



# Image formation by bifocal lenses in a trilobite eye?

József Gál<sup>a</sup>, Gábor Horváth<sup>a,\*</sup>, Euan N.K. Clarkson<sup>b</sup>, Ottó Haiman<sup>a</sup>

<sup>a</sup> Department of Biological Physics, Eötvös University, Pázmány Péter sétány 1, H-1117 Budapest, Hungary

<sup>b</sup> Department of Geology and Geophysics, Grant Institute, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW, UK

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## Abstract

In this work we report on a unique and ancient type of eye, in which the lower surface of the upper calcite lens units possessed an enigmatic central bulge making the dioptric apparatus similar to a bifocal lens. This eye belonged to the trilobite *Dalmanitina socialis*, which became extinct several hundred million years ago. As far as we know, image formation by bifocal lenses of this kind did/does not occur in any other ancient or modern animal visual system. We suggest that the function of these bifocal lenses may be to enable the trilobite to see simultaneously both very near (e.g. floating food particles and tiny preys) and far (e.g. sea floor, conspecifics, or approaching enemies) in the optical environment through the central and peripheral lens region, respectively. This was the only reasonable function we could find to explain the puzzling lens shape. We admit that it is not clear whether bifocality was necessary for the animal studied. We show that the misleading and accidental resemblance of an erroneous correcting lens surface (designed by René DesCartes in 1637 [DesCartes, R. (1637). *Oeuvres de DesCartes. La Géométrie*. Livre 2. pp. 134. J. Maire, Leyden] to the correcting interface in the compound *Dalmanitina* lens may be the reason why the earlier students of the *Dalmanitina* lens did not recognize its possible bifocality. © 2000 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The first trilobites (which first appeared in the higher part of the Lower Cambrian, about 520 million years ago) were already highly organised animals and possessed ‘compound eyes’ (Lindström, 1901; Clarkson, 1975, 1979). In the fossilized eyes of trilobites only the lenses and adjacent regions of the exoskeleton are ever preserved and this only because they were constructed of calcite. In trilobites there were three different known eye types: holochroal, abathochroal and schizochroal (Horváth, Clarkson & Pix, 1997). Schizochroal eyes originated from holochroal precursors (Clarkson & Zhang, 1991; Clarkson & Taylor, 1995), while the abathochroal eyes can be considered as intermediates between holochroal and schizochroal eyes (Jell, 1975; Gál, Horváth & Clarkson, 2000).

Visually the most enigmatic trilobite eye type is the schizochroal eye, which was confined to one trilobite

group only, the Ordovician to Devonian suborder Phacopina (Clarkson, 1975). Phacopid trilobites were generally, bottom-dwellers. The external appearance of mature schizochroal eyes was characterized by well-separated large circular lenses of relatively small number (from a few to several tens). Each lens had its own cornea. The row of lenses ran nearly vertically across the curving visual surface and each line of optical axes was separated by a significant angle from the next line. The lenses consisted of two optically homogeneous units of different refractive indices. The upper lens unit was in vivo composed of calcite with its crystallographic *c*-axis normal to the visual surface (Clarkson, 1979) thus minimising the influence of double-refraction (calcite is not birefringent along its *c*-axis). The lower lens unit may have been composed of an organic material (Horváth, 1989). The most remarkable feature of these doublet lenses was that they were corrected for spherical aberration due to an undulating interface (recalling Huygens surface) between the lens units (Clarkson & Levi-Setti, 1975; Horváth, 1989).

Although several anatomical and optical characteristics of the schizochroal trilobite eyes were brought to

\* Corresponding author. Tel.: +361-372-2765; fax: +361-372-2757.

E-mail address: gh@arago.elte.hu (G. Horváth)

light in the last decades (e.g. Lindström, 1901; Clarkson, 1966a,b, 1967, 1968, 1969, 1971, 1975, 1979; Towe, 1973; Campbell, 1975; Clarkson & Levi-Setti, 1975; Levi-Setti, 1975, 1993; Cowen & Kelly, 1976; Stockton & Cowen, 1976; Miller & Clarkson, 1980; Feist &

Clarkson, 1989; Fordyce & Cronin, 1989, 1993; Horváth, 1989, 1996; Horváth & Clarkson, 1993), many unknown features remained to be revealed. One of them is the function of an enigmatic small central bulge on the proximal lens surface in some trilobites. Recently, it was reported that the trilobite *Neocobboldia chinlinica* (Zhang & Clarkson, 1990) had calcite lenses with such a bulge (Levi-Setti, Clarkson & Horváth, 1998). Since these lenses were very tiny (their diameter was not larger than about 20  $\mu\text{m}$ ) and thus diffraction-limited, any ray optical function of this bulge may be doubted (Gál et al., 2000).

However, the proximal surface of the upper calcite unit in the great (330  $\mu\text{m}$  in diameter) doublet lens of the schizochroal-eyed trilobite *Dalmanitina socialis* described earlier by Clarkson (1968), Clarkson and Levi-Setti (1975) and Levi-Setti (1975, 1993) also possessed a similar bulge. Due to the relatively great dimension of the lens and its bulge, the latter could influence the optical performance of the lens. According to Levi-Setti et al. (1998), ‘... In view of the similarity of the lens profile in *Neocobboldia* with that of the schizochroal lenses of *Dalmanitina*, that did not conform to the Huygensian shape found in other schizochroal lenses, it is tempting to associate a bifocal function to the latter as well.’ To clear up the possible optical function of this puzzling bulge, we have reinvestigated the optics of the lens of *D. socialis* in this work.

## 2. Materials and methods

### 2.1. Anatomical reconstruction of the lens profile in *D. socialis*

*D. socialis* from the Upper Ordovician (Caradoc) Letná Formation of Bohemia is a relatively large trilobite preserved in a fine sandstone (Fig. 1A). The original exoskeletal material has been removed by percolating groundwater, leaving moulds of the outer and inner surfaces preserved in the sandy matrix. This trilobite has prominent schizochroal eyes and the shapes of the lenses are well-preserved, though in negative relief. In some internal moulds the proximal surface of the lens is preserved, in others it is the interface between the lower lens unit (called the intralensar bowl) and the upper lens unit. In such instances the intralensar bowls must have fallen out after the death of the trilobite and before it was finally preserved. All this means that there are three surfaces which may have been preserved as moulds and from these it is possible to reconstruct not only the shape of the doublet lens as a whole, but also the precise contour of the interface between the lower and upper lens units.

