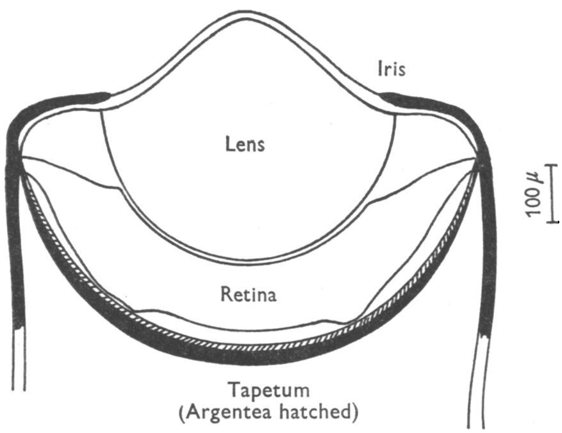
J. Physiol. (1965), **179**, *pp.* 138–153
With 1 *plate and* 9 *text-figures*
Printed in Great Britain

IMAGE FORMATION BY A CONCAVE REFLECTOR IN THE EYE OF THE SCALLOP, *PECTEN MAXIMUS*

BY M. F. LAND
From the Department of Physiology, University College London

(*Received* 13 *November* 1964)

The eye of *Pecten* has been described histologically many times (see Patten, 1886; Dakin, 1910). There has, however, been no serious attempt to examine it as an optical system, nor to assess the nature and quality of the visual image that such an eye produces. Structurally, the eye possesses many features typical of the camera eyes of vertebrates, cephalopods, and some annelids, and most workers have assumed that the optical system was analogous to that of camera eyes, with a lens forming an image on a retina lining the back of the eye (Text-fig. 1).



Text-fig. 1. Diagrammatic median section of an eye of *Pecten*.

Patten made the first observation which suggested that this eye possessed an unusual optical system. He observed that a reversed image of the surroundings was visible in the pupil of the eye. By painting fine lines on the objective of his microscope, and observing the position of their image in the eye, he concluded that the image lay close to the back of the eye, in the position occupied by the retina. Although in his diagrams Patten draws the eye as though the lens were producing the image that he observed, this could not be the case. It is not possible for the image of a distant object to be both produced by the lens, and observed in the eye through the same lens, without some form of ophthalmoscopy. The image, if it is to be visible through the lens, must be produced in some other way.

The back of the eye is lined with the argentea, an accurately spherical, highly reflecting layer. It is this layer that gives the pupil of the eye its bright iridescent appearance. The only way in which the image observed by Patten could be produced is by reflexion at the argentea. Also, since the argentea is itself visible through the pupil, the focal length of the lens must be greater than its distance from the back of the eye. The optical system of the scallop eye must therefore be a combination of a concave mirror, and a lens of long focal length (Text-fig. 5).

The aim of this paper is to establish this model by measuring the focal lengths of the argentea and the lens, and to investigate the nature and position of the image that this system produces.

RESULTS

All the experiments described in this paper were performed on large eyes, 0·9–1·0 mm diameter.

Focal length of the lens in the intact eye

The real distance from the centre of the lens to the back of the eye, and the distance from the centre of the lens to the virtual image of the back of the eye observed through the lens, can be used as U and V respectively in the thin lens formula,

$$\frac{1}{V} - \frac{1}{U} = \frac{1}{F},$$

to obtain an estimate of the focal length (F) of the lens.

Eyes were removed from the mantle and mounted, pupil upwards, in a small dish of sea water. Using the fine focus of a microscope, the distance from the cornea to the virtual image of the back of the eye was measured through the centre of the lens. Slight cracks in the argentea often make it easy to focus with precision. The microscope was calibrated to give real distances in sea water, i.e. actual distances moved $\times 1{\cdot}34$. The eye was then turned on its side on a microscope slide, and the real distance from the cornea to the tapetum was measured from outside the eye, using a micrometer eyepiece. As the centre of the lens is not visible, the distance from the centre of the lens to the cornea was estimated from frozen sections and subtracted from the 'real' and 'virtual' measurements. In addition, the thickness of the tapetum ($40\,\mu$ in the centre) was subtracted from the 'real' measurements, as these were made from outside the optic capsule.

It has been assumed in the calculations in Table 1 that the optical and geometrical centres of the lenses coincide (see below, Focal length of the isolated lens). The results obtained for seven eyes from four animals are given in Table 1.

TABLE 1. Focal lengths of lenses measured *in situ*

All dimensions are in micra.

