

FINE STRUCTURE OF THE EYE IN TWO SPECIES OF *PHACOPS* (TRILOBITA)

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ABSTRACT. The anatomy of the schizochroal eyes of *Phacops fecundus* Barrande and *P. latifrons* (Bronn) was investigated by sectioning. Intralensar structures were best preserved in *P. latifrons*, where each lens has an outer crescentic region, perhaps bipartite, surrounding a smaller 'proximal nucleus'. In *P. fecundus* lens structure was less distinct, but a sublensar structure was seen projecting into the central lumen of the eye and forming a long slightly tapering cylinder continuous with the corneal-intrascleral membrane. This may be analogous with the crystalline cone in recent arthropods.

In both species the sclera is thicker than the lenses, and each lens lies at the top of a cylindrical alveolus excavated in the sclera. The directions of these alveoli have been used in determining the probable original internal arrangement of the sublensar visual units. In horizontal section these are obliquely radial, in vertical section they are almost parallel and thus are not generally coaxial with the outwardly directed lens-axes. The functional significance of the latter phenomenon is obscure but may relate to day and night vision. The postulated internal arrangement necessitates shorter central visual units and longer outer ones. This would explain the observed size differentiation of the lenses on the visual surface.

THE schizochroal eyes of phacopid trilobites are distinguished from other trilobite eyes by having large biconvex lenses, separated from each other by an opaque interlensar sclera. These lenses, which rarely number above 500 per eye, and are generally much fewer, are arranged upon a visual surface approximating a lunate segment of a cone. The upper surface of each lens has a thin pellucid corneal covering, which continues at the lens margin to plunge below the surface of the interlensar sclera as a cylindrical ring free of contact with the lens.

The anatomical details were originally worked out by Lindström (1901), whose excellent figures of various structures in thin section have often been reproduced and commented upon (Hanström, 1926; Harrington *in* Moore, 1959). Lindström, however, only studied five phacopid species, and his illustrations showed just a few lenses and not sections through the whole eye. Some details of the anatomy of the eyes of three other phacopid species are known from the work of Clarke (1889), Exner (1891), and Rome (1936).

The eyes of several species of phacopids have now been sectioned as part of a research project on trilobite vision, in the hope of revealing further anatomical details, and in order to determine more about the structural and functional relationships of the various parts of the eye. In this paper the eyes of a well-preserved specimen of *Phacops fecundus* Barrande are described (no. 20575) (Silurian, Bohemia), and three specimens of *Phacops latifrons* (Bronn) (nos. 20576, 20584, and 20607) from the Devonian of North Germany, which were kindly donated for study by Miss H. C. Nisbet, Curator of the Grant Institute of Geology. In each of these, only a single eye-variant was studied. Lens-distribution diagrams are given (text-figs. 1*b*, 2*e*) for comparison with existing work (Clarkson, 1966*c*).

Methods of study. In order to reduce danger of disintegration during preparation, the specimens were embedded prior to grinding in blocks of clear 'Araldite', and the surfaces of these blocks were polished so

[Palaeontology, Vol. 10, Part 4, 1967, pp. 603-16, pl. 99.]

that the eyes could be clearly seen. Where specimens possessed two intact eyes the blocks were halved; one eye being used for vertical and the other for horizontal sectioning.

Horizontal sections were made by grinding the blocks parallel with the horizontal rows of lenses (for terminology see Clarkson 1966*a*). At each level when important structural detail was visible the cut face was polished with fine carborundum powder, etched for a few seconds in dilute hydrochloric acid, and then examined in reflected light using immersion oil under a coverslip. Colour changes limiting organic junctions were clearly seen by this method; they were more easily visible than in thin sections prepared as for petrography. Cellulose peels were taken as permanent records of all the sections cut prior to further grinding.

Each horizontal section was made, as far as possible, to include the full length of a single horizontal row, but because of the progressive downward widening of the spaces between dorso-ventral files these horizontal rows are not entirely planar; the central lenses lie at a lower level than the peripheral ones. In such sections the full separation between lenses of alternate files in a single horizontal row is visible only in the central parts of the eye, whereas peripherally parts of lenses belonging to adjacent horizontal rows are interposed (text-figs. 1*b*, 2*e*).

Vertical sections were usually cut exactly through the centres of the lenses of single dorso-ventral files so as to show the full height of the eye. They were made normal to the visual surface.

Phacops fecundus Barrande

Text-fig. 1*a-i*, Plate 99, figs. 1-3

The external morphology and variation in the eyes of this species was well described by Barrande (1852, p. 514), and certain functional aspects were discussed by the author (Clarkson 1966*c*, pp. 471-2). Exner (1891) figured a few lenses in thin section but was unable to distinguish any intralensar or sublensar structures.

Specimen no. 20575 was well preserved though the palpebral lobes and some of the upper lenses of both eyes were damaged. There were 18 dorso-ventral files with a maximum of 6 lenses per file and the largest lenses were of diameter 0.5 mm. The original lens distribution in files from anterior to posterior was as follows:

345 656 565 555 454 432: Total 82 (text-fig. 1*b*).

Horizontal sections were made from the left eye, vertical ones from the right one.

1. Structures seen in horizontal section

Details of the lenses, cornea, interlensar sclera, and for the first time, a sublensar structure, are visible in the single section figured here (text-fig. 1*a*).

