Evolution and morphology of the Trilobita, Trilobitoidea and Merostomata

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Evolution and morphology of the Trilobita, Trilobitoidea and Merostomata

Proceedings of a NATO Advanced Study Institute
held in Oslo 1st–8th July 1973,
organized by David L. Bruton

Edited by Anders Martinsson

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Preface

Some years ago when the informal newsletter 'Trilobite News' was first being prepared, it became obvious that a large number of people working with trilobites, trilobitoids and merostomes, were discovering a wealth of new facts only some of which were planned for publication. Meeting a number of these workers personally showed that the only way for these results to be made known and freely discussed was at some form of an international meeting designed just for them. Thus with the official backing of the University of Oslo, plans were made to hold a meeting in Oslo. For this an organising committee was later established with Professor Leif Størmer (Chairman), Professor Gunnar Henningsmoen and Dr. Valdar Jaanusson, and myself as secretary and organiser. Generous financial support for the meeting was obtained from the NATO Scientific Affairs Division and also from the International Union of Geological Sciences (IUGS) who, together with the International Palaeontological Association (IPA), also sponsored it. All three organisations are to be warmly thanked for their backing and it is the sincere hope of the committee that they will continue to support such ventures in the future.

The meeting, which became a NATO Advanced Study Institute, was held at Voksenåsen Conference Centre, Oslo 1st – 8th July 1973, and 60 people from 13 nations took part.

The programme was designed for specialists in palaeontology but zoologists, biochemists, a biophysicist and a marine biologist were also present.

This book contains the majority of papers presented at the meeting and serves to illustrate some of the current research on trilobites, trilobitoids and merostomes. Naturally not all research aspects could be covered in the time available for the meeting, but I believe that some of the exciting information presented here on the functional morphology of these groups will make this book a standard reference for years to come.

This book owes its existence to all those contributors who so willingly agreed to lecture, every participant who, without exception, so enthusiastically supported it, and to the NATO Scientific Affairs Division and the Norwegian Research Council for Science and the Humanities (NAVF) whose generous finances made its printing possible.

Finally the organising committee wish to thank Professor Anders Martinsson for all his pains with the editing of manuscripts.

David L. Bruton
Paleontologisk Museum
Oslo

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The evolution of the eye in trilobites

EUAN N.K. CLARKSON

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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.

Euan N.K. Clarkson, University of Edinburgh, Grant Institute of Geology, West Mains Road, Edinburgh EH 9 3 JW, Scotland 1st August, 1973.

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.

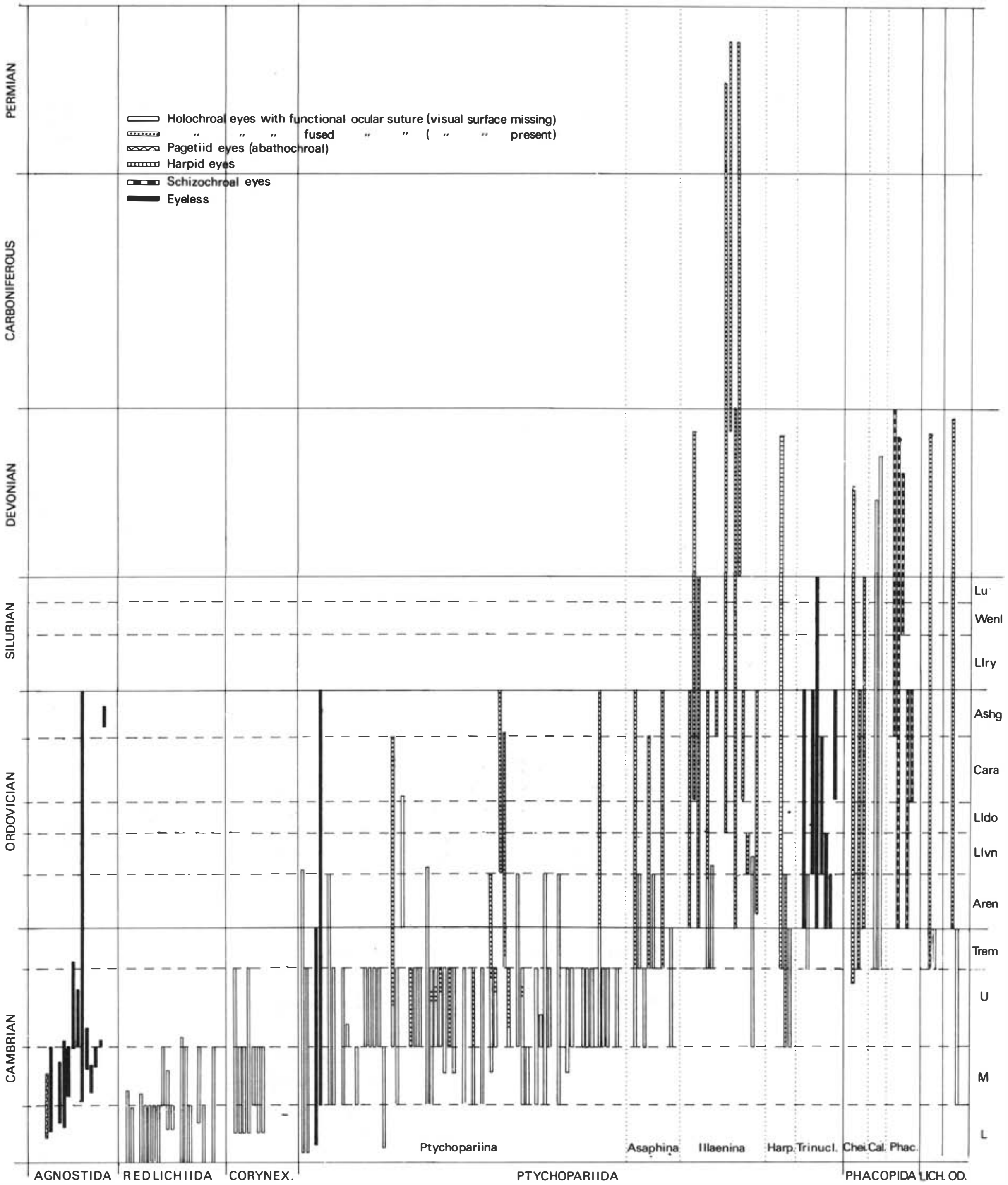

Fig. 1. Time ranges of trilobite families, showing the occurrence of different kinds of eye. Range data from the 'Treatise' (1959), modified by Cowie et al.(1967).

(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.

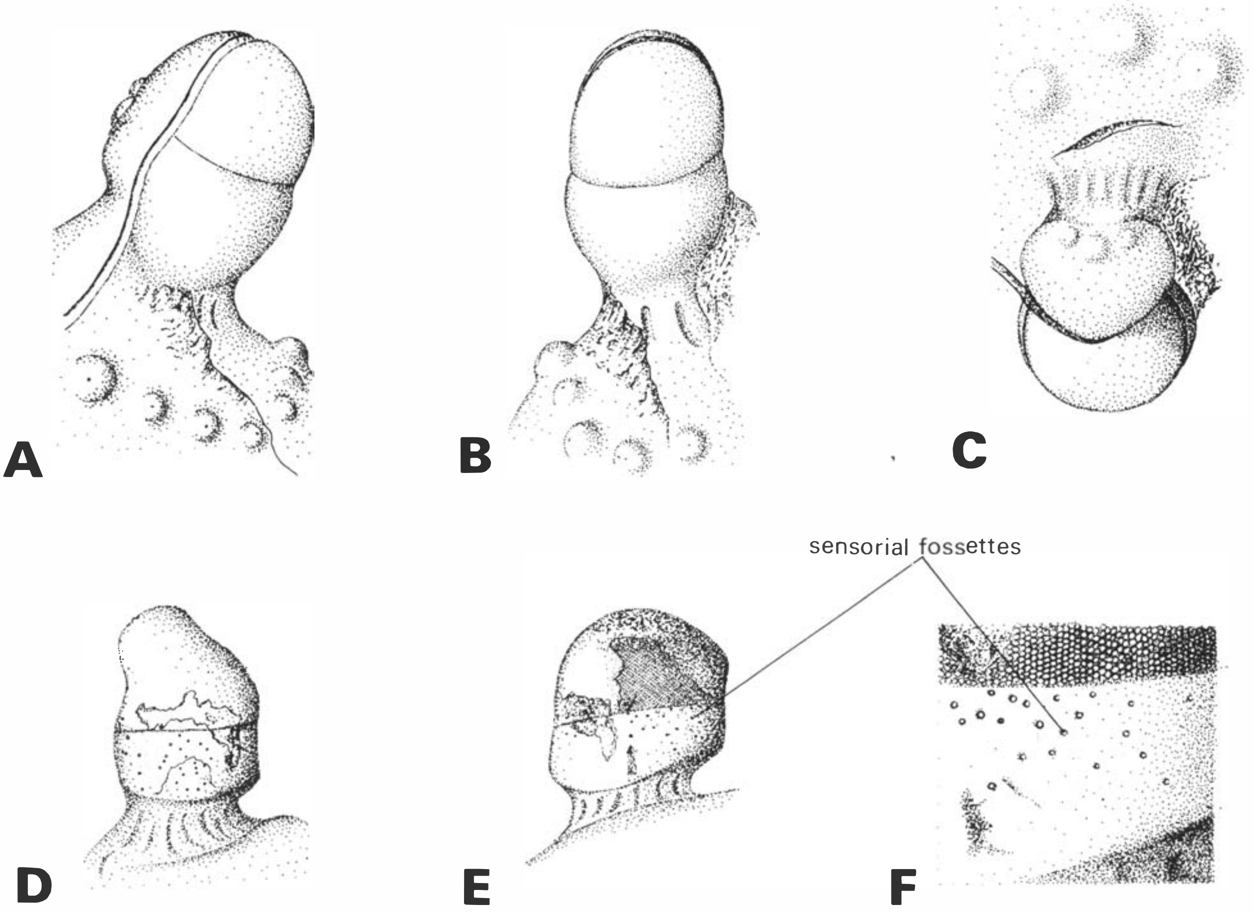

Fig. 2. A. B. C. *Encrinurus tuberculatus* (Buckland). Left eye in anterior, lateral and dorsal views. External surface slightly eroded below the eye socle, and librigena partially separated along the facial suture. SM. A. 28103 Wenlock limestone, (Middle Silurian), Dudley, England. x 18. D.E.F. *Encrinurus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

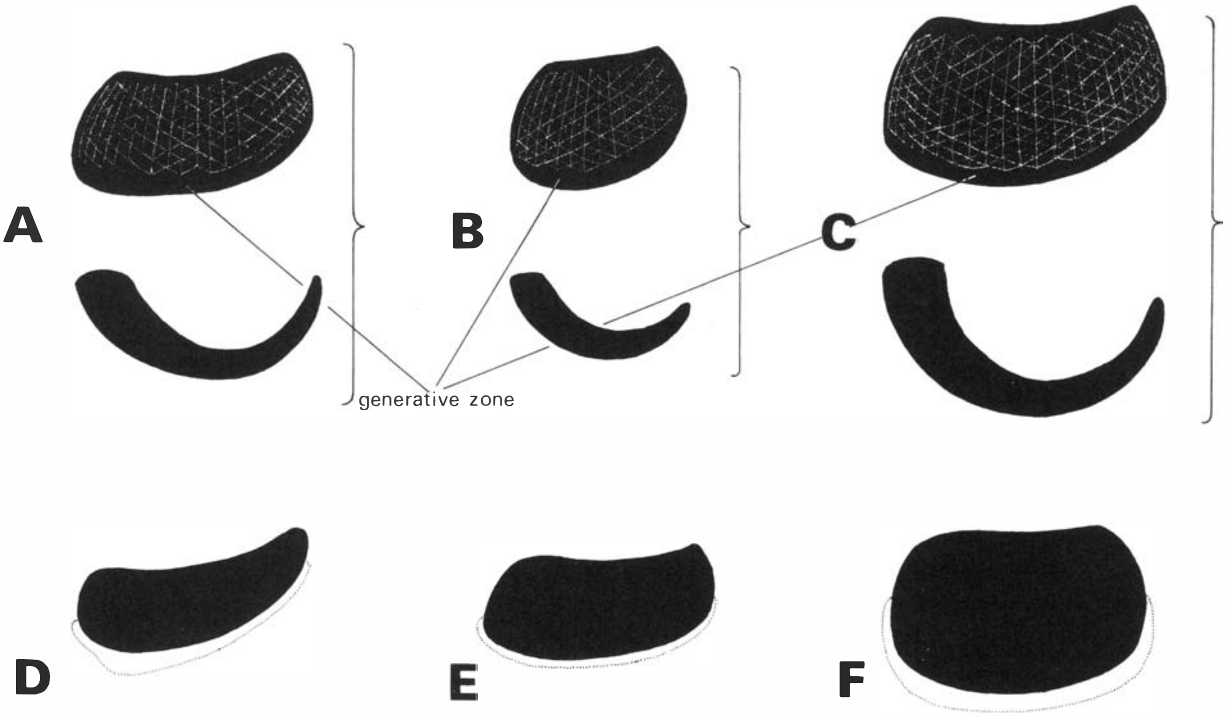

Fig. 3. Geometric structure of visual surface. A. *Reedops sternbergi.* B. *R. bronni.* C. *R. cephalotes.* Dvorce-Prokop Limestone, Devonian, Bohemia. Left eyes in lateral and dorsal views all showing logarithmic spiral form, position of generative zone, and relationships of lens-centres. D. *Niobe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

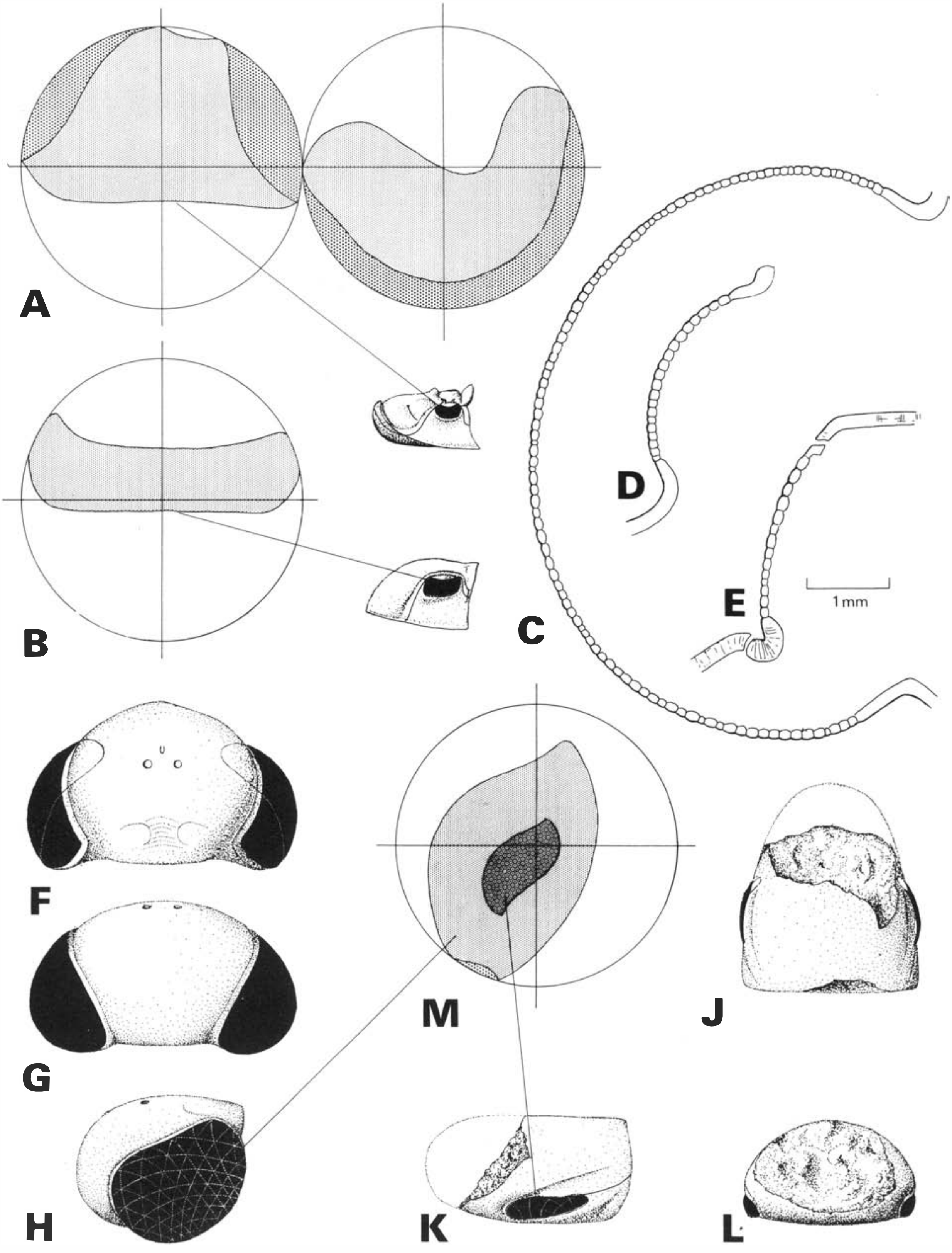

Fig. 4. A. *Bojoscutellum campaniferum* (Beyrich) Koněprusy Limestone, Devonian, Bohemia. Visual field of left eye plotted in equatorial (left) and polar (right) projection on a Lambert equal-area stereographic net. Larger stipple represents overlapping areas of the visual field. B. *Paralejurus brongniarti*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

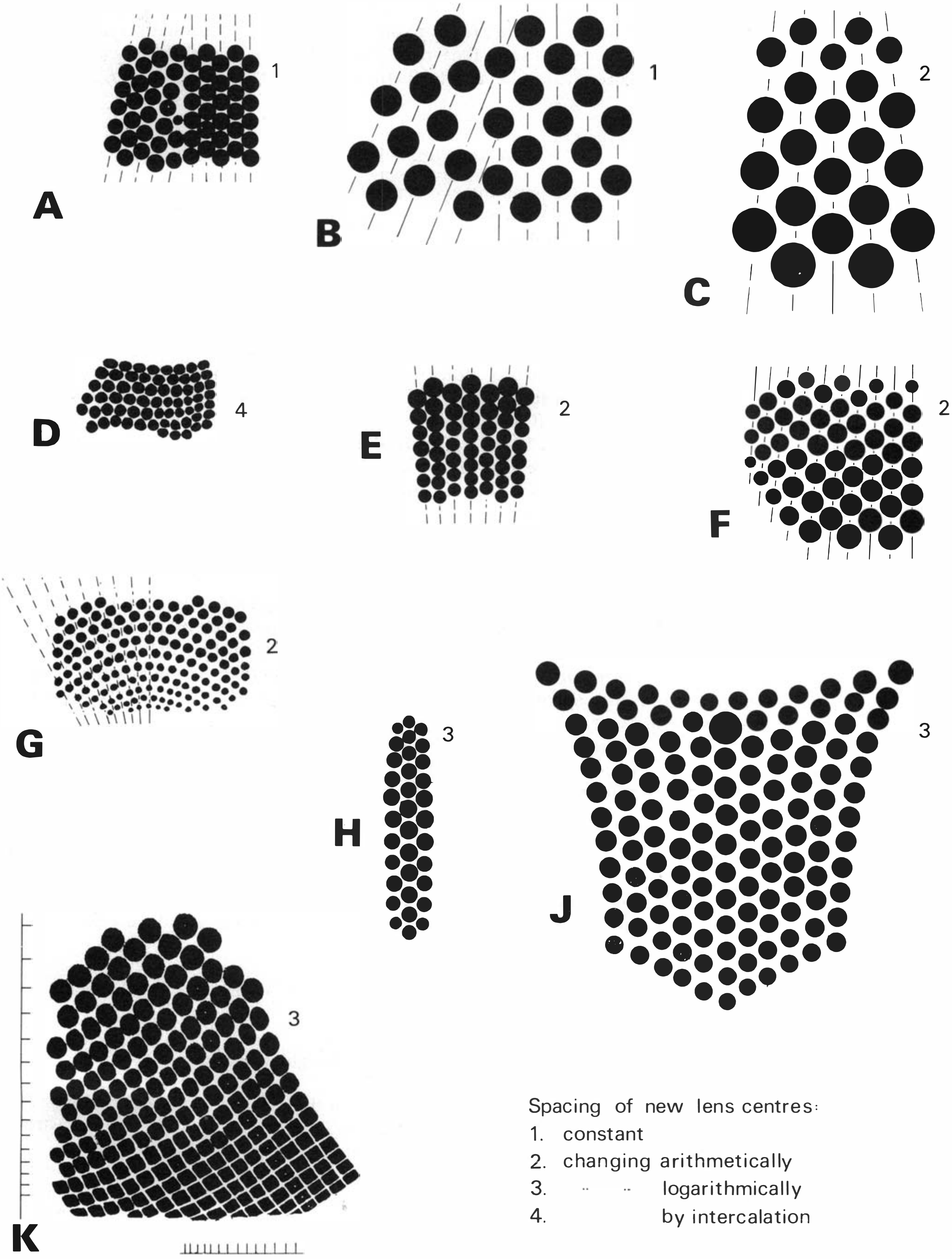

Fig. 5. Lens-packing systems in various trilobites. A. *Isotelus* (Ordovician). B. *Ormathops* (Ordovician). C. "*Phacops*". s.l. (Siluro-Devonian). D. *Ctenopyge* (Cambrian). E. *Cydonocephalus* (Ordovician). F. *Dalmanites*. (Siluro-Devonian). G. *Peltura* (Cambrian). H. *Telephina* (Ordovician). J.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

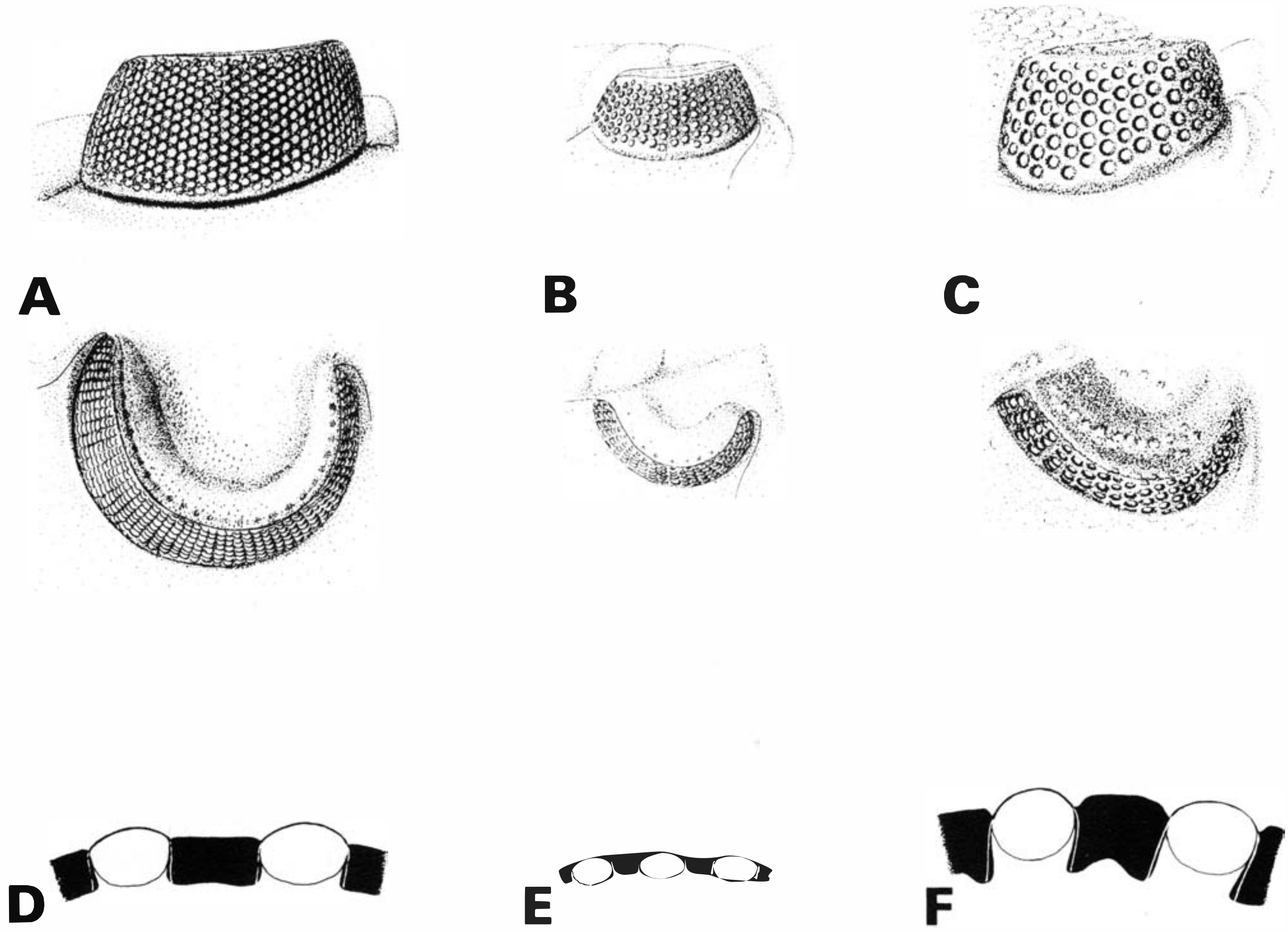

Fig. 6. The three basic kinds of eye in post-Ordovician Phacopina. A. Dalmanitiform: *Odontochile rugosa* (Hawle and Corda) Dvorce- Prokop Limestone. Emsian. Devonian. Tetin, Bohemia. D. Horizontal section through same. B. Acastiform: *Acaste downingiae* (Salter), Wenlock Lst. M. Sil. Dudley, England.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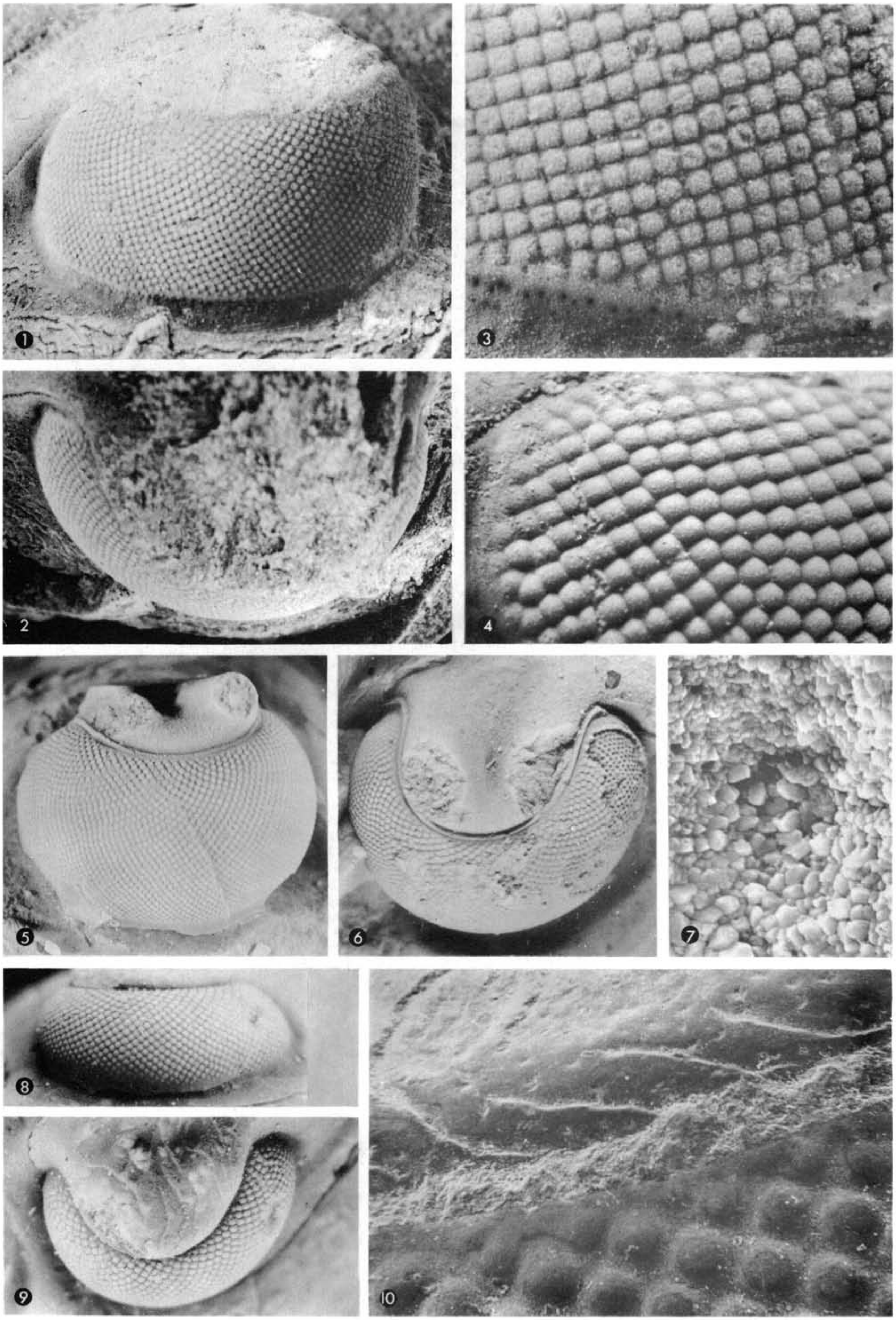

