The Physiological Optics of a Nocturnal Semi-Aquatic Spider, *Dolomedes aquaticus* (Pisauridae)

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The optics of the posterior eyes of the amphibious spider, *Dolomedes aquaticus*, are described. The lenses have strongly-curved spherical front and rear surfaces, and therefore, a fairly high light capturing ability — they have *F*-numbers of 0.9 — yet, the large amount of spherical aberration predicted by their shape is mostly corrected. The receptive segments of the receptors are arranged in rows, each row separated by pigmented glial cells, but within a row, rhabdomeres from neighbouring cells are contiguous so that coupling between cells from the same row seems a possible way of increasing absolute sensitivity for night vision. When the spider submerges, an air-layer is held over the corneal surfaces — as with a diver's face mask — so that light is focused on to the receptive layer of the retina under water as well as above. These features are considered as adaptations for the nocturnal and semi-aquatic habits of the spider.

Introduction

Dolomedes aquaticus is from a genus of large robust hunting spiders found mostly near areas of water. The behaviour of this species, and of two others from New Zealand, has been described previously [1]. During the day it conceals itself beneath boulders or debris, and at night comes out to wait for prey, generally at the water's edge; it rests its front legs on the water surface and holds on to the shore with the others. When disturbed, it usually ducks under the water surface to escape. Little use of vision seems to be made in predation, but escape can be elicited solely by visual stimuli [1].

This paper examines some optical properties of the rather large posterior eyes of *D. aquaticus* (up to 0.5 mm in diameter; *cf.* 1.4 mm, that of probably the largest single-lens eye of any land invertebrate [2]), and pays particular attention to the adaptive problems associated with nocturnal and amphibious habits. The first requires high absolute sensitivity, and the second, the ability of an eye to focus light close to the receptive layer of its retina in two media of different refractive indices — penguins, for example, have a flattened cornea to do this [3].

Materials and Methods

Adult *Dolomedes aquaticus* (Goyen) females were collected from an open, stony creek-bed in the Kaituna Valley, Banks Peninsula, New Zealand. For consistency, data were obtained only from spiders with carapace length 8 – 9 mm. Values for the dimensions of the spiders' posterior eyes were gathered from a combination of anaesthetised animals, photographs of live animals, fresh dissections under saline (0.9% NaCl), and histological preparations. For histology, eyes of daylight-adapted spiders were fixed for 1 h in 2.5% glutaraldehyde in 0.1 M cacodylate buffer (pH ∼7.3) with 0.14 M sucrose and 2 mM $CaCl_2$, and post-fixed in 1% OsO_4 in the same buffer for 1.5 h. After slow dehydration through a graded alcohol series, specimens were embedded in Araldite. Sections (2 – 3 μm) were stained with toluidine blue for light microscopy. Focal length values were obtained directly from the magnification of an object observed through a lens suspended by a drop of saline on a coverslip beneath a microscope (*i. e.* in the "hanging-drop" situation [4]). Approximately,

$$f = (I/O)\,U$$

where I and O are the sizes of image and object respectively, and U, is a large object distance. f is the front focal length (= posterior nodal distance).

Results and Discussion

Lens

The arrangement of the eyes of *Dolomedes* is shown in Fig. 1. The posterior median (PM) and posterior (PL) eyes are indentical expect for their dif-

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Fig. 1. Photograph of the ocular area of an adult female *Dolomedes aquaticus*. The posterior eyes are in a slightly recurved row above the smaller anterior eyes. The PL eyes are surrounded by long hairs, and face to the side and above the spider. Scale marker = 0.5 mm.

ferent orientation; both have corneal diameters of 0.4 mm, compared to 0.25 mm for each of the four anterior eyes. Enlarged photographs of profiles of the corneal surface and the back of the lens show that each has a spherical curvature in all planes, the latter being fully hemispherical; radii of curvature were 227 and 160 μm, respectively, accurate to about 10%. A scale optical diagram is given in Fig. 2.

