ON THE EYES OF POLYCHÆTOUS ANNELIDS.

E. A. ANDREWS.

I. INTRODUCTION.

THE most complete and satisfactory description of an annelid eye is that given by Greeff in his monograph of the Alciopidæ, in 1877 (1).

Subsequent observations in the same group have, in the main, but confirmed that account and added but little to it. The observations made from time to time upon the eyes in other families have been frequently but incidental to descriptions of the entire anatomy, yet they present great advances over the superficial knowledge utilized in the older systematic works. Some reference to these scattered observations will be made in connection with the particular forms studied in the present paper. At present we will notice only the two chief conceptions of the annelid eye to be found in the better known comparative works of Graber (2) and Carrière (3).

The former studied the eyes of many annelids, and saw in them grounds for comparison with the eyes of arthropods.

The latter observed several annelid eyes, and regarded them as similar to the gasteropod eye.

The annelid eye in Graber's conception is a duplex structure: an open, pigmented cup, the retina, closely associated with the brain, and cut off from the epidermis; a mass of epidermal cells filling the cup as a refracting accessory part of the eye, and not connected with the retina. The retina is composed of peculiar elements having at least two nuclei in each.

In Carrière's estimation, the annelid eye is a closed sac composed of the retina and the inner cornea, filled by a refracting non-cellular mass that is not connected with the epidermis. The retina is a single layer of cells in which pigmented sensory cells alternate with clear, secretory cells.

Other authors have referred the eye to one or the other of these fundamentally different interpretations.

Finding the subject by no means exhausted, and judging new observations were necessary, the following work was begun at Wood's Holl, Mass., upon material obtained in 1889 and in 1890, while enjoying the opportunities offered by the United States Fish Commission. This material was supplemented by that obtained in previous years at several of the marine stations of the Johns Hopkins University.¹

From the examination of the eyes of many adults, supplemented by some observations upon the formation of eyes, it has been possible to formulate a general idea of the simple eye of the polychætous annelids differing, as will be seen in the sequel, from those above referred to, and at the same time not contradictory to that account of the so-called compound eye of some sedentary polychætæ given in a previous paper (this Journal, Vol. V).

II. EYES OF ADULTS.

NEREIDÆ.

Nereis alacris Verrill.

The remarkable epitoke form of this annelid is found sexually mature early in July, and more abundantly in August and September, at Wood's Holl, where it may be taken swimming at the surface in great numbers in the evening and night, under various conditions of tide and weather.²

In these individuals (Fig. 1) the eyes are not only remarkably large, but also occupy a very uncommon position, the anterior ones not looking forward horizontally as is usual (Fig. 11), but partaking of the general modification of the head, and being thus directed downwards.

It is to be observed that, as compared with the common arrangement (Figs. 11, 5), the small labial palps are brought

¹ The nature of the material demands the use of many methods. Haller's liquid gave good results in general, but for the refracting part, the mixture of sea-water and H₂SO₄, as recommended to me by Professor Patten, was found excellent. Perenyi's liquid was most useful, yet various liquids containing osmic acid are sometimes necessary.

² This annelid was first described by Professor Verrill in 1873 as *Nectonereis megalops*, then in 1879, with the discovery of a female form, referred to *Nereis megalops*, and subsequently identified as the heteronereis state of the *Nereis alacris*, taken in deeper waters.

down to a ventral position next the mouth, while the antennæ no longer project forward, but hang down vertically from the peculiar anterior prolongation of the head.

The general appearance of the eyes in life is indicated in Fig. 1. The large posterior pair are approximately spherical, and have their visual axes directed dorsally, posteriorly, and somewhat outward, so that when prolonged they would tend to converge towards some point upon the anterior edge of the mouth. The anterior eyes are much larger still, less regular in shape, more elongated, and look downwards, so that the visual axes are nearly vertical, but yet, diverging somewhat outwards, would, if produced, tend to meet at some point dorsal to the head.

In this side view, both anterior and posterior eyes are well shown, but in ventral view, only the elongated elliptical retinas and circular pupils of the large anterior eyes are visible. In dorsal view, the pupils of the smaller posterior eyes are seen surrounded by the somewhat elliptical retinas, while the dorsal surfaces of the anterior eyes are also visible.

The lenses and corneas are seen only in profile views.

The size of the pupil varies much; that of the anterior is frequently greater than that of the posterior, but the reverse may occur. Moreover, amongst specimens subjected to the same treatment, some have much larger pupils than others, in all, or in some of the four eyes.

As commonly seen in life the eyes have a dark red color, modified by a golden yellow tinge. The pupils, however, appear dark blue. The explanation of this is evident when retinas are teased out in sea-water. There are two kinds of retinal pigment: the one, golden yellow, is less concealed in the superficial or peripheral part of the retina, and gives the golden reflections from its surface; the other, in mass, or in separate granules, is red by reflected, and dark blue by transmitted, light, and especially predominant in the part of the retina turned toward the centre of the eye. Hence the red and yellow light reflected from the eye, the blue light transmitted through the retina and emerging from the pupil.

In cross-sections of the head the immense eyes lie close to the brain and take up all the space between it and the epidermis. Each is innervated by a short nerve passing from the

dorsal part of the brain to the area of the retina opposite to the pupil and thence spreading out over the retina. The nerves to the anterior eyes thus pass to their inner dorsal sides, those to the posterior eyes to their inner ventral sides

The remarkable anterior process of the head is occupied by a large extension of the body cavity, the thin body wall being lined by a peritonæum that passes in over the eye to cover the brain.

A section of an eye — for all have the same structure — presents the general appearance seen in Fig. 8. This may be described under three chief heads: retina, lens, cornea.

Retina. — This is composed of pigmented cells with clear refracting ends or rods, which may be, for convenience, considered separately. The retinal cells collectively make a pigmented epithelium, forming the walls of a deep cup, the mouth of which is the pupil. The pupil, as already stated, varies much in size, but, as seen in the figure, is bounded by an inward bending of the edge of the retina, an iris-like portion of the entire retina.

When, as in the figure, the sections are made through the visual axis of the eye, the retina appears as a single layer of cells, the nuclei, in their peripheral ends, forming one zone. The dark blue pigment (red by reflected light) is especially dense along a line sharply separating the cells from the clear rods, and thence extends peripherally as irregular lines, suggesting the presence of special pigment cells and processes extending between the visible retinal cells. This is true of the dark blue pigment only: the yellow pigment appears in the interior of each cell, in its central end especially, but sometimes also extending out peripherally nearly to the nucleus. These facts are seen more clearly in very thin, highly magnified sections of part of the retina (Fig. 22), where also there is indication of the prolongation of each cell as a nerve process running parallel to the surface of the retina. Moreover, there are, here and there, in such sections, minute tubules or clear axial spaces passing from each cell through the densest blue pigment to the rod upon the central end of that cell. One is shown in Fig. 22.

In tangential sections cutting the dense pigment zone (Fig. 17) these clear passages are seen as round holes equally but irregularly distributed. Through these shines the yellow light from the axial yellow pigment of the retinal cells, or, if the

preparation is stained dark red, a red light. In a series of such sections, the one immediately peripheral to Fig. 17 shows that each round hole is continuous with the clear yellow central end of a retinal cell (Fig. 18). These bright yellow areas are full of yellow pigment spherules and surrounded by dense, dark blue pigment. The blue pigment continues to surround the clear axial parts of the cells till the level of the nuclei is reached (Fig. 19), where it is very irregular and does not separate all the cells. Final sections show only parallel cell processes, with lines of blue pigment granules extending between and along them.

Though the dark pigment would appear to be between the retinal cells, it is really in their superficial parts. For, in depigmented sections (Fig. 23) the area occupied by the blue pigment is outlined by a clear non-granular substance, presenting no nuclei nor indication of individuality other than that of the retinal cells, for which this substance forms, as it were, a thickened cell wall.

Moreover, tangential sections partly depigmented (Fig. 15) indicate that the pigment may be first removed from the thin basal disk around the axial hole (*a*) while still remaining in the very outermost boundaries of the cells (*b*). Comparing *a* and *b* with Figs. 17 and 18, we conclude the blue pigment is most refractory in the outermost surface of the cell, and may be gradually removed from the axial region outwards, with no indication of break in continuity or sign of interpolation of special small pigment cells between the large ones. When the depigmentation is complete, tangential sections (Fig. 16) present the sharp polygonal outlines of the central ends of the retinal cells, with no intervening spaces for nuclei or bodies of small pigment cells.

Macerations of the retina yield only one kind of cell (Fig. 9), which is drawn out into a slender process at one end and continued as a clear refracting rod at the other. The dark pigment adheres loosely to the cell except near the base of the rod, where a dense mass persists; this, however, may be finally removed, revealing a slender stalk connecting the cell proper with the rod. This stalk is the clear axial hole seen penetrating the dense pigment zone in sections. The yellow pigment is found as brilliant spherules in the axial parts of the cells, especially at

the end near the rod, but extending in some cells and in some eyes a very variable distance out towards the nucleus. The two kinds of pigment retain their natural colors, except that the blue granules tend to turn red in sulphuric acid macerations.

When properly stained, a large nucleus is found in the peripheral end of each cell (Fig. 14) near the cell process. These processes are nerve fibres and can be traced for some distance in a large nerve, the optic nerve, passing from the retina to the brain.

All the retinal cells are essentially alike: the swollen vacuolated form seen in Fig. 14, *a*, is common in poorly preserved sections as well as in some macerations, but is to be regarded as an artificially changed cell.

The layer of retinal rods forms a clear refracting lining to the pigmented part of the retina (Fig. 8), and is sharply defined on one side by the dense pigment zone, while on the central aspect it is but dimly¹ marked off from the clear central mass that I shall speak of as the lens. These rods are short near the pupil and largest at the bottom of the optic cup opposite the pupil. They are not all straight, but variously bent to fit into the curved space they occupy. In macerations they readily break off from the retinal cells and appear as clear rods in side view or as polygonal masses in end view (Fig. 12). Their actual continuity with the retinal cells may, however, be made out in some preparations (Fig. 9), each being partly abstricted from the end of the cell by the groove full of dark pigment surrounding the clear axial stalk. This is evident also in radial sections (Figs. 22, 23) where each rod is a continuation of a cell. Moreover, each rod has a granular axial part continued by the slender stalk of the rod into the granular, yellow, axial part of the cell, and a clearer superficial part or cell wall continuous with the part of the cell containing blue pigment.

Tangential sections of the rods near the pigment zone (Fig. 24) show the granular axes as rounded areas imbedded in a clear matrix, in which polygonal cell boundaries about each axis may also be brought out (Fig. 25).

In other stains the axes may appear light in a dark homogeneous matrix.

The axes are thick near the pigment zone, but diminish so

¹ The distinctness of this boundary is exaggerated in Fig. 8.

that tangential sections near the lens represent them as small granular circular areas separated by much intervening matrix (Fig. 26).

Lens. — The true structure of the refracting central part of the eye is not readily made out, owing to its semi-liquid consistency and liability to undergo artificial changes in various methods of treatment. In sections passing through the visual axis (Fig. 8) this central mass fills all the retinal cups, internal to the rods, and also projects from the cup as a hemispherical mass next the cornea. This projection might be called the lens proper, and the mass inside the cup the vitreous body; but as both are one, we may speak of the whole mass as the lens. When removed in sea-water, this lens (Fig. 10) is a spheroidal mass harder than glycerine, but having much the same optical appearance. Its larger lobe bears a smaller convex protuberance, the part next the cornea, and in Haller's liquid, shows longitudinal striations such as are seen in sections (Fig. 8). The groove marking off the two lobes of the lens is usually filled by the adhering pigment of the edge of the pupil or edge of the retinal cup.

