

Cyto-architecture and neuronal types of the dorsomedial cerebral cortex of the common Indian wall lizard, *Hemidactylus flaviviridis*

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ABSTRACT

The cyto-architecture and morphology of the neuronal types of the dorsomedial cortex of the lizard, Hemidactylus flaviviridis has been studied with the help of Cresyl violet staining and Golgi impregnation method. The dorso-medial cerebral cortex displayed three neuronal layers. Layer-I contains only few neuronal somas and also the dendrites ascending from the subjacent layers. Layer-II is characterized by two to three cell thick densely packed neuronal somas. Layer-III contains loosely packed neuronal somas and the dendrites and axon descending from layer-I and II. Below the layer-III an ependymal layer is observed just above the ventricle. Six classes of neurons were distinguished in the cellular layer of dorsomedial cortex of Hemidactylus flaviviridis: bitufted neurons, pyramidal neurons, inverted pyramidal neurons, bipyramidal neurons, multipolar neurons, and candelabra-like monotufted neurons. The pyramidal cells were large showing more or less single type present in the cellular layer. The multipolar neurons have mostly intracortical dendritic branching and connections. Bipyramidal neurons showed pyramidal appearance of their soma and send dendritic branches towards the superficial plexiform layer and deep plexiform layer. The candelabra-like monotufted neurons have very high dendritic branching. The comparison of the neuronal types of dorsomedial cortex of reptiles with the parahippocampal area of birds and CA3 region of mammalian hippocampus suggests possibility of their homology.

Key words

Lizard • Medial cortex • Bitufted neuron • Spinous • Golgi study

Introduction

The pallium (cerebral cortex) of the reptiles is composed of four main cortical areas: medial (MCx), dorsomedial (DMCx), dorsal (DCx) and lateral (LCx) cortices. All these cortical areas of reptilian cerebral cortex represent a laminar structure in which most neuronal cell bodies are grouped forming a principal cell layer sandwiched between the inner and outer plexiform layers (Olucha et al., 1988; Martinez-Guijarro et al., 1990; Luis De La Iglesia and Lopez-Garcia, 1997; Lopez-Garcia et al., 2002; Abhinav and Srivastava, 2006; Maurya and Srivastava, 2006; Molnar et al., 2006), which are populated by scarce interneurons and where the

afferent connections terminate in a highly laminated fashion (Lopez-Garcia et al., 2002). The inner plexiform layer (ipl) is separated from the lateral ventricle by a thin layer of ependymal cells that retain neurogenic capabilities during adulthood (Lopez-Garcia et al., 1988).

The lizard dorsomedial cortex has been considered homologous to the CA3 area of the mammalian hippocampus because it emits a prominent commissural-contralateral projection (Martinez-Guijarro et al., 1990) and because it is the main recipient of the zinc-positive "lizard mossy fibres" coming from the medial cortex (Lopez-Garcia and Martinez-Guijarro, 1988; Martinez-Guijarro et al., 1990). There are major differences in the extent of layering pattern

and distribution of pyramidal neurons in reptiles and birds. These are present in all reptilian cortices (Northcutt, 1967; Ulinski, 1976; Wouterlood, 1981), while in birds pyramidal neurons are restricted to medial hippocampus and intermediate corticoid area, whereas the parahippocampal area show little resemblance with the dorsomedial cortex, both having spiny multipolar neurons (Montagnese et al., 1996; Srivastava et al., 2007a).

Spinous bipyramidal neurons are the main neuronal type found in the cellular layer of dorsomedial cerebral cortex of the lizards *Agama agama* (Wouterlood, 1981), *Lacerta* (Berbel, 1988) and snakes (Ulinski, 1979). The somata of these neurons form the granular layer, and their dendrites extend into the outer and inner plexiform layers (Minelli, 1966; Ebbesson and Voneida, 1969; Regidor et al., 1974; Lacey, 1978; Ulinski, 1979; Wouterlood, 1981; Garcia Verdugo et al., 1983; Martinez-Guijarro et al., 1984; Berbel, 1988). The 3 acetylpyridine (3AP) induced degeneration show few pycnotic nuclei in the cell layer and in the inner plexiform layer of dorsomedial cerebral cortex and there was also a conspicuous loss of dendritic spines in bipyramidal (i.e. cell layer) neurons of the dorsomedial cortex (Font et al., 1997).

The medial and the dorsomedial cortex were collectively called as the mediodorsal cerebral cortex (Ulinski, 1974; Wouterlood, 1981). The small celled part of the mediodorsal cortex is presently called as the medial cortex and the large part as the dorsomedial cortex (Martinez-Guijarro et al., 1984; Luis De La Iglesia and Lopez-Garcia, 1997; Lopez-Garcia et al., 2002; Abhinav and Srivastava, 2006; Maurya and Srivastava, 2006; Molnar et al., 2006; Srivastava et al., 2007b). It is surprising that in recent years, most of the authors have restricted their study only to the medial cortex of reptiles describing only one type of neurons in snake genera *Natrix* and *Boa* (Ulinski, 1977), five types in the lizard *Lacerta ptyusensis* (Berbel et al., 1987) and in *Podarcis hispanica* (Luis De La Iglesia and Lopez-Garcia, 1997), seven types in *Hemidactylus flaviviridis* (Maurya and Srivastava, 2006). The detailed study in the dorsomedial cerebral cortex is dispersed and scanty describing single type in each layer of the lizard *Agama agama* (Wouterlood, 1981) and three types in the each layer of snake's dorsomedial cortex (Ulinski, 1979).

The first purpose of this study was the identification and classification of the neuronal types present in the dorsomedial cortex of the common Indian wall lizards, *Hemidactylus flaviviridis* and the second objective was to find out the homology of the lizard's dorsomedial cortex with avian and mammalian cortical structures (supposed to be homologous) (Martinez-Guijarro et al., 1984; Montagnese et al., 1996) on the basis of neuronal morphology and their connections.

Methods

Cresyl violet study

Adult animals were captured in the surroundings of Allahabad (Uttar Pradesh, India), and experiments were carried out according to animal care guidelines of ethical committee of University of Allahabad. Five anaesthetized adult lizards (*Hemidactylus flaviviridis*) were perfused with 100 ml of physiological saline followed by 10% formalin solution for 1 hour. The brain was immediately removed out from the skull and fixed in 10% formalin. The brain was dehydrated in upgrade of alcohol (30%, 50%, 70%, 90%, 100%), cleared in Xylene and embedded in paraffin at 58°C. 10 µm thick serial sections were cut with the help of rotary microtome and stained with Cresyl violet to study the cyto-architecture of the cerebral cortex of the lizard.