The surfaces of the eyes of different specimens were replicated using a rubber latex solution, so that ‘posi-

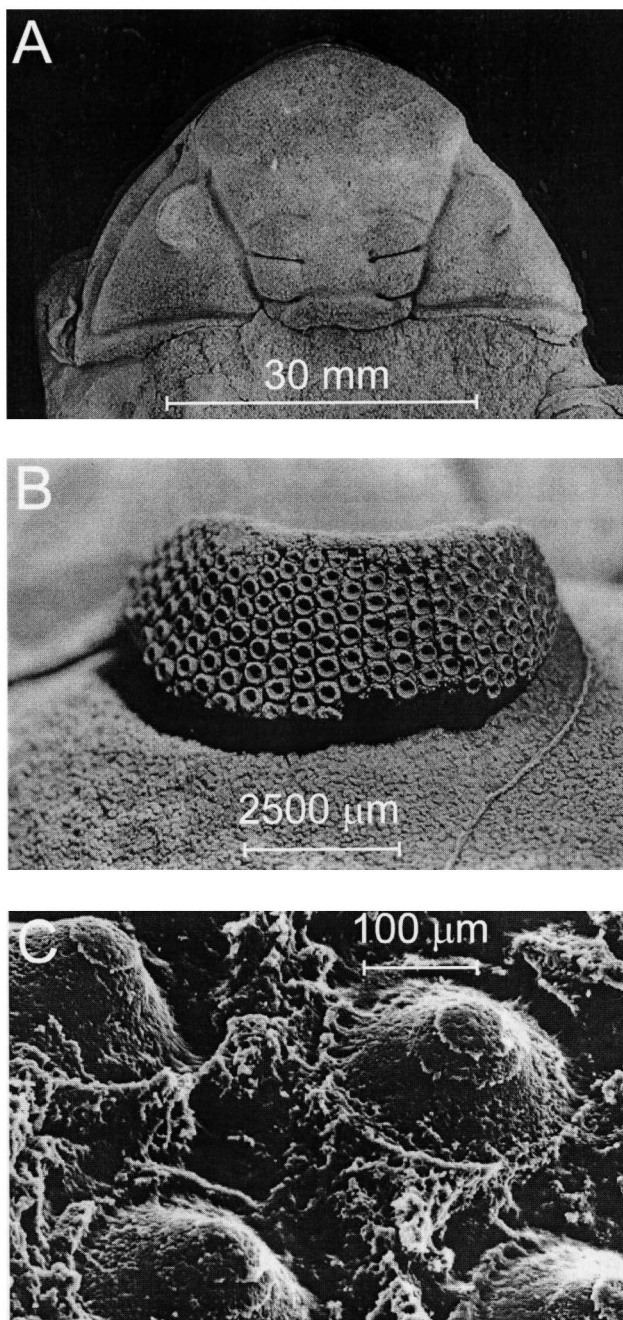


Fig. 1. Fossil remains of the Upper Ordovician (Bohemia), phacopid, schizochroal-eyed trilobite, *Dalmanitina socialis*. (A) Head of specimen preserved as an internal mould (original exoskeleton dissolved), showing position of eyes (light photomicrograph). (B) Left eye of same, showing lenses preserved as internal moulds (photomicrograph). (C) Latex replica of the lenses of same, showing the under-surface of the upper lens unit, with central nipple (SEM photograph).

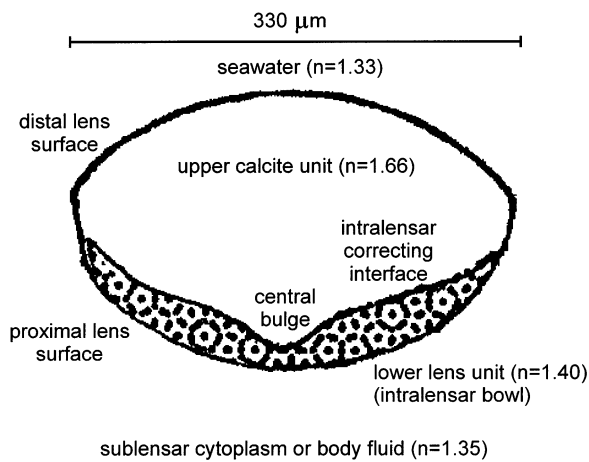


Fig. 2. The reconstructed shape (in a vertical, main cross section) of the *Dalmanitina* doublet lens. The upper calcite unit of the lens has a central bulge on its lower surface (original drawing of Clarkson, 1968).

tives' were obtained, showing the appearance of the lenses before solution; such replicas were then coated with gold-palladium and high-resolution photographs were made with a scanning electron microscope. Other replicas were made and sectioned to show the precise shape of the lens in planes parallel to the lens axis. These replicas gave all the information required for biooptical calculations.

## 2.2. Computational reconstruction of the optics of *Dalmanitina* lenses

The reconstructed shape of the *Dalmanitina* lenses was digitized with a scanner (Hewlett Packard ScanJet 6100C). In order to describe mathematically the refractive (distal or entrance, intralensar and proximal or exit) surfaces of the lenses, polynomials of different orders were fitted to the digitized points of these profiles. Using the law of refraction, a computer-aided tracing for paraxial rays of light was performed through the lenses. The paths of light rays were treated as refractions by the outer and inner lens surfaces and translations through the lenses. Thus, calculations for rays parallel to the optical axis gave the principal focal length (measured from the geometrical center of the lens) of various segments of the lenses.

Throughout the text we use the term 'back vertex distance of the focal point', which is the distance of the focal point measured from the lowermost point of the proximal lens surface. The principal focal length is the sum of the back vertex distance of the focal point and the distance of the geometrical center of the lens measured from the lowermost point of the proximal lens surface.

The rays were drawn with a greater density in those regions of the lenses for which the back vertex distance

of refracted rays remained approximately constant. It was assumed that the distal surface of the lenses was immersed in seawater with an index of refraction of 1.33, while the inside was in contact with cytoplasm (or body fluid) with a refractive index of 1.35. The refractive index of the calcite along its *c*-axis is 1.66. In the schizochroal doublet lens of *D. socialis* the refractive index of 1.4 of the lower lens unit was earlier reconstructed by Horváth (1989, 1996). The change of the back vertex distance of refracted rays of light was calculated as a function of the radial distance of the paraxially incident rays. It was assumed that there had been a small sublensar retina beneath every lens in the schizochroal trilobite eyes. On the basis of Horváth and Clarkson (1993), for both focal lengths of the lenses the depth of field in object space was calculated for different values of the receptor separation as a function of the retinal distance from the lens. The Huygensian correcting surfaces presented in Fig. 4B–D were calculated on the basis of the method described by Horváth and Clarkson (1993).

