Morphological, functional and taxonomic studies of trilobites

by

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Abstract

This dissertation contains 19 research papers published since 1967, relating primarily to the functional organisation of trilobites, and to the taxonomy of some Ordovician and Silurian trilobite faunas. These papers are preceded by a short summary in which the aims, methods and conclusions of this work are briefly explained.

The bulk of the functional work is concerned with the eyes of trilobites - the oldest known visual system. Little was known about these eyes beforehand, but the long geological record and often good preservation has enabled many details of their structure, evolution and function to be clarified. It was initially confirmed that there were two types of eye, holochroal and schizochroal; it was later established that in all cases the lenses are of primary calcite, with the c-axes oriented normal to the visual surface. The detailed structure of the visual organs of Asaphus, olenids and other holochroal eyes has been documented in detail mainly with the aid of scanning electron microscopy. The evolution of holochroal eyes has been elucidated in general terms and the construction and optics of holochroal lenses gives some basis for comparison with compound eyes in modern arthropods.

Schizochroal eyes, confined to the Ordovician-Devonian Order Phacopina, have very large disjunct lenses, and bear no close resemblance to any kind of modern eye. They are shown to have been derived paedomorphically from a holochroal ancestor, but in the earliest phacopid genus Ormathops regular lens-packing was not achieved, due to geometrical constraints.

Earlier work concentrated upon the morphology of the eye, its growth as an anteriorly expanding logarithmic spiral, the emplacement and packing of lenses upon it and the determination of the visual field through accurate measurement of the angular bearings of individual lens axes. More recent studies have been concerned with the analysis of schizochroal lens structure and optics. The phacopid lens is compound, with an upper unit of radiating calcite fibres interlocking with a lower intralensar bowl. Sometimes there is a central core of similar texture to the bowl. The lenses are aplanatic and aspheric in accordance with Cartesian principles, and the intralensar bowl and probably the core also, are subsidiary correcting structures. Some attempt is made to interpret the schizochroal eye as a whole functional organ, but in the absence of soft parts, much remains unresolved.

Other functional studies bearing upon the habits and evolution of trilobites include the original life attitude of the body in various taxa, phacopids and odontopleurids in particular, and structures concerned with enrolment. Different types of interlocking mechanisms (co-aptative structures), here described in detail, have arisen several times in different trilobite lineages.

Finally, a two-part monograph of the Silurian trilobites of the Pentland Hills (with some related forms) is included in which some 15 species are formally described. This work, together with a descriptive account of the phacopid Calyptaulax, relates also to earlier functional studies of eye-structure and enrolment mechanisms, which are of undoubted taxonmic value.

Statement

The 19 publications bound in this volume are all the result of work done in Edinburgh subsequent to my Ph.D. Three papers which came directly from my Ph.D. are not included here but are referred to in the Summary. Publication number 5 (1969) is partially based upon work undertaken in Cambridge between 1960 and 1963, and included in my Ph.D. but this was extensively reworked and altered in Edinburgh before the results were published.

In all cases of joint authorship the work was shared equally between myself and the other author, except in numbers 15 and 18 where I was the senior author, and undertook most of the work. Publications 14 and 17 were the result of equally shared work, but the topic was initially suggested by the first author. All photographs and drawings were done by me, except those made J-L. Henry in 6, 8 (part) and 11, and where stated elsewhere.

Summary

In 1960 I began work on trilobite functional morphology at the University of Cambridge and my Ph.D. dissertation entitled "Studies in the Functional Morphology of Trilobites" was examined and approved in 1964. Since then I have continued and expanded this research, and the collection of nineteen papers given here is submitted for the degree of Doctor of Science at the University of Edinburgh. Three papers (Clarkson, 1966, a, b, c) which came directly from my Ph.D. dissertation are not included in the present compendium, but since much of my later work developed from these early researches, it seems appropriate to summarise these here and to record the subsequent development of various topics and concepts.

The research in which I have been engaged since 1964 has been concerned with four inter-related topics, all of which bear upon the classification and life of these remarkable extinct invertebrates. These are, (i) the trilobite visual system (ii) the life attitudes of trilobites (iii) enrolment mechanisms in trilobites (iv) taxonomic studies.

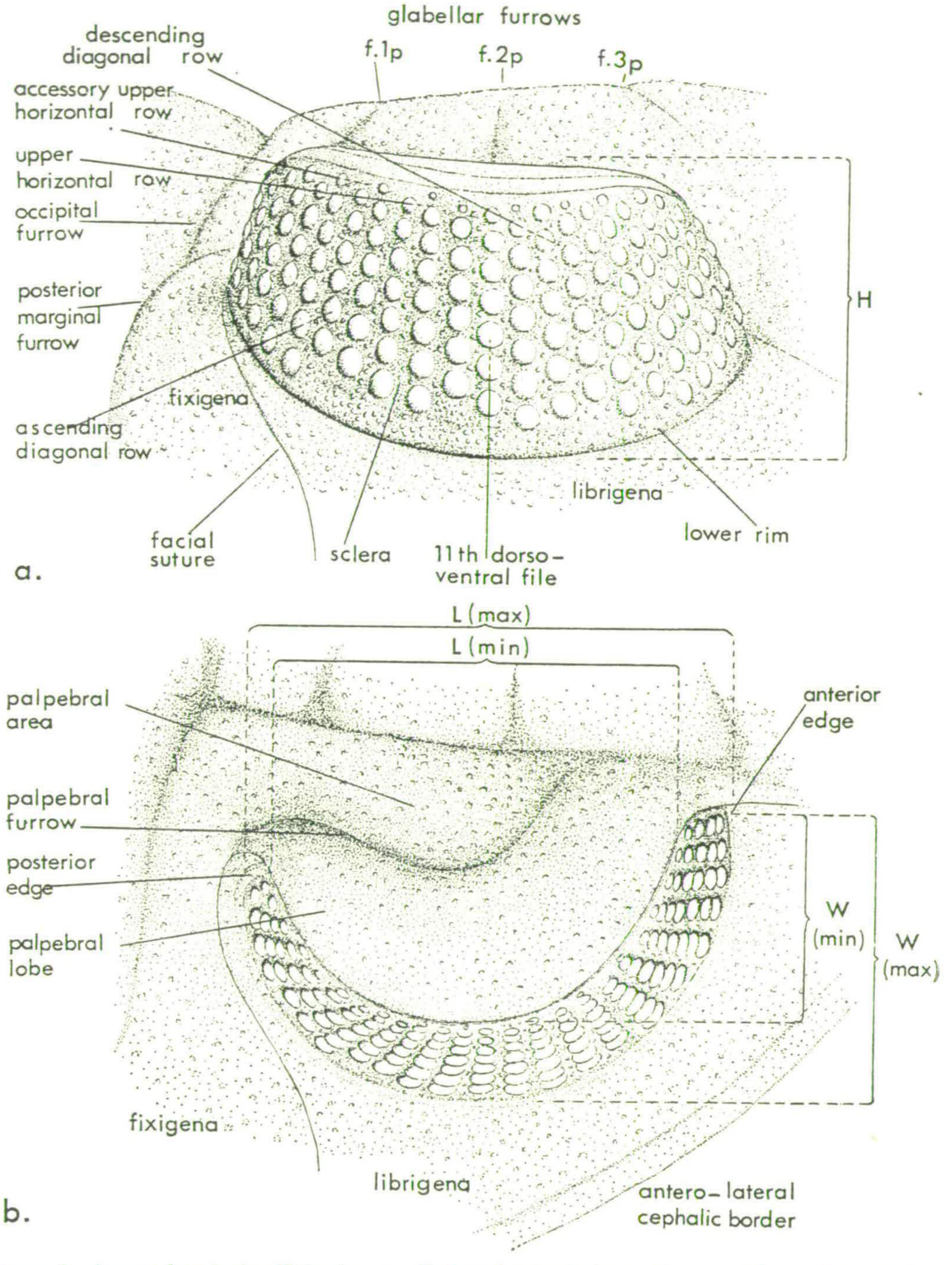
The trilobite visual system

The study of the compound eyes of trilobites was recommended to me by my Ph.D. supervisor, Dr M.J.S. Rudwick when I began research work. Whereas the eyes of trilobites are the oldest of all known visual systems they had previously been studied only by a few authors of whom the chief was Lindström (1901). This author's work was fundamental to all later studies of trilobite vision, and was of permanent and enduring value. He confirmed that there were two kinds of eye, previously defined by Clarke (1884) as holochroal and schizochroal. The former were the commonest kind, consisting of small contiguous lenses set on a curving visual surface, whilst schizochroal eyes confined to the sub-order Phacopina, possessed much larger, strongly biconvex and disjunct lenses.

Lindström figured many thin sections both of holochroal and schizochroal eyes, as well as sections through the hypostomal maculae. He believed that trilobites possessed hypostomal (ventral) eyes as well as the compound eyes of the dorsal surface, (but having re-studied this original material I regard this as inconclusive). Whilst many of the specimens he figured had been wholly or partially recrystallised, a problem which I more often than not encountered in my own work, the quality of his research set a very high standard against which all later work had to be judged.

When I began my studies of trilobite eyes in 1960, very little material was available for sectioning, and what little I had was used only to confirm Lindström's observations on the distinction between the two types of eye and the shapes of the lenses. The bulk of my early research therefore was limited to what could be understood from well-preserved museum specimens. On the advise of my supervisor I selected many specimens of Phacopina, which have schizochroal eyes normally with less than 150 lenses (Fig. 1). It proved possible (a) to construct a map of each eye showing the size, spacing and arrangement of all the lenses, and using this as a basis (b) to measure accurately the angular bearing of the axis of each lens, and thus to build up a chart of the angular range of vision of the whole eye and the distribution of lens-axes within it (Figs. 2-4).

It emerged from this work firstly, that there was a remarkable variability in lens-size across the eye and secondly that the lens-axes are often clustered to cover a particular area of the visual field, or alternatively arranged in widely spaced 'visual strips' crossing the visual field from top to bottom as in Acaste. Since schizochroal eyes bear no close analogy to the eyes of any modern arthropod, any functional interpretations of this



TEXT-FIG. 1. *Acaste downingiae* (Salter) s. str. External morphology of eye and immediate environs, After SM A 28720 (eye-variant A); *a*. Lateral view. *b*. Dorsal view. Dimensions; L, W, H, length, width, height.

Fig. 1. (after Clarkson 1966a)

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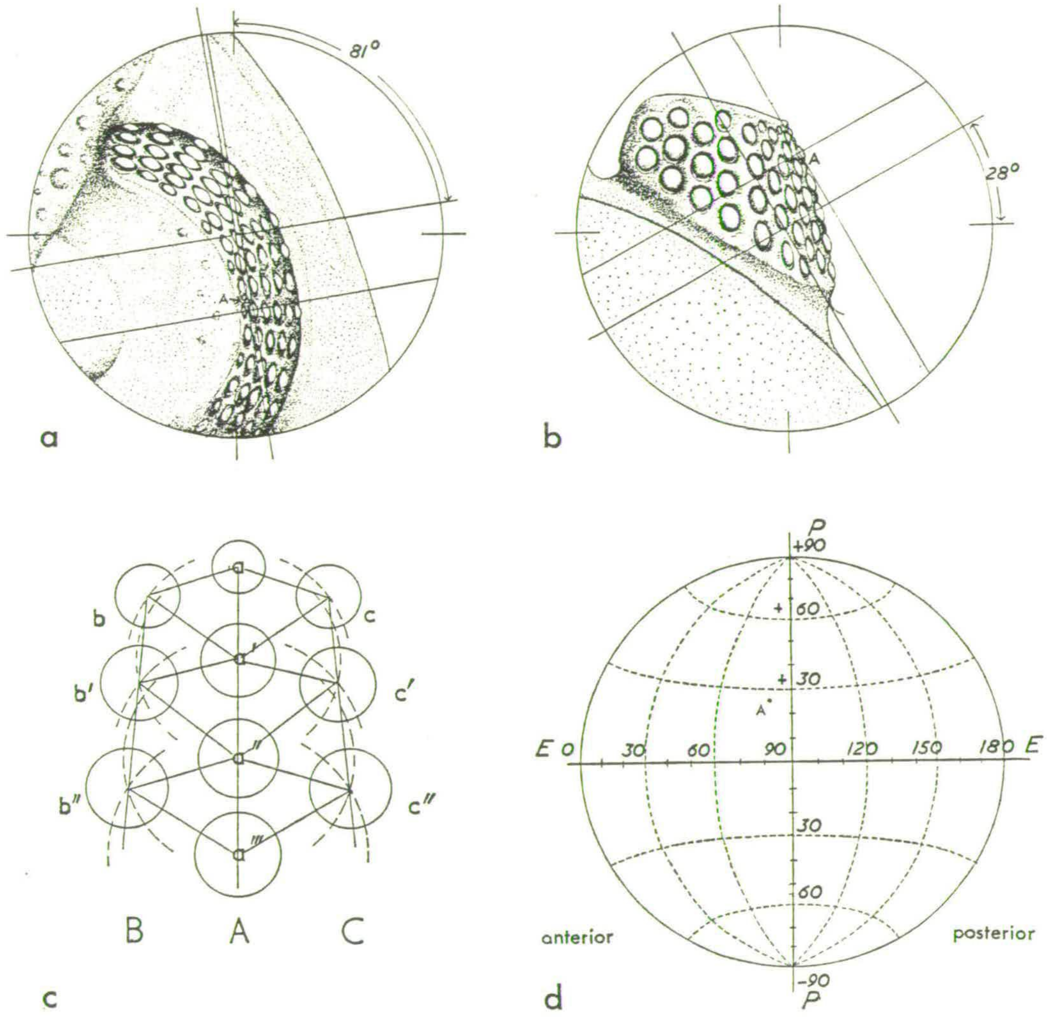
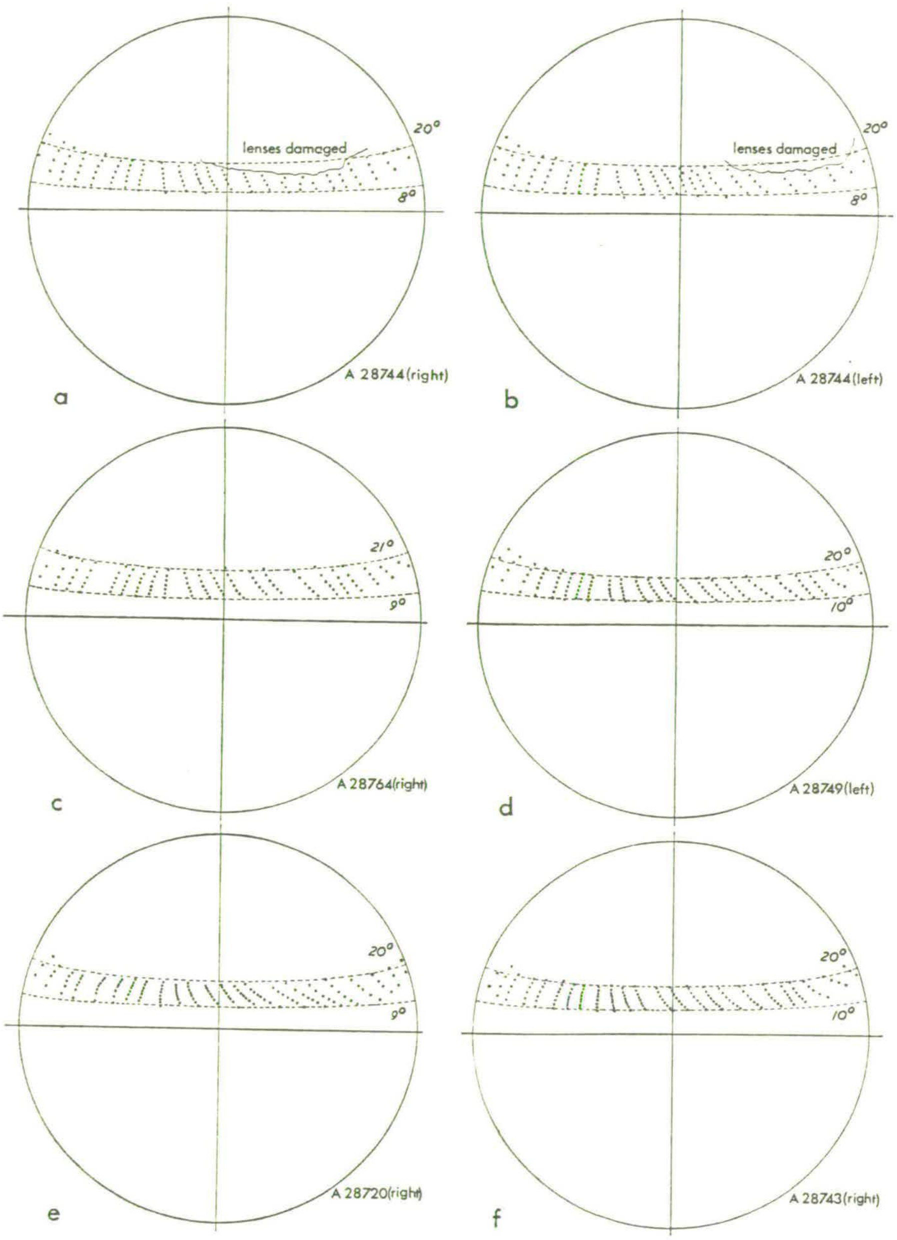


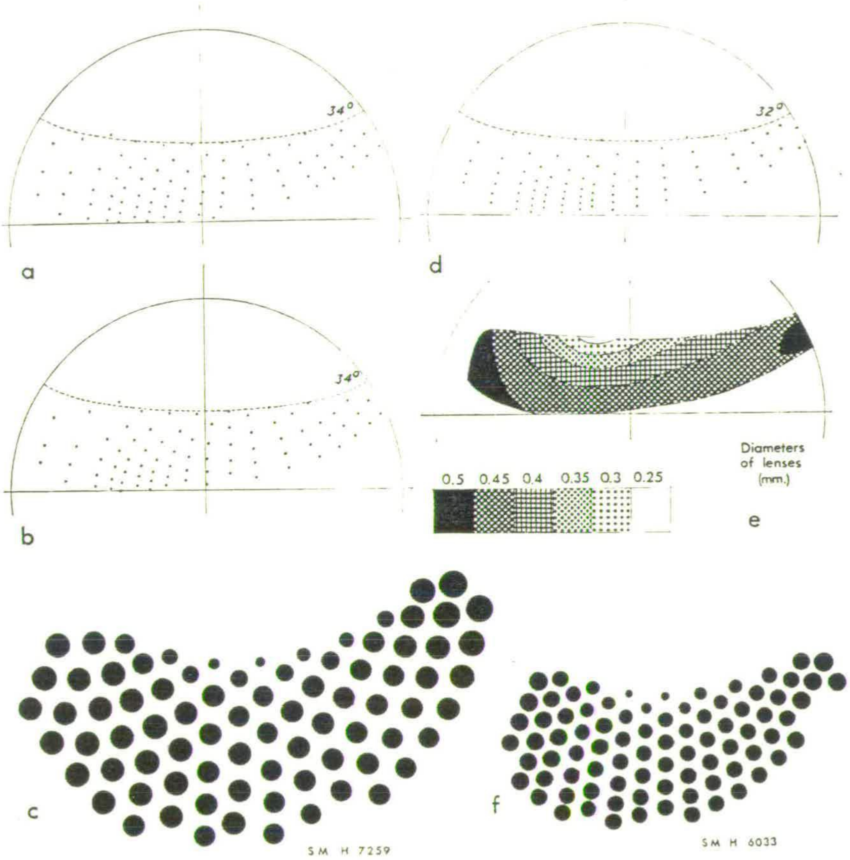
TEXT-FIG. 3. Technique of measurement of the spatial and angular relationships of the lenses. *a*, *b*, Angular directions of lens-axes of *Phacops latifrons* Bronn. The two sets of perpendicular lines represent the central cross wires of the graticule, and parallel lines following the optic axis and principal plane of the lens. Other graticular lines have been omitted for clarity. Lens A has latitudinal and longitudinal axial bearings of 28° and 81° respectively; *c*, Triangulation of lens-centres in files B and C from those of file A; *d*, Lambert equal-area net with notation adopted for recording bearings of lens-axes. The bearing of the axis of lens A (*vide* text-fig. 3*a* and *b*) is indicated.

Fig. 2. (after Clarkson 1966a)



TEXT-FIG. 5. Visual fields and axial bearings of lenses shown by stereographic projection. *a–f*, *Acaste downingiae* (Salter) s. str., eye-variant A.

Fig. 3. (after Clarkson 1966a)



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).

Fig. 4. (after Clarkson 1966b)

information were inevitably tentative. I conceived the schizochroal eye as being primarily adapted for movement perception but it was clear that much more basic data were needed in order to understand its true nature.

When I came to Edinburgh in 1963, I obtained or collected a quantity of exceptionally well preserved specimens of holochroal and schizochroal eyed trilobites ranging in age from Cambrian to Carboniferous. These specimens, collected from England, Scandinavia, Bohemia and North America allowed for the first time a detailed study to be made of the structure of various kinds of eyes and their lenses, using, in the first instance, thin sections and polished surfaces. The schizochroal eyes of Phacops (2) and Reedops (4) proved particularly amenable to analysis, even though some recrystallisation had altered the primary structures. Even so, the excellent Bohemian specimens of Reedops revealed indications of bowl-like structures within the lenses, which resembled equivalent bowls figured in one of Lindström's specimens (though he had regarded these as of diagenetic origin). The ubiquity of these intralensar bowls in Reedops and their presence also in partially decalcified lenses in Crozonaspis and Dalmanitina (3) indicated that these were indeed original parts of the schizochroal lens, though their usually imperfect preservation prohibited an understanding of their function until some time later.

Meanwhile the advent of the scanning electron microscope added a new dimension to palaeontology and proved to be a vital new tool in the study of trilobite vision. It became possible to investigate the microstructure of both holochroal and schizochroal eyes on an infinitely more detailed scale, and scanning electron microscopy was adopted as a standard technique in combination with thin-sectioning and other methods. The visual organs of Asaphus and olenids were the first holochroal eyes to be investigated in this way (9. 10), and in both the lenses proved to be of primary calcite, as had been shown independently by Towe (1973) in *Phacops*. All later studies have confirmed that the lenses of trilobite eyes were, in fact, of primary calcite with the c-axis normal to the surface of the eye. In work on the evolution of olenid eyes based upon the rich and well-documented Upper Cambrian successions in Scandinavia, the role of paedomorphosis became very evident.

Perhaps the most critical of all problems concerning the evolution of trilobite eyes was the origin of the schizochroal eye. Whilst holochroal eyes are present in the earliest Cambrian trilobites, schizochroal eyes did not appear until the early Ordovician. It seemed that one way in which to investigate this problem would be the study of the earliest of all schizochroal eyes. The phacopid genus *Ormathops* which is first found in rocks of Arenig age has a much less regular system of lens-packing than do later Phacopina, and a geometrical analysis (7. 13) showed how this arose. The eye forms an anteriorly directed logarithmic spiral, upon which lenses are emplaced in sequence. If, as in *Ormathops* the lenses are all of the same size they cannot be packed regularly, through geometrical constraints alone; but if as in all other Phacopina they increase in size ventrally, a regular system of hexagonal close packing is possible. Evidently regularity of packing must have been of importance to phacopid trilobites. This analysis finally resolved the problem of variation of lens-size over the visual surface, commented upon earlier.

A suggestion made in 1971 and subsequently confirmed in 1975 was that the earliest schizochroal eyes originated through paedomorphosis from a holochroal ancestor. When a complete meraspid specimen of the Carboniferous *Paladin eichwaldi shunnerensis* was collected in 1972 it was found to possess an eye with a small number of relatively large and separated lenses, quite different from the standard holochroal eye of the adult. It was, in effect a miniature schizochroal eye, and from such an organ the phacopid schizochroal eye could have arisen by retention of the juvenile morphology of the ancestral larva in the adult of the descendant.

By the time these studies were completed it was possible to summarise the state of knowledge of the evolution of trilobite eyes at the NATO symposium on trilobites and merostomes held at Oslo in 1973 (13). At this conference I met Professor R. Levi-Setti of Chicago, and together we conducted an investigation into the optics of schizochroal lenses. This work, carried out in Chicago in 1974, showed that the two kinds of lenses which had been demonstrated in *Crozonaspis* and *Dalmanitina* (3) (minus the intralensar bowl) conformed very closely to idealised models of thick, but aplanatic lenses designed in the 17th century by René Des Cartes and Christian Huygens. The intralensar bowl was the final correcting element of a lens which minimised spherical aberration, as was shown by a working model of *Crozonaspis* lens, which brought incident light to a very sharp focus.

Further details of lens structure and optics of both holochroal, and schizochroal eyes were given in my paper which formed the 21st Annual Address to the Palaeontological Association (16). This stage in the work on schizochroal lenses was concluded when the extremely complex lens structure of *Phacops rana milleri* was elucidated using unrecrystallised specimens collected from the Devonian of Ohio. These specimens were cut, lightly etched and photographed with the scanning electron microscope. The lenses were constructed on a radial plan, and possessed a central core as well as the intralensar bowl. These structures were of denser-textured calcite than the rest of the lens, and may both have been correcting structures. The crystal lattice of these lenses, in sections normal to the principal plane, is fan shaped, so that in addition to minimising spherical aberration they may also have minimised birefringence from oblique rays. The regeneration of the lenses after ecdysis was worked out in this species from specimens which died soon after moulting.

The only further studies I have done on trilobite eyes to date were in a taxonomic paper (ii) in which variation in the number of lenses in Calyptaulax was charted in a geographically widespread though stratigraphically limited species. There was also a theoretical discussion of blindness in trilobites and recent arthropods, with reference to deep-water environments (i) and a study of a possible light-sensitive tubercle in Nileus (14).

Whilst this 20-year study of the visual organs of trilobites has clarified certain aspects of their structure, evolution, and function, many questions remain unresolved. We have no knowledge of the origins of trilobite eyes, and although the optical perfection of the lenses of schizochroal eyes has been demonstrated, we are far from understanding how these eyes functioned as a whole. Some excellent structural work by Campbell (1975. 1977), and some promising suggestions by Stockton and Cowen (1977) have contributed to an understanding of the latter problem, but much further basic data needs to be gathered.

If suitable material becomes available, and if in particular, specimens with traces of internal structure are preserved, then some at least of the outstanding problems may be partially resolved. Useful contributions have been made recently by undergraduate zoology students working under my direction (S. Jameson, 1981 and D. Brown 1983), on structure and further such studies are planned.

Life attitudes

The eyes of many phacopid trilobites subtend a narrow latitudinal band of vision only. In life, this thin band must have been horizontal, and it could only have been so if the cephalon, as seen in profile were held in a particular attitude. Having established the original attitude of the cephalon, a reconstruction was made of the Eophacops musheni from enrolled and outstretched specimens (Clarkson 1966a) which exemplified a typical and common functional life attitude in trilobites generally, (Fig. 5).

Nevertheless, this life attitude was not universal for all trilobites, and following a comment by Whittington (1956), I began a study of the rather different structural plan in odontopleurid trilobites. The initial work on this was begun in Cambridge, but since much further study had to be done later in Edinburgh before the results were published (5) the paper more properly belongs to the present compendium. This work shed some light upon the evolution of the odontopleurids. Some incidental studies of the life attitudes of olenid trilobites were included in (10).

Enrolment

In 1970 I began a very fruitful cooperation with Dr J-L Henry (University of Rennes). This work was initially concerned with the taxonomy of some phacopid trilobites from Britanny (6) and later with the mechanism of enrolment in various trilobite groups, both from Brittany and England (8. 11).

In these works particular attention was given to the prevalence of

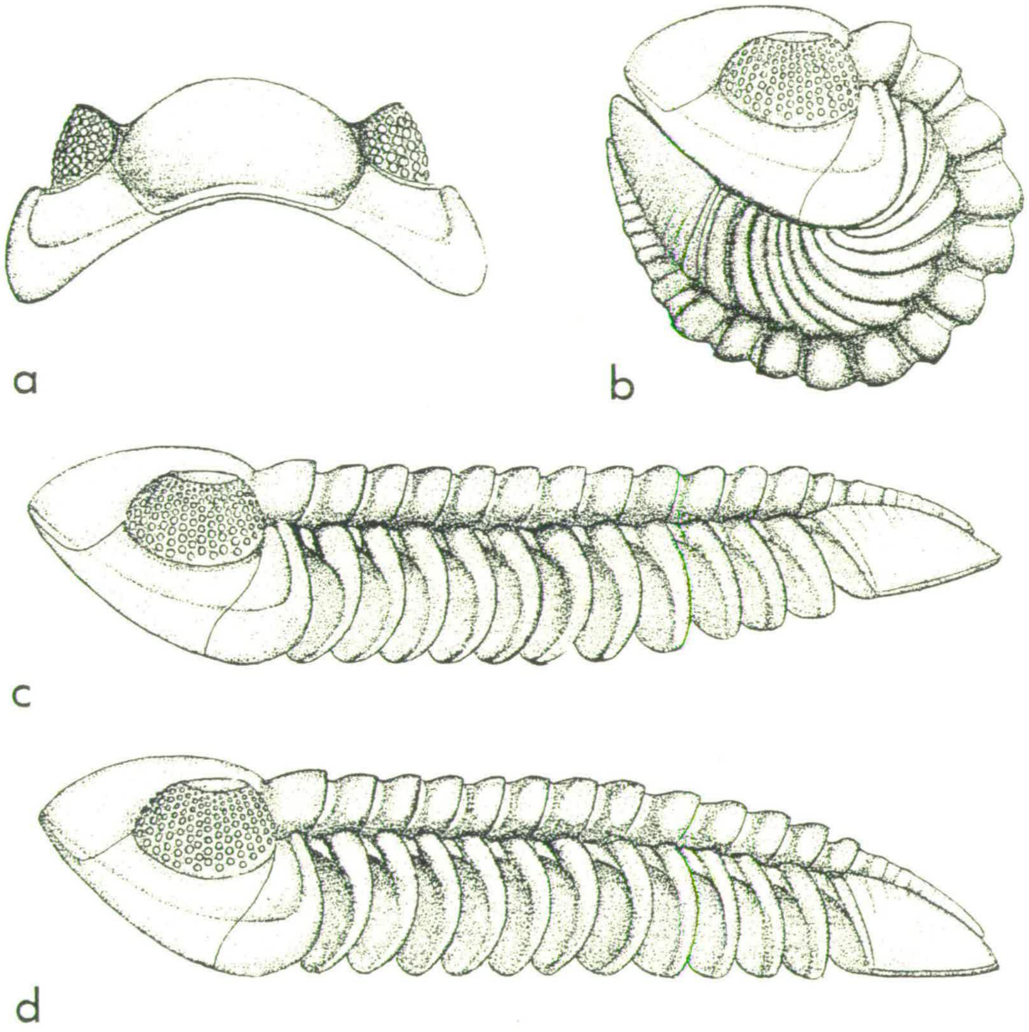


FIG. 3. *Phacops musheni:* Salter 1864. (a) Profile view of the enrolled specimen SM A 28701. In this orientation the visual field is horizontal as in Fig. 1. (b) Cephalon in the same attitude, from the front and showing the anterior arch. (c) Exoskeleton in the normal life attitude. Restored from SM A 28701 and A 28696. (d) The same with the tail unit lowered. All × 6.

Fig. 5. (after Clarkson 1966c)

different kinds of interlocking mechanisms (co-aptative structures) in trilobites of different taxa, and their importance for taxomomy.

This work was continued in a taxonomic study of the phacopid trilobites of the Pentland Hills (15) in which the use of co-aptative structures as taxonomic criteria was extended.

Taxonomy of Scottish Ordovician and Silurian Trilobites

In 1973 I began to prepare a monograph of the Silurian Trilobites of the Pentland Hills, first in cooperation with N. Eldredge and J-L. Henry and later with Yvonne Howells. This was produced in two parts, in Palaeontology (15. 18). The primary aim was to describe these hitherto poorly known, but excellently preserved faunas in detail and to record their stratigraphic occurrence. Some 15 species occur here, of which three in particular, have been found of value in correlating between other Silurian inliers in the Midland Valley of Scotland. Some functional characters were also considered in the first of these two papers.

A recent work (19) concerned one widely distributed and variable Ordovician species Calyptaulax brongniartii. The original type material was re-figured for the first time, and a detailed study of geographical variation in eye morphology was made, thus relating to other work on trilobite visual systems.

Taxonomy and functional morphology, together with ontogeny and ecology are all related: they are all inseparable and interconnected elements in the plexus of life and environment There must be an intrinsic connection between different types of research, so that, for example, a functional study of a trilobite has its roots in, and must feed back to taxonomy.

What has emerged from these and all other functional studies of trilobites, is the remarkably high quality of biological organisation and adaptation in these long-extinct organisms. Whereas the trilobites were on the one hand, limited by a confining evolutionary conservatism, yet at the same time they showed a remarkable degree of evolutionary plasticity and a capacity to colonise many different environments throughout their 350 million year time-span. Their organisation and the functional adaptations which enabled them to be so diverse and so successful for so long must begin with detailed studies of their morphology. This is the approach I have tried to follow here.

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List of Publications

(1) 1967 E.N.K. Clarkson. Environmental significance of eye-reduction in Trilobites and Recent Arthropods. *Marine Geology*, vol. 5, no. 5, 367- 375.

(2) 1967 E.N.K. Clarkson. Fine structure of the eye in two species of *Phacops* (Trilobita. *Palaeontology*, vol. 10, pt. 4, 603-616.

(3) 1968 E.N.K. Clarkson. Structure of the eye of *Crozonaspis struvei* (Trilobita, Dalmanitidea, Zeliszkellinae). *Senckenbergiana lethaea*, vol. 49, no. 6, 383-391.

(4) 1969 E.N.K. Clarkson. On the Schizochroal Eyes of Three Species of *Reedops* (Trilobita: Phacopidae) from the Lower Devonian of Bohemia. *Trans. R. Soc. Edinb.*, vol. 68, no. 8, 183-205.

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ENVIRONMENTAL SIGNIFICANCE OF EYE-REDUCTION IN TRILOBITES AND RECENT ARTHROPODS

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SUMMARY

Small phacopid and proetid trilobites lived as benthos in the trough of the Variscan geosyncline during Upper Devonian and Early Carboniferous times. The majority of these were blind or had very small, degenerate eyes, and this criterion, in addition to sedimentary evidence, has been suggested as indicative of deep-water (bathyal) conditions.

Some blind trilobites also occur in contemporaneous beds in association with normal eyed species; in view of this and other factors, the environmental significance of eye-degeneration and blindness is re-examined with reference to the origin and incidence of blindness in trilobites and in present-day marine arthropods.

Blindness in trilobites is always secondary and occurs not uncommonly; its high incidence may result from frequently occurring mutations providing viable species, capable of living in shallow water and feeding microphagously, but only becoming dominant in particular ecological conditions. The dominance of blind and small eyed trilobites of two distinct stocks in the Variscan geosyncline may reflect a dark or dim environment where predators were at a disadvantage, and selection pressure was minimal. The presence of some of those species in shallow water environments could result from contemporaneous migration from the trough. ERBEN's (1958) suggestions of the origin of blindness are considered to be tenable.

Many different present-day arthropods with reduced eyes live at depths below approximately 700 m where, in clear waters, the last traces of surface light fade. At the same depths, however, many arthropods with normal or highly adapted eyes abound, presumably sensitive to bioluminiscence.

Although this information is suggestive, it cannot directly be used to infer comparable depths in the Variscan geosyncline, as there is no means of assessing the transparency of water and relative light sensitivity of trilobite eyes. It may, however, help to give an order of magnitude of depth, i.e. hundreds, rather than tens or thousands of metres.

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INTRODUCTION

The existence of many genera of phacopid and proetid trilobites with reduced or absent eyes during Upper Devonian and Early Carboniferous times is well documented and has been discussed in detail by ERBEN (1958). Since Erben's paper various recent publications have shed extra light on the relationship of blind and reduced-eyed trilobites to their environment, and in some cases the possibility of depth control was considered. This article is intended as a review of present knowledge of the subject, mainly from a palaeobiological view-point.

RABIEN (1956) showed the existence of various facies within the Variscan geosyncline, exposed in a particular area of the eastern Rhineland. Along the northern edge of the geosynclinal trough thick beds of reef and bedded limestones accumulated together with clastics. The succession here is often discontinuous, which as Rabien suggested might result from large-scale oscillations of the shoreline during deposition. To the south, however, sedimentation was continuous and deposits were mainly argillaceous "ostracod-shales", with occasional lenses of cephalopod limestone, and thin turbidite bands.

GOLDRING (1962) noted a similar sedimentation pattern in Devon and Cornwall. He suggested that the various facies may have continued parallel with the margins of the geosyncline. It is generally accepted that the ostracod shales represent basinal deposits, and that the thin lenses of cephalopod limestone were condensed sequences deposited on submarine ridges. Several lines of evidence indicated to Rabien and Goldring that the ostracod-shale deposits were deep-water (bathyal) sequences laid down in the central trough of the geosyncline.

From the sedimentary point of view, the palaeogeographical setting of interrupted nearshore sedimentation of limestones and clastics contrasts very strongly with the undisturbed continuous deposition of predominantly argillaceous sediments with turbidite layers which occurred in the south. It has been inferred that to be unaffected by large-scale shoreline oscillations, the central part of the geosyncline must have been relatively deep, unless the oscillations were of strictly local effect. The sedimentary evidence alone, however, is not entirely unequivocal, for such sediments might be produced merely by rough conditions involving penecontemporaneous erosion near shore, and calm conditions in relatively shallow water further from shore.

The principal evidence for suggesting bathyal depths is palaeontological. There is very little benthos apart from trilobites and trace fossils. The trace fossils consist only of grazing traces, unlike the more variable shallow water assemblages described by many authors. Such grazing traces are typical of flysch deposits.

The trilobite fauna is very distinctive and individual specimens occur not infrequently. The fauna consists of diminutive phacopid and proetid trilobites, and in both these groups the remarkable phenomenon of eye-reduction occurs, affecting many of the representative species. Regarding this trilobite fauna GOLDRING (1962, p.78) has stated:

"Trilobites are not uncommon and form, apart from trace fossils, the only significant, definitely benthonic component. Of the thirteen species listed in the Famennian, eight lack eyes or have only a very few facets. Following RICHTER (1926) this blindness can only mean an evolutionary response to a dark environment. There is no evidence that these trilobites were active burrowers, no *Crossochorda* or *Cruziana* type traces having been found. The only alternative in an area of continous sedimentation is that they must have comprised vagile benthos in deep water. Not uncommonly phacopid trilobites are found showing the phacopid mode of moulting, with the cephalon overturned in front of the generally complete thorax and pygidium. Although this is not evidence for the depth of the water it does indicate its calmness."

OSMOLSKA (1958, 1962) described Famennian and Lower Carboniferous trilobites from southern Poland. She contrasted (p.81) areas of deep-water geosynclinal sedimentation where a meagre fauna consisting of blind and reduced-eyed phacopids lived, with sedimentary regions interpreted as submarine rises, carrying a rich fauna of normal eyed trilobites. The general situation is quite similar to that in western Europe.

Although in the three regions mentioned above the blind and reduced eyed trilobites seem to be more or less confined to the offshore basinal facies, contemporaneous faunas in Russia (MAKSIMOVA, 1955) contain both normal and reduced-eyed trilobites together in shallow water deposits. Maksimova believed that the blind and reduced-eyed trilobites were mud-burrowers. CHLUPÁC (1966) likewise recorded a similar contemporaneous mixed fauna in the "cephalopodmud" limestone facies of Moravia, and accepted Maksimova's conclusions as to the mode of life of the trilobites.

Thus whereas the fauna in the geosynclinal basin appears specialised, the same and related blind species also occur in shallow water in some peripheral regions though they may have been immigrants from the basin. These facts seem to cast some doubts upon the inference of bathyal depths in the basin and it is, therefore, necessary to re-examine the whole concept of eye-reduction in terms of environment.

The following questions are relevant. Do the small eyes of the phacopids and proetids associated with the entirely blind forms definitely indicate degeneration of sight? What is known of the origin and incidence of blindness in trilobites generally? What is known of the ecology and physiology of recent blind and reduced-eyed arthropods?

ERBEN (1958), with special reference to proetids, has considered the first two questions in detail. A commentary on Erben's work is given in the next section. The third question has not previously been discussed in detail and is considered separately.

ORIGIN AND INCIDENCE OF BLINDNESS AND EYE-REDUCTION

It is generally accepted that all blindness in trilobites is secondary; there are no primarily eyeless trilobites. Secondary blindness or eye-reduction occurs not infrequently, either in long-lived major taxa (e.g., agnostids and trinucleids) or sporadically in groups where eyes are normally present, and even within one known species (*Ormathops atavus*). HARRINGTON (1959) has pointed out that blindness and eye-degeneracy were commonest during Middle Cambrian, Ordovician and Upper Devonian times. In most cases, loss of the eye was usually complete; small-eyed genera are rare outside the Upper Devonian and early Carboniferous of Europe.

The small eyes of the phacopids, particularly, are peculiar and often only have 7–10 lenses, haphazardly and irregularly arranged; and often variable in number and size in the two eyes of one individual, and between individuals of the same species. This, together with the reduction of the palpebral lobe and outward migration of the facial suture (RICHTER 1926; CHLUPÁC 1966) are in all probability symptomatic of degeneracy.

Though the origin of blindness has often been considered the problem may only be approached theoretically. The most cogent analysis of the problem is that of Erben. His conclusions, though principally relating to proetids, are valid also for phacopids. According to Erben there are two theoretical explanations of the origin of eye degeneration. One suggestion implies direct adaptation to a dark environment, the other involves "mutative pre-adaptation" and thus independence of environment at least in the initial stages. He suggested that both factors had played a part, but that the first mutations affecting the early stages of eye-reduction were accidental and independent of environment. Later selection in an environment of low light intensity (provided by the offshore facies of this geosyncline, i.e., the ostracod shale facies) would enable those forms in which the first stages of eye-reduction had already taken place to survive.

Erben's arguments are not invalidated by the recent work on different Upper Devonian and Lower Carboniferous faunas, and may be supplemented by the following observations. As previously stated eye-reduction appeared sporadically in different trilobite stocks, including phacopids and proetids, at other times in geological history. Many of the reduced-eyed proetids belong to groups which seemed throughout their whole evolutionary history to be especially prone to eye-reduction. Thus, though most blind Cyrtosymbolinae are Famennian and lowermost Carboniferous, an evolutionary trend towards reduced eyes is also present in *Archegonus* which occur higher in the Carboniferous (HAHN, 1965). The genus is normally found in calcareous deposits, and probably lived in hsallow water. One species, *A. twistonensis*, inhabited reef-knolls. The high number of trilobites in which eye-reduction occurred, including shallow water forms, could indicate that degeneration of the eye was the result of recurrent mutant genes affecting different stocks, as is known to occur in some modern arthropods. In the intensively studied *Drosphila* frequently and recurrently mutating alleles for small eyes or eyelessness are well known; one mutant affecting the eye has the highest known rate of mutation in any known animal.

New species of trilobites with reduced eyes arising from such recurrent mutants obviously could live in shallow water, as is shown by their presence in the "mixed" faunas (whether these were chance migrants from other regions is uncertain). Since most trilobites did not possess biting mouth parts, as far as is known they were probably microphagous feeders rather than carnivores. Loss of the eye would not affect their feeding ability, but predation against them might well be greater.

As the blind and degenerate-eyed species (phacopids and proetids) are dominant in the ostracod-shale facies, clearly this offshore region must have provided a more suitable environment for them, and the presence of the two distinct stocks may indicate virtual environmental control, though some members were capable of migration elsewhere. If, in the ostracod-shale facies, deeper-water and darker conditions prevailed, as many authors indicate, predators would certainly have been at a disadvantage, and selection pressure against the blind and reduced eyed trilobites would be minimal.

These theoretical arguments should, however, be considered with reference to the ecology of modern arthropods.

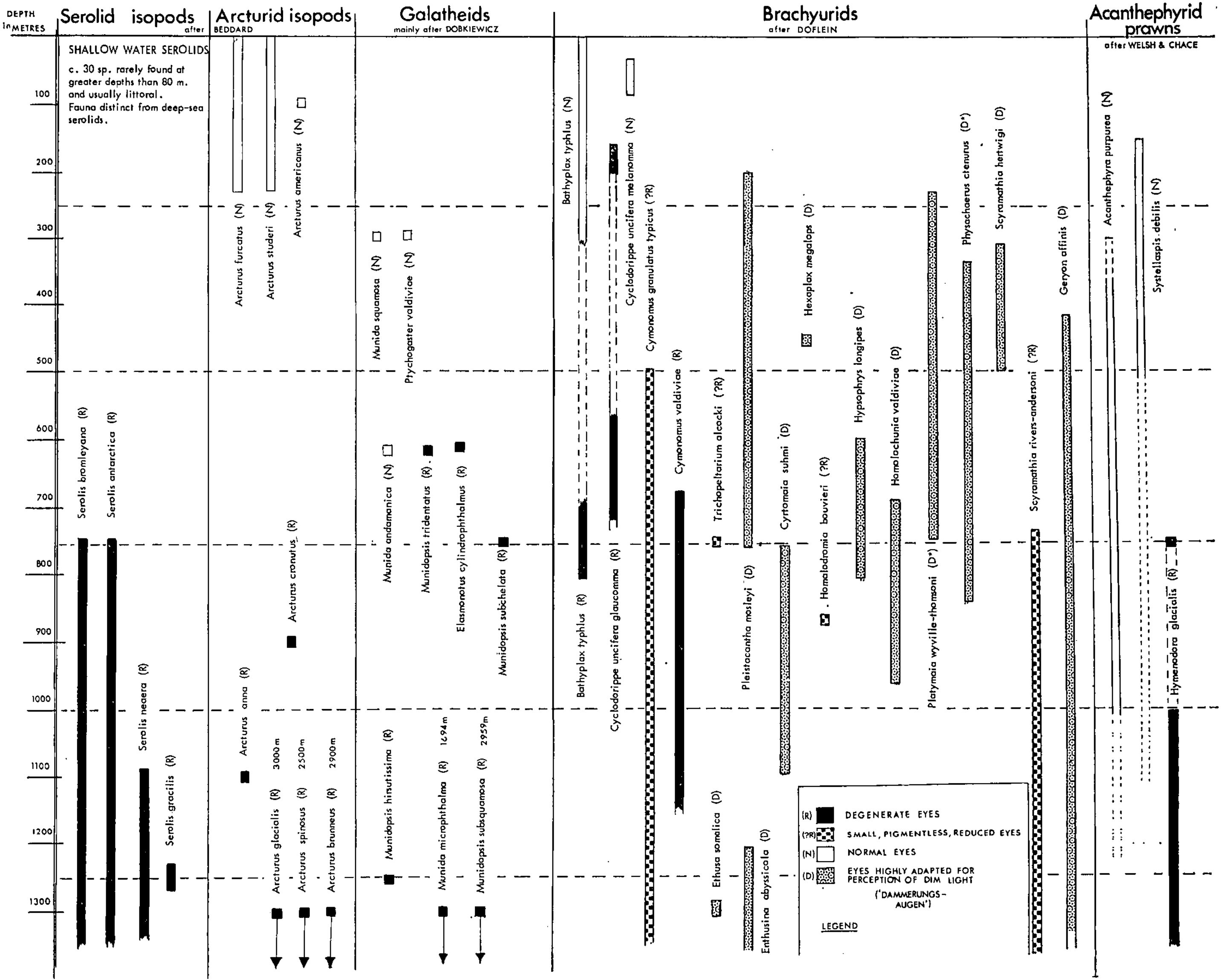
EYE DEGENERATION IN RECENT ARTHROPODS

Degenerate eyes are found in many present-day fish and arthropods living in dim or dark environments. In both cases instances have been described from cavernicolous, deep-burrowing and deep-water representatives. But as has been known for a long time it is notoriously difficult to correlate "sight" with depth. Blind and degenerate-eyed fish and arthropods may occur at the same depths as other species with normal or even enlarged and highly adapted eyes, furthermore some of the latter are restricted to depths well below those at which some blind forms occur. The reasons for this are not entirely clear, though the exact ecological niche of the animals, whether or not they have planktonic larvae, and complications due to bioluminescence of depth seem to be amongst the controling factors.

A survey of eye-degeneration and blindness in present-day deep-water arthropods has been made to show the depths at which degenerate-eyed crustaceans occur.

Shallow-water benthonic crustaceans with degenerate eyes are rare. Occasional individuals of normally deep-water species have been taken from relatively shallow sea floors in muddy water where the aphotic conditions approximate those of their more normal deep-sea environment. Thus a few specimens of *Cyclodorippe uncifera glaucomma*, a deep-sea degenerate-eyed crustacean, were collected from Sagami Bay, Japan, in depths less than 200 m (Fig.1). These waters are very muddy, and the sea floor is virtually aphotic (DOFLEIN, 1904). The blind *Polycheles* is normally deep-water but occasional individuals were taken at 200 m off Senegal. In this instance the larvae were probably transported by strong ascending currents near the African coast (MARSHALL, 1954, pp. 330–331).

Degenerate eyes are also known in the burrowing "ghost shrimps" *Gebia* and *Callianassa* (SCHEURING, 1923) which live in deep burrows in littoral and shallow waters down to 50 m (WEIMER and HOYT, 1964). These burrowers, however, are clearly


DEPTH in METRES
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
Serolid isopods
Arcturid isopods after BEDDARD
Galatheids mainly after DOBKIEWICZ
Brachyurids after DOFLEIN
Acanthephyrid prawns after WELSH & CHACE
SHALLOW WATER SEROLIDS
c. 30 sp. rarely found at greater depths than 80 m. and usually littoral. Fauna distinct from deep-sea serolids.
Serolis bromleyana (R)
Serolis antarctica (R)
Serolis neaera (R)
Serolis gracilis (R)
Arcturus furcatus (N)
Arcturus studeri (N)
Arcturus americanus (N)
Arcturus cronutus (R)
Arcturus anna (R)
Arcturus glacialis (R) 3000m
Arcturus spinosus (R) 2500m
Arcturus brunneus (R) 2900m
Munida squamosa (N)
Ptychogaster valdiviae (N)
Munida andamanica (N)
Munidopsis tridentatus (R)
Elasmonotus cylindrophthalmus (R)
Munidopsis subchelata (R)
Munidopsis hirsutissima (R)
Munida microphthalma (R) 1694m
Munidopsis subsquamosa (R) 2959m
Bathyplax typhlus (N)
Bathyplax typhlus (R)
Cyclodorippe uncifera melanomma (N)
Cyclodorippe uncifera glaucomma (R)
Cymonomus granulatus typicus (?R)
Cymonomus valdiviae (R)
Trichopeltarium alcocki (?R)
Ethusa somalica (D)
Pleistacantha mosleyi (D)
Ethusina abyssicola (D)
Cyrtomaia suhmi (D)
Hexaplax megalops (D)
Homalodromia bouvieri (?R)
Hypsophrys longipes (D)
Homolochunia valdiviae (D)
Platymaia wyville-thomsoni (D*)
Physachaerus ctenurus (D*)
Scyramathia hertwigi (D)
Scyramathia rivers-andersoni (?R)
Geryon affinis (D)
Acanthephyra purpurea (N)
Systellaspis debilis (N)
Hymenodora glacialis (R)
(R) DEGENERATE EYES
(?R) SMALL, PIGMENTLESS, REDUCED EYES
(N) NORMAL EYES
(D) EYES HIGHLY ADAPTED FOR PERCEPTION OF DIM LIGHT ('DAMMERUNGS-AUGEN')
LEGEND

special cases, as are degenerate-eyed cavernicolous crustaceans (PIKE, 1906) which need not concern us here.

Apart from the above occurrences, almost all the known cases of eye-degeneration occur in benthonic species normally living in depths of 600 m or more.

Fig.1 shows some examples of depths relationships of known degenerate-eyed crustaceans. These include benthonic isopods (BEDDARD, 1884, 1890) brachyurid crabs (DOFLEIN, 1904) and galatheid lobsters (DOBKIEWICZ, 1912) the main groups in which the eyes have been described in detail. Some diurnally migrant swimming prawns (WELSH and CHACE, 1937) are also tabulated here for comparison with the benthonic crustaceans.

Degenerate eyes are first encountered in the galatheids at 630 m though normal-eyed forms live at the same depths. Other degenerate-eyed galatheids, and also isopods and brachyurid crabs live at 700 m and deeper. Some of the crabs *Cyclodorippe uncifera*, *Bathyplax typhlus* and *Cymonomus granulatus* also occur in shallow or relatively shallow water, but individuals from shallow water have normal eyes, whereas in those taken from depths of 700 m the eyes are denegerate. In *C. granulatus* and also in some of the deep-water galatheids, the eyes have lost their visual function and are converted into tactile organs.

Fig.1 shows that degenerate-eyed arthropods appear at about 600 m, apart from the rare occurrences at lesser depths already referred to. They become a distinct element in the benthos below 700 m. This depth distribution presumably relates to depth of light penetration, a subject recently referred to by CLARKE and DENTON (1962). These authors record that in clear ocean waters the human eye can just perceive light from the surface at 700 m, where daylight is almost imperceptible but in the very clearest waters traces of faint light have been detected by bathyscaphe observers at an absolute maximum of 880 m. When surface light finally vanishes bioluminescent animals become common.

Clarke and Denton also refer to the experimental work of NICHOL (1959) who recorded that the normal-eyed crustaceans which he studied were just capable of response to light of 10^{-10} normal intensity, the equivalent intensity met with at depths of 700 m in clear water. This information is interesting in view of the depth distribution of crustaceans shown in Fig.1; eyes tend to be well developed at less than 700 m, and are often degenerate below this order of magnitude of depth.

Light will only penetrate to 700 m or below in clear transparent water. The amount of light reaching the sea floor may be greatly reduced by sediment suspended in the water, and also by high latitudes; i.e., solar radiation striking the surface at a low angle. In clear coastal water, suspended sediment may render daylight imperceptible on the sea floor at only 115 m. In view of this it is remarkable that the dark or dimly lighted environment provided by the continental shelves in shallow but cloudy water conditions should so rarely have been colonised by emigrants from the deep-water benthos. The distribution of degenerate-eyed crustaceans must be controlled by other factors besides light; pressure may be one of the most important.

This brief survey has shown that degenerate-eyed benthonic crustaceans are a distinct faunal element at depths below 700 m, but are not normally found as inhabitants of the continental shelves. Such information is useful, but limited in its application to the interpretation of past environments. For although palaeomagnetic evidence shows that the Variscan geosyncline was situated near the equator, and therefore light penetration would be good, there are other unknown factors which render direct comparisons difficult. Firstly the transparency of the water cannot easily be estimated, though since the central belt of the geosyncline was only 30 miles from the shore the water was liable to be less clear than in the deep oceans, even though sedimentation was slow. Secondly there is no way of assessing the relatively sensitivity of trilobite eyes as compared with modern arthropods. Thirdly, the exact ecological niches of the crustaceans referred to are not known with certainty, and those of the trilobites cannot always easily be inferred.

Since, however, recent arthropod faunas with degenerate eyes live commonly at depths of less than a thousand metres, there is no reason to suppose that the degenerate-eyed trilobite faunas of the Variscan geosyncline need have lived at greater depths.

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

by E. N. K. CLARKSON

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

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

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

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

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

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

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

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

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

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

Phacops fecundus Barrande

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

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

Specimen no. 20575 was well preserved though the palpebral lobes and some of the upper lenses of both eyes were damaged. There were 18 dorso-ventral files with a maximum of 6 lenses per file and the largest lenses were of diameter 0·5 mm. The original lens distribution in files from anterior to posterior was as follows:

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

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

1. *Structures seen in horizontal section*

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

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

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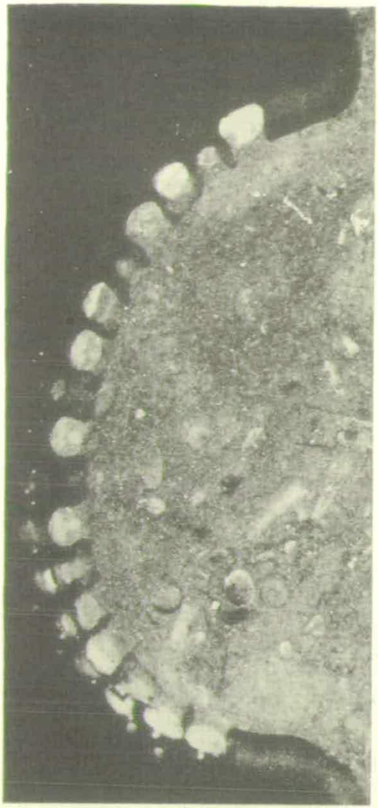
EXPLANATION OF PLATE 99

Figs. 1–3. *Phacops fecundus* Barrande. Silurian, Bohemia. Grant Institute no. 20575. 1, Left eye, sectioned horizontally as in text-fig. 1 *a*, *b*, showing a ‘cone’ below the cut lens in dorso-ventral file 14, ×10. 2, Right eye, sectioned vertically through file 14, as in text-fig. 1*h*, ×30. 3, Posterior region of left eye, showing the cone, as in text-fig. 1*c*, ×30.

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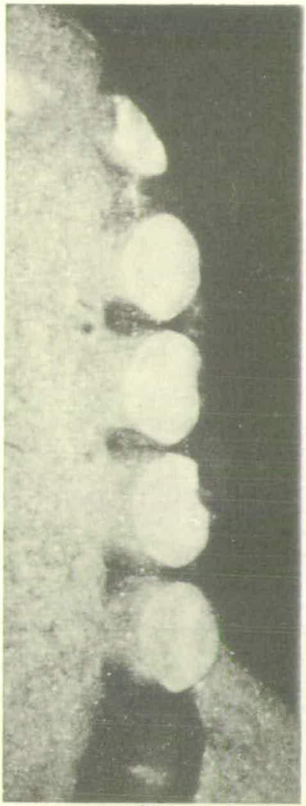
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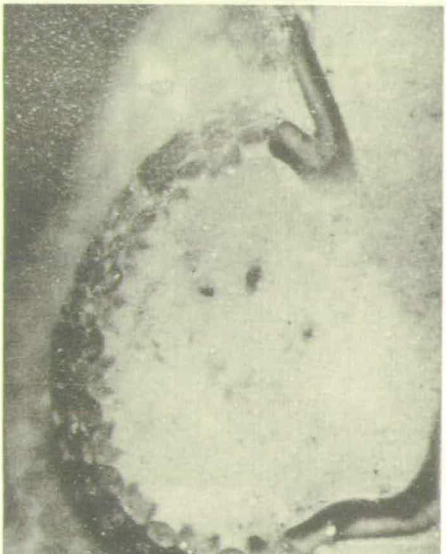
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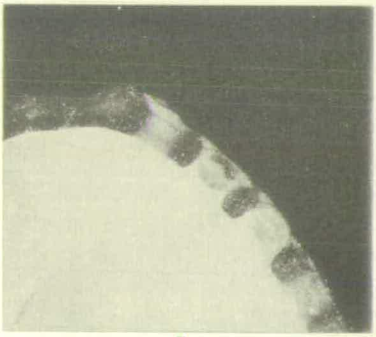
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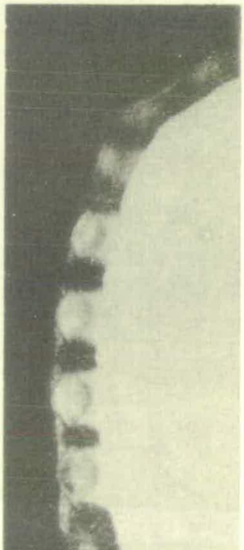
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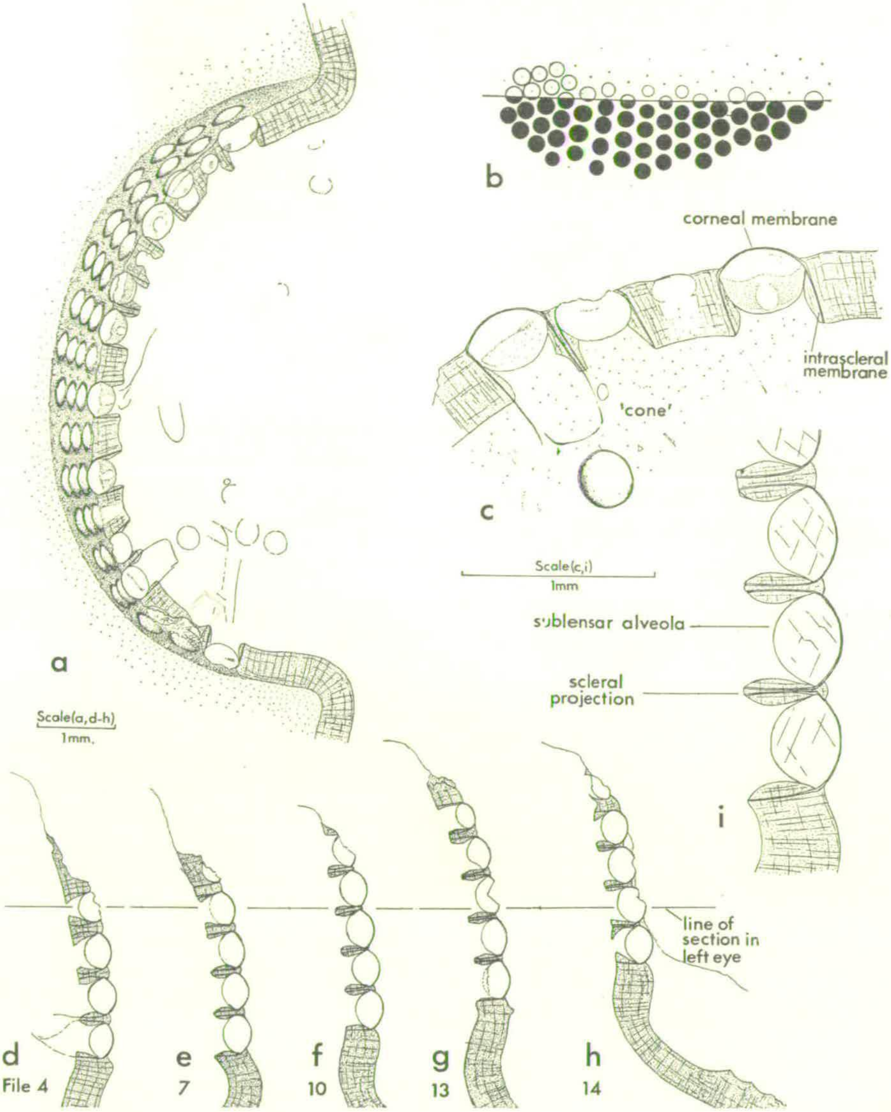
CLARKSON, Eye structure of *Phacops*



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

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

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

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

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

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

Nearly all modern arthropods have crystalline cones located below the lenses in a position analogous to that of *P. fecundus*. Acone eyes were described in *Lepisma* and other arthropods by Hesse (1901), but even in these primitive types there are nevertheless large transparent refractile Semper cells below the lenses though they are not actually modified into cones. Cones are even present in arthropods with disjunct spherical lenses, such as the copepod *Pontella*, described by Parker (1891) and some sort of cone-like refractile organ below the lens seems to be fundamental to the structure of the compound eye. Lindström believed that cones were originally present in trilobites, but had not been preserved because of their delicate nature. The opposite point of view should also be considered. In most recent arthropods the outer 'cornea' is very thin and is usually almost flat. In such cases, it can have served only as a transparent protective window, whose sole function was to let light through to the refractile cones below. It may have been possible that the corneal membrane of schizochroal trilobite eyes had a similar function and that the thick biconvex lenses would have dispensed with the need for cones. These lenses and the cones of recent arthropods might have had an identical function. The division of the lenses into an outer crescentic and an inner elliptical region (see p. 610) might indicate differences in refractive index within the lens, thus all necessary refraction may have been effected within the lens.

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

2. *Structures seen in vertical section*

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

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

Phacops latifrons (Bronn)

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

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

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

In no. 20607, which is quite typical of the species, the maximum lens diameter was 0·375 mm. There were 17 dorso-ventral files with a maximum of 5 lenses per file. The lens distribution was as follows:

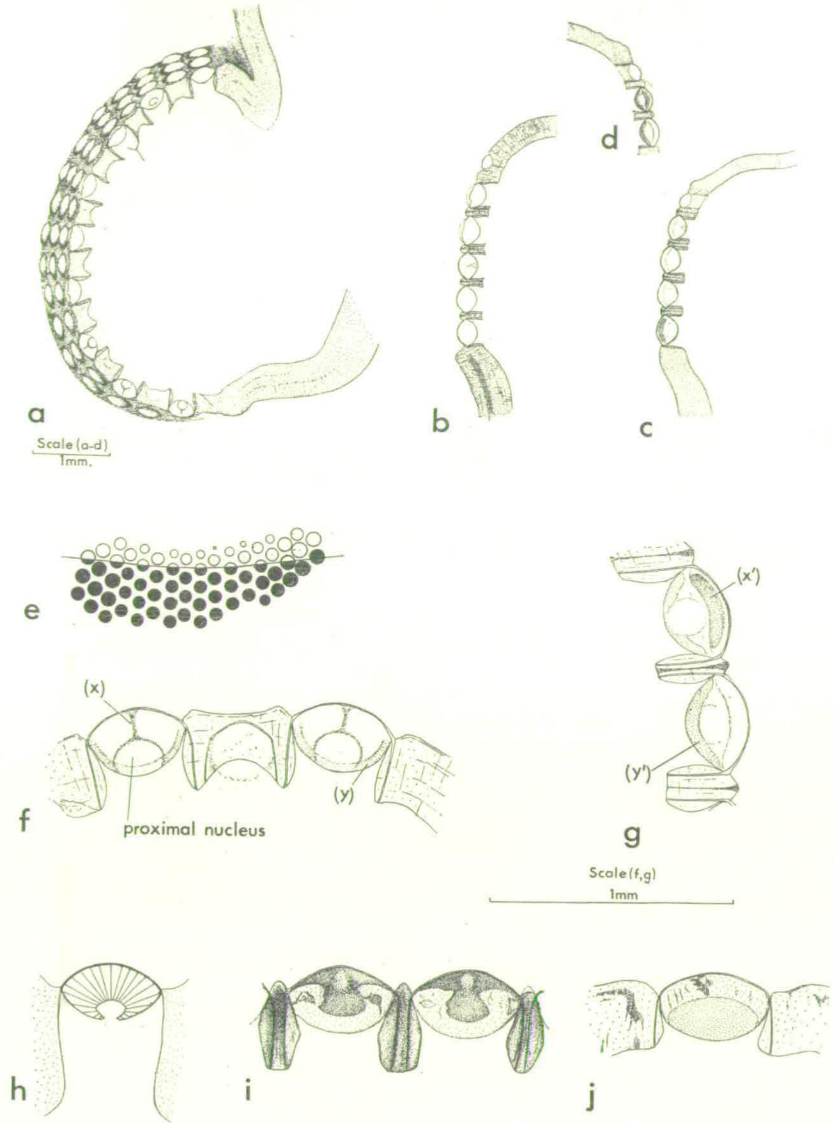
345 454 545 544 443 32: Total 68

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

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

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

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



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

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

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

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

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

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

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ENVIRONMENTAL SIGNIFICANCE OF EYE-REDUCTION IN TRILOBITES AND RECENT ARTHROPODS

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SUMMARY

Small phacopid and proetid trilobites lived as benthos in the trough of the Variscan geosyncline during Upper Devonian and Early Carboniferous times. The majority of these were blind or had very small, degenerate eyes, and this criterion, in addition to sedimentary evidence, has been suggested as indicative of deep-water (bathyal) conditions.

Some blind trilobites also occur in contemporaneous beds in association with normal eyed species; in view of this and other factors, the environmental significance of eye-degeneration and blindness is re-examined with reference to the origin and incidence of blindness in trilobites and in present-day marine arthropods.

Blindness in trilobites is always secondary and occurs not uncommonly; its high incidence may result from frequently occurring mutations providing viable species, capable of living in shallow water and feeding microphagously, but only becoming dominant in particular ecological conditions. The dominance of blind and small eyed trilobites of two distinct stocks in the Variscan geosyncline may reflect a dark or dim environment where predators were at a disadvantage, and selection pressure was minimal. The presence of some of those species in shallow water environments could result from contemporaneous migration from the trough. ERBEN's (1958) suggestions of the origin of blindness are considered to be tenable.

Many different present-day arthropods with reduced eyes live at depths below approximately 700 m where, in clear waters, the last traces of surface light fade. At the same depths, however, many arthropods with normal or highly adapted eyes abound, presumably sensitive to bioluminiscence.

Although this information is suggestive, it cannot directly be used to infer comparable depths in the Variscan geosyncline, as there is no means of assessing the transparency of water and relative light sensitivity of trilobite eyes. It may, however, help to give an order of magnitude of depth, i.e. hundreds, rather than tens or thousands of metres.

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INTRODUCTION

The existence of many genera of phacopid and proetid trilobites with reduced or absent eyes during Upper Devonian and Early Carboniferous times is well documented and has been discussed in detail by ERBEN (1958). Since Erben's paper various recent publications have shed extra light on the relationship of blind and reduced-eyed trilobites to their environment, and in some cases the possibility of depth control was considered. This article is intended as a review of present knowledge of the subject, mainly from a palaeobiological view-point.

RABIEN (1956) showed the existence of various facies within the Variscan geosyncline, exposed in a particular area of the eastern Rhineland. Along the northern edge of the geosynclinal trough thick beds of reef and bedded limestones accumulated together with clastics. The succession here is often discontinuous, which as Rabien suggested might result from large-scale oscillations of the shoreline during deposition. To the south, however, sedimentation was continuous and deposits were mainly argillaceous "ostracod-shales", with occasional lenses of cephalopod limestone, and thin turbidite bands.

GOLDRING (1962) noted a similar sedimentation pattern in Devon and Cornwall. He suggested that the various facies may have continued parallel with the margins of the geosyncline. It is generally accepted that the ostracod shales represent basinal deposits, and that the thin lenses of cephalopod limestone were condensed sequences deposited on submarine ridges. Several lines of evidence indicated to Rabien and Goldring that the ostracod-shale deposits were deep-water (bathyal) sequences laid down in the central trough of the geosyncline.

From the sedimentary point of view, the palaeogeographical setting of interrupted nearshore sedimentation of limestones and clastics contrasts very strongly with the undisturbed continuous deposition of predominantly argillaceous sediments with turbidite layers which occurred in the south. It has been inferred that to be unaffected by large-scale shoreline oscillations, the central part of the geosyncline must have been relatively deep, unless the oscillations were of strictly local effect. The sedimentary evidence alone, however, is not entirely unequivocal, for such sediments might be produced merely by rough conditions involving penecontemporaneous erosion near shore, and calm conditions in relatively shallow water further from shore.

The principal evidence for suggesting bathyal depths is palaeontological. There is very little benthos apart from trilobites and trace fossils. The trace fossils consist only of grazing traces, unlike the more variable shallow water assemblages described by many authors. Such grazing traces are typical of flysch deposits.

The trilobite fauna is very distinctive and individual specimens occur not infrequently. The fauna consists of diminutive phacopid and proetid trilobites, and in both these groups the remarkable phenomenon of eye-reduction occurs, affecting many of the representative species. Regarding this trilobite fauna GOLDRING (1962, p.78) has stated:

"Trilobites are not uncommon and form, apart from trace fossils, the only significant, definitely benthonic component. Of the thirteen species listed in the Famennian, eight lack eyes or have only a very few facets. Following RICHTER (1926) this blindness can only mean an evolutionary response to a dark environment. There is no evidence that these trilobites were active burrowers, no *Crossochorda* or *Cruziana* type traces having been found. The only alternative in an area of continous sedimentation is that they must have comprised vagile benthos in deep water. Not uncommonly phacopid trilobites are found showing the phacopid mode of moulting, with the cephalon overturned in front of the generally complete thorax and pygidium. Although this is not evidence for the depth of the water it does indicate its calmness."

OSMOLSKA (1958, 1962) described Famennian and Lower Carboniferous trilobites from southern Poland. She contrasted (p.81) areas of deep-water geosynclinal sedimentation where a meagre fauna consisting of blind and reduced-eyed phacopids lived, with sedimentary regions interpreted as submarine rises, carrying a rich fauna of normal eyed trilobites. The general situation is quite similar to that in western Europe.

Although in the three regions mentioned above the blind and reduced eyed trilobites seem to be more or less confined to the offshore basinal facies, contemporaneous faunas in Russia (MAKSIMOVA, 1955) contain both normal and reduced-eyed trilobites together in shallow water deposits. Maksimova believed that the blind and reduced-eyed trilobites were mud-burrowers. CHLUPÁC (1966) likewise recorded a similar contemporaneous mixed fauna in the "cephalopodmud" limestone facies of Moravia, and accepted Maksimova's conclusions as to the mode of life of the trilobites.

Thus whereas the fauna in the geosynclinal basin appears specialised, the same and related blind species also occur in shallow water in some peripheral regions though they may have been immigrants from the basin. These facts seem to cast some doubts upon the inference of bathyal depths in the basin and it is, therefore, necessary to re-examine the whole concept of eye-reduction in terms of environment.

The following questions are relevant. Do the small eyes of the phacopids and proetids associated with the entirely blind forms definitely indicate degeneration of sight? What is known of the origin and incidence of blindness in trilobites generally? What is known of the ecology and physiology of recent blind and reduced-eyed arthropods?

ERBEN (1958), with special reference to proetids, has considered the first two questions in detail. A commentary on Erben's work is given in the next section. The third question has not previously been discussed in detail and is considered separately.

ORIGIN AND INCIDENCE OF BLINDNESS AND EYE-REDUCTION

It is generally accepted that all blindness in trilobites is secondary; there are no primarily eyeless trilobites. Secondary blindness or eye-reduction occurs not infrequently, either in long-lived major taxa (e.g., agnostids and trinucleids) or sporadically in groups where eyes are normally present, and even within one known species (*Ormathops atavus*). HARRINGTON (1959) has pointed out that blindness and eye-degeneracy were commonest during Middle Cambrian, Ordovician and Upper Devonian times. In most cases, loss of the eye was usually complete; small-eyed genera are rare outside the Upper Devonian and early Carboniferous of Europe.

The small eyes of the phacopids, particularly, are peculiar and often only have 7–10 lenses, haphazardly and irregularly arranged; and often variable in number and size in the two eyes of one individual, and between individuals of the same species. This, together with the reduction of the palpebral lobe and outward migration of the facial suture (RICHTER 1926; CHLUPÁC 1966) are in all probability symptomatic of degeneracy.

Though the origin of blindness has often been considered the problem may only be approached theoretically. The most cogent analysis of the problem is that of Erben. His conclusions, though principally relating to proetids, are valid also for phacopids. According to Erben there are two theoretical explanations of the origin of eye degeneration. One suggestion implies direct adaptation to a dark environment, the other involves "mutative pre-adaptation" and thus independence of environment at least in the initial stages. He suggested that both factors had played a part, but that the first mutations affecting the early stages of eye-reduction were accidental and independent of environment. Later selection in an environment of low light intensity (provided by the offshore facies of this geosyncline, i.e., the ostracod shale facies) would enable those forms in which the first stages of eye-reduction had already taken place to survive.

Erben's arguments are not invalidated by the recent work on different Upper Devonian and Lower Carboniferous faunas, and may be supplemented by the following observations. As previously stated eye-reduction appeared sporadically in different trilobite stocks, including phacopids and proetids, at other times in geological history. Many of the reduced-eyed proetids belong to groups which seemed throughout their whole evolutionary history to be especially prone to eye-reduction. Thus, though most blind Cyrtosymbolinae are Famennian and lowermost Carboniferous, an evolutionary trend towards reduced eyes is also present in *Archegonus* which occur higher in the Carboniferous (HAHN, 1965). The genus is normally found in calcareous deposits, and probably lived in hsallow water. One species, *A. twistonensis*, inhabited reef-knolls. The high number of trilobites in which eye-reduction occurred, including shallow water forms, could indicate that degeneration of the eye was the result of recurrent mutant genes affecting different stocks, as is known to occur in some modern arthropods. In the intensively studied *Drosphila* frequently and recurrently mutating alleles for small eyes or eyelessness are well known; one mutant affecting the eye has the highest known rate of mutation in any known animal.

New species of trilobites with reduced eyes arising from such recurrent mutants obviously could live in shallow water, as is shown by their presence in the "mixed" faunas (whether these were chance migrants from other regions is uncertain). Since most trilobites did not possess biting mouth parts, as far as is known they were probably microphagous feeders rather than carnivores. Loss of the eye would not affect their feeding ability, but predation against them might well be greater.

As the blind and degenerate-eyed species (phacopids and proetids) are dominant in the ostracod-shale facies, clearly this offshore region must have provided a more suitable environment for them, and the presence of the two distinct stocks may indicate virtual environmental control, though some members were capable of migration elsewhere. If, in the ostracod-shale facies, deeper-water and darker conditions prevailed, as many authors indicate, predators would certainly have been at a disadvantage, and selection pressure against the blind and reduced eyed trilobites would be minimal.

These theoretical arguments should, however, be considered with reference to the ecology of modern arthropods.

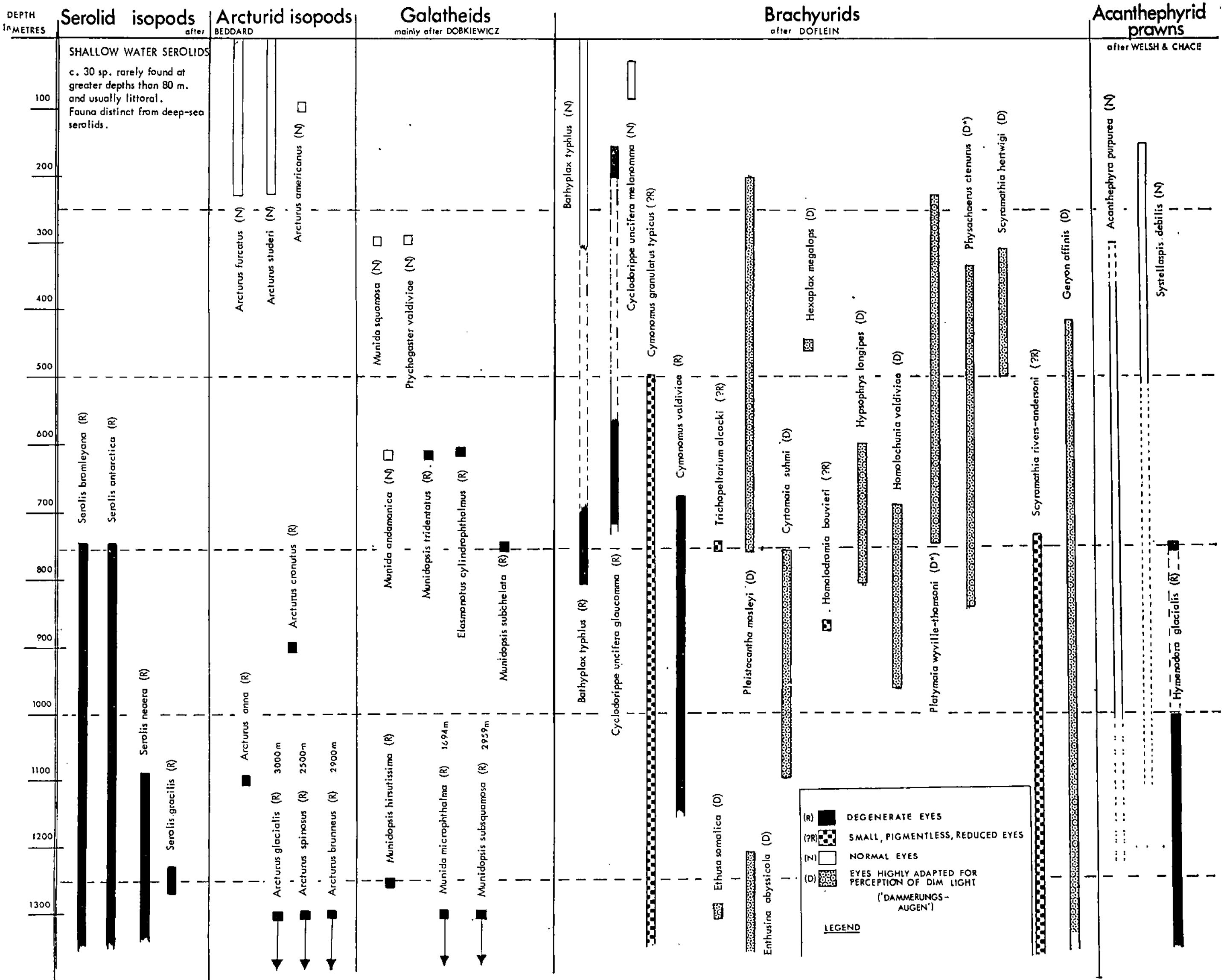
EYE DEGENERATION IN RECENT ARTHROPODS

Degenerate eyes are found in many present-day fish and arthropods living in dim or dark environments. In both cases instances have been described from cavernicolous, deep-burrowing and deep-water representatives. But as has been known for a long time it is notoriously difficult to correlate "sight" with depth. Blind and degenerate-eyed fish and arthropods may occur at the same depths as other species with normal or even enlarged and highly adapted eyes, furthermore some of the latter are restricted to depths well below those at which some blind forms occur. The reasons for this are not entirely clear, though the exact ecological niche of the animals, whether or not they have planktonic larvae, and complications due to bioluminescence of depth seem to be amongst the controling factors.

A survey of eye-degeneration and blindness in present-day deep-water arthropods has been made to show the depths at which degenerate-eyed crustaceans occur.

Shallow-water benthonic crustaceans with degenerate eyes are rare. Occasional individuals of normally deep-water species have been taken from relatively shallow sea floors in muddy water where the aphotic conditions approximate those of their more normal deep-sea environment. Thus a few specimens of *Cyclodorippe uncifera glaucomma*, a deep-sea degenerate-eyed crustacean, were collected from Sagami Bay, Japan, in depths less than 200 m (Fig.1). These waters are very muddy, and the sea floor is virtually aphotic (DOFLEIN, 1904). The blind *Polycheles* is normally deep-water but occasional individuals were taken at 200 m off Senegal. In this instance the larvae were probably transported by strong ascending currents near the African coast (MARSHALL, 1954, pp. 330–331).

Degenerate eyes are also known in the burrowing "ghost shrimps" *Gebia* and *Callianassa* (SCHEURING, 1923) which live in deep burrows in littoral and shallow waters down to 50 m (WEIMER and HOYT, 1964). These burrowers, however, are clearly


DEPTH in METRES
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
Serolid isopods
SHALLOW WATER SEROLIDS
c. 30 sp. rarely found at greater depths than 80 m. and usually littoral. Fauna distinct from deep-sea serolids.
Serolis bromleyana (R)
Serolis antarctica (R)
Serolis neaera (R)
Serolis gracilis (R)
Arcturid isopods after BEDDARD
Arcturus furcatus (N)
Arcturus studeri (N)
Arcturus americanus (N)
Arcturus cronutus (R)
Arcturus anna (R)
Arcturus glacialis (R) 3000 m
Arcturus spinosus (R) 2500 m
Arcturus brunneus (R) 2900 m
Galatheids mainly after DOBKIEWICZ
Munida squamosa (N)
Ptychogaster valdiviae (N)
Munida andamanica (N)
Munidopsis tridentatus (R)
Elasmonotus cylindrophthalmus (R)
Munidopsis subchelata (R)
Munidopsis hirsutissima (R)
Munida microphthalma (R) 1694 m
Munidopsis subsquamosa (R) 2959 m
Brachyurids after DOFLEIN
Bathyplax typhlus (N)
Bathyplax typhlus (R)
Cyclodorippe uncifera melanomma (N)
Cyclodorippe uncifera glaucomma (R)
Cymonomus granulatus typicus (?R)
Cymonomus valdiviae (R)
Trichopeltarium alcocki (?R)
Ethusa somalica (D)
Pleistacantha mosleyi (D)
Enthusina abyssicola (D)
Cyrtomaia suhmi (D)
Hexaplax megalops (D)
Homalodromia bouvieri (?R)
Hypsophrys longipes (D)
Homalochunia valdiviae (D)
Platymaia wyville-thomsoni (D*)
Physachaerus ctenurus (D*)
Scyramathia hertwigi (D)
Scyramathia rivers-andersoni (?R)
Geryon affinis (D)
Acanthephyrid prawns after WELSH & CHACE
Acanthephyra purpurea (N)
Systellaspis debilis (N)
Hymenodora glacialis (R)
(R) DEGENERATE EYES
(?R) SMALL, PIGMENTLESS, REDUCED EYES
(N) NORMAL EYES
(D) EYES HIGHLY ADAPTED FOR PERCEPTION OF DIM LIGHT ('DAMMERUNGS-AUGEN')
LEGEND

special cases, as are degenerate-eyed cavernicolous crustaceans (PIKE, 1906) which need not concern us here.

Apart from the above occurrences, almost all the known cases of eye-degeneration occur in benthonic species normally living in depths of 600 m or more.

Fig.1 shows some examples of depths relationships of known degenerate-eyed crustaceans. These include benthonic isopods (BEDDARD, 1884, 1890) brachyurid crabs (DOFLEIN, 1904) and galatheid lobsters (DOBKIEWICZ, 1912) the main groups in which the eyes have been described in detail. Some diurnally migrant swimming prawns (WELSH and CHACE, 1937) are also tabulated here for comparison with the benthonic crustaceans.

Degenerate eyes are first encountered in the galatheids at 630 m though normal-eyed forms live at the same depths. Other degenerate-eyed galatheids, and also isopods and brachyurid crabs live at 700 m and deeper. Some of the crabs *Cyclodorippe uncifera*, *Bathyplax typhlus* and *Cymonomus granulatus* also occur in shallow or relatively shallow water, but individuals from shallow water have normal eyes, whereas in those taken from depths of 700 m the eyes are denegerate. In *C. granulatus* and also in some of the deep-water galatheids, the eyes have lost their visual function and are converted into tactile organs.

Fig.1 shows that degenerate-eyed arthropods appear at about 600 m, apart from the rare occurrences at lesser depths already referred to. They become a distinct element in the benthos below 700 m. This depth distribution presumably relates to depth of light penetration, a subject recently referred to by CLARKE and DENTON (1962). These authors record that in clear ocean waters the human eye can just perceive light from the surface at 700 m, where daylight is almost imperceptible but in the very clearest waters traces of faint light have been detected by bathyscaphe observers at an absolute maximum of 880 m. When surface light finally vanishes bioluminescent animals become common.

Clarke and Denton also refer to the experimental work of NICHOL (1959) who recorded that the normal-eyed crustaceans which he studied were just capable of response to light of 10^{-10} normal intensity, the equivalent intensity met with at depths of 700 m in clear water. This information is interesting in view of the depth distribution of crustaceans shown in Fig.1; eyes tend to be well developed at less than 700 m, and are often degenerate below this order of magnitude of depth.

Light will only penetrate to 700 m or below in clear transparent water. The amount of light reaching the sea floor may be greatly reduced by sediment suspended in the water, and also by high latitudes; i.e., solar radiation striking the surface at a low angle. In clear coastal water, suspended sediment may render daylight imperceptible on the sea floor at only 115 m. In view of this it is remarkable that the dark or dimly lighted environment provided by the continental shelves in shallow but cloudy water conditions should so rarely have been colonised by emigrants from the deep-water benthos. The distribution of degenerate-eyed crustaceans must be controlled by other factors besides light; pressure may be one of the most important.

This brief survey has shown that degenerate-eyed benthonic crustaceans are a distinct faunal element at depths below 700 m, but are not normally found as inhabitants of the continental shelves. Such information is useful, but limited in its application to the interpretation of past environments. For although palaeomagnetic evidence shows that the Variscan geosyncline was situated near the equator, and therefore light penetration would be good, there are other unknown factors which render direct comparisons difficult. Firstly the transparency of the water cannot easily be estimated, though since the central belt of the geosyncline was only 30 miles from the shore the water was liable to be less clear than in the deep oceans, even though sedimentation was slow. Secondly there is no way of assessing the relatively sensitivity of trilobite eyes as compared with modern arthropods. Thirdly, the exact ecological niches of the crustaceans referred to are not known with certainty, and those of the trilobites cannot always easily be inferred.

Since, however, recent arthropod faunas with degenerate eyes live commonly at depths of less than a thousand metres, there is no reason to suppose that the degenerate-eyed trilobite faunas of the Variscan geosyncline need have lived at greater depths.

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2

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

by E. N. K. CLARKSON

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

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

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

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

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

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

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

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

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

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

Phacops fecundus Barrande

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

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

Specimen no. 20575 was well preserved though the palpebral lobes and some of the upper lenses of both eyes were damaged. There were 18 dorso-ventral files with a maximum of 6 lenses per file and the largest lenses were of diameter 0·5 mm. The original lens distribution in files from anterior to posterior was as follows:

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

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

1. *Structures seen in horizontal section*

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

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

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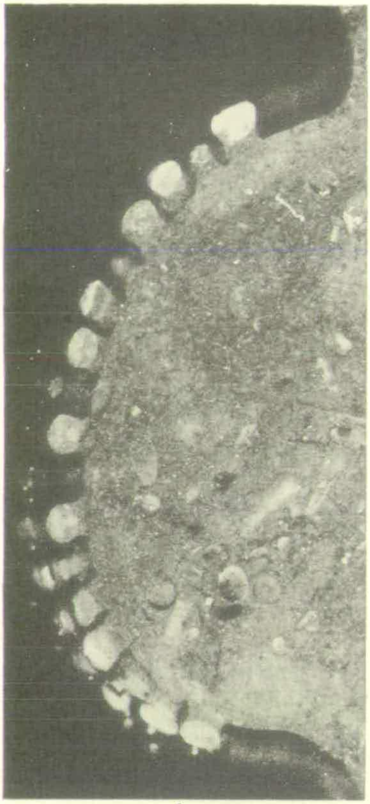
EXPLANATION OF PLATE 99

Figs. 1–3. *Phacops fecundus* Barrande. Silurian, Bohemia. Grant Institute no. 20575. 1, Left eye, sectioned horizontally as in text-fig. 1 *a*, *b*, showing a 'cone' below the cut lens in dorso-ventral file 14, ×10. 2, Right eye, sectioned vertically through file 14, as in text-fig. 1*h*, ×30. 3, Posterior region of left eye, showing the cone, as in text-fig. 1*c*, ×30.

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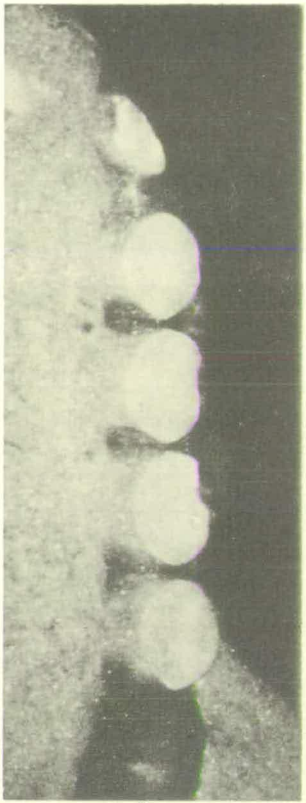
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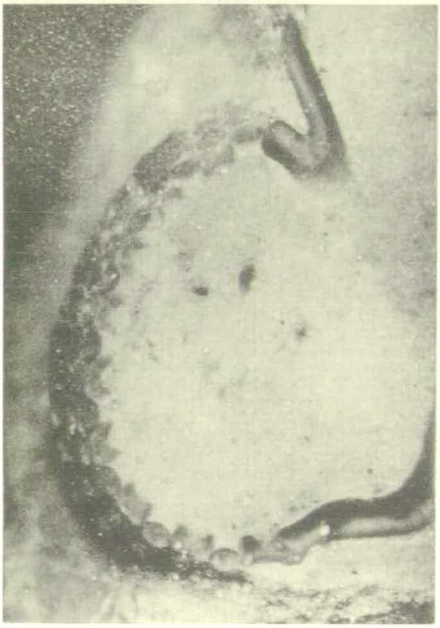
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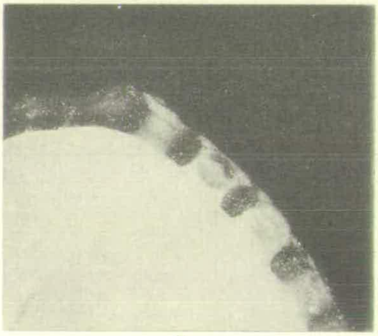
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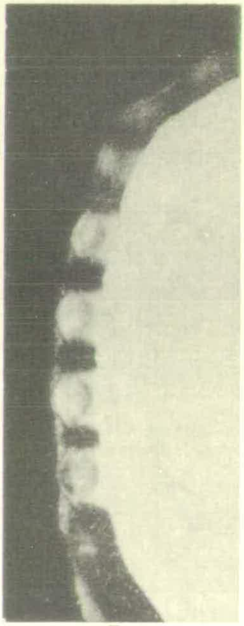
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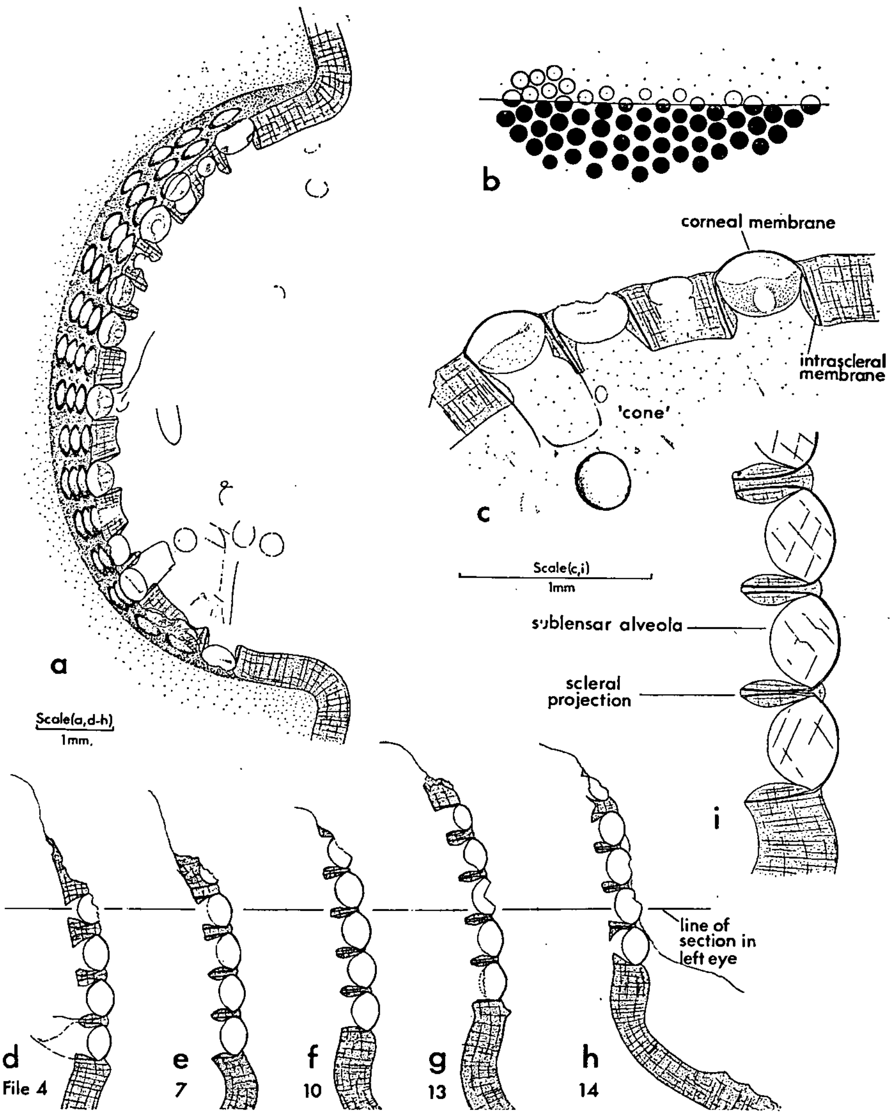
CLARKSON, Eye structure of *Phacops*



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

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

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

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

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

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

Nearly all modern arthropods have crystalline cones located below the lenses in a position analogous to that of *P. fecundus*. Acone eyes were described in *Lepisma* and other arthropods by Hesse (1901), but even in these primitive types there are nevertheless large transparent refractile Semper cells below the lenses though they are not actually modified into cones. Cones are even present in arthropods with disjunct spherical lenses, such as the copepod *Pontella*, described by Parker (1891) and some sort of cone-like refractile organ below the lens seems to be fundamental to the structure of the compound eye. Lindström believed that cones were originally present in trilobites, but had not been preserved because of their delicate nature. The opposite point of view should also be considered. In most recent arthropods the outer 'cornea' is very thin and is usually almost flat. In such cases, it can have served only as a transparent protective window, whose sole function was to let light through to the refractile cones below. It may have been possible that the corneal membrane of schizochroal trilobite eyes had a similar function and that the thick biconvex lenses would have dispensed with the need for cones. These lenses and the cones of recent arthropods might have had an identical function. The division of the lenses into an outer crescentic and an inner elliptical region (see p. 610) might indicate differences in refractive index within the lens, thus all necessary refraction may have been effected within the lens.

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

2. *Structures seen in vertical section*

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

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

Phacops latifrons (Bronn)

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

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

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

In no. 20607, which is quite typical of the species, the maximum lens diameter was 0·375 mm. There were 17 dorso-ventral files with a maximum of 5 lenses per file. The lens distribution was as follows:

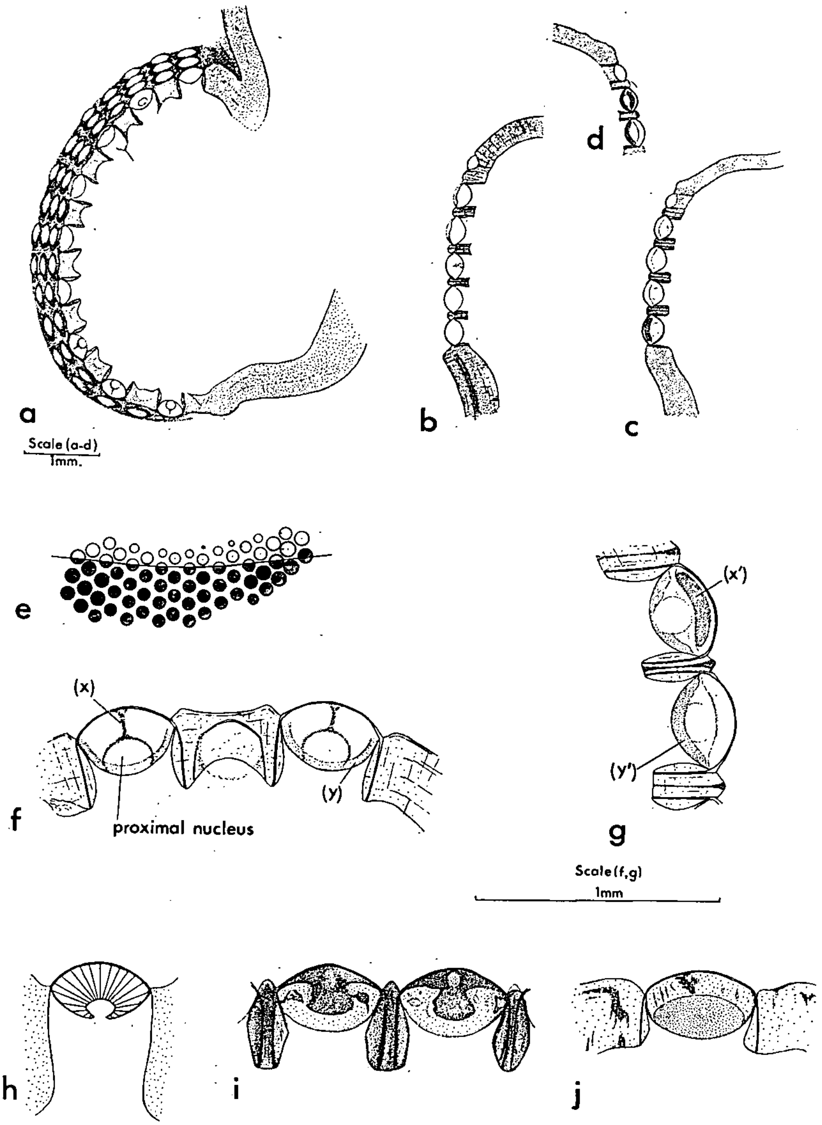
345 454 545 544 443 32: Total 68

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

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

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

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



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

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

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

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

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

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

PHYSIOLOGICAL CONSIDERATIONS

1. *Sublensar ommatidial arrangement*

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

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

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

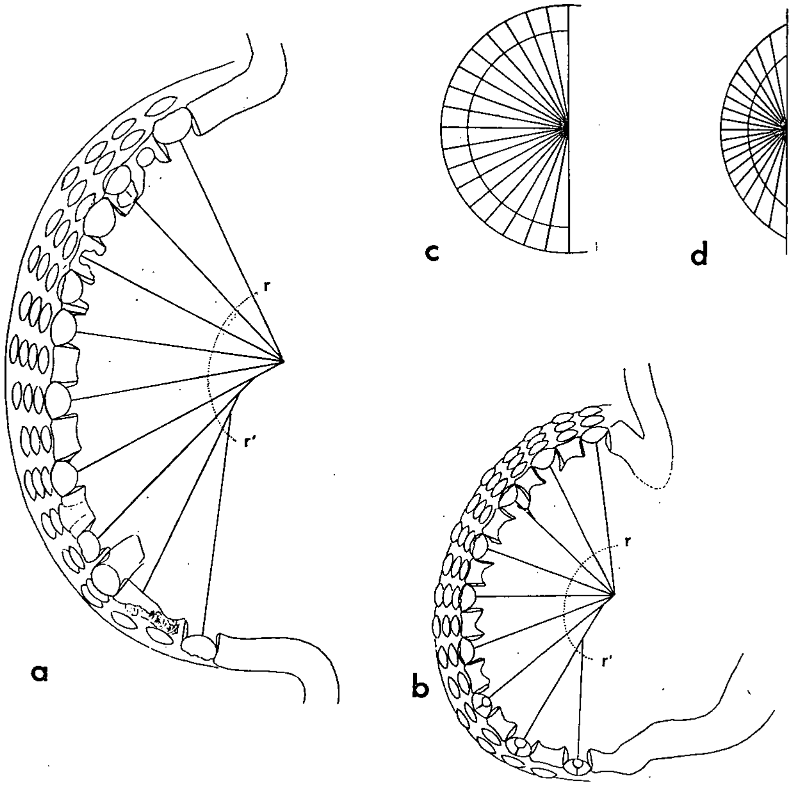
'Superposition eyes' are typical of nocturnal and crepuscular arthropods. The rhabdom of a superposition ommatidium is short and swollen, extending only a third of the total distance from the basement membrane to the cone, and connected to the latter by a thin cone-stalk. In daylight screening pigment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

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

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

All the ommatidial axes converge to a point or region whose distance is less than that from the surface to the centre of curvature of the eye. Thus the peripheral ommatidia are not normal to the visual surface.

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



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

The first model (text-fig. 3*c*) shows an eye with a perfectly hemispherical surface, having ommatidia whose axes all converge to a point at the same locus as the centre of curvature of the visual surface. Eyes of this type are not uncommon in arthropods and are usually associated with superposition-type ommatidia. The second model (text-fig. 3*d*) is more similar to those of *P. fecundus* and *P. latifrons* but is regularly curved. The point of axial convergence is only half the distance from the surface to the centre of curvature. Eyes of such a type usually have apposition-type ommatidia. An eye of the latter type can accommodate as many ommatidia with the same axial separations, and subtending as great a visual range as can one of the former variety, unless the ommatidia are very long. If they are long they can only be housed internally by reducing the length of the central ommatidia relative to the peripheral ones.

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

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

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

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

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

As far as the author is aware, nothing quite like this pattern exists in the laterally directed eyes of recent arthropods. The nearest approximation is found in certain deep-water euphausiids. In these (Chun 1896, Kampa 1965) each eye is divided into two isolated lobes, the upper of which is directly forwards and upwards, whereas the lower has a downward and backward orientation. The ommatidia of the lower lobe are radially arranged, but in the upper lobe they are all parallel. In contrast with phacopids, this parallel arrangement is constant in both sagittal and transverse planes, so that the lobe consists, in effect, of numerous ommatidia all pointing in the same direction. But as in phacopids, these parallel units with their large cones lie below a curving visual surface and individually are capped by strongly convex corneal 'facets'. In view of these structural similarities, a certain degree of physiological interpretation of the phacopid eye might be made with reference to that of the euphausiids, but little is known of the essential physiological attributes of the eyes of the latter, such as their angular light-receptivity, which would be of value in this case.

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

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

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

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

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

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

2. *Transmission of light to the deep-lying photoreceptors*

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

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

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

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

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

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

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

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Structure of the eye of *Crozonaspis struvei* (Trilobita, Dalmanitidae, Zeliszkellinae).

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With 1 plate and 2 text-figures.

Summary.

The fine structure of the eye of *Crozonaspis struvei* J.-L. HENRY 1968 is described from steinkerns and external moulds and compared with that of *Dalmanitina (Dalmanitina) socialis* (BARRANDE 1846). The nature of some hitherto little-known intralensar structures is considered, and reasons are given for suggesting that the eye of *Crozonaspis* is of a rather advanced kind, in certain respects more similar to those of Silurian and Devonian Phacopacea than to the eye of *D. (Dalmanitina) socialis* and other Zeliszkellinae.

Übersicht.

Die Feinstruktur des Auges von *Crozonaspis struvei* J.-L. HENRY 1968 wird auf Grund von Steinkernen und Abdrücken beschrieben und mit derjenigen von *Dalmanitina (Dalmanitina) socialis* (BARRANDE 1846) verglichen. Die Beschaffenheit von einigen bisher wenig bekannten Strukturen des Linsen-Inneren wird untersucht; es werden Gründe für die Vermutung angeführt, daß das Auge von *Crozonaspis* verhältnismäßig fortentwickelt und in gewisser Hinsicht den Augen der silurischen und devonischen Phacopacea ähnlicher ist als denen von *D. (Dalmanitina) socialis* und anderen Zeliszkellinae.

Introduction.

During the preparation of his manuscript on the Ordovician (Llandeilian) trilobite *Crozonaspis struvei*, Dr. J.-L. HENRY of the Institut de Géologie, Université de Rennes, kindly suggested to me that I might be interested to make a detailed study of the eye of this trilobite. Since the Zeliszkellinae are amongst the earliest Phacopina, and the fine structure of the eyes of any members of this group of trilobites is very little known, I gratefully accepted Dr. HENRY's generous offer, and was sent several free cheeks and incomplete cephalons with complete or nearly complete visual surfaces, from the Schistes de Morgat, at the type locality at Postolonnec, presqu'île de Crozon, Finistère. The eyes are finely preserved as external and internal moulds (steinkerns), and in some of the latter there are curious intralensar structures of particular interest, not previously described in any trilobites preserved in this way, but probably homologous with bowl-shaped intralensar structures found by LINDSTRÖM (1901) in a calcified Devonian phacopacean trilobite and figured by him in thin section.

In the following text the nature of these intralensar structures is considered in some detail. Comparison of the eye of *Crozonaspis struvei* with the advanced eyes of Silurian and Devonian Phacopacea (believed to be descended from Zeliszkellinae), indicates that many of the distinctive features of the latter, including the intralensar structures, were already foreshadowed in Llandeilian times in the eye of *Crozonaspis*. In the related Caradocian trilobite *Dalmanitina (Dalmanitina) socialis* (BARRANDE), however, with which *Crozonaspis* is here closely compared, the intralensar and other structures of the eye are of a different kind, and do not show the „advanced“ features typical of Phacopacea.

All morphological terminology used in the description of the eye in this paper is identical with that in the author's previous works (CLARKSON 1966a, 1966b, 1967).

All figured fragments of *Crozonaspis struvei* are deposited in the collections of the Senckenberg Museum, Frankfurt am Main (SMF). Some comparable material was donated to the Grant Institute of Geology, Edinburgh (Gr. I. Edin.) by Dr. HENRY. The figured specimen of *D. (Dalmanitina) socialis* and other similar specimens studied are in the permanent collection of the Royal Scottish Museum (RSM-Geol.).

I am especially indebted to Dr. HENRY, of the University of Rennes, for his original suggestion that I might work on this material, and for the supply of specimens, also to Dr. WOLFGANG STRUVE for advice in the preparation of this work. I also should thank Dr. C. D. WATERSTON of the Royal Scottish Museum, Edinburgh for loan of material of *D. (Dalmanitina) socialis*.

Crozonaspis struvei J.-L. HENRY 1968.

Pl. 1 figs. 1-3; text-fig. 1.

* 1968 *Crozonaspis struvei* J.-L. HENRY, *Crozonaspis struvei* n. g. n. sp.: 370-374, pls. 1-2, text-figs. 1-2, 4, ? 3.

Description of the eye.

External surface (from rubber latex replicas of external moulds):

The external morphology of the eyes has already been described by HENRY, who has noted the relatively small size of the eye and its situation, the eye-indices, and the inflation of the anterior prolongation of the palpebral lobe, amongst other details.

Some further morphological features can be distinguished in the material to me, as follows. The plan curvature of the visual surface is relatively low anteriorly, but becoming quite strong near the posterior edge. In profile the surface of the eye is almost flat. The visual surface, which rises abruptly from the cheek region, forms a slightly inflated pad upon which the lenses are set in the pattern of hexagonal close packing characteristic of Phacopina. The palpebral lobe is quite highly inflated, rising to a flat or somewhat inflated palpebral area a short distance above the upper rim of the visual surface. The palpebral area is indistinctly delimited by a faint palpebral furrow. Near the outer rim of the microtubercular palpebral lobe, which in some specimens carries a pattern of thin curving grooves, lie a number of small pits arranged in a semicircle parallel with the rim.

The arrangement of the lenses is variable and there may be 24-31 dorsoventral files; in the best preserved specimens their distribution is as follows:

Gr. I. Edin. A 4697 (right eye):
345 567 677 777 777 777 777 766 665 543 2
(184 lenses in 31 files; maximum: 7 lenses per file).

SMF 21421 (left eye):
345 677 788 878 888 877 777 765 543 2
(177 lenses in 28 files; maximum: 8 lenses per file).

Dr. Henry has figured a specimen (POC 522, coll. J.-L. Henry; Henry 1968: pl. 1 fig. 4a-b) with a maximum of 9 lenses per file, and possessing an upper horizontal row, a feature which does not appear in any of the other material examined.

The files diverge ventrally at a very low angle. Lensar spacing is variable, though as in most Phacopina the largest lenses lie near the outer edges. In the largest specimen (SMF 21420), where the eye itself is 5·0 mm long, the dimensions of the lenses are: largest 0·3 mm Ø, average 0·27 mm Ø, smallest 0·08 mm Ø. In the central parts of the visual surface the lenses may be separated by as much as three-quarters of a lensar radius, but between the larger peripheral lenses this decreases to a half-radius. Occasionally the lenses may be slightly elliptical (text-fig. 1a).

The interlensar sclera is very little inflated between the lenses.

Visual field:

Owing to the slight distortion and decalcification of the specimens, no accurate measurements of the visual field were possible, but nevertheless some empirical observations on its nature can be made. The very low profile curvature and higher plan curvature of the visual surface indicates „visual strips“ traversing the visual field as in *Acaste downingiae* (Salter 1864) s. str. (Clarkson 1966a: 11, text-fig. 5). Since, however, the files diverge at such a low angle, the radiating pattern of the strips will be less distinct than in *A. downingiae.*

Internal structure of the lenses and associated elements:

In the internal moulds (steinkerns), the lenses and interlensar sclera have normally been removed by postdepositional solution, though as shown below, such solution has sometimes been selective, and in some specimens intralensar structures are preserved. The eye-surface of a steinkern thus shows the underlying matrix moulded to the contours of the original lower surfaces of the lenses and sclera, as they were prior to their removal. The most distinct structures are thus short pillars projecting from the surface (the matrix-filled sublensar alveoli), each indented at the top by a highly concave depression or lens-cup, marking the original lower surface of the lens. A honeycomb of relatively deep channels surrounding the pillars indicates the site of the interlensar sclera. As each pillar tapers slightly downwards, the sclera must have swollen proximally and extended a little way below the base of each lens; this can be readily seen in sections made of latex replicas of steinkerns.

In some specimens the lens-cups are empty, in others somewhat recrystallised ring-shaped structures are visible within each cup; these have a central depression which extends to some depth but does not reach the floor of the lens-cup, so that each of these structures considered in three dimensions has the shape of a thick walled bowl, and they are here designated „intralensar bowls" (text-fig. 1a-e). The original material of these is uncertain, and it is not understood why in some cases they should have been retained and in others disappeared without trace, but they must have formed an integral part of each lens, differing in chemical composition from the upper part of the lens, which in the material studied is never preserved. The intralensar bowls are clearly homologous with structures figured by LINDSTRÖM (1901: pl. 6 fig. 5, reproduced by HARRINGTON in the "Treatise", p. O 90, and the present author, CLARKSON 1967: text-fig. 2i) in the Devonian *„Phacops"* *macrophthalmus* BURMEISTER, and are, as far as can be seen, little different from them in structure. Similar, though smaller, structures were also noted in *Zeliszkella (Zeliszkella) torrubiae* (VERNEUIL & BARRANDE 1855) in an excellent specimen from Brittany kindly loaned to me by Dr. HENRY, and in the Devonian *Reedops sternbergi* (HAWLE & CORDA 1847) of which a description of the eye is in preparation. Such intralensar bowls thus may be widespread throughout the Phacopina, though I have not yet seen them in any advanced Dalmanitacea. Furthermore, structures described in the lenses of *Phacops fecundus* BARRANDE and *Phacops latifrons* (BRONN), bear little resemblance to intralensar bowls (CLARKSON 1967).

The relationships of the various parts of the lenses of *Crozonaspis struvei* are shown in text-fig. 1a-e, where restorations have been made from rubber latex replicas of internal and external surfaces of different specimens, some having intralensar bowls and some without them. Significant features are the

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Text-fig. 1. *Crozonaspis struvei* J.-L. HENRY 1968. — Schistes de Morgat, Llandeilo; Postolonnec, presqu'île de Crozon, Finistère, Brittany, France.

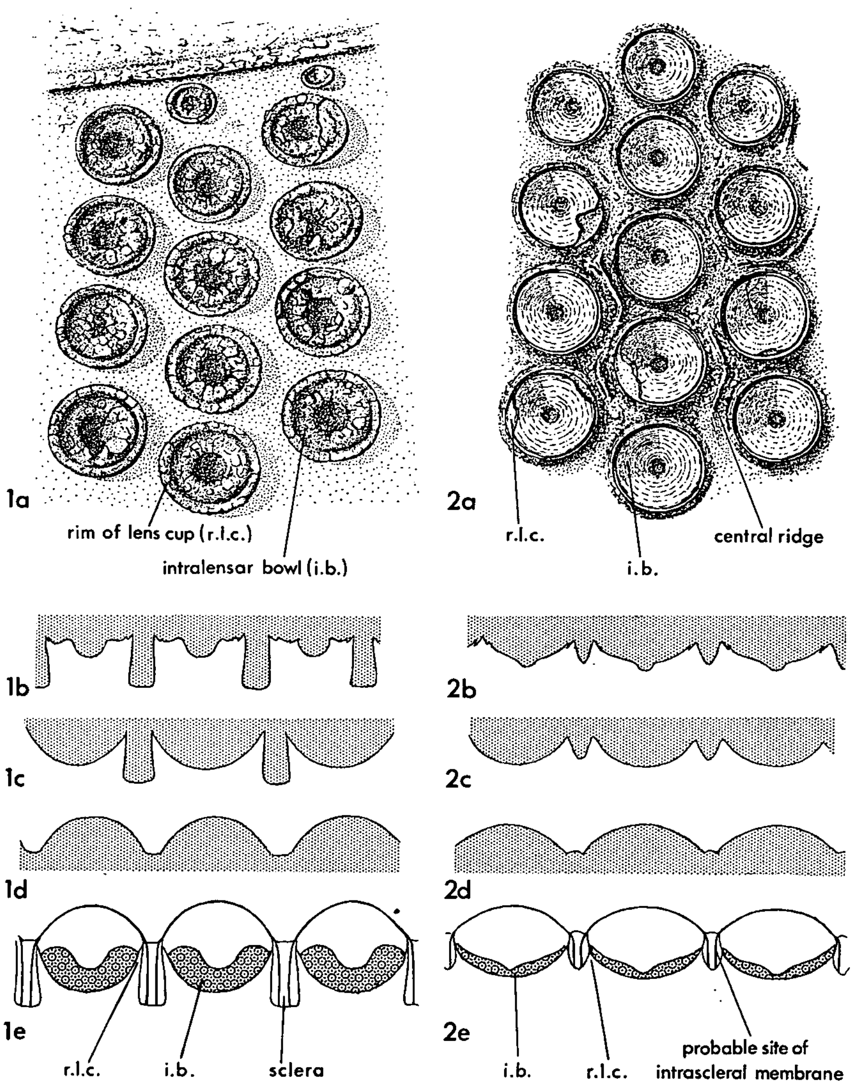
a) Part of visual surface of an internal mould (steinkern), just below the central part of the upper rim of the eye, showing lens-cups and intralensar bowls; ×50; SMF 21422.
b) Section through a single dorso-ventral file of a rubber latex replica of the same specimen; ×50; SMF 21422.
c) Similar preparation from a steinkern without intralensar bowls; ×50; SMF 21421.
d) Similar preparation from an external mould; ×50; SMF 21420.
e) Attempted reconstruction of the internal anatomy of the lenses and sclera from a, b, c, and d. Intralensar bowls are shown stippled. The site of the intrascleral membrane is inferred by analogy with other Phacopina.

Text-fig. 2. *Dalmanitina (Dalmanitina) socialis* (BARRANDE 1846). — Letná Formation, Caradocian; Veselá, Bohemia.

a) Central region of the visual surface of an internal mould (steinkern), showing lens-cups with shallow saucer-shaped intralensar bowls; the zig-zag central ridge in the matrix probably represents an indentation in the base of the sclera; ×50; RSM-Geol. 1967-32.
b-d) Sections through rubber latex replicas as in text-fig. 1b-d; ×50; RSM-Geol. 1967-32, RSM-Geol. 1957-1-9, Gr. I. Edin. 20614, respectively.
e) Reconstruction of lenses and sclera, as in text-fig. 1e.

strongly convex lensar surfaces, which is much the same for both surfaces, and the projection of the interlensar sclera to a position below the proximal surface of the lens. Such features are more typical of Silurian and Devonian genera of Phacopacea (especially *Reedops* and *Phacops)* than of the majority of Zeliszkellinae, and perhaps may be considered as "advanced".

Though the interlensar sclera is no longer present, its position, thickness, and orientation can readily be inferred from the steinkerns, and as in species of *Phacops* previously studied, all the lenses in a single file seem to have parallel



scleral projections, and in horizontal sections the peripheral lenses do not seem to be quite normal to the visual surface, as the matrix representing the sublensar alveoli may project obliquely from the eye surface.

Comparison with the eyes of other Phacopacea.

Zeliszkellinae.

Amongst the Zeliszkellinae in which the eyes are well enough preserved for detailed study, the closest resemblances in eye morphology to *Crozonaspis struvei* are to be found in *Dalmanitina (Dalmanitina) socialis* (BARRANDE 1846), and the eye of this species is described below. The eyes of many other Zeliszkellinae have been referred to in the specific descriptions of BARRANDE (1952), STRUVE (1958), HENRY (1965a, b, 1968), and other authors. There is a considerable range in form throughout the Zeliszkellinae, though as a general rule the eyes are of moderate size (150-300 lenses), except in *Ormathops* where eye-reduction is a common feature, and the palpebral lobe is normally flat or inwardly shelving [*Zeliszkella (Mytocephala)* is an exception]. Often the lenses are very close together, and the interlensar sclera cannot be discerned. Apart from in *D. (Dalmanitina) socialis* intralensar bowls have only so far been detected in *Zeliszkella (Zeliszkella) torrubiae* (VERNEUIL & BARRANDE 1855), where they are smaller than in *Crozonaspis struvei.* Before conclusive inferences about the evolutionary development of the eye in Zeliszkellinae can be drawn, it will be necessary to study other representative genera and species, and it is unfortunate that no details are available of the fine structure of the eye in Andreaspidinae, which STRUVE (1962: 161) has suggested as a subfamily of the Phacopidae, intermediate between Zeliszkellinae and Phacopinae. The visual surface of *D. (Dalmanitina) socialis,* however, is of interest in this respect and when compared with that of *Crozonaspis* helps to shed some light upon the problem of the early evolution of the schizochroal eye.

Dalmanitina (Dalmanitina) socialis (BARRANDE 1846).

Pl. 1 fig. 4; text-fig. 2.

* 1846 *Dalmania socialis* BARRANDE, Notice préliminaire sur le systême silurien et les trilobites de Bohême: 25.

1852 *Dalmania socialis.* — BARRANDE, Systême silurien du centre de la Bohême, I (I) [Trilobites]: 552, pls. 21, 22, 26, 27.

1958 *Dalmanitina (Dalmanitina) socialis.* — STRUVE, Die Zeliszkellinae: 193, text-fig. 9, pl. 3 figs. 16-17.

An extensive account of the eye was included by BARRANDE in his description of 1852 (p. 552b, pl. 26 fig. 24). Superficial similarities between the eyes of *D. (Dalmanitina) socialis* from the Letná beds[1]) near Veselá, Bohemia, and

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[1]) The Letná beds of Central Bohemia were originally considered as Llandeilian in age, but are now stated to be Caradocian (HAVLÍČEK & VANĚK 1966).

those of *Crozonaspis struvei* are to be found in their relatively small size, general shape, position on the cheek, forwardly sloping attitude, flattened visual surface, and in the number and distribution of the lenses. In typical adults these are arranged in 25-31 dorso-ventral files with a total of 180-220 lenses per eye. In two such adults their distribution was as follows.

RMS-Geol. 1957 — 1-9 (left eye):
356 778 888 888 887 677 777 665 665 43
(189 lenses in 29 files; maximum: 8 lenses per file).

Gr. I. Edin. A 265 (left eye):
235 678 898 898 988 988 787 776 665 543 2
(204 lenses in 31 files; maximum: 9 lenses per file).

The dorso-ventral files diverge ventrally at quite a high angle. An inwardly shelving palpebral lobe slopes to a flat palpebral area well below the facial suture. The separation of the lenses is variable in different specimens, though on average is slightly less than that of *Crozonaspis struvei.*

From steinkerns and rubber latex replicas of external moulds it is possible to infer the original morphology of the lenses (text-fig. 2a-e). The curvature of the lensar surfaces is relatively low, and approximately equal for upper and lower surfaces. Each matrix pillar representing the position of a sublensar alveolus is quite short and its walls have a slight outward slope; clearly the interlensar sclera tapered inwardly and did not project downwards as far as the bases of the lenses. A few thin zig-zag ridges running midway between the lenses of the dorso-ventral files are visible in one specimen (RSM - Geol. 1967 - 32), and faint traces can sometimes be seen of similar ridges running horizontally, thus forming a broken hexagonal pattern. These probably represent indentations in the lower surface of the sclera. In text-fig. 2a, they are shown as „central ridges". In most specimens the shallow lens-cups have no internal structures. Some individuals studied, however, have flattened, saucer-shaped structures, each with a small central depression, visible within each lens-cup. Where the edge of such a „saucer" is broken the matrix is visible below (text-fig. 2a). Though these „saucers" are very thin, they are undoubtedly homologous with the intralensar bowls of *Crozonaspis struvei,* and an attempt has been made here to reconstruct them for purposes of comparison (text-fig. 2e).

Silurian and Devonian Phacopacea.

There is great variation in the form of the advanced eyes of Silurian and Devonian Phacopacea (and here the large-eyed genera *Phacops* s. str. and *Reedops* may be cited), but there are nevertheless certain features which collectively distinguish them from the eyes of other Phacopina. The visual surface is normally high, with a relatively small number (c. 80-160) of very large lenses of highly convex form and separated by a thick and deep interlensar sclera. Deep intralensar bowls may be present, though considerable modifications of these have been described in two species of *Phacops* (Clarkson 1967). Inflation of the palpebral lobe is usual, though some genera have flat-topped palpebral lobes. Many of these features are already foreshadowed as early as the Llandeilian in *Crozonaspis struvei* though they are very much less developed in the stratigraphically later *D. (Dalmanitina) socialis*. The evolutionary relationship between the two types is not entirely clear; either the eye-structures in *D. (Dalmanitina) socialis* may be retained from a primitive stock from which both *Dalmanitina* and *Crozonaspis* were derived, or the features of the earlier *Crozonaspis* might actually be closer to the ancestral line. A third possible alternative involves no special relationship between the two types, and the apparent resemblance between the eyes of *Crozonaspis* and later Phacopacea may be purely fortuitous. The many points of resemblance between the two, however, seem at present to indicate a true relationship, and it is hoped that other particulars of early historical development of the eyes of early phacopids may be elucidated by further study of the eyes of Zeliszkellinae and Dalmanitinae.

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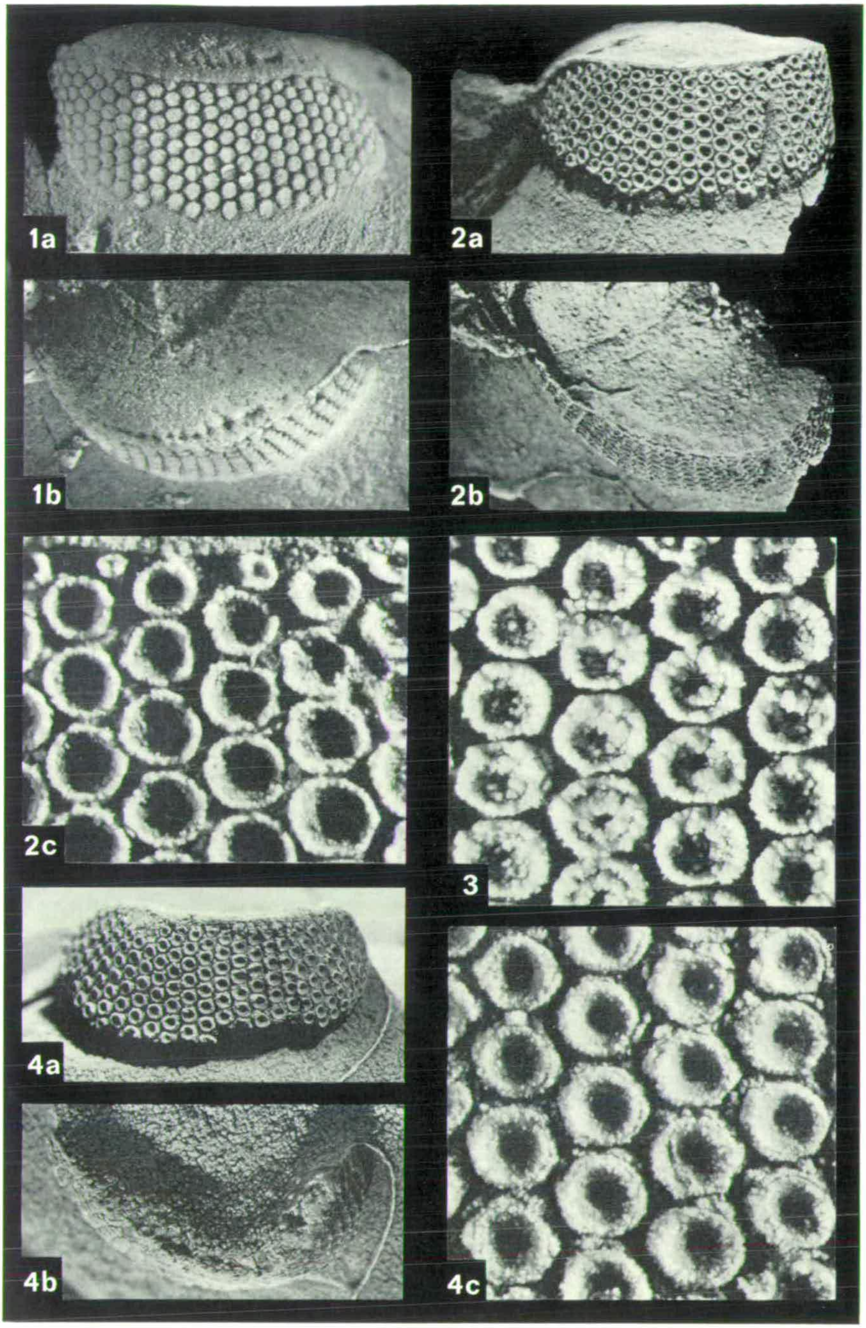
Plate 1.

All specimens are whitened with ammonium chloride.

Figs. 1-3. *Crozonaspis struvei* J.-L. Henry 1968. — Schistes de Morgat, Llandeilo; Postolonnec, presqu'île de Crozon, Finistère, Brittany, France.

1. External surface of eye (from a latex replica of an external mould), ×7·5; SMF 21420. — a) From the side. — b) From above.
2. Internal mould (steinkern) of a specimen with empty lens-cups; SMF 21421. — a) From the side; ×7·5. — b) From above; ×7·5. — c) Enlargement of part of visual surface; ×45.
3. Internal mould of a specimen with intralensar bowls in the lens-cups; part of peripheral region of visual surface enlarged, ×45; SMF 21422.

Fig. 4. *Dalmanitina (Dalmanitina) socialis* (Barrande 1846). — Letná Formation, Caradocian; Veselá, Bohemia.
Internal mould (steinkern) of a specimen with shallow intralensar bowls, RSM-Geol. 1967-32. — a) From the side; ×7·5. — b) From above; ×7·5. — c) Enlargement of part of visual surface; ×45.



E. N. K. Clarkson: Structure of the eye of *Crozonaspis struvei*.

VIII.—On the Schizochroal Eyes of Three Species of *Reedops* (Trilobita: Phacopidae) from the Lower Devonian of Bohemia.* By Euan N. K. Clarkson, B.A., Ph.D., Grant Institute of Geology, University of Edinburgh. *Communicated by* Professor G. Y. Craig. (With Three Plates and Six Text-figures.)

(MS. received January 24, 1969. Revised MS received June 2, 1969.
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SYNOPSIS

BOHEMIAN specimens of the phacopacean trilobites *Reedops cephalotes* (Hawle and Corda,) *R. sternbergi* (Hawle and Corda) and *R. bronni* (Barrande) have very well preserved schizochroal eyes. The sizes and distribution patterns of the eye lenses were studied and in *R. sternbergi* and *R. bronni* the angular bearings of all the lenses were measured, giving the visual range of the whole eye.

The internal anatomy of the eyes was also investigated, mainly from cut and polished sections. In many respects their morphology was comparable with that described previously in the Silurian and Devonian phacopaceans *Phacops latifrons* (Bronn) and *Ananaspis communis* (Barrande). The intralensar structures, however, are unlike those of *P. latifrons* and *A. communis* but bear a strong resemblance to the *intralensar bowls* of the Ordovician Zeliszkellinae, an early group believed to have been ancestral both to dalmanitaccan and post-Ordovician phacopacean stocks.

A brief history of the evolution of schizochroal eyes is given, some distinctive evolutionary trends are noted and the relationship of the structural pattern in *Reedops* is discussed with reference to that in other Phacopina.

CONTENTS

I. INTRODUCTION

TRILOBITES of the suborder Phacopina (Ordovician-Devonian) possess compound eyes whose structure is unique amongst arthropods. These eyes, originally designated "schizochroal" by Clarke (1889), are often very prominent and have extremely large and highly biconvex lenses, separated from each other by an "interlensar sclera". Each lens, unlike those of other trilobites, is covered by a separate corneal membrane. Schizochroal eyes were first studied in detail by Lindström (1901) and compared with the eyes of other trilobites; further contributions were added by Rome (1936), Brink (1951) and Beckmann (1951), and the current state of knowledge was ably summarized by Harrington (1959).

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In 1960 I began a detailed investigation of the anatomy and function of the eyes of Phacopina and the results of some of this work have already been presented (Clarkson 1966*a*, 1966*b*, 1967). The techniques and terminology there described are used also in this paper. Though I reached general agreement with Lindström's anatomical conclusions, there were some outstanding matters which could only be settled by further work. Most particularly, there were problems regarding the nature of the organic structures within the lenses. Lindström figured two sections of the eyes of "*Phacops*" *macrophthalmus* (Burmeister) showing peculiar bowl-shaped structures, of regular form, lying in the lower parts of the lenses. Whereas I likewise found (Clarkson 1967) intralensar structures in two species of "*Phacops*", these were of a quite different kind. Bowl-shaped structures were not present but instead each lens had a small "proximal nucleus" situated centrally and near its base.

Recently, Dr. J-L. Henry of the University of Rennes supplied me with specimens of Ordovician trilobites belonging to the sub-family Zeliszkellinae, a group believed to be ancestral to all post-Ordovician Phacopina. In the eyes of some of these there were structures which could best be interpreted as intralensar bowls (Henry 1968; Clarkson 1968), but there were none with "nucleate" lenses. To clarify the relationship between the two kinds of lens, the eyes of other Phacopina were studied with particular emphasis on intralensar structures.

Lindström mainly used well-preserved material from Scandinavia and North Germany, and a few specimens from Britain and North America. He did not, however, have access to the exquisitely preserved Phacopina (Ord.-Dev.) from Central Bohemia, described by Barrande between 1846 and 1872. Amongst the Bohemian Devonian material available to me were a number of specimens of *Reedops*; these were studied using the techniques discussed below.

II. MATERIAL AND TECHNIQUES

Four species of *Reedops* occur in Bohemia; *R. cephalotes* (Hawle and Corda,) *R. sternbergi* (Hawle and Corda), *R. bronni* (Barrande) and *R. modestus* (Barrande). Many specimens of such Bohemian material were sent last century to various British geological museums and institutes; some of these were originally labelled by Barrande and designated with their localities. (Hostin, Tetin and Dvorce). Others, collected apparently at a later date, were less well localized though they were probably collected from the same beds. The three species of *Reedops* studied apparently came from the Dvorce-Prokop Limestone of Lower Devonian age (Barrande's Etage E), where they occur with a fauna of odontopleurid and large-eyed dalmanitid trilobites, bivalves, brachiopods and pelagic tentaculitids. Svoboda (1966, p. 319) has described this limestone, and suggests that it was formed in relatively deep and tranquil water.

The study of the functional morphology of trilobite eyes is limited by the preservation of the material, for even in Bohemian specimens only the outer layers of structure still remain, and there is normally little trace of the internal regions. Sometimes, however, in sections made through the eyes it is possible to detect not only intralensar structures but also traces of the deeper lying sublensar organization from "ghost-structures" still remaining. Furthermore, as already shown (Clarkson 1967), it has been found possible to determine the probable original arrangement of the photoreceptive units from the inwardly-directed cavities (sublensar alveoli) in the thick sclera lying below each lens.

Techniques of preparation of the sections have been described earlier (Clarkson 1967); in this work on the eyes of *Reedops* similar methods were used.

The main problem in this work arises in differentiating between original organic units within the eye, and secondary internal "features" which arose during preservation. The quality of preservation of the intralensar elements depends on the grain size and composition of the sediments, chemical alteration during diagenesis, and many other features. But although this alteration may have gone far in some specimens, it can be assumed that these elements are original when the same kind of fairly complex structure with clear cut boundaries and a definite shape occurs within many or all of the lenses in a series of sections. Detection of such primary structures in trilobites has not proved difficult for very often distinct colour and/or compositional changes can be seen to limit well marked intralensar regions of more or less constant form. Other structures, cutting across these and usually crystalline or spherical, are undoubtedly secondary. A few features of uncertain origin occur in one or two sections; their possible significance will be discussed later.

The specimens used in this study were borrowed from the collections of various museums and are prepared as follows:— Sedgwick Museum, Cambridge (SM); British Museum (Natural History), London (BM); Royal Scottish Museum, Edinburgh (RSM); Grant Institute of Geology, Edinburgh (GrI). The sectioned specimens were all from the Grant Institute except one from the Royal Scottish Museum which was donated for study by Dr Waterston.

III. The Eye Structure of Reedops

Family Phacopidae Hawle and Corda 1847

Genus *Reedops* Richter and Richter 1925

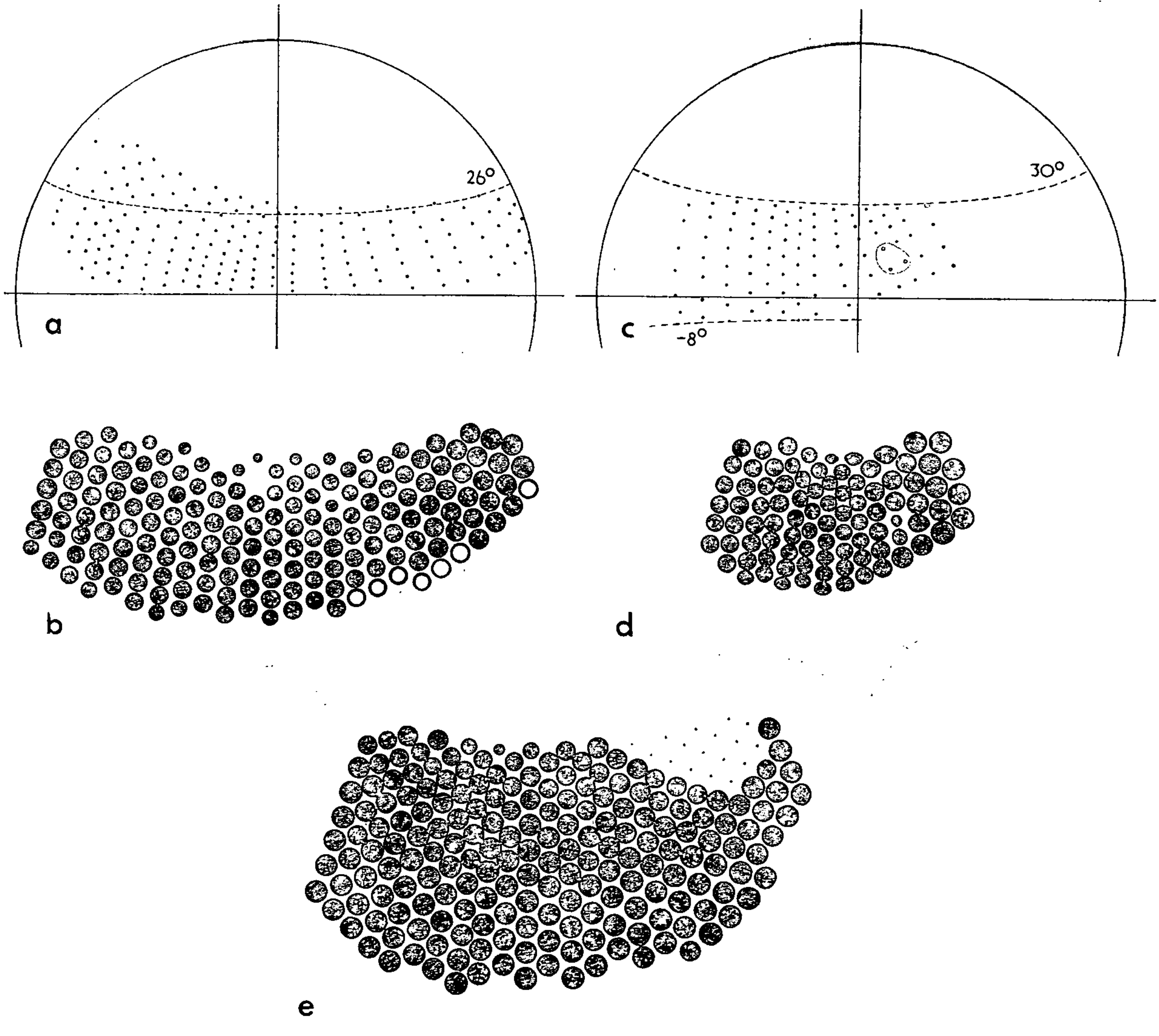
The genus *Reedops* occurs in Central Bohemia, where it is best known; endemic species also are present in the Kellerwald (Rhineland), the Harz Mountains, Germany (Alberti 1965) and from Oklahoma (Ormiston 1968). *Reedops* is closely allied to *Phacops* (s.l.) as defined in the "Treatise", but there are two main differences. First, the glabella is very large and inflated, and may as in *R. cephalotes* project far forwards. Secondly, the vincular furrow of "*Phacops*" is normally absent, though Alberti (1965) has noted that *R. bromi* has some indications of such a furrow. Much of the taxonomy has been brought up to date by Alberti, who includes synonomy lists. In the type species *R. bronni*, the eye is small; it is of moderate size in *R. sternbergi*, and very large in *R. cephalotes*. The last-named species has one of the largest eyes to be found in any phacopacean trilobite.