With lenses in the "hanging-drop", and using a microscope objective of numerical aperture (NA) 0.08 (semi-angle 6° in water) so as to include only paraxial rays, the size of the best-focus image (on the optical axis) of a 20 mm square at a distance of 125 mm was 55.3 to 59.2 μm (range for 8 eyes). Therefore, the front focal length in air (f_a) is 346 to 370 μm (mean 355 μm). Direct measurement of the position of the image behind the back of the lens (l_a) gave a real distance of about 213 μm. When the object space was filled with water so that the cornea was wet, hence possibly simulating the optical conditions that occur when the spider submerges, image sizes were 68.9 to 77.6 μm (range for 8 eyes), giving a focal length in water (f_w) of 431 to 485 μm (mean 470 μm). The distance of the best-focus image from the back of the lens (l_w) was about 318 μm.

The most useful measure of the ability of a lens to gather light from an extended field can be obtained from the posterior nodal distance/entrance

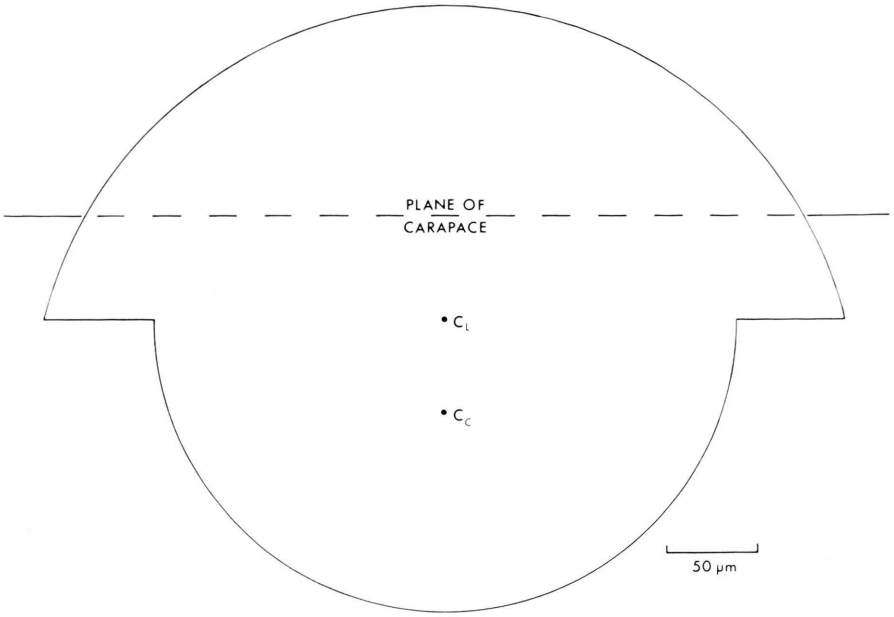

Fig. 2. Scale optical diagram of a posterior eye lens of *Dolomedes aquaticus* (carapace length 8–9 mm). The rear lens and corneal surfaces have spherical curvatures with radii 160 and 227 µm and centres about 50 µm apart at C_L and C_C, respectively. The rear of the lens is fully hemispherical. "Plane of carapace" represents the external extremity of the surrounding carapace.

pupil diameter; that is, the *F-number*, using the front focal length. The illuminance of the retina from a field of given luminance is proportional to $1/(F\text{-number})^2$. For a posterior eye of *Dolomedes*, with front face in air, and assuming that the corneal diameter corresponds to the entrance pupil diameter, the *F*-number is near 0.9. This compares to 2.1 for a relaxed human eye (front focal length 17 mm [5] and a fully dilated pupil of 8 mm). Therefore, under the same lighting conditions, a lens of *Dolomedes* would illuminate its retina $5^1/_2$ times better than that of a human eye.