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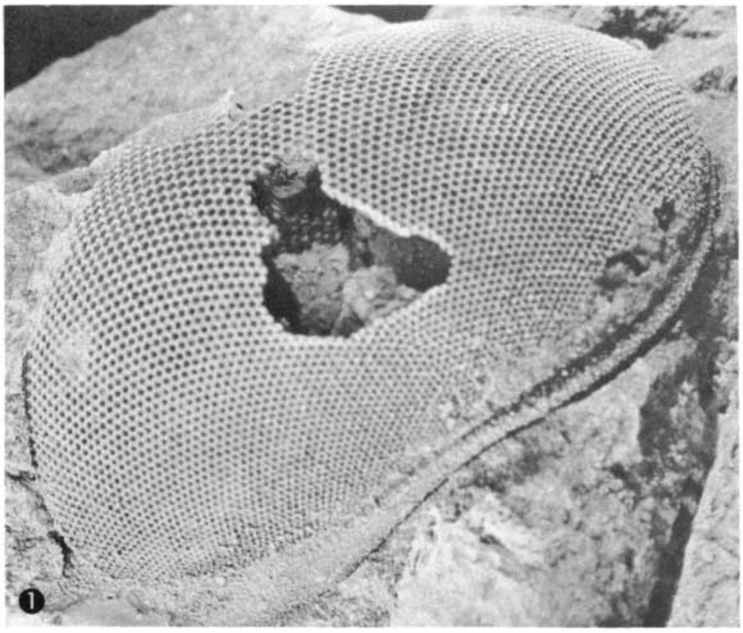

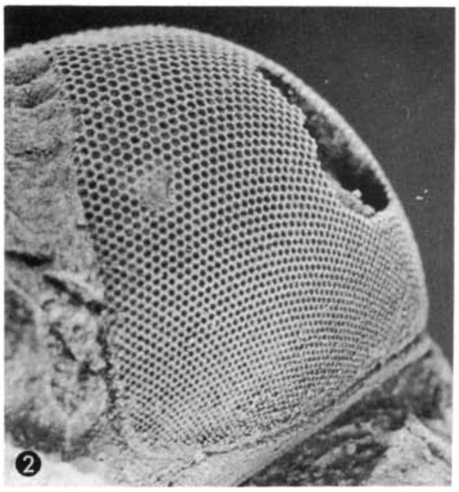

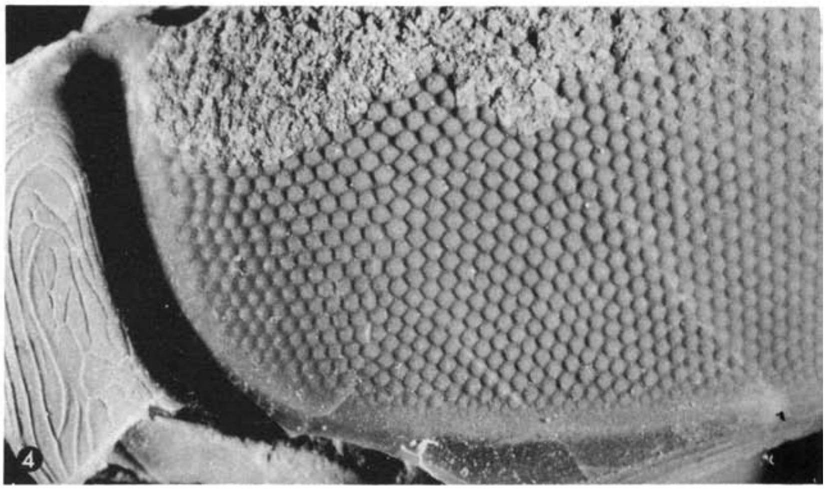

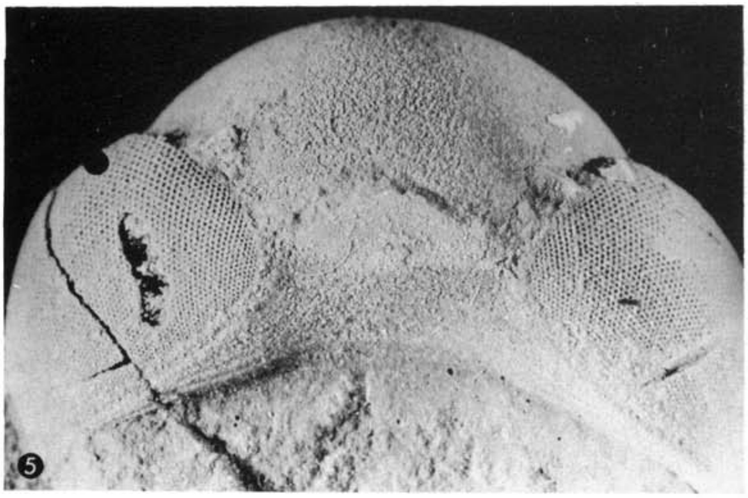

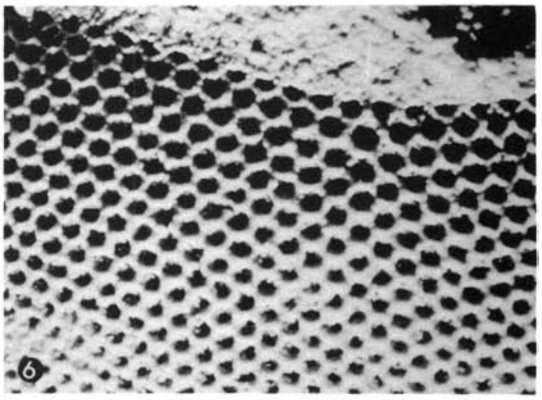

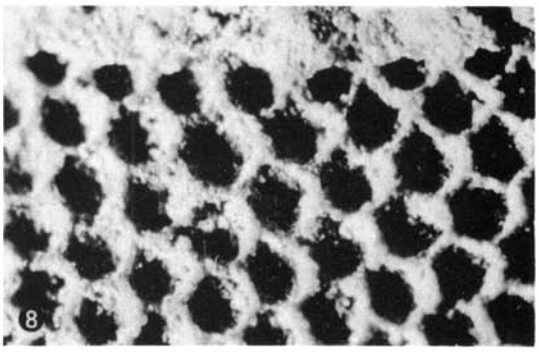

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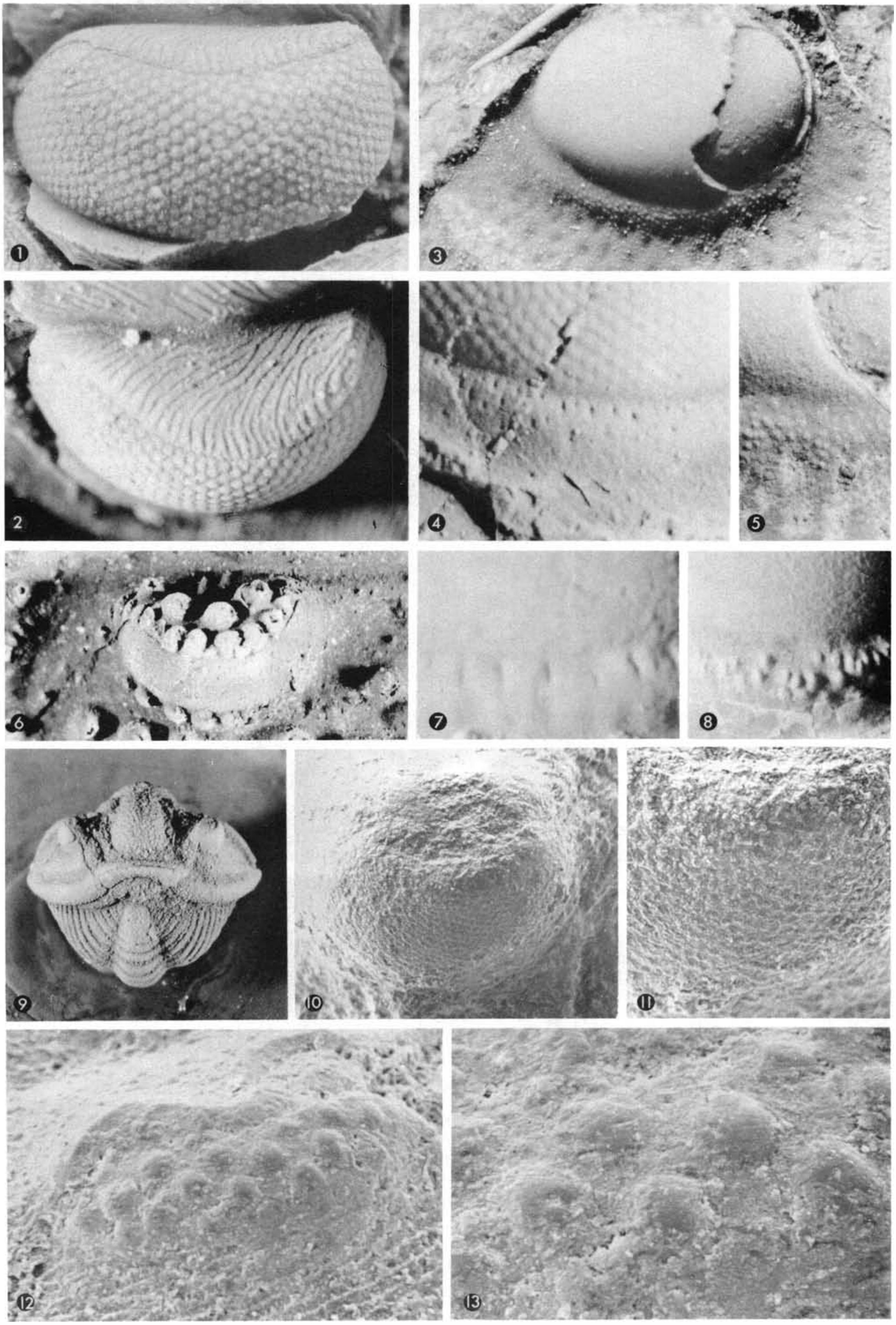

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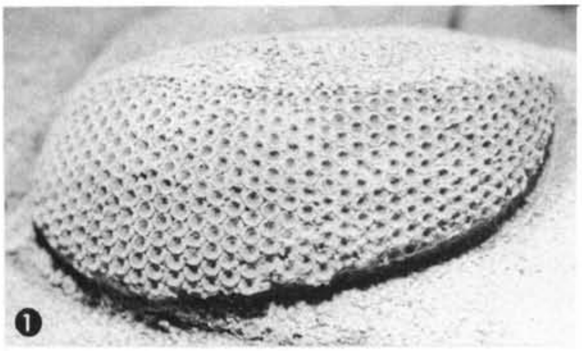

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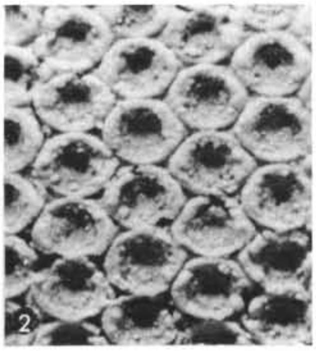

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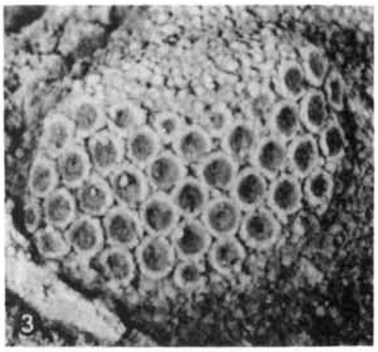

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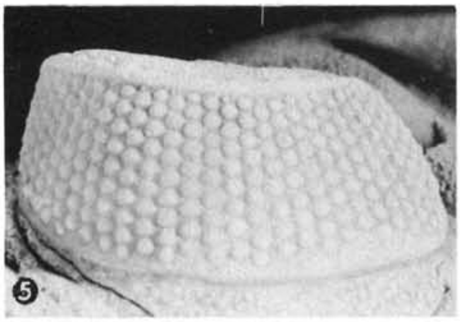

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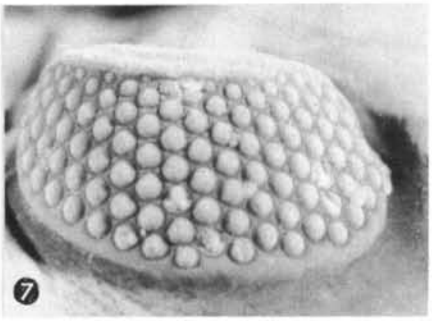

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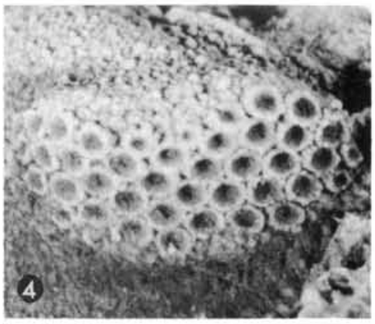

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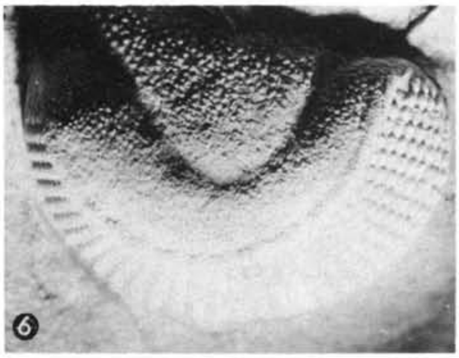

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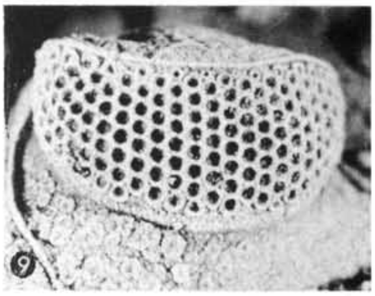

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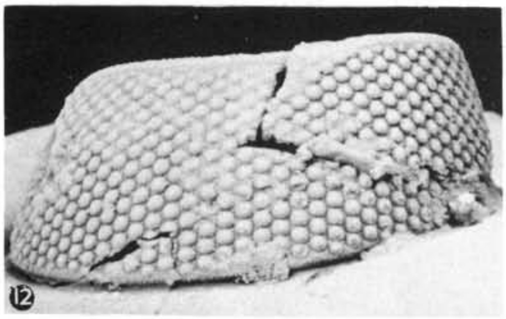

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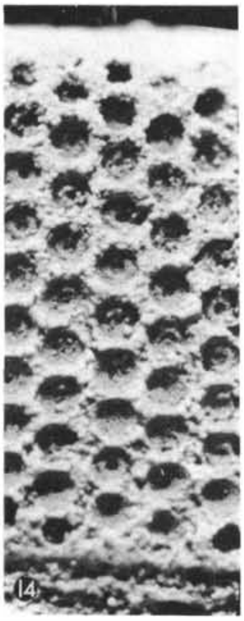

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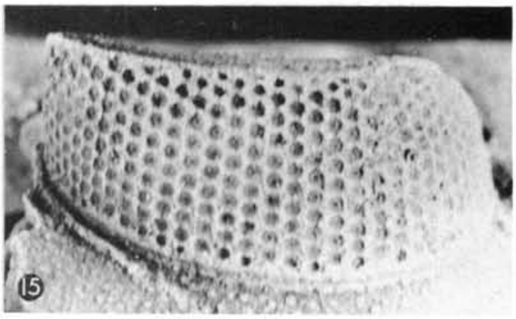

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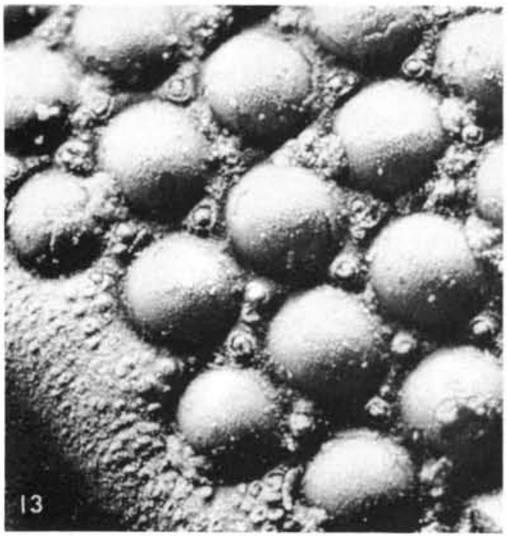

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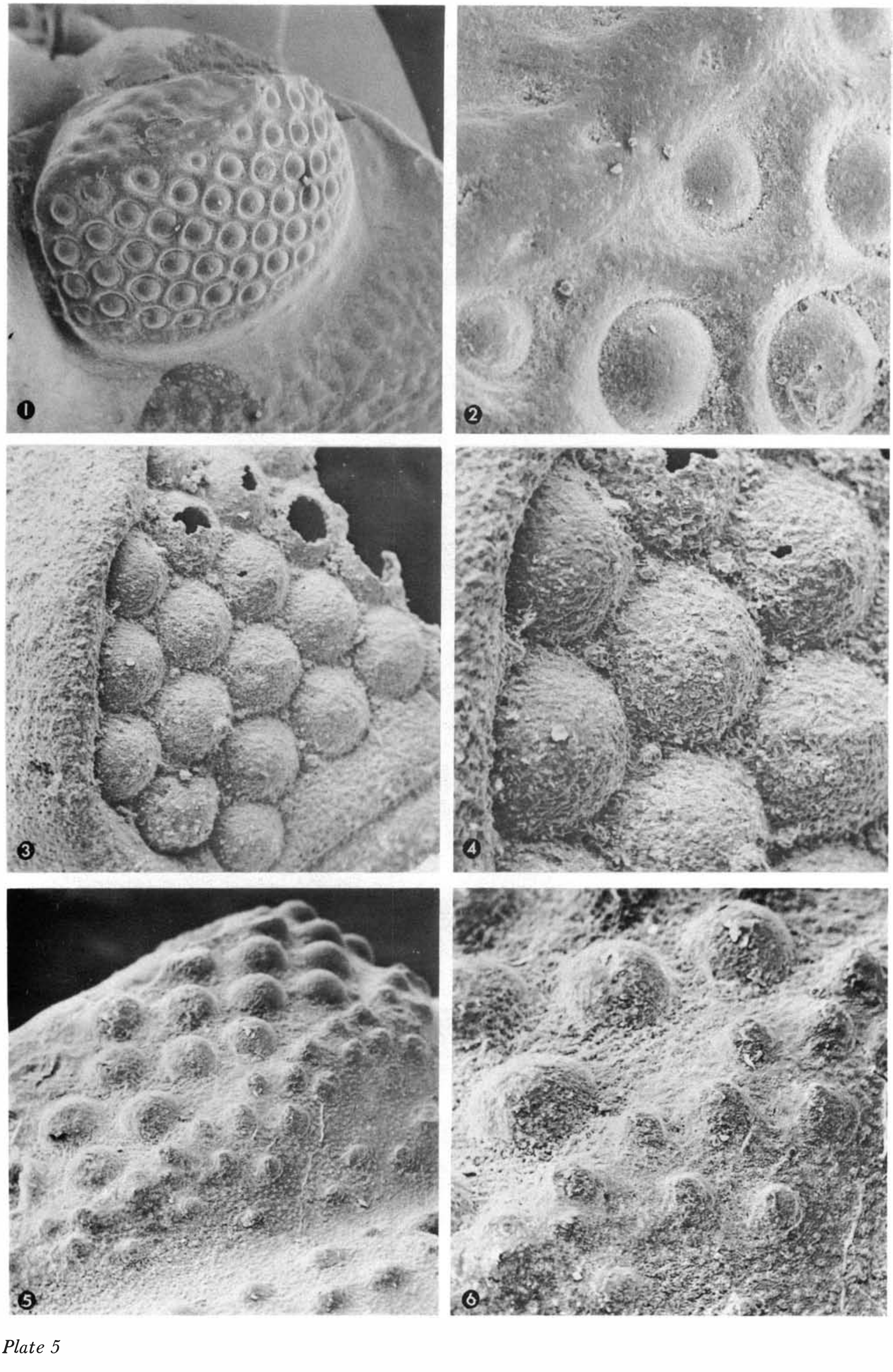
Plate 4



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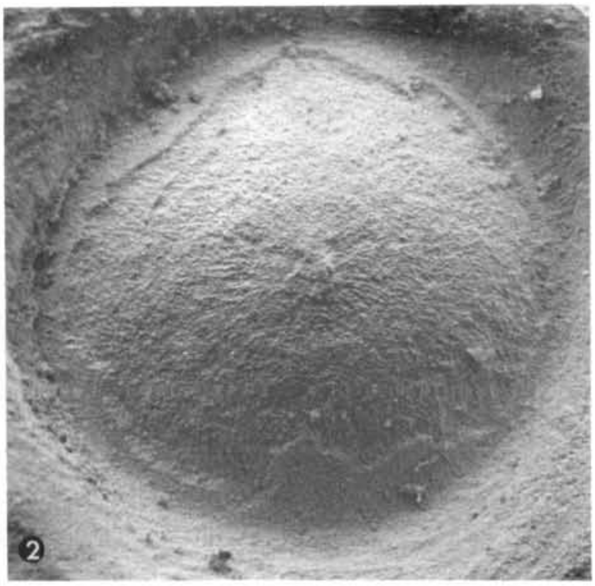

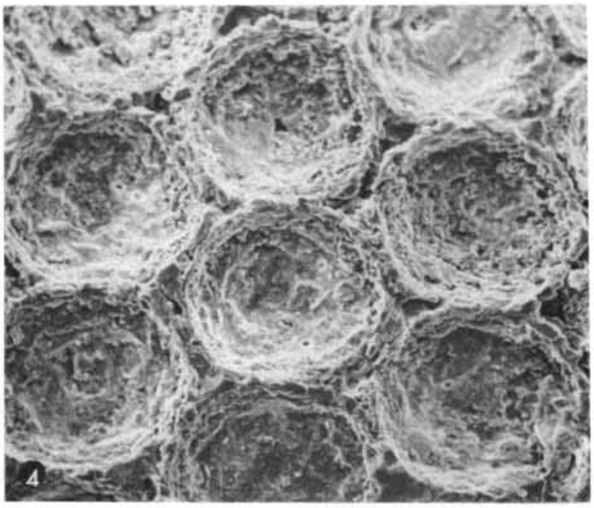

Plate 6

The abathochroal eye of *Pagetia*, a new type of trilobite eye

PETER A. JELL

Jell, P.A. 1975 07 15: The abathochroal eye of *Pagetia*, a new type of trilobite eye. *Fossils and Strata*, No. 4, pp. 33–43. Oslo. ISSN 0300-9491. ISBN 82-00-04963-9.

A third type of trilobite eye is recognized and described in *Pagetia, Opsidiscus* and an unnamed allied genus, as distinct from the well documented holochroal and schizochroal types. Although superficially similar in morphology to the schizochroal eyes of phacopids it differs most strikingly in lacking scleral projections and intrascleral membranes between the discrete ommatidia. Furthermore, the Middle Cambrian eodiscoid genera with abathochroal eyes and the schizochroal forms which first appeared in the Ordovician are not seen to be closely related. Other distinctive features of this type of eye are outlined leading to speculations on their environmental adaptations and the degeneration or loss of sight in very closely related genera.

