The Retina and Optic Ganglia in Decapods, especially in Astacus.

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With Plates 1—3.

1. Introduction.

The recent discoveries in the finer structure of the nervous system have been so numerous and so important that we may well regard the present as a period of more than usual progress in this direction. The advancement thus far made has been rendered possible mainly through the employment of two new methods of histological investigation: Golgi's method for impregnating nervous elements with salts of silver and Ehrlich's method for staining living nervous elements with methylen blue. Both these methods have yielded extraordinary results, but they have been used chiefly in elucidating the finer structure of the nervous system in vertebrates, though, as the investigations of Biedermann, von Lenhossek, Retzius, and others show, the invertebrates have by no means been neglected. It was my purpose in undertaking the present studies to attempt an application of these methods to the solution of some problem in the organisation of the nervous system in invertebrates, and, being already somewhat familiar with the structure of the retina in crustaceans, I was led to take up the study of the optic ganglia in these animals.

The results that are recorded in the following pages represent, in part, the work of two years during which I held an appointment

to a Parker Fellowship from Harvard University, Cambridge, U. S. A., a privilege that enabled me to enjoy the advantages of European travel and study. My investigations were carried on at several continental universities. During the winter semester of 1891—92 I worked in the Zoological Laboratory at Leipzig under the direction of Professor LEUCKART. The following summer semester was spent in Berlin at the laboratory of Professor F. E. SCHULZE. The succeeding winter semester was passed at Freiburg in Baden, where most of my work was done under the supervision of Professor WEISMANN, though, through the kindness of Professor VON KRIES, I also had the opportunity of making some experiments in the Physiological Laboratory of that university. From Freiburg I went to the Zoological Station at Naples, where, by the courtesy of Professor DOHRN, I had the privilege of occupying a table for some three months. The encouragement to investigation and the opportunities offered at these institutions are too well-known to require comment, and the kindliness and personal attention with which, as a student, I was invariably received make it a pleasant duty for me to acknowledge my indebtedness to the directors and assistants under whom I worked. I am also under obligations to Dr. OTTO VOM RATH of Freiburg for suggestions and help in obtaining much necessary material, as well as to Signor SALVATORE LO BIANCO for his untiring efforts in procuring for me many interesting and important crustaceans. Although my studies were completed at Naples and the manuscript of the present paper was in part prepared there, I was forced to defer the completion of it till my return to America.

2. Materials and Methods.

The two species of crayfish that I studied, were *Astacus fluviatilis* Fabr., and *Astacus leptodactylus* Esch. The optic organs in these two animals are essentially similar, and the following account is believed to refer with equal accuracy to either species. In one respect, however, I have limited my observations; to avoid the possibility of error resulting from slight specific differences, I have taken all enumerations of nerve fibres, retinal elements, etc. from one species, *Astacus fluviatilis*. Although my work has been done for the most part on the two species of crayfish mentioned, I have also studied, for the sake of comparison, representative species of the chief groups of crustaceans.

The following notes on the methods that I employed may be of assistance to those who undertake similar studies.

The rapid Golgi method as described by Kölliker (91, pag. 9) yielded good results when applied to the optic organs of the crayfish, especially when the modification suggested by Ramón y Cajal was adopted and the preparations, after having passed once through the silver bath, were again put into the solution of osmic acid and potassic bichromate, and then reimpregnated with silver. A third or even a fourth application of the silver solution seemed often advantageous. On the whole, better results were obtained from material imbedded in paraffine than from that in celloidin.

In preparations made by the Golgi method, the ganglion cells were colored less frequently than the nerve fibres or their terminal fibrillations. The relatively large size of the nerve fibres and the peculiar course that they took through the ganglia made it often difficult to prepare sections in which the entire extent of a given fibre was shown, but this difficulty was due rather to the peculiar anatomy of the ganglia than to any defect in the method. For the study of the finer structure of the rhabdome, the Golgi method was invaluable.

In employing methylen blue, I followed the general directions given by Retzius (90, pag. 24). For each crayfish experimented upon, about one tenth of a cubic centimeter of a 0.2 % aqueous solution of methylen blue was injected into the ventral blood sinus. Animals thus treated seemed to suffer no inconvenience, and, after being kept a week or so under normal conditions, they usually lost all traces of the blue coloration. When, however, they were killed and dissected some twelve or fifteen hours after they had been injected, many of the nervous elements were found to be colored intensely blue. The elements in the optic ganglia were less frequently stained than those in other parts of the nervous system, but among a dozen injected specimens there were always some three or four in which the optic ganglia were favorable for study. The ganglia in these animals were carefully removed and studied at once in the fresh condition, camera drawings being made of the more fully stained parts. It was necessary to do this without loss of time; for, soon after the death of the animal, the sharply differentiated blue stain begins to disappear, in part perhaps by fading, in part certainly by diffusion. Notwithstanding this drawback satisfactory results were easily obtained

Although the connection of ganglionic cells with nerve fibres could be very clearly demonstrated in preparations made by the method just described, it was almost impossible in such material to determine the precise location of a ganglionic cell or the exact direction taken by its nerve fibre. Since these determinations were necessary in order to gain a clear idea of the structure of the ganglia, I attempted to devise a process for making sections from material stained in this way. Two methods were finally obtained. In the first of these, a published account of which has already appeared (cf. PARKER, 92), the tissues of the ganglion were fixed and the color rendered permanent by means of aqueous corrosive sublimate. Preparatory to imbedding in paraffine, the material was dehydrated in methylal containing a little corrosive sublimate, instead of in alcohol, then transferred to xylol, and finally put into paraffine. The second method is essentially like the first except that, in place of methylal as a dehydrating reagent, alcohol containing 8% corrosive sublimate was used[1]. As this method has not yet been published, I give briefly the necessary steps in employing it. The ganglia, after being freed from the surrounding tissue, were first put into an aqueous solution of sublimate, then successively into 30%, 50%, 70%, and 95% alcohol, each grade, of course, containing its proper proportion of sublimate. The material was allowed to remain in each of these fluids about a quarter of an hour. From 95% alcohol it was transferred for an hour to absolute alcohol containing, of course, 8% sublimate, then for another hour to a mixture of one part of this alcohol and one part xylol, and finally to pure xylol. The preparation may stay indefinitely in this last fluid, from which the transfer to paraffine may be made.

In sections made in either of these ways, the methylen blue appeared in the form of a fine precipitate, and the position of ganglion cells, as well as the direction of nerve fibres, could be satisfactorily ascertained. The method, however, is not so favorable for the study of the fibrillar branches into which a nerve fibre subdivides as it is for the study of the larger fibres and cells; for the finer fibrillae,

[1] The grades of alcohol required were made by mixing strong alcohol containing 8% corrosive sublimate with water saturated with the same salt; thus 30% alcohol consisted of 30 c. c. of strong alcohol containing 8% corrosive sublimate and 70 c. c. of water saturated with sublimate. It is advisable to prepare the grades of alcohol some time before they are to be used, and to filter them after they have been standing a few days.

instead of appearing as continuous blue lines such as one sees in the fresh preparations, are represented often by a single row of disconnected bluish dots. I, therefore, usually studied the finer fibrillae in the freshly stained material, and employed sections only when it was necessary to determine the exact position of ganglion cells or nerve fibres.

Golgi's method, as well as that of Ehrlich, has the peculiarity of staining relatively only very few nervous elements. Of the more usual methods by which all the elements in a ganglion are stained, I know of none that gives such good results as the one recently suggested by vom Rath (93, pag. 102). According to this method, the tissue is fixed in a solution of osmic, acetic, and picric acids, and platinic chloride, and afterwards »reduced« in crude pyroligneous acid (Holzessig). This method presents the double advantage of being unfailing in its results and of yielding preparations remarkably clear and trustworthy.

For the study of the retina and retinal nerve fibres it was necessary to prepare depigmented sections, and for this purpose I used as a depigmenting fluid a 0.1 % aqueous solution of potassic hydrate in a way already described (cf. Parker, 90, pag. 3). In one respect, however, I have improved this former method. Instead of using, as a fixative for the sections, a Schällibaum mixture containing Squibb's flexible collodion, which sometimes allows the section to loosen in absolute alcohol, I now employ a mixture of the fixatives of Schällibaum and Mayer. When small drops of each of these fluids are thoroughly mixed on a slide, a whitish sticky paste results, which, even in extremely small amounts, resists the loosening action of both potash and absolute alcohol. The original cloudiness of the mixture is due to the presence of oil, water, and glycerine; upon dehydrating the sections in absolute alcohol, this, of course, disappears, and mounted preparations are as clear as those made with either one of the fixatives.

In the course of my work, it was necessary to make careful enumerations of retinal elements and of nerve fibres. The optic nerve fibres can be counted in good transverse sections of the optic nerve, the operation being more tedious than difficult. On account of the variation in the size of the fibres, it was necessary to count all the fibres in a nerve, the method of estimating by proportions giving rise to too great an error. The fibres were counted by means of a crossed-line eye-piece micrometer, such as is used for counting

blood corpuscles. When the magnification was so arranged that each square contained on an average about eight fibres the repeated enumeration of any group of squares gave nearly constant results. Thus ten enumerations carried out on the same four squares gave the following figures: 37, 36, 36, 36, 36, 35, 36, 35, 36, 36: average 35.9.

The number of ommatidia, or retinal elements, was determined by counting the corneal facets. Since the facets were extremely uniform in size, proportional estimates could be made without seriously impairing the final results. The method employed in this enumeration consisted in comparing the area of a facet with the area of the whole corneal cuticula in terms of weight, and was carried out in the following way. From a number of small sheets of paper of equal size, those were selected that did not vary in weight from a given sheet assumed as a standard by more than a half per cent. A complete corneal cuticula was then carefully cleaned, cut into small squarish pieces, and the outlines of the pieces traced by means of a camera on the sheets of paper previously selected. The paper areas thus outlined were cut out and weighed, the total weight being taken to represent the total area of the corneal cuticula. In a similar way outlines of small parts of each piece of corneal cuticula were made, and the exact number of facets within each one of these was accurately counted. The total weight of these pieces could then be said to represent the number of facets which they collectively contained, and in this way the value of a facet in terms of weight was easily obtained. Having the whole corneal cuticula, as well as a single facet, represented in weights, it was easy to estimate the total number of facets.

Several precautions are necessary in using this method. First, the pieces of corneal cuticula, though assumed to be flat, are in reality small parts of a nearly spherical surface, and thus must be somewhat greater in area than their outlines indicate. Further, it must be remembered that in drawing with a camera the image is somewhat distorted, its periphery being relatively larger than its central part. These sources of error partly correct each other; they can be largely eliminated, however, by judiciously selecting, in reference to the larger area, the position of the smaller one in which the facets are counted. If the smaller area stretches from the centre to the periphery of the larger one and has an appropriate form, both sources of error would be corrected; for both the unit of measure

and the part measured would be subjected to the same distortion. The method has been tested by comparing its results with actual enumerations. In all cases the estimated number has not differed from the actual number by more than 1% of the total. Thus, in one case, the estimated number of facets was 326.4, the counted number 324.75, a difference of approximately a half per cent. This seems to me to justify the employment of the method.

3. General Structure of Optic Stalks.

The nervous organs contained within the optic stalk of the crayfish are so complex in structure that it will add considerably to the clearness of the following account if, in the beginning, a few words are devoted to the shape and position of the stalks themselves. Each stalk has somewhat the form of a short cylinder movably attached by its proximal end to the animal's body and terminated distally by a nearly hemispherical surface. This surface is for the most part occupied by the retina and may be called the distal surface of the stalk; a line connecting its centre with the centre of the proximal end of the stalk defines the axis of this structure. As the stalk cannot be rotated around this axis, the surface of its cylindrical portion may be subdivided as follows: when its axis stands at right angles to the median plane of the animal, that portion of its cylindrical surface which faces dorsally may be called its dorsal surface; that which faces anteriorly, its anterior surface, etc. Thus, in addition to its distal surface, the stalk may be said to have a dorsal, a ventral, an anterior, and a posterior surface. These four surfaces border, of course, on the distal surface, whose periphery may therefore be divided into four corresponding segments — dorsal, ventral, anterior, and posterior. This method of subdividing the surface of the stalk might at first seem rather arbitrary; but, as a matter of fact, the four surfaces of the cylindrical portion are easily recognised, since the stalk is not strictly cylindrical, but flattened dorsoventrally. The terms mentioned in this paragraph have been found convenient in describing the crayfish's eye, and their usage as defined above will be adhered to in the following pages.

The nervous structures contained within the stalks have received such a variety of names that an accepted nomenclature for them can hardly be said to exist. Although no single set of terms

thus far proposed is fully satisfactory, I have not attempted to invent new ones, but have adopted such names from those already in use as seemed to me appropriate on account of their expressiveness or their more general acceptance.

When a longitudinal section of an optic stalk is examined (Pl. 1 Fig. 27), it will be observed that the cylindrical portion is covered with a layer of firm, thick cuticula (*cta*) strongly impregnated with salts of lime and resembling that which covers the greater part of the animal's body; proximally this cuticula becomes thin and flexible in the joint between the stalk and the body, and distally it passes rather abruptly into a thin transparent layer, the corneal cuticula (*crn*), which covers the retina. The thick cuticula, as well as that forming the joint of the stalk, has its inner surface covered with a thin cellular layer, the hypodermis (*h'drm*), which in the region of the corneal cuticula becomes greatly thickened, forming the retina (*r*). From the proximal surface of the retina an immense number of nerve fibres, the retinal fibres (*fbr.r*), make their way to the ganglionic mass that lies in the central part of the stalk. This mass consists of four ganglia, which may be distinguished, beginning with the one nearest the retina, as the first, the second, the third, and the fourth optic ganglion (I, II, III, IV). From the last of these the optic nerve (*n.opt*) extends to the brain. The enlargement of the brain formed by the expansion of the optic nerve may be called the optic lobe. The advantages that these terms present over some already proposed will be seen in the sequel.

4. Retina.

a. Form.

The retina in *Astacus*, even upon superficial examination, is seen to be unsymmetrically developed, its anteroposterior extent being much greater than its dorsoventral one. The ommatidia composing it are very uniform in size and regular in arrangement, and afford a convenient means of measuring its dimensions. Their positions are marked by the corneal facets, wh ch are square in outline and arranged upon what I have called the tetragonal system (cf. Parker, 91, pag. 60); i. e., they are regularly placed side by side so as to form rows extending in two directions at right angles to each other. These rows run obliquely from the anterodorsal angle

of the retina to its posteroventral one and at right angles to this; i. e., each facet is placed so that its four angles point one dorsally, one ventrally, one anteriorly, and one posteriorly (Pl. 1 Fig. 29). The facets may also be regarded as arranged in rows extending in an anteroposterior and in a dorsoventral direction; but, in such rows, the adjoining facets, instead of having their sides together, are, of course, corner to corner. These rows give an accurate measure of the extent of the retina in their respective directions. As the result of a number of measurements (vid. table below), it was found that, while the rows in the anteroposterior direction through the centre of the retina contained about 58 ommatidia, those in the dorsoventral direction had only about 31; in other words, in the adult *Astacus*, the retina is about twice as long as it is broad.

Sepcimen	Sex	Length of Specimen	Eye	Anteroposterior Curvature			Dorsoventral Curvature		
				Radius	Arc	Facets	Radius	Arc	Facets
				mm			mm		
1.	♀	12.3 cm.	R.	1.64	187°	54	1.25	130°	29
			L.	1.63	184°	54	1.25	134°	30
2.	♀	11.7 cm.	R.	1.64	190°	58	1.25	128°	29
			L.	1.69	190°	58	1.29	127°	30
3.	♂	10.6 cm.	R.	1.69	188°	58	1.22	147°	32
			L.	1.53	187°	57	1.22	142°	32
4.	♂	11.1 cm.	R.	1.55	184°	60	1.19	130°	30
			L.	1.55	184°	60	1.25	130°	30
5.	♂	11.0 cm.	R.	1.64	195°	60	1.16	150°	31
			L.	1.63	196°	60	1.19	148°	33
Average				1.62	189°	58	1.23	137°	31

Not only is the extent of the retina unequal in different directions, but the curvature of its outer surface also varies. In an anteroposterior direction as measured on perfectly fresh eyes, the radius of curvature is about 1.62 mm. and the retina extends through some 189°, while the dorsoventral curvature with a shorter radius of only 1.23 mm. has also the smaller angular extent, 137°.

The measurements upon which these statements are based are contained in the preceding table. The length of the specimen, as recorded here, was measured from the tip of the rostrum to the extreme end of the telson when the chief axis of the animal was approximately straight.

Since the ommatidia rest as a rule with their longitudinal axes vertical to the corneal surface, the divergence of the axes of any two adjoining ommatidia can be easily calculated from the data just given. Thus, in an anteroposterior row, since 58 ommatidia occupy an arc of 189°, the axes of any two adjoining ommatidia must diverge from each other at an angle of about 3° 15′; calculated in a similar way, those in the dorsoventral rows diverge at a slightly greater angle, 4° 25′. It must be remembered, however, that both in the anteroposterior and in the dorsoventral rows, adjacent ommatidia are in contact with each other only at their angles and that consequently their axial divergence is greater than that between any two adjacent ommatidia in the oblique rows where these bodies are placed with their sides together, not corner to corner. The divergence of two adjacent ommatidia in the oblique rows was found by observation to be about 3°, the smallest angle made by the axes of adjoining ommatidia.

The total number of ommatidia in the adult retina is easily determined by counting the number of corneal facets; and, as is shown by the following enumerations taken from the right eyes of five crayfishes, the number may be placed approximately at 2500.

						Average
Length of specimen in cm . . .	10.1	10.0	10.6	8.0	7.9	9.3
Number of corneal facets . . .	2696	2872	2456	2378	2375	2555

b. Structure of Ommatidia.

Notwithstanding the care and frequency with which the ommatidia in *Astacus* have been studied, the results of even the later investigators are by no means in full agreement, and I therefore venture to redescribe these organs, dwelling at length, however, only upon those points where a difference of opinion exists or where I have gained by examination a clearer insight into their structure. According to my own observations, each ommatidium in *Astacus* contains, in addition to one or more accessory pigment cells, the

following elements: two corneagen cells, four cone-cells, two distal retinular cells, one rudimentary and seven functional proximal retinular cells, making a total of sixteen cells. This number is not only characteristic for *Astacus*, but, as I have previously attempted to show (Parker, 91, pag. 114), for all decapods, a conclusion that is supported by the recent investigations of Viallanes (92) on *Palinurus* and of Herrick (92) on *Alpheus* so far as they touch this question. The enumeration of the ommatidial cells in *Astacus* as given by Szczawinska (91) supports, except in two particulars to be discussed later, this same conclusion.

The accessory pigment cells in *Astacus* fill the space between the proximal ends of the ommatidia, and extend from the distal surface of the basement membrane to the middle of the rhabdomes. Their nuclei occupy proximal positions (Pl. 1 Figs. 1 and 7, *nl.pg*), and their pigment, like that in the corresponding cells of other decapods, has the quality of reflecting light. These cells, which were first described in *Astacus* by Carrière (85, pag. 169), were also observed by Szczawinska (91, pag. 546), who believed that each ommatidium probably contained seven of them, since they seemed to alternate with the seven proximal retinular cells. The bodies that she figures (Pl. 17 Fig. 9, *pg 3*), however, do not represent each a single cell but processes from cells; and, as I ascertained by counting the nuclei, the number of these cells present for each ommatidium, though somewhat variable, was usually one, never seven.

The two corneagen cells cover the distal end of the ommatidium; their nuclei occupy the dorsal and ventral angles of this structure (Pl. 1 Figs. 1 and 3, *nl. crn*) and are separated by a line, which, though not visible in the protoplasm of their cells, is well marked in the corneal cuticula, the product of these cells. This line extends from the anterior to the posterior angle of the facet, and represents very probably the boundary between these two cells. My observations confirm those of Carrière (89, pag. 225) and of Szczawinska (91, pag. 541), according to whom there are only two corneagen cells for each ommatidium; Reichenbach's (86, pag. 91) previous enumeration of four such cells in *Astacus* is, without much question, erroneous.

The four cone-cells are in contact with the proximal surface of the corneal hypodermis, and extend from this level to the basement membrane. When seen from the side (Pl. 1 Fig. 1), they present four distinctly marked regions; first, a relatively thin distal zone

containing their four nuclei (Figs. 1 and 4, *nl.con*); secondly, a more elongated portion nearly uniform in calibre and constituting the cone (Fig. 1, *con*); thirdly, a still longer part tapering gradually from its distal to its proximal end and reaching nearly to the rhabdome (Figs. 1 and 6); and, lastly, a proximal portion in which the ends of the four cells, as separate fibres, pass around the rhabdome to terminate finally on the distal face of the basement membrane (Figs. 14, 18, and 7, *fbr.con*).

