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Reconstruction of the Shape and Optics of the Lenses in the Abathochroal-Eyed Trilobite *Neocobboldia Chinlinica*

JÓZSEF GÁL[a], GÁBOR HORVÁTH[a*] and EUAN N. K. CLARKSON[b]

[a]*Department of Biological Physics, Eötvös University, Pázmány Péter sétány 1, H-1117 Budapest, Hungary and* [b]*Department of Geology and Geophysics, Grant Institute, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW, Scotland, United Kingdom*

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Until now, the structure and optics of the calcite lenses in abathochroal trilobite eyes have not been investigated. So, the relationship of the abathochroal eye to other types of trilobite eyes has remained unclear. We have reconstructed the exact shape and optics of the lenses in the eodiscid trilobite *Neocobboldia chinlinica* to determine the mechanism of its abathochroal eye. The distal lens surface has a convex profile, while on the proximal lens surface there is a small central bulge, resulting in an undulating profile. Due to this bulge, the curvature and refractive power of the central region of the lens are greater than those of the peripheral zone. Consequently, the lens is bifocal. However, *Neocobboldia* could not take advantage of this bifocal property of its tiny lenses because of the diffraction of light and the infinite depth of field in object space. For the same reason, it is also sure that the undulating lower surface of the abathochroal lens did not evolve as a Huygensian profile, correcting for spherical aberration, as suggested earlier. This undulation is a result of the presence of the central bulge, the evolutionary significance of which remains enigmatic. On the basis of our results, we have outlined an evolutionary scenario for development of the optics of the lenses in trilobite eyes.

Keywords: Eodiscid trilobites, *Neocobboldia chinlinica*, trilobite vision, abathochroal eye, calcite lenses, optics

INTRODUCTION

In trilobites, three different types of eyes are known: holochroal, schizochroal and abathochroal (Lindström, 1901; Clarkson, 1975; Horváth, Clarkson and Pix, 1997). Holochroal eyes are found in the earliest of all trilobites, from the Lower Cambrian, and they persist throughout the history of the group. This eye represents the original, primitive form, from which other types of eyes were derived. In holochroal eyes the lenses are relatively small, numerous (several hundreds or thousands) and closely packed. Each lens was composed *in vivo* of a single calcite crystal, with its crystallographic axis normal to the visual surface (Towe, 1973; Clarkson, 1979, 1997). Holochroal eyes are sessile and kidney-shaped. In some instances, they can be very large, even hypertrophied, particularly in pelagic trilobites (Fortey, 1985; McCormick and Fortey, 1998). These were probably diurnal migrants, inhabiting deep waters of

* Corresponding author; e-mail: gh@arago.elte.hu

low light intensity during the day and rising up to the surface at night.

Schizochroal eyes are confined to one group of trilobites, the Ordovician to Devonian suborder Phacopina. Mature schizochroal eyes are characterized externally by a relatively small number (several tens) of large, well-separated, circular lenses. These lenses consist of two optically homogeneous units with different refractive indices. The upper unit of the lens was also composed *in vivo* of calcite with its crystallographic axis normal to the visual surface (Clarkson, 1979), while the composition of the lower unit was organic (Horváth, 1989). The optical function of the lower lens unit was to decrease the net reflectivity of the lens, and thus to enhance light-collecting efficiency (Horváth, 1996). These doublet lenses were corrected for spherical aberration due to an undulating interface (recalling the spherically corrected aplanatic surfaces of Huygens) between the lens units (Clarkson and Levi-Setti, 1975; Horváth, 1989). Schizochroal eyes originated from their holochroal precursors (Clarkson and Zhang, 1991; Clarkson and Taylor, 1995). Phacopid trilobites generally lived on the sea-bottom. As far as is known, none were pelagic.

A third kind of trilobite eye, the abathochroal eye, was first described by Jell (1975) in the Middle Cambrian eodiscid *Pagetia*, from Australia. These eyes have a relatively small number (50–70) of separate biconvex lenses. They are arranged in a semi-regular pattern, but there is no thick cuticular material between the lenses. They too were composed *in vivo* of calcite, with its crystallographic axis normal to the visual surface. Jell (1975) suggested that each lens had its own separate cornea, anchored to the margin of the lens.

