Review

The eyes of trilobites: The oldest preserved visual system

Euan Clarkson [a,*], Riccardo Levi-Setti [b], Gabor Horváth [c]

[a] *Grant Institute of Earth Sciences, School of Geosciences, University of Edinburgh, Kings Buildings, West Mains Road, Edinburgh EH9 3JW, UK*
[b] *Enrico Fermi Institute and Department of Physics, University of Chicago, 5630 Ellis Avenue, Chicago, IL 10024, USA*
[c] *Biooptics Laboratory, Department of Biological Physics, Lorand Eötvös University, Pazmany Peter setany 1, H-1117 Budapest, Hungary*

Abstract

The oldest preserved visual systems are to be found in the extinct trilobites, marine euarthropods which existed between about 520 and 250 million years ago. Because they possessed a calcified cuticle, they have a good fossil record, and commonly the lens-bearing surfaces of their paired compound eyes are well preserved. The sublensar structures, however, remain unknown. Three kinds of eyes have been distinguished. Holochroal eyes, apomorphic for trilobites, typically have many contiguous small lenses, set on a kidney-shaped visual surface. Lens optics, angular range of vision, and ontogeny have been established for many compound eyes. Some pelagic trilobites have enormous eyes, subtending a panoramic field of view. Schizochroal eyes are found only in one group, the phacopids (Ordovician to Devonian). These have large lenses, separated from each other by cuticular material, and the lenses have a complex doublet or triplet internal structure, which could focus light sharply. The optics of phacopid eyes are becoming increasingly well known despite the fact that there are no direct counterparts in any living arthropods today. Schizochroal eyes are apomorphic for phacopids and were derived by paedomorphosis from a holochroal precursor. Abathochroal eyes are confined to a short-lived Cambrian group, the eodiscids (of which most representatives were blind). Less is known about them than other trilobite eyes and their origins remain obscure. Some trilobite groups had no eyes, but had other kinds of sensory organs. In Upper Devonian times several groups of trilobites independently underwent progressive eye-reduction leading to blindness, related to prevailing environmental conditions of the time. The last trilobites (of Carboniferous and Permian age), however, had normal holochroal eyes, which persisted until the final extinction of trilobites at the end of the Permian.
© 2006 Elsevier Ltd. All rights reserved.

Keywords: Trilobite; Cuticle; Holochroal; Schizochroal; Abathochroal; Eye-reduction; Blindness

1. Introduction

Trilobites are extinct marine euarthropods, characterised by the head and body being divided longitudinally into three longitudinal lobes; a central raised axis and two flanking parts. The head (cephalon) is well defined, the thorax may consist of two to many segments, and the tail (pygidium) forms a fused plate. The dorsal cuticle contained, in its procuticular layer, considerable amounts of calcite. Since this material is readily preservable, trilobites have a remarkably good fossil record. The earliest trilobites are of Early Cambrian age, but whereas the base of the Cambrian is now taken as around 542 Ma (million years), trilobite history did not begin until about 520 Ma. It was preceded by a long time period, represented in the fossil record mainly by 'small shelly fossils', phosphatic tubes, coiled shells, expanding cones, and button-like objects of various kinds. Even on their first appearance, trilobites possess all characters that distinguish this group from all other euarthropods, and they have paired compound eyes. These are characteristic of Arthropoda *sensu stricto* (Maas et al., 2004; Waloszek et al., 2005) but in trilobites they are already of a highly developed type, and are the best known and studied of any fossilised visual system.

The geological history of trilobites is well documented (Fig. 1). They flourished in Cambrian times (c. 520–488 Ma), with several hundred genera and species succeeding each other

* Corresponding author.
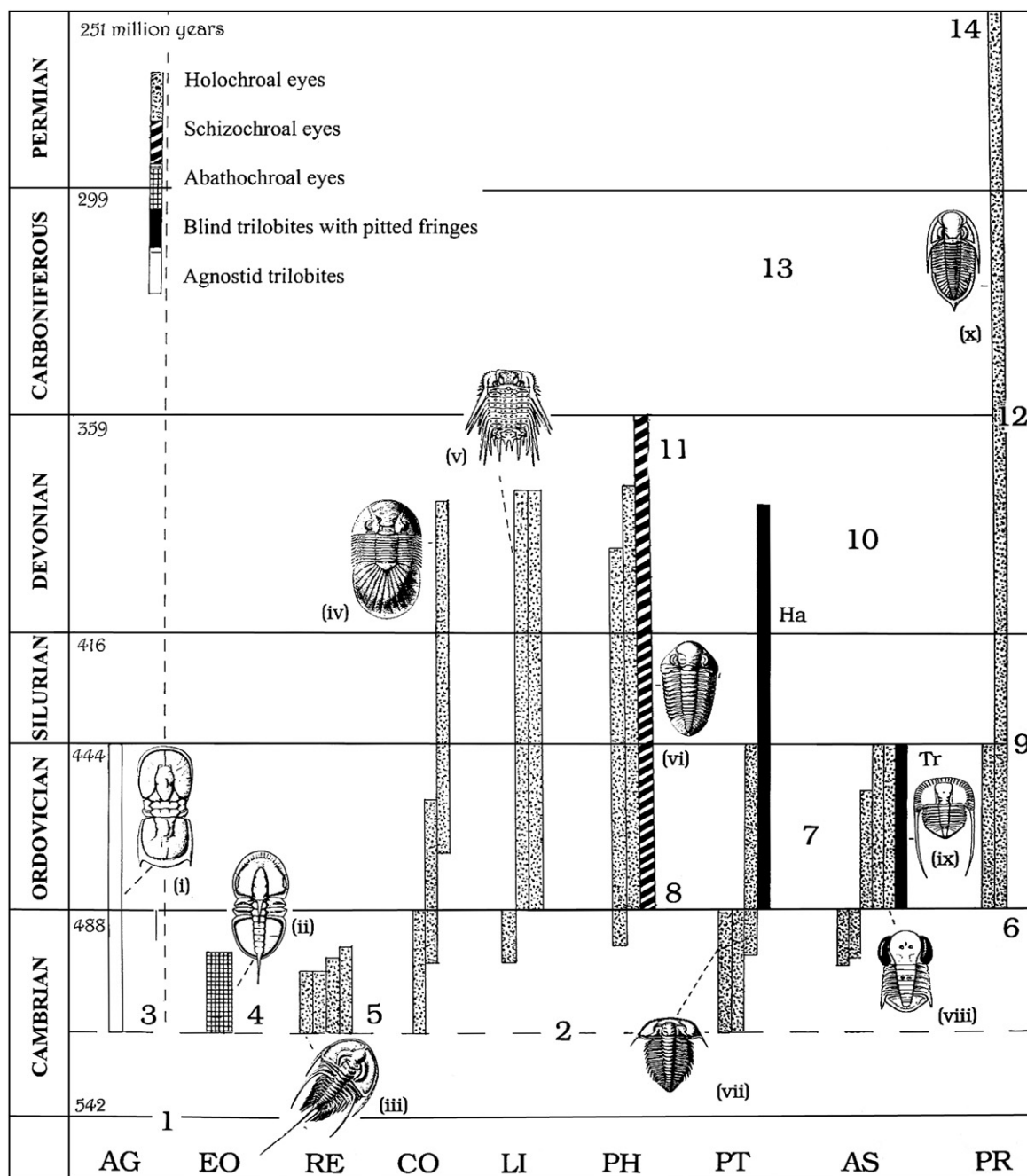*E-mail address:* euan.clarkson@ed.ac.uk (E. Clarkson).

Fig. 1. Simplified geological history of trilobites, showing various eye-types and major historical events. Single vertical bars represent suborders, grouped bundles represent orders as follows (simplified from Clarkson, 1998), though following Walossek and Müller (1990) the Agnostina are regarded as close relatives of stem-group crustaceans, and are unrelated to the Eodiscina (though traditionally classified together in Order Agnostoida). Symbols are as follows for higher taxa: EO, Eodiscina; RE, Redlichiida; CO, Corynexochida; LI, Lichida; PH, Phacopida (including schizochroal eyed Phacopina); PT, Ptychopariida (including pitted-fringed Harpina) (Ha); AS, Order Asaphida (including pitted-fringed Trinucleoidea); PR, Proetida. Major events are numbered as follows: 1. Base of Cambrian System. 2. First appearance of trilobites. 3. Origin of the unique agnostine system of a median eye and reduced ventral compound eyes. 4. The cryptic origin of the eodiscid abathochroal eyes. Most trilobites in this taxon, however, are blind. 5. The earliest holochroal eyes in Redlichiida. 6. Extinction event at the end of the Cambrian. 7. Acme of trilobites and proliferation, amongst others, of blind, pitted-fringe taxa (Harpetidae (Ha) and Trinucleoidea (Tr)) and pelagic groups with hypertrophied eyes. 8. Origin of schizochroal eyes by paedomorphosis. 9. End-Ordovician major extinction event. 10. Gradual decline and final extinction of many taxa. 11. Loss of eyes in many proetids and phacopids. 12. Late Devonian major extinction event. 13. Proetida continue to the latest Permian. 14. Final extinction of trilobites. Genera illustrated are: (i) *Machairagnostus*, (ii) *Pagetia*, (iii) *Paedumias*, (iv) *Scutellum*, (v) *Dicranurus*, (vi) *Acaste*, (vii) *Olenus*, (viii) *Pricyclopyge*, (ix) *Trinucleus*, (x) *Paladin*.

rapidly, but were quite severely affected by an extinction episode at the end of this period. In the early part of the Ordovician (c. 488–444 Ma) many new trilobite taxa arose, new niches were invaded, and it was during this period

that trilobites reached their acme. The major Hirnantian glaciation at the end of the Ordovician forced a major extinction, and for the rest of trilobite history no new body plans emerged; there were only permutations on themes already

established in the Cambrian and early Ordovician. Moreover, some ecological niches, such as the pelagic, once lost in late Ordovician times, were never re-occupied by trilobites. In the succeeding Silurian (c. 444–416 Ma) and Devonian (c. 416–360 Ma) representatives of many trilobite groups still existed, but never with the abundance and diversity of their Ordovician forebears. Several remaining groups disappeared one after the other during the Devonian, and all but one were wiped out during a major extinction episode towards the end of the Devonian. Trilobites belonging to this group, the long-lived Order Proetida continued throughout the Carboniferous (c. 360–99 Ma) and Permian (c. 299–251 Ma) until the late Permian environmental catastrophe, the greatest crisis of all, by which marine ecosystems were changed forever, and the last trilobites became extinct.

