SCHIZOCHROAL EYES AND VISION IN SOME PHACOPID TRILOBITES

by E. N. K. CLARKSON

ABSTRACT. Some aspects of vision in nine species of phacopid trilobites are described. Methods of study, which primarily consist of the investigation of the morphology of the visual surface and the extent and nature of the visual field, are identical with those of previous work.

Divergent interpretations of intraspecific variation in the lens number of *Phacops sp.* are discussed and sexual dimorphism is advanced as a tenable hypothesis. Phacopids generally have a fixed pattern of lens distribution, though the individual lens formation and arrangement varies in different species.

Individuals within a species have visual fields of similar extent and type, regardless of dimorphism. In different species, however, there is wide variation in visual type, largely as a result of distinct modes of curvature of the visual surface, affecting the angular bearings of the lens-axes.

Three principal visual types are distinguished, presumably reflecting adaptations to distinct ecological conditions. In the first, the visual field has a relatively wide vertical range and the eye is slightly astigmatic; in the second there is much greater astigmatism and a narrower visual field; the third type combines features of the other two.

INDIVIDUAL phacopid trilobites are sometimes found in an excellent state of preservation, showing no distortion and retaining their original convexity. Such specimens are of great value for functional as well as for morphological studies, since it is often possible to interpret exoskeletal structures or organs in terms of adaptive morphology. The methodology of such functional interpretation of fossil structure is fully discussed by Rudwick (1964).

Recently the author studied the eyes and some aspects of vision in a small group of well-preserved Silurian trilobites (Acastinae) (Clarkson 1966*a*). Some other phacopids, of ages ranging from Ordovician to Devonian, have also been studied and the results of these investigations are presented here. The chief limitation to this work has been the difficulty in obtaining enough perfectly preserved material; only a few adult specimens of each species were available. The methods of approach were the same as in my previous work because the material consisted of museum specimens which could not be sectioned. These methods include detailed descriptions of the external visual surface, the size and distribution of the lenses, the angular extent of the visual field, and the nature of vision as deduced from the manner in which the axes of the individual lenses are distributed within the visual field.

This information gives some conception of trilobite visual processes but needs to be supplemented by further work, and in particular by the study of the internal structure of the eyes of well-preserved specimens. The only significant research on this subject hitherto was undertaken by Lindström (1901), who obtained little information about the sublensar structure of schizochroal eyes.

Techniques of study are identical with those described in my former work. The same terminology has been retained throughout, apart from the use of the term 'genal field' proposed by Shaw and Ormiston (1964) which is substituted for 'eye platform' as used by Harrington *et al.* in the 'Treatise'.

[Palaeontology, Vol. 9, Part 3, 1966, pp. 464–87, pls. 73–75.]

The material examined includes the following species:

1. Superfamily Phacopacea. *Phacops rana* (Green), Devonian of New York State; *Phacops fecundus* Barrande, Silurian, Bohemia; *Phacops breviceps* Barrande, Devonian, Bohemia; *Phacops latifrons* (Bronn), Devonian, Germany (briefly referred to); *Phacops batracheus* Whidborne, Devonian, S.W. England; *Phacops boecki* Hawle and Corda, Devonian, Bohemia.

2. Superfamily Dalmanitacea. *Dalmanites vulgaris* (Salter) and *Dalmanites caudatus* (Brünnich), Silurian, Dudley, England; *Chasmops odini* (Eichwald), Ordovician, Estonia.

The eyes of some of these species are quite well known and have been described by systematic palaeontologists. The existing accounts of their morphology are referred to throughout but since a clear understanding of the function of any organ depends so greatly upon detailed knowledge of its structure, it has been necessary to supplement these short accounts by fuller descriptions.

The eye and its position upon the cheek are of great importance in phacopid taxonomy, and certain matters of taxonomic interest came to light in the course of this study. An example of this is the variation in lens number between adults of an apparently single species, which at least in the case of the genus *Phacops* led to divergent interpretations of systematic relationships. But although much phacopid taxonomy is rather confused, any attempt at systematic revision of the species in question would be beyond the scope of the present work. Hence existing systematic categories are used, even though some of these are known to be unsatisfactory. Such taxonomic problems as were encountered are, however, noted and described in full.

Owing to the relative scarcity of perfect specimens it has been possible to analyse only one or two adults of each species, and comparatively few other individuals were normally available for comparison. It has been already established that the number of lenses per eye and their distribution may vary considerably within a species. These factors are related to the size of the specimen and in some cases to sexual dimorphism (Clarkson 1966*a*). The problem thus arises as to how far the specimens examined are representative of the species as a whole.

This problem, as shown below, is rather complex, and in the absence of full growth stages cannot fully be eliminated. I have endeavoured to minimize it as far as possible by the following procedures: (*a*) by selecting only large sized specimens showing the most obviously adult features, (*b*) by comparison with other material and previously published descriptions, particularly in the case of the Bohemian material exhaustively described by Barrande, and (*c*) by distinguishing dimorphs where the supply of specimens was adequate.

It is worth noting that in spite of the variation in lens number, etc. within a species, the angular range of vision described for single specimens appears to be fairly constant for the species as a whole, whatever the stage of development. Increase in lens number with age does not lead to an increase in the angular range of vision. In *Acaste downingiae* (Murchison) and in *Phacops fecundus* Barrande, enough specimens were available to demonstrate that the surface curvature of the eye is established at an early stage in post-larval development, and remains much the same though the visual surface grows while new lenses are added. This leads to a larger number of lens axes covering the same area.

A short discussion of the variation in the eyes of *Phacops* is given in the next section.

FUNCTIONAL DESCRIPTIONS OF EYES

Superfamily PHACOPACEA

Variation in the eyes of Phacops *s.s.* The eyes of various species of *Phacops* s.s. have been studied in somewhat greater detail by previous authors than have those of other Phacopina. Among the best known of all are those of *Phacops rana* (Green) where the variation present has led to divergent taxonomic and developmental interpretations. This confusion is illustrated by the following history of research upon the eyes of *P. rana*.

1. A very detailed account of the morphology and development of the eyes of *P. rana* was given by Clarke (1889). From observations of the number, and manner of development of the lenses in specimens of various sizes, he concluded that lens number increased from youth to maturity following a constant pattern of development, and then declined again from maturity to senescence. This decline, as he stated, could have taken place only by the sclerosis of the lenses, or by their absorption by the palpebral lobe.

2. Beckmann (1951) worked principally upon the development of the eyes of *P.* cf. *breviceps* and *P. schlotheimi* from Germany, but referred also to *P. rana*. In the German species he found an increase in lens number from youth to maturity but no gerontological decline. He gave strong evidence that two forms of *P. rana* had been confused by Clarke, one with a larger adult number of smaller lenses than the other. The author's studies of acastid eyes (Clarkson 1966*a*) gave a general agreement with Beckmann's conclusions; two variant eye forms were distinguished and tentatively attributed to sexual dimorphism.

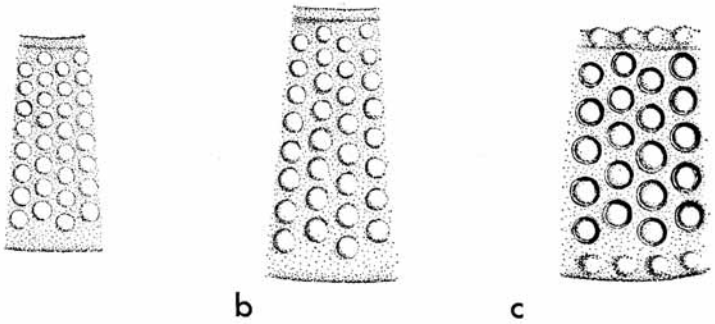
3. Systematic revision of the species *P. rana* by Stewart (1927) and Stumm (1953) led to the erection of several subspecies. The principal diagnostic features on which these subspecies were distinguished included the overall structure of the eye and the number and arrangement of the lenses, though neither author referred to Clarke's work. Typical eyes of all these subspecies were figured by Stumm.

A similar variation occurs in several species of *Phacops* related to *P. rana*. Barrande's (1852) observations on Bohemian phacopids were not mentioned by Clarke, but in many respects they are quite comparable. Barrande's fullest descriptions (1852, p. 514) were of the eyes of the common Bohemian species *P. fecundus*. With his anatomical studies he included a table showing the number and distribution in files of the lenses in the eyes of twelve specimens in various stages of development. In these the maximum number of lenses per eye ranged from 64 to 136. Barrande noted that the number of lenses depended upon the size of the specimens, but was also partially controlled by the particular conformation of the eyes of each individual. None of the largest specimens possessed the maximum number of lenses, but they did exhibit a higher degree of scleral inflation and a relatively wider degree of spacing of the lenses. He also figured the eyes of three specimens of *P. fecundus major*, reproduced here (text-fig. 1), which if considered as growth stages would indicate an exactly comparable situation to that described by Clarke, i.e. an apparent decrease of the lens number with senescence. Very large specimens of *P. breviceps* and *P. latifrons* again have larger, fewer, and more widely spaced lenses than smaller specimens.

The nature of eye-variation in *P. rana* and in all these other species is therefore a matter of some uncertainty, and has been variously interpreted by these different authors

firstly as the result of a peculiar developmental pattern; secondly as ecological or sexual dimorphism; and thirdly as merely natural subspeciation.