Zhang and Clarkson (1990) studied the abathochroal eye of the Chinese Lower Cambrian eodiscid *Neocobboldia chinlinica* which also possesses rounded and separate lenses. A complete ontogenetic series was available, showing that the eye of *Neocobboldia* could have been derived from a normal holochroal eye by paedomorphosis, in a manner directly analogous to

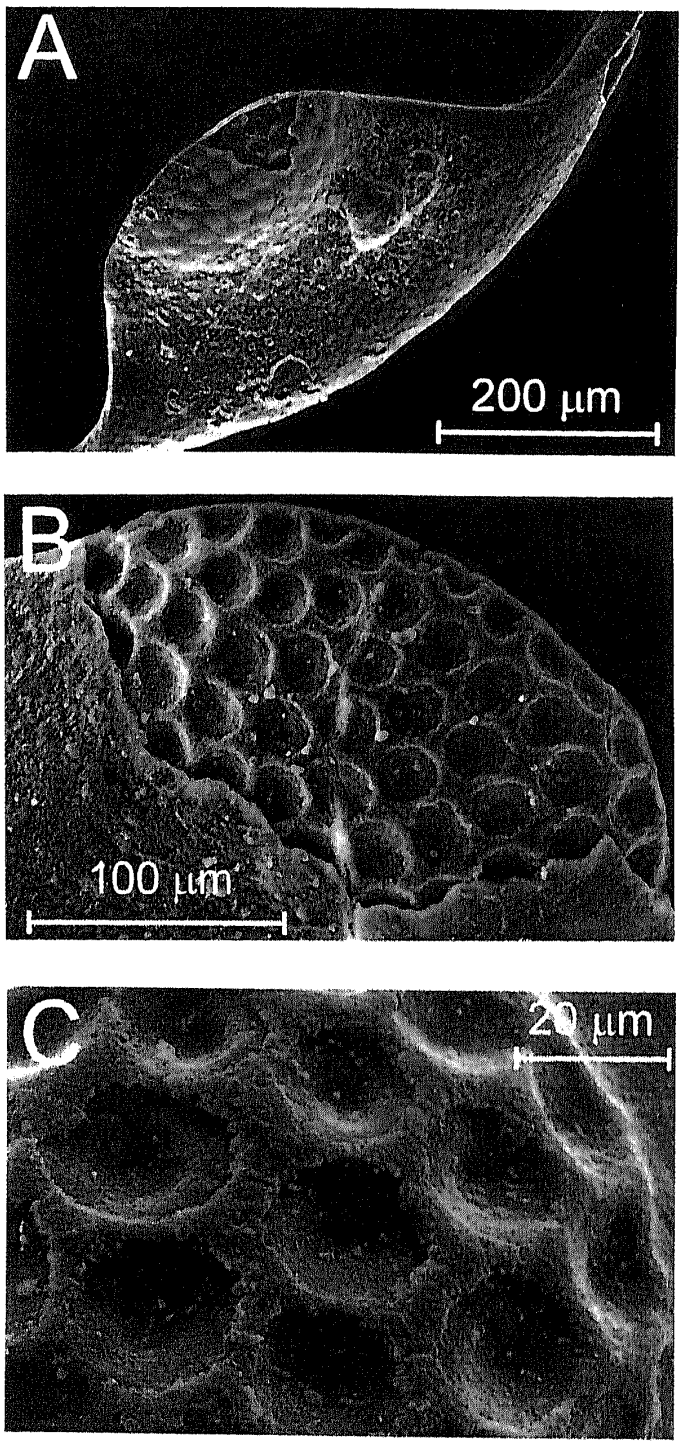

FIGURE 1 SEM photographs of fossil remains of the Lower Cambrian eodiscid trilobite, *Neocobboldia chinlinica* with abathochroal eyes, from Sichuan, China. All these specimens are preserved by phosphate encrustation; the original calcite lenses have been dissolved during acid preparation. **A.** Detached librigena (lateral part of the head), showing the outer surface of the lenses preserved as a phosphate film, partially broken to show the mould of the internal surface. **B.** Eye with the inner surface of the lenses preserved as a phosphate film, showing central dimple. **C.** Similar surface, enlarged

that envisaged for the origin of the schizochroal phacopid eye. Zhang and Clarkson (1990) cast some doubt on whether or not the abathochroal eye was truly a different kind of visual organ. In their opinion, it may simply be a kind of schizochroal eye, less specialised than that of the phacopids, rather than a distinct kind of eye. Zhang and Clarkson (1990) suggested that the undulating surface of the lower lens in the eye of *Neocobboldia* probably conforms to a Huygensian aplanatic profile, ensuring correction for spherical aberration. Recently, Levi-Setti, Clarkson and Horváth (1998) suggested that the lenses of *Neocobboldia* may be bifocal, due to a small bulge on the lower lens surface. However, up to now it has not been clear whether the optical properties of these tiny lenses (with diameters not larger than about 20 μm) are limited by diffraction or by spherical aberration.

To resolve these issues, we have reconstructed the exact shape and the optics of the lens in the abathochroal eyes of the trilobite *Neocobboldia chinlinica*. On the basis of our results, we have outlined a possible scenario for the evolutionary development of the optics of trilobite eyes.