## 3. Results

### 3.1. Lens profile and change of the back vertex distance of refracted rays

Fig. 1 shows scanning-electronmicrographs of the fossil remains of the trilobite *D. socialis*. We can see in Fig. 1B,C that the missing upper lens units of *Dalmanitina* have left an imprint with a typical central dimple. Fig. 2 represents the reconstructed shape of the lens in *Dalmanitina*. The distal surface of the lens possesses a convex profile. It is, however, of particular importance that a small but pronounced bulge occurs on the lower surface of the upper calcite unit of the lens. This bulge corresponds to the dimples in the imprint of the lenses shown in Fig. 1B,C. Due to the bulge, the curvature and the refractive power of the central region of the lens are greater than those of the peripheral zone. This means qualitatively that the lenses in *Dalmanitina* should have two different focal lengths.

The calculated ray tracing through the schizochroal lens in *Dalmanitina* is shown in Fig. 3. Fig. 3B represents the change of the back vertex distance of refracted rays in the lens as a function of the radial distance of paraxially incident rays. We can read in Fig. 3 that zones 1 and 3 of the lens are characterized by the relatively sharp focal points  $F_{\text{near}}$  and  $F_{\text{far}}$ , respectively, while in zones 2 and 4 the back vertex distance changes gradually between  $F_{\text{near}}$  and  $F_{\text{far}}$ . Using the methods described above, we have investigated several lenses of *Dalmanitina*, and obtained the same results as in Figs. 1–3.

On the basis of Fig. 3 we can establish that apart from the outermost zone 4 the lenses in *Dalmanitina* meet the requirement of bifocality: they have two distinct, sharp focal lengths which are constant for a given range of the radius. The central zone 1 has a smaller focal length than the peripheral annular zone 3, and the back vertex distance of refracted rays changes gradually in the intermediate zone 2. The most peripheral zone 4 possesses no exact focal length and its surface is relatively great in comparison with the inner zones, which would have had a disadvantageous influence upon image formation. However, *Dalmanitina* could have avoided this by a proper ring of screening pigments below and around their lenses, which ring would eliminate the most peripheral rays, as in the eyes of many recent arthropods (Land, 1981). The numerical values of the reconstructed geometric optical parameters of the *Dalmanitina* lens are shown in Table 1.

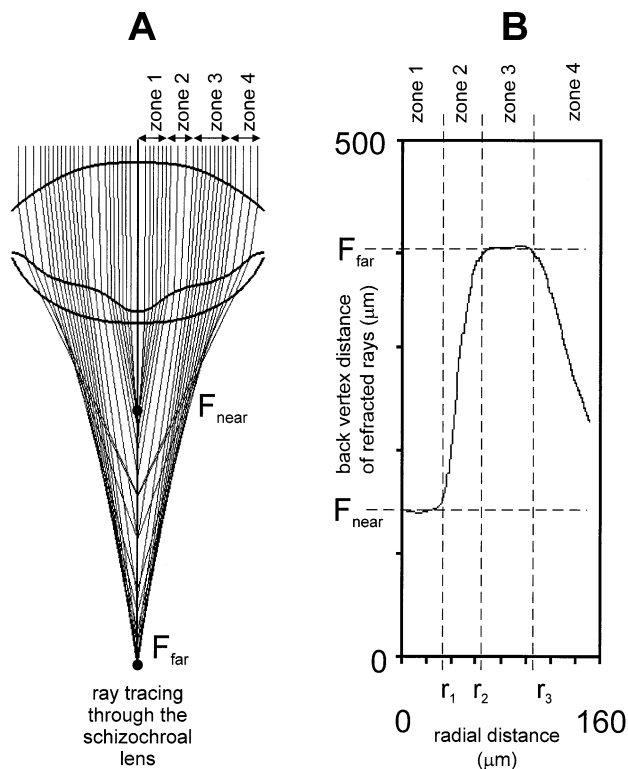


Fig. 3. Reconstruction of the change of the back vertex distance of refracted paraxially incident rays of light in the schizochroal doublet lens in *Dalmanitina socialis* portrayed in Fig. 2. (A) The tracing of paraxially incident rays of light. The density of rays was chosen to be greater in those regions of the lens (zones 1, 3) where the back vertex distance is approximately constant. The sharp focusing in zones 1 and 3 and the lack of focusing in zones 2 and 4 are clearly seen. (B) The change of the back vertex distance of refracted rays measured from the lowermost point of the central bulge as a function of the radial distance of the incident light rays. Zones 1 and 3 of the lens are characterized by the focal points  $F_{near}$  and  $F_{far}$ , respectively, while in zones 2 and 4 the back vertex distance changes gradually between  $F_{near}$  and  $F_{far}$ . Hence, apart from the most peripheral zone 4 the lens is bifocal.

Table 1

Geometric optical parameters of the reconstructed lens of the schizochroal-eyed trilobite *Dalmanitina socialis* portrayed in Fig. 2B<sup>a</sup>

Lens parameters	
Order of the polynomial fitted to the distal lens surface	6
Order of the polynomial fitted to the intralensar correcting interface	9
Order of the polynomial fitted to the proximal lens surface	6
Lens radius	165 $\mu\text{m}$
Back vertex distance of the near focal point $F_{near}$	139.1 $\mu\text{m}$
Near principal focal length $f_{near}^{principal}$	244.1 $\mu\text{m}$
Back vertex distance of the far focal point $F_{far}$	403.1 $\mu\text{m}$
Far principal focal length $f_{far}^{principal}$	508.1 $\mu\text{m}$
$r_1$	38 $\mu\text{m}$
$r_2$	62 $\mu\text{m}$
$r_3$	120 $\mu\text{m}$

<sup>a</sup>  $r_1$ ,  $r_2$  and  $r_3$  are the radial distances of the borders of the central and peripheral image forming regions of the lens in Fig. 3.

### 3.2. The erroneous central bulge of the original DesCartes design for a spherically corrected monofocal lens

According to Levi-Setti et al. (1998) ‘... In view of the similarity of the lens profile in *Neocobboldia* with that of the schizochroal lenses of *Dalmanitina*, that did not conform to the Huygenian shape found in other schizochroal lenses, it is tempting to associate a bifocal function to the latter as well.’ It is an interesting question, why the earlier investigators of the lens in *D. socialis* (Clarkson, 1968; Clarkson & Levi-Setti, 1975; Levi-Setti, 1975, 1993) did not discover the functional significance of the conspicuous central bulge, the cause of bifocality, which is a unique optical feature in the animal kingdom. The reason of this may be an erroneous calculation by René DesCartes (1637).

