

SURVEY OF MODERN COUNTERPARTS OF SCHIZOCHROAL TRILOBITE EYES: STRUCTURAL AND FUNCTIONAL SIMILARITIES AND DIFFERENCES

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Three main characters can be identified as typical of schizochroal trilobite eyes: well-separated optical units, the presence of doublet lenses, and correction for spherical aberration. Surveying the structure and function of some known modern counterparts of schizochroal trilobite eyes, an attempt is made to reveal the functional significance of these characters. First the anatomy and the possible functioning of three different known eye types in trilobites - holochroal, schizochroal and abathochroal - are briefly reviewed. Then the structure of those animal eyes are considered, which share at least one of the above-mentioned three characteristics with the schizochroal trilobite eyes. The structural and functional similarities and differences between schizochroal eyes and their modern counterparts are compared. The derivation of schizochroal eyes from holochroal ancestors are discussed. Finally, the possible evolution of the optics of trilobite lenses is outlined. Although our review supports the earlier idea that the schizochroal ommatidia probably had extended retinal structures behind them, none of the known modern counterparts considered are so compellingly similar to the trilobite eyes that they point to a clear solution of the way these ancient eyes worked. The most convincingly similar modern structure to compare with the schizochroal trilobite eye is the Strepsipteran eye that would repay further detailed studies.

Keywords: Trilobites, Schizochroal trilobite eye, Modern analogies, Functional morphology

1 INTRODUCTION

The study of the visual system of trilobites has been one of the classic functional morphology research programs in palaeontology. In the 60's and 70's the application of new techniques to the studies of trilobite eyes resulted in rapid advances in knowledge of lens structure, and minute descriptions of lenses were published covering a wide range of taxa (e.g. Clarkson, 1966a,b, 1967, 1968, 1969, 1971, 1975, 1979; Towe, 1973; Campbell, 1975; Jell, 1975; Clarkson and Levi-Setti, 1975). In the 80's the rate of advance slowed down (e.g. Miller and Clarkson, 1980; Fordyce and Cronin, 1989; Zhang and Clarkson, 1990), because much of the descriptive work had progressed as far as it could go; what was needed was the structure

of trilobite ommatidia and retina. This situation has persisted: the ommatidia are still unknown, and although there have been several recent papers on trilobite vision, most have been either descriptions of new and unusual eye structures (*e.g.* Clarkson and Zhang, 1991; Levi-Setti, 1992; Clarkson and Taylor, 1995), or detailed bio-optics (*e.g.* Horváth, 1989a, 1996; Horváth and Clarkson, 1993; Fordyce and Cronin 1993). Relatively few new conceptual advances have been made. This paper aims to move the situation forward by reviewing possible analogs in modern organisms. In this work certain modern eyes are surveyed that have varying degrees of similarity to the schizochroal condition because recent eyes possessing some of these three characters could have a good deal in common with schizochroal eyes. We are not looking for evolutionary homology but for enlightenment of the 'schizochroal enigma' by analogy.

Schizochroal trilobite eyes are of great evolutionary and paleobiological interest because they do not conform to the normal compound eye pattern in modern arthropods. The lenses are too large and too widely separated to make sense in terms of our knowledge of recent compound eyes, and the lenses have particularly interesting optical properties as well. The mature eyes of phacopid trilobites have three common structural features (Clarkson, 1966a,b, 1967, 1968, 1969, 1971, 1975, 1979; Clarkson and Levi-Setti, 1975; Horváth, 1989a; Levi-Setti, 1992): (1) Their external appearance is characterized by well-separated large circular lenses of relatively small number. This feature is called the 'schizochroal' character. (2) The lenses consist of two optically homogeneous units of different refractive indices. We refer to this, in the following text as the 'doublet' character. (3) The doublet lenses are corrected for spherical aberration by means of an undulating Huygensian interface between the lens units. This is the 'aplanatic' character. Interestingly, the post-ecdysially developing lens also was aplanatic in *Phacops rana milleri* (Miller and Clarkson, 1980; Horváth and Clarkson, 1993).

The sublensar structure of schizochroal trilobite eyes is almost entirely unknown. The exact functioning of these enigmatic eyes also remains unclear until new data are obtained from the fossil record. In the literature, there exist different hypotheses and speculations on the structure and function of schizochroal trilobite eyes (Towe, 1973; Campbell, 1975; Clarkson, 1975, 1979; Clarkson and Levi-Setti, 1975; Stockton and Cowen, 1976; Miller and Clarkson, 1980; Fordyce and Cronin, 1989, 1993; Horváth, 1989a; Zhang and Clarkson, 1990; Levi-Setti, 1992; Horváth and Clarkson, 1993). Previously, Clarkson (1975, 1979), Fordyce and Cronin (1989, 1993), and Levi-Setti (1992) attempted to find some recent analogies of schizochroal trilobite eyes, however, a comprehensive review is still lacking. The primary aim of this work is to fill this gap with illustrating some known modern counterparts of schizochroal trilobite eyes, because we believe that palaeontological reconstructions should follow living models as far as possible.

First the anatomy and the possible functioning of three different known eye types in trilobites-holochroal, schizochroal and abathochroal — are briefly reviewed. Then the structure of those animal (mainly arthropod) eyes are considered, which share at least one of the above-mentioned three characteristics with the schizochroal trilobite eyes. We compare the structural and functional similarities and differences between schizochroal

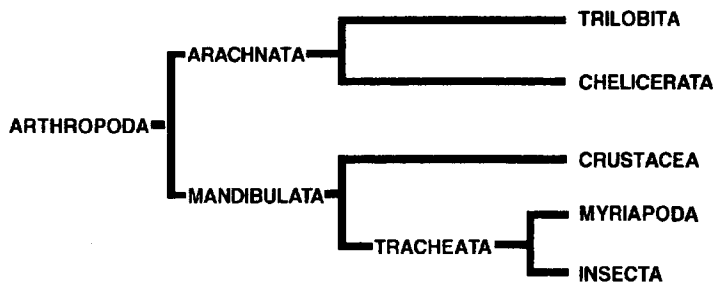


FIGURE 1 Dendrogram of possible phylogenetic relationships of various arthropod groups including the Trilobita (after Paulus, 1979).

trilobite eyes and their modern analogs. The derivation of schizochroal eyes from holochroal ancestors are also discussed. Finally, the possible evolution of the optics of trilobite lenses is outlined. According to Paulus (1979), Figure 1 shows a possible scheme of phylogenetic relationships of various arthropod groups including trilobites.

2 TRILOBITE EYE TYPES

The first trilobites appear abruptly in sedimentary rocks of early Cambrian age, some 550 million years old. They are already highly organised animals, not radically different from later trilobites, and from their earliest appearance they possess perfectly formed 'compound eyes'. Whereas these paired, laterally placed, faceted eyes constitute a primitive character for trilobites, nothing is known of their origin. Presumably there were trilobite precursors with non-mineralised shells in late Precambrian times, but the preservation potential of these is very small. Some possible candidates have been reported from the late Proterozoic of the Ediacara Hills, South Australia (Jenkins, 1992). These, however, are poorly preserved and shed no further light upon the origins of the trilobite visual system.

A fundamental problem in studying the eyes of trilobites is that only the lenses and adjacent regions of the exoskeleton are ever preserved, and we have no direct information of what originally lay below. Even so, much is now known of the detailed structure and evolution of the eye in trilobites and some useful conclusions can be drawn about how the eye functioned.

2.1 The Holochroal Trilobite Eye

Holochroal eyes are found in the earliest of all trilobites, from the Lower Cambrian, and they persist throughout the history of the group. The last trilobites became extinct at the end of the Permian, and these, too, possess holochroal eyes. The holochroal eye type represents the original, primitive condition, from which other eye types were derived.

What distinguishes holochroal eyes from others is that the lenses are numerous and closely packed, so that each lens is in direct contact with its neighbours (Figure 2).

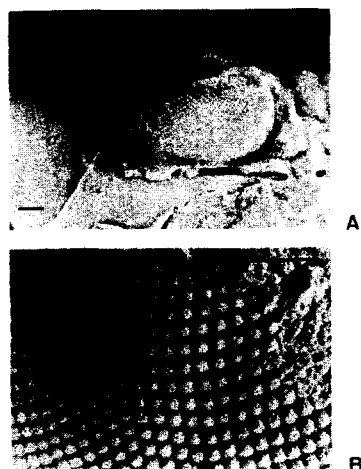


FIGURE 2 A typical holochroal eye of the trilobite *Paralejurus dormitzeri* from the Lower Devonian of Bohemia. Scale bars: 1 mm (SEM-photos).

Each lens is a single calcite crystal, with its crystallographic axis normal to the visual surface (Towe, 1973), and studies of etched lenses show that each is made up of thin laminae, radiating from the central axis (Clarkson, 1979). Apart from this, as far as is known, the internal structure of each lens is undifferentiated.

Some holochroal-eyed trilobites, especially those which lived in high-energy, nearshore environments, have relatively thick exoskeletons, and in these the lenses are remarkably elongated with a flattened outer surface and hemispherical internal terminations. Thin-shelled trilobites, conversely, tend to have thin biconvex lenses. What is important optically is not the length of the lens, but the relative convexity of its surfaces. Simple calculations (Clarkson, 1979) show that lenses of different lengths have their surfaces so curved as to have focussed light at about the same general distance below the proximal surface of the lens array. Whether a lens is thick or thin is directly correlated with the thickness of the cuticle.

Holochroal eyes are sessile and kidney-shaped, with the lentiferous surface rising above a curving band or eye-socket, which bounds the base of the eye; this may be elongated into a short stalk. The eye-socket is often covered with tiny pits, presumably the external manifestations of an internal vibro- or chemosensory system, monitoring the external environment at the same time, and from the same direction, as the visual system.

The angular range of vision is obviously related to the curvature of the visual surface. Most often the eyes are laterally directed with a latitudinal range of only 30° or so, though it may be more. In some instances holochroal eyes can be very large and hypertrophied, particularly in pelagic forms (Fortey, 1985) which were probably diurnal migrants, inhabiting deep waters of low light intensity during the day and coming up to the surface at night. Conversely in some trilobites the eyes may be lost altogether, and there are well-attested cases in both holochroal and schizochroal eyes where gradual loss of the eye is associated with the adoption of an endobenthic habit.

2.2 The Schizochroal Trilobite Eye

Schizochroal eyes are confined to one trilobite group only, the Ordovician to Devonian suborder Phacopina. They are usually prominent, and they always have thick biconvex lenses, clearly separated from one another by cuticular material (Figures 3, 4). This is known as the interlensar sclera, but is effectively identical in structure to the rest of the exoskeleton, and like it, is usually traversed by vertical canals. The lenses of schizochroal eyes are generally much larger, and fewer in number, than those of holochroal eyes. In holochroal eyes the lenses average 100 μm in diameter, whereas in large phacopids the schizochroal lenses may be as large as 750 μm across, in extreme cases reaching 1 mm in diameter.

