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Nucleus Rotundus in a Snake, *Thamnophis sirtalis*: An Analysis of a Nonretinotopic Projection

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ABSTRACT

Nucleus rotundus, a tectorecipient thalamic nucleus in reptiles and birds, is described for the first time in a snake. The morphology of rotundal neurons and tectorotundal axons was studied at the light microscopic level by using anterograde and retrograde filling with horseradish peroxidase (HRP).

Injections of HRP in the dorsal ventricular ridge retrogradely fill neurons in rotundus. Rotundus is situated centrally in the caudal diencephalon medial to the cell plate of the retinorecipient geniculate complex and ventrolateral to the lentiform thalamic nucleus. The dendrites of rotundal neurons are long and radiate, but are confined within the cytoarchitectonically defined borders of the nucleus. Injections of HRP into the optic tectum anterogradely fill axons that project to rotundus bilaterally via the tectothalamic tract. Small injections show that axons arising from a single tectal locus distribute to all sectors of rotundus. Thus, this projection may not be retinotopically organized. However, single axons reconstructed through serial sections form spatially restricted, sheetlike terminal fields that pass caudorostrally through the entire extent of rotundus.

Several hypotheses on the functional significance of such organized but nonretinotopic visual projections are discussed.

Key words: nucleus rotundus, snake, thalamus

A major feature of visual system organization in reptiles and birds is the presence of a massive, bilateral projection from the optic tectum to nucleus rotundus. Rotundus is a large, dorsal thalamic cell group (Karten and Revzin, '66; Hall and Ebner, '70a; Butler and Northcutt, '71; Braford, '72; Foster and Hall, '75; Ebbesson, '81) that in turn projects to a subdivision of the dorsal ventricular ridge in the telencephalon (Hall and Ebner, '70b; Karten and Hodos, '70; Pritz, '75; Lohman and van Woerden-Verkley, '78; Balaban and Ulinski, '81a,b).

A striking feature of the tectorotundal projection is that it is not retinotopically organized. Restricted lesions of the tectum produce degeneration scattered bilaterally throughout rotundus (Butler, '78; Rainey and Ulinski, '82b). Similarly, restricted injections of tritiated amino acids in the tectum result in widespread labeling in rotundus (Hunt and Künzle, '76). Visualization of the tectorotundal axons with horseradish peroxidase (HRP) reveals that individual axons have a widespread distribution in rotundus (Rainey and Ulinski, '82b). Conversely, focal injections of HRP in rotundus retrogradely label neurons throughout the mediolateral and rostrocaudal extents of the tectal central gray (Benowitz and Karten, '76). Consistent with these anatomical findings, rotundal units have large receptive fields that may extend over the entire visual field (reviews: Revzin, '79; Maxwell and Granda, '79). Visual system projections that lack a retinotopic organization have also been noted in the mammalian thalamus and telencephalon (Spring and Rosenquist, '80; Bruce et al., '81; Gross et al., '81). The anatomical and physiological organization of such systems is unclear, but their existence may introduce an important factor in the formation of general concepts of visual system organization.

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Although rotundus is an obvious landmark in the dorsal thalamus of most reptiles and birds, its status in snakes has been problematic. There has been no agreement on the position of rotundus in Nissl material (Warner, '46; Senn and Northcutt, '73; Halpern and Frumin, '73; Repérant, '73; Northcutt and Butler, '74; Molenaar and Fizaan-Oostveen, '80). Experimental degeneration studies (Ulinski, '77; Schroeder, '81) show a major tectal projection to the large geniculate complex, but have not clearly demonstrated a tectorotundal system. This has led to the suggestion that rotundus may be poorly developed in snakes (Northcutt and Butler, '74; Schroeder, '81). Alternatively, Ebbesson ('72, '80) has speculated that the geniculate complex in snakes represents a fusion of tectal and retinal recipient components.

This paper resolves the question of rotundal identity in snakes by using horseradish peroxidase tracing techniques to demonstrate nucleus rotundus in the eastern garter snale, *Thamnophis sirtalis*. It is also shown that – as in other reptiles and birds – the tectorotundal projection is nonretinotopically organized. The use of solid HRP filling to describe rotundal cells and reconstruct single tectorotundal axons also demonstrates a clear spatial pattern in the projection. The Discussion considers some hypotheses about the functional significance of such ordered but nonretinotopic projections.

MATERIALS AND METHODS

Forty garter snakes, *Thamnophis sirtalis*, were used. Animals received HRP injections into either the optic tectum (25 animals), the dorsal ventricular ridge (three animals), the cerebral peduncles at the level of the anterior commissure (ten animals), or the cerebral cortex (two animals). All injections were made iontophoretically (Graybiel and Devor, '74). A concentrated solution of Sigma type VI HRP in pH 8.6 TRIS buffer was injected via a glass micropipette (30-μm tip) by passing 1-5 μamp positive current for 1-5 minutes. After a 3-day survival, each animal was perfused through the heart with a phosphate-buffered solution of 1% paraformaldehyde and 3% glutaraldehyde. Brains were stored overnight in 30% sucrose and cut frozen at 40 or 100 μm. Sections were processed immediately according to the cobalt-enhanced diaminobenzidine (DAB) protocol of Adams ('77). Ortho- and retrogradely labeled elements were often solid filled with the DAB reaction product so the same material could be used for tracing rotundal pathways and for describing the morphology of rotundal cells and tectal axons.

Nissl material was derived from brains embedded in celloidon, cut at 16 μm in the coronal plane, and stained with cresyl violet.

RESULTS

The results will be presented in three stages. First, rotundus is identified by comparing anterograde labeling of axons after large tectal injections to the pattern of retrograde cell labeling after telencephalic injections. These two experiments clearly define a tectorotundal terminal field that precisely overlaps a circumscribed population of neurons projecting to the dorsal ventricular ridge. Second, small tectal injections are used to determine the spatial organization of tectal axons in rotundus. Finally, the Golgi-like filling of tectorotundal axons is used to clarify the organization of the tectorotundal projection.

Identification of nucleus rotundus

The tectorotundal pathway. Figure 1 shows the results of anterograde transport in the tectothalamic tract after a

Abbreviations

ADVR	Anterior dorsal ventricular ridge
AOT	Accessory olfactory tract
DC	Dorsal cortex
DH	Dorsal hypothalamus
DM	Dorsomedial nucleus
DTB	Dorsal tectobulbar tract
DVR	Dorsal ventricular ridge
GP	Geniculate pretectal nucleus
HC	Habenular commissure
HP	Habenulopeduncular tract (fasciculus retroflexus)
IP	Interpeduncular nucleus
LC	Lateral cortex
LFB	Lateral forebrain bundle
LH	Lateral habenula
LM	Mesencephalic lentiform nucleus
LOT	Lateral olfactory tract
LPM	Nucleus lateralis profundus mesencephali
LT	Thalamic lentiform nucleus
MC	Medial cortex
ME	Median eminence
MFB	Medial forebrain bundle
MH	Medial habenula
MLF	Medial longitudinal fasciculus
MSt	Medial striatal nucleus
MTTh	Medial tectothalamic tract
NTTh	Nucleus of the medial tectothalamic tract
NVSoD	Nucleus of the ventral supraoptic decussation
OT	Optic tract
PaG	Periaqueductal gray
PC	Posterior commissure
Pd	Posterodorsal nucleus
Pf	Perifascicular complex
Pt	Pretectal nucleus
PVH	Periventricular hypothalamus
Re	Nucleus reuniens
Ro	Nucleus rotundus
RSL	Reticularis superioris lateralis
SE	Septum
Sp	Suprapeduncular nucleus
TG	Tectogeniculate pathway
TTh	Tectothalamic tract
TThx	Crossed tectothalamic tract
VGNcp	Ventral geniculate nucleus, cell plate
VGNnp	Ventral geniculate nucleus, neuropil
VH	Ventral hypothalamus
VL	Ventrolateral nucleus
vm	Ventromedial sector of nucleus rotundus
VSoD	Ventral supraoptic decussation
VTB	Ventral tectobulbar tract
IIIr	Root of the third cranial nerve

Layers of the optic tectum

SAC	Stratum album centrale
SAP	Stratum album periventriculare
SGFSa,b,c	Stratum fibrosum griseum superficiale, sublaminae a, b, and c
SGC	Stratum griseum centrale
SGP	Stratum griseum periventriculare
SO	Stratum opticum

