

THE VISUAL SYSTEM OF TRILOBITES

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ABSTRACT. The compound eyes of trilobites are the oldest of all known visual systems and their evolution can be traced over 350 million years. Only the lentiferous surface is preserved, however, since the lenses alone are calcitic.

Holochroal eyes have many lenses closely packed together. From a study of their evolution, the morphology and optics of their lenses, various systems of lens packing, and the relationships between lens-thickness and that of the cuticle, it is possible to disentangle those features of the lentiferous surface which result purely from geometrical growth constraints from those which may have been of physiological significance. Holochroal eyes probably functioned in a manner analogous to that of many modern insect and crustacean eyes.

Schizochroal eyes, unique to the animal kingdom, have large separated lenses. They probably were derived by paedomorphosis from a holochroal precursor. The complex internal structures of these lenses has been investigated using optical and scanning electron microscopy, as well as cathodoluminescence, which has enabled primary to be distinguished from secondary structures.

Each lens, like those of holochroal eyes, when sectioned parallel with its principal plane shows calcite fibres arranged in lamellae radiating from the central axis. Sections cut along the axis, however, show first how the lower part of the lens contains an intralensar bowl of different texture to the rest of the lens, and secondly that the radial lamellae are constructed of calcite fibres (trabeculae) diverging fanwise from the axis in the upper part of the lens, to abut the upper convex surface near normally.

The complex internal structure of the schizochroal lens seems both to minimize birefringence, and to correct for spherical aberration. Such high-quality lenses must have been linked to a photoreceptive system capable of making use of their sharp images; in this and other contexts various theories of optical function in schizochroal eyes are discussed and analysed.

TRILOBITES are amongst the most ancient of all Phanerozoic marine invertebrates, but from their first appearance in the fossil record, they come equipped with remarkably elaborate sensory organs. The relics of these can be seen in the sensillar pits, terraces, pore canals, and tubercles which may cover the cuticle (Miller 1976), and most prominently in the paired compound eyes. These are the oldest of known sensors and this alone would seem to render them a viable subject for study, but if thereby the biological quality of the animals that bore them is illuminated, then their interest is all the greater.

Compound eyes are typically arthropodan, but since the arthropods are probably polyphyletic (Manton 1977), different kinds of compound eyes may have arisen in more than one evolving stock. Thus it is hard to know what kind of functional equivalence might be expected in fossilized eyes where only the outer lentiferous surfaces are preserved, the soft parts having gone with little trace. The eyes of trilobites are not the only fossilized compound eyes; they are found in ancient merostomes as well in their modern relative *Limulus* (Eldredge 1974), in eurypterids (Clarke and Ruedemann 1912; Wills 1965), and even in a Pennsylvanian centipede (Levi-Setti, pers. comm.). In trilobites, however, the record is so much more complete that their evolution can be studied through time, and this to some extent compensates for the absence of internal parts.

Since the nearest modern analogues to trilobite eyes, in the rather broad and general sense given by external appearance, are to be found in the eyes of insects and crustaceans, it is appropriate first to discuss the morphology and function of these, and then to consider what degree of similarity may be found in the eyes of trilobites.

THE COMPOUND EYES OF INSECTS AND CRUSTACEANS

In all modern arthropods possessing compound eyes the over-all structure of the optical system is relatively constant. Even though compound eyes may have arisen several times independently in different arthropod stocks they are all remarkably similar, in that the eyes are constructed of numerous identical units, the ommatidia, which are usually radially arranged so as to cover a fair angular field of vision (text-fig. 1*a, b*).

In each ommatidium there are three main functional regions:

(*a*) The dioptric structures, which comprise the corneal lens (a thickened part of the cuticle) and the crystalline cone below. Light passing through these transparent modules on its way to the underlying photoreception is refracted to focus on the distal end of the photoreceptive (reticular) cells which lay just below. The preservable lenses of trilobite eyes evidently formed part or all of an analogous dioptric system and are the only part of the eye now available for study.

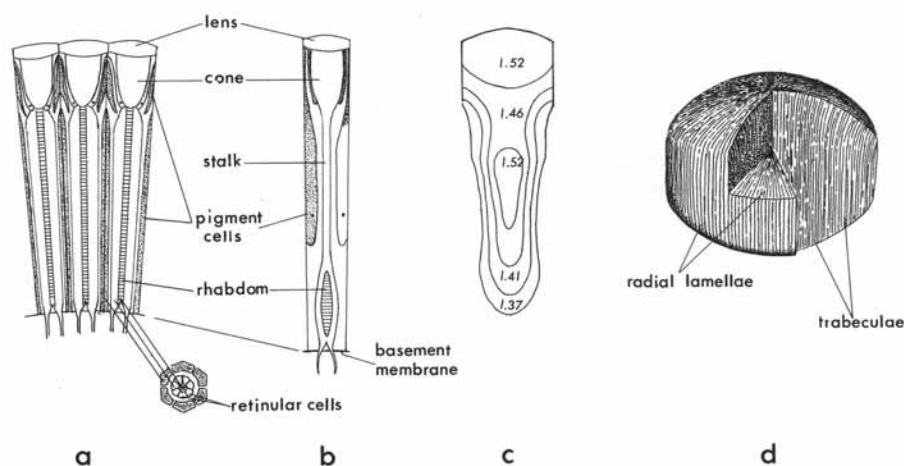
(*b*) The photoreceptive part of the ommatidium (retinula), composed of a number (usually seven or eight) of elongated reticular cells. The inward facing parts of these cells (rhabdomeres) may or may not be in direct contact, and form a closed or open cylinder, the rhabdom. These are made up of blocks of stacked microtubules, alternating along the length of the rhabdom, and containing visual pigments. When light strikes the rhabdom, the pigments are bleached by light and so trigger off nervous impulses in the optic nerves which connect the photoreceptors to the optic ganglia below.

(*c*) Pigment cells, which form an enclosing sheath normally isolating each ommatidium.

There are two main kinds of ommatidium, generally found in the eyes of diurnal and nocturnal or crepuscular arthropods respectively. The eyes bearing these two types were termed apposition and superposition eyes by Exner (1891). In apposition (daylight) eyes (text-fig. 1*a*) the rhabdom extends between the base of the crystalline cone and the basement membrane, whilst in superposition eyes (text-fig. 1*b*) it forms only a short spindle located at the base of the ommatidium and connected to the crystalline cone by a cone stalk. In superposition eyes (adapted to dark conditions) the pigment shrinks away from the cone stalk region, sometimes both proximally and distally, to aggregate round the crystalline cone and down near the basement membrane. The ommatidia are thus no longer isolated. This allows greater over-all sensitivity to dim illumination, for light striking the eye obliquely can then reach the rhabdom from all angles and not just down the axis of the eye. Resolution, however, is naturally diminished. When light-adapted, the pigment encloses the cone stalk entirely, forming a continuous cylinder so that the rhabdom is shielded from oblique rays, and as in apposition eyes only light travelling parallel with the ommatidial axis can impinge on the rhabdom.

