EYES OF MOLLUSCS AND ARTHROPODS.

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DURING the year 1885 it was my good fortune to enjoy a prolonged stay at the Zoölogical Station in Naples, that Mecca to which all good disciples of zoölogy hope to make at least one pilgrimage.

My observations there made on the eyes of Molluscs and Arthropods were published in full in the sixth volume of the *Mittheilungen aus den Zool. Stat. zu Neapel.* . The more important of those observations are described in the following summary, which has been prepared for the *Journal of Morphology*, at the suggestion of Dr. Whitman.

I found the retina of Molluscs, as well as of Arthropods, to be composed of circles of pigmented cells surrounding central, colorless ones, characterized by constant and remarkable structural features. Believing that these groups of cells constitute the structural elements of most, if not all eyes, I have called them *ommatidia;* but it must be borne in mind that, according to my observations, their structure is quite different from that which Carrière, who first suggested the term, supposed them to have in the compound eyes of Arthropods.

The simplest ommatidia that I have seen are to be found in the pigmented areas of epithelial cells distributed over the exposed parts of the body of Lamellibranchiata, especially upon the mantle and sipho. They consist of a single circle of four to six pigmented cells surrounding a colorless, central one (Fig. 6); the latter is the most important part of the ommatidium, for it is mainly upon this element that those structural improvements are consummated that lead to the formation of the most perfect eyes. This central body of the ommatidium is a double cell whose broad outer end contains two nuclei, one of which (Fig. 6, *n*, rf^2) is often difficult to see, stains faintly and, at first sight, has little resemblance to a nucleus; an axial nerve-fibre passes through the centre of the cell, and issues from its pointed inner end (*ax.n*). The inner portion of the double cell is filled with refractive and colorless globules. (Figs. 7 and 8, *ag*.)

In the undifferentiated epidermis of the mantle edge of Molluscs the nerves extend along the lateral walls of the cells. (Fig. 18, IV. and V.). The fibrillæ are applied to the surface of the cells, and usually cling so closely to it that they appear to, and probably do, penetrate the wall of the cell, and stand in direct communication with its protoplasmic contents. The nerve-fibres are therefore inter-cellular. But if two cells, whose lateral walls are well supplied with nerve-fibres, unite, and the apposed walls disappear, those nerve-fibres which were originally *between* the cells would then lie *in the centre* of a double cell. The central cells, or *retinophoræ*, of the ommatidia in Lamellibranchiata have been formed in this way, by the fusion of two cells whose apposed walls have disappeared, allowing the inter-cellular nerve-fibres to form *intra-cellular*, or axial nerves. In some cases the outer ends of the two cells composing the retinophora have failed to unite; and, as each end then contains a perfectly normal nucleus, we can clearly see the double nature of the retinophoræ. When the union is complete, as in the normal retinophoræ, one of the nuclei degenerates and often disappears. The retinophoræ are surrounded by a circle of pigmented cells, or *retinulæ*, whose inner ends are often reduced to slender hyaline stalks or *bacilli* (Figs. 7 and 8, *bc*). The retinulæ [1] are never double, and therefore never contain an axial nerve-fibre. The *cuticula*, which is often slightly thickened over the pigmented areas containing ommatidia, usually consists of two layers: a thin and structureless outer one devoid of nerve fibres, the *corneal cuticula* (Fig. 6, *c.c.*), and an inner, thicker layer, the *retinidial cuticula*. The latter contains a part of the network of nerve-fibrillæ, or *retia termi-*

[1] One meets serious difficulties in attempting to designate the pigmented cells surrounding the retinophoræ. If we regard the ommatidia as little retinas, then retinula-cells would include the retinophoræ as well as the pigmented cells. I have used, provisionally, the term *retinulæ* to designate in a general way the pigmented cells surrounding the retinophoræ, while in the Arthropods I have used it interchangably with the term retinula-cells of Grenacher, in contradistinction to those pigmented-cells surrounding the calyx. In most cases, I believe, the reader will not be misled. The term, however, as I have used it, cannot be recommended, and it is to be hoped that a better one may be suggested.

nalia, produced by the ramification of the inter-cellular nerve-fibres. Each cell, therefore, of these simple ommatidia is capped with a double cuticular layer, which may be continuous over all the cells, or divided more or less distinctly into hexagonal areas corresponding in size and shape with the outer ends of the cells.

Now we find that in *Arca* the simple ommatidia described above tend to collect in well-defined groups, forming, according to their arrangement, optic cups or convex, faceted eyes. In the formation of these eyes the ommatidia become more highly developed, the nerve-supply is increased, while the inner cuticular layer thickens and divides into distinct blocks overlying each cell. The retia terminalia extend into these blocks, which are subsequently converted into hexagonal, cuticular columns, or *rods*. These rods, which correspond to the rods found in the retina of all other eyes, contain, therefore, a specialized part of the *retia terminalia*, or a *retinidium*. Since the *retinophora* of the Molluscan ommatidium is always double, its overlying rod is also double, and contains an axial nerve-fibre like the retinophora itself, while the rods of the retinulæ are always single, and contain no axial nerves.

The *retia terminalia* form an irregular network of very fine fibrillæ, *continuous* with each other in all directions; the fibrillæ are most numerous around the outer ends of the epithelial cells, and they are arranged so that most of the fibrillæ are parallel with the surface of the cuticula. It is undoubtedly this network of nerves which gives the whole surface of the body its sensitiveness to light.

There is reason to believe that, in order to produce the greatest effect upon the fibrillæ, the rays of light must fall upon them at right angles. This result is obtained by arranging the fibrillæ in superimposed layers, and by regulating the direction of the rays of light. Axial nerves can give off radiating fibrillæ arranged in this way more easily than external nerves. The double rods of the retinophoræ, therefore, have an advantage in the possession of axial nerves, in virtue of which they gradually assume the most important rôle, while the retinulæ become modified in other directions. We therefore find in the simpler eyes of the Mollusca, as in *Haliotis* and *Patella*, that both single and double rods are present; while, in the more highly specialized eyes of Cephalopods and of *Pecten*, the double rods of the retinophoræ have alone been retained. In *Arca* the optic cups possess both single and double rods; in the convex faceted eyes found side by side with the optic cups, there are, however, only double rods, while the cells bearing single rods have been modified to serve secondary purposes.

