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A Golgi Study of the Short-Axon Interneurons of the Cell Layer and Inner Plexiform Layer of the Medial Cortex of the Lizard *Podarcis hispanica*

JOSÉ A. LUIS DE LA IGLESIA AND CARLOS LOPEZ-GARCIA*
Neurobiología, Biología Celular, Facultad de Ciencias Biológicas,
Universidad de Valencia, Spain

ABSTRACT

The medial cortex of lizards is a three-layered brain region displaying cyto- and chemoarchitectonical, connectional, and ontogenetic characteristics that relate it to the hippocampal fascia dentata of mammals. Three interneuron types located in the cell layer and ten others in the inner plexiform layer (six in the juxtasomatic zone and four in the deep zone) are described in this study.

The granuloid neurons, web-axon neurons, and deep-fusiform neurons lay within the cell layer. These neurons were scarce; they were probably gamma-aminobutyric acid (GABA)-, and parvalbumin-immunoreactive and presumably participated in feed forward as well as in feed back inhibition of the principal projection cells of the lizard medial cortex.

In the juxtasomatic inner plexiform layer, the smooth vertical neurons, smooth horizontal neurons, small radial neurons, large radial neurons, pyramidal-like radial neurons, and spheroidal neurons were found. They were all probably GABA-, and parvalbumin-immunoreactive and were involved in feed forward inhibition of principal medial cortex cells.

In the deep inner plexiform layer lay the giant-multipolar neurons, long-spined polymorphic neurons, periventricular neurons, and alveus-horizontal neurons. These neurons were probably GABA-immunoreactive and either neuropeptide- (somatostatin-neuropeptide Y) or parvalbumin-immunoreactive. They seemed to be involved in feed back or even occasionally in feed forward inhibition phenomena. J. Comp. Neurol. 385:565–598, 1997.

Indexing terms: reptiles; neuron morphology; hippocampus; fascia dentata; hilar cells

The cerebral cortex of lizards is formed by four main cortical areas, the medial, dorsomedial, dorsal, and lateral cortices. All of these areas share a common cytoarchitectonic pattern that resembles that of the mammalian hippocampus. Most neuronal somata appear closely grouped into a conspicuous cell layer that is sandwiched between the outer and inner plexiform layers. The plexiform layers are formed by the principal cell dendrites intermingled with the incoming axons, the radial glial scaffold, and a reduced population of interneurons.

The lizard medial cortex, referred to as 'the small celled part of the mediodorsal cortex' by some authors (Lacey, 1978; Wouterlood, 1981; Hoogland and Vermeulen van der Zee, 1993), has been homologized with the mammalian fascia dentata (Molowny and Lopez-Garcia, 1978) on the grounds of the similarity of their cyto- and chemoarchitecture, connectivity, late ontogenesis, and postnatal growth (see Lopez-Garcia et al., 1992). Its outer plexiform layer receives a highly laminated axonal input that resembles that of the dentate molecular layer, i.e., the lateral (olfactory) cortex axons terminate in the upper superficial third (lizard perforant path), axons coming from the dorsal cortex terminate in the intermediate third, and ipsilateral and contralateral (commissural) axons terminate in the juxtasomatic third (commissural pathway; Lopez-Garcia et al., 1992). Up to five distinct interneuronal types and two ectopic neuronal types have been identified in the outer plexiform layer of this lizard species (Luis de la Iglesia et al., 1994).

In lizards, the inner plexiform layer (the zone located between the cell layer and the ependyma) appears formed by at least three conspicuous strata (Lopez-Garcia et al.,

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*Correspondence to: Carlos Lopez-Garcia, Neurobiología, Biología Celular, Facultad de Ciencias Biológicas, Universidad de Valencia, 46100 Burjassot, Valencia, Spain. E-mail: lopezc@uv.es

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1988a), i.e., 1) the upper stratum or juxtasomatic zone, occupied by the basal dendrites of the principal medial cortex neurons, 2) the inner stratum or deep zone, highly vesicular zinc-positive, which is the primary projection field of the principal medial cortex neurons, and finally, 3) the alveus, or stratum, occupied by myelinated fibers running parallel to the ependyma. Specifically, the inner zinc-positive stratum has been considered homologous to the hilus of the fascia dentata of mammals (Lopez-Garcia et al., 1988a). Frequently, these three strata together are referred to as the medial cortex inner plexiform layer in the bibliography. The neuronal population of the medial cortex inner plexiform layer of *Squamata* (lizards and snakes) consists of scarce large solitary neurons (Molowny et al., 1972). Among them, we can distinguish 1) transitory neurons migrating from the ependymal sulcus to the cell layer (García-Verdugo et al., 1986; Lopez-Garcia et al., 1988b); 2) ectopic principal/projection neurons, which have matured without finishing their migratory schedule (Luis de la Iglesia and Lopez-Garcia, 1997); and 3) true resident neurons (interneurons) of this zone, which sometimes exhibit conspicuous morphology (Ramón y Cajal, 1904a; Ramón y Cajal, 1917; Minelli, 1966; Ebbesson and Voneida, 1969; Regidor et al., 1974; Lacey, 1978; Regidor, 1978; Wouterlood, 1981; Guirado et al., 1984; Ulinski, 1977, 1990; Berbel et al., 1987; Berbel, 1988).

Although the neuronal population of the inner plexiform layer of lizards appears to be very complex, Golgi silver-chromate impregnation studies described only one neuronal type (Ramón y Cajal, 1891, 1896; Ulinski, 1977; Guirado et al., 1984; Lopez-Garcia et al., 1988a; Bernabeu et al., 1994), two types (Ramón y Cajal, 1904a; Ramón y Cajal, 1917; Minelli, 1966; Northcutt, 1967; Ebbesson and Voneida, 1969; Wouterlood, 1981; Berbel et al., 1987), or even three (Lacey, 1978), or four types (Regidor et al., 1974; Regidor, 1978). However, some of these studies focused on one particular neuronal type (Lopez-Garcia et al., 1988a; Bernabeu et al., 1994), and others used reduced samples of Golgi processed brains and/or impregnated neurons, which did not allow a complete survey of the neuronal population of this area.

Immunocytochemical studies have revealed that most neurons of the medial cortex inner plexiform layer are gamma-aminobutyric acid (GABA)-immunoreactive (Schwerdtfeger and Lopez-Garcia, 1986; Lopez-Garcia et al., 1988a; Schwerdtfeger and Lorente, 1988a,b), and simultaneously either calcium binding protein- (parvalbumin; Martínez-Guijarro et al., 1991, 1993; Martínez-Guijarro and Freund, 1992a), or neuropeptide- (somatostatin, neuropeptide Y; Dávila et al., 1988, 1991, 1993; Medina et al., 1992) immunoreactive. A subpopulation of GABA-immunoreactive neurons does not express parvalbumin or neuropeptide immunoreactivity (Dávila et al., 1991, 1993; Martínez-Guijarro et al., 1993), but at least some of them have been identified as nicotinamide adenine dinucleotide phosphate (NADPH) diaphorase-positive in a closely related lizard species (Dávila et al., 1995).

The principal objective of this study was to make a preliminary classification of the neuronal types existing in these layers, as observed in a relatively large sample of Golgi processed brains and Golgi-impregnated neurons of this cortical area. A second objective was to compare the morphological characteristics of each neuronal type observed with those of the mammalian hippocampus, to assess some hypothetical similarities.

MATERIALS AND METHODS

Sixty lizards (*Podarcis hispanica*) of both sexes, ranging from 23 to 55 mm head-cloaca lengths (representative of individuals from perinatal to adult ages), were used in this study. Animals were captured in the surroundings of Burjasot (Valencia, Spain) and were kept in terraria until killed. Experimentation was carried out according to institutional animal care guidelines. Under ether anesthesia, animals were transcardially perfused with 30–50 ml of 1% paraformaldehyde and 1.25% glutaraldehyde in 0.12 M phosphate buffer, pH 7.2–7.4. The brains were then removed from the skulls and kept overnight in the same fixative at 4°C. For staining we used the Golgi-Colonnier method (Colonnier, 1964) with some improvements adapted to our material (i.e., 2–7 days of induration at 4°C in a mixture of 2.4% potassium dichromate and 5% glutaraldehyde, followed by 1–4 days of impregnation in 0.75% silver nitrate; Berbel, 1986). After impregnation of the brains, 125- to 200-µm-thick transverse sections were obtained with a tissue chopper and were embedded in Araldite between two cover glasses. Selected cells were video recorded, photographed, and drawn by using a Zeiss photomicroscope equipped with a camera lucida. Picture illustrations of neuronal morphology were achieved by digitizing the video image and high-quality printing. 'Collages' or composed images of dendritic trees were obtained by taking the 'in focus' dendritic fragments at different depths and collating them with the help of a computer (Screen Machine digitizing card, Corel Photo-Paint software).

From a sample of 1,174 well-impregnated cells of the medial cortex, 847 were identified as principal neurons or long-axon projection neurons, 281 were identified as interneurons, and 46 were immature neurons or nonclassified cell elements, including some microglia-like cells.

Apart from the axon length, which defined the category of interneurons, the main classification criteria were as follows: the axonal arbor configuration (ascending, descending, web-like, local plexus), the dendritic tree ramification pattern (bipolar horizontal, bipolar vertical, multipolar, or stellate), and the presence and type of dendritic spines (smooth nonspinous, sparsely spiny, and long-spined), or other dendritic excrescences (axon-like processes, spikes, long spines, microdendrites). Each neuronal archetype was given a number following some characters, referring to the layer where it lay (cl, jip, or dip for cell layer, juxtasomatic, and deep inner plexiform layer, respectively), a descriptive name based on its morphology, and a short name that facilitates its reference (e.g., type jip-i1, ascending axon, aspinous vertical neuron, or smooth vertical).

To identify and confirm the presence of some neuronal cell bodies in the different strata, a series of Nissl, Timm, parvalbumin, and somatostatin-stained transverse sections of lizard brains from our laboratory collection were used (Fig. 1); they permitted us to assess soma shapes, location, and presumable immunocytochemical nature in the cell layer and in the inner plexiform layer strata.

RESULTS

The three main strata of the inner plexiform layer were clearly identified in both Nissl, Timm, and Golgi-stained sections (Fig. 1). The careful examination of the Golgi-impregnated interneurons, whose somata were located in

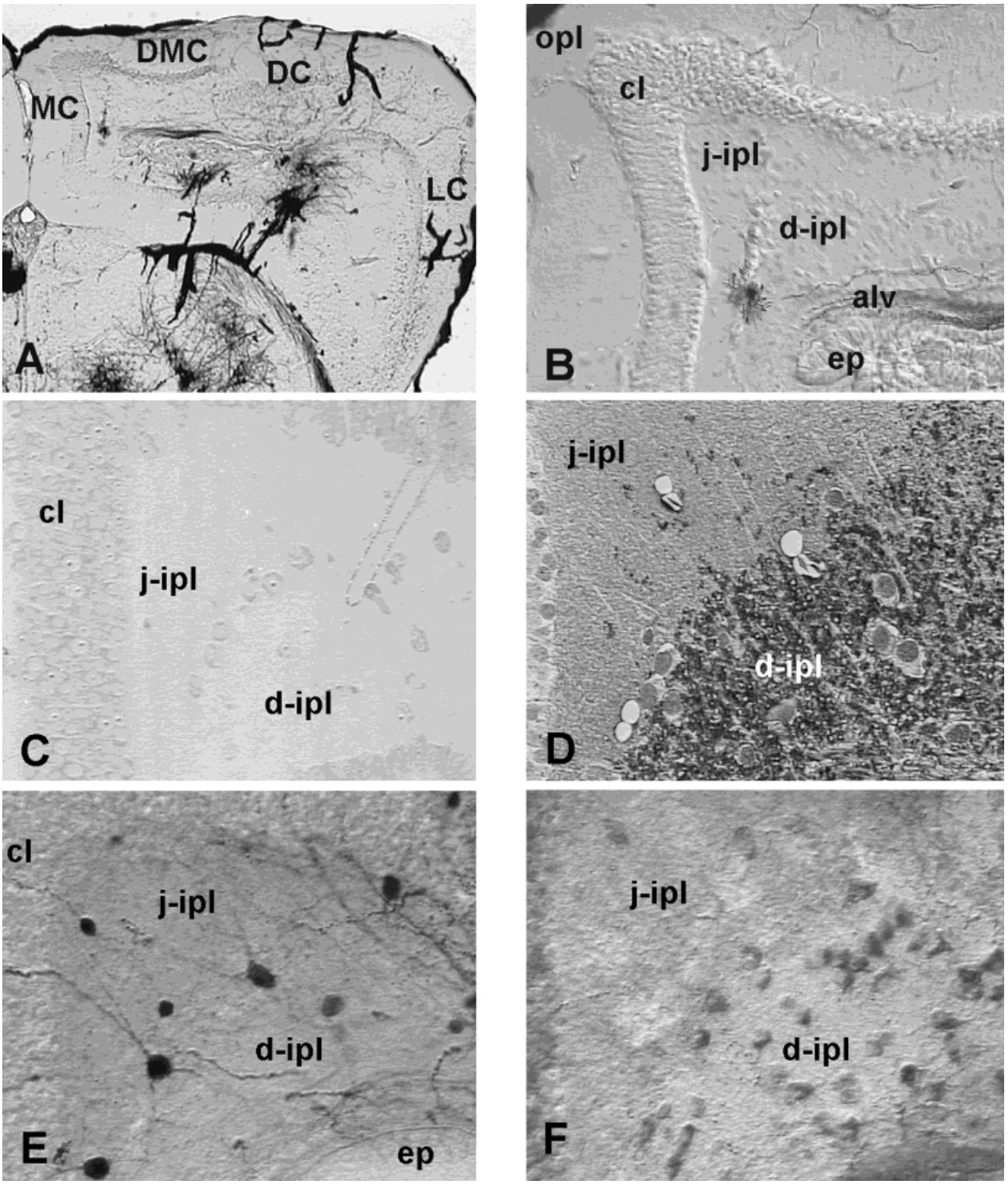

Fig. 1. **A:** Photomontage obtained with interference optics from a Golgi-impregnated brain in which the cerebral cortex is almost completely devoid of impregnated cells, thus allowing the cerebral cortical areas to be distinguished. **B:** In the same section, the trilaminar arrangement of the medial cortex is seen at a higher magnification. One impregnated microglia cell in the deep inner plexiform layer, and some impregnated fibers running in the alveus, are seen. **C:** Nissl semithin section from the brain of a lizard showing the inner plexiform layer of the medial cortex populated by some large somata. **D:** Timm-Nissl staining: the stratification of the inner plexiform layer is clearly evident after the Timm method for detection of heavy metals, due to the high content in vesicular zinc of axonal endings. **E:** Parvalbumin immunostaining: some Golgi-like immunostained neurons are seen in the juxtasomatic zone of the inner plexiform layer. **F:** Somatostatin immunostaining: abundant immunolabeled somata appear in the deep zone of the inner plexiform layer. alv, alveus; cl, cell layer; d-ipl, deep zone of the inner plexiform layer; DC, dorsal cortex; DMC, dorsomedial cortex; ep, ependyma; j-ipl, juxtasomatic zone of the inner plexiform layer; LC marks the position of the lateral cortex which terminates at a more rostral level; MC, medial cortex; opl, outer plexiform layer. Magnifications: A, ×50; B, ×150; C–F, ×260.

TABLE 1. Short-Axon Neurons in the Medial Cortex of *Podarcis hispanica*[1]

Layer type	Descriptive name	Short name	n	Percentage	Mean size (μm)
cl-i1	Ascending-axon, superficial spiny neuron	Granuloid	1	0.09	7 × 7
cl-i2	Sparsely spiny neuron with ascending-descending axon	Web-axon	2	0.17	16 × 8
cl-i3	Ascending-axon, aspinous fusiform vertical neuron	Deep-fusiform	1	0.09	25 × 14
jip-i1	Ascending-axon, aspinous vertical neuron	Smooth vertical	12	1.02	14 × 9
jip-i2	Ascending-axon, aspinous horizontal neuron	Smooth horizontal	23	1.96	12 × 8
jip-i3	Ascending-axon, small fusiform radial neuron	Small radial	3	0.26	9 × 6
jip-i4	Ascending-axon, large fusiform radial neuron	Large radial	2	0.17	20 × 12
jip-i5	Descending-axon, aspinous pyramidal-like radial neuron	Pyramidal-like radial	5	0.43	22 × 14
jip-i6	Short-axon, sparsely spiny small multipolar neuron	Spheroidal	17	1.45	7–8
dip-i7	Short-axon, giant multipolar neuron	Giant-multipolar	21	1.79	21 × 15
dip-i8	Ascending-axon, long-spined polymorphic neuron	Long-spined polymorphic	107	9.11	15 × 11
dip-i9	Ascending-axon, periventricular vertical neuron	Periventricular	9	0.77	13 × 10
dip-i10	Short-axon, alveus-horizontal neuron	Alveus-horizontal	13	1.11	13 × 7

[1]cl, cell layer; dip, deep zone of the inner plexiform layer; i1–i10, interneuron types 1 to 10; jip, juxtasomatic zone of the inner plexiform layer; n is the number of cells belonging to each type. Percentage is given as n · 100/1,174, 1,174 being the number of cells examined (see text).

the cell layer, allowed us to distinguish up to three different archetypes (granuloid, web-axon, and deep-fusiform neurons). Those interneurons whose somata were located in the upper juxtasomatic zone (adjacent to the cell layer) of the inner plexiform layer were classified into six archetypes (smooth vertical, smooth horizontal, small radial, large radial, pyramidal-like radial, and spheroidal neurons). Those located in the deeper stratum (heavily Timm-positive) were classified into three archetypes (giant-multipolar, long-spined polymorphic, and deep vertical or periventricular neurons). Finally, those located in the alveus myelinated layer were classified into only one archetype (alveus-horizontal neurons).

The list of the cell layer and inner plexiform layer interneuron types found in this study in the medial cortex of *P. hispanica*, as well as some numerical data relative to these cells, are given in Table 1.

Cell layer interneurons

Apart from those short-axon neurons from both the outer (Figs. 2A, 3A,B) and the inner (Figs. 2E,F, 3F,G) plexiform layers, that occurred occasionally in the upper and lower rows of somata of the cell layer, the following three interneuron types have been distinguished in the cell layer.

Type cl-i1, ascending-axon, superficial spiny neuron (granuloid neuron). This neuron had a round soma (9 μm in diameter) from which dendrites arose and formed an apical tuft reaching the outer plexiform layer. Dendrites bore short spherical dendritic spines but lacked the typical large elliptical and mushroom-shaped spines of the principal bitufted neurons. The axon arose laterally from the soma, took an ascending course to the outer plexiform layer, and ramified into several moderately thick branches. Axonal enlargements, bouton-like thickenings, and axonal spines might be found in the axonal arbor (Figs. 2B, 3C).

Type cl-i2, sparsely spiny neurons with ascending-descending axon (web-axon neuron). These neurons had small to medium-sized oval somata (8 × 16 μm) located in the cell layer (Figs. 2C, 3E). A striking feature was that the somata had two kinds of somatic spines: small spines and complex pedicellated multiple headed spines (black star, Fig. 3E). The poorly branched dendritic tree consisted of one thin apical dendrite, rarely ramified near the cell body, and two unbranched basal dendrites, arising from the basal edge of the soma. Dendrites showed few small spherical spines. The axon, originated from the apical dendritic trunk, took a descending course until reaching the inner plexiform layer, where it formed a short-thick segment from which several thin collateral branches arose. Some of these collaterals crossed back through the cell layer and branched in the outer plexiform layer, whereas other thin collaterals gave rise to a diffuse juxtasomatic plexus. Bouton-like thickenings and axonal spines were seen in axonal segments crossing the cell layer and in those located in the inner juxtasomatic plexus (small arrows, Fig. 3E).

