The EYE *of* PECTEN.

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THE general absence of organs of vision amongst the members of the class Lamellibranchiata meets with a curious and interesting exception in the genera Pecten and Spondylus.

These genera have long been known to possess a great number of eyes of considerable complexity, situated on the border of the mantle. The number of these eyes varies considerably in different individuals, ranging in the genus Pecten from eighty to one hundred and twenty. Their position also varies; for, although they are always situated on the border of the mantle, yet sometimes they are placed at equal distances from one another, and sometimes they are clustered together in certain localities.

Notwithstanding this indefinite element, both in their number and position, which might be expected to run parallel with a primitive and simple organisation, their anatomy is exceedingly complicated, and exhibits all the most important structural elements of the eyes of the higher Vertebrata.

The earliest investigations into the anatomy of Pecten's eye are those of Krohn,[1] who gives a drawing of the course of the optic nerve. This drawing is copied in many of the subsequent papers on the subject by other investigators, and, as far as it goes, is correct. Duvernoy,[2] in his description of the nervous system of the Pectens, gives a short description of the anatomy of the eye. This paper, however, is chiefly valuable for the excellent figures and descriptions of the distribution of the nerves in the mantle, and the filaments which are given off from the main trunks of these to supply the tentacles and the eyes.

The researches of Blanchard[3] and of Keferstein[4] which followed did not add very much to our knowledge on this subject, and it was not until 1865 that any careful histological inquiries were carried on. It was Hensen[5] who first

[1] Krohn, 'Müller's Archiv,' 1840, p. 301, pl. xi.
[2] Duvernoy, 'Mémoires de l'Academie de Sciences,' t. xxiv, 1852. 'Mémoire sur le système nerveux des Acephalés,' p. 73, pl. ii.
[3] Blanchard, 'Organisation du regne animal: Mollusques Acephalés.'
[4] Kerferstein, 'Zeit. für wiss. Zoologie,' 1863, p. 133.
[5] Hensen, 'Zeit. für wiss. Zoologie,' 1865, p. 220.

gave figures of the characters of any of the histological elements. But as the eye of Pecten forms only a very small part of the paper, his figures and description are by no means complete, and in many respects they are incorrect. Finally, J. Chatin[1] has contributed two short papers, without figures, on this subject.

Of the scanty literature Hensen's paper is by far the most important, and he alone gives any good figures of sections of the eye, or of its elements; the other observers give remarkably few figures, and consequently I have had, owing to an imperfect knowledge of the German language, some difficulty in making myself acquainted with the substance of their papers.

I have been encouraged in publishing the following researches chiefly by this scarcity of good figures, but also because I believe, and will give my reasons for believing, that these eyes deserve more mention than is usually made of them in our zoological text-books.

My investigations were chiefly carried on upon *Pecten maximus*, but I have also had the opportunity of making sections of and studying the eyes of two other species, *Pecten jacobæus* and *Pecten opercularis*. The eyes of these three species differ from one another in one or two not altogether unimportant particulars, and, as I shall afterwards point out, they form an interesting gradation, the points of difference between *P. maximus* and *P. opercularis* passing through intermediate stages in *P. jacobæus*.

The eyes of Pecten maximus—are situated amidst a number of tentacles, which run all round the border of the mantle. These tentacles are capable of considerable movement, and frequently overhang the eyes and protect them from the light. The eyes themselves are situated upon short stalks, which resemble very closely the basal part of an ordinary tentacle.

This similarity caused Duvernoy to name a tentacle a tactile pedicel, and an eye an ocular pedicel, thus to a certain extent implying that they are morphologically homologous organs respectively modified for a tactile and an ocular function. This homology is justified by certain points in their anatomy, such as the course of the nerve and the arrangement of the muscular fibres, and I believe that when the development of these eyes is studied the homology will be still further confirmed.