According to Szczawinska (91, pag. 542), who has followed Patten (86) rather closely, the cone-cells in *Astacus* do not end in fibres as described in the preceding paragraph, but are directly continuous with the rhabdome, which is formed, in fact, by an enlargement of their proximal ends. The fibres that I have mentioned as proximal portions of the cone-cells have been identified by Szczawinska (91, pag. 545), but she has interpreted them as processes from the distal retinular cells (cellules de l'enveloppe externe) and not from the cone-cells. There are, however, only two such cells in each ommatidium, not four, as she states, and thus the number of fibres does not agree with the number of cells. Moreover, in sections from the distal end of the retinula (Fig. 14), it is easy to demonstrate not only the four fibres from the cone-cells (*fbr.con*), but also two fibres (*fbr.dst*) from the distal retinular cells. Since the connection of these fibres with their respective cells can be clearly shown in maceration-preparations as well as in serial sections, I believe that Szczawinska's interpretation of the four fibres is incorrect and that they really represent the proximal ends of the cone-cells.

In a previous paper on the eye in *Homarus* (Parker, 91, pag. 545), I tried to show that the rhabdome and cone-cells were separate structures, as first maintained by Max Schultze (68), and that the fibres from the latter terminated on the basement membrane. This conclusion has been fully confirmed by Viallanes (92, pag. 361) in his account of the eye in *Palinurus*, and Patten (90, pag. 354) also now accepts it, though among recent investigators he was the first and most active to declare for the continuity of rhabdome and cone-cells. In view of these facts, it seems to me that the idea of continuity must be abandoned and that the cone-cells and the rhabdome must be regarded as separate structures.

Of the distal retinular cells surrounding the cone, one is dorsal and one ventral in position as shown by their nuclei (Fig. 5,

nl.dst). Each cell completely covers two of the four sides of the cone from its distal to its proximal end, and continues beyond this proximally as a thick fibre, which is lost between the proximal retinular cells (Fig. 14, *fbr.dst*). The part of each cell applied to the cone always contains a rich deposit of blackish pigment granules. SZCZAWINSKA (91, pag. 545) states, as mentioned above, that there are four such cells (cellules de l'enveloppe externe) for each ommatidium, but, as CARRIÈRE (85, pag. 169) first showed, and my observations confirm his, there are only two.

The seven functional proximal retinular cells, enclosing the rhabdome, have been seen in *Astacus* by GRENACHER (79, pag. 125), CARRIÈRE (85, pag. 169), and SZCZAWINSKA (91, pag. 546). Their swollen distal ends contain each a nucleus, and their proximal ones become fibrous, pierce the basement membrane, and extend as retinal fibres (Fig. 1 *fbr. r*) to the first optic ganglion where they end in many fine branches (Pl. 2 Fig. 46, *fbr. r*).

In transverse sections of the retinula, in which the mutual relations of these cells can be best studied, the rhabdome presents a squarish outline (Pl. 1 Fig. 24), its four faces being distinguished from their positions as dorsal, ventral, anterior, and posterior. The first three mentioned are occupied each by two cells, which I have numbered 1 to 6 in the figures; the fourth, the posterior side, is covered by a single cell, numbered 7. The relation of the fibrous ends of the cone-cells and distal retinular cells to these seven cells is as follows (Pl. 1 Fig. 14): the fibres from the dorsal distal retinular cell and from the dorsal cone-cell lie between cells 1 and 2, and the fibres from the corresponding ventral cells between cells 5 and 6; the fibre from the anterior cone-cell between cells 3 and 4, and that from the posterior cone-cell between either 7 and 1 or 7 and 6.

The seven nerve fibres, representing the prolonged proximal ends of the seven retinular cells, pass through the basement membrane by means of four openings, each one of which, however, is in part occupied by fibres from an adjoining ommatidium. Numbering the fibres in correspondence with the cells from which they arise, the groups that are formed in passing through the basement membrane are as follows: fibre 1 from a given ommatidium (Fig. 19) unites with fibres 4 and 5 from a neighboring one, and forms a single group; fibres 2 and 3 unite with the neighboring fibres 6 and 7, and form a second group; fibres 4 and 5 unite with a neighboring fibre 1, and form a third group; and fibres 6 and 7 unite

with the neighboring fibres 2 and 3, and form a fourth group. This arrangement explains the occurrence of groups of three and four retinal fibres immediately below the basement membrane (Fig. 20), a condition also observable in *Homarus*. In *Palinurus*, according to Viallanes (92, pag. 364), the fibres are arranged in much the same way as in *Astacus* except that there are five openings in the basement membrane instead of four, though the latter number occasionally occurs.

The axis cylinder of each retinal fibre in *Astacus* passes as a transparent shaft, the fibrillar axis, through the retinular cell to which the fibre belongs, and disappears in the region of the rhabdome without extending beyond the distal end of that structure (cf. Figs. 21, 20, 19, and 24, *ax.n*). The position at which the fibrillar axis disappears seems to me important as affording evidence in favor of the view that the rhabdome is the organ in which the optic fibres terminate. In an earlier paper (Parker, 90, pag. 29), I described a similar axis in the retinular cells of *Homarus*, and I subsequently identified like structures in a number of crustaceans (Parker, 91, pag. 116), results that have since been confirmed by Viallanes (92, pag. 362) in his study of the eyes in *Palinurus*.

In addition to the seven functional retinular cells just described, an eighth rudimentary cell is present in *Astacus*, as in many and perhaps all other decapods. The nucleus of this cell is hidden among the nuclei of the other proximal retinular cells, and is seen with certainty only when these nuclei are counted. Such an enumeration can be carried out in a series of consecutive sections through a single ommatidium as shown in figures 8—13 (Pl. 1). Here the nuclei are numbered in correspondence with the cells to which they belong. The most distal section (Fig. 8) contains parts of nuclei 1, 3, and 7, which also appear in the next section (Fig. 9) together with a portion of nucleus 6. Nucleus 7 extends through to the third section (Fig. 10), in which nucleus 6 is also represented and a part of nucleus 2. The fourth section (Fig. 11) contains the remainder of nucleus 2 and parts of nuclei 4 and 5, both of which reappear in the fifth section (Fig. 12). The sixth section (Fig. 13) contains all seven cells and the eighth nucleus in its usual position on the dorsal face of cell 7; occasionally it occurs ventral to this cell but always associated with it.

The body of the eighth cell seems reduced to a minimum, for its nucleus appears to be without surrounding protoplasm. In sec-

tions deeper than that in which nucleus 8 lies, cell 7 usually presents a small body, to all appearances a fibre, either on its cell wall or occupying a deeper position apparently through involution (Fig. 14, *y*). Whether this body is the fibrous end of the eighth cell or not, I am unable to state with certainty, but its position and numerical relations favor this view.

Herrick (92, pag. 446) believes that the eighth retinular cell is present in *Alpheus*, but he could not demonstrate it in this crustacean as clearly as in *Palaemonetes*.

The rhabdome in *Astacus* is so favorable for investigation that I have made it the subject of rather careful study, hoping thereby to gain a clearer insight into its composition. I shall therefore describe it and its surrounding structures somewhat in detail.

The axis of the retinula, as can be seen in thin longitudinal sections (Fig. 7), is occupied distally by the cone-cells (*cl.con*), which, however, separate after passing only a short distance into the retinula and make their way as fibres around the rhabdome. The level at which this separation occurs marks the distal end of a pear-shaped cavity (*x*) whose walls are made by the necks of the retinular cells and whose contents consists of a slightly coagulable fluid. This cavity reaches to the distal end of the spindle-shaped rhabdome, which, in its turn, extends almost to the basement membrane (*mb.ba*). The relations of these different structures can be seen well in transverse sections. Figures 8—11, from the distal portion of the retinula, show the cone-cells in the axis of this structure; at the level represented by figures 12 and 13, the four cone-cells have separated, and the opening in the centre is the distal end of the pear-shaped cavity, which, however, is seen to better advantage in figure 14, where the fibres from the cone-cells (*fbr.con*) are also visible. The peculiar W-shaped distal end of the rhabdome is seen in figure 16; this expands rapidly to the squarish form characteristic of most transverse sections of this organ (Fig. 24) and retained by it nearly to its blunt proximal end (Fig. 18). The relative position of the cells and fibres that surround the rhabdome remains the same throughout its length (cf. Figs. 17, 24, and 18).

Although it might seem from figure 7 that the arrangement of the pigment at the distal end of the rhabdome would prevent the direct entrance of light into that structure, such is not the case; for, as can be seen in figure 16, portions of the rhabdome lie on the near and far sides of the one process that would be effective in this

respect, that of cell 7, and thus afford on either side of the retinular axis a transparent shaft by which light can enter the body of the rhabdome directly. It is possible, too, that in the fresh condition of the rhabdome the pigmented processes are not so prominent as in the preparation figured; the latter, however, represented a very typical longitudinal section.

The rhabdome when taken directly from the live animal has a uniformly reddish pink tint, and, as can be seen in longitudinal section (Fig. 7), is composed of a series of some twenty-two plates, the flat faces of which are transverse to the retinular axis. Each plate is subdivided into two half-plates by a plane vertical to its flat face and passing through the retinular axis. The division-planes of adjoining plates do not coincide, but are at right angles to each other, thus giving rise in each rhabdome to two sets of alternating plates; when the division-planes of one set are cut transversely and are consequently seen most clearly (Fig. 7), those of the other set are, of course, not visible, since they lie parallel to the plane of section. It will be remembered that the sides of the rhabdome were designated from their positions as dorsal, ventral, anterior, and posterior, and, since the division-planes in the plates are always parallel to one or other of these sides, the resulting half-plates may be distinguished as dorsal and ventral when the division-plane cuts the plate from its anterior to its posterior side, and anterior and posterior when the plate is cut dorsoventrally.

The half-plates of a given side of the rhabdome belong to the retinular cell or cells of that side; thus, the ten or eleven posterior half-plates belong to the single posterior retinular cell, number 7 (Fig. 7, *la. p*), and represent the rhabdomere of that cell; the corresponding anterior half-plates belong to the anterior cells, numbers 3 and 4 (Fig. 7, *la. a*), and represent the united rhabdomeres of these cells; i. e., these half-plates, as I shall presently show, are to be regarded as fused pairs of quarter-plates, the rhabdomeres in this case consisting of quarter-plates instead of half-plates. In the planes of the anterior and posterior half-plates, retinular cells 1 and 2, and 5 and 6 take no part in the formation of the rhabdome, their contribution to this structure being the ten or eleven dorsal and ventral half-plates, which, of course, alternate with the pairs of anterior and posterior half-plates and which must also be regarded as composed of quarter-plates. When the retinula is macerated, as WATASE (90, pag. 299) has shown in *Homarus*, its cells or pairs of cells

separate, retaining on their axial faces the rows of half- or quarter-plates belonging to them.

From the preceding account it must be evident that the rhabdomeres in *Astacus* and *Homarus* are not single continuous bodies, as, for instance, in *Porcellio*, but consist of a series of separate pieces, the half- or quarter-plates, which project from the retinular cell like the teeth on a rack in a rack and pinion. Because of this resemblance I propose to call such rhabdomeres toothed, to distinguish them from continuous simple rhabdomeres as in *Porcellio*. The same terms may be used to designate the rhabdomes formed by the union of one or other kind of rhabdomeres.

The structure of the toothed rhabdome, as I have described it, offers, I believe, an answer to a question that GRENACHER (79, pag. 124) raised concerning the origin of this organ and that, so far as I am aware, has never been satisfactorily settled. The fact that in transverse sections the rhabdome seems to be divided into four rhabdomeres inclined GRENACHER to believe that only four retinular cells were concerned in its production, though it is surrounded by seven such. From what I have said of the two kinds of plates in the rhabdome and their alternation, it must be clear that all seven cells produce rhabdomeres and that what GRENACHER took for the planes of separation between the four supposed rhabdomeres are really the division-planes between the half-plates. These planes, since they are at right angles to each other in adjoining plates, seem, in transverse sections thicker than one plate, to divide the rhabdome into four rhabdomeres.

The structure of the half-plates in the rhabdome is most clearly seen in preparations made by GOLGI's method. A retinula prepared in this way and cut transversely is shown in figure 24; the plane of section passes through a dorsoventral plate, i. e., components of the rhabdome belonging to retinular cells 1, 2, 5, and 6, and, as often happens with this method, only a portion of the preparation is colored, in this case the quarter-plate belonging to cell 2. As is easily seen, this consists almost entirely of fine fibres, which extend from the plane of separation between the two half-plates to cell 2. This cell itself differs in appearance from the others in that its fibrillar axis is obscured by a deposit of silver precipitate similar to that which colors the fibres themselves; nor is the coloration limited to this plane only, but, as I demonstrated to my satisfaction by studying successive sections, it extends distally and proximally

through cell 2 and reappears in most of the quarter-plates belonging to this cell, the other elements of the retinula remaining almost entirely unaffected; in other words, the silver stain here, as in other cases, effects a given cell and the structure produced by it, but does not necessarily color neighboring cells. It was from seeing preparations such as this (Fig. 24) that I was led to regard the dorsal, ventral, and anterior half-plates as composed each of two quarter-plates, though I could never find a plane of separation between them as between the pairs of half-plates.

The fibres belonging to the other cells, 1, 5, and 6, in the section just mentioned are parallel to those of cell 2, as may be demonstrated in corresponding sections in which the fibres of all four cells are colored, and, as all dorsoventral plates agree in this respect, the general statement may be made that all the fibres in dorsoventral plates agree in having a common dorsoventral direction.

In the anteroposterior plates the relation of the fibres to the cells and division-planes corresponds to that in the dorsoventral ones; i. e., the direction of the fibres in the former is anteroposterior, or at right angles to that in the latter. When a rhabdome in which the fibres are colored is cut so that the section includes parts of adjoining plates, the fibres appear to cross one another (Fig. 25); of course, in such cases the two sets lie at different levels.

In longitudinal sections made parallel to one face of the rhabdome, the fibres in one set of plates would be cut longitudinally, in the other transversely. Figure 23 represents such a section, in which, however, the fibres from only two cells are colored; those belonging to the cell on the left of the rhabdome are seen in longitudinal section and appear as thick lines; those in the alternating plates of the right half of the rhabdome are cut transversely and appear as dots.

The fibres, as may be seen in the figures given, are always unbranched; of their two ends, one is buried in the retinular cell and the other usually reaches the division-plane between the two half-plates. Not infrequently fibres are seen that are not so long as this; I am uncertain whether these are really short ones, or of normal length but only partially stained (cf. Fig. 24). Occasionally some seem to pass through the division-plane and extend as rather delicate processes into the adjoining half-plate (Fig. 24); this I am inclined to regard as the result of the spreading of the silver from the deeply colored fibres of one half-plate to a few in the adjoining

half-plate and not due to the penetration of fibres from one half-plate into another.

At the base of each half-plate where the fibres meet the retinular cell (Fig. 23), the pigmented substance of the cell extends as a blunt process into the plate. In this way, transverse pigment bands are produced on the four surfaces of the rhabdome. Since each band marks the attached face of a half-plate and since antero-posterior plates alternate with dorsoventral ones, the well-known alternation of the pigment bands on adjacent sides of the rhabdome and their coincidence on opposite sides are easily understood.

The precise nature of the fibres is by no means easily determined. That they are not purely artificial products of GOLGI's method is shown, I believe, in two ways: first, they occur only in the rhabdomes and have a definite arrangement conformable with the structure of these bodies, conditions that would not be expected if they were simply artificial products, and, secondly, they can be demonstrated in some crustaceans, as, for instance, in *Porcellio* and *Serolis* without the use of this method[1]. In deciding on their nature, one structural feature that they present is of considerable importance; in ordinary sections it is not uncommon to see streaks free from pigment extending from the base of the fibres in the rhabdome through the pigmented substance of the retinular cell to its fibrillar axis as though the fibres and the axis were in direct anatomical continuity, and in preparations made by GOLGI's method, the silver salts often take this course, coloring the connecting streaks and the fibrillar axis as well as the fibres themselves. This favors the view that the fibres represent the distal terminations of the constituents of the fibrillar axis, and throws some light on the following peculiarity of the rhabdome, as contrasted with a nerve fibre, in their relations to heat. When a perfectly fresh nerve fibre is heated to 50° C., it contracts about $^1/_4$ or $^1/_5$ its original length; when a fresh rhabdome is similarly treated, it becomes thinner and

[1] The fibrous structure of the rhabdome has, in fact, already been recorded in a number of arthropods. It is probable that what MAX SCHULTZE (68, pag. 14, Pl. 1 Fig. 12) described and figured as lamellae in the plates of the rhabdome in *Astacus* were really fine fibres seen from the side. PATTEN (86, pag. 629), however, was the first that recognised fibres as such in the crustacean rhabdome. Similar structures have been observed by WATASE (90, pag. 291) and myself (91, pag. 117) in *Serolis*, by WATASE (90, pag. 303) in *Limulus*, and by WILLEM (92, pag. LXXX etc.) in *Lithobius* and *Polyxenus*.

elongates about $^1/_6$ its length, i. e., it contracts on the lines of its fibres, which are at right angles to its length, in precisely the same way that the constituents of the nerve fibre do; in other words, the substance of a nerve fibre and of the fibres of the rhabdome behave similarly towards heat. For these various reasons I have been led to regard the fibres of the rhabdome as nervous structures, the distal ends of the fibrillae of the retinal nerve fibres.

As can be seen in transverse sections of the half-plates, these nerve fibrillae constitute the greater part of the mass of the rhabdome, the interfibrillar substance being limited to a comparatively small space. Whether the fibrillae are simply fluid-filled pores in this substance or delicate rod-like bodies imbedded in it is difficult to say, but whichever they may prove to be seems to me to have little bearing on their nervous nature so long as the same question concerning nerve fibrillae in general remains open.

If the finer structure of the rhabdome, as presented in the foregoing paragraph, is not directly opposed to Grenacher's (79, pag. 158) conception that this body is the cuticular product of the retinular cells, it offers, at least, little support for that view and still less for Watase's (90, pag. 291) opinion that the organ is a chitinous product. To me the rhabdome seems in no sense a secretion, but rather a differentiation of a portion of the protoplasm of the retinular cell, much as muscle substance is the product of a muscle cell, a view already expressed by Johansen (92, pag. 353) in his preliminary account of the development of the eyes in *Vanessa*.

The diagrammatic figure 60 (Pl. 3) gives, by way of summary, the complete outline of one of the seven elements that unite to form a retinula. The swollen distal end containing a nucleus tapers into a neck, which forms part of the wall of the pear-shaped cavity and which leads directly to the body of the element. The axial side of the body is marked by about ten transverse waves, each of which carries on its crest a segment of the toothed rhabdomere. The proximal end of the body becomes fibrous, pierces the basement membrane, and, as a retinal nerve fibre, extends to the first optic ganglion where it ends in many fine branches. The fibrillae from the segments of the rhabdome unite in the body of the element to form its fibrillar axis, which is continued proximally as the axis cylinder of the retinal nerve fibre and resolves itself into fine branches in the first optic ganglion. In all parts of the element, except in the true nervous structures just mentioned and in the nucleus, there

is, as a rule, a rich deposit of fine blackish pigment granules. The whole element thus briefly outlined represents a single cell, or, adopting the term suggested by WALDEYER (91, pag. 52) for such nervous elements, a neuron.

c. Migration of Retinal Pigment.

The changes in position produced in the pigment of crustacean eyes by the action of light and darkness have been described, so far as I am aware, by only two investigators, SZCZAWINSKA and EXNER. In the account by SZCZAWINSKA (91), these changes are dealt with chiefly from an anatomical standpoint, while EXNER (91) has regarded them rather in the light of their physiological significance and has brought them into intimate relations with his theory of vision in compound eyes. Both EXNER and SZCZAWINSKA have studied the crayfish, and, though their results agree in the main, these still present differences important enough to call for reinvestigation.

The method that I finally adopted for preparing the eyes was somewhat more complicated than that formerly used, but the greater exactness of the results yielded by it seems to me to justify its employment. The extreme conditions to which I subjected the crayfishes were, on the one hand, darkness as complete as could be obtained in a closed dark-room and, on the other hand, daylight bright but diffused. As my object was to study the normal action of the eyes, I tried to reproduce, so far as the light was concerned, the extreme natural conditions under which the animal lived, and I did not resort to the use of excessively bright light, such as direct sunlight, etc., as used by SZCZAWINSKA and which, as she remarks, often kills the animals. To ward against possible individual variations in the amount of pigment in the eyes, I prepared both eyes in each animal, one after subjecting the animal to the light for four hours and the other after it had been in darkness for the same period. As the removal of one eye does not interfere with the normal action of the other, so far as I could observe, I see no objection to this method of procedure, which certainly has the advantage of allowing a closer comparison of the condition in the two eyes. The eyes subjected to darkness were prepared *without exposure to light*, usually by hardening the tissues of the animal as a whole. This I did by means of water at about 90° C.; the heat

penetrates and fixes the tissue almost at once. In this respect it is, perhaps, a safer reagent than fluids that enter the tissues more slowly and thus allow an opportunity for slight changes in the position of the pigment. However, on comparing eyes hardened in alcohol or corrosive sublimate with those prepared in hot water, I never discovered any important differences so far as the position of the pigment was concerned.