Type cl-i3, ascending-axon, aspinous fusiform vertical neuron (deep-fusiform neuron). This neuron had a large fusiform to pyramidal soma (14 × 25 μm), from which a thick apical dendrite (2.5 μm in diameter) arose. The soma gave rise to several poorly ramified dendrites in the outer plexiform layer (Figs. 2D, 3D, 4). A few apical dendrites joined the dendrites arising from the basal pole of the soma and constituted a wide tuft, which reached the deepest juxtaependymal levels. These descending dendrites showed complex spines, varicosities, and irregular thickenings along their course traversing the deep inner plexiform layer (Fig. 4B). Apical dendrites lacked spines. The axon arose from an apical dendritic segment and gave rise to a juxtasomatic plexus in the outer plexiform layer. This plexus was formed by thick and thin branches; some axonal collaterals crossing the cell layer displayed sets of bouton-like thickenings when entering the inner plexiform layer (Fig. 4A).

Inner plexiform layer interneurons (juxtasomatic zone)

Type jip-i1, ascending-axon, aspinous vertical neuron (smooth vertical neuron). These neurons had medium-sized (9 × 14 μm) somata that were located preferentially underneath the inner border of the cell layer (Figs. 5A, 6A–C), but occasionally deeper too (Fig. 6D). Somata were tuber-like to elongated in shape, and they were radially oriented. Some descending dendrites arose from the basal pole of the soma. A thick dendritic trunk (3.5 μm) arose from the apical pole; it traversed the cell layer and then gave rise to long dendrites, bifurcated with open angles. The apical dendrites ascended toward the surface, but without touching the glial limiting membrane (Fig. 6A,C,D). Very few spines, but frequent filiform varicosities resembling axon-like processes, emerged from the apical dendrites (arrowheads, Fig. 6). A very thin axon originated from a conspicuous axonal hillock, located in the apical pole of the soma or in the apical dendritic trunk. The axon ascended toward the cell layer, where it lost its chromate-silver impregnation (arrows, Fig. 6B,D).

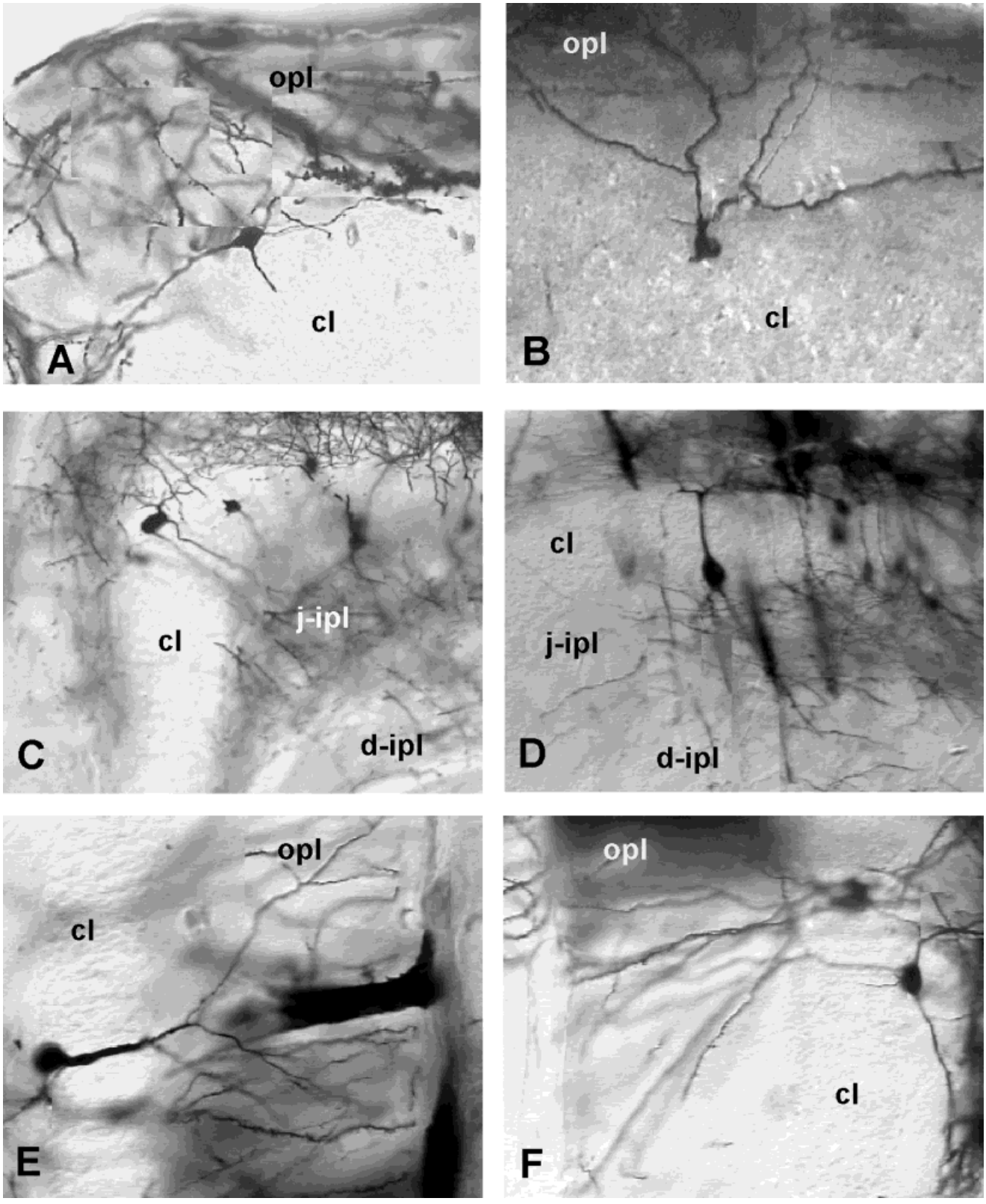

Fig. 2. Computer photomontages illustrating some interneuronal types in the cell layer. **A:** Coral neurons usually have their somata in the outer margin of the cell layer, but in some cases they lie in the first row of somata, as is shown here. **B:** Granuloid neuron. **C:** Web-axon neuron. **D:** Deep-fusiform neuron. **E:** Smooth vertical neuron. **F:** Smooth horizontal neuron. Smooth neurons (vertical and horizontal) occur in the inner margin of the cell layer, but they are also frequently seen in the juxtasomatic zone of the inner plexiform layer. Abbreviations as in Figure 1. Magnifications: A, ×420; B, ×525; C, ×315; D, ×250; E, ×670; F, ×585.

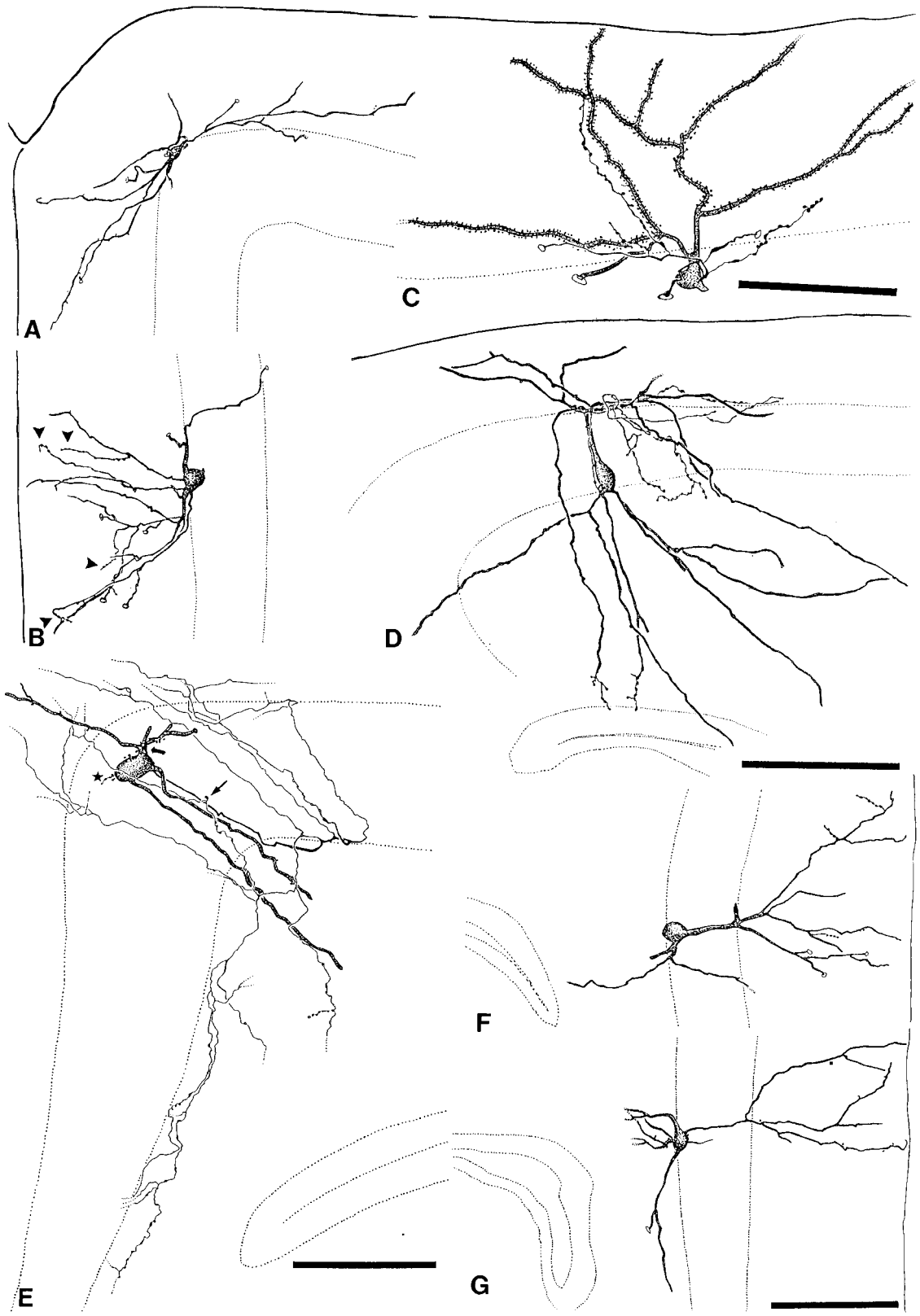

Fig. 3. Camera lucida drawings of the interneuronal types lying in the cell layer. Outer margin of the cell layer: **A:** Couchant neuron. **B:** Coral neuron; arrowheads indicate the presence of dendritic axon-like processes. Cell layer: **C:** Granuloid neuron. **D:** Deep-fusiform neuron. **E:** Web-axon neuron; the black star points to a multiple headed somatic spine, the thin arrow marks an axonal spine, and the thick arrow points to the origin of the axon. Inner margin of the cell layer: **F:** Smooth vertical neuron. **G:** Smooth horizontal neuron. (Note: in all camera lucida drawings of dendrites and axonal branches, prolonged dotted lines represent dendrites or axonal branches whose distal segments could not be drawn because of the excess of impregnation, and encircled tips represent sectioned dendrites or axons; the limits of the cell layer and ependyma are also represented by dotted lines). Scale bars = 100 μm in A, B, F, G, 50 μm in C, E, 100 μm in D.

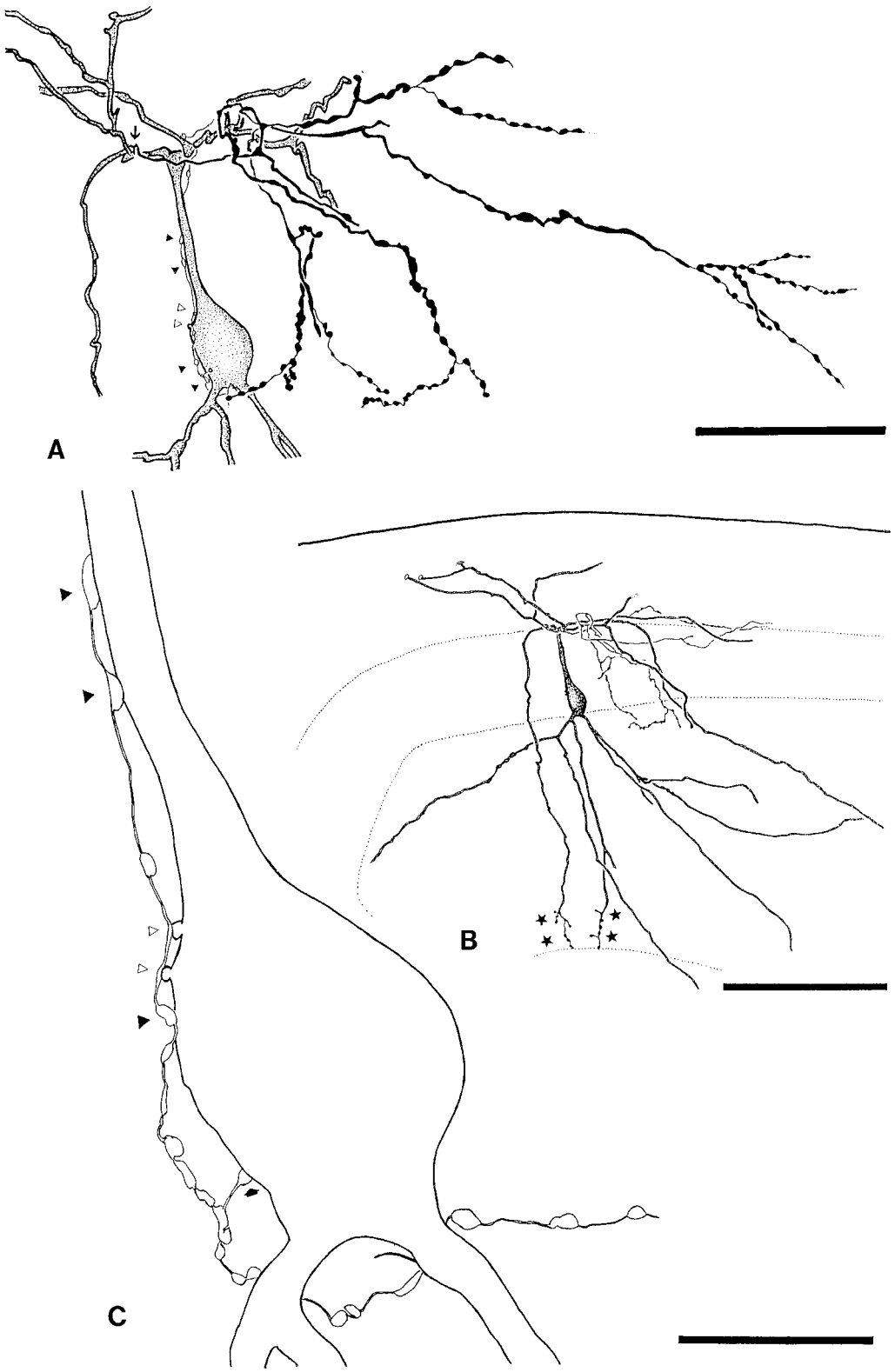

Fig. 4. **A–C:** Camera lucida drawings of the cell layer deep-fusiform neuron. Arrow in A indicates the origin of the axon. Black stars in B mark long complex dendritic spines on distal segments of deep dendrites. Note the presence in A and C of an axon climbing by the cell body and making some contacts on it; black triangles in A and C point to axonal boutons contacting the cell surface on the thick apical trunk; white triangles in A and C point to two minute somatic spines apparently contacting the axon; the thick small arrow in C marks an axonal spine contacting the cell body. Conventions as in Figure 3. Scale bars = 50 μm in A, 100 μm in B, 10 μm in C.

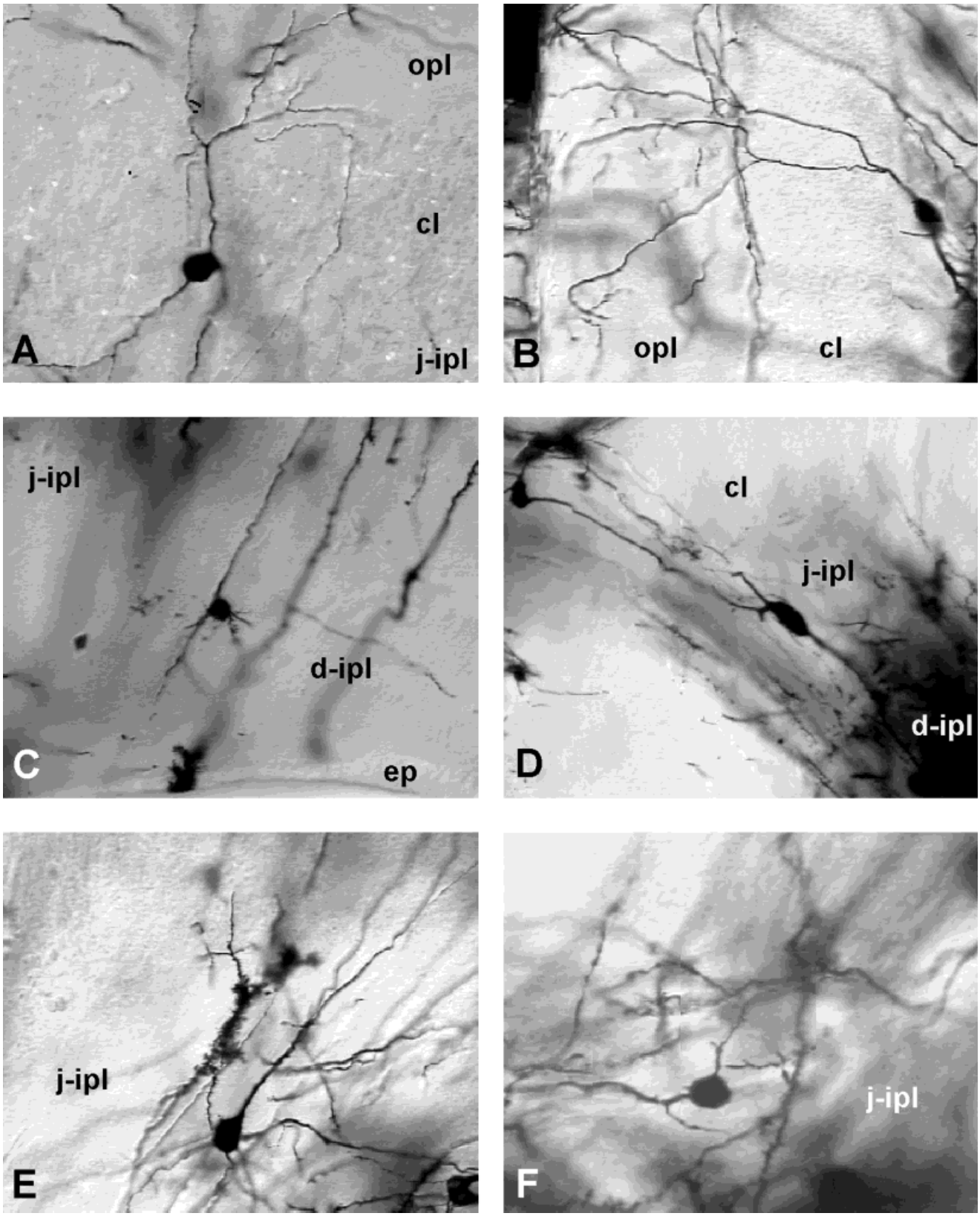

Fig. 5. Computer photomontages illustrating the interneuronal types of the juxtasomatic zone of the inner plexiform layer. **A:** Smooth vertical neuron. **B:** Smooth horizontal neuron. **C:** Small radial neuron. **D:** Large radial neuron. **E:** Pyramidal-like radial neuron. **F:** Spheroidal neuron. Abbreviations as in Figure 1. Magnifications: A, ×535; B, ×535; C, ×500; D, ×430; E, ×450; F, ×960.

