

Geometric Optics of Trilobite Eyes: A Theoretical Study of the Shape of the Aspherical Interface in the Cornea of Schizochroal Eyes of Phacopid Trilobites

GÁBOR HORVÁTH

Hungarian Academy of Sciences, Central Research Institute for Physics, Biophysical Group,
H-1525 Budapest, P.O.B. 49 Hungary

Received 1 June 1988; revised 2 January 1989

ABSTRACT

A general method is given to determine theoretically the shape of the aspherical interface that eliminates spherical aberration in an optionally shaped thick lens. The theory is applied to trilobite eyes. On the basis of the geometric optical method presented, the refractive indices and focal length of the original corneal lenses of trilobites can be determined. The shape of the aspherical interface in the cornea of some phacopid trilobites with schizochroal eyes is investigated. The theoretical aspherical interfaces agree well with the real ones.

INTRODUCTION

The structure of holochroal and schizochroal eyes of trilobites is well known [1-4]. The thick and large corneal lenses of schizochroal eyes are doublets. They consist of an upper unit of oriented calcite (with its c axis normal to the visual surface) and an intralensar bowl, the composition of which has not been determined [5].

The eyes of phacopid trilobites developed very large and thick lenses, which increased their light-collecting efficiency. The thick-lensed trilobites were nocturnal or crepuscular animals or lived in very turbid waters. For thick uncorrected lenses consisting of a simple lens, however, spherical aberration is very large. The fourth-degree aspherical interface between the lens units in the eye of phacopid trilobites eliminates the spherical aberration that would prevent the formation of a sharp image and decrease the light-collecting efficiency.

These aspherical interfaces have been investigated empirically by Clarkson and Levi-Setti [6] for the schizochroal eyes of trilobites *Crozonaspis struvei* and *Dalmanitina socialis*, for example. They determined the shape of the aspherical interfaces by two approaches: by graphical ray-tracing through

the lens structure and by construction of a large-scale model of a lens. They showed the similarity between the shape of the aspherical interface of phacopid trilobites and the shape of aplanatic surfaces described by Descartes [7] and Huygens [8] and designed such aplanatic surfaces to obtain lenses free of spherical aberration.

The refractive index of the upper lens unit and the focal length of the corneal lens of trilobites are unknown. The shape of the lens and the aspherical interface, however, can be determined experimentally, using the X-ray or electron micrograph of the thin section of the cornea, for example. Following the empirical method of Clarkson and Levi-Setti [6] these unknown parameters and the optimal shape of aspherical interfaces can be determined only slowly and with difficulty.

In this work a general theoretical method is presented for calculation of the shape of the optimal aspherical interface in the schizochroal eye of phacopid trilobites. Solving the equations of geometric optics for the real cornea of any trilobite, the shape of the aspherical interface can be determined. Fitting the theoretical interface to the real one, the above-mentioned unknown parameters of the cornea can be determined easily and quickly.

THE EYES OF TRILOBITES

There were two types of trilobite eyes [9]: a truly compound eye (holochroal) and an aggregate eye (schizochroal). The holochroal eye was characterized by close packing of the ommatidia, the entire visual surface being covered by a continuous pellucid membrane, the cornea. The ommatidia varied in shape from thin simple biconvex lenses to elongated hexagonal prisms, which were made of single calcite crystals [1]. The crystals were oriented so that the optical axis always pointed in a direction normal to the visual surface. Only along this axis does calcite behave as an isotropic medium (calcite has a strong birefringence in any other direction). The number of individual optical elements varied from about 100 to more than 15,000 in a single eye. Such holochroal eyes were characteristic of the trilobites *Ctenopyge tumida*, *Sphaerophthalmus alatus*, *Sphaerophthalmus humilis*, *Scutellum campaniferum*, *Paralejurus brongniarti*, *Priocyclopyge binodosa*, and *Asaphus raniceps*, for example [10].

In schizochroal trilobite eyes the lenses were separately encased and positioned by a cylindrical mounting, the sclera, and each lens was covered by its own cornea. The lenses were generally larger than those of holochroal eyes; the number of lenses varied from a few hundred to several hundred in each lateral eye. The lenses were doublet structures built to correct the otherwise large spherical aberration of a simple thick lens. A fourth-degree aspherical interface divided the corneal lens into two parts. The upper lens unit was made of oriented calcite (refractive index $n = 1.66$ on axis), and the

intralensar bowl was possibly made of chitin (the refractive index of dry chitin is 1.56; when hydrated the value decreases) [5]. It can be assumed that the refractive index of the medium in contact with the entrance surface was $n = 1.33$ (seawater) and that of the medium in contact with the exit surface was $n = 1.34$ (body fluid). The focal length of the corrected corneal lens is unknown.

