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# Electron Microscopy of the Dorsomedial Cortex in the Lizard *Psammodromus algirus*

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*ABSTRACT* The cellular populations and the plexiform layers of the dorsomedial cortex of *Psammodromus algirus* are described at the ultrastructural level. Solitary globous cells are located in the outermost layer of the cortex, the superficial plexiform layer. Double pyramidal cells of the cellular layer show uniform ultrastructural characteristics. Displaced double pyramidal cells, vertical fusiform cells, and globous cells are found in the deep plexiform layer. Two types of dendritic spines are described. Large spines may contain membranous sacs and mitchondira and are located at the upper third of the superifical plexiform layer; small spines do not contain organelles and are located throughout the entire cortex. Two types of axon terminals are widely distributed in both plexiform layers: terminals with only clear vesicles and terminals with both dense-core and clear vesicles. Terminals with large dense-core vesicles may be related to peptidergic synapses and are more frequent at the upper levels of the superficial plexiform layer. The neuroglia described in the dorsomedial cortex of *Psammodromus* are protoplasmatic astrocytes and oligodendrocytes.

The dorsomedial cortex is one of the cortical regions in squamate reptiles. Together with three other regions, medial, dorsal, and lateral, it forms the cerebral cortex, which lies above the lateral ventricle and presents three basic layers: a superficial plexiform layer, a cellular layer (where most of the cell bodies are present), and a deep plexiform layer. The dorsomedial cortex was first described as a large-celled mediodorsal cell plate by Unger ('06). It occupies a position between the medial and dorsal cortices, and its lateral tip overlaps with the medial portion of the dorsal cortex (superpositio medialis). P. Ramón ('17) described this region in the iguana as being formed by a row of large double pyramidal-shaped neurons (his "pyramidal curvilinear area"). Other Golgi studies confirmed the descriptions of P. Ramón (Crosby, '17; Ebbesson and Voneida, '69; Lacey, '78; Guirado et al., '84). The dorsomedial cortex plays a major role in interhemispheric relations because of its bilateral projections to the medial cortex. The dorsomedial cortex lacks efferent connections beyond the telencephalon and receives afferents from the ipsilateral medial cortex (Ulinski, '76, in *Natrix sipedon* and *Thamnophis sirtalis*). Ultrastructural descriptions of the dorsomedial cortex of reptiles are limited to those of snakes (Ulinski, '79) and a lizard (García Verdugo et al., '83, in *Lacerta galloti*).

The present work was carried out to complement a previous light microscopic study of this region in the lizard *Psammodromus algirus* (Guirado et al., '84) and the scarce data of the ultrastructural characteristics of the cells and plexiform layers of this region of the reptilian cerebral cortex. In view of the recent immunocytochemical studies on the localization of neuropeptides in different regions of the CNS of reptiles (Goossens et al., '80; Naik et al., '81; Bear and Ebner, '83), we paid special attention to the presence of terminals containing vesicles that may contain neuropeptides.

## MATERIALS AND METHODS

The brains of 18 adult lizards, *Psammodromus algirus*, body length 6–8 cm weighing approximately 9–12 gm, were used. Specimens were anesthetized via an intraperitoneal route with urethane (1.5 mg/gm body weight) and perfused intracardially with about 75 ml of a fresh solution of 1% paraformaldehyde and 1% glutaraldehyde in

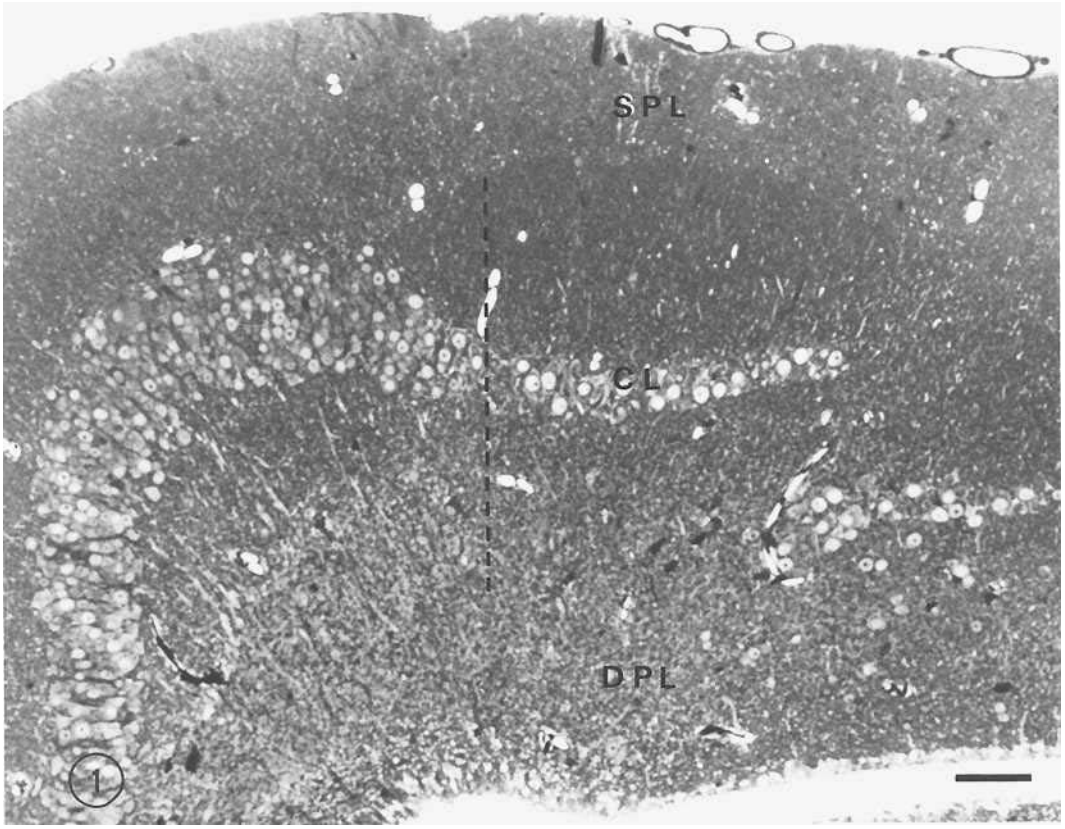



Fig. 1. Semithin coronal section through the telencephalic medial wall of *Psammodromus*. The vertical line indicates the limit between the medial and dorsomedial cortices. SPL, superficial plexiform layer; CL, cellular layer; DPL, deep plexiform layer. Toluidine blue. Bar = 80 μm.

