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A Comparative Histological Study of the Eyes of Certain Cave Animals

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A COMPARATIVE HISTOLOGICAL STUDY OF THE EYES OF CERTAIN CAVE ANIMALS

BY

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INTRODUCTION

As early as 1850 many reports of observations of the blind cave animals were made by both scientific and popular writers. Tellkampf, Agassiz, Forbes, and Silliman were some of the earlier scientists who studied the eyes of cave animals. Eigenmann made a histological study of the cave vertebrates of America. In a study of Forbesichthys papilliferus, a semi-blind cave fish, Jennie Miller Orr found important structural modifications in the eyes of this species. Since no comparative histological studies of the eyes of cave animals seem to have been made, it was decided to make such a study with a view to determining whether these structural differences are similar in different cave animals.

The animals chosen for this study are: Hadenoecus subterraneous, the so-called cave cricket; Cambarus pellucidus, the blind cave crayfish; Forbesichthys papilliferus, a semi-blind cave fish, and Typhlichthys subterraneous, a blind cave fish.

Eigenmann states that degeneration of eye tissue occurs in certain forms in the absence of light. A comparative histological study of the eyes of cave species and of those having normal eyes should reveal the nature of this degeneration.

REVIEW OF LITERATURE

Very few histological studies of the eyes of cave animals have been made, and these are for the greater part upon the eyes of the fishes. No scientific studies of the histological structure of the eyes of the cave crickets or the cave crayfishes seem to have been made.

Giovannoli[1] says that the eyes of Hadenoecus subterraneous are black and apparently well developed. In speaking of Cambarus pellucidus Giovannoli[2] states that it is not only blind but has practically lost its eyes, in that the external part of the eye is reduced to the merest rudiment, and the optic nerve, though still present, is only weakly developed.

Agassiz and Gould[3] state that Astacus (Cambarus) pellucidus has merely the pedicle for the eye, without even traces of facets.

Silliman[4] says that, though Tellkampf and Thompson speak of the eyes of Cambarus pellucidus, by examination

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1 Leonard Giovannoli, "Invertebrate Life of Mammoth and Other Neighboring Caves," Cave Life of Kentucky, Vernon Bailey (ed.) (Notre Dame, Indiana, The University Press, 1933), p. 224.

2 Ibid., p. 236.

3 William Stump Forwood, An Historical and Descriptive Narrative of the Mammoth Cave of Kentucky (Philadelphia, J. B. Lippincott and Co., 1870), p. 91.

4 Forwood, op. cit., pp. 90-91.

of several specimens he has satisfied himself that only the peduncle of the eye exists, but there are no visible facets at its extremity.

Tellkampf and Müller[5] were the first to detect the existence of rudimentary eyes in the blind cave fishes; they did not find a nerve in connection with the eye, nor did they determine the contents of the globe with certainty.

In a study of the eye of Forbesichthys papilliferus Orr[6] found that while all of the important elements of the eye are present, some are very degenerate, such as the optic nerve and the lens, but she states that the retina is very well developed.

In a study of Chologaster (Forbesichthys) papilliferus Eigenmann[7] found that the six normal eye muscles are present; the sclera and choroid are very thin; there is no nerve fiber layer, but the fibers spread out into the ganglionic layer; the pigment layer of the retina is very thick; and the retina as a whole is much simplified, with the greater point of degeneration lying between the outer nuclear and the inner

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5 Ibid., p. 26.

6 Jennie Miller Orr, Studies on a Cave Fish of Uncertain Classification (master's thesis, Western Kentucky State Teachers College, 1934), p. 16.

7 Carl H. Eigenmann, Cave Vertebrates of America (Washington, D. C., Published by the Carnegie Institution of Washington, 1909), pp. 110-115.

reticular layers. In summarizing the eyes of the Amblyopsidae family Eigenmann[8] says the eye of Chologaster (Forbesichthys) papilliferus is symetrically reduced from a larger, normal fish eye, the retina being the first structure simplified, with later the lens and the vitreous body degenerating more rapidly.

Eigenmann[9] found that the optic nerve of Typhlichthys subterraneous is connected with the brain; there is a total absence of pigment from the eye; there are no definite rods and cones; the lens, which is not present in all eyes, consists of but a few undifferentiated cells; sometimes a minute vitreal body is found surrounded by the ganglionic layer; and there are no eye muscles.

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8 Ibid., p. 146.

9 Ibid., pp. 120-126.

PROCEDURE

Collections were made from various caves in this region. Hadenoecus subterraneous is found in abundance in many caves, but the specimens used were obtained from a saltpetre cave near Anna on the Bowling Green and Monaker's Ferry road. Forbesichthys papilliferus was obtained from this cave where this species was fairly abundant. Cambarus pellucidus was found in great numbers in a cave on the McBride farm near Glasgow Junction. Two specimens of Typhlichthys subterraneous were found in this cave and three were obtained from a saltpetre cave a few miles from Glasgow.

Zenker's fixative was used for the eyes of all the forms. Much of the success in obtaining good slides might be attributed to the fact that the tissues were cleared by a special sinking process. Two of these sinking methods were used. One clearing process involved the use of equal parts of terpineol and ninety-five per cent alcohol, with the latter on top. In the other process equal parts of aniline oil, methyl salicylate, and ninety-five per cent alcohol were poured into the vial in the order named. The tissues were imbedded in paraffin to which crude rubber and a small amount of bayberry wax had been added. They were double-stained with eosin and hematoxylin.

Sections used in preparation of the drawings were taken approximately at the center of the eye from front to back. The drawings to show gross structure were made by means of a microprojector, while the Abbé camera lucida was used to make the drawings of detailed structure.