It is convenient to use the " eye-indices " devised by Struve (1958), to give a measure of the ratio of eye length to cephalic length. To derive an eye-index A is taken as the maximum eye-length, G the total length of the glabella, and Gn the total length of the cephalon, including the occipital ring (these last two measurements being taken in the sagittal plane). The large eye-index is then A/G, the small A/Gn, both expressed as percentages. The measurement H/A is also useful; H is the distance between the posterior edge of the eye and the posterior marginal furrow. Other measurements are as given previously (Clarkson 1966*a*). Thus length (min) and length (max) refer to measurements of total eye-length taken at the top and bottom of the eye respectively, in the exsagittal plane; measurements of width (max) and width (min), are the distances between the anterior edge of the eye and the top and bottom of the visual surface respectively, in the transverse plane; height includes the distance from the base of the visual surface to the top of the palpebral lobe, in the vertical plane.

(a) *Reedops cephalotes* (Hawle and Corda)

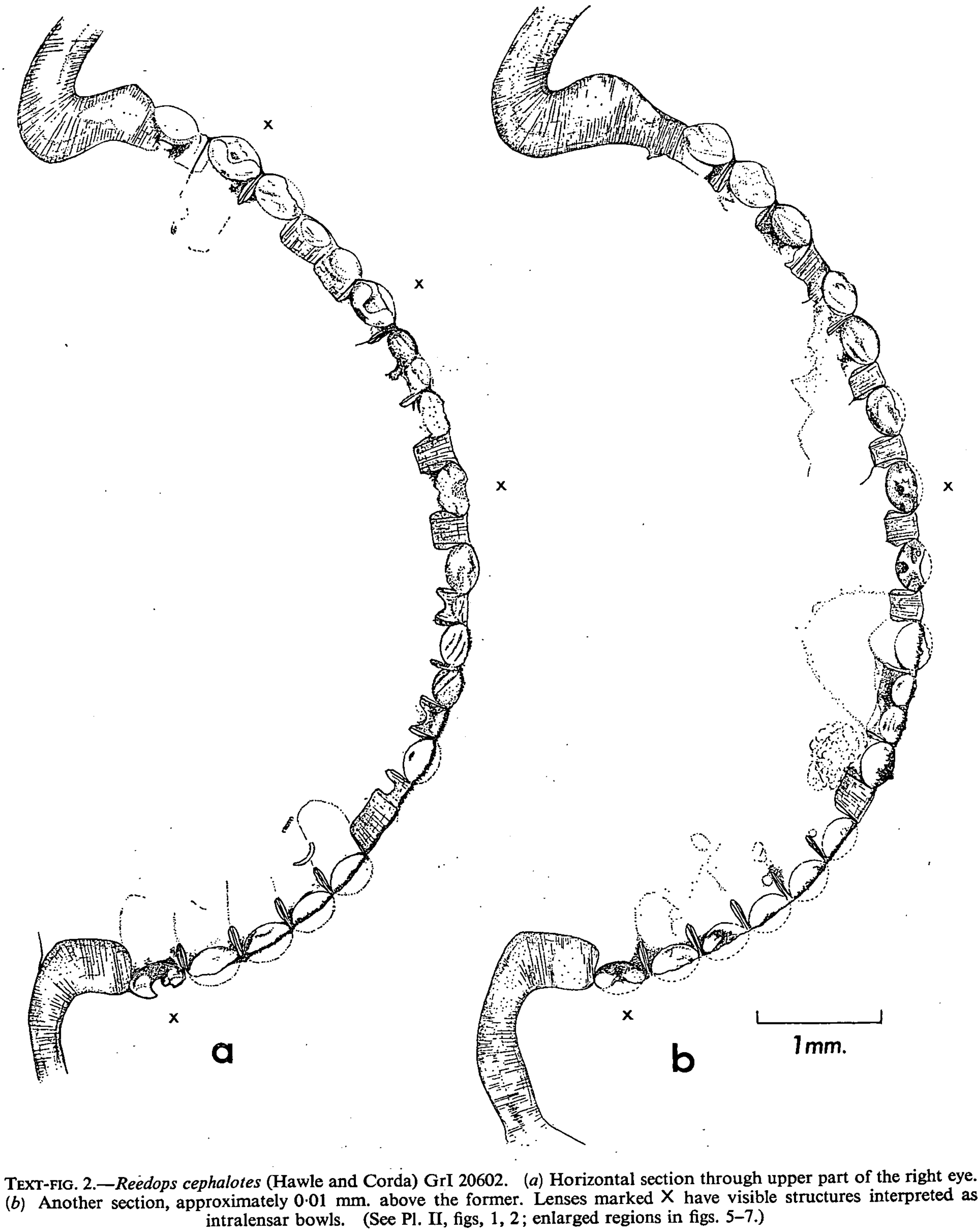
1847 *Phacops cephalotes* Hawle and Corda, p. 105.
1852 *Phacops cephalotes* Cord.; Barrande, pp. 509–510, Pl. 20.
1965 *Reedops cephalotes* (Hawle and Corda); Alberti, p. 99.

(Pl. I, figs. 4, 5; Pl. II, figs. 1–10; text-figs. 1*e*, 2, 3, 6*b*, *d*).



TEXT-FIG. 1.—(*a*, *b*.) *Reedops sternbergi* (Hawle and Corda) SM H 8451. Left eye. (*a*) Bearings of the lens-axes shown on a Lambert equal area net. (*b*) Projected visual surface of the same eye. × 7·5. The blank circles represent damaged lenses. (*c*, *d*) *Reedops bronni* (Barrande) BM I 3435, Left eye. (*c*) Visual field. (*d*) Projected visual surface. × 7·5. (*e*) *Reedops cephalotes* (Hawle and Corda) RSM 1968-45-1. Left eye. Projected visual surface. × 7·5. The upper posterior part of the visual surface has been removed entirely; the dots represent probable original lens-centres. In all cases the anterior edge of the eye faces left.

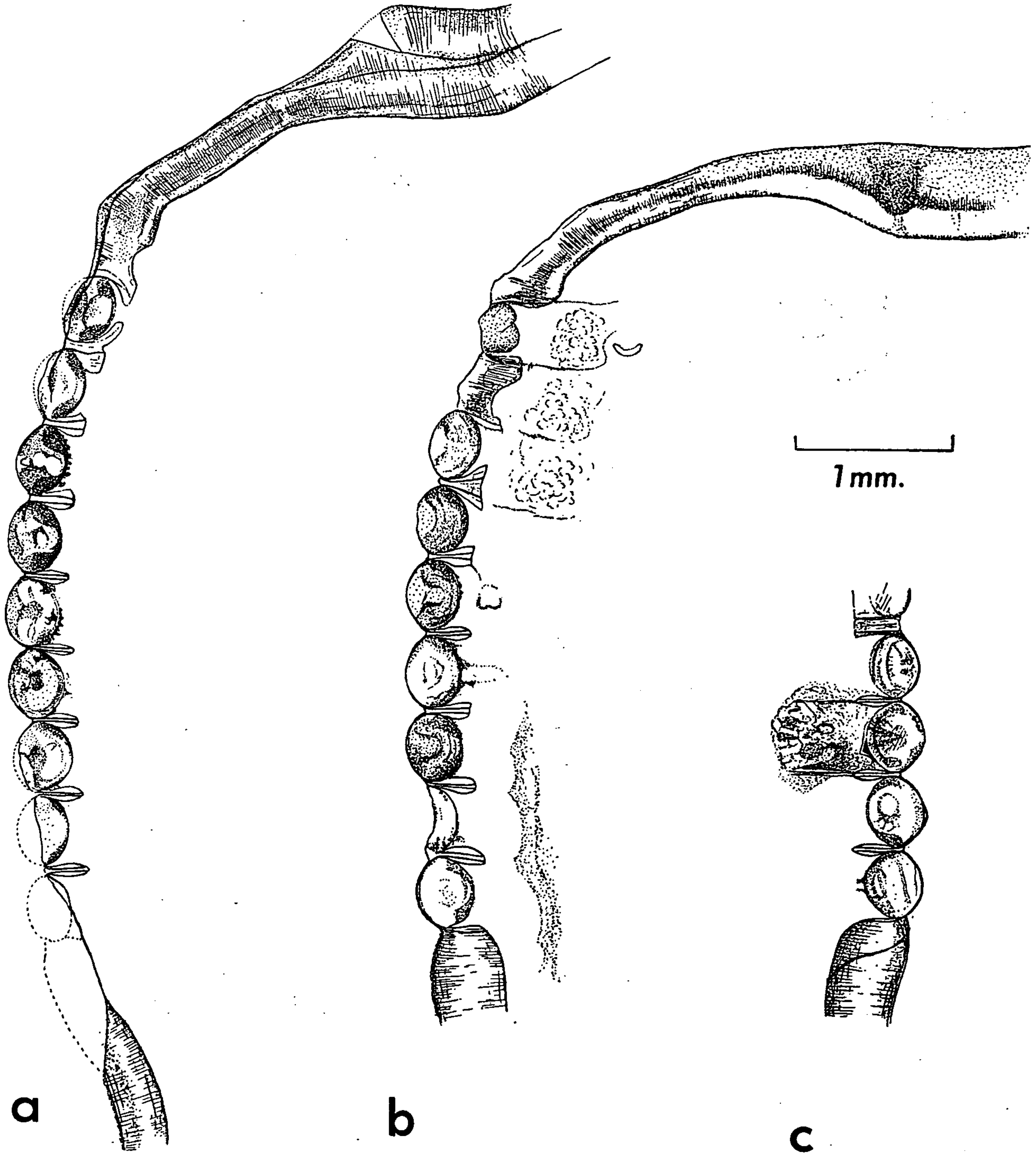
Material.—Usually specimens of *R. cephalotes* are embedded in a matrix which has proved very difficult to remove without damaging the specimen. All material examined was cleaned with a fine needle and an ultrasonic disintegrator, but even then the details of the visual surface could only be seen clearly under alcohol. In a few specimens small areas of the visual surface show undamaged lenses like those of *R. sternbergi*.



TEXT-FIG. 2.—*Reedops cephalotes* (Hawle and Corda) GrI 20602. (*a*) Horizontal section through upper part of the right eye. (*b*) Another section, approximately 0·01 mm. above the former. Lenses marked X have visible structures interpreted as intralensar bowls. (See Pl. II, figs, 1, 2; enlarged regions in figs. 5–7.)

External morphology of the eyes

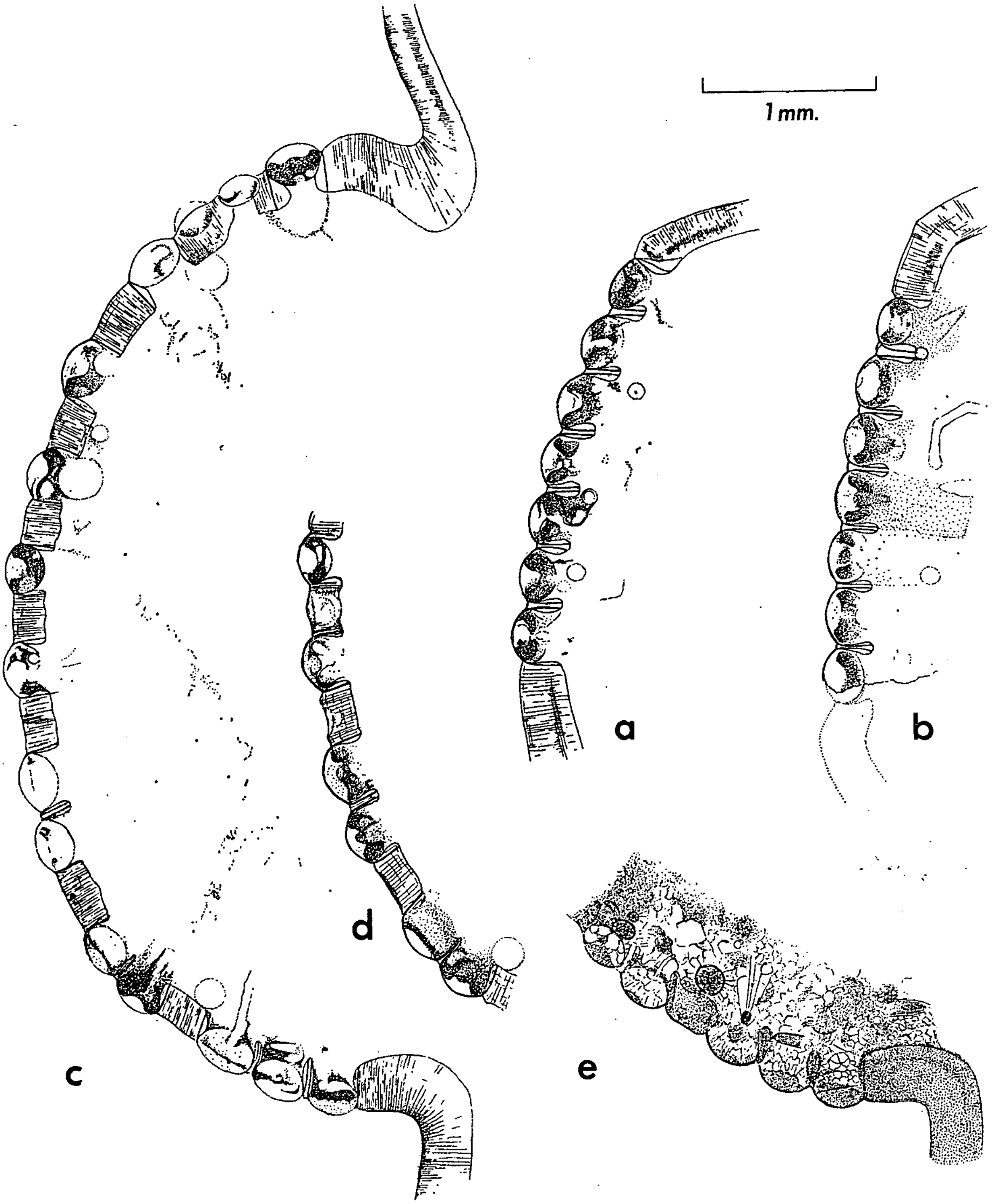
Specimens examined include: RSM 1968–45–1; RSM 1968–45–2 (external surfaces); GrI 20602; RSM 1911–62–1978 (sectioned).



TEXT-FIG. 3.—*Reedops cephalotes* (Hawle and Corda) (*a, b*) GrI 20602. Vertical sections through file 10 (*a*) and file 3 (*b*) of left eye. (See Pl. II fig 3, 4, 10.) (*c*) RSM1911-62-1978. Vertical section through file 1 of left eye showing a sublensar element. (See Pl. II, fig.9.)

Dimensions of eyes (RSM 1968–45–1). (Pl. I, figs. 4, 5). Length (max) 9 mm., (min) 7 mm.; width (max) 0·425 mm., (min) 0·3 mm.; height 5·5 mm., where cephalic length is 24 mm. and breadth 32·5 mm. Eye-indices A/G = 43 per cent, A/Gn = 37·5 per cent, H/A = 28 per cent. Maximum lens diameter 0·45 mm.

Eye very large, prominent, extending from the anterior angle of the librigena to within 2 mm. of the posterior marginal furrow. The posterior edge lies slightly further from the sagittal plane than the anterior edge. In profile, the eye is situated medially between the crown of the glabella and the lowest part of the lateral cephalic border and occupies about a third of the total length of the cephalon. The upper and lower borders of the visual



TEXT-FIG. 4.—*Reedops sternbergi* (Hawle and Corda) GrI 20599. (*a*) Vertical section through file 8 of right eye, showing distinct intralensar structures, though with indistinct lower margins to the lenses. (See Pl. III, figs. 6, 7.) (*b*) Similar section through file 3 (see Pl. III, fig, 8) (*c*) Horizontal section through upper central part of left eye (See Pl. III, fig. 1, 11). (*d*) Central part of horizontal section 0·02 mm. below the former (See Pl. III, fig. 10). (*e*.) Drawing of section (from a cellulose peel), of the posterior part of surface illustrated in (*c*), showing appearance in transmitted light.

surface are parallel. The curvature of the visual surface in plan is uniform; the curvature in profile is weak towards the base of the eye but increases dorsally. The palpebral lobe is smooth, slightly inflated, with its outer edge just overhanging the visual surface. There is only a slight trace of a palpebral furrow, but the palebral area rises slightly and is more highly inflated than the palpebral lobe and inclines steeply posteriorly.

Lens distribution within the species is relatively constant. Barrande records 24–25 files with 9–10 lenses per file, and having 200–225 lenses in the eyes of adult specimens. In RSM 1968–45–1 there are 220 lenses distributed in 25 files, with a maximum of 10 lenses per file, as follows (front to rear and grouped in threes for ease of reference):

6, 8, 9, 10, 9, 10, 10, 11, 10, 9, 10, 9,
10, 9, 9, 10, 9, 10, 9, 9, 8, 8, 7, 6, 5

(a few of the posterior files were damaged at the top, but the original lens complement could be determined from the impressions left on the matrix). Other specimens have a very similar lens distribution. The files diverge ventrally. There is little variation in lens-size throughout the eye, though the central lenses are a little larger. They are closely and strongly convex, with slightly inflated sclera between them.

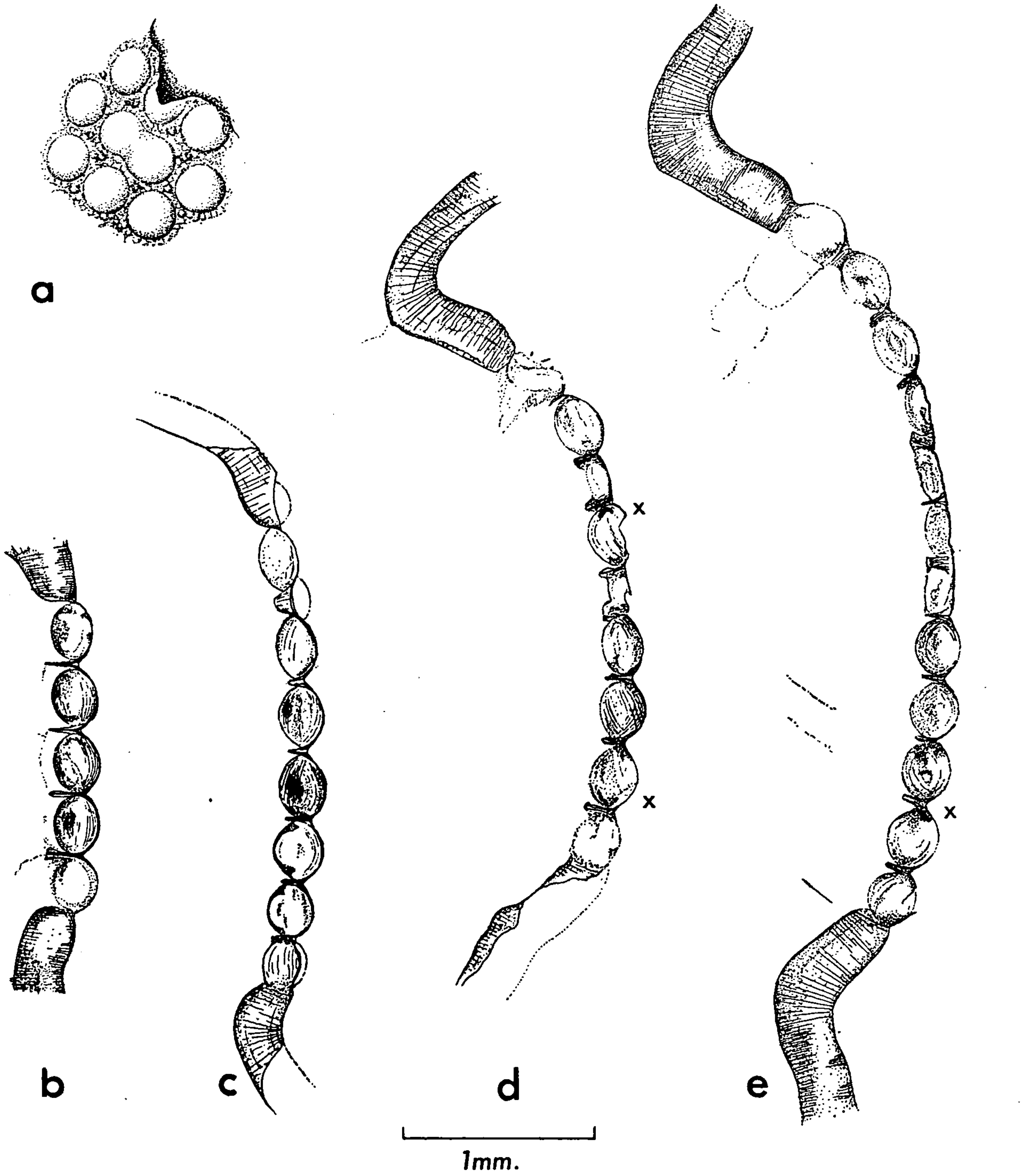
Visual field.—It has not been possible to make any determinations of the visual field since, even in the best preserved material available, the lenses had been weathered down flush with the visual surface and no trace of their original convexity was retained. Undamaged lenses were present in Gr. I. 20602, though these were incomplete. Though these weathered lenses display intralensar structures well (Pl. II, figs. 4, 5), they could not be used for accurate measurement of lensar bearings. It is estimated, however, that the horizontal visual range was around 20°–175°, and the vertical range 5°–30°. The stronger curvature of the upper part of the visual surface implies that the lens-axes would be distributed in partial strips in the lower part of the visual field, and more uniformly above, as previously described in *Phacops boecki* (Hawle and Corda 1847) (Clarkson 1966*b*, p. 476, text-fig. 6). There is a strong similarity in both the eye-morphology and the visual range of the two species.

Internal morphology of the eyes

I have previously given (1967) an account of the eye in two species of "*Phacops*" (s.l.). The general anatomy of the eye in *R. cephalotes* is quite similar to that of *Ananaspis communis* (Campbell) (formerly *P. fecundus*; see Campbell 1967). Each lens is strongly biconvex and is set at the top of a cavity or alveolus pierced through the intralensar sclera. A corneal membrane covers the external surface of each lens. At its periphery this leaves the lens and plunges through the sclera as a parallel-sided cylinder, the intrascleral membrane. In most specimens this terminates abruptly at the inner surface of the sclera. In horizontal section the alveoli are radially arranged though in vertical section they are parallel and separated by parallel scleral projections (Pl. II, figs. 3, 4, 8–10; text-fig. 3 *a–c*). (One of the vertical sections through GrI 20602 (Pl. II, fig. 4) shows scleral projections in the lower part of the eye which, though parallel, dip inwards. This displacement as revealed by further grinding, is the result of slight damage to the surface of the specimen, as though the visual surface had been pushed inwards before or after death).

As most of the anatomical details may be closely compared with that of *A. communis*, only the intralensar and sublensar structures need be discussed further.

(a) *Intralensar structures.*—The best preserved lenses are divided into three principal regions, whose limits are clearly defined by sharp compositional and/or colour differences (text-fig. 6*d*). The structures are all of the same kind, though differential alteration in some lenses has obscured the details. These different regions are as follows:—



TEXT-FIG. 5.—*Reedops bronni* (Barrande). (*a*) GrI 20603. Left eye. Upper anterior region of visual surface showing two fused lenses (See Pl. I, fig. 6). (*b*) GrI 20603. Left eye, vertical section through file 1 (See Pl. III, fig. 5). (*c*) Similar section through file 3 (See Pl. III, fig. 12). (*d*) GrI 20604. Right eye. Horizontal section near the lower rim. Lenses with intralensar "grooved rings" are marked X. (See Pl. III, fig. 4). (*e*) Similar section ·5 mm. above. (*d*) (See Pl. III, fig. 3).

(i) Except where there has been complete alteration, a fairly thin *basal layer* is present, concentric with the lower surface of the lens. Usually this has a deep brown colour. This part of the lens seems to have been most resistant to alteration, for it is almost always present. This basal layer was detected also in *A. communis* and very distinctly in *P. latifrons*, where it was indented centrally by the proximal nucleus. (Clarkson 1967, p. 610, text-figs, 1*c*, 2*f*, *g*, labelled y.y.^{1}.). It is also present in the other species of *Reedops*.

(ii) Thick-walled *intralensar bowls* are present in many sections, especially those cut in the vertical plane. They also are seen in the horizontal sections, (marked X in text-fig. 2*a*, *b*). In all cases they are preserved in yellow or white micrite. The intralensar bowls can also be seen in RSM 1968–45–1 from the external surface where the lenses have been planed down. They show up as light-coloured rings with dark centres (Pl. I, fig. 4). The central lumen of each bowl is small.

(iii) The *upper unit* of each lens, usually white in colour, has a convex upper portion forming the outer part of the lens just below the cornea, and a short central "stalk" below, filling the lumen of the intralensar bowl. The upper unit is thus mushroom shaped.

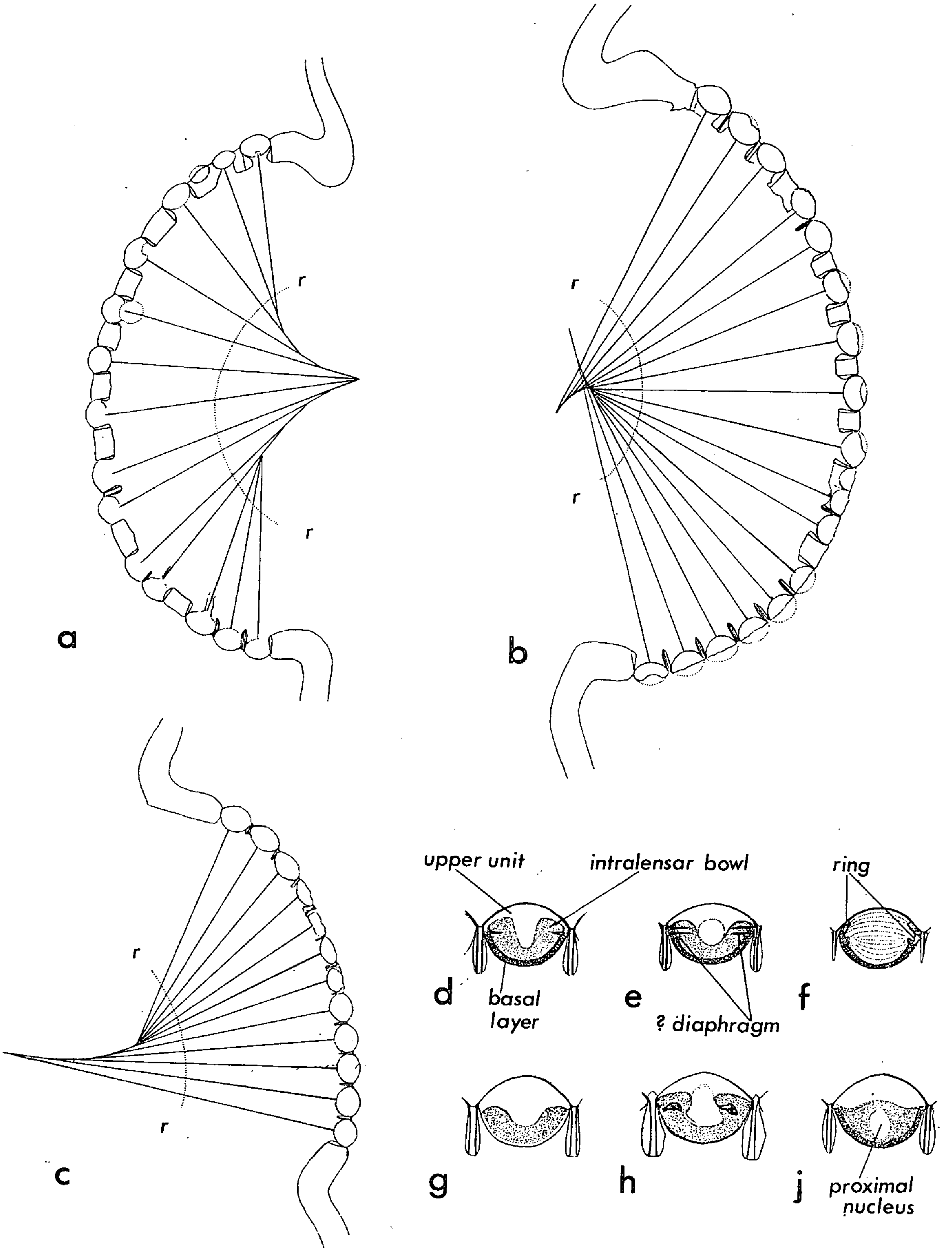
(iv) In a few lenses, especially those in the centre of the horizontal rows (as defined in Clarkson 1967), there are some other structures which certainly seem to be primary, for they can be seen in a number of the lenses of *R. cephalotes* and also in *R. sternbergi*. Their comparative rarity, however, by constrast with other intralensar structures, suggests that they were one of the first parts of the lens to be affected by postmortem alteration, and so had the least chance of being preserved. Each of these structures is a thin flat ring or diaphragm located in the principal plane of the lens and dividing the upper part of the intralensar bowl (Pl. II, fig. 6; text-fig. 2*a*, *b*). Such *intralensar diaphragms* are normally very dark brown in colour. Lindström figured a section of the eye of *P. macrophthalmus*, previously referred to, in which vague but comparable ring-shaped structures lie in an equivalent position in some of the lenses (text-fig. 6*h*).

Of the various intralensar structures which have been discussed, diagenetic alteration normally affects the intralensar diaphragm first of all. This is hardly surprising, as this diaphragm was extremely thin and occupied little space. The intralensar bowl, whatever its original material may have been, must have been much more resistant and is present in some lenses where recrystallization of the whole lens interior has been otherwise almost complete. The basal layer was affected last of all.

The reconstruction in text-fig. 6*d* has been made from structures seen in the polished sections. Cellulose peels made from the sections above gave little extra detail.

In one section, through the eye of RSM1 911–62–1978 (text-fig. 3*c*), alteration of the original structures has gone further than in GrI 20602; here the intralensar bowls are still visible but appear to be thinner; they have been invaded by calcitic material from the upper unit.

(b) *Sublensar structures.*—In all Phacopina the corneal membrane which covers the surface of each lens plunges through the sclera, normal to the surface of the eye, as the cylindrical *intrascleral membrane* (Clarkson p. 606). In *A. communis* an intact cone-shaped structure was found below one lens, formed by the continuation of the intrascleral membrane into the central lumen of the eye. A similar organic structure was seen in a vertical section of the eye of *R. cephalotes*, illustrated here (Pl. II, fig. 9; text-fig. 3*c*). Here the intrascleral membrane on both sides of the lens extends to a depth of 0·8 mm. below the inner surface of the sclera, a distance of about twice the diameter of the lens. Clearly the membranes seen in section form the walls of a cylinder comparable with the "cone" of *A. communis*, and although there are traces of a closed lower end to the cylinder, the growth of large calcite crystals partially filling the cylinder has disrupted this region. The ratio of length/



TEXT-FIG. 6.—(*a*, *b*, *c*) Diagrams illustrating the original axes of the photoreceptors, as inferred from the directions of the sublensar alveoli. The line rr shows the possible maximum depth for each basement membrane. (*a*) *R. sternbergi.* (*b*) *R. cephalotes.* (*c*) *R. bronni.* (*d-j*,) Attempted restoration of the intralensar structures of phacopid eyes. (*d*) *R. cephalotes* (Hawle and Corda). (*e*) *Reedops sternbergi* (Hawle and Corda). (*f*) *Reedops bronni* (Barrande) with structure interpreted as a "grooved ring", possibly equivalent to the intralensar bowls or to the diaphragm. The upper unit shows a distinct layered structure. (*g*) *Crozonaspis struvei* (Henry) (Zeliszkellinae, Llandeilian), redrawn from Clarkson 1968. The basal layer may have been present but is not preserved. (*h*) "*Phacops*" *macrophthalmus* (Burmeister), redrawn from Linström (1901), with a very thin basal layer. The areas marked in black may represent the remains of a diaphragm. (*j*) *Ananaspis communis* (Barrande) redrawn from Clarkson (1967).

breadth of the cylinder is about the same as in *A. communis* and there is little doubt as to its homology with the cone of the latter species.

Besides this structure there are several other sublensar "ghost structures", all of them cylindrical or subcylindrical. (text-figs. 2*a*, 3*b*). Usually these are merely dark-coloured regions of regular shape and about the same size as the cones described above, lying directly below their corresponding lenses and distinguished by colour alone. In a few cases a thin faint line was seen, enclosing a similar cylindrical region, but without colour differentiation. Such preservation recalls Denison's (1941) discovery of Devonian fish in which various major organs had been preserved by differential infilling of relatively coarse sediments. The situation in *Reedops*, though on a smaller scale, is comparable.

(b) *Reedops sternbergi* (Hawle and Corda)

1847 *Phacops sternbergi* Hawle and Corda, p. 107.
1847 *Phacops decorus* Hawle and Corda, p. 105.
1852 *Phacops sternbergi* Cord.; Barrande, p. 510, Pl. 20; figs. 18–29.
1965 *Reedops sternbergi* Hawle and Corda; Alberti, p. 99.

(Pl. I, figs. 1–3, 7–10; Pl. III, figs. 1–2, 6–11; text-figs. 1*a*, *b*, 4, 6*a*, *e*.).

Material.—SM H 8448, H 8451, H 8452 and BM 42297, all from the Lower Devonian of Hostin, Bohemia, were used for study of external surfaces. Their preservation is comparable with GrI 20599 and 20600 (labelled Dev. Bohemia), which were photographed and then sectioned; in all specimens the lens-surfaces are translucent and the details of the external surface are exceptional. As in the case of *R. cephalotes* the lithology they occur in is normally a fine argillaceous limestone, except for GrI 20599 where the matrix is bioclastic and coarser though hardly recrystallized. In GrI 20601, also sectioned, the lenses were opaque and appeared white from the outside, consisting of a very fine micrite. The preservation of the intralensar structures differs in the two matrices. The majority of specimens are from the Dvorce-Prokop Limestones, though the horizons of GrI 20599–20601 cannot be ascertained with certainty.

External morphology of the eyes

Dimensions of eyes (SM H 8451) (Pl. I, figs. 1–3). Length (max) 6 mm., (min) 5 mm.; width (max) 3 mm., (min) 2 mm.; height 3 mm., where sagittal cephalic length is 17 mm. and width 27 mm. Eye-indices: A/G = 44 per cent, A/Gn = 37·5 per cent, H/A = 50 per cent. Maximum lens diameter 0·4 mm., average 0·35–0·375, smallest 0·15 mm.

The eye is quite large and prominent, occupying the central third of the length (sag.) of the cephalon, and a third of its total height. The posterior edge of the eye is situated further than the anterior edge from the sagittal line and at a considerable distance (2·75 mm.) from the posterior marginal furrow. In profile, the curvature of the visual surface is strong anteriorly, decreasing backwards, in plan it is moderate (higher than in *R. cephalotes* or *R. bronni*) and increases slightly towards the rear. The lower rim of the eye is tuberculate, and bounded ventrally by a fairly deep groove. The palpebral lobe is somewhat inflated, sparsely tuberculate, and has a narrow outer rim. An indistinct palpebral furrow delimits the palpebral area, which lies at the same level as the palpebral lobe and is open posteriorly. (In this species the region of the librigena behind the eye is somewhat depressed, whereas the rest of the librigena is inflated. This has not been observed in any other species and may be an adaptation which enables the lowermost lenses of the rear part of the eye to have a clear field of view without being obstructed.)

The lens-distribution of several specimens is given below. Barrande mentioned an average of 136–171, distributed in 24–26 files with a maximum of 8 lenses per file.

Specimen	Lens distribution per file									Number of files	Maximum per file	Total
BM 42297 (RE)	567	777	877	777	767	666	655	443		24	8	147
GrI 20599 (LE)	577	787	878	787	877	776	655	443	32	26	8	160
SM H 8451 (LE)	678	888	988*	88*8	878	776	766	554	3	25	8	173
SM H 8451 (RE)	678	888	888	888	878	776	766	554	3	25	8	172
SM H 8452 (LE)	678	889	898	888	888	777	(776	543	21)†	26	9	177

* The lens numbers include those which have aborted and left a space.

† Estimated number in the posterior region due to slight damage.

All except the first three parallel files diverge ventrally at a moderate angle, and are close together. Within the files the spacing of the lenses decreases ventrally so that the lowermost lenses are almost contiguous; these lenses are a little larger than the upper ones. Some specimens have lenses which have either aborted completely or are much smaller than their neighbours (Pl. I, figs. 1–3). Thus in SM H 8451 the top lens in file 9 (Lens 9(i)) is absent as is 11(ii), and 15(iii) is small. In the right eye 21(iii) is also exceptionally small. Two other specimens also show this feature, and it has been noted also in *R. bronni*.

The interlensar sclera (Pl. I, fig. 3) is slightly inflated and has a finely granular surface. In the central and lower parts of the eye, where the lenses are close together, it is restricted to zigzag strips between the files, and between the bottom lenses appears as hexagons of small triangular points surrounding each lens.

Visual field (SM H 8451).—As shown in text-fig. 1*a*, there is a maximum longitudinal range of 8° anteriorly to 180° posteriorly, without any overlap. Though such a horizontal range is similar to that of many phacopaceans, the latitudinal visual limits are very unusual. The lower limit is virtually equatorial, but the elevation of the uppermost lens axes declines posteriorly from 42° at the front to only 21° latitude. Such an expansion of the anterior part of the visual field has not been encountered in any other phacopacean, though it is not uncommon in certain holochroal-eyed trilobites, notably Proetacea and Odontopleurida. The angle between individual lens-axes varies from about 4°–8° anteriorly to 12° between the lenses of the posterior files. The arrangement of lens-axes within the visual field (text-fig. 1*a*) appears to be a device whereby the whole visual range could be covered with maximum economy of lenses.

Internal morphology of the eyes

The following remarks concern GrI 20599, the best preserved of all the specimens sectioned. Here, primary structures are present and are very distinct. Intralensar bowls are present in virtually all the lenses though often the lower parts have been altered. In the dominantly biomicritic groundmass, however, there has been some recrystallization, and in some cases spherulitic structures have grown, often invading the lenses though not attacking the intralensar sclera. The appearance of the groundmass in thin section is shown in text-fig. 4*e*. Some subhedral and lath shaped crystals of calcite appear in a micritic groundmass together with secondary spherulites. Though the structure of the lens shows more clearly in polished surfaces, it is also possible to see differentiated regions in thin sections and cellulose peels. The intralensar bowls here consist of crystalline calcite often continuous with the calcite in the interior of the eye, whereas the lumen of each bowl, involving material of the upper unit, is of a very fine micrite. In thin section the boundaries between the two regions are clearly marked off from one another, though tiny needle-like points of calcite are visible, projecting from the intralensar bowls into the upper units of the lenses.

Structures in the polished surfaces show very clearly. The intralensar bowls are very dark in colour (black in the photographs), the upper units are pale grey. In the least altered lenses, the contact between the two is very sharp. The lower margins of the lenses, however, are rarely distinct; often the crystalline calcite of the bowls is continuous with that in the interior of the eye, and only in a few cases can a well-defined margin be seen. In text-fig. 4*c*, *e*, a polished surface is shown as compared with a cellulose peel of the same area.

The two vertical sections figured (Pl. III, figs. 6–8; text-figs. 4*a*, *b*) are of particular interest, for they show the disposition of the intralensar bowls within complete dorso-ventral files. As previously noted, in *Phacops*, *Ananaspis* and *R. cephalotes* the interlensar sclera, in vertical sections, appears as projections, all of which are parallel and horizontal, even though the upper lenses are inclined at an angle to them. The sections show that the axes of the bowls are likewise parallel and horizontal, aligned in the same direction as the scleral projections.

In a few cases some rather vague structures can be seen, each situated in the lumen of an intralensar bowl, (text-fig. 4*b*, *d*). Further sectioning has failed to reveal any other traces of such fillings, even though intralensar bowls were present in every section, and the existence of these as original elements of the eye is doubtful. In text-fig. 4*b*, a similar small structure, of conical form, actually cuts through the intralensar bowl. Below the same lens there is a sublensar "ghost-structure" of darker material, similar in form to the sublensar cones or cylinders already described in other species. This is the only example of such a "ghost-structure" so far encountered in *R. sternbergi.*

GrI 20506, a slightly smaller specimen, was likewise studied in horizontal section (Pl. III, fig. 2); here the lower margins of the lenses were normally entire, but otherwise no further details of structure could be determined, though the intralensar bowls were very clear, and the basal layer was usually distinct.

Though there were no traces of intralensar diaphragms in any of the above material, several vertical sections through the eye of GrI 20601, in which all the lenses were entire, but converted to very white micrite, showed definite indications of such structures (Pl. III, fig. 9). Curiously enough, the intralensar bowls, though normally present, were much less clear than in the sections already described.

It seems that the internal structures of the lenses of *R. sternbergi* were basically similar to those described in *R. cephalotes*; it is unfortunate that so few traces of sublensar units remain.

(c) *Reedops bronni* (Barrande)

1846 *Phacops bronni* Barrande, p. 84.
1847 *Phacops bronni* Barr.; Hawle and Corda, p. 106.
1852 *Phacops bronni* Barr.; Barrande p. 519, Pl. 20, figs. 15–17.
1965 *Reedops bronni* (Barrande); Alberti, p. 102.
  Taf. 1, figs. 1–5;
  Taf. 2, figs. 1–3;
  Taf. 5, fig. 8.

(Pl. I, figs. 6, 11–13; Pl. III, figs. 3–5, 12; text-figs. 1*c*, *d*, 5, 6*f*).

Material.—Preservation is excellent and the visual surfaces are normally in an almost perfect state. Of the specimens used for external examination, BM I 5435 and SM H 8445 were almost undamaged; SM H 8446 had incurred damage to areas of the visual surface, which is brittle and liable to flake off. GrI 20603, GrI 20604 and GrI 20605 were used for the preparation of polished surfaces showing internal structures.

External morphology of the eyes

Dimensions of the eye (BM I 5435): length (max) 4·7 mm., (min) 3·5 mm.; width (max) 2·0 mm., (min) 1·0 mm.; height 3·7 mm., where cephalic length is 18 mm. and breadth 28 mm. Eye-indices A/G=31 per cent, A/Gn=26 per cent, H/A=80 per cent. Maximum lens diameter 0·35 mm., average 0·3 mm., smallest 0·2 mm.

The eye is relatively small, not very prominent, occupying about the central fifth of the length of the cephalon (sag.), and situated in the anterior corner of the librigena, where the anterior edge touches the axial furrow opposite glabellar furrow 3p. Posterior edge further from the sagittal plane than the anterior edge. In profile, the eye occupies less than a third of the total height of the cephalon. The visual surface is high, flattened against the side of the cephalon ("aplatié" in the terminology of Barrande) with a relatively low plan curvature, increasing posteriorly. The curvature in profile is similar and fairly uniform.

Lens distribution within the species is relatively constant. Barrande records 13–14 files, with about 8 lenses per file, and having 100–106 lenses in all in the adult specimens. In the two perfect specimens examined their distribution was as follows:

Specimen	Lens distribution per file					Number of files	Maximum per file	Total
BM I 3435	678	787	877	665	54	14	8	91
SM H 8445	678	787	766	665	544	15	8	92

All files diverge ventrally. Within each file the spacing between lenses decreases ventrally and in all specimens examined the lowermost lenses are all elliptical (Pl. I, fig. 13), with their long axis horizontal. Elliptical lenses in the lowermost parts of the eye are sometimes present in juvenile phacopids; they have been observed in *Acaste* and *Phacops*, but have not hitherto been noticed in mature adults. All the specimens examined display this peculiar feature.

The interlensar sclera is slightly granular, appearing in the interstices of the lenses of the upper part of the visual surface as small, hardly inflated triangles surrounding each lens in hexagons. Where the horizontal rows are almost contiguous in the lower part of the eye, the hexagons coalesce and form zigzag lines between the files.

A number of irregularities and abnormalities in the lens disposition were encountered as in the case of *R. sternbergi*. In one case (GrI 20603), two lenses were united, forming a single elongate mass with only a narrow groove to show the original position of the sclera (Pl. I, fig. 6; text-fig. 5*a*). In another specimen (BM 3435) a cluster of three lenses in two files in the rear part of the eye were noticeably smaller than their neighbours (Pl. I, fig. 11; text-fig. 1*d*). Single abnormally small lenses appeared in other specimens also.

Visual field (BM I 3435) (text-fig. 1*c*, *d*).—The maximum longitudinal spread of the lens-axes is from 25° anteriorly to 146° posteriorly, and there is a vertical range from 8° below the equator to 30° above. The upper visual limit is latitudinal, the lower has a posterior lacuna; a common condition in phacopids, which seemingly prevents the high posterior border coming within the visual field of the lenses of the lowermost ascending diagonal row. Angles of separation of the lens-axes range normally from 4°–8°, and over much of the visual field are about the same in all directions though posteriorly the longitudinal separation increases to a maximum of 12°.

Internal morphology of the eyes

The internal structures of the eye of *R. bronni* are apparently different from those of the other two species; to what extent this is the result of the preservation of the material is uncertain. The sclera is quite thin, and in sections, except for the slightly oblique section drawn in text-fig. 5*b*, does not normally project as far inwards as the base of the lenses. These scleral projections are very narrow in comparison with those of the other species.

The lenses are strongly biconvex and the convexity is much the same for both surfaces. The basal layer was present in the lenses; these dark areas are however often rather ill-defined. Reasonably distinct examples occur in a few sections, and are illustrated in text-fig. 5*c*. A few lenses (marked "x" in text-fig. 5*d*, *e*) possess in addition symmetrically paired, dark coloured, V-shaped structures, lying in the principal plane of the lens, and pointing outwards towards its rim. These were undoubtedly parts of an originally continuous ring, lying in the principal plane of each lens and having a deep groove on its inner side. It is difficult to homologise this with any structures in the other species of *Reedops*. This ring might represent the upper part of a reduced and modified intralensar bowl or it could be a continuation of the basal layer, though it is never seen to join up with it. The structure is certainly different from that of the other species of *Reedops*, and further evidence must be sought before this matter is entirely clarified, meanwhile a tentative reconstruction is given in text-fig. 6*f*.

Most of the lenses are preserved as fine-grained calcite. A few have been further altered to a pure white featureless micrite (Pl. III, figs, 3, 5). Within the lenses of the former kind are very thin, clear, closely spaced and regularly curving lines, which, when the lens is cut through its centre, can be seen arching upwards in the upper parts of the lenses, and downwards below, and there is no doubt at all that these are original layers.

There is little evidence of sublensar "ghost structures". In the section illustrated in Plate III, fig. 3 and text-fig. 5*e*, the most anterior lens bears a whitish rectangular structure below, but this is very vague and cannot be accepted as evidential.

IV. DISCUSSION

(a) *The intralensar structures*

Two kinds of structures within the lenses require further comment; the intralensar bowls, and the thin semiconcentric layers found in *R. bronni* but not in the other species.

1. *Intralensar bowls.*—Lindströms' observations on the presence of intralensar bowls in "*P. macrophthalmus*" are supported by the new evidence from *R. cephalotes* and *R. sternbergi*. He did not, however, regard them as primary structures, but suggested that they resulted from differential preservation of homogeneous material. He drew attention to the eyes of isopods and spiders, where the lenses consist of thin semiconcentric layers, arched upwards in the upper part of the lenses and downwards in the lower region, and suggested that if trilobite lenses were of similar construction, bowl-like structures could have been produced by diagenesis, provided that the resistance to alteration in the lower layers was greater.

There are clear indications in the *Reedops* material that the intralensar bowls are primary structures and were discrete intralensar organs. This new interpretation is borne out by the regular and "compound" form in different lenses of the same eye, and in many individuals of the same and different species of *Reedops*. There is, furthermore, evidence of intralensar bowls in other phacopids, and particularly in some Ordovician Zeliszkellinae, a group which formed the root-stock of the post-Ordocivian Phacopina. Decalcified Zeliszkellinae from Brittany and Bohemia may carry bowl-like structures within each lens-cup though all other traces of the lens and scleral structures have disappeared (Henry 1968, Clarkson 1968). Text-fig. 6*g* shows a reconstructed lens of *Crozonaspis struvei* Henry; the basal layer may have existed but could not be detected. The precise chemical composition of the bowl structures is as yet unknown, though presumably it must have been more resistant to alteration than other parts of the lens.

The presence of the intralensar bowls gives a "compound" appearance to the lenses though, as discussed below, their function has not yet been clarified. Presumably, however, the fact that in vertical sections through the eye of *R. sternbergi* the oblique upper lenses possess bowls whose axes are parallel to the horizontal scleral projections is physiologically significant. This suggests that light entering the eye obliquely would be refracted straight down the axis of the photoreceptor to the appropriate light-accepting organs.

The lack of any comparable structures in recent arthropods makes further physiological interpretation difficult at present.

The great difference in the form of the intralensar structures in *Reedops* and in *Phacops*, *Ananaspis* and the Zeliszkellinae require some explanation. Lindström described intralensar bowls comparable with those figured here in "*Phacops*" *macrophthalmus*, though in his specimen the basal layer was much thinner, and the rim of each bowl more strongly bent inwards as a flange. This "flange effect", however, could result from sections being cut obliquely through the margin of the bowl rather than through the centre. There is therefore some doubt as to the exact shape of the bowls in *P. macrophthalmus* and I have not been able to locate Lindströms' material, and it is not certain whether it is still in existence. His figure (1901, pp. 30–31, Pl. 6, fig. 5) is redrawn here as text-fig. 6*h*.

The simplest homology of the intralensar elements is that the lens-structure in the Zeliszkellinae, *R. cephalotes* and *R. sternbergi* is primitive. The proximal nucleus in such an eye as that of *A. communis* was derived by the downward migration of the stalk of the upper unit, and its separation from the rest of the upper unit by the inward growth of the rim of the intralensar bowl, as if by closing the diaphragm (text-fig. 6*d–j*). "*P. macrophthalmus*" shows an intermediate condition morphologically. Though this explanation is tentative, it would provide a satisfactory homology for the various parts of the eye, since the structures in *Reedops* are clearly closer to the ancestral condition in the Zeliszkellinae.

2. *The layered lenses of R. bronni.*—The lenses of *R. bronni* differ from those of other species of *Reedops* and homologies of the various parts are difficult. Internal layering, which is found in this species only, immediately recalls Lindström's suggestion that semiconcentric strata like those of certain other arthropods might have originally existed, though here it is confined to the upper part of the lens only. If the reconstruction given in text-fig. 6*f* is correct, then the intralensar bowls are greatly reduced and may be represented by the "grooved ring" previously referred to, whilst the upper unit is expanded to fill most of the lens. The layering is probably visible in *R. bronni* because of the large size of the upper unit, but may have originally been present in the other species also, though destroyed by later diagenetic alteration. No similar layering has yet been detected in any other Phacopina.

(b) *Sublensar structures*

The ghost structures and remains of cone-membrane seen in *R. cephalotes* suggest sublensar cones or cylinders like the well preserved example in *A. communis* (Clarkson 1967, pp. 605–6). Though similar in relative proportions, as far as can be ascertained, they do not appear to add any new information.

(c) *Arrangement of the sublensar photoreceptors*

I have previously shown that it is possible to infer the original direction of the axes of the photoreceptors from the preserved intrascleral membranes and the sublensar alveoli alone (Clarkson 1967, p. 611). This has not been done for vertical sections, where all these axes are parallel and horizontal, but diagrams made from horizontal sections are instructive. If the axes are drawn as lines starting from the midpoint of the base of each lens, and parallel with the walls of the intrascleral membrane, (the remaining preserved part of each photoreceptor), the resulting more or less radial pattern gives information on the disposition of the internal organs before their loss. This pattern shows how the photoreceptors were arranged, and it also makes it possible to estimate their maximum depth, for the photoreceptors must have terminated short of the centre of convergence of these axes. In *R. cephalotes* (text-fig. 6*b*) the pattern is rather unusual, for though the central axes all converge to a point, the outer ones become progressively longer towards the periphery and their terminations form two overlapping curves. The photoreceptors cannot, of course, originally have extended to this depth.

R. sternbergi (text-fig. 6*a*) has the reverse of this pattern, for the central axes are the longest, and the shorter outer ones terminate on curves, whereas in *R. bronni* (text-fig. 6*c*) the posterior ones are the longest. Internal arrangements similar to those of *R. sternbergi* and *R. bronni* were shown by del Portillo (1936) in the compound eyes of various insects, but in all cases which he studied, the photoreceptive ommatidia ended internally far short of the centre of convergence of the lines. It is normal in the compound eyes of modern arthropods for the basal membrane supporting the proximal ends of the ommatidia to have a curved shape more or less concentric with the external surface, so that there is plenty of space below for the optic ganglion, nerve plexus, etc. Assuming that this principle applied in the Phacopina also, it is possible to estimate a maximum depth for the photoreceptors, which would still leave room for a ganglion below. This depth is given by the line r-r in the three cases illustrated in text-fig. 6*a–c*.

(d) *Further problems*

At present, a clear understanding of the physiology of schizochroal eyes seems remote. This is partially because of the dissimilarity of the eyes of Phacopina from those of any recent arthropod, and partially because even in modern insects and crustaceans, many aspects of vision are still not perfectly understood (Waterman 1961; Goldsmith 1964). Clearly the abrupt change from the small, simple, weakly biconvex lenses of the late Cambrian ptychopariid stock from which the Phacopina originated to the large, "compound", and highly biconvex lenses of the Phacopina is physiologically important. Yet since the refractive indices of the various parts of these fossilised lenses cannot be assessed, our knowledge of how they functioned is limited.

The kind of structural organization in schizochroal eyes appears to have evolved once only in the history of life, at the beginning of the Ordovician. Although there are many unsolved problems in the origin and physiology of these organs, there is at least the advantage that the evolution of schizochroal eyes, after the initial establishment of the basic pattern, can be studied within the framework of an extensive time perspective.

V. The Evolution of The Eye in Phacopina

(a) *History of Phacopina*

Reedops is a Devonian genus, a late product of the ancestral stock which first appeared in the early Ordovician. Campbell (1967) regards the genus as a side branch from the main *Phacops* group stock, probably derived from *Ananaspis*.

The general evolution of Phacopina is fairly well established. Whittington (1966) has shown that there was a drastic change in trilobite faunas between Late Cambrian and Early Ordovician times. Whilst most of the Cambrian stocks became extinct, many new evolutionary lines were established, some of which became dominant, persisting throughout the Ordovician and later. One of these important groups, arising in the Early Ordovician, was the suborder Phacopina.

The two earliest subgroups of the Phacopina, the families Pterygometopidae and Dalmanitidae, appeared at about the same time (Arenig), but in different faunal provinces. The pterygometopids are an exclusively Ordovician group, whose only apparent descendants were the curious Monorakidae, an isolated group virtually confined to the Siberian platform and neighbouring regions. These were extinct before the Silurian.

All post-Ordovician Phacopina were derived from the early dalmanitacean subfamily Zeliszkellinae, a group which includes many large-eyed genera. The Zeliszkellinae are now known to persist into the Middle and Upper Silurian (Rickards 1965), but reached their acme in the Middle and Upper Ordovician, when they gave rise to the remaining root-stocks of the Phacopina, which were the later dalmanitacean subfamilies, the Dalmanitidae and the Calmoniidae (a dominantly Southern Hemisphere group), and the Silurian-Devonian superfamily Phacopacea to which *Reedops* belongs. These groups remained dominant until their final extinction in the Middle and Upper Devonian. (The dates given here are from Cowie *et al.* 1967).

(b) *Evolutionary trends in the eyes of Phacopina*

(i) *Dalmanitacean line*

The eyes of the Zeliszkellinae resemble those of the later dalmanitids more closely than those of the Phacopacea. With the exception of the peculiar early genus, *Ormathops*, typical zeliszkellinid eyes are often large, with many lenses (*c.* 200) distributed in up to 40 dorso-ventral files, with relatively small and closely packed lenses, arranged in files of 8–15. Often, as in the "*Zeliszkella*" group (Struve 1955), the palpebral lobe is flat or may be raised or inflated. Typical examples have been figured by various authors. In the "*Dalmanitina*" group of the Zeliszkellinae, normally considered as ancestral to the Silurian and Devonian dalmanitaceans, the palpebral area is somewhat depressed. This structural pattern becomes extreme in the subfamily Dalmanitidae so that the palpebral lobe becomes narrow and the palpebral area very sunken, resulting in the isolation of the eye from the glabella. Such eyes have the form of a high, isolated, semicircular turret, rising very steeply and often of considerable size. An increase in the size and height of the eye, in the number of files, and in lens-size seems to be a dominant trend from the primitive "*Dalmanitina*" group pattern. The tendency for eye-degeneration, so typical a feature of the later Devonian phacopaceans, never affected the dalmanitaceans.

Intralensar bowls are certainly present in Zeliszkellinae; it has not yet been established whether they occur in their Siluro-Devonian dalmanitacean descendants.

(ii) *Phacopacean line*

The Zeliszkellinae possibly gave rise to the Phacopacea through the intermediate Upper Ordovician subfamily Andreaspidinae (Struve 1962). Little is known, however, of the eyes of this monogeneric and geographically restricted group. Amongst recently discovered genera of the Zeliszkellinae is the genus *Crozonaspis* (Henry 1968, Clarkson 1968), in which the palpebral lobe is quite strongly inflated, and there are other features like those of phacopaceans. The evolutionary relationship between this genus and the phacopaceans is still uncertain. Eyes of typical phacopaceans (*e.g. Phacops*, *Reedops*, and similar genera) when present as fully developed organs are usually fairly high, not isolated, having a flat or inflated palpebral lobe, and with rather few dorso-ventral files (up to 20). Advanced phacopaceans often only have 5–7 lenses in the central files, and possess less than 100 lenses. The lenses are always large, highly convex and widely separated by a flat or inflated sclera. In *Reedops*, lens number etc., is usually higher than in *Phacops*, and each file contains more lenses.

Reedops seemingly retained the ancestral condition with intralensar bowls, but some species of *Phacops* and related genera, evolved nucleate lenses, possibly by modification of the intralensar bowls (see p. 199), and seemingly represent an end-point in the evolution of the eye. *Ananaspis*, however, which has nucleate lenses, was cited by Campbell (1967), as probably ancestral to *Reedops*. This problem requires further work.

Discussion of the main evolutionary trends in the eyes of Phacopina would be incomplete without reference to the curious phenomenon of eye-reduction, affecting many genera of Phacopacea. In Late Devonian times the general tendency for reduction in lens number in this superfamily, which was apparent from the Ordovician onwards, reached its culmination. In some genera (*Cryphops*, *Denckmannites*, etc.), the eyes became reduced to a few small lenses, in others, *e.g. Trimerocephalus*, *Dianops*, etc., they were lost altogether. Chlupáč (1966, p. 124) has given a complete picture of the phylogeny of the last Phacopidae, and shows the geological contemporaneity of normal eye and reduced eyed forms. The last Phacopidae, belonged to the *Phacops accipitrinus* group, which had relatively large eyes with about 60 lenses each. Selwood and Burton (in preparation) suggest that the eyes of these late Devonian phacopaceans were genetically unstable and that all degrees of eye-reduction may have occurred within the one species. Some degree of environmental (deep water) control of the eye-pattern of phacopids has, however, been suggested (Erben 1958; Clarkson 1967), as with the contemporaneous Cyrtosymbolinae, which also undergo eye-degeneration in Upper Devonian time.

The history of the schizochroal eyed trilobites terminated abruptly when the last of the Phacopina, both normal and reduced-eyed stocks became extinct at the end of the Devonian.

VI. ACKNOWLEDGMENTS

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VIII. DESCRIPTION OF PLATES

PLATE I

Reedops cephalotes (Hawle and Corda), *R. sternbergi* (Hawle and Corda) and *R. bronni* (Barrande) external surfaces

Figs. 1–2. *R. sternbergi.* SM H 8451; left eye in lateral (1) and dorsal (2) views. × 10.

Fig. 3. *R. sternbergi.* SM H 8451; upper part of the visual surface enlarged. × 25.

Figs. 4–5. *R. cephalotes.* RSM 1968–45–1; left eye photographed under alcohol in lateral (4) and dorsal (5) views. × 10.

Fig. 6. *R. bronni.* GrI 20603; left eye (in lateral view) prior to sectioning, showing two fused lenses. × 10.

Figs. 7–8. *R. sternbergi.* GrI 20599; right eye prior to sectioning in lateral (7) and dorsal (8) views. × 10.

Figs. 9–10. *R. sternbergi.* BM 42297; right eye prior to sectioning in lateral (9) and dorsal (10) views. × 10.

Figs. 11–12. *R. bronni.* BM I 3435; left eye in lateral (11) and dorsal (12) views. × 10.

Fig. 13. *R. bronni.* SM H 8445; lower part of the visual surface of the right eye enlarged, showing elliptical lenses. × 25.

PLATE II

Reedops cephalotes (Hawle and Corda)—polished sections

Fig. 1. *R. cephalotes.* GrI 20602; right eye sectioned horizontally. × 10 (see text-fig. 2*b*).

Fig. 2. *R. cephalotes.* GrI 20602; similar section 0·01 mm. below that in fig. 1. × 10 (see text-fig. 2*a*).

Fig. 3. *R. cephalotes.* GrI 20602; left eye sectioned vertically through file 10. × 10 (see text-fig. 3*a*).

Fig. 4. *R. cephalotes.* GrI 20602; same section, lower part enlarged. × 45.

Fig. 5. *R. cephalotes.* GrI 20602; enlargement of anterior part of horizontal section illustrated in fig. 2. × 45. (see also text-fig. 2*a*).

Fig. 6. *R. cephalotes.* GrI 20602; enlargement of central part of horizontal section illustrated in fig. 1. × 45 (see also text-fig. 2*a*).

Fig. 7. *R. cephalotes.* GrI 20602; enlargement of posterior part of horizontal section illustrated in fig. 2. × 45 (see also text-fig. 2*a*).

Fig. 8. *R. cephalotes.* GrI 20602; uppermost lens of vertical section through file 3, showing indistinct cone-like structure. × 45, (see also text-fig. 3*b*).

Fig. 9. *R. cephalotes.* RSM 1911–62–1978; vertical section through file 1 of left eye, showing a sublensar element. × 45 (see also text-fig. 3*c*).

Fig. 10. *R. cephalotes.* GrI 20602; vertical section through lower part of file 3. × 45 (see also text-fig. 3*b*).

PLATE III

Reedops sternbergi (Hawle and Corda) and *Reedops bronni* (Barrande)—polished sections of the eyes

Fig. 1. *R. sternbergi.* GrI 20599; left eye sectioned horizontally. × 12 (see text-fig. 4*c*).

Fig. 2. *R. sternbergi.* GrI 20600; left eye sectioned horizontally. × 12.

Fig. 3. *R. bronni.* GrI 20604; right eye sectioned horizontally. × 12 (see text-fig. 5*e*.).

Fig. 4. *R. bronni.* GrI 20604; right eye sectioned horizontally near the lower rim. × 38, (see text-fig. 5*d*).

Fig. 5. *R. bronni.* GrI 20603; left eye sectioned vertically through file 1. × 57·5 (see text-fig. 5*b*).

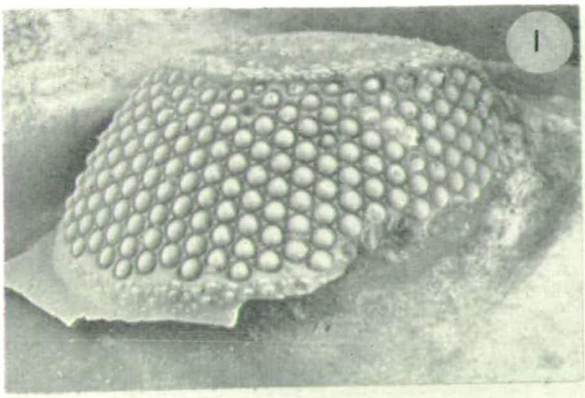
Figs. 6–8. *R. sternbergi.* GrI 20599; (6 and 7) right eye sectioned vertically through file 8 (see text-fig. 4*a*); upper and lower parts respectively, (8) similar section through central part of file 3. × 57·5 (see text-fig. 4*b*).

Fig. 9. *R. sternbergi.* GrI 20601; right eye sectioned vertically through file 12; upper part showing "intralensar diaphragms". × 57·5.

Figs. 10–11. *R. sternbergi.* GrI 20599; left eye sectioned horizontally (10) central and posterior parts of section shown in text-fig. 4*d*, (11) central part of section 0·02 mm. above (10). × 57·5 (see text fig.-4*c*).

Fig. 12. *R. bronni.* GrI 20603; left eye sectioned vertically through file 3. × 57·5 (see text-fig. 5*c*).

EUAN N. K. CLARKSON, "On the Schizochroal eyes of three species of *Reedops* (Trilobita : Phacopidae) from the Lower Devonian of Bohemia".—PLATE I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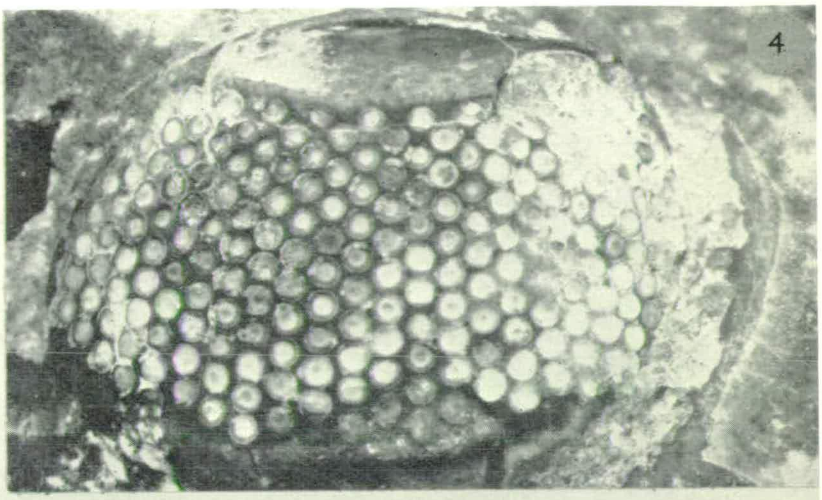
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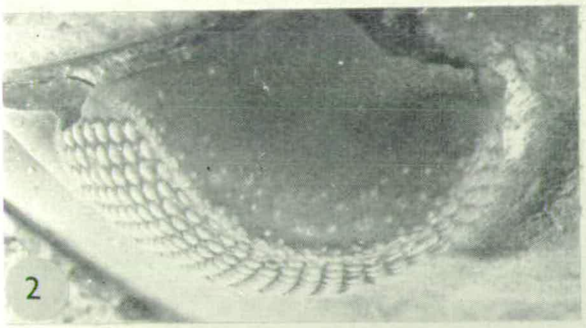
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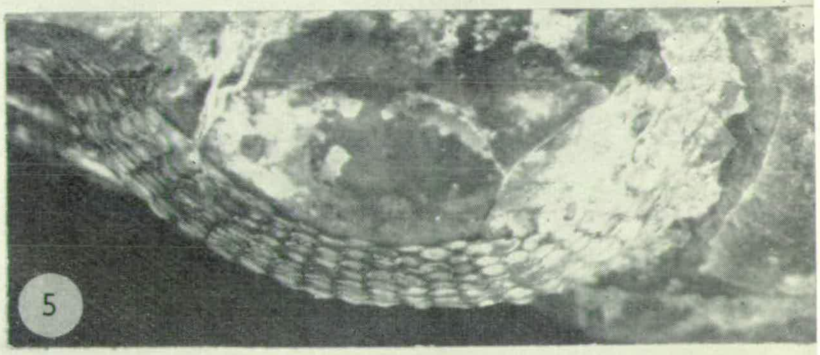
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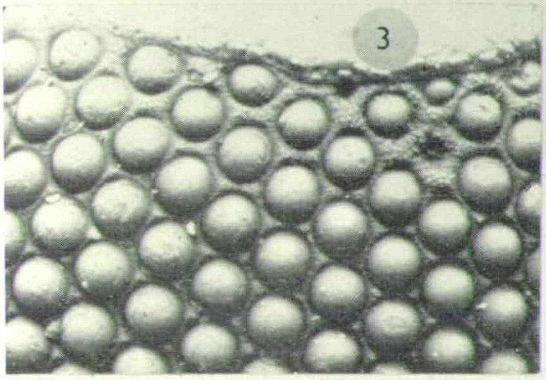
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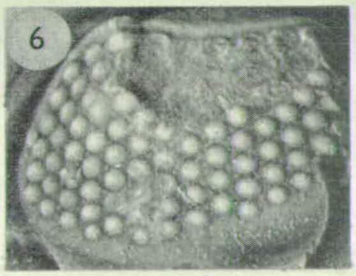
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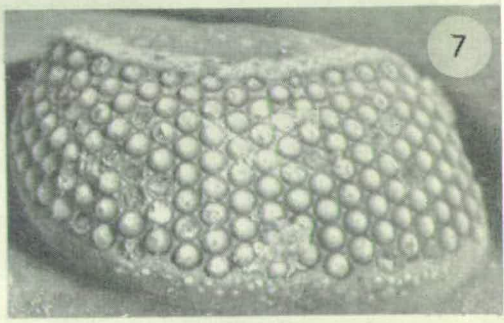
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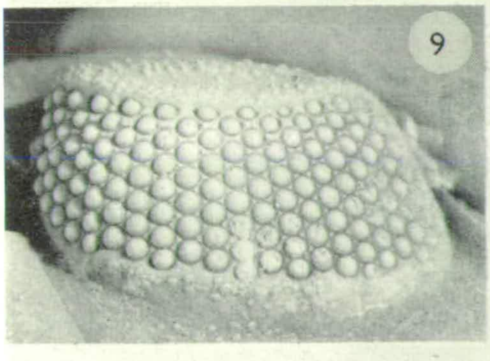
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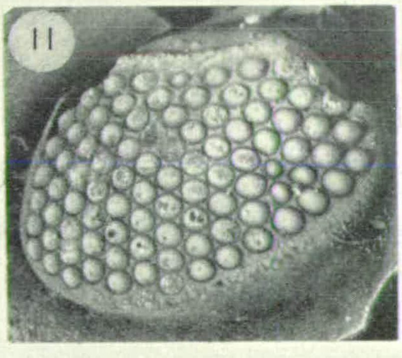
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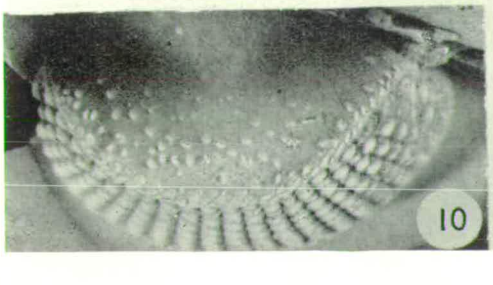
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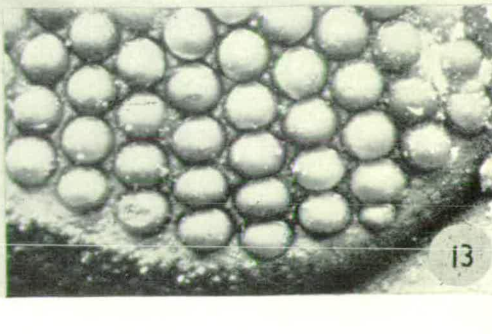
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EUAN N. K. CLARKSON, "On the Schizochroal eyes of three species of *Reedops* (Trilobita: Phacopidae) from the Lower Devonian of Bohemia".—PLATE II


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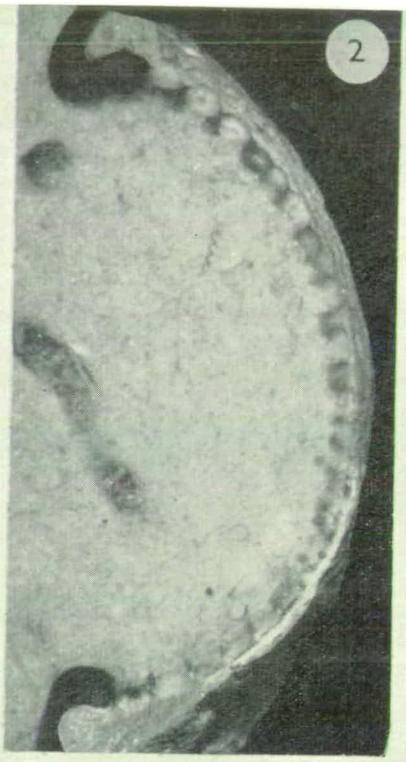
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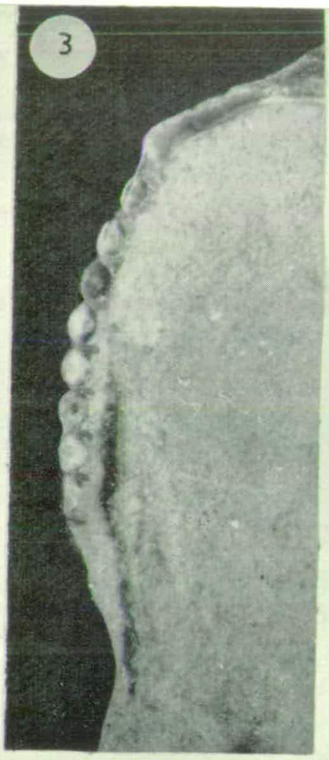
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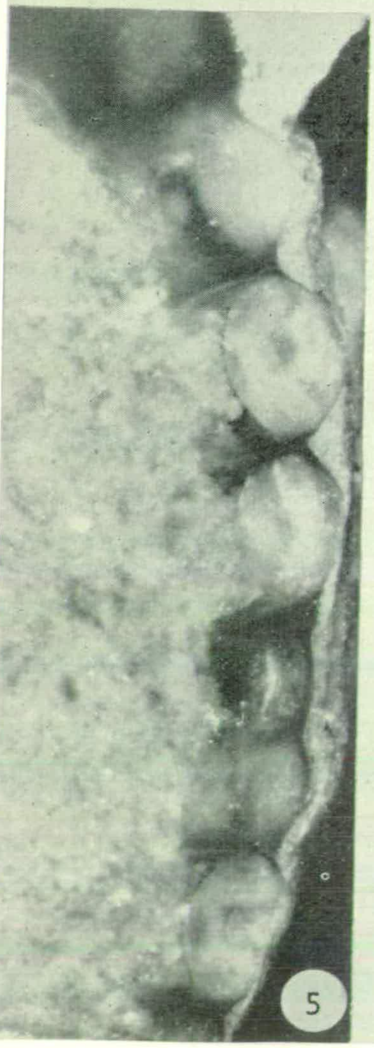
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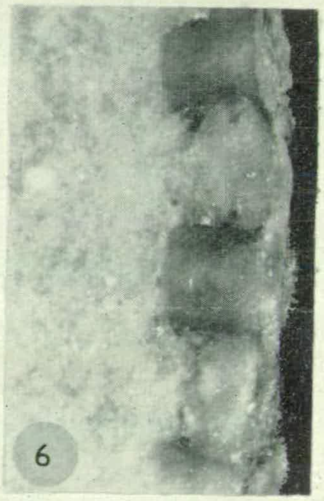
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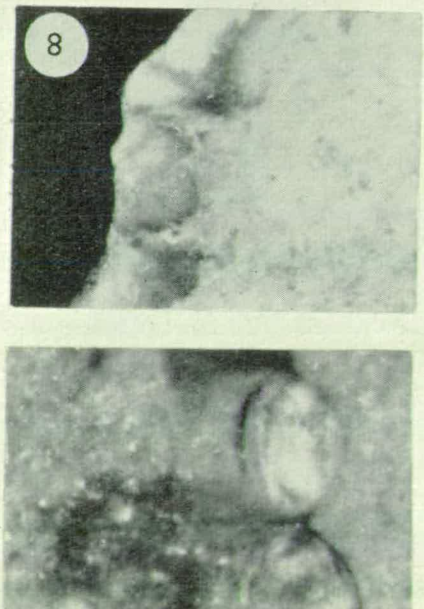
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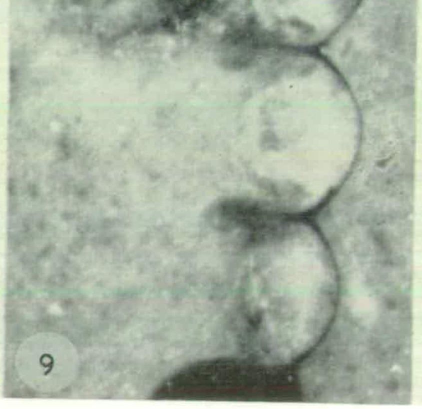
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EUAN N. K. CLARKSON, "On the Schizochroal eyes of three species of *Reedops* (Trilobita: Phacopidae) from the Lower Devonian of Bohemia".—PLATE III

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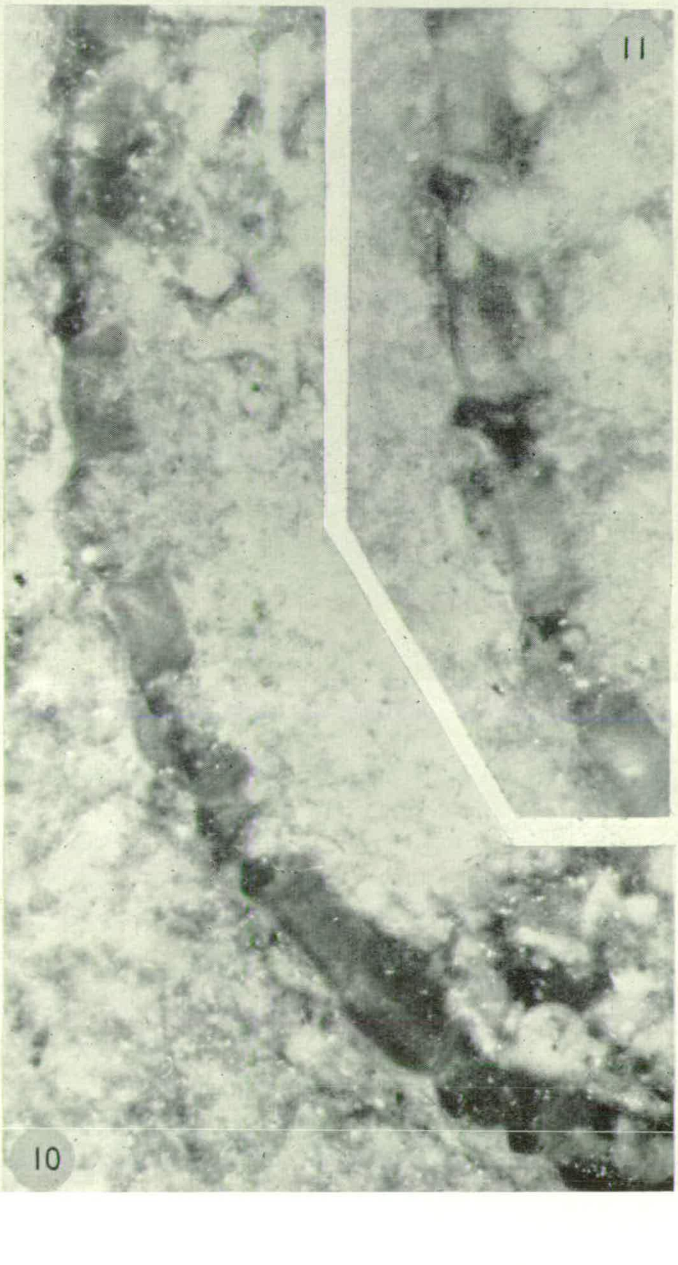

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A FUNCTIONAL STUDY OF THE SILURIAN ODONTOPLEURID TRILOBITE LEONASPIS DEFLEXA (LAKE)

EUAN N. K. CLARKSON

CLARKSON, E.N.K.: A functional study of the Silurian odontopleurid trilobite *Leonaspis deflexa* (Lake). *Lethaia*, Vol. 2, pp. 329–344. Oslo, 15th October 1969.

The odontopleurid trilobite *Leonaspis deflexa* (Lake) was functionally capable of life in two alternative attitudes. In the 'resting' attitude the whole body could lie outstretched on the sea floor, supported on the hindmost anterior denticles of the cephalon and on the genal, thoracic, and pygidial spines. In this attitude the body declined posteriorly.

In the 'active' attitude, however, the cephalon was tilted forwards through 25°, bringing the body up horizontally. The hypostome and presumably the mouth also could then have been brought into close proximity with the sea floor.

Leonaspis, *Primaspis*, *Diacanthaspis*, and *Anacaenaspis* are all functionally comparable. *Dudleyaspis*, *Acidaspis*, and other genera were specialised permanently for life in an attitude analogous to the 'active' posture of *Leonaspis*.

The life attitudes postulated for odontopleurids are compared with those of other trilobites and some comments are given on the evolution of the different patterns.

Odontopleurid trilobites arose in uppermost Cambrian times and persisted until the end of the Devonian. They were never at any time an abundant component of any fauna but they have nevertheless, on account of their physical peculiarities, attracted much attention and have been the subject of a number of papers and monographs. The most recent contributions are those of Whittington 1956a, 1956b, Whittington in Moore 1959, and Bruton 1966, 1967, 1968.

The most distinctive and characteristic feature of odontopleurid trilobites is their spinosity, a universal feature of all representatives of this group. It is largely on account of this spinosity that they have been often discussed from the point of view of adaptive morphology. Until quite recently most palaeontologists were willing to accept the view first put forward by Dollo (1909) and elaborated by Richter (1919, 1920) and Raymond (1920, 1936), that these spiny trilobites were planktonic and were able to remain suspended in the water through the frictional effect of the spines. Yet it is curious that this viewpoint should have been favoured for such a long time, for, as Seilacher (1959) clearly indicated, the increase of surface area afforded by the spines in an animal the size of a trilobite is far too low to retard appreciably the sinking of the trilobite body through the water; frictional retardation only becomes effective in a very small arthropod such as a long spined zoea larva. Furthermore, some odontopleurid genera possess spines which are both rounded in cross section and very massive (e.g., *Leonaspis*); these could hardly be imagined as aiding in the prevention of rapid sinking. Some other function of the spines must be envisaged.

Seilacher's suggestion that some odontopleurids led a partially benthonic existence was anticipated by Whittington (1956a and b), who studied the functional adaptations of some odontopleurid cephala. He showed that the heads of some odontopleurids were specially adapted for resting upon the sea floor in a particular attitude, presumably whilst feeding, the body being stretched out horizontally behind, a little above the level of the sea floor. He states (1956a, p. 505) 'In *Acidaspis* and in *Dudleyaspis* there is a row of almost vertically directed spines on the antero-lateral cephalic border. These spines are graduated in length so that the cephalon will rest on a flat surface on their tips and on the antero-lateral cephalic margin . . . (in this position) the posterior margin of the occipital ring is approximately vertical. In *Ceratocephala*, a like attitude is attained by the antero-lateral extension of the free cheeks rather than by apines. In *Whittingtonia* the cheeks show a combination of both structures. In *Leonaspis* the cephalon is less convex, but spines along the antero-lateral margin of the cephalon support it in the same position.'

The second paper (1956b, p. 185) included more evidence in support of these views and a resumé of the views of some previous authors. Particular attention was given to the structure of the anterior cephalic margin of *Ceratocephala* and *Apianurus barbatus*, in which there are paired notches on the lower surface. These were interpreted as adaptations which enabled the antennae to protrude forwards while the animal rested upon the anterior cephalic margin. It was also shown that when hypostomes were found in situ, they lay almost horizontal when the cephalon was in this orientation, above the plane formed by the base of the cephalon. This was borne out particularly by the hypostome of *Acidaspis cincinnatiensis*, which has a bevelled anterior edge which fits with that of the rostrum, in such a manner that the hypostome would normally be horizontal. There is little doubt that Whittington's conclusions are substantially valid for all the odontopleurids, but it will be shown that *Leonaspis* and allied genera could also be functional in a different attitude.

Possible life attitudes

The life attitude of *Eophacops musheni* (Salter) has previously been elucidated, using the eye and strip-like visual field as horizontal markers (Clarkson, 1966). When the head is orientated in its inferred life attitude the anterior border of the cephalon rises anteriorly, and from directly in front

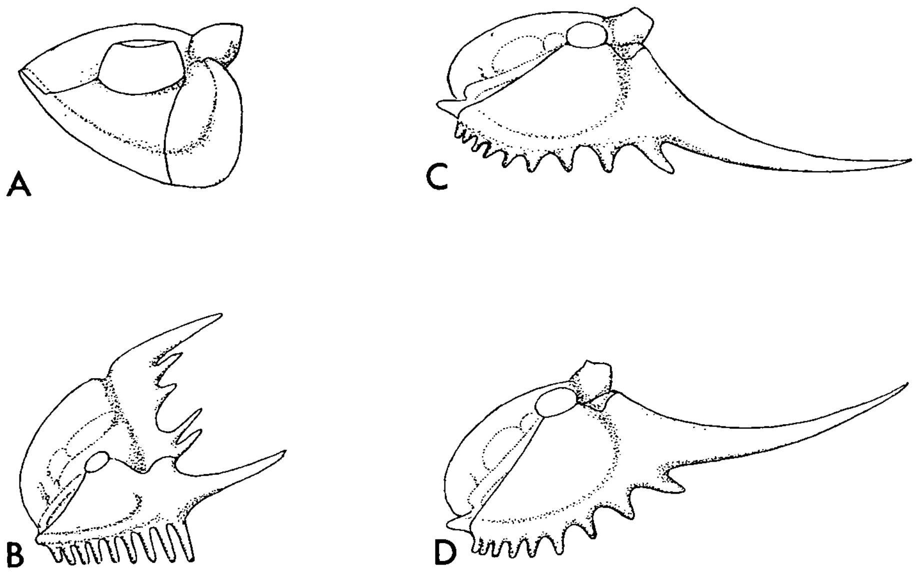

Fig. 1. Profile views of trilobite cephala. A. *Eophacops musheni* (Salter). Redrawn from Clarkson (1966). B. *Dudleyaspis quinquespinosa* (Salter). After Whittington (1965). C and D. *Leonaspis deflexa* (Lake) in 'resting' and 'active' attitudes. Not to scale.

forms an 'anterior arch' (Fig. 1A). This postulated attitude is very different from that which Whittington proposed for the odontopleurids, for if an odontopleurid cephalon such as that of *Dudleyaspis* (Fig. 1B) were to be equated with that of the phacopid it would be necessary to rotate one cephalon through 25° or so relative to the other in its plane of symmetry.

The differences in the orientation of the cephalon in these two trilobite groups (phacopids and odontopleurids) seemingly reflect adaptations for different modes of life. The problem of how these differences in orientation arose may be partially resolved by further study of odontopleurid morphology. For within the odontopleurids there are two distinct grades of functional organisation, exhibited by such genera as *Leonaspis* on the one hand and *Dudleyaspis* on the other. These may be subdivided as follows:

ODONTOPLEURIDS WITH TWO POSSIBLE LIFE ATTITUDES. – In the most primitive grade of organisation are included a number of long-ranged genera, particularly *Leonaspis* and *Primaspis*, which have been cited as one of the main root stocks of the odontopleurids (Whittington, 1956b, p. 190). *Diacanthaspis* and *Anacaenaspis* also belong here. In these the genal spines are long and tapering and have a slight ventral curvature. The tips of the antero-lateral denticles lie along a curve. These trilobites were capable of living in the attitude which Whittington postulated, with cephalon tilted forwards, and could have rested upon the tips of the *anterior* denticles (Fig. 1D). When the cephalon was so orientated the rest of the body became outstretched horizontally behind (Fig. 5A). But it is also possible to recon-

THE ANTERO-LATERAL DENTICLES. – As in other odontopleurids there are denticles produced from the antero-lateral border of the cephalon, but these are more readily comparable with those of the calymenid *Pharostoma* than the former, as their tips lie in a curve rather than in a plane. The posterior of these denticles are longer, and the points of these are in the same plane as the lowest part of the curving genal spine. In some species, e.g. *L. crenata* (Emmrich), the tip of an extra vertical spine which projects downwards from near the base of the genal spine, likewise lies in the same plane. The anterior few denticles are usually shorter and stouter and the tips of these also lie in a plane, which is inclined at 30° or so to the first plane. Thus the two extremities of the curve which passes through the tips of all the antero-lateral denticles are more or less planar, though the median section is regularly curved.

In many species of *Leonaspis*, e.g., *L. tuberculata* (Hall), and *L. williamsi* Whittington (in Whittington, 1956a), the anterior denticles are outwardly splayed rather than vertically directed, and the distal ends of all the denticles may in certain species be flattened and expanded, providing a wider area for the cephalon to rest upon.

GENAL SPINES. – The genal spines are long, rounded in cross-section and apparently unspecialised, showing greater similarity to the type of genal spines of proetids or cheirurids, rather than to the extremely modified spines of *Ceratocephala* and *Dudleyaspis*. These genal spines curve downwards, almost continuing the curve of the antero-lateral border of the cephalon, and in some species *(L. deflexa)*, they curve upwards at the tips again.

THE EYES. – Even in well preserved specimens of *Leonaspis* the eyes are frequently broken off or damaged. In species where they have been described they are sessile and may be either small and almost globular in form, or rather large and ovoid with the long axis almost vertical.

Eyes of ovoid form are possessed by *L. crenata* (Emmrich) and *L. leonhardi* (Barrande) (Bruton, 1967, 1968), and there are similar eyes in *L. cf. williamsi* (Whittington) (Whittington & Campbell, 1967). The eye of *L. cf. crenata*

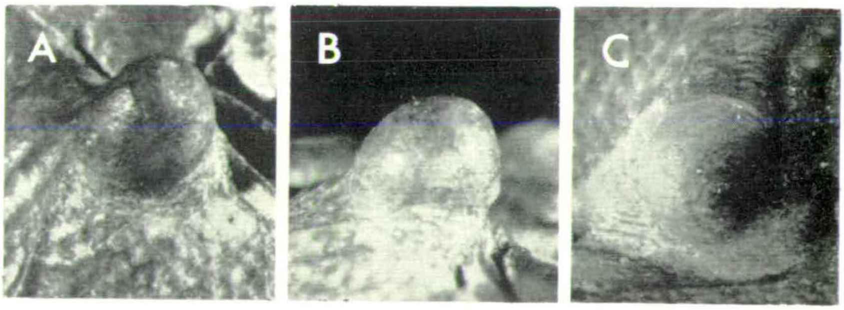

Fig. 2. Leonaspis cf. *crenata* (Emmrich). A, B, and C. BU H 389. Left eye in oblique fronto-lateral, side, and top views. × 15. Wenlock Limestone (Middle Silurian), Dudley, England.

from the British Silurian is figured here (Fig. 2). *L. coronata* has small, almost globular eyes, and so apparently has *L. deflexa*, but in none of the specimens which I have examined are they well preserved; usually the visual surface has collapsed and no longer retains its form.

The visual field of leonaspid eyes cannot be accurately determined partially because of the small size of the eye, and partially because the lenses are normally covered by a relatively thick cornea, which obscures the subsurface structures. As well preserved eyes are scarce, I have not been able to make any thin sections, and nothing is known of their internal structure apart from Lindström's observations (1901, p. 36, Pl. 1, Figs. 1–6) that the holochroal lenses were short prisms below the cornea. In view of possible inaccuracies, it seemed unwise to attempt accurate measurements of the visual range. Even so, two points concerning the eye are relevant to cephalic orientations, and can be discussed without recourse to such detailed measurements.

Firstly, the visual fields of *Leonaspis* eyes do not have the strip-like form found in phacopids. Those species with globular or otherwise highly curved visual surfaces must have had an all-round and overhead panoramic view. Such ovoid eyes as I have examined (*L. elliptica* (Burmeister) and *L. cf. crenata*) were differentially curved so that the anterior part of the visual field had a somewhat wider angular range than the posterior region. Here also, however, the overall visual range must have been high, reaching anteriorly to 80° or so above the equator, and leaving only a small 'blind spot' overhead and slightly behind the vertical plane.

Secondly, though accurate determination of the visual fields cannot be made without more material, in all cases the base of the visual surface seems to be more or less horizontal when the head is aligned in the 'resting attitude' (Fig. 1C). Presumably a resting trilobite would therefore obtain a good all-round view of the level sea floor, as far as its visual physiology allowed. When the cephalon was tilted into the 'active' attitude (Fig. 1D), and the body became stretched out behind, the eye would naturally tilt forwards. In the new attitude, this would not be disadvantageous to the trilobite because of its panoramic visual field; it would have been able to see the sea floor and region above directly ahead of it in its line of movement. Clearly this was the case also in the more specialised trilobites, *Dudleyaspis*. *Acidaspis* and *Ceratocephala*.

The three features discussed, antero-lateral denticles genal spines, and eyes indicate that the cephalon would have been functionally capable of taking up either an 'active' or a 'resting' attitude, with no apparent disadvantage in either case.

The above remarks concerning cephalic orientations are of general application in *Leonaspis*; in the next section the functional morphology of the exoskeleton as a whole is considered, with reference to the representative species *L. deflexa* (Lake).

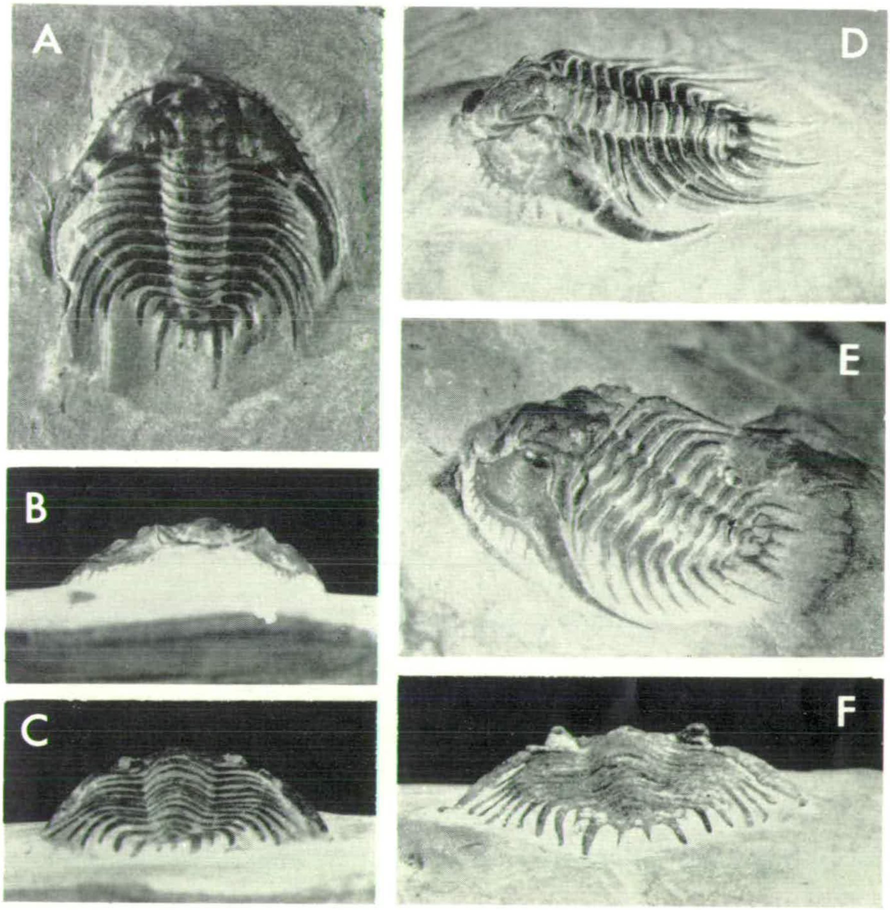

Fig. 3. Leonaspis deflexa (Lake). A, B, C, and D. BU H 258. A specimen preserved in the 'resting' attitude, shown in dorsal, anterior, posterior, and oblique lateral views. E. RSM–1951–4–1, oblique postero-lateral view. F. BU H 174, posterior view. All × 3. Wenlock Limestone (Middle. Silurian), Dudley, England.

Functional morphology of *Leonaspis deflexa* (LAKE)

SYNONYMY. – □ 1896 *Acidaspis deflexa* – Lake, p. 239, Pl. 71, Fig. 7. □ 1949 *Acantholoma (Kettneraspis) deflexa* (Lake). – Prantl and Pribyl, p. 146, 167. □ 1956a *Leonaspis deflexa* (Lake). – Whittington, p. 506, Figs. 3 and 4.

MATERIAL. – Complete extended specimens; Holcroft Collection, BU H 174, BU H 209, BU H 258; RSM 1951–4–1.

Inverted specimen with hypostome; SM A 28362.

ANATOMY OF THE EXOSKELETON. – As Lake's description is short, a few comments on basic morphology are appended. The cephalon has fairly slender but broad based genal spines, bowed outwards from the thorax; the eyes are small, sessile and panoramic, more or less globular in form, but with the long axis horizontal when the cephalon is aligned in the 'resting'

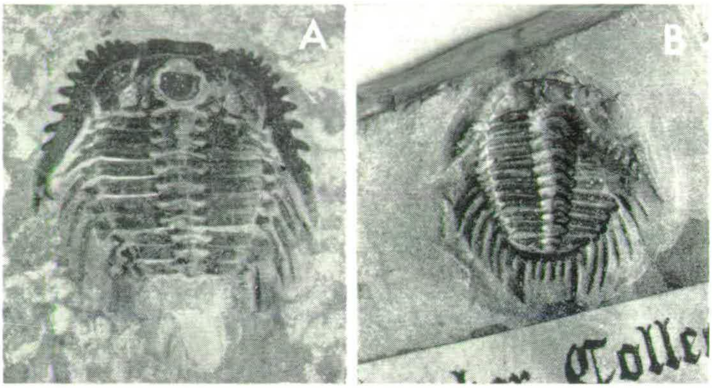

Fig. 4. A. *Leonaspis deflexa* (Lake). SM A 28362. Inverted specimen showing detached hypostome. B. *Leonaspis* cf. *coronata* (Salter) SM A 28350, showing anterior and posterior pleural spines, and the ridge encircling the pygidial margin. Both × 3. Wenlock Limestone, (Middle. Silurian), Dudley, England.

attitude. In such a posture the rear margin of the occipital ring slopes at about 25°, whereas when in the active attitude it becomes nearly vertical. There are 9 antero-lateral denticles on each side, the eighth being the longest and the ninth (counting from the front) a little shorter.

In the inverted specimen the hypostome is visible (Fig. 4A). It is broad and short, almost square in outline, and barely half the length of the cephalon. The hypostomal suture is straight.

There are ten thoracic segments, decreasing backwards in both breadth and height. The first two have shortened pleural spines, the other segments bear long slender backwardly curving pleural spines. The short peg-like anterior pleural spines project slightly forwards. They are best seen in the inverted specimens. The angle which the pleural spines make with the sagittal plane of the body likewise decreases posteriorly.

The pygidium is six-spined, the inner and outer pairs being shorter than the inner ones. It is noteworthy that the shorter spines, when seen in profile, are set at a different angle to the longer ones, and this feature enables a six-point support of the pygidium when resting. I have not seen an inverted pygidium of *L. deflexa*, but in the closely related species *L. coronata* (Salter), the inverted specimen SM A 28350, Fig. 4B, shows a low ridge running round the ventral border of the pygidium, whose ends abut against the two rows of anterior thoracic spines.

'RESTING ATTITUDE'. – The extended specimens studied are so well preserved that little restoration has been necessary to produce the profile views of the 'resting' body illustrated here. Figs. 5B and 6B have been drawn from BU H 258, and Fig. 6C from BU H 174, which lie on the bedding plane in precisely this resting attitude (Fig. 3). Accurate large scale drawings of the whole exoskeleton in profile were made from highly enlarged photographs, showing the height, size and angular relationships of the various components

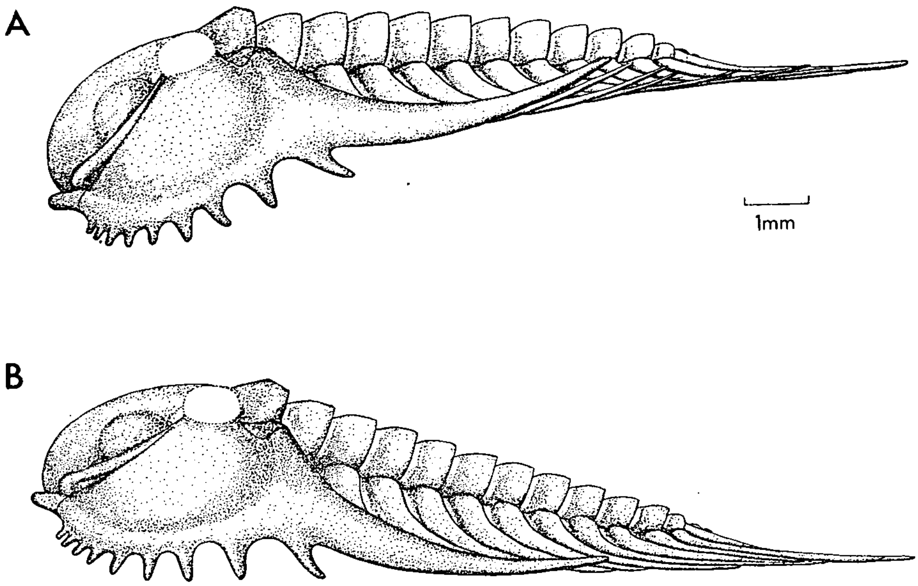

Fig. 5. Leonaspis deflexa (Lake). Reconstructions of the body in profile from BU H 258. A. Exoskeleton in the 'active' attitude (cf. Fig. 6A). B. Exoskeleton in the 'resting' attitude (cf. Fig. 6B and C).

of the exoskeleton, as they were preserved. Some of the thoracic segments in the specimens were slightly disorientated relative to one another, and in making the restorations they were realigned, with the posterior margins of their axes parallel with the rear margin of the occipital ring. A restored exoskeleton (Fig. 5B) shows that the tips of the pleural spines all lie in the same horizontal plane as the lowermost point of the genal spine and the tips of the anterior denticles; a clear indication that the resting attitude was truly functional. The thoracic axis is straight, declining backwards at about 10°, and terminating with anterior part of the pygidial axis. As previously noted, the angular offset of the various pygidial spines ensures that the pygidium shares in the support of the body. The resting attitude of the exoskeleton is not inhibited by the downwardly directed anterior pleural spines and the thickened ridge surrounding the pygidial margin, as these do not extend as far down as the sea floor.

Thus *L. deflexa* was capable of taking up a 'resting' attitude upon the sea bottom, having an open anterior arch, and with the weight of the body evenly distributed on the posterior antero-lateral denticles, the genal spines, and the distal parts of all thoracic and pygidial spines (with the exception of the short first two thoracic spines). The cephalon would be prevented from tipping forwards by the combined mass of the thorax and pygidium, and also by the counterweight of the genal and occipital spines.

'ACTIVE' ATTITUDE. – If the cephalon is tilted forwards through 25°, so that the anterior arch is closed, (Fig. 6A), and the occipital ring is vertical, then only a slight change in the articulation of the thoracic segments would bring the axial rings once more parallel with the vertical occipital ring, the thorax now being extended straight behind the cephalon (Fig. 5A). (N.B. This is the attitude in which Whittington (1956b, p. 206, Fig. 7) illustrated a species of *Leonaspis* and also *Diacanthaspis lepida* Whittington (ibidem p. 218, Fig. 10).) Here the genal spines point upwards and backwards at about 25°, but the posterior thoracic spines are horizontal. The exoskeleton of the trilobite in this attitude is quite streamlined, and thus it can be considered that this was a swimming or possibly browsing posture and may be defined as an 'active' attitude. It is noteworthy that whereas the hypostome, and thus presumably the mouth, is well clear of the substratum in the resting attitude, it could be brought down in close proximity with the sea floor in the swimming or browsing orientation. *L. deflexa* was undoubtedly functional in both attitudes, and the latter attitude may conceivably have evolved in response to a different method of feeding. *L. deflexa* was also capable of enrollment, which may account for the shortening of the first two thoracic spines.

Other species of *Leonaspis*

Whereas all the specimens of *L. deflexa* examined were preserved in the 'resting' attitude, a number of other species figured by Whittington (1956a) were lying in a posture more approximating to the 'active' posture. Richter & Richter (1952, Taf. 4, Fig. 27) figured a complete specimen of *L. aries* also in this orientation. All species of *Leonaspis*, and presumably also of *Primaspis* and *Diacanthaspis*, seem functionally capable of both modes of life. In some species there are other functional adaptations not apparent in *L. deflexa*. but which can be interpreted as of value in the life of the trilobite. Thus *L. coronata*, also from the Wenlock Limestone, has long pleural spines on the last five segments only, but these have flattened tips as though adapted for spreading the weight of the body over a wider area, when the trilobite was resting. Another apparent adaptation is that some *Leonaspis* species have a prominent occipital spine, protecting the neck-region, and covering the 'blind spot' between the eyes. Such adaptations are seemingly minor, and do not affect the general interpretation proposed here.

Function and evolution in odontopleurids

In an individual *Leonaspis* changing from the 'resting' to the 'active' attitude, the hypostome would be swung downwards and could be brought into close proximity with the sea floor. The permanent specialisation of *Dudleyaspis* would ensure that in a resting individual the hypostome would always lie close to the bottom. Such trilobites as phacopids and cheirurids did not possess this ability and the hypostome was always held high above the lowermost edges of the cephalon, between the lateral wings. This remarkable ability of the odontopleurids to change the position of the hypostome by forward rotation of the cephalon may not have been unique amongst trilobites, but it may nevertheless have been a determining factor in their ecology and evolution.

The hypostomes of odontopleurids are very short in the sagittal plane, and in the 'active' orientation of the cephalon in *Leonaspis* and others the posterior free edge of the hypostome is not far from the rostral plate. Whittington has shown that when the cephalon of *Acidaspis cincinnatiensis* is in a forwardly tilted position, the hypostome is approximately horizontal. The mouth must therefore lie near the sea floor. The anterior edge of the odontopleurid hypostome is almost plane, and rests against the straight posterior edge of the rostral plate. It may have been possible for the hypostome to articulate along this line, and if it were capable of motion through 20° of arc, the hypostome could lie horizontally in either the 'active' or 'resting' attitude. Otherwise the hypostome in the resting attitude would slope backwards and downwards, partially obscuring the anterior arch. This may or may not have been disadvantageous.

The mouth of trilobites has been generally considered to lie just behind the hypostome. Whereas in the majority of trilobites it must have been situated well above the plane of the horizontal genal spines (i.e., the sea floor in a bottom living animal), forward rotation of the odontopleurid cephalon may have allowed direct feeding from the sea bottom.

The high position of the mouth has been considered by many authors (Cannon & Manton 1927, Eriksson 1934, and Størmer 1939) as contributing towards the evidence for the trilobites being filter feeders. The evidence of the presence of the anterior arch, which could act as a channel for the flow of filter-feeding currents in stationary trilobites, tends to support this viewpoint, and one might suggest that the odontopleurids were a specialised group which adopted direct bottom feeding rather than filter-feeding, and thus that the reorientation of the cephalon in this family was connected with a change in feeding methods. All other factors connected with this reorientation such as the forward tilting of the eye, change or loss of function of genal spines, etc., may be considered as secondary.

Both methods of feeding may have been retained in *Leonaspis*, *Diacanthaspis*, and *Primaspis*, as in certain modern crustacea which feed by both filtering and raptatory mechanisms.

Whittington (1956b, p. 190) remarks that '*Acidaspis* and *Leonaspis-Primaspis* appear to be the root stocks of the Odontopleuridae', and he indicated that the pattern of evolution of this group was one of persistent main themes with relatively brief appearances of variation on these themes. He discussed (pp. 186–192) the stratigraphical range and possible evolutionary relationships of the genera of Odontopleuridae. It is probable that the *Leonaspis-Primaspis* stock, besides being morphologically and functionally intermediate between the specialised Odontopleuridae and their ancestral stock, may have been on or close to the direct evolutionary line of descent from which many later specialised types arose.

The change in the orientation of the cephalon and the body has, as already shown, the primary effect of lowering the mouth to the ground, but also has secondary effects upon certain organs, particularly the antero-lateral denticles, the genal spines, and the eyes.

ANTERO LATERAL DENTICLES. – Almost vertical denticles arranged in curving rows along the antero-lateral borders of the cephalon are found in trilobites of diverse groups. These short spines may be few and massive as in *Deiphon* and *Sphaerocoryphe*, or may resemble those of *Leonaspis* in being numerous and relatively slender. *Staurocephalus* (Cheirurina), *Glaphurus* (Komaspidae), *Pharostoma* (Calymenina), *Bouleia* (Phacopina), and *Corycephalus* (Phacopina), all have such denticles. In *Heliocephalus* (Dalmanitina) and *Coignouina* (Proetacea), they are arranged obliquely to the horizontal.

The function of such denticles is not known with certainty, but in some of these genera it may be connected with the enrollment of the trilobites. Salter (1865, Pl. 7, Figs. 14, 15a and 15b) figured enrolled specimens of *Staurocephalus murchisoni* (Barrande), in which the antero-lateral denticles interlock perfectly with the short thoracic and pygidial spines, aiding perfect enrollment. *Leonaspis* was also capable of enrollment. Barrande (1852, Pl. 37, fig. 4) figures an enrolled specimen of *L. leonhardi* (Barrande), in which the thoracic spines all lie inside these antero-lateral denticles, thus they do not interlock with them; there is no certain functional connection in Leonaspis between the faculty of enrollment and the presence of the denticles. In the specialised odontopleurids, in which the cephalon was permanently inclined forwards in the 'active' attitude, these denticles became adapted for the retention of the cephalon in that position.

GENAL SPINES. – In *Leonaspis*, *Diacanthaspis* and *Primaspis*, the genal spines are massive, and aided in the retention of the open anterior arch of the 'resting' cephalon. When the cephalon of certain Odontopleuridae became permanently adapted for life in the 'active' attitude, the genal spines which were then clear of the ground, lost their original function. In *Dudleyaspis* they became almost obsolete and reduced in size, so that they were hardly longer than the occipital and posterior marginal spines. All these spines probably functioned together as protection for the occipital region. The genal spines of *Ceratocephala*, however, became enormously extended, and more vertically inclined than horizontal, and together with the occipital spines, formed a corona at the back of the cephalon, whose function seems to have been chiefly that of protection, In other odontopleurids, e.g. *Acidaspis* and *Radiaspis*, the genal spines remained long and were permanently directed upwards and backwards.

Thoracic spines are normally much larger and usually project outwards, undoubtedly acting as protective organs, and probably also as stabilisers in swimming odontopleurids, The anterior thoracic spines are rarely visible. They are usually small and project vertically downwards (laterally in *Miraspis*). Some interesting adaptations of these spines again appear to relate to the forwardly tilted cephalon.

The posterior pleural spines of *Leonaspis* are strong and postero-laterally directed. They are apparently adapted for supporting the resting trilobite on the sea floor. In the swimming *Leonaspis* they become almost horizontal and so take up a stabilising position. The anterior spines remain minute, and when the trilobite is in the resting attitude, hardly reach the plane in which the tips of the posterior pleural, pygidial and genal spines lie. Their

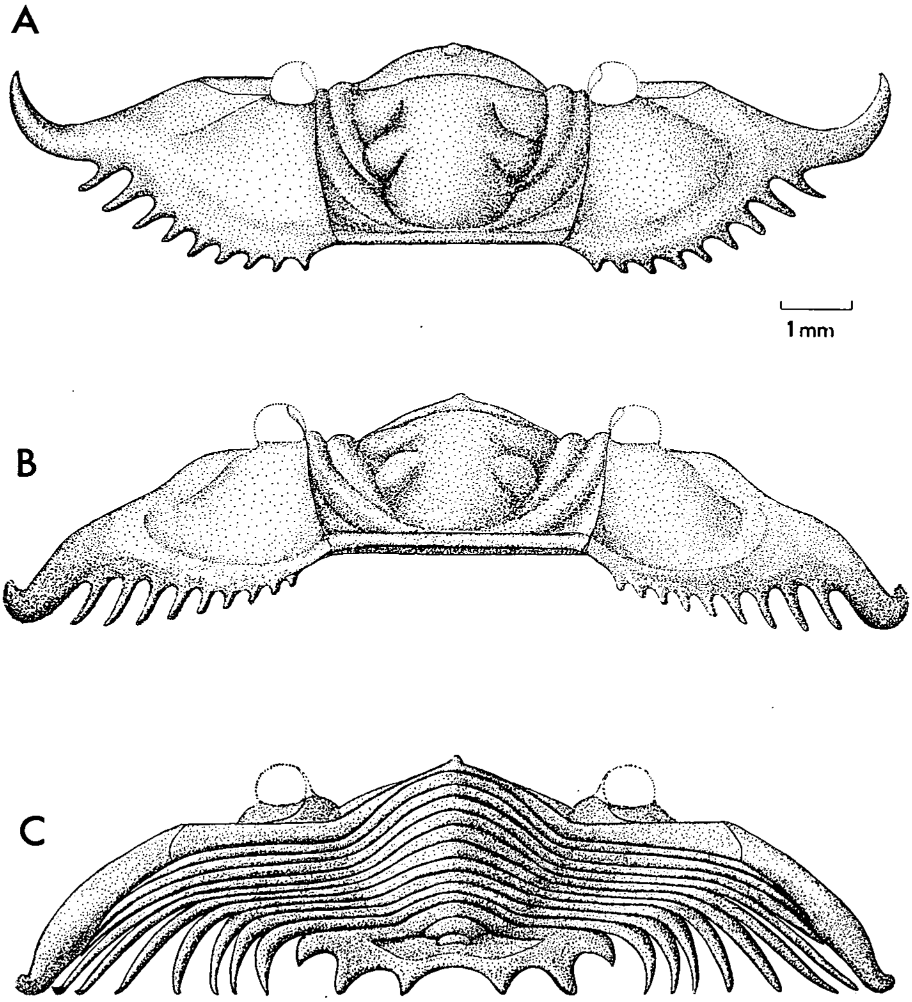

Fig. 6. Leonaspis deflexa (Lake). A and B. Reconstructions of the anterior view of the cephalon in the 'active' and 'resting' attitudes respectively, from BU H 258. cf. (Fig. 5A andB). C. Reconstruction of 'resting' exoskeleton in posterior view, from BU H 258 and BU H 174. (cf. Fig. 5B).

function is obscure, but it may be presumed that the gill appendages did not project outside them and they may have been protective in nature.

In the more specialised odontopleurids, where the cephalon is permanently tilted forwards, there are notable changes in the size and disposition of these two sets of spines. The anterior pleural spines of *Dudleyaspis* have not been visible in any of the specimens examined, but the large posterior spines, rather than being laterally directed, are bent downwards from the edges of the pleurae. As noted previously when the pygidium is lowered, their tips lie in the same plane.

In the small specimen SM A 28374 (Fig. 7A–C), the cephalon, thorax, and pygidium are perfectly preserved in what is almost their natural orientation to each other. The cephalon departs slightly from its true attitude and is tilted backwards a few degrees so that the tips of the anterior denticles do not quite lie in the horizontal plane. The almost vertical occipital ring, which is somewhat weathered so that the spines are missing, articulates with the thoracic segments, and the axial rings of the first six segments are parallel. The pleurae of these segments are all of the same height so that the tips of the pleural spines form a continuous plane with that passing through the tips of the anterior denticles. (If the cephalon were to be tipped forwards a few degrees, these would lie exactly in the horizontal plane.) The height of the last few thoracic segments decreases posteriorly so that the axial rings of the posterior part of the thorax and of the pygidium would be capable either of lying in the same plane as the preceding rings (in a fully outstretched individual), so that the pygidial spines became horizontal; or else relaxed so that the axis of the rear part of the exoskeleton was able to fall into a position in which the tips of all the posterior spines came to lie in the same horizontal plane as the anterior spines and anterior denticles of the sephalon. This specimen was buried and preserved as it lay

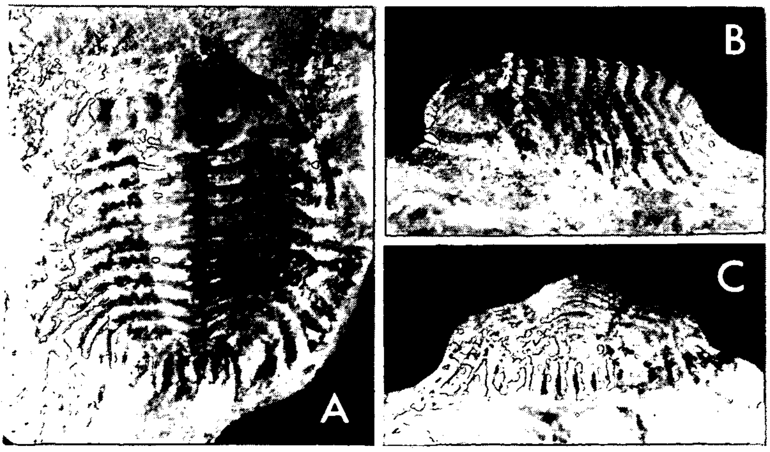

Fig. 7. Dudleyaspis quinquespinosa (Lake). A, B, C. SM A 28374. Exoskeleton in dorsal, lateral and posterior views. All Wenlock Limestone (Middle. Silurian), Dudley, England.

in the latter attitude with the tail region lowered, and all the anterior denticles, and the thoracic and pygidial spines touching the ground at once.

This seems again to indicate an obvious adaptation for bottom living, but the swimming ability of *Dudleyaspis* cannot be ruled out, for when the pygidium is raised the rear spines become horizontal, and the exoskeleton appears more streamlined, though less so than in *Leonaspis.*

The exoskeleton of *Ceratocephala,* with its corona of protective genal and occipital spines, does not appear adapted for rapid swimming. This is borne out by the massive development of the vertically directed anterior thoracic spines, for the tips of all except the most posterior, as seen in Whittington & Evitt's (1945, p. 57, Fig. 14) and Barrande's restorations (1852, Pl. 38, Fig. 6) again lie in a single plane. The posterior thoracic spines of *Ceratocephala* are horizontally directed, as are the spines of the pydigium. A certain amount of streamlining is apparent, but it is unlikely that such a heavily armoured trilobite could swim very far.

The comparatively unspecialised *Leonaspis* stock, with its dual mode of life, must have been much more versatile than the highly modified specialised odontopleurids, which no doubt accounts for the long stratigraphic range. The specialised forms appear to have occupied more restricted ecological niches, but in general, can be classified as vagrant benthos.

ACKNOWLEDGMENTS. – This work was begun in the Sedgwick Museum, Cambridge, under the supervision of Dr. M.J.S. Rudwick, to whom I am indebted for many stimulating discussions. I should also like to thank Professor O.M.B. Bulman for research facilities and Mr. A.G. Brighton, Dr. Isles Strachan, and Dr. C.D. Waterston for the loan of specimens in their care. (Specimens borrowed from the Sedgwick Museum, Cambridge, the Birmingham University Geological Museum and the Royal Scottish Museum, Edinburgh, are prefixed SM, BU, and RSM in the text.) I am also very grateful to Professor H.B. Whittington and Dr. D.L. Bruton for valuable discussions of some of the themes presented here. Mrs. C.M. Clarkson made many useful suggestions throughout.

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Sur une nouvelle espèce du genre *Crozonaspis* (Trilobite) découverte dans l'Ordovicien de la Mayenne

par Euan N. K. CLARKSON * et Jean-Louis HENRY **.

Planche I.

Sommaire. — Le genre *Crozonaspis* Henry, 1968 n'était jusqu'à présent représenté que par une seule espèce, *C. struvei*, abondante dans les schistes de Morgat (Llandeilien) de la presqu'île de Crozon (Finistère). Dans le département de la Mayenne, cette espèce existe au même niveau, associée à une forme nouvelle : *Crozonaspis kerfornei nov. sp.* Les recherches entreprises dans l'Ordovicien du Sud de Rennes (synclinorium de Martigné-Ferchaud) du Finistère et de la Mayenne permettent d'étendre à l'ensemble de la Bretagne de nouvelles observations portant sur la répartition géographique et les affinités des principaux genres et espèces de Trilobites.

Le Trilobite [1] décrit et figuré dans cet article provient des environs de Louverné, en Mayenne. Le matériel, conservé dans des nodules argileux et récolté par D. P. Oehlert et E. Buchot, est malheureusement peu abondant, mais son bon état de préservation et l'absence de déformation en ont facilité l'étude.

Les travaux consacrés à la révision des *Phacopina* ordoviciens du Massif armoricain sont encore incomplets, mais, dans l'Ouest de la France, le grand intérêt stratigraphique des représentants de ce sous-ordre est certain. Le genre *Crozonaspis* regroupe, en un ensemble homogène, des formes importantes dont l'extension verticale est le plus souvent restreinte au Llandeilien et dont la distribution géographique est vaste, puisqu'elle s'étend actuellement de la Normandie [2] et de la Bretagne au Portugal (Serra de Bussaco) [2]. La présence du taxon dans les « schistes à Calymènes » de May-sur-Orne retient particulièrement l'attention dans la mesure où ces schistes sont probablement d'âge llanvirnien [Doré et Philippot, 1962] ; le genre *Crozonaspis* apparaîtrait donc plus tôt en Normandie qu'en Bretagne.

I. Description paléontologique.

Superfamille **Dalmanitacea** Vodges, 1890.

Famille **Dalmanitidae** Vodges, 1890.

Sous-famille **Zeliszkellinae** Delo, 1935.

« Groupe de *Dalmanitina* » Struve, 1958.

Genre ***Crozonaspis*** Henry, 1968.

Espèce-type : *Crozonaspis struvei* Henry, 1968.

Crozonaspis kerfornei nov. sp.

Pl. I fig. 1 et 5 et texte-fig. 1 à 3.

Derivatio nominis : cette espèce nouvelle est dédiée à F. Kerforne.

Holotype : céphalon n° 585 (Pl. I, fig. 1) ; coll. Buchot.

Paratypes : pygidiums incomplets n° 586 (Pl. I, fig. 5) et n° 587 (non figuré) ; coll. Oehlert.

Locus typicus : lieu dit bois de Gondin, à 4 km environ au NW de Louverné (Mayenne).

Stratum typicum : schistes ordoviciens à nodules (Llandeilien).

Matériel : réduit pour le moment à l'holotype et aux deux paratypes.

Diagnose. — Une espèce du genre *Crozonaspis* caractérisée par les particularités morpholo-

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[1] Nous remercions M. P. Morzadec, qui nous a signalé la présence de cet échantillon dans les collections Buchot.

[2] Inédit ; actuellement en cours d'étude.

giques suivantes : céphalon très allongé suivant l'axe longitudinal de la carapace ; sillons glabellaires bien marqués mais fins ; sillon occipital étroit ; très large anneau occipital ; yeux moins fortement incurvés que ceux de *C. struvei* ; doublure céphalique développée dans sa partie axiale, mais réduite latéralement et apparemment dépourvue de sillon de fermeture (?) ; épine caudale du pygidium particulièrement forte.

Description. — *Céphalon.* Ogival et allongé suivant l'axe longitudinal de la carapace. La longueur totale (rostre et anneau occipital compris) est un peu inférieure à la plus grande largeur. La glabelle, en vue dorsale, a une forme élancée et elle est limitée latéralement par deux sillons dorsaux peu sinueux, étroits mais bien marqués ; comme chez *Crozonaspis struvei*, ces sillons remontent légèrement, en les entaillant, dans les parties latérales du lobe frontal. Les sillons glabellaires sont tous apparents, mais les sillons postérieurs (S 1) sont plus larges et plus profonds, bifurqués à leur extrémité interne ; les branches postérieures de ces fourches, très accusées, isolent presque les lobes latéraux postérieurs (L 1) rectangulaires. Les sillons glabellaires médians (S 2) sont convexes vers l'avant ; leurs portions distales, faiblement indiquées, s'infléchissent fortement vers l'arrière puis débouchent dans les sillons dorsaux. Les sillons antérieurs (S 3) sont peu sinueux et ne rejoignent pas les sillons dorsaux ; leurs extrémités internes s'incurvent parallèlement à l'axe de la glabelle. Le lobe frontal glabellaire porte antérieurement une granulation peu dense et, dans la région postérieure, une fossette axiale allongée. Le sillon occipital est profond, surtout latéralement, mais étroit et rectiligne dans sa partie médiane ; l'anneau occipital est large et s'élève, en vue latérale, au-dessus de la glabelle dont le profil retombe régulièrement vers l'avant. La convexité des lobes latéraux est relativement faible ; tout au plus peut-on noter un léger gonflement des lobes latéraux antérieurs (L 3).

Le bourrelet frontal est réduit, mais, dans l'axe du céphalon et en avant de la glabelle, il s'élargit brusquement en un rostre volumineux et arrondi qui correspond à un renflement de la doublure céphalique. En vue frontale, on remarquera la forte inclinaison des librigènes et des parties externes des fixigènes, à 55° environ par rapport à l'horizontale. Bourrelets marginaux bien indiqués sur toute leur longueur par des sillons qui recoupent vers l'arrière les profonds sillons postérieurs des joues. A l'exception des portions de fixigènes comprises entre les yeux et la glabelle, les joues sont entièrement sculptées de minuscules fossettes en « coups d'ongle » ; cette ornementation n'est visible que sur le moule externe.

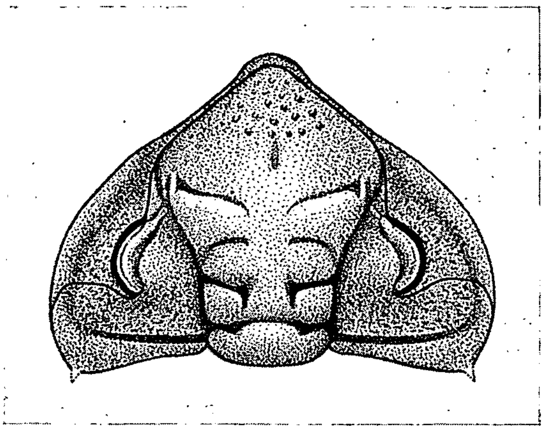

Fig. 1. — *Crozonaspis kerfornei nov. sp.*
Essai de reconstitution du céphalon en vue dorsale ; × 1,7 env.

Les branches antérieures de la suture faciale courent le long du lobe frontal glabellaire ; en vue dorsale, elles se rejoignent immédiatement en arrière du rostre en formant un angle obtus de 110° environ ; les branches postérieures suivent d'abord la courbe dessinée par l'œil ; leur tracé est ensuite rectiligne, puis elles s'incurvent rapidement vers les angles génaux et recoupent les bourrelets marginaux légèrement au-dessus des points d'intersection des sillons latéraux et postérieurs des joues.

A la face ventrale, la doublure est très développée dans sa région axiale, mais elle se réduit beaucoup latéralement et paraît dépourvue de sillon de fermeture (?). L'hypostome est inconnu.

Étude de l'œil. Dimensions : long. max. = 6,5 mm ; long. min. = 5,9 mm ; larg. max. = 2,7 mm ; larg. min. = 2,4 mm ; haut. (lobe palpébral compris) = 3,5 mm.

Terminologie descriptive : voir E. N. K. Clarkson [1966 *a*, p. 2-4, fig. 1] ; P. Hupé [1953, p. 76-81].

Description : les yeux sont proéminents, réniformes ; la surface visuelle subverticale est semblable à celle de *Crozonaspis struvei*. Vus en plan, le lobe palpébral et la surface visuelle sont toutefois plus allongés et moins fortement incurvés [3]

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[3] La différence de forme séparant les yeux des deux espèces est directement en rapport avec l'allure plus allongée du céphalon de *C. kerfornei*. Chez cette espèce, la largeur du céphalon atteint environ les 3/4 de celle de *C. struvei*. Le rapport de largeur des yeux a la même valeur. L'existence de cette relation peut être

(fig. 2). Le relief du lobe palpébral, le sillon palpébral très faiblement marqué et la présence de petites fossettes distribuées suivant un arc de cercle à proximité du bord externe du lobe palpébral sont des caractères comparables chez *C. kerfornei* et *C. struvei.*

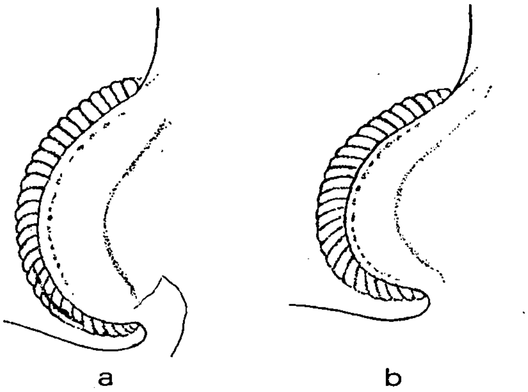

FIG. 2. — Différences morphologiques séparant les yeux des espèces *Crozonaspis kerfornei* (*a*) et *Crozonaspis struvei* (*b*). Pour la clarté des dessins, les rangées horizontales de lentilles n'ont pas été figurées. Vues dorsales ; × 5,2 env.

On compte 170 lentilles rangées en 27 files dorso-ventrales légèrement arquées, avec un maximum de 8 lentilles par file ; la distribution est la suivante :

œil gauche : 2 5 5 6 6 7 7 8 8 8 8 8 8 7 8
œil droit : — — — — — — — — — — — — — — —

œil gauche : 7 8 8 7 7 6 X X X X X X[4].
œil droit : — — — — — —[4] 6 6 5 4 3 2.

Chez l'unique céphalon connu de *C. kerfornei*, un hiatus peu important affecte les premières files, mais, par ailleurs, la disposition est parfaitement régulière. A la limite supérieure de la surface visuelle, une rangée horizontale accessoire s'étend de la file 14 à la file 26.

Les surfaces externes des lentilles sont fortement bombées et en saillie (les dimensions sont données ci-après). Les lentilles les plus volumineuses, situées dans la région centrale inférieure de la surface visuelle, sont séparées les unes des autres par une distance égale à leur rayon ; des lentilles plus petites apparaissent à la périphérie et aussi dans la partie centrale supérieure de la surface visuelle. L'espace interlenticulaire (sclera) n'est pas proéminent, mais forme au contraire une zone aplatie comportant, en quelques endroits, de petits renflements hexagonaux qui entourent les lentilles.

Les moules internes montrent de fins détails de la structure de l'œil. Les cupules des lentilles sont distinctes, bien que leurs bords soient encroûtés par une matière cristallisée ; cette même matière comble une grande partie de l'espace séparant les cupules (c'est-à-dire l'emplacement originel de la sclera), de sorte qu'il est difficile d'apprécier avec exactitude l'extension en profondeur de cette sclera. Près de la région centrale supérieure de la surface visuelle, la structure apparaît plus distinctement et l'on peut observer de légers sillons entre les cupules, sillons qui n'atteignent cependant pas le niveau de la limite interne des lentilles. Il semble que la sclera de *Crozonaspis kerfornei* était moins développée (en profondeur) que celle de *C. struvei.*

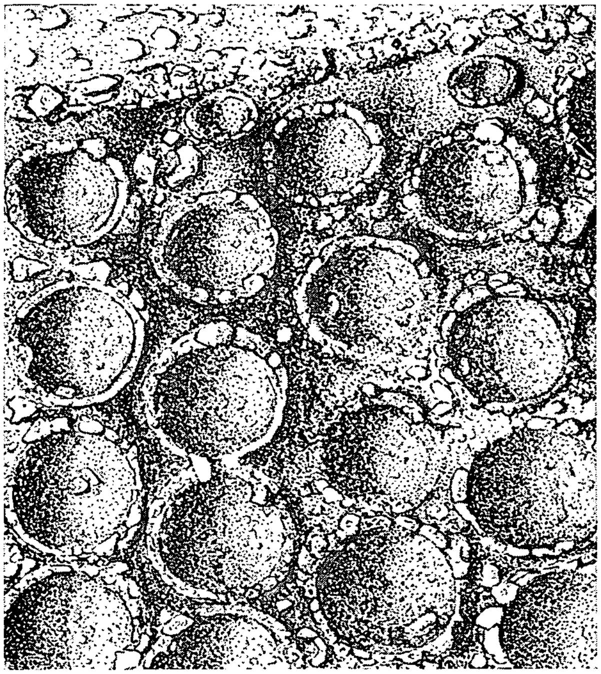

FIG. 3. — *Crozonaspis kerfornei nov. sp.*

Région centrale supérieure de la surface visuelle fortement grossie (œil gauche) ; dessin de l'empreinte en latex réalisée à partir du moule externe de l'holotype ; × 68 environ.

Il n'existe aucune trace de structures intralenticulaires, bien qu'elles aient pu exister. En effet, chez *C. struvei*, elles n'ont été observées que sur quelques individus. Mais, étant donné que l'on dispose et du moule interne et du moule externe

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géométriquement démontrée par la méthode des « grilles de transformation » de d'Arcy Thompson [1948, p. 1026]. La forme de l'œil, qui dépend donc étroitement de la croissance relative du céphalon dans une direction seulement, ne semble pas avoir de signification du point de vue adaptation.

[4] X = lentilles endommagées ; — = lentilles manquantes.

d'un même échantillon, la reconstitution de la forme originelle d'une lentille est possible. Les diamètres internes des cupules sont légèrement inférieurs aux diamètres des lentilles correspondantes sur le moule externe (respectivement 0,24 et 0,27 mm pour les grosses lentilles de la région centrale inférieure, 0,20 et 0,23 mm pour les lentilles de moyenne taille des régions périphériques) ; les lentilles n'étaient donc pas régulièrement biconvexes ; elles étaient formées d'un hémisphère externe volumineux et d'un renflement interne moins développé. Pour *C. struvei*, une telle reconstitution n'a pu être réalisée, le matériel récolté ne comprenant pas à la fois le moule externe et le moule interne d'un même œil.

Thorax. Le premier segment a été conservé avec le céphalon, mais il est trop incomplet pour que l'on puisse en donner une description précise. Il semble toutefois que le rachis thoracique était étroit et proéminent.

Pygidium. Le pygidium est connu en partie. Il ne paraît guère différent de celui de *C. struvei*. L'axe comporte probablement 7 à 8 anneaux, et les lobes pleuraux 5 côtes (?) bien délimitées par de profonds sillons pleuraux. Les sillons interpleuraux n'apparaissent jamais avec netteté, ni sur les moules internes, ni sur les moules externes. Une épine caudale particulièrement forte et large à sa base prolonge le rachis.

Dimensions. — Larg. max. du céphalon (holotype n° 585, Pl. I, fig. 1 *e-g*) = 31-32 mm ; long. max. = 24-25 mm ; long. de la glabelle, anneau occipital compris (Gn) = 23 mm ; longueur de la glabelle, sans l'anneau occipital (G) = 20 mm ; larg. max. du lobe frontal = 16-17 mm ; grand « index oculaire »[5] (A/G) = 32 % ; petit « index oculaire » (A/Gn) = 28 %.

Rapports et différences. — Les traits morphologiques séparant *Crozonaspis struvei* et *C. kerfornei* peuvent aisément se déduire de la diagnose donnée pour la nouvelle espèce ; nous les rappellerons toutefois brièvement. *C. kerfornei* possède un céphalon et une glabelle de forme plus allongée ; les sillons dorsaux, les sillons glabellaires, le sillon occipital sont beaucoup plus étroits et moins profonds ; l'anneau occipital est plus large ; la doublure céphalique semble dépourvue de sillon de fermeture (?) ; le rostre est légèrement plus volumineux et les yeux sont moins fortement incurvés. Les pygidiums paraissent très proches, mais l'épine caudale de *C. kerfornei* était sans doute plus volumineuse et plus courte.

On pourrait penser que toutes ces différences sont dues aux déformations subies par la carapace; une telle éventualité, dans le cas présent, ne doit pas être envisagée car les déformations sont extrêmement faibles. Les caractéristiques morphologiques essentielles de *C. kerfornei* résultent plutôt, comme nous avons tenté de le montrer, de la croissance du céphalon dans une seule direction.

II. Remarques sur la répartition géographique de quelques Trilobites ordoviciens dans l'Ouest de la France.

Les recherches poursuivies dans de nombreux gisements fossilifères riches en Trilobites nous conduisent à distinguer, en Bretagne, deux vastes régions fauniques bien individualisées au cours du Llandeilien [6] :

— Un « domaine nord » formé par le synclinorium médian armoricain qui s'allonge du Finistère (bassin de Châteaulin) au département de la Mayenne (bassin de Laval).

— Un « domaine sud » groupant les synclinaux paléozoïques du S de Rennes (synclinorium de Martigné-Ferchaud et synclinal d'Ancenis en particulier).

Nous étudierons brièvement dans ces deux grandes unités les associations de Trilobites et les variations qu'elles subissent durant le Llanvirnien, le Llandeilien et le Caradocien inférieur.

1. Llanvirnien. — Essentiellement schisteux, son épaisseur, de 110 à 130 m dans la presqu'île de Crozon (Finistère) et en Normandie (synclinaux des environs de Caen), est probablement la même dans le synclinorium de Martigné-Ferchaud. Riche en Graptolithes (genre *Didymograptus*), il ne renferme que peu de Trilobites généralement mal conservés ; il s'agit de rares *Asaphidae*, de *Synhomalonotidae* [*Neseuretus* (*Neseuretus*) *tristani*] localement abondants. *Dalmanitina* (*Eodalmanitina*) *macrophtalma*, l'un des plus anciens *Zeliszkellinae* connus en Bretagne, semble bien localisé à la limite Llanvirnien-Llandeilien où il accompagne souvent de nombreux Échinodermes Cystoïdes du genre *Calix* et les derniers exemplaires de *Didymograptus murchisoni*.

La distinction entre deux domaines nord et sud n'est pas encore très tranchée, bien qu'à proximité d'Ancenis (gisement fossilifère de Beau-

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[5] *Sensu* W. Struve [1958] ; A = longueur de l'œil.

[6] Ces considérations ne s'appliquent évidemment qu'aux Trilobites ; elles ne sont pas *a priori* valables pour les autres Invertébrés fossiles.