0.12 M phosphate buffer. The brains were removed after perfusion and immersed in the fixative at room temperature. After 1 hr of fixation brains were cut into transverse slices about 1 mm thick, which were then left in the fixative for an additional 1–3 hr. After this initial fixation, the slices were postfixed for 2–4 hr in 2% osmium tetroxide at 4°C in the dark. They were subsequently block stained in 2% uranyl acetate in acetate buffer, dehydrated in ethanol, cleared in propylene oxide, and embedded in Araldite. Thin sections were cut with glass knives, mounted on grids, stained with uranyl acetate and lead citrate, and examined in a Philips 201 electron microscope. Semithin sections (1–1.5 μm thick) were stained with toluidine blue.

## RESULTS

### *Light microscopy*

In semithin sections, the dorsomedial cortex of *P. algirus* has three layers (Fig. 1): 1) a superficial plexiform layer (SPL), where some myelinated fibers and solitary neuronal somata are present; 2) a cellular layer (CL), which continues the cellular layer of the medial cortex (neurons in dorsomedial cortex are less densely packed than in medial cortex); and 3) a deep plexiform layer (DPL), where numerous neurons scattered among the fibers are present (the fibers of the alveus lie in the inner part of the DPL, just above the ependyma). The lateral edge of the dorsomedial cortex overlies the cellular layer of the dorsal cortex in the superpositio medialis.

### *Electron microscopy*

#### Superficial plexiform layer

A thin glial sheet forms the most external portion of the SPL. It is formed by triangular structures (Fig. 2) that are terminal enlargements of processes of tanycytes located at the ependyma. These end feet contain many mitochondria with dense matrices and fila-

ments. The end feet extend laterally and overlap adjacent processes. Gap junctions between processes are sometimes observed (Fig. 4).

Two types of axon terminals are observed in the neuropil of the SPL: 1) terminals showing dense-core vesicles and 2) terminals with only clear vesicles. Within the first group, we have found two subtypes. In the first subtype, some axon terminals contain many dense-core vesicles of great size ($\geqslant$ 100 nm diameter) (Fig. 3). There are different forms of the vesicles, although most often they are round or oval. The dense core is separated from the vesicle membrane by a clear space. In addition to the dense-core vesicles, small clear round vesicles appear. These terminals are abundant at the upper third of the SPL. The other subtype shows clear vesicles and some small dense-core vesicles (40–60 nm). They appear uniformly distributed in the SPL. Clear vesicle terminals are the most frequent in the SPL. We have also observed two subtypes according to the vesicle shape: round vesicle terminals (S type) and flattened vesicle terminals (F type).

Most of the synapses of the external portion of the SPL are with dendritic spines of different sizes and shapes. We have observed a great number of cup-shaped dendritic spines. At the more superficial zones some large spines that almost encircle the axon terminals appear. Synapses associated with these structures are of the round, asymmetrical type, and only clear vesicles are present. The dendritic spines contain organelles: Some mitochondria and membranous sacs appear in the larger ones, whereas the smaller spines display a flocculent matrix.

The rest of the neuropil is formed by tanycytic processes, running perpendicular to the surface, dendrites, and axons, some having a myelin sheath running parallel to the surface.

At middle levels of the SPL a type of solitary neuron appears with round soma (Fig. 5). The nucleus displays one or more indentations. The chromatin is evenly dispersed, and the nucleolus is prominent. The cytoplasm, moderately electron dense, is rich in organelles. The rough endoplasmic reticulum forms Nissl bodies at the soma periphery, whereas the Golgi apparatus occupies a juxtanuclear position. Many mitochondria and free polyribosomes are found elsewhere. Scarce terminals synapse on the soma. We have observed S terminals forming axosomatic synapses.