When preserved, the lens becomes very hard and refractory, but presents striations that appear to be due to the presence of rods or columns passing from the retinal rods to the cornea. In tangential section such columnar elements may appear as polygonal bodies, shrunk from one another in Fig. 27, with radiating cracks or lines.

These component elements of the lens sometimes appear as if continuations of the retinal rods, but more often they are irregular and much less numerous. Yet some preparations show in section the continuity of each lens element with a retinal rod, as in Fig. 2, where the line of demarcation between the two is merely a series of vacuoles. This idea, however, must be regarded with much doubt, owing to the great variety of appearances produced in the coagulation of the lens. No nuclei or similar bodies were discovered in the lens, and it is not, as a whole, shut off from the retinal rod by any membrane. Although double stains with hæmatoxylin and borax-carminé may show a sharp line separating the blue rods from the red lens, this is due to a sudden change in consistency there, not to the presence of a membrane.

Cornea. — This name may be given to the thin layer of epidermis intervening between the lens and the cuticle (Fig. 8).

Though in some sections this layer seems absent, yet surface views show the epidermal nuclei scattered all over the area external to the lens. This epidermal layer is, however, very thin over the centre of the lens, consisting of but a film of protoplasm containing scattered nuclei.

The cuticle over this region might be included as part of the cornea. It is, however, not modified in any way, and is directly continuous with the similar cuticle over the neighboring parts of the head.

There is but little elevation of the surface over the eye, that indicated in the figure being due to the situation of this eye at the angle between the dorsal and lateral aspects of the head.¹

Nereis limbata Ehlers.

The mature epitoke state of this species is found with that of the former species, and equally, or even more abundantly.

The four eyes have the normal size and position (Fig. 11). The two anterior ones are somewhat the larger, and look forward and outward, nearly horizontally. The posterior eyes look backward, outward, and markedly upward. Thus the four visual axes tend to converge, when produced, towards some point within the brain. Owing to this inclination of the axes, it is almost impossible to obtain a section through the visual axes of two eyes simultaneously; yet an obliquely transverse plane cutting anterior and posterior eyes on opposite sides of the head would nearly do this.

The structure of all the eyes is the same, and identical with that just described in *N. alacris*. This identity extends to the character of the blue-red pigment and to the yellow pigment, to the arrangement of these in the nucleated retinal cells, as well as to the general structure of the retinal cups, layer of rods, lens, and cornea.

Macerated retinal cells (Fig. 4) show the dark pigment extend-

¹ As bearing upon the function, and possibly upon the evolution, of the enormous sexual eyes, it is interesting to note that the males are greatly in excess, amongst the individuals taken at the surface, and rarely present a perfect set of tentacles, even upon one side of the head. Some dorsal ones are broken off, leaving the basal joint. Is this due to a struggle amongst the males, or may the jaws be used in grasping during fertilization?

ing down the surface of the cell in lines of scarcely discernible material, suggesting processes of minute pigment cells, but regarded as shreds of the superficial pigmented portion of the large retinal cell.

In such preparations the lens is analyzed into a mass of ice-like fragments, which, however, as shown in Fig. 7, do not agree in size with the ends of the retinal cells. They are also not as numerous as those cells.¹

The eyes in the large atoke individuals, found amongst algæ upon buoys, etc., have the same structures as in the epitoke condition. The same is true of small individuals, 4 to 6 mm. long (Fig. 5), taken in such places, or in the tow net. Yet here the eye is more simple and easily understood (Fig. 21). The number of retinal cells is small, the pigment not abundant, the cornea evidently part of the epidermis converging over the lens. As the blue pigment is restricted to the dense zone, the bright yellow is less concealed, and the entire eye has a golden instead of a red color, as seen from the surface.

As the retinal cells separate more readily than in the adult, their character is beautifully and easily shown in macerations (Fig. 20).

Nereis virens Sars.

Only atoke, immature, but large specimens were studied, chiefly by section methods.

In all parts the four eyes have the same structure as that described for the two preceding species.

The eyes are far less conspicuous, owing to the thickness of the cuticle and epidermis, and to the small size of the outer lobe of the lens (Fig. 3). The cornea is composed of much elongated epidermal cells, converging over the conical outer

¹ The size of the pupil varies even more than in the previous species. The difference is not a sexual one: one specimen has one pupil remarkably small, and the other three large. That the size is constant in the individual is not proven; on the contrary, the following experiment furnishes some slight reason to judge there is a change in connection with illumination. Nine individuals kept 36 hours in total darkness show an average diameter of 1.5 in 12 eyes measured, as compared to 1 for the same in 9 kept in daylight and gaslight. The experiment was somewhat vitiated by unequal conditions of temperature and purity of water, and great actual variations in size of the pupils were noted. Those in the dark ranged from 112 μ to 182 μ ; those in light, from 42 μ to 168 μ !

lobe of the lens, so as to barely cut it off from contact with the thick cuticle.

The pigment is exceedingly dark, the rods are very short. In certain places the lens may shrink away from the rods, as on the right of the figure, in such a way as to leave slender filaments and drawn-out coagulated threads, as of a slimy material, that correspond to the retinal rods in number and position, and also are to be traced into the lens as lines.

Such connections of lens and retinal rods were seen in the epitoke *N. alacris* also.

Nereis pelagica Linné.

In sections and macerations of the eyes of atoke individuals we find here the same structure again.

In surface views of an eye there is, however, a conspicuous line corresponding to the major axis of the somewhat elliptical pupil, but not as long as it, which seems to be the line of meeting of the epidermal, corneal cells over the lens. This was observed in *N. virens* also, but not as plainly as in the present case. In anterior eyes there are vacuole-like clear bodies along this line and at one end, often, a clear ingrowth of the cuticle, seen in sections (Fig. 13) to be a conical plug of cuticular substance extending inward nearly to the lens.

This linear structure seems to correspond to a bilateral arrangement of the elements of the lens, sometimes indicated, when these elements do not run out to the cornea, but bend in toward a meridional plane.

The whole appearance, as far as understood, indicates a connection of lens and cuticle, and strongly suggests some sort of invagination or sinking in from the surface.

The retinal cells are often extremely long and slender, with short rods (Fig. 6). Moreover, they are so crowded that very slender ones amongst the less slender sort have their nuclei in a conspicuous zone near the dense pigment, and thus the retina appears as if made of two layers of cells. This is not, I judge, actually the case, but due, as above stated, to the crowding of perfect and imperfect, or greatly attenuated, cells.

In brief recapitulation, we may characterize the eye of the Nereidæ as a pigmented retinal cup, lined by clear rods, and filled by a refracting substance of doubtful origin, the entire

spheroidal mass near the brain, and scarcely separated from the cuticle by the intervening epidermal cornea. The retina is a single layer of pigmented cells, each having a clear rod as represented in the accompanying diagram. The end of the rod is continuous with the lens, and there is some reason to assume it continued into the lens as an element of it.

The above account of the eyes of *Nereis* differs considerably from that given by Graber (2), or from that of Carrière (3), the only detailed descriptions known to me.

In *N. Costæ* Graber found a membrane separating the retina from what I call the lens, and in the latter nucleus-like bodies, so that the lens seems to be a mass of epidermal cells.

These discrepancies I think due to difference in technique. Appearances such as those described for *N. Costæ* I have sometimes seen, and referred to imperfect preservation and artificial changes. Granting this to be the case, there is otherwise great similarity between the eye of that species and the forms described in the present paper.

The eyes of *N. cultrifera* studied by Carrière present, on the contrary, fundamental differences, in that the retina is a closed spherical sac, composed, except on the corneal side, of alternating clear, secretory, and pigmented, sensory, cells with no rods. Yet sections through the visual axis might show here also a central opening or pupil, and possibly other methods of preparation would demonstrate the existence of

DIAGRAM 1. — Retinal cell, rod, and part of lens of one of the *Nereidæ*.

n. nucleus; *n.p.* nerve process; *y.p.* yellow pigment; *b.p.* blue pigment; *a.* axis; *s.* sheath of rod; *l.* lens.

rods. The retina is evidently the same as those I have seen, but differently interpreted, owing to the discovery of nuclei in the blue pigment—which I regard as belonging to the surface of the yellow cells.

EUNICIDÆ.

Marphysa sanguinea Quatrefages.

Only two eyes are present, and these are buried deeply beneath the cuticle on the dorsal surface, one on each side lying as an oblique red mass external to the base of the posterior lateral antenna.

Even surface views show a clear stalk extending in from the cuticle to the eye, while macerations reveal a most interesting connection of cuticle and lens. The lens is then seen as a clear, highly refracting mass of conical form, with the base connected to the cuticle by a slender cylindrical stalk quite continuous with both cuticle and lens. In potassium hydrate, when the retinal cells are removed, the lens thus appears as a clear, hard mass hanging from the cuticle by a stalk.

Though approximately conical, the lens is yet irregular in presenting a side lobe from its base, about parallel to the cuticle, so that the large cone is but the major part of a somewhat bifurcated mass having its common base prolonged up to the cuticle as the narrow stalk.

Though nearly homogeneous, this lens has a clearer axial part, which is not liquid, however, but striated. The entire surface, except that of the stalk, is covered, in such macerations, by slender filaments or clear threads streaming out from the lens towards the retina and ending at the pigmented zone, when that has not been removed.

Vertical sections that cut the stalk lengthwise (Fig. 34) show the continuity of lens and cuticle, but give an imperfect idea of the shape of the retinal cup. This is, in fact, like the lens that fills it, somewhat bilobed, and its orifice or pupil is occupied by the cuticular stalk only at one point; elsewhere the epidermis meets over the lens, and clear elongated cells free from pigment pass continuously from one edge of the optic cup to the other, making an inner cornea.

As the eye is oblique, a transverse section (Fig. 35), near the base, will show this condition of things. The mass of clear cells on the left filling the pupil, or area between the edges of the pigmented retinal cup, comes into contact with the lens and forms a sort of raphe, ending at the stalk or connection of lens and cuticle. This mass might be called an inner cornea, the epidermis the outer cornea. The cuticle is removed from the preparation figured.

The central part of the lens, in sections, stains less deeply, and is continued in the stalk as a tubular mass of coagulated material opening to the exterior in some sections.

The retina is much as in *Nereis*, but presents some difficulties in connection with the fibrils passing to it from the lens.

The pigment is dark red, yellowish red in separate spherules, is present chiefly in the superficial parts of the cells, densely aggregated at the zone next the rods, where there are clear axial holes as in *Nereis*, and extends peripherally as irregular processes or lines, much as in *Nereis*.

The obvious arrangement of retinal nuclei in two zones (Fig. 34) is not due, I believe, to the presence of two fundamentally different sorts of cells, but to the crowding of one sort, both large and small, as represented in the portion of the retina (Fig. 38).

In macerations (Fig. 45) both thick, and slender cells are found, the former bearing clear, soft rods. These rods make a definite layer, as in *Nereis*, between the pigmented cells and the lens (Figs. 34, 35).

The peculiar clear fibrils that come off from the macerated lens are seen again in sections (Fig. 38) passing from the lens, of which they are continuations, down between the rods to the pigmented retinal cells. Again, in macerations, we find sharply defined, clear linear bodies adhering to one side of the soft rod-mass at the end of the thicker retinal cells (Fig. 45), on the left.

