

THE CYTO-ARCHITECTURE AND MORPHOLOGICAL DIVERSITY OF THE DORSAL CORTEX NEURONS IN THE GARDEN LIZARD CALOTES VERSICOLOR (DAUDIN)

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Abstract:-

The cyto-architecture and morphology of the neuronal types of the dorsal cerebral cortex of the lizard, *Calotes versicolor* has been studied with the help of Cresyl violet staining and Golgi impregnation method. The dorsal 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 three to four 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. Using different characteristics such as criteria of location, dendritic tree pattern, dendritic spine covering and soma shape seven classes of neurons were distinguished in the cellular layer of dorsal cortex of *Calotes versicolor* : multipolar neurons, pyramidal neurons, monotufted bipolar neurons, monotufted neurons, bitufted neurons, inverted pyramidal neurons and aspiny bipolar neurons. The dorsal cerebral cortex shows the pyramidal and multipolar neurons to be dominant type with 38.71% and 30.65% respectively whereas the aspiny bipolar neurons show only 2.69%. The multipolar neurons have mostly intracortical dendritic branching and connections. The spine density of dendrites of the dorsal cortex ranges from 22.67 ± 8.18 to 30.76 ± 7.64 spines in pyramidal, bitufted and multipolar neurons (moderately spinous) whereas it ranges from 10.83 ± 5.64 to 18.18 ± 02.88 spines in monotufted bipolar, monotufted and bitufted bipolar neurons (sparsely spinous) per 25 μ m-length of dendritic segment.

Keywords:- Spine density, Neuronal types, Golgi technique, Reptiles.

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 [1], [2], [3], [4], [5], [6], [7], which are populated by scarce interneurons and where the afferent connections terminate in a highly laminated fashion [4]. The inner plexiform layer (ipl) is separated from the lateral ventricle by a thin layer of ependymal cells that retain neurogenic capabilities during adulthood [8]. The lizard dorsomedial cortex has been considered homologous to the CA3 area of the mammalian hippocampus because it emits a prominent commissural-contralateral projection [2], and because it is the main recipient of the zinc-positive “lizard mossy fibres” coming from the medial cortex [9], [2]. 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 [10], [11], [12], 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 [13], [14]. Spinous bipyramidal neurons are the main neuronal type found in the cellular layer of dorsomedial cerebral cortex of the lizards *Agama agama* [12], [15], and snakes [16]. The somata of these neurons form the granular layer, and their dendrites extend into the outer and inner plexiform layers [17], [18], [19], [20], [16], [12], [21], [22], [15]. 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 [23]. The medial and the dorsomedial cortex were collectively called as the mediodorsal cerebral cortex [24], [12]. The small celled part of the mediodorsal cortex is presently called as the medial cortex and the large part as the dorsomedial cortex [22], [16], [4], [5], [6], [7], [25]. 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* [32], five types in the lizard *Lacerta ptyusensis* [26], and in *Podarcis hispanica* [3], seven types in *Hemidactylus flaviviridis* [6]. The detailed study in the dorsomedial cerebral cortex is dispersed and scanty describing single type in each layer of the lizard *Agama agama* [12] and three types in the each layer of snake’s dorsomedial cortex [16].

The first purpose of this study was the identification and Classification of the neuronal types present in the dorsal cortex of the garden lizard *Calotes versicolor* and the second objective was to find out the homology of the lizard’s dorsal cortex with avian and mammalian cortical structures (supposed to be homologous) [22], [13], on the basis of neuronal morphology and their connections.

METHODS AND 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. Four anaesthetized adult lizards (*Calotes versicolor*) were perfused with 100 ml of physiological saline followed by 10% formaline solution for 1 hour. The brain was immediately removed out from the skull and fixed in 10% formaline. The brain was dehydrated in upgrade of alcohol (30%, 50%, 70%, 90%, and 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:

Seventeen garden lizard *Calotes versicolor* were sacrificed for the Golgi study. Under ether anesthesia, animals were perfused with 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1M phosphate buffer, pH7.2-7.4 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 [27], with some improvements [28], [3], adapted to our material (i.e., 3 to 5 days of indurations 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 *Calotes versicolor* was observed to be typical vertebrate type. In the cerebral hemisphere of *C. versicolor*, 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). 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 *C. versicolor* 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. 1).