Soleil), P. Cavet et J. Pillet [1964 et 1968] aient découvert et décrit une faune de Trilobites (*Pricyclopyge, Placoparia, Colpocoryphe, Ormathops*) dont les relations avec les associations correspondantes de Bohême (couches llanvirniennes de Šárka) sont fortement accusées. Mentionnons aussi la présence, dans les départements du Finistère et de la Mayenne, de lits phosphatés riches en chamosite (bavalite) [7] ; ces lits, inconnus dans le synclinorium de Martigné-Ferchaud, ont conservé d'abondants Acritarches constituant un microbios homogène et caractéristique.

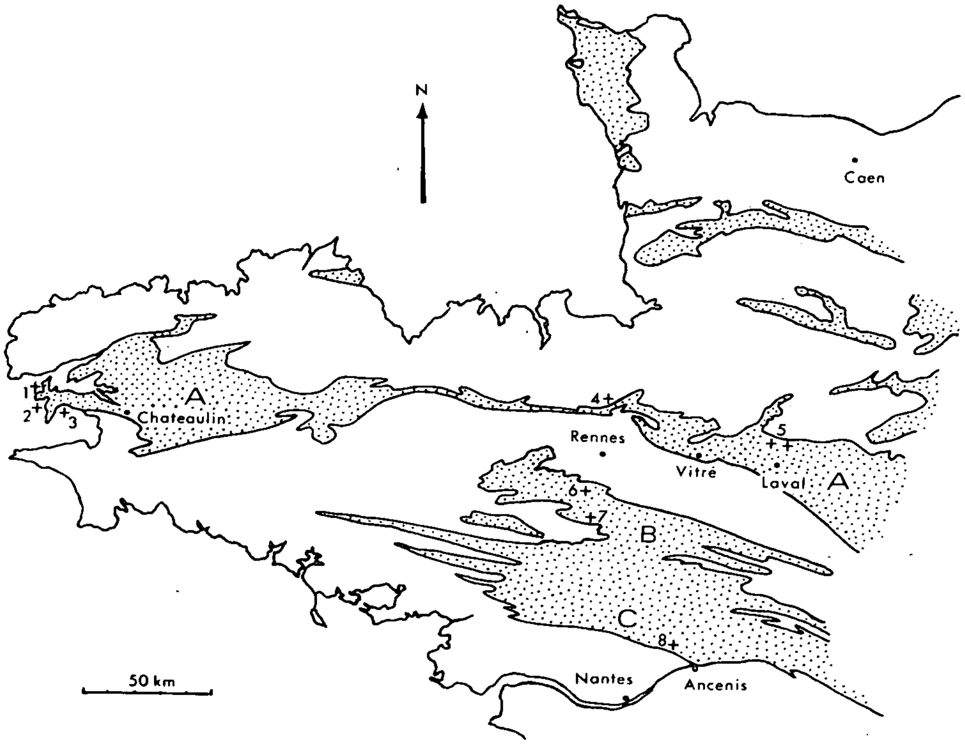

Fig. 4. — Carte schématique des formations paléozoïques sédimentaires (en pointillé) de l'Ouest de la France. D'après J.-J. Chauvel [1968].

A : synclinorium médian armoricain ; B : synclinorium de Martigné-Ferchaud ; C : synclinal d'Ancenis. — 1, 2 et 3 : schistes ordoviciens fossilifères de la presqu'île de Crozon (Finistère) (gisements de la Mort-Anglaise et du Courijou [1], du Veryac'h [2], de Morgat et de Postolonnec [3]) ; 4 : schistes llandeiliens des environs de Saint-Germain-sur-Ille (I.-et-V.) ; 5 : schistes llandeiliens des environs d'Andouillé (Mayenne) ; 6 : Traveusot-en-Guichen (I.-et-V.) ; 7 : schistes à nodules ordoviciens de Bain-de-Bretagne (I.-et-V.) ; 8 : gisement fossilifère de Beau-Soleil (Loire-Atl.).

2. Llandeilien. — Cet étage est représenté par un puissant ensemble de schistes à nombreux nodules siliceux, sans variations notables de faciès. En Ille-et-Vilaine, les schistes de Traveusot-en-Guichen, qui reposent sur le Llanvirnien à *Didymograptus*, contiennent quelques Graptolithes diplograptides (*Glyptograptus teretiusculus*) ; leur position stratigraphique est identique à celle des schistes de Morgat dans le Finistère et la Mayenne et ces deux formations ont sans doute le même âge. Les Trilobites ne sont pourtant plus les mêmes [8] :

a) Dans le synclinorium médian (domaine nord), les schistes de Morgat sont caractérisés par les principales espèces suivantes : *Plaesiacomia oehlerti, Neseuretus* (*Neseuretus*) *tristani, Phacopidella* (*Prephacopidella*) *hupei, Crozonaspis struvei*. Une zone (faunizone [9]) à *Marrolithus? bu-*

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[7] La présence de chamosite (bavalite) a été décelée par l'analyse aux rayons X (diagrammes de poudre, chambre Seeman-Bohlin 240 mm ; rayonnement non filtré du cobalt) ; raies essentielles : 14,58 Å ; 7,07 Å ; 4,63 Å ; 3,54 Å ; 2,80 Å.

[8] On remarquera à ce sujet que les Trilobites des « schistes à *Homalonotus oehlerti* » dans la Serra de Bussaco (Portugal) semblent identiques à ceux des schistes de Morgat ; par contre, pour autant que l'on puisse en juger, les genres et espèces de l'Ordovicien moyen d'Almaden (Espagne) sont très proches de ceux de Traveusot. Au Llandeilien, la distinction entre deux domaines fauniques pourrait peut-être s'appliquer à la péninsule ibérique.

[9] *Sensu* P. Hupé [1960].

reaui (Oehl.) souligne la limite supérieure du Llandeilien.

b) A Traveusot (domaine sud), *Colpocoryphe rouaulti* et *Kloucekia micheli* prédominent. L'apparition de formes telles que *Eoharpes guichenensis*, *Dionide sp.*, *Zeliszkella* (*Zeliszkella*) *torrubiae*, *Guichenia dufouri* marque d'évidentes relations avec les faunes ordoviciennes de Bohême. En dépit de longues recherches, *Plaesiacomia*, *Phacopidella* (*Prephacopidella*), *Crozonaspis* (ainsi d'ailleurs que *Marrolithus ? bureaui*) restent, à notre connaissance, inconnus dans le synclinorium de Martigné-Ferchaud.

Les Trilobites des « schistes à Calymènes » de Vitré (Ille-et-Vilaine) pourraient constituer une exception dans la mesure où ils semblent s'apparenter plutôt aux associations du domaine sud (Traveusot) ; c'est en effet de Vitré que provient l'holotype de *Guichenia dufouri*, *Zeliszkellinae* absent dans le reste du synclinorium médian [10].

3. Caradocien. — Les schistes de Raguenez dans le Finistère, la base des grès de Saint-Germain-sur-Ille au N de Rennes et dans la Mayenne, les schistes de Riadan dans le synclinorium de Martigné-Ferchaud appartiennent à la partie inférieure de cet étage. Les Trilobites des grès sont rares et encore peu connus, aussi est-il délicat de se prononcer à ce sujet ; mais l'homogénéité des associations dans les schistes, tant au S de Rennes et dans la presqu'île de Crozon qu'en Normandie (schistes d'Ecalgrain), est frappante. Au cours du Caradocien inférieur, la distinction entre un domaine nord et un domaine sud ne se justifierait donc plus. Les Trilobites importants sont : *Cryptolithus grenieri*, *Prionocheilus pulcher pulcher*, *Colpocoryphe lennieri* (Bergeron) [= *C. grandis* (Šnajdr)], *Dalmanitina* (*Dalmanitina*) *cf. socialis*, *Kloucekia dujardini*. Cette faune, bien que plus pauvre, est très comparable à celle des couches de Libeň et de Letná en Bohême.

Au Llandeilien, les associations de Trilobites des domaines nord et sud ont en commun un certain nombre de genres et d'espèces : *Eccoptochile*, *Placoparia*, *Colpocoryphe rouaulti*, *Neseuretus* (*Neseuretus*) *tristani*, *Kloucekia micheli*, *Uralichas heberti* (Rouault) [= *U. ribeiroi* (Delgado)], *Selenopeltis*... Il paraît donc difficile d'envisager l'existence de deux domaines paléogéographiques totalement isolés. Dans les sédiments actuels du delta du Niger, D. H. Porrenga [1967] a montré que le développement de la chamosite (= berthiérine, phyllite à 7 Å) dépendait étroitement de la faible profondeur (10 à 50 m) et de la température relativement élevée des eaux (supérieure à 20°). Si l'on peut admettre que la bavalite provient de la transformation d'une phyllite de type berthiérine [Caillère et Hénin, 1953] et que les conditions de formation de ce minéral étaient les mêmes au Paléozoïque, la présence de lits ou de bancs phosphatés riches en chamosite (bavalite) dans le Llanvirnien, le Llandeilien supérieur [11] et le Caradocien inférieur du synclinorium médian armoricain témoignerait en faveur d'une température élevée [12] des eaux et d'une faible profondeur de la mer ; la présence à proximité immédiate, au N de ce synclinorium médian, d'une cordillère cadomienne septentrionale [Pruvost, 1949 ; Chauvel, 1968] viendrait à l'appui de ce point de vue[13]. Du même coup, l'absence apparente de tels sédiments phosphatés à chamosite dans le synclinorium de Martigné-Ferchaud impliquerait des eaux probablement plus froides et plus profondes. Il n'est pas inconcevable de penser que ces facteurs aient pu avoir, directement ou indirectement (modifications des conditions de vie ou de milieu : extension ou disparition de champs d'Algues par exemple), une réelle influence sur la distribution géographique de certains Trilobites.

Cette hypothèse de travail, en supposant qu'elle s'avère exacte, ne suffira sans doute pas à tout expliquer ; si les associations de Trilobites du domaine sud montrent d'indiscutables affinités avec les associations correspondantes de Bohême, ces affinités — plus marquées dans le synclinal d'Ancenis que dans celui de Traveusot — s'estompent au Nord (synclinorium médian) et des formes originales comme *Crozonaspis* et *Phacopidella* (*Prephacopidella*) apparaissent. Dans l'état présent des recherches, on ne peut écarter *a priori* un éventuel rôle joué par des migrations et il sera nécessaire, à la lumière d'études plus complètes et détaillées, de reconsidérer entièrement ces problèmes, certains genres — tel *Kloucekia* — se développant plus tôt en Bretagne qu'en Bohême (voir V. Havlíček et J. Vaněk [1966, fig. 3]).

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[10] F. Kerforne [1901] signale la présence de cette espèce (sous le nom de *Dalmanites armoricanus*) dans l'Ordovicien de la presqu'île de Crozon. Il s'agit en réalité de représentants du genre *Crozonaspis*.

[11] Inédit.

[12] La découverte récente [Rohrlich, Price et Calvert, 1969] de pelotes fécales riches en chamosite (= berthiérine, phyllite à 7 Å) dans les eaux du Loch Etive (Ecosse), dont la température est comprise entre 6 et 12° C, indiquerait que l'influence de la température est discutable.

[13] M. J.-J. Chauvel a réalisé plusieurs analyses aux rayons X et a bien voulu nous faire part de ses recherches sur les minerais de fer de l'Ordovicien inférieur de Bretagne ; nous le remercions vivement de son aide.

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Légende de la Planche I.

Fig. 1 et 5. — *Crozonaspis kerfornei nov. sp.* ; schistes à nodules ordoviciens (Llandeilien) ; bois de Gondin, au NW de Louverné, Mayenne.

1 : céphalon n° 585, holotype (1 *a* : agrandissement de la partie centrale supérieure de la surface visuelle, moule interne de l'œil gauche ; × 45. — 1 *b* et 1 *d* : œil gauche, vues dorsale et latérale ; empreinte en latex tirée du moule externe ; × 7,5. — 1 *c* : moule interne de l'œil gauche vu latéralement ; × 7,5. — 1 *e*, 1 *f* et 1 *g* : céphalon (moule interne) en vues dorsale, latérale et frontale ; × 1,8. — 1 *h* : doublure céphalique ; × 1,8). — 5 : pygidium n° 586, paratype, en vue dorsale (moulage en latex) ; × 1,5.

Fig. 2 et 4. — *Crozonaspis struvei* Henry, 1968 ; schistes de Morgat (Llandeilien) ; presqu'île de Crozon, Finistère.

2 : céphalon incomplet (moule interne) n° POC 543, paratype (2 *a* : vue dorsale. — 2 *b* : doublure céphalique ; lieu dit Postolonnec ; × 1,8). — 4 : pygidium incomplet (moule interne) n° MAC 538, paratype, vue dorsale ; lieu dit la Mort-Anglaise ; × 2.

Fig. 3. — *Crozonaspis struvei* Henry, 1968 ; céphalon incomplet et déformé (moule interne) n° 588, vue dorsale ; schistes de Morgat (Llandeilien) ; Andouillé, Mayenne ; × 2.

Tous les échantillons sont déposés dans les collections du lab. de géologie et de paléontologie, Fac. des sciences de Rennes ; ils ont été blanchis au chlorure d'ammonium (fig. 1 *a-d*) ou à l'oxyde de magnésium (fig. 1 *e-h*, 2-5). Illustrations et photographies des auteurs.

Note de E. N. K. CLARKSON et J. L. HENRY

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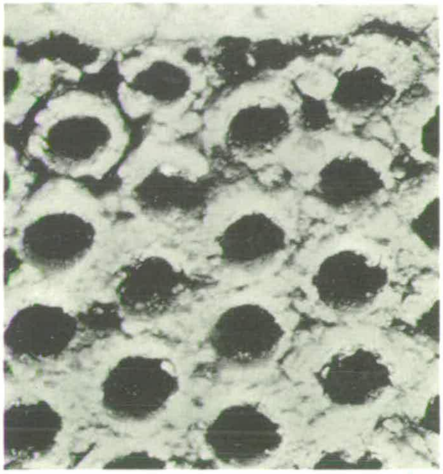
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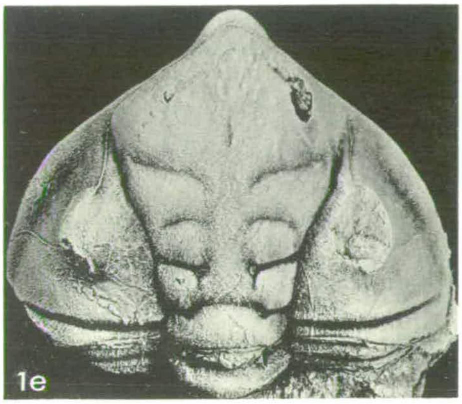
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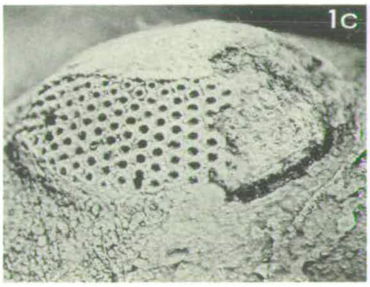
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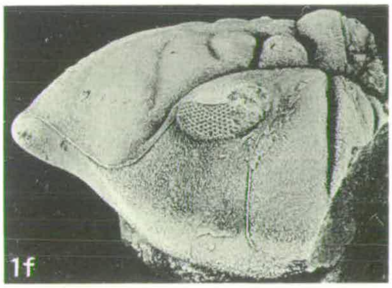
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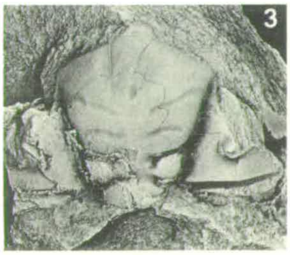
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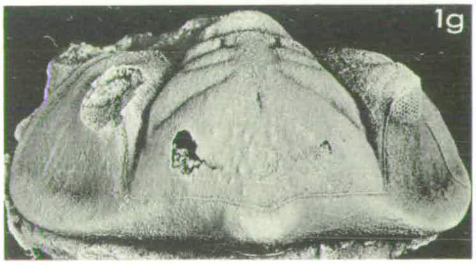
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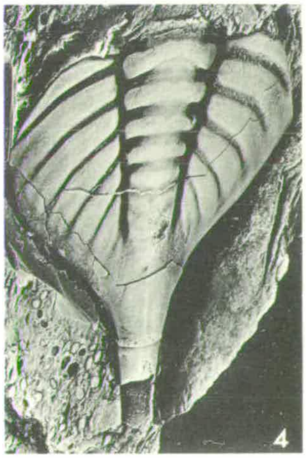
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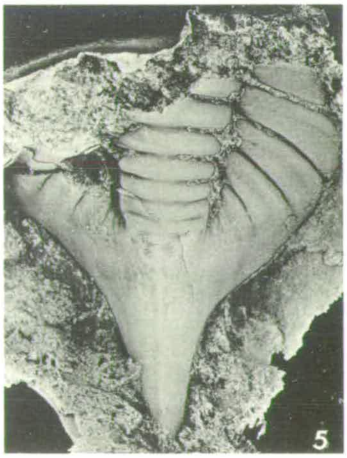
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ON THE EARLY SCHIZOCHROAL EYES OF ORMATHOPS *(TRILOBITA, ZELISZKELLINAE)*

E. N. K. Clarkson*

Résumé

Ormathops est l'un des genres les plus anciens des *Phacopina*. Toutes ses espèces ont des yeux schizochroaux dont les entilles sont grandes et éloignées les unes des autres; mais les yeux sont souvent de taille réduite. Les yeux d'*O. borni* Dean (Arenigien), de dimensions toujours normales, et les yeux parfois réduits d'*O. atavus* (Barrande), du Llanvirnien, sont l'objet le cette étude. Ces deux Trilobites possèdent, contrairement aux autres *Phacopina* connus, des lentilles de même taille listribuées irrégulièrement.

Un schéma est proposé pour le développement des yeux d'*Ormathops* et des autres *Phacopina*. Les différences s'expliquent si l'on tient compte de l'espacement constant des lentilles; chez *Ormathops*, les anomalies de répartition se comprennent ar des lentilles de même dimension, équidistantes, ne peuvent se disposer régulièrement sur une surface visuelle incurvée; 'est géométriquement impossible. Les autres *Zeliszkellinae* actuellement connus montrent des lentilles dont les dimensions ugmentent progressivement de haut en bas : le problème de leur distribution ne se pose donc pas.

Enfin, l'origine et l'évolution des premiers yeux schizochroaux est discutée.

* * *

I. INTRODUCTION

Compound eyes are present in the oldest known Lower Cambrian trilobites and were retained in most genera throughout the geological history of the class. Whenever eyelessness occurred, it was always secondary. These eyes are often well preserved and offer excellent potential for the study of a visual system in evolution.

The primary pattern of eye-structure, designated 'holochroal' by Clarke [1889] was already established in the earliest trilobites and persisted until their extinction in the late Permian. In eyes of holochroal structure the visial surface consists of very many, small, contiguous lenses covered by a common cornea. Whereas the external shapes of holochroal eyes show great variation within the class; globose, reniform, flattened, and ovoid forms having evolved independently many times over, it is clear that most, if not all, evolutionary changes in the preserved structure resulted solely from differential growth rates of the various parts. Evolution within holochroal eyes was largely a matter of permutations on a basic, established theme, involving modifications of eye shape and size, corneal thickness, and number, size and convexity of the lenses. This need not necessarily have been true, of course, for the unpreserved internal organs, (photoreceptors, nerve connections, and ganglia) as normally the external parts of the eye alone are preserved, and there is little record of the interior.

There is only one known instance, in all the 350 million years of trilobite history, of a radical and successful departure from the holochroal system to a quite different structural plan. This new visual system, the schizochroal eye, is confined to the suborder *Phacopina* (Ord. - Dev.) which arose in the Lower Arenig and persisted until the end of the Famennian. (The Harpina, (Ord. - Dev.) seem to have evolved independently a fairly similar system, but as each has only two lenses or less there is no real basis for comparison.)

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Schizochroal eyes often have relatively few lenses, but these may be very large, with a compound interior, and each has its own cornea and is separated from its neighbours by interlensar sclera [Clarkson, 1966a, b; 1967; 1969]. The *Phacopina* appear abruptly and cryptogenetically [Whittington, 1966]; there are no known intermediates between the earliest Phacopina and their late Cambrian ptychopariid ancestors, and so the origin of the schizochroal eye remains obscure.

This paper is concerned with the eyes of the first known *Phacopina*. These, though entirely schizochroal, and very clearly different from any holochroal pattern, were selected for detailed study in the hope that they might yield some information about the origins of the unique schizochroal system. There are only two very early genera of *Phacopina*, *Ormathops* and *Pterygometopus*, which appear more or less contemporaneously in the Lower Arenig, but in different faunal provinces. Whereas *Pterygometopus* does not seem to show any special features, *Ormathops* possesses a curious system of packing and arrangement of the lenses on the visual surface, which is here interpreted as primitive. The anomalous features of the visual surface, which are present in all the specimens I have examined, are described and elucidated in the following sections.

II. AGE AND RELATIONSHIPS OF ORMATHOPS

The trilobites suborder Phacopina consists of two super families, the *Dalmanitacea* (L. Ord.-U. Dev.), and the *Phacopacea* (L. Sil. - U. Dev.). *Ormathops* and *Pterygometopus*, the earliest dalmanitacean genera, belong to the subfamily *Zeliszkellinae* and the family *Pterygometopidae* respectively. Whereas the *Pterygometopidae* did not outlast the Ordovician, the *Zeliszkellinae* continued into the Silurian and were very probably ancestral to all the later Dalmanitacea. Struve [1962] has brought forward evidence that the *Zeliszkellinae* may also have given rise to the superfamily *Phacopacea*, though Eldredge (in press) on the basis of cephalic muscle scar patterns, suggests that the Phacopacea could have been derived from the *Pterygometopidae*.

Ormathops is the earliest known genus of the *Zeliszkellinae*, and first appears in the Arenig. Whittington [1966] suggested that it belonged to a short lived and sterile side-branch from the main line of dalmanitacean descent, and therefore was of little phylogenetic significance, but Henry's [1968] subsequent work on *Guichenia* casts doubt upon this interpretation. *Guichenia* is a Llandeilian genus with many characteristics intermediate between those of *Ormathops* and *Zeliszkella*; the latter genus like most other *Zeliszkellinae*, also appears first in the Llandeilian. It is thus quite possible that *Ormathops*, the earliest known zeliszkellinid, was ancestral to the later Dalmanitacea (excepting the *Pterygometopidae*), and thus occupies a most important phylogenetic position. This is certainly not proved, however, and the zeliszkellinid genera *Crozonaspis* and *Dalmanitina (Eodalmanitina)* have been found in the Llandeilian of Normandy antedating *Zeliszkella* [Henry, 1969].

Ormathops borni Dean is the earliest species, and possesses eyes of normal size. It is found in the Arenig (*Didymograptus extensus* zone) of south-western France. The rare *O. nicholsoni* (Salter), (possibly synonymous with *O. barroisi* (Kloucek)), *O. alatus* (Whittard), and *O. llanvirnensis* (Hicks), which appear in the British Llanvirnian, all have reduced eyes. Living contemporaneously in Bohemia were the reduced-eyes *O. barroisi*, and *O. atavus*, in which the eyes of different individuals range from large sized with 300 lenses or more to reduced with less than 50. There are a few other Llandeilian and later species from Bohemia; *O. inflatus* (Zelizko), *O. formosus* (Zelizko), and *O. mirus* (Snajdr), but these are less well known and have not been used in the present study and neither have the British Llanvirnian species on account of their poor preservation.

III. PREVIOUS WORK ON THE EYES OF ORMATHOPS

Like all other *Phacopina*, except the secondarily blind genera, *Ormathops* has schizochroal eyes, with large lenses separated by interlensar sclera. In *O. borni* and *O. atavus* the eye is well enough preserved for the structure to investigated in some detail. The eyes of *O. atavus* have often been referred to on account of the wide range in size and lens-number within the species. This was first recorded by Novak [1918, p. 38-41] whose work was published posthumously by Perner. Novak divided *O. atavus* into five subspecies, defined on the position and size of the eye, the lens-number, and the course of the facial suture. He gave the following ranges of lens-number for each subspecies : *O. atavus macrophthalmus* c. (300 lenses), *O. atavus transiens* (c. 250 lenses), *O. atavus atavus* (c. 150 - 200), *O. atavus intermedius* (70 - 80), *O. atavus microphthalmus* (50). The related *O. barroisi* has 15 - 20 lenses.

Richter & Richter [1926, p. 129, fig. 16] were doubtful as to the validity of this taxonomy, and preferred to regard the eye-variation as a true intraspecific reduction series. Struve [1958, p. 182-190], indicated that the boundaries between subspecies were by no means distinct and that in his material there in fact more intermediate grades than there were typical subspecies. He figured specimens showing these intermediate grades (ibid. Pl. 1, fig. 1-5). Struve did not, however, regard a continuous range in variation as entirely proved, and preferred to leave the question open until settled by statistical analysis of a large population. In the material available to me, very few specimens other than *O. atavus* have been represented. It seems probable that if *O. atavus* cannot be subdivided, as is most likely, then lens-number with respect to number of individuals would approximate a Gaussian distribution, the mode being in the *O. atavus atavus* range. It is clear, however, from ecent work by SELWOOD & BURTON [1969] that variation in the eye of some phacopids is a more complex matter than I or ther authors had realised, [BECKMANN, 1951; CLARKSON, 1966a, b] and the question of variation and subspeciation in *rmathops atavus* must be left open for the present.

Ormathops borni shows some variation in eye-size and lens-number, but variation is considerably less than in *O. atavus* nd there are no very large or small-eyed variants.

IV. EYE MORPHOLOGY OF ORMATHOPS

ORMATHOPS BORNI DEAN

1966 *Ormathops borni* DEAN : p. 292-297, Pl. 8, fig. 1-8, Pl. 9, fig. 1-13.
Text-fig. 1, b-l., Plate 1, fig. 1-6.

Material. Topotypes from DEAN's locality λ 16, Landeyran Valley, Montagne Noire, South-Western France. British Museum (Natural History), specimens BM In 56558, In 56587, In 56595, In 56599, In 57776, In 57788, In 57790, In 57806, and It 7700 were selected because the eyes were well preserved. They are all cephala, ranging in sagittal length from 2.4 (It 7700) to 7.6 mm (In 56558).

Preservation. The material is all preserved as decalcified internal and external moulds in a fine siltstone. There has been some crushing of the specimens but no apparent tectonic distortion. It is difficult to assess the original profile curvature of the visual surface in view of the slight crushing. The illustrations in Fig. 1 and 2 were all drawn from tracings of original photographs which seemed the most convenient way to allow rapid comparison.

Description. The eye is relatively small, reniform, and set in the anterior corner of the librigena, rising sharply from the visual surface. The eye indices [STRUVE, 1958] range as follows : A/G = 32-35 %, A/Gn = 26-29 %, H/A = 67-85 %. The palpebral lobe is slightly inflated and quite narrow, sharply delimited from the palpebral area by a pronounced palpebral furrow. Anteriorly the palpebral lobe is prolonged into a narrow vertical bourrelet which separates the eye from the cephalic axial furrow. The rear part of the visual surface has the strongest curvature. It is probable that the visual surface had a fairly low profile curvature, though this is difficult to assess. Lenses are distributed in dorso-ventral files, irregular in some parts of the eye, more regular in others. There are about 18-20 files, though the peculiar distribution makes it difficult to count them. Small specimens have 5-6 lenses per file, larger ones may have as many as 8-9, if the files are turned over at the top. Total lens number ranges from 68-108. Apart from the small, first formed lenses in the centre of the upper horizontal row, the lenses are all of the same size, and their spacing, even in irregular regions tends to be more or less constant (these features are not evident in later phacopids). The state of preservation gives little information on the surface ornament of the eye or of the internal structure of the lenses.

ORMATHOPS ATAVUS (BARRANDE)

1872 *Dalmanites atavus* BARR. : BARRANDE p. 28, Pl. 5, figs. 8-14, P. 15, figs. 8-14.
1915 *Dalmanites atavus* BARRANDE (and varieties) : NOVAK in PERNER p. 38-41, Taf. 3.
1935 *Ormathops atavus* (BARRANDE) : DELO p. 408-409.
1958 *Ormathops atavus* (BARRANDE) : STRUVE p. 185-186, Abb 6.
1959 *Ormathops atavus* (BARRANDE) : STRUVE *in* MOORE, p. 473-474, Fig. 375 (5a).
Text-fig. 1a, 2a-j, Plate 1, figs. 7-16.

Material. Topotypes from the Sarka Formation (Llanvirnian) (Étage d 1) of Barrande, mainly from Osek, Bohemia. Of many specimens in the British Museum (Natural History), Royal Scottish Museum, Sedgwick Museum, and Grant Institute of Geology, the following were selected as their eyes were well preserved. All the specimens examined save two of « *O. atavus microphthalmus* » have between 160 and 190 lenses so could be referred to « *O. atavus atavus* » of NOVAK. As discussed previously the subspecies are probably invalid but NOVAK's names are retained for convenience.

O. ATAVUS ATAVUS (BARRANDE)

BM 42588 (a), 42577 (b), I 4174, It 232, I 3739, SM 48944, A 48917.

O. ATAVUS INTERMEDIUS (NOVAK)

It 221 (eyes unfortunately damaged)

O ATAVUS MICROPHTHALMUS (NOVAK)

It 233, I 15221

O. ATAVUS BARROISI (NOVAK)

It 241, It 243 a, b. (eye structure very poorly preserved).

O. atavus is considerably larger than *O. borni* and cephalic length (sagittal) ranges from 14 to 22 mm in the materia examined.

Preservation. All the specimens are internal moulds, excepts I 15221, It 221, and It 243b. They are preserved in dar coloured decalcified nodules and show no evidence of crushing or other distortion. In the eyes only pit-like cavities remai to mark the place of the lenses. These were represented as black dots on the drawings (fig. 2) on account of their variabl preservation.

Description. Typical specimens of *O. atavus atavus* have moderate sized eyes set in the anterior corner of the librigenae Eye indices size as follows : A/G = 30-37 %, A/Gn = 25-31 %, H/A = 100-125 %. They are broadly similar to those o *O. borni*, though there are certain specific differences. Thus the palpebral lobe is narrow, flat, and horizontal, shelving inward anteriorly towards the rear. There is a narrow sharp palpebral furrow inside which the palpebral area rises quite steeply The anterior bourrelet, so pronounced in *O. borni*, is here indistinct and there may even be a recessed area in its place betwee the anterior edge of the eye and the axial furrow. The profile curvature of the visual surface is quite distinct and shows moderate curvature, so that a visual field would be subtended with a longitudinal extent of about 5° to 165°, and a latitudinal exten of 0° to 40° [vide. CLARKSON 1966a, b]. Lens-axes cover this whole area but are primarily concentrated in the upper par of the visual field, as the lower part of the eye is the more strongly curved.

Files are irregular, but number 25-25 altogether (including incomplete or anastomosing files). The longest files hav from 9-10 lenses and there may be 160-180 lenses in all. Apart from the lenses in the centre of the upper horizontal rov they are all of the same size. In a few specimens, notably BM 42588 (i) and (ii) intralensar bowls are preserved (Fig. 1a like those previously described in *Crozonaspis struvei* HENRY [HENRY 1968, CLARKSON 1968]. They show that the lense were compound at this early stage in schizochroal eye evolution. Lenses are sometimes elliptical and are always highly convex (Pl. 1, fig. 14). Eyes with fewer lenses are smaller and are more flattened against the visual surface, so that the narrow palpebra lobe rises upwards to the glabella and the palpebral lobe is less distinct. Relative to eyes of *O. atavus atavus*, those of *O* *atavus intermedius* and more particularly of *O. atavus microphthalmus* have been reduced anteriorly, ventrally, and posteriorly so that the shape and position of the visual surface can be compared with the upper central region of an eye of *O. atavu* *atavus*. The eye indices of *O. atavus microphthalmus* range as follows : A/G = 20-25 %, K/Gr = 16-20 %, H/A = 170-240 %

It 221 *(O. atavus intermedius)* is broken but shows clear irregularities. BM In 15221 *(O. atavus microphthalmus)* has 47 lenses in the left eye and 44 in the right. It 233 has 42 and 37 respectively. Between 12 and 14 files can be distinguished but as in the eyes of « *O. atavus atavus* » the pattern in left and right eyes is different. The visual field extends from abou 35°-115° of longitude to 20°-40° of latitude.

V. LENS — DISTRIBUTION IN ORMATHOPS

There are three definite features which distinguish the eyes of *Ormathops* functionally from those of later *Phacopina*. Firstly, the lenses, apart from those in the centre of the upper horizontal row, are all the same size. Secondly, even in areas of irregular distribution, they are all more or less equally spaced. Finally, though there is a broad distribution into a pattern of hexagonal close packing, this is never entirely regular and I have not seen any specimens which (in spite of BARRANDE's illustration of the eye (1872, pl. 5, fig. 11)) do not exhibit some degree of irregularity. The pattern, furthermore is not the same in different individuals or between the two eyes of the same specimen. Irregularity, then, is the rule in *Ormathops* whereas it is encountered but rarely in other *Phacopina*.

The disruptions affecting the regularity of distribution are most frequently found in the same general area of the visual surface, that is, the region of maximum curvature of the eye, behind the transverse plane. There may also be irregularities in the more anterior regions. The examples referred to below are mainly of *O. atavus* but these observations hold good for *O. borni* also.

Examination of many specimens has shown that there are only two main kinds of disruption, which are as follows :

(1) **Caesurae** *(Latin — « separations »)*. Since the lenses are equally sized and spaced the files are parallel, or at least there may be blocks of several parallel files. In such an example as It 232 (Text-fig. 2h) each block is abruptly truncated along a vertical line, against which the files of another and differently orientated block rest. This line of separation is here termed a « caesura ». There are two caesurae in It 232, on either side of which the lenses are arranged in a regular sequence, whereas 42588 (i) (Text-fig. 2a) only has one, upon one side of which the lenses have a rather haphazard pattern. Sometimes as in I 4174 (Text-fig. 2j), the caesura is of small effect, resulting in the interpolation merely of a short extra file. Usually, however, this is combined with a change in packing in the upper part of the visual surface.

(2) **Packing changes.** Specimen A 48944 (Text-fig. 2d, e) shows a remarkable change in the manner of packing of the lenses in the upper part of the visual surface. These are comparable changes in *O. borni* (Text-fig. 1j-1). When such changes are

present they are always in the same general area. They may occur by themselves or combined with a minor caesura. Usually the change in packing allows near-constant spacing of the lenses on the visual surface, but the curving of the files over towards the top results in an anastomosis of rows and files. Such packing changes are not uncommon.

VI. INTERPRETATION OF IRREGULARITIES IN LENS DISTRIBUTION

It is generally understood that quite complex biological structures can develop under the direction of relatively few and simple genetic instructions. Thus Raup & Mitchelson [1965] and Raup [1966] have written simple computer programmes which generated graphically models of echinoid ambulacra and various kinds of coiled shells. Gould [1970] discussed the principle fully with reference to these and other examples. Similarly in *Ormathops* on the one hand and in « regular » *Phacopina* on the other, « programmes » governing lens-packing can be deduced, differing in only minor ways in the two instances, but having quite different effects as a result of elementary geometrical principles.

(a) Lens size and spacing relationships.

In all *Phacopina* there seems to be a clear relationship between lens size and the spacing apart of the lens-centres. Various examples described previously [Clarkson, 1966a, b; 1967; 1969] show that where dorso-central files are strongly divergent ventrally, the lenses increase in size downwards in (normally) direct proportion to their spacing. Likewise wider spacing of lens-centres at the front and rear of certain eyes allows the development of exceptionally large lenses. Conversely *Dalmanites* has some files at the front and rear of the eye which converge ventrally, and the lowest lenses are correspondingly small. In *Ormathops*, the same rule applies, for the files (when regular) are parallel, and the lenses are all of the same size.

The lens dimensions eventually attained seem therefore to have been governed, in all instances, by the original distance apart of the lens-centres. Presumably the lenses continued to grow whilst they had room, and further growth may have been inhibited finally because of the relative proximity of neighbouring lenses. With each ecdyis the trilobite grew and the lens centres moved further apart so that the lenses having attained their correct relative size then all continued to grow together as the trilobite grew. In all *Phacopina,* including *Ormathops*, the lenses in the centre of the upper horizontal row are small. This probably resulted from growth-inhibition by the proximity of the downwardly bowed edge of the palpebral lobe, or the facial suture.

The internal arrangement of the photoreceptors, as I discussed previously [Clarkson, 1967] is probably in some way relevant to variation of lens-size on the visual surface, but this may be incidental, rather than primary.

(b) Development of hexagonal close packing.

Schizochroal eyes developed first by producing a single horizontal row and then by adding new lenses in regular sequence along the lower (ventral) margin of the eye where the linear generative zone lay [Beckmann, 1951; Clarkson, 1966a]. Sometimes an accessory upper horizontal row developed in the rear part of the eye above the first formed row, if there was room. The typical system of hexagonal close packing, which allows the largest possible number of lenses to be contained in a unit area, could have been achieved by the following simple rules governing development.

First the upper horizontal row was initiated in which the lens centres were of equal spacing (x). The lenses grew to a size determined by the proximity of the palpebral lobe. Secondly, during growth of the visual surface at ecdysis, new lenses arose whenever a critical threshold spacing (y) was reached vertically between the line of the first formed lenses and the generative zone below (y) is always less than (x); where the diagonal rows are at 45° then $x = 2y$. (x) and (y) increase as the specimens grow in size but always remain proportional, and as they increased the lenses grew during several ecdyses. The lenses of the second horizontal row could only have developed below and in between the lenses of the upper horizontal row and equidistant from them, as their initiation was elsewhere inhibited by the proximity of existing lenses. Thus, the foundation for a hexagonal packing system was laid which was completed by the continued action of the rules of growth. Lenses continued to develop whenever the critical threshold (y) was attained in any direction; the final growth-inhibiting factor may have been the proximity of the lower margin of the visual surface when it had attained its adult shape.

(c) The unique lens-packing system of Ormathops.

Even though the lens-packing system in *Ormathops* appears widely different from that of other Phacopina, the same kind of programme was still responsible for both. The only difference lay in the spacing of the new lens-centres in the generative zone. In *Ormathops* the original spacing (x) established in the upper horizontal row, was retained in all subsequent rows. Other phacopids however changed the spacing (x) with each new horizontal row, normally increasing it by a constant arithmetical factor. The dorso-ventral files thus came to diverge downwards, Clearly, the lenses of *Ormathops* likewise developed when spacing had reached a critical threshold because (I) where there are packing changes the spacing is more or less constant, (II) caesurae are usually present in the most highly curved parts of the eye where there was available space, (III) the observed different patterns of lens packing could have been associated with small intraspecific differences in surface curvature, affecting development.

Irregularities occurred in *Ormathops* because it is geometrically impossible to pack lenses of constant size and spacing on a conical surface in a regular pattern. If the visual surface were vertical there would have been no packing problems, bu because it approximated a segment of a cone irregularities inevitably arose as a compromise solution to several incompatible and conflicting requirements. The downward expansion of the visual surface meant that parallel blocks of lenses would usually in the more curved regions, separate, leaving spaces each of which would be filled with a new lens, usually out o phase with the others. Subsequent lenses would be produced in series with the newly formed lenses, leading to distinct blocks of lenses separated by caesurae. Packing changes are another somewhat less regular answer to the same problem, again size and spacing are constant, but regularity is disrupted.

It is strange that the rather cumbersome lens-packing system of *Ormathops* was retained for so long (Lower Arenig to late Llanvirn). After all, an entirely regular system could have been achieved merely by increasing the spacing between lens-centres with each new horizontal row, as was the norm in other *Phacopina.* The reason was probably a matter of physiology. It may have been more difficult for the trilobite's nervous system to process and integrate light impulses coming through a serie of different sized apertures than to deal with light received through lenses of constant size. Change from the *Ormathops* system, with its equidimensional lenses, to a system with regularly arranged, though different sized lenses, may not have been possible until the nervous system had achieved a level of complexity in powers of integration to make such a change functionally possible.

Ormathops is the only genus which possesses the primitive lens packing system discussed here. Its probable derivative *Guichenia*, and also *Zeliszkella*, have larger eyes with a much greater number of lenses. These are graduated in size, and are regularly packed, as is the case in all other *Zeliszkellinae*. *Ormathops*, on its first appearance in the Arenig, had established a fully schizochroal eye, but had not yet evolved a stable lens-packing system. This study therefore focuses attention on the last stages of a process of very rapid evolution, which had resulted in the production of an entirely new kind of visual system. Final stabilisation of lens-packing, though it would no doubt improve the efficiency of the eye, was secondary to the initial stages of evolution, which are still obscure. Once this stabilisation had taken place, all observable changes throughout the history of schizochroal eyes seem to be the result of allometric change alone.

What are not yet fully understood are the initial stages of this rapid, non-allometric evolutionary process and the genetic mechanism underlying such a change. It is not unlikely, however that the initial change from a holochroal to a schizochroal system resulted from neotenous retention of juvenile characters into the adult stage.

There is as yet no direct evidence of this in the trilobites but in some recent crustaceans and insects it is known that during early development a group of relatively large « simple eyes » is replaced by a compound eye with much smaller, contiguous lenses. If trilobite eyes developed in the same way then adult retention of the « simple-eyed » system could have been the first step towards the kind of schizochroal eye seen in *Ormathops.*

Such a change in organisation would no doubt have involved modifications of the structure of the unpreserved parts and in the integrative action of the nervous system as great as those changes which are actually visible.

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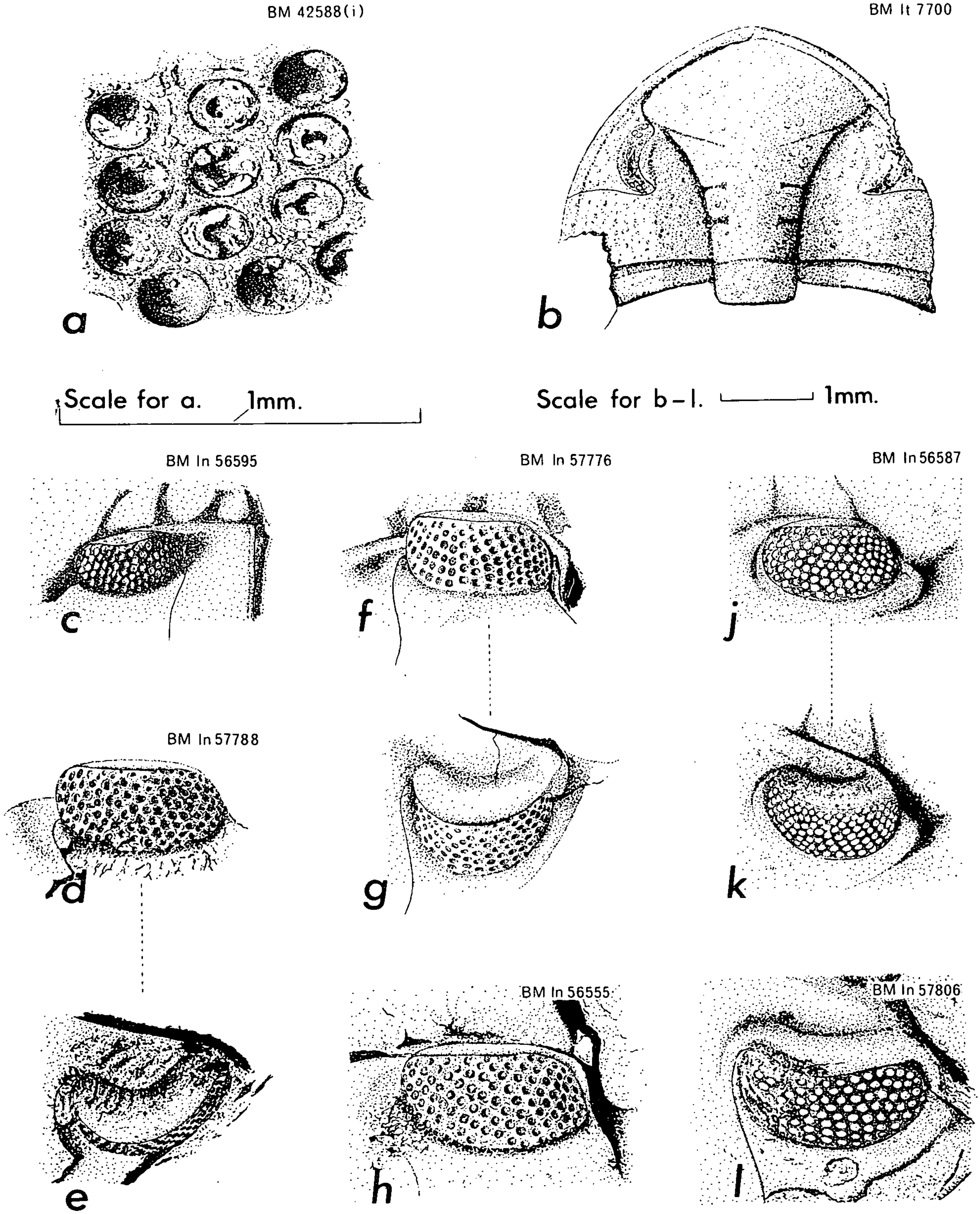
FIG. 1

a. *Ormathops atavus atavus* (Barrande). Sarka beds (Llanvirnian), Osek, Bohemia. Central part of visual surfac showing intralensar bowls.

b-l. *Ormathops borni* Dean. Couches du Landeyran (Arenig), Montagne Noire, France. Eyes of various specimer showing irregularities in lens distribution. j, k and l are external moulds in latex; the others are all original internal mould (*vide* Plate I, figs 1-6).


BM 42588(i)
BM It 7700
a
b
Scale for a. 1mm.
Scale for b – l. 1mm.
BM In 56595
BM In 57776
BM In 56587
c
f
j
BM In 57788
d
g
k
e
BM In 56555
h
BM In 57806
l

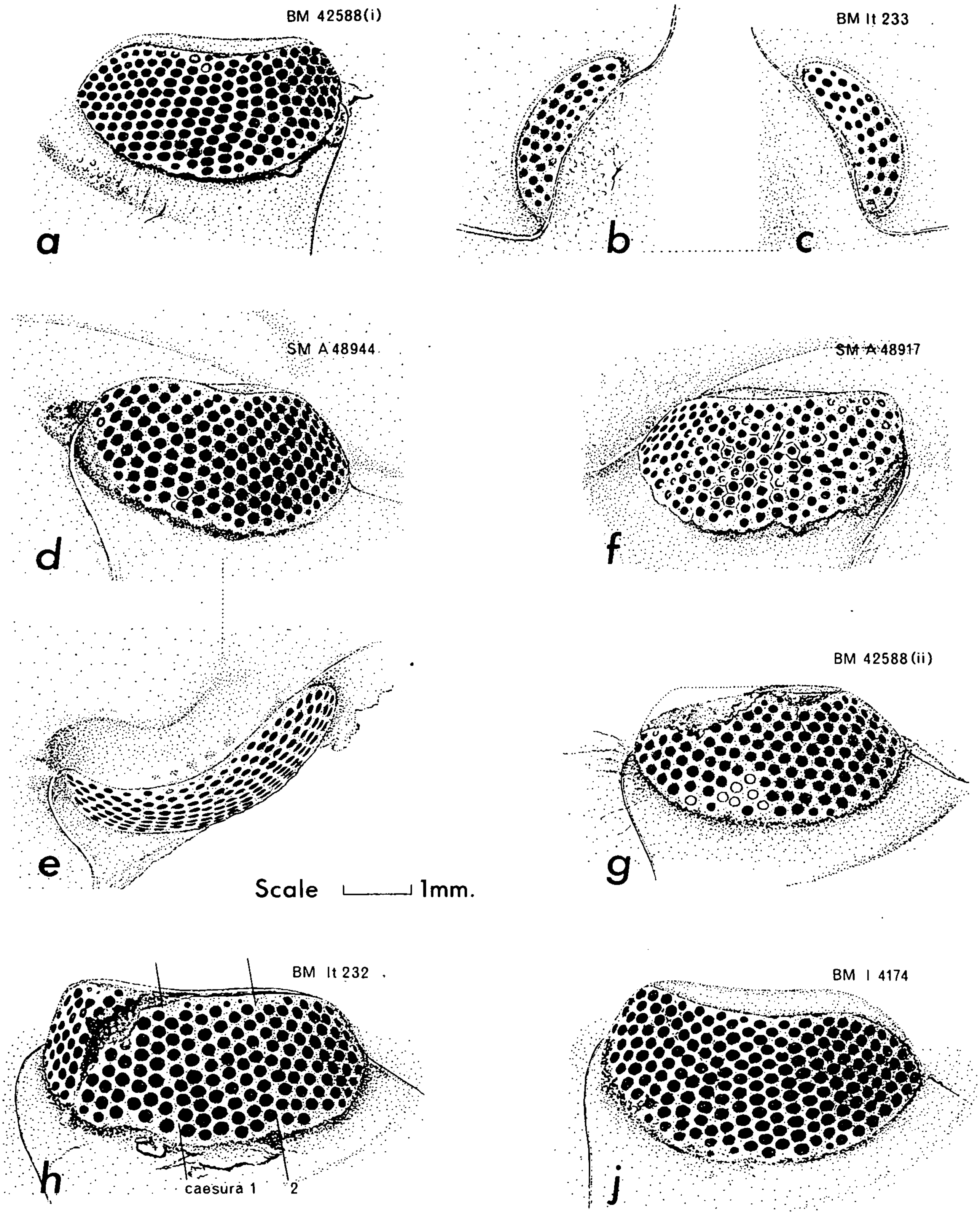

BM 42588(i)
a
b
BM It 233
c
SM A 48944
d
SM A 48917
f
e
Scale 1mm.
BM 42588(ii)
g
BM It 232
h
caesura 1
2
BM I 4174
j

PLATE I

Ormathops borni DEAN.
Couches du Landeyran supérieur (Arenigian).
Dean's (1966) locality 16, near southern end of the Landeyran Valley, Montagne Noire, France.
1 : BM In 56595, left eye x25 (*vide* Text-fig 1c).
2 : BM In 56587*, right eye x25 (*vide* Text-fig 1g).
3, 4 : BM In 57776, right eye from the side and from above x25 (*vide* Text-fig. 1f, g). **5** : In 57788, right eye x25 (*vid* Text-fig 1d, e).
6 : BM In 56555, right eye x25 (*vide* Text-fig 1h).
7, 8. *Ormathops atavus microphthalmus* (NOVAK).
Sarka beds (Llanvirnian), Osek. Bohemia.
BM It 233, left (7) and right (8) eyes x12 (*vide* Text-fig 2b, c).

9-16. *Ormathops atavus atavus* (BARRANDE).
Sarka beds (Llanvirnian), Osek, Bohemia.
9 : BM 42588 (i) left eye x12 (*vide* Text-fig 2a).
10, 11 : SM A 48944, right eye from the side and from above x12 (*vide* Text-fig 2d, e). **12, 13** : SM A 48917, left eye fron the side and from above x12 (*vide* Text-fig 2f). **14** : BM 42588 (i)* external surfaces of lenses near the posterior edge of th eye x50. **15** : BM 42588 (ii) right eye x12 (*vide* Text-fig 2g). **16** : BM It 232, right eye x12 (*vide* Text-fig 2h).

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* Specimens marked with an asterisk are external latex moulds. All others are internal moulds, original except for BM It 232 and 233 which are fibreglass. All specimens are whitened with ammonium chloride.
Specimens prefixed BM are from the British Museum (Natural History), London; SM refers to the Sedgwick Museum, Cambridge.


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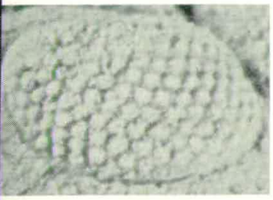
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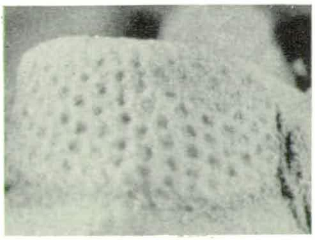
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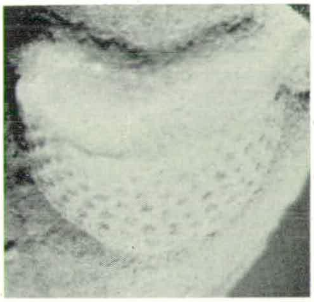
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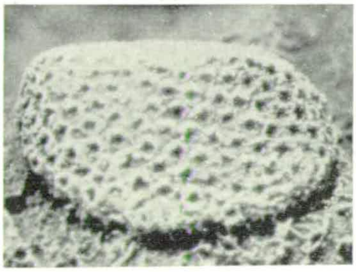
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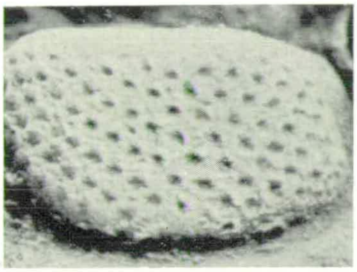
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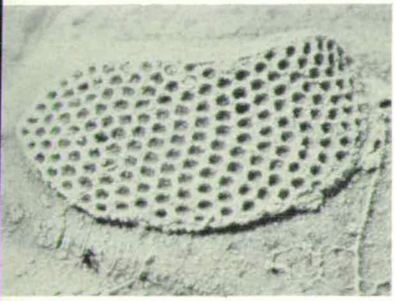
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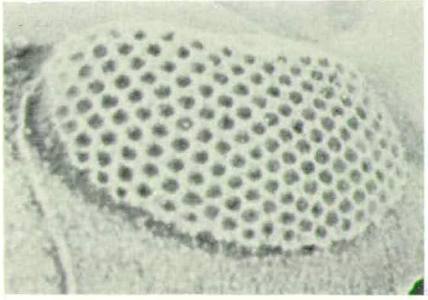
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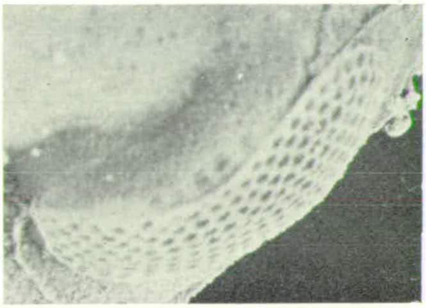
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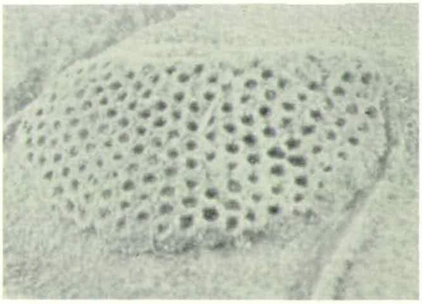
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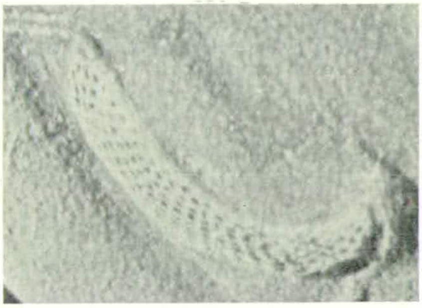
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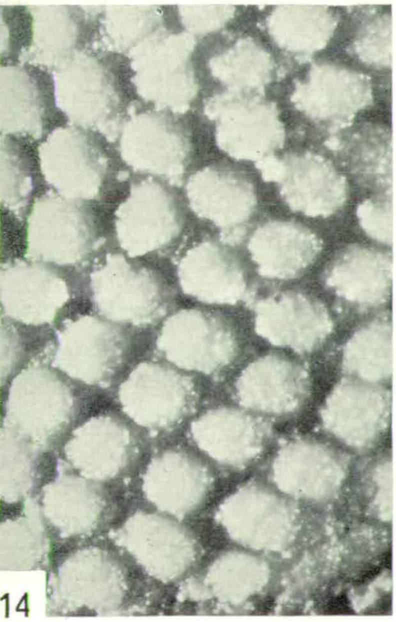
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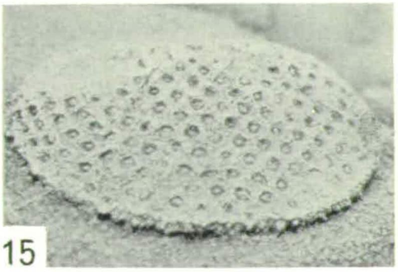
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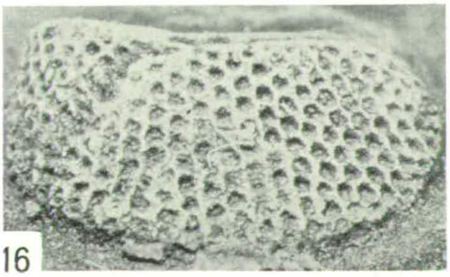
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Structures coaptatives et enroulement chez quelques Trilobites ordoviciens et siluriens

EUAN N. K. CLARKSON ET JEAN-LOUIS HENRY

Clarkson, E. N. K. & Henry, J. L.: Structures coaptatives et enroulement chez quelques Trilobites ordoviciens et siluriens. [Coaptative structures and enrollment in some Ordovician and Silurian trilobites.] *Lethaia*, Vol. 6, pp. 105–132. Oslo, 15th April, 1973.

Certain trilobites possessed highly adapted structures on the cephalon and pygidium, and sometimes also the thorax, which ensured very close interlocking of opposing surfaces during enrollment. Different kinds of structures are described in detail in selected Ordovician and Silurian genera. There is a simple 'press-stud' mechanism axially situated on the opposing cephalic and pygidial doublures of *Kloucekia micheli*, whereas in various species of *Crozonaspis* and in *Kloucekia dujardini* a projecting cephalic beak fits into an excavation under the caudal spine. The cephalic beak and corresponding pygidial excavation seemingly evolve towards a more pronounced form in successive species throughout time. *Colpocoryphe rouaulti*, by contrast, has a pygidial protuberance interlocking with a cephalic excavation. Complete specimens of *Encrinurus tuberculatus* and *E. variolaris* have very complex contact surfaces along opposing doublures, with various kinds of interlocking structures.

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A l'exception de rares observations isolées (Henry 1968), aucune recherche approfondie n'avait été jusqu'alors consacrée à certaines particularités remarquables (rostre céphalique par exemple) de plusieurs Trilobites ordoviciens de Bretagne. Le matériel restait en effet insuffisant. De nouvelles et abondantes récoltes, durant ces dernières années, ont livré, parmi les Zeliszkellinae (*Crozonaspis*, *Kloucekia*) et Colpocoryphidae (*Colpocoryphe*) recueillis, des spécimens entiers et enroulés mettant en évidence le rôle important joué, dans l'enroulement, par ces structures morphologiques particulières désignées sous le nom de structures coaptatives.

Deux espèces du genre *Encrinurus*, bien conservées dans les calcaires wenlockiens de Dudley (Angleterre), possèdent également des dispositifs coaptatifs perfectionnés qui font l'objet, dans cet article, d'une étude détaillée.

Le matériel décrit appartient aux collections du Sedgwick Museum de Cambridge (SM), de l'Institut de Géologie de Rennes (IGR) et de l'Institut de Géologie de Caen (IGC). Dans le Massif armoricain, il a été récolté, soit dans des schistes et nodules siliceux d'âge llanvirnien et llandeilien, soit dans des schistes calcareux et nodules décalcifiés caradociens.

Terminologie et techniques utilisées

La terminologie employée pour les descriptions est celle proposée par Hupé (1953a) et par Harrington (1959). De l'arrière vers l'avant, les sillons glabellaires ont été numérotés S1, S2, S3 et les lobes latéraux correspondants L1, L2, L3. Nous désignons, sous le nom de coaptation (sensu Cuénot 1919), l'ajustement mécanique de deux parties indépendantes de l'animal lors de l'enroulement. Le rostre (cephalic beak) est, au sens français du terme, une partie saillante située en avant de la tête dans le plan de symétrie du Trilobite; ce nom ne doit pas être confondu avec celui de rostrum. Nous entendons par zone de contact ou zone de jonction (contact surface) l'ensemble des surfaces suivant lesquelles s'ajustent, au cours de l'enroulement, les différents éléments de la carapace. Les index oculaires (sensu Struve 1958) sont les rapports A/G et A/Gn; A représente la longueur de l'oeil, G la longueur de la glabelle sans l'anneau occipital et Gn la longueur de la glabelle anneau occipital compris.

La lettre 'a' qui suit un numéro d'échantillon indique un moule interne, la lettre 'b' un moule externe. Tous les échantillons figurés ont été légèrement blanchis au chlorure d'ammonium ou à l'oxyde de magnésium. Les photographies et dessins ont été réalisés par les deux auteurs.

Les coaptations chez quelques Zeliszkellinae et Colpocoryphidae ordoviciens

Chez tous les exemplaires appartenant aux genres et espèces étudiés, les segments thoraciques sont imparfaitement conservés; les observations porteront donc essentiellement sur les dispositifs appartenant au céphalon et au pygidium. Les structures coaptatives de *Phacopidella* (*Prephacopidella*) *hupei* (Phacopidellinae) ayant été déjà décrites (Henry & Nion 1970), elles ne seront pas évoquées dans cet article.

Kloucekia micheli (Tromelin 1877)

Synonymie. – ☐ ? 1856 *Dalmanites phillipsi* Barrande – Verneuil & Barrande, pp. 976–977 Pl. 26: 5. ☐ 1876b *Dalmanites micheli*–Tromelin & Lebesconte, p. 599. ☐ * 1877 *Dalmanites micheli*–Tromelin, p. 10. ☐ 1886 *Dalmanites micheli* Tromelin & Lebesconte – Lapparent & Fritel, Pl. 2: 11–14. ☐ 1900 *Dalmanites phillipsi* Barrande, var. *micheli* Tromelin – Bureau, p. 168, Fig. 27 b–c. ☐ 1901 *Dalmanites micheli* Tromelin – Kerforne, p. 182. ☐ 1963 *Kloucekia micheli* (Tromelin) – Henry, p. 261, Fig. 1 a–b. ☐ 1965 *Kloucekia micheli* (Tromelin) – Henry, pp. 199–210, Figs. 1–2, Tabl. 1, Pls. 1–2.

Neotype. – Une carapace incomplète IGR N° 31 a, figurée par Henry 1965, Pl. 1: 2.

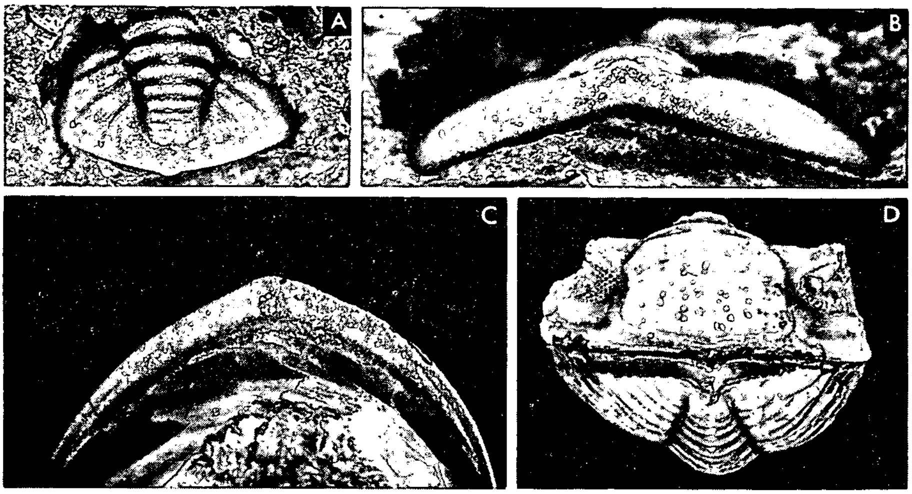

Fig. 1. Kloucekia micheli (Tromelin). A. Dorsal view of a pygidium. IGR No. 5300a. ×4. B. Posterior view of the same specimen. ×8. Note the slight depression under the base of the terminal axial spine. Couches de Morgat (Llandeilian), Postolonnec, Crozon peninsula, Finistère. C. Cephalic doublure showing the vincular furrow and the small median protuberance. IGR No. 11a figured by Henry (1965, Pl. 2:1) ×4. D. Frontal view of an enrolled specimen. IGR No. 1586a. ×4. Llandeilian shales of Traveusot near Guichen, Ille-et-Vilaine.

Étage type et localité type. – Llandeilien terminal, zone (faunizone sensu Hupé 1960) à *Marrolithus ? bureaui* (Oehlert); lieu dit la Touche, Andouillé, Mayenne.

Cette espèce, précédemment décrite (Henry 1965) ,est abondante dans les schistes et nodules siliceux du gisement llandeilien de Traveusot en Guichen (Ille-et-Vilaine). Sur la doublure céphalique relativement étroite, dans le plan axial de la carapace, on observe une excroissance arrondie, peu proéminente, constante chez tous les individus examinés (Fig. 1C). L'extrémité postérieure du pygidium porte une épine large à sa base, à peine ébauchée, aplatie et redressée (Fig. 1A) et sous laquelle se creuse une faible dépression circulaire, située légèrement en retrait par rapport aux bords latéraux du pygidium. Sur les moules internes complets et enroulés (Fig. 1D), l'épine terminale est toujours brisée, mais il est vraisemblable que, lors de l'enroulement, le mamelon de la doublure céphalique s'emboîtait dans la dépression pygidiale, la limite externe du pygidium coïncidant alors avec celle du céphalon. Au préalable, les extrémités des plèvres thoraciques postérieures prenaient place dans le sillon de fermeture bien marqué latéralement (Fig. 1C). Les terminaisons pleurales sont dépourvues d'épines, mais elles montrent des facettes articulaires développées facilitant le recouvrement partiel des plèvres pendant l'enroulement.

Ce dispositif de fermeture, très simple, est semblable à celui que réalise un bouton-pression. Il est, selon Tétry (1969), relativement rare chez les Invertébrés actuels; on le connaît toutefois chez des Crustacés tels que *Carcinus moenas*.

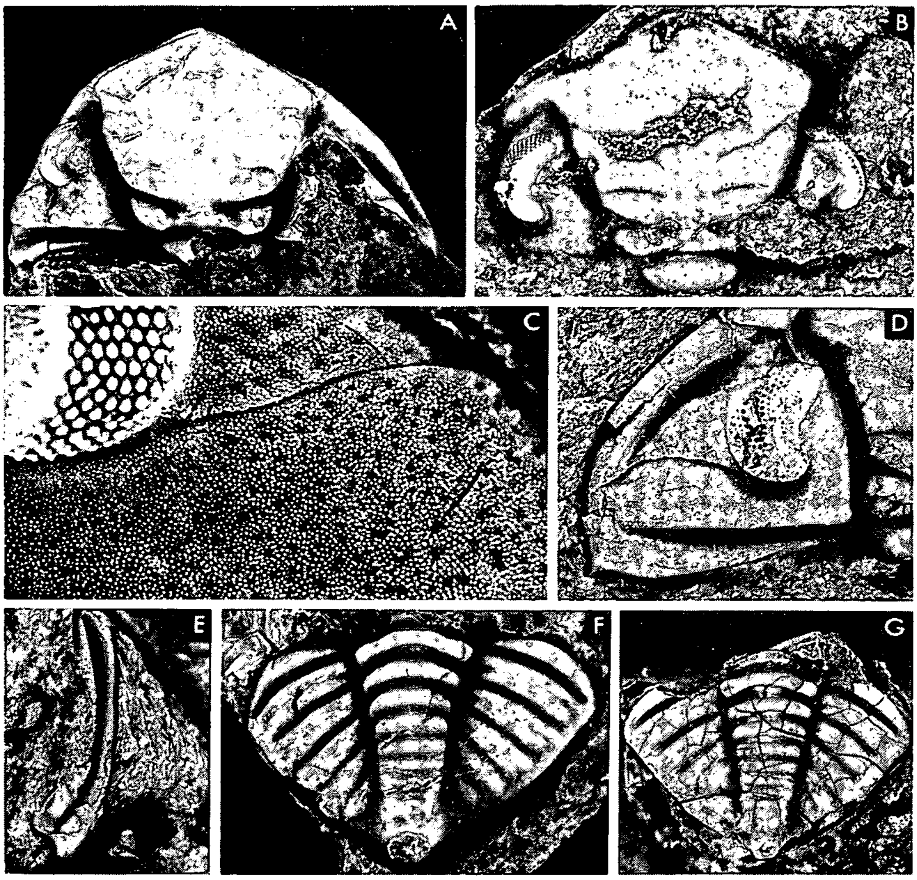

Fig. 2. Crozonaspis mayensis n. sp. A. Holotype, cephalon in dorsal view. IGR No. 606a. ×2. B. Paratype, latex replica of a cephalon in dorsal view. IGR No. 607b. ×4. C. Holotype, latex replica showing the ornamentation of the genae, IGR No. 606b. ×10 (approx.). D. Paratype, cephalon partially shown, in dorsal view. IGR No. 601a. ×6. Note the small fixigenal spine. E. Paratype, thoracic pleura. IGR No. 605a. ×4. F. Paratype, pygidium in dorsal view. IGR No. 627a. ×2.5. G. Paratype, pygidium in dorsal view. IGR No. 638a. ×4. All the specimens come from the Llanvirnian shales of May-sur-Orne, Calvados, Normandie.

Crozonaspis mayensis n. sp.

Holotype. – Un céphalon presque complet IGR No. 606a–b, figuré dans ce travail Figs. 2A, 2C.

Étage type et localité type. – Llanvirnien, 'schistes à Calymènes' de May-sur-Orne, Calvados, Normandie. Affleurements le long de la rive droite de l'Orne.

Paratypes. – Céphalons: IGC No. 402a (1 céphalon et quelques segments thoraciques), IGR No. 600a–b, IGR No. 601a – IGR No. 605a (1 céphalon et 1 plèvre thoracique isolée), IGR No. 607b, IGR No. 608a (1 céphalon et 1 pygidium), IGR No. 620a – IGR No. 622a, IGR No. 624a, IGR No. 628a–b, IGR No. 629a, IGR No. 630a.

Pygidiums: IGC No. 407a (1 pygidium et 9 segments thoraciques), IGR No. 591a, IGR No. 592a, IGR No. 593a–b, IGR No. 594b, IGR No. 595a – IGR No. 598a, IGR No. 599b, IGR No. 626a, IGR No. 627a, IGR No. 636a–b, IGR No. 637a – IGR No. 640a.

L'hypostome est inconnu.

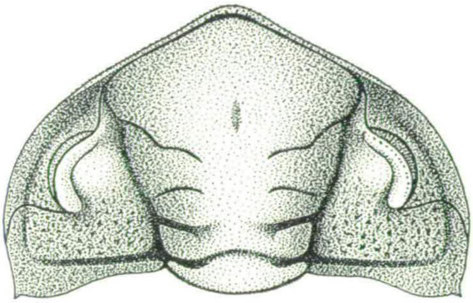

Fig. 3. Crozonaspis mayensis n. sp. Reconstruction of the cephalon, dorsal view. ×4 (approx.).

Diagnose. – Une espèce du genre *Crozonaspis* présentant les particularités suivantes: céphalon dépourvu de rostre, mais possédant un bourrelet antérieur granuleux et gonflé dans sa partie médiane (Fig. 4B); index oculaires: A/G = 32 à 36 %, A/Gn = 27 à 33 %; bande postérieure d'une plèvre thoracique se prolongeant distalement en une forte excroissance arrondie (Fig. 2 E); pygidium ne comportant, sur chaque lobe pleural, que quatre côtes et demie (la cinquième côte semble incomplète); échancrure peu prononcée sous la base de l'épine pygidiale (Fig. 4 A).

Cette espèce nouvelle, abondante dans les schistes llanvirniens de May-sur-Orne, appartient indiscutablement au genre *Crozonaspis* dont elle présente tous les caractères, à savoir: céphalon ogival; glabelle nettement élargie vers l'avant, portant des sillons Sl larges et profonds, des sillons S2 et S3 fins et peu marqués; présence de minuscules pointes génales chez les individus adultes (Fig. 2D); pygidium relativement petit, triangulaire, à faible nombre de côtes pleurales sur lesquelles les sillons interpleuraux sont toujours obsolètes. *Crozonaspis mayensis* n. sp. se distingue des autres espèces déjà connues (*C. struvei* Henry, *C. kerfornei* Clarkson & Henry, *C. incerta* (Deslongchamps), du Llandeilien du Massif armoricain) par les caractères cités dans la diagnose, tout particulièrement par l'absence remarquable de rostre. Il en résulte que ce trait morphologique ne peut plus être considéré comme une caractéristique de *Crozonaspis* et doit disparaître de la diagnose générique énoncée par l'un de nous (Henry 1968:368).

Quelques carapaces incomplètes et imparfaitement enroulées montrent que *Crozonaspis mayensis* possédait la faculté d'enroulement. Le fort bourrelet antérieur du céphalon et l'échancrure située sous la base de l'épine pygidiale représentent certainement des structures coaptatives. Si le bourrelet céphalique est bien conservé sur le moule externe IGR No. 607b (Fig. 4B), la forme exacte de l'échancrure reste difficile à apprécier car cette dernière n'est connue que sur des moules internes (IGC No. 407a, Fig. 4A). L'ajustement précis de ces structures coaptatives en fin d'enroulement ne peut donc être actuellement démontré et c'est la raison pour laquelle il n'a pas été représenté sur la Fig. 17A.

Crozonaspis struvei Henry 1968

Synonymie. – ☐ 1968 *Crozonaspis struvei* n. g. n. sp. – Henry, pp. 370–374, Figs. 1–2, ? 3, 4, Pls. 1–2. ☐ 1968 *Crozonaspis struvei* Henry – Clarkson, pp. 384–388, Fig. 1a–e, Pl. 1, Figs. 1–3. ☐ 1970 *Crozonaspis struvei* Henry – Clarkson & Henry, p. 119, Fig. 2b, Pl. 1, Figs. 2–4.

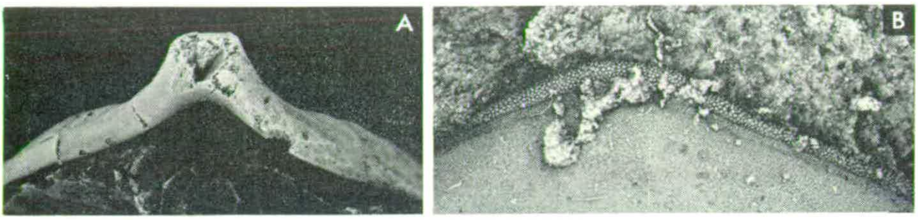

Fig. 4. Crozonaspis mayensis n. sp. A. Paratype, posterior view of a pygidium. IGC No. 407a. ×4. Note the slight indentation under the basis of the terminal axial spine. B. Paratype (see Fig. 2B), part of latex replica showing the granular anterior border. IGR No. 607b. ×10. (approx.). Llanvirnian shales of May-sur-Orne, Calvados, Normandie.

Holotype. – Un céphalon (moule interne) légèrement déformé IGR No. 520a, figuré par Henry (1968, Pl. 1:1).

Étage type et localité type. – Llandeilien, couches de Morgat (sensu Henry 1969); lieu dit Postolonnec, presqu'île de Crozon, Finistère.

Paratypes. – La liste des paratypes a été publiée par Henry (1968:370).

Cette espèce est communément répandue dans tout le synclinorium médian, depuis le Finistère jusqu'à la Mayenne (Clarkson & Henry 1970); elle est surtout abondante sous la zone à *Marrolithus ? bureaui*, à la partie supérieure du Llandeilien. Le céphalon de *Crozonaspis struvei* présente, antérieurement, dans le plan axial, un rostre largement arrondi et bien individualisé en vue dorsale, déjà décrit par l'un de nous (Henry 1968:372). Sous la base de la longue et forte épine pygidiale, on retrouve une échancrure relativement marquée (Fig. 5A). La doublure céphalique porte latéralement un léger sillon de fermeture. Chaque plèvre thoracique est pourvue d'une facette articulaire et son extrémité distale se prolonge en une courte épine acérée dont le rôle de butoir stoppant le recouvrement des plèvres pendant l'enroulement paraît probable (Henry 1968:373, Pl. 2:9). Bien que les carapaces soient généralement incomplètes et qu'aucun individu entier et enroulé n'ait été découvert, l'importance du rostre et de l'échancrure pygidiale en tant que structures coaptatives ne fait aucun doute; si l'on tient compte des déformations d'origine tectonique, la forme de ces structures, étudiée sur des moules internes et externes, est telle que leur ajustement précis en fin d'enroulement peut être considéré comme vraisemblable.

Remarques. – Le lobe frontal glabellaire montre, en son centre, une profonde fossette linéaire (Fig. 5C) correspondant sans doute à une insertion musculaire (voir à ce sujet Eldredge 1971). A l'exception des sillons, le test de *Crozonaspis struvei* est recouvert d'une fine granulation; les dimensions et la densité des granules sont toutefois plus élevées sur le rostre et la doublure céphalique que sur le reste de la carapace (Fig. 5C). On notera enfin qu'à proximité du point α, le tracé des tronçons pré-oculaires de la suture faciale subit une faible inflexion dont la courbure tend à épouser celle du rostre (Fig. 5B).

Crozonaspis rouaulti (Tromelin & Lebesconte 1876)

Synonymie. – ☐ v. 1851 *Dalmannia incerta* (Deslongchamps) – Rouault, p. 371. ☐ 1876a *Dalmanites rouaulti* Tromelin & Lebesconte, p. 687. ☐ 1968 *Crozonaspis rouaulti* (Tromelin & Lebesconte) – Henry, p. 374.

Holotype. – Une carapace enroulée et incomplète IGR No. 589a, figurée pour la première fois dans ce travail Fig. 6 A–E.

Étage type et localité type. – ? Llandeilien, ? Caradocien; 'nord nord est de Gahard' (Ille-et-Vilaine), seule mention d'origine rédigée de la main de Rouault.

Un seul exemplaire de cette espèce est actuellement connu; récolté par Rouault, il porte une indication d'origine malheureusement trop imprécise pour que l'on puisse émettre une opinion quant à la localisation géographique et la position stratigraphique du gisement fossilifère dans lequel cet holotype a été découvert.

Les caractères morphologiques de céphalon (profil et forme de la glabelle, segmentation glabellaire, position et dimensions des yeux, tracé de la suture faciale) sont, de toute évidence, ceux d'un *Crozonaspis* ordovicien. Au premier abord, en vue dorsale, le céphalon de *Crozonaspis rouaulti* ne paraît guère différent de celui de *C. struvei*, à l'exception toutefois du rostre plus saillant, mieux individualisé, et des sillons glabellaires S2 et S3 moins marqués; mais la doublure bien conservée de *C. rouaulti* montre quelques particularités remarquables: de part et d'autre d'une volumineuse excroissance arrondie, prolongement ventral du rostre, s'allongent deux surfaces planes, grossièrement rectangulaires, se confondant distalement avec les bords latéraux arrondis de la doublure. Immédiatement sous ces deux surfaces s'étend une troisième facette également plane, en forme de triangle isocèle dont la base serait constituée par la suture hypostomale et les deux côtés par deux fines arêtes rectilignes (voir Fig. 6E). Une telle 'structure géométrique' de la région médiane de la doublure céphalique n'a encore jamais été observée chez les autres espèces connues du genre *Crozonaspis*; elle devait certainement permettre un ajustement particulièrement précis des doublures céphalique et pygidiale en fin d'enroulement.

Le sillon de fermeture est discontinu, mais il est très large et profond latéralement; il est orné de granulations apparentes. Sur l'holotype, seules les extrémités pleurales gauches des sept premiers segments thoraciques sont conservées, 'en place', dans le sillon de fermeture; mais la longueur de la partie inoccupée de ce sillon correspond à la largeur totale (sag.) de quatre terminaisons pleurales. Le nombre de segments thoraciques étant de onze chez *Crozonaspis*, on peut conclure que les extrémités distales de toutes les plèvres s'emboîtaient, lorsque le Trilobite s'enroulait, dans le sillon de fermeture. Le pygidium s'appliquait alors sur la région médiane de la doublure céphalique, le rostre s'encastrant dans une échancrure (?) placée sous la base d'une hypothétique épine pygidiale.

Remarques. – En 1876, lorsque de Tromelin & Lebesconte créèrent cette espèce fondée sur l'unique échantillon de Rouault, ils la citèrent dans une

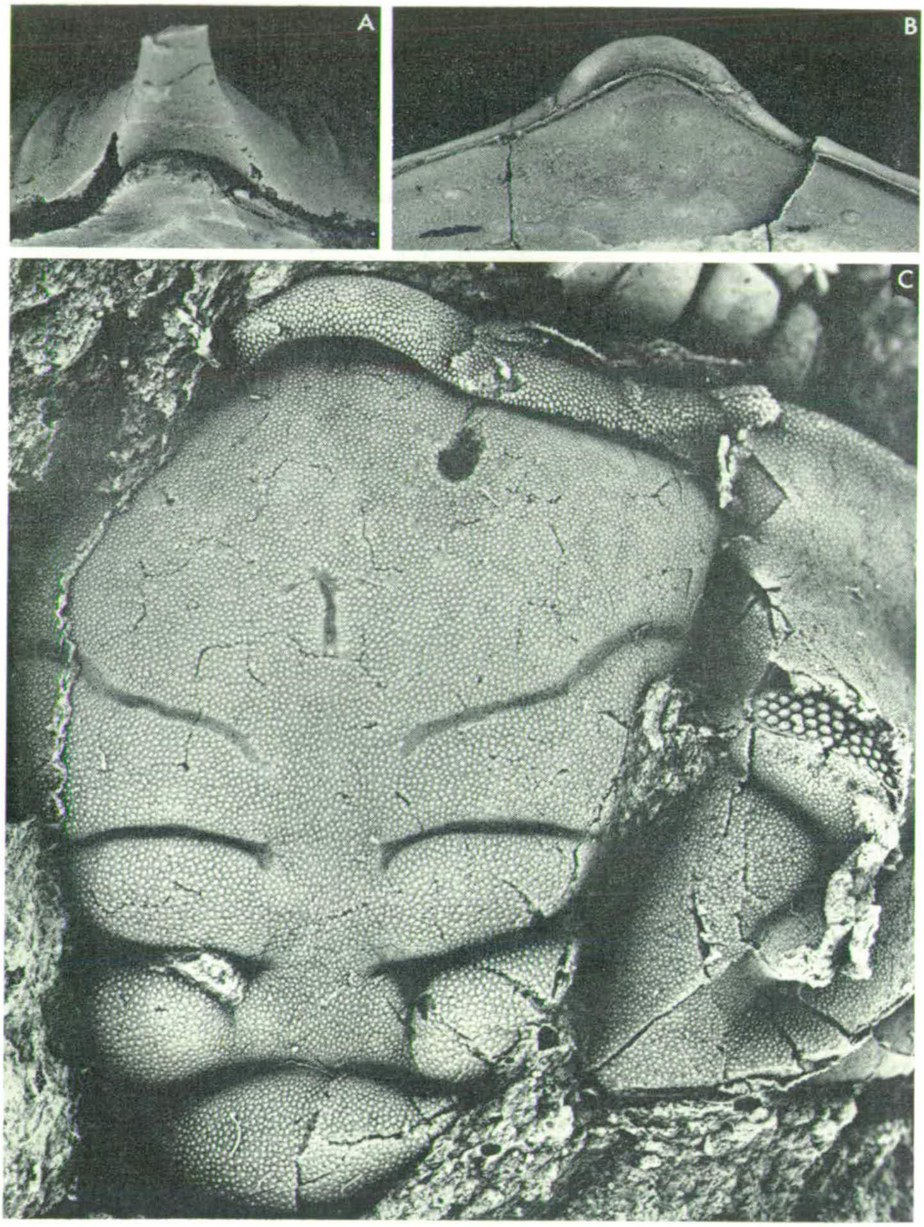

Fig. 5. Crozonaspis struvei Henry. A. Posterior view of a pygidium, showing the indentation under the terminal axial spine. IGR No. 1592a. ×4. B. Cephalon partially shown, in dorsal view. IGR No. 651a. ×4. Note the slight incurvation of the facial suture behind the cephalic beak (rostre). Couches de Morgat (Llandeilian), Postolonnec, Crozon peninsula, Finistère. C. Latex replica of an incomplete cephalon in dorsal view showing the ornamentation of the exoskeleton. Courbouleix coll., Catholic University of Paris. ×9. 'Schistes à *Homalonotus oehlerti*' (Llandeilian), Serra de Buçaco, Portugal.

liste de fossiles dévoniens des environs de Gahard, localité d'Ille-et-Vilaine située à 22 km au NE de Rennes. L'holotype ayant été momentanément égaré

Fig. 6. Crozonaspis rouaulti (Tromelin & Lebesconte). Holotype, IGR No. 589a. A, C, D. Dorsal, lateral and frontal views of the cephalon. ×3. B. Left part of the cephalic doublure. ×6. E. Median part of the cephalic doublure. f = facets. ×3. Ordovician (? Llandeilian, ? Caradocian), 'nord nord est de Gahard', Ille-et-Vilaine.

dans les collections du Musée de Rennes, les auteurs contemporains pensèrent qu'il s'agissait d'un représentant du genre *Acastella*, commun en Bretagne dans les grès à *Platyorthis monnieri* du Siegenien inférieur. Cette confusion semble d'ailleurs avoir été commise par de Tromelin & Lebesconte eux-mêmes. Comme nous l'avons déjà écrit (Henry 1968:374), le terme spécifique *rouaulti* doit être rapporté au seul Trilobite ordovicien décrit et figuré dans cet article.

Kloucekia dujardini (Rouault 1847)

Synonymie. – □ v 1847 *Phacops dujardini* Rouault, p. 320, Pl. 3:5. □ ? 1856 *Dalmanites dujardini* (Rouault) – Verneuil & Barrande, p. 977, Pl. 26:6. □ 1894 *Calymene* aff. *tristani* Brongniart – Bergeron, pp. 42–43, Pl. 6:1–2. □ 1901 (pars) *Dalmanites incertus* (Deslongchamps) – Kerforne, pp. 182–183. □ 1967 *Kloucekia (Phacopidina) dujardini* (Rouault) – Coates, p. 88, Figs. 5–6. □ 1969 *Kloucekia (Phacopidina) dujardini* (Rouault) – Pillet & Robardet, pp. 70–71, Fig. 3, Pl. 2:1, ? 2. □ 1969 *Kloucekia dujardini* (Rouault) – Henry, p. 17.

Lectotype. – Le matériel utilisé par Rouault lors de la création de l'espèce a été retrouvé. Il comprend: deux céphalons (IGR No. 1601a, IGR No. 1602a), un thorax incomplet et un pygidium (IGR No. 1603a), une carapace brisée et incomplète (IGR No. 1604a) et un céphalon accompagné de quatre segments thoraciques (IGR No. 1605a). Tous ces syntypes sont très mal conservés, mais, à l'exception de l'exemplaire IGR No. 1605a qui pourrait être un

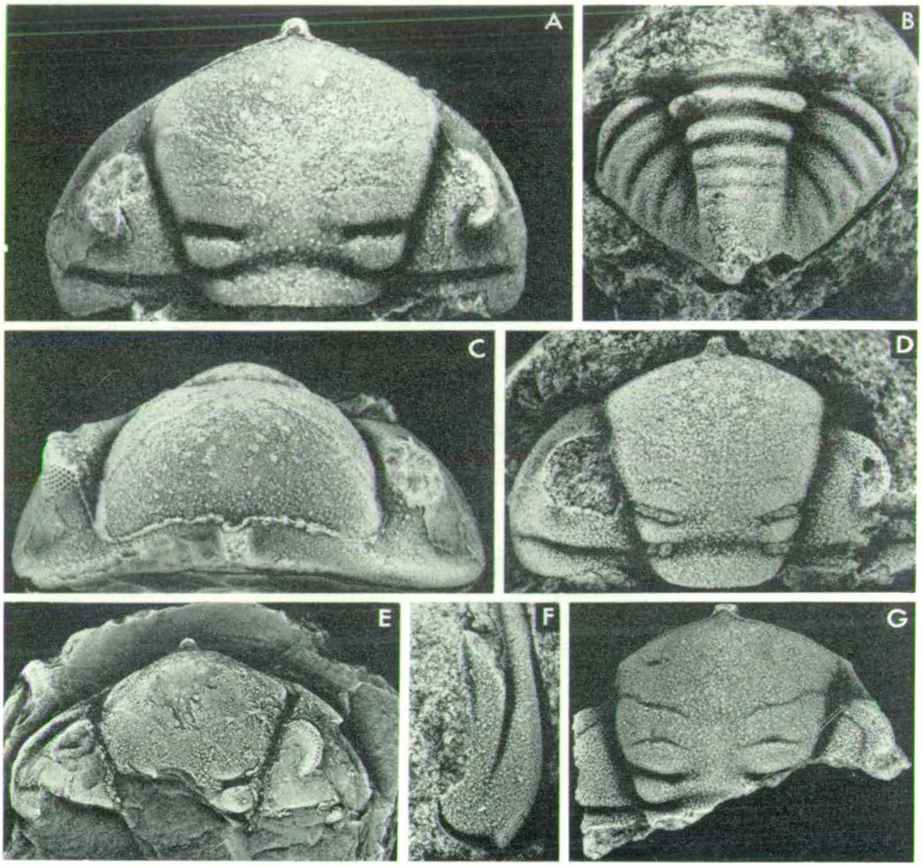

Fig. 7. Kloucekia dujardini (Rouault). A, C. Cephalon, dorsal and frontal views. IGR No 1590a. ×3. Ile de l'Aber. B. Pygidium, dorsal view (the terminal axial spine is broken) IGR No. 1591a. ×3. Plage de Raguenez. D. Cephalon, dorsal view. IGR No. 1587a. ×6 Ile de l'Aber. Schistes de Raguenez (Caradocian), Crozon peninsula, Finistère. E. Lectotype (here selected), incomplete cephalon in dorsal view. IGR No. 1601a, Rouault coll. ×2.5. Schistes de Riadan (Caradocian), Riadan near Poligné, Ille-et-Vilaine. F. Distal part of a thoracic pleura. IGR No. 1606a. ×5. Plage de Raguenez. G. Incomplete cephalon, dorsal view. IGR No. 1589a. ×4. Ile de l'Aber. Schistes de Raguenez (Caradocian), Crozon peninsula, Finistère.

Eodalmanitina, ils appartiennent probablement à l'espèce *Kl. dujardini*. Le céphalon IGR No. 1601a (Fig. 7 E) est désigné comme lectotype dans ce travail.

On remarquera qu'aucun des syntypes ne ressemble au dessin publié par Rouault (1847, Pl. 3:5); cette illustration n'est sans doute qu'un essai de reconstitution réalisé à partir de plusieurs spécimens.

Étage type et localité type. – Caradocien, schistes de Riadan; anciennes exploitations ardoisières de Riadan, situées au bord de la route nationale Rennes – Nantes, au Sud de la localité de Poligné (Ille-et-Vilaine).

Des descriptions et figurations de ce Trilobite, basées sur du matériel récolté dans des schistes caradociens du Cotentin (Normandie), ont été récemment publiées par Coates (1967) et par Pillet & Robardet (1969). Les exemplaires des schistes de Raguenez (presqu'île de Crozon, Finistère, mieux conservés,

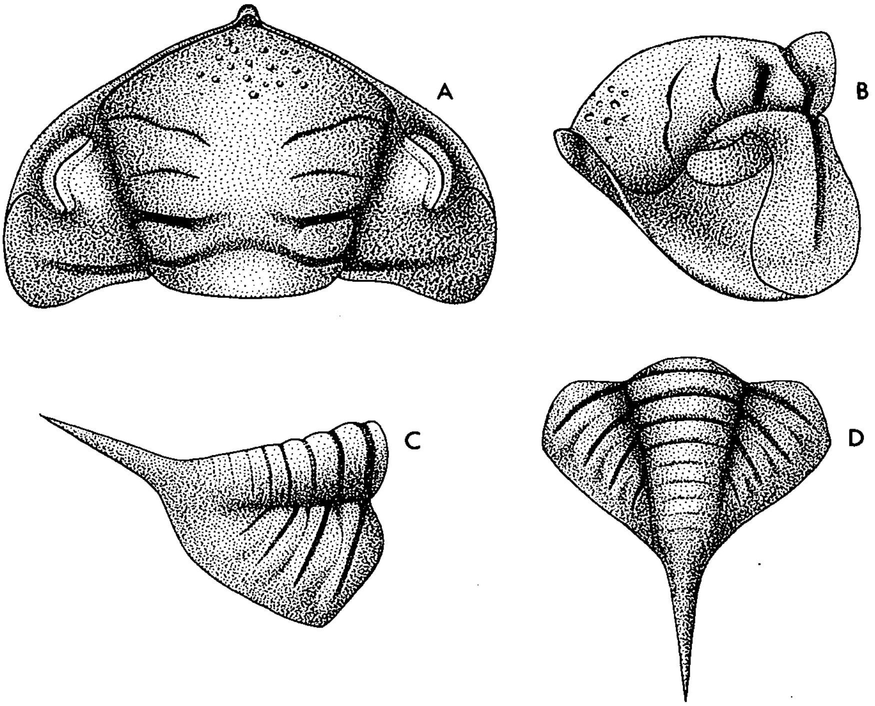

Fig. 8. Kloucekia dujardini (Rouault). A–B. Reconstruction of the cephalon, dorsal and lateral views. × 3 (approx.) C–D. Reconstruction of the pygidium, lateral and dorsal views. × 3 (approx.).

permettent de compléter les observations antérieures. Chez *Kloucekia dujardini*, la section de l'épine pygidiale est circulaire; le pygidium figuré par Pillet & Robardet (1969, Pl. 2: 1e) est écrasé, et la forme spatulée de l'épine caudale dont parlent les deux auteurs résulte d'une déformation d'origine tectonique.

Les structures coaptatives du céphalon et du pygidium de *Kloucekia dujardini* sont particulièrement bien développées. En vue dorsale, le rostre est une courte pointe mousse, fine et proéminente; la protubérance qu'il forme sur la doublure est bordée de deux sillons subverticaux (Fig. 9D). La partie médiane de la doublure, très comparable à celle de *Crozonaspis rouaulti*, est constituée de trois régions séparées les unes des autres par le rostre et deux arêtes rectilignes. A l'exception du sillon de fermeture moins profond latéralement, les seules différences notables, par rapport à *Crozonaspis rouaulti*, résident dans la grande taille relative des deux facettes rectangulaires (placées symétriquement de part et d'autre du rostre) et dans la réduction de la région postérieure triangulaire (voir Fig. 9A).

Les plèvres thoraciques sont pourvues de facettes articulaires nettes et chaque terminaison pleurale porte, postérieurement, une robuste et courte épine (Fig. 7F); lorsque le Trilobite s'enroulait, ces épines stoppaient le glissement des plèvres les unes sur les autres.

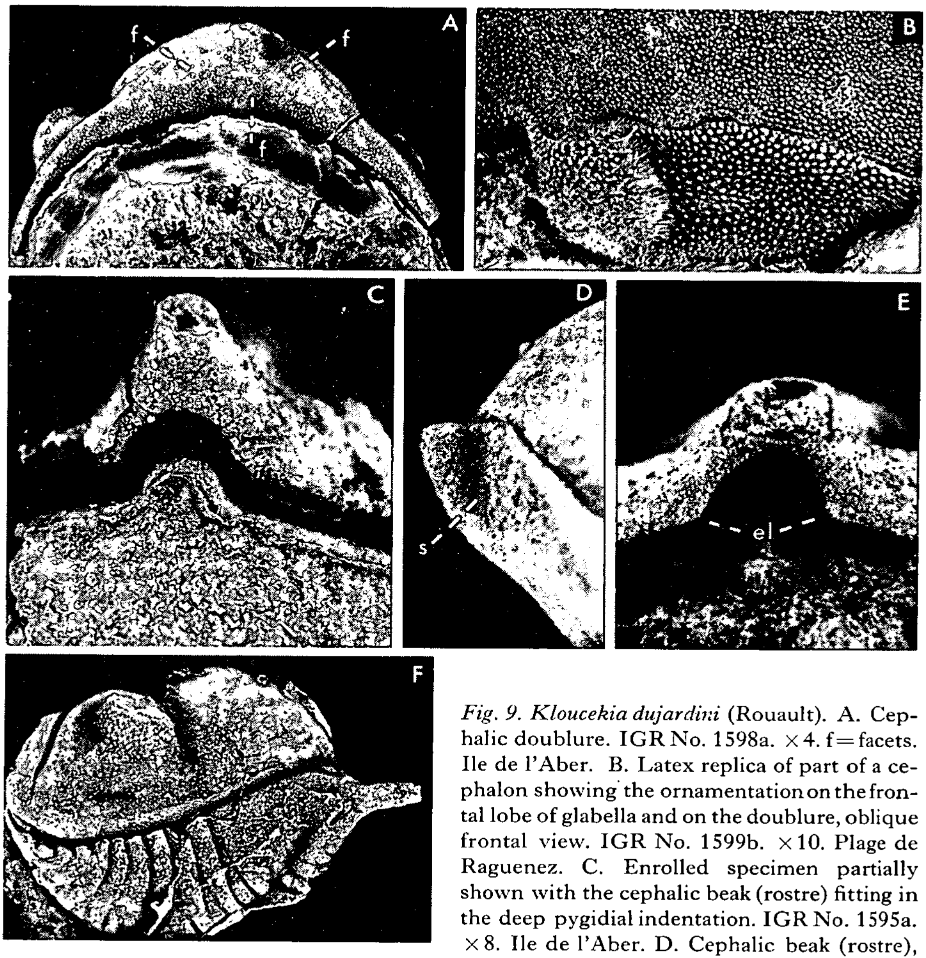

Fig. 9. Kloucekia dujardini (Rouault). A. Cephalic doublure. IGR No. 1598a. ×4. f = facets. Ile de l'Aber. B. Latex replica of part of a cephalon showing the ornamentation on the frontal lobe of glabella and on the doublure, oblique frontal view. IGR No. 1599b. ×10. Plage de Raguenez. C. Enrolled specimen partially shown with the cephalic beak (rostre) fitting in the deep pygidial indentation. IGR No. 1595a. ×8. Ile de l'Aber. D. Cephalic beak (rostre), latex cast in lateral view. IGR No. 1600b. ×8.s = furrow (sillon). Ile de l'Aber. E. Posterior view of a pygidium showing the deep indentation under the base of the terminal axial spine. IGR No. 1588a. ×9. el = two flattened protuberances (excroissances en lames) at the opening of the indentation. Plage de Raguenez. F. Lateral view of an enrolled specimen, latex cast. IGR No. 1593b. ×3. Plage de Raguenez. All the specimens come from the schistes de Raguenez (Caradocian), Crozon peninsula, Finistère.

Sous la base de l'épine terminale du pygidium, dans un plan vertical perpendiculaire au plan de symétrie de la carapace, le test dessine une profonde et étroite échancrure dont les bords subparallèles forment, au niveau de l'ouverture de cette échancrure, deux petites excroissances semi-circulaires, en forme de lames à peine ébauchées (Fig. 9E).

Au cours de l'enroulement, les extrémités pleurales prenaient appui sur les parties latérales de la doublure céphalique, les terminaisons distales des plèvres thoraciques postérieures s'emboîtant dans le léger sillon de fermeture. Le pygidium, dont la doublure n'est malheureusement pas conservée, s'appliquait alors sur la partie médiane de la doublure céphalique, sa limite externe coïncidant avec le bord antérieur du céphalon (Fig. 9F). L'ajuste-

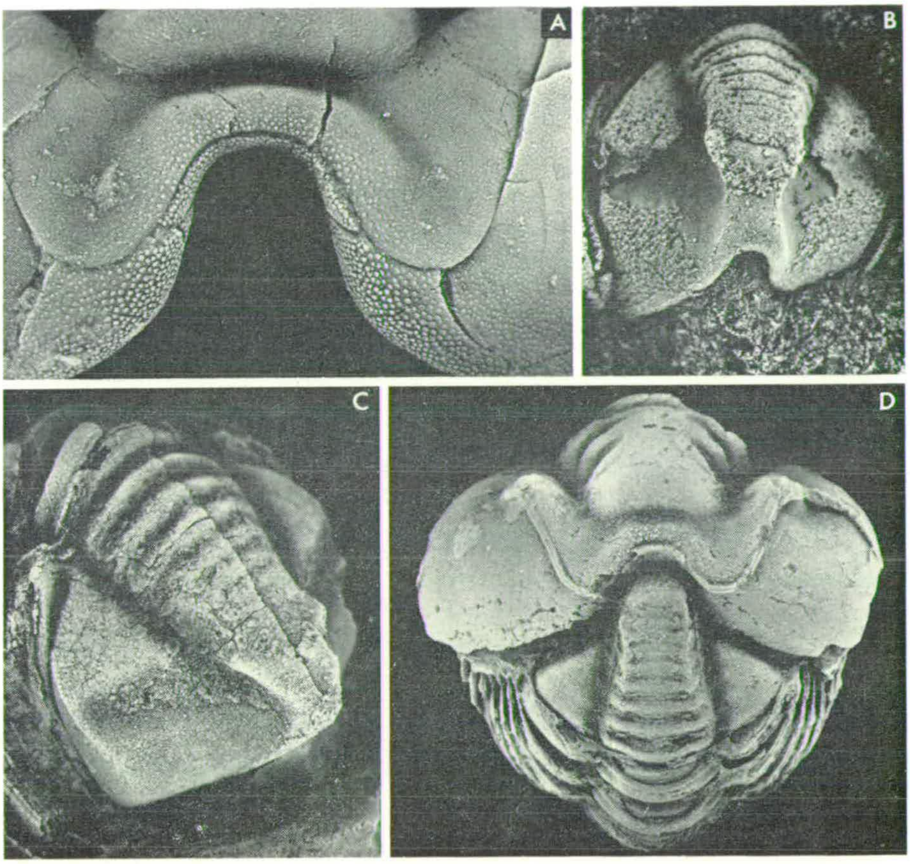

Fig. 10. Colpocoryphe rouaulti Henry. A. Cephalic indentation, frontal view. IGR No. 2032. ×6. ? Llandeilian. Les Elaunais, Montsûrs, Mayenne. B. Latex replica of a pygidium, posterior view. IGR No. 1594b. ×6. C. Lateral oblique view of a pygidium. IGR No. 2003a figured by Henry (1970, Pl. B:3a–c.). ×4. D. Enrolled specimen, frontal view. IGR No. 2007a figured in part by Henry (1970, Pl. B:5). ×2. Llandeilian shales of Traveusot near Guichen, Ille-et-Vilaine.

ment des structures coaptatives (rostre et échancrure) marquait la fin de l'enroulement, les protubérances en lames situées à l'ouverture de l'échancrure prenant place (ou peut-être coulissant) dans les deux rainures délimitant latéralement la partie ventrale du rostre.

Remarques. – En vue dorsale, immédiatement en arrière du rostre, la suture faciale est 'déformée' et décrit une boucle prononcée (Fig. 9C). On notera aussi que les granulations qui couvrent toute la doublure céphalique (rostre compris) sont beaucoup plus denses et plus volumineuses que sur le reste de la carapace (Fig. 9B).

Colpocoryphe rouaulti Henry 1970

Synonymie. – Une synonymie détaillée a été publiée par Henry (1970).
Holotype. – Une carapace entière IGR No. 2000a figurée par Henry (1970, Pl. B:1a–b).

Étage type et localité type. – Schistes et nodules siliceux contenant *Glyptograptus teretiusculus*, Llandeilien; lieu dit Traveusot en Guichen, Ille-et-Vilaine.

L'enroulement de ce Trilobite ayant été précédemment décrit (Henry 1970: 17) nous n'ajouterons aux observations antérieures que quelques remarques. En fin d'enroulement, la pièce terminale du rachis pygidial, pourvue latéralement de deux excroissances aliformes, s'emboîte dans la profonde échancrure du céphalon (Fig. 10D). Cet emboîtement est stoppé par les excroissances aliformes prenant appui sur les bords de l'échancrure céphalique, tandis que les bourrelets latéraux des joues s'engagent dans les deux sillons de fermeture du pygidium (Fig. 11).

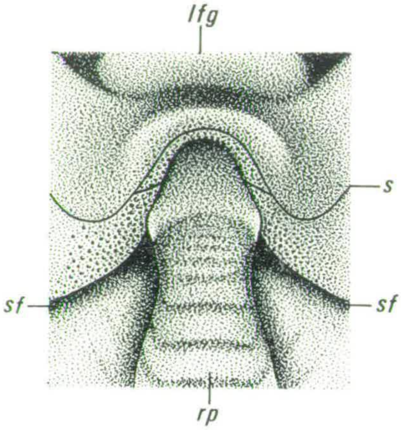

Fig. 11. Colpocoryphe rouaulti Henry. Interlocking of the cephalic and pygidial coaptative structures when fully enrolled, frontal view. × 4 (approx.). lfg = frontal lobe of glabella (lobe frontal glabellaire), s = facial suture (suture faciale), sf = vincular furrows of the pygidium (sillons de fermeture du pygidium), rp = axis of the pygidium (rachis pygidial).

On notera, à l'inverse de ce que l'on observe chez *Crozonaspis*, que c'est le pygidium, chez *Colpocoryphe rouaulti*, qui porte les principales structures coaptatives. Ce même type de coaptation se retrouve chez *Colpocoryphe salteri* (Rouault) et *C. lennieri* (Bergeron). Des recherches portant sur l'évolution des dispositifs coaptatifs de quelques Calymenacea ordoviciens sont actuellement en cours et feront l'objet d'une publication ultérieure.

Coaptations in two species of the genus *Encrinurus*

The Wenlock Limestone (Silurian) of Dudley, England, has long been known to yield excellently preserved trilobites. Several of the genera occurring therein were capable of enrollment, some possessing relatively simple contact surfaces, such as *Acaste*, others having much more elaborate mechanisms for ensuring tight closure. Of all the genera examined, *Encrinurus* showed the most complex and interesting series of interlocking structures along the contact surface; these were briefly referred to by Temple (1954), and are very well shown in the two species discussed below.

Encrinurus tuberculatus (Buckland 1836)

Synonymy. – ☐ 1822 *Calymene variolaris* Brongniart, Pl. 1: 3a (non fig. 3b). ☐ 1836 *Asaphus tuberculatus* Buckland, p. 74, Pl. 46: 6 (= Pl. 1: 3a in Brongniart 1822). ☐ 1850 *Cybele*

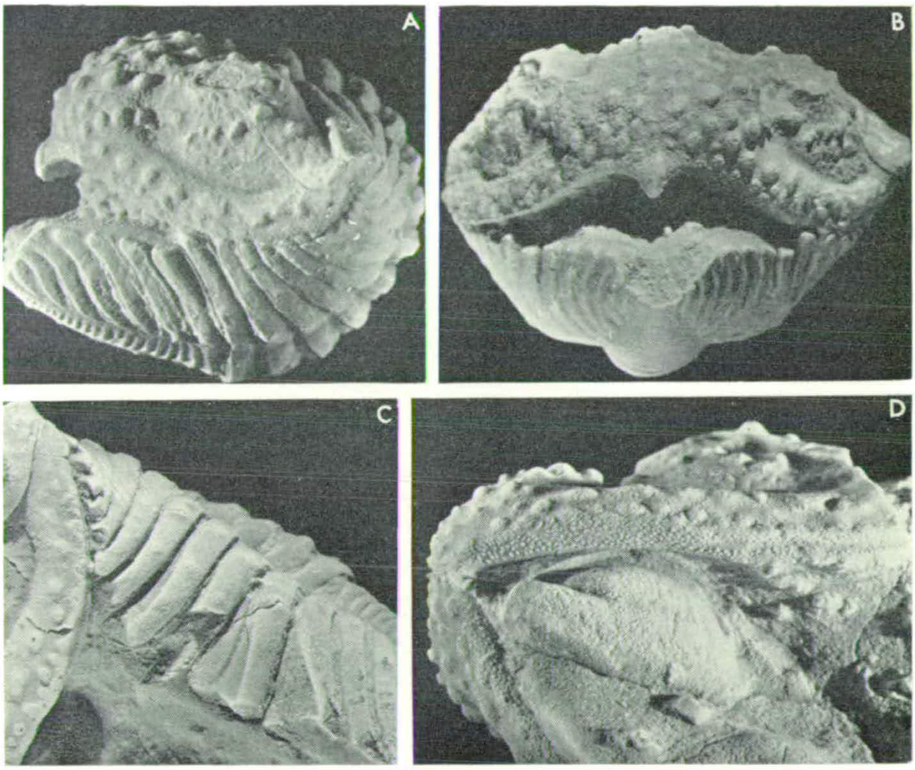

Fig. 12. Encrinurus tuberculatus (Buckland). A–B. Lateral and anterior views of anin completely enrolled specimen. SM A 28417. ×4.2. C. Lateral view of a specimen showing part of the flanged cephalic doublure, and partially extended thorax and pygidium. Articulating facets are visible (cf. Fig. 16 C). SM A 28413. ×3.25. D. Ventral surface of a slightly distorted cephalon; flanged doublure visible; hypostome somewhat displaced. SM A 28410. ×5.2. Wenlock Limestone, Dudley.

punctata Fletcher, p. 402, Pl. 32:1–5. □ 1853 *Encrinurus punctatus* Salter, p. 6, Pl. 4:15–16 (non fig. 14). □ 1962 *Encrinurus tuberculatus* (Buckland) – Tripp, p. 467, Pl. 65:5–8, Pl. 66:4–11, Pl. 67:9–10, Pl. 68:4–6.

Tripp's account of this species contains illustrations of enrolled specimens. Such enrolled individuals are not uncommon in collections, but they are less frequently encountered than those of *E. variolaris*, where perfectly enrolled specimens abound. In *E. tuberculatus* furthermore, even in well preserved enrolled individuals, the cephalon and pygidium are rarely found in contact, so that partial enrollment is the norm.

When the animal is fully enrolled the hypostome is enclosed completely, and its projecting central body is housed within the triangular space circumscribed by the pygidial doublure. But since the tip of the pygidium projects well beyond the front of the head, the distal part of this triangular cavity is exposed externally to the interlocked cephalon and pygidium. This is an unusual adaptation amongst enrolled trilobites and is not shared by *E. variolaris*.

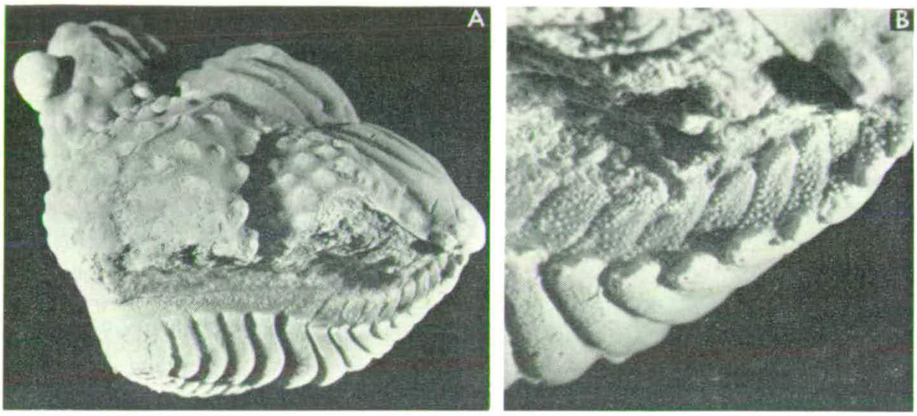

Fig. 13. Encrinurus variolaris (Brongniart). A. Antero-lateral view of a specimen, where the librigena has been broken away showing the doublures of the thorax and pygidium forming a contact surface. ×3. B. Enlargement of the thoracic doublures. SM A 28430. ×10. (cf. Fig. 16F–G). Wenlock Limestone, Dudley.

Interlocking devices

Cephalon. – The undersurface of the cephalon has various coaptative structures which enable it to interlock effectively with the tips of the thoracic pleurae and the pygidium. On following the cephalic doublure from the front of the cephalon posteriorly, four successive structural regions are encountered (Figs. 12D, 16A). Firstly, there is a beak-like rostral plate, which projects ventrally, and to which the edge of the central body of the hypostome is attached. Behind this plate is an elongated region where the doublure is narrow and its inner edge shelves very steeply dorsally to meet the recessed lateral edge of the hypostome. Further back, the doublure changes shape abruptly, becoming broader and indented by a groove, on the inner surface of which a vertical flange arises, projecting ventrally. Posteriorly again, the groove and flange disappear, and the doublure narrows once more, finally merging with the genal spine.

Thorax. – Each thoracic pleura has two parts, an anterior articulating facet, with a central vertical groove, and a posterior band or rib. The facets slid below the preceding pleurae when the animal enrolled, so that the edges of the posterior pleural bands just touched one another. The facet of the first thoracic segment slid below the posterior cephalic border. Each thoracic rib is strong and well-developed, but in lateral view the ribs become broader and less strongly curved towards the rear of the trilobite. This adaptation, similar to that of *Eophacops musheni* (Salter), discussed previously (Clarkson 1966), enables the front and back of the pleural ribs to fit together with precision during spheroidal enrollment without telescoping or overlapping. All the pleural ribs have the same kind of termination; a short projection or point arising from the outer part of the pleura. These are here referred to as pleural spines (Harrington, Moore & Stubblefield 1959:O124). When the

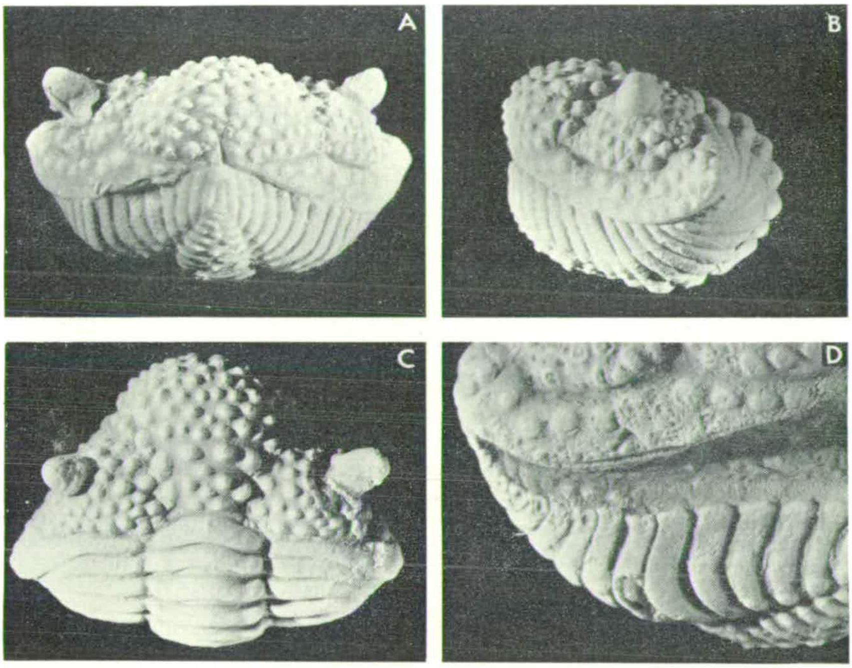

Fig. 14. Encrinurus variolaris (Brongniart). A–C. Anterior, lateral, and dorsal views of an enrolled specimen, very slightly crushed. SM A 28429. ×3.75. D. Contact surfaces of an incompletely enrolled specimen showing the flanged cephalic doublure (above), and the thoracic and pygidial doublures (below). SM A 28422. ×5. (cf. Fig. 16E). Wenlock Limestone, Dudley.

trilobite is enrolled these pleural spines are lodged in the groove in the ventral surface of the cephalic doublure on each side of the trilobite. Their inner surfaces rest against the outer edge of the ventrally projecting flange. The groove and flange are of equivalent length to the closed-up pleural spines of the enrolled thorax, thus the cephalon and thorax can hold together by themselves forming a rigid box independently of the pygidium. Normally the pygidium would be held close against the cephalon, but it is possible that some relaxation of the musculature could allow raising or lowering of the pygidium without disturbing the cephalon and thorax.

Pygidium. – The shape of the pygidial doublure is well adapted for closure with the cephalon. An isolated pygidium in lateral view shows that the pleural field actually terminates some distance before the true pygidial 'base', i.e. the inner edge of the doublure (Figs. 12A, 16C, D). Anteriorly, the doublure itself shelves inwards and ventrally from the base of the pleural field to its inner edge, but posteriorly the inclination becomes less strong becoming almost flat below the mucro. In an enrolled specimen the anterior part of this sloping pygidial doublure lies close against, and parallel with, the inclined cephalic doublure. Where the antero-lateral border of the cephalon

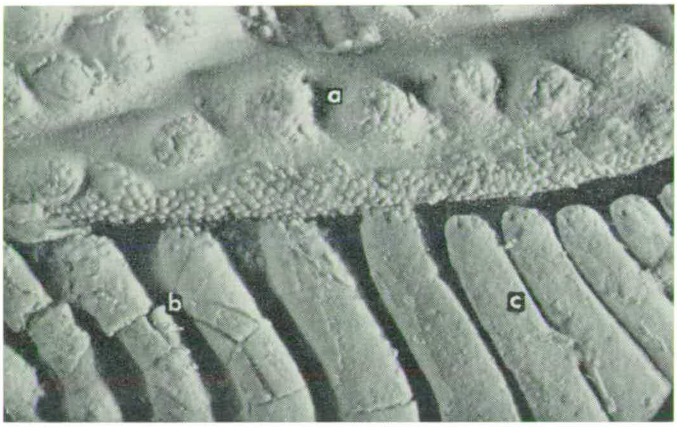

Fig. 15. Encrinurus variolaris (Brongniart). Part of a completely enrolled specimen with (a) cephalon (b) pygidium and (c) thorax, showing extreme tuberculation in region of contact surface. SM A 10266. × 8. Wenlock Limestone, Dudley.

is actually traversed by the pygidial doublure, on the other hand, the latter is flattened, again being parallel with that part of the cephalon which it contacts, and so ensuring tight closure. There remains, as noted earlier, a small triangular open space inside the inner margin (Fig. 16A), where the pygidium projects beyond the cephalon and as a result of this, water could circulate freely whilst the trilobite was enrolled.

Shape of the contact surface

When the thoracic and pygidial doublures close with the cephalic doublure, they contact each other in such a way that the two opposing surfaces are mirror-images of each other over much of their length. The line of junction or contact surface was not fully exposed in any of the specimens of *E. tuberculatus* examined, but its shape could be worked out from the convexity and slope of the different doublures. It is clear that the anterior part of the contact surface (cephalon – pygidial contact) is orientated in a different plane to the posterior region (cephalon – thorax contact). Whereas the anterior section of the contact surface has an upward and inward slope (where the proximal part of the pygidium fits inside the cephalon), the pleural projections surround the cephalic flange on the outside, and the flange fits into the angle between the cephalic thoracic doublures and the sharply reflexed pleural spines. There are better details of the precise shape of the contact surface in a specimen of *E. variolaris* described later, and so no further discussion is needed here.

Both surfaces which meet together along the contact surface and sometimes the neighbouring regions also, are densely covered with small tubercles not present in other areas. Better examples in *E. variolaris* are described later.

Encrinurus variolaris (Brongniart 1822)

Synonymy. – ☐ 1822 *Calymene variolaris* Brongniart, Pl. 1:3b. ☐ 1850 *Cybele variolaris* Brongniart – Fletcher, p. 404, Pl. 32:6–10. ☐ 1853 *Encrinurus variolaris* Brongniart – Salter, p. 7, Pl. 4:12–14. ☐ 1954 *Encrinurus variolaris* (Brongniart) – Temple, p. 315, Figs. 1–2.

This species is less common than *E. tuberculatus*, but a higher proportion of specimens are found perfectly enrolled. In this species there are no genal or dorsal spines, and the pygidial tip is not mucronate, but is rounded and during enrollment fits exactly underneath the cephalon (Figs. 13, 14). It does not project beyond the cephalon during enrollment, and so there is no open space between cephalon and pygidium such as is visible in *E. tuberculatus*.

Interlocking structures and the shape of the contact surface

Although most of the interlocking structures along the doublures are broadly comparable with those of the former species, some details of their precise relationship during enrollment are better shown in *E. variolaris*. In one fully enrolled specimen (SM A No. 28430) the left librigena and the eye have been broken away and subsequently prepared so that the surfaces of the thoracic and pygidial doublures are revealed, lying adjacent to one another in an unbroken series, extending from the rostrum nearly to the genal angle (Figs. 13A, B, 16F, G). This ribbon-like strip is a mirror-image of the cephalic doublure, which it rests against during enrollment, and defines the contact surface between the two surfaces. The contact surface undergoes an interesting series of changes of shape and direction from front to rear. The pygidial doublure is somewhat convex, with a strong outward slope that meets the pleural field. Thus in the pygidial region of an enrolled specimen, the contact surface inclines outwards and downwards, but towards the (true) anterior of the pygidium there are small projections arising from the tips of the pleural ribs (a feature absent in *E. tuberculatus*), so the contact surface turns up again at the edges.

In the thoracic region the contact surface is gently concave along its length. It not only curves upwards to meet the genal angle but is outwardly twisted so that just before it terminates, the thoracic doublures lie almost vertically.

The small, pointed, pleural spines form a sharp angle with the pleural doublures and when the trilobite is enrolled, point vertically upwards, embracing the flange, as in *E. tuberculatus*. Axially to this region, the inner part of the cephalic doublure fits neatly onto the gently concave thoracic and pygidial doublures.

Though the shape of the contact surface is not shown so clearly in any specimens of *E. tuberculatus* it seems to be similarly twisted. From the functional point of view both species seem to be adapted for an extended mode of life similar to that of *Eophacops musheni*, but they are also very well adapted to enrollment. The twisted contact surface, and the embracement of the cephalic doublure by the small pleural spines, seem particularly

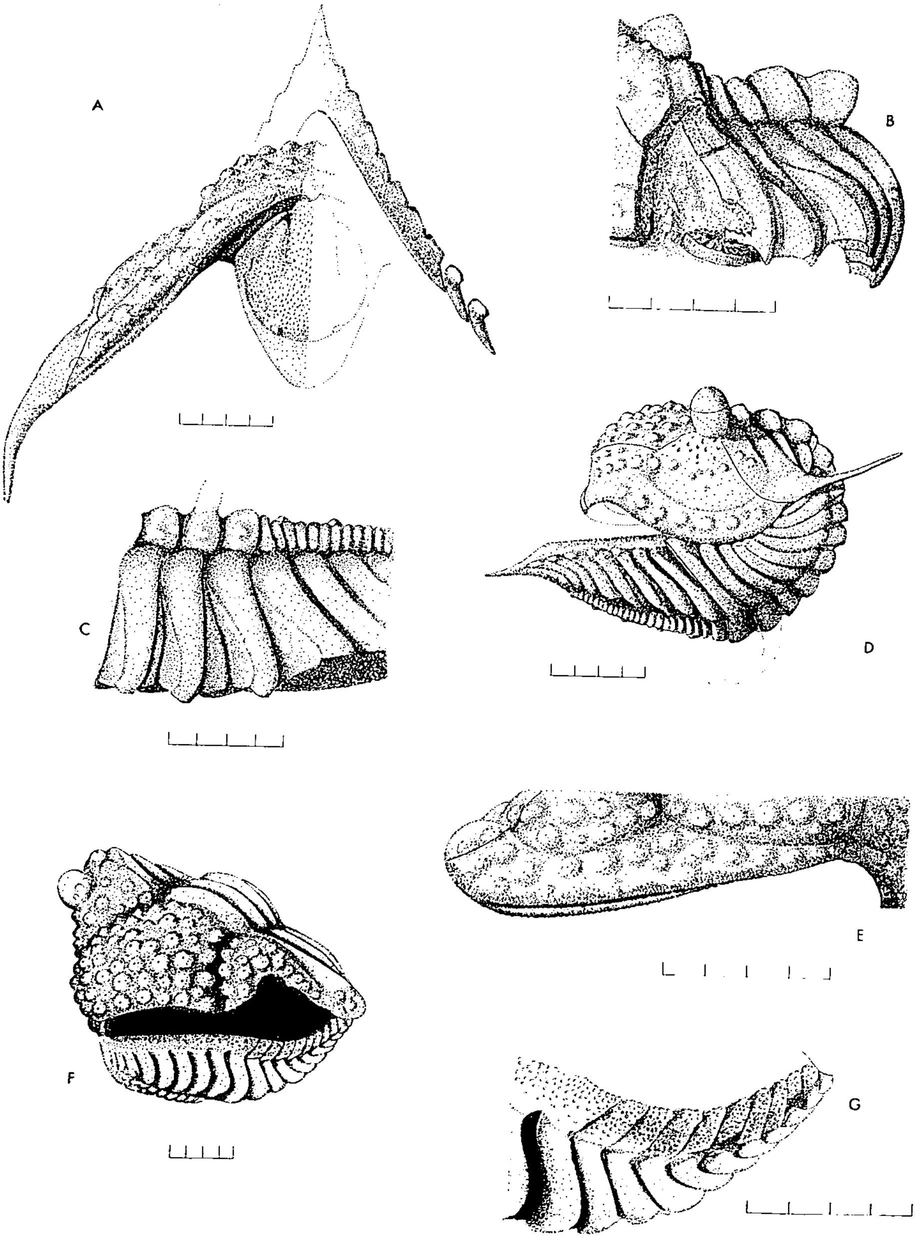

Fig. 16. Encrinurus tuberculatus (Buckland). A. Restoration of the ventral surfaces of the cephalon (with hypostome in place) and the pygidium. The pygidium together with two adjacent thoracic segments, with pleural spines visible, is shown in its correct relationship to the cephalon during enrollment. From SM A 10207, and A 28410. B. Part of SM A 28410. The broken posterior border of the cephalon reveals the facets of the first thoracic segment; other facets are also visible. The discoidal object is a crinoid ossicle. C. Part of SM A 28413, showing the last three thoracic segments and the front of the pygidium. The tips of two of the thoracic spines are restored. D. Restoration of an almost completely enrolled specimen (from SM A 28417) with the eye, genal and dorsal spines and position of the hypostome marked in with reference to other specimens. *Encrinurus variolaris* (Brongniart). E. Cephalic doublure and flange of A 28442, from slightly below. Tuberculation restored from A 10266. F. En-

well adapted to prevent torsion or lateral shearing of an enrolled specimen. A predator would have found it difficult to unroll or twist open such an enrolled animal, even in the case of *E. tuberculatus*, where the pygidium projects, affording greater leverage to the predator. The presence of the pygidial 'breathing-hole' in the latter raises the question of why it evolved in *E. tuberculatus* and not in other trilobites; one might assume that the advantage lay in the longer periods of time which the latter could spend in the enrolled state when danger threatened.

As in *E. tuberculatus*, there are abundant, small tubercles distributed on both sides of the contact surface, but not elsewhere. They are very distinct along the outer surface of the cephalic and on the pygidial doublure (Fig. 15). The tips of the thoracic pleurae have smaller, less distinct tubercles, and the surface of the groove and flange into which they fit is entirely smooth. Along the lower edge of the flange tubercles are encountered once more. These small tubercles may have been the sites of contact-sensory organs, responding both to contact with the sea floor, when the trilobite was extended, and to contact between the two surfaces when it was enrolled. They may also have aided in locking the surfaces together by providing a rougher contact. Contact-sensory systems concerned with enrollment in trilobites have been suggested previously. Hupé (1954) proposed that the 'panderian organs' present on the lateral parts of the pleurae in asaphids and other trilobites might have been the sites of sensory organs (avertisseurs pandériens) responding to the proximity of neighbouring pleurae when the trilobite had enrolled completely. Though there is no proof, the likelihood that contact-sensory organs were present in trilobites seems reasonable.

Discussion: intérêt des structures coaptatives chez les Trilobites

Pour chaque espèce ordovicienne, à l'exception de *Crozonaspis rouaulti*, de nombreux spécimens adultes ont été examinés: nous n'avons jamais observé de variations morphologiques, si faibles soient-elles, au niveau des structures coaptatives. A l'intérieur d'une même espèce, celles-ci sont toujours remarquablement stables, non seulement chez des individus provenant d'un seul et même lit fossilifère, mais aussi chez les exemplaires récoltés dans des horizons stratigraphiques différents et appartenant par conséquent à plusieurs générations. Des observations et expériences de greffes montrent que les coaptations d'Invertébrés actuels sont héréditaires, et qu'elles sont 'conditionnées génétiquement' (Tétry 1969). Si l'on fait abstraction de quelques cas douteux, un moulage des parties coaptantes durant l'ontogénèse ne peut être invoqué (Sahuc 1969:50–58; Tétry 1969:490). Les stades

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rolled specimen (A 28430, with left librigena and eye removed), showing thoracic and pygidial doublures. Left anterior tuberculation restored. G. Enlargement of the thoracic doublures. A 28430. Each scale division represents one millimetre. Wenlock Limestone, Dudley.

meraspis et holaspis jeunes des Trilobites décrits dans cet article restent encore trop peu nombreux pour qu'une étude détaillée des dispositifs coaptatifs et de leurs modifications possibles au cours de la croissance soit entreprise dans l'immédiat. Mais l'invariance de ces structures chez les adultes est un argument non négligeable en faveur de leur appartenance au patrimoine héréditaire. Lorsqu'elles sont présentes, les coaptations permettraient donc d'aboutir à des déterminations spécifiques sûres.

Les coaptations sont-elles utiles ? Si l'on entend par utile '. . . ce qui favorise une fonction sans lui apporter une condition indispensable' (Sahuc, 1969:66), la réponse ne peut appartenir qu'au domaine de l'hypothèse. En effet, de nombreux genres et espèces de Trilobites, apparemment dépourvus de structures coaptatives développées, pouvaient s'enrouler; il est par conséquent difficile de savoir si la présence de telles structures facilitait ou non l'enroulement d'un Trilobite. Par contre, si l'on considère l'utilité de ces dispositifs, non plus par rapport à la fonction proprement dite (enroulement), mais par rapport aux avantages qui pouvaient en découler, il semble bien que les coaptations, du moins les plus élaborées, aient été réellement bénéfiques. L'enroulement d'un Trilobite est généralement interprété comme une réaction de défense, l'animal assurant ainsi la protection d'une région ventrale fragile et vulnérable (Richter 1920; Hupé 1953a). Certaines coaptations, telles que l'emboîtement des plèvres thoraciques dans un sillon de fermeture ou l'ajustement précis d'un rostre céphalique et d'une échancrure pygidiale, permettaient un blocage parfait des différents éléments de la carapace et prévenaient toute tentative de torsion par déplacement latéral du pygidium ou du céphalon. Un prédateur, pour atteindre la face ventrale, devait donc nécessairement 'ouvrir' le Trilobite en forçant le jeu de muscles, sans doute puissants, qui maintenait l'animal en position d'enroulement. Les Trilobites ne sont pas les seuls Arthropodes qui possèdent la faculté d'enroulement, puisque

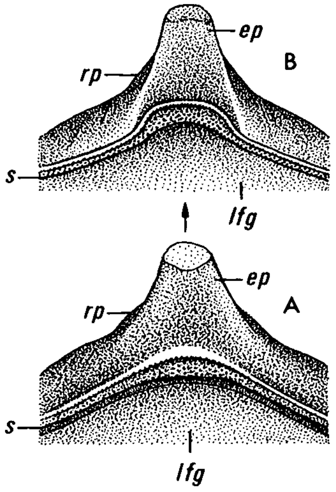

Fig. 17. Interlocking of the cephalic and pygidial coaptative structures, when fully enrolled, in the Ordovician genus *Crozonaspis*, dorsal views. A. *C. mayensis* n. sp. ×10 (approx.). Llanvirnian. B. *C. struvei* Henry. ×2 (approx.). Llandeilian. lfg = frontal lobe of the glabella (lobe frontal glabellaire), s = facial suture (suture faciale), rp = axis of the pygidium (rachis pygidial), ep = terminal axial spine of the pygidium (épine terminale du pygidium).

certains Isopodes (cf. Gruner 1953) et Diplopodes Oniscomorphes (Myriapodes) peuvent s'enrouler en une sphère compacte (cf. Gruner 1953; Manton 1954). La présence de structure coaptatives à la fois chez les Oniscomorphes et les Trilobites est particulièrement intéressante. Manton (1954) a montré que ces structures sont très bien développées chez les genres *Sphaerotherium* et *Glomeris*, dont les angles des plaques dorsales sont tronqués, antérieurement sur la face externe et postérieurement sur la face interne. Cette particularité morphologique rappelle les facettes articulaires des Trilobites et assure un ajustement parfait des segments se recouvrant pendant l'enroulement. Il existe, de plus, un mécanisme de fermeture: le bord postérieur de chaque segment porte une crête qui s'engage, lors de l'enroulement, dans une rainure placée près du bord antérieur du segment suivant; l'animal peut ainsi se maintenir fermement en position d'enroulement. L'évolution indépendante de telles structures coaptatives chez deux groupes différents d'Arthropodes renforce l'hypothèse suivant laquelle ces structures auraient une réelle valeur fonctionnelle.

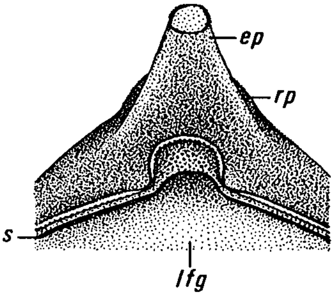

Fig. 18. Kloucekia dujardini (Rouault). Interlocking of the céphalic and pygidial coaptative structures, when fully enrolled, dorsal view. × 7 (approx.). Caradocian. lfg = frontal lobe of glabella (lobe frontal glabellaire), s = facial suture (suture faciale), rp = axis of the pygidium (rachis pygidial), ep = terminal axial spine of the pygidium (épine terminale du pygidium).

Les coaptations évoluent-elles ? Comme l'écrit Sahuc (1969: 62), '. . . pour répondre objectivement à cette question, il faut commencer par établir, à l'aide de critères autres que celui des coaptations elles-mêmes, la filiation des différentes catégories animales et leur ordre d'apparition dans le temps. Nous ne saurions nous baser sur l'évolution supposée des structures coaptatives pour soutenir ensuite qu'elles ont évolué'. Considérons le cas de *Crozonaspis*. Nous avons montré que les trois espèces *C. mayensis*, *C. struvei* et *C. rouaulti* présentaient de nombreux et importants caractères communs et que l'on pouvait sans réserve les rapporter à un seul et même genre. La succession dans le temps de ces Trilobites est connue, au moins pour deux d'entre eux: *C. mayensis* est abondant dans les 'schistes à Calymènes' de May-sur-Orne, d'âge llanvirnien; ces schistes reposent en effet sur les grès feldspathiques cambriens (le grès armoricain manque) et sont surmontés par le grès du 'petit May' daté du Llandeilien (voir à ce sujet Doré & Philippot 1962; Henry 1969). *Crozonaspis struvei* est une forme stratigraphiquement plus 'jeune' que *C. mayensis* dont elle semble issue, puisqu'elle se développe à la partie supérieure des couches de Morgat (Llandeilien) dans le synclinorium médian armoricain. Du Llanvirnien au Llandeilien, la localisation des dispositifs coaptatifs sur la carapace de *Crozonaspis* ne subit aucune modification, mais ces structures évoluent indéniablement dans le sens d'un perfectionnement: en effet, à partir du fort bourrelet céphalique de *C. mayensis* s'individualise, chez *C. struvei*, un véritable rostre tandis que l'échancrure correspondante du pygidium paraît s'approfondir. Un troisième stade évolutif pourrait être illustré par *Crozonaspis rouaulti* dont la doublure du céphalon porte trois facettes et un sillon de fermeture particulièrement marqué. On ne connaît malheureusement pas l'âge exact de cette dernière espèce.

Les exemplaires de *Crozonaspis incerta* (Deslongchamps), du grès de May inférieur ('petit May') de Normandie, sont mal conservés et une comparaison précise avec les autres formes connues du genre *Crozonaspis* reste actuellement malaisée. *C. incerta*, également pourvue d'un rostre céphalique, est proche de *C. struvei*, mais il est préférable de maintenir, au moins momentanément, l'indépendance des deux espèces.

Reste le cas de *Kloucekia dujardini*. Les structures coaptatives de ce Trilobite caradocien, bien que plus marquées, sont très comparables à celles de *Crozonaspis rouaulti*. On pourrait penser que *Kl. dujardini* est un descendant direct des *Crozonaspis* llandeiliens. La forte gibbosité glabellaire chez cette espèce ne contredit pas une telle supposition dans la mesure où l'on admet, avec Hupé (1953b:47), que les 'formes gibbeuses dérivent certainement de formes à glabelle normale'. Dans ce rameau phylétique, tout se passerait alors comme si le développement progressif du rostre céphalique pendant l'Ordovicien entraînait, immédiatement en arrière de ce rostre, une déformation de plus en plus prononcée de la suture faciale. Cette hypothèse est séduisante, mais elle appelle quelques réserves; il n'est pas impossible que des coaptations de même type puissent apparaître chez des Trilobites n'ayant entre eux aucun lien de parenté. Les structures coaptatives d'Invertébrés actuels 'présentent . . . parfois des convergences très nettes' (Sahuc 1969:65). D'autre part, on sait que l'augmentation du nombre de côtes pleurales au pygidium pendant l'Ordovicien semble être la règle chez les Zeliszkellinae; or le pygidium de *Kl. dujardini* ne compte que trois paires de côtes, chiffre sensiblement inférieur à celui des *Crozonaspis* stratigraphiquement plus 'anciens'.

L'origine des coaptations est un problème biologique qui prête à de nombreuses discussions. Si nous nous référons aux travaux récents de Sahuc, c'est parce que certaines observations de ce chercheur sont en accord avec les nôtres. Pour Sahuc, plusieurs facteurs, externes et internes, participent à la réalisation des structures coaptatives; le comportement de l'animal (facteur externe indirect) est à l'origine de pressions matérielles et de frictions (facteurs externes directs) se produisant dans les zones de contact des différentes parties anatomiques. Ces résistances physiques, jouant le rôle de stimulations externes, induiraient dans des régions précises une intensification de l'activité auto-organisatrice du vivant (facteur interne). Si l'on tente d'appliquer cette perspective de recherche, sommairement exposée ici, aux Trilobites étudiés dans cet article, on peut admettre que la faculté d'enroulement constitue un facteur externe indirect responsable des pressions matérielles existant dans les zones de contact. Chez *Crozonaspis*, la poussée évolutive (facteur interne) se traduirait alors, dans la partie antérieure du céphalon, par l'apparition d'un fort bourrelet se développant progressivement en un véritable rostre. Cette poussée évolutive (sensu Sahuc) diffusant au niveau du pygidium, un 'moulage actif' aurait pu s'accomplir sous forme d'une échancrure placée sous la base de l'épine caudale (cf. Sahuc 1969: 115). Sahuc (pp. 123–124) note également que dans les zones de stridulation de certains Coléoptères (*Xylotrupes lorquini*), les fines épines des régions avoisinantes se transforment en 'de grosses épines écourtées et aplaties en forme de carènes'. De semblables observations peuvent être faites sur tous les Trilobites adultes bien conservés que nous avons examinés: les granules deviennent progressivement plus denses et plus volumineux à proximité immédiate de l'échancrure céphalique de *Colpocoryphe rouaulti* (Fig. 10A), ainsi que sur la doublure du céphalon et le rostre de *Crozonaspis struvei* (Fig. 5C). Chez *Encrinurus tuberculatus* et *E. variolaris*, on peut aussi constater le développement de la granulation dans les zones de contact. Selon Sahuc (1969: 110), ces '. . . détails structuraux . . . semblent bien être des produits de l'activité inductive du vivant . . .'.