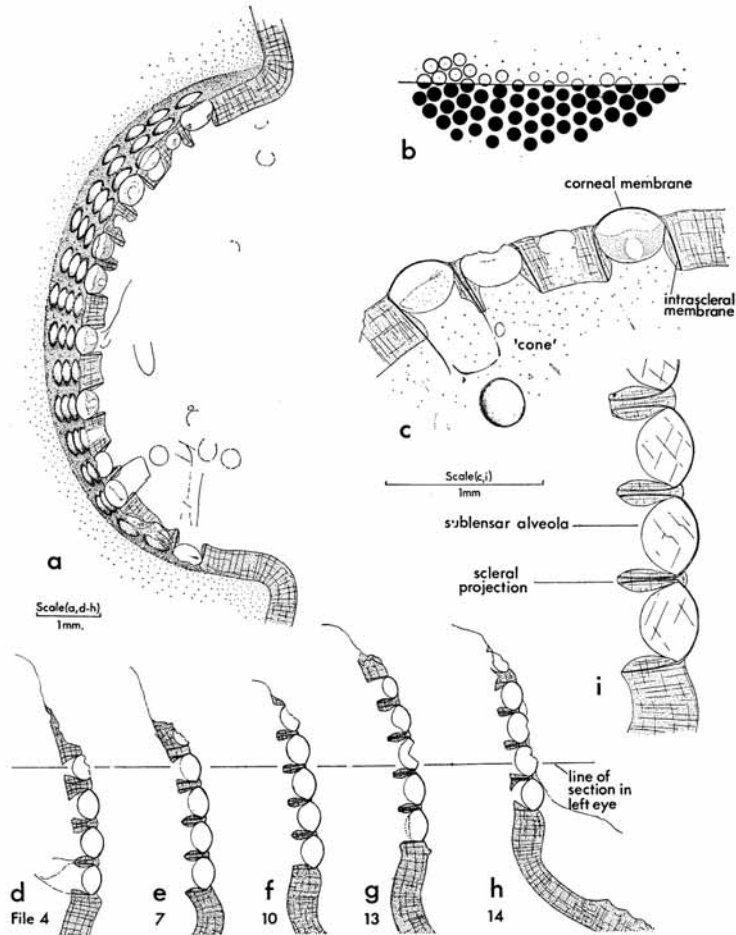
Each lens is set at the summit of a cylindrical cavity, or sublensar alveolus, excavated in the sclera (text-fig. 1*i*). The thick lenses are unequally biconvex; their inner surfaces have the higher radius of curvature. A narrow flange at the edge of each lens interlocks with a corresponding indentation just below the surface of the interlensar sclera. The

EXPLANATION OF PLATE 99

Figs. 1-3. *Phacops fecundus* Barrande. Silurian, Bohemia. Grant Institute no. 20575. 1, Left eye, sectioned horizontally as in text-fig. 1*a, b*, showing a 'cone' below the cut lens in dorso-ventral file 14, $\times 10$.

2, Right eye, sectioned vertically through file 14, as in text-fig. 1*h*, $\times 30$. 3, Posterior region of left eye, showing the cone, as in text-fig. 1*c*, $\times 30$.

Figs. 4-7. *Phacops latifrons* (Bronn). Devonian, N. Germany. 4, Left eye of Grant Institute no. 20607, sectioned horizontally as in text-fig. 2*a, e*, $\times 15$. 5, Left eye of specimen 20584, sectioned vertically through file 5, showing intralensar structures as in text-fig. 2*d, g*, $\times 25$. 6, Posterior region of left eye of specimen 20607, showing intralensar structures as in text-fig. 2*a, f*, $\times 25$. 7, Right eye of specimen 20584, sectioned vertically through file 5, as in text-fig. 2*c*, $\times 25$.



TEXT-FIG. 1. Anatomy of the eye of *Phacops fecundus* Barrande, Grant Institute no. 20575. *a*, Horizontal section through left eye along the line shown in fig. *b*. A 'cone' is visible under the sectioned lens of the 14th dorso-ventral file. Some of the other internal structures are fragmentary cones but most are organic debris. $\times 10$. *b*, Projected visual surface of left eye, showing the line of the section fig. *a*. The blank circles represent lenses, originally present, which have been removed during preparation, the dots indicate the probable centres of lenses damaged prior to preparation. $\times 5$. *c*, Enlargement of part of the above horizontal section showing the 'cone' in the 14th dorso-ventral file, and the continuous corneal-intrascleral membrane. Traces of intralensar structure are visible. The ring below the cone is an extraneous organic fragment, possibly of algal origin and is not part of the eye. $\times 25$. *d-h*, Vertical sections through the centres of numbered dorso-ventral files. File 10 has not been cut quite normal to the visual surface. Sublensar structures in file 4 seem to represent a collapsed cone. These sections are aligned for reference according to the line of the horizontal section in the other eye. $\times 10$. *i*, Enlargement of part of file 7. The lenses of this eye have undergone recrystallization, obliterating the internal structures, and showing traces of calcite cleavage planes. $\times 25$.

outer surfaces of the lenses are always regularly curved, but their inner surfaces are not always so, for in parts of the eye where the visual surface is most strongly curved, there may be some discrepancy between the axial bearing of the outer part of the lens and the direction of the sublensar alveolus, and in such cases the inner surface is drawn out into a slight bulge in the direction of the alveolus. It may be assumed here that the sublensar ommatidium was coaxial with the alveolus, and thus that light incident on the lens in the direction of its axis would be refracted towards the photoreceptors in a slightly different direction.