The actual connection of these lens fibrils with the retinal cells is not satisfactorily made out, though sections (Fig. 38) show pretty clearly that they are only the attenuated ends of the more slender, reduced retinal cells, and not, as macerations (Fig. 45) lead one to infer, parts of a superficial case about each soft rod.

The former view is strengthened by the appearances seen at the pupil where, as on the left of Fig. 35, the clear not pigmented cells have filaments connecting, almost certainly, the slender cells with the lens.

It would thus appear that in this eye the retina is continuous with the rods and with the lens, and the latter with the cuticle.¹

Unice ornata Andrews.

Sections of the limited material of this species from North Carolina suffice to show that the eye in this genus may agree closely with that of *Marphysa*.

The lens (Fig. 33) connects with the cuticle by a cylindrical stalk, and is somewhat bilobed from the point of attachment of this stalk. The pigment in the retina is like that in *Marphysa* (is represented in the figure as nearly removed by acid), and is also absent from a pupil-like area of clear cells along one side of the lens, as in Fig. 35, of *Marphysa*.

The axial part of the lens appears nearly liquid, is vacuolated and shrunk: the denser peripheral part when shrunk away from the retinal rods, as on the left of the figure, leaves clear fibrils or strands passing in between the rods. These appear to be the same as those seen in *Nereis* (Fig. 3), and also are identical, as far as sections tell, with the lens filaments of *Marphysa*.

Thus in depigmented sections of the retina (Fig. 37) the lens is continued as large fibres passing between the granular protoplasm-like rods into the area depigmented. These fibres are swollen and vacuolated just after leaving the lens, so that there is formed a zone of rounded bodies suggesting minute nuclei, but really comparable, I judge, to the vacuoles sometimes seen in *Nereis* between rods and lens (Fig. 2).

Another resemblance to *Nereis* is to be found in the presence of an interrupted line, in depigmented sections, marking off the rods from the cell bodies, being the limit of pigmentation. This line is the expression of what seems a perforated membrane, through which each large retinal cell continues as a rod, but

¹ An additional reason for associating the sipunculids with the annelids may be found in the resemblance between the eyes of the two groups, as seen in comparing the figures of the cephalic sense organs of *Phrynosoma* as given by Shipley (*Q. J. Mic. Sci.*, 1890), with the above figures of the eyes of *Marphysa* (Fig. 34), especially.

which is, perhaps, merely the aggregate of the more dense polygonal bases of the retinal cells.

The interpolation of slender cells and occurrence of nuclei in two zones increase the difficulty in interpretation from sections alone. The arrangement appears to be as in *Marphysa*, and again there is some evidence that, as too diagrammatically indicated in Fig. 37, the lens filaments are but the continuations of the more attenuated retinal cells.

Eunice violaceo-maculata Ehlers.

Specimens from Green Turtle Cay, Bahamas, have eyes like those of the two preceding annelids, and serve to clear up some doubtful points in the interpretation of these eyes.

The cuticular stalks of the large eyes have definite perforations or axial canals (Fig. 32); that is, the cuticle is invaginated as a short tube, and then thinning out, becomes continuous with the surface of the lens.

The epidermis following this ingrowth becomes here, as in the preceding cases, continuous with the pigmented retinal cup. Moreover, the greatly elongated, slender cells of the epidermis are repeated in the correspondingly elongated retinal cells (see also Fig. 43, as compared with Fig. 37 or 38).

The lens would appear to be nearly liquid at its centre but more dense at the periphery. Here it is continuous with the cuticle, which does not extend far into the optic cup, but gradually becomes less refracting and dense till it merges into, and is one with, the peripheral part of the more granular, less refracting lens.

In the retina there is little doubt that the much-attenuated, slender cells that are crowded in amongst the thicker but very long ones are actually continued out to the lens as slender fibrils between the rods (Fig. 43). These fibrils, lens fibrils, appear thus to perforate the line indicating the boundary of the rod pigment, just as the clear axes of the larger rod cells do.

Some views of the common epidermis of the head lead one to infer that here also the attenuated cells amongst the larger epidermal cells have a close connection with the cuticle, like that of the above cells with the lens. In tangential sections across the rods (Fig. 36), we meet again with these slender lens filaments, or attenuated rods of slender cells as they seem to be,

in the small amount of matrix or fused cell wall between the rods.

Such sections across the central zone of nuclei show them to be much smaller than the peripheral nuclei of the common larger retinal cells; these smaller nuclei seem generally to be those of the attenuated cells (Fig. 43).

Arabella opalina Verrill.

The eyes, as seen through the thick cuticle and epidermis, form a transverse series of dark spots, usually four, sometimes six. The pair nearest the mid-line is much the largest, at least twice the diameter of the outer. When six are found, the outermost are much the smallest. The pigment is very dense and dark red or red-brown.

All these eyes lie imbedded in the dorsal, ganglionic part of the brain separated from the surface by cuticle, epidermis, and brain substance, and, in most places, by an intervening part of the body cavity (Fig. 47).

The structure is as in *Marphysa*, save that the lens is scarcely at all developed, and no connection with the cuticle is discoverable. The optic cup is partly filled by an intrusion of cells somewhat resembling those forming the inner cornea or pupil in *Marphysa* (Fig. 35), but, in part at least, like the ganglion cells of the surrounding brain.

The retina presents long and short, thick and slender cells, as in *Marphysa*; the soft rods are intermingled with slender fibres resembling those of *Marphysa*.

The two largest eyes are often very irregular; the intrusion of brain cells may penetrate through the retina in such a way as to cut off a few pigmented retinal cells from the rest.

These insulated retinal cells surrounded by brain cells have no rods, but are merely elongated, pigmented, columnar cells.

There is thus some reason to believe these eyes to be degenerating.¹

¹ An examination of *Diopatra cuprea*, *Cipd.*, confirms the absence of eyes in this genus. The *Nackenwülste* (*Spengel, Oligognathus. Mith. z. s. Neapel.* 3.) are, however, very evident as a pair of horseshoe-shaped ciliated grooves, each embracing a rounded elevation. The cuticle in the groove is markedly thin and perforated by the cilia from a ridge of elongated, modified epidermal cells. These are connected with nerves, and so arranged as to present the outlines of a "taste-bud" in transverse section.

From the above it appears that the eye in the Eunicidæ is fundamentally like that in the Nereidæ. The retina, however, has some attenuated cells which bear imperfect rods or slender ends passing into the lens. The lens shows no sign of being made of elements corresponding to the retinal cells, but is more like a secreted mass. It is, however, connected with the cuticle, is a part of the cuticle, and not separable from the cuticle, though when this is invaginated a short distance, it may appear as a secretion morphologically external to the cuticle.

The continuity of lens and cuticle, as well as the existence of the retinal rods, was recognized by Graber (1) in *Eunice vittata* and *E. Harassii*. His account of the retina and rods is, however, quite different from that given above in the presence of a definite membrane separating these two zones and the interpretation of small bodies in the adjacent ends of rods and pigment cells as being two zones of nuclei.

I do not regard the membrane-like line found in my material as a true membrane, and have not seen the nuclei.

Pruvot (4) describes and figures the eye of *Hyalinæcia tubicola* as a spheroidal mass of two concentric zones of elongated cells all buried in and not separated from the brain. These cells have swollen, nucleated ends towards the brain, and then extend as slender processes or bodies to the lens, from which they are not separated by any line whatever, but rather penetrate into it. This lens is, moreover, merely a small rounded inward growth or process of the cuticle. The pigment appeared to be between the bodies of the cells; the eye figured is that of an *albino*.

The eyes of *Eunice torquata* are said to have the same structure. These, however, as well as the eyes of *E. Harassii* have been most excellently figured by Jourdan (5). This author finds no separation of retina and rods in the species in which Graber figures so evident a membrane, but recognizes the fact that each rod is but the clear end of a retinal cell. All the retinal cells are pigmented and end in rods.

The nuclei nearest the pigment end of the cells he regards as their true nuclei, while the more peripheral ones are in a peculiar zone of anastomosing ganglion cells continuous with the pigmented retinal cells. (Some of my preparations incline one to suppose this may be the true state of the case, though another interpretation has been preferred.)

A minute pore is found leading in through the cuticle to the axis of the lens. A double contour between lens and rods is regarded as a continuation of the cuticle inward to line the whole retinal cup, and hence the soft lens is interpreted as a secreted mass external to the cuticle and comparable to the mucous the animal secretes elsewhere.

This separating layer is evidently what I have regarded as merely the dense or more firmly coagulated superficial part of the lens next the rods, and not as a continuation of the cuticle.¹

The structure of the eyes of the Eunicidæ as discovered by Jourdan finds, in some respects, a parallel in the case of one of the Chloræmidæ, *Siphonostoma diplochætos*, as elucidated by the same author (6). Here also the retinal cells are pigmented, and their enlarged bases are connected with the brain by pigmented nerve fibres. There is also a refractory mass composed of radiating elements or rods filling the retinal cups. Whether there is any connection with the epidermis or not does not appear from this preliminary note.

SYLLIDÆ.

*Autolytus prolifer Langerhans.*²

The beautiful adult forms of this annelid were taken in immense numbers during July 1 to 15, 1889 and 1890, swimming at the surface in the evening.

The females appear to be much less numerous than the males, but this may be in part due to their tending to sink below the surface. The males present two marked color varieties, the one bright red, the other green. No other differences are apparent,

¹ The eye of the Eunicidæ appears to be repeated in the Nephthydæ, to judge from the figures given by Graber for the eye of *Nephthys margaritacea*; these are strikingly like Fig. 34 of the present paper. No connection of lens and cuticle was seen, however, but the rods and retina are represented just as in that author's figure of Eunice. An examination of *Nephthys buccera* and of *N. picta* failed to furnish eyes for comparison with the above.

² This identification is only provisional: the males are much like the *Polybostrichus* of Müller and of Keferstein, which is but the male sexual form of *A. prolifer* of Langerhans. This annelid has been noted on our coast by Webster as *A. hesperidum*, *Clpd.*, and also by Verrill as *A. varians*, I believe. A non-sexual form producing several of these males was observed. This seems, however, to differ much from the *Syllis prolifera* of older authors.

and some green specimens have red pigment also. The eyes studied are thus chiefly those of the mature male, either variety being used; both are about equally abundant and have the same eyes.

As in the sexual form of *Nereis alacris* (Fig. 1), the posterior eyes (Fig. 39) look upward, the larger anterior eyes downward. The large anterior eyes have become so far removed ventrally as to be vertically beneath the small posterior or dorsal ones. The eyes are red-brown, the isolated pigment granules yellowish.

The lens is very conspicuous as a somewhat conical, clear body, evidently connected with the cuticle by a slender stalk or pedicle. This connection is also seen in sections, but as it is very minute it is not often cut, and a condition like that shown in Fig. 44 is more common.

This is, however, owing to the shrinkage, not the natural relation. In fact, there is less protuberance of the cuticle over the lens, and a distinct intervening space between the lens and epidermis, save at the point where the small stalk is. The true condition is then more like that indicated for another annelid in Fig. 41.

When teased out fresh, the lens is a solid, homogeneous, highly refracting mass, and is markedly bilobed, the larger lobe filling the optic cup, the smaller projecting from the pupil.

The connection with the cuticle is obvious even in macerations; when potash is added, the lens dissolves save for a granular matrix and a few oil-like drops, but this faint residue remains attached firmly to the cuticle at one point.

Hæmatoxylin stains the lens readily, osmic acid gives it a brown color, while nitric acid turns it orange. In hardened specimens it is brittle and refractory.