As Levi-Setti (1975, 1993) pointed out ‘... Long before trilobites were even recognized as ancient inhabitants of our planet, DesCartes in his *La Géométrie* (1637) ... had derived the general shape that the second refracting surface of a lens should have in order to eliminate spherical aberration ...’ In his famous book on trilobites Levi-Setti (1975, 1993) and also Clarkson & Levi-Setti (1975) cited the original drawing of DesCartes, which is here reproduced again in Fig. 4A. One can see that the correcting surface designed by DesCartes possesses also a small bulge on the optical axis. Clarkson and Levi-Setti (1975) and Levi-Setti (1975, 1993) recognized that ‘... The intermediate surface [in the lens of *Dalmanitina socialis* (Fig. 2B)] is shaped in remarkable accord with the design by DesCartes [Fig. 4A] ...’ However, Horváth (1989) computed the shape of the intralensar correcting interface for the doublet lens in *D. socialis* and found that the

resulting profile does not possess any central bulge. Thus, DesCartes (1637) must have made a mistake. This is proven in Fig. 4B–D.

Fig. 4B–D shows the correcting profiles of three spherically corrected lenses — with spherical (Fig. 4B), parabolic (Fig. 4C) and hyperbolic (Fig. 4D) entrance (distal) surface — computed for different object distances as in the design by DesCartes (Fig. 4A). One can see that the computed correcting surfaces are centrally quite different from the correcting profile of DesCartes. The reason of this is that DesCartes made a simplification in his calculations so that he applied Fermat's

principle of least time erroneously. According to Levi-Setti (1975, p. 35), DesCartes did not impose the thickness of the lens.

Thus, the correcting lens surface designed by DesCartes is erroneous and its misleading resemblance to the correcting interface in the lens of *D. socialis* is accidental. In our opinion it is due to this unfortunate coincidence that the earlier students of the *Dalmanitina* lens did not recognize its possible bifocality.

Clarkson and Levi-Setti (1975) traced rays and made a large-scale optical model to show that the wavy interface between the upper and lower lens units in the trilobite *Crozonaspis struwei* corrects for spherical aberration. This evidence is convincing. The reader of the present work must not, however, think that the earlier analyses of Clarkson and Levi-Setti (1975) were totally erroneous because DesCartes has got his sums wrong. We would like to emphasize that Clarkson and Levi-Setti (1975) misinterpreted only the doublet lenses of *D. socialis* but not the spherically corrected, monofocal doublets in *C. struwei*. Ray tracing was performed and optical model was built and tested in water by Clarkson and Levi-Setti (1975) only in the case of the *Crozonaspis* lens resembling the Huygenian, spherically corrected, monofocal lens design, which is correct. Only the *Dalmanitina* doublets recall the Cartesian, spherically corrected, monofocal lens design, which however, is unfortunately erroneous.

### 3.3. Estimation of the influence of light diffraction on the optics of *Dalmanitina* lenses

The focal points of the bifocal trilobite lenses are blurred to some extent because of the diffraction of light. The image blur due to diffraction can be characterized by the so-called Airy disk. This is the bright patch of light surrounded by light and dark rings of decreasing intensity corresponding to the image of a point source. The radius of the Airy disk on the retina is  $R = 1.22f\lambda/2r$ , where  $f$  is the principal focal length and  $r$  the radius of the imaging apparatus;  $\lambda$  is the wavelength of light (Land, 1981).

We calculated the ratio  $q_c = R_c/r_1$  ( $R_c = 1.22f_{\text{hear}}^{\text{principal}} \lambda/2r_1$ ) for the central and  $q_p = R_p/r_3$  ( $R_p = 1.22f_{\text{far}}^{\text{principal}} \lambda/2r_3$ ) for the peripheral region of the bifocal lenses in *Dalmanitina* (see Table 1) for  $\lambda = 470$  nm, which is the typical wavelength of the quasi-monochromatic light under water due to selective absorption (Jerlov, 1976). This ratio gives the relative linear dimension of the image blur due to diffraction with respect to the linear dimension of the image forming (central or peripheral) lens region. In *Dalmanitina*  $q_c \approx 4.8\%$ ,  $q_p \approx 1\%$ . The numerical value of  $q_p$  can be considered, however, only as a first approximation, because zone 3 (Fig. 3) of the bifocal trilobite lenses is an annulus, at the inner rim of which light diffraction