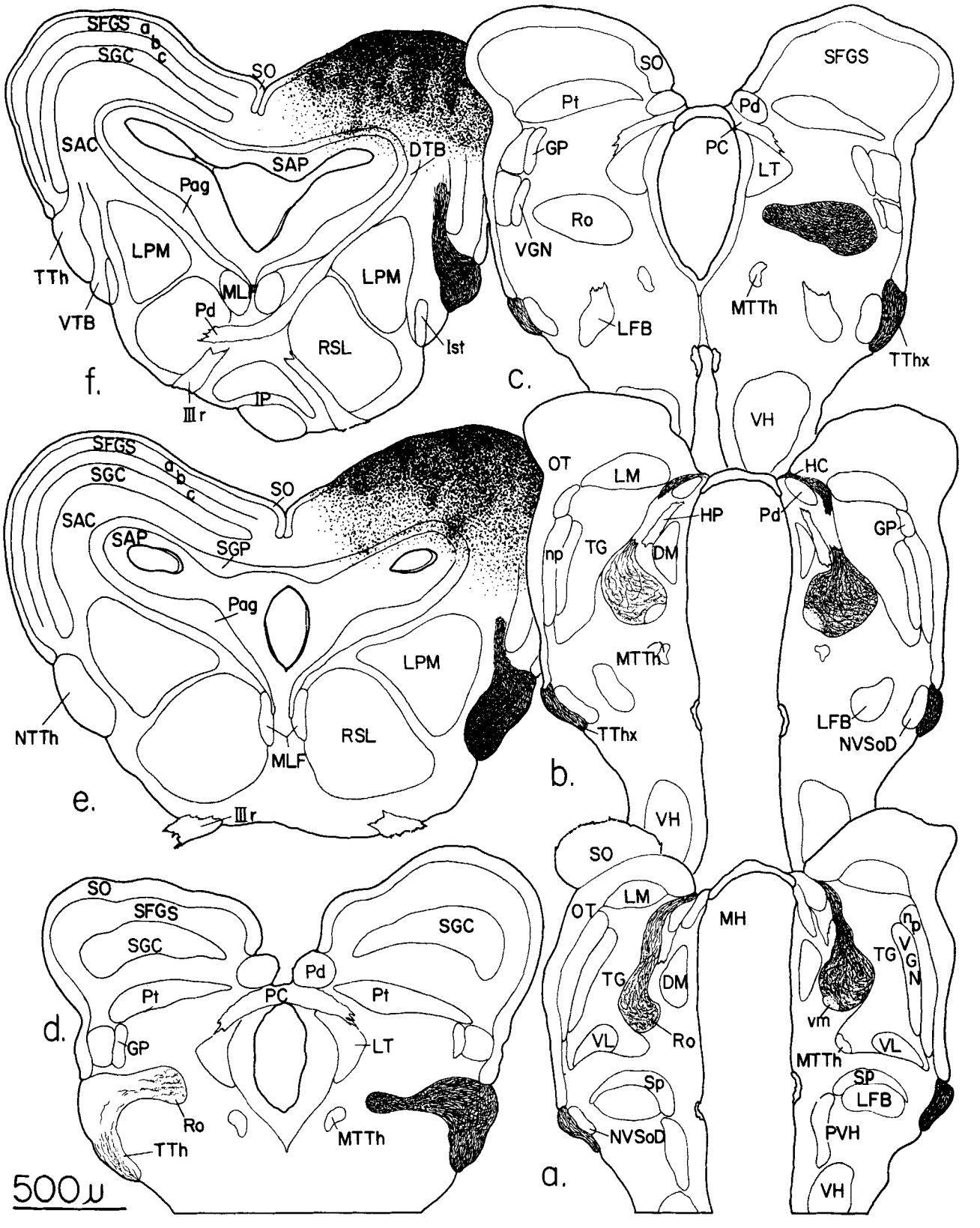


Fig. 1. The tectorotundal pathway. HRP injections into the optic tectum (shown stippled in sections e and f) anterogradely fill tectorotundal axons. Tectal fibers reach rotundus (Ro, sections d–a) ipsilaterally via the habenular commissure and the ventral supraoptic decussation. The point of crossing is rostral to section a and is not shown.

large HRP injection into the superficial and central tectal layers. Solid filled axons can be followed laterally from the injection site, through the central fiber layer of the tectum, and to the ventrolateral margin of the tectum. They gather in the tectothalamic tract, a distinct bundle that forms a prominent bulge on the lateral surface of the midbrain (Fig. 1). Tectothalamic fibers continue forward, just ventral to the optic tract, to caudal pretectal levels where a large contingent of their fibers makes a sharp medial turn caudal and ventral to the cell plate of the retinorecipient geniculate complex (Fig. 1d). A dense meshwork of fine, beaded collaterals forms a large, disc-shaped terminal field ventral to the lentiform thalamic nucleus (LT) and medial to the geniculate cell plate. Labeled fibers turn rostrodorsally and expand into a more spherical field near the border between the lentiform thalamic and dorsomedial nuclei (DM). This terminal field overlaps a well-defined nucleus that is distinguishable in Nissl material by its cell-poor capsule. It is this group of cells that has been identified as nucleus rotundus.

In addition to this direct ipsilateral tectothalamic pathway, there are two distinct crossed projections to rotundus. The first arises at the point where the tectothalamic fibers turn medially to enter the caudal diencephalon (Fig. 1). There, some fibers continue ascending ventral to the optic tract and cross the midline in the ventral supraoptic decussation. Fibers in this crossed tectothalamic pathway (Tthx, Fig. 1) join the ipsilateral tectothalamic tract and enter rotundus at its caudolateral border. There is also a substantial contingent of tectothalamic fibers that does not end at the rostral pole of rotundus, but continues to ascend dorsomedially (Fig. 1). Situated medial to the pretectum, lateral to the dorsomedial nucleus (DM), and ventral to the lateral habenular nucleus, these fibers cross the midline in the habenular commissure to enter rotundus from its rostrodorsal pole. Both crossed pathways distribute a significant, but lighter input that completely overlaps the ipsilateral projection.

The rotundodorsal ventricular ridge pathway. Figure 2 shows the results of a telencephalic injection of HRP. Section a indicates the area of the injection. The fine stippling depicts diffuse reaction product in anterior dorsal ventricular ridge (ADVR) and the lateral forebrain bundle (LFB). The charting shows the labeling of one thalamic nucleus identified as rotundus. Other thalamic groups (e.g., DM) were also labeled in all cases, but are not described here.

Solid filled fibers can be traced from the dorsal ventricular ridge to the lateral forebrain bundle, in which they descend. Fibers leave the forebrain bundle dorsally (Fig. 2e) at rostral pretectal levels. They are situated in a cell-poor area ventral to the dorsomedial nucleus and medial to the geniculate cell plate. The cells of origin of these fibers appear just medial to the rostral pole of the lentiform thalamic nucleus, where they form a spherical mass. Further caudally they flatten into an egg shape (Fig. 2e, LT) until they appear as a thin plate of fusiform cells at the caudal pole of the lentiform thalamic nucleus. The caudal pole of rotundus overlaps the entrance of the tectothalamic tract into the diencephalon (Figs. 2f, 1d), and the dorsoventrally compressed appearance of rotundus at this level is correlated with the lateral to medial orientation of incoming tectorotundal fibers. Rotundus was labeled after all large peduncle injections and after small injections confined to dorsal ventricular ridge. Rotundus was not labeled in two cases in which HRP injections were restricted to cortex.

A comparison of the anterograde and retrograde experiments demonstrates that the nucleus identified as rotundus is the primary recipient of heavy, bilateral input from the tectothalamic tract. It, in turn, projects massively to the dorsal ventricular ridge.

Appearance of rotundus in Nissl material. Figures 3-5 show three transverse sections through the diencephalon of *Thamnophis*. These sections pass through the rostral, middle, and caudal regions of rotundus. Each section is accompanied by a higher-magnification view of rotundus at approximately the same level. Rotundus is present caudally (Fig. 3) at the level of the posterior commissure, just caudal to the conspicuous, nut-shaped nucleus posterodorsalis (Pd) in the pretectum. Dorsal to rotundus is the caudal pole of the wedge-shaped lentiform thalamic nucleus (LT); it is separated from rotundus by a narrow, cell-poor region. Ventrally, rotundus is bounded by a cell-poor area that marks the origin of the lateral forebrain bundle. Laterally, the tectothalamic tract forms a prominent bulge on the surface of the brainstem. Fibers in the tract make a sharp medial turn into the caudolateral pole of rotundus at this level. The caudal region of rotundus is disc-shaped in the horizontal plane and its cells are also flattened in this plane. Rotundus becomes egg-shaped and is encapsulated by a distinct cell-poor zone at intermediate levels (Fig. 4). It is situated medial to the caudal pole of the geniculate cell plate (Gn) and ventral to the mesencephalic lentiform nucleus in the pretectum. Rotundus shifts medially as it extends rostrally to abut on a cell-poor area close to the midline (Fig. 5). It lies dorsomedial to the caudal pole of the dorsal hypothalamus. The rostral pole of rotundus is situated just ventrolateral to the caudal pole of the dorsomedial thalamic nucleus and dorsal to the lateral forebrain bundle and suprapeduncular nucleus (SP).

Rotundal neurons range in shape from spherical to fusiform and in size from medium (20–25 μm in diameter) to small (7–10 μm in diameter). The small cells have scant, lightly stained cytoplasm and their evenly stained nuclei thus stand out against a light background. They can be easily distinguished from glia which have darkly stained, bean-shaped nuclei and no visible cytoplasm. The larger rotundal neurons have more abundant, evenly stained cytoplasm with dispersed Nissl substance.

Neurons of different sizes are preferentially distributed in rotundus. Large, fusiform cells predominate caudally in rotundus where they are sandwiched among the tectal fibers that enter the nucleus from lateral to medial (Fig. 3). They are densely packed and evenly distributed with an average spacing of about 10 μm. Most cells are spherical and smaller further forward as rotundus expands into a large egg shape. Rostrally, there is a distinct, dense aggregation of small, darkly staining cells at the ventromedial pole of rotundus. These cells form a dense whorllike grouping that can be distinguished from the vertically oriented small cells of DM, just dorsal to rotundus (Fig. 8). This region corresponds to an area in which tectal input is largely excluded (Fig. 8). These cells, however, are included in the rotundal capsule and were labeled in the retrograde experiments.