The *compound eyes* of *Arthropods* consist of two parts: a thin outer layer of cells, the *corneal hypodermis* (Fig. 14, *c.hy.*), which secretes the corneal facets; the remaining portion of the eye, or *ommateal hypodermis*, although it is often extremely thick, represents but a single layer of cells. These facts are of importance in determining the homologies of the compound eye. While Grenacher and his followers have either overlooked or misunderstood the corneal hypodermis, they have maintained that the crystalline-cone cells and the surrounding pigmented ones constitute a distinct outer layer, and the retinulæ and so-called rhabdoms an equally distinct inner layer of the ommateum. That the ommateum proper, which does not include the corneal hypodermis, is not a double layer is shown by the fact that the retinulæ and other pigmented cells extend through the whole thickness of the ommateum; and, above all, by the fact that the so-called rhabdom is not produced by the retinulæ, but by the inward prolongation of the crystalline-cone cells. It follows, therefore, that generalizations founded upon the supposition that the ommateum is two-layered are no longer tenable.

We find good reasons for believing that the ocelli are also composed of ommatidia having essentially the same structure as those of the compound eye. The ocelli of spiders consist of groups of cells, each cluster containing a double colorless cell with either double apical rods, as in Molluscs, or with double axial rods and overlying nuclei. The rods in the latter case coincide essentially with the crystalline cones of the compound eye, and we therefore consider them as homologous structures.[1] The compound cells, or retinophoræ, of the Arachnid ocellus, like those in the compound eye, are surrounded by circles of pigment-cells. Although the retinophoræ of spiders, as far as

[1] My recent observations on the eyes of *Phalangium* show that its ommateum is composed of ommatidia in all essential points like those of the compound eye. The resemblance of the threefold conical rods of *Phalangium* to the fourfold crystalline cone is especially evident. *Vide* my preliminary account in this journal.

known, contain double rods only, the crystalline-cone cells, or retinophoræ, of the compound eye are usually quadruple, although in Amphipods and related Crustacea they are double. On the other hand, the rod-bearing cells, or retinophoræ, of *Scorpio* and *Limulus* are respectively five and ten or fifteen fold.

It is probable that ommatidia are present in various modifications in all eyes. In Vertebrates the axial nerve-fibre of the rods, and the presence of two nuclear-like bodies in the rod-bearing cells, afford good reasons for supposing that the rods, and the cells which bear them, are double. The ommatidia are, therefore, essential elements, and a classification of eyes must be founded mainly on the modifications which they have undergone. I distinguish three principal kinds of light-sensitive layers, according to the modification of the ommatidia.

A *retineum* is a collection of ommatidia in which the rods of both retinulæ and retinophoræ, or of the latter alone, form a continuous layer, the retinulæ retaining their pigment and primitive arrangement around the retinophoræ; *e.g.*, invaginate eyes of all Molluscs, except *Pecten*, and worms (?).

An *ommateum* is a group of ommatidia in which the rods, produced only by the retinophoræ, are completely isolated; *e.g.*, faceted eyes of Molluscs and Arthropods, and some Arthropod ocelli.

A *retina* is composed of ommatidia whose retinulæ, having lost their rods, are transformed into colorless ganglionic cells; *e.g.*, Pecten and Vertebrates.

PART I.

Molluscs.

Arca Noæ is extremely sensitive to slight changes in the intensity of light. In a normal condition it never fails to close its shell when any shadow is cast upon it. This perception of light gradations may be so delicate that if a small object, such as a lead-pencil, is brought with extreme caution within two and a half or three inches of the open shell, and in such a manner that no perceptible shadow falls upon the animal, it at once closes its shell, and with the same energy as when a deep shadow is cast upon it. On examining the exposed parts of the mantle edge, one readily sees numerous dark spots of various sizes, which, upon closer inspection, prove to be highly-organized eyes. They are, undoubtedly, the light-sensitive organs which the foregoing experiment showed must be present in *Arca*. The mantle edge of *Arca*, as well as all other Lamellibranchiata that I have examined, is divided into three longitudinal folds, — an outer one, or *shell fold*, an inner one, the *velar fold*, or *velum*, and a median one, or *ophthalmic fold*. At the base of the furrow, separating the shell fold from the ophthalmic one, is the gland secreting the cuticular-like covering of the shell. The whole mantle edge of *Area* is well supplied with patches of pigment which are especially abundant on the inner face of the ophthalmic fold. These pigmented areas are composed of columnar, pigmented cells, among which are a number of colorless cells provided with two nuclei and an axial nerve-fibre. These colorless cells are usually surrounded by a circle of four pigmented ones, distinguished from the surrounding cells by their color and sharp configuration. These pigmented patches, with their clusters of cells, or ommatidia, and with no special thickening of the cuticula, belong to the simplest light-sensitive organs known. Along the summit of the ophthalmic fold, the ommatidia are collected into well-defined groups to form either the *pseudo-lenticulate*, the *invaginate*, or the *faceted* eyes.

The *pseudo-lenticulate* eyes, of which there are about two hundred in each individual, are scattered irregularly over the surface of the ophthalmic fold. They consist of groups of ommatidia, over which the cuticula is thickened to form a lens-like body. The latter is composed of a number of cuticular rods, each one overlying the cell by which it is secreted. The whole cuticular mass is richly supplied with prolongations of the nerve-fibres found between the ommatidial cells, and the whole network of nerve-fibre in the cuticular mass is simply an extended and modified part of the *retia terminalia* of the simple epithelial cells.

There are about eight hundred *invaginate* eyes in each full-grown specimen of *Arca Noæ*. The groups of ommatidia which constitute these eyes are sunken beneath the surface to form minute cups, the mouths of which may be reduced to narrow slits. The rods of the ommateal cells form a thick cuticular floor for each cup.

