Resumen por el autor, S. R. Detwiler.

Estudios sobre la retina.

Respuestas fotomecánicas en la retina de Eremias argus.

La retina de Eremias argus, un lagarto diurno común en las inmediaciones de Peking, China, posee conos dobles y sencillos, pero carece por completo de bastones, asemejándose por esta causa a la de otros saurios diurnos. Se caracteriza también por la posesión de una fovea ligeramente desarrollada situada en el centro de un "área" bastante prominente. Los conos de la fovea son mucho más numerosos y más delgados que los situados en la porción extrafoveal de la retina. Exhiben, sin embargo, todas las características de los conos típicos. La iluminación del ojo mediante la luz diurna difusa produce una contracción media de los conos de 2.3 micras en la fovea, y de 2.9 micras en la región extrafoveal. También causa la emigración del pigmento epitelial en una extensión de 4. 1 micras en la fovea y 3.4 micras en la región extrafoveal. Estos resultados sirven como otro ejemplo de la existencia de cambios fotomecánicos en retinas des provistas de bastones, y de este modo viene a confirmar la idea de que, aunque no sirven para ningún propósito, según la teoría de la duplicidad, en la contracción de los conos y la emigracion del pigmento vemos un ejemplo de la respuesta del protoplasma irritable a un estímulo adecuado definido.

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STUDIES ON THE RETINA

PHOTOMECHANICAL RESPONSES IN THE RETINA OF EREMIAS ARGUS

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TEN FIGURES

INTRODUCTION

The literature dealing with the structure of the reptilian retina and the photomechanical changes occurring there has been reviewed in previous communications (Detwiler, '16, Detwiler and Laurens, '20, and Laurens and Detwiler, '21). From this we see that in the majority of reptilian forms, the retina possesses cones only, the exceptions being certain nocturnal animals, e.g., the geckos (in which cones are entirely lacking), the crocodiles, and the boa.

In the light of the Duplicity Theory and of the generally accepted explanation of the functional significance of retinal photomechanical changes, the reptilian retina offers an interesting field for study owing to the fact that in the majority of forms cones, or rods, alone occur. In a number of such forms, however, pigment migration and cone contraction have been observed.

The retina under consideration is that of Eremias argus, a diurnal lizard common in the vicinity of Peking, China. According to Stejneger ('07) Eremias argus occurs commonly throughout north-eastern China, specimens having been gathered from Chefu, Kiautshou, Tsingtau and Peking. It has also been recorded as inhabiting eastern Mongolia and Korea. Three specimens gathered from Seoul, Korea by P. L. Jouy in 1883 are now on exhibit in the U. S. National Museum at Washington.

METHODS

Specimens of Eremias were placed in a dark room for approximately twenty-four hours, at the expiration of which time one was removed to diffuse daylight (north light) for about six hours. After proper exposure to light or darkness, the upper jaws containing the eyes were rapidly removed by means of heavy scissors and dropped into a dish of fixing fluid. This procedure required only a few seconds in the light and not more than twenty seconds in the dark. The jaws containing the eyes were allowed to remain in the fixing fluid for about a half hour in the light and dark respectively. The eyes were then removed and placed in fresh fixative where they remained for four hours. Both Perenyi's and Kleinenberg's picro-sulphuric fluids were used. Sagittal sections 10 μ thick were made and stained with Ehrlich's haematoxylin and erythrosin.

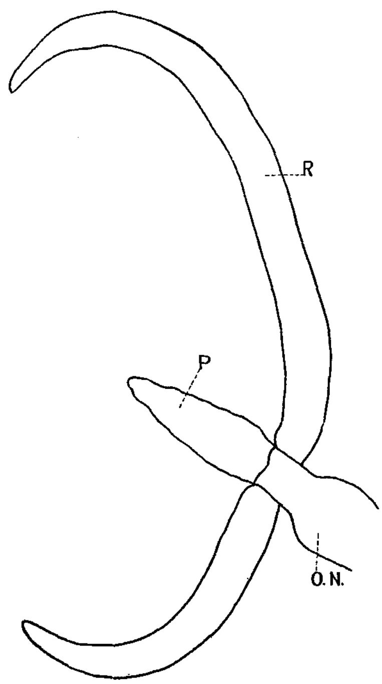


Fig. 1 Outline drawing showing the retina and the pecten. $\times$ 27. *P.*, pecten; *R.*, retina; *O.N.*, optic nerve.