Eye	*A* Cornea–argentea, measured through pupil	*B* Cornea–tapetum, measured from the side	*C* Cornea–centre of lens, estimated from sections	*D* Real distance of argentea from centre of lens $= B-C-40$	*E* Apparent distance of argentea from centre of lens $= A-C$	*F* Focal length of lens $= \frac{ED}{E-D}$
1	760	625	225	360	535	**1100**
2	792	560	201	319	591	**695**
3	831	660	237	383	594	**1080**
4	633	575	207	328	426	**1430**
5	594	510	183	287	411	**950**
6	755	700	252	408	503	**2160**
7	755	640	230	370	525	**1250**
Means	731	610		351	512	**1238**
					S.D.	470

TABLE 2. Position of the reflected image measured *in situ*

All dimensions are in micra. *C* and *D* refer to Table 1.

Eye	*F* Focal length of lens	*G* Cornea–image, measured through pupil	*H* Apparent distance of image from centre of lens $= G-C$	*I* Real distance of image from centre of lens $= \frac{HE}{F+H}$	*J* Real distance of image from argentea $= D-I$
2	695	459	258	188	**131**
3	1080	562	325	250	**133**
4	1430	396	189	167	**161**
6	2160	495	243	218	**190**
7	1250	480	250	208	**162**
Means	1323	478	253	206	**155**
				S.D.	24

Image position in the intact eye

The image, produced by reflexion at the argentea, of a grid placed above the eye can be seen in the pupil of the eye (Pl. 1). Its apparent position relative to the cornea can be measured. However, since the reflected image is being observed through the lens, its real position must be calculated from its apparent position, using the focal length of the lens.

A grid of 1 cm squares was suspended 7·5 mm above the dish in which the eye was lying in 2·4 mm of water. Thus the apparent distance of the grid, viewed from the cornea of the eye, was $(7{\cdot}5 \times 1{\cdot}34) + 2{\cdot}4$ mm $= 12{\cdot}4$ mm. Measurements of image position were made with the same microscope arrangement as the focal length measurements.

In Table 2 the position of the reflected image is found by taking its observed position as V in the lens formula, where F is the focal length of the lens of the same eye. The eyes used here are five of those used for the focal length measurements.

Two corrections must be applied to the position of the reflected image measured in this way.

(i) The grid which was used as the object in this experiment was not at infinity, but at an effective distance of 12·4 mm from the cornea. With a reflector of focal length 205μ (see below, Calculated position of the reflected image), the image of a point at infinity will be about 4μ nearer to the argentea than the image of the grid.

(ii) The image produced by a spherical reflector is not flat, but spherical and concentric with the reflecting surface. The central square of the object grid subtended an angle of 44° at the eye, and hence approximately the same angle would be subtended at the centre of curvature of the argentea by the image. Because of the image curvature, the axial part of the image will be nearer the argentea than the sides of the observed square by $205(1-\cos 22°)\mu$, i.e. 15μ.

In making these corrections the effect of the lens has been ignored as it would make only a few percent difference to the already small alterations.

The mean, corrected, axial image–argentea distance is 136μ.

Focal length of the isolated lens

An alternative method of measuring the focal length of the lens is to dissect it out, and measure the distance from its centre to the point at which parallel light is brought to a focus.

A hole was cut in one side of the eye with a razor blade, and the lens, which is loosely attached to the inside of the cornea, was gently squeezed out. The lens is soft, and must be handled carefully to prevent deformation. The lens was transferred to a flat-bottomed glass cell containing sea water, orientated so that the optical axis was perpendicular to the bottom of the cell, and was illuminated with parallel light from below. When viewed from the side the lenses were not visibly distorted by contact with the flat surface. The distance from the rim of the lens to the brightly focused spot above it was measured with the microscope fine focus, calibrated to measure real distances in sea water. The microscope objective had a wide enough aperture (N.A. 0·28) to receive light focused over an angle of 32°, which includes all light passing through the lens.

The results obtained from the lenses of six eyes from different animals are given in Table 3. Axial distances from the rims to the geometrical centres of the lenses have not been taken into account, as they are small (50–100μ), by comparison with the measured focal lengths.

