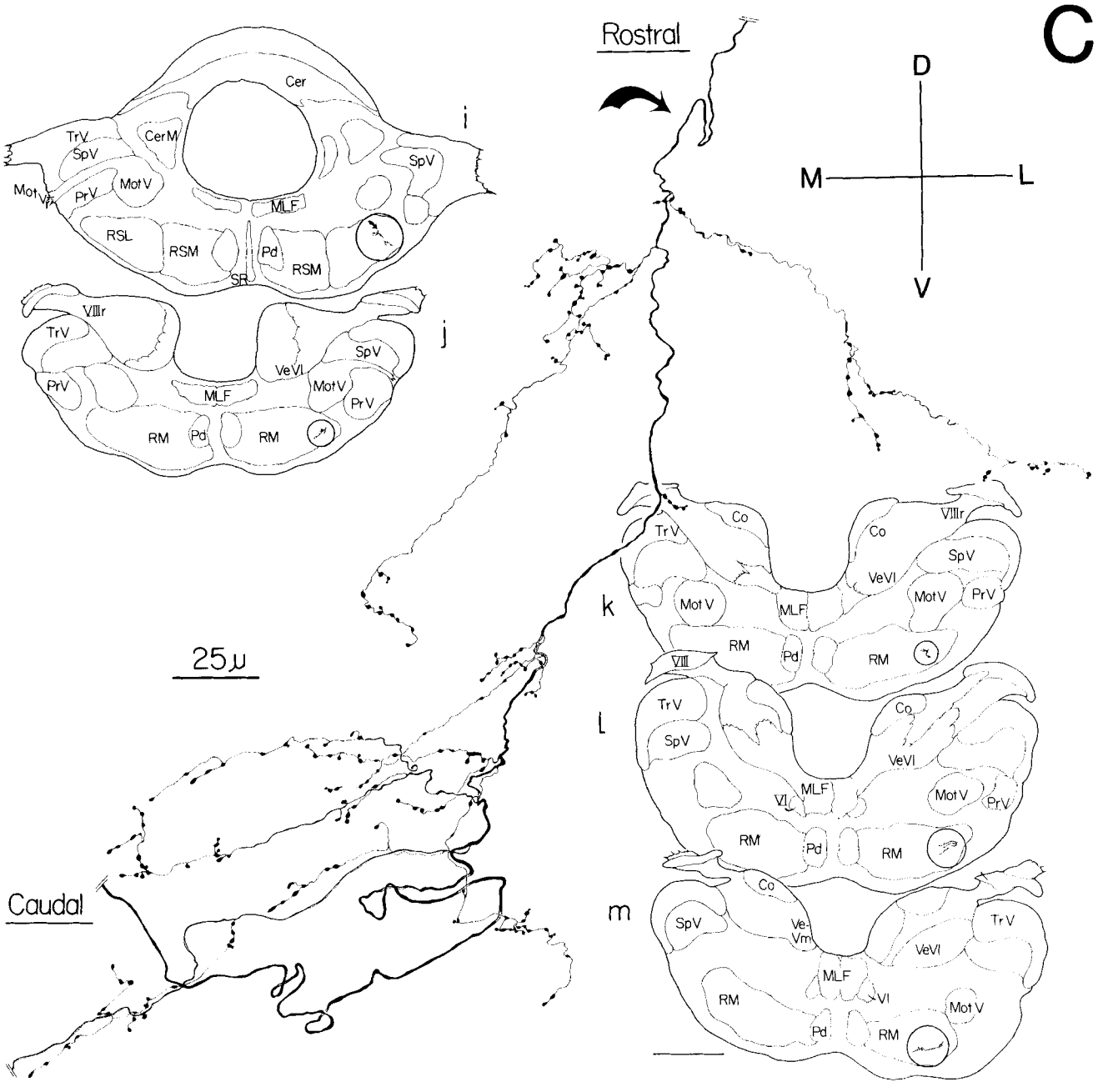

Figure 9 (cont'd)

