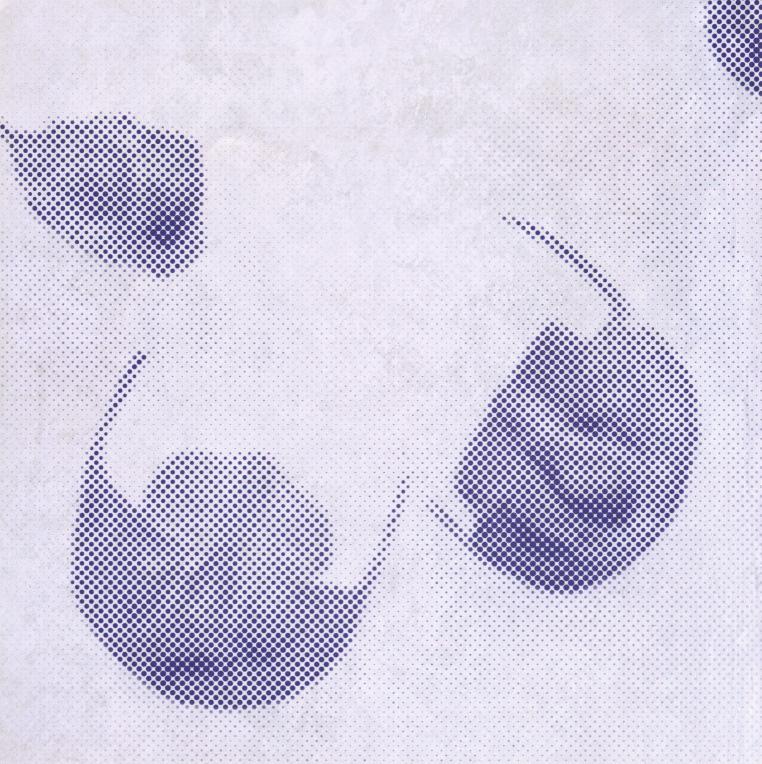# The eyes of trilobites:

the oldest preserved visual system

The eyes of trilobites:
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Eyes and the fossil record

Vision, which is surely the most essential and useful of all the senses to most animals, developed very early in the history of animal life, as the fossil record tells us. The first 'eyes' were probably no more than patches of light–sensitive cells, as in the 'spot–eyes' of living flatworms, but we do not know when they originated in geological time. What is remarkable, however, is that highly developed eyes are present in some of the earliest known marine arthropods – the long extinct trilobites. We shall shortly describe them, and put them in the context of geological time.

Our planet is some 4600 million years old, and life on Earth began during the first 30% of its history. By late Precambrian times bacteria, algae and probably small multicellular animals thrived, in simple ecosystems with short food–chains. We know relatively little of these, however, since these organisms are not greatly preservable. Ice sheets spread to low latitudes, the time of 'Snowball Earth', some 700 million years ago. When these eventually melted, the rising temperatures favoured the diversification of life. There came the strange creatures of the widespread Ediacara Fauna, like flat mattresses with ridged surfaces, lacking guts and possibly harbouring symbiotic algae. Then there was the most dramatic event of all, the so–called Cambrian 'explosion of life', from about 543 million years onwards, and phased over several million years. It was at this time when the first hard–shelled and preservable marine fossils originated. First came the 'small shelly fossils', phosphatic tubes, expanding cones, coiled shells and little buttons, some of these being parts of larger animals. And at about 520 million years ago came the earliest trilobites, with which we are primarily concerned here; the last ones became extinct at about 250 million years ago, so they lasted altogether for some 270 million years.

Trilobites are easily recognisable; they are all constructed on a basic plan, however much variability they displayed through time (Fig. 1). They all have a bilaterally symmetrical body, divided from front to rear into three parts; a raised central axis with two flanking regions. The head (cephalon) is well–defined, and possesses a pair of eyes, the thorax may consist of two to many segments, and the tail (pygidium) is an arched plate made up of fused segments. In the head were three or four pairs of 'appendages' each being two–branched with a leg and a gill, there was one pair for

each thoracic segments and usually several of diminishing size in the tail (Clarkson 1998, Levi–Setti 1993, Whittington 1992). It is surprising how much is known about trilobite biology and ecology despite these remarkable animals having been extinct for so long a time. Here, however, we are concentrating on the structure and function of the visual system alone and all these other fascinating dimensions must remain untold.