The strongly-curved spherical front and rear profiles would give the lens its high power, but in addition imply that it should suffer from spherical aberration. If the lens is assumed homogeneous, its refractive index (n) can be calculated from the thick-lens formula for the distance, l, where

$$-l_{\mathrm{a}} = \frac{1.33\, r_2([n\, r_1/(n-1)]-d)}{n\, r_2-(n-1.33)\,([n\, r_1/(n-1)]-d)}\,^{*} \qquad [6]$$

for a lens with front surface in air and rear in water. Using the measured values for l_{a}, r_1, r_2, and d (Fig. 2), n thus equals 1.54, and the degree of spherical aberration can be predicted by graphical ray tracing (Fig. 3). Such spherical aberration is not observed. When using objectives of increasing NA in the "hanging-drop", the quality and position of the best-focus image was found to change little: values for f_{a} with objectives whose NAs were 0.08, 0.25, 0.32 and 0.75, were 350, 348, 370 and 352 µm, respectively. In addition, with an objective of NA 0.75, a distant point source was focused to an only slightly distorted shape, less than a maximum of 20 µm across, instead of a blur circle of 65 µm diameter as predicted by Fig. 3.

The actual defects of the point source image are probably due to minor irregularities in the dioptric system, possibly due in part to damage either during or after dissection. If image quality is limited by diffraction, the Airy disc should have a dark ring whose diameter is $2.44\,\lambda\, f_{\mathrm{a}}/\text{aperture}$ [6], *i. e.* only about 1 µm in diameter for green light. As it is, the partial correction of spherical aberration which is achieved provides an image of sufficient quality to match the receptor size (see below).

Spherical aberration is probably corrected by the lens being non-homogeneous. This was suggested for the lenses of the PM eyes of the spider, *Dinopis*, a nocturnal visual predator, which have both their rear and corneal faces fully hemispherical and *F*-numbers of 0.58 [2]. Blest and Land [2] showed that they have a double structure with a front element of lower refractive index and an inner spherical lens, and

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* r_1 and r_2 are the radii of curvature of the front and rear faces of the lens, respectively, and d its thickness. Signs are according to Cartesian convention with light entering from the left; therefore r_2 and l_{a} are negative.