The layers were outermost layer-I (outer plexiform layer), middle layer-II (cell layer) and inner layer-III (inner plexiform layer) (Fig. 2). The thickness of outermost layer-I ranged from 15-52 μ m. This layer showed only a few neuronal somas and also the dendrites ascending from subjacent middle layer. Layer -II was characterized by densely packed neuronal cell bodies (somata). It also had dendrites descending from outer layer-I and ascending from inner layer-III. The thickness of layer-II ranged from 11-25 μ m. Layer-III was 16-67 μ m thick having loosely packed neuronal cell bodies. It also showed dendrites descending from layer-I & II and ascending processes from ependymal layer. Below the inner plexiform layer an ependymal layer was seen just above the ventricle (V).

The four cortical regions of cerebral cortex were not continuous with each other and the sheet of somata 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. 1). 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.

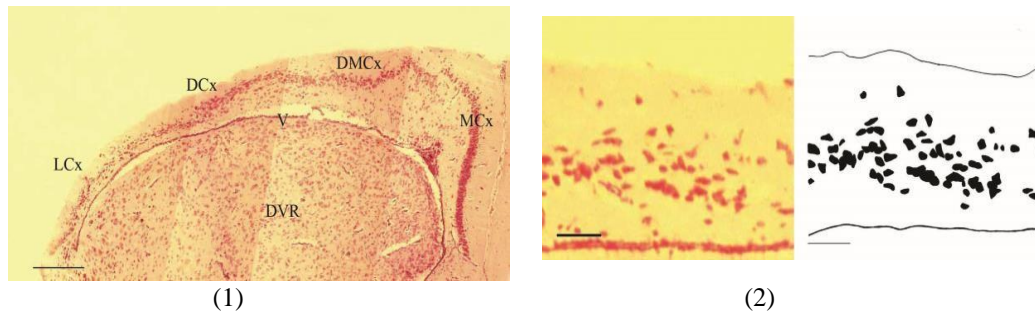


Fig. 1. Photomicrograph of the cresyl violet stained transverse section at the intermediate level showing the three layered structure of the cerebral cortex. Scale bar =100 μ m.

Fig. 2. Photomicrograph and drawing showing the enlarged view of the dorsal cortex at higher magnification. Scale bar =10 μ m.

Golgi study:

A Golgi analysis was made of the cell types present in the dorsal cerebral cortex of the lizard *Calotes versicolor*. 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 dorsal cortex displays three distinct neuronal layers and an ependymal layer. The neurons of the dorsal cortex have their cell body mostly located in the cellular layer and solitary cell bodies are observed in the upper periphery of cell layer. All these neurons send their dendritic branches towards the outer and inner plexiform layer. The dendritic tree of projection neurons, dendritic thickness, dendritic spine frequency and shape appeared variable feature. The thickness of apical dendrites of the neurons of dorsal cortex ranged between 1.22 \pm 0.02 μ m to 2.26 \pm 0.53 μ m in bitufted neurons and pyramidal neurons respectively (table. 1).

Dendrites of the neurons of cell layer-II were covered with many short spherical to long-oval or mushroom headed dendritic spines (fig. 3). Densities of spines were observed to be different on the dendrites (table. 2). The spine density of dendrites ranged from 30.76 \pm 7.64 spines to 10.83 \pm 5.64 spines per 25 μ m length of dendritic segment in moderately spinous and sparsely spinous respectively. The length of spines present on apical dendrites ranged between 1.97 \pm 0.55 μ m to 2.50 \pm 0.64 μ m, while the diameter of spine head varied from 1.18 \pm 0.02 μ m to 1.44 \pm 0.18 μ m on the apical dendritic of the neurons. Length of axon observed in multipolar, pyramidal and bitufted neurons were up to 65 μ m, 85 μ m and 48 μ m long respectively. Surface of axon was devoid of spines and collaterals were not seen in all the presently studied neurons. It ran down towards deeper layer of the inner plexiform layer. Using characteristics such as criteria of location, soma shape and size, dendritic tree pattern/dendritic field shape, and dendritic spine covering, seven types of neurons have been distinguished in the cellular layer of dorsal cortex viz. bitufted, pyramidal, inverted pyramidal, multipolar, monotufted, monotufted bipolar and aspiny bipolar neurons. The characteristics of the dorsal cortex neurons have been summarized in the table 3.