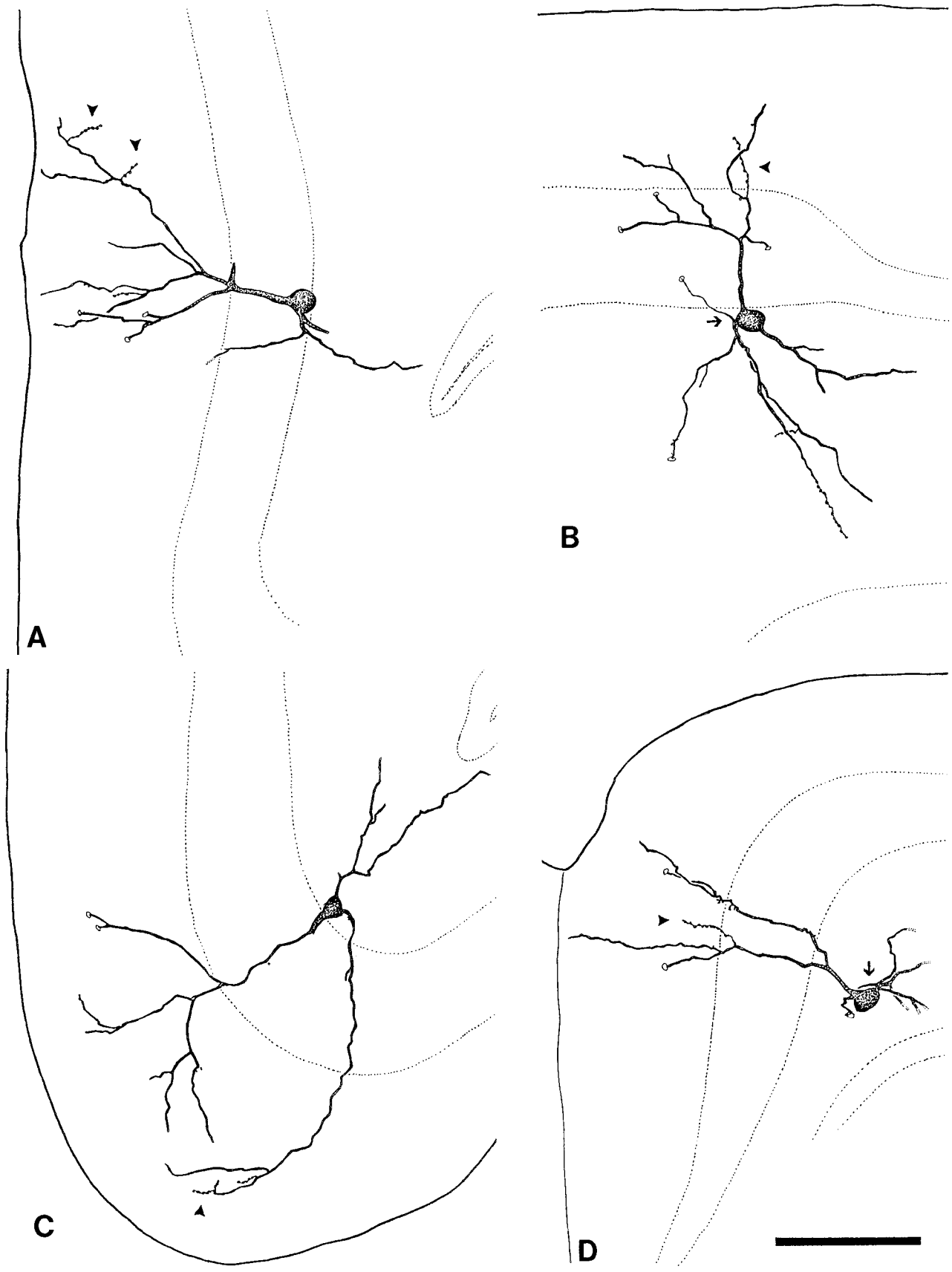

Fig. 6. Camera lucida drawings of smooth vertical neurons. Arrowheads in **A–D** indicate axon-like processes; the arrows in B and D point to the origin of the axon. Conventions as in Figure 3. Scale bar = 100 μm.

Type jip-i2, ascending-axon, aspinous horizontal neurons (smooth horizontal neuron). These neurons had fusiform somata (8 × 12 μm) that were located close to the inner border of the cell layer with the long axis parallel to it (Figs. 5B, 7). In some cases, the cell body lay deeper (Fig. 7E,F) or was obliquely oriented (Fig. 7C). Sometimes, a short cilium was seen to protrude from the soma (asterisk, Fig. 7B), a feature that was rarely observed on interneurons. Two dendritic trunks arose from the soma poles; they usually curved toward the cell layer, traversed it, and then ramified in the outer plexiform layer. The apical dendrites did not reach the glial limiting membrane but sometimes bent behind it (Fig. 7C). Some short, poorly ramified dendrites were seen in the inner plexiform layer. The dendrites were smooth or carried very few spines; occasionally, they showed some fine filiform axon-like processes in both plexiform layers (arrowheads, Fig. 7E,F). The axon started from the soma and took an ascending course toward the cell layer, where it lost its chromate-silver impregnation (arrows, Fig. 7B,C).

Type jip-i3, ascending-axon, small fusiform radial neurons (small radial neuron). These neurons (Figs. 5C, 8) had oval radially arranged somata (5–10 μm) with occasional somatic spines. One or two thin dendrites arose from the apical pole of the soma, traversed the cell layer, and ramified in the outer plexiform layer without reaching the glial limiting membrane. The secondary and tertiary dendrites were smooth or bore rare spines or varicosities; occasionally, they showed axon-like processes (arrowheads, Fig. 8C,E). Basal dendrites were short and poorly ramified. The axon was very thin; it arose from a juxtasomatic dendritic segment and followed an ascending trajectory until reaching the cell layer, where it lost its chromate-silver impregnation. One impregnated neuron, with the same somatic and dendritic morphology, displayed an axon directed to the alveus, a characteristic that raises the question of whether it represents another neuronal type (Fig. 5C, 8F).

Type jip-i4, ascending-axon, large fusiform radial neurons (large radial neuron). These neurons had large fusiform somata (12 × 20 μm) radially arranged and located in a particular zone of the inner plexiform layer, i.e., that defined by the flexion of the dorsal edge of the medial cortex and the medial most part of it (Figs. 5D, 9, 10A). One or two dendrites ascended from the apical pole of the soma, traversed the cell layer, and finally reached the outer plexiform layer, where they showed a short trajectory (short segments into the outer plexiform layer). One or two basal thick dendrites took a descending course; sometimes one of them suddenly turned outward, toward the outer plexiform layer (Fig. 9). Basal dendrites might have round-headed spines or long-filiform spines (5–8 μm long) on particular segments. The axon arose from the apical pole of the soma, took an ascending course, crossed the cell layer, and gave off thick branches, which emitted beaded collaterals (bouton-like series) juxtacellularly distributed. Those nonjuxtacellular axonal collaterals did not display bouton-like thickenings (Fig. 9A).

Type jip-i5, descending-axon, aspinous pyramidal-like radial neuron (pyramidal-like radial neuron). These neurons were located in the corner defined by the dorsal and vertical parts of the medial cortex cell layer (Figs. 5E, 10B,C). They had pyramidal somata with short basal dendrites and a thick apical dendrite, which traversed the cell layer and gave off collateral dendrites, both in the inner and in the outer plexiform layers. These apical collateral dendrites formed close angles with the primary apical dendrite, thus constituting a characteristic narrow dendritic tree. The axon arose from the basal pole of the cell body, followed an initially descending course to reach the deep zone where it became unimpregnated. Contrary to the typical projection axons in the medial cortex, these axons did not display enlargements, thickenings, or beaded collateral branches along their trajectory (arrowheads, Fig. 10C).

Type jip-i6, short-axon, sparsely spiny small multipolar neuron (spheroidal neuron). Spheroidal neurons (Figs. 5F, 11) had round small somata (6–10 μm) sometimes bearing small spines (arrowhead, Fig. 11F) or a short cilium (asterisks, Fig. 11A,F). Two or three poorly ramified dendrites formed a reduced dendritic tree in the inner plexiform layer; occasionally, one dendrite crossed the cell layer, reaching the outer plexiform layer. Dendrites were progressively thinner at distal ends; they might bear a few short spherical dendritic spines. Axons were very slender; they arose from the soma or from a proximal dendrite and ramified close to the cell layer (arrows, Fig. 11C–E,G). Frequently, the axons displayed incomplete impregnation.

Inner plexiform layer interneurons (deep zone)

Type dip-i7, short-axon, giant multipolar neuron (giant-multipolar neuron). These neurons had polygonal medium-sized to large somata (from 9–20 to 15–26 μm) located preferentially in the virtual borderline between the juxtasomatic and deep zones of the inner plexiform layer (Figs. 12A,B, 13–15). Their cell bodies were usually smooth, but they sometimes bore small spines (arrowheads, Fig. 13B). Three to six very long, thick dendritic trunks arose from the vertices of the soma. The dendrites tapered progressively at each branching point and at the distal segments. Frequently, these dendrites spread throughout the width of the cortex, reaching even the dorsomedial cortical parenchyma (Figs. 14C, 15B). Dendrites were generally smooth, but some of them bore occasional or even abundant spines (Fig. 15B). In some cases, one dendrite appeared spiny, whereas the rest of the dendrites of the same neuron were smooth (Fig. 14A, 15A). In addition to dendritic spines, filiform axon-like excrescences (arrowhead, Fig. 14A), 'microdendrites' (Fig. 14B,C), and 'spikes' (white arrows, Fig. 13B,D) were seen protruding from the dendrites. The axon arose from a primary dendrite, took an ascending course, traversed the cell layer, and gave off several thick branches (most likely myelinated distribution branches) from which abundant collaterals arose forming a superficial plexus (Figs. 13A, 14A). These collaterals had a series of large bouton-like thickenings. Frequently, a dense plexus was formed in the juxtasomatic zone of the inner plexiform layer; this plexus consisted of axonal branches provided with abundant elliptical boutons, coming from either the superficial plexus or directly from the principal axonal branch (Fig. 15B). There was a marked degree of variability in the axonal arbor of these neurons, a characteristic that poses the question of whether different subtypes may be distinguished.

Type dip-i8, ascending-axon, long-spined polymorphic neuron (long-spined polymorphic neuron, LSPN). These were the most conspicuous neurons of the inner plexiform layer of the medial cortex (Figs. 12C,D, 16, 17),

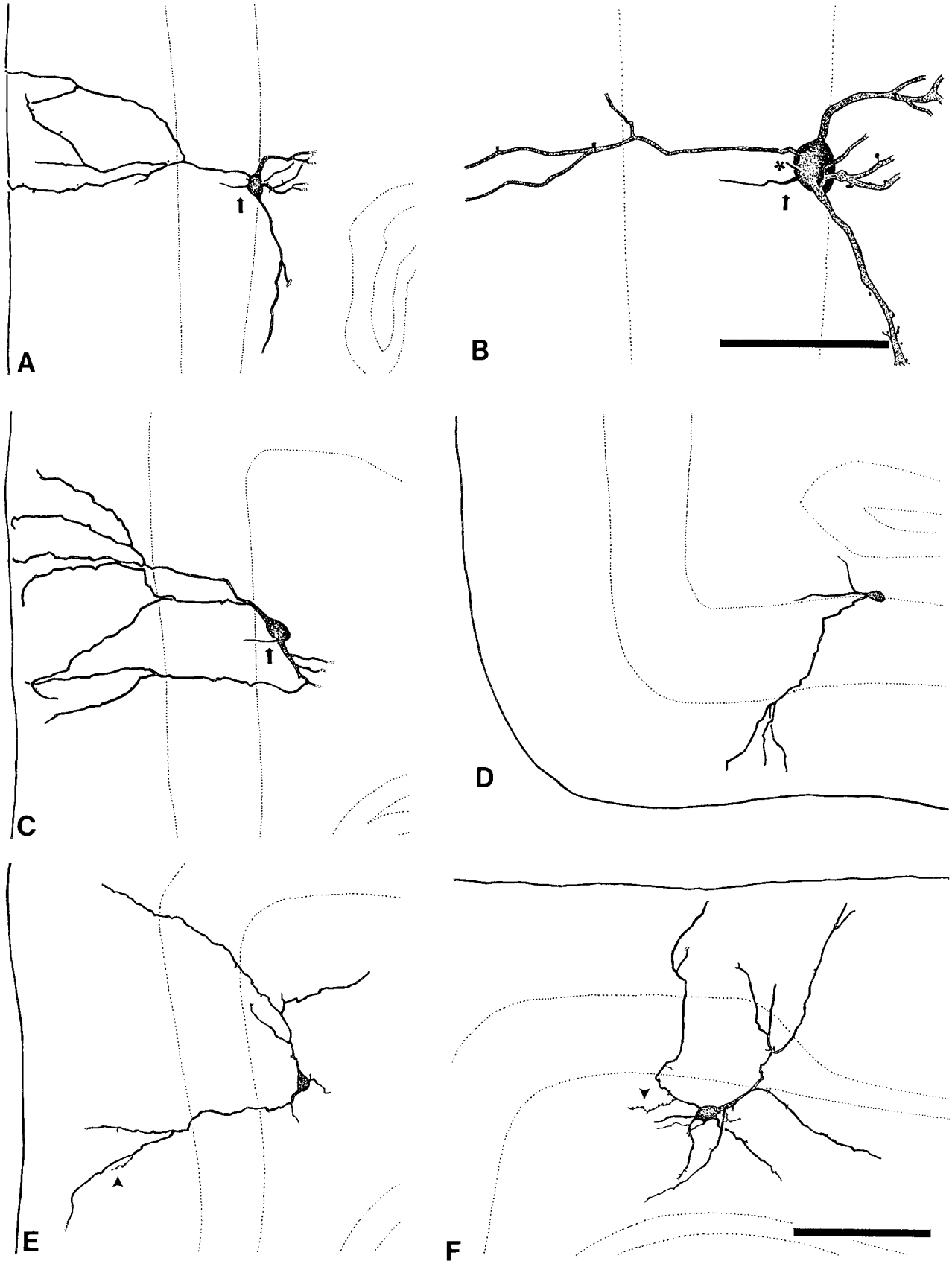

Fig. 7. **A–F:** Camera lucida drawings of smooth horizontal neurons. The thick arrows in A–C point to the origin of the axon; the asterisk in B indicates a short somatic cilium; the arrowheads in E and F indicate axon-like processes. The cell body of the neuron in A is shown in B at a higher magnification. Conventions as in Figure 3. Scale bars = 100 μm in A, 50 μm in B, 100 μm in C–F.

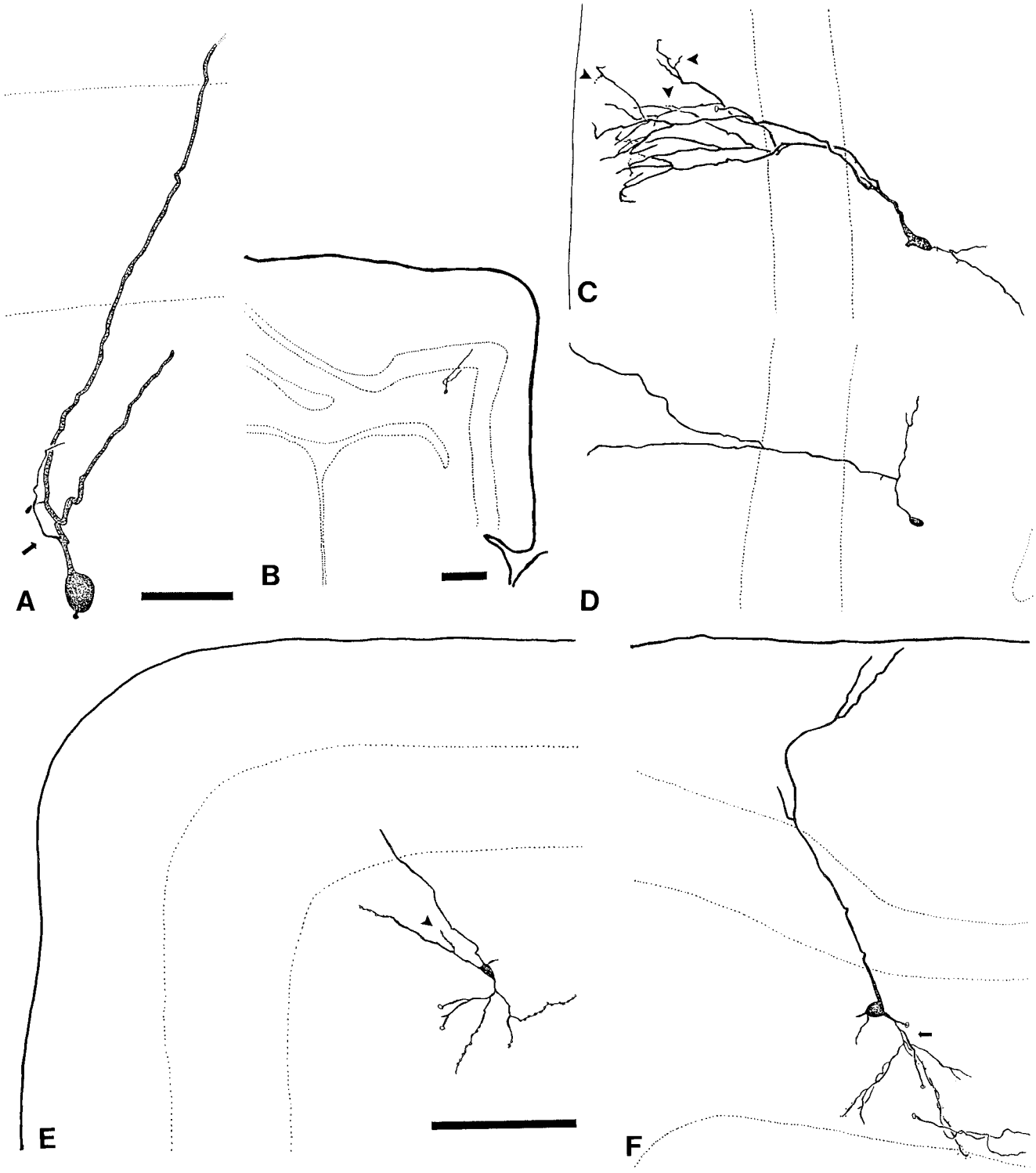

Fig. 8. **A–F:** Camera lucida drawings of small radial neurons. The position of the cell in A is indicated in the panoramic drawing in B. The thick arrows in A and **F** point to the origin of the axon; note that the axon is initially ascending in A but descending in F. Arrowheads in C and E indicate axon-like processes. Conventions as in Figure 3. Scale bars = 25 µm in A, 100 µm in B, 100 µm in C–F.

which also occurred in all of the cortical projection fields of the medial cortex (Fig. 12D). They had variably sized somata (from 8–15 to 11–21 µm) and showed frequent long spines or microdendrites (see below) when they lay in their preferential location, i.e., the deep zone of the inner plexiform layer (vesicular zinc-positive synaptic fields). Two to four long, thick dendrites arose from the soma and followed tortuous courses through the inner plexiform

Fig. 9. **A,B:** Two camera lucida drawings of the same large radial neuron. Conventions as in Figure 3. Scale bars = 50 μm in A, 100 μm in B.