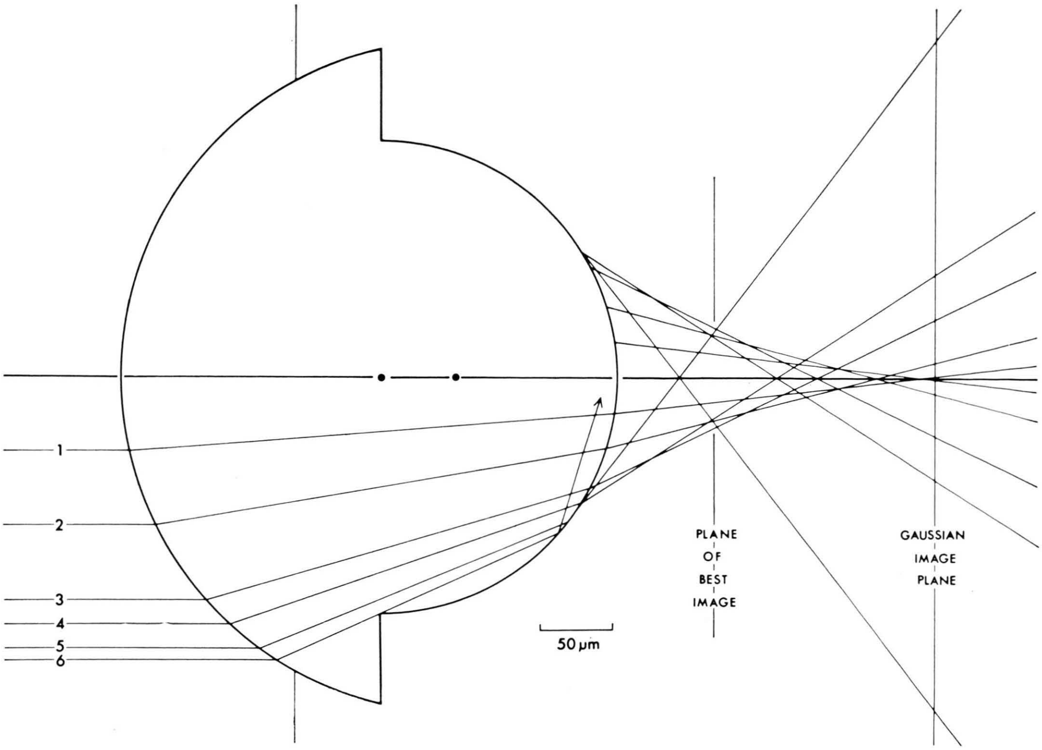


Fig. 3. Graphical construction of rays of light parallel to axis through a lens of the shape that was deduced for a posterior eye of *Dolomedes aquaticus*, and of a uniform refractive index of 1.54. Ray 6 is totally internally reflected, since it meets the rear interface at 65 °, compared to the critical angle of 59.7 °. Ray 5 meets the rear face of the lens at the critical angle and therefore exits at right angles to it, intersecting the optical axis a mere 36 µm behind the lens. It meets the caustic 63 µm behind the lens, where a "circle of least confusion", the best-focus image of a point source, is found [7]; it is 65 µm in diameter. Paraxial rays focus close to the Gaussian image plane, which was found by direct measurement using an objective of NA 0.08 in the "hanging drop" (see text) 213 µm behind the back of the lens.

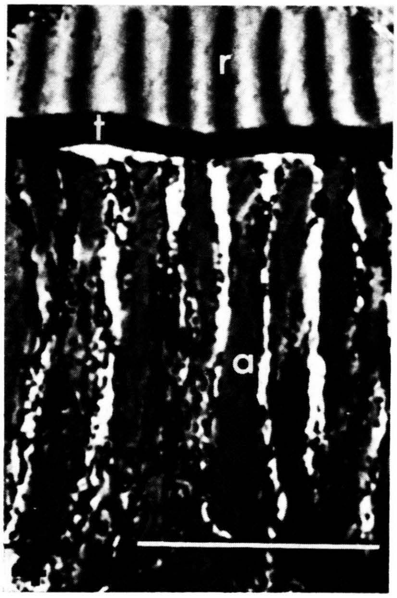
proposed, as the only possible theoretical solution, that the latter is constructed like a fish-lens: that is, non-homogeneously in such a way that the refractive index decreases from centre to periphery.

It is relevant that spherical aberration is not inherent in the posterior eyes of *Dolomedes*, since it shows that this defect is also corrected in more modest spider eyes and not merely a specific adaptation by the extremely specialized PM eyes of *Dinopis*. A means for correcting spherical aberration, however, is only necessary in nocturnal spiders, which have lenses with strongly-curved surfaces to increase their light capturing ability. In the diurnal Salticid spider, *Metaphiddipus*, the anterior median eyes have spherical lens surfaces with large radii of curvature relative to eye diameter. Consequently, there is only little deviation between a wavefront of light and their surfaces, which would cause only minor spherical aberration. The receptor spacing (a mere 1.7 µm – *cf.* 27 µm for *Dolomedes*) matches the limit of lens performance that this predicted spherical aberration would impose [8], implying that it is not corrected.

Retina

The gross arrangement of the retinal components of *Dolomedes* has been described by Homann [9] and Blest and Day [10.] Each receptor cell soma gives rise to a receptive segment whose rhabdomere is seated on a strip of tapetum; there is a swollen intermediate segment proximal to the tapetum [10] (Fig. 4).

The retinae are not hemispherical; in dissection they appear trough-shaped and measure about 950 µm in length and 400 µm wide. A central pigment layer runs lengthwise, bisecting each retina. Within each half, the receptive segments are aligned to form a strand which is continuous and folded back and forth on itself, so they effectively lie in two columns of parallel rows (Fig. 5). Each row, about