In spite of intensive research on compound eye physiology over the last 80 years, there is still no clear agreement on how the various parts of the compound eye give an over-all visual sense (Goldsmith and Bernard 1974). Most students, however, accept some sort of 'mosaic-vision' theory, as first put forward by Müller (1829), and elaborated by Exner (1891). According to this theory each ommatidium, when light-adapted, should be sensitive only to light coming down the axis or at only a small angle to it, since the pigment sheath absorbs the oblique light. Relatively little overlap should therefore be expected between the visual fields of neighbouring ommatidia, and the over-all 'image' formed at the retinular level would be a mosaic pattern of individual bright dots like a silk-screen photograph. The coarseness of this mosaic would depend on the number and size of the lenses and the angular separation of the ommatidia. The dioptric apparatus of each ommatidium focuses light on the tip of the rhabdom, and a 'blur-circle' rather than a sharp point of light is formed because of diffraction at each small lens. The sensitivity of ommatidia to incident light has been shown to be greatest along the optic axis, dropping off sharply as the angle of light to the axis increases.

Whilst the incident light always seems to focus on the distal tip of the rhabdom, and the rhabdomere ends are contained within the focal plane, the rhabdom itself acts as a wave guide, and the incident light is conducted down to its base. Besides this, however, an inverted image is formed in the rhabdom itself at a fixed distance below the lens, and further diffraction images may occur at lower levels. Whether any of these images are actually used by visual system or whether they are merely inevitable, but unnecessary by-products of the optical system is still debatable.



TEXT-FIG. 1. (a) structure of apposition-type ommatidium in a longitudinal section and (below) in transverse section, as compared with; (b) superposition-type ommatidium; (c) variation in refractive index within the lens and cone of the firefly *Phausis* (redrawn from Seitz 1969); (d) reconstruction of a single lens of a holochroal-eyed trilobite, based on *Paladin eichwaldi shunnerensis* (King).

In insect and crustacean eyes a very sharp focal point is sometimes assured by variation in the refractive index of the crystalline cone (text-fig. 1c). As within the spherical lenses of fish eyes (Locket 1977) gradation in refractive index allows light to come to a perfect focus, and a very clear image results. Elegant maps of several such dioptric systems in insect eyes have been prepared, e.g. the optical system of the firefly *Phausis* described by Seitz (1969). Not all insects have dioptric apparatus of this kind, however; in the eyes of some fireflies refractive index is constant throughout the cone.

In all compound eyes the size of the lenses seems to be a compromise between two conflicting requirements. High sensitivity to light ideally needs a large lens, whilst high resolution needs large numbers of small lenses in order to pick out fine detail by making the mosaic finer. How large the lenses are in any given arthropod seems to be related to the actual use of its eyes, and to the environment it inhabits. The upper size limit of an ommatidial lens, according to Horridge (1977 *a, b*), should theoretically be no more than 30 μm , but in some insects and crustaceans there are areas with much larger lenses; up to 80 or even 120 μm , concentrated in special foveal areas in which the angular separation of the ommatidia is very low. In these foveas, high resolution and high sensitivity are combined. These are the areas of most intense and acute vision. Horridge has mapped these in several insects and has measured variation in angular separation ($\Delta\Phi$), and in diameter of the lenses (D) across their eyes. Eyes with a large eye parameter ($D\Delta\Phi$), i.e. large lenses with a wide angular separation, are generally adapted for night or deep-sea vision, whilst those with very many small lenses, of low angular separation (i.e. with a low $D\Delta\Phi$, approaching the theoretical limits set by diffraction), occur in insects living in bright sunlight. The eye parameter may vary horizontally across the eye. Horridge associates the latter phenomenon with the fact that in flying insects objects at the side have greater angular velocity than those at the front, and the size gradation and separation seems to relate to this.

The mosaic theory, in the light of much experimental evidence, is a useful model or first approximation to understanding the function of the compound eye, but no more, and whilst many problems have been illuminated there are many others which for the moment seem intractable.

Some of this information of the function of compound eyes may be useful in interpreting the mode of operation of trilobite eyes; indeed, the above discussion has been largely confined to those aspects of its operation which can be understood from the dioptric system alone.

In order to form a reasonably clear picture of the visual system in trilobites the following properties should be established:

The morphology, fine structure, and mineralogy of as many different trilobite eyes as possible, based on well-preserved material. In particular the various kinds of eyes must be defined, and primary structures within them must be distinguished from secondary diagenetic effects.

The evolution and diversification of the various kinds of eye through geological time, with documentation of any main evolutionary trends.

The time and mode of origin of new eye types.

The form, growth patterns, and geometry of the lentiferous surface, especially the size, manner of packing, and spacing of the lenses.

The optics of the lenses, functioning both individually and collectively as a complete or partial dioptric system.

The angular range of vision of the eye, and if possible the angular bearings of individual lens-axes within the visual field.

Any striking comparisons or contrasts between trilobite eyes and those of modern arthropods.

HOLOCHROAL TRILOBITE EYES

Holochroal eyes are by far the commonest type and occur in trilobites of all ages from Cambrian to Permian. They possess many lenses of relatively small size (30–100 μm , rarely larger), closely packed together and in contact. The lenses are covered by a thin common cornea which is no more than an extension of the outer layer of the cuticle.

Little is known of the early history of holochroal eyes, and indeed our knowledge of these for the first 60 million years of trilobite history is very scanty and is based solely upon a few meraspids of Lower Cambrian age. Adult Lower and Middle Cambrian trilobites rarely have the visual surface preserved, for an ocular suture was emplaced below the visual surface in the early adult stage of development, so that the lentiferous surface was not attached to the librigena and fell out after death. In the later Upper Cambrian, however, the ocular suture became obsolete in certain groups, and in the Ordovician most trilobites retained the visual surface for it was welded to the librigena. Only in a few groups, such as the Calymenina, was the ocular suture retained. Its obsolescence and the consequent retention of the visual surface is probably a paedomorphic phenomenon, at least in the olenids (Clarkson 1973 *b*), and probably in other trilobites too.

From the early Ordovician to the late Permian the record of holochroal trilobite eyes and their associated sensory zones is good, and details of structure are known in olenids, *Asaphus*, scutelluids, some illaenids, and proetids and cyclopygids (Lindström 1901; Clarkson 1975). In some respects there is quite a considerable range of variation in characters such as, for instance, lens size, form, thickness, and number, and in the size and shape of the visual surface and the angular range subtended by the lens array. In other respects, however, the holochroal eye was a very conservative organ, in which growth of the visual surface as an anteriorly expanding logarithmic spiral and the emplacement of lenses in a generative zone along the lower rim of the eye almost always seems to have taken place in the same general way. Indeed it seems fairly clear that throughout the 350 million year history of the eye in trilobites there were only three main controls: changes in proportion, size, and surface curvature of the visual surface due to differential relative growth; paedomorphosis; and the incorporation of cuticular sensillae into discrete sensory zones marginal to the eye.

There is now a useful body of information on the structure and evolution of the eye in trilobites, but there are acute problems in trying to interpret this functionally in terms of modern compound eyes since the soft parts have all gone. There remains the possibility, however, of disentangling those morphological characters which result purely from geometrical constraints during growth, from those which may have been physiologically significant. Certain characters seem to be especially amenable to

analysis in this way, and of these the form of the visual surface, the geometry of growth and lens packing, and the form, geometrical optics, and internal structure of the lenses are here selected for further discussion.

The visual surface

Lens-packing systems. The genetic programmes which governed the growth of many Palaeozoic organisms were relatively simple, as witness, for instance, the independent occurrence of dichotomous branching in pteridophytes, graptolites (especially as seen in anisograptids), and in crinoids. A very straightforward generative instruction suffices for this: i.e. bifurcate when the branch has reached length X. Length X may remain constant for successive zones of growth, but usually decreases by an arithmetic or logarithmic factor. Similarly uncomplicated genetic instructions sufficed to generate the lentiferous surface of most trilobite eyes, and it is possible to work these out from the morphology of the eye alone.