In Figures 1–3 the reconstructed corneal lens of *Crozonaspis struwei*, *Dalmanitina socialis*, and a Silurian *Dalmanites* can be seen in horizontal section [6]. In *Dalmanitina socialis* the intralensar bowl is thin and indented centrally with a small dimple (Figure 2). In *Crozonaspis struwei* the lens is highly convex, with a large and relatively thick intralensar bowl, indented not with a small dimple but with a wide depression (Figure 1). In the Silurian *Dalmanites* the shape of the upper surface of the bowl is intermediate between the two end types mentioned above (Figure 3). There seem to be two basic kinds of structure of schizochroal eyes (*Dalmanitina socialis* and *Crozonaspis struwei*) with a range of intermediates between them (Silurian *Dalmanites*) [6].

Schizochroal eyes were features of trilobites such as *Dalmanites pratteni*, *Dalmanitina socialis*, *Reedops sternbergi*, *Crozonaspis struwei*, *Dalmanites*

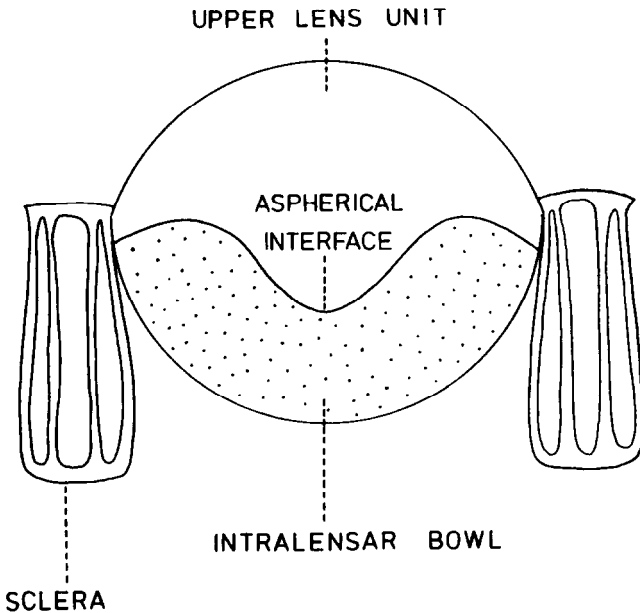


FIG. 1. Reconstructed corneal lens of the phacopid trilobite *Crozonaspis struwei* with schizochroal eye [6].

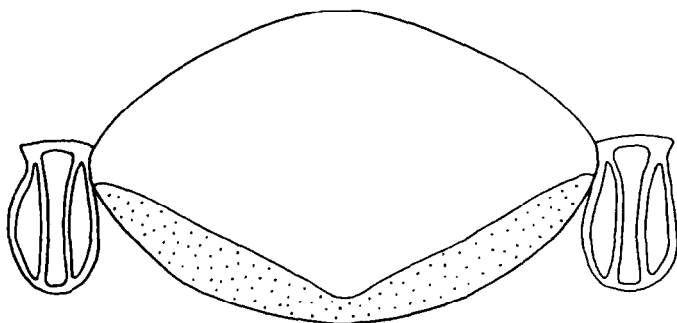


FIG. 2. Reconstructed corneal lens of the phacopid trilobite *Dalmanitina socialis* [6].

verrucosus, *Phacops rana crassituberculata*, *Phacops rana milleri*, *Eophacops trapeziceps*, *Chasmops odini*, and *Denckmannites volborthi*, for example [10].

The structure of the cornea of a water bug, the backswimmer (*Notonecta glauca*), is similar to that of phacopid trilobites—that is to say, the corneal lenses of the backswimmer have a doublet structure—and there is a bell-shaped thin transition layer (aspherical interface) between the lens units [11, 12].

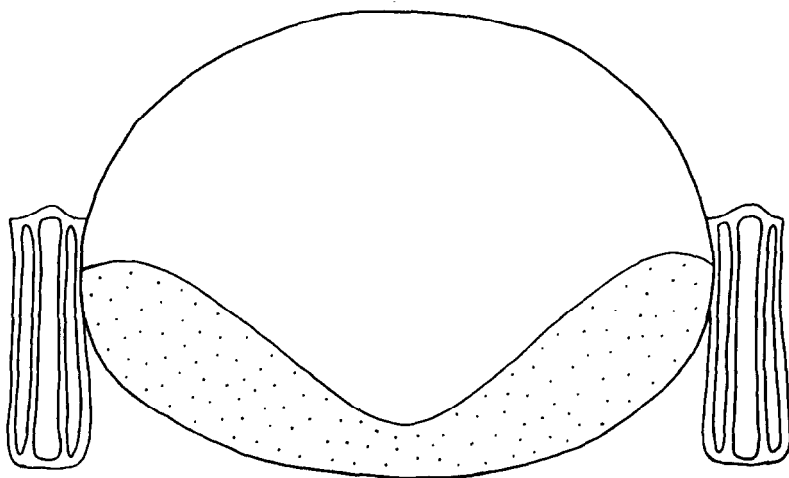


FIG. 3. Reconstructed corneal lens of a Silurian *Dalmanites* [6].