Morphology of rotundal cells. Figure 7B is a photomicrograph of a section through midrotundus retrogradely labeled after an HRP injection into the cerebral peduncle. Many neurons of all sizes are solid filled and almost every neuron within rotundus shows granular or diffuse labeling. Figure 7A is a low-power camera lucida tracing of the more

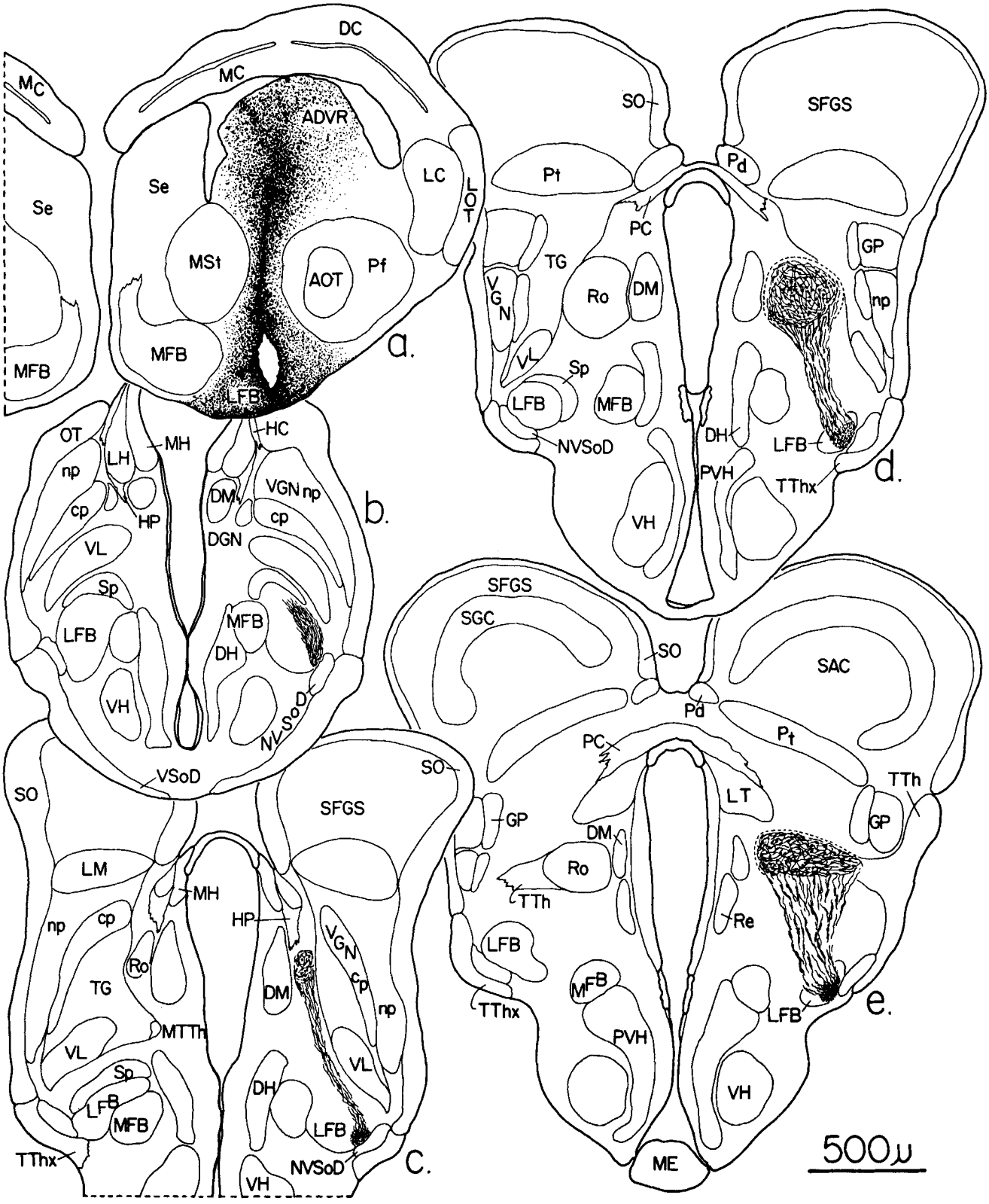
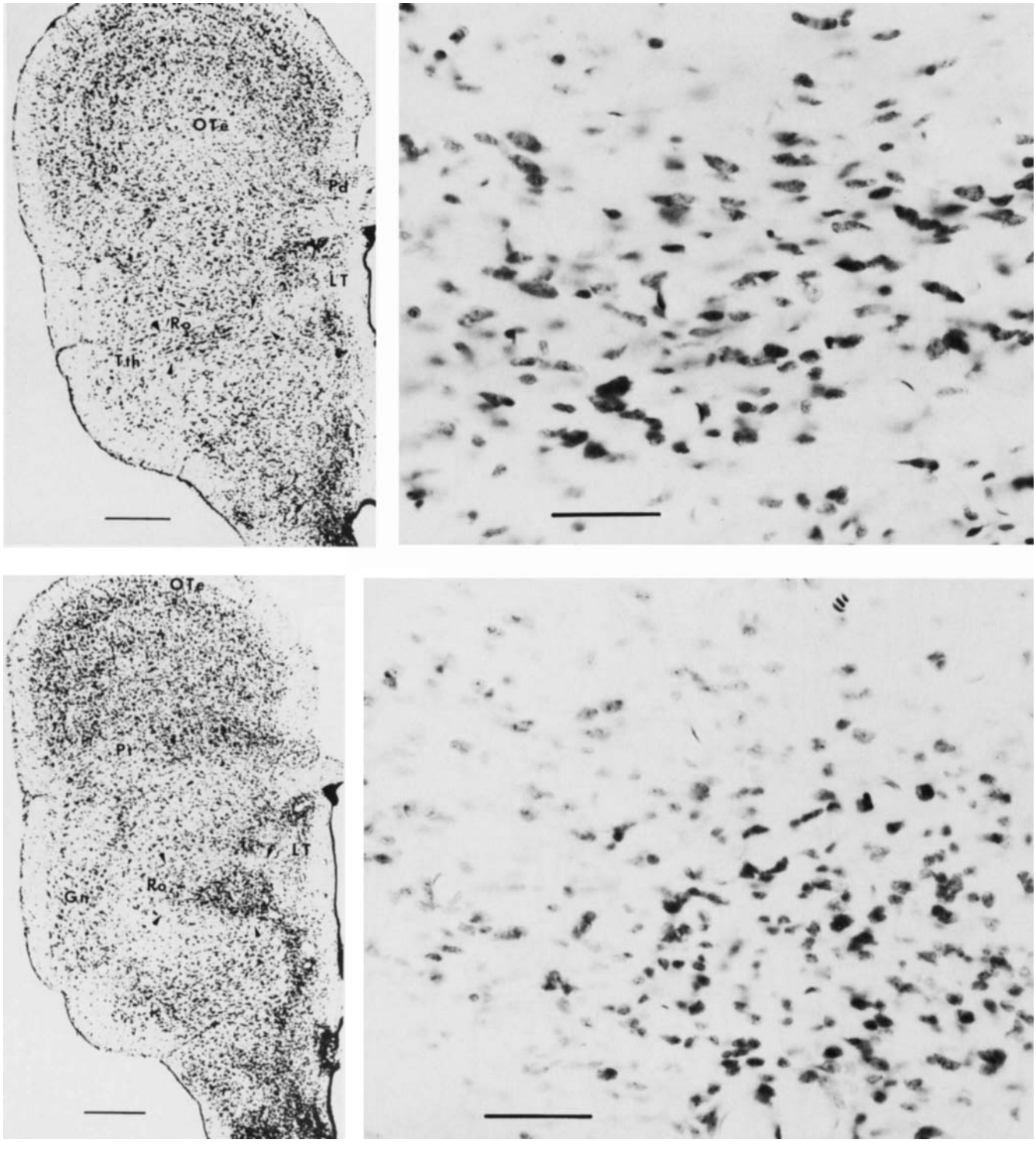


Fig. 2. The rotundo-DVR pathway. HRP injections into dorsal ventricular ridge or lateral forebrain bundle (shown stippled in section a) retrogradely fill rotundal neurons (sections d–e). The caudal pole of rotundus is situated ventrolateral to the lentiform thalamic nucleus (LT). It extends rostrally to the border between LT and the dorsomedial nucleus (DM). Rotundal efferent fibers descend vertically to enter the peduncle of the lateral forebrain bundle.



Figs. 3-5. Cytoarchitecture of nucleus rotundus in *Thamnophis*. The position and appearance of rotundus in Nissl preparations is illustrated in rostral (Fig. 3), middle (Fig. 4), and caudal (Fig. 5) sections through the nucleus at low (scale bar = 1 mm) and high (scale bar = 40 μm) magnifications.