It has been established (Beckmann 1951; Clarkson 1971, 1975) that almost all trilobite eyes, holochroal or schizochroal, begin their growth as a thin strip of exoskeletal material (the generative zone) just below the palpebral suture, which is in this case a logarithmic spiral. The lenses are produced from the generative zone which moves downwards as the eye enlarges, always forming the base of the visual surface and adding new lenses at each ecdysis until the eye is fully grown. Thus the new lenses are tacked on to the ends of dorso-ventral files which form as a result of this mode of growth. These files form characteristic patterns, sometimes confined to certain taxonomic groups only; a number of these have been illustrated elsewhere (Clarkson 1975).

In all cases the size of the lenses is controlled by the spacing of the lens centres, which may remain constant or may alter as the visual surface grows. The new lenses can only grow as far as the proximity of neighbouring lenses will permit, and then their growth is arrested. Thus, for example, the spacing of the lens centres in most scutellid eyes decreases by a constant logarithmic factor as the eye grows, and if the locations of the individual points in the generative zone from which the lenses are budded off shift laterally during growth, then the eye will come to have large lenses at the top and small ones towards the base, arranged in curving diagonal dorso-ventral files (Clarkson 1975, fig. 5κ, pl. 1, figs. 1-10).

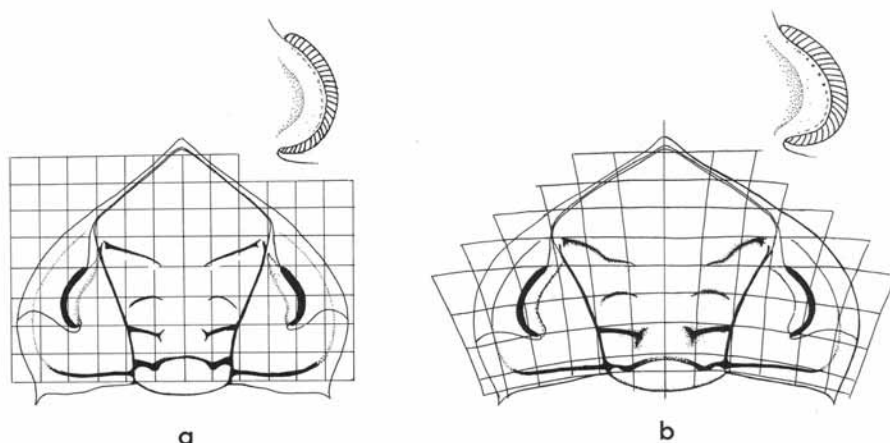
The important point here is that whilst the change in lens size of the visual surface may have been useful to the trilobite, it results from nothing more than an answer (one of many viable ones), to the problem of packing lenses regularly from a single marginal generative zone, on to a curving surface. Whilst the fact that the lenses were larger in one region of the visual surface was primarily controlled by geometric necessity alone, some interest attaches to whether trilobites actually did find this useful, and indeed they may well have done so.

In many modern arthropods variation in the size of the lenses is not uncommon, and may be more pronounced than in trilobites, reaching an extreme form in the remarkable bilobed eyes of euphausiids (Chun 1896; Kampa 1965). As mentioned before, some insects have different parts of the eye specialized for particular functions, especially where differential surface curvature and change in facet size allows certain parts of the visual field to be covered by a 'fovea', where relatively large lenses with

very small interommatidial angles between them provide high resolution as well as good capacity for light gathering.

The examples I have found in trilobites which might suggest a similar function are somewhat equivocal. As an example, the eyes of *Pseudogygites*, aff. *latimarginatus* (Pl. 1, fig. 6) have large biconvex lenses occupying the upper part of the eye and covering the latitudes between about 45° and 90° above the equator. Below these upper lenses are smaller ones, decreasing regularly in size downwards, but with small, laterally directed axial angles. Whilst it is clear enough that this growth pattern, like the ones previously described, is a geometrical phenomenon, the possible value of this to the trilobite cannot be established, for the level of functional differentiation in terms of pronounced bilobation as found in the eyes of mantis shrimps by Horridge, and in some euphausiids by Chun, is never approached by trilobites.

The curvature of the visual surface, and the extent of the visual field. It might be expected that the angular range subtended by the eye would of necessity be adaptive, and indeed this may often be so. Nevertheless, even this frequently seems to be related to the over-all form of the trilobite as much as to any specific adaptation. Thus independently in cheirurids and scutelluids highly vaulted genera such as *Crotalocephalus* and *Paralejurus* have laterally directed eyes with a latitudinal visual range of only some 30° or so, whilst their more flattened close relatives *Cheirurus* and *Scutellum* have panoramic eyes with a range of more than 90° of latitude. Whilst this might just be the result of a purely fortuitous convergence, there can be little doubt that in two closely related species of the French Ordovician phacopid genus *Crozonaspis*, the actual form of the schizochroal eye, and hence its visual range, is directly controlled by the form of the cephalon. Simple Cartesian transformations (text-fig. 2), using the celebrated methods of D'Arcy Thompson (1961), make this abundantly clear.



TEXT-FIG. 2. Cephalon of (a) *Crozonaspis kerfornei* Clarkson and Henry, 1970; and (b) *Crozonaspis struvei* Henry, 1968; closely related Phacopina from the Ordovician of Brittany, plotted on Cartesian transformation grids showing that the different shapes of the eye are a function of relative growth alone.

The difference in the visual field of the two species is adaptive only in the sense that the morphology of the whole animal is adaptive, and for the moment one cannot go beyond this.

Lens structure and function

Radial structure of holochroal lenses. Lindström (1901) figured a number of thin sections of holochroal eyes with their lenses ground parallel with their principal planes. In many of these there seems to be a pronounced radial symmetry (as shown by *Dysplanus centrotus* Dalman (ibid.), p. 55, pl. III, figs. 53–54; *Iliaenus chiron* Holm, p. 58, pl. IV, figs. 22–23; and *Symphysurus palpebrosus* Dalman, p. 62, pl. IV, figs. 16–17, though in the latter case the radial structure is largely obscured by diagenesis).

The presence of a radial pattern within the lenses has been amply confirmed by etching the surfaces of various well-preserved holochroal eyes with EDTA. *Paladin eichwaldi shunnerensis* (King) is a magnificently preserved Namurian trilobite found in the North of England (Osmólska 1970), whose eyes have already been studied in some detail (Clarkson 1969b, 1975). Etched specimens (pl. 1, figs. 1–5; text-fig. 1d), show that each lens consists of thin lamellae, radially arranged around the *c*-axis, and probably originally contiguous. The radial structure is less pronounced in the central part of the lens, where it is interrupted by concentric rings. This central part seems as a whole to etch more rapidly, perhaps suggestive of a slightly different mineralogy and hence refractive index.