MATERIALS AND METHODS

Anatomical Reconstruction of the Lens Shape in Neocobboldia chinlinica

The specimens of *Neocobboldia chinlinica* which we have investigated were collected from Lower Cambrian limestones in Sichuan, South China. They are very small and consist of isolated fragments. The heads, tails, thoracic segments, and the librigenae upon which the eyes are borne are all disarticulated (Figure 1). These various components have been preserved by encrustation of their outer and inner surfaces by a thin film of phosphate. This is an unusual mode of preservation, but it is not uncommon in the Lower Cambrian of Sichuan. Here, there was a very high concentration of phosphate in the early Cambrian environment. Calcium phosphate precipitated on both surfaces of recently dead arthropods, probably by bacterial action. In the limestones which yield *Neocobboldia*, several other species of trilobites and bradoriid arthropods are preserved in the same way, at all growth stages. Even arthropod egg cases have been reported.

The isolated exoskeletal components of the trilobites can be freed from the limestone by solution with 5 % acetic acid. The original calcite lenses of the eyes are dissolved by this treatment, but the phosphate moulds preserve the original shapes of the lenses in negative relief. The very delicate specimens can then be prepared for scanning electron micrography (SEM).

SEM photographs in the magnification range from x500 to x1000 have proved most useful in establishing the actual shapes of the eye lenses from the phosphatic moulds. Whereas the external surface of the lens is uniformly curved, the broad, prominent central bulge on its cambered proximal surface is very distinct. Initial drawings were prepared, but to estimate the exact shape of the lens, it was necessary to use latex replication. This proved very difficult, due to the small size and delicacy of the specimens. A few unfigured *Neocobboldia* librigenae bearing eyes remained from the work of Zhang and Clarkson (1990), and latex replication proved possible with one or two of these specimens. The original phosphatic shell was picked off, so it was destroyed in the process, but adequate replicas of the inner and outer surfaces of the lenses were obtained. From these, accurate drawings could then be prepared with a high-powered microscope. These drawings proved to correspond very closely with those made by eye alone.

Computational Reconstruction of the Optics of the Lens

The reconstructed shapes of the trilobite lenses were digitized with a scanner (Hewlett Packard

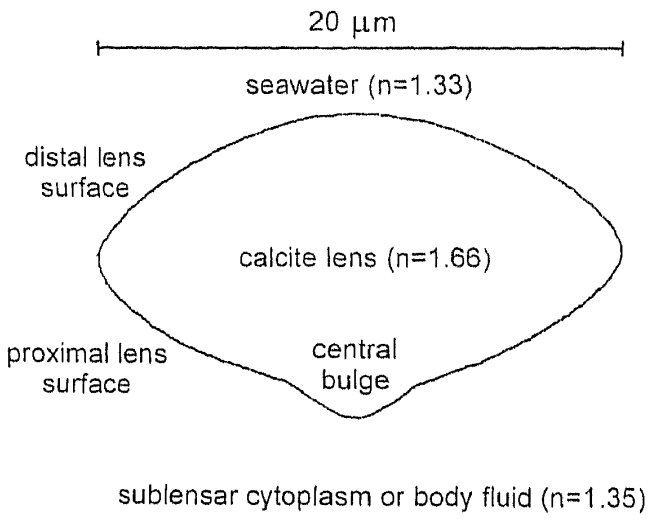

FIGURE 2 The reconstructed shape (in a vertical, main cross section) of the calcite lens in the abathochroal eye of *Neocobboldia chinlinica*. The lens possesses a characteristic central bulge on its proximal surface

ScanJet 6100C). In order to describe the distal (or entry) and proximal (or exit) refractive surfaces of the lenses mathematically, polynomials of different orders were fitted to the digitized points along these profiles. Using the law of refraction, a computer-aided tracing of paraxial rays of light passing through the lenses was performed. The paths of light rays were treated as refractions at the lens surfaces and as translations through the optically homogeneous lenses. 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.

In this paper, we use the term "back vertex distance of the focal point" to refer to the distance between the focal point and 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 between the geometrical center of the lens and the lowermost point of the proximal lens surface.

The rays were drawn with a greater density in those regions of the lens for which the back vertex distance of refracted rays remained approximately constant. It was assumed that the distal surface of the lens was immersed in seawater with an index of refraction of 1.33, while the inner surface was in contact with cytoplasm (or body fluid) with a refractive index of 1.35. The refractive index of calcite along its c-axis is 1.66. Change in the back vertex distance of refracted rays of light was calculated as a function of the radial distance of the paraxially incident rays. Supposing that there was a small sublensar retina beneath each lens in the abathochroal eye, following Nussbaum and Phillips (1976) and Horváth and Clarkson (1993), both the focal lengths of the lenses and their depths of field in object space were calculated for different values of the receptor separation, as a function of the retinal distance from the lens.

RESULTS

Lens Profile in Neocobboldia chinlinica

Scanning-electronmicrographs of fossils of *Neocobboldia chinlinica* show imprints of the missing eye lenses with a typical central dimple (Figure 1B, C). Figure 2 represents the reconstructed shape of the lens. The distal surface of the lens has a convex profile, while there is a small central bulge on the proximal surface. This bulge corresponds to the dimple in the imprint of the lenses shown in Figure 1B, C. Due to the bulge, the curvature and the refractive power of the central lens region are greater than those of the peripheral zone. This means qualitatively that the lenses in *Neocobboldia* may have two different focal lengths, that is that they may have been bifocal.