Golgi study

Thirty three common Indian wall lizards (*Hemidactylus flaviviridis*) were sacrificed for the Golgi study. Under ether anesthesia, animals were perfused with 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1M phosphate buffer, pH 7.2-7.4 by immersion in the fixative. Then the brain was immediately removed out from the skull and kept overnight in the same fixative at 4°C. For staining, the Golgi-Colonnier method was used (Colonnier, 1964) with some improvements (Berbel, 1986; Luis De La Iglesia and Lopez-Garcia, 1997) adapted to our material (i.e., 3 to 5 days of induration's at 4°C in a mixture of 2.4% potassium dichromate and 5% glutaraldehyde followed by 1 to 2 days of impregnation in 0.75% silver nitrate). After impregnation the brain was dehydrated in different grades of alcohol, cleared in xylene and embedded in paraffin wax (m. p. 52-56°C). 60 to 100 µm thick transverse sections

were cut by the rotary microtome. Sections were cleared in xylene and mounted in DPX. Selected neurons were photographed by using "Computer aided Photomicroscope (Nikon Eclipse 80i)" and Camera-Lucida drawing was made at the magnification 400X (40 x 10X) with the help of microscope equipped with Camera Lucida.

Results

Cresyl violet study

The brain organization of *Hemidactylus flaviviridis* was observed to be typical vertebrate type. In the cerebral hemisphere of *H. flaviviridis*, a roof (pallium) and a floor (subpallium) had been recognized.

In the pallium (cerebral cortex) four cortical regions were observed and named according to their relative mediolateral position as medial cortex (MCx), dorsomedial cortex (DMCx), dorsal cortex (DCx) and lateral cortex (LCx) (Fig. 1A-C). The septal area occupied the medial portion of the subpallium, whereas the lateral portion organized by the dorsal ventricular ridge (DVR) and the striatum (SE).

The cerebral cortex of *H. flaviviridis* displayed three distinct neuronal layers and an ependymal layer. The basic pattern of three continuous layers could be seen in the cresyl violet stained transverse sections through the cerebral hemisphere at the intermediate level (Fig. 1B). The layers were outermost layer-I (outer plexiform layer), middle layer-II (cell layer) and inner layer-III (inner plexiform layer)

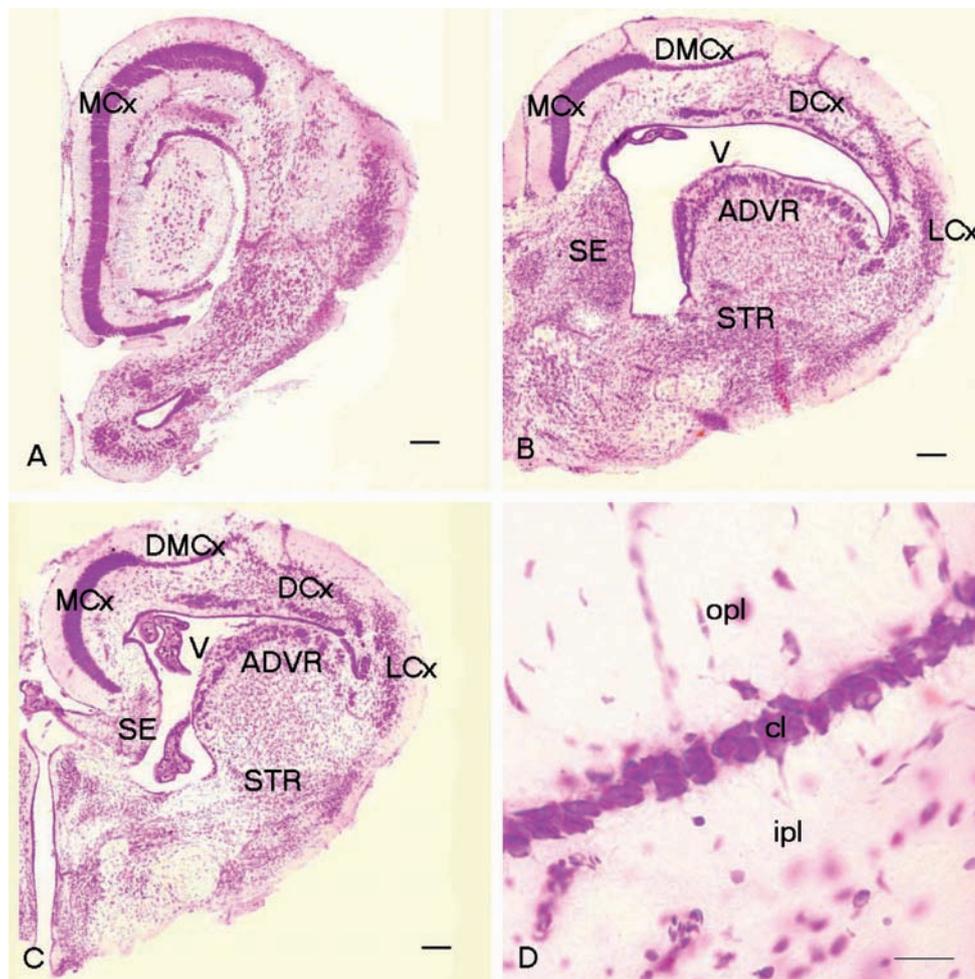


Fig. 1. - Cresyl violet stained photographs showing position of four cortical areas in the sections passing through (A) rostral, (B) intermediate, and (C) caudal level of the cerebral hemisphere. (D) Photograph shows the enlarged view of dorsomedial cortex at higher magnification. ADVR: anterior dorso ventricular region; MCx: medial cortex; DMCx: dorsomedial cortex; SE: septum; DCx: dorsal cortex; LCx: lateral cortex; V: ventricle; opl: outer plexiform layer; cl: cell layer; ipl: inner plexiform layer; STR: striatum. (Scale bar A-C = 100 μ m; D = 25 μ m)

(Fig. 1D). The thickness of outermost layer-I ranged from 28-210 μm . This layer had only few neuronal somas and also the dendrites ascending from subjacent layer-II. Layer-II was characterized by densely packed neuronal cell bodies. It also contained dendrites descending from outer layer-I and ascending from inner layer-III. The thickness of layer-II ranged from 19-93 μm . Layer-III was 28-269 μm thick having loosely packed neuronal cell bodies. It also contained dendrites descending from layer-I and II and ascending processes from ependymal layer. Below the inner plexiform layer an ependymal layer was also observed to be present just above the ventricle (V). This layer was observed in all the cortical areas except the lateral cortex.

The thickness of the three layers: outer plexiform layer, cell layer and inner plexiform layer of the dorsomedial cortex have been given in the Table I at the rostral, intermediate and caudal level of cerebral hemisphere of the *H. flaviviridis*.

The four cortical regions of cerebral cortex were not continuous with each other and the sheet of somas in the cell layer-II was interrupted by a discontinuity in the different regions. The dorsomedial cortex was overlapped with the medial extreme of the dorsal cortex whereas the lateral portion of the dorsal cortex overlapped by the lateral cortex (Fig. 1B, 1C). The result of this discontinuity and overlap was that the basic tri-laminar pattern was replaced by five-layered cortex within the annulus of overlap.