Peter A. Jell, Dept. of Geology, Australian National University, P.O. Box 4, Canberra, 2600, Australia, 1st August, 1973.

Of the multitude of trilobites described from Cambrian sediments only a handful have so far been discovered with the visual organs or their impressions preserved. Knowledge of trilobite eyes has been obtained, almost exclusively, from those of Ordovician age or younger. Since the classical works of Clarke (1889) and Lindström (1901) the existence of two readily recognizable types of trilobite eyes has been generally accepted. Apart from those described herein, all the Cambrian specimens known and many younger trilobites have holochroal eyes. These are considered the 'primitive' type from which the schizochroal eyes of Ordovician and younger members of the Phacopida evolved.

Holochroal eyes are characterized by the presence of many small lenses packed closely together in direct contact with one another and a single continuous cornea that covers the entire eye and grades laterally into the exoskeleton. Schizochroal eyes on the other hand consist of fewer and larger biconvex lenses each having its own corneal covering and separated from one another by thick interlensar sclera. (Clarkson, 1966a, 1966b, 1967a, 1968, 1969, 1971) has described schizochroal eyes in considerable detail.

Öpik (1963:57) described the eye of a species of *Pagetia* from 'Alexandria Downs' on the Barkly Tableland as of the schizochroal type. However, he did not figure the material nor describe the details of its structure and preservation. The line drawing that he did provide does not show the correct arrangement of lenses nor does it allow anything but the most superficial comparison with the eyes of other trilobites. Nowhere in any of his papers has Clarkson made any comment on this description of a schizochroal eye. Moreover, he states (1971:51) that 'There is only one known instance, in all the 350 million years of trilobite history, of a radical and successful departure from the holochroal system to a quite different structural plan. This new visual system, the schizochroal eye is confined to the suborder Phacopina . . .'.

The detailed morphology of the eye of *Pagetia* resembles the schizochroal type but is separable from it in several features. In this paper these distinguishing features are described and a new name – abathochroal (derived from the Greek *abathos* meaning shallow and *chroa* meaning surface of the body) – is given to this type of eye.

MATERIAL

BURTON BEDS, *Xystridura templetonensis Zone.* – Queensland Museum locality 145 (lat. 19°03'S., long. 136°40'E.) on the road to 'Brunette Downs' 4 km west of Alexandria Downs Homestead, Barkly Tableland, Northern Territory, many internal and external moulds of free cheeks with the visual surface attached are present in a large collection of an undescribed species of *Pagetia (Pagetia* sp. nov. A). Öpik (1963:57) identified *Pagetia significans* (Etheridge Jnr.) from this locality but did not figure the material. During a review of Australian eodiscoids

(Jell, in press) all material from this locality is described under a new specific name. Although the explanation of his fig. 15 states that it is based on CPC4308, 4309 & 4310 the text on page 57 (lines 3 to 6) indicates otherwise. However, examination of the specimens cited and the non-recognition of any other species at this locality indicate that Öpik was probably not describing *P. significans* but *Pagetia* sp. nov. A of this paper.

BEETLE CREEK FORMATION, *Ptychagnostus gibbus Zone.* – University of Queensland locality 927 (lat. 19°55'S., long. 138°59'E.) at the crossing of Dingo Creek by the road from 'Ylvertoft' to the Paradise Goldfields (i.e. the road to the Lady Annie Mine) northwestern Queensland, many internal and external moulds of free cheeks with the visual surface attached in a large collection of an undescribed species of *Pagetia (Pagetia* sp. nov. B).

Queensland Museum locality 113 (lat. 21° 05'S., long 139° 58'E.) 2 to 3 km north of Mount Murray, Chatsworth Holding, northwestern Queensland, many free cheeks with visual surface attached among a large collection of *Pagetia ocellata* Jell, 1970 in insoluble residues from limestone.

CURRANT BUSH LIMESTONE, *Ptychagnostus atavus Zone.* – Queensland Museum locality 128 (lat. 19°34'S., long. 138°55'E.) 5 m above the base of the formation on the hill 7.5 km south of Thorntonia Homestead forming the left bank of the West Thornton River, northwestern Queensland, several specimens with free cheek, visual surface of eye and cephalon still attached in the insoluble residues from the limestone. This material belongs to an undescribed species *Pagetia* sp. nov. C.

V CREEK LIMESTONE, *Ptychagnostus nathorsti Zone.* – Bureau of Mineral Resources locality M243 (lat. 20°04'S., long 138°30'E.) on the flood plain of Whistler Creek 0.8 km north of its junction with the Buckley River, 42 km west of Yelvertoft Homestead, northwestern Queensland, a small number of specimens including complete enrolled individuals of an undescribed species of *Opsidiscus (Opsidiscus* sp. nov.).

Several specimens of the visual surface of other undescribed species of *Pagetia* from northern and central Australia have also been collected and studied but are not figured herein. They have visual organs comparable with those described below.

DISPOSITION OF SPECIMENS. – All specimens examined for this paper including those illustrated are deposited in the Queensland Museum or the Commonwealth Palaeontological Collection and are numbered with the prefixes 'QMF' and 'CPC' respectively.

PRESERVATION

Description of components of the visual organ in trilobites is based on the external surface, internal mould and horizontal and vertical cross-sections. However, the eye of *Pagetia* is so small that sectioning would be very difficult and no material suitable for sectioning (i.e. in which the original carbonate of the lenses etc. is still preserved) has yet been collected.

Pagetia spp. nov. A and B are represented by internal (Fig. 2B, D, E, G, H) and external moulds in a fine hard siliceous shale. Latex casts of their external moulds (Figs. 2A, C) provide details of the external surface. The specimens of *P. ocellata* (Figs. 4B–D) are phosphatic and have been liberated from the limestone matrix by acetic acid treatment. The external surface of the eye is clearly visible but the internal surface is covered by adhering phosphatic material in all specimens examined.

The external surface of the cranidium of *Pagetia* sp. nov. C is sparsely punctate whereas the surface of exfoliated specimens (i.e. internal moulds) is, like that of the insoluble phosphatic specimens, smooth. The specimens of that species described and figured herein are therefore interpreted as phosphatic replacements of the matrix forming the internal moulds. The specimens of *Opsidiscus* sp. nov. are also replacements of the internal filling but in their case the replacement mineral is limonite.

It should also be noted that the ocular suture (Öpik, 1967:54), which is fused in many specimens, may have been functional in most, as free cheeks without the visual surface attached and complete specimens with the visual surface absent are common.

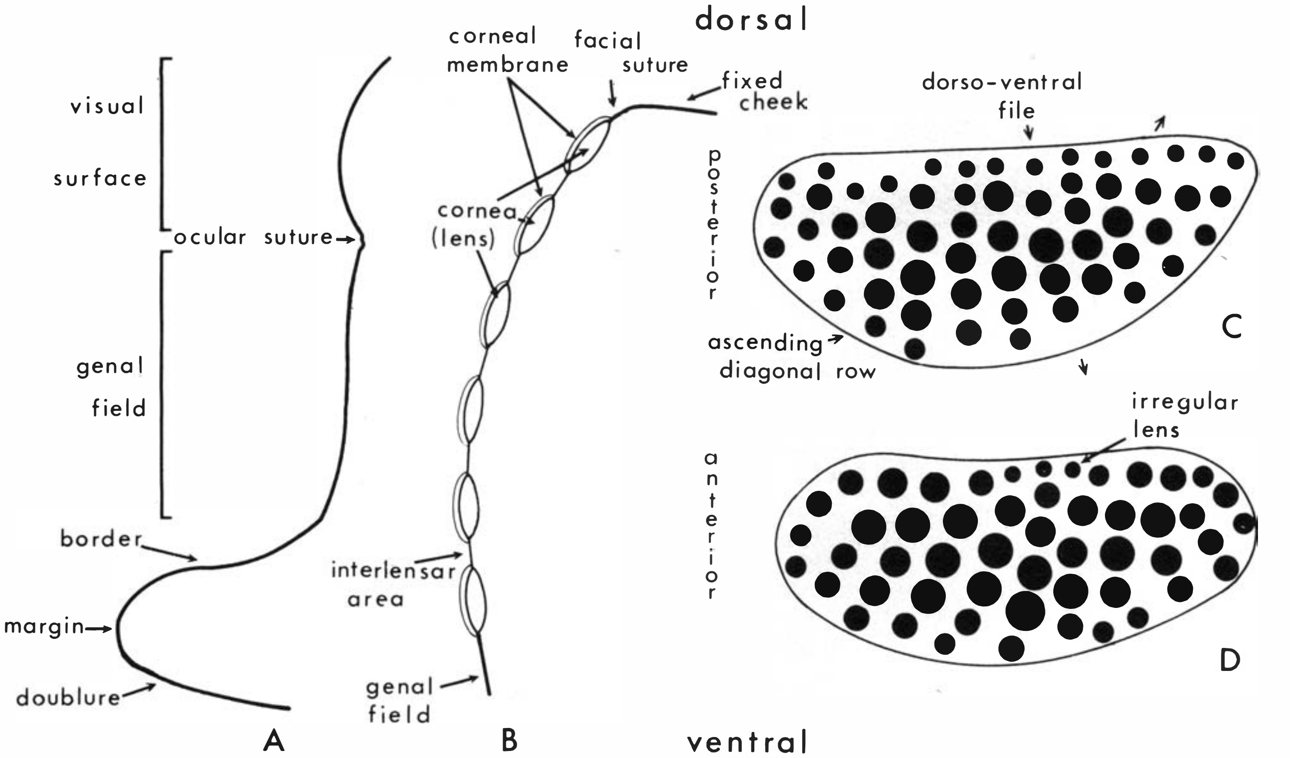

Fig. 1. A. Transverse section of the free cheek of *P. ocellata* with the visual surface attached dorsally. Drawn from QMF6942 (Fig. 4B), X240. B. Diagrammatic transverse section of the visual surface of *Pagetia.* Compiled from QMF6945 & 6852 (Figs. 4D & 3D respectively) X1000 approx. C. Arrangement of lenses in the right eye of an individual belonging to *Pagetia* sp. nov. B showing the regular files and diagonal rows, CPC13377 (Fig. 2A), X200. D. Arrangement of lenses in the left eye of an individual belonging to *Pagetia* sp. nov. C showing some irregularity near the posterior, QMF6853 (Fig. 3C), X200.

MORPHOLOGY OF THE EYE OF *PAGETIA*

As no major differences are observed between the eyes of the four species referred to herein they are described collectively. Interspecific variation is noted where observed.

The eyes of *Pagetia* are situated just behind the midlength of the cephalon and occupy 20% or less of the cephalic length just abaxially from the highest points of the very tumid fixed cheeks. In plan view they offer an extremely narrow profile occupying only a small part (5% approx.) of the transverse width. Their surfaces are almost vertical with the genal field falling away vertically to the border furrow where it becomes almost horizontal to form the border (Fig. 1A and Öpik, 1963, Fig. 15). The facial sutures are proparian. The free cheeks are small and subquadrangular with their greatest length at the margin and their marginal corners drawn out into points (Fig. 4B) as the facial suture runs over the margin and the extremely narrow doublure (Fig. 2F). The narrow border of internal moulds is ornamented with several (3 to 9) radial scrobicules which are not apparent on the external surface. Except for a very poorly impressed one in some specimens of *Pagetia* sp. nov. B, the border furrow is not impressed, its position is defined only by the change in slope between border and genal field. The eyes are not prominent and their anterior and posterior ends are in an exsagittal plane with a slight abaxial convexity at the midlength. The eye is 'kidney shaped', elongate exsagittally with well rounded ends and slightly more convex ventral margin than dorsal margin which is only very slightly concave around the palpebral lobe. Each eye has a well defined border around it (often a shallow furrow) in each species except in *P. ocellata,* where it is absent abaxially. This furrow represents the facial suture dorsally and the ocular suture ventrally. Whereas the visual surface occupies only a small part of the free cheek in *P. ocellata* it may be up to half the vertical height of the free cheek in *Pagetia* spp. nov. A & B and as much as 75% in *Pagetia* sp. nov. C.

The visual surface of the eye has overall convexity both sagittally and transversely. It is covered by a large number of smaller convexities (lenses) arranged in regular dorso-ventral files and diagonal rows (Figs. 1C, D). Internal moulds show a shallow concavity corresponding to these smaller external convexities. This is interpreted to mean that a thin biconvex lens occupied each of these sites. Öpik (1963:57) described small specimens (probably of *Pagetia* sp.

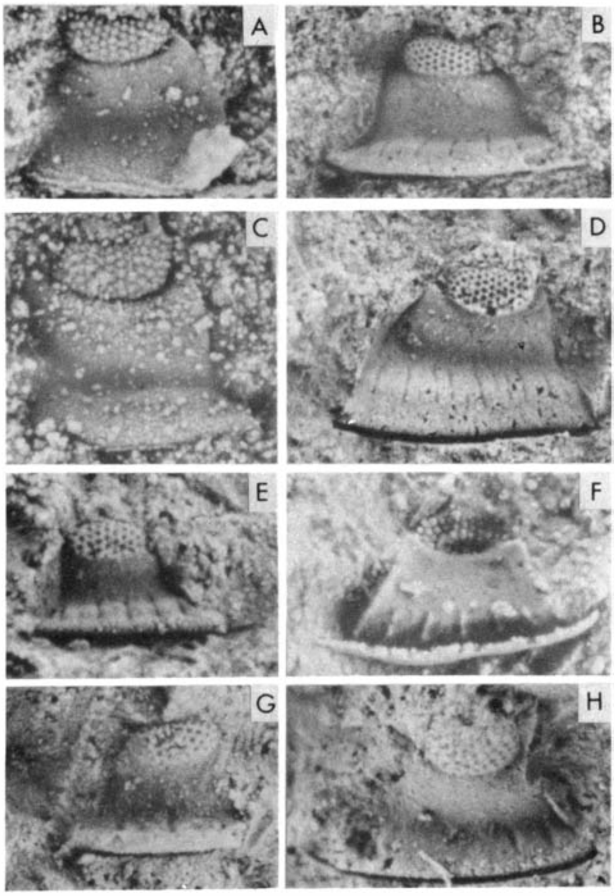

Fig. 2. A-D. *Pagetia* sp. nov. B. A, C. Lateral views of latex rubber casts from moulds of right and left oculate free cheeks respectively, the fine grained porous shale matrix has preserved the fine structure of the lenses and the terrace lines but a sugary surface texture is evident where the latex has run into pore spaces, X47 and 43, CPC13377 and 13373. B, D. Internal moulds of right and left oculate free cheeks respectively, X28 and 29, CPC13375 and 13374. E-H. *Pagetia* sp. nov. A. E, G, H. Lateral (E, G) and oblique lateral (H) views of a right and two left oculate free cheeks respectively, X50, 47 and 44, QMF6873, 6874 and CPC13465. F. Latex rubber cast of internal mould on E, X55, QMF6873.

nov. A) with 11 or 12 lenses. These may be interpreted as juvenile individuals, the subsequent mature representatives of which would have the 30 or more observed in large specimens. *P. ocellata* has approximately 25 to 30 lenses in its eye, this total lens number appears to be a specific character distinguishing it from *Pagetia* spp. nov. A, B & C. Specimens of *Pagetia* sp. nov. B have between 50 and 60 lenses in each eye so that there is considerable variation in the number of lenses between individuals, between different growth stages and between species. The lenses are regularly arranged both dorso-ventrally and diagonally but no regularity in the horizontal rows has been observed. Table 1 gives the distribution of lenses in files for the better preserved material on which most of the files can be counted.

The dorso-ventral files are parallel and very nearly straight near the midlength (Fig. 1C) except in *Pagetia* sp. nov. C where they are slightly curved anteriorly and posteriorly in the front and rear halves respectively (Fig. 1D). Near the anterior and posterior ends in all species they diverge ventrally towards the more adjacent end. This divergence is quite marked in *Pagetia* sp. nov. C and *P. ocellata* but only very slight in *Pagetia* spp. nov. A and B. The size of the lenses varies within each eye with smaller ones at each end and along the dorsal edge. The lens size increases gradually from each end but those in the most dorsal row are generally much smaller than the next row abaxially. The lenses are surrounded and separated by a narrow area of exoskeleton which does not appear to have been covered by cornea; this area is best exhibited separating the lenses on the latex casts from external moulds of *Pagetia* sp. nov. B (Figs. 2A, C). It is also seen separating the lenses on the internal cast (Fig. 2F). The external surface was very irregular and these interlensar areas appear to have been covered by a thin layer of normal exoskeleton on *P. ocellata* (Figs. 4C, D). Although no cross-sections have been cut, a fairly accurate schematic reconstruction can be made (Fig. 1B). The internal moulds (Figs. 2B, D, E-H, 3A, C-F) show that the interlensar areas were very thin and underlain by soft unpreserved parts of the animal but do not show any scleral projection or intrascleral membrane. No structures are

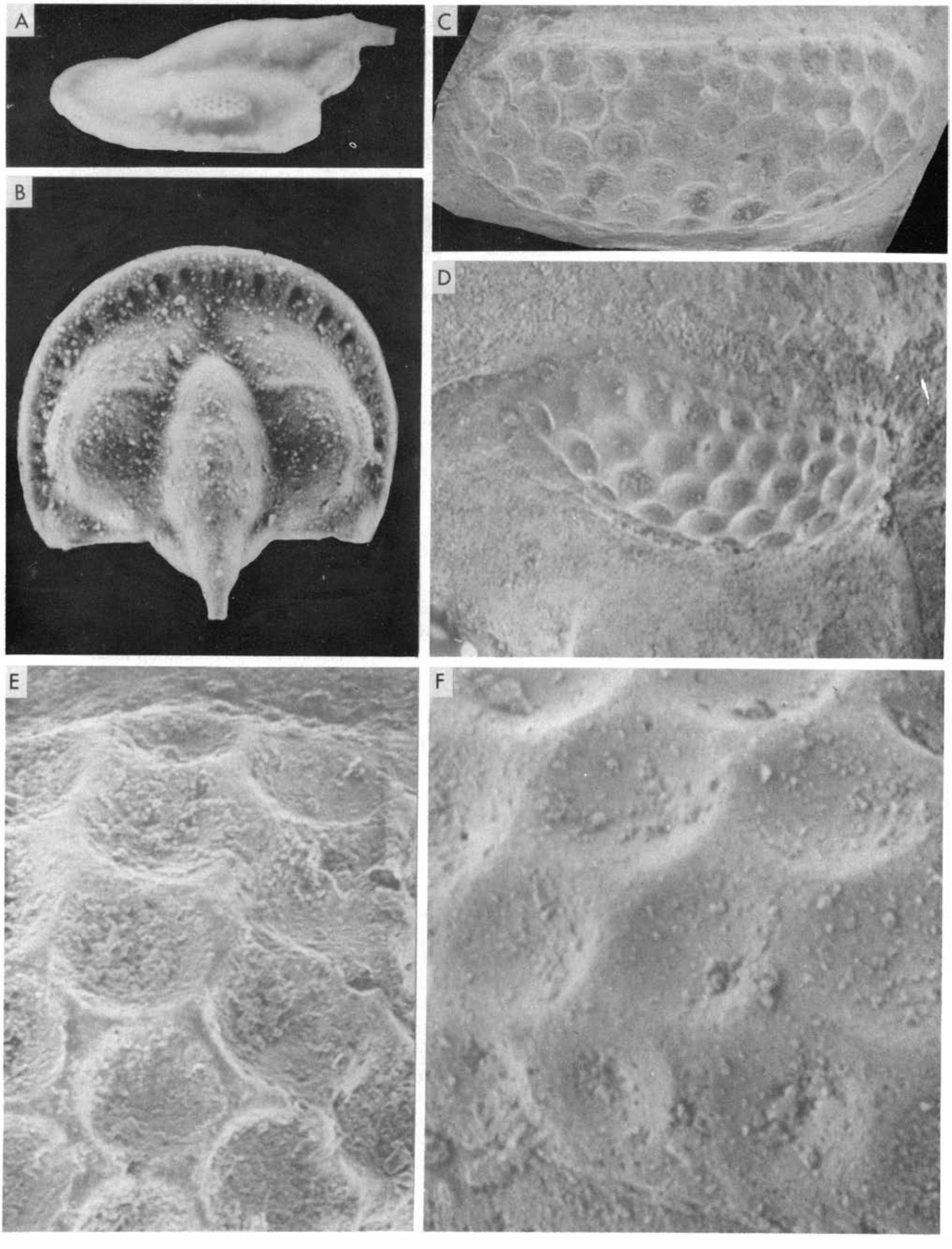

Fig. 3. Pagetia sp. nov. C. A, B. Left lateral and dorsal views of a complete internal mould showing the position of the eye, the facial suture and the vertical component of the field of view, X48, QMF6846. C-F. Scanning electron micrographs of internal moulds of two left eyes showing the shallow regular lens cups, the interlensar areas (ridges), the facial suture (D) and the possible sublensar structure (lower part of F), E is an enlargement of the upper portion of D, X300, 260, 900 and 800, QMF6853 and 6852.

Table 1. Numbers of lenses per dorso-ventral file (posterior to anterior) and the total lens numbers in the visual surface of selected specimens.

Pagetia sp. nov. A		
QMF6873	2, 3, 4, 4, 5, 5, 4, 3, 2	= 32
Pagetia sp. nov. B		
CPC13373	?, ?, 4, 5, 6, 6, 5, 6, 5, 5, 4, 3, 2, 1	= 52 (+ 7?) = 59
CPC13374	3, 4, 5, 5, 6, 6, 5, 6, 5, 5, 4, 3, ?, ?	= 57 (+ 3?) = 60
CPC13375	3, 4, 5, 5, 5, 6, 5, 6, 5, 5, 4, 3, 2, 1	= 59
CPC13377	3, 4, 4, 5, 6, 6, 6, 5, 5, 5, 4, 3, 2, 1	= 59
Pagetia sp. nov. C		
QMF6846	2, 3, 4, 5, 5, 5, 4, 4, 3, 2	= 37
QMF6852	3, 3, 4, 4, 4, 5, 4, 4, 3, 2	= 36
QMF6853	3, 4, 5, 5, 6, 6, 5, 5, 4, 3	= 46
Pagetia ocellata		
QMF6942	1, 2, 3, 3, 2, 3, 2, 2, 1	= 19
QMF6945	1, 2, 3, 3, 2, 3, 3, 2, 1	= 20

apparent in the bottoms of the concavities except perhaps in a few on Fig. 3F where a small star shaped depression is observed. Such structures are, however, present in only a few lens cups and they may not represent any organic structure. Some irregularities in the arrangement of lenses do occur (Fig. 1D).

THE EYE OF *OPSIDISCUS*

The eye of a Tasmanian species referred to *Opsidiscus* has been figured and described by Jago (1972:230-231), pl. 44, Figs. 4, 6, 9). This species along with an undescribed species from north-western Queensland is elsewhere assigned to a new genus, closely related to *Opsidiscus* (Jell, in press). However, the structure of Jago's species appears comparable with that described for *Opsidiscus* sp. nov. herein.

Opsidiscus lacks a facial suture so that the eye is completely surrounded by fixed cheek (Figs. 5A, B). The eye is extremely small occupying less than 15% of the cephalic length and only 1% of the width. The visual surface is almost vertical and oriented parallel to an exsagittal plane in which direction it is also elongated (Fig. 5C). It has well rounded ends between which the dorsal and ventral margins are parallel. Situated just abaxial to the highest point of the cheek the eye stands above the vertical slope to the border furrow. It is convex out both exsagittally and transversely.

Only internal moulds are available and these show very minute concavities as on internal moulds of *Pagetia* eyes. Jago's figures show the corresponding external convexities, thus indicating that both the Queensland and Tasmanian material probably had a very thin biconvex lens shape. Only 15 to 20 lenses arranged in regular dorso-ventral files of 2 to 4 lenses each are present in each eye. Diagonal rows may be present but preservation is not good enough to be certain. Regular horizontal rows are not apparent. The few specimens of *Opsidiscus* sp. nov. are not well enough preserved to allow the exact number of lenses in each file to be counted. The lenses appear to be of generally uniform size with slightly smaller ones at the anterior and posterior ends. The files are parallel throughout. The interlensar area is apparently present although not as clearly observable as in *Pagetia.* The material is too poorly preserved and photographed at too low a magnification to exhibit intralensar structures.

INTERPRETATION OF THE EYE OF *PAGETIA*

The position of the eye near the highest point of the cephalon, its protuberant nature and its overall convexity, indicate that each eye had a wide angle of vision. Its field of vision was mainly in a lateral direction, with respect to the attitude of the cephalon but the row of lenses along the facial suture was directed upwards at a fairly high angle (Figs. 3B, 5C). A quantitative assessment of this field similar to those obtained by Clarkson (1966a, 1966b, 1967a) for phacopinid eyes, is precluded by the extremely small lens size.