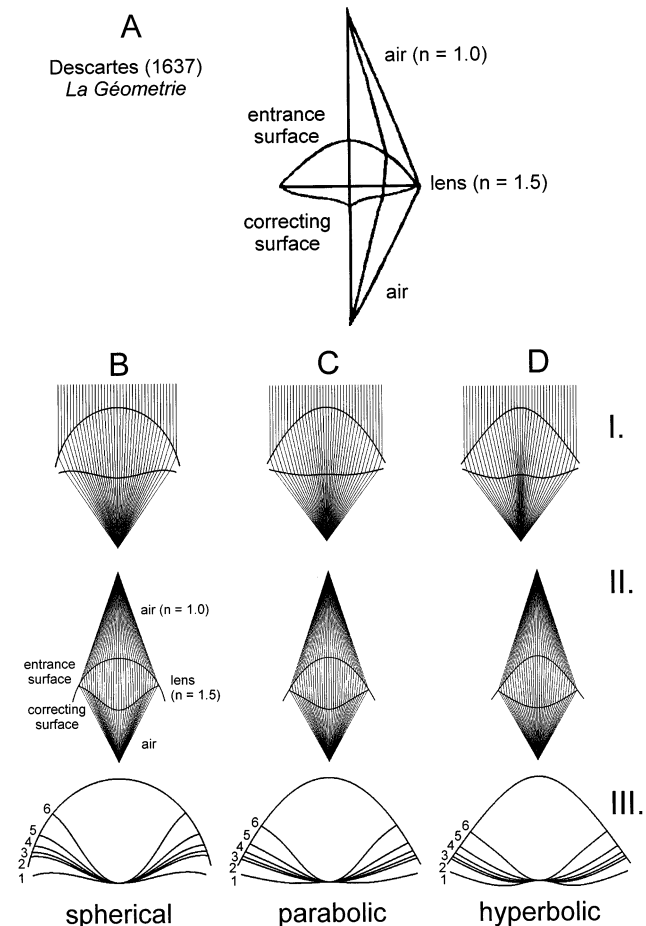


Fig. 4. (A) A monofocal lens with an index of refraction of 1.5 in air ( $n = 1.0$ ) free of spherical aberration constructed by Descartes (1637). The undulating shape of the correcting surface ensures that the lens has an exact focal point (with a small modification after Levi-Setti, 1993). (B–D) Profiles of different spherically corrected lenses ( $n = 1.5$ ) in air ( $n = 1.0$ ) computed for different object distances. As with the Descartes design, the undulating exit surface of the lens ensures the correction for spherical aberration for a given entrance surface, which is spherical (B), parabolic (C), or hyperbolic (D). (I) Ray tracing through the lens when the object is at infinity (for paraxial incident light rays). (II) Ray tracing for a finite object distance. (III) Profiles of the correcting surface as a function of the object distance, which is infinity for profile 1, and gradually decreases from profile 2 towards profile 6.

occurs too. This enhances, however, only slightly the value of  $q_p$ .

On the basis of these data we conclude that in *Dalmanitina* the image blur because of diffraction was negligible due to the relatively great aperture of the image forming central and peripheral lens regions. Thus, the bifocal feature of the lenses in *Dalmanitina* was not destroyed by diffraction; these schizochroal lenses possessed apparently two sharp focal points.

#### 3.4. Relative brightness of the two images formed by the bifocal *Dalmanitina* lenses

Since there is no doubt about the bifocality of the schizochroal doublet lens in *Dalmanitina* it is worth while to estimate the retinal illuminance produced by the central and peripheral lens regions when the eye views an extended surface of luminance  $L$ . According to Land (1981), the retinal illuminance can be calculated by  $E = L\pi(r/f)^2$ , where  $f$  is the principal focal length and  $r$  is the radius of the lens region considered. Then the retinal illuminance produced by the central and peripheral lens regions are given by  $E_c = L\pi(r_1/f_{\text{near}}^{\text{principal}})^2$  and  $E_p = L\pi(r_3^2 - r_2^2)/f_{\text{far}}^{\text{principal}^2}$ , respectively (see Table 1). For the *Dalmanitina* lens we obtain  $E_p = 1.7E_c$ . Thus, if the eye viewed an extended surface with a homogeneous illuminance, then the retinal illuminance produced by the peripheral lens region was 1.7 times greater than that produced by the central region.

This, however, does not mean that the image formed by the peripheral lens region in *Dalmanitina* was 1.7 times as bright as that formed by the central region because the peripheral region imaged distant objects while the central region imaged near objects (Fig. 6). Under water the intensity of light originating from an object decreases exponentially as a function of the distance from the object because of absorption and scattering (Jerlov, 1976). The more turbid the water, the stronger is the attenuation of light therein. In turbid and clear sea water the intensity of light originating from an object can decrease by a factor of 1.7 within a few decimetres and some metres, respectively (Lythgoe, 1979). Moreover in turbid water the contrast of remote objects is also reduced. Thus, the greater light collecting efficiency of the peripheral lens region in the *Dalmanitina* eye might compensate the contrast reduction and greater attenuation of light originating from distant aquatic objects. Unless they are well above the horizon such remote aquatic objects may well be brighter than nearby ones (Jerlov, 1976; Lythgoe, 1979).

#### 4. Discussion

What could *D. socialis* have seen with its bifocal lenses? In order to answer this question, some knowl-

edge of the photoreceptors beneath the lens is needed. Unfortunately, the sublensar tissues in trilobite eyes have disappeared during fossilization and diagenesis, thus one can only speculate about their structure.

Fordyce and Cronin (1993) gave evidence suggesting that each of the individual lenses of the holochroal trilobite eye had its single photoreceptor and that the eye as a whole functioned in a manner similar to that of modern arthropods, being especially adapted to moderate to dim light. On the other hand, in its structure and optical optimization, the schizochroal dioptric apparatus recalls the ocellar eye of larvae of the sawfly *Perga* (Meyer-Rochow, 1974), therefore Campbell (1975) suggested that the sublensar tissue in schizochroal-eyed trilobites might also be similar to an ocellar retina. Most investigators (e.g. Campbell, 1975; Clarkson and Levi-Setti, 1975; Stockton and Cowen, 1976; Fordyce and Cronin, 1989; Horváth, 1989; Levi-Setti, 1993) share the belief that each lens in the schizochroal trilobite eyes had a tiny retina behind it, thus the schizochroal eye type might have been a 'stemmataran compound eye' (Horváth et al., 1997). Furthermore bifocality would be entirely valueless if the individual lenses possessed only a single photoreceptor behind them. Thus one may suppose that there was a small retina below every bifocal lens in *Dalmanitina*.

Supposing that *Dalmanitina* had sublensar retinae with a given receptor separation  $RS$ , and that the retinae were a single plane of negligible depth (which was true if the photoreceptors were short or if they were long but were optically isolated from each other; Land, 1981), the depth of field in object space over which the image is 'in focus' can be estimated for both the near and far focal points as a function of the retinal distance measured from the lens. The depth of field in object space means the range of object distances that produces blurs on the retina whose radii do not exceed the receptor separation. From Fig. 5A the definitions of the different terms associated with the depth of field can be read. If a point object is positioned in the sharp point  $SP$  in front of the lens, its image  $I_{SP}$  is formed on the plane of the retina. When the point object is displaced by the far depth of field towards the far point  $FP$ , or by the near depth of field towards the near point  $NP$ , its image is formed in front of ( $I_{FP}$ ) or behind ( $I_{NP}$ ) the retina, respectively, and thus, the image is blurred in the plane of the retina. In spite of this image blur  $IB$  (which is the diameter of the blur circle), however, the retina perceives the point object as being sharp until  $IB$  is not greater than about twice  $RS$ .

