PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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N. A. Locket

Phil. Trans. R. Soc. Lond. B 2000 **355**, 1167-1169
doi: 10.1098/rstb.2000.0660

THE ROYAL SOCIETY

doi 10.1098/rstb.2000.0660

On the lens pad of *Benthalbella infans*, a scopelarchid deep-sea teleost

N. A. Locket

Department of Anatomical Sciences, University of Adelaide, South Australia 5005, Australia (*adam.locket@adelaide.edu.au*)

The tubular eye of scopelarchids contains a lens pad, derived from cornea, lateral to the lens and opposite a gap in the iris. The pad, transparent in life, is formed of optically dense lamellae arranged at *ca.* 45° to the sagittal plane of the fish. The lamellae are *ca.* 155 nm thick, separated by *ca.* 185 nm. The pad does not deviate light passing normally through the lamellae, but does deviate light at an acute angle to the lamellae unequally through *ca.* 40°, converting a spot to a streak. Light from *ca.* 20° to the vertical below the fish will be projected onto the accessory retina of the dorsally pointing tubular eyes. The pad also disperses white light, blue light *ca.* 34° and red light *ca.* 44°. The deviation of light from below may enable the fish to detect predators below, and the dispersion may play a role in breaking camouflage by spreading photophore light over an area of retina.

Keywords: lens pad; optics; deviation; dispersion; camouflage breaking

1. INTRODUCTION

The scopelarchid fishes, like many other deep-sea taxa, have tubular eyes, in which the main visual axis is directed upwards, at least in adults. The lens is large with respect to the eyecup, and the retina divided into two main portions, a main retina in the ventral part of the cup, and an accessory retina lining the medial wall and extending anteriorly and posteriorly. The two portions of retina, separated from each other by the choroidal fissure, have different structures. The main retina is complex, and itself subdivided into regions with differing structures (Locket 1971; Collin *et al.* 1998), which will not be considered further here. The accessory retina is simpler in structure, but like part of the main retina contains receptor groups set in reflective pits and thus optically isolated from each other. The main retina is located at the focal distance from the lens, i.e. it conforms to Matthiessen's ratio (Matthiessen 1880), but the accessory retina is at varying distances from the lens, and dorsally they almost touch. Thus the accessory retina will not receive a focused image, so a function in resolution is unlikely.

Unlike most tubular-eyed fishes, the scopelarchids have a structure in the eye called the 'Linsenpolster' by Brauer (1908), usually translated as lens pad. The pad, drawn by Brauer, lies between the ventrolateral part of the cornea and the lens, opposite a dip in the iris forming the lateral wall of the eyecup (figures 1 and 2). The deep surface of the pad is close to the lens, but the superficial surface is separated from the dense cornea by some tissue which Brauer believed to be unstriated muscle. The striated appearance of the pad in transverse section led Brauer to suggest that it is composed of fibres; these were shown by Locket (1977) to be lamellae. The pad in life is transparent, as reported to the author by M. V. Angel (personal communication), but in preserved material the transparency is usually lost, and the pad then looks pearly. This led to the name pearleye for the scopelarchid fishes and to the erroneous suggestion that it might be a light organ.

An illustrated description of the pad, and suggestions on its function, were given by Locket (1977). A summary of these findings follows. The pad in the intact eye is roughly elliptical, and is deeper beneath the corneal surface ventrally than it is dorsally. When transparent it is visibly optically denser than surrounding tissues, and from some angles shows iridescent reflections. In sections the pad is convex laterally, and less so medially; the outer third of the pad stains less darkly than the rest, and the whole appears finely striated, the striae in the dark part being parallel and running inferolaterally, at *ca.* 55° to the plane of the pad. Measured from a scale drawing, they lie at an angle of *ca.* 43° to the sagittal plane of the fish. The striae in the paler part are directed approximately along the radii of the lens.

2. METHODS AND RESULTS

Electron microscopy showed that the pad of *Benthalbella infans* is derived from the cornea. The corneal endothelium and Desçemet's membrane are continuous from the normal cornea dorsally over the deep surface of the pad. The pale-staining tissue lateral to the pad ventrally, which Brauer believed to be muscle, is composed of collagen fibres loosely disposed in a matrix, and lies against the deep surface of the stroma proper. This has the usual structure of corneal stroma; fibres of uniform size and separation arranged in layers at large angles to each other. A layer of keratocytes between diffuse and compact cornea resembles at first sight an epithelium, but is not associated with a basement membrane.