The lenses are thin, biconvex and not in contact with their neighbours. Therefore in the absence of an intrascleral membrane, a corneal membrane covering the entire visual surface or a separate membrane over each lens must be postulated. Whether or not this membrane extended across the interlensar regions is not clear. However, the similarity of texture of the cheek and in-

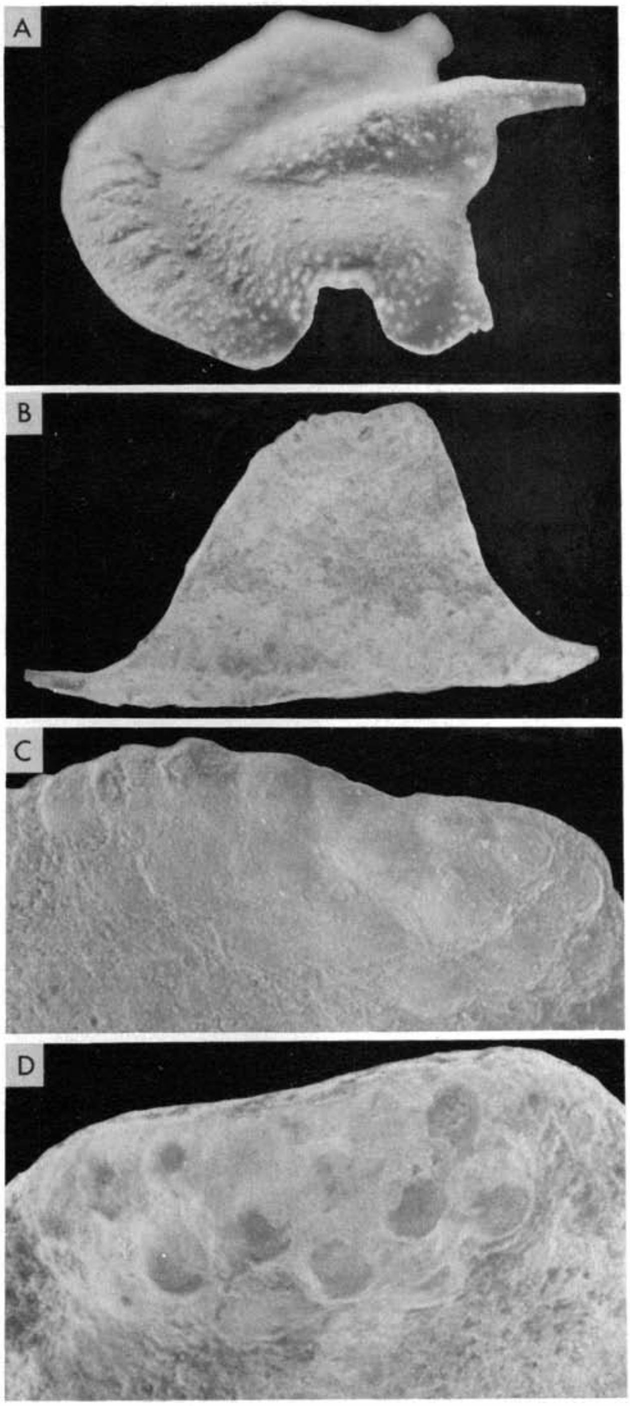

Fig. 4. Pagetia ocellata Jell, 1970. A. Oblique left lateral view of a cranidium showing the space for the free cheek and eye laterally, X40, QMF6937. B, C. Scanning electron micrographs of the eye attached to the free cheek showing the pointed marginal corners, general shape, convex lenses and interlensar areas with the same surface texture as the cheek, X120 and 430, QMF6942. D. Scanning electron micrograph of the oblique lateral aspect of the visual surface, X500, QMF6945.

terlensar areas (Figs. 4C, D) would tend to suggest that it did not. Therefore this membrane was probably anchored at the margins of each lens (Fig. 1B). In that case a very strong attachment to the surface must have existed since the membrane was clearly not embedded in any scleral projection as it was in schizochroal eyes. The answer to this problem may not be clearly decided at present.

Since the lenses were not contiguous (Figs. 2A, C, 4C, D) and since there were no scleral projections, which in the schizochroal eye acted as light guides to ensure that ommatidia received only light from their own lens, it is apparent that either movement of pigment fulfilled this function or that the ommatidia were of the superposition type (Waterman, 1961:23) (i.e. able to receive light through several lenses). In the light of other features, expressed below, the former choice is thought to be more likely.

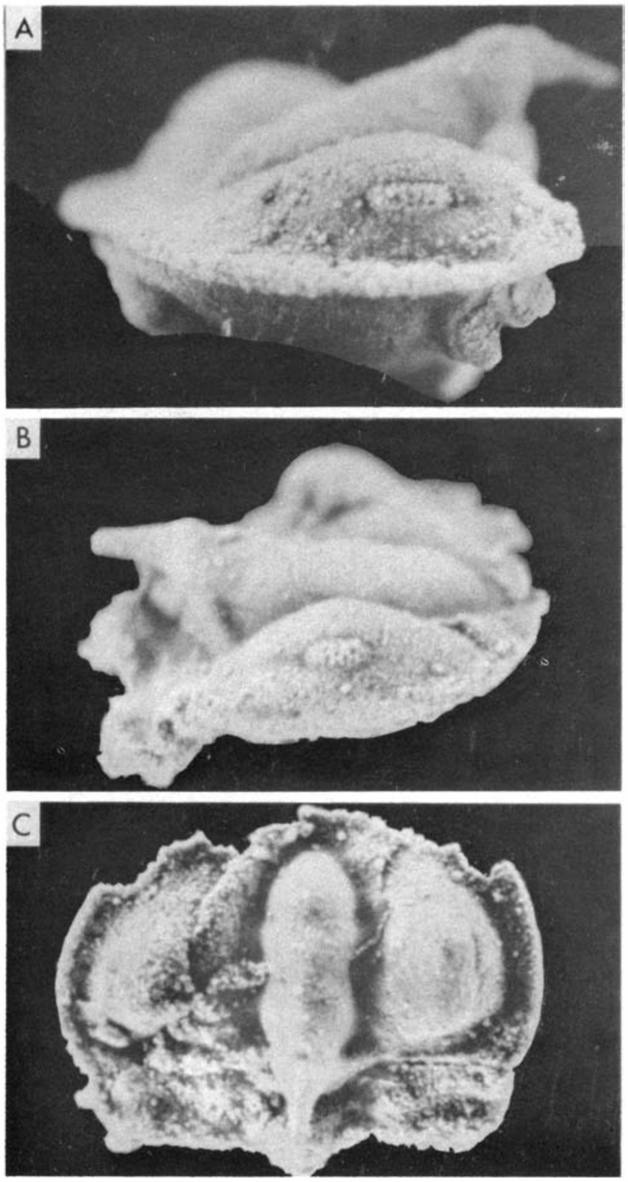

Fig. 5. Opsidiscus sp. nov. A. Lateral view of a complete enrolled specimen showing the eye without facial suture, X39, CPC13506. B, C. Right lateral and dorsal views of a damaged cephalon, X37, CPC13502.

According to Clarkson (1971:51) the schizochroal eye type first appeared in the Early Ordovician (Arenig) in the earliest representatives of the suborder Phacopina (e.g. *Ormathops)* and continued in members of that group into the Late Devonian. On the other hand *Pagetia* is a member of the superfamily Eodiscoidea which first appeared in the Early Cambrian and had disappeared by the beginning of the Late Cambrian leaving no recognizable descendants except the blind superfamily Agnostoidea. The three major evolutionary lineages of the Eodiscoidea all evolved blind forms. The size of the eyes degenerated through the species of *Pagetia* to the very small eyes of *Opsidiscus.* These stratigraphic and phylogenetic considerations show that the phacopinid eye could not have evolved from that of *Pagetia.*

COMPARISON OF TRILOBITE EYE TYPES

Öpik (1963:57) and Jell (1970:306) described the eye of *Pagetia* as schizochroal and Jago (1972:230) considered the eye of *Opsidiscus argusi* as schizochroal also. However, the more detailed morphological examination (above) of material from those genera does not bear out these interpretations.

The eyes of the different species of *Pagetia,* of *Opsidiscus* sp. nov. and of *O. argusi* Jago, 1972 are considered to be of the same type since the differences between them (e.g. number of lenses per file, number of files per eye, divergence of files, shape of the eye) are also seen to vary between the eyes of different representatives of other eye types (e.g. between the schizochroal phacopinids). This possession of a common eye type is not surprising in view of the fact that *Pagetia* and *Opsidiscus* share a large number of other characters and are obviously phylogenetically related.

The eye of *Pagetia* resembles the schizochroal type in that 1, there are a relatively small number of lenses widely separated on the visual surface, 2, the lenses are biconvex and not in contact with any of the surrounding lenses, 3, the lenses are arranged in regular dorso-ventral files and diagonal rows, 4, the interlensar area of schizochroal eyes has an ornament which passes transitionally into the ornament of the lower rim or the eye (Clarkson, 1966a) and in *Pagetia* the interlensar areas have the same texture as the free cheek ventral to the eye, 5, it is associated with a proparian facial suture. These two eye types are, however, distinguished by the following features 1, the eye of *Pagetia* has no deep interlensar scleral projection as present in the schizochroal eye, 2, nor does it appear to have the intrascleral membrane of schizochroal eyes, 3, it appears likely that a corneal membrane covered the lenses and was anchored to the interlensar areas around each lens margin, 4, the adult eye of *Pagetia* is much smaller than the schizochroal eyes and at maximum development contains fewer (maximum 70 compared to 500+) and smaller lenses, 5, the shape, 6, the number of lenses per file, 7, thickness of the lenses, 8, structure of the inner part of the lens (internal moulds of the lens cups show this point). The first three of these differences are fundamentally important since the almost complete lack of sclera in *Pagetia,* except perhaps for a thin, near surface, interlensar layer, the different method of holding the lenses in place (i.e. in schizochroal eyes the intrascleral membrane performs this task whereas in *Pagetia* it appears to be the role of a soft tissue covering the lenses and anchored at the surface) and the different type of control of the cornea indicate a different type of photoreception, possibly for different types of stimuli. This evidence is sufficient to establish that the eyes of *Pagetia* are not of the schizochroal type.

Of the two holochroal eye subtypes defined by Lindström (1901:27,28) those of the first (i.e. with prismatic, plano-convex lenses) are easily distinguished from the eyes of *Pagetia* by their smooth outer surface, close packed lenses, prismatic sublensar structure and continuous cornea of constant thickness. However, the second subtype with biconvex lenses is less easily distinguished. The internal moulds of the eye of *Peltura scarabaeoides* Wahlenberg (Lindström, 1901, pl. 3:37) and *Pagetia* (Figs. 2B, D, E, G, H, 3A, C-F) are very similar indeed. The shallow lens cups, smooth elevated interlensar areas and similar relative lens to eye size and distribution are features which give this similar appearance. However, Lindström (1901, pl. 3:38-41) shows the outer surface of the eye to be smooth and the lenses to be not only contiguous but also fused which is not the case in *Pagetia.* Once again these major differences are probably adaptations for receiving different light stimuli (e.g. movement, light intensity, form and colour) and for different responses. The eye of *Pagetia* cannot therefore be interpreted as holochroal.

Since it cannot be classified within either of the well established eye types, I propose the name abathochroal for this new type of eye.

The eye of *Acanthoparypha, Holia* and *Sphaerexochus* described by Whittington and Evitt (1953:15, 16) as schizochroal resemble, fairly closely, in their external morphology the eyes of *Pagetia.* However, the short scleral projections and outwardly concave inner surface of the lens cups indicate that they are not of the abathochroal type. These eyes do not fit readily into either of the other types but further investigation of them is outside the scope of this paper.

FUNCTION AND ECOLOGY

Waterman (1961:52) in a review of vision and light sensitivity in crustacea considered that detailed structural information and comparative studies of physiological optics are much needed to understand the function of the lateral eyes. At the present level of knowledge of vision in living marine arthropods it is difficult to propose functions for homologous structures in trilobites. Therefore the following discussion is necessarily of a speculative nature.

The abathochroal eye with a relatively small number of thin, widely separated lenses probably operated as an apposition eye as described in modern crustacea (e.g. branchiopods, copepods and others) by Exner (1891). Light received by each ommatidium would be passed to its own receptor cells and the total image made up as a mosaic combined from all lenses. In contrast with the schizochroal eye where the scleral projections probably acted as light guides between the ommatidia it must be assumed that this task was performed by pigments which have not been preserved. The animal had its main field of view in a lateral direction with respect to the cephalon as a whole. There was also some vertical vision imparted by the dorsal row of lenses. The eyes probably functioned mainly for the recognition of changes in the intensity of light. Waterman (1961) states that the primary dependence of diurnal vertical migrations of pelagic organisms upon changes in light intensity has been clearly shown. I believe all miomerid trilobites had this capacity either through the lateral eyes, where present, or the median eye (represented by a glabellar node) in supposedly blind forms (e.g. agnostoids). The lateral eye of *Pagetia* may also be able to recognize movements especially if eye tremors occurred as have been observed in living crustacea (e.g. *Triops, Artemia, Daphnia)* by Fox (1949) and Heberday & Kupka (1942). No evidence is available to indicate whether or not forms could be distinguished by this type of eye.

Degeneration of the lateral eyes throughout the superfamily Eodiscoidea is interpreted as an adaptation to the supposed pelagic mode of life. The presumed evolution (Jell, in press) from Eodiscoidea to the Agnostoidea is further evidence of this interpretation. A pelagic animal would need a minimal capacity for photoreception. The glabellar node of most agnostoids may represent the median eye as suggested by Ruedemann (1916) and Størmer (1930). This would be in accord with living pelagic animals where generally only a median eye is retained to provide photoreception as proposed above, the lateral eyes have presumably been lost during evolution from eodiscoids. The genus *Pagetia* retained its lateral eyes through the late Early Cambrian and most of the Middle Cambrian, although it evolved blind genera in many different areas at different times. The lateral eyes degenerated in the late Middle Cambrian species of *Pagetia* and *Opsidiscus* but no descendants of that lineage are known which lack them completely except perhaps the younger species of *Opsidiscus* from Sweden and Siberia in which their presence or absence has not been made clear from the available descriptions. Clearly, then, there was no selective pressure to retain or further specialize the eodiscoid eye and its retention in the *Pagetia* lineage for a much longer period than in the other lineages of the superfamily may have been because of a slower adaptation to a pelagic mode of life. Furthermore, it may be that once the eodiscoid form without lateral eyes had been evolved the stage was set for evolution to the agnostoid form. Within the same superfamily two lineages which began with oculate genera *(Neocobboldia* and *Hebediscus)* are interpreted (Jell, in press) as having given rise to blind eodiscoids *(Chelediscus* and *Tannudiscus* respectively) which then gave rise to agnostoids (Ptychagnostidae and Quadragnostidae respectively). It would not be surprising, therefore, if in the future an early Late Cambrian phylogeny between *Opsidiscus* and some agnostoid group, whose origins are presently unknown, were defined.

Clarkson's (1967b) interpretation that eye reduction in phacopid trilobites was an adaptation to life in deeper darker water is not completely accepted for the eye reduction observed in this group. These pelagic animals may have spent the daytime in dark water near, the level of maximum light penetration and risen to the surface at night. Others, however, lived on the shelf in shallow well illuminated water.

CONCLUSIONS

Although several morphological similarities between the eye of *Pagetia* and each of the holochroal and schizochroal types exist there are differences which clearly distinguish the three types and prompt introduction of the name – abathochroal.

The observed degeneration of the eodiscoid eye is interpreted as being compatible with adoption of a pelagic mode of life. This would then indicate that miomerids evolved from a polymerid stock, perhaps by neotony (e.g. in their retention of only two thoracic segments, their equidimensional cephalon and pygidium, the pelagic mode of life and their small size), as they adopted a new mode of life. However, photoreceptors capable of distinguishing light intensity variation for control of vertical diurnal migrations must be present. The lateral eyes of *Pagetia, Opsidiscus* and other oculate forms and the median eye of supposedly blind eodiscoids and agnostoids are seen as carrying out this function.

The eyes of *Pagetia* were capable of recognizing light intensity changes and could possibly recognize movements. The reason for the assumed Precambrian evolution of the abathochroal from holochroal eye remains a mystery.

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Anatomy of *Triarthrus* and the relationships of the Trilobita

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Radiographic study of over 100 specimens of *Triarthrus eatoni* from Beecher's Trilobite Bed has revealed the anatomy of the exoskeletal, skeletomuscular, and digestive systems in fine detail. The head includes one preoral antennal segment and three postoral segments bearing biramous limbs somewhat differentiated from trunk limbs. The abdomen is divided into pygidial and postpygidial portions. In the conformations of the food groove and thoracic musculature, *Triarthrus* is quite similar to cephalocarid crustaceans. The Trilobita provide a link at a very primitive organizational grade between Crustacea and Chelicerata. The Trilobita-Crustacea-Chelicerata comprise a monophyletic assemblage, and the gap between them and the Uniramia extends virtually to the origins of the Arthropoda.

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This paper presents a description of the anatomy of the exoskeletal, skeletomuscular, and digestive systems of the Ordovician trilobite *Triarthrus eatoni* (Hall) that is based on a high resolution radiographic study of over 100 pyritized specimens from Beecher's Trilobite Bed in the Frankfort Shale near Rome, New York (cf. Cisne 1973b). In addition to the internal anatomy, which has been known for trilobites only in the most fragmentary fashion, the paper reveals a number of unexpected points of external anatomy. It brings to light previously missing evidence on the relationships of the Trilobita and on the still larger problem of the origins of the Arthropoda, and it briefly interprets this evidence. This is a short summary of an extensive account with full documentation and discussion (Cisne 1973 MS) which will be published elsewhere.

Research has been carried out in the Department of Geophysical Sciences, University of Chicago, and in the Department of Geology, Field Museum of Natural History. Among the many I wish to thank are Dr. Ralph G. Johnson, University of Chicago, who supervised my work, Dr. Robert R. Hessler, Scripps Institution of Oceanography, who has been my constant and constructive critic, and Dr. Rainer Zangerl, Field Museum, who supervised my radiographic work. Through the courtesy of Dr. Karl M. Waage, Yale University, Dr. Stephen J. Gould, Harvard University, Dr. Niles Eldredge, American Museum of Natural History, and Dr. Eugene S. Richardson, Field Museum, specimens were made available to me from, respectively, Peabody Museum (YPM), the Museum of Comparative Zoology (MCZ), the American Museum, and Field Museum. Research has been supported by a National Science Foundation Graduate Fellowship, the American Association of Mineralogical Societies Fellowship, and the William Rainey Harper Fellowship of the University of Chicago, and by grants from the Hinds Fund, Gurley Fund, and Salisbury Fund, University of Chicago.

MATERIALS AND METHODS

Among the specimens on which this study is based are those made famous in the works of Beecher (e.g., 1894, 1895a, 1896, 1902), Raymond (1920), and Størmer (1939, 1951). From examination of over 600 *Triarthrus* specimens from Beecher's Trilobite Bed, 171 were selected for study. After a radiographic survey of all but the tiny protaspids and meraspids, the 68 best and most interesting were selected for intensive study using a Siemens Beryllium Window X-ray apparatus, a "soft" X-ray apparatus with a continuously water-cooled head which allowed arbitrarily long exposures. Stereoscopic negative pairs were made for each specimen until altogether suitable exposures were obtained. Exposure times usually ranged between one and two hours. Six specimens were subsequently cut into serial slices which were then X-rayed stereoscopically. More than 1000 individual enlargements on paper for over 150 stereoscopic pairs, and paired enlargments on 8 x 10" film sheets for the 20 best specimens were prepared and studied.

Stürmer (1970) described the numerous advantages of radiographic techniques over traditional means of preparation and study of pyritized fossils. Combined with stereoscopy, radiography affords a means of examining all parts of a fossil and of studying their anatomical relationships in three dimensions without damaging or otherwise biasing the specimen itself. In the present study, it has been possible to repeatedly find small setae down to 10μ in diameter. This observation suffices to illustrate the resolution obtainable with the technique as well as the resolution of the preservation itself.

The taphonomy of the fossil assemblage, the necessary background for interpretation of the trilobite fossils, has been dealt with elsewhere (Cisne 1973a, b). The specimens have been somewhat deformed in compaction of the siltstone matrix, yet they are strongly three-dimensional. Typically, the body cavity is collapsed. A small amount of silt material within it, probably introduced during decomposition, forms the matrix for pyritized internal structures.

Fossilized parts of the trilobite were identified on the basis of their form, structure, and relationships to other parts using a knowledge of comparative arthropod anatomy. Structures considered to be real and original features of the trilobite were distinguished from preservational artifacts and debris on the basis of their recurrence from specimen to specimen. Serially repeated structures that are reported in this paper have been identified in at least four specimens in which they are actually serially repeated. Major paired and unpaired structures have been identified in at least 10 specimens. Usually, structures have been found to recur many more times than this. Parts of the intestine, for example, have been identified in about two-thirds of the 68 specimens intensively studied. A number of seemingly real anatomical structures, including some resembling ganglia and ovaries, have been discounted for reasons of rarity or poor preservation.

Reconstructions of the trilobite were built up and refined through combined optical and radiographic study of the entire suite of specimens. A critical problem has been the shape and dorsoventral dimensions of the body cavity, and it was solved to a good approximation through considerations of several lines of evidence. From a morphometric study of development (Cisne 1973 MS), it can be demonstrated that proportions of the major body parts remained essentially constant over a five-fold increase in length during the holaspid period. There is thus reason to assume that the shape of the axial region of the tergum, which defines the dorsal contour of the body cavity, should also have remained constant. Measurements on the width and height of the first, fifth, and fourteenth thoracic tergites in about 20 specimens confirm that, in the most convex specimens, these parameters of shape grew in direct proportion to one another. Barring systematic error, there is thus reason to believe that these specimens give approximately the shape of the axial region in the living animal. Using measurements of the lengths of dorsoventral muscles and endoskeletal bars in specimens deformed severely enough that the muscles were exposed in lateral view, and knowing the shape of the axial region, it was then possible to geometrically reconstruct transverse sections through individual specimens.

ADULT ANATOMY

External anatomy

DESCRIPTION. – In dorsal aspect, the body proper is oval in outline and surrounded laterally by the distal parts of the limbs (Pl. 1:1, Fig. 1). In ventral aspect, the body proper is concave ventrally (Pl. 1: 1, Fig. 2). Holaspids range from 8 to 39 mm in overall length of the tergal exoskeleton. No clear indications of sex or sexual dimorphism have been found at any developmental stage.

The body is divided longitudinally into head, thorax, and abdomen. The head bears a single pair of uniramous, annulated antennae preorally, and bears three pairs of biramous limbs postorally. The mouth cavity (atrium oris) opens between the hypostoma and metastoma (m) (Figs. 2, 9). The abdomen is divided into an anterior pygidial portion of five limb-bearing segments (P_1 –P_5 , Fig. 10) which bear the pygidium, a tergum, and a posterior post-pygidial portion of six to 12 limb-bearing segments (P_6 –P_{11-17} , Fig. 10). The sclerotized parts of the exoskeleton are the tergum (tergal or dorsal exoskeleton) – which includes the head tergum ("cephalon"), 14 thoracic tergites, and the pygidium – and two sternal structures, the hypostoma and metastoma. A rostrum has not been identified.

Postoral limbs of the head and trunk all conform to the same biramous pattern (Figs. 2, 3).

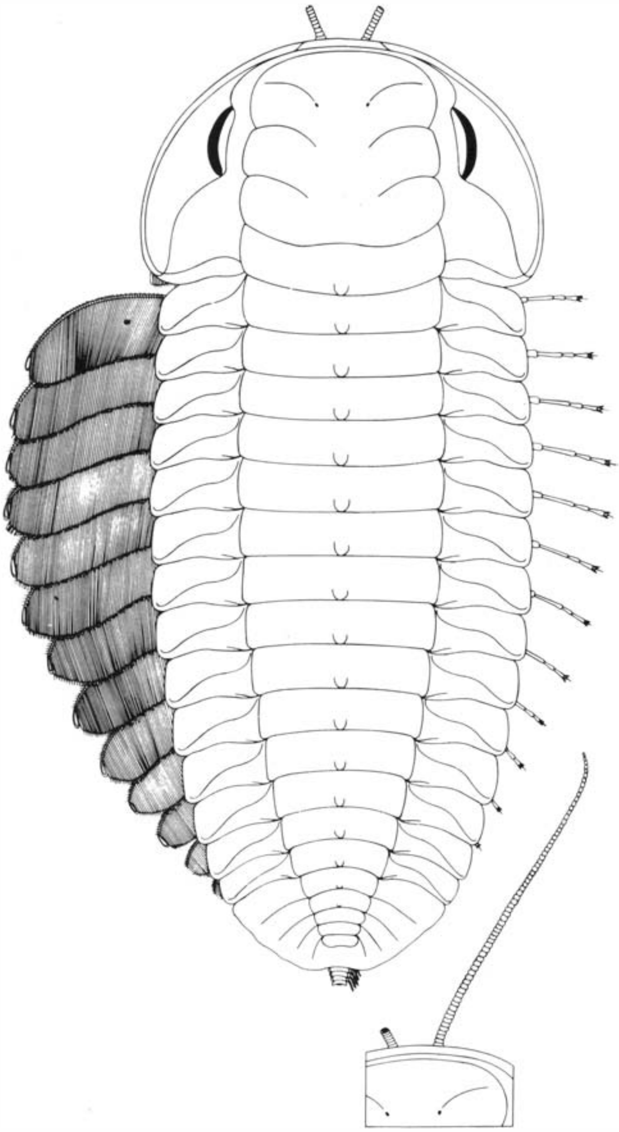

Fig. 1. Dorsal view of large adult *Triarthrus eatoni* (Hall).

A typical trunk limb (e.g., the fifth thoracic limb, T_5 in Fig. 3) is composed of a large, blade-like coxa which bears two rami: a feather-like exite inserted medially and a telopod inserted distally. The exite is composed of a thin annulated rhachis that terminates distally in a spatulate segment. The annuli, up to about 100 in number, each bear one or more blade-like filaments, each of which terminates distally in a seta. The telopod is composed of seven segments which Størmer (1939) designated according to the terminology applied to arachnid limbs. In the absence of a detailed knowledge of the intrinsic musculature, it is impossible to determine the podomeric composition of the limb. The term "coxa" is used loosely. It is quite possible that the structure is a complex of fused or incipiently divided podomeres like the crustacean sympod or protopod. It is impossible to determine which, if any, of the telopod segments represent secondarily divided podomeres, and whether the terminal segment (pretarsus) represents a podomere at all.

Postoral limbs are graded in size and in proportions of parts along the body, and head limbs are somewhat differentiated from trunk limbs (Figs. 2, 3). As compared with a mid-thoracic limb (T_5, Fig. 3), the head limbs (C_1-C_3, Fig. 3) have the coxal endites progressively reduced in dorsoventral depth and have the exite and telopod reduced in relative size and more and more ventrally directed about their articulations to the coxa. Along the trunk, limbs past the middle of the thorax become progressively reduced in size (e.g., P_3, Fig. 3). Owing to poor preservation, it is not known whether post-pygidial limbs bore exites. All along the postoral part of the body, paired endites closely approach one another along the midline. The midventral space between them forms an uninvaginated food groove (vt, Fig. 7). Thoracic exites are imbricated, the posterior part of one lapping dorsally over the anterior part of the exite behind it.