The *faceted eyes*, of which there are about two hundred in each individual, are the most highly developed of all; and they are of special interest, since they possess all those characters which distinguish the so-called compound or faceted eyes of Arthropods. The faceted eyes of *Arca* are collections of about eighty highly specialized ommatidia to form minute hemispherical projections, lineally arranged along the summit of the ophthalmic fold, at the anterior and posterior portion of the mantle edge. In these eyes, the colorless cells, or *retinophoræ*, are quite large (Fig. 8), and contain two nuclei, and an axial nerve-fibre; on their outer ends is a large, double rod which projects slightly above the surface. Carrière mistook these refractive rods for minute lenses. The inner part of the conical retinophora is filled with a mass of brilliantly refractive globules which act as reflectors, causing the light to pass a second time through the rods. Both nuclei are situated at the outer end of the retinophora; one is large, stains deeply, and contains a well-marked nucleolus (*n. rf.*[1]); the other (*n. rf.*[2]), is usually smaller, and seldom absorbs coloring matter.

One often finds, however, cases in which both nuclei are quite alike, while the outer end of the cell is strongly bifurcate, proving beyond doubt that the retinophora is formed by the fusion of two cells. Each retinophora is surrounded by eight retinulæ, arranged in two circles of four cells each. In one circle the four retinulæ are pigmented only at their inner ends, which form a complete sheath for the inner ends of the retinophoræ (*pg.*[2]) The outer third of each cell is reduced to a very thin and colorless membrane, which unites with the similar prolongations of the three other cells to form a delicate sheath around the outer ends of the retinophoræ. In the other circle (*pg.*[1]), the inner ends of the four retinulæ are reduced to slender and colorless stalks, or *bacilli*, (*b.c.*[1]) while their swollen outer ends form a complete sheath of pigment around the double rod. It is important to notice that the retinulæ of the evaginate eye have lost their rods, and now serve simply as a covering to exclude lateral rays of light from the highly developed rods of the retinophorae. The first step towards the formation of the eyes in *Arca* is the collection of the isolated ommatidia into groups. At the same time there is a thickening of the retinidial cuticula, to form over each cell a cuticular column, or rod, which contains a part of the "*retia terminalia.*" The corneal cuticula remains as a thin membrane covering the outer ends or the rods. (Fig. 7.) If the rods formed a lens-like thickening over such a cluster of ommatidia there would be formed a *pseudo-lenticulate* eye. If such an eye were invaginated an optic cup would be formed; if it were evaginated, and the ommatidial cells slightly modified, one of the faceted eyes would be the result.

Arca Noæ, therefore, is a valuable subject for the study of the origin of the eyes; for there we have a complete series of transitional forms between highly specialized visual cells and simple epithelial ones; but, what is of still more value, we have all stages in the development of the nerve-fibres of the undifferentiated epithelium up to those supplying the most specialized visual cells. In Arca we have conclusive proof that the so-called rods of the eye are derived from cuticular thickenings over sense-cells, and that the cuticula serves no other purpose than as a support for a system of minute nerve-fibrillæ, which are the real sensitive elements of the eye.

We have in Arca a sluggish, and for the most part fixed, animal lavishly supplied with over twelve hundred well-developed light-sensitive organs, not to mention the innumerable isolated ommatidia scattered everywhere over the surface of the mantle. The presence of all these organs in such an animal may well excite surprise especially when we consider that *Avicula*, a related genus, and one that is not provided with specialized eyes (so called), is exactly as sensitive, if not more so, to changes in the amount of light as is Arca.

Pectunculus has about twenty-five faceted eyes, similar in structure to those of *Arca*, upon the right mantle edge, and twenty-two on the left. No invaginate or pseudo-lenticulate eyes are present.

Anatomy of the Eyes of Pecten.

The eyes of *Pecten*, since Poli first described them as such, in 1795, have attracted the attention of many zoölogical students, not a few of whom have made them the object of special study. The general structure of the organs in question is, therefore, well known.

I have shown that the control of the dioptric apparatus was more perfect than had been supposed. The curvature of the cornea and of the outer surface of the lens can be modified by radiating and circular contractile fibres. The size of the pupil may be modified by increasing the curvature of the cornea. The lens may be raised bodily, or lowered, by the combined action of what I have called the *ciliary muscle*, and of an elastic cushion, the *septal membrane*. That the body in question is a true lens, and that its change of shape and of position is to modify the position of an image, is shown by placing the eye in such a position that one may observe the inverted image of any neighboring object formed by the lens upon the retina.

On focusing between the *argentea* and the place where the image formed by the lens is seen with the greatest distinctness, one sees a double image, less distinctly toward the argentea, but increasing in sharpness toward the focal point of the eye, where the two images coincide. The only explanation I have to offer for the origin of the second image is that it is a reflected one of the first, formed by the curved surface of the argentea.

The eyes of *Pecten*, like the faceted ones of *Arca*, are disposed more or less distinctly in pairs, and show several peculiarities in arrangement and coloration.

The eyes of the flat, left valve are larger and more numerous than those of the curved, right one. In *Arca* there is a difference between the eyes of the right and left sides, but none in the shape of the valves. In most *Pectens* the maximum difference in the shape of the valves is accompanied by a maximum difference in the size and number of the eyes on both sides. One occasionally finds an eye, in those species in which eyes are especially numerous, — *Pecten varius* and *P. opercularis*, — the pupil of which is entirely covered with pigment. I have taken especial pains to examine these organs, which could no longer function as eyes, and have found that the retina with its rods and nerve-fibres is perfectly developed. The corneal cells are provided with median transverse teeth, and with longitudinal folds at their inner ends. The teeth and folds fit into corresponding indentations of neighboring cells, giving firmness and flexibility to the cornea. The longitudinal folds are continuous with fine fibres which cross the pseudo-cornea and unite with the outer surface of the lens.

Beneath the iris there is a nucleated layer of fibres, some of which terminate at the edge of the cornea in an outward curve as though attached to the epithelium at that point, forming what I have called the *ciliaris;* other fibres are continued onward between the cornea and lens, forming an almost structureless layer, the *pseudo-cornea*, in which nuclei are seldom seen.

