

Fine Structure of the Retina in the Reptilian Third Eye.* BY RICHARD M. EAKIN AND JANE A. WESTFALL. (From the Department of Zoology, University of California, Berkeley.) ‡

Recently Stebbins and Eakin (1) revived in modified form a concept of a photothermal function of the parietal eye of reptiles. Laboratory and field studies indicated that surgical removal of the "eye" from the lizard, *Sceloporus occidentalis*, leads to increased activity and exposure to light. They postulated that under stimulation the retina of the "eye" produces a hormone which, perhaps after accumulation in the cavity of the organ, passes into capillaries and exerts an inhibitory effect upon the activity of the animal probably *via* the pineal, pituitary, thyroid, and other endocrine glands. Because of these findings it seemed desirable to examine the parietal eye with the electron microscope. "Eyes" of juvenile *S. occidentalis* were fixed in 1.25 per cent osmium tetroxide buffered to pH 7.4 for 24 hours at 2°C., sectioned at less than 0.1 μ , and examined in a RCA EMU-2-E electron microscope. The electron photomicrographs (Figs. 2 and 3) add several structural details to the anatomical picture worked out by Nowikoff (2). Fig. 1, a photomicrograph of a thick section of the parietal eye taken with a light microscope, will orient the reader on the region of the retina included in Figs. 2 and 3.

Receptor cells (*r*) possess at their outer ends complex processes which may extend more than 15 μ into the lumen (*l*) of the organ. The distal segment of each process, tapering and sometimes branched at the base, contains 100 to 200 transversely arranged discs or flattened sacs (*rs*) which are strikingly like those in the outer segments of the rods and cones of the lateral eyes of vertebrates (3). Each disc or sac, consisting of a dense membrane and a narrow cavity is about 200 A thick. The sacs are ordinarily slightly separated; the occasional wide gaps are interpreted as artifacts. The surface membrane of the distal segment in this specimen has been damaged or lost altogether in the course of fixation and embedding. The rims of the sacs appear to be rounded or slightly tapered (insert, Fig. 2), in which respect the sacs resemble those of the cones in the rabbit's retina as described by De Robertis and Lasansky (3). In the basal part of the distal segment the periodicity of the flattened sacs is broken by

vesicles (*rv*) which are like those designated by De Robertis and Lasansky as "unoriented cone sacs" in the rabbit. Clumps of granular material adhere to the sides of the distal segments; others lie free in the lumen of the "eye."

The proximal segments of the processes have a very different organization. Internally there are longitudinally arranged tubules (*rt*, Fig. 3), embedded in a fine cytoplasmic matrix, which appear to enter numerous slender microvilli (*rmv*, Fig. 2) extending distally from the proximal segment. Proximally, the tubules continue in parallel array into the body of the receptor cell. A few mitochondria (*rm*) occur in the proximal segment of the process; they are numerous, however, in the cell proper (Fig. 3). They are exceedingly long bodies arranged lengthwise in the cell, and appear to possess internal longitudinal tubules. Pigment granules are very few in the receptors or else completely absent.

The proximal and distal segments of the receptor processes shown in Fig. 2 may seem to be separated by a gap, because the connecting piece lies out of the plane of section. It is a very short narrow element which is seen infrequently. The insert of Fig. 3 shows a longitudinal section through the connecting cilium (*cc*) of a receptor from another section. Its surface membrane is clearly continuous with that of both proximal and distal segments. It contains longitudinally arranged filaments (*f*), three of which may be seen (embedded in a clear matrix) in the section shown. Proximally these fibrils arise from electron dense areas which may correspond to a basal body (*b*). They extend into the distal segment where, in this specimen, their course through the granular matrix is not clear. The picture presented is remarkably similar to that of the rabbit cone described and figured by De Robertis and Lasansky (3, Fig. 7).

Pigment cells (*p*, Fig. 3) alternate, more or less, with the receptor cells, as shown by Nowikoff in *Lacerta* (2). They contain ovoid granules (*pg*), about 1.9 μ by 0.6 μ in size, of seemingly uniform structure. In slender parts of the cell the granules may occur in single file. From the distal end of the pigment cell, long narrow microvilli (*pmv*) project into the cavity of the organ. Vesicles or tubules (*pl*) appear to be connected to the bases of the

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villi. Mitochondria (*pm*) in the pigment cell are shorter, larger in diameter, less numerous, and more irregularly distributed than those in the receptor.