Change of the Back Vertex Distance of Refracted Rays in the Lens

The calculated ray tracing through the abathochroal lens in *Neocobboldia* is shown in Figure 3A. Figure 3B represents the change in the back vertex distance of refracted rays in the lens as a function of the radial distance of the

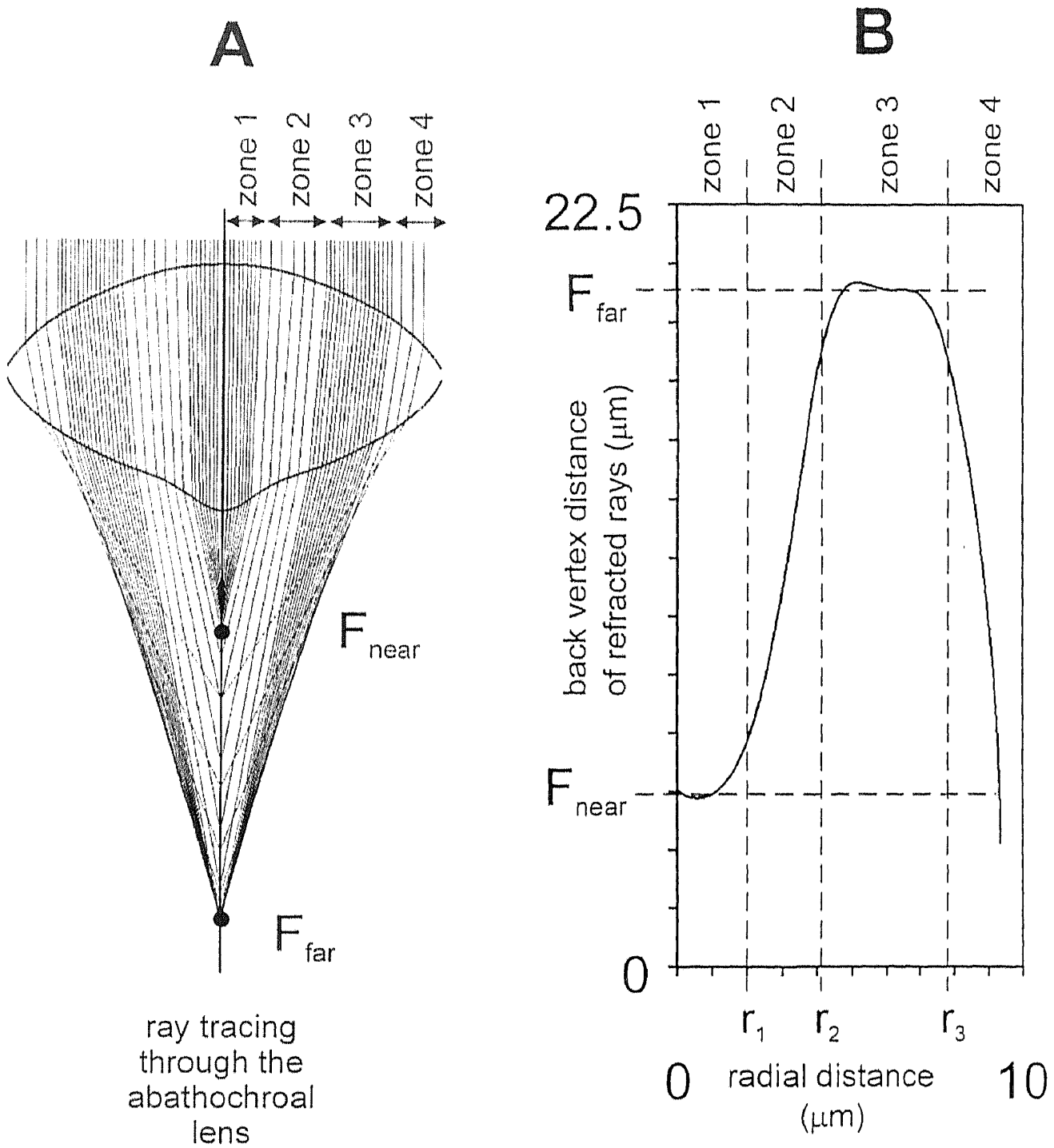

FIGURE 3 Reconstruction of the change in back vertex distance of refracted, paraxially incident rays of light in the abathochroal lens of *Neocobboldia chinlinica* portrayed in Figure 2. **A.** The tracing of paraxially incident rays of light. A greater density of rays is shown in those regions of the lens (zones 1, 3) where the back vertex distance is approximately constant. The sharp focus in zones 1 and 3, and the lack of focus in zones 2 and 4 are clearly seen. **B.** The change in 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}

paraxially incident rays. We can see from Figure 3 that zones 1 and 3 of the lens are characterized by the relatively sharp 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}. Using the methods described above, we have investigated several lenses of *Neocobboldia*, obtaining the same results as those shown in Figures 2 and 3.