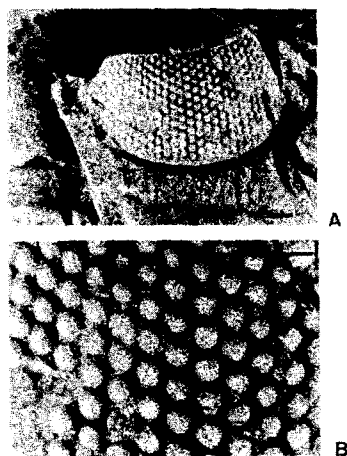


FIGURE 3 A typical schizochroal eye of the trilobite *Odontochile haussmanni* from the Lower Devonian of Bohemia. Scale bars: 1 mm (SEM-photos).

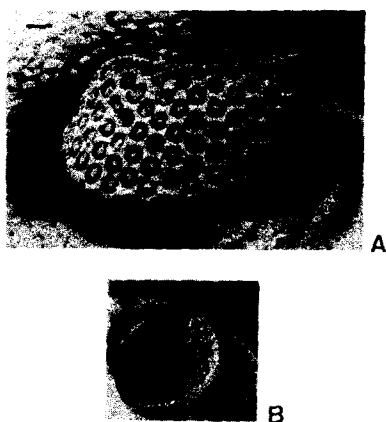


FIGURE 4 Two schizochroal trilobite eyes (from the Middle Devonian of Ohio) with a relatively small number of lenses sunken into the sclera. Scale bars: 1 mm. (A) *Phacops rana crassituberculata*; (B) *Phacops rana rana* (SEM-photos).

Within the phacopid trilobites a number of different types of schizochroal eye can be distinguished. Ordovician genera such as *Zeliskella* and their immediate derivatives (*e.g.* *Acaste*) have about 150 lenses with a diameter of some 200 μm , and the interlensar sclera in these is less than the thickness of the lenses. There is a general trend towards larger eyes with larger lenses through time, but two clear lines of descent can be distinguished. One led to the very large turret-like eyes of such genera as the Devonian *Odontochile*, where there may be as many as 500 lenses of up to 450 μm in diameter (Figure 3). In these the interlensar sclera remains thinner than the lenses. The other evolutionary pathway led to the large-lensed eyes of the Devonian *Phacops*, where may only be 50–60 lenses, up to 750 μm in diameter (Figure 4). In these the sclera is as thick as, or thicker than, the lens.

In all schizochroal eyes each lens has its own cornea, a thin pellucid sheet of calcium carbonate which overlies the outer surface and then plunges down through the sclera, as a cylindrical ring. There is some evidence (Clarkson, 1967; Campbell, 1975) that at least in the thick-shelled *Phacops* this cylinder terminates below the lens as a capsule in which the photoreceptors lay.

The large, well-separated lenses, and the presence of the thick interlensar sclera give an unmistakable appearance to a schizochroal eye (Figures 3, 4); as such it could never be confused with a visual organ of holochroal type (Figure 2). The lenses of the phacopid eye are arranged, as in other trilobites, on a laterally-directed, curving visual surface, but by contrast with some 'panoramic' holochroal eyes the angular range of vision is always less than 40° above the animal's equator. The lenses in the schizochroal eye are arranged in dorso-ventral rows. The lines of lens axes with low angular separation called 'visual strips' (Clarkson, 1966a) run nearly vertically across the visual field and each line of axes is separated by a significant angle from the next line (Figures 3, 4).

Phacopid trilobites were generally bottom-dwellers, and as far as is known, none were pelagic. The eye tends, in consequence, to be a fairly conservative organ, and although the eyes of some phacopid trilobites may be large, as in the superfamily Dalmanitacea, the great range in form found in holochroal eyes is nowhere evident. As noted above, however, the eyes may be reduced in size or lost altogether in endobenthic or deep-water forms. Such reduced-eyed or blind trilobites are especially common in the Upper Devonian. At this time in geological history, the firm, calcareous, shallow water sea-floor substrates which had provided a habitat for a great range of marine invertebrates, including oculated trilobites, disappeared altogether. They were replaced by a vast blanket of fine mud which extended over an immense area of Europe and Asia (Feist and Clarkson, 1989; Feist, 1991). In surviving the loss of their former habitat, many trilobites became adapted to an endobenthic life within this mud, and the gradual reduction and sometimes the final loss of the eye has been demonstrated, in parallel, in both holochroal and schizochroal-eyed trilobites at this time.

Since holochroal-eyed trilobites had already been in existence for some fifty million years before the first schizochroal eyes, the origin of the latter must have been from a holochroal precursor. This has been confirmed by the discovery of larval holochroal eyes (Clarkson and Zhang, 1991; Clarkson and Taylor, 1995) in which the lenses are relatively large and separated from one another. The larval holochroal eye is effectively schizochroal,

and the earliest schizochroal eyes are believed to have originated from such an immature form, by paedomorphosis. The earliest schizochroal-eyed genus *Ormathops*, had a somewhat irregular system of lens-packing, and this seems to have arisen from the geometrical constraints of packing lenses of identical size on a curving surface which is wider at the base than at the top (Clarkson, 1971). In all later phacopids, the lenses are graduated in size, being larger at the bottom, and this mechanism ensured that regular hexagonal close packing was possible. This was presumably important, in some way, for the functioning of the schizochroal eye.

Nearly a century has passed since Lindström (1901) drew attention to bowl-like structures within the lenses of schizochroal trilobite eyes. The existence of such lens-doublets (Figure 5) has been confirmed since (Clarkson and Levi-Setti, 1975; Clarkson, 1979; Miller and Clarkson, 1980), but well-preserved and readily available material which allows sophisticated anatomical reconstructions to be undertaken is very rare. Even if many specimens can be obtained, in which the eyes are present and seem to be well-preserved, the percentage of these unaffected by diagenesis (alteration and recrystallisation of the lens-structure) is usually small. — This fact may be the main reason of why the 'doublet model' of schizochroal lenses presented by Clarkson and Levi-Setti (1975) was so violently disputed by Towe (1979). — Our understanding of the internal structure of the lenses in schizochroal trilobite eyes, therefore, is based upon relatively limited data, and it is sought to rectify this in the years to come.

2.3 The Abathochroal Trilobite Eye

A third kind of trilobite eye, the abathochroal, was described by Jell (1975) in Middle Cambrian eodiscid trilobites from Australia. In these the individual lenses are separate, as in schizochroal eyes, and Jell suggested that each had its own cornea, anchored to the margin of each lens. In a study of Lower Cambrian eodiscids, however, Zhang and Clarkson (1990) cast some doubt upon whether the abathochroal eye was truly a different kind of visual organ (Figure 6). The Chinese eodiscids *Shizhudiscus* and *Neocobboldia* were examined; the former has a normal holochroal eye with the lenses in contact, whereas in the latter the lenses are rounded and separate. A complete ontogenetic series

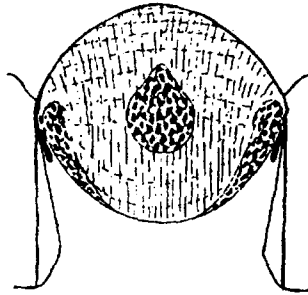


FIGURE 5 Sketch of longitudinal section of the schizochroal lens in the eyes of *Phacops rara milleri*. The 'intralensar bowl' and core are spotted, and the crystallites of the upper lens unit are also represented (after Miller and Clarkson, 1980).

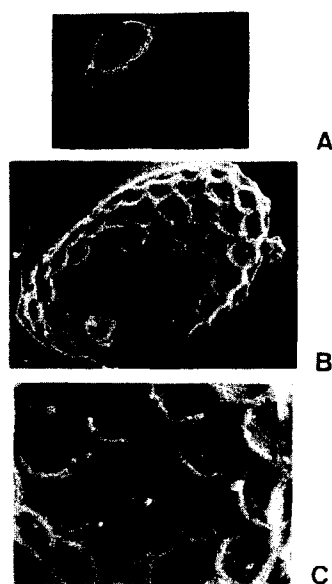


FIGURE 6 The abathochroal eye of the trilobite *Neocobboldia chinlinica* (Zhang and Clarkson, 1990). (A) External mould, scale bar: 200 μm ; (B) internal mould, scale bar: 100 μm ; (C) internal mould, scale bar: 20 μm (SEM-photos).

-was available for both, showing that the eye of *Neocobboldia* could have been derived from a normal holochroal eye by pedomorphosis, in a manner directly analogous to that envisaged for the origin of the schizochroal phacopid eye. The 'abathochroal' eye may simply be an eye of schizochroal kind, though less specialised than that of the phacopids, rather than a separate kind of visual organ in its own right.

2.4 Previous Views on the Functioning of the Schizochroal Trilobite Eye

The giant lenses of the schizochroal eye suggest that their bearers may have lived in an environment of low light intensity. Since phacopid trilobites usually occur in sedimentary rocks of shallow water origin, the most parsimonious interpretation suggests that they were active at night, and that their large biconvex lenses picked up as much of the available light as possible. Phacopid trilobites may indeed have been nocturnal, but there are other factors to be taken into account also. The problem with the schizochroal eyes is that the lenses are just too big, for a standard compound eye. Whatever assumptions one makes the eye parameter or the sensitivity, give values that are only consistent with environments dimmer than starlight (see Fordyce and Cronin, 1989, 1993).

It has proved possible to measure the axial direction of each of the lenses of a schizochroal eye (Clarkson, 1966a, b). When these are plotted on a chart, for example a stereographic net, the total angular range of vision can readily be established, as can the distribution of lens-axes within it. Because of the differential curvature of the visual

surface, there is usually some clustering of lens-axes; they tend to be more densely grouped in the central, equatorial part of the visual field, which might be an adaptation to a flat visual world (Zeil *et al.*, 1989). Where, however, the curvature of the visual surface in the horizontal plane is much greater than that in the vertical plane, the latitudinal range of vision is narrow ($\leq 10^\circ$), and the lens-axes traverse the visual field in 'visual strips'. Thus the vertical separation of the axial bearings within these is only 1–2 degrees, but the strips themselves may be separated by 10–12 degrees. The suggestion by some authors (*e.g.* Clarkson and Levi-Setti, 1975; Campbell, 1975) that each lens had a tiny retina behind it could explain some way the separation of the schizochroal lenses. Clearly, a passing predator would touch off responses in successive visual strips as it went by, but if it were approaching, it would trigger off a series of responses within a visual strip as it came nearer. In the early days of the study of schizochroal eyes, therefore it seemed that such organs were adapted for no more than movement perception (Clarkson, 1966a). When the internal structure of the lenses became known, however, and the lens optics analysed (Clarkson and Levi-Setti, 1975), it became clear that the eye was of much higher optical quality than had previously been imagined.