Pour Harrington (1959: 0102), certains Trilobites du Cambrien inférieur ne possédaient pas la faculté d'enroulement. Rasetti (communication personnelle) pense que la plus grande partie des Trilobites cambriens 'au moins tous ceux possédant une carapace compacte et convexe', pouvaient s'enrouler. Quoiqu'il en soit, les dispositifs coaptatifs des formes cambriennes, lorqu'ils existent, sont simples; les renseignements qui nous ont été donnés à ce sujet concordent parfaitement et il est probable que ces structures n'ont jamais atteint le degré de complexité et de perfectionnement qu'elles montrent fréquemment à l'Ordovicien. On sait par ailleurs que si des prédateurs susceptibles de s'attaquer aux Trilobites ne sont pas connus avec certitude pendant le Cambrien, il n'en est plus de même à partir du Tremadocien supérieur puisque certaines classes d'Invertébrés (Mollusques Céphalopodes par exemple) prennent un essor considérable (cf. Whittington 1966: 732). Cet essor rapide des prédateurs à l'Ordovicien aurait eu une influence sensible sur le comportement des Trilobites et l'enroulement, en tant que moyen de défense, aurait alors acquis, du moins chez certaines formes, une fréquence qu'il n'avait peut-être pas auparavant. Dans le cadre de l'hypothèse suggérée par Sahuc, l'augmentation du nombre des prédateurs constituerait un des facteurs externes participant indirectement à l'élaboration de dispositifs coaptatifs. Ces idées sont en accord avec celles exposées par Monod (1971: 142): 'Le fait que, dans l'évolution de certains groupes, on observe une tendance générale, soutenue pendant des millions d'années, au développement apparemment orienté de certains organes, témoigne de ce que le choix initial d'un certain type de comportement (devant l'agression d'un prédateur par exemple) engage l'espèce dans la voie d'un perfectionnement continu des structures et performances qui sont le support de ce comportement'. Chez les

Trilobites, l'enroulement considéré comme réaction de défense face à un prédateur n'est pas a priori la seule interprétation possible. En effet, l'enroulement de *Glomeris* paraît être plutôt lié à 'l'économie de l'eau': l'animal lutterait ainsi contre les variations brutales (saisonnières par exemple) des facteurs de l'environnement; en milieu aquatique, le phénomène de tamponnage rend toutefois cette hypothèse moins plausible, sauf dans le cas d'eaux peu profondes.

Les réflexions que nous avons exprimées dans cet article ne sont pas originales: empruntées à des travaux de biologistes, elles ont été 'adaptées' au cas des Trilobites et illustrées par quelques exemples choisis. Dans notre esprit, il ne saurait s'agir, ni d'une prise de position concernant l'origine des coaptations, ni de conclusions générales s'appliquant à toute la classe des Trilobites. Toutefois, par leur variété, leur stabilité au niveau de l'espèce, les dispositifs coaptatifs des Trilobites sont d'un intérêt certain en systématique. Ils devraient aussi s'avérer très utiles dans l'étude des problèmes phylogéniques.

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THE EYES OF *ASAPHUS RANICEPS* DALMAN (TRILOBITA)

by E. N. K. CLARKSON

ABSTRACT. The holochroal eyes of the Lower Ordovician trilobite *Asaphus raniceps* Dalman have been studied using light and electron microscopy.

In these eyes the refractive elements are elongated calcite prisms underlying a cornea which is continuous with, although structurally dissimilar to, the 'outer cuticular layer' described by Dalingwater. The prisms are orientated with their *c*-axes normal to the surface. Some of the material studied (from Öland) showed the effects of at least two phases of diagenesis, which in one case had resulted in the production of secondary prisms growing syntaxially on the primary prisms, and confusingly similar to primary structures.

The visual surface approximates a segment of an almost perfect spheroid whose radii of curvature in vertical and horizontal planes all converge to a single point, in a manner very similar to that of some superposition eyes in modern arthropods, with which analogies are drawn.

Problems in the use of calcite as a primary refractive medium are discussed, and it is concluded that the effects of birefringence could have been minimized by suitable pigment screens, like those of insects and crustaceans, underlying the prismatic layer.

The 'sensory fossettes' on the eye-socle are craters, each with a central perforation communicating with the internal surface.

TRILOBITES of the family Asaphidae have distinctive compound eyes whose range in form is quite well known from palaeontological literature. These eyes, often well preserved, are usually rather large and prominent, and often rise above the glabella; one remarkable species, *Asaphus kovalevskii* Lavrov, has eyes situated upon very elongated bases resembling long stalks. Asaphid eyes were referred to by various authors working in the nineteenth and early twentieth centuries; Schmidt's (1904) monograph, for instance, contains good illustrations. More recent authors have also described and figured asaphids with intact eyes, and Whittington's studies (1963, 1965) included many details of external eye morphology. Hupé (1953) has provided an excellent figure of the eye of *Asaphus cornutus* (Pander), reproduced in the 'Treatise' by Harrington (1959), and Rose (1967) has shown that in *Nileus* and *Isotelus* growth of the visual surface is accomplished by the addition of new lenses round the lower margin of the eye.

Although we possess a reasonably good understanding of the range in form and external morphology of asaphid eyes, there have been only two serious attempts to investigate their internal morphology; the first being that of Lindström (1901), who described sections and fracture surfaces of the eyes of several Scandinavian asaphids. He showed that the refractive elements were elongated prisms (rather than lenses) underlying the cornea, and gave a good account of their anatomy. Balashova (1948) confirmed that the eye had a prismatic structure, and further indicated that the eye-socle (Lindström's reticulate or spongious zone) was permeated with very fine pore-canals and that there were 'fossae' on the socle opening downwards into fine calcite-filled tubes, to which she imputed a sensory (tactile) function. The advent of the scanning electron microscope stimulated further study of the eyes of asaphids, and, as expected, revealed many details invisible to Lindström.

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In 1967 Dr. John Dalingwater kindly sent me a number of finely preserved specimens of *Asaphus* which he had collected from Böhlin's (1949) locality where the glauconitic '*raniceps*' limestone is exposed at the cliff of Haget, northern Öland. Tjernvik (1972, p. 305) gives the age of this limestone as lower Llanvirnian (*bifidus* zone). Specific identification of these was somewhat difficult as most of the specimens were fragmentary, but Dr. Dalingwater and I agree that they most closely approximate *A. raniceps* Dalman, *sensu* Angelin (1878, p. 53).

During the investigation of these eyes, using light and electron microscopy, it became evident that different specimens had been variously affected by diagenesis. This made the interpretation of the original structure difficult, for it was not immediately apparent in all cases which structures were primary and which were the results of secondary recrystallization. In one specimen, for instance, there were radially arranged microstructures extending quite deep inside the eye, these were so regularly formed that they could have been mistaken for primary structures, but they proved, in fact, to be secondary, growing syntaxially upon primary elements of the 'refractive' zone.

Part of this study has been therefore orientated towards an understanding of the nature of primary structures and how they were affected by diagenesis; the rest is more closely concerned with the organization of the eye as a functional visual organ.

The specimens were prepared for examination as follows. The prefix 'Gr I' refers to the collections of the Grant Institute of Geology, University of Edinburgh.

External surface only. Gr I 5501.

Internal structure using thin sections, polished surfaces, and cellulose peels. Gr I 5502, 5503, 5510, 5511, 5512.

External and internal features (fracture surfaces and etched sections) using the Stereoscan. Gr I 5504, 5505, 5506, 5507, 5508, 5513.

THE CUTICLE OF *ASAPHUS*

Dalingwater (in press) in a study of the structure of trilobite cuticles has shown that *Asaphus raniceps* (from the same locality as my material) has a cuticle of two distinct layers. The outer layer, less than one-tenth of the total thickness, is composed of fairly regular perpendicular crystallites which have a fibrous appearance. The thick inner area is less distinctly structured, and no individual crystallites could be seen. Neither layer extinguished uniformly in polarized light implying that the calcite of which the bulk of the cuticle is composed does not occur in regularly arranged crystallites. There was also some organic matter remaining, which could be isolated by decalcifying the cuticle with EDTA.

These two cuticular layers have their direct counterparts in the eye. The thin outer layer passes laterally into the cornea, losing its fibrous appearance at the periphery of the eye-socle, and becoming thinner. The thick inner cuticular area is directly equivalent to that part of the eye underlying the cornea, consisting of large hexagonal prisms of calcite, which acted as refractive units, directing light to the photoreceptive organs below. These large prisms unlike the inner cuticular area are regularly structured and have their *c*-axes orientated near normal to the outer surface of the eye.

VISIBLE STRUCTURES IN THE EYE OF *ASAPHUS RANICEPS*

External surface. The external form of the eye (text-fig. 1*a–c*) closely approximates that of *Asaphus cornutus* Pander, from the Ordovician of Estonia, figured by Hupé (1953, p. 77, fig. 31) and reproduced by Harrington (1959, p. O.88, fig. 64i). It is large and strongly curved in plan, projecting well above the glabella. The visual surface, which has a much higher profile curvature anteriorly, is situated upon a vertical 'eye-socle' rising abruptly from the librigena (*sensu* Shaw and Ormiston 1964), upon which are shallow funnel- or basin-shaped cavities, irregularly distributed and decreasing in size towards the base of the eye-socle. These were described by Hupé as sensory fossettes. The facial suture is semicircular, separating the visual surface from the palpebral lobe, which slopes sharply down to the glabella, and carries terrace-line ornamentation.

There is a thin pellucid cornea covering the surface, merging laterally into the outermost layer of the cuticle (text-fig. 4*c*; Pl. 50, fig. 9). Through this cornea the many quadrate or hexagonal lenses can be seen by translucence, especially if the specimen is immersed in a medium of high refractive index. Hupé's specimen showed patches of larger irregularly distributed lenses, which he thought had resulted from damage during ecdysis.

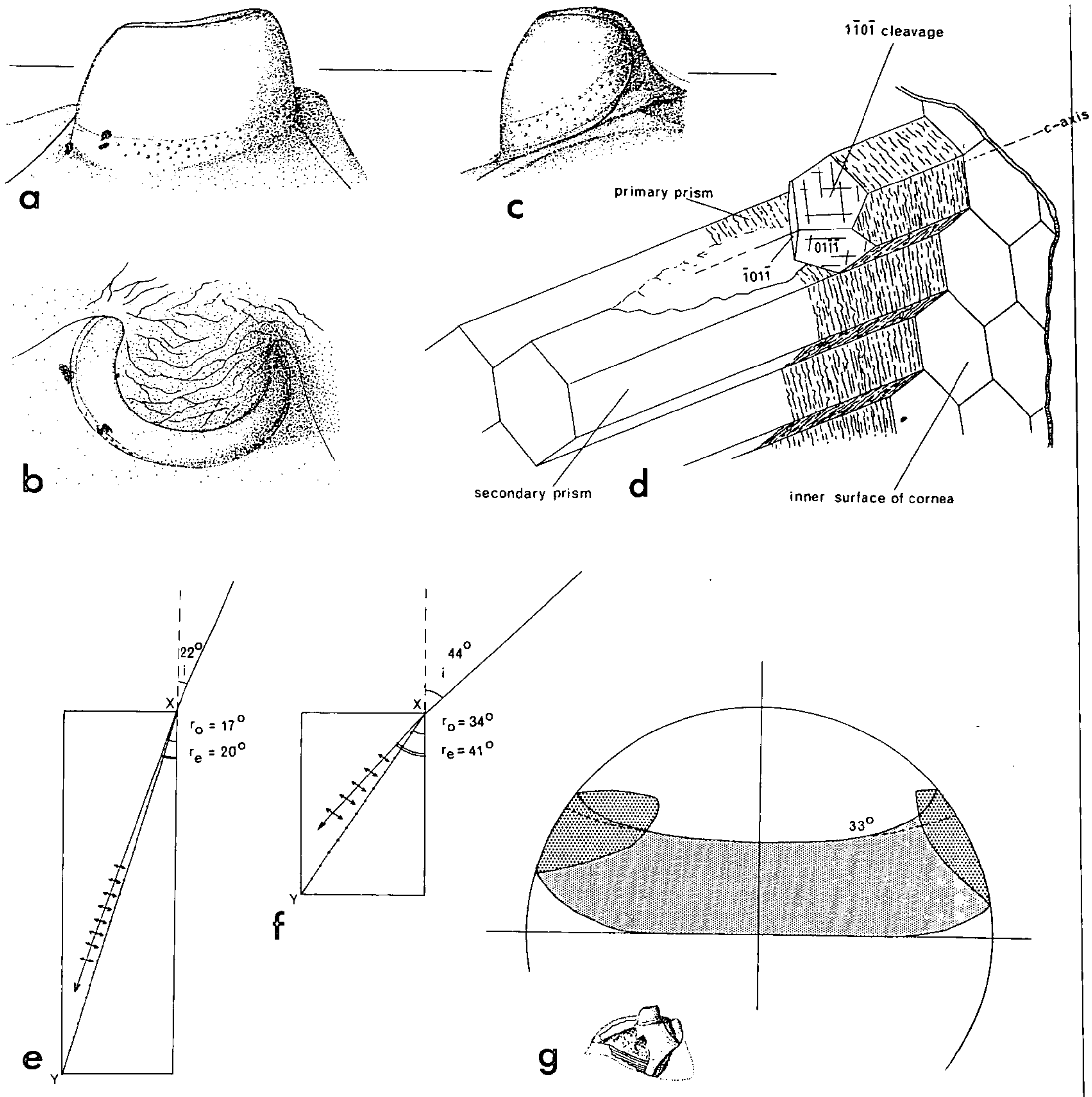
Even with the Stereoscan the external surface of the best-preserved specimens appears to be smooth and structureless; a micrograular effect is not evident until magnifications of over ×500 is reached. Relative granularity, however, varies according to the quality of preservation of the material.

Internal structure. Lindström (1901, pp. 28, 37–43, pl. 1, figs. 8–30) gave a good account of the eye structure in asaphids as known to him, and noted the following main points. Welded to the inner surface of the cornea are the refractive organs, appropriately termed prisms, which are closely packed hexagonal pillars, arranged radially. (This zone is here termed the primary prismatic region.) If the eye is fractured the prisms separate cleanly from one another, and can be seen under low magnification like columns of basalt lying on their sides. Vertical sections show that the prisms generally become longer and thinner near the margins of the eye, and especially towards the lower rim of the visual surface.

Above and below the visual surface the prisms pass into a rather structureless 'marginal zone', twice as thick (in section) as the primary prismatic region. Lindström referred to this also as the 'spongious' or 'reticulate' zone, in view of its spongy appearance in slightly decomposed specimens. He noted the fossettes on the eye-socle also but did not impute a sensory function to them.

The use of the Stereoscan has given more information upon the nature of most of these regions, and most particularly of the primary prismatic layer.

In the best-preserved specimens, each prism is a single crystal of calcite with its optic axis normal to the surface (text-fig. 1*d*). The optic axes of neighbouring prisms diverge slightly. Thin sections made horizontally through a complete eye and examined using crossed nicols show that the prisms undergo extinction in the NS. and EW. positions; this pattern remains constant on rotation. Tests with a sensitive tint plate show that the *c*-axes of the calcite crystals are normal to the surface. It is difficult to imagine how such a system as this, with regularly diverging optic axes, can be other than primary, for although further impregnation with calcite during diagenesis might take place in optical continuity with the existing crystal lattices, more extensive recrystallization would very likely destroy the regularity of the pattern, as has actually happened to some extent in some of the less well-preserved specimens. The eyes in living specimens of *Asaphus raniceps* must therefore have had a high



TEXT-FIG. 1. *a–c.* Left eye of *A. raniceps* Dalman. ×6·5. Gr I 5501, in lateral, dorsal, and posterior views. The black specks are adherent glauconite grains. *d.* Diagrammatic construction showing crystallography of the primary and secondary (diagenetic) prisms underlying the cornea. *e–f.* Polarization of light rays passing through a peripheral (*e*) and a central (*f*) primary prism. The o-ray (*XX*) is shown passing along the long diagonal (*XY*). For full explanation see text, p. 438. *g.* Minimal visual field of *A. raniceps*, from Gr I 5501, orientated as in the small diagram (the latter ×2/3).

proportion of calcite, each prism being a single calcite crystal, presumably associated with protein and other organic material.

It is not surprising to find calcite used as a structural component in the eyes of trilobites, for many modern arthropods which have cuticles reinforced with calcite are found to have calcite in the eye as well. It is not, however, used in the same way, for although the prisms of *A. raniceps* have an extremely regular arrangement, there is no regularity of structure in the rest of the cuticular inner area. The arrangement of calcite crystals in the eyes and cuticle of many modern arthropods is singularly irregular. According to Richards (1951, pp. 103–105), crystallization of calcite in very many modern arthropods begins independently at various loci and each crystal simply continues growth until it contacts another crystal. This is true for the calcite crystals within the eye as well, as Düdich (1931) clearly showed; for randomly orientated calcite crystals cut across the ommatidia at all angles without any relationship at all to organic boundaries. In *A. raniceps* on the other hand each visual unit, or at least the upper part, was individually calcified, and, as argued later, calcite was probably the primary refractile material.

In thin sections the cleavages in the prisms often appear distinct, each prism having its own set of cleavages, orientated slightly differently to its neighbours. Not infrequently, however, two or three neighbouring lenses in some sections can be seen to have the same cleavages running through all of them, and the small block or 'domain' of lenses goes into extinction as a unit with sharply marked edges. Rotation of the stage thus produces a stepwise rather than a regular extinction. It is likely that such domains were secreted together and retained their optical continuity throughout life. It has been suggested to me by C. Eccles that this may have resulted from a crystallographic constraint, and that neighbouring prisms had to grow in the same optical orientation as the angle of divergence of individual prisms was too small to permit crystallographic separation. Only when there was a critical angle of divergence could another domain grow at a different crystallographic orientation. It is not clear whether new prisms were always secreted in domains but it is not unlikely, for the individual prisms often seen in section with separate orientation could belong to a small domain of three or four lenses of which only one was cut in the plane of the section.

The tendency for small groups of neighbouring lenses to have the same crystallographic orientation is shown also in Stereoscan photographs, such as Pl. 49, fig. 3 where two adjacent prisms lying below the cornea have cleavages running through both of them without a break.

The sides of intact prisms as shown in Stereoscan photographs are remarkably rough, with corrugated granular surfaces (Pl. 48, figs. 1–3; Pl. 49, fig. 5). These corrugations are always parallel with the cornea, and are related to the underlying cleavage directions (text-fig. 1*d*). Usually, though not always, the prisms become long and thin towards the top and particularly the bottom of the visual surface (Pl. 48, fig. 2). Here they may be up to twice the length in other parts of the eyes. In some specimens, however, this tendency is far less evident. It is possible that the former condition occurs only in immature specimens. It is clear that the new visual units must, as in Phacopina (Beckmann 1951; Clarkson 1966*a*) have been produced in a generative zone at the periphery of the eye and the work of Rose (1967) confirms that they were added only at the base of the visual surface. In *Asaphus* the generative zone seems to have lain at the lower junction of the visual surface and the marginal zone. New prisms were first of all the same width (in section) as the marginal zone and very thin; they shortened and grew thicker as they became functional.

Some of Lindström's specimens showed concentric layering within the lenses. Such concentric structure was not visible in any of my material, and neither did etching with dilute acid (Pl. 48, fig. 5) reveal any structures other than the cleavages which were picked out by the acid. The apparent absence of layering may have been because Lindström's material was less fresh than mine, and that mild weathering might have revealed primary structures in his specimens which were not clear or evident in mine though they may have been present.

The sensorial fossettes. Hupé (1953) noted a series of irregularly distributed, shallow excavations on the eye-socle, which he described as sensorial fossettes. Lindström (1901) had previously noted the presence of these little pits, but imagined them to be the excavations of some boring organism. Some thin sections and polished surfaces made in the present study showed that each fossette is set at the summit of a narrow canal (now calcite filled) which can be traced to the inner surface of the eye-socle though little structure can be seen, even in the posterior part of the socle where the best and largest examples are normally located (text-figs. 4*a*, *b*, *c*; Pl. 50, fig. 9). Stereoscan photographs of the external surface simply show the fossettes as shallow rimless craters and contribute nothing further to our knowledge (Pl. 48, fig. 6).

Hupé's interpretation of the fossettes as sensory structures seems appropriate; similar structures in the neighbourhood of some insect eyes are the sites of vibro-sensory organs whose nerves are connected with the third optic lobe (Burtt and Catton 1966*a*). Very many trilobite eye lobes are provided with pit-like structures, narrow vertical grooves, small tubercles (often only properly visible with the Stereoscan), or other such organs, usually located on the eye-socle; these may all be the sites of sensory organs of some kind, hence the fossettes of *Asaphus*, though exceptionally large, are not unusual amongst the trilobites.

EFFECTS OF DIAGENESIS

Recrystallization of the primary prisms. The course of diagenesis was followed in thin sections of the eyes of different specimens following Friedman (1964). Some sections, or parts of sections, showed the original form of the calcite prisms, either as single crystals or as small domains. In these, the cleavages are always distinct

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EXPLANATION OF PLATE 48

Asaphus raniceps Dalman (Stereoscan photographs all of fracture surfaces except figs. 5 and 6).

Fig. 1. Prisms near lower margin of the visual surface. × 110. Gr I 5505.

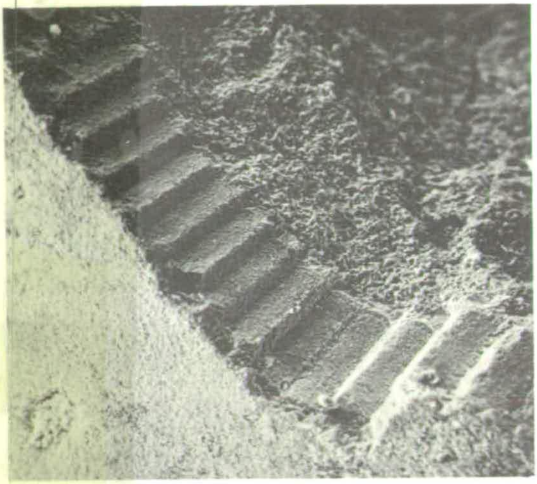
Fig. 2. Elongated prisms near the lower margin of the visual surface. × 440. Gr I 5504.

Fig. 3. Corrugated surfaces of prisms in the central part of the eye. × 2300. Gr I 5507.

Fig. 4. Similar prisms showing cleavages parallel with the corrugations. × 1100. Gr I 5507.

Fig. 5. Horizontal ground surface, cutting through prisms and etched with dilute HCl. × 525. Gr I 5510.

Fig. 6. Surface of the eye-socle in the posterior region, showing sensory fossettes. × 110. Gr I 5507.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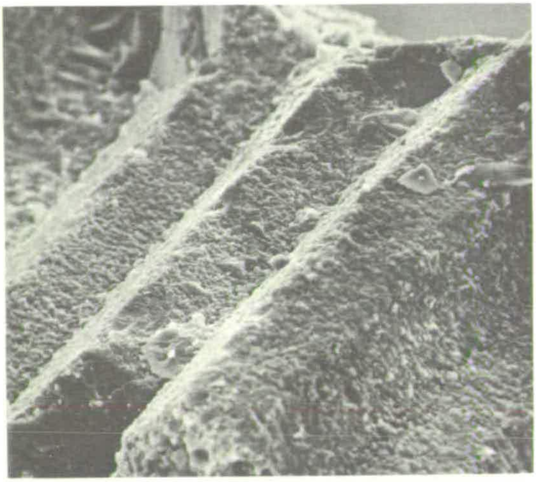
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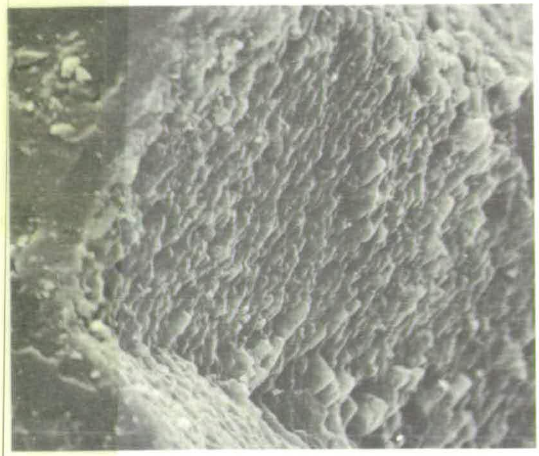
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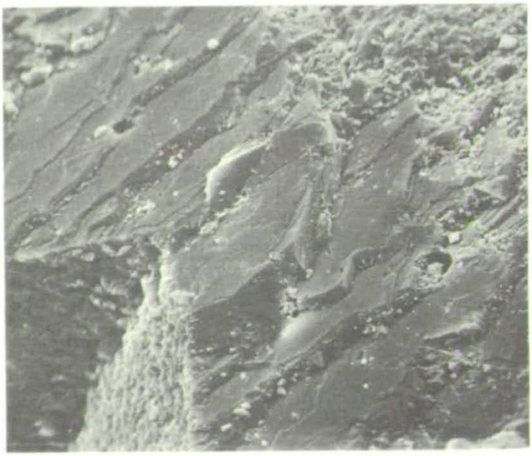
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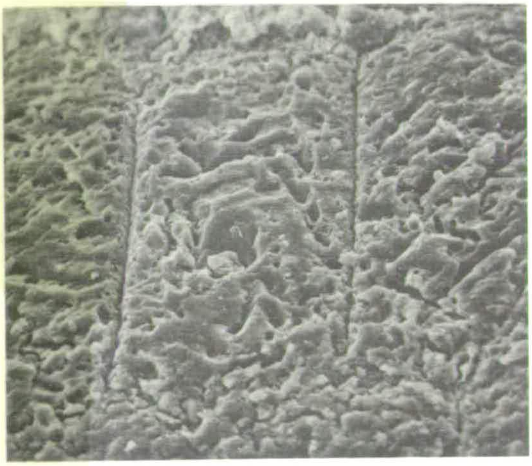
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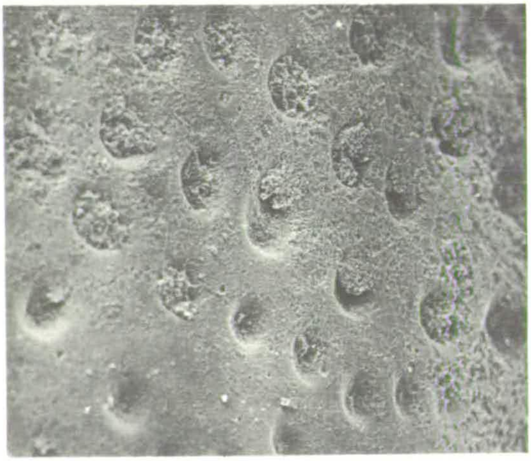
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CLARKSON, *Asaphus* eyes

(Pl. 50, fig. 1), and extinction follows a stepwise pattern. The lower ends of the prisms may be rounded or somewhat ragged in appearance, but never show crystal faces.

Two stages of diagenesis have been differentiated. The first stage involved some degree of recrystallization of calcite *in situ*, into a microcrystalline form, resulting in the crystal boundaries and cleavages becoming indistinct, and blurring the extinction pattern (Pl. 50, fig. 6). This was seen in its early stages in certain parts of otherwise unaltered eyes. The recrystallized areas (yellow-brown under crossed nicols) are often darker in colour than the primary crystals.

In some sections diagenesis has been carried a stage further, with a second development of microcrystalline calcite invading the already altered primary prismatic region (Pl. 50, figs. 7, 8). This second stage microcrystalline calcite is variable in colour, but is usually a very light yellow, contrasting with the darker yellow-brown of the first-stage diagenetic material. Sometimes it appears as randomly orientated flecks or patches within the prisms. Often it is seen as a 'front' which has advanced into the prismatic region from either surface. On occasion it has picked out the boundaries of the altered prisms, which then appear as thin yellow lines, and it may have invaded the interior of each prism from all its edges at once. In such cases all that is left of the original prismatic layer is a series of elongated kernels (already altered during the first stage in diagenesis) surrounded by lighter coloured microcrystalline calcite of the second stage. These kernels may be regular in appearance, but are sometimes truncated by a 'front' of second-stage microcrystalline material, where the latter has grown more rapidly in one direction than in others (Pl. 50, fig. 8).

Recrystallization of primary structures is less easy to recognize in fracture surfaces or in etched sections using the Stereoscan. It has been observed, however, that whereas certain calcite prisms have sharp, well-defined corrugations on the surface, parallel with the cleavages, other calcite crystals in the same eye may have much less regular corrugations, and only a rough granularity to the surface. As unaltered primary crystals have well-defined cleavages, it would seem likely that the crystals with roughly granular surfaces have undergone some measure of diagenesis.

Secondary growths below the primary prisms. In one specimen (Gr I 5508), both fracture surfaces and thin sections revealed inward extensions of the primary prisms.

EXPLANATION OF PLATE 49

Asaphus raniceps Dalman (Stereoscan photographs, all of fracture surfaces).

Fig. 1. Slightly oblique view of primary prisms (corrugated), with smooth secondary (diagenetic) prisms growing syntaxially upon them. ×180. Gr I 5508 (cf. text-fig. 2).

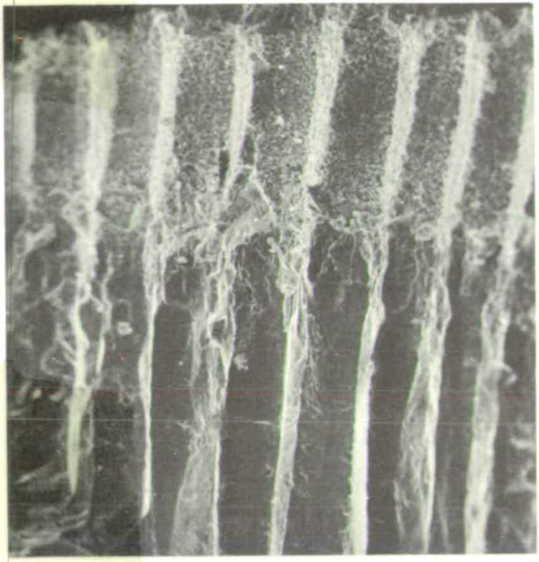
Fig. 2. Lower terminations of the same secondary prisms and subjacent area of recrystallized calcite. ×130. Gr I 5508 (cf. text-fig. 2).

Fig. 3. Several prisms underlying the cornea, visible as an upstanding wall near the top of the photograph. Two adjacent prisms are fractured showing a common cleavage direction running through both. ×325. Gr I 5506.

Fig. 4. Junction between primary and secondary prisms (cf. Pl. 49, fig. 1). ×485. Gr I 5508.

Fig. 5. Enlarged surface of corrugations on the outer surface of a prism (cf. Pl. 48, fig. 2). ×2400. Gr I 5504.

Fig. 6. Prisms near the lower margin of the visual surface. ×65. Gr I 5505.



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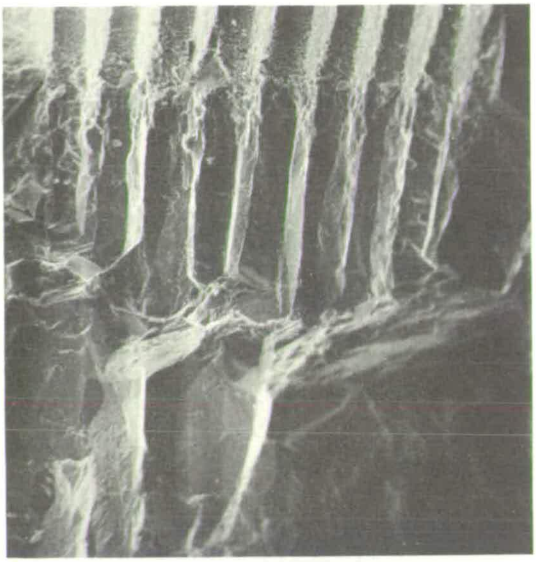

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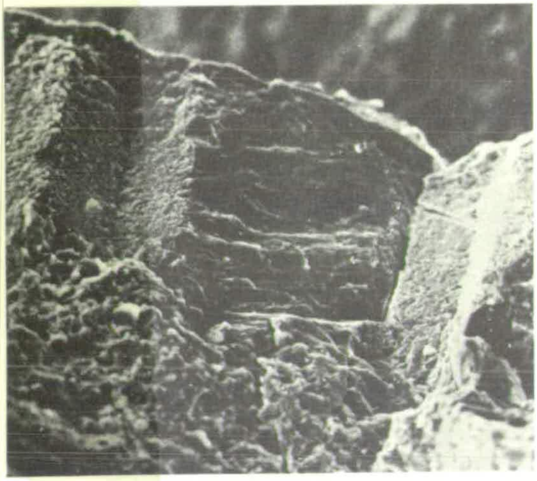

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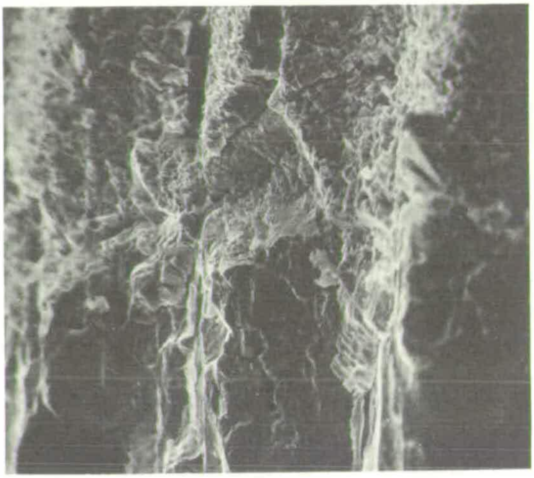

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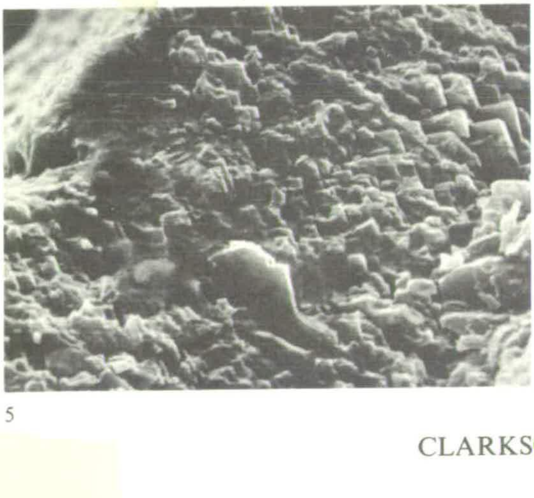

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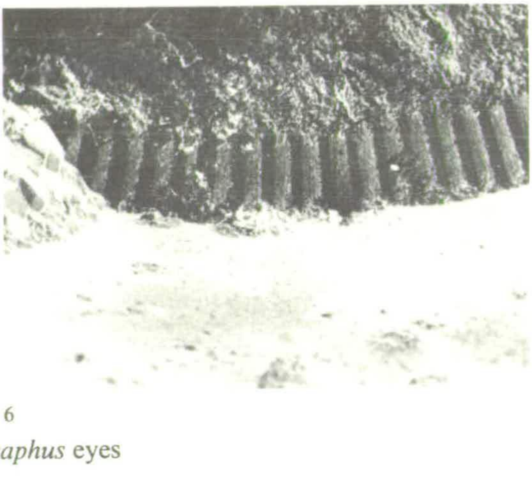

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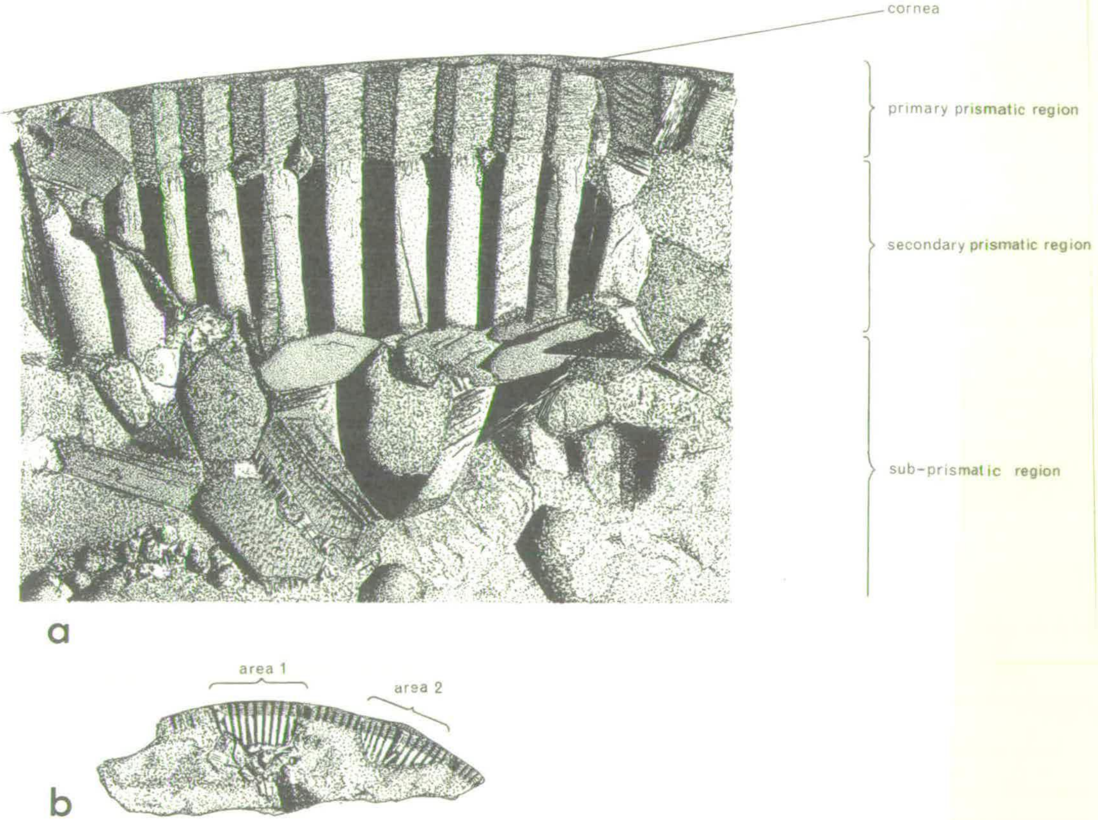
CLARKSON, *Asaphus* eyes

Stereoscan photographs showed these to be of extremely regular form, being syntaxial, pillar-like extensions of the outer prisms (Pl. 49, figs. 1, 2; text-fig. 2*a*, *b*). They are found only in certain parts of the eye, and in all the Stereoscan preparations extend to about the same level. Between and around these areas lie micrite and finely recrystallized sparite, in patches. These extensions, referred to as 'inner' or 'secondary prisms', have very smooth outer surfaces, and the transition from the corrugated outer zone is sharp, being marked usually by a line of somewhat irregular fractures (Pl. 49, fig. 4). One example showed the edges of a primary prism being met by the sides of an inner prism, but normally the edges of a primary prism are continuous with those of a secondary one.

Below the inner prisms (sub-prismatic region in text-fig. 2) are large, equant calcite crystals with patches of micrite and sparite. Some of these are syntaxial with the inner prisms. Several orientated crystals of dog-tooth spar cemented together by a calcitic jacket were noted in one area; these had near-perfect crystal faces.

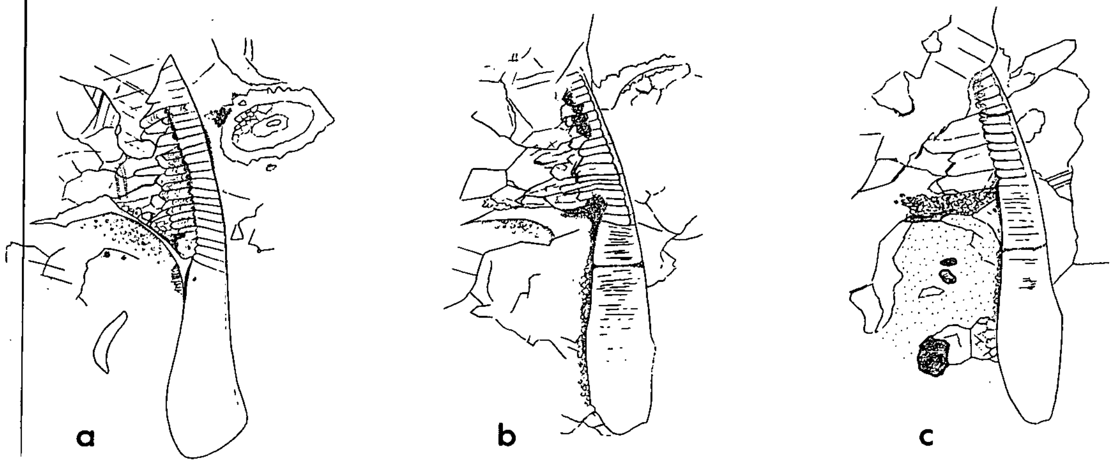
Though there would be little doubt that all the structures in this sub-prismatic



TEXT-FIG. 2. Drawings made from fracture surface of Gr I 5508 showing areas of primary and secondary (diagenetic) calcite. *a*. Enlargement of area 1 × 120. *b*. Fragment of eye showing the two areas of secondary prisms, one of which is enlarged in *a*. × 18.

region are secondary, the regular appearance of the inner prisms in the Stereoscan photographs might suggest that at least these could be of primary origin, though other Stereoscan evidence is equivocal. Thin sections, however, indicate that the inner prisms are very probably secondary. The series illustrated in text-fig. 3*a*–*c* are vertical sections made obliquely through the posterior region of the eye of Gr I 5508.

Text-fig. 3*a* (Pl. 50, fig. 3) shows a cellulose acetate peel stained with methylene blue (Dickson 1966). The primary layer has been differentially affected by first-stage diagenesis, though crystal boundaries are clear in places. There is a pronounced line of demarcation between the primary and the inner prisms. The latter, though regular in places, are elsewhere of differing lengths, and sometimes overgrow one another. They show clear evidence of secondary growth on the bases of the primary prisms in that a record is left of the past position of the euhedral crystal faces. The structure becomes very irregular at depth, but even here some crystals are still more or less syntaxial with the primary prisms. Similar, though much smaller, secondary growths were visible in other calcitic shells in the same section.



TEXT-FIG. 3. Effects of diagenesis shown in thin sections and cellulose peels of Gr I 5502. *a*. Oblique vertical section near posterior margin stained with methylene blue, showing primary and secondary prisms. *b*. Similar section, stained with alizarine red-S and acid fuchsine, with very irregular secondary prisms. *c*. Thin section through the same area, showing complete recrystallization of the secondary and partial alteration of the primary prisms. All ×20.

Cellulose peels stained with alizarine red-S and acid fuchsine (Pl. 50, fig. 2; text-fig. 3*b*), through the same general region but more posteriorly, showed much the same kind of structural elements but picked out slightly different details. The section illustrated was more strongly affected by second-stage diagenesis, and the boundary between primary and secondary structures was indistinct. In general, there was far less regularity, which emphasizes the secondary nature of the inner prisms. This section also showed a fringe of small secondary calcite crystals, elongated and with axes normal to the surface of the cuticle, growing on the inside of the eye-socle. These are clearly analogous to the inner prisms.

In an optical thin-section (Pl. 50, fig. 8; text-fig. 3*c*), there are very large elongated euhedral crystals, growing below the primary layer, each encompassing the bases of several (altered) primary prisms. They are in optical continuity with the latter, though these are altered by first-stage diagenesis, but they are not in optical continuity with the light yellow material of the second diagenetic stage. Probably these large euhedral crystals resulted from the coalescence of several smaller crystals which originated in contact with the primary prisms.

It is clear from the foregoing observations that all the calcitic elements below the primary prismatic layer are of secondary origin. The great regularity of their structure in some parts of the eye (which is not always maintained in other regions) is merely a reflection of the regular arrangement of the large prisms above, which provided suitable foci for continued growth of calcite, provided that there was a void below. It may have been that there were partially calcitized elements below the primary prisms which could have controlled the direction of subsequent calcitization, but there is no direct evidence of this.

VISION IN *ASAPHUS RANICEPS*

Visual field. A provisional determination of the visual field has been made, using similar apparatus and techniques to those described formerly (Clarkson 1966*a*, *b*). Since the prisms are normal to the surface it was possible to use a graticule and protractor to measure the inclination of the upper and lower margins of the visual surface, every 10° of longitude from front to rear, in a manner comparable with the measurement of the axial bearings of individual phacopid lenses. Plotting these inclinations on a Lambert net gave an angular range of vision quite similar to that of many phacopids (text-fig. 1*g*), overlapping at front and rear to give some degree of binocular vision. The relatively narrow latitudinal extent of vision may be contrasted with that of many holochroal eyes, where latitudinal ranges of up to 120°

EXPLANATION OF PLATE 50

Asaphus raniceps Dalman (Photomicrographs of thin sections, except Figs. 2 and 3 which are acetate peels).

Fig. 1. Horizontal section through eye showing the cleavages running through the prisms and the rounded terminations of the latter. Plane polarized light. ×80. Gr I 5512.

Fig. 2. Oblique vertical section (acetate peel) stained with alizarine red-S and acid fuchsine, with very irregular secondary prisms. ×65. Gr I 5502 (cf. text-fig. 3*b*).

Fig. 3. Similar section (acetate peel) stained with methylene blue, showing primary and secondary prisms. The latter are rather irregular and exhibit growth lines. ×65. Gr I 5502 (cf. text-fig. 3*a*).

Fig. 4. Oblique vertical section showing primary prisms only. ×18. Gr I 5511.

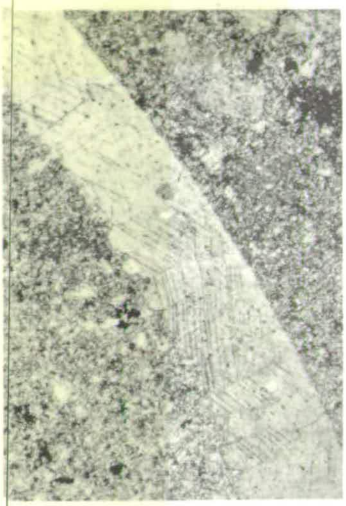
Fig. 5. The same under crossed nicols. ×18. Gr I 5511.

Fig. 6. Part of vertical section through an eye somewhat altered by first-stage diagenesis, showing primary prismatic layer, with indistinct prisms, and the thin cornea (lower part of this section in fig. 9). ×40. Gr I 5503 (cf. text-fig. 4*c*).

Fig. 7. Part of a vertical section, showing advanced diagenesis, passing through the uppermost part of the visual surface (upper marginal zone of Lindström). ×80. Gr I 5503.

Fig. 8. Oblique vertical thin section showing complete recrystallization of the secondary prisms and partial alteration of the primary prisms. ×37. Gr I 5502 (cf. text-fig. 3*c*).

Fig. 9. Downward continuation of section in Pl. 50, fig. 6, showing inward extension of a sensory fossette and the upward passage of the vertically laminated outer cuticular layer of Dalingwater into the cornea at the base of the eye-socle. ×40. Gr I 5503 (cf. text-fig. 4*c*).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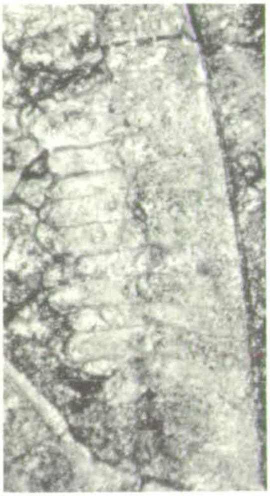
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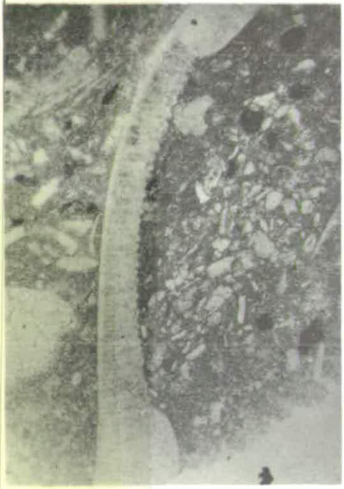
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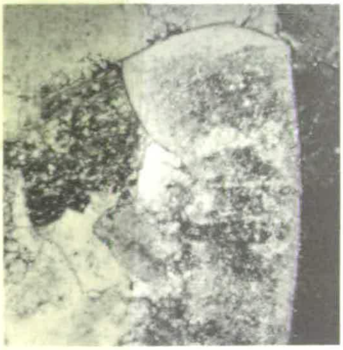
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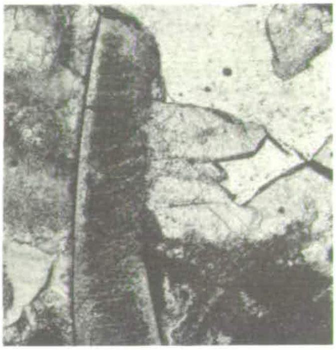
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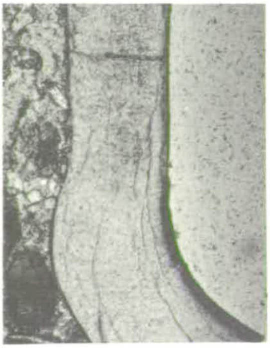
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CLARKSON, *Asaphus* eyes

for each eye, with marked overlap above, are not uncommon. This plot represents the minimum possible range of vision, assuming that the peripheral prisms receive only light coming parallel with the *c*-axis. The eye may have actually been capable of receiving light from outside this zone and transmitting it to the photoreceptors; this would depend upon whether or not screening pigment was present, isolating the ommatidia as in modern compound eyes.

Optics of the calcite prisms. Calcite was used as a primary structural component in trilobite cuticle. It was also present in the eye, where it was of particular value, being rigid, easily secreted in the same way as the rest of the cuticle, and above all refractive and transparent. But calcite is an anisotropic mineral with the property of double refraction, and its use in an optical system raises problems. Some modern arthropods have an irregular mosaic of calcite crystals within the eye as mentioned earlier.

In the following discussion on calcite optics each prism is considered as an individual calcite crystal, though it is recognized that each was probably penetrated throughout by organic matter. How far this would have altered the refractive index, if at all, cannot be assessed but the birefringent properties of calcite would not have been eliminated by such interpenetration. The calcite cornea may also have had an organic association.

Each prism is a single hexagonal crystal with its optic axis (*c*-axis) normal to the surface of the eye. Any light rays entering the crystal normal to the visual surface (i.e. parallel with the optic axis) would be transmitted, unpolarized, straight through the crystal without any change of direction. A light ray entering obliquely, however, will be resolved into two linearly polarized rays vibrating perpendicular to each other. The ordinary ray has constant velocity whatever the direction of incidence, but the extraordinary ray increases in velocity as the angle of incidence increases from the normal. Oblique incident rays not only polarize, but produce double images at different depths. Herein lies the disadvantage of calcite; some interference with the visual process would be expected, unless there were some system within the eye for ensuring that only normal or near normal rays were actually let through to the photoreceptive organs below.

Let us consider the angular light receptivity of each crystal. Median sections of two crystals, of the dimensions actually found in different parts of the eye, are illustrated in text-fig. 1*e*, *f*. Text-fig. 1*f* is the typical form, occurring in all but the peripheral regions of the eye, whereas text-fig. 1*e* is a crystal from the generative zone hear the lower margin. If each prism is considered as an isolated unit, the most oblique incident ray which it could transmit would be refracted along the line *XY* which is the path and wave-normal of the ordinary ray.

Light entering at a higher angle of incidence would be refracted against the wall of the prism. The angle of incidence for such a refracted ray travelling along the line *XY* can be calculated using Snell's Law and the following refractive indices ($n_{\text{water}} = 1{\cdot}33$, $n_{\text{o-ray}} = 1{\cdot}66$). The highest angles of incidence are then 44° and 22° respectively for the two prisms. If $n_{\text{e-ray}} = 1{\cdot}48$, then using the optical indicatrix for calcite, the path of the extraordinary ray incident at *O* may be constructed as in the diagram; as it travels faster it is less highly refracted. Thus each prism, considered by itself, has quite a high range of angular receptivity.

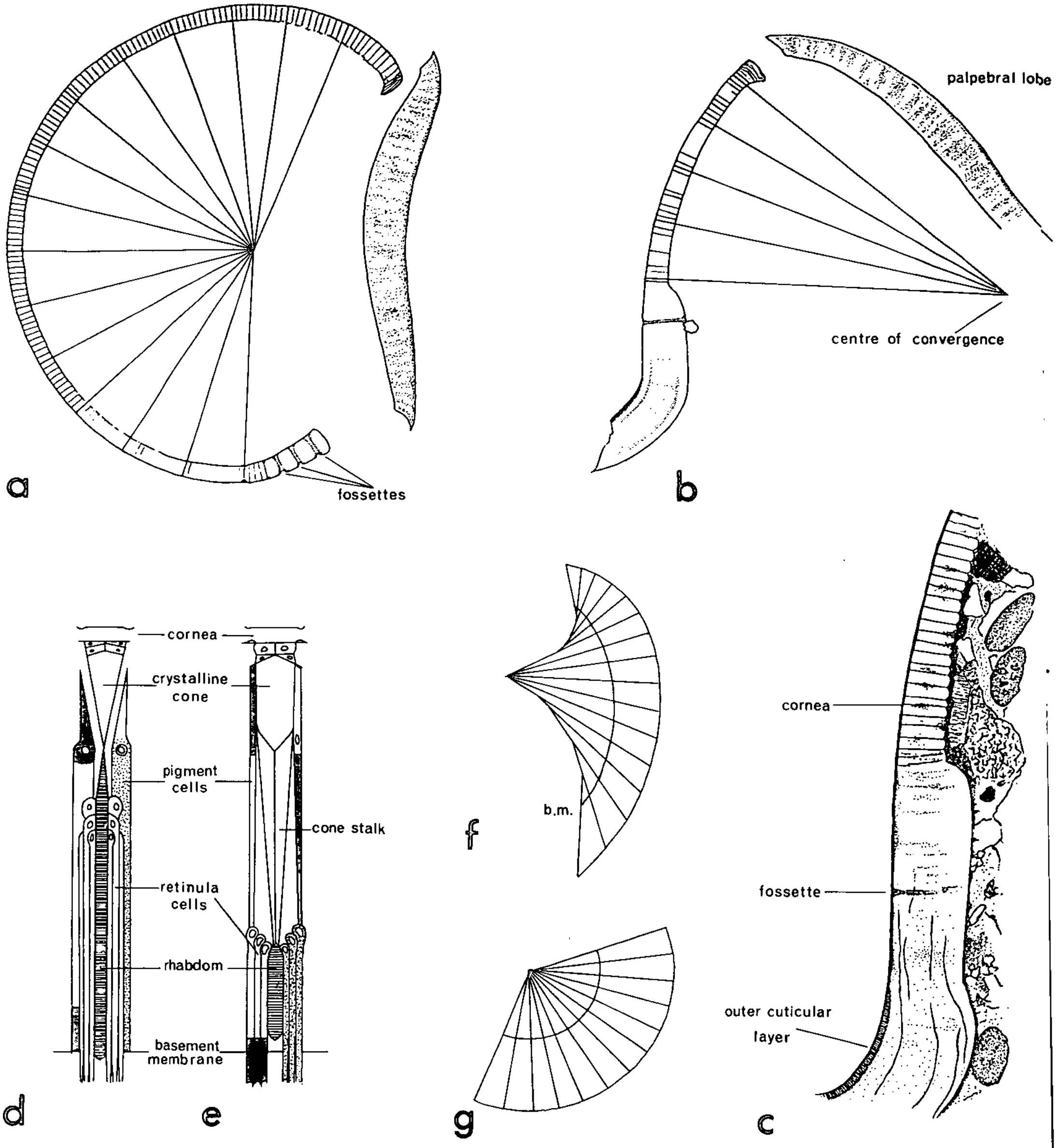
The prisms in the eye do not, however, exist in isolation, but are contiguous one with another. It is not known, of course, whether in life they were optically separated by organic layers along their walls. There is no evidence of such layers, and their former presence is rendered unlikely both by the close contiguity of the prisms and the fact that there are small domains of optically associated prisms where the cleavages pass through from one crystal to another. The lenses of modern insect and crustacean eyes, where contiguous like those of *Asaphus*, are sometimes optically isolated one from another by such highly refractive layers but not always, and indeed the superposition system of vision, as mentioned later, depends upon their close optical contiguity.

If, therefore, as we assume, the prisms of *Asaphus* were originally in optical contiguity, then the dioptric system as a whole would actually be receptive to a much higher range of light incidence, for the light could pass through neighbouring crystals. In such a case the divergence between the path of the extraordinary and the ordinary ray would increase, resulting in more extreme double refraction and hence double images at different depths.

Such double images, however, could have been virtually eliminated and not transmitted to the photoreceptors if the *Asaphus* eye were provided with a layer of absorbing pigment, just below the prismatic region, exactly as with the 'distal retinal pigment' of many known crustaceans (text-fig. 4*d*, *e*), which occurs in both apposition and superposition eyes. In the latter, there is a cylindrical sleeve of black or brown pigment surrounding the upper parts of each ommatidium below the lens, embracing the crystalline cone and the area below it, which absorbs unwanted light rays. A similar pigment sleeve in *Asaphus* located just below the prisms, would fulfil an identical function, and if the central bore were narrow, would effectively restrict most of the oblique rays, and screen them from the other ommatidia. If this were the case a mosaic-type image could then be formed by the eye, using only rays parallel with the axis or only slightly oblique and thus cutting out most of the adverse effects of double refraction. Such a system would allow a degree of mosaic vision not greatly inferior to that of modern arthropods. The extreme sphericity of the visual surface would give a more or less undistorted image of the mosaic kind, and it might also relate to a kind of superposition vision, as discussed in the next section.

Arrangement of deeper-lying structures. The visual surface of *Asaphus raniceps* has an almost constant horizontal curvature, the radius of which is slightly less than that in the vertical plane, though the latter is less regular, and decreases towards the top of the eye. Thus the visual surface approximates a segment of a prolate spheroid in which the vertical axis is slightly greater than the horizontal ones.

The eye has a slightly higher profile curvature anteriorly than posteriorly, and the visual field is expanded latitudinally towards the front (text-fig. 1*g*). Apart from this slight difference the curvature of the eye is otherwise regular, and follows the almost perfectly radial arrangement of the primary prisms. In horizontal and vertical sections of well-preserved specimens the edges of the prisms are clearly visible, and may be used as a basis for some reconstruction of the internal parts. If lines are drawn along the edges of adjacent prisms and extended inwards, they are found to meet at a common centre.



TEXT-FIG. 4. *a*. Horizontal section through *A. raniceps* eye, with radii of curvature passing through every tenth prism marked. From a thin section. × 12·5. Gr I 5512. *b*. Vertical section. × 12·5. Gr I 5503. *c*. Thin section through lower part of visual surface and eye-socle. The outer cuticular layer of Dalingwater passes upwards into the cornea at the base of the eye-socle. × 30. Gr I 5503. *d*. A single ommatidium of the apposition eye of a shore crab. *e*. Ommatidium of the superposition eye of a lobster.

In *d* and *e*, the left-hand side is shown as dark-adapted, the right as light-adapted. Both after Kampa (1965).

f, *g*. Diagrams illustrating surface convexity and centres of ommatidial convergence in the eyes of the insect *Apis mellifica* (apposition eye), and *Samia cecropia* (superposition eye). Both redrawn from Portillo (1936).

The radii of curvature in the two directions are illustrated in text-fig. 4*a*, *b*. It is very probable that those parts of the eye, now destroyed, lying below the primary prisms, were elongated ommatidia, following the radii of curvature more or less exactly, just as in the eyes of many insects and crustaceans, though how deep they were cannot be assessed. In modern arthropods the first optic ganglion of synaptic region occupies the central part of the underlying space and the same was probably true of the trilobites. Almost certainly the ommatidia must have terminated some distance short of the centre of curvature.

The regularity of surface curvature, ommatidial separation, and radial arrangement of the ommatidia, evident in *Asaphus raniceps*, is also characteristic of the structure of many superposition eyes in modern arthropods. In this respect the eye of *A. raniceps* is unlike both modern apposition eyes, and those of phacopid trilobites.

Anatomical differences between apposition and superposition eyes are very well known, and have been synthesized in various reviews (Waterman 1961; Goldsmith 1964; Wigglesworth 1965). Apposition eyes (text-fig. 4*d*) have the rhabdom in contact with the crystalline cone, whereas in superposition eyes (text-fig. 4*e*), the cone and rhabdom are separated by a long cone-stalk, believed to be a light conductor. The rhabdom here is very much shorter than in apposition eyes.

These anatomical differences have been greatly discussed since the time of Exner (1891), but their physiological significance is still controversial (Goldsmith 1964; Miller *et al.* 1968).

Superposition eyes, which are typical of nocturnal crepuscular or deep-water arthropods, have an elaborate system of adaptation to dark conditions. In light-adapted superposition eyes, when screening pigment surrounds each ommatidium, the visual system probably forms a mosaic image rather like an apposition eye. (Actually the 'mosaic theory' of image formation, first propounded by Müller in 1826, is now held to be too simple, and Burtt and Catton (1962, 1966*a*, *b*) have shown the important role of diffraction processes in arthropod vision, so as to modify greatly and extend the mosaic theory.)

In dark-adapted superposition eyes, the pigment migrates away from the cone-stalk region so that the isolation of the ommatidia is lost. In this way light coming through many lenses can pass freely to any rhabdom, and is not confined to any specific ommatidium. Sensitivity seems to be increased thereby, though resolution is lost.

It is interesting that the only modern arthropod eyes of spherical, geometrically perfect form with the radii meeting at the centre are of superposition type (Portillo 1936), though not all superposition eyes do, in fact, have such perfect form. Portillo believed that such a structure was highly desirable for superposition vision, both optically and physiologically.

The parallels between the regular structure of the eye of *Asaphus raniceps*, and typical modern superposition eyes are illustrated in text-fig. 4*a*, *b*, *f*, *g*; it is possible that the number of points in common may imply some degree of functional similarity.

Some recent work by Stuermer (1970) appears at first sight to militate against the above suggestions. Stuermer subjected the schizochroal eyes of some Devonian phacopid trilobite to X-ray examination and found within the eyes very long, closely packed bundles of fibres extending from the lentiferous region right into the axial part of the body of the trilobite. He interpreted these as light guides (presumably equivalent to very long cone-stalks in modern arthropods), which conducted light from the lenses to the photoreceptors.

I have assumed that in *Asaphus raniceps*, as in virtually all recent arthropods, the photoreceptive organs were of ommatidial kind, arranged radially, following the radii of curvature more or less exactly and that optic ganglion was present centrally. Though Stuermer's material is tectonically distorted, it is clear that the structures he described do not follow this pattern; they are numerous and quite thick and because of their extreme length a radial pattern is not evident. As far as can be seen they terminate outside the optic region altogether so that if they were really light guides the optic ganglion would be displaced towards the central part of the body.

Thus the eye as interpreted by Stuermer bears very little resemblance to any other kind of arthropod eye. Even in certain mysids and euphausiids where the cone-stalks are of exceptional length (thus accommodating multiple diffraction images at different depths), the optic ganglion remains centrally located, and the external part of the eye becomes expanded outwards during ontogeny to accommodate the extra length. It is difficult to see what purpose could be served in the large-lensed phacopids by such an improbable distance between lens and photoreceptor, and it is likely that the fibre-bundles are not part of the optical system at all. They could be part of a circulatory system like the alimentary prosopon of many Cambrian trilobites (Öpik 1961) only located below the surface, or, as Dr. J. Bergström (pers. comm.) has suggested, filaments of the 'gill' or exite branch of the appendages. Various factors seem to support this suggestion, and in particular the random and oblique orientation of the fibre-bundles, and their indistinct preservation directly below the palpebral furrow, which would have acted as a ridge crushing against the filaments. Such filaments may have been preserved only where trapped in the void below the eye and the glabella, and that is why they extend only to the visual surface and not beyond, thus giving the impression of being part of the optical system.

Until further evidence is forthcoming, therefore, Stuermer's structures cannot be unequivocally accepted as being light guides. And though the internal organization of the schizochroal system may well have differed from that of holochroal eyes the external morphology of the latter approximates that of insects and crustaceans in so many ways that it seems more appropriate to infer some internal resemblance, at least in so far as having radially arranged photoreceptors and a centrally placed ganglion.

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10

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 he '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 he 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 n the structure and shape of the eye are clear in different lines of descent. Some of the observed modifications are hought 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 lentiferous 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 lentiferous surfaces in Cambrian pagetiids, where the eye has a 'schizochroal' appearance.

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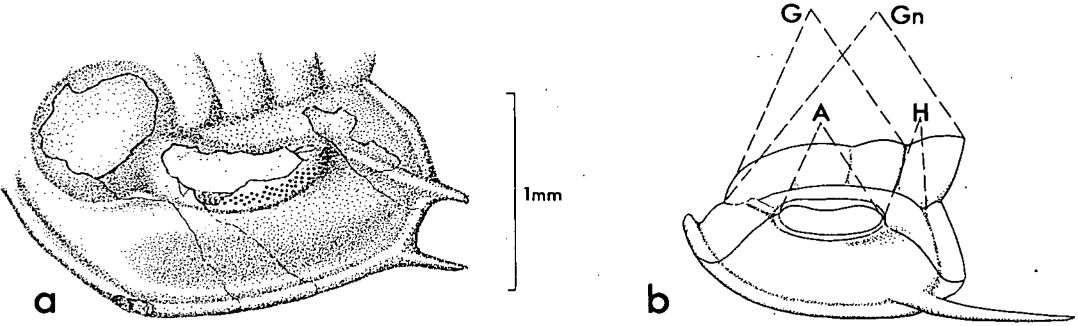
I am not aware that any visual surfaces are known to be preserved in Middle Cambrian trilobites, but amongst the Upper Cambrian fauna certain genera with intact eyes occur sporadically, and different kinds of eyes may be preserved within particular groups such as the family Olenidae, which are the subject 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 cranidium. 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. 2*a*), 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-socle, 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. 1*a*) 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.



TEXT-FIG. 1. *a. Olenellus gilberti* Meek. Meraspid figured by Walcott (1910, pl. 36, fig. 4*c*; 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. Cn = 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-socle, 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 (2aβ).

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-socle) 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-socles 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.).

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 eye-socles 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 paedomorphic 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*

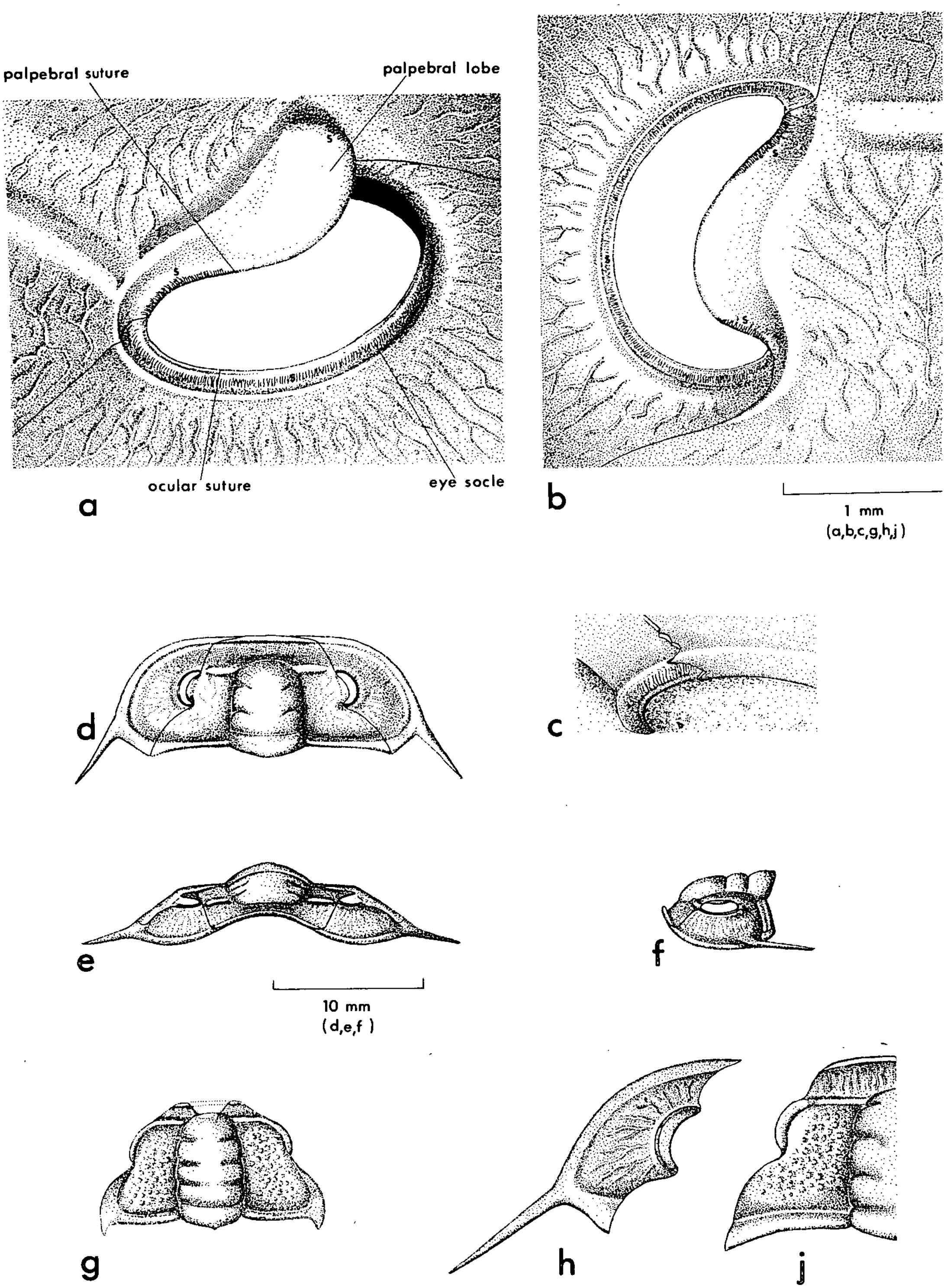
Material. Twenty-two blocks of topotype material from Andrarum, Zone II (2aβ). Gr I 5514–5536.

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 1966*b*) 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 × 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


palpebral suture
palpebral lobe
s
s
ocular suture
eye socle
a
s
s
s
b
1 mm
(a,b,c,g,h,j)
d
c
e
f
10 mm
(d,e,f)
g
h
j

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-socle 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 meraspids the palpebral lobe is at first very narrow, and is connected to the ocular ridge (text-fig. 1*g*). 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. 2*j*, 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° with the exsagittal plane. This contrasts with the situation in meraspids where the equivalent angle may be up to 45°. Eye-indices (Struve 1958): A/G 37%, A/Gn 30%, H/A 108% (text-fig. 1*b*). 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-socle. 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 prospon 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-socle, 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-socle is a prominent band, which could on superficial inspection be taken for the visual surface itself. The true shape of the eye-socle 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. 2*c*, it was

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-socle. Mainly from Gr. I. 5521.

c. Part of specimen showing undamaged anterior horn of the eye-socle, 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.

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-socle. 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-socle are confined to a median horizontal band, above which the socle 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-socle, 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*

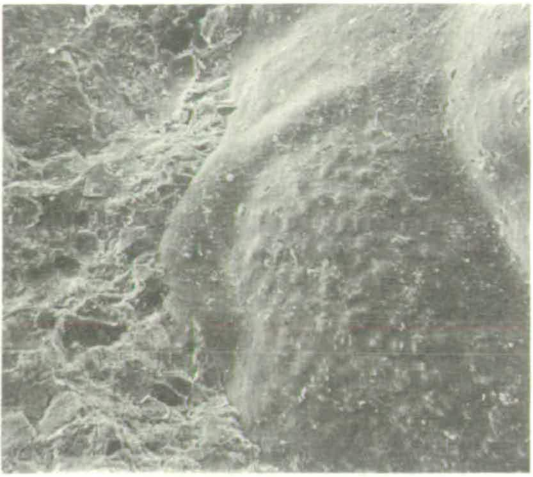
Material. Five blocks from Westergård's collection, University of Lund, Andrarum. Zone III (2*b*). LO 4527–31.

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-socle. 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 meraspids of *Olenus*. Ridges of the alimentary prospon 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-socle (inverted) showing faint striations of the sensory zone and undamaged upper rim. Gr. I. 5517, ×65. 5, Outer surface of eye-socle, with prominent striations. Upper rim damaged. Gr. I. 5518, ×120. 6, Same, showing striations highly magnified, ×2400. Bar = 5 μm.



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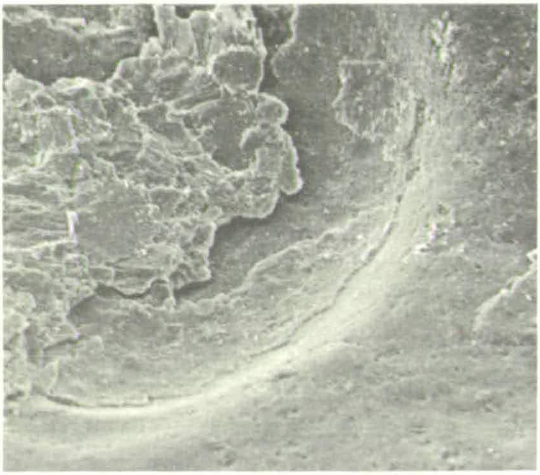

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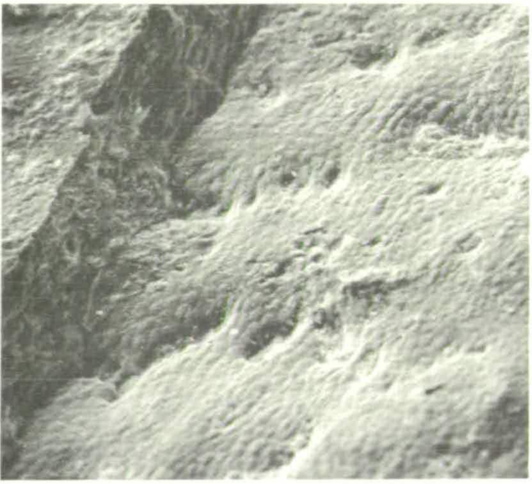

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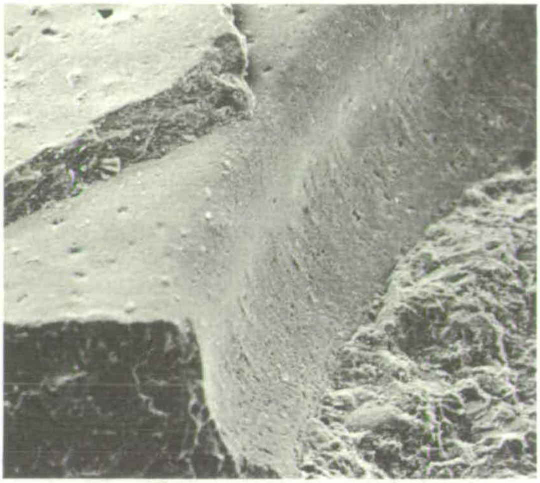

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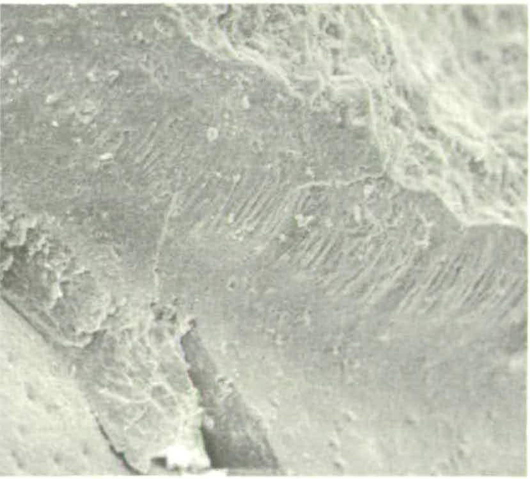

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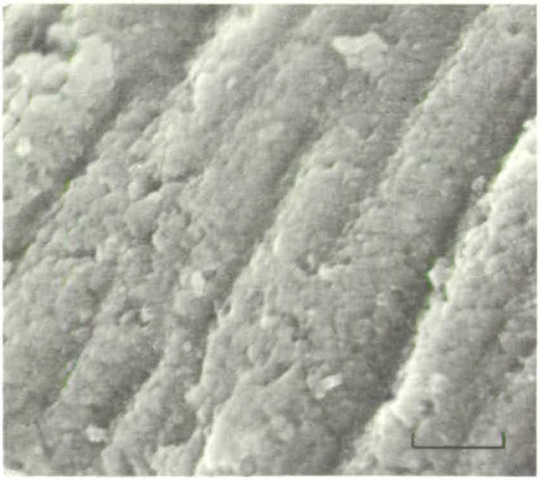

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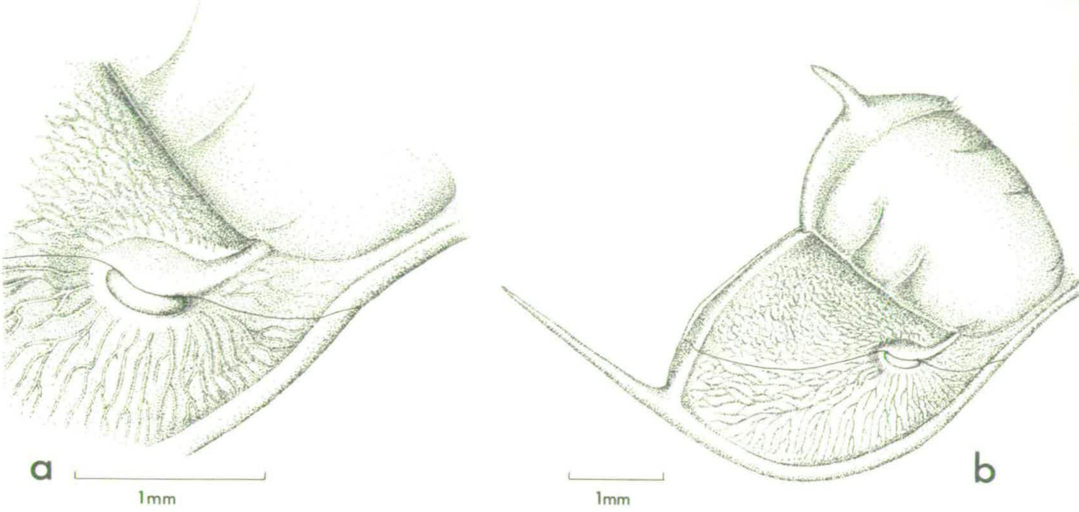
CLARKSON, *Olenus* eyes



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

Features of the eye of *Parabolina* which bear resemblance to the eyes of meraspids of *Olenus* suggest tha the *Parabolina* eye was derived from the eye of *Olenus* by paedomorphosis. These include: (i) The retentio of the visual surface and obsolescence of the ocular suture; (ii) Confluence of the palpebral lobe with th 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 th palpebral lobe, are not paedomorphic 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

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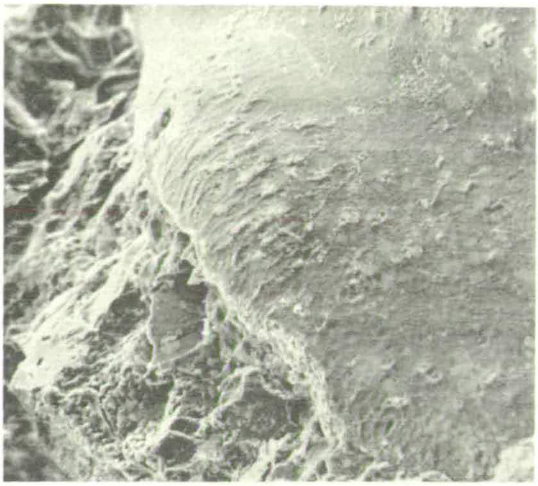
EXPLANATION OF PLATE 92

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

Figs. 5, 6. *Parabolina spinulosa* (Wahlenberg 1821). Zone III. Andrarum, Scania. 5, Librigena with eye. LO 4527, ×46. 6, The same, magnified ×125.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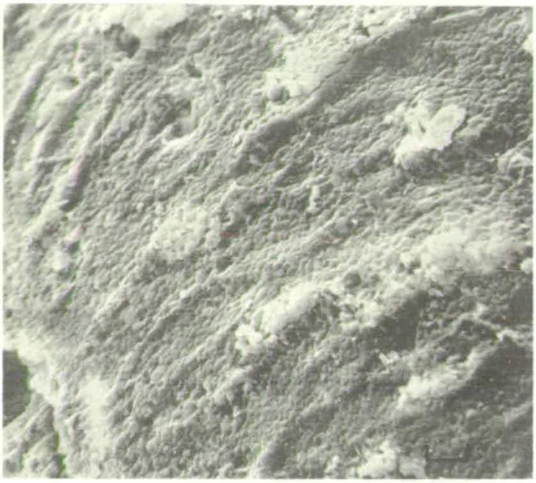
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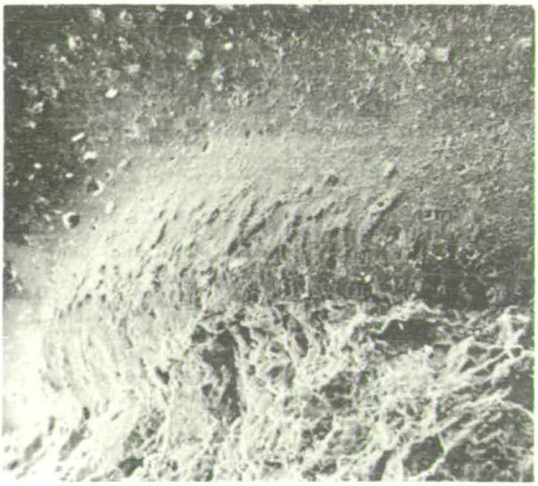
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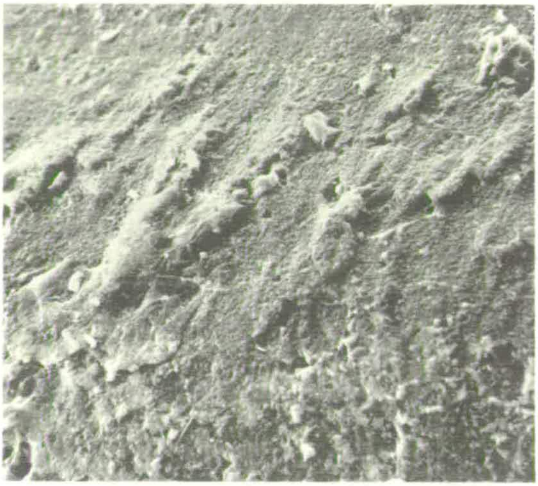
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CLARKSON, *Olenus* and *Parabolina* eyes specimens of both genera suggest breakage rather than the presence of an ocular suture. Indeed, it seems fairly certain that *Protopeltura* had an eye similar to that of *Peltura*.

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)

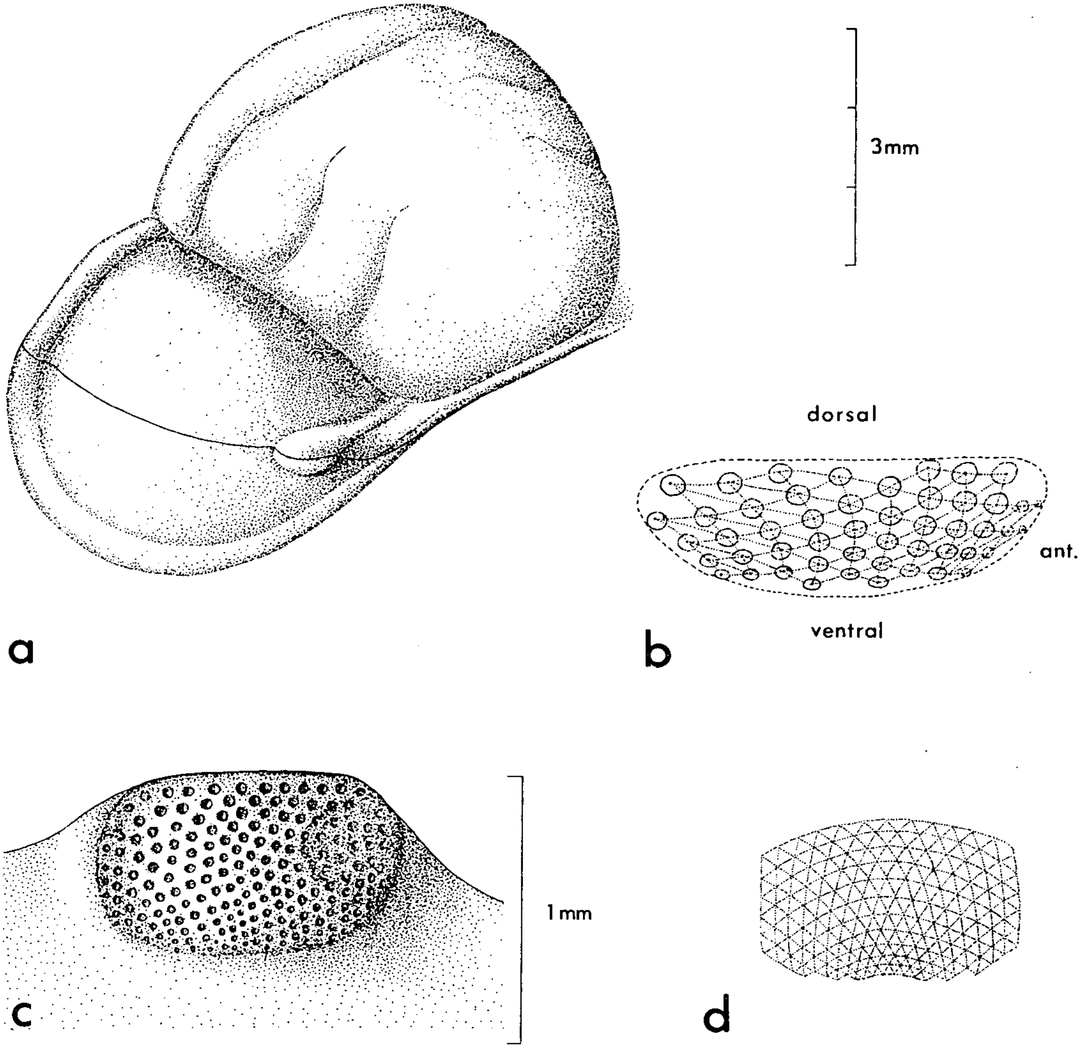
1821 *Entomostracites scarabaeoides*; Wahlenberg, p. 41, pl. 1, fig. 2.
1854 *Peltura scarabaeoides* Wahl.; Angelin, p. 45, pl. XXV, fig. 8.
1922 *Peltura scarabaeoides* (Wahlenberg); Westergård, p. 173, pl. XV, figs. 12, 13, 18.
1957 *Peltura scarabaeoides scarabaeoides* (Wahlenberg 1821); Henningsmoen, 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 (2dγ) P.M.O. 29268, 29270, 29272. Also ontogenetic series BM It. 5516–9. One block from Andrarum, Scania associated with *Ctenopyge linnarssoni*, 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 cranidium posed no problems, it is very much more difficult to be certain as to how the cranidium and librigena fit together. Several camera-lucida drawings were made of the cranidium 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 cranidium. Each librigena in turn was then manœuvred 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. 4*c*); 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 4*c*.

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* meraspids, 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 Lindstrom'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. 4*b*

Material. One specimen from Gamlebyen, Oslo, associated with *Sphaerophthalmus alatus*, Zone Vb (2dβ). 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

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EXPLANATION OF PLATE 93

Figs. 1, 2. *Peltura minor* (Brögger, 1882). Gamlebyen. Oslo. Zone Vb. (2dβ). 1, Internal mould of visual surface (right edge = anterior). P.M.O. 87558, ×135 (vide text-fig. 4*b*). 2, Same, upper part of visual surface, ×500. Bar = 10 μm.

Figs. 3–6. *Ctenopyge* (*Mesoctenopyge*) *similis* Henningsmoen 1957. Sars Gate. Oslo. Zone Vb (2dβ sim.). 3, Palpebral lobe showing nearly structureless surface (top right = anterior). P.M.O. 87567, ×120. 4, Adult visual surface in lateral view showing dorso-ventral files and eye-socle with faint vertical striations. P.M.O. 87566, ×85. 5, Oblique dorsal view of adult visual surface. P.M.O. 87565, ×65. 6, Oblique dorsal view of visual surface of a young specimen (right edge = anterior), (see also text-fig. 5*e*), (enlargement of left-hand specimen in Pl. 94, fig. 5). P.M.O. 87564, ×120. (Figs. 5 and 6 are illuminated from the south).

PLATE 93


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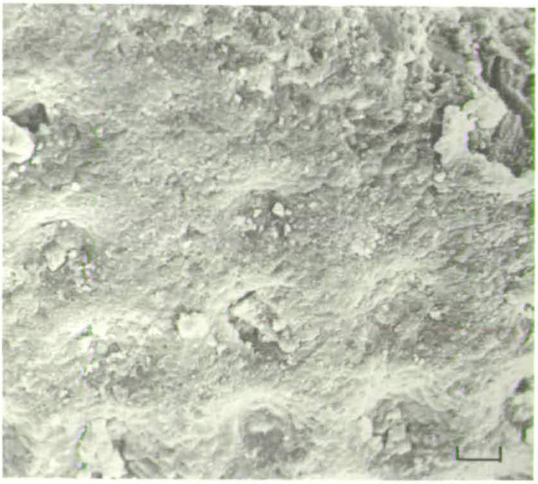
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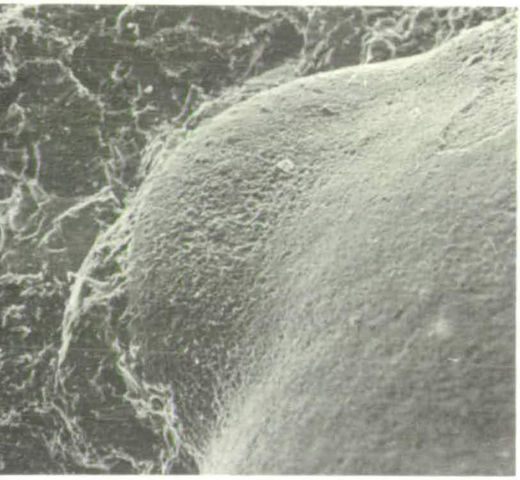
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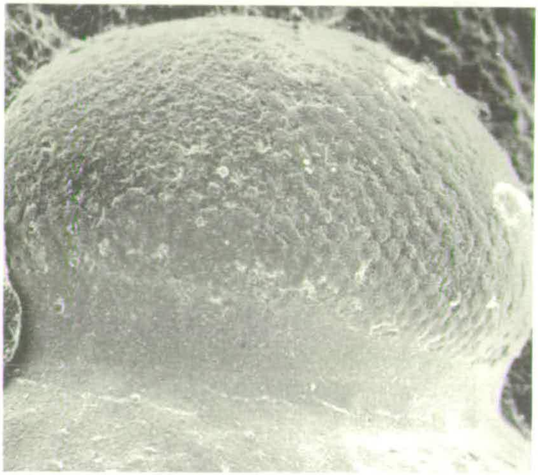
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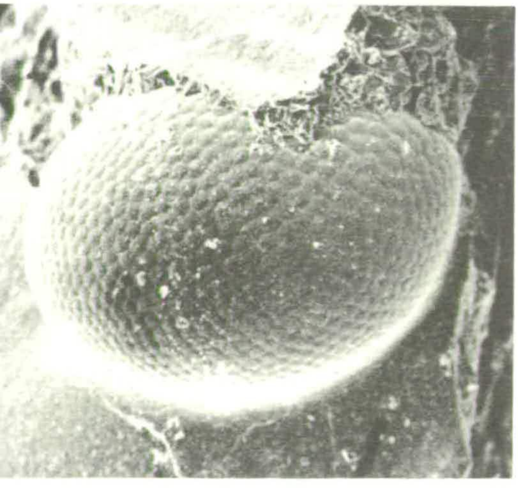
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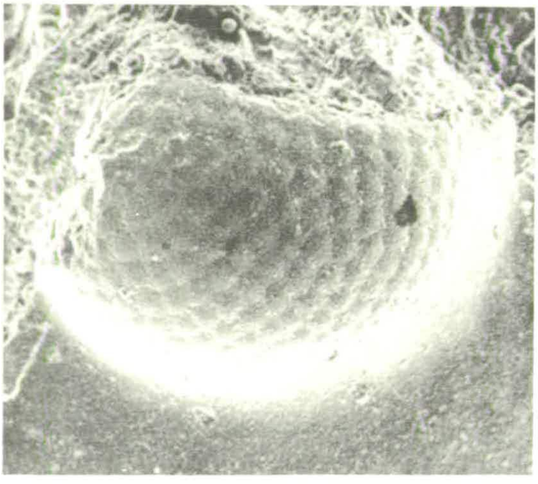
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CLARKSON, *Peltura* and *Ctenopyge* eyes axes centred on an axis 45° from the sagittal plane, and directed downwards at 10–20° below the 'equator', towards the sea floor.

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. 4*c*, but apart from these the lens centres are arranged in a regular geometric sequence, idealized in text-fig. 4*d* 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.

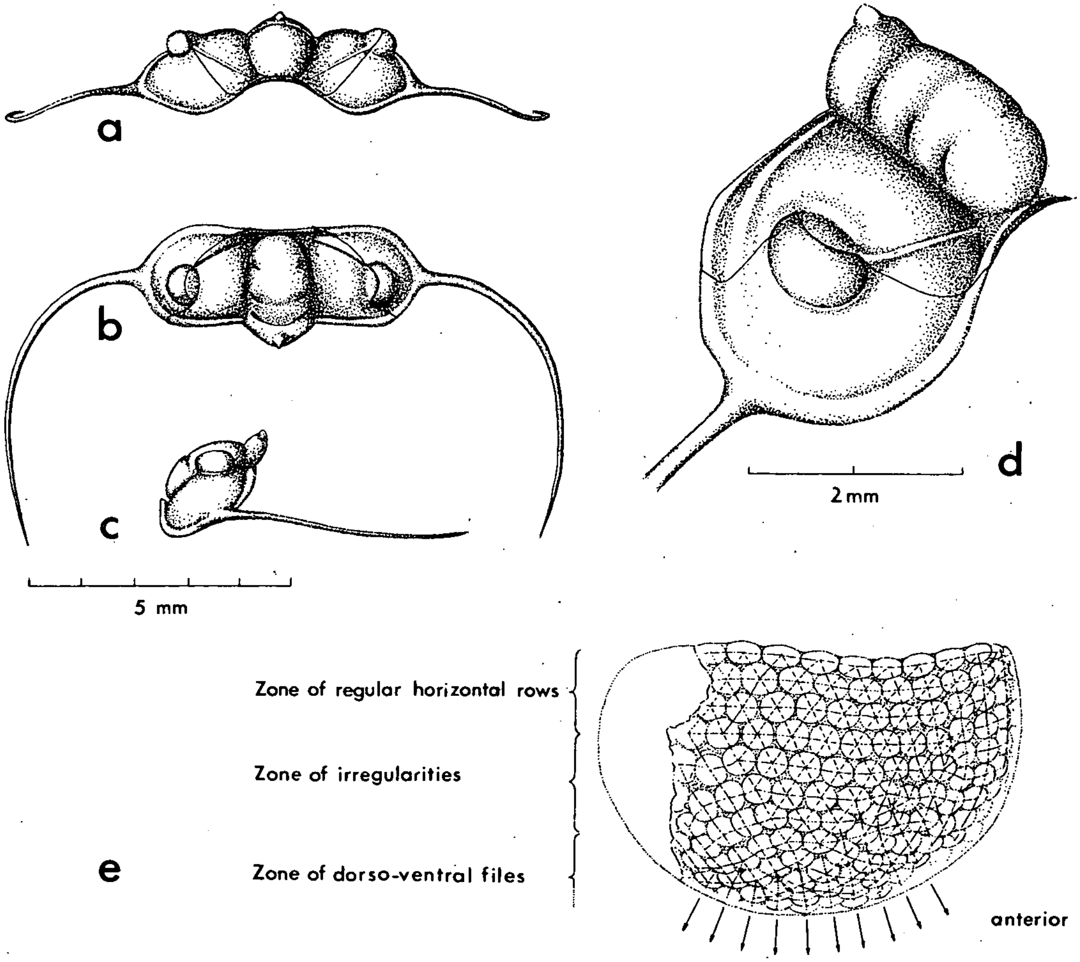
Ctenopyge (*Eoctenopyge*) *modesta* Henningsmoen 1957

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 (2dβ 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 1966*b*) 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-socle, about one-fifth the height of the whole eye. In the material to hand there are no vertical ridges on the socle. Some specimens have an eye of symmetrical form: a regular oblate spheroid truncated below by the upper edge of the eye-socle, 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); Westergard, 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. 5*e*, 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-socle.

Ctenopyge (*Mesoctenpyge*) *tumida* Westergård 1922

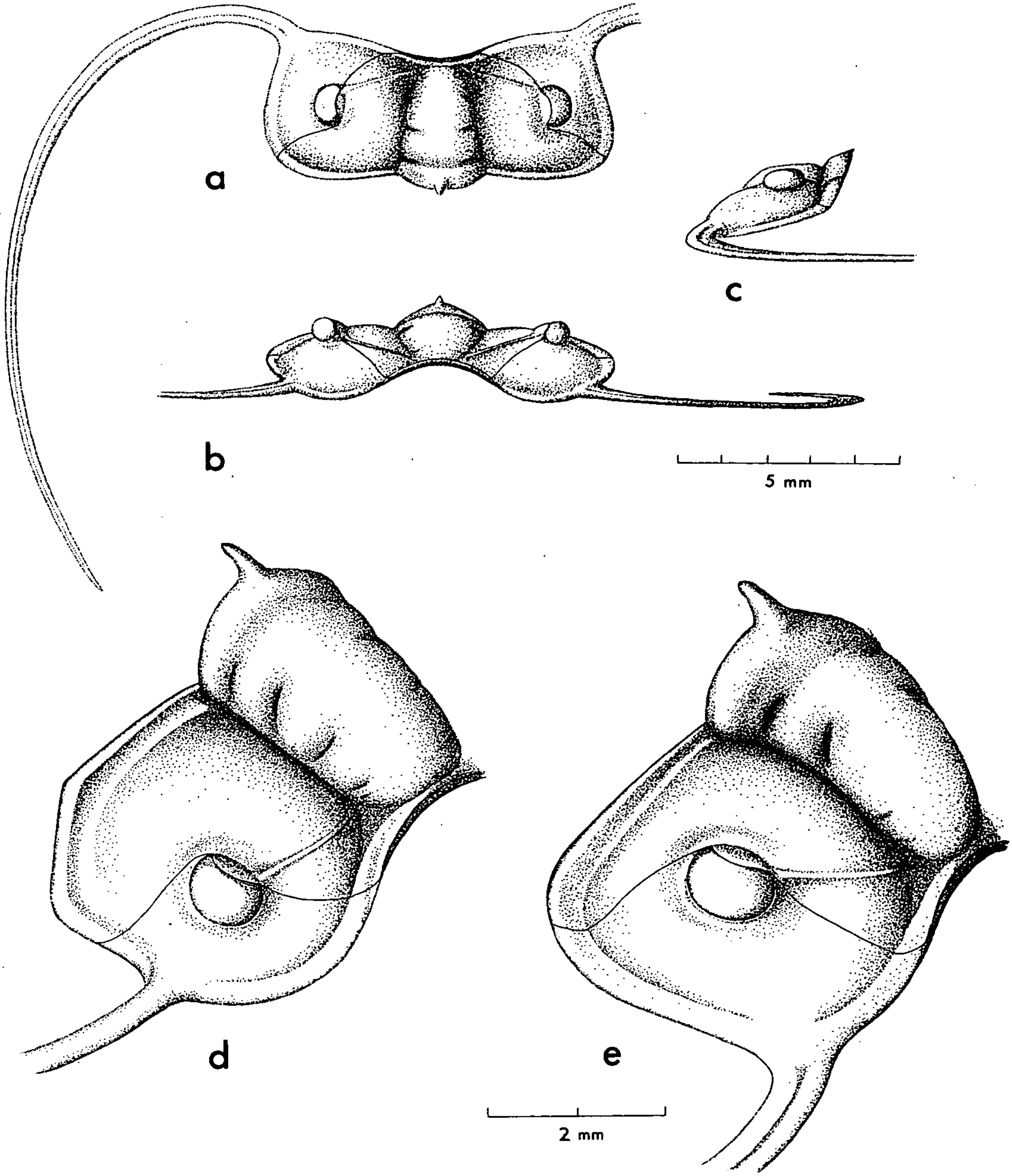
1922 *Ctenopyge tumida* n. sp. (partim.); Westergård, p. 155, pl. XI, figs. 15–18.
1957 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård 1922: Henningsmoen, p. 198, pl. 5; pl. 20, fig. 16.

Plate 94, figs. 1–4; text-fig. 6*d*

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. 6*a–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. 7*a–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-socle is extremely narrow, more so than in any species previously discussed, though faint vertical striations are visible.

Sphaerophthalmus humilis (Phillips 1848)

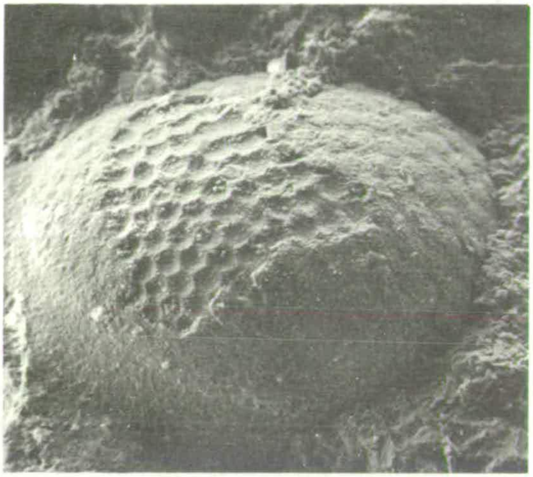
1848 *Olenus humilis* n.s.; Phillips, p. 55, figs. 4–5, p. 347.
1901 *Sphaerophthalmus alatus* Angelin (*sic*); Lindström, p. 29, pl. III, figs. 31–34.
1913 *Sphaerophthalmus alatus* (Boeck sp.); Lake, p. 74, pl. VIII, fig. 1–5.
1957 *Sphaerophthalmus humilis* (Phillips 1848); Henningsmoen, p. 215, pl. 5; pl. 22, figs. 7, 11–15.
1968 *Sphaerophthalmus humilis* (Phillips); Rushton, p. 415, text-fig. 2, 3*a*, 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-socle of large adult eye; faint vertical striations visible on eye-socle. 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-socle. 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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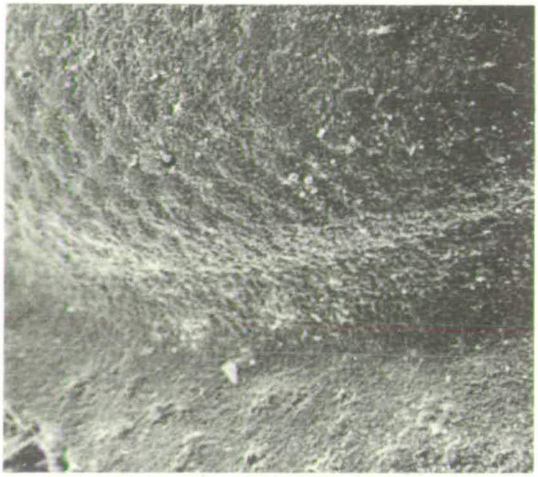
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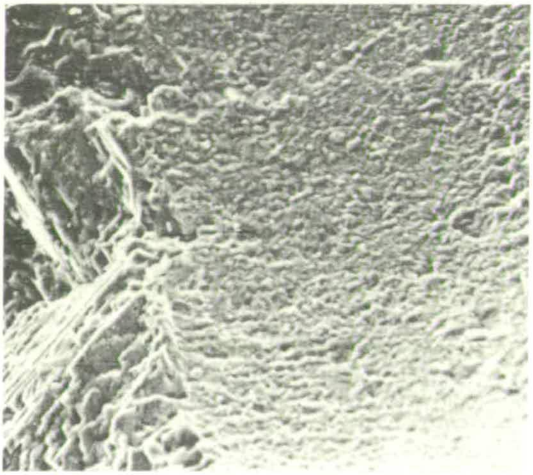
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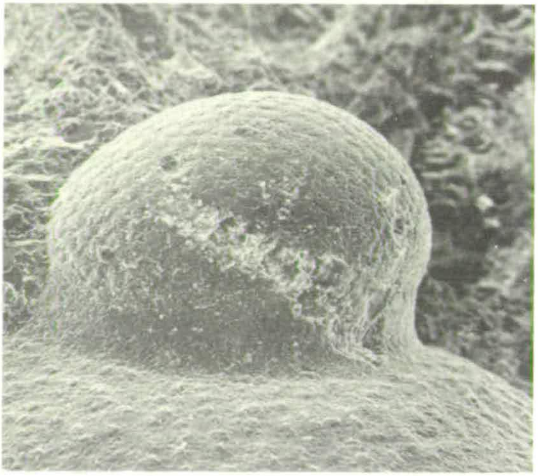
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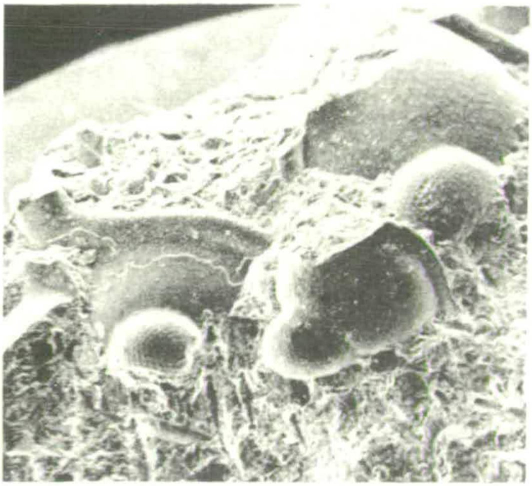
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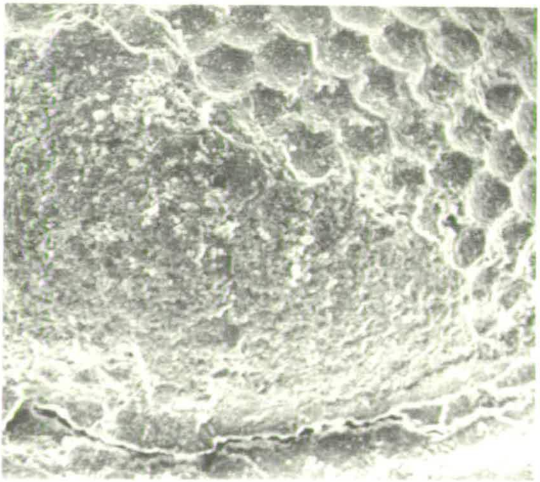
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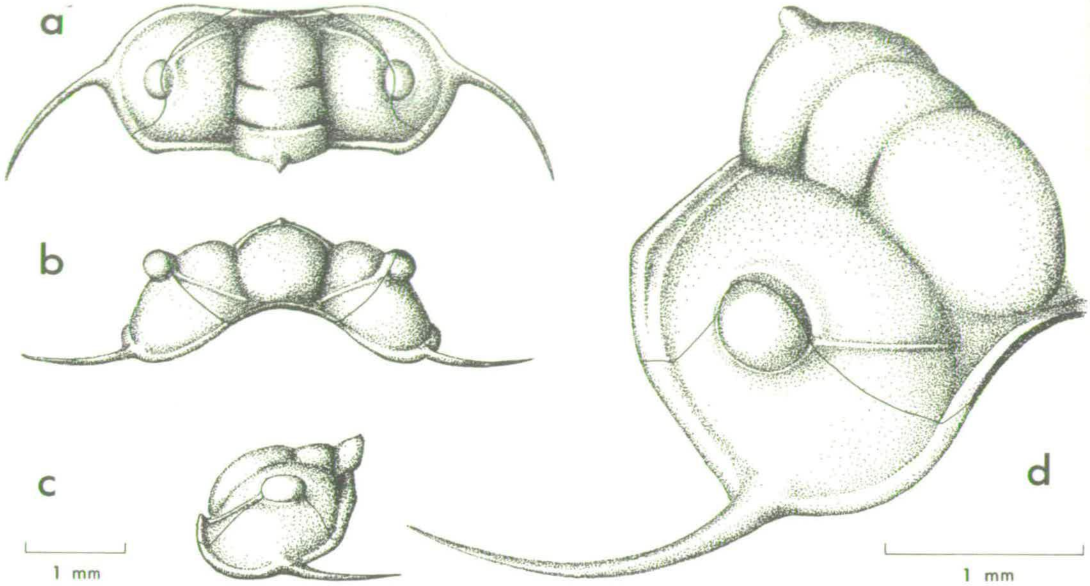
CLARKSON, *Ctenopyge* and *Sphaerophthalmus* eyes



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 (2dγ). Old collection, Gr. I. 20706, 20803, 5537.

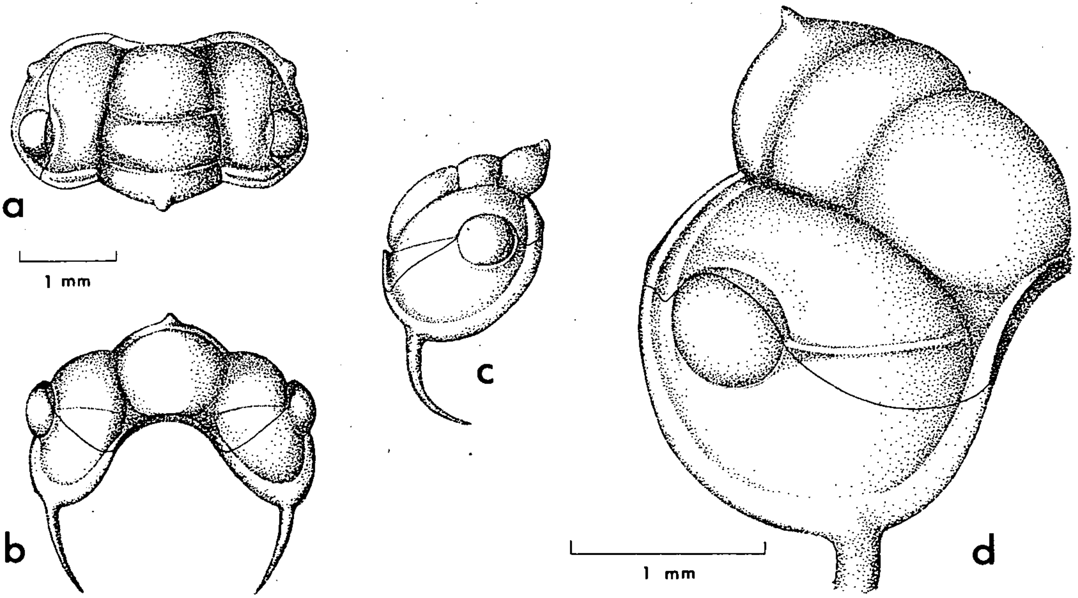
Remarks. S. humilis is an extremely convex trilobite with a very pronounced anterior arch and almost vertical librigenae. The peculiar attitude of the genal spines in this species was first noted by Rushton (1968, p. 415). He reconstructed the cephalon with steeply sloping librigenae, and ventrally projecting 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-socle 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 1966*a*). 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 1966*b*). 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. 5*e*) 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.

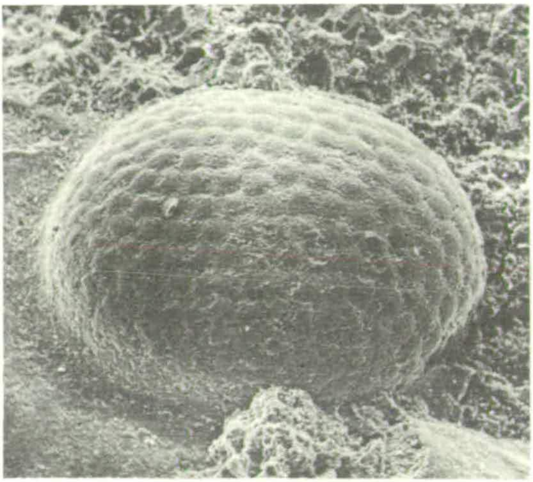
The lower third of the eye lies below the ambitus (this term used as in an echinoid) where the eye has reached its greatest horizontal circumference and thereafter decreases slightly in diameter. Since the visual surface is no longer increasing no new lenses are added by intercalation and it is hardly 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 hiatoses.

EXPLANATION OF PLATE 95

Figs. 1, 2. *Sphaerophthalmus alatus* (Boeck 1838). Andrarum, Scania. Zone Vb (2dβ). 1, Dorso-lateral and 2, anterior view of young eye. Gr. I. 20775, × 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, × 1200. Bar = 10 μm. 4, Internal mould of adult eye with a few lenses still adherent. Left edge anterior. Gr. I. 20803, × 60. 5, Very young eye; outer surface Gr. I. 5537, × 200. 6, Internal mould of lenses near base of eye. Gr. I. 20803, × 500. Bar = 10 μm.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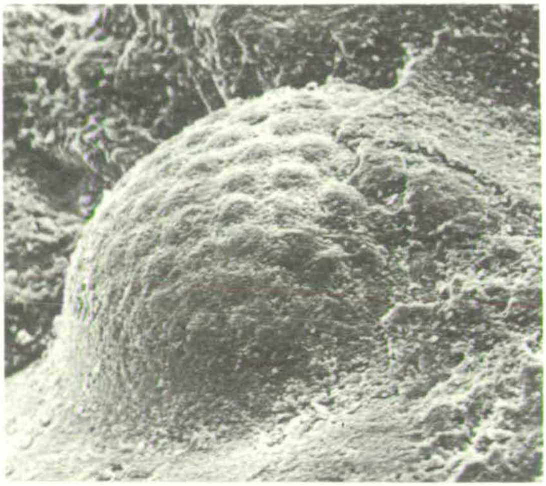
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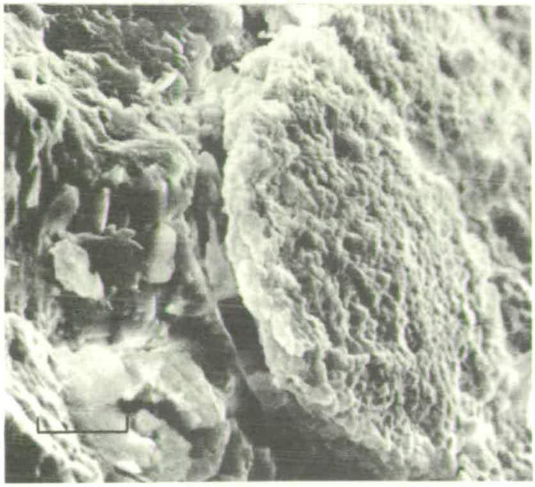
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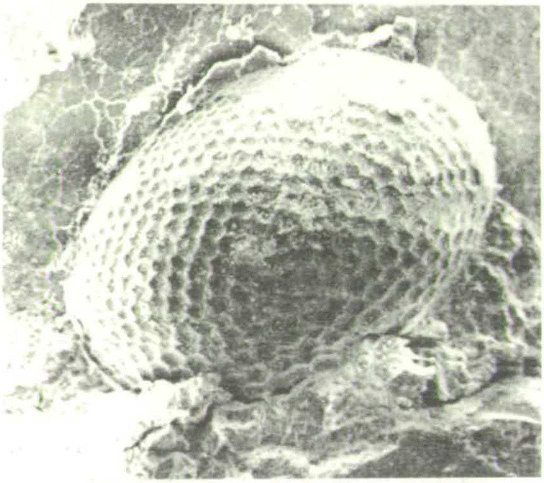
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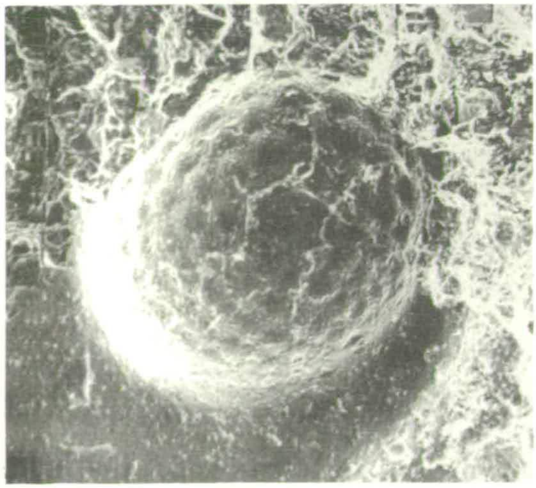
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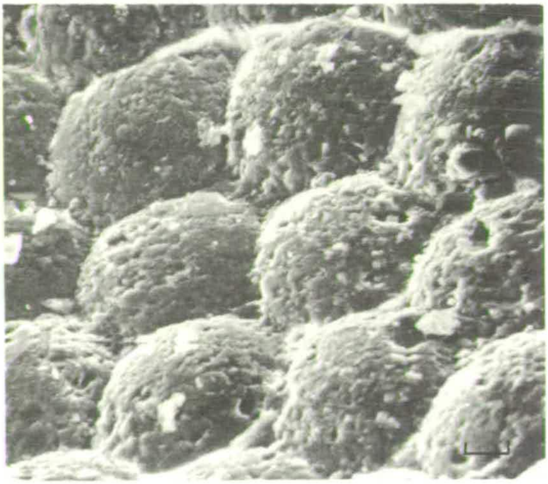
6

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 (Orlowski, 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 cephala (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.

11

Enrollment and coaptations in some species of the Ordovician trilobite genus *Placoparia*

JEAN-LOUIS HENRY AND EUAN N.K. CLARKSON

Henry, J.-L. & Clarkson, E.N.K. 1974 12 15: Enrollment and coaptations in some species of the Ordovician trilobite genus *Placoparia. Fossils and Strata,* No. 4, pp. 87–95. Pls. 1-3. Oslo ISSN 0300-9491.
ISBN 82-00-04963-9.

The species *Pl.* (*Placoparia*) *cambriensis, Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni,* described by Hammann (1971) from the Spanish Ordovician, are found in Brittany in formations attributed to the Llanvirn and the Llandeilo. The lateral borders of the librigenae of *Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni* bear depressions into which the distal ends of the thoracic pleurae and the tips of the first pair of pygidial ribs come and fit during enrollment. These depressions, or coaptative structures sensu Cuenot (1919), are also to be observed in *Pl.* (*Placoparia*) *zippei* and *Pl.* (*Hawleia*) *grandis,* from the Ordovician of Bohemia. However, in the species *tournemini* and *borni,* additional depressions appear on the anterior cephalic border, and the coaptations evolve towards an increasing complexity. From *Pl.* (*Placoparia*) *cambriensis,* an ancestral form with a wide geographic distribution, two distinct populations seem to have individualised by a process of allopatric speciation; one of these, probably neotenous, is represented by *Pl.* (*Coplacoparia*) *tournemini* (Massif Armoricain and Iberian Peninsula), the other by *Pl.* (*Placoparia*) *zippei* (Bohemia). Geographic isolation may be indirectly responsible for the appearance of new coaptative devices.

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The genus *Placoparia* is common in some Ordovician formations of the Massif Armoricain, but so far no detailed account of the species occurring in Brittany has yet been published. The only recent studies were made by Cavet & Pillet (1964, 1968), who described and figured a *Placoparia* occurring in nodular shales of Llanvirnian age in the synclinorium of Redon-Ancenis, which in 1968 was only provisionally assigned to the species *zippei.*

In 1876, De Tromelin & Lebesconte (pp. 636-637) recognized two species among the specimens found in the Palaeozoic synclines south of Rennes: *Placoparia tourneminei* (Rouault) and *Pl. zippei* (Boeck). which differ essentially in that they have respectively 11 and 12 thoracic segments. Later on, in the thesis he devoted to the Ordovician and the Silurian of the Crozon peninsula, Kerforne (1901:53, 178-179) mentioned one form only: *Placoparia tourneminei;* the author added that he never collected any *Pl. zippei,* "dont l'aire geographique n'est pas assez grande en Bretagne pour qu 'on puisse s'en servir comme fossile caractéristique". Let us add that, what with the lack of good illustrations in the early studies and the loss of part of the material, it is impossible to draw up detailed lists of synonyms.

Now that Hammann (1971a, 1971b, 1971c) has provided a firm systematic basis for the subfamily Placopariinae, it seemed to us pertinent to describe the coaptative devices and the enrollment of the *Placoparia* of Brittany.

TERMINOLOGY AND TECHNIQUES USED

The terminology used in the present paper is that established by Hupé (1953). From rear to front the glabellar furrows are numbered S1, S2, S3, and the corresponding lateral lobes L1, L2, L3. The word coaptation, first introduced by the French biologist Cuénot in 1919, refers to the mechanical adjustment or fitting together of two independent parts of the same animal. The coaptative structures are peculiar morphological devices (cavities, protuberances, notches, furrows etc. . . .) such as for instance interlock in a fully enrolled trilobite.

All the specimens and the latex casts figured here have been slightly whitened with ammonium chloride, and the background in some of the photographs has been partially blocked out with Indian ink. Photographs and drawings are those of the first author.

MATERIAL

The specimens studied are most often small, hardly exceeding 3 or 4 cm in length when complete. All of these come from formations assigned to the Llanvirn and to the Llandeilo. Though frequently distorted in lutites, the *Placoparia* are, however, finely preserved, the ornamentation of the test being perfectly visible on the external moulds.

In the species known from the Ordovician of Brittany, the dorsal exoskeleton is comparatively thick, being about 0.1 mm in individuals whose overall length does not exceed 3 cm. Thus the more delicate coaptative structures of the cephalon are very hard to distinguish, or are even invisible, on internal moulds. Precise determination of the species is therefore possible only in latex replicas obtained from external moulds, except of course when the test itself has been preserved.

The material comprises exoskeletons which are often incomplete and sometimes enrolled, and isolated pygidia and cranidia. Complete cephala with their fixigenae are rather rare. In some cases the hypostoma is preserved "in situ". All the specimens are part of the collections of the Geology Institute in Rennes (IGR). Theu are numbered from IGR N° 1798 to TGR N° 1966. The letter "a" following a sample number indicates an internal mould, the letter"b" an external mould.

THE SPECIES OF THE GENUS *PLACOPARIA* IN BRITTANY AND THEIR VERTICAL DISTRIBUTION

In this paper we have abandoned the stratigraphic nomenclature which students of the Ordovician of the Massif Armoricain have been using for more than a century. This out-of-date nomenclature, which is often misleading, and has become increasingly less useful as research progresses, has been replaced (in all but exceptional cases) by geographical names applying to local lithologically homogeneous units. These units have been known for quite a long time, and besides, they are those referred to on geological maps. They retain, at least for the time being, a deliberately broad meaning so as to avoid an excessive multiplication of names.

The trilobites figured in this paper come from two large geological domains: the Median Armorican synclinorium and the synclinorium of Martigné-Ferchaud (Fig. 1). They have been collected from lutites or from areno-lutites with siliceous nodules, generally known as "schistes à Calymènes". The latter, varying in thickness from about 200 to 400 m, lie over the Armorican Sandstone Formation which probably dates back to the Arenig (Deunff & Chauvel 1970). Let us add that the use of the expression "Armorican Sandstone" for the region of Brittany does not imply, in our meaning, that the lower or the upper limit of this lithological unit is everywhere synchronous.

In the Median synclinorium, the very discontinuous character of the outcrops (there is an almost total lack of continuous sections) justifies the adoption of three different denominations replacing that of "schistes à Calymènes": Postolonnec Formation for the Crozon peninsula in the West, Bas-Couyer Formation in the North of Rennes, for the region of Menez-Belair studied recently by Paris (1971, 1972), and Andouillé Formation for the northern side of the Bassin de Laval in the East. In the Crozon peninsula some quartzites forming broad layers having an overall thickness of about 14 m, appear within the Postolonnec Formation and constitute the Kerarvail Member. South of Rennes, in the synclinorium of Martigné-Ferchaud, we shall refer to the "schistes à Calymènes" under the name of Traveusot Formation. These different lithological units are described in detail and their names defended in a publication which is now in press.

The three species of genus *Placoparia* identified with certainty in the Ordovician of Brittany, namely *Pl.* (*Placoparia*) *cambriensis* Hicks, *Pl.* (*Coplacoparia*) *tournemini* (Rouault), *Pl.* (*Coplacoparia*) *borni* Hammann, have already been described from Spain by Hammann (1971a).

Pl. (*Placoparia*) *cambriensis* has been found in the Lower Llanvirn of the Iberian peninsula; the observations that may be added to Hammann's excellent description need only be minor

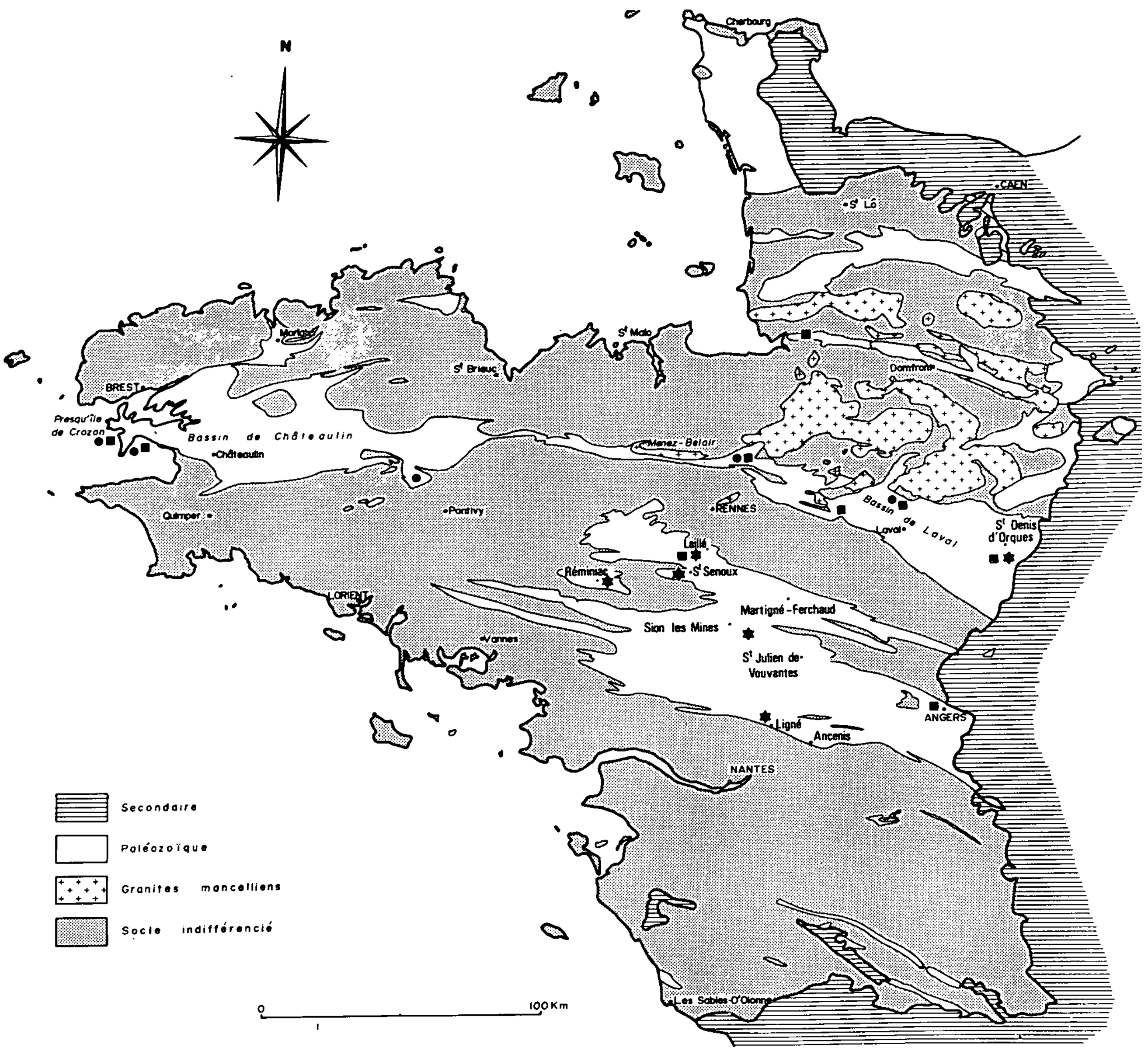

Fig. 1. Geographical distribution, as known at present, of the species *Pl. (Placoparia) cambriensis* (★), *Pl. (Coplacoparia) tournemini* (■) and *Pl. (Coplacoparia) borni* (●) in the Massif Armoricain.

ones. The specimens from the Massif Armoricain are identical with those from Spain, but the few cephala collected near Laillé, in the locality named "cote 85", are remarkably well preserved and make it possible to describe the most minute ornamentation of the exoskeleton. Three distinct elements of surface sculpture are evident. Firstly, all parts of the cephalon are densely perforated with tiny pits; these are largest and most numerous on the regions bordering the cephalic furrows and near the posterior border and near edge of the occipital ring. Secondly, the fixigenae are pitted with about 50 to 60 much larger deep cavities, roughly oval or round in shape. Irregularly distributed, and differing even on the two fixigenae of one single cephalon (Pl. 1:4), these cavities are scattered over a trapezoidal surface separated from the dorsal glabellar furrows and the posterior furrows of the cheeks by a margin ranging from 0.3 to 0.4 mm in breadth. It will be noted that the most distinct cavities lie close against the facial suture, on the external lateral portions of the fixigenae. Three similar cavities are present near the anterior glabellar border, in the plane of symmetry of the cephalon. Thirdly, between the cavities the test carries a fine and dense granulation. The whole cephalon is covered, the furrows excepted, with granules: these are of small size on the occipital ring and on the posterior borders of the cheeks, as well as on the lateral lobes L1, L2, L3, but their dimensions increase on the frontal glabellar lobe (Pl. 1:1; Pl. 3:1). The anterior cephalic border is gently arched and its breadth (sag.) remains more or less uniform over its whole length; the granulation which covers it is identical with that which ornaments the frontal lobe of the glabella. Librigenae have not been found in the material from Brittany, though Hammann (1971a, Pl. 1:9a-b) illustrates a pyritised enrolled specimen with the librigenae in place.

The specimens discovered by Cavet & Pillet (1964) in the nodular shales of Ligné (synclinorium of Redon-Ancenis) are certainly *Pl.* (*Placoparia*) *cambriensis*. The typical ornamentation of the fixigenae, and the presence of 12 thoracic segments and of 3 clear rings on the pygidial axis, make this indisputable. The specimens of the Ordovician shales of Sion-les-Mines (Loire-Atlantique), mentioned by De Tromelin & Lebesconte (1876) as *Placoparia zippei*, must also be assigned to the species *cambriensis*.

In the synclinorium of Martigné-Ferchaud, in Laillé, Saint-Senoux, and Sion-les-Mines, *Pl.* (*Placoparia*) *cambriensis* has been collected at the base of the Traveusot Formation, in black shales containing *Didymograptus* cf. *bifidus*. In addition to this graptolite there occur, in the locality named "cote 85", *Trinodus* sp. and *Pseudosphaerexochus* (*Pateraspis*) sp. *Pl.* (*Placoparia*) *cambriensis* is also present at the same level in the syncline of Réminiac (Quété 1975). Finally, in siliceous nodules from the Ligné region, the species is found together with *Pricyclopyge binodosa* and *Ormathops* cf. *atavus* (Cavet & Pillet 1968). Apart from the genus *Trinodus*, all these trilobites occur in the Šárka Formation (Llanvirn) in Bohemia (Marek 1961; Havlíček & Vaněk 1966). *Ormathops nicholsoni* and *O. alatus* also accompany *Pl.* (*Placoparia*) *cambriensis* and *Pricyclopyge binodosa* in the Hope Shales (Lower Llanvirn) of Shropshire (Whittard 1966; Dean 1967). Though the determination of the *Didymograptus* is uncertain owing to distortion and poor preservation, all other criteria lead us to conclude that the shales containing *Pl.* (*Placoparia*) *cambriensis* belong, in the Massif Armoricain, to the Lower Llanvirn.

In Brittany, the species *cambriensis* has only been recorded, so far, in the Palaeozoic synclines south of Rennes and at the extreme eastern end of the Median synclinorium (region of Saint-Denis-d'Orques : locality called "Butte du Creux").

When Rouault (1847:320, 326) first cited *Calymene tournemini*, he wrote *tournemini*, and not *tourneminei*. Whatever the origin of this specific name may be, and even if there has been an incorrect transliteration, there is no need to amend and modify the name originally given by Rouault. *Pl.* (*Coplacoparia*) *tournemini* is the most common species of this genus in the whole Median synclinorium and in the Palaeozoic synclines south of Rennes. It differs from *Pl.* (*Placoparia*) *cambriensis* in the number both of its thoracic segments (11 instead of 12), and in the clearly individualized rings in the pygidial axis (4 instead of 3). Moreover, the external edges of the librigenae each bear 12 deep cavities, and on the lateral parts of the anterior cephalic border there are two depressions expanding transversely lengthwise; they are a constant feature in all the individuals examined (Pl. 1:6–8). Though the large cavities of the fixigenae remain clearly visible, they are more faintly impressed than those of *Pl.* (*Placoparia*) *cambriensis*. The very small pits, however, are similar in size and distribution to those of that species. Finally, it will be noted that the granules covering the anterior border of the cephalon are smaller, but far more numerous, than those which ornament the frontal glabellar lobe (Pl. 1:8; Pl. 3:4).

The hypostoma has been found "in situ" in several specimens from Traveusot (IGR N° 1873b, Pl. 1:14; IGR N° 1883a–b; IGR N° 1891b, Pl. 1:13). It is oval-shaped; its maximum breadth, measured at the level of the triangular anterior wings, is somewhat greater than its maximum length. The hypostomal suture is a curve, slightly convex towards the front. The median body, strongly curved, has neither an anterior furrow nor distinct maculae, but it displays laterally, half-way down its length, two extremely faint short notches obliquely directed rearwards and inwardly (Pl. 1:14). At the level of these two notches, just where the posterior furrow disappears, the lateral edges of the hypostoma swell into two projecting protuberances. The narrow border constituting the buccal edge carries perhaps one or two pairs of tiny points (?).

In the Crozon Peninsula, *Pl.* (*Coplacoparia*) *tournemini* appears, according to Kerforne (1901:53), above the Kerarvail Member. At about 30 m in thickness under the *Marrolithus bureaui* Zone, this species is still represented by a few specimens only, then it becomes extinct. Its vertical range appears to be identical in both the Bas-Couyer Formation (Menez-Belair) and the Andouillé Formation (Bassin de Laval). To the south of Rennes, *Pl.* (*Coplacoparia*) *tournemini* is present in the middle and upper part of the Traveusot Formation, in micaceous areno-lutites which are of unknown thickness but which overlie black lutites containing *Pl.* (*Placoparia*) *cambriensis*. The areno-lutites of Traveusot en Guichen contain a few *Glyptograptus*, unfortunately incomplete and poorly preserved, which makes their precise determination impossible; these *Glyptograptus* might belong to the species *teretiusculus*, or to a new species (information communicated by V. Jaanusson). Overlying the Traveusot Formation in ascending sequence are the Chatellier Sandstones, about 50 to 60 m thick, then the Shales of Riadan whose trilobite fauna (very similar to that collected from the top of the Postolonnec Formation in the Finistère) shows strong affinities with the fauna known in the Libeň Formation in Bohemia (Middle and Upper Llandeilo, and Lower Caradoc; cf. Williams & al. 1972 : Fig. 2 for

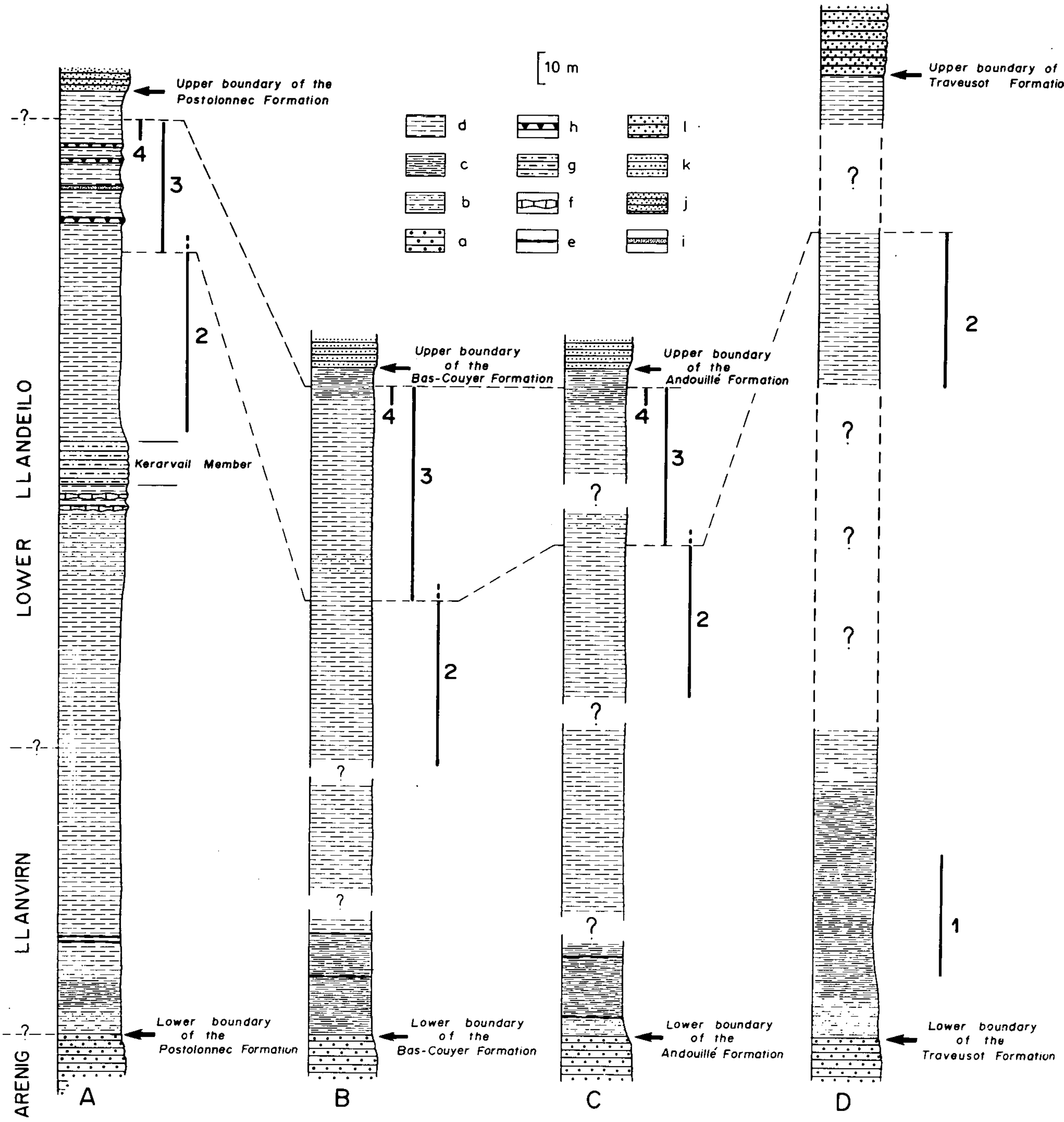

Fig. 2. Vertical distribution, as known at present, of the species *Pl. (Placoparia) cambriensis* (1), *Pl. (Coplacoparia) tournemini* (2), *Pl. (Coplacoparia) borni* (3), *Marrolithus bureaui* (4). A. Postolonnec section, Crozon peninsula. B. Menez-Belair region. C. Bassin de Laval. D. Martigné-Ferchaud synclinorium.
a. Armorican Sandstone Formation (Grès armoricain). b. Sandstone – shale alternations. c. Lutites. d. Areno-lutites. e. Oolitic beds. f. Lenticular beds of calcareous sandstone. g. Kerarvail sandstone. h. Sill. i. Thick sandstone bed. j. Sandstones of the Kermeur Formation. k. Sandstones of the Saint-Germain-sur-Ille Formation. l. Sandstones of the Chatellier Formation.

further information). In the absence of unequivocal criteria and since the sedimentary sequence is apparently conformable, it would seem for the moment that to attribute part of the Formations of Postolonnec (the *Marrolithus bureaui* Zone included) and of Traveusot to the Lower Llandeilo remains the only logical possibility.