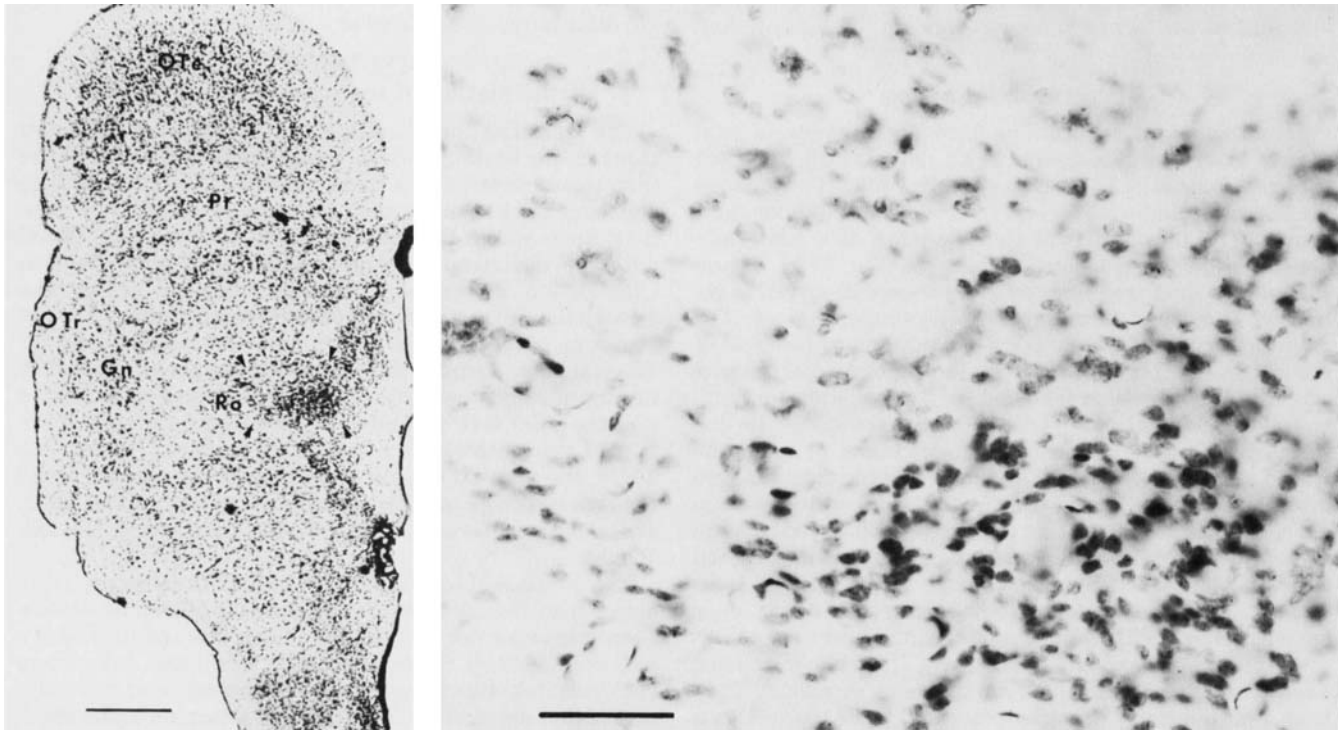


Figure 5

densely filled rotundal cells and their axons at approximately the same level as Figure 6A. Cells near the center of rotundus have long dendrites that radiate in all directions toward the periphery of the nucleus. These dendrites gently curve and follow the oval contours of the nucleus. Peripherally located cells have dendrites that run either directly into the center of the nucleus or along its borders. The effect is a concenric swirl of dendrites that are confined to and define the nuclear borders of rotundus. Many dendrites thus run in the horizontal (mediolateral) plane. The cell-poor region surrounding rotundus contains concentrically organized rotundal dendrites and tectorotundal axons. Fascicles of axons from rotundal neurons leave the nucleus ventrally and laterally to enter the lateral forebrain bundle. The details of the morphology of central and peripheral rotundal neurons are illustrated by higher-magnification tracings in Figure 8 and 9.

Figure 8 is a solid-filled cell from the core of rotundus at about the level shown in Figure 7. The spherical soma issues an axon that travels in a direct course ventrolaterally to exit the nucleus. It is smooth and does not appear to be myelinated within rotundus. No collaterals were observed on this or any other axon in rotundus. Four or five primary dendrites branch dichotomously close to the soma and then run for long distances to the periphery of the nucleus where they curve and follow its contours. The dendrites bear two kinds of specializations. The primary dendrites occasionally issue a long, thin appendage close to the soma that is intricately lobulated at its tip (Fig. 8). The distal dendrites bear a low to moderate density of short, spinelike protrusions that are often beaded at their tips. When dendrites can be traced to their tips they usually bear a small, beaded arborization (see the ventralmost dendrite in Fig. 8).

Figure 9 is a tracing of two cells located at the periphery of rotundus. Like central cells, their axons pass ventrolaterally and enter the forebrain bundle. The dendrites of these cells are also long and could be traced up to 300 μm before leaving the plane of the section. None of the dendrites shown could be traced completely. Peripheral cells send their dendrites either radially into the center of rotundus or concentric with its borders. They bear a variety and density of dendritic appendages similar to those described for central cells.

The tectorotundal projection is nonretinotopic

Fourteen animals received restricted HRP injections into the tectum. The injection sites ranged from a tectal quadrant to a small patch approximately 150 μm in diameter. A small fascicle of fibers could be traced from the injection site into the tectothalamic tract in all cases. In contrast to the spatial order seen in the optic tract (personal observations), fibers originating from any tectal locus distributed evenly throughout the ascending tract. In a few cases, two nonoverlapping injections placed into the medial and lateral fringes of a single tectal lobe produced similar results. There was, thus, no evidence for any tectotopic order in the tectothalamic tract. All injections produced a qualitatively similar pattern of terminal labeling in rotundus: a widespread, uniform distribution of fine-diameter terminal collaterals filled the nucleus throughout its rostrocaudal extent.

Figure 10 shows the relationship of injection size to the density of terminal labeling in two representive cases. Small injections produce a very light scattering of fine-diameter collaterals (FIg. 10A), whereas larger injections produce a more dense terminal network (Figs. 10B, 6B).

The axonal morphology that accounts for such a terminal distribution will be considered in detail in the next section.

Tectorotundal axons

Tectal axons enter rotundus from its caudolateral pole, stream from lateral to medial in its caudal third, and then turn rostrodorsally to reach its anterior pole. These axons are heavily collateralized and interlaced throughout their course. The terminal field thus appears as a uniformly dense meshwork of beaded collaterals (Fig. 11A). Figure 11B shows the types of axon morphology observed in rotundus after solid filling of the tectothalamic tract. The axons are from the caudal third of rotundus where most of the incoming tectal fibers have a lateral to medial orientation and could thus be followed for some distance in individual coronal sections. Three types of axons could be distinguished. First, smooth axons about 1 μm thick could be traced into rotundus from the tectothalamic tract and are interpreted as the parent or primary axons of tectorotundal cells. Other axons of this caliber were observed to issue collaterals to rotundus and continue forward in the crossed tectothalamic tract. Second, thinner axons about 0.5 μm thick are lightly studded with varicosities along their lengths. They could often be seen arising as primary collaterals of parent axons. Third, very fine-caliber beaded axons less than 0.5 μm thick are the most abundant. They bear a high density of varicosities and issue many short, beaded branchlets. They most often originate from the primary collaterals, but occasionally arise directly from parent axons.

The number of axons labeled in small injection cases was often small enough to permit single tectorotundal axons to be followed through serial sections. Figure 12 is a reconstruction of four such axons traced through five 80-μm transverse sections. The axons depicted are relatively large-caliber parent axons and their collaterals. The reconstructed axons share several structural features. First, single axons extend from the caudal to rostral pole of rotundus without forming focal terminal fields. In fact, some have been traced from the tectothalamic tract to the habenular commissure, where they contribute to the second crossed rotundal projection. Second, each axon runs in a fairly straight line through the nucleus from caudolateral to rostrodorsal. In its course, each may issue one or more primary collaterals (arrows in Fig. 12) that run in parallel with the parent axon. Third, both parent axon and primary collateral give rise to fine-diameter secondary collaterals along their length. Collaterals extend in the mediolateral axis for several hundred microns across the nucleus while those radiating in the dorsoventral axis are short (50–100 μm) and often more branched.

A consequence of these structural features is that single axons maintain a relative spatial order in their course through rotundus. Thus, for example, the most ventral axon in Figure 12 maintains this relative position throughout its course, and its terminal field does not overlap that of the dorsally situated axons. The terminal fields of single axons can therefore be viewed as forming horizontally oriented slabs that run the entire length of the nucleus. The slabs extend in the mediolateral plane but are compressed in the dorsoventral plane so that a relative spatial order is realized. It should be remembered, however, that the spatial order does not reflect the retinotectal map because a cluster of axons arising from a single tectal locus (as in Fig. 12) distributes to all parts of rotundus.

DISCUSSION

Identification of rotundus in *Thamnophis*

The identification of rotundus in *Thamnophis* rests on three major findings. First, the massive projection of the tectothalamic tract to a large nucleus in the central diencephalon and the subsequent projection to dorsal ventricular ridge matches the overall plan of the tectofugal visual pathway described in other reptiles and birds (review: Ulinski, '83). The course and relative position of both the tectothalamic tract and the rotundal projection is virtually the same in all of these studies as that described here for *Thamnophis*. Second, the tectorotundal projection is not retinotopically organized in *Thamnophis*. The lack of a point to point tectorotundal map is a well-documented feature of this pathway in other forms (review: Ulinski, '83). Third, the internal organization of rotundus and its tectal input is strikingly similar to the pattern in the pond turtle *Pseudemys scripta* (Rainey, '79, '80; Rainey and Ulinski, '82a,b).

