

# MORPHOLOGY AND EVOLUTION OF THE EYE IN UPPER CAMBRIAN OLENIDAE (TRILOBITA)

by E. N. K. CLARKSON

**ABSTRACT.** The eyes of selected olenid species from Scandinavian concretionary shales were examined with the scanning electron microscope. Though these eyes are small, many previously unknown details were visible, including the 'peripheral zone' of *Olenus wahlenbergi* and other genera. Reconstructions, prepared by camera-lucida techniques, show the eye and the whole cephalon of certain species.

In early olenids the visual surface was dehiscent in the adults and is preserved only in meraspids; in later genera the ocular suture became fused and the visual surface was retained. Details of lens distribution and manner of emplacement are described in *Peltura minor*, *P. scarabaeoides*, and *Ctenopyge (Mesoctenopyge) similis*. Evolutionary changes in the structure and shape of the eye are clear in different lines of descent. Some of the observed modifications are thought to be due to paedomorphosis.

Some comments on the mode of life of olenids are also given.

## THE EYES OF CAMBRIAN TRILOBITES

AT the end of the Cambrian there was a major crisis in the history of the trilobites. Most of the rather undifferentiated Upper Cambrian stocks became extinct and were replaced, first by a number of short-lived Tremadoc groups, and then soon afterwards by several very distinct suborders which came to dominate the Ordovician trilobite fauna (Whittington 1966).

This late Cambrian crisis had far-reaching effects on the evolution of trilobites. Certain morphological features which had remained rather conservative during Cambrian times became much more diversified and novel kinds of functional organization came into being. Amongst the characters affected was the visual system, and the new trilobite stocks of the early Ordovician evolved eyes exhibiting greater variety than those possessed by their Cambrian forebears. Not only did the primitive holochroal organization, which was already established in the earliest Cambrian trilobites, become modified in many different ways, but there first appeared an entirely new kind of visual organ, the schizochroal eye (which may have been derived from a holochroal ancestral pattern by paedomorphosis according to Clarkson (1971). This kind of eye is probably confined to the suborder Phacopina, which persisted from Arenig to Famennian times.

Though some of the many different kinds of eye in Ordovician and later trilobites have been quite extensively studied there is at present so little information on the eyes of Cambrian genera that we do not have a comprehensive picture of the evolution of the eye in trilobites. One good reason for this is that the eyes in adult specimens of Cambrian trilobites are not very often preserved, though in a few cases intact lenti-ferous surfaces have been reported. Thus Walcott (1910) noted lenses in the eyes of meraspids of the Lower Cambrian *Olenellus gilberti* Meek and Öpik (1961, p. 57) and later Jell (1970, p. 306) and Jago (1972, p. 230) discussed the presence of lenti-ferous surfaces in Cambrian pagetiids, where the eye has a 'schizochroal' appearance.

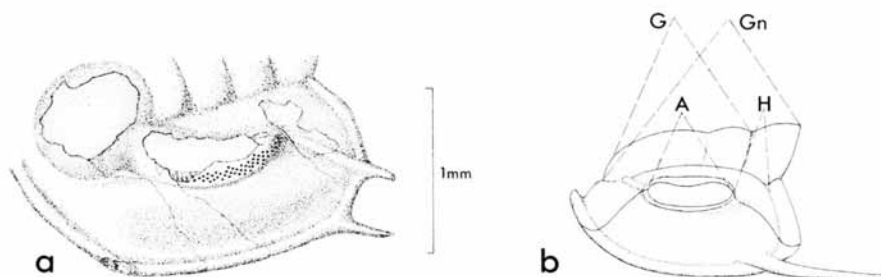
[Palaeontology, Vol. 16, Part 4, 1973, pp. 735-763, pls. 91-95.]

I am not aware that any visual surfaces are known to be preserved in Middle Cambrian trilobites, but amongst the Upper Cambrian fauna certain genera with intact eyes occur sporadically, and different kinds of eyes may be preserved within particular groups such as the family Olenidae, which are the subject of the present study. Lindström (1901, p. 29, pl. III) in his monograph on trilobite eyes figured the visual surfaces of the olenid genera *Peltura*, *Sphaerophthalmus*, and *Ctenopyge*, illustrating highly magnified lenses, thin sections, and the librigenae in position on the cranium. As a matter of historical interest, he regarded the olenids as the oldest known 'oculate genera', and did not think that earlier trilobites had functional eyes. Upper Cambrian trilobite eyes were also described by Öpik (1967) in his monograph of the Mindyallan fauna of Queensland, where, amongst others, the large and well-preserved eyes of *Blountia mindycrusta* Öpik were illustrated.

Öpik (1967, p. 54) discussed the question of the preservation of the eye in Cambrian trilobites very thoroughly. Noting that the visual surface is rarely preserved, he suggested that in life the visual surface had been bounded by a peripheral *circumocular suture*, and that during ecdysis or after death the whole lentiferous area would fall out and not be preserved. This suture comprised the *palpebral suture* and the *ocular suture* (text-fig. 2a), which ran along the upper and lower borders of the visual surface respectively, meeting at the front and rear. He pointed out that in post-Cambrian trilobites, the lower part of the circumocular suture or *ocular suture* became fused, so that during ecdysis, the visual surface separated only along its contact with the palpebral lobe. The visual surface adhered to the librigena and thus stood a much higher chance of preservation. Some of the Upper Cambrian trilobites also had non-functional ocular sutures and, as Öpik pointed out, fusion of the visual surface with the librigena became reasonably common in Upper Cambrian times in unrelated groups, and is not a character of phylogenetic significance. The only alternative possibility is that in many Cambrian trilobites the visual surface was so delicate that its preservation in any case would be unlikely; but then one would expect there to be a ragged edge to the eye-socket, to which the visual surface was attached, and this is not so. I therefore agree entirely with Öpik's suggestions, adding that there is some evidence of the ocular suture having been functional only in adult trilobites. The meraspids of *O. gilberti* Meek described by Walcott (text-fig. 1a) and sometimes very small holaspids of Ordovician *Flexicalymene* species from the Waynesville formation, Ohio, have intact visual surfaces with visible lenses. Adult individuals of these species, however, never have visual surfaces preserved, although in mature *Flexicalymene* the lower surface of the palpebral lobe, along the line of the palpebral suture, may be denticulate as if elongate prisms or 'lenses' had originally rested there.

In the course of the present study, I found some small but complete visual surfaces in meraspids of *Olenus wahlenbergi* Westergård. The retention of the visual surface in *Parabolina* and other derivatives of *Olenus* may be seen as an example of paedomorphic development, in which the ocular suture, which had been functional only in the adult, was even there dispensed with. The role of paedomorphosis in the evolution of olenid and other eyes is discussed later.

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TEXT-FIG. 1. *a.* *Olenellus gilberti* Meek. Meraspid figured by Walcott (1910, pl. 36, fig. 4c; pl. 43, fig. 5, 6) in oblique lateral view with the individual lenses visible. Where the visual surface has been broken away at x, impressions of the lenses are left on the underlying matrix. Lower Cambrian, Ptarmigan Pass, Alberta. Smithsonian Institution Catalogue number 56828f.

*b.* *Olenus wahlenbergi*. Lateral view of cephalon reconstructed, showing the 'eye-indices' of Struve (1958). A = length of visual surface. H = Distance from posterior edge of eye to posterior border furrow. G = preglabellar to occipital furrow. Gn = preglabellar furrow to rear edge of occipital ring.

#### THE OLENIDS

Because so many Cambrian trilobites had functional ocular sutures, it is unlikely that we shall ever obtain a good record of the evolution of the most ancient trilobite eyes. Studies of the detailed morphology of the eyes of single species can, however, contribute towards this end, and when the phylogeny of Cambrian trilobites becomes better known these may be seen more clearly in an evolutionary perspective. In addition, it is fortunate that there is one family at least, the Olenidae, where the phylogeny is well known and in which material for study is so well preserved and abundant that at least some features of the evolutionary history of the visual system within this family can be elucidated.

The Olenidae are a geographically widespread family, which arose early in Upper Cambrian times and abounded to the end of the Tremadoc. A few genera persisted into the Ordovician, and *Triarthrus* until the close of the Middle Ordovician. Olenid faunas are best known in Scandinavia where they have been the subject of many studies culminating in the major monographs of Westergård (1922) and Henningsmoen (1957); they are common throughout the Acado-Baltic province and in the Tremadoc of South America (Harrington and Leanza 1957), and there are isolated occurrences elsewhere.

In the alum shales of the Oslo region and the old quarries of Andrarum, in Scania, there occur stinkstone concretions with vast numbers of disarticulated olenid fragments, frequently with very fine structure preserved, and in full relief with no trace of flattening. In the early genera, *Olenus*, *Leptoplastus*, *Eurycare*, and others, the lenses are preserved only in small meraspids. The visual surface in adults is unknown, but even so there remains, at least in the best-preserved adults of *Olenus*, a wealth of interesting detail on the palpebral lobe and the lower rim or eye-socket, which suggests that the whole region peripheral to the visual surface may have been a highly sensory zone. Later genera, which include *Sphaerophthalmus*, *Ctenopyge* s.l., *Peltura*,

and *Parabolina*, retained the visual surface, often with excellent details of the lenses and peripheral zones. Though no details of subsurface layers in the eye are preserved, but only the lenses, it is hoped that the present study will be a useful contribution to olenid morphology in general, and to the understanding of the evolution of trilobite visual systems. Because the olenid faunas of Scandinavia are so well known I have made extensive reference to Westergård (1922) and Henningsmoen (1957) in which full accounts of morphology and complete synonymies are given. Following Henningsmoen both proposed international and local Norwegian zones are given, e.g. *Olenus wahlenbergi* occurs in Zone II (2a $\beta$ ).

#### METHODS AND TECHNIQUES

Since all the material available to me consisted of disarticulated fragments the work on olenid eyes fell naturally into two parts. The first task was to reconstruct the cephalon with the cranidium and librigenae fitting together as they were originally assembled in the living animal. This was to show the visual surface (where present) in its original relationship to the palpebral lobe, and the eye in its true relationship to the cephalon. The second phase of the work was the detailed study of the visual surface and the bordering regions (palpebral lobe and eye-socket) with the scanning electron microscope (SEM). With this information, certain inferences could be made about the evolution of the eye in the family, though it was not possible to study all the genera.

*Technique of reconstruction.* The reconstructions were made from cranidia and librigenae, accurately drawn with a Wild-Heerbrugg microscope with an M5 drawing tube or 'camera-lucida'. For each species several undamaged or nearly complete cranidia were drawn in dorsal, lateral, and frontal views; the plane of the palpebral lobe being normally taken as horizontal. High magnification drawings were also made in oblique lateral view. Where the specimen was slightly damaged appropriate details could be filled in with reference to other cranidia.

Librigenae of equivalent size were also selected. Each was drawn in an orientation where its camera-lucida image fitted the drawing of the reconstructed cranidium, with the slope of the cheek region, and the edges of the librigena and fixigena matching all the way along the suture. In the final drawing the dimensions of the parts of the reconstructed cephalon were the same in all the different views.

*Scanning electron microscopy.* Both gold-palladium and aluminium coatings were used; the latter were found to be equal to the former in conducting properties. Visual surfaces, palpebral lobes, and eye-sockets were all examined in different orientations, to build up a complete picture of the eye. Where the lenses had become detached from the eye in some areas, their total thickness was apparent. Unexpected features visible with the SEM were the remarkable peripheral zones in the eye of *Olenus wahlenbergi*, which are recorded in detail below.

