HOMOLOGIES OF THE VERTEBRATE CRYSTALLINE LENS.[1]

BY BENJAMIN SHARP, M. D., PH. D.

I cannot better introduce my subject than by quoting the following passage from Chas. Darwin: "To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection seems, I freely confess, absurd in the highest possible degree. Yet reason tells me that, if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if, further, the eye does vary ever so slightly, and the variations be inherited, which is certainly the case; and, if any variation or modification in the organ be ever useful to an animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can be hardly considered real. How a nerve comes to be sensitive to light, hardly concerns us more than how life itself first originated; but I may remark that several facts make me suspect that any sensitive nerve may be rendered sensitive to light, and likewise to those coarser vibrations of the air which produce sound. . . ."[2]

"If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. But I can find out no such case. No doubt many organs exist of which we do not know the transitional grades, more especially if we look to much-isolated species, round which, according to my theory, there has been much extinction. . . ."[3]

"In the cases in which we know of no intermediate or transitional states, we should be very cautious in concluding that none

---

[1] Being the principal part of an address delivered before the Biological Section of the Academy of Natural Sciences of Philadelphia, December 15, 1884.

[2] Darwin, Chas., "On the Origin of Species, by Means of Natural Selection, etc." New York (Appleton), 1861, p. 167.

[3] Darwin, Chas., Orig. of Species, etc., p. 169.

could have existed, for the homologies of many organs, and their intermediate states, show that wonderful metamorphoses in function are at least possible."[1]

It will be my endeavor to show the stages of development of the eye from the simple deposit of pigment in an epithelial cell to the highest form known to us, that of the vertebrata.

Invagination seems to be the most simple, as well as one of the commonest, methods by which organs are formed in the animal series. The formation of the gastrula, of the medullary canal, the development of glands, etc., etc., by invagination, are cases too well-known to require further comment. The formation of the eye, ear, and nose, form no exception to this rule.

In a previous paper[2] I have endeavored to show that the simplest expression of an organ of sight is found in the Lamellibranchiata. These simple organs, however, are not morphologically the primitive visual organs of the group, but *adaptive organs*, the ancestral eyes being present, in a few forms, only for a short time during the free larval stage of the animal; it is lost when the animal becomes fixed and the head excluded from the light.

FIG. 1.—Visual cells of *Ostrea virginica*. *c*, cuticle; *p*, pigment; *n*, nucleus.

We will hastily review these simple eyes. One of the simplest cases is found in *Ostrea virginica* (fig. 1), in which we have, on the free edge of the mantle, a number of epithelial cells containing a nucleus (*n*), a deposit of pigment (*p*) in their exterior extremities, and on the outer surface a fine transparent, refractive cuticula (*c*). There seems to be no protection for the organ, save the power of withdrawal of the whole mantle within the valves of the shell. Experiment conclusively proves that sight exists in these animals, as shown by Ryder.[3]

We next find these pigmented visual organs confined to a certain point of the mantle which has become specialized into the so-called siphon. In *Venus mercenaria* we have these cells, unprotected on the external surface of the siphon, but at the same time some cells are more or less protected at the base of the tentacles; but as this animal is able to retract the entire

[1] Darwin, Chas., Orig. of Species, p. 182.

[2] Sharp, B., On the Visual Organs in Lamellibranchiata. Mittheil. a. d. Zool. Stat. zu Neapel, Bd. v, 1884, p. 447.

[3] Ryder, J. A., Primitive Visual Organs. Science, vol. ii, No. 44, 1883, p. 739.

siphon within the shell, protection is thus afforded to these delicate organs.

When we find forms which are unable to wholly retract the siphon within the shell, the visual cells are confined to grooves at the bases of the tentacles. In the rapid withdrawal of the siphon through the sand, in cases of danger, we can easily see that the sharp particles would irritate any delicate organ, and protection must be afforded to them. Now, the possession of sight at the only exposed portion of the animal, would be of the highest value, in the struggle of life, to its possessor, if, when a shadow, like that of a rapacious fish, is thrown upon the organ of sight, a rapid retraction will save it from being nipped off.

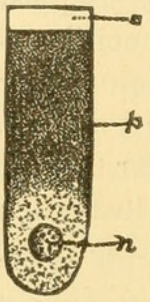

FIG. 2.—One visual cell of *Solen vagina*. *c*, cuticle; *p*, pigment; *n*, nucleus.