In stratigraphic sequence *Pl.* (*Coplacoparia*) *borni* succeeds *Pl.* (*Coplacoparia*) *tournemini*, but this trilobite has never been reported, as far as we know, in the synclinorium of Martigne-Ferchaud. It is well represented, however, throughout the Armorican Median synclinorium, where it is found in association with *N.* (*Neseuretus*) *tristani, Plaesiacomia oehlerti, Crozonaspis struvei, Morgatia hupei;* it is still abundant in the *Marrolithus bureaui* Zone, but then disappears suddenly. One of the remarkable features of *Pl.* (*Coplacoparia*) *borni* is the presence of 4 semicircular depressions on the inner edge of the anterior cephalic border, a border which is covered with extremely close-set granules (Pl. 3:7–8). On the fixigenae the large cavities are barely visible and not numerous, but, as can be observed in the species *tournemini,* a few deep cavities remain on the outer region of the fixigenae. The distribution of the tiny pits remains as in the preceding species.

ENROLLMENT AND COAPTATIVE STRUCTURES

An abundance of well preserved samples, and partially or totally enrolled specimens, has made it possible for us to describe in detail the coaptative devices of *Pl.* (*Coplacoparia*) *tournemini* and of *Pl.* (*Coplacoparia*) *borni,* two species in which the enrollment is exactly alike.

When an individual trilobite enrolled, the rounded distal ends of the thoracic pleurae fitted into well marked cavities, each with a smooth bottom and set in a spiral on the lateral borders of the cheeks. These small depressions, from point ω onwards, have been numbered from 1 to 12 on each border (Pl. 2:6). From rear to front they are first located sub-ventrally, then they gradually become marginal. It is into the two foremost cavities of the librigenae that the blunt tips of the first two ribs of the pygidium come and fit. The tips of the second pair of ribs fit into the lateral depressions of the anterior cephalic border, whereas the tips of the third and fourth pairs of pygidial ribs lock into the preglabellar furrow (Pl. 2:8–10). It will be noted that the posterior border of the fixigenae bears distally a wide and short spine which fits, at the beginning of the enrollment, into a corresponding depression located on the first thoracic pleura (Pl. 2:11–12).

Hammann (1971a, Pl. 1:9a–b) has given two excellent photographs of an enrolled *Pl.* (*Placoparia*) *cambriensis.* Despite appearances, the position of the pygidium in respect to that of the cephalon at the end of the enrollment, does not differ, in that species, from that observed in *Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni.* Indeed, from the lateral view of the specimen figured by Hammann, it may be seen that the distal ends of the thoracic pleurae (from the fifth to the eleventh) are not in contact with the lateral margin of the cheek. Such incompletely enrolled specimens are frequently observed (Barrande 1872, Pl. 8:33; Prantl & Šnajdr 1957, Pl. 1(31):5; Hammann 1971, Pl. 2:13a–b; Pl. 2:7 in the present paper), not only in the genus *Placoparia* but also in *Colpocoryphe* (unpublished). Incomplete enrollment might be explained, in certain cases at least, by a partial relaxation of the musculature after death, together with rapid burial in the sediment.

Pl. (*Placoparia*) *zippei* (Dobrotivá Formation) was also capable of enrollment, as Prantl & Šnajdr (1957, Pl. 2(32):15) have figured the cast of one cheek revealing, on the lateral border, a few depressions which are very similar to those observed on *Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni.* We have not examined any enrolled individual of *Pl.* (*Placoparia*) *zippei,* but there is no reason to assume that in this species the enrollment differed from that of Ordovician forms from Brittany. The same applies to *Pl.* (*Hawleia*) *grandis* (Libeň and Letná Formations) in which the lateral margins of the cheeks also bear depressions (Barrande 1872, Pl. 8:43–44). The samples of *Pl.* (*Hawleia*) *prantli* (Ashgill of Poland) figured by Kielan (1959, Pl. 23:4–6) are poorly preserved and it is therefore impossible to comment upon the presence or the absence of coaptative structures.

EVOLUTION OF THE GENUS *PLACOPARIA* DURING THE LLANVIRN AND THE LLANDEILO

The most ancient representative of the genus so far known is *Pl. (Placoparia) cambriensis.* The lateral margin of the cheeks belonging to the specimen figured by Hammann (1971a, Pl. 1:9b) seems to reveal very slight depressions in the anterior part. These seem to be present also, and similarly located, on an external mould coming from the Šárka Formation in Bohemia. If the existence of these barely excavated depressions were confirmed by the examination of more abundant material it would reinforce the suggestion that *Pl.* (*Placoparia*) *zippei* and *Pl. (Coplacoparia) tournemini* derived from *Pl. (Placoparia) cambriensis.* Indeed, in the two Llandeilian species the depressions into which the distal ends of the thoracic pleurae interlock are already quite clear. But on the anterior border of *Pl. (Coplacoparia) tournemini* two additional excavations are present. These coaptative structures, like the ones already (described in the case of Ordovician and Silurian t_r)

described in the case of Ordovician and Silurian trilobites (Clarkson & Henry 1973), are remarkably regular features of the adults throughout the whole time range of the species. The same applies to *Pl. (Coplacoparia) borni* in which the cephalon bears, besides the two deepening lateral cavities, four new depressions located on the inner edge of the anterior cephalic border, and not on the outer edge as figured by Hammann (1971a: Fig. 3). It is as though the blunt tips of the pygidial ribs, which come to rest in the preglabellar furrow when enrollment is complete, were imprinted into an exoskeleton which was still soft; yet researches upon the coaptations of contemporary invertebrates have revealed that such mutual moulding of the coapting parts during ontogeny cannot be invoked as an explanation, and that the coaptative devices are genetically inherited (Tétry 1969; Sahuc 1969).

In the Armorican Median synclinorium, *Pl. (Coplacoparia) borni* succeeds *Pl. (Coplacoparia) tournemini* from which it probably derived, but the two trilobites may perhaps have coexisted for a short while, since they are encountered together in the same locality (foundations of the house named "les Atlantes" in Postolonnec). One of the cranidia collected (IGR N° 1851b, Pl. 3:6) shows an interesting peculiarity : although it has most of the characteristics of the species *borni,* the total number of depressions on the anterior border is 4 rather than 6. The two small hollows located immediately on each side of the plane of symmetry are missing. This "absence" originates neither in the distortion it underwent – which is very faint – nor in the preservation – which is excellent since the granulation is perfectly preserved. This specimen could either be representative of an intermediate stage, indicating a gradual transition from *Pl. (Coplacoparia) tournemini* to *Pl. (Coplacoparia) borni,* or else a hybrid, signifying the interfecundity of two distinct populations.

Parallel with the increasing complexity of the coaptative structures throughout time, and perhaps in close connection with this evolution, some characters already observed by Curtis (1961) and by Hammann (1971a) undergo gradual changes. Thus one may observe the decrease in number and size of the small pits on the fixigenae, the increase of the degree of curvature and of the length of the pygidial ribs, the increase of the density of the granules on

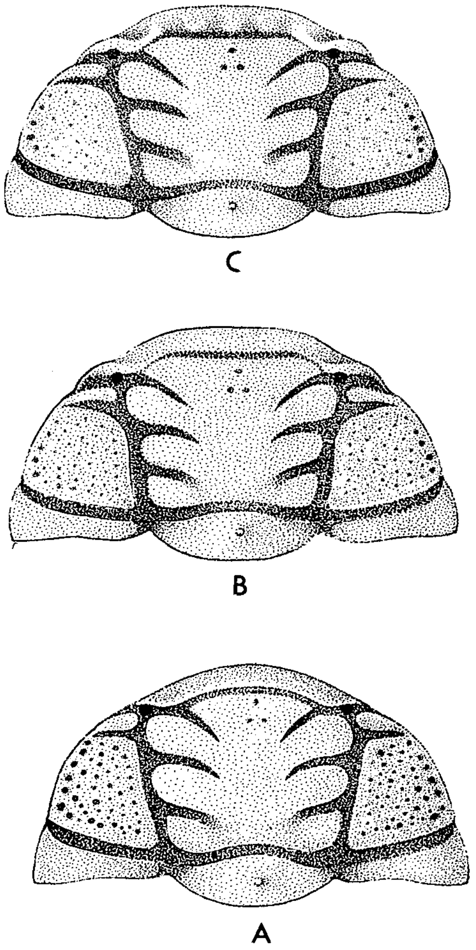

Fig. 3. Pl. (Placoparia) cambriensis (A), *Pl. (Coplacoparia) tournemini* (B), *Pl. (Coplacoparia) borni* (C). Reconstruction of the cranidia.

the anterior cephalic border of the species *tournemini* and *borni*. Along the contact surfaces between two coapting parts, this increase of the granulation has been observed, without any exception, in all the Ordovician trilobites of Brittany having coaptative devices (Clarkson & Henry 1973). In our estimation, this corroborates the ideas of Sahuc (1969) on the direct part played by mechanical rubbing and pressure in the elaboration of the coaptative structures.

In Bohemia, during the Llandeilo and the Caradoc (Dobrotivá Formation, Libeň and Letná Formations), the coaptative devices of *Pl. (Placoparia) zippei* and *Pl. (Hawleia) grandis* do not seem to undergo any improvement. In contrast to what is observed in the species from Brittany, no depressions appear on the anterior border of the cephalon whose granulated ornamentation, at least in the case of *Pl. (Placoparia) zippei,* is not different from that of the glabella. It is difficult to show for the moment, as direct evidence is lacking, that the two species *Pl. (Coplacoparia) tournemini* and *Pl. (Placoparia) zippei,* with their limited geographical distribution, constituted two strictly contemporaneous populations, but it is logical to assume that they are both derived, through allopatric speciation, from *Pl. (Placoparia) cambriensis,* a widely distributed ancestral form, since it is known in Great Britain, in Spain, in Bohemia, and in Brittany. As Devillers (1973:32) puts it: " . . . á partir d'une population ancestrale divergent progressivement des populations entre lesquelles s'établit une barrière, géographique, physiologique ou autre qui, en supprimant les croisements, empêche le brassage génétique. Dans chaque population s'accumulent, peu á peu, des caractères qui vont accentuer sa physionomie particulière et contribueront, avec l'isolement génétique qui progresse, à lui donner le statut d'espèce". Confirmatory evidence from further observations might give additional weight to some of the ideas recently expressed by Eldredge (1971, 1973) regarding allopatric speciation in Palaeozoic invertebrates.

In a paper published recently (Clarkson & Henry 1973), we wrote that the development of of predators (cephalopods) might be an indirect cause of the increasing complexity of the coaptative structures in some of the Ordovician and Silurian trilobites. This suggestion remains reasonable, but, as Hammann (1971a:66) wrote, geographical isolation, leading to particular modes of life in a given region, must not be forgotten. Whereas enrollment is often considered as a defence reaction against predators, it may also be interpreted as a reaction of the animal living in shallow waters liable to rapid variations of ecological factors (temperature, salinity, etc. . . .). In a temporarily isolated palaeogeographical province (Massif Armoricain and Iberian Peninsula), an unfavourable and unstable environment might be indirectly responsible for the appearance of new morphological devices among the representatives of genus *Placoparia.* Such a possibility is not unreasonable since the trilobite faunas known in the Spanish and Armorican Ordovician are poor; they only contain a limited number of genera and species. Moreover, in some fossiliferous localities from Brittany, where the exoskeletons are often complete (Traveusot for instance), the proportion of enrolled individuals is always very high.

The presence of 11 thoracic segments only in *Pl. (Coplacoparia) tournemini* and *Pl. (Coplacoparia) borni,* as compared with the other known species which have 12, remains to be explained. During ontogeny, the posterior elements of the exoskeleton are the last to become differentiated and the growth is directed forwards. This is clear from a number of ontogenetic series, particularly that of *Breviscutellum (Meridioscutellum),* as Feist (1970) has shown. There is no reason to suppose that growth and development in *Placoparia* was any different. Thus to be equivalent to *Pl. (Placoparia) cambriensis,* the pygidium of the *tournemini* and *borni* species would have to release an additional segment towards the thorax, one pair of pleurae then simultaneously originating in the posterior extremity of the pygidium. It may therefore be assumed that *Pl. (Coplacoparia) tournemini* and *Pl. (Coplacoparia) borni* constitute a neotenous line in which there occurs" . . . un retard dans le developpement des structures corporelles relativement à celui des organes reproducteurs" (Hupé 1953:85). To assume that evolution along this line resulted from arrested development, as R. Feist (personal communication) has suggested to us, appears to be the most plausible explanation.

In Brittany, the biozones of the species *cambriensis, tournemini,* and *borni,* such as are illustrated in Fig. 2, certainly could be improved upon, but they are still very useful in an area where the outcrops are scarce and where continuous sections are lacking.

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EXPLANATION OF PLATES

Plate 1.

The following figures are based on latex replicas: 1, 3, 5–11, 13–14. *Figs. 1–4. Placoparia (Placoparia) cambriensis* Hicks. *Fig. 1.* Cranidium, dorsal view. IGR N° 1690b. x10. *Figs. 2–3.* Pygidium, dorsal and oblique posterior views. IGR N° 1939a–b. x16.(approx.). *Fig. 4.* Cranidium, dorsal view. IGR N° 1692. x10. All the specimens come from the Traveusot Formation. "Cote 85" near Laillé, Ille-et-Vilaine. *Figs. 5–10. Placoparia (Coplacoparia) tournemini* (Rouault). *Fig. 5.* Cephalon partially shown, in lateral oblique view; note the depressions on the lateral border of the librigena. IGR N° 1894b. x8 (approx.). Traveusot Formation. Traveusot en Guichen, Ille-et-Vilaine. *Fig. 6.* Two cranidia, dorsal view. IGR N° 1854b. x10. Postolonnec Formation. Morgat, Crozon peninsula, Finistère. *Fig. 7.* Incomplete cephalon and three thoracic segments, dorsal view. IGR N° 1823b. x5. Andouille Formation (?). Butte du Creux near Saint-Denis-d'Orques, Sarthe. *Fig. 8.* Cranidium, dorsal view. IGR N° 1852b. x14 (approx.). Postolonnec Formation. Foundations of the house named "les Atlantes", Postolonnec, Crozon peninsula. *Figs. 9–10.* Incomplete pygidium, dorsal and posterior views. IGR N° 1899b. x7. Traveusot Formation. Traveusot en Guichen. *Fig. 11. Placoparia (Coplacoparia)* sp. Hypostoma. IGR N° 1856b. x6. Postolonnec Formation. Morgat, Crozon peninsula. *Figs. 12–14. Placoparia (Coplacoparia) tournemini. Fig. 12.* Hypostoma. IGR N° 1581a. x6. Bas-Couyer Formation. Bas-Couyer en Mélesse, Ille-et-Vilaine. *Figs. 13–14.* Hypostoma "in situ". IGR N° 1891b (Fig. 13) and IGR N° 1873b (Fig. 14). x8. Traveusot Formation. Traveusot en Guichen.

Plate 2.

The following figures are based on latex replicas: 2, 6–8, 12. *Figs. 1–5. Placoparia (Coplacoparia) borni* Hammann. *Fig. 1.* Cranidium, dorsal view. IGR N° 1832. x6. Andouillé Formation. Les Monneries, Andouillé, Mayenne. *Fig. 2.* Incomplete cranidium, dorsal view. IGR N° 1853b. x6. Postolonnec Formation. Postolonnec, Crozon peninsula. *Figs. 3–5.* Pygidium in dorsal, posterior and lateral views. IGR N° 1806. x5. Andouillé, Formation (*Marrolithus bureaui* Zone). La Touche, Andouillé, Mayenne. *Figs. 6–8. Placoparia (Coplacoparia) tournemini. Fig. 6.* Incomplete cephalon partially shown, frontal oblique view; note the depressions (from the fifth to the twelfth) on the lateral border of the librigena. IGR N° 1966b. x10. Traveusot Formation. Traveusot en Guichen. *Fig. 7.* Incompletely enrolled specimen, dorsal view. IGR N° 1822b. x4. Andouillé Formation (?). Butte du Creux near Saint-Denis-d'Orques. *Fig. 8.* Incomplete, but fully enrolled specimen, partially shown in dorsal view. IGR N° 5400b. x6 (approx.). Bas-Couyer Formation. Bas-Couyer en Mélesse. *Figs. 9–11. Placoparia (Coplacoparia) borni. Figs. 9–10.* Fully enrolled specimen, lateral and dorsal views. IGR N° 1805a. x3.5 (approx.). *Fig. 11.* Enrolled specimen partially shown, in lateral view, with the distal extremities of five thoracic pleurae fitting into corresponding depressions of the lateral border of the librigena. IGR N° 1818. x10. Andouillé Formation (*Marrolithus bureaui* Zone). La Touche, Andouillé. *Fig. 12. Placoparia (Coplacoparia) tournemini.* Part of an enrolled specimen, lateral view. IGR N° 5400b (see Fig. 8). x10. Bas-Couyer Formation. Bas-Couyer en Mélesse.

Plate 3.

The following figures are based on latex replicas: 1–9. *Figs. 1–3. Placoparia (Placoparia) cambriensis. Fig. 1.* Part of a cranidium showing the anterior cephalic border. IGR N° 1690b (see Pl. 1:1). x15. *Fig. 2.* Fixigena of the same specimen. x15. *Fig. 3.* Incomplete cranidium partially shown; the distortion is very faint. IGR N° 1821b. x15 (approx.). Butte du Creux near Saint-Denis-d'Orques. *Figs. 4–5. Placoparia (Coplacoparia) tournemini. Fig. 4.* Enlargement of part of a cranidium showing the two depressions and the extreme tuberculation on the anterior cephalic border. IGR N° 1852b (see Pl. 1:8). x20. *Fig. 5.* Dorsal oblique view of a fixigena. IGR N° 5400b (see Pl. 2:8, 12). x10. *Fig. 6. Placoparia (Coplacoparia)* cf. *borni.* Enlargement of a cranidium partially shown; the anterior cephalic border bears only four depressions. IGR No 1851b. x15. Foundations of the house named "les Atlantes", Postolonnec, Crozon peninsula. *Figs. 7–10. Placoparia (Coplacoparia) borni. Figs. 7–8.* Two incomplete cranidia partially shown, dorsal views; note the depressions located on the inner edge of the anterior cephalic border. IGR N° 1855b (Fig. 7) and IGR N° 1853b (Fig. 8). x15. Postolonnec Formation. Foundations on the house named "les Atlantes", Postolonnec, Crozon peninsula. *Fig. 9.* Enlargement of a fixigena belonging to the specimen IGR N° 1855b (see Fig. 7). x15. *Fig. 10.* Part of a cranidium in dorsal view showing the six depressions on the anterior cephalic border. IGR N° 1813. x18 (approx.). Andouillé Formation. Les Monneries, Andouillé, Mayenne.

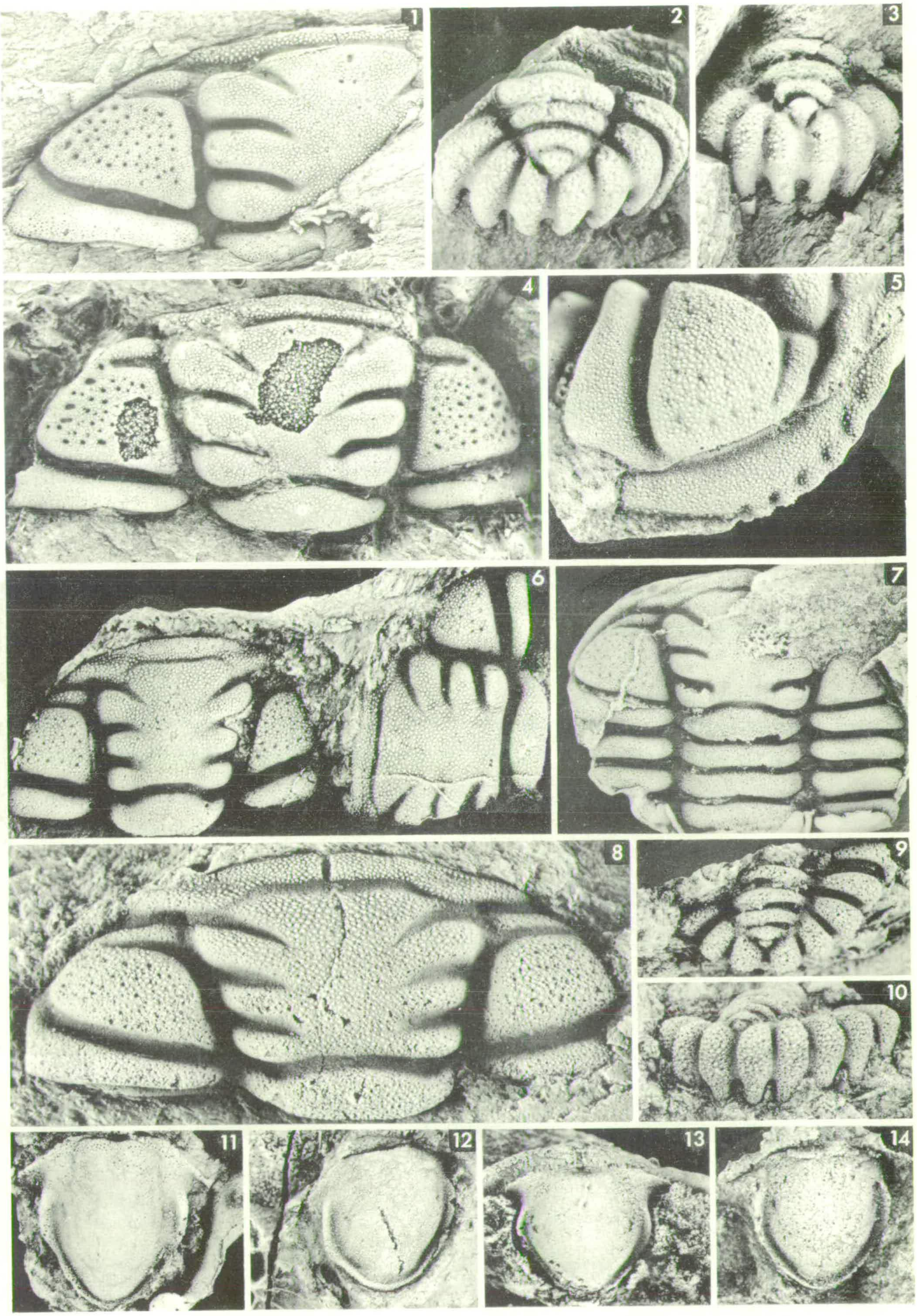

Plate 1.

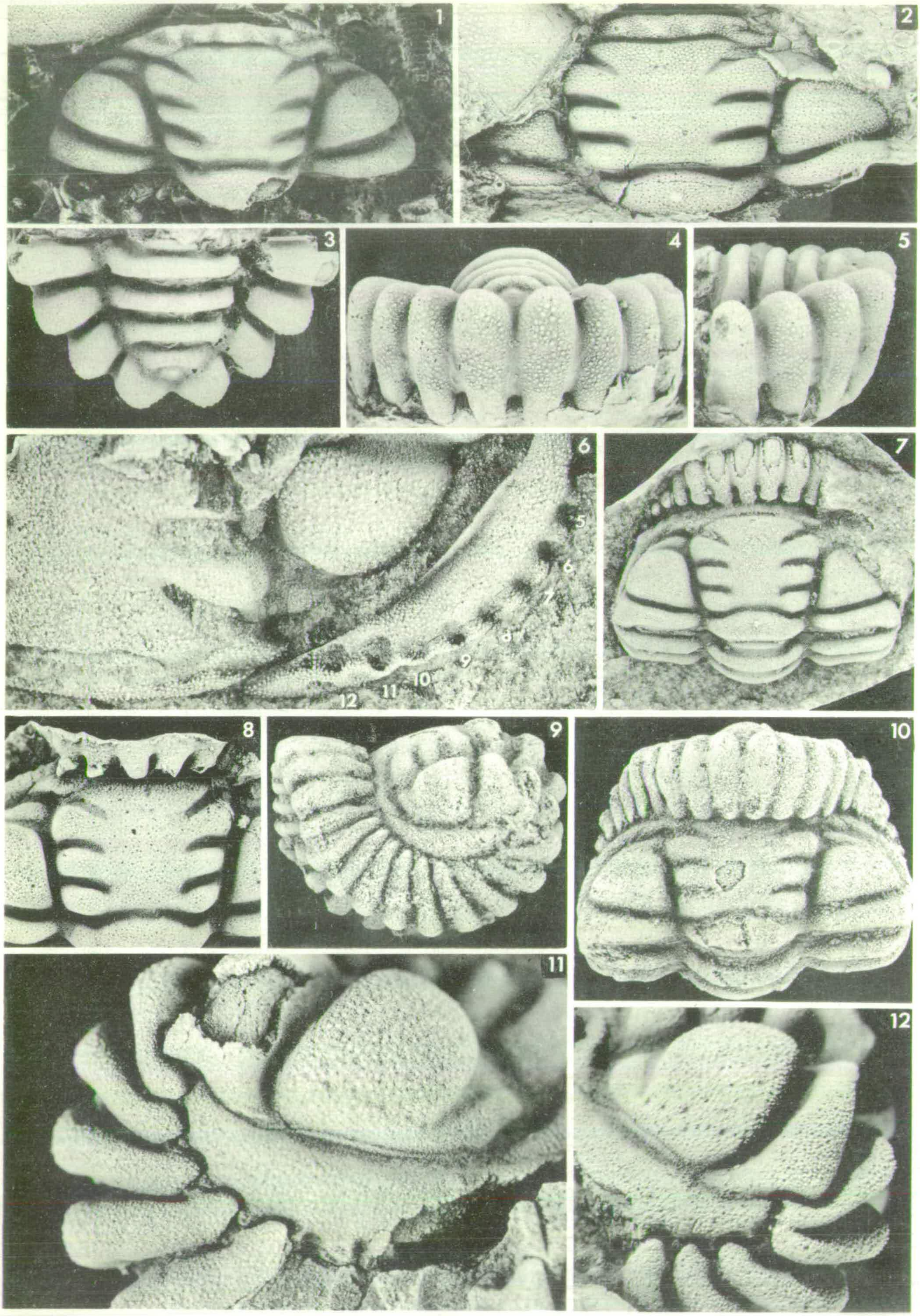

Plate 2.

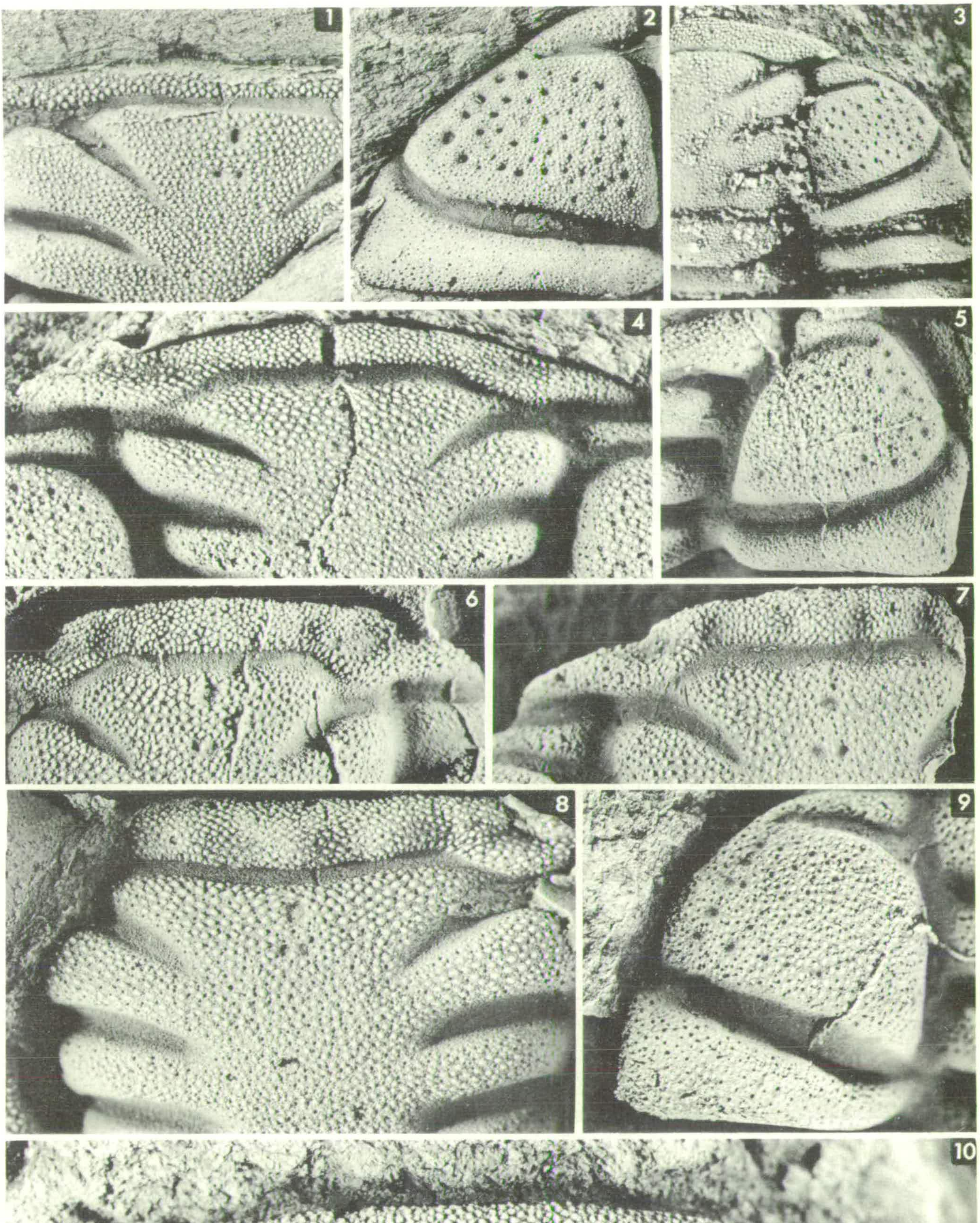

Plate 3.

(Reprinted from Nature, Vol. 254, No. 5502, pp. 663–667, April 24, 1975)

Trilobite eyes and the optics of Des Cartes and Huygens

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The thick lenses in the aggregate eyes of a group of trilobites were doublet structures designed to eliminate spherical aberration. The shape of the optically correcting interface is in accord with constructions by Des Cartes and Huygens and is dictated by a fundamental law of physics. Trilobites may have evolved such sophisticated eye-lenses to maximise optic neurone response in a dimly lit environment.

TRILOBITES, which occur in rocks ranging from Lower Cambrian (600 Myr old) to Upper Permian (250 Myr old), have the most ancient visual system known. From the beginning of their fossil record, compound eyes are present, symmetrically paired on the sides of the head. These compound eyes are primary structures and blindness in trilobites, which is not infrequent, is invariably secondary.

The primordial or holochroal eye, first found in the earliest genera, and thereafter taking many forms has numerous closely-packed lenses or prisms, each represented by a single crystal of calcite with its *c*-axis usually directed normal to the visual surface[1]. Most trilobites had such eyes, the main exception being the schizochroal eye, which is confined to the Ordovician–Devonian suborder Phacopina.

Schizochroal eyes, which are the subject of this study, have large thick biconvex lenses, each separated from its neighbours by a sclera; material similar in composition and structure to the rest of the cuticle. Eyes of this kind are present in the earliest Phacopina and there is some evidence that they were derived from the eyes of holochroal ancestors by paedomorphosis.

The structure of schizochroal eyes has been described in several publications[2,3] and it is now clear that in all known cases the lenses are doublets each of which has an upper unit of oriented calcite[4] (with its *c*-axis normal to the visual surface) interlocking with a proximally located intralensar bowl, the composition of which has not been determined. The distinction between these two units is apparent both in specimens which are preserved in limestone and thus retain their original structure, and in those preserved in silt or mudstone and subsequently decalcified. In the former case a compositional difference between the bowl and the upper lens unit is clearly visible in thin sections or polished surfaces unless diagenetic processes have destroyed or altered the primary structure; this is usually marked by a pronounced colour change. Invariably the lenses within any one eye are identical in structure. Where specimens are decalcified, the upper lens unit disappears, but the shape of its base may be preserved on the internal mould of the fossil. This is because the bowl has become detached or has decayed shortly after the death of the trilobite, and its former space is filled with silty or sandy matrix, preserving exactly the shape of the upper unit–bowl interface. The shape of this interface is clear in both kinds of preservation; there seem to be two basic kinds of structure with a range of intermediates between. The two fundamental kinds of lens structures were first described by Clarkson[3] from Ordovician Phacopina preserved as decalcified siltstone moulds. In *Dalmanitina socialis* (Barrande) from the Caradocian (Middle Ordovician) of Bohemia, the intralensar bowl is thin and indented centrally by a small dimple (Fig. 1*a*). Really well preserved specimens (RSM Geol. 1967–32; FMNH

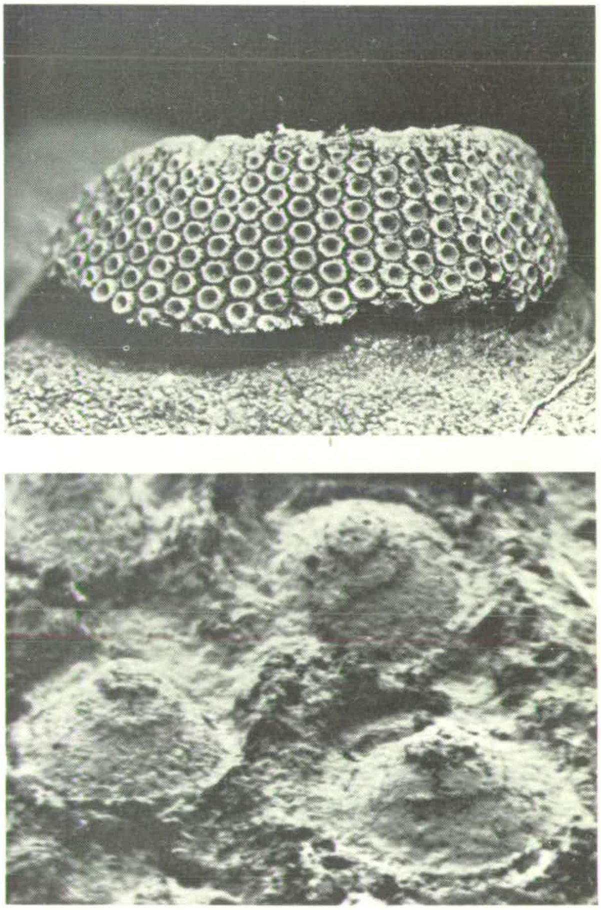


Fig. 1 *Dalmanitina socialis* (Barrande), RSM-Geol—1967–32 Letná Formation, Veselá. Bohemia. Caradocian (Ordovician). *a*, Left eye of a decalcified internal mould (steinkern) showing the intralensar bowls with central dimples. Slightly whitened with magnesium oxide (×11). *b*, Latex replica of the eye surface of the same specimen showing the central dimple of each intralensar bowl in positive relief. Scanning electron micrograph (×110).

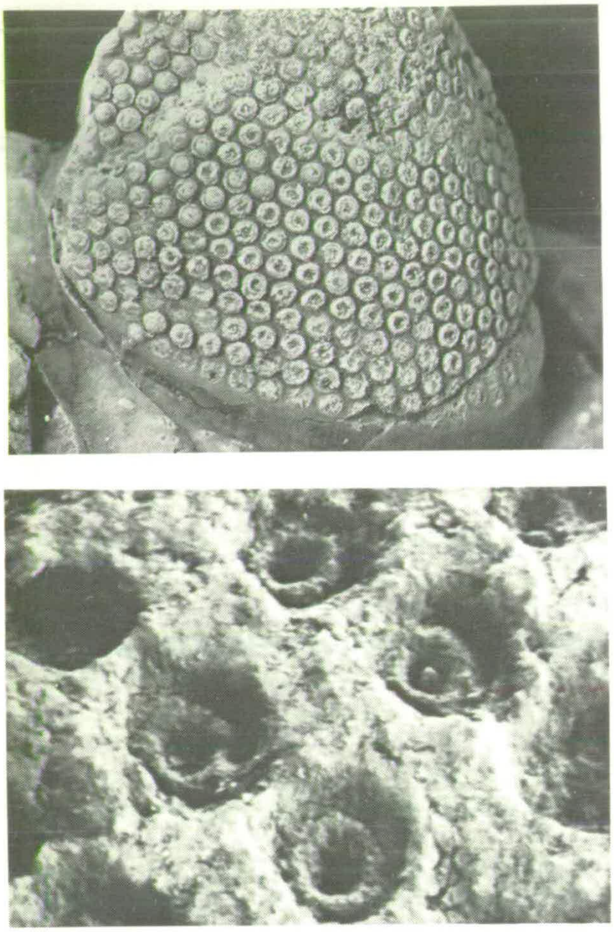


Fig. 2 *a*, *Dalmanites pratteni* Roy, FMNH P 16704, Devonian, Devil's Backbone, near Grand Tower, Jackson County, Illinois. Left eye of decalcified internal mould (steinkern) with intralensar bowls, partially filled with matrix (×4). *b*, *Zeliszkella lapeyrei* (Bureau), Gr. I. 40192. Llandeilian. (Ordovician). Traveusot-en-Guichen near Rennes, France. Part of the left eye of a decalcified internal mould showing an intralensar bowl in each lens cavity. Scanning electron micrograph (×110).

UC–1707) are rare, but from these, latex replicas can be made showing, as an average over many lens units, the surface shape as in Fig. 1*b*. The original reconstruction of Clarkson[3] has been slightly modified after a re-examination of the same material and some new material: the bowl is deeper and the upper surface is slightly more hyperbolic. Such lenses occur in other Dalmanitidae also.

The other kind of structure originally described from the species *Crozonaspis struvei* Henry[3], from the Llandeilian (Middle Ordovician) of Brittany, is perhaps better seen in the eye of *Dalmanites pratteni* Roy[5] from the Devonian of Illinois (Fig. 2*a*) and in *Zeliszkella lapeyrei* (Bureau) also from the Llandeilian of Brittany (Fig. 2*b*). Here the lens is highly convex with a large and thick intralensar bowl, indented not by a small dimple, but by a wide and hemispherical depression. Lenses of this kind are not only found in these species of Dalmanitidae, but are the norm in the Siluro-Devonian family Phacopidae, especially in the genera *Phacops* and *Reedops* in which the lenses of the eye are very large, highly biconvex and relatively few in number[6].

The example shown in Fig. 3 is a lens in horizontal section of a large-eyed Silurian *Dalmanites*. Dark field illumination shows the difference between the intralensar bowl and the upper unit. The latter has typical calcite cleavages showing it to be a single crystal (with the *c*-axis aligned along the lens axis); these stop short at the edge of the bowl. The shape of the bowl's upper surface is intermediate between the two end types mentioned above.

Corrected optics in phacopid lenses

We first discussed the possible function of schizochroal lens structure at the NATO sponsored Trilobite and Merostome Conference in Oslo in July of 1973. Subsequently, Levi-Setti recognised that the two basic patterns of the intermediate refracting surfaces in *Dalmanitina* and *Crozonaspis* approximated in shape to that of the aplanatic surfaces described respectively by Des Cartes[7] and Huygens[8].

Such generally aspheric refracting surfaces belong to the class of so-called Cartesian Ovals. They were originally designed to obtain lenses free of spherical aberration. The original constructions by Des Cartes and Huygens are reproduced in Fig. 4*a* and 4*c* respectively, where for comparison, the structure[3] of the lenses of *Dalmanitina socialis* (Fig. 4*b*) and *Crozonaspis struvei* (Fig. 4*d*) are also shown. The similarity between the shape of the upper unit in *Dalmanitina* and the Des Cartes construction, as well as in that of the upper unit in *Crozonaspis* and the Huygens construction is strikingly apparent.

Cartesian Ovals

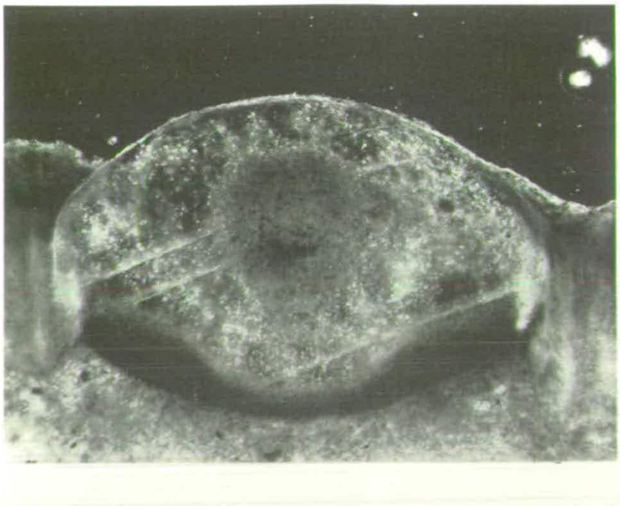
The physical principles underlying the function of the ovals of Des Cartes as optical refracting interfaces are derived from regarding these surfaces as the geometric representation of the stigmatic condition for an optical system (the requirement that a point in object space be mapped on to a point in image space). Their analytic expression, which is in general that of a fourth degree surface in Cartesian coordinates, takes a particularly significant form when cast in bipolar coordinates[9]. If the distances of a point P from two fixed points O and O' are called r and r' respectively, then r and r' are called bipolar coordinates of P. An equation connecting r and r' defining a locus for P, is called a bipolar equation. The ovals of Des Cartes are defined by the bipolar equation:

$$mr \pm nr' = k \tag{1}$$

where m, n and k are constants. If we now consider a system of two conjugate points O and O' in object (refractive index n_1) and image (refractive index n_2) space respectively, and r and r' the distances traversed by a light ray going from O to O' through a point P on the surface separating the two media, we can write the stigmatic condition as:

$$n_1 r + n_2 r' = c \tag{2}$$

Fig. 3 *Dalmanites* sp. Silurian. Locality unknown. Single lens in thin section in dark field illumination, showing the dark intralensar bowl, and calcite cleavages truncated by a diagenetically altered central mass. Diagenetic effects within other lenses of the same eye are very variable; in some lenses it is only incipient, whereas in others irregular masses of amorphous calcite have filled up much of the interior. This section is cut in the horizontal plane and passes through the centre of the lens (×70).



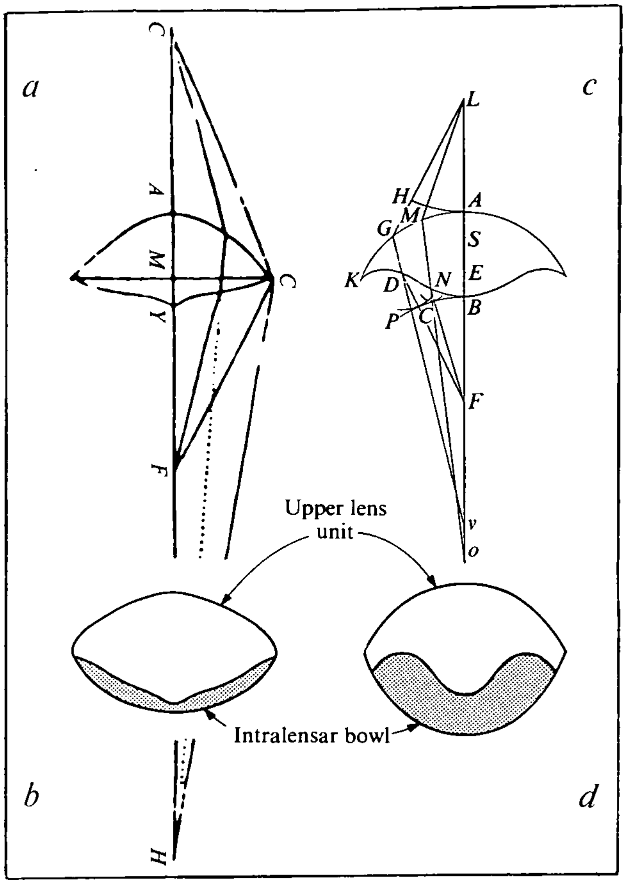


Fig. 4 *a*, Original construction by Des Cartes of an aplanatic lens in air, making use of two Cartesian Ovals. *b*, Reconstructed lens of *Dalmanitina socialis*. *c*, Original construction by Huygens of aplanatic lens in air making use of spherical first surface, and a Cartesian second surface. *d*, Reconstructed lens of *Crozonaspis struvei*[3].

with c as a constant. This equation implies that whatever the position of the point P on the interface of the two media, the optical paths (represented by the left hand side of equation (2)) between the conjugate points O and O' must be the same. Alternatively, the shape of the interface must be such that light will traverse the path from O to O' in equal times, either travelling along the straight line connecting the two points (the shortest path hence the shortest time) or any other off-axis path. In his construction of a lens free of spherical aberration, Huygens[8] adhered explicitly to this condition. Ultimately, equation (2) is a specialisation of Fermat's principle of least times, which states that no matter to what kind of reflection or refraction a ray is subjected, it travels from one point to another in such a way as to minimise the time taken. We recognise that equation (1), restricting to the + sign, and equation (2) have identical forms. The bipolar representation of the ovals of Des Cartes thus acquires an immediate physical meaning through fulfilling the stigmatic condition when describing the shape of an optical interface. In this sense the ovals of Des Cartes represent the most natural economical solution to the problem of constructing optical elements free of spherical aberration. In our derivation, the only physics involved consists of Fermat's principle: Snell's (or Des Cartes') law of refraction is in fact already an implicit consequence of the former, as first demonstrated by Huygens on the basis of the wave theory of light. The ovals of Des Cartes could of course be described more laboriously with recourse only to the (weaker) refraction laws[7].

Optical function of phacopid lens doublets

Were it not for the presence of the intralensar bowl in the trilobite lenses, there would be virtually a one-to-one correspondence in shape and function between trilobite lenses and the optimal construction of Des Cartes and Huygens (allowing for differences arising from the fact the trilobite lenses operate in water rather than in air).

The function of the intralensar bowl has been investigated empirically by two approaches: first, graphical ray-tracing through the lens structure for example, that of *Crozonaspis*, and second, constructing a large-scale model of a *Crozonaspis* lens.

In the problem at hand we assume that the refractive indices of the media in contact with the entrance surface (seawater, $n = 1.33$) and the exit surface (body fluid, $n = 1.34$) are known. We also assume that the refractive index along the axis of the upper lens unit is equal to that along the c-axis of calcite ($n = 1.66$).

Given the interface profile actually observed, the unknowns are the refractive index of the intralensar bowl and the focal distance of the lens doublet as a whole. In principle the problem is completely determined by making use of the two constraining conditions: the stigmatic condition as an extension of equation (2); and the requirement of continuity of the light rays at each refracting surface. (It should be noted that since equation (2) satisfies Fermat's principle, the law of refraction does not represent an independent constraint.)

Using both approaches, by trial and error, we have determined that the intralensar bowl of *Crozonaspis* should have a refractive index of about 1.63, and the resulting focal length equals approximately one lens thickness measured from the exit surface. The f/number (inverse of the relative aperture) of this lens, operating in water is $\sim f/1.1$.

Given the shape of the upper unit as observed in *Crozonaspis* the intralensar bowl is thus seen as a necessary element to ensure convergence of an incident parallel beam of light to a sharp focus, when the lens is immersed in water. The intermediate Cartesian interface acts as a correcting surface, to make the doublet aplanatic.

The graphical ray tracing construction for the corrected lens versus a similar uncorrected one is shown in Fig. 5*a*, where the effect of spherical aberration for the latter case can be appreciated. The experimental verification of the function of the *Crozonaspis* lens is illustrated in Fig. 5*b*, which shows the focusing of a parallel beam of white light by a large scale model of the lens. Considering the uncertainties inherent in this reconstruction of the profile of the lens and the imperfections in the manufacture of the model, the focal plane of the corrected lens is remarkably well defined. The value of refractive index derived for the intralensar bowl may give a clue to its unknown chemical composition. Calcite was probably present, possibly together with organic material such as chitin.

Advantages and disadvantages

The fact that this remarkable lens doublet system functions in the manner empirically determined, provides independent evidence for the presence of oriented calcite[4] in the upper unit *in vivo*. It can, moreover, easily be appreciated that such a system is adapted for light collection and for the formation of a sharp and undistorted image in its focal plane.

Calcite is the basic structural component of the trilobite exoskeleton[10], but its orientation in the lenses is optimised to the function being performed. In the first place, this orientation is the direction along which the ordinary and extraordinary rays of calcite propagate with equal velocity, thus eliminating birefringence for paraxial rays. In the second place, along the c-axis the refractive index is maximal ($n = 1.66$), thus yielding the largest possible relative aperture (and thus optimising light-gathering) for a lens of the shape given.

The production of a good quality image, however, may not have been the main advantage to the trilobite of evolving such lenses. Because it is (to a first approximation) free of spherical aberration, the distribution of light intensity along the axis peaks more sharply in the region of the focal plane than it would in

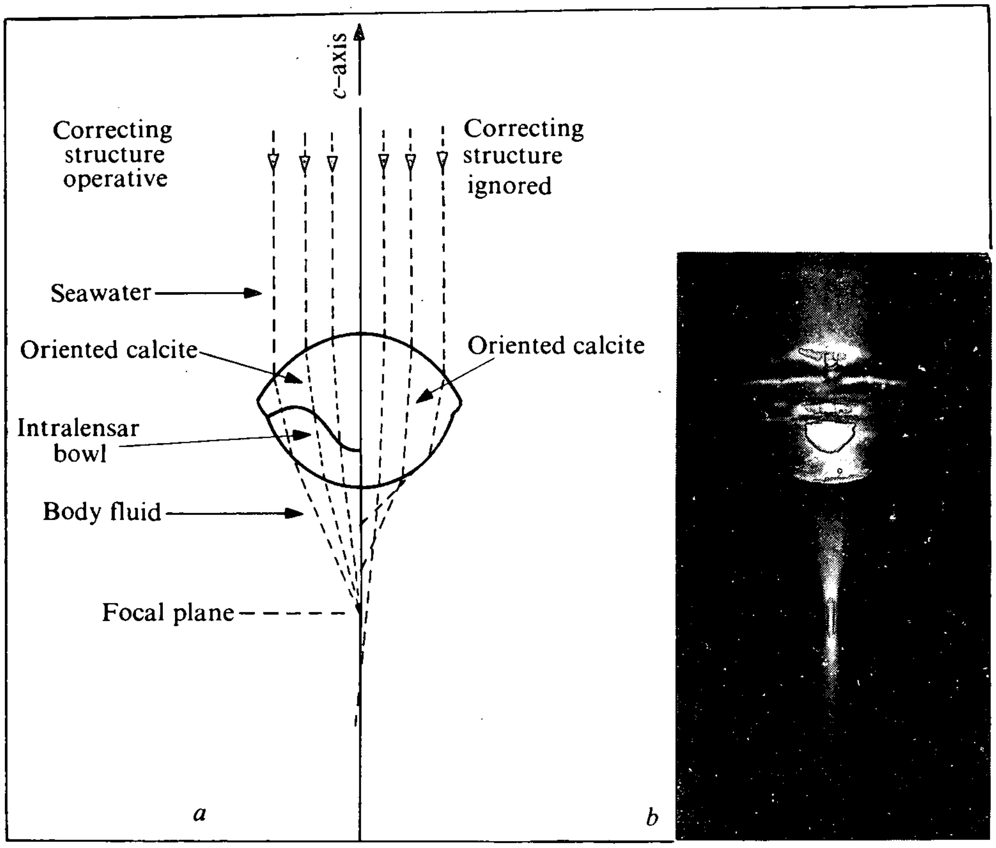


Fig. 5 *a*, Ray tracing through tl lens of *Crozonaspis struvei*. On tl left of the axis, the correspondi structure is assumed operative f indices of refraction: seawater 1.3 oriented calcite of upper unit 1.6 intralensar bowl 1.63, body flu 1.34. On the right of the axis, tl lens is assumed to have no intern structure, and made of oriente calcite $n = 1.66$. *b*, Parallel bea of white light incident upon a lar scale model of a *Crozonaspis* le immersed in water, where the upp unit is made of oriented calci ($n = 1.66$), and the intralens bowl is made of polysulpho ($n = 1.63$). The light beam is ma visible by a small amount of mi mixed with the water tank. Tl combination of refractive indic represent an optimum conditio arrived at after testing with intr lensar bowls made of vario plastics.

an uncorrected lens. A measure of this improvement is the full width at half maximum of such distribution. Scaled down to the actual size of the *Crozonaspis* lens (250 μm), we estimate the above width at about 20 μm, and possibly less. If the lenses were uncorrected, the corresponding width would approximate to about 100 μm. The increased concentration of light in the focal plane could conceivably raise the level of illumination in a dimly lit environment above the neural response threshold at the retina.

The use of a doubly refracting mineral such as calcite to construct a lens may seem disadvantageous. This drawback has been shown to be minimised by the orientation of the *c*-axis to coincide with the optic axis of the lens. Only for an object placed considerably off-axis would a secondary (extraordinary) image be formed, at varying depths, depending on the angle of incidence, but always deeper than the ordinary (o ray) image. As a consequence, the e ray image will not coincide with that formed by the o ray, nor will it focus in the same plane. One could envisage several means by which this ghost image could have been eliminated, although in any case it may have been of little consequence. A retina of limited thickness located in the image plane of the o ray would automatically filter out the e ray image: although accommodation of the eye would require a movable retina, a remarkable depth of field would still be available even with a fixed one. From the optical parameters of phacopid lenses, and requiring a circle of confusion in the retinal plane of diameter as small as 1 μm (the resolution limit due to diffraction), the depth of field would extend from several mm (~1 trilobite length) to infinity. Alternatively, one could invoke the use of photoreceptors sensitive only to the direction of polarisation of the o ray, thus eliminating the effect of the e ray image (the polarisation analysing capability of the rhabdomes is well known).

Finally, one could object that chromatic aberration may have offset the correction of spherical aberration. This is unlikely, however, since the environment under the sea is essentially monochromatic even at moderate depths.

Visual function of schizochroal eye

The function of schizochroal eyes can be better appreciated whe contrasted with that of holochroal eyes. Holochroal eyes i trilobites normally have pronounced curvature in both th azimuthal and vertical planes (often assuming a toroidal shape and have numerous optical elements which could, as in insec and crustacean eyes, have formed a true visual mosaic. Schizochroal eyes, however, have too few optical units to form detailed mosaic image. Furthermore, the arrangement of th lenses in files often widely separated and pointing in divergin directions, leads to a discontinuous coverage of the object space Such eyes as these were formerly thought[2] to be capable only o gross movement perception, though the discovery of correcte lenses now calls this view into question.

What use did phacopid trilobites actually make of their corrected lenses? They may have been used primarily as light concentrators, as has recently been proposed[11] for *Limulus polyphemus*. Alternatively, they may have served a more comple function. If the photoreceptor had the form of a thin retina, a suggested by the aplanatic properties of the lens, and if it wa composed of numerous subunits, then the corrected imag formed by the lens at the level of the focal plane or immediatel beneath it, could be perceived as a micromosaic. The schizochroal eye could then be regarded more as an aggregate o individual eyes, each surveying a different part of the objec space, rather than as a true compound eye. Evolution would hav in this case proceeded from the external mosaic scheme of th ordinary compound eye towards the utilisation of an interna mosaic, much as in the lens–retina eye system of more advance life forms. It is unfortunate that the genetic information of suc a perfected visual apparatus became lost to further evolution i the animal kingdom, when the phacopid trilobites becam extinct.

The presence of crystallised *in vivo* calcite in the lenses of fossilised trilobite specimens may prove valuable in a differen context. It is conceivable in fact, that this primary minera retained its original isotopic composition, in equilibrium wit the depositional environment. If so, trilobite lenses may afford an unprecedented opportunity for determining the temperatures of Palaeozoic seas using the $^{18}O/^{16}O$ relative abundance method[12].

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The evolution of the eye in trilobites

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The earliest trilobites have fully differentiated compound eyes, and the subsequent evolution of the eye seems to have been controlled by only three factors: (1) Changes in proportion, surface curvature, etc., through differential relative growth. (2) Paedomorphosis, which was probably the main factor in the origin of the schizochroal eye. (3) Incorporation of cuticular sensillae into discrete sensory zones peripheral to the eye. Cambrian eyes are rarely preserved due to the functional ocular suture. In post-Cambrian trilobites, the visual surface is normally intact, and an analysis is presented of its growth and form (controlled by a logarithmic spiral generative zone), different systems of lens-packing, and visual ranges. The schizochroal eye is shown to have had an internal muscular system, and may have been an organ for night vision.

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VISUAL SYSTEMS IN THE ANIMAL KINGDOM

The origin and evolution of different kinds of visual system has been the subject of discussion for a very long time. This debate was originally based upon the knowledge of anatomy and embryology of various kinds of eyes which had been established during the era of classic light microscopy (c. 1870–1920). At this time, much research was done upon the comparative anatomy of many different eyes, especially in the various German schools, and we have a fine heritage of beautifully executed studies of eye morphology dating from this period, detailed as far as the limits of resolution of the existing light microscopes would allow. In eyes of all kinds the really basic structures are the photoreceptors, normally located deep within the eye, and their structure is so fine that it eluded the early microscopists altogether. It was not until the advent of the electron microscope that the ultramicroscopic details of the photoreceptors became visible. And the one striking conclusion to emerge from their study was the fundamental homogeneity of photoreceptors throughout the animal kingdom. In all kinds of living organisms which possess eyes; protistans, molluscs, arthropods and vertebrates, there is similarity both of photoreceptor structure and photochemical processes operating within the photoreceptors. They normally consist of ultramicroscopic tubules, stacked in regular blocks containing visual pigments which are altered chemically by light and trigger a series of electrochemical reactions which end by stimulating the optic nerve; (Eakin, 1968 Wolken, 1970).

Though the photoreceptors are basic, they form only one part of the eye. The rest consists of accessory structures which direct and focus light onto the photoreceptors. These on the one hand and the nervous complex which integrates the electrical stimuli triggered off by the light impulses on the other, are complementary and highly important parts of the whole organ.

One evolutionary path seemingly led from simple eye-spots to an aggregate of photoreceptors in a pit, thence to a lensless pinhole camera type of eye, and finally to a true "camera-eye" with a lens. This path was followed independently by many groups of animals, culminating in the eyes of cephalopods and vertebrates, but the visual organs of spiders and the median eyes of insects and some other arthropods can be regarded as less elaborate versions of the same kind of eye.

A second type of eye is the compound eye, characteristic of most arthropods, some polychaete worms (Bekhlemishev, 1964), and possibly, the peculiar Silurian chordate *Anikitizoon* (Ritchie, 1964). Compound eyes are composed of repeated organs of similar kind, the ommatidia, each being a hollow cylinder capped by a lens, with the photoreceptor or rhabdom situated in the bottom half of the cylinder. The ommatidia all point in slightly different directions, usually encompassing a wide visual field, and their bases are linked to nerve ganglia whose complexity almost rivals the vertebrate brain, but whose integrative action is as yet poorly understood.

Trilobites possess compound eyes, which are the most ancient visual system of which we have knowledge. Their evolutionary history can be followed through some 350 million years of geological time. It is perhaps surprising that they have so long been neglected in discussions of the evolution of visual systems especially after the promising work of Clarke (1889) and Lindström (1901) for they provide the only real evidence of an eye evolving through time; the compound eye of trilobites is the only visual system with a good evolutionary history (though fossilised eyes are also found in a few eurypterids and in scorpions and insects). And though the only remains of their internal structure are occasional, tantalising traces, the lentiferous region and associated areas are often quite beautifully preserved, and can provide us with a remarkable body of information.

VISUAL SYSTEMS IN ARTHROPODS

Paired, laterally positioned compound eyes are present in myriapods, insects, crustaceans, and in certain living and fossil merostomes, as well as in trilobites. The median eye or ocellus, which may have a single lens overlying the photoreceptive layer, so commonly present in insects and crustaceans, is absent in trilobites. Some zoologists believe that the compound eyes in some or all of these various arthropodan stocks were derived independently from aggregates of simple eyes and that this may have happened several times. But the trilobites give no assistance in elucidating this problem, nor do they tell us anything about the origin of the compound eye. For the earliest Cambrian trilobites had fully developed compound eyes; those of the Lower Cambrian olenellid trilobites not being radically different to the eyes of most later genera and there seems to be no reason to regard them as functionally inferior to modern compound eyes.

Many excellent reviews have extensively treated the anatomy and physiology of modern arthropod eyes (Waterman 1961; Wigglesworth 1965; Dethier 1967, amongst others), and I have previously written brief accounts of compound eye functional organisation in relation to that of trilobites (Clarkson, 1973); no further discussion is given here.

STRUCTURE AND EVOLUTION OF TRILOBITE EYES

Composition and preservation

The lenses of trilobite eyes were composed of calcite, which was probably secreted by cells underlying the visual surface. This calcite was primary, but may have mixed with some undetermined organic component.

Several lines of evidence support this determination. Firstly, the cuticle of trilobites, which grades laterally into the eyes, is largely calcite, arranged in small needles normal or near normal to the visual surface (Dalingwater, 1973), but often with an external calcite layer of little crystals in a different orientation. The fine straight or coiled canals described by Dalingwater, which penetrate the cuticle would not have been preserved had the calcite forming the cuticle been other than primary. Secondly, thin sections show that all the lenses or prisms of which the eyes are made are single crystals with their c-axes normal to the external surface of the eye. This arrangement is functionally desirable for the elimination of unwanted polarised rays; light passing along the c-axis is unpolarised (Clarkson, 1973a). Such structure has been described in *Asaphus* and in olenids (Clarkson, 1973a, b), and also in *Isotelus* and phacopids (Towe, 1973). Towe has shown how inverted images are produced by the calcite lenses of *Phacops* over a large depth of focus. Stereoscan photographs of asaphids and olenids (Clarkson, 1973a, b) showing fracture surfaces of lenses and prisms confirm that this interpretation is correct, for they exhibit typical calcite cleavages such that the crystallographic orientation of each prism can be established.

How much information can be gained from the study of trilobite eyes depends entirely upon their preservation. Limestones and argillaceous calcareous muds normally preserve the details excellently, but on occasions the micritisation of the cuticular surface by invading algae may have damaged the surface (Miller, 1972). The finest details of all have invariably been found in specimens preserved in finegrained, medium to dark-coloured limestones, often somewhat pyritous. Examples are the Upper Cambrian alum shales of Scandinavia, the Dvorce-Prokop Limestone (Emsian, Bohemia), and other Bohemian Limestones (Svoboda, 1966); Devonian Limestones of the Traverse Group, Michigan, Shunner Fell Limestone (Namurian, Yorkshire, U.K.), and others. Pure reef limestones may preserve very good details of external surfaces, but there is usually, rather disappointingly, less good detail of structure seen in cross-section, because of minor recrystallisation which shows up distinctly in stereoscan photographs and has often obliterated small structures.

Thus stereoscan photographs of the Devonian scutelluid *Paralejurus brongniarti* (Barrande), from the Dvorce-Prokop limestone of Bohemia, show remarkable details of not only the lenses, but also small pits just below the visual surface, some 10 mμ in diameter. (Pl. 1: 3.7). Such pits probably existed in the related *Bojoscutellum paliferum* (Beyrich), from the pure Koneprusy Limestones but there is no trace of them, and the surface at equivalent magnification is clearly recrystallised, often very coarsely. Similar recrystallisation affects the Upper Ordovician reef limestones of Kiesley, Kildare and Dalarna.

Good details are often preserved in red limestones (e.g. the Suchomasty limestone of Bohemia) and in certain glauconitic limestones (such as the Lower Ordovician limestones of Öland). Silicified trilobites (Whittington & Evitt 1954; Whittington 1959), are of limited value owing to the surface granulation visible at quite low magnifications (Pl. 5: 3.4 by contrast with Pl. 5: 1.2. 5.6.).

Some trilobites which appear to be extremely well preserved, such as those from the English Wenlock Limestone, prove to have less good structural details than might have been expected; through the softness of the matrix and almost invariable micritisation, and syndepositional abrasion of the cuticle.

It therefore seemed appropriate to study in detail, through stereoscan and thin section work, those trilobites which were of exceptional preservation and to use the others for studies of gross morphology, and for the measurement of visual fields, so as to build up a scheme of the evolutionary history of trilobites eyes inevitably most firmly based in some parts than in others. Some valuable information can also be gained from internal and external moulds of specimens in decalcified mudstones and siltstones, which can at least give information of the basic anatomy of the eye, and the shape of the lenses. In some schizochroal eyes preserved in this way there are puzzling intralensar bowls lying in the bottoms of the pits orginally occupied by the lenses, usually of the same composition as the matrix. It is probable that these parts of the lenses did not consist of calcite but of some other material. A new interpretation of the lens structure in schizochroal eyes is given on p. 24.

Very rarely there are preserved specimens which appear to have suffered virtually no post-mortem diagenetic processes at all. An example is a specimen of *Cyclopyge kindlei* Cooper, from the Whitehead Formation, Upper Ordovician, Percé, in which the external surfaces of the lenses are exceptionally glossy appeared remarkably smooth, even at a magnification of x10,000 ! This surface appears to represent the original unaltered exterior of the trilobites; it would be interesting to know the state of degradation of the organic matter.

Holochroal and schizochroal eyes

The basic division of trilobite eyes into holochroal and schizochroal kinds, as originally defined by Clarke (1889) and later clarified in Lindström's (1901) work, has been fully substantiated. Holochroal eyes, with a single cornea covering the outer surfaces of the lenses are of many varied forms, and persisted in trilobites of Lower Cambrian to Permian age. They are poorly understood in Cambrian genera, however, because the visual surface of these was normally encompassed by the circum-ocular stuture which meant that the lentiferous region dropped out after the death of the trilobite and was not preserved except in juveniles.

Schizochroal eyes, as understood here, with their large separated lenses, are confined to the suborder Phacopina. They are of much more restricted range in form than holochroal eyes, normally being truncated cones with a laterally directed visual field. Though in other groups such as Cheirurina, the eyes have sometimes been reported to be schizochroal, these are not comparable in structure to the eyes of Phacopina, resembling them only in having lenses slightly separated from one another. In these, however, there is still a common corneal covering, which happens to be somewhat flattened in the interstices of the lenses, but is otherwise undifferentiated. They cannot therefore be regarded as truly schizochroal in the sense originally defined by Clarke, for the cornea does not, as in Phacopina, leave the margin of each lens to plunge as a cylinder through the interlensar sclera.

Harpid eyes have two or three large separate lenses, of elliptical form, with the long axis horizontal. Lindström's figure (1902, Pl, IV: 19) illustrated concave bases but Richter (1919) showed that this was a preservational feature and that they are really ovoid. Neither author gave evidence of a plunging peripheral cornea. Harpid eyes could perhaps be regarded as an independent evolutionary experiment towards a schizochroal condition, but their structure is so different from that of phacopid eyes that it would be unwise to term them schizochroal.

Another example where a member of a normally holochroal group has departed from the usual condition towards a more "schizochroal" form is provided by the eye of *Pricyclopyge binodosa* (Salter), from the Llanvirnian of Sarka, Bohemia, (Pl. 2: 3). Here the lenses arranged in the "rhombic" system typical of all cyclopygids, are of thinly biconvex form. But each lens is surrounded by a deep cylindrical groove and is separated from its neighbours by interstitial material, so that it has a very schizochroal appearance. It is not clear whether the cornea continues over the interstitial material or otherwise, but it is interesting that this odd structure appears in a group where all other members are holochroal in the ordinary way, and that in all other respects the eye is similar to theirs. If the schizochroal eyes of phacopids originally arose through paedomorphosis, it would not be surprising to find other examples to appear occasionally in unrelated groups, and such may be the case in *P. binodosa.*

A new type of eye (abathochroal), in Middle Cambrian *Pagetia* is described by Jell (this volume), as having separated lenses with disjunct corneas.

The schizochroal lenses of Phacopina are generally much larger than those of most holochroal eyes, but there is some overlap in size range. Normally lenses in holochroal eyes average less than 100 mμ across, but range in diameter from about 30 mμ in *Remopleurides, Apatolichas* and other genera, through c. 60 – 80 mμ in most Proetacea and Illaenidae, to 120–170 mμ in the large scutelluids *Bojoscutellum* and *Paralejurus,* and even up to 200 mμ in certain Cyclopygidae.

In the early Phacopina the lenses are not as large as they became later. In *Kloucekia micheli* (Tromelin) they average 120 mμ across, though most other Zeliszkellinae and in Acastinae they are consistently around the 200 mμ range. Very large lenses are found only in the later Phacopina. The Devonian genera *Reedops* has lenses of diameter 450 mμ, and in *Phacops* they range from 350 mμ to a normal maximum of 750 mμ though Brink (1951) figured a specimen in which they were over 1 mm across. Similar ranges are found in the large Devonian Dalmanitidae.

It is interesting to contrast these size ranges with the diameters of the lenses in *Limulus* (200 mμ), and in certain salticid spiders (350 mμ). Most insect, crustacean, and myriapod eyes, however, have lenses smaller than those of holochroal eyed trilobites, being in the region of 8–45 mμ.

Major features of the evolution of the eye in trilobites

Though compound eyes are known to be present in Lower Cambrian trilobites, evidence as to their organisation is very limited.

Intact visual surfaces with lenses are present in meraspids of *Olenellus gilberti,* from the Lower Cambrian of Alberta (Walcott 1910: 239, Pl. 43: 5.6; Clarkson, 1973b), and also in *Holmia kjerulfi* (Kiaer, 1916: 61, 65; Pl. 7: 1–3) and *Kjerulfia lata* (Raw, 1957: 152, who rightly remarks, "How ancient already in the Lower Cambrian must the compound eye have been". The pagetiids of the Middle Cambrian also had eyes (Jell, this volume) with up to 20 lenses each, but no Upper Cambrian or later Agnostida had any visual organs.

The eyes of Cambrian trilobites are not well known, and only those of Upper Cambrian olenids have been studied in any detail. Nevertheless there are certain details of the history of the eye in Cambrian times which are well established (Fig. 1). All known Cambrian trilobite eyes except for those of pagetiids appear to have been of holochroal type, but very rarely, except in some Upper Cambrian groups, is the visual surface preserved. This is because, as Öpik (1967) 54) pointed out, the visual surface of most Cambrian forms was encircled by a circum-ocular suture, consisting of two branches, the palpebral (upper) and ocular (lower) sutures, so that the lentiferous region normally dropped out of its "socket" after death and was lost. In most post-Cambrian trilobites, as well as some of the Upper Cambrian genera, the ocular suture became fused so that the visual surface was retained by the librigena, and thus was preserved. I have shown (Clarkson, 1973b), that at least in olenellids and in some olenids, the ocular suture was not functional in meraspids, which therefore retained an intact visual surface. The same was probably true of most other Cambrian groups, and a search among Cambrian meraspids may reveal many more eyes. But as far as is known, pagetiids excepted, the eyes of Cambrian trilobites seem to have the following characters: –

(a) The lenses are thin and biconvex, arranged in a hexagonal close packing system which may or may not be regular.

(b) The eyes are normally reniform, though some are globular. No pedunculate eyes are known.

(c) The ocular suture was normally functional in adults, but in several independent groups of Upper Cambrian age, it became obsolete. Öpik (1967, p. 55) lists a number of Australian forms in which the visual surface is retained; in addition, the later olenids, the Catillicephalidae (Rasetti, 1954), and genera such as *Acheilus, Tatonaspis,* and *Stenopilus* (Rasetti, 1944, 1945) may be cited.

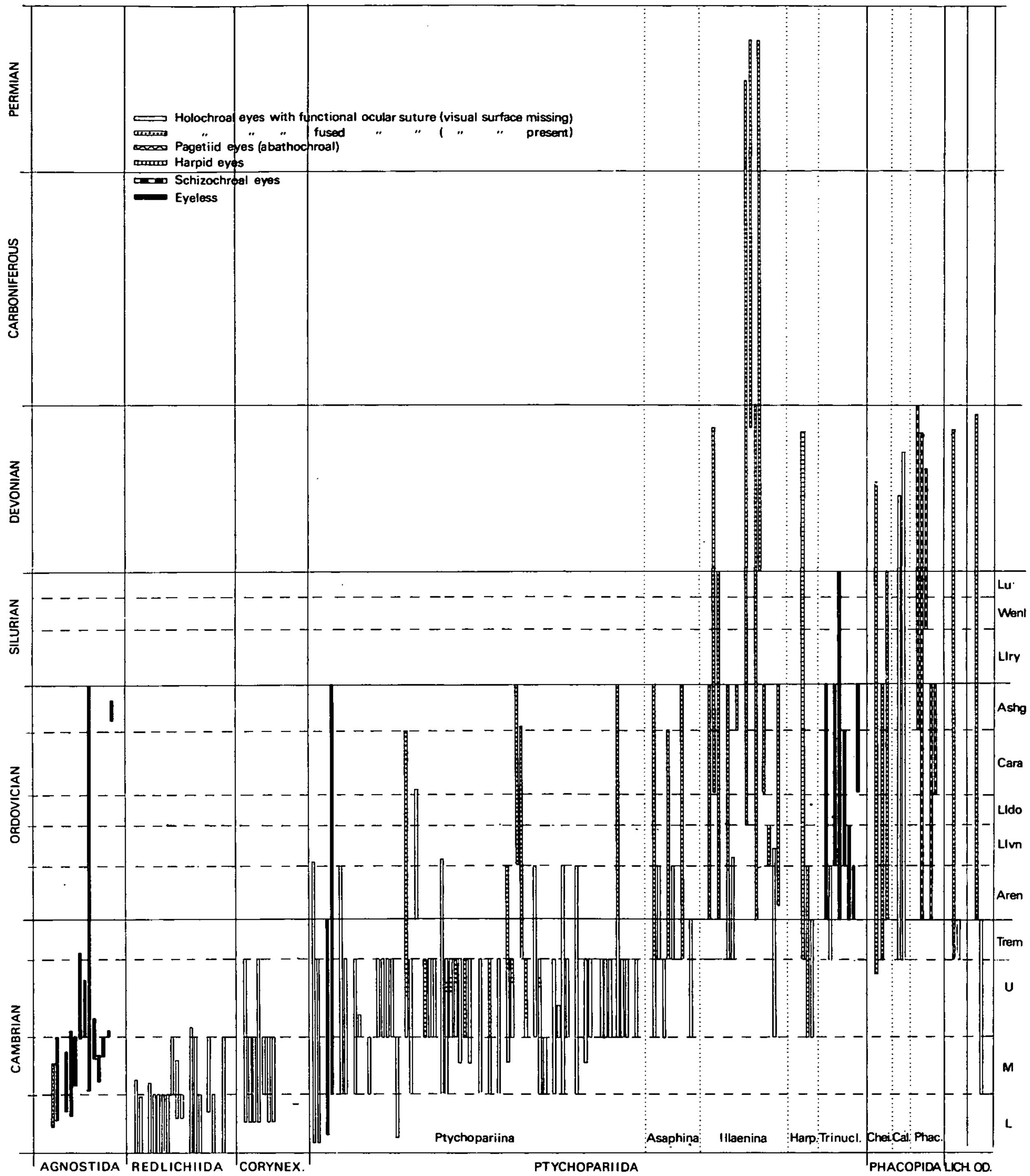

Fig. 1. Time ranges of trilobite families, showing the occurrence of different kinds of eye. Range data from the 'Treatise' (1959), modified by Cowie et al.(1967).

(d) Peripheral sensory zones were certainly present in *Olenus,* and probably in other Cambrian trilobites, but the state of preservation in other genera has not been adequate to show how representative these are.

(e) The ocular ridge, connecting the palpebral lobe with the glabella, is an almost constant feature of Cambrian trilobites, but together with most of the other caecal ornament or prosopon tended to disappear in the Ordovician and later trilobites. In some of the well preserved Upper Cambrian trilobites of Australia (e.g. Öpik, 1967) the ocular ridge appears to be double stranded internally.

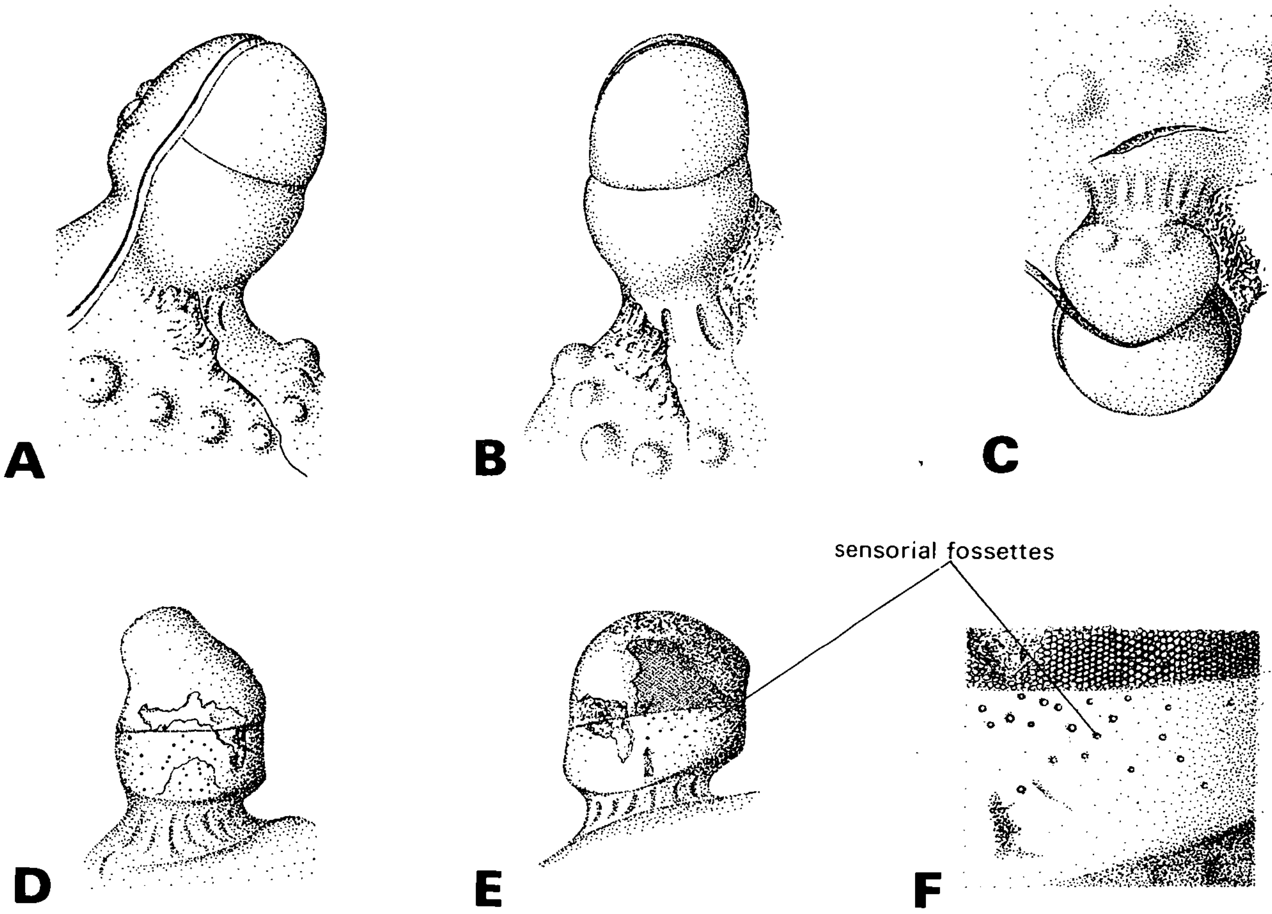

Fig. 2. A. B. C. *Encrinurus tuberculatus* (Buckland). Left eye in anterior, lateral and dorsal views. External surface slightly eroded below the eye socle, and librigena partially separated along the facial suture. SM. A. 28103 Wenlock limestone, (Middle Silurian), Dudley, England. x 18. D.E.F. *Encrinurus calgach* Lamont. D.E. Internal mould of distorted and eroded left eye in anterior and lateral views. F. Enlargement of eye-socle showing sensory fossettes and moulds of the lenses. Gr. I. 40203. Plectodonta mudstones of Wetherlaw Linn, Upper Llandovery, Pentland Hills, Scotland. x18.

In spite of our limited knowledge of the eyes of Cambrian trilobites there is no reason to assume that they were "inferior" to those of their Ordovician successors; there was simply less diversity of form and structure, but this is true of Cambrian trilobites generally, and not just their eyes.

With the beginning of the Ordovician there came some remarkable modifications of the structure of the eye. Most post-Cambrian trilobites retained their holochroal structure, but the earliest known Phacopina, with their schizochroal eyes also originated at this time. Particular evolutionary changes in holochroal eyes seem to have been as follows:

(a) The thin convex lenses so typical of Cambrian trilobites, became modified either as elongate prisms as in *Asaphus, Proetus,* and others, or as very thick lenses with biconvex surfaces (*Scutellum, Paladin,* etc.), Lindström's (1901) plates show these very well. Relatively few trilobites retained the very thin lenses of Cambrian genera.

(b) Reniform eyes continued to be the most common type. But in certain independent groups, (e.g. most encrinurids, some odontopleurids, a few asaphids), growth and modification of the eye socle resulted in true stalked or pedunculate eyes. In the encrinurids, the stalk was the site of a highly modified peripheral sensory zone (Fig. 2). Globose, conical and strip-like eyes also arose, some groups lost their eyes altogether, and in cyclopygids, telephinids, and the komaspid *Carolinites,* the visual surfaces became hypertrophied, sometimes fusing anteriorly.

(c) Retention of the visual surface in the adult became the norm, and the ocular suture fused, but in the Calymenidae (other than in *Prionocheilus*) the visual surface of juveniles is retained (Pl. 3: 9—11), but that of adults very rarely so.

(d) The peripheral sensory zones in some groups became very elaborate and though the vertical ridges and grooves of the eye of *Olenus* have their counterparts in many post-Cambrian trilobites, certain other structures appeared for the first time in the Ordovician which replaced them. These pits are the surface expression of canals perforating the cuticle, and are very well shown in asaphids, encrinurids, and scutellids.

(e) The ocular ridge normally disappeared, though in some cases the palpebral lobe remained close to the glabella. Possibly the pronounced eye ridges of the odontopleurids are homologous with those of their Cambrian forebears; their appearance in the Cambrian Eoacidaspidae would certainly suggest this.

Within each taxonomic group, whether family, superfamily, or even order, the eye once established tended to remain a rather conservative structure. The basic pattern in most families did not alter very much, and thematic variations were usually minor: i.e. size, number of lenses etc. There are however, certain exceptions to this general rule, notably the Cheiruridae, within which there is probably more variation of eye structure than in any other suborder. To a lesser extent, the eyes of the family Olenidae, whose evolution is now known (Clarkson, 1973b), show a rather wide range in form.

In general, it seems that new eye-types were established rapidly, and thereafter evolution in any one type was largely a matter of mild variations upon a theme. Often, as in the Phacopidae, there was a considerable profusion of eye types early in evolution, most of which soon vanished, whilst certain lineages were selected and persisted thereafter. As is general with trilobites, most new kinds of eye structure were introduced in early Ordovician times, and there were few if any, major innovations thereafter.

Blindness was a sporadic occurrence in trilobites, affecting many groups and sometimes environmentally controlled, as in the deep-water Famennian phacopids and proetids of the Variscan geosyncline (Clarkson, 1967 a).

The last trilobite eyes of all belonging to Permian proetaceans were large, well-developed holochroal eyes, with many lenses arranged in regular hexagonal packing on a reniform visual surface.

In spite of the diversity which is evident amongst the eyes of trilobites the whole of their evolutionary history since the earliest Cambrian can be related to three factors alone, and with the possible exception of the internal differentiation of the lenses in phacopids, no other factors need to be invoked. They are as follows:

(a) Changes in proportions of the different parts of the eye resulting from differential relative growth.

(b) Rapid changes resulting from paedomorphosis.

(c) Incorporation of cuticular sensillae into discrete and often complex sensory zones surrounding the eye.

Each of these will be considered in turn in the next section.

GROWTH AND FORM OF THE EYE

Geometry of the visual surface

During the ontogeny of trilobites, the eyes first appear in the protaspid stages at the antero-lateral margin. In successive moult stages they migrate inwards and backwards, and the facial suture migrates with them. During this inward translation there appears to be some degree of rotation of the eye relative to its original position, and the posterior edge migrates towards the sagittal axis more quickly than does the anterior edge. This is most evident where the two edges of the eye lie in the same exsagittal plane.

The first lenses in any eye are emplaced in a generative zone which lies directly below the palpebral suture, and form a single horizontal row. It has become clear that in all trilobites the generative zone has the form of an anteriorly expanding logarithmic (equiangular) spiral as does the palpebral suture (Fig. 3 A—C). Subsequent lenses are always emplaced below existing ones at the bottom of the visual surface, so that as the eye grows, the generative zone moves away from the palpebral suture, all the while contributing lenses in regular sequence to the base

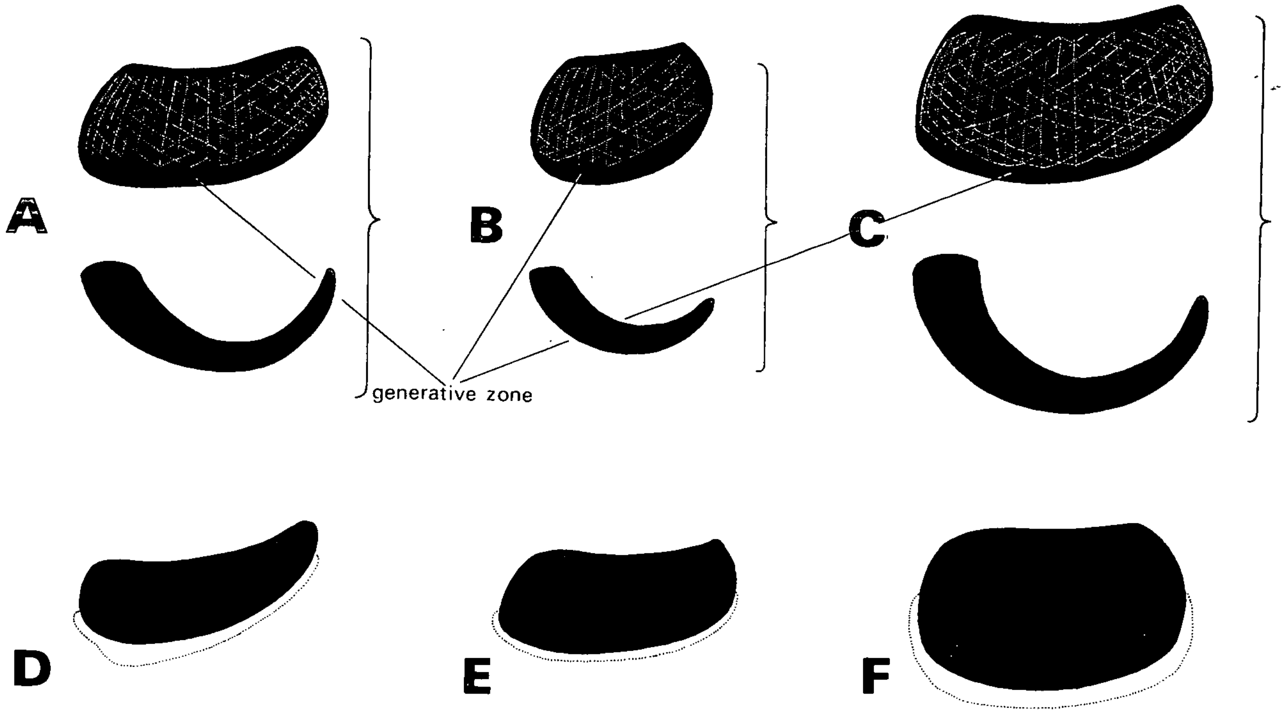

Fig. 3. Geometric structure of visual surface. A. *Reedops sternbergi.* B. *R. bronni.* C. *R. cephalotes.* Dvorce-Prokop Limestone, Devonian, Bohemia. Left eyes in lateral and dorsal views all showing logarithmic spiral form, position of generative zone, and relationships of lens-centres. D. *Niobe quadraticaudata* (Billings). Table Head Formation, Newfoundland. Redrawn from Whittington (1965) Pl. 24: 4. E. *Cornuproetus sculptus* (Barrande) BM 42388, Devonian, Bohemia. F. *Proetus tuberculatus* (Barrande) BM In 56035, Suchomasty Limestone, Bohemia. All left eyes, with shape of eye-socle indicated below.

of the visual surface above it. Characteristic patterns of lens-packing emerge, which are normally constant for the species, and sometimes even within a family or superfamily.

If the growth and form of the eye is understood as governed by a developmental programme of several stages, then the first part of this is the initial spiral growth of the generative zone and palpebral suture. The growth of this spiral zone, at the anterior end, may cease before the second, and quite distinct phase of the programme (lens emplacement) begins.

On the other hand, lens addition may begin whilst the spiral zone is still growing anteriorly. This would account for the accessory upper horizontal rows of the rear part of the dalmanitid eye, (p. 15).

Much of the geometry of the visual surface is controlled by the logarithmic spiral form of the generative zone. Most trilobite eyes, especially the reniform holochroal kind, or the truncated cones of Phacopina, have constant morphological features which could be explained in terms of some simple laws of growth. To take an example, the schizochroal eye of *Reedops sternbergi* has a logarithmic spiral generative zone, expanding forwards like the palpebral suture. The posterior edge of the eye is higher than the anterior, so that the palpebral suture is oblique to the horizontal and forms a distinct "sutural angle" (Fig. 3A). In side view the visual surface appears relatively steep posteriorly and only slightly curved; anteriorly the curvature increases and the visual surface becomes progressively more oblique, With this change in shape the visual field is affected, and the latitudinal range expands anteriorly and in the same direction the lower visual limit rises from the equator (Clarkson, 1969, Text-fig. 1). Though this anterior expansion in visual range may be of some importance in the life of the animal it is in reality no more than a consequence of the laws of growth. For such an eye, over most of its area is of identical morphology to part of a whorl of a coiled shell of a helicocone gastropod. Though the gastropod shell grows by accretion at the apertural margin, and the trilobite's eye by addition of new lenses along its lower margin, the geometric rules governing their form are the same.

The consequences of spiral growth in living organisms have been discussed by D'Arcy Thompson (1942) in a masterly chapter in his Growth and Form ("The Equiangular Spiral"). The fundamental property of this spiral were described in the following words" . . . the shell retains its unchanging form in spite of its asymmetrical growth; it grows at one end only . . . And this remarkable property of increasing by terminal growth, but nevertheless retaining unchanged the form of the entire figure is characteristic of the equiangular spiral and of no other mathematical curve".

In view of the gastropod analogy it seems appropriate to consider Raup's (1966) study of theoretical coiled-shell morphology. In a now-classic paper he demonstrated that computer simulated models of different coiled shells could be generated simply by varying the four basic parameters. These were D (the distance of the generating curve from the axis), W (the rate of whorl expansion), T (the rate of whorl translation in helical coiling) and S (the shape of the generating curve). The same parameters can be used in understanding the growth and form of the trilobite's eye. It is clear, of course, that the visual surface of the eye is not a circular tube as in Raup's model, but merely an outwardly curving surface as in the whorls of fusiform and other gastropods. Furthermore the growing edge or generative zone of the eye lies along the lower margin of the visual surface and is not equivalent to the accretionary apertural margin. But as in the case of the gastropods relatively slight variations in the basic parameters could account for a whole range of different kinds of eye.

In some trilobite species D is constant throughout growth, as in the Phacopacea. *Reedops sternbergi* shows a generative zone of almost perfectly logarithmic spiral form, in which D. is relatively low, whereas the related *R. bronni* (Fig. 3B) has a higher spiral angle. In some dalmanitaceans on the other hand the spiral angle changes throughout growth, which results in strangely curved eyes, but in the rootstock Zeliszkellinae, on the other hand, the spiral angle is constant. Similar rules apply to holochroal eyes and many examples could be cited; usually when the spiral angle diminishes anteriorly, as in most Scutelluidae, whilst rounding off the anterior edge of the eye, this change is normally accompanied by a change in the regularity of lens-packing (Pl. 4.).

W is rarely large in trilobites, and the upper and lower borders of many eyes are subparallel though this is not very clear when the anterior and posterior lower edges are truncated. Some Nileidae (e.g. *Nileus macrops* Billings 1865) (figd. Whittington 1965, Pl. 33: 4) and Asaphidae (e.g. *Niobe quadraticaudata* Billings, 1865) (Pl. 24: 4) redrawn in Fig. 3D), have relatively large values of W and the eye expands forwards considerably. Parallels are also found in schizochroal eyes.

T, the rate of whorl translation, ranges from zero to relatively large. Thus in *R. cephalotes* it is rather low and the eye is only slightly inclined, whereas the greater value of T in *R. sternbergi* is made evident by the more oblique palpebral suture; there is a perceptible sutural angle, as in a gastropod spire. Dalmanitids may have an exceptionally large T value, so that the eye is much higher posteriorly, and accommodates one two, or even three partial or accessory horizontal rows at the top of the eye towards the rear, above the first complete horizontal row of lenses. Though Beckmann (1951) believed that in Phacopina some lenses were added at the top of the eye it now seems that accessory horizontal rows were merely the first formed parts of the eye and that the descending whorl with its high T value had to grow forwards almost to its full length before a full horizontal row could be emplaced. The series illustrated in Fig. 3D–F shows a morphological series in holochroal eyes with extreme, average, and minimal values of T.

S-variations in Raup's coiled shell models (normally coincident with the shape of the generating curve) were limited, and in gastropods there are very many aperture shapes which have not yer been simulated or even analysed. In gastropod shells the simplest shapes are the regularly curved surfaces of circular form. Other models depart from this by regular expansion of the central part of the whorl. But there are other shells again where the eventual shape of the aperture is irregular and must have been controlled by more than one factor, requiring further elucidation.

Likewise in trilobites there are many kinds of S-values, some simple, others quite complex, though the mathematical analysis of these is beyond the scope of this paper. Throughout the whole range of structure of trilobite eyes, variation in the forms of their visual surfaces appears to be entirely the result of the interplay of these four controlling factors, just as in the gastropod shell. And even small changes in any one of these can have substantial effects upon the morphology of the eye.

It is clear, furthermore, that some or all of these factors relate to the geometrical coordinates of the whole trilobite. In the two zeliszkellinid species *Crozonaspis struvei* (Henry, 1968) and *C. kerfornei* (Clarkson & Henry, 1969, p. 117–18, fig 2), the different shapes, in plan view of the generative zones and palpebral sutures are directly associated with the relative widths of the cephala in the two cases. Likewise the eyes of the highly vaulted scutelluid *Paralejurus* have a laterally directed visual field, whereas those of the much flatter *Bojoscutellum* have a more panoramic range (Fig. 5A, B); there is a parallel case in the vaulted cheiruid genus *Crotalocephalus,* as compared with the flattened *Hadromeros.* The visual fields here may well

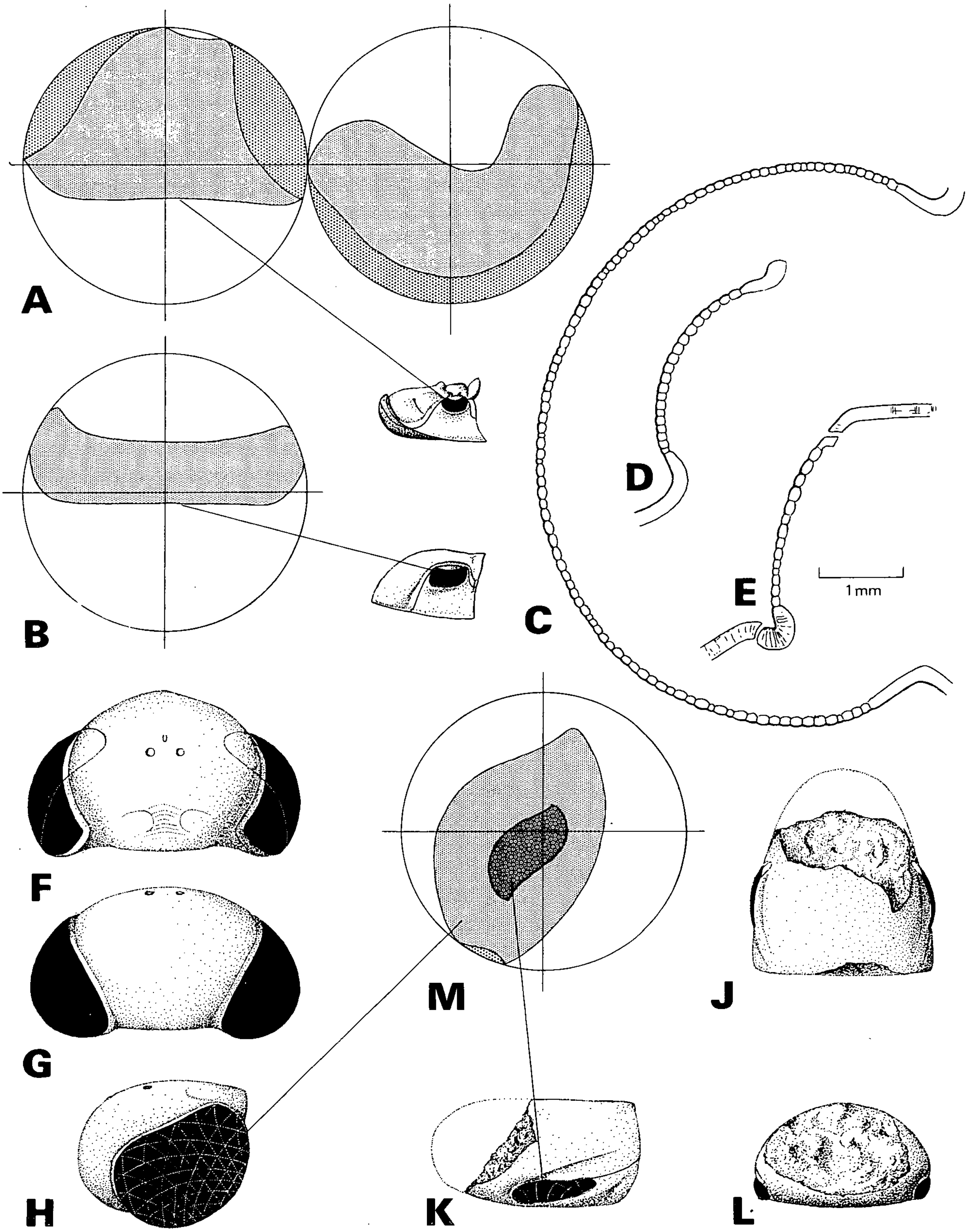

Fig. 4. A. *Bojoscutellum campaniferum* (Beyrich) Koňeprusy Limestone, Devonian, Bohemia. Visual field of left eye plotted in equatorial (left) and polar (right) projection on a Lambert equal-area stereographic net. Larger stipple represents overlapping areas of the visual field. B. *Paralejurus brongniarti* (Barrande) (vide Pl. 1, fig. 5). Dvorce-Prokop Limestone. Devonian, Bohemia. Visual field of left eye in equatorial projection. (vide Pl. 1: 1, 2). C. D. *B. campaniferum.* Gr. I 40202.3. Horizontal and vertical sections through left eye. Drawn from polished surfaces with camera-lucida. E. *P. brongniarti.* Gr. I. 40201. Vertical section through left eye. F. G. H. *Pricyclopyge binodosa* (Salter). Sarka beds, Ordovician, Bohemia. Reconstruction of cephalon and eye from BM. I. 15232 in dorsal anterior, and lateral view, showing (F) shape of the visual surface turning under the cephalon, and (H) course of lens-rows. J.K.L. *Microparia praecedens* Kloucek Sarka beds, Ordovician, Bohemia. Partial reconstruction of cephalon from BM. I. 15277, in dorsal, anterior and lateral view, as above. M. Visual fields, in equatorial projection, of *P. binodosa* and (inset) *M. praecedens.*

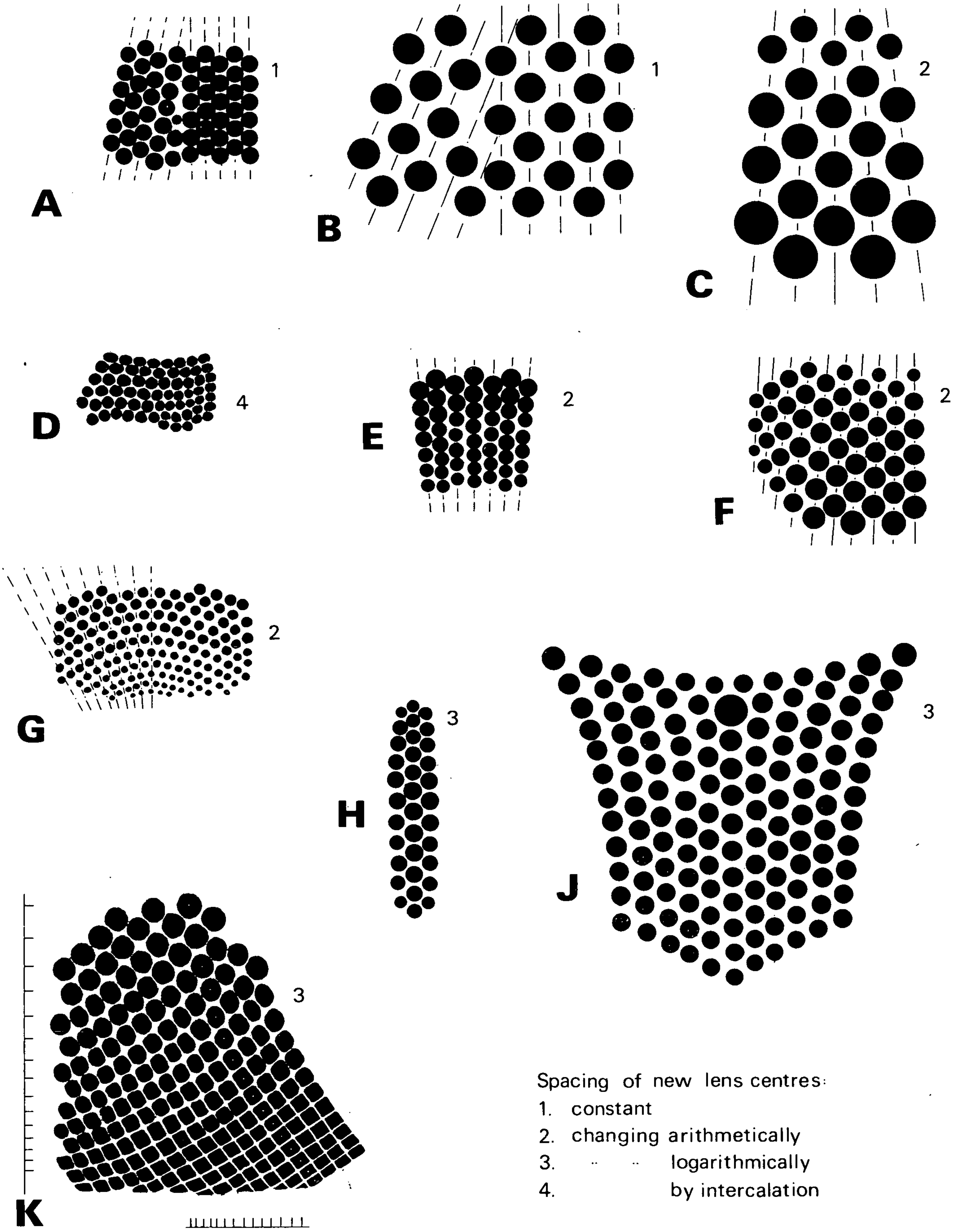

Fig. 5. Lens-packing systems in various trilobites. A. *Isotelus* (Ordovician). B. *Ormathops* (Ordovician). C. *"Phacops"*. s.l. (Siluro-Devonian). D. *Ctenopyge* (Cambrian). E. *Cydonocephalus* (Ordovician). F. *Dalmanites.* (Siluro-Devonian). G. *Peltura* (Cambrian). H. *Telephina* (Ordovician). J. *Pricyclopyge* (Ordovician). K. *Paralejurus* (Devonian) (showing logarithmic spacing of marked lenses). For explanation see text. D. G. J. and K. are made from camera-lucida drawings, the rest are diagrammatic.

be adaptational in themselves, but they are also to a large extent associated with the relative vaulting or flattening of the body; a further point to add to the existing information on the significance of the vaulted "paliferum" and flattened "campaniferum" types of body plan in scutelluids discussed by Richter (1926), R. and E. Richter (1934), and Selwood (1966).

Visual fields

The angular range of vision of any compound eye depends upon the surface curvature, the relative inclination of the peripheral ommatidia, and the angular receptivity of each ommatidium about its axis. The latter factor cannot be assessed in trilobites, and it is convenient to use the term "minimal visual field" for the visual ranges which can be established by simple measurement. In trilobite eyes, as in those of modern arthropods, the peripheral lens-axes may be normal to the surface or may be inclined, and this inclination may vary in different parts of the eye. In holochroal-eyed species, where they are normal to the surface, the minimal visual field may readily be plotted on a graph simply by measuring the angle which the visual surface makes with the horizontal at specific points all the way along its periphery. This has been done for a number of species with a special turntable apparatus, originally used for measuring the bearings of the lens-axes in schizochroal eyes (Clarkson, 1966 a). The eyes of the Devonian scutellids (from the Bohemian fauna of Snajdr, 1960) *Bojoscutellum paliferum* (Beyrich) and *Paralejurus brongniarti* (Barrande) (Fig. 4, A—E) exemplify the two basic types of visual field most commonly encountered amongst trilobites with reniform eyes, the former being panoramic, the latter latitudinally restricted; intermediates also occur. The visual field of *B. paliferum* expands anteriorly, as do those of *Reedops sternbergi,* and other holochroal eyes with both panoramic and latitudinal vision. Such visual fields are always associated with an eye in which W is proportionally high, relative to T. The visual field of *P. brongniarti* on the other hand, like that of *Asaphus raniceps* (Clarkson, 1973a) lies mainly within parallel upper and lower limits, even though the eye of this species and others like it appear from the side to be obliquely set upon the cephalon. This is because in the normal logarithmic whorl, of which the trilobite's eye is a part, the upper edge makes a constant angle with the horizontal so that the upper visual limit is latitudinal provided that the cephalon is correctly orientated. Only where W increases over T, does the angle likewise increase.

Peculiar visual fields occur in some trilobites, such as those of Bohemian cyclopygids (Marek, 1961) (Fig. 4, F—L), in which a substantial part of the visual surface was downwardly directed; this must have implications in interpreting its mode of life.

Lens-packing systems

In the eyes of all trilobites the lenses are arranged in the economical system of hexagonal close packing. There is however, considerable variation in the type of hexagonal close packing and two main categories can be distinguished: —

(a) Systems in which the lenses are all of the same size. In all known cases the visual surface always has marked irregularities in packing in certain regions.

(b) Systems in which the lenses are graduated in size and are regularly arranged.

At first sight there appears to be a true relationship between the packing of the intersecting rows of lenses and the basic geometry of the visual surface, as with the growth lines of a gastropod shell. Such a relationship is, however, much less direct than it appears, for the developmental programme governing the emplacement of the lenses is quite separate from that determining the shape of the visual surface, and quite often visual surfaces of similar shape have very different packing systems. As regards the generation of the new lenses, there is one rule which seems always to be observed, throughout the whole range of trilobite eyes, as originally stated in my earlier work on *Ormathops* (Clarkson, 1971). This is that the size to which the lenses will grow in any eye depends upon the relative spacing of the lens centres, when newly introduced in the generative zone. If the lens-centres are "programmed" to develop in sequence directly below their predecessors without any change in spacing, then these lens-centres will lie in parallel dorsoventral files. Growth is somehow inhibited by the proximity of neighbouring lenses, thus all the lenses grow to the same size. If on the other hand the developmental programme contains instructions to increase or decrease the spacing of the new lens-centres by an arithmetical or logarithmic factor each time, then the lens-centres will come to lie in diverging or converging dorso-ventral files which may be straight or curved. The lenses within these files will then regularly change in size from top to bottom of the eye. Some examples of these two basic kinds will be discussed and treated in evolutionary perspective.

Lenses remaining of constant size

(a) *Ormathops* (Fig. 5B). – The schizochroal eyes of this early genus of the Zeliszkellinae have already been fully discussed (Clarkson, 1971). It is sufficient to say here that since it is geometrically impossible to pack uniform lenses in perfect regularity on a curving surface, irregularities in lens-packing are the rule. Sometimes these are merely areas of loose and irregular packing on an otherwise regular surface. In other specimens blocks of parallel, regular dorso-ventral files lie against the truncated edges of other such blocks, the line of junction being termed a caesura. New lenses arise when a certain critical spacing arises between the generative zone and the lenses above it, presumably at each moult stage. As this critical threshold remained constant the new lenses would normally arise directly below existing ones, hence the parallel blocks of files, but with the downward expansion of the visual surface there would be extra space and this would be filled by one or more new lenses which would arise through the automatic operation of the programme. Each new intercalated lens would then act as a focal point for the generation of further lenses either in parallel blocks truncated by caesurae or in irregular packing, depending on the precise conformation of the eye.

All these packing irregularities are evident in *O. atavus* (Barrande) and *O. borni* (Dean) but caesurae are also very clear in the new species *O. clariondi* Destrombes from Morocco (Destombes, 1972, Pl. 1b).

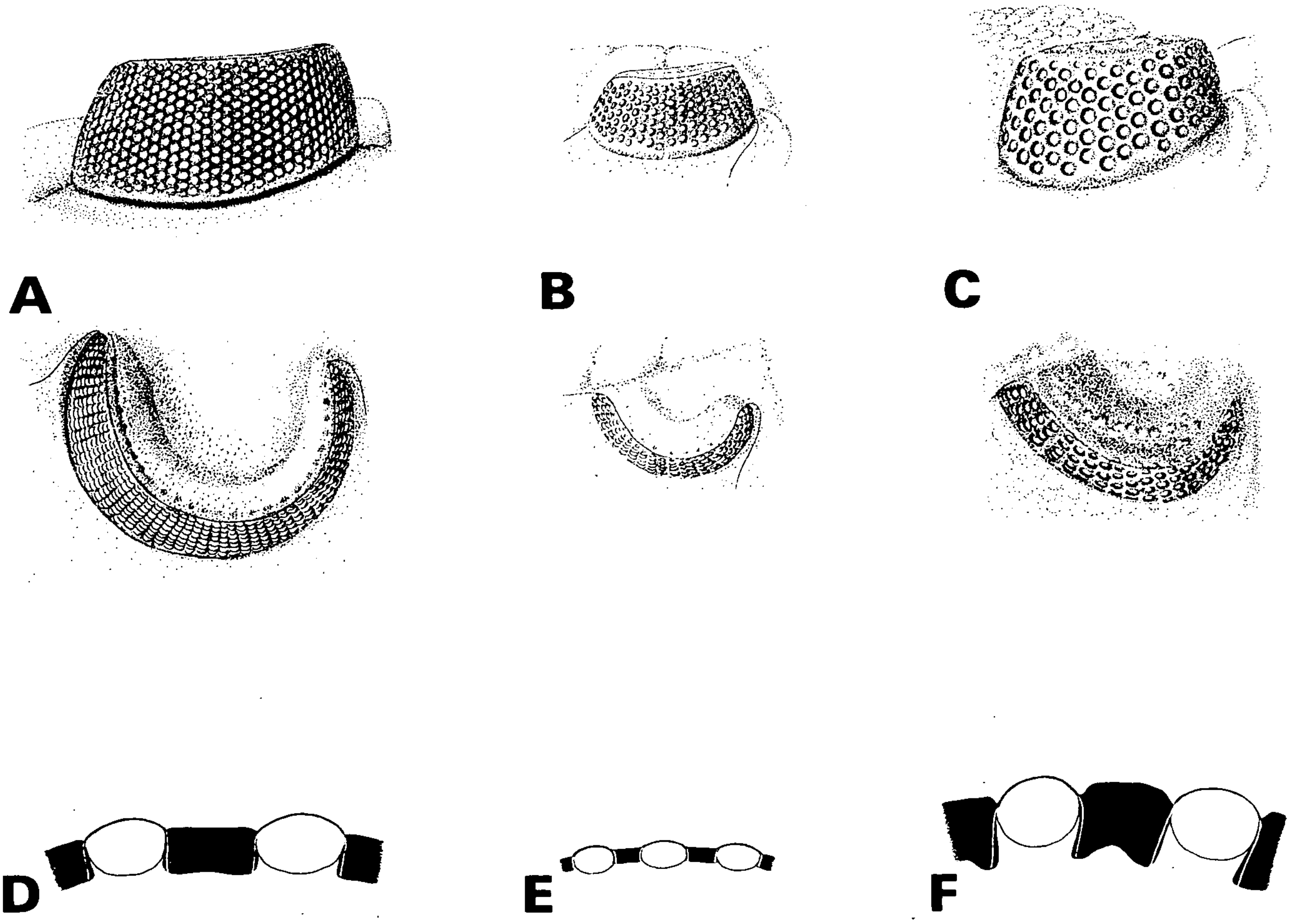

Fig. 6. The three basic kinds of eye in post-Ordovician Phacopina. A. Dalmanitiform: *Odontochile rugosa* (Hawle and Corda) Dvorce- Prokop Limestone. Emsian. Devonian. Tetin, Bohemia. D. Horizontal section through same. B. Acastiform: *Acaste downingiae* (Salter), Wenlock Lst. M. Sil. Dudley, England. E. Horizontal section. C. Phacopiform: *Phacops rana crassituberculata.* Stumm, 1953. Silica Formation. Lucas Co., Ohio. F. Horizontal section.

(b) Lenses of constant size are also present in many holochroal eyed genera, which usually have caesurae, or patches of irregular packing, like *Ormathops.* Such packing is the norm amongst Proetacea, and is usual in Bathyuridae (e.g. *Bathyurellus nitidus* Billings, 1865, figd. Whittington 1963, Pl. 10, fig. 16); amongst the Asaphidae it is evident in *Isotelus* (Fig. 5A), and Whittington and Evitt's figure (1954, Pl. 16: 5, 6) of the eye of *Acanthoparypha perforata* shows that such a packing system was present in some Cheiruridae. Presumably the schizochroal eye of *Ormathops* may have been derived from that of a holochroal precursor with a similar packing system.

(c) The eye of the Upper Cambrian olenid *Ctenopyge* (Fig. 5D) has already been described in detail (Clarkson, 1973b) and the prominent horizontal zone of irregularities which it displays has been related to intercalation of new lenses as the eye widened. In this case, however, new lenses were intercalated between existing ones at random, and a highly irregular system emerged.

These packing systems are all different solutions to the problem of generating and packing uniform lenses with maximum economy of space on convex surfaces. It may be assumed that the primary necessity in such cases was that the size of the lenses be maintained as constant. Regularity was evidently a secondary consideration; this might suggest that these eyes had a somewhat different physiology to those in which the lens-sizes were graduated.

Lenses graduated in size

(a) Lenses increasing in size downwards. These have been found in the schizochroal eyes of Phacopina (Fig. 5C) and in no other trilobites. Such a packing system seems to be ideally designed for the visual surfaces of low convexity present in the phacopids. The change from the *Ormathops* system where the lenses are of uniform size, to the packing mode of the derivatives of that genus, where graduated lenses arise simply through increase in spacing through a constant arithmetical factor has already been described (Clarkson, 1971).

Some dalmanitids have a system in which the lenses near the anterior and posterior edges actually become smaller downwards and the dorso-ventral files converge, but the functional significance of this is unclear (Fig. 5F). Though other trilobites have visual surfaces of relatively slight profile convexity, like those of phacopids, it is curious that this simple, arithmetically based system is not found outside the Phacopina.

(b) Lenses decreasing in size downwards. This is perhaps the commonest type of packing in the holochroal eyed trilobites. The decrease in lens size and consequent spacing may be arithmetical or logarithmic.

(1) Arithmetic decrease. There are relatively few examples of arithmetic decrease. A good one, figured by Whittington (1963, Pl. 10), is provided by the eye of *Cydonocephalus scrobiculus* Whittington (Fig. 5E). Here the dorso-ventral files, which traverse a nearly globular eye, converge ventrally about a ventral vertical file. The outer files are, of course, shorter than the central ones and their uppermost lenses were generated later. Since the files converge and are straight, the horizontal rows are upwardly bowed in the centre. This is perhaps more evident in the eye of *Peltura scarabaeoides,* in which, as previously described (Clarksom, 1973b), there is a much greater distance between the lenses within each dorso-ventral file than between adjacent files (Fig. 5G).

(2) Logarithmic decrease. Various patterns based upon a logarithmically changing pattern of lens-spacing are to be found in trilobites. The most striking patterns are to be found amongst the cyclopygids and scutelluids. Some Bohemian cyclopygids (Marek, 1961), such as *Microparia* (Fig. 4J, K, L) have a very clear pattern of lens-packing, which is rather like that of *Peltura,* though the dorso-ventral files converge centrally with lenses reducing in logarithmic sequence and so are curved. The eye of *Microparia* is relatively small for a cyclopygid and in the large hypertrophied eye of *Pricyclopyge binodosa*, a curious modification of this pattern is clear. Each eye has grown from two similar generative zones, each being a logarithmic spiral. One grows forwards, the other backwards and the two meet along an inclined line towards the rear of the eye (Fig. 4H, 5J). This median line is formed by the two distal files of each system, which are separate just below the palpebral suture, but unite as a single vertical file below the third or fourth horizontal row. The point of junction is marked by a single enormous lens, which has been able to grow larger than any other in the eye simply because there was more room for it, well illustrating the normal rule that lenses will grow until inhibited by the proxi-

mity of neighbouring structures. In general the first formed lenses are more widely spaced than the later ones, and so can grow larger, and there is no need to postulate a "relay" system which would mean that the lowermost lenses are smaller because they were formed later. Each half of the eye has its own packing system, but the anterior half is the larger.

All Scutelluidae have large prominent eyes in which the spiral generative zone is displayed to perfection (Pl. 1: 1—10). The well preserved specimens of *Paralejurus brongniarti* (Barrande) from the Dvorce-Prokop Limestone of Bohemia, show not only the lens-structure clearly but the strip of sensory pits just below the generative zone. Normally the lenses are arranged in a pattern (Fig. 5K) where the dorso-ventral files themselves are log. spirals not easily distinguished from the curving diagonal rows. The lenses decrease in size downwards and become rhombic in shape. The following three generative factors can be isolated and would have sufficed to generate this pattern if they themselves constituted the genetic instructions.

(A) Each new lens introduced in the generative zone is offset from that in the dorso-ventral file directly above it by a logarithmically increasing factor. Thus the dorso-ventral files, which are nearly vertical below the palpebral suture, grow downwards as posteriorly directed logarithmic spirals.

(B) The actual distance between successive lens-centres within each dorso-ventral file decreases ventrally in a logarithmic manner.

(C) There is a very small decrease in the lateral spacing of the files towards the base of the eye, which together with factor B results in the compression of the lenses so that they become quadrate. This change is probably logarithmic but is very small.

Near the lower anterior edge of the eye, there is an abrupt change in the direction of the dorso-ventral files, which affects the packing of the lenses (Pl. 1: 4). This is clearly associated with W, the rate of whorl expansion, which suddenly decreases to round off the anterior edge of the eye.

A few scutelluids have a hexagonal close packing system without the offset effect, examples being *Dentaloscutellum hudsoni* Chatterton (Chatterton 1971, Pl. 1: 15), and *Perischoclonus capitalis* Raymond (Whittington 1963, Pl. 22: 7), in the latter the files converge logarithmically to the base of a straight central file.

Lenses decreasing in size in both directions away from the ambitus

This system, paralleling that of the plating of *Echinus*, would seem to be an ideal method of lens-packing, but it is very uncommon. Only certain Telephinidae and perhaps also *Chasmops* (Clarkson, 1966b, Pl. 95: 7—11; Fig. 9) appear to have evolved this method, which must depend upon instructions to increase the spacing of lens-centres up to a certain point and then to decrease it.

Most telephinids have very large, highly convex eyes with a regular packing system based upon regular dorso-ventral files. The diagonal files are inclined more highly than in most trilobites (45°). From the figures of Ulrich (1930), and Whittington (1965, Pl. 37: 14—17) it is clear that the distance between lens-centres decreases constantly and arithmetically in both directions away from the ambitus (Fig. 5H), so that of all known trilobite eyes, those of the Telephinidae exhibit the most perfect and regular symmetrical arrangement of lenses.

But the rarity of this system implies that such perfection is difficult to achieve and it is not hard to understand why. For in other trilobites a few standard genetic instructions would suffice to generate an entire visual surface with all its lens complement, and no alteration in developmental programme is needed once it has begun. Telephinid eyes require an extra instruction written into their programme to decrease the lens-size constantly in the lower part of the eye. This may be geared in some way to the instructions generating the shape of the visual surface. One may compare the rather clumsy lens-system packing in *Ctenopyge,* where the visual surface is of similar shape and which was generated by a programme lacking instructions to change the lens-size, with the perfect geometry of telephinid eyes, where the developmental instructions must have been more complex. Such additional instructions were either unnecessary or too complex for the genetic systems of other trilobites and seem to have evolved in this one group only, with possible isolated instances elsewhere.

The above analysis, though not exhaustive, illustrates many of the main kinds of lens-packing systems in trilobites. Different systems are characteristic of particular taxa, and their further analysis may prove to be of real systematic value. One clear conclusion to emerge from this study is that various quite different systems are all governed by the same simple rules of generation, and the wide variety of packing types arises simply because of arithmetic or logarithmic variation in the basic parameters.

Changes resulting from paedomorphosis

The important evolutionary concept of paedomorphosis was developed by Garstang in the 1920s. It involves the retention of the juvenile characters of the ancestor into the adult phase of the descendant. When coupled with the related concept of neoteny (the onset of sexual maturity in juveniles), it has been used by zoologists to account for a number of puzzling evolutionary problems. Amongst these may be cited Garstang's (1928) view of the origin of chordates on the one hand from the larvae of tunicates, and siphonophores on the other, from floating actinula larvae. Another fine example is Gurney's (1942) suggestion that copepods were derived from the planktonic larvae of bottom living decapods. De Beer (1940) has given the subject very extensive treatment and Hardy (1956: 194–8) has written that "Garstang, with his concept of paedomorphosis has altered our whole outlook on the process of evolution." As Gould (1968) has shown, paedomorphosis coupled with allopatric speciation might well account for some of the very rapid evolutionary developments so familiar in the fossil record. After all, one of the major features in the record of life is the very rapid establishment of entirely new groups by what Simpson called tachytelic evolution. In such cases there is usually no trace of intermediate links between ancestors and descendants and even if migrations are taken into account it may not be unlikely that such "instantaneous" evolution might result from neotenous or paedomorphic change.

Whereas neotenous change involves the whole body of the animal, in paedomorphic evolution the development of certain organs or parts alone may be retarded, so that when the animal is mature, the said organs resemble those of the ancestral juveniles. Evidently the full cycle of development may be arrested only in one part of the body or in different parts of the body at different times.

Recently I proposed (Clarkson, 1971) that the origin of the schizochroal eye might have been paedomorphic. There is a parallel in the eyes of some modern arthropods where the compound eye arises through coalescence of separate, simple eyes, and the disappearance of the tissues between them. If the full development of such an eye were arrested whilst in this early stage and the animal became an adult with an eye of juvenile type, the lens-arrangement would approximate a schizochroal condition. If this process had taken place in trilobites, an eye of this kind could have been the precursor of the kind of eye seen in the early phacopacean *Ormathops* (p. 19). Here, apart from the primitive lens-packing system and relatively small lenses, the eye is properly schizochroal in all other respects. It is interesting that schizochroal eyes are associated with proparian sutures which are believed on other grounds to be paedomorphic. Perhaps the whole eye-complex, including the suture, is here paedomorphic.

That paedomorphic evolution has happened in the history of trilobite eyes is clear from studies of olenid eye morphology (Clarkson, 1973b). The remarkable similarities of the adult eyes of *Peltura* and *Parabolina* to the meraspid eyes of their probable ancestor *Olenus*, the obsolescence of the ocular suture in the later olenids (it is not developed in meraspids), and various other morphological criteria, were all cited as evidence of paedomorphic evolution as a factor affecting the evolution of the eye. In addition many of the described examples of eye-reduction could likewise be paedomorphic, as they normally involve the outward migration of the facial suture to a juvenile position and the reduction of the visual surface to a very small size.

The real confirmation of the hypothesis of the origin of schizochroal eyes would come from the study of the eyes of meraspid and protaspid trilobites. These, however, are very rarely preserved. In a fine suite of larval and postlarval specimens of *Paladin eichwaldi shunnerensis* (King), Miller (personal communication) has found a degree 1 meraspis with an intact visual surface, and has kindly allowed me to use it (Pl. 3: 12, 13). In this the lenses are large, slightly separated, and highly convex unlike those of the adult (Clarkson, 1969b), so that this juvenile eye has some similarities to a schizochroal eye.

This discovery offers some support for the hypothesis that the eyes of trilobites began their development by the coalescence of single units, and that schizochroal eyes were paedomorphic. It is hoped that material of other meraspid eyes will be forthcoming for further study.

Peripheral sensory zones

In many trilobites the eye socle is provided with accessory structures which may have fulfilled a sensory role. Sometimes the surface of the palpebral lobe is also of complex structure, and especially in holochroal eyes the pits, ridges, and tubercles which cover the surface are of a different kind to those on the eye socle. Not all trilobites appear to have eye socles with sensory structures preserved, and the outer surface may be smooth. In such cases the internal face of the eye socle may likewise be devoid of structure, and often the apparent absence of small accessory sense organs may simply be a preservational feature. On the other hand, as in *Encrinurus* (Fig. 2) the eye socle is penetrated by fine canals, which have minute external orifices, but which flare internally, like the cuticular sensillae of many insects, so that the wider internal openings appear as numerous small circles on the internal moulds.

The well preserved peripheral sensory zones described in the Upper Cambrian trilobite *Olenus wahlenbergi* (Clarkson, 1973b) are currently the oldest known, but similar zones may have been in existence in more ancient trilobites.

The sensory zones peripheral to the eye are a differentiated part of the whole complex of sensillae covering the trilobite cuticle, which has been studied in detail by Miller (in press), and Dalingwater (1973).

Since these authors discuss in detail the nature of sensory structures in both trilobites and modern arthropods, it is only necessary here to record the various kinds of structure visible in the zones peripheral to the eye, rather than to interpret.

According to Dethier (1963) all sensillae except for photoreceptors are believed to be homologous, even though they are of diverse function, and were probably initially derived from setae.

The major types of structure found in the peripheral zones of holochroal eyes are as follows:

(1) Structures on the eye socle

(a) Simple canals, running through the eye socle and normal to its outer surface. These are very small, and the outer and inner surface of the eye socle is smooth.

(b) Funnel shaped canals, perforating the eye socle as in (a), but flaring and making distinct external orifices. These are usually randomly distributed and concentrated close to the lower rim of the visual surface. Examples are *Asaphus* where they are some 150 mμ in diameter at the aperture, and *Paralejurus* (diameter 10 mμ).

(c) Funnel shaped canals, flaring internally and often distributed as in (b). The external orifices are minute, the internal ones in *Encrinurus* about 75 mμ (Fig. 2, D–F).

(d) Tubercles, usually similar to the glabellar tubercles, though normally smaller. Such tubercles may be perforated by a central tube. There may be a few large tubercles, many smaller ones, or a combination of these *(Eocyphinium seminiferum* (Phillips) (Osmolska 1970: 97, Pl. XII: 15); (Pl. 3: 6) *Proetus bohemicus* Hawle and Corda (Pl. 3: 3, 5), and the schizochroal eye of *Signatops signatus* (Hawle and Corda) (Pl. 5: 3,4).

(e) Ridges and grooves, which are very clear in many trilobites, especially in *Olenus wahlenbergi* Westergård (Clarkson, 1973b), and *Cummingella brevicauda* (Goldring) (Osmolska, 1970: 59. Pl. VI: 3c) *Paladin eichwaldi shunnerensis* (King) (Pl. 3: 4) and various other proetids. The deep grooves probably lead into canals below.

(f) Other structures, described by various authors, but not investigated here, which include various modifications of the eye socle itself. Whittington (1961: 920, Pl. 102: 16, 17) described the peculiar central depression on the eye socle of *Colobinion julius* (Billings 1865), and later (1965, Pls. 24, 26 and 28) figured the eyes of *Niobe quadraticaudata* (Billings 1865), and *N. morrisi* (Billings, 1865) in which the antero-lateral parts of the eye were peculiarly inflated.

(2) Structures on the palpebral lobe

(a) Simple canals, as on the eye socle and other parts of the cuticle.

(b) Tubercles of various kinds, often arranged in a single or double row, concentric with the palpebral suture.

(c) Small pits, scattered over the surface.

(d) Terrace lines, continuous with those on the rest of the cephalic cuticle. These are normally arranged in a pattern roughly concentric with the suture, but occasionally, as in *Peraspis lineolata* (Raymond, 1925), figured by Whittington (1965, Pl. 34: 9) and in *Cornuproetus sculptus* (Barrande) (Pl. 3: 1, 2), each diverges from near the posterior edge of the eye and curves round to about the palpebral suture nearly at right angles to it.

(e) In schizochroal eyes, tubercles and pits exist both on the eye socle and on the palpebral lobe. These are normally very similar to those on the rest of the cuticle and especially the glabella (Miller, this volume).

(f) Prosopon, (alimentary caecae) like that of the whole cuticular surface, but on a smaller scale. Occasional swollen regions can be seen which could possibly be sensory organs of some kind. This has been fully described in *Olenus wahlenbergi* (Clarkson, 1973b).

In most holochroal eyed trilobites the palpebral structures normally differ from those of the eye socle, but in *Phacops* and other trilobites with schizochroal eyes they are the same (Miller, in press). Such structures of the peripheral zone as have been studied are normally genus specific, but even within a single superfamily such as the Proetacea, the range of structures and the number of combinations in which they may exist is considerable. Proetaceans have most of the different kinds of structures mentioned above on the eye socle and the palpebral lobe (except for prosopon) amongst their various species. The history of peripheral sensory zones is obviously complex and is a challenging problem, but one which will have to wait until we have a fuller understanding of the nature and function of all cuticular sensillae.

Many of the structures may have borne setae, others were perforations through the cuticle accommodating different sensillae, and different kinds of structures may have functioned as tactile, chemosensory, or auditory organs, like those of insects and crustaceans, but since even in modern arthropods the functions of many of the sensillae are little known, it is not very easy to relate sensillar structure to precise function in trilobites.

An unusual and interesting case of possible replacement of the visual surface with sensory tubercles (as is known from some modern deep-sea crustaceans) has been described in *Coignouina decora* by Miller (1973).

The close association of the compound eyes and peripheral sensillae, so evident in trilobites, does not seem to have been described in any detail from modern arthropods, and I have found little reference to the functional significance of such proximity. But it seems clear that the elevation and curving surface of the eye socle must have been a convenient structure for the location of sensillae, which could receive tactile, auditory, or chemical stimuli from the same directions and at the same time at the photoreceptors. The attributes of any object moving within the field of view could then be analysed by more than one kind of organ simultaneously; it would be interesting to know at what level the two kinds of information were processed, whether within the optic ganglia, or in the cephalic ganglia, further away from the eyes.

THE SCHIZOCHROAL EYE

In all the animal kingdom there are no other visual organs quite like the schizochroal eyes of phacopid trilobites, which have been the subject of extensive study (Clarke, 1889; Lindström, 1901; Rome, 1936; Beckmann, 1951; Brinkmann, 1951; Clarkson 1966a, b, 1967, 1968, 1969a, 1971; Eldredge, 1971; Towe, 1973).

All schizochroal eyes have very large lenses, which are normally in the range of 200–500 mμ, but sometimes can reach 750 mμ or more. These lenses are separated by interlensar sclera, and each has its own separate cornea, which plunges through the sclera at the margin of the lens to join with a "cone" lying below the sclera. The deeper lying structures are unknown, though it is possible to infer their direction from the orientation of the cavities in the interlensar sclera each of which is capped by a lens. Evidently the photoreceptive structures were radially arranged in horizontal section, but in vertical section they were parallel. Each of the lenses has a compound interior, often modified through differential preservation. The sclera in the Phacopidae is usually thicker than the lenses, so that the cylindrical cavity or alveolus below each lens is quite pronounced, but in the Dalmanitidae, the sclera is actually thinner than the lenses (Fig. 6, D–F).

These facts are well established, but recent work has revealed some new information, which supplements and slightly modifies our existing knowledge.

Structure of the schizochroal eye

(a) Lens structures: Different kinds of structure have been described within the lenses, and I previously distinguished "proximal nuclei" and "intralensar bowls" in *Phacops* and *Reedops* (Clarkson 1967, 1969). It is now clear that the proximal nuclei are secondary structures, found only within recrystallised lenses, though in such lenses some traces of the intralensar bowls occasionally remain. In material of both *Reedops* and *Odontochile* from the Devonian Dvorce-Prokop Limestone of Bohemia, some specimens have lenses of clear calcite, with intralensar bowls present, but others have opaque white lenses in which the original material has been recrystallised, usually as small needles of random orientation, destroying most of the primary structures. This normally seems to take place by the invasion of new material from the external surface of the lenses to the more proximal regions. Sometimes this is complete; in other cases there is left a small area of original material left as a proximal nucleus, clearly secondary, in others again the lenses show partial, non-uniform recrystallisation. Within the same eye different lenses may be variously affected, some being untouched by recrystallisation, and others almost totally altered.

The original structure of schizochroal eyes appear to be upper units interlocking with intralensar bowls with a thin basal layer underneath; all other previously described structures are merely diagenetic modifications. The thin concentric layers and intralensar "diaphragms" of *Reedops* might also be primary.

Intralensar bowls are present in the earliest phacopids. Amongst the Zeliszkellinae they have been reported in *Ormathops, Crozonaspis* and *Dalmanitina,* and they are illustrated here in *Zeliszkella* (Pl. 4: 14—16). In all the above they are visible in the internal moulds of decalcified mudstone in which these fossils are preserved. They have also been noted in the Devonian *Reedops,* preserved in limestone, and seem also to be present in some Silurian and Devonian dalmanitaceans, though the lenses of the latter are commonly recrystallised. The bowls were undoubtedly different in composition from the upper units of the lenses, but what was their original material?

Various lines of evidence indicate that though the upper units were calcitic, the intralensar bowls were not. Towe (1973) shows that the corneal calcite is radially orientated, and that the subcorneal part of the lens acts as a single calcite crystal, with its c-axis directed outwards. This is confirmed by stereoscan photographs of *Phacops breviceps* Barrande, amongst others (Pl. 6: 1, 2) which show that the radial structure of the cornea is impressed upon the upper part of the subcorneal region, as an "aster". The subcorneal region described by Towe as a lens is actually only an upper unit, with its base forming a characteristic bulge. On his photographs there is no trace of intralensar bowls, as in my photographs (Clarkson, 1969a, Pl. III; Fig. 4) of sections though the eyes of *R. sternbergi,* (Hawle and Corda), where the lower margins of the intralensar bowls are often indistinct, and the (secondary) calcitic material of which they are made extends below the lens into the limestone matrix.

Where the intralensar bowls are preserved in Ordovician Zeliszkellinae that occur as internal and external moulds, they are always of identical composition to the matrix; they are siliceous in specimens collected from siliceous nodules.

These facts suggest that the intralensar bowls may have originally been organic, possibly either solid or gelatinous, and perhaps bounded proximally by a thin calcitic membrane (the basal layer), which if kept intact has allowed the original form of the lenses to be retained during the infilling of the bowl with diagenetic material. If the basal layer was destroyed the matrix would become moulded to the lower surface of the upper unit, and a matrix-filled intralensar bowl would result. Until more details of the intralensar structures are known their function must remain uncertain but at first sight it appears that they may have corrected spherical and chromatic aberration on the well known lens-doublet principle (R. Levi-Selti. pers. comm.).

Palpebral musculature

Several kinds of structure are present on the palpebral lobes of Phacopina. First there is the surface sculpture on the site of pseudotubercles, and of setal ducts of various sizes (microtrichs and macrotrichs), the larger ducts being often concentrated towards the edge of the lobe (Miller, in press). Frequently there occurs, especially in the Dalmanitacea, though also in some Phacopacea, a line of deep pits near the edge aligned in a row concentric with the palpebral suture. These are geometrically related to the pattern of lenses on the visual surface, for each of the pits lies directly above one of the small lenses of the second horizontal row. They normally leave slightly indented impressions of the internal moulds, which are particularly clear in the Zeliszkellinae.

Unrelated to either of the above features are a third kind of structure, so far only observed in *Phacops* and *Reedops*. These are excavations in the lower surface of the palpebral lobes which stand up in internal moulds as prominent little nodes, arranged in a semicircle concentric with the palpebral suture (Pl. 6: 3, 5–8). These are very similar to. though often more deeply impressed than the cephalic muscle scars described by Eldredge (1971). Dr. Eldredge who kindly sent me a specimen of *P. rana milleri*, in which both cephalic and palpebral muscle scars are preserved, has commented upon the deeper impression of the scars towards the external surface, and suggests that these muscles were impressed at some 45° to the surface of the palpebral lobe.

These may have been the site of muscle attachments, but their function is unclear. Many modern compound eyes have ocular muscles, which sometimes produce a "flicker", permitting image-scanning. On the other hand the large, single-lensed eyes of salticid jumping spides are provided with muscles which can move the retina to and fro across the field of view as well as partially rotating the retina about the visual axis of the eye – another form of scanning, which might be a pattern-recognition procedure (Land, 1969).

It is conceivable that palpebral musculature is associated in some way with the peculiar parallel arrangement of the photoreceptors in vertical section. One might envisage an eye in which the photoreceptors could be moved up and down, slowly or rapidly, for scanning, or for increasing the field of view. Whatever the explanation the palpebral musculature does seem to be closely associated with the eye, and may well have been an integral part of the schizochroal visual system.