The lens is held in place by a *suspensory ligament* attached to the periphery of its outer surface, which is supplied with a layer of concentric, circular fibres superimposed by a layer of radiating ones.

The inner surface of the lens is sparingly supplied with branching fibres, which, in *Pecten opercularis*, accumulate near the centre to form a nucleated mass of fibres connecting the lens with the septal membrane.

In *Pecten opercularis* there is a special accumulation of circular fibres to form two contractile rings, situated close together, one on the outer and the other on the lateral surface of the lens. The inner surface of the lens is much more convex than the outer.

The posterior portion of the eye consists of a concave disc, completely enclosed within a membranous sac. The thick anterior wall of the sac, or the *septal membrane*, serves to protect the retinal cells, and as an elastic cushion for the lens. The inner wall constitutes a tough, double-layered *sclerotica*. At the confluence of these two membranes the wall of the sac is much thinner, and is perforated by innumerable passages for the entrance of nerve-fibres from the axial branch of the optic nerve. The cells within the ommateal sac constitute a closed vesicle whose anterior and posterior walls touch each other, thus obliterating the central cavity. The wall of the vesicle was originally composed of a single layer of cells, an arrangement which is subsequently obscured by the division of both anterior and posterior walls into several secondary layers. The posterior wall of the ommateal vesicle consists of four layers,— the *vitreous net-work*, the double-layered *argentea*, and the *tapetum*. The anterior wall is likewise composed of four layers,— an *outer ganglionic layer*, an *inner ganglionic layer*, the *retinophoræ*, and the *rods*.

The *retinophoræ* (Fig. 15) are long, bent cells, one end supplied with an inwardly directed rod, while the other is drawn out to a slender tube continuous with the axial nerve. Each retinophora contains a large, oval nucleus and a small, faintly stainable one. The flanged walls of the inner ends of the retinophoræ unite at the same level with those of neighboring cells, producing a sharp division between the rods and the inner ends of the cells. This *pseudo-membrane* was named the "*sieve membrane*" by Carrière. A delicate wall, the *terminal membrane*, separates the retinophora from its rod; on the edge of the retina are many slender and rodless retinophoræ.

The rods are cylindrical, and consist of a refractive cap or sheath, surrounding a pyramidal, axial core. The axial nerve is continued through the distal end of the rod, and immediately divides into two branches, one of which unites with a similar branch from a neighboring rod, while the other is bent over and distributed in fibrillæ over the surface of the rod. I have called these nerves the *axial nerve-loops*. That portion of the axial nerve within the rod gives rise to successive *étages* of radiating fibrillæ which unite with the nerve-fibres upon the surface of the rod. These cross fibrillæ constitute the *retinidium*, which is composed of fibrillæ similar to those seen in the rods of *Haliotis*, but arranged in a more systematic manner. There are also circular fibrillæ arranged around the axial core of each rod, and connecting the radiating fibrillæ.

Above the retinophoræ is the *outer ganglionic layer*, which consists of large ganglionic cells ($g.\ c.^{1\text{-}5}$), terminating at either end in a varying number of fibrous prolongations; those of the outer end are continued into the ganglionic branch of the optic nerve, while those of the opposite extremity extend along the walls of the retinophoræ to the rods, over the surface of which they form a net-work of fibres. This layer contains cells in instructive stages of ganglionic perfection.

The *inner ganglionic layer* consists of a single row of minute ganglionic cells ($g.\ c.^5$), which, when seen at all by previous writers, have been mistaken for the nuclei of the retinophoræ. Each cell, which is nearly filled by its nucleus, is provided with several fibrous prolongations, one of which is directed outwards, passing into the ganglionic nerve-branch, while five or six others extend inwards to help form the net-work of fibres on the surface of the rods. Many of the nerve-branches from both ganglionic layers terminate upon the walls of the retinophoræ in one of two ways, — either a single fibre impinges directly upon the cell-wall, and there divides into several short fibrillæ, connected at their distal extremities with a circular fibril enclosing the whole (*y.*), or a nerve-fibre follows the cell-wall for some distance, giving off at intervals smaller, lateral branches, and finally becoming so minute as to disappear (*z.*).

The outer prolongations of the ganglionic layer form, beneath the septal membrane, a mass of free fibres, which were mistaken by *Carrière* for nucleated cells, and by *Hensen* for fibres pulled out of the retina by shrinkage. The layer of free nerve-fibres is, however, a normal condition, and is necessarily so in order to give the lens space for focal adjustment without injury to the retina.

A system of circular fibres surrounds the periphery of the inner face of the retina, forming a *membrana circularis.*

Beneath the rods there is a thin layer of a vitreous substance forming a net-work, the meshes of which constitute a hexagonal crown for the inner end of each rod. On the periphery of the retina the *vitreous net-work* is transformed into a thin plate, pierced by numerous and irregularly-shaped holes.

The *argentea* is formed by the modification of two cell layers into refractive membranes. Each membrane is composed of minute square plates, whose edges are bevelled in such a manner that their outer faces are smaller than the inner, which rest upon the undifferentiated, under surface of the membrane by which all the plates are held together. In passing inwards the membranes become thinner, less distinct, and refractive, while the plated structure entirely disappears. The thick outer layer of the *argentea* in the adult never contains nuclei, although one or two may occasionally be found in the inner layer.

The *tapetum*, the red-pigment layer of previous writers, usually consists of a single layer of cells, decreasing in thickness from the axial part of the eye toward the periphery, and terminating with the argentea at the entrance into the retina of the fibres from the axial branch of the optic nerve.

The thickened central part of the outer layer of the septum, a little to one side of the optic axis, is perforated by the ganglionic nerve-branch. The peripheral part, gradually diminishing in thickness toward the edge of the retinal sac, consists of nucleated connective-tissue cells modified into circular fibres.

The inner layer of the *sclerotica* is marked with short parallel cross-lines; the thick outer layer consists of longitudinal fibres, which may contain a few nuclei.

There are numerous refractive fibres which arise from the periphery of the eye-stalk, and, converging toward the base of the eye, penetrate the sclerotica and the superimposed layers as far as the inner ends of the rods. In the sclerotica they expand into refractive spindle-shaped bodies, often of a faint pink color.