At present the state of taxonomic confusion of the genus *Phacops* renders it difficult to distinguish the most probable of these alternatives. It is quite likely that more than one factor is involved. Abandonment of Clarke's hypothesis is, however, strongly advocated by Beckmann's work, and this conclusion is substantiated by the extreme variability of *P. rana* as shown by its number of possible subspecies. The similarity between the different eye-variants of *P. rana* and those of related species would indicate, nevertheless, that natural subspeciation could be complicated by sexual dimorphism occurring in all these



TEXT-FIG. 1. *Phacops fecundus major* Barrande. Parts of the visual surface of the eyes of three specimens increasing in size from *a* to *c*. The last may possibly be interpreted as a different eye-variant from *a* and *b*, hence this series may reflect a sexually dimorphic condition. (Redrawn from Barrande 1852.) (*a* ×8, *b* ×8, *c* ×6.)

related species. The possibility of such dimorphism has not always been taken account of by systematists.

It has been necessary to defer complete studies of eye development and variation within these species until such taxonomic revisions have been made which would provide a sounder basis for such studies. The purpose of the present study is to show something of the range of visual types within phacopid trilobites. Thus the course adopted here has been to describe and analyse functionally, as individual visual organs, one or two of the representative eye forms of each species or subspecies in question.

Phacops rana (Green 1832)

1832 *Calymene bufo* var. *rana* Green, p. 42.
1888 *Phacops rana* (Green); Hall and Clarke, pp. 19–26, pl. 7, figs. 1–11; pl. 8, figs. 1–8; pl. 8*a*, figs. 21–33.
1889 *Phacops rana* (Green); Clarke, pp. 253–70, pl. 21.
1940 *Phacops rana* (Green); Delo, p. 22, pl. 1, figs. 1, 2.

All available material was referred to the two subspecies *P. rana milleri* Stewart and *P. rana crassituberculata* Stumm. Stumm remarks that the only characters whereby the subspecies may be distinguished are the structure of the eyes and their number of lenses. It is therefore of particular interest to compare the functional characteristics of their eyes.

Phacops rana milleri Stewart 1927

Plate 73, figs. 10–11; text-fig. 2 *d–f*

1927 *Phacops rana* var. *milleri* Stewart, pp. 58–60, pl. 5, figs. 14–17.
1940 *Phacops rana* var. *milleri* Stewart; Delo, p. 23, pl. 1, fig. 3.
1953 *Phacops rana milleri* Stewart; Stumm, pp. 137–8, pl. 9, figs. 1–4, pl. 10, figs. 1–10.

A single adult specimen, SM H 6033, from the Hamilton Group, Devonian, Western New York State, was analysed. Both eyes are preserved, the left is slightly warped, the right is in perfect condition apart from the very bottom of the central region, which is slightly dislodged from its true position. The external morphology of the specimen accords with *P. rana milleri* but there are slightly fewer lenses than in *P. rana rana* which has 104–124. Nevertheless the comparative diameters and the degree of spacing of the lenses is identical with Stewart's type specimens.

Eye morphology (left eye SM H 6033). Dimensions of eye: L. (max.) 7·5 mm. (min.) 5·8 mm.; W. (max.) 4·8 mm. (min.) 4·0 mm.; H. 4·8 mm., where cephalic length (sag.) is 14 mm. and breadth 26 mm.

Eye large and prominent, occupying much of the upper part of the librigena, about half the length and two-thirds the total height of the cephalon but not rising quite as high as the crown of the glabella. The anterior and posterior edges lie approximately in the same exsagittal plane. The eye, which is in the form of a lunate segment of a cone, stands out laterally from the librigena, its base being bounded by a deep groove. In plan the visual surface is rather flattened anteriorly, but very sharply reflexed behind; in profile, the lower part of visual surface again is flattened but the curvature increases upwards, becoming very strong just below the facial suture. Palpebral lobe broad (*tr*), coarsely tubercular, slightly inflated, rising gently from the narrow rim above the facial suture, and declining to the distinct palpebral furrow. Palpebral area lying below the level of lobe, open posteriorly and continuous with surface of librigena.

Lenses disposed in 17 files, which diverge ventrally at a moderate angle, as follows:

466 767 676 655 442* 2* 2; Max. 7; Total 84. (* denotes irregularity.)

(The lower ascending diagonal row is complete apart from the bottom lenses of rows 15 and 16. If this row were unbroken, as would probably be the case in a more normal eye, there would be 86 lenses.) Lenses rather widely spaced between files, but within each file the lowermost lenses are almost contiguous, the spacing increasing upwards so that the top lenses are quite far apart. Lens diameters: Maximum 0·5 mm. (in the upper lenses of

---

EXPLANATION OF PLATE 73

Figs. 1–4. *Phacops rana crassituberculata* Stumm. SM H 7259. Silica Formation, Devonian, Lucas Co., Ohio. Right and left eyes in lateral and dorsal aspects. ×5.

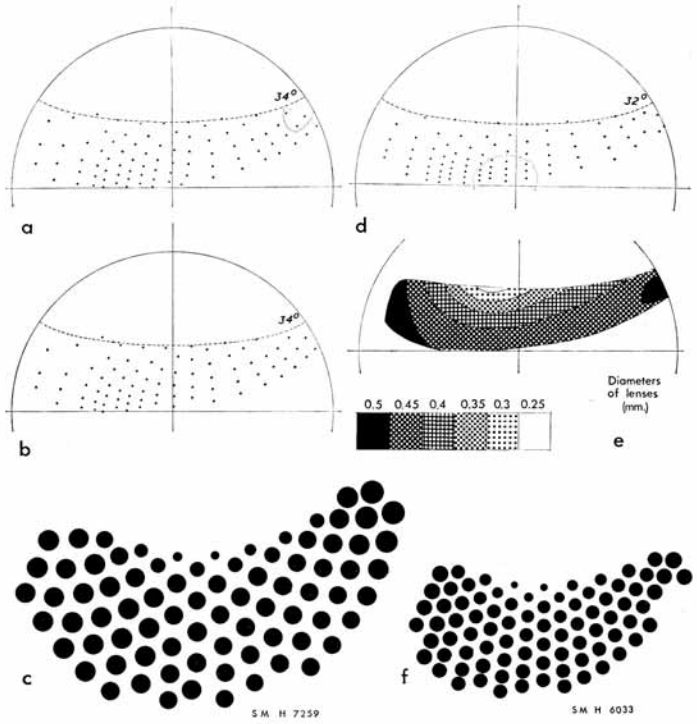
Figs. 5, 6. *Phacops latifrons* (Bronn). SM H 4840. Devonian, Rhineland. Right eye in dorsal and lateral aspects. ×5.

Figs. 7–9. *Phacops fecundus* Barrande. SM A 49374. Stage E_2, Silurian, Dlauha Hora, Bohemia. 7, Central region of the left eye, showing irregular distribution of the lenses. ×25. 8, 9, Left eye in lateral and dorsal aspects. ×5.

Figs. 10, 11. *Phacops rana milleri* Stewart. SM H 6033. Hamilton Group, Devonian, New York State. Right eye in lateral and dorsal aspects. ×5.

the first and last few files), average 0·4 mm. (in the central files), minimum 0·2 mm. (in the centre of the upper horizontal row). Apart from in the latter region and in the first and last files, the lens diameters are fairly constant.

Interlensar sclera only slightly inflated, generally giving the appearance of indistinct intersecting hexagons but flattened above the upper horizontal row, so that the upper



TEXT-FIG. 2. *a–c. Phacops rana crassituberculata* Stumm. SM H 7259. *a*, *b*, Stereograms showing visual fields of left and right eyes respectively. *c*, Projected visual surface of left eye (×5). This eye has one more lens (file 9) than the right eye and the bottom lens of file 8 is slightly displaced. *d–f. Phacops rana milleri* Stewart. SM H 6033. *d*, Stereogram of right eye. *e*, Contoured stereogram showing coverage of different regions of the visual field by lenses of various sizes. *f*, Visual surface of right eye (×5).

rim of the inflated part of the sclera appears undulose, with each lens of the upper row lying in a trough. Each lens is situated in a shallow crater-like depression, above which the crown of the lens just projects, but in the posterior few files these depressions become shallower so that the bases of the lenses are almost flush with the surface of the sclera. All the lenses of the upper horizontal row are set at an angle to the surface of the sclera so that their axes have a lower latitudinal bearing than would be expected from the declination of the surface of the eye.

Character of visual field. The maximum range of vision is 16–184° longitudinally and 0–32° latitudinally. The upper visual limit is latitudinal, but the elevation of the lens-axes of the lower ascending diagonal row increases posteriorly, hence there is a postero-ventral lacuna in the potential visual field. The coverage of different regions of the visual field by lenses of various sizes is shown in text-fig. 2*e*.

The strong differentiation in the curvature of certain regions of the visual surface in plan and profile results in a high concentration of lens-axes in the lower region of the visual field between 45° and 80° long., which is covered by files 3–10. Here the longitudinal axial angles average 6°, but increase anteriorly to 14°, and posteriorly where the curvature is extreme, to 20°. Latitudinal axial angles about 3° in the region of maximum concentration, increasing upwards to 14°; in other parts of the visual field averaging 10°. The axes of the lenses of the upper horizontal row are latitudinal, those of the lower rows are sublatitudinal.

Whereas in each of the anterior and central files, the lens-axes all have about the same longitudinal bearing, in the posterior files there is a marked change in axial direction from top to bottom, and this arrangement of lens-axes enables a considerable angular range to be covered with a maximum economy of lenses.

Phacops rana crassituberculata Stumm 1953

Plate 73, figs. 1–4; text-fig. 2*a–c*

1953 *Phacops rana crassituberculata* Stumm, pp. 136–7, pl. 9, figs. 5–13, pl. 10, figs. 19–21.

The available material was an enrolled and complete topotype, SM H 7259, of very large size with both eyes perfectly preserved.

Eye morphology (SM H 7259). Dimensions of eyes: L. (max.) 11 mm. (min.) 8 mm.; W. (max.) 5·5 mm. (min.) 4·5 mm.; H. 6 mm., where cephalic length (sag.) is 22 mm., and breadth 38 mm.

