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The Eye: Paleontology

The trilobites, a group of marine arthropods that emerged out of the Cambrian explosion of advanced life forms, have left an impressive fossil record of the earliest known visual organs. Because the lens elements of the compound eyes of trilobites were made of crystalline calcite, and their encasing framework also mineralized, the structure of the visual surface of these ancient eyes is preserved in outstanding detail. Several evolutionary steps leading to improved visual function can be identified throughout the trilobite's life span, culminating in the development of lens structures apt to correct for spherical aberration. Although nothing is preserved of the internal structure of the eye of trilobites, the optimization of the visual function of their dioptric apparatus is telltale evidence of a parallel increase in complexity of their photoreceptors and neural system in response to selective pressures. Although trilobites became extinct, seemingly by convergent evolution and within the canons of optics, several modern life forms developed perfected dioptric apparatuses quite similar to those evolved by their unrelated predecessors.

Vision and the Eye

Vision, undoubtedly the most essential and advanced sensory function of animal life, developed very early in the animal kingdom, as we learn from the fossil record. The most ancient known eyes of any kind belong to the extinct trilobites, a group of marine arthropods which flourished from the early Cambrian until the Late Permian, a time range of approximately 325 million years. The eyes are compound, like those of insects and crustaceans, and they are present in the earliest trilobites of all. They are paired and placed laterally on the head of the trilobites. Before continuing the description of what is found in the fossil record of trilobites, and to appreciate what is missing, it is important to introduce an overview of the process of vision as we know it from extant life.

The compound eye represents one of two basic schemes for vision, the other being that developed by cephalopods and vertebrates also quite early in the history of life, resembling the structure of a photographic camera. Although differing in the resulting physical structure of the eye, both schemes rely on mechanisms that are indeed quite similar.

Requirements for Vision

Basic factors in vision are the ability to perceive and react to light, the ability to locate the light source and to sense movement, the ability to perceive form and depth (relative distance of objects), and the ability to distinguish colors and (in many cases) polarization of light. At the lowest level of complexity, to accomplish these tasks there must be a light detector or sensor — some kind of device that will respond to the stimulus of light. Then there must be a directionally

selective optical device, or dioptric apparatus, that can transfer a pattern of light (the seen object) to the vicinity of the light sensor and, finally, a “brain”—a neural structure to coordinate and interpret the signals received by the sensor, ultimately to “reconstruct” as an image the object seen. At a higher level of vision, where more precise and versatile perception is required, additional refinements of structures and systems are necessary. To be able to sense movement, eyes must have the ability to follow the evolution of a visual pattern through time. To be able to perceive depth, visual systems must have the ability to compare images obtained from different viewpoints, and to be able to distinguish colors and polarization eyes must have a more complex structure of sensors.

Basic Structures of the Eye

The light-sensing devices, similar in all types of animals, are the photoreceptors. Normally located deep within the eye, the photoreceptors act in a manner analogous to the film in a camera: They react chemically to light. In the invertebrates, they take the form of orderly networks of stacked microtubules, replaced by disks in the vertebrates. These structures contain pigments (rhodopsins) which are altered chemically by light. The chemical reactions within the rhodopsins create a series of electrical stimuli that are conveyed by an optic nerve to the neuromotor center (the brain).

In all kinds of eyes (Fig. 1), the link between the photoreceptors and the outside world is created by an *optical interface*—a transparent device that gathers and concentrates light from the outer world (the object) and conveys light patterns (images) to the photoreceptors. Whatever the structure of the optical interface, a single lens or a set of lenslets, the images must be broken down into many “point elements” so that individual units in the photoreceptor network can each perceive a part of each image. Here resides the common denominator of all schemes of vision: The im-

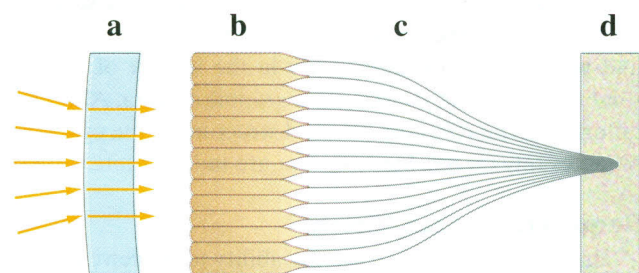


FIGURE 1 The basic structures of all types of eye. A directionally sensitive optical device (a) gathers light from the outside world and transfers a pattern of light, the image, to a light sensor (b). Here, a chemical reaction converts the light stimulus to a neural stimulus which is conveyed by an optic nerve (c) to the neuromotor center (“brain”) (d).

age must be sampled in bits and pieces by the network of photoreceptors; up to a point, the finer the mesh of photoreceptors, the greater the ability of the eye to discern details. (There is a practical limit to how small the elements of this mesh can be made since the aperture of the optical interface causes diffraction effects that will always blur the image somewhat). Photography and television are two familiar man-made examples of this optical sampling process, which seems to be basic to the reconstruction of any image.

Two Functional Approaches to Vision

Now we can view the two basic schemes for vision, the *camera eye* versus the *compound eye*, as two equivalent solutions to the problem of sampling the image into discrete point elements (Fig. 2).

In the camera eye, the photoreceptors are arranged in a closely packed array that covers the innermost surface of the eye cavity (the retina). In its simplest form, the retina is illuminated through a pinhole. In the more advanced forms, such as our own eyes, the pinhole is replaced by a focusing lens provided with a variable aperture, which accommodates to focus the image and adjusts the level of illumination to optimize the retinal response. The lens projects a continuous image, but the photoreceptors (≈ 130 million rods and cones in the human retina) break up the image into many discrete point elements and “sample” the image. Then, the nervous system, culminating in the visual cortex of the brain, reconstructs the numerous discrete stimuli into a final image perception. Focusing is accomplished in this camera eye by a lens whose focal length can be varied, by a movable lens, or in a few cases by a movable retina. Other structural components of the eye, including the cornea and the refracting vitreous fluid which fills the eye cavity, are accessories of the optical interface. Two eyes of this kind are normally needed to gauge distances and obtain stereoscopic vision (stereopsis), although eye movement coupled with visual memory can sometimes substitute for stereopsis. In a variety of animal eyes, the visual field is scanned to accomplish the image sampling. An extreme example of this is found in the microscopic marine organism *Copilia quadrata*, in which the images projected by a pair of eye lenses are respectively scanned by a single sweeping photoreceptor. From the amazingly complex retina (which performs a kind of parallel readout of incoming visual data) to the scanning photoreceptor (which performs a serial or sequential readout), all eye “cameras” are effectively performing the same kind of function.

In the second major scheme for vision, the compound eye, the retina does not break up the image into point elements. This is done instead by the optical interface. Given the overwhelming number of animal species that have adopted this approach (it suffices to think of the insects), there is no question as to the success of this alternative scheme. The visual surface of this type of eye is composed

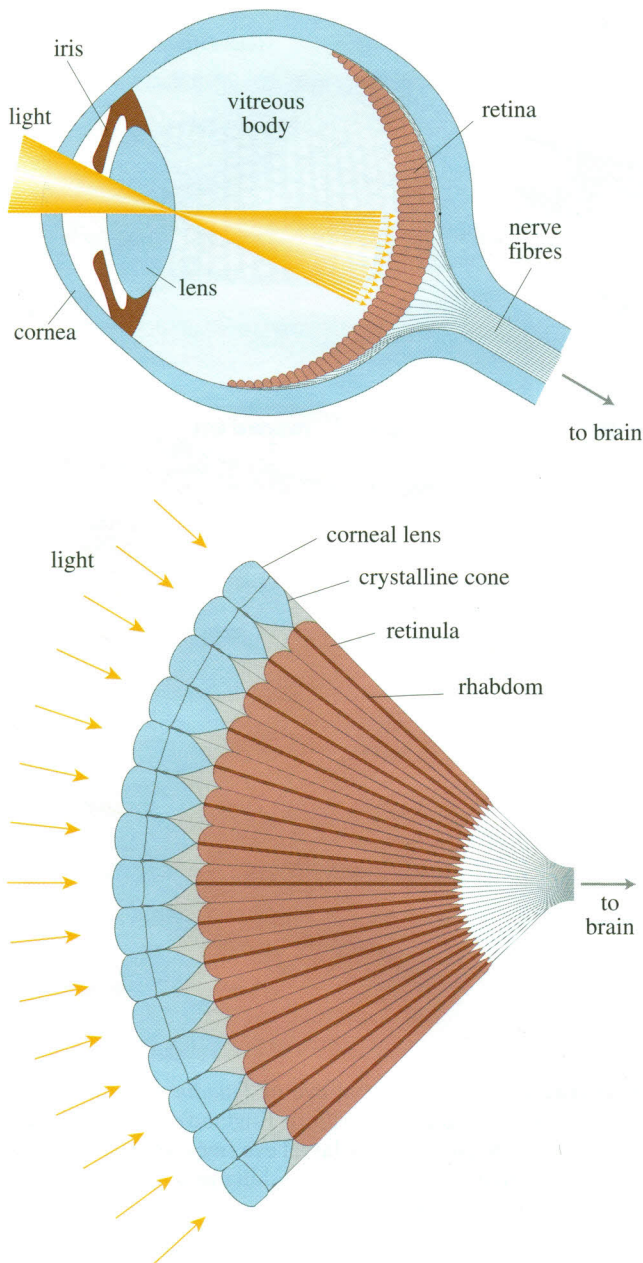


FIGURE 2 The two fundamental schemes for vision found in nature. The optical interface of the camera eye (top) projects a continuous image on a retinal array of photoreceptors, which break the image into numerous discrete “point elements.” In the compound eye (bottom), the optical interface breaks up the image into point elements.