Not a great deal of internal structure is visible in the lenses. They consist of microcrystalline calcite, which might indicate an element of calcite in their original constitution. Some of the lenses sectioned horizontally show a banded structure. A few have a central capsule or nucleus located near the proximal edge of the lens. Similar, but better-preserved structures were observed in the eye of *P. latifrons*.

The upper surface of each lens has a disjunct corneal membrane which plunges through the interlensar sclera as a cylindrical ring and ends abruptly on the inner surface of the sclera. This structure was correctly described by Lindström in *P. macrophthalmus* (1901, p. 65, pl. 6, figs. 3-5). The membranous cylinder is here termed the *intrascleral membrane*. It is always coaxial with the sublensar alveolus and is separated from the latter by a thin layer of sclera.

The horizontal section illustrated (text-fig. 1 *a, c*, Pl. 99, figs. 1, 3) cuts through a lens in the 14th dorso-ventral file, which carries clear traces of a sublensar structure. Here the intrascleral membrane continues below the inner margin of the sclera to form a slightly tapering flat-based cylinder; the membrane is ruptured in one place. There are two interpretations of this structure. Either, it could be a structure analogous to the crystalline cone of recent arthropods, in which case the photoreceptive organs must have lain below it, or simply a membrane within which these organs were contained. It has been shown by Exner (1891) that whereas in insects the crystalline cones are quite hard and rigid structures, those of marine arthropods are often gelatinous. If the cones of phacopids were likewise gelatinous, decay or rupture of the delicate membrane investing them would destroy them entirely. This seems to have happened in most cases for sometimes loose ends of the membrane can be seen projecting from the inner surface of the sclera in *P. fecundus* and in other phacopids. Preservation of the membrane entire would certainly be a rare event. Within the lumen of the eye are a number of branching cylindrical tubes, possibly of algal origin. One of these tubes lies directly below the base of the only preserved cone, and may have protected it from decay.

Lindström observed fine vertical threads below the lenses of *Dalmanites vulgaris* (Lindström 1901, pl. 3, fig. 50), but they are unlike the structure described here. He did not think that they were organic in origin. Likewise the hexahedral calcite crystals below the lenses of *P. quadrilineata* (*ibid.*, p. 15, fig. 38) were not considered as having any relationship to the original structure of the eye.

Nearly all modern arthropods have crystalline cones located below the lenses in a position analogous to that of *P. fecundus*. Acone eyes were described in *Lepisma* and other arthropods by Hesse (1901), but even in these primitive types there are nevertheless large transparent refractile Semper cells below the lenses though they are not actually modified into cones. Cones are even present in arthropods with disjunct spherical lenses, such as the copepod *Pontella*, described by Parker (1891) and some sort

of cone-like refractile organ below the lens seems to be fundamental to the structure of the compound eye. Lindström believed that cones were originally present in trilobites, but had not been preserved because of their delicate nature. The opposite point of view should also be considered. In most recent arthropods the outer 'cornea' is very thin and is usually almost flat. In such cases, it can have served only as a transparent protective window, whose sole function was to let light through to the refractile cones below. It may have been possible that the corneal membrane of schizochroal trilobite eyes had a similar function and that the thick biconvex lenses would have dispensed with the need for cones. These lenses and the cones of recent arthropods might have had an identical function. The division of the lenses into an outer crescentic and an inner elliptical region (see p. 610) might indicate differences in refractive index within the lens, thus all necessary refraction may have been effected within the lens.

In those recent arthropods with truly biconvex lenses (e.g. *Oniscus*, described by Debaisieux 1944), the lenses do, however, have cones, and they must therefore have been essential in such cases. The weight of evidence would indicate that the sublensar structure described here is indeed the equivalent of the crystalline cone of recent arthropods. If this is so, then the photoreceptive organs would need to be located below the bases of such cones, and in *P. fecundus* there is adequate space in which to accommodate them. The only other organ necessary within the eye is the optic ganglion, and even if this was of fair dimensions, as is common in eyes of the apposition type (see below), relatively long ommatidia could nevertheless have been present.

2. Structures seen in vertical section

Progressive grinding of the right eye resulted in sections being exposed through several complete dorso-ventral files (text-fig. 1 *d-i*, Pl. 99, fig. 2). These sections were usually made normal to the outer surface of the eye, but one or two were deliberately ground askew to show the nature of lens/scleral contacts in oblique section.

As each lens is situated at the top of a sublensar alveolus the lenses are separated by thin scleral projections. The intrascleral membranes of each lens appear very close together in these sections. The scleral projections are thin between the principal planes of the lenses, widening out above and below this level and they all have square-cut ends. A curious and unexpected feature is that these projections are all virtually horizontal and parallel with each other rather than being radially divergent, even though the lenses and particularly the uppermost ones may be inclined at an angle to them. In the specimens examined the palpebral lobes were broken, but in row 13 the upper lens belongs to the upper horizontal row and the same condition appears. This parallel arrangement applies both to the scleral projections themselves and to the intrascleral membranes running through them. It is unlikely to be the result of freak preservation, as it is found in other phacopids also. In *Reedops cephalotes* (Barrande) a similar condition has been noted in an eye with ten lenses per file; all the scleral projections are parallel. The functional significance of this structural pattern is difficult to assess, though some comments are appended below.

Phacops latifrons (Bronn)

Text-fig. 2 *a-g*. Plate 99, figs. 4-7

P. latifrons possesses an eye similar to that of *P. fecundus*, but it is larger relative to

the cephalon, and the lenses are more deeply sunken within the interlensar sclera. Burmeister (1846, p. 89, pl. 4, fig. 12) figured the eye, and Clarkson (1966c, p. 474) has briefly commented upon the external morphology, but variation within the eyes of this species has not yet been worked out in detail. Barrande (1852, pl. 3, fig. 16) illustrated a partly weathered eye exhibiting the effects of erosion which removed the outer parts of the lenses but left central stumps (noyaux).