The paired compound eyes of trilobites are the best known of all fossil visual systems. They have many lenses composed of calcite, which had their origin as a specialised part of the calcified dorsal cuticle. Unfortunately, almost nothing is preserved of the sublensar structure, which decayed after death,

and almost everything that we know about trilobite compound eyes is based on the visual surface with its calcitic lenses. More detailed treatments of trilobite vision are given in previous works (Clarkson, 1975, 1979; Levi-Setti, 1993; Clarkson *in* Kaesler, 1997; Levi-Setti et al., 1998; Thomas, 2005).

Most trilobite eyes are of the so-called *holochroal* type (Figs. 1–3). This type is characterised by having many contiguous lenses, fairly small, and often of similar size throughout the eye. The lenses are set on a kidney-shaped visual surface, which usually subtends a considerable angular range of vision, though this varies with the curvature of the eye. The earliest trilobites, of Early Cambrian age, had eyes of such a kind, as did the last of all in the Late Permian, and holochroal eyes are to be regarded as the ancestral eye type for trilobites. The holochroal eye remained the standard kind of visual organ throughout the 270 million years of trilobite history, and it is likely that below the lenses lay an array of ommatidia, similar to those of living insects and crustaceans. Presumably holochroal eyes are apomorphic for trilobites, and derived from an unknown, basic type of euarthropodan eye.
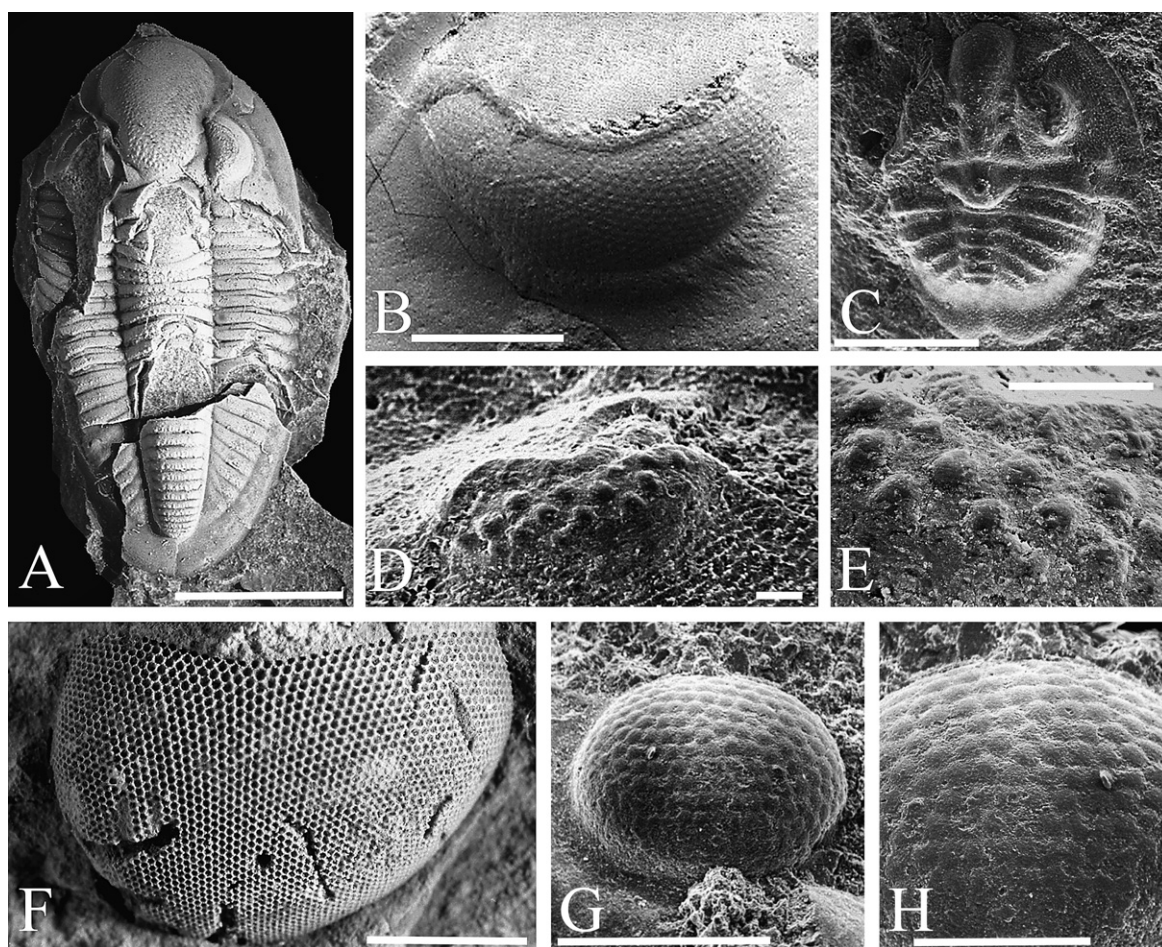

Fig. 2. Holochroal eyes (A–H) *Paladin eichwaldi shunnerensis* King, 1914 (Middle Carboniferous, Yorkshire, England). (A) Adult, lectotype (scale bar 5 mm). (B) Holochroal right eye of same (scale bar 0.5 mm). (C) Larval form (degree 0 meraspis) (scale bar 0.5 mm). (D) 'Schizochroal' right eye of same (scale bar 0.1 mm). (E) Same, enlarged. All specimens have original calcitic cuticle (scale bar 0.1 mm). (C–E) are scanning electron microscopy (SEM) photographs. (F) *Pricyclopyge binodosa* Salter, 1849 (scale bar 2.5 mm). Hypertrophied left eye preserved as an internal mould after the original exoskeleton has been leached by acid groundwater (Ordovician, Sarka, Bohemia). (G, H) *Sphaerophthalmus alatus* Boeck, 1838 (Upper Cambrian, Andrarum, Skåne, Sweden). (G) Left eye in lateral view (scale bar 0.25 mm). (H) Same, enlarged (scale bar 0.1 mm).
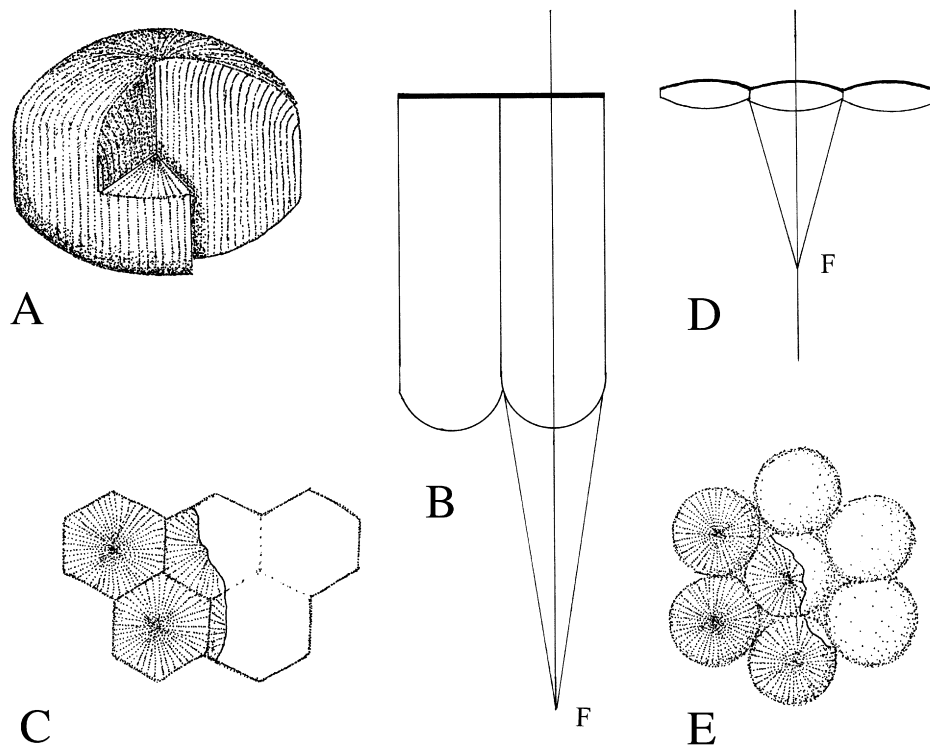
Fig. 3. Holochroal eyes. (A) *Paladin eichwaldi shunnerensis* King, 1914 (Middle Carboniferous, England). Reconstruction of a single lens, cut to show radial lamellae and vertical trabeculae. (B, C) *Asaphus raniceps* Dalman, 1827 (Lower Ordovician, Sweden). (B) Vertical section through adjacent lenses showing thin cornea (black), hemispherical lower terminations and focal point (F). (C) Surface view, with cornea removed at left hand side to show radial lamellae. (D, E) *Sphaerophthalmus alatus* Boeck, 1838 (Upper Cambrian, Sweden). (D) Section through adjacent lenses and focal point (F) (E). Surface view of lenses, cornea removed on left hand side to show radial lamellae.