*Deposition of specimens.* All olenid specimens used in this study are in the collections of the following institutes: Palaeontologisk Museum, Oslo (P.M.O.); Geology Department, University of Lund (LO); British Museum (Natural History), London (BMNH); Grant Institute of Geology, Edinburgh (Gr. I.).

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## OLENID EYE MORPHOLOGY

## Subfamily OLENINAE

*Olenus* s.s. is the earliest olenid genus and seems to have been the rootstock of the whole family. The eye of *O. wahlenbergi*, described below from exceptionally well-preserved material, is representative of early olenids as a whole and eyes of this kind were retained by various later genera which include *Leptoplastus* and *Eurycare*. Later leptoplastines, however, had eyes of modified form.

In adults of *Olenus* the visual surface has not been found, but small meraspids have been found with the visual surfaces still intact, so that some details of their structure can be determined. In the adults, fine details of the palpebral lobes and eyesocles remain, and these can be reconstructed in their original relationship.

Only two genera of the Oleninae, *Olenus* and *Parabolina*, have been studied. *Parabolina* is probably a derivative of *Olenus* (see p. 744) in which the adult has a visual surface of similar kind to that in the meraspids of *Olenus*. The palpebral lobe, moreover, though inflated and of peculiar form, is confluent with the ocular ridge, again as in immature specimens of *Olenus*. These two factors amongst others are suggestive of a pedomorphic origin for the eye of *Parabolina*, a situation paralleled by *Peltura* and more distantly by other olenids.

*Olenus wahlenbergi* Westergård, 1922

1922 *Olenus Wahlenbergi* n. sp.; Westergård, p. 128, pl. IV, figs. 5-14.

1957 *Olenus wahlenbergi* Westergård 1922; Henningsmoen, p. 110, pl. 3 (with complete synonymy).

Plates 91, figs. 1-6; 92, figs. 1-4; text-fig. 2 a-j

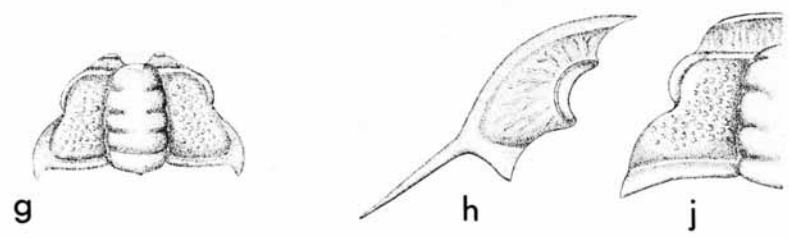
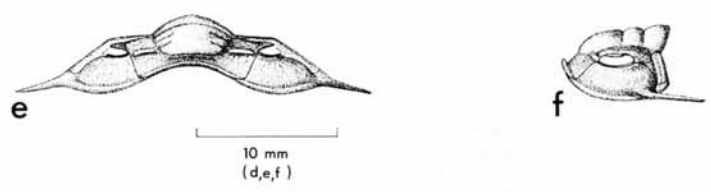
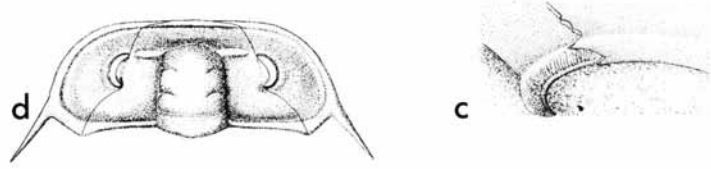
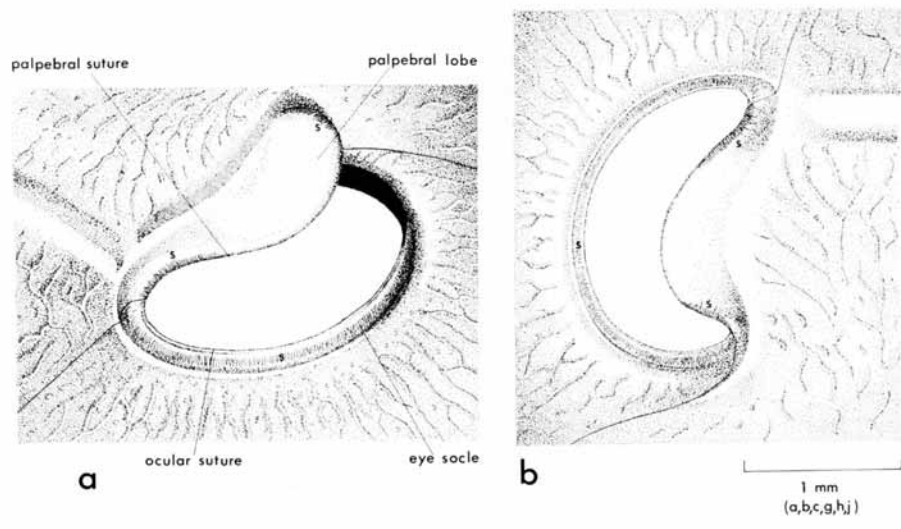
*Material.* Twenty-two blocks of topotype material from Andrarum, Zone II (2aβ). Gr I 5514-5536.

*Remarks.* The gross morphology described by Westergård is supplemented by my reconstruction which shows the librigenae in place (text-fig. 2, c-e). Both lateral and frontal views show how the genal spines were in life directed horizontally and may be interpreted as props for supporting the cephalon on the sea floor. The anterior arch (Clarkson 1966b) is well developed, though it might have been partially blocked by the hypostome.

*Development.* Though the ontogenetic development of *O. wahlenbergi* has not been documented in detail, Strand's (1927) description of ontogeny in *O. gibbosus* show a broadly comparable mode of development. Many larval stages of *O. wahlenbergi* are present in the material which I studied, those figured in text-fig. 1 g, h, and j being close in morphology to Strand's stages 8 or 9 (length 0.70-0.71 mm) and 11 (length 1 mm). Strand remarks upon the presence of continuous eye-ridges from the earliest stages, though the severance of these from the palpebral lobe in later development was not noted. The equivalent stages to Strand's stages 8 and 9 are here referred to as meraspids, following Whitworth (1970).

*Structure of the cuticle.* At high magnifications (over  $\times 1000$ ), the external surface of the palpebral lobe, eye-socle, and other parts of the exoskeleton can be resolved into raised polygons, all of the same general size and of semi-regular form (Pl. 91, fig. 3). Such polygons also underlie the ridges of the alimentary prosopon. They are found only on the external surface and have no internal expression. They seem to be similar to the 'cell polygons' of modern arthropod cuticles (Dalingwater, in press); each of the underlying cells which secretes the cuticle contributes a single 'tile' to the mosaic which forms the whole cuticle, and its form is retained on the outside of the cuticle. Though cell-polygons are present in other olenids they have not been found so clearly preserved as in *O. wahlenbergi*. Fractured cuticular surfaces show radial structures though these have not been investigated further.

*Eye-morphology: Meraspid eyes.* The visual surface is present in meraspids where the length of the eye



does not exceed 0.45 mm. In these the external surface of the lentiferous area is smooth, though examination of internal surfaces shows the undersides of the lenses, which are small and weakly convex. Preservation of these small structures is not particularly good, and therefore details of their structure and arrangement are indeterminate. The eye-socket is distinct from the visual surface, though at this stage in development does not exhibit the vertical ridges of the adult (Plate 91, fig. 2).

In meraspid the palpebral lobe is at first very narrow, and is connected to the ocular ridge (text-fig. 1g). Later it widens and eventually, when the eye has attained a length of more than 0.75 mm, it becomes separate from the ocular ridge. The specimen illustrated in text-fig. 2j, in which the ornament of the fixigena is still pustulose, shows the beginnings of separation of the palpebral lobe from the ocular ridge. In adult specimens, the pustulose ornament is replaced by the ridges of the prosopon (Öpik, 1961), and the ocular ridge does not connect with the palpebral lobe, but is separated from it by a pronounced channel. It is noteworthy that the visual surface in juveniles is first of all directed more anteriorly, and only later commands a more lateral field of view.

*Adult eyes.* Sometime after the meraspid stages illustrated in text-fig. 2 h, j, the ocular suture must have been effective, for there is never any trace of the visual surface thereafter. The visual surface must have been reniform and of moderate height, though not spherical or globular. It was set opposite S2 with its posterior edge set slightly further from the mid-line so that the long axis of the eye (line joining the anterior and posterior edges) made an angle of about  $10^\circ$  with the exsagittal plane. This contrasts with the situation in meraspid where the equivalent angle may be up to  $45^\circ$ . Eye-indices (Struve 1958): A/G 37%, A/Gn 30%, H/A 108% (text-fig. 1b). The palpebral lobe is reniform, separated from the fixigena by a distinct palpebral furrow, depressed centrally, and rising anteriorly and posteriorly to low elevations (the rear elevation is the more prominent). From these elevations the surface plunges very steeply and the palpebral lobe narrows as it joins the eye-socket. The surface of the palpebral lobe is rather smooth but becomes highly ornamented in the outer region near the facial suture. Two separate elements can be distinguished. The first kind of structure (Pl. 92, figs. 1-4) consists of thin elongated ridges, nearly normal to the outer edge of the palpebral lobe and especially prominent on its anterior and posterior elevations. On these raised areas the ridges resemble alimentary prosopon and bifurcate as they approach the edge. In the outer central part of the lobe, which lies between the two elevations, the ridges are less prominent and anastomose, forming an area of irregular polygons (Pl. 92, fig. 2), again confined to the outer part of the lobe.

Secondly, there are a number of peculiar swellings, usually elongate, situated along, or sometimes between, some of the ridges. They sometimes show a well-developed crystalline structure (Pl. 92, fig. 2), but are otherwise of indeterminate morphology. These alone have some similarity of appearance to the much more highly developed corrugated surface of the eye-socket, and might have had a similar function. They might have been the sites of glands or sensory organs. In addition, the surface of the palpebral lobe, like that of the rest of the cuticle, has many round pits, possibly the openings of perpendicular canals in the cuticle (Dalingwater, in press).

The eye-socket is a prominent band, which could on superficial inspection be taken for the visual surface itself. The true shape of the eye-socket was determined by excavating inverted librigenae, which retained their upper edges within the rock matrix and were more likely to possess intact anterior and posterior edges than specimens with the dorsal surface uppermost. From librigenae such as that figured in text-fig. 2c, it was

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TEXT-FIG. 2. *Olenus wahlenbergi* (Westergård 1922). Zone II, Andrarum, Scania.

a, b. Reconstructions of the eye region of a medium-sized adult in antero-lateral and dorsal views showing the visual surface missing because of the functional ocular-suture. 's' marks the position of peripheral (possibly sensory) zones on the palpebral lobe and eye-socket. Mainly from Gr. I. 5521.

c. Part of specimen showing undamaged anterior horn of the eye-socket, lying ventral side uppermost and excavated from above. Gr. I. 5526.

d, e, f. Reconstructions of complete cephalon in dorsal, frontal, and lateral views from Gr. I. 5521 and 5522.

g. Early meraspid, slightly damaged anteriorly, approximating Strand's (1927) stages 8 or 9. Gr. I. 5523.

h. Librigena of meraspid still retaining the visual surface. Gr. I. 5524.

j. Cranidium of meraspid of about the same size, approximating Strand's stage II. Gr. I. 5525.

