The evolution and acuity of the schizochroal eye in trilobites

Steven C. Haack
5011 Glade St.
Lincoln, NE 68506

ABSTRACT: The schizochroal eyes of trilobites of the suborder Phacopina consist of arrays of large, optically sophisticated lenses which were probably associated with retinas rather than ommitidia. Arguing from a proposed evolutionary scheme, it is suggested that the lenses were diffraction limited. The resulting estimated resolution is about ten times that of modern compound eyes. The limits imposed by diffraction upon stereoscopic vision are determined and the influence this has upon the evolution of the schizochroal eye is discussed.

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Several characteristics of the schizochroal eye found in trilobites of the suborder Phacopina establish it as unique in the history of life on the planet. Comprised of arrays of large lenses, typically numbering a few hundred, each lens was an individual unit separated from its neighbors by intervening cuticle material. This is unlike the more common holochroal eyes of other trilobites which, like modern compound eyes, had a single corneal membrane covering the entire complex of lenses. Each lens of the schizochroal eye was comprised of two elements of slightly different refractive index which corrected for spherical aberration (Clarkson and Levi-Setti, 1975) and, indeed, rendered a quite respectable image (Towe, 1973). The lens material was largely calcite which was oriented to minimize the effects of birefringence.

It is likely that the holochroal eye of other trilobites operated in a manner like that of the modern compound eye, each lens corresponding to a single ommatidium which registered the level of light coming from the direction immediately surrounding the axis of the lens. The animal then integrated the numerous pieces of data to construct a rough mosaic of its surroundings. While the limit of resolution of the modern compound eye is about one degree, the lenses of the holochroal eyes of trilobites were somewhat larger (30 to 100 μm as opposed to the 8 to 30 μm lenses found in modern arthopods) and their placement upon an eye surface of roughly the same diameter resulted in a resolution of typically 2 or 3 degrees.

Although it has been suggested that the schizochroal eye was also ommitidial (Levi-Setti, 1975, pp. 33–38), with the enormous lenses being an adaptation to darkness (Clarkson, 1975) it seems quite unlikely. Among extant sea creatures, there is no systematic tendency toward larger eyes in dark conditions. Eye reduction or blindness is more often the case. Furthermore, the highest possible resolution would be in the vicinity of 15 degrees, rendering a very low level of information content. This seems unlikely when one considers the sophistication of its design. It has been argued quite convincingly (Campbell, 1975) that the lenses of the schizochroal eye were associated with retinal surfaces like the ocelli found in the larvel eyes of the sawfly and a number of other modern arthropods. The fine images which can actually be produced by some of the beautifully preserved lenses underscores the likelihood of this possibility.

It is proposed here that the schizochroal eye resulted from a unique evolutionary attempt to increase the acuity of vision and that it was, in fact, quite successful.

In the course of the early evolution of sight, the quality of vision rendered by simple ommatidial eyes could have been improved in one of two ways. One would have been to replicate the lens-ommatidia structure, producing more of them and packing them closer together. It is such a pattern of evolution which has resulted in the holochroal eye of other trilobites and the modern compound eye. In the course of its development, the resolution increased until the limit imposed by diffraction was

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reached as in the case of the modern compound eye.

The other possibility consists of an increase in the number of light detectors behind each lens. The lens would probably have been initially convex in order to better direct light onto a single rhabdom, so it may have had a rough image—producing capacity which would have justified the addition of more rhabdoms. At this point, the eye would have evolved along a line quite different from that of the simple compound eye.

If the process were initiated in a lens of typical holochroal dimensions, the most severe constraint upon resolution would not have been imposed by the quality of the lens, but rather by diffraction.

The phenomenon of diffraction, or the bending of light around objects, limits the resolution of any optical system to angles larger than 1.22 λ/A radians, where λ is the wavelength of light involved and A is the diameter of the aperture. Although this rule, known as Rayleigh's Limit, is most commonly applied to large optical systems such as telescopes, it has been shown to be an excellent rule of thumb for biological optics as well (Palka and Pinter, 1975).

In the case of the holochroal eye, regardless of the quality of the lens involved, an increase in lens diameter would have been necessary before the addition of more rhabdoms beyond a very few would improve the acuity of vision. For example, if a lens were 50 μm in diameter, the limit of resolution would be about .70 degrees. It would be of no value to add more rhabdoms beyond the point at which each one of them accepted the light from an area .70 degrees in diameter. In the typical holochroal eye, such a lens would cover an angular area of about 2.5 degrees in diameter. The number of rhabdoms necessary to cover this area would be $(2.5/.70)^2$ or about thirteen. The addition of more rhabdoms would either be rendered useless by diffraction or, if the angle of acceptance of the lens were larger, they would replicate the vision of neighboring lenses. Only the increase of lens diameter would make the addition of more rhabdoms beneficial. Upon this occurring, a refinement of the retinal surface would eventually demand the improvement of the optics of the lens until the diffraction limit was reached again. The scenario, then, entails a cycle of selection pressures brought to bear upon lens size, optical quality, and retinal development to bring about large lenses of high quality casting their images upon commensurately refined retinas.