Sensory zones

Organs of sense other than visual are normally found as part of the schizochroal eye-complex. Where the surface of the intralensar sclera is well-preserved, it may be covered with tiny tubercles, or if it is smooth, may be perforated with tiny pits of diameter about 1 mμ (fine examples are illustrated in *P. rana rana* in Pl. 5:1, 2). These may be comparable with the pore-canals of recent arthropods (Miller, pers. comm.). The palpebral lobe is often of complex structure with pits and tubercles, the latter usually being arranged in a semicircle, concentric with the palpebral suture. Similar tubercles often lie along the lower margin of the eye. Both the pits and tubercles are identical with those elsewhere on the cephalon, and the pits have been interpreted as setal pits. The highly tuberculate peripheral zones of *Signatops signatus* (Hawle & Corda) figured in Pl. 5: 5, 6, have very large and very small tubercles, but unfortunately the structure of the interlensar sclera is indistinct.

Evolution of the schizochroal eye

The phylogeny of the Phacopina is somewhat controversial, and a full analysis of the evolution of their eyes is not yet possible. Even so certain points are clear.

(a) Schizochroal eyes were probably paedomorphic in origin.

(b) The primitive lens packing system in the early genus *Ormathops* was abandoned in all later genera for a regular system with graduated lenses.

(c) The Ordovician Phacopina (Zeliszkellinae and Pterygometopidae) had eyes of much more diverse kind than did their Silurian and Devonian successors. Only a few basic patterns of eye construction, within each of which there is only minor variation, are present in the post-Ordovician Phacopina.

Amongst the Zeliszkellinae the range of variation is seen in such genera as *Ormathops* (Clarkson, 1971, Pls. 1–3), *Dalmanitina (Eodalmanitina)* (Henry, 1965, Pl. V: 1, 4), *Crozonaspis, Dalmanitina* (Henry, 1968; Clarkson, 1968), *Kloucekia* (Henry, 1963) and *Mytocephala* (Pl. 4: 1). In most of these the lenses diameters are some 150–250 mμ. The eyes of Pterygometopidae are less well-known, but there is again a fair range in form as witness the variety in eye form in *Calyptaulax* (Pl. 5: 3, 4) *Pterygometopus, Achatella* and other genera whose eyes were illustrated by Delo (1940, Pls. 11–13) and *Chasmops* (Clarkson 1966b. Pl. 75: 7–11).

Though the Pterygometopidae became extinct at the end of the Ordovician, the Zeliszkellinae persisted, giving rise to all post-Ordovician Dalmanitacea.

There are only three main patterns of eye-construction in the post-Ordovician Phacopina, two of which occur in the Dalmanitacea (Fig. 6). One of these types, exemplified by *Dalmanites* is a large eye with many lenses of relatively large size. (c. 350 mμ), strongly curved in plan, and with a sunken palpebral area (Clarkson 1966b, Pl. 75: 1–6; this paper Pl. 4: 12, 13). Eyes of this kind are shared with minor variations by all members of the Dalmanitidae and Asteropoyginae. Such eyes are closely similar to those of the Ordovician *Dalmanitina (Eodalmanitina), Dalmanitina,* and *Zeliszkella,* and were presumably derived from these. The other kind of Dalmanitacean eye, which is much smaller, and has fewer lenses of diameter averaging 200–250 mμ, is representative of Calmoniidae. Such well-known examples are the eyes of *Acaste* (Clarkson 1966a, Fig. 1), which are almost identical to those of the ancestral zeliszkellinid *Kloucekia.* Within the Calmoniidae the morphology of the eye does not vary much and is always distinctive, even in such bizarre genera as *Bouleia,* as Eldredge (1972) has recently shown. Both "dalmanitiform" and acastiform" eyes could have been derived from such an eye as that of *Dalmanitina* (Pl. 4: 5, 6).

Selection at the end of the Ordovician eliminated all those dalmanitaceans except those bearing the two kinds of eye just mentioned, and subsequent evolution of these eyes was within a narrowly circumscribed range; each kind must therefore represent an "adaptive peak" in the sense of Sewell Wright (1932).

A third kind of eye is present in the Phacopacea, but here the range of variation is much greater, so that Campbell (1967: 30) has stated that within the Phacopinae and Phacopidellinae eye size and shape show no systematic changes with time. Large and small eyes may occur, as in *Reedops,* within different species of the same genus, and eye-reduction and blindness are common. Examples are figured in Pl. 4: 3, 4, 7–11. Evidently the evolutionary potential of the phacopacean eye was greater than that of the two patterns of dalmanitacean eye. The orgin of the phacopacean eye is as yet not certain; there are conflicting views on the origin of the Phacopacea, as show by Eldredge (1971). But there is some resemblance between the eye of some pterygometopid genera (e.g. *Calyptaulax*) and that of *Acernaspis* and other early phacopacean genera, which may add weight to Eldredge's suggestions of a pterygometopid ancestor for the phacopaceans.

There seems to have been a general tendency for the later Phacopacea to have large, fewer lenses than their early Silurian precursors, and the Devonian *Phacops* eye may have lenses as large as 750 mμ across. The Middle Devonian *Phacops rana* complex has recently been the subject of a masterly evolutionary study by Eldredge (1971), who documented an overall reduction by allopatric speciation, in the number of dorso-ventral files. He also confirmed that as Clarke (1889) had originally stated, the lenses decrease in number with age in gerontic individuals.

Though the lenses of some of the earlier Phacopina are only 150–200 mμ in diameter (which is within the range of the largest lenses of some holochroal eyes, especially those of Scutelluidae), the Siluro-Devonian Phacopina may have lenses of up to 750 mμ across (*P. rana crassituberculata*). Why were these lenses so enormous?

In the absence of any modern analogues, any answer must be conjectural. If Eldredge's (1970) suggestions are correct that *Phacops,* like *Limulus,* spent part of its time buried in the substrate, then *Phacops* could have been a nocturnal animal. The huge lenses of *Phacops* and other phacopids could have been adapted to gather as much of the dim light available as possible.

Though the possibility that the schizochroal eye was a night-adapted visual organ seems reasonable, it can never be more than just a suggestion, and in conclusion, it must be said that though the morphological information available to us suggests that the eyes of trilobites were elaborate, complex organs, of a high degree of biological organisation, our knowledge of their function must remain strictly limited, unless more details of their internal structure happen one day to be found.

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All stereoscan photographs were taken by Mr. Jim Goodall, Department of Electrical Engineering, Edinburgh University.

EXPLANATIONS OF PLATES

Asterisks indicate stereoscan photographs

Plate 1

1 – 4, 7. 10. *Paralejurus brongniarti* (Barrande) Dvorce-Prokop Limestone. Emsian. Tetin, Bohemia.

1. 2. Lateral and dorsal views of left eye with abraded palpebral lobe. BM. I1 42629. x9. 3. Lower part of visual surface with sensory fossettes just below the generative zone. BM. I1 42629. x40. 4. Anterior part of visual surface, showing change in lens-packing. BM. 42513. x40. 7. Sensory pit from below generative zone. BM. 42513. x2700*. 10. Upper part of visual surface separated along facial suture from palpebral lobe showing pits and terrace-lines. BM. 42513. x65.

5. 6. *Bojoscutellum campaniferum* (Beyrich) Upper Koněprusy Limestone. Eifelian. Koněprusy, Bohemia.
5. Left eye with broken palpebral spines, lateral view. BM. 42507.x12.

6. Right eye in dorso-lateral view. Some anterior lenses missing. Gr. I. 40200.x12.

8. 9. *Scutellum edwardsi* (Barrande) Kopanina beds. Near Králóv Drův, Bohemia. Right eye in dorsal and lateral view. BM: 42524.x30.

Plate 2

1 – 3, 5 – 7, 8. *Pricyclopyge binodosa* (Salter). Sarka Formation. Llanvirnian (Diγ). Sarka, Bohemia.
1. Ventrolateral and 2. anterior views of internal mould of left eye. SM A 48913.x10. 3. Part of intact visual surface with "schizochroal" appearance. BM. 15231.x13. 5. Ventral view of cephalon (internal mould) with both eyes preserved BM: I 15232.x7. 6. Enlargement of internal mould (left eye) showing central dorso-ventral file (marked) separating the two 'halves' of the eye. See also Fig. 4H and 5J. BM. I 5504.x16.5.
8. Same.x40.

4. *Symphysops spinifera,* Kindle & Cooper. Whitehead Formation. Grand Coupe, Percé, Quebec. Lens-packing changes are visible anteriorly. BM. It 7168.x13.

7. *Microparia praecedens* (Kloucek). Sarka Formation. Llanvirnian (Diγ). Sarka, Bohemia. Lateral view of left eye. BM. I 15277.x7.

Plate 3

Structure of holochroal eyes

1. 2. *Cornuproetus sculptus* (Barrande). Pragian. Lower Devonian. Hostin, Bohemia. Intact surface of left eye showing terrace lines. BM. 42388.x35.

3. 5. *Proetus bohemicus* Hawle and Corda. Koňeprusy Limestone. Pragian. Lower Devonian. Koňeprusy, Bohemia. Surface of left eye, showing partially exfoliated lentiferous surface and tuberculate eye socle. Gr. I 40201. 3. x17. 5. x50.

4. 12. 13. *Paladin eichwaldi shunnerensis* (King). Shunner Fell Limestone. Namurian. Great Shunner Fell, West Yorkshire England.

4. Lower part of visual surface and sensory zone of the eye socle. Gr. I. 1933. (Figd. Clarkson 1969c. Pl. 13: 5). x50. 12. 13. Visual surface of a degree 1 meraspid, showing schizochroal appearance of the lenses. Gr. I 40187. 12.x250*. 13.x620*.

6. *Eocyphinium seminiferum* (Phillips). Visean. Lower Carboniferous. Matlock, Derbyshire, England. Latex replica of left eye showing strong tuberculation on the palpebral lobe and the eye socle. BM. I 3194. (Figd. Osmolska, 1970, Pl. XII: 15).x16.

7. *Cummingella carringtonensis* (Woodward). Visean. Narrowdale, Staffs., England. Lower part of visual surface and sensory pits on eye socle. BM. In 27930. (Figd. Osmolska, 1970, Pl. VII: 3). x45.

8. *Proetus tuberculatus* Barrande. Pragian. Mnenian. Bohemia. Lower part of visual surface and tubercles on eye socle. BM. In 56035.x45.

9 – 11. *Flexicalymene cf. quadrata.* Ordovician (Richmondian) Waynesville Formation, Ohio.

9. Enrolled specimen of small size with intact visual surfaces. Gr. I 40186.x16. 10. 11. Left eye of same. 10. x87*. 11. x175*.

Plate 4

Range in form of some schizochroal eyes

1. 2. *Mytocephala hawlei* (Barrande). Dobrotiva Formation. Llandeilian. Bohemia. BM. 42343.x10.

1. Internal mould of left eye, x10. 2. Lens-pits of same, x35.

3. 4. *"Phacops"* sp. with reduced eyes. Frasnian. Weipoltshausen, Nr. Giessen, Hesse, Germany. Gr. I 40189.
3. Left eye.x12.

4. Right eye.x12.

5. 6. *Dalmanitina arkansana* van Ingen. St. Clair Limestone. Ordovician. Batesville, Arkansas. Right eye. USNM. 79146.x10.

7. 8. *Eophacops trapeziceps* (Barrande). Kopanina beds. Silurian. Listice, Bohemia. Right eye in lateral and dorsal views. Gr. I 40188.x9.

9. 10. *Phacopidella. (Prephacopidella) hupei* Nion & Henry. Schistes de Morgat, Llandeilian, Postolonnec. Presqu'ile de Crozon, Finistere. Right eye. Gr. I 40190.x10.

11. *Denckmannites volborthi* (Barrande). Kopanina beds. Silurian. Lochkov, Bohemia. Left eye in oblique posterolateral view. Gr. I 40191.x50*.

12. 13. *Odontocheile rugosa* (Hawle & Corda). Dvorce-Prokop Limestone. Emsian. Tetin, Bohemia. 12. Left eye, lateral view. BM. I 3435.8. 13. Lower part of visual surface showing large interlensar and smaller marginal tubercles. SM H 8447.x40.

14 – 16. *Zeliszkella (Zeliszkella) lapeyri* (Bureau). "Schistes à Calymènes". Llandeilian. Traveusot-en-Guichen, south of Rennes, Brittany. 14. Part of visual surface of an internal mould showing intralensar bowls. Gr. I 40192.x30. 15. 16. The same eye in dorsal and lateral views.x11.

Plate 5

Surface structure of schizochroal eyes

1. 2. *Phacops rana rana* (Green, 1832). Silica Shale. M. Devonian. Ohio. Left eye in antero-lateral view. Gr. I 40193. 1x26*. 2x140*, showing large and small pits on the palpebral lobe and small pits on the interlensar sclera.

3. 4. *Calliops strasburgensis* Ulrich & Delo 1940. Edinburg Limestone. Middle Ordovician. Virginia. Posterior part of visual surface of silicified specimen showing small tubercles in the interstices of the lenses, and recrystallisation of surface structure. Gr. I 40194. 3.x75*. 4.x150*.

5. 6. *Signatops signatus* (Hawle & Corda, 1847). Vinarice-Kalke. Siegenian, Menany, Beroun, Bohemia. Visual surface and eye-socle, showing large tubercles and small pustules on the latter. Gr. I 40195. 5.x60*. 6.x120*.

Plate 6

Lens-structure and muscle-scars of schizochroal eyes

1. 2. *Phacops breviceps* Barrande. Koneprusy Limestones. Eifelian. Bohemia. Visual surface with corneas partially removed, showing that the radial structure is impressed upon the surface of the upper unit. Gr. I 40196. 1.x90. 2.x180.

3. 5. *Phacops rana milleri* Stewart. Silica Shale. Middle Devonian. New York State. Internal mould of palpebral lobe of left eye showing muscle scars. Gr. I 40197 3.x34. 5.x14.

4. *Phacopidella (Prephacopidella) hupei* Nion & Henry . Schistes de Morgat. Llandeilian. Postolonnec, Finistere. Internal mould of visual surface. Gr. I 40178. x130*.

6 – 8. *Reedops cephalotes* (Hawle & Corda). Dvorce-Prokop Limestone. Emsian, Bohemia. Internal moulds of palpebral lobe showing muscle scars. 6. Gr. I 40198.x16. 5. 7. 8. Gr. I 40199 in lateral and dorsal view. x16.5.

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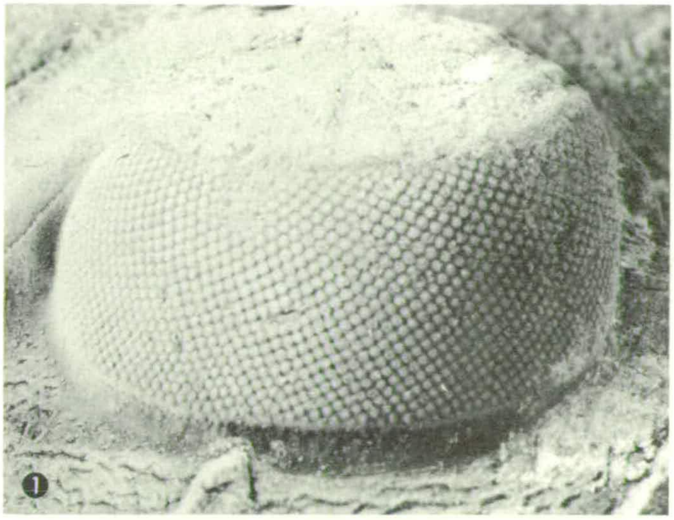
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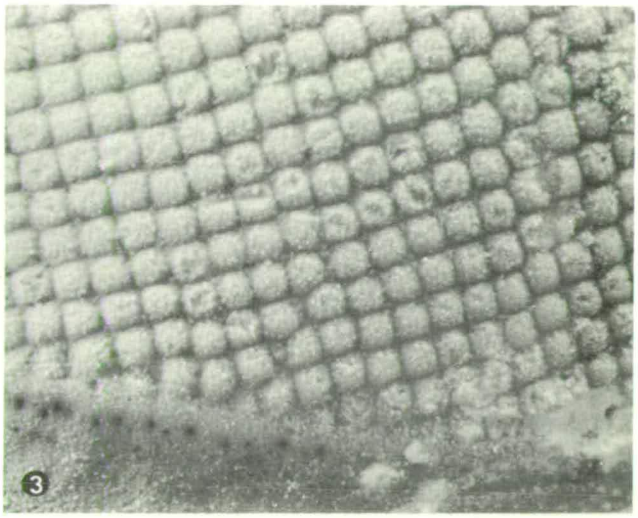
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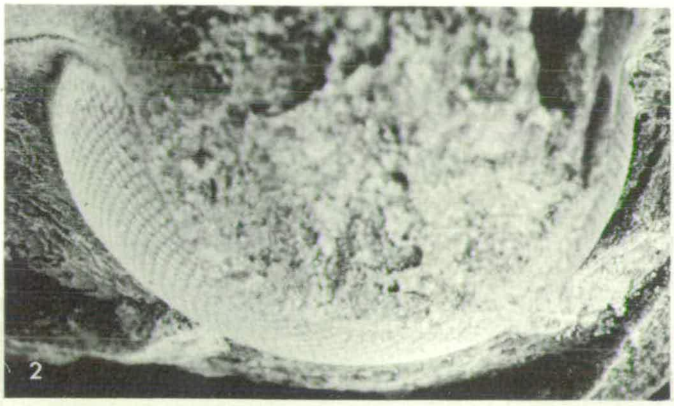
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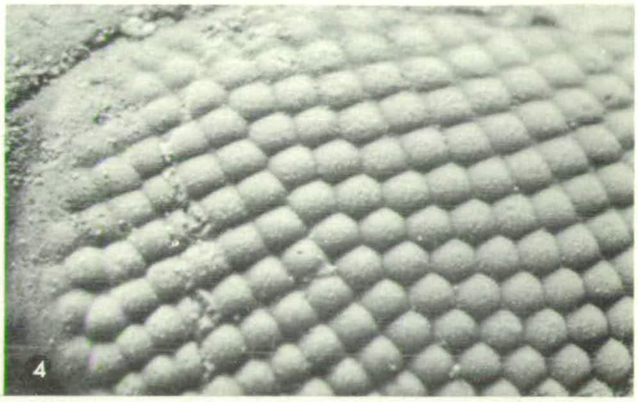
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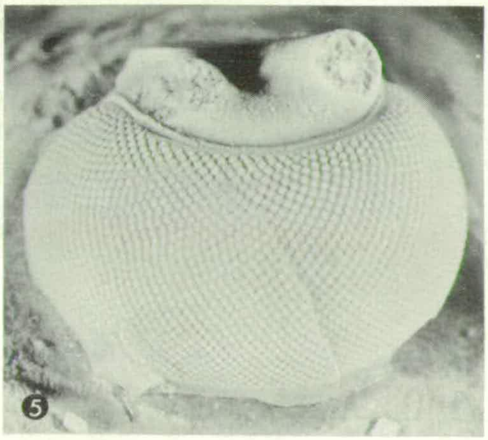
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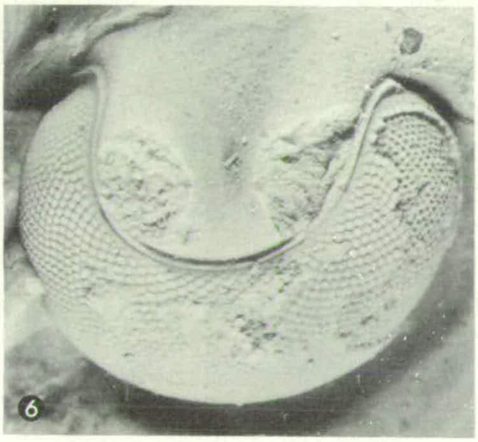
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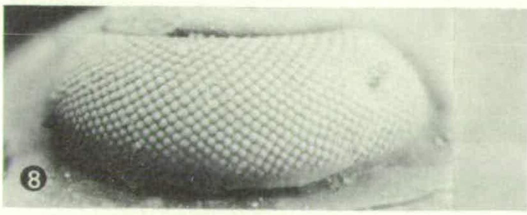
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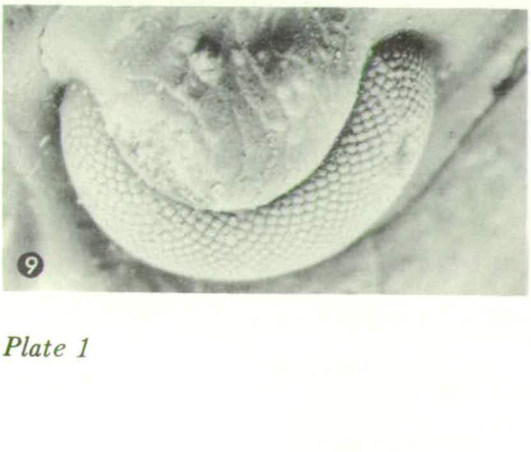
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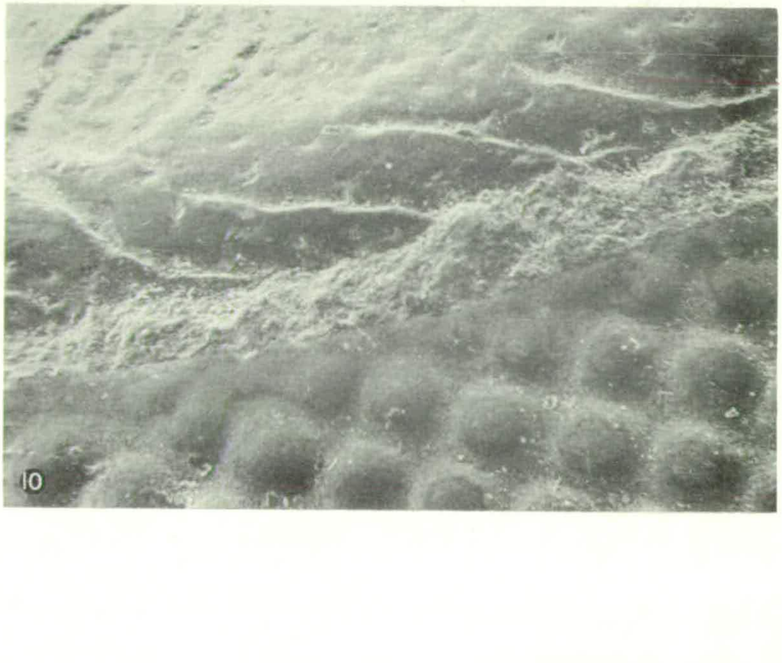
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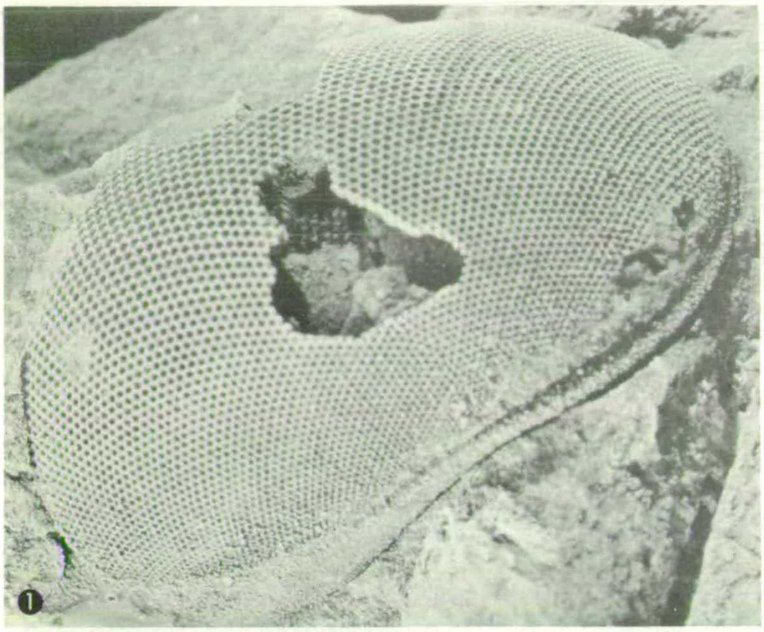

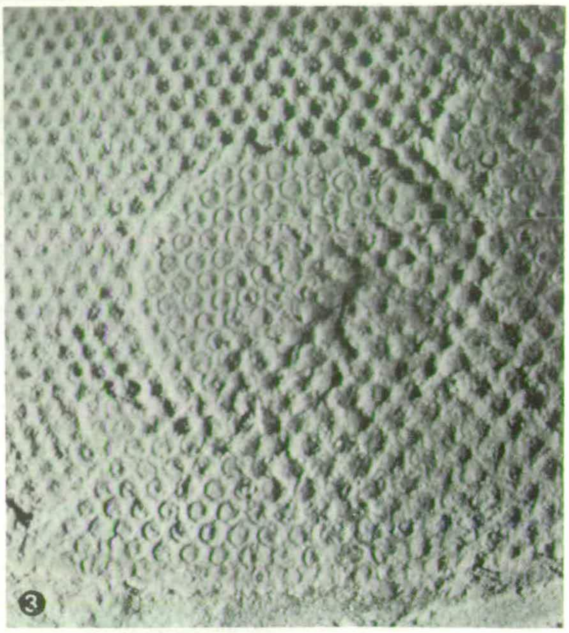

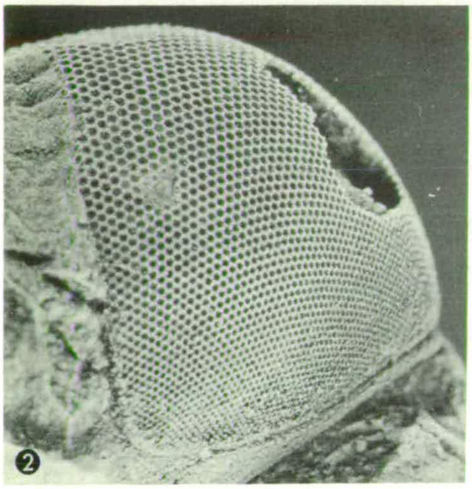

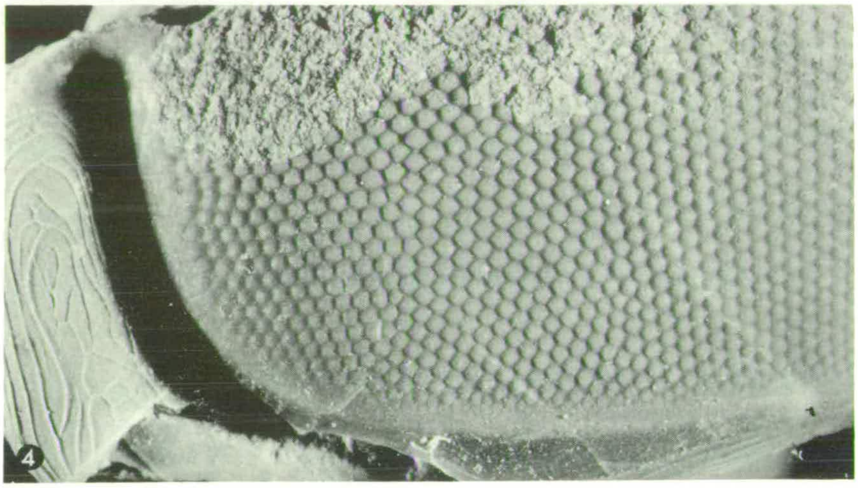

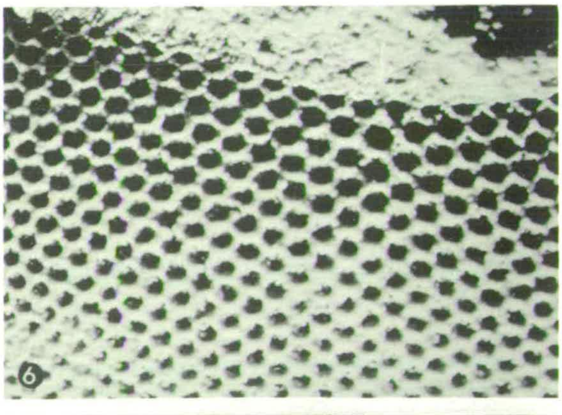

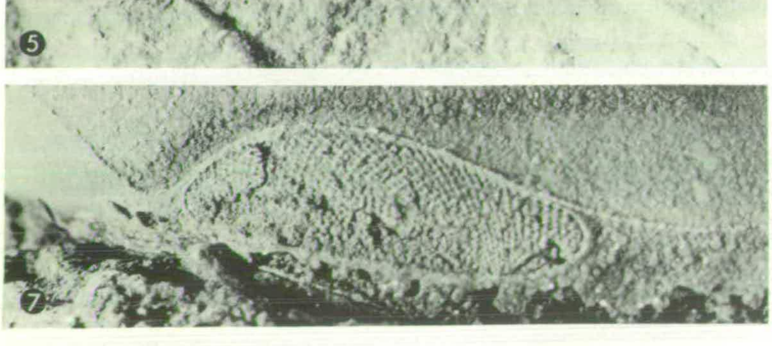

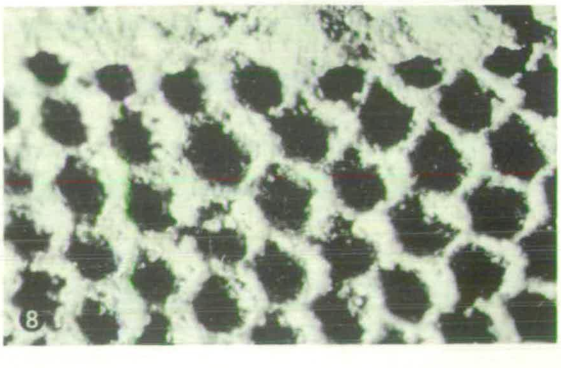

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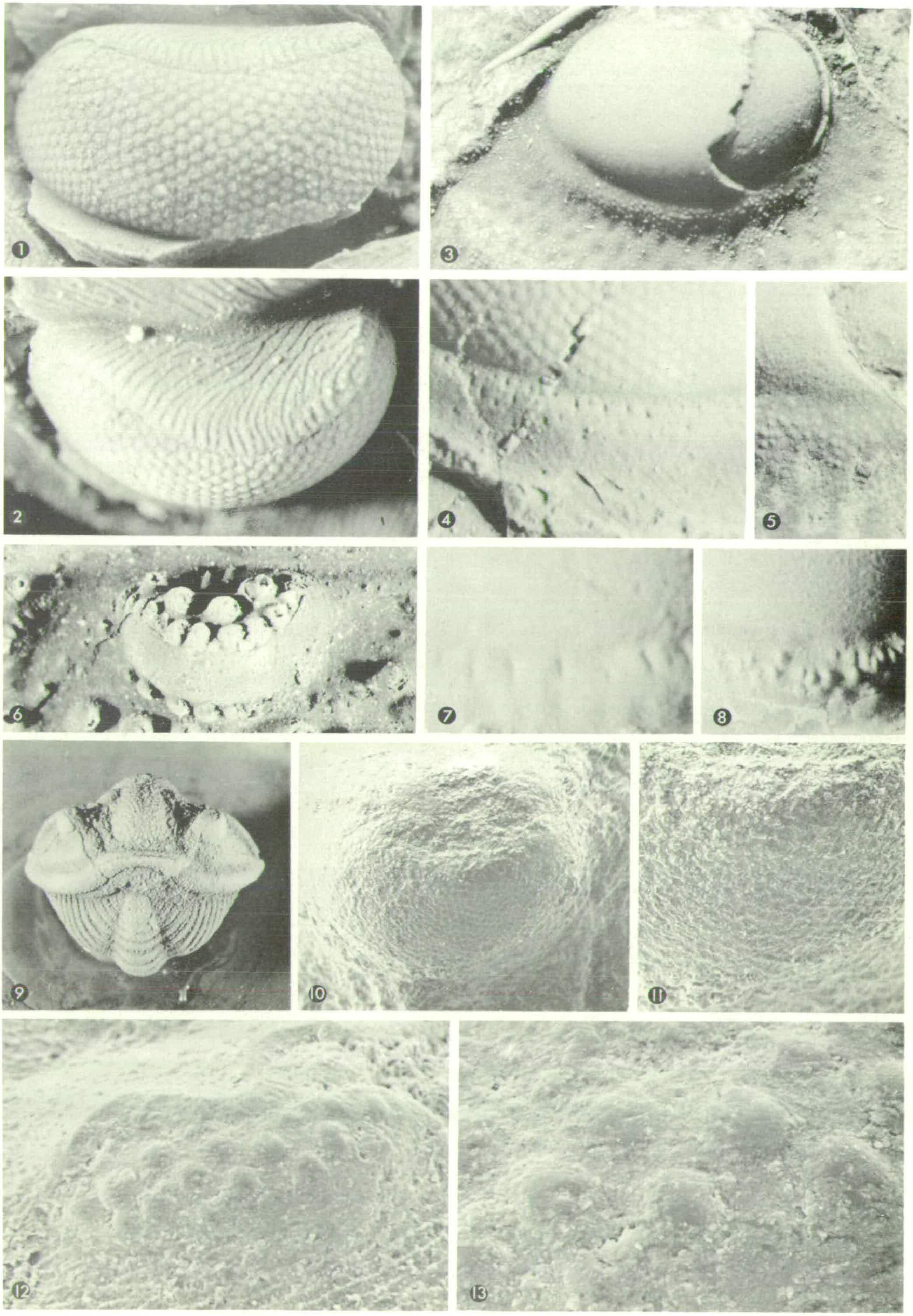

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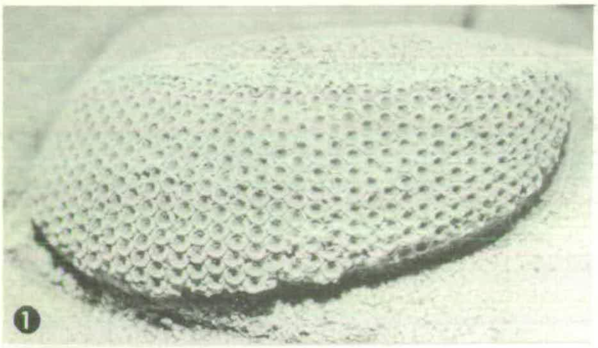

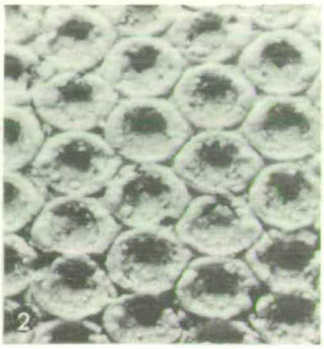

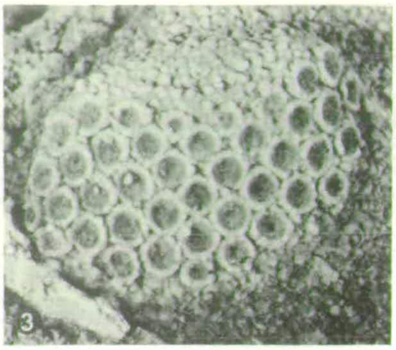

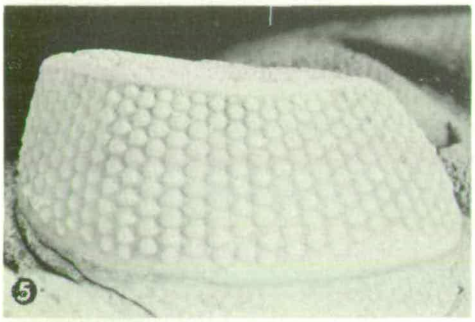

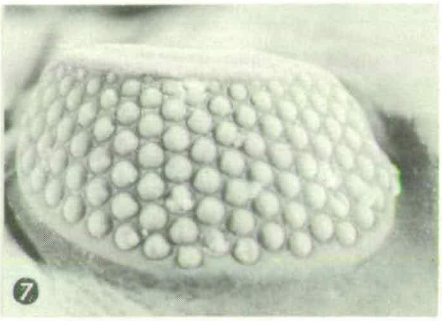

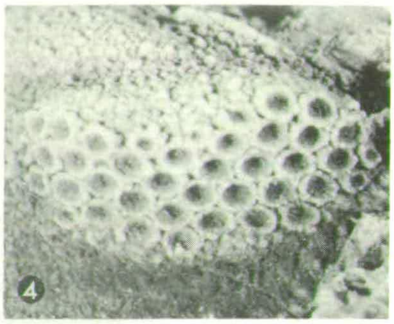

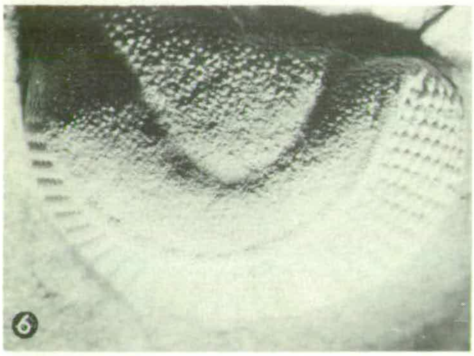

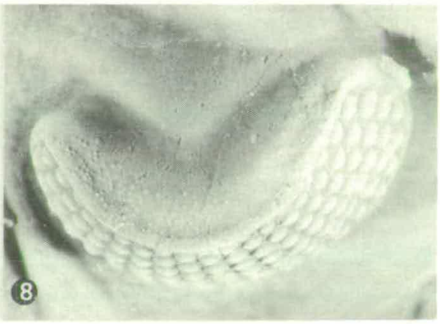

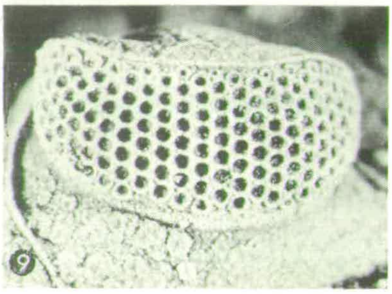

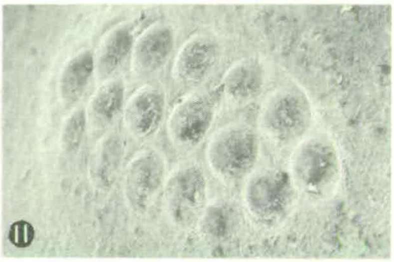

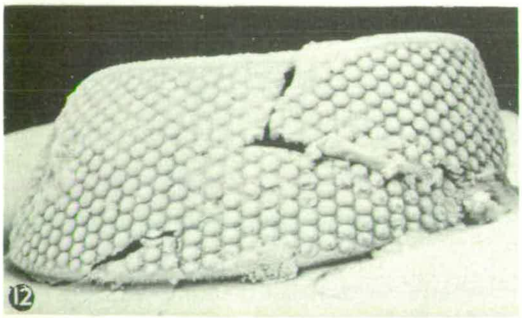

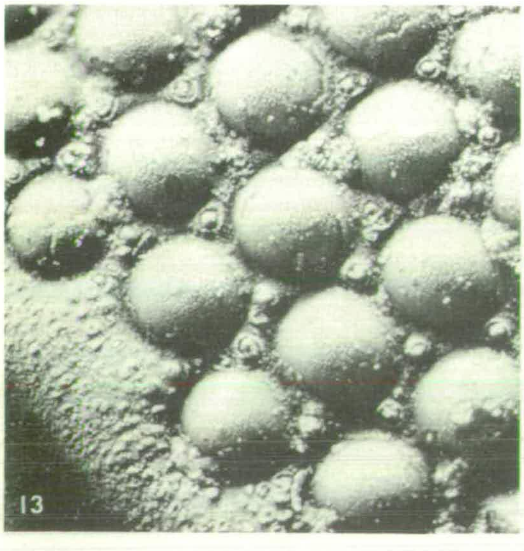

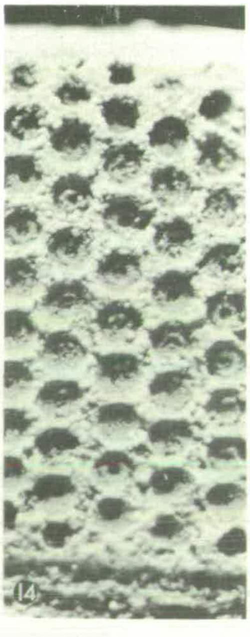

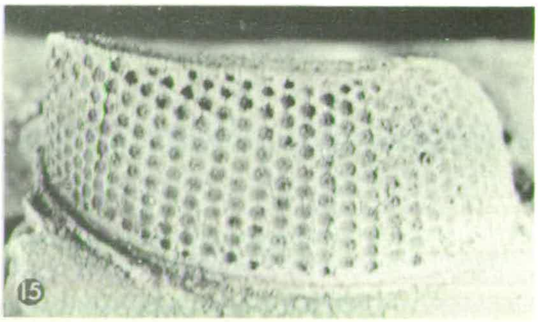

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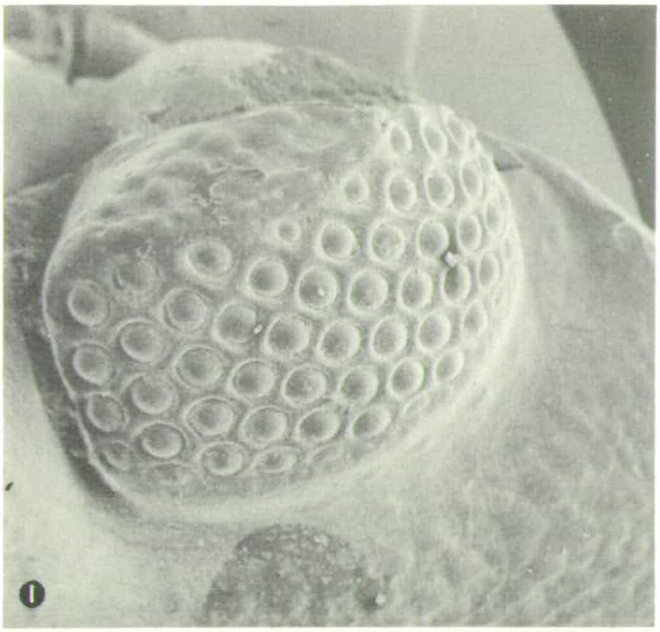
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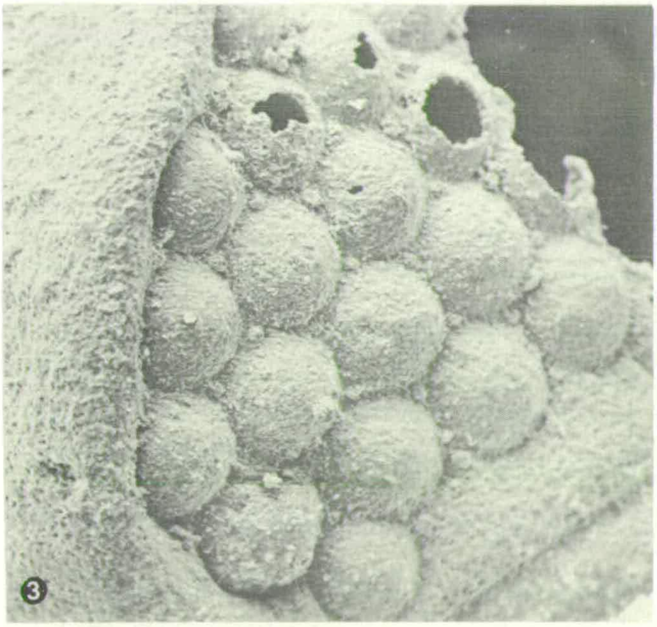
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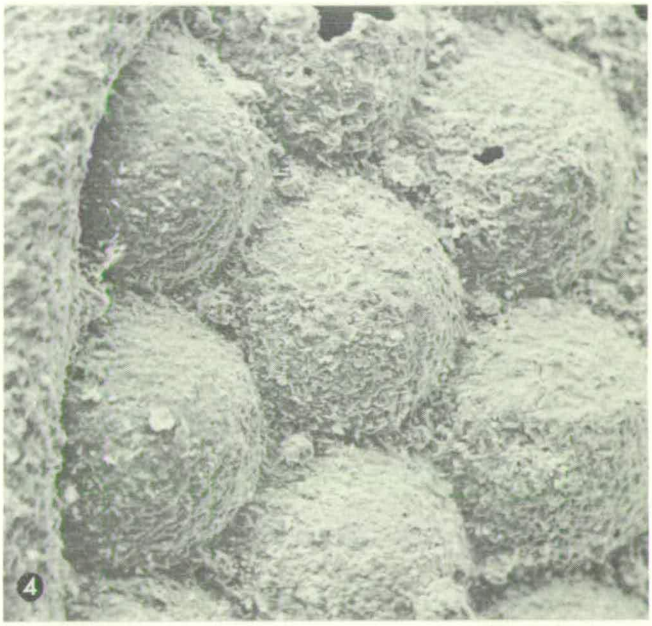
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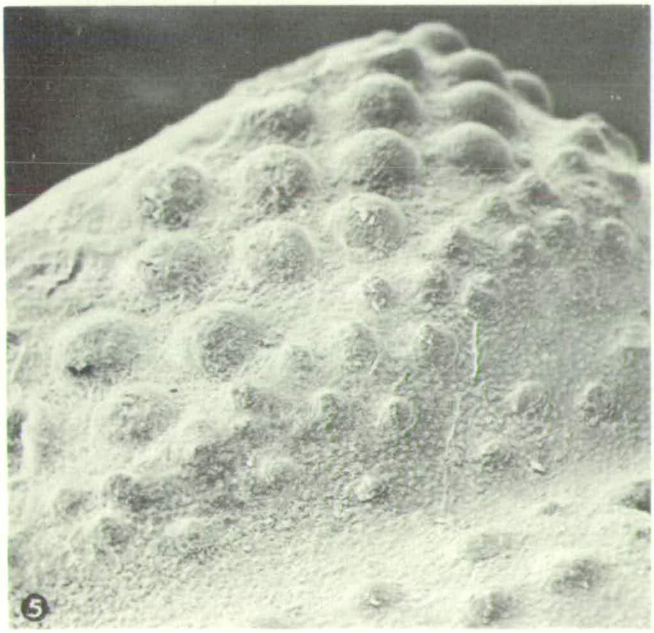
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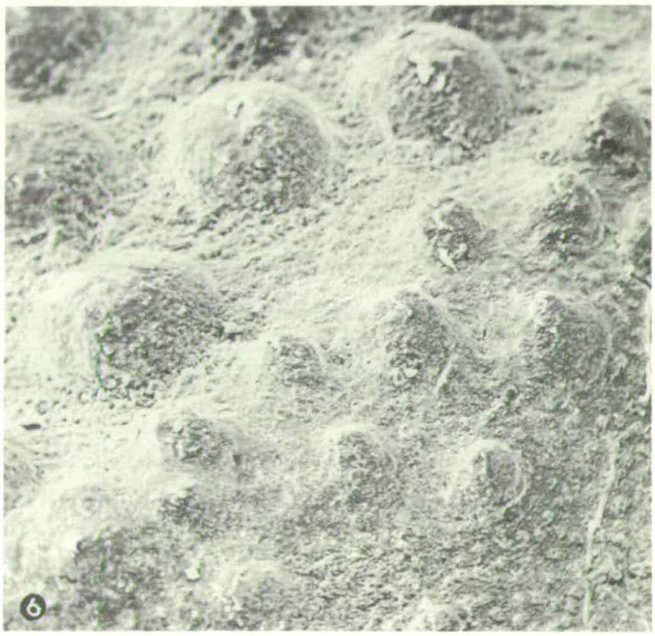
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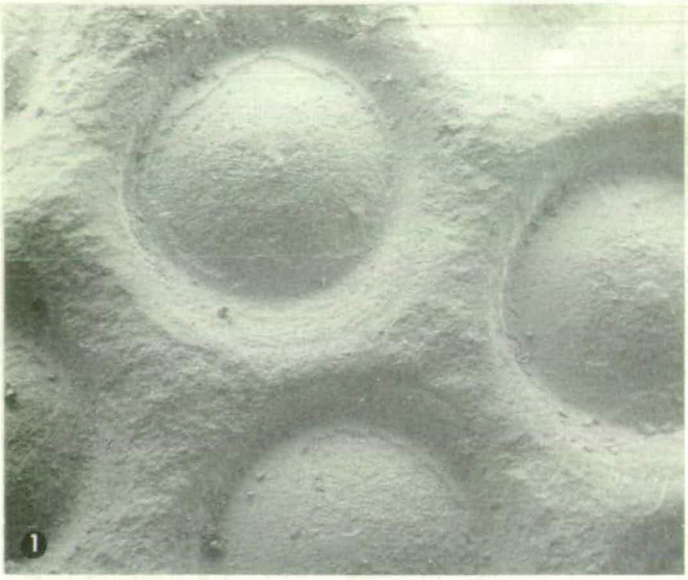

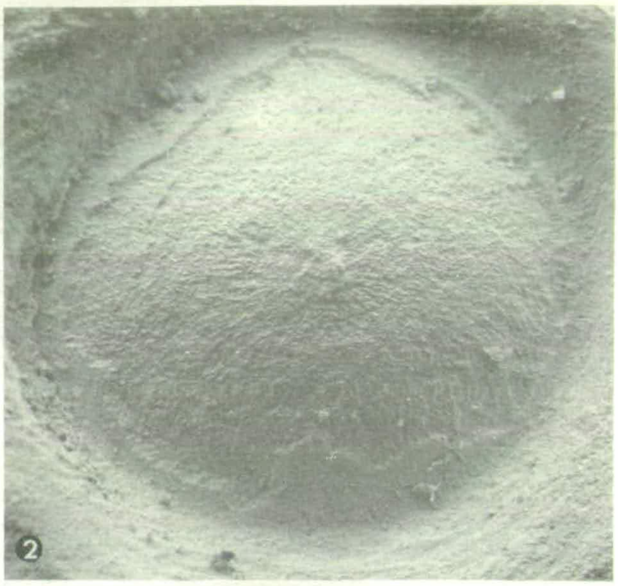

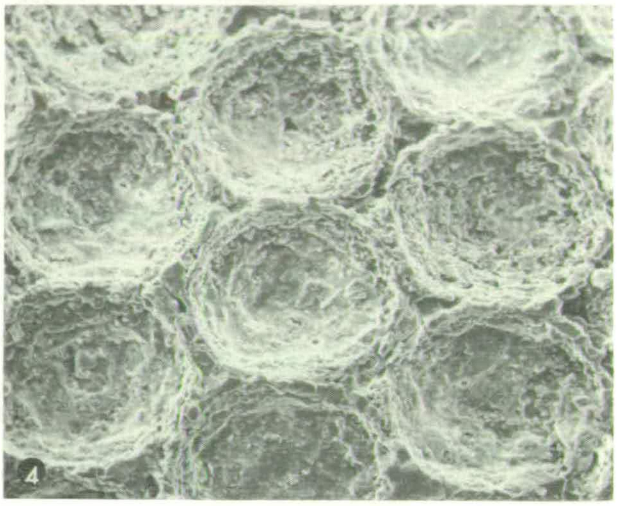

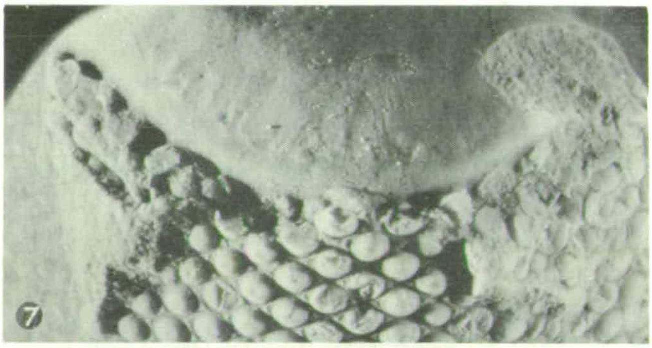

Plate 6

The function of the glabellar ‘tubercle’ in *Nileus* and other trilobites

RICHARD A. FORTEY AND EUAN N. K. CLARKSON

LETHAIA

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The glabellar ‘tubercle’ of *Nileus armadillo* (Dalman) is an inverted funnel-shaped thinning in the cuticle, covered by the outer cuticular layer. Its structure is consistent with a function as a light-sensitive organ, whose angular range of light receptivity complements that of the lateral eyes. Median cephalic tubercles of most other trilobites are unlike that of *Nileus* and are different in structure and position; hence they are unlikely to have been homologous.

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Many trilobites possess a median tubercle or node on the glabella. The structure is invariably small, in no examples exceeding 1 mm in diameter, and often as small as 100 μm. The presence of such tubercles was noted by Barrande (1852) and Beyrich (1846), and further observations have been added in many systematic papers over the last 100 years. The function of the tubercle has been debated since the time of these early authors.

Two theories are now considered probable:

(1) That the tubercle functioned as a median eye or ocellus, a theory originally proposed by M’Coy (1849:410).

(2) That the tubercle represents a ‘sensorial complex’ comparable to cephalic organs of living crustacea, including tactile and pressure-sensitive organelles, as originally suggested by Hanström (1926).

The purpose of this paper is to examine in particular the glabellar ‘tubercle’ of *Nileus,* which in our opinion probably had a light-sensitive function. We also briefly review the types of tubercle known from other trilobites and attempt to assess their homology or otherwise with that of *Nileus.* Because in some cases there are similarities between glabellar tubercles and those present on the occipital ring, these latter are also included in the discussion. No trilobites possess together both an occipital and glabellar tubercle.

The glabellar ‘tubercle’ of *Nileus*

On *Nileus armadillo* (Dalman) and other Nileidae the glabellar ‘tubercle’ is visible only as a small (0.2 mm) protuberance situated opposite the palpebral lobes on internal moulds. The dorsal surface of the exoskeleton (Fig. 1) is completely smooth over the region of the tubercle, which is detectable only as a ‘spot’ (dark or pale, according to the colour of the internal matrix) due to thinning of the cuticle at that point. The *Nileus* ‘tubercle’ differs markedly from those of many other trilobites, discussed below, in which it is a node visible equally on dorsal and ventral surfaces of the cuticle. We have never seen any indication of symmetrically disposed pits over the position of the *Nileus armadillo* ‘tubercle’ on the dorsal surface.

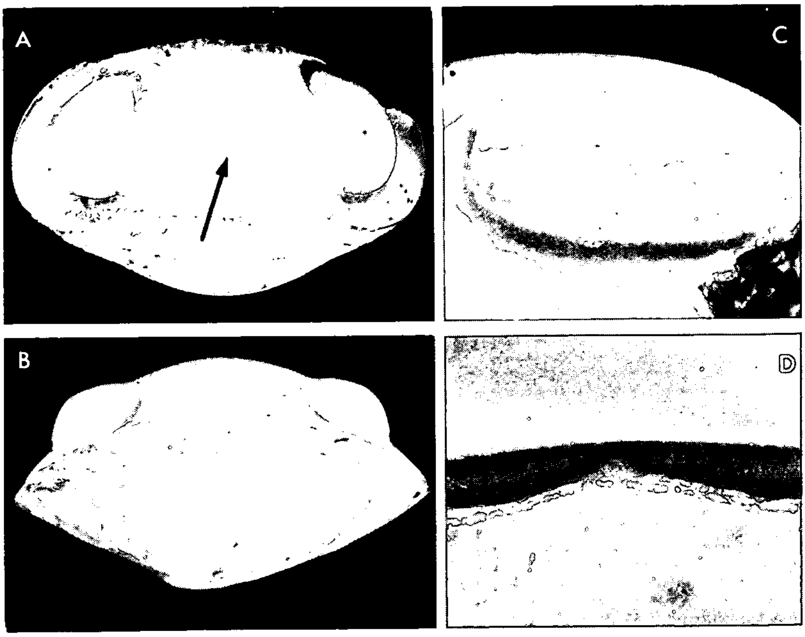

Fig. 1. Nileus armadillo (Dalman). □ A. Enrolled individual used later for sectioning, with position of glabellar 'tubercle' marked. Brit. Mus. (Nat. Hist.) In 28439. Old collection from Expansus Limestone, Sweden. ×2.25. □ B. Same in frontal view. ×2.25. □ C. Right eye of same. ×5. □ D. Glabellar 'tubercle' of same in section. Surface ground, polished, and photographed in immersion oil. ×25. (Vide Fig. 2A, C.)

Hypothesis. – It is proposed that the glabellar 'tubercle' of *Nileus* acted as a light receptive organ. Its function was to complement exactly the field of view of the lateral eyes to allow light sensitivity over more or less complete 180° vision, and its position on the glabella is uniquely designed for this function.

Visual fields of *Nileus*

The optics of vision in trilobites with holochroal eyes have recently been clarified (Towe 1973; Clarkson 1973). The lateral eyes of *Nileus* are holochroal, the dioptric units being calcite prisms closely similar to those of *Asaphus* described by Clarkson (1973). The direction and field of view of each lens is given by the orientation of the c-axis of the calcite crystal comprising each lens and is generally normal to the external visual surface, except at the lower surface of the eye where the prisms are angled to give equatorial coverage. By plotting the orientation of the peripheral prisms, the total field of vision of the eyes of *Nileus armadillo* was obtained from well preserved, undistorted, complete specimens (Figs. 2A, 3) using the technique of Clarkson (1966). Each eye has about 5600 lenses arranged in dorso-ventral files of up to 40 lenses. The field of view is latitudinally confined to a broad band, extending from the equator to a minimum of 50° and expanding slightly both anteriorly and posteriorly. This leaves a large, dorsomedian area of amplitude about 40° from the pole which is not 'covered' by the field of view of the lateral eyes.

Sections made transversely and sagitally indicate that the glabellar 'tubercle' is symmetrical, i.e. that the inner surface of the cuticle thins evenly in all directions on the mid-line. Detailed sections were made exactly through the middle of the 'tubercle' by grinding the same enrolled *Nileus* specimen on which measurements of the extent of view of the lateral eyes were made (Fig. 1D; 2A, C). Cellulose acetate peels were also taken from a second well preserved enrolled *Nileus armadillo* (Fig. 2B).

The cuticle of *Nileus* shows a bilaminate structure comparable to that of other trilobites (Dalingwater 1973:836), the inner laminate layer greatly exceeding in thickness the outer prismatic layer. In this case the cuticle seems to consist of darker and lighter laminae but their colour may be secondary. The inner layer thins abruptly about the glabellar 'tubercle'. Over the apex of the 'tubercle' only the outer, prismatic part remains, although this layer is

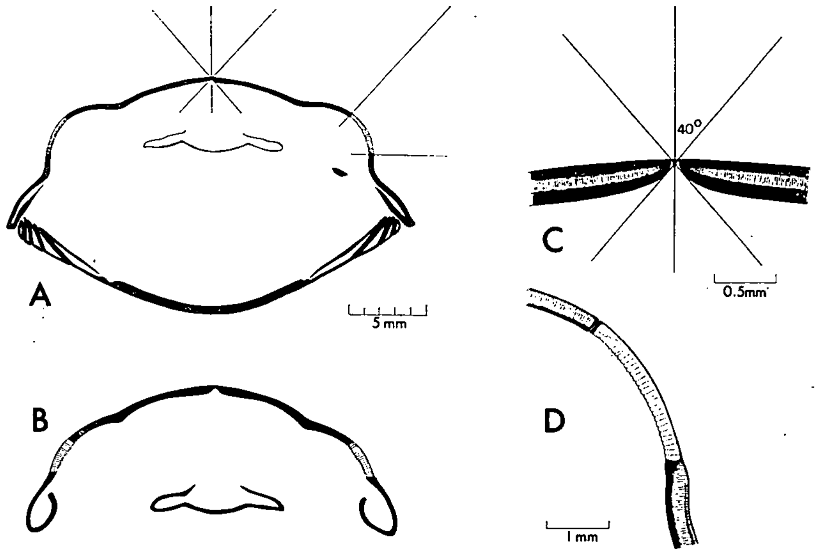

Fig. 2. Nileus armadillo (Dalman). ☐ A. Brit. Mus. (Nat. Hist.) In 28439 in vertical section passing through the glabellar 'tubercle'. Angles of light acceptance by the eye and glabellar 'tubercle' shown. ☐ B. B.M.(N.H.) In 28440 in slightly oblique, near vertical section. ☐ C. Section through glabellar 'tubercle' of B.M.(N.H.) In 28439, showing maximum angle of possible light acceptance. Lighter area within the cuticle is probably secondary. ☐ D. Vertical section through right eye of B.M.(N.H.) In 28439. All drawings were made with a camera lucida.

very thin and frequently tears in acetate peel preparations. The prismatic cap on the 'tubercle' enables a function much like that of a normal trilobite eye lens or prism – unimpeded passage of light along the calcite c-axis – a function impossible through the 'normal' trilobite cuticle even in the absence of pigmentation. Detailed orientation of individual units in the prismatic layer are on too fine a scale to be observed, but it is clear that the limit of vision is dictated by the angle at which the perimeter walls of the 'tubercle' converge on the internal surface of the cuticle (Fig. 2C). This indicates a potential angular range of amplitude at 40° to the pole of the 'tubercle'.

When this field is plotted sterographically with that of the lateral eyes, it covers almost exactly the dorsal 'blind' area (Fig. 3). A small shift of the 'tubercle' of only 1 mm anteriorly or posteriorly would again result in part of the blind spot being 'unguarded'. Such a precise correspondence is surely not mere coincidence.

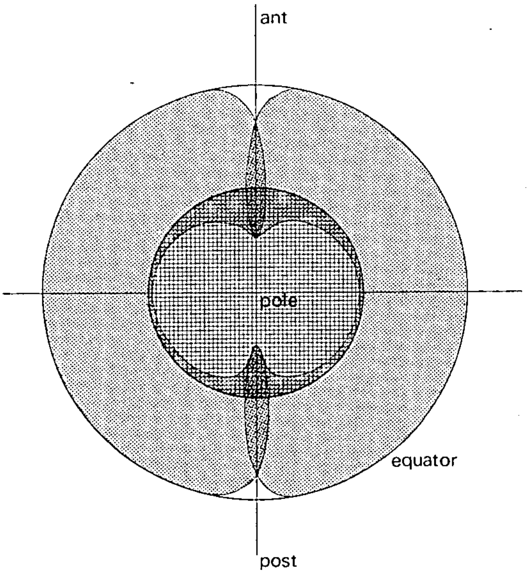

Fig. 3. Polar projection (Lambert equal area net) showing correspondence between the angle of light acceptance of the glabellar 'tubercle' (cross-hatched), and the visual fields of the eyes (stippled). The latter extend from the equator to approx. 60° latitude, and overlap slightly in the midline.

Both the position of the 'tubercle' and its structure are consistent with the hypothesis of a visual function. How efficient such a structure would have been is difficult to assess in the absence of data on the detailed microstructure, but its efficiency could scarcely have been comparable with that of the lateral eye with its thousands of lenses. It is possible that the 'tubercle' was only light/dark sensitive, for example. *Nileus* was a benthic trilobite (Fortey 1975), concerned mainly with food-gathering on and about the sea bottom, for which its lateral eyes were specifically adapted. Separation of this visual function from the monitoring of illumination from above, can be regarded as adaptive. In the same way modern euphausiids (Chun 1896; Kampa 1965) have divided compound eyes, and it is possible that the upwardly directed part is an intensity assessor.

Sensory cephalic tubercle on other trilobites

We have found few other trilobites that possess a cephalic 'tubercle' of a form similar to that of *Nileus,* i.e. a marked thinning of the cuticle not reflected on the dorsal surface. The most plausible examples are found in the family Illaenidae, particularly *Illaenus* (Whittington 1965:149, Fig. 7, Pl.50:5) and *Panderia* (Bruton 1968, Pl. 1:1, Pl. 10:1). The exact position of the 'tubercle' will depend on the location of the complementary position for the field of view of the eyes. In some Nileidae low convexity is associated with a more posterior position of the 'tubercle', for example in *Poronileus fistulosus* (Fortey 1975a Pl. 13:1). The extreme of this tendency occurs in *Peraspis lineolata* (Raymond) (see Whittington 1965, Pl. 34:9), the convexity of which is at a minimum for the family and where the 'tubercle' has attained a suboccipital position (Fig. 4C).

A distinct type of cephalic organ consists of a (usually low) tubercle on which there are four symmetrically disposed pits (Fig. 4D). These have been described on Odontopleuridae (Whittington 1956; Chatterton 1971; Bruton 1967) and Scutelluidae (Whittington 1965, Pl. 55:9, Pl. 55:10) and Asaphidae (Fig. 4D). In Trinucleidae, Størmer (1933) described a comparable structure but with a large central pit surrounded by four smaller ones. It seems improbable that this sort of organ had a direct visual function and it is certainly very different from the nileid tubercle. There is apparently no drastic thinning of the cuticle over these organs and it is improbable that the inner laminar cuticular layer is missing. In some examples (e.g. *Diacanthaspis orandensis* Whittington 1956, Pl. 11:20) the tubercle is prolonged into a spine. This type of tubercle has been compared with the median 'sensorial complex' of syncarid crustacea (e.g. Hanström 1934). The function of this organ in the recent forms has not yet been resolved, but in view of the structural similarity, analogy of function seems the best explanation at the moment.

It is of importance to note that the placing of this type of organ in Odontopleuridae and Scutelluidae is occipital. In Trinucleidae and Asaphidae it is found well in front of the occipital ring and probably belongs to a different segment. It is surprising to find that such a peculiar organ is segmentally non-uniform and therefore likely to be independently derived, but the contrary argument that the tubercle is developed on a constant segment would involve the unorthodox notion that there is an 'extra' cephalic segment in Asaphidae and Trinucleidae compared with odontopleurids and scutelluids. In some asaphids the glabellar tubercle is so far back as to be in an 'occipital' position. But in *Ogygiocaris* the tubercle is believed to have migrated to the 'occipital' position from a more anterior preoccipital position as is usual in *Niobe* (Fig. 4D). In the process the occipital furrow has been pushed backwards so that it is represented only by remnants on the lateral posterior parts of the glabella.

Many occipital tubercles represent simple homologues of mid-thoracic tubercles which are usually present along the length of the thorax (Fig. 4A). These show neither pits nor marked internal thinnings of the exoskeleton, but they do seem to retain the potentiality for protrusion into axial or occipital spines. Such tubercles are present in many families from the early Cambrian onwards.

Many trilobites possess a single occipital tubercle which has no equivalent on the thoracic axial rings and which does not seem to possess symmetrically disposed pits, nor the distinctive structure and position of the nileid tubercle. Such tubercles (Fig. 4B) tend to be dome-like excrescences visible in both the internal and external .moulds. A tubercle of this kind is often present on Proetidae (e.g. Owens 1973, Fig. 8A, 104) and Phillipsiidae. That this structure is distinct functionally from mid-thoracic axial tubercles is shown by such species as *Eremiproetus notabilis* (Alberti 1969:126, Figs. 1–5) which possess both types together on the occipital ring. On tuberculate or commonly granulate families such as Cheiruridae and Phacopidae, it is often difficult to distinguish the occipital tubercle from similar-sized tubercles distributed elsewhere over the dorsal exoskeleton; in many cases it is doubtfully present. In such cheirurids as *Xystocrania* (e.g. Whittington 1965, Pl. 62:1–3; Ross 1972, Pl.

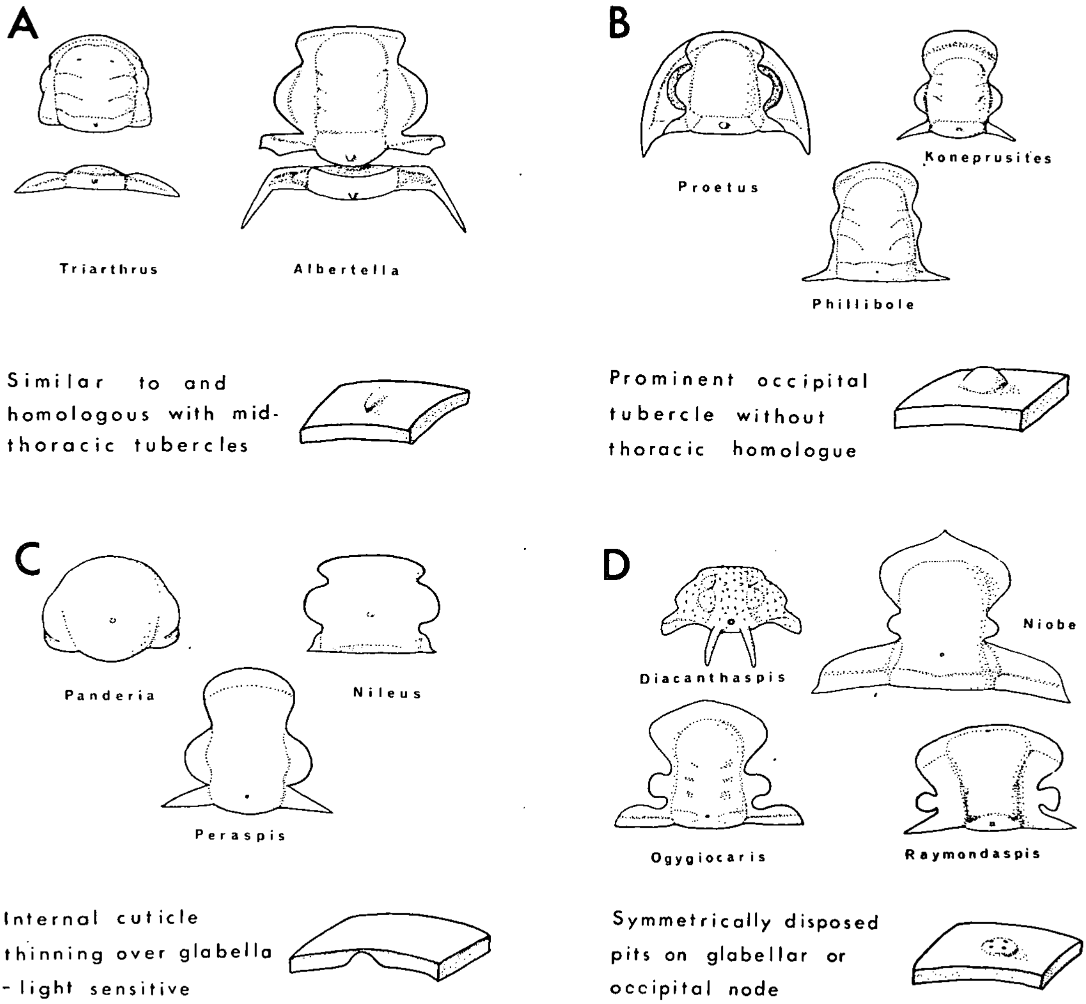

Fig. 4. Different kinds of median cephalic tubercle in trilobites. For explanation, see text.

17:20) a stout spine is developed on the glabella in a comparable position to the glabellar 'tubercle' of *Nileus.* Homology is very improbable, but it does seem possible that such spines provided an alternative method of protecting the 'blind' area uncovered by the lateral eyes.

The anterior glabellar tubercle of *Ampyxina* (Whittington 1959, Pl. 34:13, 15, 21) and *Mendolaspis* (Fortey 1975a, Pl. 30:8) is the remnant of a reduced anterior spine; in the former genus a prolonged anterior spine becomes reduced to a tubercle during ontogeny. Other Raphiophoridae lacking spines such as *Pytine* and *Globampyx* (see Fortey 1975a) possess prominent glabellar tubercles, but much more posteriorly positioned than that of *Ampyxina.* Since no raphiophorid possesses both a posterior glabellar tubercle and an anterior spine it is evident that the two structures are mutually exclusive and probably homologous.

To summarise, only a few examples are known in which the glabellar tubercle has the structure of that of *Nileus,* which is considered to have been light-sensitive. Other median cephalic tubercles differ in positioning and structure, and are unlikely either to have been homologous or to have had identical functions. The taxonomic significance of this diversity remains to be explored. Some of the main types of cephalic median tubercles are shown on Fig. 4.

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SOME PHACOPINA (TRILOBITA) FROM THE SILURIAN OF SCOTLAND

by E. N. K. CLARKSON, N. ELDREDGE, *and* J.-L. HENRY

ABSTRACT. *Acernaspis* (*Eskaspis*), a new subgenus, and *Podowrinella*, a new genus of Phacopina from Silurian inliers of the Midland Valley of Scotland, are here proposed. *A.* (*Eskaspis*) is restricted to the Telychian (upper Llandovery) and is referred to the subfamily Phacopinae. *A.* (*E.*) *sufferta* (Lamont) from the *M. crenulata* Zone of the Pentland Hills and *A.* (*E.*) *woodburnensis* from the upper *M. sedgwickii* Zone of Girvan are described. *Podowrinella*, which is found in the lower Wenlock of Girvan, and in the Telychian (upper Llandovery) of the Hagshaw and Pentland Hills, can probably be assigned to the Pterygometopidae, but possesses some character states normally considered representative of Phacopidae. Coaptative structures on the ventral doublures of *A.* (*Eskaspis*) and *Podowrinella* are described in detail, and information is given on the auxiliary impression system on the glabella of *A.* (*E.*) *sufferta*.

SILURIAN rocks in the Midland Valley of Scotland lie in a chain of inliers extending from Girvan to within a few kilometres of Edinburgh (text-fig. 1). At Girvan, in the Hagshaw Hills, and in the North Esk Inlier of the Pentland Hills, the Llandovery succession begins with turbidites or subturbidites, and passing upwards through shallow-water marine horizons (with shelly faunas well developed at certain horizons at Girvan and in the North Esk Inlier) the sequence changes to thin brackish or freshwater deposits and finally into redbeds, early in the Wenlock.

The large inlier of Lesmahagow, lying further to the north, has dominantly fresh or brackish water beds followed by redbeds.

In Telychian (upper Llandovery) mudstones and siltstones of the North Esk Inlier there occur abundant faunas, especially in the beds which have been referred to as the '*Plectodonta* mudstones' by Lamont (1947) and others.

Fossils were first discovered here in 1838 by Charles Maclaren of the Geological Survey, and Howell and Geikie listed them in 1861. The fine preservation and richness of the faunas led to much palaeontological activity in the next few decades, mainly by members of the Edinburgh Geological Society and associates (Haswell 1865; Henderson 1867; Brown and Henderson 1867; Henderson and Brown 1869; Etheridge 1874; Davidson 1874). But although extensive faunal lists were compiled, only Haswell (1865) and Davidson (1874) described any of the faunal elements. Haswell's descriptions and plates were very sketchy, but Davidson's monograph of the brachiopods was a valuable and enduring contribution to the palaeontology of the region.

The U.K. Geological Survey's faunal notes were updated by Peach and Horne (1899) and Mykura and Smith (1962), who described the area in detail.

Meanwhile, Lamont (1947, 1948, 1949, 1952) discussed the fauna at length primarily in a stratigraphical context, recognizing for the first time that the faunas were pre-Wenlock. New bivalves and chelicerates were later described (Lamont 1954, 1955). Though the starfish from well-known horizons in the Gutterford Burn were formally described by Spencer (1914–1940), most of the other elements in the

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rich and diverse fauna of the Pentland Hills remained imperfectly known or undescribed until very recently. Interest in the fauna has revived of late, however, and various elements have been revised or described for the first time by various authors. In recent works there have been described a new echinoid (Kier 1973), crinoids (Brower 1975), and the trilobite *Scotoharpes* (Norford 1973).

Tipper (1976) has remapped the region, revised the stratigraphy, erected new formation names, and distinguished three successive faunal assemblages from the upper Deerhope and lower Wether Law Linn Formation (Tipper 1975). In the present paper Tipper's formation names have been used throughout, replacing the older stratigraphical divisions (text-fig. 1).

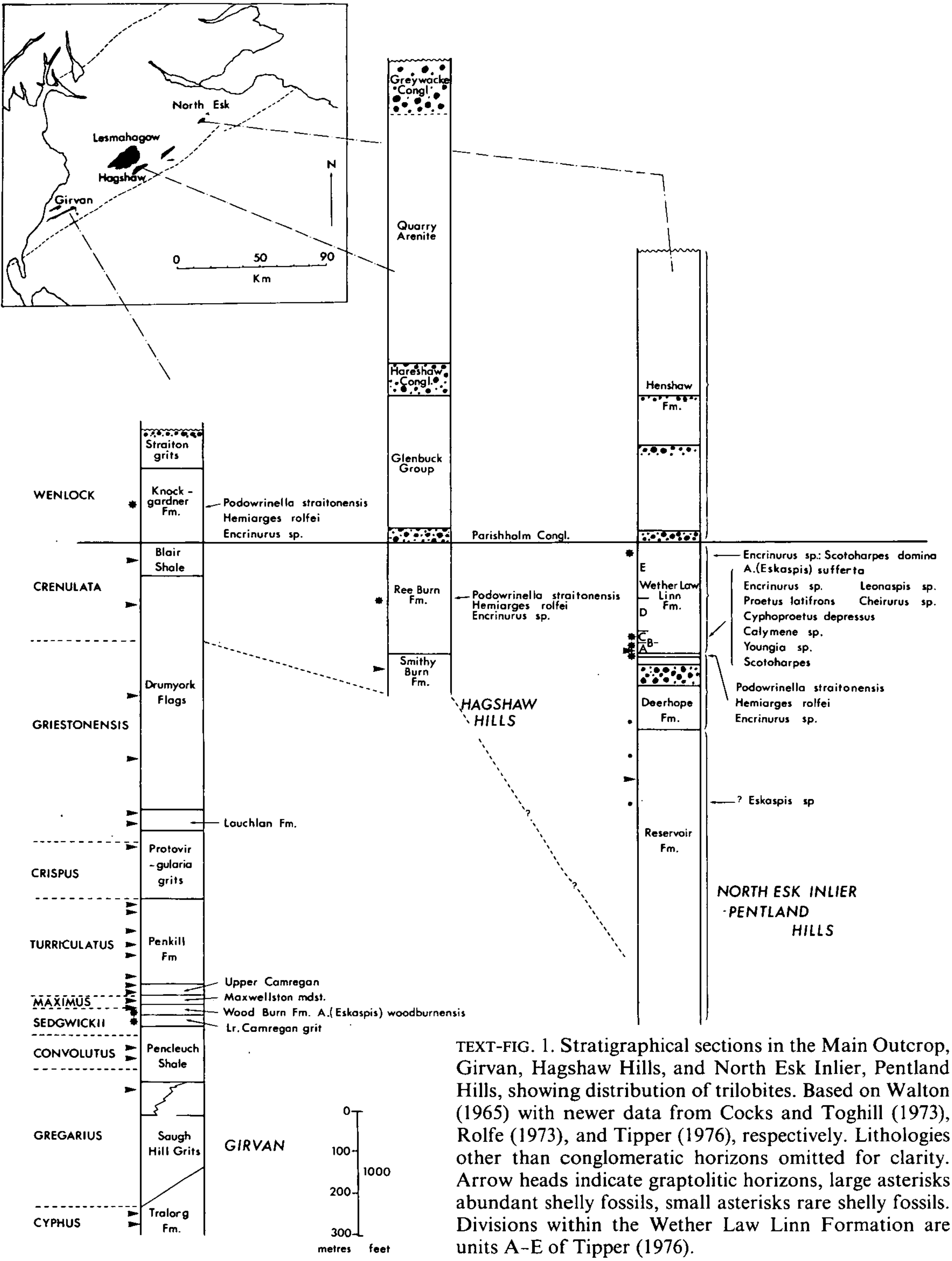
Trilobites, amongst many other fossils, especially brachiopods, are abundant at certain horizons within the upper Llandovery, and though the fauna is restricted to a comparatively few genera and species, individuals of these may be frequently encountered. In the Reservoir Formation these include occasional phacopids, probably *Acernaspis* (*Eskaspis*), n. sg. otarionids and odontopleurids, whereas *Podowrinella straitonensis*, *Encrinurus*, and *Hemiarges* together with less-common elements are present at the top of the Deerhope Formation. In the immediately overlying Wether Law Linn Formation (which includes the *Plectodonta* Mudstones), there is a rich fauna with *A.* (*E.*) *sufferta* (Lamont) (150 examples), *Encrinorus* sp. (*c.* 150 ex.), *Proetus latifrons* (M'Coy) (25 ex.), *Cyphoproetus depressus* (Barrande) (16 ex.), *Scotoharpes domina* (Lamont) (2 ex.), *Youngia* (6 ex.), *Calymene* sp. (6 ex.), *Cheirurus* sp. (1 ex.), and possibly other genera and species listed by Lamont (1948), though the validity of these has not yet been ascertained.

In the Wether Law Linn Formation the most abundant trilobites are found only at the base (in units A and C of Tipper) becoming less common towards the top of unit C of the succession. *Encrinurus* occurs quite abundantly, however, in the uppermost part of this formation, in unit E, in which the only other trilobite to have been collected is *Scotoharpes*. Tipper (1975) has shown that trilobites occur independently of the brachiopod communities which he described in this sequence.

In this paper the Phacopina of the Pentland Hills are described, these being *A.* (*E.*) *sufferta* (Lamont, 1947) and *Podowrinella straitonensis* (Lamont, 1965). *A.* (*E.*) *sufferta* is known from the Pentland Hills alone, but an earlier species, *A.* (*E.*) *woodburnensis*, n. sp. from the older Wood Burn Formation at Girvan can also be referred to that genus, and is the only other species known at present.

P. straitonensis is known from the Ree Burn Formation in the Hagshaw Hills, from which it was first described from specimens collected by Rolfe, and also from the lower Wenlock Knockgardner Formation at Girvan. In the Pentland Hills it occurs in a coarse siltstone, whereas both in the Hagshaw Hills and at Knockgardner, specimens are found at the base of coarse turbidite flows where they occur with brachiopod faunas (Rolfe 1973; Cocks and Toghill 1973). In all these cases *Encrinurus* and *Hemiarges* occur in the same fauna, which, judging by its anomalous stratigraphic position (younger in the west), strongly indicates either a facies fauna (perhaps controlled in some way by the regressive sequence), or else inaccuracies in correlation.

The present work is the first of a series of papers in which the trilobite fauna of the Pentland Hills is described. The rest of the fauna will be described in later papers, some by other authors.



TEXT-FIG. 1. Stratigraphical sections in the Main Outcrop, Girvan, Hagshaw Hills, and North Esk Inlier, Pentland Hills, showing distribution of trilobites. Based on Walton (1965) with newer data from Cocks and Toghill (1973), Rolfe (1973), and Tipper (1976), respectively. Lithologies other than conglomeratic horizons omitted for clarity. Arrow heads indicate graptolitic horizons, large asterisks abundant shelly fossils, small asterisks rare shelly fossils. Divisions within the Wether Law Linn Formation are units A–E of Tipper (1976).

TAXONOMY

Nomenclature

Lamont (1965) described *Phacops straitonensis* from the Hagshaw Hills and Knockgardner. The discovery of this species in the Pentland Hills, and the collection of more material from all three localities gave the incentive for a more detailed study. No question arises over the validity of the specific name, though the holotype has been lost (Lamont, pers. comm.).

Podowrinella is here described as a new genus. It seemed to us initially that the poorly known, but suggestively named, genus *Pterygometopidella* Wedekind, 1912 (based on *Phacops quadrilineata* Angelin) might be available as a generic taxon for *P. straitonensis.* Wedekind (1912) described *Pterygometopidella* very inadequately from only two specimens collected from the c-marl (Silurian) of Gotland, and figured only one of them in a poor and tiny photograph which allowed few details to be seen but which seemed to indicate a close resemblance to *Eophacops musheni* (Salter). The two specimens, deposited in the collections of the Geologisch-Paläontologisches Institut der Universität Göttingen, are no longer in the Institute (Jahnke, pers. comm. 1974), and may have been destroyed. Struve (pers. comm. 1974) suggests that Wedekind may have erected the subgenus on an erroneously determined species and Schrank (1972) regards Wedekind's specimens of *P. quadrilineata* as incorrectly determined individuals of *E. musheni* (Salter), indicating that *Eophacops* is a junior synonym of *Pterygometopidella.*

Though the taxonomic problem of *Pterygometopidella* may not be entirely resolved, it is clear that this generic name is not available for *Phacops straitonensis.*

A. (*E.*) *sufferta*, on the other hand, was figured, though not described, by Lamont (1948) as *Eophacops sufferta*, in a paper in which many other trilobites from the Pentland Hills were also figured but for which no formal descriptions were given. There thus arises the question of the validity of the nomenclature, a matter which Norford (1973) has also referred to in dealing with *Scotoharpes. S. domina* Lamont was also figured in the same paper by Lamont (1948), and Whittington (1950) rejected the name as being invalid. Norford (p. 12), however, revived the name on the basis of Lamont's recognizable photograph and few words of description.

For the same reasons the specific name *sufferta* is here considered to be valid, since the photographs of Lamont's (1948, pl. 1, figs. 21, 22) which show a complete internal mould are clearly recognizable, and Lamont (pers. comm. 1974) has confirmed that the common phacopid trilobite at Wether Law Linn is, in fact his '*Eophacops*' *sufferta*, though the type, formerly in his possession, has now been lost. Though Lamont did not name the species in his 1947 paper on the stratigraphy and faunas of the region he states (p. 290) that 'a large *Eophacops* is very common at Wetherlaw Linn. It has more than 6 facets per radius in the eye, which rules out *E. elliptifrons* (Esmark).... The rather long pygidium with numerous axial segments, however, points to comparison with *E. elliptifrons* var *glaber* Marr & Nicholson . . .'. Lamont's notes which annotate the Grant Institute Library copy of Haswell's (1865) guide to the geology and faunas of the Pentland Hills refer to Haswell's figures (p. 6) of '*Phacops stokesii*' as '*E. sufferta*' and state, 'It should have shown 7-8 rings in the pygidial axis' and, 'Eye usually has 7 facets per column'.

There thus seems to be no question that the common and only species of phacopid trilobite from the Wether Law Linn Formation is what Lamont recognized as a new species and called *E. sufferta*, and it is here redescribed, under the generic name *Acernaspis* (*Eskaspis*).

SYSTEMATIC DESCRIPTIONS

Order PHACOPIDA Salter, 1864
Suborder PHACOPINA Struve, 1959
Superfamily PHACOPACEA Hawle and Corda, 1847
Family PHACOPIDAE Hawle and Corda, 1847
Subfamily PHACOPINAE Hawle and Corda, 1847
Genus ACERNASPIS Campbell, 1967
Subgenus ESKASPIS n. sg.

Type species. Eophacops sufferta Lamont, 1947. Upper Llandovery (Telychian). Wether Law Linn Formation, North Esk Inlier, Pentland Hills, Peeblesshire, Scotland.

Diagnosis. Relatively small Phacopinae. Cephalon roughly 1·8 times as wide as long; genae somewhat truncate postero-distally (in dorsal view) so that the cephalon is widest just anterior to the posterior branch of the facial suture. Anterior glabella lobe moderately inflated, rather flat on top and shelving more steeply anteriorly.

Axial furrows deeply emplaced. Glabellar furrows 3p and 2p lightly impressed; 3p in two distinct, unjoined parts with distal ramus straight, running at an exsagittal angle of 45°, not confluent with axial furrow; proximal ramus of 3p furrows convex anteriorly, inclined slightly antero-laterally. 2p furrows likewise convex and not confluent with axial furrows.

Glabellar furrows 1p confluent with axial furrow, concave anteriorly and not coalesced mesially, with stout apodemes developed in distal portion of 1p external surface. Intercalating ring thus confluent mesially with anterior glabellar lobe; intercalating ring depressed, with distal nodes. Occipital furrow deeply incised laterally. Occipital ring longest (sag.) at the midline, depressed laterally with nodes partially set off by exsag. furrows, not reaching height of anterior glabellar lobe in lateral view.

Posterior border furrow lightly impressed, becoming nearly obsolescent laterally but merging with lateral border furrow. Eyes large, nearly reaching, or some distance from, posterior border furrow, and, anteriorly, lateral border furrow, with eye socle developed only as small, depressed area beneath visual surface. Visual surface with sixteen to nineteen dorsoventral files of lenses, all protruding well beyond bounding sclera. Palpebral lobe flat, rather narrow, set off from palpebral area by faint palpebral furrow.

Anterior cephalic margin distinct laterally and smoothly continuous with anterior glabellar lobe, disappearing antero-medially. No anterior border furrow developed.

Anterior doublure fairly long (sag.), with inflated central lobe sometimes present. Vincular furrow present anteriorly only as paired subfrontal depressions meeting at midline, deeply impressed postero-laterally and bearing nine notches for pleural tips. Anterior and posterior regions of vincular furrow unconnected, or connected by a faint furrow. Hypostoma unknown.

All parts of exoskeleton minutely granular; auxiliary impression system ovate, developed as depressions devoid of granules on anterior glabellar lobe, and as scars viscerally.

Thorax with distinct axial nodes set off by short non-communicating furrows inclined postero-proximally on both the anterior and posterior sides of axial ring. Pleural tips gently rounded. Pygidium with well-defined axial furrows, with about six axial rings and terminal piece. Axis rounded posteriorly, not meeting posterior margin of pygidium. Five pairs of pleurae present; pleural furrows becoming progressively fainter posteriorly; inter-pleural furrows present, but weakly impressed.

Remarks. Our diagnosis of *Acernaspis* (*Eskaspis*) includes character states inclusive of some other, particularly Silurian, Phacopinae. All characters included in the diagnosis do, in fact, vary in general amongst Phacopinae and are of potential value as diagnostic elements. Furthermore, inclusion of 'primitive' as opposed to strictly autapomorphous ('derived') characters, in a diagnosis, is of value in recognizing distinct genera, for only one or at most a few subordinate taxa in a defined group may in fact retain a particular primitive feature, hence its valid inclusion in a diagnosis. The minute granulation of *A.* (*Eskaspis*), for instance, is close to the primitive condition for all Phacopinae, yet is typical only of species of *A.* (*Eskaspis*) and *A.* (*Acernaspis*) among all known Phacopinae.

As written, the diagnosis of *A.* (*Eskaspis*) embraces some features of only three additional genera known to us: *Murphycops* Lespérance, *A.* (*Acernaspis*) Campbell, and in ventral morphology *Ananaspis* Campbell. We emphasize here the distinctly diagnostic traits of *Acernaspis* (*Eskaspis*) which serve to distinguish it from these other genera. *A.* (*Eskaspis*) shares with *Murphycops* some similarity in the coaptative device of the cephalic doublure, but otherwise differs from *Murphycops* in the cuticular granulation, development of auxiliary impression system, presence of a distinct palpebral furrow separating the palpebral lobe from the palpebral area, and the presence of nodes developed on the thoracic axial rings just proximal to the axial furrows.

A. (*Acernaspis*) and *A.* (*Eskaspis*) are dorsally very similar to one another, their over-all shape, degree of glabellar inflation, and auxiliary glabellar impressions, for instance are almost identical, and perhaps the only significant difference is the reduction of the anterior border in *A.* (*Eskaspis*), so that it is not visible in dorsal view. But we would here draw attention to the ventral morphology of the cephalon, as did Campbell (1967), and because of the coaptative enrolment mechanisms, to the pygidial doublure. Coaptative morphology has not yet been fully explored in Phacopina, but is clearly very important in taxonomy.

The ventral cephalic morphology of *A.* (*Acernaspis*), here represented by the Idwian *A.* (*A.*) *elliptifrons* (Esmark) from Girvan, Ayrshire, Scotland, is substantially different from that of *A.* (*Eskaspis*) *sufferta*. There are some variations within *A.* (*Acernaspis*) judging by the photographs of the doublures of various species given by Campbell (1967), Männil (1970*a*, *b*), and Sherwin (1972), but nowhere is there the kind of conformation illustrated by *A.* (*E.*) *sufferta*. Both *elliptifrons* and *sufferta* have nine vincular notches, the last one being indistinct in *elliptifrons* (text-fig. 3*a*–*c*). In *elliptifrons* the vincular notches are narrow and all about the same width forming a more or less parallel-sided row deeply indenting the flat surface of the doublure and subparallel with its edges. The notches are all centrally excavated to about the same depth and are joined by shallower passages. The anterior notch runs into a deep vincular furrow behind which the doublure forms a pronounced flat shelf. *Sufferta*, on the other hand, has a much wider series of obliquely set vincular notches, becoming broader and deeper posteriorly and evidently adapted for receiving a flattened pleural end rather than a more pointed tip. The two ridges separated by the vincular notches are oblique to one another when seen in lateral view, and the outer one is indented by continuations of vincular notches. *A.* (*E.*) *sufferta*, the type species, has no trace of a vincular furrow, but has a pair of shallow subfrontal depressions meeting on the midline. *A.* (*E.*) *woodburnensis* has these subfrontal depressions as well, but also has a shallow vincular furrow joining each of them to the vincular notches. It is not a deeply incised furrow like that of *elliptifrons*, however, but a lightly impressed indentation. The vincular morphology of *woodburnensis* is in many ways intermediate between that of *elliptifrons* and that of *sufferta*, being anteriorly more similar to the former, and posteriorly resembling the latter; the three are illustrated here as a morphological series (text-fig. 3). In many ways, however, there is a fair resemblance between the vincular morphology of *woodburnensis*, to that of *Ananaspis* species (Campbell 1967, pl. 14, figs. 9, 13–15), though the presence of the subfrontal depressions links it with *Acernaspis* (*Eskaspis*) to which it is, with slight reservations, assigned here.

A. (*Eskaspis*) seems to have been a localized late Llandovery derivative of the *A.* (*Acernaspis*) stock, retaining most of its plesiomorphic (primitive) features of dorsal cephalic morphology, but having more advanced ventral morphology. This in *woodburnensis* is rather like that of the 'derived' genus *Ananaspis*, which it does not closely resemble in dorsal morphology, though it also has features pointing towards the more extreme, and indeed unique construction of the doublure of *Acernaspis* (*E.*) *sufferta*, which seems to have been a terminal endpoint.

Acernaspis (*Eskaspis*) *sufferta* (Lamont, 1947)

Plate 18, figs. 1–9; Plate 19, figs. 1–7, 10; text-figs. 2*a*, *f*, 3*a*, *b*, 4*a*, *c*

1861 *Phacops Stokesii* M.-Edw.; Howell and Geikie, p. 134.
1865 *Phacops Stokesii* Haswell, p. 37, pl. 4, figs. 6, 7.
1867 *Phacops Stokesii* Henderson, pp. 22–23.
1869 *Phacops Stokesii* Brown and Henderson, p. 31.
1899 *Phacops Stokesii* (M.-Edw.); Peach and Horne, p. 597.
1947*a* *Eophacops* cf. *elliptifrons* var. *glaber*. Marr and Nicholson; Lamont, p. 290.
1947*b* *Eophacops sufferta* n. sp. Lamont, p. 6, pl. 1, figs. 21, 22.
1962 *Phacops* aff. *stokesii* (Milne-Edwards); Mykura and Smith, p. 138.
1975 *Acernaspis* sp. Tipper, p. 297.

Material. Neotype, IGS 1034. Pl. 18, fig. 1, is here selected since Lamont's holotype is lost.

Other figured material. Gr. I. 40282, Pl. 18, fig. 2; Gr. I. 40279, Pl. 18, figs. 3, 7; IGS 5783, Pl. 18, fig. 4; Gr. I. 40269, Pl. 18, fig. 5; Gr. I. 40270, Pl. 18, fig. 6; Gr. I. 40262, Pl. 18, fig. 8; Gr. I. 40281, Pl. 18, fig. 9;

Gr. I. 40257, Pl. 19, fig. 1; Gr. I. 40243, Pl. 19, fig. 2; Gr. I. 40281, Pl. 19, fig. 3; Gr. I. 40260, Pl. 19, fig. 4; Gr. I. 40280, Pl. 19, fig. 5; Gr. I. 44093, Pl. 19, fig. 6; Gr. I. 40261, Pl. 19, fig. 7; Gr. I. 40275, Pl. 19, fig. 8; Gr. I. 44094, Pl. 19, fig. 10.

Additional material examined. Approximately 150 specimens from the Wether Law Linn Formation (Tipper's units A and C) from the Deerhope Burn and Wether Law Linn localities from the collections of the Grant Institute (Gr. I.) (mainly Tipper and Clarkson Collections), the Royal Scottish Museum (RSM), and the Institute of Geological Sciences (IGS) of Edinburgh.

Distribution. This species is confined to the lower Wether Law Linn Formation in the North Esk Inlier, Pentland Hills. It occurs quite abundantly and in good preservation as internal and external moulds at all levels, and complete specimens are not infrequently found. Fragmentary specimens recently discovered by S. Wood in the Reservoir Formation may belong to this species.

Diagnosis. A species of *Eskaspis* lacking connection between the subfrontal depressions of the anterior region of the doublure and the posterior, notched portion of the vincular furrow. Eyes large, with nineteen files (rarely eighteen in adults) with a general lens formula of 565 787 877 765 543 2 and about 116 lenses in all. Smaller specimens (approximately half adult size), with eighteen files of no more than six lenses. Lowermost lenses very small, elliptical in some specimens.

Dimensions. Holotype: total length (sag.) 20·0 mm, cephalic length (sag.) 5·7 mm, width 13·0 mm. Range in cephalic length 2·2–9·0 mm, width 5·0–17·5 mm.

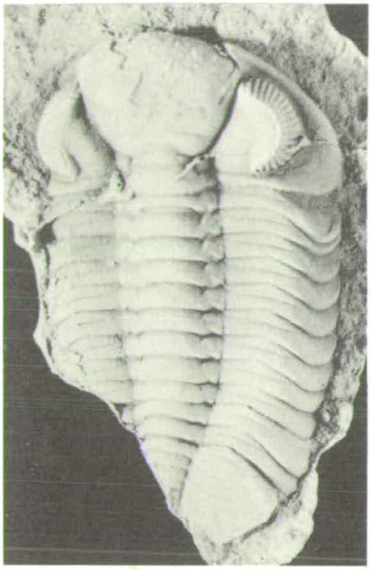
Description. Cephalon relatively broad, width/length ratio being approximately 2:1, and with an almost rounded (subangular) anterior margin (text-fig. 2*a*). Glabella half the cephalic width at its widest, broadly heptagonal, expanding anteriorly, widest in front of eyes where it is about as broad as its length. Glabellar crown (in profile) slightly higher than palpebral lobes (text-fig. 2*d*). In lateral profile the glabella is rather flattened on top, but slopes with increasing steepness to meet the anterior margin at about 80° with no real preglabellar furrow or preglabellar field, so that the glabella is directly in contact with the cephalic doublure. Axial furrows moderately deeply impressed, running forwards from lobe 1p at about 45° to an exsagittal line and changing direction where the palpebral furrow contacts glabellar lobe 3p, thence diverging from the exsagittal line only by some 10°, its course being indented slightly by the anterior edge of the eye. Axial nodes small, usually round but sometimes elongate.

All glabellar furrows faintly impressed and approximately equidistant from one another. 1p is the deepest; it is discontinuous and anteromedially directed at 45°.

EXPLANATION OF PLATE 18

Figs. 1–9. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Wether Law Linn Formation (Telychian), North Esk Inlier, Pentland Hills. 1, neotype. Wether Law Linn (WL), IGS 1035,* ×3·5. 2, complete specimen. Deerhope Burn (DB), Gr. I. 40282,† ×2·3. 3, almost complete, somewhat disarticulated specimen (DB), Gr. I. 40279,† ×2·5. 4, partially enrolled specimen (WL), IGS 5783,* ×3·5. 5, anterior doublure, showing subfrontal depressions, antero-ventral view (WL), Gr. I. 40269,* ×4·5. 6, eye and vincular notches, ventro-lateral view, Gr. I. 40270,* ×5. 7, right eye, Gr. I. 40279,† ×10. 8, doublure (cf. text-fig. 3) (DB), Gr. I. 40262,* ×5. 9, almost complete specimen in lateral view (DB), Gr. I. 40281,† ×4.

* Latex replica of external mould. † Internal mould.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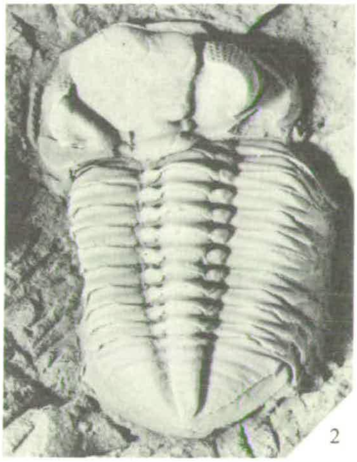
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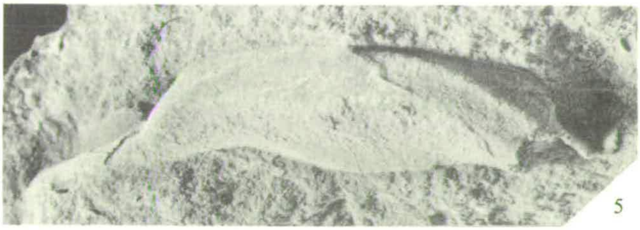
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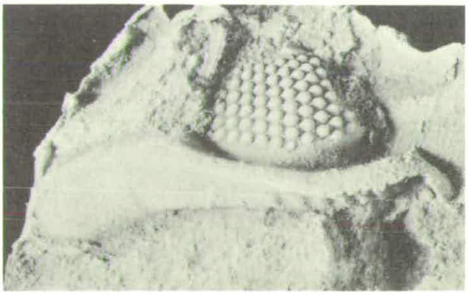
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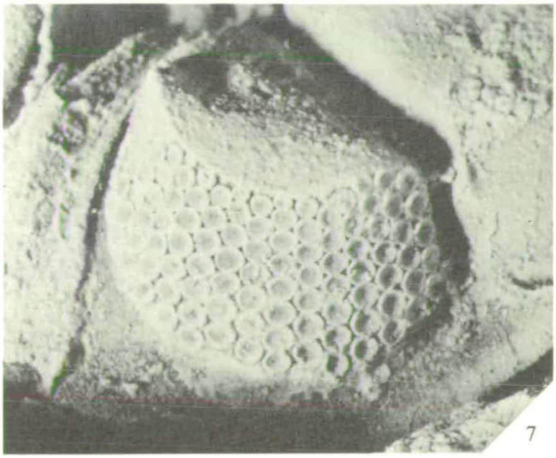
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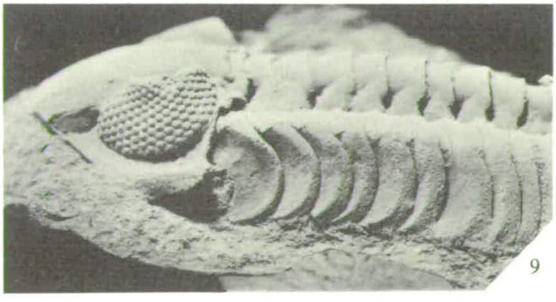
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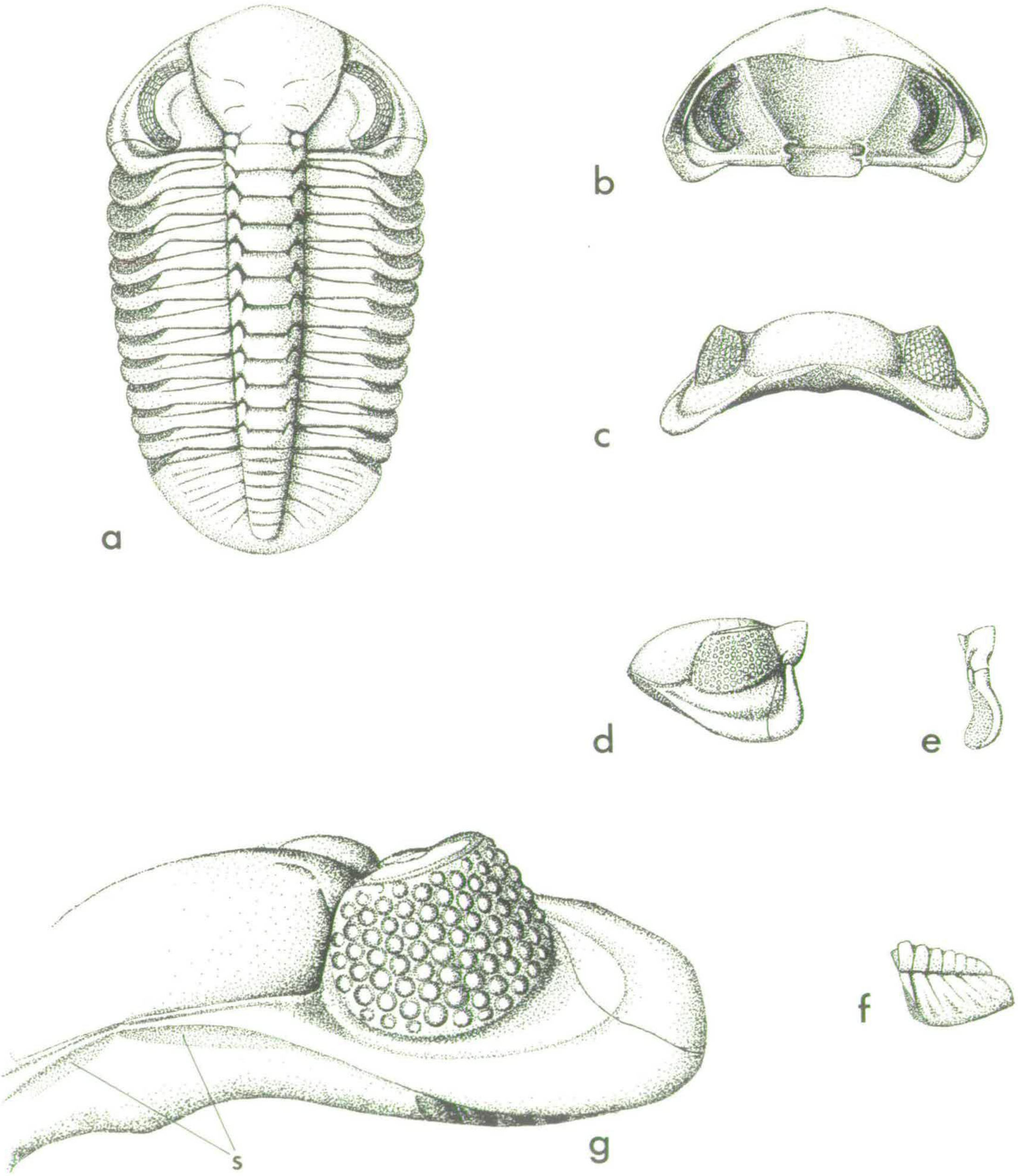
CLARKSON, ELDREDGE and HENRY, *Acernaspis*



TEXT-FIG. 2. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Reconstructions of *a*, whole animal in dorsal view. *b–d*, cephalon in ventral, frontal, and lateral view. *e*, thoracic segment showing facet in lateral view. *f*, pygidium in lateral view. *g*, cephalon in oblique lateral view, showing subfrontal depressions (s). *a–f*, ×3·5; *g*, ×8·5.

Furrow 2p nearly transverse with the outer tip recurved; 3p in two distinct unjoined parts, inner part directed slightly forwards, outer part at 45° and not reaching the axial furrow. Intercalating ring not sharply demarcated anteromedially, but confluent with composite glabellar lobes. Anterior lobe half the total length of the glabella. Auxiliary glabellar impressions form a circular pattern, some are quite deeply impressed (text-fig. 5) (cf. *Acernaspis* figured by Eldredge 1971, text-fig. 2J).

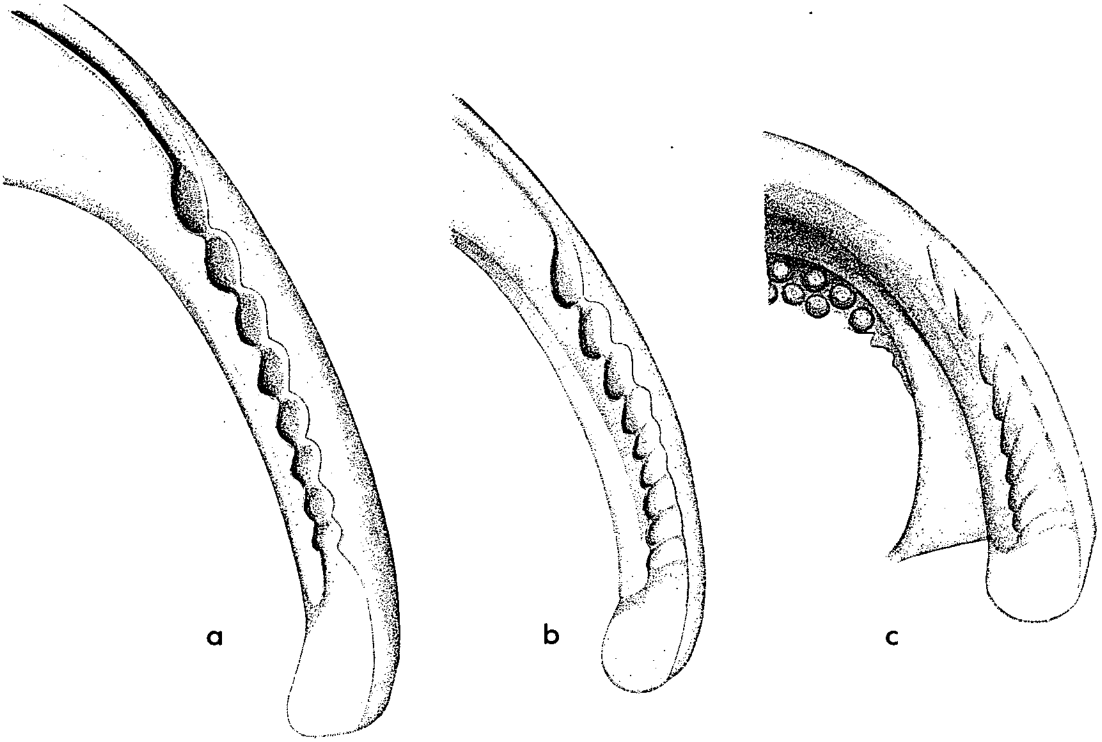
Occipital furrow straight and shallow medially, more deeply impressed laterally, at the apodemal pit, occipital ring very large (as wide as the posterior part of the glabella including lateral nodes) and with prominent lateral lobes directed forwards and outwards at 45°. Genal region with a definite lateral border which is widest postero-laterally, and delimited by a broad, shallow, lateral border furrow, less distinct below the eye, but becoming more incised anteriorly and nearly reaching the glabella. Posterior border furrow straight and deeply incised. Genal angles truncated, projecting somewhat posteriorly and subangular.

Palpebral lobes large, slightly inflated, and with a faint external rim extending from furrow 3p to the occipital furrow. Palpebral furrow usually distinct though may be rather vaguely defined in the central part. Palpebral area quite broad, triangular, mainly flat or slightly inflated. Eyes very large, nearly half the total height of the cephalon, the posterior edge slightly further from the midline than the anterior (Pl. 18, fig. 7; text-fig. 1*g*).

Lenses projecting beyond the sclera, not sunken, arranged in nineteen dorsoventral files (commonly eighteen in juveniles but rarely in adults) with a general lens formula:

567 787 877 765 543 2. Maximum per file eight. Total 116.

In some specimens the lowermost lenses are very small and elliptical. Eye socle very reduced. Facial suture apparently functional in holaspids, the anterior branch cutting antero-lateral corners of the anterior face of the glabella, meeting at a distinct point on the midline. Posterior branch directed at first anteriorly, then curving outwards and backwards again to reach the border opposite the posterior edge of the eye. The suture appears again on the postero-lateral part of the doublure making a posteriorly convex, symmetrical U-shaped lobe behind the course of the dorsal part of the suture (text-fig. 3). Cephalic doublure nearly a third the length of the glabella sagittally its rear margin convex posteriorly, the central part convex downwards. Vincular furrow marked anteriorly only as a pair of elongate, contiguous, and shallow subfrontal depressions on either side of the midline (text-fig. 1*b*, *g* (marked 's')). Where the depressions meet, there is a tiny forwardly projecting point. Subfrontal depressions separated from the notched lateral vincular furrow which extends from below the anterior edge of the eye to nearly below its posterior edge. The inner lamella of the lateral doublure is less steeply inclined in lateral aspect than the outer lamella which forms the postero-lateral margin of the cephalon. Posteriorly, the inner lamella ends abruptly below the dorsal facial suture in front of the U-shaped lobe; the outer lamella extends further back (text-fig. 3). The most anterior notches are less deeply impressed than those which lie posteriorly; nine notches are evident in all, and are arranged radially from a point posterior to the U-shaped lobe defined by the doublural suture. The doublure turns abruptly at the



TEXT-FIG. 3. The lateral part of the ventral doublure, showing vincular structures and coaptative morphology in *Acernaspis* (*Acernaspis*) and *A.* (*Eskaspis*). *a*, *A.* (*Acernaspis*) *elliptifrons* (Esmark), from the Newlands Formation (Idwian), Girvan, Ayrshire. BM It 9121. *b*, *A.* (*Eskaspis*) *woodburnensis* n. sp. from Wood Burn Formation (lowermost Telychian), Lauchlan Burn, Girvan, Ayrshire. IGS 5777. *c*, *A.* (*Eskaspis*) *sufferta* (Lamont), Wether Law Linn Formation (upper Telychian), Pentland Hills, near Edinburgh. Gr. I. 40262 (see Pl. 18, fig. 8), all × 14. All these illustrations are camera-lucida drawings made from latex replicas of external moulds.

genal angle and tails off to terminate just behind the posterior edge of the eye. Occipital and 1p apodemes distinct on ventral surface of the cephalon.

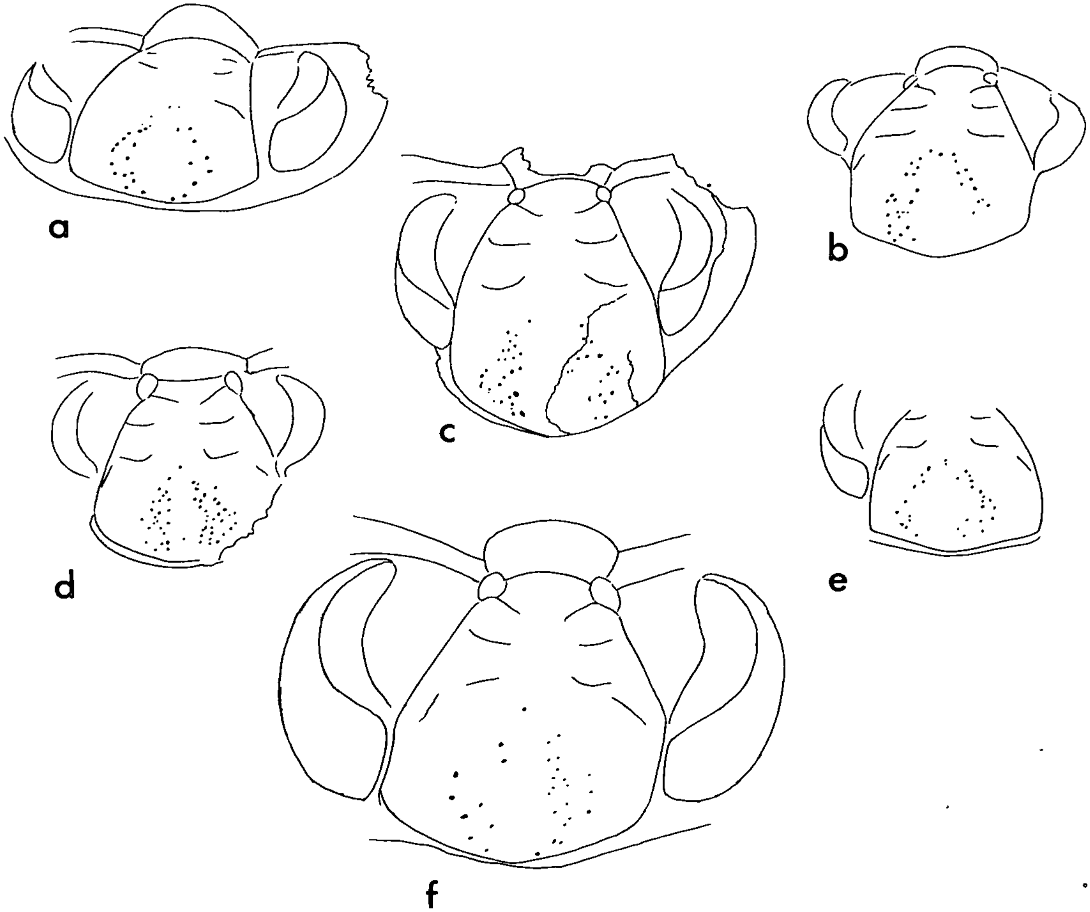
Thorax of eleven segments tapering backwards slightly, having quite strongly arched rings. Axis is quarter the total width. Each axial ring is indented anteriorly by deep paired incisions, which together with shallower posterior incisions placed closer to the axial furrows delimit chevron-shaped axial lobes, set further forward than the axial part of the ring but are not swollen as nodes (text-fig. 2*a*, *e*). Posterior border of each axial ring high and sharp. A distinct furrow divides the articulating half-ring from the axial ring.

Pleural regions flat but strongly bent down distally. Pleural furrows straight or slightly curving, narrow, of moderate depth, and extend as far as the articulating facets. Facets very pronounced anteriorly while the pleural ribs are very narrow and curved, but diminishing in size and curvature posteriorly. The rear edge of the flat top of each pleuron has a narrow flange articulating with a corresponding anterior groove on the next segment.

Pygidium with rounded or almost imperceptibly pointed margin with nine to ten rings diminishing in size posteriorly (text-fig. 2*a*, *f*). The last two axial rings are indistinct, the first three or four have a pseudo-articulating half-ring. There are four or five pleural furrows whose obliquity increases backwards, the first being quite deep, the others increasingly shallow, interpleural furrows weakly impressed, and disjunct. All pleural and interpleural furrows fade out some distance before the pygidial margin, leaving a broad smooth border zone.

Pygidial doublure broad, with two lateral parts forming a small notch in the sagittal line and shaped to fit the two vincular depressions on the cephalon.

All parts of the exoskeleton are covered with dense microgranular sculpture except for the subocular groove which is smooth. On the doublure, glabella, and axial rings and pleural ribs this sculpture is especially dense, though it is sparser on the flat tops of the pleurae.



TEXT-FIG. 4. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Camera-lucida drawings showing auxiliary impression patterns on the anterior glabellar lobe. All ×5. *a*, Gr. I. 40271; *b*, Gr. I. 40263; *c*, Gr. I. 40281; *d*, Gr. I. 40265; *e*, Gr. I. 40264; *f*, Gr. I. 40257.

Acernaspis (*Eskaspis*) *woodburnensis*, n. sp.

Plate 19, figs. 9, 11-13; text-fig. 5*a*, *b*

1899 *Phacops stokesi* (M.-Edw.). Peach and Horne, p. 538.
1906 *Phacops elegans* Sars and Boeck. Reed, p. 155.

Locus typicus. Lauchlan Burn (Bargany Pond Burn, Girvan, Ayrshire).

Stratum typicum (Wood Burn Formation, lowermost Telychian) (Cocks and Toghill 1973, p. 225)

Diagnosis. Axial furrows straight, diverging forwards to a point in front of the eye. Eyes fairly large, not particularly high, posterior edge more distant than the anterior edge from the sagittal line. Lenses distributed in sixteen files as follows:

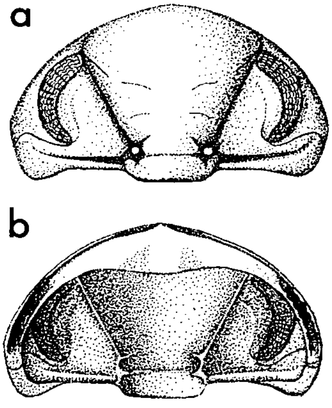
566 677 776 766 534 3. Maximum per file seven. Total 90.

Posterior section of doublure has ?nine vincular notches on each side connected by a shallow vincular furrow to the subfrontal depressions.

Types. Holotype IGS 5777. Paratypes IGS 5778-5779, 5780-5781 (parts and counterparts).

Other material. Ten specimens in IGS collections.

Remarks. A. (*E.*) *woodburnensis* is the oldest member of this subgenus known at present but is stratigraphically younger than the middle Llandovery *A.* (*A.*) *elliptifrons* of the Newlands Formation. It is particularly interesting that here a



TEXT-FIG. 5. *Acernaspis* (*Eskaspis*) *woodburnensis*, n. sp. *a*, *b*, cephalon reconstructed in dorsal and ventral view, ×2·25.

EXPLANATION OF PLATE 19

Figs. 1-7, 10. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Wether Law Linn Formation (Telychian), North Esk Inlier, Pentland Hills. 1, cephalon with auxiliary impression patterns, Gr. I. 40257,* ×3·5. 2, cephalon and part thorax, oblique anterolateral view, Gr. I. 40243,* ×3·75. 3, almost complete specimen, oblique antero-lateral view, Gr. I. 40281,† ×5·25. 4, pygidium, Gr. I. 40260,* ×6. 5, almost complete enrolled specimen, Gr. I. 40280,† ×2·75. 6, genal point, visible only on internal mould, Gr. I. 44093,† ×15. 7, small cephalon, Gr. I. 40261,† ×4. 8, almost complete specimen, Gr. I. 40275,* ×3·75. 10, doublure of small specimen, Gr. I. 44094,† ×5·5.

Figs. 9, 11-13. *A.* (*Eskaspis*) *woodburnensis*, n. sp. Wood Burn Formation (lowermost Telychian). 'Bargany Pond Burn' = Lauchlan Burn, Maxwellton Hill, Girvan. 9, ventral view of holotype cephalon showing doublure with shallow furrow connecting vincular notches to subfrontal depressions, IGS 5777, ×3·5. 11, holotype, IGS 5777,† ×2·5. 12, 13, anterior and dorsal views of complete specimen retaining its cuticle though altered and exfoliated in places, IGS 5780, ×2.

* Latex replica of external mould. † Internal mould.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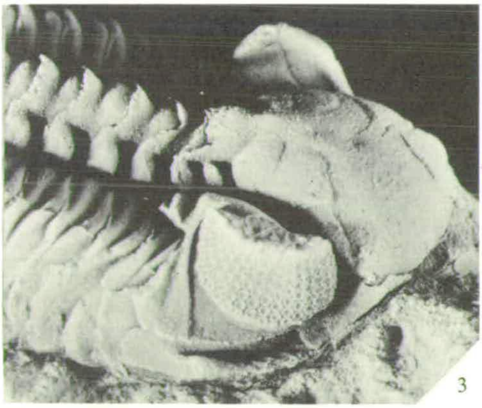
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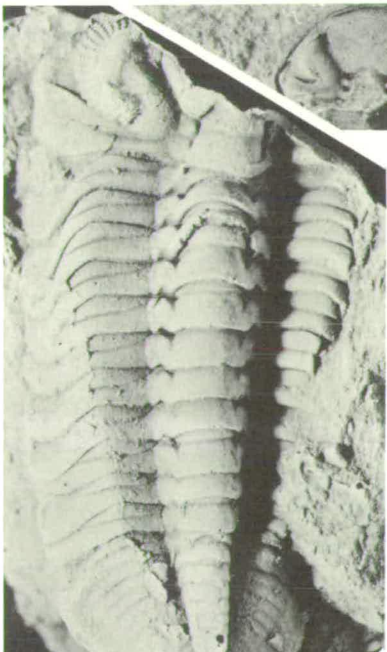
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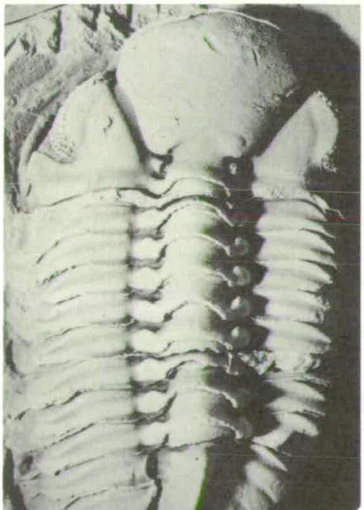
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CLARKSON, ELDREDGE and HENRY, *Acernaspis* shallow vincular furrow is present, though absent in the otherwise quite similar *A.* (*E.*) *sufferta.*

Dimensions. Holotype: total length (sag.) 28·0 mm, cephalic length (sag.) 10·0 mm, width 18·5 mm. Range in cephalic length 9·5–11·0 mm, width 17·0–20·0 mm.

Superfamily DALMANITACEA Vogdes, 1890
Family PTERYGOMETOPIDAE Reed, 1905
Genus PODOWRINELLA gen. nov.

Type species. Podowrinella straitonensis (Lamont, 1965) by original designation and monotypy, from the Knockgardner Formation (?Wenlock) of the Blair-Straiton district near Girvan, Ayrshire, and the Ree Burn Formation (?Telychian, upper Llandovery), Hagshaw Hills, and the Deerhope Formation (Telychian), North Esk Inlier, Pentland Hills.

Etymology. From the Podowrin Burn in the Hagshaw Hills where the Ree Burn Formation outcrops and where fossils are common in the turbidites.

Diagnosis. Small Phacopina combining features of both phacopid and pterygometopid organization. Cephalon roughly triangular but with truncated genal angles. Glabella pear-shaped with furrow 1p connected to 3p as in Pterygometopidae but 3p in two distinct parts as in Phacopidae, and confluent with axial furrows. Eyes with about eighteen files with up to seven lenses each, about 100 lenses altogether. Cephalic doublure traversed by deep, broad coaptative grooves, continuous laterally, becoming dorso-medial just before they meet. Thorax with axial nodes and strongly downturned outer parts of the pleurae. Pygidium somewhat triangular with a rounded or occasionally slightly pointed margin.

Podowrinella straitonensis (Lamont, 1965)

Plate 20, figs. 1–14; text-fig. 6*a*–*h*

1962 *Phacops* sp. nov. Rolfe, p. 252.
1965 *Phacops straitonensis* sp. nov. Lamont, p. 39, pl. V, fig. 5.
1973 *Phacops straitonensis.* Rolfe, p. 109.

EXPLANATION OF PLATE 20

Podowrinella straitonensis (Lamont). 1, neotype cranidium, figured by Lamont (1965, pl. V, fig. 5), almost undistorted. Ree Burn Formation, Hagshaw Hills (Rolfe's loc. 31), BU 1900,* ×6. 2, cranidium in W-mode deformation. Top of Deerhope Formation, Deerhope Burn, North Esk Inlier, Pentland Hills (locality B), Gr. I. 40340,* ×5·5. 3, thoracic segment in lateral view. Pentland Hills (loc. B), Gr. I. 40348,† ×3·5. 4, 5, anterolateral and ventrolateral view of detached librigena showing vincular furrows and eye, small quarry in the Ree Burn Formation, nearly opposite junction of Shiel Burn with Monk's Water, Hagshaw Hills (loc. A), RSM 1975-43-2,† ×6·5. 6, ventral surface showing vincular furrows, RSM 1975-43-3,† ×6. 7, undistorted cranidium. Knockgardner Formation, Knockgardner, IGS M 13219,† ×3·5. 8, cranidium. Pentland Hills (loc. B), Gr. I. 40310,* ×5·55. 9, lateral view of compressed pygidium. Pentland Hills (loc. B), Gr. I. 40345,* ×7·5. 10, ventral surface W-mode deformation). Pentland Hills (loc. B), Gr. I. 40358,† ×6. 11, left eye and subjacent librigena. Hagshaw Hills (loc. A), RSM 1975-43-4,* ×7·5. 12, pygidium. Hagshaw Hills (loc. A), RSM 1975-43-5, ×5·5. 13, pygidium (L-mode deformation). Pentland Hills (loc. B), Gr. I. 40349,* ×5. 14, pygidium showing accessory half-ring on segment 1. Pentland Hills (loc. B), Gr. I. 40307,* ×6·5.

* Latex replica of external mould. † Internal mould.

PLATE 20


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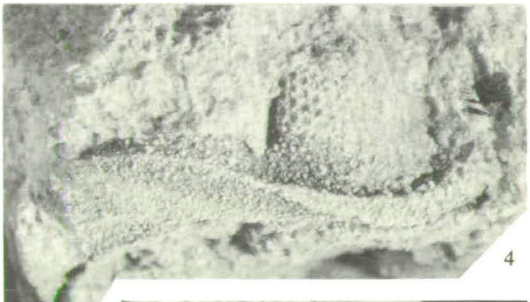
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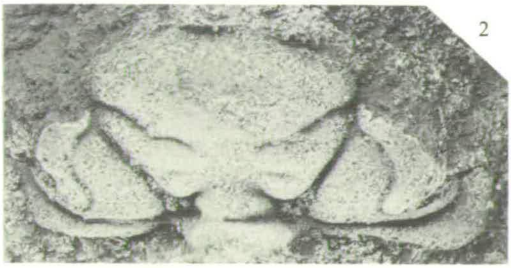
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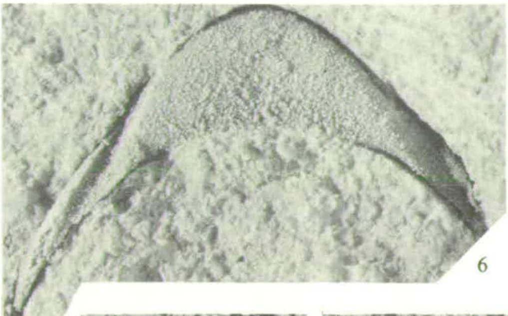
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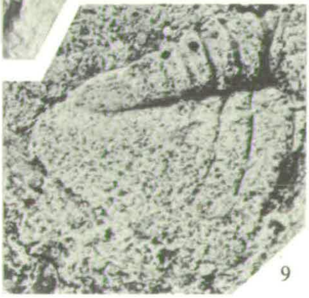
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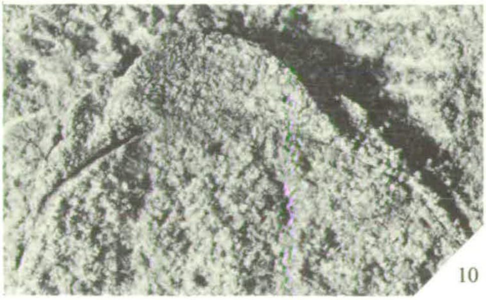
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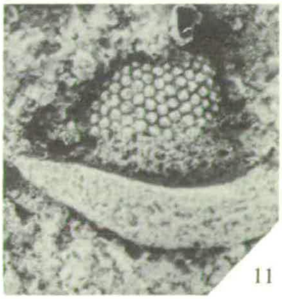
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CLARKSON, ELDREDGE and HENRY, *Podowrinella*

Material

(*a*) Hagshaw Hills.

(1) Twenty-five specimens from the Rolfe Collection, University of Birmingham, including BU 1900a, b figured by Lamont (1965, pl. V, fig. 5), which is herein designated as neotype, since the unfigured holotype from Knockgardner is now lost (Lamont pers. comm.).

Neotype. BU 1900a, b (from Rolfe's locality 31/48 in unpublished thesis; University of Birmingham 1960).

Other material. Thirty other specimens in the collection of the Department of Geological Sciences, University of Birmingham.

(2) One hundred specimens from the Ritchie Collection, Royal Scottish Museum, collected from a small quarry in the Ree Burn Formation on the east bank of the Monk's Water, opposite the mouth of the Shiel Burn, Hagshaw Hills. These include the paratypes RSM 1975-43-1, RSM 1975-43-2 (Pl. 20, figs. 4, 5), RSM 1975-43-3 (Pl. 20, fig. 6), RSM 1975-43-4 (Pl. 20, fig. 11), RSM 1975-43-5 (Pl. 20, fig. 12).

Also twenty-five RSM specimens from the foot of the Podowrin Burn, east of Monk's Water, Hagshaw Hills.

In addition, fifty-five other specimens from the same localities in the Grant Institute Collections (Gr. I.).

(*b*) North Esk Inlier. Specimens from Tipper and Clarkson Collections. Top of Deerhope Formation, Deerhope Burn. Paratypes Gr. I. 40340, Pl. 20, fig. 2; Gr. I. 40348, Pl. 20, fig. 3; Gr. I. 40310, Pl. 20, fig. 8; Gr. I. 40348, Pl. 20, fig. 9; Gr. I. 40358, Pl. 20, fig. 10; Gr. I. 40349, Pl. 20, fig. 13; Gr. I. 40307, Pl. 20, fig. 14.

(*c*) Knockgardner. Blair-Straiton Inlier, east of Girvan. Maconochie Collection. IGS M 13219 (Pl. 20, fig. 7) and twenty-five other IGS specimens. Also thirty specimens in Grant Institute of Geology.

Range. Telychian (North Esk, Hagshaws)—?lower Wenlock (Knockgardner).

Remarks. The material available from Knockgardner and the Hagshaw Hills is all preserved as disarticulated fragments collected from the base of turbidite flows. Specimens are found in all orientations and most individuals have suffered some distortion. The notable variation in width and length between specimens resembling the L and W forms of Henningsmoen (1960, p. 207) and Sadler (1974, pp. 81, 85) is attributed to stress due to crushing pressure of the mass of unconsolidated turbidite after deposition. Some sheared specimens occur also. The reconstructions were made from the less distorted specimens.

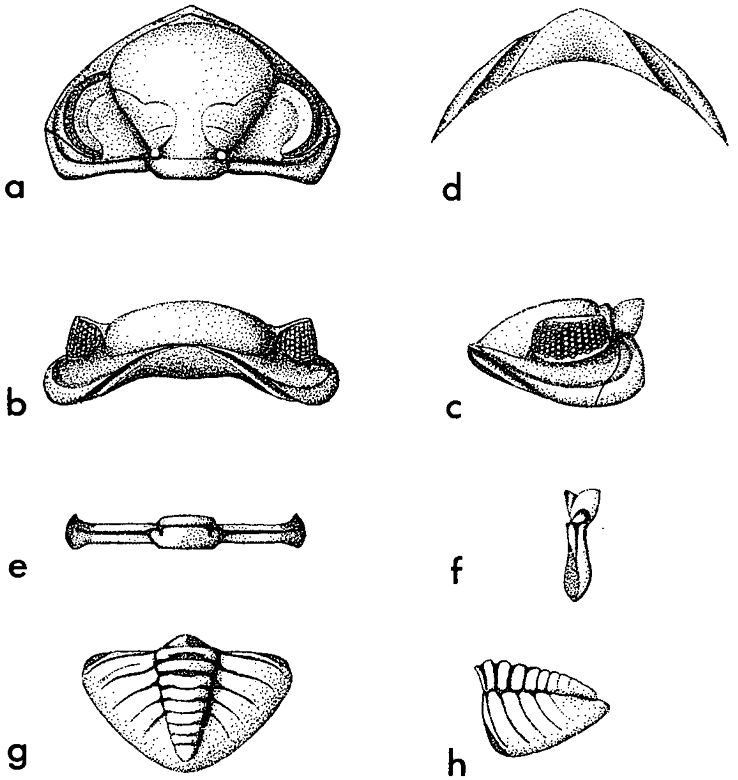
Dimensions. Holotype: cephalic length (sag.) 5 mm, width 10 mm. Range in cephalic length 4–6 mm, width 8–12 mm.

Description. Small Phacopidae with roughly triangular cephalic outline (in dorsal view), modified by truncated genal angles. Cephalon widest at distal librigenal/fixigenal junction. In lateral view (text-fig. 6*c*) (in standard orientation), glabella depressed anteriorly, sloping regularly postero-dorsally, with central region of glabella extending above level of palpebral lobes. Large anterior arch developed in frontal view.

Axial furrows moderately deeply implaced, diverging at an angle of approximately 65° then abruptly reflected directly in front of the anterior edge of the palpebral lobe, and curving smoothly around anterior glabellar lobe, becoming confluent with anterior and lateral cephalic border furrows.

Glabella pear-shaped, with anterior, 3p, 2p, and medial portion of 1p lobes united to form composite glabellar lobe (text-fig. 6*a*). Anterior glabellar lobe subovate, continuous with medial portion of remainder of glabella. Anterior margin of anterior glabellar lobe rounded, bounded by furrow bearing anterior ramus of facial suture antero-laterally. Facial suture continuous with anterior border furrow medially; anterior border, border furrow, and facial suture thus meeting in a distinct point medially, delimiting a small, triangular pre-glabellar field proximal to facial suture. Anterior border thin, though distinct in front of this field; concentric with facial suture, but disappearing marginally.

Glabellar furrow 3p in two parts, with sharp bend between distal and proximal branches; branches generally connected at bend by shallow furrow, occasionally wholly disconnected on internal and external moulds. Distal branch of 3p furrow deepest proximally, confluent with axial furrow just opposite anterior margin of visual surface, slightly convex anteriorly, running at an angle of approximately 55° from the midline. Proximal branch of 3p furrow comma-shaped, with proximal terminus slightly posterior to distal terminus. Proximal terminus continuous with a broad, shallow, variably developed longitudinal glabellar furrow running posteriorly and communicating smoothly with 1p glabellar furrows. Glabellar furrow 2p short, comma-shaped (convex anteriorly) with distal and proximal tips in transverse line, and not communicating with axial furrow distally, but confluent with



TEXT-FIG. 6. *Podowrinella straitonensis* (Lamont). *a–c*, reconstructions of cephalon in *a*, dorsal, *b*, frontal, *c*, lateral aspects. *d*, cephalic doublure in ventral view. *e*, *f*, thoracic segment in dorsal and lateral view. *g*, *h*, pygidium in dorsal and lateral view. All ×4.

longitudinal glabellar furrow medially. Glabellar furrow 1p deeply incised distally. confluent with axial furrow, and recurved antero-proximally. Glabellar furrow 1p apparently continuous medially as broad, shallow furrow, delineating an intercalating ring.

Glabellar lobe 3p hypertrophic distally; ratio of glabellar lobe lengths along axial furrow roughly: 4·7:2:1 for 3p:2p; 1p. 2p lobe small, ovate, 1p lobe longest medially, reduced to nodes distally, and depressed below concordant surface of anterior glabellar region and occipital ring. Occipital furrow shallow, straight; occipital ring of approximately equal length (sag.) throughout.

Posterior border furrow shallow, communicating with axial furrow, running nearly transversely, distally becoming more shallow and recurved antero-distally, confluent with lateral border furrow of librigena. Posterior border distinct, roughly transverse proximally, becoming thickened distally near genal margin, thereby causing slight deflection to posterior margin of cephalon. Posterior border sharply reflected antero-distally, forming a bluntly pointed genal angle of approximately 100°. Lateral cephalic border reflexed antero-proximally at point where crossed by posterior ramus of facial suture. Lateral border continuous with anterior border; anterior border becoming progressively thinner approaching midline.

Lateral border of librigena steeply inclined, capped by sharp ridge; lateral border furrow broad, smoothly confluent with concave distal portion of librigena (text-fig. 6*c*). Librigena becoming steeply inclined proximally, merging with eye socle (not distinctly defined because of lack of ornamental features due to poor preservation). Visual surface nearly vertical, with eighteen d-v files with up to seven lenses per file, about 100 lenses in all. Eye moderately long, not reaching posterior border furrow. Palpebral lobe quite narrow, inflated above palpebral area and set off from it by a sharply implaced palpebral furrow. Palpebral area relatively flat, sloping postero-proximally and smoothly confluent with fixigenal area posterior to eye.

Cephalic doublure produced anteriorly into flat trapezoidal spatulate process, inclined at an angle of approximately 25° (in lateral view) and visible in frontal view. Spatulate process bounded distally by deep, broad grooves traversing doublure, and inclined antero-proximally at an exsagittal angle of approximately 35°. Grooves continuous laterally, becoming dorsal where converging at midline (text-fig. 6*b*, *d*). Anterior-most medial portion of cephalon a thin ridge where anterior border, vincular groove, and spatulate process coterminate. Cephalic doublure developed as thin ridge postero-distally to vincular grooves; inner wall nearly vertical. Hypostoma unknown.

Auxiliary impression pattern and details of cephalic ornament unknown; cephalon apparently smooth (based on study of external moulds).

Thorax incompletely known; most of the thoracic segments examined (probably the anterior ones) with the axis one-quarter the width of the whole, axial nodes set off by short, deep anterior furrows (text-fig. 6*e*, *f*). Pleural furrows relatively shallow, of moderate depth, and straight. Inner part of pleura flat, outer third sharply turned down; pleural tips pointed. Pleural facets present but not very distinct.