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seen that these edges curved upwards sharply to meet the descending edges of the palpebral lobe, which are slightly recessed where they meet the eye-socket. Text-fig. 2 (*a, b*), showing the reconstructed eye, was constructed from camera-lucida drawings of a perfectly preserved palpebral lobe, and a nearly perfect librigena of a similar-sized specimen.

The vertical ridges on the eye-socket are confined to a median horizontal band, above which the socket thins abruptly (Pl. 91, figs. 4-6). These ridges are more or less vertical and parallel, but sometimes lie obliquely and anastomose with neighbours. The ridges of the palpebral lobe and eye-socket, though not really similar in appearance, form a continuous zone peripheral to the visual surface and may have been the sites of accessory sensory organs; a concept discussed in more detail later on. Since their function is not proved, it is convenient to refer to the whole complex of ridges and grooves as the 'peripheral zone', and this term is used hereafter. Many other trilobites have a similar peripheral zone, sometimes in the form of ridges and grooves, sometimes as tubercles, and sometimes as funnel-shaped pits. The existence of such a zone in *Olenus* is the earliest recorded occurrence, and it is of interest that it should apparently be much less well developed, at least in external expression, in later olenid derivatives.

#### *Parabolina spinulosa* (Wahlenberg 1821)

- 1821 *Entomostracites spinulosus*; Wahlenberg, p. 38, pl. 1, fig. 3.  
 1854 *Parabolina spinulosa* Wahl.; Angelin, p. 46, pl. XXV, fig. 9; pl. XXVII, fig. 3.  
 1922 *Parabolina spinulosa* (Wahlenberg); Westergård, p. 134, pl. VI, figs. 14-20.  
 1957 *Parabolina spinulosa* (Wahlenberg); Henningsmoen, p. 126, pl. 1, fig. 2; pl. 3, fig. 12 (with complete synonymy).

Plate 92, figs. 5, 6; text-fig. 3 *a, b*

*Material.* Five blocks from Westergård's collection, University of Lund, Andrarum. Zone III (2*b*). LO 4527-31.

*Remarks.* The morphology of this species is very well known and I have not attempted complete restorations, but only antero-lateral views primarily to show the eye and the alimentary prosopon, drawn with a camera-lucida.

*Eye-morphology.* As no juveniles were available for examination this description is based upon adults. The eye is small, and set relatively close to the anterior border. It lies obliquely, and the long axis (line connecting the anterior and posterior edges) makes an angle of some 20° to the exsagittal plane. Eye-indices: A/G 25%, A/Gn 19%, H/A 270%. By contrast with an adult *Olenus*, the ocular ridge contacts the glabella and runs laterally and slightly backwards, expanding to become confluent with the swollen palpebral lobe. The palpebral lobe which is defined by a shallow palpebral furrow, is smooth with no evidence of a peripheral zone, nor is there any indication of such a zone on the (very narrow) eye-socket. The visual surface is reniform and not strongly curved, so that it subtends a rather restricted field of view directed antero-laterally. The external corneal surface is smooth and structureless (Pl. 92, figs. 5, 6), and the lenses below, which seem to be welded to the lower corneal surface, are poorly preserved, but their lower surfaces are weakly convex as in the case of meraspid of *Olenus*. Ridges of the alimentary prosopon radiate from near the base of the eye, branching towards the cephalic border and anastomosing towards the rear of the librigena.

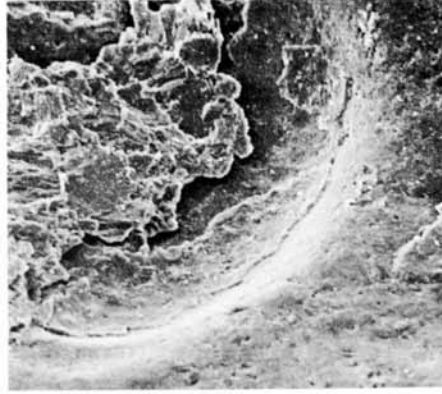
#### EXPLANATION OF PLATE 91

Figs. 1-6. *Olenus wahlenbergi* (Westergård 1922). Zone II. Andrarum, Scania. 1, Meraspid cephalon showing confluence of palpebral lobe and ocular ridge. Gr. I. 5514, ×90. 2, Meraspid. External mould of visual surface with some parts of the cornea and underlying lenses still adherent. Gr. I. 5515, ×175. 3, External mould of the surface of an adult cephalon, with cell-polygons and tubercles. The full thickness of the cuticle is seen on the left. Gr. I. 5516, ×220. 4, External mould of eye-socket (inverted) showing faint striations of the sensory zone and undamaged upper rim. Gr. I. 5517, ×65. 5, Outer surface of eye-socket, with prominent striations. Upper rim damaged. Gr. I. 5518, ×120. 6, Same, showing striations highly magnified, ×2400. Bar = 5 μm.





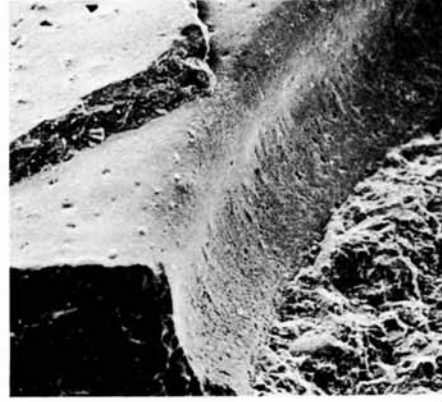
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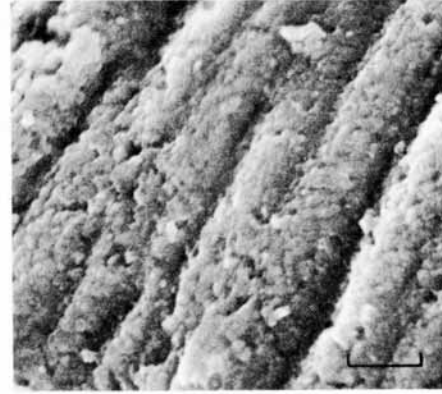
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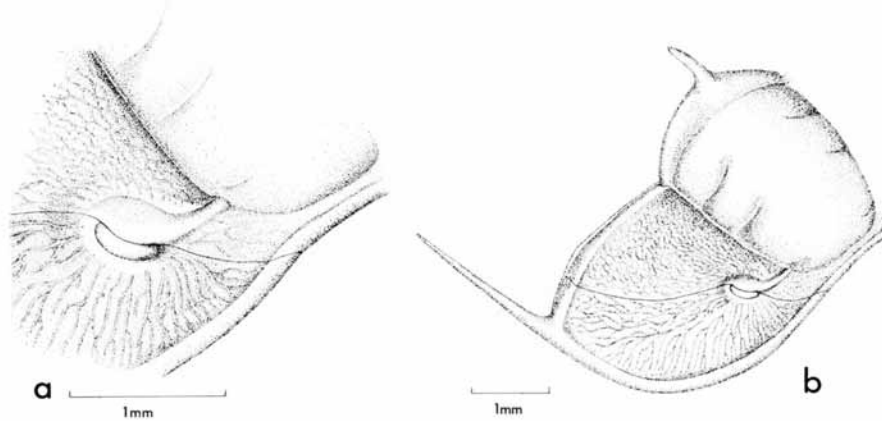


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CLARKSON, *Olenus* eyes



TEXT-FIG. 3. *Parabolina spinulosa* (Wahlenberg 1821). Zone III, Andrarum, Scania.  
*a.* Eye region reconstructed from cranium and librigena with a near-perfect visual surface. *b.* Whole cephalon restored. From LO 4259, 60.

Features of the eye of *Parabolina* which bear resemblance to the eyes of meraspids of *Olenus* suggest that the *Parabolina* eye was derived from the eye of *Olenus* by pedomorphosis. These include: (i) The retention of the visual surface and obsolescence of the ocular suture; (ii) Confluence of the palpebral lobe with the ocular ridge; (iii) The anterior position of the eye and its high inclination to the exsagittal plane, and possibly (iv) the absence of surface features of the peripheral zone. Other features, such as the inflation of the palpebral lobe, are not pedomorphic and have a separate origin.

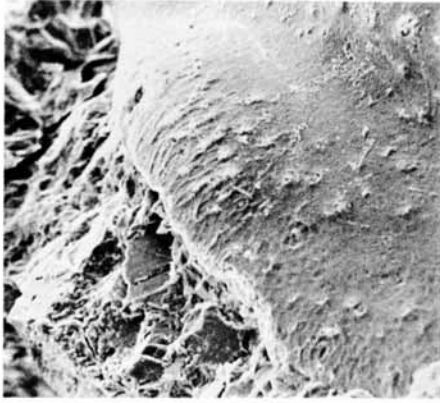
#### Subfamily PELTURINAE

As far as is known, all Pelturinae have eyes of the same general kind. They are small, placed far forward, shaped so as to cover only the anterior hemisphere of vision, and are normally preserved with the visual surface intact. The palpebral lobe is swollen and connected to the glabella by an unbroken ocular ridge, though this may become indistinct near the glabella. In such material of *Protopeltura* as was available for study, the eye was not well preserved, and there is less certainty about ocular morphology. Some of Westergård's figures of various species of *Protopeltura* (1922, Taf. XIV, figs. 4, 27), suggest that the visual surface is absent whereas others (Taf. XIV, fig. 20; Taf. XV, fig. 1) seem to indicate its presence; but as he also figured species of *Peltura* both with and without the visual surface, its absence in some

#### EXPLANATION OF PLATE 92

Figs. 1-4. *Olenus wahlenbergi* (Westergård 1922). Zone II. Andrarum, Scania. 1, Palpebral lobe, anterior region with structures of sensory zone. Gr. I. 5519,  $\times 190$ . 2, The same showing 'prosoxon' and 'sensory nodes',  $\times 935$ . Bar = 5  $\mu$ m. 3, Palpebral lobe of another specimen, anterior region with structures of 'sensory' zone. Gr. I. 5520,  $\times 130$ . 4, The same, magnified  $\times 500$ .

Figs. 5, 6. *Parabolina spinulosa* (Wahlenberg 1821). Zone III. Andrarum, Scania. 5, Librigena with eye. LO 4527,  $\times 46$ . 6, The same, magnified  $\times 125$ .



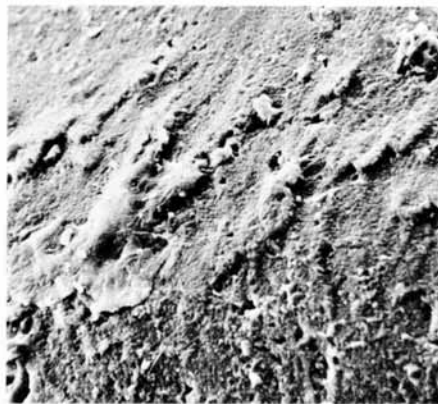
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CLARKSON, *Olenus* and *Parabolina* eyes

specimens of both genera suggest breakage rather than the presence of an ocular suture. Indeed, it seems fairly certain that *Protopeltura* had an eye similar to that of *Peltura*.