The retina (Fig. 44) has the same structure as in the eye of a young *Nereis* (Fig. 21). When macerated the cells seem to carry much of their pigment upon the outside, where it is easily removable (Fig. 40), but the use of high powers convinces one that there are also many yellowish granules in the axial parts of the cells. The part readily removed is to be regarded as also in the cells, but in the superficial parts only.

Most of the cells are alike as in Fig. 40: the peculiar branching or anastomosing cell in the left was observed but once.

This, however, suggests a connection of retinal cells and ganglion cells like that observed by Jourdan in Eunice.

Sections of one female specimen show the same structure as that found in the male. A single non-sexual form bearing three males, one nearly perfect, also presents the same structure, though the eyes are smaller.

Sections of two adult male *A. longisitosus* Ver. reveal eyes that are even larger than those of the male *A. prolifer*, but with identity in structure. No connection of lens and cuticle was actually observed in this limited material.

Procærea tardigrada Webster.¹

The non-sexual forms of this brightly banded annelid occur amongst the hydroids upon the wharves, late in the summer, while the sexual forms are sometimes taken in the surface net.

In the non-sexual form, the four eyes are all dorsal, the anterior pair much the larger. Surface views demonstrate that the pigmented retinas are sunk beneath the cuticle, and that a large conical part of the lens projects from this pigment towards the cuticle, with which it is connected by a slender stalk. This protuberant part of the lens is surrounded by clear, epidermal cells, and is marked by few longitudinal lines, as though it were made up of a few pyramidal masses applied together.

This connection of lens and cuticle is also seen in sections.

When macerated, the lens is plainly bilobed (Fig. 42), the constriction being embraced by the edges of the optic cup.

The retina has the same structure as in *Autolytus*. The isolated pigment granules are large, yellow-red spherules adhering to and contained within the cells: only the nucleus may remain free from pigment.

In the adult female with blue eggs, or larvæ carried in the ventral sac, the eyes have the same structure as in the non-sexual form, though the position is as shown in the male *Autolytus* (Fig. 39). In section the connection of lens and cuticle by a slender cylindrical stalk was well shown, as indicated in the simplified drawing (Fig. 41).

¹ This annelid I regard as the same as *P. ornata* of Verrill.

Odontosyllis lucifera Verrill.

These annelids are found very abundantly, swimming at the surface with *Autolytus*. While *Autolytus* is positively heliotropic, these syllids are markedly negatively heliotropic, and at the same time able to secrete an unusual amount of mucous and to give out a brilliant green phosphorescent light.

The eyes are four, and dorsal in position; the anterior pair much the larger. The pigment is golden-red when fresh; in Perenyi's liquid it dissolves, in part, as a golden liquid. From surface views there is no evidence of a lens; but in sections, a peculiarly constructed lens connected with the cuticle is demonstrable. The long retinal rods (Fig. 46) appear directly continued as rod-like elements of the clear refracting mass, or lens, filling the optic cup. Within this mass, however, there are rounded highly refracting bodies or miniature lenses of various sizes, not divisible into rod-like elements. One of these is quite large, as seen in the figure. A few others are present, scattered about, and often so small as to be contained within one of the rod-like elements of the lens, as on the right. The entire lens, or refracting mass central to the retinal-rod layer, is thus composed of continuations of these rods, except where the large especially refractory globules are found. The smaller globules are within the continuations of the retinal rods.

A slender cylindrical stalk connects the lens with the cuticle (Fig. 46), and this presents longitudinal situations suggesting that the attenuated lens elements are here continued up to the cuticle!

The retina is like that of *Autolytus*, but is not separable from the brain. Its isolated cells are densely pigmented, even along the nerve processes, as represented in Fig. 48.

Pedophylax longiceps Verrill.

In an adult female with sexual setæ the four eyes have yellow-red pigment and dense lenses sending up conical slender stalks to the cuticle, much as seen in the last annelid (Fig. 46). The lens, however, has the appearance of that in *Autolytus* (Fig. 44), though not projecting from the retinal cup.

A summary of the results obtained in this family seems scarcely necessary, as the eyes here repeat much that is found

in the Nereidæ, and structures found in the Eunicidæ in addition. In the case of *Odontosyllis*, however, we have also evidence of the composite nature of the lens; a suggestion that it may be only the partly fused ends of the rods, that it is composed of the modified retinal cells themselves.

No account of the eyes of the Syllidæ giving more than the general appearance of lens and pigment appears to have been hitherto published.

HESIONIDÆ.

Podarke obscura Verrill.

The anterior of the four dorsal eyes are, as usual, the larger. The lenses are not prominent, and look outward; the anterior, also forward; the posterior, backward.

The isolated retinal cells are much as in *Nereis*, and contain a pigment that is red-brown when fresh.

Even surface views show depressions of the cuticle passing in as hollow stalks to connect with the lens. On section the cuticle actually rolls in at one point, to form a hollow tube (Fig. 49), open to the exterior, but closed by the lens. The inflected cuticle spreads out parallel to the surface, to fade away as the superficial part of the lens next the retinal rods, the relationship of lens and cuticle being as shown on a larger scale in *Eunice* (Fig. 32). The lens, as in *Odontosyllis*, has radiating elements, appearing at places to be continuous with the retinal rods; but it has no special refracting globules in addition.

Depigmented sections show plainly that each retinal cell ends as a clear rod. There is, moreover, an appearance as of a perforated membrane marking off the cell bodies from the rods, just as in *Nereis* and the Eunicidæ; but this is to be interpreted as due to the greater amount of pigment in the superficial than in the axial parts of the cell body and to its sudden cessation, usually, where the rod begins.

In two cases, a small extra eye was found closely applied to the usual posterior eye upon one side of the head. This eye does not appear directly connected with the cuticle, but is a side lobe of the normal eye, somewhat as found in *Marphysa*, but more widely separated and independent.

In *Hesione pantherina* Graber (2) finds no slender lens-stalk, but a large mass passing from the cuticle into the retinal cup,

and regarded as a plug of epidermal cells, separated from the retina by a sharp membrane. The retina is composed of pigmented cells with clear rods. In the presence of that membrane and in the presence of nuclei, both in the retinal rods and in the element of the lens, this eye would appear to differ from that of Podarke fundamentally. Leaving out the membrane and nuclei, the eye agrees essentially and closely with those here described. Both membrane and nuclei I regard as probably artificial products, produced by the methods employed.

POLYNOIDÆ.

Lepidonotus squamatus Kinberg.

These annelids remain closely appressed against the surfaces upon which they crawl, and do not lead as free a life as do most of those hitherto described in this paper.

The four small eyes are on the dorsal aspect of the head, the anterior further apart but not larger than the posterior pair.

When isolated the retinal cup is found filled by a lens mass that projects from its orifice or pupil in the form of highly refracting conical bodies resembling pieces of ice. The whole cup is filled with these lens elements or separate lenses, each connected at one end with the layer of retinal rods, by means of a delicate thread or process that may be drawn out as if viscid.

When macerated the retinal cells (Fig. 51) are found to be very short and thick with short clear rods and abundant black pigment in the rod end of the body of the cell. This pigment is composed of very fine granules having a sooty black color, even when isolated. In one case a retinal rod was seen continuous with one of the lenses or lens elements (Fig. 50). Here the short retinal rod expands as a swollen oil-like mass, the lens element, surrounded by a membrane-like contour that continues down over the retinal rod.

Owing to the great thickness of the cuticle and to the hard refractory nature of the lens good sections of the entire eye are difficult to obtain. The best show, as in Fig. 52, some of the lens elements still remaining, and in places connected with the rods, though elsewhere much shrunken.

All these lens elements are in life closely packed to form a solid lens projecting towards the cuticle. In sections, this projection is seen to extend up to the cuticle and even, at one point, to pierce it as a dim line or strand differing from the rest of the cuticle (Fig. 52).

In depigmented sections the retina is a single layer of cells, each bearing a retinal rod.

Harmathoë imbricata Malmgren.

Sections show the same compound lens and its connection with the cuticle. Macerations furnish retinal cells like those of the last animal; in fact, as far as observed, the eyes in these two species are identical.

Sthenelais picta Verrill.

Here again, four dorsal eyes are met with having compound lenses and dark, smoky-black pigment. No connection of lens and cuticle was discovered, but such may well exist.

In highly magnified views of a part of a depigmented retina (Fig. 53), the continuity of retinal cell and rod is well shown, as also the close application of these rods to the lens elements, with which, moreover, there is some general agreement in number. A few retinal cells have nuclei in the pigment zone; these cells seem, as those figured, to be crowded in amongst the more common kind, and are not special pigment cells.

The eyes of the Polynoidæ thus furnish additional evidence of the continuity of the various parts of the eye and of its connection with the cuticle. They also indicate that the elements of the lens are but the ends of the retinal cells or else formed by these cells individually.

Graber (2) has represented the composite nature of the lens in *Polynæ elegans*, *P. areolata*, and in *Hermione hystrix*; and also shown the continuity of retinal cells and rods. In most other respects his account may be interpreted as above in the case of the Hesionidæ.

AMPHINOMIDÆ.

Amphinome Pallasii Quatrefages?

Specimens probably belonging to this species and taken at Green Turtle Cay, Bahamas, and some from Florida, present four red dorsal eyes, the anterior the larger.

As seen in section (Fig. 30), the retina is peculiar in that lines of pigment granules extend along the cell processes, even to a distance of ten times the length of a retinal cell, thus passing in the mass of nerve fibres proceeding towards the *punct-substanz* of the brain.

A lens scarcely exists as distinct from the retinal rods; each rod is continued as a clearer, more liquid and tapering part toward the stout cylindrical pedicle that connects the eye with the cuticle. The sum of these watery tips may be called the lens as distinguished from the less transparent, more deeply staining layer of retinal rods. Graff (7) has described the eyes in three species of *Spinther* as deep spoon-shaped pigmented cups¹ filled by converging clear rods. His figures are given incidentally, and obviously do not give the entire structure satisfactorily. No connection with the cuticle is seen, but I infer such may exist. These eyes are interpreted as agreeing with the eye of *Nereis* as described by Carrière, but the figures I think may as readily be interpreted as agreeing with the structure found in *Amphinome*.

Beddard (8) finds in *Chlocia merguiensis* Bed. four eyes having retinas much like that described above for *Nereis*. The elongated cells each bear a clear rod and are pigmented. Some of the pigment is inside the cell, some in dark masses as if between the rod ends of the cells: from surface views and tangential sections this latter pigment appears as a black mass perforated by clear holes, the bases of the rods (as shown for *Nereis*, Fig. 17). There is also some orange-colored pigment in one area of the retina.

The lens is remarkably like the cuticular plug shown for *Nereis* in Fig. 13; it is larger and comes into contact with the

¹ From references to the work of R. v. Drasche, I infer that he found the eyes in one of these species of *Spinther* to be nearly closed retinal cups, with but small pupils.

retinal rods; is, in fact, a laminated part of the cuticle filling the small retinal cup.

Beddard would interpret this eye as Carrière has done that of Nereis, thinking that separate minute pigment cells might be found in the pigmented zone of the retina.

PHYLLODOCIDÆ.

Eulalia annulata Verrill?

The two large eyes look upward and outward and are buried beneath the surface. The retinal cells when isolated have much the form of those found in *Lepidonotus* (Fig. 51), but the pigment in them is red, not black. In section (Fig. 31) the retina is buried in the brain, but sharply marked off from it and from the epidermis also, except at one point; here the retina and epidermis are continuous. The cuticle penetrates this region as a slender stalk continuous with the lens.

The lens is much shrunken both by Perenyi's liquid and by chromic acid, and presents an unusual appearance, being a mass of darkly staining round granules. How far this is merely artificial could not be determined from the material at command.