All specimens sectioned came from Gerolstein, Eifel, North Germany. Horizontal sections were cut from both eyes of specimen no. 20607, vertical sections from both eyes of no. 20584 and from the left eye of no. 20576. The right eye of the latter was damaged.

In no. 20607, which is quite typical of the species, the maximum lens diameter was 0.375 mm. There were 17 dorso-ventral files with a maximum of 5 lenses per file. The lens distribution was as follows:

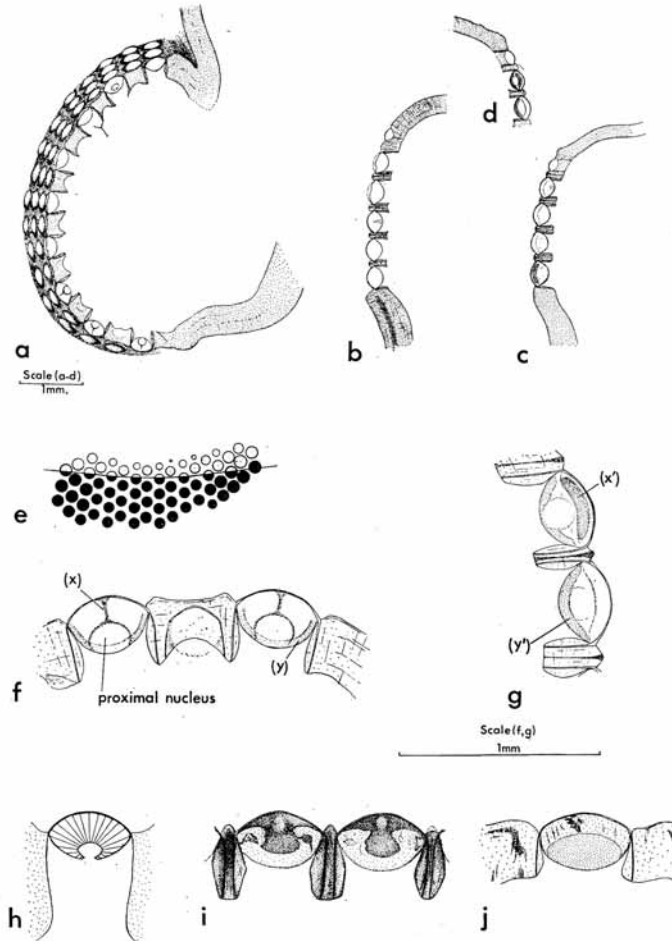
345 454 545 544 443 32: Total 68

The principal differences from *P. fecundus* are as follows. The dorso-ventral files diverge downwards at a lesser angle, thus the horizontal sections include almost complete horizontal rows without the peripheral interpolation of the lenses of adjacent rows (text-fig. 2a, Pl. 99, fig. 4). In these sections the inner surface of the interlensar sclera is indented between the lenses rather than planar as in *P. fecundus* but is otherwise similar. The palpebral lobes of *P. latifrons* were intact and the complete sections show that all the scleral prolongations are parallel. There are no traces of sublensar structure. As previously noted, internal structures in the lenses of *P. fecundus* were not very clear though distinct traces of a proximally placed 'nucleus' were visible in some of the lenses. The intralensar structures of *P. latifrons* are better preserved, though recrystallization of calcite within the lenses has resulted in the partial obliteration of the elements originally present. As not all the lenses have been preserved in the same way the interpretation put forward here is necessarily tentative and there is some difficulty in reconciling the internal construction according to this interpretation with the rather diverse structures reported in different species by Clarke, Lindström, and Rome.

P. rana, studied by Clarke (1889, p. 258, pl. 21, figs. 1-6, 27, redrawn in text-fig. 2h), possesses a small spherical indentation in the lower surface of each lens. This proximal cavity becomes filled with sediment after the death of the trilobite, and thus appears in section and in internal moulds as a small central boss or tubercle.

P. macrophthalmus, the best-preserved of the species studied by Lindström (1901, pp. 30-31, pl. 6, fig. 5, redrawn in text-fig. 2i), has lenses with an upper mushroom-shaped unit interlocking with a lower bowl-shaped structure. There is no trace of a proximal cavity in this or any of Lindström's species. Lindström suggested that the lenses originally consisted of thin layers, arched downwards below and upwards above, as in the eyes of recent crustaceans and spiders.

Rome's figures (1936, p. 4, pl. 2, figs. 9-12, redrawn in text-fig. 2j) of the eye of *P. accipitrinus maretioensis* illustrate lenses with an outer crescentic part enclosing a smaller inner proximal region. The difference between this structure and that of *P. rana* is that the proximal region in *P. accipitrinus maretioensis* is larger and seems actually to be an intrinsic part of the lens, and not merely a cavity within it.



