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.

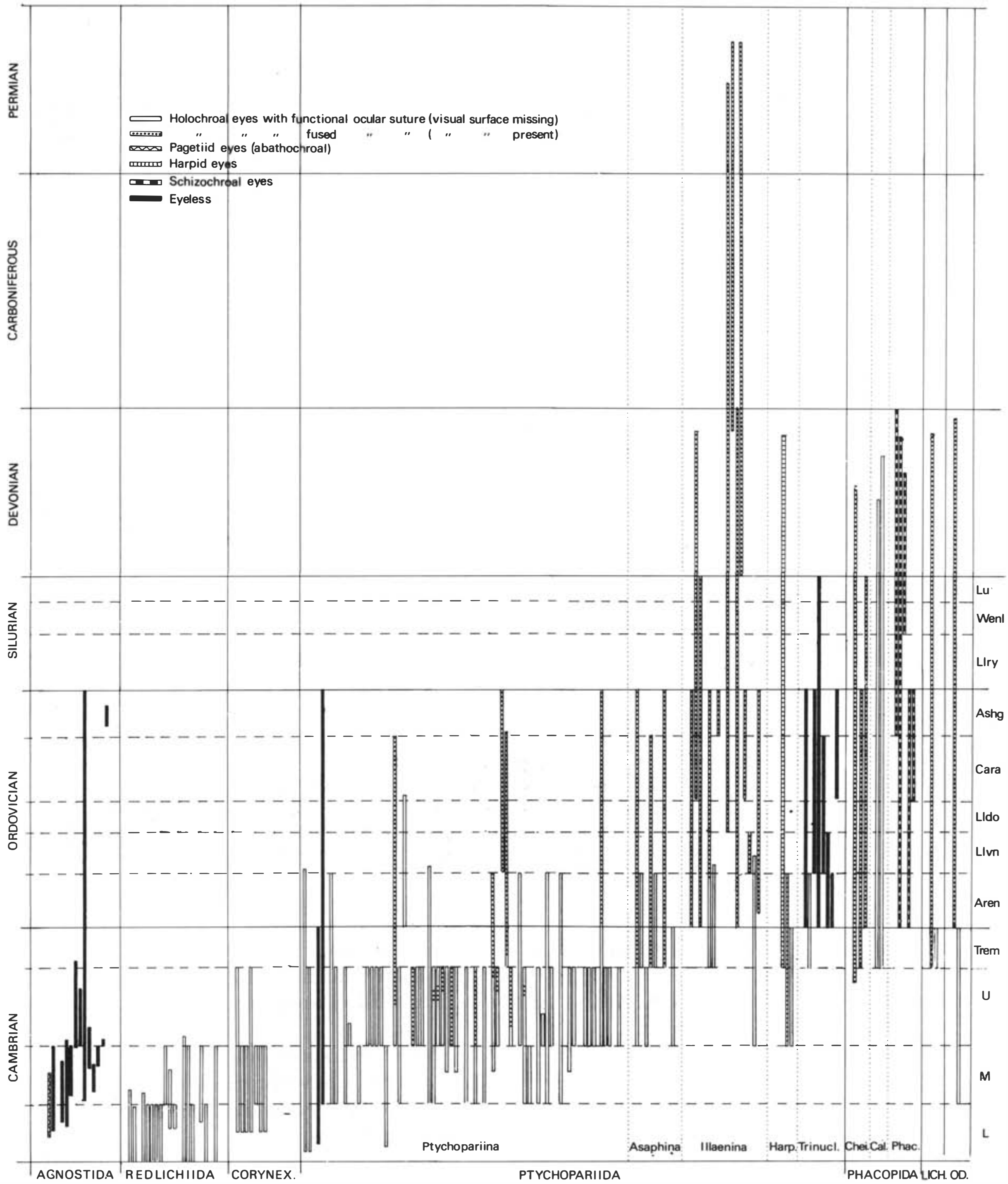

Fig. 1. Time ranges of trilobite families, showing the occurrence of different kinds of eye. Range data from the 'Treatise' (1959), modified by Cowie et al.(1967).

(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.