Lateral to Desçemet's membrane of the pad is a layer of cells that lie against the membrane, but amongst which are others that align with the lamellae of the pad

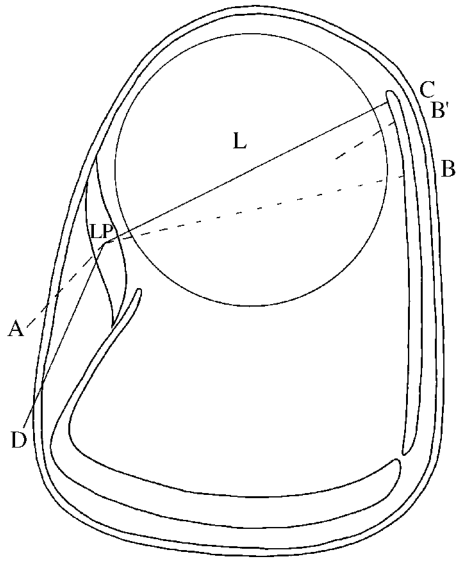

Figure 1. Diagram of a transverse section of the *Benthalbella* eye. Light from A would be deviated by the lens pad, LP, to B on the accessory retina, were it not for the lens, L. The lens would deviate the ray to B′. Tracing back, light arriving at the top of the accessory retina, C, and passing through the centre of the lens, would have been deviated from D, about 26° from the vertical below the fish. See § 2 for further discussion.

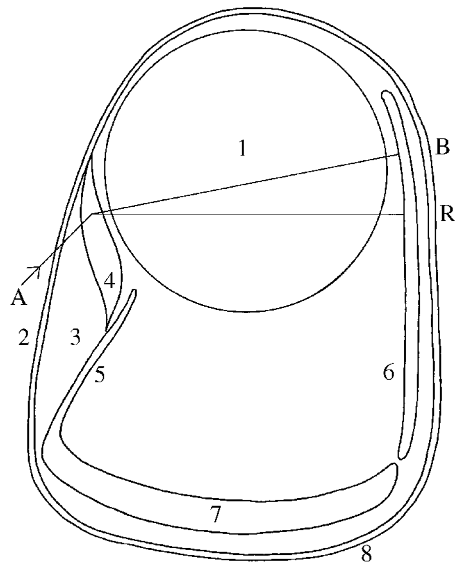

Figure 2. To show dispersion. White light from A is dispersed through about 10°. In the absence of the lens, blue would be projected to B, and red to R. The effect of the lens will be to reduce this separation. 1, lens; 2, compact cornea; 3, diffuse cornea; 4, lens pad; 5, iris; 6, accessory retina; 7, main retina; 8, sclera.

substance. The edges of these flat cells are of normal staining properties, abut the deep margins of the dense lamellae, and give the impression that they become transformed into lamellae as they grow superficially. The dense lamellae themselves are mostly of very even thickness and separation, interrupted in places by local dilatations of a central membrane-bounded space, probably representing endoplasmic reticulum. The lamellae are separated by pale-staining amorphous material; measurements of the thickness of lamellae and spaces are 155 and 184 nm, respectively, the lamella plus space average being 339 nm, and half this *ca.* 170 nm.

The lateral third of the pad is formed by flattened cells like those of the dense part, but pale-staining like those beneath Desçemet's membrane. These cells are in a parallel array like the dark ones, which they abut edge to edge; these abutments occupy a zone *ca.* 40 μm thick. The outer ends of the pale cells abut the layer of keratocytes marking the inner surface of the diffuse cornea, which send short flat processes between the lamellar cells in places. There is no basement membrane between the keratocytes and lamellar cells.

The findings summarized above were made on a lens pad observed and fixed at sea by the author. The fresh fish was manipulated while immersed in a dish of seawater, and observed with an ophthalmoscope through the surface. Attempts were made to obtain a clear view of the retina, and observations made on the directions from which a reflex could be obtained, and the colours of such reflexes. A further fixed eye of *B. infans*, in which the lens pad had remained transparent, was kindly made available by S. P. Collin (Department of Anatomical Sciences, The University of Queensland). The eye was drawn and measured, and the lens pad excised. The optics were investigated by suspending the pad in a cell containing buffer, a beam of light, white, or red from a laser, being directed through it and observed on the far end of the cell, which was of finely ground glass. An image of an illuminated pinhole was focused on the pad by a convex lens. The image on the ground glass was viewed and the location of the beam under different conditions measured. Measuring the distance of the pad from the screen enabled angles of deviation and dispersion to be obtained. The pad was turned with respect to the beam to simulate light coming from above or below the horizontal in the intact fish.