Type 1. Bitufted neurons:

The neurons of this type had fusiform medium sized somata (15 \times 11 μ m in diameter), which were large or small. The soma was either vertically arranged or horizontally arranged (fig. 9 A-C; 8 A-C). Cell bodies of these neurons were always located in the upper periphery or the center of the cell layer. Two thick dendritic shafts arising from each pole of the soma gave off the two dendritic tufts, and they extended up to 163 μ m. The tuft of apical dendrite sent primary dendrites towards the outer plexiform layer, and showed subsequent branches, which sometimes reached to beneath the outer limiting membrane. Apical dendrite (1.22 \pm 0.02 μ m thick) had one to three branching points and acute bifurcation angles. The basal dendritic tuft emerged from the basal pole of the soma, which traversed the cell layer and ramified just on the border in the inner plexiform layer. Basal tuft was less developed than the apical tuft. Dendrites of these neurons were moderately spinous. The spine density was 23.52 \pm 5.49 spines per 25 μ m-length dendritic segment on the apical dendrites, while the length of spines present on apical dendrites was long (2.38 \pm 0.48 μ m) and the diameter of spine head was observed to be

1.18±0.02µm. The axon (48µm long) emerged from the soma or from the basal dendritic shaft, and ran down towards the inner plexiform layer.

Type 2. Pyramidal neurons:

These neurons had medium sized somata (14×9 µm) situated in the center of cell layer (fig. 5E, F; 6A; 7A). Soma shape varied from pyramidal, conical, and triangular to pyriform shaped. Apical dendritic trunk ramified quite away from the soma at the limit of the outer plexiform layer, giving rise to two to three primary dendrites, which bifurcated again once or twice to give off secondary and tertiary dendrites. Apical dendrites were (2.26±0.53 thick) more developed than the basal dendritic. The basal dendritic was composed of two to three primary dendrites, which ramified, giving off secondary and tertiary dendrites. They ran deep into the inner plexiform layer or sometimes ran horizontally in the cell layer. The dendrites of these neurons extended up to 217µm and showed moderately spinous covering. The mean spine density per 25µm-length dendritic segment on the apical dendrites was found to be 30.76±7.64 and means of spine length and diameter of spine head were 2.50 ±0.64µm and 1.44±0.18µm respectively. Axon (85µm long) originating from the basal part of the soma could be characterized by absence of spines, and ran towards the inner plexiform layer.

Type 3. Inverted pyramidal neurons:

The inverted pyramidal neurons with medium sized somata (15×8µm) showed all the characteristics of pyramidal neurons except that its apical dendrites get oriented towards the inner plexiform layer (fig. 6 E, F; 7 E, F). Cell bodies were usually located in the center of the cell layer. The dendritic field in this type of neurons extended up to 154µm towards the outer and inner plexiform layer. Apical dendrites (1.39±0.19µm thick) bifurcated giving off secondary and tertiary dendrites, which showed sparsely spinous covering (18.18±2.88 spines per 25µm-length dendritic segment) as they entered to the inner plexiform layer. The spine length observed on apical dendrite and diameter of spine head are mentioned in table 3. From the basolateral side of the soma, more than two shafts like primary basal dendrites originated, which may bifurcate in the outer plexiform layer to give off secondary and tertiary dendrites. In this type of neurons, axon usually arose from the basal end or from basal primary dendrite and ran along the cell layer to reach in the inner plexiform layer.

Type 4. Multipolar neurons:

These neurons had polygonal or ovoid large sized somata (20×12µm) located in the middle of the cell layer. Three to six very long dendrites arose from the soma. These dendrites spread throughout the outer/inner plexiform layers, and also in the cell layer. Dendritic field was observed to be 237 µm (fig. 4A-D; 5A-D). The ascending dendrites (1.29±0.03 thick) crossed the cell layer, and reached to the upper strata of the outer plexiform layer, where they ran beneath the limiting membrane. Descending dendrites crossed the cell layer, and reached to the inner plexiform layer. The primary dendrites ramified near or after a short distance from the soma to give off secondary and tertiary dendrites. The dendrites of these neurons had spinous covering. The corrected spine density per 25µm-length dendritic segment was found to be moderately distributed 22.67±8.18 on the apical dendrite. The length of spines present on apical dendrites was 1.97±0.55µm and the diameter of spine head was 1.26±0.11µm. The axon (65µm long) arose from the basal pole of the soma or from a primary dendrite, and ran down towards the inner plexiform layer. Collaterals were not found in this type of neurons.