The border of the mantle which bears the tentacles and

[1] J. Chatin, 'Bulletin de la Société Philomatique.' Paris, 1877.

eyes is covered with an epithelium, consisting of columnar, non-ciliated, and slightly granular cells bearing nuclei, situated near the base of the cells. As this epithelium passes over the eye-bulbs, it undergoes two interesting modifications. It becomes considerably thicker and filled with a dark brown pigment (Pl. XXXIV, fig. 1 *c*) as it passes round the sides of the eyes, but immediately in front of the eye (Pl. XXXIV, fig. 1 *a*), it again diminishes in thickness, and becomes perfectly transparent. By thus surrounding the eye on all sides with a dark-coloured pigment, leaving only a round spot in front, clear and transparent, the epithelium, by limiting the entrance of the light to a small diaphragm in front, here performs the function of an iris. The epithelium which runs over this transparent part, and which forms the epithelial layer of the cornea, differs from the ordinary epithelium covering the rest of the mantle in that their cells are rather larger, are perfectly transparent in the living condition, and the nuclei are large and spherical, and situated in the centre of the cells.

The eye consists of the following parts, which I shall now describe in order. The cornea, covered externally by its transparent epithelium, protects a large elliptical lens. Close up to the lens is the retina, but separated from it by the optic nerve, which spreads out over the anterior surface of the retina. The retina rests upon a tapetum, and behind this, occupying all the posterior concavity of the eye-cup, there is a red pigment.

The *cornea*—consists of two parts, the outer epithelium, which has already been described, and a basement membrane, consisting of a thin layer of connective tissue. As before stated, this epithelium is merely a modification of the general epithelium of this part of the mantle; and the pigmented epithelium surrounding the eye-bulbs (in like manner, a modification of the same tissue) is continuous with it all round its edge. The passage of the cells of the pigmented epithelium into those of the corneal epithelium is signalised by two important changes in the characters of the cells. In the first place the pigment entirely disappears, and the nuclei, which in the former case were obscured by the pigment, now becomes apparent, and in the second place the cells are considerably diminished in their longitudinal axis. The diminution in size of the cells causes the edge of the cornea to be sunk below the level of the pigmented epithelium; and a shallow trough runs round the line of its juncture with it (Pl. XXXIV, fig. 3). The convexity of the cornea is not great, and the dome of it frequently only just

reaches the level of a line drawn from the highest points of the pigmented epithelium on either side of it. This appearance is not often seen in sections, as the pigmented epithelium rapidly shrinks, when the tissue dies, and under most reagents; but I am fully persuaded of the accuracy of this statement from an examination of the eyes of living specimens of *Pecten maximus* and sections of *Pecten opercularis*.

The delicate epithelial cells of the cornea, in consequence of being entirely unprotected by any membrane similar to the conjunctiva of the higher animals, are quite naked, and very liable to injury from the rough edges of the tentacles which surround them. The arrangement just described, however, probably prevents the tentacles from coming into immediate contact with them. The little trough which runs round the margin of the cornea always contains a little liquid, even when the eye itself is removed from the water; and the pressure of the tentacles when folding over the eye causes it to spread out as a thin layer over the cornea, and thus the cells are prevented from coming into immediate contact with the tentacle.

Thus, the two remarkable modifications, namely, the presence of a large quantity of pigment, and a greater longitudinal axis of the cells which the pigmented epithelium exhibits, are of considerable value to the eye, firstly, to prevent very divergent rays from entering, and secondly, to prevent any damage to the cornea caused by the rubbing of the adjacent tentacles over the sides of the eye.

The second layer of the cornea is about half as thick as the epithelial layer, and, like it, is perfectly colourless and transparent. It consists merely of a thin continuation of the connective tissue of the stalk. It may be called the basement membrane of the corneal epithelium, as from the absence of any definite cellular elements its only function probably is to support these cells.

Beyond the cornea this membrane becomes much thicker, and supports the pigmented epithelium, and at the same time structural elements make their appearance in it. From thence it passes into the connective tissue of the eye-stalk without further modifications.

The *lens*—is one of the most interesting parts of the eye. It is comparatively large, and is composed of a number of nucleated cells. In the fact that the lens is formed by more than one cell the eye of Pecten bears an interesting resemblance to that of the Vertebrata. The shape of the lens has been a subject of much dispute amongst the authors

who have written on this subject. Krohn and Keferstein believed it to be spherical. Hensen has figured it filling up the space between the cornea and retina, and consequently of an irregular bi-convex shape.

It is difficult to see how a controversy on such a simple subject could have arisen, unless it is because different authors have examined different species, and described them for the genus.