The lenses of phacopid trilobites are doublets, as previously noted. In these the upper unit alone forms an elegant lens whose lower surface is so shaped as to correct for spherical aberration. Two primary kinds of upper unit have been distinguished. In *Dalmanitina* the lower lens surface has a small central nipple, whereas in *Crozonaspis* the more biconvex lens has a wavy lower surface. These two types conform respectively to the two alternative models proposed for aplanatic lenses designed by René Descartes in 1637, and by Christian Huygens in 1690. As far as our present knowledge goes, however, these two types seem to be the end points of a whole range of equally functional intermediates.

In all cases the upper lens unit is a single calcite crystal, and as in holochroal eyes it is constructed of thin radial lamellae. The crystallographic axis, from which the fibres radiate, is orientated normal to the principal plane of the lens, and light travelling parallel with this axis does not suffer double refraction. Along this c-axis, the refractive index is $n = 1.66$.

The lower part of the doublet system, the intralensar bowl, fits directly against the lower surface of the upper unit. It acts as the final optical element. When a working model of a Cartesian lens was made, with the upper unit of orientated calcite, it was found that a plastic intralensar bowl where $n = 1.63$ sharpened the image still further (Clarkson and Levi-Setti, 1975). Such a lowered refractive index could be achieved simply by the presence of organic inclusions within the lens, or by slightly altered mineralogy. Horváth (1989a) reconstructed computationally the possible value of the refractive index n of the lower lens unit and of the focal length f of the doublet lens in three phacopid trilobites. In *Dalmanitina socialis*, a Silurian *Dalmanites* and *Crozonaspis struvei* $n = 1.40$, $f = 213 \mu\text{m}$; $n = 1.40$, $f = 234 \mu\text{m}$ and $n = 1.53$, $f = 175 \mu\text{m}$, respectively. These refractive index values refer to a hydrated soft jelly-like substance and a chitinous material. The intralensar bowl is a requirement, in water, for focussing the more peripheral rays (Levi-Setti, 1992), but Horváth (1993, 1996) has

argued also that its presence diminishes reflectivity, and thus more of the available light is transferred to the photoreceptors below. The transmissivity enhancement by the bowl in a typical schizochroal doublet lens can reach more than 10 percent in comparison with a single calcite lens as Horváth (1996) estimated recently.

Some phacopid trilobites have additional refinements in their eyes. The highly biconvex lenses of *Phacops* have an intralensar bowl, but it becomes vanishingly thin centrally, and there is also a central core. The function of these organs remains to be clarified.

Despite our present understanding of the elegant bio-optimisation of the schizochroal lenses, a number of problems remain to be resolved. For example, the highly convex outer surface of the lens seems to be adapted for wide-angle light receptivity. Yet the more oblique the incident rays are, the higher the double refraction, with double images being produced at different depths. If there were a pigment ring below each lens, as in most compound eyes today, it would screen out the more peripheral rays, but it would seem to defeat the purpose of the highly convex external surface.

Most investigators incline to the view that the schizochroal eye was more an aggregate of simple lens-eyes, with overlapping visual fields, than an analogue of the eyes of modern insects or crustaceans. This concept is generally coupled to the belief (Campbell, 1975; Clarkson, 1979; Fordyce and Cronin, 1989), that below each lens there lay a short ocellar capsule, floored by a flat retinal layer of cells, rather than a small set of retinula cells. If this is correct, the schizochroal eye is thus a unique kind of organ, with no direct modern analogues; a contention we explore more fully in this paper. Fordyce and Cronin (1993), by comparison, gave evidence suggesting that the individual lenses of the holochroal eye each had a single photoreceptor, presumably some kind of rhabdom, and that the eye as a whole functioned in a similar manner to that of modern arthropods, being especially adapted to moderate to dim light.

Adopting the ocellar model, and recognising the high optical quality of the lenses, Cowen and Kelly (1976), and Stockton and Cowen (1976) proposed that the highly convex outer surfaces of schizochroal lenses would have been capable of using adjacent lenses, within the same eye, for stereoscopic vision. They calculated that an approaching predator would be picked up by a set of lenses, and as it came towards the trilobite, its movement would be detected by successive triggering of the reticular cells on opposite sides of two adjacent lenses. If appropriate neural networks existed, then the distance of the predator could be registered stereoscopically by comparison of images at successive times, on a very short time scale. This model accounts for the visual strips, whose high angular separation could actually be useful for stereoscopic vision, and also for the need for regular packing of lenses on the visual surface. According to this model, therefore, the schizochroal eye is adapted for the perception of depth as well as movement.

Further considerations are dependent upon our current understanding of schizochroal lenses as bio-optimised image-formers, which retain their capacity for sharp focussing even when the new lens is developing after moulting (Horváth and Clarkson, 1993).

3 SURVEY OF THE MODERN COUNTERPARTS OF SCHIZOCHROAL TRILOBITE EYES

No paper reviewing modern counterparts of trilobite eyes can be complete without a discussion of the eyes of the night-active horseshoe crab *Limulus*. Since the *Limulus* eye possesses corneal singlet lenses with a gradient index of refraction (Land, 1979), and on the other hand, the ommatidia are not separated from each other (Levi-Setti *et al.*, 1975), it can be an analog of the holochroal rather than the schizochroal trilobite eye. This is the reason of why we do not discuss the *Limulus* eye in this work.

3.1 Modern Eyes with 'Schizochroal' Character

We have seen in the Introduction that the eye of phacopid trilobites possesses a special external feature, the schizochroal character, which distinguishes it from the holochroal eye type. Many recent animal eyes bear the schizochroal character, some of them are briefly reviewed in this subsection, using mainly the fundamental work of Paulus (1979).

- i. Lateral eyes dispersed into five lenses occur among Chelicerata, in Scorpiones, Palpigradi, Uropygi, Amblypygi and Araneae, for example. According to Paulus (1979), the four lenses on each prosomal side in Arachnida correspond to the whole faceted eye, which has become separated into five parts, each part with many ommatidia that persisted, and the single cornea is a modified fused lens.
- ii. The deep-sea ostracode, *Macrocypridina castanea* lives at a depth of about 700 m. In such a dimly lit environment it uses an eye with a high sensitivity due to its enormous, well-separated facets. In front of the moveable, paired, dorsally situated, cylindrical eyes there is a transparent circular window in the carapace. Each eye contains 27 ommatidia in an approximately hexagonal lattice (Figure 7). The interommatidial angle ranges from about 6° to 20°. A dense pigmentation forms a dark shell around the eye, penetrated only by the crystalline cones. The cones contain a refractive index gradient. The crystalline cone is composed of two cells. Each ommatidium contains six retinula cells contributing equally to a very wide and short rhabdom. The largest cones acceptance angles of 15–20° and the smallest cones 50–60°. The myodocopid ostracodes, *Cypridina norvegica* (from a depth of about 400 m) and *Philomedes globosa* (which lives in the surface waters down to 50 m) have similar but much smaller eyes than *Macrocypridina*. The number of ommatidia is 16 in *Cypridina* and 35 in *Philomedes*. *Daphnia* has also such compound eyes where there are only 22 ommatidia (Land and Nilsson, 1990).
- iii. Myriapoda usually have two groups of up to 40 relatively large, well-separated circular lenses of different sizes. They are frequently reduced or even absent, as in Pauropoda, Symphyla, some Chilopoda, and some Diplopoda. The retina is multi-layered, and contains up to 100 cells. The eye of *Lithobius*, for instance, is very similar to the stemmata of some insect larvae, especially those of Coleopteroidea (Paulus, 1979).

- iv. Collembola possess dispersed faceted eyes consisting of up to eight relatively large and well-separated circular lenses. These eyes are typical ommatidia. The rhabdom is formed by eight retinula cells and has a two-layered arrangement in Poduromorpha; the other Collembola have a single-layered rhabdom. The crystalline cone is formed by four cells. In Arthropleona the cone is a large extracellular homogeneous ball. The cone in Symphypleona is intracellular, and therefore tetrapartite as in other insects. In some cave species of the Hypogastruridae or Poduridae the dioptric system becomes more and more reduced, with a subsequent loss of the crystalline cone (Paulus, 1979).
- v. Some Zygentoma (*e.g.* silverfish and firebrats) possess a reduced, dispersed compound eye consisting of well-separated ommatidia, whose number is 12 in *Lepisma*, *Thermobia*, *Ctenolepisma*, and 40–50 in *Tricholepidion gertschii*. The Zygentoma have a biconvex cornea, four Semper cells, and two primary pigment cells. The retinula consists of eight cells, forming a two-layered rhabdom (Paulus, 1979).
- vi. The larvae of most Mecoptera have dispersed faceted eyes consisting of 30–35 typical ommatidia with two-layered retinula. Before pupation, the larva loses this faceted eye, which does not increase in size during the larval period. The eyes are reduced in some mecopteran larvae with a special mode of life. The larva *Boreus hiemalis*, for example, lives in deep moss pillows, and has only three small lenses on each side of the head, and the crystalline cones are completely reduced (Paulus, 1979).
- vii. The caterpillars of the Lepidoptera and Trichoptera normally have six isolated circular biconvex lenses, widely distributed on each side of the head. In Micropterygidae, for instance, there are five small lenses only. Representatives of

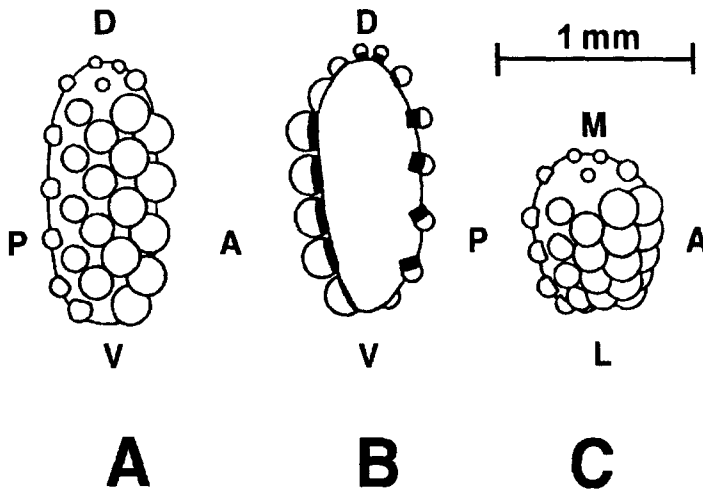


FIGURE 7 The right eye of the deep-sea ostracode, *Macrocypridina castanea* in lateral (A), medial (B) and dorsal (C) views showing the size and location of the lenses (after Land and Nilsson, 1990). A: anterior, P: posterior, D: dorsal, V: ventral, M: medial, L: lateral.

the Limnephiloidea have only six stemmata, one of which is apparently a double-stemma. This fusion of stemmata is advanced in the genus *Philopotamus* (Hydropsychoidea). Externally, there appear to be only two stemmata, however, in sections each crystalline cone is fused with those of several stemmata (Paulus, 1979). Interestingly, the ocellar lenses of the larval Lepidoptera *Pieris brassicae* consist of two optically homogeneous units with refractive indices of 1.541 and 1.491 (doublet character) (Barrer, 1971).