of an array of separate lenses, or other light-gathering and ray-selecting devices, with each element on the visual surface connected to its own photoreceptor. The modules that make up the compound eye are called *ommatidia*. In general, each ommatidium is a cylinder of transparent material, terminated at the end which faces the outside world (distal

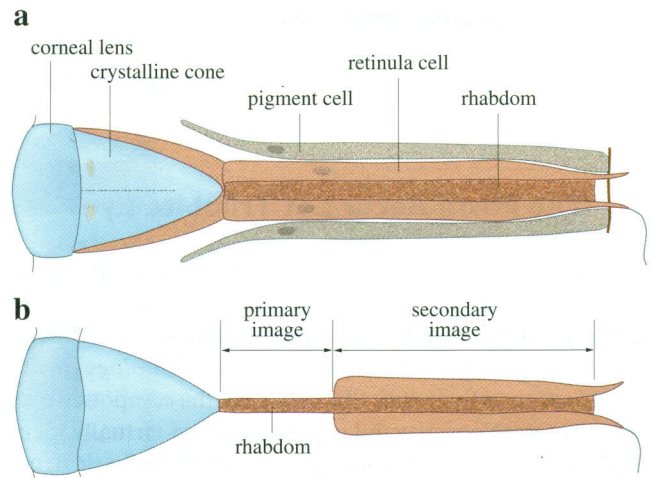


FIGURE 3 (a) Structure of ommatidia, the modules that make up the compound eye. Many thousand of ommatidia can be grouped together to form a visual surface, and because each one points in a slightly different direction the compound eye often has an unusually broad field of vision. (b) Structure of an ommatidium in which secondary patterns of images (Fourier images) are repeatedly formed deep within the eye. This phenomenon, found in some compound eyes, is made possible by the overlapping of contiguous primary images. This gives the compound eye extreme sensitivity to movement of forms in the visual field.

end) by a corneal lens, a crystalline cone, or a combination of both (Fig. 3). At the other (inside or proximal) end of each ommatidium is a photoreceptor (or *rhabdom*) which is linked by a nerve cell (*neuron*) to the nervous system and, ultimately, to the “brain.” With this arrangement, a parallel readout of electrical stimuli emerges from the network of individual photoreceptors via a bundle of neurons. Also, a brain of some kind is still needed to coordinate the mosaic of point elements provided by the optical interface to produce a perception of image. The mesh of receptors is relatively coarse when compared with that of the retina in the camera eye, but the functioning of this system is essentially the same. The major difference is in the structure of the optical interface and optical phenomena that such structure may originate. A compound eye often has an unusually broad field of vision because the many ommatidia (visual modules) are all arranged to point in slightly different directions. In fact, the fields of view of a pair of compound eyes may actually overlap in front and back of the carrier, making stereo vision possible over the entire surroundings. (In principle, a limited amount of stereo vision may even be available to each compound eye separately, in the region in which the fields of view of neighboring ommatidia overlap). A further advantage of the compound eye that is seldom recognized is its inherently large depth of field. Since it is an optical instrument that, to a good approximation, can

be regarded as a two-dimensional array of pinhole apertures, it needs no focusing or accommodation to obtain relatively sharp images of both close and distant objects simultaneously.

The Fossil Record of Trilobite Eyes

It is perhaps no coincidence that the modular approach to the construction of the eye was pioneered by arthropods in general and by trilobites in particular since these creatures exhibit a high degree of modularity (*serial homology*) in the construction of their entire bodies. Like the compound eye, trilobites were constructed of a sequence of virtually identical segments, each originally provided with the basic structures needed to carry out the functions of life. The eyes of trilobites are often well preserved because the lenses, like the rest of the exoskeleton, are made of calcite, which has a high preservation potential, especially in limestones. Although in some instances the lenses have been recrystallized by postmortem diagenesis, in other instances the original mineralogy and structure of the lenses may be preserved virtually intact. However, it is only the lenses and adjacent regions of the cuticle, making up the optical interface, which are preserved because the soft parts which underlay the lentiferous surface decayed without trace shortly after death. Even so, a remarkable amount is known about the structure, growth, and evolution of these eyes (Clarkson, 1975, 1979) and about the function and optics of the trilobite visual system. Two main kinds of trilobite eye have been distinguished, designated *holochroal* and *schizochroal*. A possible third kind, the *abathochroal* eye, has also been proposed.

Holochroal Trilobite Eyes

In most trilobites the eyes are holochroal; that is, the calcitic lenses are small and numerous, in direct contact with one another, and closely packed (Fig. 4). They are usually round or hexagonal. A single thin sheet of calcite covers the lens array, and this cornea is continuous with the outer surface of the cuticle. Below the visual surface there is often a narrow platform, the eye socle, which may be provided with sensory pits. Directly above the visual surface runs part of the facial suture, a line of weakness which enables the old exoskeleton to break up into separate components during molting. On the other side of the suture lies the palpebral lobe, which is part of the central part of the head (cranium); it forms a kind of “upper eyelid” with an outwardly curving outer edge.

Holochroal eyes are present in the earliest Cambrian trilobites (olenelloids), and although the visual surface of Cambrian trilobites is not often preserved the record of holochroal eyes of different kinds from the Late Cambrian

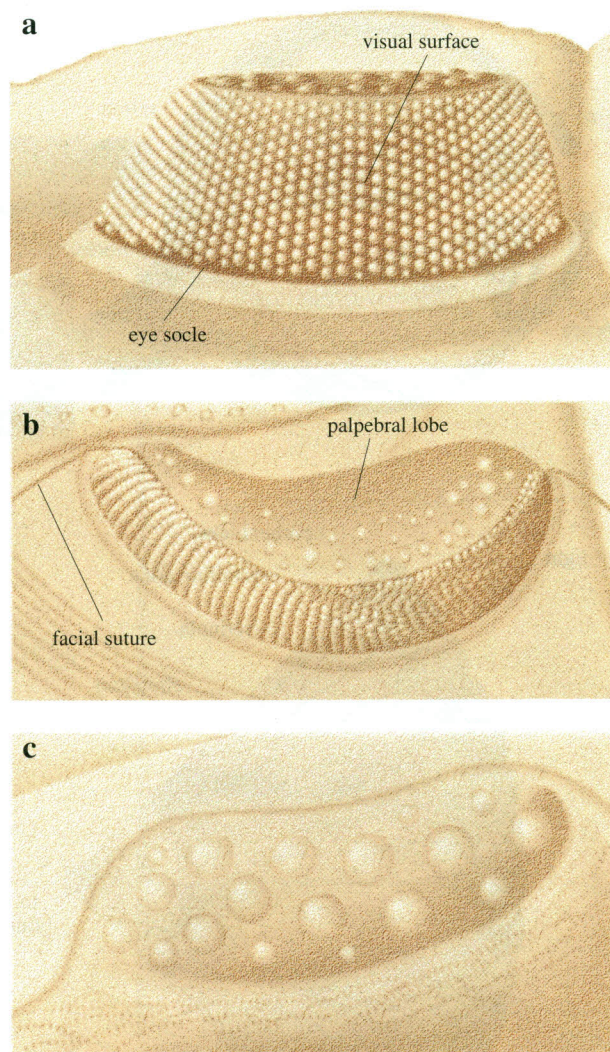


FIGURE 4 The holochroal eye of *Paladin eichwaldi shunnerensis* (Carboniferous, northern England): (a) lateral view, (b) dorsal view, and (c) early larval eye (meraspid) with a typical schizochroal morphology. The adult eye is 3.5 mm long and the larval eye is 0.2 mm.

until the end of the Permian is very rich. In fact, the earliest forms (except in certain young individuals), the visual surface was released upon molting or death, and only the palpebral lobe and the eye socle outline the eye profile (Fig. 5). Toward the end of the Cambrian, and during post-Cambrian times, the visual surface became fused to the eye socle and was preserved as part of the mineralized exoskeleton. Most holochroal eyes are kidney shaped and sessile with at most a few hundred lenses, but in the Ordovician there appeared a great diversity of eye types. The pelagic niche was colonized, probably for the first time, and in such swimming trilobites as *Opipeteur* (Fig. 6) and *Cyclopyge* the eyes became immense, and in some cases even fused an-

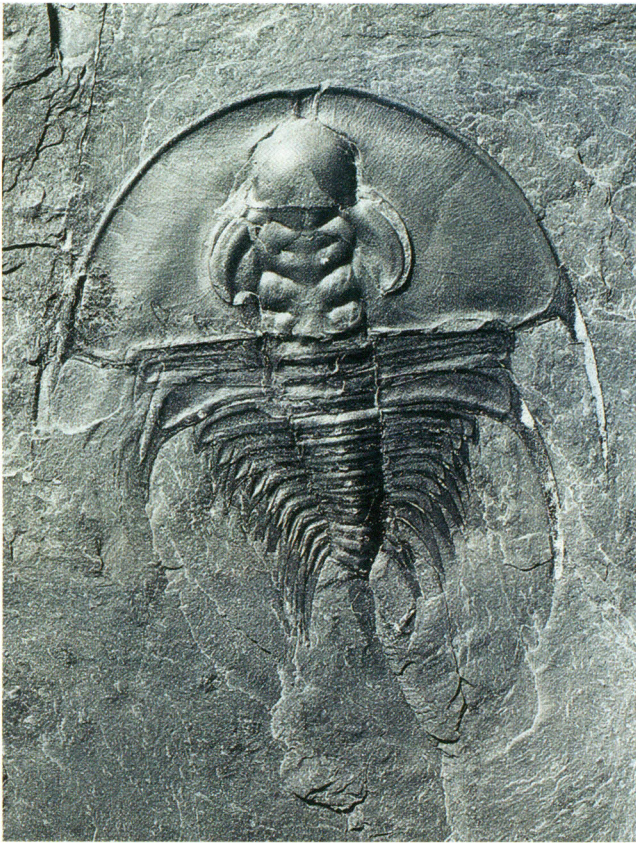


FIGURE 5 The eye in these exuviae of *Olenellus clarki* (Lower Cambrian, California), indicated by the arrow, is determined by the palpebral lobe and the eye socle, and the visual surface was released and lost in the molting process. The trilobite is 2.8 cm long (reproduced from Levi-Setti, 1993, with permission of the University of Chicago Press).

teriorly. In most post-Ordovician trilobites, the eyes, where holochroal, are usually reniform with well-developed lenses, and this kind of conservative organization persisted until the end of the Permian.