As may be gathered from the anatomical description already given, the pigment in the retina of *Astacus* is of two kinds, fine blackish grains, and flakes of an irregularly crystalline substance, yellowish by transmitted light but whitish in reflected light. These two substances are contained in different cells; the flaky material fills the accessory pigment cells and constitutes what Exner calls the tapetum, while the blackish grains are found in the distal and proximal retinular cells, corresponding to what Exner has termed the iris and the retinal pigment respectively.

The pigment in the proximal retinular cells is easily affected by light. In diffused daylight, it is present throughout the retinular cell from its distal nucleated end to a point in its fibrous prolongation some distance below the basement membrane, the concentration of the pigment, however, being around the distal end of the rhabdome (Pl. 1 Fig. 1); in other words, by means of this pigment the whole rhabdome is protected from the approach of light except at its distal end, where light can gain access to it through the small aperture by which the four cone-cells penetrate the distal end of the retinula, as previously described. Under similar circumstances, essentially the same arrangement of pigment was observed by Szczawinska (91, pag. 552) and by Exner (91, pag. 109).

In eyes that had been prepared in perfect darkness, the pigment of the proximal retinular cells was found to have migrated completely into the retinal fibres below the basement membrane (Pl. 1 Fig. 2); in other words, in complete darkness, no part of the rhabdome remains covered by black pigment; and, except for the protection that its proximal end receives from the accessory pigment cells, it is accessible to the light from all sides. The extreme position of the pigment by which this condition is produced has been observed by Exner (91, pag. 109). According to Szczawinska (91, pag. 552), however, the pigment does not retreat proximally further than the middle of the rhabdome. I have observed this condition in crayfishes that have been kept in the dark and whose

eyes have been preserved immediately on exposing the animals to the light. As this seems to have been SZCZAWINSKA's usual method of procedure, it is easy to understand why she never observed the pigment in its more extreme position as seen by EXNER and myself. In all cases, however, in which the eyes were prepared in darkness after having been kept there some hours, the absence of retinal pigment on the distal side of the basement membrane was easily demonstrated.

In dim light, as might be expected, this pigment occupies a position intermediate between the two extremes just described and covers the proximal half or two-thirds of the rhabdome. From its action it seems to be a means of controlling the access of light to the rhabdome; when much light enters the eye, it covers the rhabdome all but the distal end; on decreasing the amount of light the exposed surface of the rhabdome is increased, till finally in perfect darkness the whole rhabdome is uncovered.

Since the changes shown by the pigment in the distal retinular cells are not so easily observed as those in the cells last described, it is not surprising that the accounts of SZCZAWINSKA and EXNER do not agree in this instance as well as in the former. Each distal retinular cell, it will be remembered, consists of two parts: a flat portion, which may be called the body of the cell and which covers two adjacent faces of the cone, and a process, which extends from the proximal edge of the body to the retinula. In regard to the distribution of pigment in these parts, considerable individual variation occurs, and I begin by describing a case that may be said to represent one extreme of these differences.

In a left eye prepared in darkness, pigment was observed only in the bodies of the distal retinular cells (Pl. 1 Fig. 2), their proximal processes containing none of this substance; in other words, the pigment was lodged entirely between the cones as observed by EXNER (91, pag. 73) and by SZCZAWINSKA (91, Pl. 17 Fig. 1). In the other eye from the same animal prepared in daylight, the pigment had evidently migrated proximally (Pl. 1 Fig. 1), not, however, as a pigmented cylinder sliding over the cone as described by EXNER, but as pigmented processes, one for each cell as stated by SZCZAWINSKA (91, pag. 545). When viewed from the side, however, these processes seem like the edges of a cylinder cut longitudinally, an appearance that probably misled EXNER. In serial transverse sections, however, the fibrous form of the processes can be demonstrated

beyond doubt (Pl. 1 Fig. 6, *cl.dst*). These pigmented processes, as might be expected, are not new structures, but are the transparent processes of the distal retinular cells partly filled with pigment from the body of the cell. The largest migration that the pigments made, was over a distance about equal to the length of the cone. EXNER (91, pag. 73) states that, after the proximal migration has taken place, only a few traces of pigment are left between the cones; and SZCZAWINSKA (91, pag. 552) says that the change renders the pigmented cylinder of the cones in part imperfect. Although the subtraction of pigment granules from between the cones may render that region somewhat less impervious to light, certainly more pigment remains behind than passes into the processes, and I never observed such a deficiency in what was left as SZCZAWINSKA (91, Pl. 17 Fig. 2) figures. In this case, then, the change from darkness to light induces the migration of a small part of the pigment from the body of the cell into its proximal process.

The opposite extreme to the case just described was as follows: the pigment of the distal retinular cells, when prepared in darkness, occupied not only the body of these cells, but also the distal portion of their proximal processes, so that their appearance was almost identical with that produced by the action of light in the former instance. The light, in this case, caused the pigment in the processes to migrate still farther till it nearly touched the proximal retinular cells. In both cases, then, the light produced the same effect, a proximal migration of the pigment; in the first instance, this began in the body of the cell, but, in the second, it began in the process itself. Since in these experiments the action of light and of darkness was tried one on the right and the other on the left eye of the same crayfish, and since in all preparations the pigment of the proximal retinular cells reacted normally and fully, I believe that I am justified in interpreting the conditions in these two extreme cases as due to individual variations and not caused by pathological changes. This conclusion is supported by the fact that, in the four pairs of eyes that I have cut, the changes in the pigment of the distal retinular cells show considerable variation as contrasted with the uniformity of the changes in the proximal cells.

Although the pigment in the distal retinular cells migrates in the direction that EXNER has stated, the fact that it has the form of a narrow process instead of a cylinder might at first sight seem to offer a serious objection to his explanation of these changes and

open the question as to whether his descriptions of the corresponding changes in other crustaceans are not faulty in this respect. With a view to partially answering this question, I studied the changes in the pigment of *Palaemon*, one of the best instances given by EXNER, and I can fully confirm his statements regarding this crustacean; *Palaemon* certainly possesses a pigmented cylinder, which, under the influence of light or darkness moves proximally or distally over the united cone-cells. This shows that, though EXNER's view may require some modification for certain crustaceans, as, for instance, *Astacus*, it may still hold good for others. Nor do the modifications required by *Astacus* necessitate any serious changes, for, if, in the presence of increased light, a pigmented cylinder is an optical advantage below the cones in obstructing oblique rays, pigmented processes in a similar position would answer the same purpose, though, of course, their action would probably be less complete. I regard the proximal processes of the distal retinular cells in *Astacus* as an apparatus of this kind, incomplete in one sense and yet efficient enough doubtless to meet the requirements of the animal.

Concerning the accessory pigment cells with their whitish pigment, SZCZAWINSKA (91, pag. 552) states that under the influence of light they shorten and swell slightly. EXNER (91, pag. 105), however, was unable to identify with certainty any movement in these cells in *Palaemon*, and regards the changes that they appeared to undergo as due to the fact that in different conditions of illumination they were differently covered by the blackish pigment of the proximal retinular cells. My own observations on *Astacus* support EXNER's conclusion; in eyes preserved in darkness, as well as in those prepared in light, the accessory pigment cells extend from the middle of the rhabdome to the distal face of the basement membrane, and in these two conditions showed, as far as I could observe, no difference in form. I therefore conclude that they are not affected by light or darkness.

In a retina exposed to light, the black pigment in the proximal retinular cells lies between the accessory pigment cells and the rhabdome; but, in one from which the light is excluded, the black pigment migrates to a region below the basement membrane, and there is no opaque substance intervening between the accessory cells and the rhabdome. If, under such circumstances, a small amount of light were to enter the retina and pass to the proximal end of the rhabdome without being absorbed, it would probably be reflected

through the rhabdome again by these cells, thus doubtless increasing the stimulation of that organ. The fact that reflection would be most needed in faint light and that under such circumstances the accessory cells are in a position to act most efficiently as reflectors suggests this as their function.

The blackish pigment grains are contained within the distal and proximal retinular cells, and in their migrations they remain entirely within the walls of these cells. Since the cells have about the same form after the migration of the pigment as before, I find it difficult to explain this change without assuming that it is produced as in vertebrates by a protoplasmic streaming. Certainly in *Astacus* no muscles are concerned in the change, though the case may be different in *Palaemon*.

By way of summary it may be stated that the black pigment of the distal and proximal retinular cells is a means of controlling the amount and quality of the light that reaches the rhabdomes. In comparative darkness, the absence of pigment around the rhabdome, as well as the absence or shortness of the pigmented processes from the distal retinular cells, renders the rhabdome far more easily accessible to light than in the conditions presented in the brightly illuminated eye. In faint light, rays from a variety of directions can reach the rhabdome; in bright light, the more oblique rays are excluded and only those more nearly parallel with the ommatidial axis enter it. When least light enters the retina, the accessory pigment cells are most exposed and can consequently act most effectively as a reflecting apparatus.

d. Theories of vision.

The numerous theories that have been proposed to account for vision in compound eyes differ from one another in one or both of the following particulars: first, as to which structure in the eye is the perceptive organ, i. e., is concerned with the reception of light and the production of the impulse transmitted by the optic nerve; and, secondly, as to the number of simultaneous but distinct impressions that each such organ can receive, i. e., whether each organ is a perceptive surface for a whole picture or for only one element in a picture.

In determining which are the perceptive organs, facts concerning the structure of the eye are of no small importance; these organs

must, on the one hand, be connected with the exterior by means of structures capable of transmitting light to them, and, on the other hand, they must have nervous connections with the brain. Of the various views known to me concerning their location, that suggested by LOWNE (84) seems least successfully in meeting the requirements mentioned above. According to this investigator the perceptive elements do not occur in what is usually termed the retina, but in what I have designated the first optic ganglion, where they are represented by a layer of bodies called by VIALLANES (92a, pag. 391) the neurommatidia. This layer, however, as I shall presently show, is not accessible to light nor does it represent the distal termination of the optic fibres, two facts that appear to me fatal to LOWNE's view. So, too, WAGNER's (35, pag. 372) opinion that the pigmented sides of the cone form a perceptive surface, as well as LEYDIG's (55, pag. 416) and PATTEN's (86, pag. 692) belief that the cone itself is the perceptive body, seems to me erroneous, since these structures, though accessible to light, have been shown to be without nervous connections. Objections can also be raised against VIALLANES' opinion that the pigmented distal ends of the proximal retinular cells are the perceptive structures and that the pigment itself plays an essential part in the production of the visual impulse. If these cells act as VIALLANES believes they do, it is not easy to understand why the axis cylinder extending through each of them does not terminate in their distal ends instead of in the rhabdome as admitted by VIALLANES himself. Moreover the fact that albino animals, such as rabbits (cf. ANGELUCCI, 78, pag. 377) are able to see, though the postretinal epithelium of their eyes is devoid of pigment, shows conclusively that this pigment does not play the essential part in vision that VIALLANES ascribes to it; and, further, since this view, like that of WAGNER, LEYDIG and PATTEN, offers no explanation for the presence of the rhabdome nor for the migration of the pigment in the retinular cells, I believe that it, like the others, must be abandoned.

Unsatisfactory as these different opinions are, there is still one against which it seems difficult to raise serious objections and that is the opinion first clearly expressed, I believe, by MAX SCHULTZE (68, pag. 12) and afterwards defended by GRENACHER (79, pag. 157) that the rhabdome is the perceptive organ. The fact that the dioptric apparatus of the eye transmits light to the rhabdome but no further, that there are nervous connections between rhabdome and

brain, and that no other structure in the retina possesses both of these peculiarities, is strong evidence in favor of the perceptive nature of this body. Moreover, granting this conclusion, the changes undergone by the pigment become perfectly intelligible, for they are obviously directed toward controlling the quantity and the quality of light that reaches the rhabdome. These various reasons, I believe, justify the conclusion that the rhabdome is the perceptive organ of the retina.

Having reached this point, there still remains the question concerning the character of the impressions made upon the rhabdomes: does each rhabdome perceive a complete picture or only one element in a picture? This problem may be approached from two sides; we may first try to ascertain the character of the image thrown on the rhabdome by the dioptric apparatus, and secondly, by examining the finer structure of the rhabdome itself, we may attempt to determine to what extent it is capable of perceiving an image.

Concerning the character of the image thrown by the dioptric apparatus, there are already a number of conflicting observations and opinions. From the time of LEEUWENHOEK, investigators have been more or less familiar with the fact that each facet in the corneal cuticula is capable of projecting at a short distance behind itself a small inverted image of an object held in front of it. In a carefully prepared fly's eye, GOTTSCHE (52, pag. 488) believed that this image was to be seen at the proximal end of the cone, and, regarding it as functionally significant, he raised the question of how and where it is perceived. MAX SCHULTZE (68, pag. 27), who, as we have already seen, correctly interpreted the rhabdome as the perceptive organ of the retina, took the suggestion from ZENKER that the denser material of the proximal part of the cone-cells might cause a proximal displacement of one of the foci of the dioptric apparatus, and believed that in this way an image might be thrown on the rhabdome. VIALLANES (92, pag. 372) states that, in the eyes of insects and crustaceans prepared by a method essentially similar to GOTTSCHE's, a small inverted image could be observed at the distal end of each retinula. It is, then, a matter of observation that for each ommatidium in freshly prepared eyes a small inverted image occurs not far from the distal end of the rhabdome.

These observations are directly opposed to those of EXNER (91), who, after preparing the rather resistant dioptric apparatus of *Lam-*

pyrus by carefully removing the nervous layer of the retina and all pigment, observed, near the level formerly occupied by the perceptive layer of the retina, a single erect image produced by the combined action of the separate dioptric organs of the eye. These organs when uninjured never gave rise to small inverted images as described by other investigators. The contrast between EXNER's observations and those summarised in the preceding paragraph must be evident.

The grounds upon which these two opinions are based are not wholly unassailable; in the method of preparation used by GOTTSCHE and VIALLANES, the uncertainty as to whether the structures left in the eye retain their normal positions or not must be evident to any one who has attempted such experiments, and the complete removal of pigment, as practised by EXNER, obviously leaves the dioptric apparatus in a condition far from normal. It is also important to bear in mind that neither EXNER nor the advocates of the opposing theory have ever observed images in or on the perceptive organs themselves; what they have seen has been located near the perceptive elements or at best in a position formerly occupied by these bodies. That the character of the image in the rhabdome itself has not been ascertained is due in great part to the technical difficulties involved in such an operation. *Astacus*, however, on account of the very large size of its ommatidia, is more favorable for such experiments than other crustaceans; and it is chiefly due to this fact, rather than to any technical advance, that I have been able to observe the image in the rhabdomes of this crustacean.

For this purpose I prepared the eyes in the following manner. A perfectly fresh eyestalk was so placed in a freezing microtome that, beginning at its proximal end, transverse sections could be cut from it till only the hemispherical distal end containing the retina remained. It was easy to determine from the appearance of the pigment on the cut surface what plane in the retina had been reached, and there was no difficulty in making preparations for any desired level. The preparation having been cut, it was removed from the ice and placed on a cover-glass, its flat face being next the glass. This transfer was made before the retina had thawed out; for, after it had become soft, it was found impossible to move it without seriously displacing the ommatidia. The preparation was usually fixed to the cover-glass by a very small amount of Canada balsam, care being taken, however, to keep the balsam from entering

the retina or spreading over the face of the corneal cuticula. The preparation was then inverted over a small glass box containing enough water to bathe its convex surface, and the whole apparatus was placed under the microscope so that the cut surface of the preparation could be inspected. In preparations that had been carefully made, the ommatidia were found still regularly arranged as in life, and, since the front face of the eye was bathed in water and the retina was permeated with normal fluids, and, further, since all the refracting surfaces artificially introduced were rendered ineffective by being at right angles to the light, it was assumed that the requirements for exact observation were complied with. Since it was necessary to make the preparations in the light, the experiments were conducted on eyes in which the pigment had taken the position characteristic for a retina brightly illuminated.

The results obtained were briefly the following. Light never penetrated the eye to the depth of the basement membrane; for this always appeared uniformly black, even when the front face of the retina was illuminated with sunlight reflected from a plane mirror or with the rays from a strong electric arc-light. This observation, if correct, seems to me, as previously stated, to render LOWNE's theory untenable. When the preparation was made so that the proximal ends of the rhabdomes were exposed and the retina was illuminated with strong sunlight or light from an electric lamp, the rhabdomes appeared as small irregular pinkish areas, but the light which they contained was so faint that the presence or absence of an image in them could not be satisfactorily determined. When the preparation was made so that the distal ends of the rhabdomes were exposed, these bodies appeared, even when illuminated with diffused daylight, as small pinkish areas set in an opaque black field. Each rhabdome was uniformly bright and presented not the least indication of an image within its area. When a lamp was used and the amount of light given out by it was made to vary, these variations, even when very slight, were observable in the rhabdome. When an opaque object, such as a pencil, was held in the light between the lamp and microscope, its position was marked by the darkening of certain rhabdomes, and, when it was moved to and fro, the order of succession in which the rhabdomes became dark showed conclusively that it was represented in the retina as a whole by a single erect image.

In preparations that were made for a level slightly beyond the distal ends of the retinulae and that showed, consequently, only the

proximal ends of the groups of cone-cells, the presence of the single erect image just mentioned was easily verified, and, though its outline could not be called sharp, its general form could be easily recognised. It was, of course, only well seen in the central part of the retina; for, owing to the radial arrangement of the ommatidia, the sides of preparations made as I have described are always unfavorable for study. In this central region I never observed the small inverted images claimed by VIALLANES to be present at this level in each ommatidium.

These observations are important in two respects; they show that, when the rhabdome is surrounded by pigment, its whole length can be penetrated only by very strong light, though its distal end can always be illuminated even by diffused daylight, and, secondly, they confirm the belief entertained by MÜLLER, GRENACHER, and EXNER that the image in the compound eye is a single upright one for the whole retina, whose perceptive elements, the rhabdomes, receive each a single impression.

Granting this conclusion, it might fairly be asked, what, then, are the small inverted images seen by so many investigators? The presence of these images under certain conditions is beyond question. When the corneal cuticula is carefully cleaned and properly mounted under the microscope, each facet produces a remarkably sharp, bright image of objects in front of it, even the comparatively flat faced facets of *Astacus* being no exception to this rule. These images, as ZENKER surmised, can be made to occupy more proximal positions by filling the region in which they are formed with denser media, as the following observations on the facets of *Carcinus maenas* show. When the distal face of the cleansed corneal cuticula of this crustacean is immersed in water and the proximal concavity occupied with air, the image is seen at a distance of 9 μ behind the proximal face of the facet; with water in the proximal concavity it is formed at a distance of 17 μ, and with glycerine, at 21 μ. I have made preparations of the eyes of *Musca* and *Carcinus* as GOTTSCHE and VIALLANES did, and in both cases I saw the small inverted images described by these investigators. As is implied by VIALLANES, these images are certainly produced by the corneal facets and displaced proximally by the denser transparent material of the retina, but that their formation is a normal process is by no means so certain. In both *Musca* and *Carcinus*, the substance of the cones is so soft that when these bodies are freshly removed from the eye it flows like a thick

liquid; and, when a number of cones are removed together, though their outlines are at first distinguishable, they soon melt into an almost homogeneous, transparent mass. This usually takes place also when the retina is prepared according to GOTTSCHE's method, and thus a homogeneous mass is produced by which the images from the facets are simply displaced to a deeper region in the eye. As these images were not observed in preparations in which the structure of the cones was unaltered, it seems to me that they must be regarded as functionally unimportant, and I account for them by the fact that one part of the dioptric apparatus, the facet, has remained intact, while another part, the cone, has been rendered ineffective by an alteration in its structure.

Having reached the conclusion that the normal retinal image is of such a character that each rhabdome receives only a single impression, there still remains the question: Does the finer structure of the rhabdome justify this conclusion? Granting the fibrillar structure of this body, it might be assumed that each fibrilla represents an isolated perceptive organ, the whole rhabdome thus constituting a perceptive field like the human retina. The distribution of the fibrillae, however, does not favor this view; for, whether we assume them to be effected by light only at their free ends or throughout their entire length, they never present a mutual arrangement favorable for the reception of separate impressions. The fact that the quarter-plates of fibrillae from one retinular cell alternate vertically with those from another so that the same kind of light would effect both sets of fibrillae, is directly opposed to the idea that each rhabdome receives numerous separate impressions. In fact, the structure of the rhabdome seems admirably adopted for destroying precisely this difference. VIALLANES (91a, pag. 396), however, assumed that each retinula represented seven perceptive organs capable of perceiving each a single impression. Without raising the question why these seven elements are united to form a retinula, I believe we can grant what VIALLANES claims and still have difficulties enough to explain how seven perceptive organs, such as the retinular cells, can be very effective in perceiving an image such as that which VIALLANES believes to be thrown on them. The images figured by him are altogether too rich in details for such a retina, and I side with GRENACHER (79, pag. 152) in the opinion that, if seven is the greatest number of separate perceptive elements that can be assumed for each retinula, it is more likely that the retinula receives only

one impression than many. Owing, however, to the peculiar overlapping of the quarter- and half-plates of adjoining rhabdomes as previously described, even this assumption seems to me inadmissible; for, in conformity with this overlapping, there can in reality be only three retinal elements in each rhabdome. This number is obviously too small to constitute any serviceable retina, and I, therefore, believe that, both from the character of the image thrown on the rhabdome and from the structure of this body itself, we are justified in concluding that each rhabdome is a perceptive organ for a single impression.