The suborder Phacopina, ranging from the early Ordovician to late Devonian, possessed a different kind of visual system, the so-called *schizochroal* eye. This type normally had fewer, but relatively much larger lenses, separated from each other by interlensar cuticle (sclera) (Figs. 1, 4A–F, 5). The lenses have a complex internal structure which has been the focus of much recent investigation. As discussed later, schizochroal eyes are autapomorphic for Phacopida, and were derived by paedomorphosis from a holochroal-eyed ancestor.

A third kind of eye, the *abathochroal* type, is confined to the Eodiscina, a suborder of small Lower and Middle Cambrian trilobites (Figs. 1 and 4G,H). The lenses are tiny, slightly separated from each other, and each lens may have had its own external calcitic membrane. These are amongst the earliest of all trilobite eyes to appear in the fossil record, and are well formed. It is most likely that such eyes, autapomorphic for eodicids, were derived from a holochroal ancestor. It is interesting to note that most eodiscids underwent secondary eye loss. All the later eodiscids were blind.

2. Holochroal eyes

These are the ancestral type of trilobite compound eyes, present in the majority of trilobites from the lower Cambrian to the Permian. As an example we shall consider the superbly well-preserved eyes of the Carboniferous (Namurian) proetid *Paladin eichwaldi shunnerensis* King, 1914, (Figs. 2A–E

and 3A) from Northern England. The uppermost part of this eye is the palpebral lobe, a flattish shelf projecting laterally, and with a curving outer rim. Running along the outer edge of this lobe is the palpebral suture, the central part of the facial suture, along which the trilobite cephalon could split during moulting, thereby facilitating the shedding of the old cuticle. Below this is the curving visual surface, with its many small contiguous lenses. These are arranged in a hexagonal close-packing system, but the geometrical constraints that arise when similar-sized discs are arranged on a curving surface lead to evident, and irregular discontinuities. This curving visual surface subtends an angular visual range of about 180 degrees horizontally, and c. 35 degrees vertically, from just below the trilobite's equator upwards. Below the visual surface comes the eye socle, a raised band with vertical lineations, probably the external expression of a sensory system. In section the lens array is seen to be covered with a thin, continuous, pellucid sheet of calcite, the cornea. Each of the lenses, lying below, is a short cylinder of calcite, about as broad as it is long, and with rounded outer and inner surfaces. A lens cut parallel with the principal plane shows thin sheets of calcite (lamellae) radiating from the centre, and each of these lamellae in turn consists of thin rods (trabeculae) (Fig. 3A). The trabeculae, as seen in lenses cut normal to the principal plane (i.e. parallel with the mineralogical *c*-axis) turn out fanwise towards the cambered outer surface. Whereas the mineralogical *c*-axis (along which light is not doubly refracted) is normal to
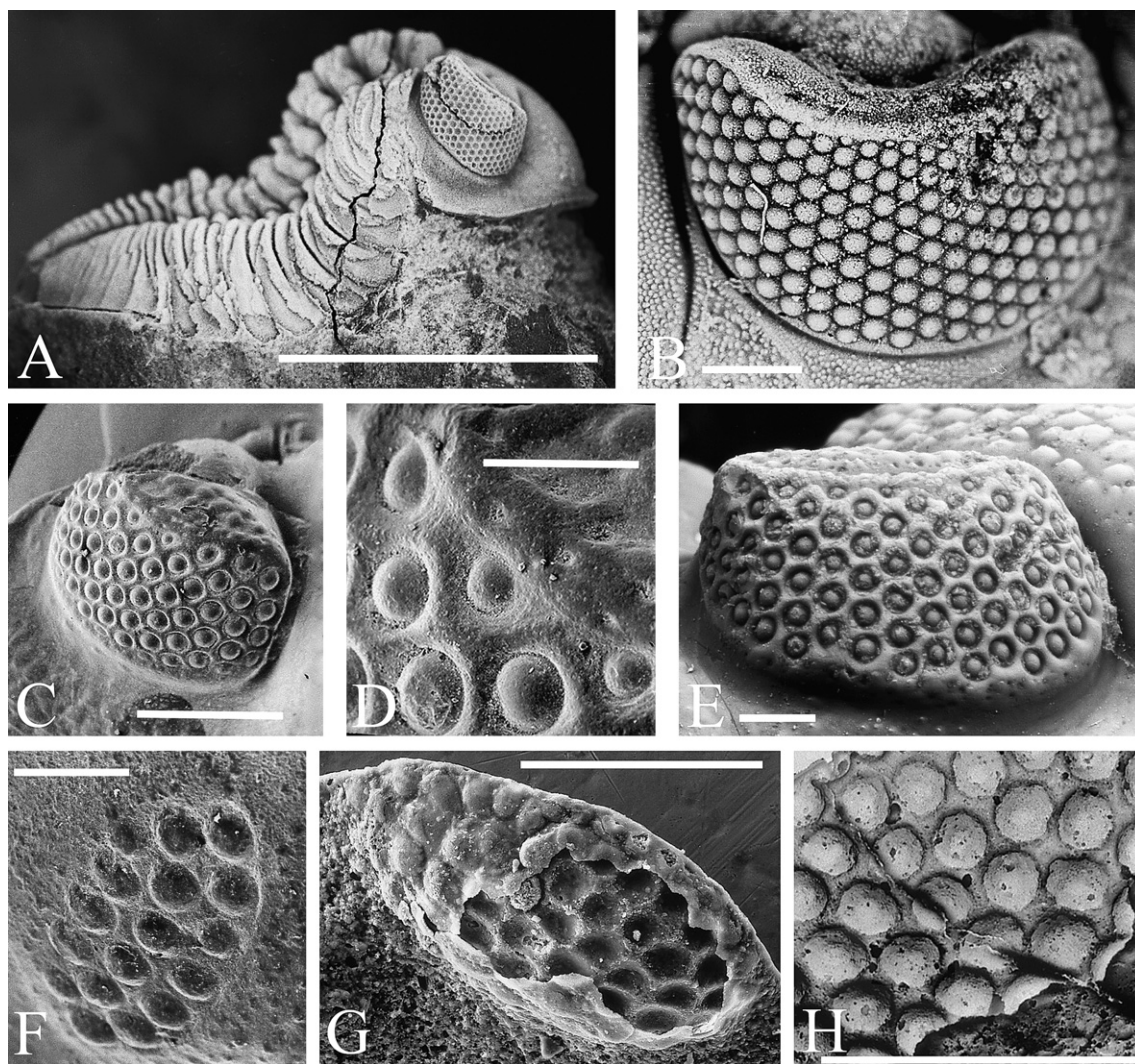
Fig. 4. (A–F) Schizochroal eyes. (A) *Calyptaulax brongniartii* Portlock, 1843 (Upper Ordovician, Girvan, Scotland). A mould of the internal surface of a complete trilobite in lateral view (the original cuticle having been leached away by acid groundwater), showing the large schizochroal eye (scale bar 10 mm). (B) *Calyptaulax brongniartii* Portlock, 1843 (Ayrshire, Scotland). Right eye, latex replica of an external mould (scale bar 1 mm). (C, D) *Eldredgeops rana rana* Green, 1832 (Middle Devonian, Silica Shale Ohio, USA). Right eye (SEM photo of original exoskeleton) (scale bar 1 mm). (E) *Eldredgeops rana crassituberculata* Stumm, 1953. (Middle Devonian, Silica Shale, Ohio), large specimen. Right eye (scale bar 0.25 mm). (F) *Denckmannites volborthi* Barrande, 1852 (Silurian, Lochkov, Bohemia, Czech Republic). Left eye, showing reduced lens number (SEM photo of original exoskeleton).0.5 mm). (G, H) Abathochroal eyes. *Neocobboldia chinlinica* Lee. (Lower Cambrian, Xichuan, Henan). (G) Right eye showing outer surface, revealing inner surface where broken, both preserved as phosphate films. The original calcite has been dissolved by solution in acetic acid when freeing the specimens from the matrix. SEM photo (scale bar 0.1 mm). (H) Internal surface of lenses showing central dimple; SEM photo (scale bar 0.1 mm).

the principal plane, the outwardly twisted trabeculae may have assisted in directing peripheral light rays into the lens.

P. eichwaldi shunnerensis was the first holochroal-eyed trilobite in which the early developmental stages were described, and in these the lenses are separate from each other and large relative to the visual surface, like a tiny schizochroal eye (Fig. 2D).

