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Neural organization of the retina of the turtle *Mauremys caspica*: a light microscope and Golgi study

HELGA KOLB[1], IDO PERLMAN[2] AND RICHARD A. NORMANN[3]

[1]Physiology Department, University of Utah School of Medicine
[2]Department of Physiology, Technion-Israel Institute of Technology, Haifa, Israel
[3]Bioengineering Department, University of Utah, Salt Lake City

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Abstract

The organization of the retina of the turtle species *Mauremys caspica*, found in fresh water ponds of Israel, has been examined by light microscopical techniques including examination of fresh wholemount retina, one micron blue-stained vertical sections and Golgi-stained material. The anatomical findings on *Mauremys* retina have been compared with those of the *Pseudemys* retina (Kolb, 1982) which is more commonly used for electrophysiological and neurochemical studies in the USA. The photoreceptors of *Mauremys* are similar in type and oil droplet content to *Pseudemys* photoreceptors except for the double cone in *Mauremys*. This cone type appears more abundant than in *Pseudemys* and the principal member contains a yellow oil droplet instead of an orange oil droplet. Golgi staining reveals that all the cell types that have been seen in *Pseudemys* are found in *Mauremys* with identical morphology. In addition, two amacrine cell types that were not before described for *Pseudemys* have been added to the classification. One of these is the tristratified dopaminergic amacrine cell described in immunocytochemical studies (Witkovsky et al., 1984; Nguyen-Legros et al., 1985; Kolb et al., 1987). We have used these anatomical studies on *Pseudemys* and *Mauremys* retina to form a catalogue of neural types for the turtle retina in general. We conclude with an attempt to combine findings from anatomy, electrophysiology, and neurochemistry to form an overview of the organization of this reptilian retina.

Keywords: Turtle retina, photoreceptors, Golgi technique, amarcine cells

Introduction

Mauremys caspica (formerly called *Clemmys caspica*) is a species of turtle occupying fresh water ponds of the Mediterranean coast of Israel. The retina of this turtle has been used in electrophysiological investigations of retinal neural pathways (Itzhaki & Perlman, 1984, 1987) and intracellular recordings from photoreceptors and horizontal cells indicate no significant differences from those obtained in *Pseudemys scripta*, which is most commonly used in retinal research in the United States. For these electrophysiological studies it has been assumed that the *Mauremys* retina is identical to the *Pseudemys* retina in photoreceptor and neural types; a detailed anatomical study, however, has not been done in order to verify this supposition. The purpose of this study, then, is to examine the *Mauremys* retina by anatomical methods that reveal the cell types and make a comparison with the findings from *Pseudemys* retina (Kolb & Jones, 1982, 1984; Kolb, 1982) so that we can be confident that there are no significant species differences of concern for the physiological findings. We hope that the combined morphological investigations of the two species, *Mauremys* and *Pseudemys*, will increase our knowledge of the neural organization of this particular vertebrate retina, where physiological, pharmacological, and behavioral investigations are rapidly progressing.

Golgi staining has revealed that the photoreceptor types, bipolar, horizontal, amacrine, and ganglion cell types in *Mauremys caspica* are identical to those seen in *Pseudemys scripta*. In particular, we note that the horizontal cell types of *Mauremys* have exactly the same morphology as those described for *Pseudemys* (Leeper,

Reprint requests to: Helga Kolb, Department of Physiology, 410 Chipeta Way, Research Park, Salt Lake City, UT 84108, USA.

1978*a*, *b*). This finding suggests that the physiological responses of the various luminosity and chromaticity types are likely to be identical in both species: a fact already confirmed (Itzhaki & Perlman, 1984, 1987). Examination of fresh wholemount retina reveals that the photoreceptors and oil droplets contained within them are similar to those of the *Pseudemys* with the exception that the principal member of the double cone contains a small yellow oil droplet instead of an orange one.

A number of Golgi-stained cell types that were not seen in the original study on the *Pseudemys* retina (Kolb, 1982) have been added in this morphological study. In particular, the dopaminergic amacrine cell described in immunocytochemical studies of *Pseudemys* retina (Witkovsky et al., 1984, 1987; Nguyen-Legros et al., 1985; Kolb et al., 1987) has been stained by the Golgi procedure in this study. We present a catalogue of the nerve cell types for the turtle retina based on the findings of Golgi staining, immunostaining techniques (Eldred & Karten, 1983, 1985; Eldred & Carraway, 1987; Eldred et al., 1985, 1987; Eldred & Williamson, 1987; Weiler & Ball, 1984; Weiler & Schutte, 1985; Weiler, 1985), and intracellular staining techniques after recording response patterns to light (Marchiafava, 1983; Marchiafava & Weiler, 1980, 1982; Weiler & Marchiafava, 1981; Weiler & Ammermuller, 1986; Jensen & DeVoe, 1982, 1983). We discuss the correspondence of the electrophysiological response types and the immunostained cell types with the morphological cell types described in this study.

Methods

Adult turtles, *Mauremys caspica*, with carapace size of 8 in. were used for the study. Animals were decapitated and the eyes removed under normal room lighting. The retinas were processed in one of the following three ways:

1. *Light microscopy of fresh, unfixed, wholemounts*

The posterior pole of the hemisected eye was placed in normal saline for a few minutes, to aid the removal of the retina from the pigment epithelium. It was then cut in half though the optic nerve on the vertical meridian and the retina teased off the pigment epithelium with a small spatula. The retina was then mounted photoreceptor side up on a glass slide and viewed by light microscopy.

2. *Light microscopy of 0.5 μm sections*

The hemisected eyecup was placed in ice-cold 1% Dalton's chrome-osmium fixative (Dalton, 1955) for 2 h. The retina and pigment epithelium were dissected from the choroid and sclera and the pieces of retina washed in cold chrome-saline mixture. Dehydration, *en bloc* staining in uranyl acetate in 70% alcohol overnight, and embedding in Araldite followed the usual procedures. Semithin sections (0.5 μm) were cut on an ultramicrotome and the sections stained with Richardson's stain.

3. *Golgi preparations*

The Golgi technique used has been described previously (Kolb, 1982). Briefly, several retinas, cut in half along the vertical meridian were mounted between filter papers in a sandwich between glass coverslips. The sandwich was placed in glass jars in the dark in the Colonnier (Colonnier, 1964) primary mixture of glutaraldehyde and potassium dichromate for 4 d, and then in the secondary silver nitrate solution for 2 d. Dehydration, clearing with cedarwood oil, and mounting in Permount on a glass slide, ganglion cell side up, followed routine methodology. Cells were drawn with a camera lucida or photographed. Shrinkage is estimated to be approximately 10%.

Results

Overall appearance of the Mauremys retina

The isolated, flattened *Mauremys* retina measures 9 mm in diameter in the specimens we used for the anatomical studies. The optic nerve is visible as a 0.5-mm diameter white spot in the center of the eyecup and the retina appears a black color with an orange sheen as a result of reflecting oil droplets in the photoreceptors. In *Mauremys* retina the linear visual streak situated 1 mm dorsal to the optic nerve and running across the whole retina on the horizontal meridian, is not easily distinguishable compared with *Pseudemys* where a clear black line in the eyecup is seen. Once the retina is removed from the eyecup, however, and mounted flat on a glass slide the visual streak is evident as a red line and under the light microscope it is seen to consist of very small closely packed photoreceptors and oil droplets.

Photoreceptors and oil droplets as seen in fresh wholemount retina

A view of freshly excised retina with the photoreceptor side up is shown in the light micrograph of Fig 1. As in other species of turtle, the different cone types can be recognized by the characteristic colored oil droplet contained within their inner segments. Although microspectrophotometry has not been performed on *Mauremys caspica* to relate the visual pigment of the different cone types with the morphology of the cones and the color of their oil droplets, it is probably reasonable to assume that the photoreceptors in this species are similar to those of the other species where the spectral types have been studied, i.e. *Pseudemys scripta*, *Chrysemys picta*, *Chelydra serpentina*, *Geoclemys reevesii* (Fujimoto et al., 1957;

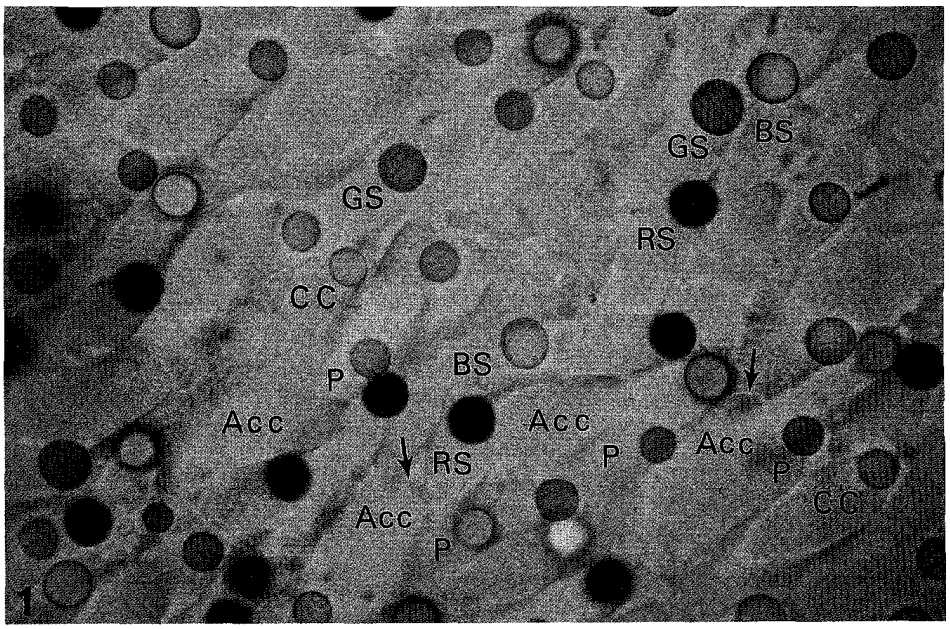


Fig. 1. Wholemount view of fresh (unfixed) photoreceptors of the *Mauremys* retina. The different spectral types of cone can be recognized by their associated colored oil droplet. Red single cones (RS) contain a large red oil droplet and green single cones (GS) contain a large orange oil droplet. Two types of cones contain colorless oil droplets and the largest belongs in the blue single cone (BS) while the smaller (CC) is contained in a possible ultraviolet sensitive cone type. Double cones consist of a principal member (P) with a small yellow oil droplet and an accessory member (Acc) lacking an oil droplet but containing a yellow pigmentation instead (arrow). (×900).

Liebman & Granda, 1971; Liebman, 1972; Ohtsuka, 1978, 1985*a*, *b*; Lipetz & MacNichol, 1982*a*, *b*, 1983; Lipetz, 1985). In fact, action spectra of red and green cones and of L- and C-type horizontal cells in *Mauremys* retina are similar to those in *Pseudemys* retina (Perlman, unpublished).

Thus, the large red oil droplet is contained within the red single cone (RS), the large deep yellow/orange oil droplet is in the green single cone (GS), the large colorless oil droplet is in the blue single cone (BS), and the small colorless oil droplet is in a red or possibly ultraviolet absorbing cone type (CC) (Lipetz, 1985; Kolb & Jones, 1987). The double cones consist of a principal member (P) containing the small yellow oil droplet and arranged alongside it is the accessory member (Acc) containing no oil droplet but an aggregation of yellow globules (arrows, Acc, Fig. 1): both members of the double cone are probably red cones (Lipetz & MacNichol, 1983; Ohtsuka, 1985*a*, *b*). No rods are visible in this particular micrograph (Fig. 1) but they are seen occasionally and have the same appearance, as in *Pseudemys* retina (Lasansky, 1971; Leeper, 1978*b*; Kolb & Jones, 1982). We have made counts of the different spectral types of cone in the *Mauremys* retina and find the following approximate proportions of cones in peripheral retina: red single cones, 32%; green single cones, 20%; double cones, 29%; blue single cones, 13%; and clear colorless oil droplet cones, 6%. The oil droplet combination with spectral photoreceptor type and the proportions of these photoreceptors in the turtle retinas studied to date is shown in Table 1.

Table 1. *Percentage of cones and their oil droplet colour in turtle retinae*

Species	Percent cones				
	RS	GS	DC	BS	CC
Mauremys caspica	32 R od	20 O od	29 Y od	13 F od	6 C od
Pseudemys scripta	40 R od	20 Y od	20 O od	14 F od	6 C od
Geoclemys reevesii	28 R od	19 O od	30 Y od	14* F od	8# C od

Pseudemys scripta from Kolb & Jones, 1987.
Geoclemys reevesii data from Ohtsuka, 1985 (* is a red cone and # is a blue cone according to Ohtsuka).
RS: red single; GS: green single; DC: double cone; BS: blue single; and CC: clear colorless single.
R: red; O: orange; Y yellow; F: fluorescent; C: clear; and od: oil droplet.

Light microscopy of radial sections of the Mauremys retina

Figure 2 shows a 1 μm radial section through mid-peripheral retina of the turtle *Mauremys caspica* to show the major cell layers and plexiform layers of this retina. The appearance of *Mauremys* retina in section is very similar to *Pseudemys*. The photoreceptors (Ph), consisting primarily of cones, occupy one-quarter of the thickness of the retina. The single and double cones can be recognized and the other types can be classified into spectral types by the size and density of staining of the oil droplets contained in their inner segment. Where no oil droplet is present the cone is an accessory member of the double cone. A portion of a rod, also lacking an oil droplet, with a characteristic wide outer segment is seen (R). The outer plexiform layer (OPL) is delimited by the cone pedicles and the outer nuclear layer (ONL) on the one side and by the horizontal and bipolar cell bodies of the inner nuclear layer (INL) on the other. The peripheral retina of turtle has particularly prominent Muller fibers running throughout the retina. The INL is characterized by large expanses of Muller fiber and occasional clusters of "white streaks" (arrows, Fig. 2) which are bundles of bipolar cell axons. A layer of amacrine cell bodies delimits the lower INL border.

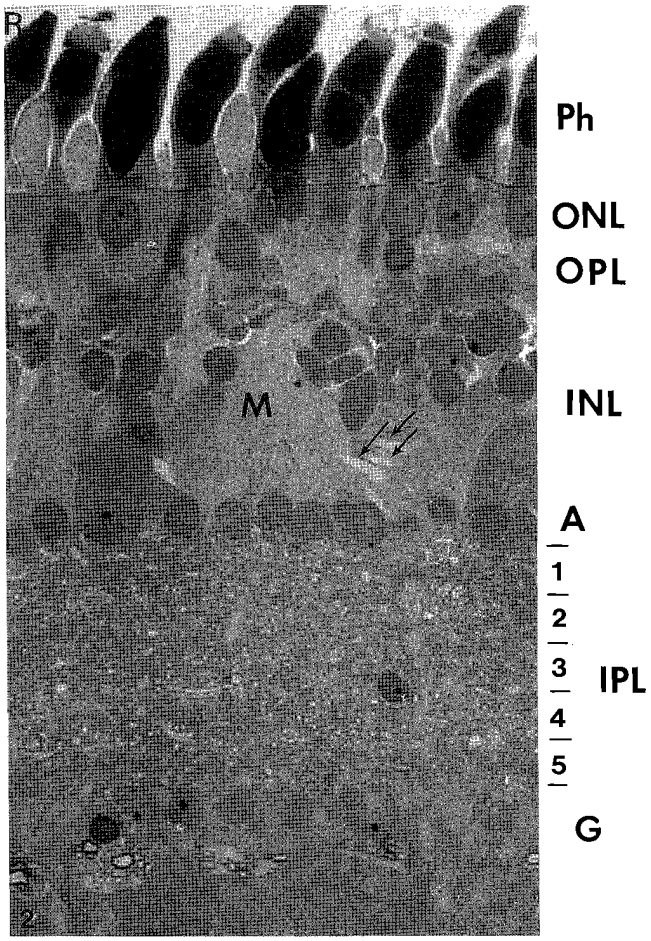


Fig. 2. One micron thick vertical section of peripheral *Mauremys* retina. Photoreceptors are mainly cones with an occasional rod (R) visible in the material, and photoreceptor pedicles are clearly seen in the outer plexiform layer (OPL). The three nuclear layers, outer nuclear layer (ONL), inner nuclear layer (INL), and ganglion cell layer (G) are separated by the two plexiform layers, outer plexiform layer (OPL) and inner plexiform layer (IPL). Amacrine cell bodies (A) line the INL/IPL boundary and white streaks in the INL are bipolar cell axons (arrows). The IPL can be divided into 5 equally thick strata or sublayers. The nuclear layers contain a large content of fibrous looking Muller cell processes. (×700).