Eulalia pistacia Verrill.

The eyes here differ in not being as far removed from the surface as in the preceding species, and in having a stouter connection with the cuticle. The lens seems to extend out to the cuticle without a very marked stalk; but it is poorly preserved, presenting the appearance of a reticulated coagulum containing some dark granules seen in the other species.

The dark red, retinal pigment is in strong contrast to the brightly refracting green-yellow spherules found, in this species, aggregated in the cuticular ends of the ordinary epidermal cells.

Phyllodoce catenula Verrill.

Here again we find the same structure; the retinal cells are longer and the lens comes into direct contact with the cuticle, presenting also the finely granular appearance of a coagulated liquid mass.

Some imperfect observations upon *Anaitis picta* Verrill indicate that here again the eyes are much as in *Phyllodoce*.

In the Phyllodocidæ, then, we fail to find any indication of a composite nature in the lens, though it is connected with the cuticle, and not sharply separated from the retinal rods.

The detailed description of the very large eyes of *Genetyllis oculata* M'Int., given by M'Intosh (9), shows clearly that the retinal cells are pigmented and bear rods, but does not clear up the nature of the lens. The material obtained was, however, one specimen that had been "slightly dried."

ALCIOPIDÆ.

Asterope candida Claparède.

Through the courtesy of Professor Patten I have been able to examine well-preserved material from Naples, but only in sections, thus leaving much unobserved.

Owing to the great size and refractory nature of the lens, and to its close approximation to the cuticle, no clear conception of the nature of the cornea could be obtained. No connection of lens and cuticle was discovered, the epidermis apparently continuing all over the region of the pupil. Moreover, the retinal cup itself seems to be closed by an inner cornea passing across the pupil, and thus making two cell layers between the lens and the cuticle, as has been described by Graff (1) and by Carrière (3) and denied by Graber (2). However, the material is insufficient to decide this point, and from similar results in *Nereis* and other annelids, I am inclined to think the optic cup here also may be an open one when seen in true meridional sections.

The retina, as one would judge from the majority of previous observations, is undoubtedly a single layer of cells, each bearing a clear rod, very easily studied. The pigment is restricted to a sharply circumscribed zone where cell body and rod unite and is, I judge, actually in the cells of the retina, not in any special pigment cells, nor outside the retinal cells. Moreover, in my section at least, there are no clear axial regions as in *Nereis*, but on the contrary, the pigment is densest at the axis of each cell, where the rod arises. This concentration of pigment may account for the nucleus-like bodies observed here by some authors.

The very large refracting mass central to the layer of retinal rods is clearly divisible into a peripheral coagulum, the "glas-

körper" of Graff, and a lens proper, or dense spheroidal mass near the pupil. I find, however, no membrane separating those two regions, nor any between the whole mass and the retinal rods; more granular parts of the coagulum represent what have been described as membranes in other genera.

Thus, in a radial section passing through the centre of the lens, there are in *Asterope* the following regions, as shown in Fig. 28:—

1. The expanded optic nerve on the periphery of the retina.
2. The single layer of elongated retinal cells.
3. The zone of yellow-red pigment granules.
4. The layer of long retinal rods.
5. A granular zone comparable to the area of vacuoles seen in *Nereis* (Fig. 2), between the rods and the lens.
6. A thick zone, peripheral part of the "glaskörper," composed of reticulated coagulum.
7. A sharp line of granules.
8. A very thick zone of reticulations, closer than those in the peripheral part.
9. A second granular line forming the boundary of the granular, hard, refracting lens.
10. This is often broken into parallel pieces, but presents a central, more dense part, with concentric structure. The lens proper (10) and the "glaskörper" (5-8) are thus all one continuous mass of coagulum of varying density in successive concentric zones. Both together may be called the lens in the wide sense.

The large eyes of the *Alciopidæ*, so often studied, do not, apparently, agree with those of the other families as elucidated here.

The chief differences lie in the closed state of the optic cup and in the nature of the lens. The former character may prove to be an erroneous conception derived from imperfect knowledge of the difficult corneal region of the eye. The structure of the lens as made out in *Asterope* shows at least its continuity with the retina, and allowing for the important difference obtained by various methods of preparation, we cannot deny that the peripheral part at least, the "glaskörper," may be really composed of separable, rod-like elements. In fact, Graber has figured such elements in *Alciope Contrainii*, as well as their continuity with the epidermis. Yet it would be unjust to accept those results when denying the reality of the membranes and supernumerary nuclei also figured there.

SPIONIDÆ.

A species of *Polydora* having long setal hooks upon the posterior somites as in *P. hamata* of Webster, but inhabiting soft tubes upon the piles of wharves, has four minute eyes buried in the superficial ganglionic layer of the brain. Each eye is a cup of dark brown pigment granules, partly surrounding a clear lens that does not appear to be separated from the surrounding brain mass.

A similar minute eye is seen in sections of *Polydora commensalis* Andrews.

In a peculiar and apparently undescribed *Spio*, taken at Wood's Holl, there are four eyes, the anterior larger and farther apart, as is the rule in the higher Polychætous annelids. Each is buried amongst the ganglion cells of the brain, and has the same simple structure as in *Polydora* (Fig. 71). In some sections there is little doubt that the pigment lies in a few, a very few, cells between the nucleus of the cell and the part next the lens.

The Spionidæ thus present a state of simplification that may be regarded as in some sense a reduction from the degenerated condition found in *Arabella* (Fig. 47); yet, at the same time, it appears to be largely a retention of larval characteristics.

Jacobi (10) has figured the eyes of *P. quadrilobata* and *P. ciliata* as bean-shaped masses of pigment granules applied to a hemispherical lens, and sending a few nerve fibres to the brain. The whole is imbedded in the epidermis, while continuous with the brain. The anterior eyes have scattered pigment near them, and are irregular, thus giving the appearance of more than four eyes. This would favor the supposition that the eyes of the Spionidæ are to some extent degenerate structures.

TOMOPTERIDÆ.

Examination of an immature specimen of *Tomopteris*, taken off the New England coast by the U. S. Fish Commission, shows that the two eyes are buried in the brain (Fig. 72). In each we recognize a lens, somewhat granular, as in *Eulalia*, separated from the pigment cup by a clear zone that may be interpreted as the rod-like ends of a few very large cells. The

pigment in these cells lies where the rod and cell body meet, but leaves a central axial region of the cell clear, as in *Nereis*.

No nuclei could be found in these large retinal cells in the imperfect material at hand, but nuclei are plainly shown in this region in the figures given by Graff (11).

We may thus regard the eye of the Tomopteridæ, provisionally at least, as intermediate between that of the Spionidæ and the more complex forms met with in the Nereidæ, etc.

The simple character of the eyes in this family of pelagic annelids, as compared with the perfect forms found in the free-swimming Alciopidæ, Nereidæ, and Syllidæ, may possibly be connected with the great transparency of the body in Tomopteris, that rendering a projecting convex eye less necessary.

OPHELIADÆ.

Here again I am indebted to Professor Patten for specimens of *Polyopthalmus* from Naples.

The eyes lie in the brain as masses of pigment surrounding, in part, a clear body separable into a denser more easily stained zone, next the pigment, and a central lens at the mouth of the pigment cup and not separated from the surrounding brain substance.

These very imperfect observations would thus reduce the eye to a structure like that of *Spio* (Fig. 71).

Meyer (12) has found greater complexity in the refracting and corneal part of the eye in *P. pictus*, while Lessona (13) found merely a bifid lens mass in a pigmented cup.

The "lateral eyes" of *Polyopthalmus*, so often referred to, are not, judging from my sections, eyes at all, but peculiar epidermal organs composed largely of gland-like tubular bodies, parts of a system of epidermal tubules.

From the notice in the work of Albert (14), it appears that Meyer has abandoned the interpretation of these organs as eyes, and inclines to regard them as possibly light organs.

Another form of reduced or degenerate eye has been discovered in the Capitellidæ, by Eisig (15). The eyes are here collections of scattered pigment cells. In the adult these are in the brain, but in the young may be in the epidermis.

Toward the cuticle the cell has a clear lens-like part in which

there may be a nucleus. This clear end extends amid the epidermal cells towards the cuticle, while the pigmented end extends inward, and is thought to connect with ganglion cells by means of a nerve process.

These cells, I judge, may be compared with the retinal cells of the more perfect eyes; here scattered and not aggregated in such a way that their clear ends could unite to form a large refracting mass.

III. FORMATION OF EYES.

The following observations upon the forming and the immature eyes of several polychætous annelids are unfortunately very unsatisfactory, owing to the lack of sufficient knowledge of the technique necessary to obtain clear results. As far as they extend, however, they aid in completing and in strengthening the general conception arrived at in the study of the adult eye.

Nereis limbata.

The eggs are readily fertilized and the larvæ reared up to a stage represented in Fig. 55. The four eyes then present are obviously the same in position, and are also the same in structure as those in the young *Nereis* (Fig. 56) taken in the surface net. These in turn are identical with the eyes of small specimens four to six millimetres long (Figs. 5, 21), and thus agree with the adult structure.

The four larval eyes are, then, converted into the four of the adult.

In an earlier state (Fig. 54) there are six eye-spots: the posterior four are the permanent ones; the anterior two, the provisional eyes.

The study of the formation and early condition of the four posterior eyes of the larva is thus the study of the formation of the adult eyes.

The first eye-spots appear about the tenth hour after fertilization, as minute golden red areas, one on each side, between the region of the apical pole and the equatorial ciliated band. The larva is now a spherical gastrula inside the egg-membrane.

Surface views and macerations of an eye show a limited number of pigment spherules, less than one hundred, irregularly

scattered over an area about $5\ \mu$ wide, corresponding in size to one of the nuclei of an epidermal cell. These granules are near the cuticle, the nuclei are farther in, so that the pigment appears to be in the outer end of an epidermal cell, or of several cells. The granules are golden yellow, yet reflect reddish light.

The number of granules increases and the mass reflects more red light; at the same time the pigment is arranged in a compact disk, sending a few granules deeper into the ectoblast, and becoming depressed, saucer-shaped, even in a larva of twelve hours. When the cell boundaries are brought out by silver nitrate, the pigment appears to fill the end of a single cell.

At twenty-one hours, when the larva is free-swimming, the pigment cup is filled by a clear, refracting body or lens.

At thirty-six hours, the somewhat pear-shaped larva swims actively towards the light. It has two parts of parapodia represented by setæ sacs, and has a conspicuous band of red pigment about the prototroch. This pigment is obviously different from that of the eyes, and also dissolves in alcohol, while the eye pigment does not. The peculiar greenish pigment at the anal end is also conspicuous at this time.

Each eye has a lens, filling a deep cup of pigment, and reaching out to the cuticle. In side views the cup appears as a crescent.

Similar eyes are found in *N. alacris* reared to this stage.

Near each eye is a clear vesicle, in the ectoblast.

Sections of such eyes, of one at thirty-three hours, give the appearances indicated in Fig. 59 for one fifty hours old.

At this latter period the larva has assumed the form shown in Fig. 54, and the eye (Fig. 59) has an apparently semi-solid lens surrounded by large pigment spherules. No cell walls were seen, but the pigment seems to be in a few cells that have elongated so as to bring their nuclei and the pigment next them away from the cuticle into a deeper position.

These two eyes remain in this condition for some time, as shown by surface views and by sections; but about the seventieth hour we find them more on the ventral side, and moving in from the surface, as irregular streaks of pigment enclosing a clear mass.