Certain morphological characters of the eyes of Pelturinae can be interpreted, as with *Parabolina*, as being paedomorphic in origin. Into this category fall the small size, forward position and inclination of the long axis of the eye, the unbroken ocular ridge, the retention of the visual surface in the adult, and the over-all similarity of structure to the eyes of meraspids of *Olenus*. Henningsmoen (1957, p. 114) pointed out the resemblance between the earliest *Parabolina* species, *P. brevispina* and *Protopeltura*, suggesting that the two are closely related descendants of *Olenus*. The similarity of eye structure in *Peltura* and *Parabolina* accords with this relationship; presumably this kind of eye arose once only.

The two species discussed below were selected as having eyes representative of Pelturinae, and both of them displayed excellent structural details showing the arrangement of lenses on the visual surface.

*Peltura scarabaeoides scarabaeoides* (Wahlenberg 1821)

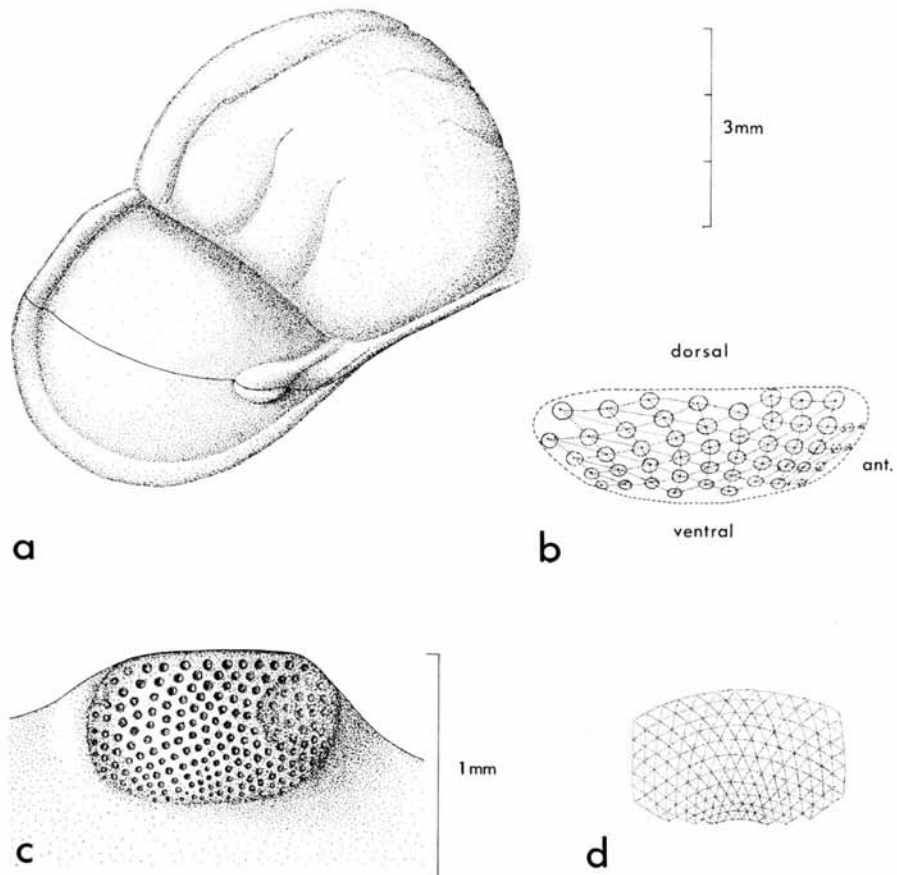
- 1821 *Entomostracites scarabaeoides*; Wahlenberg, p. 41, pl. 1, fig. 2.  
 1854 *Peltura scarabaeoides* Wahl.; Angelin, p. 45, pl. XXV, fig. 8.  
 1922 *Peltura scarabaeoides* (Wahlenberg); Westergård, p. 173, pl. XV, figs. 12, 13, 18.  
 1957 *Peltura scarabaeoides scarabaeoides* (Wahlenberg 1821); Henningsmoen, p. 237, pl. 2, fig. 1; pl. 6; pl. 25, figs. 6, 13, 14; pl. 26, figs. 1, 2.  
 1958 *Peltura scarabaeoides* (Wahlenberg 1821); Whittington, p. 200, pl. 38, figs. 1-18.

Text-fig. 4 a, c

*Material.* Three blocks from Slemmestad, Norway Zone Vc (2d $\gamma$ ) P.M.O. 29268, 29270, 29272. Also ontogenetic series BM It. 5516-9. One block from Andrarum, Scania associated with *Ctenopyge linarssoni*, and *Sphaerophthalmus humilis*. Zone Vc Gr. I. 20803.

*Remarks.* Of all the cephalic reconstructions made to show the true position of the eye that presented here for *P. scarabaeoides* is the most tentative. Though the restoration of the cranium posed no problems, it is very much more difficult to be certain as to how the cranium and librigena fit together. Several camera-lucida drawings were made of the cranium in different orientations. Various librigenae were then successively examined under the camera lucida microscope so that the image of the librigena could be seen adjacent to the previously drawn cranium. Each librigena in turn was then manoeuvred into an orientation such that the image of the whole cheek region showed a smooth unbroken curve; this was then taken as the most lifelike construction. Such a reconstruction shows that the librigenae slope down quite steeply at about 45° and that there is a moderately well-developed anterior arch, though this was probably partially blocked by the hypostoma.

*Eye-morphology.* The eye is small, placed far forward on the cephalon and quite near the glabella. Its long axis is inclined at 45° to the exsagittal plane. Eye-indices: A/G 20%, A/Gn 15%, H/A 350%. Whittington (1958) showed that the palpebral lobe is poorly defined, though present early in ontogeny. Thereafter it becomes more distinct and the visual surface is present in the smallest known librigenae (*ibid.*, Pl. 38, figs. 12, 13). The material of *P. scarabaeoides* is not particularly good, and did not photograph well, hence the drawing (text-fig. 4c); lens arrangement in the early stages is better shown in *P. minor*. The palpebral lobe of adult specimens is entirely smooth, swollen near the facial suture, and confluent with the short ocular ridge which connects with the glabella, though in some specimens the ocular ridge becomes faint and ill defined towards the glabella. The lenses themselves are not preserved, and the material is found as internal and external moulds. External moulds show that the cornea must have been entirely smooth and without any distinct structure, whereas impressions of the lower surfaces of the lenses appear distinctly on internal moulds. Lindström (1901, p. 29, Pl. III, figs. 35-42) illustrated the fine structure of the eye of



TEXT-FIG. 4. *a*, *Peltura scarabaeoides scarabaeoides*. (Wahlenberg 1821.) Zone Vc, Slemmestad, Norway. Cephalon in oblique lateral view, restored from Gr. I. 20803.

*b*, *Peltura minor* (Brögger 1882). Diagram exhibiting the spatial relationships of the lenses. From P.M.O. 87558 (vide Pl. 93, fig. 1). *c*, *Peltura scarabaeoides scarabaeoides* (Wahlenberg 1821). Right eye of a large specimen drawn from photographs and camera-lucida. From BM It. 5519. *d*, Idealized hexagonal close-packing system showing geometrical relationships between lens centres typical of pelturines. Based on 4c.

*P. scarabaeoides* from material with the lenses preserved. He showed that the lenses are plano-convex with a smooth upper surface. As Lindström saw no trace of an organic junction between the lenses and the cornea, he regarded them, not as 'free lenses', but as inwardly bulging extensions of the cornea like those of *Limulus*. My present study has given no evidence for or against this suggestion, neither in *Peltura* nor in the similar *Olenus meraspidis*, where the lenses and cornea apparently can only be detached together. It seems more likely, considering that the olenids are a close-knit group, that the lenses are in fact free structures of plano-convex form, closely welded to the lower surface of a very thin cornea, which did not show in Lindström's

sections because of recrystallization. Nevertheless, the extraordinarily wide spacing of the upper lenses in *P. minor*, and their curious distribution could accord with either hypothesis, and Lindström's suggestion should not be discounted.

*Peltura minor* (Brögger 1882)

- 1882 *Cyclognathus costatus* n. sp. var *minor*; Brögger, p. 110, pl. II, figs. 10-11.  
 1922 *Peltura minor* (Brögger); Westergård, p. 175, pl. XV, figs. 3-11.  
 1957 *Peltura minor* (Brögger, 1882); Henningsmoen, p. 235, pl. 6, pl. 25, figs. 2-5.

Plate 93, figs. 1, 2; text-fig. 4b

*Material.* One specimen from Gamlebyen, Oslo, associated with *Sphaerophthalmus alatus*, Zone Vb (2d $\beta$ ). P.M.O. 87558.

*Eye-morphology.* Only the visual surface is present, preserved as an internal mould. There appears to be little difference in eye structure between this species and *P. scarabaeoides*. The lenses are represented by the impressions of their lower surfaces. There is considerable variation in the spacing of these lenses; those near the facial suture being very widely spaced, and almost certainly disjunct, whereas those near the lower margin are somewhat smaller and much closer together, probably being contiguous.

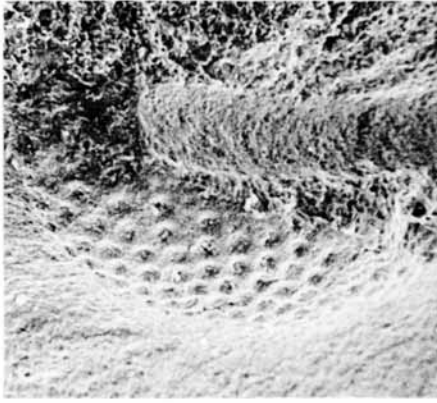
*Development of the eye in pelturines.* In young pelturines the lenses have an unusual pattern of arrangement, unlike that of leptoplastines or indeed of other Cambrian trilobites. There may have been a similar system in the Oleninae, but the preservation is not good enough to determine this. This basic pattern is retained, though modified by the addition of many more lenses in fully grown pelturines. The beautifully preserved eye of *P. minor*, figured in Pl. 93, figs. 1, 2, serves as a model showing an early stage of development; young *P. scarabaeoides* eyes are very similar though less well preserved.

Here the pattern is a form of hexagonal close packing, but the dorso-ventral files radiate dorsally, diverging in a fan-like manner. The uppermost lenses are the most widely spaced; they are also somewhat larger than the others. By analogy with other trilobites these were presumably the first-formed lenses. This odd pattern, with the files converging as they plunge downwards seems to be adapted to accommodate more lenses in the lower central part of the visual field, whilst giving wide-ranging though less intensive coverage elsewhere. The approximate maximum visual range for this eye, which has fifty lenses, is 0° to 90° (long.) and -20° to 50° (lat.). Vision is thus entirely confined to the anterior hemisphere, with the main clustering of lens

EXPLANATION OF PLATE 93

- Figs. 1, 2. *Peltura minor* (Brögger, 1882). Gamlebyen. Oslo. Zone Vb. (2d $\beta$ ). 1, Internal mould of visual surface (right edge = anterior). P.M.O. 87558,  $\times 135$  (vide text-fig. 4b). 2, Same, upper part of visual surface,  $\times 500$ . Bar = 10  $\mu$ m.
- Figs. 3-6. *Ctenopyge (Mesoctenopyge) similis* Henningsmoen 1957. Sars Gate. Oslo. Zone Vb (2d $\beta$  sim.). 3, Palpebral lobe showing nearly structureless surface (top right = anterior). P.M.O. 87567,  $\times 120$ . 4, Adult visual surface in lateral view showing dorso-ventral files and eye-socket with faint vertical striations. P.M.O. 87566,  $\times 85$ . 5, Oblique dorsal view of adult visual surface. P.M.O. 87565,  $\times 65$ . 6, Oblique dorsal view of visual surface of a young specimen (right edge = anterior), (see also text-fig. 5e), (enlargement of left-hand specimen in Pl. 94, fig. 5). P.M.O. 87564,  $\times 120$ . (Figs. 5 and 6 are illuminated from the south).