- viii. The coleopteran and megalopteran larvae have up to six well-separated stemmata on each side of the head, the Neuroptera and Raphidioptera up to seven, and the Strepsiptera five. The stemmata of the Neuropteroidea and Coleopteroidae have a strongly biconvex lens, formed by a number of corneagenous cells. Just beneath the lens is a multilayered rhabdom, consisting of numerous retinula cells. The coleopteran larval stemmata might have been evolved by fusion of several ommatidia with reduced crystalline cones (Paulus, 1979).

3.1.1 The 'Schizochroal Compound Eye' of Male Strepsiptera

The systematic position of the small cosmopolitan insect order Strepsiptera has yet to be determined (Kinzelbach, 1990). These holometabolous insects parasitize other insects of various orders (Kathirithamby, 1989) and some of their modified characters are considered to be related to their endoparasitic life history (Ulrich, 1943). The adult female is always wingless. With the exception of the few species in the Mengenillidia, the females stay resident in their hosts throughout their lifetime. The male imago is an agile, winged insect with its forewings modified as sense organs of equilibrium (Pix *et al.*, 1993). After emergence from the puparium the males spend about one hour's life on the wing searching for receptive females. They are attracted by female odors (Linsley and MacSwain, 1957).

A conspicuous character of adult male Strepsiptera is the blackberry-shaped faceted eye with well-separated ommatidia (Figure 8; Pix, 1994). As the head is so wide in proportion to its length, the hemispherical eyes appear to be stalked (the genus name *Stylops* means 'stalked eye'). Strohm (1910) and Rösch (1913) found a large number of retinula cells beneath the individual corneal lenses. The authors identified more than one rhabdom beneath a common lens and thus considered each facet to be an ocellus and the whole eye to be an 'ocellar complex eye'. Bohart (1941) pointed out that the eyes may equally well have been reduced to their present form from normal ommatidia. The investigations of Kinzelbach (1967) and Wachmann (1972) have revealed features associated with compound eyes, particularly the mode of innervation via *Lobi optici* and the presence of crystalline cones. The eyes of male Strepsiptera are therefore interpreted as modified compound eyes. They have been considered as 'paedomorphic' (Kinzelbach, 1971) or 'stemmataran' (Paulus, 1979), with reference to their appearance in early larval stages and to the arrangement of photoreceptors, which resembles more closely that found in the larval stemmata of Neuroptera (Paulus, 1986a) and several families of Coleoptera (Paulus, 1986b) than that in the ommatidia of adult insects.

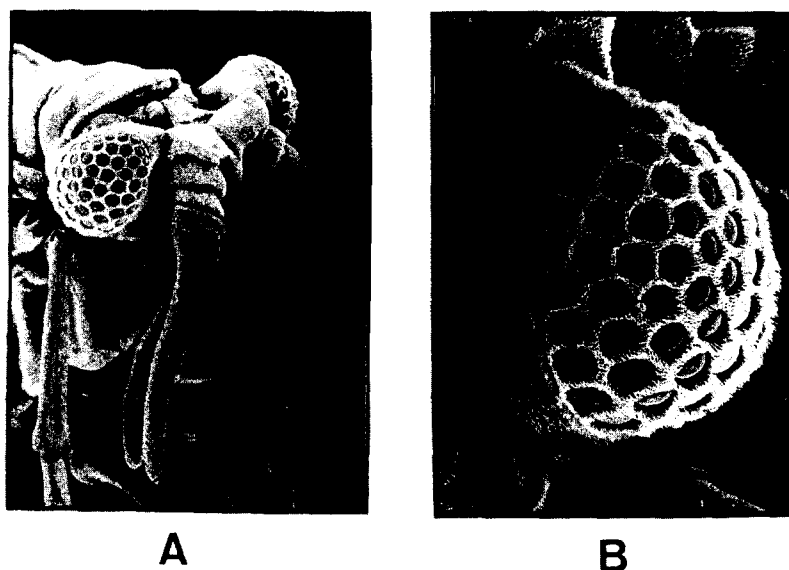


FIGURE 8 The 'schizochroal compound eye' of the male Strepsiptera *Xenos vesparum* (SEM-photos). (A) head, lateral view, scale bar: 400 μm ; (B) dorsal view of the left eye with corneal lenses and interlensar hairs, scale bar: 100 μm (Pix, 1994).

Depending on the species, each compound eye has 10–150 ommatidia (Kinzelbach, 1971). The large, circular lenses are well-separated from one another by broad cuticular stripes which are in most species densely covered with microtrichia (Figure 8). The dioptric apparatus consists of a biconvex lens and a crystalline cone in the case of *Stylops*), for instance, which may be reduced as in the case of *Coriophagus* or replaced by other refractive tissue, for example in *Xenos* (Kinzelbach, 1990). A number of striae can be seen within the lens, which are probably the result of a layered construction, which might alter the refractive index. The optical elements are surrounded by several pigment cells. One ommatidium contains approximately 60 retinula cells which in *Stylops* seem to form a single rim-like rhabdom (Wachmann, 1972).

Adult male Strepsiptera of various families are attracted by light traps (Riek, 1970; Kathirithamby, 1989) suggesting that the short-lived males are nocturnal. In particular, those of the plesiomorphic Mengenillidae are known to emerge at night (Hans Pohl, personal communication). On the other hand, emergence of males belonging to the family Stylopidae occurs on bright days (Pix, 1994) and males were observed flying around during the day (Riek, 1970). The unique structure of the compound eyes with few but relative to the animal's dimensions unusually large lenses may well be an adaptation to an original nocturnal mode of life of male Strepsiptera. The diurnal life of male Stylopidae which also possess the characteristic 'schizochroal compound eye' may be a secondary evolutionary event.

3.2 Recent Eyes with 'Doublet' and 'Aplanatic' Character

3.2.1 The Eyespots of Some Extinct and Modern Ostracodes

Ostracode eye tubercles or eyespots are shell structures located in the anterodorsal region of the valves of some ostracodes that have eyes (Figure 9A) (Kontrovitz, 1985; 1987). These structures are small, circular or oval, transparent and outwardly convex areas. The lens in the eyespot consists of clear calcite allowing light to enter the eye at the distal tip of the ocular sinus which is to some degree stalked in most marine podocopids. The proximal surface of an eyespot is undulating with a central convexity and posterior concavities, while the distal surface is approximately spherical (Figure 9B). The ocular sinus is a channel in the shell, lying between an internal opening called the ocular pit and the distal surface of the eyespot (Kontrovitz and Zhao, 1991).

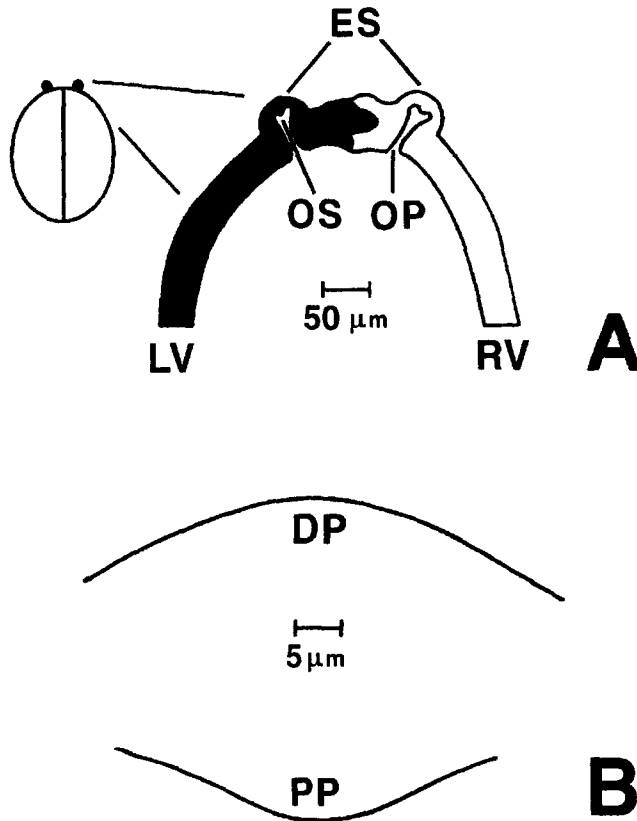


FIGURE 9 (A) Schematic diagram of a section through the ocular region of an ostracode shell in an anterior view with the left (black) and right (white) valves (after Kontrovitz, 1985). LV: left valve; RV: right valve; ES: eyespot; OS: ocular sinus; OP: ocular pit. (B) Profiles (in longitudinal section) of the calcite lens in the eyespot of *Echinocythereis margaritifera* (after Kontrovitz and Myers, 1984). DP: distal profile; PP: proximal profile.

Comparison of a modern (*Echinocythereis margaritifera*) and an extinct Oligocene (*Echinocythereis jacksonensis*) ostracode species indicates similar eyespot morphology and presumably similar functioning (Kontrovitz and Myers, 1984). The eyespot morphology relates to light levels, which in turn are related to water depths; thus a possible means of reconstructing water depths is available for sediments with ostracodes that had eyes (Kontrovitz and Myers, 1988), unless they were nocturnal.

According to Kontrovitz and Myers (1984), the geometry of these ostracode eyespots is similar, in a superficial way, to the configuration of schizochroal trilobite lenses (Clarkson, 1967). Light is focussed in the underlying eye space. In *Echinocythereis jacksonensis*, paraxial rays are focussed at a distance which falls beyond the eye cavity, unless light rays undergo reflections by the eye's tapetal layer (Myers and Kontrovitz, 1988). In the case of the modern and fossil species mentioned it is doubtful if they had highly-developed vision. The small number of rhabdoms (9–18 per cup) reported for modern forms and probably present in the fossil forms, would preclude precise vision with high resolution (Kontrovitz and Myers, 1984). On the other hand, the f-number of the lens-mirror system in podocopid ostracodes is limited to a range between 0.50 and 0.25, which are among the smallest known for organisms. Therefore these animals seem to be well adapted for efficient viewing in dim light (Kontrovitz and Myers, 1988).

3.2.2 *The Compound Eye of the Backswimmer Notonecta*

The dioptric apparatus of the apposition compound eye in the water bug backswimmer, *Notonecta glauca* consists of the corneal lens and the crystalline cells, at the proximal end of which an open rhabdom begins. The acone type eye has four crystalline cells in place of a secreted cone, which are optically homogeneous (Schwind, 1980). Bedau (1911) observed that the corneal lens is composed of two layers (doublet character). Schwind (1980) found that both lens units are optically homogeneous and that the refractive indices of the distal and proximal units are 1.54 and 1.46, respectively. Between the two units there is a thin transition layer; its refractive index varies continuously and its thickness increases from the optical axis towards the margin of the cornea (Figure 10A, Schwind, 1980, 1985). Schwind (1980) and Horváth (1989b) showed that this transitional layer reduces the spherical aberration of the lens. Measurements on intact corneal lenses confirmed that they have only very low spherical aberration in air as well as in water (aplanatic character) (Schwind, 1980, 1985). Horváth (1989b) calculated the optimal form of the lens of *Notonecta* and the optimal shape and position of the correction layer (Figure 10B), and found that the dioptric apparatus of backswimmer is highly optimized. The entrance surface of an individual corneal lens is only slightly convex, therefore there is little change in the position of the plane of focus in the eye when the amphibious bug leaves the water. The diameter of the lenses is about 40 µm (Schwind, 1980).