Fig. 5B shows qualitatively the change of the object distance as a function of the retinal distance  $RD$  from the lens if the object is positioned in the far ( $FP$ ), sharp ( $SP$ ) or near ( $NP$ ) point in front of the eye. It is a general rule that the near, sharp and far object distances, and furthermore the near and far depth of field

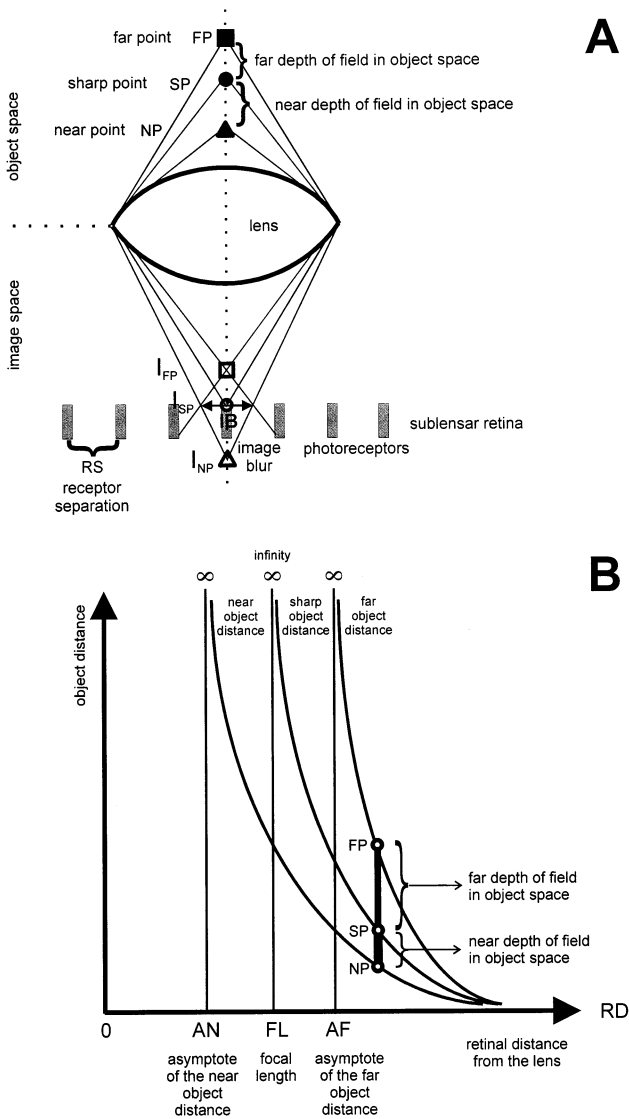


Fig. 5. (A) Definition of the far point FP, sharp point SP, near point NP, image blur IB, far and near depth of field in object space of a point object in front of an eye composed of a lens and a sublensar retina with a given receptor separation RS. If the object point is positioned in SP, then its sharp image  $I_{SP}$  is formed on the retina. When the object is displaced towards FP or NP, its image is formed in front of ( $I_{FP}$ ) or behind ( $I_{NP}$ ) the retina, respectively, and thus the image is blurred in the plane of the retina. In spite of this blur however, the retina perceives sharply the object point as long as  $IB < RS$ . (B) The change of the object distance as a function of the retinal distance from the lens if the object is positioned in the far (FP), sharp (SP) or near (NP) point in front of the eye.

increase as RD decreases. The far, sharp and near object distances become infinite if RD is smaller than AF (asymptote of the far object distance). FL (focal length) and AN (asymptote of the near object distance), respectively. Thus, the far and near depth of field is finite if  $RD > AF$  and  $RD > FL$ , respectively.

Fig. 6 summarizes the image formation by a ‘facet’ (composed of a bifocal lens and a sublensar retina) of the supposed stemmataran compound eye in *Dalman-*

*itina*. If the retina was placed between the lens and  $F_{near}$ , no image could be formed on it (Fig. 6A). If the retina was at  $F_{near}$ , sharp images could be formed on it by the central region (bulge) of the lens (with greater refractive power) from objects positioned in the far field or infinity (Fig. 6B). If the retina was placed between  $F_{near}$  and  $F_{far}$ , sharp images could be formed on it by the central lens region from intermediate-field objects (Fig. 6C). If the retina was placed at  $F_{far}$ , sharp images could be formed on it either by the central lens region from intermediate-field objects, or by the peripheral lens region (with smaller refractive power) from far-field objects or from objects being at infinity (Fig. 6D). If the retina was placed beyond  $F_{far}$ , sharp images could be formed on it either by the central lens region from near-field objects, or by the peripheral lens region from far-field objects (Fig. 6E).

On the basis of Fig. 6 we can establish that *Dalmanitina* could have taken advantage of the bifocality of its lenses only if its sublensar retinæ were placed at or beyond the far focal point  $F_{far}$  (Fig. 6D,E). The optimal position of the retina is apparently the far focal point  $F_{far}$  (Fig. 6D).

Let us compare the features of bifocal lenses in *Dalmanitina* with features of common monofocal trilobite lenses. If the lenses possessed only a single focal length and a finite depth of field in object space, the image of objects placed either in the near-field or in the far-field of the optical environment would have been out of focus. Thus, the evolutionary importance of the bifocal trilobite lenses may be that: (1) using such lenses, trilobites could monitor their distant visual environment in order to detect approaching enemies, conspecifics or the features of their habitat at a remote distance, and at the same time, (2) the trilobites could inspect the finer details of the objects (e.g. food particles or tiny preys) next to them.

If the depth of field of an eye with a fixed and rigid dioptric apparatus is small (either due to a small receptor separation in the retina, or because of a large lens diameter; see Fig. 5A), then a bifocal lens is advantageous, because it ensures sharp image formation and simultaneous but separate perception for both remote and near objects, that is, it extends the depth of explorable field in object space. Perhaps this is the reason why *Dalmanitina* used bifocal lenses. Another possible solution to this optical problem is, of course, to use a visual system, the depth of field of which practically overlaps with the biologically important object distances. This might have been the case generally in most schizochroal trilobite eyes (Horváth and Clarkson, 1993).

Beside the lens diameter, the depth of field depends, as already mentioned, greatly on the density of photoreceptors in the retina. Unfortunately, nothing is known about this parameter in the eyes of trilobites,

thus the value of the receptor separation RS can only be estimated on the basis of modern counterparts (Horváth et al., 1997). In the eye of *Perga* intersegmental spacings are between  $RS = 15$  and  $20 \mu\text{m}$  (Meyer-Ro-

chow, 1974), for instance. In the distal retina of the pallial eye of scallop *Pecten* the receptor separation  $RS \approx 3\text{--}5 \mu\text{m}$  in the centre, and  $RS \approx 8\text{--}10 \mu\text{m}$  towards the edges (Land, 1968).