As regards *Pecten maximus*, an examination of the fresh eye has convinced me that in this species the lens is elliptical, the major axis being parallel to the plane of the mantle. A section of the eye made in a plane at right angles to the plane of the mantle and the direction of its margin—that is, the plane which is most convenient for section-cutting, and the one which is apparently usually adopted—would consequently cause the lens to appear circular in section. In the diagrammatic representation of the eye (fig. 1) I have for convenience sake represented the lens as being at right angles to the plane of the mantle in order that the true shape of the lens may not be overlooked.

A fresh examination of the lens, when teased out from the rest of the eye, exhibits one or two interesting points. The lens is not, as in most eyes, perfectly colourless, but possesses a well-marked brown colouration, and a number of fine striæ may be seen running in the direction of the major axis. The lens does not appear so perfectly elliptical in the fresh condition as in certain sections I have made; it is drawn out somewhat longitudinally, so as to be more like a double cone than an ellipse. This is probably due to the lens being released from the ligaments and connective-tissue pressures, which cause it to retain its proper shape.

Hensen says that the lens is very soft, and the cells are light, polygonal, and nucleated. A careful examination of the lens of *P. maximus* has led me to a very different conclusion. The lens seemed to be of exactly the same nature as in the higher forms, and when teasing it out I found some difficulty in holding it with a needle, as it slipped away from under it when a slight pressure was exerted. As regards the shape of the cells composing the lens, they are not all polygonal, as would be inferred from Hensen's remarks on the subject. In the centre they are polygonal, but as they approach the periphery they become more and more flattened and elongated, until at the periphery they are strap-shaped. They are nucleated. As Hensen, I could find no membrane covering the lens, and no muscular fibres connected with it; but in a few cases I have observed a liga-

ment, such as I have represented diagrammatically in fig. 1 *f*, which, I believe, forms a support for the lens. This ligament is usually broken by the action of reagents, and then hangs down by the side of the cavity, and thus becomes difficult to observe; at the same time the lens sinks down, and rests upon the anterior surface of the retina.

The lens is suspended in the space which corresponds with the vitreous humour in the higher animals. This space is filled with an aqueous humour in Pecten. The lens is larger, and, consequently, the space occupied by aqueous humour relatively smaller in *P. maximus* than it is in either *P. jacobæus* or *P. opercularis*, and in *P. jacobæus* it is larger than in *P. opercularis*.

The *retina*—does not line the concavity of the eye-cup, as it does in most well-developed eyes, but is nearly flat, and a considerable space is left between it and the floor of the cup, which is filled up by the red pigment. In consequence of this the retina appears in section to be a thick band crossing the eye from side to side. Thus, just as the lens was remarkable for the way in which it approached the retina by hanging back into the cavity, so the retina is remarkable for the manner in which it leaves the posterior concavity of the eye-cup to approach the centre. The eye of Pecten, in fact, presents the interesting peculiarity of the approach of the lens and the retina towards the centre, so that in *P. maximus* they almost touch.

The anterior surface of the retina is convex at the sides and concave in the middle, but these convexities and concavities vary in different species. The different layers of the retina will be described from behind forwards, as it will be easier to trace the transitions in that way than if described from before backwards. They are—1°. Posterior limbs of the rods. 2°. Anterior limbs of the rods. 3°. Spindle-shaped nucleated rods. 4°. Molecular and nuclear layer. 5°. Nerves.

The posterior limbs of the rods stand upon a membrane, which runs along the posterior side of the retina; at their anterior ends they pierce a very delicate membrane, and pass into the anterior limbs of the rods. The anterior limbs are about twice as long as the posterior limbs, and are usually smaller in diameter, and situated farther apart than the posterior limbs. That they are circular in section may be seen from Pl. XXXV, fig. 7*a*, which is a drawing of a section made at right angles to the eye-stalk. The anterior limbs of the rods are sometimes swollen so as to appear oval;

this condition occurs especially in the rods at the side convexities. Fig. 6 represents an isolated rod in this condition.

The anterior ends of the rods contract considerably, and again expand into spindle-shaped bodies, each of which contains a nucleus; so that in *P. jacobæus*, where the retinal elements of this region are difficult to distinguish, there may be seen a single row of nuclei running from end to end of the retina, and following its sinuosities (Plate XXXV, fig. 11 *b*).