TEXT-FIG. 2. *a-g*. Anatomy of the eye of *Phacops latifrons* (Bronn). *a*, Horizontal section through the left eye of Grant Institute no. 20607 along the line shown in fig. *e*. $\times 10$. Internal structures can be seen in some of the lenses. *b*, Section through 6th file of left eye, no. 20576. The section was cut slightly askew and does not pass through all the lens-centres. $\times 10$. *c*, Vertical section of file 5, right eye, of no. 20584. $\times 10$. *d*, Vertical section of file 5, left eye, no. 20584. $\times 10$. *e*, Line of section in fig. *a*, no. 20607. $\times 5$. *f*, Enlargement of two lenses of the rear part of the eye in fig. *a*, left eye, no. 20607. The lenses each display a proximal nucleus, and above this a thin median strand (*x*) running normal to the upper surface as well as traces of layering in the lower parts (*y*). $\times 40$. *g*, Enlargement of part of fig. *d*. Left eye, no. 20584. $\times 40$. This section is cut diagonally and thus passes directly through the centre of the proximal nucleus in the upper lens, but slightly to one side of it in the lower. The crescentic strip in the upper lens, (*x'*) may be the equivalent of the median strand (*x*) in the horizontal section in fig. *f*, in this case cut sagittally. *h*, *Phacops rana* (Green). Schematic representation of lens structure, redrawn from Clarke (1889) (not to scale). *i*, *Phacops macrophthalmus* Burmeister. Vertical section through a dorso-ventral file, redrawn from Lindström (1901) (not to scale). *j*, *Phacops accipitrinus maretioleensis* (R. and E. Richter), redrawn from Rome (1936) (not to scale).

The original structure of the lenses of both species may have been the same, but in *P. rana* the lower margins of the lenses have been disrupted so as to let in sediment which filled the proximal cavity when the original contents had disappeared, whereas in *P. accipitrinus maretiolensis* the lenses were left intact and the contents of the proximal cavity could not be removed. It is probable that the latter were originally gelatinous.

In *P. latifrons* some lenses show distinct indications of a spherical proximal nucleus surrounded by an outer crescentic region (text-fig. 2*f, g*, Pl. 99, figs. 4, 6). Normally the two regions are separated by a thin dark line but do not show major compositional differences. There is no evidence that the proximal nucleus is actually a cavity connected with the sublensar alveolus for the inferior rims of the lenses are never indented. Barrande's figure showing the weathered surface of an eye of *P. latifrons*, already referred to, shows correctly the nature of the central lens-nuclei (noyaux) which are part of the original structure of the lenses rather than intralensar continuations of the sublensar alveoli. The proximal nucleus of this species is evidently similar to, but smaller than, that described by Rome.

Some sections, cut in the vertical plane, show an additional kind of proximal structure, in the form of a thin downwardly convex layer of transparent calcite, following the lower surface of the lens and separated from the upper regions by a distinct compositional change (text-fig. 2*f (y), g (y')*, Pl. 99, figs. 5, 7). The proximal nucleus lies in a central indentation in the upper surface of this layer and abuts directly against the lower margin of the lens. Whilst the existence of the proximal nucleus and the thin proximal layer just described seem to be well established, there are still some uncertainties in interpreting the remaining structures.

Horizontal sections of both the eyes sectioned show certain lenses with thin medial strands co-directional with the lens-axes (text-fig. 2*f (x)*, Pl. 99, fig. 6) and extending from the proximal nucleus to the upper surface. These were only visible in some of the lenses but, where present, they seemed to be persistent throughout each lens as the eye was ground down horizontally.

Vertical sections, on the other hand, show some lenses with an apparently different internal constitution. Two such lenses are illustrated in sections through different files of specimen no. 20584 (text. fig. 2*c, d, g*, Pl. 99, figs. 5, 7). Each of the sections illustrated was ground normal to the surface along the length of the file but somewhat diagonally and not through the centres of all the lenses. The internal structures only appeared in their entirety where the section passed through the median vertical plane of each lens. In such cases a regularly arched mass or plate of transparent calcite (*x'*), was seen overlying the proximal nucleus, parallel with the upper surface of the lens (text-fig. 2*c, d, g*). It is possible that the structures here shown as *x* and *x'*, appearing in different planes, are in fact different views of the same type of intralensar organ which can be interpreted as a medial vertical plate, dividing the upper part of the lens, above the nucleus, into two regions. This bipartite effect may be the result of the original secretion of the lens by two underlying cells, but may also be part of a mechanism for concentrating light as it passed through the lens. If the proximal nucleus was of higher refractive index than the rest of the lens it could in itself have acted as a discrete source transmitting light received from above to the deeper-lying photo-receptors

PHYSIOLOGICAL CONSIDERATIONS

1. *Sublensar ommatidial arrangement*

Though no traces of sublensar ommatidial structure are preserved apart from the 'cone' already described in *P. fecundus*, it is nevertheless possible to infer much about the deep-lying structural arrangement of the eyes of both species from the directions of the sublensar alveoli and the intrascleral membranes alone.

It is important first to note, for comparative purposes, the main ommatidial types present in modern arthropods. There are only two basic types of ommatidial element, defined by Exner (1891) as apposition and superposition ommatidia.

Eyes with apposition ommatidia ('apposition eyes') are perhaps the simplest kind. They are characteristic of diurnal arthropods living in bright light. The photoreceptive units (rhabdoms) of the ommatidia are very long and extend from the base of the crystalline cone to the basement membrane of the eye. Each ommatidium is virtually isolated from its neighbours by screening pigment.