Development of the Eyes of Pecten.

On the branchial wall of the ophthalmic fold of *Pectens*, 2 mm. long, are a few minute, pigmented and transitory cups, undoubtedly homologous with the invaginated eyes of *Arca*.

The stalked eyes first appear as oval optic thickenings at the base of the ophthalmic fold. By a continued proliferation of the cells on the outer side of the optic thickening, an oval knob-like papilla is formed, containing a solid core of hypodermic cells. At first the core is ill-defined; several of the more deeply situated cells separate from the rest to form the ganglionic cells, which later provide the eye with nerve-fibres. The whole papilla then elongates, and a disc-shaped cavity appears in the centre of the core, transforming it into an *optic vesicle*.

In the following stages the posterior wall becomes more sharply defined, and there, for the first time, the cells of the optic vesicle are provided with distinct cell-walls. The inner wall of the optic vesicle divides into two layers, — the inner one giving rise to the *tapetum*, and the outer one to the *argentea*. The latter is formed by the transformation of cells into superimposed plated membranes, the nuclei being retained, in some cases, until the eye has completed its development. The outer wall of the optic vesicle divides into three zones, consisting of the fibrous, the ganglionic, and the retinophoric layer of the retina.

Some of the connective-tissue cells surrounding the optic vesicle give rise to the retinal-sac, a nucleated membrane, the anterior wall of which develops into the *septum*, and the posterior into the *sclerotica*.

The connective-tissue cells above the septum give rise to the *lens*. The cells of the *tapetum* are at first filled with coarse, colorless granules, which subsequently acquire a characteristic red color. The nuclei of the retinophoræ, which at first are situated in a peripheral thickening of the retina, gradually push their way towards the centre of the eye. It is not till quite late in the devolopment, after the appearance of the rods, that their cell-walls become visible.

The only difference between the rods, when first seen, and those of the adult, was the large size of the axial core, and the extremely thin shell, or sheath, scarcely visible except at the tips of the rods. As soon as the rods could be clearly distinguished they were seen to contain an axial nerve-fibre. The nuclei of the argentea decrease in size until they finally disappear, with the exception of those in the inner layers, where, in the adult even, one or two aborted nuclei may occasionally be seen.

The *vitreous net-work*, in contrast with its subsequent condition, forms at first a thick homogeneous and structureless layer.

The innumerable isolated fibres which, even in the earlier stages innervated the eye, subsequently unite to form a single, loose bundle of nerve-fibres, — the primitive optic nerve, which divides later into the *axial* and *ganglionic* branches of the definite optic nerve. All the nerve-fibres supplying the optic vesicle are not collected to form the optic nerve; for many entering the base of the vesicle retain their primitive arrangement, and appear to penetrate the sclerotica, tapetum, and argentea, as far as the rods. The circumpallial nerve contains as many ganglionic swellings as there are optic nerves. In many, if not all, of these ganglia there is a peculiar infolding dividing them into halves.

The free edge of the ophthalmic fold contains, at regular intervals, large ova-like cells, which may be seen in preparations of the whole mantle edge, as well as in sections. In the neighborhood of the hinge the branchial wall of the mantel of younger specimens is thrown into a variety of thick ciliated folds, the nuclei of which are, in most cases, several rows deep. In some cases one of the folds becomes especially enlarged at its extremity, the walls thickening to form a kidney-shaped body with a great many small, deeply-stained nuclei. The surface is covered with a cuticula, provided with minute papillæ, from each one of which arises an enormously long cilium.

The *sense-hair papillæ*, which originate at any place along the outer surface of the velum, first appear as thickenings of the hypodermis which soon become conical, and provided with a tuft of stiff sense-hairs at the apex. The inward proliferation of the cells at the apex of the thickening gives rise to an ectodermic core, which becomes transformed into the longitudinal nerve with which every tentacle is provided. As the papillæ increase in length, tufts of sense-hairs are formed on the sides, each connected with one or two ganglionic cells. In those papillæ which do not develop into tentacles no distinct nerve is formed; but two or three cells separate from the summit of the papilla and wander into the underlying tissue, there forming ganglionic cells, the nerve-like ends of which may terminate in a small number of sense-hairs; or, if the cells are more highly specialized, the sense-hairs may be absent, while the terminal fibres divide into numerous fibrillæ which supply the adjacent cells.

We have found the same sensitiveness to changes in the intensity of light in *Ostrea*, *Mactra stultorum*, *M. solidissima*, *Pinna*, and *Avicula*, that was so marked in *Arca*. In these cases, however, there were no well-defined eyes, but large pigmented and shallow grooves, or slightly depressed areas over which the cuticula was but little thickened. In these pigmented patches were numerous ommatidia having essentially the same construction as those in the pseudo-lenticulate and invaginate eyes of *Arca*. They undoubtedly belong to the simplest of light-sensitive organs; but, in spite of their simple structure, they are in some cases wonderfully delicate organs. In *Avicula*, for instance, the simple and diffuse ommatidia, the only visual organs present, are able to perceive the difference in light produced by holding such a small object as a pencil between them and the source of light. Under such circumstances a shadow so faint as to be imperceptible to the experimentor caused immediate contractions of the whole animal.

At the end of each siphonal tentacle of *Cardium edule*, beneath a semicircular band of pigment is a minute eye. It consists of a roughly spherical mass of large cells, which emit, when living, a faint red color, reflected by the underlying argentea. I have counted, with a pocket lens, fifty-one eye-bearing tentacles on one individual.

The extremely simple retina, which is oblong in shape, — the short diameter being at right angles to the pigmented covering, — consists of five or six rows of cells, the ends of which, being directed inwards, rest upon the mass of connective-tissue fibres which serves at once as a capsule and tapetum. The opposite extremities of the retinal cells, where the large oval and sharply stained nuclei are situated, appear to terminate in single nerve-fibres, which pass out of the capsule and, bending at right angles, extend along the axis of the tentacle. At the angle of each of these cells, nearly opposite the large nuclei, is a small and poorly defined cell containing a minute but deeply stained nucleus.