The chief morphological differences between the eyes of this subspecies and *P. rana milleri* consist only of the relative size of the eye, the number and arrangement of lenses, and the degree of inflation of the sclera. The lenses in SM H 7259 are disposed as follows in 18 files:

Right eye: 345 565 655 555 544 323; Max. 6; Total 80

Left eye: 345 565 656 555 544 323; Max. 6; Total 81

The files diverge ventrally as in *P. rana milleri*, but the lenses are much more widely and evenly spaced, and none are contiguous. Variation in lens-size in different parts of the visual surface resembles that in *P. rana milleri*. Lens diameters: Max. (posterior two files) 0·7 mm., average (central and anterior files) 0·6 mm., Min. (centre of upper horizontal row) 0·25 mm.

Interlensar sclera more highly inflated than that of *P. rana milleri*, hence all the lenses are more deeply sunken, and the depressions in which the posterior lenses lie are more profound, though less deep than those in the central region.

Character of visual field. In both eyes, the visual range is almost identical in extent with that of *P. rana milleri* in spite of the difference in arrangement of lenses (15–180°, long., 0–34° lat.), and there is a similar concentration of lens-axes anterior to the polar

meridian. There is less extreme variation in latitudinal axial angles owing to the shorter dorso-ventral files; here they range from 4 to 12°. The difference in longitudinal bearing between the upper and lower lenses of the posterior files is rather higher than in H 6033, hence the rows of points indicating the axes of the lenses of these files on the stereogram appear more slanted.

Phacops fecundus Barrande 1846

Plate 73, figs. 7–9, Plate 74, figs. 3, 6; text-fig. 3 *a–d*

1846 *Phacops fecundus* Barrande, p. 46.
1852 *Phacops fecundus* Barrande; Barrande, pp. 514–18, pl. 21, figs. 1–27, pl. 22, figs. 32, 33.
1872 *Phacops fecundus* Barrande, and vars. *communis* and *degener* Barrande, pp. 24–25, pl. 13, figs. 1–14.

Variation in the eye of *P. fecundus* as described by Barrande, has already been noted (p. 466). In subsequent accounts of recorded occurrences of *P. fecundus* and varieties (Erben 1952, p. 328–30, with synonomies), no further details as to the morphology of the eyes have been given. Only one adult eye-variant has been examined. Several specimens, SM A 49374, 49375, from Stage E_2 (Barrande 1852), Silurian, Dlauha Hora, Bohemia, and others were examined. The former is the best preserved, and shows an interesting irregularity in the disposition of the lenses.

Eye morphology (left eye SM A 49374). Dimensions of eye: L. (max.) 4·3 mm. (min.) 4·0 mm.; W. (max.) 2·8 mm. (min.) 2·0 mm.; H. 2·0 mm., where cephalic length (sag.) is 12 mm., and breadth 20 mm.

Eye of moderate size, not very prominent, situated near the anterior angle of the librigena, and occupying the central third of the total cephalic length. The anterior edge almost touches the axial furrow; the posterior edge lies further from the sagittal line and is separated from the axial furrow by a broad inflated palpebral area. In this specimen the latter edge falls far short of the posterior marginal furrow, but Barrande regarded this character as variable. In profile the base of the eye lies about half way between the plane of the genal angle and the glabellar crown; the palpebral lobe lies well below the latter.

Curvature of visual surface moderate and fairly uniform, in plan slightly increasing posteriorly. Lenses set on a thickened inflated pad, which is bounded ventrally by a deep groove, and which projects laterally outwards from the librigena, but does not reach as far as the plane of the cephalic border. Outer tuberculate rim of palpebral lobe greatly thickened, projecting outwards above facial suture, and separated adaxially from the slightly inflated centre of the palpebral lobe by a smooth deep groove. Palpebral area strongly inflated, slightly higher than lobe, opening posteriorly to the outwardly declined librigena.

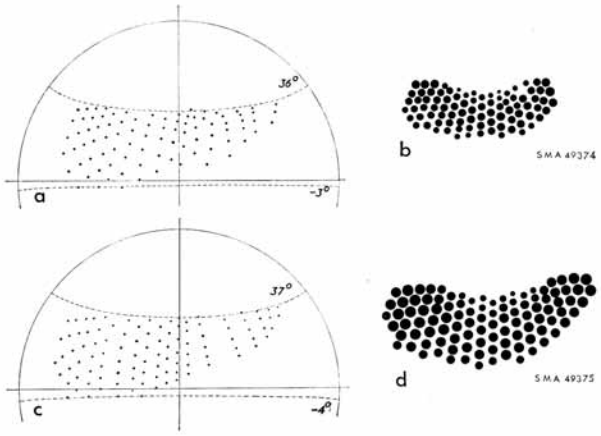
Lenses disposed in 17 files, regularly arranged apart from in the hiatus which lies between the 12th and 16th dorso-ventral files.

456 666 666 664* 655 43; Max. 6; Total 90. (* denotes irregularity.)

The first three files converge ventrally, the rest diverge at a moderate angle. Spacing of lens centres within files is almost uniform. The lens pattern is complicated by the great variation in lens size, which decreases ventrally in the outer files. Lenses of central files separated by more than a lensar radius; elsewhere they may be almost contiguous.

Largest lenses 0·25 mm., average 0·2 mm., smallest 0·1 mm. Very small lenses occur at the bottom of the diagonal rows as well as in the centre of the upper horizontal row. The former are immature. Accessory upper horizontal row present, arising in file 11, but disrupted by hiatus in files 12–16, where the upper lenses are displaced anteriorly from their true position.

Interlensar sclera hardly inflated, finely granular, with larger tubercles in places, forming irregular zigzag rows between the dorso-ventral files.



TEXT-FIG. 3. *Phacops fecundus* Barrande. *a*, *b*. SM A 49374. Visual surface of left eye (×5) and stereogram. The hiatus breaking up of the regularity of the lenses, and the effects of this hiatus upon the dispersal of lens-axes are visible. *c*, *d*. SM A 49375. Visual surface of right eye (×5) and stereogram.

Text-fig. 3*d* represents for comparison the visual surface of a slightly larger specimen SM A 49375, in which the lenses (maximum diameter 0·35 mm.) are disposed regularly in 19 files as follows:

346 676 767 667 665 543 2; Max. 7; Total 102.

Character of visual field. In SM A 49374 the maximum visual range is 27–150° longitudinally, and −3 to 36° latitudinally. A large postero-ventral lacuna is present. The lens-axes are dispersed more uniformly than in *P. rana*, except for the region of the described hiatus. Axial separations in both directions range between 4 and 7°, increasing slightly posteriorly and ventrally. The visual field of SM A 49375 is very similar in extent, 25–153° long., and −4 to 39° lat. Owing to the larger number of lens-axes covering a visual field of similar extent to SM A 49374, latitudinal separations are slightly less and are more uniform.

Phacops breviceps Barrande 1846

Plate 74, figs. 1, 2, 4, 7; text-fig. 4*a–e*

1846 *Phacops breviceps* Barrande, p. 71.
1852 *Phacops breviceps* Barrande; Barrande, pp. 518–19, pl. 22, figs. 24–31.
1951 *Phacops* cf. *breviceps* Barrande; Beckmann, pp. 126–41, pl. 10, 16 figs.

Barrande (1852) recorded 18–22 files per eye, each file containing 5–8 lenses (normally 7), the overall number of lenses ranging from 83–128 according to the age of the specimen. He noted that in the larger specimens the lenses were much more widely spaced and the degree of scleral inflation was greater.

Beckmann (1951) did not distinguish any notable variation in the number and arrangement of the lenses in *P.* cf. *breviceps*, but in the species defined by Barrande variation similar to that of *P. fecundus major* (text-fig. 1) occurs in different specimens found in the same beds. The two principal adult eye-variants found here are for convenience designated eye-variant A and B. Nine cephala, all from Koněprusy Limestone, Stage F_2 (Barrande 1852), Devonian, Koněprus, Bohemia, were examined. A specimen of average size, H 8442 (eye-variant A), and the largest specimen, SM H 8440 (eye-variant B) are described here.

Eye-Variant A (right eye SM H 8442). Dimensions of eye: L. (max.) 6·5 mm. (min.) 5·0 mm.; W. (max.) 3·5 mm. (min.) 2·0 mm.; H. 3·0 mm., where cephalic length is 10 mm. and breadth 22 mm.

Eye medium-sized, quite prominent, visual surface extending from the axial furrow just anterior to the median transverse line, almost to the posterior marginal furrow. Both edges lie approximately in the same exsagittal plane, but owing to the strong rearward convergence of the axial furrows, the posterior edge is separated from the glabella. In profile, the eye occupies the central third of the height of the cephalon, hence the palpebral lobe falls short of the glabellar crown. Plan curvature of visual surface moderate, increasing behind transverse line; in profile the lower part of the eye is seen to be flattened; the degree of flexure increases upwards, becoming extreme just below the facial suture. Eye surface projects outwards above the shallow groove at its base, reaching laterally almost to the plane of the antero-lateral cephalic border. Palpebral lobe sparsely tubercular, rising gently from thickened rim above the facial suture to the curved palpebral furrow, beyond which the smooth palpebral area shelves adaxially to the axial furrow. Lenses disposed as follows in 18 dorso-ventral files:

456 566 666 565 544 332; Max. 6; Total 87.

All files diverge ventrally at a high angle, which is less in the first three files. Lenses quite closely packed, showing little variation in spacing within each file, almost contiguous in outer files. Size distribution as in *P. rana*, largest lenses 0·45 mm., average 0·35–0·4 mm., smallest 0·15 mm. In the ascending diagonal rows there is a rearward increase in diameter, and in the descending diagonals a forward increase.