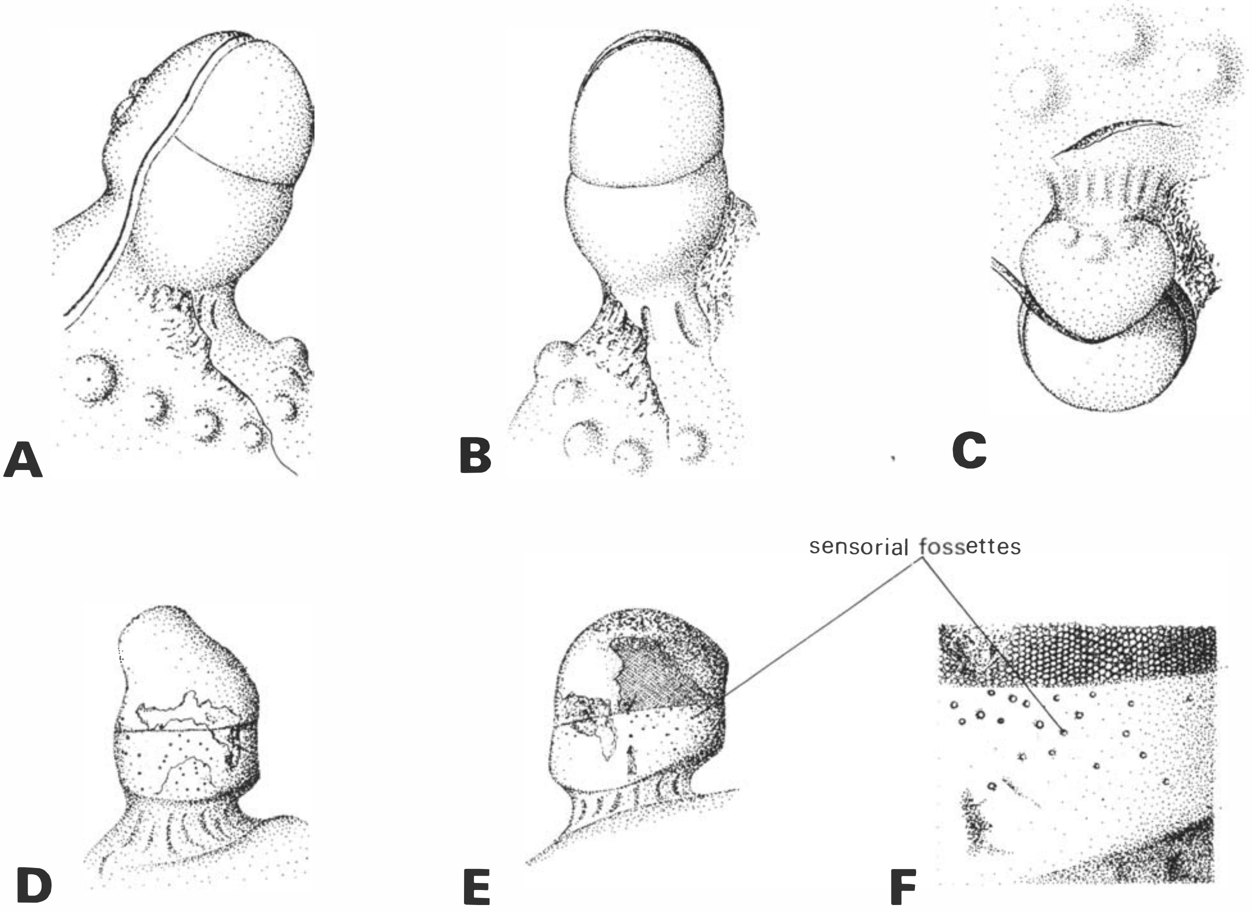

Fig. 2. A. B. C. *Encrinurus tuberculatus* (Buckland). Left eye in anterior, lateral and dorsal views. External surface slightly eroded below the eye socle, and librigena partially separated along the facial suture. SM. A. 28103 Wenlock limestone, (Middle Silurian), Dudley, England. x 18. D.E.F. *Encrinurus 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. x 18.

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 anterolateral 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

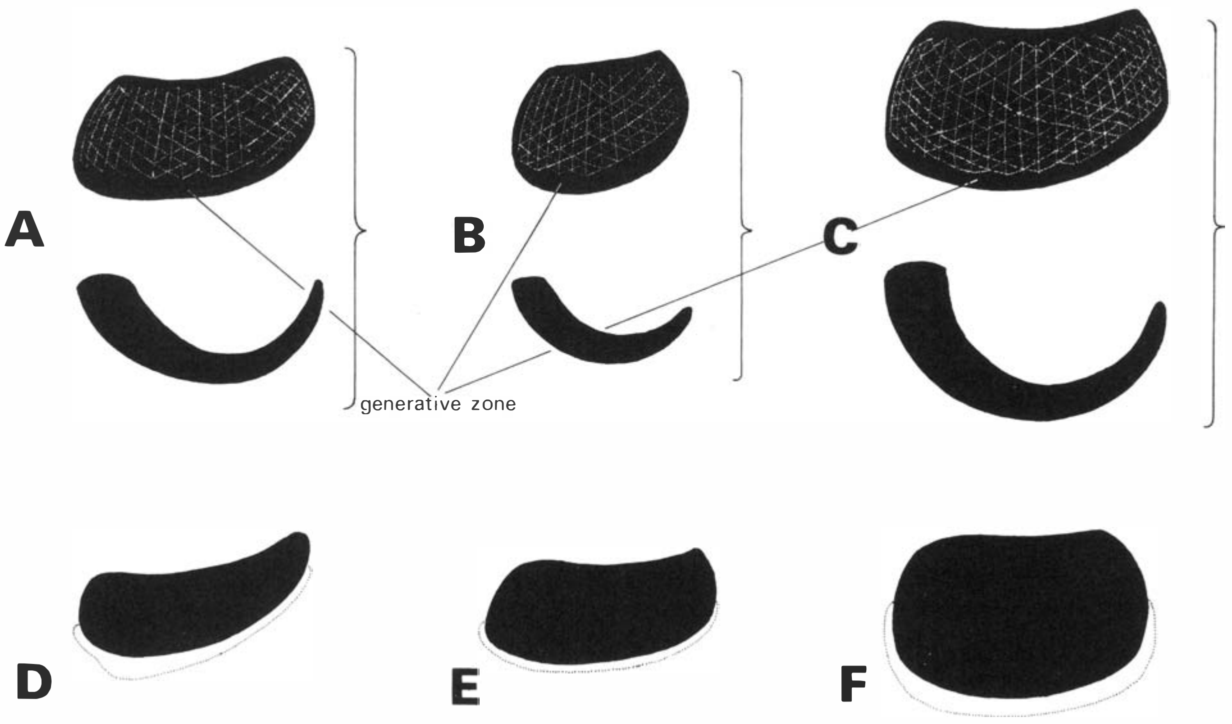

Fig. 3. Geometric structure of visual surface. A. *Reedops sternbergi*. B. *R. bronni*. *C. R. cephalotes*. Dvorce-Prokop Limestone, Devonian, Bohemia. Left eyes in lateral and dorsal views all showing logarithmic spiral form, position of generative zone, and relationships of lens-centres. D. *Niobe 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