The argentea is similar to that of *Pecten*, and consists of nucleated connective-tissue cells, the bodies of which are flattened into membranes, composed of minute refractive squares. The argentea envelops the whole eye, but is thickest on the sides next the pigment, and toward the base of the tentacle. Whether the inner ends of the retinal cells are provided with rods similar to those of Pecten could not be determined with certainty.

The round cellular body situated in front of the retina is composed of large, characteristic cells, which, however, are not confined to this region alone, but extend thence, in a double row, nearly half the length of the tentacle.

In *Cardium tuberculatum* the tentacles are also provided with eyes, although the pigmented patches at the tips of the tentacles are absent.

In *Cardita sulcata* isolated ommatidia are present, but no tentacular eyes.

The most important fact obtained by studying the eyes of *Haliotis* was that the colorless cells are not gland-cells or of secondary importance to the retina, but are true retinophoræ, having double rods, two nuclei, and an axial nerve fibre. The pigmented cells, or retinulæ, are provided with single, club-shaped rods, which contain a net-work of fibrillæ formed by the ramification of intercellular nerve-fibres. The most satisfactory proof of the intercellular nature of the nerves and of the nervous structure of the rods was obtained by dissolving the cuticula, leaving the net-work of nerve-fibrillæ free and uninjured. It is then seen that the fibres of the optic nerve penetrate the basal membrane and pass outwards between the cells of the ommatidia. As they pass beyond the outer end of the cells the nerves break up into innumerable branches, which do not end freely, but unite with each other in all directions to form a network of continuous fibrillæ.

On the upper side of each tentacle of Haliotis is a longitudinal groove, the floor of which consists of thick columnar cells, filled with a dark-brown or black pigment; the cuticula is not especially developed, neither could any colorless cells be seen. The similarity of these pigmented bands to those on the sipho and mantle edge of the Lamellibranchiata is apparent.

II.

Crustacea.

Each square corneal facet of *Pinæus* is secreted by two underlying oblong cells belonging to the corneal hypodermis.

The centre of each ommatidium is occupied by four colorless cells, — the retinophoræ, — united to form an inverted pyramid, whose base abuts against the corneal hypodermis, while the apex rests upon the basal membrane. The inner end of the pyramid is reduced to a slender, hollow stalk, — the *style,* — whose inner end enlarges into a solid, pyramidal thickening, the *pedicle;* the latter rests upon the basal membrane by a delicate stalk composed of the attenuated, inner ends of the four retinophoræ, two of which are united with each other. Each leg of the stalk is divided at its inner end into several fibres by which it is united to the basal membrane. This fact is important, for it shows that the segments of the so-called rhabdom of Grenacher are not secretions of the retinulæ, but merely the inner ends of the retinophoræ (or crystalline-cone cells), which terminate in the same root-like fibres seen in nearly all hypodermic cells.

The pedicle, whose abaxial walls are very thick, entirely obliterating the central canal, is composed of plates varying in thickness in different parts. Each plate is marked by a set of parallel lines at right angles with a similar set in the adjacent plate. The plates of the pedicles resemble, in some respects, the plates in the argentea of *Pecten* and other Molluscs, and I have suggested that they may have a similar function; *i.e.*, they act as reflectors to intensify the light impressions in cases where a great deal of light is necessary, or when there is little light at the animal's disposal. The fact that the pedicles are usually present in nocturnal insects harmonizes with this interpretation. The rounded outer ends of the retinophoræ are capped with protoplasmic thickenings, in which the nuclei are situated.

Below the nuclei is an enormous crystalline cone nearly half as long as the ommatidium. Near the centre of the eye, almost at the inner ends of the crystalline cone, the opposite halves of the calycal wall develop granular thickenings, sickle-shaped in cross-sections, which increase in size as the diameter of the retinophoræ diminishes.

Surrounding the retinophoræ are seven oddly-shaped retinulæ of different apparent lengths, four of which are nearly black, while the remaining three are filled with light-brown pigment.

The retinulæ seem to terminate at the apex of the pedicle in the knob-like swellings containing the nuclei; this, however, is not so, for they are continued outwards as extremely delicate membranes, similar to those of the retinulæ of *Arca*. Toward the outer surface of the eye the united terminal membranes of each group of retinulæ form a delicate sheath, loosely surrounding the style and calyx. Toward the outer surface of the eye the sheath divides into seven hyaline thickenings, which abut against the inner face of the cornea, to form, at the corner of each facet, regular four-armed figures. Each thickening of the sheath represents the outer end of a retinula.

One of the retinulæ is remarkable for its great size and peculiar shape. At the beginning of the laminated structure of the pedicle the axial wall of this cell becomes scalloped, each fold projecting into the end of a plate.

The pigmented collar of the retinophoræ is formed by a circle of four cells arranged in two pairs. Each cell is continued inward as a slender colorless rod, or *bacillus*. The outer edges of the collar cells contain refractive granules, which, in reflected light, are yellowish-white and perfectly opaque. The cells are continued outwards as four delicate fibres, which produce four minute impressions at each corner of a corneal facet.

In the spaces between the inner ends of the ommatidia is a third group of cells, the boundaries of which cannot be distinguished, and it is therefore difficult to determine the exact number belonging to each ommatidium. The nuclei are arranged at various niveaux around the inner ends of the pedicles. These cells contain yellowish fat-like crystals which form, at the inner surface of the ommateum, a narrow and intensely white band. The crystals are insoluble in absolute alcohol, clove-oil, creosote, chloroform, or ether. But a very dilute solution of caustic potash dissolves them at once, with the formation of a purple solution.

In the spaces between adjacent facets which have been treated with caustic potash, may be seen four groups of fibres, or impressions of the same. They are probably the outer ends of the basal cells just described, although I have not been able to trace any connection between the structures in question. This supposition, if correct, would fix the number of these cells at four, which agrees very well with what appears to be present.