On the basis of Figure 3 we can draw the following inferences. The lenses in *Neocobboldia* have two distinct, relatively sharp focal lengths which are approximately 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 abruptly in the intermediate zone 2. The most peripheral zone 4 has no exact focal length. Its surface is relatively great in comparison with the inner zones, which would have had a disadvantageous influence upon image formation. However, *Neocobboldia* could have avoided this if it had a proper ring of screening pigments below and around its lenses. Such a ring would eliminate the most peripheral rays, as in the eyes of many recent arthropods (Land, 1981). Numerical values of the reconstructed geometric optical parameters of the abathochroal trilobite lens are shown in Table I.

TABLE I Geometric optical parameters of the reconstructed abathochroal trilobite lens portrayed in Figure 2. 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 Figure 3

order of the polynomial fitted to the distal lens surface	5
order of the polynomial fitted to the proximal lens surface	9
lens radius	10 µm
back vertex distance of the near focal point F_{near}	5 µm
near principal focal length $f_{near}^{principal}$	10.8 µm
back vertex distance of the far focal point F_{far}	22.6 µm
far principal focal length $f_{far}^{principal}$	28.4 µm
r_1	1.6 µm
r_2	4.4 µm
r_3	7.4 µm

Estimation of the Influence of Light Diffraction on the Optics of the Lens

Images at the two focal points of these abathochroal trilobite lenses are blurred to some extent because of the diffraction of light. 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 $R = 1.22\, f\, \lambda/2r$, where f is the principal focal length and r is the radius of the imaging apparatus; λ is the wavelength of light (Land, 1981).

Using the data of Table I, we calculated the ratio $q_c = R_c/r_1$, where

$$R_c = 1.22\, f_{near}^{principal}\, \lambda/2r_1$$

for the central region and the ratio $q_p = R_p/r_3$, where

$$R_p = 1.22\, f_{far}^{principal}\, \lambda/2r_3$$

for the peripheral region of the bifocal lenses in *Neocobboldia*. We assumed $\lambda = 470$ nm, which is the typical wavelength of quasi-monochromatic light under water, due to selective absorption (Jerlov, 1976). These ratios indicate the relative linear dimension of the image blur due to diffraction, with respect to the linear dimensions of the central and peripheral image forming regions of the lens. In *Neocobboldia*, $q_c \approx 121$ % and $q_p \approx 15$ %. These numbers must be considered only as first approximations of the true values of q_p, as zone 3 (Figure 3) of the bifocal lens is an annulus, at the inner rim of which light diffraction also occurs. However, this only slightly enhances the value of q_p.

On the basis of these data, we conclude that the near focal point of the abathochroal lens in *Neocobboldia* is totally blurred by the diffraction of light. Thus, the lens is not in fact bifocal, and the function of the central bulge is therefore enigmatic.

Depth of Field in Object Space

To estimate the depth of field in object space, some knowledge of the photoreceptors beneath the lens of *Neocobboldia* is required. Unfortunately, the sublensar tissues of trilobite eyes have disappeared during fossilization, so one can only speculate about their structure.

Fordyce and Cronin (1993) cited evidence suggesting that each individual lens of the holochroal trilobite eye had its own, single photoreceptor, arguing that the eye as a whole functioned in a manner similar to that of modern arthropods, being especially adapted to moderate or 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). Consequently, Campbell (1975) suggested that the sublensar tissue in trilobites with schizochroal eyes might be also similar to an ocellar retina. Most investigators (Clarkson and Levi-Setti, 1975; Campbell, 1975; Stockton and Cowen, 1976; Fordyce and Cronin, 1989; Horváth, 1989; Levi-Setti, 1975, 1993) share the belief that each lens in the schizochroal trilobite eye had a tiny retina behind it. Thus, the schizochroal eye might have been a "stemmataran compound" type of eye (Horváth, Clarkson and Pix, 1997), like the eye of the male strepsipteran insect *Xenos peckii* (Buschbeck, Elmer and Hoy, 1999). The abathochroal eye seems to be intermediate between the holochroal and schizochroal types of eyes, so below each lens there might have been either a single photoreceptor or a small retina.

We suppose that *Neocobboldia* had sublensar retinae with a fixed receptor separation RS, and that the retina was a single plane of negligible depth, which holds true if the photoreceptors were short or if they were long but optically isolated from one another (Land, 1981). Then, 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 is defined as the range of object distances that produce blur on the retina with radii that do not exceed the separation of the receptors.

In addition to the diameter of the lens, the depth of field depends greatly on the density of photoreceptors on the retina. Nothing is known about this parameter in the eye of *Neocobboldia*, so the magnitude of the receptor separation RS can only be estimated on the basis of modern counterparts (Horváth, Clarkson and Pix, 1997). In the eye of *Perga*, interrhabdomal spacings are between RS = 15 and 20 μm (Meyer-Rochow, 1974). In the distal retina of the pallial eye of the scallop *Pecten*, the receptor separation RS $\approx$ 3–5 μm at the centre, and RS $\approx$ 8–10 μm towards the edges of the eye (Land, 1968).