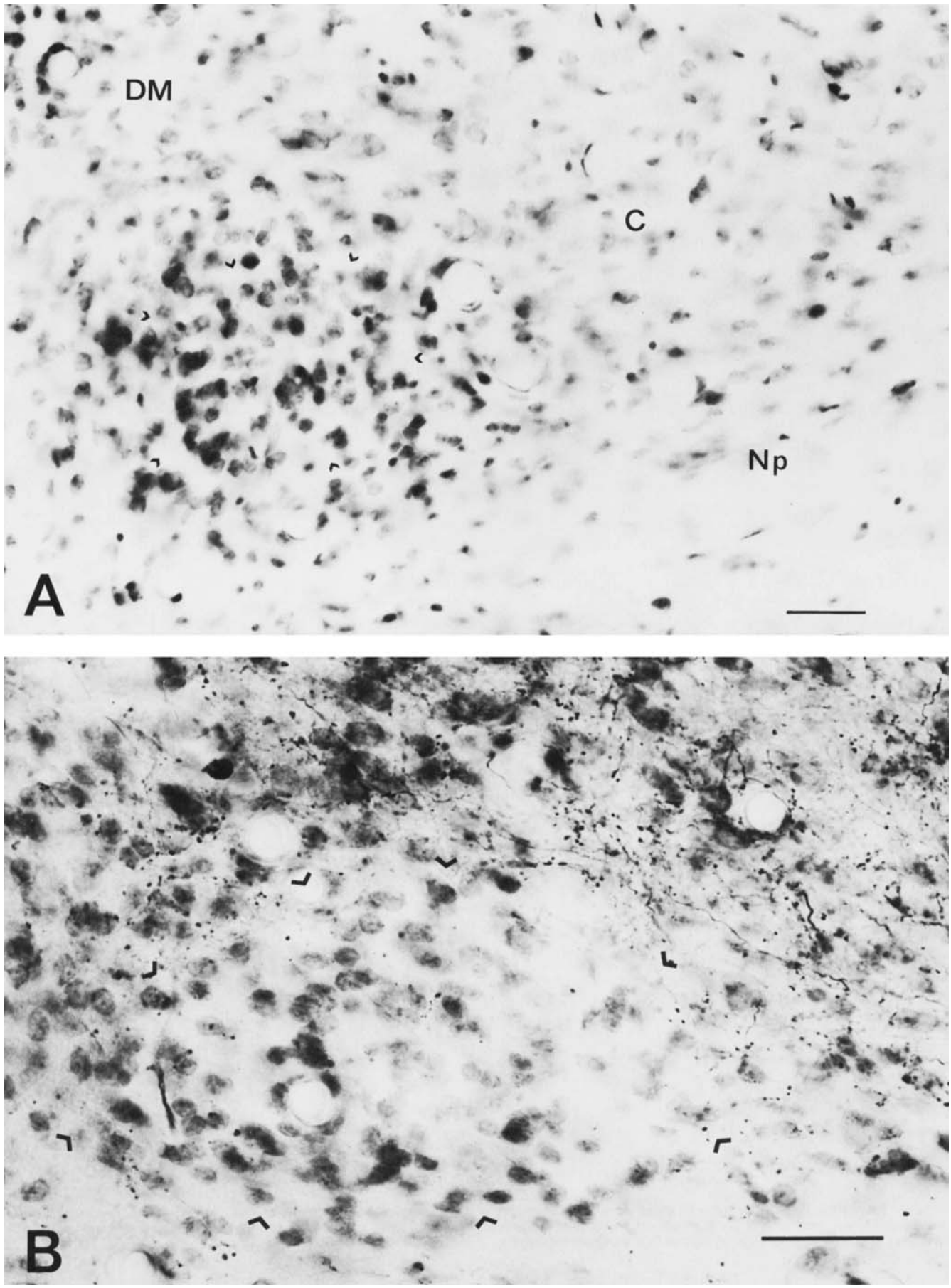
The problem of identifying rotundus in snakes probably stems from its apparently more caudal position relative to the other major dorsal thalamic cell groups and its lack of a well-defined shell. Thus, Warner ('31, '46) and Armstrong ('51) mistook the large, well-demarcated, and rostrally placed dorsomedial nucleus (DM) for rotundus. Later studies of retinal projections in various snake genera (Halpern and Frumin, '73; Northcutt and Butler, '74) corrected this, but there was no subsequent agreement as to the location of rotundus (compare, for example, Repérant, '73; and Molenaar and Fizaan-Oostveen, '80). Northcutt and Butler ('74) suggested that rotundus was poorly developed in snakes while the retinothalamic system appeared to be larger than in other reptiles. They included rotundus (as identified here) as part of the lentiform thalamic nucleus (LT), noting that it was in the same position as is rotundus in other reptiles. Recent experimental studies of tectal projections in snakes also did not identify a tectorotundal system (Ulinski, '77 – *Natrix*; Schroeder, '81 – *Crotalus*). They conclude that rotundus may be poorly developed, although Schroeder did describe a massive, bilateral projection from the tectothalamic tract to the lentiform thalamic nucleus and observed that this nucleus seemed to extend farther caudolaterally than in other reptiles.

Comparison With *Pseudemys*

A thorough comparative review of rotundal structure in reptiles and birds has recently been published (Rainey, '79). The following discussion will focus on a comparison of rotundus in snakes and rotundus in the pond turtle, *Pseudemys scripta*, where the most detailed information exists.

Rotundus in *Pseudemys* is characterized by its strikingly large size relative to surrounding thalamic nuclei and by a single layer of cells (the rotundal shell) that sets rotundus off from surrounding nuclei. The shell is penetrated by incoming tectal fibers at its caudolateral pole and surrounds a cell-poor zone and a central core. Rotundus does

Fig. 6. A. The ventrolateral sector of rotundus, shown in a Nissl preparation, is cytologically distinguishable as a dense whorllike grouping of smaller cells ventrolateral to the dorsomedial nucleus (DM). B. Tectal terminals are conspicuously absent from this region in orthograde HRP experiments. Approximate borders of the ventromedial region are marked by arrows. Scale bars in A and B = 40 μm.


DM
C
Np
A
B

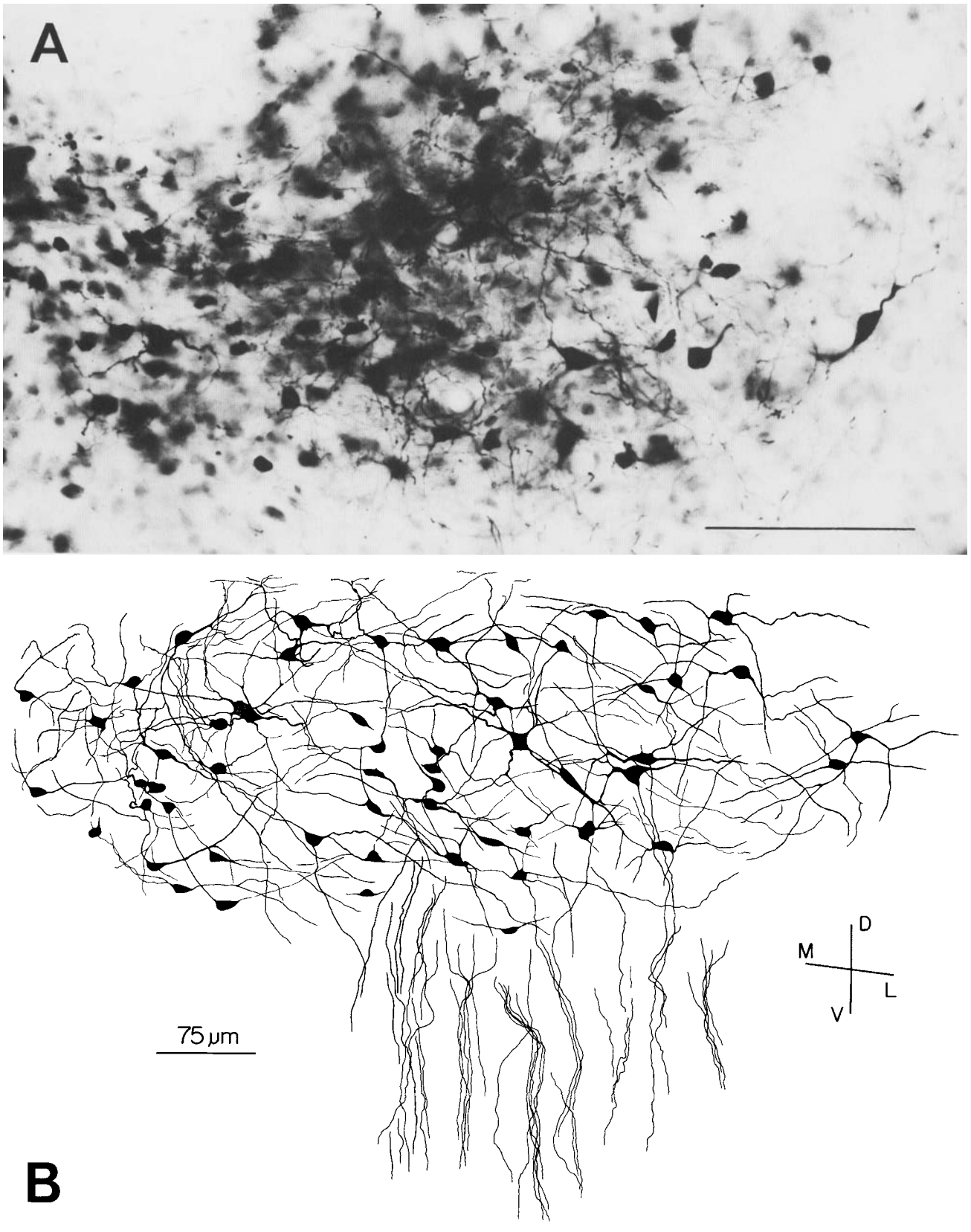


Fig. 7. Retrograde HRP fill of rotundal cells. A. A section through midrotundus shows most cells of various sizes either solidly or diffusely filled after HRP injections into the cerebral peduncles. Diaminobenzidine (DAB) reaction, Nissl counterstain. Scale bar = 100 μm. B. Camera lucida tracing at about the same level as in A shows the encapsulated or closed pattern of rotundal dendritic organization.