This method gives a mean value for the focal length about 45% greater than that measured *in situ*. The probable reason for this is that the lens has no single focal point, and that each method measures a different aspect of a complex pattern of focus. In the measurements made on the intact eye, only the central part of the lens was used, as the apparent depth of the central, deepest part of the argentea was being measured. Hence the focal length measured here is the focal length for rays close to the optical axis of the lens. As the N.A. of the objective used to make these measurements was 0·18, only a 20° cone of light from the back of the eye was used in making these measurements, and such a cone would occupy only the central 200μ at the front surface of the lens. The second method, however,

TABLE 3. Focal lengths in sea water of isolated lenses (μ)

Lens	Distance from rim of lens to point of brightest focus (μ)	
1	1580	light incident on anterior face of lens
2	1970	
3	1625	
4	1570	light incident on posterior face of lens
5	2055	
6	1923	
Mean	1787	

measures the position of the circle of least confusion produced by the whole lens, and this might well be different from the focal length for rays close to the axis (see Text-fig. 2). An indication that the lens has an extended region of focus is given by the fact that, if a grid is used instead of parallel light to produce a real image, a series of images of varying magnification can be seen through the microscope at different distances from the lens.

Another possible explanation for the discrepancy between the values for the focal lengths given in Tables 1 and 3 is the error introduced by the assumption, in measurements made on the intact eye, that the optical and geometrical centres of the lens coincide. A lens with a front profile as non-uniform as this has no single optical centre from which to make the measurements required in using the thin lens formula. However, estimates of curvature based on photographs of frozen sections suggest that the optical centre for rays close to the axis may be up to 100μ nearer the front face of the lens than the geometrical centre, while for rays 100μ from the axis the optical centre may be either side of the geometrical centre. The error introduced by taking all measurements from the estimated position of the geometrical centre will be significant in the estimates of focal length given by this method. A discrepancy of 50μ between the geometrical centre and the mean position of the optical centre for rays up to 100μ from the axis would give a value for the focal length about 25% greater than that quoted in Table 1. However, the error in the final position of the reflected image (J in Table 2) will be only about 5%, i.e. about 8μ further from the argentea than the figure quoted. The exact profiles of the front surfaces of the lenses are too variable to apply this correction with certainty.

If the refractive index of the retina differed significantly from that of sea water, this would also lead to a difference in the results of the two methods of measuring focal length. However, observations on the isolated retina in sea water and in sucrose solutions, and on individual cells under phase contrast, indicate that only the outer segments (see Text-fig. 6) have a refractive index substantially higher than sea water. The effect of such a layer, less than 40μ thick, on the measured focal length or the position of the reflected image would be negligible.

Focal length of the lens by construction

To examine in more detail the properties of the lens it is necessary to know:

(i) the shape;

(ii) the refractive index;

(iii) whether the refractive index is uniform throughout the lens.

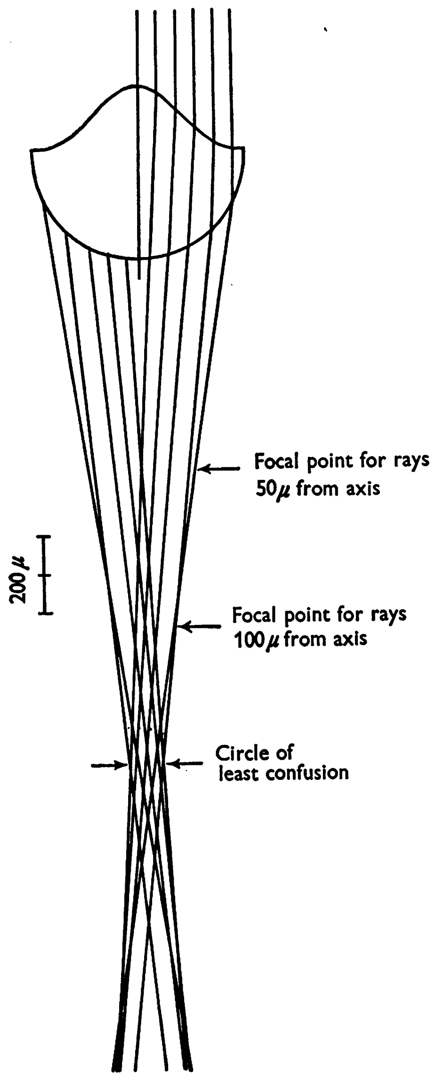
The shape of the lens was obtained from photographs of frozen sections. Eyes were fixed in a neutralized 4% solution of formaldehyde in sea water for $\frac{1}{2}$ hr, and sectioned at 25μ on a freezing microtome. Central sections from each series were photographed in sea water. The sections showed no measurable change in the external dimensions, compared with the unfixed eyes.

To determine the refractive index, lenses were dissected out and placed in glass cells containing sucrose solutions of concentrations from 0 to 70% (wt./wt. solution). The slides were illuminated with parallel light from below, and observed microscopically. If a bright spot was produced above the lens, the lens was acting as a converging lens, and hence had a higher refractive index than the surrounding medium. If the light appeared to diverge from a bright spot below the lens, then, as the lens is biconvex, it must be of lower refractive index than the medium. A value for sucrose concentration and refractive index was found in which the lens neither diverged nor converged light. These observations must be made in the first minute after immersion in the sucrose solution, as dehydration and increase in refractive index were found to occur rapidly in the higher strength solutions.