As trilobites grow from the early stages, the eyes appear at the anterolateral edges and with successive molts migrate inwards and backwards taking the facial suture with them. The lenses are emplaced in a generative zone lying below the facial suture, and new lenses are always added below existing ones. The mature eye has a curving surface, and the angular range of vision thereby subtended, may be either strip-like with a latitudinal range of no more than 30° from the horizontal or panoramic, extending from below the horizontal to 90° above; the visual fields of such eyes overlap at front and rear. The packing arrangement of the lens elements in this eye type is remarkable in many respects (Clarkson, 1975). On a small scale, the lenses are arranged in a hexagonal pattern, much like the cells of a beehive. On a broader scale, a pattern of intersecting logarithmic spirals

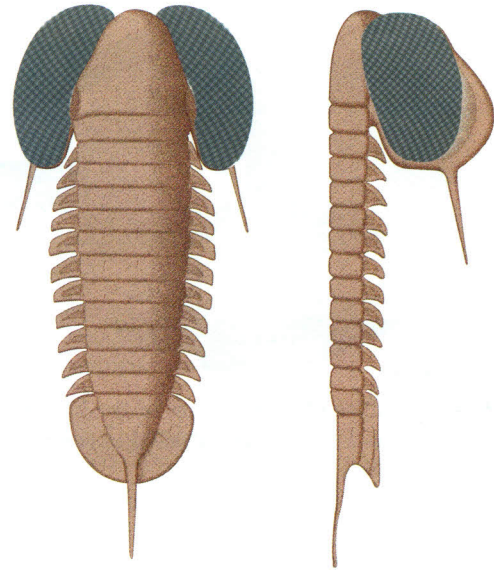


FIGURE 6 *Opipeuter inconnivus*, an Ordovician pelagic trilobite from Spitzbergen with hypertrophied eyes (black). Total length of the adult individual is 2.2 cm.

emerges, much like the arrangement of florets in a giant sunflower (Fig. 7). The properties of the logarithmic (or equiangular) spiral have fascinated naturalists and poets for centuries (D'Arcy Thompson, 1942). It arises in nature whenever growth (linear expansion) combines with the necessity of preserving circular forms (rotational symmetry). The growth of the trilobite eye, most noticeably of the holochroal variety, was dominated by this theme.

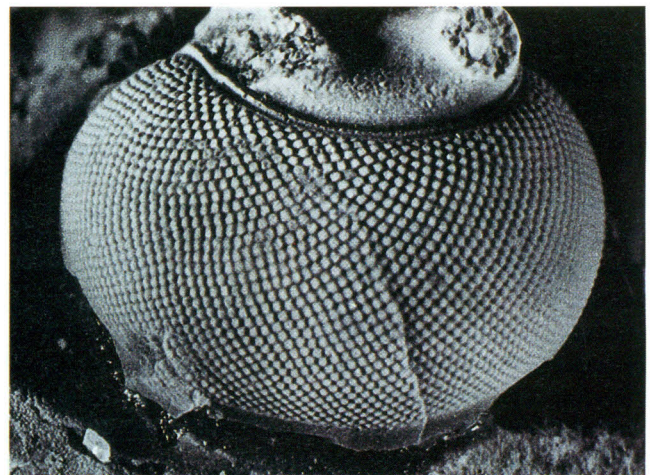


FIGURE 7 Intersecting logarithmic spiral arrangement of the lenses in the holochroal eye of *Scutellum (Paralejurus) campaniferum*. This Devonian trilobite from Bohemia could cover an almost spherical visual field. The horizontal width of the eye is 7.3 mm (reproduced from Levi-Setti, 1993, with permission of the University of Chicago Press).

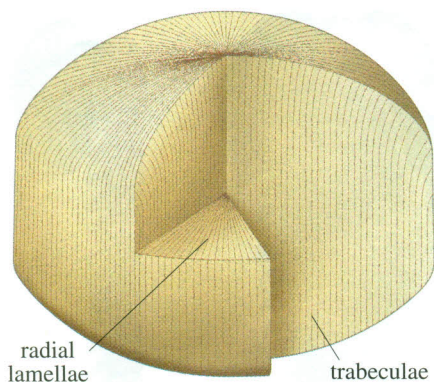


FIGURE 8 Structure of a single lens of the holochroal eye of *Paladin* (see also Fig. 4), reconstructed to show the radial lamellae.

Each lens is a single crystal of calcite, constructed of radial lamellae around its axis; presumably the lens grew by adding new calcite at the outer edge of each lamella (Fig. 8). The crystallographic *c*-axis is oriented along the lens axis, normal to the visual surface, thereby minimizing double refraction. The lenses of thin-shelled trilobites are usually thin and biconvex, but where the shell of the trilobite is thick the lenses form elongated prismatic columns, with semicircular terminations. The crystal nature and crystal orientation of each element is evident in the thin section of Fig. 9, cut across the visual surface of one of the latter forms, in which cleavage planes can be seen crossing the prisms at a constant angle to the axis of each element. Ray

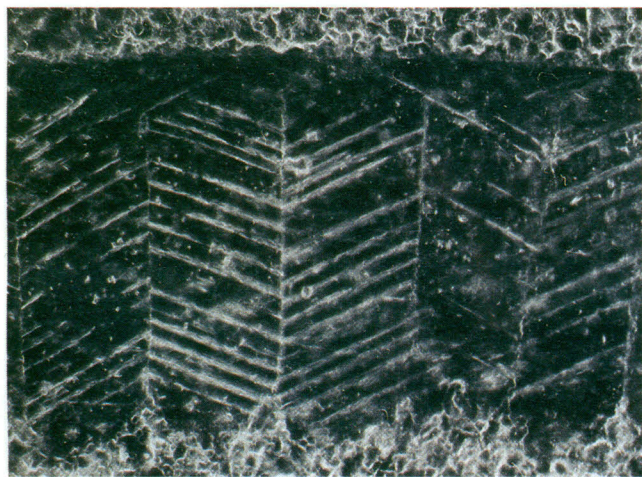


FIGURE 9 Thin section cut through the visual surface of the Ordovician *Asaphus raniceps*. The cleavage planes through each columnar lens elements show that these are made of calcite single crystals, whose *c*-axis coincides with the lens axis. The horizontal length of the section is 291 μm (reproduced from Levi-Setti, 1993, with permission of the University of Chicago Press).

tracing shows that holochroal lenses, whatever their form, focus at about the same relative distance below the lens; what is important optically is the relative convexity of the lens surfaces. Nothing is known of the internal structure of the eyes, but they probably had an ommatidium-like unit below each lens, and functioned like the eyes of crustaceans.

Schizochroal Trilobite Eyes

Only one group of trilobites possesses schizochroal eyes: the suborder Phacopina, which appeared in the Lower Ordovician and became extinct at the end of the Devonian. These eyes are unique: There is nothing quite like them elsewhere in the animal kingdom. They are usually large, with a curving visual surface, and the lenses are remarkably large, strongly biconvex, and separated from each other by cuticle, like that of the rest of the exoskeleton (Fig. 10). The lenses are normally arranged in a regular system of hexagonal close packing, oriented in such a way as to give rise to rectilinear vertical rows, the *dorsoventral files*, and are normally far less numerous than those of holochroal eyes. It is when schizochroal eyes are cut in section that

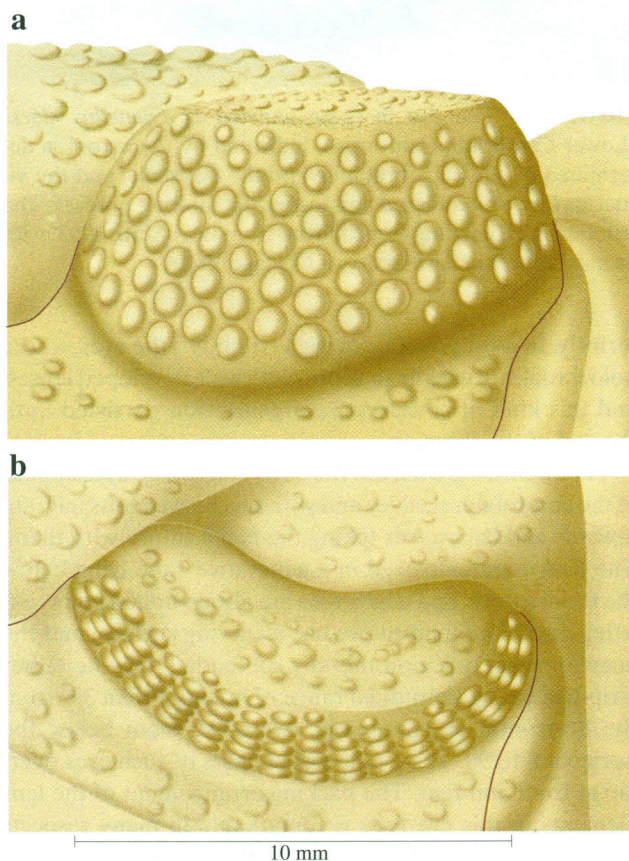


FIGURE 10 Schizochroal eye of *Phacops rana crassituberculata* (Ohio, Devonian): (a) lateral view and (b) dorsal view. The eye of a typical adult individual is about 10 mm wide.