2.1. Evolution of holochroal eyes

Most trilobites may have lived as vagrant benthos, particularly those with holochroal eyes that seem to have been well adapted for this mode of life. The visual fields, on the whole were like those of *P. eichwaldi shunnerensis,* sometime more highly curved vertically, thereby extending the angular range of vision towards the poles. This adaptation to a particular habitat through hundreds of millions of years, probably explains the remarkable conservativism of the visual organs in holochroal-eyed trilobites, which on the whole remain much the same from the Cambrian to the Permian. Yet whereas some Cambrian trilobites retained their visual surfaces, a larger number of them (belonging to different taxa) do not, especially those of the Lower and Middle Cambrian. This is because, in the adults of those taxa, an additional suture is emplaced along the upper surface of the eye socle, below the lens array. This, the ocular suture, joins with the palpebral suture so that the visual surface is encircled by a continuous line of weakness, and during moulting it falls out. Not much is known,

in consequence, of the structure of the visual surface in adult eyes possessing such a suture. Yet the eyes of juveniles, where preserved, are commonly found with the visual surfaces intact, for the ocular suture does not become functional until relatively late in development. It has been argued (Clarkson, 1973, 1979) that the retention of the visual surface in some later Cambrian and most Ordovician and later trilobites is the result of paedomorphosis.

Those trilobites that have thinly calcified cuticles have thin biconvex lenses. Best known amongst these are the upper Cambrian (Furongian) Subfamily Leptoplastinae of the Family Olenidae, where the visual surface is always retained in the adult (Clarkson, 1973). These eyes usually have narrow palpebral lobes, and are often almost spherical, like tiny golf balls, with many lenses subtending an almost panoramic field of view (Figs. 2G,H and 3D,E). Those trilobites with thicker cuticles have thicker lenses, and in the most extreme cases, such as the Asaphidae, the lenses are calcitic columns with flat outer surfaces and semicircular inner surfaces (Fig. 3B,C). Yet in all these kinds of lenses, the external and internal surfaces are so shaped that simple Gaussian formulae can be used to demonstrate that light would be focussed at approximately the same distance below the surface of the lens (Clarkson, 1979).

In early Ordovician times two groups of pelagic trilobites originated independently, derived from benthic ancestors. One group, exemplified by the genus *Carolinites* occupied equatorial waters. Species of this genus occur in various kinds of sedimentary rock, such as limestones, mudstones and shales, unlike benthic trilobites, which are usually confined to one kind of sediment alone. This is one line of evidence suggesting that they lived in the water column. Fortey (1985) interpreted *Carolinites* as an epipelagic genus. A second group of trilobites, the cyclopygids, including species of *Pricyclopyge* (Figs. 1 and 2F) was confined to high latitudes round the margin of the great southerly continent named Gondwana. These cyclopygids occur either alone, or with an assemblage of blind, or nearly blind benthic trilobites. Such assemblages of pelagic trilobites with enormous eyes, and blind forms which lived in deep waters below the limits of light penetration was termed 'atheloptic' (Fortey and Owens, 1987). Both *Carolinites* and *Pricyclopyge* have hypertrophied eyes, often enormous and fused anteriorly, with the lenses extending to the ventral surface. These were evidently pelagic trilobites which, like living species of the amphipod *Cystisoma* and other eucrustaceans with very large eyes, probably underwent some degree of vertical migration diurnally. In *Carolinites killaryensis utahensis* Hintze 1951, the lenses are larger in size and fewer in number than they are in *Pricyclopyge binodosa* Barrande, 1852. McCormick and Fortey (1998) measured the 'eye parameter' p for both kinds of eyes, a product based on lens diameter (D) and ommatidial angles (the angle between adjacent lenses). For a square lens array $p = D\Delta\varphi$, while for hexagonal packing $p = D3^{1/2}\Delta\varphi/2$. These formulae can be used to establish the approximate light intensity to which these two kinds of eye were adapted. The eye parameter for *Pricyclopyge* is appreciably higher than that for

Carolinites. Thus *Pricyclopyge* had an eye optimally adapted to function at relatively low levels of illumination, while that of *Carolinites* was adapted to brighter light. This is much in line with previous interpretations of the former genus as mesopelagic and the latter as epipelagic. With the extinction of both these groups at the end of the Ordovician the pelagic niche does not seem to have been colonised thereafter by trilobites, and certainly there were no more trilobites with such hypertrophied eyes.

Although the sublensar parts of the holochroal eye remain unknown it is generally believed that it consisted of a radial system of ommatidia, one below each lens. The diameter of the facets, and interommatidial angle lie within the same range as nocturnal compound eyes of living euarthropods (Fordyce and Cronin, 1993), and the holochroal eyes of trilobites were most likely adapted to dim to moderate light intensities.

3. Schizochroal eyes

3.1. Morphology

These eyes are confined to one group only, the Suborder Phacopina (Lower Ordovican to Upper Devonian), for which they are autapomorphic (Figs. 1, 4A−F, 5, 6). They are unique amongst Arthropoda (*sensu* Maas et al., 2004; Waloszek et al., 2005). Accordingly, they have been the focus of intensive research, and to some extent their structure and function remain controversial. In such an example as the Devonian *Eldredgeops rana crassituberculata* Stumm, 1953 (Fig. 4E) the eyes are large, with about 70 lenses, set upon a curving surface that expands forwards as a logarithmic spiral. The lenses are much larger than those of holochroal eyes, they are highly biconvex, and are separated from each other by cuticular material, the interlensar sclera. This sclera is appreciably thicker than the lenses, so that each lens is set at the outer end of a cylindrical cavity, the sublensar alveolus. Each lens has an external thin epicuticle, the cornea, which continues at the periphery to run through the sclera, plunging downwards as a cylindrical ring. In a few cases this is seen to continue as a thin-walled tapering cylinder below the lens, closed off below, and evidently an integral part of the visual system (Fig. 5A). These have been described in *Phacops fecundus* Barrande, 1852 and *Reedops cephalotes* Barrande, 1852 by Clarkson (1967, 1969), and a much stouter, thicker walled capsule has been illustrated by Bruton and Haas (2005) in *Geesops sparsinodosus* Struve, 1970. These capsules probably contained a retina of tens to hundreds of photoreceptors.

3.2. Lens-packing on the visual surface

As is the case with holochroal eyes, the growth of the visual surface and the emplacement of the lenses upon it seem to have been governed by separate developmental programmes. The lenses were emplaced in a generative zone, which initially underlie the palpebral suture, and as the visual surface expanded downwards and at front and rear, so lens-emplacement continued on a rolling-programme basis in a system of
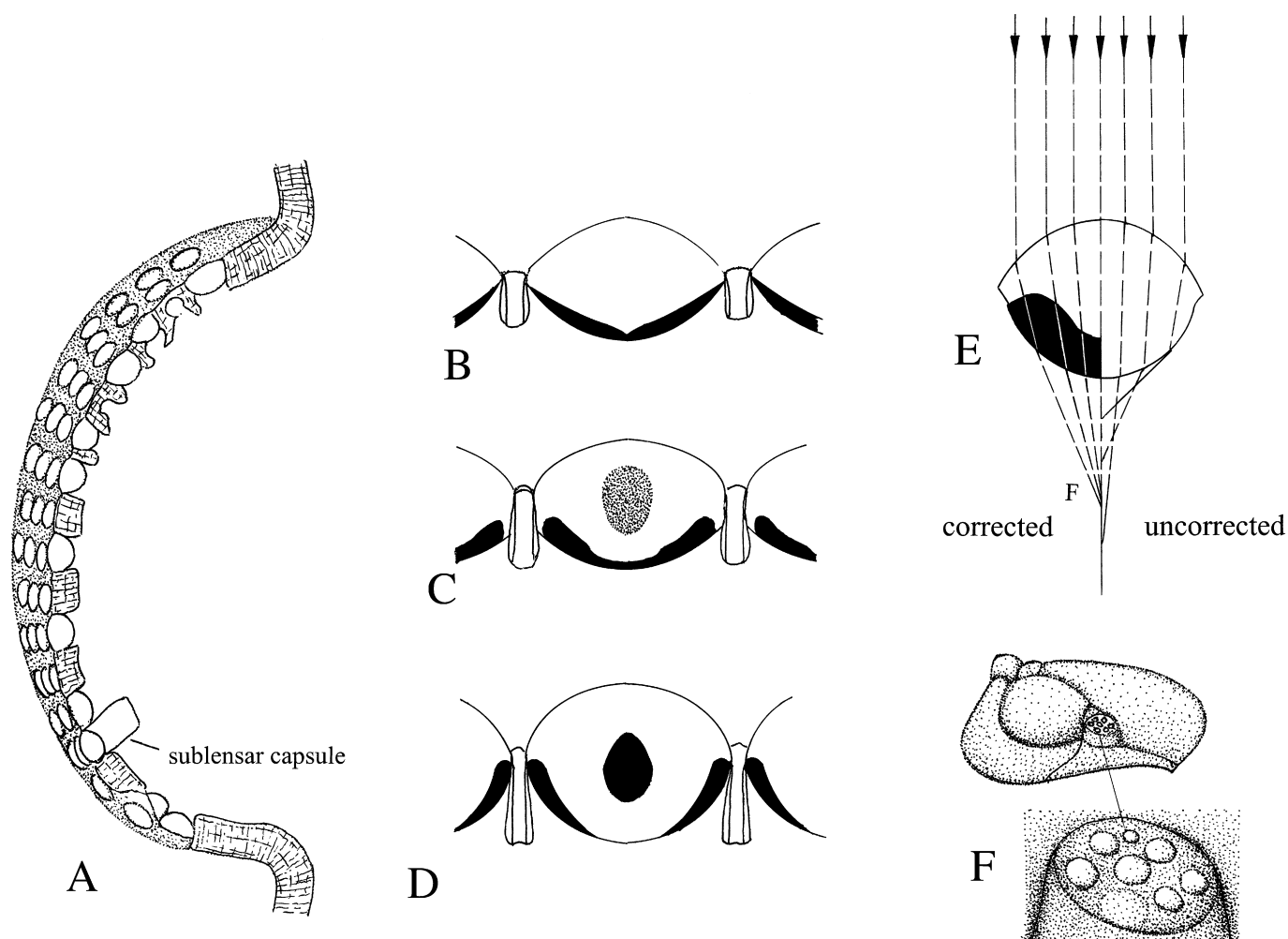
Fig. 5. Schizochroal eyes. (A) *Phacops fecundus* Barrande, 1852 (Silurian, Czech Republic), eye cut horizontally, showing a single sublensar capsule. (B) *Dalmanitina socialis* Barrande, 1852 (Ordovician, Czech Republic). Section of lenses showing intralensar bowl (black). It is not known if a core was present. (C) *Dalmanites* sp. (Silurian, locality unknown). Here a core is present though less well defined than in (D). (D) *Eldredgeops rana rana.* Green, 1832 (Middle Devonian, Ohio, USA). A highly biconvex lens in which the core is well developed and of the same appearance as the bowl. The bowl thins out and vanishes proximally. (E) *Crozonaspis struvei* Henry, 1968 (Ordovician, Brittany, France). Ray tracing through the lens. Simplified from Clarkson and Levi-Setti (1975). (F) *Acuticryphops acuticeps* Kayser, 1878 (Upper Devonian, Southern France). Cephalon in lateral view and (below) an enlargement of the reduced eye. The swelling at the bottom centre may be an imperfectly formed lens (Simplified from Crônier and Feist, 2000).