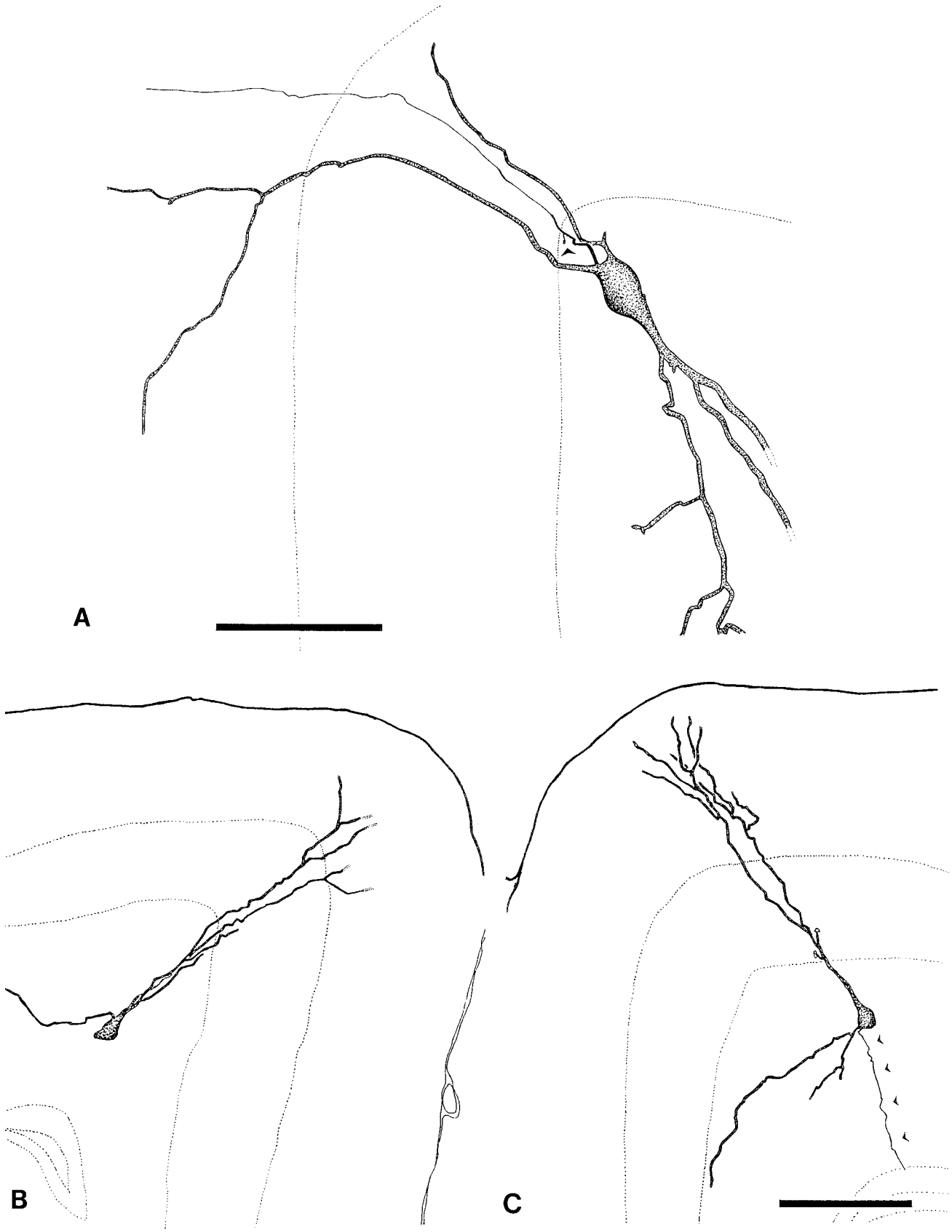

Fig. 10. Camera lucida drawings of one large radial neuron (**A**) and two pyramidal-like radial neurons (**B,C**). Arrowhead in A indicates the presence of an axonal spine. Arrowheads in C mark an initially descending axon. Conventions as in Figure 3. Scale bars = 50 µm in A, 100 µm in B,C.

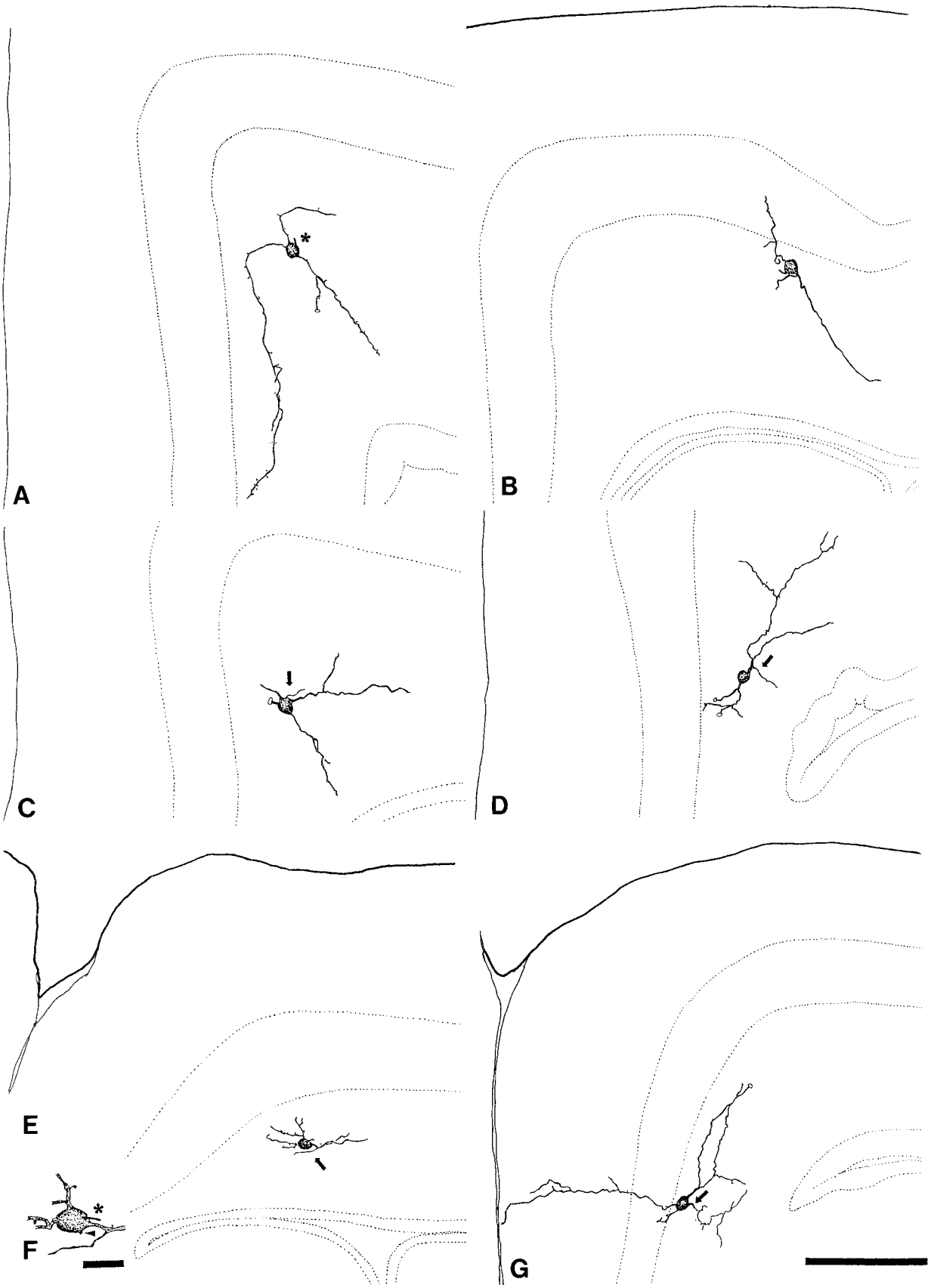

Fig. 11. **A–G:** Camera lucida drawings of spheroidal neurons. The soma of the cell in E is shown in F at a higher magnification. The asterisks in A and F indicate the presence of short somatic cilia. The thick small arrows in C, D, E, and G point to the origin of the axons. The arrowhead in F points to a minute somatic spine. Conventions as in Figure 3. Scale bars = 100 μm in A–E, G, 10 μm in F.

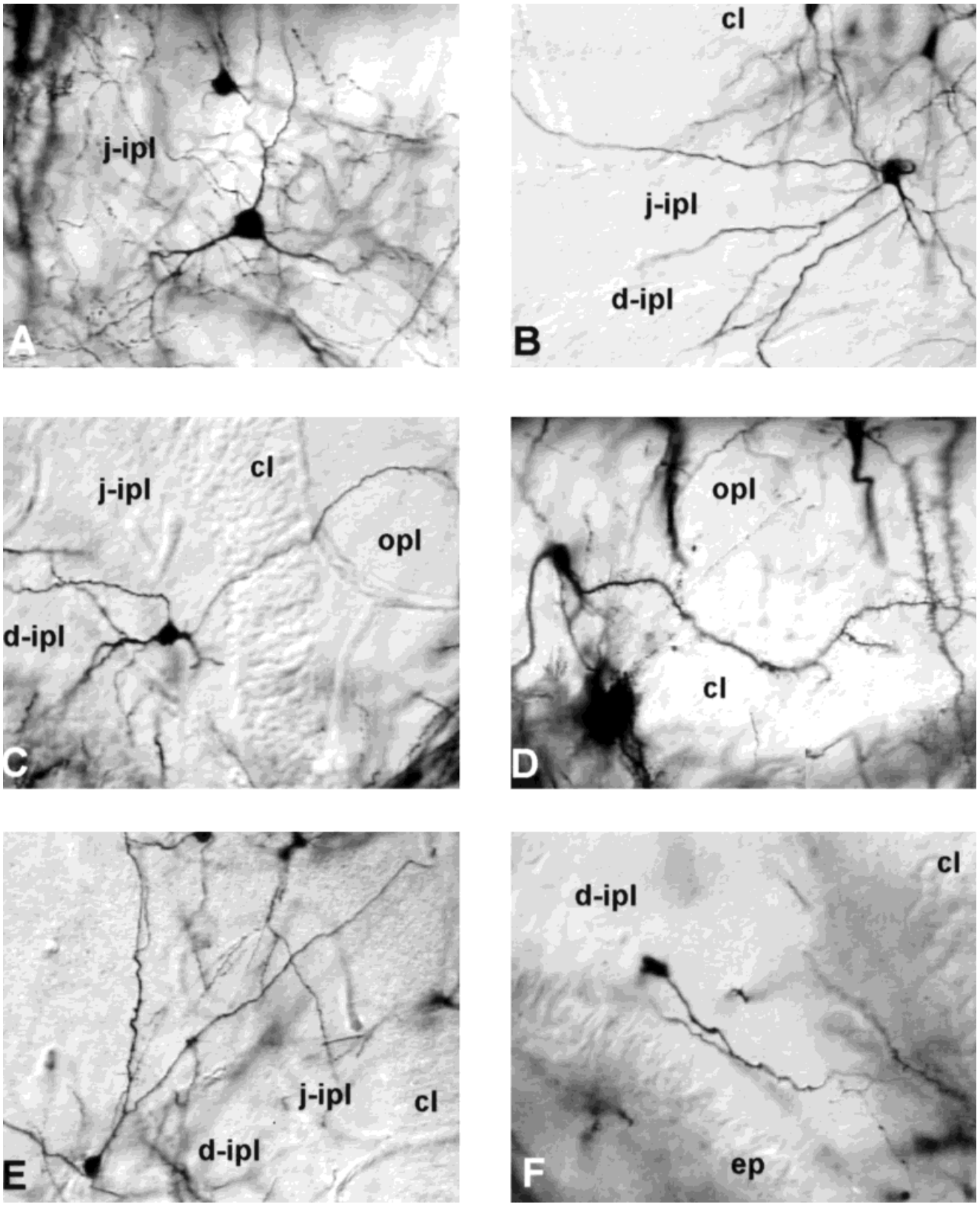

Fig. 12. Computer photomontage illustrating the interneurons of the deep zone of the inner plexiform layer. **A,B:** Giant-multipolar neurons. **C:** Long-spined polymorphic neuron. **D:** Ectopic long-spined polymorphic neuron located on the cell layer at the limit between the medial and dorsomedial cortices. **E:** Periventricular neuron. **F:** Alveus-horizontal neuron. Abbreviations as in Figure 3. Magnifications: A, ×395; B, ×250; C, ×250; D, ×470; E, ×230; and F, ×500.

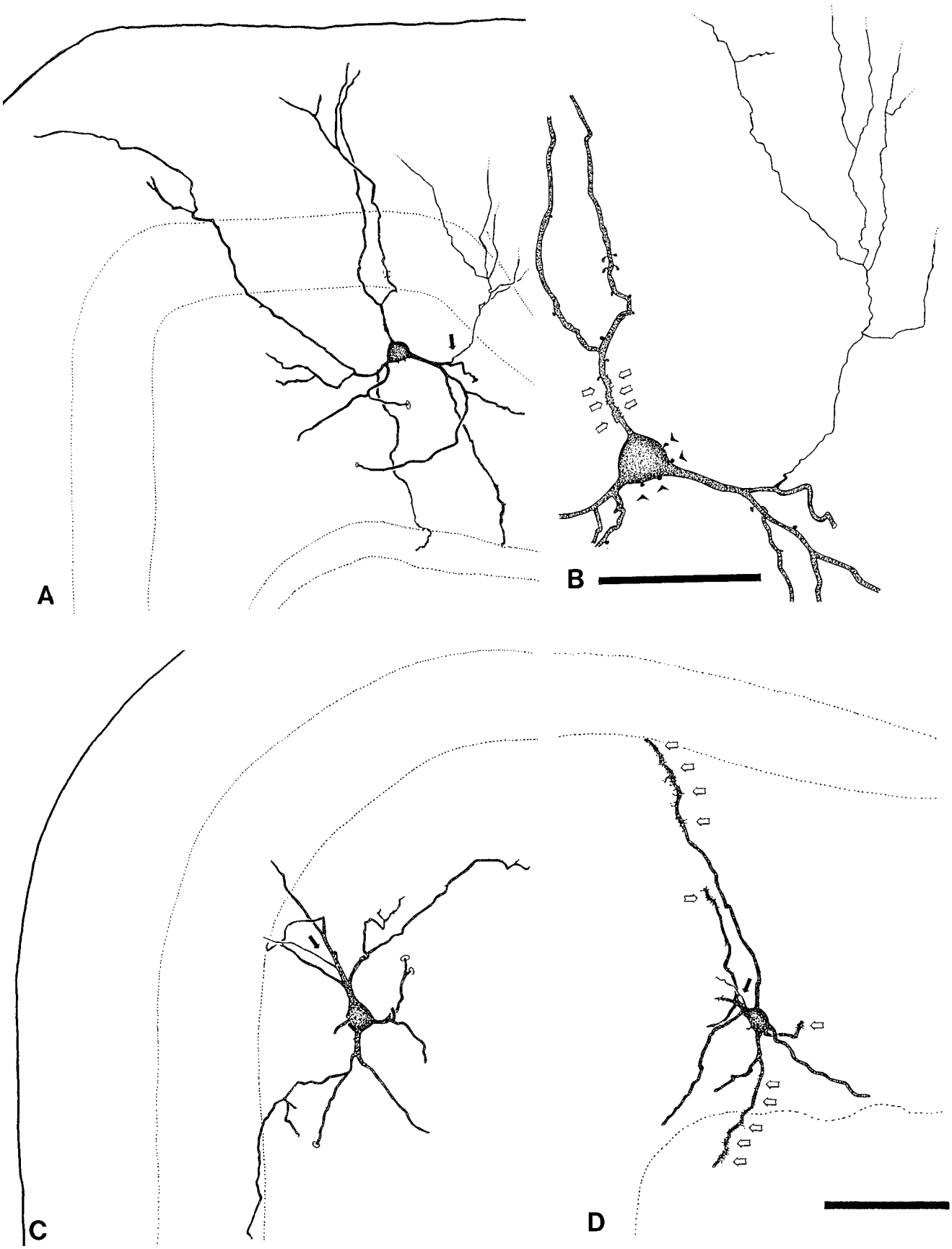

Fig. 13. Camera lucida drawings of giant-multipolar neurons. Thick small arrows in **A, C,** and **D** point to the origin of the axon. White thick arrows in **B** and D indicate the presence of some minute dendritic spikes. Arrowheads in B mark some small somatic spines. The soma of the neuron in A is shown in B at a higher magnification. Conventions as in Figure 3. Scale bars = 100 μm in A, C, D, 50 μm in B.