The suggestion that neighboring lenses could have been used to determine distances stereoscopically (Stockton and Cowen, 1976) is interesting to consider incorporating the assumption that the lenses were diffraction limited. In Figure 1, two lenses of aperture A, focal length f and separation S produce images upon their respective retinas. When the two images of an object are shifted by a distance
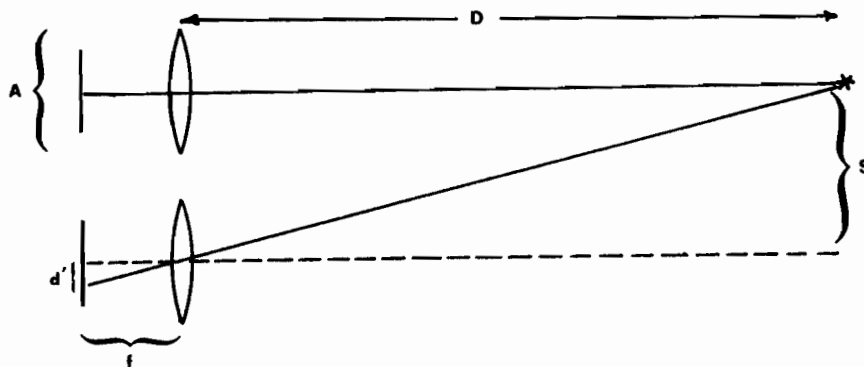

Fig. 1. Two neighboring lenses produce an image of an object upon their respective retinas. When the shift between the two images is just inside the limit of resolution of the retinas, the object is at the maximum stereoscopically detectable distance.

just large enough to be perceived, the object is at the maximum distance which can be determined stereoscopically. If d' is the diameter of the light detecting elements of the retina, then

$$f/d' = D/S$$

or the maximum distance which can be perceived stereoscopically is

$$D = S \cdot f/d'.$$

If the optics are diffraction limited, the smallest resolvable angular separation would be 1.22 λ/A. This would correspond to an angular measure across the retina of d'/f radians. Substituting into the above equation we have

$$D = S \cdot A/1.22\lambda.$$

It is nice that both the focal length and rhabdom diameter cancel out and we are left with two easily measured quantities.

Figure 2 shows the maximum distance which can be determined stereoscopically by a pair of diffraction limited optical units as a function of their apertures and separation. It is assumed that λ is 5000 Angstroms. Since the center to center
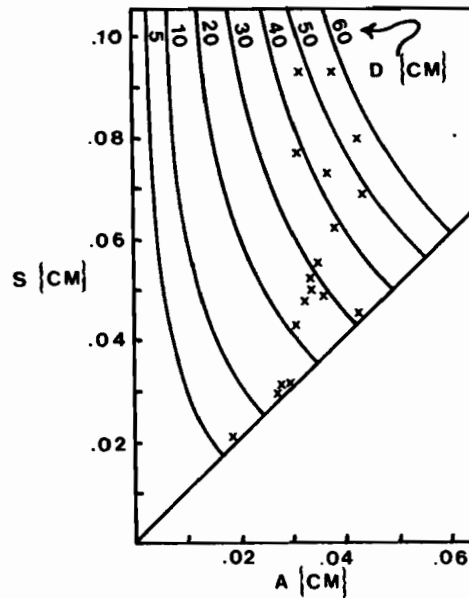

Fig. 2. Maximum distance, D, which can be determined stereoscopically by a pair of diffraction limited lenses of aperture A and separation S.
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separation must be equal to or greater than the lens diameter, the region below the diagonal is not meaningful. The values of A and S of a number of schizochroal eyes as measured from photographs (Levi–Setti, 1975 and Clarkson, 1975) have been plotted.

Although evidence exists that stereoscopic distance determination is possible even when d' is less than the diameter of a cone (Andersen and Weymouth, 1923), D should still be considered to be the outer limit of useful stereoscopic detection. As the distance of the field being inspected increases, the distinction which can be made within the field grows poorer. The object being scrutinized would lie well within the limit D before the differences between the two images would render useful information concerning its depth or the rate of its approach.

It can be concluded from Figure 2 that the optics of the schizochroal eye would have to have been at least very good, if not diffraction limited, for the proposed stereoscopic capacity to have been useful.

An interesting feature of Figure 2 involves the increase in lens separation as the aperture increases beyond .03 cm. It is possible that stereoscopic vision became adaptively significant as the increasing lens diameter entered this region. At this point, increasing lens diameter would have improved the stereoscopic vision, but would also have increased the information capacity of the system by an amount

proportional to the square of the aperture. The stereoscopic vision could be
improved without necessitating the commensurate growth of the information processing
system by simply increasing the separation S.

Although the utility of stereoscopic vision has been proposed as the selective
advantage which initially caused the development of the schizochroal eye from the
holochroal eye (Stockton and Cowen, 1975), this appears unlikely. The largest holo-
chroal lens is about .01 cm. in diameter. Even if it were diffraction limited, the
maximum range at which it could detect distances stereoscopically would be about 1.6
cm., a range too small to be of any survival significance.

A more reasonable picture for the evolution of the schizochroal eye entails
its development from the holochroal eye due purely to the increased acuity of vision.
Stereoscopic vision may well have become of adaptive significance as lens diameter
increased.

The scenario outlined above also provides an explanation for the schizochroal,
or separated, nature of the lenses. As the evolution proceeded, it is probable that
the lens-retina assemblage became the phenotypic unit subjected to selection as
opposed to the entire lens array, as in the case of the holochroal eye. This could
have led to the genetic de-coupling of the individual lenses and have resulted in
their synthesis as isolated components of sight. When stereoscopic vision became of
significance, this trait could have been exploited in the form of an increase in
separation of the already distinct elements.

If we can assume that the schizochroal eye was diffraction limited, it is a
simple matter to estimate its actual resolution. Using Rayleigh's Limit, we find
that a lens .04 cm. in diameter (lenses from .02 cm. to .05 cm. were common) has a
diffraction limit of .0015 radians or about .09 degrees for a wavelength of 5000
Angstroms. This is about ten times the resolution of most modern compound eyes and
falls short of the resolution of the human eye by a factor of six. Indeed, these
creatures appear to have had excellent vision, about comparable to that of a frog.
Not only was resolution high, but vision was panoramic with the battery of lenses
covering the marine horizon all around the animal with the exception of a small blind
area in the rear.

Acknowledgements

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