Since both the retinal distance and receptor separation in the eye of *Neocobboldia* are unknown, the most that we can do is to determine whether or not there exist receptor separations at which *Neocobboldia* could have taken advantage of its tiny bifocal lenses. In this case, the near and far depths of field should be at least partially separated. They must not completely overlap, or else there would be no reason to employ two different focal lengths. Using the data of Table I, we established from geometric optical calculations that no such situation exists. Due to the small diameter of the abathochroal lens in *Neocobboldia*, the depth of field is infinite for both the near and far focal points, for every imaginable separation of the receptors (RS $\geq$ 2–3 μm). Thus, whatever its distance from the eye, *Neocobboldia* could see an object sharply through the central as well as the peripheral regions of the lens. In this case, there is no advantage to a bifocal lens, and the use of monofocal lenses with the same diameter would be a simpler solution.

DISCUSSION AND CONCLUSION

On the basis of the above analysis, we conclude that *Neocobboldia chinlinica* could not take advantage of the bifocal optics of its tiny abathochroal lenses because of the diffraction of light and the infinite depth of field in object space. For the same reasons, it is also sure that the undulating lower surface of the abathochroal lens is not a Huygensian profile, correcting for spherical aberration as Zhang and Clarkson (1990) had suggested. This undulation results from the presence of a central bulge, the evolutionary importance of which remains enigmatic, in the base of the lens. Perhaps the central bulge had no optical function, and its bifocal character arose only an accidental byproduct of some other attribute.

Recently, Gál et al. (2000) discovered similar calcite lenses, with a central bulge, in the schizochroal-eyed phacopid trilobite *Dalmanitina socialis*. They suggested a possible optical function for this bulge. They demonstrated that, in the eye of *Dalmanitina*, bifocal vision may be a reasonable function, actually the only one they could find. They suggested that the central region of the lens could have been used to detect food particles and tiny prey animals floating next to the trilobite, while the peripheral region of the lens would have made it possible for the trilobite to see the entire, remote optical environment sharply.

Although the biological significance of this optical organization is evident, a similar function is out of the question in the case of the tiny, diffraction-limited lenses of *Neocobboldia*, with their infinite depth of field. In the schizochroal eye of *Dalmanitina*, the lenses are sufficiently large that their bifocal optics is not countermanded by diffraction, and their depth of field is not infinite.

There is at least one other possible example of bifocal optics in trilobites. The compound calcite lenses of the schizochroal-eyed trilobite *Phacops rana milleri* were the object of extensive, earlier investigations (Clarkson, 1966, 1975, 1979; Miller and Clarkson, 1980; Horváth and Clarkson, 1993; Horváth, Clarkson and Pix, 1997). In adults, the upper unit of these lenses exhibits a pear-shaped central core, with an optical function that remains unknown. Adjacent to the projection of this core, in a plane normal to the optical axis, the lower unit of the lens has vanishing thickness. This suggests a function for the core quite similar to that of the central bulge on the proximal surface of the upper unit of the lens in *Dalmanitina socialis*. *Phacops rana milleri* appears in the Devonian, while *Dalmanitina socialis* is Ordovician in age. So, the core could represent a later incorporation of the bulge into the upper unit of the lens to provide bifocal vision (Riccardo Levi-Setti, personal communication). Study of this possibility is in progress.

EVOLUTION OF THE OPTICS OF TRILOBITE LENSES

The schizochroal eye in *Dalmanitina socialis* is of great evolutionary and palaeobio-optical interest, because it does not conform to the pattern of normal compound eyes in modern arthropods. The bifocal lenses of *Dalmanitina* differ in their optical characteristics from those of all known compound eyes of recent animals and of other extinct trilobites. The abathochroal lens of *Neocobboldia*, with its central bulge, differs from both holochroal and schizochroal trilobite lenses. Thus, the abathochroal eye may be considered as a separate kind of visual organ in its own right.

The main characteristics of the holochroal, abathochroal and schizochroal eyes of trilobites are summarized in Table II, and Figure 4 represents an evolutionary scheme for the optics of trilobite eyes. Large, spherically-corrected doublet lenses appeared relatively late in trilobite evolution (Clarkson, 1975, 1979). Only the schizochroal-eyed phacopids possessed such doublets. In ancestral, holochroal eyes, only small singlet calcite lenses were present. This is also true of abathochroal trilobite eyes, which