In some of the rods at the side of the retina a second spindle-shaped body follows the first one, as represented in the isolated rods in figs. 5, 6, but usually the anterior end of the spindle is drawn out into a delicate thread, which occasionally possesses nuclear swellings. Finally, this thread breaks up into a network, which bears a number of nuclear-like bodies at its nodes, and several round molecular bodies appear to be caught in its meshes. These bodies are so much like the ordinary nuclei of the network that I am inclined to believe that they are, in reality, merely modifications of them, and in some way connected with the network (fig. 6 *a*). Anteriorly the fibres of the network bend at right angles and enter the nerve layer, which covers the anterior surface of the retina. This nervous layer will be described with the description of the optic nerves.

The above is a description of the retina as I found it in *P. maximus*, and I believe it holds good for the other members of the genus. The elements of the retina are so much larger in this species, and the spaces between the rods and network, &c., so much more considerable, that it is a great deal easier to investigate; but I believe careful examination of the other species would show that they do not differ from this in any important detail.

The *tapetum*—is placed immediately behind the retina, and may help in its support. When fresh,[1] the tapetum exhibits a display of colours, and it is this membrane which gives the eyes their beautiful metallic lustre. When examined with a $\frac{1}{2}$th-inch obj. it seems to be composed of a great number of little black specks separated by a fine yellow membrane, but careful examination with a higher power shows that it is composed of a great number of fine fibrils crossing at right angles.

The space between the tapetum and the posterior part of

[1] I have one series of sections stained in osmic acid, and mounted in Canada balsam, which has retained this display of colours.

the eye-cavity is filled with a red fluid *pigment*. In the fresh condition the pigment readily flows on to the slide when the eye is pricked, but in sections of the eye which has been hardened by alcohol or other reagents the pigment adheres to the tapetum or posterior wall of the eye-cup.

Hensen figures a layer of cells in this position, but I have never been able to observe anything of the kind; the pigment contains no cellular elements at all, nor is there a layer of cells lining the cavity which contains the pigment. The pigment consists of a number of bright red granules floating freely in a colourless fluid.

The *nervous supply*—of the eye of Pecten is perhaps the most interesting of the many peculiarities of this eye. The nervous system of Pecten is well described by Duvernoy in the paper referred to above. The mantle is supplied by a number of branches given off from the principal ganglia. These branches all fall into a large nerve, which runs round the margin of the mantle, and which Duvernoy calls the "circumpalial" nerve. This nerve is figured in section in fig. 1, Pl. XXXIV, one of the nerves joining this nerve being figured at fig. 1, *q*. This "circumpalial" nerve gives off filaments to supply the tentacles and eyes.

Krohn first gave a drawing of the optic nerve, and described it as a single nerve passing off from this trunk, and dividing into two branches as it aproaches the eye. Later observers have, however, drawn and described two nerves passing off from the "circumpalial" nerve. My researches have led me to believe that Krohn is right, and that such a figure as Hensen gives in his paper, representing two main trunks passing up to supply the eye is erroneous. Plate XXXV, fig. 9, of *P. maximus*, shows the division of the single nerve into its two branches. In fig. 1 the course of the optic nerve, before its division into two branches, was carefully drawn from one of a complete series of sections, and in none of the other sections could I find a trace of any other nerve proceeding from the "circumpalial." The branching of the nerve takes place in a plane at right angles to the plane of the mantle. When the optic nerve approaches the eye it divides into two branches, which may be called the "retinal nerve" and the "complementary nerve." The former passes up the side of the eye cavity, and spreads over the anterior surface of the retina; the latter soon loses its sheath, and divides up into a number of branches, which supply the tissues surrounding the eye. The course which the retinal branch takes may be seen in Pl. XXXIV, fig. 1, and in Pl. XXXV,

figs. 8 and 9. In figs. 8 and 9, the first section is cut through the optic nerve, and shows the manner in which the retinal branch runs up the side of the eye-cavity; the second section shows the manner in which the branch bends over on to the retina and spreads out. The distribution of the complementary branch is diagrammatically represented in fig. 1 *n*; it seems to divide into a number of branches which envelope the eye-cup, and probably send filaments to the cornea, lens, tapetum, and epithelium.