Pygidium (text-fig. 6*g*, *h*) equilaterally triangular with, however, its posterior apex truncated, having approximately eight axial rings and terminal piece; two or more accessory half-rings present. Axis not reaching posterior pygidial margin, acutely rounded posteriorly. At least four pairs of pleurae present; inter-pleural furrows obscure. Pleural furrows becoming fainter posteriorly, and nowhere reaching pygidial border. Most specimens have a rounded pygidium, but in some examples the posterior border is slightly pointed, especially in those from the Pentland Hills.

Remarks. This genus cannot be readily confused with any other taxon known to us. To clarify its diagnosis and to aid in recognition of related forms we briefly discuss which features are peculiar to the taxon alone, and which are 'phacopid-like' and 'pterygometopid-like'.

There is no question that *Podowrinella* is, in the great majority of its features, pterygometopid in aspect. In fact, *Podowrinella* is very similar indeed to the Ordovician pterygometopids *Calyptaulax* and *Eomonarachus*, in particular to those species of *Calyptaulax* from Europe which, as Shaw (1974, p. 42) has noted, have a 'noticeable bend' along glabellar furrow 3p. Pterygometopid-like features of *Podowrinella* include over-all conformation of cephalon; possession of a distinct lateral and anterior border (reduced anteriorly in *Podowrinella*); glabellar segmentation, generally, including size and shape of glabellar lobes and presence of longitudinal glabellar furrows; narrow palpebral lobes; anterior branch of facial suture meeting in a distinct point; presence of a spatulate medial projection of the cephalic doublure; and a somewhat triangular pygidium, pointed in some examples.

Podowrinella is phacopid-like in the following features: presence of a 3p glabellar furrow divided into two parts, discontinuous in some specimens of *P. straitonensis*, with the proximal moiety nearly transversely oriented (the distal ramus remains pterygometopid-like in conformation); a smoothly rounded anterior glabellar margin; truncated genal angles, without genal spines; nearly complete loss of inter-pleural furrows, and sharp reduction in the number of pleural furrows, on the pygidium. We hasten to add that some species of *Calyptaulax*, particularly *C. callicephala*, are very much like *Podowrinella* in having a smoothly rounded anterior glabellar margin and truncated genal angles; supposed 'phacopid-like' characters. Finally, *Podowrinella* appears to be rather unique in the coaptative doublure morphology, though some pterygometopid species, again, particularly *C. callicephala*, are somewhat similar in possessing a vincular furrow traversing the doublure and converging antero-dorsally at the midline.

Though we have been unable to reach a final agreement on the taxonomic position of *Podowrinella*, the unusual combination of characters which it displays does reinforce Eldredge's (1971) suggestions as to a close relationship between Phacopidae and Pterygometopidae. There are some interesting resemblances between *A.* (*Eskaspis*) and *Podowrinella*, in terms of glabellar furrowing, eye size and position, and genal angles. Sometimes specimens of *A.* (*E.*) *sufferta* show traces of extended glabellar furrows, so that 1p and 3p are faintly connected (e.g. the slightly crushed specimen in Pl. 19, fig. 1). There seem to be possible grounds for restructuring the current classification of Phacopina and the curious morphology of *Podowrinella* could be critical.

Coaptative structures in A. (Acernaspis), A. (Eskaspis), *and* Podowrinella: *some remarks*

Within trilobites of the Phacopina and other suborders there have been described a substantial array of structures on the ventral doublure of the cephalon which interlock during enrolment with mirror-image structures on the thorax and the pygidium. Examples have been figured by Campbell (1967), and others have been discussed in detail by Henry and Nion (1970), Clarkson and Henry (1973), and Henry and Clarkson (1975). These have arisen independently in a number of trilobite groups and have been defined (Hupé 1953; Clarkson and Henry 1973) as coaptative mechanisms. They have, in our estimation, much potential value in taxonomy, as well as their intrinsic interest from the functional and evolutionary point of view, but before this can be effectively realized, it is essential to illustrate and document the various types present in different trilobite groups.

This study gives information of the nature of coaptative mechanisms of *A.* (*Acernaspis*), *A.* (*Eskaspis*), and *Podowrinella.* In *A.* (*Eskaspis*) (text-fig. 3*c*) there are nine vincular notches on each side which receive the tips of the thoracic pleurae. Though no complete enrolled specimens have been found which might enable further details of the mechanism to be elucidated, it appears that these notches are for the reception of the last nine pleural tips; the first two pleurae are shorter and have wider facets. During enrolment, they probably locked in against the end of the inner ridge of the doublure (text-fig. 3) close together with the tip of the third pleuron. The more posterior pleurae were fitted into depressions which became progressively more spaced out towards the anterior of the doublure, whilst becoming less deeply impressed. By contrast with *A.* (*Acernaspis*) which has a well-marked semicircular vincular furrow connecting the two lateral sets of vincular notches (text-fig. 3*a*), *A.* (*E.*) *woodburnensis* has only a very shallow furrow, connecting with the two subfrontal depressions, whilst *A.* (*E.*) *sufferta* only has the two depressions, and no furrow at all. In both species of *A.* (*Eskaspis*) two slightly swollen areas on the pygidial doublure fit into the subfrontal depressions; otherwise the pygidium comes to rest freely against the flat (or only slightly indented in the case of *A.* (*E.*) *woodburnensis* surface of the anterior part of the cephalic doublure. This difference between the coaptative morphology of the doublure of *A.* (*Acernaspis*) and *A.* (*Eskaspis*) is coupled with the fact that in the former subgenus the surfaces of the parallel vincular ridges lie in the same plane, whereas in the latter they are somewhat oblique to one another, so that the inner ridge as seen in lateral profile having the higher angle to the horizontal; there are other differences also as previously mentioned (p. 125). It is not certain whether the morphological sequence illustrated in text-fig. 3, and previously referred to is a true evolutionary sequence. Had the specimens all been collected from a single vertical section it would be almost unequivocal. Even so, the morphology, confined distribution, and stratigraphically sequential changes suggest a definitive evolution towards the grade of organization in *A.* (*E.*) *sufferta* within a fairly localized area.

Podowrinella has no separate notches for the reception of individual pleural tips, but only a pair of elongated furrows, deepening posteriorly and becoming slightly twisted in the process. With this type of structure the pleural tips come to rest in the groove, as does the doublure of the pygidium, and presumably the triangular point at the extreme anterior of the cephalon forms a seal with the similarly angular sagittal edge of the said pygidial doublure. Such coaptative morphology resembles that of some Pterygometopidae though in a more extreme form.

The range in morphology of coaptative structures amongst Phacopina is considerable; compare, for example, the ventral morphology of the doublure in *Kloucekia*, *Morgatia*, and *Crozonaspis* species (Henry and Nion 1970; Clarkson and Henry 1973), with that of the trilobites discussed in this paper. The value of these in taxonomy is probably very great, but there is, as present, a need for detailed study covering a wider spectrum than is presently known, and only then will their actual value be able to be established.

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Finally, Dr. Archie Lamont of Carlops, Peeblesshire, who encouraged us to work on these trilobites, corresponded with us throughout, and helped with many queries.

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THE VISUAL SYSTEM OF TRILOBITES

by E. N. K. CLARKSON

(*Twenty-first Annual Address, delivered 8 March 1978*)

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

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

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

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

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

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

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

[Palaeontology, Vol. 22, Part 1, 1979, pp. 1–22, pl. 1.]

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

THE COMPOUND EYES OF INSECTS AND CRUSTACEANS

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

In each ommatidium there are three main functional regions:

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

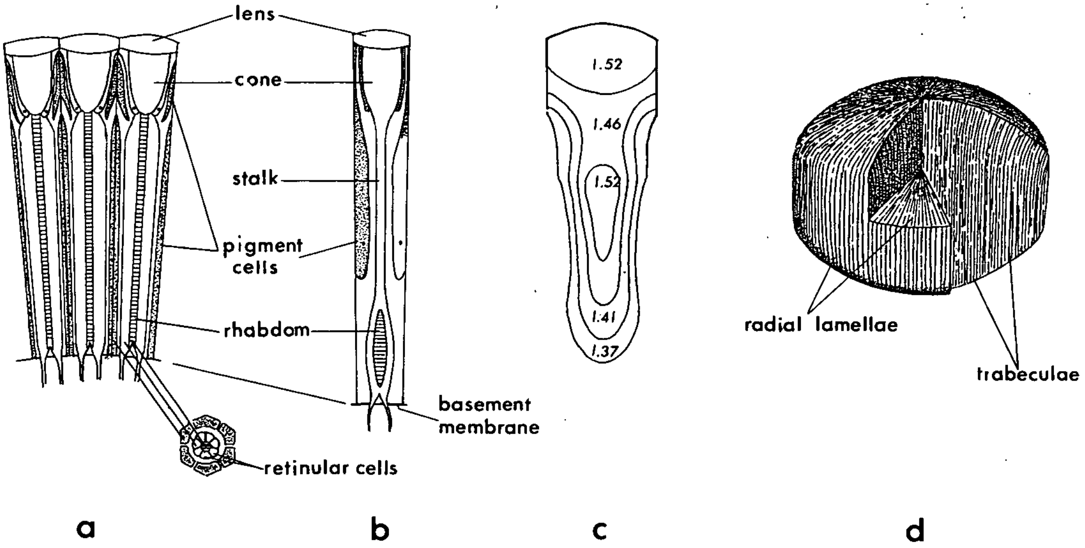
(*b*) The photoreceptive part of the ommatidium (retinula), composed of a number (usually seven or eight) of elongated retinular cells. The inward facing parts of these cells (rhabdomeres) may or may not be in direct contact, and form a closed or open cylinder, the rhabdom. These are made up of blocks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

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

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

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

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



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

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

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

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

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

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

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

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

The time and mode of origin of new eye types.

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

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

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

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

HOLOCHROAL TRILOBITE EYES

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

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

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

There is now a useful body of information on the structure and evolution of the eye in trilobites, but there are acute problems in trying to interpret this functionally in terms of modern compound eyes since the soft parts have all gone. There remains the possibility, however, of disentangling those morphological characters which result purely from geometrical constraints during growth, from those which may have been physiologically significant. Certain characters seem to be especially amenable to analysis in this way, and of these the form of the visual surface, the geometry of growth and lens packing, and the form, geometrical optics, and internal structure of the lenses are here selected for further discussion.

The visual surface

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

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

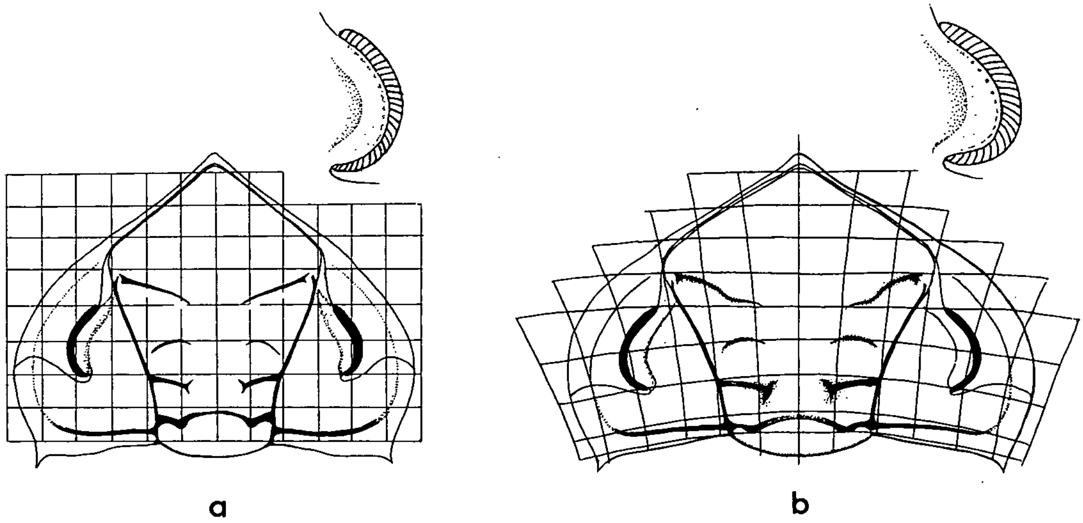
In all cases the size of the lenses is controlled by the spacing of the lens centres, which may remain constant or may alter as the visual surface grows. The new lenses can only grow as far as the proximity of neighbouring lenses will permit, and then their growth is arrested. Thus, for example, the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

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

In many modern arthropods variation in the size of the lenses is not uncommon, and may be more pronounced than in trilobites, reaching an extreme form in the remarkable bilobed eyes of euphausiids (Chun 1896; Kampa 1965). As mentioned before, some insects have different parts of the eye specialized for particular functions, especially where differential surface curvature and change in facet size allows certain parts of the visual field to be covered by a ‘fovea’, where relatively large lenses with very small interommatidial angles between them provide high resolution as well as good capacity for light gathering.

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

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



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

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

Lens structure and function

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

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

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

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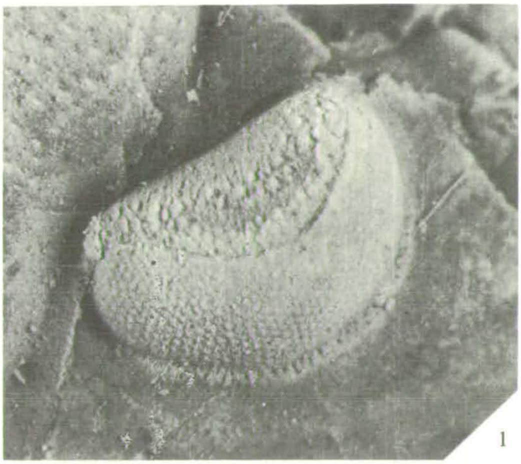
EXPLANATION OF PLATE 1

Structure of holochroal eyes.

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

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



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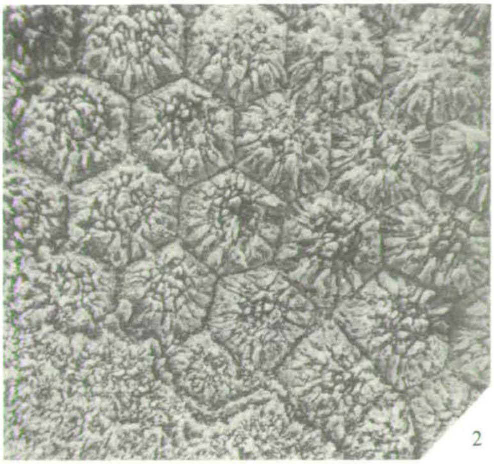

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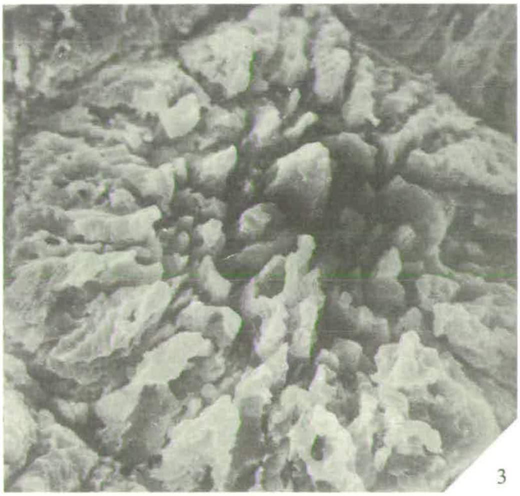

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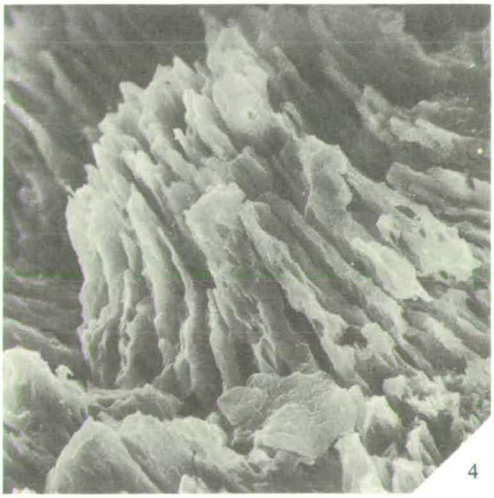

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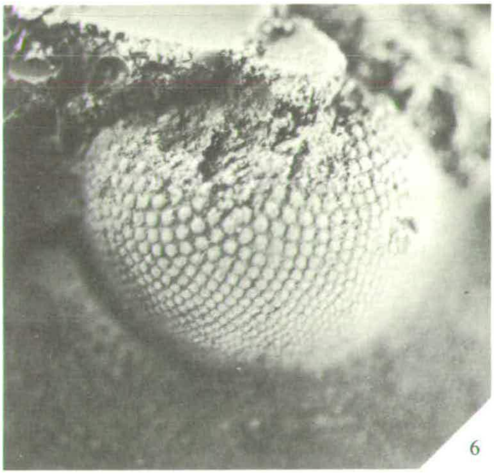


6

CLARKSON, trilobite eyes

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

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

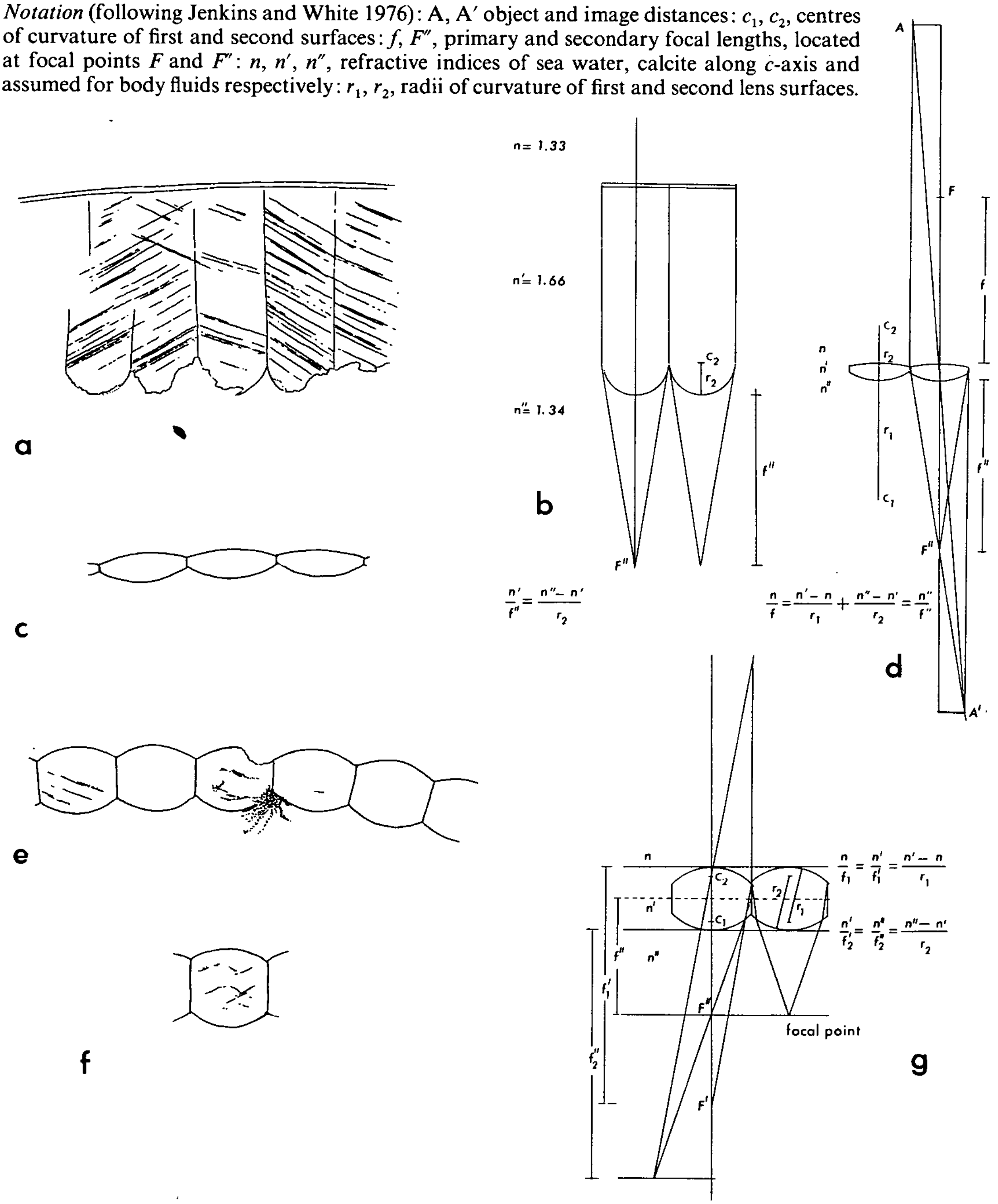
Geometrical optics of the lenses. In holochroal-eyed trilobites the thickness of the lenses is widely variable. As Lindström (1901) first showed some trilobites have very thin biconvex lenses. Those Cambrian trilobites which have been studied in detail (e.g. the olenids), all have lenses of this kind,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

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

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

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

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



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

Again in *Asaphus*, the hemispherical proximal surface of the prism compensates for the virtually flat distal surface so that light is brought to a focus at a similar relative distance below the proximal surface to that of the biconvex lens of *Ctenopyge*. The two lenses have similar f numbers ((f/D) (focal length f divided by diameter D) in this case $f/{=}2{\cdot}5$). The actual length of the lens or prism is not important for the focusing of the light; what is significant is the relative curvature of the two surfaces. Since both kinds of lenses focus light at a similar relative distance below the proximal surface, and indeed as do lenses of intermediate length and curvature, differences in axial length of the lens or prism are clearly not an optical necessity. It is more likely that this is a simple structural requirement or growth necessity. The relatively simple genetic instructions of a trilobite could not grow a thick cuticle without also growing a thick lens, but the terminations of the lenses would need to be of a particular form if the eyes were to function effectively.

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

SCHIZOCHROAL TRILOBITE EYES

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

Lens structure

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

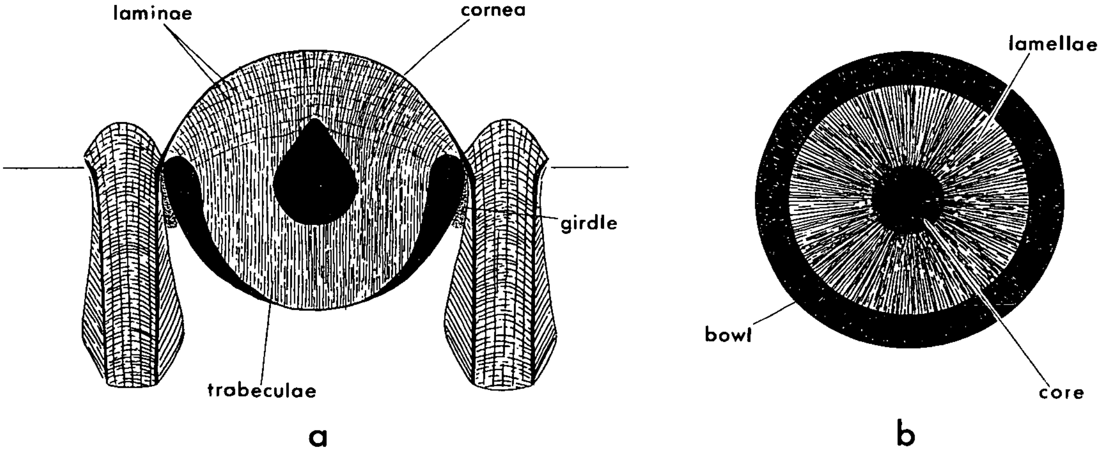
Campbell (1975) likewise used thin sections and polished surfaces and has reported the existence of intralensar bowls and other internal structures in several Phacopina. In all cases the bowl was found to be present, though in members of a dimorphic pair its precise shape varied from one dimorph to another.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

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

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

In *P. rana milleri* the highly biconvex upper unit is of quite complex, though regular, form and it is somewhat difficult to interpret, for the etching process modifies the original structure whilst accentuating the details. In sections parallel with the principal plane a radial structure is apparent, though this is less distinct in the intralensar bowl. The calcite is arranged in thin lamellae radiating out from the central core; these lamellae are particularly clear at the top of the lens which is the first part to be reformed after ecdysis. Sections cut parallel with the axis, however, show that each of the radial lamellae, like those of holochroal eyes, are made of a large number of fibrous calcitic trabeculae, running parallel with the axis in the lower part of the eye, but diverging outwards towards the outer surface of the lens, each trabecula abutting this surface near normal to it.

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



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

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

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

Optics of the lenses

Towe (1973) ground phacopid lenses parallel with the principal planes of schizochroal lenses and was able to take quite sharp photographs through the clear calcite of the remaining half lens. This simple experiment conclusively proved the existence of orientated calcite, with the *c*-axis normal to the principal plane, but could not, of course, establish the optical nature of an intact biconvex lens. Following Levi-Setti's discovery of the remarkable correspondence between the shapes of the upper units in *Dalmanitina socialis* and *Crozonaspis struvei*, and the ideal aplanatic lenses of Des Cartes (1637) and Huygens (1690), optical models were made of the same shape. The upper unit was constructed of a block of orientated calcite ($n=1{\cdot}66$), machined to shape, bowls shaped to fit and made of various plastics were tried in turn. A polysulphone bowl with refractive index ($n=1{\cdot}63$), brought parallel beams of light to a sharp focus below the lens; the result of a combination of slightly different refractive indices, separated by a Cartesian surface (Clarkson and Levi-Setti 1975).

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

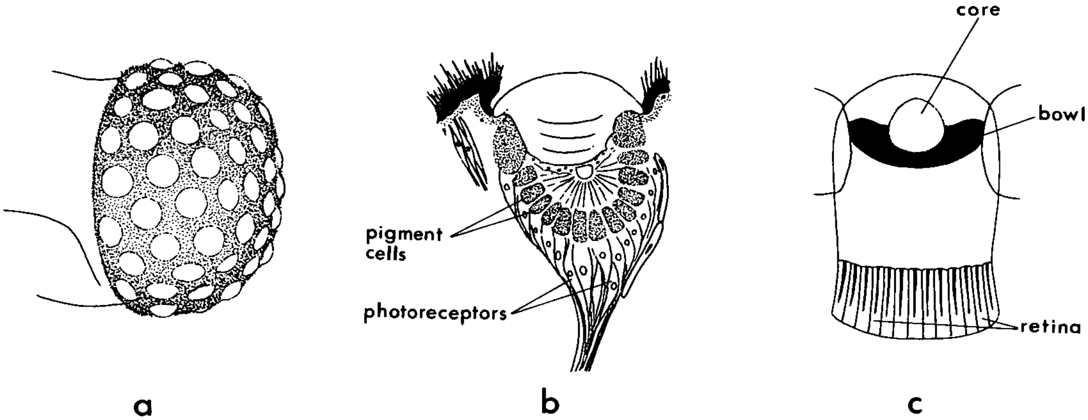
Thus although the model proposed by Clarkson and Levi-Setti appears to hold good, the complex upper unit with its core and radial structure appear to be designed for further optical refinement, particularly in minimizing the acute problems of birefringence caused by the lens being made of calcite.

The nature of the original sublensar structures

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

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

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



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

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

Origins, function, and use of the schizochroal eye

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

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

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

Amongst early Phacopina only *Ormathops* has an eye of this kind, presumably retaining the identical size of the lenses from a holochroal ancestor. There must have been strong selection pressure in favour of regularity of packing at the expense of identical size, for all other Phacopina have achieved regularity simply by increasing the distance between lens centres in the generative zone to accommodate for the increasing girth of the eye as it grows. The lenses therefore become larger towards the base of the eye. Whilst this might seem too optically disadvantageous, it is possible that a slight change in biconvexity of the lenses from the top to the bottom of a file could have altered the focal length (f), and since the f number of the lens is f/D, where D is the diameter, might have allowed a constant f number whatever the lens diameter. The sensitivity of the lens can be measured as $1/f^2$, and hence if the f number remains the same so does the sensitivity. So far it is not entirely certain whether or not this theoretical model was adopted by trilobites; it is merely one of a number of ways in which the trilobites eye could have come to terms with the problems of change in lens size.

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

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

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

Previously I proposed (Clarkson 1966*a*) that the schizochroal eyes of trilobites were adapted for no more than movement perception. This was upon the understanding that an approaching object would progressively occlude more lens-axes, as Professor Rudwick first pointed out, and that a passing object would register as a flicker across the visual field. This view, however, was propounded before the remarkably elegant structure of the lenses was known. A more embracing theory of the function of the whole eye, has recently been proposed by Cowen and Kelley (1976), and elaborated by Stockton and Cowen (1977). This seems to be a good model for many aspects of schizochroal eye function.

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

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

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

The 'stereoscopic model' depends, largely, however, upon whether the basic assumption is justified, i.e. whether there was a short ocellar lens capsule or an ommatidium below each lens. If it were the latter the model would need each serious modification.

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

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

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THE POST-ECDYSIAL DEVELOPMENT OF THE CUTICLE AND THE EYE OF THE DEVONIAN TRILOBITE *PHACOPS RANA MILLERI* STEWART 1927

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[Plates 1–7]

CONTENTS

Specimens of the Devonian trilobite *Phacops rana milleri* Stewart 1927 from the Silica Shale of Ohio are sometimes preserved in the early stages of the post-ecdysial cycle. Individuals that died in this early stage have pale, thin and wrinkled cuticles; in later stages the cuticle became rigid as it thickened and darkened. The post-ecdysial development of the cuticle and the schizochroal compound eye has been studied in a suite of specimens representing various stages, culminating in the intermoult condition.

Scanning electron microscope studies on etched specimens, supplementing cathodoluminescence and light microscopy, have enabled primary structures to be distinguished from secondary diagenetic effects, and have been used to elucidate diagenetic changes.

In our earliest post-ecdysial cuticle the 10 μm thick outer prismatic layer is already formed and the principal layer below this is only about 25 μm thick. The later thickening of the cuticle affects the principal layer alone. In subsequent development there is a division into three zones with a variety of vertical canals. The final intermoult cuticle can be up to 500 μm thick.

In the developing eye, each of the post-ecdysial lenses has initially the form of a small, simple calcite cone hanging from the lower surface of the cornea. In later stages this lens spreads to the full width of the lens capsule, losing its conical form, taking on a Huygensian shape, and eventually acquiring its mature form in which there is a central core of massive texture and, proximally, a thin intralensar bowl, of much the same appearance as the core. The upper unit of the lens consists of thin calcite lamellae, radially arranged around the *c*-axis, each lamella consisting of palisade-like fibres, parallel in the lower part of the lens, but radiating outwards where they meet the convex outer lens surface. When the lens is mature, a ring of scleral material forms on the inside of the cylindrical wall of the lens capsule, together with an annular girdle of fine-grained material at the junction of lens and sclera.

Some suggestions are made regarding function in the developing eye, and the need for complete replacement of calcium carbonate at each ecdysis is discussed.

1. INTRODUCTION

Like modern arthropods, trilobites shed their exoskeletons periodically to accommodate changes in size and shape produced by their growth. Palaeontologists have, therefore, long been aware that the majority of trilobite remains represent cast-off shields or exuviae and not dead animals. The moulting process in trilobites has twofold significance for palaeontology. First, there are considerable implications to follow from a knowledge of where, when and how trilobites moulted. Certain trilobites have left undisturbed associations of dorsal shield components in characteristic and consistent configurations. These occurrences are similar to those produced by modern crustaceans and are considered to represent exuvial assemblages reflecting distinctive types of moulting behaviour (Miller, in press). Henningsmoen (1975) has provided a comprehensive review of this aspect of moulting in relation to trilobite morphology.

The second field where moulting is of importance is that of trilobite biology. Little or no evidence, beyond studies of the number of moult stages accumulating during ontogeny (Hunt 1967), has, so far, been forthcoming in this field. It is now recognized that the various stages in the arthropod moulting cycle are more or less continuous, the recovery from one moult being followed by renewed storage of metabolic reserves in preparation for the next. Ecdysis itself is a period of considerable physiological stress, accounting for a large percentage of arthropod mortality. Trilobite cuticle is exceptional in arthropods, being composed almost entirely of calcite, and, until now, no clear evidence has been available to suggest how trilobites regrew their cuticles after ecdysis.

In this paper, we describe a suite of specimens of *Phacops rana milleri* Stewart 1927 from the Middle Devonian of Ohio (Eldredge 1972). These are preserved in various stages of the early post-ecdysial cycle and have allowed us to determine how much cuticle carbonate was removed and renewed during moulting, how the layers of cuticle were built up post-ecdysially and how specialized cuticular organs, especially the schizochroal eyes, were reconstructed immediately after exuviation. We make some attempt to consider how the solution of some problems facing trilobites in moulting reflects on studies of their functional morphology in particular and their evolutionary history in general.

2. MATERIAL AND METHODS

(*a*) *Location of material*

The specimens of *Phacops rana milleri* are all from the Middle Devonian Silica Shale and were collected from the north quarry of the Medusa Portland Cement Company, Silica, Ohio. They include a uniquely informative slab collected by Mr Mullard Widener of Tulsa, Oklahoma, and registered AMNH 29282 (American Museum of Natural History). Other material was donated by Dr N. Eldredge and Dr R. Levi-Setti, and is deposited in the Royal Scottish Museum (R.S.M.). Cuticle and eye fragments of *P. rana africanus* Burton & Eldredge 1974 from the Eifelian of the Spanish Sahara, together with those from *P. rana crassituberculata* and *P. rana rana* from the Silica Shale, were also examined for comparative purposes. Professor A. D. Wright, Queen's University of Belfast (Q.U.B.), provided an early post-ecdysial specimen of *Cheirurus* sp. from the Silurian Wenlock Limestone of Dudley, England.

(*b*) *Description of post-ecdysial specimens*

(i) AMNH 29282 (figure 5†)

A 7 cm square slab of pale grey calcareous mudstone with an outstretched intaglio (complete specimen) of *P. rana milleri* having a pale honey-coloured cuticle that is extremely thin (30 μm) and transparent. Almost at right angles to this individual lie the exoskeletal parts of another *P. rana milleri*, with dark brown cuticle of thickness typical of intermoult stage (300–500 μm). On the right is the thoracopygon (term defined by Henningsmoen 1975, p. 182), with the pygidium inclined at 45° to the horizontal. A small, inverted fragment of hypostome lies between the thoracopygon and the intaglio, and the cephalon partly underlies the left side of the intaglio. Most of the hypostome appears to have been removed in the preliminary preparation of the specimen.

(ii) RSM GY 1979.11.1 (figures 8, 9) (This specimen was figured intact by Levi-Setti (1975, p. 13, pl. 5).)

An intaglio 4.6 cm long, with pale translucent brown-grey cuticle 40 μm thick; dark areas due to disseminated pyrite. Immediately underlying the pygidium of this intaglio is a partial thoracopygon of a slightly narrower specimen with its anterior 180° opposed to the intaglio. The cuticle of the thoracopygon is dark brown and of typical intermoult thickness.

(iii) RSM GY 1979.11.2.

A damaged specimen; thorax, 2.6 cm width, but asymmetrically compacted; cuticle, light brown, semi-translucent.

(iv) RSM GY 1979.11.3 (figure 7)

An almost complete specimen 6.6 cm long, undistorted by compaction. Cuticle glossy, pale brown and translucent; 135 μm thick.

(v) RSM GY 1979.11.4 (figure 10)

An intaglio 3 cm long, somewhat compacted, left eye missing. Cuticle very thin (20 μm), pale honey colour, opaque, not glossy.

(vi) RSM GY 1979.11.5

An enrolled specimen from which many preparations have been made. Cuticle thin (30 μm), mid-brown, highly glossy.

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† Figures 5–47 appear on plates 1–7.

(vii) QUB 2732 (figure 6)

A specimen of *Cheirurus centralis* Salter from the Silurian Wenlock Limestone of Dudley, England, preserved in light olive coloured calcareous mudstone; cuticle light to medium brown, semitransparent and very thin (20 μm). No visual surface preserved. It is figured here to show a comparable developmental stage in a different taxon.

(*c*) *Other material*

Numerous preparations have been made for scanning electron microscopy (Grant Institute: Gr I 46150-61) and cathodoluminescence (Museum of Paleontology, Michigan: MPM 27063a), all from mature intermoult specimens.

(*d*) *Interpretation of specimens*

All the specimens of *P. rana milleri* described above have an unusually thin, fragile and light-coloured cuticle compared with the typical intermoult cuticle, which is dark brown and ranges in thickness from 250–500 μm (Miller 1976). Only the disarticulated exoskeletal material underlying the intaglio of AMNH 29282, and that of RSM GY 1979.11.1 have the character of fully developed intermoult cuticle. Therefore, those specimens with pale thin cuticles appear to be in various stages of cuticle calcification and thickening following ecdysis, and probably themselves represent the remains of animals that died before post-ecdysial development was complete. The conclusion that the individuals with thin cuticles are in immediate post-ecdysial condition is supported both by our detailed studies on cuticle structure and by the development of the schizochroal eye as described in §§ 4–6.

In both AMNH 29282 and RSM GY 1979.11.1 it seems reasonable to suppose that the trilobite died shortly after completing exuviation and rests partly upon its own exuviae. The cephalon–hypostome–thoracopygon configuration of AMNH 29282 is within the typical range shown by Salterian moulting (N. Eldredge, personal communication; Henningsmoen 1975, p. 192). Bearing in mind the larger degree of compaction undergone by the very thin and apparently flexible cuticle of the intaglio, and the fact that aquatic arthropods rapidly swallow water once free of the old exoskeleton to increase their size, the relative sizes of the exuviae and the adjacent 'paper-shell' individuals are compatible. It has, unfortunately, not proved possible to count accurately the number of lens files on the intaglio of AMNH 29282 owing to considerable flattening and distortion of the eyes. Thus we were not able to verify Clarkson's (1966*a*) suggestion that a new lens row is injected at every moult in *Phacops* holaspids.

(*e*) *Methods*

For studies of the cuticle structure, fragments of exoskeleton were removed both from intaglios and from exuviae, broken cleanly across to give transverse sections. These were etched in saturated solutions of EDTA (disodium salt) before mounting for scanning electron microscopy (s.e.m.). Etching was controlled by observation under a high power binocular microscope. Etch times varied between 5 and 35 min. Fragments of visual surface from post-ecdysial eyes were similarly treated, but in one the cuticle was entirely dissolved away and the internal mould examined (figures 46, 47). Whole eyes were removed from intermoult specimens. They were then trimmed into small blocks with a diamond blade of 1 cm radius. Vertical sections were made by grinding flat faces passing vertically through one of the dorso-ventral files;

horizontal sections were made with the line of section cutting through lenses at different levels (cf. Clarkson 1967, text-figs 1, 2) and passing tangentially, parallel with the principal plane of each lens.

Final smoothing of the cut faces was done with 1000 grade carborundum, and, after rinsing, the specimens were etched in EDTA as described above. Distilled water and, finally, absolute alcohol were used for gentle washing after etching. The specimens, after coating in gold–palladium, were scanned, on the s.e.m., from one end of the cut face to the other. A series of overlapping photographs were taken to provide a large scale montage (see, for example, figure 19), facilitating examination of the eye as a whole. Tilting specimens in the s.e.m. enabled three-dimensional correlation of cut planes at various angles with the outer lens surfaces.

Slides from a serially sectioned, enrolled *P. rana milleri* were used for cathodoluminescence microscopy. The trilobite was embedded in Araldite before slicing, and sections were polished on both sides and were attached to the slides with Araldite. Slices passing through the eyes were examined in a Nuclear Enterprises Inc. Luminoscope, with cold cathode discharge at 18 kV and 0.35 mA, at low pressure. Paired photographs were made by transmitted light and cathodoluminescence (see, for example, figures 42, 43), with exposures of 1 s for transmitted light and 5 s for luminescence, on Ilford FP4 film uprated by development to ASA 200. The Luminoscope proved invaluable in revealing structural details in preparations where little was visible optically, and also gave significant information about diagenesis.

3. Diagenetic modification of the cuticle and eye structure

All the specimens examined by us had undergone some degree of diagenesis, which wholly or partially obliterated the primary structure. Neomorphic replacement of primary calcite appears to have been the major process involved. In several instances, indications of primary microstructure are revealed in the arrangement of neomorphosed calcite crystallites, which were based on an organic matrix (cf. Sandberg 1975). In others, neomorphic replacement has been very coarse, obliterating any primary microstructure. Using relatively unaltered specimens as a reference, we have charted the different degrees of alteration that lenses in our material had suffered (figure 1).

The main problem in interpretation of the primary structures is that, while the etching process greatly clarifies the internal organization of the lens, it also partially dissolves it. Hence, cleavage planes in the calcite are highly accentuated, and so are the primary voids that may exist in the calcite of the lens, but it is not very clear what the *in vivo* dimensions of the latter actually were.

However, the various internal zones of both cuticle and eyes, as revealed by textural differences in etched specimens, were also confirmed by luminescence microscopy. Sommer (1972*b*) has shown that invertebrates with calcareous skeletons incorporate trace amounts of Mn^{2+} into their calcite, which produces a characteristic red luminescence under electron excitement. Structures and layers grown at different times and of different constructions can luminesce more or less brightly according to their manganese content. The iron content of the calcite also affects luminescence; increasing iron quenches the red manganese luminescence. It appears that, during neomorphism, manganese ions in the calcite lattice retain their relative concentrations, so that, even in highly crystallized material, primary structures can still be revealed by luminescence microscopy (figures 35–37, 42, 43). There is thus no doubt that the structural elements observed in the visual apparatus, as well as finer architectural details such as lamination, were originally present and are not artefacts produced either by diagenesis or preparation.

Neomorphism has affected all cuticle calcite, but is most noticeable in the eye lenses. Lens crystallites were optically well oriented, providing preferential sites for epitaxial cement overgrowths which occluded the small intercrystallite spaces, probably at a very early stage in diagenesis. The excellent optical orientation of the lens calcite is further indicated by later large syntaxial cement crystals growing into sublensar cavities, where they have successfully competed with other cements (figure 36).

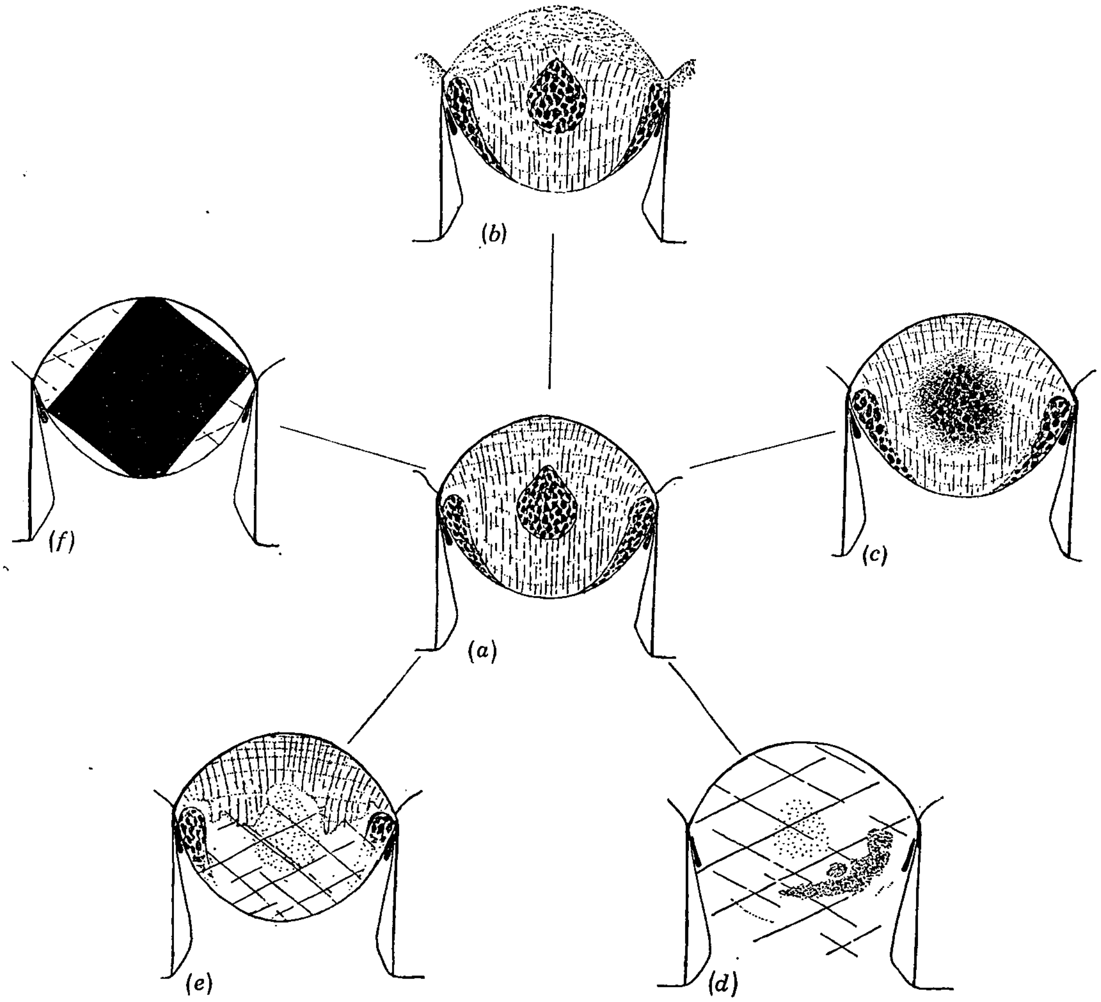


FIGURE 1. Diagenetic changes that have been observed in the eyes of *Phacops rana milleri* Stewart 1927 from the Silica Shale of Ohio. (*a*) Intact lens with bowl and core; (*b*) micritization of the outer part by endolithic algae; (*c*) apparent expansion of core by outward migration of core material; (*d*) complete recrystallization of lens and sublensar alveolus involving neomorphism and occlusion of primary voids by epitaxial cements; (*e*) recrystallization of part of lens; (*f*) partial or complete pyritization, in this case replacement of calcite by a large single pyrite crystal.

4. THE STRUCTURE AND THE POST-ECDYSIAL DEVELOPMENT OF THE INTERMOULT CUTICLE

(*a*) *Terminology*

The terms used herein to describe the *P. rana milleri* cuticle are those suggested by Dalingwater & Miller (1977), who recognized an outer prismatic layer and an inner principal layer, the latter composed of three texturally distinct zones. Terminology of accessory (sensory) structures in the cuticle follows Miller (1976).

(*b*) *Intermoult cuticle* (figures 14–16)

A general description of intermoult cuticle has been given by Miller (1976) for several subspecies of *P. rana*. Fragments of thoracic pleura from the exuvial thoracopygon of AMNH 29282 (figure 5) show similar features to other *P. rana milleri* cuticle samples, whether from isolated exuviae or from enrolled individuals, and are also typical of intermoult cuticles in all other subspecies of *P. rana* so far examined.

The cuticle ranges between 300 and 500 µm in thickness and is heavily pigmented brown or almost black. Its glossy surface is due to the presence of a thin outer layer, possibly analogous to an epicuticle. The 10 µm thick prismatic layer is not readily seen in etched preparations because it etches back far more rapidly than the other layers or zones. Electron microprobe scans across the thickness of cuticle failed to reveal any significant differences in chemical composition between prismatic and principal layers, and this consistent response to EDTA etching may probably be attributed to the larger size and coherent *c*-axis normal orientation of the prismatic layer calcite crystallites.

The principal layer, comprising the bulk of cuticle thickness, is clearly divided into three distinct zones. The innermost and outermost zones are composed of finely textured calcite crystallites and show traces of narrow laminae about 10–20 µm apart, while the central zone crystallites are very much coarser and there are only a few, widely spaced laminae. The triple zonation is present throughout most of the cuticle but is lost at the doublure and at the intersegmental articulations (figure 16). Scleral cuticle also shows the triple zonation, but its laminate character is far more marked than that elsewhere (figure 19). Much of the upper zone in the scleral region has been lost by etching, but this and the lower zone show a finely laminate, compact arrangement of calcite crystallites (figure 26). Laminae of the lower zone appear to continue across the corneal membrane bounding the lens capsule, passing into the alveolar ring; on either side of the membrane, the laminae become steeply divergent in a distal direction. The middle zone of the scleral areas is more coarsely laminated than is cuticle elsewhere. The scleral cuticle appears to lack the characteristic widely spaced 'major' laminar boundaries seen in non-specialized cuticle, and a general impression is gained that the scleral organization is differentiated for its function in support and regeneration of the visual complex (see § 6).

Both scleral and non-scleral cuticle are richly supplied with vertical elements opening into surface pits. These have been described in detail by Miller (1976, pp. 346–353), and are considered to represent the sites of former sensory setae varying in size, strength and flexibility.

Pseudotubercles (Miller 1976, p. 351) are local raised thickenings of cephalic cuticle, which contain mushroom-like bundles of ducts. They are considered to be differentiated sensory organs, possibly with a long distance chemoreceptory (olfactory) function.

Close comparisons of cuticles from enrolled *P. rana milleri* (which may be presumed to represent dead intermoult-stage animals), with isolated ecdysed cephala and pygidia have revealed no detectable differences in their layering, zonation, or thickness. In particular, the exuvial cuticle of AMNH 29282 is indistinguishable from the cuticle of a comparably sized enrolled individual. Intermoult and ecdysed cuticles from *P. rana rana*, *P. rana crassituberculata* and *P. rana africanus* are also identical, as far as can be determined. It must be concluded that during moulting these trilobites shed the entire intermoult exoskeleton without significant prior resorption of carbonate. This conclusion is borne out by our study of the *Phacops* visual system and its post-ecdysial regeneration, and, as discussed in the final section, has considerable implications for the biology of trilobites.

(*c*) *Post-ecdysial cuticle* (figures 4*a*, 11–13)

Apart from their being considerably thinner, the post-ecdysial cuticles are comparable to intermoult cuticles in possessing a well developed epicuticle and prismatic layer; they have, however, a very much thinner principal layer. The epicuticle is illustrated in figure 12; its appearance under s.e.m. is that of a somewhat fibrous film with small embedded calcite crystals. It burns away rapidly in the electron beam above 10 kV potential, especially if the beam is directed on one particular spot.

Beneath the epicuticle is a prismatic layer of typical trilobite type and of normal thickness (10 μm) for *P. rana milleri*. The large calcite crystallites are arranged with their *c*-axes normal to the surface, and the surface shows an even and regular crystal texture (figure 13).

The principal layer varies in thickness from 25 to 500 μm in the suite of post-ecdysial specimens. Its calcite crystallites are smaller and lack the uniform orientation of the prismatic layer. No traces of laminar organization have been observed, nor is there any indication of zonation in the principal layer at this early stage.

Vertical ducts opening into pits are present in all the post-ecdysial cuticles (figures 12, 13); the typical intermoult size ranges of duct appear, and surface socket pits and fossettes are distributed exactly as in intermoult cuticles. However, the pseudotubercles are undifferentiated; they are represented by inflated areas without cuticular thickening and without the differentiated mushroom bundle of ducts characteristic of final intermoult stages.

The thinnest cuticles in the suite of post-ecdysial specimens have all been wrinkled as the trilobites were subject to post-mortem compaction. In many instances, double folds have been developed, especially near the eyes (figure 44, 45). Some brittle fracture of the cuticle has occurred, but it seems that in the early stages the cuticle was essentially flexible, as would be expected if calcification was incomplete. Later stages (e.g. RSM GY 1979.11.1) are nearly undistorted and have cuticles with comparatively thicker principal layers, though still thinner overall than in the intermoult stage. This supports the contention that trilobite cuticles developed their strong calcification on a matrix or template of organic matter (Dalingwater 1973; Dalingwater & Miller 1977).

(*d*) *Post-ecdysial development of the cuticle*

Prior to ecdysis the new epicuticle and prismatic layer must have been formed above the hypodermis and the moulting split must have occurred between the neo-epicuticle and the proximal margin of the old principal layer. Presumably, as in modern crustaceans, sensillae, ducts etc. were already formed within the new cuticle, and, in the same way, setae were probably everted by friction during shedding of the exuviae.

It is impossible to be certain if any of the principal layer was laid down before ecdysis, although evidence from the eye (pp. 474–478) might suggest that only the epicuticle and prismatic layer were complete at ecdysis. The subsequent development of the cuticle must have involved the inward progress of calcification, thickening of the principal layer and development of the characteristic intermoult zones.

5. The mature eye and its lens structure

The gross morphology of the eye of many phacopacean and dalmanitacean trilobites has been described (Lindström 1901; Rome 1936; Clarkson 1966*a*, *b*, 1967, 1969, 1979; Campbell 1975) and needs little further comment. In all schizochroal eyes the lenses are separate (figures 3, 4*b*) and each has its own corneal membrane which leaves the periphery of the lens to plunge through the interlensar sclera as a cylindrical ring (intrascleral membrane). The lens is evidently compound, with an 'intralensar bowl', whose function has recently been interpreted (Clarkson & Levi-Setti 1975; Clarkson 1979) as an optical correcting element, within it. In dalmanitacean trilobites the sclera is normally thinner than the lenses (Clarkson 1975), but in phacopaceans it is thick, so that the lens is set at the top of a cylindrical cavity, the sublensar alveolus.

Our new information contributes to the understanding of the microstructure of the cuticular intralensar sclera, which is broadly comparable with that of the rest of the cuticle, and to the minute structure of the lenses.

(i) *The lens capsule*

The lens, the corneal membrane and its prolongation, and the intrascleral membrane, together with the scleral material lying within the intrascleral membrane, all form parts of a developmentally discrete structure, here termed the lens capsule. It is only through the study of the post-ecdysial development of the lenses that this has become clear (*q.v.*), for in the mature eye it is solely apparent in the real discontinuity of the laminae within and without the intrascleral membrane.

(ii) *The structure of the lens in* P. rana milleri *as shown by s.e.m. and cathodoluminescence microscopy* (*figures* 3 *and* 4)

Much has been written about the structure of the mature lenses in adult phacopacean trilobites, but interpretations, by various authors, of intralensar structures have tended to be contradictory and sometimes confusing. This is almost entirely because of diagenetic modification of primary structure. Indeed, such alteration has often gone so far that virtually all trace of primary structure has disappeared (see, for example, figure 34 compared with figure 41). To disentangle the primary from the secondary elements it has been necessary to use new techniques. We have found that the EDTA etching process, previously applied to the study of trilobite cuticle by Miller (1975, 1976), is highly satisfactory, and, together with luminescence microscopy, has helped to resolve not only what the primary structures are, but also the various diagenetic pathways that lead to interpretative problems. In previous work (Lindström 1901; Clarkson 1966*a*, *b*, 1967, 1968, 1969; Clarkson & Levi-Setti 1975) the existence of the intralensar bowl in many phacopid species was established.

Towe (1973) made thin sections of the eyes of *P. rana milleri* and found no trace of intralensar bowls. But, as shown later, one diagenetic pathway leads from a highly structured lens with real internal differentiation to an altered lens of clear or cloudy calcite, crystallographically syntaxial with the original structure and looking deceptively primary in origin.

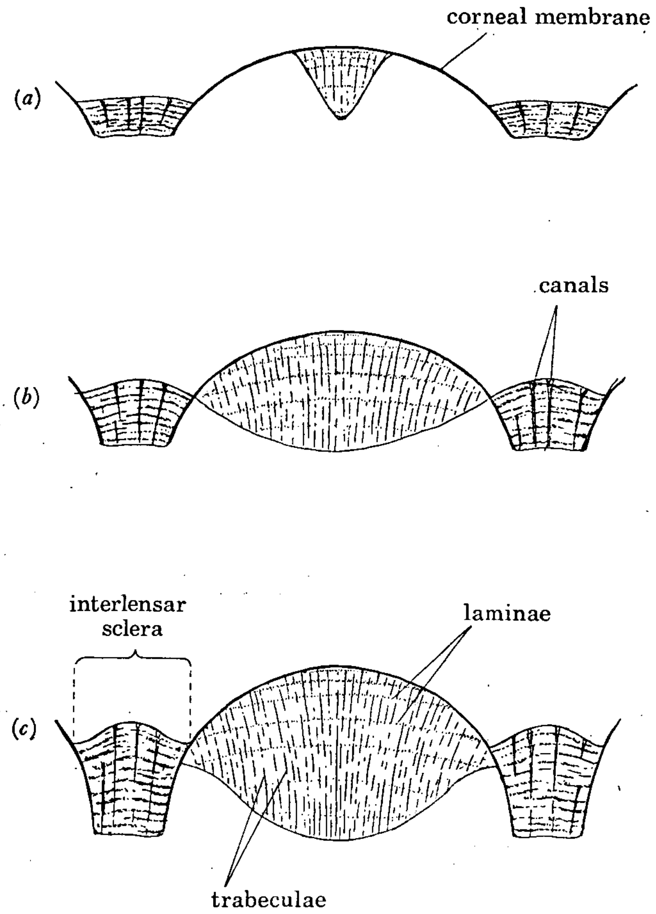


FIGURE 2. *Phacops rana milleri* Post-ecdysial development of the lens. (*a*) Initial conical lens (cf. figure 39, plate 6; figures 46, 47, plate 7); (*b*) thin biconvex lens (cf. figure 18, plate 3); (*c*) Huygens lens, before the differentiation of the core and addition of the intralensar bowl (cf. figure 20, plate 3).

The most recent work on the fine structure of phacopacean lenses is that of Campbell (1975), who worked on *P. rana milleri*, *Phaciphacops raymondi*, and other North American Devonian Phacopacea. This valuable study has given much new detail of lens structure, as well as confirming previous work. The techniques used by Campbell included examination of the surfaces of silicified specimens where the outer cornea has broken away revealing the internal structures, and also the preparation and examination of thin sections and polished surfaces, which were observed under oil.

The important elements distinguished by Campbell were the intralensar bowl 'formed of calcite with many inclusions', below which is a basal layer of 'clear, randomly oriented microcrystalline calcite', and a large pear-shaped central core, sometimes in contact with the basal layer, at other times located well above it, and always with its *c*-axis parallel with the lens axis.

In the upper unit the *c*-axes of the more peripheral calcite crystals turn outwards fanwise, so as to make a lesser angle with the external surface than if they had been horizontal. Within the upper unit there are laminations, probably organic in nature, and with a somewhat lesser curvature than the outer lens surface. The outer cornea appeared to Campbell to be multi-layered and probably with random crystallographic orientation.

The observations that we have made with our etching technique largely confirm Campbell's studies on the eyes of *P. rana milleri*, but extend them so that for the first time it is possible to

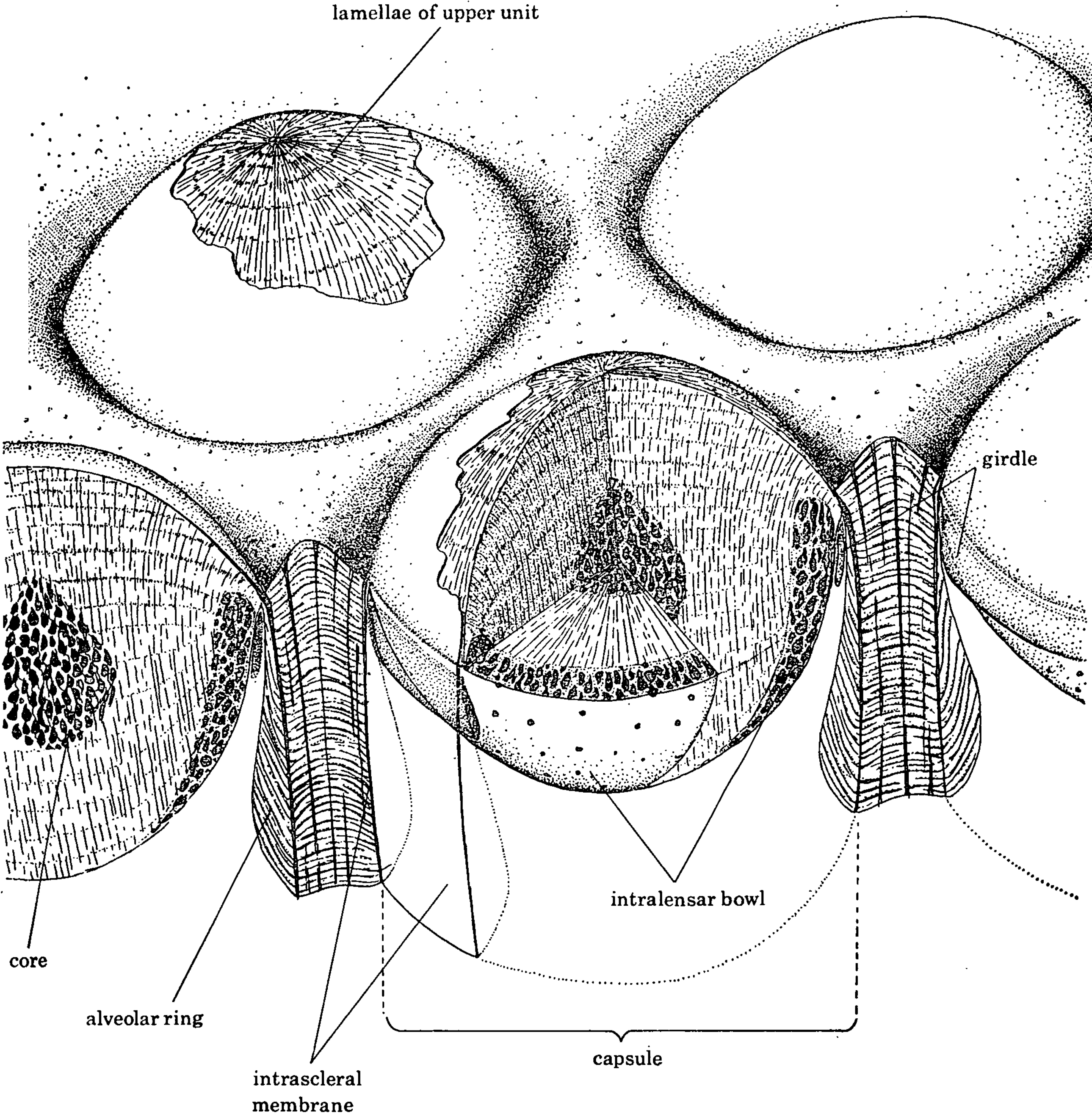


FIGURE 3. Diagrammatic representation of the mature eye of *Phacops rana milleri*, with lenses dissected to show internal structure. Details of corneal structure have been omitted for clarity.

visualize the lens as a three-dimensional structure and to determine its detailed micro-organization.

The elements of lens structure are broadly as Campbell described them, and the core, bowl and laminae in the upper unit are all confirmed as real internal parts, regarding which the s.e.m. reveals a wealth of detail.

A new and important fact to emerge from the study of tangential sections is that the whole lens, like that of the holochroal eye (Clarkson 1979), is constructed of calcitic plates arranged radially round the central axis (shown vertical in standard orientation). This radial appearance shows most clearly in sections cut normal to the axis and parallel with the principal plane of the lens, and in external elements exposed when the cornea is stripped off. All other internal elements within the lens relate in some way to this radial organization, which is here described in detail for the first time. It has hitherto been tacitly assumed that schizochroal lenses were constructed as simple, single crystals of calcite since they behaved optically in this way. We now realize that their open mesh construction is analogous to that of echinoderm ossicles and plates, presumably reflecting a similar strategy of economy in fabrication combined with functional efficiency.

(*a*) *The cornea*

Campbell (1975, p. 174) described this as the 'outer layer', and correctly indicated that it is composite. He describes it as three-layered, with a central dark layer sandwiched between two clear layers, of which the inner one thickens peripherally and interdigitates with the distal part of the upper unit. He regards it as being continuous with the basal layer of the lens. Our s.e.m. preparations also show that there are three layers, indicated on figure 4 together with their correspondences to scleral layers. The cornea (figures 4*b*, 22, 23) consists of an outermost organic epicuticle which covers both lens and sclera, below which is the corneal layer, continuous with and homologous to the cuticular prismatic layer. The corneal layer does not continue into the lens capsule (figure 4*b*) but wedges downwards at the periphery of the lens.

Below the cornea is a corneal membrane (continuous with the intrascleral membrane), which plunges through the scleral pillar and bounds the lens capsule (figure 26). There is a marked change in orientation of cuticular laminae in the sclera on either side of the intrascleral membrane.

(*b*) *The upper unit*

In tangential section the radial structure of the upper unit is very clear. In the specimen shown in figures 31 and 32 there has been an incipient diagenesis; nevertheless, the radial plates are visible, especially in the outer part of the eye. This slice is cut just above the level of the intralensar bowl, but goes through the core, which has been expanded through diagenesis. The appearance here is like a lacy meshwork with the radial lamellae being dominant; these seem to retain constant thickness, but new radial lamellae were intercalated between them as the lens grew. In a vertical slice (figures 19, 33, 34) the same kind of meshwork is evident, but the main elements are more or less vertical (parallel to the lens principal axis), though turning out in a fanlike structure just below the cornea. Hence, the radial plates seen in transverse section are not solid, but more like individual net curtains, with a generally vertical pattern. The calcite needles of which they are formed (trabeculae) are parallel with the lens axis in the lower part of the lens, but veer outwards towards the top so as to make an angle of some 70° to the upper lens surface at its periphery. This accords with Campbell's description of the arrangement of the calcitic axial structure, which he deduced from the study of extinction patterns between crossed nicols.

The upper unit, like the core of the lens, is traversed by well marked subconcentric laminae, which become increasingly closely spaced towards the cornea (figure 19), and which are shown clearly by cathololuminescence (figures 35–38). These laminae are bounded by deeply etched slots, which were observed during etching to contain a thin, fragile, translucent membrane, presumably organic in composition. These observations are closely comparable to those made for laminar units of *Asaphus* cuticle (Dalingwater & Miller 1977), and the membranes are probably laminar membranes. Such laminae have been described in *Reedops bronni* (Clarkson 1969, p. 196–8, text-fig. 5; pl. 3, figs 5–6) and, by Campbell, in various phacopids (1975, p. 175, pl. B, fig. 6). Campbell's most striking photograph shows a specimen of *Phaciphacops birdsongensis* (Delo) (Campbell 1975, pl. 5, fig. 3), having silicified laminae through which the top of the central core projected.

The laminated region of the upper unit corresponds to an inverted bowl-like region in the lens of *P. latifrons* (Clarkson 1967, pl. 99, fig. 5; text-fig. 2*g*, where it is marked as 'x'), suggesting that the latter is a diagenetically modified version of the same structure bounded by the lowermost lamina. Some of Campbell's figures show a similarly accentuated laminar zone (Campbell 1975, pl. B, figs 3, 4), which may seem to be disproportionately pronounced in abaxial sections, not because of a real difference in composition, but by virtue of the change in direction of the calcite crystallites within the upper unit. The organic interfaces of the laminae seem, in addition, to have acted as centres of diagenesis modifying the structure further.

(*c*) *The core*

The pyriform core of Campbell is probably equivalent to the 'proximal nucleus' described by Clarkson (1967). But, since diagenesis had modified the original structure of the *Ananaspis* specimens upon which the original term was based and since Campbell's concise term 'core' refers to an apparently unmodified and real structure, Campbell's term is to be preferred. The core consists of very dense ferroan calcite (figures 19, 24, 25), clearly distinct from that of the upper unit. When subjected to longer periods of EDTA treatment than normal, it is etched into cavities, but whether or not there were original cavities within it is unknown. The reconstruction (figures 3, 4*b*) shows such cavities, since they appear in most of our preparations. There is a striking equivalence in the appearance of the calcite of the core and that of which the ferroan calcite intralensar bowl is constructed. Campbell (1975, pl. B, fig. 7) illustrates a core and bowl of similar dimensions to those of our material. In other sections, however, the core seems to be appreciably larger. We have noticed a similar effect in several of our thin sections and also on a few of our etched tangential faces. The excess dimensions of the core appear to be related to a diagenetic front growing out from the core and enlarging it preferentially, with calcite cements epitaxially growing and occluding primary void fabric (figure 1). The dimensions of the core given in our reconstruction appear to us to be in keeping with its shape and size in unaltered material. Laminae passing through the core are seen by cathodoluminescence microscopy (figure 37), though these are less evident in s.e.m. preparations.

(*d*) *The intralensar bowl*

In schizochroal lenses the bowl is one of the constant structures to be found in nearly all preparations. In *P. rana milleri* the upper rim of the bowl is thick and rounded, but below this lip the bowl becomes much thinner, almost vanishing centrally below the core (figures 17, 19, 26, 34, 37, 38). Such a bowl structure seems to be a little unusual in Phacopina, though in *Reedops* species the bowl may also be reduced in thickness axially. The bowl in the species under discussion is very deep, rising high up the sides of the lens. Such morphology contrasts strongly with the much flatter bowl of the Dalmanitacea, which has been the subject of independent study elsewhere (Clarkson & Levi-Setti 1975).

The similarity in its texture and composition to that of the core has already been noted. Both bowl and core may be coarsely recrystallized high ferroan replacements, perhaps of original high magnesium calcite structures. Richter & Füchtbauer (1978) have suggested such replacements to be common in former high magnesium skeletal calcites. Electron microprobe studies show that *P. rana* cuticles are presently low in magnesium, but magnesium is lost during neomorphism and it is not otherwise possible to determine if all cuticle and intralensar structures were originally rich in magnesium or if the bowl and core were differentiated in this respect. Certainly, were the calcite composition of both bowl and core different in this way, this might give the required shift in refractive index to enable them to function as correcting elements as discussed on page 478. No lamination of the bowl has been observed with the s.e.m., but cathodoluminescence microscopy shows very clear concave laminae in the bowl (figure 38).

(*e*) *The girdle* (*figures* 26, 40, 41)

This constant feature of phacopid lenses has hitherto escaped description. It is an annulus of very fine-grained calcite crystallites encircling the lens parallel with its principal plane and just below its widest part, at the junction of the lens with the sclera. It appears dense, whitish or pale grey in thin section. It consistently etches far more rapidly than other lens elements. The girdle is always present, and, though not part of the lens itself, is apparently an integral component of the visual system, as it lies within the lens capsule. Its function, however, can only be speculated on.

(*f*) *Sublensar cylinders*

In one specimen of *P. rana africanus* wherein the lens was incomplete (in that the bowl had not been added), a pair of symmetrical calcitic horns are seen projecting from the bottom of one of the lenses into the matrix (figure 41). These must be part of a downwardly flaring cylinder, whose upper aperture seems to be attached to the curving lower surface of the lens, though well within its circumference. The symmetry would suggest that this is an original part of the visual complex, though, in the absence of other evidence, it cannot be fully substantiated. No such structures have so far been seen in *P. rana milleri*.

6. Post-ecdysial development of the lenses

Enough material has been available for us to have been able to trace the nearly complete development of the lens from a very early post-ecdysial stage to maturity.

(*a*) The earliest stage in post-ecdysial development (figures 2*a*, 39, 46, 47) is shown by the newly moulted intaglio of AMNH 29282. Here, the cornea was apparently flexible, as the wrinkling of the eye surface shows. Where the cornea is translucent the embryonic upper unit of the lens can be seen through the transparent cornea as a clear, small, dark circle, 150 μm across in the centre of the lens. The whole corneal surface is about 650 μm across and the lens hangs suspended from the proximal surface of the cornea. At this stage the lens forms a steep-sided cone whose proximal point lies in approximately the same plane as the lower surface of the sclera.

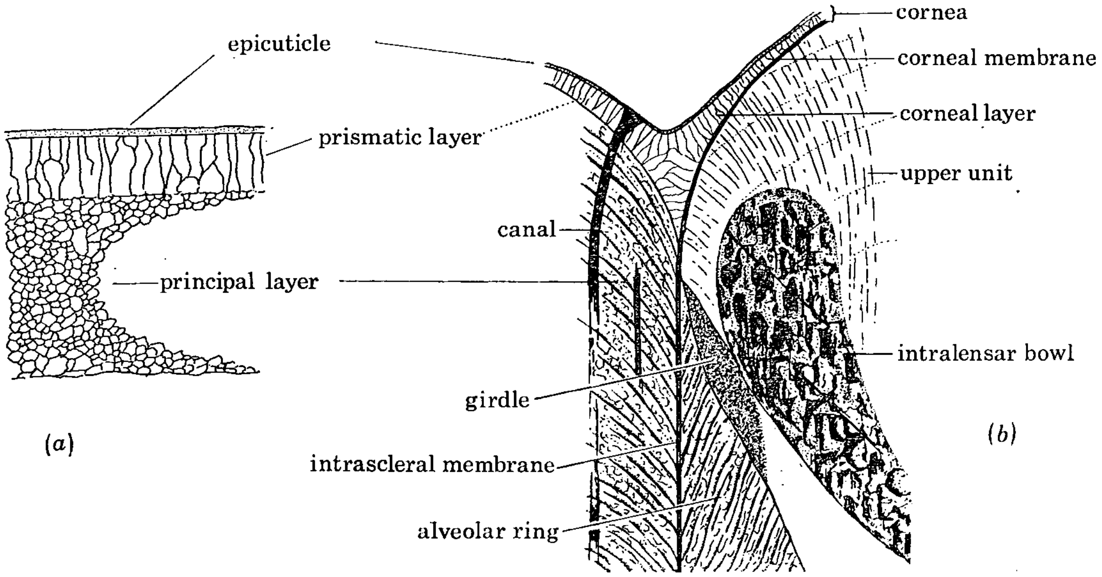


FIGURE 4. (*a*) Structure of thin (30 μm) post-ecdysial cuticle of *Phacops rana milleri* (cf. figure 11, plate 2); (*b*) structure of edge of mature lens and sclera, showing terminology and relation of the various parts.

The true shape of the early post-ecdysial lens has been determined by removing a fragment of the eye of AMNH 29282 and dissolving out the lens so that the internal mould could then be photographed (figures 46, 47). The sides of the cone are slightly incurved and the tip truncated. In addition, the form of the lens shows up, though not so clearly , in a s.e.m. photograph of an etched surface of part of RSM GY 1979.11.5 (figure 39). As the specimen is severely recrystallized, however, the shape is less evident and nothing can be made of the internal structure of the lens. This early stage in the development of the lens must have been constructed on a radial plan, however, as it is retained in the mature intermoult lens as the small central 'aster' (figures 29, 30).

(*b*) The next stage in development is shown by figures 2*b*, 18. Here the lens has grown right to the periphery of the cornea and has lost its conical form, becoming biconvex, the lower surface being slightly more curved, as in the olenids (Clarkson 1973). The lowermost part of the lens still lies in approximately the same plane as the proximal edge of the sclera. In our material, unfortunately, all examples displaying this stage in development have been slightly recrystallized.

(*c*) A little later, the lens has become thicker, as has the sclera, and the proximal surface of the lens has assumed a Huygensian form (figures, 2*c*, 20). In some of our specimens at this stage there are good indications of curved laminations in the upper part of the lens, even though there has been some degree of recrystallization.

DESCRIPTION OF PLATES 1–3

PLATE 1

Phacops rana milleri Stewart 1927, Middle Devonian, Silica Shale, Ohio.

FIGURES 5, 7–10. Mature and post-ecdysial specimens in various stages of development.

FIGURE 5. A large, thin-cuticled (30 μm), recently ecdysed individual (left) overlies an exuvial cephalon, and (right) thoracopygon (AMNH 29282). Magn. × 1.7.

FIGURE 7. Thick-cuticled (135 μm) and nearly completed intermoult intaglio (RSM GY 1979.11.3). Magn. × 1.35.

FIGURE 8. Specimen with cuticle of intermediate thickness (40 μm), showing patches of darker material. Right eye now removed. Specimen figured by Levi-Setti (1975, p. 13, pl. 5) (RSM GY 1979.11.1). Magn. × 1.5.

FIGURE 9. Left eye of same. Magn. × 6.

FIGURE 10. Thin-cuticled (20 μm), post-ecdysial intaglio, indifferently preserved (RSM GY 1979.11.4). Magn. × 1.5.

FIGURE 6. *Cheirurus centralis* Salter 1853, Wenlock Limestone, Dudley. Thin-cuticled (20 μm) specimen shown for comparative purposes; cf. Lane 1971, pl. 5, figs 1–6, 8–12 (QUB 2732). Magn. × 1.5.

PLATE 2

Phacops rana milleri. Structure of post-ecdysial and mature cuticle.

FIGURE 11. Broken fracture surface of thin post-ecdysial cuticle, 35 μm thick, showing outer prismatic layer and thicker principal layer (AMNH 29282). Magn. × 650.

FIGURE 12. External surface of cuticle of same specimen, etched with EDTA and showing calcite crystallites of the prismatic layer; openings of 10 μm wide setal canals partially overlain by thin organic epicuticle (AMNH 29282). Magn. × 650.

FIGURE 13. External surface of unetched intermoult cuticle showing calcite crystallites of outer prismatic layer with a setal pit (AMNH 29282). Magn. × 2000.

FIGURE 14. Ground and etched section of intermoult cuticle showing etched outer prismatic layer (above), setal canals filled with secondary calcite, and triple layering (Gr I 46150). Magn. × 65.

FIGURE 15. Polished and etched section through intermoult cuticle, 300 μm thick, showing deeply etched outer prismatic layer and triple layering in the principal layer (Gr I 46151). Magn. × 45.

FIGURE 16. Similar section through intersegmental articulation of pleura showing loss of triple zonation (Gr I 46151). Magn. × 45.

PLATE 3

Phacops rana milleri.

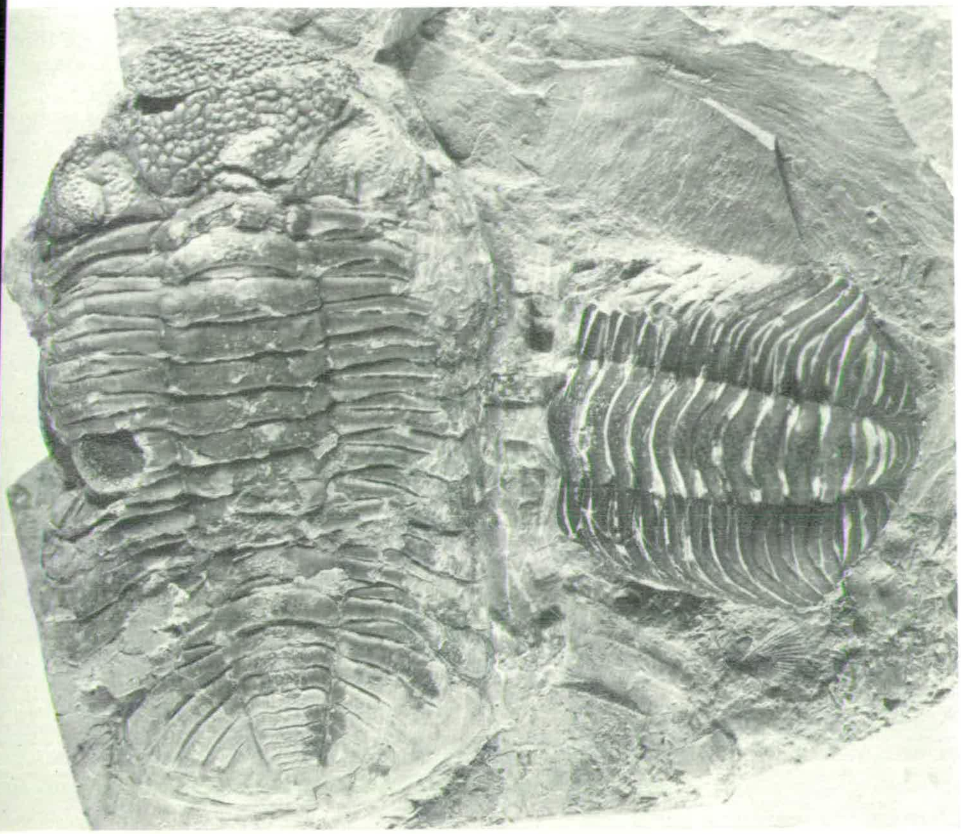
FIGURE 17. A single, etched, unaltered lens, cut obliquely off centre, showing radial lamellae of the upper unit, and bowl partially obscured by matrix (Gr I 46153). Magn. × 100.

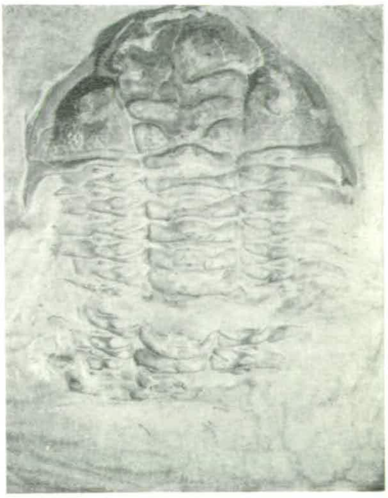
FIGURE 18. Post-ecdysial lens of biconvex form equivalent to stage 2 of figure 2*b*, somewhat micritized, cuticle 20 μm thick (RSM GY 1979.11.4). Magn. × 45.

FIGURE 19. Montage scanning a slightly oblique vertical section etched with EDTA, through four adjacent lenses of a single dorso-ventral file. This specimen has suffered very little diagenetic alteration. Lens A is grazed at the edge, showing the more massive texture of the intralensar bowl and the finer texture of the upper unit (see also figure 5 and plate 4). Lens B, cut almost centrally, shows the core (c.), intralensar bowl (i.b.), and upper unit (see also figure 26*j*). Deeply etched cleavage planes show the crystallographic structure of the calcite. Lens C, cut off centre, shows the bowl and the upper unit; only the edge of the bowl in lens D is present (Gr I 46152). Magn. × 100.

FIGURE 20. Post-ecdysial lens of Huygensian shape equivalent to stage 3 of figure 2*b*, somewhat altered, but with traces of laminae still present; cuticle, 50 μm thick (Gr I 46162).

FIGURE 21. Partially altered and recrystallized lens, which still retains traces of the bowl and pronounced laminae (Gr I 46154). Magn. × 100.





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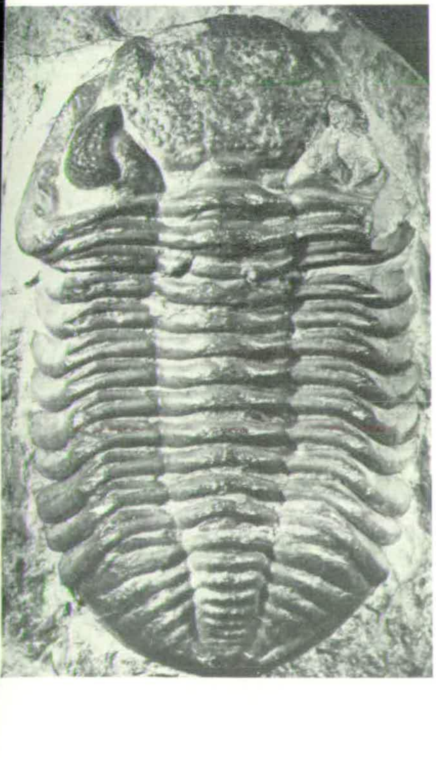

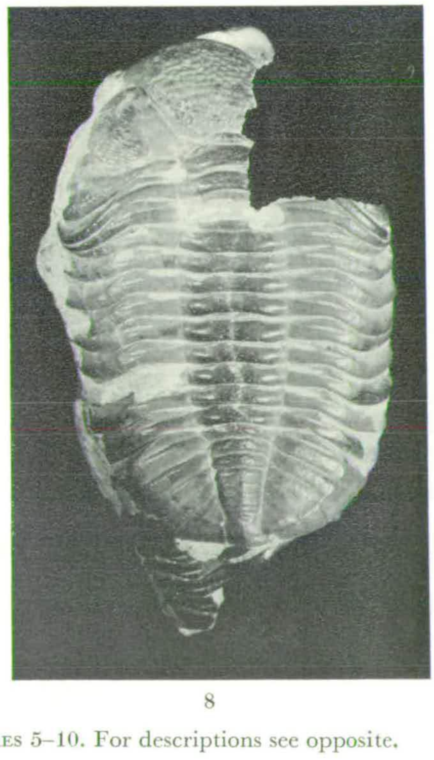

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FIGURES 5–10. For descriptions see opposite.

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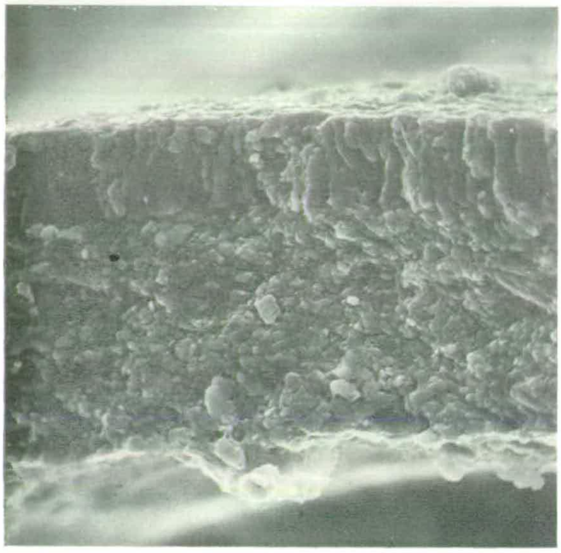

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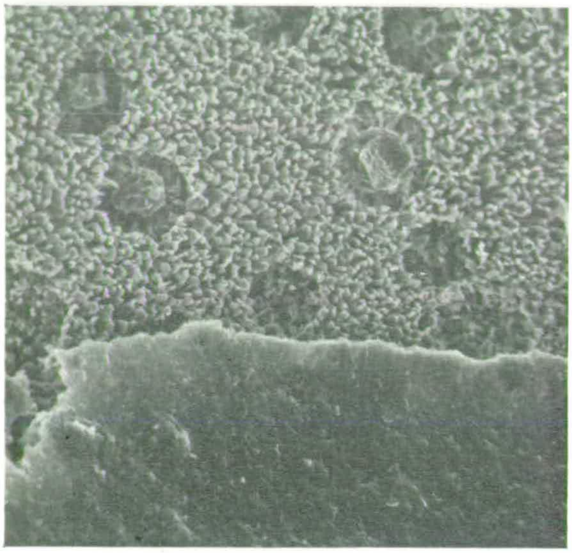

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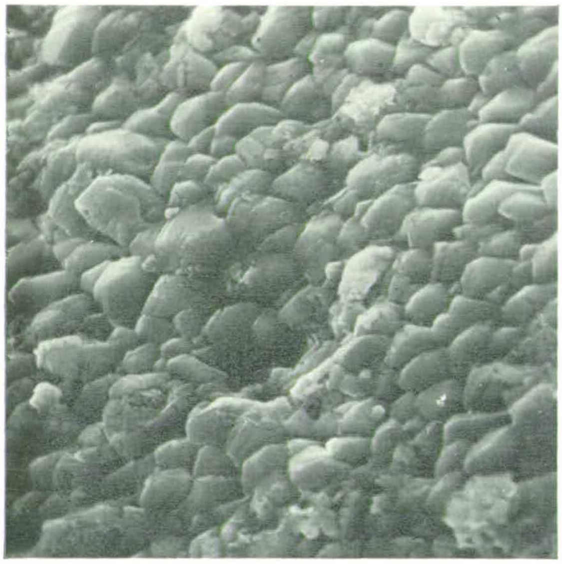

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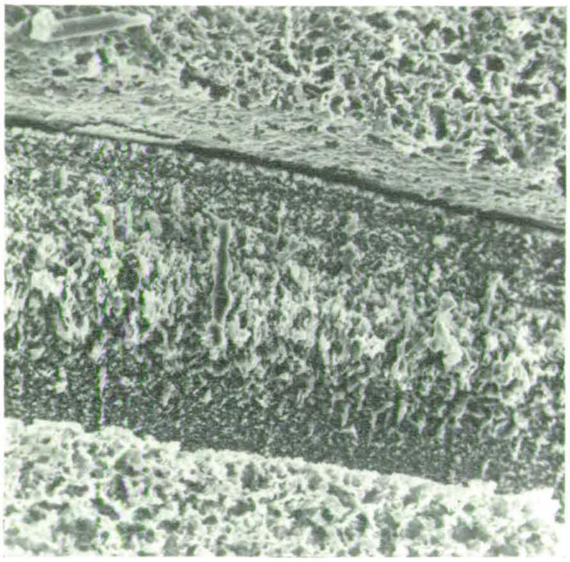

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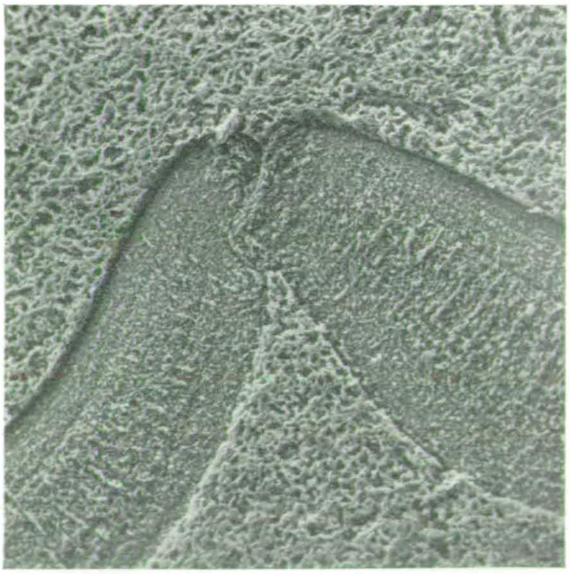
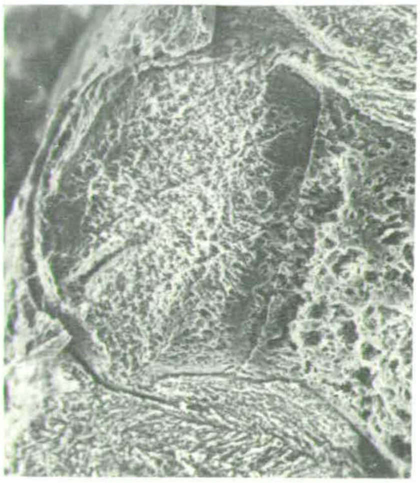


FIGURES 11–16. For description see page 476.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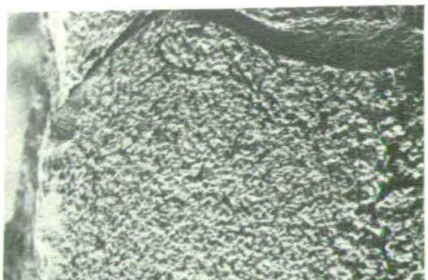
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FIGURES 17–21. For description see page 476.

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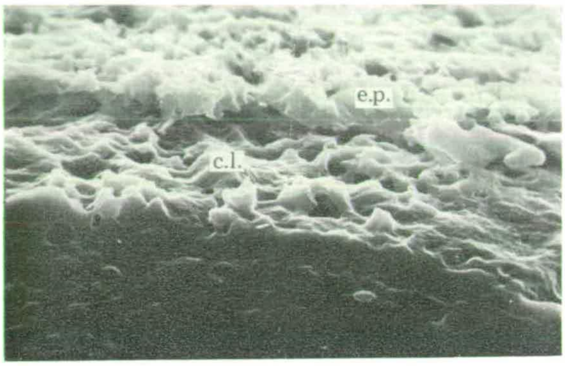

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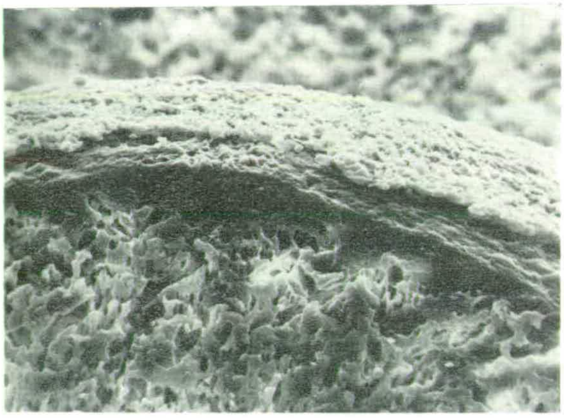

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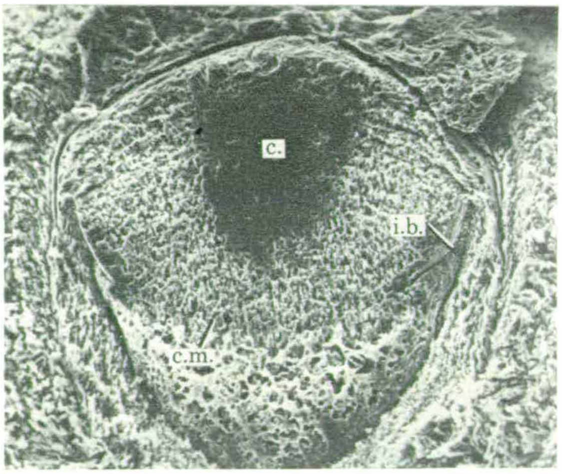

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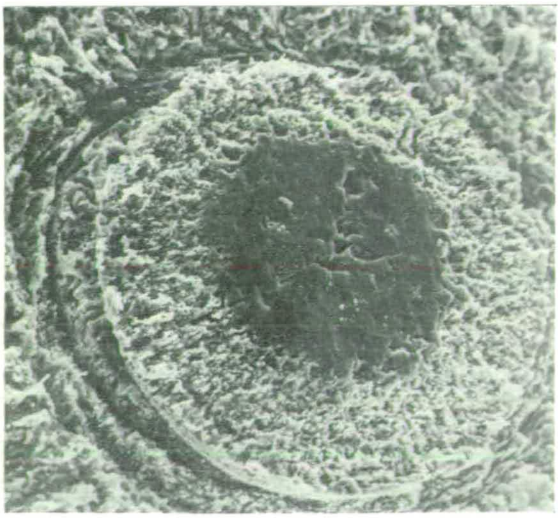

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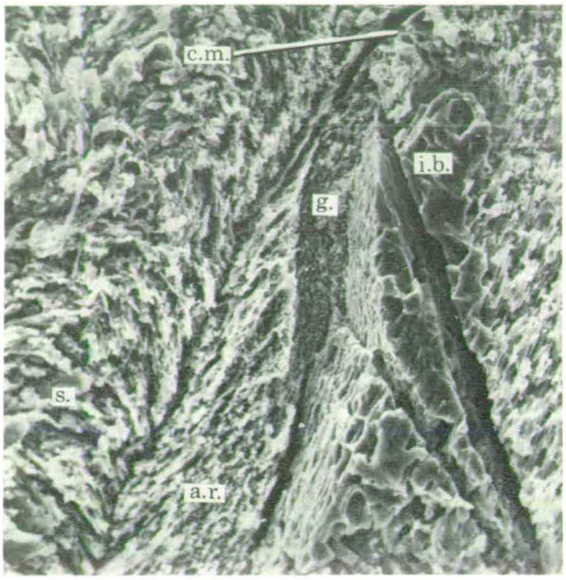

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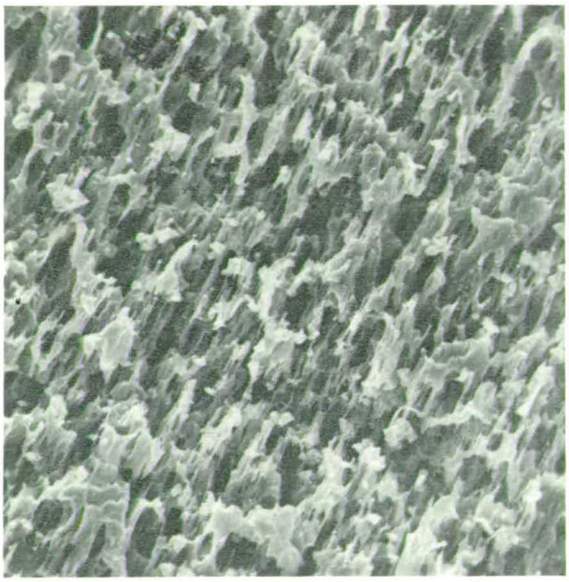

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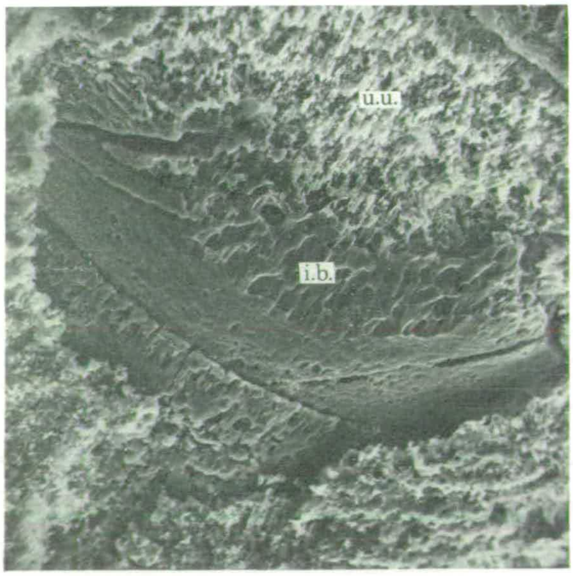

FIGURES 22–28. For descriptions see opposite.

DESCRIPTION OF PLATE 4

Phacops rana milleri.

FIGURES 22 AND 23. Oblique view of outer surface of vertically sectioned and etched lens, showing epicuticle (ep.), with surface of corneal layer (cl.) below lying above slightly recrystallized upper unit (Gr I 46155). Figure 22 magn. × 1800; figure 23 magn. × 435.

FIGURE 24. Single lens, cut obliquely and etched showing core (c.), slightly enlarged by diagenesis, radial lamellae, laminae, thin edges of intralensar bowl (i.b.), and, below, matrix filling of alveolus and corneal membrane (c.m.) (Gr I 46156). Magn. × 100.

FIGURE 25. Section cut in principal plane of lens, showing core, probably expanded by incipient diagenesis, slightly altered radial lamellae of upper unit, intralensar bowl (crescent on left hand side) and deeply etched ring of corneal membrane (Gr I 46157). Magn. × 100.

FIGURE 26. Left hand edge of lens B in figure 19, plate 3, with well marked calcitic bowl (i.b.) and upper unit traversed by a deeply etched cleavage plane; girdle (g.), sclera (s.), corneal membrane (c.m.) and alveolar ring (a.r.) (Gr I 46152). Magn. × 200.

FIGURE 27. Same lens showing etched trabeculae of upper unit in vertical section (Gr I 46152). Magn. × 400.

FIGURE 28. Enlargement of obliquely cut and etched lens A in figure 19, plate 3, showing junction of massive textured bowl (i.b.), and more open textured upper unit (u.u.) (Gr I 46152). Magn. × 200.

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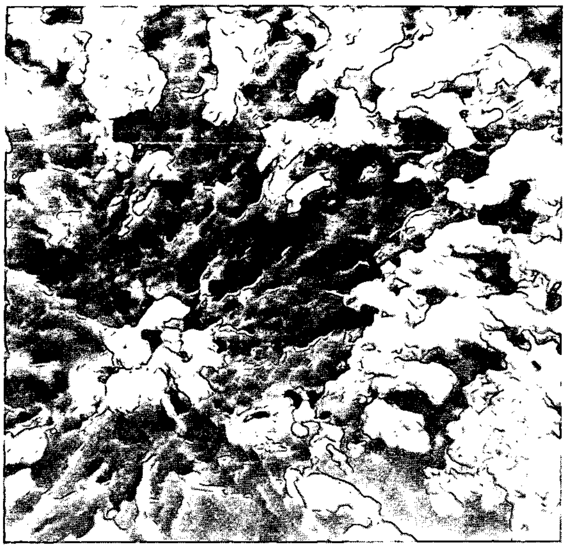

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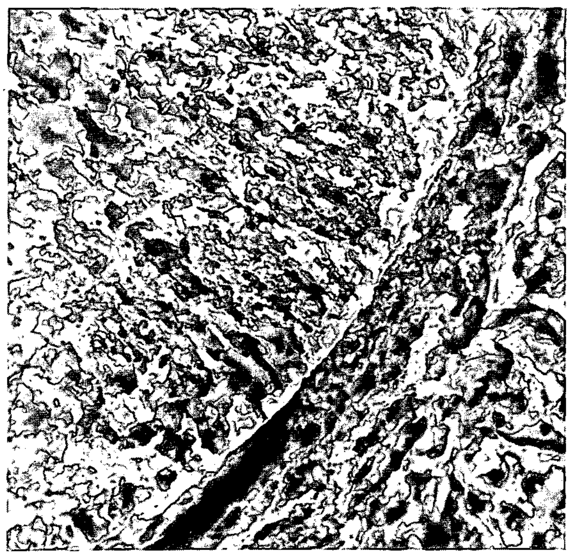

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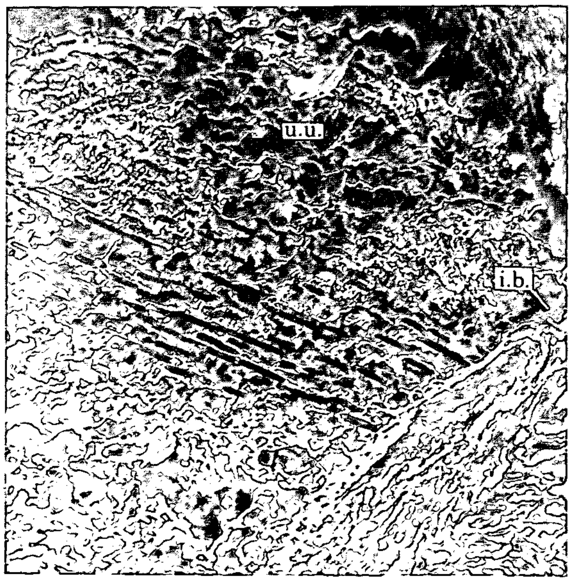

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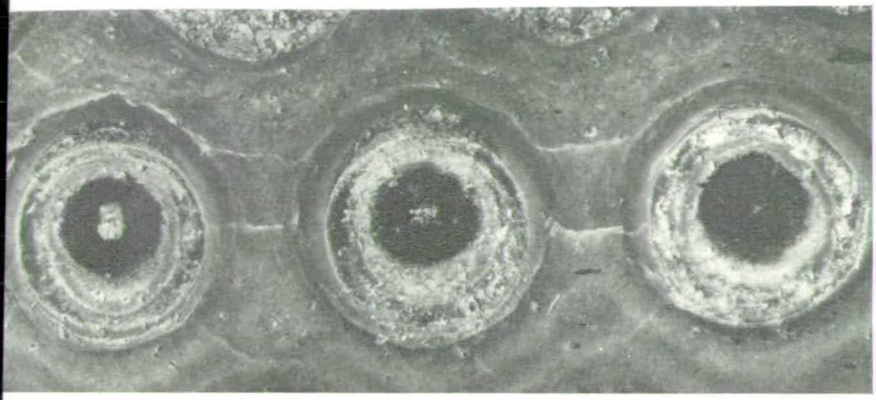
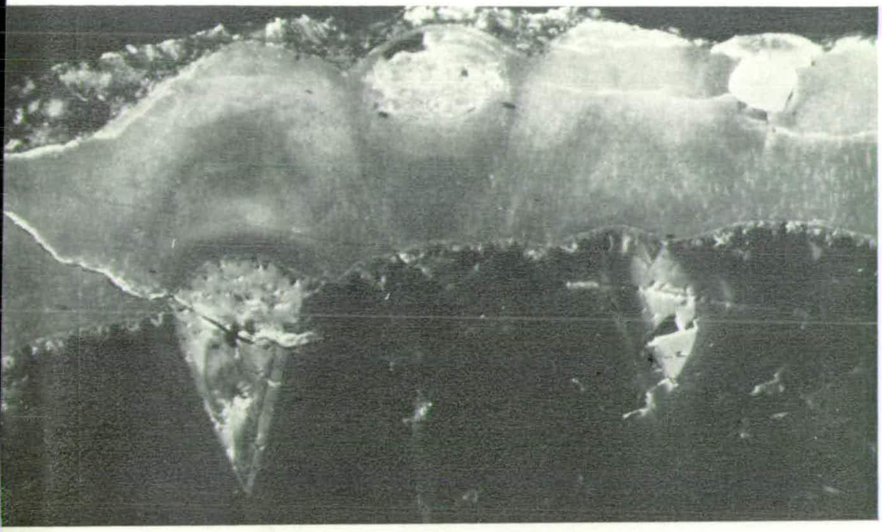
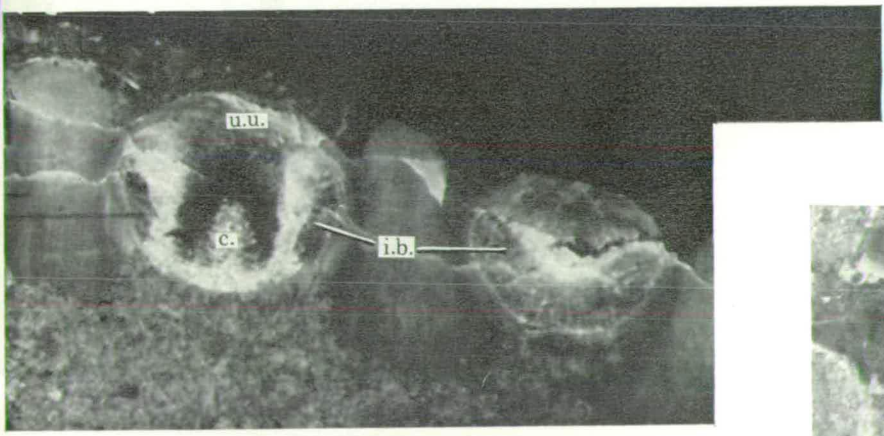
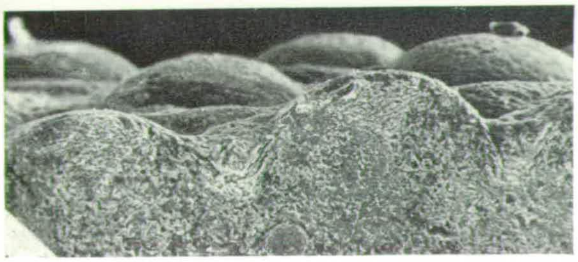
FIGURES 29–34. For description see page 477.









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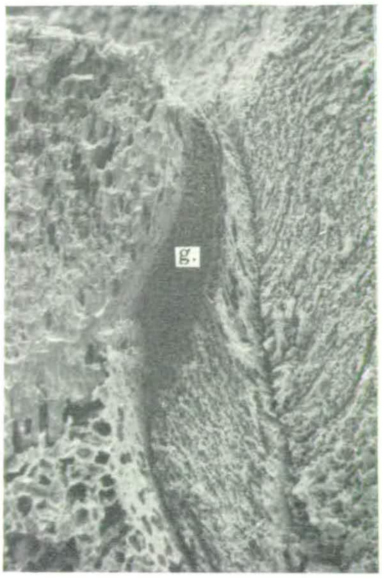

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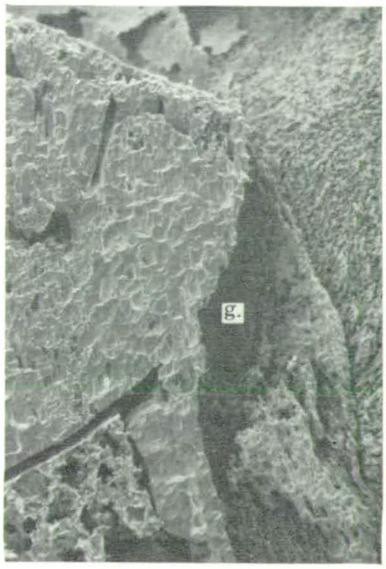

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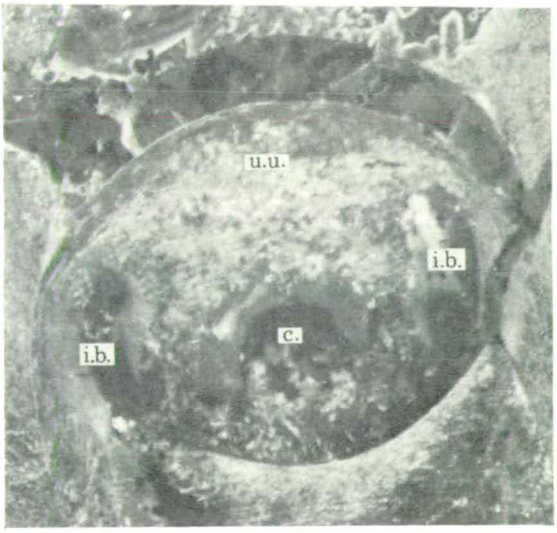

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FIGURES 35–41. For description see page 477.

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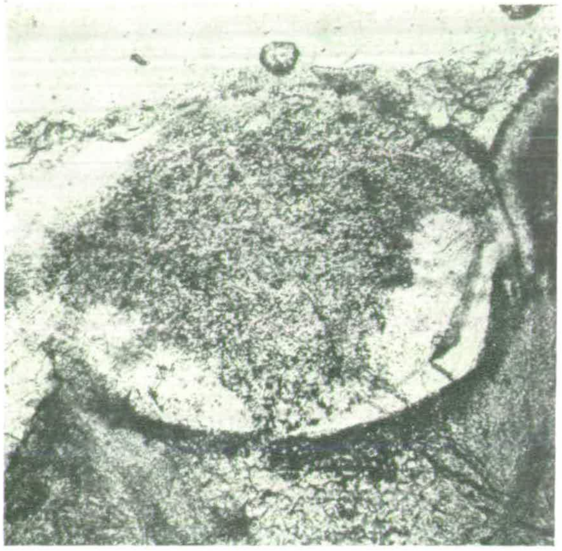

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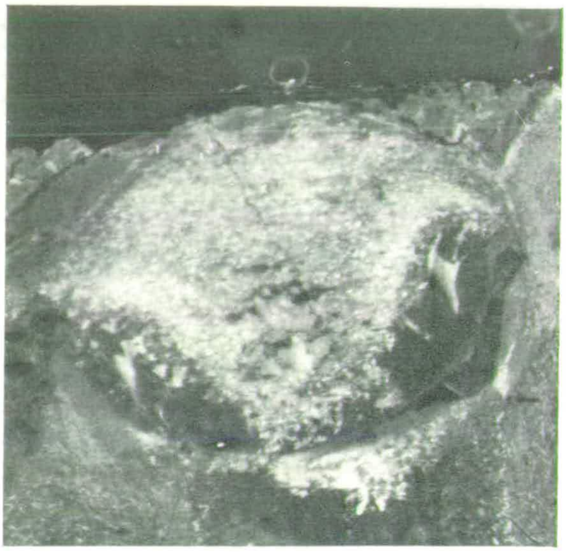

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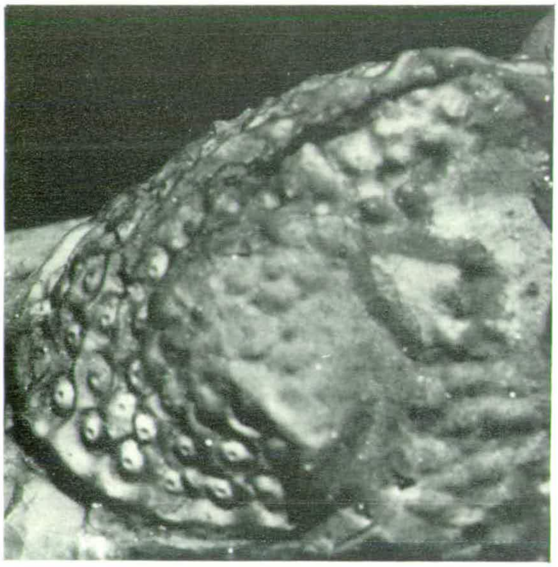

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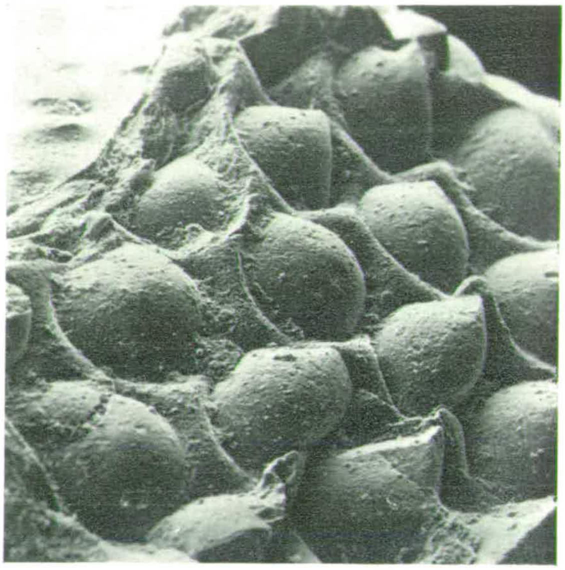

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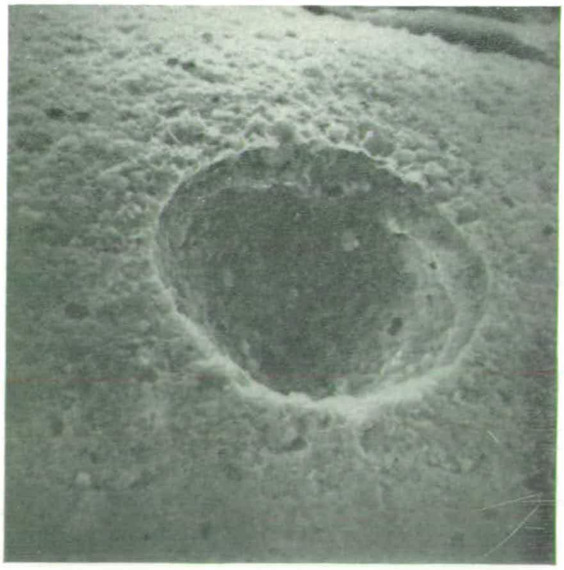

FIGURES 42–47. For descriptions see opposite.

DESCRIPTION OF PLATES 5–7

PLATE 5

Phacops rana milleri.

FIGURE 29. Etched upper surface of lens showing radial subcorneal structure and evidence of growth of upper unit in concentric zones (Gr I 46158). Magn. × 450.

FIGURE 30. Similar preparation of another lens (Gr I 46159). Magn. × 900.

FIGURE 31. Etched section of lens, cut parallel to principal plane, above the intralensar bowl. Core evidently expanded through diagenesis, but radial lamellae of the upper unit unaffected (Gr I 46160). Magn. × 180.

FIGURE 32. Radial lamellae of the same lens. Magn. × 450.

FIGURE 33. Substantially altered lens, cut tangentially, parallel with axis and etched. Intralensar bowl (i.b.) still discernible peripherally, but largely replaced below by recrystallizing calcite with pronounced cleavage planes. Upper unit (u.u.) also largely recrystallized (Gr I 46161). Magn. × 480.

FIGURE 34. Lens B of plate 3, figure 19, enlarged, showing unaltered bowl (i.b.), core (c.), trabeculae and laminae. The etching has opened up the cleavage planes in the calcite. Magn. × 180.

PLATE 6

Phacops rana milleri.

Figures 35–38. Lens structure revealed by cathodoluminescence microphotography.

FIGURE 35. Section parallel with principal plane of three lenses, showing core, upper unit, bowl, alveolar ring, corneal membrane and sclera in sequence away from the centre. A neomorphic calcite crystal is growing in the left hand lens (MPM 27063a). Magn. × 45.

FIGURE 36. Vertical section through cuticle with setal canals and zoned syntaxial crystals of secondary calcite cement below lenses (the latter out of the plane of section) (MPM 27063a). Magn. × 45.

FIGURE 37. Altered lenses in vertical section, which still retain parts of the bowl (i.b.), altered core (c.), dark central structure and upper unit (u.u.). Note intralensar laminae (MPM 27063a). Magn. × 15.

FIGURE 38. Single lens (MPM 27603a), cut in oblique vertical section, showing altered bowl (i.b.), part of core (c.) and laminations in upper unit (u.u.). Magn. × 80.

FIGURE 39. Post-ecdysial lenses in earliest stage of development, cut in vertical section and etched, showing initial conical shape of lens and thin cuticle, with only slight diagenetic alteration (RSM GY 1979.11.5). Magn. × 45.

FIGURES 40–41. *Phacops rana africanus* Burton & Eldredge, Devonian, Spanish Sahara.

FIGURE 40. Vertical section of edge of etched lens, partially recrystallized, with possible original trabeculae and bowl. The girdle (g.) is very distinct (BMNH 5687696). Magn. × 160.

FIGURE 41. Edge of another etched lens completely recrystallized and penetrated by borings, showing girdle and one of a pair of sublensar 'horns' seemingly continuous with the original lens structure and presumably forming a conical ring (BMNH 5687696). Magn. × 160.

PLATE 7

Phacops rana milleri.

FIGURES 42 AND 43. A tangential vertically sectioned lens, photographed in plane polarized light (figure 42) and with cathodoluminescent microphotography (figure 43), showing neomorphic partial replacement of the bowl and laminations in the upper unit. The core is mainly out of the plane of section (MPM 27063(a)). Magn. × 80.

FIGURES 44–47. The earliest stages in post-ecdysial development (all AMNH 29282).

FIGURE 44. Left eye, slightly crushed, photographed under alcohol. The dark spot seen through the transparent cornea is the early conical lens. Magn. × 9.

FIGURE 45. Wrinkled surface of right eye of same specimen. Magn. × 42.

FIGURE 46. Etched surface showing moulds of small conical lenses which have been dissolved out with EDTA. Magn. × 95.

FIGURE 47. Detail of a single etched conical lens. Magn. × 450.

Figures 45–47 are scanning electron micrographs.

(*d*) The mature lens (figures 3, 19, 34) has a properly developed intralensar bowl, and a central core. It is much thicker than in stage (*c*), but, for the first time, the sclera has thickened greatly so that its proximal surface lies well below the base of the lens. At all previous stages of development the lens capsule has been bounded internally by the inner face of the corneal cylinder, but in the mature lens both the girdle and the alveolar ring have grown inside the cylinder and are clearly very late-stage developments. Though all these new developments apparently happened quite rapidly, it has not been possible for us to tell from the material at hand whether they took place in a particular sequence or developed more or less simultaneously.

The post-ecdysial development of the lenses is therefore a process involving several stages of growth. There seems to be little change in the curvature of the upper surface of the lens, but new material, as would be expected, is accreted exclusively on the lower part of the lens and on the inner wall of the lens capsule.

7. Function in the developing eye

It seems pertinent to consider whether the conical shape of the immediately post-ecdysial lens was a functional adaptation or was merely a record of the only way in which the lens could grow. An analysis of the optics of the different developmental stages is beyond the scope of this paper, but one or two points seem clear. First, the optical function of the lens optimized as the lens developed and as the components within it differentiated. The eye must have reached maximum efficiency only when the cuticle had achieved its full thickness. The time scale of this process is not known, but the thickness of the cuticle is such that it must have been some time, perhaps even several days after ecdysis, before visual acuity could be returned to an optimal level. This seems to have been, at least to some extent, a limitation on trilobite organization to add to those occasioned by ecdysis itself.

The conical shape of the early lenses apparently was retained only during the period while the cuticle was flexible, so that the trilobite would not have been capable of much movement. In this state the animal probably had to hide, as do many newly ecdysed arthropods. Though there is not an exact equivalence, these conical lenses resemble the parabolic exocones of *Limulus* described by Levi-Setti *et al.* (1975) as ideal light concentrators. For a recently moulted trilobite, which needed to keep out of sight (possibly either by partial burial or by timing ecdysis at night-time), there would be a great value in having eyes highly sensitive to light for detection of potential enemies. The conical lenses could therefore have been optimized, at this early and most critical stage, for the best possible vision given their incomplete formation. The early lens shapes were certainly neither constructively the simplest nor the most economical of material. In the later stages of development the change in optical function is reflected in the change in shape of the lens.

8. The cuticular carbonate metabolism of *P. rana milleri*

Trilobites are exceptional among arthropods in their high degree of cuticular calcification (Dalingwater & Miller 1977). Crustaceans, the other major group to use calcification as a method of strengthening cuticle, rely on a combination of a histochemically tanned organic matrix impregnated with calcite and calcium phosphate in varying concentrations.

Considerable amounts of metabolic energy are expended in accumulating inorganic ions from the external environment and secreting them as cuticle deposits. Most crustaceans maximize efficiency by reducing loss of these materials in their cast exoskeleton through pre-ecdysial resorption of inorganic salts (Passano 1960). The resorbed calcium is added to newly acquired material for redeposition in early post-ecdysial calcification stages.

In *P. rana milleri*, *P. rana rana*, *P. rana crassituberculata* and *P. rana africanus* the entire calcified visual apparatus was shed along with the rest of the cuticle and was completely reformed after each ecdysis. Such a complete periodic renewal of a relatively thick calcite cuticle must have demanded considerable metabolic effort on the part of these trilobites, contributing considerably to the high physiological stress of their ecdysial cycle. If it is shown that most trilobites failed to resorb their cuticular carbonate, then we may speculate that the inefficiencies of this system might have put trilobites at a selective disadvantage compared with crustaceans competing for the same niches. Further, the demands of this high-turnover calcium carbonate metabolism could also have influenced both local (ecological) and stratigraphic (evolutionary) distribution of trilobites according to fluctuations in calcium availability and/or partial pressure of carbon dioxide. Further investigations along these lines could shed new light on the evolutionary biology of trilobites.

We are indebted to Dr N. Eldredge, Dr R. Levi-Setti and Professor A. D. Wright for donating specimens upon which this study is based. Dr J. E. Dalingwater provided much useful discussion on cuticular matters. S.e.m. photography was carried out at the Institute of Terrestrial Ecology, Bush, Midlothian, where Lynn Lamont gave valuable technical assistance. Mr D. Ince helped with macrophotography, and Mrs Janette Brunton typed the manuscript.

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UPPER LLANDOVERY TRILOBITES FROM THE PENTLAND HILLS, SCOTLAND

by EUAN N. K. CLARKSON *and* YVONNE HOWELLS

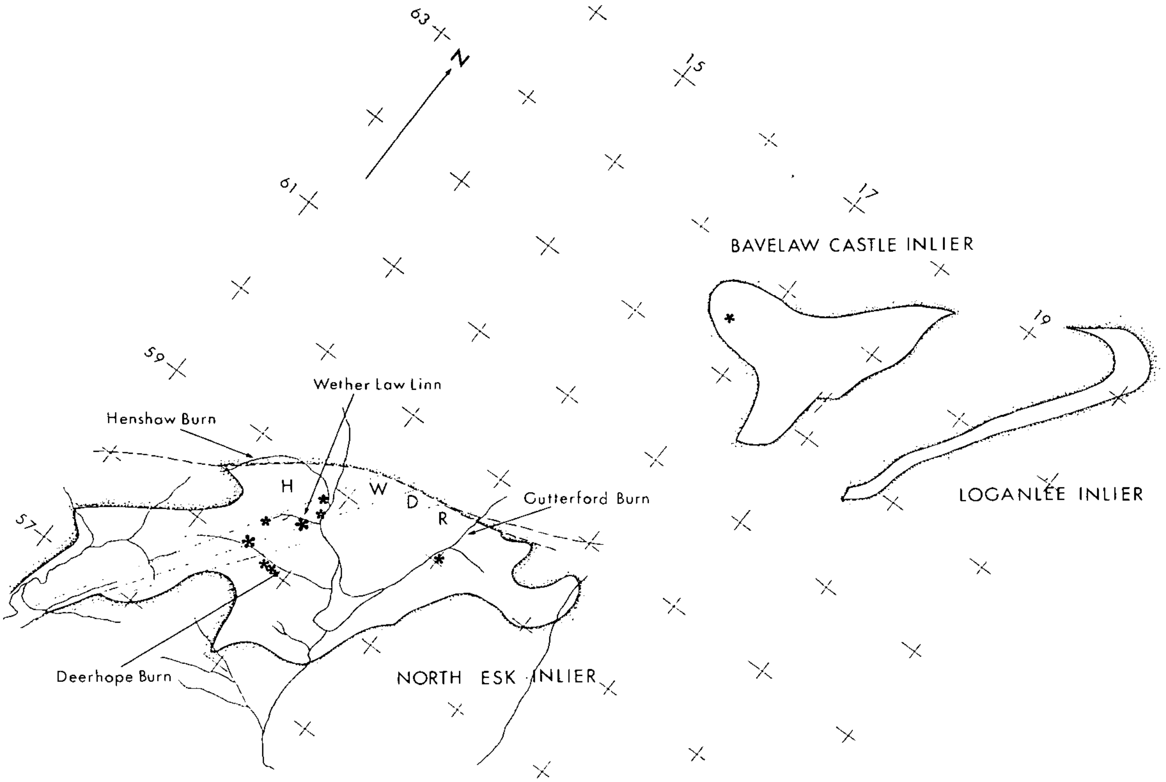
ABSTRACT. Well-preserved trilobites of Upper Llandovery age are reported from two of the three Silurian inliers in the Pentland Hills. In addition to two species of Phacopina previously described, there are some fifteen species belonging to Proetidae, Aulacopleuridae, Harpetidae, Cheiruridae, Encrinuridae, Calymenidae, Odontopleuridae, and Lichidae. In the older beds (Reservoir and Deerhope formations) trilobites are relatively rare and appear to be endemic to the Midland Valley of Scotland. In the succeeding lower part of the Wether Law Linn Formation the more abundant trilobites occur together with a rich brachiopod fauna and bear pronounced affinities with trilobites from the East Baltic. The hypostome of *Acernaspis* (*Eskaspis*) *sufferta* (Lamont) is described for the first time. New taxa described are *Cyphoproetus comitilis* n. sp. and *Harpidella* (*Harpidella*) *thomasi* n. sp.

SOUTH-WEST of Edinburgh, the Pentland Hills form an elevated chain some 35 km long, consisting mainly of Old Red Sandstone sediments and volcanics, and rising to a maximum height of about 600 m. The Old Red Sandstone rests unconformably upon almost vertical Silurian sediments, exposed in three inliers (text-fig. 1) (Mykura and Smith 1962; Tipper 1975, 1976). The largest and most westerly of these is the North Esk Inlier, within which are exposed Upper Llandovery marine sandstones and siltstones, passing up into a non-marine redbed sequence of Wenlock age. This latter is similar in facies to the overlying Lower Old Red Sandstone, but is separated from it by a pronounced angular unconformity. The Upper Llandovery beds are very fossiliferous in places, and the preservation is excellent, as has long been known; Geikie (1924) relates how he first discovered fossils therein and Haswell (1865) wrote that 'most of the eminent geologists with whom I have been corresponding . . . were quite astonished at their fossiliferous character'.

Many of the fossils are still undescribed, or have been figured only as photographs and sketches (Lamont 1948, 1965, 1978). Most of the trilobites described in the present work are from the highly fossiliferous Deerhope and Wether Law Linn Formations of the North Esk Inlier, of which a geological summary has been given by Mykura and Smith (1962), and Tipper (1975, 1976). Descriptions of the phacopid trilobites from the North Esk Inlier have already been presented as the first part of this study and a historical and geological summary given in Clarkson, Eldredge and Henry (1977). The Bavelaw Inlier consists of poorly fossiliferous pale-green mudstones but contains, in addition to a few inarticulate brachiopods, finely preserved specimens of *Leonaspis lothiana* (Lamont). Very little fossiliferous material is preserved in the Loganlee-Craigenterrie Inlier, where the lithology is similar.

Of the four formations defined by Tipper (1976) in the North Esk Inlier, the lower part of the Reservoir Formation is very patchily fossiliferous, other than the beds containing starfish (Spencer 1914–40) and eurypterids (Waterston 1979) and has yielded only a few indeterminate *Acernaspis* and *Encrinurus* specimens along the Gutterford Burn. The upper part of the Reservoir Formation has more fossils, chonetid brachiopods and bivalves (Lamont 1954) being especially common, and there is a highly productive coral bed (NT 147580), from which very rich coral-brachiopod faunas as well as *Proetus* (s.l.) cf. *latifrons* were obtained by S. D. G. Campbell in 1976 and 1977. Trilobites are relatively rare, but when found may be complete. Several well-localized specimens, in variable preservation (*Acernaspis*, *Encrinurus*, *Harpidella thomasi* n. sp.), were found by Peach, Horne, and McConochie at localities along the Deerhope Burn, below the coral bed, and are in the collections of the Institute of Geological Sciences, Edinburgh.

[Palaeontology, Vol. 24, Part 3, 1981, pp. 507–536, pls. 77–82.]



TEXT-FIG. 1. Sketch map showing the three Silurian inliers in the Pentland Hills relative to National Grid co-ordinates. Larger asterisks mark the most significant fossil localities, small asterisks show less important localities. R—Reservoir Formation; D—Deerhope Formation; W—Wether Law Linn Formation; H—Henshaw Formation. (Based on Tipper 1976.)

The overlying Deerhope Formation consists mainly of cross-bedded sandstones and conglomerates, but the upper part yields very abundant trilobites; *Podowrinella straitonensis* (Lamont) fragmentary *Encrinurus* specimens, and rare *Hemiarges rolfei* (Lamont), occuring along with the brachiopods *Isorthis* and *Glassia*.

Above this comes the highly fossiliferous Wether Law Linn Formation exposed at NT 145582 in the Deerhope Burn and NT 148586 in Wether Law Linn, of which faunal lists have been given by Tipper (1975, 1976). Whilst Tipper has documented a substantial change in the brachiopod faunas from unit A to unit C, marked by a white volcanic clay band, unit B, the trilobite fauna seems to have been relatively unaffected by this rapid pyroclastic deposition, so that in both units A and C there occurs *Proetus* (*Lacunoporaspis*) sp., *Cyphoproetus comitilis* n. sp., *Cyphoproetus depressus* (Barrande), *Calymene frontosa* (Lindström), *Encrinurus expansus* Haswell, *Youngia douglasi* Lamont, *Acernaspis* (*Eskaspis*) *sufferta* (Lamont), and *Anacaenapis dealgach* (Lamont).

A single large cheirurine hypostome was found by Tipper in unit C, in which very rare *Scotoharpes domina* Lamont also occurs, and a single unidentified odontopleurid pygidium was present at the junction of the upper Deerhope and Wether Law Linn Formations.

Unit D of the Wether Law Linn Formation is virtually unfossiliferous, though the holotype of *S. domina* came therefrom, but unit E, exposed in the Henshaw Burn yields *Encrinurus pagei* (Haswell), and from here also was collected a single *Scotoharpes* cephalon, and a fauna of brachiopods dominated by the Zygospirid *Pentlandella*.

A veteran student of trilobites from the Pentland Hills for more than thirty years has been Dr. A. Lamont, who in 1948 published a short paper with photographs of several trilobite species which were named but not described, and the validity of these names has in consequence been called into question. Whittington (1950) did not recognize *Scotoharpes* Lamont as a valid taxon, but Norford (1973) who had access to a plasticine replica of Lamont's material considered that it was, in fact, an available name. Likewise the specific name *sufferta*, for which *Acernaspis* (*Eskaspis*) was erected, was considered to be valid by Clarkson, Eldredge and Henry (1977). Recently Lamont (1978) published privately a more detailed work giving short descriptions of Pentland Hills trilobites, which were illustrated by sketches.

Dr. Lamont has kindly donated many of these specimens to the Royal Scottish Museum, so it has generally been possible to study these in detail. Lamont's nomenclature is accepted provided that Article 13a of ICZN is satisfied; such acceptance has been facilitated where the type specimens are well preserved and localized, and can be matched with equivalent material from the same horizons. The following species named by Lamont (1948, 1978) appear to come in this category: *Scotoharpes domina* (see Norford 1973; Clarkson *et al.* 1977); *Anacaenaspis dealgach* (*Bruxaspis dealgach* of Lamont 1978, syntypes available; *Leonaspis lothiana* (*Dudleyaspis lothiana* of Lamont 1948, 1978) holotype available; *Youngia douglasi*, holotype available; *Hemiarges rolfei*; (See Howells, in press). *Cyphoproetus glaudii* on the other hand is here considered *nomen nudum*. This species was figured in 1948 from two very poor specimens, a cranidium and a pygidium, but there was no accompanying description. In 1978 a hypostome and another cranidium were shown by sketches, but though there was a description the species cannot be identified from these alone and the specimens are now so abraded as to be unidentifiable. Hence the name *glaudii* should be suppressed. The other Pentland species figured (1948) or described and figured (1978) by Lamont, can be synonymized with established species (see following descriptions).

SYSTEMATIC DESCRIPTIONS

Family PROETIDAE Salter, 1864
Subfamily PROETINAE Salter, 1864
Genus PROETUS Steininger, 1831
Proetus (s.l.) cf. *latifrons* (McCoy, 1846)

Plate 77, fig. 6

1846 *Forbesia latifrons* McCoy, p. 49, fig. 11.
1973 *Proetus* (s.l.) *latifrons* (McCoy, 1846); Owens, p. 21, pl. 1, figs. 11, 12; pl. 2, figs. 1, 2, 4 (with synonymy).
1978 *Proetus* (s.l.) *latifrons* (McCoy, 1846); Thomas, p. 40, pl. 9, figs. 12, 13.

Figured Material. A single external mould of an incomplete specimen collected from the coral bed in the Upper Reservoir Formation at NT 147580, Deerhope Burn by S. D. G. Campbell, RSM GY 1978. 61. 524.

Dimensions. Cephalic length (sag.) 5 mm, width 5 mm, total preserved sagittal length of specimen (9 mm).

Remarks. The single specimen is incomplete, the front of the cephalon being broken, and only eight partial thoracic segments are still present. Nevertheless diagnostic features remaining include the broadly conical glabella, slightly wider than the axis of the occipital ring and the axis of the thorax, and the large occipital lobes.

Owens (1973) has shown that *P.* (s.l.) *latifrons* is probably confined to the Upper Llandovery of north-western Ireland, and the Wenlock Shale of the Mendip Hills, though some poorly preserved trilobites from Tortworth, May Hill, Shropshire, and Pembroke may also pertain to this species. If the specimen from the Reservoir Formation is truly *P.* (s.l.) *latifrons*, then the only point to be added to Owens's description is that the cranidium seems to be weakly granular.

Subgenus LACUNOPORASPIS Elkin, 1966
Proetus (*Lacunoporaspis*) sp.

Plate 77, figs. 4, 8-12

1948	*Proetus peeblesi*; Lamont, pl. 1, fig. 5.
1977	*Proetus latifrons* (McCoy); Clarkson *et al.*, pp. 120, 121 (list only).
1978	*Proetus* (*Forbesia*) *pitcairni* sp. nov. Lamont, p. 265, pl. xxx, figs. 1-4.
1978	*Proetus* (*Scotoproetus*) *fergali* subgen. et sp. nov. Lamont, p. 266, pl. xxx, fig. 5.
1978	*Proetus* (*Cornuproetus*) *dicuili* sp. nov. Lamont, p. 266, pl. xxx, figs. 8-10.
1978	*Praedechenella peeblesi* (Lamont, 1948); Lamont, p. 268, pl. xxx, fig. 13.

Figured material. Cranidia; RSM GY 1978. 61. 391, (Pl. 77, fig. 8): —399 (Pl. 77, fig. 9); —395, (Pl. 77, fig. 10); —393 (Pl. 77, fig. 11) (also figured Howells, in press); —394 (Pl. 77, fig. 12) and RSM GY 1979, 45. 3 (Pl. 77, fig. 4) (also figured Lamont? 1948, 1978 as *Praedechenella peeblesi*).

Other material. Cranidia; RSM GY 1978. 61. 384, —386, —90, —392.

Distribution. Cranidia of this species are quite common in units A and C of the Wether Law Linn Formation at NT 145582 and NT 148586, but they are often distorted or laterally compressed, giving rise to a rather wide variety of forms and hence to the range of separate 'species' described by Lamont. Thus the specimen upon which Lamont (1948) based the name '*Proetus peeblesi*' though unrecognizable from the photograph was described as having 'a remarkably long narrow conical central lobe' which might seem to validate the name under Article 13a of the Rules. Comparison with other specimens, however, shows that this morphology is quite atypical and is entirely due to lateral compression. The name '*peeblesi*' should be therefore suppressed as *nomen nudum*. Whilst some distorted librigenae and pygidia might belong to this species better material is awaited before figuring them.

Dimensions. Cranidia range in size from 4·0 to 5·5 mm in length, and have a glabellar width across the base 3·5 to 4·5 mm.

Description. Cranidium about as wide as long. Glabella tapering forwards to bluntly rounded point, as long as wide across base, slight constriction opposite 2S, moderately inflated, normally reaching anterior border. 1S abaxial branch opposite midpoint of palpebral lobe transverse, adaxial branch running backwards at about 50° to exsagittal line dying out before reaching occipital furrow. Small shallow depression continuing line of abaxial branch. 2S opposite anterior limit of palpebral lobe, shallower than 1S, backwardly directed, about one-third way from 2S to anterior end of glabella. Anterior border not greatly inflated, one-eighth length (sag.) of cranidium. Occipital furrow deep, median part transverse, laterally curving anteriorly. Occipital ring as wide as glabella, one-seventh length (sag.) of cranidium, with median tubercle. Occipital lobes small, ovate, depressed below level of glabella. Anterior branch of facial suture diverging at about 10° to exsagittal line from anterior limit of palpebral lobe, curving adaxially as crosses anterior border. Posterior facial suture diverging slightly and

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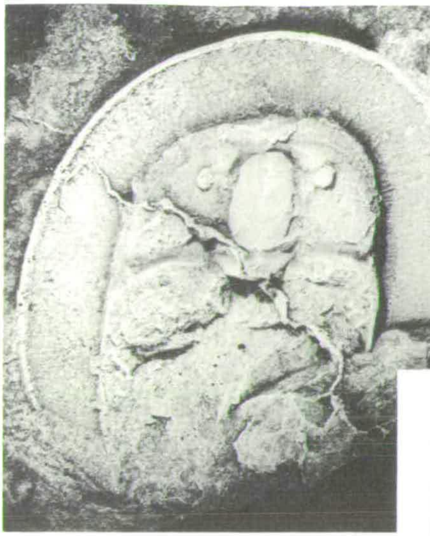
EXPLANATION OF PLATE 77

Figs. 1, 2. *Scotoharpes domina* Lamont. Wether Law Linn Formation, unit E, Henshaw Burn. North Esk Inlier. 1. Latex replica of external mould, RSM GY 1978. 61. 504b, × 3. 2. Lower lamella of fringe, RSM GY 1978. 61. 504a, ×6·5.

Figs. 3, 5, 7. *Cyphoproetus comitilis* n. sp. Wether Law Linn Formation, unit A, Deerhope Burn; paratypes. 3. Incomplete specimen, internal mould. RSM GY 1978. 61. 419, ×8. 5. Latex replica of thoracopygon, RSM GY 1978. 61. 411, ×6. 7. Librigena, internal mould, RSM GY 1978. 61. 416, ×6·5.

Figs. 4, 8-12. *Proetus* (*Lacunoporaspis*) sp. Wether Law Linn Formation, units A and C, Deerhope Burn and Wether Law Linn; cranidia. 4. RSM GY 1979. 45. 3, figured by Lamont 1978 as *Praedechenella peeblesi*, ×5·25. 8. Internal mould, RSM GY 1978. 61. 391, ×6. 9. RSM GY 1978. 61. 399, ×6. 10. RSM GY 1978. 61. 395, ×6. 11. RSM GY 1978. 61. 393 (also figured Howells, in press), ×6. 12. RSM GY 1978. 61. 394, ×6 (9-12; latex replicas of external moulds).