DISCUSSION. – The single most important finding on external anatomy is that *Triarthrus* has three pairs of postoral head limbs, not four as supposed by Beecher (1895a, 1896), Raymond (1920), Størmer (1942, 1944, 1951), Bergström (1973), and Stürmer and Bergström (1973).

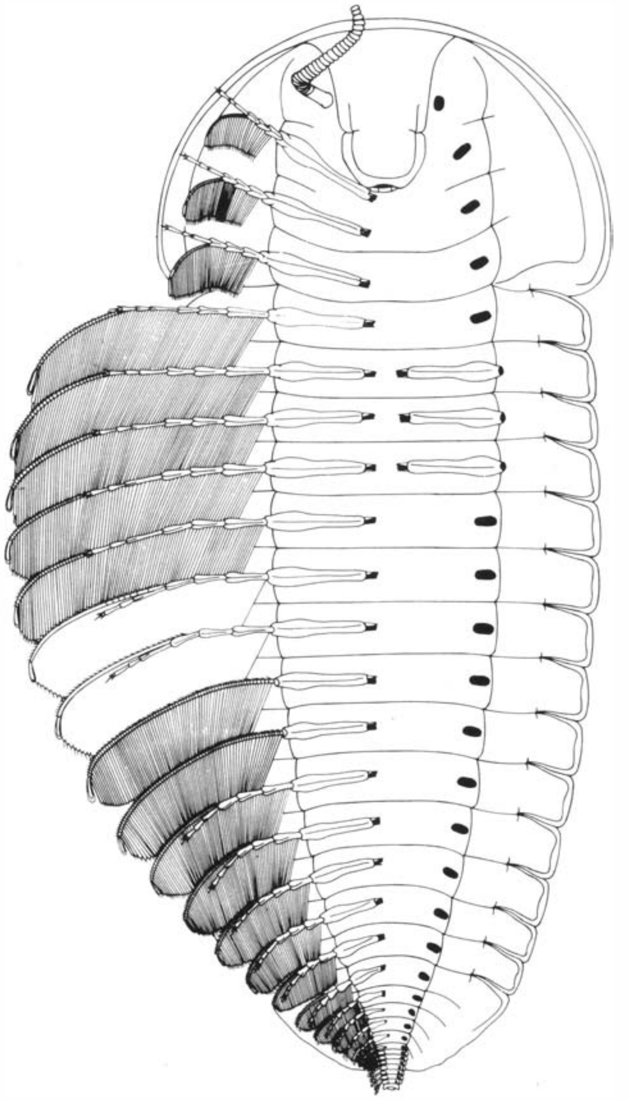

Fig. 2. Ventral view of large adult *Triarthrus eatoni* (Hall).

The construction of the skeletomusculature confirms that only three postoral segments were present in the head. Previous interpretations of head segmentation in trilobites, which have been largely based on Beecher's (1895a) interpretation of *Triarthrus,* are thus in error.

Beecher's (1895a) original count, which has been accepted by subsequent workers, is based on an incorrect interpretation of fossil anatomy. His error is quite understandable in view of the rather small number of specimens that he had time to prepare so painstakingly, and in view of the study techniques he had available to him. Radiographic study of a much larger number of specimens has revealed that the limb interpreted by Beecher (1895a) as the fourth postoral head limb is in fact the first thoracic limb. Quite commonly, limbs of the head and anterior part of the thorax have fallen forward in post-mortem deformation of the body, though in a number of specimens they have remained in their natural, upright positions. After having fallen forward, the first thoracic limb usually rests with its coxa lying across the posterior margin of the head tergum and, with its broad posterior face exposed to view ventrally, has all the appearance of a fourth postoral head limb. Radiographs of the specimen on which Beecher (1895a) particularly based his interpretation (YPM 220) revealed it to be deceptively deformed in this way. Specimen MCZ 7190/18 (Fig. 4) most clearly illustrates the problem. Thoracic limbs on the left side in the figure have remained upright. But the corresponding limbs on the right side have fallen forward. The first thoracic limb on the right lies at the back of the head and, in the apparent shape of the coxa, has much the appearance of head limbs, which have fallen forward on both sides of the body.

If indeed the predominant pattern of head furrow development among trilobites corresponds to a single pattern of head segmentation (cf. Whittington, 1957), it is most probably that pattern represented in *Triarthrus.* Probably, the trilobite head characteristically included four limb-bearing segments, one preoral and three postoral. At least in *Triarthrus,* the antennal segment corresponds to the first lateral glabellar lobe, and the postoral segments correspond to the second and third lateral glabellar lobe and the occipital ring. Only three pairs of postoral head

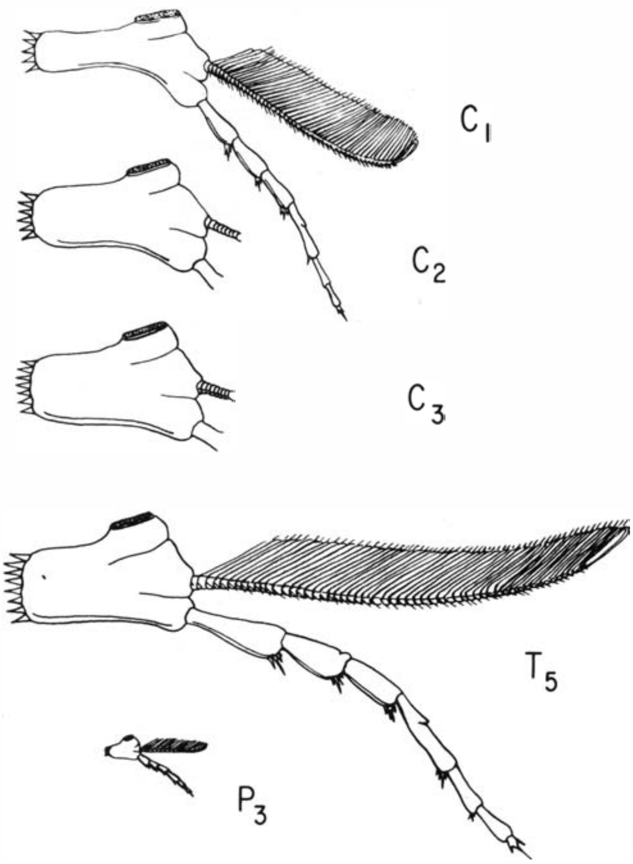

Fig. 3. Anterior views of the first, second, and third postoral head limbs (C_1—C_3, only the basal parts of the second and third limbs are shown), the fifth thoracic limb (T_5), and the third abdominal limb (P_3).

limbs are present in the other best known trilobites: *Phacops* sp. and *Asteropyge* sp. (Bergström 1973 and Stürmer & Bergström 1973), *Cryptolithus bellulus* (Cisne in preparation), and likely *Olenoides serratus* (Whittington 1975 and personal communication). Head structure in other trilobites is not so well known. Raymond (1920) reported that he found evidence of only three pairs of postoral head limbs in *Isotelus* spp., and that he reconstructed the fourth limb pair by analogy with *Triarthrus*. Størmer's (1951) interpretation of four pairs of postoral head limbs in *Ceraurus pleurexanthemus,* which is based on models of parts of the limbs in parts of the head in three specimens, must remain open to question.

The post-pygidial abdomen (Pl. 2 : 2, Figs. 1, 2, 10) is another unexpected finding. Though the posterior part of it was described by Walcott (1918) and Raymond (1920) as a post-segmental "anal plate", it was entirely unexpected that there should be a series of limb-bearing segments posterior to the pygidium. Each pair of post-pygidial limbs probably corresponds to a segment. However, it must be pointed out that more than one pair of limbs may correspond to a single body segment, as in the abdomen of notostracan branchiopods. From the largest meraspid stage to the largest holaspid stages, the post-pygidial abdomen is a constant feature of body organization. Its length, measurable in over 20 specimens, most of those including the extreme posterior part of the body, grew in direct proportion to the overall length of the tergal exoskeleton (Cisne, 1973 MS). Hence it would seem unlikely that the post-pygidial abdomen represents an asexual bud or deciduous reproductive structure like the epitoke in polychaetes (cf. Lemche, 1957).

The pygidial abdomen in *Triarthrus* thus did not include the telson (t, Fig. 10), which was a tiny, limb-less structure at the tip of the post-pygidial abdomen. The small, semicircular, unsegmented pygidium of most olenellid trilobites is probably homologous with the telson in *Triarthrus,* not the multisegmented pygidium. If this be correct, the multisegmented pygidium found in the great majority of trilobites is not strictly characteristic of the Trilobita.

Skeletomusculature

The present reconstruction of the skeletomusculature is necessarily incomplete and simplified. Some muscles that there is good functional reason to expect (e.g., muscles governing the hypo-

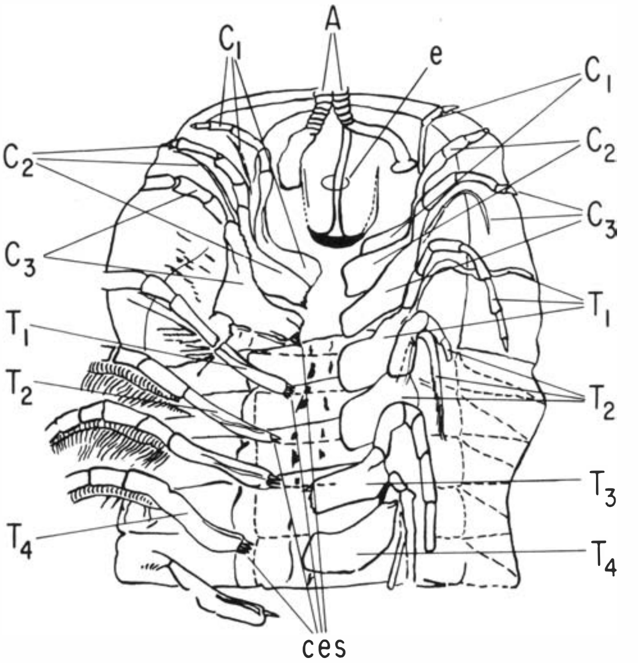

Fig. 4. Ventral view of MCZ 7190/18 showing in particular the three pairs of postoral head limbs (C_1-C_3), coxal enditic setae (ces) on head and trunk limbs, and the esophagus (e). While thoracic limbs (T) on the left side in the figure have remained upright, thoracic limbs on the right side have fallen forward on their anterior faces such that the first thoracic limb (T_1) takes on much the appearance of head limbs, which have fallen forward on both sides of the body. The figure is a tracing from an enlargement made on film.

stoma) have not been recognized in fossils. What might be called the resolution of preservation is consistently high enough to reveal the larger body muscles and fibers within them, and sufficient in many cases to reveal the gross form of smaller muscles. But it is not sufficient to reveal, for example, the numerous fibers that might have comprised a given extrinsic limb muscle and to reveal functionally important differences as to the exact origins and insertions of those fibers. For this reason, it has not been possible to distinguish promotor and remotor extrinsic limb muscles.

DESCRIPTION. – The skeletal muscles can be divided into five sets: (1) longitudinal body muscles (dlm, vlm, Figs. 5-7, 10), (2) dorsoventral body muscles (dva, dvp, dvv, Figs. 5-7, 10), (3) horizontal body muscles (hom, Figs. 5, 7), (4) extrinsic limb muscles (dam, dmm, dpm, vam, vpm, Figs. 5-7), and (5) intrinsic limb muscles (poorly known, cem, Fig. 7). An additional component of the skeletomusculature is the probably tendinous endoskeleton, which consists of a ladder-like series of bars (fb, b, Figs. 5-10).

The paired dorsal longitudinal muscles (dlm) form a sheet of parallel fibers along the underside of the tergal exoskeleton in the trunk. Progressively more medial slips of the lateral part of the muscle take origin beneath the first, second, and third lateral glabellar furrows. The medial slips take origin beneath the occipital furrow. Along the thorax, the muscle is inserted on each articulating half ring. The ultimate insertions of the muscle in the abdomen are not known.

The ventral longitudinal muscles (vlm) are a pair of bundles that run in parallel along the body. The muscle takes origin in the vicinity of the anterior border of the head tergum. Segmental blocks of the muscle are inserted end to end on endoskeletal bars (fb, b) in the head and thorax. The bulk of the muscle probably inserted ultimately in the anterior part of the abdomen.

The endoskeletal bars are rods that extend between segments. The frontal bar (fb) is larger than the rest. At least post-frontal bars (b) were presumably connected to the sternal exoskeleton by connecting ligaments (cl), which have been identified in only one specimen (YPM 228, Pl. 1:1, Fig. 11). It is not known whether the endoskeleton extended into the abdomen.

The dorsal and ventral longitudinal musculature is linked by dorsoventral muscles of three variaties: the anteriorly descending muscle (dva), the posteriorly descending muscle (dvp), and the ventrally descending dorsoventral muscle (dvv). In the second and third postoral head segments (C_2, C_3) and in each thoracic segment, this set of muscles forms a box truss on either side of the body cavity. The muscles take origin on the tergal exoskeleton and descend to insert near the ends of endoskeletal bars. Dorsoventral muscles other than in much modified form were probably absent in the first postoral head segment owing to the extent of the stomach in

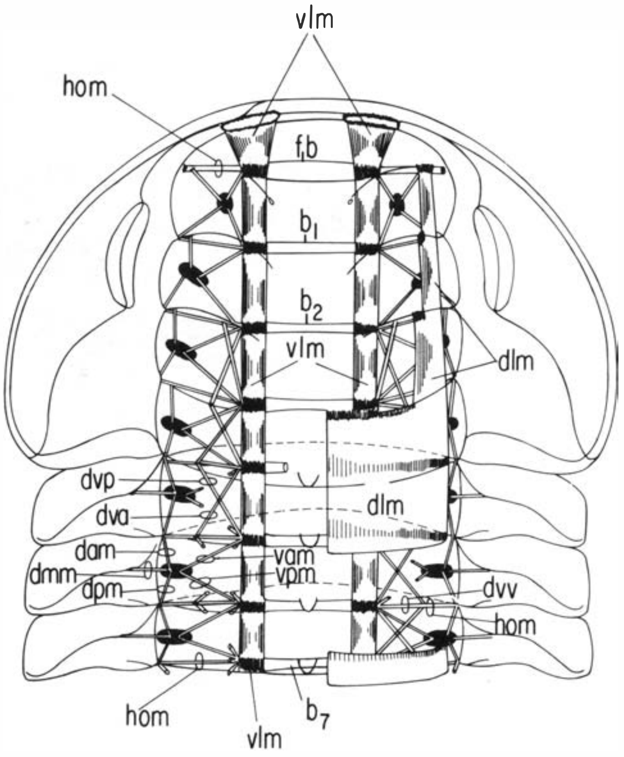

Fig. 5. Dorsal view of the head and first three thoracic segments showing the musculature.

this region (Figs. 8, 9). It is not known whether dorsoventral muscles were present in the abdomen.

The horizontal muscles extend laterally from the tips of endoskeletal bars to insert on the sternal exoskeleton in the vicinity of the ventral axial furrow.

The extrinsic muscles of thoracic limbs fall into five major masses, each of which may include more than one discrete muscle: the dorsoanterior muscle (dam), the dorsomedial muscle (dmm), the dorsoposterior muscle (dpm), the ventroanterior muscles (vam), and the ventroposterior muscle (vpm). The dorsal extrinsic limb muscles (dam, dmm, dpm) take origin on the tergal exoskeleton, the dorsomedial muscle (dmm) taking origin beneath the pleural furrow and the other two (dam, dpm) taking origin on the tergal posterior apodeme (tpa, Fig. 8). The ventral extrinsic limb muscles (vam, vpm) take origin near the ends of endoskeletal bars. The details of the insertions of these muscles within the coxa are poorly known. The extrinsic muscles of head limbs (A, C_1 –C_3) conform to the same pattern as do those of thoracic limbs except in that dorsomedial muscles (dmm) are probably absent.

Intrinsic limb muscles, or rather strands of pyrite that appear to be bits and pieces of them, have been found in the proximal third of the antenna and throughout the telopod in postoral limbs. Only two seemingly complete muscles were repeatedly found in more than five biramous limbs: the coxal enditic muscle (cem, Fig. 7) and a muscle extending between the distal part of the second and the proximal part of the fourth telopodal segments (prefemur and patella of Størmer 1939).

DISCUSSION. – The numbers of specimens in which the various elements of the skeletomusculature have been identified among the 68 specimens intensively studied are as follows: dorsal longitudinal muscle (39), ventral longitudinal muscle (10), frontal bar (24), post-frontal bars (20), dorsoventral muscles (5), horizontal muscles (4), extrinsic muscles of the antenna (4) and of postoral limbs (18), and intrinsic muscles of the antenna (4) and of postoral limbs (18). The anterior portion of the ventral longitudinal muscles (vlm) is shown in association with the frontal bar (fb) and the first three post-frontal bars (b_1 –b_3) in YPM 228 (Pl. 1:1, Fig. 11). Connecting ligaments (cl) are shown on the third post-frontal bar (b_3). Parts of the dorsal longitudinal muscle (dlm) and sets of dorsoventral muscles (dva, dvp, dvv) in association with part of the ventral longitudinal muscle (vlm) in the second and third postoral head segments (C_2 , C_3) are shown in YPM 204. (Pl. 1:2, Fig. 2). The dorsal longitudinal muscle (dlm) is shown in YPM 28264 (Pl. 2:1, Fig. 13) together with endoskeletal bars (b) and horizontal muscles (hom) associated with the ventral longitudinal muscles (vlm).

Movements of the trilobite's exoskeleton were governed by a complex musculature. Dor-

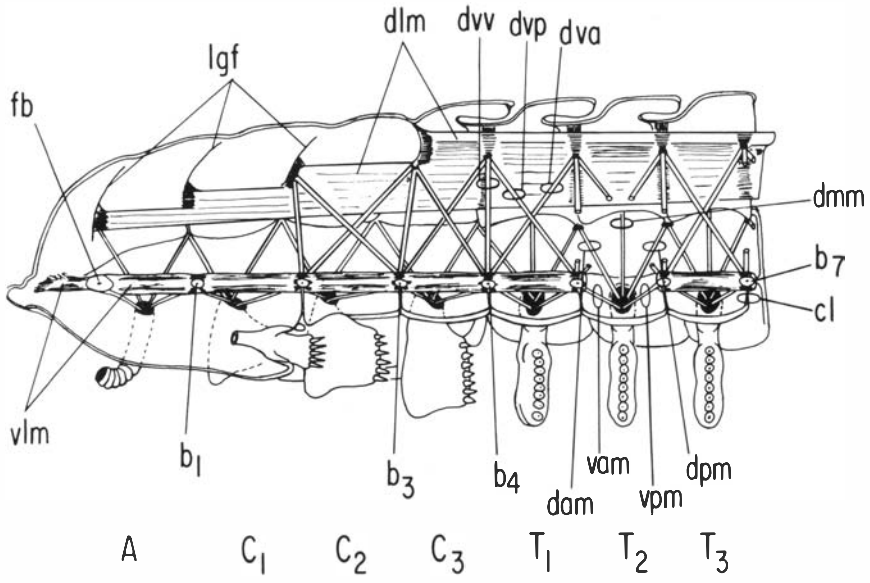

Fig. 6. Interior view of the head and first three thoracic segments showing the musculature. Only the coxae of postoral limbs are shown.

sally, muscles acted against the sclerotized tergal exoskeleton. Ventrally, muscles acted against an endoskeleton, which in turn was anchored to the thin, little sclerotized sternal exoskeleton by ligaments and horizontal muscles. The dorsal and ventral longitudinal muscles should have functioned in flexing the body dorsally and ventrally, respectively, about paired intertergal hinge points located at the level of the dorsal axial furrow (cf. Cisne 1973 MS). The dorsoventral and horizontal muscles were probably adjustors. The lateral slips of the dorsal longitudinal muscle that extend far forward beneath the head tergum may have acted in supporting the head during locomotion (cf. Whittington 1975).

No evidence has been found to support Størmer's (1939) suggestion that exterior dorsal muscles extended between tergites. Indeed there is no a priori reason to believe that such muscles necessarily existed. While they are found in a variety of configurations in insect abdomens (Snodgrass 1931), they are absent in many crustaceans (e.g., *Hutchinsoniella macracantha,* cf. Hessler 1964).

Digestive System

DESCRIPTION. – The basic parts of the digestive tract discernible in fossils are the mouth cavity (mca, Figs. 8, 9), esophagus (e, Figs. 8, 9), stomach (s, Figs. 8, 9), intestine (i, Figs. 7–10), and anus (a, Fig. 10). Presumably, the esophagus and stomach were stomodaeal and had a cuticular lining. The esophague as here recognized presumably includes a pharynx adjacent to the mouth cavity as well as the esophagus proper. It has not been possible to distinguish these two regions in fossils. It is not known what length of the intestine, if no more than a tiny lip inside the telson, corresponds to the proctodaeum. Parts of the gut musculature and caeca (cca, Fig. 9), most probably digestive glands, are also known.

The mouth cavity (mca, an atrium oris) is posteriorly directed and opens between the hypostoma and metastoma (m). At its sides are the endites of the first postoral (C_1) limbs. Anteriorly, the mouth cavity tapers into the esophagus (e). This narrow tube (e) extends forward ventral to the first post-frontal (b_1) and frontal (fb) bars. It (e) loops anteriorly around the frontal bar and tapers into the stomach (s), which lies beneath the anterior part of the glabella. The intestine (i), into which the stomach tapers posteriorly, extends as a cylindrical tube through the posterior part of the head and the thorax. But in passing through the abdomen, it tapers down to about the diameter of the esophagus.

The digestive tract probably had a complex musculature associated with it. Ventral dilator muscles (vdm, Figs. 8, 9) took origin at least on the first post-frontal bar (b_1) and inserted on the region of the esophagus adjacent to the mouth cavity. A complex of muscles, including hypothetical frontal dilator muscles (fdm, Figs. 8, 9) probably extended from the exoskeleton and endoskeleton to the esophagus and stomach. The stomach is surrounded circumferentially by a complex of muscle fibers. Likely, it was to an extent developed as a triturating crop, though denticles have not been found in it.

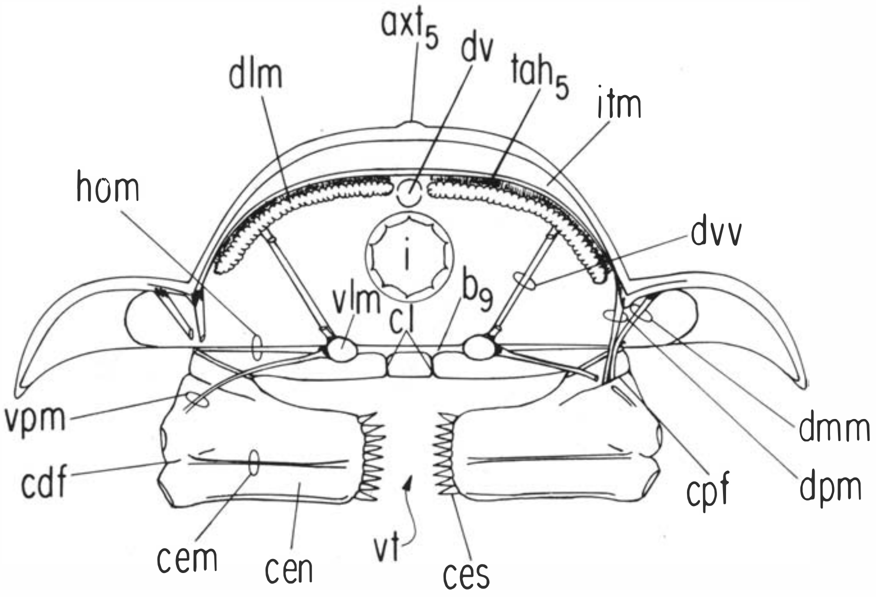

Fig. 7. Anterior view of the posterior half of the fifth thoracic segment showing the musculature, the dorsal vessel (dv), and the intestine (i). Only the coxae of the paired limbs are shown.

Highly ramified caeca (cca) are present in the genal regions and lateral glabellar regions of the head. Large ducts have been identified within the caecal mass, but these have not been observed to connect to the gut. Most likely, such glandular ducts would have arisen at the junction of the stomach and intestine and, owing to spatial limitations imposed by the musculature, would have passed laterally outward through the first postoral segment (C_1). No indications of division of caeca into segmental masses have been found.

DISCUSSION. – The numbers of specimens in which the various elements of the digestive system have been found among the 68 specimens intensively studied are as follows: esophagus (30), ventral dilator muscles of esophagus (2), stomach (20), intestine (44), caeca (11). The esophagus (e) is shown in MCZ 7190/18 (Fig. 4) and in YPM 228 (Pl. 1:1, Fig. 11), where a ventral dilator muscle (vdm) and endoskeletal bars (fb, b) are shown in relation to it. The posterior part of the intestine (i) is shown in YPM 28264 (Pl. 2:1, Fig. 13). Specimen MCZ 7190/15 (Pl. 2:2) shows the intestine extending from the thorax through the abdomen to the anus. The cloud of fine particulate material behind the specimen can be seen to emanate from the anus. It evidently represents gut contents squeezed out during post-mortem compression of the body.

REMARKS ON THE FEEDING MECHANISM. – Several lines of evidence indicate that *Triarthrus* had a trunk limb feeding mechanism of the same general sort found in particle feeding cephalocarid, branchiopod, and phyllocarid crustaceans. First, the trilobite evidently fed on such material. Even in the largest specimens, the esophagus and anus are only a fraction of a millimeter in diameter. The weakly developed masticatory mechanism would not seem suited for breaking down large food items. Squeezed out gut contents, seen in two specimens, reveal only fine particulate material. Second, *Triarthrus* has a food groove, an integral part of trunk limb feeding mechanisms (except perhaps in notostracan branchiopods). Moreover, the food groove is lined with deep, setose endites as it is in cephalocarid and phyllocarid crustaceans. This particular conformation is associated with mechanical transport of collected material on endites (Cannon 1927, 1933; Sanders 1963). Paired food transport chambers dorsal and lateral to the limb bases as depicted by Bergström (1969) are not developed in *Triarthrus*.