Type 5. Monotufted neurons:

The monotufted neurons showed medium sized fusiform somata (16×9µm), situated in the center of the cell layer (fig. 8D; 9D). The soma had single dendritic shaft originating from one pole of the soma and giving rise to subsequent dendritic branches in the outer plexiform layer, and extended up to 114µm. Dendrites (1.27±0.03µm thick) of these neurons were sparsely spinous. The spine density was observed to be 15.84±3.49 spines per 25µm-length dendritic segment, and the spine length and the diameter of spine head were 2.17±0.17µm and 1.28±0.03µm respectively. In this study, the axon could not be seen in these types of neurons.

Type 6. Monotufted Bipolar neurons:

These neurons had fusiform somata with average size 17×8µm. They always had their cell bodies located in the middle of cell layer (fig. 6B-D; 7B-D). One thick dendritic shaft arose from the one pole of the soma having single dendritic tuft on apical side, and sent their dendrites towards the outer plexiform layer. The basal pole of the soma gave rise to single dendritic shaft, which showed one basal dendrite towards the inner plexiform layer. Dendrites of these neurons extended up to 134µm. Apical tuft showed two to four primary dendrites which bifurcated once or twice to give rise to secondary and tertiary dendrites. The apical dendrites (1.33±0.19µm thick) showed sparsely spinous 10.83±5.64 spines per 25-µm-length dendritic segment on all their branches. The spine length and diameter of spine head are mentioned in table 3. The axon in this type of neurons failed to impregnate.

Type 7. Aspinous Bipolar neurons:

These neurons had ellipsoidal or fusiform somata (16×11µm) located in the center of cell layer. The soma had apical and basal tapering ends. Apical dendrite traversed the cell layer and reached up to outer plexiform layer and the basal dendrite traversed the cell layer and reached just on the border of the inner plexiform layer. Both the apical and basal dendrites were without spine covering (fig. 8E, F; 9E, F).

DISCUSSION

The study of the neuronal classes in the dorsal 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 method to reveal the morphology of the neurons and neuropil in the cerebral cortex of lizards [24], [11], [29], [12], [22], [26], [15], [3], [6], [7], [4], [5], [25]. By using characteristics such as criteria of location, shape of soma, dendritic tree pattern and dendritic spine covering we have reported seven types of neurons in the cellular layer of *C. versicolor* namely pyramidal, multipolar, inverted pyramidal, bitufted, monotufted, monotufted bipolar and aspinous bipolar neurons. Five types monotufted, bitufted, candelabra, pyramidal and bipyramidal neurons have been found in the cellular layer of dorsal cortex in *M. carinata* [25], while in lizard *H. flaviviridis* four types of neurons namely monotufted, bitufted, multipolar and pyramidal have been reported [6]. In the *Lacerta galloti*, while considering the size and location within the dorsal cortex only single type of neuron have been described in the granular stratum [21]. The dorsal cortex of the lizards *Iguana* [10], and *Psammotromus algirus* [30], has been divided into two subdivisions, medialis and lateralis. Four neuronal types have been reported in the cell layer-II of the dorsal cortex of the lizard *Psammotromus algirus* which were pyramidal, bitufted, multipolar and bipolar neurons [30]. Thus the classification criteria used in considering the types of neurons may play a major role. Due to this reason two or more previously reported types match with the single type in latter studies or viceversa. In addition difference in the morphology of the neurons between the different species can be expected since there is a considerable variation between them.