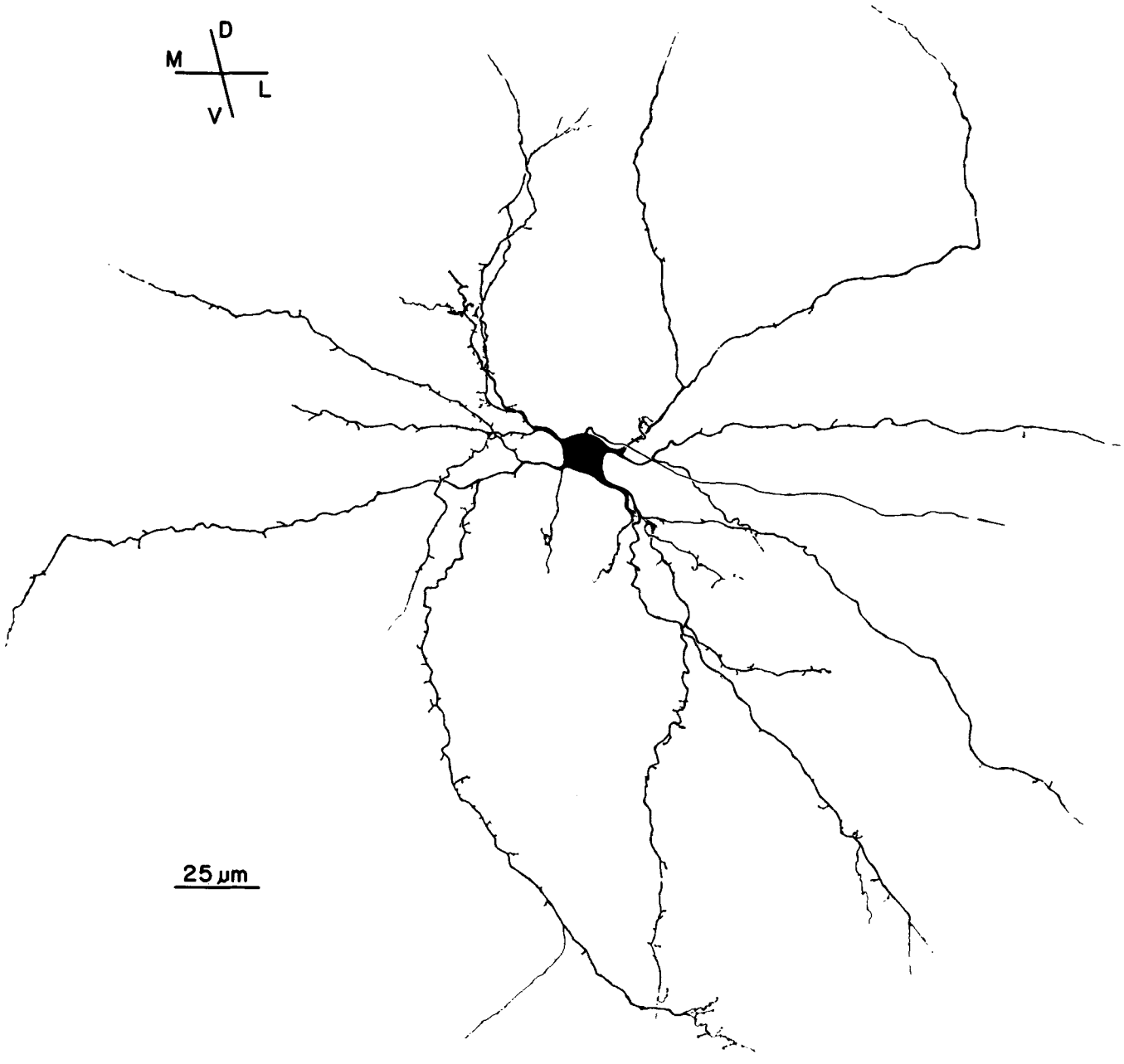


Fig. 8. HRP fill of a rotundal core cell. Dendrites are smooth and radiate but bear a sparse distribution of short spinelike protrusions on dendritic shafts and longer, lobulated appendages on the proximal dendrites. The axon courses ventrolaterally without collateralizing.

not appear as large and conspicuous in *Thamnophis* as it does in *Pseudemys* (or other reptiles). However, it is clearly one of the largest dorsal thalamic nuclei in *Thamnophis* when its boundaries are outlined by visualizing its tectal input or by retrogradely filling its cells (Figs. 1, 2). It too is encapsulated by a cell-poor neuropil, but it is not demarcated by a rind of shell cells. It is comparable in this respect to most other reptiles, where a distinct shell is not apparent (Rainey, '79). However, as in *Pseudemys*, the tectothalamic fibers penetrate rotundus at its caudolateral pole and remain confined to its cell-poor zone and core. Further, cells in the shell (Fig. 7) structurally isolate rotundus from direct retinal input in both *Pseudemys* and *Thamnophis*.

Rotundus contains a distinct region of densely packed, darkly staining cells in both *Pseudemys* and *Thamnophis*. This region is situated along the ventromedial edge of the nucleus and receives only a sparse tectal input. In *Pseudemys*, it is located caudally and is called the caudomedial region (Rainey, '79). In *Thamnophis*, it forms a cylindrical column that extends through the rostral two-thirds of rotundus. It is cytologically more distinct than in *Pseudemys* and tectal input appears to be more completely excluded (Fig. 6). Other inputs to this region have not yet

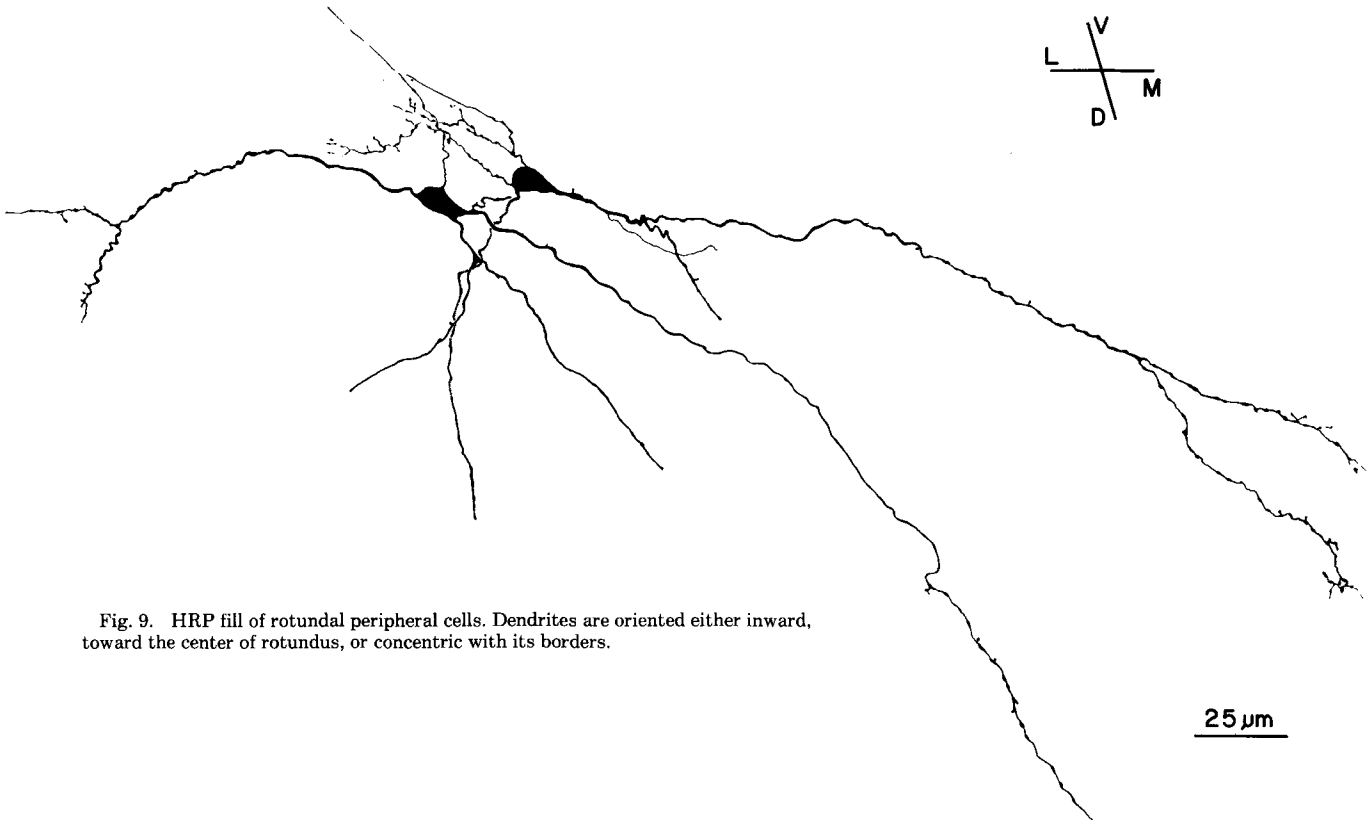


Fig. 9. HRP fill of rotundal peripheral cells. Dendrites are oriented either inward, toward the center of rotundus, or concentric with its borders.

been discovered in *Pseudemys*, but preliminary evidence in *Thamnophis* indicates that the ventromedial region receives a heavy input from the basal optic nucleus (personal observations).

Neuronal structure is remarkably similar in *Pseudemys* and *Thamnophis*. The core contains neurons with a range of soma sizes, all of which project to dorsal ventricular ridge. Axons always arise from somata and there is no axon collateralization within rotundus. Core or central cells have radiating, sparsely branched dendrites that extend to the cell-poor zone, but not beyond it. The dendrites bear scattered, spinelike protrusions and longer complex appendages. There is no evidence for an intrinsic neuron population. The only major structural difference between rotundal cells in *Pseudemys* and *Thamnophis* is the absence of a distinct shell, but the shell is a variable feature in rotundus among reptiles and birds (Rainey, '79).