Though the occurrence of a food groove would seem to leave little doubt as to how food material was transported to the mouth once it was collected in the midventral space, it does not elucidate the problem of how the distal parts of the limb, the exite in particular, might have functioned in generating a feeding current. The coxa in *Triarthrus*, which bears a striking resemblance to the blade-like protopod of cephalocarid crustaceans, might likewise have produced a feeding current in its immediate vicinity with metachronal movement of the limbs (cf. Sanders 1963, Cannon and Manton 1927 describe the principle of this mechanism, a peristaltic paddle pump). Unfortunately, there is no close analogue for the trilobite exite among crustaceans or other modern arthropods. It can only be said that the exite, which was rather stiff and rigidly attached to the coxa, is different in form and deployment from exites in cephalocarid and

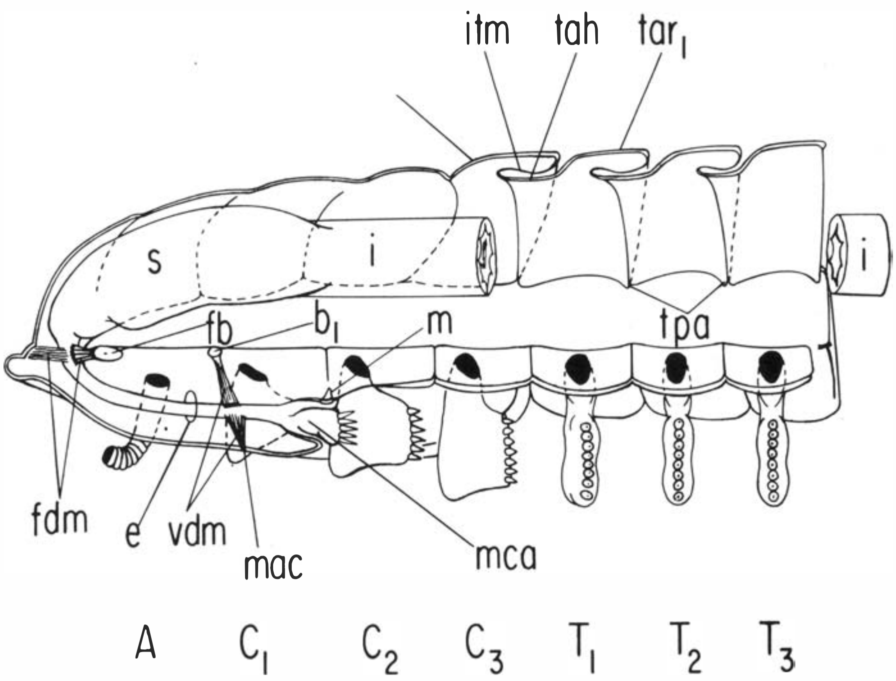

Fig. 8. Interior view of the head and first three thoracic segments showing the digestive tract and related musculature. Only the coxae of postoral limbs are shown.

phyllocarid crustaceans and must have produced different fluid mechanical effects. Study of working models would seem to offer the only hope for solving this problem.

The endites of head limbs are developed as parts of a masticatory mechanism. From posterior to anterior, the axes of swing of the coxa-body articulations shift from transverse to oblique in nearly horizontal planes (cf. Cisne 1973 MS). As a consequence, paired head endites should have moved forward and together on the forestroke in a weak biting action. The first endite pair (C_1) should have pressed inward on food masses between them in pressing masses forward into the mouth cavity. It is quite possible that the metastoma, like paragnaths in crustaceans, served as a body against which this pair of endites acted in comminuting food. Yet the trilobite's gnathobasic masticatory mechanism would seem to be weakly developed. Development of a suctorial foregut and perhaps a triturating stomach would seem consistent with such a masticatory mechanism.

COMPARATIVE ARTHROPOD ANATOMY

Tagmatization

GENERAL. – Four body tagmata can be recognized in *Triarthrus.* Distinctions between them are slight and are drawn primarily along discontinuities in the development of the tergal exoskeleton. The head bears a fused tergum, but the thorax bears articulated tergites. The pygidial abdomen bears a fused tergum, but the post-pygidial abdomen lacks such strong sclerotization of its dorsal exoskeleton. The most distinct division of the body is between head and trunk. But even this lies across gradients in structure and so is less distinct than it might appear. Elements of the skeletomusculature show a high degree of serial homology among all limb-bearing segments and present continua that bridge discontinuities in the development of the exoskeleton. Dorsal and ventral longitudinal muscles and the ventral endoskeleton occur in all limb-bearing head and thoracic segments (Figs. 5, 6). The same set of dorsoventral muscles occurring in thoracic segments is repeated in the two posterior head segments (Figs. 5, 6). Head and trunk limbs are quite similar in basic structure, and gradation in the development of the coxa (Fig. 3) makes the differentiation between head and trunk limbs in part gradational.

It has long been appreciated that trilobites correspond to a very primitive grade in tagmosis (e.g., Lankester 1904a, b). Trilobites would in fact appear to come close to the hypothetical condition of an arthropod ancestor having all postoral segments built on the same pattern. The degree of serial homology found in *Triarthrus* is unparalleled among modern arthropods. Even onychophorans, the most primitive living arthropods, have the three head segments much more strongly differentiated among themselves and from trunk segments (cf. Manton 1937).

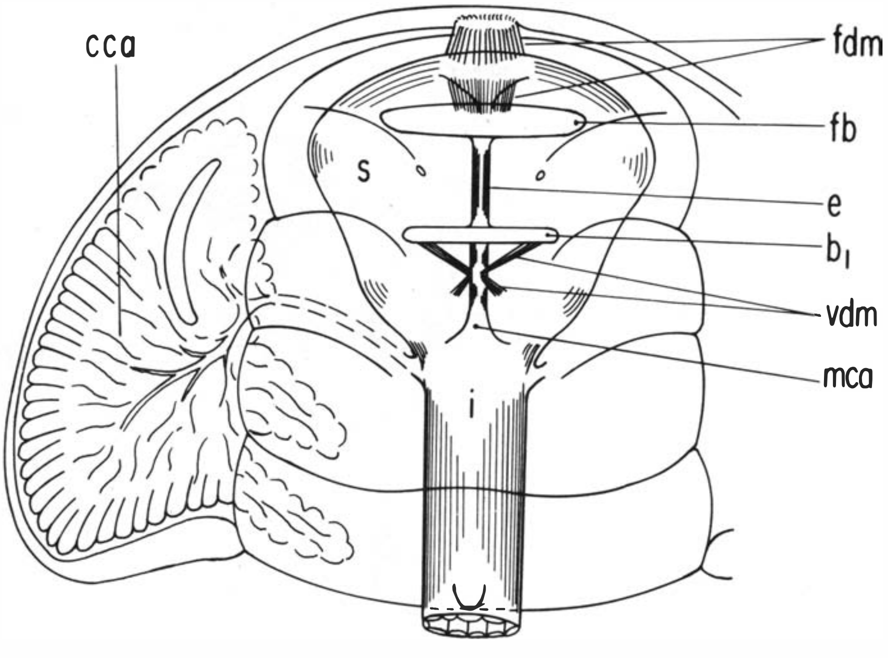

Fig. 9. Dorsal view of the head showing the digestive tract, related musculature, and caeca (cca).

As pointed out by Tiegs & Manton (1958), the multisegmented trilobite pygidium represents a tagma unique among arthropods, unique in that it usually maintains its integrity as a tagma composed of a fixed number of segment through the course of meraspid development. The meraspid transitory pygidial region appears to represent a zone of gradation in ontogenetic development through which segments passed in going from the zone of segment formation adjacent to the telson to their final locations in the thorax or abdomen of the holaspis. The pygidial abdomen would seem to persist in the adult as a relict of earlier ontogeny once the process of segmental addition stopped. In *Triarthrus,* the pygidial abdomen remains as a zone of transition in the development of the tergal exoskeleton between the sclerotized, jointed tergites of the thorax and the little sclerotized segmental rings of the post-pygidial abdomen. At least for more primitive, micropygous trilobites like *Triarthrus,* the concept of the pygidial abdomen as a tagma reflecting a gradient in ontogenetic development of segments helps explain two riddles of trilobite structure: why this tagma should remain so stable through the course of ontogenetic development, and why trilobites of the same or closely related species should have very similar pygidia despite differences in the holaspid number of thoracic segments. This number varies from population to population in *Triarthrus eatoni* (Cisne 1973a).

HEAD STRUCTURE. – Head structure is the primary basis for classification of arthropods at the superclass level (Lankester 1904a; Manton 1969). Trilobites have a head structure that sets them apart from modern superclasses. Discounting a possible pre-antennal segment, which would be the apparent homologue of the pre-antennal segment in crustaceans, myriapods, and hexapods, and of the pre-cheliceral segment in chelicerates (cf. Manton 1949, 1960), trilobites appear characteristically to have had a head comprised of four segments, a unique number. Crustaceans, myriapods, and hexapods have five head segments, again discounting the pre-antennal segment. In contrast to trilobites, two of these segments are anatomically preoral in the adult. Chelicerates have the prosoma, their head region, composed of seven limb-bearing segments. Like trilobites, they have a single anatomically preoral segment. But it bears a chelicera, not an antenna. The weakly developed masticatory mechanism in *Triarthrus* shows no particular anatomical similarities to mandibular mechanisms in crustaceans, myriapods, and hexapods, nor to masticatory mechanisms in chelicerates. It seems to be specialized in no one direction.

Limb structure

At the highest levels of classification, fundamentals of limb structure divide the Arthropoda into two groups. Tiegs & Manton (1958) noted the distinction between the Onychophora-Myriapoda-Hexapoda, which have a primitively uniramous limb, and the Trilobita, Chelicerata, and

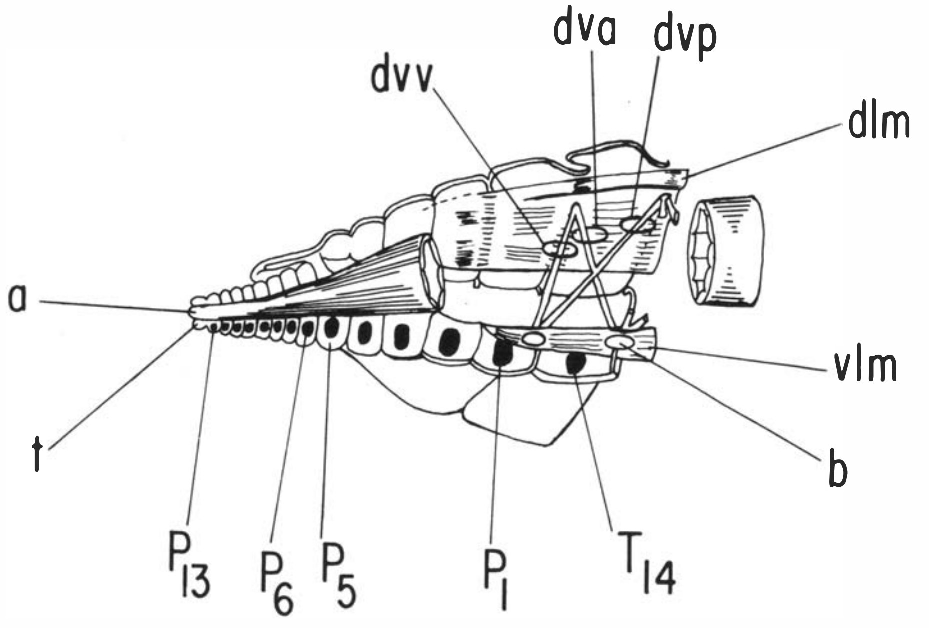

Fig. 10. Interior view of the last thoracic segment and the abdomen showing the body musculature and the intestine (i). The limbs and their extrinsic musculature are omitted.

Crustacea, which were then thought to all have a primitively biramous limb. Manton (1972) named the Onychrophora-Myriapoda-Hexapoda the Uniramia in recognition of this one of their characteristics. Most recently, Hessler & Newman (1975) demonstrated the probably triramous structure of the archetypal crustacean limb. Several times, and in several ways, the triramous limb has come to be simplified to biramous structure.

In the past, much has been made of limb structure as a basis for classification of class-level arthropod groups. More recently, it has emerged that the general homology of corresponding limb segments between members of different superclasses (e.g., between malacostracan crustaceans and insects) is an illusion (Tiegs & Manton 1958). There is no a priori reason to assume that trilobite limb structure must conform to the pattern found in one or another modern superclass.

The postoral limb in *Triarthrus* (Fig. 3) indeed presents an unusual combination of features. In the shape of the coxa and somewhat in the ambulatory-type of the telopod, the limb is quite reminiscent of the trunk limb in cephalocarid crustaceans. But it has a biramous, rather than triramous, structure. Størmer (1933, 1939, 1944, 1951) pointed out that the trilobite exite is more like the gill exites in the chelicerate *Limulus* than it is like crustacean exites. It is most unusual that the trilobite telopod contains seven segments. To attempt to draw homologies with telopod segments in modern arthropods, it is necessary to assume that at least two of these segments represent parts of secondarily divided podomeres, for no more than six telopodal podomeres occur among modern forms (Snodgrass 1952). In the absence of detailed knowledge of the intrinsic limb musculature, the external anatomy of the telopod can be interpreted equivocally as regards segmentation. In having relatively many telopodal segments, trilobites would appear to be more similar to chelicerates than to crustaceans. Pycnogonids, chelicerate allies that have the trochanter secondarily divided, are almost alone among modern arthropods in having seven freely articulated telopodal segments, just as in trilobites. While limb structure remains as a feature to be explained in making phylogenetic interpretations, it does not appear to provide solid evidence linking trilobites to any one of the major modern groups.

The postoral limb in *Triarthrus* clearly does not conform to the pattern of the trilobitan limb as reconstructed by Størmer (1939, 1944) in having the exite inserted medially on the coxa, in having a large coxal endite, and in lacking a clearly defined precoxa. This finding raises doubts as to the validity of the trilobitan limb as a feature uniting a group so inclusive as the Trilobitomorpha of Størmer (1944).

Skeletomusculature

The skeletomusculature of *Triarthrus* is built on the same basic pattern found among primitive crustaceans. Hessler (1964) demonstrated the existence of a common plan for crustacean skele-

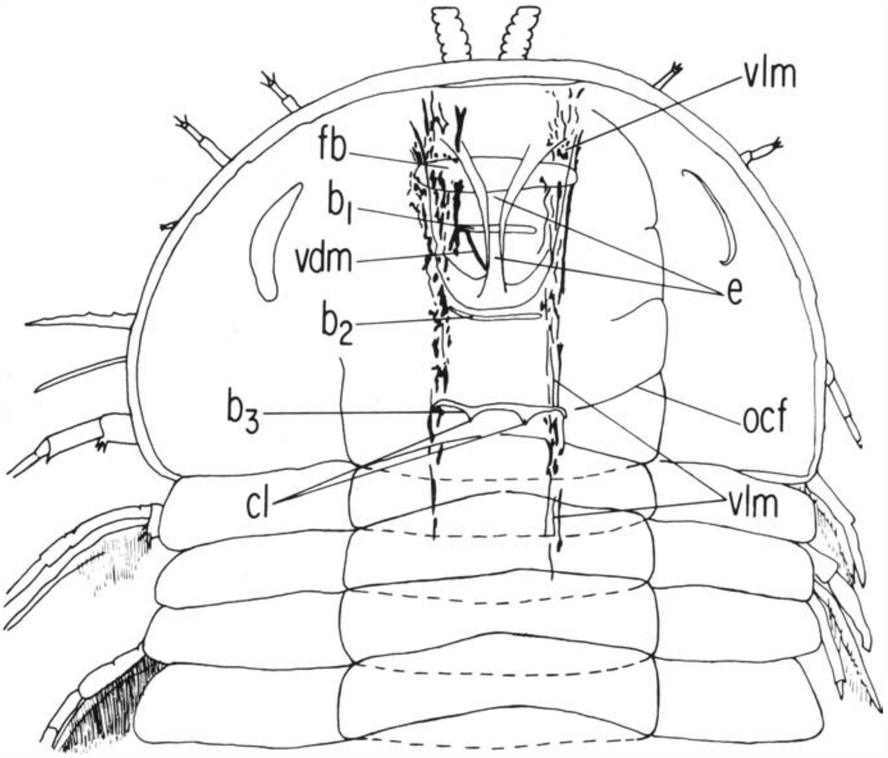

Fig. 11. Ventral view of the anterior part of YPM 228 (Pl. 1:1) showing tips of postoral limbs, showing the ventral longitudinal muscle (vlm), endoskeletal bars (fb, b) and a ventral dilator muscle (vdm) of the esophagus (e), and showing connecting ligaments (cl) of the third post-frontal bar (b_3). The figure is a tracing from an enlargement made on film.

tomusculature, a plan seen in its most primitive form among cephalocarids, branchiopods, and phyllocarid malacostracans. As in crustaceans, the ventral skeletomusculature is serially arranged. The endoskeleton consists of a ladder-like series of bars, not a series of endophragms as in many myriapods (cf. Manton 1961, 1965), and not a radially arranged endosternite as in chelicerates (cf. Lankester 1885, 1904b). The similarity in thoracic musculature between *Triarthrus* and the cephalocarid *Hutchinsoniella* is striking (compare Figs. 5–7, 10 with Hessler 1964, Figs. 1–5). In both cases (and in notostracan branchiopods as well), the dorsal longitudinal muscles form a sheet of parallel fibers along the top of the body cavity, and the ventral longitudinal muscles fall into paired bundles, segmental blocks of which are inserted end to end on endoskeletal bars. Horizontal muscles are present in both. The dorsoventral muscles fall into the same pattern, a box truss in each segment. The phylogenetically important similarity here is not simply in the fact that the basic elements of the skeletomusculature are very similar but in the fact that the entire body mechanical systems are basically the same. Dorsoventral muscles conforming to the pattern of a box truss are, for example, also found in geophilomorph chilopods, but in an otherwise much different body musculature (cf. Manton 1965).

The principal differences between *Triarthrus* and *Hutchinsoniella* are related to the much lower degree of cephalization in the trilobite. One more segment is present in the cephalocarid head, and the individual segments are much more strongly modified over the pattern of trunk segments. In particular, the endoskeleton of the three postoral segments is fused into a ventral cephalic tendon, which is the endoskeletal foundation for the mandibulate and caridoid conditions. Unlike *Hutchinsoniella, Triarthrus* has the endoskeleton continuing into the preoral part of the head. Though it is unusual among crustaceans, the anostracan branchiopod *Eubranchipus* has a preoral endoskeletal bar (study of Hessler's undescribed sections).

Digestive system

Crustacea and Chelicerata are distinguished from Uniramia in having, primitively, a posteriorly directed mouth and in having an often extensive prolieration of digestive glands in the head region (Tiegs & Manton 1958; Manton 1972, 1973). In the development of the digestive system, trilobites are clearly more similar to crustaceans and chelicerates than to uniramians.

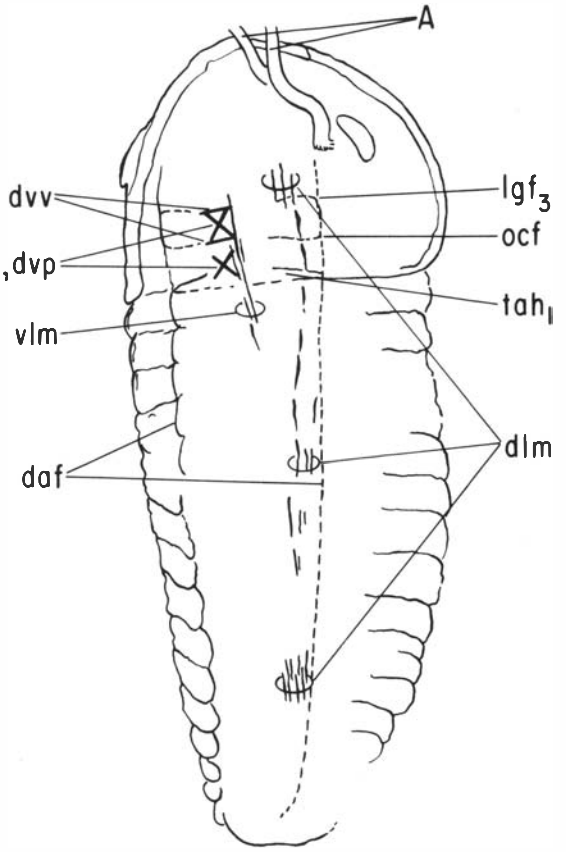

Fig. 12. Ventral view of YPM 204 (Pl. 2:2) showing the dorsal and ventral longitudinal muscles (dlm, vlm) and dorsoventral muscles (dva, dvp, dvv) and their relationship to the third lateral glabellar furrow (gf$_3$) and occipital furrow (ocf). The figure is a tracing from an enlargement made on film.

Feeding mechanism

MASTICATORY MECHANISM. – Crustacea and Chelicerata are distinguished from Uniramia in having gnathobasic, rather than whole-limb, masticatory mechanisms (Manton 1964, 1972). Taking *Triarthrus* as representative for the group, trilobites have a gnathobasic mechanism developed among postoral head limbs.

FOOD COLLECTION MECHANISM. – Trunk limb mechanisms for particle feeding set primitive crustaceans apart from chelicerates, which have much different mechanisms for predaceous feeding, and from uniramians, which have direct mandibular mechanisms (Cisne 1973 MS, Manton 1973). Such mechanisms are quite conservative in their basic features among cephalocarid, branchiopod, and phyllocarid crustaceans (Sanders 1963). Likely, the occurrence of this mechanism underlies the conservatism in trunk musculature among these crustaceans (cf. Hessler 1964). Hence the presence of a trunk limb feeding mechanism in *Triarthrus,* or at least the presence of some of the anatomical features associated with one, would seem to be an important feature linking trilobites and crustaceans (cf. Hessler & Newman 1975).

Development

The ontogenetic development of trilobites is primitive in that it is (so far as can be told) very gradual and in that it includes an early-hatching larva (cf. Whittington 1957, 1959). Interestingly enough, the life history of *Triarthrus* was divided into a pelagic larval and juvenile phase and a probably nektobenthic juvenile and adult phase despite gradual and continuous development (Cisne 1973a).

Though little is known of its anatomy, inferences from adult anatomy suggest that the trilobite protaspis was a primitive and distinctive larva. It included at least the complement of segments present in the adult head. It is a reasonable guess that the four pairs of head limbs were present in non-rudimentary form. The crustacean nauplius, in contrast, includes at least three non-rudimentary segments bearing limbs. From the outset, the second antenna and mandi-

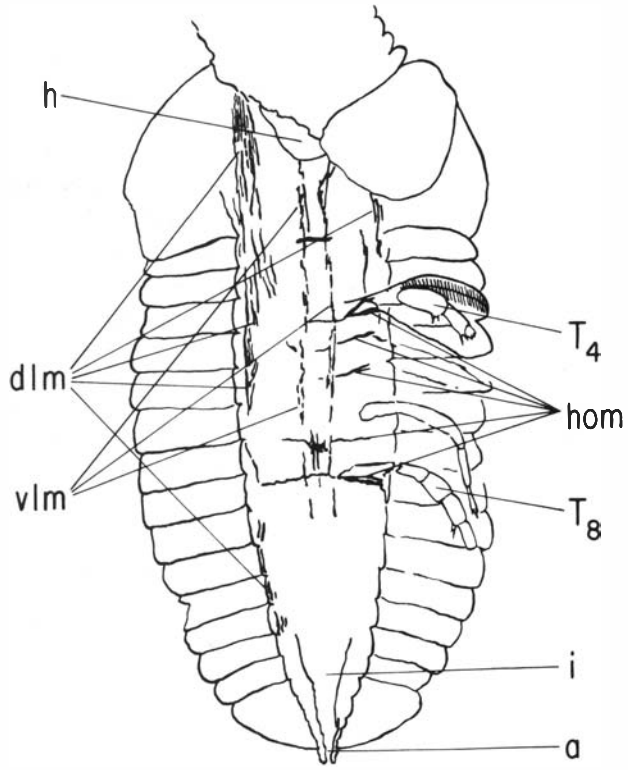

Fig. 13. Ventral view of YPM 28264 (Pl. 2:1), showing the dorsal and ventral longitudinal muscles (dlm, vlm), endoskeletal bars (unlabelled) linking the paired bundles of ventral longitudinal muscles, horizontal muscles (hom), and the intestine (i). The figure is a tracing from an enlargement made on film.

bles are differentiated in form and function. Beecher (1895b) and Garstang & Gurney (1938) regarded the nauplius as a specialized larval type and suggested it to be derived from a protaspis-like form. The naupliar net-sweep feeding mechanism is one obvious specialization (Gauld 1959). As a very primitive feature, this larval feeding mechanism may be retained in the adult (Cannon 1933; Sanders 1963). Yet there are no indications from adult anatomy that *Triarthrus* had a feeding mechanism different in principle from the trunk limb mechanism of the adult. Perhaps the protaspis had this sort of mechanism developed among both head and trunk limbs. Otherwise, the protaspis bears little resemblance to the bizarre protonymphon larva of pycnogonids, the only other early-hatching larva among modern arthropods.

Adult trilobites bear certain very interesting similarities to crustacean nauplii. Garstang & Gurney (1938) pointed out their similarity in having only one preoral segment. The resemblance between the adult *Triarthrus* and late naupliar *Hutchinsoniella* is striking (compare Fig. 2 with Sanders 1963, figs. 23, 24). Not only is the second antenna postoral, and not only does it bear a naupliar enditic process like the first postoral limb in the trilobite, but the mandibles and first and second maxillae all conform to the pattern of trunk limbs.

Størmer (1944) listed the presence of four primary segments in the embryo of *Limulus* as a phylogenetically important similarity to what he took to be the four postoral head segments in trilobites. Certainly this similarity may be important, but not exactly for the reasons he stated. First, the four primary segments in *Limulus* probably correspond instead to the four limb-bearing head segments in trilobites, including the antennal segment. Second, primary and secondary segments are not fundamentally different as thought by Iwanoff (e.g., 1933) and Størmer (1944, 1951) (cf. Manton 1949). Rather, the phenomenon of heteronomy of segments in embryos undergoing direct development, such as the embryo of *Limulus,* probably reflects the presence of a small, early-hatching larva in antecedent phylogenetic stages (Manton 1949). While it is significant that *Limulus* has one more primary segment than crustaceans, it is quite conceivable that four-segmented larvae evolved among chelicerate ancestors independent of the evolution of the trilobite protaspis.