The refractive index of all lenses used was $1{\cdot}42 \pm 0{\cdot}01$.

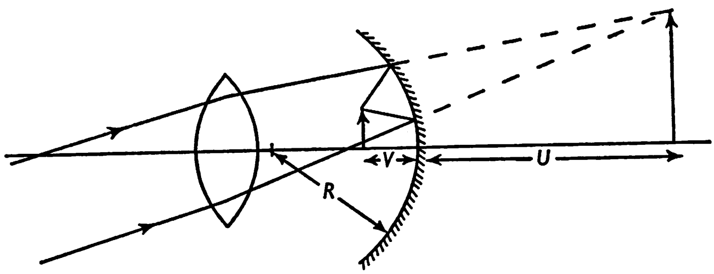
Several observations suggest that the refractive index of the lens is uniform. The fact that it is possible to produce a simple refractive index match as described here suggests uniformity. Unlike the lenses of the eyes of fish, the lens of *Pecten* is soft throughout. There is no hard protein core and soft periphery, as in the fish lens, and one would not expect there to be the same gradation of refractive index through the lens as there is in fish lenses. Histologically, the lens is uniform, except for a slight flattening of peripheral cells.

Text-figure 2 is a geometric construction of the paths of paraxial rays through an axial section of an actual, fairly typical, lens. A uniform refractive index of 1·065 relative to sea water (1·42 relative to air) was assumed.



Text-fig. 2. Construction of the paths of paraxial rays of light through a typical lens.

In this construction, and similar ones, the rays nearest the axis are brought to a focus nearer to the lens than more peripheral rays. The distance from the centre of the lens to the circle of least confusion is 1590μ in this construction, and 1820μ in another. However, the values of the focal length for rays 100μ either side of the axis, from the same constructions, are 1180 and 1350μ. These figures are consistent with the results obtained from the two methods of measuring the focal length.



Text-fig. 3. Position of the reflected image. $1/V = 2/R + 1/U$.

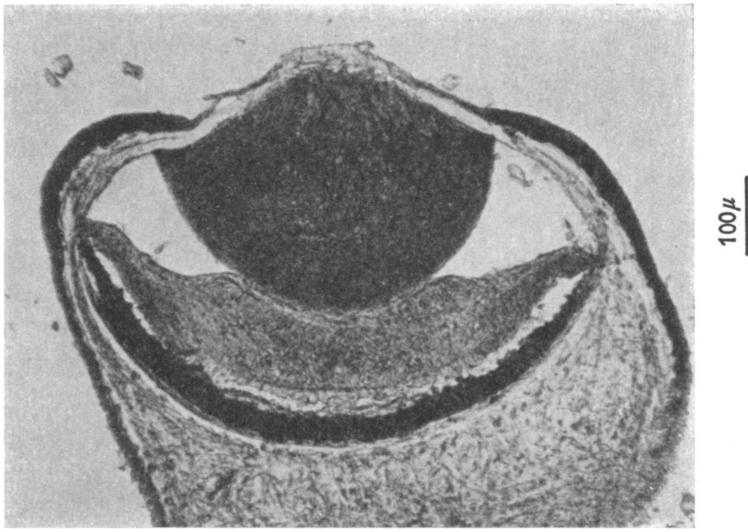
Calculated position of the reflected image

The mean radius of curvature of the argentea from four sections was 410μ; all four were within 50μ of the mean. The focal length of the argentea for a narrow pencil of parallel light is half this, 205μ. The position of the reflected image can be calculated by taking the focal point of the lens as the virtual object of the argentea (Text-fig. 3).

Taking the axial focal length of the lens as 1238μ, the value obtained from *in situ* measurements, and the distance from the centre of the lens to the argentea as 375μ, the calculated distance from the argentea to the image is 166μ. If the focal length is taken as 850μ, the value obtained by construction for rays 50μ from the axis of the lens, the image–argentea distance becomes 143μ, which agrees well with the corrected, measured axial distance of 136μ.