The inner plexiform layer (IPL) is very thick in turtle retina, varying from 45 μm thick in peripheral retina to 90 μm thick in visual streak. The IPL in this mid-peripheral region is approximately 65 μm thick and consists of processes of bipolar, amacrine, and ganglion cells separated by Muller cell processes. In this Golgi study, we classify all these cells primarily according to their dendritic or axonal stratification in the IPL. We, therefore, divide the IPL into the 5 strata or sublayers of equal thickness as first described by Cajal (1933). The ganglion cell layer contains a single layer of similar-sized cell bodies of ganglion cells in addition to several varieties of displaced amacrine cell bodies, amongst Muller cell end feet and bundles of ganglion cell axons, many of which are myelinated (Fig. 2).

Golgi staining of the neurons of the Mauremys caspica retina

Golgi-staining procedures have revealed an enormous variety of stained neurons in the *Mauremys caspica* retina. Almost all of the neural types stained in the *Pseudemys* retina (Kolb, 1982) have been stained in *Mauremys* retina and in addition some types that were not originally seen in *Pseudemys* have been revealed. The following description is not intended to be an exhaustive one for every cell type. Rather, we have picked out cells of particular interest from a physiological or immunocytochemical perspective. The cells have been given the same nomenclature as in the *Pseudemys* study and are considered to be the same cell types as described there. The two descriptions, taken together, give us a more complete analysis of the neurons of the turtle retina in general.

a. Bipolar cells

Nine different morphological types of bipolar cell are seen in *Mauremys* retina. They differ primarily by the number and stratification of their axon terminals in the IPL. All nine types appear to exhibit Landolt clubs and similar-sized dendritic tree. The dendritic tree area and the numbers of clusters of terminals are very small for the bipolar cells of the visual streak (typically there are

5 or 6 clusters of terminals) but in more peripheral retina, there is an increase in size and numbers of clusters. The cells of Fig. 3 were located 2–3 mm from the visual streak and bear from 8–12 clusters of terminals. Each cluster of terminals probably contacts a cone or a rod pedicle. The exact spectral types of cone pedicle contacted by the terminals is only known for B4 and B6 cells in turtle retina (Kolb et al., 1986*a*).

Wholemount views of Golgi-stained bipolar cells (Fig. 3) indicate their typical obliquely running axons, but the stratification levels of their axon terminals are difficult to represent. However, by focusing up and down through the IPL, measuring the distance between the amacrine cells and the ganglion cells, and dividing this distance into 5 equal steps, the stained profiles (axon terminals in this case) can be assigned a level of branching in the IPL. Thus, B1 and B2 cells, which are both monostratified (have a single axonal ending) stratify in S5 and S4 through S5, respectively. B1 has a dendritic field with a more radiate display of dendrites than B2 which has, in contrast, a very bushy dendritic tree design. The axon of B1 is again wider and more strictly confined to one plane in S5 than that of B2. The latter cell has a clumped and vertically directed axon terminal passing down through two strata, S4 and S5 of the IPL.

Bipolar cells B4 and B6 are the commonly recorded center-hyperpolarizing and center-depolarizing bipolar cells respectively of the turtle retina. B4 is distinguished from B6 by its bistratified axon terminal having branches in S1 and on the S2/3 border, compared with B6 axons which branch in S3 and S5 (Fig. 3).

A very curiously shaped cell type that can best be described as a centrifugal bipolar after Cajal's (1933) description, has been seen on several occasions in the *Mauremys* retina. This cell type (Fig. 3, cen. b) has a very expansive dendritic branching pattern (more than 100 μm in diameter) in the OPL compared with the more restricted arbors of regular bipolars. The loosely ramifying OPL processes do not contain clear clusters of terminals either. There are terminal-like projections that could be contacting photoreceptors but they could also be interpreted as ending on profiles in the neuropil of the OPL. The cell body sits in the middle of the inner nuclear layer, in a bipolar-like fashion, and the descending process to the IPL is another loosely organized branching process that passes down through most of the strata of the IPL and is typically much smaller in field diameter than the processes in the OPL (Fig. 3). These "centrifugal bipolar cells" have also been seen in Golgi stained *Pseudemys* retina but were not included in the original paper on that species (Kolb, 1982).

b. Horizontal cells

Four types of horizontal cell are seen in the *Mauremys* retina as in *Pseudemys* retina. The different types are distinguished on the morphological features described by Lepeer (1978*a*, *b*), Ohtsuka (1983), and Ohtsuka & Kouyama (1986). It is probable that the spe-

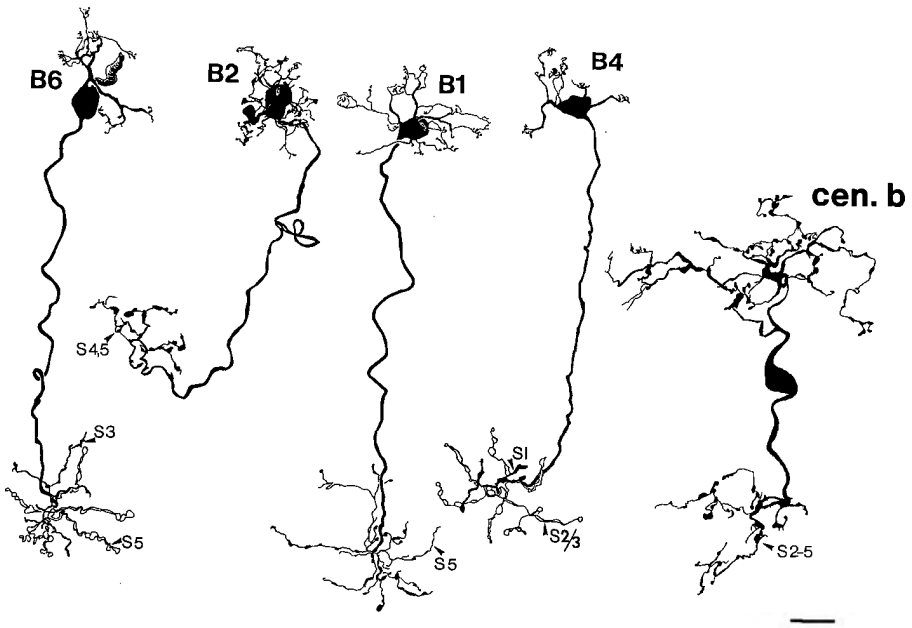


Fig. 3. Camera lucida drawings of Golgi-stained bipoplar cells as seen in wholemount views. Bipolar cells are distinguished primarily on the branching pattern of their axon terminals. The strata of the IPL in which the axons branch are indicated. A putative centrifugal bipolar cell (cen. b) has a widely ramifying dendritic tree in the OPL and a more narrow, vertically directed, diffuse axon terminal in the IPL. Scale bar = 15 μm.

cific connectivity between horizontal cells and the different spectral types of cones in *Mauremys* will be the same as in *Pseudemys* (Leeper, 1978*a*, *b*). Thus, type H1 cells (H1 CB, Fig. 4) are small-field cells with bushy overlapping dendrites bearing many clusters of terminals. These cells are termed L2 units based on electrophysiological studies (Leeper, 1978*a*, *b*; Ohtsuka & Kouyama, 1986). They are the only variety bearing an axon ending in the bulbous and sinuous axon terminal (H1AT, Fig. 4) known as the luminosity L1 unit electrophysiologically. H2 cells are large-field stellate cells lacking an axon. Their dendrites are thick and heavy-appearing and bear numerous clusters of terminals. H3 cells are distinguished from H2 cells by their finer caliber curved dendrites bearing fewer but widely spaced terminal clusters, but they have a similar-sized dendritic field and are also axonless. Type H4 is a more rarely staining horizontal cell type with a smaller overall size and more spindly appearance (Fig. 4, H4) than any other type. It could almost be mistaken for a large bipolar cell type but, of course, lacks the descending axonal process and the Landolt club. Whereas the specific spectral connectivity of H1, H2, and H3 cell types have been elucidated (Leeper, 1978*a*, *b*; Ohtsuka & Kouyama, 1986), little is known concerning the spectral connections of the H4 cell type.

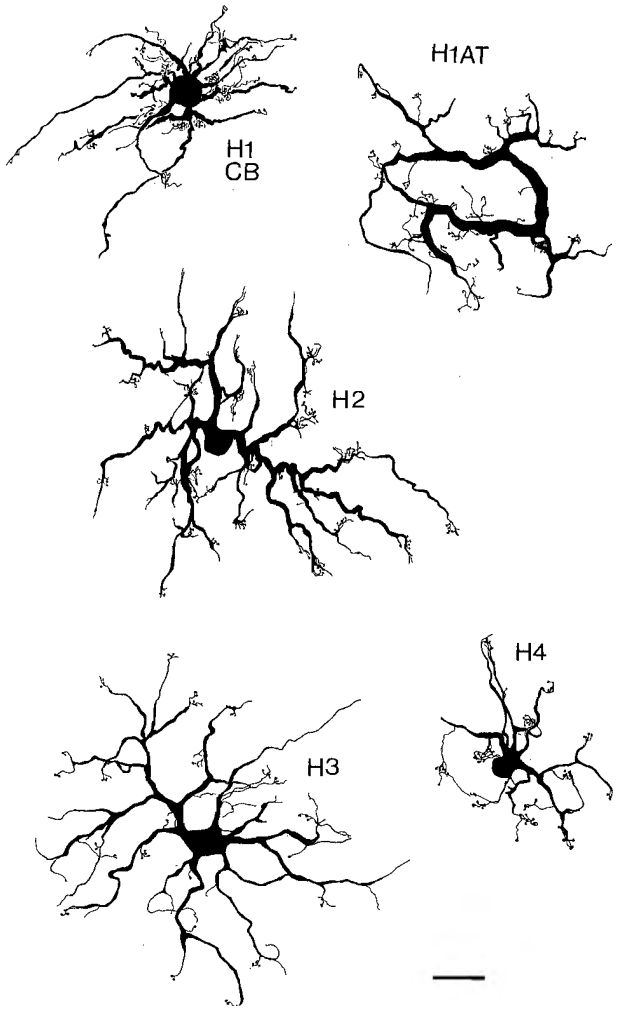


Fig. 4. Camera lucida drawings of Golgi-stained horizontal cells of the *Mauremys* retina. H1, H2, H3, and H4 types can be distinguished. H1 cell body (CB) is the bushiest type and exhibits an axon and axon terminal (H1AT) which looks like another morphological type of cell when stained in isolation. Scale bar = 15 μm.

c. Amacrine cells

There are probably more than 30 different types of amacrine cell in the turtle retina. All 27 types of amacrine cell described for *Pseudemys* retina (Kolb, 1982) have been seen in *Mauremys* retina and two more types, A28 and A29, have been added here. The different amacrine cell types are distinguished on the basis of dendritic field size, dendritic morphology, branching patterns, and levels of arborization in the different strata of the IPL. Almost certainly different amacrine and ganglion cell types will have dendritic tree sizes that increase with eccentricity from the visual streak. Furthermore, in turtle retina all cell types tend to have an elongated dendritic tree oriented parallel to the visual streak particularly when they lie close to, in, or along the edge of the streak. Thus, classifying amacrine and ganglion cells on dendritic field size alone is problematical. In the previous study (Kolb, 1982), these cells were grouped into types that had very narrow fields (30–150 μm diameter), small fields (150–300 μm diameter), medium fields (300–700 μm diameter), and wide fields (over 700 μm diameter) and we will adhere to this same scheme in this paper.

Narrow-field amacrine cells. Five different morphological types of amacrine cells (A1–A5) fall into the narrow-field category, two of which (A4 and A5) are illustrated for *Mauremys* in Figs. 5, 6, 14A, and 14B. These amacrine cell types have profusely branched dendrites forming compact bushy dendritic trees that usually occupy several strata of the IPL. In essence, these amacrines are more vertically directed in their dendritic tree expanse rather than covering large lateral expanses of neuropil. The bistratified nature of A4 is seen in the micrographs (Figs. 14A and 14B) where it is rather clearly seen that the tier of dendrites in S3 has a wider and more profusely branched spread than the tier of rather simpler varicose dendrites in stratum 4 deeper in the IPL from the cell body. The A5 cell type is illustrated at higher magnification and its three tiers of branching are separated out in the drawing of Fig. 6. The dendrites that branch deeper in the IPL, i.e. on the S2/3 and S4/5 borders, are again slightly wider field and more varicose

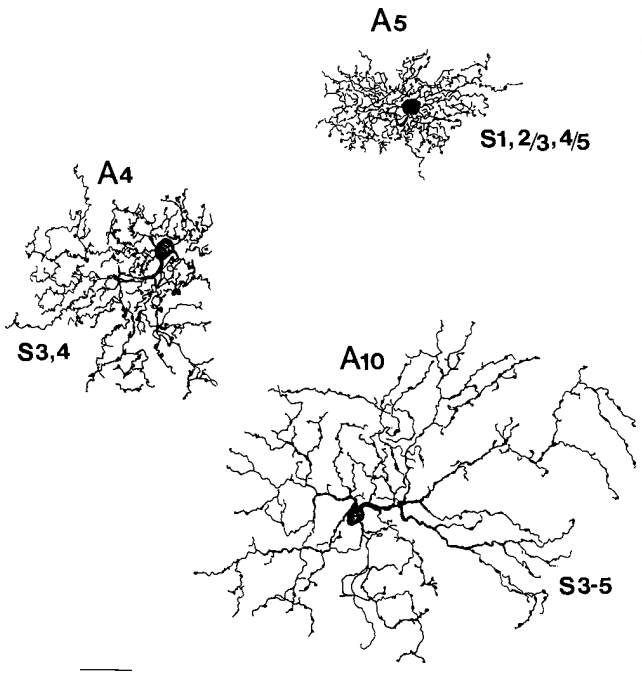


Fig. 5. Three examples of narrow- and small-field amacrine cells in the *Mauremys* retina as seen in wholemount. A4 is bistratified, A5 is tristratified, and A10 is broadly stratified through three strata. A5 is shown at higher magnification and separated by its dendritic tiers in Fig. 6. Another example of an A4 is illustrated in the micrographs of Fig. 14A and 14B. Scale bar = 25 μm.

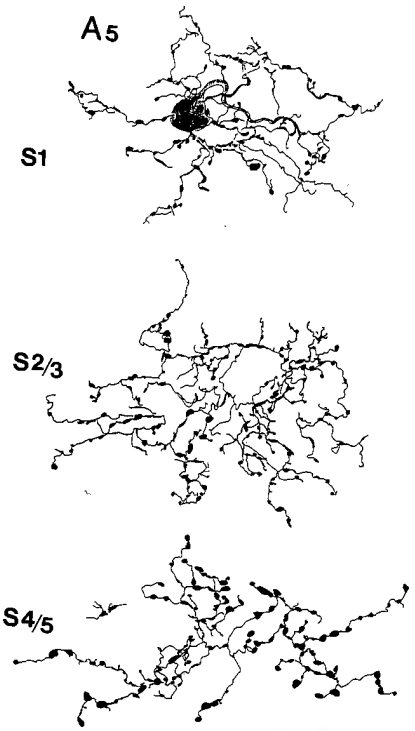


Fig. 6. Type A5 amacrine cell drawn from wholemount at the three different levels in the IPL where the dendrites branch to show the different morphology of each dendritic tier. The dendrites in S1 close to the cell body are finer than the dendrites in the deeper strata where they become pronouncedly beaded. Scale bar = 10 μm.

than the slender, wispy dendrites of the top tier in S1 (Fig. 6).

Small-field amacrine cells. The seven small-field amacrine cell types that were seen in *Pseudemys* have also been seen in *Mauremys*. In addition, another small-field amacrine cell, called A29, seen for the first time in this study, can be added to this group of amacrine cells. Cells A9, A10, and A12 that were seen in *Pseudemys* retina are illustrated in Figs. 5, 7, 16A, 16B, and 18. Amacrine A9 (Fig. 7) is a small-field, loosely branched cell with thick major dendrites and several curvilinear secondary and tertiary branches bearing occasional spines. It is monostratified on the S3/4 border and is a far peripheral cell with a dendritic field diameter of 280 μm. A10 (Figs. 5 and 18) has a more compact dendritic tree of thicker varicose dendrites exhibiting many more appendages than A9. The dendrites also occupy more depth of the neuropil of the IPL by passing through three strata S3–S5. A12 (Fig. 16A,B) is a tristratified cell with loose branches ramifying in S1, S3, and S5. Only the branching in S1 and S3 is shown in the two micrographs. A curious feature of the A12 cell type is that in all the examples we have seen, both in *Pseudemys* and *Mauremys* retina, their dendritic trees are asymmetrical relative to the cell body. In some examples seen in the original *Pseudemys* study, but not illustrated here, each layer of dendrites of A12 cells had a different orientation or directionality.