hexagonal, or occasionally square packing. The model proposed by Clarkson (1975) has been refined and extended by Thomas (1998, 2005). Thomas noted that in the living eu-arthropod insect *Drosophila melanogaster* Meigen, 1830 an indentation known as the morphogenetic furrow sweeps across the imaginal disc during eye formation. This wave-like front of differentiation leaves behind it rows of perfectly spaced ommatidia. It is quite possible that this process is operated by ancient, highly conserved programmes, and that the trilobite visual system became differentiated in the same way.

It seems clear that the spacing of the lens centres determines the size to which the lenses can grow. Constant spacing will ensure that all the lenses grow to the same size, as in some of the early Ordovician phacopids such as *Ormathops atavus* Barrande, 1852 and *O. borni* Dean, 1966 (Clarkson, 1971). Here some parts of the same eye exhibit normal hexagonal close packing, but in other areas there are distinct irregularities. This is because, as in most holochroal eyes (the ancestral

state), the lenses are all of the same size, and it is not possible to develop perfect packing on a downwardly expanding visual surface. In this sense the eyes of *Ormathops* inherited the ancestral system from their holochroal forebears. This was readily corrected by introducing a constant arithmetical increase in lens-spacing as the eye expanded downwards during ontogeny, as is shown by derived phacopids such as *Eldredgeops* and *Phacops* where the lenses increase in size downwards and towards front and rear (Clarkson, 1971, 1975). Clearly it was important to have a regular system of packing, and the functional model of Schoenemann, discussed later, may explain why this was so.

In the Devonian trilobite *Erbenochile erbeni* Alberti, 1981 the schizochroal eyes extended prominently upwards and each had an extraordinary visual surface in the form of a straight sided tower of about 560 lenses, with 18 lenses in a vertical file (Fortey and Chatterton, 2003). Due to the high elevation of the eyes the animal could even see backwards

over its thorax. The palpebral lobe extended outwards over the whole of the visual surface as an eyeshade. According to Fortey and Chatterton (2003) the eye was so straight-sided that this hood might protect the visual surface from glare derived from surface light. This adaptation suggests that this trilobite was probably diurnal, living in brightly illuminated shallow waters since an eyeshade would be of little use in the dark.

3.3. The internal structure of the lenses

The internal structure of the lenses of schizochroal eyes is important in understanding how they worked. Towe (1973) first recognised that the lenses consisted of primary calcite, and subsequently Clarkson (1967, 1969, 1975) and Clarkson and Levi-Setti (1975) demonstrated that the phacopid lens consisted of an upper lens unit and a lower intralensar bowl (Fig. 5). The upper lens unit was composed of primary calcite with the crystallographic axis (c-axis) normal to the principal plane of the lens. Light passing through calcite is broken into two rays; it is doubly refracted producing different images at different depths. Light travelling parallel with the c-axis, however, is not doubly refracted, and clearly the orientation of the calcite lens relative to the eye is an adaptation for improved vision. The interlensar bowl is separated from the upper lens unit by an undulating, regularly formed surface. There is some variety amongst Phacopina, both in the shapes of the lenses, and in the form and disposition of these internal structures. In the Ordovician *Dalmanitina socialis* Barrande, 1852, for example (Fig. 5B), the lenses are elliptical in cross-section, and in each the upper calcite unit has a small central bulge on its lower surface, so that the intralensar bowl has a matching dimple. The upper lens unit here is very similar in shape to the original aplanatic thick lens designed by René Des Cartes in 1637, designed to bring light to a sharp focus. Another kind of lens, represented by the Ordovician *Crozonaspis struvei* Henry, 1968, is more highly convex, the intralensar bowl is thicker and has a wider hemispherical concavity on its upper surface, rather than just a dimple. The upper lens unit of this trilobite greatly resembles the alternative design for an aplanatic lens designed by Christian Huygens in 1690. A model of this latter kind of lens was constructed in Chicago by Levi-Setti, with an upper unit of oriented calcite ($n = 1.66$). Various intralensar bowls of clear plastic and of different refractive indices were fitted, and the sharpest focus, in water, was obtained with a bowl where $n = 1.63$ (Fig. 5E).

A third kind of lens was described by Miller and Clarkson (1980) in the Devonian *Eldredgeops rana milleri* Stewart, 1927. Here the intralensar bowl is thinned out completely at the base of the lens, but an additional structure, the core, of apparently similar material to the bowl is present in the centre of the upper lens unit (Fig. 5D). The above summary represents our state of knowledge up until the end of the 20th century, summarised by Clarkson (1997).

Bruton and Haas (2003) studied the Devonian phacopid *Geesops sparsinodosus* Struve, 1970, using thin-sections and polished surfaces. They illustrated somewhat irregular intralensar structures, which we regard as diagenetically degraded residues of the core and bowl. They consider these, however, and by default all other described intralensar structures, to be artefacts. These authors, however, fail to account for the facts that perfectly symmetrical structures within the lenses have been described in better-preserved material, that all the lenses within one eye are invariably identical in internal structure, that the Cartesian surfaces previously recognised operate ideally according to known principles of geometrical optics, and that these same principles operate at all stages during the re-formation of the lenses after ecdysis (Miller and Clarkson, 1980; Horváth, 1996). Even in the imperfectly preserved material of *Geesops*, the relics of the bowl and core are in the same positions as in the phacopid lenses described previously in other phacopids. The presence of both bowl and core have been further confirmed during work in progress by Catherine Crônier (personal communication) and Brigitte Schoenemann (personal communication). Moreover, current, though as yet unpublished work, in progress at Glasgow University, especially on a species of *Dalmanites* (Clare Torney, Alan Owen and Martin Lee) has confirmed not only that the bowl and core exist, but has shed light on their chemical composition. Several techniques have been used in the Glasgow study; transmitted light microscopy, cathodoluminescence microscopy, electron microprobe analysis with X-ray mapping, and Electron Backscatter Diffraction (ESBD). These latter two techniques had not previously been applied to trilobite eyes. It is clear from this work that in *Dalmanites* sp. the intralensar bowl consists of high magnesian calcite, as did the core, although the concentration of magnesium was less. There was an increased concentration of iron in both the bowl and the core, being highest in the latter. The rest of the lens, like the cuticle (Wilmot and Fallick, 1989), consisted of low magnesian calcite. This work has also revealed that the trabeculae are real structures, each following a curving path through the lens, and are currently interpreted as dispersing doubly refracted rays, towards the periphery of the lens, thereby minimising the problem of double images at different depths. In the original study of the eyes of *Dalmanites* by Clarkson and Levi-Setti (1975) a somewhat fuzzy area in the centre of the lens, interrupting the cleavage planes of the calcite, was thought be diagenetic. Working on the same material, Torney et al. show that it is a real structure, though as noted the percentage of high-magnesian calcite is lower than in the core (Fig. 5C). It is possible that it was only in the later phacopids, such as *Eldredgeops rana milleri* (Stewart, 1927) (Fig. 5D) that the core became more fully defined and the proportion of high-magnesian calcite increased.

3.4. Functioning of phacopid lenses

Two alternative models have been proposed for the functioning of the lenses of phacopid trilobites. These two models depend entirely upon whether the internal structures within the lenses are interpreted as primary or otherwise. The first model, initiated by Clarkson and Levi-Setti (1975), is based upon the upper lens unit and the core being primary, as argued above.