Different kinds of eyes

Vision, in its most basic sense, involves the ability to perceive light and to react to it, to locate the source of the light, and to sense movement; these can be accomplished by a relatively simple eye. More advanced kinds of eyes can distinguish form and distance, as well as colour and polarisation. The light–sensing devices, the most important parts of any kind of eye, especially an advanced eye, are the photoreceptors, which collect and process the light. These are usually numerous, they are normally found within the inner part of the eye, and they contain visual pigments which react chemically to light. This chemical energy is converted into electrical signal, and conveyed by the optic nerve to a series of nervous complexes and the brain. Here all the signals sent by the different photoreceptors are converted into an image, to which the animal can respond. Apart from reflection of biological mirrors (multilayered interference structures, e.g. in the lens–mirror–eyes of the scallop, *Pecten*), (Levi–Setti 1993, Fig. 13, p. 69) the only way in which the light can reach the photoreceptors is through some kinds of transparent surface, the 'optical interface'. This gathers light and passes it from the outside world to the photoreceptors. The image received and processed by the brain is made up of very many tiny point elements; each individual photoreceptor can only process a small part of the whole image, which is reconstructed by the brain as a mosaic, or like pixels on a computer screen. The more photoreceptors there are, the more detailed the image (Clarkson *et al.* 2006, Levi–Setti *et al.* 1998).

Two main kinds of eyes are found in the animal kingdom, both perfectly good solutions to image formation (Levi–Setti *et al.* 1998). Firstly there are camera eyes, as in vertebrates (ourselves included), in cephalopods (octopuses, squids, and *Nautilus*), and even in some kinds of jellyfish (Fig. 2). Secondly there are compound eyes, as in insects, crustaceans and trilobites (Fig. 3)

Camera eyes. In camera eyes, the photoreceptors (and there are millions of them) are arranged in a curving shell at the back of the eye, and collectively connected by an optic nerve to the brain. In the simplest form of camera eye light illuminates the retina through a small, pinhole–like aperture at the outer surface of the eye, but in more elaborate kinds a lens focuses the light on the retina, usually by varying its focal length. The space between the lens and the retina is filled with transparent, refracting fluid. The stimuli from each of the photoreceptors are reconstructed by the brain into a final image.

Compound eyes. Here the retina does not break up the image into point elements; this is done instead at the optical interface, which consists of many separate small lenses, arranged on a curving surface, and thus pointing in slightly different directions. There may be hundreds or thousands of these. Below each lens is a single ommatidium. All ommatidia are very similar; the eye is constructed on a modular principle.

Each ommatidium is a tapering cylinder, with its outer surface capped by a lens, and often with another transparent unit, the crystalline cone, below. This is connected to the rhabdom, a central light–sensitive rod surrounded by several photoreceptors, and the whole is linked to underlying 'ganglia' and to the brain, which process the various signals and form a mosaic image. This would seem to be rather coarse by comparison with the finely resolved image of a camera eye, but it had a great angular range of vision, and a good depth of field. Judging by how widespread these eyes are in arthropods, they are evidently a highly successful kind of eye.

Trilobites and their eyes through time

The external skeleton of trilobites is made of calcite ($CaCO_3$, or Iceland Spar), set in an organic base, and such material has a high potential for preservation, especially in limestone, but also in other kinds of sedimentary rock. The eyes are simply a specialised part of the exoskeleton (otherwise known as the cuticle), and the preservable parts, the lens array are made of calcite too (Towe 1973, Clarkson 1979, 1997). Accordingly, the fossil record of trilobites is remarkably good and is well known. We shall summarise it here, with reference to Figure 4. The first trilobites are found from rocks about 520 million years old, some distance above the base of the Cambrian. These belong to several groups, they are already highly differentiated, and it is very likely that they were derived from earlier ancestors in which the exoskeletons did not consist of calcite but were unmineralised. And even amongst the earliest there are perfectly good compound eyes. There was a continuous relay of trilobites throughout the Cambrian, but they were nearly all bottom–dwelling types.