In *Solen vagina* and *S. ensis*, the former being the species on which I first satisfactorily proved the existence of a visual sense,[1] we find the cells have become much more developed, as is seen in fig. 2 (this being drawn to the same scale as that of fig. 1), but are essentially on the same plan as those in *Ostrea*. These cells line deep grooves at the bases of the tentacles and are found nowhere else, thus being amply protected from any injury. The nerves supplying these visual cells are probably the nerves of general sensibility, perhaps somewhat specialized.

The remarkable organs of *Pecten* and *Spondylus*, I will not here consider, as they throw no light on our immediate subject, and have been considered by me elsewhere.[2]

In passing next to a higher group, the Gastropoda, from which the Lamellibranchiata have probably degenerated, marked steps in advancement are to be noted.

In *Patella* we find that the pigment spots, or visual organs, take their morphological position, namely in the oral end of the body, and consist of a single pair in the base of the broad tentacle. More than a single pair of eyes are not found in the Gastropoda.[3]

---

[1] Sharp, B., On Visual Organs in *Solen*. Proc. Acad. Nat. Sci. Phila., Nov. 6, 1883, p. 248 ; also, On the Visual Organs in Lamellibranchiata.

[2] Sharp, B., On the Visual Organs in Lamellibranchiata.

[3] The adaptive dorsal eyes of *Onchidium* form an exception, but the normal pair of cephalic eyes are present. See Semper, Carl, Ueber Sehorgane von Typus der Wirbelthiereaugen am Rücken von Schnecken. Wiesbaden (Kreidel), 1877.

In *Patella*, as shown by Fraisse,[1] there is a simple sphere, made up of pigmented cells, similarly formed as those described for the Lamellibranchiata. This sphere is open in front and allows the entrance of the external media.

Haliotis[2] gives us an advance ; here we have an open sphere as in *Patella*, but instead of the refractive cuticula to each cell, they are physiologically combined into one mass, forming a lens. This lens is the product of the cells of the eye, and is purely a secretion—a simple cuticular lens, as is found in all the eyes of the invertebrata—while the lens of the vertebrata, where it exists, is always cellular. The cellular lens-like bodies found in the so-called eyes of *Pecten* and *Spondylus*, and the dorsal eyes of *Onchidium*, are exceptional, and will be treated of elsewhere.

Fissurella[1] gives us an eye that goes practically as far as any gastropod eye, the higher forms merely carry out, a little more in detail, this plan. This results in a closed eye containing a lens, the transparent epidermal covering acting as a cornea. The pigmented layer is as in *Haliotis*, namely, the cells composing it are devoid of a transparent cuticula, the lens and cornea serving as the refractive bodies.

The phylogenetic development of the molluscan eye, therefore (cephalopoda excepted), is as follows: (1), a pigmental surface of epithelial cells; (2), pigmented invaginated grooves for protection, at centralized points of the body, each visual cell having a cuticular body; (3), this groove contracting to an open sphere which closes; (4), the refractive bodies of each cell being centralized into a cuticular lens. A distinct nerve, specialized for sight, is developed (*Haliotis* and *Fissurella*), which connects the eye with the superior cephalic ganglia.

Now, let us see how the ontogenetic development agrees with the phylogenetic.

Bobretzky[3] and Haddon[4] have given us the development of

---

[1] Fraisse, Paul, Ueber Mollusken Augen mit embryonalem Typus. Zeitschr. f. wis. Zool., Bd. xxxv, 1881.

[2] Fraisse, Paul, Ueber Mollusken Augen mit embryonalem Typus. Zeitschr. f. wiss. Zool., Bd. xxxv, 1881.

[3] Bobretzky, N., Studien über die embryonale Entwickelung der Gastropoden, Arch. f. mikr. Anat. Bd., xiii, 1877.

[4] Haddon, A. C., Note on the Development of Mollusca, Quart. Jour. Mic. Sci., n. s., vol. xxii, 1882.

the gastropod eye, the former in *Fusus*, and the latter in *Murex.* I have carefully investigated the embryological growth of this same organ in *Nassa*, and lastly, Carrière[1] gives an account of the regeneration of the eye after amputation in the Pulmonata.

We find that ontogeny merely recapitulates phylogeny, as we would naturally anticipate. There is first an invagination, which closing forms a sphere ; in the cells of this invagination there is a deposit of pigment, and from them a cuticular lens is formed, which increases in size by the addition of concentric layers. A nerve is there developed and connects this eye with the superior cephalic ganglia.

We will now pass to consideration of the eyes of the vertebrata, which, with a few exceptions, are remarkable for the similarity in general plan of organization throughout the whole group.