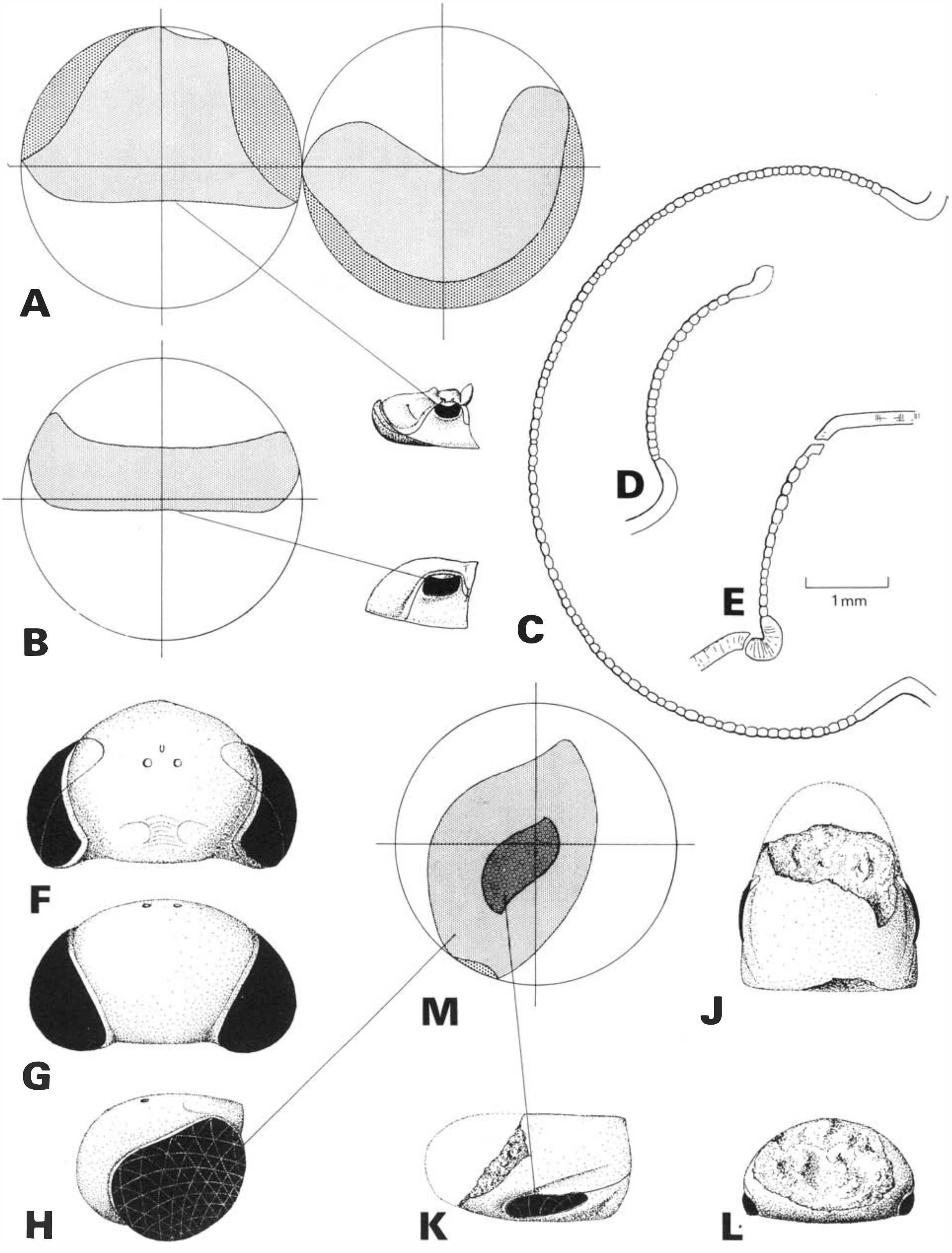

Fig. 4. A. *Bojoscutellum campaniferum* (Beyrich) Koňeprusy Limestone, Devonian, Bohemia. Visual field of left eye plotted in equatorial (left) and polar (right) projection on a Lambert equal-area stereographic net. Larger stipple represents overlapping areas of the visual field. B. *Paralejurus brongniarti* (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.*

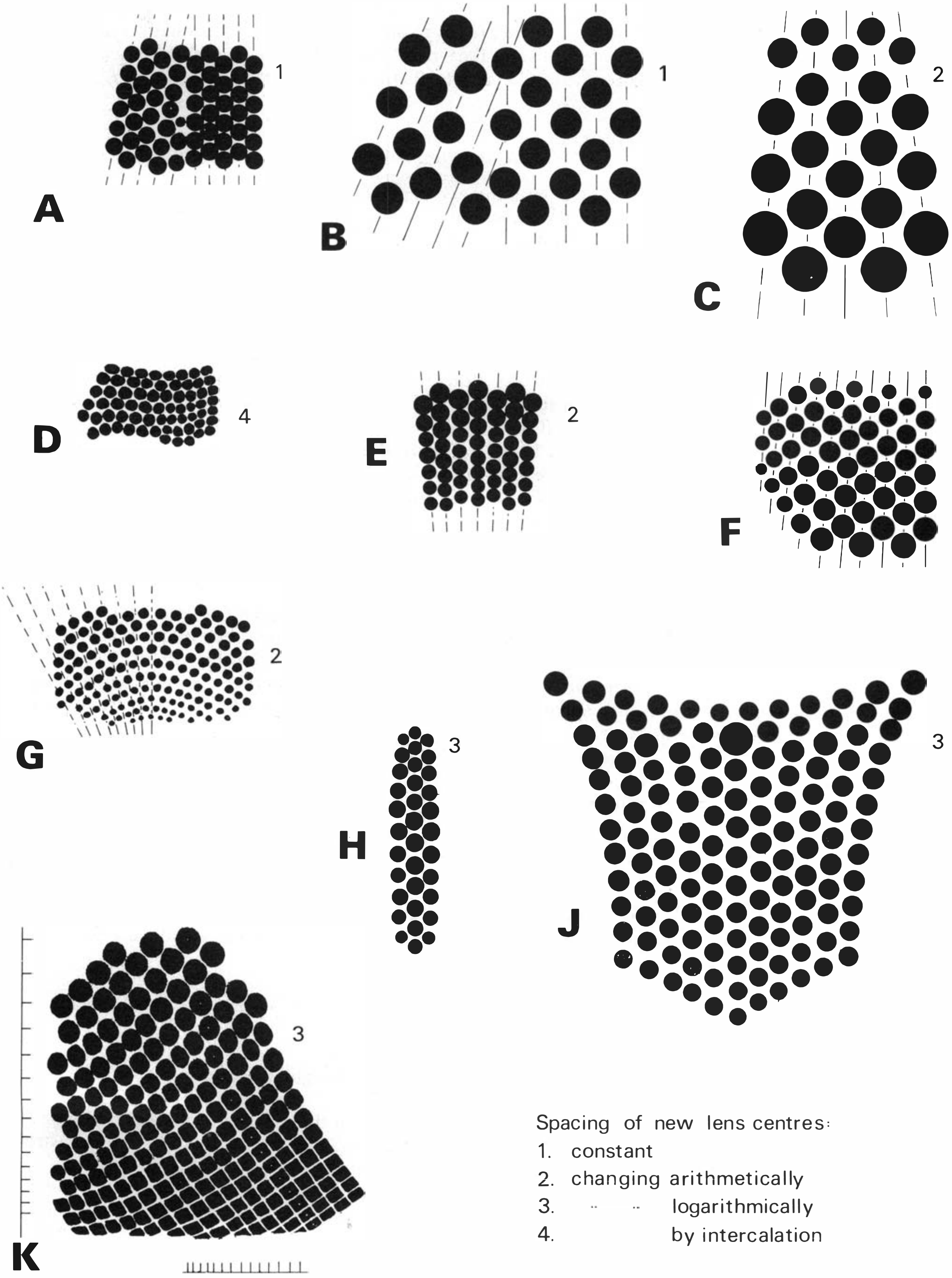

Fig. 5. Lens-packing systems in various trilobites. A. *Isotelus* (Ordovician). B. *Ormathops* (Ordovician). C. "*Phacops*". s.l. (Siluro-Devonian). D. *Ctenopyge* (Cambrian). E. *Cydonocephalus* (Ordovician). F. *Dalmanites.* (Siluro-Devonian). G. *Peltura* (Cambrian). H. *Telephina* (Ordovician). J. *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).