These streaks remain up to the one hundred and eighty-fifth hour, and lie close to the above vesicles, which have become very

large, and extend to the ventral face near the base of the palp, right and left.

Though no later stages were examined, it seems that these eyes disappear, or at least have no connection with the eyes of the adult.

The four definitive eyes are seen at fifty hours, in Fig. 54; at the first they have a more nearly transverse arrangement than here figured. Each is a collection of red-yellow pigment granules, in every respect like the provisional eye at ten hours.

By fifty-seven hours the pigment granules are aggregated in a disk-shaped mass which, in maceration, seems to fill the outer end of one cell. These eyes grow quickly, so that at sixty hours the larva has three pairs of nearly equal reddish eye-spots.

A clear lens appears in each cup, and at seventy hours the posterior eyes still look upward, while the anterior, permanent eyes have turned over, so that they look forward, and present a crescentric outline viewed from above.

Sections at eighty-four hours give the same structure as in the provisional eyes at fifty (Fig. 59). Macerations lead one to infer that the pigment is in a few cells, in the ends close to the lens.

At ninety-six hours, the pigment cup has become dark blue, almost black, with a few scattered yellow granules passing inward from it, as seen in the section (Fig. 60).

At one hundred and fifty-six hours, the eyes are blue or dark red, and contain a prominent lens. Moreover, surface views of the bottom of the cup, seen in tangential sections, reveal minute clear spaces in the dark pigment, as shown in the adult (Fig. 17).

Larvæ one hundred and sixty and two hundred and two hours old are no farther advanced than one only eighty hours old, reared in the warmer climate of Beaufort, N.C. (Fig. 55). Sections of these two periods show stages intermediate between Fig. 60 and Fig. 61.

This last figure is that of the young *Nereis* (Fig. 56), and presents an advance, in that the lens and the rods are now distinguishable as two well-defined parts of the refracting mass. Owing to poor preservation, this figure does not approach as near to the adult condition as the eye itself probably does, as indicated by the faint traces of a division of the rod region into separate rods.

It thus appears that in the formation of the eyes of *Nereis* there is no sign of any invagination. The eye arises as a solid mass in the epidermis. The pigment recedes from the cuticle, leaving a clear mass next it, which subsequently is distinguishable as rods and lens, and later separates more or less from contact with the cuticle. The arrangement of nuclei as seen in section and the appearances seen in macerations strongly suggest that the whole eye is merely a collection of epidermal cells with clear ends.

Procærea tardigrada.

The larvæ, while still in the brood sac, but capable of swimming when liberated, have the form indicated in Fig. 58, and are about .15 mm. long. The eyes are four: two larger ventrolateral ones very far apart; two small dorsal, posterior eyes, near together. At an earlier stage all four are nearly in the same transverse line.

Each is a spheroidal mass of bright yellow-red pigment, near the cuticle, but sending inwards a few lines of granules. In each is a clear, spheroidal, refracting lens (Fig. 57), partly surrounded by the pigment granules and in contact with the cuticle. In this transverse section of the head there is a solid mass of ectoblast between the cuticle and the "punctsubstanz." In this no cell boundaries are seen, but the arrangement of the nuclei about the eye may be explained if it is made up of a few epidermal cells. Macerations, give, as in Fig. 63, a collection of elongated cells closely associated with the pigment and with the lens. These cells have processes at the inner ends, and one is seen connected with a cell, probably a ganglion cell. That the pigment is in the outer ends of these cells, and thence passes down along their surfaces, seems probable from macerations in Haller's liquid, osmic acid, acetic acid, and potassium bichromate; yet this could not be satisfactorily demonstrated. In fact, the last reagent gives results suggesting that the pigment is in a special pigment cell sending processes down between the columnar cells, but no nucleus was found in this pigment mass.

The posterior eyes are as yet very small, and furnish early stages in the formation of the eye.

The earliest observed is that in which there are seventeen

clear golden pigment spherules occupying almost exactly one of the polygonal areas representing the epidermal cells as seen from the surface. The pigment granules are scattered so as to leave part of this area free.

The other posterior eye had in this case about twice as many granules.

In another case a macerated posterior eye presents a lens about one-half the diameter of a cell nucleus and imbedded in a mass of pigment granules in the end of what seems to be a single cell, but which may be several cells. A similar stage is represented in the section (Fig. 62) where the minute posterior eye is composed of a few epidermal cells having clear ends next the cuticle, and containing only a few pigment granules between the nuclei and the cuticle.

From the position and structure of these larval eyes and from the facts observed in *Nereis*, we may infer that they become the adult organs.

The formation of eyes in *Procaerea* would then be much as in *Nereis*.

The formation of the eyes of the sexual adults, when compared with the above formation of the adult eyes in the non-sexual form arising from the egg, presents on the whole a fundamental identity. This has been studied by sectioning the new heads borne upon the sexual part of the trunk. The new head is found just posterior to the thirteenth somite; posterior to this the somites may be as many as eighty before the new animal separates. Then the original thirteen somites soon form new ones. The eyes arise as parts of the dorsal thickening of epidermis, making the new head (Fig. 64). As in the larva, the anterior eyes appear first, and thus become larger than the posterior ones and farther apart.

In the earliest stages only the anterior eyes are present as scarcely discernible pigment specks. In section each is a thickening of the epidermis near the base of the lateral antenna (Fig. 65). There is no change in the cuticle, but many elongated epidermal cells here have clear outer ends. These are cut off from the rest of the cells by a delicate membrane-like line passing out to the cuticle on either side. Under the highest powers used this is not a continuous line, but interrupted as in the similarly situated structure seen in adult *Eunice* (Fig. 43).

The pigment begins abruptly at this line and extends inward as if in one cell or between two cells; very little is present in the whole eye, perhaps no more than shown in this section. The epidermal cells are not as yet marked off from the deeper cells, which may become ganglion cells.

A later stage is represented by the transverse section through a posterior eye (Fig. 69).

Several epidermal cells contain the pigment and pass out through the above-mentioned curved line as clear rods extending towards the cuticle. In this hemispherical clear region there are, however, a number of small refracting spherules or minute lenses, of varying size, surrounding the largest central lens. Some of these seem to lie inside the rods or cell ends. Beneath the eye, towards the body cavity, there is now some granular nerve substance. This stage may be compared with the adult condition in *Odontosyllis* (Fig. 46).

A much later stage is represented in the longitudinal section (Fig. 70), which passes through one of the anterior eyes and shows the entire extent of the epidermal thickening forming the new head.

The epidermis is sunk in as an oblique mass to form the eye, and is separable from the underlying ganglion mass.

The amount of pigment is much greater, though still confined to a part of the optic cup.

The bright yellow-red granules pass in irregularly as lines along and apparently between the cells, but there is a sudden cessation of pigment at the curved line marking off the rods. These have now much the same appearance as in the adult.

The main lens is surrounded by many very small ones, which in tangential sections form a complete circle about the largest central one.

Older heads present stages of transition from that of Fig. 70 to the condition found in the adult sexual animal.

Thus in the formation of eyes in the budded sexual form there is the same absence of invagination as in the formation of larval eyes.

In other respects there is also fundamental agreement. In the bud the process differs in that the eye is formed from more numerous, larger cells, and is thus somewhat abbreviated as compared with the formation in the egg larva.

Pedophylax longiceps.

As is well known, the larvæ remain attached to many of the parapodia of the mother, one on each. The epidermis on a rounded elevation, apparently around the opening of the nephridium, secretes a cement which fastens this part of the parent to the posterior end of the larva.

When 2 mm. long, the larva has four dorsal eyes, the anterior larger and farther apart. There is now a mouth, a digestive tract full of purple yolk, and four well-marked somites without parapodia or setæ.

Each eye is a collection of red-brown pigment granules, which, upon maceration, seem to be in the cuticular ends of a few cells, in the youngest posterior eye perhaps in only one cell. As far as the limited observations extend, these eyes agree with the earliest larval eyes of *Procærea*.

The same may be affirmed of the larval eyes of the undescribed *Polydora* mentioned in the previous part of this paper. In larvæ with thirteen somites and long provisional setæ there are four eye spots, the anterior larger and farther apart. In section each eye has a lens in contact with the cuticle and partly surrounded by a cup of brown pigment.

In the adult the eye retains this simple character, though it sinks away from the cuticle and, as far as known, loses all connection with it, as in *Spio* (Fig. 71).

Lepræa rubra?

Small annelids that may be the young of this species are found abundantly upon the wharves. They have a conspicuous series of dark red spots on the dorsal and lateral aspects of the buccal somite posterior to the origin of the tentacles. These spots number about thirty, and are arranged in two irregular transverse rows.

Each spot (Fig. 66) is a somewhat hemispherical clear mass partly enveloped by a cup of large red spherules, and produced as a delicate filament that extends nearly or quite to the cuticle.

The pigment cup is buried deeply in the epidermis where continuous with the brain, and may open in various directions, so that the lens stalk may be variously curved on its passage toward the cuticular surface. Depigmentation reveals no nuclei

in the pigment mass, but a tendency of this to break up into a few smaller masses, suggesting that it is in as many cells.

Provisionally, these eye-spots may be interpreted as having the same structure as the larval eyes hitherto considered.

In the adult *Lepræa* no eyes were found, so that these larval eyes seem to disappear; yet it is possible that these young belong to some other member of the Terebellidæ.

The foregoing observations upon the formation of eyes in the Polychætæ leaves much to be inferred regarding their cell structure; yet this is unfortunately true of most of the previous publications upon this subject, as will appear from the following review.

With reference to the formation of eyes in the budding syllididæ, it is interesting to note that Albert (14) has described pigment spots in *Haplosyllis spongicola* Gr. closely resembling the earliest stages in the formation of the sexual eyes in *Pro-cærea* (Fig. 65). Though no sexual head nor brain is formed in the epitoke or reproductive part of the animal, there are in this separable, free-swimming region many pairs of pigment spots, one on the dorsal base of each parapodium. Each is a collection of elongated, pigmented epidermal cells forming a convex elevation. Each cell has a clear end next the cuticle, these collectively making a "lens." The author regards these organs as the homologues of head eyes, and supposes that they represent eyes in an arrested stage of development, since they have no optic nerve, and so cannot function as eyes.

Larval eyes are represented by Salensky (16) for *Pileolaria*, *Aricia*, and *Terebella*. In sections they appear as pigment cups from which project clear lenses that may reach up to the cuticle much as in Figs. 59, 66. There is, however, a clear nucleus figured in the lens.

No special description of the eyes is given, and these nuclei may possibly be merely those of surrounding cells projected out of their true plane on to the lens.

Meyer (17) has given much more detailed representations of the larval eyes of *Psymbranchus protensus*. Each eye is a pigment cup in a thickening of the ectoblast, and contains a clear lens passing from the cup to the cuticle. Later the cup elongates, becomes conical or urn-shaped, and the lens loses its contact with the cuticle. The arrangement of nuclei about

the eye shows plainly that the epidermis passes in to surround the lens, as in Fig. 70.

Actual sections show cell walls also round about the pigment cup; later the eye sinks away from the surface and appears in section much as in Fig. 71. Here again a nucleus is seen in the lens; this may be explained in the way suggested for the eyes figured by Salensky. Yet it is to be observed that Meyer speaks of the eyes as at first "bestehend aus je einer am proximalen Theile ihres Peripherie mit rothbraunem pigment angefullten Zelle" surrounded by a many-celled thickening of the ectoblast. So he would regard the nucleus as really in the clear part of the cell, not peripheral to the pigment, as I have maintained in this paper.