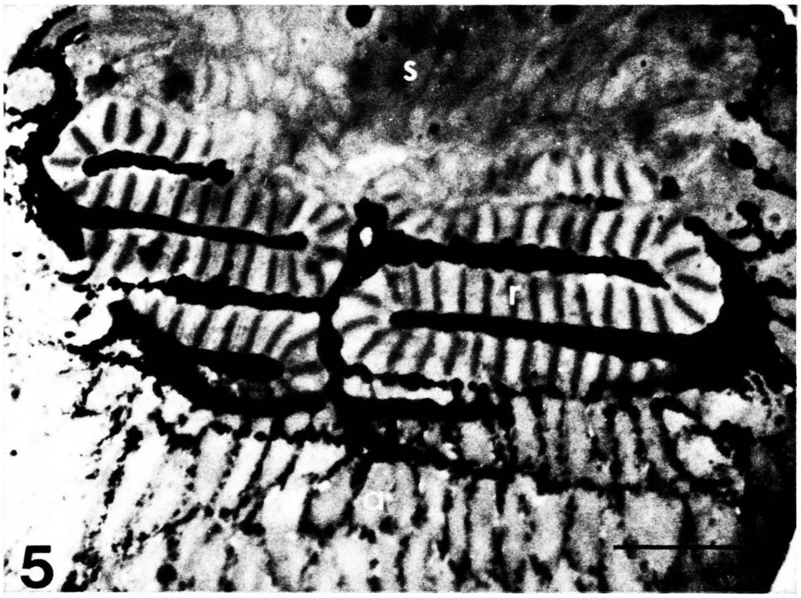


Fig. 4. Longitudinal section of part of a row of receptive segments (r) seated on a tapetal strip (t). Swollen intermediate axons (a) extend below the tapetum. Scale marker = 50 μm.

Fig. 5. Part of a sagittal section through the retina of a posterior eye showing receptive segments (r) in near transverse section. Within each half of the retina, they are arranged in a continuous strand which is folded back and forth on itself along the length of the retina, so that they effectively lie in two columns of parallel rows. Successively deeper elements appear from top to bottom. s, area of cell somata; a, swollen intermediate axons. Scale marker = 50 μm.

20 μm wide, is optically insulated along most of its length by a 7 μm wide row of pigmented glial cell processes, but the receptive segments within each row are not. Thus, each receptive segment contains two rhabdomeres derived from opposite faces of their cells and separated by cytoplasm [10], so that a single darkly-stained "unit" in Figs. 4 and 5 represents two continuous rhabdomeres from adjacent receptive segments. Retinae from the PM and PL eyes differ only in the orientation of their receptive segment rows (Fig. 6).

In the phylogenetically close Lycosid spiders, the retina is arranged similarly, although in the diurnal genus *Lycosa* there is some pigment, especially proximally, also between receptor cells in the same row, thus providing total optical isolation of individual receptive segments [11]. By contrast, the retinal arrangement of nocturnal Lycosids is exactly like *Dolomedes* with pigment only between receptor rows [12]. This arrangement allows the possibility of one ray of light passing through and being absorbed by more than one photoreceptor (the extent of this depends on the accuracy of tapetal reflection), and electrical coupling between adjacent receptors in the same row. Either could increase absolute sensitivity in these nocturnal spiders, albeit at the expense of resolution. But, at least in *Dolomedes,* resolution would not be lost along the length of the retina (*i. e.* perpendicular to the receptive segment rows): the lens is capable of focusing light from a distant point source on to an area of diameter less than the width of one receptive segment row, thus each row receives light from a unique angle of object space. One row subtends an angle of $20/f_{\mathrm{a}}$ rad, or 3.2°, at the posterior nodal point, and therefore in object space. The receptor row spacing is $27/f_{\mathrm{a}}$, or 4.4°. This is the case for both day and night adapted retinae, since the receptive segments do not change their cross sectional dimensions under natural lighting conditions [10].

An angle of 4.4° would not allow resolution of fine spatial detail by the standards of diurnal eyes, but it is feasible that the posterior eyes of *Dolomedes* might operate as movement detectors with orientational selectivity, functional at night, and maximally able to detect movement along the longer axis of their retinae. The PM eyes should be more sensitive to movement in the longitudinal axis of the spider's body, while the PL eyes, whose retinae are orientated differently (Fig. 6), should detect movement along more lateral axes best. Behavioural observations in fact show that *Dolomedes* will flee in visual response to the overhead movement of a large object, such as one's hand [1]. With these retinae, combined with high light-capturing lenses, birds, which are probably the main predators of *Dolomedes (Dolomedes* sp. have been found in stomach contents of the morepork *(Ninox novaeseelandia)*, a nocturnal bush-dwelling bird of New Zealand [13]), should be detectable as they fly overhead against the night sky.