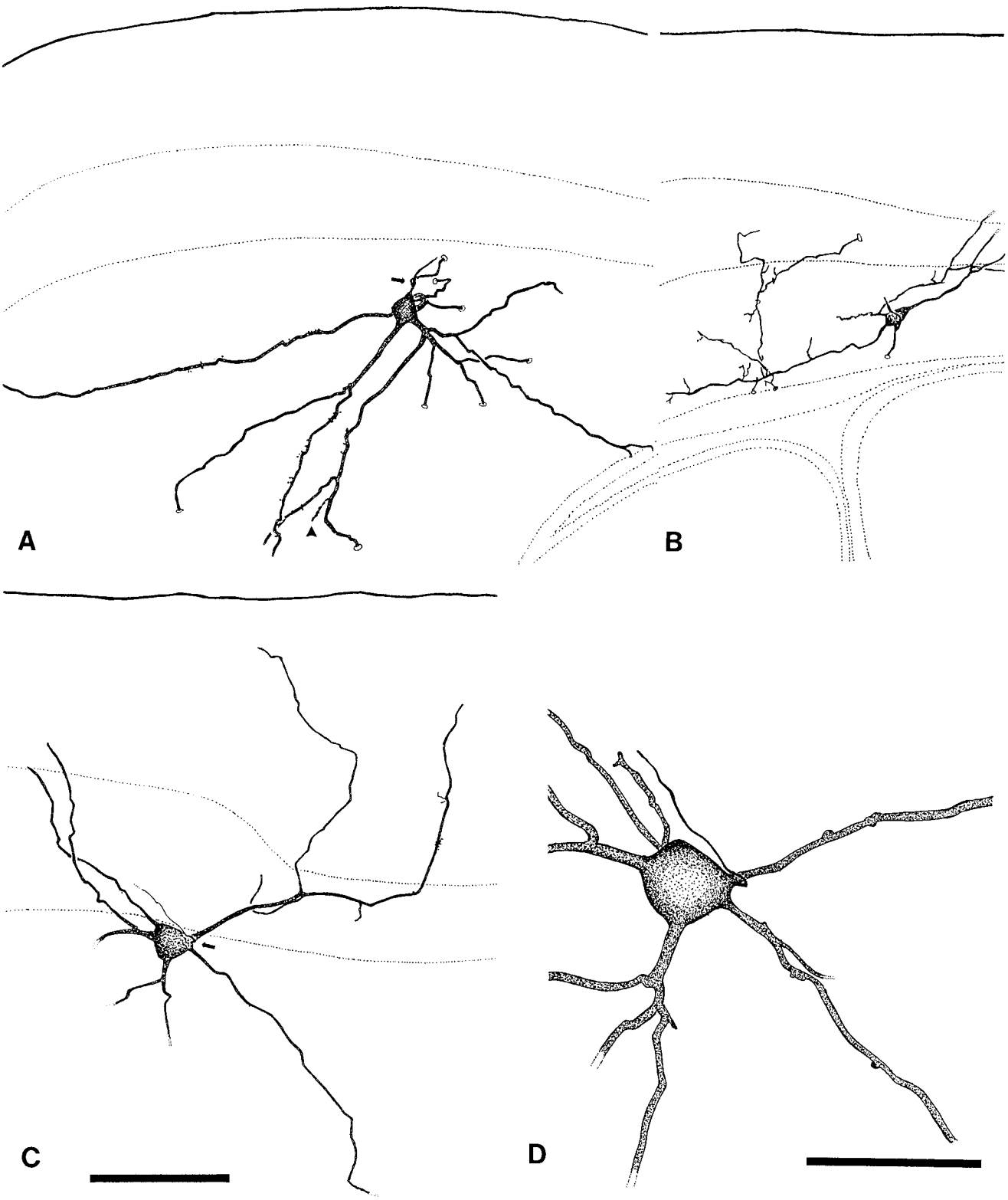

Fig. 14. **A–D:** Camera lucida drawings of giant-multipolar neurons. The thick small arrows in A and C indicate the origin of the axon. The arrowhead in A marks the presence of one axon-like process. The soma of the neuron in C is shown in D at a higher magnification. Conventions as in Figure 3. Scale bars = 100 µm in A–C, 50 µm in D.

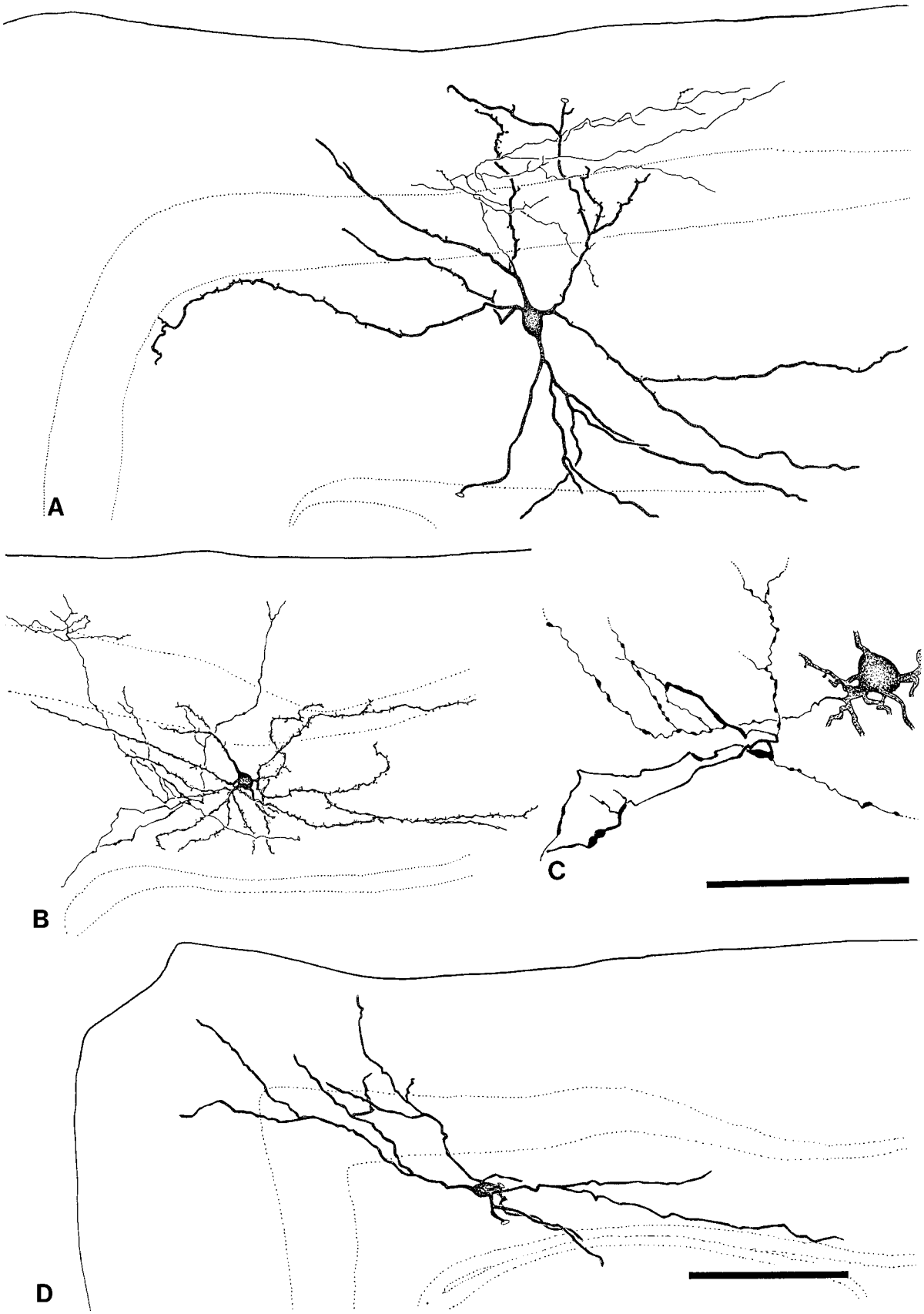

Fig. 15. **A–D:** Camera lucida drawings of giant-multipolar neurons. The soma and the proximal branches of the axon of the neuron in B is shown in C at a higher magnification. Conventions as in Figure 3. Scale bars = 100 µm in A, B, D, 50 µm in C.

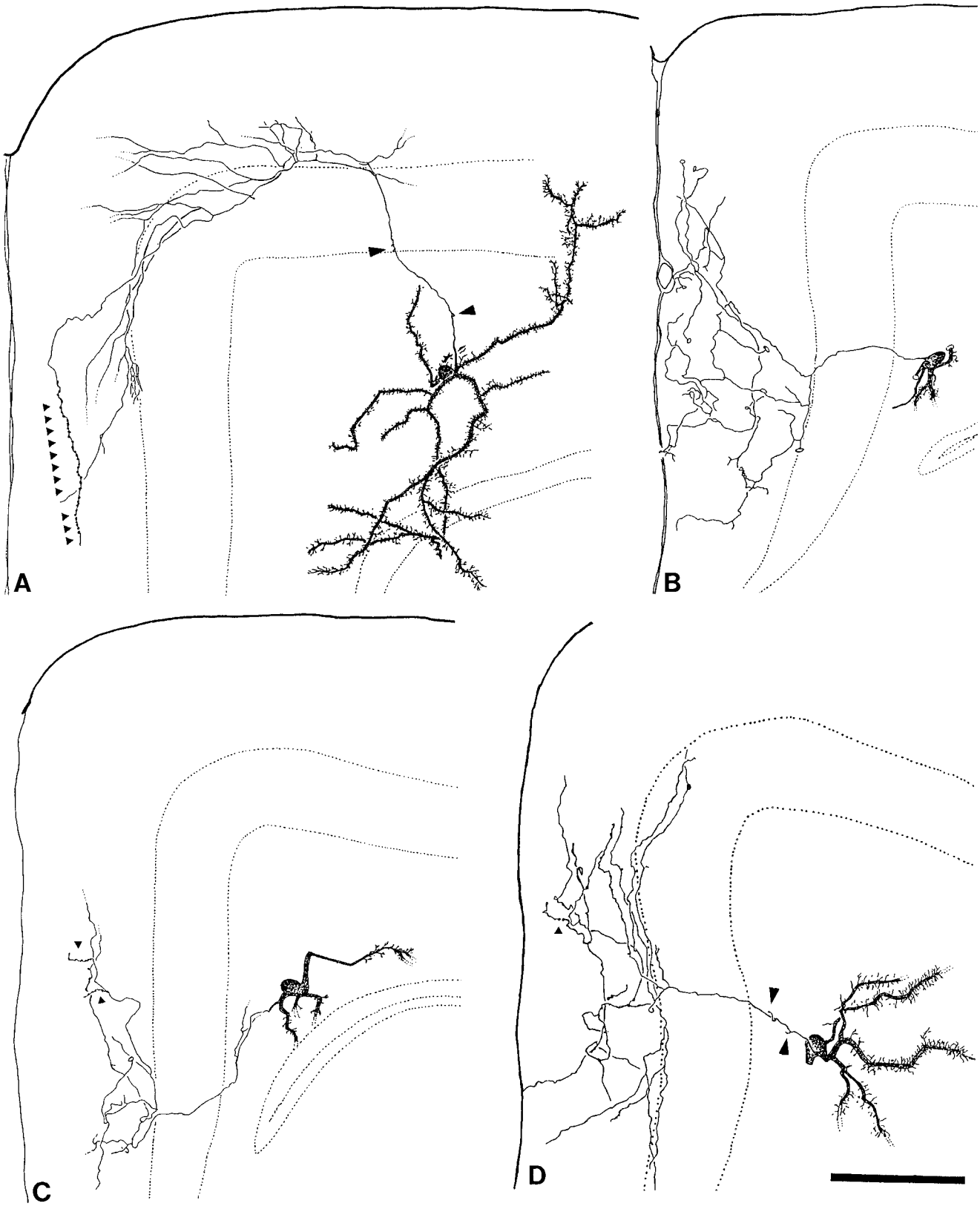

Fig. 16. **A–D:** Camera lucida drawings of long-spined polymorphic neurons. Small black triangles in A, C, and D indicate the presence of small axonal boutons on distal axonal segments. Arrowheads in A and D point to small axonal spines. Conventions as in Figure 3. Scale bar = 100 µm.

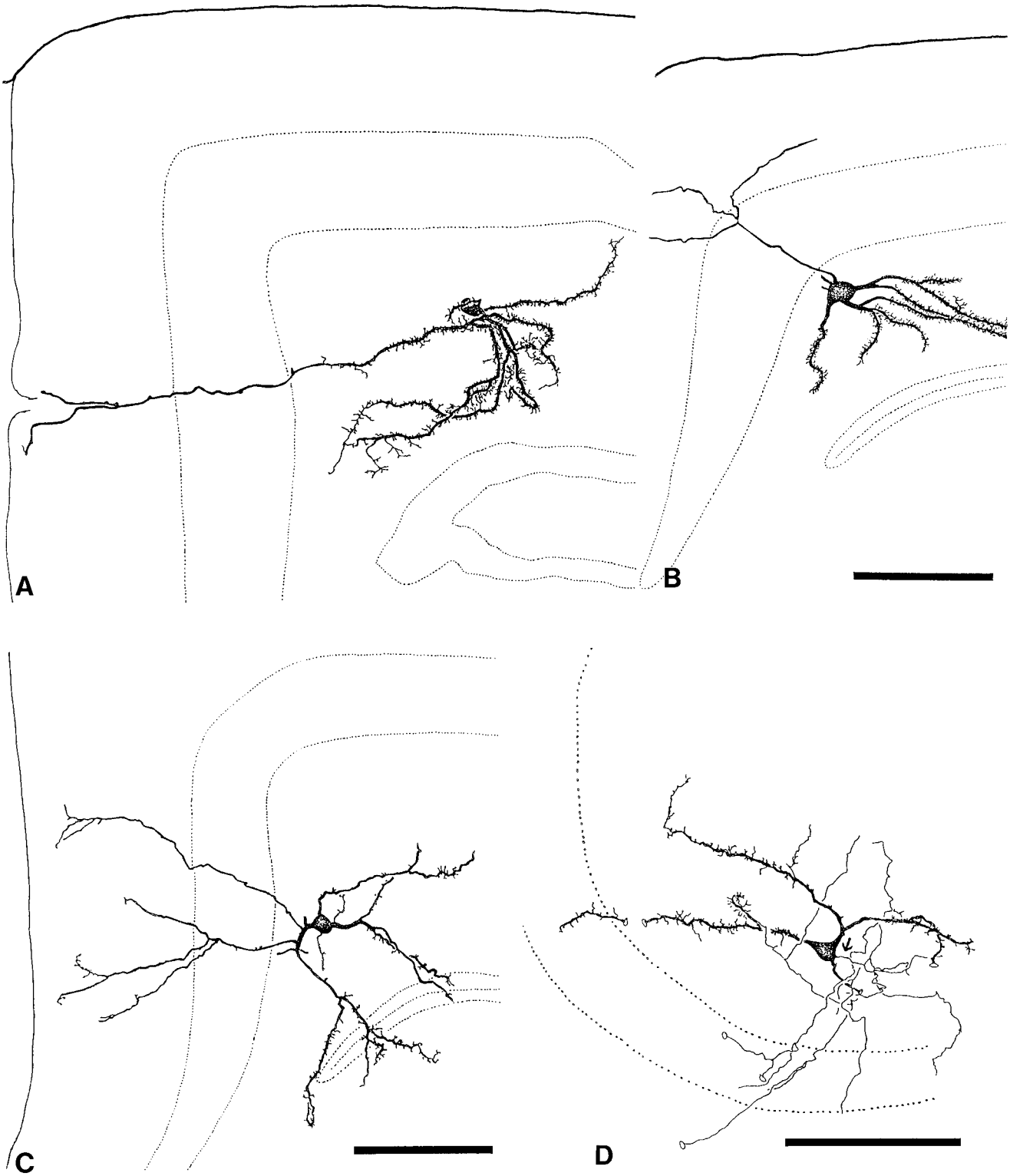

Fig. 17. **A–D:** Camera lucida drawings of long-spined polymorphic neurons. The arrow in D points to the origin of the axon. Conventions as in Figure 3. Scale bars = 100 µm in A,B, 100 µm in C,D.

layer; they showed three to four bifurcation points. Secondary dendrites were progressively thinner at distal segments. The dendrites bore a dense covering with conspicuous long spines and microdendrites. Long spines were filiform or bifurcated excrescences 5–10 µm long; microdendrites were thin longer branches (up to 30–50 µm long). Long spines and microdendrites were present in the dendritic segments in the deep zone of the inner plexiform

layer (as well as other medial cortex projection fields), but they disappeared from any dendritic segment leaving the medial cortex projection fields; there, the dendritic segments were smooth, or bore normal headed spines, or even varicose filiform axon-like processes (Fig. 17A,C). The axons arose from the soma or from a proximal dendrite, followed an ascending trajectory, traversed the cell layer, and finally ramified profusely in the outer plexiform layer (Fig. 16). Occasionally, a few collaterals were distributed in the inner plexiform layer (Fig. 17D). Axonal branches might bear spines on the intermediate segments (arrowheads, Fig. 16A,D), but small bouton-like thickenings in the distal segments, especially in the external third of the outer plexiform layer (black triangles, Fig. 16A,C). In one case, we observed an axonal collateral taking a descending course and entering the alveus, where it could be followed to the anterior commissure (not shown).

Type dip-i9, ascending-axon, periventricular vertical neuron (periventricular neuron). These neurons had radially arranged fusiform-pyriform somata (from 5–10 to 12–16 μm) located close to the ependyma, in the limits between the medial and dorsomedial cortices (Figs. 12E, 18). Three to four smooth poorly ramified dendrites arose from the soma. The apical dendrite appeared comparatively thicker, showed two branching points, traversed the cell layer, and finally ended in the outer plexiform layer; it bore occasional axon-like processes (arrowheads, Figs. 18A,B,D). Short smooth basal dendrites ran through the deep zone of the inner plexiform layer. The axon originated from the soma or from a proximal dendrite (arrows, Fig. 18A,D,E) and followed an ascending course, giving off collaterals that ran in the deep inner plexiform layer. The complete axonal arbor could not been followed in our material, but morphologically similar neurons of the dorsomedial cortex displayed axonal arbors resembling those of the giant-multipolar neurons.

Type dip-i10, short-axon, sparsely spiny alveus horizontal neuron (alveus-horizontal neuron). These neurons had small to medium-sized oval somata (from 5–8 to 10–15 μm) arranged in parallel to the ependyma and located close to it (Figs. 12F, 19). The cell bodies might bear a somatic spine or a short cilium (Fig. 19F). Two smooth poorly ramified dendrites arose from the poles of the soma; they ran parallel to the ependyma intermingling with alvear fibers over long distances. Occasionally, one dendrite bent upward, even crossing the cell layer (Fig. 19A). Sometimes immature-like processes were seen protruding from the soma (Fig. 19E). The axon originated from the soma, ran by the deep zone of the inner plexiform layer, and gave off some collaterals that displayed some bouton-like thickenings. Occasional axonal spines might be seen on them.

A comprehensive survey of the interneuron types lying in the cell layer and the inner plexiform layers of the medial cortex of *P. hispanica* is shown in Figure 20; ectopic principal neurons, indicated with 'e,' are also included in this illustration for comparative purposes.

DISCUSSION

On the classification criteria

As in many other studies, the morphology and distribution of the axonal arbors have been the principal criteria for classifying the complex neuronal population of the lizard medial cortex. The axonal morphology permitted us to distinguish the two main neuronal groups of the lizard medial cortex, i.e., the principal projection neurons and the interneurons (Luis de la Iglesia, 1994, 1995). Projection axons of principal neurons always displayed the same pattern (Luis de la Iglesia and Lopez-Garcia, 1997), whereas those of the interneurons exhibited a high variability, e.g., short local versus long (presumably commissural), ascending versus descending courses, or both, with abundant bouton-like thickenings, or axonal spines, or without them, etc. Unfortunately, the targets of the different axonal arbors could not always be identified in this light microscopy study.

On the other hand, a second important feature was the pattern and location of the receptive dendritic trees in the different and highly laminated synaptic fields of the lizard medial cortex. In this way, a secondary criterion for classification was the dendritic morphology, a characteristic that sometimes was not discriminative (e.g., some projection spiny bitufted neurons and granuloid neurons had identical location and quite similar dendritic patterns). Nevertheless, the dendritic morphology frequently allowed us to identify certain interneuron types (e.g., long-spined polymorphic neuron), even though they were located in an unusual place, (in the latter example, ectopic outer plexiform layer long-spined neurons, Fig. 12D; Desfilis, 1989; Luis de la Iglesia et al., 1994).

In some instances, the use of such criteria resulted in including archetypes that were actually represented by only one or two well-impregnated cells in our sample (i.e., the granuloid, and the deep-fusiform neurons). The apparent complexity of the interneuronal population of the medial cortex and the limitation imposed by the unknown selection mechanisms of Golgi staining, make the sample of studied impregnated neurons probably incomplete. Thus, the classification described here may still be open to the addition of new types that could be subsequently detected.