These new findings provide additional evidence that the parietal eye of reptiles is more than a vestige of an ancient, presumably visual, organ. The microanatomy of the "eye" of *Sceloporus occidentalis* suggests that its retina contains photoreceptors, which in several respects resemble the cones of the lateral eyes. In view of the nature of the connecting piece we conclude that the receptor processes, like the cone and rod outer segments of the lateral eyes, have evolved from cilia (flagella). The large number of mitochondria, the system of internal tubules (could they be a Golgi apparatus?) which seem to lead into microvilli protruding into the lumen of the "eye" suggest, additionally, that the receptors (and perhaps the pigment cells) may be secretory. Studies are now being conducted to determine whether cytological or cytochemical differences exist between the "eye" of an animal receiving continuous

illumination for several days and that of a control animal maintained in total darkness.

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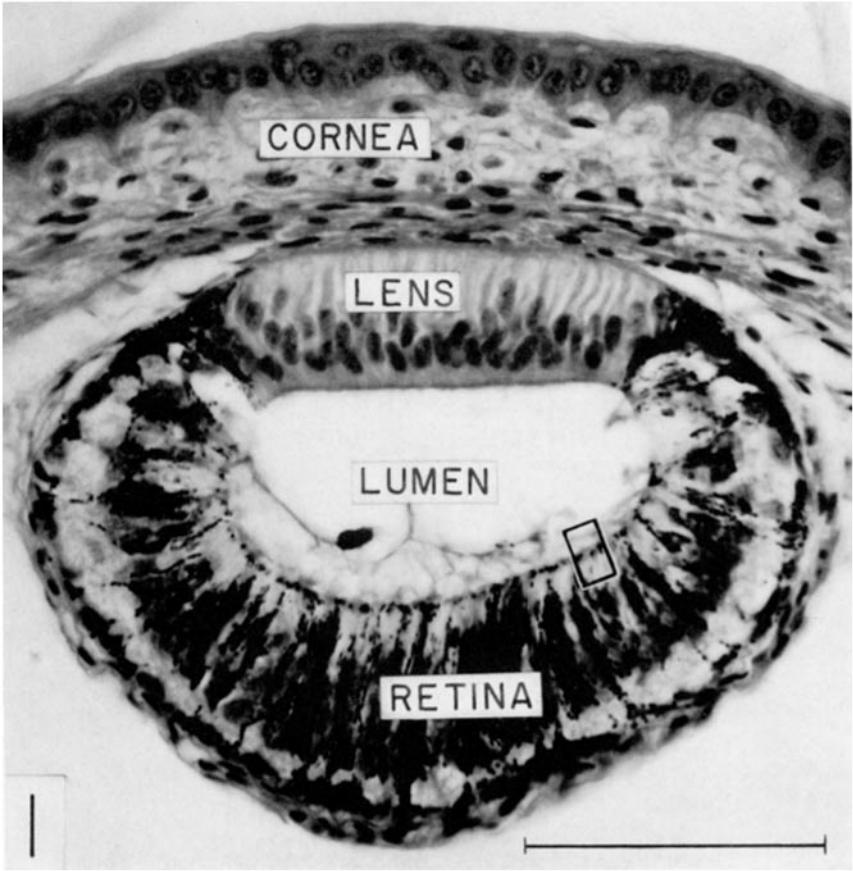
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Addendum in proof: After this paper was submitted a note by W. Steyn of Johannesburg, South Africa, on the ultrastructure of the pineal eye of *Cordylus polyzonus* appeared in *Nature* (Vol. 183, No. 4663, p. 764, 1959). Our study, begun in September of 1958, was conducted at the same time as that of Steyn's.

EXPLANATION OF PLATES

PLATE 84

FIG. 1. Parietal eye of *S. occidentalis*. Rectangle indicates region of retina shown in Figs. 2 and 3. Horizontal line represents 0.1 mm.