Comparison of the eyes of the three species, *P. maximus*, *P. jacobæus*, and *P. operularis*.—The eye of *P. maximus* is undoubtedly the most highly developed, the eye of *P. operularis* is the simplest, whilst *P. jacobæus*, although more like *P. operularis* than *P. maximus*, shows many points in which it is intermediate between the two.

The lens in *P. operularis* is separated from the retina by a considerable space (Pl. XXXV, fig. 10), and consequently the chamber containing the humour is relatively large. In *P. jacobæus* the lens is larger than in *P. operularis*, and the chamber consequently smaller; and in *P. maximus* the lens is very large, and nearly touches the retina, the chamber of the eye being sometimes very small. A gradation is thus observed in the character of this part of the eye in the three species. In *P. maximus* but a small space is filled with humour, in *P. jacobæus* a much larger space is filled with it, and in *P. operularis* there is a larger space still.

Again, when the retinas of the three species are compared, a similar gradation is found. The retina of *P. operularis* is comparatively thin, and the concavity and convexities of its anterior surface slight. In *P. jacobæus* the retina is decidedly thicker, and the anterior surface is more convex at its sides than in *P. operularis*; moreover, it may be noticed that the delicate membrane which separates the anterior from the posterior limbs of the rods has become bent up in the regions corresponding with the anterior convexities of the retina. In *P. maximus* all these variations become much exaggerated. The retina is much thicker than in either of the other species; and the side convexities of its anterior surface are much bolder (Pl. XXXV, fig. 11, *a*, *b*, *c*). The anterior concavity does not undergo much variation.

The shape of the membrane separating the anterior and posterior limbs of the rods is greatly altered. In *P. operularis* this membrane is observed, in section, to stretch from side to side without any well-marked curves; in *P. jacobæus* two well-marked curves, corresponding with the anterior con-

vexities of the retina, are observed; but in *P. maximus* these curves are converted into two distinct folds, which run up into the substance of the retina. The membrane between the folds does not sink again as low as it is at the commencement of the folds, and consequently the central part of the retina is raised in the form of a table above the level of its sides. This elevation of the central part of the retina may be also seen in *P. jacobæus*, though it is not nearly so well marked. The folds which occur in *P. maximus* cause the rods to appear to be given off in a pinniform manner at the sides of the retina, and before I found the intermediate condition in *P. jacobæus* I had some difficulty in determining the true relationship between the retinas of *P. maximus* and *P. opercularis*. (Compare *a*, *b*, *c*, fig. 11).

In addition to those just mentioned there are other minor points in which the eyes of these species differ from one another, such as in the shape of the cells composing the lens and in the distribution of the retinal nerve, &c., but they are comparatively slight.

General considerations.—Having thus described, in some detail the anatomy of the various parts which compose the eyes of Pecten, I shall, before leaving the subject, point out some of their interesting morphological peculiarities. It is, in itself, a remarkable thing to find a large and variable number of eyes situated on an area at some considerable distance from any central nerve-ganglion; and, when it is remembered that the class and even family (with one other exception, *e. g.* Spondylus) to which the genus belongs, possess no organs of vision at all in the adult condition, it is altogether surprising that they should be of such extraordinary complexity as they have proved to be. The high structural development that this eye has attained is, however, not so remarkable as the fact that in many ways it differs from the ordinary Invertebrate eye, and resembles that of the Vertebrata.

In the first place, the lens is built up of a large number of distinct nucleated cells, which undergo a flattening at its circumference very similar to that found in the eye of the Vertebrata. Whether the lens is developed from the cells of the epiblast, as in the Vertebrata, or from the mesoblast, must at present be left unsettled, but it will probably be found, when the development of the eye is studied, that in this respect also it resembles the eyes of the Vertebrata. The tapetum, a structure which is of considerable im-

portance to animals which are nocturnal or aquatic in habit, has hitherto been described only in the Vertebrata. That Pecten possesses a tapetum as highly developed as any found amongst the Vertebrata is anatomically a point of considerable interest; but it also indicates to a certain extent the physiological capability of the eye.