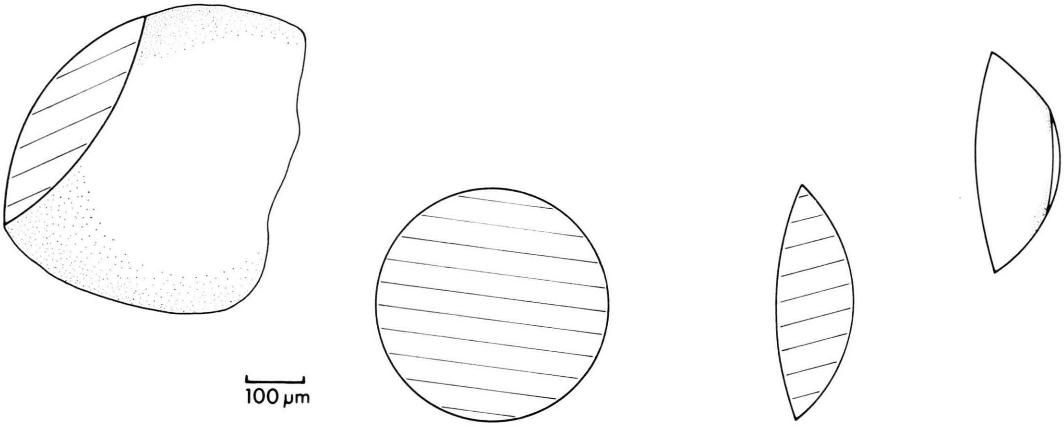


Fig. 6. Diagram of the four posterior eyes viewed slightly to the left of Fig. 1. The black lines represent the orientation of the receptive segment rows or the rows of pigment between them. It is hypothesized that with this retinal arrangement, absolute sensitivity would be increased by inter-receptor coupling, and *Dolomedes* would be able to detect primarily movement above it, thus enabling the perception of potential predators against a night sky.