RELATIONSHIPS OF THE TRILOBITA

The Trilobita are distinguished from members of other arthropod superclasses by the presence of antennae on the single limb-bearing preoral segment and by the presence of three postoral head segments bearing biramous limbs little differentiated from those of the trunk which together served in a gnathobasic masticatory mechanism. A trilobate tergal exoskeleton and a distinctive biramous postoral limb are characteristic of the group, and a multisegmented pygidium is characteristic of all but certain olenellids. Beecher (1897) pointed out the necessity and the dangers of generalizing from a few well known species in the attempt to categorize the Trilobita.

These characteristics could be used as a basis for erecting the Trilobita as a superclass. However, this would not seem prudent in the present state of knowledge. Characterization of the modern arthropod superclasses is based on features that have remained phyletically conservative through later Phanerozoic time. There is no assurance that these features were really so conservative during the initial adaptive radiations of arthropods early in the Paleozoic. Many of the Burgess Shale arthropods, for example, would seem to represent evolutionary experiments on basic patterns of head tagmatization. The fossil record provides no assurance that the major modern groups were really so discrete in the Cambrian. Moreover, Burgess Shale arthropods suggest that the major modern groups formed only parts of what then was a more continuous spectrum (cf. Tiegs & Manton 1958; Hessler & Newman 1975. Consequently, different criteria may have to be developed for a phylogenetic classification of primitive Early Paleozoic arthropods. But first, more detailed knowledge of these forms is necessary. In the future, it may emerge that the Trilobita would best be ranked as a class within some larger category that is not now possible to clearly define.

Because the Trilobita are a very primitive group, the question of their relationships takes on especial importance with regard to the current problem of the monophyletic versus polyphyletic origin of the Arthropoda. Contrary to the traditional view, Tiegs & Manton (1958) and Manton (e.g., 1964, 1972) proposed that the Uniramia, Crustacea, and Chelicerata each originated from ancestors which were not themselves arthropods. But because the anatomy of trilobites has been so incompletely known, it has not been practical to approach the question of their relationships in the neontological terms of current work on arthropod phylogeny.

Through the work of Størmer (1933, 1939, 1942, 1944, 1951), it has come to be generally accepted that trilobites and chelicerates are rather closely related. Chelicerates probably arose through adaptation of a primitively trilobite-like body plan for predaceous feeding. Despite differences in feeding adaptations, the two groups have the same number of anatomically preoral limb-bearing segments, though there is some question as to the homologies of the cheliceral segment (cf. Manton 1949, 1960, Bullock & Horridge 1965). The principal change in going from the trilobite condition to the chelicerate condition would be the formation of the prosoma through fusion of three additional segments to the trilobite head and through modification of cephalized segments around the endosternite, the endoskeletal foundation of the locomotory and feeding mechanisms. Størmer (1939, 1944) has shown how chelicerate limbs can be derived from trilobite limbs. A series of large coxae as found in *Triarthrus* would seem to represent a generalized condition from which the masticatory apparatus of *Limulus* could readily be derived (cf. Manton 1964). Aglaspids, perhaps the most primitive known chelicerates, provide a link between trilobites and more specialized modern forms. Raasch (1939) demonstrated ambulatory-type opisthosomal telopods in an aglaspid, a trilobite-like feature known in no modern chelicerate. Had not Raasch (1939) also demonstrated a chelicera and five pairs of prosomal telopods, some aglaspids could almost be taken for abherrant trilobites. The Burgess Shale arthropod *Sidneyia* also combines features of trilobites and chelicerates (Bruton in preparation).

Hessler & Newman 1975 convincingly argue that the crustacean ancestor was a trilobitomorph. Indeed trilobites are more similar in anatomy and ecology to primitive crustaceans than to chelicerates. So strong are the similarities that it would be much more interesting to argue their meaning in terms of relative closeness of relationship of Trilobita to either Cephalocarida-Malacostraca or Branchiopoda than in terms of profound convergence. Derivation of the cephalocarid condition from the condition represented in *Triarthrus* follows directly along the lines of the general evolutionary trend toward progressive specialization and tagmatization of segments (cf. Lankester 1904a). The essential changes are: (1) movement of an additional segment to an anatomically preoral position in the adult, (2) fusion of an additional segment to the head posteriorly, and (3) progressive serial differentiation of the resultant set of three postoral head limb pairs to conform to a steeper morphological gradient terminated anteriorly by mandibles. These changes would convert any generalized trilobite to a very primitive, generalized crustacean. Cephalocarids conform beautifully to the expected result. In *Hutchinsoniella,* the second antenna, postoral in the nauplius, remains at the side of the mouth in the adult, much as does the first postoral limb in *Triarthrus* (Sanders 1963). The second maxillary segment, the new segment fused to the head, conforms in many ways very precisely to the pattern of trunk segments (Sanders 1963, Hessler 1964). The derivation conveniently explains why the second maxilla should be virtually identical with trunk limbs, which is perhaps the most obvious feature distinguishing cephalocarids as the most primitive living crustaceans (Sanders 1955). As noted, postoral head limbs in naupliar *Hutchinsoniella* are structurally graded, and all conform to the pattern of trunk limbs. With continued development, the morphological gradient among them steepens, and the larval mandible progressively takes on its adult form as a palpless mandible (Sanders 1963, Hessler 1964). Otherwise, differences in limb structure can be resolved by supposing that both cephalocarid and trilobite limbs were derived by reduction and specialization of a more complex, multiramous archetype. Sanders (1963) has shown how such derivations may have taken place in going from primitive to complex crustacean limbs.

The phylogenetically important similarities that trilobites share with crustaceans and chelicerates suggest that the three groups shared a common ancestry from forms not unlike trilobites. The Trilobita provide a link at a very primitive organizational grade between the Crustacea and Chelicerata, two superclasses that are in the present quite distinct. It is possible to characterize the Trilobita-Crustacea-Chelicerata as a group united by these features: (1) a single anatomically preoral limb-bearing segment in the free-living larva if not in the adult, (2) a primitively multiramous limb, (3) primitively, a posteriorly directed mouth, (4) often extensively proliferated digestive glands in the head region, and (5) a gnathobasic masticatory mechanism. However, the Trilobita-Crustacea-Chelicerata is probably only an approximation to a still larger group including a variety of other primitively marine arthropods such as many trilobitoids and pycnogonids.

Though the Trilobita occupy a very primitive organizational grade, they show none of the features of the Uniramia. There is thus revealed a dichotomy between the Trilobita-Crustacea-Chelicerata and the Uniramia. Except for the marine Protonychophora, this dichotomy closely corresponds to the division between primitively marine and primitively terrestrial arthropods. A common ancestor for the two groups would have to combine the minimal arthropodization of an onychophoran (cf. Manton 1965) with the minimal degree of segmental differentiation of a trilobite. The protonychophoran *Aysheaia* comes close to meeting these requirements (cf. Hutchinson 1930, 1969). Yet even at this grade, the Uniramia would be distinguished in having a uniramous limb, a subterminal mouth, and a whole-limb masticatory mechanism and in lacking extensive digestive glands (Manton 1972). Perhaps these fundamental differences indicate an essentially diphyletic origin for the Arthropoda. On the other hand, perhaps quintessentially primitive arthropods, forms which might not have been unlike *Spriggina* of the Ediacara fauna, bridged this gap.

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Abbreviations

A	antenna/antennal segment
a	anus
axt	axial tubercle
b	post-frontal endoskeletal bar
C	postoral head limb/postoral head segment
cca	caeca
cdf	coxal distal furrow
cem	coxal enditic muscle
cen	coxal endite
ces	coxal enditic seta
cl	connecting ligament
cpf	coxal proximal furrow
dam	dorsoanterior extrinsic limb muscle
dlm	dorsal longitudinal muscle
dmm	dorsomedial extrinsic limb muscle
dpm	dorsoposterior extrinsic limb muscle
dv	dorsal vessel
dva	anteriorly descending dorsoventral muscle
dvp	posteriorly descending dorsoventral muscle
dvv	ventrally descending dorsoventral muscle
e	esophagus
fb	frontal endoskeletal bar
fdm	frontal dilator muscle of esophagus
h	hypostoma
hom	horizontal muscle
i	intestine
itm	intertergal membrane
lgf	lateral glabellar furrow
m	metastoma
mac	macula
mca	mouth cavity
ocf	occipital furrow
P	abdominal limb/abdominal segment
s	stomach
T	thoracic limb/thoracic segment
t	telson
tah	thoracic articulating half ring
tar	thoracic axial ring
tpa	tergal posterior apodeme
vam	ventroanterior extrinsic limb muscle
vdm	ventral dilator muscle of esophagus
vlm	ventral longitudinal muscle
vpm	ventroposterior extrinsic limb muscle
vt	food groove

EXPLANATION OF PLATES

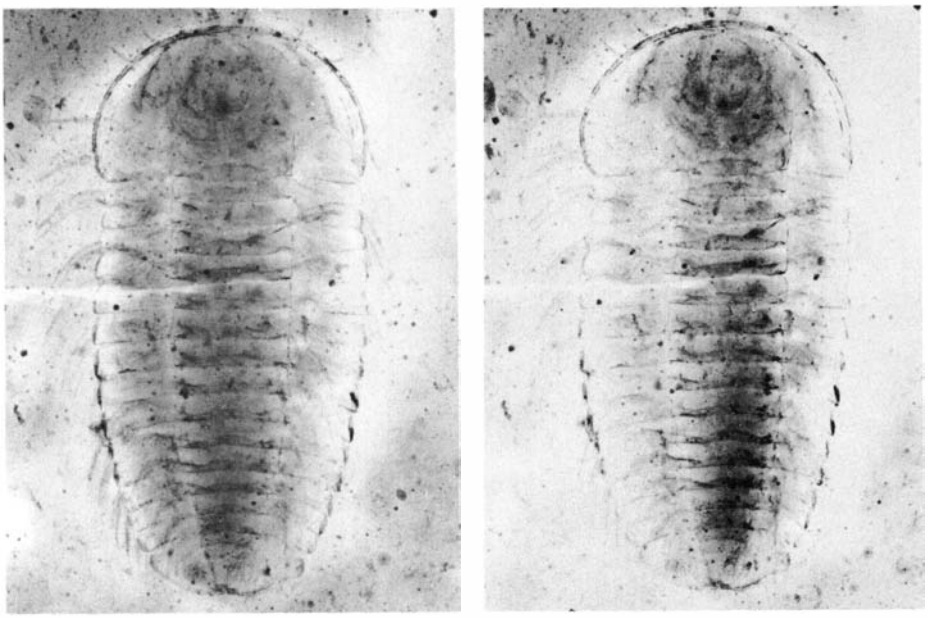
Stereoscopic radiographs of *Triarthrus eatoni* (Hall).

Plate 1

Fig. 1. Ventral view of YPM 228 (Fig. 11). x1.94. Fig. 2. Ventral view of YPM 204 (Fig. 12) x3.42.

Plate 2

Fig. 1. Ventral view of YPM 28264 (Fig. 13). A small individual lies across the front of the head. x2.36. Fig. 2. Ventral view of MCZ 7190/15. x3.28.



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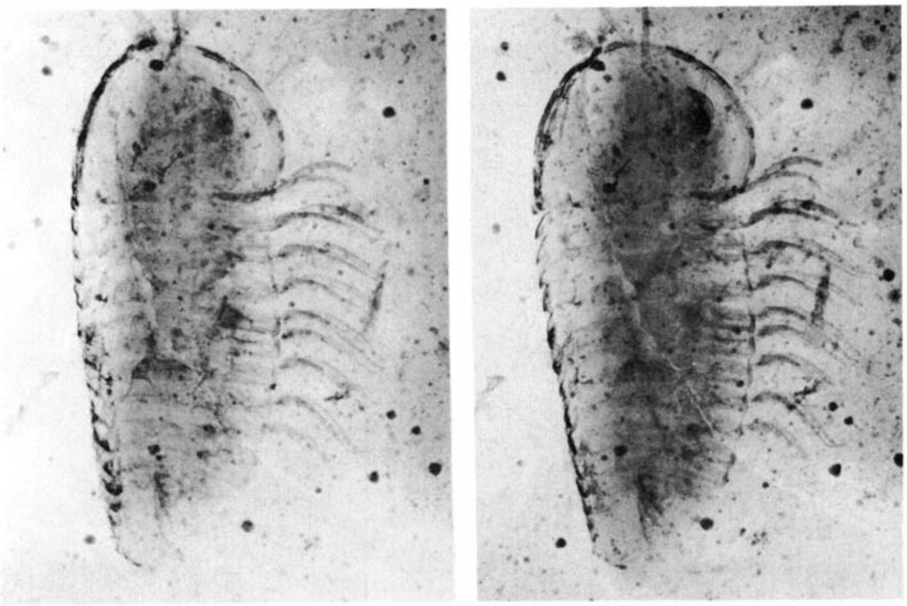

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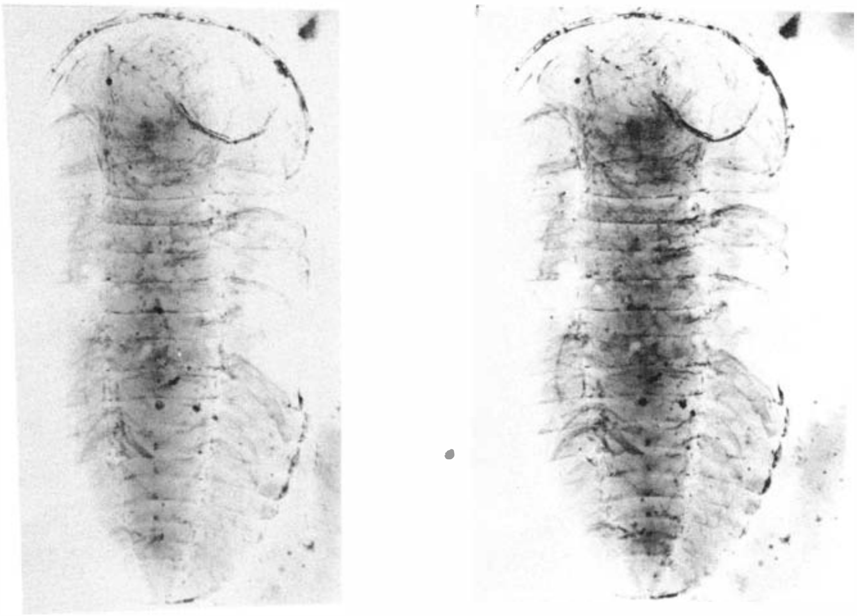

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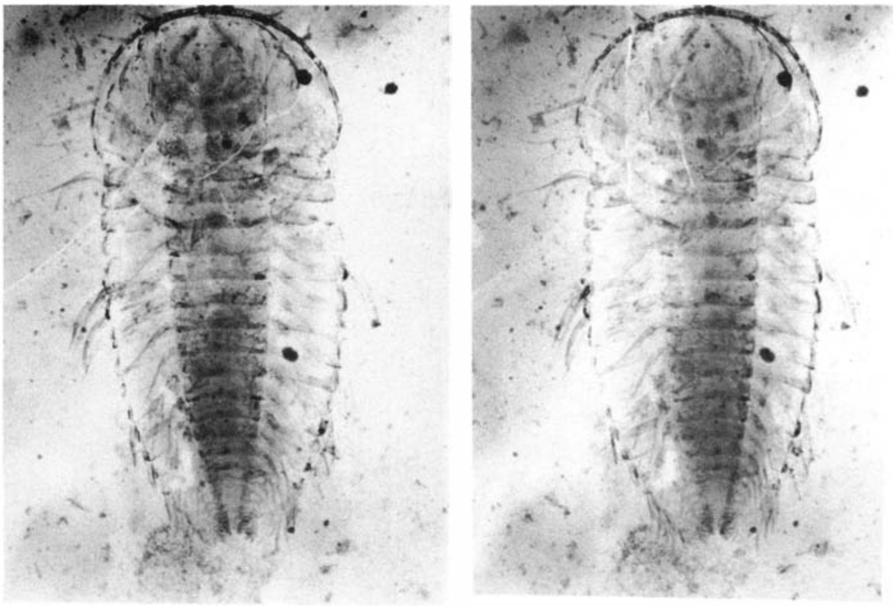

2

The functional morphology of *Cryptolithus*

KENTON S.W. CAMPBELL

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Details of the exoskeleton of *Cryptolithus* are listed and commented upon, using *C. tesselatus* (Green) and *C. bellulus* (Ulrich) as the prime sources. Features important for the functional interpretation of the organism, but tending to be missed in taxonomic work, are emphasised. Trace fossils produced by various species of the genus are examined in detail. Using a stated system of interpretation, the soft tissues of the animal are reconstructed. Then an attempt is made to describe the morphology in functional terms.

The main conclusions reached are as follows. (1) The animal was a benthonic mud feeder. (2) It was able to burrow vertically with both telepodites and exites, to produce detritus for feeding. (3) The animal did not plough its head into the sediment, but either burrowed backwards or made discrete, partly overlapping burrows. (4) The numerous appendages on the pygidium kept detritus in suspension behind the burrows and also increased the area of the respiratory surfaces. (5) The bulbous glabella contained an enlarged stomach. (6) The space between the upper and lower lamellae of the cephalic fringe was filled with large digestive glands supplied with blood from a marginal artery, and drained by a venous sinus lying in the cavity formed by the girder. (7) The thorax and pygidium were strongly articulated and capable of being outrolled rapidly by a highly developed trunk musculature. (8) Locomotion was by walking and a limited amount of swimming with the aid of both the appendages and movement of the pygidium and thorax. (9) The animal was stable in currents directed from the front, but unstable in currents from other directions. (10) The fringe was a sensory receptor to indicate changes in current direction.

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Cryptolithus, and the trinucleid trilobites in general, have often engaged the attention of palaeontologists because of their bizarre fringes which catch the eye of collector and systematist alike. Much effort has been put into classifying the group and attempting to use it biostratigraphically. In addition, some remarkably preserved specimens that show unusual detail have come to light. The silicified material from Virginia (Whittington, 1959), the appendage-bearing individuals from New York (Beecher, 1895; Raymond, 1920), the moulds with the alimentary canal preserved (Beyrich, 1846; Barrande, 1852), and the trace fossils that can be definitely assigned to *Cryptolithus* (Osgood, 1970), have made it possible to prepare an analysis of the morphology and habits of the animal with a degree of confidence that is unusual for an organism from so remote a period. Despite this wealth of information the functional interpretations of different authors are anything but consistent, and no satisfactory interpretation of the most outstanding feature, the fringe, has ever been offered. The reason for the divergence of views is, in my opinion, the failure to attempt an analysis of the whole animal, most workers being concerned to interpret only one structure or set of structures – for example, the appendages or the fringe – at a time. Moreover there has been a tendency to ignore much of the unique morphology of the group in making interpretations.

In the following work, therefore, the distinctive morphological features of the genus *Cryptolithus* are set out *seriatim.* Then the observed features of the *Cryptolithus* trace fossils are listed. With these observational data as a basis, an attempt is made to reconstruct the soft anatomy in accordance with an explicit set of principles. Then, finally, the life habits of the animal are inferred.

SKELETAL MORPHOLOGY

The cephalon

(1) The cephalon is highly arched overall. In anterior profile there is a broad high arch in the anterior margin.

(2) The long genal spines do not continue the arch of the margin, but project downwards and backwards.

(3) The glabella is highly domed in both lateral and anterior profiles.

(4) The anterior (antennulary) pit is always well developed.

(5) The occipital apodeme and apodeme lp project ventrally as short pegs. The occipitals are closer together than the lp pair.

(6) There are no apodemes in front of lp, but there are three pairs of muscle scars. (In some genera, for example, *Tretaspis,* there is a pair of 2p apodemes.) These muscle scars, which are well figured by Whittington (1968, Fig. 1) decrease in size from rear to front. The most posterior scars are the largest and are placed dorsad of, and a little anterior to, apodemes lp. The next two pairs are also well up on the flanks of the glabella, high above the axial furrows.

(7) On the anterior slope in well preserved specimens there is a pair of faint ridges joining in front of the median tubercle to form a V. Anteriorly these ridges expand as they reach the anterior furrow where they join a similar ridge that appears to run anteriorly and laterally around part of the axial furrow (Whittington, 1968, Pl. 89: 1, 10).

(8) The occipital ring is short (sag. & exsag.), inclined markedly backwards, and projected into an occipital spine that is inclined at a low angle to the horizontal.

(9) There is a short, thick ventrad projection from the posterior edge of the occipital ring, but no true doublure (see Pl. 2: 12, 13).

(10) The pit pattern of the fringe is well described by several authors and it shows little intrapopulational variation. The details are not of consequence for functional work.

(11) The walls of the pits of the upper and lower lamellae are in contact, and at least on silicified specimens it is difficult to detect the contact (part of the facial suture). It is clear, however, that the bases of the upper and lower pits are not always in contact. Sometimes there is a narrow open annulus around the central capilliary (see Whittington, 1959, Pl. 21 : 17). This has also been confirmed by my observation of other silicified material.

(12) The inner edge of the lower lamella is not closely appressed to the dorsal exoskeleton, so that the gaps between the pillars forming the walls of the opposed pits open into the central space of the cephalon. Laterally, where the pits are smallest and most closely spaced, the inner edge of the lower lamella is frilled so that the size of the openings is maximised (see Pl. 2:10).

(13) The largest opening into the fringe is the most posterior one which is on the continuation of the posterior border of the cephalon. There, the inner edge of the lower lamella is slightly cut away to increase the size of the opening (see Pl. 2:11).

(14) Inside the girder the exoskeleton is not thickened, and hence that is the site of the largest concentric canal inside the fringe.

(15) Medially the inner part of the lower lamella stands very steeply and it is also slightly embayed (Whittington, 1959, Pl. 20: 1).

(16) Hypostomes are rare. The only ones known are small and only slightly sclerotised, Since the hypostomal suture must have been along the medial edge of the lower lamella, the hypostome must have been situated high up under the glabella.

The thorax

(1) The thorax is short, its length being approximately threequarters that of the saggital length of the cephalon.

(2) The axial rings are moderately arched and are clearly divided into four in dorsal view – a flat posterior band that is not quite as long as the doublure that underlies it, a higher and slightly longer main band, a well defined articulating furrow, and a short articulating half ring (see Pl. 2:1,6).

(3) The articulating half ring on the first segment is almost colinear with the leading edges of the pleurae in dorsal view, but its posterior edge cuts back between the inner edges of the apodemes, displacing the articulating furrow and the convex band backwards. The half rings on the more posterior segments do project in front of the line of the front edge of the pleurae.

(4) The pleurae on all segments are flat over most of their width, only the short distal extremity being downturned, and this not vertically, but at an angle of 40°–60° to the horizontal on most segments and 20°–30° on the first.

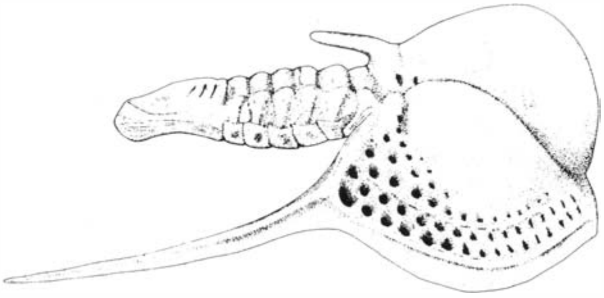

Fig. 1. Lateral view of a whole specimen, drawn from the individual figured on Pl. 2:7–9. Note the shape of the ends of the thoracic pleurae and the position of the cephalic muscle scars.

(5) The pleural furrow is deep and extends to the distal extremity. Put another way, the posterior band is strong, and forms a line with the convex part of the axial ring. However, the exoskeleton is thickened so that on the ventral surface of the pleurae the furrow and the pleural bands are much less clearly defined.

(6) The articulation at the axial furrows is complex. On the anterior edge of the segment, a large socket is flanked on each side by a short projection. On the posterior edge the large process is flanked by a corresponding pair of small sockets (Whittington, 1959, Pl. 21: 1–6, Pl. 2: 1–6 herein). The sockets are only about half filled by the processes. This arrangement is more complex than that of other trilobites which have either a simple process and socket, or an axial process and socket flanked on the inside by a ring process and socket (Whittington & Evitt, 1954; Bergström, 1973).

(7) Small fulcral processes are present and are opposed to much larger sockets.

(8) On the first segment the fulcral process is very tiny and it is opposed by a very faint socket *underneath* the posterior border of the cephalon (Pl. 2:11).

(9) The posterior edge of each pleura has a sharply defined straight articulating furrow between the axial furrow and the fulcrum. However, this furrow is situated *above* both the fulcral socket and the axial articulating process (Whittington, 1959, Pl. 21:6). This is unusual. Compare, for example, the specimens of *Lonchodomas* figured by Whittington (1959).

(10) On the posterior border of the cephalon this articulating furrow is just visible in posterior view. It lies on the downturned *postero-ventral* edge of the border, and like those of the subsequent segments, it lies *above* the line of the fulcral socket and the axial articulating process.

(11) The downturned pleural tips have an anterior process that articulates into a marked socket on the posterior of the next segmental tip. That is, one pleural tip is not able to swing inside that of the next segment but articulates into a slight cavity within it. The gap between process and socket is very small (Whittington, 1959, Pl. 21:5). Although Panderian notches are developed within the thoracic doublures, *those on successive segments do not engage one another to prevent further enrollment.*

(12) The facet on the first segment is modified. It has a large, slightly concave anterior face that fits against a special wide flange on the back of the cephalon (Pl. 2:4, 11–13). Its tip has a small anterior projection, but there does not appear to be a special pit to receive it on the under surface of the cephalon, though it could possibly move into one of the fringe pits.

(13) The downturned pleural tips form a continuous lateral wall to the thorax. The tips of successive segments are not rectangular in lateral view, but tend to be rhombic. Their anterior and posterior edges are curved to permit some relative movement during enrollment (Pl. 2: 8–9, Fig. 1).

(14) The apodemes are wide and high. At their inner extremities they have a slightly bulbous expansion that projects ventro-medially. The size of this expansion and the extent to which it projects increases on progressively more posterior segments. On the anterior segment the gap between their inner ends is about one-third of the total width of the axial ring, but on more posterior segments it is only one-quarter to one-fifth.

(15) In the antero-dorsal face of the apodeme there is a slight cavity. Joining these cavities is the flattened inner face of the articulating furrow.