I will not enter here into a detailed account of the work that has been done on this subject, nor into a description of the finer anatomy, except where necessary to illustrate points under consideration. I leave these to a future and more exhaustive work upon the "Anatomical and Physiological Evolution of the Organ of Vision," upon which my friend, Dr. Charles A. Oliver, and myself are now engaged, and which is to appear under our joint names.

The general structure of the eye of the vertebrata is well known, and I will here simply draw attention to some of the cardinal points.

The eye consists of a more or less spherical body, bounded in front by a transparent plate, the *cornea*, which is a continuation of the white opaque enveloping sheath of the eye-ball, called the *sclerotica.* Internal to this *sclerotica* is a layer of pigment (*choroïdea*), passing forward to about the position of the junction of the *cornea* and *sclerotica*, and also extending over the posterior wall of the iris. Lying on this pigmented layer is the *retina*, the sensory portion of which is considered to be a continuation of the optic nerve, and which passes beyond the equator of the eye to a point called the *ora serrata.* The cavity of the eye-ball is divided anterio-posteriorly into two principal chambers, the anterior one is again subdivided into two, called the anterior and the posterior chamber, and includes all the space anterior to

[1] Carrière, Jus., Studien über die Regenerationserscheinungen bei den Wirbellosen. I. Die Regeneration bei den Pulmonaten. Würzburg, 1880.

the lens. The anterior chamber is divided from the posterior by the iris, the latter being a flattened projection of the vascular layer of the *choroïdea*. The hole in its centre is called the pupil. These two chambers are filled with a fluid called the *humor aqueus*. Back of the lens and *iris* is the largest chamber of the eye-ball, called the vitreous chamber, and contains a semi-fluid mass, known as the *corpus vitreum*.

The lens is a *cellular* body, suspended from the *process ciliaris* by the suspensory ligament; the *process ciliaris* of the *iris*, is an extension of the vascular layer.

The *retina* is composed of many layers; one of the most external, that which is directed toward the *choroïdea*, is called the layer of the rods and cones. The innermost layer, that next to the *corpus vitreum*, is the layer of fibres of the optic nerve; between these two are several ganglionic layers. The whole retina is practically transparent, and the light passes through it unchanged to the point of contact of the rods and cones with the pigmented layer. Here the light-motion is transferred into a "nerve-energy," which is transmitted to the perceptive centres of the brain,[1] no light-motion, of course, passes beyond the receiving sensory fibres internally. The optic nerve pierces the retina a little on the nasal side of the optic axis. It will thus be seen that the extraneous color-waves have, in their impinging upon the sensory tips of the rods and cones, passed through the entire thickness of the retina, before it has been put in a position to give a proper sensory impression. In fig. 3, I have given a diagrammatical representation. *R* is a ray of light passing through the retina, and impinging on the point of a rod or cone, *n* representing the return through the cells of the retina (*r*) to the nerve-fibres, and then passing by them to the brain, *B*.

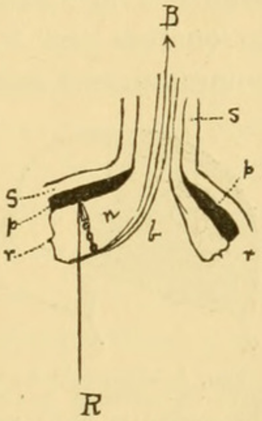

FIG 3.—Diagram representing the course of light, *R*, in the eye of a vertebrate, and "nerve-energy" through the retina to the brain, *B*. *S*, sclerotica; *p*, pigment; *r*, retina; *b*, blind spot; *n*, is the return through the retina of the nerve-energy.

Now, to consider the development of the eye, we find that in

[1] For a detailed account of this, see the forthcoming paper of Oliver, Charles A., "A Correlation Theory of Color Perception," Amer. Jour. Med. Sci., Jan., 1885. Dr. Oliver has kindly allowed me access to the manuscript of this article.

an early stage of the embryology of a vertebrate, the anterior end of the medullary groove, or canal, as the case may be, is divided into three segments, which later form the brain. The anterior of these is known by the name of fore-brain, or *proencephalon*; the middle one, or mid-brain, is called *mesencephalon*; and the posterior, the hind-brain, or *metencephalon.*