A29 (Figs. 7, 20) is a cell type seen for the first time in the *Mauremys* retina, although most certainly it is also present in the *Pseudemys* retina. This amacrine has a "star-burst"-like branching pattern, i.e. the primary dendrites emerge in a radial pattern and branch repeatedly into cascades of secondary and tertiary branches with all the dendrites being adorned with small delicate appendages. Even the cell body is covered with these delicate appendages (Fig. 7, 20). The dendrites run in lower S1 of the IPL.

Medium-field amacrine cells. The three amacrine cells belonging to this group (A13–A15) that were seen in *Pseudemys* have also been seen in *Mauremys* retina. An A13 type amacrine cell is illustrated in the micrograph of Fig. 15. The cell has a 200 × 300 μm dendritic field size and the dendritic branching pattern is profuse with wavy, overlapping dendrites bearing characteristic spines

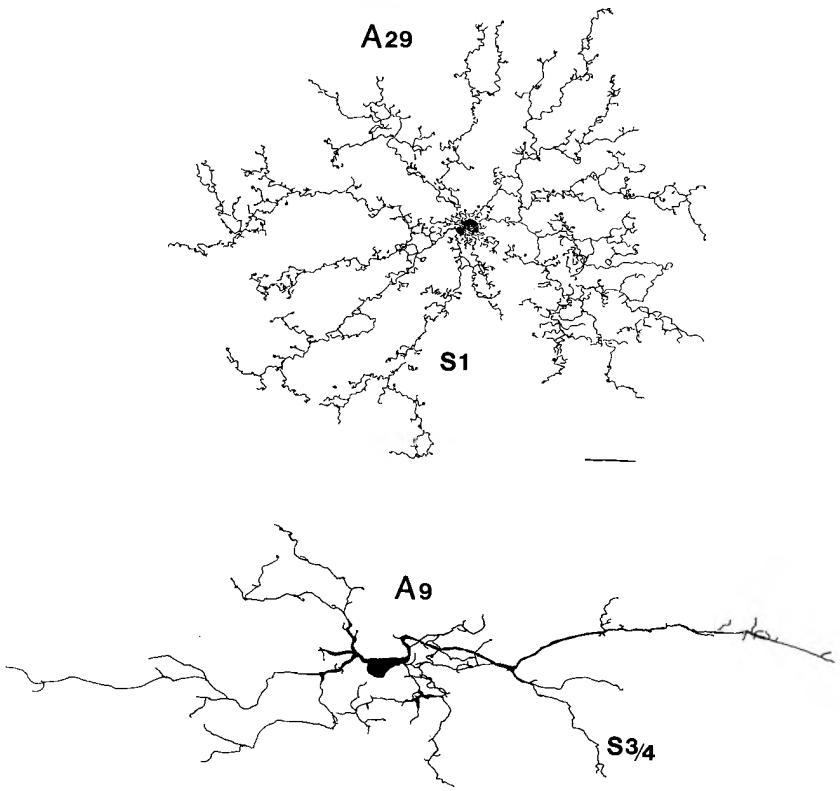


Fig. 7. A medium- and a small-field amacrine cell of the *Mauremys* retina. A9 is monostratified on the S3/4 border with a simple dendritic tree shape, while A29 is a delicate "star-burst" shaped cell covered with fine terminals and appendages stratifying in S1. An A29 is also illustrated on Fig. 20. Scale bar = 25 μm.

and clusters of appendages. The whole dendritic tree remains rather broadly stratified in stratum S2. A new medium-field amacrine cell, A28, not originally seen in the Golgi study of *Pseudemys*, has now been stained in *Mauremys* retina (Fig. 8). This cell also occurs in *Pseudemys* retina; a tristratified medium-field amacrine cell of similar morphology has been stained with the antibody to tyrosine hydroxylase in immunocytochemical studies in this species (Witkovsky et al., 1984; Nguyen-Legros et al., 1985; Kolb et al., 1987).

The A28 cell exhibits a large cell body (diameter 10 × 12 μm) which emits 2 to 4 thick major dendrites. These subdivide and branch profusely in a fine cobweb-like dendritic tree at three levels of the IPL, S1, lower S2, and on the S4/5 border. The cell illustrated in Fig. 8 was found close to the visual streak and is the smallest sized of these cell types, with a dendritic field diameter of 250 μm. In peripheral retina, according to the immunocytochemical study in *Pseudemys* retina, the A28 cells typically reach dendritic field diameters of 700 μm (Kolb et al., 1987).

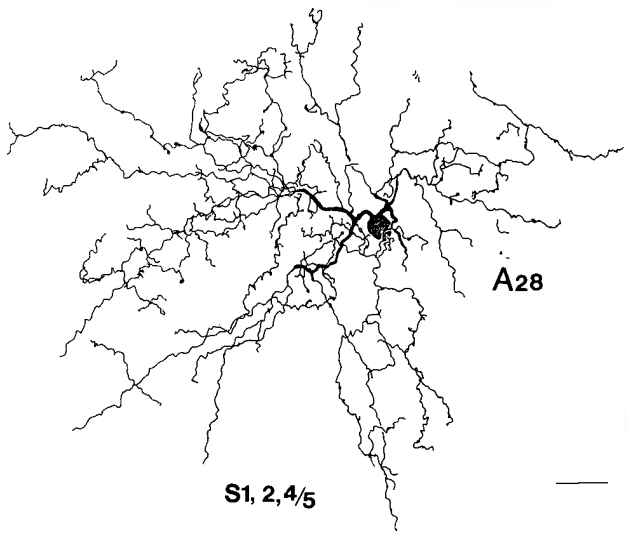


Fig. 8. A28 is a tristratified medium-field amacrine. A28 is the dopaminergic amacrine cell. Scale bar = 25 μm.

Large-field amacrine cells. There are many varieties of large-field amacrine cells in the turtle retina. In fact these cell types are probably the commonest amacrine cell of this reptilian retina. Thus, amacrines A16–A27 are different morphological varieties of large-field amacrine cell common to *Mauremys* retina as well as the *Pseudemys*. These amacrine cell types have simple branching patterns and are all very narrowly stratified to one stratum or to

the border between two strata. Some have dendritic fields that exceed 1 mm in diameter; often the dendrites are extremely fine for some hundreds of microns and then thicken at their termination, e.g. A22.

A17, A18, A19, and A23 illustrated in Figs. 9, 10, 17, 12, and 21 are large-field amacrines that ramify in S1 of the IPL. Clearly, cells A17, A18, and A23 have entirely different morphologies, but cells A17 and A19 look somewhat similar. A17, on the one hand, has a small cell body and seemingly fine smooth dendrites and a very simple, relatively unbranched dendritic tree (Fig. 9). A19 (Fig. 17), on the other hand, appears to have a larger cell body and coarser, thicker dendrites than A17, which exhibit occasional spines and large appendages on long stalks.

A18 has a small cell body but extremely long, wavy, curvilinear dendrites that cover a dendritic field diameter of 1.7 mm in the example drawn (Figs. 10, 13 and 21). This dendritic tree is almost certainly understained and each of the dendrites probably run as great a distance as the longest one shown on Fig. 13 (arrow). A22 (Figs. 11, 13) is a cell that has been studied physiologically and whose neurotransmitter is known (see Discussion). This cell has a very characteristic morphology and branches strictly on the S2/3 border of the IPL. The cell body is large (12 μm diameter), the thick primary den-

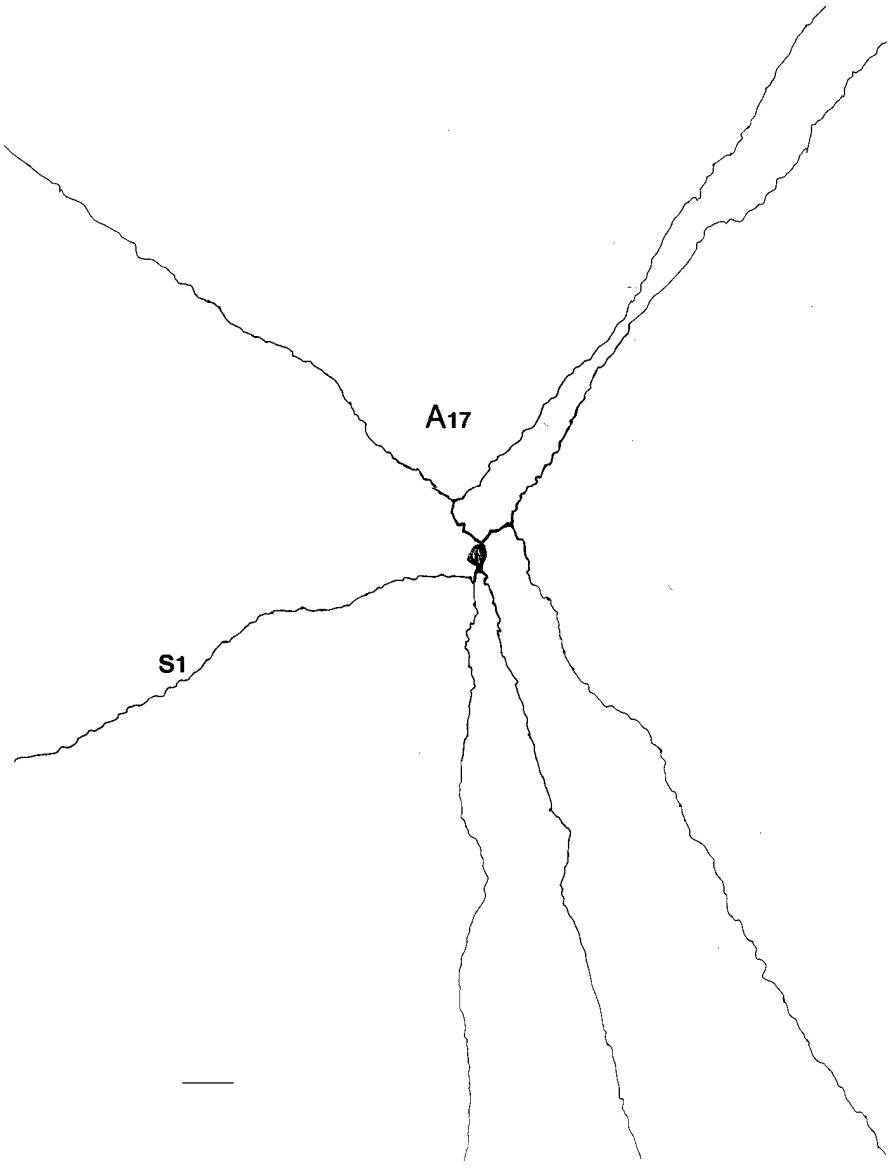


Fig. 9. Camera lucida drawing of an A17 wide-field amacrine cell. The cell has a simple radiate monostratified dendritic field stretching 1.6 mm which is not shown in full on the figure (see Fig. 13). Scale bar = 25 μm.

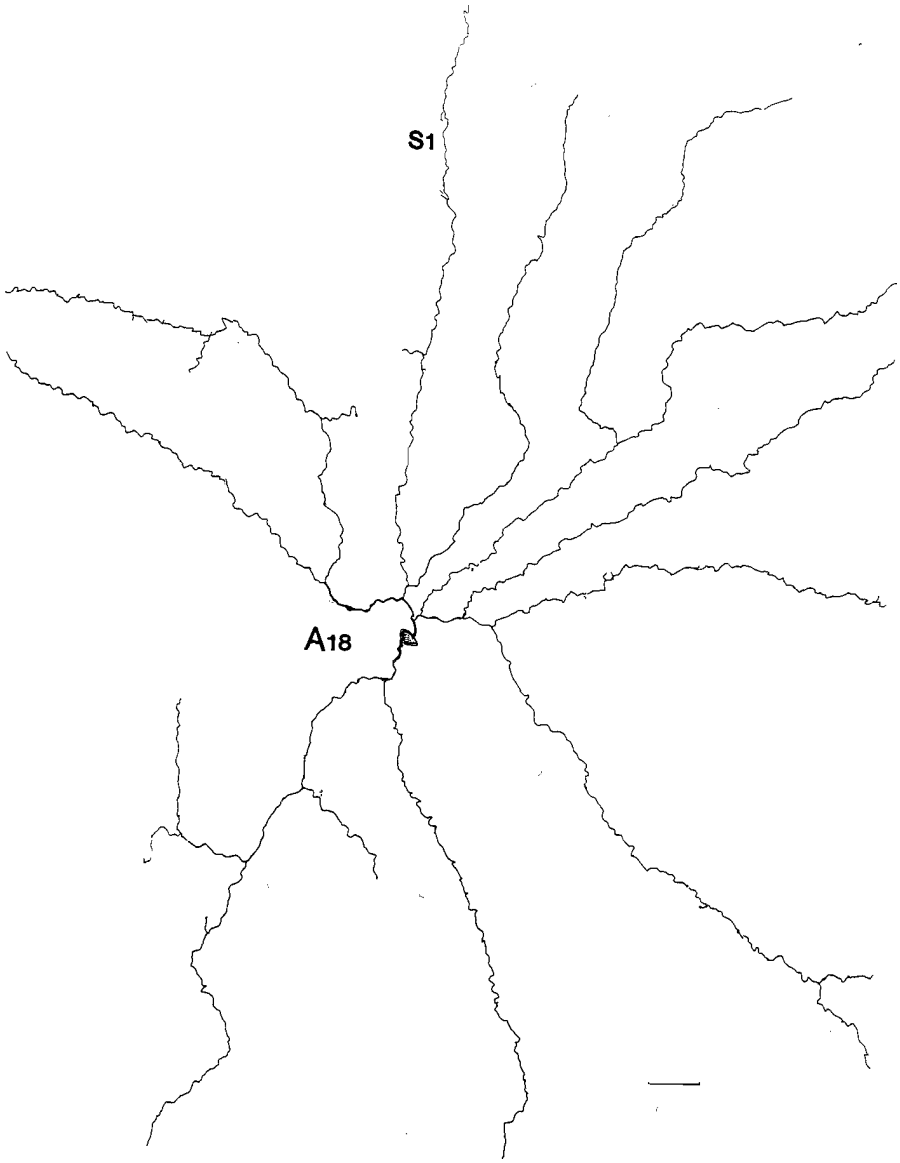


Fig. 10. A wide-field monostratified amacrine A18 has a different morphology compared to A17 and is therefore a different cell type. The dendrites are wavy and curved and bear occasional appendages. The full dendritic field may cover 5 mm as judged by the extent of one dendrite (as illustrated on Fig. 13). An A18 is also illustrated on Fig. 21. Scale bar = 25 μm.

drites fall immediately to lower S2 and radiate out for 150 μm as very thick branches (2–3 μm diameter), and then become extremely fine (less than 0.5 μm, arrowheads, Fig. 11) and run for 800 μm before becoming enlarged and varicose at their ending.

A23 (Figs. 12, 19) is one of the amacrine cell types with branching patterns like the "radiating spokes of a wheel." There appears to be one of these types of amacrine cells branching in every stratum of the IPL (see Kolb, 1982). A23 branching in S1 has the largest number of dendrites emanating from the cell body, dividing once or twice and then running unbranched straight out from the center of the dendritic field to cover a 800–1000 μm diameter field (Fig. 12, Fig. 19). A25 (Fig. 15), on the other hand, gives rise to fewer primary dendrites and dendritic spokes than A23 (compare Figs. 15 and 19). It restricts its dendrites to S3 of the IPL. In *Pseudemys* retina we saw A25 type amacrine cells with dendritic fields of 2.7 mm diameter, but the example in *Mauremys* was not that completely stained.