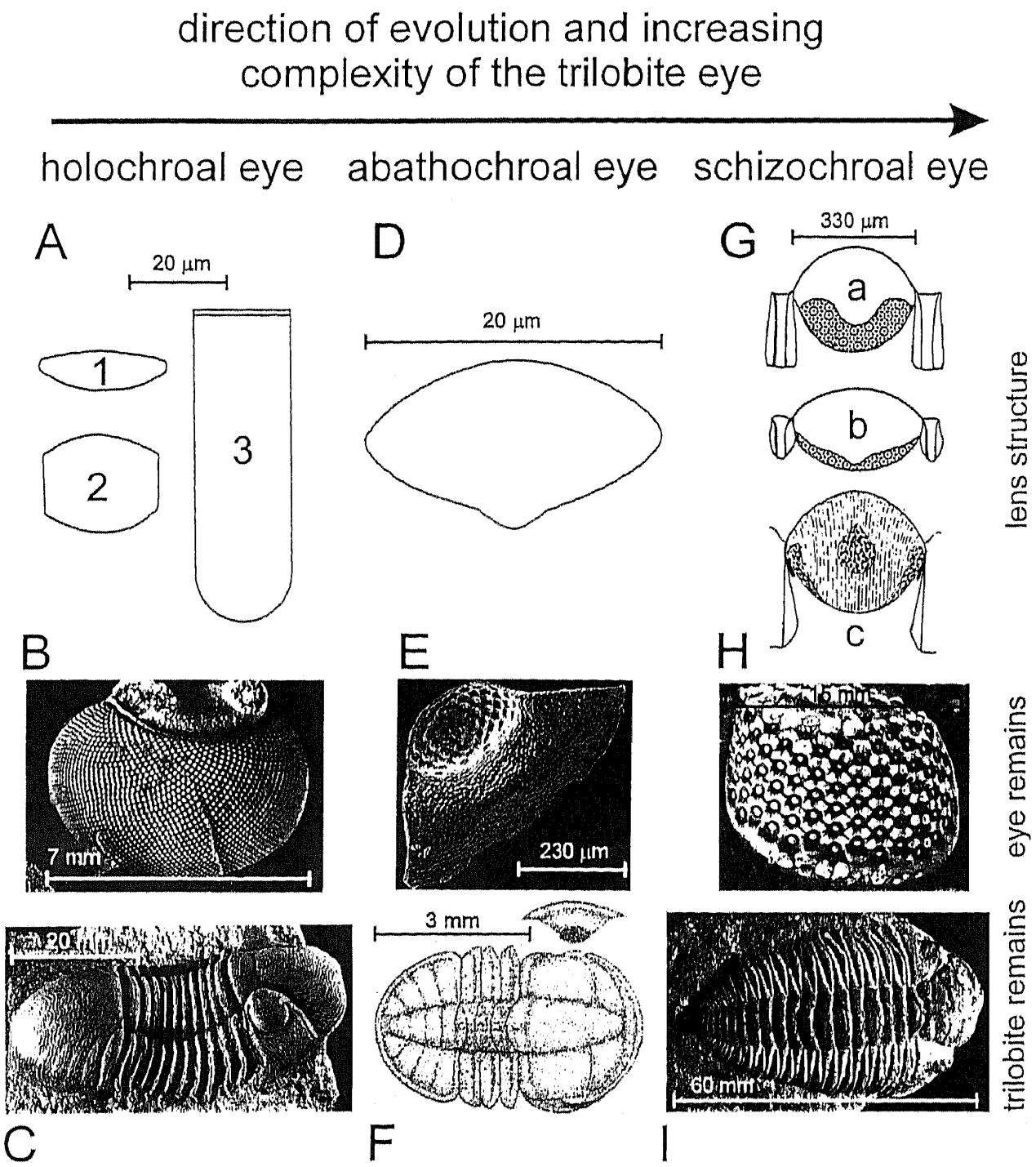

FIGURE 4 The evolutionary scheme of trilobite eyes. **A.** Examples of calcite lenses with different thicknesses in holochroal eyes of **1**, *Sphaerophthalmus humilis*; **2**, *Bojoscutellum campaniferum*; and **3**, *Asaphus raniceps* (after Clarkson, 1979, Figure 3). **B.** The holochroal eye of *Scutellum campaniferum* (after Levi-Setti, 1993, Plate 17). **C.** The holochroal-eyed trilobite, *Scutellum dormitzeri* (after Levi-Setti, 1993, Plate 214). **D.** Vertical main cross section of the bifocal calcite lens in the abathochroal eye of *Neocobboldia chinlinica*. **E.** The abathochroal eye of *Neocobboldia chinlinica* (after Zhang and Clarkson, 1990, Figure 8c). **F.** Reconstruction of the abathochroal-eyed trilobite *Neocobboldia chinlinica* with the left librigena detached and illustrated as if lying on a flat surface. In life, it was in a more nearly vertical position, as shown on the right hand side. **G.** Examples of doublet lenses in the schizochroal eyes of **a**, *Crozonaspis struvei* (after Clarkson, 1968, Figure 1e); **b**, *Dalmanitina socialis* (after Clarkson, 1968, Figure 2e); **c**, *Phacops rana milleri* (after Miller and Clarkson, 1980, Figure 1a). **H.** The schizochroal eye of *Phacops megalomanicus* (after Levi-Setti, 1993, Plate 33). **I.** The schizochroal-eyed trilobite, *Dalmanitina socialis* (after Levi-Setti, 1993, Plate 155)