All the peripheral rhabdomeres of the backswimmer contain a pigment with an absorption maximum at 560 nm (Schwind *et al.*, 1984). This is associated with adaptation of the spectral sensitivity of the peripheral visual cells to the illumination conditions in the bodies of water inhabited by *Notonecta*. Backswimmers prefer turbid, still water with

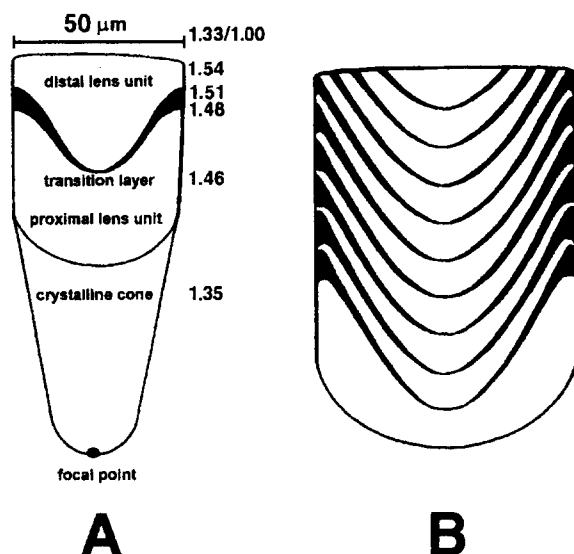


FIGURE 10 (A) Longitudinal section and refracting indices of the dioptric apparatus in the backswimmer, *Notonecta glauca*. Between two optically homogeneous lens units there is a thin bell-shaped transition layer (black) with a refractive index gradient (after Schwind, 1980). The corneal doublet lens is corrected for spherical aberration by means of this transition layer. (B) Calculated optimal correction layers (black) in the aplanatic corneal doublet lens of *Notonecta* as a function of the thickness of the upper lens unit (after Horváth, 1989b).

a dense growth of aquatic plants and phytoplankton (Giller and McNeill, 1981). The peripheral rhabdomeres in the eye of *Notonecta* serve as a scotopic system, they are used for perception of dim light in turbid water (Schwind *et al.*, 1984).

The proximal lens unit in the backswimmer constitutes a refractive index transition between the distal lens unit and the crystalline cone, therefore it inevitably reduces the reflectivity of the eye. Horváth (1993) suggested that this reduction in reflectivity is the optical function of the lower lens unit, which produces both decreased reflection and increased transmission. He calculated the reflectivity of the doublet in *Notonecta* and compared it with the reflectivity of two corresponding aplanatic singlets of different refractive indices for contact with air and water. He found, that due to the lower lens unit, the absolute reflection suppression ΔR in the dioptric apparatus is about 2% in water and the relative reflectivity reduction $\Delta R/R$ amounts to 65%. The intralensar bowl in schizochroal trilobite eyes has a similar reflectivity reduction. In *Crozonaspis struvei*, for example, the transmissivity enhancement by the lower lens unit amounts to about 10% (Horváth, 1996).

3.2.3 The stemmata in Larvae of the Sawfly *Perga*

Larvae of the sawfly *Perga* live in colonies and feed at night on eucalypt leaves (Evans, 1934). In broad daylight they seek the shade to protect themselves from direct sunlight (Meyer-Rochow, 1972). Sawfly larvae have only one pair of stemmata. Each one possesses

a biconvex circular lens, which increases in diameter from 0.18 mm in the third larval instar to 0.35 mm in the sixth and final stage before pupation. Below the cornea are long cylindrical corneagenous cells devoid of pigment. Below the lens there is an extensive retina with 8 retinula cells, the rhabdomeres of which fuse centrally to form a butterfly-like rhabdom. The microvilli of the rhabdomeres are arranged in two perpendicularly oriented subsystems and have a high polarization-sensitivity (Meyer-Rochow, 1974).

Interference microscopic observations of longitudinal sections of the corneal lens of the stemmata reveal that the lens consists of two optically homogeneous layers of different refractive indices (Figure 11A) (doublet character). The thicker distal unit has a refractive index of 1.525, while that of the proximal one is 1.482. The opaque edges of the body cuticle project into the transparent lens between the middle and proximal layers, and form a permanent, stiff aperture of about 0.15 mm in the fourth larval instar. The refractive index of the sublensar corneagenous clear-zone is 1.35 (Meyer-Rochow, 1974).

It was found by means of geometric optical ray tracing (Figures 11B,C) that the stemmata is corrected for spherical aberration (aplanatic character) and receives light over a total angular range of about 210° with a 50 percent value of about 140° . From this ray tracing it became evident that only a small portion of the stemmata, the focal region

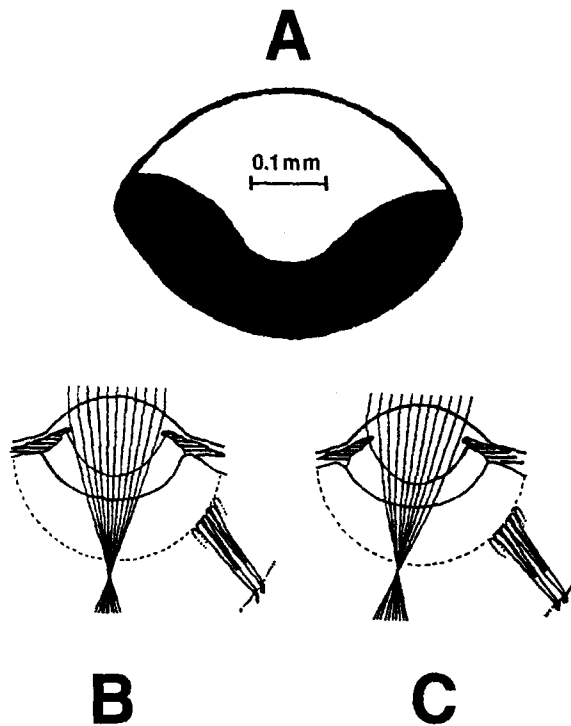


FIGURE 11 (A) Schematic diagram of the longitudinal section through the corneal doublet lens in the larva of the sawfly *Perga*. The lens consists of two optically homogeneous units, which are coloured white and black. (B, C) Ray tracing through the spherically corrected stemmata of the *Perga* larva for two different incident angles $\theta = 0^\circ$ (B) and $\theta = 10^\circ$ (C) measured from the optical axis of the lens (after Meyer-Rochow, 1974). For paraxial rays the light beam is sharply focussed at a level roughly at the distal end of the rhabdom.

of the lens, has a high resolution with acceptance angles of about 4° . The nocturnal sawfly larvae can increase sensitivity by 2 to 3 log units in the dark without losing acuity (Meyer-Rochow, 1974). Behavioural observations (Weiss *et al.*, 1944; Wellington *et al.*, 1957; Carne, 1962; Meyer-Rochow 1974) suggest that the little stemmata of sawfly larvae are capable of polarization sensitivity, motion detection, form and colour perception. In general, it appears that the eye of the sawfly larvae is a simple, but efficient visual organ, and its lens is very similar to the schizochroal trilobite lens.

3.2.4 The Pallial Eyes of the Scallop *Pecten*

The scallop *Pecten maximus* has about 60 well-separated (schizochroal character) pallial eyes (Figure 12A); their diameter amounts to about 1 mm (Land, 1965). A real image is formed in the eye by refraction through a thick lens and by reflection at the argentea, a multilayered structure composed of guanin crystals, which functions as a highly efficient reflector (Land, 1996a). The spherical argentea lines the whole of the back of the eye (Figure 12B). The refractive index of the soft and homogeneous lens is 1.42; its rear surface is spherical, the front face is bell-shaped, but its profile varies considerably (Land, 1965).

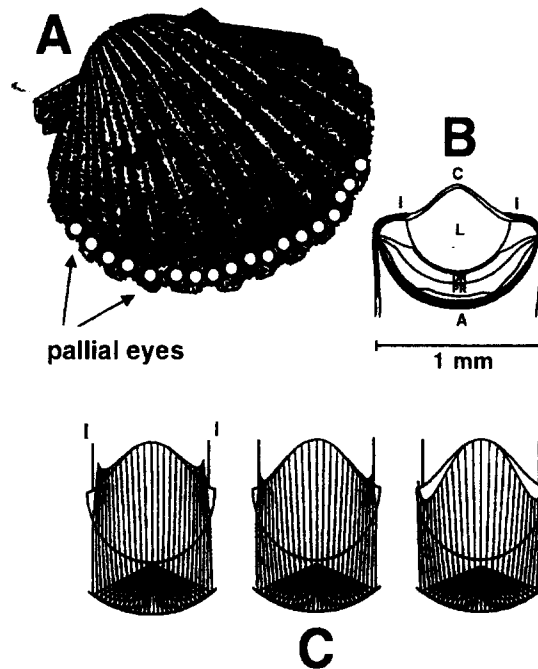


FIGURE 12 (A) The scallop *Pecten maximus* has about 60 pallial eyes (here represented not to scale). (B) Schematic diagram of the longitudinal section of the *Pecten* eye (after Land, 1965). C: cornea, I: iris, L: lens, DR: distal retina, PR: proximal retina, A: reflecting argentea. (C) Longitudinal section of the eye of *Pecten* showing the calculated front surface and the real lens shape with ray tracing for three different values of the focal length (after Horváth and Varjú, 1993).

The retina occupies the space between the lens and the argentea (Figure 12B). It consists of two main cell layers. Since the proximal retina is very close to the argentea, no image is formed on it. Between the proximal retina and the lens is a second layer of cells, the distal retina, where the image is formed. There are approximately 5000 receptors in each retina in *Pecten maximus*, and each gives rise to a fibre in the optic nerve (Land, 1968). Two aspects of the visual environment are important to scallops: the overall level of illumination, and its small local or total changes caused by shadows or image movements. Information relating to these two aspects is extracted by two separate receptor systems in the retina (Hartline, 1938; Buddenbrock and Moller-Racke, 1953; Land, 1965, 1966a,b, 1968): The distal retina is involved in movement perception, and the proximal retina, where no image is formed, monitors the level of illumination.