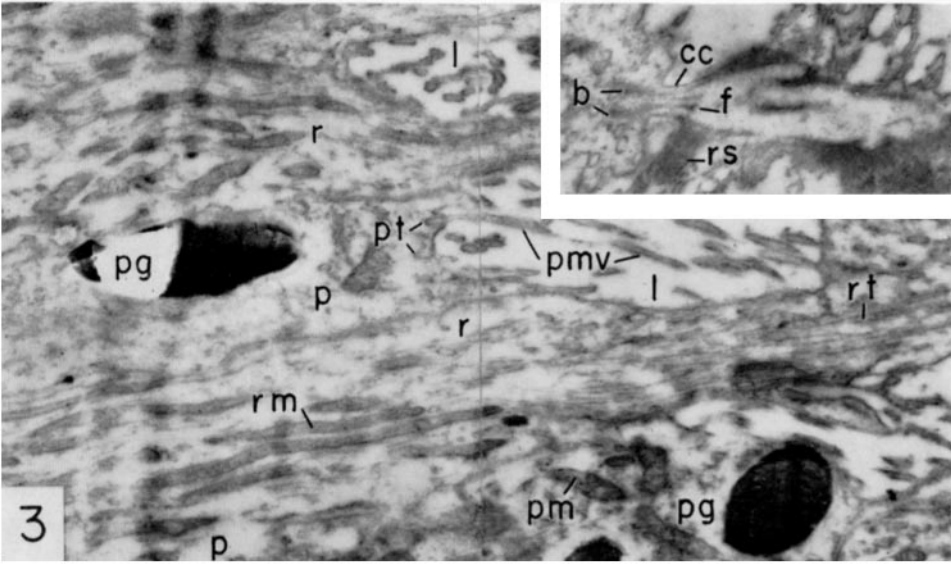
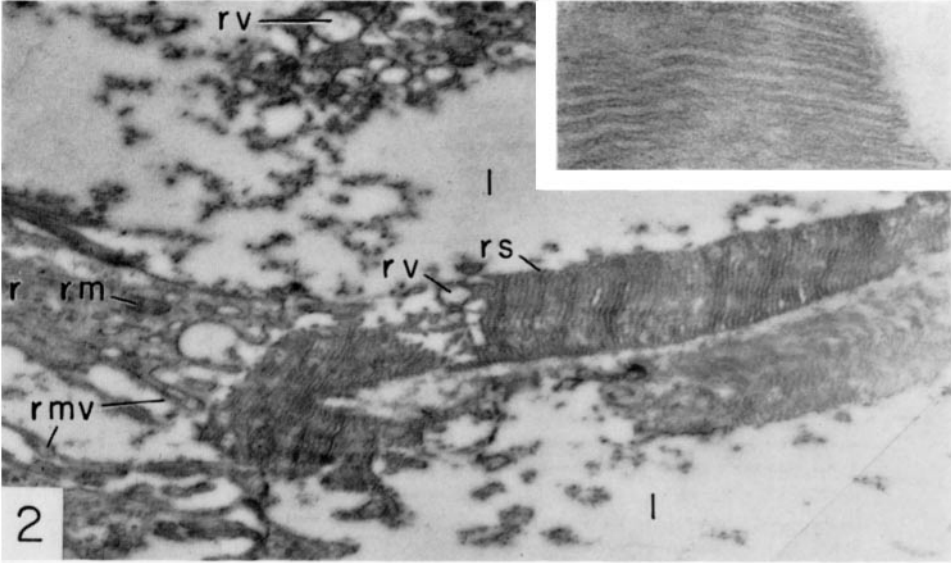
(Eakin and Westfall: Structure of retina)

PLATE 85

FIG. 2. Distal segment (branched) of a receptor process and the outer part of its proximal segment, $\times 20,000$.
Insert, high magnification of the discs or flattened sacs, $\times 70,000$.

FIG. 3. Receptors and pigment cells at retinal surface (right side of figure matches left side of Fig. 2), $\times 20,000$.
Insert, connecting cilium of a receptor, $\times 20,000$.

b, basal body; *cc*, connecting cilium; *f*, filaments in connecting cilium; *l*, lumen of parietal eye; *p*, pigment cell; *pg*, pigment granule; *pm*, mitochondria of pigment cells; *pmv*, microvilli of pigment cell; *pt*, tubule or vesicle of pigment cell; *r*, receptor cell; *rm*, mitochondria of receptor; *rmv*, microvilli of receptor; *rs*, discs or flattened sacs; *rt*, tubule of receptor; *rv*, vesicular sacs (?).



(Eakin and Westfall): Structure of retina)