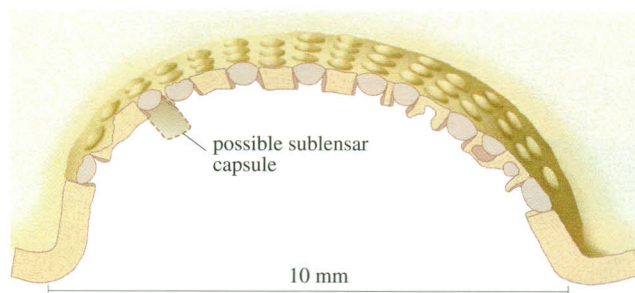


FIGURE 11 Horizontal section through the left eye of *Phacops fecundus* (Bohemia, Devonian) showing partially recrystallized lenses and a possible sublensar capsule. The section is 10 mm long.

their difference from holochroal eyes becomes most evident. Each biconvex lens is set at the outer end of a hollow cylindrical cavity, and its outer surface has a thin calcitic cornea. This plunges down through the cuticle, and in rare instances it can be seen to continue as a tapering cylinder, closed off below (Figs. 11 and 12). The lenses are doublets, constructed of two components, and the function of these is discussed later.

Schizochroal eyes grow by a system of lens emplacement like that of holochroal eyes, made out of intersecting logarithmic spirals (Fig. 13), and the visual surface expands downwards as the eye grows. However, within any one dorsoventral file the lenses are graduated in size, becoming larger toward the base of the eye, and usually to front and rear. If the lenses were all the same size, as is common in holochroal eyes, they would lie in parallel rows, but the downward expansion of the eye will create extra space. It is geometrically impossible to pack uniformly sized lenses in regular sequence on an expanding surface and growth anomalies are likely to result. This is common in holochroal eyes (see Fig. 4), but it is also the case in one of the earliest of all schizochroal-eyed trilobites, the Early Ordovician genus *Ormathops* (Fig. 14), in which areas of loose and irregular packing are evident on an otherwise regular surface, or lenses, set in parallel rows, lie truncated against other blocks. The downward increase in lens spacing in most schizochroal-eyed genera is a simple solution to the lens-packing problem.

As with holochroal eyes, the schizochroal lenses are constructed of thin lamellae, radiating from the *c*-axis. In sections normal to the principal plane, it is evident that each lens is actually a doublet, in which a proximal intralensar bowl interlocks with an upper unit along a wavy surface (Clarkson, 1968). It is also evident, from the orientation of cleavage planes in the upper unit (Fig. 15), that the *c*-axis of the calcite crystal composing the lens was oriented along the lens axis (Clarkson and Levi-Setti, 1975, Levi-Setti, 1993). Although Gustav Lindström (1901), an eminent Swedish pa-

leontologist, described doublet structures nearly 100 years ago, he thought that the structures might have been diagenetic artifacts. Their primary nature, however, has been interpreted (Levi-Setti, 1975, Clarkson and Levi-Setti, 1975) in terms of their function to correct the spherical aberration of thick lenses, and this description (discussed later) has been amply confirmed by other work (Horváth, 1989a, Horváth and Clarkson, 1993). There are at least three patterns of lens construction in the Phacopina, although their function was most likely based on the same optical principles. The lenses of such early phacopids as the Ordovician *Dalminitina* have a seemingly hyperboloidal first surface and the intralensar bowl was rather flattened, with a central dimple. The contemporaneous *Crozonaspis*, on the other hand, had more convex lenses, and here the bowl was thicker, with a wavy upper surface (Fig. 16). In the Middle Devonian *Phacops*, the bowl consists of dense calcite and thins out to be absent proximally (Miller and Clarkson, 1980). However, there also seems to be a dense central core, the function of which is uncertain (Miller and Clarkson, 1980). After molting, the lenses regenerate and it has been possible in *Phacops* to determine how they developed from a series of thin-shelled specimens which died directly or shortly after molting. In the earliest postecdysial stages the cuticle was still flexible, and each lens had the form of a small cone suspended from the center of the cornea. Subsequently, the lens spread to the periphery, thickening and becoming saucer shaped, and ultimately acquiring its characteristic wavy proximal surface. The bowl and core differentiated last of all. Horváth and Clarkson (1993) have shown that the lens was optimized for correction of spherical aberration at all stages of development.

The earliest schizochroal eyes were almost certainly derived pedomorphically from a holochroal-eyed ancestor. In the few holochroal eyes in which the earliest stages are known, the Cambrian *Olenus* and the Carboniferous *Pala-din* (see Fig. 4c), the lenses are relatively large and separated from each other by cuticle; they are, in effect, miniature schizochroal eyes (Clarkson and Zhang, 1991). As the eye develops the interstitial cuticle disappears and the eye becomes holochroal. The retention of this juvenile structure into the adult stage through pedomorphosis would be the first and most important step in the origin of the schizochroal eye. In such early Phacopina as *Ormathops*, the identical lens size was probably retained from a holochroal precursor, but in later phacopids, regularity in packing, presumably important to the proper functioning of the eye, was achieved by a simple increase in lens diameter.

It is generally believed that a relatively short ocellar capsule, rather than an ommatidium, lay below each lens in schizochroal eyes (Fig. 12; Campbell, 1975; Clarkson, 1979). It is tempting to hypothesize that this type of eye may represent an aggregate of simple lens eyes in a transition from the compound to the camera eye. This assumption (Clarkson

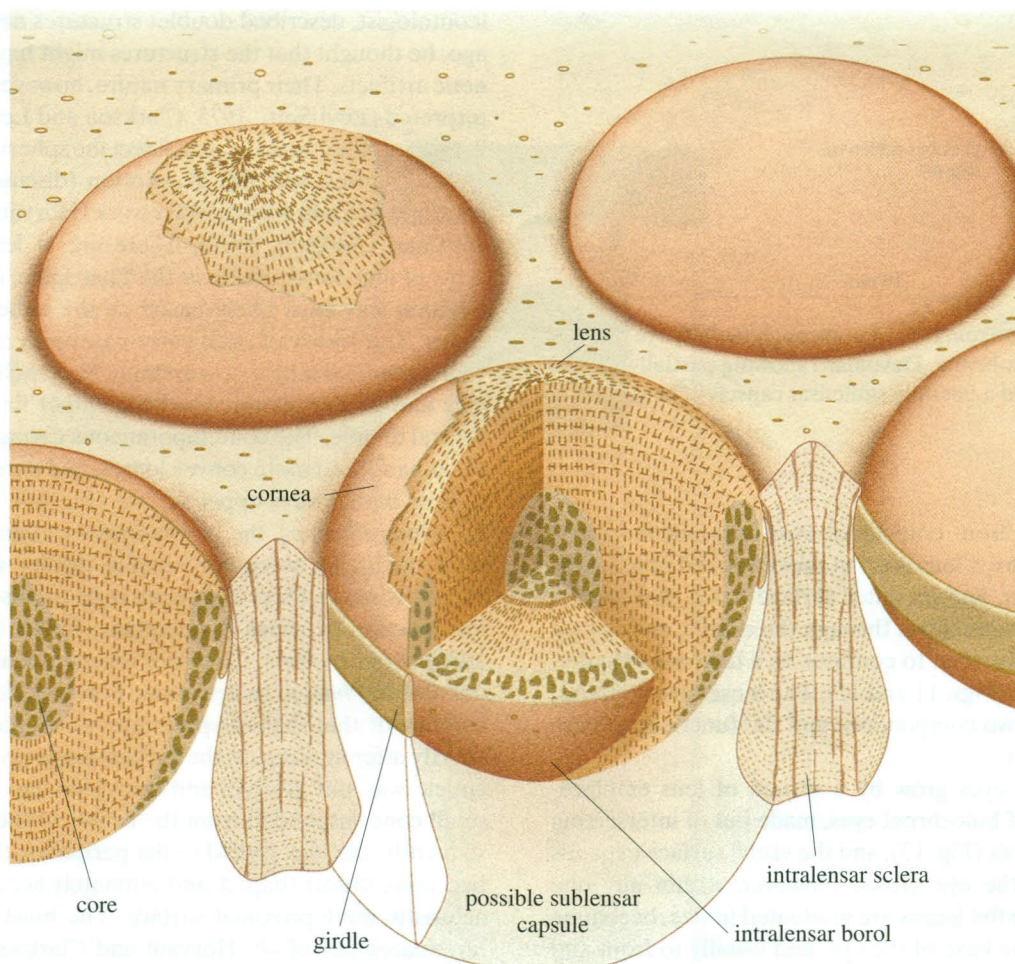


FIGURE 12 Reconstruction of the lens structure of *Phacops rana milleri* (Ohio, Devonian) showing an intralensar bowl and core (ornamented) and radial lamellae.