The eye of *Pecten* collects light very efficiently. The visual field of each eye extends to 90–110° (Buddenbrock and Moller-Racke, 1953; Land, 1965). The extremely small focal ratio $A = 0.6$ provides an aperture wider than that of the most known lens eyes. The *Pecten* mirror with such a large aperture, however, has great spherical aberration, and therefore poor resolution. Land (1965) suggested that the bell-shaped front profile of the lens corrects for this spherical aberration like the corrector plate in the Schmidt telescope. This idea was computationally tested by Horváth and Varjú (1993). They calculated the shape of the front surface of the scallop lens as a function of the refractive indices and geometrical parameters of the eye (Figure 12C). Comparing the theoretical profiles to the real ones, they could estimate to what degree the spherical aberration of the *Pecten* eye is corrected for. They demonstrated that with proper parameters the peculiar front profile of the lens compensates well for spherical aberration caused by the spherical argentea (Figure 12C). Small deviations of the parameters from the optimal values, however, causes substantial deviations from the optimality. Experimental investigations reveal great variability of the eye parameters (Land, 1965). Horváth and Varjú (1993) pointed out that the degree of correction of the *Pecten* lens for spherical aberration is not as good as it could be. It seems reasonable to assume that the actual shape of the correcting surface of the lens results from a compromise that would optimize the lens function over a wide cone of acceptance. In addition, inadequacies of a single eye might be compensated for with respect to visually guided behaviour by interaction with other pallial eyes.

4 DISCUSSION

4.1 Structural and Functional Similarities and Differences between Schizochroal Trilobite Eyes and their Modern Counterparts

Table I summarizes the main features of the recent eyes considered in our survey. As we have already mentioned in the Introduction, the schizochroal trilobite eye has three typical characters: schizochroal, doublet and aplanatic. In Table I a given character is designed by '+', if it also characterizes a given modern counterpart, otherwise it is marked by '–'.

The anatomical descriptions of animal eyes generally contain information, on the basis of which one can easily establish whether a given eye possesses the schizochroal and doublet character. However, it is more difficult to decide if a dioptric apparatus is aplanatic or not. To test this, one has to measure (*e.g.* Towe, 1973; Clarkson and Levi-Setti, 1975; Schwind, 1980) or calculate (*e.g.* Meyer-Rochow, 1974; Myers and Kontrovitz, 1988; Horváth, 1989a,b; Horváth and Clarkson, 1993; Horváth and Varjú, 1993) the degree of correction for spherical aberration in the eye. Unfortunately, there is only a restricted number of such investigations in the literature. In many cases we did not find any references to studies on spherical aberration of the modern eyes. In this case the aplanatic character is questionable and is designed by '?' in Table 1.

TABLE 1 The modern counterparts, their main features, the literature cited, and the three typical characters (S: schizochroal, D: doublet, A: aplanatic) of schizochroal trilobite eyes. The common characters of modern counterparts and schizochroal trilobite visual systems are designed by '+', and the uncommon ones by '-'. In some cases no information was available from the literature whether the dioptric apparatus of a given recent eye is aplanatic or not. These instances are marked by '?'

MODERN COUNTERPARTS OF SCHIZOCHROAL TRILOBITE EYES	MAIN FEATURES OF THE EYES	LITERATURE	COMMON CHARACTERS WITH SCHIZOCHROAL TRILOBITE EYES		
			S	D	A
lateral faceted eyes of some Chelicerata	- unicorneal faceted eye, - 5 well-separated lenses, - many sublensar persisted ommatidia	Paulus (1979)	+	-	?
eye of the deep-sea ostracode <i>Macrocypidina castanea</i> (similar eyes in: <i>Daphnia</i> : 22 lenses, <i>Cypridina</i> : 16 lenses, <i>Philomedes</i> : 35 lenses)	- moveable cylindrical dispersed faceted eye, - well-separated enormous facets, - 27 typical ommatidia, - 6 retinula cells, - wide and short rhabdom, - crystalline cone-lens with refractive index gradient	Land and Nilsson (1990)	+	-	?
lateral faceted eyes of some Myriapoda	- stemmataran compound eyes, - 2-40 large well separated circular lenses, - small multilayered sublensar retinae with up to 100 cells	Paulus (1979)	+	-	?
faceted eyes of Collembola	- dispersed faceted eyes, - large well-separated circular lenses, - up to 8 typical ommatidia, - 8 retinula cells	Paulus (1979)	+	-	?
reduced lateral faceted eyes of some Zygentoma	- dispersed faceted eyes, - large well-separated circular lenses, - 12, 40-50 ommatidia, - 8 retinula cells, - two-layered rhabdom	Paulus (1979)	+	-	?

TABLE 1 (Continued)

MODERN COUNTERPARTS OF SCHIZOCHROAL TRILOBITE EYES	MAIN FEATURES OF THE EYES	LITERATURE	COMMON CHARACTERS WITH SCHIZOCHROAL TRILOBITE EYES		
			S	D	A
larval faceted eyes of some Mecoptera	<ul style="list-style-type: none"> - dispersed faceted eyes, - 30–35 typical ommatidia, - two layered retinula 	Paulus (1979)	+	-	?
larval eyes of Lepidoptera	<ul style="list-style-type: none"> - stemmataran compound eyes, - 5, 6 well-separated stemmata sometimes partially fused, - circular biconvex corneal lenses 	Barrer (1971) Paulus (1979)	+	- (+ in Pieris sp.)	?
larval eyes of Neuropteroidea and Coleopteroidae	<ul style="list-style-type: none"> - stemmataran compound eyes, - 5, 6, 7 stemmata, - strongly biconvex well separated circular lenses, - multilayered sublensar retinae 	Paulus (1979)	+	-	?
faceted eyes of male Strepsiptera	<ul style="list-style-type: none"> - dispersed compound eyes, - 10–150 large well-separated circular strongly biconvex lenses, - dense interlensar hair - laminar lens structure - sublensar crystalline body, - 60 retinula cells - many rhabdomeres 	Strohm (1910), Rösch (1913), Bohart (1941), Ulrich (1943), Linsley and MacSwain (1957), Kinzelbach (1967, 1971, 1990), Riek (1970), Wachmann (1972), Paulus (1979, 1986a,b), Kathirithamby (1989), Pix <i>et al.</i> (1993), Pix (1994)	+	-	?
ostracode eyespots (modern and fossil)	<ul style="list-style-type: none"> - a pair of large circular single calcite lens, - spherical outer lens surface, - undulating inner lens surface, - lens corrected for spherical aberration, - reflecting tapetum, - large light collecting efficiency (small f-number), - small retina (9–18 rhabdoms) 	Kontrovitz & Myers (1984, 1988) Kontrovitz (1985, 1987), Myers and Kontrovitz (1988), Kontrovitz and Zhao (1991)	-	- (lens mirror)	+
compound eye of <i>Notonecta glauca</i>	<ul style="list-style-type: none"> - apposition compound eye, - corneal doublet lens corrected for spherical aberration, - two optically homogeneous 	Bedau (1911), Schwind (1980, 1985), Giller and McNeill (1981), Schwind <i>et al.</i> (1984), Horváth (1989b, 1993)	-	+	+

TABLE 1 (Continued)

MODERN COUNTERPARTS OF SCHIZOCHROAL TRILOBITE EYES	MAIN FEATURES OF THE EYES	LITERATURE	COMMON CHARACTERS WITH SCHIZOCHROAL TRILOBITE EYES		
			S	D	A
	<ul style="list-style-type: none"> lens units of different refractive indices, - thin bell-shaped intranlensar correction layer, - large light-collecting efficiency, - 8 retinula cells, - open rhabdom, - reflectivity reduction and transmissivity enhancement due to the lower lens unit 				
larval eye of the sawfly <i>Perga</i>	<ul style="list-style-type: none"> - a pair of typical stemmata, - biconvex circular doublet lens corrected for spherical aberration, - two optically homogeneous units of different refractive indices, - extensive retina, - 8 retinula cells, - fused rhabdom 	Evans (1934), Weiss et al. (1944), Wellington <i>et al.</i> (1957), Carne (1962), Meyer-Rochow (1972, 1974)	-	+	+
pallial eyes of <i>Pecten maximus</i>	<ul style="list-style-type: none"> - 60 large well-separated circular pallial eyes corrected for spherical aberration, - thick single lens with spherical proximal surface and undulating distal correction profile, - spherical reflecting argentea, - two-layered retina with 2×5000 photoreceptors, - large light-collecting efficiency (small f-number), - analogy with Schmidt astronomical telescope 	Hartline (1938), Buddenbrock and Moller-Racke (1953), Land (1965, 1966a, b, 1968), Horváth and Varjú (1993)	+	- (lens-mirror)	+

4.1.1 The Dimensions of the Optical Units

Although the qualitative features of modern counterparts more or less mimic some of the characteristics of schizochroal trilobite eyes, in some instances there are remarkable differences in the dimensions of the optical units (ommatidia, stemmata, pallial eyes,

eyespots). The diameter of typical schizochroal lenses is between 500–1000 μm . This range is matched only by the pallial eyes of *Pecten* (700–1000 μm). The diameter of the optical units in all other modern counterparts is much smaller: 180–350 μm in *Perga* larvae, 40–50 μm in *Notonecta* and ostracodes, 20–30 μm in male *Strepsiptera*. A larger schizochroal trilobite eye is of much greater dimensions than the whole body of a male *Strepsiptera*, *Perga* larva or *Notonecta*, for example. The tiny dioptric apparatuses in *Strepsiptera* may be diffraction limited, and also the aplanatic eyespots in ostracodes and the spherically corrected corneal lenses in *Notonecta* approach the diffraction limit. On the other hand, the optical resolution of the larger lenses in *Pecten*, *Perga* and phacopid trilobites is controlled by correction for spherical aberration; these dioptric apparatuses are far from the diffraction limit (see *e.g.* Land, 1981).

4.1.2 The Schizochroal Character

It is clear from Table 1 that there are many arthropod eyes, which possess the schizochroal character. Some modern counterparts, however, have only a few lenses: *e.g.* dispersed faceted eyes of some Chelicerata, Collembola, and larval eyes of Lepidoptera, Neuropteroidea, Coleopteroidae. These recent eyes with a considerably reduced number of lenses resemble the schizochroal eyes of Upper Devonian trilobites (Feist, 1991), for instance, which have also only a few calcite lenses. Other modern counterparts are more typical, because they possess several ten lenses (but less than a hundred), which is a better approximation of the lens number in schizochroal trilobite eyes: *e.g.* eyes of *Macrocypidina*, *Daphnia*, *Cypidina*, *Philomedes*, some Myriapoda and Zygentoma, male *Strepsiptera*, *Pecten*, and larval dispersed faceted eyes of some Mecoptera.

In our opinion the most impressive modern counterpart with respect to the schizochroal character is the dispersed compound eye of male *Strepsiptera*. The SEM-photographs in Figures 8A,B of the eye of *Xenos vesparum* demonstrate what a typical schizochroal eye of a Devonian phacopid trilobite might have looked like. A brief discussion on the possible function and evolutionary importance of the schizochroal character of compound eyes was given in an earlier subsection, however, the function of the schizochroal feature of the eyes in phacopid trilobites remains rather enigmatic until the sublensar structure of these ancient visual systems will be revealed.

4.1.3 The Doublet Character

Unfortunately it is still unclear whether the above-mentioned 'schizochroal modern eyes' are corrected for spherical aberration or not. On the other hand, their single lenses are surely not doublets. The only exception is the larval eye of *Pieris brassicae*.