ANATOMICAL

Cones. The retina of Eremias argus possesses both single and double cones, but is entirely devoid of rods. The ratio of single to double cones is approximately 4:1. Both kinds of cones throughout the retina possess conical outer segments. The inner segments exhibit slight variability in shape and structure. In the region of the ora serrata, they are typically stout (fig. 2). In the fundus of the retina they are somewhat more narrow whereas at the fovea they are very slender.

The predominant type of single cone is characterized by the possession of a prominent paraboloid, a typical ellipsoid, a short myoid and an oil drop (fig. 3). The double cones are composed of a principal member and an accessory member. The former possesses a very long narrow myoid, an ellipsoid and an oil drop, but lacks a paraboloid. The accessory member is much broader and stouter than the principal member. It possesses a short myoid, a prominent paraboloid, and ellipsoid, but lacks an oil drop (fig. 3). The double cones are very similar in shape to those previously described for Chrysemys picta and Sceloporus undulatus (Detwiler '16). Although double cones occur throughout the parafoveal portion of the retina, they can not be seen in the region of the fovea. In this portion, the cones are much more numerous in a given area and are much more slender. They possess, however, paraboloids and oil drops (fig. 5) which is in contrast with the conditions found at the fovea in Phrynosoma cornutum (Detwiler and Laurens '20), where the cones are more rod-like in their general shape and lack both paraboloids and oil drops. No single cones without paraboloids were to be found such as occur in the retina of Phrynosoma (Detwiler and Laurens '20).

Fovea. The fovea of Eremias is very similar to that of Lacerta viridis as described by Chievitz ('89). It consists of a slight depression situated in the center of a rather well developed area centralis (fig. 6). It is located slightly dorsal and lateral to the entrance of the optic nerve. At the very apex of the fovea, the cones, as previously stated, are quite slender and very numerous. Here also the external nuclear layer is considerably thickened (fig. 6) whereas this same layer beyond the limits of the area consists typically of one row of nuclei, bordered on its vitreal side by a few rounded cells (fig. 7) which have been considered by Chievitz ('89) to be the nuclei of supporting cells.

The nuclei of the foveal visual cells are more or less spindle-shaped (fig. 9) and those deeply situated are connected with their respective cones by long drawn out central processes. In Phrynosoma, the external nuclear layer was found to be entirely interrupted at the apex of the fovea—the cone nuclei occupying a parafoveal situation (fig. 3 and 4, Detwiler and Laurens, op. cit.).

The internal nuclear layer at the fovea in Eremias is only slightly less narrow than in the parafoveal region whereas the molecular and the ganglionic layer are essentially the same in thickness as they are beyond the limits of the fovea (fig. 6).

Pecten. The pecten is a conical shaped structure approximately 1 mm. in length with its base applied to the inner surface of the optic nerve as it enters the eye and its apex directed dorsally into the posterior chamber of the eye (fig. 1). Its general shape and structure is very similar to that of Phrynosoma (Detwiler and Laurens '20). As in Phrynosoma, the pecten is deeply pigmented particularly at its apex and is extremely vascular.

Pigment epithelium. The pigment epithelium is similar to that occurring in other reptile eyes, with the exception of Alligator mississippiensis, previously described. The pigment is abundant and is present in the form of brownish needle-like granules which, when massed, appear almost homogeneously black. The pigment layer varies in breadth and intensity according to the conditions of illumination as will be described later.

EXPERIMENTAL

Cone contraction. When sections of eyes which have been exposed to diffuse light are compared with those of animals kept in darkness, an average difference of 2.3μ is seen in the length of the cone myoid at the fovea and of 2.9μ in the length of the parafoveal cones (v. table and figs. 3 and 4).