'Superposition eyes' are typical of nocturnal and crepuscular arthropods. The rhabdom of a superposition ommatidium is short and swollen, extending only a third of the total distance from the basement membrane to the cone, and connected to the latter by a thin cone-stalk. In daylight screening pigment effectively isolates each ommatidium, but in dim light this pigment migrates towards the upper and lower ends of the ommatidia, so that light can pass through the translucent ommatidial walls. Thus individual rhabdoms may be illuminated by light passing through many lenses. This device apparently increases the light sensitivity of the eye, though definition may be lost. There is, however, no clear agreement over many points in the differential physiology of the two kinds of eye. Full and detailed accounts of apposition and superposition are given in Waterman (1961) and Goldsmith (1964).

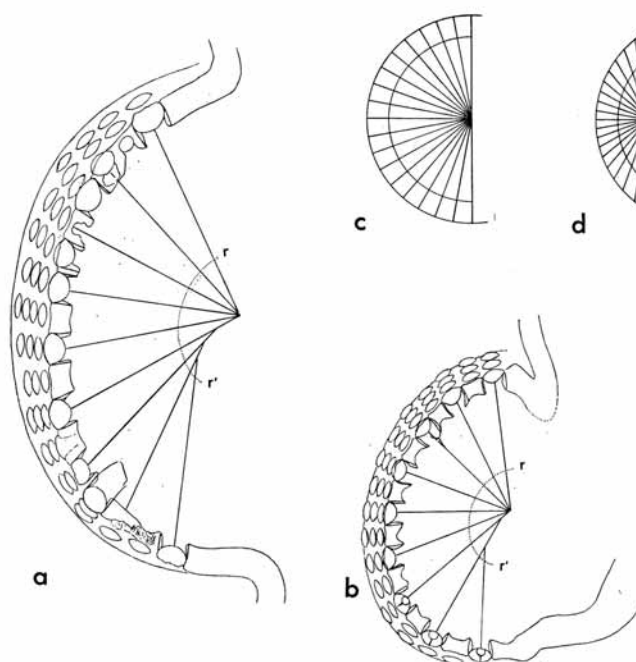
This information on the two basic eye-types is useful in interpreting the possible sublensar structures in *Phacops*, especially in their horizontal arrangement.

(a) *Horizontal arrangement.* In horizontal sections the sublensar alveoli show a markedly radial pattern, which must indicate an originally radial ommatidial arrangement. Diagrams (text-fig. 3 *a, b*) show the inferred directions of the ommatidial axes, which are taken as having lain vertically below, and parallel with, the sublensar alveoli and intrascleral membranes. Lines were drawn from the centre of each lens of the horizontal row in question in directions given by the walls of the alveoli. (Where the lens does not appear on the section owing to the curvature of the horizontal rows, directions could be surmised from the arrangement of neighbouring lenses.) As in the insect eyes described by del Portillo (1936), using a somewhat similar method, these lines do not all converge to a single point. Projected ommatidial axes of the central and anterior lenses are perfectly convergent, but those of the more posterior lenses lie on a curve, the 'Brennkurve' or curve-of-focus of del Portillo. They are shorter than the anterior axes. The differential curvature of the visual surface which is mainly responsible for this phenomenon results in a larger number of lenses covering the anterior part of the visual field (Clarkson 1966c, text-fig. 3); a situation which is presumably of some adaptive significance.

All the ommatidial axes converge to a point or region whose distance is less than that

from the surface to the centre of curvature of the eye. Thus the peripheral ommatidia are not normal to the visual surface.

To show the significance of this feature two simple theoretical models are illustrated showing different types of radial ommatidial arrangement.



TEXT-FIG. 3. Internal arrangement of the visual units. *a. Phacops fecundus* Barrande. Grant Institute no. 20575. Horizontal section as in text-fig. 1*a*. Diagram illustrating original internal arrangement of the ommatidia, as inferred from the directions of the sublensar alveoli. The lines represent ommatidial axes. A possible maximum depth for the basement membrane is given by the line rr' . *b. Phacops latifrons* (Bronn). Grant Institute no. 20607. Horizontal section as in text-fig. 2*a*. Inferred ommatidial arrangement, as above. *c*, Model of an arthropod eye where the ommatidial axes converge to the centre of surface curvature. *d*, Model of an eye where the axes converge to a point only half the depth of the centre of surface curvature. This more nearly approximates the phacopid condition.

The first model (text-fig. 3*c*) shows an eye with a perfectly hemispherical surface, having ommatidia whose axes all converge to a point at the same locus as the centre of curvature of the visual surface. Eyes of this type are not uncommon in arthropods and are usually associated with superposition-type ommatidia. The second model (text-fig. 3*d*) is more similar to those of *P. fecundus* and *P. latifrons* but is regularly curved. The point of axial convergence is only half the distance from the surface to the centre of curvature. Eyes of such a type usually have apposition-type ommatidia. An eye

of the latter type can accommodate as many ommatidia with the same axial separations, and subtending as great a visual range as can one of the former variety, unless the ommatidia are very long. If they are long they can only be housed internally by reducing the length of the central ommatidia relative to the peripheral ones.

Although it is not possible to infer the maximum depth of the ommatidia and hence the basement membrane in *P. fecundus* and *P. latifrons*, it cannot, at its maximum, have been as deep as the region of internal convergence of the anterior lenses. In text-fig. 3*a, b*, the line rr' shows the deepest possible position for both species which would allow room for a small optic ganglion. It is probable, however, that the ommatidia were somewhat shorter than this.

Although some superposition eyes have an irregularly curved surface, the majority approximate the ideal condition of text-fig. 3*c*, in order that they may function efficiently for night-vision in the manner described by Exner (1891). The principal advantage of the second model, where the eye is not of superposition type, is that the same organs may be more efficiently stowed inside the eye. Less of the eye projects, giving greater protection, and there is less internal wasted space. Only enough room is needed below the ommatidia to accommodate the optic ganglion, thus to some extent the degree of curvature of the visual surface must depend on the size of the latter.