From the fore-brain proceeds outwards and laterally a swelling, which increases in size, and passes on to the epidermis. Here an invagination takes place, inward, to meet this outward brain-growth. This invagination finally closes, and soon becomes cut off, to form a hollow vesicle, the cavity of which is finally obliterated, and, becoming transparent, forms the lens of the adult eye. In the meantime, the growth from the brain has arched over and above this vesicle, and then folds over laterally to enclose the lens. This process of the brain is hollow, and communicates with the ventricular cavities of the brain.[1] This differentiation which has taken place, to form the so-called "secondary optic vesicle," is hardly an invagination in the true sense of the word, but is rather a double-walled plate, which folds downwards around the lens, this is indicated in the diagrammatic representation in fig. 4. The lens fills up the anterior opening of the cavity of the secondary optic vesicle, and as the two edges, *a* and *b*, close around the under surface of the lens, a certain amount of mesodermic tissue is included, which later forms the transparent *corpus vitreum.* After the closure is completed, there is a double-walled vesicle, the interior wall is the thicker of the two, and later gives rise to the many-layered *retina;* the external wall forms the pigment layer of the *choroïdea.* It not unfrequently happens that we find incomplete closure of the secondary optic vesicle, and when this is the case in the adult eye, the pathological condition known to physicians as *coloboma* exists. This may take place in the *iris* (*coloboma iridis*), or in the *retina*

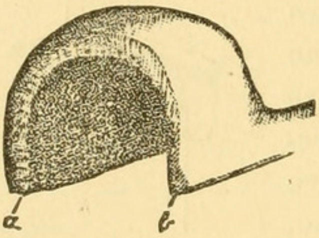

FIG. 4.—Diagram to illustrate the method by which the secondary optic vesicle encloses the lens which should fill up the open end. Eye of vertebrate.

[1] It must be borne in mind that the interior of the lens was once a part of the general surface of the body, and also the interior of the secondary optic vesicle, proceeding first by the formation of the medullary groove, and then from that inward.

(*coloboma retinæ*); in the latter case, on examining the eye with an ophthalmoscope, we can see a wedge-shaped white patch, the base downwards, at the inferior part of the background of the eye, the white is the sclerotica shining through. This is merely a reversion to a primitive state—a failure in the union, posteriorly, of the two lateral walls of the secondary optic vesicle.

The optic nerve is formed by the bending over, and union below, of the connecting portion of the secondary optic vesicle with the fore-brain. The portion of mesoderm included by this process is later termed the *arteria centralis retinæ*. The *sclerotica* and the vascular layer of the *choroïdea* are formed from the mesoderm, and are merely organs for the nourishment and the protection of the nerve-elements within.

It seems to me that the steps taken in ontogenic development of the eye, point out to us that the course which has been pursued in its phylogenesis from a simple epithelial pigmentary deposit, is as follows: The first visual organ primarily consisted of a deposit of pigment, centralized at that portion of the animal where it will be of the most use, viz.: at the oral pole. Since animals as a rule proceed with this extremity forward, they are developed in this situation; but in some cases, as in the Lamellibranchiata, as pointed out above, they are developed at that portion of the body which needs their protection. The next step in advance is to protect these important organs, and as a consequence invaginated grooves result, which gradually shorten to form a sphere. The refracting media of separate cells soon coalesce, to produce a cuticular lens. The nerves of general sensibility, connecting this eye with the brain, soon become specialized, and form a distinct (primitive) optic nerve. As the eye increased in importance and usefulness to its possessor, a corresponding stimulation took place in the brain, where sight is without doubt seated. Increased activity in any organ causes a corresponding increase in blood-supply—or better, *nutriment-supply*—and an increase of development took place all along the tract, from the eye to the seat of vision in the brain. As this increased, that part of the brain nearest the eye enlarged, and proceeded by steps *toward* the eye, similar to the process now taking place in the development of the eyes of the *Vertebrata*, the primitive optic nerve still connecting the two. We then have a stage in which a part of the brain closes over the superior part of the eye, being separated by a layer of fibres, which is the much-shortened and flattened primitive optic nerve. The pedicle connecting this advanced part of the brain, which may be looked upon as a ganglion, we will now call the "secondary optic nerve," the optic nerve of the eyes of the adult *Vertebrata*. A similar state of affairs as this is found to-day in the eyes of the *Cephalopoda dibranchiata*. This ganglion soon becomes the most important part of the eye, and receives the light-waves upon its exterior wall, the primitive eye becoming transparent, and later forming the lens. This "*ganglion opticum*," as it may be provisionally called, gradually proceeds downwards about the primitive eye, joining below. As development and importance advance, we find the hollowing out of the *ganglion opticum*, this structure later is filled with the *corpus vitreum*, which is included, as was shown in the development of the eyes of the *Vertebrata*. Thus, I hold, if this hypothesis be a true one, that (1) the lens of the eyes of the *Vertebrata* is homologous with a primitive invaginated eye, such as we find to-day in the gastropoda; that (2) the layer of optic fibres of the *retina* is homologous with the primitive optic nerve. As the *retina* below has become the sensory part of the eye, the rays of light must necessarily pass through it, to reach a point where nerve-energy is developed. The *nervus opticus* of the eyes of the *Vertebrata* is, therefore, according to this view, really a secondary optic nerve.