A COMPARISON OF THE EYE OF HADENOECUS SUBTERRANEOUS WITH A NORMAL COMPOUND EYE

Definite structures are very difficult to distinguish in an ommatidium of the eye of Hadenoecus because the cells are filled with a dark brown pigment, but occasionally some ommatidia could be found where the pigment was less dense, and in these could be found all the structures present in the normal compound eye. In the drawing of the ommatidia of the eye of Hadenoecus (Figure 1), it is shown that the crystalline-cone cells, the rhabdomes, and the retinula or visual cells are all well developed.

By a superficial general examination of this eye it is readily seen that it is much smaller than the eye of the normal members of the Tettigoniidae family to which it belongs. There is a great reduction in the number of ommatidia composing the eye. The average number of ommatidia counted in each cross-section was seventeen, which is approximately one-fourth the number found in a cross-section of the eye of Amblycorypha, a member of the same family. With a decrease in the number of ommatidia there seems to be an increase in the size of each. In a comparison of the ommatidia of Hadenoecus with those of Camburus sp. which are drawn to the same magnification (Figure 3), it can be seen that the ommatidia of the former are proportionately much shorter and broader than those of the latter. Both the decrease in number and the corresponding increase in the size of the ommatidia may be taken as

evidences of degeneration, since the acuteness of vision of a compound eye depends to a great extent upon these two factors. for the details of an object can be seen better by a greater number of small ommatidia than by a few large ones, in that the smaller the portion of the object viewed by each ommatidium the more detailed will be the complete mosaic image.[10]

As was mentioned previously there is an unusual amount of pigment present in the eye of Hadenoecus as compared with the normal eye; there is so much pigment that no part of the ommatidium took the stain except the crystalline-cone cells. This may be taken as another evidence of degeneracy, for Eigenmann[11] states that a great amount of pigment is usually to be found in degenerate eyes.

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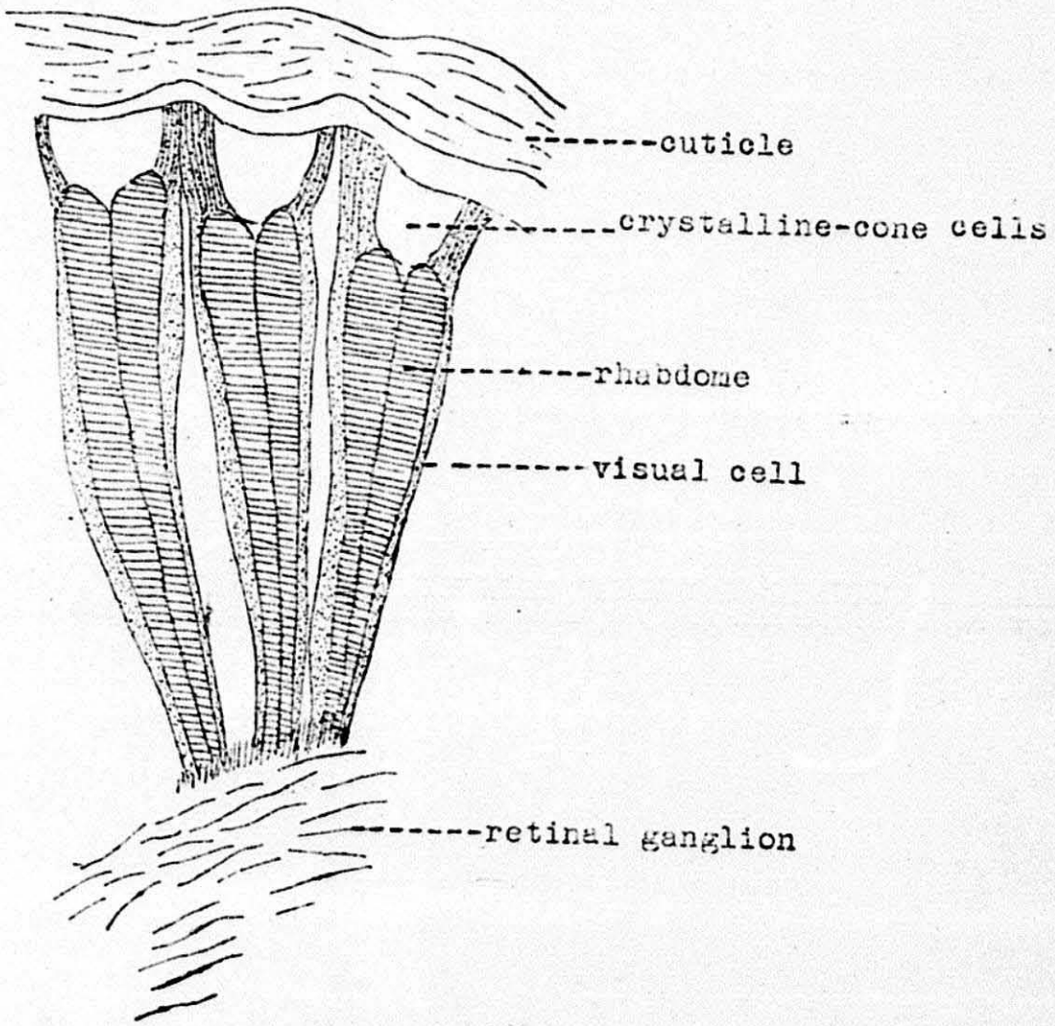
10 John Henry Comstock, An Introduction to Entomology (Ithaca, N. Y., The Comstock Publishing Co., 1930), p. 142.

11 Eigenmann, op. cit., p. 113.

FIGURE 1

Ommatidia from the Eye of Hadenoecus subterraneous (x-550)



A COMPARISON OF THE EYE OF CAMBARUS PELLUCIDUS WITH THE EYE OF CAMBARUS SP.