GEOMETRIC OPTICAL METHOD FOR CALCULATION OF THE SHAPE OF THE ASPHERICAL INTERFACE

In Figure 4 the path of a ray of light through a thick lens can be seen. Only half of the cross section of the lens, which has a cylindrical symmetry, is represented. The incident ray of light is parallel to the optical axis of the lens. The parameters n_1, n_4 and n_2, n_3 are the refractive indices of the media in contact with the entrance and exit surfaces of the lens and the refractive indices of the upper lens unit and the intralensar bowl, respectively.

The entrance and exit surfaces of the lens and the aspherical interface can be described by the functions $f_1(x_1)$, $f_2(x_2)$, and $y(x)$, respectively, in the system of coordinates of Figure 4. The definition of the geometric parameters a, c, d, r can be read in Figure 4. The focal length of the lens is L from the exit surface. The elimination of longitudinal spherical aberration is required by the aspherical interface for incident rays of light parallel to the optical axis of the lens. This means that any such incident ray crosses the same focal point F after being refracted by the entrance, aspherical, and exit surfaces. Such refractions can be described by the law of Snellius and Descartes:

$$\frac{\sin \alpha}{\sin \beta} = \frac{n_2}{n_1}, \quad \frac{\sin \delta}{\sin \omega} = \frac{n_3}{n_2}, \quad \frac{\sin \eta}{\sin \theta} = \frac{n_4}{n_3}. \tag{1}$$

On the basis of Figure 4 we can write

$$\tan \alpha = -f_1'(x_1) \equiv -\frac{df_1}{dx_1}, \quad \tan \gamma = y'(x) = \frac{dy}{dx},$$

$$\tan \nu = f_2'(x_2) \equiv \frac{df_2}{dx_2}, \tag{2}$$

$$\delta = \alpha - \beta + \gamma, \tag{3}$$

$$\eta = \nu + \omega - \delta + \alpha - \beta, \tag{4}$$

$$x = x_1 - \tan(\alpha - \beta)[f_1(x_1) + a - y(x)], \tag{5}$$

$$x_2 = x - \tan(\omega - \delta + \alpha - \beta)[y(x) - a + c - f_2(x_2)], \tag{6}$$

$$L + f_2(x_2) = \frac{x_2}{\tan(\theta - \nu)}. \tag{7}$$

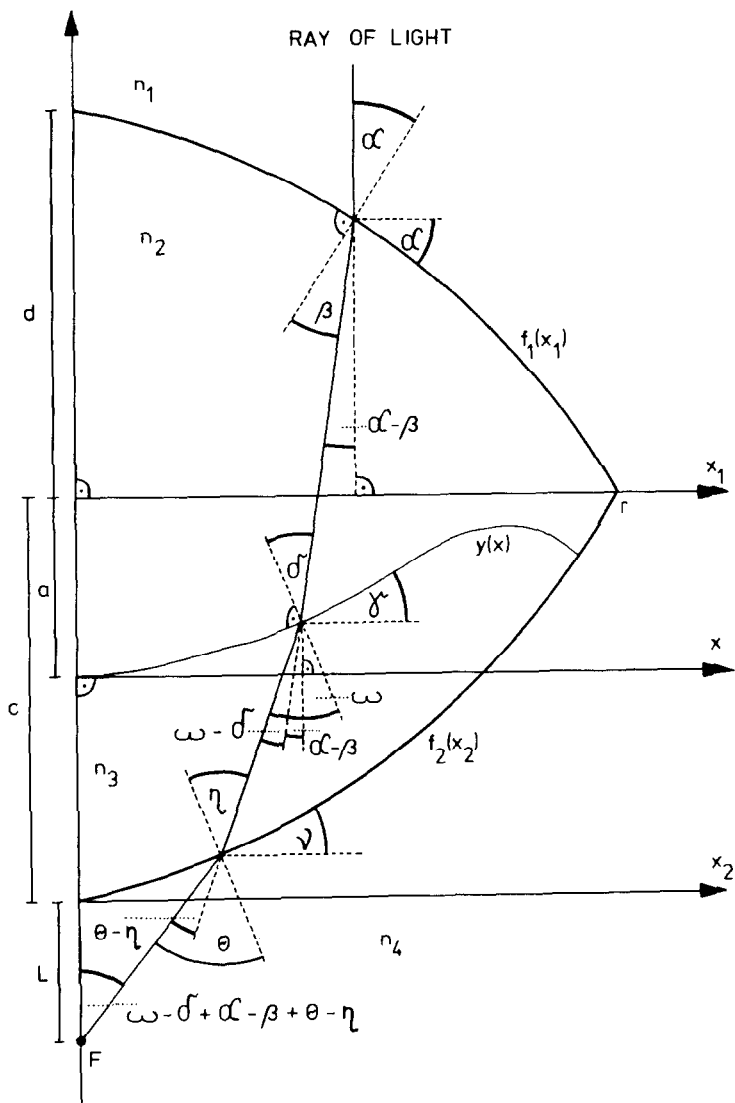


FIG. 4. Path of a ray of light through a thick lens. Only half of the cross section is represented.