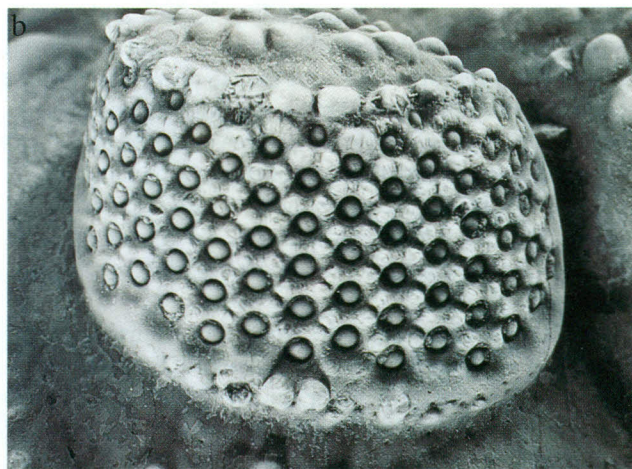
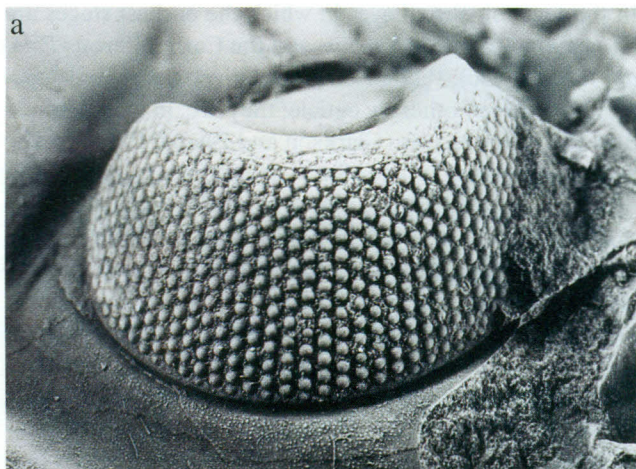


FIGURE 13 (a) Right eye of *Odontochile hausmanni* (Bohemia, Lower Devonian) showing how vertical dorso-ventral files emerge from a pattern of intersecting logarithmic spirals in the schizochroal eye. The eye is 7 mm long. (b) Right eye of the giant *Phacops (Drotops) megalomanicus* (Morocco, Lower Devonian), also showing the same highly ordered lens emplacement, when the lenses are fewer and widely spaced. The eye is 15 mm long (reproduced from Levi-Setti, 1993, with permission of the University of Chicago Press).

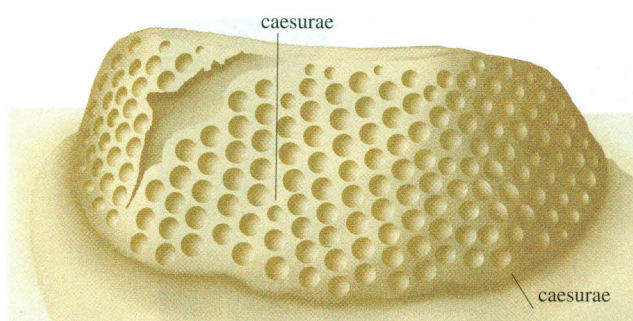


FIGURE 14 Left eye of *Ormathops atavus* (Bohemia, Ordovician): an early schizochroal eye with discontinuities in lens packing (caesurae). The eye is 5 mm long.

and Levi-Setti, 1975; Fordyce and Cronin, 1989) implies that each lens had a tiny retina behind it rather than a single, ommatidium-like photoreceptor composed of a small set of retinula cells, as in the holochroal eye and that of modern arthropods. This can explain the separation and the need for perfect image formation of the schizochroal lenses. In fact, if there had been only a single rhabdom in the sub-lensar capsule, then the spatial resolution would have been very poor due to the rather small number of point elements provided by the well-separated lenses in the schizochroal eye. Such a regressive step would defy the sophisticated optimization of the optical function demonstrated by the doublet structure of the schizochroal lenses, which could only

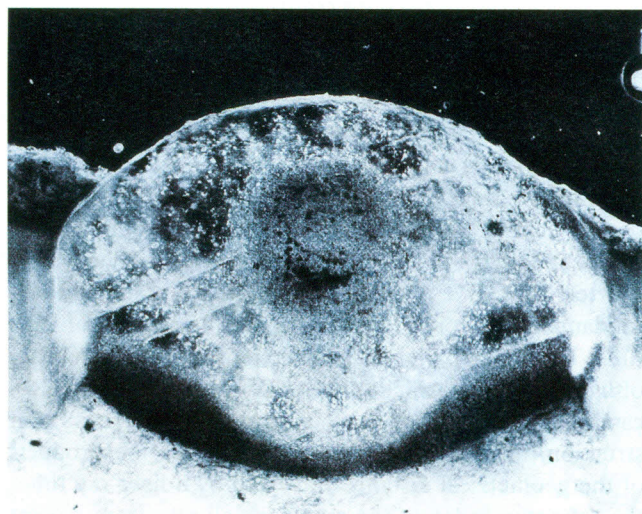


FIGURE 15 Thin section through the equatorial plane of a lens of a Silurian *Dalmanites*, showing a doublet structure with a Huygensian interface. The cleavage planes in the upper unit indicate that the *c*-axis of the single calcite crystal is oriented along the lens axis. The horizontal length of the section is 0.74 mm (reproduced from Clarkson and Levi-Setti, 1975, with permission of *Nature*).

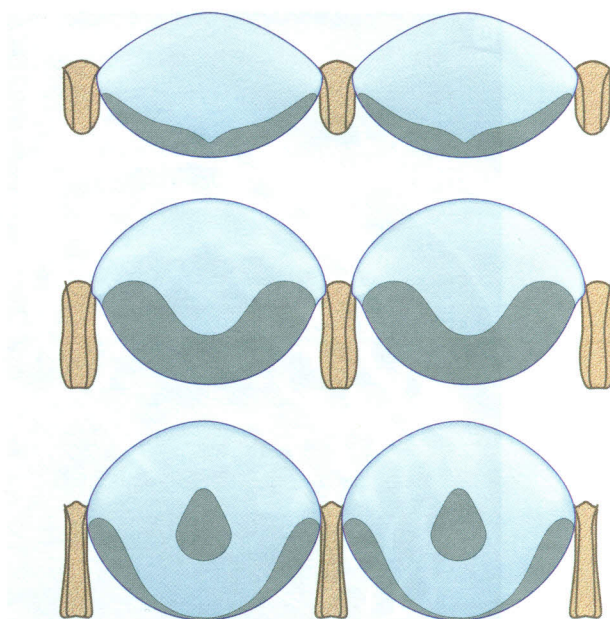


FIGURE 16 Doublet structures observed in the Ordovician *Dalmanitina* (top), *Crozonaspis* (middle), and the Devonian *Phacops* (bottom).

be properly exploited via sampling by a high-resolution retinal array of photoreceptors.

Abathochroal Trilobite Eyes

Some authorities believe that the eyes of the Lower to Middle Cambrian eodiscids constitute a third kind of eye, intermediate between the holochroal and schizochroal types — the abathochroal eye. These eyes, first described by Jell (1975) for the Middle Cambrian *Pagetia* from Australia, superficially resemble small schizochroal eyes. They have a relatively small number (50–70) of separate biconvex lenses, arranged in a semiregular pattern, but there is no thick cuticular material between the lenses and, as Jell suggested, it is possible 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 on whether the abathochroal eye was truly a different kind of visual organ. The Chinese eodiscids *Shizhudiscus* and *Neocobboldia chinlinica* were examined; the former has a normal holochroal eye with the lenses in contact, whereas in the latter the lenses are rounded and separate (Fig. 17). A complete ontogenetic series 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. Zhang and Clarkson (1990) suggested that the abathochroal eye may simply be an eye of schizochroal kind, though less specialized than that of the phacopids. In support of this view was the discovery that the

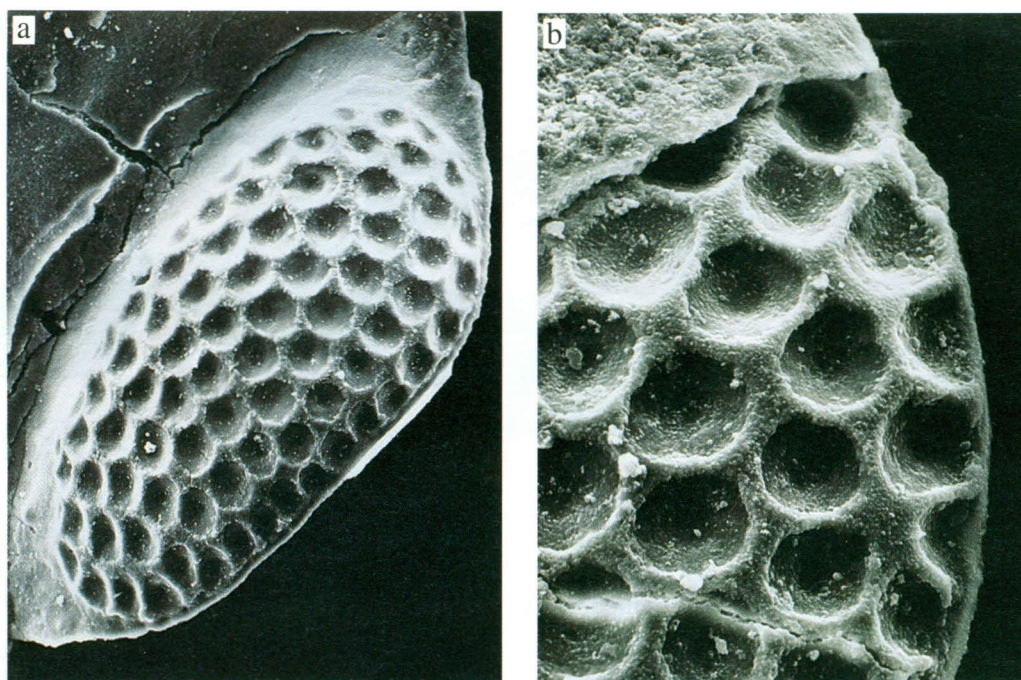


FIGURE 17 (a) Scanning electron microscope image of the abathochroal eye of the Lower Cambrian eodiscid trilobite *Neocobboldia chinlinica*. The missing eye lenses have left an imprint with a central dimple. The eye is 294 μm long. (b) Magnified detail of another eye of the same kind of trilobite. The horizontal width of the image is 100 μm .

lens profile in *Neocobboldia*, although not exhibiting a doublet structure, was provided with an aspherical proximal surface with a central nipple (Fig. 17), quite similar to that of the upper unit in the lenses of the early schizochroal eye of the Ordovician *Dalmanitina*, likewise believed to have risen by neoteny (Clarkson and Levi-Setti, 1975). (Neoteny refers to a reduced rate of development of particular characters — in this case the eye — relative to that of the rest of the individual.) As will be discussed later, a particular optical function may be associated with such lens profile in regards to initial steps in the process of vision optimization.