Interlensar sclera somewhat inflated and smooth.

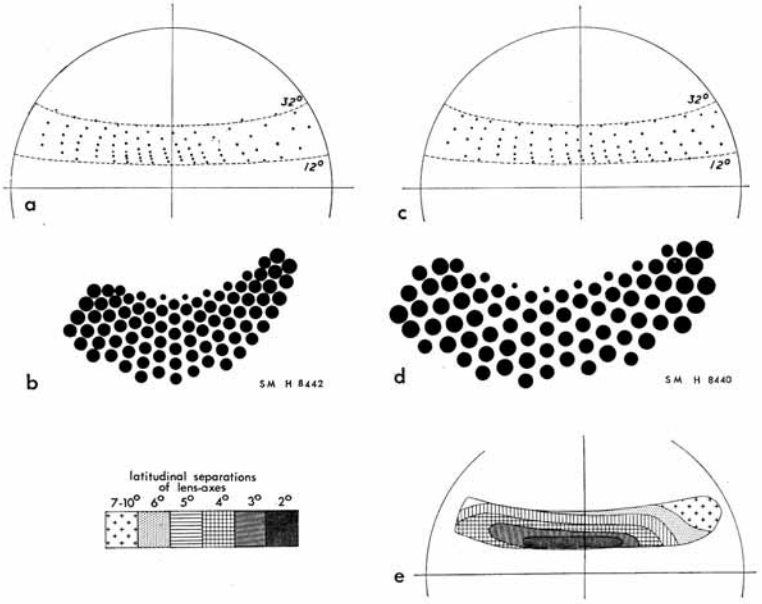
Eye-Variant B (left eye, SM H 8440). Dimensions of eye: L. (max.) 10 mm. (min.) 7·0 mm., W. (max.) 6·0 mm. (min.) 4·5 mm., H. 4·5 mm., where cephalic length (sag.) is 18 mm. and breadth 38 mm.

The position and overall appearance of the eye is not dissimilar to that of SM H 8442 (eye-variant A), but the palpebral lobe shows a higher degree of inflation and is more coarsely tuberculate, and its outer edge where it contacts the facial suture is thickened. As seen directly in lateral aspect this ridge is slightly downwarped. The chief morphological differences between the two eye-variants are exhibited by the visual surface. In this specimen the last two files have been broken off. Impressions of the inner surfaces of

the lenses have, however, been left on the underlying matrix, and have been used for spatial and angular measurements. Lenses disposed as follows in 19 files which diverge ventrally as in eye-variant A:

345 455 555 454 544 443 1; Max. 5; Total 79.

Lenses quite widely spaced, the periphery of each generally lies at a distance of more than a lensar radius from that of its neighbours, but in the first and last few files, where their diameter is particularly large, they are almost contiguous.



TEXT-FIG. 4. *Phacops breviceps* Barrande. *a*, *b*, SM H 8442 (eye-variant A). Stereogram and visual surface of right eye (× 5). *c–e*, SM H 8440 (eye-variant B). *c–d*, Stereogram and visual surface of left eye (× 5). *e*, Contoured stereogram showing latitudinal separations of lens-axes. Longitudinal separations average 7–10°.

Largest lenses (files 17, 18, 19), 0·55 mm. diam., average 0·4 mm., smallest 0·15 mm., those of the first file (1) increasing ventrally from 0·45 mm. to 0·525 mm.

Interlensar sclera inflated so that each lens lies in a shallow cup, but the top of each lens projects above the level of this sclera.

Characters of visual field. The species *Phacops rana*, *P. fecundus*, *P. latifrons* (Pl. 73, figs. 5–6), and *P. breviceps* all exhibit a fairly similar pattern of lens number and distribution. The visual fields of the first three are likewise similar, having a wide latitudinal range, (*c.* 35°), and a strong postero-ventral lacuna. The visual field of *P. breviceps* however, differs radically from these, having a comparatively narrow latitudinal range and no

lacuna. In both eye-variants the total range is about 15–175° longitudinally, and 12–32° latitudinally.

The pattern of lens-axis dispersal is peculiar. The profile surface curvature of the eye in the lower part of the visual field is slight, and axial separations are only 2° or so, but owing to increasing upward curvature, they may reach 10°. The plan curvature is much higher and axial separations vary between 7 and 10°. There are thus partial visual strips, strongly evident in the lower and central parts of the visual field, but which become less distinct towards the top. In eye-variant B there are fewer lenses per file, and the strips are not quite so apparent. Anteriorly the strips are longitudinal, but in the central and posterior regions they run diagonally across the visual field.

Phacops batracheus Whidborne 1889

Plate 74, figs. 5, 8; text-fig. 5 *a*, *b*

1889 *Phacops batracheus* Whidborne, pp. 2–4, pl. 1, figs. 2–7.

Whidborne (1889, p. 2) commented in his full description of this species that the lenses of the eyes were 'very large and convex, in 18 perpendicular rows of from four to six lenses each, between 80 and 90 in all'. He figured the cephalon and left eye of SM H 4072 (1889, pl. 1, fig. 5), which is described here.

All Whidborne's syntypes from the Middle Devonian, at Lummaton, Devon (SM H 4067–74), and many other specimens were available. There is apparently only one eye-variant present, typified by Whidborne's figured specimen, which is perfectly preserved and undistorted, though the surfaces of a few lenses are slightly damaged.

Eye morphology (right eye SM H 4072). Dimensions of eye: L. (max.) 4·5 mm. (min.) 3·5 mm.; W. (max.) 2 mm. (min.) 1·5 mm.; H. 1·75 mm., where the length (sag.) of the cephalon is 9·5 mm., and breadth 20 mm.

Eye large, prominent, lunate, lying in the posterior half of the cephalon, occupying half its total length (sag.), extending from just anterior to the median transverse line to within 0·5 mm. of the posterior marginal furrow. The posterior edge is further from the sagittal line. In profile the eye occupies less than a third of the total height of the cephalon. The base of the visual surface is situated midway between the plane of the genal angle and the glabellar crown. Since the vertical extension of the eye is small as compared with its longitudinal span, the palpebral lobe lies well below the level of the glabella. The visual surface projects laterally almost to the antero-lateral cephalic border.

Plan curvature moderate, increasing posteriorly; profile curvature similar increasing ventrally. Palpebral lobe sparsely tuberculate, rising adaxially above narrow outer rim, becoming horizontal near axial furrow. Palpebral area continuous with lobe; there is no palpebral furrow.

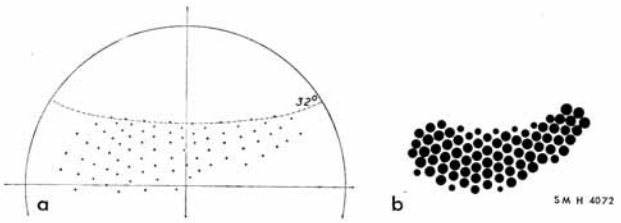
Lenses strongly convex, disposed in 18 files:

355 565 656 554 444 332; Max. 6; Total 80.

The first three files are parallel, the others diverge ventrally at a rather high angle. Individual lenses quite closely packed, almost contiguous in outer files, elsewhere there is about half a lensar radius between them. Within the files each lens centre is situated at a uniform distance from its neighbours. Lens diameters: largest (files 17 and 18) 0·4 mm.

diam.; average 0·375 mm., minimum 0·15 mm., in the centre of the upper horizontal row, and at the lower ends of the longest diagonals. There is no accessory upper horizontal row.

Interlensar sclera only slightly inflated, each lens projects conspicuously from the visual surface. The lenses of the upper horizontal row lie in shallow crater-like depressions, each of which has a prominent scleral rim. The lower edges of the rims are more strongly pronounced, and the lenses set obliquely to the surface of the sclera, and



TEXT-FIG. 5. *Phacops batracheus* Whidborne. SM H 4072. *a*, *b*. Visual surface of right eye (×5) and stereogram.

are thus directed at a lower angle to the horizontal than if they had been normal to the surface (cf. *P. rana*).

Characters of visual field. The maximum range of vision is 20–156° longitudinally, 3–32° latitudinally. The upper visual limit is latitudinal and there is a deep postero-ventral lacuna present. The lens-axes are dispersed regularly and uniformly without any tendency to cluster or form visual strips. Both the latitudinal and longitudinal separations are about the same, averaging 7°. The separations in the lower part of the visual field are slightly greater.

Phacops boecki Hawle and Corda 1847

Plate 74, figs. 9, 10; text-fig. 6 *a*, *b*

1847 *Phacops boeki* Hawle and Corda, p. 107.
1852 *Phacops boecki* Corda; Barrande, p. 513, pl. 20, figs. 30–32.

The fullest previous description is that of Barrande (1852) who recorded 18–21 files per eye, with 5–8 lenses as a maximum depending on the size of the specimen. The total number of lenses ranged from 66–134.

EXPLANATION OF PLATE 74

Figs. 1, 2, 4, 7. *Phacops breviceps* Barrande. Koněprusy Limestone, Stage F_2, Devonian, Koněprus, Bohemia. 1, 2, SM H 8440 (eye-variant B). Left eye in lateral and dorsal aspects. ×5. 4, 7, SM H 8442 (eye-variant A). Right eye in lateral and dorsal aspects. ×5.

Figs. 3, 6. *Phacops fecundus* Barrande. SM H 49375. Stage E_2, Silurian, Dlauha Hora, Bohemia. Right eye in lateral and dorsal aspects. ×5.