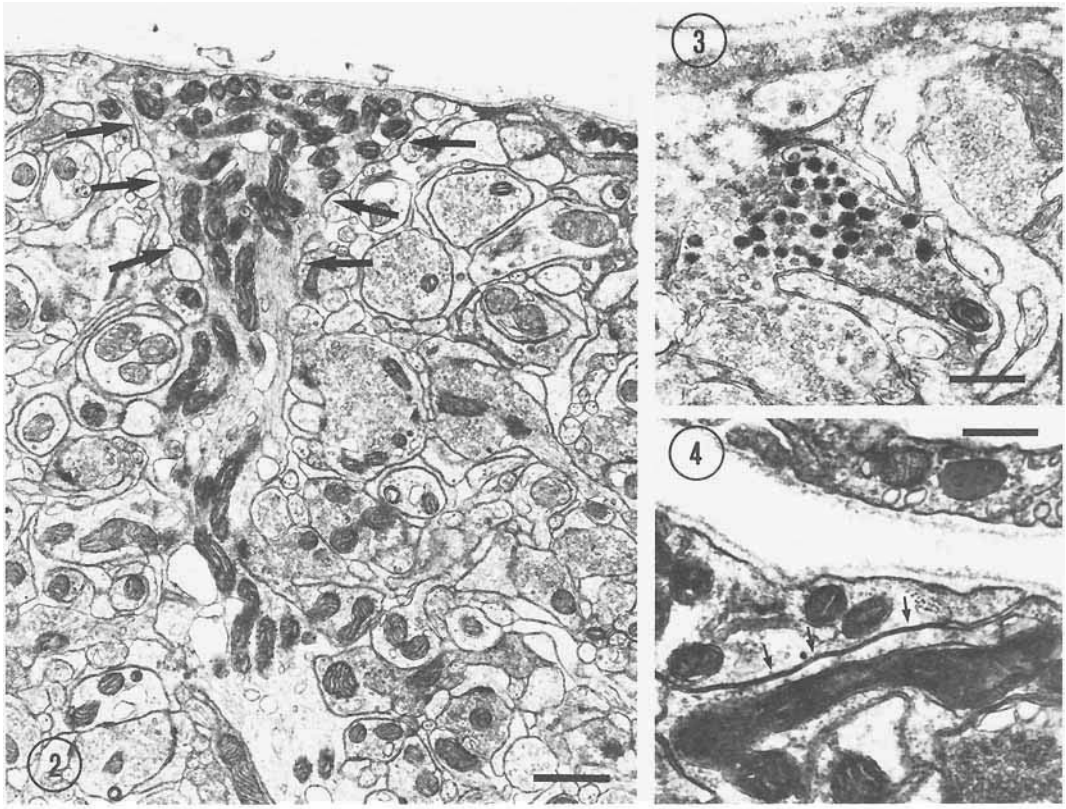
### Cellular layer

The cellular layer is formed by one or two rows of large cells separated from each other by narrow zones of neuropil (Fig. 6). All the cells present similar ultrastructural characteristics, and thus we consider them a single neuronal type: the double pyramidal neuron. They are large neurons (maximum diameter, 20 $\mu$m) with triangular or fusiform somata and oval nuclei in a basal position. The nuclear chromatin is evenly dispersed. The major axis of the neuronal cell body is perpendicular to the surface. At the apical portion the cytoplasm grows thin and forms a thick primary aspiny dendrite that ascends through the SPL. Some neurons at the lateral end of the dorsomedial cortex have two ascending primary dendrites resembling those of candelabra cells, but their ultrastructural characteristics do not differ from the other cells described here (Fig. 7). A basal process is frequently observed running towards the ventricle.

The cytoplasm of the double pyramidal neurons is somewhat clearer than the surrounding neuropil (Figs. 6, 7). The perinuclear cytoplasm is rich in organelles. The rough endoplasmic reticulum is abundant and displays a variable position. The Golgi apparatus occupies a supranuclear position and is preferentially oriented parallel to the major cellular axis. Vesicles with a very electron-dense content covered by a membrane are sometimes associated with the Golgi apparatus (Fig. 8). These are similar to the vesicles found in the superficial plexiform layer. Many mitochondria of different sizes and shapes are located elsewhere in the cytoplasm.

The plasma membranes of adjacent neurons are separated from each other by small bands of neuropil, but they may be in contact over wide areas. In some of the contact zones, small protrusions of cytoplasm, which may present subsurface densities (Fig. 9), evaginate from one cell into the other (Fig. 10).

The somata and primary dendrites of the double pyramidal neurons have many synaptic contacts. We observed axosomatic synapses of the round, asymmetrical as well as the flat, symmetrical type (Fig. 11). Axon terminals containing large dense-core vesicles may appear near the somata, but we did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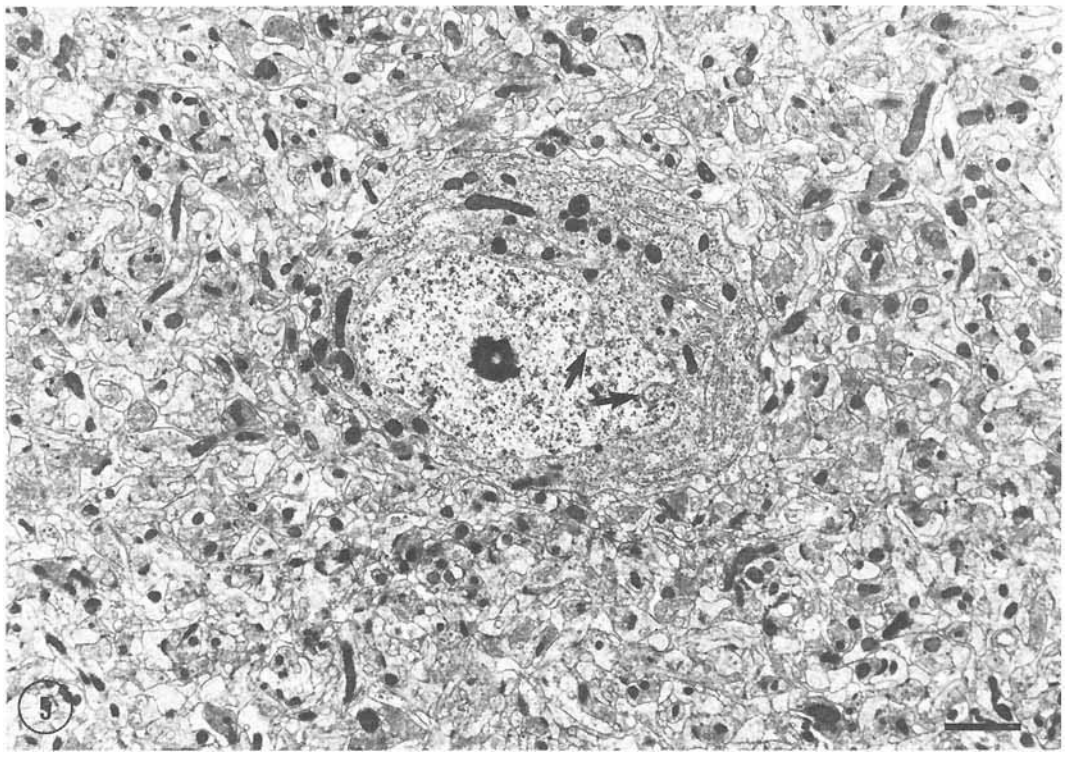
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not observe axosomatic synapses with this type of terminal (Fig. 12).