The cones under conditions of illumination, in addition to being slightly contracted, are seen also to be less slender than

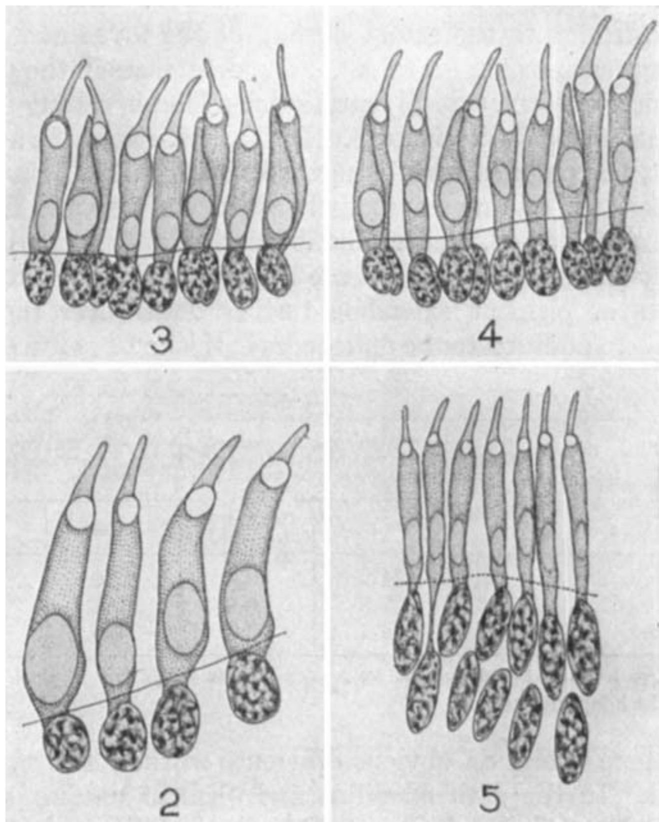


Fig. 2 Four single cones taken from the region of the ora serrata. × 1080.
Fig. 3 Single and double cones selected from the posterior portion of the retina of a light adapted eye. × 1080.
Fig. 4. Single and double cones selected from the posterior portion of the retina of a dark adapted eye. × 1080.
Fig. 5 Foveal cones from a dark adapted eye. × 1200.

are those in the dark-adapted condition (cf. figs. 3 and 4). This slight but measurable contraction compares favorably with the conditions found in the turtle retina in which light was also seen to produce shortening to the extent of 2.3μ (Detwiler '16, table 1, page 173).

Pigment migration. Differences in the position of the pigment in light and dark eyes, though slight, are measurable.

A series of measurements of three light and three dark eyes show migration to the extent of 4.1μ at the fovea and 3.4μ in the extrafoveal region (v. table). The differences in the position of the pigment in a typical extrafoveal region is readily seen by comparing figure 7 with figure 8. In the dark eye, in the majority of cases, the pigment band is narrower than in the light and in most cases the oil drops are clearly visible as is seen in figure 8. On the other hand, under illumination the pigment band is typically broader, covering the oil drops, and with finger-like processes of pigment extending further down over the cones (fig. 7). In addition to the differences in thickness of the pigment

TABLE 1[1]

CONDITIONS	DISTANCE FROM EXTERNAL LIMITING MEMBRANE TO NEAREST PIGMENT NEEDLE IN μ		DISTANCE FROM CONE NUCLEUS TO OUTER SEGMENT IN μ	
	Foveal region	Extra-foveal region	Foveal region	Extra-foveal region
Dark	11.9	9.4	18.0	17.6
Light	7.8	6.0	15.7	14.7
Difference	4.1	3.4	2.3	2.9

[1] Figures based on averages of 200 measurements taken from 3 dark adapted and 3 light adapted eyes.

band, there is also an obvious difference in the intensity of the pigment. In the dark condition the pigment needles are less massed whereas in the light, they are aggregated so as to form an almost homogeneously black mass (cf. figs. 7 and 8),

At the fovea the difference in the position of the pigment was found to be slightly more than in the extrafoveal region (v. table.) Here also, the pigment, in addition to being closer to the external limiting membrane, was found to be considerably more massed in the light than in the dark condition (cf. figs. 9 and 10). Although the breadth of the pigment layer in the dark, as shown in figure 10, is seen to be slightly greater than in the light (fig. 9), examination of a number of eyes shows that this is not typical and that the greater breadth as indicated in figure 10, is the effect of distortion owing to imperfect technique.