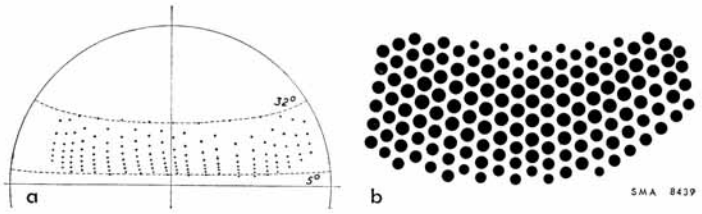
Figs. 5, 8. *Phacops batracheus* Whidborne. SM H 4072. M. Devonian, Lummaton, Devon. Right eye in lateral and dorsal aspects. ×5.

Figs. 9, 10. *Phacops boecki* Hawle and Corda. SM H 8439. Dvorce Limestone Stage G_1 (lower part), Devonian, Dvorce, Bohemia. Left eye in lateral and dorsal aspects. ×5.

Only one well-preserved specimen was available, so only the one eye-variant has been noted. SM H 8439 is a very large adult from Dvorce Limestone, Stage G_1 (lower part) (Barrande 1852), Devonian, Dvorce, Bohemia. Both eyes are well preserved, though the surfaces of some of the lenses are slightly roughened by weathering.

Eye morphology (left eye SM H 8439). Dimensions of eye: L. (max.) 7 mm. (min.) 5 mm.; W. (max.) 4 mm. (min.) 3 mm.; H. 4 mm., where cephalic length is 13 mm., and breadth 23 mm.

Eye very large, prominent, occupying almost half length (sag.) of cephalon, visual surface extending from just anterior to median transverse plane of cephalon almost to the posterior marginal furrow. Both edges lie in approximately the same exsagittal plane. In profile, the eye base is set low on the cephalon, the palpebral lobe standing not quite as



TEXT-FIG. 6. *Phacops boecki* Hawle and Corda. SM H 8439. *a*, *b*. Visual surface of left eye (× 5) and stereogram.

high as the glabellar crown. The visual surface forms a conic segment, with parallel upper and lower borders, whose height/base ratio, if projected to form a cone would be 5:1. Eye surface bounded ventrally by an inwardly shelving flat strip, projecting laterally so as to overhang cephalic border. Plan curvature uniform, moderate; profile curvature very low ventrally, increasing dorsally. Palpebral lobe smooth, bounded laterally by thickened rim, somewhat inflated, shelving adaxially to indistinct palpebral furrow. Palpebral area flat, open posteriorly.

Lenses, as far as can be ascertained, strongly convex, disposed in 21 files:

678 788 888 888 878 776 654; Max. 8; Total 150.

All files diverge ventrally at a very low angle.

Lenses rather widely spaced, generally separated by distance of a lensar radius and remarkably constant in size throughout the visual surface, peripheral lenses generally slightly smaller. Largest lenses 0·35 mm., diam. smallest 0·2 mm.

Interlensar sclera only slightly inflated between lenses of central files.

Character of visual field. The maximum range of vision is 25–172° longitudinally, 5–32° latitudinally. Both the upper and lower limits are almost entirely latitudinal. In spite of the proximity of the posterior edge of the eye to the rear border of the cephalon, there is only a slight upward deflection of the lower limit in the hindermost part of the visual field, posterior to 140° long. and covered by files 18–21.

Owing to the extremely low profile curvature of the visual surface near the base of the

eye, the axes of the lower lenses of the dorso-ventral files are concentrated in visual strips, in which axial separations are as low as 1°; but the upward increase in curvature results in separations of up to 12° near the top of the visual field and the strips fade out dorsally. The visual strips are quite regularly spaced, and the angles separating them vary between about 7 and 10° of longitude.

Superfamily DALMANITACEA

Dalmanites vulgaris (Salter 1849)

Plate 75, figs. 1–4; text-fig. 7 *a–e*

1822 *Asaphus caudatus* Brongniart, p. 22, pl. 2, figs. 4 *a–d*.
1845 *Dalmannia caudatus* (Brünnich); Emmerich, p. 38.
1849 *Phacops caudatus* (Brünnich) var. *vulgaris* Salter, pp. 1–6, pl. 1, figs. 1–12, 15.
1864 *Phacops* (*Odontochile*) *caudatus* (Brünnich) var. *vulgaris* Salter; Salter, pp. 49–53, pl. 3, figs. 4–17. (= *Dalmanites caudatus* (Brünnich) of later writers.)
1935 *Dalmanites vulgaris* (Salter); Delo, pp. 424–6, pl. 48, figs. 8, 9.

Salter's descriptions of 1849 and 1864 include good illustrations of the eye. He recorded about 240 lenses per eye, and 8–10 per file. He also noted that in some specimens the eyes were larger than in others and referred this difference to sex, concluding that the male had larger eyes.

Many specimens from the Wenlock Limestone have been examined, but although some variation is apparent within the species there is as yet no conclusive evidence of sexual dimorphism.

In the best-preserved specimen examined, SM A 28635, both eyes are well preserved, though part of the left eye is chipped and two patches of polyzoa have encrusted the upper rim of the right eye, obscuring a few lenses. The lenses retain their full convexity.

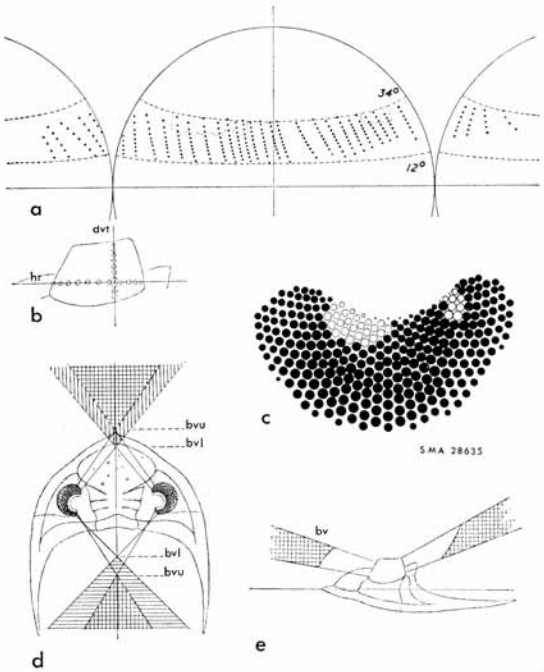
Eye morphology (right eye SM A 28635). Dimensions of eye: L. (max.) 5 mm. (min.) 3 mm.; W. (max.) 4 mm. (min.) 2·5 mm.; H. 3 mm., where cephalic length (sag.) is 17 mm., and breadth 30 mm.

Eye large, situated posteriorly on the cephalon, standing high above the glabella, and forming a truncated cone whose height/base ratio, if projected to form a cone would be 4:1. The anterior edge is separated from the axial furrow, and the posterior edge lies further from the sagittal line. The eye base occupies the summit of the librigena, and is surrounded by a moat-like depression, with an external concentric ridge, which limits the genal field. Plan curvature very strong and fairly uniform, but in profile the visual surface is almost flat and inclined at about 80° to the horizontal. In the 'natural attitude' (text-fig. 7 *b*, *e*). the upper rim is oblique to the horizontal, and the eye appears to slope forwards and downwards, though the 'horizontal' lens-rows actually lie in a horizontal plane.

The narrow (*tr*) palpebral lobe is almost uniformly curved in plan and consists of a narrow strip with a shallow concentric groove running parallel with the facial suture. It plunges steeply adaxially to the palpebral furrow, which lies a short distance below the upper rim of the eye. The tuberculate palpebral area declines with increasing steepness towards the axial furrow.

There are 34 dorso-ventral files in which the lenses are disposed as follows:

467 899 10 9*10* 10*11*10* 11*10*11* 10*11*10 11 10 10 10 10 9 9 8 8 7 8 8 765 2; Max. 11; Total 294 (* In the regions where the eye surface is covered by polyzoa, the number of lenses in the other eye have been counted.)



TEXT-FIG. 7. *Dalmanites vulgaris* (Salter). SM A 28635. *a*, *c*, Stereogram and visual surface of right eye (×5). The blank circles and the corresponding enclosed areas on the stereogram represent lenses covered by polyzoa. The equivalent lenses and lens-axes of the left eye are substituted here. *b*, Left eye in 'natural orientation' showing a horizontal row (*hr*) and one of the dorso-ventral files (*dvf*), which in this attitude appears vertical. *d*, Limits of binocular vision shown by the bearings of the upper (*bvu*) and lower (*bvl*) lenses of the first and last files. *e*, Profile view of the cephalon showing limits of binocular vision with respect to the upper surface of the head. Apparent angular bearings are shown here (apparent latitude = $\tan\theta \cos\phi$ where θ is the latitudinal and ϕ is the longitudinal bearing of the lens-axis in question).

Apart from the first and last three dorso-ventral files, which are parallel, the files diverge ventrally at a very high angle (the highest observed so far in any Phacopina). Within the files the lenses are closely packed together. In the lower part of the visual surface the lenses of adjacent files are quite widely spaced owing to the high downward divergence of the files so that there is about the distance of a lensar radius between them; but in the median and upper parts of the eye they are almost contiguous. The distance between the lenses within the files gradually increases upwards. The largest lenses

(diam. 0·3 mm.) occur in the central region of the visual surface. On the periphery of this region they are smaller and all round the borders of the visual surface lenses of diameter less than 0·2 mm. are present. Hence the lowest two or three ascending and descending diagonal rows contain small lenses.

Minute lenses are found in the centre of the upper horizontal row and in an incipient accessory upper horizontal row which is present at the top of files 26, 28, and 30.

Interlensar sclera is indistinguishable in the region of the large closely packed lenses, but is visible at the bottom of the eye, and is tuberculate. Each lens here is surrounded by an irregular polygon of fine points.