DISCUSSION

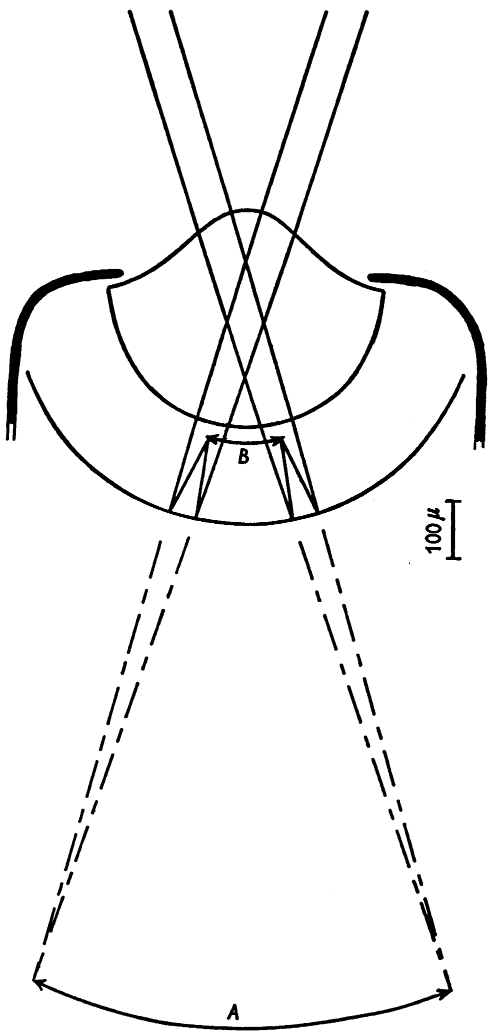
In the eye of *Pecten* a real image is formed by reflexion at the spherical argentea. This image is the only image formed in the eye, and is eligible for consideration as a 'visual' image provided it can be shown that it falls on a photoreceptive region. This is not a reflector designed to increase sensitivity in low light intensities, as in the eyes of some mammals and fishes. In such eyes the visual image is formed by a lens. In *Pecten* the lens alone would form an image well outside the eye. Text-figure 4 is a photograph of a median frozen section of a *Pecten* eye, and Text-fig. 5 is an optical diagram of the same eye, summarizing the results of the optical measurements described in this paper.



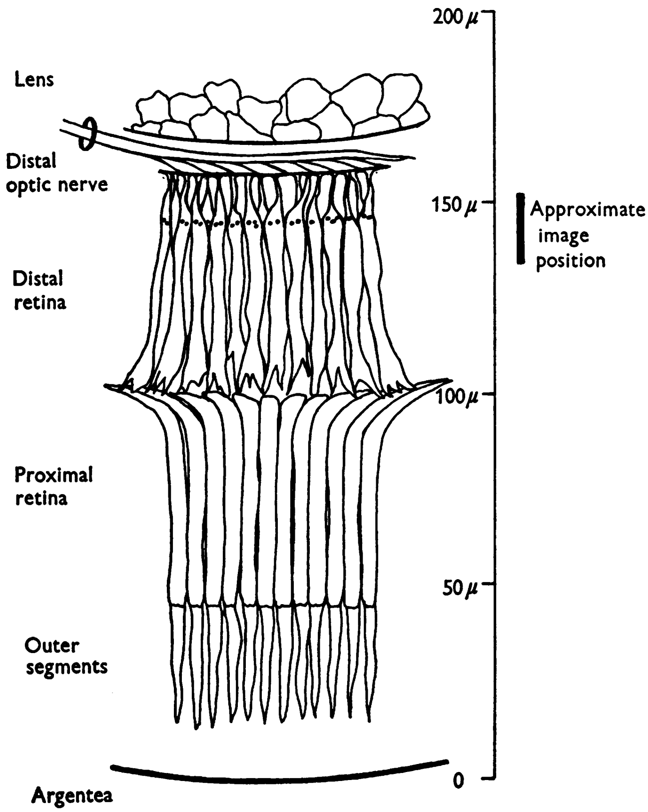
Text-fig. 4. Median frozen section of an eye.

Structure of the retina and position of the image

The retina occupies the whole of the space between the lens and the argentea. It is composed of two main layers of cells. That nearest the argentea, the proximal retina, contains cells which resemble typical photoreceptors in possessing an elongated body, terminating adjacent to the argentea in an 'outer segment'. Dakin (1910) emphasizes that there is no gap between the proximal retina and the argentea. The region of the outer segments is so close to the argentea (10–40μ in front) that there is no image produced or observable in this region. Between the proximal retina and the lens is a second layer of cells, the distal retina. The distal extremities of these cells are drawn out into a number of fine processes which stain deeply with silver techniques. These either synapse with, or are continuous with, the fibres of the distal optic nerve, which runs between the retina and the rear face of the lens. At the roots of these processes there are, in each cell, a number of small bodies, 1–2μ in diameter, which are visible with phase contrast in frozen sections, and in stained preparations. Miller (1958) showed in electron micrographs that these bodies are each derived from several basal bodies and ciliary stalks, coiled into concentric lamellae. It is on the region containing these bodies that the reflected image falls (Text-fig. 6). While neither optical nor histological techniques are adequate to localize the image precisely, the only structures which might have a photoreceptor function, and lie in the region of the plane of the image, are these bodies. The fact that, like the image, the distal retina is roughly spherical and concentric with the argentea suggests that it is capable of receiving a reflected image over its entire area.