To this conclusion the objection might be raised that the function ascribed to the rhabdome is altogether too simple to require such a complicated structure as this organ possesses. But this objection seems to me falsely grounded, for, though each rhabdome cannot receive more than a single impression at a time, it does not follow that the impressions themselves cannot be complex; in fact, I believe we must assume them to be so, since the animals give every evidence of distinguishing between lights of different intensity as well as of different colors. It, therefore, seems to me possible that the complex structure of the rhabdome is necessitated by its complex function. Thus, as was previously stated, diffused daylight enters only the distal portion of the rhabdome, while strongest light is required to penetrate to its proximal end. Since diffused daylight can, therefore, stimulate only the more distal fibrillae, while light of greater intensity effects not only these but also fibrillae in more proximal positions, it is conceivable that the difference in intensity between any two impressions might be expressed by the difference in numbers of fibrillae thrown into functional activity in the two cases. If this be true, an efficient rhabdome would consist of numerous fibrillae placed at different levels in respect to the light. Why, as is actually the case, there should also be many fibrillae at the same level is not easily understood, unless we assume that there are different ones for the perception of different colors, in which case the series might be repeated at successive levels. But whether this be true or not, it must be remembered that on the sides of our own retinas, the elements are more numerous than the impressions we receive, and, though I am as unable to explain this excess as I am that in the rhabdome of *Astacus*, the facts that such an excess really exists, proves, I believe, that the objection mentioned in this paragraph is, after all, without weight.

Although the foregoing conclusions that each rhabdome receives a single impression and that the retinal image is a single erect one, supports, in all essential respects, MÜLLER's theory of mosaic vision, it is possible, as EXNER has recently shown, that in some instances the retinal images are not formed in precisely the way that MÜLLER supposed. MÜLLER believed that, of the rays of light entering a given ommatidium, only such as were approximately parallel to its longitudinal axis were conducted to the perceptive organ at its base, the rest being absorbed by its pigmented walls, and, further, that the light received by one ommatidium had no influence upon the perceptive elements of adjacent ommatidia. In this way each ommatidium produced independently one block in the upright mosaic image formed by the mutual action of all ommatidia. EXNER, likewise, believes that retinal images can be formed essentially in this way and has called them apposition images. In eyes in which a complete pigment sheath extends from the cone to the rhabdome, only apposition images would be possible, but there are also eyes in which the region between rhabdome and cone proper contains little or no pigment, and in such cases it is conceivable that the light entering the cone of one ommatidium might reach the rhabdome of another or possibly, several others, as EXNER believes. This might seem at first sight to interfere with the clearness of vision, but, as EXNER has shown in some instances at least, the dioptric organs of the eyes in question are so constituted that they each form a relatively large erect image near the level of the rhabdomes, and these images overlap one another so that the details in one coincide with the details in another, thus giving rise to a single erect image for the whole retina; in other words, the light that emanates from one small luminous object in the field of vision and enters the retina, even though it does so by means of many cones, is finally concentrated at one point in the sensory layer. The image thus formed has been appropriately called by EXNER a superposition image and differs from an apposition image, all other things being equal, only in its greater brightness; i. e., one mosaic block in an apposition image is formed by the axial rays from one cone; the corresponding block in a superposition image is formed by the corresponding rays plus many others that, after entering the retina through neighboring cones, are turned by these so as to meet the given axial rays at the level of the perceptive layer.

It is not my purpose to enter into a discussion of the optical means

by which such superposition images may be produced. So far as my own observations are concerned, I know of nothing that is in disagreement with EXNER's belief that each dioptric organ acts as a »lens-cylinder«, an optical contrivance that this author (cf. EXNER, 91, pag. 1) has ably described and that seems perfectly capable of producing the requisite images.

A question more directly connected with the present studies concerns the character of the retinal images in *Astacus*: are they apposition or superposition images? The fact that the pigment plays so important a part in determining the kind of image in a given eye, and, further, that in *Astacus* it presents two extremes in its arrangement, one for bright and one for dim light, requires that this question be asked for both conditions. Since the region of the retina between the cones and the rhabdomes is for the most part devoid of pigment, a superposition image might be expected; but, for a satisfactory answer, evidence of a more conclusive nature must be had. This I have tried to obtain in the following manner.

A frozen preparation of a fresh retina, such as I have already described (cf. pag. 29), was made for the distal end of the rhabdome, placed in the usual way under the microscope, and illuminated by rays from a lamp some two metres distant. It will be remembered that in a superposition image each rhabdome receives light from a number of cones, whereas in an apposition image the light entering any rhabdome comes from a single cone. With this difference in mind, I placed directly below the preparation, i. e., between it and the source of light, a sliding diaphragm composed of a glass plate carrying a piece of tinfoil in which there was an opening a little smaller in diameter than a facet. By moving this back and forth I could illuminate either one cone or the whole retina. In using the apparatus two precautions were to be observed; first, it was necessary to bring the diaphragm to rest with its opening opposite a facet and not between facets. The correct position could easily be judged from the rhabdomes, for it was possible to place the diaphragm so that only one rhabdome showed light. The second precaution was to place in the eye piece of the microscope a diaphragm with a very small opening so that the light that passed through the sides of the retinal preparation when fully illuminated could not reach the experimenter's eye and thus interfere with accurate observation. Having set up the apparatus, I attempted to decide whether a given rhabdome, after being illuminated by light entering it

through a single cone, became brighter when the same kind of light fell on the surrounding cones. Repeated trials convinced me that this was not the case; at least, on sliding the diaphragm, I could perceive no change in the brightness of the rhabdome, though, when a piece of slightly smoked glass was introduced between the source of light and the microscope, the light in the rhabdome was perceptibly diminished. I therefore believe that the image received by the retina in *Astacus* when the pigment is arranged for bright illumination is an apposition image.

The character of the image in eyes in which the pigment is arranged for dim light was not easily determined on account of the difficulty of making preparations. This was necessarily done in the light, and, though the eyes were prepared immediately on being taken from the darkness, the exposure to light sufficed often for a complete return of the pigment to its position for bright illumination. I was, therefore, finally obliged to experiment with preparations cut, not at the level of the rhabdomes, but far enough distal to these to avoid all pigment. Taking as the body to be illuminated, the cut proximal end of a group of four cone-cells, I repeated the experiment which I had previously tried with the rhabdome, and found the group of cone-cells very much brighter when light was admitted to the retina through many cones than when it entered through only one, an observation that indicated to my mind the presence of a superposition image. The image itself could be easily seen; thus, when a small lead-pencil was held in front of the prepared eye, its image appeared as a dark band in the retina, and I could readily demonstrate by moving it that the image was an erect one. The image was sharp enough to enable me to distinguish the pointed from the blunt end of the pencil, and, so far as I could see, the sharpness increased slightly on focusing proximally, so that the image may have been clearer at the level of the rhabdomes than where I observed it. These observations left no doubt in my mind that when the retinal pigment in *Astacus* was adjusted for very dim light, the image formed by the dioptric apparatus was a superposition one. Hence *Astacus* may be classed, so far as its dioptric organs are concerned, with those crustaceans whose retinal images, as Exner has pointed out, are formed at one time as apposition, at another as superposition images.

5. Optic Ganglia.

a. Composition.

The mass of nervous tissue that occupies the central part of the optic stalk is composed of four distinct ganglia so placed that they constitute a series extending from the retina toward the brain (Pl. 1 Fig. 27). These ganglia have been designated, beginning with the most distal one, as the first, the second, the third, and the fourth optic ganglion (I—IV). The retina is connected with the first of these by the retinal fibres (*fbr.r*), and from the fourth the optic nerve (*n.opt*) extends proximally to the brain. The three spaces between the ganglia are bridged over by systems of nerve fibres. The chief constituents of the ganglia are ganglionic cells, nerve fibres, and »Punktsubstanz«; but, in addition to these, the ganglia also contain capillaries, connective tissue cells, and possibly a neuroglia.

The capillaries that ramify in the substance of the ganglia are derived from the subdivision of a single small artery that makes its way over the posterior face of the ganglionic mass. In preparations in which these capillaries have been injected with haematoxylin, it is easy to demonstrate the distribution of these vessels. They are about as abundant in the fibrous regions between the ganglionic centres as in these centres themselves, and within each ganglion they are noticeably more numerous in the »punktsubstanz« than among the surrounding ganglionic cells.

Connective tissue cells occur not infrequently throughout the ganglia, being rather more abundant on the periphery of these structures and among the nerve fibres between them than in other places. The presence of a neuroglia like that in Vertebrates will be considered in connection with the first ganglion, in which this kind of tissue probably occurs.

The ganglionic cells are superficial in position, forming an incomplete external coating to each ganglion. They are always absent from the distal and proximal faces of these structures, and, in the cases of the second and third ganglia, from the posterior faces also (Pl. 1 Figs. 34, 35, 36); the remainder of the ganglionic surfaces is covered with cells. The ganglionic cells can be satisfactorily studied in preparations stained with methylen blue, and in such preparations two types of cells can be distinguished: apolar and unipolar.

The apolar cells, which are unquestionably shown to be such

by the clearness of their outlines in well-stained preparations, are distinguishable from the unipolar cells only in that they possess no processes. They occur in regions where the ganglia are still growing; for, as will be shown presently, these structures increase by the addition of new elements even after the animal has reached maturity. It seems to me probable that the apolar cells represent the undifferentiated material from which unipolar cells will be ultimately formed. If this be so, then the apolar cells as such have no physiological rôle to play in the nervous functions of the ganglion.

The unipolar cells (Pl. 2 Figs. 48, 49, 51), which are vastly more numerous than the apolar ones, are of an extremely simple type. They consist of roundish or oval masses of protoplasm containing a single relatively large nucleus. Their single process is so simple and their surface so smooth that there is nothing that can be interpreted in the sense of protoplasmic processes. In this respect they agree very closely with the great majority of cells from the central nervous system of the crayfish, which, as RETZIUS (90, pag. 49) has already shown, are, as a rule, of this simple unipolar type.

Two kinds of unipolar cells, large and small, can be distinguished. Almost all the cells of the first, second, and third ganglia are small (Pl. 1 Figs. 34, 35, 36, *cl.gn*), there being only a few large ones in the last two ganglia named (Fig. 36, *x*). Conversely, almost all the cells of the fourth ganglion are large (Fig. 37, *cl.gn*). So far as I have been able to observe, small cells are always associated with fine short fibres, and large cells with coarse and usually long fibres. This relation is so invariable that the size of a ganglionic cell is a sure indication of the character of the fibre connected with it and vice versa; thus the large ganglionic cells that cover the fourth ganglion belong to the fibres that constitute the optic nerve and that are the longest fibres in the optic tracts, whereas the small cells that surround the first, second, and third ganglia are connected with the smaller, shorter fibres that intervene between the retina and the fourth ganglion.

The nerve fibres that enter into the composition of the optic ganglia are essentially similar to those found in other parts of the crayfish. Each fibre consists of a relatively large axis cylinder surrounded by a SCHWANN's sheath, the nuclei of which occur at rather irregular intervals. Different fibres vary considerably as far as the development of their SCHWANN's sheaths are concerned. In one part of the optic nerve (Pl. 2 Fig. 38, *n.d*), for instance, the axis cylinders are nearly devoid of sheaths and are so intimately pressed

together that it is often impossible to distinguish their exact limits, whereas, in the other parts of this nerve, each axis cylinder usually has a perfectly discrete sheath of its own. In the fresh condition the axis cylinders seem to be composed of a homogeneous substance in which there is no evidence of fibrillation, but in those treated with osmic acid a faint but distinct longitudinal striation is visible.

The third essential constituent of the ganglia, the »Punktsubstanz«, is separated into four masses, which form, so to speak, the cores of the four optic ganglia (Pl. 1 Fig. 27, I—IV). As is well known, this material is composed of a vast number of extremely fine fibrils, which, in preparations stained with methylen blue or made by the Golgi method, can be shown to result from the repeated division of the axis cylinders of the innumerable nerves which enter it. In no instance that came under my observation was there any evidence of direct union between different systems of fibrils; apparently, fibrils derived from different nerve fibres are at most only in contact with one another. In addition to the fibrillar material, which is, of course, the essential portion of the »Punktsubstanz«, the latter also contains a few connective tissue cells and a rather rich supply of capillaries.

Before proceeding to a description of the optic ganglia, it is necessary to say a word or so about the general relations of the three nervous elements already described. So far as I am aware, all the functional ganglionic cells in the optic ganglion of the crayfish are unipolar. Moreover, the one process that each of these cells gives rise to is always directly continuous with a nerve fibre. This process, however, does not represent one end of the fibre, but rather meets that structure somewhere on its length as the upright of a letter T meets the transverse part. The nerve fibre at its two ends, which correspond of course to the tips of the arms of the T, breaks up into fibrillations thus giving rise to a portion of the »Punktsubstanz«. The nervous fibrillar constituent of the »Punktsubstanz« seems always to arise from the repeated division of a nerve fibre, and there are no nerve fibres that are not connected with ganglionic cells; hence, fibrillae, as well as nerve fibres, may be regarded as processes from ganglionic cells. Nervous cells with their appended processes, as I have already mentioned, have been designated by Waldeyer as neurons, and, as this term is a convenient one, I shall adopt it in the following description.

b. Topography of Ganglia.

First Optic Ganglion. The first optic ganglion (Fig. 27, I) is a relatively thin, dome-shaped structure with a convex distal face and a concave proximal one, in both of which the curvature conforms very closely to that of the retina. In passing through the ganglion from its proximal to its distal side, four layers can be distinguished, which may be designated as follows: the external nuclear layer (Pl. 2 Fig. 46, 2), the fibrous layer (3), the internal nuclear layer (4), and the layer of »Punktsubstanz« (5). The retinal fibres make their way into the ganglion through its distal face, and from its proximal one emerge the fibres that connect it with the second ganglion.

The distal nuclear layer, which forms, of course, the distal surface of the ganglion, consists of a number of large oval or roundish nuclei imbedded in what is apparently an irregularly fibrous mass (Pl. 2 Fig. 41). Berger (78, pag. 199) noticed in *Squilla* the resemblance between these nuclei and the nuclei of connective tissue cells, and much the same interpretation of them is implied by Grenacher (79, pag. 120) in his account of the ganglion in *Mysis*. Viallanes (92a, pag. 395), however, who has studied them in *Palinurus*, regards them as true ganglionic nuclei. In Golgi preparations (Pl. 2 Fig. 46, *fbr.r*), the retinal fibres can be seen passing between these nuclei without entering into any definite relations with them. In preparations stained in methylen blue, the cells to which these nuclei belong are often clearly outlined; they are usually spindle-shaped with their longer axes parallel to the retinal nerve fibres, with which, however, they show no connections. The fact that these cells do not send processes into the »Punktsubstanz«, as well as their lack of connection with nerve fibres, justifies the conclusion, I believe, that they are not nervous, but rather sustentative in function. The layer that they form can be traced directly into a mass of ectodermic tissue that lies on the anterior face of the ganglion, and the resemblance between the nuclei in the distal nuclear layer and those in the ectodermic mass is so striking that, though these cells are most probably sustentative in function, I believe them ectodermic in origin. If this is so, it is probable that we have to do in this instance with a tissue not unlike the ectodermic neuroglia in vertebrates.

The second or fibrous layer (Pl. 2 Fig. 46, 3) is composed of a close felt of fibrous material almost entirely devoid of cellular

elements. As one can see in GOLGI preparations (Fig. 46), as well as in ordinary transverse sections (Fig. 42), this layer is completely penetrated by the bundles of retinal fibres.

The proximal nuclear layer (Fig. 46, 4) is precisely similar to the distal one except that it contains on the whole fewer cells. What has been said concerning the nature of the distal cells applies with equal force to those in this layer. These two nuclear layers, the distal and the proximal, have the appearance of having been originally a single layer, which became divided by the formation of the fibrous layer. The fact that the fibrous layer contains almost no cells leads one to look for the elements from which it arose in the layers adjacent to it. Whether it is a joint product of the two nuclear layers or not is still to my mind an open question, though the position that it occupies inclines me strongly to the opinion that it is produced by these layers.

The last layer in the ganglion is the layer of »Punktsubstanz« (Fig. 46, 5). To this the retinal fibres make their way and from it emerge the fibres that connect the first and second ganglia. The »Punktsubstanz« of this layer is not of uniform consistency, but is divided into small masses that are so regularly arranged that in transverse sections (Pl. 2 Fig. 44) they have somewhat the appearance of honey comb. Their arrangement and size are such that the question naturally suggests itself, are not these bodies the ganglionic representatives of the retinal ommatidia? VIALLANES (92a, pag. 391), who has studied them in *Palinurus*, believes that they do correspond to ommatidia and supports this opinion by the statement that each ganglionic body, which he calls by the very appropriate name of neurommatidium, contains seven fibres, the exact number given out by each ommatidium. Owing to the unfavorable condition presented by the ganglion in the crayfish, I have been unable to obtain decisive evidence for or against this opinion, and the only pertinent observation that I was able to make was in regard to the total number of retinal and ganglionic elements. In an eye with 1798 ommatidia the estimated number of neurommatidia was 1833. This, though not a perfect coincidence, is near enough to lead me to believe that VIALLANES is correct in his opinion that the neurommatidia agree in number with the ommatidia.

Another question of importance concerning the »Punktsubstanz« has to do with the fibres that enter and leave it. VIALLANES (92a, pag. 392) states that the retinal fibres pass directly through the first

ganglion, their continuations serving to connect that ganglion with the second one. Grenacher (79, pag. 120) makes a more guarded statement when he says that in *Mysis* the retinal fibres become lost in the first ganglion. He is, moreover, unable to decide whether they pass completely through the ganglion or not. To any one that has studied ordinary histological preparations of these structures, the difficulties in the way of deciding such a question must be obvious, and it was not until I had seen preparations made by the Golgi method, as well as those stained in methylen blue, that I was able to answer the question to my own satisfaction. In such preparations all the stained distal (retinal) fibres ended in a fibrillation in the ganglion (Pl. 2 Fig. 46, *fbr.r*); moreover, all fibres that emerged from the proximal side of the ganglion took their origin in fibrillations (Fig. 47, *fbr.n*), and in no case did I observe a fibre that passed through the ganglion. These observations lead to the conclusion that all optic fibres are interrupted in the first optic ganglion. It will be remembered that the retinal nerve fibres are really proximal processes from the proximal retinular cells and that these cells with their processes constitute the most distal set of neurons in the optic apparatus of the crayfish. For convenience they may be designated as neurons of the first order, while those fibres that lead centrally from the first ganglion mark the beginnings of neurons of the second order. The first optic ganglion may, therefore, be defined as the structure in which the neurons of the first order end and those of the second order begin.

First Decussation. Although the retinal fibres take the most direct course from the retina to the first optic ganglion, being arranged like the radii of a spherical system, the fibres between the first and second ganglia have such peculiar relations to the two masses of »Punktsubstanz« that, in their passage from one to the other, as Berger (78, pag. 199) long ago pointed out, they decussate more or less completely. The exact character of this decussation, though described and figured by several more recent investigators, has never been more accurately portrayed than by Grenacher (79, pag. 120), whose account I can confirm in every respect.

In the crayfish the decussation is most satisfactorily studied in sections made through the axis of the optic stalk in its anteroposterior plane (Pl. 1 Fig. 27). In such a section the first and second ganglia would be seen cut from their anterior to their posterior edges. The arrangement of fibres is such that one which starts from

the extreme posterior edge of the first ganglion passes to the extreme anterior edge of the second ganglion; and, conversely, one from the extreme anterior edge of the first ganglion passes to the extreme posterior edge of the second one; the two fibres thus cross one another like the arms of a letter X. The other fibres occupy intermediate positions, i. e., in proportion as the fibre's point of origin in the first ganglion is removed from the anterior end of that ganglion, so is its point of insertion in the second ganglion removed from the opposite end of the second ganglion. It follows from this that a fibre coming from the centre of the first ganglion should enter the centre of the second one, and, as a matter of fact, such is the case. These relations will perhaps become clearer on consulting the diagrammatic figure 59 (Pl. 3), as well as figure 57 (Pl. 2), in which the courses of a few fibres are given.

The decussating fibres form bundles that lie almost entirely in the anteroposterior plane, and consequently the decussation is best seen in sections cut in this plane (Pl. 1 Fig. 27); when the ganglia are cut dorsoventrally (Fig. 26), all traces of the decussation are lost, as is also the case in transverse sections of the fibrous regions (Pl. 1 Fig. 34, *cx. 1*). Such sections when more highly magnified (Pl. 2 Fig. 45) show usually some bundles of fibres parallel to the plane of section and others cut either transversely or more or less obliquely.