In a comparison of the eye of Cambarus pellucidus with that of Cambarus sp. we can find very few points of resemblance (Figures 2 and 3). In the eye of the blind crayfish the cuticle has become greatly thickened and heavily chitinized; it is especially thick at the anterior end, where a small dome-like projection is found. On the exterior of this eye no facets can be found as are on the eye of Cambarus sp. Within the eye several striated muscle fibers are found at one side beginning at the anterior end and extending with a diminishing width to the posterior end. At the other side and occupying the greater amount of space in the eye is a circle of tissues which may be the remains of the corneal cells. Within this circle and separated from it by a great amount of connective tissue is another circle within whose bounds are several layers of nuclei which are probably the degenerate rhabdomes and retinular cells. No ommatidia can be seen, for they appear to have coalesced into these indistinguishable masses.

Giovannoli[12] says that the optic nerve though poorly developed is still present, but in the present study the optic nerve was not located in connection with the eye.

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12 Giovannoli, op. cit., p. 224.

Figure 2

Cross Section of the Eye of Cambarus pellucidus (x-110)

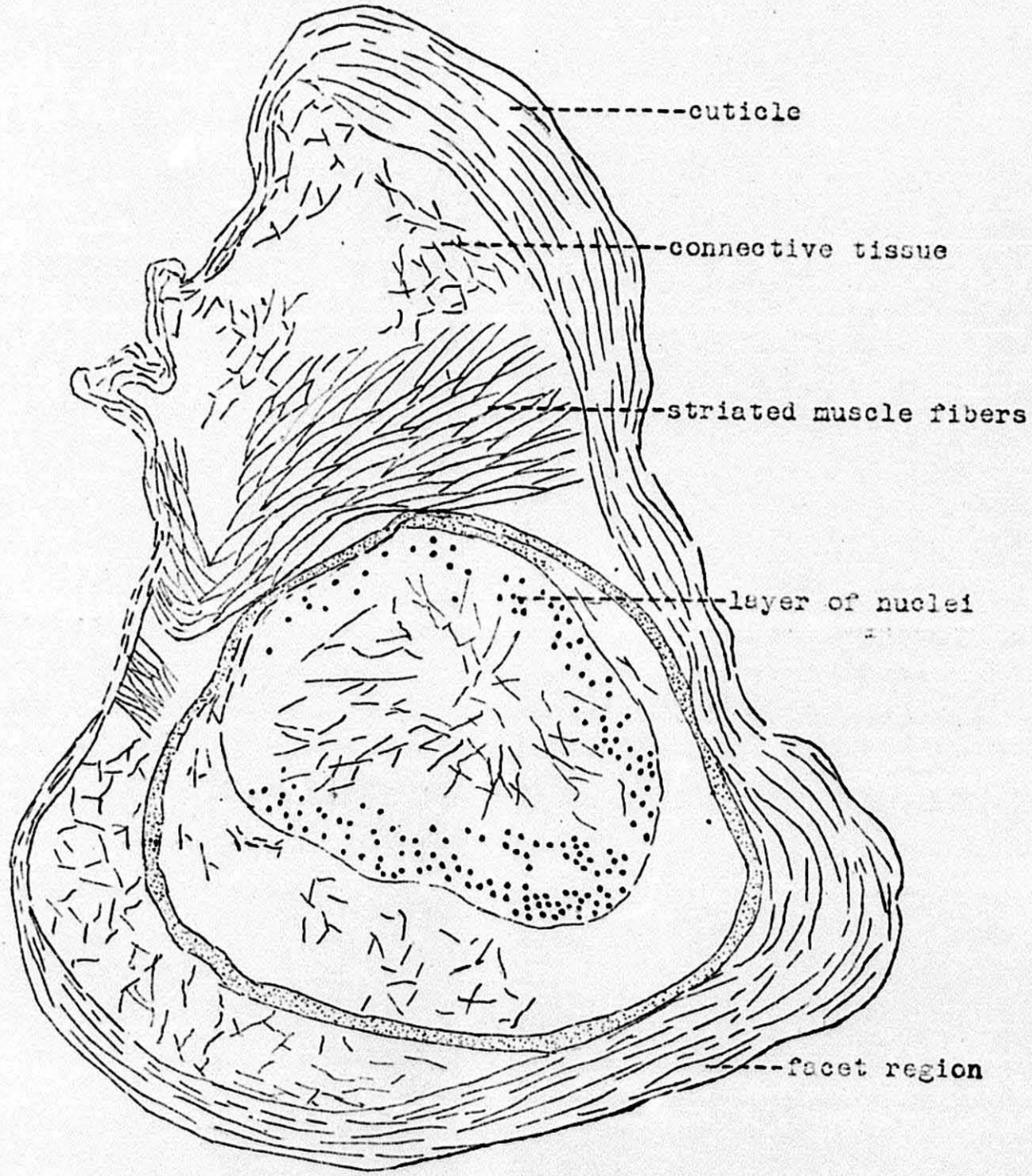
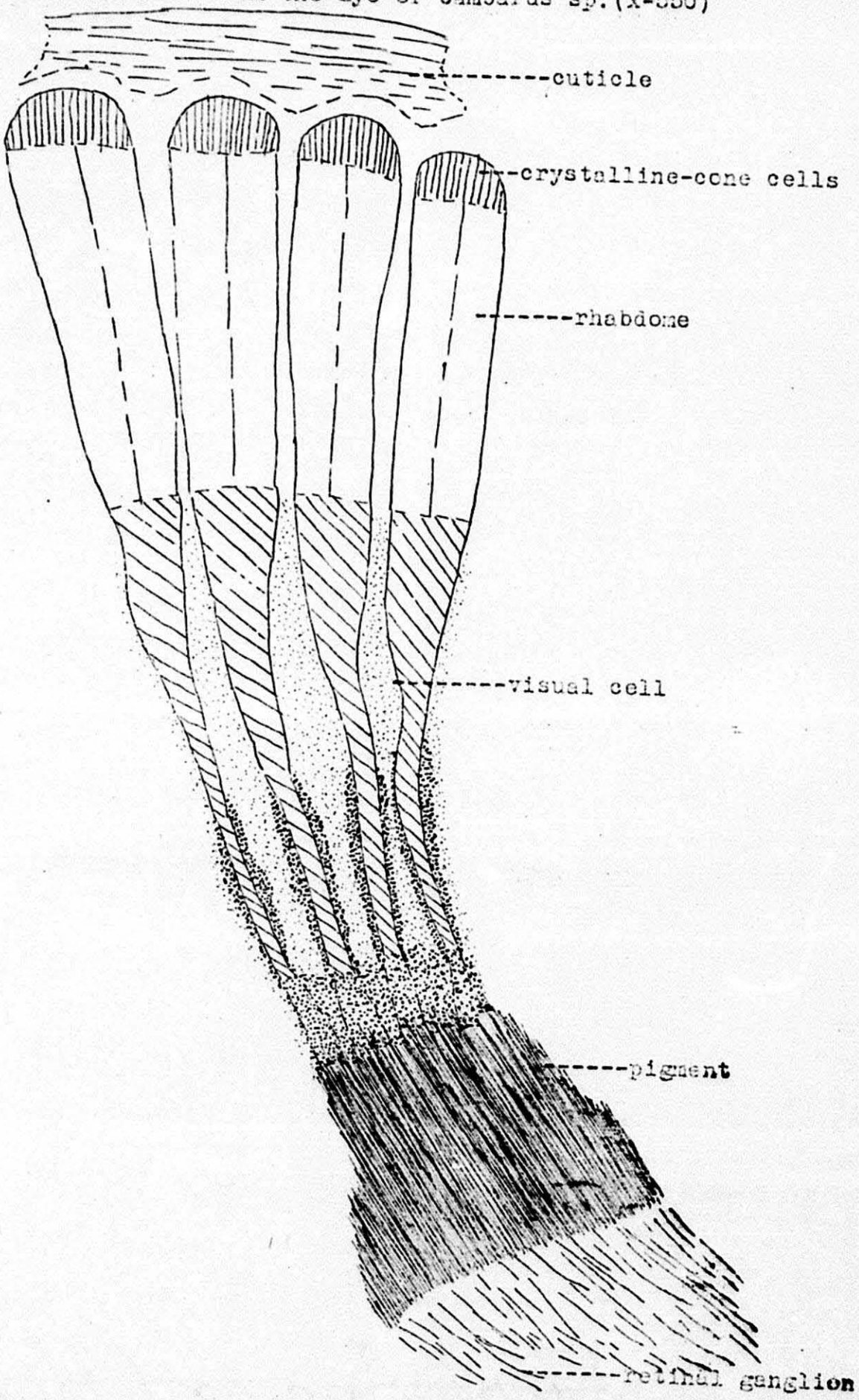