The lenses were aplanatic, despite being thick; they were doublets that brought light to a sharp focus and eliminated spherical aberration. The interface between the upper lens-unit and the intralensar bowl acts as a correcting surface. The intralensar bowl was interpreted as the final and necessary element in the lens, ensuring a sharp focus some distance below the lens. This model has been refined and modified by Gál et al. (2000b). In this work it was pointed out that a mathematical error by Des Cartes led to the assumption that a small central 'nipple' was an essential component of this kind of aplanatic lens. Computation by Horváth (1989), as discussed by Gál et al. (2000b) shows that the central nipple would not be necessary for sharply focusing the light. If this is so, then what was the central nipple for? Gal et al. (2000b) suggested that these lenses were bifocal. The central areas of the lens, defined by the nipple, would have had a depth of field ranging from 0 to 0.5 cm. It could detect small floating objects, food particles and tiny prey, in the immediate vicinity. The peripheral region, by contrast, with a depth of field from 0.5 cm to infinity could enable the trilobite to pick up sharply focused objects much further away; the sea floor, potential mates, and predators. No known recent euarthropod compound eye resembles that of *Dalmanitina socialis*, but interestingly, as Gál et al. (2000b) noted, concentric bifocal optical lenses, recently developed and used as artificial implants in human eyes, are of remarkably similar form. These also allow near and far vision.

Two other questions remain. The first is whether the intralensar bowl had more than one function. According to Horváth's, (1996) detailed calculations one of the possible functions of the intralensar bowl could be a reduction in reflectivity, and the enhancement of transmissivity in passing through the lens. This increase has been estimated to be as much as 10.5%. The optical elegance of these lenses could not have been conceived of a generation or two ago. Horváth and Clarkson (1993) showed that the upper lens unit in the schizochroal eye of the Devonian trilobite *E. rana milleri* was more-or-less corrected for spherical aberration even during post-ecdysial aberration. This is also a remarkable feature demonstrating the sophisticated optics of the schizochroal eye.

The second question concerns the core. In *E. rana milleri* it is a real structure, and in the highly biconvex lenses of this trilobite, it is associated with an intralensar bowl which thins out entirely proximally (Miller and Clarkson, 1980). From the work in progress by Torney et al. mentioned earlier, it is now evident that it was a primary structure also in *Dalmanites*. It is not yet clear, whether the core is present as a mineralogically differentiated unit in all schizochroal eyes, or only in the later phacopids. Its function requires still to be determined.

The alternative Gradient Refractive Index (GRIN) model has been elegantly set out by Bruton and Haas (2003). This model assumes that the refractive index of the calcite lens was graded from the outer to the inner surface of the lens, and this by itself would bring light to a sharp focus. Eyes fitting this model are present in the euchelicerate 'horseshoe-crabs' such as *Limulus polyphemus* Linnaeus, 1776. It would indeed be a possible model for the functioning of phacopid

lenses too, but it depends upon the interpretation of internal structures as artefacts, and there is no evidence of the lenses of phacopids being singlets with a gradient index of refraction; it remains a theory. Until such evidence is forthcoming we feel that no further discussion is required.

3.5. How did the schizochroal eye function as a whole?

We have noted that the schizochroal eyes of phacopid trilobites are unlike the compound eyes of any living euarthropod. There are no direct counterparts or analogues, which is unfortunate since palaeontological reconstructions should ideally relate, where possible, to living models.

Horváth et al. (1997) defined schizochroal eyes as possessing three common structural features (i) the 'schizochroal' character, i.e. well separated, relatively few, and large lenses (Figs. 4A–F and 6B–F), (ii) the 'doublet' character, i.e. two (or three) internal units of different refractive indices, and (iii) the 'aplanatic' character, i.e. correction for spherical aberration. A survey was made (Paulus, 1979; Horváth et al., 1997) of living animals with eyes of 'schizochroal' character. These include some chelicerates, deep-sea ostracodes, myriapods, some insects and insect larvae. But by far the closest analogue is with the compound 'schizochroal' eyes of males of the pterygote insect group Strepsipterida. The eyes of these ephemeral, and usually night-flying insects are almost spherical, with large and separated lenses; the intervening cuticle is covered by tiny hairs. Below each thick singlet lens the photoreceptors are arranged in a concave layer as in an ocellus rather than an ommatidium. According to Buschbeck et al. (1999), in the male strepsipteran *Xenos peckii* an independent retina lies below each image-forming lens, on which the image of the world within the visual field is formed and sampled by numerous photoreceptors. While such eyes resemble those of phacopids, they are very much smaller. Eyes of 'doublet' character (i.e. having the equivalent of an upper lens-unit and an intralensar bowl) in living invertebrates are present in the larval insects *Pieris* and *Perga*, and in the backswimmer *Notonecta* amongst others and the 'aplanatic' character is found in some ostracodes, *Notonecta*, and larval *Perga*. Independently the scallop *Pecten* has likewise an 'aplanatic' character. In the arm ossicles of the light-sensitive brittlestar *Ophiocoma wendtii* the periphery of the labyrinthic calcite skeleton extends into a regular array of biconvex microlenses that guide and focus the light inside the photosensitive tissue (Aizenberg et al., 2001). Each microlens is designed to minimise spherical aberration (by having a Huygensian lower lens surface: aplanatic character) and birefringence (by having the crystallographic *c*-axis parallel to the optical axis of the lens), and to detect light from a particular direction. The optical performance of the lens array is further optimised by phototrophic chromatophores that regulate the dose of illumination reaching the dermal photoreceptors. *Pieris*, larval *Perga*, and *Pecten* share two of the three characteristics with schizochroal eyes of phacopids, but there is no modern eye which shares all three.

Critical to our understanding of the function of the schizochroal eye of phacopids is the nature of the sublensar
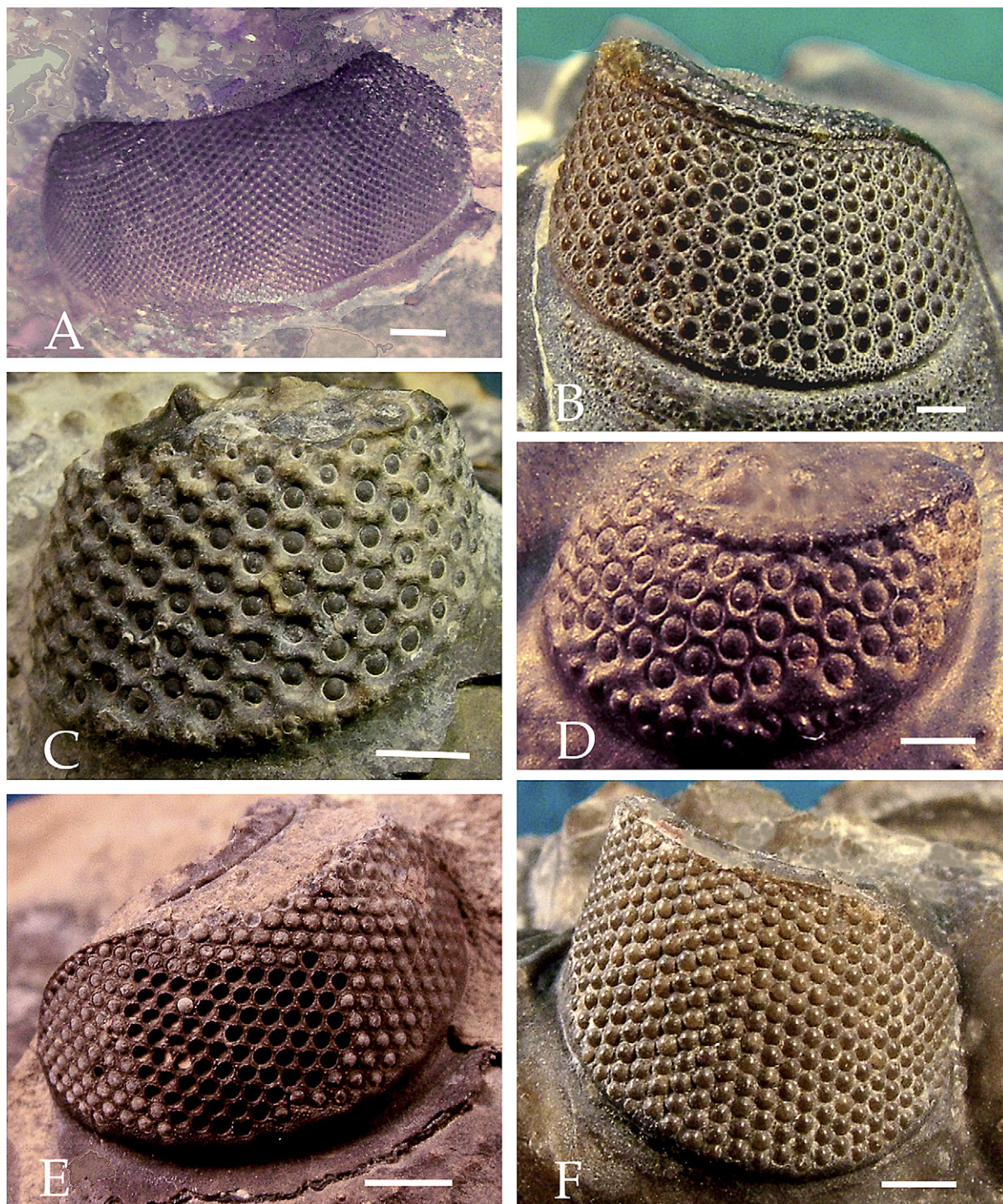
Fig. 6. Digital camera images of trilobite eyes (Fuji FinePix S7000, 6.1. Mpxl, in Super macro mode) (photos by R. Levi-Setti). (A) Holochroal eye of *Platyscutellum massai* Alberti, 1981 (Lower Devonian, Tafilalt, Hamar Laghdad, SE Morocco). The pattern of intersecting logarithmic spirals, a leitmotif in the lens arrangement of both holochroal (as in this example) and schizochroal trilobite eyes, is particularly noticeable in this image. (B–F) Schizochroal eyes (B) Right eye of *Hollardops mesocristata* Le Maitre, 1952 (Middle Devonian, Máder, Jbel Issoumour, SE Morocco). A fine hexagonal decoration of dots is portrayed here on the sclera surrounding each lens. Similar decoration was first pointed out by Barrande (1852) in dalmanitid eyes. To be noted also is the progressive increase in width of the lenses in each dorsoventral file, away from the generative zone, following the increased lens spacing. (C) Left eye of *Drotops armatus* Struve, 1995 (Middle Devonian, Máder, Jbel Issoumour, SE Morocco). Here small lenses are widely separated and encased in dominant hexagonal patterns of scleral protrusions. (D) Left eye of *Phacops tafilaltensis* Alberti, 1983 (Lower Devonian, Zguilma (SE of Foum Zguid), SE Morocco). In contrast to the eye in (C), this phacopid exhibits a few wider and closely-spaced lenses in each dorsoventral file. (E) Left eye of *Odontochile* (*Zlichovaspis*) aff. *rugosa* Barrande, 1852 (Middle Devonian, Máder, Jbel Issoumour, SE Morocco). In this eye, many lenses have been dislodged, leaving empty alveoli. (F) Right eye of *Coltraneia oufatenensis* Morzadec, 2001 (Lower Devonian, Máder, Oufatène, SE Morocco). In this remarkable eye, the calcite lenses, protruding well above the sclera, are translucent. (All scale bars are 1 mm.)