(Ebbesson, '84; Huerta and Harting, '84; Hunt and Brecha, '84; Lazar, '84; Northcutt, '84; Vanegas et al., '84). The present results have extended our knowledge with a description of the morphology of axons contained in these pathways, permitting a discussion of their function that considers the geometry or spatial distribution of their terminal arbors. Perhaps the most interesting general result is that while some of the axons—such as those involved in the tectogeniculate and tectoisthmi projections—show the spatially restricted terminal arbors characteristic of point-to-point or topographic connections that have been demonstrated in other species (e.g., Crossland and Uchwat, '79; Grobstein et al., '78; Gruberg and Udin, '78), other axons show a widespread or spatially distributed morphology whose significance is less clear. Hypotheses about the func-

Fig. 10. The crossed tectobulbar axon. This large-caliber axon (3 μm in diameter) was reconstructed through 25 serial sections from the rostral midbrain to the caudal medulla. A. The parent axon descends through the midbrain tegmentum in the dorsal tectobulbar tract (DTB) issuing several primary collaterals that radiate throughout the rostral two-thirds of lateralis profundus mesencephali (LPM). B. As the axon approaches the midline at the level of the root of the third cranial nerve (IIIr) it issues two fine-diameter terminal collaterals in the vicinity of the oculomotor nucleus (III) and the medial longitudinal fasciculus (MLF). C. After the axon crosses the midline it begins to issue a series of long primary collaterals that radiate laterally and dorsally into reticularis superioris pars medialis, bearing a sparse and patchy distribution of terminal boutons. D–G. This pattern continues through the pontine and medullary reticular fields resulting in a rostrocaudally elongate cylindrical zone of termination in reticularis medialis and reticularis inferioris pars dorsalis. The overall spatial distribution of the terminal field for this single axon is coextensive with the tectal terminal field of this pathway. Scale bars for lowercase-lettered sections = 500 μm.