After these two eyes have moved away from the surface with the brain, they become bilobed, suggesting to Meyer that they subsequently divide to give rise to the groups of eyes subsequently present.

Kleinenberg (18) shows the larval eyes of a *Phyllodoce* in section, resembling Fig. 21 save that cell walls and rods are not present.

The most detailed, the only detailed, account of the formation of the annelid eye is that given by Kleinenberg (18) for certain *Alciopidæ*.

These remarkably large and complex eyes appear to be formed in an even more remarkable manner, which opposes a strong barrier to the extension of the conception advanced in the present paper to include all the eyes of *Polychætæ*.

In these *Alciopidæ* the first appearance of the retina is a solid ectoblastic thickening, one for each eye. These become pinched off from the surface, without the appearance of any invagination; by a separation of the cells of this solid mass, a central cavity is formed, in which a lens subsequently appears, being secreted by the surrounding cells into the closed central cavity. This retinal vesicle establishes a close connection with the brain, even gives off some of its cells to the brain, but later this connection is reduced to the stalk forming the optic nerve. The part of the vesicle near the epidermis becomes thin, and forms the inner cornea, while the rest remains as the retina. The lens is from the first inside a closed sac; is at first granular, then homogeneous. It does not increase as

rapidly as the vesicle, but lies near the cornea, so that a space is left between it and the retina. This space is lined next the retina by a layer of retinal rods, which appear with the pigment, and perforate it. At first, there is a mass composed of a few rods, to judge from the figures, which then becomes split up into as many rods as there are cells; meanwhile, the pigment spreads from one point as a thin layer where the rods and retinal cells are united. There still remains a large space between the rods and the lens, represented in the adult *Asterope* by the coagulated material in Fig. 28, 9-5.

The formation of the vitreous body filling this space is the most unexpected part of the whole process. It is secreted by a single large cell. This is found in the brain before the retina has begun to form at the surface, but later it introduces itself into one side of the retinal vesicle, and subsequently breaks through its walls, so as to pour a secretion into the central cavity. This secretion passes out from near the enormous reticulated nucleus through the cell to the above space, and forms all the vitreous body between the lens proper and retinal rods.

Such unicellular "glaskörperdrusen" are said to occur in other annelids with highly developed eyes.

That these bodies have a remarkable appearance is indicated by the fact that Graff (1) found and figured them as auditory sacs, one near each eye in the adult, connected by a nerve with the circumoesophageal commissures, and containing an otolith. Yet he recognized that each has at first sight somewhat the appearance of a cell.

Since the *Alciopidæ* are at once among the few parasitic annelids, and possess the largest and most complex eyes, we may assume that there is considerable chance of secondary changes having taken place, so that their present ontogeny does not repeat the primitive method. Thus, the formation of the lens inside a closed sac, and the secretion of a large part of the refracting material by the action of a single cell having no direct connection with the retina, may well be recent innovations, and offer no objection to the acceptance of other methods as the more primitive and general.

Polygordius.

Considering the simplicity of *Polygordius*, whether ancestral or secondary, it is interesting to find its larval eyes closely resembling those of *Polychætæ*. Thus, in a section of the apical plate (Fig. 68), each eye-spot is a cup of large yellow-red pigment granules, partly surrounding a clear, refracting lens, that extends up to the cuticle, while the surrounding nuclei suggest that the eye is composed of a few ectoblastic cells. When depigmented (Fig. 67), there is a clear space representing the pigmented region, while the faintly discerned cell boundaries point plainly to the conclusion that the whole eye is made up of a few long cells having refracting substance at the cuticular end, a large nucleus in the other end, and pigment in the intermediate portion.

Hatschek (19) figured the larval eye of *Polygordius* as a thin pigment layer over the inner side of a spherical refracting body or lens, in which nuclei are seen. He regarded the lens as probably made up of clear prismatic cells with small, faint nuclei, but could not decide if the pigment was in those cells, or in the surrounding cells of the apical plate.

In the figures of Fraipont (20) the pigment is a thicker layer, the lens a projecting mass composed of two clear halves side by side, and each containing in its outer end a body that is probably the nucleus spoken of by Hatschek.

Until these eyes are reinvestigated, and those nuclei-like structures shown to be actually nuclei in the cuticular ends of the component elements of the lens, I am inclined to regard the true nature of the eye that indicated in Fig. 67, and to consider the clear ends of the few cells composing it to be the parts seen from the surface as a bilobed or as a single lens.

In addition to the study of the formation of eyes in larvæ and in buds, there is a third method that has not been sufficiently utilized in the annelids. A few observations were made, however, upon the formation of eyes in regenerated heads of the species of *Amphinome* mentioned in the second part of this paper.

From the large number of individuals collected at Green Turtle Cay, Bahamas, it was possible to pick out some in which the heads had been lost, and were in process of regeneration along with a varying number of anterior somites.

Unfortunately, the youngest stages observed (Fig. 29) have already much of the character of the adult eyes. The distinction of rods and lens is, however, less marked, while the whole organ is very minute.

An early connection of lens and cuticle is indicated by the fact that these small eyes have already acquired stalks as long and thick as those of the adult, though the retinal cup is very much smaller.

In the example figured there are, abnormally, two posterior eyes on this one side of the head, each eye having its separate stalk extending from the lens to the cuticle.

IV. SUMMARY AND CONCLUSIONS.

An examination of the eyes in a majority of those families of the Polychætæ in which they are well developed, has shown that there is fundamental agreement in the following general characters.

The eyes are epidermal organs and generally remain connected with the epidermis.

Each is a pigmented cup filled by a refracting mass which projects more or less from the orifice, the pupil, and there usually comes into contact with the cuticle.

The pigmented cup is composed of a single layer of epidermal cells, forming the retina, all essentially alike, though some may be much attenuated.

These cells have nerve processes and contain a pigment that is yellow, red, blue, or black, and may, perhaps, be converted from a lighter into a darker color, two appearing in some cells.

Each cell bears a clear rod, having an axis continued from the cell through the densest part of the pigment; these rods form the peripheral part of the refracting mass, but are part of the retina.

The remaining, central, refracting material is more liquid in nature; it may be nearly a homogeneous lens, or divided into a denser lens proper near the pupil, and a less dense part, vitreous body, next the retinal rods.

The refracting mass is often continuous with the cuticle and by the intervening rods with the retina also.

It may appear as a liquid secreted by the retinal cells or may

show indications of being formed by the fused ends of the retinal cells.

The invagination of the cuticle concerns at the most the stalk of the lens; the main mass is to be regarded as a part of a thickening of the cuticle, or else as a fusion of cell ends abutting against the cuticle.

The whole eye is thus a spheroidal collection of elongated epidermal cells ending in a clear mass that may be secreted, but appears rather to be the modified ends of these cells. Such cells agree essentially with that represented in Diagram 1.

A review of previous work upon such eyes enables us to bring most of it into agreement with this conception, allowing sufficient weight to the differences attributable to insufficient material and imperfect methods.

Some observations upon the formation of eyes in larvæ and in budded heads show that the eye is formed from the epidermis with no invagination, that the epidermal cells become pigmented and elongate, that the rods are the ends of these cells, that the other refracting media appear next the cuticle and may be parts of these same cells.

The opinion that the nuclei of the larval eyes lie peripheral to the pigment as in the adult is, however, not supported by previous descriptions.

The origin of the eyes in the Alciopidæ presents complications that may be regarded as secondary and unusual.

Cases in which eyes are found buried in the brain and separate from the surface are to be considered secondary, either the results of degenerative reductions from the above type or else retentions of larval characters with the addition of separation from the cuticle.

In conclusion we may restate the above facts and ideas with the aid of the accompanying diagram illustrating the presumptive phyllogenetic history of the annelid eye.

Primitively certain areas of epidermis became specially sensitive to light, one or more cells. Such areas (1) contained cells with clear receptive protoplasm near the cuticle, and probably pigment also.¹

¹ This pigment may be regarded rather as one of the secondary concomitants of special activity in translating vibrations than as a necessary antecedent to such special activity.

Such simple areas appear as the first indications of the eyes in the larval Polychætæ, and may, perhaps, remain upon the cephalic branchiæ of some sedentary adults (Serpulidæ), as organs sensitive to changes in illumination.

With the increase in the amount of the clear receptive protoplasm and increase in the efficiency of the organ, there was an elongation of the cells (2) and restriction of the pigment to

DIAGRAM 2.—1-5, successive stages in hypothetical formation of annelid eye. Cuticle represented by long parallel lines; lens and vitreous body by short lines; pigment by large dots, and protoplasm by fine ones. The rods remain clear.

their less sensitive areas. Such eyes may reappear in the formation by budding (Fig. 65), and seem to be retained in some larvæ, as Fig. 66, and in *Polygordius* (Figs. 67, 68), and are probably represented by the stages shown in Figs. 57, 60.

The cuticular ends of the cells next become modified as refracting bodies (3), perhaps a spherical lens in each cell, next the cuticle, as indicated in Figs. 46, 69, 70.

With a greater elongation of the cells (4), a pigmented retinal cup was formed containing the lens mass, now more efficient and gradually divided, in some cases, into a lens proper near the cuticle and an intervening vitreous body next the rods. Such eyes remain as the perfect adult structures in many cases (Figs. 3, 8, 30, 31, 32, 33, 34, 46, 49, 52).

Any component cell will have the parts represented in Diagram 1, a nerve fibre passing to the brain, a pigmented part, a clear rod, and a part of the common refracting mass in contact with the cuticle.

Finally, in some perfect eyes, as seems the case in the *Alciopidæ*, and in some degenerating eyes, the sinking in from the surface may extend so far that the eye is entirely removed from the cuticle (5), and may then, apparently, become closed in to form a complete vesicle with no connection with the epidermis. This last phase is, however, an unusual one, and may possibly not really exist in any described eye.

In all that precedes, reference has been had to the eyes upon the cephalic lobe proper, near the brain, and especially well developed in errant *Polychætæ*. The peculiar branchial eyes of some sedentary groups may, however, be brought under the same general conceptions, at least as to their origin.

As illustrated in a former article in Vol. V. of this Journal, the numerous epidermal eyes upon the branchial processes of the heads of some tubicolous *Polychætæ* differ from the eyes described in the present paper, in that each cell has its refracting body isolated from that of the others. There is thus no multicellular lens, but a compound eye or aggregate of separate cells each an eye in itself.

These may be regarded as originating in a simple epithelium represented in 1, Diagram 2. Subsequently, however, the clear part of the cell became specialized only in the axial part of the cuticular end, not throughout it as in the stage 2. In this axial part, also, the lens-like body was found still in contact with the cuticle as in 3.

The elongation of the cells, each having a refracting body *within* its cuticular end, did not result in the formation of a large lens mass and, moreover, there was no sinking, but rather an elevation of the entire region. This elevation is, perhaps, connected with the necessities of a functional compound eye, but

may have been in part due to the presence of a hard skeleton immediately beneath the epidermis.

Though this is the character of the branchial eye in general, the peculiar eyes met with in *Hypsicomus* present what may be regarded as a transition towards the "camera" eyes of the annelids. Each eye here has a single conical lens or rod and lens combined, continuous with the cuticle and springing from a single cell at its apex. The pigmented cells round about this elongated lens are, however, applied against it as if taking part in its formation. The eye might thus be compared with 2, Diagram 2, supposing only one cell to have a rod-lens and the adjacent cells bent over towards this refracting part. This eye is then formed upon the sunken-in type, and seems to have arisen without invagination. At the same time the central cell of this peculiar eye presents a refracting inclusion comparable to that found in the separate cells of the compound eye.

