No. 6. *The Eyes in Scorpions.* By G. H. Parker.*

The subject discussed in the following pages has already attracted the attention of able investigators, and were it not that the authors of the later papers have pointed out questions only partially answered, a reconsideration of the subject might appear presumptuous. It is hoped that, in discussing these questions from an embryological as well as histological standpoint, the additional evidence obtained may throw some light on their solution.

The study of the eyes in Arthropods requires so much technical skill that until very recently satisfactory work in this field has been almost impossible. Aside from papers mainly of historical interest, the most comprehensive publication for the student to-day is Grenacher's "Untersuchungen über das Sehorgan der Arthropoden." This appeared in 1879, and contained an admirable study of the eyes in spiders; it did not, however, touch upon the organs of sight in scorpions. The same year, Graber, in his paper entitled "Ueber das unicorneale Tracheaten-Auge," severely criticised Grenacher's conclusions. Grenacher, in order to answer his critic, turned his attention to the eyes in scorpions, and, in his paper on the eyes in Myriapods, published in 1880, he included a reply to Graber. Three years later a comparison of the eyes in the scorpion and king-crab was published by Lankester and Bourne. The substance of these four papers, when viewed in the light of newly discovered embryological facts, has recently been fully discussed by Mark. Previous to the appearance of Mark's paper, Patten, after having made a comparative study of the eyes in certain mollusks and arthropods, included in his general description an account of the histology of the eyes in scorpions. The five papers quoted, namely, those of Graber ('79), Grenacher ('80), Lankester and Bourne ('83), Patten ('86), and Mark ('87), are the only ones in which the histology of the eyes in scorpions is considered.

The publications on the development of the eyes are even less extensive than those on the histology. Metschnikoff ('71, p. 225), in his

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paper on the development of the scorpion, barely alludes to the eyes. Their probable method of development is described by Patten ('86, p. 672). His conclusions as far as they touch upon the eyes in scorpions are based upon inferences drawn from the method of development in other forms, not from actual observations. In a preliminary communication by Kowalevsky and Schulgin ('86, pp. 530–532) the method of development for the median eyes is described at some length. On account of incompleteness in their studies, these authors were forced to omit a description of the lateral eyes. Later in this paper, the substance of their communication will be considered.

The species of scorpions previously studied have been numerous. Graber ('79, p. 71) examined the eyes in *Scorpio europæus*, Schr., and *Buthus afer*, L. Grenacher's investigations ('80, p. 42) were made upon *Buthus afer*, *Ischnurus caudicula*, and *Lychas americanus*. *Androctonus funestus*, var. *citrinus*, Ehr., *Euscorpius italicus*, Roess. and *E. carpathicus*, were the species studied by Lankester and Bourne ('83, p. 180). The embryological researches of Kowalevsky and Schulgin were made upon *Androctonus ornatus*.

The species which I have studied belongs to the genus Centrurus.* In July and August, 1886, through Mr. C. W. Johnson, gravid females were obtained from Florida. At intervals during the following winter Mr. Johnson and Mr. F. S. Schaupp of Texas supplied me with fresh material. I am also indebted to Dr. H. A. Hagen for some alcoholic specimens from Arkansas.

In preparing the eyes for study by means of sections, the two chief difficulties encountered were the presence of chitinous lenses and dense pigment. It is difficult to cut the lens, and often this structure is in part torn away, thus destroying the surrounding tissue. In the median eyes, by careful dissection, the soft parts may be separated from the lens and cuticula, and cut without the interference of these hard structures. The separation is best accomplished after the tissues have been hardened. The method of dissection cannot be applied to the lateral eyes, for they are almost completely surrounded by chitine. In these eyes the best results were obtained by trimming off the chitine around the eyes, and cutting the retina and the lens after the removal of as much chitine as possible.

The pigment is so abundant and so dense that even the thinnest sec-

* I am unable to state what species this is. I have not succeeded in finding it described anywhere. Specimens in the collection of the Museum marked by Simon as "Centrurus sp. incog." are of the same species as those here described.

tions cannot be studied to advantage until they have been depigmented. For this purpose I know of only two classes of successful reagents, acids and strong alkalis. Grenacher has generally employed the first, Graber the second.

Of the acid reagents strong solutions are required. Lankester and Bourne ('83, p. 180) employed 5 or 10% solutions of nitric acid. In the eyes which I have studied, this mixture did not remove the pigment, even after the lapse of a week; and I was forced to use stronger and stronger grades, till 50% was reached. This mixture gives fair results, but must be made and used with much caution. A given volume of acid should be poured slowly into an equal measure of alcohol, never the reverse, and the mixture should be kept cool, otherwise the acid may attack the alcohol. In such an event the solution is rendered worthless, and, should the specimens be in it at the time, the heat generated by the reaction gives the acid such additional dissolving power that the sections are at once destroyed. A more efficient acid reagent is a mixture of equal parts hydrochloric and nitric acids. A 35% solution of this mixture in strong alcohol gives better results than the pure nitric acid at 50%, and does not so readily attack the alcohol.

Of the alkalis, weak ammonia, sodic hydrate, and potassic hydrate are most serviceable. The solids are to be preferred to the ammonia, since from them solutions of a definite strength can more easily be made. An aqueous solution of $\frac{1}{3}$ or $\frac{1}{4}$% potassic hydrate has given the most satisfactory results.

The method of using the depigmenting fluid is as follows. Unstained material is cut in paraffine; the ribbons are mounted on a slide with Schällibaum's fixative; when the sections are fixed, the paraffine is removed with turpentine; the slide with the sections is then successively washed with alcohol of 98%, 90%, 70%, and so on, till a grade homogeneous with the depigmenting fluid is reached. Into a shallow white dish filled with the depigmenting fluid the slide is now gently lowered. In a *few seconds* the pigment, dissolving, will be seen as a reddish cloud. The process is usually completed in less than a minute, and the slide is promptly transferred to a dish of clean water or alcohol and there gently rinsed. The sections are next stained by exposure to the dye in a shallow dish. After being sufficiently stained, they may be washed and mounted in glycerine, or, after the proper steps in dehydrating and clarifying, mounted in benzol-balsam or other mounting medium.

The dyes which have been found the most serviceable are some of the carmines and hæmatoxylin. The aniline dyes have almost invariably

given poor results. For general purposes Grenacher's alcoholic borax-carmine is excellent. In both embryonic and adult material Czoker's alum-cochineal gave fine nuclear outlines. In the adult eyes, the rhabdomes and the cell boundaries were most distinctly shown by Kleinenberg's hæmatoxylin. A very faint coloration with this dye gave the best results for nerve-fibres.

For the isolation of the retinal elements two maceration fluids were used. A weak solution of chromic acid, as employed by Patten ('86, pp. 736, 737), gave good results; but since the mycelium of a fungus is often developed in very dilute solutions of this reagent, it can be used only when it is carefully watched and its results are controlled by another method. It was employed in the following manner. The retina, after the removal of the lens and surrounding tissue, was placed for five or ten minutes in a $\frac{1}{5}\%$ solution. After this treatment, which slightly hardened the tissues, the first solution was replaced by a second of $\frac{1}{50}\%$. In this the retina remained for three or four days, at the end of which time the retinal cells were easily separable. The most satisfactory method of isolating the cells is to place on a slide in dilute glycerine a small portion of the macerated retina, and, having protected it with a cover-glass raised on wax feet, to gently tap the cover-glass till the cells are separated. One part of 0.2% solution of acetic acid in sea-water mixed with an equal volume of 0.04% osmic acid in sea-water, although only partially successful as a maceration fluid for the retina in scorpions, is a reliable check for the results obtained from chromic acid.

After the cells have been isolated, the abundance of pigment which they contain so obscures their contents that scarcely more than their outlines can be studied. The removal of the pigment is on the whole more successfully accomplished before than after isolation. For this process, as for simple isolation, the retina should be subjected to the action of $\frac{1}{5}\%$ chromic acid for five or ten minutes, and then transferred to a solution of $\frac{1}{3}\%$ potassic hydrate. In this the pigment dissolves, forming a reddish cloud. After about a minute the retina should be removed to distilled water, rinsed, and transferred to Grenacher's alcoholic borax-carmine. This reagent performs both the office of a maceration fluid and a dye. In from twelve to twenty-four hours the retinal cells can be isolated, and present in different regions of the retina three principal conditions. First, those from the exterior of the retina are seriously altered by the continued action of the potash; second, those from the centre of the retina remain almost unchanged, still retaining most of their pigment; third, those from an intermediate position, without being other-

wise much altered, lose most of their pigment. It is from these last that the best results were obtained.

The *eyes in scorpions* are situated on the prosomatic shield. According to their position they may be classed into two natural groups, the median and the lateral eyes. As their name implies, the median eyes are situated close to the sagittal plane. They are a little in advance of the centre of the shield, two in number, and always symmetrically placed. The lateral eyes form two isolated groups, one on either side, at the edge of the shield where its anterior border meets its lateral margin. In different genera, the number of eyes in each group varies from two to seven. Two kinds of lateral eyes have been distinguished; the larger or "principal," and the smaller or "accessory" eyes. As will be shown later, no essential difference exists between these two groups; the smaller and larger eyes are constructed on the same plan.

On account of the marked dissimilarity in the structure of the median and lateral eyes, they will be described separately.

The Median Eyes.

Grenacher ('79, p. 40) first pointed out that the vitreous and retinal layers in the eyes of spiders were separate. Graber in the same year confirmed this discovery, and showed that the median eyes of scorpions had a similar structure. These two-layered eyes were designated by Lankester and Bourne ('83, p. 195) as diplostichous, and among them were included the median eyes in scorpions. Up to this time all authors agreed that the median eyes of scorpions were two-layered.

One of the results of Locy's work ('86, p. 85), as Mark has indicated ('87, p. 71), is that in spiders the so-called diplostichous eyes are in reality three-layered, or triplostichous. The embryological facts on which this statement is based will be referred to later. For the present it is sufficient to note that an interesting question presents itself, namely, if the so-called diplostichous eyes in spiders have been shown to be triplostichous, may we not look for a similar condition in the median eyes of scorpions? Some of the reasons for believing this have already been stated by Mark ('87, pp. 55–58), but the final settlement of the question can only be reached through embryological means. It was my principal object in beginning these studies to reach a satisfactory conclusion in this matter.

Patten ('86, p. 672) had already claimed that the median eyes in

scorpions were three-layered, and that they were probably formed from a cup-like involution of ectoderm. The closure of the cup produced an optic vesicle, the deeper half of which became retina, while the more superficial half was probably represented by a structure to be described hereafter, the preretinal membrane. The details of this method of development, as will be seen later, are not confirmed by my observations; but nevertheless it remains to Patten's credit that he was the first to insist that the eyes in scorpions were three-layered, and not two-layered as had been previously held.