All the neurons of the cell layer of dorsal cortex in *C. versicolor* were found to be uniformly distributed. The monotufted neurons observed in the presently studied lizard have not been reported in any lizard except in *M. carinata* [25], and *H. flaviviridis* [6]. The bitufted neurons, multipolar neurons and pyramidal neurons observed in the *C. versicolor* have clear matching types reported in the *Psammotromus algirus* [30], *M. carinata* [25], and *H. flaviviridis* [6], on the basis of their similar morphology. Inverted pyramidal and monotufted bipolar neurons have been observed in the layer-II of the dorsal cerebral cortex which have not been reported in dorsal cerebral cortex of the lizard *H. flaviviridis* [6], and *M. carinata* [25], may be because of its low impregnation frequency. Aspinous bipolar neurons were described as only single type of aspinous neurons in the cell layer-II of dorsal cortex of *C. versicolor*, which have not been reported in dorsal cerebral cortex of lizards except in the *Psammotromus algirus* [30]. The three neurons of reptilian dorsal cortex namely bitufted neurons, multipolar neurons and pyramidal neurons have formed the basis for comparing the medial aspect of dorsal cortex being homologous to the mammalian hippocampal formation [20], whereas the lateral aspect of the dorsal cortex has been compared to the mammalian isocortex, or at least to part of it [31]. The subdivision in the dorsal cortex of *C. versicolor*, could not be observed, which shows its less developed condition.

Anatomically the dorsal cortex of lizards differ from the isocortex in being three layered instead of six layered and in lacking columnar organization [32]. The dorsal cortex is a structure unique to reptiles, and its relationship to structures in mammalian brain is of great theoretical interest [32], [33], [34]. 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.

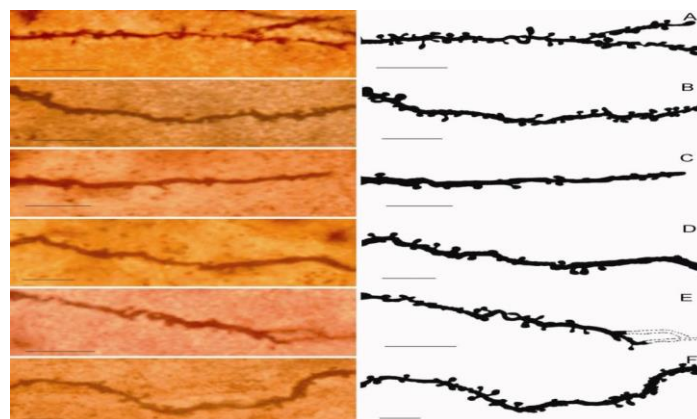


Fig. 3. Photomicrographs and drawings of intermediate segment showing Golgi- impregnated apical dendrites of the neurons of dorsal cortex with spines arising from the dendrites; pyramidal neuron (A), multipolar neuron (B), monotufted bipolar neuron (C), monotufted neuron (D), bitufted neuron (E), inverted pyramidal neuron (F). Scale bar =10 μ m.

Table 1. Mean diameter of dendrites (\pm S.D.), spine length (\pm S.D.), and diameter of spine head (\pm S.D.) for apical dendrites of the different types of dorsal cortex neurons of *Calotes versicolor*.

No.	Type of Neuron	Diameter of dendritic (Dd). Mean \pm SD, μ m	Spine length (Sl). Mean \pm SD, μ m	Diameter of spine head (Sd). Mean \pm SD, μ m
1	Multipolar neurons	01.29 \pm 0.03	01.97 \pm 0.55	01.26 \pm 0.11
2	Pyramidal neurons	02.26 \pm 0.53	02.50 \pm 0.64	01.44 \pm 0.18
3	Bitufted neurons	01.22 \pm 0.02	02.38 \pm 0.48	01.18 \pm 0.02
4	Inverted pyramidal neurons	01.39 \pm 0.19	02.39 \pm 0.30	01.27 \pm 0.17
5	Monotufted bipolar neurons	01.33 \pm 0.19	02.11 \pm 0.41	01.24 \pm 0.14
6	Monotufted neurons	01.27 \pm 0.03	02.17 \pm 0.17	01.28 \pm 0.03
7	Aspinous bipolar neurons	01.28 \pm 0.04	-	-

Table 2. Mean spine densities (\pm S.D.) for apical dendrites of different types of dorsal cortex neurons of *Calotes versicolor*.