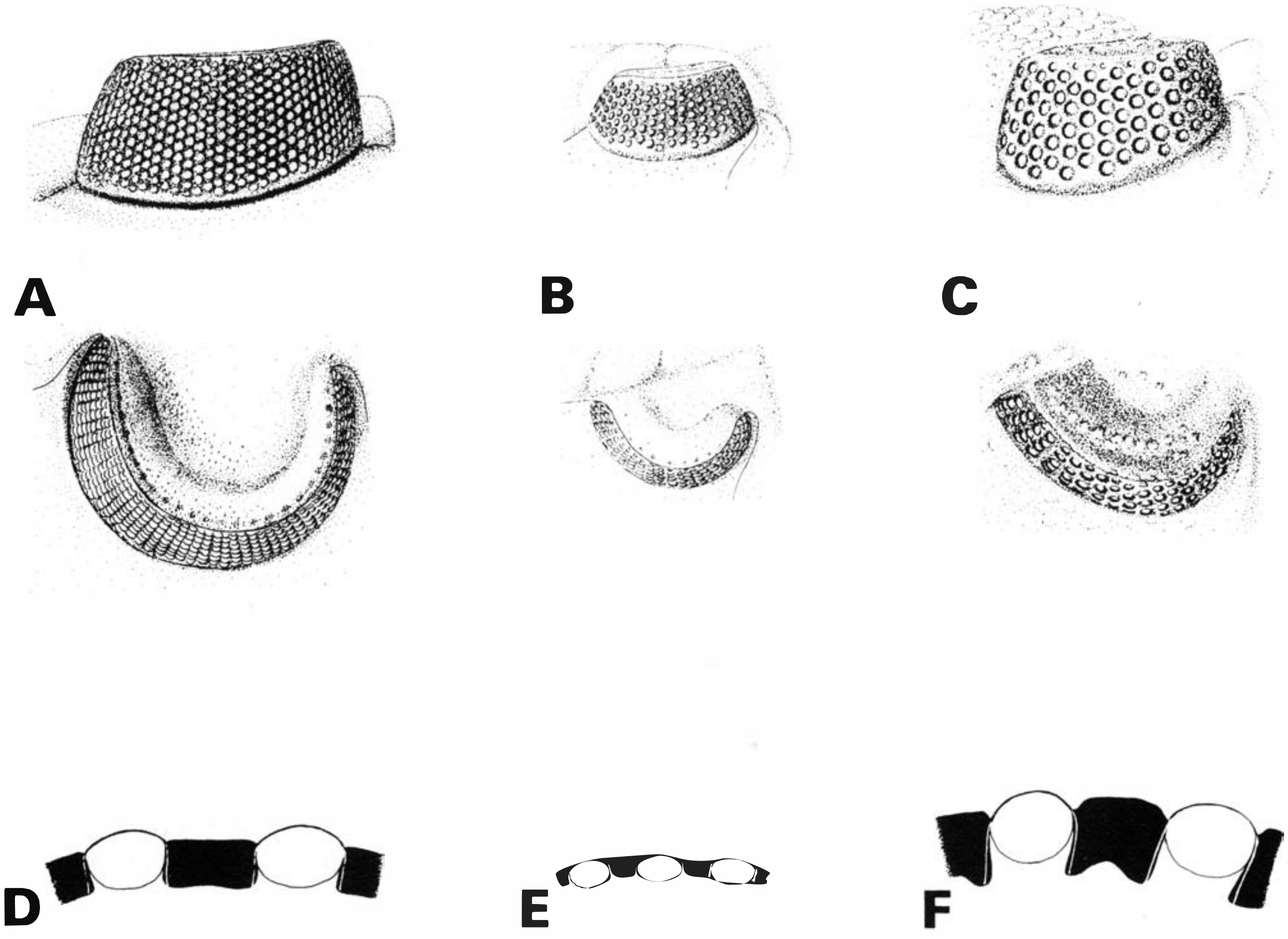

Fig. 6. The three basic kinds of eye in post-Ordovician Phacopina. A. Dalmanitiform: *Odontochile rugosa* (Hawle and Corda) Dvorce- Prokop Limestone. Emsian. Devonian. Tetin, Bohemia. D. Horizontal section through same. B. Acastiform: *Acaste downingiae* (Salter), Wenlock Lst. M. Sil. Dudley, England. 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.

(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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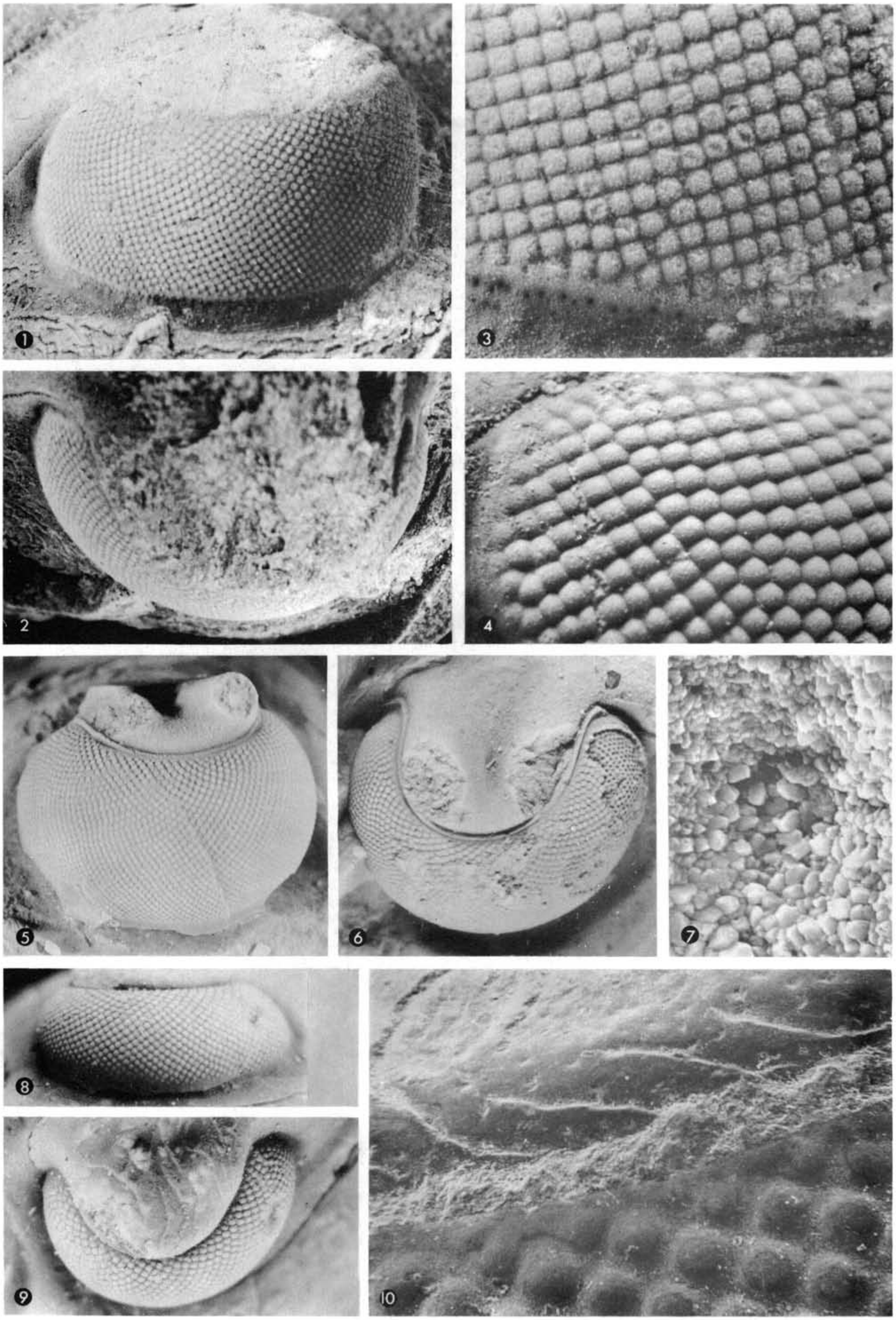