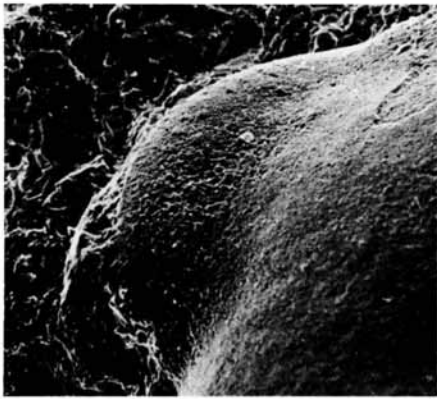




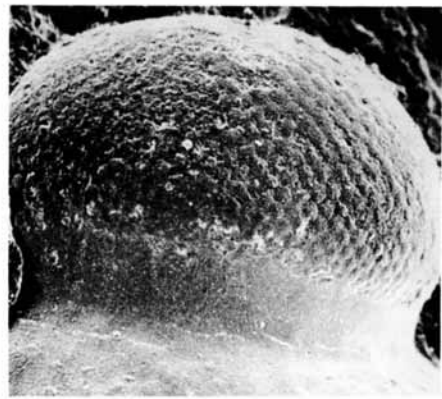
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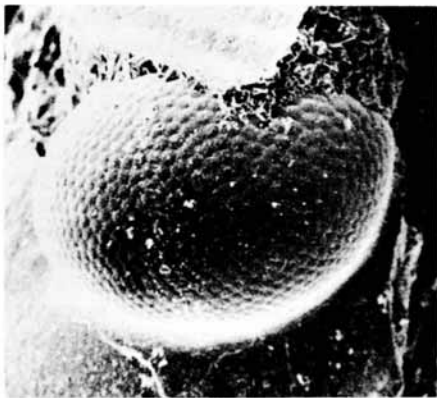
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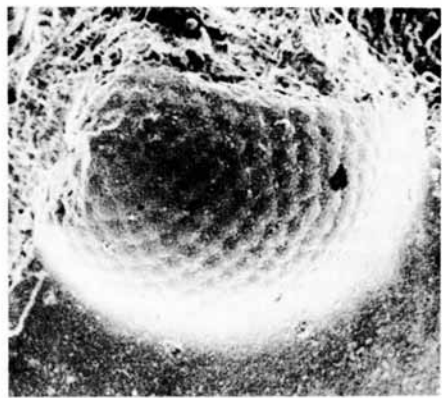
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6

CLARKSON, *Peltura* and *Ctenopyge* eyes



axes centred on an axis  $45^\circ$  from the sagittal plane, and directed downwards at  $10\text{--}20^\circ$  below the 'equator', towards the sea floor.

Though no large adults of *P. minor* were available for study, the fully developed pelturine system of lens arrangement was seen in mature specimens of *P. scarabaeoides scarabaeoides*. Here there are some 180 lenses, arranged in a pattern like that of *P. minor*, though modified through growth. Most specimens have some fortuitous irregularities, like those figured in text-fig. 4c, but apart from these the lens centres are arranged in a regular geometric sequence, idealized in text-fig. 4d. This is clearly a hexagonal close-packing scheme, but one in which the distances between lens-centres decrease arithmetically towards the base of the eye. Three intersecting component rows are evident, as follows: (a) arching latitudinal rows, becoming closer together ventrally, (b) a set of files converging ventrally towards the anterior ventral edge of the eye, vertical near the anterior edge and curving more and more obliquely towards the posterior edge, (c) an identical set, vertical near the posterior edge and curving towards the anterior.

The lenses are largest at the top and decrease in size ventrally and it is probable that their growth is inhibited by the proximity of neighbouring lens-centres, as suggested in my analysis of the eye of *Ormathops* (Clarkson 1971). One advantage of having lenses graduated in size is that irregularities in distribution are avoided. When the lenses are all the same size, as in *Ormathops* or *Ctenopyge*, irregularities are inevitable. The eyes of *Ctenopyge* are similar to those of the pelturines in that the dominant files, which are diagonal near the top of the eye, swing into a more nearly vertical position towards the base but these do not converge in *Ctenopyge*, and identical-sized lenses with inevitable irregularities in distribution result (see p. 737). A full analysis of different systems of lens-packing in trilobites is beyond the scope of this paper, but it is worth noting that the system exhibited by pelturines is found also in certain post-Cambrian trilobite groups and is especially distinct in cyclopygids, though here the decrease in spacing may be logarithmic.

#### Subfamily LEPTOPLASTINAE

The eye of *Leptoplastus stenotus* Angelin was less well preserved than that of *O. wahlenbergi* in the material studied. Basically, it is of the same general type, though relatively smaller. The visual surface is absent, and none of the small meraspids were preserved showing the visual surface. No detailed structure was visible on the palpebral lobe or the eye-socle, due to poorer preservation. *Eurycare* again has an eye of similar type, with the visual surface missing.

Though the similarities between the eyes of early Leptoplastinae are clear, there was a great change with the incoming of *Ctenopyge* and *Sphaerophthamus*. Not only was the visual surface retained but there were substantial modifications in the palpebral lobe and associated regions. The visual surface furthermore departed from the primeval reniform shape and became larger, and elliptical or nearly spherical, often projecting laterally from the head. Though the peripheral zone is less clearly marked than in *Olenus*, ridges and grooves are still detectable in some cases on the palpebral lobe and the eye-socle. Preservation of the eyes in the later Leptoplastinae was good, though less perfect than in *O. wahlenbergi*. The granular structure seen at high magnification implies at least some diagenetic alteration.

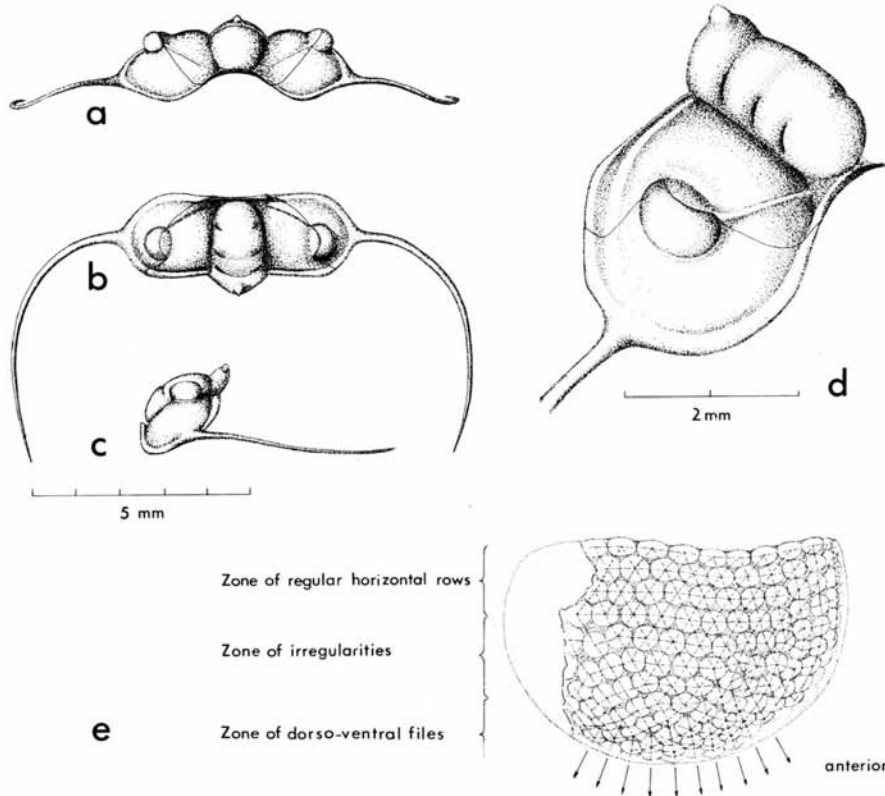
*Ctenopyge (Eoctenopyge) modesta* Henningsmoen 1957

1922 *Ctenopyge flagellifera angusta* n. var. (partim); Westergård, p. 185, pl. XI, fig. 6-7.  
 1957 *Ctenopyge (Eoctenopyge) modesta*; Henningsmoen, p. 191, pl. 5; pl. 19, figs. 1-10.

Plate 94, fig. 5; text-fig. 5 a-d

*Material.* Four blocks from Sars Gate, Oslo, associated with *Ct. similis*, *Protopeltura bidentata*, *Parabolina mobergi*. Zone Vb (2d $\beta$  sim.) P.M.O. nos. 87564-7.

*Remarks.* The reconstructions, made from camera-lucida drawings, show how the slender genal spines emerge on the librigenae opposite the eye, and thence springing away at right angles to the cephalon curve



TEXT-FIG. 5. a-d. *Ctenopyge (Eoctenopyge) modesta*. Henningsmoen 1957.

a, b, c. Restoration of the cephalon in frontal, dorsal and lateral views, from P.M.O. 87564-7. d. Same, enlarged, in antero-lateral view.

e. *Ctenopyge (Mesoctenopyge) similis* eye drawn from stereoscan photograph (vide Pl. 93, fig. 6) showing relationships of the lenses, the different zones, and the development of the dorso-ventral files. Arrows represent the directions of the emergent dorso-ventral files. P.M.O. 87564.

backwards and downwards coming to lie in the same plane as the antero-lateral border of the cephalon. Such a cephalon could be given support to rest upon the sea floor by these spines, and as with many other trilobites (Clarkson 1966b) the base of the eye would then be horizontal.

*Eye-morphology.* The eye is one-third the total length (sag) of the cephalon, and set opposite S1, high on the cheek towards the rear. Eye-indices are A/G 44%, A/Gn 34%, H/A 36%. The palpebral lobe, relatively large and defined by a pronounced palpebral furrow, rises outwards and in some specimens carries prominent radial ridges, all the way round, and normal with the facial suture. A thin ocular ridge connects the palpebral lobe to the anterior region of the glabella. The visual surface, of elliptical form, is set upon a vertical eye-socket, about one-fifth the height of the whole eye. In the material to hand there are no vertical ridges on the socket. Some specimens have an eye of symmetrical form: a regular oblate spheroid truncated below by the upper edge of the eye-socket, in others the anterior part of the spheroid is depressed, and the highest curvature is posterior. This may, however, be a preservational feature. The visual field commanded by such an eye is panoramic, and the visual fields of the two eyes meet, though hardly overlap, in front, above and behind. Laterally, the limit of vision is directed a few degrees below the equatorial or horizontal plane.

*Ctenopyge (Mesoctenopyge) similis* Henningsmoen 1957

1922 *Ctenopyge erecta* n. sp. (partim); Westergård, p. 156, pl. XI, figs. 26–27.

1957 *Ctenopyge (Mesoctenopyge) similis* n. sp.; Henningsmoen, p. 195, pl. 5; pl. 20, figs. 10–14.