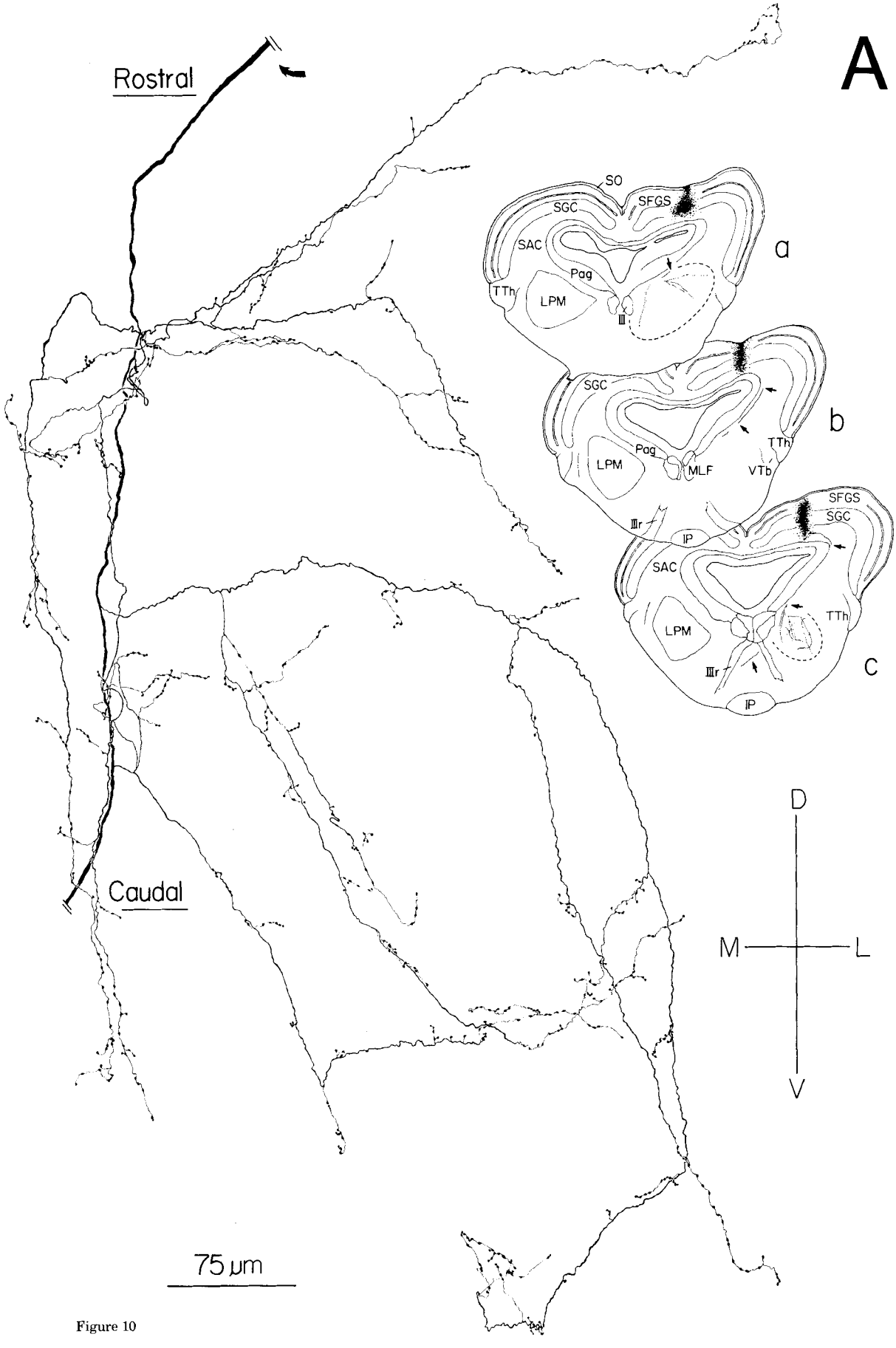
A
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