These considerations upon the original internal anatomy of the eye bear upon the differentiation in lens size observed in *P. fecundus*, *P. latifrons*, and most other phacopids. The ommatidia or visual units of a single eye may be assumed to have been of similar construction and shape. Large lenses must be associated with large ommatidia, and small lenses with smaller and, as ommatidia of all sizes are of identical form, consequently shorter ommatidia. Thus the peripheral large lenses of *P. fecundus* and *P. latifrons* indicate deeper ommatidia, and the smaller central ones similar though shorter ones. These conditions may be compared directly with the hypothetical second model (text-fig. 3*d*), which exhibits a very similar structure. It is possible that the ancestral phacopid eye approximated this form. In phacopids derived from such an ancestor, differential curvature of the visual surface relating to distinct visual adaptations was superimposed upon it; many of these adaptations have been previously described (Clarkson 1966*c*).

Summarizing, there is some evidence that the ommatidia of *P. fecundus* and *P. latifrons* were moderately long. In the horizontal plane they were arranged radially, though the outer lenses were not normal to the surface. This arrangement would almost certainly preclude any superposition image being formed. The eye could only have functioned as an apposition eye, and the internal structures reflect adaptation to apposition-type vision, with maximum economy of spacing internally as many ommatidia as could be accommodated in a superposition eye of much greater size.

(*b*) *Vertical arrangement.* The physiological significance of the parallel arrangement of ommatidia in vertical section is obscure.

As far as the author is aware, nothing quite like this pattern exists in the laterally directed eyes of recent arthropods. The nearest approximation is found in certain deep-water euphausiids. In these (Chun 1896, Kampa 1965) each eye is divided into two isolated lobes, the upper of which is directly forwards and upwards, whereas the lower has a downward and backward orientation. The ommatidia of the lower lobe

are radially arranged, but in the upper lobe they are all parallel. In contrast with phacopids, this parallel arrangement is constant in both sagittal and transverse planes, so that the lobe consists, in effect, of numerous ommatidia all pointing in the same direction. But as in phacopids, these parallel units with their large cones lie below a curving visual surface and individually are capped by strongly convex corneal 'facets'. In view of these structural similarities, a certain degree of physiological interpretation of the phacopid eye might be made with reference to that of the euphausiids, but little is known of the essential physiological attributes of the eyes of the latter, such as their angular light-receptivity, which would be of value in this case.

The structural dissimilarities furthermore, may outweigh the similarities and thus preclude fruitful comparison. Not only is the phacopid eye a laterally, rather than upwardly directed organ, but the visual units of phacopids are parallel only in the vertical plane. Likewise, there is no pigment between the ommatidia of the euphausiid upper lobe and thus no isolation of the visual units, but in the phacopids, prolongation of the sclera between the lenses must inevitably isolate the ommatidia. Finally, the lenses of phacopids are immensely larger than those of the euphausiids.

The eyes of these euphausiids are highly modified, and are adapted to function in deep-water conditions where bioluminescence and dim illumination from above are the only light sources. The resemblance between these eyes and those of phacopids may not be entirely fortuitous, but one cannot go further at present with this particular topic.

A possible explanation of the parallel arrangement of the visual units would relate it to different adaptations to day and night vision. In recent arthropods, such adaptations are controlled by internal movements of pigment, but the presence of pigments in trilobites is not known, though they may well have existed.

The externally directed optic axis of each lens defines the centre of its cone of vision. As the outer lens-surfaces are strongly convex, the cones of vision must have been relatively wide, though as in *Limulus* (see Waterman 1954) the threshold of visual stimulation probably increased away from the axis. Hence though the eye is adapted to receive light from the whole visual field, i.e. the region covered by all the lens axes, and its penumbra (Clarkson 1966a), it is also directly susceptible to horizontal light rays, parallel with the ommatidial axes. These rays would pass at an angle through the lens, but straight towards the photoreceptors with little change in direction. As shown below, they may have effected total internal reflection within the cone, if the latter were of high refractive index.

In this way the dorso-ventral files would have a similar function to those of *Acaste downingiae*, where their lens-axes form widely separated visual strips, capable of detecting the movement of bottom-living animals. Such a mechanism would mainly be effective in daylight on a brightly illuminated sea-floor. During daylight also there would presumably be some side effect from the weaker illumination above the sea-floor, but at night or in twilight, when the sea-bed became dark, illumination from above was the only available light.

The strong convexity, large size, and high angular separation of the lenses enabled this dim light to be received over a wide visual range, and thus would give a reasonable degree of night vision. This was probably supplemented by pigment migrations.

2. Transmission of light to the deep-lying photoreceptors

In both horizontal and vertical sections there is a definite discrepancy between the angular bearings of the lens-axes and the inward directions of their associated ommatidia, as inferred from the courses of the sublensar alveoli. The eye is adapted to gather light from a particular region of the trilobite's external environment and this adaptation controls the external bearing of the lens axes. The internal arrangement of the ommatidia facilitates maximum spatial economy for the number and size of the ommatidia, and may also, as already explained, be related to the possibility of day and night vision.

Thus the collection of light from the external environment and its internal transmission to the photoreceptors are controlled by a number of factors, and in order that all requirements are satisfied a change in the direction of light within the eye may be necessary.

Exactly how this is accomplished is a problem which can only be discussed in a theoretical sense, though there are three or more factors involved.