All the fibres that enter into the distal decussation have their origins, as I mentioned before, in the »Punktsubstanz« of the first ganglion (Pl. 2, Fig. 47, *fbr.n*), and, so far as my observations go, they all terminate in fibrillations in the second ganglion. Each fibre is attached to a ganglionic cell (Pl. 2 Figs. 48, 49), and these cells together constitute the horseshoe-shaped mass that surrounds the second ganglion (Pl. 1 Fig. 35). The cells and fibres have a rather definite arrangement, which has been represented in the diagrammatic figure 59. The fibres that arise from the posterior end of the first ganglion have their cells in the most proximal portion of the cellular mass, and those from the anterior portion of the ganglion are connected with cells in the distal portion of the mass. Fibres intermediate in position are, of course, united with cells in a middle place in the cellular mass. Although the great majority of cells are of the small type (Pl. 2 Fig. 48), the proximal portion of the ganglion contains usually a number of the larger kind of cells (Pl. 2 Fig. 49). These are connected with large nerve fibres that extent from the posterior end of the first ganglion to the anterior end of the second.

It is interesting to observe (cf. Fig. 49) that the body of these large fibres seems to pass over directly and almost entirely into their fibrillations and that the ganglionic cell is attached to the fibre by a relatively delicate process. This condition rather favors the idea that the ganglionic cell does not participate directly in the nervous functions and that the latter have their seats in the fibre and the »Punktsubstanz«.

By way of summary, it may be said that the fibres of the distal decussation begin in the first ganglion and terminate in the second one and with their attached ganglionic cells constitute a series of neurons that, from their relation with those connecting the retina and first ganglion, may be called the neurons of the second order.

Second Optic Ganglion. The mass of »Punktsubstanz« that forms the centre of the second ganglion is much thicker than that in the first ganglion; it is slightly convex distally and concave proximally and usually rests in a position somewhat oblique to the axis of the optic stalk, its anterior edge being proximal to its posterior one (Pl. 1 Fig. 27, II). In structure it is much simpler than the »Punktsubstanz« of the first ganglion. It is not surrounded by anything that can be called a neuroglia and its substance is not divided into neurommatidia. It consists, in fact, of a rather uniformly matted mass of fibrillae derived from the two sets of nerve fibres in connection with it and surrounded laterally by ganglionic cells (Pl. 1 Fig. 35).

Second Decussation. The nerve fibres that emerge from the proximal side of the second ganglion decussate in their passage to the third ganglion in almost exactly the same way as do those in the first decussation. Even the plane in which this crossing occurs, the anteroposterior, is the same in the two cases. Each fibre, so far as my observations go, is connected with a ganglionic cell usually of the small type and the layer formed by these cells surrounds the »Punktsubstanz« of the third ganglion in the characteristic horseshoe pattern (Pl. 1 Fig. 36, *cl. gn*). All these fibres begin in the fibrillar material of the second ganglion and almost all of them end by breaking up into fibrillae in the third ganglion; a few, however, pass proximally beyond this ganglion. In preparations stained with methylen blue, it is not uncommon to find one or two large fibres (cf. Pl. 3 Fig. 59, green) extending from the anterior end of the second ganglion to the posterior end of the third, where they each are united with a ganglion cell, in this instance of the large

type (Pl. 1 Fig. 36, *x*), and whence they proceed by a superficial course to pass obliquely over the dorsal face of the fourth ganglion till they finally enter the dorsal part of the optic nerve and make their way to the brain. The fibres of the second decussation together with their appended ganglionic cells constitute the neurons of the third order.

Third Optic Ganglion. This ganglion (Pl. 1 Fig. 27, III) consists of a nearly spherical mass of »Punktsubstanz« almost identical in composition with that of the second ganglion. The great majority of the neurons of the third order enter it distally and terminate in it; some few, however, as already mentioned, pass over it and enter the optic nerve directly. From its proximal face spring the fibres that connect it with the fourth ganglion. It is surrounded laterally, except on its posterior side, by small ganglionic cells (Pl. 1 Fig. 36, *cl.gn*), which belong, as already mentioned, to the neurons of the third order. Near its posterodorsal angle is a group of large cells (*x*), to which are connected the fibres that pass directly from the second ganglion to the brain.

Third Decussation. This decussation, as GRENACHER (79, pag. 121) long ago pointed out, is by no means so regular as the first and second, and, in fact, the fibres cross in such an erratic way that it is almost impossible to be sure that there is a true decussation present. The most that can be said about the character of the crossing is that the fibres from the posterior end of the third ganglion pass over to the dorsal part of the fourth and that those from the anterior end of the third gain a ventral position in the fourth. Beyond this it is difficult to make any very definite statements, and this, as will be seen, involves only a partial crossing of the fibres. Excepting the few fibres already mentioned as passing directly from the second ganglion to the optic nerve, all the fibres in the third decussation take their origin in the »Punktsubstanz« of the third ganglion and terminate in that of the fourth. They are connected with ganglionic cells of the small type, which fill the space between the third and fourth ganglia, and, together with these cells, constitute a system of neurons of the fourth order.

Fourth Optic Ganglion. This ganglion, the largest of the four masses, differs from the others in several important particulars. Its surface, except about its distal and proximal ends, is irregularly covered with large instead of small ganglionic cells (Pl. 2 Figs. 55, 56, *cl.gn*); and the substance of the ganglion, instead of consisting

of almost pure fibrillar material, is a confused mass of fibrillae and nerve fibres. Facts concerning the courses taken by the fibres in this ganglion are rather scanty. So far as my observations extend, all the neurons of the fourth order terminate in this ganglion, and, excepting the fibres that enter the optic nerve directly from the second ganglion, all optic fibres likewise terminate here. The courses taken by the fibres are, however, not easily worked out. The fibres that come from the posterior end of the third ganglion (neurons of the fourth order) make their way into a relatively small eminence on the dorsal side of the fourth ganglion (Pl. 2 Figs. 55, 56, *x*), and terminate there in the characteristic fibrillation. From this eminence a new and peculiarly marked set of fibres (Fig. 56, *n.d*) proceeds proximally through the ganglion to the dorsal part of the optic nerve, whence they can be traced to the brain. A second system of fibres, though less easily demonstrable, can be traced through the ventral part of the ganglion. The fibres from the anterior portion of the third ganglion terminate in the ventral part of the fourth ganglion, from which region a new set of fibres passes directly to the brain through the ventral part of the optic nerve. These two systems are the only ones about which I can speak with confidence; the others that must occupy intermediate positions I have been unable to identify with certainty.

c. Optic Nerve.

The optic nerve, a conspicuous structure in ordinary dissection, extends from the fourth optic ganglion to the optic lobe of the brain. Its finer structure is best understood from transverse sections (Pl. 2 Fig. 38), where it will be seen to be composed of a vast number of fibres, of which the dorsal ones (*n.d*) form a peculiar group eccentrically surrounded by the others. These dorsal fibres arise, as already mentioned, in an eminence on the dorsal face of the fourth ganglion and make their way through the dorsal part of the optic nerve to the brain. They were recognised long ago by Dietl (76, Pl. 37 Fig. 24), and they differ from the other fibres of the optic nerve in that their individual limits are very poorly defined. This is due, I believe, to the imperfect development of their sheaths of Schwann. If the frequency with which the nuclei of these sheaths occur be taken as an indication of the degree to which the sheaths are developed, a striking difference in this respect will be noticed between the two parts of the optic nerve. Comparing the

averages from ten enumerations made on equal areas in the dorsal and in the ventral parts of the nerve, it was found that, when the nuclei in the ventral part were represented by 9, those in the dorsal part were represented by only 5.3. This difference leads me to believe that the sheath of SCHWANN are poorly developed in the dorsal part of the nerve and that, in consequence of this, the limits of the separate fibres are more poorly marked there than in the ventral part.

Excepting the few fibres that enter the nerve directly from the second optic ganglion, all optic fibres take their origin, so far as I am aware, in the fibrillations of the fourth ganglion (Pl. 2 Fig. 51) and terminate in a similar way in the optic lobes of the brain (Fig. 54). Whether there is a partial optic chiasma in the brain, as mentioned by several authors, I am unable to say. Although I have seen appearances which indicate that there is one, in neither GOLGI nor methylen blue preparations have I ever seen an optic fibre enter one side of the brain and pass across to the other side before breaking up into a fibrillation. Of the many preparations studied all have shown the optic fibres to terminate on the same side of the brain as that which they entered.

The relation of the fibres in the optic nerve to ganglionic cells is not easily determined. In preparations of the fourth ganglion stained with methylen blue, the fibres of the optic nerve are seen to terminate in three ways: first, in a ganglionic cell of the large type and in a fibrillation (Pl. 2 Fig. 51); secondly, in a ganglionic cell only (Fig. 52); and, thirdly, in a fibrillation only (Fig. 53). In the optic lobe of the brain these fibres, so far as my observations extend, always terminate in fibrillations (Fig. 54) and are unconnected with ganglionic cells. As every fibre very probably has a ganglionic cell directly connected with it, and as the region for these connections seems to be the fourth ganglion, I have regarded preparations such as that represented in figures 53 as incompletely stained; and, had the process been completed, I believe a ganglionic cell would have been found connected with the fibre. Similarly, preparations such as those seen in figure 52 are probably instances in which the fibrillation has failed to take up color, though the cell and fibre have. It seems to me probable that the whole truth of these relations is shown in figure 51 and that the other conditions (Fig. 52 and 53) are but partial representations of it. These observations lead me to conclude that those optic nerve fibres that connect the fourth gang-

lion with the brain terminate in each of these places in fibrillations and are connected with ganglionic cells only in the region of the fourth optic ganglion.

This statement, however, may not be without its exceptions, for, according to RETZIUS (90, pag. 37), in some cases at least, the optic fibres are connected with cells in the brain. Granting that there are such fibres, then terminations in the fourth ganglion without ganglionic cells (Fig. 53) would be a normal relation, for it is improbable that a nerve fibre is connected with ganglionic cells both in the brain and in the fourth optic ganglion. Although I am unable to give a final decision on this question, I feel confident that, while a few optic nerve fibres may possess ganglionic cells located in the brain, the great majority of them are connected with cells in the fourth optic ganglion only. Whether these fibres have their cells in the one position or in the other, they represent the last system of neurons between the retina and the brain, neurons of the fifth order.

Before leaving the subject of the optic nerve, it is necessary to say a word or so about certain of its peculiarities. Although most of its fibres are true optic fibres, it contains a few belonging to other categories. Immediately before the fourth ganglion is reached, the optic nerve gives off a few fibres to the muscles that move the optic stalk. These fibres can be traced easily to their distribution among the muscle fibres, and I have no hesitation in pronouncing them motor fibres. There are probably not more than eight or ten of them in the whole nerve. They are unconnected with ganglionic cells outside the brain, and, as they are probably united with cells within this structure, it may be possible that these were the fibres that RETZIUS observed to be connected with cerebral cells.

Another peculiarity of the optic nerve is the possession of a few delicate fibres that, taking a superficial course, extend over the surface of the optic ganglia even to the first of these and terminate in cells from which a few branching processes extend still further over the ganglionic mass (Pl. 2 Fig. 58). These nervous elements, which represent single neurons, terminate in the brain with the optic fibres and yet apparently have no direct connection with the optic mechanism, for they do not pass through the decussations nor reach the retina. I regard them as similar to nervi nervorum, i. e., deep-seated sensory neurons surrounding the delicate optic ganglia. Judging from the number that appear stained, these elements cannot be very numerous, possibly as numerous as the motor fibres.

The optic nerve of the crayfish must, therefore, be regarded as mixed in character; for, in addition to its multitude of optic fibres, it contains eight or ten motor fibres and a few special sensory fibres resembling nervi nervorum.

d. Systems of Neurons.

So far as the succession and course of the neurons are concerned, the diagrammatic figure 59 (Pl. 3) may be taken as a convenient summary of the preceeding description. The four masses of »Punktsubstanz« represent as many interruptions in the course of the nerve fibres from the retina to the brain; in other words, each mass marks the end of one system of neurons and the beginning of another. An impulse in passing from the retina to the brain would, therefore, ordinarily travel over five neurons beginning with one of the first order and ending with one of the fifth. The only exception to this statement is to be found in the case of those peculiar fibres that, starting from the anterior end of the second ganglion, pass over the third and fourth and make their way directly to the brain. In this case the impulse would necessarily pass over only three neurons. Whether in any part of the eye there is a series of four neurons, intermediate between this series of three and the usual one of five, or not, is a question on which I have no conclusive evidence. If there were such a series, one might expect the distal three of its members to extend, as the ordinary neurons do, from the retina to the third ganglion, from which the fourth one would make its way directly to the brain. I have never seen any conclusive evidence on this question, but among my earlier observations is recorded a fibre that extended directly from the optic nerve to the third ganglion, where it separated into fibrillae, precisely what would be expected if a series of four neurons were present. The fact that this observation is a single one and that it was made before I fully appreciated the significance it might have, leads me to refrain from concluding that a series of four neurons does exist, though it seems to me highly probable that such may be the case.

Finally, the connections established by the different series of neurons may be thus briefly summarised. The series beginning at the posterior side of the retina (Pl. 3 Fig. 59, green) passes first to the corresponding side of the first ganglion, then to the anterior side of the second ganglion, to the posterior side of the third ganglion,

to the dorsal side of the fourth ganglion, and, finally, through the dorsal part of the optic nerve to the brain. The series beginning at the anterior side of the retina (Fig. 59, black) passes from that side of the retina to the corresponding side of the first ganglion, then to the posterior side of the second ganglion, to the anterior side of the third ganglion, to the ventral side of the fourth ganglion, and, finally, through the ventral part of the optic nerve to the brain. The series starting from near the middle of the retina (Fig. 59, blue) passes through the middle regions of all four ganglia and probably of the optic nerve.

e. Numerical Relation of Nerve Fibres.

From several standpoints it would be of considerable interest to determine the number of neurons in the series of five orders extending from the retina to the brain. The arrangement of the nerve fibres within the ganglionic mass is, however, so complicated that such an enumeration was impossible and I succeeded only in ascertaining the number of retinal fibres and the number of fibres in the optic nerve, i. e., the number of fibres that enter the optic ganglia as a whole and the number that emerge from them.

The determination of the number of fibres that leave the retina is a comparatively simple process. As previously shown each ommatidium gives rise to seven fibres; as the number of ommatidia equals the number of corneal facets it follows that seven times the number of corneal facets must equal the number of fibres leaving the retina. These fibres remain distinct from one another in their passage to the first ganglion, and hence as many fibres enter that ganglion as emerge from the retina.

The enumeration of the fibres in the optic nerve is by no means so simple an operation. This nerve, it will be remembered, is composed of two parts (Pl. 2 Fig. 38), in one of which the outlines of the fibres are clearly marked and their enumeration a simple matter of counting, while in the other the fibres are so indistinctly outlined that, though I have attempted to count them, I believe a method of estimates has yielded better results. In making these estimates the number of fibres and ommatidia were accurately compared in two crayfishes of different ages. The two specimens on which the enumerations were carried out may be called specimen *A* and specimen *B*; the former was a crayfish 3 centimetres long, and the latter was 7.9 centimetres in length. In both the right eye was studied.

Specimen *A* had 1155 corneal facets, and the number of retinal fibres must, therefore, have been seven times as many or 8085. Specimen *B* had 2375 facets, and its retinal fibres must have numbered 16,625.

In determining the number of fibres in the optic nerve it is important to bear in mind the two parts of the nerve: the dorsal portion, in which the separate fibres are distinguishable only with difficulty, and the ventral part, in which the individual fibres are clearly outlined. As I shall show presently, it is to the ventral part that new fibres are added in the gradual growth of the optic nerve, the dorsal part being unaffected by these changes. In specimen *A*, the ventral part of the nerve contained by actual count 1291 fibres; the corresponding part of the nerve of specimen *B* contained 3430 fibres. To form some idea of the number of fibres in the dorsal parts of the two nerves, I proceeded in the following manner. The difference in the number of facets in the two specimens, 2375 less 1155, or 1220, shows the number of new ommatidia that have been added to the retina of specimen *B* in its growth beyond the condition represented by specimen *A*. The difference between the number of fibres in the two optic nerves, 3430 less 1291, or 2139, shows the number of new fibres added to the optic nerve in this growth. The ratio between the new ommatidia and the new optic nerve fibres is now easily found by dividing 2139 by 1220, the result being that the ommatidia are to the fibres of the optic nerve as 1 to 1.75. Assuming this relation to be constant for the retina as a whole, the total number of fibres in the optic nerve can easily be estimated from the number of ommatidia. Thus in specimen *A* with 1150 ommatidia the total number of optic nerve fibres would be 1.75 times the number of ommatidia, or 2021; and in specimen *B* with 2375 ommatidia the total number would be 4156. That these estimates come very near the truth is seen from the following relation. I have already stated that the dorsal part of the nerve does not receive new fibres in the further development of the optic apparatus, but the new fibres are added to the ventral part. The difference, then, between the total number of optic fibres and the number in the ventral part ought to be about the same in specimens *A* and *B*, provided the estimates are nearly correct. Taking 3430, the number of fibres in the ventral part of *B*'s nerve, from 4156, the estimated total for the same nerve, a difference of 726 is obtained. Applying the same operation to the case of specimen *B*, a difference of 730 appears. These results

seem to me to argue strongly for the accuracy of the total number of optic fibres as estimated in the way described, and, further, they show that the number of fibres in the dorsal part of the nerve is approximately 700. The one actual enumeration of this region that I have made was carried out on specimen *B* and gave as a result 506 fibres. Where it is difficult to distinguish fibres, it is more probable that an actual enumeration would fall short of the real number than that it would exceed it, and the discrepancy between the estimated number and the number obtained by actual enumeration is to be explained, I believe, in this way.

The following table gives by way of summary the results of the preceding enumerations.

	Length	Ommatidia	Retinal Fibres	Optic Nerve Fibres
Specimen *A*.	3 cm.	1155	8085	2021
Specimen *B*.	7.9 cm.	2375	16 625	4156
Ratio of fibres to ommatidia . . .		1	7	1.75

As this table indicates, seven retinal fibres extend from each ommatidium to the first optic ganglion, and fibres to the proportion of 1.75 for each ommatidium connect the fourth optic ganglion with the brain. Granting that each ommatidium originates a single visual impulse, the 1155 impulses produced in the retina of specimen *A*, to take a specific example, are transmitted, probably, over all the 8085 retinal fibres to the first optic ganglion, and are transferred from the fourth optic ganglion to the brain over the 2021 optic nerve fibres. This reduction in the number of fibres concerned with the transmission of the impulses, as they pass through the optic tracts from the retina to the brain, is the chief observable anatomical change effected in the optic ganglia. It is of interest to notice that in no place in the course of the optic tracts is there a smaller number of fibres than the assumed number of retinal impulses.

6. Comparison of Optic Ganglia in Crustaceans.

In attempting to gain some understanding of the complicated structure of the optic ganglia in the crayfish, a comparative study of the corresponding organs in other crustaceans naturally suggests

itself. To carry out such a line of research to anything approaching completeness would, however, extend the present investigations far beyond what I originally set as their limits, and I content myself, therefore, with a few brief comparisons, in the belief that they will indicate the more important conclusions to which such studies would lead.

For matters of comparison with the crayfish one of the most instructive crustaceans is *Branchipus*. The optic ganglia of this animal have already been carefully studied, especially by CLAUS (86), and there is little to add to his extended account of them. As can be seen in Figure 28 (Pl. 1), the ganglionic mass in *Branchipus* consists of two portions; the distal of these is tongue-shaped (I), receives the retinal fibres, and gives off from its proximal face fibres that connect it with the second or proximal portion; this (II) is considerably elongated and tapers proximally into the optic nerve (*n.opt*). These two masses are not only connected by bundles of nerve fibres, but they are actually confluent at their dorsal extremities (*x*).

In spite of repeated attempts, I never succeeded in obtaining good preparations of the optic ganglia in *Branchipus* stained either with methylen blue or by the GOLGI method, and I am, therefore, obliged to depend entirely upon ordinary preparations for the finer anatomy of these organs.

The distal ganglion in *Branchipus* has many resemblances to the first optic ganglion in the crayfish. Like the latter, it is dome-shaped with its convexity facing the retina. It is composed of two layers, a distal one of nuclei closely set and a proximal one of »Punktsubstanz«. In position the nuclear layer corresponds to the two nuclear layers and the fibrous layer in *Astacus*, for the single layer in *Branchipus* extends from the distal surface of the ganglion to the »Punktsubstanz«. It is also penetrated by the retinal fibres as the three layers in *Astacus* are. If these three layers in *Astacus* are equivalent to the single one in *Branchipus*, the condition in the latter probably represents the more primitive one, an assumption agreeing well with what is known about the relations of these two crustaceans. The »Punktsubstanz« in *Branchipus* is divided into neurommatidia as in *Astacus*; the retinal fibres pass into it, and from it emerge the fibres that lead to the next ganglion as in *Astacus*. These facts seem to me to show that what I have called the distal ganglion in *Branchipus* is without doubt homologous with the first optic ganglion in *Astacus*.