Metschnikoff ('71, p. 225), in his paper on the development of the scorpion, did not discuss the formation of the eye further than to claim for it a hypodermal origin. His evidence on this point can scarcely be considered as conclusive, for his studies were made from superficial views only.

The youngest material at my disposal was already somewhat advanced; but the eyes were still sufficiently undifferentiated to give adequate evidence as to their origin, and thus to afford a trustworthy basis for the interpretation of structures in the adult.

In the earliest stage examined, the eyes appear on surface view as a pair of oval, slightly pigmented areas. They are situated at the anterior end of the head, one on either side of the median line, and somewhat above the mouth. In a slightly older stage a sagittal section a little at one side of the median plane shows the region of the pigmented areas to be already composed of three layers of hypodermis (Pl. III. fig. 12, *pr r.*, *r.*, and *p r.*). The hypodermis of the prosomatic shield (*pr r.*) extends downward toward the mouth, and preserves its indifferent condition; before reaching that opening, it is folded upon itself, the deeper arm (*r.*) of the fold passing dorsally in contact with the deep face of the external portion. The ventral third of the infolded layer is as thin as the external layer of hypodermis, but the remaining two thirds are considerably thickened and contain much pigment. This thickened layer, becoming rapidly thinner at its dorsal end, is also folded upon itself to form a third layer (*p r.*), which passes ventrally next the deep face of the thickened portion, and at the point of first folding becomes continuous with the external hypodermis as it proceeds in the direction of the mouth.

This condition is practically an involution of the hypodermis. The infolded layers take the form of a flattened sac, or pocket, the open end of which is situated in the median plane between the mouth and the previously described pigmented areas. From its opening the pocket extends vertically upward, and its anterior face is closely applied to the deep surface of the permanent hypodermis.

At the stage represented in Fig. 12, the cavity of the pocket is scarcely noticeable. It should appear, of course, between the second (*r.*) and third (*p r.*) layers, and at the deep end of the infolding a trace of it is visible (*cav.*). The second and third layers, however, are quite distinct, and show no indications of fusion. The cavity of the pocket is obliterated only by its opposite walls coming in contact, so that even in Fig. 12 a pocket may be spoken of without inconsistency. In stages earlier than that given in Fig. 12, the cavity of the pocket is very noticeable, and from its external opening to its deep end it is a continuous open space.

In a *horizontal* section of the earliest stage examined, the region just above the external opening of the pocket presents the appearance of a slightly irregular tube cut crosswise (Pl. III. fig. 13). The wall of the tube is made up of a single layer of hypodermis, whose deep surface is covered with a delicate basement membrane (fig. 13, *mb.*). The cavity of the tube is continuous with the pocket of the infolding (fig. 13, *cav.*). At about half the distance from its opening to its deep end, the pocket is divided in the median plane into a right and left compartment (Pl. III. figs. 14, 15). Each compartment has the form of a sac flattened from before backwards. The sacs extend dorsally on either side of the median plane, and end blindly.

One can distinguish, then, in the invagination a common neck, and two symmetrically placed sacs which arise from it. In the sagittal section (Pl. III. fig. 12) already described, the thin ventral third of the infolded hypodermis corresponds to the neck, and the thickened dorsal two thirds to the anterior wall of the sac. The position of the sacs is indicated externally by the areas of pigment already alluded to; the sacs are destined to become the retinas. The neck soon disappears, but some time before this takes place the outer wall of each sac is thickened still more and becomes more deeply pigmented. The thickened faces form the essential part of the retina, with which, after the closure of the pocket, the posterior thinner layer fuses.

The three hypodermal layers which enter into the composition of the eye, have received special names. That portion of the permanent hypodermis which is directly external to the optic sac, constitutes the first layer. At a later stage it produces the lens, and consequently has been termed by Mark ('87, p. 77) the "lentigen." By other authors it has been generally designated as the "vitreous." Directly under the lentigen, and forming the thick external wall of the optic sac, is the second or retinal layer. Behind this layer the thin internal wall of the sac forms

the third or post-retinal layer. At the sides and blind end of the sac, the two deeper layers, the retina and post-retina, are continuous.

Granting the optic sacs to have arisen by involution, it is important to notice that of the three layers described the retinal layer is inverted; i. e. that face which before involution is external becomes after involution internal. A similar inversion in the retinas of the anterior median eyes of Agelena has already been demonstrated by Locy ('86, p. 87). In fact, at this early stage, the only striking difference between the eyes in Agelena and Centrurus is, that in the scorpion the two sacs are united by a common neck, whereas in the spider they are independent involutions. It seems scarcely possible that this is an essential difference, and I therefore believe that the median eyes of scorpions, like the eyes of spiders, arise from hypodermal involutions not immediately connected with the formation of other organs.

Since the above conclusion was arrived at, Kowalevsky and Schulgin ('86, pp. 530–532), who have studied the development of Androctonus, have published in a preliminary communication the results of their work. In their description of the nervous system the development of the eye occupies several paragraphs. On account of the absence of figures their necessarily brief account is somewhat difficult to follow, and in one place I am not sure of their meaning.

Their statements on the median eyes are substantially as follows. A pair of semicircular depressions occur in the cephalic plate. From the anterior margin of each depression a fold grows down toward the mouth. The closure of each depression by its fold gives rise to a right and left cephalic vesicle. From the region at which the mouth of each vesicle has just closed, a new fold develops. Each of the new folds opens toward the animal's mouth, and takes on the form of a pocket. The right and left pockets thus formed are the first traces of the median eyes. The authors then describe the connection of the two pockets by a common neck, and the thickening of the retinal layer, in the ventral part of which pigment is deposited.

As will be noticed, the description summarized has to do with the earliest condition in the formation of the eye. The youngest stage of my material is too advanced to permit me to make positive statements on this subject. The point about which I have had difficulty relates to the description of the brain and eye folds. In describing the formation of the brain vesicles the authors speak of an *accessory fold* (eine accessorische Falte, p. 530). When the development of the median eyes is described, they speak of a *new fold* (eine neue Falte, p. 531). Finally,

in the paragraph especially devoted to the median eye (p. 531), the following occurs: "Die Mittelaugen werden von *der gleichen Falte** gebildet, welche am Baue der Kopflappen Antheil nimmt, nur mit dem Unterschiede, dass für den Bau des Hirns die tiefen Theile der Falte verwendet werden, während die Augen Derivate der peripherischen Theile *derselben Falte** sind." After speaking of an accessory fold and a new fold in connections already alluded to, the statement that the cephalic lobe and median eye are derived from the *same* fold seems to me contradictory.

The involution of the optic sacs in spiders, as Locy has shown ('86, Pl. XI. fig. 70), takes place at a much later period than the formation of the cephalic ganglia, and to all appearances independently of the latter. Whether in scorpions the growth of these two structures is connected or not, is a question for the determination of which I have not yet secured the requisite material. Besides the statements of Kowalevsky and Schulgin, which are somewhat obscure, there remains as a guide only the analogous case in spiders; the fact that the later stages in the eyes of spiders are essentially the same as those of the scorpion, lends support to the view that the eyes in scorpions, as in spiders, arise from folds independently of those concerned in the formation of the brain.

The most noticeable changes which the pair of sacs undergoes in the further development of the eyes are, first, an obliteration of their cavities, and, second, a considerable change in position. The closure of the sacs is first effected in the region where they unite with the common neck. From this point the fusion of the retinal and post-retinal layers proceeds toward the blind end of each sac, and the neck, becoming detached from the sacs, is slowly withdrawn to form a part of the permanent hypodermis (Pl. II. fig. 11, *col.*). The line of demarcation between the retina and post-retina at the deep end of the sac is the last trace of the already obliterated cavities (Pl. II. fig. 10, *cav.*).

The change in position undergone by the eyes is correlated with a change in the form of the animal's body. In the embryo the region of the prosomatic shield occupies the anterior face of the animal, and therefore lies in a plane approximately perpendicular to the long axis. The optic sacs are situated near the centre of this region, the plane of their flattening being nearly vertical, and the lines corresponding to the future axes of the eyes being horizontal. As the animal develops, the shield assumes a position more nearly horizontal, till at length it becomes entirely so. The axes of the eyes, having shifted through an arc of 90°,

* The Italics are not in the original.

then have a vertical direction. The only planes which in both the adult and embryo cut the eyes similarly are those parallel with the sagittal plane. In a horizontal section of a young embryo the eye shows the same relation of parts as one sees in a transverse section of an adult.

As previously stated, the eye in the embryo consists of three cell layers, lentigen, retina, and post-retina. These three layers are recognizable in the adult eye, and in considering the histology of this structure the three layers will be treated in the order named.

The *lentigen*, as Grenacher ('79, p. 40) first clearly demonstrated in spiders, is distinct from the retina, and is directly continuous with the hypodermis. Graber ('79, p. 61) established the existence of a similar condition in the median eyes of scorpions.

The lentigen results from a modification of the hypodermis directly external to each optic sac. For some time after involution this hypodermis consists of undifferentiated cells, whose positions are indicated by their spherical nuclei. About the time when pigment is deposited in the retina, the hypodermis in front of each pigmented area thickens, and the outlines of its cells become visible (Pl. III. fig. 15, *pr r.*). This is the first modification in the formation of the lentigen. The thickening of the lentigen increases, and each cell assumes the form of a long pyramid, whose base rests upon a membrane between retina and lentigen, and whose slightly truncated apex reaches the forming lens (Pl. II. figs. 9 and 10). In immature eyes the sides of the lentigenous cells are perpendicular to the surface on which they rest. In a transverse section of the head of an adult (Pl. I. fig. 2), the cells are curved. About three fourths of the lentigen, extending from the median toward the lateral margin of the eye, has its cells convex toward the sagittal plane; in the lateral fourth, the cells are concave toward the sagittal plane, and in the small intermediate region they are straight (compare Lankester and Bourne, '83, pl. X. fig. 8). In a longitudinal section of an adult head (Pl. I. fig. 1), the lentigenous cells all appear perpendicular to the surface on which they rest.

The nuclei of the lentigen cells, at the first indications of a thickening in the lentigenous region, keep to its deeper parts, and form in the adult eye a continuous line close to the deeper face of the lentigen (Pl. I. fig. 2, *nl. pr r.*).

The lentigen as a whole is of glassy transparency. In young stages the hypodermis at the edge of the lens nearest the median plane shows a deposit of pigment. This pigmented region in time extends around the

edge of the lens, and, as Graber has indicated ('79, p. 62), forms in the adult a complete circle, — the iris. In the iris proper the whole of each cell contains pigment granules, while in the adjoining hypodermis the granules are scattered in small groups through the cells, and are especially abundant at their outer ends.