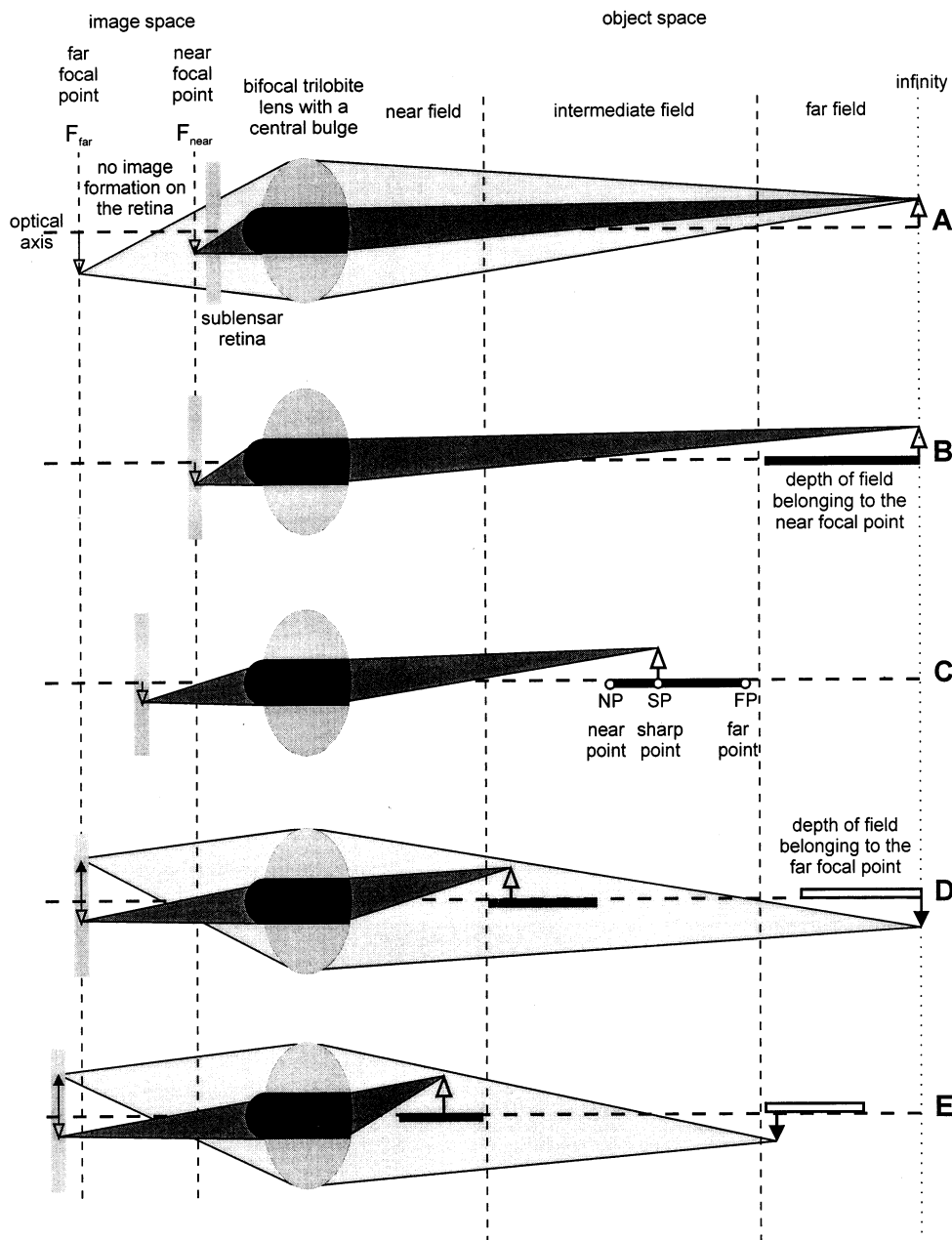


Fig. 6. Diagrammatic representations of image formation by a bifocal trilobite lens as dependent on the position of the sublensar retina and the object distance. The retina is represented by a vertical grey bar. The objects and their reverted images are symbolized by arrows. The central and peripheral regions of the lens with different focal lengths are shaded in different grey tones. The depths of field belonging to the near and far focal point are represented on the optical axis by horizontal black and white bars, respectively. The near (NP) sharp (SP) and far (FP) points of the object are represented in row C. The object space is divided into three zones: near field, intermediate field and far field. In the object space the infinity is symbolized by a vertical dotted line. (A) If the retina is placed between the lens and  $F_{\text{near}}$ , no image can be formed on it. (B) If the retina is at  $F_{\text{near}}$ , sharp images can be formed on it by the central region (bulge) of the lens (with greater refractive power) from objects positioned in the far field or at infinity. (C) If the retina is placed between  $F_{\text{near}}$  and  $F_{\text{far}}$ , sharp images can be formed on it by the central lens region from intermediate-field objects. (D) If the retina is placed at  $F_{\text{far}}$ , sharp images can be formed on it either by the central lens region from intermediate-field objects, or by the peripheral lens region (with smaller refractive power) from far-field objects or from objects being at infinity. (E) If the retina is placed beyond  $F_{\text{far}}$ , sharp images can be formed on it either by the central lens region from near-field objects, or by the peripheral lens region from far-field objects.



Table 2  
The distance of the near point NP, sharp point SP and far point FP from the proximal lens surface<sup>a</sup>

Retinal distance	Receptor separation	Central lens region			Peripheral lens region		
		NP	SP	FP	NP	SP	FP
404 $\mu\text{m}$	15–20 $\mu\text{m}$	0 $\mu\text{m}$	300 $\mu\text{m}$	0.5 cm	0.5 cm	43 cm	$\infty$

<sup>a</sup> Computed for the central and peripheral regions of the bifocal lens in *Dalmanitina socialis* (Figs. 2B and 4) for receptor separations ranging from 15 to 20  $\mu\text{m}$  when the retina is placed at the far focal point  $F_{\text{far}}$  (Fig. 6D).

Both the retinal distance and receptor separation in the eye of *Dalmanitina* are unknown. Thus, the most that we can do — after trilobites have extincted several hundred million years ago — is to find out whether there exist such receptor separations at which *Dalmanitina* could take advantage of its bifocal lenses. In this case the near and far depth of field should be separated as represented in Fig. 6D, or else there would be no reason to use two different focal lengths. Table 2 proves that there exist such situations for *Dalmanitina*.

*Dalmanitina* could take advantage of the bifocality of its schizochroal lenses if the receptor separation was about 15–20  $\mu\text{m}$  and the retina was placed at the far focal point. We can see in Table 2 that for *Dalmanitina* the depth of field of the central lens region ranges up to 0.5 cm from the lens and the depth of field of the peripheral lens region extends from 0.5 cm to infinity, if  $RS = 15\text{--}20 \mu\text{m}$  and  $RD \approx 404 \mu\text{m}$ , for instance.