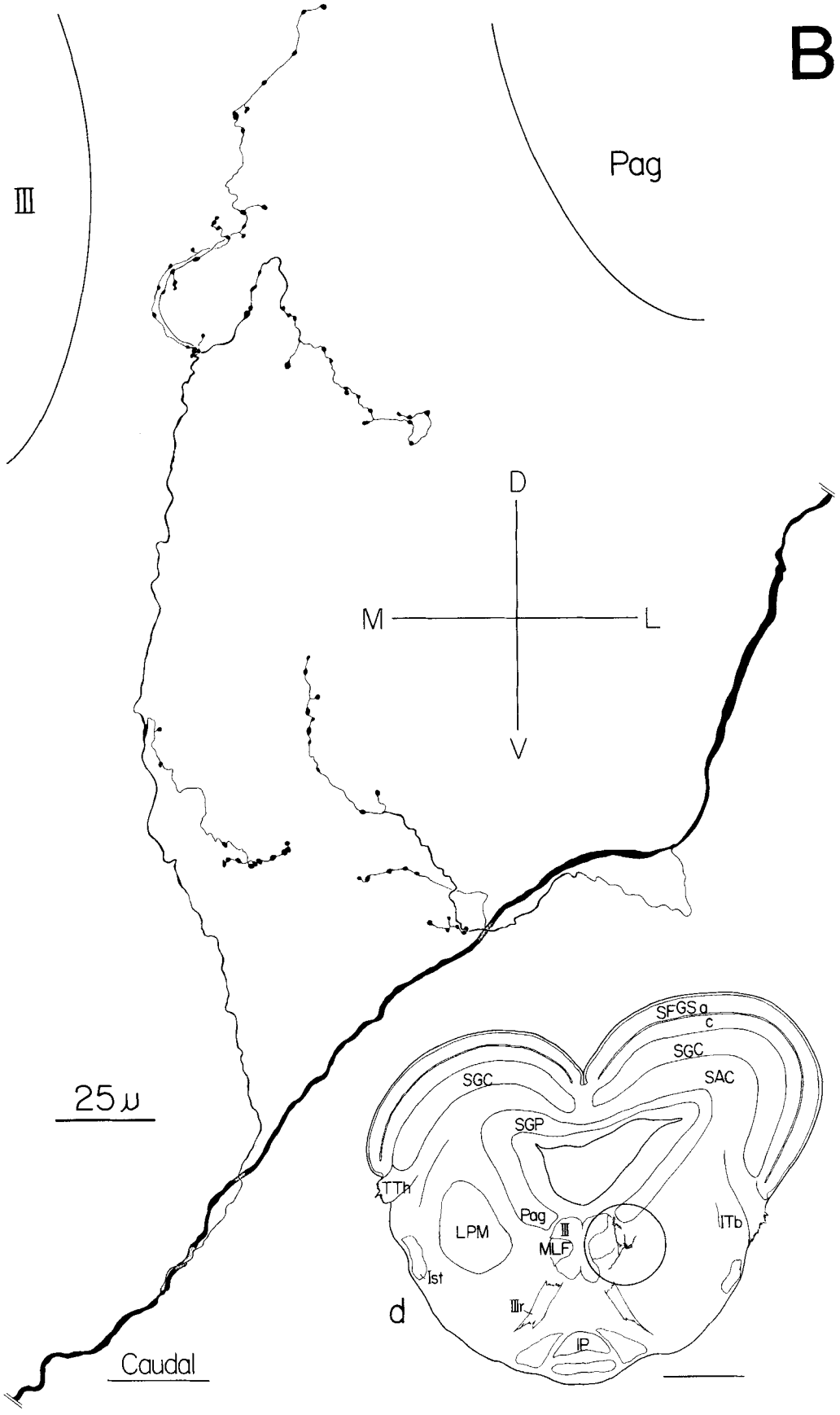
Figure 10