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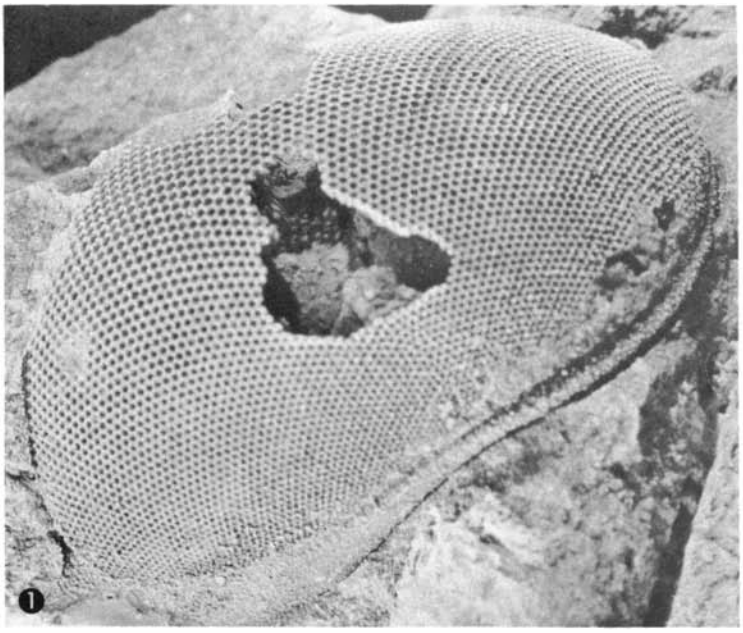
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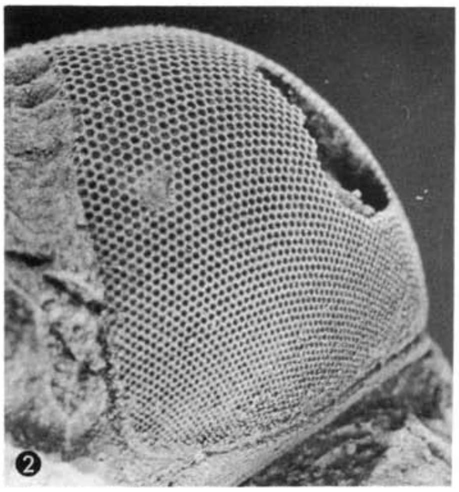
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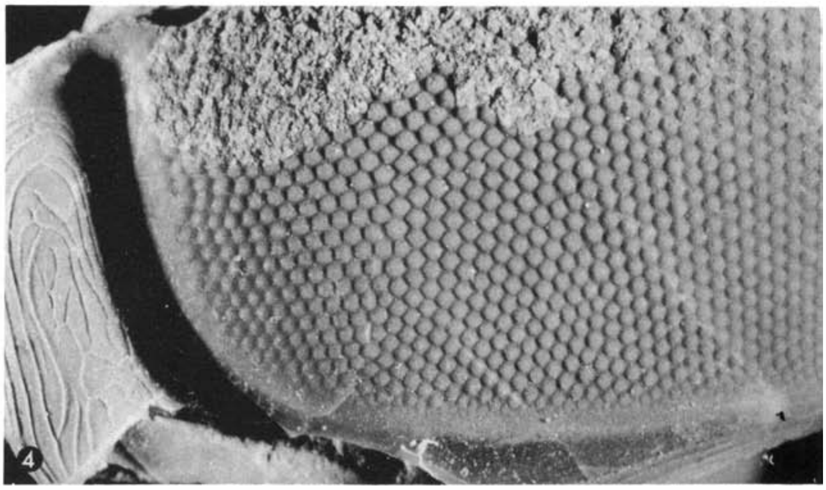
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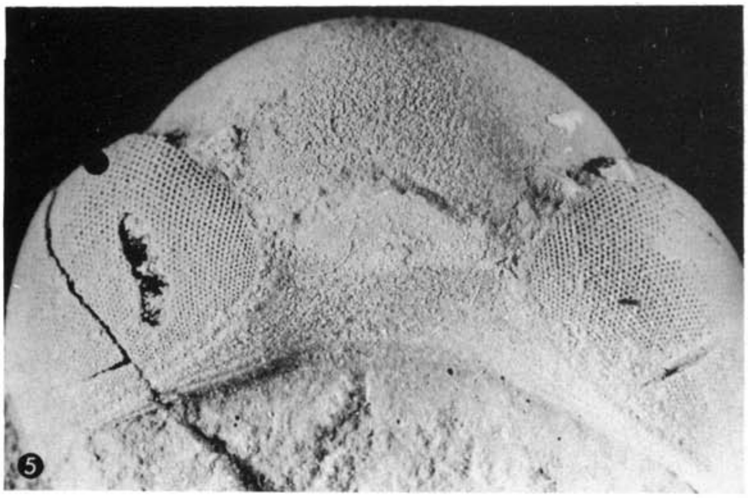
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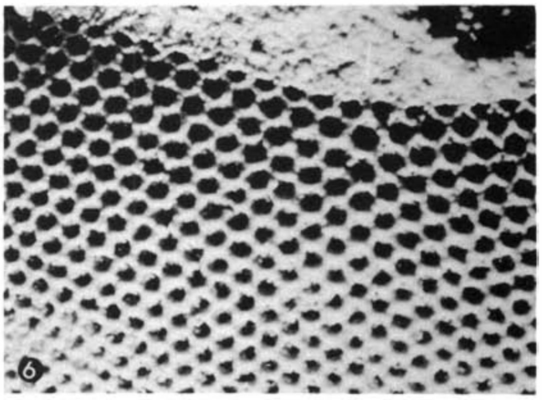
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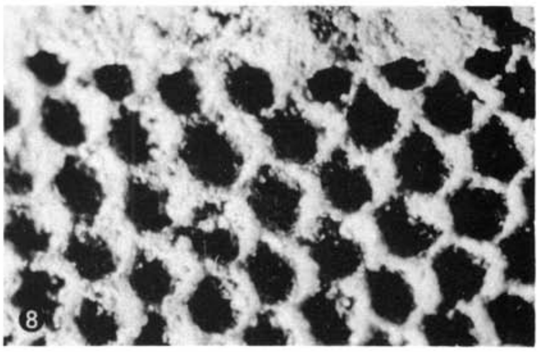
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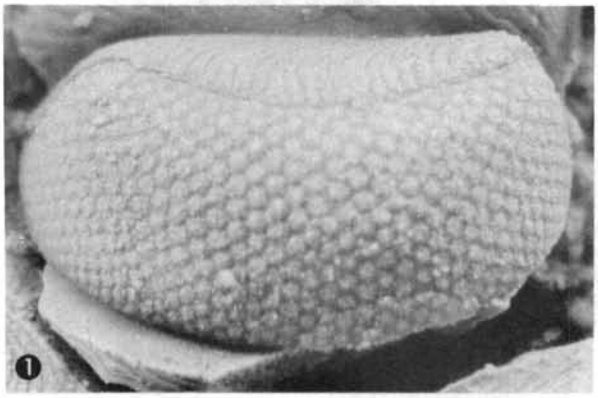
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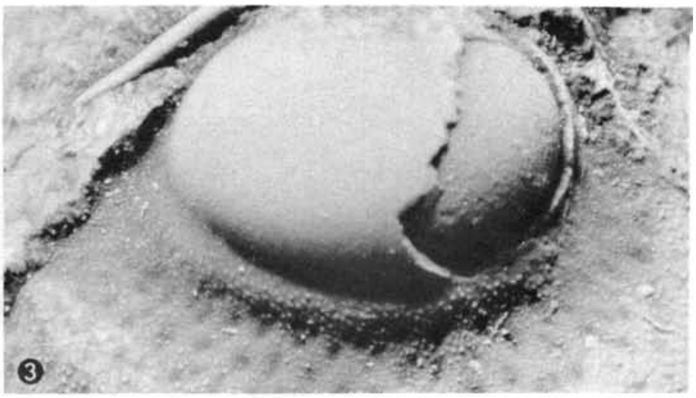
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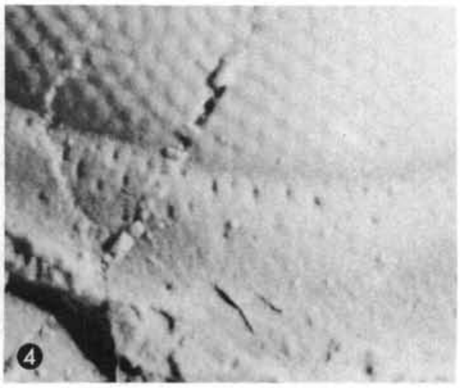