From Equations (1)–(7) we obtain

$$\tan(\alpha - \beta) = \frac{-f_1'(x_1) + \frac{[f_1'(x_1)(n_1/n_2)]/[1 + f_1'^2(x_1)]^{1/2}}{\left[1 - \frac{f_1'^2(x_1)(n_1/n_2)^2}{1 + f_1'^2(x_1)}\right]^{1/2}}}{1 + f_1'^2(x_1) \frac{(n_1/n_2)/[1 + f_1'^2(x_1)]^{1/2}}{\left[1 - \frac{f_1'^2(x_1)(n_1/n_2)^2}{1 + f_1'^2(x_1)}\right]^{1/2}}}. \quad (8)$$

From (2) and (3) we get

$$\tan \delta = \frac{\tan(\alpha - \beta) + y'(x)}{1 - \tan(\alpha - \beta) y'(x)}. \quad (9)$$

Using (1) and some trigonometric transformations, we obtain

$$\tan(\omega - \delta) = \frac{\frac{(\tan \delta)(n_2/n_3)/(1 + \tan^2 \delta)^{1/2}}{\left\{1 - [(\tan \delta)(n_2/n_3)]^2/(1 + \tan^2 \delta)\right\}^{1/2}} - \tan \delta}{1 + \frac{(\tan^2 \delta)(n_2/n_3)/(1 + \tan^2 \delta)^{1/2}}{\left\{1 - [(\tan \delta)(n_2/n_3)]^2/(1 + \tan^2 \delta)\right\}^{1/2}}}, \quad (10)$$

$$\tan(\theta - \nu) = \frac{\frac{(\tan \eta)(n_3/n_4)/(1 + \tan^2 \eta)^{1/2}}{\left\{1 - [(\tan \eta)(n_3/n_4)]^2/(1 + \tan^2 \eta)\right\}^{1/2}} - f_2'(x_2)}{1 + f_2'(x_2) \frac{(\tan \eta)(n_3/n_4)/(1 + \tan^2 \eta)^{1/2}}{\left\{1 - [(\tan \eta)(n_3/n_4)]^2/(1 + \tan^2 \eta)\right\}^{1/2}}}. \quad (11)$$

Using (2) and (4) we can write

$$\tan \eta = \frac{\tan(\omega - \delta + \alpha - \beta) + f_2'(x_2)}{1 - \tan(\omega - \delta + \alpha - \beta) f_2'(x_2)}. \quad (12)$$

Equations (5)–(12) constitute a system of equations for the calculation of the shape of an aspherical curve (the section of aspherical interface) $y(x)$. We

introduce the following notation.

$$a_1 = f_1'(x_1) [1 + f_1'^2(x_1)]^{-1/2} n_1/n_2, \quad a_2 = a_1(1 - a_1^2)^{-1/2},$$

$$a_3 = \frac{a_2 - f_1'(x_1)}{1 + a_2 f_1'(x_1)}, \quad f_1'(x_1) \equiv \frac{df_1}{dx_1}, \quad (13)$$

$$b_1 = \frac{x - x_2}{y - a + c - f_2(x_2)}, \quad b_2 = \frac{b_1 - a_3}{1 + b_1 a_3}, \quad b_3 = \frac{b_1 + f_2'(x_2)}{1 - b_1 f_2'(x_2)},$$

$$b_4 = b_3(1 + b_3^2)^{-1/2} n_3/n_4, \quad b_5 = (1 - b_4^2)^{1/2}, \quad (14)$$

$$b_6 = b_4/b_5 - f_2'(x_2), \quad b_7 = 1 + f_2'(x_2) b_4/b_5.$$

From (5), (7), and (10) we obtain

$$F(x_1) \equiv x_1 - x - a_3 [f_1(x_1) + a - y] = 0, \quad (15)$$

$$G(x_2) \equiv L + f_2(x_2) - x_2 b_7/b_6 = 0, \quad (16)$$

$$H(t) \equiv t^4 \left[1 - \frac{n_2^2}{n_3^2} (1 + b_1^2) \right] + 2t^3 b_1 + t^2 \left(1 - \frac{n_2^2}{n_3^2} \right) (1 + b_1^2) + 2t b_1 + b_1^2 = 0, \quad (17)$$

where $t = \tan \delta$. From (9) we get

$$y'(x) = \frac{t - a_3}{1 + t a_3}. \quad (18)$$

Then the system of equations (5)–(12) can be solved in the following way. First we solve (15) numerically for x_1 , using the tangent method of Newton, for example; namely, using the recursion