The *basal membrane* is composed of Greek-cross-shaped masses of connective-tissue. From the centre of the inner surface of each cross a group of fibres projects inwards and unites with the connective-tissue cells underlying the basal membrane. The squares enclosed by the crosses are bridged by a bundle of diagonal fibres. A series of cross-sections of the inner ends of the ommatidia enable us to determine the position that each cell occupies upon the basal membrane. Beyond the base of the pedicle the retinulæ suddenly separate, and the stalk of the pedicle dissolves into two groups of fibres, which become attached to the outer surface of the cross. One group is formed of two separate bundles, while the other is also composed of two bundles, but so closely placed as to form one figure, the outline of which indicates its dual composition. These four bundles are the inner ends of the retinophoræ and the fibres are their root-like terminations.

To each basal-membrane square are also attached, in regular and constant order, the inner ends of the bacilli and retinulæ. Thus each cross of the basal membrane furnishes the support for a single ommatidium, and both these structures correspond in number.

In longitudinal sections one sees that a bundle of pigmented nerves-fibres passes to each of the openings leading into the square spaces enclosed by the crosses; just before reaching the basal membrane it breaks up into smaller branches, one of which goes to each cell attached to a basal-membrane cross. Besides the pigmented fibres there are four colorless ones which, arising from as many main nerve-branches, ascend the four angles of the cross, and extend along the outer surface of the four cells composing the retinophora. Lastly, a single colorless branch enters the base of the cross and issues from the centre of the opposite surface, to be continued straight upward through the centre of the style to the crystalline cone. Although the basal-membrane crosses, and the enclosed squares, as well as the principal nerve-bundles, coincide in number, each ommatidium is supplied with nerve-fibres from four different bundles. It is probable that the superficial fibres distributed over the wall of the calyx communicate with the axial nerve by means of cross fibrillæ, just as in *Pecten* and *Arca*. In the outer ends of the crystalline cone, in that part which is densest and most hyaline, I have not been able to demonstrate anything like cross lines or fibres.

In *Galathea*, *Palæmon* and *Pagurus*, one may easily observe the corneal hypodermis the general characters of which differ but little from that of *Penaeus*. In both *Palæmon* and *Pagurus* there are two peripherally placed nuclei for each quadrilateral facet. In *Galathea* there is a remarkable modification of these cells to form, for each ommatidium, an iris with a slit-like contractile opening, the walls of which may be expanded by means of radiating contractile fibres. In *Galathea* I have followed the external longitudinal nerve-fibres of the style, as well as the central, axial fibres, up to the calyx, where the latter nerves extend into the centre of the crystalline cone, and the former give rise to branching fibres spread over the wall of the calyx. In *Galathea* there are four lateral thickenings of the calycal wall. In *Galathea*, *Palæmon*, and *Pagurus*, the pedicles are composed of two sets of plates similar to those of *Pinæus*, the markings in one set being at right angles to those of the other.

In *Branchipus* the nuclei of the retinophoræ are situated in protoplasmic thickenings over the outer ends of the rods. A corneal hypodermis is present, composed of indefinitely arranged cells.

The *style* is a flattened tube, containing an axial nerve-fibre.

In *Mantis religiosa* there are two corneal cells beneath each facet. Each ommatidium has seven retinulæ and at least six light-brown pigment-cells surrounding the calyx. There are also two large black cells enclosing the neck of the calyx. Their inner ends terminate abruptly at the outer end of the style. Three of the retinulæ are longer and more deeply pigmented than the others.

The *basal membrane* is a thick layer of nucleated connective-tissue, permeated by canals corresponding in number with the ommatidia; through each canal passes a bundle of pigmented nerve-fibres.

Just beyond the narrow neck of the calyx the four axial nerves contained in the style break up into four bundles, one entering each chamber of the calyx. There each fibre gives rises to innumerable horizontal fibrillæ, which unite with each other to form a complete nervous net-work.

The style is surrounded by six nerve-fibres, which appear in cross-sections as so many small dots. They may be followed as far as the calyx, where they break up into numerous smaller branches, continuous with those inside the calyx, by means of minute cross fibrillæ. The outer ends of the retinulæ are reduced to structureless membranes which unite to form a sheath around the calyx. The abaxial face of each retinula is provided with longitudinal nerve-fibres connected with each other by circular fibrillæ. Around the retinulæ are several, probably eight, bacilli. The nerve-fibres surrounding each bacillus supply the outer pigmented ends of the same.

The various stages in the formation of ganglionic cells out of sensory ones may be studied in the mantle edge of Molluscs. They arise in the following manner: The nucleus of a slender sense-hair cell, which terminates inwardly in a long fibre exactly similar to the prolongations of the neuro-epithelial cells of Coelenterates, wanders below the basal membrane (Fig. 18, III.), while the outer end of the cell is reduced to a fine fibre, still terminating in one or more sense-hairs.

The outer end of the fibre then gives rise to minute cross-fibrillæ, which either adhere to the wall of the neighboring sense-cell, or unite with similar fibrillæ from older nerve-fibres; lastly, the tuft of sense-hairs disappears, and the conversion of the sense-cell into a bipolar ganglionic one is complete. (IV.) Subsequently the body of the bipolar cell gives rise to numerous secondary fibres, which unite with those from other cells, and so convert the bipolar cell into a multipolar one, whose primitive, outer end still retains its original position between the epithelial cells. (V.) This process of nerve formation may occur at any part of the mantle edge, and is not confined to the larval stage, but takes place also in the nearly full-grown individual. Here, then, is the explanation of the intercellular nerve endings in the Mollusca; and unless degeneration of the outer ends of the nerves has taken place, they should always extend to the cuticula. In no case do nerves from the central nervous system unite directly with the sense-cells of the epidermis. All the nerve-ends in the hypodermis mark approximately the places where ganglionic cells originated. The latter alone are directly united on the one hand with the hypodermis and on the other with the central nervous system.

The *basal membrane* of Molluscs is formed by the union of the root-like ends of ordinary epithelial cells. I consider that the latter cells and the basal membrane represent the myo-epithelial cells and the underlying layer of fibres of Coelenterates.