At the caudal level all the four cortical areas were clearly demarcated; while at the most rostral level only medial cortex was observed forming a continuous layer. The lateral cortex was clearly observed at the intermediate level and it became smaller at caudal level.

Golgi study

A Golgi analysis was made of the cell types present in the dorsomedial cerebral cortex of the lizard

H. flaviviridis. The Golgi impregnation procedure gave highly variable results depending on individual animals or unknown experimental factors; i.e., from almost no impregnated cells in the cerebral cortex to large quantities of impregnated cells (Fig. 2A). The Golgi impregnation study of dorsomedial cortex was made in the experiments in which the maximum number of impregnated neurons were achieved. The neurons were carefully selected for the study that showed well-developed dendritic tree pattern and clear dendritic branching. The axonal branching pattern was also traced for exploring the connections. The dorsomedial cortex showed four-layered cortical structure: the outer plexiform layer (200 μm thick), the cell layer (30 μm thick) and inner/deep plexiform layer (250 μm thick) with an additional fibre layer just above to ependymal layer (Fig. 2A). The cellular layer of the medial cortex, which mostly populated by the spinous bitufted neurons, was continued in the dorsomedial cortex. The cell layer of dorsomedial cortex was thinner (2 to 3 cell thick) than the cell layer of medial cortex (6-8 cell thick). The cell layer of the dorsomedial cortex was not found to be continuous with the cell layer of dorsal cortex instead it became interrupted in between. The cell layer of dorsal cortex was found to be extending up to the third layer of dorsomedial cortex below the second layer.

All the projection neurons of dorsomedial cortex had their cell body located in the cell layer and sent their dendritic branches towards the outer and inner plexiform layer (Fig. 2A). Solitary cells were observed in the superficial & deep plexiform layer and also in the fiber layer. Different types of neurons were classified on the basis of the soma shape and dendritic tree pattern as bitufted, pyramidal, inverted pyramidal, bipyramidal, multipolar and candelabra like monoftufted neurons (Fig. 2B-G). Dendrites of these projection neurons of cell layer-II were covered with many short spherical to long-oval dendritic spines. The morphology of the den-

Table I. - Thickness of the three layers of dorsomedial cortex of the lizard, *Hemidactylus flaviviridis* at the rostral, intermediate and caudal level.

Layers	Rostral	Intermediate	Caudal
L-I	131-170 μm	106-177 μm	99-177 μm
L-II	21-28 μm	18-35 μm	21-32 μm
L-III	156-195 μm	205-248 μm	181-269 μm

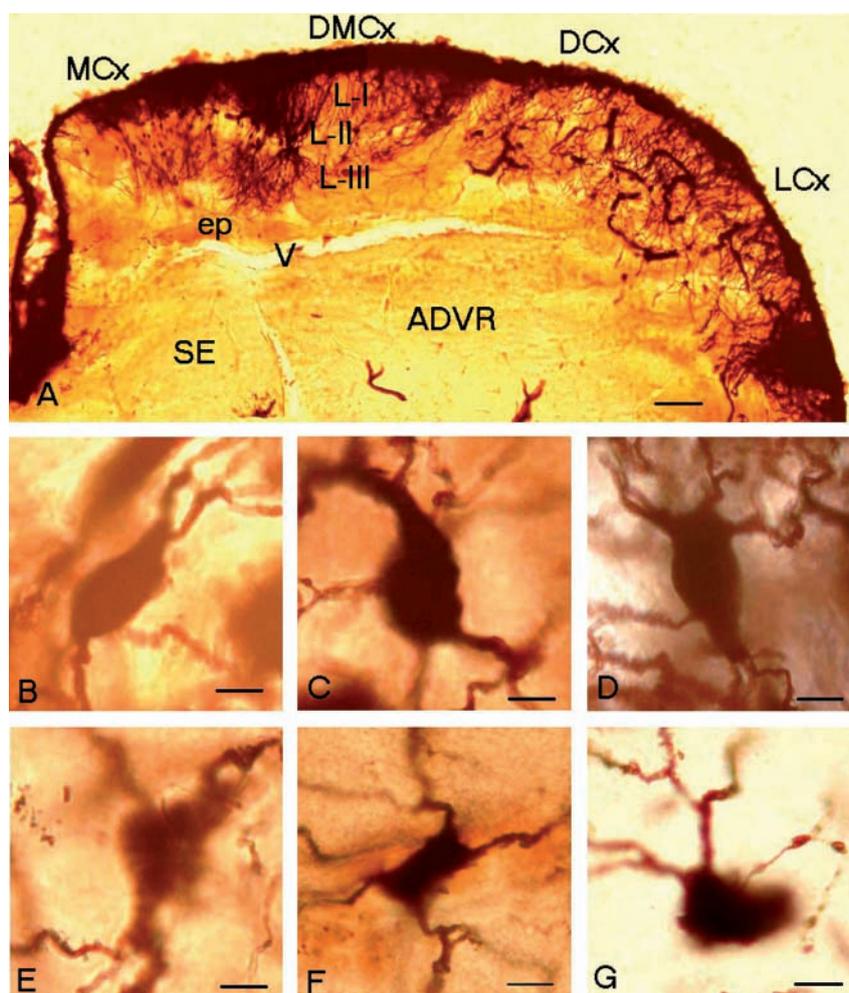


Fig. 2. - (A) Typical aspect of the cerebral cortex of a well Golgi impregnated brain. Morphology of the principal neuron cell bodies; (B) bitufted; (C) pyramidal; (D) inverted pyramidal; (E) bipyramidal; (F) multipolar; and (G) candelabra like monotufted neuron. ADVR: anterior dorso ventricular region; MCx: medial cortex; DMCx: dorsomedial cortex; SE: septum; DCx: dorsal cortex; LCx: lateral cortex; V: ventricle; ep: ependymal layer. (Scale bar: A = 100 μm ; B-G = 10 μm)

dritic spines was highly variable: some were long and pedunculated with large oval and mushroom shaped head, while other had a short peduncle with round head. The axonal arbors of these neurons had vertical and horizontal branches that sometimes invaded the adjacent cortical layers. In the layer-III of dorsomedial cortex projections of the neurons of cell layer-II seemed to extend towards the cell layer of dorsal cortex.

Using characteristics such as criteria of location, soma shape and size, dendritic tree pattern/dendritic field shape, and dendritic spine covering six classes of neurons could be distinguished in the cellular layer of dorsomedial cortex of *H. flaviviridis*. Table II summarizes the percentage and mean soma size of the neurons of dorsomedial cortex of *H. flaviviridis*.