$$x_1^{(i+1)} = x_1^{(i)} - \frac{F[x_1^{(i)}]}{F'[x_1^{(i)}]}, \quad F'(x_1) \equiv \frac{dF}{dx_1}, \quad (19)$$

for the approximate roots $x_1^{(i)}$. Then we solve (16) and (17) numerically for x_2 and t , respectively, using the recursions

$$x_2^{(i+1)} = x_2^{(i)} - \frac{G[x_2^{(i)}]}{G'[x_2^{(i)}]}, \quad G'(x_2) \equiv \frac{dG}{dx_2}, \quad (20)$$

$$t^{(i+1)} = t^{(i)} - \frac{H[t^{(i)}]}{H'[t^{(i)}]}, \quad H'(t) \equiv \frac{dH}{dt}. \quad (21)$$

Then substituting the root x_1 into the expression for a_3 and substituting the

roots t and a_3 into (18), we obtain $y'(x)$. Using the boundary condition

$$y(x = 0) = 0 \tag{22}$$

we can determine the aspherical curve $y(x)$, because it is clear that

$$y(x + \Delta x) = y(x) + y'(x) \Delta x, \quad \Delta x = r/m, \tag{23}$$

where r is the radius of the lens and m is a large number. The larger the number m is, the better the numerical solution for $y(x)$ is.

The method presented above for determining the shape of the aspherical interface of a thick lens without longitudinal spherical aberration is general. The shape of the lens, that is, the functions $f_1(x_1), f_2(x_2)$, the geometrical parameters a, c, d, r, L , and the refractive indices can be arbitrary.

THEORETICAL ASPHERICAL INTERFACES IN THE CORNEA OF SOME PHACOPIID TRILOBITES

The method just presented can be used for any corneal lens. It can be applied for the aspherical interface in the cornea of phacopid trilobites of Figures 1–3, for example. The entrance and exit surfaces of the corneal lens of these trilobites can be well described as follows.

Crozonaspis struwei (Spherical Surfaces)

$$\begin{aligned} f_1(x_1) &= (R_1^2 - x_1^2)^{1/2} - R_1 + d, & R_1 &= (d^2 + r^2)/2d, \\ f_2(x_2) &= R_2 - (R_2^2 - x_2^2)^{1/2}, & R_2 &= (c^2 + r^2)/2c. \end{aligned} \tag{24}$$

Dalmanitina socialis (Elliptic-Parabolic, Elliptic Surfaces)

$$\begin{aligned} f_1(x_1) &= kd \left[1 - \left(\frac{x_1}{r} \right)^2 \right] + d(1 - k) \left[1 - \left(\frac{x_1}{r} \right)^2 \right]^{1/2}, & k &= 0.6, \\ f_2(x_2) &= c - c \left[1 - \left(\frac{x_2}{r} \right)^2 \right]^{1/2}. \end{aligned} \tag{25}$$

Silurian Dalmanites (Elliptic Surfaces)

$$f_1(x_1) = d \left[1 - \left(\frac{x_1}{r} \right)^2 \right]^{1/2}, \quad f_2(x_2) = c - c \left[1 - \left(\frac{x_2}{r} \right)^2 \right]^{1/2}. \tag{26}$$

The geometrical parameters a, c, d, r and the refractive indices n_1, n_2, n_4 are

TABLE 1

Known Refractive Indices and Geometric Parameters in the Corneal Lens
of Three Phacopid Trilobites [6]

For all three trilobites investigated,

n_1 (seawater) = 1.33, n_2 (calcite along the c axis) = 1.66, n_4 (body fluid) = 1.34

Crozonaspis struvei

$a = 75 \mu\text{m}$, $d = 113 \mu\text{m}$, $c = 138 \mu\text{m}$, $r = 163 \mu\text{m}$, $Q = 0.25$

Dalmanitina socialis

$a = 88 \mu\text{m}$, $d = 105 \mu\text{m}$, $c = 100 \mu\text{m}$, $r = 165 \mu\text{m}$, $Q = 0.06$

Silurian *Dalmanites*

$a = 240 \mu\text{m}$, $d = 310 \mu\text{m}$, $c = 310 \mu\text{m}$, $r = 460 \mu\text{m}$, $Q = 0.11$

The parameter $Q = (c - a)/(c + d)$ is the relative thickness of the intralensar bowl.

known; their numerical values are given in Table 1. The focal length L and the refractive index n_3 of the intralensar bowl are unknown.

I have solved numerically the system of equations (5)–(12) using the method described above for the corneal lenses described by (24)–(26). I varied the parameters L and n_3 and looked for the theoretical aspherical curve most similar to the shape of the real aspherical interface. The approximate values of L and n_3 can thus be determined for the investigated corneal lenses.