Text-fig. 5. Optical diagram of an eye based on the measurements described in the text. *A* is the position of the image produced by the lens, and *B* is the real reflected image in the eye.



Text-fig. 6. Structure of the retina and position of the image. The scale is of axial distance from the argentea, and is based on measurements made on frozen sections.

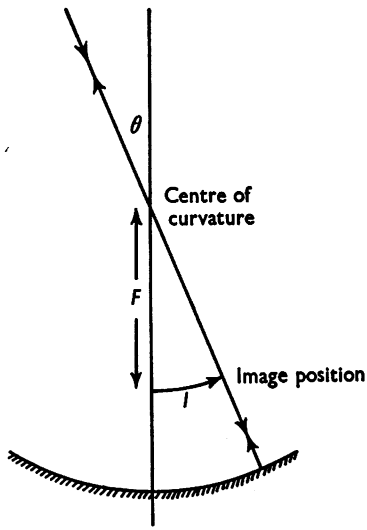
Quality of the image

The eye of *Pecten* is a very efficient light-collecting system. The aperture may be expressed as the *f* number of the system, which is the ratio of the focal length of the system to the diameter of the pupil. The focal length is defined as:

$$\frac{\text{size of image}}{\text{angle in radians subtended at the eye by object at infinity}}.$$

Since, in this case, the angle subtended at the eye by an object at infinity is approximately the same as the angle subtended by its image at the centre of curvature of the argentea, the focal length of the eye is given by the radius of curvature of the argentea minus the image–argentea distance (Text-fig. 7).

For a typical eye this is $410 - 140\mu = 270\mu$. The *f* number of the system is thus $\frac{270}{450} = 0{\cdot}6$. This will be an accurate measure of the ability of the eye to concentrate light on the retina only if the argentea is a perfect reflector. It is, however, a wider aperture than that of any known eye which forms an image with a lens. The best of these, the eyes of fish, have an aperture of about f 0·8. A spherical mirror of such large aperture, however, has a great deal of spherical aberration, and hence poor resolution. Ignoring the effect of the lens, the image of a point object produced by the mirror alone would be, not a point, but a circle of confusion, whose diameter is a function of the aperture of the mirror. In this case the diameter of the circle of confusion, constructed geometrically, is about 25μ. The packing distance of the cells of the distal retina is only about 5μ in the centre, and 10μ towards the edges. Thus, if the eye were a simple uncorrected mirror system,



Text-fig. 7. Focal length of the eye. Focal length $= I/\theta$ (radians) $= F$.

one might expect its visual resolution to be limited by the quality of the image rather than by the 'grain' of the retina. A parabolic argentea would improve the image axially, but this does not appear to be the case either in life or on sections of the eye. Furthermore, the field of vision of each eye, i.e. the angle at the eye over which an image is formed on the retina, is large. When reconstructed on frozen sections this comes to 90–100°, which agrees with the estimate of von Buddenbrock & Moller-Racke (1953) of 90–110° from behavioural observations on *P. jacobaeus*, a closely related species. A parabolic mirror would be useless over so wide an angle, as the image of points more than a few degrees off the axis would be worse than with a spherical mirror.

The possibility was considered that the lens of *Pecten* has the function of correcting for the spherical aberration of the argentea. A biconvex lens where both faces are spherical would worsen rather than improve the resolution, as both it and the mirror would produce spherical aberration in the same direction. However, while the rear face of the *Pecten* lens is hemispherical, the front face is rather curious. Its appearance is shown on the tracing of a section in Text-fig. 8, which is fairly typical of lenses as they appear in life.

It is possible to construct for the eye of *Pecten* a lens that will correct at least the axial spherical aberration of the argentea. Making the assumptions that:

(*a*) the refractive index of the lens is 1·42, and uniform throughout;

(*b*) the back of the lens is hemispherical;

a front profile for the lens can be constructed such that rays drawn from an axial point on the image would emerge as a parallel beam. Text-figure 9 shows such a construction. The radii of curvature of the argentea and the rear face of the lens are taken from Text-fig. 8.