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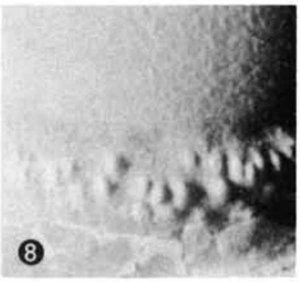
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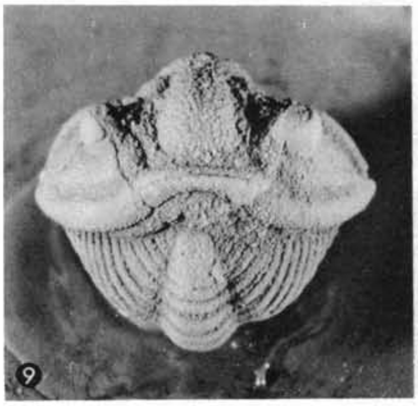
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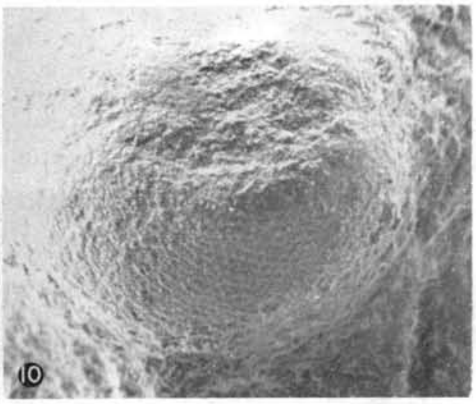
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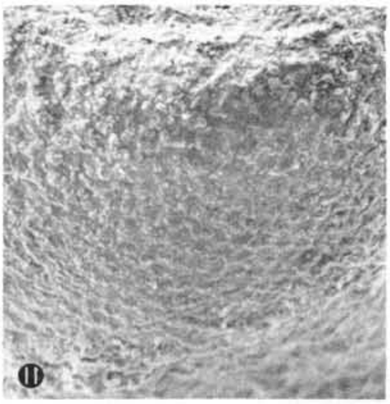
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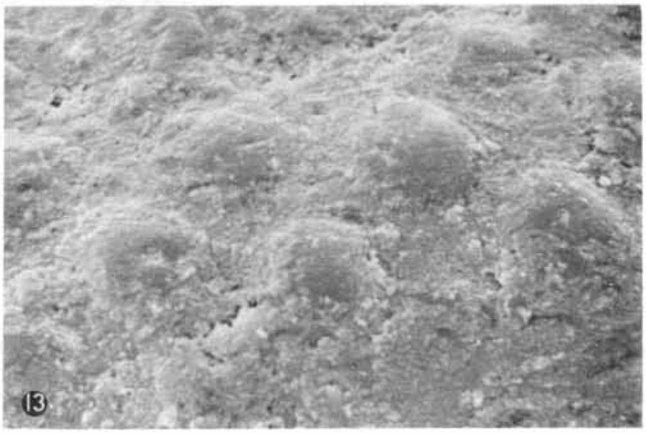
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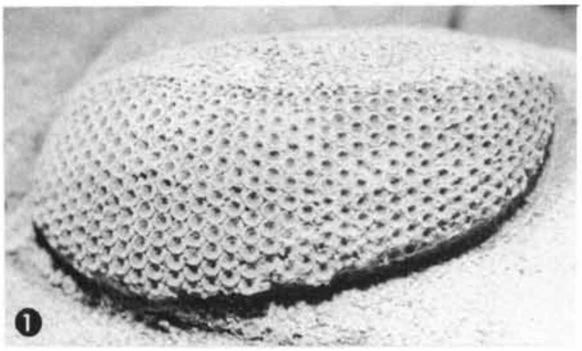
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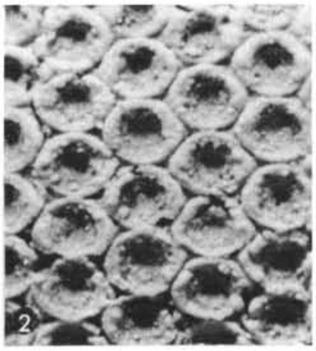
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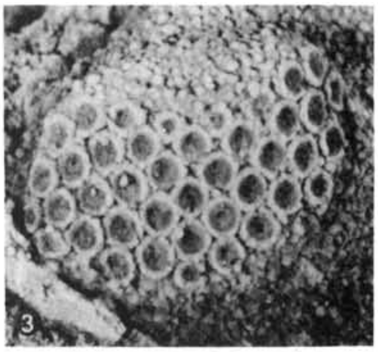
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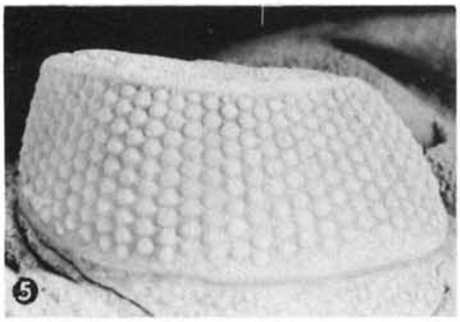