Character of visual field. The maximum range of vision is 265° longitudinally, and 12–34° latitudinally. The visual fields of the two eyes overlap anteriorly and posteriorly and, as in all dalmanitids, the lenses covering the overlapping parts are small. The axes of the top and bottom lenses of the first files have slightly different longitudinal bearings (40 and 35°) and meet just in front of the glabella and the anterior margin of the cephalon respectively. Lens-axes of the last file likewise have different bearings (—35 and 45°) and meet at some distance behind the occipital ring clearing it by a fair angle (text-fig. 7 *d*, *e*). The upper limit is largely latitudinal, as is the lower over the anterior region, but posteriorly there is a shallow lacuna.

As in *Acaste downingiae* the strong differential curvature of the visual surface results in the arrangement of the lens-axes of the files into very distinct visual strips. Within the strips axial separations are usually less than 2° and never more than 4°. Between strips axial angles are about 6–7° though axial separations twice this figure occur between files 19 and 20, just posterior to the polar meridian. A unique feature of this eye is that all the visual strips slant the same direction and the top lens-axis in each file has about the same angular bearing as the bottom lens-axis of the preceding file. This condition may be contrasted with that in *A. downingiae*, where the strips follow a radial pattern, and that in *Chasmops odini* where they are curved. It may be considered as an adaptation whereby the whole longitudinal field of view is covered, with maximum economy of lenses.

In the overlapping parts of the visual field the separation of the visual strips is rather more variable.

Dalmanites caudatus (Brünnich 1781)

Plate 75, figs. 5, 6; text-fig. 8 *a–j*

1781 *Trilobus caudatus* Brünnich, p. 392.
1839 *Asaphus longicaudatus* Murchison, p. 656, pl. 14, figs. 11–14.

EXPLANATION OF PLATE 75

Figs. 1–4. *Dalmanites vulgaris* (Salter). SM A 28635. Wenlock Limestone, Silurian, Dudley, England. 1, 2, 4, Right eye in lateral, dorsal, and dorso-lateral aspects. ×7·5. 3, Lenses near the lower rim of the visual surface. ×20.

Figs. 5, 6. *Dalmanites caudatus* (Brünnich). SM A 28644. Wenlock Limestone, Silurian, Dudley, England. Left eye in lateral and dorsal aspects. ×5.

Figs. 7–11. *Chasmops odini* (Eichwald). SM A 53427. C_2 Kukruse shale or C_3 Itfer shale, Caradocian, Estonia. 7, Right eye, lenses near the lower rim of the visual surface. ×25. 8–11, Right eye in lateral, frontal, dorso-lateral, and dorsal aspects. ×5.

1845 *Dalmannia longicaudata* (Murchison); Emmerich, p. 40.
1849 *Phacops caudatus* (Brünnich) var. *longicaudatus* (Murchison); Salter, pp. 1–6 (pars), pl. 1, figs. 13–14.
1864 *Phacops* (*Odontochile*) *longicaudatus* Murchison; Salter, pp. 55–56, pl. 3, figs. 19–28. (=*Dalmanites longicaudatus* of later authors.)
1935 *Dalmanites caudatus* (Brünnich); Delo, pp. 424–6, pl. 48, figs. 6, 7.

The fullest previous descriptions of this Wenlock Limestone species are those of Salter (1849, 1864). He made only brief reference to the eye.

Many specimens have been examined but only one eye-variant has been distinguished. SM A 28644 is well preserved, though the lensar surfaces have in some cases been planed off. Both eyes are identical.

Eye morphology (left eye SM A 28644). Dimensions of eye: L. (max.) 5 mm. (min.) 3·5 mm.; W. (max.) 3·5 mm. (min.) 3 mm.; H. 3 mm., where cephalic length is 13 mm. and width 20 mm.

The form and situation of the eye resembles that of *D. vulgaris*; the major differences lie in the degree of curvature, the character of the palpebral lobe, and the number and arrangement of the lenses. The visual surface is very strongly and regularly curved in plan, whereas in profile the degree of curvature of the anterior part of the visual surface is considerable but lessens posteriorly so that in the region of the last few files the eye is almost flat. The palpebral lobe is extremely narrow (*tr*), and plunges very steeply to the U-shaped palpebral furrow, which lies well below the upper rim of the eye.

Lenses disposed as follows in 32 files:

457 889 899 999 989 899 999 988 888 776 52; Max. 9; Total 249.

The outer files converge ventrally, but the central ones diverge at quite a high angle. Within files lens spacing increases ventrally. In the upper regions they are so closely packed as to be hexagonal, elsewhere they are rounded. The largest lenses (0·25 mm.) occur in a wide crescent running through the upper anterior, lower central, and upper posterior parts of the visual surface. Outside this crescent lie smaller lenses (0·175 mm.). In SM A 28644 the central lenses of the upper horizontal row have failed to develop. Three minute lenses at the top of files 25, 27, and 29 represent an incipient accessory upper horizontal row.

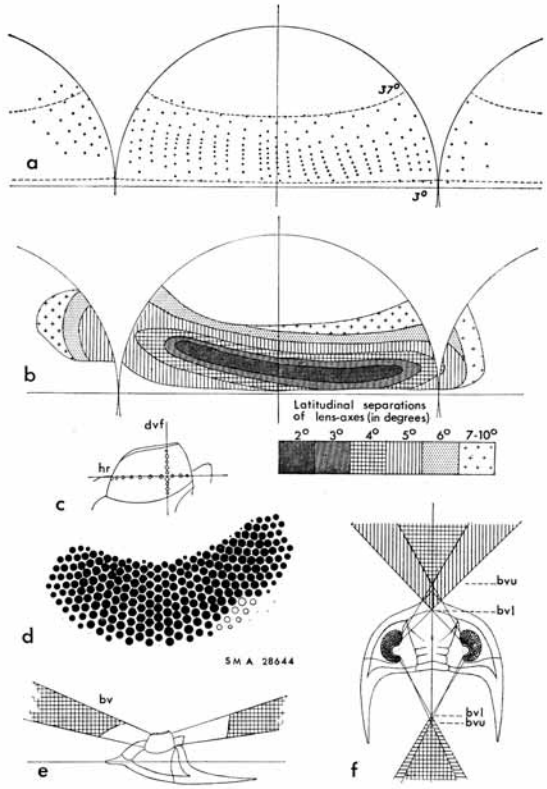
The lenses are so closely packed that no interlensar sclera can be seen.

Character of visual field. The maximum range of vision is 254° longitudinally, 3–37° latitudinally. There is an overlap of the visual fields of the two eyes comparable with that of *D. vulgaris* (text-fig. 8*e*, *f*), though there is a greater difference (15°) between the longitudinal bearings of the top and bottom lenses of file 1, which seems to be associated with the relatively longer distance between the front of the glabella and the anterior point.

Lens-axes of the dorso-ventral files form visual strips which are separated by angles of 5–8°. Some of these strips are longitudinal, others, particularly those associated with the more posterior files, are divergent. Although the strips are quite regularly spaced they are quite unlike those of *D. caudatus* because of the strong differentiation in profile curvature of the eye from front to rear. On the contoured stereogram (text-fig. 8*b*) this change in curvature is shown by a band of closely spaced lens-axes which traverses the visual field diagonally in the anterior part of the visual field, and lies almost horizontally

posteriorly. Within this band latitudinal axial separations average 2–3°, outside it they may be as high as 10°, and normally approximate the longitudinal separations.

The elevation of the lens-axes within the horizontal rows declines gradually backwards, but as the three small lenses of the accessory upper horizontal rows have elevations of 37°, the upper visual limit is unbroken.



TEXT-FIG. 8. *Dalmanites caudatus* (Brünnich). SM A 28644. *a*, *d*, Stereogram and visual surface of left eye (×5). *b*, Contoured stereogram showing latitudinal separations of lens-axes. The diagonal band containing the lowest separations is distinct. Longitudinal separations average 6–8°. *c*, Left eye in natural orientation. *e*, *f*, Limits of binocular vision, notation as in text-fig. 7.

Chasmops odini (Eichwald 1840)

Plate 75, figs. 7–11; text-fig. 9 *a*, *b*

1840 *Calymene odini* Eichwald, p. 62.
1851 *Chasmops odini* (Eich. sp.); M'Coy, p. 164, pl. 1*g*, figs. 22, 23.
1881 *Chasmops odini* (Eichwald); Schmidt, p. 101, tab. 2, figs. 1–13.
1937 *Chasmops odini* (Eichwald); Öpik, p. 77, tab. 9, figs. 5, 6, text-figs. 23–25.

In Eichwald's original description of this species little reference was made to the eye, but Schmidt gave a very detailed account, noting about 240 lenses in 20–22 files, and about 12 lenses per file. His excellent figures (1881, figs. 2, 8, 9) showed the almost flat visual surface. No new information was recorded by Öpik.

The material studied was a single cephalon, SM A 53427, from the Caradocian of Estonia (C_2 Kukruse shale or C_3 Itfer shale (after Öpik)). It is preserved in full relief and both eyes are present. The upper surface of the left eye is broken, but the right is undamaged apart from the posterior upper rim and a few of the topmost lenses which have been broken off.

Eye morphology (right eye SM A 53427). Dimensions of eye: L. (max.) 5·5 mm. (min.) 5·0 mm.; W. (max.) 4·5 mm. (min.) 4·0 mm.; H. 5·5 mm., where cephalic length (sag.) is 16 mm. and breadth 30 mm.

Eye very prominent and set high on the cephalon forming a high truncated cone, which if projected to form a cone would have a height/base ratio of 10:1. The anterior edge is situated almost exactly half way between the anterior border and the occipital ring, on a level with glabellar furrow (3p), and the posterior edge lies some way (2 mm.) anterior to the posterior marginal furrow. Both the anterior and posterior edges of the eye lie almost in the same exsagittal plane, the former being separated from the axial furrow by the highly inflated fixigena. The visual surface reaches almost to the antero-lateral border.