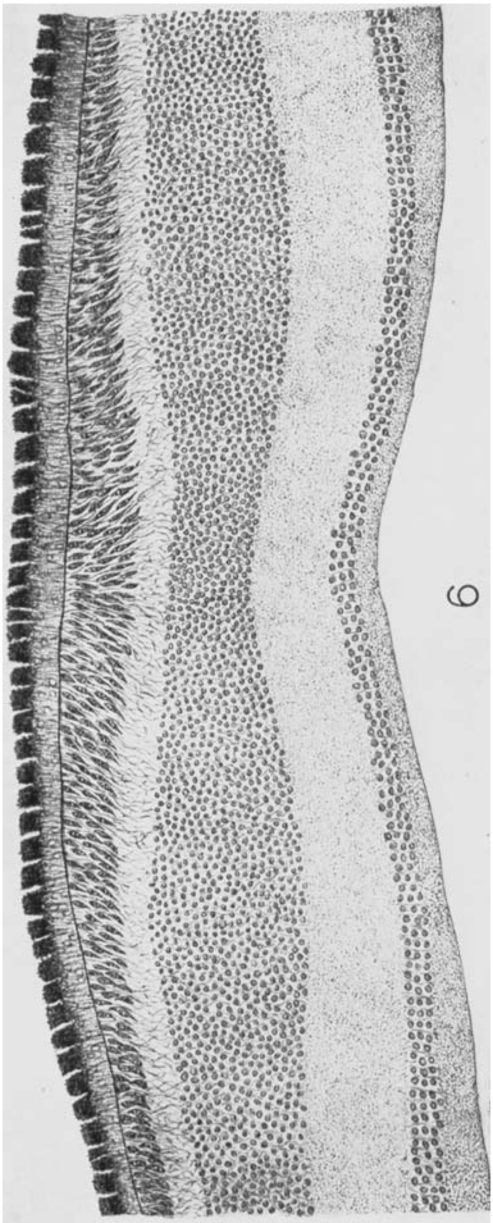
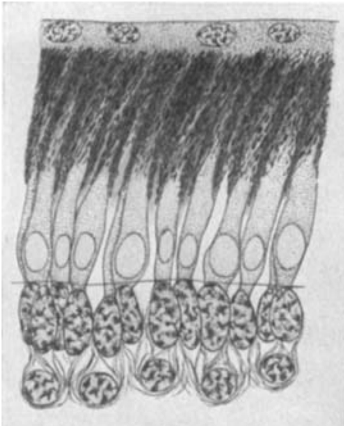