Plate 93, figs. 3–6; text-figs. 5e, 6 a–c, e

*Material.* Four blocks from Sars Gate, Oslo, associated with *E. modesta*, *Protopeltura bidentata*, and *Parabolina mobergi*. Zone Vb (2dβ sim.) P.M.O. nos. 87564–7.

*Remarks.* The most striking feature of the reconstructed cephalon is the pair of large genal spines, which project forwards and curve round to the rear, terminating behind the body. Though such long spines have sometimes been used in inferring a planktonic mode of life through frictional retardation of sinking, their orientation, as the front and side views show, is much more suggestive of an adaptation for supporting not just the cephalon, but also the whole body upon the sea floor. The flattening of these massive spines suggests their functioning as a gigantic snowshoe giving support to the body when resting on a muddy sea-floor.

*Eye-morphology.* The eye is one-fifth the total length (sag.) of the cephalon, and set high on the cheek opposite S2 with its anterior edge about midway between the anterior and posterior borders. Eye-indices: A/G 33%, A/Gn 38%, H/A 125%. The palpebral lobe is relatively small and narrow, with distinct ridges, though these are not so deeply impressed as in *O. wahlenbergi* or *E. modesta*. The visual surface is very similar to that of *E. modesta* though the lenses are relatively smaller, and it commands a similar visual field. Some specimens have faint vertical ridges on the eye-socket.

*Ctenopyge (Mesoctenopyge) tumida* Westergård 1922

1922 *Ctenopyge tumida* n. sp. (partim); Westergård, p. 155, pl. XI, figs. 15–18.

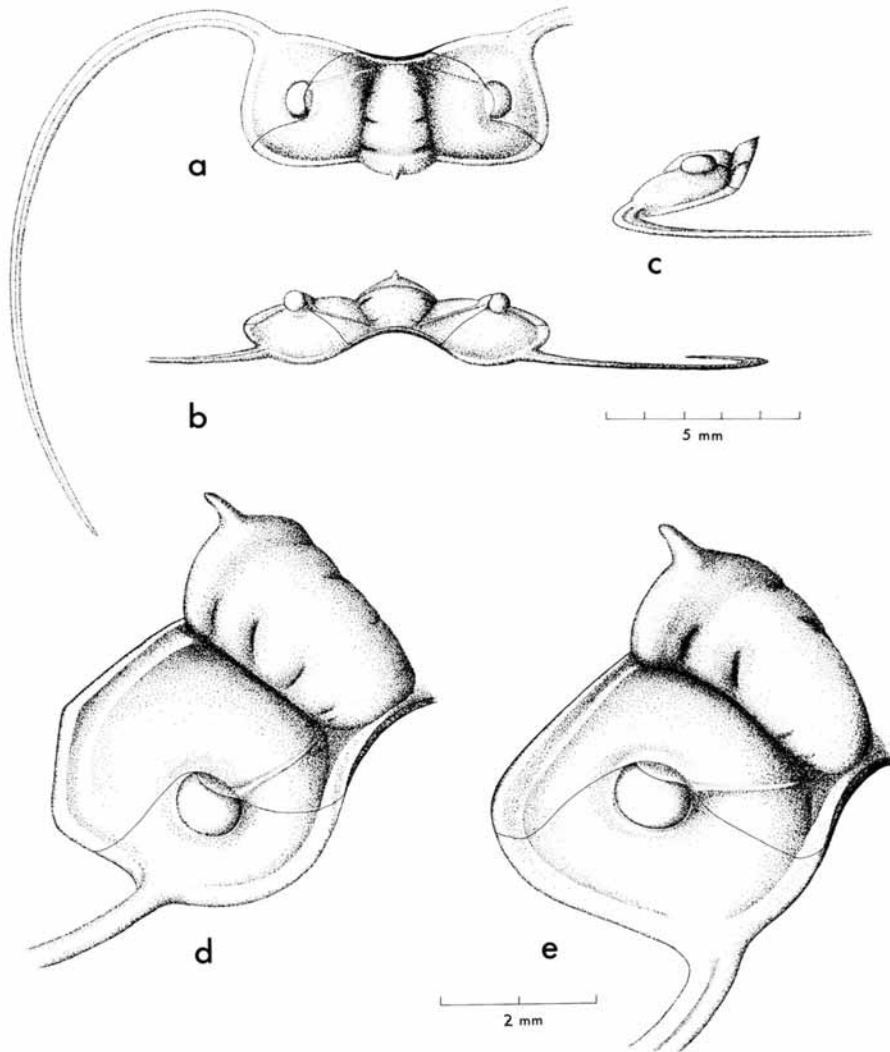
1957 *Ctenopyge (Mesoctenopyge) tumida* Westergård 1922: Henningsmoen, p. 198, pl. 5; pl. 20, fig. 16.

Plate 94, figs. 1–4; text-fig. 6d

*Material.* Five blocks from Naersnes, Røyken, associated with *Peltura acutidens*. P.M.O. no. 87551–5. Also two blocks from Sars Gate, Oslo of *C. cf. tumida* associated with *C. angusta*, Zone Vb (2dβ). P.M.O. nos. 29751, 29757.

*Remarks.* Though the genal spines are less massive, less flattened, and jut out laterally rather than first being directed anteriorly, they could still have been used for the support of the cephalon and body on the sea floor. The morphology of this species does, however, seem to be less ideally adapted for that purpose than does that of *M. similis*.

*Eye-morphology.* The eye is of almost identical morphology to that of *M. similis*, except in position. It is set further forward and lower down, so that the posterior edge of the eye lies about midway between the anterior and posterior borders of the cephalon, and the orientation of the ocular ridge and other structures is correspondingly altered. Palpebral lobes lie opposite S2. Eye-indices: A/G 28%, A/Gn 35%, H/A 150%.



TEXT-FIG. 6a-c, e. *Ctenopyge (Mesoctenopyge) similis* Henningsmoen 1957. Zone Vb. Sars Gate, Oslo. Restoration of the cephalon in dorsal, frontal, and lateral aspects, and (c) in enlarged antero-lateral view from P.M.O. 87564-87567.

d. *Ctenopyge (Mesoctenopyge) tumida*. Westergard 1922. Zone Vb. Royken. Cephalon in antero-lateral view restored from P.M.O. 87551-87555.

*Sphaerophthalmus alatus* (Boeck 1838)

- 1838 *Trilobites alatus* mh.; Boeck, p. 143.  
 1857 *Sphaerophthalmus alatus* Boeck; Kjerulf, p. 92.  
 1922 *Sphaerophthalmus major* Lake; Westergård, p. 163, pl. XIII, figs. 9–19.  
 1957 *Sphaerophthalmus alatus* (Boeck); Henningsmoen, p. 212, pl. 2, fig. 15; pl. 5; pl. 22, figs. 18–26.  
 1968 *Sphaerophthalmus alatus* (Boeck): Rushton, p. 414.

Plate 95, figs. 1, 2; text-fig. 7a–d

*Material.* Three blocks from Gamlebyen, Oslo, labelled *S. major*, and associated with *Peltura minor*. Zone Vb (2dβ). P.M.O. 87556–8. Also two blocks from Andrarum (old collection) associated with *Peltura? acutidens*. Zone Vb (2dβ) Gr. I. 20775–6.

*Remarks.* Three-dimensional material shows that the genal spines of *S. alatus* (in standard orientation) spring out laterally from the librigenae and are not bent downwards below the cephalon as in *S. humilis*. Even in the best specimens studied, the tip of the genal spine was always broken, but can be restored from the illustrations of previous authors, especially Henningsmoen and Rushton. The anterior arch is of moderate height, and the postero-lateral border rises from the genal spine obliquely. Thus the cephalon could rest upon the sea floor upon the antero-lateral border and the genal spines; a position impossible for the related *S. humilis*.

*Eye-morphology.* Eye one-quarter the total length of the cephalon, and set high on the cheek, opposite S1. Eye-indices: A/G 35%, A/Gn 27%, H/A 108%. The palpebral lobe is relatively narrow with a curving outer edge, and is confluent with the long narrow and backwardly curving ocular ridge. In side view it forms a nearly semi-circular arch, with a slightly flattened top, where it is widest. The upper surface of the palpebral lobe flares outwards and upwards from the deeply incised palpebral furrow at about 45°. There is little trace of surface ornament apart from scattered indistinct tubercles, but the granular surface seen at high magnifications implies that some recrystallization has taken place. The visual surface is closely similar to that of typical representatives of *Ctenopyge*, and is a nearly perfect oblate spheroid in form with irregularities in lens distribution typical of all later leptoplastines. The eye-socket is extremely narrow, more so than in any species previously discussed, though faint vertical striations are visible.

*Sphaerophthalmus humilis* (Phillips 1848)

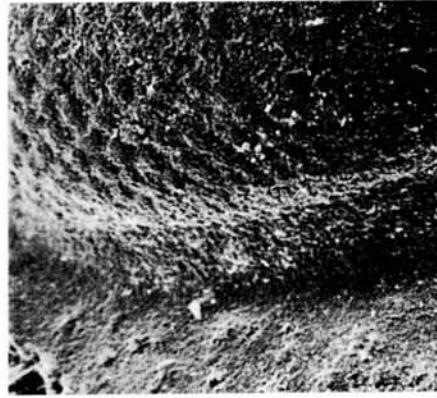
- 1848 *Olenus humilis* n.s.; Phillips, p. 55, figs. 4–5, p. 347.  
 1901 *Sphaerophthalmus alatus* Angelin (*sic*); Lindström, p. 29, pl. III, figs. 31–34.  
 1913 *Sphaerophthalmus alatus* (Boeck sp.); Lake, p. 74, pl. VIII, fig. 1–5.  
 1957 *Sphaerophthalmus humilis* (Phillips 1848); Henningsmoen, p. 215, pl. 5; pl. 22, figs. 7, 11–15.  
 1968 *Sphaerophthalmus humilis* (Phillips); Rushton, p. 415, text-fig. 2, 3a, pl. 78, figs. 11–15.

## EXPLANATION OF PLATE 94

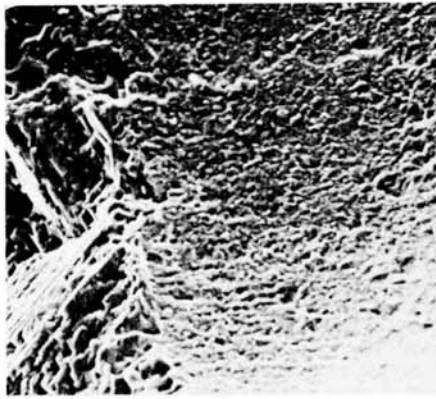
- Figs. 1–4. *Ctenopyge (Mesoctenopyge) tumida* Westergård 1922. Naersnes, Royken. Zone Vb (2dβ).  
 1, Anterior region of small adult eye with some lenses missing. P.M.O. 87552, × 105. 2, Lowermost lenses and eye-socket of large adult eye; faint vertical striations visible on eye-socket. P.M.O. 87554, × 135.  
 3, Palpebral lobe, outer central region with striations nearly normal to the outer edge. P.M.O. 87552, × 250. 4, Adult eye in lateral view showing eye-socket. Visual surface damaged. P.M.O. 87553, × 75.  
 Fig. 5. Block with librigenae and eyes of *Ctenopyge (Mesoctenopyge) similis* Henningsmoen 1957 (left), and *Ctenopyge (Eoctenopyge) modesta* Henningsmoen 1957 (centre and right). Sars Gate, Oslo. Zone Vb (2d sim.). P.M.O. 87564, × 26.  
 Fig. 6. *Sphaerophthalmus humilis* Phillips 1848. Andrarum, Scania. Zone Vc. Lower central part of eye; external surface of cornea and internal moulds of lenses. Gr. I. 20706, × 180.