The shape of the constructed front face corresponds well with the actual shape. In particular three features are common to all such constructions and all actual lenses.

(i) The greatest curvature is in the centre of the lens.

(ii) There is a nearly uniform slope from the central region of the lens to just inside the periphery.

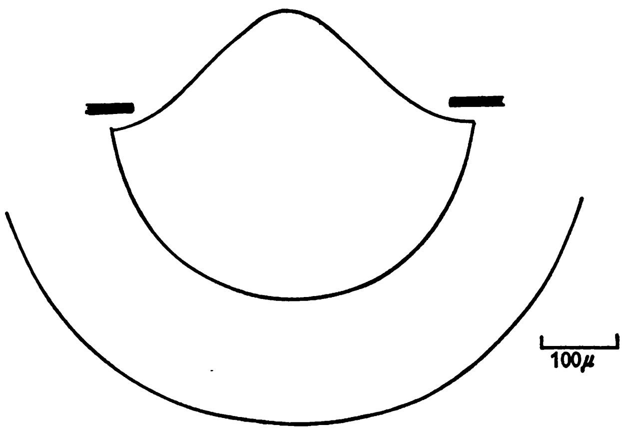
(iii) In constructed lenses the sign of the curvature changes abruptly about 50μ from the periphery. In real lenses this region is covered by the iris, and is flat.

If the refractive index, or the image position, is changed slightly in drawing the constructions, the central curvature of the front face is altered, but the shape as defined by the three features above is not affected. In Text-fig. 9 a slightly better match would have been obtained by taking the refractive index as 1·43. With a lens acting in the manner suggested, the angular resolution in the axial part of the image could approach the minimum value given approximately by $1{\cdot}2\lambda/D$, where D is the diameter of the pupil. The diameter of the Airy disk on the retina would be less than a micron. The improvement in definition will be limited to the central region of the retina, the image at the edges being no better than it would be with an 'uncorrected' mirror.

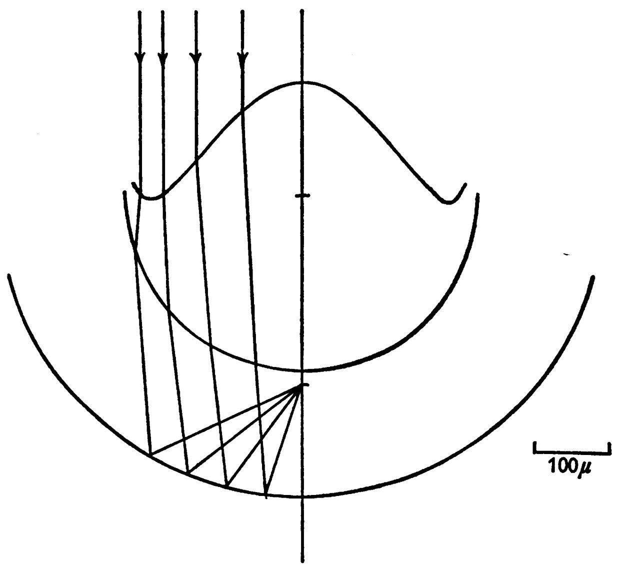
Action of the retina

Hartline (1938) recorded a response in the distal branch of the optic nerve of *Pecten irradians* to cessation of illumination. An 'on' response, continuing during the period of illumination, was recorded from the proximal branch. Hartline, however, was illuminating the whole retina. If the cells of the distal retina do initiate the 'off' response, it is possible that a response limited to a small area of the retina might be produced by a dark image on that part of the retina. The presence of a dark moving object in the environment could produce a series of responses as its image crossed successive cells of the distal retina. It has been shown many times that the whole animal reacts, by closing, to the presence of moving objects, light or dark. The 'off' response could be the basis of movement perception.

One qualification to this suggestion is that, light having already passed through the retina once, the reflected image of a small dark object can



Text-fig. 8. Tracing of a median section of a typical lens.



Text-fig. 9. Construction of a lens producing no axial spherical aberration of the image formed by reflexion at the argentea.

only reduce the light intensity on the distal cells to one half that on the cells on which no dark image falls. There is no evidence that the distal receptors are in any way shielded from light on its first passage through the retina. The cells would have to be able to produce a response to quite small changes of light intensity. My own observations (unpublished) indicate that slight dimming of the light incident on the whole eye does produce a short duration response in the optic nerve. Von Buddenbrock & Moller-Racke (1953) showed that *P. varius* responded by closing to a reduction of light intensity of 0·3 %: three other species were rather less sensitive.