Figure 3
Ommatidia from the Eye of Cambarus sp. (x-550)



A COMPARISON OF THE EYE OF FORBESICHTHYS PAPILLIFERUS WITH THE EYE OF NOTROPIS ATHERINOIDES

For a comparison of the eye of Forbesichthys with a normal eye, the minnow Notropis atherinoides was selected, and eyes from individuals of approximately the same size were used. In comparing the two eyes (Figures 4 and 5), several differences are apparent.

The entire eye of Forbesichthys is much smaller than that of Notropis. In Forbesichthys the skin is extended entirely over the eye; however, it can be seen that the accessory glands, although plentiful around it, are not found in the skin covering the eye. The optic nerve is well developed in the eye of Forbesichthys, but it is comparatively much smaller than in Notropis. In the latter the diameter of the optic nerve is equal to the width of the retina, while in Forbesichthys the width of the optic nerve is approximately one-fourth that of the retina. In Forbesichthys the lens is proportionately much smaller than it is in Notropis.

The major differences are found in the retina (Figures 6a and 7). In the retina of Notropis there is a definite nerve fiber layer on the inner side of the ganglionic layer, but there is no differentiated nerve fiber layer in the retina of Forbesichthys. Eigenmann[13] says the optic nerve spreads out in all directions as soon as it has passed the pigmented

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[13] Eigenmann, op. cit., p. 113.

part of the retina, some of the fibers passing behind the ganglionic cells and being distributed among the nuclei of this layer. There is only one layer of nuclei in the ganglionic layer of the retina as compared with the two layers of nuclei found in the corresponding layer of Notropis. In the inner nuclear layer of Forbesichthys there are two or three layers of nuclei, while in this layer of Notropis there are six layers of nuclei. A reduction of nuclei is also found in the outer nuclear layer. There are only two or three layers of nuclei in this stratum in Forbesichthys, while there are four layers in this section in the Notropis eye. The rods and cones of Forbesichthys, though apparently well developed, are greatly reduced in number. As in the eye of the cave cricket, there is an excessive amount of pigmentation, the pigment layer being approximately one-half the width of the entire retina. In general, there has been a decrease in the width of the other layers and an increase in the extent of the pigment layer in comparison with the normal eye, and, as in the cave cricket, this shows degeneration. A very interesting phenomenon is observed in the eye of a Forbesichthys which had been exposed to daylight for three months before the eye was removed. As can be seen (Figure 6b) the retinal pigment has migrated into the region of the rods and cones and has completely obscured them by its density.