In the lizard species *P. hispanica*, the neuronal population of the inner plexiform layer has been estimated to be approximately five thousand neurons per hemisphere (Lopez-Garcia et al., 1984). With the inherent limitations of the Golgi method for quantitative studies, the impregnation frequency for each neuronal archetype described (see Table 1) may be regarded as an index of its actual numbers, because preferential impregnation of a particular type has not been demonstrated.

Comparisons and terminology of the interneurons in this study

Five intrinsic types of interneurons were reported in the outer plexiform layer of *P. hispanica* (Luis de la Iglesia et al., 1994; Luis de la Iglesia, 1995). The short-axon, aspinous bipolar neurons (or sarmentous neurons) have medium-sized somata, smooth dendrites with occasional axon-like processes (which give them their sarmentous appearance) and an axon that forms a loose plexus of beaded collaterals that overlap the dendritic field. The short-axon, aspinous juxtasomatic neurons (or coral neurons; Figs. 2A, 3B) have a fan-like dendritic tree, dendrites with axon-like processes, and local axons showing thickenings, but lacking axonal boutons. The short-axon, sparsely spiny multipolar neurons (or stellate neurons) have long, distally varicose dendrites arranged in parallel to the cell layer, and an axonal plexus that overlaps the dendritic field, displaying small boutons in the distal collaterals. The short-axon, sparsely spiny juxtasomatic multipolar

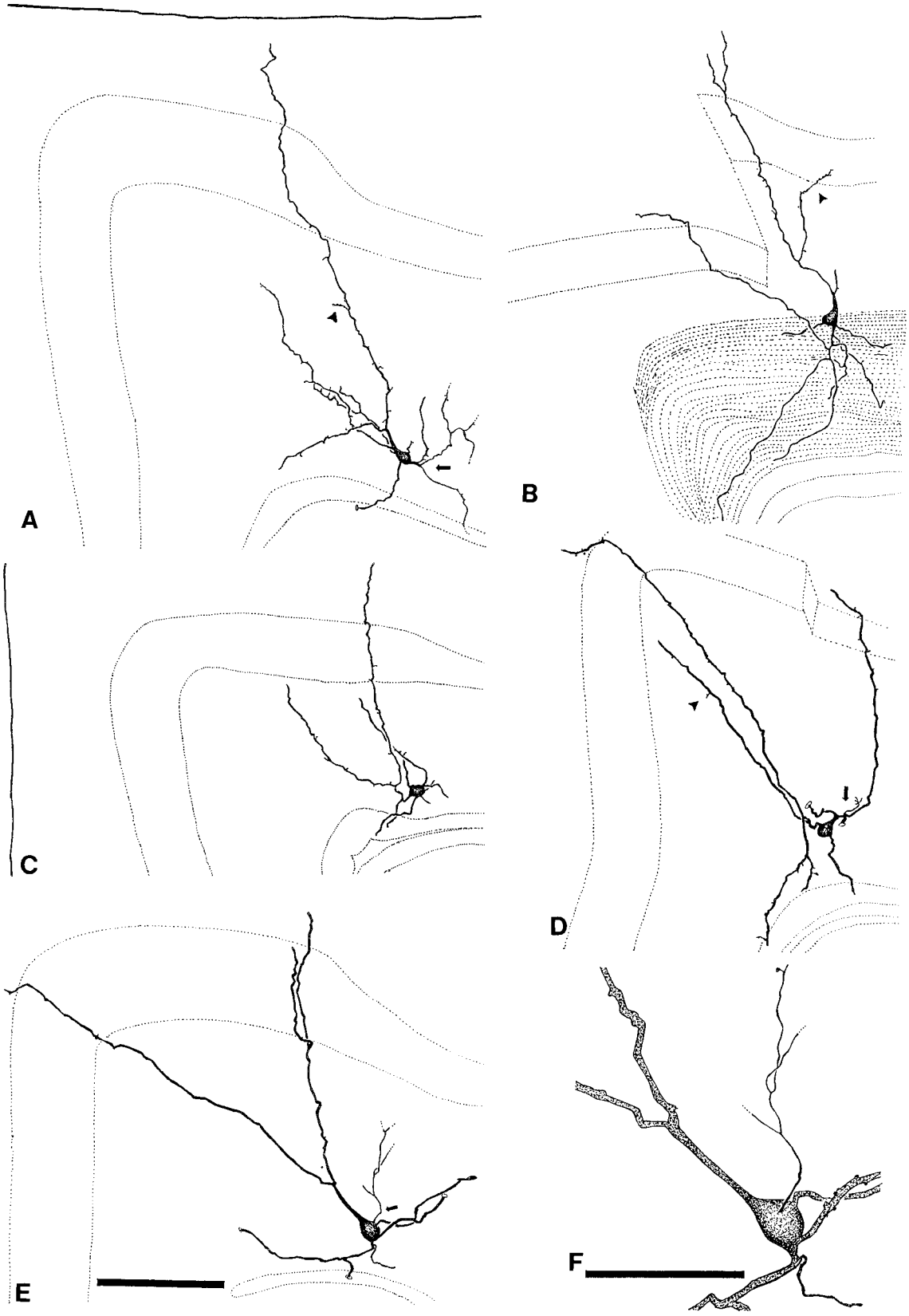

Fig. 18. **A–F:** Camera lucida drawings of periventricular neurons. The soma of the cell in E is shown in F at a higher magnification. Thick small arrows in A, D, and E point to the origin of the axon. Arrowheads in A, B, and D indicate the presence of axon-like processes. Conventions as in Figure 3. Scale bars = 100 μm in A–E, 50 μm in F.

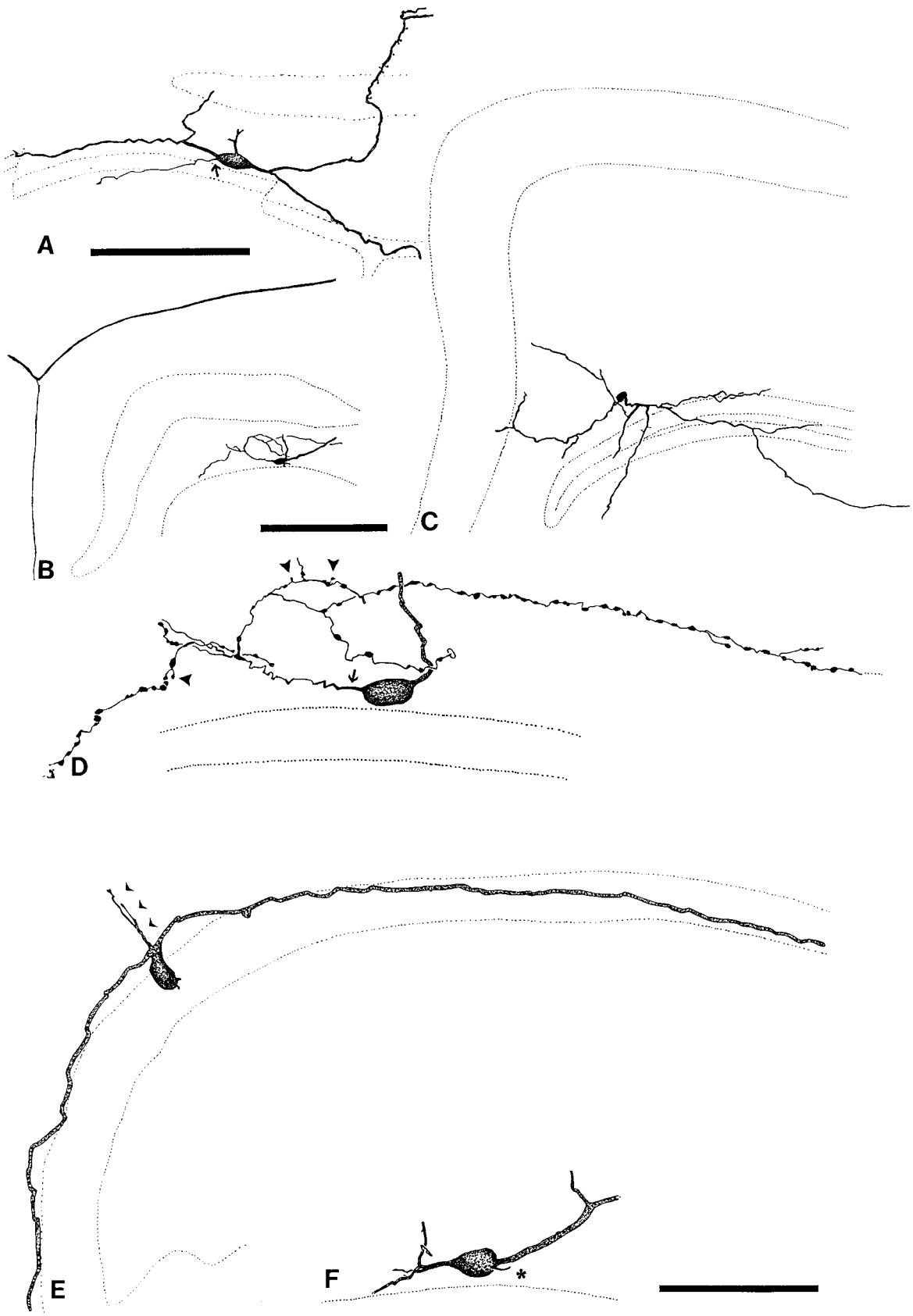

Fig. 19. **A–F:** Camera lucida drawings of alveus-horizontal neurons. The cell bodies of neurons in A and F lie at the limit between the dorsomedial and dorsal areas. Thick small arrows in A and D point to the origin of the axon. The arrowheads in D indicate the presence of small axonal spines. The small arrowheads in E point to the growing axon of an immature-like alveus-horizontal neuron. A short somatic cilium in F is marked by an asterisk. Conventions as in Figure 3. Scale bars = 100 μm in A, 100 μm in B,C, 50 μm in D–F.

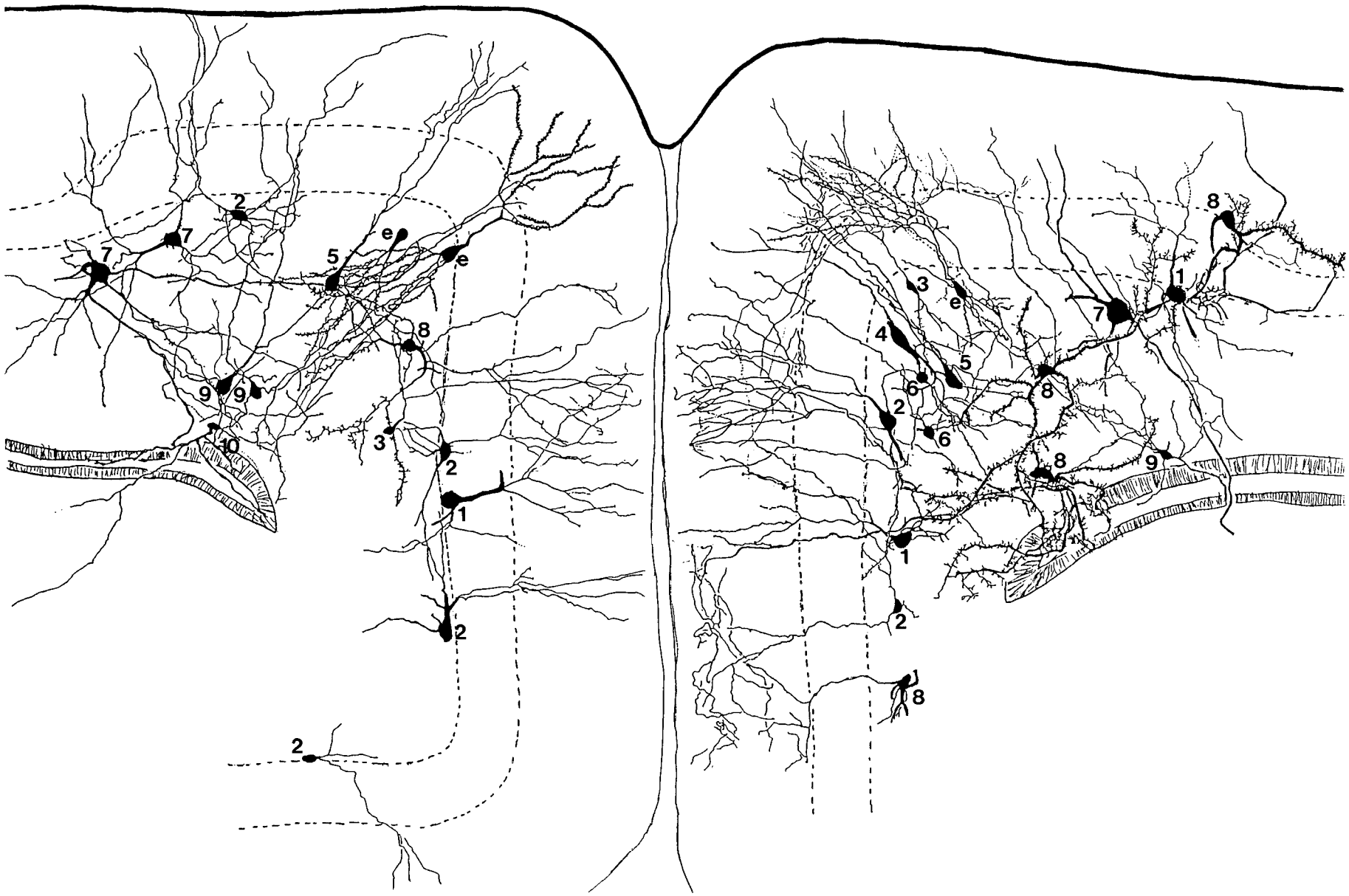

Fig. 20. Line drawing composition illustrating the different interneuronal types found in the inner plexiform layer of the lizard medial cortex. Some ectopic projection (e) neurons located in the juxtasomatic zone of the inner plexiform layer are also represented. Numerals 1–10 coincide with those ordinal names i1–i10 shown in Table 1. Dotted lines indicate the borderlines of the cell layer.

neurons (or deep-stellate neurons) are characterized by their deep dendrites (similar to those descending dendrites of deep-fusiform neurons) and by their thin axons that give off many distal collaterals studded with abundant small boutons. Finally, the sparsely spiny juxtasomatic horizontal neurons (or couchant neurons; Fig. 3A) have thin, poorly branched dendrites and a slender axon that loses its impregnation as it enters the cell layer (see Luis de la Iglesia et al., 1994, and Luis de la Iglesia, 1995, for a more detailed description of the morphology and immunocytochemical nature of these interneurons). The sarmentous and stellate interneurons lie preferentially in the two outer thirds of the outer plexiform layer, but the coral, deep-stellate, and couchant neurons lie in deeper strata, sometimes even inside the upper rows of somata of the cell layer.

There is no equivalent of the granuloid, web-axon, and deep-fusiform interneurons of the cell layer in precedent Golgi studies; thus, this study gives a first description of them. The actual existence of these neuronal types was predicted from electron microscopic studies, which described the presence in the cell layer of occasional somata with the ultrastructural characteristics of interneurons, i.e., abundant perinuclear cytoplasm, deep nuclear invaginations, etc. (Ulinski, 1977; Wouterlood et al., 1981; García-Verdugo et al., 1984; Dávila et al., 1985). Immunocytochemical studies reported multipolar and vertical fusiform to pyramidal GABA-immunoreactive somata inside the cell layer (Schwerdtfeger and Lopez-Garcia, 1986; Schwerdtfeger and Lorente, 1988a,b), some of them being parvalbumin-immunoreactive (Martínez-Guijarro et al., 1993). Those large parvalbumin-immunoreactive fusiform neurons receiving serotonergic axonal endings, reported in this latter study, are very similar to the deep-fusiform neuron illustrated in Figure 4C. Similarly, some HRP transport studies (Olucha et al., 1988; Martínez-García et al., 1990) have reported contralateral, retrogradely labeled somata in the medial cortex cell layer of *Podarcis* (i.e., putative commissural neurons), whose morphological features coincide with those of web-axon neurons.

The terminology applied and the possible correspondence of the ten interneuronal types populating the juxtasomatic and deep zones of the inner plexiform layer, with other neuronal types reported in related reptilian species are shown in Table 2. Nevertheless, some points of the proposed equivalencies should be further explained. Thus, the smooth vertical neuron is compared with some (but not all) of the sparsely spiny class C1 of neurons in *Agama* (Wouterlood, 1981), on the basis of their somatic and dendritic morphology. Similarly, the cell layer class 4 neuron found in *Sceloporus* (Lacey, 1978), represented in his Figure 7C, displayed a clearly ascending axon and should rather be considered as an interneuron, probably a smooth vertical neuron. With regard to the deep zone, both giant-multipolar, and long-spined polymorphic neurons have been found in the inner plexiform layer of other cortical layers, namely, the dorsomedial and dorsal cortices (Lopez-Garcia et al., 1988a; Desfilis, 1989; Martínez-Guijarro et al., 1990; Bernabeu et al., 1994). Moreover, the conspicuous long-spined polymorphic neurons seem to be distributed throughout the cortical medial cortex projection fields, including the less frequent locations in the outer plexiform layer of the dorsomedial (Fig. 12D) and dorsal (Desfilis, 1989) cortices. It seems clear that their characteristic long spines and microdendrites are specialized structures that receive specific contacts from medial cortex zinc-enriched axonal endings (Lopez-Garcia et al., 1988a). Consequently, somata and dendrites outside the medial cortex projection fields lack these kind of specializations (see the long dendrite in Fig. 17A). Periventricular neurons were also found in the dorsomedial cortex, and alveus-horizontal neurons were present in the dorsomedial and dorsal cortices (Fig. 19A,F). Hence, the zone comprising the deep inner plexiform layer of the medial cortex and the inner plexiform layers of dorsomedial and dorsal cortices share some common types of interneurons, although each area shows specific neuronal populations.

The interneurons of the cell layer: Axo-somatic, axo-axonic, or commissural interneurons?

Unfortunately, the precise axonal targets of granuloid, web-axon, and deep-fusiform interneurons could not be characterized in this study. By comparison with its homologous center, i.e., the mammalian fascia dentata granule layer, they could be either axo-axonic and/or axo-somatic interneurons. Five types of axo-somatic basket cells have been identified in the mammal dentate granular layer (Ramón y Cajal, 1904b, 1911; Lorente de Nó, 1934; Seress and Pokorny, 1981; Ribak and Seress, 1983; Seress and Ribak, 1983); moreover, one additional axo-axonic or chandelier cell (Soriano and Frotscher, 1989; Soriano et al., 1990), and one subgranular axo-dendritic cell, whose axons arborize in the molecular layer (Soriano and Frotscher, 1993a), have been described. The molecular layer basket cells, located in the outer margin of the granular layer (Seress and Pokorny, 1981; Ribak and Seress, 1983; Seress and Ribak, 1983), are morphologically identical to the deep-stellate neuron of the medial cortex outer plexiform layer (Luis de la Iglesia et al., 1994). They both have a large cell body with an apical and a basal plume of nonspinous, distally varicose dendrites, display deep dendrites reaching the hilus or the deep zone of the inner plexiform layer, and form dense supragranular plexuses making typical perisomatic baskets in the fascia dentata, but undifferentiated primitive basket-like contacts in lizards (Luis de la Iglesia et al., 1994). The axonal trajectories of deep-fusiform neurons (Fig. 4A) are similar to those of deep-stellate neurons; although primitive baskets are not present, bouton-like thickenings may make perisomatic contacts suggesting that they are axo-somatic neurons.