Large-field amacrine cells of strata 4 and 5 are also present in *Mauremys* retina, resembling those described for *Pseudemys* (Kolb, 1982). Figure 13 is a composite drawing at very low magnification to allow the reader to

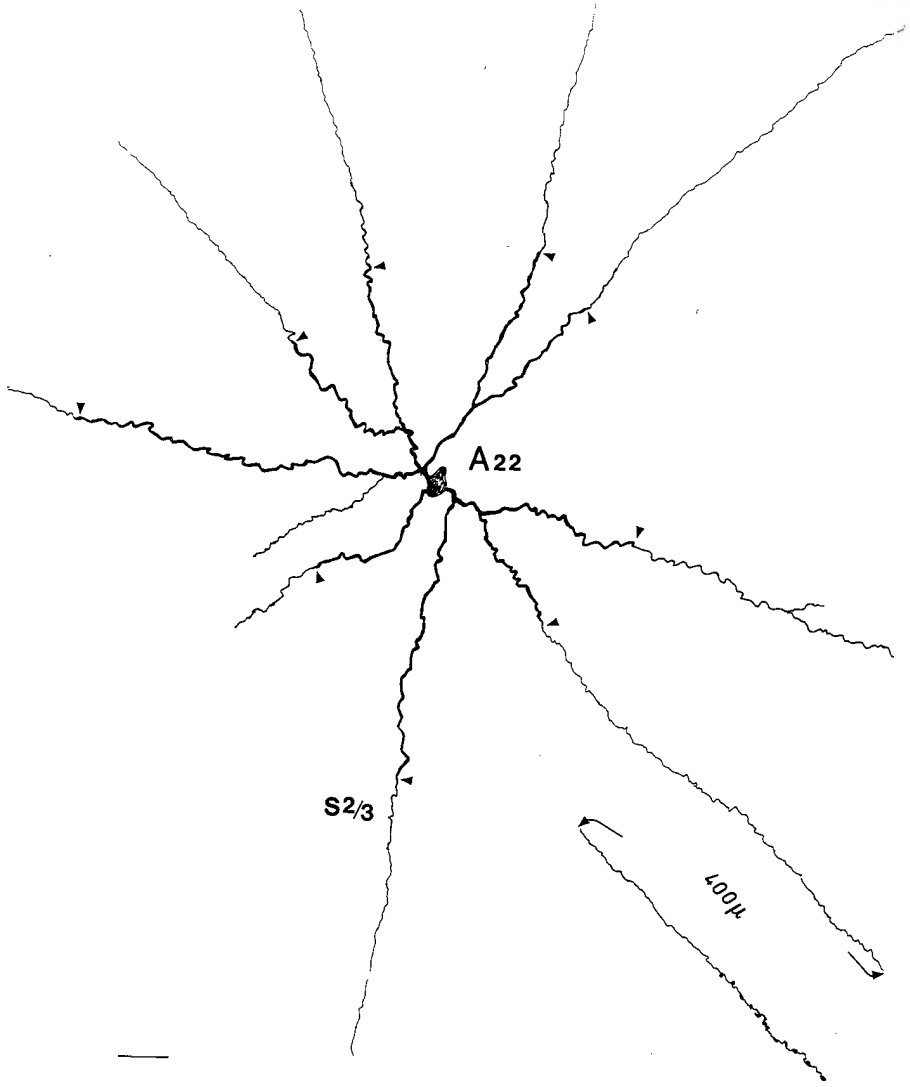


Fig. 11. Wholemount view of an A22 cell. The characteristics of this wide-field cell are described in the text. The arrow heads indicate where the major dendrites thin to the fine long running extensions of the dendritic field. The end of the fine dendrites swell into varicosities. Arrows 400 μm indicate distance from one arrow to the other where the dendrite runs unbranched. The cell is also illustrated on Fig. 13. Scale bar = 25 μm.

appreciate the full extent of some of these large-field amacrine cells. Clearly any fine details concerning dendritic thickness, caliber, and presence or absence of appendages cannot be depicted on such an illustration. Hence, the larger magnifications drawings are also shown (Figs. 9, 10 and 11).

d. Ganglion cells

There is no reason to suspect that the ganglion cells of *Mauremys caspica* retina are any different from those in the *Pseudemys scripta* retina, judging by our Golgi-stained material. Not all the types that were seen in *Pseudemys* were observed in the present study but those varieties that were stained seemed identical in morphology to those already described (Kolb, 1982). Thus, there are at least 21 identified different morphological varieties of ganglion cell in the turtle retina.

Figure 22 illustrates the extreme types of morphology ganglion cells exhibit. G2 is one of the very smallest with a small cell body (10-μm diameter) and a narrow diffuse dendritic tree of tiny, fine dendrites and appendages, while G20 is one of the largest types of ganglion cell. The latter cell has a cell body as large as is seen for any turtle ganglion cell at 26 μm diameter. The narrowly stratified dendritic tree of large-diameter curved, coarse dendrites covered with fine hair-like spines covers an area 500–800 μm in diameter. The majority of ganglion cell types seen in Golgi preparations of turtle retina appears to be small to medium-field sized with profusely branched dendrites and are commonly bi-stratified or tristratified. Large

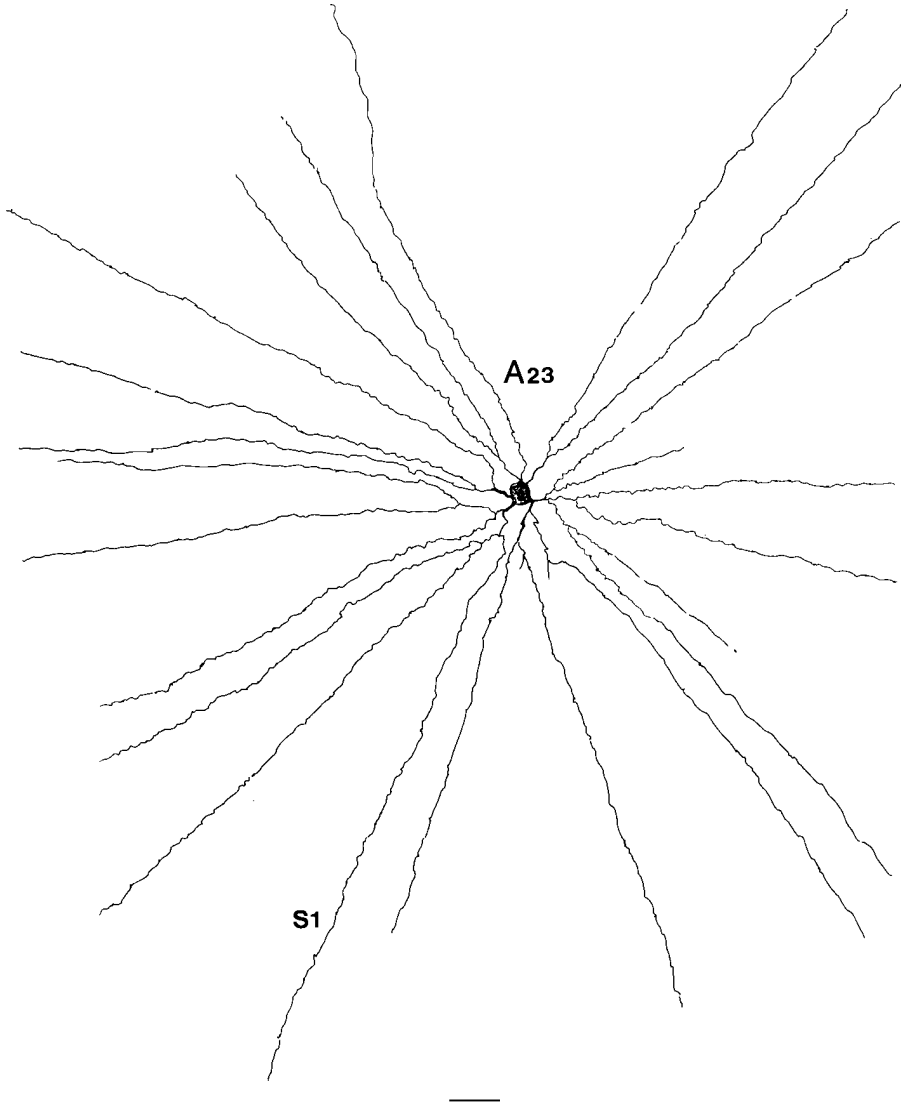


Fig. 12. Drawing of the A23 cell in wholemount retina. The cell has a "spokes of a wheel" like branching pattern of strictly monostratified dendrites that range much further than the drawing depicts (approximately 800–1000 μm). Another A23 is shown in the micrograph of Fig. 19. Scale bar = 25 μm.

cells such as G20 constitute fewer morphological varieties in our experience.

G3, G6, and G8 (Figs. 23, 25A, 25B) are small in dendritic field size but each has a unique branching pattern of delicate fine processes. Thus, G3 is very sparsely branched sending only a few curled fine dendrites up diffusely through the IPL (Fig. 23). G6, on the other hand, is clearly a bistratified cell with two distinct tiers of profusions of curving, overlapping fine dendrites on the S4/5 border and the S1/2 border (Fig. 23). G8 is a very commonly stained type of ganglion cell in turtle retina (Fig. 25). The cell has a narrowly stratified dendritic tree of fine, delicate profusely branched dendrites. Its dendritic tree occupies stratum 3 of the IPL.

Ganglion cells G7, G10, and G12 are all medium field in dendritic tree size, and again each is unique in branching pattern and stratification level. Thus, G7 (Fig. 24) is a bistratified cell with a tier of fine, cobweb-like dendrites on the S4/5 border and another tier in lower S2. If this cell were to have a tier of branches in S1, it would be an exact morphological ganglion cell counterpart of the A28 amacrine cell. This cell is clearly a ganglion cell, however, as can be seen from the long stretch of axon that was stained (Fig. 24). The two other ganglion cells, G10 (Fig. 26) and G12 (Fig. 24), look superficially rather alike but on careful inspection differ with respect to their dendritic stratification. Thus, G12 has a very elongated dendritic tree oriented parallel to the visual streak and lies within 1 mm of the long axis of the streak. The cell has thick primary dendrites that emerge in bipolar fash-

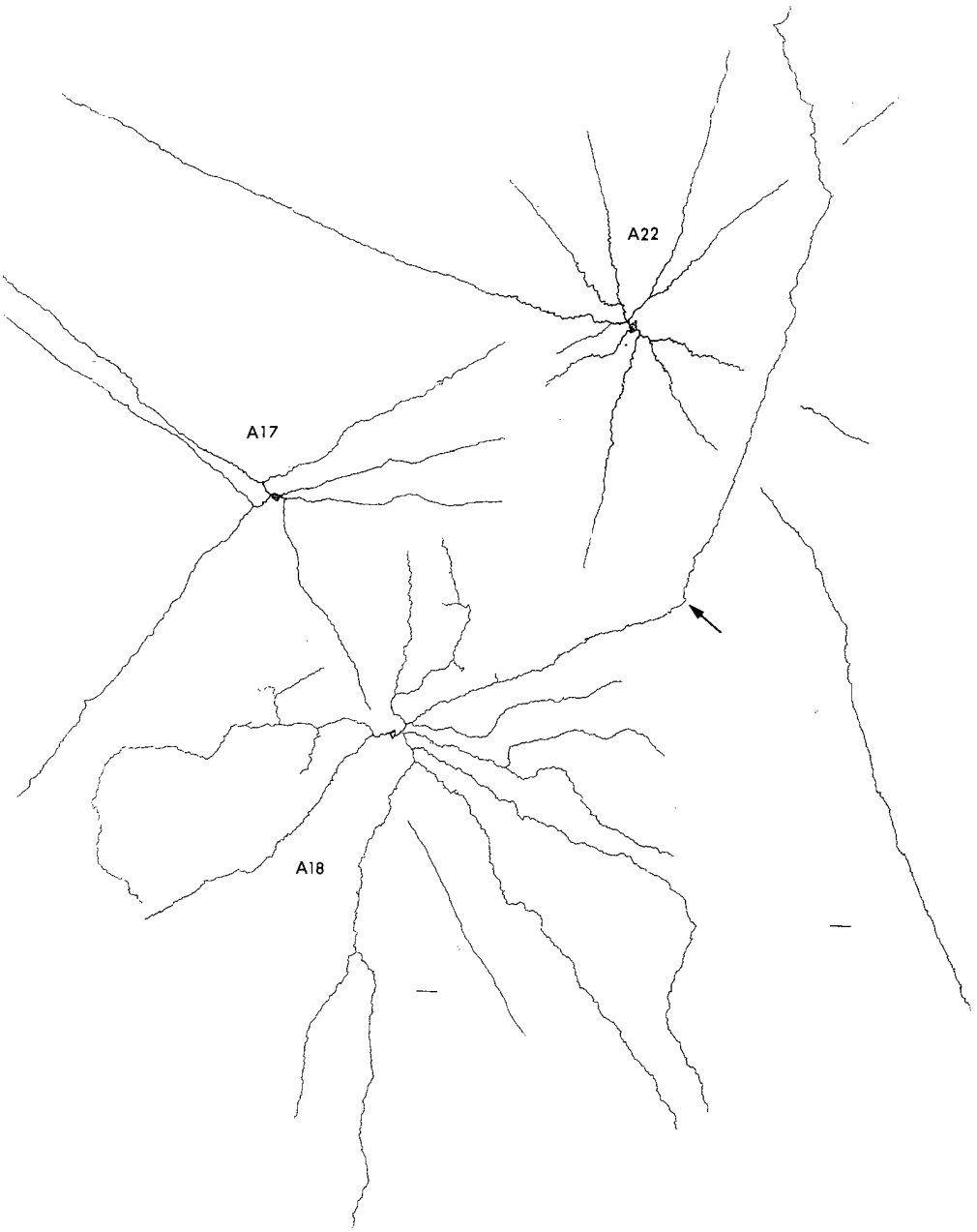


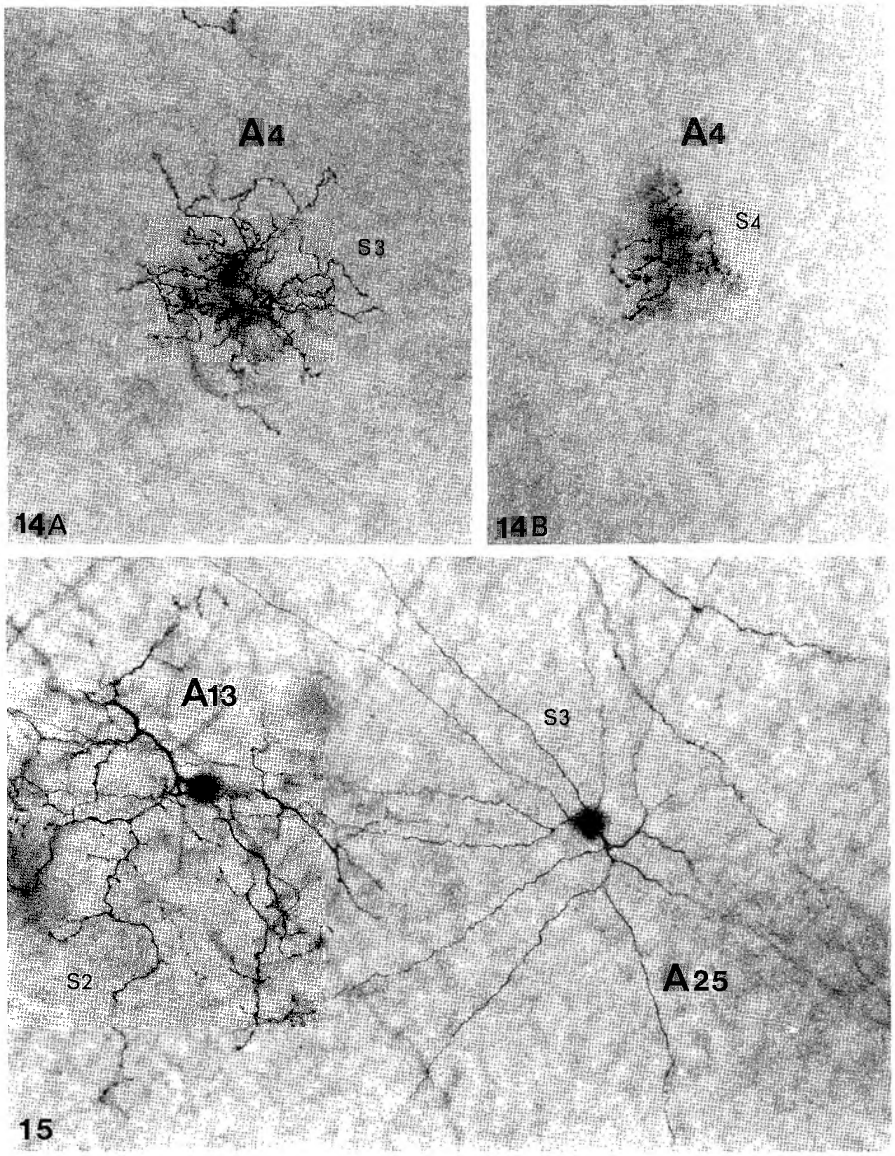
Fig. 13. Drawing of the three largest field amacrines of the turtle retina to show their entire dendritic field. A17 covers 1.6 mm, A22 covers 3.6 mm, and A18 might cover 5 mm if all the branches were completely stained. Scale bar = 50 μm.

ion from the cell body but then split into several secondary and tertiary branches covered with spines and appendages. The cell's dendrites ramify exclusively in S2 of the IPL. The G10 ganglion cell (Fig. 26A) is a more loosely branched cell with fewer fine dendrites some of which ramify in S5 and others rise to S3. The dendrites contain relatively few appendages compared with G12 although its overall dendritic tree shape is elongated and oriented parallel to the visual streak like the G12 cell. A fine axon is clearly emerging from one of the major dendrites and curving around to run in the direction of the optic nerve head (Fig. 26B).