Very few invaded the planktonic realm, in other words living as passive drifters or feeble swimmers in the upper waters of the sea; one tiny, and undoubtedly planktonic form is known from the upper Cambrian. There then came an environmental crisis of some kind, and many of the Cambrian groups died out, to be replaced by a greatly diverse trilobite fauna early in the Ordovician. This was the high point of trilobite evolution, and these animals diversified into many different kinds of habitat, the sea floor, carbonate reefs, and the pelagic realm, the domain of active swimmers in the mid to upper waters of the oceans. But at the end of the Ordovician, a major glaciation spread ice to low latitudes, sea–levels were lowered, habitats were lost, and for the rest of trilobite history no new body plans originated, only permutations on themes established already in the early Ordovician. Silurian trilobite faunas are rather like impoverished versions of those of the Ordovician; there were no more pelagic forms, and the upper waters of the sea were never re–colonised. During the Devonian major groups became extinct one after the other, there was a further major extinction in the late Devonian, environmentally induced, and only one group, the Order Proetida survived for the next 50 million years. These small and rather 'typical–looking' trilobites were adapted to certain habitats only. And then came the most severe environmental crisis through which life passed, at the end of the Permian, marine ecosystems were changed for ever, and the last trilobites became extinct.

The fossil record of trilobite eyes

We have noted that the lenses in the eyes of trilobites are constructed of calcite, like the rest of the cuticle, and hence their potential for preservation is high, especially in

limestones. Not infrequently, the internal structure of the lenses is preserved, though in many cases chemical alteration (diagenesis) after the death of the trilobite has destroyed or modified the original structure. It is, however, only the lenses and adjacent regions of the cuticle which are preserved, and all the photoreceptors and other structures which lay below have decayed without trace. Almost certainly, however, at least in the primordial type, the holochroal eyes, there were ommatidia, as in modern compound eyes. Despite this loss during preservation, a remarkable amount is known about trilobite vision, which we shall now explore. Three separate kinds of eyes are known in trilobites, holochroal, schizochroal, and abathochroal (Clarkson 1975, 1979, 1997, Levi–Setti *et al.* 1998).

Holochroal eyes

Most trilobite eyes are of this kind, which represents the ancestral type (Fig. 5, 6, 7). They are usually kidney–shaped and have many small calcitic lenses, closely packed, and in contact with one another; the lenses are usually round or hexagonal. A thin calcitic sheet, the cornea, covers the lenses, and is continuous with the outer layer of the cuticle. At the top of the lentiferous surface is a suture, part of a line of weakness that split when the trilobite moulted, facilitating the shedding of the old cuticle. Above this is the palpebral lobe, a kind of outwardly curving upper eyelid. At the base of the eye is a thin band, or socle, which often bears sensory pits. Each lens is made of calcite, with rounded outer and inner surfaces. Now calcite has the advantage of being transparent, and in this respect ideal for letting the light though to the photoreceptive units blow. But there is a disadvantage, it is a birefringent mineral which means that light passing through is broken into two rays, which would produce double images at different depths. There is, however, one direction in which light travels through without being thus affected and that is the so–called crystallographic or c–axis, which normally runs the length of any calcite crystal. The lenses of both holochroal and schizochroal eyes are remarkable in that in every case the c–axis is the same as the lens–axis, so that light travelling parallel with the axis is not broken into two rays. This minimisation of birefringence, while retaining all the advantages of transparency, is surely a magnificent feat of evolutionary optimisation. Looking at the lens in detail, we see that it consists of thin plates (lamellae) radiating from the centre, these in turn are made of thin rods, the trabecula, which turn out fanwise towards the upper surface.

Since the lentiferous surface is curved, it subtends a considerable angular range of vision. In most instances it is about 180° horizontally and from a little below the equator to about 35° above, though in some trilobites it is almost panoramic (Clarkson 1975).