The *lens* owes its origin exclusively to the activity of the lentigen. As is well known, it consists of a thickening of the external cuticula. The lentigen bears the same relation to the lens as the hypodermis does to the indifferent cuticula.

In Centrurus the cuticula at most points on the body consists of three layers. The outermost, first recognized as distinct by Graber ('79, p. 59), is a thin, homogeneous, colorless layer (Pl. I. fig. 2, *ll*). Under this is a second layer of about equal thickness with the first, but usually of a deep yellow color (Pl. I. fig. 2, *ll'*). These two layers together form about one fourth the whole thickness of the cuticula. The third layer (Pl. I. fig. 2, *ll''*), embracing the remaining three fourths, is distinctly laminated. The deepest lamella of this third layer readily takes up borax-carmine. The remaining lamellæ are distinguishable from the second layer chiefly by their want of color. The cuticula is very commonly penetrated by two sets of pore-canals (Pl. I. fig. 2, *can. po.* and *can. po.'*), fine and coarse.

As the indifferent cuticula passes into the region of the lens, the following conditions are noticeable. The external hyaline layer passes unchanged either in thickness or texture over the front of the lens. The second or colored layer becomes perfectly colorless, and by its increased thickness adds to the convexity of the lens. The bulk of the lens, however, is produced by a thickening of the third layer.

Whereas in the indifferent cuticula only its deepest lamella is colored with borax-carmine, in the lens all parts below the outer homogeneous layer readily take up this dye. A similar condition has been observed in several other local thickenings in the general cuticula, especially on the ventral side of the animal. The conclusion to be drawn from these observations is, that the lens in its composition is more closely related to the last-formed cuticular lamella than it is to the older lamellæ.

The coarse pore-canals never occur in the lens. Grenacher ('79, p. 90) was unable to find fine pore-canals in the lens of Phalangium, although Leydig had previously claimed them to be found in such lenses. Graber stated ('79, p. 60) that all arthropod lenses which he had examined contained fine pore-canals. In Centrurus, notwithstanding that many sections of lenses have been examined, fine pores have never been visible, although in the adjoining cuticula they are plainly evident.

Graber ('79, p. 59) raised the question whether the lens consists of only the normal cuticular layers thickened, or contains additional layers. This is a question upon which evidence is not easily obtainable, for it deals with layers which in the lens may be of considerable thickness and yet remain so thin as to be almost imperceptible in the indifferent cuticula. The condition of the lens in young individuals offers some evidence. About the time a young scorpion leaves the mother's back, the indifferent cuticula appears to consist conclusively of what in later stages corresponds to the external hyaline layer. Careful search has failed to show any subjacent cuticula, and yet in the region of the lens a very perceptible layer of stainable cuticula is visible. This seems to indicate that the lentigen has the power of producing cuticula independently of that produced by the indifferent hypodermis. Admitting this, it seems probable that of the many lamellæ in the lens some may be peculiar to the lens itself and unrepresented in the adjacent cuticula.

The separation of the retina and lentigen, as discovered by Grenacher, was further emphasized by Graber's discovery ('79, pp. 64–67) of a limiting membrane ("praeretinale Zwischenlamella") between them. This preretinal membrane, as Graber showed, is continuous with the "sclera" and the basement membrane of the hypodermis. The explanation of these structures which is offered by the formation of the eye from a hypodermal sac, has already been discussed by Mark ('87, p. 71). He has claimed that the sclera is the basement membrane of the post-retinal layer, and that the preretinal membrane is the fused basement membranes of the lentigen and retina. The explanation given in the case of the infolded eyes of spiders applies equally well to the median eyes in scorpions.

As to the nature of the basement membrane, especially in the region of the sclera and preretinal membrane, two opposing theories have been advanced. Graber ('79, pp. 63, 64) maintains that the basement membrane including the sclera is cuticular, not cellular, and as its matrix he claims cells whose nuclei were found both by Grenacher ('79, p. 60, fig. 34) and himself ('79, p. 64, fig. 18). For the preretinal membrane Graber ('79, pp. 64, 65) also claims a cuticular nature and states that it contains no nuclei. Lankester and Bourne ('83, p. 189) describe the ommateal capsule or sclera as laminate and devoid of nuclei. Mark ('87, p. 71) believes that the basement membrane with its modifications is a cuticula derived from the basal ends of the hypodermal cells.

Opposed to these views Schimkewitsch ('84, pp. 8, 9, 11, 12) maintains that the basement membrane and its modifications are connective

tissue, and consequently cellular. His first argument is for the basement membrane of the unmodified hypodermis. He shows that this membrane passes off from the hypodermis and invests muscles. Arguing by analogy from Froriep's conclusion that the sarcolemma of striate muscles in vertebrates is connective tissue, he maintains that the investment of the muscles in spiders and the continuous basement membrane are connective tissue. This argument of itself is scarcely convincing, for we do not know that the sarcolemma in vertebrates and arthropods has necessarily the same structure. Schimkewitsch used a second argument, which was more weighty, namely, that in the envelope of the eye (sclera) nuclei had been found. But the figures which illustrate this point are, as Mark ('87, p. 70) has stated, open to criticism.

In the developing eye in Centrurus, the basement membrane appears as a thin sharply defined structure bounding the deep ends of the hypodermal cells. It is continuous over the optic nerve, and unites with the membrane investing the brain (Pl. III. fig. 16, *mb.*). In the region of the preretinal membrane it is double, one layer limiting the lentigen, the other the retina (Pl. II. fig. 9, *mb.*). This confirms Mark's theoretic conclusion. In the earliest stages studied, mesodermic nuclei occur at intervals between the two membranes, except directly over the centre of the eye, where the two membranes are in contact (Pl. III. figs. 14, 15, *nl. ms d.*). Although mesodermic nuclei occur between the two retinas, and also between the retina and the brain, they are never found within the basement membrane of the eye region, as they are within the envelope of the brain. As the two layers of the preretinal membrane unite, the mesodermic cells, instead of being included between them, migrate toward the margins of the eye, and leave the preretinal membrane when completed destitute of cellular elements. In the region of the sclera, however, mesodermic nuclei, often very much flattened and always closely applied to the outside of the membrane, are distinguishable almost up to the adult state (Pl. III. fig. 15, Pl. II. fig. 9, *nl. ms d.*). It is, therefore, nearly certain that some of the substance of this mesodermic covering enters into the formation of what is known as the "sclera." In the adult sclera, however, no nuclei are visible, and besides it is by no means certain that these mesodermic cells form a continuous investment over the basement membrane, — perhaps nothing more than a network.

The nuclei in the eye on the right of Schimkewitsch's Figure 11 (Pl. III.) are almost identical in appearance with those found in the young eyes of Centrurus, where they *appear* to occupy the middle of the membrane; they are in reality outside it, as can be readily demonstrated

when, as sometimes occurs, one finds a place where the mesodermic element with its nucleus has been loosened from the sclera, and both nucleus and sclera remain uninjured.

The nuclei which Schimkewitsch has drawn in Fig. 4 (Pl. II.) and Fig. 11 (Pl. III.) are undoubtedly mesodermic, and represent a thin tissue on the outside of the sclera.* Those in his diagramatic figure (Pl. III. fig. 4), if they are, as Schimkewitsch says, identical with those of the other two figures, are mesodermic nuclei drawn on the wrong side of the sclera; if, on the other hand, their position is correct, they are not the same nuclei as those in Figs. 4 and 11, but, as Mark ('87, p. 70) maintains, the nuclei of the post-retinal layer.

From what has been said it will be inferred that in the adult neither the sclera nor preretinal membrane contains nuclei. It is conceivable that in some cases mesodermic nuclei might be surrounded in either of these structures. Such, of course, would be exceptional. Of the twenty preretinal membranes studied in section only one has shown nuclei; but, strange as it may seem, half † of this one contained no less than fourteen. They were uniformly distributed, and always elongated parallel to the striations of the membrane. In position they were appreciably nearer the retina than the lentigen (Pl. II. fig. 8, *nl. ms d.*). This instance shows that the preretinal membrane may at least have a central layer of mesodermic tissue, although the greater part of it is ectodermic cuticula.

The great thickness of the preretinal membrane in scorpions has already been noticed by Graber ('79, p. 67). In Centrurus, as in others, it presents a fibrous laminate appearance, and in specimens treated with potassic hydrate it is slightly swollen and vacuolated.

At the edge of the preretinal membrane, where its two constituents separate, the one which passes around the retina is much thinner than the one which continues under the hypodermis. This is an indication of the relative amount of substance contributed respectively by the retina and the lentigen in the formation of the membrane. The line which would separate the lentigenous from the retinal part must be drawn somewhat nearer the retina than the lentigen. It is on this line, more-

* This limitation of the meaning of the word "sclera" seems desirable in view of the possibility that a mesodermic covering may be altogether wanting, but it is not intended as a criticism of Schimkewitsch's statement that the sclera contains nuclei; for the "sclera" as previously understood may evidently be in part mesodermic, and therefore cellular, as Schimkewitsch has claimed.

† The remaining half of this membrane was mounted on a second slide, and treated by a method which did not make its nuclei distinguishable.

over, that one would expect to find mesodermic elements if any were present, and naturally enough it is in this region that the exceptional nuclei previously referred to occur (Pl. II. fig. 8).

The fact that mesodermic tissue is incorporated in the preretinal membrane makes it highly probable that the mesodermic cells noticed on the sclera really contribute to that layer, and that the sclera is in part mesodermic and in part ectodermic. To summarize, then, the preretinal membrane, like all parts of the basement membrane, appears first as an ectodermic cuticula. Mesodermic elements may be included between its two layers, but this is the exception. The most of the membrane is in any event cuticula, of which the greater part is produced by the lentigen, the lesser by the retina.

The *retinal* and *post-retinal* layers. — The intimate connection into which these two layers enter in forming the retina is a sufficient reason for considering them together. Grenacher's ('79, pp. 39–57) researches on the eyes of arachnids led him to believe that the retina consisted of a number of similar elements, each of which contained a rod-like body, or bacillus, and a nucleus. Each element was, therefore, to be considered a single cell. He also discovered that there were two different types in the disposition of the nucleus and bacillus. Either, as in the anterior median eyes of Epeira ('79, pp. 43–45, fig. 18 A), the bacilli were in front of the nuclei, or, as in the posterior median eye (fig. 18 B), they were behind the nuclei. In the structure of the eye this interesting dimorphism, as Grenacher has termed it, has proved to be a feature of common, if not universal, occurrence with spiders.

Graber, who based his conclusions on the study of the retina in scorpions as well as spiders, opposed Grenacher's views, and claimed to have found in the median eye of Buthus ('79, pp. 71, 72) at least two nuclei to each element, — a large, basal, ganglionic nucleus, and, near the outer end of the element, a smaller apical one. The equivalent of Grenacher's bacillus lay between these. In the case of the lateral eyes * of Buthus (Pl. V. fig. 5), as well as in the anterior and posterior median eyes of Epeira (Pl. VII. figs. 25, 26), Graber figured a third small nucleus directly behind the bacillus.