In a system such as this resolution would be important, as the contrast between light and dark regions of the image is already reduced by the nature of the system. A poorly resolved dark spot would be indistinguishable on a poorly resolved light background. Fine resolution is probably limited to the central region of each retina, and this may partly account for the fact that *Pecten* has a large number of eyes (about 60 in *P. maximus*) to cover about 300 degrees.

The function of the proximal retina is less clear, but in the absence of a resolved image it may function as a monitor of light intensity. Interaction between the two retinae is clearly a possibility.

SUMMARY

1. The optical system of the eye of *Pecten* was investigated by measuring the focal length of the lens and the radius of curvature of the reflecting back of the eye.

2. The image visible in the eye is produced by reflexion at the back of the eye. The lens by itself does not produce an image in the eye.

3. The reflected image falls on the distal receptor cells of the retina. There is no image on the proximal retina.

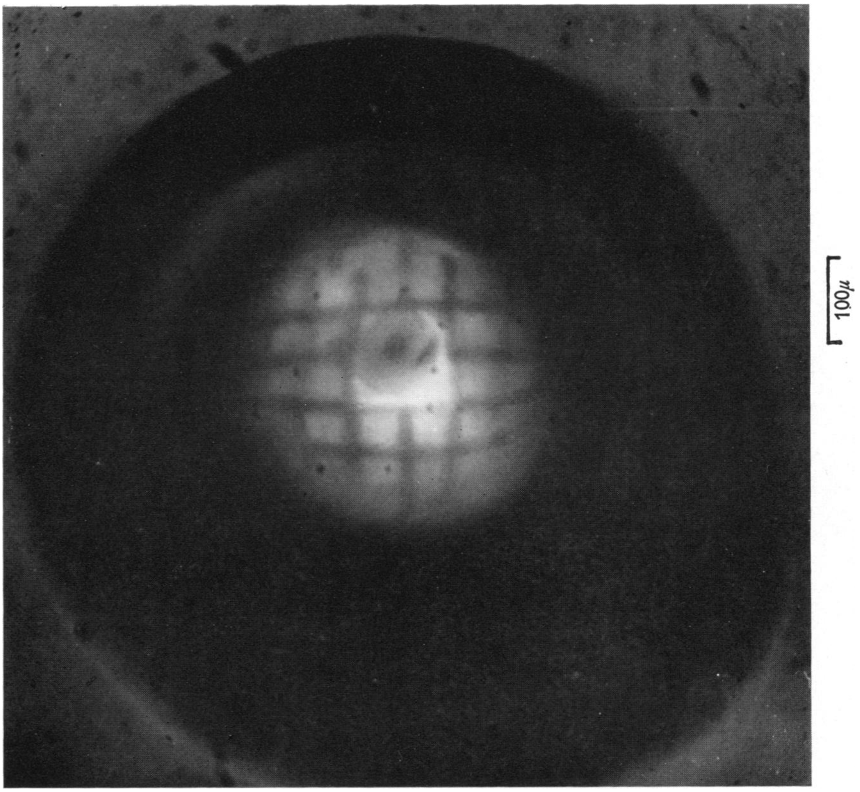
4. The possibility of the lens correcting the spherical aberration of the reflector was considered.

5. The aperture of the eye is *f* 0·6, and the field of view is 90–100°.

6. The lens is of uniform consistency. Its refractive index is 1·42.

My thanks are due to Professor J. A. B. Gray for encouragement and guidance throughout the work, and to Professor A. F. Huxley for advice on optical problems. I am in receipt of a Medical Research Council grant for training in research.

The Journal of Physiology, Vol. 179, *No.* 1 Plate 1



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REFERENCES

BUDDENBROCK, W. VON & MOLLER-RACKE, I. (1953). Über den Lichtsinn von *Pecten* *Pubbl. zool. Staz. Napoli*, **24**, 217–245.

DAKIN, W. J. (1910). The eye of *Pecten*. *Quart. J. micr. Sci.* **55**, 49–112.

HARTLINE, H. K. (1938). The discharge of impulses in the optic nerve of *Pecten*, in response to illumination of the eye. *J. cell. comp. Physiol.* **11**, 465–477.

MILLER, W. H. (1958). Derivatives of cilia in the distal sense cells of the retina of *Pecten*. *J. biophys. biochem. Cytol.* **4**, 227–228.

PATTEN, W. (1886). Eyes of molluscs and arthropods. *Pubbl. zool. Staz. Napoli*, **6**, 542–756.

EXPLANATION OF PLATE

PLATE 1

Reflected image of a grid photographed in the pupil of an eye. The object grid was 1·5 cm from the eye. The lines were 1 mm wide, and 3 mm apart.