Tectal input to rotundus is not retinotopically organized in *Thamnophis*, consistent with findings in other squamates, crocidilians, turtles, and birds (see beginning of article for references). Small HRP injections produce a widespread but light scattering of terminal labeling throughout rotundus. The density, but not the location, of labeling is related to the injection size. Orthograde HRP filling has been used to study the terminal morphology of tectorotundal axons in *Thamnophis* and *Pseudemys*. These axons travel from caudal to rostral through the nucleus, collateralizing in their course. However, the present observations on single, solid filled axons extend our understanding of the tectorotundal system by showing that, although axons arising from a single tectal locus can be positioned throughout rotundus, they maintain a spatial order in their relative positions. Fibers enter rotundus and travel in straight lines through the nucleus, issuing terminal fields that form rostrocaudally aligned slabs, flattened in the horizontal plane but extending some distance in the mediolateral axis. These slabs are overlapping, but are partially shifted in the dorsoventral axis. They form the basis for a divergence of single tectal axons to many rotundal cells and a convergence of many tectal axons to single rotundal cells. However, the topography of single terminal fields suggests that a spatial pattern is present. The radiate dendritic fields of rotundal neurons constitute highly overlapping but spatially unique spherical domains; tectal axons pass through rotundus such that each dendritic domain has a unique intersection with the tectal terminal field. The kind of signal transformation that this structural pattern may represent is considered in the next section.

Functional significance of nonretinotopic organization

The significance of the lack of retinotopy in the tectorotundal projection is not apparent at this time. However, some hypotheses may serve to guide future thinking and experimentation. Four will be considered here.

First, it is conceivable that the tectorotundal projection encodes information about position in visual space in spite of the extensive convergence in the projection. This hypothesis is consistent with behavioral data implicating rotundus in pattern vision and acuity discriminations in

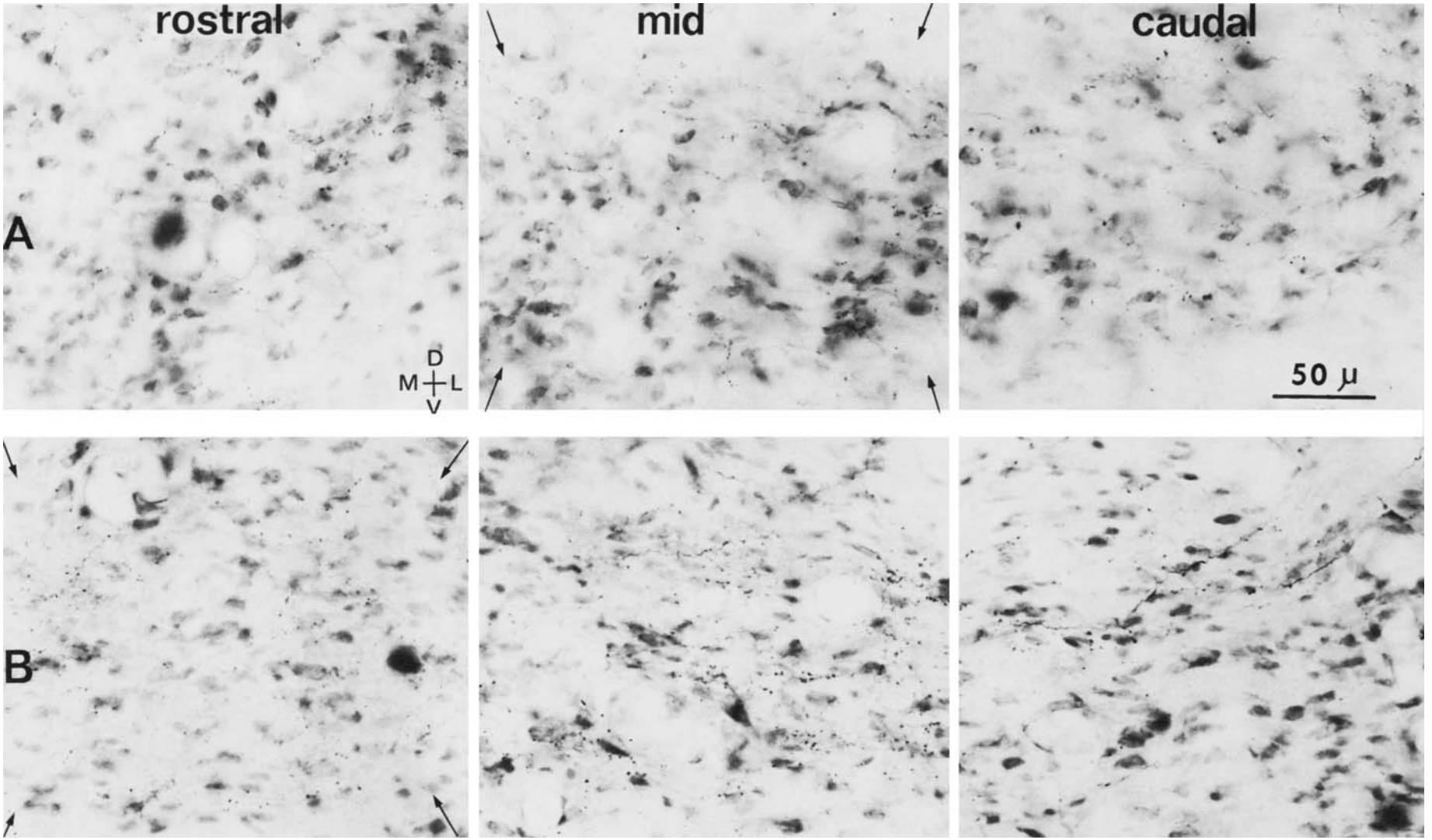


Fig. 10. Terminal distribution of HRP-filled tectal axons in rotundus. All small HRP injections produce a light labeling throughout the rostrocaudal and mediolateral extent of rotundus. However, the density of the terminal labeling is related to the size of the HRP injection. The smallest injection (A) produced a light scattering of labeled terminals at rostral, middle, and caudal levels. A larger injection produced a denser labeling (B). The borders of rotundus are noted by the arrows.

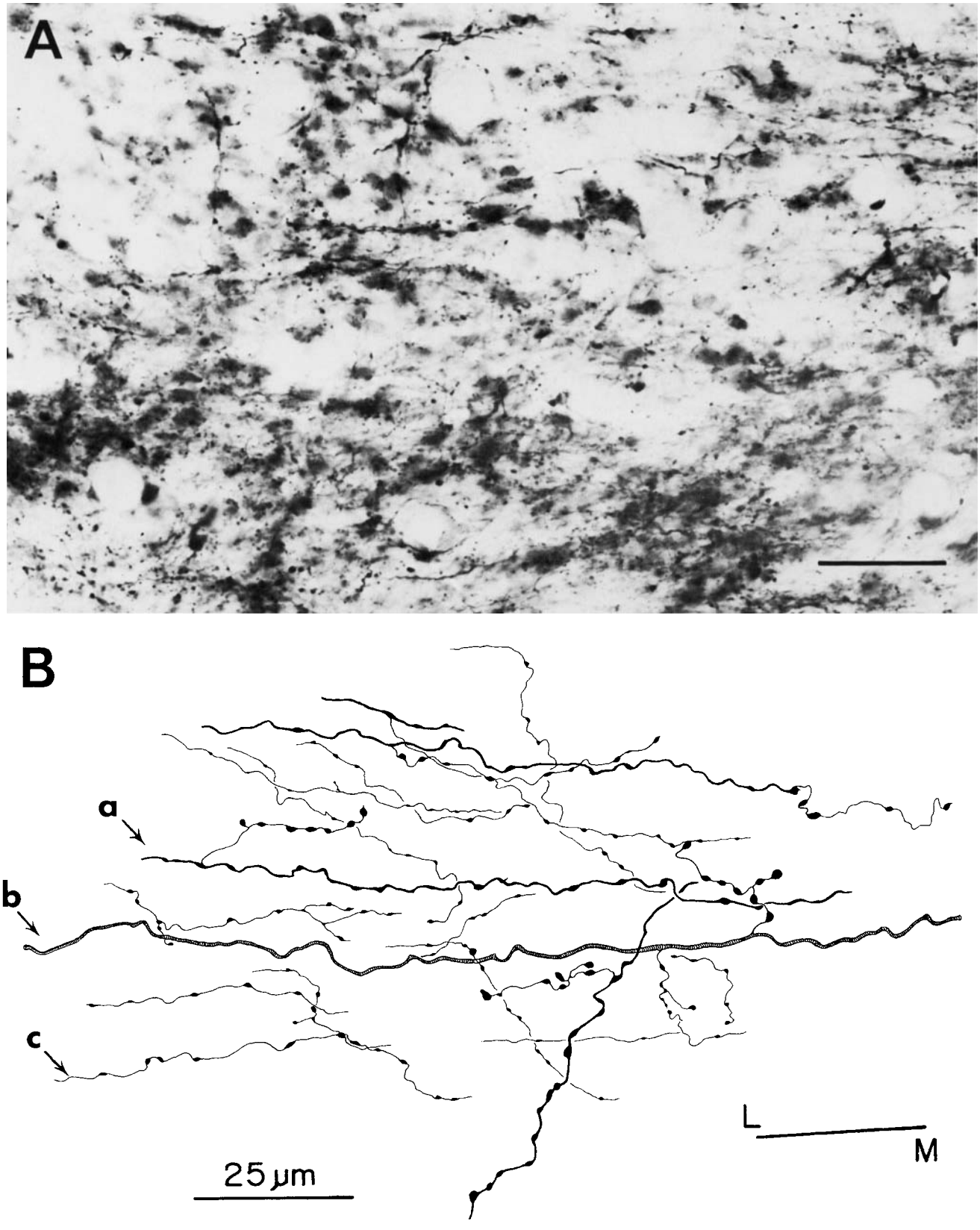


Fig. 11. Tectorotundal axon morphology. A. A dense meshwork of axon terminals after a large tectal injection of HRP (DAB reaction). Scale bar = 40 μm. B. Camera lucida tracing of axons in this material demonstrates smooth parent axons (b), primary collaterals (a), and fine beaded terminal collaterals (c). Terminal collaterals can arise from either parent axons or primary collaterals.

