THE LOWER LENS UNIT IN SCHIZOCHROAL TRILOBITE EYES REDUCES REFLECTIVITY: ON THE POSSIBLE OPTICAL FUNCTION OF THE INTRALENSAR BOWL

GÁBOR HORVÁTH

Biophysics Group, Department of Atomic Physics, Loránd Eötvös University, H-1088 Budapest, Puskin u. 5–7., Hungary

It is shown that the lower lens unit (or intralensar bowl) in the corneal doublet lens of schizochroal-eyed trilobites decreases reflectivity. The reflectivity of geometric optically equivalent distally and proximally Huygensian (spherically corrected) singlet lenses is calculated and compared with the reflectivity of the aplanatic doublet lens in the trilobite *Crozonaspis struvei*. The maximum reflectivity reduction by the intralensar bowl in the doublet lens amounts to 10.5% and 3% by comparison with the corresponding distally and proximally Huygensian singlet lenses, respectively. From this it is concluded that one of the possible functions of the intralensar bowl might be reflectivity reduction and transmissivity enhancement.

KEY WORDS: Phacopid trilobites, Schizochroal trilobite eyes, *Crozonaspis struvei*, Corneal doublet lens, Lower lens unit, Reflectivity reduction.

INTRODUCTION

The most important palaeobiooptical features of the corneal lens in schizochroal-eyed phacopid trilobites are the doublet structure and the aplanatic character (Clarkson, 1979). All schizochroal trilobite lenses were doublets. They had an upper unit of oriented calcite (with c-axis normal to the visual surface and parallel to the optical axis) interlocking with a proximally located lower lens unit called the "intralensar bowl". The doublets were aplanatic, that is, corrected for spherical aberration (Clarkson and Levi-Setti, 1975; Levi-Setti, 1975, 1993; Horváth, 1989a). The original material of the intralensar bowl has disappeared and has been replaced during fossilization and diagenesis, but its probable original composition, and the focal length of the doublet lens can be computationally reconstructed (Horváth, 1989a). R. Levi-Setti discovered the remarkable correspondence between the shape of the upper lens units described by Clarkson (1968, 1969) in phacopid trilobites and the aplanatic lenses of Descartes (1637) and Huygens (1690) (this work was first presented at the Oslo International Conference on Trilobites in 1973). Clarkson and Levi-Setti (1975) and Levi-Setti (1975, 1993) proposed that the optical function of the intralensar bowl is correction for spherical aberration. At a given focal length and aperture, however, the problem of correction for spherical aberration can be simply solved by means of a singlet lens, the distal or proximal surface of which has a Huygensian profile that makes the lens aplanatic. From this the following question arises: Why did

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Phone: (36)-1-266-7902 Fax: (36)-1-266-0206 E-mail: gh@hercules.elte.hu

use schizochroal-eyed trilobites aplanatic doublet lenses instead of the simpler Huygensian singlets to correct for spherical aberration?

Recently, Horváth and Clarkson (1993) - building on the earlier anatomical work of Miller and Clarkson (1980) - have computationally shown that the schizochroal-eyed trilobite *Phacops rana milleri* used spherically corrected Huygensian singlet lenses in its post-ecdysially developing eye. On the other hand, Zhang and Clarkson (1990) demonstrated that in the eye of the Lower Cambrian eodiscoid trilobite *Neocobboldia chinlinica* the lenses were singlets probably conforming to a Huygensian aplanatic lens (in this species the lenses are separated from one another, as in schizochroal eyes proper). These two examples of the occurrence of Huygensian singlets in fossil trilobite eyes arise the counterpart of the earlier question: What is the optical function of the intralensar bowl in the schizochroal doublet lens?

The probable index of refraction n_i = 1.53 of the intralensar bowl (Horváth, 1989a) falls between the refractive indices of the upper lens unit (n_c = 1.66, calcite) and sublensar medium (n_b = 1.34, body fluid). Since the lower lens unit implies such a refractive index transition, the amount of light reflected from the refracting surfaces is smaller in the doublet lens than in the corresponding Huygensian singlet lenses. Is one of the possible functions of the intralensar bowl in schizochroal-eyed trilobites reflectivity reduction? To test this hypothesis I calculate the reflectivity of geometric optically equivalent distally and proximally Huygensian singlet lenses and compare it with the reflectivity of the aplanatic doublet lens of the trilobite *Crozonaspis struvei*.