photoreceptive structures, and in the absence of direct analogues this remains speculative. Some investigators (Campbell, 1975; Clarkson, 1979) have suggested that below each lens lay a short ocellar capsule floored by a layer of retinal cells. Evidence for this is limited to the capsule of *Phacops fecundus* and *Geesops sparsinodosus* referred to earlier, and another possible analogue with strepsipterid insects. Conversely Fordyce and Cronin (1989) inclined to the view that a single photoreceptor underlay each lens, and that the eye was adapted to dim light.

In some schizochroal eyes, such as in various species of the Devonian *Phacops* and *Eldredgeops*, the axial bearings of the lens-axes are more or less evenly spaced though somewhat clustered in the lower part of the visual field (Clarkson, 1966b). Such an eye could form a coherent image only if the individual images for each lens are superimposed, without blind spaces between (Brigitte Schoenemann, personal communication). The retina may have had over 1000 photoreceptors, as Schoenemann calculates from the sizes of phacopid lenses, and the dimensions of photoreceptors in the compound eyes of living arthropods. According to Schoenemann, light transmitted from a particular point in the visual field would stimulate a receptor, or group of receptors, in the retina below one particular lens. But it would also be scanned by orienting the different parts of the retina in neighbouring lenses. Thereby the phacopid visual system could unite all the individual images with their overlapping fields into a single coherent and total image. In phacopids such as the Silurian *Acaste downingiae* (Salter, 1864), as described by Clarkson (1966a) the visual surface is much more highly curved in the horizontal plane than it is in the vertical. The result is that the axial bearings of the lenses are arranged in widely spaced 'visual strips' crossing the visual field obliquely from top to bottom. Such an eye would not, at first sight, seem to be able to form a coherent image, but further explanations are forthcoming (Brigitte Schoenemann, personal communication). Several other factors require further explanation, such as a net evolutionary change towards fewer and larger lenses in Devonian species of *Phacops* and its relatives through time, and the nature of the neural network to name but two. Yet Schoenemann's model has considerable potential for the further understanding of how phacopid eyes worked, and what they saw.

3.6. Origin of the schizochroal eye

The great majority of holochroal eyes are known only from adult trilobites, but in a few cases the juvenile eyes have also been described from very well preserved material. Perhaps surprisingly, these proved to be schizochroal with relatively few and separate lenses, large for the visual surface (Fig. 2C—E). They have been described so far in *Paladin eichwaldi shunnerensis* King, 1914 (figs 8c, 9a in Clarkson and Zhang, 1991), and in *Olenus wahlenbergi* Westergård, 1922 (fig 5j in Clarkson and Taylor, 1995). It is highly probably that such juvenile eyes were universal in all trilobites with holochroal adult eyes. The adult schizochroal eye is apomorphic for phacopids but retention of the juvenile morphology

of the ancestor in the adult of the descendant, in other words classical paedomorphosis, is a very probable scenario for the origins of schizochroal eyes from a holochroal-eyed ancestor.

4. Abathochroal eyes

This kind of eye is confined to the Lower to Middle Cambrian Suborder Eodiscina, a group of very small trilobites with no more than two or three thoracic segments (Figs. 1 and 4G,H). Abathochroal eyes are apomorphic for eodiscids, though in most eodiscids the eyes have been lost secondarily. Both blind and oculate forms may occur in related groups. The eye structure has been described by Jell (1975) and Zhang and Clarkson (1990). Abathochroal eyes superficially resemble very small schizochroal eyes, as the lenses are usually separated from each other, but they have no interlensar sclera (thick cuticular material between the lenses). It may be that each lens had an individual thin corneal membrane, fixed round the margin. The best known abathochroal eyes are of phosphatised material from China, belonging to the species *Shizhudiscus lonquanensis* S-G. Zuang and Zhu, 1980 and *Neocobboldia chinlinica* Lee, 1977. In the latter, moulds of the inner surface show a little dimple in the centre of each lens. Such lenses as this are aplanatic, bringing light to a sharp focus, despite their being relatively thick. Gál et al. (2000a) suggested that the optical function of this lens bulge in *Neocobboldia chinlinica* could be to make the lens bifocal, even though one of the two focal points (the one belonging to the central lens region possessing the tiny bulge) was not sharp due to diffraction of light. It is not known why so many eodiscids were blind; the eyes of these early trilobites, where present, were of elegant design and were clearly functional. We can only presume that eye loss, as in other trilobites, was environmentally related, though nothing further is known. Apart from those eodiscids referred to above, little else is known, and the origin of this ancient eye type remains tantalisingly obscure.

The Suborder Eodiscina has been traditionally grouped with the Suborder Agnostina in a single Order Agnostida, which are likewise diminutive and which have only two thoracic segments. Waloszek and Müller (1990), however, and Stein et al. (2005) have shown that on the basis of limb morphology and other characteristics, these groups are quite unrelated. This has now been confirmed by the discovery of hypostomes (a hypostome is a hard ventral plate lying below the glabella (Peter Cederström, personal communication) of 'standard' trilobite type in eodiscids. The hypostomes of agnostoids are quite unlike those of any other trilobite. *Agnostus,* usually regarded as blind, has actually a median eye, but also compound eyes, situated ventrally and reduced to small lobes. The limbs and ventral morphology are greatly similar to those of stem group crustaceans.

5. Eye-reduction and blindness

Compound eyes are primary structures in trilobites, because they have been plesiomorphically retained from Arthropoda *sensu stricto*. Secondary blindness is not uncommon, however,

in certain species. Absence of any kind of eye is characteristic of some important groups such as the Ordovician Trinucleoida, and Ordovician to Devonian Harpetidae (Fig. 1). These trilobites posses a large pitted fringe, which curves round the anterior margin of the head, and which may well have had a vibro- or chemosensory function. If so it would seem to have 'replaced' the compound eye as a primary sense organ. The abathochroal eyes of Eodiscida, and their secondary loss in many species, has already been discussed. The Agnostida have no external eyes but a probable median dorsal ocellus and reduced ventral compound eyes, represented by pimples in front of the hypostome, and the soft areas on the hypostome may well indicate a light sense.

There are, however, many examples of progressive eye-reduction through time. The best known examples come from the Upper Devonian of Europe and China; such eye-reduction affected both holochroal and schizochroal-eyed trilobites simultaneously. The Montagne Noire of Southern France yields a precisely zoned succession of Tropidocoryphinae, a long-ranged in-group of holochroal-eyed trilobites of the Order Proetida. The earlier, large-eyed tropidocoryphines had been a stable group for some 40 million years, and then in their last few million years the eyes, in two separate lineages, degenerated progressively through time, leading to blindness (Feist and Clarkson, 1989). In the representatives of another proetid group, *Drevermannia* from Thuringia, Germany, eyes are likewise absent, but this genus has no known direct ancestry from forms with normal or reduced eyes, and blindness must have been acquired very early in its evolutionary lineage. In early developmental stages of species of this genus ocular ridges, which presumably carried the optic nerves, are still retained. This is an example of centripetal eye reduction, where the external parts of the visual system are first affected, as opposed to centrifugal reduction where the internal nerves degenerate before the lenses begin to diminish (Lerosey-Aubril, 2006). Contemporaneous eye reduction is known in other proetides, but also in phacopids where the eyes are schizochroal (Crônier et al., 1999; Crônier and Clarkson, 2001; Crônier and Feist, 2000) (Fig. 5F). Feist (1995) recorded an equivalent unidirectional 'trend' in late Devonian phacopids, showing it to result from progressive paedomorphosis. During trilobite ontogeny the eyes invariably appear on the anterior margin, and as the trilobite grows, they enlarge and migrate inwards, 'dragging' the facial suture with them. During eye loss in Feist's phacopids, the reverse happens, the eyes becoming increasing small and marginal, i.e. morphologically more and more 'juvenile' through time, and eventually they disappear altogether. Thomas (2005) has most recently discussed the developmental processes that lead to secondary eye-reduction and blindness.