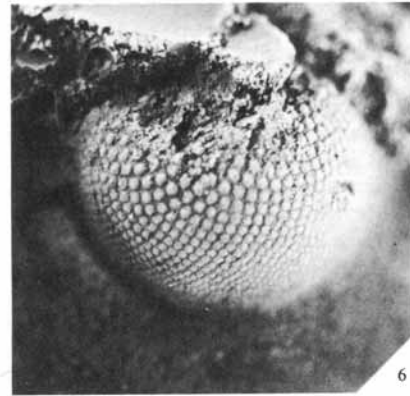
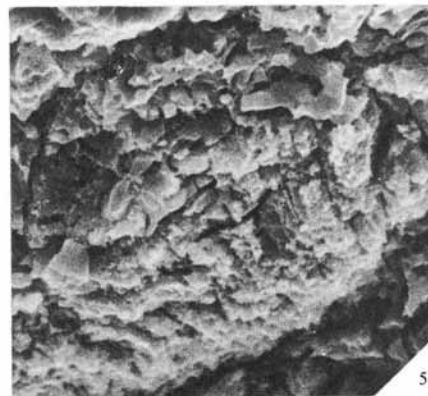
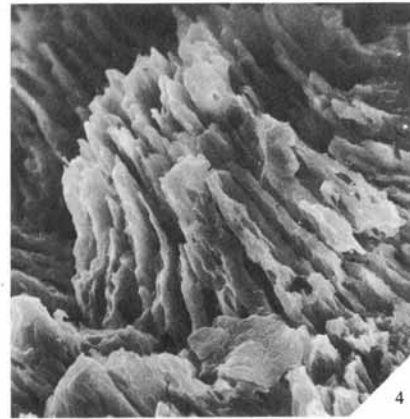
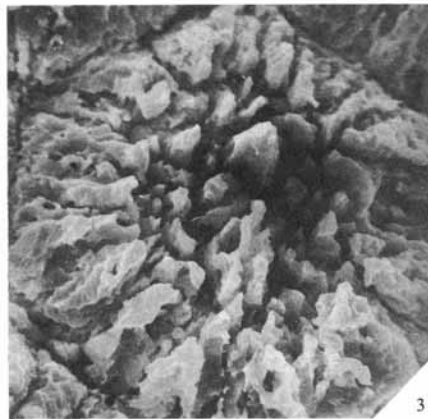
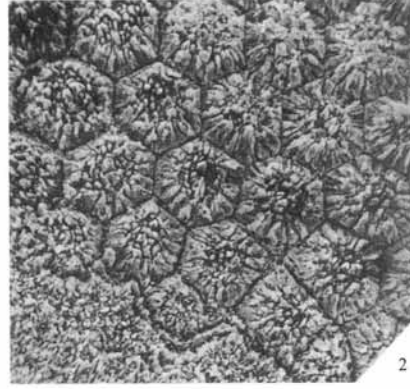
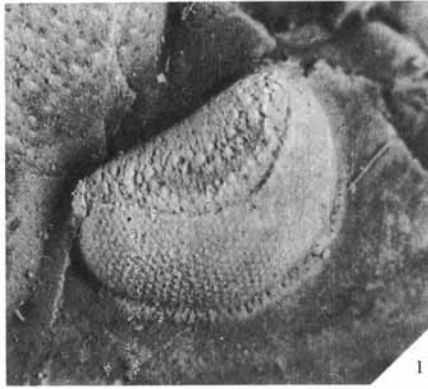
Etched sections normal to the principal plane show that the radial lamellae themselves consist of slender calcite fibres here termed trabeculae, which turn outwards in a fan-like manner so that their distal terminations lie near normal to the convex outer surface of the lens. This is only found in eyes with convex lenses; in *Asaphus raniceps*, which has prismatic lenses with a flat outer surface, though the lenses are made of radial lamellae, the trabeculae of which they consist do not turn outwards distally. Presumably the outward torsion of the trabeculae in convex lenses is associated with the minimization of birefringence for oblique incident light rays, which would thus be conducted down the curving *c*-axis of each trabecula without being doubly refracted. Although the radial-lamellar and trabecular construction is made visible by the etching process, it is also thereby modified. The actual structures which are illustrated are thus to some extent artefacts, and it is not possible to tell whether the trabeculae and lamellae were originally in contact. Despite the

EXPLANATION OF PLATE I

Structure of holochroal eyes.

Figs. 1–5. *Paladin eichwaldi shunnerensis* (King), Namurian E2, Shunner Fell Limestone, near summit of Great Shunner Fell, North Yorkshire, England. 1, left eye of holotype SM E 10497, $\times 14$. 2, lower part of visual surface of Gr I 45,668, etched with EDTA to show radial structure of the lenses, $\times 200$. 3, the same, a single lens enlarged, $\times 100$. 4, oblique lateral view of deeply etched lens, showing radial lamellae, $\times 1000$. 5, polished and etched surface, ground nearly parallel with the lens axis, showing curving trabeculae on the right-hand side. Gr I 45,669, $\times 800$ approx.

Fig. 6. *Pseudogygites* aff. *latimarginatus* (Hull). Ashgill, Allen Bay, Devon Island, Canada. Right eye on detached librigena, GSC C-22858, $\times 45$.



CLARKSON, trilobite eyes

complex internal structure of the lenses each still consists of a single crystal of calcite and like the stereom of echinoderms, the whole lens has crystallographic unity. It is hard to assess the functional significance of this kind of internal organization. It may be no more than a growth phenomenon, the addition of trabeculae at the ends of radial lamellae being simply an easy way to grow a calcitic lens. Whether this is so or not, the system has been found useful, for without it it might have been more difficult to eliminate or minimize birefringence in this remarkable fashion.

The radial-lamellar and trabecular structure in schizochroal lenses is virtually identical with that in holochroal eyes, indeed it was first noted in the schizochroal eyes of *Phacops rana milleri* (text-fig. 4). The only real difference in the detailed structure of the lenses is that schizochroal lenses have intralensar bowls whilst, to the best of our knowledge, bowls are absent in holochroal lenses. But this correspondence in fine structure suggests a basic unity, and provides a link between two otherwise very dissimilar-looking kinds of eye. The schizochroal eye was certainly derived from a holochroal precursor, probably by paedomorphosis (p. 17), and in the process retained this fundamental radial plan.