METHODS

Two different Huygensian singlet lenses are studied: (i) The distal profile of the so-called 'distally Huygensian singlet' (DHS) is Huygensian, that is, corrected for spherical aberration, and the proximal surface corresponds with that of the schizochroal doublet lens of the trilobite *Crozonaspis struvei* (Clarkson and Levi-Setti, 1975; Horváth, 1989a). (ii) In the 'proximally Huygensian singlet' (PHS) the proximal lens profile is Huygensian and the distal surface coincides with that of the schizochroal aplanatic doublet (AD) lens in *Crozonaspis struvei*. The calculation of the distally and proximally Huygensian lens surfaces is the same as presented in Horváth and Clarkson (1993). The profile of the intralensar correcting interface of an aplanatic doublet lens in schizochroal-eyed trilobites was determined by the method of Horváth (1989a). The focal length measured from the proximal lens surface of the doublet lens is L_{AD}, which is the same as the focal length of the distally and proximally Huygensian singlet lenses.

A possible way to compare trilobite eyes with different corneal lenses is in terms of their sensitivity, an appropriate measure of the number of photons absorbed per receptor, per unit of luminance in the visual field being imaged (Land, 1981). The sensitivity S is given by $S = (1 - A - R)(r_a/F)^2 \pi^2 r_r^2 [1 - \exp(-kl)]$, where r_r and l are the radius and length of photoreceptors, k is the absorption coefficient of the visual pigment in photoreceptors, r_a and F are the radius of aperture and the principal focal length (or posterior nodal distance) of the corneal lens (Land, 1981). In the above expression of S the loss of light passing through the lens is taken into consideration by means of the absorption A and reflectivity R of the lens, which are the measure of amount of light absorbed by the lens substance and reflected by the refracting surfaces. Since the absorption A can be neglected in the ocular media of arthropods in the visible range of the spectrum (Miller, 1979), one can see from the above expression of the sensitivity that S depends on R and $Q \equiv r_a/F$ at a given type of photoreceptors, that is, at a given r_r, l and k. So, if one intends to study the sensitivity difference between

trilobite eyes with singlet and doublet corneal lenses, then one has to compare the reflectivity R versus the relative radius of aperture $Q = r_a/F$. On the basis of the above, lenses with the same relative radius of aperture can be geometric optically considered equivalent. In Appendix A the reflectivity of a trilobite doublet lens is calculated. The principal focal length F of distally and proximally Huygensian singlet lenses and the schizochroal doublet lens in *Crozonaspis struvei* is calculated in Appendix B.