Fig. 6. *Proetus* (s.l.) cf. *latifrons* (McCoy), Coral bed in Reservoir Formation, Deerhope Burn. Incomplete specimen, latex replica of external mould, RSM GY 1978. 61. 524, ×6.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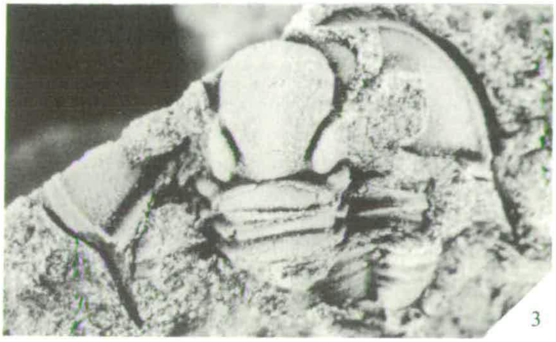
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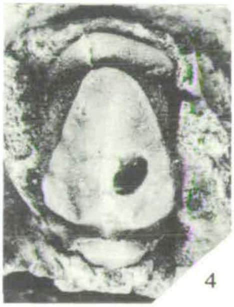
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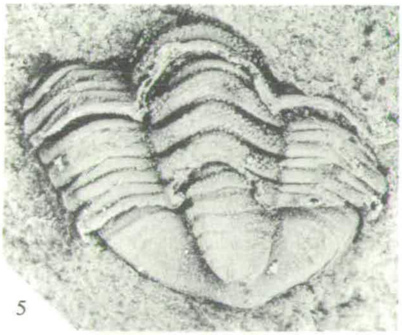
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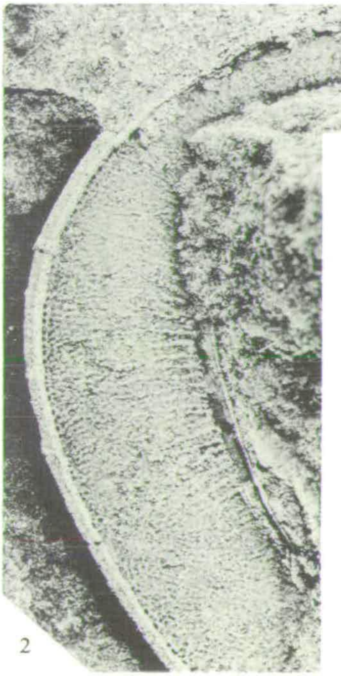
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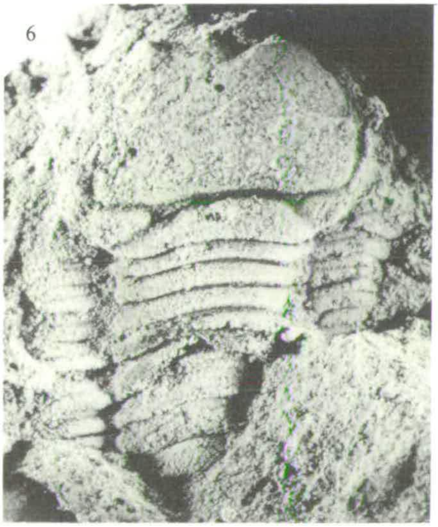
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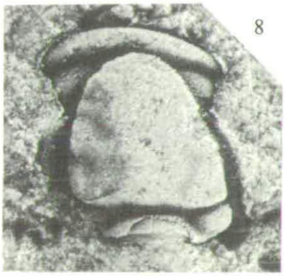
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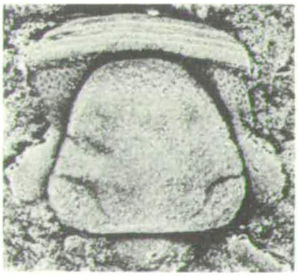
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CLARKSON and HOWELLS, Silurian trilobites

then more sharply posteriorly, but crossing posterior borders a short distance from the glabella (above the width of the occipital lobes). Palpebral lobe about one-third sagittal length of cranidium. Surface sculpture of cranidium nearly smooth, with slight granularity.

Discussion. The cranidia from the Pentland Hills resemble those of *P*. (*L*.) *confossus* Owens, 1973 in form, but the glabellar furrows are more deeply impressed and the glabella is less inflated. the palpebral lobe is appreciably longer and is set further back than that of *P*. (*L*.) *confossus*, resembling more that of *P*. (*L*.) *oppidanus* Thomas, 1978. The latter, however, has a longer and narrower glabella, as has *P*. (*L*.) *obconicus* (Lindström, 1885) and 1S and 2S in these species do not connect with the axial furrow. Librigenae occurring in the same beds which may belong to this species are poorly preserved but do not seem to have the characteristic pitting of *P*. (*L*.) *confossus* and *P*. (*L*.) *obconicus* and in view of this and their longer genal spines are closer to those of *P*. (*L*.) *oppidanus*.

The species does not closely resemble *P*. (s.l.) *latifrons* (McCoy, 1846) as described by Owens (1973), since in the latter the base of the glabella is relatively wider and the glabellar furrows not at all impressed.

In the absence of good librigenae and pygidia no further determinations can yet be made. The specific name *pitcairni* may be available for this species but since the material gathered to date consists of isolated fragments only, we feel for the moment that it is wisest to leave this under open nomenclature until more complete specimens come to hand.

Genus CYPHOPROETUS Kegel, 1927

Cyphoproetus comitilis n. sp.

Plate 77, figs. 3, 5, 7; Plate 78, figs. 1, 2, 4, 5, 7, 9–11.

?1948 *Cyphoproetus glaudii* Lamont, pl. 1, figs. 3–4.
1977 *Cyphoproetus depressus* (Barrande,1846); Clarkson *et al*., pp. 120, 121 (list only).
?1978 *Cyphoproetus* (*Carlopsia*) *glaudii* Lamont; Lamont, p. 267, pl. xxx, figs. 6, 7.
?1978 *Cyphoproetus* cf. *puncticillosus* (Lindström); Lamont, p. 267, pl. xxx, fig. 12.

Type material. Holotype; RSM GY 1978. 61. 400a, b (complete specimen, part and counterpart) (Pl. 78, figs. 1, 2, 4, 11). Paratypes; (complete or partial specimens) RSM GY 1978. 61. 401 (Pl. 78, fig. 5); —404 (Pl. 78, fig. 9); —411 (Pl. 77, fig. 5); —413 (Pl. 78, fig. 7); —419 (Pl. 77, fig. 3); —416 (Pl. 77, fig. 7).

Other material. About thirty other specimens in the Royal Scottish Museum collections, including RSM GY 1978. 61. 406, —410, —412, —414, and —415.

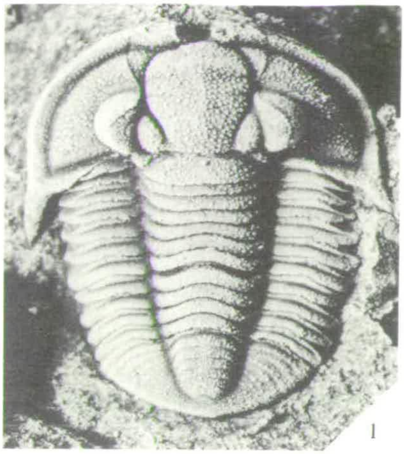
Etymology. *comitilis* (Latin) means 'small companion', since the species occurs in association with the larger, closely related *C. depressus* at the same horizon.

Distribution. This species occurs not infrequently in units A and C of the lower Wether Law Linn Formation both at NT 145582 and NT 148586. It is especially common just below the white clay band, (unit B of Tipper, 1975, 1976). It seems to be confined to this horizon in the Telychian.

EXPLANATION OF PLATE 78

Figs. 1, 2, 4, 5, 7–9, 11. *Cyphoproetus comitilis* n. sp. Wether Law Linn Formation, units A and C. Deerhope Burn (1, 2, 4, 5, 11) and Wether Law Linn (7–9). 1, 2, 4, 11. Holotype, RSM GY 1978. 61. 400a. 1, 2. Latex replica of external mould of intaglio, ×6. 4. Internal mould of holotype, RSM GY 1978. 61. 400b, ×6. 11. Enlargement of glabella showing surface sculpture, ×14. 5. external mould of partial specimen RSM GY 1978. 61. 401*, ×6. 7. Latex replica; external mould of enrolled specimen, RSM GY 1978. 61. 413*, ×7. 9. Internal mould of almost complete specimen, RSM GY 1978. 61. 404*, ×6. * paratypes.

Figs. 3, 6, 8, 10. *Cyphoproetus* cf. *depressus* Lindström. Wether Law Linn Formation, units A and C, Deerhope Burn (6, 8, 10) and Wether Law Linn (3). 3. Almost complete specimen, latex replica external mould, RSM 1978. 61. 404, ×3·5. 6. Partial, crushed specimen, latex replica of external mould, RSM 1978. 61. 403, ×3·75. 8. Damaged cranidium, internal mould, RSM GY 1978. 61. 417, ×5. 10. Cranidium internal mould; RSM GY 1979. 45. 4, figured by Lamont (1978, pl. xxx, fig. 6) as *Cyphoproetus* (*Carlopsia*) *glaudii*, ×5.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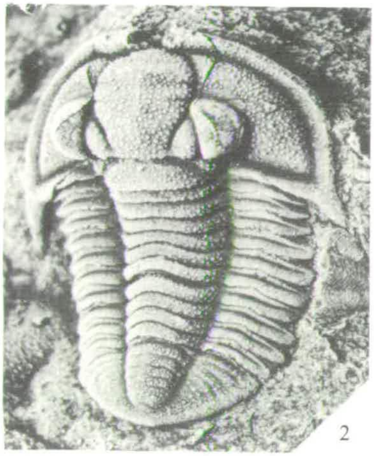
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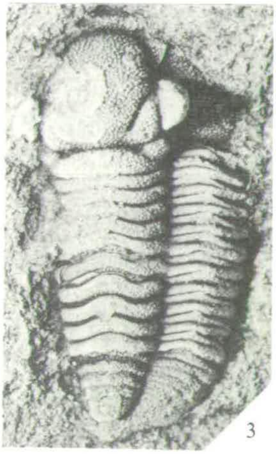
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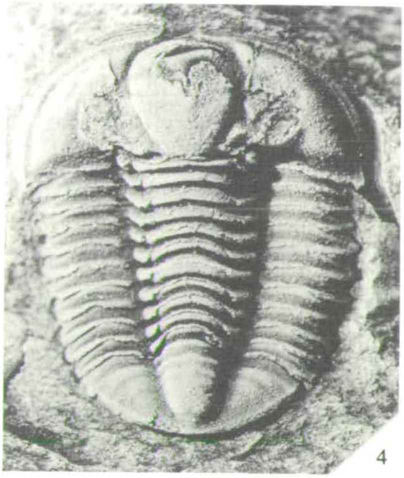
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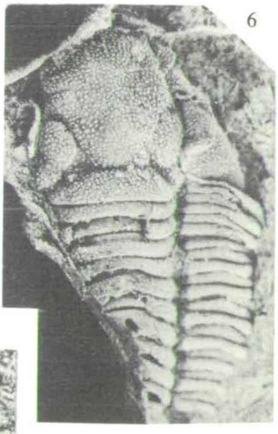
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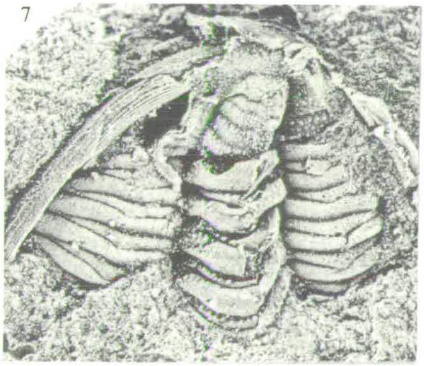
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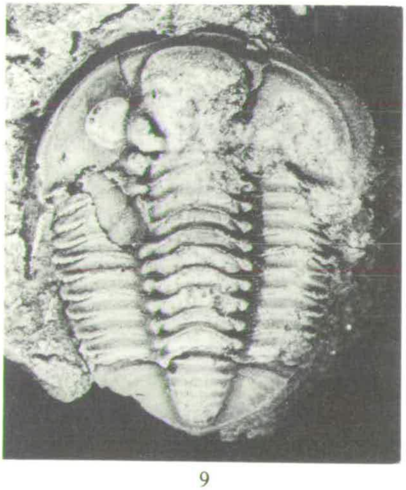
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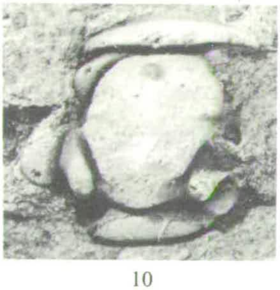
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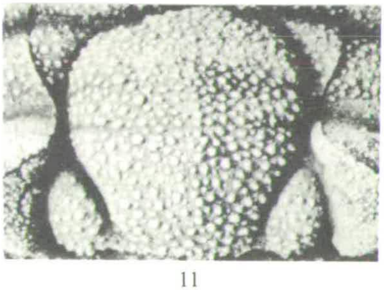
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CLARKSON and HOWELLS, *Cyphoproetus*

Diagnosis. Small *Cyphoproetus* with deep 1S, 2S, and 3S clearly defined, 4S very shallow, anterior border not sagitally widened, lacking pre-glabellar field sagittally, lateral cephalic margin incurved at base of genal spine, a faintly defined glabellar lobe adaxial to 1S and opposite 1L is visible on internal moulds.

Dimensions. Holotype. Total length 8·5 mm, width 8·0 mm, cephalic length (sag.) 2·6 mm. Range in total length 8–11 mm.

Description. Cephalon moderately convex, virtually twice as wide (tr.) as long (sag.), one-third length of dorsal shield. Glabella only very slightly longer (sag.) than wide (tr.), weakly inflated, straight-edged anteriorly. 1S deep and wide at its midlength shallowing more rapidly posteriorly and merging into occipital furrow, remaining relatively deep anteriorly until just before axial furrow where it shallows rapidly, aligned at 20° to exsagittal line, running backwards from opposite anterior limit of palpebral lobe and defining 1L. 1L ovate, two-fifths exsagittal length of glabella, one-sixth its basal width (tr.), rounded posteriorly, slightly pointed in outline anteriorly. 2S transverse, shallowing adaxially, just anterior to anterior limit of palpebral lobe. 3S transverse or running forwards slightly, just a little shorter (tr.) than 2S. ?4S very shallow transverse depression seen only on internal mould midway between 3S and anterior limit of glabella. In some specimens and particularly on internal moulds, a faintly defined rounded lobe about half the length of 1L appears to lie adaxial to 1S (see Pl. 78, figs. 2, 9). Occipital furrow narrow (sag.), well-defined, deepening a little where it curves laterally and posteriorly around posterior limit of 1L. Occipital ring one-sixth length (sag.) of cranidium, as wide (tr.) as anterior border, five times wider than long. Median tubercle anteriorly placed. Occipital lobe small, ovate, about three-quarters length (exsag.) of occipital ring.

Anterior border, convex, one-eighth length (sag.) of cranidium. Anterior border furrow of cranidium deep and well-defined. Preglabellar field absent sagittally but present laterally as subtriangular area, convex, but depressed below level of glabella and anterior border. Anterior branch of facial suture diverging abaxially forwards at 20° from opposite 2S, curving adaxially forwards from anterior border furrow. Posterior branch of facial suture initially almost transverse then running at 70° to the exsagittal line, cutting the posterior border midway along its length. Palpebral lobe subparabolic, abutting against 1L. Visual surface of eye strongly curved in plan and profile and with many tiny lenses and shallow subocular furrow.

Field of librigena moderately convex. Lateral border widens a little posteriorly but incurved at base of genal spine. Lateral border furrow shallower than anterior border of cranidium. Posterior border furrow deeper and narrower than lateral border furrow. Posterior border slightly narrower than lateral border, merging with lateral border to produce short genal spine without median furrow and which extends at least as far as fourth thoracic segment. All raised surfaces very finely granulated. Cephalic doublure with terrace ridges, reaching at least as far as limit of raised border.

Thorax of ten segments. Axis one-third width (tr.) of thorax narrowing posteriorly to three-quarters anterior width. Axial ring short (sag.) eight times wider than long. Adaxial part of pleuron horizontal and transverse recurving ventrally beyond fulcrum. Pleuron terminating laterally as blunt point.

Pygidium approximately twice as wide as long. Axis about one-third total pygidial width anteriorly, tapering backwards to blunt point, with very weak postaxial ridge present on internal moulds. Five axial rings delimited by shallow axial ring furrows. Pleural areas with four pairs of ribs which curve gently backwards abaxially. Pleural and interpleural furrows shallow and both extending close to margin. Thoracic axis and pygidium have smaller and less dense granules than those of cephalon.

Discussion. From Owens (1973, p. 28, Table 5) the non-sagittally widening anterior border of the Pentland Hills species is also found in *C. facetus* Tripp, 1954, *C. rotundatus* (Begg, 1939), both Ordovician, and *C. externus* (Reed, 1935), Llandovery. However, *C. comitilis* can be distinguished from *C. externus* which possesses a minute preglabellar field, and from the two Ordovician species in that the lateral cephalic margin incurves at the base of genal spine. The other Silurian forms *C. depressus* (Barrande, 1846), *C. binodosus* (Whittard, 1938), *C. strabismus* (Owens, 1973), and a new species from the Llandovery of Girvan are distinct from the Pentland form in possessing a sagittally widened anterior border. The specimens upon which Lamont based the name *C. glaudii*, though available, are now so badly abraded that it is not possible to tell from these whether the species represented is *C.* cf. *depressus* or *C. comitilis*. Likewise the drawings in Lamont's 1978 work and his photograph (1948, pl. 1, fig. 3) are of distorted and poorly preserved specimens which cannot be assigned to either species.

Cyphoproetus cf. *depressus* (Barrande, 1846)

Plate 78, figs. 3, 6, 8, 10

1846 *Cyphaspis depressus* Barrande, p. 60.
1946 *Cyphoproetus depressus* (Barrande), Přibyl, p. 36, pl. 1, figs. 9, 9*a*.
1948 ?*Cyphoproetus glaudii* Lamont, pl. 1, figs. 3, 4.
1978 ?*Cyphoproetus* (*Carlopsia*) *glaudii* subgen. et sp. nov. Lamont, p. 267, pl. xxx, figs. 3, 4.

Material and remarks. Specimens include RSM GY 1978. 61. 403 (Pl. 78, fig. 6); —405 (Pl. 78, fig. 3) —417 (internal moulds of cephala); —402 (a partially decalcified external mould, not figured); and 1979. 45. 4 (Pl. 78, fig. 10 figured by Lamont, 1978 as *C. glaudii*). This species is appreciably larger than *C. comitilis* though well within the size range of *C. depressus*, quoted by Owens for the species, the sagittal lengths of the cranidia for specimens —403, —405, and —407 being 6·5, 5·75, and 6·0 mm respectively. The sagittal flattening and widening of the anterior border is most clearly seen in 1979. 45. 4, though in neither of the large complete specimens are the genal spines preserved. In all other respects, e.g. the shape and dimensions of the 1L lobes, the form of the glabella, and the granulation of the exoskeleton, the specimens approximate *C. depressus*. 1S in 1978. 61. 405, very deeply incised medially, is very like that of specimens from Dolyhir figured by Thomas (1978, pl. 11, figs. 1, 2). All specimens come from unit A of the Wether Law Linn Formation at NT 145582, just below the white clay band, unit B.

Family AULACOPLEURIDAE Angelin, 1854
Genus HARPIDELLA McCoy, 1846

Remarks. Thomas and Owens (1978) have discussed the taxonomic status of the genus and Thomas (1978) has listed the known species.

Harpidella (*Harpidella*) *thomasi* n. sp.

Plate 79, figs. 1, 2, 16

Holotype. The holotype and only known specimen (part and counterpart, GSE 13519 —20), 6·5 mm broad to tips of genal spines, was collected by W. MacConochie on the south bank of the Deerhope Burn and comes from the uppermost beds of the Reservoir Formation at NT 148580. An isolated pygidium 3·5 mm broad (GSE 13517) may possibly belong to this species.

Etymology. After Dr. A. T. Thomas, in respect of his work on Aulacopleuridae.

Diagnosis. A *Harpidella* (*Harpidella*) species with anterior border of uniform length sagittally and exsagittally, smooth exoskeleton, glabella half total length (sag.) of cephalon and stout recurved genal spine.

Description. Cephalon semicircular to subtrapezoidal, border most strongly curved where cut by anterior branch of facial suture and twice as wide (tr.) as it is long (sag.) (to base of genal spine). Cranidial length more than three-quarters its width. Occipital ring convex nearly as wide (tr.) as distance from occipital furrow to anterior border furrow, with a low occipital granule. Occipital furrow deep and narrow. Glabella flush with general convexity of cephalon, about half length of cranidium three-quarters as long (sag.) as greatest width at the lobes, anterior outline a slightly flattened semicircle. Axial furrow narrow, continuous, and deeply incised, except directly opposite 1L. 1S very deep, arising from axial furrow half-way along glabella and isolating relatively large 1L, which is elliptical sagittally, half the length of glabella and a quarter of its total width, hardly delimited from fixigena by axial furrow. 2S barely perceptible, approximately a quarter the distance from front of glabella. Occipital, axial, the pre-glabellar furrows, and 1S all about same width and depth, axial furrow shallow opposite 1L. Preglabellar field two-thirds length of glabella, a little inflated, and slightly peaked anteriorly, descending to broad and deep anterior border furrow. Anterior border forming strong ridge of constant width as far as base of genal spine, half that (tr.) of preglabellar field. Anterior section of facial suture diverging outwards at about 30° from exsagittal plane, curving in again as it crosses anterior border. Palpebral lobe semicircular, remote from axial furrow, anterior edge of eye directly opposite preglabellar furrow, posterior edge opposite centre of 1L; nearly as long as glabella. No indication of ocular ridge. Posterior branch of facial suture at about 80° to exsagittal line, nearly straight, terminating nearly at base of genal spine.

Librigena relatively narrow (tr.) with strong convex border and wide and deep lateral border furrow; posterior border furrow shallower, posterior border narrow. Visual surface of eye large and semicircular, extending laterally to within short distance of lateral border. Librigenal field thus long (sag.) and narrow (tr.), inclined at about 45° and almost flat. Genal spine broader (tr.) at its base than lateral border with which it is continuous, about as long (sag.) as cephalon, curving away from the cephalon and turning in again in a continuous curve at about half-way along its length, tapering posteriorly. Concentric terrace ridges on both upper and lower surface of genal spine parallel with length of spine. Cephalic doublure narrow with concentric terrace ridges, rostral plate unclear. No other surface sculpture present.

Thorax of holotype probably incomplete, ten segments are known; axis convex, one-third the total width of thorax, broadest at second and third thoracic segment where it is slightly broader than glabella, but slightly tapering posteriorly. Axial spine present on sixth segment but incompletely preserved. Each axial ring narrowing slightly laterally and turning forwards to join with flat pleuron at distinct axial furrow. Pleura with narrow transverse furrow, more clearly defined posteriorly and possessing distinct pleural facets on first few segments.

The poorly preserved single isolated pygidium (GSE 13517) is subtriangular, nearly twice as broad (tr.) as long (sag.), axis convex, one-third of the pygidial width anteriorly and with four or five axial rings. Pleural field with only faint traces of segmentation, border absent.

Discussion. *H*. (*H*.) *thomasi* is probably closest to *H*. (*H*.) *aitholix* Thomas from the Wenlock Coalbrookdale formation (Thomas 1978, p. 32, 1. 8), but in the latter the anterior border is widened sagittally, the glabella is relatively larger, and fairly large tubercles are rarely present on the glabella and preglabellar field. It is also distinct from *H*. (*H*.) *helenae* Lane 1979, which likewise has a distinct tubercular sculpture and a larger glabella also a broader and more pointed anterior border.

Family HARPETIDAE Hawle and Corda, 1847
Genus SCOTOHARPES Lamont, 1948
Scotoharpes domina Lamont, 1948

(Plate 77, figs. 1, 2)

1948*a* *Scotoharpes domina* Lamont, p. 532, fig. 2, p. 534.
1948*b* *Scotoharpes domina* Lamont; Lamont, pp. 376–377, fig. 2.
1973 *Scotoharpes domina* Lamont; Norford, p. 14, pl. 1, figs. 1–3.

Remarks. Norford (1973) has already accepted the validity of the genus and has given a full description based upon the unnumbered holotype, of which a plasticine replica was furnished by Dr. Lamont. This came from the lower part of unit D of the Wether Law Linn Formation at

EXPLANATION OF PLATE 79

Figs. 1, 2, 16. *Harpidella* (*Harpidella*) *thomasi* n. sp. upper Reservoir Formation, Deerhope Burn 1, 2. GSE 13519–20, holotype. 1. Latex replica of external mould, ×9. 2. Internal mould of same. 16. Pygidium, latex replica of external mould, GSE 13517, ×5.

Figs. 3–11. *Calymene frontosa* Lindström. Wether Law Linn Formation, Deerhope Burn and Wether Law Linn. 3. Internal mould of cranidium (figured by Lamont 1949 as holotype of *Calymene carlops*), Gr. I. 1518, ×5·5. 4. Internal mould of small pygidium, RSM GY 1978. 61. 541, ×3·5. 5. Smallest known pygidium, latex replica of external mould, RSM GY 1978. 61. 540b, ×4·5. 6. Complete specimen, latex replica of external mould, GSE 1013, ×6·75. 7. Same, internal mould, GSE 1014, ×6·75. 8. Cranidium, internal mould, RSM GY 1978. 61. 539, ×4·25. 9. Pygidium, internal mould, RSM GY 1978. 61. 545, ×4·25. 10. Pygidium, latex replica of external mould, RSM GY 1978. 61. 544, ×4·75. 11. Cranidium, latex replica of external mould, RSM GY 1978. 61. 537, ×3·25.

Fig. 12. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Hypostome, slightly distorted anteriorly, internal mould. Wether Law Linn Formation, unit C, Deerhope Burn, RSM GY 1978. 61. 510a, ×10.

Figs. 13–15. *Hemiarges rolfei* Lamont. Upper Deerhope Formation, Deerhope Burn. 13. Cranidium, internal mould, RSM GY 1979. 45. 2 (figured by Lamont as holotype of *H. hendersoni*), ×5·5. 14. Partial pygidium, latex replica of external mould, RSM GY 1978. 61. 511b, ×4. 15. hypostome, internal mould, Gr. I. 40306, ×5.

PLATE 79


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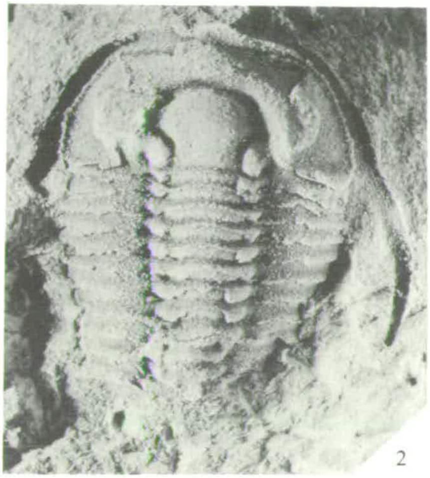
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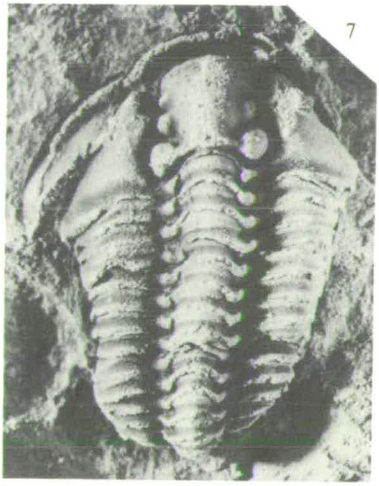
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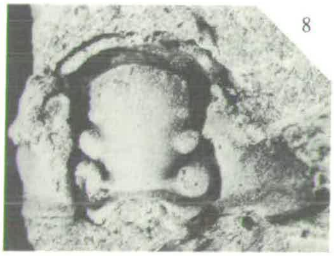
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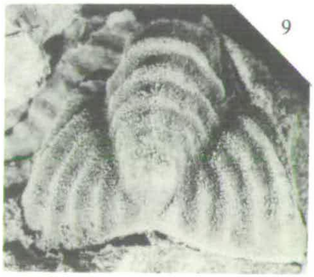
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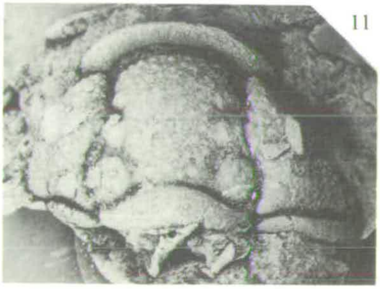
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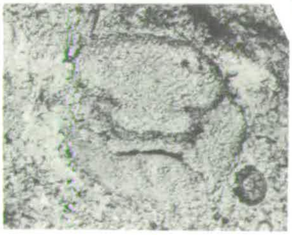
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CLARKSON and HOWELLS, Silurian trilobites

NT 149587 in the Henshaw Burn. Three other specimens are known of which one is here figured, RSM GY 1978. 61. 504a, b; an almost complete cephalon 18 mm long, including the brim; the dorsal and part of the ventral lamella of the brim preserved, from unit E of the Wether Law Linn Formation. The specimen was collected in 1971 by Mr. Hugh Mackenzie. The other specimens are RSM GY 1978. 61. 547, a partial fringe from unit C, and RSM GY 1965. 18. 3 from unit E at NT 144585 collected by R. W. Lamond.

Some additional details of morphology can be added to Norford's description from RSM GY 1978. 61. 504a, b. The eye-tubercles are very prominent and are connected to the glabella by slender ocular ridges, the apparent lack of sculpture of the glabella and adjacent regions mentioned by Norford is confirmed, though extremely faint continuations of the radial ridges of the fringe extend some distance up the cheek roll, though do not cover the genal surface as in *S. loma* (Lane). The structure of the fringe, and especially the lower lamella is more clearly displayed in this specimen than in the holotype. The rim is substantially raised above the fringe and has a flat surface indented by a narrow concentric groove from which the inner face of the rim shelves to a single row of pits at the junction of rim and fringe. A less well-defined second row of pits lies immediately within the first row; interior to this the pattern of fringe pits is less regular, though towards the inner margin the pits become orientated between the smooth radial ridges which are more pronounced near the girder but fade out midway across the fringe towards its outer edge. These ridges are most prominent at the antero-lateral corners of the cephalon and seem to be more pronounced on the ventral lamella. The girder forms a narrow curving ridge sculptured with a single row of tiny granules.

Family CHEIRURIDAE Hawle and Corda, 1847
Subfamily CHEIRURINAE Hawle and Corda, 1847
Cheirurinae indet.

Plate 80, fig. 3

Material. A single large cheirurid hypostome, RSM GY 1978. 61. 533, 18 mm long (sag.) and 20 mm wide (tr.), excellently preserved as an internal and external mould, was found in Unit C of the Wether Law Linn Formation at NT 148586 by J. C. Tipper.

Description. Hypostome slightly longer (sag.) than wide (tr.) including wings. Anterior border semicircular. Central body large and convex, very nearly reaching anterior border, and with its frontal margin more strongly curved than the latter, being separated from it by a deep and narrow furrow, broadening laterally. Posteriorly the central body narrows to a distinct waist at the middle furrows and then broadens slightly to terminate in a posterior lobe about a fifth the length of the central body and with a semicircular posterior margin. Middle furrows deeply cut, inclined backwards at 50–60° to the exsagittal plane. Anterior section of lateral border rather swollen indenting central body, postero-lateral border of constant width behind middle furrow, sharply angled to meet transverse posterior border. Surface of hypostome densely granulate, granules more pronounced on the postero-lateral border.

Remarks. No other evidence of large cheirurines in the Pentland Hills has been forthcoming other than this single hypostome. Since cheirurine hypostomes are all rather similar it is hard to know which, if any, of the known Llandoverian cheirurine genera it might pertain. *Cheirurus*, *Ktenoura*, *Hadromeros*, and *Proromma* all occur at this horizon (Lane 1971) but this specimen cannot be matched exactly with any of those previously figured.

Subfamily ACANTHOPARYPHINAE Whittington and Evitt, 1954
Genus YOUNGIA Lindström, 1885
Youngia douglasi Lamont, 1948

Plate 80, figs. 1, 2, 5, 6, 11

1948 *Cheirurus* (*Youngia*) *douglasii* Lamont, pl. 1, fig. 12.
1978 *Youngia douglasii* Lamont; Lamont, p. 274, pl. xxx, figs. 14, 15.

Type material. Holotype: RSM GY 1979. 77. 38 cranidium, internal mould figured by Lamont (1948, 1978) is well preserved (Pl. 80, fig. 11) but the librigena (1978, fig. 15) is barely recognizable and is not figured again here.

Other figured material. Four cranidia: RSM GY 1978. 61. 505 (Pl. 80, fig. 1); —507a (Pl. 80, fig. 5); —508 (Pl. 80, fig. 6); —516 (Pl. 80, fig. 2).

Other material. Cranidia: RSM GY 1978. 61. 507b; —525; —526.

Distribution. This species occurs in units A and C of the Wether Law Linn Formation at NT 148586 and NT 145582.

Diagnosis. A species of *Youngia* lacking a large occipital spine but with a small spine on the lateral border below the genal spine.

Dimensions. The size range of the known cranidia is considerable. The smallest cranidium is that of the holotype with a length of 4·5 mm, whilst the largest cranidium (—507a) is 11 mm long and if complete would be 20 mm broad.

Description. Glabella inflated, widest across 1L, wider than long. 1L two-fifths width (tr.) of glabella, not delimited adaxially. 2L and 3L progressively narrower (tr.) than 1L and slightly shorter. 1S deep and well-defined, abaxially obliquely aligned, adaxially curving towards but not reaching occipital furrow. 2S and 3S not so deeply impressed as, and parallel to, abaxial part of 1S, reaching not so far across the glabella. Occipital furrow as wide and as deep as 1S. Occipital ring narrower (tr.) than glabella, five times wider than long, longer sagittally than medially to accommodate 1L. No occipital spine preserved and seemingly absent. Axial furrow deep and well-defined.

Fixigena, excluding spines, subrectangular in outline. Posterior border short (exsag.) adaxially, expanding laterally into long genal spine at least half length of glabella. Posterior border furrow wide and deep. Lateral border wide with very small spine just below posterior branch of facial suture. Eye not preserved. Anterior branch of facial suture parallel to axial furrow, posterior branch transverse turning posteriorly as it crosses lateral border. Surface of cranidium covered with coarse, irregularly sized granules. These are almost in contact with each other on the glabella, but smaller and most distantly spaced on the fixigena and occipital ring, becoming fewer and less distinct towards the tip of the genal spine.

Discussion. Y. douglasi differs from the type species *Y. trispinosa* in the absence of an occipital spine and that 1L is not circumscribed; it also has a lateral border spines on the fixigena. *Youngia* sp. 1 and 2 described by Perry and Chatterton (1977) also has 1L circumscribed. Of these, sp. 1 has a long occipital spine whilst sp. 2 has only a 'short spinose tubercle'. *Y. copelandi* (Perry and Chatterton, 1979) has a short occipital spine, two short spines on the lateral border below the genal spine, and has much larger granules whilst 1L is circumscribed. The closest resemblances seem to be with Lindström's (1885) species *Y. inermis* and *Y. globiceps* from Gotland in which the occipital spine is reduced or absent. These two species, however, are poorly known.

Family ENCRINURIDAE Angelin, 1854
Subfamily ENCRINURINAE Angelin, 1854
Genus ENCRINURUS Emmrich, 1844
Encrinurus expansus Haswell, 1865

Plate 80, figs. 4, 7-9, 10, 12

1865	*Encrinurus expansa* (sic.) Haswell, p. 36, pl. IV, figs. 4, 5.
?1948	*Encrinurus pluc* Lamont, pl. 1, fig. 14 (no description; poor illustration).
?1948	*Encrinurus calgach* Lamont, p. 6, pl. 1, figs. 15, 16 (no description; poor illustration).
1975	*Encrinurus calgach* Lamont; Clarkson, pp. 12, 23, figs. 2D-F (illustration of eye).
1978	*Calgachia calgach* Lamont; Lamont, p. 270, pl. XXXI, fig. 5. (*nomen nudum*).

Figured material. Haswell's types being lost, the description is based on other material; intaglio of length 2·2 mm collected by Dr. J. L. Henry, RSM GY 1978. 61. 427a, b (Pl. 80, fig. 12); partly enrolled external mould, RSM GY 1978. 61. 420 (Pl. 80, fig. 7); external mould of ventral surface with hypostome, —421 (Pl. 80, fig. 8); internal mould of librigena with eye, —448 (Pl. 80, fig. 9); external mould of small intaglio lacking librigenae, —438 (Pl. 80, fig. 4); internal mould of cranidium, —453 (Pl. 80, fig. 10).

Distribution. All material comes from the Wether Law Linn Formation (units A and C) at NT 145582 and NT 148586.

Dimensions. The largest intaglio is 25 mm long and has a cephalon 8 mm long by 15 mm broad; the smallest cephalon is 6 × 12 mm, the largest 9 × 22 mm.

Diagnosis. 1L reduced to very small ridge. Lateral glabellar lobes larger than tubercles on glabellar lobe. General tubercle formula: II—1_*; iii—0; III—1. Anterior border with single row of ten tubercles. Short genal spine. Lateral part of field of fixigena with very few tubercles but many pits. Lateral border of librigena with one row of tubercles; field of librigena with five or six faintly raised tubercles and with shallow pits; precranidial lobe with two or three rows of tubercles. Pygidium with seven pleural ribs (eighth pair fused behind axis); fifteen to twenty axial rings; terminating posteriorly in upturned mucro.

Description. Cephalon a little over twice as wide (tr.) as long (sag.) width taken at posterior border. Glabella approximately twice as long as width across 2L lobes, expanding anteriorly to twice width across 2L lobes. Occipital ring five times wider than long. Occipital apodeme short and circular in outline. Occipital furrow combined with 1S medially producing broad furrow between occipital ring and 2L. 1L present only laterally as very small, ridge-like swelling between occipital apodeme and 1S apodeme. 2L, 3L, and large tubercle overhanging axial furrow anterior to these much larger than glabellar tubercles and roughly circular in outline. 1S apodeme, circular in outline, long and larger than occipital apodeme. 2S apodeme, as 1S apodeme; 2S furrow distinguishable only between 2L and 3L. 3S apodeme, circular in outline, shorter and smaller than 2S apodeme; 3S furrow present only between 3L and large overhanging tubercle. Preglabellar furrow broad, more deeply impressed laterally, terminating by very deep and wide anterior pit. Tubercle formula: II—1_*; iii—0; III—1; III—2_* sometimes present. Anterior border of cranidium with single row of ten tubercles with lateral tubercle as large as 3L. Occipital ring and all furrows lack sculpture. Remainder of glabella with irregularly placed tubercles. Fixigena subtriangular in outline, wide and narrow laterally. Posterior border short (exsag.) adaxially, lengthening abaxially and projected into short genal spine. Posterior border furrow broad and shallow. Lateral border present only close to genal angle, where narrow, merging with posterior border. Anterior section of facial suture running diagonally forwards from eye crossing axial furrow at anterior pit and defining outline of anterior border of cranidium. Posterior section of facial suture crossing lateral border opposite occipital apodeme. Four tubercles overhanging axial furrow alternating in position with lateral glabellar lobes. Remainder of convex part of cheek with few large tubercles and pits increasing in number laterally. Borders and furrows without sculpture.

Pedunculate eye with wide base equalling width of two tubercles overhanging axial furrow; about as wide as high; visual surface tapering to blunt point dorsally. Librigena very gently convex, over twice as long as wide, width taken at position of eye. Lateral border of librigena wide (tr.) a quarter width of librigena at eye position narrowing rapidly and merging with very narrow anterior border of cephalon. Single row of large tubercles on lateral border increasing in size and definition anteriorly. Anterior border with few low tubercles. Lateral border

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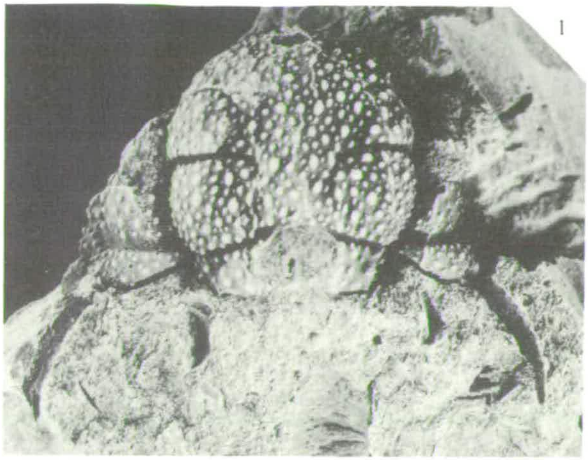
EXPLANATION OF PLATE 80

Figs. 1, 2, 5, 6, 11. *Youngia douglasi* Lamont. Wether Law Linn Formation, units A and C. Deerhope Burn. 1. Cranidium with spines, internal mould, RSM GY 1978. 61. 505, × 5·25. 2. Partial cranidium in dorso-lateral view, latex replica of external mould, RSM GY 1978. 61. 516, × 4·5. 5. Almost complete cranidium, latex replica of external mould, RSM GY 1978. 61. 507a, × 3·5. 6. Glabella, internal mould, RSM GY 1978. 61. 508, × 3·75. 11. Holotype; glabella, internal mould. RSM GY 1979. 77. 38a, × 5·5.

Fig. 3. Cheirurinid hypostome, latex replica of external mould, RSM GY 1978. 61. 533, × 2.

Figs. 4, 7–10, 12. *Encrinurus expansus* Haswell. Wether Law Linn Formation, units A and C. Deerhope Burn (8, 12) and Wether Law Linn Formation (4, 7, 9, 10). 4. Small intaglio devoid of librigenae; latex replica of external mould, RSM GY 1978. 61. 438, × 4. Partly enrolled external mould, latex replica, RSM GY 1978. 61. 420, × 4. 8. Latex replica of cephalic doublure and hypostome, RSM GY 1978. 61. 421, × 3·5. 9. Internal mould of left librigena with eye, RSM GY 1978. 61. 448, × 3·75. 10. Internal mould of cranidium, RSM GY 1978. 61. 453, × 2·5. 12. Intaglio devoid of librigenae, latex replica of external mould, RSM GY 1978. 61. 427a, × 3.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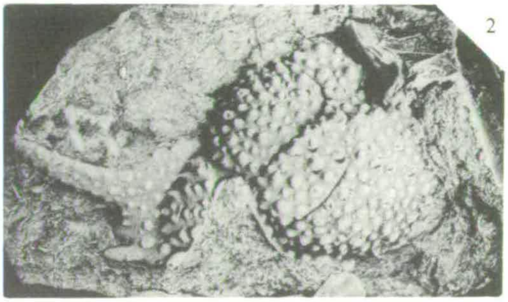
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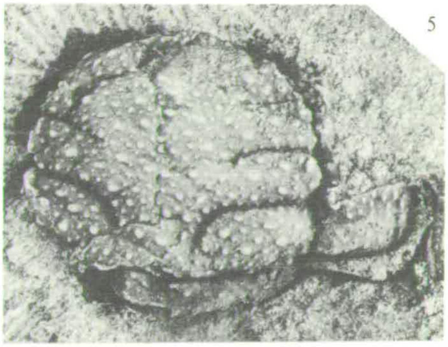
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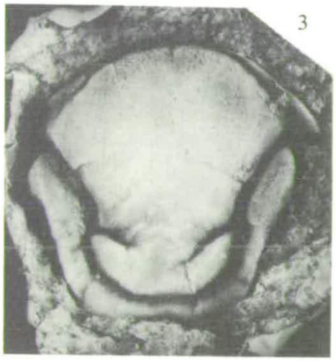
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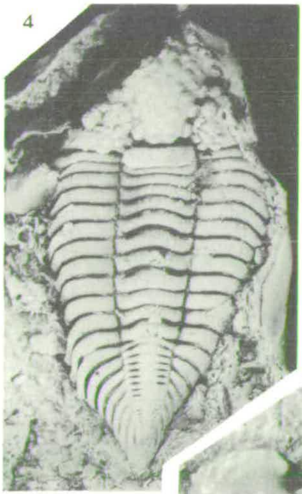
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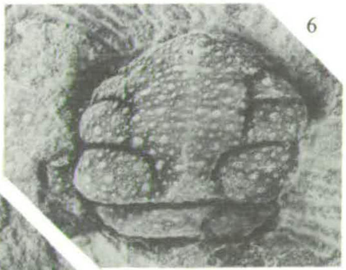
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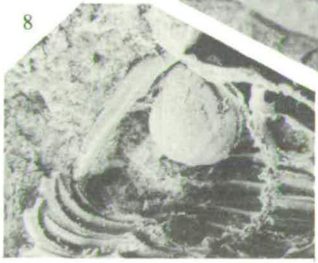
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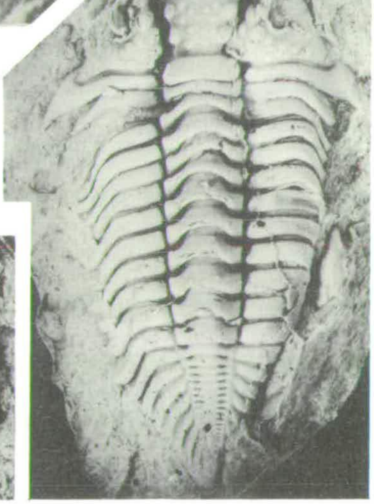
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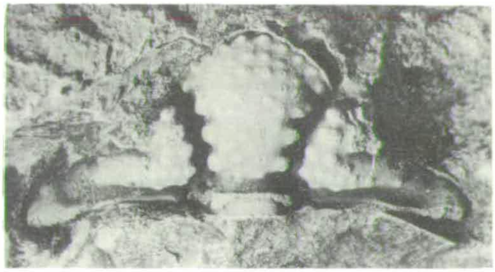
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CLARKSON and HOWELLS, Silurian trilobites

furrow well-defined, deepening anteriorly. Anterior border furrow very shallow. Field of librigena quite flat, sculpture as five to six very faintly raised tubercles vaguely arranged around base of eye socle, and with shallow pits randomly arranged. Precranidial lobe with two or three rows of tubercles.

Rostral plate unknown. Hypostome, only middle body known. Middle body only slightly longer than wide, diamond-shaped in outline, rhyncos projecting forwards as far as anterior border furrow, narrowing rapidly anteriorly. Macula oval in outline, obliquely aligned. Surface very finely granulated.

Thorax of eleven segments. Axis a quarter width of thorax. Central half of axial ring arched forwards, posterior margin transverse. Inner half of pleural field horizontal, outer half flexed down and backwards. Posterior pleural band parallel-sided for horizontal region, increasing markedly in length (exsag.) laterally. All surfaces with very fine granulation.

Pygidium triangular in outline, as wide as long. Pygidial axis a little over three-quarter length of pygidium, one-third width (tr.) of anterior margin, tapering posteriorly almost to a point, only slightly raised above the convexity of the pleural field. Fifteen to twenty axial ring furrows, distinct for full width behind most anterior three or four rings, increasingly effaced medially and laterally posteriorly so that only seen as two rows of transverse slits posteriorly. Up to four, not greatly raised, median tubercles present on axial rings (population not large enough to determine frequency of occurrence). Seven pleural ribs, eighth pair probably fused behind pygidial axis; anterior two ribs with free lateral margins, distal parts of posterior five ribs fused to form posterior border; progressively curving inwards posteriorly, merging into upturned mucro of unknown length. First pleural rib and first axial rib separated by very shallow furrow. All surfaces very finely granulated.

Remarks. *E. expansus* would appear to be a member of the *E. schmidti* group (Männil, 1968) from West Estonia (Upper Llandovery), in the general characters of the cephalon, including the short genal spine, and the shape and formation of the pygidium. However, *E. expansus* has fewer glabellar tubercles, although the glabellar tubercle formula is quite similar, and tubercles of the fixed cheek which overlap the axial furrow are larger, the eye is longer (exsag.), and the pygidial mucro is shorter. In Scotland *E. expansus* can only be compared with an undescribed encrinurine from the Wood Burn Formation (Fronian), Girvan especially in the form of the elongate glabella, genal spine, and mucronate pygidium. However, the Pentland form can be distinguished by the presence of a 1L ridge, a different glabellar tubercle formula, and the glabellar tubercles being smaller than the glabellar lobes.

Encrinurus pagei (Haswell, 1865)

Plate 81, figs. 5, 8, 9, 10, 12

1865 *Zethus pagei* Haswell; p. 37, pl. 4, figs. 1–3.
?1948 *Cromus*(?) *dris* Lamont, pl. 1, fig. 17 (no description; poor illustration).
?1948 *Cromus* sp.; Lamont, p. 7, pl. 1, fig. 18 (no description; poor illustration).
1948 *Cromus pagei* (Haswell); Lamont, p. 7, pl. 1, fig. 19 (no description).
1978 *Paracalgachia henshawensis* (Lamont); Lamont, p. 271, pl. XXXI, fig. 6 (*nomen nudum*).
1978 *Wallacia expansa* (Haswell); Lamont, p. 271, pl. XXXI, fig. 7.

Figured material. As with *E. expansus*, the types cannot be located, and figured specimens include an almost complete intaglio 25 mm long, RSM GY 1978. 61. 425a, b (internal and external moulds), lacking librigenae (Pl. 81, fig. 10). Partial specimens: —528, 530 (Pl. 81, figs. 12, 9); thoracopygon —529a, b (Pl. 81, fig. 5); cephalon with librigenae, figured by Lamont 1948, RSM GY 1897. 32. 6 (Pl. 81, fig. 8).

Dimensions. Cephalic length (sag.) 6·0–7·5 mm, width (tr.) 16–18 mm.

Distribution. All specimens come from unit E of the Wether Law Linn Formation at NT 148588 on the west bank of the Henshaw Burn when they occur with a fauna of conulariids, bivalves, gastropods, and the brachiopod *Pentlandella*.

Diagnosis. 1L present as large ridge. Lateral glabellar lobes larger than tubercles on glabellar lobe. General tubercle formula: I—1*, 2; ii—0; II—1, 2*; iii—0. Anterior border of cranidium with single row of eleven tubercles. Very short genal spine. Field of fixigena and field of librigena with many tubercles. Pygidium with eight pleural ribs and seventeen axial rings.

Description. Differs from *E. expansus* in the following features. 1L as larger ridge protruding as far as other lateral glabellar lobes but not as swollen. Lateral glabellar lobes as rectangular protruberances overhanging axial furrow, tuberculate. All apodemes shallower. Occipital furrow and 1S separate. 1S, 2S, and 3S deeply impressed extending a little way across glabellar lobe. Preglabellar furrow as very shallow depression. Tubercle formula: I—1*, 2; ii—0; II—1, 2*; iii—0. Anterior border of cranidium with single row of eleven tubercles, one placed sagittally. Longitudinal median glabellar furrow as broad shallow depression. Posterior border of fixigena projecting into very short genal spine. Field of librigena with more, better-defined, tubercles.

Eye not preserved in full detail. Librigena poorly known but considerably more tuberculate; lateral border wide, and possessing a single row of tubercles. Rostral plate and hypostome unknown.

Pygidium slightly wider than long, flattened. Pygidial axis hardly raised above convexity of pleural field, about one-third width of anterior margin; about seventeen axial ring furrows decreasing in definition posteriorly. Pygidial axial furrow deeply impressed anteriorly, shallowing rapidly beyond 4th pleural rib. Median tubercles present on some rings. Eight pleural ribs, anterior four ribs with free lateral margins, posterior ribs fused to form posterior border.

Remarks. This species was very poorly described by Haswell (1865) and is largely unrecognizable from his illustrations. Even so, the horizon given (Locality I) and the associated conulariids mentioned by Haswell indicate that the specimens were collected from unit E, in which this *Encrinurus* species alone occurs; it is therefore considered to be a valid species. *E. pagei* is closest to *E. variolaris* (Brongniart, 1822) from the Wenlock and Ludlow series of the West Midlands and Welsh Borderlands. However, the Pentlands form differs particularly in having a sagittally placed tubercle on the anterior border of the cranidium, 1L continuing as a ridge across the glabella, more pygidial axial rings, and less tuberculate pygidium over all.

Family CALYMENIDAE Burmeister, 1843
Subfamily CALYMENINAE Burmeister, 1843
Genus CALYMENE Brongniart, 1822
Calymene frontosa Lindström, 1885

Plate 79, figs. 3-11

1885	*Calymene frontosa* n.; Lindström, p. 69, pl. 15, figs. 1-4.
?1894	*Calymene frontosa* Lindström; Schmidt, p. 18, pl. 2, figs. 4, 4*a*, *non* figs. 5, 5*a*, 6, 7.
1936	*Calymene frontosa* Lindström; Shirley, p. 387.
1949	*Calymene carlops* sp. nov.; Lamont, p. 319, pl. 18, figs. 13-19.
1970	*Calymene carlops* Lamont, 1949; Schrank, pp. 115, 119.
1970	*Calymene frontosa* Lindström, 1885; Schrank, p. 116, pl. 1, figs. 1, 2.
1977*a*	*Calymene frontosa* Lindström, 1885; Männil, p. 244, pl. 2, figs. 1, 2.
1978	*Calymene carlops* Lamont, 1949; Lamont, p. 274.

Types. Lectotype: RM Ar6210, figured Lindström 1885, pl. 15, figs. 1-3, from the Lower Visby Beds (topmost Llandovery), Visby, Gotland. Paralectotype: RM Ar6211, figured Lindström 1885, pl. 15, fig. 4; RM Ar6212—both enrolled specimens from Visby, Gotland.

Figured material. Cranidium Gr I 1518 (figured by Lamont as holotype of *Calymene carlops*, 1949, pl. viii, fig. 15 (Pl. 79, fig. 3); Intaglio GSE 1013-14. (Pl. 79, figs. 6, 7); Cranidia RSM 1978. 61. 537 (Pl. 79, fig. 11), —539 (Pl. 79, fig. 8); small pygidium 540a, b (Pl. 79, fig. 5); pygidium —541 (Pl. 79, fig. 10), —545 (Pl. 79, fig. 9).

Other material. RSM 1876. 42, A, B, C. (Specimens collected by John Henderson and figured by Lamont 1949, pl. XVIII, figs. 16, 18, and 19 as *Calymene carlops*. These are poorly preserved and are not refigured here.) Also RSM GY 1978. 61. 536, —538, —542, and —543.

Distribution. As Lamont (1978) noted this species appears to be confined to unit A of the Wether Law Linn Formation, at NT 145582 and NT 148586. Tipper likewise records this distribution. The only complete specimens known to us are that figured in Plate 69, figs. 6, 7 and a larger specimen in the collection of Mr. Andrew Poland.

Dimensions. The size range of this species is considerable. The figured complete specimen is small, only 9·0 mm long; cephalic length otherwise (sag.) ranges from 3·5 to 10·0 mm and width from 7·0 to 14·0 mm, pygidial width from 3·0 to 9·5 mm.

Diagnosis. Glabella about as wide as long, anterior margin almost transverse. Preocular part of fixed cheek about one-third as wide as glabella at 2L. Anterior border of cranidium rolled. Pygidium strongly convex with six axial rings and five wide pleural furrows. All raised surfaces with irregularly sized and spaced granules.

Description. Cephalon twice as wide as long. Glabella almost as wide as long, anterior margin almost transverse. Occipital ring about four times wider than long medially, decreasing in length laterally to accommodate 1L lobe. 1L a quarter width of glabella, oval in outline. 1S curving backwards and inwards, shallowing posteriorly. 2L half size of 1L, also oval in outline, 2S, as depression between 2L and 3L. 3L as swelling on side of glabella, only slightly shorter (exsag.) than 2L. Shallow anterior pit positioned midway between 3L and anterior margin of glabella. Preglabellar furrow deep and wide, slightly undercutting anterior margin of glabella. Anterior border rolled, slightly longer laterally than medially. Posterior border of fixed cheek lengthening (exsag.) laterally. Posterior border furrow distinct and wide. Palpebral lobe slightly longer than, and positioned opposite, 2L. Preocular part of fixed cheek about one-third as wide as glabella at 2L, narrowing anteriorly; anterior inner corner pointed. Anterior branch of facial suture running forwards to anterior margin. Posterior branch of facial suture running transversely for short distance, then running diagonally backwards crossing posterior margin obliquely. All raised surfaces with irregularly sized and spaced granules.

Librigena subtriangular in outline. Lateral border rolled, wide. Lateral border furrow deep and wide. External surface of librigena with scattered granules. Hypostome unknown.

Thorax of thirteen segments. Axis one-third width of thorax. Articulating half ring about half width of axial ring. Axial ring transverse posteriorly, produced into nodes laterally. Pleural region horizontal for adaxial half, flexed downwards abaxially. Pleural furrow positioned anteriorly on rib, running transversely.

Pygidium roughly triangular in outline. Pygidial axis strongly convex, narrowing slightly posteriorly to blunt point, with six axial rings; axial ring furrows becoming less distinct posteriorly. Axial furrow well-defined. Pleural region deflected downwards so that posterior margins almost transverse; five wide pleural furrows; interpleural furrows more distinct distally. All raised surfaces with scattered granules, pleural furrows with some granules.

Remarks. The Pentland calymenid is considered to be conspecific with *C. frontosa* because of the overall similarity of their exoskeletons, especially in the deep and wide preglabellar furrow, the deep and wide axial furrow in front of lobe 2L, the pointed, projecting anterior corner to the fixed cheek, small palpebral lobe, and the cranidial ornamentation. Lamont (1949, p. 231) considered that the Pentland

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EXPLANATION OF PLATE 81

Figs. 1, 3, 4, 11. *Leonaspis lothiana* (Lamont). Quarry near Bavelaw Castle, Bavelaw Castle Inlier (see also Pl. 82). 1. Thoracopygon, latex replica of external mould, RSM GY 1897. 32. 242, ×4·5. 3. Incomplete thoracopygon, latex replica of external mould, Gr. I. 22226, ×7. 4. Damaged cephalon and part of thorax, GSE 13487, ×5·5. 11. Details of ventral morphology, latex replica of external mould, RSM 1978. 61. 520, ×8.

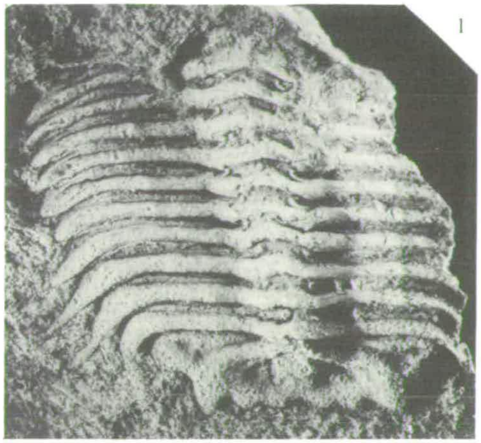
Fig. 2. *Anacaenaspis dealgach* (Lamont). Wether Law Linn Formation (unit A or C). Syntype cephalon, internal mould, RSM GY 1979. 77. 45a, ×8 (see also Pl. 82).

Figs. 5, 8, 9, 10, 12. *Encrinurus pagei* (Haswell). Unit E, Wether Law Linn Formation, Henshaw Burn. 5. Pygidium and last thoracic segments of thoracopygon, latex replica of external mould, RSM GY 1978. 61. 529a, ×3. 8. Flattened cephalon, internal mould, (figured Lamont 1948, pl. 1, fig. 13), RSM GY 1897. 32. 61, ×2. 9. Cephalon lacking librigenae, retaining seven thoracic segments, latex replica of external mould, RSM GY 1978. 61. 530, ×3. 10. Almost complete specimen, latex replica of external mould, RSM GY 1978. 61. 425a, ×2. 12. Cephalon lacking librigenae, with two thoracic segments, latex replica of external mould. RSM GY 1978. 61. 528a, ×2·5.

Fig. 6. *Acernaspis* sp. upper Reservoir Formation. Internal mould, outer surface somewhat recrystallized, RSM GY 1978. 61. 534, ×5.

Fig. 7. *Anacaenaspis* sp. upper Reservoir Formation, Deerhope Burn. Internal mould of cranidium, GSE 13518, ×5·5.

PLATE 81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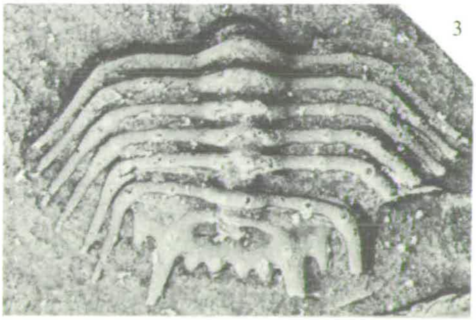
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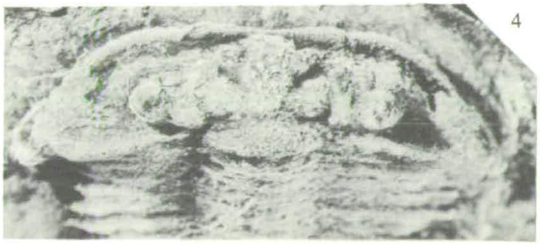
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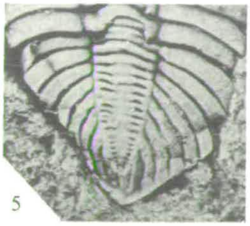
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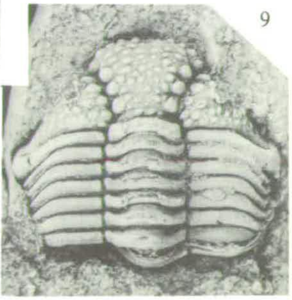
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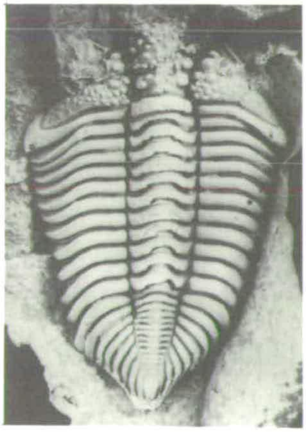
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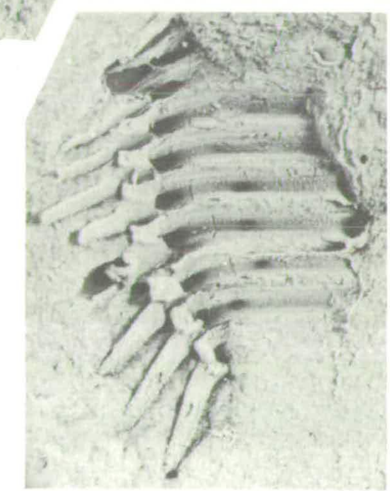
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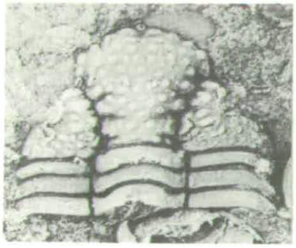
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CLARKSON and HOWELLS, Silurian trilobites

calymenid form could be separated from *C. frontosa* in that it had a less tapering and longer frontal glabellar lobe and possessed finer surface granulation. Study of populations of the Scottish and Gotland forms indicates that these two features vary and are not considered specific differences.

Family PHACOPIDAE Hawle and Corda, 1847
Subfamily PHACOPINAE Hawle and Corda, 1847
Genus ACERNASPIS Campbell, 1967
Acernaspis sp.

Plate 81, fig. 6

1978 *Cyphoproetus* (*Otadenus*) *alacer* Lamont; p. 267, pl. XXX, fig. 12.

Material and remarks. A number of specimens of *Acernaspis*, usually small, have been found in the upper Reservoir Formation, but their preservation is such that no specific determinations can be made. The oldest known are GSE EM 1108/9 from a locality 'in the Gutterford Burn, below the starfish beds'; whose precise horizon is unknown. These are respectively a partially enrolled cephalon with two thoracic segments and a pygidium, both preserved as internal moulds in a red mudstone. Higher in the Reservoir Formation at localities along the Deerhope Burn there have been found two small complete specimens occurring in association with *Encrinurus* fragments and strophochonetids. They are internal moulds with the surface encrusted by silica and little structural detail can be distinguished (RSM GY 1978. 61. 534, 535). There is also a large partially enrolled thorax (GSE EM 1230) and a pygidium (GSE EM 1268). It is probable that all those from the Upper Reservoir Formation belong to the same species, but their preservation does not permit more detailed analysis.

Subgenus ESKASPIS (Clarkson, Eldredge and Henry, 1977)
Acernaspis (*Eskaspis*) *sufferta* (Lamont, 1947)

Plate 79, fig. 12

1947 *Eophacops sufferta* n. sp. Lamont, p. 6, pl. 1, figs. 21, 22.
1977 *Acernaspis* (*Eskapsis*) *sufferta* (Lamont, 1947); Clarkson *et al.*, p. 126, pl. 18, figs. 1–9; pl. 19, figs. 1–7, text-figs. 2*a*, *f*, 3*a*, *b*, 4*a*, *c*.

Material. A single phacopid hypostome, consisting of a partial external and complete internal mould, RSM GY 1978. 61. 510a, b, from unit A, Wether Law Linn Formation at NT 148586, probably belongs to *A.* (*Eskaspis*) *sufferta*. The moulds are somewhat distorted, fragile, and only lightly impressed on the matrix, and the anterior border is slightly abraded.

Description. Hypostome about as broad (to tips of wings) as it is long (sag.) Anterior border nearly straight, curving posteriorly at the wings. Central body about two-thirds total width of hypostome, weakly convex medially, and declining laterally and posteriorly. Faint lateral swellings (? maculae) present half-way down its length. Anteriorly central body defined by broad, shallow anterolateral furrow turning in from lateral border at its deepest point.

Hypostomal border parallel-sided and in plan almost horizontal, not quite reaching the anterior border, and projecting outwards anteriorly as a flange. Border abruptly changes course at about half-way along its length, where the hypostome is deepest, sloping posteriorly at about 45° to the horizontal curving inwards to form the elliptical posterior border. Hypostomal wings broadly triangular and (in plan) sloping forwards at some 45° to the horizontal.

Surface sculpture of closely spaced granules, just like those on the dorsal surface of the cephalon.

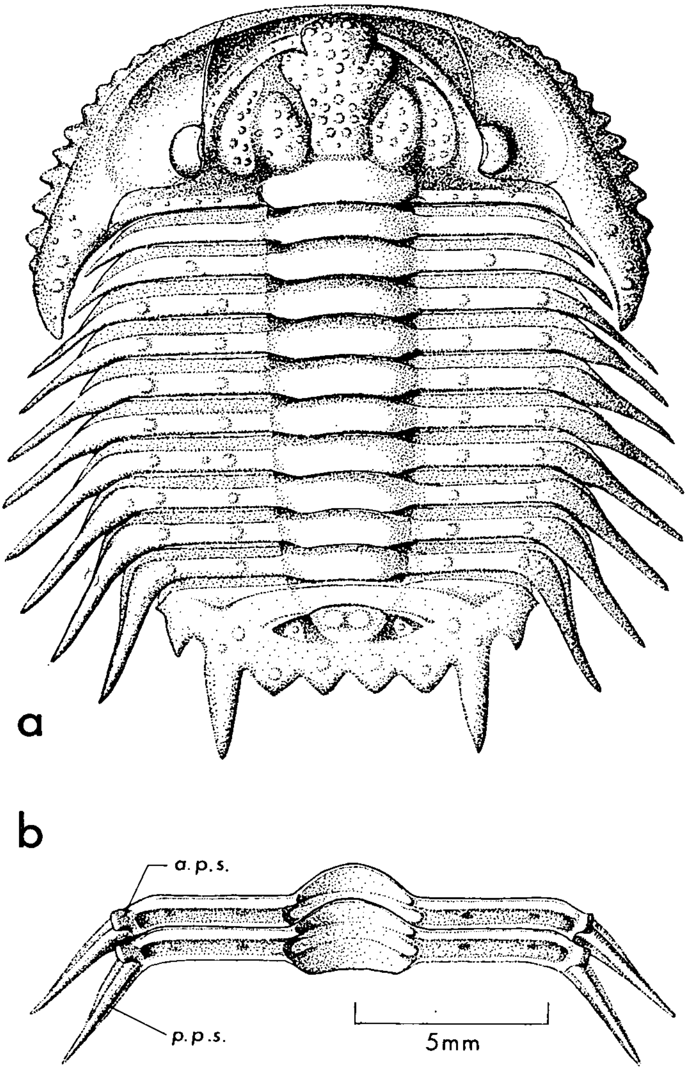
Remarks. Very few hypostomes of Llandoverian Phacopina have been described. Campbell (1967) noted that the hypostomes of *Acernaspis* and *Eophacops* were then unknown, but described and figured that of *Ananaspis communis* (Barrande) (ibid., Pl. 13) which has a 'short posterior border, and ornament of granules and is strongly tapered'. Männil (1970*a*) figured the hypostome of *Acernaspis konoverensis* (ibid., fig. 1*a*, *b*, Table 1, fig. 9) with its posteriorly curved anterior border and (1970*b*, fig. 1*a*, *b*, Table 2, fig. 9) that of *A. rectifrons*, both of which bear some similarity to that of *A.* (*E.*) *sufferta*, though the wings of the latter are broader and the posterior border more pronounced.

Family ODONTOPLEURIDAE Burmeister, 1847
Genus LEONASPIS Richter and Richter, 1917
Leonaspis lothiana (Lamont, 1948)

Plate 81, figs. 1, 3, 11; Plate 82, figs. 5, 7-10; text-fig. 2*a*, *b*

1899 *Acidaspis* sp. Peach and Horne, p. 605 (list only).
1947 *Acidaspis* aff. *erinaceus* Marr and Nicholson; Lamont, p. 290 (list only).
1948 *Acidaspis lothiana*; Lamont, pl. 1, figs. 6, 7.
1978 *Dudleyaspis lothiana* (Lamont, 1948, *pars*); Lamont, p. 276, pl. xxx, fig. 21.

Figured material. Lamont (1948) illustrated this species, the only odontopleurid, and the only common trilobite in the Bavelaw Inlier, by a small photograph of an articulated thorax and pygidium, and another showing a cephalon in frontal view. These two syntype specimens are no longer available but in 1978 Lamont illustrated (GSE 13487) a damaged partial external mould, originally from the Hardie collection. This is refigured here (Pl. 82, fig. 4); other figured material includes a thoracopygon, Gr I 22226 (Pl. 81, fig. 3); an external mould of the



TEXT-FIG. 2 *a*. *Leonaspis lothiana* (Lamont) Reconstruction. *b*, Ventral morphology of thoracic segments; reconstruction. (a.p.s.—anterior pleural spine; p.p.s.—posterior pleural spine.)

ventral surface, RSM GY 1978. 61. 520 (Pl. 81, fig. 11); a pygidium with moulds of both surfaces, and thoracic segments on the same slab, RSM GY 1978. 61. 522. 3 (Pl. 82, figs. 5, 6); a partial cranidium, —518 (Pl. 82, fig. 8); and a slab with an enrolled specimen and another largely complete specimen, —517 (Pl. 82, figs. 9, 10).

Other material. An abraded intaglio, RSM GY 1897. 32. 242; and various fragmentary specimens, RSM GY 1978. 61. 518-521.

Distribution. This species does not occur in the North Esk Inlier and is known only from a small quarry near Bavelaw Castle (NT 168627, locality 2 of Mykura 1975). It is presumed that these beds are of Upper Llandovery age, but their precise horizon is unknown.

Dimensions. Total length (estimated average) 15 mm, width 13 mm. Cephalic length (average) including spines 6 mm, width 11 mm, glabellar length 2·5 mm, pygidial length 2·5 mm, width 5·5 mm.

Diagnosis. Leonaspis with short, blunt genal spines, posterior thoracic spines with swollen bases, increasing in length and inclination posteriorly, and pygidium with two short outer pairs of spines, one pair of major thoracic spines enclosing four short pairs of spines all of equal length.

Description. All known specimens are incomplete, and the description and reconstruction are composite and based upon several specimens with measured parameters.

Exoskeleton longer than broad by a factor of five-sixths, circumference round spine tips subelliptical verging on quadrate. Cephalon broad (tr.) semi-elliptical in outline, in plan view somewhat flattened anteriorly, maximum width just anterior to tips of genal spines, twice sagittal length including genal spines, three times length to edge of occipital ring.

Cranidium with large smooth occipital ring, devoid of occipital spine, occipital furrow distinct though rather shallow medially, but becoming deeply marked posterior to the basal glabellar lobes (1L) where the occipital ring is laterally indented. Glabella at maximum width (just anterior to the eye) about as wide as it is long with more or less rectangular median anterior glabellar lobe which is rather flat-topped, declining anteriorly to deep anterior furrow. 1L large, half total glabellar length and nearly twice as long (sag.) as wide, slightly pointed anteriorly, with its axis about 25° to the sagittal plane. 1L bounded anteriorly but shallowing and narrowing inwards and backwards, where it joins (normally) broad and rather poorly defined axial furrow. 1L steepest postero-laterally where it becomes nearly vertical. 2L small (one-fifth total length of the glabella), rounded, of similar convexity to 1L, bounded sagittally by a very weak axial furrow which is a sagittal extension of that bounding 1L. Large curving fixigenal area running forward from behind 1L, forwards and inwards to connect with 2L across a broad shallow furrow directly anterior to 1L. Very deep furrow separating this area from high palpebral lobe which continues forward opposite the centre of 1L as slender continuously curving ocular ridge, in its median part about 45° to the sagittal plane. Anterior border furrow very deep, anterior border high, with a flat upper surface, rounded in plan but somewhat flattened anteriorly, curvature increasing postero-laterally. Palpebral lobe opposite posterior edge of 1L, approximately one-third the length of the glabella. Anterior branch of facial suture initially parallel with sagittal line just in front of eye, but curving slightly inwards anteriorly. Posterior branch in transverse plane, and parallel to posterior border, which forms a low, flat, transverse ridge, lower than occipital ring, truncated by posterior branch at a distance from occipital ring slightly greater than width of occipital ring itself.

Librigena triangular with rather blunt and stout genal spine less than one-third of total length, eye conical, with very small lenses visible on visual surface, no eye socle, but eye separated from smooth, steeply sloping librigenal surface by very poorly defined junction. Lateral border furrow deep and clearly defined anteriorly, shallowing backwards and merging with posterior border furrow. Lateral border forming strong curving ridge merging posteriorly with genal spine. Beneath this border are fourteen short, stout spines inclined outwards at some 15° from the vertical, increasing in size posteriorly, the largest opposite posterior border and with the two smaller spines directly below the anterior curve of genal spine. Librigenal doublure extending inwards to the level of the lateral border furrow.

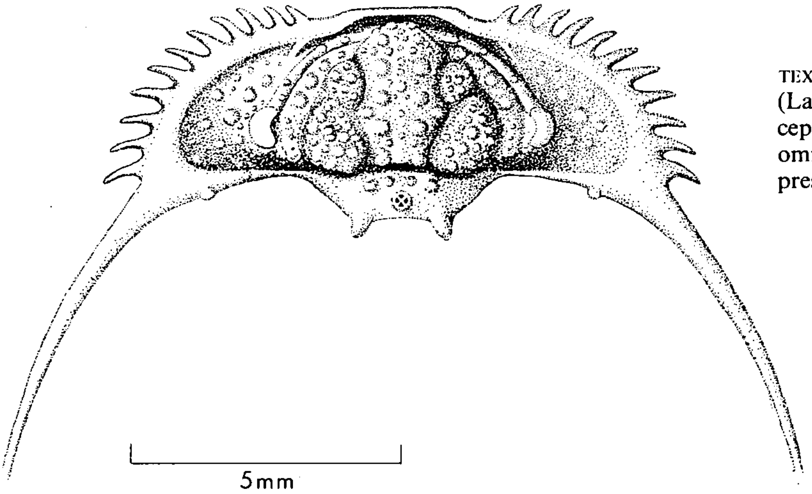
Cranidium (glabella, glabellar lobes, ocular ridges, and fixigena) sculptured with rounded granules, more or less symmetrically placed, spaced more widely than their diameter, slightly larger and more clustered on anterior glabellar lobe. Numerous large granules are also present towards the point of the genal spine. Cephalon otherwise smooth other than a few small granules on occipital ring, and dense granulation on antero-lateral border and denticles of librigena. Hypostome unknown.

Thorax of ten segments, with broad convex axis about a quarter of total width, and with pronounced articulating half ring about same length (sag.) as the axial ring. Axis parallel-sided, slightly narrowing posteriorly. In ventral view a pair of slightly raised platforms, with rounded ends directed outwards are visible which is poorly preserved and is not figured again here. These are recognizably the same as four specimens collected by J. C. Tipper from unit A of the Wether Law Linn Formation at NT 148586, RSM GY 1978. 61. 512 (Pl. 82, fig. 2), a largely complete internal mould of a cephalon, two incomplete external cephalic moulds, RSM GY 1978. 61. 513 and 514 (Pl. 82, figs. 1, 3), and an almost complete internal mould of a pygidium, RSM GY 1978. 61. 515 (Pl. 82, fig. 4), which represent all the available material.

Dimensions. Cephalic length exclusive of genal spines approximately 4 mm, breadth 10 mm. Pygidial width approximately 7 mm.

Diagnosis. Small *Anacaenaspis* with subtrapezoidal glabella, long curving genal spines, eleven pairs of lateral spines, rather elongate glabella with constricted base, and relatively large 1L and 2L. Occipital ring broad with two small occipital spines. Pygidium with five pairs of symmetrically spaced spines, all of equal lengths.

Description. Cephalon (exclusive of genal spines) subtrapezoidal, some two and a half times broader (tr.) than long (sag.). Occipital ring trapezoidal, three times longer than broad anteriorly, decreasing posteriorly to half anterior width, with pair of short, stout occipital spines directed slightly outwards from posterior angles. Occipital furrow sharply incised. Glabella twice as long as broad, parallel sided but indented by 1L and 2L, subpentagonal anteriorly, descending steeply anteriorly and almost reaching anterior border. 1L very convex, half length of glabella, axis parallel with basal glabellar furrow, some 25° to the sagittal plane, indenting glabella quite distinctly. 2L ovoid, half length of 1L, separated from 1L by strong axial furrow, shallowing posteriorly.



TEXT-FIG. 3. *Anacaenaspis dealgach* (Lamont). Reconstruction of cephalon; course of facial suture omitted since it is not visible in the preserved material.

EXPLANATION OF PLATE 82

Figs. 1-4. *Anacaenaspis dealgach* (Lamont). Wether Law Linn Formation, unit A, at Wether Law Linn (see also Pl. 81). 1. Partial cephalon, fronto-dorsal view, latex replica of external mould, RSM GY 1978. 61. 513, × 8. 2. Cephalon, internal mould showing genal spine, RSM GY 1978. 61. 512, × 8. 3. Partial cephalon, dorsal view, RSM GY 1978. 61. 514, × 8. 4. Pygidium, internal mould, RSM GY 1978. 61. 515, × 8.

Figs. 5, 7-10. *Leonaspis lothiana* (Lamont). Quarry near Bavelaw Castle, Bavelaw Castle Inlier (see also Pl. 81). 5. Pygidium, ventral view, latex replica of external mould and two thoracic segments, RSM GY 1978. 61. 522, × 6. 6. Pygidium dorsal view, latex replica of external mould, RSM GY 1978. 61. 523 (counterpart of 522), × 6. 7. Partial cranidium, latex replica of external mould, RSM GY 1978. 61. 518, × 8. 9. Enrolled specimen, latex replica of external mould. RSM GY 1978. 61. 517 (i), × 5. 10. Partial cranidium, thorax, and detached librigena on same slab, RSM GY 1978. 61. 517 (ii), × 5.

Fig. 6. *Leonaspis* sp. internal mould of pygidium from junction of Deerhope and Wether Law Linn Formations, Deerhope Burn, RSM GY 1978. 61. 516, × 8.

within axial ring, just posterior to flat and poorly defined apodemes (text-fig. 2*b*). Principal pleural ridge broad, flat-topped continuous with posterior pleural spine; anterior pleural band broad (exsag.), flat, depressed, terminating in backwardly curved edge laterally; posterior pleural band narrow (exsag.), depressed, fulcrum swollen with single large tubercle which becomes more pronounced with each succeeding posterior pleura. Anterior pleural spine, short in ventral view, rectangular, and blunt ended; inclined outwards at angle of some 45° to sagittal plane. Posterior pleural spine thin, straight, and sharply pointed, becoming much longer and more highly inclined to transverse plane posteriorly, with angles ranging from 40° at front to 80° at rear.

Pygidium (exclusive of spines) three times as broad (tr.) as long, with two-ringed rhachis. Axial furrow of first ring barely perceptible, second ring sharply marked off, rounded posteriorly with pair of large swellings, and with short transverse groove behind, surrounded by deep transverse boat-shaped depression. Articulating half-ring highly convex with deep articulating furrow behind; one pair of apodemes below, for ventral surface. First axial ring joining with strong flat pleural ridge, curving backwards to meet pronounced broad posterior border, opposite point of origin of major (second pair) posterior spine, with which, however, it is not directly connected. Posterior border flat, over one-third width (sag.) of pygidium. Five pairs of pygidial spines; anterior pair very short, directed slightly forwards, and probably homologous with anterior pleural spine of the thorax (cf. Whittington 1956, p. 509); second pair short and pointed; third pair strong major pygidial spines, same length as pygidium (sag.), twice as thick as posterior pleural spines at rear of thorax, and slightly swollen just behind their bases; between these four short, broad-based, rather blunt spines, set in transverse plane, and all of similar size and shape. Doublure forms broad flange turned inwards as far as posterior border furrow, with slightly raised transverse band, narrowing antero-laterally, and inclined forwards terminating in small anterior spine. Dorsal surface of pygidium with large tubercle on border, anterior to base of major spines, and on four median spines. Ventral surface of pygidium and spines densely granulated, this granulation is present on sides of spines but dies out dorsally.

Remarks. *L. lothiana* is close to *L. marklini* (Angelin) from the Upper Wenlock–Lower Ludlow Halla and Mulde beds of Gotland, especially in the form of the glabella, though it is relatively smaller in *L. lothiana*, and in the short and stumpy genal spine. The pygidial spines of *L. marklini* are relatively longer and the swollen bases of the thoracic spines are less pronounced. Bruton (1967) has listed the characters whereby *L. marklini* is distinguished from other species.

Leonaspis sp.?

Plate 82, fig. 6

Material. A single small pygidium, RSM GY 1978. 61. 516, of width 3·5 mm, preserved as an internal mould was found at NT 145582 in the Deerhope Burn at the boundary of the Deerhope and Wether Law Linn Formations.

Description. Pygidium (including spines) about as broad as long, semicircular with broad subparallel-sided rhachis one-third total width with three axial rings. Three pairs of rather slender marginal spines. Outer pair short, curving slightly adaxially; middle pair longer, about half total pygidial length, straight directed slightly adaxially; internal pair continuing line of axial furrows, shorter and not reaching so far posteriorly, almost parallel with axis. Large tubercle located on pleural field near base of each middle spine; pair of smaller tubercles lie just within axial furrows in front of third segment of rhachis.

Remarks. This pygidium cannot be matched with that of any known Silurian species. *L. deflexa* (Lake, 1896) has a somewhat similar though narrower pygidium and that of *L. angelini* (Prantl and Přibyl) (Bruton 1967, pl. 34, fig. 4) also resembles that of the Pentland species though the spines are much longer. Until further material is forthcoming the species is left under open nomenclature.

Genus ANACAENASPIS Bruton, 1967

Anacaenaspis dealgach (Lamont 1978)

Plate 81, fig. 2; Plate 82, figs. 1–4; text-fig. 3

1948 *Acidaspis dealgach* Lamont, p. 5, pl. 1, figs. 8, 9 (no description; poor illustration, *nomen nudum*).
1978 *Bruxaspis dealgach* (Lamont 1948) [*sic*]; Lamont, p. 275, pl. xxx, figs. 19, 20 (poor illustration).

Material and distribution. The syntypes are two specimens figured by Lamont (1948) and later sketched (1978). One of these is a partial cephalon, (internal mould) RSM GY 1979. 77. 452, the other a pygidium devoid of spines

PLATE 82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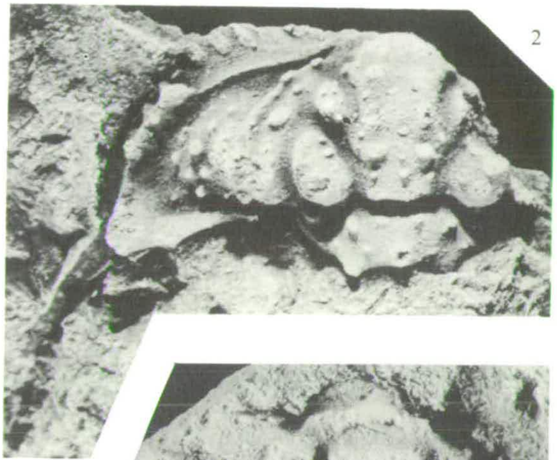
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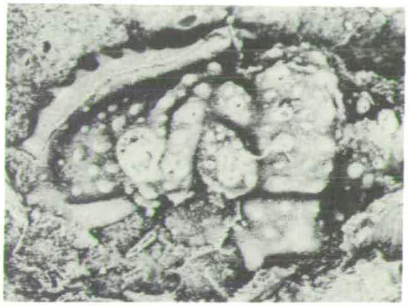
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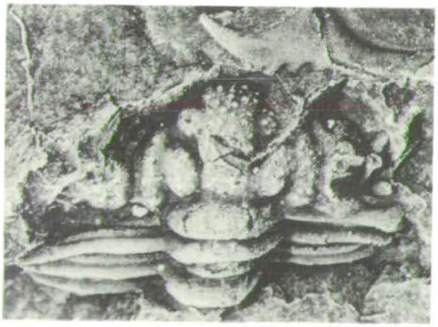
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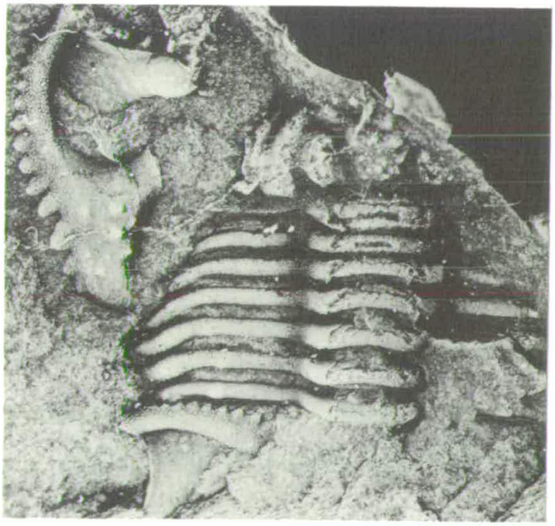
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CLARKSON and HOWELLS, Silurian trilobites

Fixigena ridge-like swollen, bounded externally by very narrow ocular ridge emerging from front of eye at some 30° to sagittal plane, curving in forwards to run almost transversely and finally terminating against the glabella. Eye about one-third length of glabella, set opposite centre of 1L. Genal field broad, sloping outwards to broad and deep border furrow. Anterior border narrow and straight, reflexed at corners to join broad antero-lateral border, which has eleven radial spines, projecting some 45° to vertical, equally spaced and all of about the same length, with last three directed posteriorly. Sutural ridge emerging from inner edge of lateral border opposite first radial spine running subparallel to, and close to, ocular ridge for short distance, tapering posteriorly and dying out on genal field.

Posterior border narrowing abruptly towards the occipital ring, being very thin just outside 1L. Genal spine very long, broadest at base, becoming slender posteriorly, continuously curving, full length unknown, but at least one and a half times length of cephalon.

Surface sculpture of larger and smaller granules, more or less symmetrical and finer granulation. Glabella with a sagittal line of small granules, and five pairs of large tubercles outside this running parallel with it; with many smaller tubercles. 1L and 2L densely covered with many somewhat smaller tubercles. Row of large tubercles running along fixigenal ridge; genal field with other large tubercles; borders with few ill-defined tubercles, with large pair lying on posterior border. Occipital ring with four tubercles of intermediate size in transverse plane, single median occipital tubercle has four symmetrical depressions. Hypostome and thorax unknown.

Pygidium known only from internal moulds, three times broader (tr.) than long, axis quite broad, rounded posteriorly (but not well preserved in available specimens), first axial ring very pronounced, with pleural band extending postero-laterally to cross flat pleural field. Postero-lateral border well-defined with five symmetrical pairs of nearly straight spines extending subradially, equally spaced, and all about half axial length of pygidium.

Remarks. This species is very similar to *A. emarginata* (Schmidt, 1885) from the Upper Wenlock of Estonia, redescribed by Bruton (1967, p. 237), differing mainly in the relatively longer glabella with its more constricted base, and the somewhat larger 1L and 2L. The axis of 1L in addition is about 25° to the sagittal plane rather than nearly parallel to it as in *A. emarginata.*

Anacaenaspis cf. *dealgach* (*Lamont*)

Plate 81, fig. 7

Remarks. A single incomplete internal mould of a cephalon GSE 13518, which was collected from the uppermost Reservoir Formation, in the Deerhope Burn bears a close resemblance to *A. dealgach*, but the cephalon is less broad, the pleural field especially being narrower. No more precise definition is possible.

Family LICHIDAE Hawle and Corda, 1847
Subfamily CERATARGINAE Tripp, 1957
Genus HEMIARGES Gürich, 1901
Hemiarges rolfei Lamont, 1965

Plate 79, figs. 13–15.

1904 *Lichas* (*Corydocephalus*) *anglicus* (Beyrich), 1846; Reed, p. 95.
1961 *Hemiarges* sp.; Lamont (*in* Rolfe, p. 252) (list).
1965 *Hemiarges rolfei* Lamont, p. 33, pl. 5. figs. 1, 1A.
1965 *Hemiarges* sp.; ibid., p. 34.
1965 *Hemiarges hughmacdiarmidi* Lamont; ibid., p. 34.
1977 *Hemiarges rolfei*; Clarkson *et al.*, p. 121 (list).
1978 *Hemiarges hendersoni* Lamont; Lamont, p. 275, pl. xxx, figs. 17, 18.

Holotype. BU 1896, incomplete internal mould of cranidium with counterpart, figured Lamont 1965, pl. 5, figs. 1, 1A; from the Ree Burn Formation (*crenulata* Zone), Hagshaw Hills, Scotland.

Figured material from Pentland Hills. Internal mould of cranidium figured by Lamont (1978, pl. xxx, fig. 17) as type of *Hemiarges hendersoni*, RSM GY 1979. 45. 2 (locality unknown) (Pl. 79, fig. 13); partial pygidium, part and counterpart RSM GY 1978. 61. 511a, b (Pl. 79, fig. 14); hypostome, part and counterpart Gr. I. 40. 306, 308 (Pl. 79, fig. 15).

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Other material. Partial pygidium (internal mould), Gr. I. 40. 307.

Distribution. All known specimens other than the cranidium come from the Upper Deerhope Formation at NT 145582. The species also occurs in the Ree Burn Formation in the Hagshaw Hills and in the Knockgardner Formation at Girvan together with *Podowrinella straitonensis* (Lamont) and *Encrinurus* fragments.

Diagnosis. Cranidium not greatly convex. Frontomedian lobe parallel-sided for most of length (sag.). Bullar lobe small, rounded anteriorly, pointed posteriorly. 1L long (exsag.), greater in length laterally than bullar lobe. Pygidium with long (sag.) tapering axis. Posterior raised ridges of pygidial pleura and border of pygidium with short, pointed spines.

Dimensions of holotype. Cranidial sagittal length, 5 mm; half cranidial width, 3 mm.

Description. Cephalon known in the Pentland Hills only by a single laterally compressed glabella. Whilst this was taken by Lamont as the type of *H. hendersoni* it compares with better-preserved material from Knockgardner in all aspects save the convexity, imparted by lateral compression. Frontomedian lobe parallel-sided for most of length expanding anteriorly to three times midlength width. Longitudinal furrow deep. Occipital ring one and a half times as wide as base of frontomedian lobes. Occipital lobe not preserved. Occipital furrow, shallower than longitudinal furrow, transverse behind frontomedian lobe. Bullar lobe circumscribed, approximately one-third length (exsag.) of cranidium, equal in width (tr.) to narrowest part of frontomedian lobe; kidney-shaped in outline, with small indentation at midlength adjacent to longitudinal furrow, rounded anteriorly, pointed posteriorly. 1L delimited from frontomedian lobe by shallow depression, somewhat inflated. Fixed cheek, palpebral lobe, anterior border and facial suture not preserved. All convex surfaces with irregular, scattered tubercles. Librigena unknown.

Hypostomal outline forms an equidimensional hexagon. Middle body very gently convex, more than three-quarters total width of hypostome, about one and a half times wider (tr.) than long (sag.), expanded anteriorly into large transverse lobes occupying two-thirds its total length, sharply indented behind these and tapering posteriorly to smaller pair of transverse lobes. Middle furrow transverse, quite broad and deep, defining a distinct narrow transverse ridge half total width of hypostome, and separated from posterior border by narrow and deep posterior furrow. Postero-lateral borders flat, about as wide as a quarter of total length of hypostome, and arising just in front of median transverse plane. Thorax unknown.

Pygidium approximately one and a half times wider (tr.) than long (sag.). Axis tapering gradually posteriorly to half axial anterior width (tr.), anteriorly with five distinct axial rings with two more faintly defined rings behind, terminating bluntly but merging into postaxial ridge. First and second lateral pleurae with raised posterior borders produced into short pointed spines. Faintly raised border produced into short spines. Some symmetrical arrangement of granules on axis but not clearly defined, remainder of pygidium with scattered granules.

Discussion. The parallel-sided frontomedian lobe and long 1L, and the pygidial morphology indicate that the Pentland form is identical to *H. rolfei* from the Hagshaw Hills and Knockgardner. *H. hughmacdiarmidi* Lamont (1965, p. 34) from the Knockgardner locality appears to be a *nomen nudum* as no description, type specimen, or type locality is given for this species and no prior reference to it has been traced. The cranidium referred to by Reed (1904, p. 95) cannot be traced. The spinosity of the pygidium of *H. rolfei* separates it from the other *Hemiarges* species found in older rocks of the Girvan Inlier.

FAUNAL AFFINITIES

The Reservoir and Deerhope Formations contain trilobites which appear to be endemic to the Midland Valley of Scotland, whereas the closest affinities of the Upper Llandovery trilobite faunas of the Wether Law Linn Formation are found in the East Baltic (Gotland and Estonia), and the faunas do not resemble those of the Girvan area. Following Schmidt's classic work (1881-1907), and that of Lindström (1885), Öpik (1937), and others, many of the Silurian faunas have been described in detail by Männil (1958; 1968; 1970*a*, *b*; 1977*a*, *b*, *c*) who has given full stratigraphic detail; and both morphological and stratigraphic parallels with the faunas from the Pentland Hills are close. Several successive species of *Acernaspis* in the Llandovery of Estonia show morphological changes in the vincular furrow. Männil (1970*b*, p. 34) notes that early Llandoverian species have a continuous vincular furrow (*A. semicircularis*, *A. estonica*), whereas by Middle Llandovery times the furrow was becoming faint anteriorly (*A. rectifrons*, *A. incerta*), and by the Upper Llandovery the vincular furrow is absent anteriorly (*A. konoverensis*). A parallel reduction in the anterior part of the vincular furrow is apparent in the Scottish species of *Acernaspis* though the stratigraphic section is less complete than in Estonia (Clarkson *et al.* 1977): *A. konoverensis* is in any case closely similar to *A.* (*Eskaspis*) *sufferta* and would seem to belong to the same subgenus.

Almost all the other trilobites in the Wether Law Linn Formation likewise seem to belong to species groups which are well-established in the East Baltic, especially in the Fronian–Telychian Adavere stage of Estonia. Thus the Pentland *Encrinurus expansus* belongs to the *E. schmidti* group, *Proetus* (*Lacunoporaspis*) sp. resembles the Baltic species *P.* (*L.*) *obconicus*, and *Calymene frontosa* is present both in the Pentland Hills and in Estonia. *Youngia douglasi* has perhaps its closest counterpart in *Y. inermis* and *Y. globiceps*, poorly known species from Gotland, whilst, the odontopleurid *Leonaspis lothiana* is close to *L. marklini* and *L. mutica* from Gotland; *Anacaenaspis dealgach* resembles *A. emarginata.*

Youngia does not seem to occur in Estonia. The Estonian Upper Llandovery faunas are more diverse, including trilobites of the families Scutelluidae and Illaenidae which are absent in the Pentlands, and a richer fauna of Encrinuridae and Calymenidae. Faunas in other parts of Britain and Ireland are quite different. This suggests an extension of open marine conditions between eastern Scotland and the Baltic area in Upper Llandovery times.

The presence of well-preserved phacopid and encrinurid specimens in the Silurian rocks of Ringerike, Norway, has been kindly brought to our attention by M. P. A. Howe and Dr. J. H. McD. Whitaker, who have let us borrow their collections. In Stage 8A (lowermost Wenlock) (Kiaer 1908; Whitaker 1977) occurs a phacopid species virtually indistinguishable from *A.* (*Eskaspis*) *sufferta* and an *Encrinurus* very close to *E. expansus.* Such faunal similarities again reinforce the likelihood of an open marine connection between eastern Scotland and Balto-Scandia during this part of the Silurian, whereas there may have been a physical or ecological barrier between eastern and western Scotland at this time.

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The Ordovician trilobite *Calyptaulax brongniartii* (Portlock)

E. N. K. Clarkson and R. P. Tripp

ABSTRACT: *Calyptaulax brongniartii* (Portlock) from the Caradocian Bardahessiagh Formation, Pomeroy, Northern Ireland is redescribed. Equivalent material from Scottish horizons (Balclatchie and Ardwell groups) is regarded as belonging to separate populations. Campbell's system of notation is used to describe variation in the arrangement and number of lenses in the eye. The most closely related species is *C. strasburgensis* (Ulrich & Delo) from the Edinburg Limestone of Virginia, U.S.A.

KEY WORDS: Caradocian, distribution, eyes, Northern Ireland, Phacopina, redescription, Scotland.

Calyptaulax brongniartii is a common trilobite in the Caradocian of Northern Ireland and southern Scotland, and is widely distributed (Fig. 1). In revising this species and in attempting to establish whether the variations seen are of stratigraphical value, it became clear that they are not, but that separate geographical populations can be distinguished, in the main based upon variation in number and arrangement of the eye lenses.

Portlock (1843, p. 282, pl. 2, figs 8 a–d, pl. 3, fig. 8d) founded his *Phacops Brongniartii* upon material which, from the lithology, is from the Bardahessiagh Formation of Pomeroy; we have here selected IGS GSM 13983 as lectotype for *Calyptaulax brongniartii*, herein refigured on Figure 3a. Portlock's *Phacops Dalmanni* (1843 p. 283, pl. 2, figs 7 a–c, pl. 3, fig. 7d) and his *Phacops Murchisonii* (1843 p. 283, pl. 2, figs 9a, b, pl. 3, figs 9c, d), are also from the Bardahessiagh Formation (Fig. 3b, c). Salter (1853, pl. 1, p. 10, 1864, p. 34) placed both "*P. Dalmanii*" and "*P. Murchisonii*" in the synonymy of *brongniartii*, regarding "*P. Dalmanii*" as the female form (or variety). We have no hesitation in agreeing with Salter that the three Portlock species must be regarded as synonymous, and the two specimens IGS GSM 13984 and 13987, the types of *Murchisonii* and *Dalmanni* (Fig. 3 b–c) respectively are also lectotypes.

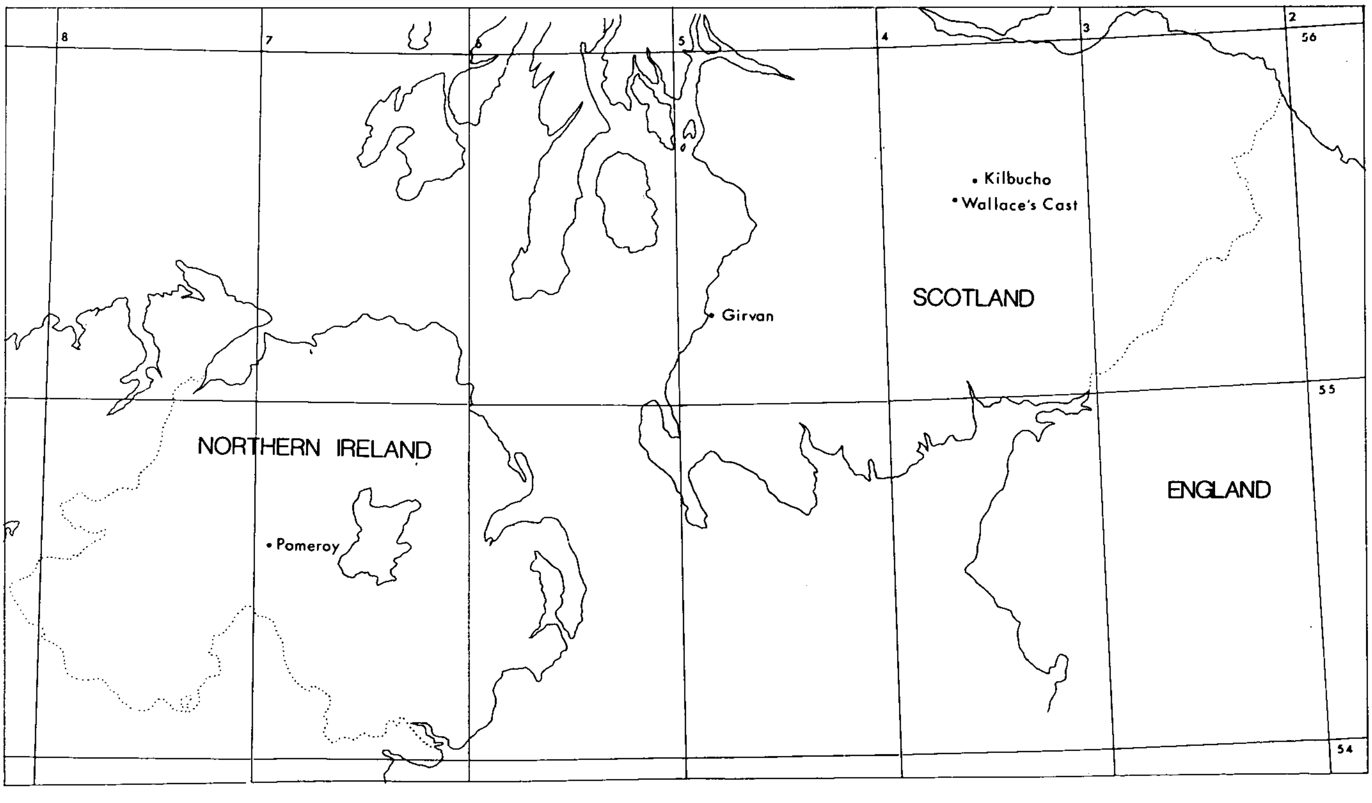


Figure 1 Locality map for *Calyptaulax brongniartii* populations.

1. Systematic descriptions

The terminology used is essentially that adopted in the *Treatise on Invertebrate Paleontology, O*. The system of recording the number of specimens with each individual lens of the eye, introduced by Campbell (1977, text-fig. 12) has been adopted. Terms used in describing the eye are those of Clarkson (1966, p. 2). All dimensions are given in millimetres. A list of specimen numbers, sizes, and lens 'formulae' has been deposited with, and may be purchased from the British Library, Boston Spa, Yorkshire LS23 7BQ, Great Britain, as Supplementary Publication No. 90064 (9 pages).

Order	PHACOPINA	Struve, 1959
Family	DALMANITIDAE	Vogdes, 1890
Genus	*Calyptaulax*	Cooper, 1930

Diagnosis. Cephalon highly vaulted. Frontal lobe of glabella may be prolonged laterally in extensions of free cheek cut off by facial suture. Neck of glabella with or without independent convexity. 3L large, triangular, extending laterally a little less than frontal lobe; 2L small; 1L short with discrete nodular lateral node. 2S convergent forwards, fainter abaxially than adaxially, may become obsolete, apodeme absent; 1S subparallel with 2S, apodeme alongside 1L node. Genal spine usually absent, sometines present in adult. Occipital ring wider than preoccipital segment. Anterior border furrow usually present mesially. Eye long, commencing at rachial furrow opposite 3S, reaching, or almost reaching posterior border furrow, marked off by a strong palpebral furrow. Posterior border short adaxially. Pygidium highly vaulted, usually non-mucronate, generally subtriangular; seven or more rings and two or more pleural ribs distinct. Inter-rib furrows reach rachial furrow, rib fur-

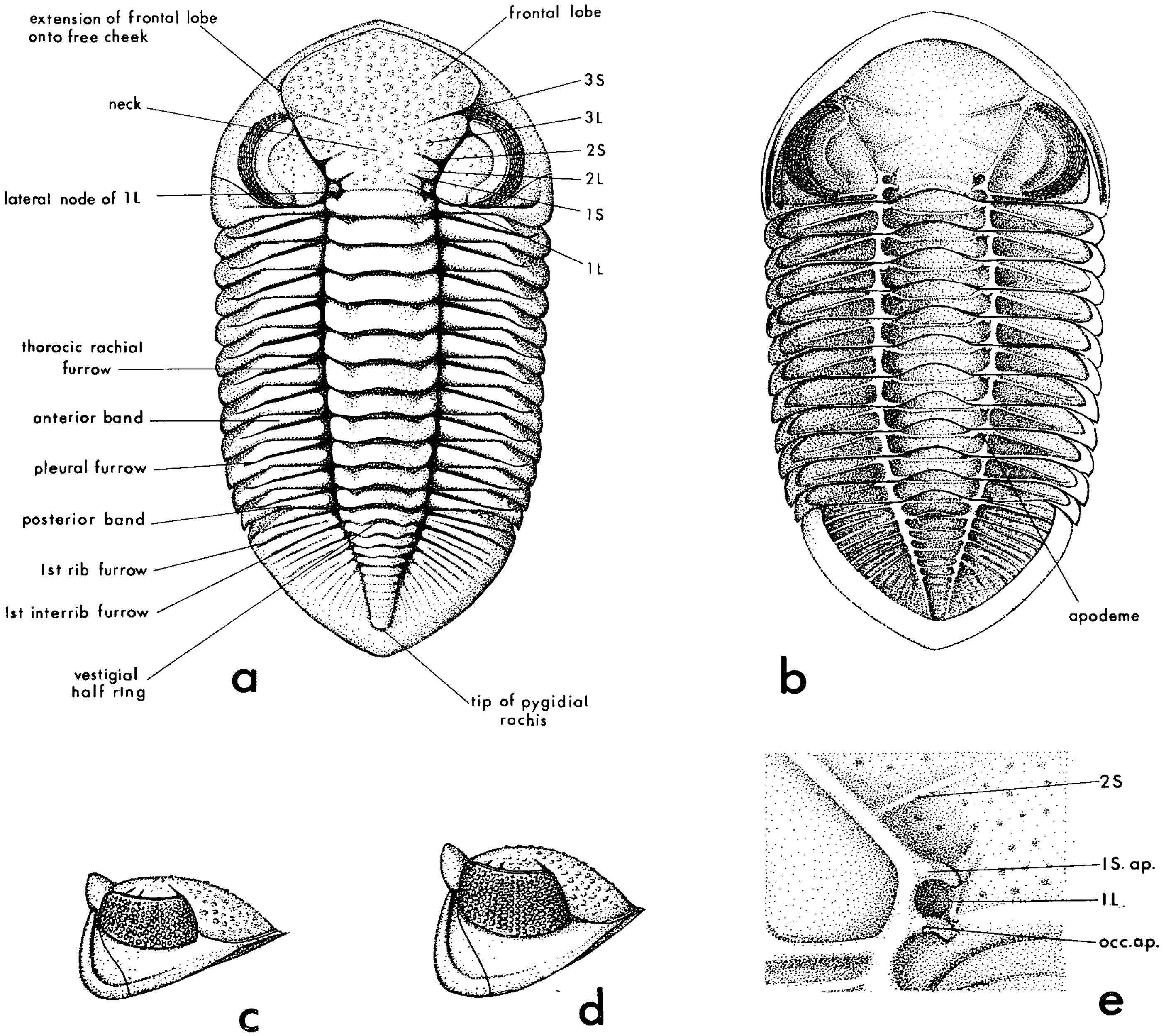


Figure 2 *Calyptaulax brongniartii* (Portlock).
(a, b) Reconstruction of dorsal and ventral morphology, based on specimens of the Ardmillan population, with terminology used here.
(c) Reconstruction, in lateral view, of cephalon, from the Bardahessiagh population.
(d) From the Ardmillan population.
(e) Reconstruction of part of cephalon in ventral view showing apodemes of occipital ring (occ. ap.) and 1S (1S ap).

rows posterior to first are shallower than pleural furrows adaxially. Surface of cranidium usually granulate.

We follow Shaw (1968, p. 83) and other authors in preferring to use *Calyptaulax* in a wide sense, rather than the insecurely founded *Calliops* Delo (1935, p. 417).

Calyptaulax brongniartii (Portlock, 1843)

1843 *Phacops Brongniartii* Portlock, p. 282, pl. 2, figs 8a–d, pl. 3, fig 8d.
1843 *Phacops Dalmanni* Portlock, p. 282, pl. 2, figs 7a–c, pl. 3, fig 7d.
1843 *Phacops Murchisonii* Portlock, p. 283, pl. 2, figs 9a, b, pl. 3, figs 9c, d.
1853 *Phacops Brongniartii* Portlock; Salter, p. 10.
1864 *Phacops* (*Acaste*) *Brongniartii* Portlock; Salter, p. 34–36, pl. 1, figs 21, 25, *non* fig. 20.
1878 *Phacops Brongniartii* Portlock; Nicholson & Etheridge, p. 99, pl. 7, fig. 1, *non* fig. 2.
1879 *Phacops Brongniartii* Portlock; Nicholson & Etheridge, pp. 201–202, pl. 14, fig. 8, *non* fig. 7.
1906 *Phacops* (*Pterygometopus*) *brongniartii* Portlock; Reed, p. 154, (*pars*) pl. 19, figs 17, 18.
1945 *Phacops* (*Calliops*) *jukesi*; Salter var. nov. *vicina*; Reed pp. 314–315, pl. 4, fig 6.
1952 *Phacops* (*Calliops*) *brongniartii* (Portlock); Reed, p. 122.
1954 *Calliops brongniartii* (Portlock); Tripp, pp. 685–686, pl. 4, figs 34–38.
1980 *Calyptaulax brongniartii* (Portlock); Tunnicliff, pp. 41, 42.

Diagnosis. Glabella wide anteriorly, extended onto free cheek; rachial and palpebral furrows deep; anterior border flattened and smooth. Lateral node of 1L usually depressed. Eye extends to posterior border furrow, composed of 134–225 lenses. Posterior border depressed adaxially. Genal angle rounded. Doublure not embayed anteriorly. Pygidium composed of up to twelve rings and seven pleural ribs; first rib furrow longer than subsequent rib furrows.

Lectotypes. All internal moulds of dorsal shield; Bardahessiagh Formation, Tyrone, Northern Ireland.

(i) IGS GSM 13983. Figured Portlock 1843, pl. 2, figs 8a, pl. 3, fig. 8d; Salter 1864, pl. 1, fig. 22; this paper Fig. 3a.

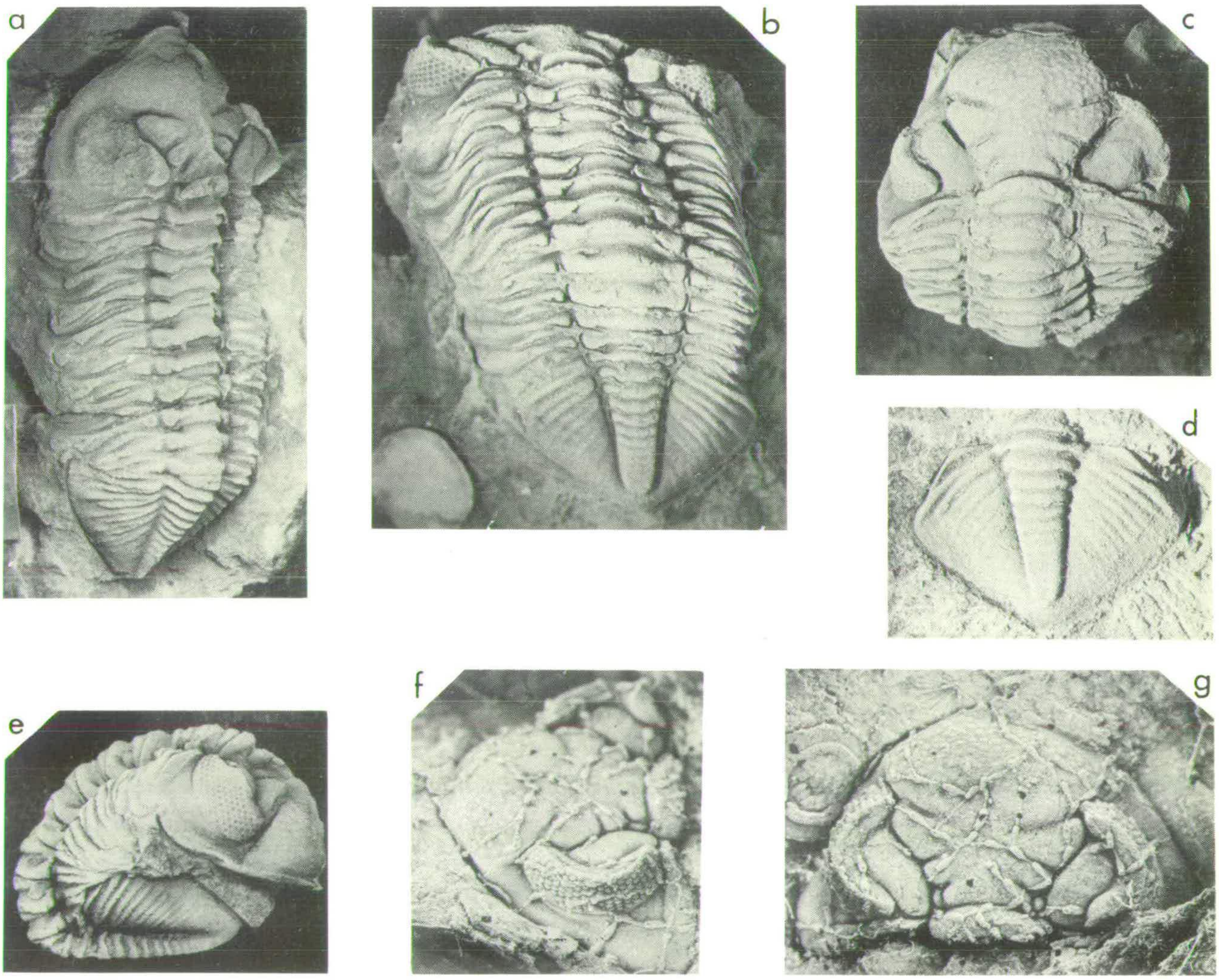
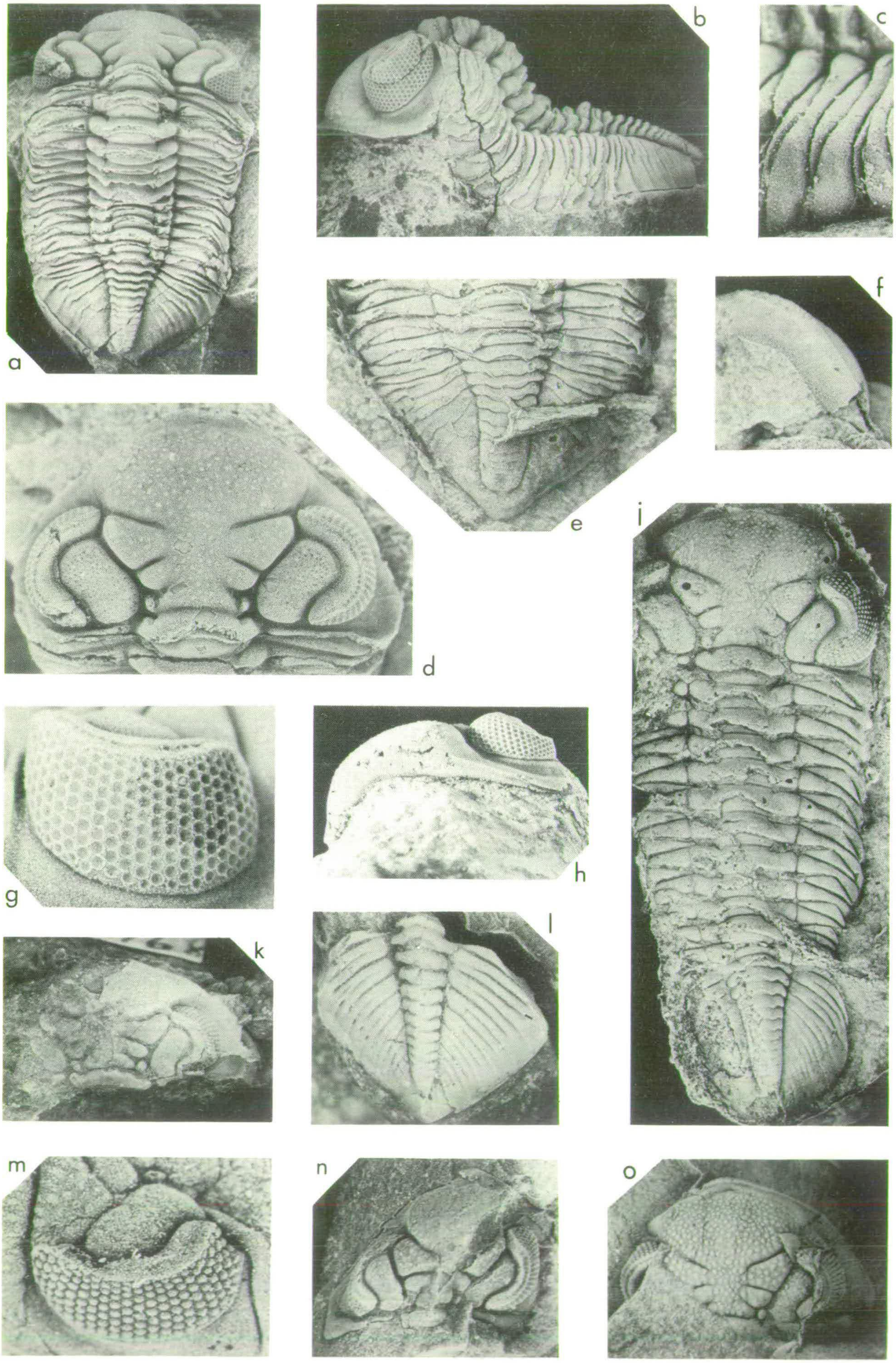


Figure 3 *Calyptaulax brongniartii* (Portlock) from the Bardahessiagh Formation, Pomeroy, Northern Ireland.
(a) Lectotype, IGS GSM 13983, figured by Portlock 1843, as type of *Phacops brongniartii*; ×2.5.
(b) Lectoype, IGS GSM 13981, figured by Portlock 1843, as type of *Phacops Murchisonii*; ×3.5.
(c) Lectotype, IGS GSM 13987, figured by Portlock 1843 as type of Phacops *Dalmanni*; ×3.5.
(d) Pygidium, IGS GU 1727, internal mould; ×4.
(e) Enrolled specimen, IGS GSM 13984, internal mould, figured by Portlock, 1843, pl. II, fig. 8d; ×2.8.
(f, g) Cephalon, IGS GY 1337, overgrown by the bryozoan *Corynotrypa delicatula* (James) previously known only from the Middle and Upper Ordovician and Lower Silurian of North America and the Middle Ordovician of the Baltic provinces—*fide.* Bassler), ×0.5.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(ii) IGS GSM 13987. Figured Portlock 1843, p. 282, pl. 2, figs 7a, b, c; ?pl. 3, fig. 7d, as *Phacops Dalmanii*; cited Salter 1853, 1864 and Reed (1952) as above; this paper, Fig. 3c.

(iii) IGS GSM 1. Figured Portlock 1843, p. 283, pl. 2, figs 9a, b; pl. 3, figs 9c, d. *Phacops Murchisonii*; cited Salter 1853, p. 10, p. 1; Salter 1864, p. 34, Reed 1952, p. 123; this paper Fig. 3b.

Dimensions of IGS GSM 13983. Sagittal length of cranidium (normal projection) 10.9; sagittal length of thorax 16.8; sagittal length of pygidium (normal projection, excluding occipital ring) 8.9; length of eye (exs.) 5.2; width of cephalon (estimated) 20.3.

Occurrences. (Fig. 1) (a) Northern Ireland; Bardahessiagh Formation (see Mitchell 1977, p. 5; Tunnicliff 1982, p. 45), Pomeroy (over 50 specimens including dorsal shields, cranidia, thoracic segments and pygidia; outnumbers all other trilobites together); (b) Scotland: Girvan district: lower Balclatchie Group—Knockbain Burn (very rare), Glendrissaig (rare), Dow Hill (common); upper Balclatchie Group—Balclatchie (common), Penwhapple Burn (Balclatchie Conglomerate) (common); lower Ardwell Group—Ardmillan (very common); upper Ardwell Group—Kiln Mudstones, Craighead Quarry (rare); (c) Scotland: central Southern Uplands (Northern Belt); Kilbucho (common but in a state of preservation inadequate for precise analysis); Wallace's Cast, Wandel Water (common) (see Peach & Horne 1899, pp. 224–225, 242–243).

Description. Sagittal length of cephalon about 50% width. Glabella wider than long, moderately to strongly convex, more strongly so anteriorly than posteriorly. Frontal lobe 60% length (sag.) of glabella adaxially. Anterior border up to 10% length of glabella, marked off by a depression (faint abaxially), by less steep inclination and by absence of sculpture mesially. Neck of glabella may have slight independent convexity but not marked off by longitudinal furrows. 3L large, subtriangular, gently convex. 2L oblique, well defined 1L with rounded, discrete lateral node, generally

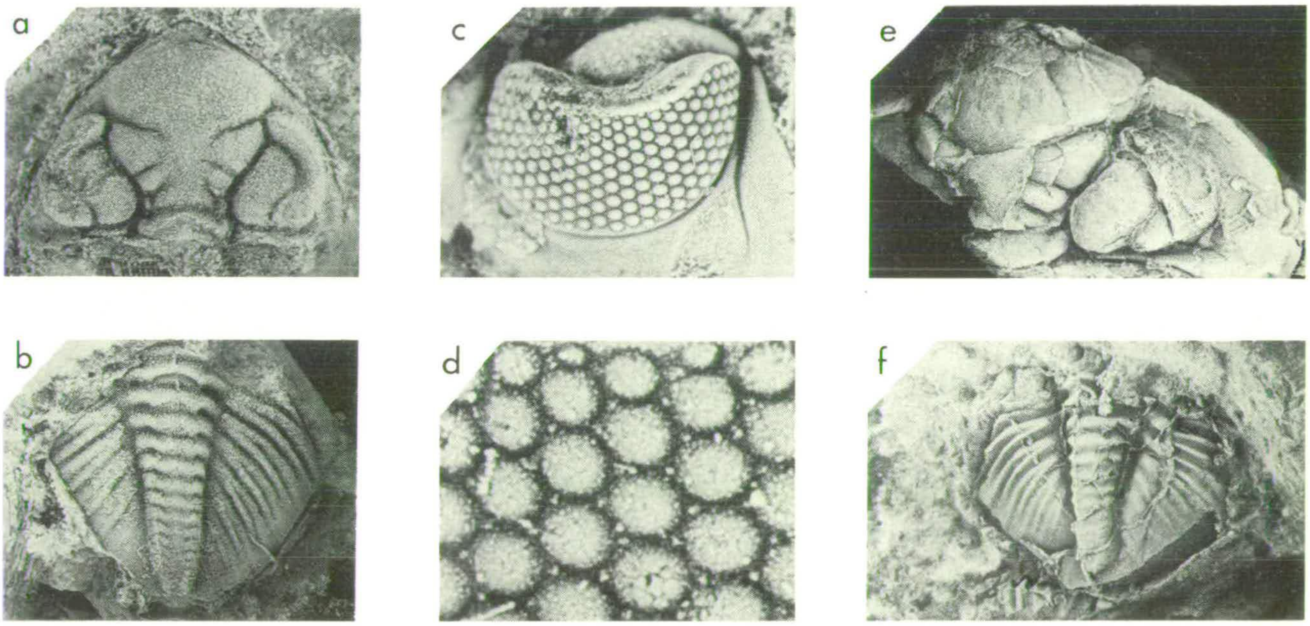

Figure 5 *Calyptaulax brongniartii* (Portlock) Central Southern Uplands (Northern Belt), strata coeval with Balclatchie and Ardwell groups of Girvan.
(a–d) Wallace's Cast, Wandel Water, e.f. Kilbucho.
(a) Cephalon. IGSE 13755, internal mould; ×4.
(b) Pygidium, IGSE 13754, internal mould; ×4.
(c) Eye, IGSE 32907, latex replica of external mould; ×10.
(d) Same, showing granules surrounding each lens; ×50.
(e) Partial cephalon, IGSE 13753, internal mould; ×3.25.
(f) Pygidium, IGSE 13752, internal mould; ×2.5

Figure 4 *Calyptaulax brongniartii* (Portlock) from the Girvan district.
(a–h, k.j) Lower Ardwell Group, Ardmillan.
(a–e, g.h) Complete specimen, BMNH In 23550.
(a, b) Dorsal and left lateral views, internal mould; ×3.
(c) Anterior thoracic pleura with articulating facets; latex replica of external mould, left lateral view; ×7.
(d) Cephalon, internal mould; ×4.75.
(e) Pygidium and last thoracic segments, latex replica of external mould; ×4.5.
(f) Doublure of partial cephalon internal mould, IGSE 13751; ×5.
(g) Right eye, internal mould; ×9.
(h) Cephalon in oblique ventral view showing doublure and vincular furrow, internal mould; ×4.
(j) Complete specimen BMNH In 23553, latex replica of external mould; ×3.25.
(k) Cephalon retaining partially altered cuticle, HM A 5370, Upper Balclatchie Group, Penwhapple Burn (figured Reed (1945) as *Phacops* (*Calliops*) *jukesi*. var. *vicina*); ×3.
(l) Pygidium with original cuticle, BMNH In 20253, Upper Balclatchie Group, Balclatchie; ×8.5.
(m–o) Lower Balclatchie Group, Dow Hill.
(m) Eye and adjacent regions of cephalon BMNH In 43710, latex replica of external mould; ×10.
(n) Cephalon. BMNH In 43799, internal mould; ×4.
(o) Cephalon. BMNH In 43710, latex replica of external mould; ×3.5.

depressed abaxially. 3S almost straight, strong, set at 70° to midline. 2S distinct, set at 110° to midline, 1S short and deep, curving inwards and forwards adaxially to lateral node: apodeme directed inwards and backwards at abaxial extremity. Occipital ring extends further sideways than 1L, longest sagitally; lateral node faintly indicated anteriorly. Occipital furrow shallow behind glabella, deepening abaxially into transverse apodeme. Rachial furrow merges with 3S anteriorly, broad, deepening opposite 2L and 1L. Fixed cheek strongly defined, gently convex, extending backwards beyond occipital furrow. Palpebral lobe extends from rachial furrow opposite 3L to posterior border furrow, narrow, of uniform width, marked off from fixed cheek by a broad palpebral furrow which deepens adaxially; anterior and posterior extremities approximately follow exsagittal line. Palpebral lobe level with upper extremity of eye mesially, deepening towards palpebral furrow anteriorly and posteriorly and marked by a chain of punctuations close to and parallel with outer edge. Posterior border transverse, short (exs.), depressed below level of fixed cheek, well defined only adaxial to palpebral lobe. Abaxially border dies out and posterior margin curves backwards, usually extending some distance posterior to backward extremity of occipital ring. Posterior border furrow deep, transverse, placed posterior to occipital furrow. Genal angle broadly but variably rounded.

Facial sutures submarginal, merging anteriorly in a tight curve, then curving outwards and backwards and cutting off the lateral extension of glabellar frontal lobe onto the free cheek. Posterior branch short, curving lateral margin opposite 1L; sutural ridge faintly discernible.

Eye gently rounded in plan view, subtending 180° visual range, composed of 134 to 225 lenses, arranged in 22 to 26 files, hexagonally close-packed, with 8 to 11 lenses in longest files; lens formulae (number of lenses in successive files and relative positions of basal lenses of files) are recorded in deposition material. Lenses increase gradually in size from top to bottom of files except for the bottom lens of a few files; part-formed lenses included in counts. In profile, visual surface is slightly curving, inclined at about 10° to vertical. Well-preserved specimens show a ring of six minute tubercles surrounding each lens (Fig. 5d, cf. *C. strasburgensis* in Clarkson 1975, pl. 5, figs 3, 4). Occasional anomalies in size and arrangement of lenses occur in specimens from all localities. Socle weakly developed, marked off from eye by a narrow, continuous furrow and from cheek anteriorly only. Free cheek comparatively wide abaxially, not strongly downturned although much liable to distortion. Broad lateral border marked off by broad, shallow furrow. lateral doublure extends half way to eye.

Doublure 20% sagittal length of cephalon, not embayed anteriorly, inner margin forms a broadly rounded curve. Doublure flattened anteriorly, more convex and narrowing (tr.) posteriorly becoming indented by a pronounced vincular furrow commencing opposite 3S and deepening backwards. Apodemes of occipital ring and 1S distinct, each being a round knob set on a sloping, backwardly curved spur (Fig. 2e.)

Granulation on cephalon varies in strength and size between specimens, stronger on frontal lobe and neck of glabella, than on 3L, 2L, palpebral lobe and occipital ring in that order, absent on posterior border and on extension of glabella on free cheek. Anterior border smooth mesially, faintly granulate abaxially. Fixed cheek adaxial to palpebral furrow finely pitted on external surface only (Fig. 4d).

Hypostome not known with certainty.

Thorax about 150% length of cranidium, composed of eleven thoracic segments. Rachis 35% width of thorax, first ring wider than occipital ring, moderately arched transversely; lateral nodes faintly developed on internal moulds. Articulating half-ring and furrow strongly developed, blade-like apodeme at abaxial extremity of furrow. Rachial furrow straight and narrow. Pleurae directed only slightly backwards; inner part horizontal, outer part curved downwards, fulcrum at 40% width of thorax. Abaxially to fulcrum a large, bevelled articulating facet develops anteriorly, and lateral part of pleura curves slightly forwards. Pleural furrow deep, running outwards and strongly backwards to fulcrum, then curving forwards and dying out before lateral margin. Adaxial parts of pleura anterior and posterior to furrow with strong independent convexity. Thoracic doublure flat and relatively narrow with inner margin U-shaped and strongly curving to cut posterior pleural border at fulcrum and anterior border a third of the distance between distal tip of pleura and fulcrum.

Pygidium 80% length (sag.) of cranidium, ogive-shaped in outline, weakly convex longitudinally, moderately so transversely 60–80% as long as wide. Rachis 30% anterior width of pygidium, bowed inwards, moderately convex transversely, up to twelve rings, posterior rings faint, and a terminal piece. Vestigial half-ring sometimes present at back of first ring, smaller half-rings occasionally found behind second and third rings. Ring furrows deep anteriorly, becoming shallower posteriorly, anterior furrows bowed backwards mesially. Apex of rachis narrowly rounded. Rachial furrow narrow. Up to seven pleural ribs, widening slightly abaxially, directed increasingly strongly backwards. Rib and inter-rib furrows (equivalent respectively to interpleural and pleural furrows) decreasing in strength successively towards back, great variation in strength between specimens; inter-rib furrows deeper than rib furrows adaxially, reaching rachial furrow, dying out well before lateral margin; rib furrows obsolete adaxially, deepening rapidly to equal inter-rib furrows and extending further than they do towards lateral margin. First pleural rib thus demarcated therefore constituted by posterior band of first pleurae and anterior band of second pleurae separated by interpleural furrow between first and second pleurae; this (first rib) furrow disproportionately stronger than subsequent rib furrows. Posterior part of pleural lobe continuous with postrachial area. Doublure extends to apex of rachis, convexity strongest posteriorly, inner margins meeting at an acutely rounded angle. Articulating ring and furrow strongly developed. Articulating facet cuts obliquely across anterior band of first pleura and first pleural rib.

2. Populations

Certain geographical populations differ from the topotype material (Figs. 4, 5.) distinguished mainly on the structure of the eye.

The other characters which might be considered in separating these populations are of rather limited value. These include glabellar tuberculation and the convexity of the exoskeleton. The size and density of tubercles varies from one population to another but not enough to make tuberculation a reliably diagnostic criterion for distinguishing populations. Thus although the Bardahessiagh and Dow Hill populations (which are very close morphologically) usually have larger and more densely packed tubercles than those of the Ardmillan population, there is enough variation in each population to allow some overlap.

In the Ardmillan population the cephalon is strongly convex (Fig. 4b, h), but is less so in the Bardahessiagh and Dow Hill populations (Figs 2, 4). The eye is likewise deeper in the Ardmillan population, and seems to be geometrically related to the stronger convexity of the cephalon simply because of a more convex head can accommodate a deeper eye. The other populations are usually represented by distorted and flattened material and quantitative expression of convexity cannot be determined. Only the specimens from Wallace's Cast retain an original convexity (Fig. 5a–d), which is intermediate between that of Dow Hill–Bardahessiagh and Ardmillan, and this again seems to relate to an eye of intermediate depth.

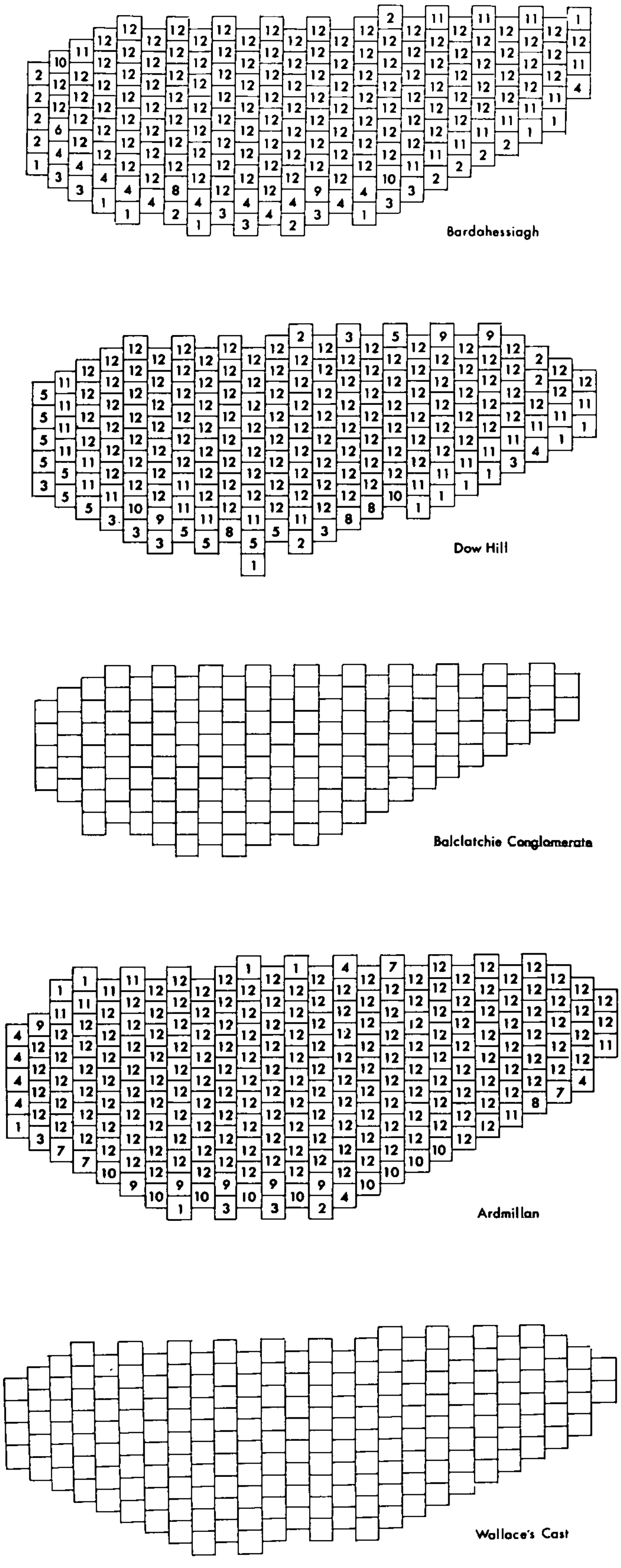

Figure 6 Lens—distribution in various populations of *Calyptaulax brongniartii*, (left is anterior); for explanation see section 2.

Of these various populations the only one which has been separately named is a form from the Balclatchie Conglomerate described by Reed (1945, pp. 314–316) as *Phacops* (*Calliops*) *jukesi* var. *vicina* (Fig. 4k). We regard this as a representative of another population, but not to be distinguished by a separate name, and as such it is included in our synonymy. The arrangement of the lenses in the eye does not differ greatly from that of the Dow Hill population, and although 1L is not much depressed, this feature is quite variable, for instance in *C. strasburgensis* from various localities.

In order to show the variation in eye structure populations, a notational system of lens-distribution has been adopted, with slight modification, from Campbell (1977). The eye is represented by a grid pattern, each square corresponding to a lens and in each population the eye and hence the grid has a characteristic shape (Fig. 6). The diagrams record the number of specimens examined (twelve specimens selected for each population where possible) carrying a lens at each position. Since the eye expands forwards (as a logarithmic spiral) and downwards as it grows it has been possible to equate individual files and lenses in various specimens by working forwards from the posterior file, and this is confirmed by a harmonious matching of the patterns of all other files. These diagrams show that not all specimens have the anterior file developed, and, of course, some of the smaller specimens lack the lowermost one or two lenses of each file.

Whilst the eye lens-distribution charts confirm the similarities in the Bardahessiagh and Dow Hill populations, they also display minor differences between these two, and indicate clearly that the other populations have indeed a different lens-distributional structure. Unfortunately the material from Kilbucho is so distorted that accurate lens-counting is not possible, and the Balclatchie Conglomerate and Wandel Burn are each represented only by a single usable specimen.

A summary of the eye characters for each of the populations is given in Table 1.

3. Discussion

Calyptaulax brongniartii is a Caradoc species, occurring in Northern Ireland and in southern Scotland from Girvan to Kilbucho. It is distinguished from other species of the genus by characters including depression of the lateral node of 1L, by the strength of the rachial and palpebral furrows and by the eye reaching to the posterior border furrow. The lens formula provides a sensitive diagnostic character and it has been used to discriminate geographical populations. Such variation in lens number and arrangement does not seem to be of any stratigraphic significance.

The closest resemblance between *C. brongniartii* and other described species is to *C. strasburgensis*, (Ulrich & Delo) (see Delo 1940, pp. 99–100, p. 12, figs 8–10) from the Lower Edinburg Formation of the Southern Appalachian region. *C. brongniartii* differs from *C. strasburgensis* in having more lenses in the eye. In the latter 1L is less depressed, and 3L, 2L and the palpebral lobe are as tuberculate as the rest of the glabella. In ventral view, *C. strasburgensis* has a strongly medially embayed doublure, whilst this feature is less evident in *C. brongniartii*.