Vision Optimization in Trilobites Eyes

The Canons of Optics

It was recognized by Levi-Setti (1975) and further elaborated by Clarkson and Levi-Setti (1975) that the profiles of the upper units of the doublet lens structures observed in the schizochroal eyes of several phacopid trilobites bore a striking resemblance to the profiles of aspherical aplatic lenses derived by René Descartes (1637) and Christian Huygens (1690). Such thick lenses, made of glass and operating in air, would convey a bundle of light rays emerging from a point source (the object) to a point focus (a perfect image), satisfying the so-called stigmatic condition for

an optical system. Such system is free of spherical aberration, whereby the image of a point object is not a point anymore but a diffuse distribution of points along the optical axis. Des Cartes derived his construction geometrically by applying the law of refraction that he had discovered (also attributed independently to Snell). Huygens based his construction on the wave optics principle that carries his name, and he stated that the previous requirement (the stigmatic condition) is met when all rays from the point source to the point image, through the lens, traverse their path in equal times (inclusive of the path along the straight line joining object and image points — the shortest path and hence the shortest time). We recognize in the latter a statement of a fundamental canon of optics — Fermat's principle of least time: The actual path between two points taken by a beam of light is the one which is traversed in the least time. Recasting Fermat's principle, when applied to Huygens's construction, in terms of optical path lengths (the products of the geometrical distance traversed by a light ray times the refractive index of the medium), all rays from a point source, traversing whatever sequence of refracting media, will converge to a point image if they traverse minimal and identical optical paths. In the case of an interface separating two media (a diopter) of refracting indices n_1 and n_2 , the previous principle leads to an equation of the form

$$l_1 n_1 + l_2 n_2 = \text{constant},$$

which defines the shape of the interface, one of a family of curves called *Cartesian ovals*. For example, a parallel bundle of rays (point source at infinity) in air will converge to a point in glass when the Cartesian oval convex interface is an ellipsoid of revolution. Similarly, rays from a point source in air will converge to an image point at infinity in glass (a parallel beam) when the Cartesian oval convex interface is an hyperboloid of revolution. If we are dealing with two interfaces as in the case of the thick lenses considered by Descartes and Huygens, one or both interfaces will be Cartesian ovals to satisfy the stigmatic condition. Thus, for example, a doubly hyperboloidal convex lens is a perfect lens. In Huygens's construction, the first refracting surface is spherical, and the exit surface is a Cartesian oval of wavy contour. Figure 18, in a computer-aided reconstruction of Descartes and Huygens "burning glasses," shows how the wavy exit surface changes as the object distance is varied for two profiles of the first surface. In a modern restatement of Fermat's principle in variational form, a range of trajectories deviating slightly from the ideal construction are still allowed without affecting the result. It should be noted that in applying Fermat's principle to calculate the profile of an interface, such interface need not be an abrupt transition between two media of different refractive index. A gradual change in refracting properties will not affect the final result, as in a mirage in which a cushion of air of varying density behaves, for a distant observer, as a mirrored surface.

The Optics of the Schizochroal Lens Doublets

On the basis of the previous discussion of Cartesian or Huygensian optics, it is compelling to view the wavy proximal surfaces of the upper units in the doublet structures of phacopid eye lenses as Cartesian ovals, serving the function of making such a unit a stigmatic, aplanatic lens or, in other words, a lens yielding images free of the blur caused by spherical aberration. Important differences, however, relative to the constructions in Fig. 18 for a glass lens in air are the media involved in the actual trilobite environment: oriented calcite (refractive index $n = 1.66$ along the c -axis) for the upper lens unit, seawater ($n = 1.33$) in front of the lens, body fluid ($n = 1.35$) in back of the doublet, and the presence of the intralensar bowl of unknown refractive index. In our early empirical reconstructions by ray tracing and experimental modeling — a solution of which made the all-doublet assembly aplanatic for the *Crozonaspis* profile for example — the index of the intralensar bowl was determined with a value intermediate between that of the calcite and that of the body fluid. Its function seemed to be primarily that of focusing the more peripheral rays. Although the composition of this unit is unknown, the fact that it is preserved as a fossil suggests that a mineral component was involved, possibly a layered composite of calcite and organic material. A more rigorous fit by Horváth (1989b) to, among others, the *Crozonaspis* profile, by means of a math-

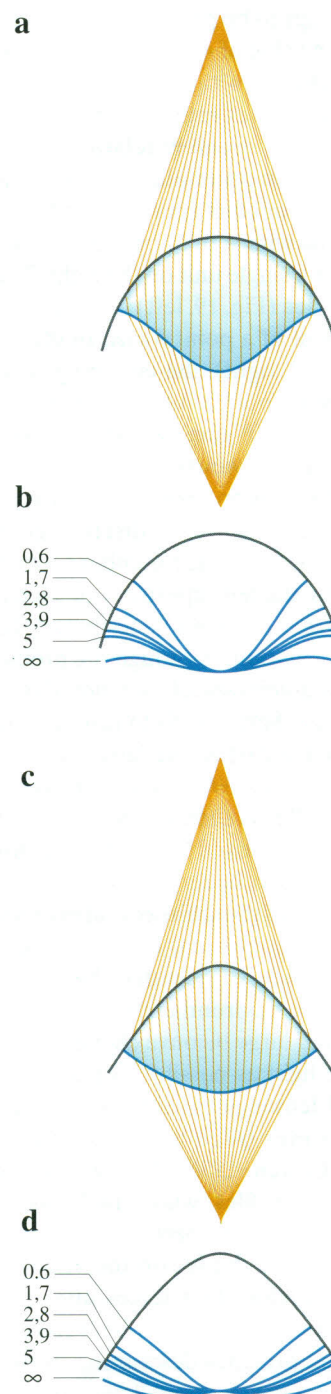


FIGURE 18 Computer-aided ray tracings through aplanatic Huygensian lenses made of glass ($n = 1.5$) in air ($n = 1.0$). (a) Ray tracing for a spherical distal surface and an object distance of 1.7 times the focal length. (b) Changes in the proximal lens profile (also for a spherical distal surface) for object distances of infinity (bottom) and 5, 3.9, 2.8, 1.7, and 0.6 (top) times the focal length. (c and d) As in a and b for a hyperboloidal distal surface.

ematical model apt to be programmed for computer simulations, yielded a value of $n = 1.53$ for the intralensar bowl. Its role was further investigated by Horváth (1996) and it was determined to be effective in enhancing the transmittivity of the doublet assembly relative to that of a singlet Huygensian lens. Computer-aided ray tracings based on the previous index parameters are shown in Fig. 19. Figure 19a shows a split lens with a fully operative doublet structure on the left and as a single unit on the right. The shape of the correcting interface (Fig. 19, left) is determined by the stigmatic requirement of a point focus. In the absence of this correction (Fig. 19, right), the emerging rays intersect the axis over a range of focal points, such as to originate severe spherical aberration. Figure 19b shows how the shape of the interface varies as a function of object position: the lowermost curve indicates an object at infinity, and the uppermost curve indicates an object distance equal to the lens thickness. Remarkable is the f /number (defined as the focal length divided by the lens aperture) of such a lens operating in water, $\sim f/1.1$, comparable to that of the best camera lenses on today's market. Although the profile of the upper lens unit of *Dalmanitina socialis* was noted (Levi-Setti, 1975; Clarkson and Levi-Setti, 1975) to resemble that given in a construction by Descartes, the latter could not be reproduced by Horváth's (1989b) computer ray tracings on the assumption that all rays should converge to a unique focus. This point will be discussed later when we discuss the optical function of the abathochroal eye lenses.