RESULTS

As Horváth (1989a) has computationally reconstructed, the probable value of the refractive index n_i of the intralensar bowl and the focal length L_{AD} measured from the proximal surface of the doublet lens in *Crozonaspis struvei* was $n_i = 1.53$ and $L_{AD} = 175$ μm. The height of the distal (H_1) and proximal (H_2) lens surfaces, the radius r_{AD}, the thickness a_u and the refractive index n_c of the upper lens unit of the doublet are $H_1 = 113$ μm, $H_2 = 138$ μm, $r_{AD} = 190$ μm, $a_u = 188$ μm, $n_c = 1.66$. The doublet lens has a spherical entrance (distal) and exit (proximal) surface. The thickness of the doublet is $a_{AD} = H_1 + H_2 = 251$ μm.
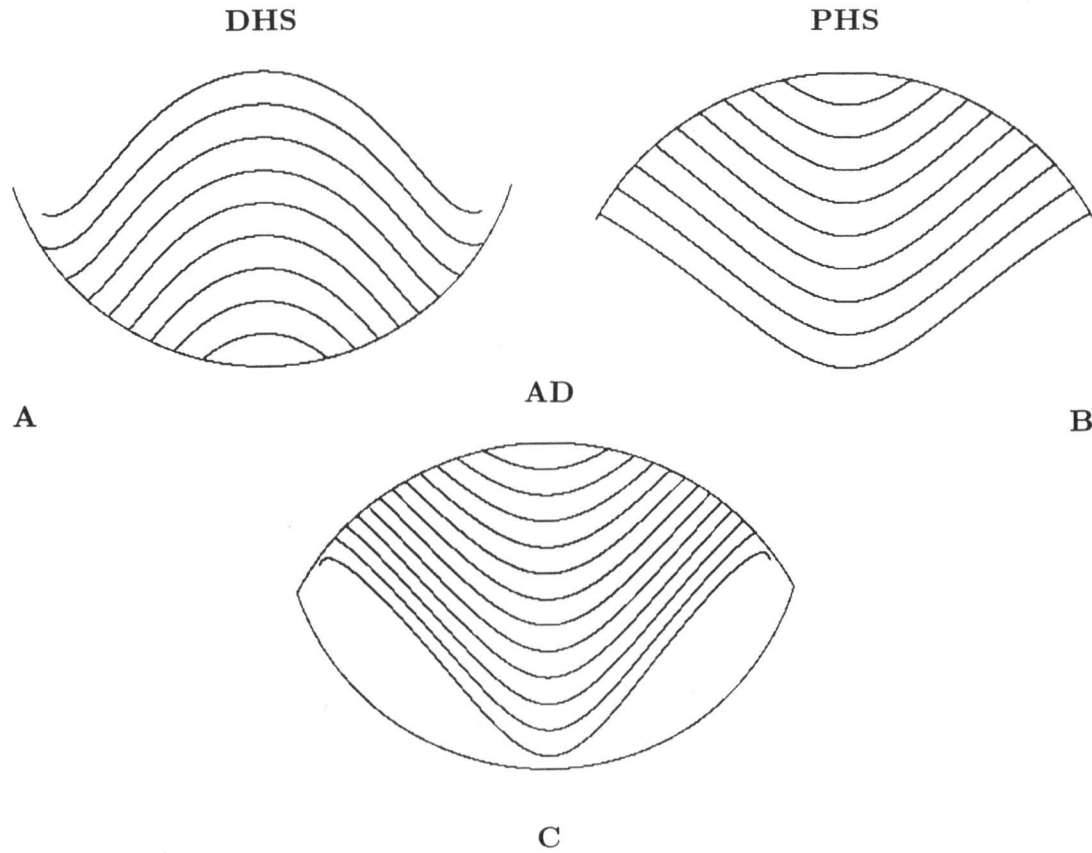
Consider first a distally Huygensian singlet (DHS) lens composed of calcite ($n_c = 1.66$), the proximal surface of which corresponds with the exit surface of the doublet lens in *Crozonaspis struvei*. Let the focal point of the DHS be at a distance $a + L_{AD}$ measured from the distal surface, where a is the lens thickness. The shape of the Huygensian distal profile of the DHS can be seen in Figure 1A as a function of a. If the distal surface of the singlet lens coincides with the entrance surface of the doublet lens in *Crozonaspis struvei*, then the proximal surface of the singlet must by Huygensian. The shape of the exit surface of the proximally Huygensian (PHS) singlet lens is shown in Figure 1B as a function of the lens thickness. Figure 1C shows the intralensar correcting interface of the doublet lens in *Crozonaspis struvei* as a function of the thickness a_u of the upper lens unit.

Figure 2A, B and C show a DHS, PHS and AD, which are geometric optically equivalent with the same relative radius of aperture $Q = r_a/F = 0.548$. Figure 2 represents also the ray tracing through the lenses in order to demonstrate their aplanatic character. In Figure 3 we can see the calculated relative reflectivity R/R_{AD} versus Q/Q_{AD} of the DHS, PHS and AD, where $R_{AD} = 2.9\%$ is the reflectivity and $Q_{AD} = r_{AD}/F_{AD} = 0.511$ the relative radius of aperture of the doublet lens in *Crozonaspis struvei*.