There is thus agreement in all the eyes of *Polychætæ* to the extent that the visual cells are pigmented, epidermal cells having some sort of clear, refracting material next the cuticle.

In the compound eye this is within separate cells. In *Hypsicomus* it is in one cell and also forms a single cuticular ingrowth. In the camera eyes of the higher *Polychætæ* it forms rods and lens structures, together with various ingrowths of the cuticle.

Not knowing how far the annelid cuticle is a true secretion from the cells, rather than a transformation of their ends, no sharp distinction has been drawn between it and the various refracting bodies so often continuous with it.

JOHNS HOPKINS UNIVERSITY,

May 23, 1891.

REFERENCES.

1. GREEF. — Die Alciopiden: *Nova Acta Leopold.* 39 (2). 1877.
2. GRABER. — Augen der freileben marinen Borstenwürmer: *Arch. f. mik. Anat.* 17. 1880.
3. CARRIÈRE. — Die Sehorgane der Thiere. 1885.
4. PRUVOT. — System nerveux des annélides: *Arch. Zool. Ex.* 2, s. T. 3. 1885.
5. JOURDAN. — Eunice: *Ann. Sci. Nat. Zool.* T. 1. 1886.
6. JOURDAN. — Siphonostoma: *Comptes Rendus.* T. 102. 1888.
7. GRAFF. — Spinther: *Zeit. f. Wiss. Zool.* 46. 1888.
8. BEDDARD. — Mergui Archipelago Annelids: *Journ. Linn. Soc.* 21. 1888.
9. M'INTOSH. — Annelida Polychæta. *Challenger Reports.* XII. 1885.
10. JACOBI. — Polydoren der Kieler Bucht. 1883.
11. GREEF. — Pelagische Anneliden: *Zeit. f. Wiss. Zool.* 32. 1879.
12. MEYER. — Polyopthalmus: *Arch. f. mik. Anat.* 21. 1882.
13. LESSONA. — Sull' anatomia dei polioftalmi: *Mem. Reale Acad. Torino.* T. 35. 1884.
14. ALBERT. — Haplosyllis: *Mith. Zool. Sta. Neapel.* 7. 1886.
15. EISIG. — Die Capitelliden: *Fauna und Flora des Golfes von Neapel.* 16. 1887.
16. SALENSKY. — Développement des Annélides: *Archives de Biologie.* IV. 1883.
17. MEYER. — Körperbau der Anneliden: *Mith. Zool. Sta. Neapel.* 8. 1888.
18. KLEINENBERG. — Lopadorhynchus: *Zeit. f. Wiss. Zool.* 44. 1886.
19. HATSCHKE. — Entwicklungsgeschichte der Anneliden: *Arb. Zool. Inst. Wien.* 1. 1878.
20. FRAIPONT. — Polygordius: *Fauna und Flora des Golfes von Neapel.* 14. 1887.

EXPLANATION OF PLATE IX.

[All figures drawn with camera and lenses of Zeiss.]

FIG. 1. Side view of anterior end of male *Nereis alacris* V., heteronereis state, showing position of eyes. Proboscis protruding. $\times 50$.

FIG. 2. Part of section of eye of the same, showing union of rods (*r*) and coagulated lens (*l*). $\times 700$.

FIG. 3. Section of outer part of eye of *Nereis virens*, showing approximation of lens to cuticle. On right the lens is shrunk away from the rods. $\times 325$.

FIG. 4. Retinal cell with rod, *Nereis limbata*, epitoke state. Macerated in seawater and H_2SO_4 . $\times 425$.

FIG. 5. Dorsal view of anterior end of a young *N. limbata*, 6 mm. long. $\times 50$.

FIG. 6. Isolated retinal cell and rod of *Nereis pelagica*. $\times 1000$.

FIG. 7. Isolated retinal cell and rod, with fragments of lens, *N. limbata*, epitoke state. Haller's liquid. $\times 425$.

FIG. 8. Entire section through centre of posterior eye of *N. alacris*, heteronereis state. $\times 325$.

FIG. 9. Isolated retinal cells and rods of *N. alacris*, heteronereis state. Hertwig's liquid, followed by Haller's. $\times 700$.

FIG. 10. Isolated lens of the same. $\times 175$.

FIG. 11. Side view of anterior end of *N. limbata*, epitoke. Proboscis extruded. $\times 20$.

FIG. 12. Isolated rods of the same, side and end views. $\times 700$.

FIG. 13. Portion of section of an eye of *N. pelagica*, showing a process of the cuticle approaching the lens. $\times 175$.

FIG. 14. Two retinal cells and rods of *N. alacris*, heteronereis state. The one on the left vacuolated, probably by macerating liquid. $\times 1000$.

EXPLANATION OF PLATE X.

[Figures drawn with Zeiss camera and lenses.]

FIG. 15. Tangential sections of retina of *Nereis alacris*, heteronereis state. Partly depigmented in Grenacher's liquid. *a*, at level of clear axial passages; *b*, just peripheral to *a*. $\times 930$.

FIG. 16. Section like *a* of Fig. 15, but entirely depigmented in eau de Javelle. $\times 930$.

FIG. 17. Tangential section as in 15, *a*, but not depigmented. $\times 930$.

FIG. 18. Tangential section peripheral to Fig. 17. Not depigmented. $\times 930$.

FIG. 19. Tangential section nearer periphery of retina, cutting nuclei. Not depigmented. $\times 930$.

FIG. 20. Isolated retinal cell and rod of young *N. limbata*, 6 mm. long. $\times 930$.

FIG. 21. Section of entire eye of same. $\times 430$.

FIG. 22. Radial section, part of retina of *N. alacris*, heteronereis state. Partly depigmented in eau de Javelle. $\times 930$.

FIG. 23. Same as last, but entirely depigmented in Grenacher's liquid. $\times 930$.

FIG. 24. Tangential section across bases of rods near retinal pigment. *N. alacris*, heteronereis state. $\times 930$.

FIG. 25. Same as last, showing boundaries of rods as well as granular axes. $\times 930$.

Fig. 26. Tangential section across rods near the lens. $\times 930$.

Fig. 27. Tangential section of part of lens when shrunk into polygonal, rod-like masses. $\times 930$.

FIG. 28. *Asterope candida* Clpd. Radial section through retina and all of the refracting media of the eye. 1, optic nerve fibres; 2, retinal cells; 3, pigment zone; 4, retinal rods; 5, granular material at ends of rods; 6, zone of coarsely reticulated coagulum; 7, granular line of demarcation; 8, zone of finely reticulated coagulum; 9, granular line of demarcation at periphery of lens proper, 10. $\times 230$.

FIG. 29. *Amphinome Pallasii*? Section of young eyes in regenerated head. Case of duplication of a posterior eye. $\times 230$.

FIG. 30. Section of entire eye. Same as Fig. 29. $\times 560$.

FIG. 31. Section of entire eye of *Eulalia annulata*? $\times 560$.

EXPLANATION OF PLATE XI.

[Figures drawn with Zeiss camera and lenses.]

- FIG. 32. *Eunice violaceo-maculata*. Section of outer part of eye, with connection of cuticle and lens. $\times 175$.
- FIG. 33. Section of an entire eye of *Unice ornata*. $\times 175$.
- FIG. 34. Section of entire eye of *Marphysa sanguinea*. $\times 175$.
- FIG. 35. Same, but transverse to greatest axis of eye. Partly depigmented. $\times 325$.
- FIG. 36. Tangential section of portion of retina of *E. violaceo-maculata*. Depigmented. $\times 1020$.
- FIG. 37. Radial section of part of retina and periphery of lens. *E. ornata*. Depigmented. $\times 670$.
- FIG. 38. Similar section of *Marphysa sanguinea*. Not depigmented entirely. $\times 475$.
- FIG. 39. Side view of anterior end of red male *Autolytus prolifer*. $\times 75$.
- FIG. 40. Isolated retinal cells of same. Macerated in sea-water and H_2SO_4 . On the left an unusual branched cell. $\times 1000$.
- FIG. 41. Connection of cuticle and lens, by means of a slender stalk in adult female *Procarea tardigrada*.
- FIG. 42. Isolated lens of *Procarea tardigrada*, non-sexual form. $\times 175$.
- FIG. 43. Section of part of retina and periphery of lens of *Unice violaceo-maculata*. Depigmented. $\times 475$.
- FIG. 44. Section of entire dorsal eye of *Autolytus prolifer*, male. $\times 675$.
- FIG. 45. Isolated retinal cells and rods of *Marphysa sanguinea*. $\times 1000$.
- FIG. 46. Section of entire eye of *Odontosyllis lucifera*. Partly depigmented. $\times 750$.
- FIG. 47. Section of one of the largest eyes of *Arabella opalina*. $\times 175$.
- FIG. 48. Isolated retinal cell and rod of *Odontosyllis lucifera*. $\times 1000$.
- FIG. 49. Section of entire eye of *Podarke obscura*. $\times 400$.
- FIG. 50. *Lepidonotus squamatus*. Isolated element of lens attached to pigmented end of a retinal cell. $\times 750$.
- FIG. 51. Two isolated retinal cells and rods of above. $\times 675$.
- FIG. 52. Section of entire eye of the same. $\times 400$.
- FIG. 53. *Sthenelais picta*. Part of a radial section, showing retinal cells and rods and some lens elements. $\times 1020$.

EXPLANATION OF PLATE XII.

[Figures drawn with Zeiss camera and lenses.]

- FIG. 54. Dorsal view of larva of *Nereis limbata*, 50 hours old. $\times 175$.
 FIG. 55. The same, eighty hours old, reared at Beaufort, N.C. $\times 175$.
 FIG. 56. Young *Nereis* taken in tow-net, Beaufort, N.C. $\times 50$.
 FIG. 57. Half of section across head of larva of *Procareia tardigrada*, showing larval eye. $\times 750$.
 FIG. 58. Dorsal view of above larva. $\times 250$.
 FIG. 59. Section of provisional eye of larval *Nereis limbata* at stage shown in Fig. 54. $\times 1775$.
 FIG. 60. Section of definitive eyes of same, ninety-six hours after fertilization. $\times 1775$.
 FIG. 61. Section of eye of young *Nereis* seen in Fig. 56. $\times 1070$.
 FIG. 62. Section of posterior eye of larval *Procareia tardigrada*. $\times 750$.
 FIG. 63. Maceration of same larval eye, showing lens, pigment granules, and neighboring cells. $\times 1000$.
 FIG. 64. Dorsal view of non-sexual form of *P. tardigrada* where head of male is forming. Beaufort, 1884. $\times 50$.
 FIG. 65. Section of epidermis of new-formed sexual head of same; the earliest appearance of an anterior eye as elongated cells, one containing pigment. $\times 475$.
 FIG. 66. Section of part of head of young *Lepraea rubra*, showing one of eye-spots. Depigmented thirty-six hours in Grenacher's liquid. $\times 1020$.
 FIG. 67. Section of one side of cephalic plate of a *Polygordius* larva. Depigmented in acidulated alcohol. $\times 1020$.
 FIG. 68. The same, but not depigmented. $\times 1020$.
 FIG. 69. Part of transverse section of new sexual head of *Procareia tardigrada*, representing one of the posterior eyes seen in Fig. 64. $\times 1020$.
 FIG. 70. Longitudinal section of same, showing an anterior eye. $\times 470$.
 FIG. 71. Section of eye and surrounding brain cells in a species of *Spio*. $\times 470$.
 FIG. 72. Similar section from a species of *Tomopteris*. $\times 470$.