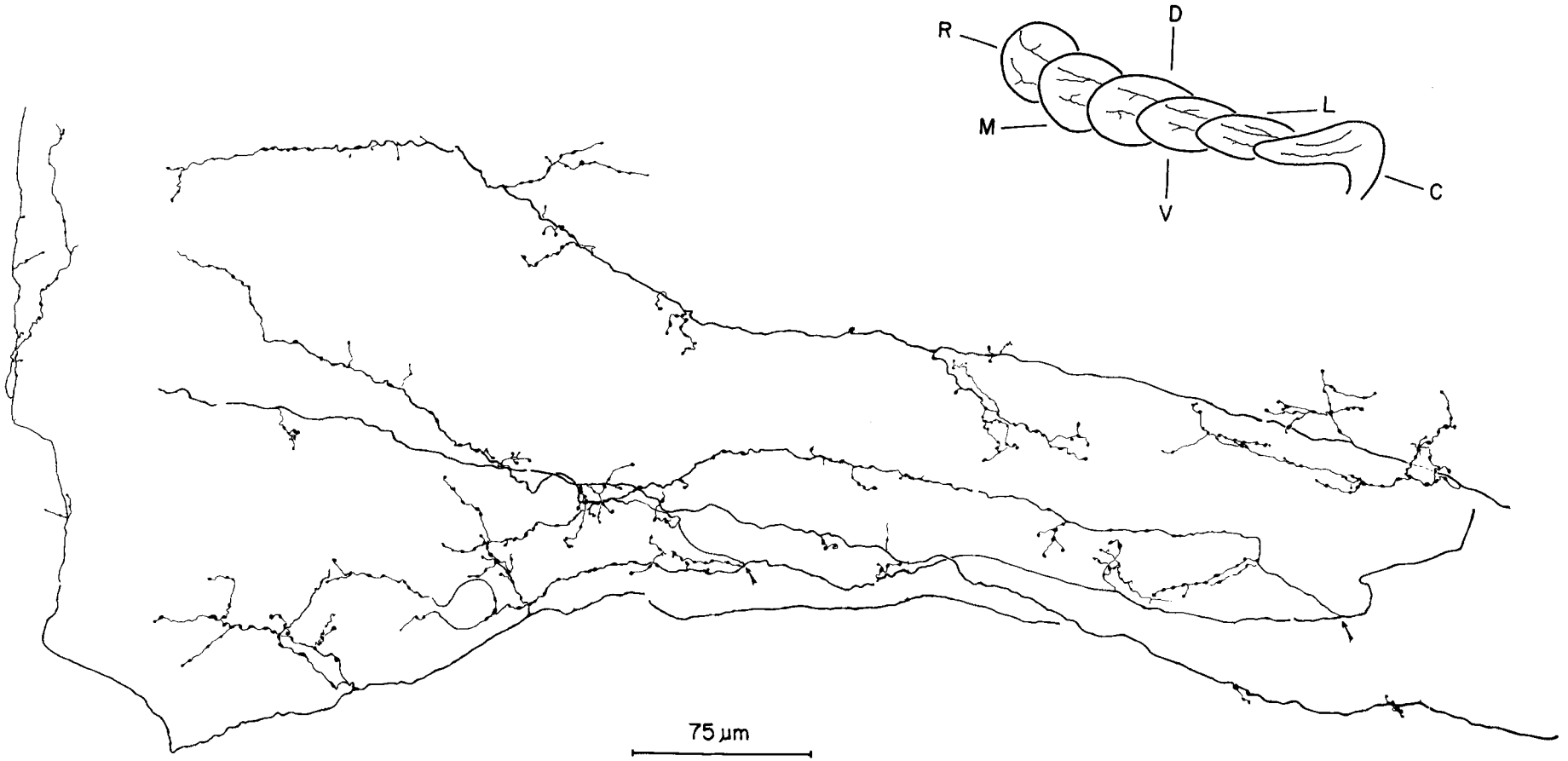


Fig. 12. Reconstruction of single tectorotundal axons. Inset at top is a schematic of the orientation of the tectal axons as they pass through coronal sections of rotundus from caudal to rostral. Origin of two primary collaterals is marked by the arrows. Axon that turns dorsally at the far left is ascending rostrally toward the habenular commissure.

pigeons (Macko and Hodos, '79; Mulvanny, '79). One mechanism that would preserve information about position in visual space involves coding spatial position in discharge frequency. In *Pseudemys*, for example, tectal neurons are distributed nonhomogeneously within the tectum (Ulinski, '78). In the periventricular gray layer of the tectum there is an increase in the density of neurons within the representation of the retinal visual streak, a linear area of increased ganglion cell density (Peterson and Ulinski, '79). If this variation in density is preserved in the tectorotundal projection, then a given rotundal neuron might receive a sample of information from all regions of visual space, but with a greater synaptic input from within the streak representation than from the representation of the peripheral retina. Thus, rotundal neurons would be stimulated by visual stimuli anywhere in visual space, but with a greater synaptic strength by stimuli within the visual streak. Consistent with this model, there is some evidence that rotundal units with large receptive fields in turtles respond preferentially to stimuli within certain regions of visual space (Morenkov and Pivavarov, '75). Visual units in dorsal ventricular ridge also have large receptive fields that respond preferentially to stimuli within the visual streak (Dünser et al., '81). A similar model has been suggested for the spatial to frequency transformation in the projection from the superior colliculus to the paramedian pontine reticular formation in primates (Wurtz and Albano, '80).

A second hypothesis is that spatial information is not encoded in rotundus, but that rotundal neurons encode information about some other parameters of visual stimuli. Thus, there is evidence from physiological studies of avian rotundus suggesting that large field units with different stimulus preferences are differently distributed within rotundus (Revzin, '79; Maxwell and Granda, '79). Rotundus would then resemble other sensory structures that lack a receptotopic organization but contain neurons that encode other features of sensory stimuli. The space mapped component of the torus semicircularis of owls is an auditory structure that lacks a tonotopic organization but contains neurons that code position in auditory space (Knudsen and Konishi, '78). Similarly, the FM-FM region of auditory cortex in the mustache bat is not tonotopically organized but contains neurons that are tuned to particular delays between the bat's high-frequency pulse and its echo (O'Neill and Suga, '82).

A third hypothesis is that rotundus contains a distributed representation of a spatiotemporal pattern of activity in the tectum. This idea is made tenable by the presence of both convergence and spatial order in the tectorotundal projection demonstrated here in *Thamnophis*. In a distributed representation information is coded in the patterned activity of a population of cells. (See Anderson and Hinton, '81 for a discussion of distributed representations.) Thus, no individual unit would uniquely specify a particular position in space or be selective for a single feature. Instead, it would respond to many input patterns with information being coded as a variation in the strength and temporal position of a unit's output relative to others. This hypothesis would also be compatible with the proposed role for rotundus in pattern discrimination and is consistent with the finding that many rotundal cells respond to any change in a visual stimulus (Revzin, '79). It suggests that physiological analysis of rotundus may profit by recording from several units simultaneously, so that the relative activities of single cells can be correlated with changes in the stimulus pattern.

A fourth hypothesis suggests that the information represented in rotundus is related not to the representation of some specific visual parameter (e.g., movement, position), but to a tectally mediated sensory-motor transformation. This hypothesis is motivated by the structural relation between those tectal neurons that project to rotundus and those that project to the reticular formation (Dacey and Ulinski, in preparation). Tectorotundal neurons have narrow dendritic fields that extend into the retinal terminal layers and are small enough to receive a retinotopic input. In contrast, tectoreticular neurons have large dendritic fields that are confined to the deeper tectal layers and do not extend into the retinal recipient layers. However, the tectorotundal cells possess massive collateral systems that project into the dendritic domains of tectoreticular cells and might thus be a major source of input to these cells. Physiological studies of the sequence of connections from tectal neurons to oculomotor neurons in primates provide ample evidence that there is a spatial to temporal transformation from a retinotopic map, coding location, to a nonretinotopic map, coding frequency of motoneuron discharge (review: Wurtz and Albano, '80). Perhaps the putative connection between tectorotundal and tectoreticular cells is a stage in a comparable spatial to frequency transformation, and the ascending nontopographic component of the tectorotundal axon is also part of a circuitry mediating the sensory to motor transformation. In this view, the sequence of connections through dorsal ventricular ridge and the striatum back to the tectum (review: Ulinski, '83) constitute a feedback system involved in modulating visuomotor behavior.

The tectorotundal projection may also be involved in the nonvisual localization of prey by those snakes that possess heat-sensitive pit organs. The distribution of receptotopically organized infrared input to the tectal central gray in rattlesnakes (Kass et al., '78) is positioned to contact the basal dendrites of tectorotundal cells. These efferent neurons might then be equivalent to the bimodal units recently observed (Newman and Hartline, '81) that respond to both visual and infrared stimuli. Thus, the tectorotundal projection in infrared snakes may utilize a bimodal receptotopic representation to encode a movement signal.

These hypotheses may not be mutually exclusive (for example, the hypothesized sensory-motor transformation could be encoded in a distributed representation), and there certainly are other models that are equally plausible. It does seem clear, however, that progress in this area will lie outside of the classical framework of receptotopic maps and sequential models of information processing.

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