DISCUSSION AND CONCLUSION

Figure 1 demonstrates that the shape of the correcting profiles in Huygensian singlet and aplanatic doublet lenses depends greatly on the lens thickness. Increasing the thickness a of DHS and PHS and the thickness a_u of the upper unit of AD, the radius of aperture r_a increases, too, as we can see in Figure 1. We showed in the Methods that the reflectivity of different singlet and doublet lenses in trilobite eyes should be compared as a function of their relative radius of aperture $Q = r_a/F$, because they are geometric optically equivalent only in that case, when they have the same Q. Figure 2 represents such three geometric optically equivalent lenses (DHS, PHS, AD) with ray tracing. One can see that these lenses can have quite a different shape.

Figure 3 shows that the reflectivity of the singlet and doublet lenses increases monotonously as a function of Q, because the profile of the correcting surfaces (distal, proximal, intralensar) becomes steeper and steeper for thicker lens (Figure 1). One can

DHS

PHS

AD

A

B

C

Figure 1 (A) Front profile of a distally Huygensian singlet (DHS) lens as a function of the lens thickness. (B) Exit profile of a proximally Huygensian singlet (PHS) lens as a function of the lens thickness. (C) Intralensar correcting interface as a function of the thickness of the upper lens unit in an aplanatic doublet lens (AD) of the schizochroal-eyed trilobite *Crozonaspis struvei*.
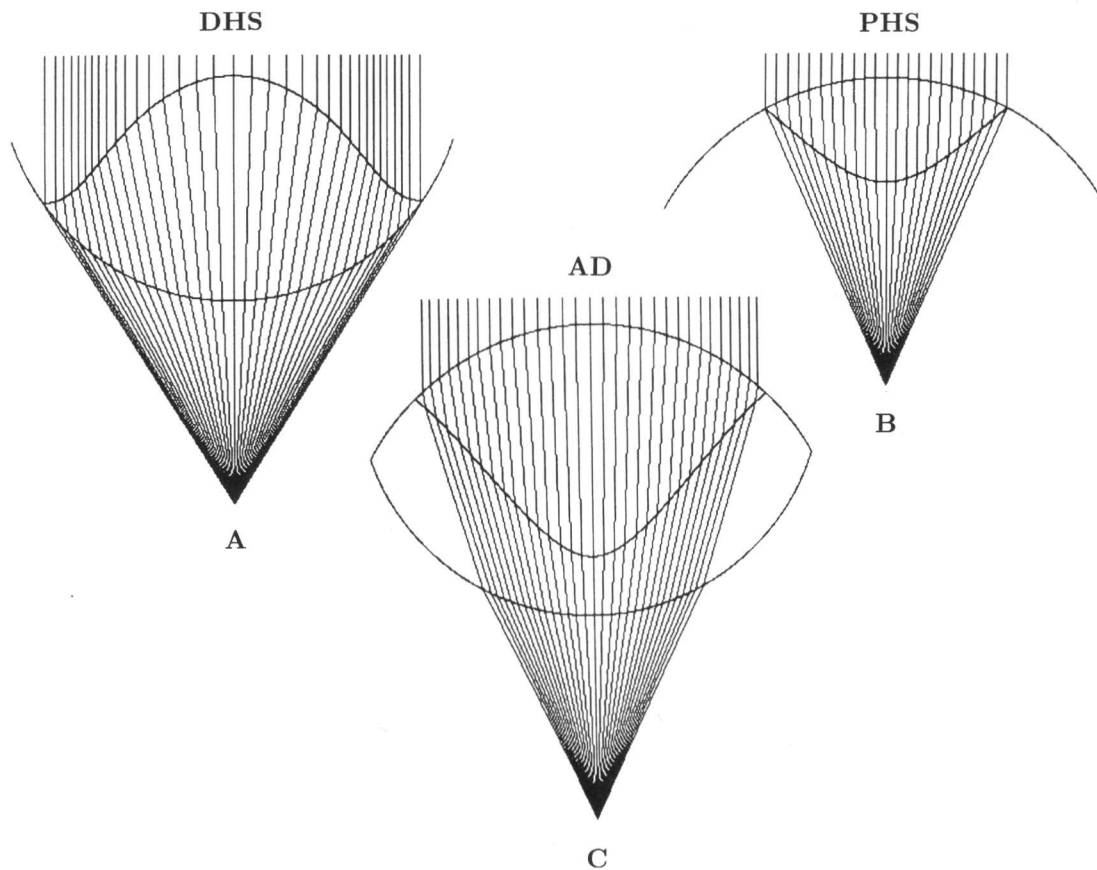
Figure 2 Ray tracing through geometric optically equivalent, spherically corrected corneal lenses with the same relative radius of aperture $Q = r_a/F = 0.548$, where r_a is the radius of aperture and F the principal focal length of the lens. (A) Distally Huygensian singlet lens (DHS), (B) proximally Huygensian singlet lens (PHS), (C) aplanatic doublet lens (AD).
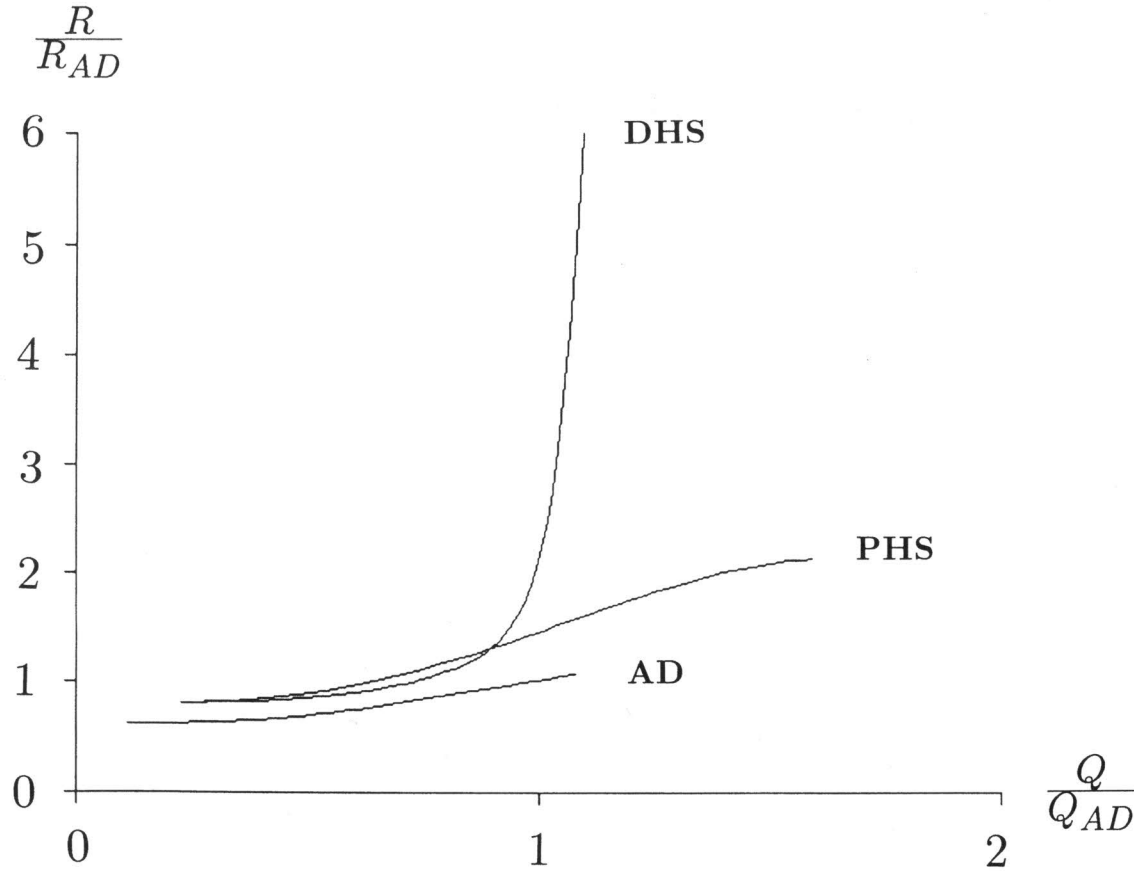
Figure 3 Relative reflectivity R/R_{AD} of distally (DHS) and proximally (PHS) Huygensian singlet lenses and the aplanatic doublet lens (AD) in *Crozonaspis struvei* as a function of Q/Q_{AD}, where $R_{AD} = 2.9\%$ is the computed reflectivity, $Q_{AD} = 0.511$ is the relative radius of aperture of the doublet lens.