Not much is known about holochroal eyes of most Cambrian trilobites, the reason being that in most of these early forms, an additional suture was present between the lentiferous surface and the socle, so that all the lenses fell out during moulting. But this suture did not become functional until late in development, and the juvenile stages retain the eye. In the upper Cambrian, however, one group (Family Olenidae) retains the lentiferous surface through life, which is some cases is almost spherical, so that the eye looks like a tiny golf ball (Clarkson 1973, 1997, Clarkson *et al.* 2003) (Fig. 7G, H) In the succeeding Ordovician, at the time when trilobites proliferated exceedingly, holochroal–eyed trilobites flourished. While most of these lived on or near

the sea floor, two groups independently became pelagic, living as swimmers in the upper or mid–waters of the sea. *Carolinites* and its relatives lived in equatorial waters and it has a pair of enormous eyes, with great numbers of lenses, extending to the ventral surface. Like some living crustaceans, it probably migrated to the surface at night and went down into deeper waters during the day. At the same time *Pricyclopyge* (Fig. 7F) and related forms inhabited the pelagic realm in southerly latitudes, round the margin of the great continent of Gondwana. All these species have greatly enlarged eyes, in some instances fused anteriorly. It has been calculated, from the sizes of the lenses, and the angle between adjacent lenses, that the eyes of *Carolinites* were adapted to relatively bright light, while those of *Pricyclopyge* functioned at lower levels of illumination, the latter genus living deeper in the sea (Fortey 1985, McCormick & Fortey 1998). These trilobites became extinct at the end of the Ordovician, there were no more large–eyed trilobites thereafter, and it seems that the pelagic niche was never colonised again. Trilobites, usually with kidney–shaped holochroal eyes, adapted to dim or moderate light intensities, persisted until the close of the Permian, when so many marine invertebrates became extinct.

Schizochroal eyes

These eyes are quite unlike anything else in the animal kingdom (Figs. 8–13). They are absolutely fascinating but how they worked is still controversial. In such a typical form as the Middle Devonian *Eldredgeops* the eyes are large, with about 70 lenses (Clarkson 1975, 1979, 1997, Miller & Clarkson 1980). These lenses are much larger than those of any holochroal eye and they are almost biconvex. Moreover they are separated from each other by cuticle (sclera). This sclera is somewhat thicker than the lenses, so each lens is set at the outer end of a cylindrical cavity, the alveolus. Each lens has its own thin cornea, which continues through the cuticle as a cylindrical ring, and occasionally has been seen to continue as a thin–walled tapering cylinder below the lens (Clarkson 1967).

The internal structure of the lenses is of special interest. In the year 1901 the Swedish palaeontologist Gustav Lindström published a remarkable work entitled 'Researches on the Visual Organs of Trilobites' (Lindström 1901). In this he illustrated many trilobite eyes, and in particular he showed a thin section through a phacopid eye which he had specially prepared. At the base of lenses which had not been chemically altered after death (diagenesis) there was shown a bowl–like structure, interlocking with the curving upper part of the lens along a wavy surface. Actually Lindström wondered if this bipartite internal structure was an artefact, the result of diagenesis after the death of the trilobite, but later investigations showed that very similar structures were present in other phacopids too, all of the same kind within adjacent lenses and thus unlikely to be artefacts. As research on these lenses continued, it became clear that their internal structure was remarkably complex, but not always the same in different phacopids. In the early Ordovician *Dalmanitina*, for example, the upper surface of the bowl is indented with a tiny dimple, whereas in the contemporaneous *Crozonaspis*, the bowl is much thicker with a wavy upper surface (Fig. 13 B–E). In 1975 Riccardo Levi–Setti, working in Chicago, recognised that these two shapes corresponded almost perfectly to separate designs for thick, but aplanatic lenses, which would bring light to a sharp focus, produced by René Descartes in 1637 and