This discovery, if corroborated, would invalidate Grenacher's view of dimorphism in the eyes of spiders, and one would be forced to admit that the retinal elements are multinuclear, and therefore not single cells. Grenacher's ('80, pp. 415–430) reply to Graber, at least so far as the

* When the discussion of the lateral eyes is reached, the subject of their nuclei will be considered more at length.

retina in scorpions is concerned, is based on a study of the median eyes only. He ('80, pp. 422–425) shows conclusively that for a ganglionic nucleus Graber has described and figured a body which is not a nucleus. Grenacher, after a careful search for Graber's middle and anterior nuclei, positively denies their existence. This, as Grenacher says, leaves the retinal elements in scorpions devoid of nuclei; he then proceeds to show that in the region of Graber's so-called ganglionic nucleus there exists a true nucleus essentially unlike the latter. Therefore, according to Grenacher, the retinal elements in scorpions are to be placed in the category to which the anterior median eyes of Epeira belong.*

Lankester and Bourne ('83, p. 188) agree with Grenacher that each retinal cell contains a single nucleus; but they also maintain that Graber's anterior and middle nuclei are to be found in the retina. These nuclei, however, do not belong to the retinal elements proper, but to small intrusive pigment cells.

The composition of the adult retina in Centrurus has been studied by means of sections and maceration preparations. A horizontal section of an adult retina (Pl. I. fig. 1) presents a concavo-convex outline; a portion of the convex face occupies the median plane of the body, and is fused to the corresponding part of the opposite retina. The concave face is limited by the preretinal membrane. The concave region is composed of a series of deeply pigmented club-shaped masses, which taper off into the lighter middle region. Behind the lighter area, which occupies fully half of the thickness of the retina, many of the bands and lines of pigment become thickened into irregular dark blotches, which make up a poorly defined mottled area. This soon merges in the median plane into the retina of the opposite side, and elsewhere into a densely pigmented zone limited behind by the sclera. This pigmented zone can be traced around the side of the retina till at the edge of the latter it becomes confluent with the pigmented area first mentioned.

After removing the pigment and staining the section in Grenacher's alcoholic borax-carmine, the outermost pigmented region (Pl. I. fig. 2) is seen to consist of a very granular substance, in which cell-walls can be traced from the preretinal membrane backward to the pointed, rod-like structures, or rhabdomes. The latter cause the lightness of the large

* Graber ('79, p. 69) designated those elements in which the nuclei were behind the bacillus as "post-bacillar"; those in which the nucleus was in front of the bacillus, "pre-bacillar." Mark ('87, p. 73) has proposed for these terms pre- and post-nuclear, respectively. Since these present advantages over the older terms, they will be adopted in the following pages.

middle area. This granular substance (Pl. II. fig. 4) extends down between the rhabdomes, and merges with a less regularly granular substance behind. The rhabdomes at their deep ends merge imperceptibly into this irregularly granular substance. In the region where the deep ends of the rhabdomes disappear, large slightly granular nuclei occur (Fig. 4, *nl. r.*). All the nuclei in the retina of Centrurus are found in what has been described in the pigmented eye as the mottled area. The nuclei nearest the concave surface of the retina are the largest, and, as has been previously mentioned, are slightly granular. Behind these, in the middle of the nuclear region, smaller oval nuclei (Fig. 4, *nl. pig.*) occur. Here also nerve fibres are abundant, and those curious bodies mistaken by Graber for nuclei and designated by Lankester and Bourne under the name of phaospheres (Fig. 4, *pha sp.*). The deepest nuclei (Fig. 4, *nl. p r.*) in the retina are flattened, and more deeply colored than the rest. They lie upon the internal surface of the densely pigmented zone, previously mentioned, and form a line of separation between that zone and the coarsely granular substance in front. The substance of the deepest zone is almost identical in character with that of the outer portion of the retina, and its granular appearance, like that of the external layer, is largely due to the colorless remains of pigment granules. The smaller anterior and median nuclei of Graber do not exist in Centrurus, either *in* the retinal cells or *between* them, as claimed by Lankester and Bourne ('83, pp. 192, 193). The latter authors state ('83, p. 192) that the reason Grenacher overlooked these nuclei was that the acid which he used to remove the pigment destroyed them. In the case of Centrurus sections depigmented with the 35% mixture of nitric and hydrochloric acids, with $\frac{1}{3}$% solution of potassic hydrate, or *unaffected* by depigmenting reagents, but colored with borax-carmine and cut three micromillimeters thick, show no trace whatever of anterior or middle nuclei. The examination of fresh material and of maceration preparations has given the same results. Moreover, since the nuclei in the brain after treatment with $\frac{1}{3}$% potassic hydrate are not to be distinguished from those in the same organ unaffected by that reagent, it seems scarcely possible that the same reagent could *destroy* nuclei in the retina. It is therefore safe to conclude that at least in the retina of Centrurus no nuclei exist external to the band of larger nuclei already described.

Having shown that the retinal nuclei are limited to the deeper region of the retina, and that these nuclei are of three principal types, we are now prepared to inquire into the cellular composition of the retina. This is best done by means of isolation preparations. In the retina

there are at least three kinds of cells. Two can be readily isolated; the third has been studied only in sections.

The retina extending from the line of deepest flattened nuclei to its outer margin breaks up into two very distinct forms of cells, — retinal or nerve-end cells, as Lankester and Bourne ('83, p. 182) have called them, and pigment cells. The retinal cells (Pl. II. fig. 5) are elongated and rounded at their outer ends; they terminate below in nerve fibres. From the rounded external end the calibre is uniform till the region of the rhabdomeres is reached. Here the cells increase in diameter, and then continue for some distance uniform in size. Finally, each cell, enlarging slightly at its deep end, rapidly tapers into a nerve fibre. Throughout its whole extent the retinal cell contains pigment, which is principally concentrated, however, at its rounded outer end.

The pigment cells (Pl. II. fig. 6) at their anterior ends, like the pigmented tops of the retinal cells, abut against the preretinal membrane. From this they pass backward, and in the region of the rhabdome, where the retinal cells enlarge, they contract to thin fibres, which, after the rhabdome has been passed, again expand into irregular pigment sacs at the deep part of the retina. When isolated, they present the appearance (Pl. II. figs. 6, 7) of two sacs of pigment connected by a slender rigid fibre.

The large round or slightly oval nuclei have been identified as belonging to the retinal cells (Pl. II. fig. 7), and the smaller oval nuclei occupy the deep swollen ends of the pigment cells. It is possible that some of the pigment cells may not be prolonged in front of the rhabdomes, and therefore not possess anterior sacs; but I have never been able to discover such. The filamentous middle portion connecting the two extremities of the long pigment cells is so constant and characteristic in maceration preparations, that pigment cells which do not extend to the front of the retina must form the exception, if in fact they exist at all.

Another method employed in studying the cells of the retina, and one especially instructive for the region of the anterior zone, was by the aid of sections perpendicular to the retinal cells. The retina has the form of a shallow bowl; consequently in sections perpendicular to its axis the deeper portions of the retina will lie at the periphery of the section, and its centre will be the region nearest the preretinal membrane.

Figure 3 represents a portion of a retinal section whose centre, and consequently highest portion, is toward the right, and whose periphery or deeper portion is toward the left. The relatively higher portion of the

section is at that point below the preretinal membrane where the rhabdomeres diminish into simple cell boundaries, and the five cells which make a single group are here easily distinguishable. To the left the rhabdomes are much larger, and have assumed their usual outlines. The rhabdomes have increased in size at the expense of the cells. It will be noticed that each of the cells present belongs to some group of rhabdomeres, and consequently *all* are retinal cells.

The section (Fig. 3, *a*) which was the next external to the one just described shows practically the same condition, except that, being slightly nearer the front of the retina, the rhabdomes are not quite so distinct, especially in the extreme right, where in one or two groups scarcely any trace of the rhabdomeres can be seen. Nevertheless, all the cells of the former section can be identified, and moreover between the groups in the upper right hand corner an additional cell is noticeable. This cell, which by a comparison of the two sections is seen to be a supernumerary element, is not a retinal (nerve-end) cell; but since in maceration preparations the outer expanded ends of the pigment cells were always found near the preretinal membrane, there is every reason for considering this such a cell. Moreover, when sections nearer and nearer the preretinal membrane are examined, these additional cells become more numerous, until finally they are with difficulty distinguished from the retinal cells. The anterior sacs of the pigment cells, then, can be demonstrated on sections as well as by maceration.

The rhabdomes never reach the anterior face of the retina, but fall short of it by the thickness of several sections. This space between the rhabdomes and preretinal membrane corresponds to the anterior zone of deep pigmentation seen in longitudinal sections. The pigment in this region is so dense that the outlines of the cells can be traced only with difficulty.

The phaospheres, as Lankester and Bourne ('83, pp. 185, 186) have called the curious bodies mistaken by Graber for nuclei, are abundant in the nuclear zone of the retina (Pl. II. fig. 4, *pha sp.*). They are as small as the oval nuclei around them, and often smaller, but differ from these in containing usually one, and sometimes two, three, or even four highly refractive dots. Lankester and Bourne state that they are usually behind the nucleus of the retinal cell. In isolated cells I have never succeeded in satisfactorily identifying them, therefore in Centrurus I cannot feel sure of their position. In one section only has a phaosphere occurred in a prenuclear position; in all others they have been strictly behind the neighboring nuclei.

As to their nature two suggestions have been made. Lankester and Bourne ('83, pp. 185, 186) imply that they are of the nature of rhabdomes; in this light they are further discussed by Mark ('87, p. 93). Patten ('86, p. 684) is inclined to look upon them as degenerate nuclei. In Centrurus the phaospheres, being of nearly the same size as the nuclei, present less favorable opportunities for study than in those scorpions where they are much larger. Those in Centrurus stain in much the same way that the surrounding nuclei do, and in fact are to be distinguished from these mainly through their highly refractive dots. In many cases, however, these dots are not well marked, and it is then difficult to determine whether a given body is a nucleus or a phaosphere. The nuclei are constantly oval in form; the phaospheres are more or less irregular in outline. This irregularity, however, is only noted in phaospheres which have very refractive dots, and never in those which seem to be transitional in form between nucleus and phaosphere.

The third type of cell occurs as a single layer of pavement-like elements at the back of the retina (Pl. II. fig. 4). It has been correctly stated by Graber ('79, p. 84) that this pavement layer is the matrix of the sclera. Lankester and Bourne ('83, p. 192, pl. X. fig. 8, *p*) have also observed it in Androctonus, where the cells are relatively much smaller than in Centrurus. In sections of Centrurus the outlines of these cells are visible, though faint; in form they are broadly columnar. Their nuclei, as previously stated, take a deep color, are flattened, and are always located at the end of the cell farthest from the sclera.