We find in the vertebrata, and much more frequently in the invertebrata, blind animals, the near relatives of which have well-developed organs of sight. This blindness is due to the peculiar environments of the animal, such as cave life, where light is excluded; parasitism, etc., etc.

The *Proteus* of the Adelsberg grotto is an animal that is practically devoid of pigment. The eye of this practically blind animal is remarkable, inasmuch, that no lens is developed in the adult state. Our literature is unfortunately deficient in the embryology of this interesting form, so it is at present a matter of impossibility to state whether there *ever* exist a lens in the early development of the eye. The primitive optic vesicle has the form of that of the embryos of those vertebrates which have well-developed eyes in the adult state; the retina is a thick, many-celled layer, lying on the *stratum pigmentum*, which contains a very meagre deposit of pigment; the anterior edge of this double-walled cup, formed by the retina and pigmented layer, come together, owing to the absence of the lens. It is stated[1] that no *corpus vitreum* is present. This degenerate eye is of little use to the animal, and, besides the loss of the lens, it is covered by the general integument of the body. Now it may be argued, upon my hypothesis, that the lens should be last to disappear, being phylogenetically the *first* to appear; but as the secondary optic vesicle has taken up the principal function of the eye, viz.: the developing of nerve-energy, we would naturally expect that the *accessory* organs would be the first to disappear in the process of degeneration; hence, the lens modified to an organ of refraction, although the most primitive part of the eye, would disappear before the secondary optic vesicle, since it has lost its function as an eye and acts merely as a refractive agent.

Another objection may be raised, which may be well to insert here, viz.: Why should the process from the proencephalon start before the invagination, to form the lens, the former being a secondary state in the phylogeny of the animal? I would explain this by the fact that as the optic vesicle, being now the most important part of the eye, and so established for many generations, now appears *first* and disappears *last* in degeneration.

In *Myxena glutinosa*, as described by Wm. Müller,[2] we have an eye consisting of the secondary optic vesicle, as in the case of *Proteus*, but open in front and filled with a plug of mesodermal tissue. The eye is entirely devoid of pigment and lies buried beneath a layer of muscle underlying the skin. The optic nerve passes into the vesicle, and terminates *in* the retina, there being no layer of optic nerve-fibres present at all. This eye has proceeded a step further in its degeneration, than the eye of *Proteus*, being *entirely* devoid of pigment, and having become more deeply imbedded, is covered by a layer of mesodermal tissue, the muscular stratum.

Thus in degeneration, the eye proceeds, step by step, backwards towards the brain, after first losing its accessories, such as the lens, *cornea*, *sclerotica*, etc.

---

[1] Semper, Carl. Animal life as affected by the natural conditions of existence. Intern. Sci. Series, vol. xxx, New York (Appleton), 1881, p. 78.

[2] Müller, Wm. Ueber die Stammesentwickelung des Sehorganes der Wirbelthiere. Festgabe an Carl Ludwig. Leipzig (Vogel), 1875, p. vii.

In *Branchiostoma lanceolatum* we find the degeneration has reached its greatest extreme. There exists no trace of the eye, in form, and we recognize its existence only by a slight deposit of pigment on the anterior end of the neural canal. The brain itself has disappeared in this degenerate form, it going hand in hand with the eye, so that the only remnant of it is a spot of pigment on the anterior end of the neural canal.

Now this deposit of pigment that we find in *Branchiostoma*—and a similar deposit in the nerve-centres of some of the larvæ of the Ascidia, looked upon at one time as the ancestors of the Vertebrata, while they are if Vertebrata at all, greatly degenerated ones—led Lankester[1] to regard the primitive type of the Vertebrata as a transparent animal with eyes sessile on the brain. I am of the opinion that forms so degenerate as *Branchiostoma* and the *Ascidia* should not be taken as a standard, on which to base our conclusions for the origin of the Vertebrata.

In conclusion I may quote a passage from Tyndall,[2] which we have taken for our motto : " The eye has grown for ages *toward* perfection, but ages of perfect*ing* may still be before it."

---

[1] Lankester, E. R., Degeneration, a Chapter in Darwinism. Nature series. London, 1880.

[2] Tyndall, John, Six Lectures on Light. London, 1873.