see in Figure 3 that for all Q values the reflectivity of the doublet lens is smaller than that of the Huygensian singlet lenses, and there is not a significant reflectivity difference between the DHS and PHS for relative radii of aperture Q smaller than about 0.9 Q_{AD} (Q_{AD} = 0.548). If $0.8 \leq Q/Q_{AD} \leq 1.2$, then the reflectivity of the DHS and PHS is about 2.2–4.5-times and 1.5–2-times larger than the reflectivity of the AD, respectively. This implies about 3.6–10.5% and 1.5–3% reflectivity difference between the Huygensian singlets (DHS, PHS) and the aplanatic doublet (AD).

From the above analysis, one can draw the conclusion that the intralensar bowl in the doublet lens of the schizochroal-eyed phacopid trilobite *Crozonaspis struvei* reduces reflectivity by comparison with the corresponding Huygensian calcite singlet lenses. So it seems pertinent to suppose that the enigmatic function of the lower lens unit may be the reflectivity reduction and transmissivity enhancement of the dioptric apparatus in order to enhance the light-collecting efficiency and sensitivity of the eye.

Clarkson and Levi-Setti (1975) suggested that schizochroal-eyed phacopid trilobites might have lived in dimly lit environment (turbid water, or activity at night, for example). Under such conditions it is very important to collect as much light as possible by the eyes, and the use of an intralensar bowl in the lens is, therefore, advantageous. In my opinion, the transmissivity enhancement of 3.6–10.5% explains the evolutionary importance of the intralensar bowl in phacopid trilobites. This recalls the 2% transmissivity enhancement by the lower lens unit in the compound eye of the water bug backswimmer, *Notonecta glauca* (Schwind, 1980; Horváth, 1989b, 1993) and the 4% reflectivity reduction by the corneal nipple array in the compound eyes of nocturnal lepidoptera and trichoptera (Miller, 1979). Backswimmers prefer turbid water with a dense growth of aquatic plants and phytoplankton (Giller and McNeill, 1981), and the peripheral photoreceptors in their ommatidia function as a scotopic system in the dimly lit aquatic environment (Schwind *et al.*, 1984). In all probability, the lower lens unit of the doublet lens in the larval ocelli of the sawfly Perga (Meyer-Rochow, 1974) has similar transmissivity enhancement. These larvae are also night active animals.

The phacopid trilobites applied three optical methods to ensure a high quality imaging and to enhance the light-collecting efficiency, transfer of contrast and sensitivity of their schizochroal compound eyes. (i) The c-axis of the calcite crystal in the upper lens unit was parallel to the optical axis in order to minimize the effect of double-refraction of the calcite. (ii) The corneal lenses were corrected for spherical aberration by means of an undulating intralensar correcting interface between the optically homogeneous lens units. (iii) The lenses were doublets; an intralensar bowl (composed probably of hydrated chitinous material) was added to the calcite upper lens unit to reduce reflectivity.

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APPENDIX

Reflectivity of Trilobite Lenses

Consider a trilobite doublet lens receiving a paraxial light beam of constant intensity I through its aperture of radius $r_a(\leq r_{AD})$. The lens receives an elementary amount of light $2\pi Ix_1dx_1$ through the coaxial ring with radius x_1 and infinitesimal thickness dx_1. If the angle of incidence of this annular beam is $\varphi_1(x_1)$ and the amplitude reflection coefficient of the entrance lens surface is $\rho_1 \equiv \rho[\varphi_1(x_1), n_w, n_c]$, then the amount of light reflected from the annular area of the entrance surface is $2\pi Ix_1\rho_1^2dx_1$. The total amount of light reflected from the whole entrance surface is $E_{reflected} = \int_0^{ra} 2\pi Ix_1\rho_1^2dx_1$, and the

total amount of light received by the lens through its entire aperture is $E_{received} = r_a^2 \pi I$. So the reflectivity of the entrance lens surface is

$$R_1 \equiv \frac{E_{reflected}}{E_{received}} = \frac{2}{r_a^2} \int_0^{ra} x_1 \rho[\varphi_1(x_1), n_w, n_c]^2 dx_1, \; r_a \leq r_D. \tag{1}$$