Christian Huygens in 1690, respectively. The optical principles they discovered had already been used by trilobites some 490 million years earlier! (Clarkson & Levi–Setti 1975). A model *Crozonaspis* lens was made in Chicago, and if a pure calcite upper lens unit was coupled with a plastic intralensar bowl of slightly lower refractive index, light was brought to a perfect focus. It worked ideally. But as was shown later some phacopid lenses at least have a still more complex internal structure. The lower surface of the upper lens unit in *Dalmanitina socialis*, for instance, has a little nipple (Fig. 13B), and it has been shown (Gál *et al*. 2000a) that this bulge made the whole doublet lens bifocal (with two sharp focal points below the lens) so that the trilobite could see simultaneously far and near in spite of the fact that its rigid lens was not able to accommodate. Another example is *Eldredgeops*, (Figs. 8E, 13D) in which the bowl thins out and vanishes centrally, while an additional structure, the core, of similar appearance to the bowl, is placed in the centre of the lens (Miller & Clarkson 1980). In some other phacopids there seems to have been a core as well, but less highly differentiated. The lenses of *Eldredgeops*, like those of holochroal eyes are constructed of radial lamellae, themselves comprised of a palisade of trabeculae, and the existence of these, and the bowl and core has been amply confirmed in a recent study (Lee *et al*. 2007) using new methods, and in unprecedented detail. The core and bowl have been shown to be richer than the upper unit in magnesium, and the trabeculae in some species appear to fan out downwards rather than upwards. While there remain many problems to be solved regarding the structure and optics of the lenses of schizochroal eyes, there is more clear evidence about how such eyes originated in the first place, and it comes from a study of juvenile trilobites.

Trilobites, like other arthropods grew by moulting (ecdysis). This process involves a new soft shell being secreted below the old hard exoskeleton, while the lower part of the latter is dissolved by a corrosive fluid from special glands. Eventually the old exoskeleton is cast off, and the new, and slightly larger soft shell thickens and hardens. In fine sediments the cast off shells of all growth stages may be preserved, and is only necessary to study them as a gradational size series to discover how the trilobite grew and how their organs developed. With the aid of the scanning electron microscope, the smallest details may be revealed, and the juvenile forms of holochroal eyes turn out to be schizochroal; they have relatively few, large, and separate lenses (Clarkson & Zhang 1991) (Figs. 2A–E, Fig. 14). This has been confirmed in other trilobites. Schizochroal eyes must have been derived from holochroal precursors, and the earliest schizochroal eyes arose by retaining the juvenile form of the ancestor into the adult of the descendant. This is a well known biological process, known as paedomorphosis, and evidently results from a minor genetic malfunction. The earliest phacopid eyes did not have quite the perfection of the later ones, for very often the packing of the lenses on the eye surface was irregular. Now in both holochroal and schizochroal eyes, new lenses were added at the bottom of the eye, in sequence (Thomas 2005), and the irregularities resulted from the lenses being all of the same size (a legacy of the holochroal condition). Such lenses cannot be neatly arranged in a system of hexagonal close packing, on a lentiferous surface which expands downwards; there are always discontinuities (Clarkson 1997). But in later phacopids, the diameter and spacing of the lenses became greater towards the bottom of the eye, and thereby a perfect system of packing was achieved. Clearly this must have been important to the trilobite, and we should consider this factor in terms of the overall functioning of the schizochroal eye.

How did the schizochroal eye function as a whole?

We noted earlier that schizochroal eyes have no living counterparts, so there is no direct analogue which can be invoked in understanding their function (Horváth *et al.* 1997). The nearest is in males of the short–lived night–flying insects known as strepsipterans. These have separated lenses, large for the size of the eye, but the eye itself is tiny. But below each lens, rather than there being an ommatidium, there is instead an independent retina, with many photoreceptors, on which the image of the insect's world is formed and sampled by many photoreceptors (Buschbeck *et al.* 1999). This may, to some extent, be a guide in interpreting what lay below the lenses of schizochroal eyes, and most students of the subject have concluded that under each lens was a short capsule, floored by retinal cells, of which there may have been 1000 or more (Fordyce & Cronin 1993, Clarkson 1997). But could such an eye form a coherent image? A new model (Schoenemann 2007) suggests that it could, but only if the individual images formed by each lens were superimposed, without blind spaces in between. According to this model, light coming from a particular point within the animal's visual field would stimulate a receptor, or group of receptors in the retina below one particular lens. But it would also stimulate different areas of the retina in neighbouring lenses. The phacopid visual system could therefore unite all the images formed in the separate retinas into a single, coherent and total image. This would work very well for an eye where the curvature was more or less the same in horizontal and vertical planes, so that the directions of the lens–axes (axial bearings) had the same kind of spacing. Where the eye is much more curved horizontally than vertically, the axial bearings of the lenses are clustered in widely–spaced 'visual strips'. Might such an eye still have been able to form a good image? If it was a rapidly moving trilobite, perhaps so.