Bitufted neurons

These neurons had vertically arranged fusiform somata, which were long, slender, or short thick (20 x 9 μm , mean size), but they always had their cell bodies located in the center of the cell layer (Fig. 3C-1, 3D-3). Two thick dendritic shafts arising from each pole of the soma gave rise to the two dendritic tufts. Apical dendrites spread into the outer plexiform layer and showed subsequent branches which sometimes reached beneath the outer limiting membrane (Fig. 3A-1, 5A-1). The basal dendritic tuft emerged from the basal shaft, which traversed the cell layer and ramified just on the border with the inner plexiform layer (Fig. 5A-1). The basal dendrites were less ramified and spread into the upper part of the inner plexiform layer. The axon arose

Table II. - Characteristics features of the projection neurons, present in the cell layer-II of dorsomedial cortex of the lizard, *Hemidactylus flaviviridis*.

Type	Descriptive name	Layer	n	Percentage	Mean soma size (μm)
1.	Bitufted neurons	cl	25	10.25%	20 x 9
2.	Pyramidal neurons	cl	47	19.27%	19 x 13
3.	Inverted pyramidal neurons	cl	17	6.97%	21 x 12
4.	Bipyramidal neurons	cl	89	36.49%	20 x 12
5.	Multipolar neurons	cl	49	20.09%	19 x 12
6.	Candelabra like monotufted neurons	cl	16	6.56%	14 x 11

Cl: cell layer.
Percentage is given as n.100/243, 243 is the number of neurons examined in this study, immature neurons are not included in this table.

from the basal pole of the soma, from the basal dendritic trunk, or from a basal dendrite, and went down to the alveus, giving rise to beaded collaterals in the deep inner plexiform layer (Fig. 5A-1).

Pyramidal neurons

These neurons had conical to pyramidal shaped somata (19 x 13 μm , mean size) situated in the inner rim of the cell layer (Fig. 3B-1, 3C-2, 3D-1). The length of soma ranges from 15 to 23 μm while width ranges from 10 to 16 μm . An apical dendritic trunk traversed the cell layer and ramified at the limit with the outer plexiform layer, giving rise to two to five primary dendrites, which showed spine covering. These primary dendrites bifurcated again once or twice which gave rise to subsequent secondary and tertiary dendrites, which soon acquired intense spine covering as they traversed the outer plexiform layer. Their distal segments ran underneath the brain surface, closely attached to the limiting membrane. The basal tuft was composed of two to four primary dendrites arising from the basolateral sides of the soma. These may bifurcate into secondary dendrites, which represented spine covering. The basal dendrites might run deep in to the inner plexiform layer or sometimes they ran horizontal to the inner plexiform layer (Fig. 3C-2). A typical projection axon originated directly from the basal part of the soma or sometimes from the juxta somatic segment of a basal dendrite (Fig. 3B-1).

Inverted pyramidal neurons

These neurons have conical to pyramidal shaped somata (21 x 12 μm , mean size), whose apical dendrite oriented towards the inner plexiform layer (Fig. 3D-2, 5D-2). The length of soma ranges from 13 to 30 μm while width ranges from 8 to 12 μm .

The apical dendrites bifurcate in to secondary and tertiary dendrites, which show intense spine covering as they traverse the inner plexiform layer. From the basolateral side of the soma more than two shafts like primary basal dendrites are originated which may bifurcate in the outer plexiform layer. These subsequent secondary and tertiary dendrites extend in the outer plexiform layer, sometimes up to the underneath of outer limiting membrane (Fig. 5D-2). All these dendrites show intense spine covering at distal segment and fewer spines on the proximal end of the primary dendrites. The axon originated from the basal end or from basal primary dendrite and run along the cell layer to reach in the inner plexiform layer (Fig. 5D-2).

Bipyramidal neurons

These neurons have biconical or bipyramidal shape cell body (20 x 12 μm , mean size), whose length varies from 14 to 26 μm and width ranges from 6 to 15 μm (Fig. 4A-D). The apical and basal pole gave rise to two to four primary dendrite, which show moderate, or no spine covering at beginning but moderate to intense spine covering at distal end. The subsequent secondary and tertiary dendrites show intense spine covering. At the both lateral side of the soma dendrites were observed which ran some distance in the cell layer and then goes either outer or inner plexiform layer (Fig. 6A-D). This is the characteristic feature of these neurons, which differentiate them from the pyramidal and bitufted neurons. The axon originated from the basal pole of the soma or from the basal primary dendrite and run along the basal dendritic branches, which soon gave rise to many distal collaterals that spread in to the deepest part of inner plexiform layer (Fig. 4C, 4D).