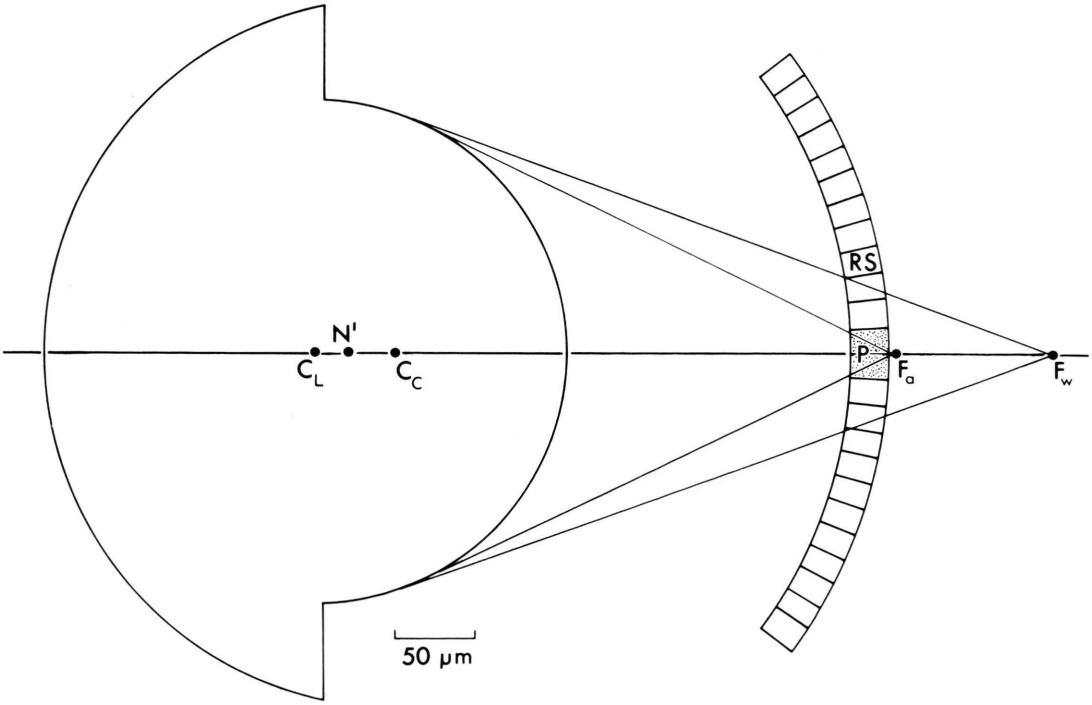


Fig. 7. Diagram of a posterior eye to illustrate the hypermetropia that exists with the cornea wet. The focal point in this situation (F_w) is 105 µm further from the lens, and the position of the posterior nodal point differs little, compared to when the cornea is in air (F_a, N′ respectively). F_a is close to the average position of the receptive segments (RS) found from histology. The receptive segments drawn here constitute a row from both halves of the retina; it is as if the retina has been sectioned widthwise; thus, the only pigment (P) is that of the central pigment layer. C_C and C_L as for Fig. 2.

Vision under-water

The non-hemispherical shape of the retina suggests that all receptors might not be the same distance from the posterior nodal point (N′) of a lens with front surface in air, and that some might be displaced to receive a best-focus image when the cornea was wet, being an optical adaptation to the habit of submerging during escape by the spider. N′, found from f_a and l is approximately 18 μm to the right of C_L with the cornea in air (Fig. 7). Longitudinal sections of eyes that were taken through the centre of the eye and at several different orientations, however, showed that the rhabdomeres of a retina differed in distance from N′ by only 0 – 40 μm, depending on the specimen. Even a 40 μm "displacement", which was in fact probably due to artefactual distortion prior to embedding, is considerably less than half of the displacement expected were the retina fully adapted for amphibious vision: the position of the focal point (*i. e.* pole of focal hemisphere), found by direct measurement *(l)*, was 105 μm further from the lens for a lens with front face in water (F_w) than for a lens with front face in air (F_a), and the position of N′ differs only minimally between the two conditions. The average distance from N′ of the rhabdomeres (which are 25 μm long, although effectively 50 μm because of tapetal reflection) was 325 μm for their distal ends. This compares favourably with f_a (Fig. 7).

Further indication that all rhabdomeres are positioned to receive a best-focus image in air, and none for when the cornea is wet, comes from observations of the retinae in *intact* spiders, which are not subject to inaccuracies from measurements and histological artefacts. In this method, light from orthodromic illumination is reflected back by the tapetal strips to produce an image of the pigment around the receptive segments rows, observable from outside the eye. The pigment rows from all parts of the retina appeared in-focus when the cornea was wet, but none were in-focus when it was in air. If there was any part of the retina displaced for underwater vision, it would not have been in-focus with a wet cornea: its image would focus near infinity. Instead it should have been possible to find a real in-focus image of that part of the retina with the cornea in air.

Since the eyes become so markedly hypermetropic when their corneas are wet, what then happens when the spider submerges? Closer observations of submerged spiders, and examination of carapaces dipped in and out of water in fact showed that *Dolomedes* might not need a displaced retina to focus light underwater, as the corneal surfaces, especially of the PL eyes, often did not get wet. Instead the air layer that adheres to all the body hairs when the spider submerges [1], usually extends over the eyes. Thus it appears that at least the PL eyes, which are well surrounded by long hairs or "eyeashes" (Fig. 1), are able to focus light underwater by effectively using a face-mask as employed by skin divers. This adaptation for amphibious vision has the advantage over a flattened cornea or a displaced retina in that it can be combined with high sensitivity because the refractive power of the cornea is maintained.

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