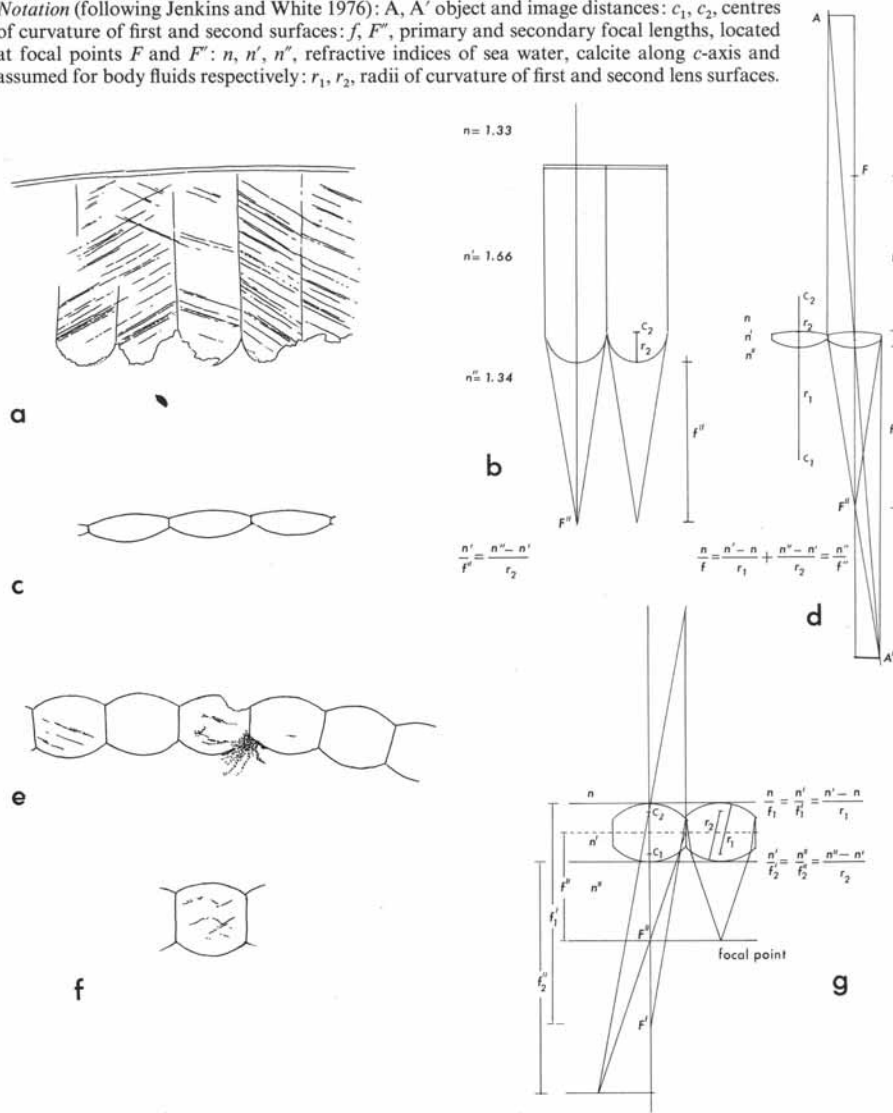
Geometrical optics of the lenses. In holochroal-eyed trilobites the thickness of the lenses is widely variable. As Lindström (1901) first showed some trilobites have very thin biconvex lenses. Those Cambrian trilobites which have been studied in detail (e.g. the olenids), all have lenses of this kind, but they are found also in the Ordovician *Pseudogygites* aff. *latimarginatus* and others. Scutelluids and proetids tend to have lenses of intermediate type whilst many other kinds of trilobite possess very elongated and prismatic lenses; of these *A. raniceps* is well known (Clarkson 1973a). Are there any significant functional reasons for this diversity? Certain lines of evidence suggest that this too may be a matter of geometric rather than physiological necessity. Firstly, in the examples mentioned above and in most others there is a general correlation between the thickness of the lenses and that of the cuticle. Where the cuticle is thin the associated lenses are thin, whilst prismatic lenses are associated with a thick cuticle. In general, lens thickness is about two-thirds that of the cuticle, whatever the form of the lens or prism.

Secondly, the surfaces of these various kinds of lenses are so shaped as to bring incident light to a focus at approximately the same relative distance below the proximal surface of each lens. The lenses of the Upper Cambrian olenid *Ctenopyge* (Clarkson 1973b) are biconvex in form, the lower surface being of slightly greater curvature. Given the known refractive indices of the external sea water, of calcite along the *c*-axis, and that assumed for internal body fluids, as in modern marine arthropods (Clarkson and Levi-Setti 1975), the focal length is readily calculated using Gaussian lens-formulae (e.g. Jenkins and White 1976), and ray paths may then be traced (text-fig. 3).

In the case of *Asaphus* (Clarkson 1973a), the upper surface of the prism is virtually flat. The proximal surfaces of the prisms in most of the material which I originally studied were damaged, probably by solution during ecdysis, for all the specimens appeared to be exuviae. There are a number of lenses, however, which still retain most of their original form, showing hemispherical proximal ends of near perfect shape. The drawing (text-fig. 3a) constructed from a high magnification photograph shows

TEXT-FIG. 3. Optics of the lenses of holochroal eyes: (a) *Asaphus raniceps* Dalman. L. Ord., Öland, Sweden. Part of horizontal section through Gr I 5512, (figured by Clarkson 1973a, pl. 50, fig. 1); (b) same, reconstruction of lenses based on (a), with ray paths traced for incident light normal to surface; (c) *Sphaerophthalmus humilis* (Phillips), Andrarum, Scania. Reconstruction of lenses in horizontal section (based on Gr I 20803, figured by Clarkson 1973b, pl. 95, fig. 3); (d) same, with ray paths traced for incident light normal to the surface; (e) *Bojoscutellum campaniferum* L. Dev. Koneprusy, Bohemia. Horizontal section through lenses in the centre of the eye. Gr I 14202 (figured by Clarkson 1975, fig. 4c); (f) same, thicker lens at the periphery of the eye; (g) same, lenses illustrated in (e), ray paths traced for incident light parallel with the axis, using Gaussian thick-lens formulae. The effects of curving trabeculae are minimal for incidence of light along the axis and are not considered here.

Notation (following Jenkins and White 1976): A, A' object and image distances: c_1, c_2 , centres of curvature of first and second surfaces: f, F' , primary and secondary focal lengths, located at focal points F and F' : n, n', n'' , refractive indices of sea water, calcite along c -axis and assumed for body fluids respectively: r_1, r_2 , radii of curvature of first and second lens surfaces.



how the radius of curvature is readily measured so that the focal length can be calculated. Likewise the focal length of thicker biconvex lenses, e.g. those of *Bojoscutellum*, are readily calculated using the oblique ray method for thick lenses as described by Jenkins and White (1976, ch. 5).

Again in *Asaphus*, the hemispherical proximal surface of the prism compensates for the virtually flat distal surface so that light is brought to a focus at a similar relative distance below the proximal surface to that of the biconvex lens of *Ctenopyge*. The two lenses have similar f numbers ((f/D) (focal length f divided by diameter D) in this case $f/D=2.5$). The actual length of the lens or prism is not important for the focusing of the light; what is significant is the relative curvature of the two surfaces. Since both kinds of lenses focus light at a similar relative distance below the proximal surface, and indeed as do lenses of intermediate length and curvature, differences in axial length of the lens or prism are clearly not an optical necessity. It is more likely that this is a simple structural requirement or growth necessity. The relatively simple genetic instructions of a trilobite could not grow a thick cuticle without also growing a thick lens, but the terminations of the lenses would need to be of a particular form if the eyes were to function effectively.

In insects and crustaceans, light is always focused on the distal tips of the rhabdoms (apposition eyes) or on the tip of the cone stalk (superposition eyes). These lie at a very similar relative distance below the dioptric apparatus as do the focal planes calculated for the lenses of various holochroal-eyed trilobites. This tends to support the assumption that these trilobite eyes contained some kind of ommatidia, one below each lens. Within such eyes there is plenty of room for ommatidia as well as for a large central optic ganglion. Despite the obviously greater diameter of the lenses in trilobites than in modern insects and crustaceans (30–100 μm as opposed to 8–30 μm) on average, there seems to be fair grounds for interpreting the holochroal trilobite eye as having some structural and functional equivalence to the eyes of insects and crustaceans. And whilst the programmes responsible for its growth seem to have been generally rather simple, the elegant structures which minimized birefringence do not suggest that the holochroal trilobite eye was an organ of inferior or inadequate biological quality.

SCHIZOCHROAL TRILOBITE EYES

Schizochroal eyes appeared quite suddenly in the early Ordovician. They were presumably derived from a holochroal ancestor. They are confined to the Ordovician to Devonian suborder Phacopina, though the eyes in some other taxa also have certain features in common with the schizochroal condition. Schizochroal eyes are usually large, with thick biconvex lenses, often relatively few in number, and in some cases as much as 1 mm across. They are arranged on an inclined, curving visual surface, but their visual range is never more than some 40° above the equator. The lenses are not in direct contact with one another but are separated by cuticular material or, as it is known, intralensar sclera. Whilst the gross morphology, and the angular bearings of the lenses axes within the visual field have been known for many phacopids for some time, most of the current interest in schizochroal eyes is concerned with detailed microstructure and optical properties of the lenses, and the significance of this in understanding the function of the whole eye.