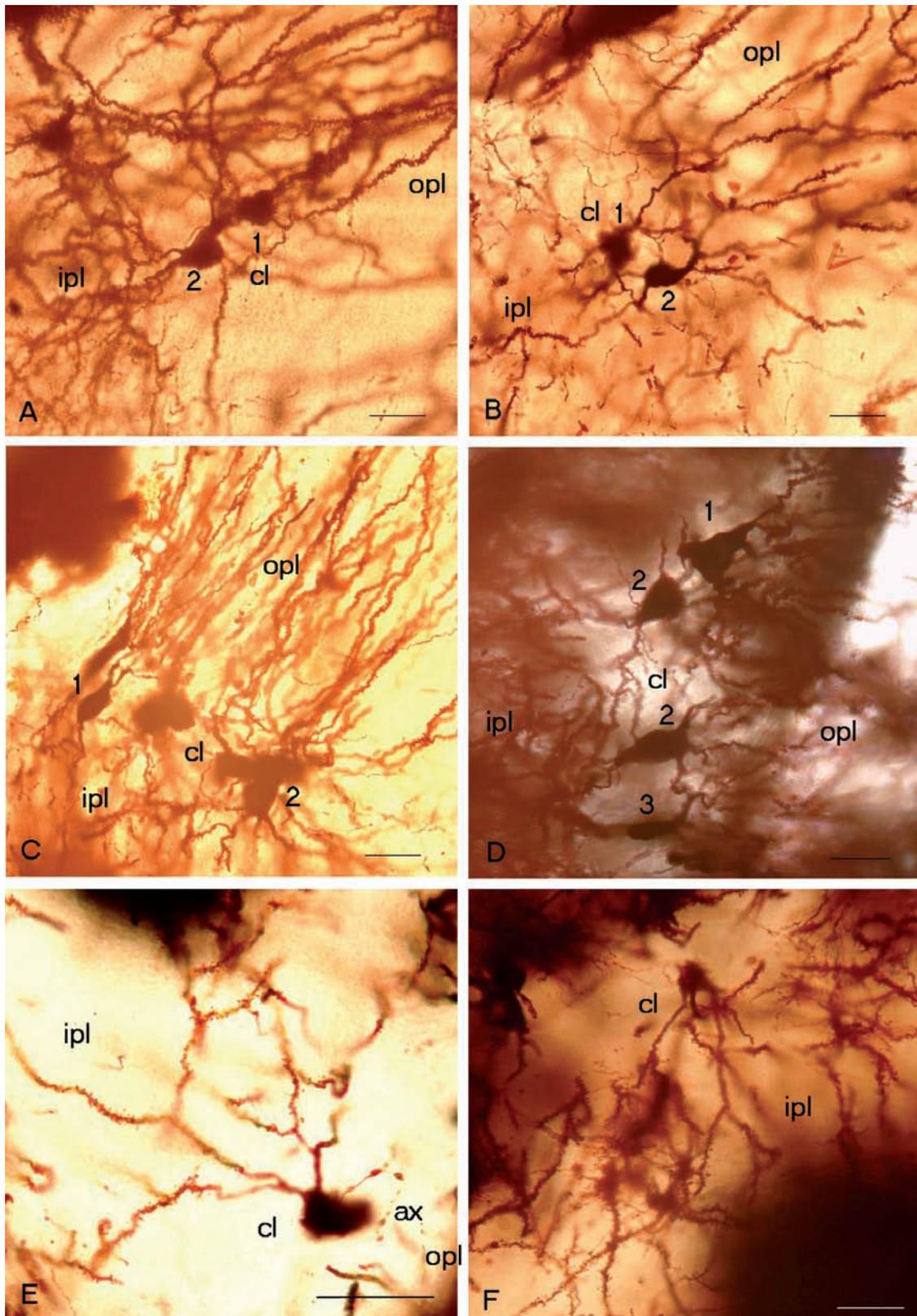


Fig. 3. - Computer photographs illustrating dorsomedial cortex neurons: (A) 1- bitufted neuron, 2- bipyramidal neurons; (B) 1- pyramidal neuron, 2- bipyramidal neuron; (C) 1- bitufted neuron, 2- pyramidal neuron; (D) 1- pyramidal neuron, 2- inverted pyramidal neurons, 3- bitufted neuron; (E-F) candelabra like monotufted neuron. opl: outer plexiform layer; cl: cell layer; ipl: inner plexiform layer; ax: axon. (Scale bar = 25 μm)

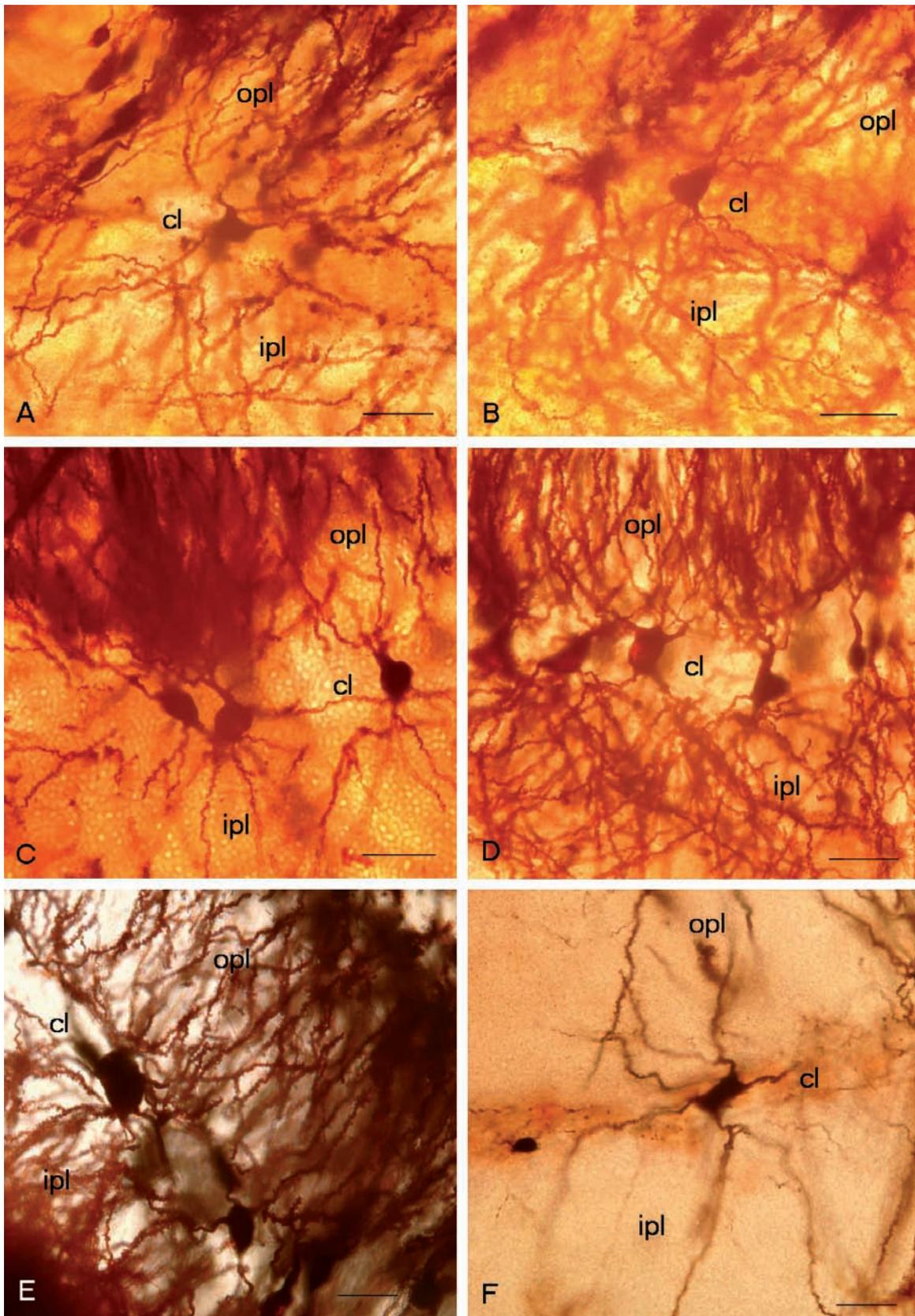


Fig. 4. - Computer photographs illustrating dorsomedial cortex neurons: (A-D) bipyramidal neurons; (E-F) multipolar neurons. opl: outer plexiform layer; cl: cell layer; ipl: inner plexiform layer. (Scale bar = 25 μ m)