This deep layer of cells envelops the convex face of the retina, passing up on its sides till it reaches the edge of the retinal cup (Lankester and Bourne, '83, pl. X. fig. 8, *p*). Here, as Graber has shown ('79, Pl. V. fig. 14), it becomes continuous with the retinal layer. Only in the region where the retinas of the two median eyes fuse does this basement layer fail to cover the deep surface of the retina proper.

The principal histological changes which take place during the development of the eye relate to nuclei, the pigment, and the optic nerve. The formation of the optic sacs, the disappearance of their common neck, and the fusion of the post-retinal with the retinal layer has already been described.

While the eye is yet an ectodermic pocket (Pl. III. figs. 12–15), the *nuclei* are distributed through the whole of the thickened retinal layer; in the post-retina they form a single row. At this stage the nuclei of the different cells are indistinguishable. Their outlines are round or

slightly oval; their contents, except for a few sharply marked granules, are very transparent. Somewhat later, but before the optic sacs have closed, they are less abundant near the front face of the retina, but otherwise no special arrangement is as yet evident.

The rhabdomeres play an important part in the future distribution of the nuclei. They first appear as light streaks, which, beginning close to the preretinal membrane, gradually extend backward. With the extension of the rhabdomeres, the nuclei recede to the deeper parts of the eye, and with very few exceptions* never occupy a place in front of the rhabdomeres.

At about the time the young scorpion is born, the cavity of the optic sac having disappeared, the nuclei of the retinal layer are found to have arranged themselves in two groups. In axial sections of the eye (Pl. II. fig. 9) one group forms an irregular line at the base of the rhabdomeres, the other a broad band in the deeper part of the eye. The space separating these two groups is considerable, and contains only a few scattered nuclei. The deeper nuclei in the broad band, i. e. those nearer the sclera, are to be referred to the post-retinal layer.

At this stage the nuclei are still undifferentiated, and even after the young scorpion has left the mother's back it is some time before one can recognize differences between them. It is only in the fully developed adult that a marked differentiation is reached. By this time the nuclei of the retinal cells have become slightly more homogeneous (Pl. II. fig. 4, *nl. r.*) and somewhat reduced in size. The nuclei of the post-retinal cells have become much flattened and stain more deeply. These, as well as the nuclei of the pigment cells, are reduced in size, and have become more homogeneous. The columnar "matrix" cells previously described, and to which these flattened nuclei belong, constitute the post-retina; and their transition at the rim of the optic cup into the retinal layer is only a preservation of the relation they have sustained to that layer from the time of the original involution. This interpretation of the "matrix" cells has already been maintained by Mark ('87, p. 56).

The phaospheres appear at a very late date. In young scorpions which have left the mother's back no trace of phaospheres was discoverable, and it was only in those eyes in which the three forms of nuclei were already distinguishable that the structures were noticed. The time of their appearance — a period of nuclear differentiation — is evidence in favor of their nuclear origin.

* In only one instance out of the many in which developing eyes have been examined has a nucleus remained in a prebacillar position

That the retinal cells and the post-retinal cells, as well as the pigment cells, *contain* pigment, has already been stated. Lankester and Bourne ('83, p. 194) were somewhat in doubt whether the retinal cells in the median eyes of scorpions contained any pigment. Patten ('86, p. 728) believes that they do not contain pigment. The evidence furnished by sections perpendicular to the length of the cells (Pl. II. fig. 3, *gra. pig.*) is, I think, conclusive.

Under the head of "intrusive pigmentary connective tissue," Lankester and Bourne ('83, p. 191) include the pigment cells in Androctonus, and, with less confidence, their so-called intracapsular pavement. The pigment cells proper are considered by them as of mesodermic origin. This they defend by several arguments, but admit that their reasons cannot be regarded as offering a sufficient basis for a final conclusion.

During early stages in the development of Centrurus, mesodermic tissue is often seen making its way into the substance of the brain, and its appearance is characteristic. It penetrates into the nervous system as thin continuous sheets of cells, which in cross-section appear as lines. During the development of the eye no such appearances have been encountered, and it is fair to conclude that mesodermic tissue has not gained access to the eye by the same means that it has to the brain.

Lankester and Bourne suggest that it may have entered the eye capsule at the opening for the optic nerve; but the capsule (sclera) is reflected on to the optic nerve, and, even admitting that mesodermic tissue did gain access here or from the brain, where it undoubtedly exists, one would naturally expect the pigment to appear first in the region of the optic nerve. Contrary to this, as Kowalevsky and Schulgin ('86, p. 531) have shown, — and my own observations confirm theirs, — pigment first appears in the front of the retina on its ventral — afterward becoming its anterior — edge, at a point farthest from that where the optic nerve joins the retina. Taking all the evidence into account, it seems that the nerve-end cells, the intracapsular pavement cells (post-retina), and the pigment cells are alike ectodermic, and that the retina contains no tissue that can be referred to a mesodermic source.

The *optic nerve* in the adult scorpion joins the eye at a point on the under side of the eye capsule. From this point bundles of fibres pass anteriorly through the base of the retina in front of the post-retinal layer, and from small secondary bundles are given off single fibres which join the *bases* of the retinal cells.

In the youngest stages studied, the optic nerve was already formed, and its fibres (Pl. III. fig. 17, *n. fbr.*) passed over the front of the retina,

apparently connecting with the *external* ends of the retinal cells. At least the fibres disappear here, and cannot be traced into the retina. The optic nerve (Pl. III. fig. 16, *n. opt.*) at this stage emerges from the retina by passing over the rim of the optic cup in a region corresponding to the outer edge of the pocket. The region extends from the dorsal margin half-way down toward the ventral margin of the cup.

During the further development there is but little change in the point of exit for the optic nerve. It simply shifts from its posterior lateral position in the embryo, to a posterior ventral one in the adult. The change in the course of the intracapsular fibres is much more significant.

There is reason to believe that in the embryo the nerve fibres are attached to the *external* ends of the retinal cells (Figs. 14–17). In the adult they certainly emerge from the *deep* ends of these cells. The steps which connect the earliest with the final condition consist of a migration of the point of attachment for the nerve fibre from the external end of the cell to the deep end. The migration of the fibres takes place at the same time that the nuclei recede into the deeper parts of the eye, and seems to be controlled by the same influence, namely, the growth of the rhabdomeres. An analogous condition in the eyes of Agelena has been described by Mark ('87, pp. 84–87). There is, however, a difference; the nerve fibres in Agelena never come to have a post-nuclear attachment to the retinal cell, whereas in the figures of Graber and those of Lankester and Bourne, and certainly in the retina of Centrurus, the nerve fibres emerge from the cell behind the nucleus. Mark ('87, pp. 91, 92) has claimed for these facts an important significance, and concludes that they point to a functional condition of the retina before involution. The bearing of this will be further considered under the head of theoretic conclusions.

The Lateral Eyes.

The lateral eyes in scorpions, although in some respects more interesting than the median eyes, have on the whole received less attention. Grenacher in his two papers previously quoted makes no mention of them; for our present knowledge of their structure we are indebted to the researches of Graber ('79) and of Lankester and Bourne ('83). The results of these inquiries are in so far unsatisfactory that in several essential points they are directly opposed to each other. The points upon which there is a conflict of opinion are (1) the origin of the retina, and (2) the presence or absence of a lentigen.

On the question of the origin of the retina in arthropods, two unreconcilable opinions have been held. Some authors have maintained that the retina was an outgrowth from the brain, and others that it was a modification of the hypodermis. Graber may be taken as a representative of the former school, Grenacher of the latter. The evidence upon which they based their opinions was derived in the two cases from quite different kinds of eyes. Grenacher believed, since he had found in eyes like those of the larval Dytiscus a retina which was continuous with the hypodermis, that therefore the retina in the more complex eyes was derived from the same hypodermal source. Graber, arguing from those eyes in which the retina is separated from the hypodermis by a preretinal membrane, maintained that the retina is an outgrowth from the brain, and not derived from the hypodermis. Such an eye as the larval eye of Dytiscus would, even in the absence of other evidence, seriously weaken the force of Graber's argument. As an explanation of such structures, Graber is inclined to think that the larval eye of Dytiscus really possesses a preretinal membrane, with hypodermis in front of it; but that, on account of the thinness of this structure, Grenacher has overlooked it. In other words, Graber considers the arthropod ocellus as a two-layered structure, the outer layer of which is hypodermal, and the inner layer, or retina, neural in its origin.

In Graber's figures and description of the lateral eye in scorpions, the two essential parts of the median eyes, the lentigen and retina, are represented; but the lentigen, unlike that of the median eyes, is reduced to a very thin layer of cells. This is perfectly consistent with Graber's theory; but whether it represents the actual structure of the eye or not is questionable, since Lankester and Bourne ('83, pp. 182 and 187) expressly state that the lateral eye of Androctonus is composed of a single layer of cells, — a thickening of the superficial hypodermis, — and claim that Graber is incorrect in describing a separate layer concerned in the formation of the lens.

Since the publication of these papers, Locy's discovery of the method of development in spiders' eyes has firmly established the hypodermal origin of the retina. It has also offered a perfectly rational explanation for the presence of Graber's preretinal membrane. Thus the hypothesis of the neural origin of the retina is no longer tenable.

The presence or absence of a *lentigen* and preretinal membrane is, as Mark ('87, p. 55) has stated, important in determining whether a given eye has been formed by involution with inversion or not. Although the hypodermal nature of the retinas in both the lateral and median eyes of

scorpions is unquestionable, yet whether the lateral eyes, like the median, have been formed by an involution with inversion, or whether their formation is accompanied simply by a thickening and more or less extensive depression in the hypodermis, is still an open question. Graber's figure ('79, Pl. V. fig. 4), with its preretinal membrane and lentigen, would indicate that the eye arose by involution. Lankester and Bourne's figures ('83, Pl. X. figs. 2, 3, and 4), in which these structures are absent, would favor the explanation that the eye is only a hypodermal thickening.

The position of the lateral eyes in scorpions has already been described. In the adult Centrurus each group consists of four eyes, three of which are large and are designated by systematists as "principal" eyes, and the fourth is small and known as an "accessory" eye. The larger eyes are arranged in a horizontal line at the antero-lateral angle of the shield; the small eye is above a point midway between the posterior and middle larger eyes.