Discussion

General conclusions

In this paper, we have examined the retina of the fresh water turtle *Mauremys caspica* by various light microscopic techniques in order to compare the morphologies



Figs. 14–15. 14A: Light micrograph of a narrow-field amacrine cell A4 at the level of one of the tiers of dendrites of its bistratified dendritic field. 14B: A4 cell in a plane of focus at the second tier of dendrites. 15: Two different morphological types of amacrine cell (A13 and A25) as seen in wholemount views. (×450).

of the different neurons with those in the retina of the better studied species *Pseudemys scripta*. We conclude that the organization of both retinas is very similar and that neurons of the exact same morphology can be found in both. Some new cell types, not seen in the original study on the *Pseudemys* retina (Kolb, 1982), have been revealed by the Golgi method in this study but these are not considered to be unique to *Mauremys* retina. We suggest that the morphological investigations of the two turtle species can be taken together as an extensive catalogue, which is almost certainly not yet complete, of the cell types found in general in turtle retinas.

Photoreceptors

The six different types of photoreceptors normally present in the *Pseudemys* retina are also seen in the *Mauremys* retina. Thus, rods are present as a minority photoreceptor (less than 10% of the photoreceptors) in addition to five different cone types: red single cones, green single cones, blue single cones, double cones, and a fifth class of single cone that might be an ultraviolet receptor (Kolb & Jones, 1987; Arnold & Neumeyer, 1987). *Pseudemys* and *Mauremys* retina differ in their proportions of double cones. There appear to be a larger fraction of dou-

ble cones in *Mauremys* than in *Pseudemys* retina (see Table 1). Furthermore, whereas in *Pseudemys* the principal member of the double cone contains a large orange oil droplet, in *Mauremys* it contains a small yellow droplet instead. In fact this configuration of oil droplets in *Mauremys* is the same as in *Geoclemys reevesii* (Ohtsuka, 1985*b*).

Bipolar cells

At least nine different types of bipolar cells are found in the turtle retina, all with different patterns of axonal stratification in the IPL. Undoubtedly, they also have specific connectivity with the different classes of cone in the OPL too, but this information is still lacking for all but B4 and B6 types, which are known to contact red cones primarily and some green cones (Kolb et al., 1986). A morphologically different "centrifugal bipolar" type has also been observed in turtle retina whose connectivity in the OPL and whose interactions in the IPL are still a matter of speculation. Since the turtle retina does not appear to have a dopaminergic interplexiform cell *per se* (Witkovsky et al., 1984; Nguyen-Legros et al., 1985; Kolb et al., 1987), it is tempting to think of the "centrifugal bipolar" cell as possibly subserving some kind of interplexiform cell-like role in this species retina. We will have to await further evidence concerning this cell type.

Horizontal cells

Morphologically, the horizontal cells in the *Mauremys* retina appear identical to those of the *Pseudemys* retina. Four different types can be discerned in Golgi preparations, H1, H2, H3, and H4 types. Only the H1 type has an axon and axon terminal system which are known to correspond to the L2 and L1 units of electrophysiological investigations, respectively. H2 and H3 correspond to chromaticity types electrophysiologically while the physiology of H4 is still unknown. There is no reason to doubt that the photoreceptor contacts of the *Mauremys* horizontal cells are the same as in the *Pseudemys* retina (Leeper, 1978*a*,*b*) and electrophysiology suggests that identical luminosity and chromaticity types of responses are obtained from these cells in *Mauremys* (Ihtzaki & Perlman, 1984, 1987).

Amacrine and ganglion cells

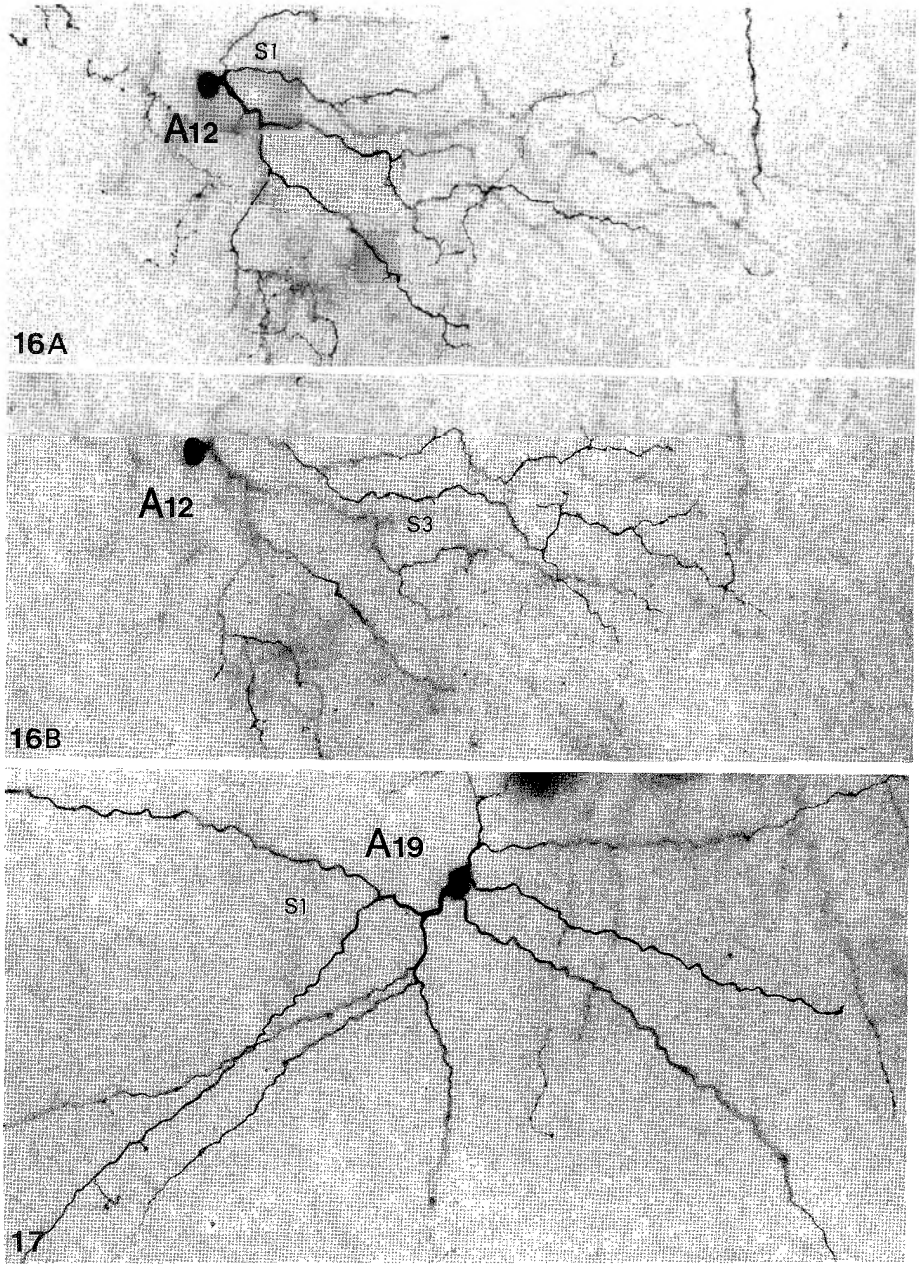
Twenty-nine different amacrine cell types and 21 different ganglion cell types have been observed to date in the turtle retina. Two new types of amacrine cells have been added to the classification stemming from the *Pseudemys* Golgi study (Kolb, 1982), and undoubtedly this indicates that further morphological types will be revealed in future Golgi-staining, immunostaining or intracellular staining of these retinas. This large variety of amacrine and ganglion cells is not unique to turtle retina. In cat, human, and rabbit just as many different morphological varieties exist (Kolb et al., 1981; Kolb et al., 1986; Linberg et al., 1986; Famiglietti, 1987). In fact, a recent Golgi study of the roach retina (Wagner & Wagner, 1987) describes 43 different amacrine cell types alone.

Amacrine cells in turtle retina appear most typically to be large field and monostratified. There are several varieties with dendritic fields in excess of a millimeter in diameter and the dendrites of these cells occupy a narrow stratum of the IPL. Less common varieties of amacrine are small or very narrow field and such cells are more frequently diffusely branched with tortuous interdigitating, appendage-laden dendrites occupying several strata of the IPL and directed in the vertical direction rather than the horizontal. A few varieties are bistratified or tristratified and these can be narrow, small, or medium field. Yet each are distinctly different morphologically and usually occupy a unique set of strata of the IPL. They are not simply smaller or larger versions of the same cell types.

Ganglion cells of the turtle retina, on the other hand, are more typically small to medium field in size. The large-field varieties are probably a minority of ganglion cells. The small-field types are typically bistratified or tristratified with intricate, but delicate dendritic branching patterns which often correspond in appearance to the smaller amacrine cell types. These smaller ganglion cells probably have a complex organization of inputs available to different tiers of their dendrites from multitiered amacrine cell dendrites and bipolar axons. It seems likely that the intricate morphology of these multibranched varieties of neurons in the turtle IPL underlies the complex receptive field physiology of turtle ganglion cells (see below).

Correlation of Golgi staining with immunostaining and intracellular recording and staining in the turtle retina

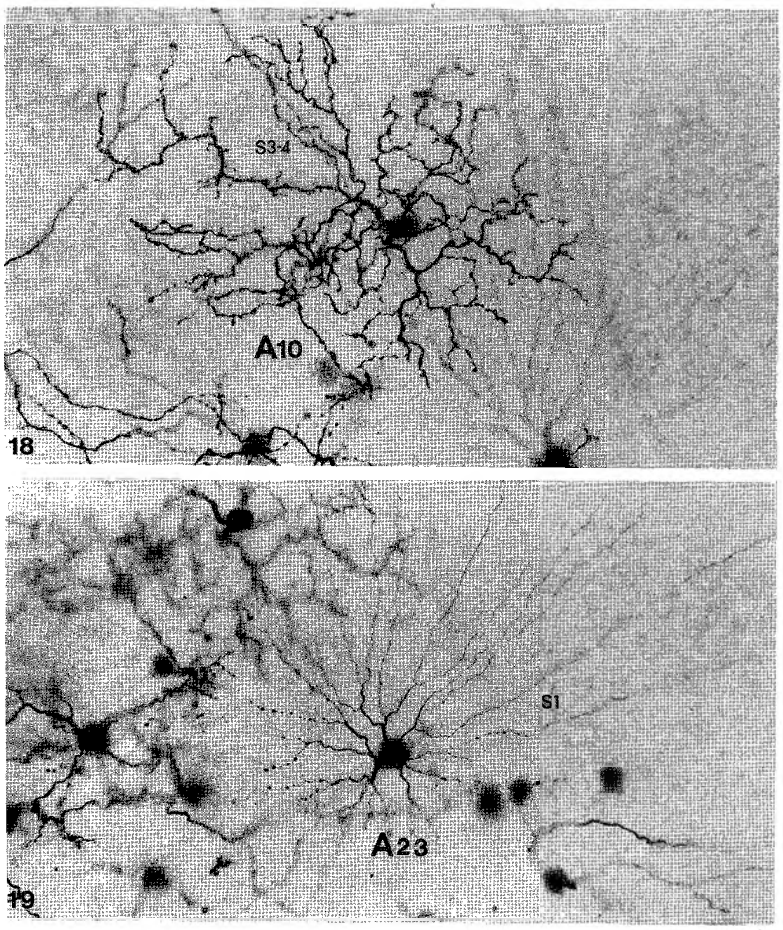
Vision researchers have tried to classify turtle retinal neurons from a number of points of view, using morphological, neurochemical or electrophysiological approaches. As a result the literature on the functional neurocircuitry of the turtle retina is perplexing, fragmented, and incomplete in many areas. Sixty-nine different types of retinal neurons can be distinguished in the turtle retina by Golgi and light microscope techniques such as those described in this paper, but immunocytochemical studies have demonstrated various neurotransmitter substances in only 15 or so discrete subpopulations of neurons. Electrophysiological studies combined with dye injection have elucidated the morphology and response patterns of some of



Figs. 16–17. 16A and B: Two views of a tristratified amacrine A12 at levels of focus of two of the tiers of dendrites. 17: An A19 amacrine cell contrasts with A17 in being a larger, coarser cell with large appendages on the dendrites. (All ×425).

the photoreceptors, 3 of the 4 horizontal cell types, 3 or 4 different bipolar types and about 8 different amacrine cells, and 12 different ganglion cells. We have attempted to integrate the findings coming from these different disciplines into a table (Table 2) so one can see the progress to date on the neural organization of the turtle retina and appreciate the large gaps that still exist in our knowledge concerning this interesting vertebrate retina. As more electrophysiological data from intracellularly dye-marked neurons becomes available, it will be interesting to learn if there are functional correlates to the large number of morphologically different cell types or whether diversely shaped cells can have a common physiology and common role to play in the neurocircuits of the turtle retina.

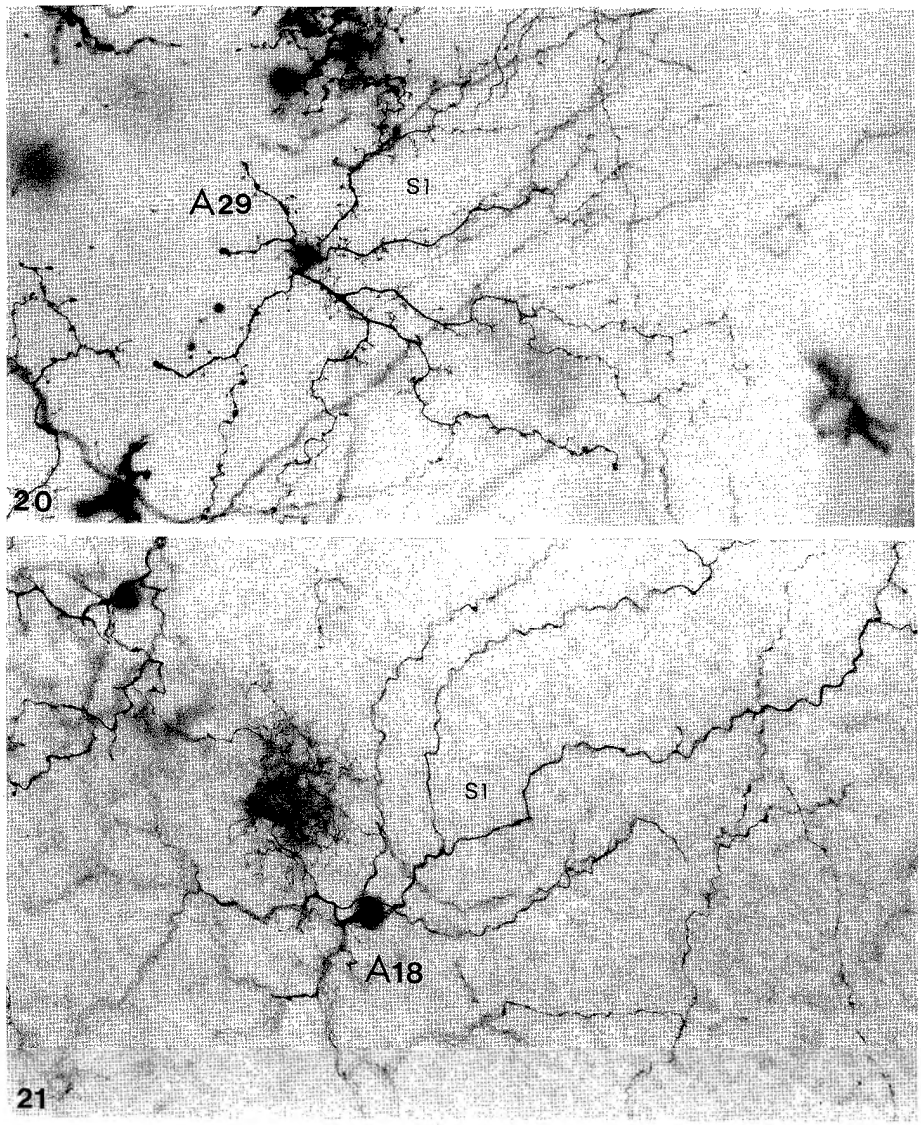
What general principles emerge from information provided by this table? Firstly, it becomes obvious that the turtle retina has some advantages over other vertebrate retinas in that at the very first stage of retinal processing we are able to recognize the different spectral



Figs. 18–19. Multibranched, broadly stratified small-field amacrine, A10, has dendrites branching at a different level of focus from a wide-field "spokes of a wheel" type of amacrine A23. (Both ×350).

types of photoreceptor, so that the formulation of chromatically distinct pathways can be initiated based on this knowledge. Thus, the spectral connections of the B4 center-hyperpolarizing and B6 center-depolarizing bipolar cells are known (Kolb et al., 1986*a*), and the manner in which these particular bipolar cells contribute to the ON- and OFF-center organization of inputs to ganglion cells is well established (Marchiafava & Weiler, 1980; Kolb et al., 1986*a*). Photoreceptor inputs to the different variety of horizontal cells have been studied morphologically (Leeper, 1978*a*,*b*; Ohtsuka & Kouyama, 1986) and electrophysiologically (Miller et al., 1973; Fuortes & Simon, 1974; Yazulla, 1976; Leeper & Copenhagen, 1979; Perlman & Normann, 1979) and models of how luminosity and chromaticity types are driven and feedback to photoreceptors (Baylor et al., 1971) occurs, can be derived from these findings (Leeper, 1978*a*, *b*; Lipetz, 1985; Ohtsuka & Kouyama, 1986).