The results can be seen in Figures 5–7 for the phacopid trilobites mentioned above. It can be seen that the theoretical aspherical interfaces in Figures 5(a) and 7(a) agree well with the real ones in Figures 1 and 3, respectively. The theoretically reconstructed numerical values of the parameters L and n_3 are given in Table 2. In Figures 5(b), 6(b), and 7(b) a family of curves can be seen for the theoretical aspherical interfaces depending on the geometrical parameter a .

CONCLUSIONS

Spherical aberration becomes important when the size of the blur circle is larger than the size of the Airy disk due to diffraction. While the diameter of the diffraction disk decreases with increasing relative aperture $\rho = r/L$, the diameter of the blur circle increases approximately as the cube of ρ . The intersections of these curves show that spherical aberration becomes important at smaller apertures as the lenses increase in focal length (or size) so that for a lens of focal length $L = 100 \mu\text{m}$, ρ can be as large as 0.56, but ρ is reduced to 0.33 when $L = 10^3 \mu\text{m}$ and to 0.18 when $L = 10^4 \mu\text{m}$ [13]. The theoretically reconstructed focal length L and relative aperture ρ are presented in Table 2 for the trilobites investigated. The wide aperture of the lenses of phacopid trilobites and their comparatively large diameter indicate

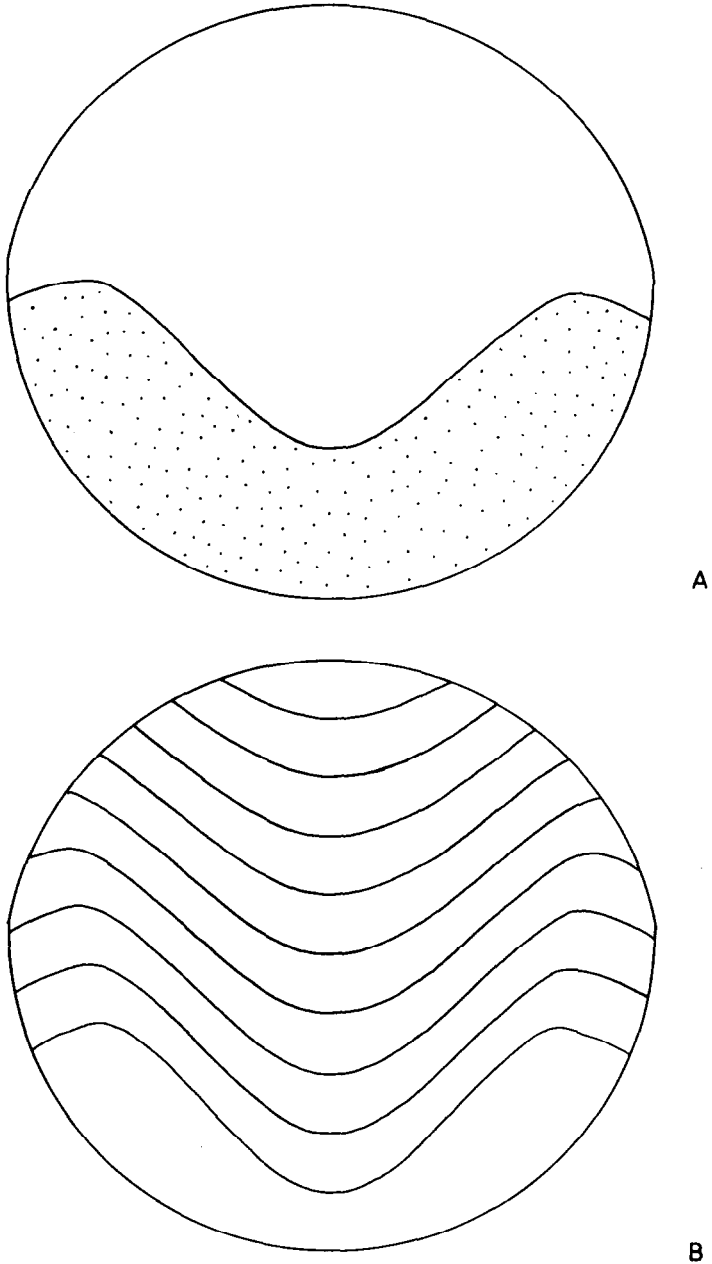


FIG. 5. (a) The theoretical aspherical curve most similar to the real aspherical lens interface of the trilobite *Crozonaspis struwei*. (b) Family of theoretical aspherical lens curves obtained by varying the parameter a . The other parameters are equal to those in Figure 5(a).