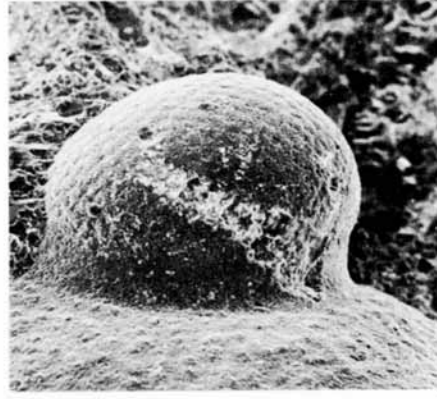
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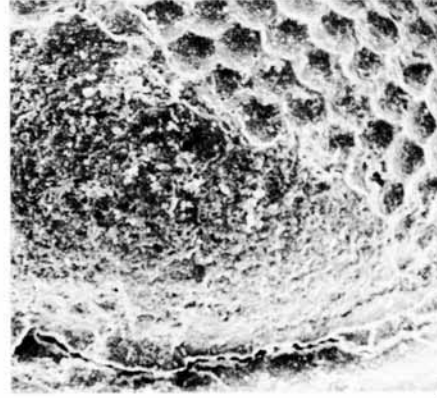
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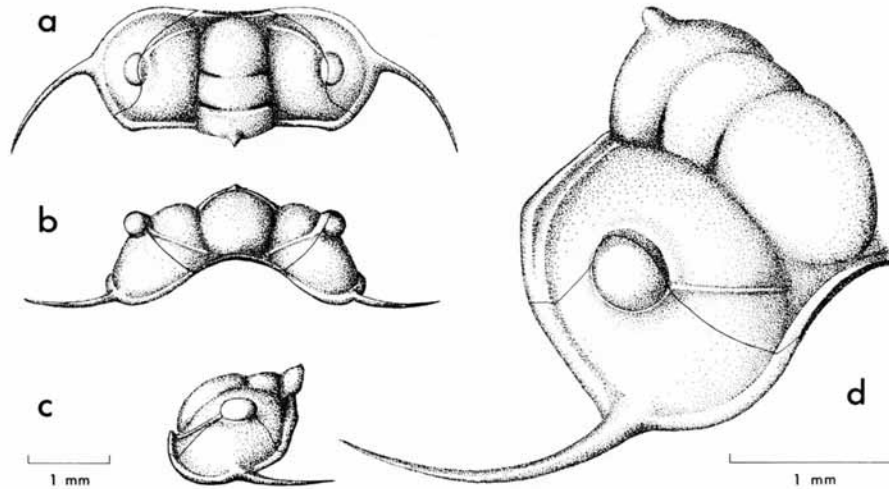


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6

CLARKSON, *Ctenopyge* and *Sphaerophthalmus* eyes



TEXT-FIG. 7. *a-d*. *Sphaerophthalmus alatus* (Boeck 1838). Zone Vb. Gamlebyen, Oslo. Restoration of the cephalon in dorsal, frontal, and lateral aspects and (*d*) enlarged in antero-lateral view from P.M.O. 87556-87558.

Plate 94, fig. 6; Plate 95, figs. 3-6; text-fig. 8*a-d*

*Material*. Three blocks from Andrarum, associated with *P. scarabaeoides scarabaeoides*, *Ct. linnarssoni*, and *Ct. teretifrons*. Zone Vc (2*d*<sub>y</sub>). Old collection, Gr. I. 20706, 20803, 5537.

*Remarks*. *S. humilis* is an extremely convex trilobite with a very pronounced anterior arch and almost vertical librigenae. The peculiar attitude of the genal spines in this species was first noted by Rushton (1968, p. 415). He reconstructed the cephalon with steeply sloping librigenae, and ventrally projecting genal spines, curving in under the cephalon. I have been able to confirm that the genal spines do plunge downwards as Rushton described, so that the cephalon could not rest upon the sea floor. In my restoration, these spines do not curve inwards quite so strikingly, but in all other respects I agree with Rushton.

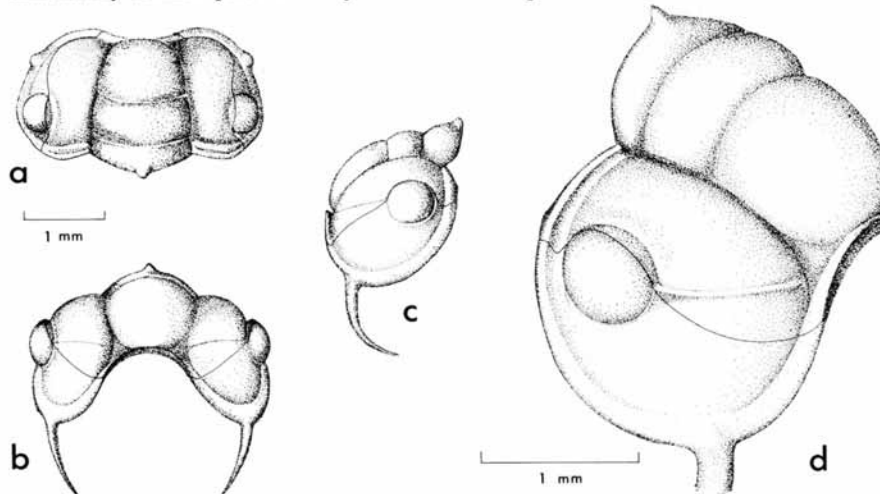
*Eye-morphology*. This species is unusual because of the relatively enormous size of the eye, and its very far posterior position. It is one-third the total length of the cephalon, with its anterior edge opposite S1. Eye-indices: A/G 38%, A/Gn 30%, H/A 335%. The palpebral lobe, which is jointed to the ocular ridge, is similar in form to that of *S. alatus*, though narrower. No surface ornament has been detected in the material examined. Since the palpebral lobe is placed slightly behind the widest part of the cranidium, the anterior edge of the visual surface appears to be slightly recessed. The visual surface forms about a third to a half of a slightly oblate spheroid, with the long axis horizontal. Its edge lies in an exsagittal plane, inclined at some 10° from the vertical. In side view the eye appears nearly globular. Each eye subtended a visual field whose lower limits are 70° to 80° below the equator, and which just overlap at the front, rear, and above so as to give an almost entirely panoramic range not found in other olenids, and, indeed, in few other trilobites. Juvenile eyes are of similar form, but have fewer lenses (*c.* 70 as compared with *c.* 200). Both in juvenile and adult eyes the eye-socket is very narrow and shows no definite structure.

In the material to hand the thin biconvex lenses are easily detached. Where they are partially removed from the matrix each is preserved as a single calcite crystal with a very slightly convex upper surface and a more strongly convex inner face. Distinct cleavages are visible, from which it can be deduced that the *c*-axis of each crystal is normal to the surface. Sometimes the finer detail has been destroyed by recrystallization, but the impressions left by the lower surfaces of the lenses show their arrangement very clearly (Pl. 95, figs. 3-4).



*Development of the eye in later leptoplastines.* In most trilobites the first-formed lenses are emplaced in an initial horizontal row parallel with the facial suture. New lenses are added below these, in parallel horizontal rows. The new lenses are offset relative to those above so that there develops an array of lenses arranged in a regular system of hexagonal close packing. This pattern is most clearly shown in the phacopids, where the lenses are large and separate; dorso-ventral files can be seen intersecting with ascending and descending diagonal files (Clarkson 1966a). In some phacopid eyes new small lenses may actually develop in an accessory row above the initial horizontal row, but this seems to be confined to certain genera only (Beckmann 1951; Clarkson 1966b). The eyes of *Ct. (E.) modesta*, *Ct. (M.) similis*, and *Ct. (M.) tumida* are closely similar to one another, and though there are differences in size and position the resemblance in detailed structure is such that though most of the comments given here are based upon *Ct. (M.) similis* (Pl. 94, fig. 2, text-fig. 5e) they are appropriate also to the others. In most respects they apply also to *Sphaerophthalmus* eyes, though the latter have more lenses.

All these olenid eyes begin their development in much the same way as phacopids, though being holochroal the lenses are contiguous and they are all much the same size. The first-formed lenses lie in a horizontal row following the curve of the facial suture. When seen from above this row and subsequent rows appear to be concentric and curving outwards like parallel strings of beads. In the upper (i.e. the oldest) part of the eye the close-packing system is regular and arranged with respect to the dominant elements—the horizontal rows. But some distance below the facial suture, usually after the first half-dozen rows, irregularities are encountered which break up this clearly defined pattern. Why do these develop?



TEXT-FIG. 8. *a-d. Sphaerophthalmus humilis* (Phillips 1848). Zone Vc. Andrarum, Scania. Restoration of the cephalon in (a) dorsal, (b) frontal, and (c) lateral aspects and (d) enlarged in antero-lateral view, from Gr. I. 20706.

It has long been established that in trilobites generally new lenses are usually added only along the lower margin of the visual surface, and that each normally arises below and directly between two existing lenses of the preceding horizontal row. Irregularities come into being when extra lenses are intercalated into this system, in other words when at a few loci two new lenses are emplaced instead of one. If, as I discussed previously in the phacopid *Ormathops* (Clarkson 1971), the developmental system is 'programmed' to produce new lenses when a particular spatial threshold has been reached, then such new intercalated lenses will necessarily be emplaced to fill the 'extra space' as the visual surface expands in circumference. Each of the new intercalated lenses will in turn act as a focus for lens-initiation in successive horizontal rows, and the effects of these small, though inevitable irregularities are clearly visible. Had these olenids possessed lenses graduated in size such irregularities would never have arisen, but since they are all much the same size, disruptions of the regular packing system are, as in *Ormathops*, a geometrical requirement.

The lower third of the eye lies below the ambitus (this term used as in an echinoid) where the eye has reached its greatest horizontal circumference and thereafter decreases slightly in diameter. Since the visual surface is no longer increasing no new lenses are added by intercalation and it is hardly surprising to find another change in the manner of lens emplacement. What usually happens is that one of the two original sets of diagonal rows swings into a vertical orientation, these becoming the vertical files characteristic of the lower part of the eye, though they are not homologous with the dorso-ventral files of the phacopids. The lenses in this region are slightly smaller than the upper ones, accommodating the slight decrease in the diameter of the eye.

Thus the eyes of olenids of this type have three horizontal zones, an upper regular zone where the horizontal rows are the dominant elements, a zone of intercalation, where the horizontal rows are still dominant though there are notable irregularities, and a lower zone of dorso-ventral files where the system of hexagonal close packing is based upon one set of diagonal rows which has now become vertical in response to packing requirements. This system resembles that of the pelturines only in so far as the diagonal rows change direction and become more vertical. But the pelturine system is based upon arithmetical change in distances between lens-centres, whereas in later leptoplastines, distances between lens-centres remain constant, except where the increasing girth of the eye promotes hiatuses.