TABLE II The main characteristics of holochroal, abathochroal and schizochroal trilobite eyes

		holochroal trilobite eye	abathochroal trilobite eye	schizochroal trilobite eye
external features of the eye	total length of the eye	1-8 mm	500 µm -1.1 mm	5-20 mm
	lens number	100–15000	20-90	Ordovician: 150 Devonian: 50-500
	arrangement of the lenses	closely packed lenses (absence of interlensar sclera)	more or less separated lenses	well separated lenses (presence of interlensar sclera)
	angular range of vision above the animal's equator	"panoramic"	20°-30°	less than 40°
internal features of the lenses	number of units in the lens	1	1	*2 (upper and lower unit) **3 (upper unit, central core, lower unit)
	composition of the lens units	calcite	calcite	*upper: calcite lower: organic **upper: calcite central core: calcite with organic inclusions lower: organic
	focal length	150–250 µm	***$F_{near} \approx 5$ µm ***$F_{far} \approx 23$ µm	****$F_{near} \approx 140$ µm ****$F_{far} \approx 400$ µm
	lens dimension	diameter: 20-100 µm thickness: 10-70 µm	diameter: 20 µm thickness: 10 µm	Ordovician: 150-200 µm Devonian: 450-750 µm
	correction for spherical aberration	unknown	to a certain extent (bifocal)	yes
	diffraction limited	perhaps yes in the case of the smallest lenses	more or less	no
sublensar structures	medium beneath the lens	unknown (possible body fluid/cytoplasma)	unknown (possible body fluid/cytoplasma)	unknown (possible body fluid/cytoplasma)
	possible number of photoreceptors in an ommatidium	1 – a few	1 – a few	several (small retina)
possible eye type		apposition/superposition compound eye	apposition/superposition compound eye	stemmataran compound eye

**Crozonaspis struvei*, ***Phacops rana milleri*
****Neocobboldia chinlinica*, *****Dalmanitina socialis*

arose independently, representing an intermediate morphological stage between holochroal and schizochroal eyes. On the basis of the data accumulated from the visual systems of trilobites, we propose the following evolutionary scenario for the optics of trilobite lenses (Table II, Figure 4).

1. The first stage of development took place in the ancestral, holochroal eye (Figure 4A-C). It involved minimizing the influence of the birefringence of calcite within a single lens. This problem was solved by appropriate orientation of the c-axis of the calcite crystals, so as to be aligned parallel to the optical axis of the lenses. This, in turn, is normal to the visual surface of the eye. The problem is resolved because calcite is not birefringent along its c-axis. The smallest holochroal lenses perhaps were not, as yet, corrected for spherical aberration. Judging from their tiny dimensions, their imaging might have been diffraction-limited. If this was so, there would have been no selective advantage associated with correction for spherical aberration.

2. A second evolutionary step was the appearance of abathochroal eyes (Figure 4D-F) which are present only in Cambrian eodiscid trilobites. Here, the lenses possessed a characteristic central bulge on their proximal surfaces. The function of this bulge remains obscure, as shown in this paper. It made the lens bifocal, but the near focal point was entirely blurred by diffraction. The actual shape of the lens ensured some correction for spherical aberration, at least in the case of the far focal point. The relatively steep rise of the proximal profile and the difference in refractive index between the lens (calcite: $n = 1.66$) and the sublensar material (probably body fluid: $n = 1.35$) resulted in disadvantageous internal reflections on the proximal refracting surface. This would have reduced the transmissivity and so, also, the light-collecting efficiency of the eye. Judging from their average diameter, abathochroal lenses approached the diffraction limit. Nevertheless, there must have been some selective pressure to correct for spherical aberration and to develop the enigmatic central bulge of the lenses.

3. The problem of light loss due to internal reflection was solved in the schizochroal eye of phacopid trilobites, which possessed spherically corrected, large doublet lenses (Figure 4G-I). The origin of such structures might have been induced by a nocturnal or a predatory mode of life. Bifocal vision, the feature first developed by the abathochroal-eyed trilobites, reappeared in the schizochroal eye of the Ordovician *Dalmanitina socialis*, and perhaps yet again in the schizochroal-eyed Devonian trilobite *Phacops rana milleri*. Subsequently, it disappeared entirely in the later evolution of schizochroal eyes. This may have been the last attempt to extend the depth of field of sharp vision, using bifocal lenses to enable the trilobite to see objects both far away, through the peripheral region of the lens, and close-up through the central part of the lens region. The schizochroal eye may be considered as a functional end-point in evolution. The lower unit of the lens reduced intralensar reflection, enhancing the transmissivity of the doublet lens. The birefringence of the lens was minimized by a proper orientation of the c-axis of calcite crystals in its upper unit, whose undulating proximal surface ensured correction for spherical aberration.

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