A vertical section through the axis of one of the larger eyes (Pl. III. fig. 18) shows at the surface a strongly convex lens (*lns.*) beneath which a relatively small retina (*r.*) appears. The outline of the latter is marked by the basement membrane (*mb.*), and on its dorsal and ventral edges it is seen to be continuous with the hypodermis (*hd.*). In an eye from which the pigment has not yet been removed, the whole retina is intensely black. The pigment extends up to the margin of the lens, as figured by Lankester and Bourne ('83, Pl. X. fig. 1), and spreads out above and below into the adjacent hypodermis. It is far more abundant in the dorsal hypodermis than in the ventral.

The *lens* in the adult eye consists of essentially the same parts as in the median eye, and contains no pore-canals. Its substance except the front hyaline layer is stained throughout by alcoholic borax-carmine. In young individuals (Pl. III. fig. 21) the lenses of the lateral eyes, even better than those of the median eyes, show a formation of stainable cuticula (*ll''*) under the hyaline layer (*ll*) before a similar secretion has taken place from the general hypodermis.

In the adult eye not the least appearance of a *lentigen* or preretinal membrane is to be found, even after careful depigmentation. The fact that the pigmentiferous tissue extends up to the lens is of itself suggestive of the absence of a lentigen, for in ocelli generally this layer is remarkable for its transparency. When to this is added the fact, that no nuclei exist in the front part of the eye, and that in no place does the basement membrane extend as a preretinal membrane across the front of

the eye, the evidence against the presence of a lentigen is apparently complete.

The composition of the *retina* in the lateral eyes is much more difficult to study than in the median eyes. This is due in part to the small size of the lateral retinas, and in part to their almost complete chitinous investment. To make isolation preparations is wellnigh impossible, by far the best results being obtained from the study of sections.

Graber ('79, Pl. V. fig. 5), believing that the composition of the median and lateral retinas was essentially the same, has figured in the lateral eyes of Scorpio retinal elements with three nuclei. Moreover, the retinal elements are grouped, as in the the median eyes, in fives (Pl. V. fig. 8).

Lankester and Bourne ('83, pp. 181–187) claim that the retina consists of unicellular elements, or nerve-end cells, as they call them, and of indifferent cells. The indifferent cells occur both *between* the nerve-end or retinal cells, as "interneural cells," and *around* the edge of the retina, as "perineural cells." The indifferent cells all contain pigment; the retinal cells, in their opinion, are probably pigmented on their peripheries.

In Centrurus the nuclei (Pl. III. fig. 18, *nl. r.* and *nl. pi n.*), as in the median retinas, are limited to the deeper portion and to the periphery of the eye, and Graber's anterior and median nuclei are not present. The nuclei (*nl. r.*) belonging to the deep portion of the retina are slightly larger than those (*nl. pi n.*) on the periphery, and very uniform in size. The fact that in this part of the retina there is only one form of nucleus leads to the conclusion that the retina in Centrurus is composed of only one kind of cells, and that here the interneural cells described by Lankester and Bourne do not exist.

Sections perpendicular to the axis of this retina show immediately under the lens the sharp outlines of cells which deeper in the retina have their walls thickened into rhabdomeres. No additional cells, like those in the median eyes, appear in the outermost sections of the retina, and therefore the interneural cells, if present, must be limited to the deeper portion of the retina. The fact that there is no difference in the nuclei of this region leads me to believe that interneural cells are entirely wanting. In Centrurus the retinal cells (Pl. III. fig. 19) show no tendency to be arranged in groups of five, and the rhabdomeric thickening (*rhb m.*) takes place on all sides of the cell. This is particularly noticeable in examining the region nearest the lens. In the outermost sections the cells are sharply outlined and their walls are very thin. In the second or third section from the lens, the walls suddenly become

thicker around the whole circumference of the cell, and take on a lustrous appearance. With Kleinenberg's hæmatoxylin the substance of the rhabdomeres can be colored, and the line of demarcation between products of the separate cells can be distinguished. This structural condition can be traced to the deeper part of the retina, where the cell outlines become indistinct, the rhabdomeres incasing each retinal cell for a half or two thirds of its length.

Pigment (Pl. III. fig. 19, *gra. pig.*) is uniformly distributed through the retinal cells, as well as the perineural cells to be described later. This is best seen in sections perpendicular to the axis of the eye. Phaospheres, although present in the median eyes, do not occur in the lateral eyes. The optic nerve (Pl. III. fig. 18, *n. opt.*) emerges from the deep end of the retina, and its course is so oblique to the axis of the eye that a section which shows the retina well seldom shows much of the optic nerve.

The perineural cells surround the depressed retinal area, and their attenuated ends, especially on the ventral side of the eye, often reach out, even in the adult condition, in front of the retinal cells themselves (Pl. III. fig. 18). The positions that the nuclei occupy in the ventral portion of the perineural ring suggest that these cells may at one time have extended far enough to have completely covered the retina, and the fact that in young individuals (Pl. III. fig. 21) the retina is largely covered by the perineural cells indicates that in all probability the lens is the product of these cells. In that event the perineural cells are the physiological equivalent of the lentigen. The peripheral margin of this lentigenous ring passes by insensible gradations into the surrounding hypodermis.

The *development of the lateral eyes* is referred to by Kowalevsky and Schulgin ('86, p. 531) as follows: "Die Seitenaugen entwickeln sich unabhängig von den Mittelaugen, und bei ihrer Ausbildung nimmt die Vertiefung der obern Schicht der Kopfplatte Antheil. Die Einzelheiten dieses Vorganges sind von uns noch nicht bearbeitet." This is the only reference which they or other students have made to the development of the lateral eyes.

The "ocular areas," as Lankester and Bourne designate the regions occupied by the lateral eyes, appear in Centrurus as pigmented tracts of hypodermis on either side of the head and a little below and behind the median optic sacs. Horizontal sections of the embryo cut these areas in the most advantageous way for a general study; they show that the whole ocular area is produced by a thickening of the hypodermis.

The horizontal sections shown in Figs. 22–27 (Pl. IV.) are arranged to represent the characteristic features of the ocular area of the *left* side of the head, as one would observe it in passing from a dorsal to a more ventral position. Calling that of Fig. 22 the first section, they are the 1st, 3d, 6th, 13th, 16th, and 21st sections in a series from a single animal. Fig. 22 represents the hypodermis directly above the eyes and at the edge of the ocular area. The extent of this area is indicated by the thickened region. Two sections below this (Fig. 23) the ocular area is more extended, and shows a single simple depression (No. 1). It will be observed that the band of nuclei indicates a more marked depression even than the outline of the hypodermis itself. This simple depression in the hypodermis indicates the position of a lateral eye. The cells which compose the wall of the cup are wedge-shaped; their nuclei are below the middle of the cells, and those cells which occupy the central portion of the depression are so attenuated at their free ends as scarcely to reach the surface. The basement membrane (*mb.*) closely invests the deep face of this structure, as it does any ordinary hypodermal thickening. The sixth section, Fig. 24, exhibits a region in which the ocular area is greatly thickened, but it shows no depressions, and the nuclei extend very near to the surface. Fig. 25, seven sections deeper than Fig. 24, presents four cup-shaped depressions (Nos. 2, 3, 4, 5), each essentially like the depression previously described. The two central depressions (Nos. 3, 4) are the largest; next in size is the anterior one (No. 2), and smallest of all is the posterior one (No. 5). As in the case of depression No. 1 (Fig. 23) the band of nuclei in the region of each depression forms a much deeper cup than the outer surface of the hypodermis. The basement membrane (*mb.*), as in Fig. 23, invests only the deep surface of each hypodermal cup. From this plane ventrally the hypodermis gradually becomes thinner, and at the extreme edge of the dorsal shield the indifferent hypodermis is reached. (Compare Figs. 18, 20.)

The five depressions just described are early stages in the development of the lateral eyes. In the adult Centrurus only four eyes are present. Of the five depressions seen in the embryo the most posterior (No. 5) of the ventral four disappears, and three remaining form the "principal" lateral eyes. The fourth or "accessory" eye arises from the dorsal depression (No. 1), which, even in the embryo, occupies a position above the space between the second and third depressions (Nos. 3 and 4) of the lower row. The presence in the embryo of a rudimentary fifth eye is interesting, in view of the fact that there are five eyes in the *adult* of Androctonus, as has been shown by Lankester and Bourne. It is proba-

ble that one of these five eyes in Androctonus is represented by the rudimentary eye in Centrurus, although this can be definitely settled only by a careful comparison.

In the embryo the fibres of the optic nerve (*n. opt.*) emerge from the *base* of the retina (Pl. IV. fig. 25). This, moreover, is their position throughout the life of the scorpion (Pl. III. fig. 18).

The further changes which affect the form of the optic depressions before they become matured eyes are unessential modifications of the already established plan. At the time of the production of a lens (Pl. III. fig. 21) the lentigenous (perineural) cells stretch over from all sides and overtop the retina. The external ends of the lentigenous cells contain no pigment (Pl. III. fig. 20).

The basement membrane, from the time when the depressions are formed till the eye is completed, covers the modified hypodermis as it covers a simple hypodermal thickening. There is never any indication of a preretinal membrane, nor, from the structure of the eye, should we expect to find one. In all stages the basement membrane presents the appearance of a single delicate lamella, and at no time is there an additional sheet of mesodermic tissue, as in the median eyes.

The evidence derived from the anatomy of the adult eye, the absence of a preretinal membrane and permanent lentigen, and the continuity of the retina with the hypodermis, together with the facts derived from a study of the development of the eye, show conclusively that in scorpions the retina of the lateral eye is what Lankester and Bourne have called monostichous, and that this retina, unlike that of the median eyes, is normal, not inverted.

Theoretic Conclusions.

The striking similarity in the structure and development of the median eyes in scorpions and the anterior median eyes in spiders has already been indicated. In both cases the retina by a process of involution has become inverted. The question whether the retina was functional during the phylogenetic involution of the eye is, as Mark has maintained, answered in the affirmative by the phases noted in the development of the optic nerve. At least, the fact that the fibres of the optic nerve are at first attached to the morphologically deep ends of the retinal cells, and only at a later date come to emerge from the opposite end, is most easily explainable on the supposition that the retina was functional before involution. The primitive eye would, then, consist of a single layer of retinal

cells from the deep ends of which the nerve fibres emerge. Admitting that in the ancestral eye the rhabdomeres were in their usual position, namely, at the outer end of each retinal cell, an inversion of this retina would not only place the optic fibres on the front face of the retina, but the rhabdomeres would come to occupy the deep ends of the cells. The prenuclear rhabdomeres of a normal retina would, therefore, be homologous with the postnuclear rhabdomeres of an inverted retina. The prenuclear rhabdomeres of the median eyes in scorpions must, then, be secondary structures, developed in such a way as to replace functionally the older postnuclear structures.*

The phaospheres, as Mark ('87, p. 93) has already suggested, may represent the remains of postnuclear rhabdomeres. These are to be regarded, then, in the nature of disappearing organs, and the fact that in some species of scorpions they are present, while in others they are absent, would favor this view. As Mark has stated, the phaospheres, if they represent postnuclear rhabdomeres, should be found only in eyes with inverted retinas. Lankester and Bourne, as previously mentioned, have described them in the lateral eyes of Euscorpius. Mark hesitated, in the case of the lateral eyes, as to whether he should follow Graber's observations and consider them triplostichous, with inverted retinas, or whether he should follow Lankester and Bourne and consider them monostichous. In the former case the phaosphere might readily represent postnuclear rhabdomeres ; in the latter, this interpretation would be out of the question. In Centrurus the structure and development of the lateral eyes show conclusively that they are monostichous, and there seems to be small room to doubt that the same is the case with the lateral eyes in Euscorpius. In these eyes, however, Lankester and Bourne claim the presence of phaospheres. I have had no material from Euscorpius to examine ; but since in Centrurus the median eyes contain phaospheres, while the lateral eyes are devoid of them, it is a matter of interest to see whether, upon further investigation, the presence of phaospheres in the lateral eyes of Euscorpius is confirmed, or whether that genus, like Centrurus, has phaospheres in the median eyes only. If they should not be found in the lateral eyes, there would still be reason for considering them the remnants of rhabdomeres; but if they should be found there, this view would be no longer reasonable.