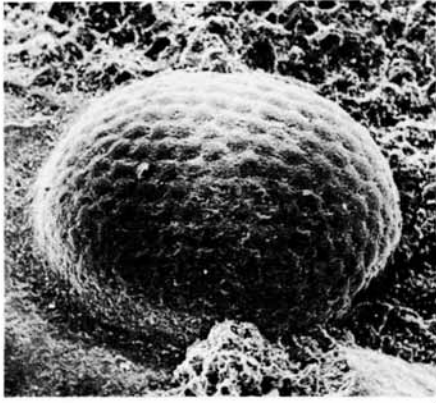
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EXPLANATION OF PLATE 95

Figs. 1, 2. *Sphaerophthalmus alatus* (Boeck 1838). Andrarum, Scania. Zone Vb (2d $\beta$ ). 1, Dorso-lateral and 2, anterior view of young eye. Gr. I. 20775,  $\times 140$ . In 1 right edge is anterior.

Figs. 3-6. *Sphaerophthalmus humilis* (Phillips 1848). Andrarum, Scania. Zone Vc. 3, Single lens, partially detached from matrix, and internal moulds of missing lenses. Gr. I. 20803,  $\times 1200$ . Bar = 10  $\mu\text{m}$ . 4, Internal mould of adult eye with a few lenses still adherent. Left edge anterior. Gr. I. 20803,  $\times 60$ . 5, Very young eye; outer surface Gr. I. 5537,  $\times 200$ . 6, Internal mould of lenses near base of eye. Gr. I. 20803,  $\times 500$ . Bar = 10  $\mu\text{m}$ .

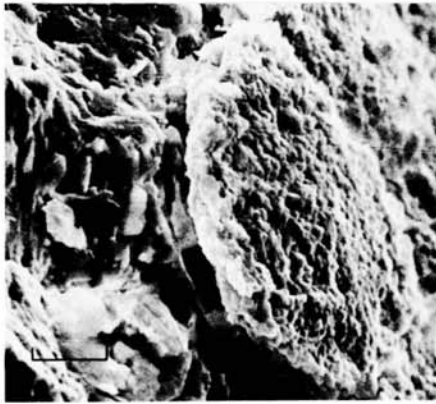
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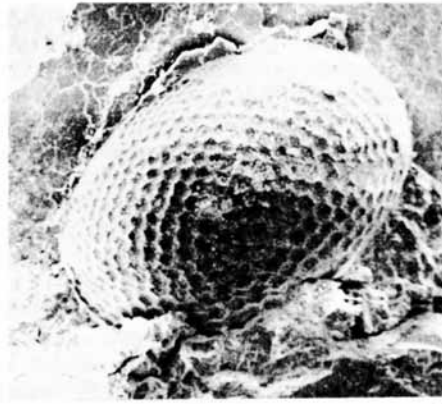
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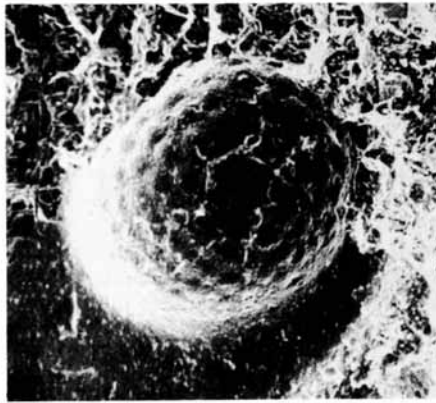
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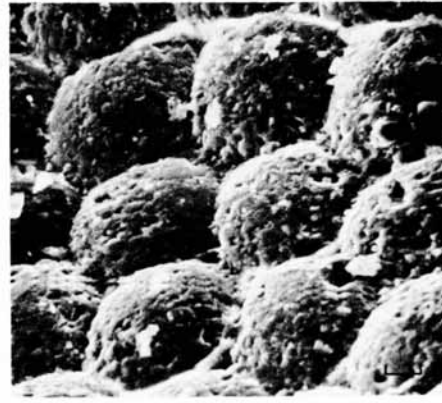
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6

CLARKSON, *Sphaerophthalmus* eyes

## SUMMARY AND CONCLUSIONS

*Evolution of the eye in the Olenidae.* In this summary of observations I have largely followed the phylogenetic scheme of Henningsmoen (1957, Chart 6), and though this will certainly need to be modified in the light of recent and future observations, it still forms a useful provisional basis for discussion of phylogeny.

According to Henningsmoen, *Olenus*, which was the earliest Upper Cambrian genus, persisting through Zones I and II only, gave rise to three lines of descent. The most conservative line led to *Parabolina* (Zone III to Lower Tremadoc), and to other Olenidae. At about the same time (Zone III), the first pelturine genus *Protopeltura* appeared, and was followed later (Zone Vb), by *Peltura* and other Pelturinae. From *Olenus* also descended a third group, the Leptoplastinae, which began with *Leptoplastus* in Zone IV, a genus which gave rise to the elaborate leptoplastines *Ctenopyge* and *Sphaerophthalmus* which flourished in the time of Zone V.

Though the Triarthrinae and various other genera of the established families appeared and evolved in Tremadoc and later times, none of these have been studied in detail in my present work: in most of them the eye is small and rarely well preserved, though some of the Argentinian olenid species, e.g. *Parabolina argentina*, *Saltaspis steinmanni*, have relatively large eyes (Harrington and Leanza 1957, pp. 83, 95).

Öpik (1963) included the monogeneric Australian subfamily Rhodonaspidinae Öpik in the Olenidae. Because of the marked similarity of the pygidium of *Rhodonaspis* to that of *Parabolina*, he suggested a close relationship between these two genera, and noted that *Parabolina* may not have been derived from *Olenus*, but was part of another complex (including *Rhodonaspis*), which had persisted from the early Upper Cambrian. The evidence for this rests on the pygidial resemblance alone.

Study of the eye-morphology of Scandinavian genera, however, supports the other criteria used by Henningsmoen in erecting his phylogenetic scheme; the similarity of the eyes of *Olenus* meraspids and adult *Parabolina* has already been pointed out. *Rhodonaspis* has very large eyes of unusual form, having the palpebral lobe and probably the ocular ridge also as double structures, divided by an ocular striga. The ocular ridge is separated from the glabella, as in adult *Olenus*.

Further descriptions and discussions of new olenid material may help to resolve conflicting suggestions as to olenid phylogeny, and it is to be hoped that the rich Cambrian successions of Queensland may furnish yet more material of olenids and related trilobite families. For the moment, however, I have preferred to take a conservative view of olenid phylogeny.

The principal conclusions which have emerged from the present studies are as follows:

(a) The 'primeval' olenid eye from which all other kinds ultimately derived is exhibited by *Olenus*. Here the ocular suture is functional in the adult, so that the visual surface is found only in meraspids. Large adults have a highly structured and possibly sensory zone surrounding the visual surface, well supplied with alimentary prosopon. This peripheral zone is, however, weakly developed in meraspids. In the latter the lenses are plano-convex, and are probably welded to the inner surface of the cornea, sometimes being quite widely spaced.

(b) In both the later Oleninae and in all the Pelturinae, the eyes have many features

very similar to those of meraspids of *Olenus*. These include their small size and forward position, the inclination of the long axis to the exsagittal plane, the non-functional ocular suture, structure of the visual surface, poorly developed peripheral zone, and the confluence of the palpebral lobe with the ocular ridge. All these are suggestive of a paedomorphic origin for these adult eyes. Pelturine eyes have lenses decreasing in size ventrally, arranged in a geometrically regular system with logarithmic diminution of distances between lens-centres. It is probable that the eyes of most Tremadoc and later olenids are also of this type.

(c) Early Leptoplastinae had eyes like those of *Olenus*, though their generally poorer preservation precludes very detailed comparison. The later leptoplastines *Ctenopyge* and *Sphaerophthalmus* retained the visual surface in the adult, and the eye is often strikingly well developed, though the peripheral zone is not greatly in evidence. Some features of these eyes may likewise be regarded as paedomorphic. Eyes of this kind are usually spheroidal, and have thin biconvex lenses underlying a very thin cornea. They are variable in size, position, and in the shape of the palpebral lobe and the range of the visual field (the most extreme form being *S. humilis*). The visual surface has a peculiar pattern of development, which is very clear in *Ct. (M.) similis*, but seems to be constant throughout the group. In this the lenses are all of the same size, and have a distinct zone of irregularities. Following the extinction of the last species of *Ctenopyge* and *Sphaerophthalmus* before the close of the Upper Cambrian, no other olenids evolved such remarkably developed visual organs.

*Adaptations of the olenid cephalon.* Henningsmoen (1957, pp. 70–82) has written extensively about the mode of life and environment of the olenids. He suggested that although most olenids were capable of swimming above the sea floor, they could also sojourn for certain periods on the floor of the stagnant Olenid Sea, and were probably adapted for life in waters with a restricted oxygen content. Further evidence of bottom-dwelling habits in some olenids is provided by recent trace-fossil analysis (Orłowski, Radwański, and Roniewicz 1970; Birkenmajer and Bruton 1971).

The cephalic reconstructions presented here, which were made to show the eye in its correct relationship to the rest of the cephalon, also seem to indicate, in some cases, functional adaptations for a benthonic mode of life. Most olenid cephalons (with the notable exception of *S. humilis*), seem to be well adapted for resting upon the sea floor. The short genal spines of most species of *Olenus*, *Parabolina*, and *Leptoplastus*, together with *S. alatus*, project horizontally from the cephalon, so that the trilobite could lie on the sea floor, with its cephalon propped in a stable position and having its anterior arch open. Such support is even more evident in genera with long genal spines. Thus the genal spines of *E. modesta* are long and elegantly curved, in such a manner that the cephalon could be supported on four points; the lowest parts of the two antero-lateral borders, and the lower surfaces of the genal spines just in front of their tips. *Ct. similis* and *Ct. tumida* have very long flattened and horizontal genal spines, which would give support over their whole length. In these the height of the occipital ring above the base level, and the oblique appearance of the postero-lateral border, when seen from the side suggest that the body was carried high above the sea floor, a habit which no doubt carried real functional implications. I have elsewhere contended (Clarkson 1969) that long spines in the odontopleurid trilobites are

support structures rather than being used to prevent sinking through frictional retardation. Judging by the structure of the cephalon in the long-spined olenids, the same principle seems to apply, but it will be necessary to prepare complete lateral reconstructions with the thorax and pygidium in place before these suggestions can be fully worked out. The immensely long thoracic spines of *Ctenopyge*, and their relationship to the rest of the body still pose intriguing problems.

Clearly *S. humilis* was very differently modified, as witness the nearly vertical genal spines and the very large eye with its greatly expanded visual field. Though the purpose of such adaptations is far from certain, it is evident that even within the confines of the organization of such a close-knit family as the Olenidae, there was still a substantial degree of evolutionary plasticity, and the possibility of individual functional differentiation.

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All the SEM photographs were taken using a Cambridge 'Stereoscan' by Mr. J. Goodall of the Department of Engineering, Edinburgh University, to whom I am greatly indebted for his continued skill and patience. I gratefully acknowledge a grant towards plate cost from the Carnegie Trust for the Scottish Universities.

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*Discussion on Dr. Clarkson's paper:*

Chaloner: Did you clean the surface in any way prior to examination?

Clarkson: Yes. I used a Directional Ultrasonic Cleaner, which is a gun device manufactured by the Simms Group R. & D. Ltd. The specimen is placed under water and 'blasted' for two or three seconds by a stream of high-velocity bubbles from the gun. This suffices to remove all the loose dirt and dust; but if the gun is operated for longer than a few seconds the surface of the specimen may be damaged by abrasion.