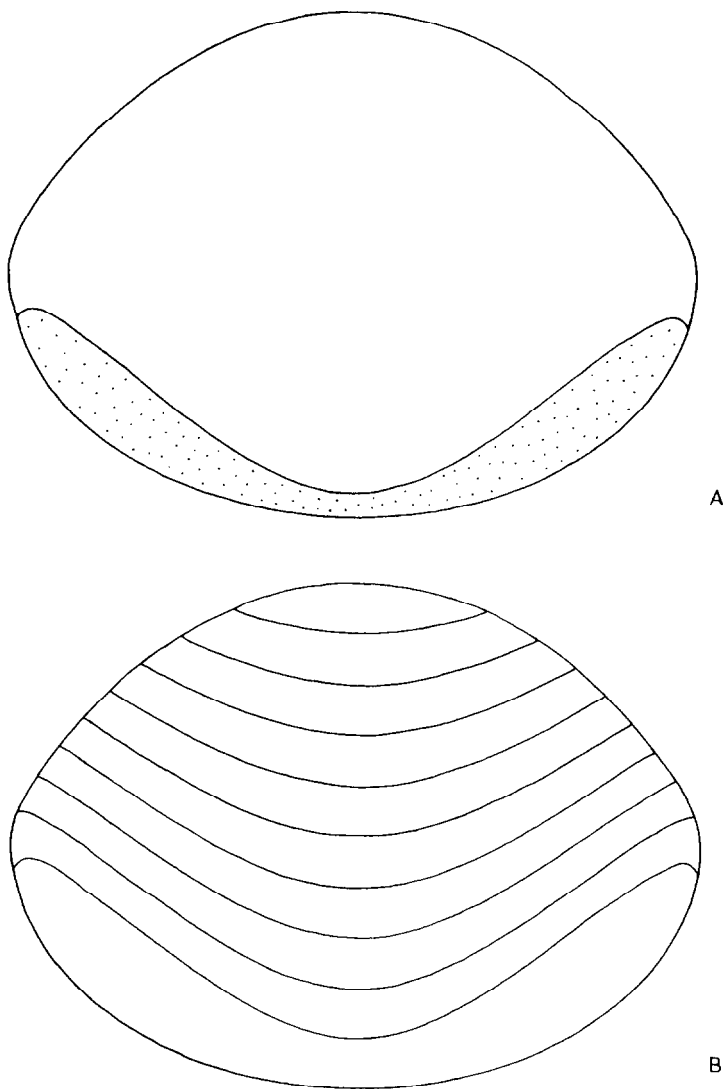


FIG. 6. Theoretical aspherical curves for *Dalmanitina socialis*.

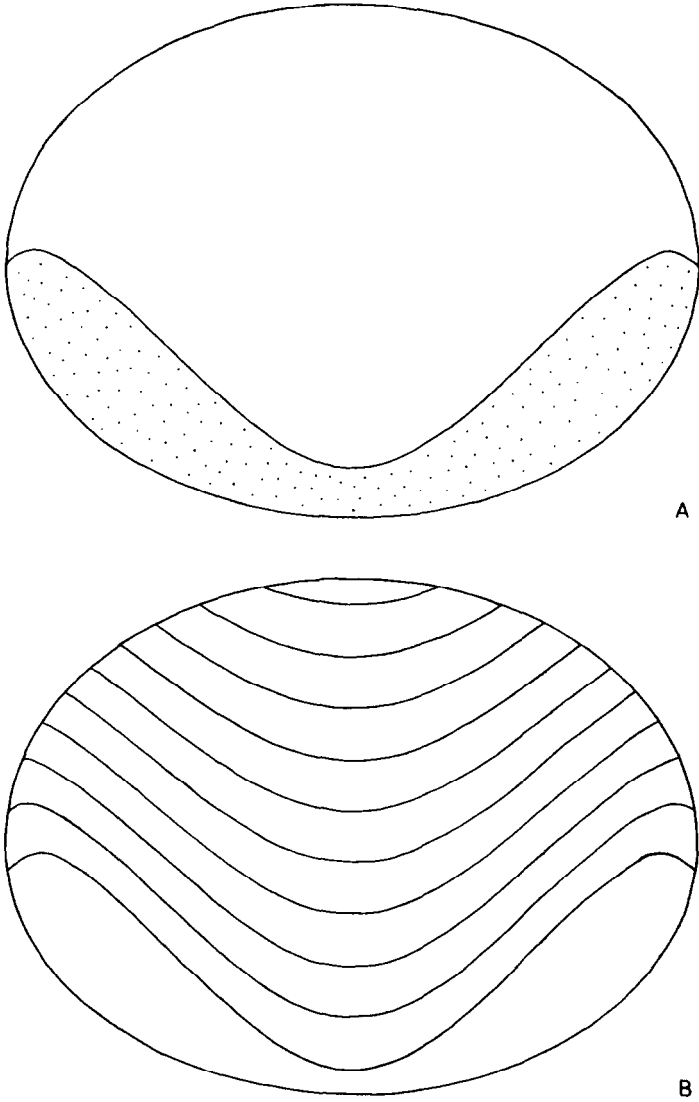


FIG. 7. Theoretical aspherical curves for a Silurian *Dalmanites*.