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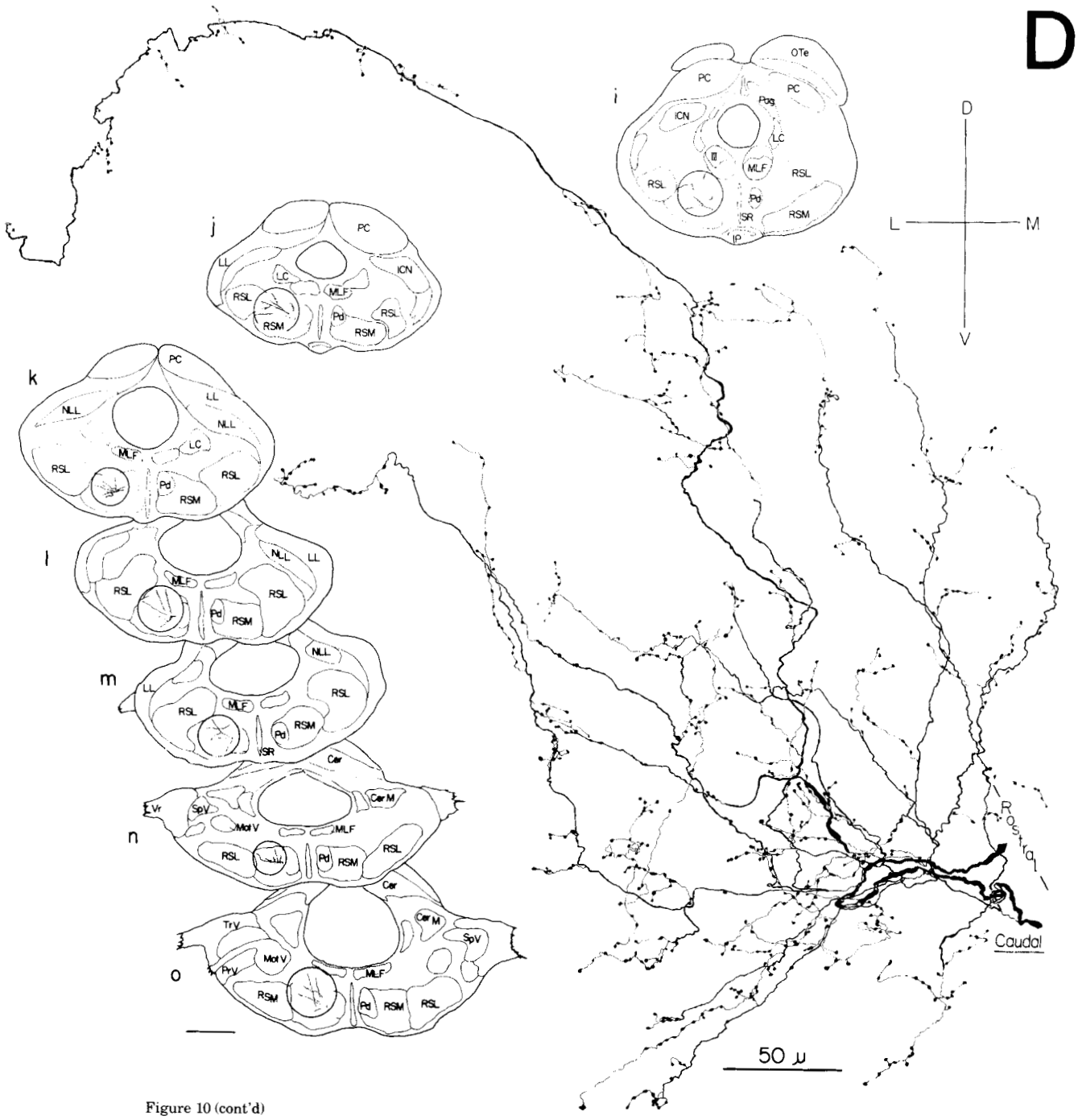
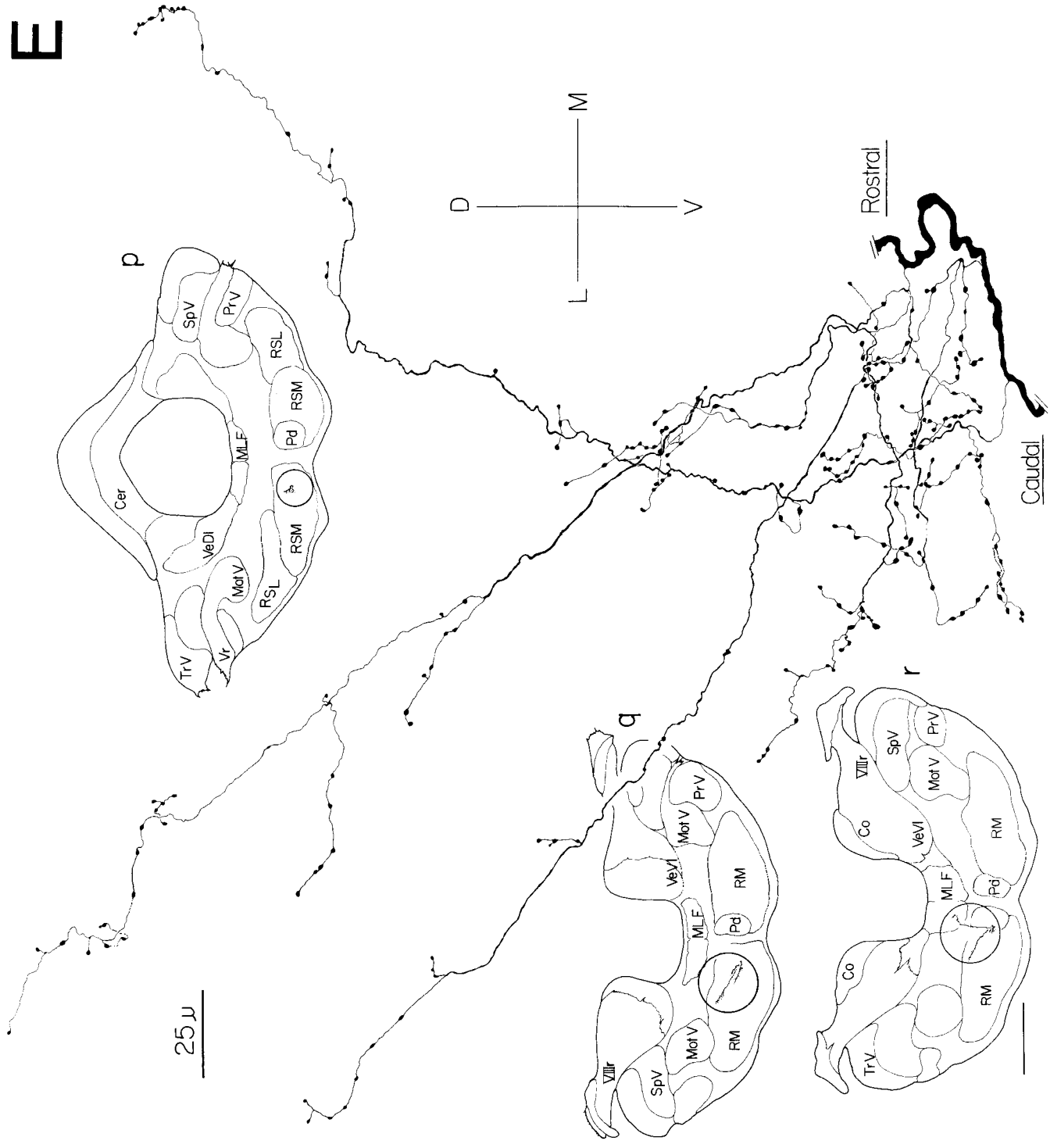