To satisfy Fermat's principle (condition for an aplanatic optical system), it is necessary to introduce aspherical surfaces in the dioptric apparatus. This is true for reflecting as well as refracting systems. This can be accomplished in a number of ways, in one step, or two steps, or more, depending on the medium in which the visual system operates, the

refractive indices of the available materials, etc. Many solutions are possible. The Huygensian doublet is one of the two-steps solutions, which uses only refracting elements. The eyes of *Pecten* and the ostracode eyespots represent another two-steps solution, using a refracting and a reflecting element. These different solutions are in a way, equivalent, since they lead to the same result, namely they both satisfy Fermat's principle. From an evolutionary or survivalistic standpoint, the two different solutions are completely equivalent, representing optimization of the optical function. In this sense, the aplanatic doublet lens is one of two-steps solutions, and the *Pecten* eyes and ostracode eyespots are just another two-elements solutions.

Like the eye of *Pecten*, the modern and fossil ostracode eyespots consist of a single lens underlain by a reflector. On the other hand, the ostracode eyespots contain a calcite lens, in which the c-axis of the calcite crystal is parallel to the optical axis, as in trilobite eyes, which minimises the influence of the disadvantageous double-refraction of calcite. This is one of the known instances among recent visual systems with calcite in the dioptric apparatus. Isopod crustaceans, for instance, possess also calcite in their corneal lenses, however, usually its c-axis is not parallel to the optical axis (Wolsky, 1929; Dudich, 1931). An other example of the occurrence of calcite in modern eyes is the cornea of decapod crabs (Nilsson and Labhart, 1990).

The lenses in the stemmataran compound eye of *Pieris brassicae*, in the apposition compound eye of *Notonecta glauca*, and in the larval stemmata of the sawfly *Perga* are typical doublets with optically homogeneous lens units. with respect to the doublet character, the latter three eyes have the greatest resemblance to the schizochroal trilobite eye (Table 1).

What is the optical advantage of a doublet lens in comparison with a singlet? As we have seen above, the optical function of the lower lens unit in the corneal doublet lens of the water bug *Notonecta glauca* is reflection reduction and transmission enhancement to increase the light-collecting efficiency of the eye. To collect as much light as possible is important for vision in dim light, and *Notonecta* lives in dimly lit turbid water with a dense growth of aquatic plants and phytoplankton (Giller and McNeill, 1981). It might not be fortuitous that the nocturnal larvae of the sawfly *Perga* also possess doublet lenses in their stemmata. We have already mentioned that also the intralensar bowl in a typical schizochroal trilobite eye had a considerable reflectivity reduction and transmissivity enhancement. This supports the view that schizochroal-eyed trilobites might have been nocturnal animals, or at least they might have lived in dim, turbid water (Clarkson and Levi-Setti, 1975; Levi-Setti, 1992).

4.1.4 The Aplanatic Character

As we have mentioned above, determination of the degree of correction for spherical aberration is the task of future studies in the case of most of the modern counterparts we have considered here. In this subsection, we therefore discuss only those few cases, where experimental or computational investigations were performed to reveal the aplanatic character of the eyes (Table 1).

Ostracode eyespots (modern and fossil) are corrected for spherical aberration by means of the proximal undulating Huygensian profile of the single calcite lens (Kontrovitz and Myers, 1984; Myers and Kontrovitz, 1988). Since these eyespots possess also a sublensar reflecting tapetum, their optics are the same as that of the pallial eyes of the scallop *Pecten* (Land, 1965; Horváth and Varjú, 1993). The only difference between them is that in the eye of *Pecten* it is not the proximal but the bell-shaped distal lens surface that ensures correction for spherical aberration.

The eyes of trilobites may not have possessed reflectors, but the aplanatic single calcite lens in the abathochroal trilobite eyes (Zhang and Clarkson, 1990) and the Huygensian single calcite lens in the post-ecdysially developing schizochroal eye of *Phacops rana milleri* (Miller and Clarkson, 1980; Horváth and Clarkson, 1993) recall the aplanatic single lens in the eyespots of ostracodes and in the eyes of scallops. Considering the aplanatic character, the most closely corresponding modern counterparts of the spherically corrected schizochroal trilobite lens are the lenses in the apposition compound eye of *Notonecta* and in the larval stemmata of *Perga*. Moreover, these lenses are not only aplanatic, but also doublets.

The function of correction for spherical aberration in the above-mentioned dioptric apparatuses is quite clear: to enhance the light-collecting efficiency and transfer of contrast, that is, to assure a brighter and sharper image of the environment.

4.2 Evolution of Schizochroal Trilobite Eyes

4.2.1 Derivation of Schizochroal Trilobite Eyes from Holochroal Ancestors, and Some Modern Analogies

According to Clarkson (1975, 1979) and Clarkson and Zhang (1991), schizochroal trilobite eyes have been derived from the ancestral holochroal eyes by paedomorphosis. While this seems to be well-attested, only the lentiferous surface is present in trilobites, and what happened below this region is unknown. Since schizochroal trilobite eyes resemble some larval and adult arthropod eyes (Table I), it is worth briefly considering the evolution of holometabolan larval insect eyes and that of arthropod ommatidia and faceted eyes in order to provide possible analogies for the derivation of schizochroal trilobite eyes from holochroal ones, especially the sublensar units.

Figure 13 shows the evolutionary pathways of holometabolan larval insect eyes. According to Paulus (1979), there are at least four evolutionary radiations in different orders: (1) In the Coleoptera, Strepsiptera and Neuropteroidea the evolution of the larval eyes is characterised by a complete modification: decrease in number of ommatidia, fusion of ommatidia, crystalline cone reduction, layering of the retina. (2) The Hymenopteran larvae have unicorneal compound eyes due to corneal fusion and crystalline cone reduction. The eyes of scorpions, Arachnida and the lens eyes of the Anoplura are developed in a truly analogous way. (3) The evolution of the larval eye in Mecoptera and Diptera took place through stepwise modifications: decrease in the number of ommatidia,

fusion of ommatidia, cessation of development at an early embryonic stage, crystalline cone fusion or reduction. (4) Trichopteran and lepidopteran larval eyes evolved by ommatidial modifications: decrease in number of ommatidia, isolation of individual ommatidia, rearrangement of the dioptic apparatus to give three crystalline cones and three primary pigment cells. Since schizochroal trilobite eyes are reminiscent of some larval insect eyes (see Table 1), the interior parts of schizochroal eyes could have been modified in any or all of the above ways.

According to Paulus (1979), the ancestors of the Arthropoda in their early evolution possibly had some isolated lens eyes without fixed numbers of elements. During the

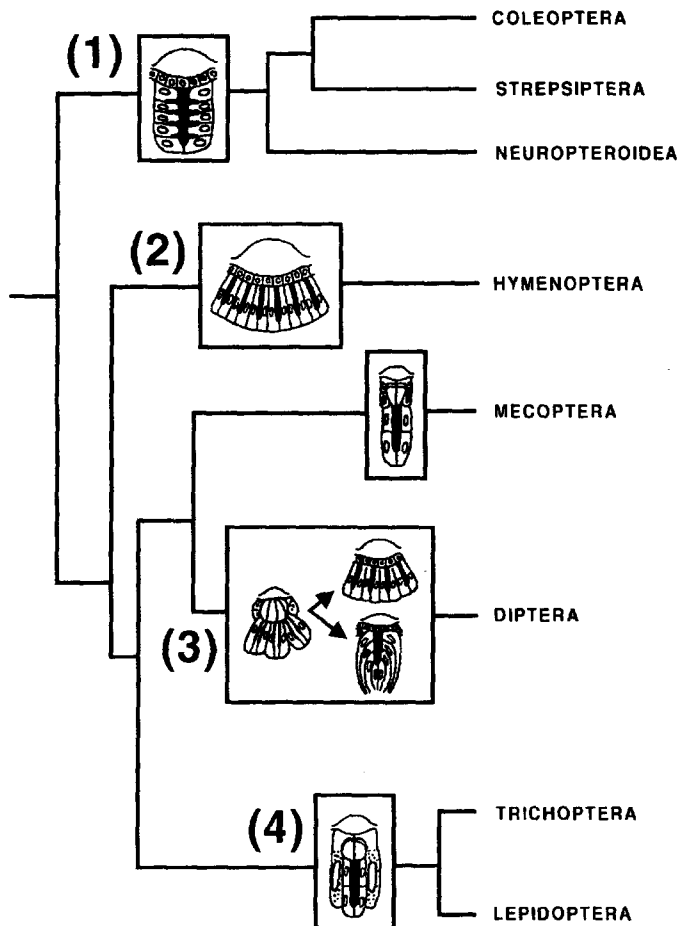


FIGURE 13 Distribution and evolutionary pathway of holometabolous larval insect eyes (after Paulus, 1979). There are at least four evolutionary radiations in different orders: (1) Complete modification: decrease in number of ommatidia, fusion of ommatidia, crystalline cone reduction, layering of the retina. (2) Unicornal compound eye: corneal fusion, crystalline cone reduction. (3) Stepwise modification: decrease in number of ommatidia, fusion of ommatidia, development cessation at an early embryonic stage, crystalline cone fusion or reduction. (4) Ommatidial modification: decrease in number of ommatidia, isolation of individual ommatidia, rearrangement of the dioptic apparatus to give 3 crystalline cone and 3 primary pigment cells.

evolution of the different arthropodan characters, these eyes had a chitinous (in trilobites also a calcitic) lens, an epidermal lentigenous layer, and beneath it a cup-like retina. By composing and increasing many of these eyes, an aggregate eye has developed — in which, however, the optical units were still well-separated — for more perfect movement perception and form resolution. The characters of this developmental stage resemble the main features of schizochroal trilobite eyes. Later, by decreasing the interommatidial angles, a typical facettted eye has developed, like the holochroal trilobite eye. Within the Chelicerata this facettted eye has been reduced at least twice: in the Pantopoda and Arachnida during occupation of land. The Arachnida modified the facettted eye by forming a unicorneal compound eye as the first step (as in *Scorpiones*). Schizochroal trilobite eyes originated by similar reductions and modifications from the ancestral holochroal facettted eye (Clarkson, 1975, 1979); in one sense reverting to a more ancestral form, though much more specialized.

The ancestors of Myriapoda had facettted eyes, as is known from fossil material which became modified because these ancestors had just come out of the water and had no good protection against evaporation from their cuticle. For this reason, they could be active only by night. In insect larvae, this eye reduction possibly started with a wood-boring mode of life. The result of these two different modes of life was a remarkably identical eye, at least in some insect larvae due to parallel evolution (Paulus, 1979). The eye modification of schizochroal-eyed phacopid trilobites might be associated with a change in their mode of life: activity at night or in dimly lit (*e.g.* turbid) water, or predatory behaviour, for example.