The neurochemical interactions in the OPL of turtle have also received much attention in both immunocytochemical and electrophysiological investigations (Table 2). Excitatory amino acids such as L-glutamate are still regarded as the most likely neurotransmitters of the cones (see Miller & Slaughter, 1985, for a review) and receptors for this amino acid have been demonstrated on isolated cones of the turtle retina (Kaneko & Tachibana, 1987). However, the effectiveness of the latter agents or their analogs upon luminosity (L1 units) horizontal cells and field potentials is more complex than expected for the photoreceptor transmitter (Normann et al., 1986; Perlman et al., 1987). Acetylcholine (ACh) is actually the only transmitter to have been demonstrated by uptake and immunocytochemistry in turtle photoreceptors (Lam, 1972; Sarthy & Lam, 1979*b*; Criswell & Brandon, 1987). In addition, various bipolar cell types in the turtle retina have been shown to have alpha-bungarotoxin receptors, a probe for nicotinic receptors, upon dendrites, cell bodies, and axons (James & Klein, 1985) but muscarinic, not nicotinic, antagonists block cone to horizontal cell transmission (Gerschenfeld & Piccolino, 1977). The luminosity type horizontal cells of the turtle retina are thought to use the inhibitory neurotransmitter



Figs. 20–21. The A29 and the A18 cell have distinctly different morphologies despite branching in the same stratum of the IPL. (Both ×450).

gamma-aminobutyric acid (GABA) (Table 2) as in other nonmammalian species (Lam et al., 1978; Marc et al., 1978; see review by Yazulla, 1986). Furthermore, there is evidence that feedback to cone photoreceptor pedicles (Baylor et al., 1971) from horizontal cells is mediated by GABA sensitive receptors (Tachibana & Kaneko, 1984; Kaneko et al., 1985).

It is evident that for as much as is known concerning the organization of functional pathways in the turtle OPL as much still remains elusive. For example, how horizontal cells uncouple in the OPL (Gerschenfeld et al., 1982) without the presence of a dopaminergic interplexiform cell (Witkovsky et al., 1984, 1987; Nguyen-Legros et al., 1985; Kolb et al., 1987), and how much the organization of the bipolar cells is influenced by direct synapses upon them from horizontal cells (Kolb & Jones, 1984) as opposed to indirect actions by feedback to cones and then feedforward is still not fully understood for the turtle.

In terms of organization of the IPL in the vertebrate retina, turtle may again be one of the most advantageous model retinas. The stratification of the IPL is particularly obvious in this species for all the cell types that contribute to this neuropil. Thus, mono-, bi-, and tristratified bipolars cells interact with many possible permutations of diffuse and multistratified in addition to very strictly monostratified amacrine and ganglion cells (see Table 2). Furthermore, the cells of the IPL are not only architecturally distinctly arranged but are also segregated into specific pathways by their neurotransmitter content.

Thus, a putative glutamine-containing bipolar cell

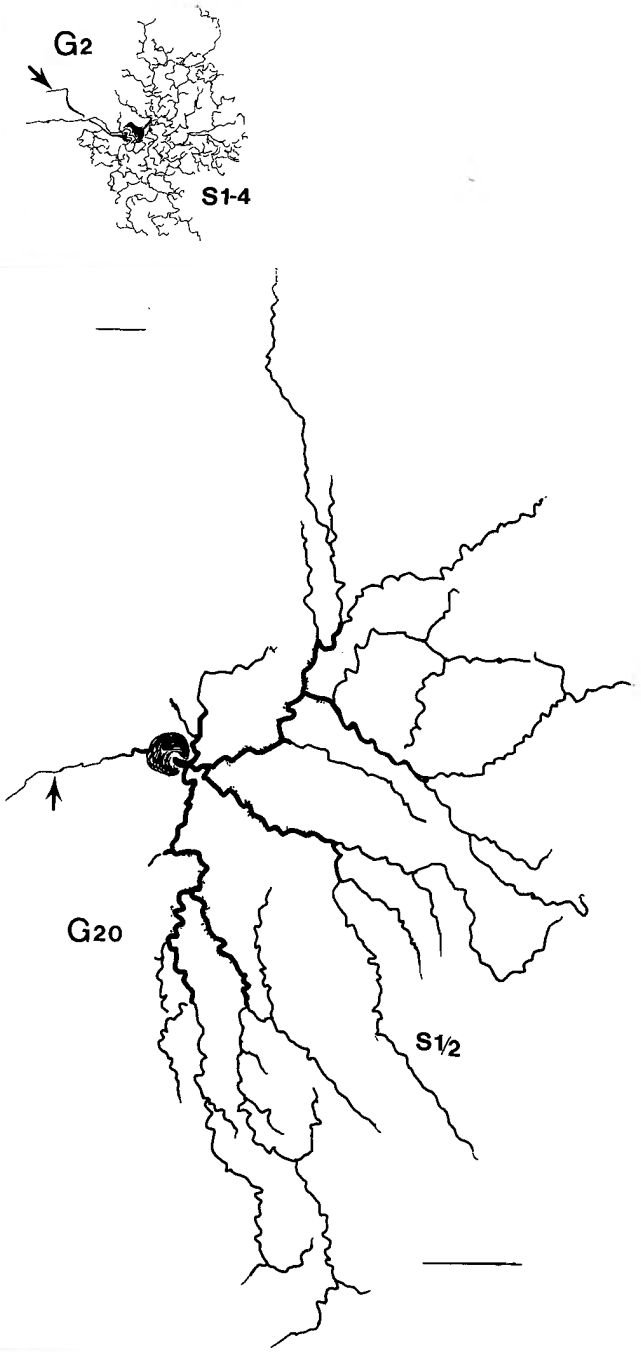


Fig. 22. Camera lucida drawing of the two extremes of ganglion cell morphology in turtle retina. G2 is one of the smallest field ganglion cells with a small cell body and diffuse dendritic tree of fine interlaced dendrites. Scale bar = 25 μm. Arrow points to the axon. G20 has a large cell body and thick "hairy" dendrites covering a 500–600 μm dendritic field. Scale bar = 50 μm. The arrow indicates the axon.

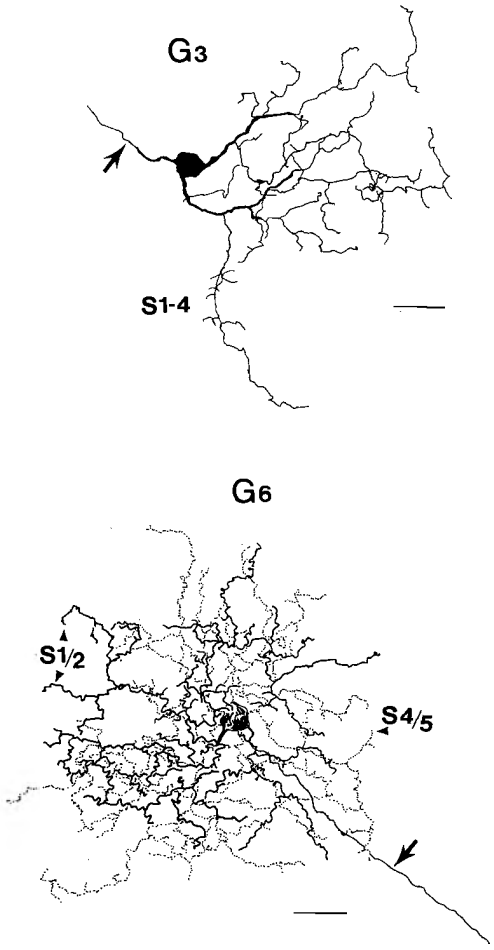


Fig. 23. Drawings of two common but different morphological types of ganglion cell. The cell bodies and dendritic fields are medium sized. G3 is diffuse while G6 is bistratified. The lower tier of dendrites of G6, in S4/5, are drawn with dotted lines. The axons are indicated by arrows. Scale bar = 25 μm.

(B2) (Ehinger, personal communication) has a distinctly different potential for interactions with different sets of amacrine and ganglion cells compared with the bipolar cell that is known to contain serotonin (B9) (Table 2, Witkovsky et al., 1984; Weiler & Schutte, 1985; Schutte and Weiler, 1987). Bipolar cells B4 and B6, although not yet assigned a neurotransmitter, are clearly important for the architecture of the functional ON-center and OFF-center lamination of the turtle IPL (Marchiafava & Weiler, 1980; Kolb et al., 1986).

Concerning neurochemically specific amacrine and ganglion cells in the turtle IPL, it is evident that just about every neuroactive substance found to date can be assigned to amacrine cells of the turtle retina (see Table 2). The neurotransmitters of ganglion cells in turtle are still elusive though, with substance P having been found in one ganglion cell type (Kolb et al., unpublished), serotonin in another (G9, Weiler & Ammermuller, 1986), and LANT-6, although seen in many varieties of ganglion cell, still has no known function (Eldred et al., 1987).

The classic excitatory transmitter ACh is demonstrable in turtle IPL (Criswell & Brandon, 1987) and is thought to be involved somehow in inputs to directionally selective ganglion cells (Ariel & Adolph, 1985).

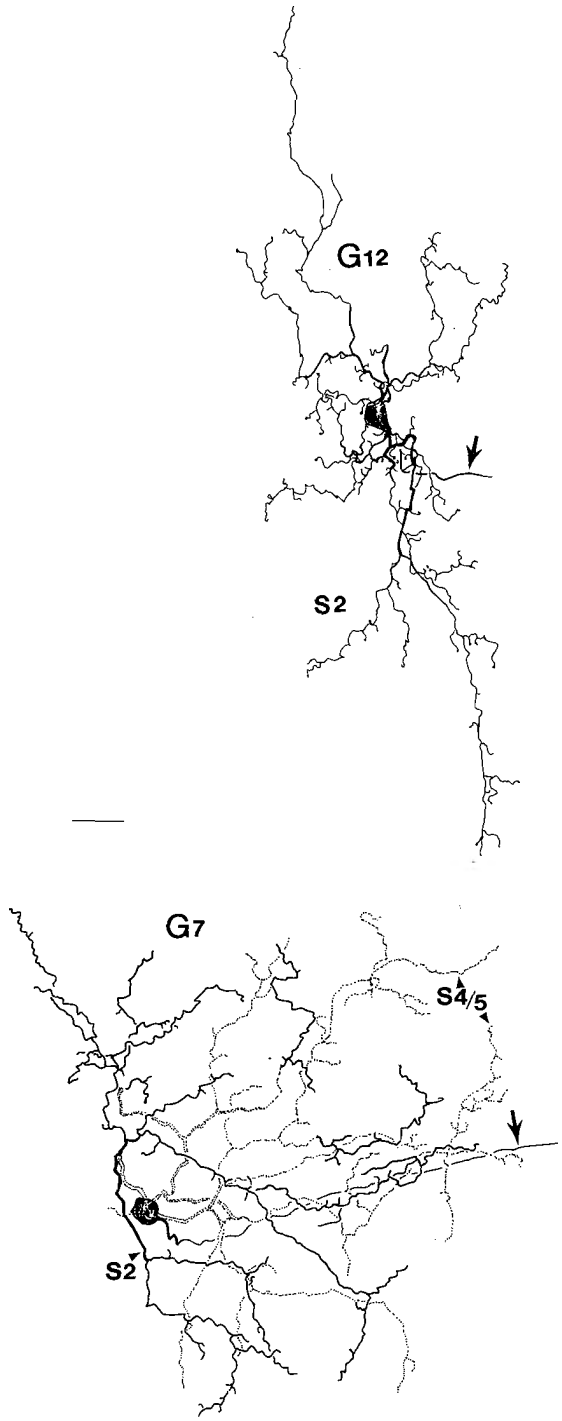


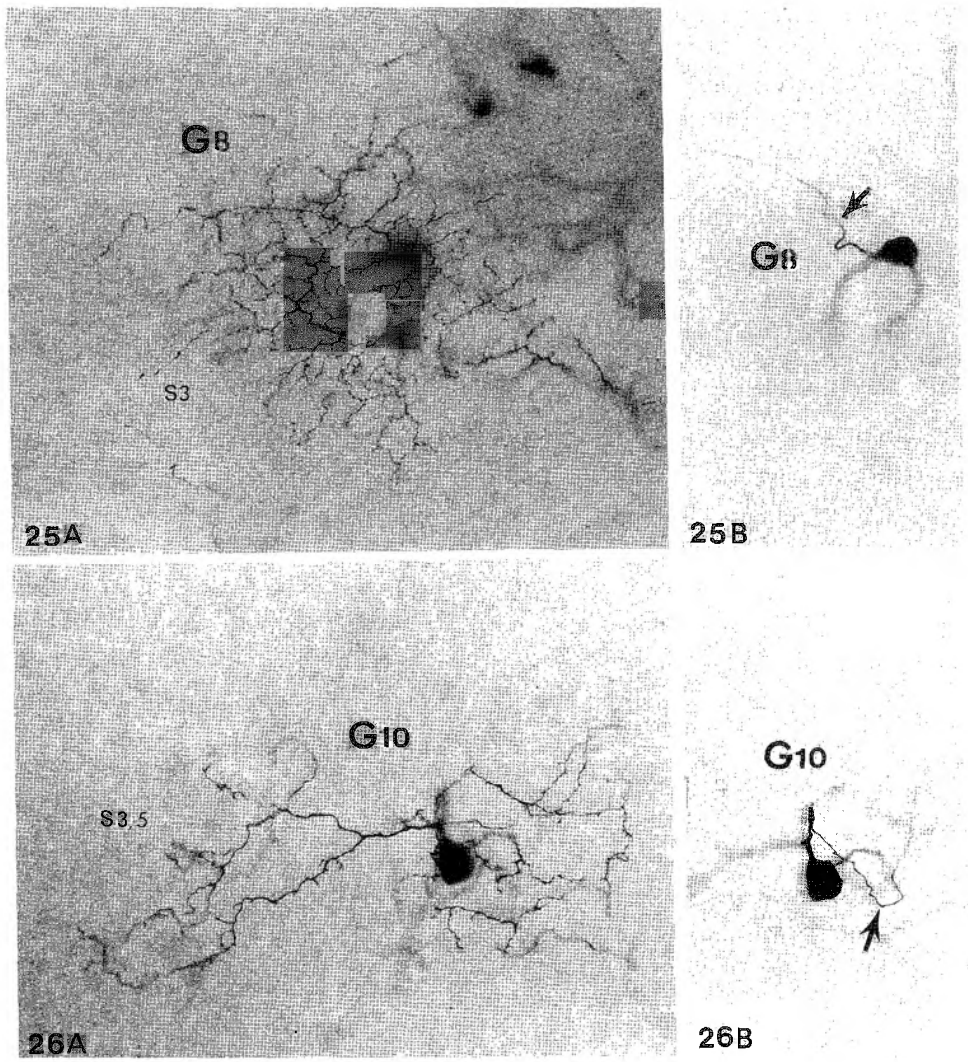
Fig. 24. Drawings of G12 and G7 type ganglion cells. These are larger in dendritic field sizes than G3 and G5 but still have fine, appendage-ladened dendrites. G12 is monostratified while G7 is bistratified. Scale bar = 25 μm.