Deep plexiform layer

The DPL is formed by an extensive neuropil where many scattered neuronal somata as well as some glial cells appear. The DPL is bound by the ependyma, which consists of a monolayer of prismatic cells bordering the lateral ventricle. Just above the ependyma a great number of axons run parallel to the ventricle (Fig. 16). This zone is where the myelinated axons are more frequent. The axons form part of the alveus system and the same disposition is found in the deep third of the DPL of the medial and dorsal cortices. Axon terminals are of the same type as described in the SPL. Large dense-core vesicle terminals appear, but not extensively (Fig. 14). We have also observed axon terminals with round clear vesicles and with flattened vesicles.

Neurons in the DPL are of three morphological types:

1. At the middle level of the DPL, neurons with triangular somata may appear. The nucleus is oval or round and eccentrically located. The electron-lucent cytoplasm contains many organelles. Approximately 20 to 30 mitochondria can be seen in each section. The Golgi apparatus is highly developed with elongated cisternae. Short and numerous cisternae of rough endoplasmic reticulum are observed at the basal pole. Some free polyribosomes and dense bodies, the former preferentially located at the apical pole, complete the organelles in the cytoplasm. S and F terminals synapse on the somata of these neurons. We classify these cells as double pyramidal neurons displaced from the cellular layer.

2. Other neurons present fusiform somata with the major axis perpendicular to the ventricle: vertical fusiform neurons (Fig. 15). This cell type is found at the middle level of the DPL. The cells have oval nuclei, with the chromatin evenly dispersed, and a large nucleolus. The apical cytoplasm is extensive and tapers distally to form a thick dendrite. The granular reticulum occupies a supranuclear position and is oriented parallel to the major cell axis. Mitochondria, sometimes very long, are observed, as well as many dense bodies and free polyribosomes. The soma and the primary process are surrounded by many axon terminals, but we did not observe axosomatic synapses.

3. The third neuronal type has a large round soma: globous neurons. These cells are located without any special distribution in the DPL. The nucleus may be oval or kidney shaped, with small clumps of chromatin and a large nucleolus eccentrically located (Fig. 13). The nucleus is displaced toward a cell pole, and the cytoplasm contains many organelles. The Golgi apparatus is highly developed, showing several profiles per section. It occupies a supranuclear position and is composed of very long cisternae and many vesicles. Short cisternae of rough endoplasmic reticulum are located at the periphery of the cell. Many mitochondria (30–40) of various forms are evenly distributed in the cytoplasm. Heterogenous dense bodies and free polyribosomes are also present. Four to five S and F terminals synapse on the soma in each section.

Glial cells with typical characteristics of protoplasmic astrocytes are scattered in the DPL. We have observed some oligodendrocytes, more frequent in the deep third of the DPL. Criteria for identification of neuroglia were those described by Mugnaini and Walberg ('64).

Ependyma

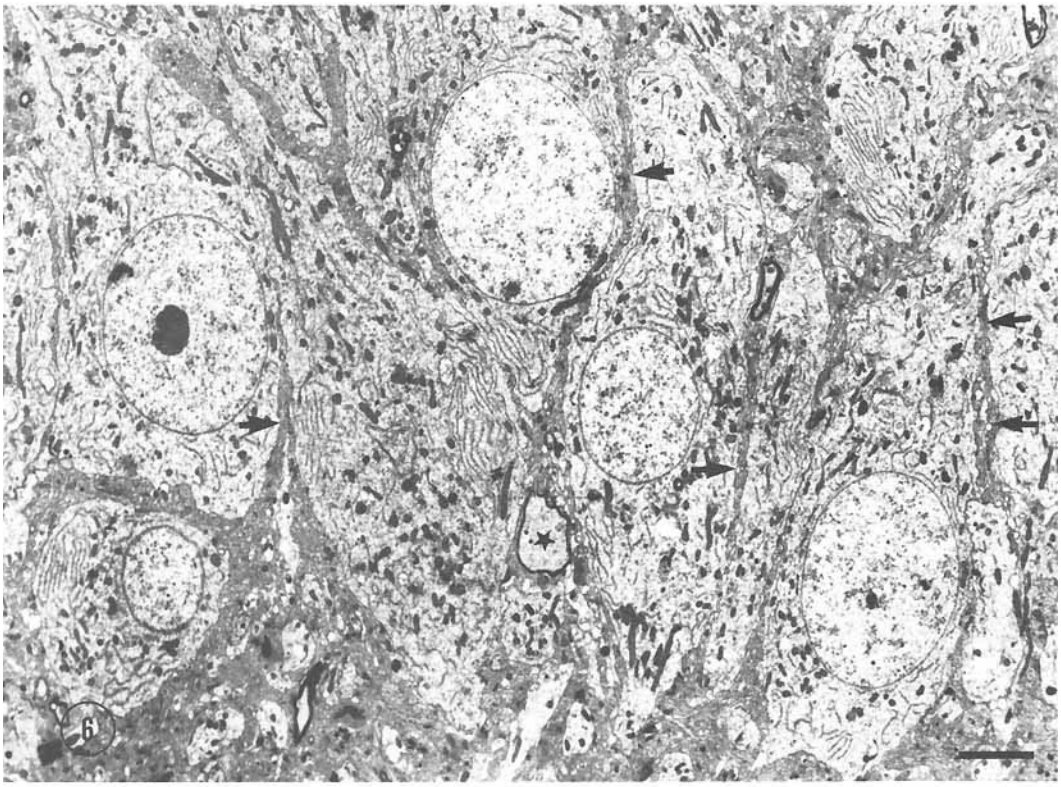
The border of the DPL is formed by a monolayer of cells limiting the ventricle (Fig. 16). The cells are prismatic, and nuclei are polymorphic and occupy a basal position with respect to the apical, ventricular surface. Nuclei show frequent depressions produced by the large lipid droplets that may occupy a large portion of the cell cytoplasm. Most of the organelles are located at the apical pole, where many mitochondria can be observed. The cytoplasm is vacuolated, causing the cell to be electron lucent. Junctional complexes appear between adjacent cells at their apical borders. Many cilia and microvilli project into the ventricle. From the basal pole, a process arises that ascends toward the cortical surface.