No.	Type of Neuron	Number of Visible Spines (n)	Estimated True Total Number of Spines (N)
1	Pyramidal neurons	12.80 \pm 01.80	30.76 \pm 07.64
2	Multipolar neurons	08.70 \pm 02.79	22.67 \pm 8.18
3	Bitufted neurons	10.70 \pm 02.41	23.52 \pm 05.49
4	Inverted pyramidal neurons	07.60 \pm 01.35	18.18 \pm 02.88
5	Monotufted bipolar neurons	03.60 \pm 0.84	10.83 \pm 05.64
6	Monotufted neurons	06.00 \pm 01.00	15.84 \pm 03.49
7	Aspinous bipolar neurons	Aspinous	Aspinous

Table 3. Characteristic features of the projection neurons of the dorsal cortex of *Calotes versicolor*.

No.	Types of Neuron	Soma Diameter	Dendritic field	Axonal length*	Percentage**
1	Bitufted neurons	15 \times 11 μ m	163.00 μ m	48.00 μ m	10.75 %
2	Pyramidal neurons	14 \times 9 μ m	217.00 μ m	85.00 μ m	38.71 %
3	Inverted pyramidal neurons	15 \times 8 μ m	154.00 μ m	Absent	09.14 %
4	Multipolar neurons	20 \times 12 μ m	237.00 μ m	65.00 μ m	30.65 %
5	Monotufted neurons	16 \times 9 μ m	114.00 μ m	Absent	03.22 %
6	Monotufted Bipolar neurons	17 \times 8 μ m	134.00 μ m	Absent	04.84 %
7	Aspinous bipolar neurons	16 \times 11 μ m	168.00 μ m	Absent	02.69 %

*- Distance from the soma to the point where the axon disappears either by leaving the plane of section or by failure to impregnate. **- Percentage is given as $n \times 100 / 186$, 186 is the number of neurons examined in this study.

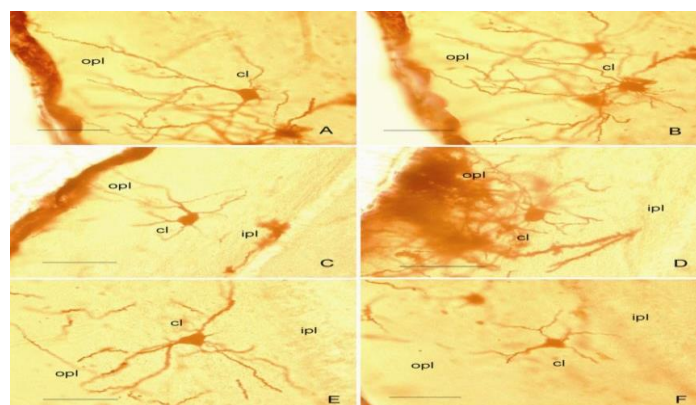


Fig. 4. Photomicrographs showing neurons of the dorsal cerebral cortex of *Calotes versicolor*: multipolar neurons (A-D); pyramidal neuron (E-F). Scale bar =50 μ m.

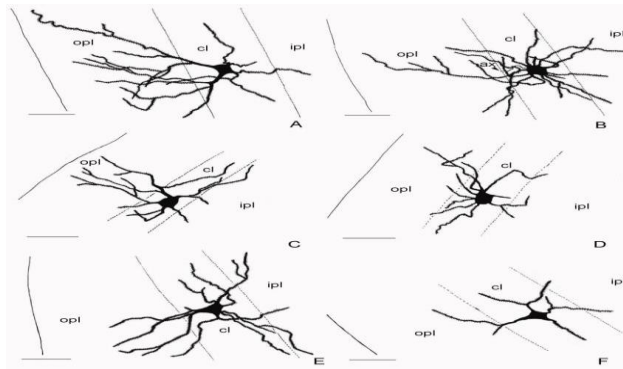


Fig. 5. Camera lucida drawings of the dorsal cerebral cortex neurons of *Calotes versicolor*: multipolar neurons (A-D); pyramidal neuron (E-F). Scale bar = 50µm.

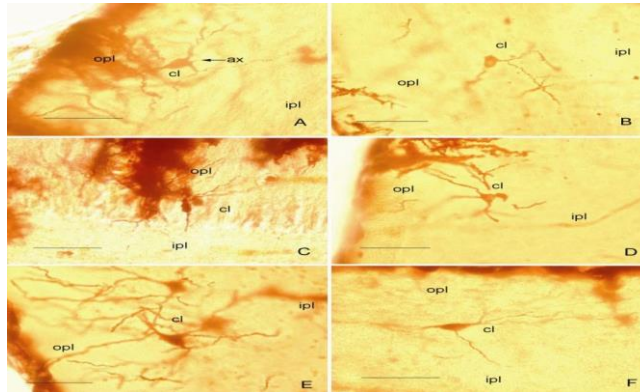


Fig. 6. Photomicrographs showing neurons of the dorsal cerebral cortex of *Calotes versicolor*: pyramidal neuron (A); monotufted bipolar neuron (B-D); inverted pyramidal neuron (E-F). Scale bar =50µm.