The chief interest, however, lies in the relative positions of the optic nerve, the retina, and the pigment. In the eyes of the Cephalopods the pigment layer is situated in front of the rods, and the nerve-fibres enter the rods from behind. In the eyes of the Gasteropoda, the Crustacea, &c., down to the simplest form of eye, such as that of the Rotifera, the same relationship of these parts holds good. In the Vertebrata, however, their relative positions are reversed; the optic nerve pierces the retina, and distributes itself over the front of the retina, whilst the pigment is situated behind it. In Pecten the relationship of these parts is the same as that in the Vertebrata; the nerve passing up the side of the eye-cup bends over, and spreads itself over the anterior surface of the retina. The pigment also is situated behind the retina. Pecten is not, however, the only Invertebrate whose eyes are built up on this type. Semper[1] has recently pointed out that on the backs of certain slugs (Onchidium) a number of eyes are found, and that in these the nerves pass to the front of the retina before being distributed. On account of this distribution of the optic nerve he says that they belong to the Vertebrate type of eye (typus der Wirbelthieraugen), so that two animals are now known, each belonging to a large and important class of Invertebrata (Gasteropoda and Lamellibranchiata respectively) that possess eyes which are built up on this type. The eyes of Pecten are even more deserving of the name of Wirbelthieraugen than those of Onchidium, for they are much more highly developed, and possess, in addition to this relationship of the nerve and retina, other Vetebrate peculiarities. The lens is multicellular, a character which, although not unknown amongst the Invertebrates, is much more characteristic of the Vertebrata. The tapetum, too, a structure which doubtfully exists in any other Invertebrata is found in Pecten and some Vertebrates. But, although the application of this word Wirbelthieraugen to these eyes is convenient for the adult condition, it must be carefully remembered that the development of these eyes is essentially

[1] Semper, 'Uber sehorgane vom Typus der Wirbelthieraugen auf dem Rücken der Schnecken.' Wiesbaden, 1877.

different from that of the Vertebrate eye. The Vertebrate eye is formed in the embryo from a hollow process given off from the brain, and the future eye-cup is formed by an invagination of this process. It is impossible for the eyes of Pecten or Onchidium to be formed by any process similar to this. Thus, in the young state these eyes are essentially different from those of the Vertebrata, and the resemblance in the adult is merely accidental, and by no means due to morphological identity.

Little is known and little can be said concerning the function of the eyes of Pecten. The presence of such a well-formed tapetum makes it probable that they are capable of appreciating very diffused light, and the close approximation of the lens to retina makes it exceedingly improbable that any image is formed upon the latter.

A few experiments have been made on the extent of their visual power, which make it very doubtful whether they are of much value to the animal in avoiding its enemies. The most reasonable theory of their function seems to be that, when on the ebbing of the tide, a probability arises that they will be left high and dry on the shore, they can appreciate the fact by the growing intensity of the light, and, by that peculiar flapping motion of their valves the Pectens are so remarkable for, move away into deeper water.

These researches were entirely carried on in the morphological laboratory of the University of Cambridge, and my best thanks are due to Mr. Balfour for his valuable advice and encouragement during the whole course of my researches. Owing to his kindness, also, I have been enabled to examine some of Semper's preparations of the eye of Onchidium, to which reference has been made in the text.

Methods.—For a general examination of the eye the best method is to harden in alcohol and stain by immersion in hæmatoxylin for twenty-four hours. Of the osmic-acid acid preparations the best were obtained by immersion in a 1 per cent. solution for fifteen minutes, followed by absolute alcohol for three or four days. This method is of great value for studying the retina and lens. I have also used gold chloride for staining the nerves with some success. For examining the tapetum the best preparations I have were made from some eyes given me by Mr. Haddon, which had been treated with picric acid. This reagent seems to have dissolved away the red pigment, and consequently left the tapetum free from the numerous little red granules which

generally cling to it. For examining the isolated rods of the retina I have allowed the eyes to remain in a solution of chloral hydrate for four or five days. I have then dissected out the retina with needles as carefully as possible, and poured a drop or two of hæmatoxylin on to the slide. When the retina had been standing in hæmatoxylin in this manner for some hours it was washed with water, teased out with fine needles, and mounted in glycerine.