Figure 10 (cont'd)

tional significance of the spatially distributed tectorotundal projection have been considered elsewhere (Dacey and Ulinksi, '83) and will not be discussed further here. This discussion is devoted to an analysis of the spatially distributed organization of the tectoreticular pathways because they are likely to subserve orienting movements.

The organization of the tectoreticular axon systems described here in *Thamnophis* is virtually identical to recent descriptions of these axons in the pond turtle *Pseudemys* (Sereno, '85) and in cats (Grantyn and Grantyn, '82; Grantyn and Berthoz, '85). Such reconstructions of single tectoreticular axons elucidate several important features that may be of functional significance. The first is that tectoreticular axons and their collaterals do not bear an obvious spatial relation to their point of origin in the tectum. Small injections of HRP into various tectal loci fill a small number of tectoreticular axons. These axons do not maintain a constant spatial relation in their course through the reticular formation. Instead, they distribute in a seemingly random way within the brainstem pathway. The distribution of their terminals in any given region in the reticular formation is similar, regardless of the locus of the injection. It may be, then, that no information about tectal locus is encoded in terms of the relative position of single tectal



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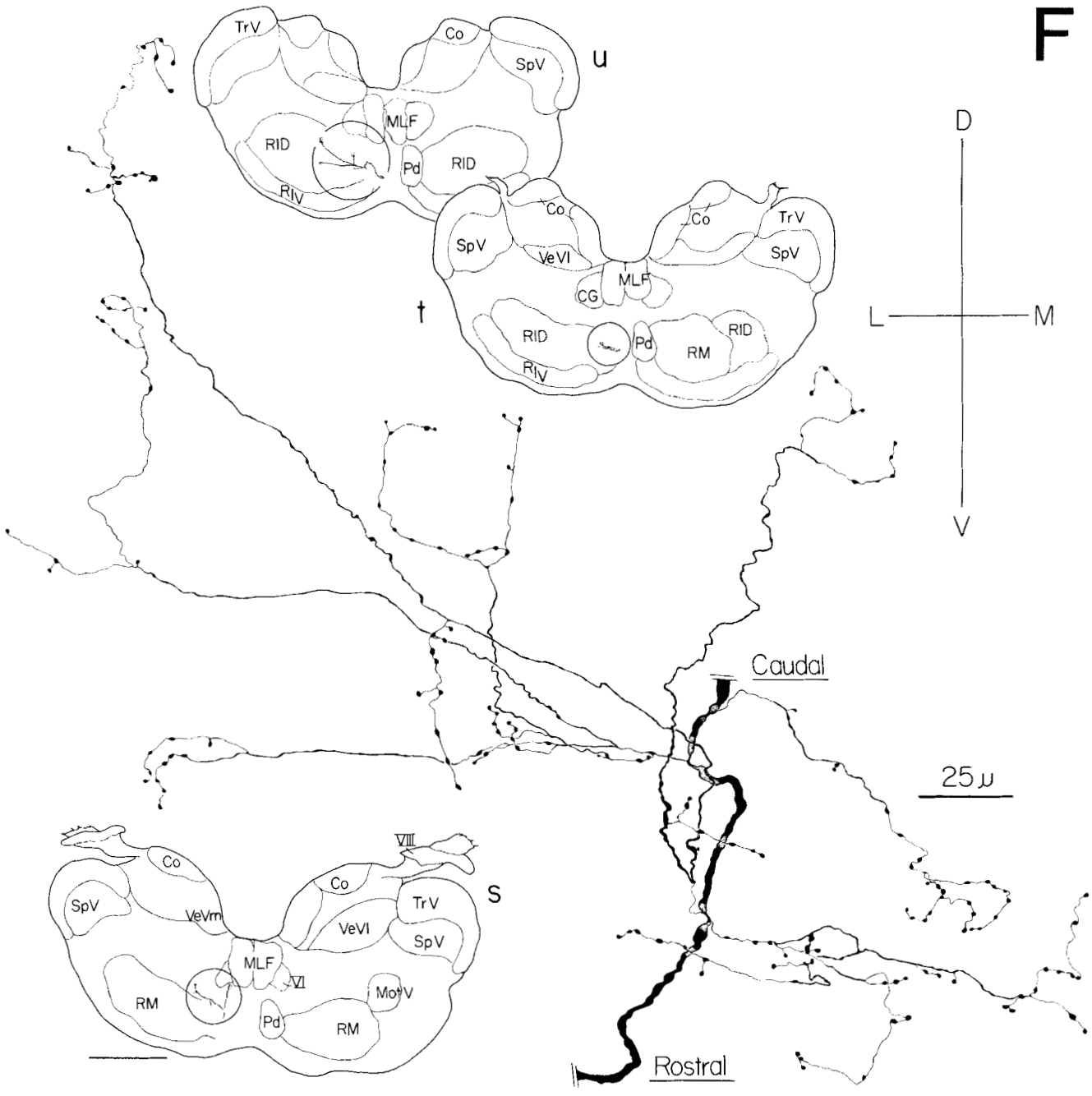