My observations on the structures of the compound eye have led me to the conclusion that it is a modified ocellus. The primitive Arthropod ocellus I regarded as a closed optic vesicle, the inner wall forming the retina whose rods are therefore upright. The outer wall of the optic vesicle in most cases is not visible. The hypodermis overlying the optic vesicle is represented by the "*vitreous-layer*," or what I have called the *corneal hypodermis*. In the compound eye the same layer is present, which I have also called the corneal hypodermis, as a thin stratum of cells over the crystalline cones. The crystalline-cone cells are, therefore, not the homologue of the vitreous layer of the ocelli, but of the colorless rod-bearing cells, or retinophoræ, with which they have a common function. If this be true, then the crystalline cones are not dioptric organs, but the essential, light-sensitive elements. If this also be true, it must of necessity follow that by far the majority of compound eyes are not adapted for "*mosaic vision,*" as commonly understood, but for the perception of inverted images formed by the corneal facets upon the crystalline cones.

I also claimed, on theoretical grounds, that neither the ommateum nor the retina of Arthropods could have arisen as an outgrowth of the brain, and I may add that my recent observations on the development of the eyes of *Vespa* have confirmed this conclusion.

Certain facts in the anatomy and distribution of the simplest kinds of eyes, as well as other sense-organs, lead me to suppose that their function was originally not that of sense-organs; that is, organs by means of which their possessor became cognizant of changes in external conditions; they were rather the receivers and transmitters of external changes which had in themselves a stimulating and beneficial effect upon the organism. The constant association of certain sensory impressions with changes in external condition finally led to the so-called "recognition" of such changes, and the organ which recorded those changes then became a true sense-organ. This supposition may explain the multiplication of highly complicated "sense-organs" in animals which can apparently make no use of so many to *perceive* objects. The great number of sense-organs present in some animals is intelligible when we assume that they have a phagous function; and as, on any supposition, they are especially affected by *changes* in external conditions, I have called them *Dynamophagous* organs.

MILWAUKEE, April 11.

EXPLANATION OF PLATE III.

ax.n., axial nerve.
bc., bacillus.
b.m., basal membrane.
c.c., corneal cuticula.
c.c.c., crystalline-cone cells.
c.hy., corneal hypodermis.
ex.n., external nerve-fibres.
g.c., ganglionic cells.
l.ax.^{1} and *l.ax.*^{2} axial-nerve loops.
n f., nerve-fibres.
n.rf., nuclei of retinophoræ.
n.rf.^{1}, nucleolated nucleus of retinophoræ.
n.rf.^{2}, aborted nucleus of retinophoræ
pd., pedicle.
pg., pigment cells.
pg.$^{1-3}$, first, second, and third circle of pigment cells.
rf., retinophoræ.
rf.^{1}, innermost ends of crystalline cone cells, or retinophoræ.
rh., rod, or crystalline cone.
rt., retinula.
rt.$^{1-3}$, hyaline continuation of the retinulæ.
st., style of the retinophoræ, or crystalline-cone cells.
v.l., vitreous cell layer.
v.b., vitreous body.
v., crystalline cone, or vitrella.

1. Ancestral arthropod eye.
2. Same of larval insect.
3. Ocellus of *Scorpio;* only one ommatidium is represented.
4. Posterior ocellus of spiders.
5. Diagram of compound eye, to illustrate its origin as a modified ocellus.
6. One of the isolated ommatidia from the hypodermis of a Mollusc.
7. An ommatidium from a Molluscan retineum.
8. Ommatidium from the compound eye of *Arca* or *Pectunculus*; the retinulæ *pg.*^{12} have lost their rods, as is the case in all the succeeding diagrams, and serve only to protect the rod of the retinophoræ, or become transformed into ganglionic cells.
9. Same, with cross-section from the anterior ocellus of a spider.
10. The same, from the ocellus of Scorpio.
11. The same, from posterior ocellus of a spider.
12. The same, from the compound eye of Insects and Crustacea.
13. Two ommatidia from a vertebrate retina, without the outer ganglionic layers.

13*a*. Is a cross-section of the rods.

14. Diagram of an ommatidium, with the corneal facet and its cells, from a compound arthropod eye. The pedicle, walls of the retinophoræ, and the style, have been drawn in red for the sake of clearness; in all other cases the red indicates nerve-fibres; *x* is the refractive division between adjacent facets; *a*, that between the halves of each facet; *y*, thickening, sometimes present, of the abaxial walls of the calyx; the crystalline cone may be present or absent, but it can never fuse with the facet, as is supposed to be the case in *Lampyris*.

14*a* and 14*b* are cross-sections through the calyx and middle of the style, respectively.

15. Two retinophoræ with their ganglionic cells, from the retina of *Pecten*, showing the loops of the axial, and external nerves of the rods, the two nuclei of the retinophoræ, and five characteristic forms of ganglionic cells; *b.m.*, basal membrane, or septum, of the eye; *x*, a nerve-fibre terminating on a small ganglionic cell; *z*, and *y*, two methods of nerve endings upon the cell wall of the retinophoræ.

16. Diagram of compound eye, constructed according to Grenacher's views.

17. An ommatidium from a compound eye, constructed according to Grenacher's statements; he does not recognize the corneal hypodermis, and separates the eye into two layers at $b.m^1$; the dotted line, *y*, shows the position of the crystalline cone in certain cases where it appears to be absent.

17*a*, is a cross section of the retinulæ, showing the seven (or four) rods which they are supposed to secrete.

18. Diagram showing five stages in the transformation of a pair of epithelial cells; m^1 represents a myo-epithel cell connected with the sensory cell s^1. In II. and III., s^1 becomes a neuro-epithel cell, and m^1 has become a contractile cell. In IV., the neuro-epithel cell unites with a neighboring sense-cell by fine fibrillæ. In V., the outer end of the neuro-epithel cell has lost its sense-hairs, and is united to a neighboring sense-cell by numerous fibrillæ. Its outer end has become a true nerve-fibre, while its nucleated inner part develops new fibres uniting it with neighboring ganglionic cells. These five changes result in the transformation of the original epithel cell s^1, into the multipolar ganglionic one s^5.

The three cells s^6, s^4 and m^5 represent the three extremes in the modification of epithelial cells, at the same time, they represent the simplest combination of cells to form a mutually dependent sensory, nervous, and contractile system.