Since the intermediate zone 2 of the bifocal lens is almost as wide as the central zone 1, furthermore the effect of off-axis rays on the image formation was not quantitatively investigated, the following questions arise: Does zone 2 not obliterate the near-field image? How do zones 2 and 3 degrade the near field image when extended sources are viewed? Is the near field image washed out by off-axis light from zones 2 and 3?

Since there are about 30 lenses in a horizontal row of the *Dalmanitina* eye having an overall field of view of ca. 300° in a horizontal plane, the field of view of an individual lens is not larger than about 10°. In the case of such a relatively narrow field of view off-axis rays cannot do too serious mischief. This is the reason why only tracing of axial rays is presented. The near field image are not washed out by off-axis light from zones 2 and 3.

Of course, the intermediate zone 2 reduces slightly the contrast of both the near- and far-field images. However, the back vertex distance of refracted rays changes gradually in zone 2, the area of which is smaller than that of zone 3. Thus, the illuminance produced by the converging (but not focussed) rays passing through zone 2 is much smaller than that of the near- and far-field images.

This situation is quite similar to the problem of converging light rays in the mirror-lens eye of the

scallop *Pecten*, for instance, investigated accurately by Land (1965, 1968) and Horváth and Varjú (1993). In the *Pecten* eye sharp image is formed on the upper retina placed between the lens and spherical mirror (called the *argentea* or *tapetum lucidum*). The contrast of the image is considerably reduced by the converging rays passing twice through the retina: after (i) refraction at the lower lens surface and (ii) reflection from the mirror. This effect, however, does not obliterate the image formed on the upper retina (Land, 1965; Horváth and Varjú, 1993).

The effect of the converging rays from zone 2 on the near-field image in the *Dalmanitina* eye is smaller than the influence of the converging rays on the image formed at the upper retina of the *Pecten* eye, because the latter rays pass twice the plane of focus. Consequently, light rays passing through zone 2 does not obliterate the near-field image.

On the basis of the above arguments we conclude that zone 1 of the bifocal *Dalmanitina* lens is not too small at all, and the rays that it admits are not swamped by off-axis rays from the outer lens regions. The near field image is not degraded by rays from zones 2 and 3. One might wonder which swamping would be more dangerous for the animal: that one by outer-zone light (affecting images formed by the inner-zone lens component, the bulge), or that one by the inner-zone light, i.e. from near objects, affecting outer-zone images, e.g. of potential enemies. This may have been a reason for developing seemingly too small bulges.

The aim of this work was to suggest a possible optical function of the bulge of the *Dalmanitina* lens. Table 2 shows that in the eye of *D. socialis* bifocality is a reasonable function, actually the only one we could find till now. The central lens region with its depth of field ranging from 0 to 0.5 cm could help to detect food particles and tiny animals (prey) floating next to the trilobite, for example. On the other hand, the peripheral lens region with its depth of field ranging from 0.5 cm to infinity made it possible to the trilobite to see sharply its entire remote optical environment.

Fig. 1A shows that the head of *Dalmanitina* protrudes quite a bit below the eyes, thus the question arises how objects can get much closer to the eyes than a few millimetres. The solution is that *Dalmanitina*, like

all phacopid trilobites, was a sea-bottom-dweller. Such trilobites could usually dig themselves in the mud or sand of the sea floor in such a way that only their tower-like compound eyes looked out. In this case floating food particles and/or tiny preys could get quite close to the eyes.

Bifocality was the only reasonable function we could find to explain the puzzling lens shape in *Dalmanitina* that could see 'sharply' with its great lenses (of 330  $\mu\text{m}$  diameter) from infinity up to closer than half the head diameter, and only a few vertebrate eyes with accommodation can focus up so close. We admit that it is not clear whether it was necessary for the animal studied. Since the sublensar tissues in trilobite eyes have unfortunately disappeared during fossilization, there is no way to resolve the basic problem: In spite of the fact that the lenses investigated possess two distinct focal lengths, it remains unsafe that the peculiar lens shape has really evolved for bifocality. The only puzzling thing is the shape of the upper lens unit that looks like a bifocal lens. But it is not clear whether it is necessary for *Dalmanitina*. Perhaps, some unknown ancestor with larger eyes has used such a design and it was conserved also in the very small abathochroal trilobite eyes (Gál et al., 2000).

As far as we know, there is no known recent eye that possesses concentric bifocal lenses similar to those used by the trilobite *D. socialis*. Interestingly, it was only recently that the concentric bifocal intraocular lens implants (Fig. 7) were developed; the only optical prostheses (Krause, 1991) that mimic exactly the ancient bifocal corneal lenses in *Dalmanitina*, which became extinct several hundred million years ago, thus also its bifocal lenses disappeared from the scene of evolution. However, these unique ancient dioptric apparatuses were recently revived by men.

Finally, we emphasize that no paper dealing with trilobite vision can generally be complete without a discussion of the eyes of the night-active horseshoe crab *Limulus*. The *Limulus* eye possesses corneal singlet

lenses with a gradient index of refraction (Land, 1979), the ommatidia are not separated from each other (Levi-Setti, Park & Winston, 1975), and there are no sublensar retinæ in the ommatidia (Land, 1979). Thus, the *Limulus* eye is an analogy of the holochroal trilobite eyes rather than the schizochroal eye of *Dalmanitina*. This is the reason why we did not refer to the *Limulus* eye and did not bring it into connection with the *Dalmanitina* eye in this work.

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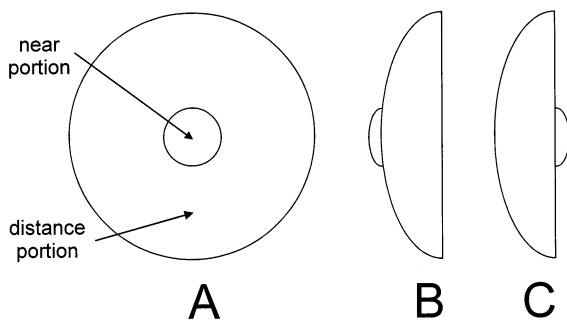


Fig. 7. The structure of concentric refractive bifocal intraocular lens implants (with the distant and near region at the periphery and the center, respectively) the only known analogy for bifocal trilobite lenses (after Krause, 1991). (A) front view; (B, C) side view.

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