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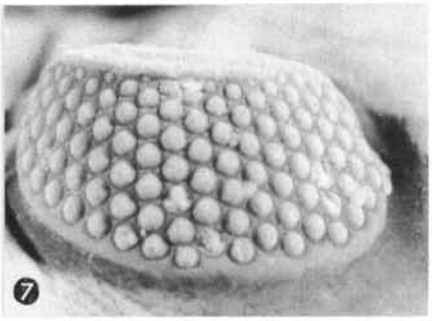
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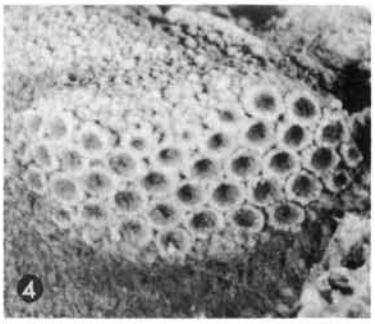
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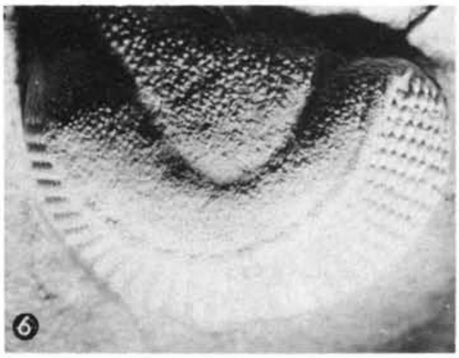
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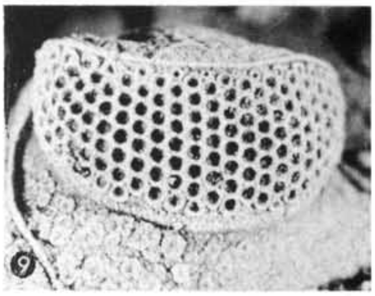
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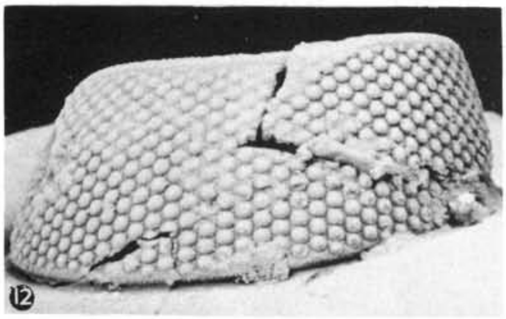
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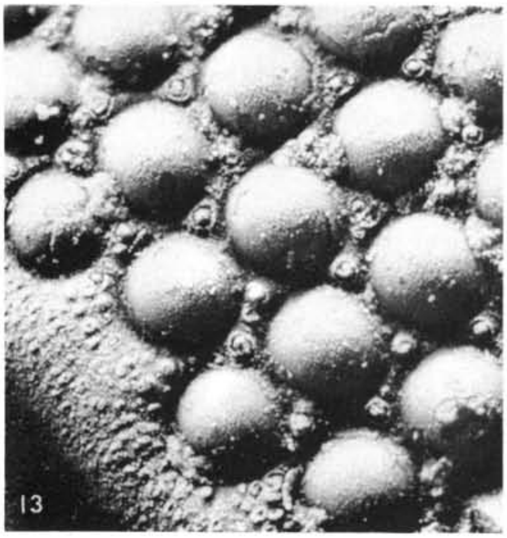
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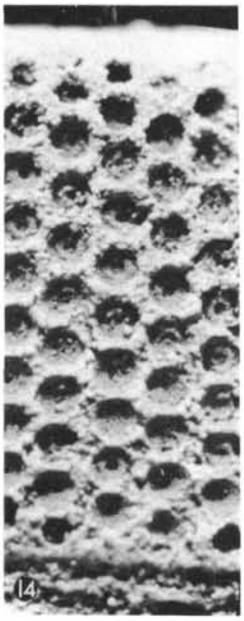
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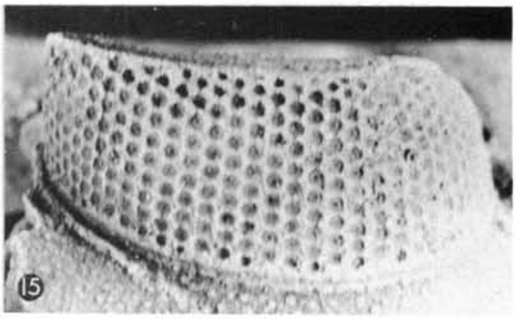
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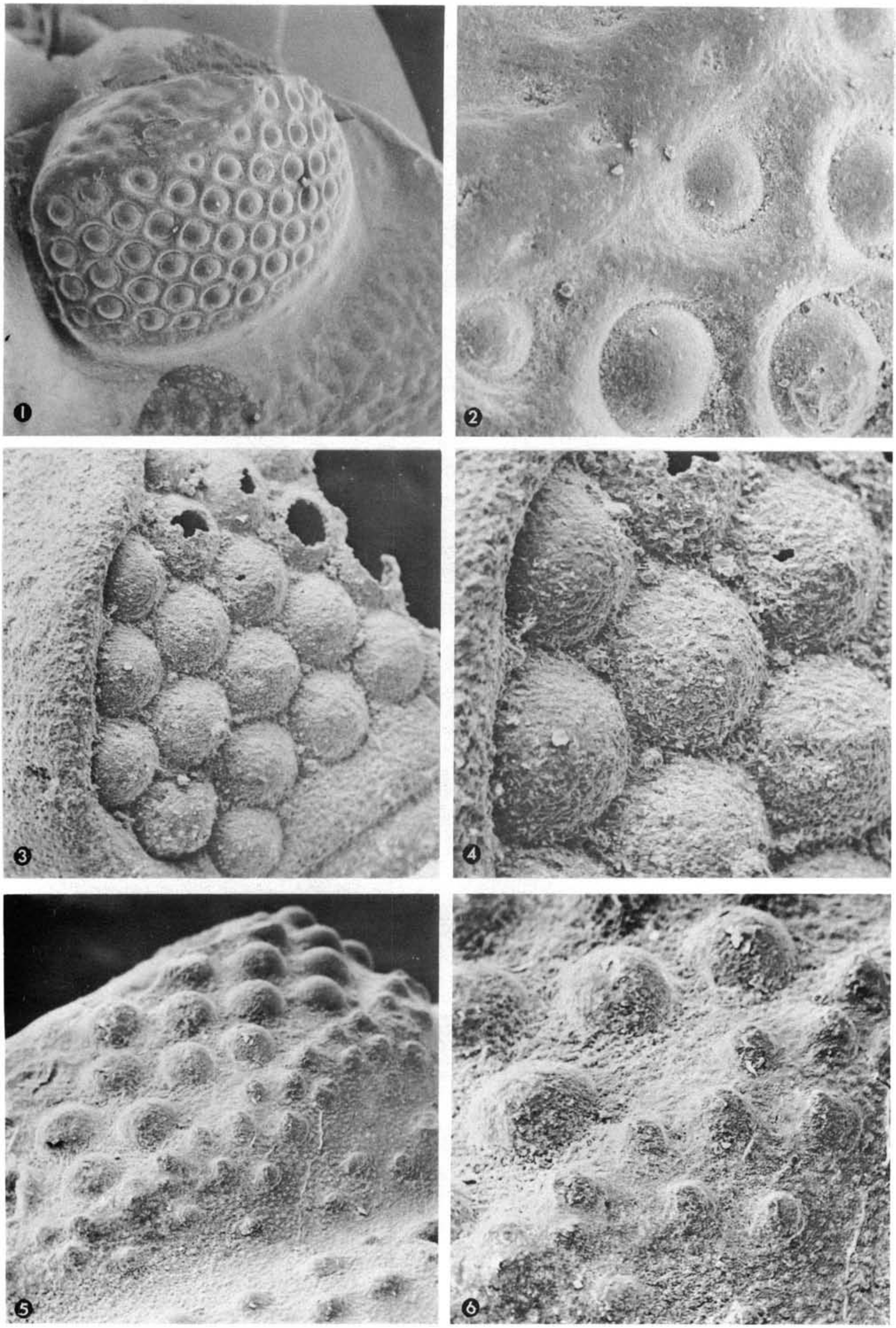