The homologies of the proximal ganglion in *Branchipus* are, perhaps, not so easily determined. This ganglion may be said to be composed of three layers: on its ventral face is a layer of nerve fibres (Fig. 28 *fbr.n*) derived in part at least from the first ganglion, next to this dorsally is a layer of »Punktsubstanz« (II), and finally on its dorsal side is a layer of ganglionic cells (*cl.gn*). In regarding this ganglion from a comparative standpoint, the question arises: does it correspond to some one of the remaining optic ganglia in *Astacus* or to several of them united? An answer to this question could, of course, be found if the exact extent of the neurons were known in *Branchipus*. Unfortunately, I have been unable to determine this, but there is still other evidence, beside that derived from Golgi or methylen blue preparations, that may lead to a satisfactory conclusion. In *Branchipus* there are, as I have just mentioned, two masses of »Punktsubstanz«, that in the first ganglion and that in the one in question. These masses, judging from the conditions in *Astacus*, must represent the termination of one system of neurons and the beginning of another, and it is, therefore, probable that in passing from the retina to the brain in *Branchipus* three sets of neurons would be traversed. An inspection of figure 28 (Pl. 1) will show rather clearly the extent these three neurons must have. The neurons of the first order would be represented by the retinular cells and their processes, the retinal fibres, which together reach from the retina to the »Punktsubstanz« of the first ganglion. The neurons of the second order would reach from the »Punktsubstanz« of the first ganglion to that of the second one. As the most ventral of these terminate at the proximal end of the »Punktsubstanz« of the second ganglion, one is justified, I believe, in assuming only another set of neurons to reach to the brain. These neurons would be represented by the fibres of the optic nerve and would constitute a third order. In *Branchipus*, therefore, only three neurons are necessarily concerned in connecting retina with brain. These observations lead me, therefore, to conclude that the whole of what I have called the proximal ganglion in *Branchipus* is homologous with the second optic ganglion in *Astacus* and that the third and fourth optic ganglia in the crayfish are not represented in *Branchipus*.

Although the first and second optic ganglia in *Branchipus* show many points of resemblance to the homologous structures in *Astacus*, there are, nevertheless, some important differences. It will be remembered that in *Astacus* a decussation occurs among the

fibres between the first and second ganglia. In *Branchipus*, however, as figure 28 shows, there is no indication of such a crossing; the fibres that arise from one end of the first ganglion extend to the corresponding end of the second one, not to the opposite end as in *Astacus*. CLAUS (86, pag. 311, Pl. 30 Fig. 4), in his account of *Branchipus*, describes and figures a crossing of fibres (Faserkreuzung) between the first and second ganglia, but does not commit himself to the statement that this crossing represents the first decussation in the higher crustaceans. A critical comparison of his figure with one showing the decussation as in *Astacus*, will demonstrate at once that the crossing figured by CLAUS lacks the essential features of a true decussation. Moreover, in spite of careful search I have failed to detect in *Branchipus* even the crossing described by CLAUS. The fibres that enter the »Punktsubstanz« of the second ganglion often cross those lying parallel to the surface of this structure, but such crossings are so limited that they could not give rise to the general appearance figured by CLAUS. I cannot, therefore, confirm his observation, and, being thrown back upon my own, I conclude that, between the first and second ganglion in *Branchipus*, there is, in contrast to *Astacus*, no real decussation and only a limited crossing of fibres.

Another difference between *Astacus* and *Branchipus* is in the sequence of the materials of the second ganglion. In passing transversely through the ganglion in *Astacus* (Pl. 1 Fig. 35), the materials are met with in the following order: ganglionic cells (*cl.gn*), nerve fibres (*cx. 1*), »Punktsubstanz« (II); in *Branchipus* (Pl. 1 Fig. 28) the sequence is ganglionic cells (*cl.gn*), »Punktsubstanz« (*II*), nerve fibres (*fbr.n*), the last two constituents being inverted in their relations to each other.

The structure of the optic ganglia in *Branchipus*, as this account shows, is obviously much simpler than that in *Astacus*. Of the four optic ganglia in the crayfish, only the first and second are represented in *Branchipus*. In the first, a single nuclear layer represents the two nuclear layers and the fibrous layer in *Astacus*. The decussation present between the first and second ganglia in *Astacus* is lacking in *Branchipus*. A further point of difference between the two forms is that the nerve fibres which enter the second ganglion in *Branchipus* are external to its »Punktsubstanz« instead of being between this and the ganglionic cells as in *Astacus*.

Of the other crustaceans the structure of whose optic ganglia I am acquainted with either from observation or from the work of

other investigators, all may be classed under either the type of *Branchipus* or that of *Astacus*. Ganglia essentially like those in *Branchipus* are to be found in *Apus*, *Estheria*, *Argulus*, and, judging from the figure given by Claus (76, Pl. 26 Fig. 10), in *Daphnia*. Ganglia of the type in *Astacus* occur in *Squilla* according to the figure given by Berger (78, Pl. 16 Fig. 32), in *Mysis* according to Grenacher (79, pag. 120), and, though somewhat differently described, in *Nebalia* according to Claus (88, pag. 65), the last two cases being confirmed also by my own observations. Ganglia of this type are likewise found in the decapods *Palaemon* and *Homarus* and in the isopod *Anilocra*. The optic ganglia in the amphipods are so crowded together that they are extremely unfavorable for study. Della Valle (93), in his exhaustive account of the Gammarini, does not even give the number of ganglia present, nor have I been able to determine it.

Meagre as these observations are, it will be seen at a glance that so far as present information extends, the type represented by the optic ganglia in *Branchipus* is characteristically entomostracan, while that represented in *Astacus* is peculiar to the malacostraca. Notwithstanding the fact that these conclusions are based upon the examination of comparatively few species, their validity seems to me largely assured by the fact that the species have been chosen from widely separated groups.

Although not directly connected with this question, it is of interest to observe that the optic ganglia in hexapods are almost identical in their structural features with those in *Astacus*, the similarity being so striking that one is tempted to hypothecise a direct derivation of the ganglia in insects from those in crustaceans, though, as will be seen from the next section, this resemblance may also be explained by assuming that the requirements of growth for these nervous structures have been similar in the two groups of organisms.

7. Growth of Retina, Ganglia, and Optic Nerve.

Several investigators, notably among them Claus, have suggested that the anatomical complications of the optic ganglia in the higher crustaceans were to be explained as a mechanical necessity of the method of growth in these structures; but no one, so far as I am aware, has attempted to formulate the exact steps by which this

degree of complication could be arrived at. It is the purpose of this section to attempt such a formulation.

The growth of the optic tracts in *Astacus* can be satisfactorily studied only at two places, the retina and the optic nerve. These will be considered separately, beginning with the growth of the retina.

The retina in an adult crayfish, as will be remembered, has an elongated form, its anteroposterior dimension when measured in ommatidia being about 58, its dorsoventral extent, when similarly measured, approximating 31. If, with the intention of ascertaining how these dimensions have been produced, the corneal cuticula on the margin of the retina be examined, it will be seen that on the dorsal, ventral, and posterior edges the transition from the faceted to the non-faceted cuticula takes place abruptly or at least with the intervention of only a very few imperfect facets (Pl. 1 Figs. 30, 31, 32); on the anterior edge (Fig. 33), however, the region of transition is conspicuous and contains a considerable number of irregular facets and outlines of cells apparently in process of forming facets. This condition is characteristic of the whole anterior edge as contrasted with the other three edges, and suggests at once that the excessive anteroposterior extension of the retina is due to continued growth on this edge.

To ascertain whether the retina has grown in this way or not, the eyes in several young crayfishes were examined. In a newly hatched specimen measuring 8.5 mm. from the tip of its rostrum to the end of its telson, the retina contained in its dorsoventral curvature 29 ommatidia and in its anteroposterior 27. When these numbers are compared with the corresponding ones in an adult, it will be observed that, though at this early stage the retina has acquired almost the full number of ommatidia in its dorsoventral curvature, in its anteroposterior dimension it has only about half as many as it must have ultimately; so that, between this stage and that of an adult, the ommatidia must approximately double their number and the growth must be either on the anterior or on the posterior edge of the retina or on both. When these two edges were compared in the young crayfish just mentioned, the mass of hypodermal cells, as well as the occurrence of small ommatidia on the anterior edge and the absence of these peculiarities from the posterior one, left no doubt that only the anterior was concerned in the extension of the retinal area.

In an older crayfish whose length was 2.4 cm., the dorsoventral

curvature contained 28 ommatidia, the anteroposterior 39, or 12 more than in the corresponding dimension of the previous stage. In a still larger and presumably older crayfish measuring 3 cm. in length, the number of ommatidia in the dorsoventral rows was 29, while in the anteroposterior ones there had been an increase to 43. In both these animals the growing edge of the retina was the anterior one, and it therefore seems safe to conclude that after the crayfish has been hatched the retina continues to grow only on its anterior margin. This method of growth probably also characterised the development of the retina previous to hatching; at least, such is the case in the closely allied genus *Homarus*, and I believe we would not be far wrong in assuming that the anterior edge has always been the growing edge and that the posterior one represents approximately the region from which the retina has grown; in other words, the posterior edge is ontogenetically the oldest and the anterior the newest part of the retina.

In dealing with the growth of the optic nerve, it is necessary to keep clearly in mind the two parts of which it is composed: the smaller dorsal portion (Pl. 2 Fig. 38 *n.d*) and the larger ventral one. In a young crayfish whose length was 3 cm. the area of the ventral part of the nerve as seen in transverse section was about 2.3 times that of the dorsal portion (Fig. 39). In the adult these proportions are considerably changed (Fig. 40); for, while the area of the dorsal part has increased by about one third (from 1 in the young to 1.34 in the adult), the area of the ventral part has nearly tripled (from 2.3 in the young to 6 in the adult). This general increase has probably been produced by two causes: first, the individual fibres, like the retinal element, have simply each increased in calibre slightly, thus enlarging the whole nerve; and, secondly, the addition of new nerve fibres has certainly increased parts of the nerve. There is no evidence that new fibres are added to the dorsal part of the nerve, and I believe that the slight increase in that region is due entirely to the enlargement of individual fibres; in the ventral part, however, the fibres have multiplied nearly three times, from 1291 in the young to 3430 in the adult; i. e., the increase in the number of fibres has been about in the same proportions as the increase in the area of transverse section. These observations lead to the conclusions that the optic nerve grows by the addition of new fibres to its ventral part, a unilateral method essentially like that in the retina, and that the dorsal part of the nerve may be regarded as ontogenetically older

than the ventral part. It is probable indeed that the dorsal part represents what may be called the embryonic optic nerve, i. e., that part of the nerve formed during embryonic development, a time when individual fibres are less likely to gain mesodermic sheaths than later. This interpretation, though somewhat gratuitous, does not clash with any facts known to me about the optic nerve, and offers an explanation for several peculiarities otherwise difficult to understand.

In this connection it is of considerable importance to observe the relations between the various parts of the retina and of the optic nerve as established through their nervous connections. These connections have already been described (cf. Fig. 59), and it need only be mentioned here that the fibres which leave the part of the retina ontogenetically oldest (green) pass into the oldest part of the optic nerve, and, conversely, fibres from the newest part of the retina are connected with fibres in the newest part of the nerve; in other words, the retina and the optic nerve have increased hand in hand. It is also of interest to observe that that part of the optic tract which is ontogenetically the oldest presents a very different condition from the rest. As can be seen in the diagrammatic figure 59, an impulse starting from the newer parts of the retina (red, blue, or black) would necessarily pass over five neurons in reaching the brain, whereas one coming from the older part (green) would necessarily pass over only three neurons. In *Branchipus* an impulse may reach the brain from any part of the retina by passing over three neurons. This primitive condition is reproduced in *Astacus* only in the ontogenetically oldest part of the optic tracts, a position, however, in which, if a primitive condition occurred at all, one would expect to find it.

The essential similarity in the method of growth followed by the retina and the optic nerve suggests at once the idea that the intervening ganglia probably likewise follow the same lines of growth. In fact by tracing the course of the newest fibres it is comparatively easy to state which is the growing end of most of the ganglia. Thus the first ganglion (cf. Fig. 59) grows like the retina anteriorly, the second posteriorly, and the third again anteriorly. The direction of growth in the fourth ganglion is less easily defined, and the most that I can state is that the growth must be in a ventral direction, at least where the optic nerve emerges.

In *Branchipus*, as might be expected, the growth of the optic

tracts is simpler than in *Astacus*. As can be seen in dorsoventral sections (Pl. 1 Fig. 28), the retina in *Branchipus* continues to grow along its dorsal margin, a region that, as Claus (86, pag. 310) has clearly shown, has been the region of growth even from the earliest stages of development. Further, from this same region, material is also added to both ganglionic masses, so that all the nervous structures in the stalk, the retina and the two optic ganglia may be said to originate from this one centre. In *Branchipus*, then, the plane of growth is dorsoventral, and the growing ends in the three nervous structures just mentioned are the dorsal ones.

In comparing the method of growth in *Branchipus* and in *Astacus* several important differences will be observed. In *Branchipus* the plane of growth for all the nervous structures of the stalk is dorsoventral; in *Astacus* only the optic nerve grows in this way, the retina and the first, second and third ganglia growing in the anteroposterior plane. This difference, which might at first sight seem fundamental, is, however, readily explained if it be admitted that the stalk in *Astacus*, together with much of its distal contents, has been twisted on its axis, so that what is dorsal in *Branchipus* has come to be anterior in *Astacus*. Such a change as this, which in itself is easily conceivable, would offer a sufficient explanation for the fact that the retina and the first three ganglia in *Astacus* bear the same relation to the anterior face of the optic stalk in that animal as the corresponding structures in *Branchipus* bear to the dorsal face of the stalk in this form. It would also explain the imperfect decussation of fibres between the third and fourth ganglia, the region in which the twisting is actually felt, as well as the fact that the optic nerve, the portion of the optic tracts too deep to be effected by the twisting, retains the primitive dorsoventral plane of growth.

Another difference between *Branchipus* and *Astacus* concerns the centres of growth. In *Branchipus*, all the nervous organs in the optic stalk grow from a common centre. In *Astacus*, there is a centre of growth for the retina and for each ganglion: thus, the retina grows from the hypodermis, and each ganglion from the ganglionic cells that surround it. This more differentiated condition of the centres of growth in *Astacus* offers, however, no serious obstacle to the comparison of the sets of organs in the two animals, but is in harmony with the more complex organisation in *Astacus*. In the development of the optic stalks, *Astacus*, together with other decapods, passes through a stage that strongly recalls the permanent

condition in *Branchipus*. At an early stage in the growth of the optic lobes in *Astacus*, as the researches of REICHENBACH show, an area of cell proliferation appears in a position corresponding to that seen permanently in *Branchipus*. This proliferation is in fact accompanied by a temporary involution, and the cells resulting from it go in part into the growing retina and in part into the optic ganglia. The same is true of the optic lobes in *Homarus* (cf. PARKER, 90, pag. 34), except that in this instance no involution has been observed, and the conditions in this respect are almost identical with those in *Branchipus*. Eventually in *Homarus* and probably also in *Astacus* the ganglia lose their connection with this centre of growth, which continues as a growing area for the retina only. It is incidentally of interest to observe that, of the two conditions shown by the decapods, the one in which there is a simple cell proliferation, as exemplified in *Homarus*, reproduces the primitive condition in *Branchipus* more accurately than the involution in *Astacus* does: in the latter a centre of cell proliferation has apparently been replaced by an involution cenogenetically acquired rather than the reverse.

The last important point of comparison in the optic tracts of *Branchipus* and *Astacus* pertains to the direction of growth in the different parts. The third and fourth ganglia in *Astacus*, as already indicated, have no homologues in *Branchipus* and it is necessary, therefore, to consider only the first and second ganglia. Admitting that the dorsal side of the stalk in *Branchipus* corresponds to the anterior side in *Astacus*, the direction of growth in the retina and the first ganglion is the same in both, namely dorsal in *Branchipus* and anterior in *Astacus*. In the second ganglion, however, a very different condition of affairs obtains, for this ganglion in *Astacus*, at least so far as its »Punktsubstanz« is concerned, grows posteriorly, a direction, mutatis mutandis, precisely contrary to that taken by its homologue in *Branchipus*. Coupled with this peculiarity in the growth of the second ganglion in *Astacus*, is the fact that the fibres which enter or leave it are involved in either the first or the second decussation, an arrangement altogether different from that in *Branchipus*, where, as before mentioned, there is no indication of a true decussation. If, then, with a change in the direction of growth in a ganglion, decussations appear on either side of it, one would naturally suspect that the new method of growth had some connection with the formation of the decussations. Precisely what this connection may be can be clearly seen, I believe, if one attempts to convert a

second ganglion of the type in *Branchipus* into one of the type in *Astacus*.

In attempting such a conversion it is necessary at the outset to appreciate clearly the relations of the various structures involved. The second ganglion in *Branchipus* (Pl. 1 Fig. 28) is composed of a dorsal layer of ganglionic cells (*cl.gn*), a middle layer of »Punktsubstanz« (II), and a ventral layer of nerve fibres (*fbr.n*). The first two of these grow dorsally at their distal ends. In the second ganglion in *Astacus*, these three layers reappear. The ganglionic cells (Fig. 27, *cl.gn*) occupy a position corresponding to that of their homologues in *Branchipus*, and, moreover, grow in a like direction (cf. Fig. 59). The »Punktsubstanz« (Fig. 27, I), however, does not lie next the ganglionic cells, as in *Branchipus*, but projects and grows ventrally, allowing the nerve fibres (*cx. 1*) from the first ganglion to intervene between it and the ganglionic cells. These are the more essential differences between the two types of ganglia, and any change that would lead from one type to the other would obviously involve either »Punktsubstanz« or nerve fibres.

Assuming as a beginning a stage in *Branchipus* in which a few of the oldest fibres (the ventral ones) were established between the first and second ganglia and in which the proximal end of the »Punktsubstanz« of the second ganglion was formed, it is easy to point out the paths by which, on the one hand, the condition in *Branchipus* will be realised and, on the other, that in *Astacus*. If from this indifferent stage the »Punktsubstanz« grows distally and dorsally, it will always remain between the nerve fibres and the ganglionic cells as in *Branchipus*; if, however, it grows ventrally, it will pass between the nerve fibres already formed and finally occupy a ventral position as in *Astacus*. Starting from this indifferent stage, then, the condition in either *Branchipus* or *Astacus* will be arrived at depending entirely upon the direction that this growth of the »Punktsubstanz« takes.

The change in the direction of growth by which the condition in *Astacus* would be brought about would also induce the formation of two decussations, one in front of and the other behind the second ganglion, precisely as they occur in that crustacean. Thus, in the growth of the optic tracts, any newly added fibres in the region between the first and second ganglia would necessarily have their distal fibrillations in the anterior end of the first ganglion and their proximal ones in the posterior end of the second, thus

requiring that the new fibres should cross the course of those already established. Under such circumstances, the continuous addition of new fibres would only add to the fulness of the decussation. In the same way the nerve fibres connecting the second and third ganglia would suffer a decussation, since the third ganglion grows in the same direction as the first. Thus both the first and second decussations may be said to be the result of the change in the direction of growth in the second ganglion.

If this explanation of the origin of the decussations is true, it follows that the two decussations should lie in the same plane and that this plane should coincide with the plane of growth in the given part of the optic stalk. As the preceding account has shown, such is really the case: in both decussations in *Astacus* the fibres cross in the anteroposterior plane and this plane is also the plane of growth for the optic structures of that region. Moreover, this explanation makes clear the course of certain anomalous nerve fibres that have been observed in the second ganglion. These fibres (Pl. 2 Fig. 57 *x*) connect what is ontogenetically the older part of the first ganglion with the corresponding part of the second one, and represent the fibres between which the »Punktsubstanz« might be expected to grow in gaining the position characteristic of it in *Astacus*. Such fibres, as figure 57 shows, are either involved in the »Punktsubstanz« or lie posterior (= ventral in *Branchipus*) to it, thus recalling the primitive position occupied by these fibres in *Branchipus*. These observations lead me to believe that the explanation which I have offered for the two decussations is a true one.

What could have led to the change in the direction of growth in the second ganglion is a question that I cannot definitely answer. Possibly the crowding of the first and second ganglia on one another, as new nervous elements were added, pressed the »Punktsubstanz« of the second ganglion into a new channel. But such answers can be at most only suggestive. That the change in the direction of growth in the second ganglion is an adequate explanation of the two adjoining decussations seems evident enough. Whether the cause of this change can be discovered or not is another question.