Lens structure

A knowledge of the mineralogical composition and detailed microstructure of the lenses is a necessary prerequisite for understanding their optics. Early work by Lindström (1901) was based on thin sections prepared for optical micrography, and it was he who first recognized intralensar structures, though he thought that they were probably secondary rather than primary. Working with Bohemian phacopids I found (Clarkson 1967a, 1969a) that polished surfaces showed more detail than thin sections. In these, though it was sometimes hard to distinguish primary from secondary microstructure, one consistent element in the lenses of nearly all the specimens was a bowl-shaped unit in the base of the lens, similar to those which Lindström figured. This intralensar bowl was found to be of very variable shape amongst Phacopina. In some Ordovician Dalmanitinae, evidence of the three-dimensional shape of the bowls came from internal and external moulds (*Dalmanitina*, *Crozonaspis*, *Zeliszella*), whilst in Silurian dalmanitids the bowl appeared as a dark, symmetrical, centrally indented element at the base of the lens (Clarkson 1968; Clarkson and Levi-Setti 1975; Levi-Setti 1976). Towe (1975), however, has not detected bowls in the material he studied.

Campbell (1975) likewise used thin sections and polished surfaces and has reported the existence of intralensar bowls and other internal structures in several Phacopina. In all cases the bowl was found to be present, though in members of a dimorphic pair its precise shape varied from one dimorph to another. In addition he gave clear evidence of subconcentric laminae within the upper unit of the lens, similar to those described by Clarkson (1969a) in *Reedops bronni*.

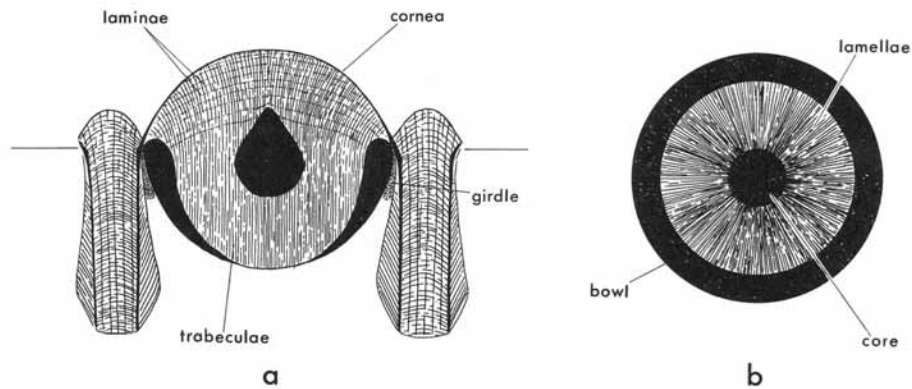
Campbell (1975) also described a pyriform central core in a number of phacopid eyes. It was most clearly identifiable as a primary structure in silicified specimens of *Paciphacops birdsongensis*, in which the outer parts of the lenses had been removed by weathering to expose individually silicified laminae, indented centrally by the distal tip of the core. Campbell's photographs (ibid., pl. c, figs. 3-6), leave no doubt that this is a real structure and not a diagenetic artefact.

Miller and Clarkson (in prep.) have been able to confirm these observations in *Phacops rana milleri* from the Devonian Silica Shale of Ohio. We have used thin sections, polished surfaces, ground surfaces etched with EDTA, and examined with the scanning electron microscope, and cathodoluminescence micrography, which enables some of the primary structures to be distinguished from diagenetic artefacts. Diagenetic effects were common, and unmodified structure is found only rarely. The etched and scanned material shows that the bowl and the core are of regular form, and of much denser texture than the upper unit of the lens. Rather curiously, the bowl is very thin or absent directly below the core, though the lip is quite thick and rounded (text-fig. 4). The upper part of the lens is traversed by laminae, convex upwards and more closely spaced towards the top.

In *P. rana milleri* the highly biconvex upper unit is of quite complex, though regular, form and it is somewhat difficult to interpret, for the etching process modifies the original structure whilst accentuating the details. In sections parallel with the principal plane a radial structure is apparent, though this is less distinct in the intralensar bowl. The calcite is arranged in thin lamellae radiating out from the central core; these

lamellae are particularly clear at the top of the lens which is the first part to be reformed after ecdysis. Sections cut parallel with the axis, however, show that each of the radial lamellae, like those of holochroal eyes, are made of a large number of fibrous calcitic trabeculae, running parallel with the axis in the lower part of the eye, but diverging outwards towards the outer surface of the lens, each trabecula abutting this surface near normal to it.

Whilst relatively few of the specimens we have examined are entirely unaffected by diagenesis, and the above observations are based on a small number of unaltered eyes, comparative details are present in a number of other schizochroal-eyed genera and species.



TEXT-FIG. 4. *Phacops rana milleri* Stumm. Devonian, Silica Shale, Ohio. Reconstruction of lenses in (a) vertical, and (b) horizontal section.

We have also studied the post-ecdysial growth of the eye in *P. rana milleri*, which has shown that the post-ecdysial lenses are very thin and biconvex, they thicken as the cuticle thickens, becoming of Cartesian form and eventually adding the intralensar bowl last of all. With the thickening of the lens and cuticle, the cylindrical alveolar cavity below the lens deepens. At about the time when the bowl is added there appears an annular girdle preserved as grey micrite just below the ambitus of each lens. Finally, more cuticular material, obliquely laminated, is secreted on the cylindrical wall of the alveolus, as an alveolar ring lying against the intrascleral membrane which is continuous with the cornea.

Whilst the 'phacopiform' lenses of *P. rana milleri* are in many ways typical of advanced Phacopina, other shapes of bowl and lens occur. In the more primitive 'acastiform', and 'dalmanitiform' eyes the lenses are more numerous, smaller, more closely packed, and less strongly biconvex. These have flatter bowls, which in *Dalmanitina* closely approximate to the ideal aplanatic lens first described by Des Cartes in 1637. It is not yet known whether these lenses typically contain cores or not.

Optics of the lenses

Towe (1973) ground phacopid lenses parallel with the principal planes of schizochroal lenses and was able to take quite sharp photographs through the clear calcite of the remaining half lens. This simple experiment conclusively proved the existence of orientated calcite, with the *c*-axis normal to the principal plane, but could not, of course, establish the optical nature of an intact biconvex lens. Following Levi-Setti's discovery of the remarkable correspondence between the shapes of the upper units in *Dalmanitina socialis* and *Crozonaspis struvei*, and the ideal aplanatic lenses of Des Cartes (1637) and Huygens (1690), optical models were made of the same shape. The upper unit was constructed of a block of orientated calcite ($n=1.66$), machined to shape, bowls shaped to fit and made of various plastics were tried in turn. A polysulphone bowl with refractive index ($n=1.63$), brought parallel beams of light to a sharp focus below the lens; the result of a combination of slightly different refractive indices, separated by a Cartesian surface (Clarkson and Levi-Setti 1975).

Campbell (1975) pointed out that the core should have some effect on the lens optics, and indeed this should be the case, so should the fan-like arrangement of the calcite trabeculae in the upper unit. If each trabecula or lamina did act as a light guide, then oblique light impinging on the lateral part of the exposed lens surface would, as in holochroal eyes, then be conducted down the *c*-axis of each curving trabecula without being broken into two rays.