A deep lunate depression surrounds the base of the eye, external to which lies the narrow genal field from which the librigena plunges vertically. In plan the visual surface is strongly curved and parabolic about the transverse line but in profile it is almost flat with only the slightest curvature. The prominent outer rim of the palpebral lobe surrounds the whole of the upper edge of the visual surface and projects outwards over it, becoming thicker where it plunges downwards subparallel with the anterior and posterior dorso-ventral file. Adaxially to the rim the inner face of the palpebral lobe slopes to meet the palpebral furrow, which in its central part is very sharply reflexed so as to be almost V-shaped (the point of the V being directed outwards). At the base of the eye the palpebral furrow joins with the deep groove surrounding the bottom of the visual surface, so that the whole eye is encircled by one continuous furrow. The palpebral area is inflated and open to front and rear.

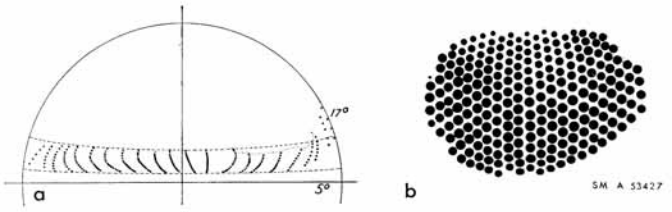
There are 22 dorso-ventral files, with the following lens distribution:

5 7 10 11 12 13 14 14 14 14 14 14 14 13 12 12 11 10 9 7 5 4; Max. 14; Total 239.

In all other phacopids which have been investigated the dorso-ventral files are straight, but here only the central files are straight and the outer files are curved outwards, the degree of flexure increasing in opposite directions away from the centre. (In text-fig. 9 the curvature of these files is shown as accurately as possible, but in representing the distance apart of the outer lenses there is some inevitable distortion.) Thus the files diverge from the top downwards at a moderate angle from each other and just below the median plane they being to converge again. All the lenses are quite closely packed, but there is a gradual upward increase in the distance between the lenses in the dorso-ventral files, hence the lowest lenses are elliptical and almost contiguous, whereas the smaller upper

lenses are rounded and are nearly their own diameter apart. In certain files elliptical lenses occur near the top of the eye but generally they are round. Between the lenses of adjacent dorso-ventral files the separation is generally greater than the vertical distance between lenses within a file.

The lenses of the lower central and outer parts of the visual surface are the largest (0·3 mm.) and are of relatively uniform diameter. In the central files the lenses become progressively smaller upwards from the median region, decreasing to 0·15 mm. diam. Those of the upper horizontal row are of about the same diameter, and only increase slightly in size away from the centre. The interlensar sclera is flat but furnished with small round tubercles in the interstices of the lenses which form irregular polygons surrounding each lens. At the base of the visual surface these tubercles are very numerous and completely cover the lower rim.



TEXT-FIG. 9. *Chasmops odini* (Eichwald). SM A 53427. *a*, *b*. Stereogram and visual surface of right eye (× 5).

Characters of visual field. The maximum range of vision is 180° longitudinally, 5–17° latitudinally. Both visual limits are latitudinal, except at their posterior extremities, where the elevation of the lenses of the last few files increases greatly.

The pattern of lens-axis dispersal, as shown on the stereogram, is one of the most remarkable observed in any phacopid. The axes of the numerous lenses in the dorso-ventral files are accommodated within the visual field in very distinct, widely separated, and peculiarly curved visual strips. The curved appearance of these strips obviously relates to the curving files themselves; both are bowed outwards in opposite directions away from the central file, whose equivalent strip has a bearing of about 105° long. Within strips the latitudinal axial separations of the lens-axes may be as low as $\frac{1}{2}$°, though towards the extremities it increases to 2° or 3°. Longitudinal separations between strips may be as high as 15°. Apart from those in the last few files, where there is a sudden increase in elevation, all the lens axes of the horizontal rows have approximately constant bearings.

SUMMARY

This paper, together with my previous one (Clarkson, 1966*a*) describes the relationship between eye-form and the spatial and angular characteristics of the lenses, in a number of typical schizochroal trilobite eyes. Full physiological interpretations of this and other information relating to trilobite vision are to be made in a later paper but a brief concluding summary of observations to date can be given.

External morphology of eyes

(i) Lenses upon the visual surface are normally arranged in a regular pattern of hexagonal close packing. Breakdown in regularity occurs in a few cases.

(ii) During postlarval ontogeny there is an increase in lens number until full maturity is reached. The adult lens-number within species is approximately constant, though in some species there are apparently two distinct adult eye-variants, which may reflect a sexually dimorphic condition. In the present state of taxonomic confusion it is not yet possible to elucidate this matter further.

(iii) Within the visual surface of individual specimens of the Phacopina there is normally considerable variation in lens-size. Small lenses are always found in the upper central region, and the newly emplaced lenses at the lower ends of the dorso-ventral files are likewise small. The pattern is distinct in all the species investigated except *Chasmops odini*.

(iv) Lens size, number, and spacing vary greatly within the Phacopina as a whole. Eyes with very large lenses, e.g. *Phacops rana crassituberculata*, normally only have a limited lens number. In some eyes increased lens number has been achieved by the close packing of the lenses so that they become hexagonal. Characteristic patterns of the arrangement of lenses upon the visual surface relate to systematic categories and presumably reflect evolutionary relationships.

(v) Variation in lens-size within the visual surface of individuals is normally independent of differential surface curvature.

(vi) The lenses are not always set normal to the visual surface but owing to their large size their axial directions may readily be inferred from the external morphology of the eyes.

Characters of visual fields. Three main patterns of the arrangement and dispersal of lens-axes are found within Phacopina, largely as a result of distinct modes of curvature of the visual surface. In species with two adult eye-variants the visual fields of both may be of similar extent, although the lens-axes may have a slightly different arrangement. These patterns are as follows:

(i) Visual fields of wide (*c.* 30–40°) latitudinal extent, normally associated with eyes of 100 lenses or less, in which the plan curvature is rarely more than twice the profile curvature. The upper visual limit is normally latitudinal, though a deep triangular postero-ventral lacuna is commonly present which truncates the equatorial lower limit. This device apparently prevents occlusion of vision in this region by the high posterior cephalic border. Axial separations are high though some of the lens-axes may be clustered together in the lower anterior part of the visual field. Examples are *Phacops rana milleri*, *P. rana crassituberculata*, *P. latifrons*, *P. fecundus*, *P. batracheus*, *P. musheni* (see Clarkson, 1966*b*), *Acastoides constricta*.

(ii) Visual fields of narrow (10–20°) latitudinal extent usually relating to eyes with upwards of 100 lenses, curving very much more in plan than in profile. Both visual limits are generally latitudinal; if there is a lacuna it is shallow. The lower visual limit lies at 10° or more above the equator. Such eyes are highly astigmatic, as the lens-axes are dispersed in visual strips which are present from a very early stage in postlarval development. These strips cross the visual field from top to bottom and may be disposed either radially as in *Acaste downingiae*, diagonally in *Dalmanites vulgaris*, or may themselves be curved, e.g. *Chasmops odini*.

(iii) Visual fields which combine many of the features of (i) and (ii). The number of lenses in the eye is variable. Both visual limits are latitudinal, the lower normally lying a few degrees above the equator (12° in *P. breviceps*). Incomplete visual strips are developed which run in a band normally parallel with the visual limits (apart from *Dalminites caudatus*) but which do not extend the full latitudinal width of the visual field. In *P. breviceps* and *P. boecki* this band of partial visual strips lies at the base of the visual field; in *Acaste downingiae macrops* it is above this level; and in *D. caudatus* it runs diagonally across the anterior part of the visual field and posteriorly runs parallel to and just above the lower limit.

Acknowledgements. The author's thanks are due to Prof. O. M. B. Bulman for research facilities in the Sedgwick Museum, Cambridge, and to Mr. A. G. Brighton for the loan of specimens in his charge. Dr. M. J. S. Rudwick offered stimulating supervision throughout the work, and Mrs. C. M. Clarkson gave helpful advice, and assisted with the preparation of the manuscript.

Much of the original research was carried out while the author was in receipt of a D.S.I.R. Research Studentship.

REFERENCES

BARRANDE, J. 1846. *Notice préliminaire sur le Systéme silurien et les Trilobites de Bohême.* 1–97, pl. 1. Leipzig.

—— 1852. *Système silurien du Centre de la Bohême. Ière partie; Crustacés; Trilobites.* **1,** 1–935, pl. 1–51. Prague and Paris.

—— 1872. *Système silurien du Centre de la Bohême; Supplément au vol. I. Trilobites, Crustacés diverses et Poissons.* 1–647, pl. 1–37. Prague and Paris.

BECKMANN, H. 1951. Zur Ontogenie der Sehflache großäugiger Phacopiden. *Paläont. Z.* **24,** 126–41, pl. 10.

BRONGNIART, A. and DESMAREST, A. G. 1822. *Histoire naturelle des Crustacés fossiles, sous les rapports zoologiques et géologiques.* 1–154, pl. 1–11. Paris.

BRÜNNICH, M. T. 1781. Beskrivelse over Trilobiten. *K. danske Vidensk. Selsk. Skr.* N.S. **1,** 1–384.

CLARKE, J. M. 1889. The structure and development of the visual area in the trilobite *Phacops rana* Green. *J. Morph.* **2,** 253–70, pl. 21.

CLARKSON, E. N. K. 1966*a*. Schizochroal eyes and vision of some Silurian Acastid Trilobites. *Palaeontology*, **9,** 1–29, pl. 1–3.