8. Derivation of Ommatidia.

The numerical relations of the cells in the ommatidia of crustaceans, as I have already pointed out (cf. Parker, 91), have such a remarkable uniformity that the idea of ommatidial types definable by the number and arrangement of their cells almost naturally suggests itself. As an example of the most complex of these types, the ommatidium in *Astacus* may be taken. The numbers of cells that it contains, omitting the accessory pigment cells, are as follows: corneal hypodermal cells, two; cone cells, four; distal retinular cells, two; proximal retinular cells, seven functional and one rudimentary. The arrangement of these elements as seen in the longitudinal and transverse aspect of the ommatidium is shown in the diagrammatic figures 64 to 66. One of the simplect ommatidia is that in *Branchipus* in which there are two corneal hypodermal cells, four cone cells, and five retinular cells. In some ommatidia, notably those in schizopods, the cones consist of only two cells, a condition which suggests that the ommatidia in *Branchipus*, at least so far as their cones are concerned, probably do not represent the simplest type. The least number of cells that we should be justified in assuming for the simplest type of ommatidium would then be two corneal hypodermal cells, two cone cells, and five retinular cells. The arrangement of these elements is indicated in figures 61 and 62.

These two types of ommatidia, the simplest and the most complex, are without doubt genetically connected, and, as there is no evidence to show that the former is a degenerate product of the latter, it is probable that the simplest type is a primitive one from which the other has been derived. The numerical relation of the ommatidial cells indicates the way in which this derivation could have been accomplished. Thus a cone composed of two cells could be easily converted into one formed of four cells by a division of each original cell into two, and the simpler group of five indifferentiated retinular cells could by differentiation and division give rise to the two distal and eight proximal retinular cells of the more complex type (cf. Parker, 90, pag. 56).

The necessary steps in the conversion of an ommatidium of the simpler type into one of the more complex type are indicated in the diagrammatic figures 61 to 66. These changes effect only the retinular and cone cells, the corneal hypodermal cells being essentially alike in both types. The cone cells, originally two in number

(Fig. 62), could by division (Fig. 63) become four (Fig. 65), and by their elongation the rhabdome (*rhb*) would come to lie some considerable distance from the cone proper (Fig. 64). These two changes, the increase in number and the elongation, are the chief modifications noticeable in the cone cells. The changes in the retinular cells are more complex. Each of the five retinular cells in the simpler type (Fig. 61) gives rise to a part of the rhabdome and forms a portion of the sheath of the cone. In the complex type, these two functions are carried out by separate cells, the distal retinular cells forming the sheath of the cone and the proximal ones producing the rhabdome. Beginning with the simpler type, it is conceivable that one of its retinular cells (Fig. 62, *9—10*) might come to be chiefly concerned with sheathing the cone, while the remaining four might become more or less limited to the rhabdome. If the retinular cell that partially envelopes the cone were to divide, the ommatidium would then contain two distal retinular cells and four proximal ones, a condition precisely that found in *Serolis* (cf. PARKER, 91, pag. 89). From this stage, by a division of the four proximal retinular cells into eight, a stage in which the numerical relations of the cells are exactly those in *Astacus* would be reached. The elongation of the cone cells would separate the proximal from the distal retinular cells, the latter being limited to the cone, the former to the rhabdome (Fig. 64). The details of this process are clearly enough shown in the diagrammatic figures already referred to, and require comment in only one particular. The position in the simpler ommatidial type of the cell (Fig. 62, *9—10*), from which the two distal retinular cells of the more complex type were derived, is such that it is probable that the two descendants of this cell do not remain in the same ommatidium, but that one of them (*10*) applies itself to an adjoining ommatidium, while the other (*9*) remains with the ommatidium to which it originally belonged (cf. Figs. 63 and 65).

The type of optic ganglia found in *Branchipus* has already been shown to be a primitive one, and the exclusive association of ommatidia containing only five retinular cells with this type is evidence in favor of the primitive nature of the ommatidia. In a similar way, the regular occurrence of ommatidia of ten retinular cells with a derived type of ganglionic structure, as in *Astacus*, supports the conclusion already reached that these ommatidia, like the connected ganglia, are also structures of a derived type. Deductions such as these lead to the general conclusion that, beginning with a stage

somewhat like that in *Branchipus*, the optic ganglia and retina in crustaceans have grown in complexity hand in hand till a condition like that in *Astacus* was reached. This mutual growth is quite natural when one reflects on the intimate physiological dependence of the retina and the ganglia.

Aside from the question of the relation of ommatidia to one another is that concerning their origin. This topic has already been discussed (cf. PARKER, 91, pag. 118), and I recur to it only to add some fresh evidence. This evidence bears directly upon the opinion expressed by WATASE (90) that each ommatidium is an elongated ectodermic involution whose cavity has been obliterated by the approximation of its walls, the cells of which, however, still retain their power of secreting chitinous substance. The secretion of the deeper cells forms the rhabdome, that of cells nearer the surface gives rise to the cone, and the superficial cells produce the facet; in one sense, then, these three structures, rhabdome, cone, and facet, are homologous. I have already advanced arguments against this theory (cf. PARKER, 91, pag. 128): the arrangement of the cells in different ommatidia does not favor this idea; the small number of cells in the more primitive forms of ommatidia makes involution mechanically difficult; there are no transitional forms between those simple ocelli that are produced by involution, and ommatidia; and, finally, there is absolutely no embryological evidence that ommatidia are formed by involution. To these objections I must now add the further one that the composition of the rhabdome as portrayed in the preceding pages does not favor the idea that this structure is in any wise a secreted body, but rather that it is a living product of the retinular cell in much the same sense that muscle substance is the product of a muscle cell. These objections seem to me to afford sufficient ground for abandoning the theory that ommatidia have arisen by involution. They offer no difficulty, however, to the idea already expressed (PARKER, 91, pag. 130) that the simplest type of ommatidium has been derived from a cluster of cells in a continuous unfolded epithelium and that by a process of cell division and differentiation the simpler type of ommatidium gave rise to the more complex.

Papers Quoted.

Angelucci, A. (78), Histologische Untersuchungen über das retinale Pigmentepithel der Wirbelthiere. in: Arch. Anat. Phys. Phys. Abth. 1878 pag. 353.

Berger, E. (78), Untersuchungen über den Bau des Gehirns und der Retina der Arthropoden. in: Arb. Z. Inst. Wien 1. Bd. pag. 173.

Carrière, J. (85), Die Sehorgane der Thiere vergleichend-anatomisch dargestellt.

—— (89), Bau und Entwicklung des Auges der zehnfüßigen Crustaceen und der Arachnoiden. in: Biol. Centralbl. 9. Bd. pag. 225.

Claus, C. (76), Zur Kenntnis der Organisation und des feineren Baues der Daphniden und verwandter Cladoceren. in: Zeit. Wiss. Z. 27. Bd. pag. 362.

—— (86), Untersuchungen über die Organisation und Entwicklung von *Branchipus* und *Artemia* nebst vergleichenden Bemerkungen über andere Phyllopoden. in: Arb. Z. Inst. Wien 6. Bd. pag. 267.

—— (88), Über den Organismus der Nebaliden und die systematische Stellung der Leptostraken. ibid. 8. Bd. pag. 1.

Della Valle, A. (93), Gammarini del Golfo di Napoli. in: Fauna Flora Golf. Neapel 20. Monogr.

Dietl, M. J. (76), Die Organisation des Arthropodengehirns. in: Zeit. Wiss. Z. 27. Bd. pag. 488.

Exner, S. (91), Die Physiologie der facettirten Augen von Krebsen und Insecten.

Gottsche, C. M. (52), Beitrag zur Anatomie und Physiologie des Auges der Krebse und Fliegen. in: Arch. Anat. Phys. 1852 pag. 483.

Grenacher, H. (79), Untersuchungen über das Sehorgan der Arthropoden, insbesondere der Spinnen, Insecten und Crustaceen.

Herrick, F. H. (92), *Alpheus*: A study in the Development of Crustacea. in: Mem. Nation. Acad. Sc. Washington Vol. 5 Mem. No. 4 pag. 370.

Johansen, H. (92), Über die Entwicklung des Imagoauges von *Vanessa*. in: Z. Anzeiger 15. Jahrg. pag. 353.

Kölliker, A. (91), Zur feineren Anatomie des centralen Nervensystems. in: Zeit. Wiss. Z. 51. Bd. pag. 1.

Leydig, F. (55), Zum feineren Bau der Arthropoden. in: Arch. Anat. Phys. 1855 pag. 376.

Lowne, B. T. (84), On the Compound Vision and the Morphology of the Eye in Insects. in: Trans. Linn. Soc. London (2) Vol. 2 pag. 389.

Parker, G. H. (90), The Histology and Development of the Eye in the Lobster. in: Bull. Mus. Comp. Z. Harvard Coll. Vol. 20 pag. 1.

—— (91), The Compound Eyes in Crustaceans. ibid. Vol. 21 pag. 45.

—— (92), A Method for making Paraffine Sections from Preparations stained with Ehrlich's Methylenblue. in: Z. Anzeiger 15. Jahrg. pag. 375. Also in: Sitz. Ber. Ges. Nat. Freunde Berlin 1892 pag. 97.

Patten, W. (86), Eyes of Molluscs and Arthropods. in: Mitth. Z. Stat. Neapel 6. Bd. pag. 542.

—— (90), Is the Ommatidium a Hair-bearing Sense Bud? in: Anat. Anzeiger 5. Jahrg. pag. 353.

Rath, O. vom (93), Beiträge zur Kenntnis der Spermatogenese von *Salamandra maculosa*. in: Zeit. Wiss. Z. 57. Bd. pag. 97.

Reichenbach, H. (86), Studien zur Entwicklungsgeschichte des Flusskrebses. in: Abh. Senckenbg. Ges. Frankfurt 14. Bd. pag. 1.

Retzius, G. (90), Biologische Untersuchungen. (2) 1. Bd.

Schultze, M. (68), Untersuchungen über die zusammengesetzten Augen der Krebse und Insecten.

Szczawinska, W. (91), Contribution à l'étude des yeux de quelques Crustacés et Recherches expérimentales sur les mouvements du pigment granuleux et des cellules pigmentaires sous l'influence de la lumière et de l'obscurité dans les yeux des Crustacés et des Arachnides. in: Arch. Biol. Tome 10 pag. 523.

Viallanes, H. (92), Recherches anatomiques et physiologiques sur l'oeil composé des Arthropodes. in: Ann. Sc. N. (7) Tome 13 pag. 349.

—— (92a), Contribution à l'histologie du système nerveux des Invertébrés: la lame ganglionnaire de la Langouste. ibid. pag. 385.

Wagner, R. (35), Einige Bemerkungen über den Bau der zusammengesetzten Augen der Insecten. in: Arch. Naturg. 1. Jahrg. pag. 372.

Waldeyer, W. (91), Über einige neuere Forschungen im Gebiete der Anatomie des Centralnervensystems. in: Med. Wochenschr. No. 44.

Watase, S. (90), On the Morphology of the Compound Eyes of Arthropods. in: Stud. Biol. Lab. J. Hopkins Univ. Vol. 4 pag. 287.

Willem, V. (92), Les Ocelles de *Lithobius* et de *Polyxenus*. in: Bull. Soc. Mal. Belg. Tome 27 pag. 79.

Explanation of Figures.

All the drawings were made with the aid of an Abbe camera.

Abbreviations.

a Anterior.
ax.n Fibrillar axis.
cl.con Cone cell.
cl.crn Corneal hypodermal cell.
cl.dst Distal retinular cell.
cl.gn Ganglionic cell.
cl.pg Accessory pigment cell.
con Cone.
crn Corneal cuticula.
cta Cuticula.
cx.1 First decussation.
cx.2 Second decussation.
cx.3 Third decussation.
d Dorsal.
fbr.con Fibre of cone cell.
fbr.dst Fibre of distal retinular cell.
fbr.n Nerve fibre.
fbr'.n Nerve fibrilla.
fbr.r Retinal fibre.
h'drm Hypodermis.
la.a Anterior half plate.
la.p Posterior half plate.
mb.ba Basement membrane.
mu Muscle.
n.d Dorsal part of optic nerve.
nl.con Nucleus of cone cell.
nl.crn Nucleus of corneal hypodermal cell.
nl.dst Nucleus of distal retinular cell
nl.ex Outer nuclei of I.
nl.in Inner nuclei of I.
nl.ms'drm Nucleus of mesodermic cell.
nl.pg Nucleus of accessory pigment cell.

nl.px Nucleus of proximal retinular cell.
n.opt Optic nerve.
p Posterior.
r Retina.
rhb Rhabdome.
rhb' Rhabdomere.
v Ventral.
va.sng Blood vessel.
I. Punktsubstanz of first ganglion.
II. » of second »
III. » of third »
IV. » of fourth »

The numbers 1 to 8 are used to designate the proximal retinal cells, the same number referring always to corresponding cells.

Plate 1.

Fig. 1—6 are magnified 130 diameters; Figs. 7—22, 430 diameters; Figs. 23—25, 640 diameters. The figures of all transverse sections are placed upon the plate so that their upper edge is dorsal, their lower ventral, their right side anterior, and their left posterior (cf. pag. 7).

Figs. 1 and 2. Longitudinal sections of ommatidia showing the arrangement of pigment as influenced by light (Fig. 1) and by darkness (Fig. 2). The numbers at the right of Fig. 2 indicate the levels at which the sections for Figs. 3—6 were taken.

Fig. 3. Transverse section through the corneal hypodermis; the tip of the cone appears in the centre of the section.

Fig. 4. Transverse section through the cone cells at the level of their nuclei.

Fig. 5. Transverse section through the cone and nuclei of the distal retinular cells.

Fig. 6. Transverse section through the cone cells proximal to the cone.

Fig. 7. Longitudinal section of a retinula; *x* cavity filled with fluid; the numbers at the left indicate the levels at which sections for Figs. 8—20 were made.

Figs. 8—13 represent consecutive transverse sections through the region occupied by the nuclei of the eight proximal retinular cells.

Fig. 8. The most distal section in the series, containing parts of the nuclei of cells 1, 3, and 7.

Fig. 9. The second section, containing, in addition to parts of the three nuclei just named, part of the nucleus of cell 6.

Fig. 10. The third section, containing the proximal portions of the nuclei in cells 6 and 7 and the distal part of the nucleus of cell 2.

Fig. 11. The fourth section, containing, in addition to a part of the nucleus in cell 2, parts of the nuclei of cells 4 and 5.

Fig. 12. The fifth section, containing the proximal ends of the nuclei in cells 4 and 5.

Fig. 13. The sixth section, containing, in addition to cells 1—7, the nucleus of cell 8.

Fig. 14. Transverse section of a retinula at the level of the fluid-filled cavity (*x*) distal to the rhabdome (compare Fig. 7), showing the two fibres (*fbr.dst*) from the distal retinular cells, the four fibres (*fbr.con*) from the cone cells, and a fibre (*y*) probably representing a proximal process from the eighth proximal retinular cell. Depigmented in potassic hydrate.

Fig. 15. Transverse section from near the distal end of the rhabdome showing the transparent central axis leading to that structure.

Figs. 16 and 17. Transverse sections from the distal end of the rhabdome to show the peculiar W-shaped outline of this structure; Fig. 17 was taken from the section proximal to that from which Fig. 16 was drawn.

Fig. 18. Transverse section of the proximal end of the rhabdome surrounded by its seven proximal retinular cells and the four fibrous prolongations of the cone cells. Depigmented in potassic hydrate.

Fig. 19. Transverse section from near the distal surface of the basement membrane. The fibrous ends of the proximal retinular cells as indicated by their fibrillar axes (*ax.n*) are forming groups of threes or fours preparatory to passing through the basement membrane. The fibres belonging to one ommatidium are numbered 1 to 7. The axis of each ommatidium is indicated by the slight elevation (*fbr.con*) on the basement membrane where the ends of the fibres from the cone cells terminate.

Fig. 20. Transverse section of groups of three and four retinal fibres immediately proximal to the basement membrane.

Fig. 21. Transverse section of retinal fibres approximately halfway between the retina and the first optic ganglion.

Fig. 22. Transverse section of a bundle of retinal fibres at the distal surface of the first optic ganglion.

Fig. 23. Longitudinal section of a rhabdome cut in such a place that one set of fibrillae appear in transverse section (dots) and another set in longitudinal section (lines). Rapid Golgi method.

Fig. 24. Transverse section of a rhabdome in which the fibrillae belonging to cell 2 and a few from cell 5 are colored. Rapid Golgi method.

Fig. 25. Transverse section of a rhabdome in such a plane that some of the fibrillae of both cells 1 and 7 appear. Rapid Golgi method.

Fig. 26. Right optic stalk of *Astacus* cut dorsoventrally; the right side is ventral; the left, dorsal. × 30.

Fig. 27. Right optic stalk of *Astacus* cut anteroposteriorly; the left side is anterior; the right, posterior. × 30.

Fig. 28. Right optic stalk of *Branchipus* cut dorsoventrally; the left side is dorsal; the right, ventral; owing to a twisting of the stalks, the anteroposterior position in *Astacus* (Fig. 27) corresponds to the dorsoventral one in *Branchipus* (Fig. 28); *x* region of growth. × 77.

Figs. 29—33 represent pieces of corneal cuticula that were cleaned in potassic hydrate and studied in water. × 130.

Fig. 29. Four facets from the centre of the corneal hypodermis, i. e., the distal pole of the optic stalk. The figure is placed as though it were a transverse section (see above).

Figs. 30—33. Pieces of corneal cuticula from the margins of the retina: Fig. 30, from the dorsal margin; Fig. 31, from the posterior margin; Fig. 32, from the ventral margin; and Fig. 33, from the anterior margin.

Figs. 34—37. Transverse sections of the optic ganglia. × 65.

Fig. 34. Transverse section through the first decussation (cf. Fig. 27), the surrounding ganglionic cells (*cl.gn*), and the »Punktsubstanz« of the first ganglion (I).

Fig. 35. Transverse section through the »Punktsubstanz« of the second ganglion (II), a part of the first decussation (*cx.1*), and the surrounding ganglion cells (*cl.gn*).

Fig. 36. Transverse section through a part of the second decussation (*cx.2*), the »Punktsubstanz« of the third ganglion (III), and the surrounding ganglionic cells (*cl.gn*); *x* a group of especially large ganglionic cells whose fibres extend from the second ganglion directly to the brain (cf. Fig. 59, green).

Fig. 37. Transverse section through the fourth ganglion: its substance is composed of a mixture of fibres and »Punktsubstanz«.

Plate 2.

All figures of transverse sections are so placed that their dorsal edges are above, their ventral below, their anterior to the right, and their posterior to the left (cf. pag. 7).

Fig. 38. Transverse section of the optic nerve at a plane midway between the fourth optic ganglion and the brain. The outlines of the individual fibres, which are usually readily distinguishable, can scarcely be made out in the dorsal part of the nerve (*n.d*). × 140.

Fig. 39. Transverse section of the optic nerve of a crayfish 3 cm. long. × 65.

Fig. 40. Transverse section of the optic nerve of an adult crayfish. × 65.

Figs. 41—44. Transverse sections at different levels through the first ganglion. × 410.

Fig. 41. Transverse section at the level of the outer nuclei (cf. Fig. 46, 2).

Fig. 42. Transverse section at the level of the fibrous layer (cf. Fig. 46, 3).

Fig. 43. Transverse section at the level of the inner nuclei (cf. Fig. 46, 4).

Fig. 44. Transverse section through the »Punktsubstanz« of the first ganglion showing four neurommatidia.

Fig. 45. Section from a part of the first decussation; the plane of section is such that some bundles of fibres are cut longitudinally, some transversely. × 410.

Fig. 46. Section through the first optic ganglion: 1) layer of retinal fibres; 2) outer nuclei; 3) fibrous layer; 4) inner nuclei; 5) »Punktsubstanz«; and 6) nerves fibres of the first decussation. A retinal fibre (*fbr.r*) is seen to form a fibrillation in the »Punktsubstanz«. × 410.

Fig. 47. A section similar to that shown in Fig. 46, but in which a fibre (*fbr.n*) from the first decussation is seen terminating in the »Punktsubstanz«. × 410.

Fig. 48. A nerve fibre and ganglion cell of the small type from the first decussation; the fibrillation forms a part of the »Punktsubstanz« of the second ganglion. Methylen blue. × 140.

Fig. 49. A similar fibre and cell of the large type. Methylen blue; fixed with corrosive sublimate. × 140.

Fig. 50. Fibrillation of a fibre from the second decussation and of one from the third decussation in the »Punktsubstanz« of the third ganglion. Rapid Golgi method. × 140.

Fig. 51. Termination of a fibre from the optic nerve in its ganglionic cell and in fibrillations in the fourth optic ganglion. Methylen blue. × 140.

Fig. 52. Termination of two optic nerve fibres in ganglionic cells of the fourth ganglion without apparent fibrillations. Methylen blue. × 140.

Fig. 53. Termination of an optic nerve fibre in a fibrillation in the fourth ganglion without any apparent connection with a ganglionic cell. Methylen blue. × 140.

Fig. 54. Fibrillation of an optic nerve fibre in the optic lobe of the brain. Rapid Golgi method. × 140.