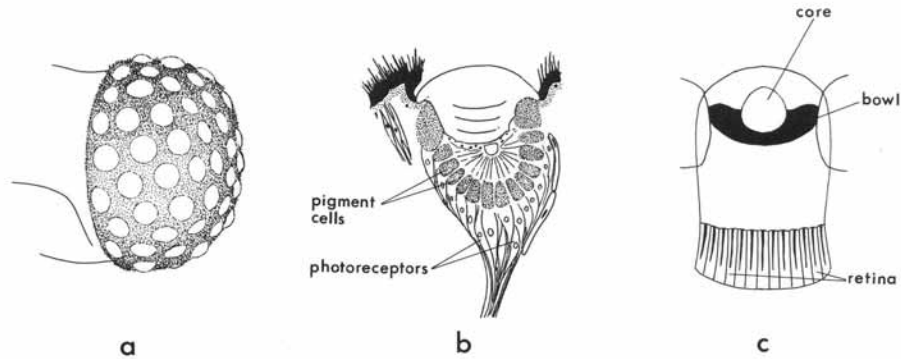
Thus although the model proposed by Clarkson and Levi-Setti appears to hold good, the complex upper unit with its core and radial structure appear to be designed for further optical refinement, particularly in minimizing the acute problems of birefringence caused by the lens being made of calcite.

The nature of the original sublensar structures

Three possibilities have been suggested for the original structures which underlay each lens of a schizochroal eye: an ommatidium, analogous with those of modern insects or crustaceans (Clarkson 1967a); a relatively short ocellus with a flat layer of narrow reticular cells some distance below the lenses (text-fig. 5c) (Campbell 1975; Clarkson and Levi-Setti 1976; Stockton and Cowen 1976); a structure with no known modern analogues, and therefore hard to interpret (Stuermer 1970; Stuermer and Bergström 1973).

In defence of the ocellar theory Campbell points out that 'the indirect evidence suggests that the character of the optic units in phacopid eyes are not those associated with ommatidia', and notes that even the best ommatidia could not resolve objects subtending an angle less than the angle of separation of the ommatidia, which may be very high. He also shows that in most modern eyes, thick biconvex lenses are most commonly associated with ocelli. The ocellar lens of the larval sawfly *Perga* even has an intralensar bowl. Campbell suggests that the sublensar cone I described in *Ananaspis communis* (= *Phacops fecundus*) and the somewhat vaguer equivalents in *Reedops cephalotes* (Clarkson 1967a, 1969b), rather than being equivalent to the crystalline cone, were more likely ocellar capsules at whose base lay the reticular layer (text-fig. 5c). In all these respects I agree with Campbell that an ocellar hypothesis is more plausible than the others.

Perhaps the closest analogue to the schizochroal eye of trilobites is to be found in the compound eye of Strepsiptera (Insecta), (text-fig. 5*a, b*), to which Dr. R. A. Crowson of Glasgow University kindly drew my attention. These eyes, described most recently by Kinzelbach (1967), are large and hemispherical, with relatively enormous and separated lenses. In different genera and species the lens size and number varies considerably, but they usually have Cartesian proximal surfaces. The size of the lenses varies within a single eye. Below each lens is a short, modified ommatidium, which retains the neural structure of normal ommatidia, but in which the retinulae are more spread out in a concave layer, and hence much more like an ocellus.



TEXT-FIG. 5. (*a, b*). *Xenos* (Strepsiptera) a 'schizochroal-eyed' insect: (*a*) external view of eye showing large, separated lenses; (*b*) a single ommatidium in vertical section (redrawn from Kinzelbach 1967); (*c*) Campbell's reconstruction of an optical unit of a phacopid trilobite (redrawn, slightly modified, from Campbell 1975).

While this would seem a good model for a complete visual unit, the remarkable structures described by Stuermer (1970), and Stuermer and Bergström (1973) from X-radiographs, must be taken into consideration. These have the form of very elongated fibres extending from near the visual surface to deep down in the body, converging on the midline of the trilobite. The specimens in which they occur are somewhat distorted and the fibres do not connect with the lenses, hence Campbell (1975) and I (Clarkson 1973*a*) have suggested that these are not part of the visual system. Nevertheless, in stereoscopic X-ray pairs which Professor Stuermer kindly sent me, the fibres do appear to be coming from different levels inside the eye and are certainly not all in one plane, as would be expected if they were merely gill lamellae. If these are actually part of the visual system as Stuermer and Bergström claim, then they could actually be very elongated ommatidia or some kind of cone stalks, alternatively they might be nerves connecting the bases of unpreserved, immediately sub-lensar structures (and there is no reason why these could not have been ocelli), to a deep ganglion, which for some reason was most curiously placed in the centre of the body. There are thus conflicting lines of evidence as to what structures lay below the lenses and until this is resolved, our understanding of the functions of the schizochroal eye must remain to some extent speculative.

Origins, function, and use of the schizochroal eye

The schizochroal eye, as developed in *Phacops* and related genera, at first sight seems so different from any holochroal precursor that a search for its origins may seem futile. Yet there are resemblances both in the logarithmic spiral form of the visual surface and in the radial pattern of the lenses, which show a clear relationship. Some meraspid trilobites begin with relatively large lenses, separated by intervening cuticular material; and as the eye grows a small patch of lenses which retains to some extent this morphology, may be left in the centre of the eye, just below the palpebral suture. The larval eye of *Paladin eichwaldi shunnerensis* is of this type (Clarkson 1975, pl. 3, figs. 12, 13) and the small eyes of *Pagetia* described by Jell (1975) as 'abathochroal' seem to be remarkably similar in external appearance to such meraspid holochroal eyes, though their fine structure is not well known.

It is quite probable that the earliest schizochroal eyes were derived paedomorphically from a holochroal ancestor by retaining the relatively large and separated lenses of the juvenile condition into the adult phase. Further evidence from these rare and unusual eyes must be sought, however, before this is confirmed.

Assuming such a paedomorphic holochroal precursor what would be the next stage in development? Examination of the earliest schizochroal-eyed genera shows that in most respects they are typically schizochroal and of dalmanitiform structure. Even these, however, come too late in the early evolution of the schizochroal eye for the processes of their origin to be readily determined, in all respects except one. For in the Arenig Llanvirnian genus *Ormathops* the lens packing system is significantly different and all eyes examined have a less than regular distribution of lenses on the visual surface (Clarkson 1971, 1975). These lenses, unlike those of other Phacopina, are all of identical size. Since in *Ormathops*, the spacing of the lens centres stayed the same as new lenses were added to the generative zone at the base of the eye, the lenses were unable to grow beyond a certain size. But as the eye grew downwards the visual surface expanded, leaving room for the more lenses whenever there was a large enough space; these were automatically emplaced by the simple genetic programme and once formed, acted as a focus for new lens files as the eye grew larger still. In all the eyes of *Ormathops* species, there are normally two or three blocks in which the lenses are regularly arranged and the dorso-ventral files are parallel. These blocks are separated by discontinuities, which may be sharp and angular (caesurae) or simply less distinct zones where the lenses are irregularly distributed; in the latter case the emplacement of lenses in these zones seems to have been partially controlled from both sides.