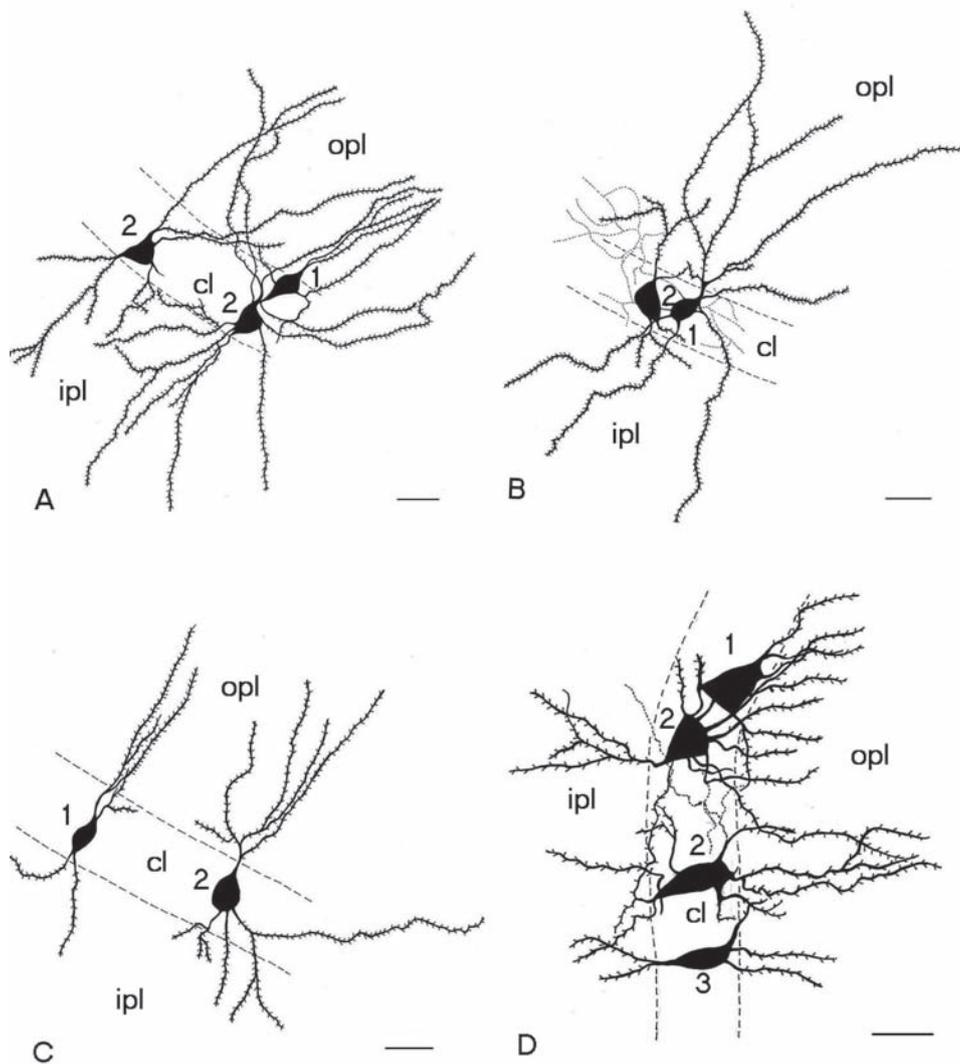


Fig. 5. - Camera lucida drawing of dorsomedial cortex neurons: (A) 1- bitufted neuron, 2- bipyramidal neurons; (B) 1- pyramidal neuron, 2- bipyramidal neuron; (C) 1- bitufted neuron, 2- pyramidal neuron; (D) 1- pyramidal neuron, 2- inverted pyramidal neurons, 3- bitufted neuron. opl: outer plexiform layer; cl: cell layer; ipl: inner plexiform layer. (Scale bar = 25 μ m)

Multipolar neurons

These neurons have polygonal or ovoid cell bodies located in the cell layer. The length of soma ranges from 15 to 25 μ m while width ranges from 10 to 16 μ m (Fig. 4E-F). The cell body (19 x 12 μ m, mean size) of these neurons gave rise to three to six primary dendrites that ramify near the soma with acute angles. Primary dendrites are thicker and spines may be seen on dendrites but they are sparsely distributed at the beginning and intense spine covering could be seen after some distance in primary dendrites. Secondary dendritic branches were observed to mostly populated by the intense spine covering.

Spine covering in these neurons seems to be more regular than the other dorsomedial cortex neurons. The ascending dendrites that cross the cell layer and reach the upper strata of the outer plexiform layer, where they ran beneath the limiting membrane. The long descending dendrites cross the cell layer and reach the deepest strata of the inner plexiform layer, where they sometimes ramify (Fig. 7A-B). The dendrites are devoid of spine when they are located in the cell layer and also some distance in the inner plexiform layer, but they show moderate number of spine covering at the distal segment. Generally the spine density increases as the distance from the

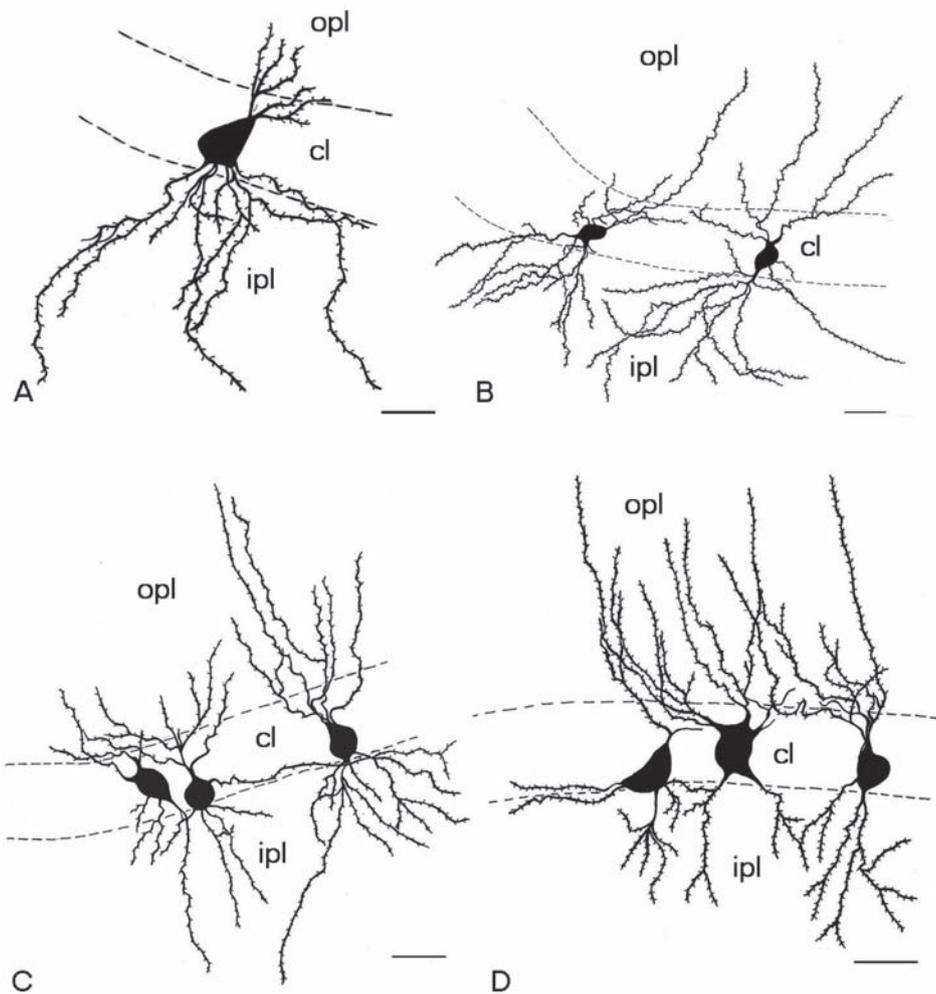


Fig. 6. - Camera lucida drawing of dorsomedial cortex neurons: (A-D) bipyramidal neurons. opl: outer plexiform layer; cl: cell layer; ipl: inner plexiform layer. (Scale bar = 25 μm)

soma increases. The axon emerges from the soma or from a primary dendrite and gives off many distal collaterals which run along distances over the cell layer and deepest part of the inner plexiform layer (Fig. 7B).