Fig. 6 Drawing of the central portion of the area centralis showing slightly developed fovea. Drawn area = 0.65 mm. in length. × 240.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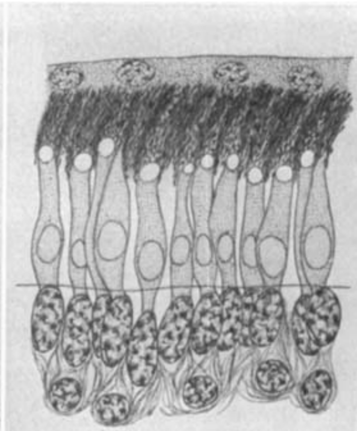
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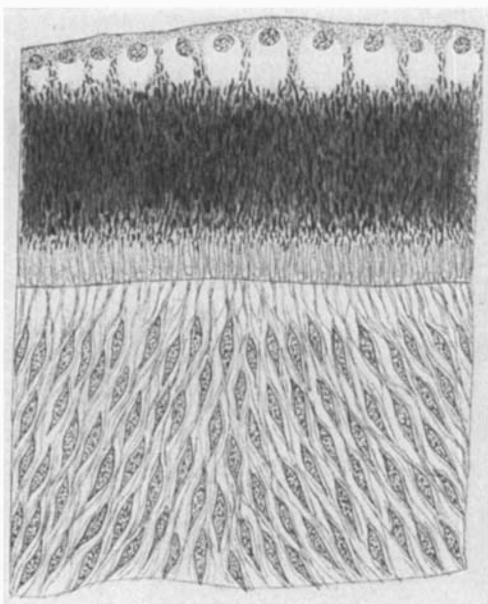
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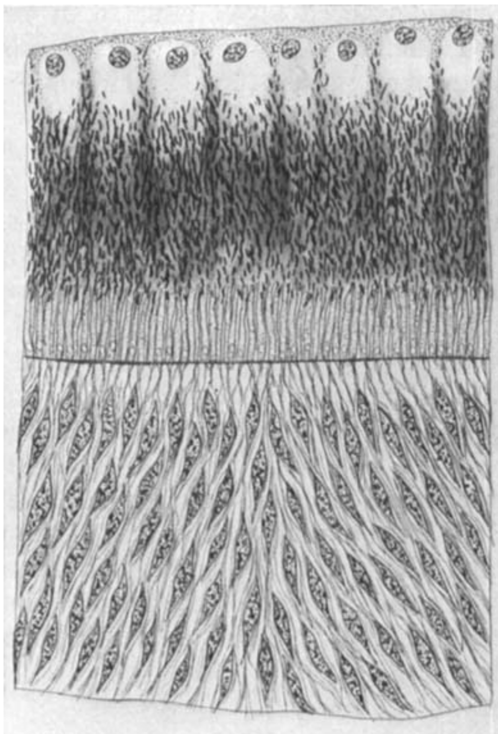

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Fig. 7 A portion of the retina showing visual cells and epithelial pigment. Animal kept in diffuse light for 6 hours. × 1080.

Fig. 8 A portion of the retina showing visual cells and epithelial pigment. Animal kept in darkness for 24 hours. × 1080.

Fig. 9 A portion of the retina taken from the fovea of a light adapted eye. × 1000.

Fig. 10 A portion of the retina taken from the fovea of a dark adapted eye. × 1000.

SUMMARY AND CONCLUSIONS

The retina of Eremias argus possesses single and double cones and is entirely devoid of rods, resembling in this respect that of other diurnal saurians. It is also characterized by the possession of a slightly developed fovea, situated in the center of a prominent 'area' (fig. 6). It also contains a prominently developed conical shaped pecten (fig. 1) which is highly vascular and deeply pigmented.

The foveal cones are much more numerous and much more slender than those in the extrafoveal region. They exhibit, however, all of the characteristics of typical cones in possessing conical outer segments, oil drops and paraboloids (fig. 5).

Illumination of the eye by diffuse day-light brings about a slight contraction of the cones and a migration of the pigment. The extent of the cone contraction averages 2.3μ in the foveal region and 2.9μ in the extrafoveal region. The pigment migration averages 4.1μ at the fovea and 3.4μ in the extrafoveal region.

The photomechanical responses as observed in this eye, as well as those obtained from a study of the eyes of the turtle, Chrysemys picta, and the lizard, Sceloporus undulatus have a distinct bearing upon the question of the functional significance of pigment migration and changes in the visual cells in light and dark adaptation.

LITERATURE CITED

CHIEVITZ, J. H. 1889 Untersuchungen über die Area centralis retinae. Arch. f. Anat. (u. Physiol.) Suppl. Bd., S. 139–196.

DETWILER, S. R. 1916 The effect of light on the retina of the tortoise and the lizard. Jour. Exp. Zoöl., vol. 20, pp. 165–191.

DETWILER, S. R., AND LAURENS, H. 1920 Studies on the Retina. The structure of the retina of Phrynosoma cornutum. Jour. Comp. Neur., vol. 32, pp. 347–356.

LAURENS, H., AND DETWILER, S. R. 1921 Studies on the Retina. The retina of Alligator mississippiensis and its photomechanical changes. Jour. Exp. Zoöl., vol. 32, pp. 207–234.

STEJNEGER, L. 1907 Herpetology of Japan and adjacent territory. Smithsonian Institution, U. S. National Museum. Bulletin 58.