Axo-axonic or chandelier cells of the outer border of the granular layer give rise to axons making synaptic contacts on the initial axonal segments of granule cells (Soriano and Frotscher, 1989; Soriano et al., 1990). In the lizard medial cortex, comparable neurons remain unidentified, but similar axo-axonic synaptic contacts, made by parvalbumin-immunoreactive axonal endings, have been found (Martínez-Guijarro et al., 1993). Web-axon neurons share the axonal characteristics of both axo-somatic and axo-axonic cells (see axonal trajectory in Fig. 2E), a feature that may represent a primitive property in lizards. Nevertheless, whether this neuronal type represents chandelier cells in the lizard medial cortex is still a point to be elucidated.

Some interneurons whose somata are located juxtaposed to the cell layer, either to the external or the internal sides, are likely contralateral projection neurons. The locations of their somata and dendrites clearly match those of some GABA-immunoreactive neurons (Schwerdtfeger and Lopez-Garcia, 1986; Schwerdtfeger and Lorente, 1988a,b) and those of some neurons that resulted heavily labeled after HRP injections in the contralateral hemi-

TABLE 2. Comparison of Short-Axon Neurons Reported in the Inner Plexiform Layer of the Squamate Medial Cortex. I. Golgi Studies[1]

	Juxtasomatic zone of the inner plexiform layer						Deep zone of the inner plexiform layer			
	Smooth neurons		Radial neurons				Multipolar neurons		Bipolar neurons	
Author, Year; (Species) Present study, 1997; *(Podarcis hispanica)*	Type i1: Vertical	Type i2: Horizontal	Type i3: Small	Type i4: Large	T. i15: Pyramidal-like	Type i6: Spheroidal	T. i7: Giant-multipolar	T. i8: Long-spined polymorphic	T. i9: Periventricular	T. i10: Alveus-horizontal
Ramón, 1891; *(Lacerta agilis, L. viridis)*					Thick pyramidal					
Ramón, 1896; *(Chamaeleo chamaeleo)*		Ascending-axon globous & fusiform cells								
Ramón y Cajal, 1904a; *(Ch. chamaeleo)*		Ascending-axon globous & fusiform cells						Ascending-axon fusiform cells		
Ramón y Cajal, 1917; *(L. agilis, Iguana iguana)*					Fusiform pyramidal			Cells with peripheral axon		
Minelli, 1966; *(L. viridis, L. muralis)*		Horizontal bipolar						Highly branched multipolar cells		
Northcutt, 1967; *(I. iguana)*						Type Golgi-II		Pluripolar cells		
Ebbesson & Voneida, 1969; *(Tupinambis nigropunctatus)*							Multipolar neuron		Vertical neuron	
Regidor et al., 1974; *(L. galloti)*		Type m1-F					Type m1-I	Type m1-G		
Ulinski, 1977; *(Boa constrictor, Natrix sipedon)*									Periventricular	
Lacey, 1978; *(Sceloporus undulatus)*	Class 4 (C) (cell layer)				class 1 (IPL)			Class 2 (inner plexiform layer)		
Wouterlood, 1981; *(Agama agama)*	Type C1 (cell layer)							Type S2		
Guirado et al., 1984; *(Psammodromus algirus)*		Class 1 (IPL)								
Berbel et al., 1987; *(P. pytiusensis)*		T.F: Sp-sp multipolar						Type G: Large spiny polymorphic		
Lopez-Garcia et al., 1988a; *(L. galloti, P. pytiusensis, P. hispanica)*								Long-spined polymorphic		
Ulinski, 1990; (reptiles)		Horizontal							Periventricular	
II. Electron Microscopy, Immnocytochemical, and Histochemical Studies										
Schwerdtfeger & Lopez-Garcia, 1986; *(P. hispanica);* GABA-ICCh	Asp & Sp-sp (GABA-IR)	Horiz-bi-polar (GABA-IR)					Spherical & multipolar cell bodies (GABA-IR)			
Lopez-Garcia et al., 1988a; *(L. galloti, P. pytiusensis, P. hispanica)* GABA, EM								Large polymorphic (GABA-IR)		
Schwerdtfeger & Lorente, 1988a,b; *(P. hispanica);* GABA-ICCh; EM	Pyram-like (GABA-IR)		Vertical fusiform (GABA-IR)				Horizontal & multipolar cell bodies (GABA-IR)			
Olucha et al., 1988; *(P. hispanica, G. stehlinii);* HRP; EM			Ascending-axon polymorphic & stellate neurons				Ascending-axon polymorphic & stellate neurons			
Martínez-García et al., 1990; *(P. hispanica, G. stehlinii);* HRP; EM	Aspinous commissural (inner margin of the cell layer)									
Martínez-Guijarro et al., 1993; *(P. hispanica);* PV, NPY-ICCh; EM	Pyramidal-like (PV-IR)		Vertical bipolar (PV-IR)		Pyramidal-like (PV-IR)		Multipolar (PV-IR)	Neuro-peptide Y-IR	Pyramidal-like (PV-IR)	
Martínez-Guijarro et al., 1994a; *(P. hispanica);* PV, NPY, opioid, 5HT-ICCh		Juxtasomatic inner plexiform layer PV-IR cell bodies receiving 5HT-IR axonal endings								
Bernabeu et al., 1994; (P. hispanica); HRP intracellular injection, GABA-ICCh							A-S&A-D-Mp (GABA-IR)			

[1]5HT, serotonin; Asp, aspinous; A-S&A-D-Mp, axosomatic and axodendritic multipolar; EM, electron microscopy; GABA, gamma-amino butyric acid; Horiz, horizontal; HRP, horseradish peroxidase transport; i1–i10, inteneuron types 1–10 -ICCh, immunocytochemistry; IPL, inner plexiform layer; -IR, immunoreactive; NPY, neuropeptide Y; Pyram, pyramidal; PV, parvalbumin; Sp-sp, sparsely spiny; T, type.

sphere (Olucha et al., 1988; Martínez-García et al., 1990). Unfortunately, their complex axonal trajectories could not be traced in our Golgi-impregnated material.

The interneurons of the juxtasomatic dendritic layer: A parvalbumin-immunoreactive population?

In the lizard inner plexiform layer, GABA-immunoreactive cells include two nonoverlapping populations: those located in the juxtasomatic zone (Fig. 1E), which are also parvalbumin-immunoreactive (Martínez-Guijarro and Freund, 1992a; Dávila et al., 1993; Martínez-Guijarro et al., 1993), and those lying in the deep zone (Fig. 1F), which are also neuropeptide-immunoreactive (Dávila et al., 1988, 1991, 1993; Martínez-Guijarro et al., 1993). Parvalbumin antibody gives a Golgi-like immunostaining of neuronal processes; this allows comparisons with Golgi-impregnated neurons. Those parvalbumin-immunoreac-

tive neurons located in the outer rim of the cell layer have been compared with the coral, deep-stellate, and couchant neurons in a previous work (Luis de la Iglesia et al., 1994), and those located in the inner side of the cell layer (Martínez-Guijarro et al., 1993) probably represent the deep-fusiform, smooth vertical, and smooth horizontal neurons described here.

In the mammalian fascia dentata, parvalbumin-immunoreactive neurons are mostly found in the cell layer and especially in the hilus (Kosaka et al., 1987; Katsumaru et al., 1988; Ribak et al., 1993; Seress et al., 1993). Among them, axo-somatic basket cells and axo-axonic chandelier cells have been identified (Nitsch et al., 1990a; Soriano et al., 1990). Parvalbumin-immunoreactive neurons in the lizard medial cortex show a similar morphology (Martínez-Guijarro and Freund, 1992a; Martínez-Guijarro et al., 1993).

In this study, the interneurons populating the juxtasomatic inner plexiform layer showed characteristic features of parvalbumin-immunoreactive cells, i.e., cell body shape and size, and dendritic tree morphology. Their aspect is similar to those of basket cells (Seress and Pokorny, 1981; Ribak and Seress, 1983), identified as GABA- (Seress and Ribak, 1983) and parvalbumin-immunoreactive (Seress et al., 1993) in the mammal fascia dentata, including the presence of the characteristic axon-like processes (Hazlett and Farkas, 1978), referred to as filopodial-like appendages after parvalbumin immunocytochemical and electron microscopy studies (Ribak et al., 1993). Thus, medial cortex smooth vertical and horizontal neuronal types resemble pyramidal and horizontal fusiform basket cells of dentate subgranular layer, whereas small, large, and pyramidal-like radial neurons are quite similar to certain cell types of the hilar fascia dentata (see Table 3). Finally, the spheroidal neuron resembles the spheroid cell (Amaral, 1978), some hilar cells with ascending-axons (Ramón y Cajal, 1911), and the oval subgranular cell with extensive axonal arborization in the molecular layer (Soriano and Frotscher, 1993a).

The interneurons of the inner plexiform layer or primary projection field of the medial cortex: a lizard hilus neuronal population?

Dentate hilar interneurons display a great variability in shape and size, especially those of the deep hilar region called polymorphic cell zone (Ramón y Cajal, 1904b, 1911), or polymorphic layer (Lorente de Nó, 1934). A complex and heterogeneous population of polymorphic cells, difficult to classify, has been described in several studies in the dentate hilus (Ramón y Cajal, 1904b, 1911; Lorente de Nó, 1934; Stensaas, 1968; Amaral, 1978; Seress and Ribak, 1983; Soriano et al., 1989; Soriano and Frotscher, 1993b; Al-Hussein and Al-Ali, 1995).

In the deep zone of the inner plexiform layer, two or three neuronal types have been reported in earlier studies (see Table 2). Here we describe four types, one of them lying in the alveus, and three others being highly pleomorphic. There is no neuronal type in lizards comparable with the hilar mossy cell, perhaps the most conspicuous cell type in the dentate hilus (Amaral, 1978; Ribak et al., 1985; Frotscher et al., 1991). However, the various types of multipolar, stellate, or semistellate hilar neurons resemble the group of giant-multipolar cells in the deep inner plexiform layer (see Table 3). The hilar long-spined, multipolar cell (Amaral, 1978), and the spiny nonpyramidal neuron of stratum lucidum in the CA3 region of the rat hippocampus, being considered as the same archetype lying in a different ubication (Soriano and Frotscher, 1993b), are identical to the long-spined polymorphic neuron of the lizard medial cortex. They both occur in the projection fields of either dentate granule cells (i.e., the dentate hilus and stratum lucidum of the hippocampal CA3 region in mammals) or medial cortex principal neurons (i.e., the cortical zinc-enriched Timm-positive areas in lizards). In these neurons, long spines and microdendrites occur profusely distributed on dendrites and somata only in the dentate mossy fiber zone of mammals (Soriano and Frotscher, 1993b) and in its equivalent zone in lizards. Dendrites running out of this area suddenly lose these excrescences both in mammals (Soriano and Frotscher, 1993b) and in lizards (Fig. 17A,C). In mammals, an inductive role of mossy fibers in the growth of complex spines and thorny excrescences on dendrites of CA3 region pyramidal cells has been argued for (see references in Soriano and Frotscher, 1993b). A similar effect has been proposed for the long spines of long-spined, multipolar cells and spiny nonpyramidal cells of the stratum lucidum (Soriano and Frotscher, 1993b). This may well be the case for some of the specific dendritic specializations in the medial cortex, such as long spines of long-spined polymorphic neurons and long complex spines of deep dendrites seen on more superficial cell types.

A fraction of hilar cells in the mammalian fascia dentata constitutes a subpopulation of neuropeptide-containing cells (Swanson et al., 1987; Deller and Leranth, 1990; Leranth et al., 1990; Holm et al., 1992), most of them also being GABA-immunoreactive (Kosaka et al., 1988). Somatostatin and neuropeptide Y show a high degree of coexistence in the same cells (Deller and Leranth, 1990), but they constitute a nonoverlapping population with parvalbumin-immunoreactive cells (Nitsch et al., 1990b). Hilar neuropeptide-containing cells display peripheral axons that make symmetrical synapses preferentially on dendritic shafts of granule cells (Deller and Leranth, 1990) and participate both in feed back and feed forward inhibition mechanisms (Gulyás et al., 1990; Leranth et al., 1990; Miettinen and Freund, 1992). Similarly, some of the deep inner plexiform layer interneurons of the lizard medial cortex, presumably the polymorphic neurons, display GABA, somatostatin, and/or neuropeptide Y immunoreactivities (Dávila et al., 1988, 1991, 1993; Lopez-Garcia et al., 1988a; Martínez-Guijarro et al., 1993; Nacher et al., 1996). Both neuropeptides show a high coexistence between themselves and with GABA (Dávila et al., 1991,1993), but they do not coexist with parvalbumin (Martínez-Guijarro et al., 1993), which is present in other deep inner plexiform layer interneurons (Fig. 1E), probably giant-multipolar, and periventricular neurons. Neuropeptide-containing neurons have peripheral axons that innervate distal dendritic shafts of medial cortex principal neurons (Dávila et al., 1993; Martínez-Guijarro et al., 1993, 1994a). Moreover, they also are thought to participate in feed back and feed forward inhibition (see below). Hence, the deep inner plexiform layer interneurons of the lizard medial cortex, taken together with similar neurons occurring in the inner Timm-positive zone of the dorsomedial and dorsal cortices, may be regarded as a lizard hilus neuronal population.

The horizontal juxtaependymal interneurons of the medial cortex: are they a lizard alveus neuronal population?

In the cerebral cortex of reptiles, the alveus is a thick transverse fiber bundle situated between the inner plexi-

TABLE 3. Comparison of Short-Axon Neurons in Dentate Area of Mammals and in the Medial Cortex of *Podarcis hispanica*[1]

Author, year; species, procedure	Mammalian fascia dentata	Lizard medial cortex
Ramón y Cajal, 1904b, 1911; Rabbit, Golgi	Molecular Zone	Outer Plexiform Layer
	—Short-axon, superficial, pyriform, ovoid or fusiform cell	—Sarmentous/Stellate
	—Small cell	—Stellate
	—Short-axon, deep triangular or stellate cell	—Deep-stellate/Coral
	Polyorphic Cells Layer	Inner Plexiform Layer
	Limitans Subzone	Inner Border of the Cell Layer
	—Ascending-axon, pyramidal cell	—Smooth vertical
	—Descending-axon, stellate or fusiform cell	—Smooth horizontal (?)
	Plexiform Subzone	Juxtasomatic Zone
	—Ascending-axon, fusiform cell (axon branched in molecular zone)	—Smooth horizontal
	—Ascending-axon, stellate cell (axon branched in granule layer)	—Giant-multipolar/Large radial
	—Descending-axon, fusiform cell	—Pyramidal-like radial
	—Descending-axon, stellate cell	—Spheroidal/Giant-multipolar (?)
	—Short-axon, stellate cell	—Giant-multipolar
	Fusiform Cell Subzone	Deep Zone
	—Descending-axon, stellate or triangular cell	—Long-spined polymorphic
	—Horizontal cell	—Alveus-horizontal
	—Short-axon, stellate or triangular cell	—Periventricular
Lorente de Nó, 1934; Mouse, Golgi	Molecular Layer	Outer Plexiform Layer
	—Superficial cells	—Sarmentous/Stellate
	—Deep cells	—Coral/Deep-stellate
	Polymorphic Layer	Inner Plexiform Layer
	—Pyramidal-like basket cell	—Smooth vertical
	—Horizontal basket cell	—Smooth horizontal
	—Polygonal basket cell	—Giant-multipolar
	—Ascending-axon, horizontal cell	—Smooth horizontal
	—Horizontal-axon cell	—Giant-multipolar
Stensaas, 1967; Fetal rabbit, Golgi	Marginal Layer (Prospective Molecular Zone)	Outer Plexform Layer
	—Small bipolar cell	—Stellate
	—Large cell (Cajal-Retzius cell)	—Sarmentous
Stensaas, 1968; Fetal rabbit, Golgi	Polymorphic Layer	Inner Plexiform Layer
	—Ascending-axon pyramidal cells	—Smooth vertical
	—Ascending-axon semistellate cells	—Giant-multipolar
	—Descending-axon semistellate cells	—Pyramidal-like radial
	—Ascending-axon, small horizontal cells	—Smooth horizontal
	—Descending-axon, small horizontal cells	—Smooth horizontal (?)
	—Immature polymorphic cells	—Long-spined polymorphic
Amaral, 1978; Rat; Golgi	Hilus /CA · 4: Zone 1	Inner Plexiform Layer
	—Pyramidal basket cell	—Smooth vertical
	—Pyramid-like, stellate cell	—Long-spined polymorphic
	—Giant aspiny stellate cell	—Giant-multipolar
	Hilus /CA · 4: Zone 2	
	—Inferior region unipolar (IRU) interneuron	—Small radial (?)
	—Large spiny stellate cell	—Giant-multipolar
	—Wavy multipolar cell	—Large radial/Giant-multipolar
	—Multipolar cells	—Giant-multipolar
	—Peanut cell	—(?)
	—Small pauci-spined stellate cell	—Spheroid
	—Suprapyramidal aspiny stellate cell	—Giant-multipolar
	Hilus /CA · 4: Zone 4	
	—Dentate pyramidally-shaped basket cell	—Smooth vertical
	—Dentate horizontal basket cell	—Smooth horizontal
	—Spheroid cell	—Spheroid/Giant-multipolar
	—Cells of the D/H border with ascending and descending axon	—Giant-multipolar
	—Fusiform cells	—Smooth horizontal
	—Small aspiny multipolar cell with web-like axonal plexus	—Spheroidal/Giant-multipolar
	—Mossy cell	—(?)
	—Oviform cell	—Giant-multipolar
	—Long-spined multipolar cell	—Long-spined polymorphic
	—Aspiny stellate cell	—Giant-multipolar
Hazlett & Farkas, 1978; Opossum; Golgi	Molecular Layer	Outer Plexiform Layer
	—Short-axon molecular layer neurons	—Sarmentous/Coral
Seress & Pokorny, 1981; Rat; Golgi	Molecular Layer	Outer Plexiform Layer
	—Molecular layer basket cell (type V)	—Deep-stellate
	Granular Layer	Cell Layer
	—Pyramidal basket cell (type I)	—Smooth vertical
	—Horizontal basket cell (type II)	—Smooth horizontal
	—Triangular basket cell (type III)	—Smooth vertical
	—Granular layer large bipolar basket cell (type IV)	—Deep-fusiform
Ribak & Seress, 1983; Rat, Golgi	Molecular Layer	Outer Plexiform Layer
	—Molecular layer basket cell	—Deep-stellate
	Granular Layer	Cell Layer
	—Pyramidal basket cell	—Smooth vertical
	—Fusiform basket cell	—Deep-fusiform
	—Horizontal basket cell	—Smooth horizontal
	—Inverted fusiform basket cell	—Coral (?)