Eye-reduction and blindness on a global scale during the Late Devonian is likely to be associated with periods of ocean deepening. During such episodes a blanket of mud spread over huge areas of the sea floor, beyond the limits of light-penetration (Feist, 1991). The trilobites became adapted to this habitat, with loss of their eyes and very small size, but even this did not save them for they perished during the great Late Devonian mass-extinction crisis, which followed shortly after. The remaining trilobites persisting through the Carboniferous and Permian were all Proetida. They were derived from shallow-water ancestors and largely kept to this habitat, and they all had 'normal' holochroal eyes. With the extinction of the last trilobites at the end of the Permian, some 250 million years ago, during the most severe environmental crisis of all, the 270 million year history of the best-known fossil visual system came to its final conclusion.

References

Aizenberg, J., Tkachenko, A., Weiner, S., Added, L., Hendler, G., 2001. Calcitic microlenses as part of the photoreceptor system in brittlestars. Nature 412, 819–822.

Bruton, D., Haas, W., 2003. The puzzling eye of *Phacops*. Special Papers in Palaeontology 70, 349–361.

Campbell, K.S.W., 1975. The functional anatomy of trilobites: musculature and eyes. Journal and Proceedings of the Royal Society of New South Wales 108, 168–188.

Clarkson, E.N.K., 1966a. Schizochroal eyes and vision in some Silurian acastid trilobites. Palaeontology 9, 1–29.

Clarkson, E.N.K., 1966b. Schizochroal eyes and vision is some phacopid trilobites. Palaeontology 9, 464–487.

Clarkson, E.N.K., 1967. Fine structure of the eye in two species of *Phacops* (Trilobita). Palaeontology 10, 603–616.

Clarkson, E.N.K., 1969. On the schizochroal eyes of three species of *Reedops* (Trilobita, Phacopidae) from the Devonian of Bohemia. Transactions of the Royal Society of Edinburgh 68, 168–188.

Clarkson, E.N.K., 1971. On the early schizochroal eyes of *Ormathops* (Trilobita: Zeliszkellinae). Mémoires du Bureau des Recherches Géologiques et Minieres 73, 51–63.

Clarkson, E.N.K., 1973. Morphology and evolution of the eye in Upper Cambrian Olenidae (Trilobita). Palaeontology 16, 735–765.

Clarkson, E.N.K., 1975. The evolution of the eye in trilobites. Fossils and Strata 4, 7–31.

Clarkson, E.N.K., 1979. The visual system of trilobites. Palaeontology 22, 1–22.

Clarkson, E.N.K., 1997. The eye: morphology, function, and evolution. In: Kaesler, R.L., et al. (Eds.), Treatise on Invertebrate Paleontology, part O Arthropoda 1, Trilobita, Revised. The University of Kansas Press and Geological Society of America, pp. 114–132.

Clarkson, E.N.K., 1998. Invertebrate Palaeontology and Evolution, fourth ed. Blackwell Science, Oxford, 452 pp.

Clarkson, E.N.K., Levi-Setti, R., 1975. Trilobite eyes and the optics of Des Cartes and Huygens. Nature 254, 663–667.

Clarkson, E.N.K., Taylor, C.M., 1995. Ontogeny of the trilobite *Olenus wahlenbergi* Westergård, from the upper Cambrian Alum Shales of Skåne, Sweden. Transactions of the Royal Society of Edinburgh: Earth Sciences 86, 13–34.

Clarkson, E.N.K., Zhang, X.-g., 1991. Ontogeny and structure of the Carboniferous trilobite *Paladin eichwaldi shunnerensis* (King, 1914). Transactions of the Royal Society of Edinburgh: Earth Sciences 82, 277–295.

Crônier, C., Bartzsch, K., Weyer, D., Feist, R., 1999. Larval morphology and ontogeny of a late Devonian phacopid with reduced sight from Thuringia, Germany. Journal of Paleontology 73, 240—255.

Crônier, C., Clarkson, E.N.K., 2001. Variation of eye-lens distribution in a new late Devonian phacopid trilobite. Transactions of the Royal Society of Edinburgh: Earth Sciences 92, 103—113.

Crônier, C., Feist, R., 2000. Évolution et systematique du groupe Cryphops (Phacopina, Trilobita) du Devonien superiere. Senckenbergiana Lethaea 79, 501—515.

Feist, R., 1991. The late Devonian trilobite crises. Historical Biology 5, 197—214.

Feist, R., 1995. Effect of paedomorphosis in eye reduction on patterns of evolution and extinction in trilobites. In: McNamara, K.J. (Ed.), Evolutionary Change and Heterochrony. John Wiley and Sons, pp. 225—244.

Feist, R., Clarkson, E.N.K., 1989. Environmentally controlled phyletic evolution, blindness and extinction in Late Devonian tropidocoryphine trilobites. Lethaia 22, 359—373.

Fordyce, D., Cronin, T.W., 1993. Trilobite vision: A comparison of schizochroal and holochroal eyes with compound eyes of modern arthropods. Paleobiology 19, 288—303.

Fortey, R.A., 1985. Pelagic trilobites as an example of deducing the life habits of extinct arthropods. Transactions of the Royal Society of Edinburgh: Earth Sciences 76, 219—230.

Fortey, R.A., Chatterton, B.D.E., 2003. A Devonian trilobite with an eyeshade. Science 301, 1689.

Fortey, R.A., Owens, R.M., 1987. The Arenig Series in South Wales: Stratigraphy and palaeontology. 1. The Arenig Series in South Wales. Bulletin of the British Museum (Natural History). Geology 41, 67—307.

Gál, J., Horváth, G., Clarkson, E.N.K., 2000a. Reconstruction of the shape and optics of the lenses in the abathochroal-eyed trilobite Neocobboldia chinlinic. Historical Biology 14, 193—204.

Gál, J., Horváth, G., Clarkson, E.N.K., Haiman, O., 2000b. Image formation by bifocal lenses in a trilobite eye? Vision Research 40, 843—853.

Horváth, G., 1996. The lower lens unit in schizochroal eyes reduces reflectivity: on the possible optical function of the intralensar bowl. Historical Biology 12, 83—92.

Horváth, G., Clarkson, E.N.K., Pix, W., 1997. Survey of modern counterparts of schizochroal trilobite eyes: structural and functional similarities and differences. Historical Biology 12, 229—263.

Levi-Setti, R., 1993. Trilobites, second ed. University of Chicago Press, Chicago and London, 342 pp.

Levi-Setti, R., Clarkson, E.N.K., Horváth, G., 1998. Paleontologia dell'occhio, in: Frontiere della Vita: Enciclopedia Italiana (English language version The Eye: Paleontology). pp. 365—379.

Lerosey-Aubril, R., 2006. Ontogeny of Drevermannia and the origin of blindness in late Devonian proetoid trilobites. Geological Magazine 143, 89—104.

McCormick, T., Fortey, R.A., 1998. Independent testing of a palaeobiological hypothesis: the optical design of two Ordovician pelagic trilobites reveals their relative paleobathymetry. Paleobiology 24, 235—253.

Maas, A., Waloszek, D., Chen, J.-Y., Braun, A., Wang, X.-G., Huang, D.-Y., 2004. Phylogeny and life habits of early arthropods—predation in the Early Cambrian sea. Progress in Natural Science 14, 158—166.

Miller, J., Clarkson, E.N.K., 1980. The post-ecdysial development of the cuticle and the eye of the Devonian trilobite Phacops rana milleri Stewart 1927. Philosophical Transactions of the Royal Society of London, Series B 28, 461—480.

Paulus, H.F., 1979. Eye structure and monophyly of the Arthropoda. In: Gupta, A.P. (Ed.), Arthropod Phylogeny. Van Nostrand Reinhold, New York, pp. 299—383.

Stein, M., Waloszek, D., Maas, A., 2005. Oelandocaris oelandica and its significance to resolving the stem lineage of Crustacea. In: Koenemann, S., Vonck, R. (Eds.), Crustacea and Arthropod Relationships. CRC Press, Boca Raton, pp. 55—71. Crustacean Issues 16.

Thomas, A.T., 1998. Variation in the eyes of the Silurian trilobites Eophacops and Acaste and its significance. Palaeontology 41, 897—911.

Thomas, A.T., 2005. Developmental palaeobiology of trilobite eyes and its evolutionary significance. Earth Science Reviews 71, 77—93.

Towe, K.M., 1973. Trilobite eyes; calcified lenses in vivo. Science 179, 1007—1009.

Waloszek, D., Müller, K.J., 1990. Stem-lineage crustaceans from the Upper Cambrian of Sweden and their bearing on the position of Agnostus. Lethaia 23, 409—427.

Waloszek, D., Chen, J.-Y., Maas, A., Wang, X.-G., 2005. Early Cambrian arthropods—new insights into arthropod head and structural evolution. Arthropod Structure and Development 34, 189—205.

Wilmot, N.V., Fallick, A.E., 1989. Original mineralogy of trilobite exoskeletons. Palaeontology 32, 297—303.

Zhang, X.-G., Clarkson, E.N.K., 1990. The eyes of lower Cambrian eodiscid trilobites. Palaeontology 33, 911—933.