However, the morphology of such an amacrine cell is as yet unknown. The inhibitory neurotransmitter GABA is, of course, also present in amacrine cells in the turtle retina and likewise has effects upon ganglion cell physiology (Ariel & Adolph, 1985). As in all other vertebrate retinas (see Massey & Redburn, 1987, for a recent review), GABA is accumulated by more than one morphological variety of amacrine cell and immunocytochemical or uptake studies demonstrate many cell bodies in the INL and several bands of staining in the IPL without yet definitive morphological cell types having been identified.

Amacrine cells using catecholamines as neurotransmitters are well characterized in turtle retina (Witkovsky et al., 1984; Weiler & Schutte, 1985; Nguyen-Legros et al., 1985; Kolb et al., 1987) and correspond to amacrine cells A15 (serotonin) and A28 (dopamine). The latter cell type was first described in radiolabeling and immunocytochemical studies without a Golgi-stained equivalent cell having been seen. In this study on *Mauremys* retina, however, we have been able to stain the cell by the Golgi method. The dopaminergic amacrine cell in the turtle (A28) is quite clearly a medium-field tristratified amacrine cell. There is no dopaminergic interplexiform cell in turtle retina (Witkovsky et al., 1987).

Antibodies to neuropeptides often stain two distinctly different varieties of amacrine cell in turtle retina (Table 2). For example, neurotensin quite clearly stains the A10 and the A22 types of amacrine cell. These cells have distinctly different morphologies and, more importantly, stratify in different strata of the IPL, thus placing them in positions to modulate or influence different varieties of bipolar and ganglion cell pathways. The antibody to corticotropin-releasing factor (CRF) is particularly striking in its diverse staining characteristics (Eldred & Williamson, 1987) for not only does this antibody stain two distinct populations of amacrine cells (A26 and A27, see Table 2) but also each of those populations has a unique distribution. A27 occurs primarily in the visual streak while A26 occurs only in ventral retina (Eldred & Williamson, 1987). Perhaps such data suggests that particular amacrine cell types which are important for certain features of the visual image become segregated so as to influence specific functional types of ganglion cells, i.e. A27 may be important for orientation sensitivity while A26 might be concerned with color coding or movement detection from the superior visual field that looks to the sky in this species.

Results of these immunocytochemical studies (primarily those done by Eldred and his group, Table 2) have given us important perspectives on the density and topographical distribution of transmitter-specific amacrine cells in the turtle retina. Thus, we know that dopamine-containing cells occur at a low density, have a nonrandom distribution, and a small dendritic overlap, in contrast to cells such as those that show glucagon-like immunoreactivity which occur at very high density and have tremendous dendritic field overlap. Further information on topographical distributions will become use-



Figs. 25–26. 25A and B: Small-field ganglion cell with a monostratified dendritic tree. The axon (arrow) is clear on the cell body at a diferent plane of focus from the dendrites. 26A and B: Dendrites and cell body of a bistratified medium-field ganglion cell. The axon (arrow) arises from a primary dendrite and curves down and to the side of the cell body. (All ×420).

ful for our understanding of how ganglion cell receptive fields are formed and where in the retina certain functional classes of ganglion cell may be preferentially located.

So far intracellular investigation on amacrine and ganglion cells have yielded intriguing but equivocal results for turtle retina. Despite the paucity of detailed physiological data, some general principles emerge concerning functional amacrine and ganglion cell types that can be related to their morphology. Thus, amacrine cells which respond in a sustained manner appear more often to have a diffuse spread of their dendrites through all strata of the IPL, while the transient varieties are most commonly monostratified (Marchiafava & Weiler, 1982). Interestingly, sustained amacrine cells in the cat retina are also diffuse in dendritic spread (Kolb & Nelson, 1985, for a review). In contrast, the opposite situation prevails for ganglion cell physiology. Diffuse and multibranched ganglion cells exhibit transient responses to light while the monostratified types give sustained responses (Marchiafava & Weiler, 1980).

Most of the amacrine cells recorded electrophysiologically give ON–OFF responses to light (see Table 2) as might be predicted from the fact that most amacrine cells in the turtle retina appear to be large-field monostratified or bistratified (see Table 2). The ON–OFF amacrine cells can be further subclassified on details of their receptive field organization that can often be correlated to distinctive morphological features. For example, the ON–OFF cell corresponding to A22 (Weiler & Marchiafava, 1981;

Table 2. *Classification of turtle retinal neurons*

Cell type	Morphological distinctions	Physiological properties	Transmitter candidates
Photoreceptors	Red, yellow, orange, clear		
R,G,B,UV cone	Oil droplets, telodendria	Hyperpolarizing photoresponse Small RF (28)	ACh. content, GABA and glutamate receptors (2)(4)(5)
Rod	No oil droplet	Slight inhibitory surround	
Horizontal cells			
H1 cell body	Small bushy, axon containing. contacts all cones	Luminosity (L2 type) (27) Hyperpolarizing Slight inhibitory surround	Glutamate and muscarinic receptors, GABA containing
H1 axon term	"Worm like," axon containing. contacts R cones, rods	Luminosity (L1 type) (27) Hyperpolarizing large RF	Glutamate and muscarinic receptors
H2	Large, stellate, axonless, contacts G and B cones	Chromaticity, R/G type (27)	
H3	Large, spindly, axonless, contacts B cones	Chromaticity, B/G type (27)	
H4	Small, axonless		
Bipolar cells			
B1	Monostr., a.t. S5		ACh nicotininc receptors (6)
B2	Broad str. a.t. S4–5		Glutamate containing (1)
B3	Tristr. a.t. S2, S3, S4		ACh nicotinic receptors (6)
B4	Bistr. a.t. S1, S2/S3	Off center, red sensitive (23)	ACh nicotinic receptors (6)
B5	Monostr. a.t. S1		ACh nicotinic receptors (6)
B6	Bistr. a.t. S3, S5	On center, red sensitive (23)	ACh nicotinic receptors (6)
B7	Tristr. a.t. S3, S4, S5		ACh nicotinic receptors (6)
B8	Bistr. a.t. S2, S5		ACh nicotinic receptors (6)
B9	Bistr. a.t. S1, S5	Off center (29)	Serotonin containing (7)(10)
Cent. B	Large field in OPL; small, diffuse field in IPL		
Amacrine cells			
A1	Narrow, diffuse		
A2	Narrow, varicose, monostr. S2		
A3	Narrow, beaded, monostr. S2		
A4	Narrow, broad str. S3, S4	On–Off, slow/transient (22)	
A5	Narrow, tristr. S1, S3, S5		
A6	Small, diffuse	Sustained on, univarient (20)(22)	
A7	Small, coarse, monostr. S1		
A8	Small, append., monostr. S1		
A9	Small, monostr. S2/3		
A10	Small, broad str. S3–5		Glycine, neurotensin (3)(13)(15)
A11	Small, bistr. S2, S5		Enkephalin (13)(14)
A12	Small, tristr. S1, S3, S5		Glucagon (13)(16)
A13	Medium, multibr., monostr. S2	On–Off, slow/transient (22)	
A14	Medium, elongated, bistr. S1, S3		
A15	Medium, bistr. S1/2, S4/5	On, transient/sustained (20)	Serotonin (7)(10)(11)
A16	Wide, bipolar, monostr. S5		
A17	Wide, simple, monostr. S1		
A18	Wide, curved, monostr. S1		
A19	Wide, coarse/fine, monostr. S1		
A20	Wide, coarse, irreg. monostr. S3	On–Off, fast transient (22)	Substance P (19)
A21	Wide, simple, elong., monostr. S4	On–Off, slow/transient (22)	
A22	Wide, coarse/fine, monostr. S2/3	On–Off, transient, r sens. (20)(21)	Neurotensin, Lant-6 (13)(15)(3)(17)
A23	Wide, wheel-like, monostr. S1		
A24	Wide, wheel-like, monostr. S3		
A25	Wide, simple, monostr. S3	On–Off, slow/transient (22)	
A26	Wide, simple, monostr. S5		CRF (12)
A27	Wide, coarse/fine, oriented, monostr. S1		CRF (12)
A28	Medium, tristr. S1, S2, S4/5		Dopamine (7)(8)(9)
A29	Small, star-burst appendages, monostr. S1		
Ganglion cells			
G1	Small, monostr. S3/4		
G2	Small, broad str. S1–4		
G3	Small, beaded, diffuse	Sustained, On to small, On–Off to large (25)	
G4	Small, tristr. S1, S2, S3	D.S. On–Off (25)	
G5	Small, tristr. S2, S2/3, S4/5	Sluggish, On transient (23)(25)	
G6	Small, bistr. S1/2, S4		

Table 2. *Continued*

Cell type	Morphological distinctions	Physiological properties	Transmitter candidates
G7	Small-medium, bistr. S1, S4	D.S. On (25)	
G8	Medium, fine, monostr. S3		
G9	Medium, beaded, monostr. S2/3		
G10	Medium, bistr. S3, S5		
G11	Medium, tristr. S1, S2/3, S5		
G12	Medium, coarse, append, broad S1–2		
G13	Medium, diffuse	Transient (23)(24)	
G14	Medium, curved, bistr. S1/2, S3	On–Off to small, On to large (24)(25) On–Off color coded (26) Serotonin (11)	
G15	Large, bistr. S1, S4	On–Off (25)	
G16	Large, coarse/fine, bistr. S1/2, S4		
G17	Large, tristr. S1/2, S2/3, S3/4	On–Off (25)	
G18	Large, (Dogiel) monostr. S1		
G19	Large, diffuse	D.S. Off (25)	
G20	Large, coarse, monostr. S1/2	Sustained Off (23)(24)(25) Antagonistic surround	
G21	Large, coarse, monostr. S4	Sustained On (23)(24)(25) Antagonistic surround	

Source: (1) Ehinger, personal communication; (2) Criswell & Brandon, 1987; (3) Weiler & Ball, 1986; (4) Lam, 1971; (5) Sarthy & Lam, 1979b; (6) James & Klein, 1985; (7) Witkovsky et al., 1984; (8) Nguyen-Legros et al., 1985; (9) Kolb et al., 1987; (10) Weiler & Schutte, 1985; (11) Weiler & Ammermuller, 1986; (12) Eldred & Williamson, 1987; (13) Eldred & Karten, 1983; (14) Eldred & Karten, 1985; (15) Eldred & Carraway, 1985; (16) Kolb et al., unpublished; (17) Eldred et al., 1987; (18) Eldred et al., 1985; (19) Kolb et al., unpublished; (20) Weiler & Marchiafava, 1981; (21) Jensen & DeVoe, 1982; (22) Marchiafava & Weiler, 1982; (23) Marchiafava & Weiler, 1980; (24) Marchiafava, 1983; (25) Jensen & DeVoe, 1983; (26) Weiler & Ammermuller, 1986; (27) Miller et al., 1973; (28) Baylor & Fuortes, 1970; (29) Schutte & Weiler, 1987.

Jensen & DeVoe, 1982; Marchiafava & Weiler, 1982) has a characteristic morphology where very fine dendrites emitted from the thick major dendrites run for 500 μm before ending in beaded varicosities (see Fig. 11). This morphology is reflected in the cell's receptive field properties in that this cell is ON–OFF to spots of light in the center of the receptive field that covers the extent of the larger thick dendrites, but becomes ON-center when the spot size stimulates the whole receptive field where the small diameter dendrites extend (Jensen & DeVoe, 1982). Another transient ON–OFF amacrine cell A20 (Table 2) gives responses similar to A22's but without the latter's change to an ON response with larger spot size stimulation, yet it branches in similar portions of the IPL (S3) and covers a similar planar large field. However, differences in morphological details (more irregular branching pattern and no thinning of peripheral dendrites for A20) coincide with different physiological responses from those of A22. Almost certainly these cells have compartmentalized and independent physiology for different portions of the cell, as is known to occur in axon terminals of the H1 horizontal cells (Ohtsuka, 1983) and in certain amacrine cells of rabbit (acetylcholine cells) and cat retina (A17 cells) (Miller & Bloomfield, 1983; Nelson & Kolb, 1985). Many more of the turtle amacrine cells will probably prove to have similar intriguing behaviour when future morphophysiological studies are done on them.

The various types of slow transient amacrine cells also appear to be unique morphological types. Thus, each of the slow transient types is bistratified or broadly stratified in its spread of dendrites compared with the narrowly monostratified fast ON–OFF cells, yet each branches in a different set of strata and has slightly different physiological responses (see Table 2). It is particularly interesting that the smallest amacrine cell type A4 (Table 2) is a bistratified cell with branches in the OFF- and ON-center laminae (Nelson et al., 1978; Kolb, 1982) and has a characteristic ON transient with a sustained portion to its response. This physiology is very reminiscent of the AII, small-field bistratified amacrine cell of the cat and rabbit retinas (Nelson, 1982; Dacheux & Raviola, 1986).

The turtle retina, like other vertebrate retinas with visual streaks, has a large proportion of ganglion cells responsive to movement, directional selectivity (DS), and orientation selectivity (Marchiafava, 1979; Baylor & Fettiplace, 1979; Bowling, 1980; Fulbrook, 1982; Jensen & DeVoe, 1983). The ON center and OFF center DS cells are medium-field ganglion cells that branch in the respective ON and OFF sublaminae of the IPL while the ON–OFF DS type is a very small field cell ramifying in

both the OFF and the ON sublaminae (Table 2). Curiously the ON-OFF DS ganglion cell is tristratified and the DS ON cell is bistratified, for in the rabbit retina the former is bistratified and the latter monostratified (Amthor et al., 1984). These ganglion cells appear to have lost a tier of dendrites in the course of evolution.

The ON-center and OFF-center ganglion cells of the turtle retina stratify appropriately in the two sublaminae of the IPL as in the cat retina (Nelson et al., 1978) and there are appropriate ON- and OFF-center bipolar cells available for input to the two sublaminae (i.e. B4 and B6, see Table 2). Diffusely branched or bistratified and tristratified ganglion cells that have dendrites spanning the two sublaminae of the IPL are typically ON-OFF cell types (Table 2). In many cases the overlap of ON-OFF ganglion cells with ON-OFF amacrine cells could account for the former cell types physiological responses. For example, an ON-OFF color-coded ganglion cell (Weiler and Ammermuller, 1986) corresponding to G14, is bistratified on the S1/2 border and in 53. These are positions occupied by the monostratified amacrine A25 and by one tier of dendrites of the bistratified A15, both of which are ON-OFF amacrine cells (Table 2). However, neither of these amacrines is reported to be color specific. Thus, it appears that this ganglion cell's excitation by red and blue light and inhibition by green light must come from sources other than the amacrines that are optimally positioned to have synaptic input to it in the neuropil. Interactions, not yet fully understood, from different cell processes in different strata must converge on these ganglion cells.

As can be seen there are still many intriguing questions concerning the functional organization of the ganglion cell response and receptive field in the turtle retina. Further investigations using these species are clearly warranted and we hope that such studies will build on the morphological description of *Pseudemys* and *Mauremys* turtle retinas presented in this paper.

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References

Amthor, F.R., Oyster, C.W. & Takahashi, E.S. (1984). Morphology of on-off direction-selective ganglion cells in the rabbit retina. *Brain Research* **298**, 187–190.

Ariel, M. & Adolph, A.R. (1985). Neurotransmitter inputs to directionally sensitive turtle retinal ganglion cells. *Journal of Neurophysiology* **54**, 1123–1143.

Arnold, K. & Neumeyer, C. (1987). Wavelength discrimination in the turtle (*Pseudemys scripta elegans*). *Vision Research* **27**, 1501–1511.

Baylor, D.A. & Fuortes, M.G.F. (1970). Electrical responses of single cones in the retina of the turtle. *Journal of Physiology* (London) **207**, 77–92.

Baylor, D.A., Fuortes, M.G.F. & O'Bryan, P.M. (1971). Receptive field of cones in the retina of the turtle. *Journal of Physiology* (London) **214**, 265–294.