The possible relation of the median to the lateral eyes in scorpions has already suggested itself, for in pointing out the probable nature of

* This relation of the structures of the normal and inverted retina has been fully discussed by Mark ('87, pp. 87–94).

the phylogenetic antecedent of the median eyes, a condition has been implied which agrees with the essential features of the lateral eyes. Of all the eyes in spiders and scorpions, the lateral eyes in scorpions are undoubtedly the least complicated, and they may be looked upon as deviating least from the probable ancestral type.

Summary of Results.

Nos. 2–11 refer to the median eyes; Nos. 12–17 refer to the lateral eyes.

1. The *retinas* of the median and lateral eyes are strictly *hypodermal* in their origin.
2. The *median eye* is *triplostichous*, and is formed by an involution of hypodermis accompanied with an *inversion* of the middle layer, which forms the retina proper.
3. The first layer or *lentigen*, is modified hypodermis immediately external to the pocket of involution, and, in addition to secreting the lens, serves a purpose which gave to it its earlier name of "vitreous."
4. The *lens* is the specialized cuticula produced by the lentigen. It differs from ordinary cuticula in containing *no* pore-canals, and, excepting the external hyaline layer, in being stainable throughout.
5. The *lentigen* can produce cuticula independently of the general hypodermis.
6. The second layer, or *retina*, is inverted, and consists of two kinds of cells, — retinal (nerve-end) cells and pigment cells. It contains phaospheres.
7. The *retinal* (*nerve-end*) *cells* contain pigment; their walls are thickened into prenuclear rhabdomeres, and a nerve fibre emerges from their deep ends. They are so arranged in groups of five, that five rhabdomeres are united to form one rhabdome.
8. Each of the *pigment cells* is reduced to two sacs, connected by a stiff fibre. The external sac contains pigment; the internal, the nucleus and pigment.
9. The third or *post-retinal layer* is the "sclera matrix" of Graber. It becomes intimately fused with the retina.
10. The fibres of the *optic nerve* in the embryo emerge from the external ends of the inverted retinal cells; in the adult, from the opposite ends.

11. The *basement membrane* is a cuticula produced by the inner ends of the hypodermal cells. The *preretinal membrane* is the united basement membranes of the lentigen and retina. It may or may not contain mesodermic elements. The *sclera* is the basement membrane of the post-retina. It is usually overlaid with a delicate mesodermic tissue.
12. The *lateral eyes* are *monostichous*, and arise from a simple thickening and depression of the hypodermis.
13. A ring of "*perineural*" *cells*, forming the margin of the depression, secretes the lens, and therefore constitutes the lentigen. Since, owing to subsequent recession, they do not remain interposed between the lens and retina, they have not the double function of lentigen and "vitreous" which the outer layer of the median eye has.
14. The *lens* has the same structure as in the median eye.
15. The *retinal cells* occupy only the deeper portion of the depression. There are no interneural cells. Along the external portion of each retinal cell its lateral walls are thickened into rhabdomeres. The nucleus is near the deep end of the cell, and from this end the nerve-fibre emerges. Phaospheres are not present.
16. The *basement membrane* (sclera) contains no mesodermic elements. There is no preretinal membrane.
17. The *lateral eyes* may be fairly taken to represent the *ancestral type* of the *median eyes*.

CAMBRIDGE, July 1, 1887.

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EXPLANATION OF FIGURES.

ABBREVIATIONS.

a.	Anterior.	*n. fbr.*	Nerve fibre.
can. po.	Fine pore-canals.	*n. opt.*	Optic nerve.
can. po.'	Coarse pore-canals.	*nl. ms d.*	Nucleus of mesodermic cell.
cav.	Cavity of infolding.	*nl. pig.*	" pigment "
cl. pig.	Pigment cell.	*nl. pi n.*	" perineural "
col.	Neck of invagination.	*nl. p r.*	" postretinal "
enc.	Brain.	*nl. pr r.*	" lentigen "
env. em.	Embryonic envelop.	*nl. r.*	" retinal "
gra. pig.	Pigment granule.	*p.*	Posterior.
h d.	Hypodermis.	*pha sp.*	Phaosphere
ir.	Iris.	*p r.*	Post-retina.
ll.	Outer hyaline layer of cuticula.	*pr r*	Lentigen.
ll'.	Middle " " "	*r.*	Retina.
ll''.	Deep " " "	*rhb.*	Rhabdome.
lns.	Lens.	*rhb m.*	Rhabdomere.
mb.	Basement membrane.	*scl.*	Sclera.
mb. pr r.	Preretinal "	1, 2, 3, 4, 5.	Lateral eyes.
mu.	Muscle.		

All the figures were drawn with the aid of an Abbé camera. Except where otherwise specified, all the preparations were examined in benzol-balsam.

Figures 1 to 18 represent the structure of the *median* eyes. Figures 1 to 9 illustrate the *adult* eye.

PLATE I.

Fig. 1. A horizontal section of the retinas of the two median eyes seen from the dorsal side. The tissue has been simply hardened and cut, the pigment remaining intact, and no dye being employed. ×195.

Fig. 2. A transverse section of the retina of the right median eye seen from the posterior face. The pigment has been removed by potassic hydrate and the tissue stained in Grenacher's alcoholic borax-carmine ×195.

PLATE II.

Fig. 3. The outer face of a frontal section through the retina of a median eye. The portion of the figure nearer the right side is close to the centre of the retina, that to the left is nearer the periphery. Colored with Klei-

nenberg's hæmatoxylin. The outline figure on thin paper (Fig. 3a) is taken from the section directly external to the one just described. ×475.

Fig. 4. Posterior face of a part of a transverse section of the retina described in Fig. 2. ×475.

Fig. 5. A retinal cell isolated in $\frac{1}{50}\%$ solution of chromic acid, and examined in a mixture composed of equal parts of water and glycerine. ×475.

Fig. 6. A pigment cell isolated and examined in the same manner as that shown in Fig. 5. ×475.

Fig. 7. A retinal cell with an attached pigment cell. The pigment was removed with a solution of potassic hydrate, and the cell was isolated and stained in Grenacher s alcoholic borax-carmine. Examined in a mixture of glycerine and water. ×475.

Fig. 8. The posterior lateral portion of a horizontal section of a retina seen from the dorsal side. Partially depigmented with a solution of potassic hydrate, and subsequently stained with Czoker's cochineal. In several places the lentigen has been artificially ruptured. ×475.

Figs. 9 to 17 represent the structure of the median eyes in young scorpions.

Fig. 9. The posterior face of a transverse section of the right retina in a young scorpion about the age at which it leaves the mother's back. Depigmented with potassic hydrate; stained in Czoker's cochineal. ×195.

Fig. 10. The left face of a section through the right eye parallel to the sagittal plane. Pigment unchanged; stained in Grenacher's alcoholic borax-carmine. This specimen was taken about the time of birth. ×195.

Fig. 11. Right face of a section from the sagittal plane of an individual somewhat younger than that seen in Fig. 10. In this section the neck of the invagination (*col.*) is seen to reach almost to the retina. In the sections on either side of this the neck appears much reduced, and at no point does it unite with the retina. ×195.

PLATE III.

Fig. 12. The right face of a section almost in the sagittal plane of an embryo. The lower part of this section was exactly in the median plane. The upper part was somewhat to the right of that plane. Pigment unaffected; stained in Grenacher's alcoholic borax-carmine. ×195.

Figs. 13 to 17 represent the dorsal faces of a series of horizontal sections in the region of the median eyes. In all the pigment is unchanged, and all have been stained with Grenacher's alcoholic borax-carmine. The region of the eye extends through forty-four sections. ×195. Beginning with the most ventrally situated and passing dorsally, Fig. 13 represents the seventh. It will be noted that the sections are not strictly horizontal, but that they dip slightly to the left; consequently in Fig. 13 the wall of the pocket is cut on the right in the thickened or retinal region, but on the left nearer the orifice of the pocket.

Fig. 14, the fourteenth section, shows the cavity of involution just before it is divided into a right and left compartment.

Fig. 15, the twenty-third section, shows the cavity divided.

Fig. 16, the thirty-first section, shows the right compartment reduced in size.

Fig. 17, the forty-first section, represents the wall of the deep (dorsal) end of the pocket cut tangentially.

Figs. 18 to 27 inclusive relate to the structure of the *lateral* eyes. Figs. 18 and 19 are from preparations of adult eyes.

Fig. 18. The anterior face of a vertical axial section of the right eye (No. 2); compare Pl. IV. Depigmented with a solution of potassic hydrate; stained with Grenacher's alcoholic borax-carmine. × 325.

Fig. 19. Anterior face of a frontal section. Partially depigmented with potassic hydrate; stained with Kleinenberg's hæmatoxylin. × 475.