Fig. 2. Tanycytic process reaching the cortical surface. Note the terminal expansion (arrows) filled with mitochondria and gliofilaments. Bar = 680 nm.

Fig. 3. Axon terminal with large dense-core vesicles at the outermost region of the superficial plexiform layer. Bar = 465 nm.

Fig. 4. Gap junction (arrows) between adjacent glial processes at the limiting glial sheet. Bar = 335 nm.

Fig. 5. Solitary globous neuron in the SPL. Typical nuclear indentations (arrows) of this cell type can be observed. Bar = 1,680 nm.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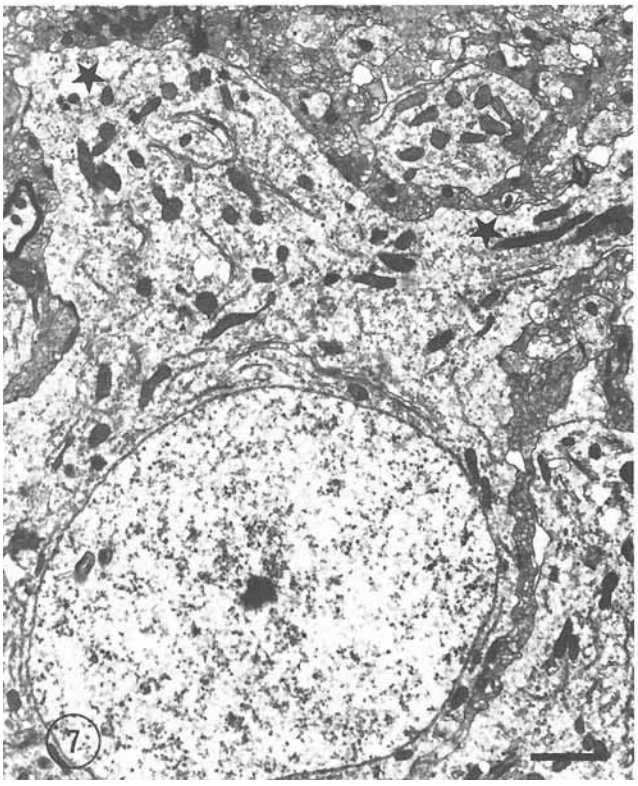
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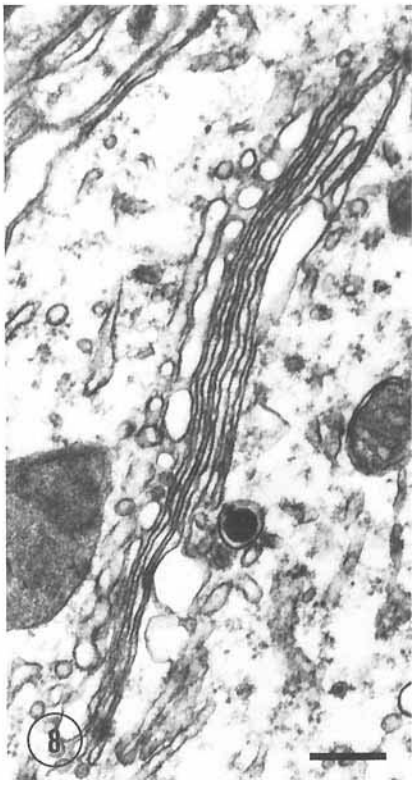
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## DISCUSSION

The dorsomedial cortex of *Psammodromus* shows a trilaminar organization as occurs in other lizards (Meyer, 1893; Unger, '06; Shanklin, '30; Goldby, '34; Curwen, '37; Northcutt, '67, '78; Ebbesson and Voneida, '69; Beckers et al., '71; Butler, '76, '78). When the dorsomedial cortex has been studied using Golgi methods, it has been described as containing a homogenous cell population of double pyramidal cells in the cellular layer (Ramón, 1891, 1896, '17; Minnelli, '66; Northcutt, '67; Ebbesson and Voneida, '69; Lacey, '78), stellate cells in the superficial plexiform layer (Ramón, '17; Lacey, '78; Ulinsky, '79), and horizontal and stellate cells in the deep plexiform layer (Ramón, '17; Minelli, '66; Ebbesson and Vonedia, '69; Lacey, '78). It is usually difficult to establish a correspondence between the neuronal types described with the Golgi method and descriptions of the cell ultrastructure; this has been resolved using combined Golgi and EM techniques or by intracellular injection of horseradish peroxidase (HRP). However, in the case of very homogenous neuronal populations, as is found in the dorsomedial cortex, a correct assignment of ultrastructural characteristics to each neuronal type is possible without using special techniques.