Fig. 55. Transverse section of the fourth optic ganglion showing the dorsal eminence (*x*) into which pass fibres from the dorsal part of the optic nerve (*n.d*) and from the cells (*cl.gn*) on the anterior face of the ganglion. Vom Rath's method. × 65.

Fig. 56. Longitudinal section of the fourth optic ganglion showing the dorsal eminence (*x*) and the dorsal part of the optic nerve (*n.d*). Vom Rath's method. × 65.

Fig. 57. An outline of portions of a longitudinal section of optic ganglia in which numerous fibres had been stained with methylen blue: fixed in corrosive sublimat; *x* a nerve fibre with an anomalous course. × 65.

Fig. 58. Nervi nervorum (?) from the surface of the fourth ganglion. Methylen blue. × 140.

Plate 3.

Fig. 59. A diagram representing the nervous structure of the optic tracts in *Astacus*. The optic stalk is supposed to be cut on its axis in an antero-posterior plane; in the fourth ganglion and in the optic nerve those fibres and cells that would lie dorsal to the plane of section are drawn in solid colors; those ventral to this plane are represented in dotted lines. Whereas the path indicated by the green fibres involves only three neurons between the retina and the brain, the other paths require five. Although the diagram represents the actual conditions rather fully, it must be born in mind (cf. pag. 52) that for each nerve fibre entering the brain, there are about four emerging from the retina. The arrows indicate the direction of growth. × 40.

Fig. 60. A diagrammatic figure of a neuron of the first order (cf. pag. 20); the nervous portions are colored red.

Fig. 61—66. Diagrams to illustrate the transition from a simple (Fig. 61) to a complex ommatidium (Fig. 64). Different kinds of cells are designated by different colors: cone cells, green; the dorsal undifferentiated retinular cell and its derivatives, the distal retinular cells, blue; the four remaining undifferentiated retinular cells and their derivatives, the proximal retinular cells, red; other parts, gray. The longitudinal sections (Figs. 61 and 64) are supposed to be cut in the dorsoventral plane. The transverse sections are placed with their dorsal sides uppermost. The numbering of the retinular cells is such that in the simpler type each cell that gives rise by division to two cells, is indicated by the same numbers as are used to designate its descendants.

Fig. 61. Longitudinal section of an ommatidium of the simpler type.

Fig. 62. Diagram showing the position of the cells in the transverse aspect of an ommatidium of the simpler type.

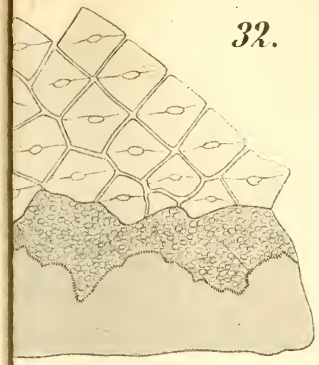
Fig. 63. Diagram illustrating the necessary change in position and the division of cells in passing from the simpler to the more complex type. The planes of division are indicated by dotted lines.

Fig. 64. Longitudinal section of an ommatidium of the more complex type. For the sake of simplicity the fibres of the distal retinular cells (blue and gray) are not carried proximally farther than the distal ends of the proximal retinular cells.

Fig. 65. Transverse section of an ommatidium of the more complex type at the level of its cone.

Fig. 66. A similar section at the level of the rhabdome.

32.



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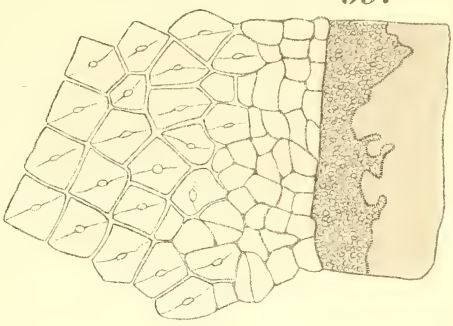

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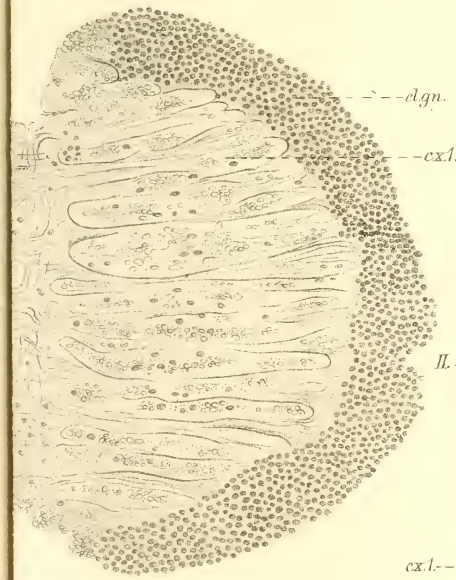

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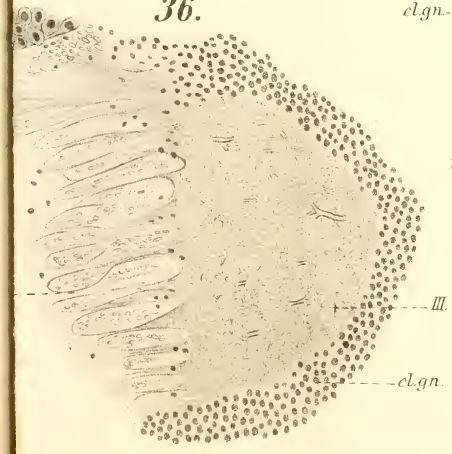

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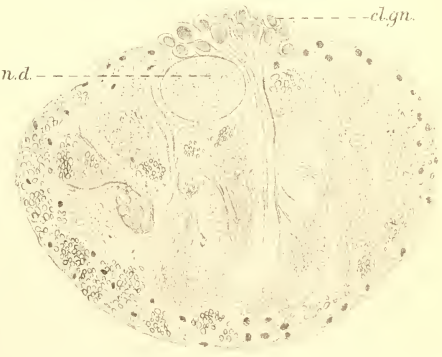

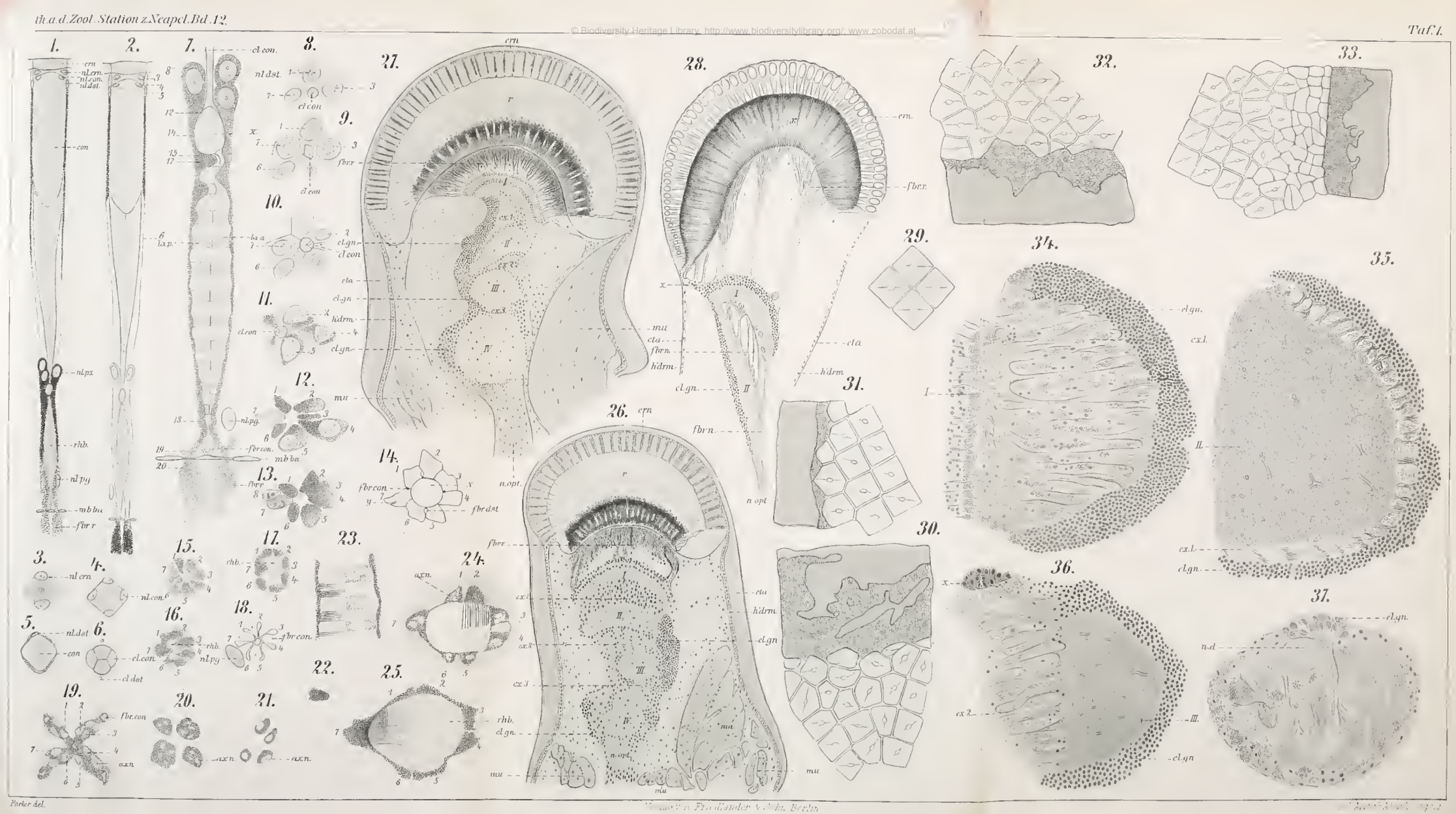

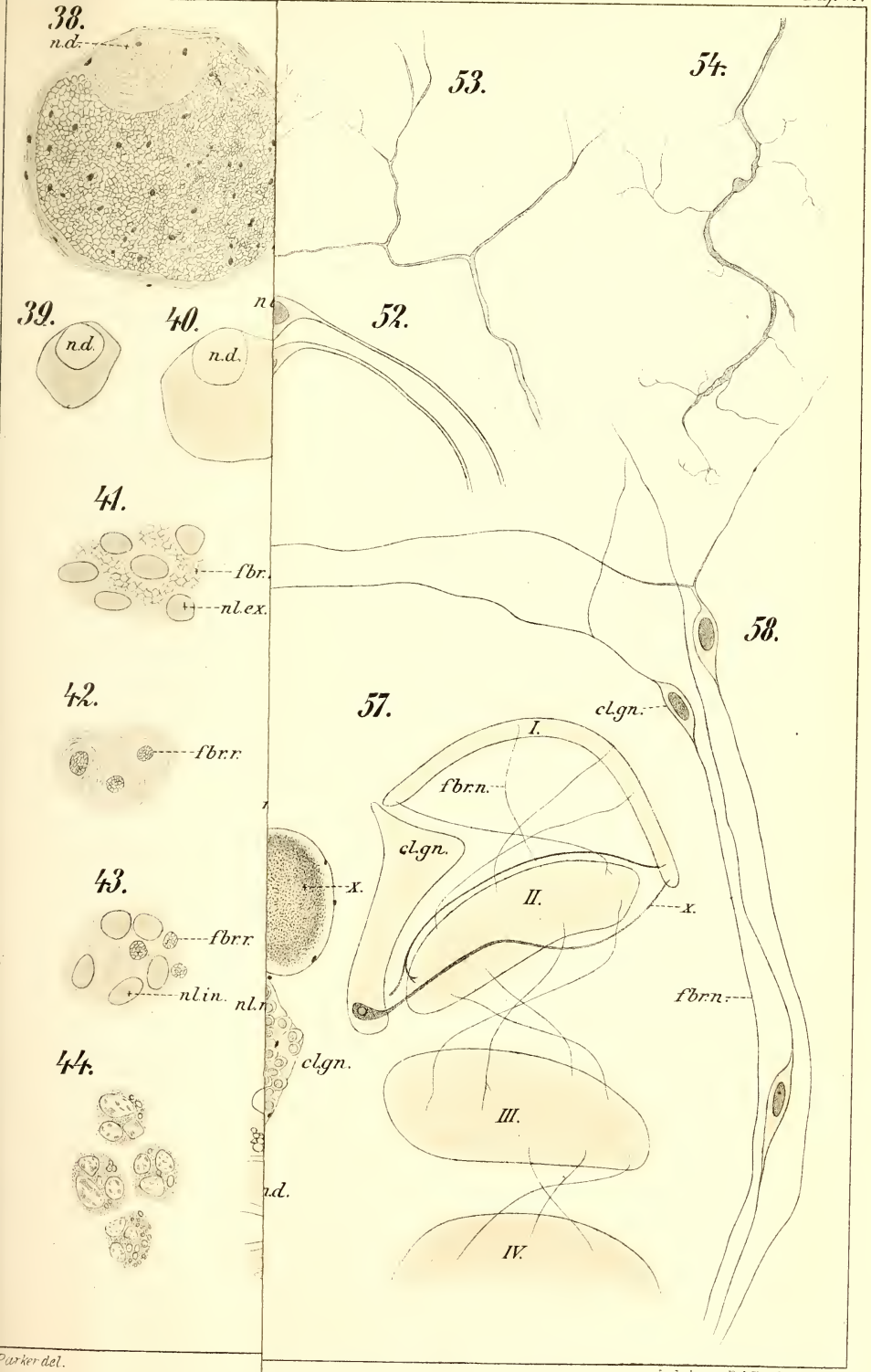

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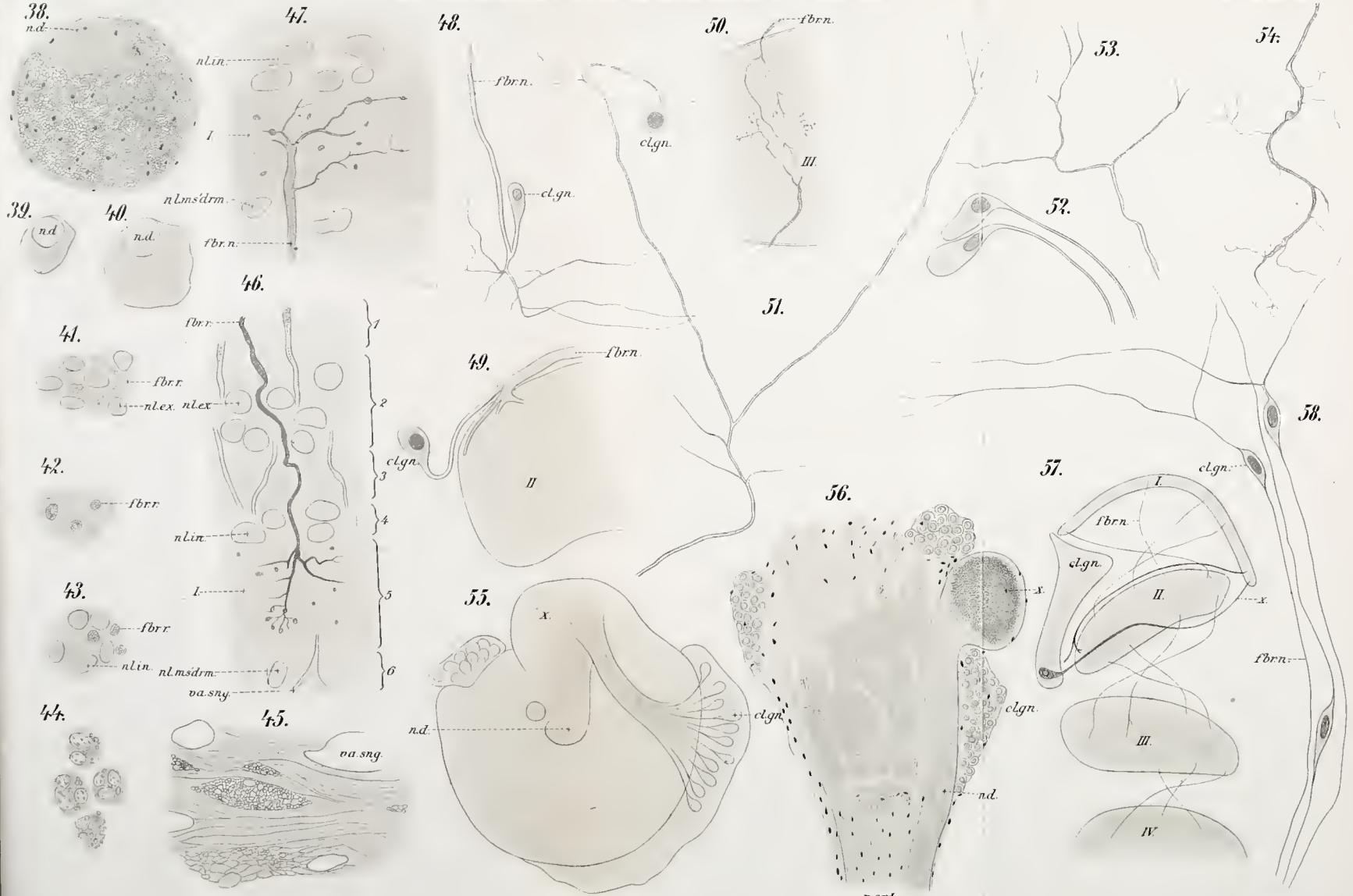

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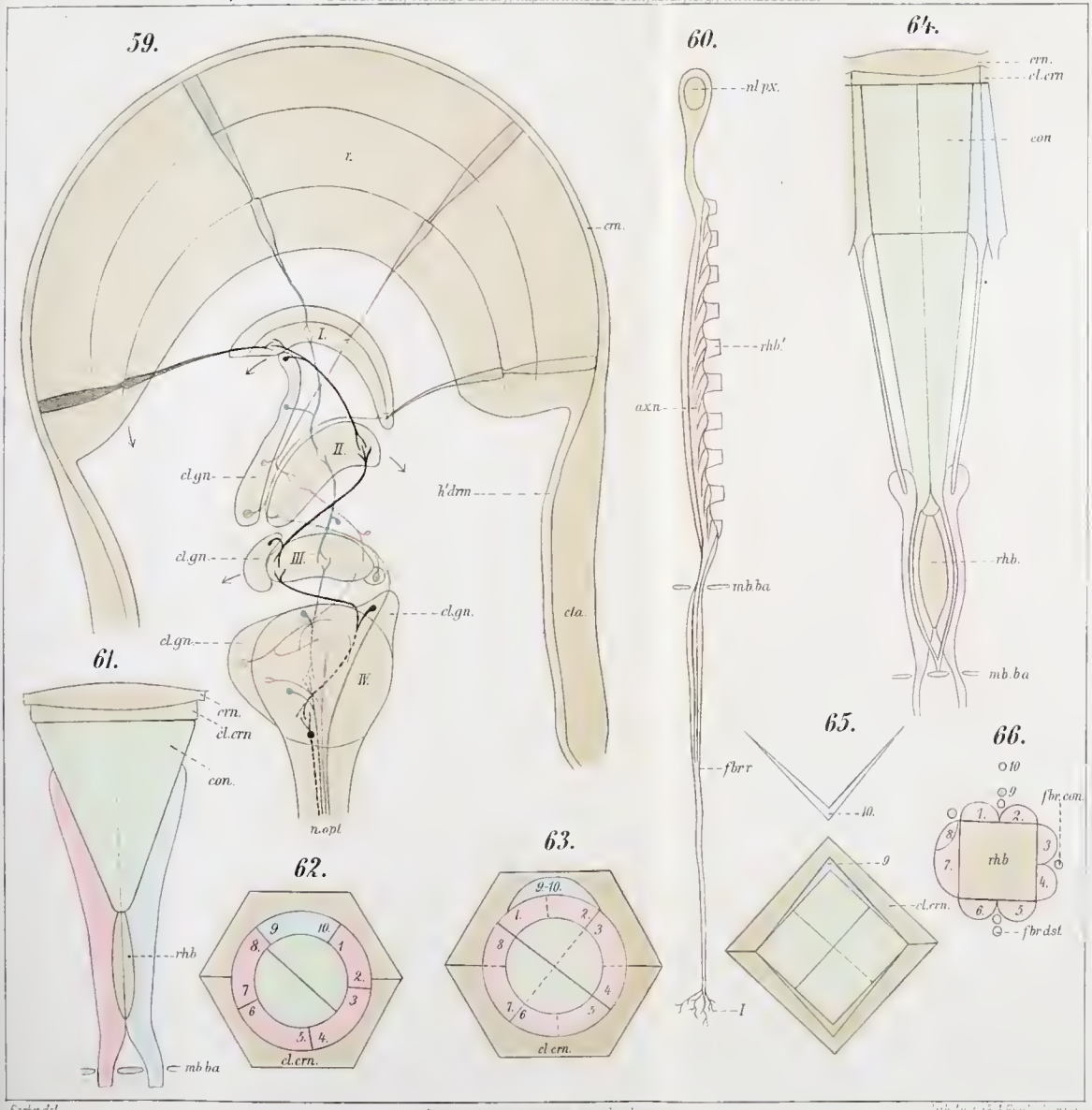

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