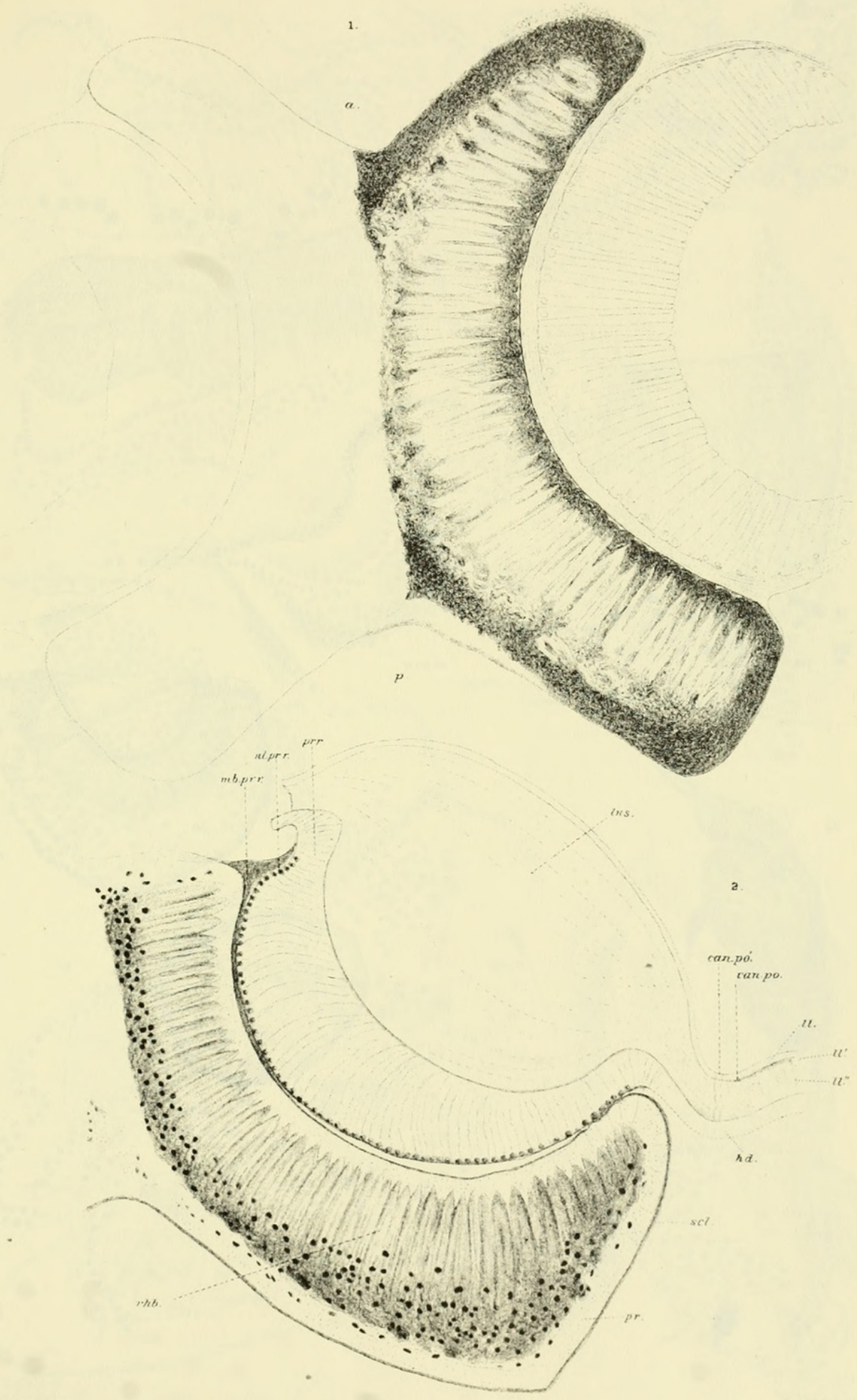
Figs. 20 to 27 inclusive give the structure of the eyes in young scorpions. Figs. 20 and 21 are from material of the same age as Fig. 9.

Fig. 20. Anterior face of a vertical axial section of left eye (No. 3). The pigment is unaffected, and no dye has been used. The edge of eye No. 1 is seen above. × 325.

Fig. 21. Anterior face of a vertical axial section of left eye depigmented in potassic hydrate and stained with Grenacher's alcoholic borax-carmine. × 325.

PLATE IV.

Figs. 22 to 27 inclusive are taken from the dorsal faces of a set of sections of the youngest embryos at hand (of the same age as those from which Figs. 13 to 17 are taken). The sections have been depigmented with a solution of potassic hydrate and stained in Grenacher's alcoholic borax-carmine. × 325. The figures represent the left cluster of lateral eyes. Beginning dorsally and proceeding ventrally, Fig. 22 is the first section, Fig. 23 the third, Fig. 24 the sixth, Fig. 25 the thirteenth, Fig. 26 the sixteenth, and Fig. 27 the twenty-first.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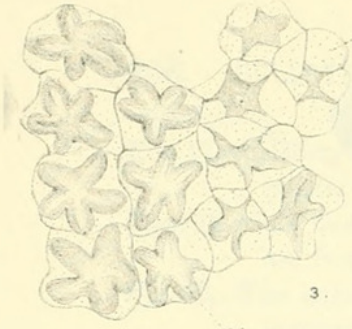
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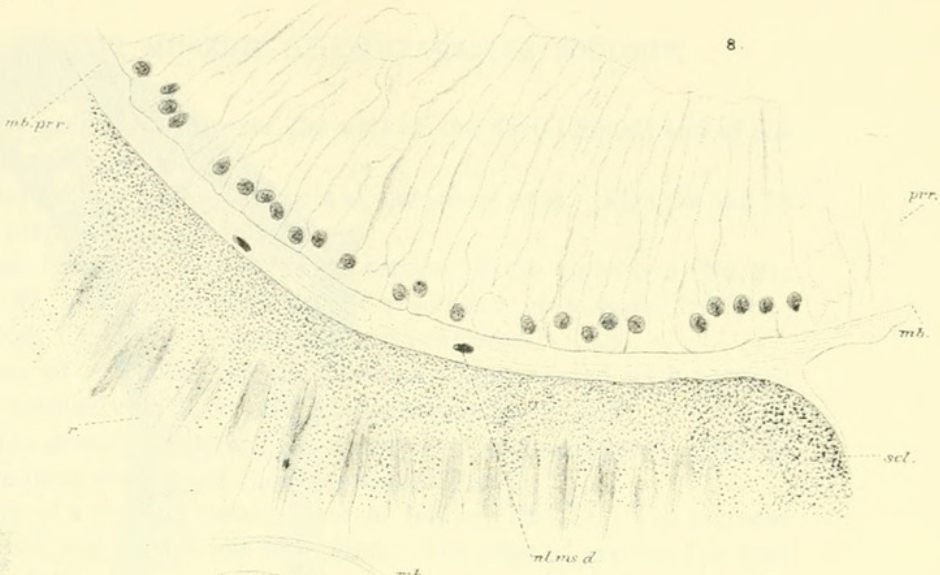
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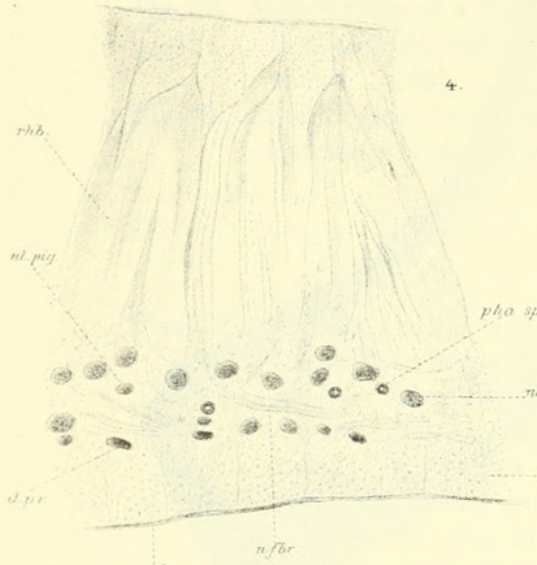
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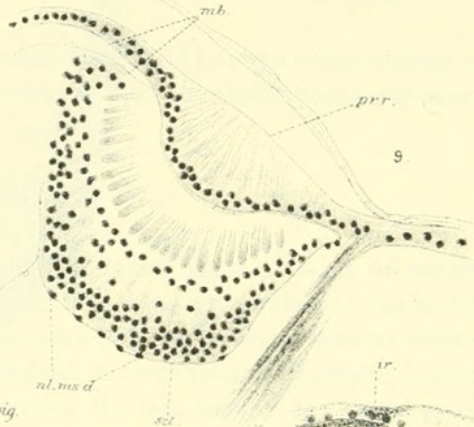
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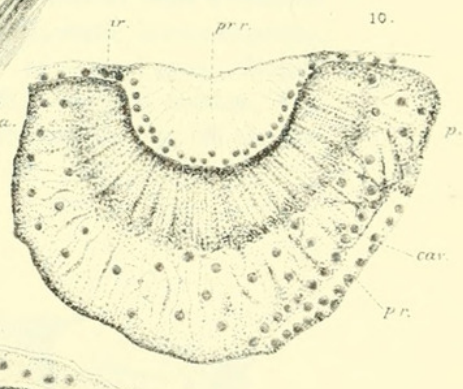
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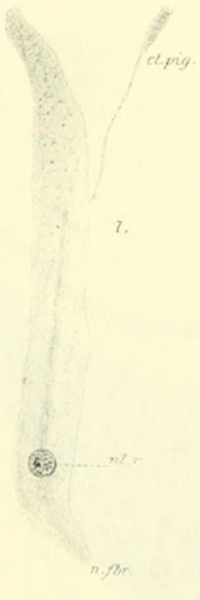
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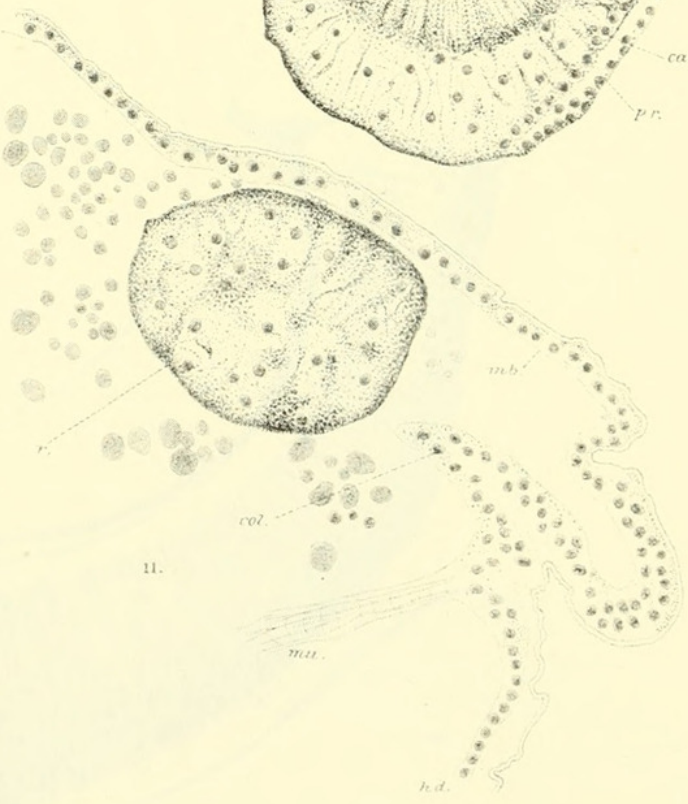
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