Figure 4

Cross Section of the Eye of Forbesichthys pupilliferus (x-350)
(Pigment obscures rods and cones because of exposure to light)

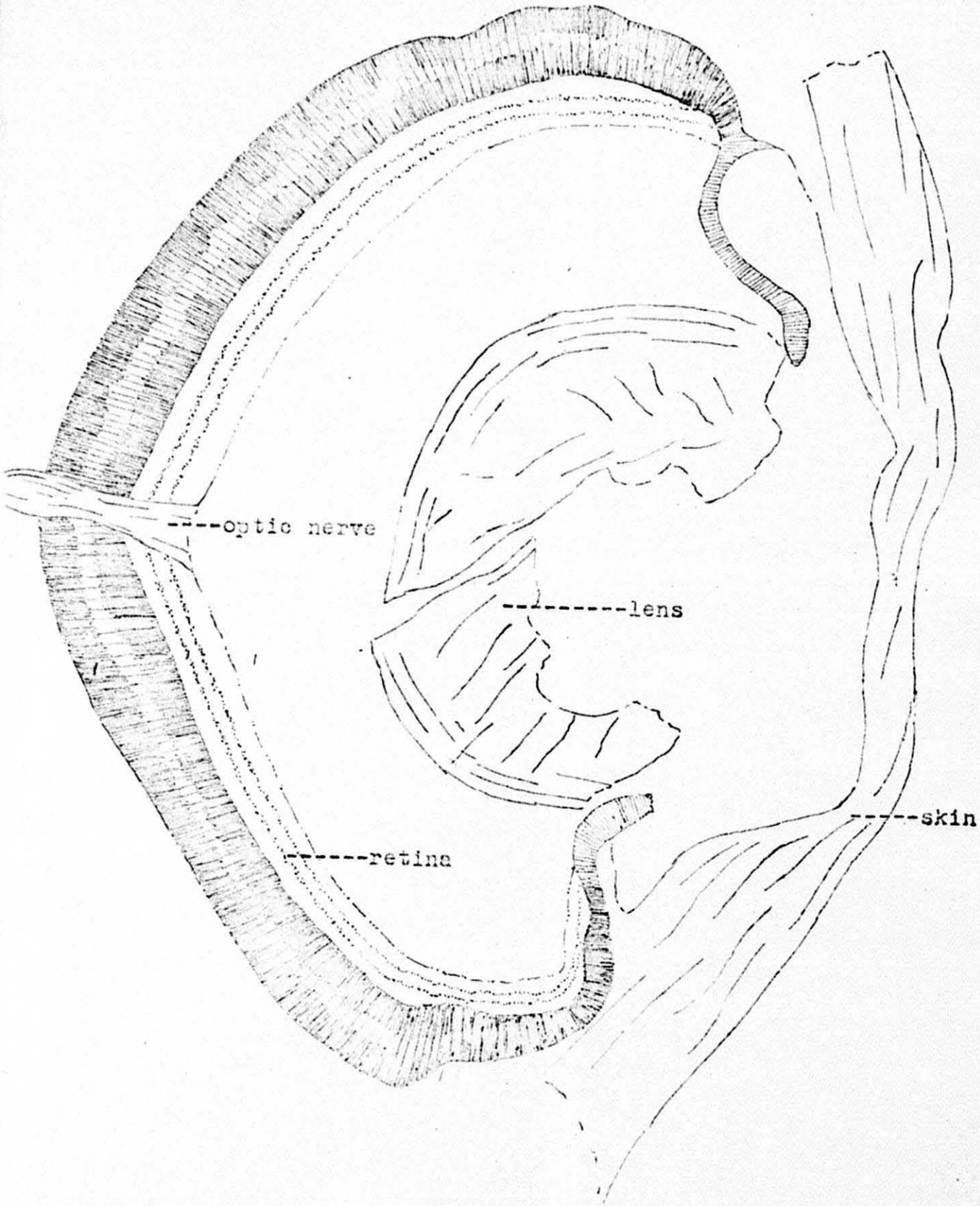


Figure 5
Cross Section of the Eye of Notropis atherinoides (x-350)