The giant lenses of the schizochroal eye (when compared with those of the holochroal eye), and their exceptional light-gathering power, suggest that their bearers may have lived in a dimly lit environment or were night-active animals and that their large biconvex lenses picked up as much of the available light as possible. Since the outer surfaces of schizochroal lenses are highly convex, adjacent lenses within the same eyes could have been used for stereopsis (Stockton and Cowen, 1976). This would account for the vertical dorsoventral files, whose high angular separation would be useful in this respect, and also for the need for regular packing of the lenses on the visual surface. Trilobites had to redevelop their lenses after each molt since the old lenses remained with the discarded exoskeleton. As mentioned in the previous description of the schizochroal eye, initially the new lens is small and conical; thereafter it spreads to the periphery of the cornea and develops further. The optical function of the lens was already optimized from the early stages of development and would have reached the maximum efficiency possible by using the Huygensian proximal lens surface for correction of spherical aberration, thereby increasing its light collecting efficiency and transfer of contrast. The eye was myopic at the earliest developmental stage but thereafter it could see sharply at a distance of a few millimeters to a few centimeters from the visual surface (Horváth and Clarkson, 1993). After molting and while the cuticle remained flexible, trilobites were not capable of

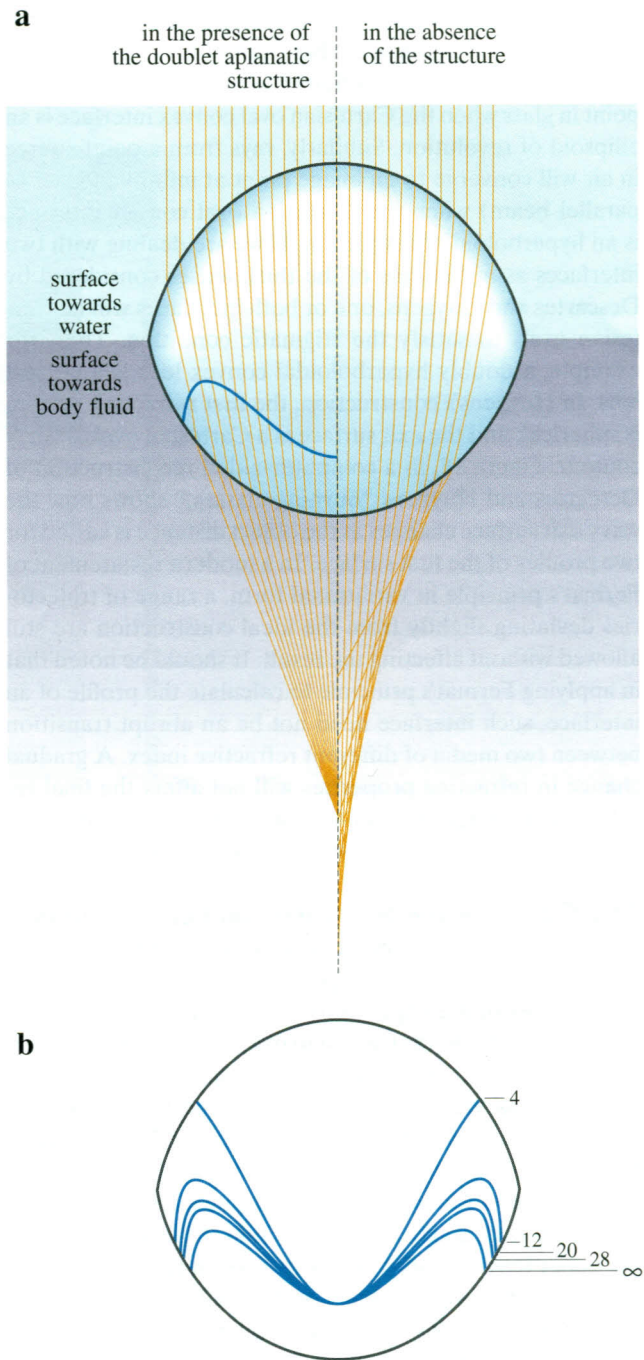


FIGURE 19 Computer-aided ray tracing through a doublet aplanatic structure (left) simulating the structure of the schizochroal biconvex eye lens with the spherical surface in contact with seawater ($n = 1.34$) in front and body fluid ($n = 1.35$) behind. The upper lens unit is made of oriented calcite ($n = 1.66$), and the Huygensian interface is calculated for an intralensar bowl of unidentified mineralized organic material ($n = 1.53$). For comparison, the right half shows what the ray tracing would be without the correcting doublet structure, clearly indicating that the source of spherical aberration is due to the absence of a sharp focal point. (b) Variations in the profile of the Huygensian interface as a function of the object distance, from infinity (bottom) to respectively 28, 20, 12, and 4 times the focal length.

much movement. In this state the animals probably had to hide, as do many newly ecdysed arthropods. For recently molted trilobites, which needed to keep out of sight (perhaps either by partial burial or by nocturnal ecdysis), there was great value in having eyes highly sensitive to light for detection of predators. Perfect image formation as soon as possible after molting was clearly of great importance. Optical maturation in schizochroal eyes differs from that found in the dioptric apparatus in some modern compound eyes. In the eyes of modern arthropods optical maturation is relatively slow, and image quality is poor immediately following ecdysis. As the eye matures, the lenses become more effective. This difference probably relates to the different postecdysial life styles of trilobites and recent arthropods.

The Optics of the Abathochroal Trilobite Eye: Image Formation by Bifocal Lenses

Since the classification of the abathochroal eye remains uncertain, its optical system has been studied in detail with particular reference to the trilobite *N. chinlinica*, whose eye lenses (as noted previously) provide evidence of some kind of corrected optics. A section through the main vertical plane of the lens was reconstructed (Fig. 20a) on the basis of SEM photographs, and the distal (entrance) and proximal (exit) lens profiles were digitized with a scanner. Computer-aided ray tracing for paraxial rays, assuming that the distal surface of the calcite lens was immersed in seawater with an index of refraction of 1.33 while the inside was in contact with cytoplasm with a refractive index of 1.35, is also shown in Fig. 20a. Two regions of convergence are indicated—for rays crossing the peripheral region of the lens and the central bulge of greater refractive power, as can also be appreciated quantitatively from a plot of the focal length as a function of the radial ray distance (Fig. 20b). Hence, the abathochroal lens of *Neocobboldia* is effectively bifocal, with a central region of much smaller focal length than the peripheral annulus, and there is a fairly rapid transition between the two regions. Large spherical aberration affected the most peripheral region of the lens unless a stop of screening pigment below and around the lens was present, as in recent arthropods. The relatively steep rise of the proximal profile and the considerable refractive index difference between the lens (calcite: $n = 1.66$) and the sub-lensar material (probably body fluid: $n = 1.35$) resulted in large internal reflection at the proximal refracting surface, and this reduced the transmissivity and also the light-collecting efficiency of the eye. In view of the similarity of this lens profile with that of the schizochroal lenses of *Dalmaniina*, which did not conform to the Huygensian shape found in other schizochroal lenses, it is tempting to associate a bifocal function to the latter as well. This hypothesis is under investigation. Aside from the issue of classifying the abathochroal eye as a third trilobite eye type, distinct from the holochroal and the schizochroal eye, the abathochroal eye acquires particular evolutionary significance because it

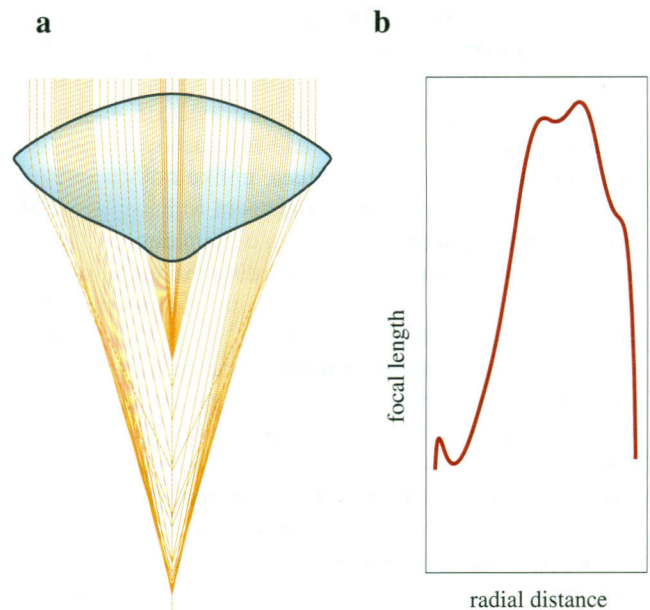


FIGURE 20 (a) The reconstructed shape of the corneal lens of the abathochroal-eyed trilobite *Neocobboldia chinlinica* in a vertical main section with the tracing of paraxially incident rays of light. The density of rays is greater in those two regions of the lens in which the focal length is more or less constant. The diameter of the lens is $30\ \mu\text{m}$. (b) Change of the focal length of the lens as a function of the radial distance of the incident light rays. It can be seen that, apart from the most peripheral zone, the lens is approximately bifocal.

provides evidence of a first step, albeit not optimal, toward the correction of spherical lens aberration (the latter successfully attained in later trilobite stocks).

It is surprising to find such an attempt at optimization of the visual function at the very onset of trilobite evolution and, as for the ideally optimized phacopid doublets, one may speculate as to which selective pressure this may have been a response. From this standpoint, other factors in addition to the correction of spherical aberration may have contributed to optimize vision. For example, the depth of field (the conjugate of the depth of focus), namely, the distance range over which objects can be distinctly discerned with a rigid dioptric–photoreceptor system, acquires particular relevance for the monitoring of the environment and the preservation of life. If indeed the abathochroal eye of *Neocobboldia* was provided with miniature retinas, as envisaged for the schizochroal eye, then bifocality may be viewed as a response to the need for an extended depth of field (bifocality would be valueless if the individual lenses possessed only a single photoreceptor).

Evolution of the Optics of Trilobite Lenses

Large, spherically corrected (aplanatic) doublet lenses appeared relatively late in trilobite evolution (Clarkson, 1975, 1979); only the schizochroal-eyed phacopid trilobites

possessed such doublets. In the ancestral holochroal trilobite eyes, only small calcite singlet lenses were present. This is also true for the abathochroal trilobite eyes, which arose independently and represent an intermediate evolutionary stage between holochroal and schizochroal eyes. The abathochroal eyes of *N. chinlinica*, unlike holochroal and schizochroal eyes, are bifocal and seem to have been corrected for spherical aberration to a certain degree. On the basis of the data accumulated regarding the visual systems of trilobites, we propose the following evolutionary scenario of the optics of trilobite lenses.