Similarly can be derived the reflectivity of the intralensar correcting interface and the exit surface of the lens

$$R_2 = \frac{2}{r_a^2} \int_0^{ra} x_1 \{1 - \rho[\varphi_1(x_1), n_w, n_c]^2\} \rho[\varphi_2(x_1), n_c, n_i]^2 dx_1, \tag{2}$$

$$R_3 = \frac{2}{r_a^2} \int_0^{ra} x_1 \{1 - \rho[\varphi_1(x_1), n_w, n_c]^2\} \{1 - \rho[\varphi_2(x_1), n_c, n_i]^2\} \rho[\varphi_3(x_1), n_i, n_b]^2 dx_1. \tag{3}$$

The resultant reflectivity of the schizochroal aplanatic doublet lens (AD) is

$$R_{AD} = R_1 + R_2 + R_3. \tag{4}$$

The reflectivity of a Huygensian singlet lens can be similarly derived. Using Fresnel's formula (Guenther, 1990), the amplitude reflection coefficient of a refracting interface between two optical media of refractive indices n_i and n_j at angle of incidence φ for unpolarized light is

$$\rho(\varphi, n_i, n_j) = \sqrt{\frac{S_1(2 - S_1 - S_2)}{2S_2(1 - S_1)}}, \; S_1 = \frac{1 - cos^2\varphi}{n_j^2} \; (\sqrt{n_j^2 - n_i^2 + n_i^2 cos^2\varphi} - n_i cos\varphi)^2,$$

$$S_2 = \frac{1 - cos^2\varphi}{n_j^2} \; (\sqrt{n_j^2 - n_i^2 + n_i^2 cos^2\varphi} + n_i cos\varphi)^2 \tag{5}$$

if the light propagates from medium i to j.

The Principal Focal Length of Trilobite Lenses

Using the geometric optical formulae of thick lenses (Nussbaum and Phillips, 1976), the principal focal length F of the distally (F_{DHS}) and proximally (F_{PHS}) Huygensian singlet lens is the following

$$F_{DHS} = \frac{n_b}{\dfrac{n_c - n_w}{r_d} - \dfrac{n_b - n_c}{r_2} + \dfrac{a(n_c - n_w)(n_b - n_c)}{n_c r_d r_2}},$$

$$r_d = \frac{n_c - n_w}{n_c} \cdot \frac{a(a_{AD} + L_{AD} - a)(n_c - n_b) - r_2[an_b + (a_{AD} + L_{AD} - a)n_c]}{(a_{AD} + L_{AD} - a)(n_c - n_b) - r_2 n_b}, \tag{6}$$

$$F_{PHS} = \frac{(a_{AD} + L_{AD} - a)r_1 n_c}{n_c r_1 - a(n_c - n_w)} \tag{7}$$

where r_1, r_2 are the radius of curvature of the distal and proximal surfaces of the doublet lens in the trilobite *Crozonaspis struvei*, and r_d is the radius of curvature of the distal

profile of the Huygensian singlet lens. The principal focal length F_{AD} of the aplanatic doublet lens is

$$F_{AD} = \frac{n_b}{(k_1 + k_2 - \frac{a_u k_1 k_2}{n_c})(1 - k_3 \frac{H_1 + H_2 - a_u}{n_i}) + k_3(1 - \frac{a_u k_1}{n_c})},$$

$$k_1 = \frac{n_c - n_w}{r_1}, \quad k_2 = \frac{(L_{AD}k_3 - n_b)(k_1 \frac{H_1 + H_2 - a_u}{n_i} + \frac{a_u k_1}{n_c} - 1) - L_{AD}k_1}{(1 - \frac{a_u k_1}{n_c})[L_{AD}(1 - k_3 \frac{H_1 + H_2 - a_u}{n_i}) + n_b \frac{H_1 + H_2 - a_u}{n_i}]}, \quad k_3 = \frac{n_b - n_i}{r_2} \quad (8)$$

where k_1, k_2 and k_3 are the refractive power of the distal surface, correcting interface and proximal surface of the doublet lens, respectively.