In middle levels of the SPL we described solitary globous cells, with an indented nucleus, and at the periphery we described the rough endoplasmic reticulum forming Nissl bodies. Ulinski ('79) describes in snakes stellate cells in the SPL, preferentially located in the inner two thirds of this layer. García Verdugo et al. ('83) in *Lacerta galloti* show a single neuronal type located at the outer third of the SPL, with a highly developed Golgi apparatus and one or two nuclear invaginations. There are variations in the localization of these solitary neurons, but their ultrastructural characteristics are very similar to each other, and they resemble the cells found in the SPL of the medial cortex of *Psammodromus*. Solitary cells in the SPL of the dorsomedial cortex have been seen, with Golgi methods, by Ramón ('17) in *Lacerta* (small stellate cells); Minelli ('66) describes aspiny cells with vertical orientation in *Lacerta muralis*, and Lacey ('78) reports in *Sceloporus undulatus* aspiny stellate cells in this layer. In our previous Golgi report the impregnation of cells failed in the SPL of the dorsomedial cortex.

Neurons of the cellular layer showed uniform ultrastructural characteristics: We describe them as double pyramidal cells. In the Golgi study (Guirado et al., '84) we found two morphological cell types, double pyramidal cells and candelabra cells at the tip of the layer. In this position we have described cells whose primary dendrites show the typical features of candelabra cells, but their ultrastructure does not differ from other neurons in the layer. Double pyramidal cells have been seen in *Lacerta* (Ramón, 1891, 1896, '17; Minelli, '66), in the green iguana (Northcutt, '67), in *Tupinambis* (Ebbesson and Voneida, '69), in *Sceloporus* (Lacey, '78), in snakes (Ulinski, '79), and in *Lacerta galloti* (García Verdugo et al., '83). There is a general consensus among investigators, and only García Verdugo et al. ('83) found small paired cells with ultrastructural characteristics different from those of the double pyramidal cells described here.

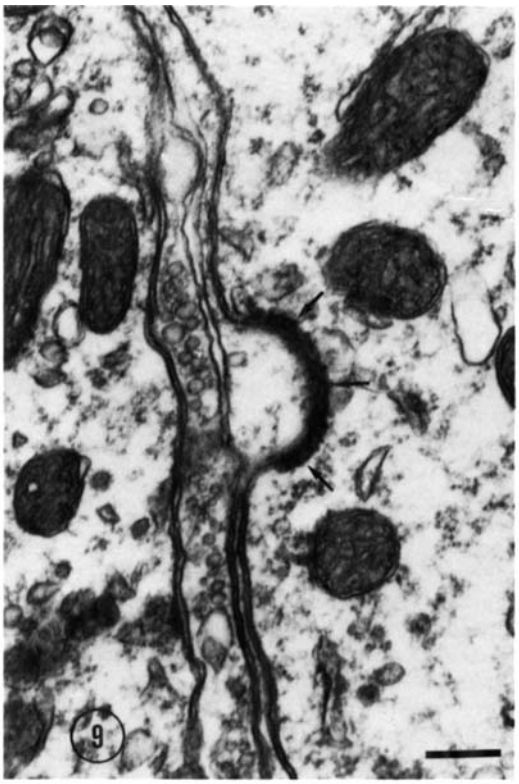
Regarding the small protrusions of cytoplasm between neurons in the cellular layer, these zones could represent cohesion structures between neighboring cells that help to maintain the integrity of a cell layer formed by only one or two rows of cells.

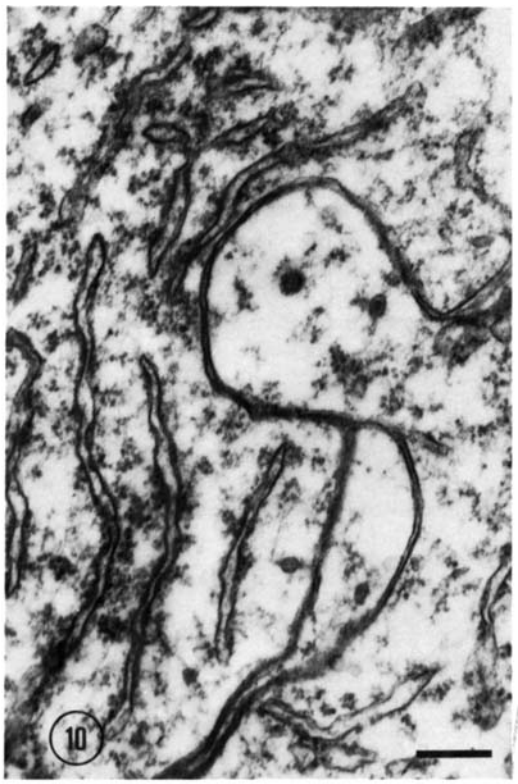
We have observed displaced double pyramidal cells in the deep plexiform layer of the dorsomedial cortex, and such cells have been described previously by Ramón (1891, 1896), Ebbesson and Voneida ('69), Lacey ('78), and Ulinski ('79). We have also described vertical fusiform cells and globous cells in the DPL. In the Golgi study we found neurons with vertically oriented somata and dendrites that could correspond to the vertical fusiform cells of this study. There is no clear correlation between the horizontal cells described by Ramón (1896, '17), Minelli ('66), Lacey ('78), and Ulinski ('79) and any of the cells of the DPL described in the present work. The globous neurons of the DPL, because of their morphology and localization, may correspond to the stellate cells described by the former investigators.