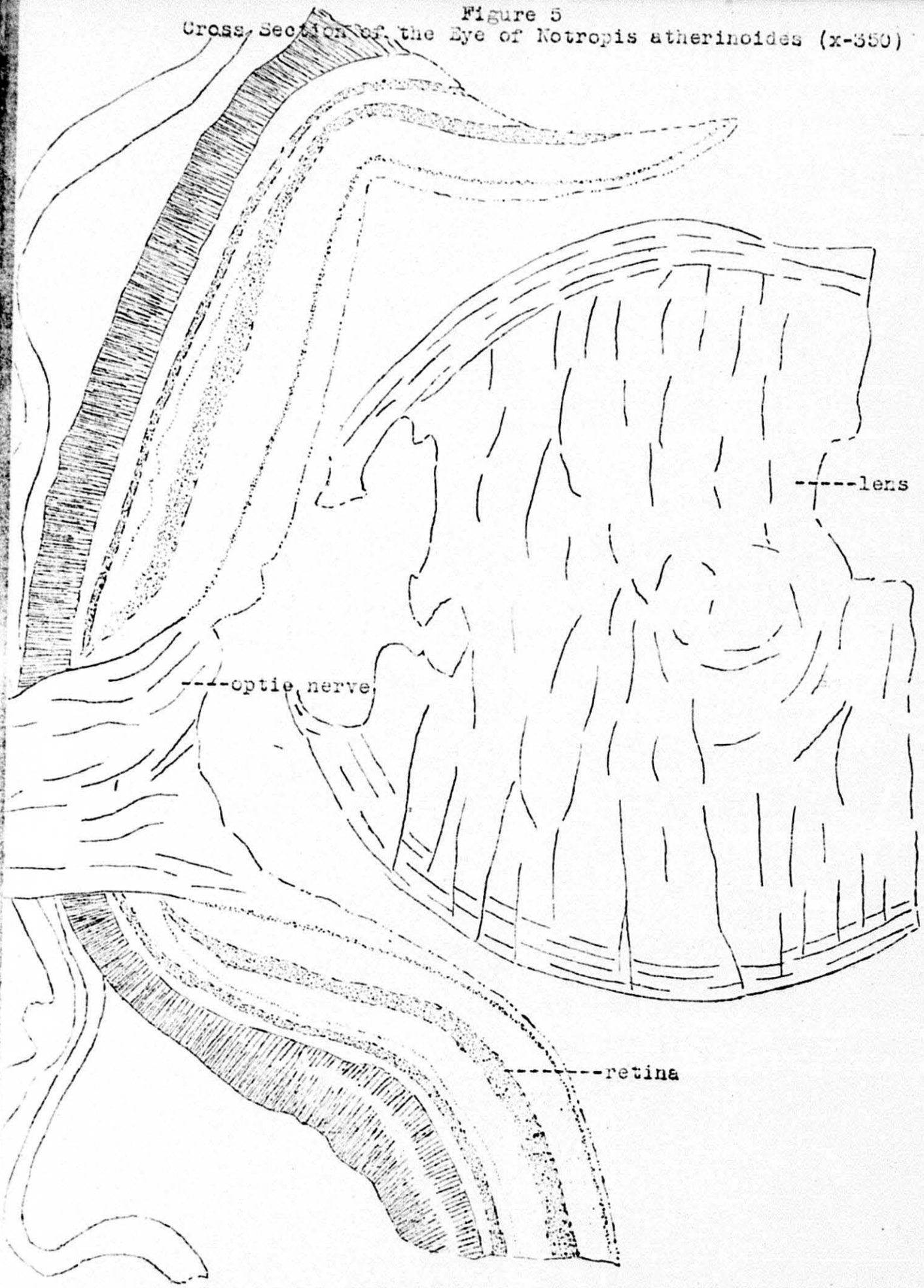
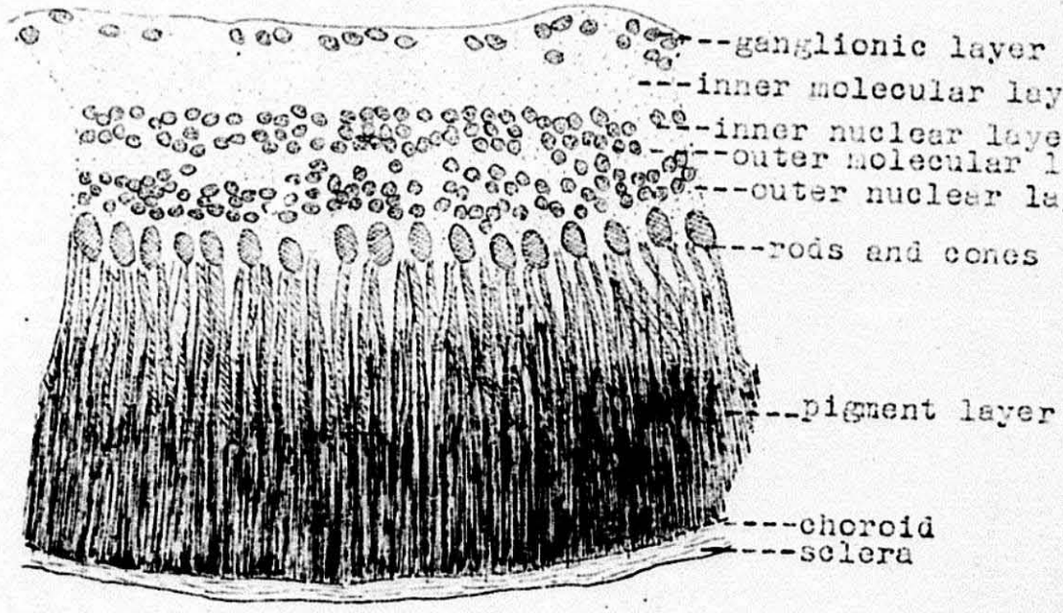
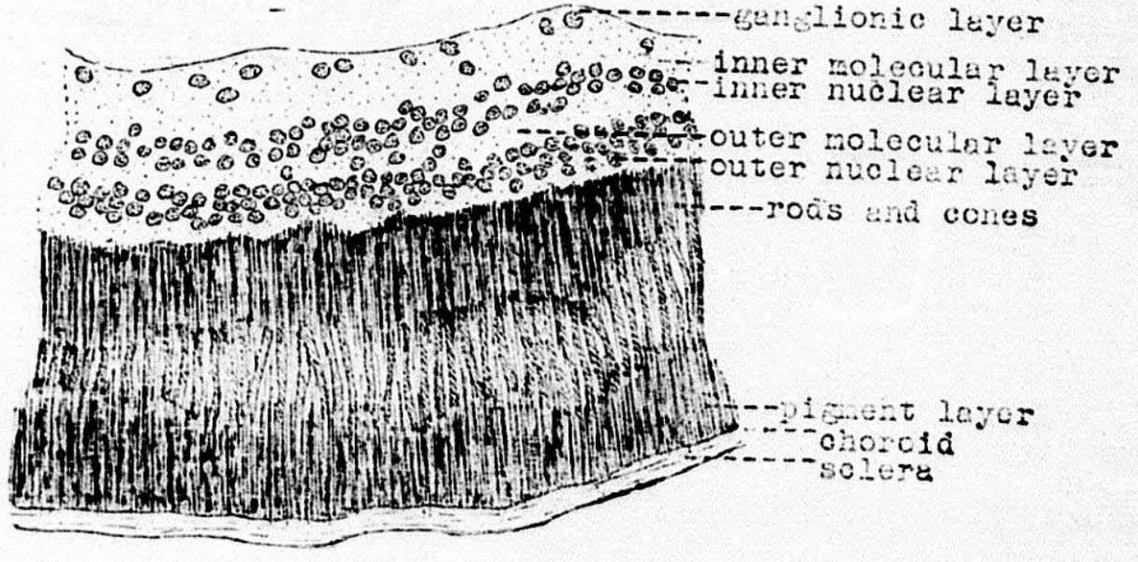


Figure 6

Cross Section of the Retina of the Eye of Forbesichthys papilliferus (x-550)