TABLE 2

Focal Length L of the Corneal Lens, Refractive Index n_3 of the Intralensar Bowl, and Relative Aperture $\rho = r/L$ Reconstructed Theoretically for Three Trilobites

<i>Crozonaspis struwei</i>
$L = 175 \mu\text{m}$, $\rho = 0.930$, $n_3 = 1.53$ (hydrated chitinlike substance)
<i>Dalmanitina socialis</i>
$L = 213 \mu\text{m}$, $\rho = 0.775$, $n_3 = 1.40$ (wet jellylike substance)
Silurian <i>Dalmanites</i>
$L = 234 \mu\text{m}$, $\rho = 1.965$, $n_3 = 1.40$ (wet jellylike substance)

that spherical aberration would have been severe enough to warrant correction.

In this work I have presented a general, theoretical, geometric optical method to calculate the shape of the aspherical interface that eliminates longitudinal spherical aberration in a thick lens with a doublet structure. I applied this method for the large and thick corneal lenses of some phacopid trilobites with schizochroal eyes. I looked for those theoretical aspherical interfaces that are the most similar to the shape of the real ones of the investigated trilobites. I varied the value of the focal length of the corneal lens and the refractive index of the intralensar bowl. Thus I could reconstruct the real value of these parameters quickly and easily.

The lower unit of the corneal lens has disappeared in the fossils and been replaced; therefore its composition can be reconstructed only theoretically. The following can be assumed on the basis of Table 2. The thick intralensar bowl of *Crozonaspis struwei* was made possibly of hydrated chitin, because $n_3 = 1.53$ is nearly high enough to be chitin or a similar dry protein (the refractive index of dry chitin is 1.56; when hydrated the value decreases). The thin intralensar bowls of *Dalmanitina socialis* and Silurian *Dalmanites* were made possibly of a jellylike substance, because $n_3 = 1.40$ implies a fairly wet jelly.

The shape of the theoretical aspherical interface agrees well with the real one for *Crozonaspis struwei* and a Silurian *Dalmanites*. In the former the intralensar bowl is relatively thick; in the latter it is thinner, and in both it is indented with a wide depression. In the trilobite *Dalmanitina socialis* the theoretical intralensar bowl is thin, like the real one, but the aspherical surface, the shape of which is similar to that of the other two investigated trilobites, is not indented centrally with a small dimple.

The corneal lens of phacopid trilobites near the optical axis can be approached with a plane-parallel lens for any trilobite, so the curvature of the theoretical aspherical surfaces is quite constant near the optical axis. Thus it is clear that in the trilobite *Dalmanitina socialis* also the theoretical aspherical interface is indented with a wide depression. The central small

dimple in the real cornea of *Dalmanitina socialis* cannot be explained on the basis of the presented geometric optical theory.

I also investigated the shape of the aspherical interface for different values of the parameter a and obtained a family of curves from which the following can be concluded. If the intralensar bowl is thin ($a \approx c$), then the aspherical interfaces cross the exit surface of the corneal lens [see Figures 5(b), 6(b), and 7(b)], so the whole of the cornea can be aplanatic (without longitudinal spherical aberration). If the intralensar bowl is very thick ($a \ll c$), then the aspherical interfaces cross the entrance surface of the corneal lens [see Figures 5(b), 6(b), and 7(b)], so only a central part of the cornea can be aplanatic. The phacopid trilobites had very large lenses, which increased the intensity of light received by an individual cornea in the dim light of their environment [14]. These trilobites, then, did not have a very thick intralensar bowl in their lenses, or the spherically corrected corneal lenses would have been disadvantageously smaller in diameter.

Why does the composition of the intralensar bowl of *Crozonaspis struwei* differ from that of *Dalmanitina socialis* and the Silurian *Dalmanites*? The relative thickness of the intralensar bowl, $Q = (c - a)/(c + d)$, can be seen in Table 1 for these trilobites. It would be disadvantageous if a considerable part of the corneal lens consisted of a soft, jellylike substance; therefore the lower lens unit consists of hard chitin in the cornea of *Crozonaspis struwei*, which has a thick ($Q = 0.25$) intralensar bowl, whereas thin ($Q = 0.06$ or 0.11) intralensar bowls can consist of soft jelly in the cornea of *Dalmanitina socialis* and the Silurian *Dalmanites*.

Thanks are due to Professor P. Greguss, Applied Biophysics Laboratory, Technical University, Budapest; Dr. Z. I. Nagy, Institute of Paleontology, Hungarian National Museum; Dr. A. Galácz, Department of Paleontology, R. Eötvös University, Budapest; and I. Jánosi, Department of Surface Science, R. Eötvös University, for their continuous help, advice, and support.

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