Much more work needs to be done on schizochroal eyes, so that we can understand them more fully. But what is already known is dramatic.

Abathochroal eyes

This kind of eye is confined to the Lower and Middle Cambrian Suborder Eodiscina, a group of tiny trilobites with no more than two or three thoracic segments (Fig. 8 F–H). They look rather like tiny schizochroal eyes, with separated lenses, but there is no interlensar sclera, and the packing system is somewhat irregular (Zhang & Clarkson 1991). The eyes of exquisitely preserved Chinese *Neocobboldia* specimens show that the lower surface has a little nipple, and it has been suggested (Gál *et al.* 2000b) that as with *Dalmanitina*, mentioned earlier, this bulge made the lens bifocal so that it could see both near and far, even though the focal point below the bulge was not sharp, due to diffraction. However elegant and clearly functional these tiny early eyes may have been, it is a remarkable fact that many eodiscids were blind, more of them, in fact, than there are sighted forms. Sometimes blind and oculate species occur together. Presumably eye–loss was environmentally related in some way, but this remains tantalisingly obscure. And this leads us on to the final section.

Eye reduction and blindness

We noted earlier that compound eyes are primary structures in trilobites, as typical of most arthropods. Yet throughout geological time we see that various groups lost their eyes, and became secondarily blind. It seems remarkable that such useful organs

should disappear, but they did, many times. Eye loss is most striking in some long ranged groups, the exclusively Ordovician Trinucleidae (Figs. 4, 15), and the Ordovician to Devonian Harpetidae. In all species eyes are effectively lacking. But both these groups have an extensive pitted fringe surrounding the front and sides of the cephalon, which may have functioned as a kind of 'compound ear' in other words a vibro–sensory organ. Or it may have been an organ of chemical sense. Whatever it was, it seems to have replaced vision as a primary sense.

But in addition, there are examples of progressive eye–reduction through time, and the best examples of this are in the late Devonian. At this period in trilobite history only two main groups were left, the holochroal–eyed Proetida and the schizochroal–eyed Phacopida. The former survived the end–Devonian extinction, the latter did not. It has been known for a long time that during the late Devonian, the eyes of many species, in both groups simultaneously became progressively smaller through time, the lenses fewer and more irregularly arranged (Fig. 5F), and in some cases the eyes had disappeared completely. One attested case, based upon material from Germany and especially from southern France concerns a group of the Order Proetida known as the Tropidocoryphinae (Feist & Clarkson 1989). The earlier Silurian and Devonian representative of this group had normal large eyes. In the mid to late Devonian, however, we see progressive eye reduction through time, in two separate lineages, one after the other; this is calibrated against a time–scale given by conodonts. There are other examples too, and in one study of eye–reduction in Phacopida, the unidirectional trend has been shown to result from progressive paedomorphosis (Feist 1995). During ontogeny, as the trilobite develops from the early juvenile stages onwards, the eyes appear on the anterior margin of the cephalon, and as the trilobite grows they enlarge and migrate inwards, 'dragging'

the facial suture in with them. During eye–reduction and loss, however, the reverse happens, the eyes become small and more marginal, in other words more and more 'juvenile' through time, and eventually they disappear altogether. Many examples are now known from Europe, but also contemporaneously from China and Australia. But although we know that eye–reduction leading to blindness happened, and when it happened, and up to a point how it happened, there remains the question of why it happened. The likely driver is environmental change (Feist 1991). For during the later Devonian, the oceans deepened, a vast blanket of mud spread over huge areas of the sea floor on a global scale, and beyond the limits of light penetration. The trilobites became adapted to this habitat with their very small size and loss of eyes. Some became mud–burrowers, with even less need for visual organs. An eye is an 'expensive' piece of equipment to maintain, and where there is no need for it, in lightless conditions, natural selection will soon eliminate it; we see equivalent eye loss for example in deep–sea fish and crustaceans and in burrowing and cave–dwelling amphibians. But all these highly adapted forms perished during the subsequent late Devonian mass–extinction crisis, and the surviving Proetida had normal holochroal eyes, right up to the end of the Permian, when they were environmentally driven to extinction, and the history of the trilobites, and their eyes, came to its final end.