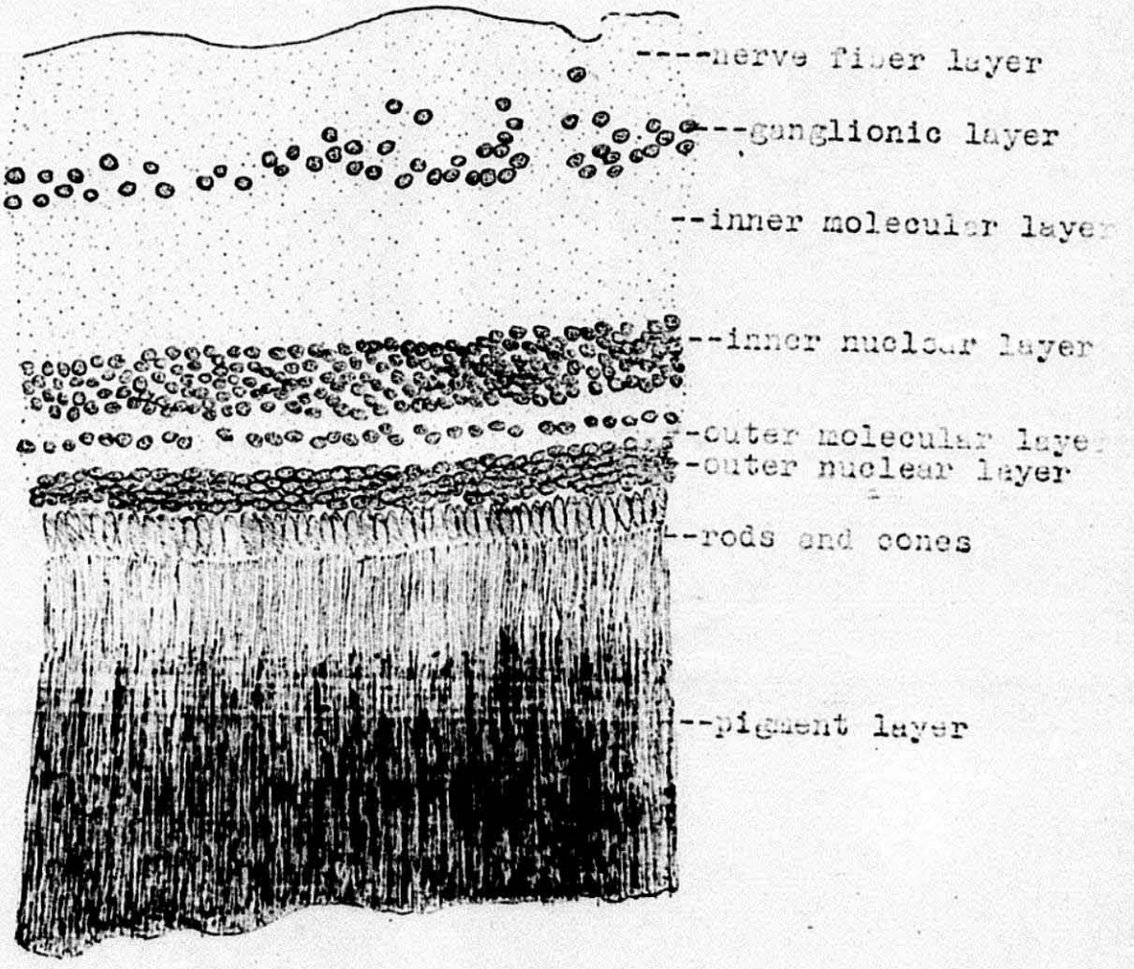
a. From an individual that has been exposed to no light



b. From an individual that has been exposed to light

Figure 7

Cross Section of the Retina of the Eye of Notropis atherinoides (x-550)



A COMPARISON OF THE EYE OF TYPHLICHTHYS SUBTERRANEOUS WITH THE EYE OF FORBESICHTHYS PAPILLIFERUS

The eye of Forbesichthys is easily seen by casual examination, but the eye of Typhlichthys cannot be seen from the surface because it is very minute, without pigment, and is deeply embedded in an orbital fat mass (Figure 8b). Eigenmann[14] says that in this species he did not find a connective tissue membrane separating the orbital fat mass from the other fatty tissues that are found in this region. In the section used in this study such a membrane can be found extending for the major part of the distance at the posterior side of this fat mass (Figure 8b). In Forbesichthys it is noticed that the skin extends over the eye continuous with the skin covering the head, but the accessory glands of the skin are absent over the eye. In Typhlichthys the skin is also found covering the eye, but with a difference in that the accessory glands are present in as great numbers as they are elsewhere on the head.

As in Forbesichthys, the sclera and choroid are very thin in Typhlichthys and are still more insignificant. The optic nerve is very indistinct in its entrance into the eye of Typhlichthys in contrast to the prominence of the optic nerve in Forbesichthys (Figures 4 and 8 a).

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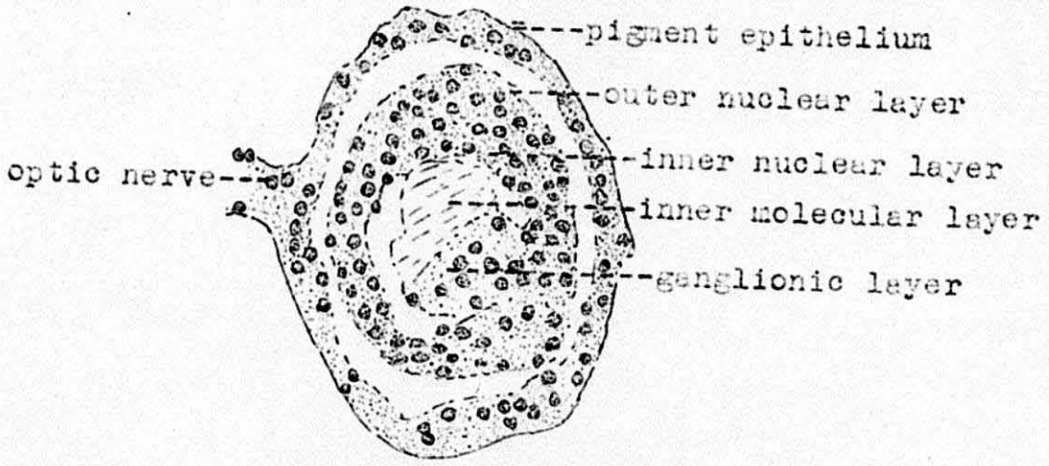
[14] Eigenman, op. cit., p. 121.