—— 1966*b*. The life attitude of the Silurian trilobite *Phacops musheni* Salter 1864. *Scot. J. Geol.* **2,** 76–83, pl. 1.

DELO, D. M. 1935. The genotype of *Dalmanites. J. Palaeont.* **9,** 424–6, pl. 48.

—— 1940. Phacopid trilobites of North America. *Spec. Pap. geol. Soc. Am.* **29,** 1–135, pl. 1–13.

EICHWALD, C. E. VON. 1840. *Sur le système silurien de l'Estonie.* 1–122. St. Petersbourg.

EMMERICH, H. F. 1845. Ueber die Trilobiten. *Neues Jb. Miner. Geol. Paläont.* (Bd. 1845), 18–52, pl. 1.

ERBEN, H. K. 1952. Trilobiten aus dem älteren Hercyn (Unterdevon) des Unterharzes. *Neues Jb. Geol. Paläont.* Abh. **94,** 150–362, pl. 17–24, 64 figs.

GREEN, J. 1832. *A monograph of the Trilobites of North America.* 1–93, pl. 1–4. Philadelphia.

HALL, J. and CLARKE, J. M. 1888. Trilobites and other Crustacea. *Paleontology of New York*, **7,** 1–236, pl. 1–36. Albany.

HAWLE, I. and CORDA, A. J. C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. *K. Böhm. Ges. Wiss.* Abh. **5,** 129–212, pl. 1–7.

LINDSTRÖM, G. 1901. Researches on the visual organs of the trilobites. *K. Svensk. Vetensk. Akad. Handl.* **34,** 1–86, pl. 1–6.

M'COY, F. 1851. *British Palaeozoic Fossils in the Geological Museum of the University of Cambridge.* 1–661, pl. 1A–3K. London and Cambridge.

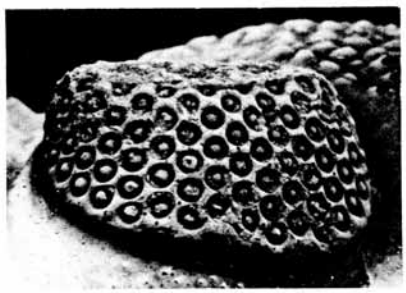
MURCHISON, R. I. 1839. *The Silurian System.* 1–768, pl. 1–40. London.

ÖPIK, A. A. 1937. Trilobiten aus Estland. *Acta Comment. Univ. tartu.* **A.** *Math.—Phys.—Med.* **32,** 1–163, pl. 1–26, figs. 1–42.

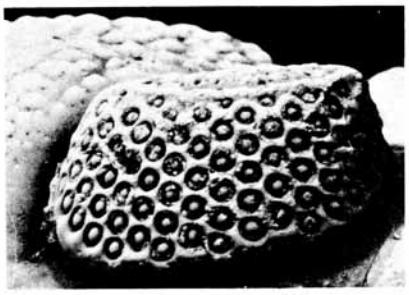
RUDWICK, M. J. S. 1964. The inference of function from structure in fossils. *Br. J. Phil. Sci.* **15,** 27–40.
SALTER, J. W. 1849. Figures and descriptions illustrative of British Organic Remains. Decade II. *Mem. geol. Surv. U.K.*
—— 1864–83. A monograph of British Trilobites. *Palaeontogr. Soc.* [*Monogr.*], 1–224, pl. 1–30.
SCHMIDT, F. 1881. Revision der ostbaltischen silurischen Trilobiten nebst geognostiche Übersicht des ostbaltischen Silurgebiets. Abt. 1 Phacopiden, Cheiruriden, und Encrinuriden. *Mem. Acad. imp. sci. St.-Petersbourg*, **30,** 1–237, pl. 1–16.
SHAW, F. C. and ORMISTON, A. R. 1964. The eye socle of trilobites. *J. Paleont.* **38,** 1001–2, fig. 1.
STEWART, G. A. 1927. Fauna of the Silica Shale of Lucas County. *Bull. geol. Surv. Ohio*, **32,** 1–76, pl. 1–5.
STUMM, E. C. 1953. Trilobites of the Devonian Traverse Group of Michigan. *Contr. Mus. Paleont. Univ. Mich.* **10,** 101–57, pl. 1–12, 1 map.
WHIDBORNE, G. F. 1889–92. A monograph of the Devonian Fauna of the South of England. Vol. 1. *Palaeontogr. Soc.* [*Monogr.*], 1–344, pl. 1–31.

E. N. K. CLARKSON
Grant Institute of Geology,
University of Edinburgh,
Edinburgh, 9

Manuscript received 12 August 1965

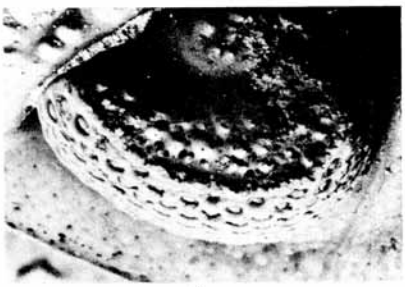


1



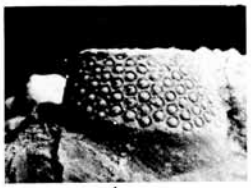
2

3

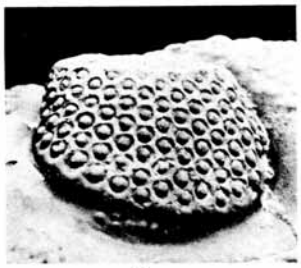


4

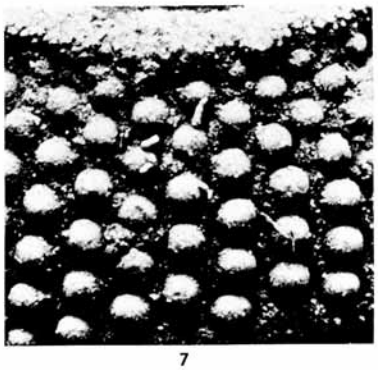
5



6



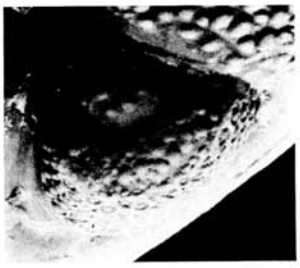
10



7

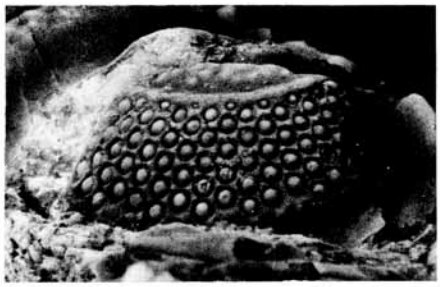
8

9



11

CLARKSON, Schizochroal eyes in phacopid trilobites

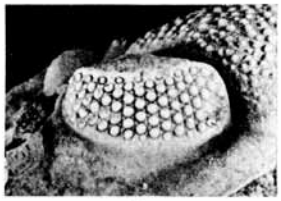


1

2

3

4

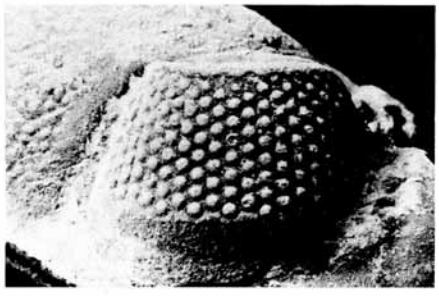


5

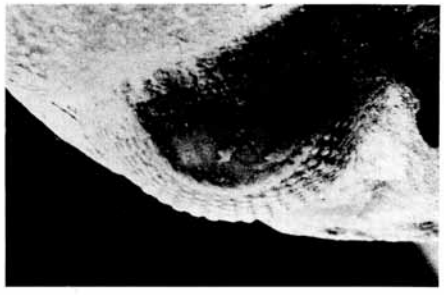
6

7

8



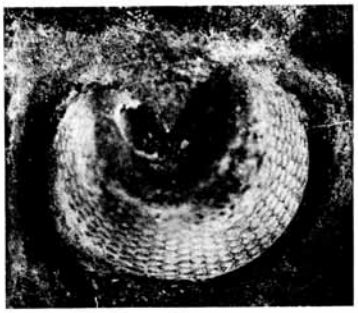
9



10

CLARKSON, Schizochroal eyes in phacopid trilobites

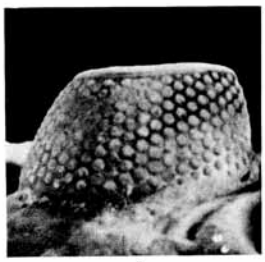
1



2

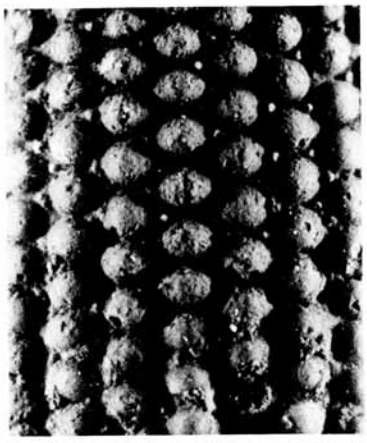
3

4



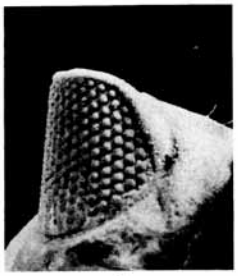
5

6

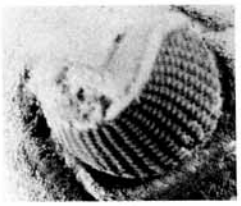


7

8



9



10

11

CLARKSON, Schizochroal eyes in phacopid trilobites