The appearance of the fresh lens pad depends on the point from which it is illuminated and viewed, but it always appears to be optically dense, unlike the tissue between it and the corneal stroma proper. Seen from laterally in the intact eye and illuminated from above the pad gives an orange reflection, the colour not changing with the angle of illumination. The orange disappears if the lens, but not the pad, is shaded. If the light is from antero- or posterosuperior, the orange is absent and the pad looks transparent. Illuminated from above and viewed from *ca.* 30° above the horizontal, a narrow vertical strip of iridescent colours appears. From above moving downwards these are; green, yellow, orange, red, blue, unsaturated blue and unsaturated green. Viewed from below the horizontal, the pad is transparent, without colours. Ophthalmoscopy gives a blue to blue-green reflex viewing from below the horizontal, which is extinguished as the horizontal is approached. This reflex comes from the accessory retina; that from the main retina viewed from above through the lens alone is orange.

Ophthalmoscopy had shown that light is deviated by the pad when striking it from below the horizontal, but not when coming from above, though transmitted in both cases. To test this, further experiments with the isolated pad were performed. A beam from above the horizontal was deviated little if at all, but was diffused to some extent, forming a larger spot on the screen than was present without the pad. From below the horizontal the results were markedly different. Laser light striking the pad from 40° below the horizontal was deviated downwards through about 40° and additionally drawn out into a streak. With white light, marked dispersion into a spectrum was also seen, the angle of dispersion between blue and red being about 10°, blue being deviated 34° and red 44°. This degree of dispersion would, in the absence of the lens, give a spread from blue to red that would cover some 35 receptor groups in the eye examined; the spread will be lessened to some extent by convergence through the lens (figure 1).

3. DISCUSSION

The nature and function of the lens pad has aroused interest since Brauer's first description of it, and several functions have been assigned to it on the basis of what was known at the time. We can now comment on the effect of the pad on light passing through it, though it is less clear what the fish makes of these effects. The deviation of a beam from below the horizontal enables light that would not otherwise be received to reach the upper part of the accessory retina. This may enable the fish to detect luminous objects to within *ca.* 20° of the vertical below it, helpful perhaps in avoiding predators. The spreading of a point source into a streak will mean that unfocused light from such a source will be projected onto a vertical band of accessory retina, not in focus, but containing grouped receptors. These may well function as 'macro-receptors', in which the individual receptors do not function singly, being optically coupled by the reflecting pit in which they are located (Locket 1971, 1977; Collin *et al.* 1998). The point-to-streak conversion will mean that a luminous point inferolateral to the fish will be strongly signalled as to the horizontal meridian, but with little resolution in the vertical meridian.

In the deep mesopelagic to bathypelagic depths in which the fish lives, there is little if any ambient light, and any there is will be virtually monochromatic. Under these conditions the marked dispersion may be of little importance. If, however, a potential prey object or predator has photophores with a different or wider waveband than ambient, the dispersion may cause the different wavelengths to be projected onto different areas of retina, of potential importance in breaking camouflage.

The occurrence of structural colours due to thin film interference are well known, and the optics well explained by Land (1981). Usually the colours appear on reflection, but in the present case, though iridescent reflections are visible, the more pronounced effect is in transmitted light. Another example of this phenomenon occurs in the photophores of euphausiids (Herring & Locket 1978), in which cylindrical lamellar structures act to direct light from the luminous tissue in a particular direction. The lamellar structure in a single plane shown by the lens pad and acting like a transmission diffraction grating is a further intriguing example of biological optics.

REFERENCES

Brauer, A. 1908 Die Tiefseefische. Part II. *Anatomische Teil. Wiss. Ergebn. Dtsch. Tiefsee Exped. Valdivia* **15**, 2–432.

Collin, S. P., Hoskins, R. V. & Partridge, J. C. 1998 Seven retinal specializations in the tubular eye of the deep-sea pearleye, *Scopelarchus michaelsarsi*: a case study in visual optimization. *Brain Behav. Evol.* **51**, 291–314.

Herring, P. J. & Locket, N. A. 1978 The luminescence and photophores of euphausiid crustaceans. *J. Zool.* **186**, 431–462.

Land, M. F. 1981 Optics and vision in invertebrates. In *Handbook of sensory physiology*, VII/6B (ed. H. Autrum), pp. 471–592. New York: Springer.

Locket, N. A. 1971 Retinal anatomy in some scopelarchid deep-sea fishes. *Proc. R. Soc. Lond.* B **178**, 161–184.

Locket, N. A. 1977 Adaptations to the deep-sea environment. In *Handbook of sensory physiology*, VII/5 (ed. F. Crescitelli), pp. 67–192. New York: Springer.

Matthiessen, L. 1880 Untersuchungen über dem aplanatismus und die Periskopie der Kristallinsen in den Augen der Fische. *Pflüger's Arch. Ges. Physiol.* **21**, 287–307.