In the pigmentary layer is found the greatest divergence in the respective degenerations of the two eyes. In the case of Forbesichthys there is an excessive amount of pigment present, but no pigment granules are observed in the pigmentary layer of the Typhlichthys eye. In Forbesichthys rods and cones are present, although in reduced numbers, but in Typhlichthys nothing resembling these structures can be seen.

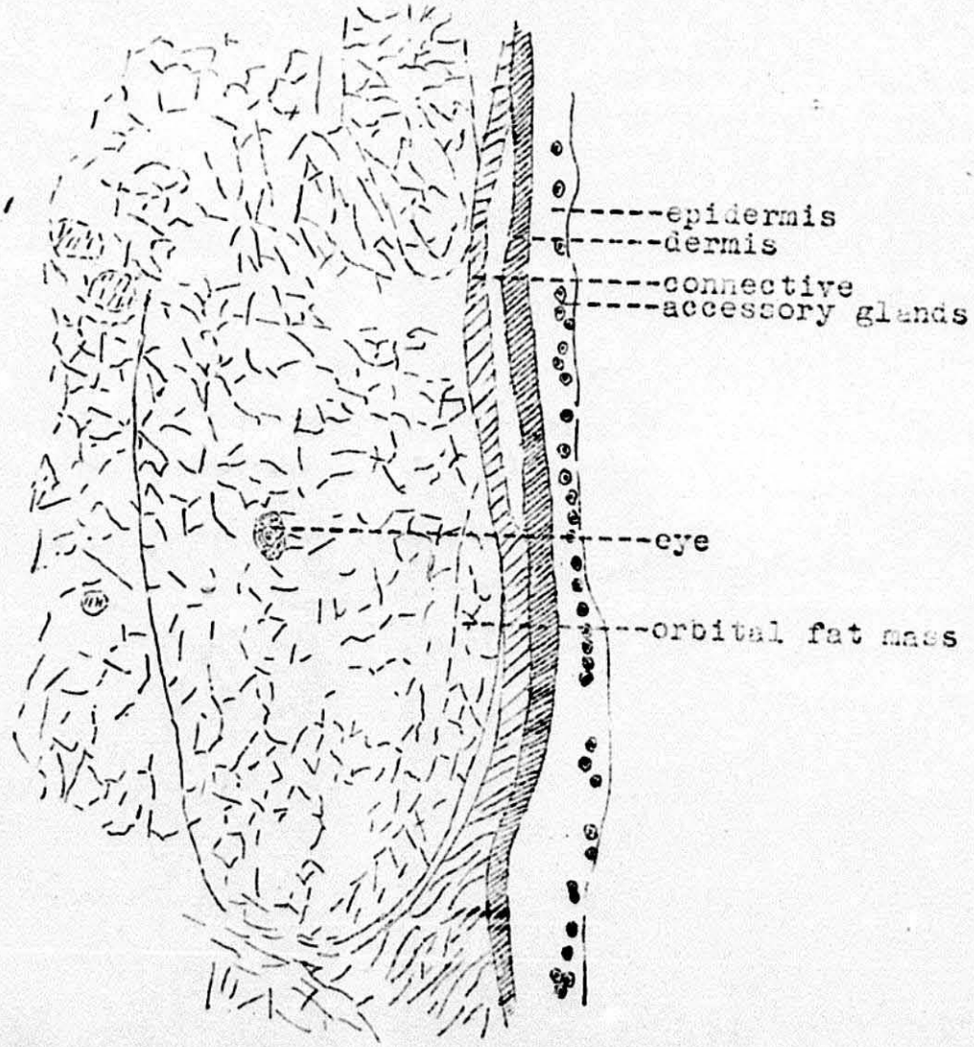
The outer and inner nuclear layers are little if any more degenerate in Typhlichthys than in Forbesichthys; in both are found the same number of layers of nuclei. Also, the outer molecular and ganglionic layers are still present with practically the same degeneracy in the blind as in the semi-blind, with the important difference that the inner surfaces of the retina touch in Typhichthys, thus throwing the ganglionic layer into one mass. As in the eye of Forbesichthys there is no nerve fiber layer in the eye of Typhlichthys.

Figure 8

Cross Sections of the Eye of Typhlichthys subterraneous



a. Eye removed from orbital fat mass (x-550)



b. Eye enclosed in orbital fat mass (x-67)

SUMMARY

The purpose of this study was to make a histological comparison of the eyes of certain cave animals and of related normal species and in this manner to observe the evidences of degeneration in the former.

It is found that the degeneration of the eye of Hadenoecus has resulted in a reduction of the size of the eye, a decrease in the number of ommatidia with an increase in the size of each, and in a very dense pigmentation of the eye, while in Cambarus pellucidus the cuticle has become thickened and chitinized, shutting out the light, and the ommatidia have apparently coalesced forming inseparable and indistinguishable bodies.

In Forbesichthys the important differences from a normal eye are: the skin forms a covering over the eye; the entire eye as well as most of its parts are greatly reduced in size; there is no nerve fiber layer; the ganglionic, inner nuclear, and outer nuclear layers have been reduced in width, but the pigmentary layer is greatly increased.

In comparing the eyes of Typhlichthys and Forbesichthys it is found that the eye of the former is very much smaller and is inclosed in an orbital fat mass; in the latter there is an increase of pigment with degeneracy, while in the former there is a total absence of pigment; there is very little more degeneracy in the layers of the retina of

Typhlichthys than of Forbesichthys; accessory glands are present in the skin covering the eye of Typhlichthys, while there are none in Forbesichthys; and while there is a reduction of rods and cones in the retina of Forbesichthys, there are probably no rods and cones in Typhlichthys.

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