Baylor, D.A. & Fettiplace, R. (1979). Synaptic drive and impulse generation in ganglion cells of turtle retina. *Journal of Physiology* (London) **288**, 107–127.

Bowling, D.B. (1980). Light responses of ganglion cells in the retina of the turtle. *Journal of Physiology* (London) **299**, 173–196.

Cajal, S.R.Y. (1933). Die Retina der Wirbeltiere. Wiesbaden: Bergmann. *The Structure of the Retina*. Translation by S.A. Thorpe and M. Glickstein (1972). Thomas, Springfield.

Colonnier, M. (1964). The tangential organization of the visual cortex. *Journal of Anatomy* **98**, 327–344.

Criswell, M.H. & Brandon, C.J. (1987). Immunocytochemical evidence that turtle cones are cholinergic. *Investigative Ophthalmology and Visual Science* (Suppl.) **28**, 278.

Dacheux, R.F. & Raviola, E. (1986). The rod pathway in the rabbit retina: a depolarizing bipolar and amacrine cell. *Journal of Neuroscience* **6**, 331–345.

Dalton, A.J. (1955). A chrome-osmium fixative for electron microscopy. *Anatomical Record* **121**, 281–287.

Eldred, W.D. & Karten, H.J. (1983). Characterization and quantification of peptidergic amacrine cells in the turtle retina: enkephalin, neurotensin, and glucagon. *Journal of Comparative Neurology* **221**, 371–381.

Eldred, W.D. & Karten, H.J. (1985). Ultrastructure and synaptic contacts of enkephalinergic amacrine cells in the retina of turtle (*Pseudemys scripta*). *Journal of Comparative Neurology* **232**, 36–42.

Eldred, W.D. & Carraway, R.E. (1987). Neurocircuitry of two types of neurotensin containing amacrine cells in the turtle retina. *Neuroscience* **21**, 603–618.

Eldred, W.D., Howard, E. & Polak, J.M. (1985). Quantitative analysis of neuropeptide-Y containing amacrine cells in the turtle retina. *Society for Neuroscience Abstracts* 1216.

Eldred, W.D., Isayama, T., Reiner, A. & Carraway, R.E. (1987). Ganglion cells in the turtle retina contain the neuropeptide LANT-6. *Journal of Neuroscience* (in press).

Eldred, W.A. & Williamson, D. (1987). Corticotropin releasing factor containing amacrine cells in turtle retina. *Investigative Ophthalmology and Visual Science* (Suppl.) **28**, 351.

Famiglietti, E.V. (1987). The ganglion cells of the rabbit retina: shape, stratification of dendritic trees, and relationship to cholinergic amacrine cells. *Investigative Ophthalmology and Visual Science* (Suppl.) **28**, 279.

Fujimoto, K., Yanase, T. & Hanaoka, T. (1957). Spectral transmittance of retinal colored oil globules reexamined with microspectrophotometer. *Japanese Journal of Physiology* **7**, 339–346.

Fulbrook, J.E. (1982). Motion sensitivity of optic nerve axons in turtle *Pseudemys scripta elegans*. Dissertation, University of Delaware.

Fuortes, M.G.F. & Simon, E.J. (1974). Interactions leading to horizontal cell responses in the turtle retina. *Journal of Physiology* (London) **240**, 177–198.

Gerschenfeld, H.M. & Piccolino, M. (1977). Muscarinic antagonists block cone to horizontal cell transmission in the turtle retina. *Nature* **268**, 257–259.

Gerschenfeld, H.M., Neyton, J., Piccolino, M. & Witkovsky, P. (1982). L-horizontal cells of the turtle: network organization and coupling modulation. *Biomedical Research* **3**, 21–34.

Itzhaki, A. & Perlman, I. (1984). Light adaptation in luminosity horizontal cells in the turtle retina. *Vision Research* **24**, 1119–1126.

Itzhaki, A. & Perlman, I. (1987). Light adaptation of red cones and LI horizontal cells in the turtle retina: effects of the background spatial pattern. *Vision Research* **27**, 685–696.

James, W.M. & Klein, W.L. (1985). α-Bungarotoxin receptors on neu-

rons isolated from turtle retina: molecular heterogeneity of bipolar cells. *Journal of Neuroscience* **5**, 352–361.

Jensen, R.J. & DeVoe, R.D. (1982). Ganglion cells and (dye-coupled) amacrine cells in the turtle retina that have possible synaptic connection. *Brain Research* **240**, 146–150.

Jensen, R.J. & DeVoe, R.D. (1983). Comparisons of directionally selective with other ganglion cells of the turtle retina: intracellular recording and staining. *Journal of Comparative Neurology* **217**, 271–287.

Kaneko, A., Tachibana, M. & Ohtsuka, T. (1985). GABA sensitivity in solitary turtle cones: evidence for the feedback pathways from horizontal cells to cones. In *Neurocircuitry of the Retina: A Cajal memorial*, eds. Gallego, A. & Gouras, P., pp. 89–98. New York: Elsevier.

Kaneko, A. & Tachibana, M. (1987). Effects of L-glutamate on isolated turtle photoreceptors. *Investigative Ophthalmology and Visual Science* (Suppl.) **28**, 50.

Kolb, H. (1982). The morphology of the bipolar cells, amacrine cells, and ganglion cells in the retina of the turtle (*Pseudemys scripta elegans*). *Philosophical Transactions of the Royal Society B* **298**, 355–393.

Kolb, H., Nelson, R. & Mariani, A. (1981). Amacrine cells, bipolar cells, and ganglion cells of the cat retina: a Golgi study. *Vision Research* **21**, 1081–1114.

Kolb, H. & Jones, J. (1982). Light and electron microscopy of the photoreceptors in the retina of the red-eared slider (*Pseudemys scripta elegans*). *Journal of Comparative Neurology* **209**, 331–338.

Kolb, H. & Jones, J. (1984). Synaptic organization of the outer plexiform layer of the turtle retina: an electron microscope study of serial sections. *Journal of Neurocytology* **13**, 567–591.

Kolb, H. & Nelson, R. (1985). Functional neurocircuitry of amacrine cells in the cat retina. In *Neurocircuitry of the Retina: A Cajal Memorial*, eds. Gallego, A. & Gouras, P., pp. 215–232. New York: Elsevier Press.

Kolb, H., Wang, H.H. & Jones, J. (1986*a*). Cone synapses with Golgi-stained bipolar cells that are morphologically similar to a center-hyperpolarizing and a center-depolarizing cell type in the turtle retina. *Journal of Comparative Neurology* **250**, 510–520.

Kolb, H., Linberg, K.A. & Fisher, S.K. (1986*b*). A Golgi study of ganglion cells in the human retina. *Investigative Ophthalmology and Visual Science* (Suppl.) **27**, 203.

Kolb, H. & Jones, J. (1987). The distinction by light and electron microscopy of two types of cone containing colorless oil droplets in the retina of the turtle. *Vision Research* **27**, 1445–1458.

Kolb, H., Cline, C., Wang, H.H. & Brecha, N. (1987). The distribution of dopaminergic amacrine cells in the retina of the turtle (*Pseudemys scripta elegans*). *Journal of Neurocytology* **16**, 577–588.

Lam, D.M.K. (1972). The biosynthesis of acetylcholine in turtle photoreceptors. *Proceedings of the National Academy of Science of the U.S.A.* **69**, 1987–1991.

Lam, D.M.K., Lasater, E.M. & Naka, K-I. (1978). γ-aminobutyric acid: a neurotransmitter candidate for cone horizontal cells of the catfish retina. *Proceedings of the National Academy of Science of the U.S.A.* **75**, 6310–6313.

Lasansky, A. (1971). Synaptic organization of cone cells in the turtle retina. *Philosophical Transactions of the Royal Society B* **262**, 365–381.

Leeper, H.F. (1978*a*). Horizontal cells of the turtle retina. I. Light microscopy of Golgi preparations. *Journal of Comparative Neurology* **182**, 777–794.

Leeper, H.F. (1978*b*). Horizontal cells of the turtle retina. II. Analysis of interconnections between photoreceptor cells and horizontal cells by light microscopy. *Journal of Comparative Neurology* **182**, 795–810.

Leeper, H.F. & Copenhagen, D.R. (1979). Mixed rod-cone responses in horizontal cells of snapping turtle retina. *Vision Research* **19**, 407–412.

Linberg, K.A., Fisher, S.K. & Kolb, H. (1986). A Golgi study of amacrine cells in the human retina. *Investigative Ophthalmology and Visual Science* (Suppl.) **27**, 203.

Liebman, P.A. (1972). Microspectrophotometry of photoreceptors. In *Handbook of Sensory Physiology*, vol. VII/I, pp. 481–528. Berlin: Springer.

Liebman, P.A. & Granda, A.M. (1971). Microspectrophotometric measurements of visual pigments of two species of turtle (*Pseudemys scripta* and *Chelonia mydas*). *Vision Research* **11**, 105–114.

Lipetz, L.E. (1985). Some neuronal circuits of the turtle retina. In *The Visual System*, eds. Fein, A. & Levine, J.S., pp. 107–132. New York: Alan R. Liss, Inc.

Lipetz, L.E. & MacNichol, E.F. Jr. (1982*a*). Photoreceptor types and their visual pigments in a turtle. *Investigative Ophthalmology and Visual Science* (Suppl.) **22**, 120.

Lipetz, L.E. & MacNichol, E.F. Jr. (1982*b*). Photoreceptors of freshwater turtles: cell types and visual pigments. *Biology Bulletin* **163**, 396.

Lipetz, L.E. & MacNichol, E.F. Jr. (1983). Visual pigments of two freshwater turtles. *Biophysical Journal* **41** (2/2), 26a.

Marc, R.E., Stell, W.K., Bok, D. & Lam, D.M.K. (1978). GABAergic pathways in the goldfish retina. *Journal of Comparative Neurology* **182**, 221–246.

Marchiafava, P.L. (1979). The responses of retinal ganglion cells to stationary and moving visual stimuli. *Vision Research* **19**, 1203–1212.

Marchiafava, P.L. (1983). The organization of inputs establishes two functional and morphologically identifiable classes of ganglion cells in the retina of the turtle. *Vision Research* **23**, 325–338.

Marchiafava, P.L. & Weiler, R. (1980). Intracellular analysis and structural correlates of the organization of inputs to ganglion cells in the retina of the turtle. *Proceedings of the Royal Society of London B* **208**, 103–113.

Marchiafava, P.L. & Weiler, R. (1982). The photoresponses of structurally identified amacrine cells in the turtle retina. *Proceedings of the Royal Society of London B* **214**, 403–415.

Massey, S.C. & Redburn, D.A. (1987). Transmitter circuits in the vertebrate retina. *Progress in Neurobiology* **28**, 55–96.

Miller, W.H., Hashimoto, Y., Saito, T. & Tomita, T. (1973). Physiological and morphological identification of L- and C-type *S*-potentials in the turtle retina. *Vision Research* **13**, 443–447.

Miller, R.F. & Bloomfield, S.A. (1983). Electroanatomy of a unique amacrine cell in the rabbit retina. *Proceedings of the National Academy of Science of the U.S.A.* **80**, 3069–3073.

Miller, R.F. & Slaughter, M.M. (1985). Excitatory amino acid receptors in the vertebrate retina. In *Retinal Transmitters and Modulators: Models for the Brain*, ed. Morgan, W.W., vol. **II**, pp. 123–160. Boca Raton, Florida: CRC Press.

Nelson, R., Famiglietti, E.V. & Kolb, H. (1978). Intracellular staining reveals different levels of stratification for on- and off-center ganglion cells in cat retina. *Journal of Neurophysiology* **41**, 472–483.

Nelson, R. (1982). A11 amacrine cells quicken time course of rod signals in the cat retina. *Journal of Neurophysiology* **47**, 928–947.

Nelson, R. & Kolb, H. (1985). A17: a broad-field amacrine cell in the rod system of the cat retina. *Journal of Neurophysiology* **54**, 592–614.

Nguyen-Legros, J., Versaux-Botteri, C., Vigny, A. & Raoux, N. (1985). Tyrosine hydroxylase immunohistochemistry fails to demonstrate dopaminergic interplexiform cells in the turtle retina. *Brain Research* **339**, 323–328.

Normann, R.A., Perlman, I. & Daly, S.J. (1986). The effects of continuous superfusion of L-aspartate and L-glutamate on horizontal cells of the turtle retina. *Vision Research* **26**, 259–268.

Ohtsuka, T. (1978). Combination of oil droplets with different types of photoreceptor in a fresh-water turtle (*Geoclemys reevesii*). *Sensory Processes* **2**, 321–325.

Ohtsuka, T. (1983). Axons connecting somata and axon terminals of luminosity-type horizontal cells in the turtle retina: receptive field studies and intracellular injections of HRP. *Journal of Comparative Neurology* **220**, 191–198.

Ohtsuka, T. (1985*a*). Relation of spectral types to oil droplets in cones of turtle retina. *Science* **229**, 874–877.

Ohtsuka, T. (1985*b*). Spectral sensitivities of seven morphological types of photoreceptors in the retina of the turtle (*Geoclemys reevesii*). *Journal of Comparative Neurology* **237**, 145–154.

Ohtsuka, T. & Kouyama, N. (1986). Electron microscopic study of synaptic contacts between photoreceptors and HRP-filled horizontal cells in the turtle retina. *Journal of Comparative Neurology* **250**, 141–156.

PERLMAN, I. & NORMANN, R.A. (1979). Short-wavelength input to luminosity-type horizontal cells in the turtle retina. *Vision Research* **19**, 903–906.

PERLMAN, I., NORMANN, R.A. & ANDERTON, P.J. (1987). The effects of prolonged superfusions with acidic amino acids and their agonists on field potentials and horizontal cell photoresponses in the turtle retina. *Journal of Neurophysiology* **57**, 1022–1032.

SARTHY, P.V. & LAM, D.M.K. (1979*b*). Endogenous levels of neurotransmitter candidates in photoreceptor cells of the turtle retina. *Journal of Neurochemistry* **32**, 455–461.

SCHUTTE, M. & WEILER, R. (1987). Morphometric analysis of serotonergic bipolar cells in the retina and its implications for retinal image processing. *Journal of Comparative Neurology* **260**, 619–626.

TACHIBANA, M. & KANEKO, A. (1984). γ-aminobutyric acid acts at axon terminals of turtle photoreceptors: difference in sensitivity among cell types. *Proceedings of the National Academy of Science of the U.S.A.* **81**, 7961–7964.

WAGNER, H.-J. & WAGNER, E. (1987). Differentiation and layering of amacrine cells in the roach. *Investigative Ophthalmology and Visual Science* (Suppl.) **28**, 262.

WEILER, R. (1985). Afferent and efferent peptidergic pathways in the turtle retina. In *Neurocircuitry of the Retina: A Cajal Memorial*, eds. GALLEGO, A. & Gouras, P., pp. 245–256. New York: Elsevier.

WEILER, R. & MARCHIAFAVA, P.L. (1981). Physiological and morphological study of the inner plexiform layer in the turtle retina. *Vision Research* **21**, 1635–1638.

WEILER, R. & BALL, A.K. (1984). Colocalization of neurotensin-like immunoreactivity and 3H-glycine uptake system in sustained amacrine cells of turtle retina. *Nature* **311**, 759–761.

WEILER, R. & SCHUTTE, M. (1985). Morphological and pharmacological analysis of putative serotonergic bipolar and amacrine cells in the retina of a turtle (*Pseudemys scripta elegans*). *Cell Tissue Research* **241**, 373–382.

WEILER, R. & AMMERMULLER, J. (1986). Immunocytochemical localization of serotonin in intracellularly analyzed and dye-injected ganglion cells of the turtle retina. *Neuroscience Letters* **72**, 147–152.

WITKOVSKY, P., ELDRED, W. & KARTEN, H.J. (1984). Catecholamine- and indoleamine-containing neurons in the turtle retina. *Journal of Comparative Neurology* **228**, 217–225.

WITKOVSKY, P., ALONES, V. & PICCOLINO, M. Morphological changes induced in turtle retinal neurons by exposure to 6-hydroxydopamine and 5-6-dihydroxytryptamine. *Journal of Neurocytology* **16**, 55–67.

YAZULLA, S. (1976). Cone input to horizontal cells in the turtle retina. *Vision Research* **16**, 727–735.

YAZULLA, S. (1986). GABAergic mechanisms in the retina. *Progress in Retinal Research* **5**, 1–52.