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 were not as yet aplanatic. Judging from their dimensions, they might have been diffraction limited, and so there would have been no selective pressure correcting for spherical aberration.

A second evolutionary step was the appearance of the abathochroal eyes, in which larger lenses were present than in those holochroal eyes, probably associated with a dimly lit optical environment. Without any correction the larger abathochroal lenses could have suffered from considerable spherical aberration. The actual shape of the lens ensured some correction for spherical aberration, and the central bulge on the proximal lens profile resulted in bifocality and consequent increased effective depth of field. Internal reflection may have reduced somewhat the light-collecting efficiency of this lens. 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. Judging from their average diameter of about 20–30 μm , abathochroal lenses might have approached the diffraction limit. Nevertheless, there must still have been some selective pressure correcting for spherical aberration and developing the bifocality of the lenses. The latter, newly developed feature, however, may have reappeared in some of the early examples of schizochroal eye.

By and large the most remarkable evolutionary development occurred in the schizochroal eye. Both the ordered structure in the lens packing and the perfected Huygensian profile of the spherically correcting interface in the doublet structure of the phacopid eye lenses suggest a response to selective pressures that may have gone well beyond the mere gathering of the maximum amount of light. Even though the correction of spherical aberration may have reduced the threshold level for light detection due to the increased concentration of light at the sharply defined focal plane, and the presence of the intralensar bowl may have improved the light-gathering power of the lenses by reducing internal reflection, much simpler solutions to maximize

light collection have been developed by other marine arthropods, e.g., the crystalline cones in *Limulus* (Levi-Setti *et al.*, 1975). The most important evolutionary step implicit in the structure of the schizochroal eye may actually reside in the surmised increased complexity of the photoreceptors and neural network apt to take advantage of stereopsis and perfected images of the environment — in other words, the development of a true, albeit primitive, brain. Due to the extinction of the trilobites, the schizochroal eye remains an evolutionary endpoint. However, the canons of optics guided convergent evolution to develop similarly optimized visual systems in other life-forms.

Eye Reduction and Blindness in Trilobites

Compound eyes are primary structures present in most trilobites. They are particularly evident in trilobites that were capable of rolling up in a ball for protection, and presumably they acted as early warning sensors, detecting the approach of predators. Therefore, it may seem strange that independently in many groups of trilobites, the eyes became reduced or absent altogether. In such cases, the loss of the eye is related to the adoption of a dark, deep-sea or infaunal environment, but in some entirely blind groups sense organs of a quite different kind have developed and are the dominant environmental monitor (e.g., in the Ordovician Trinucleidae, in which the broad pitted cephalic fringe was probably a vibrosensory organ).

The clearest examples of progressive eye reduction and eventual blindness are found in Middle and Upper Devonian Proetida (with holochroal eyes) and Phacopida (with schizochroal eyes). There are several distinct lineages in which the facial suture migrates laterally outwards as the eye diminishes in size. They have been best documented in Germany and southern France (Feist and Clarkson, 1989; Feist, 1991), where progressive loss of the eye can be traced through several million years. However, parallel and contemporaneous eye loss is known in Chinese trilobites. Because each successive phase in eye reduction resembles a more juvenile condition of the ancestral form, the process seems to have been under pedomorphic control. The affected trilobites had become adapted to an endobenthic mode of life when the firm shallow seafloors of Silurian and Lower Devonian time were replaced throughout many areas of the world by a soft mud blanket. In this respect, eye reduction and blindness are not so much degenerate as they are adaptive.

Beyond Trilobites: Other Fossil Visual Systems

The Morphology and Dioptrics of the Eyespots of Fossil Ostracodes

As in the trilobites, the extinct ostracodes possessed dioptric apparatuses which in life were composed of calcite so

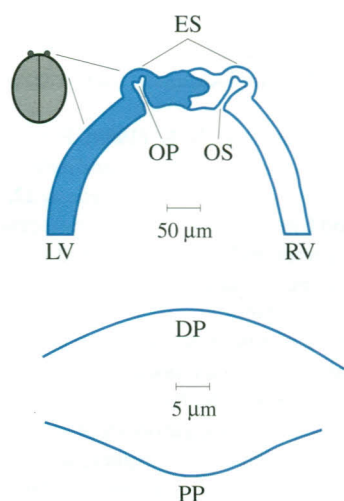


FIGURE 21 (a) Schematic diagram of a section through the ocular region of an ostracode shell in an anterior view with the left valve in blue and the right valve in white (reproduced with permission from Kontrovitz, 1985). LV, left valve; RV, right valve; ES, eyespot; OS, ocular sinus; OP, ocular pit. (b) Profiles in longitudinal section of the calcite lens in the eyespot of the ostracode *Echinocythereis margaritifera* (reproduced with permission from Kontrovitz and Myers, 1984). DP, distal profile; PP, proximal profile.

that fine details of their eyes were preserved. On the other hand, fossil ostracodes have many modern relatives, and their visual system is relatively well-known. Eye tubercles or eyespots are shell structures located in the anterodorsal region of the valves of some fossil and modern oculated ostracodes (Fig. 21a) (Kontrovitz and Myers, 1984). These structures are small, circular or oval, transparent, and outwardly convex areas and have diameters that vary from ≈ 30 to $60\ \mu\text{m}$. The lens in the eyespot consists of clear oriented calcite, even in modern ostracodes, allowing light to enter the eye at the distal tip of the somewhat stalked ocular sinus. The ocular sinus (a passageway for axons) is a channel in the shell, lying between an internal opening called the ocular pit and the distal surface of the eyespot. The distal surface of the lens is convex and approximately spherical. The proximal lens surface is undulating with a central convexity and anterior and posterior concavities (Fig. 21b). This geometry is similar, in a superficial way, to the shape of the upper lens unit in schizochroal-eyed trilobites. According to Kontrovitz and Myers (1984), light is focused by the lens of ostracode eyespots in the underlying eye space. In the fossil ostracode *Echinocythereis jacksonensis*, paraxial light rays are focused at a distance which falls behind the eye cavity, unless rays undergo reflections by the eye's tapetal layer (Kontrovitz and Myers, 1988).

Comparison of the modern ostracode *Echinocythereis margaritifera* and the Oligocene *E. jacksonensis* indicates the same eyespot morphology and presumably similar func-

tioning (Kontrovitz and Myers, 1984). The genus *Echinocythereis* is of particular interest because 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. Benson (1984) indicated a general decrease in eyespot size of fossil ostracodes with increasing water depth and that at depths of 600–900 m the eyespots disappear. Kontrovitz and Myers (1984, 1988) have shown that the eyes of podocopid ostracodes would be of little use below depths of ≈ 300 m in the oceans because of the design of the eye and the low light levels. Modifications to the eyespot–tapetum system could do little to enhance vision below that depth.

Using geometric optical ray tracing, Kontrovitz and Myers (1984) were able to establish that the eyespots of both fossil and modern ostracodes are more or less corrected for spherical aberration by means of the proximal undulating Huygensian profile of the calcite lens, like the aplanatic corneal lens in schizochroal-eyed trilobites. However, it is doubtful that modern and fossil ostracodes 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 high-resolution vision (Kontrovitz and Myers, 1984). On the other hand, the f -number of the lens–mirror system in podocopid ostracodes (similar to that of the eye of *Pecten*, described in the next section) is limited to a range between 0.50 and 0.25, the smallest known for any organism. These animals therefore seem to be well adapted for efficient viewing in dim light (Kontrovitz and Myers, 1988). Thus, the aim of correction for spherical aberration in the ostracode eyespots may be the enhancement of the light-collecting efficiency in a dimly lit optical environment.

Corrected Optics in Modern Invertebrates

Aside from the use of calcite crystal lenses, varying degrees of similarity to the structure of the schizochroal trilobite eyes are found in many modern invertebrates, some of them nonarthropods. These recent animal eyes share at least one of the three typical characteristics—(i) well-separated optical units, (ii) the presence of doublet lenses, and (iii) correction for spherical aberration—with the schizochroal trilobite eyes. The most convincingly similar modern structure that compares with the special external feature of schizochroal trilobite eye is the stemmata compound eye of adult male *Strepsiptera*, a blackberry-shaped faceted eye with well-separated ommatidia (Strohm, 1910; Roesch, 1913).

Some recent eyes possess doublet lenses which are aplanatic like the lenses in schizochroal-eyed trilobites. One of these modern visual systems is the compound eye of the water bug backswimmer *Notonecta* (Schwind, 1980). Both lens units in every ommatidium are optically homogeneous with different refractive indices. Between the two lens units

there is a thin bell-shaped transition layer which reduces the spherical aberration of the lens in air and in water (Horváth, 1989b). The larvae of the sawfly *Perga* have only one pair of stemmata possessing a biconvex circular lens. The lens consists of two optically homogeneous layers of different refractive indices. Below the lens there is an extensive retina (Meyer-Rochow, 1974). It has been found by means of geometric optical ray tracing that the stemmata is corrected for spherical aberration.

The scallop *Pecten* has approximately 60 well-separated pallial eyes; their diameter is approximately 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. The spherical argentea lines the whole of the back of the eye. The rear surface of the homogeneous lens is spherical, and the front face is bell shaped. This wavy front profile of the lens corrects for spherical aberration in a similar manner to that of the corrector plate in the Schmidt astronomical telescope (Horváth and Varju, 1993). The retina occupies the space between the lens and the argentea. It consists of two main layers of photoreceptors (Land, 1966). The image is formed on the distal retina, which is involved in movement perception. The proximal retina, in which no image is formed, monitors the level of illumination.

Acknowledgments

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