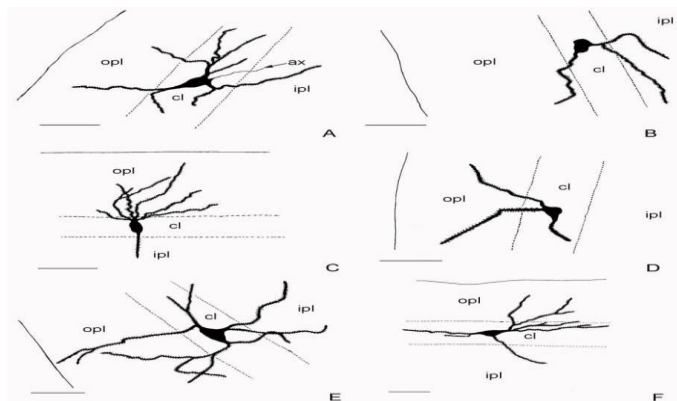


Fig. 7. Camera lucida drawings of the dorsal cerebral cortex neurons of *Calotes versicolor*: pyramidal neuron (A); monotufted bipolar neuron (B-D); inverted pyramidal neuron (E-F). Scale bar = 50µm.

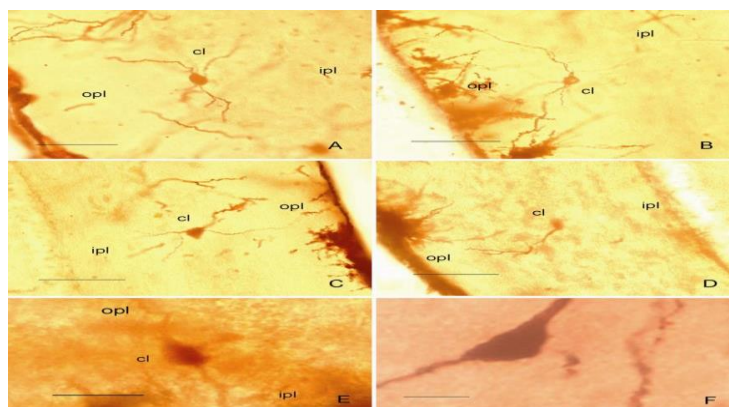


Fig. 8. Photomicrographs showing neurons of the dorsal cerebral cortex of *Calotes versicolor*: bitufted neuron (A-C); monotufted neuron (D); aspiny bipolar neuron (E-F). Scale bar; A-E =50 µm, F=10µm.

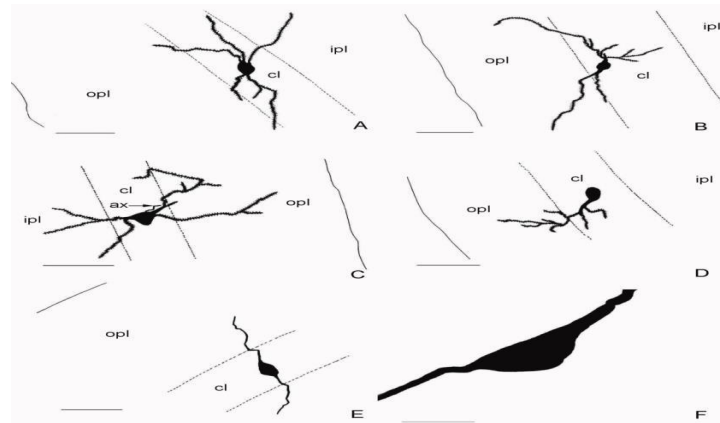


Fig. 9. Camera lucida drawings of the dorsal cerebral cortex neurons of *Calotes versicolor*: bitufted neuron (A-C); monotufted neuron (D); aspiny bipolar neuron (E-F). Scale bar; A-E=50µm.

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