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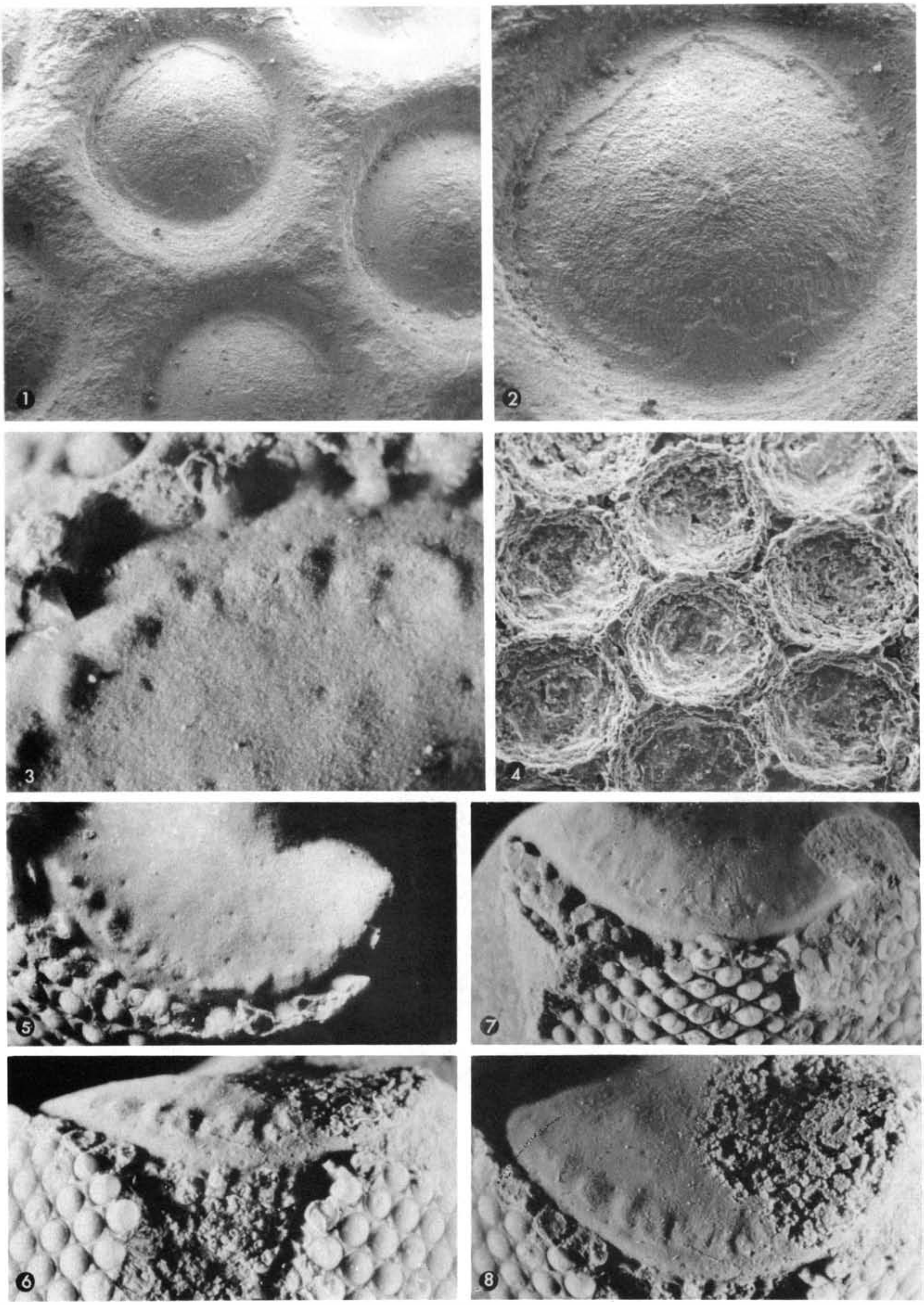

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