Candelabra like monotufted neurons

These neurons had their cell body (14 x 11 μm , mean size) located in the cellular layer of dorsomedial cortex (Fig. 3E-F). These neurons represent 6.56% of total population. 75% of these neurons sent their dendrites towards the inner plexiform layer, while 25% towards the outer plexiform layer. The dendritic branching in these neuronal types was very high and represents candelabra like profuse

branching pattern, which is comparable with those of the monotufted neurons of the medial cerebral cortex (Fig. 7C-D). These neurons have heavily spinous covering on their dendritic branches. These neurons show short axon, which may run parallel to the dendrites towards the respective plexiform layers (Fig. 7C).

Discussion

The study of the neuronal classes in the dorsomedial cortex of the lizard is important for a better understanding of the evolution of the cerebral cortex in vertebrates. Several authors have used the Golgi

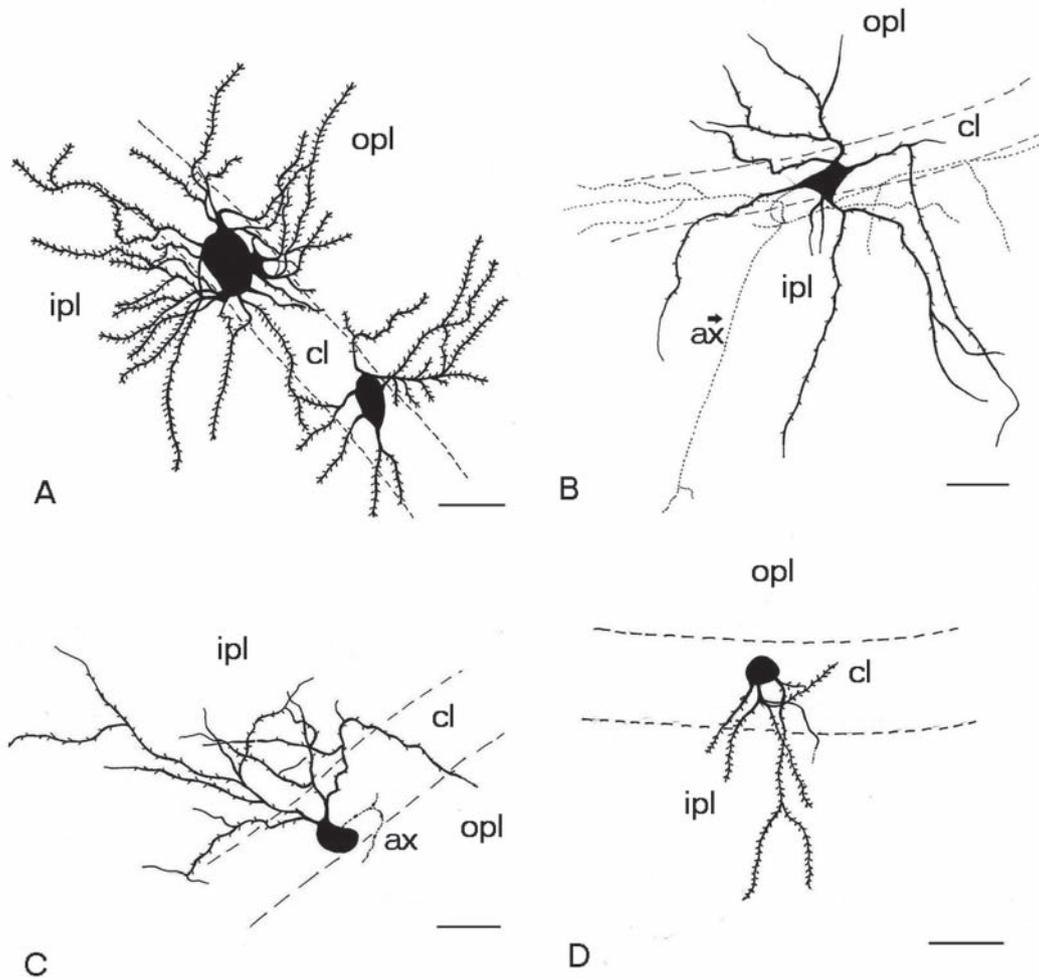


Fig. 7. - Camera lucida drawing of dorsomedial cortex neurons: (A) multipolar neurons; (B) multipolar neuron; (C) candelabra like monotufted neuron; (D) candelabra like monotufted neuron. opl: outer plexiform layer; cl: cell layer; ipl: inner plexiform layer; ax: axon. (Scale bar = 25 μ m)

method to reveal the morphology of the neurons and neuropil in the cerebral cortex of lizards (Ulinski, 1974, 1976, 1977; Wouterlood, 1981; Martinez-Guijarro et al., 1984; Berbel et al., 1987; Berbel, 1988; Luis De La Iglesia and Lopez-Garcia, 1997; Maurya and Srivastava, 2006; Molnar et al., 2006; Lopez-Garcia et al., 2002; Abhinav and Srivastava, 2006; Srivastava et al., 2007b). By using Nissl and Golgi methods six neuronal types have been distinguished in the dorsomedial cerebral cortex of *H. flaviviridis* namely bitufted neurons, pyramidal neurons, inverted pyramidal neurons, bipyramidal neurons, multipolar neurons, and candelabra-like monotufted neurons. In the cellular layer of the dorsomedial cortex of reptiles the number of neuronal types varies

considerably. In the lizard *Agama agama* six types of pyramidal-like candelabra cells (Wouterlood, 1981) and in *Lacerta* only two types namely spinous bipyramidal neurons and smooth neurons (Berbel et al., 1987) have been observed, while in case of snakes single type of double pyramidal cells were reported (Ulinski, 1979). The increased number of neuronal types may be explained on the basis of the classification criteria used in the present study such as dendritic tree pattern, dendritic tree orientation, soma shape, spine covering and location of somata. It is possible that different neuronal types described here may show resemblance with previously reported neuronal types in cell layer of dorsomedial cortex of other reptiles.