(i) In *P. fecundus* extreme discordance between the direction of the external optic axis and sublensar alveolus is often associated with the bulging of the lower surface of the lens in the direction of the ommatidial axis. The optic axis of the lens seems to be bent below the principal plane, which might result in an intralensar change in light direction.

(ii) *P. latifrons* has lenses internally differentiated into two regions. The proximal nucleus may have had a higher refractive index, and light would then be trapped within it. The base of this nucleus would then act as a discrete internal light source, transmitting light in all directions including the line of the ommatidial axis. Pigment screening would effectually trap most of this available light within the ommatidial cylinder, resulting in the stimulation of the photoreceptors. As far as can be made out, the intralensar structures in *P. fecundus* would work in the same way.

(iii) A third possibility involves total internal reflection within the cone, if the latter had a high refractive index. Numerous authors working with recent arthropods have suggested that this simple and well-known physical phenomenon might have the effect of trapping light within the crystalline cone and guiding it towards its appropriate light-accepting organ. Many examples taken from insects were cited by Goldsmith (1964), and Kampa (1963, p. 77) has suggested the possibility in a crustacean. Confinement of light within phacopid cones and its subsequent transmission to the deeper-lying photoreceptors could account for the necessary internal change in light direction.

Further physiological studies on trilobite vision must be delayed until the internal structures of other eyes have been investigated.

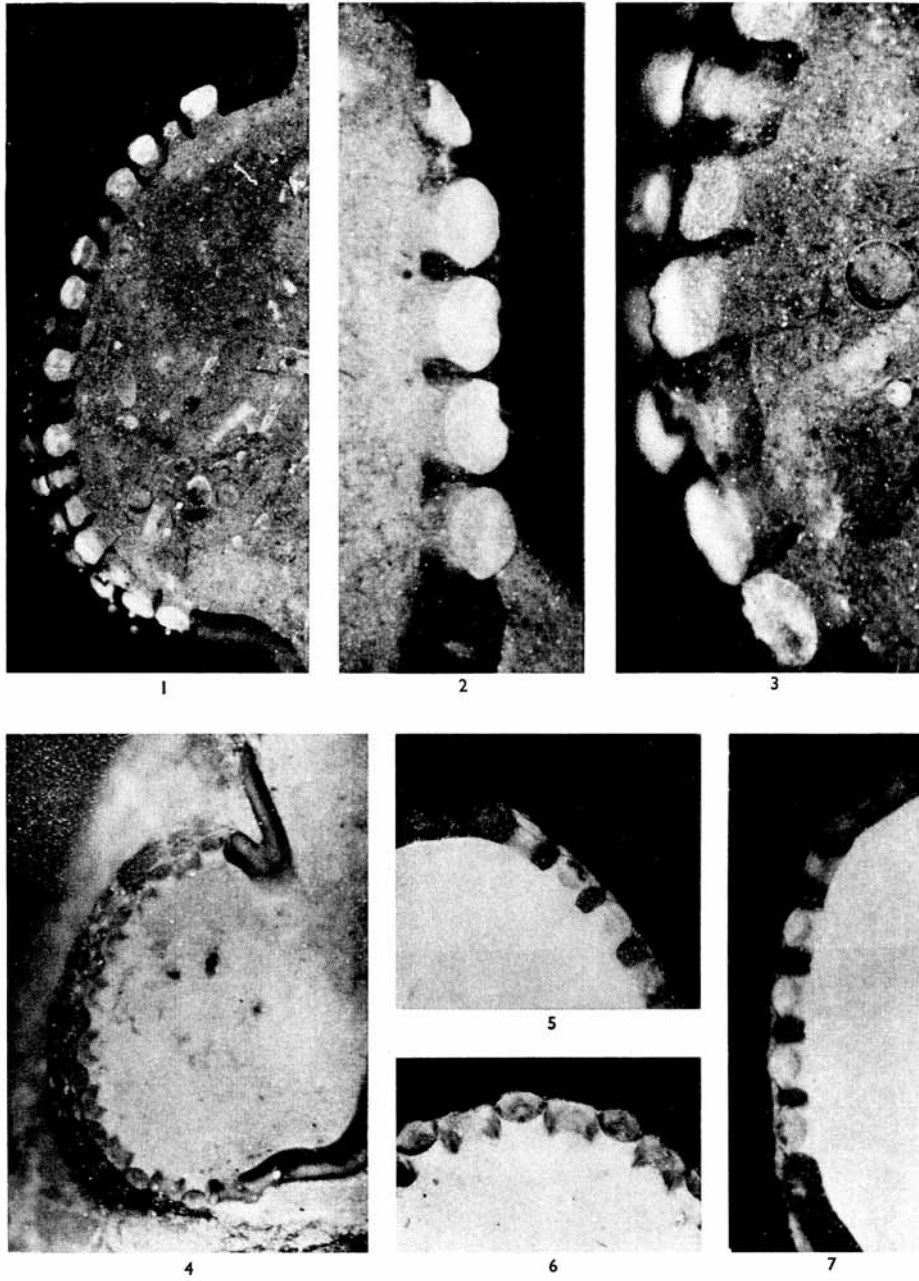
Acknowledgements. I am indebted to Drs. Elizabeth M. Kampa (Mrs. Boden) and Brian P. Boden of the Scripps Institute of Oceanography for helpful discussions connected with this work. I also wish to thank Miss H. C. Nisbet for access to material and Dr. W. B. Heptonstall for critical reading of the manuscript.

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