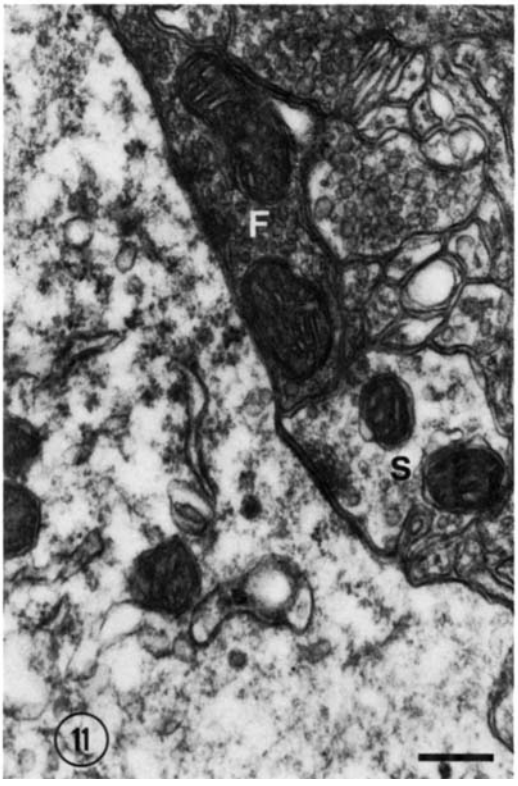
Fig. 6. Low-power magnification of the cellular layer. Large double pyramidal neurons are separated from each other by a narrow neuropil (arrows). Note the myelinated axons (star) within the layer. Bar = 3.5 $\mu$m.

Fig. 7. Detail of the soma of a double pyramidal cell. Two primary dendrites (stars) arise from the apical region. Bar = 1,560 nm.

Fig. 8. Golgi apparatus of a cellular layer neuron. Large dense-core vesicles can be observed close to the Golgi cisternae. Bar = 270 nm.



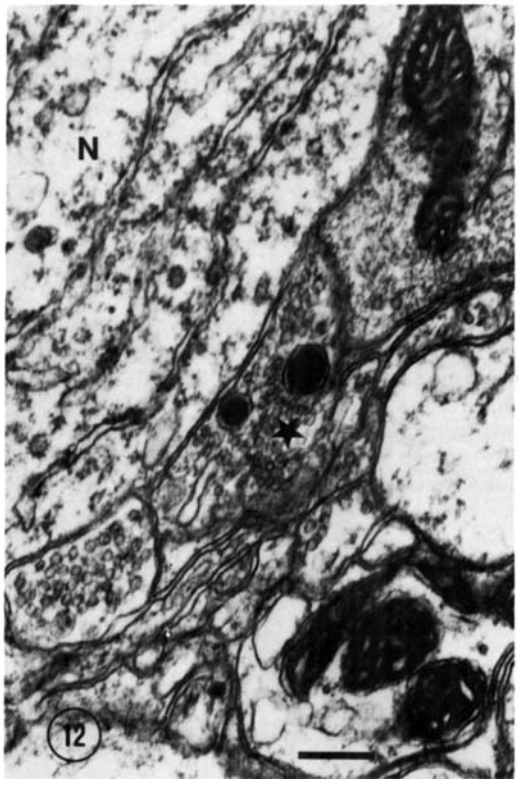
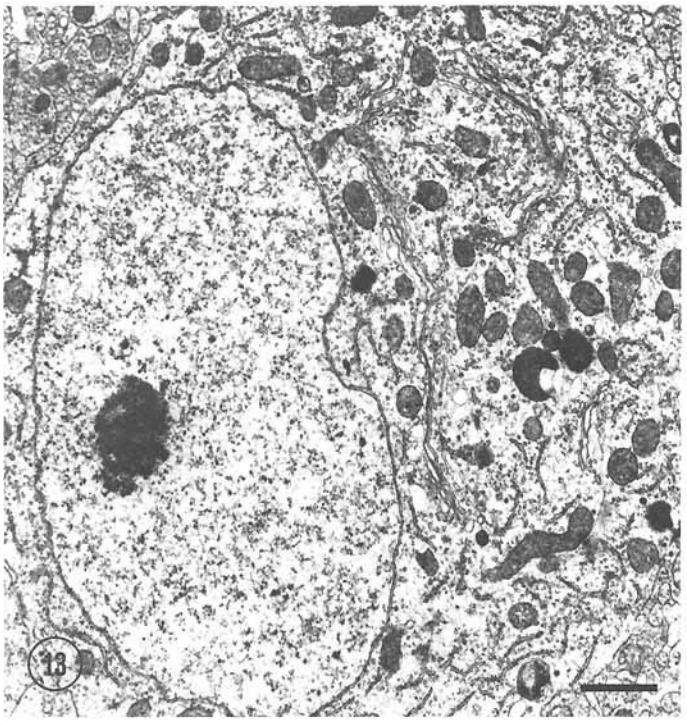



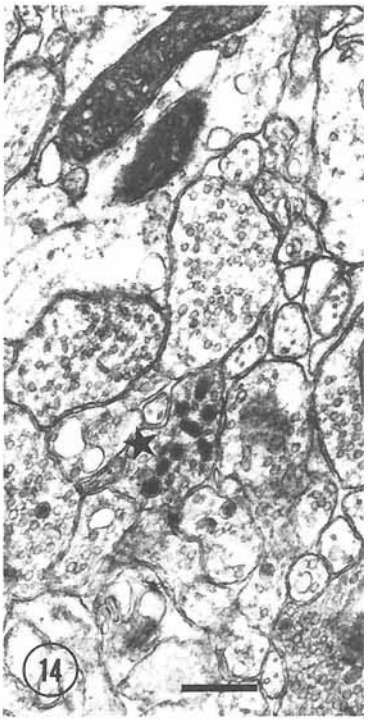

Fig. 9. Subsurface densities (arrows) are frequently associated with contacting zones of the plasma membranes of adjacent cells. Bar = 270 nm.