TABLE 3. (continued)

Author, year; species, procedure	Mammalian fascia dentata	Lizard medial cortex
Seress & Ribak, 1983; Rat, GAD-ICCh	Molecular Layer —Small superficial cell —Large juxtasomatic multipolar cell Granular Layer —Pyramidal basket cell —Large fusiform cell —Horizontal basket cell —Inverted fusiform cell Hilus —Multipolar cells —Bipolar cells —Fusiform cells	Outer Plexiform Layer —Sarmentous/Stellate —Deep-stellate/Coral Cell Layer —Smooth vertical —Deep-fusiform Smooth horizontal —Coral (?) Inner Plexiform Layer —Giant-multipolar —Radial neurons/Periventricular —Long-spined polymorphic
Soriano et al., 1989; Rat, GAD-ICCh	Molecular Layer —Small spheroid or fusiform cells —Large juxtasomatic cells Granule Cell Layer —Spheroid cells —Fusiform cells —Deep pyramidal cells Subgranular Zone (Inner Border of the Cell Layer) —Horizontal fusiform cell Hilus —Medium-sized spherical or ovoid cells	Outer Plexiform Layer —Sarmentous/Stellate —Deep-stellate/Coral Cell Layer —Granuoid/Web-axon —Deep-fusiform —Smooth vertical Inner Border of the Cell Layer —Smooth horizontal Inner Plexiform Layer —LSPN/Giant-multipolar
Soriano & Frotscher, 1989; Rat, Golgi & GABA-ICCh	Molecular Layer & Granule Cell Layer —Axo-axonic fusiform GABA-IR cell	Cell Layer —Web-axon (?)
Soriano et al., 1990; Rat, Golgi, GABA & PV-ICCh	Molecular Layer & Granule Cell Layer —Chandelier axo-axonic GABA/PV-IR cell	Cell Layer —Web-axon (?)
Soriano & Frotscher, 1993a; Rat, Golgi, GABA & Glu-ICCh	Inner Margin of the Cell Layer (Subgranular Zone) —Ascending-axon oval GABA-IR cell	Cell Layer —Spheroidal (?)
Soriano & Frotscher, 1993b; Rat, Golgi & GABA-ICCh	Stratum Lucidum of CA-3 —Spiny nonpyramidal glutamate-like-IR neurons in the CA-3 region	DMC & DC OPL & IPL —LSPN of DMC & DC
Al Hussein & Al-Ali, 1995; Human, Golgi	Molecular Layer —Type M1: Aspinous horizontal fusiform neuron —Type M2: Small ovoid-round neuron with short aspinous dendrites —Type M3: Aspinous multipolar neuron —Type M4: Aspinous triangular neuron Granule Cell Layer —Type nG1: Sparsely-spinous vertical fusiform neuron —Type nG2: Aspinous inverted pyramidal neuron Hilus (Type H1: hilar; types H2-H10; subgranular) —Type H1: Large multipolar neuron with complex dendritic spines —Type H2: Spinous elongated neuron —Type H3: Medium-sized, multipolar neuron —Type H4: Descending-axon, horizontal fusiform aspinous neuron —Type H5: Small aspinous, vertical fusiform neuron —Type H6: Aspinous, triangular vertical neuron —Type H7: Aspinous fusiform-ovoid neuron —Type H8: Ascending-axon, sparsely-spinous fusiform-ovoid neuron —Type H9: Large aspinous multipolar neuron —Type H10: Small horizontal fusiform neuron	Outer Plexiform Layer —Stellate —(?) —Sarmentous/Coral —Stellate/Deep-stellate Cell Layer —Smooth vertical —Deep-fusiform Inner Plexiform Layer —Long-spined polymorphic (?) —Long-spined polymorphic —(?) —Smooth horizontal/Giant-multip —Smooth vertical —Smooth vertical —Giant-multipolar —Giant-multipolar (?) —Giant-multipolar —Spheroidal

[1]DMC, dorsomedial cortex; DC, dorsal cortex; GABA, gamma-amino butyric acid; GAD, glutamic acid decarboxilase; Glu, glutamate; -ICCh, immunocytochemistry; IPL, inner plexiform layer; -IR, immunoreactive; LSPN, Long-spined polymorphic neuron; multip, multipolar; OPL, outer plexiform layer; PV, parvalbumin.

form layer and the ependyma. No specific neuronal type lying in the alveus of lizards has been reported in the literature; here we provide a first description of these alveus-horizontal scarce neurons. The existence of immature cells with dendrites running between the fibers of the alveus and a growing axon taking an initially ascending trajectory (Fig. 19E) suggests that they might be postnatally generated, a possibility that has been shown for some GABA- and parvalbumin-immunoreactive interneurons in the lizard cerebral cortex (Martínez-Guijarro et al., 1994b).

In the mammalian hippocampus, the alveus is situated between the ependyma and the stratum oriens. The fascia dentata lacks an alveus because of its folded structure capping the terminal blade of the hippocampal regio inferior. Nevertheless, alveus triangular, or horizontal fusiform neurons with ascending peripheral axons were described in old classical Golgi studies (Ramón y Cajal, 1904b, 1911; Lorente de Nó, 1934). These neurons are similar to the lizard alveus-horizontal neurons.

Participation of the interneurons in the medial cortex circuitry

The lamination of afferents to the medial cortex, the fate of its projections, and the ubication, axonal trajectories, and immunocytochemical nature of the different interneuronal types, allow speculation about the role of these interneurons in the local circuitry. Their presumable role is schematized in Figure 21.

Most nonprincipal neurons in the medial cortex are GABA-immunoreactive. GABA has been shown to be an inhibitory neurotransmitter in reptiles (Kriegstein and Connors, 1986; Blanton et al., 1987; Kriegstein et al., 1988). Thus, these interneurons are probably GABAergic and inhibitory neurons. Taking into account their putative synaptic relationships, deduced from the position of their dendritic trees, these interneurons are thought to participate in feed back, feed forward, or in both control mechanisms. Thus, the outer plexiform layer sarmentous and stellate neurons displaying parvalbumin or enkephalin

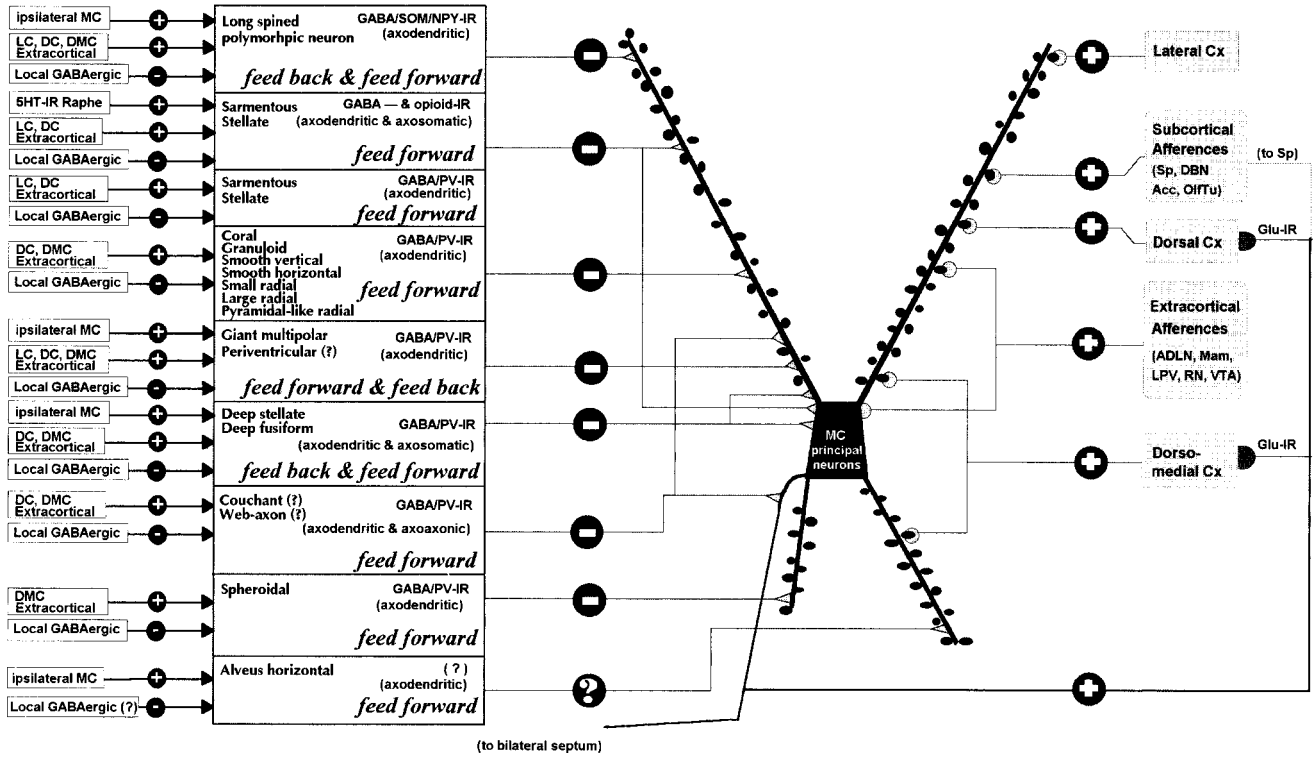

Fig. 21. Schematic drawing summarizing the putative role of each interneuron type in the circuitry of medial cortex. Axonal inputs to the medial cortex terminate in a laminated fashion as indicated on the right of the drawing: afferents from the lateral cortex (olfactory) end in the external sublayer of the outer plexiform layer, those from dorsal cortex end in the intermediate sublamina, and those from the dorsomedial cortex end in the inner sublamina of the outer plexiform layer, and in the juxtasomatic zone of the inner plexiform layer. Subcortical afferents from septal nuclei terminate diffusely distributed in the outer plexiform layer. Extracortical afferents from thalamic, hypothalamic, and mesencephalic nuclei are mainly concentrated in the middle sublayer of the outer plexiform layer. Projections from medial cortex principal neurons end ipsilaterally in the deep zone of the inner plexiform layer of the medial cortex, in the juxtasomatic outer and inner plexiform layers of the dorsomedial and dorsal cortices, and bilaterally in the septum (here indicated by a dotted line; see Lopez-Garcia et al., 1992, for references). The main control on the principal cells is exerted by the local short-axon interneurons, which also innervate them in a laminated fashion, as shown on the left of the drawing. This inhibition is exerted at distal and proximal dendritic shafts, as well as at perisomatic and initial axonal segment level. Abbreviations: 5HT-IR, serotonin-immunoreactive inputs; Acc, nucleus accumbens; ADLN, thalamic anterior dorsolateral nucleus; Cx, cortex; DBN, diagonal band nuclei; DMC, dorsomedial cortex; DC, dorsal cortex; GABA— & opioid-IR, γ-aminobutyric acid-negative, opioid-immunoreactive interneurons; GABA/PV-IR, γ-aminobutyric acid-, parvalbumin-immunoreactive interneurons; GABA/SOM/NPY-IR, γ-aminobutyric acid-, somatostatin- and/or neuropeptide Y-immunoreactive interneurons; Glu-IR, glutamate-immunoreactive medial cortex principal neurons; LC, lateral cortex.; LPV, lateral preoptic area; Mam, mammilary nuclei; MC, medial cortex; OlfTu, olfactory tubercle nucleus; RN, raphe nuclei; Sp, septum; VTA, ventral tegmental area. A white 'plus' symbol inside a black circle indicates exciting inputs; a white 'minus' symbol inside a black circle indicates inhibitory inputs. A white question mark inside a black circle indicates the unknown type of control exerted by alveus-horizontal neurons, because their presumable immunocytochemical nature could not be assessed in this study.

immunoreactivity may be involved in feed forward control (either excitatory-inhibitory or inhibitory-disinhibitory) of medial cortex principal neurons. This control may be driven by the afferents coming from the lateral cortex, which terminate in the external third of the outer plexiform layer (Luis de la Iglesia et al., 1994). Moreover, raphe nuclei exert a powerful control on the medial cortex principal neurons via the opioid interneurons, which are strongly innervated by serotonergic axonal endings from raphe nuclei (Martínez-Guijarro et al., 1994a). Similarly, parvalbumin-immunoreactive coral (Luis de la Iglesia et al., 1994) and granuloid neurons should play a feed forward control on principal neurons, driven by extracortical (thalamic, hypothalamic, mesencephalic), and cortical (dorsal, dorsomedial) afferents. The axons of these cells innervate principal neurons on apical dendritic shafts.

The outer plexiform layer deep-stellate neuron (Luis de la Iglesia et al., 1994) and the cell layer deep-fusiform neuron (Fig. 4) are thought to establish perisomatic symmetrical synaptic contacts on the principal cells. They are probably parvalbumin immunoreactive and have dendrites spreading in the two inner thirds of the outer plexiform layer, but they also have deep dendrites reaching the primary projection field of the medial cortex. There, they probably receive zinc-enriched synaptic contacts from principal neuron axonal boutons, which represent as many as 97% of all axonal boutons present in that region (Martínez-Guijarro et al., 1987). Consequently, they may exert a complex feed forward (driven by extracortical, corticodorsal, and corticodorsomedial afferents), and feed back control on the principal neurons of the medial cortex.

Although further confirmation is needed, the couchant neuron (Luis de la Iglesia et al., 1994), and the web-axon neuron (Fig. 3E) are the best candidates for the axo-axonic interneurons in the medial cortex of *Podarcis*. They are probably parvalbumin immunoreactive (Luis de la Iglesia et al., 1994; Martínez-Guijarro et al., 1993), and their dendritic trees spread under the zone of influence of extracortical, corticodorsal, and corticodorsomedial afferents, thus being presumably involved in feed forward

control of principal neurons. The strong effect of the inhibition at initial axonal segment level should compensate for the paucity of cells belonging these two types.

Smooth vertical (Fig. 6) and horizontal (Fig. 7) neurons, together with small (Fig. 8), large (Figs. 9, 10A), and pyramidal-like (Fig. 10B,C) radial interneurons are likely to be parvalbumin immunoreactive (Martínez-Guijarro et al., 1993). Although the complete axonal trajectories of these neurons have not been observed in every case, they followed an initially ascending course in most cases. This suggests that they have ascending axons that arborize in the outer plexiform layer and that they innervate principal neurons on dendritic shafts, where parvalbumin-immunoreactive axonal endings are seen to contact (Martínez-Guijarro et al., 1993). Hence, these neuronal types should participate in feed forward control of medial cortex principal neurons. This control should be driven by afferents reaching the inner two-thirds of the outer plexiform layer and the juxtasomatic zone of the inner plexiform layer, i.e., again the axons coming from extracortical nuclei and from dorsal and dorsomedial cortices. However, the spheroidal neuron (Fig. 11), whose dendritic and axonal arborizations are mostly restricted to the juxtasomatic inner plexiform layer, is likely to be exerting a feed forward control on principal neurons, mainly driven by afferents coming from the dorsomedial cortex.

The presumably parvalbumin-immunoreactive giant-multipolar neurons have lengthy dendrites spreading throughout the width of medial cortex and adjacent areas (Figs. 13–15). Their axons arborize in both plexiform layers of medial cortex and may also reach dorsomedial and dorsal areas (Bernabeu et al., 1994). Consequently, they may be involved both in feed forward and feed back control of principal neurons in the medial cortex and adjacent areas.

The GABA- and neuropeptide-immunoreactive long-spined polymorphic neurons are, probably, the most abundant cells in the deep zone of the inner plexiform layer. In that zone they receive multiple synaptic contacts from the principal cell zinc-enriched axonal endings on their long spines (Lopez-Garcia et al., 1988a). Their peripheral axons establish symmetrical synaptic contacts on distal dendritic shafts of medial cortex principal neurons. Thus, this group of neurons may exert a feed back inhibition on principal neurons in the medial cortex but a feed forward control (driven by medial cortex projection neurons) in the dorsomedial and dorsal cortices. On the other hand, long-spined polymorphic neurons are innervated by GABA-immunoreactive axonal endings (Lopez-Garcia et al., 1988a). In addition, somatostatin- and/or neuropeptide Y-immunoreactive neurons in the cerebral cortex of lizards, have been found to be extensively innervated by GABAergic axons originating in the septum (Martínez-Guijarro and Freund, 1992a), but they are only poorly innervated by serotoninergic axons from the raphe nuclei (Martínez-Guijarro et al., 1994a). Finally, at least some long-spined polymorphic neurons display long dendrites reaching the outer plexiform layer and even areas adjacent to the medial cortex. Taken together, all of these findings strongly suggest that these cells exert an increased feed forward control of the principal projection neurons of the medial cortex, driven by complex afferents of diverse origin, probably including the lateral, dorsal, and dorsomedial cortices, thalamic and hypothalamic structures, septum, and, to a lesser degree, the mesencephalic nuclei.

Periventricular neurons are similar to the parvalbumin-containing pyramidal-like neurons, which are abundant in the deep inner plexiform layer of the dorsomedial cortex (Martínez-Guijarro and Freund, 1992b; Martínez-Guijarro et al., 1993). Although their axonal trajectories are not well known in the medial cortex, they probably follow identical trajectories as in the dorsomedial cortex, where they have been characterized, and if so, they form extensive axonal arborizations in the two plexiform layers. As they populate the primary projection field of the medial cortex, they probably establish feed back loops with medial cortex principal neurons. And, as with long-spined polymorphic neurons, they are thought to be involved in more complex feed forward control mechanisms of principal neurons, both in the medial cortex and in adjacent areas.

Finally, the role of alveus-horizontal neurons is not clear, but they seem to be involved in feed back control of principal cells, because some dendrites run in the deep inner plexiform layer of the medial cortex. In the dorsomedial and dorsal cortices, these cells may exert a feed forward control of principal cells driven by the medial cortex projection.

In sum, there is a certain lamination in the interneuronal innervation of the principal projection neurons of the medial cortex. The situation described above closely resembles what happens in the interneuron innervation of dentate granule cells. A significant part of the dentate hilar interneurons sends dendrites reaching the molecular layer, where they are excited by the perforant path axonal endings. Moreover, the excitation threshold of most hilar interneurons is lower than that of granule cells, and stimuli under that threshold invoke extensive inhibition of granule cells via hilar interneurons (Scharfman, 1991). In addition, there is a marked subdivision and lamination of dendritic and axonic arborizations of local GABAergic interneurons in the area dentata of mammals (Halasy and Somogyi, 1993), which have been electrophysiologically characterized (Han et al., 1993). Briefly, dentate basket cells inhibit granule cells at perisomatic, or apical primary dendritic shaft levels (Ribak and Seress, 1983; Seress and Ribak, 1983); axo-axonic or chandelier cells make inhibitory symmetric synaptic contacts on initial axonal segments (Soriano and Frotscher, 1989; Soriano et al., 1990), and a third group of inhibitory interneurons innervates the intermediate segments of apical granule dendrites (Soriano and Frotscher, 1993a). Most of those neurons are parvalbumin immunoreactive. On the other hand, the hilar somatostatin- and/or neuropeptide Y-immunoreactive interneurons make symmetrical synaptic contacts on the distal dendritic shafts of apical granule cell dendrites, and, to a lesser extent, at perisomatic level (Deller and Leranth, 1990; Leranth et al., 1990). Because many of these hilar cells have dendrites reaching the dentate molecular layer, they will participate in both feed back and complex feed forward control mechanisms.

However, a major difference in the local circuitry of these two centers is the existence of a strong GABAergic component in the commissural projection of the mammalian fascia dentata that has its origin in the dentate hilus (Seroogy et al., 1983; Seress and Ribak, 1984; Swanson et al., 1987; Deller and Leranth, 1990). In lizards, a commissural pathway coming from unidentified neurons in the medial cortex has been reported (Martínez-García et al., 1990). In the medial cortex, some interneuronal types displaying initially descending axons (Figs. 3A, 8F, 10C) or descending collaterals have been observed. This was the case with a long-spined polymorphic neuron displaying a collateral that could be followed to the anterior commissure (not shown). This finding suggests that some deep

hilar commissural interneurons might exist in the lizard fascia dentata.

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