Amongst early Phacopina only *Ormathops* has an eye of this kind, presumably retaining the identical size of the lenses from a holochroal ancestor. There must have been strong selection pressure in favour of regularity of packing at the expense of identical size, for all other Phacopina have achieved regularity simply by increasing the distance between lens centres in the generative zone to accommodate for the increasing girth of the eye as it grows. The lenses therefore become larger towards the base of the eye. Whilst this might seem too optically disadvantageous, it is possible that a slight change in biconvexity of the lenses from the top to the bottom of a file

could have altered the focal length (f), and since the f number of the lens is f/D , where D is the diameter, might have allowed a constant f number whatever the lens diameter. The sensitivity of the lens can be measured as $1/f^2$, and hence if the f number remains the same so does the sensitivity. So far it is not entirely certain whether or not this theoretical model was adopted by trilobites; it is merely one of a number of ways in which the trilobites eye could have come to terms with the problems of change in lens size.

In nearly all Phacopina, the result of such packing control is the establishment of a regular system of hexagonal close packing on the eye surface, but an unusual case of cubic close packing has been described recently in *Phacops turco* aff. *praecedens* Haas by Fortey and Morris (1977), who state that it could be accounted for by a relatively small initial difference in lens spacing during ontogeny within the dorso-ventral files. So far, however, this is the only case of such close packing described. It is associated in this case with lenses of a fairly constant size, but the functional significance of the system is presently unknown.

Having assessed something of the origin of the schizochroal eye, and knowing that individual lenses were sensitive (because of their large size) and capable of producing sharp images, it remains to consider the function of the schizochroal eye as a whole. One way of approaching this is through the measurement of the visual field, and of the angular bearing of lens axes within it. In the eyes of all Phacopina the visual field normally forms a relatively narrow strip, latitudinally aligned, with the upper limit of vision rarely rising above 40° of latitude, and it is usually below 30° , contrasting with the frequently panoramic visual field of many holochroal eyes (Clarkson 1966a, b). Dr. A. W. A. Rushton (pers. comm.) has suggested that since the lenses are very large, and capable of point focusing, it is possible that they could have overloaded the photo-receptors had they been directed straight upwards at the source of light, and this may be one of the reasons why the schizochroal eye never faces direct illumination. On the other hand, the orientation of the visual field must also be an adaptation to their mode of life.

One of the most striking characters in the whole visual system is the peculiarly unhomogeneous distribution of the lenses within the phacopid visual field. The plan curvature of the visual surface may be much greater than the profile curvature so that the lens-axes of the dorso-ventral files tend to be clustered together with small latitudinal axial angles, whilst their longitudinal separation is quite wide. This is perhaps most extreme in *Acaste* where a narrow visual field, directed 10° above the equator and covering only 10° of latitude is traversed by distinct 'visual strips', within which the axial angle is only $1-2^\circ$, but between which it may be as much as $10-15^\circ$ longitudinally. Not all schizochroal eyes show this extreme condition, but there is always some difference between latitudinal and longitudinal axial angles and frequently the lens axes are clustered towards the base of the visual field. To what extent these differences and indeed the pattern of lens-axis distribution within the Phacopina as a whole are actually adaptive, is for the moment hard to determine.

Previously I proposed (Clarkson 1966a) that the schizochroal eyes of trilobites were adapted for no more than movement perception. This was upon the understanding that an approaching object would progressively occlude more lens-axes, as Professor Rudwick first pointed out, and that a passing object would register as a

flicker across the visual field. This view, however, was propounded before the remarkably elegant structure of the lenses was known. A more embracing theory of the function of the whole eye, has recently been proposed by Cowen and Kelley (1976), and elaborated by Stockton and Cowen (1977). This seems to be a good model for many aspects of schizochroal eye function.

These authors draw attention to the extreme convexity of the lenses and suggest that adjacent lenses in the one eye, especially those within a dorso-ventral file, could have been used for stereoscopic vision provided that there were appropriate neural links and relays connecting the photoreceptive units. These authors adopt the ocellar theory and assume a flattish retina of individual photoreceptors at the base of a lens capsule lying some short distance below the lens. The lens capsule is partially contained within the sublensar alveolus. This would accord with the fact that the uppermost lenses in the dorso-ventral files of many phacopids are set at an angle to the alveoli. There are many analogues for this system in modern arthropods, the eyes of spiders, the larval eyes (stemmata) of beetles, and the ocelli of various insects. Indeed, as Campbell mentions, the larval eye of the sawfly *Perga*, has a large thick lens, provided with an intralensar bowl, and a short lens capsule below, with a basal retina (Meyer-Rochow 1974).

A pair of adjacent lenses covering a particular region of the visual field would both see the same object but it would appear on opposite sides of their respective retinas. As it moved towards or away from the lens-pair, it would register as a movement of the stimulated points on the two retinas—hence 'the distance of an object would be inferred by comparison of images in adjacent lenses at one time; movement of an object could be detected by comparison at successive times'. Stockton and Cowen therefore see the schizochroal eye as designed to give a warning of the presence and movement of near-by objects, and in particular a three-dimensional appreciation of actual distance. These authors estimate, using simple geometry, that stereoscopic vision would be effective at up to 25 cm away from the eye, and even up to 2 m if lenses at opposite ends of the dorso-ventral files were neurally connected, though they did not especially favour this latter idea. It is clear that such a system would operate best for adjacent lenses of dorso-ventral files (hence the selection pressure to dispense with the less regular lens array of *Ormathops*). There may also have been a possibility of stereoscopic vision between adjacent files, though this would have involved a much more complex neural relay system.

This model seems to account for a number of the remarkable features of the schizochroal eye, especially if the f -number, and hence sensitivity of the lenses could have been made constant through slight changes in surface curvature, from top to bottom of a file. As has been shown, the calcitic trabeculae of which the lenses are constructed radiate outwards so as to abut the lens-surface near normally and could act as non-birefringent light guides for the conduction of strongly oblique light, emphasizing the role of the lens in collecting light over a wide angle. This, too, is in accordance with Stockton and Cowen's model. It is in fact, quite probable that there were other features of the schizochroal eye of equal functional importance, and which have not yet been detected.

The 'stereoscopic model' depends, largely, however, upon whether the basic assumption is justified, i.e. whether there was a short ocellar lens capsule or an

ommatidium below each lens. If it were the latter the model would need each serious modification.

Whilst we are still far from a good understanding of the schizochroal eyes of Phacopina, it is clear that they were in no way primitive or inferior organs, or that their biological function was very limited. The elegance of the lens design at least and the various corrections of which the lenses were capable do not imply a low-grade nervous system associated with them. The not infrequent incidence of blindness in Phacopina and many holochroal-eyed trilobites may in some cases at least be environmentally related (Clarkson 1967*b*), and does not imply that the eyes were of poor enough quality to be easily dispensed with.

Finally, what did trilobites, especially those with schizochroal eyes, actually use them for? Many trilobites seem to have been mud ingesters or filter feeders, though as Whittington (1975) has shown, the gnathobasic jaws and spiny appendages may have enabled some species to pick up and triturate small worms from the substrate. Even if they were predators to this degree, the eyes would not have been much use to them in their search for worms, since they are located on the dorsal surface of the cephalon, and the interpretation of hypostomal maculae as ventral eyes by Lindström (1901) is still *sub judice*. There is, however, a fair general correlation between the possession of large and well-developed eyes, and the ability to enroll. It is common, though not invariable to find that those trilobites with large eyes, whether holochroal or schizochroal, frequently have superior enrollment ability and fine vincular (coaptative) structures. The primary function of trilobites eyes as distant early warning sensors for the detection of approach of predators, seems to be a reasonable deduction from the evidence, especially since major changes both in eye structure and in enrollment ability seems to have taken place in many of the early Ordovician groups at around the same time. The combination of advanced visual and protective systems may well have been a major factor in prolonging the existence of trilobites until the end of the Palaeozoic even in the face of fierce competition and predation.

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