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axons. Said another way, each tectal locus has the same spatial representation in the reticular formation.

A second feature is that the terminal collaterals of single tectoreticular axons have a widespread distribution throughout a given terminal field. For example, collaterals from a single tectobulbar axon in the nucleus lateralis profundus mesencephali (Fig. 9A) are coextensive with the terminal field defined by the entire projection (Fig. 3). Single collaterals radiate with no apparent spatial restriction throughout the terminal zone. All of the axons contributing to a terminal field have widespread and highly overlapping distributions. This pattern differs from the nontopographical tectorotundal system where axons are not distributed according to tectal position, but their terminal fields do maintain a relative spatial topography within nucleus rotundus.

The third feature is that the number of boutons arising from a single axon is large, but their distribution throughout a terminal zone is sparse and patchy. Multiple collaterals from a single axon issue hundreds of terminal boutons within a given terminal zone (e.g., Fig. 10D). However, collaterals typically radiate away from each other with boutons distributed sparsely and in small clusters along their length. The result is that the boutons of a single axon do not show any zone of concentration but are dispersed at low density over a widespread area. This pattern contrasts

Figure 10 (cont'd)

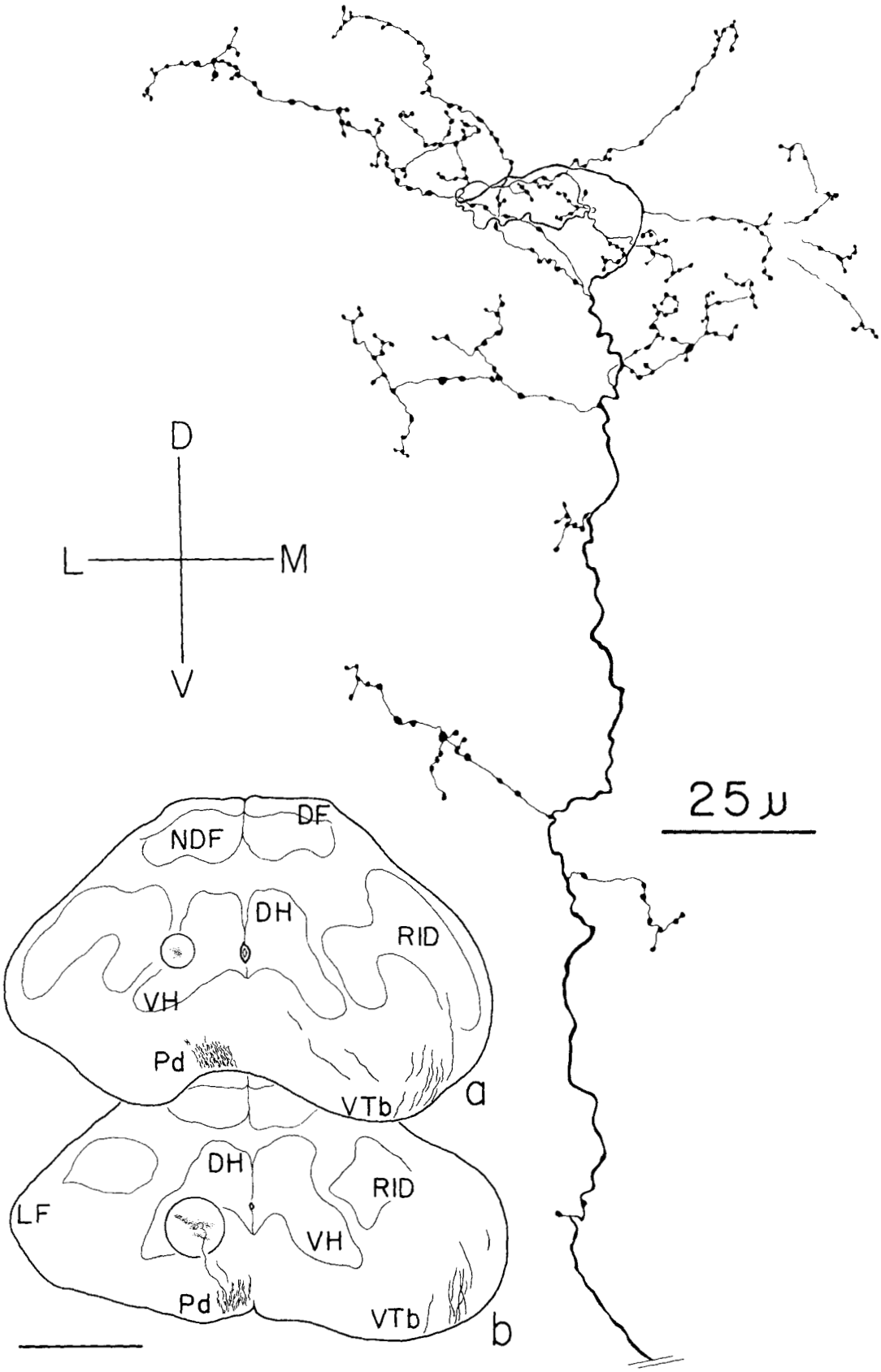

Fig. 11. Tectospinal terminals. Crossed tectobulbar axons were traced to the cervical spinal cord where they ascend vertically from the predorsal bundle to terminate in the ventral horn of the spinal cord. These axons end in a single terminal arbor just dorsal to the region of the motoneuron somata. Scale bar for lowercase-lettered sections = 500 μm.

sharply with the situation in the topographically organized systems, where larger numbers of boutons are concentrated in a small space. Small clusters of tectal terminals were never found apposed to or surrounding somata in the reticular formation, suggesting that synaptic contacts are on dendrites. Reticular neurons are multipolar with long, radiating dendrites (Dacey and Ulinski, '86d; Ramon-Moliner and Nauta, '66). Dendrites from many neurons thus form a highly overlapping meshwork and single reticular neurons receive a convergent input from many tectal axons. Conversely, tectal axons are positioned to have divergent input to a large number of reticular cells. This anatomical pattern is consistent with physiological studies in other species that demonstrate that single reticular neurons are monosynaptically excited from a variety of different stimulating sites in the tectum (Peterson et al., '76; Raybourn and Keller, '77). The sparse distribution of boutons suggests further that the number of contacts made by a single tectal axon on a single reticular cell may be small relative to the total number of boutons.

The final feature of the tectoreticular projection is that the overall density of terminals distributed to terminal fields by single tectoreticular axons can vary. For example, there is a marked variation in the number of collaterals and terminal boutons contributed by different tectobulbar axons to the midbrain tegmentum. This variation appears to be related to axon diameter in that smaller axons have fewer collaterals and terminals than do larger axons. The number of collaterals contributed to a given nucleus appears to vary with the locus of the injection, but too few axons were studied to establish any pattern. A corollary of this feature is that any single axon contributes more or less extensively to different terminal zones. Tectobulbar axons, for instance, sometimes show a heavy bouton distribution in the midbrain tegmentum and a relatively light distribution in the pontine medullary reticular fields; other tectobulbar axons show the converse pattern.

The next paper in this series (Dacey and Ulinski, '86a) continues this analysis of tectal efferent neurons by relating the axon morphology of tectal neurons to the morphology of their parent somata and dendrites.

ACKNOWLEDGMENTS

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