The insect larval eye is definitively derived from the normal insect ommatidium. All reductions and modifications start with a diminution of the facettted eye and a decrease in the number of ommatidia. According to Paulus (1979), in insect larvae, as well as in some adult insects one can distinguish at least three possible pathways of eye modification, which are demonstrated in Figure 14. (1) Reduction of the remaining ommatidia to isolated lenses: These remaining ommatidia are either unchanged in structure (*e.g.* in *Collembola*), or slightly modified (*e.g.* trichopteran and lepidopteran larvae). The first step of modification is the formation of a two-layered rhabdom with distribution of the eight cells in two layers. (2) Fusion of all corneae into one single giant lens without modification of the retina, but with reduction of the superfluous crystalline cones: the unicorneal composite eye developed in this way (*e.g.* in all hymenopteran and some dipteran larvae). (3) Fusion of ommatidia: such cases are found frequently in trichopteran and dipteran larvae, which have double stemmata showing complete fusion, at least of the crystalline cone. In cases where the two ommatidia or stemmata fuse, the retinula cells very often distribute in many layers. Often the crystalline cone no longer develops (*e.g.* in coleopteran and some neuropteroidean larvae).

All these observations testify to the remarkable evolutionary plasticity of the arthropod compound eye, and its potential for modification, and should be borne in mind when considering the derivation of schizochroal trilobite eyes from a holochroal ancestral type.

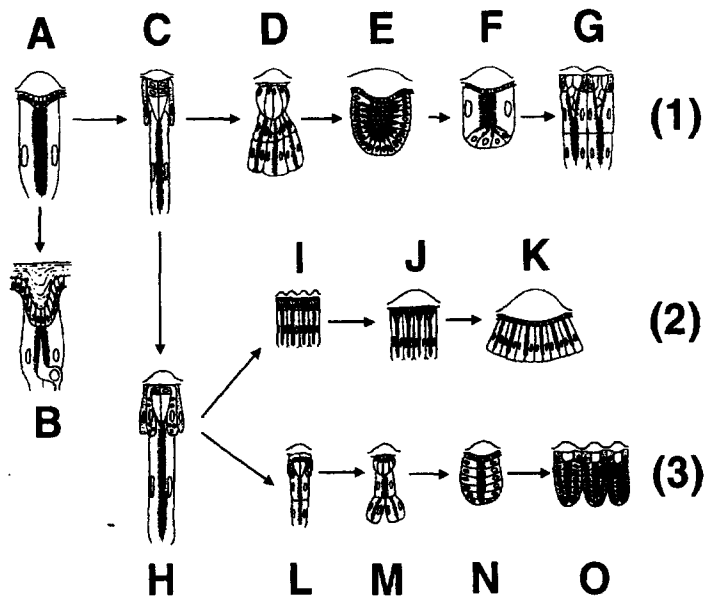


FIGURE 14 Three possible evolutionary pathways of arthropod ommatidia and faceted eyes; for further details see subsection 4.2.1 (after Paulus, 1979). (1) A: Simple protarthropodan ommatidium; B: ommatidium of *Limulus*; C: ommatidium of Protomandibulata as seen today unchanged in Crustacea (from this type developed by reduction different myriapodan eyes); D: intermediate stage in a myriapodan ancestor; E: ommatidium of *Scolopendra*; F: ommatidium of *Lithobius*; G: pseudofaceted eye of *Scutigera*; H: insect type of ommatidium developed from C; (2) I: normal faceted eye; J: intermediate stage; K: unicornal compound eye as in hymenopteran larvae; (3) L: larval ommatidium of Mecoptera; M: double ommatidium of Trichoptera; N: multilayered stemmata of Coleoptera; O: stemmataran compound eye in adult male Strepsiptera.

4.2.2 Possible Evolution of the Optics of Trilobite Lenses

Large doublet lenses appeared relatively late in the trilobite evolution (Clarkson, 1975, 1979), only the schizochroal-eyed phacopid trilobites possessed such doublets. In the ancestral holochroal trilobite eyes, as far as is known only small calcite singlet lenses occurred. This is also true for the abathochroal trilobite eyes, which arose independently but evidently, and represent an intermediate evolutionary stage between holochroal and schizochroal eyes. Abathochroal eyes, unlike holochroal eyes, seem to have been corrected for spherical aberration (Zhang and Clarkson, 1990) like schizochroal eyes (Clarkson and Levi-Setti, 1975; Horváth, 1989a). If it could be shown by more detailed anatomical and computational studies that abathochroal trilobite lenses were also aplanatic, then it would be pertinent to suppose the following evolutionary scenario of the optics of trilobite lenses:

- i. The first stage of development took place in the ancestral holochroal eye: minimization of the influence of double-refraction of calcite within the single

corneal lens. This problem was solved by a proper orientation of the c-axis of calcite crystals in such a way that it was aligned always parallel with the optical axis of the lenses, which in turn was normal to the visual surface of the eye. The small holochroal lenses, however, were not aplanatic. Judging from their dimensions, they might have been diffraction-limited, and so there would have been no selective pressure correcting for spherical aberration.

- ii. A second evolutionary step might have been the appearance of the abathochroal eyes (probably due to dimly lit optical environment), in which larger lenses occurred than in holochroal eyes. Without any correction the larger abathochroal lenses could have a considerable spherical aberration. The proximal undulating (Huygensian?) lens profile observed by Zhang and Clarkson (1990), however, might ensure correction for spherical aberration. The relatively steep rise of this proximal Huygensian profile and the considerable refractive index difference between the lens (calcite: $n = 1.66$) and the sublensar material (probably body fluid: $n = 1.35$) resulted in large internal reflections on the proximal refracting surface, and this reduced the transmissivity and so also the light-collecting efficiency of the eye. This kind of eye is confined to Lower and Middle Cambrian eodiscid trilobites. Many eodiscids lost their eyes altogether, and the group died out leaving no descendants.
- iii. The problem of loss of light because of internal reflections was solved in the schizochroal eye (perhaps induced by nocturnal and/or predatory mode of life), which may be considered as an endpoint in evolution: the lower lens unit (intralensar bowl) reduced these reflections and enhanced the transmissivity of the aplanatic doublet lens, as in the eye of *Notonecta*, for instance.

5 CONCLUSIONS

- i. The eyes of the extinct phacopid trilobites have three typical structural characteristics: The large circular lenses are well-separated from each other ('schizochroal' character), they possess two optical units ('doublet' character) and are corrected for spherical aberration ('aplanatic' character).
- ii. With respect to the 'schizochroal' character, the following eyes might be modern counterparts of the eyes of phacopid trilobites, for example: the unicorneal lateral faceted eyes of some Chelicerata; the dispersed faceted eyes of *Daphnia*, *Cypridina*, *Philomedes*, *Macrocypridina castanea*, Collembola, male Strepsiptera and some Zygentoma; the stemmataran compound eyes of some Myriapoda; the larval dispersed faceted eyes of some Mecoptera; the larval stemmataran compound eyes of Lepidoptera, Neuropteroidea, Coleopteroidae; the eyes of *Pecten*. Externally, perhaps the best example for a 'recent schizochroal eye' is the dispersed compound eye of male Strepsiptera. It would be possible to add further arthropod eyes with schizochroal character to the above list.

- iii. Considering the 'doublet' character, the larval stemmataran compound eyes of *Pieris brassicae*, the apposition compound eyes of *Notonecta*, and the larval stemmata of *Perga* are modern counterparts of schizochroal trilobite eyes. The eyespots of modern and fossil ostracodes and the eyes of scallops may also be considered as recent counterparts with an optimized, two-component (lens-mirror) dioptric apparatus.
- iv. The ostracode eyespots, the compound eyes of *Notonecta*, the larval stemmata of *Perga* and the eyes of *Pecten* are modern counterparts of schizochroal trilobite eyes, because their dioptric apparatus is corrected for spherical aberration, like the aplanatic mature or post-ecdysially developing lenses in the schizochroal-eyed trilobite *Phacops rana milleri*, for instance.
- v. The eyespot of ostracodes and the cornea in eyes of decapod crabs are modern counterparts, in which the dioptric apparatus consists of calcite with its c-axis parallel to the optical axis, like in trilobite eyes. Isopod crabs, for example, possess also calcite in their cornea; the c-axis of the calcite crystals, however, is not parallel to the optical axis.
- vi. The lens diameter in schizochroal-eyed trilobites matches the diameter of the eyes in the scallop *Pecten*. Schizochroal trilobite lenses are about three times larger than the larval stemmata of the sawfly *Perga*. The diameter of the optical unit (ommatidium or eyespot) of the visual system in *Notonecta*, male *Strepsiptera* and ostracodes is about twenty times smaller than in the schizochroal trilobite eyes.
- vii. There is not any recent eye, according to Table 1, which satisfies the all three conditions typical of the schizochroal trilobite eye. The eyes of *Pieris brassicae*, *Perga* larvae, *Notonecta* and *Pecten* have two characters, which are common with the schizochroal trilobite eye.
- viii. The optics of the eyespots of ostracodes, and the eyes of *Notonecta* and *Perga* larvae seems to indicate a convergent evolution. All these animals live in a dimly lit optical environment: in deeper layers of the sea, in turbid water with aquatic plants and phytoplankton, or they have a nocturnal mode of life. A similar convergent evolution occurs in the case of eyespots of ostracodes and eyes of scallops, whose visual systems consist of an aplanatic lens and a reflecting tapetum. Interestingly, the males of most Strepsiptera species, possessing 'schizochroal eyes', are also night-active. It is consistent with this argument that the deep-sea ostracodes, many mining insects and insect larvae have 'schizochroal eyes'.
- ix. The function of correction for spherical aberration ('aplanatic' character) in schizochroal trilobite eyes is to ensure as large light-collecting efficiency as possible for vision in dimly-lit optical environment. The lower lens unit ('doublet' character) in schizochroal-eyed trilobites reduces the reflectivity and enhances the transmissivity of the dioptric apparatus. The function of the 'schizochroal' character of the eyes in phacopid trilobites remains rather enigmatic until the sublensar structure of these ancient visual systems is revealed.

- x. Larval forms of holochroal-eyed adult trilobites have miniature schizochroal eyes, and pedomorphosis may be invoked in considering the origin of schizochroal eyes in adults. Their sublensar structure is unknown, but reference to the evolutionary pathways of holometabolous larval insect eyes shows the kind of modifications that may have taken place internally also in trilobite eyes. These modifications might involve: decrease in number of ommatidia, fusion of ommatidia, crystalline cone fusion or reduction, layering of the retina, corneal lens fusion, ceasing of the development at an early embryonic stage, isolation of individual ommatidia.
- xi. All reductions and modifications of the eyes of phacopid trilobites might have started with a pedomorphic diminution of the eye and decrease in the number of ommatidia. Possible pathways of further modification in trilobite eyes might have been similar to those in insect larvae as well as in some adult insects: (1) Reduction of the remaining ommatidia to isolated optical units with either unchanged, or slightly modified structure. (2) Fusion of ommatidia resulting in multiple optical units with complete fusion of the crystalline cones and distribution of the retinula cells in many layers. (3) Fusion of all corneae into one single giant lens without modification of the retina, but with reduction of the superfluous crystalline cones, resulting in a unicorneal compound eye.

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