In the lizard *H. flaviviridis* the neurons of the dorso-medial cortex have medium/large (14 x 11 μm to 21 x 12 μm) sized somata in comparison to the small/medium (10 x 7 μm to 12 x 8 μm) sized somata of the neurons of medial cortex (Maurya and Srivastava, 2006). The spine density over the dendritic branches increases as the distance from the soma increases in the neurons of dorsomedial cortex. Three neurons namely pyramidal, bipyramidal and multipolar neurons seems to be dominated in the dorsomedial cortex, which clearly differentiate this region from the small celled medial cortex neurons which is populated by bitufted, granular and candelabra neurons (Luis De La Iglesia and Lopez-Garcia, 1997; Maurya and Srivastava, 2006; Srivastava et al., 2007b).

In the dorsomedial cortex of the lizard *Agama agama*, large pyramidal cells of one type have been reported in the cellular layer (Wouterlood, 1981), while in case of snakes the dorsomedial cortex has double pyramidal cells with their somata loosely packed in layer-II (Ulinski, 1979). In the lizard *Podarcis hispanica* aspinoous multipolar neurons have been reported in the inner plexiform layer of dorsomedial cortex (Bernabeu et al., 1994), while in *M. carinata* spinous multipolar neurons are observed in the layer-II (Srivastava et al., 2007b). In the presently studied lizard bitufted, pyramidal, inverted pyramidal, bipyramidal, multipolar and pyramidal like candelabra neurons were found in the layer-II of the dorsomedial cortex which are also reported in *M. carinata* except the bitufted neurons (Srivastava et al., 2007b). Pyramidal neurons of the lizard *H. flaviviridis* and *Agama agama* (Wouterlood, 1981) are comparable with respect to their morphology, while bipyramidal neurons observed in the presently studied *H. flaviviridis* are in consistence to the double pyramidal cells reported in dorsomedial cortex of snakes (Ulinski, 1979). The candelabra neuron of the dorsomedial cortex seems to be characteristic of the presently studied lizard and of *M. carinata* (Srivastava et al., 2007b) which has not been reported in other lizards and snakes (Ulinski, 1979; Wouterlood, 1981).

Usually no immunoreactive somata could be observed in the cell layer of the dorsomedial cortex of *Podarcis hispanica*, although several short processes immunoreactive for PSA-NCAM were observed intermingled in between the pyramidal neurons of dorsomedial cortex of *Podarcis hispanica*. Some fusiform immunoreactive cells similar to

those found in the medial cortex were observed in the inner plexiform layer of dorsomedial cortex of *P. hispanica*. These cells were always located in the medial end of the dorsomedial cortex and appeared towards the medial cortex cell layer (Ramirez-Castillejo et al., 2002). The bitufted neurons of dorsomedial cortex of *Hemidactylus*, that are not reported in literature show poor impregnation and located close to the medial cortex which could correspond with fusiform immunoreactive cells of the inner plexiform layer of dorsomedial cortex of *P. hispanica* (Ramirez-Castillejo et al., 2002).

The bipyramidal, pyramidal, inverted pyramidal and multipolar neurons of the dorsomedial cerebral cortex of the *H. flaviviridis* extend their dendrites towards the outer limit of outer plexiform layer and occasionally they turn up towards the outer plexiform layer of medial cortex, which seems to be connected with the incoming axons from the medial cortex. The dendrites of these neurons extend throughout the thickness of the cortex and represent the intra cortical connections while the main source of extracortical efferent originates from the medial cortex (Lohman and Mentink, 1972; Ulinski, 1976; Bruce and Butler, 1984). The projections of these neurons are quite similar to the two systems of the *Gecko*, one arising from the dorsal part of the medial cortex and terminating on the proximal parts of the apical and basal dendrites while the second system originates in the ventral part of medial cortex and terminates mainly on the more distal parts of both the apical and basal dendrites of the dorsomedial cortex neurons (Bruce and Butler, 1984; Hoogland and Vermeulen-Van Der Zee, 1993). The dendrites of these neurons receive synaptic input from a variety of sources of which the most prominent is that of zinc-positive boutons coming from granule cells of the medial cortex (Lopez-Garcia et al., 1984).

In reptiles, the telencephalic roof (pallium) has developed in to a three-layered cortical structure and divided into four cytoarchitecture areas: medial, dorsomedial, dorsal, and lateral cortices (Ulinski, 1990; Luis De La Iglesia and Lopez-Garcia, 1997; Maurya and Srivastava, 2006; Srivastava et al., 2007b). Similarities between reptilian medial and dorsomedial cortex with avian hippocampus and parahippocampus include the position medial and dorsal to the ventricle, a more or less pronounced three layered organization (Lohman and Mentink, 1972;

Ulinski, 1976; Guirado et al., 1989), neuronal types (Northcutt, 1967; Ulinski, 1976; Wouterlood, 1981; Luis De La Iglesia and Lopez-Garcia, 1997; Maurya and Srivastava, 2006), and efferent and afferent projections (Ulinski, 1976; Bruce and Butler, 1984; Casini et al., 1986; Hoogland and Vermeulen-Van Der Zee, 1989). The dorsomedial cortex of presently studied lizard show resemblance with the parahippocampal area of birds due to its position dorsal to the ventricle and medial hippocampus, and the presence of multipolar neurons in the parahippocampal area of birds with medium/large cell body and four to six spinous dendritic branches (Montagnese et al., 1996; Srivastava et al., 2007a).

The pattern of extra cortical afferences and efferences of the dorsomedial cortex neurons (Bruce and Butler, 1984), and the intra cortical scheme of connections of the lizard cerebral cortex have a clear resemblance to that of the mammalian hippocampus and the entorhinal olfactory cortex (Olucha et al., 1988). The dendritic tree pattern of pyramidal and bipyramidal neurons with their dendritic spines of dorsomedial cerebral cortex of *H. flaviviridis* and other lacertilian (Martinez-Guijarro et al., 1984) are comparable with the corresponding elements on pyramidal neurons of the CA3 (Cornu ammonis 3) area of the mammalian hippocampus because it emits a prominent commissural-contralateral projection (Martinez-Guijarro et al., 1990) and also because it is the main recipient of the zinc-positive "lizard mossy fibers" coming from the medial cortex (Martinez-Guijarro et al., 1984; Lopez-Garcia and Martinez-Guijarro, 1988).

The difference in the type of neurons in this study and the previous ones may be explained by the following reasons. Golgi procedure used in this study may impregnate neuronal types at random and number of experiments may have some effect. The dendritic morphology may be influenced by location of the neurons. In addition, a certain difference in the neuronal types between the different species can be expected since there is considerable variation of behavior between them. The interconnection of neuronal morphology with the behavior needs more experiments of lesion regeneration. Consideration of homology between the distant vertebrate groups should be taken with care as the living species of these classes are much different than their ancestors who may have their origin from the same stock.

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