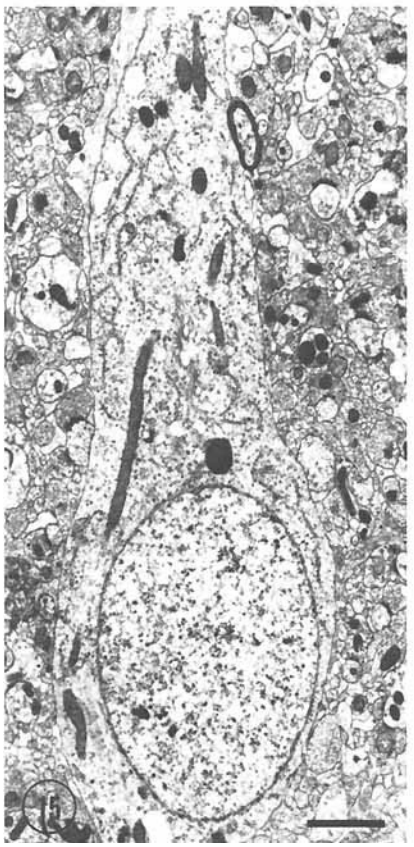
Fig. 10. Cytoplasmic protrusion between adjacent neurons in the cellular layer. Bar = 270 nm.

Fig. 11. Two axon terminals containing round (S) and flattened (F) vesicle synapses with a double pyramidal soma. Bar = 270 nm.

Fig. 12. An axon terminal containing large dense-core vesicles (star) is found in the neuropil surrounding the neurons (N) in the cellular layer. Bar = 270 nm.



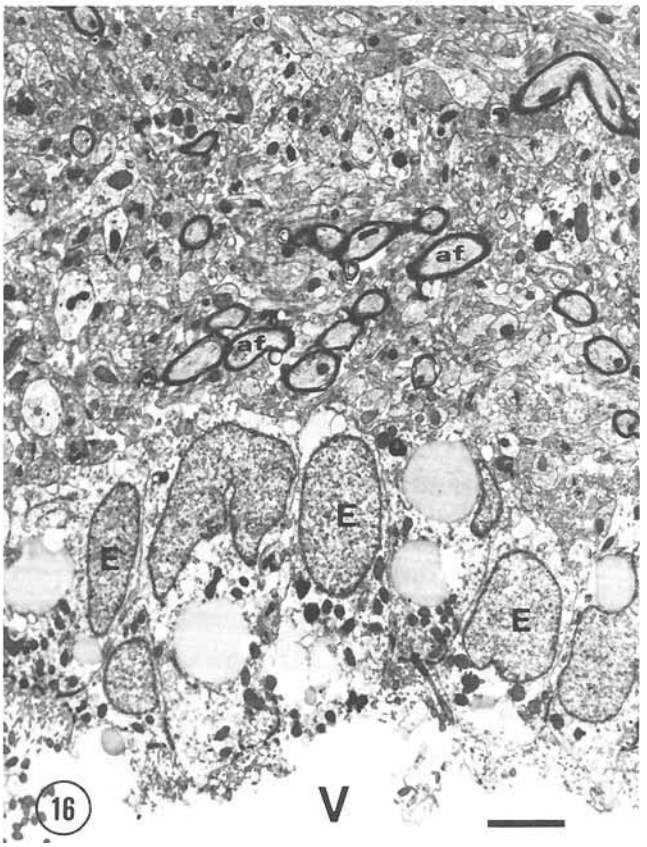




Fig. 13. Globous neuron in the deep plexiform layer. Note the highly developed Golgi apparatus. Bar = 950 nm.

Fig. 14. Possible peptidergic terminal (star) in the deep plexiform layer. Bar = 430 nm.

Fig. 15. Vertical fusiform cell in the deep plexiform layer. Bar = 1.65 $\mu$m.

Fig. 16. Low-power magnification of the inner third of the DPL. Just beneath the alveus fibers (af) a monolayer of ependymal cells (E) lines the ventricle (V). Bar = 2.2 $\mu$m.

Two types of dendritic spines have been described. Large spines have a cup-shaped form or may encircle the axon terminal almost completely. The spines may contain membranous sacs and, less frequent, mitochondria, and they are found in the upper third of the SPL. This type of spine has been described by Davydova and Smirnov ('69) and Ebner and Colonnier ('75, '78) in turtles and by Dávila et al., ('85) in the medial cortex of *Psammodromus*. The rest of the spines are small, do not contain organelles, and are located throughout the entire cortrex. This distribution of spines may correspond to a different specialization along the dendrites of the double pyramidal neurons in the stimuli reception.

Immunocytochemical studies have demonstrated the presence of neuropeptides in the cerebral cortex of reptiles, in fibers as well as in neuronal somata (Goossens et al., '80, *Ctenosauria pectinata*; Naik et al., '81, *Anolis carolinensis*; Bear and Ebner, '83, *Pseudemys*; Fernández-Llebrez, personal communication, *Natrix*). In *Psammodromus* we have observed large dense-core vesicles, similar to those of the peptidergic terminals, in the cytoplasm of pyramidal neurons of the cellular layer.

In this report we have described two types of axon terminals widely distributed in both plexiform layers: terminals with only clear vesicles and terminals with dense-core and clear vesicles. Clear vesicle terminals form round, asymmetrical or flat, symmetrical synapses. Terminals containing dense-core vesicles can be subdivided into two groups: 1) those with small dense-core vesicles and 2) those with large dense-core vesicles. The former are probably related to aminergic fibers (Panzica et al., '82). They are uniformly found in all layers. The latter may be related to peptidergic terminals (Panzica et al., '82) and are more frequently found at the upper levels of the SPL. Although the terminals with dense-core vesicles are observed in the cellular layer, they have never been seen to synapse on a pyramidal cell body located in the cellular layer.

In spite of the morphological uniformity of the neurons in the cellular layer of the dorsomedial cortex, as observed both in Golgi and EM studies, the presence of possible peptidergic neurons within the layer and a variety of afferents mediated by different axon terminals and dendritic spines give to this region a great functional variability, which needs further investigations.

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