(16) With the segments arranged so that the pleurae are coplanar, the anterior edge of the half ring lies a little behind the anterior edge of the doublure of the preceding segments.

The pygidium

(1) The axis is only moderately convex, and the pleural regions are flattened to slightly concave.

(2) The 'border' is downturned all round, and it bears characteristic terrace lines. There is no infolded doublure or only a very narrow shelf. This, together with the fact that the pleural furrows stop short of a border flange on the dorsal surface, suggests that the so-called border is really the doublure. It has a very characteristic shape. At its anterior extremity it is downturned about the same amount as the last thoracic pleural tip. It maintains this height laterally, but then increases to produce a pair of enlarged posterior lobes separated by a distinct emargination.

(3) The fulcral points are tiny and are situated almost at the lateral extremities.

(4) The axial articulating sockets are small and are also situated *below* the articulating line on the pleural edge.

(5) The first appendifer is like those of the thorax, though the expansion of its inner end is much smaller and does not project so far ventrad. The second and third appendifers are progressively further reduced and are inclined antero-medially. At the inner end of the third one, a small differentiated mound can be distinguished. Subsequent segments carry slight transverse elevations or muscle scars laterally, and small more equidimensional scars toward the axis. The axial rings arch forwards strongly, and consequently each medial scar is situated well in front of the corresponding lateral scar. Including the apodemes there are as many as sixteen pairs of muscle attachment on the pygidium.

The appendages

By courtesy of Dr. John Cisne, who is producing a detailed account of the material, I have been able to examine two X-radiographs of the appendages of *Cryptolithus bellulus* (Ulrich) from Beecher's trilobite bed in the Frankfort Shale of New York. These have been used to supplement, and to some extent correct, the description of the same material given by Raymond (1920).

(1) The uniramous antennules are usually preserved pointing backwards, and reach as far as the end of the thorax. Raymond (1920, p. 65–5, 70) comments that this does not necessarily indicate that they were incapable of being directed forwards. If the animals were preserved in a burrowing attitude, the antennules would necessarily be turned backwards.

(2) The telopodites of the thorax and pygidium were reasonably well known from Raymond's material. They are all strongly bent, sometimes through more than a right angle. The segments are distinctly compressed, and some of them give the impression of being almost blade-like. Some of the segments of the telopodites on the posterior segments of the thorax and on the pygidium are almost as wide as they are long. Each axial ring of the thorax probably had an associated pair of limbs.

Raymond was of the opinion that the telopodites were only slightly flexible, and the reconstruction of Bergström (1972, Fig. 2) certainly implies that they could not straighten. So far as I am aware, no straightened limbs have ever been observed. The radiographs show some limbs broadly flexed in the manner shown on Raymond's Fig. 20, and others geniculated at a segment about half way along the length of the limb. It seems reasonable to conclude that the normal relaxed shape of the thoracic and pygidial telopodites was the broadly arched position, that they were able to flex inwards to a large extent (which would be necessary for enrollment), but that they were incapable of straightening to increase the angle between their proximal and distal parts to more than 120°–130°.

(3) It is apparent that the telopodites on the first four thoracic segments were long, and had it been possible to straighten them and place them horizontally, they would have extended well beyond the line of the margin of the cephalon. Raymond's reconstruction has them too short. Behind the fourth segment, the telopodites rapidly decrease in length. Those on the pygidium are normally flexed, but if straightened out laterally would extend a little beyond the pygidial margin.

(4) The telopodites of the cephalon were poorly known from the material described by Raymond. I am unable to determine their number from the radiographs, but it is clear that there are at least three pairs of long limbs similar in form to the anterior ones of the thorax, though the most anterior ones may have been proximally directed antero-laterally and recurved at their tips.

(5) Exites were developed on all limbs. There is no evidence from the radiographs to support the view of Bergström (1972, 1973) that they formed a distal tuft set, with or without an abaxial set, nor is there any evidence of a terminal rake-like element. Filaments seem to be

borne along almost the whole length of a poorly defined branch. However, instead of the branch flexing backwards abaxially, as shown by Raymond, it seems to be directed laterally, and the filaments are directed posterolaterally throughout. The filaments are much longer than Raymond indicates, and in this regard are more similar to those figured by Bergström (1973, Fig. 15). On the cephalon the filaments extend about as far laterally as the girder; on the anterior thoracic segments they extend beyond the lateral extremity of the exoskeleton; and on the pygidium and the posterior part of the thorax, they lie within the lateral limits of the exoskeleton.

As regards orientation, the filaments seem to be preserved with those of successive limbs lying over one another in *en echelon* fashion. There is no evidence of how they were held with respect to a horizontal plane.

TRACE FOSSILS

Burrows

There are several references in the literature to trace fossils said to be made by trinucleids. The most convincing is that of Osgood (1970) who has described and figured specimens of *Rusophycus cryptolithi* from the Cincinnatian of Ohio. Professor K.E. Caster has provided me with casts of these and other specimens, and Dr. R.G. Osgood has sent further notes. The evidence for the assignment of these traces to *Cryptolithus* seems to me to be conclusive for the following reasons:

(1) The outline of the trace is identical with the outline of a trinucleid.

(2) The markings within the trace are of a size and form that are consistent with the size and shape of trinucleid appendages.

(3) There are numerous associated drag marks that could be produced by the movement of trinucleid genal spines.

(4) The front face of one of the burrows shows imprints of the fringe.

(5) '*R. cryptolithi* is quite rare and is confined to strata that contain abundant *Cryptolithus* fragments ' (Osgood, *pers. comm.*).

The following comments supplement Osgood's description of the basic morphology of *R. cryptolithi.*

The deepest burrows have a maximum depth of 4-5 mm. Compaction must have diminished the depth of the originals, and it would not be surprising if these were 8-10 mm. The floors of the deep burrows show very closely similar structures. The front and lateral walls are steep, varying a little on either side of vertical, whereas the rear wall slopes at 45-60 degrees to the horizontal. The front and side walls bear traces of the imprints of the fringe and the borders of the cephalon. In specimen UCGM37601 there are five of these impressions of the border one above the other in the anterior face of the burrow. These give the impression that the animal thrust forward a millimetre or two then settled back before renewing excavation. The presence of these bands and the steepness of the anterior face indicate that the cephalon was not used as a shovel to scrape the front wall of the burrow vertically. The burrow was being enlarged downwards, but there was some shuffling both fore-and-aft and sideways in the excavation during construction.

The floor of each burrow has a median ridge that begins about one-third of the length from the front of the burrow and continues up the posterior wall. This ridge is narrow and rather sharp-crested towards the front, and somewhat broader and more rounded to the rear. In front of the ridge is a smooth broadly V-shaped area that extends to the edge of the burrow. It carries very fine striations as shown on Fig. 2.

Lateral to the ridge is a pair of sausage-shaped depressions, variable in width and depth between specimens. On one individual they are shallow and narrow, and on another they are two or three times as deep and extend almost to the mid-line. They form part of the margin of the V-shaped area mentioned above, and then arc back to the posterior wall into which they are incised to varying degrees.

On one individual of UCGM37587 (the one figured by Osgood on Pl. 58:2, which incidentally has the cephalon towards the lower side of the plate) it is possible to distinguish scratch marks in places. These are arranged as is shown on Fig. 2. There is little doubt that they were excavated by the tips of the telopodites. The shape of the excavation and the direction of movement of the telopodite tips may imply that the most anterior telopodites were directed almost anteriorly from their proximal ends, then curved backwards and inwards distally. This matches neither the reconstruction of Raymond (1920, Fig. 20), nor

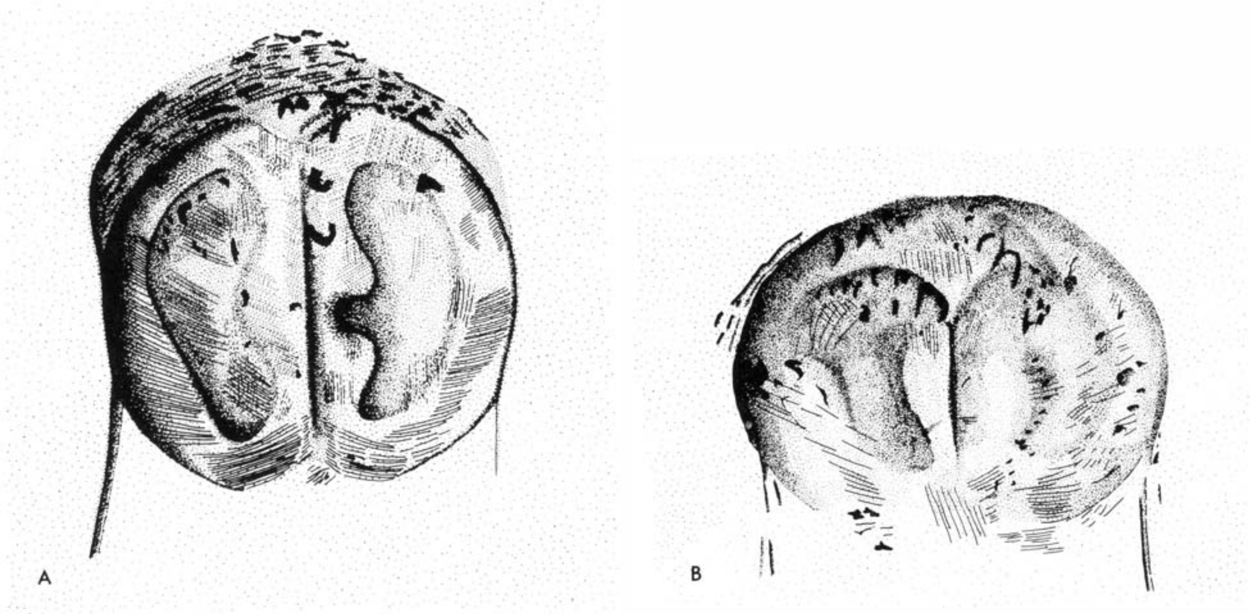

Fig. 2. The burrows of *Cryptolithus bellulus* (Ulrich) drawn from University of Cincinnati 37587. Both figures show the impressions of the genal spines, the median ridge and the paired sausage-shaped depressions bounded laterally by striated, steeply inclined surfaces. Much of this striation is probably due to compaction emphasising the original bedding of the sediment. Figure A also shows the series of impressions in the front wall of the burrow representing successive positions of the cephalic margin, and showing that the animal moved slightly backwards at successive depths (see Pl. 1:1–5). Fine lines are striations and the larger darker markings in the floor of the burrows represent impressions made by the telopodites.

that of Bergström (1972, Fig. 2), but does support the new observations reported above. The second and third pairs of telopodites probably had a similar orientation and shape, though their proximal ends would have been turned a little more laterally. The more posterior limbs must have been similar to those shown by both these authors.

The floor between these depressions and the lateral walls of the burrows is covered with postero-medially oriented striations. These continue up the back wall of the burrow and those of the opposite sides meet on the median ridge behind the end of the telopodite-excavated areas. These striations must have been produced by the ends of the exites that moved so as to shift sediment backwards and inwards towards the mid-line. Their distribution demonstrates that the exites of the cephalic appendages must have extended as far as the girder on the fringe, and those on at least the anterior thoracic segments must have reached the pleural tips.

On specimens in which the telopodite-excavated areas do not meet the mid-line, there is a rather smooth area carrying only fine striae arranged on the same pattern as those on the V-shaped area in front. The significance of the striations is not understood. They can scarcely be the result of movement of hairs on the coxal segments because these are placed well above sediment level, and they are not oriented correctly. They may possibly be due to movement of the bristles on the end of the telopodite, but the sharp inner edge on the telopodite-excavated burrow argues against this. It is more probable that they result from the systematic movement of the antennules which are known to have extended back between the telopodites.

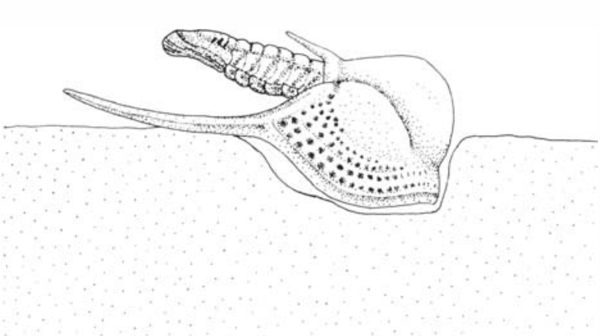

Fig. 3. Individual in its burrow. The angle at which the thorax and pygidium are held is that of the feeding position, during which detritus would be suspended in a cloud and filtering would be taken place on the exites. During burrow formation the pygidium and thorax would be lowered so that the anterior appendages could come into contact with the sediment more effectively.

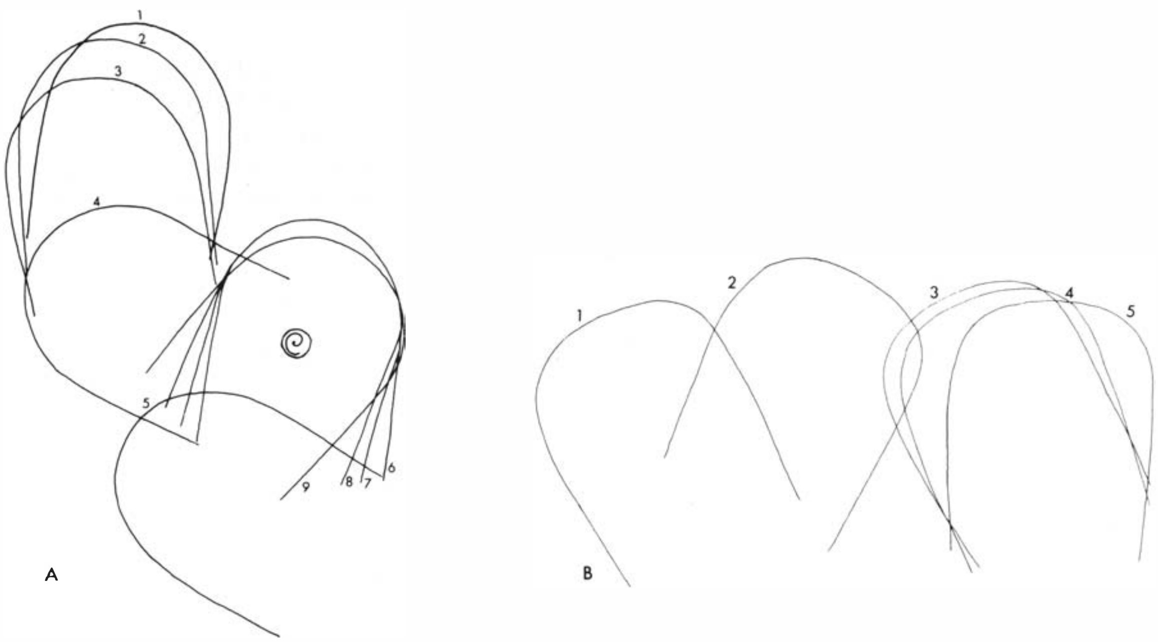

Fig. 4. A. Series of burrows reconstructed from University of Cincinnati 37567 (see Pl. 1:9). The outlines are those inferred for successive positions of the cephalon and genal spines and show the movement of the animal during burrowing, from position 1 to position 9. The spiral structure in the centre of the 6-9 sequence is a piece of hard shell. The animal has moved backwards from 1 to 5, then forward head-on into the current. Subsequently it had to modify its position because of the above mentioned shell. Current from top of page. B. Diagram similar to the one above, reconstructed from second individual on University of Cincinnati 37587. The animal has moved laterally to make a series of burrows while keeping its head directed into the current.

Short imprints of the genal spines are present on several specimens, as Osgood noted. These are not usually simple pairs but groups of impressions which become progressively deeper. These show that the animal sometimes rotated 10-15 degrees during the excavation of a simple burrow. These movements probably accompanied the fore-and-aft movements mentioned above.

The animal must have sat in its burrow with the head tilted downwards and the pygidium upwards as shown in Fig. 3. This conclusion is reached because — 1. the genal spine impressions are very short and hence their ends must have been above the sediment surface, 2. the length of the burrow is always less than the width whereas specimens of the genus *Cryptolithus* are slightly longer than wide, 3. the posterior face of the burrow is emarginate rather than pointed, thus showing that the pointed pygidium was not in contact with the sediment, 4. the area behind the step posterior burrow wall never shows evidence of limb movement such as would be expected if the pygidial appendages were in contact with the sediment.

These facts, together with the sharp posterior edge on the area excavated by the telopodites, and the meeting of the exite-produced striations on the mid-line of the posterior wall of the burrow, indicate an abrupt reduction in size or an abrupt change in orientation of the telopodites on the pygidium or the posterior segments of the thorax. The exites may also have been reduced. It is difficult to see how a gradation in size of the appendages as shown by Bergström can be reconciled with the evidence of these burrows. Further, the evidence indicates that the function of the more posterior appendages was different from those on the cephalon and the front of the thorax. Since there is no pile of sediment behind the burrow, part of this function was probably the dispersal of material removed from the excavation.

Osgood comments that the fossil was rheotaxic, and this is certainly a striking feature of the specimens available to me. Two of them are of particular interest. On the left side of slab numbered UCGM37587 (Pl. 1:8) there is an area that shows a series of burrows formed by the one migrating individual. The animal formed shallow burrows in the order shown on Fig. 4B, but it maintained a more or less uniform direction consistent with the drag marks on the slab as well as the other independent burrows.

The other specimen, UCGM37567, shows another series (see Pl. 1:9, Fig. 4A) in which the animal has evacuated one burrow then moved *backwards* to the next which is partly superimposed on the previous one, and so on. The series is linear and oriented parallel with the drag marks. This specimen has to be interpreted as the result of discontinuous backward burrowing because of the partly superimposed disjunct nature of the outlines. On the right side of the same specimen is another burrow that seems to be oriented at a high angle to the current direction. Fortunately it can be interpreted from four successive positions of the right genal spine that are progressively deeper. The right hand one is the shallowest and indicates that when the animal first settled it was almost parallel with the current. As it burrowed deeper the orientation changed progressively until it was at about 45 degrees to the current direction. The reason for this change was that in the bottom of the burrow it encountered a small shell that it could not remove and hence it progressively re-arranged itself so that the shell came into the mid-line between the ends of the telopodites. Hence even this evidence supports the view that the *natural* orientation of the animal was head-on into the current.

Tracks

There seem to be no accounts in the literature of tracks that can be ascribed to *Cryptolithus* with certainty. Those described as *Trachomatichnus numerosum* Miller (see Osgood 1970: 366–8) are only related to the genus by indirect arguments, and as Osgood has noted "it is puzzling that no evidence of long genal spines is preserved with the trail". Consequently, little weight should be placed on this type of evidence in determining the function of *Cryptolithus*. The *Cruziana*-like track figured by Osgood is likewise suspect, and in any case it is difficult to see how the fringe margins of *Cryptolithus* could produce a bent outline like that of his Pl. 65:7 without the genal spines leaving some kind of impression lateral to the main burrow.

Seilacher (1970:468) has produced drawings of what he terms procline resting tracks that he named *Cruziana perucca* from the Caradocian of Jordan. These are associated with linear furrowed trackways. There is no necessary connection between the two types of trace fossil, nor is there strong evidence that they were formed by trinucleids. However, Seilacher suggests that a trinucleid may have been responsible in view of a similarity to some of the assumed trinucleid traces figured by Osgood. In the present context they are of interest in that they are preserved in sediments at the bottom of a major channel fill, and they are clearly rheotaxic.

INFERRED SOFT ANATOMY

In reconstructing the soft anatomy certain explicit principles are adopted. These are as follows:

(1) No organs or tissue will be inferred unless similar organs or tissues are known in living arthropods or are known to have existed in extinct arthropods.

(2) The positions and interrelations of soft parts will be inferred according to three principles.

(a) Relationships that are observed in a wide spectrum of living forms will be assumed to be primitive, and hence shared by the trilobites, which are early members of the phylum. For example, the axial nervous system is placed dorsad of the alimentary canal because this is its position in almost all living forms.

(b) When relationships differ between living groups, that shown by the most primitive group showing similar gross morphology to the trilobites is preferred. For example, although merostomes are probably more closely related taxonomically to the trilobites than are the crustaceans (see Størmer, 1944), the high degree of fusion of the exoskeletal elements in merostomes obviously makes them a much less appropriate model for trilobite trunk musculature than many primitive crustaceans.

(c) Where close analogies cannot be drawn with living forms, the organs and tissues will be inferred to be of a size and position consistent with available space and maximum functional efficiency. This is in essence a modification of the paradigm method formulated by Rudwick (1961). Skeletons of the precise shape of the trilobite obviously cannot be found among living forms, and hence the musculature that activates them has to be reconstructed according to efficient mechanical principles. However, to be consistent with the previous principles, no groups of muscles can be inferred unless there is either evidence from the skeleton of their presence, or they are known to occur in primitive groups.

The alimentary canal

It can be inferred from the position of the hypostome that the mouth was high, probably between the bases of the first or second pair of biramous appendages. The celebrated Bohemian specimens of *Onnia ornata* (Sternberg) indicate that in trilobites of this type the stomach was large and occupied much of the space in the swollen glabella (for discussion see Raymond, 1920:80–81). Also the alimentary tract in the thorax was one-fifth or one-quarter the width of the axial rings and, as in living arthropods, it occupied a dorsal position. It is clear therefore that most of the space in the tunnels outlined by the apodemes must have been occupied by the alimentary canal. The same specimens indicate that the anus was at the posterior extremity, and it probably opened through the emargination in that position.

The digestive system

The cheeks of many trilobites show traces of variously branching channels on their inner surfaces. These are generally referred to by the non-committal name 'genal caeca'. Because the cheek regions of merostomes such as *Limulus* are largely occupied with digestive glands and many crustaceans and other arthropods also have similar large midgut glands, and because the caeca of trilobites tend to focus on the glabella which houses the stomach, the caeca are believed to represent the sites of the ramifying trunks of a digestive gland. This view receives support from the fact that in primitive trilobitomorphs from the Burgess Shale, caeca are known to connect with the alimentary tract. Bergström (1973) has questioned this interpretation of the caeca on some polymerids, and has suggested that they are vascular in origin. I cannot accept this view. The caecal pattern in *Papyriaspis* does not resemble a vascular pattern. Even if it were vascular, presumably it would exist only to serve some organ such as alimentary diverticulum. The blood vessels in living anthropods are usually sunken in the soft tissue they serve and do not lie immediately beneath the exoskeleton, and hence only their broadest patterns might be expected to be preserved. There is little reason to extrapolate the gut pattern observed by X-ray study of *Phacops* to other trilobites with very differently shaped glabellas as Bergström does.

There is little direct evidence of what underlay the smooth inner parts of the cheeks of *Cryptolithus* except that in a very few well preserved specimens (Raymond, 1920, Fig. 25; Whittard, 1958, Pl. 10:6, 7, 10) there are faint 'nervures' that originate opposite the first glabellar muscle scar. These nervures are strongest in a direction towards the genal angle where they disappear with the fringe canals, but a few weak ones can be distinguished running antero-laterally across the cheeks.

There is an approach to this problem by analogy with other Ordovician trilobites with similar fringes – particularly the Harpidina. The genus *Harpides* has an enormous fringe with multiple opposed pits in the upper and lower lamellae joined at their bases (see Whittington, 1965, Pls. 5–7). Within the fringe the radial canals dominate and are connected back to the glabellar region *via* a series of anastomosing canals, many of which are connected to the eye ridge. In addition there are smaller, flatter concentric canals in the fringe. This pattern is commonly regarded as indicating an extensive digestive caecal organ. Various genera of the Harpidae show a similar but less regular and less entrenched caecal pattern extending into the fringe. In addition, the lower lamella of these genera has a distinct girder which is opposed on the upper lamella to a slight concentric swelling – that is this swelling and the girder make a concentric canal much larger than any other except the marginal canal.

It is reasonable, therefore, to suggest that the fringe of the trinucleids also contained digestive caeca despite the lack of evidence for extensive connections between the fringe and the glabella. Of course this does not preclude the possibility that other tissues, for example blood vessels, were also present. In fact, their presence is necessarily implied.

The circulatory system

Since in all arthropods, primitive and advanced, the axial part of the circulatory system lies dorsad of the alimentary canal, the same position can be inferred for it in trilobites. Further, if it is accepted that the cheeks were largely filled with caecal tissue, they must have had a rich supply of blood with copious arteries and venous sinal systems. Little has been written about these systems in trilobites, but since arteries occupy a dorsal position they, at least, should leave some traces on the dorsal exoskeleton.

An approach to the problem is through the thorax. Each segment will of necessity have had its own branches of the arterial system extending out into the pleurae. When one considers how these branches could be related to the axial vessels, which lay in a rather confined space above the alimentary canal, there is only one place for them – namely in the

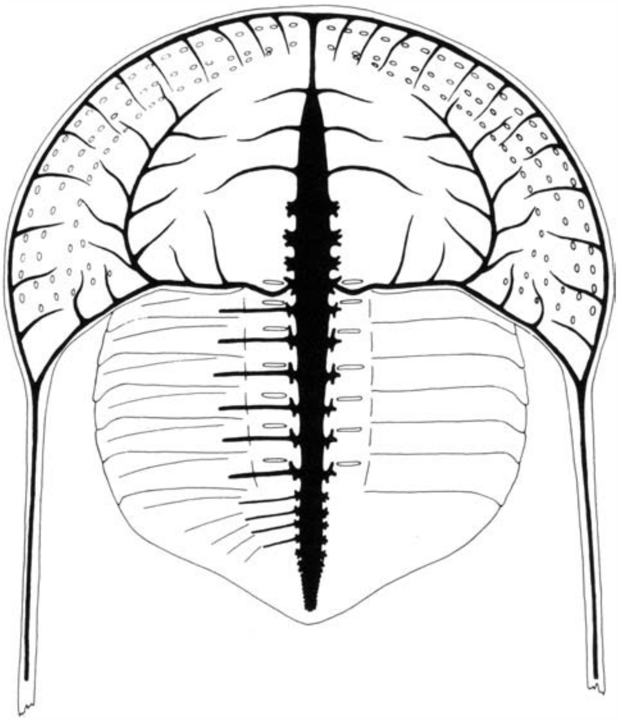

Fig. 5. Schematic reconstruction of the arterial system of *Cryptolithus* (see text).

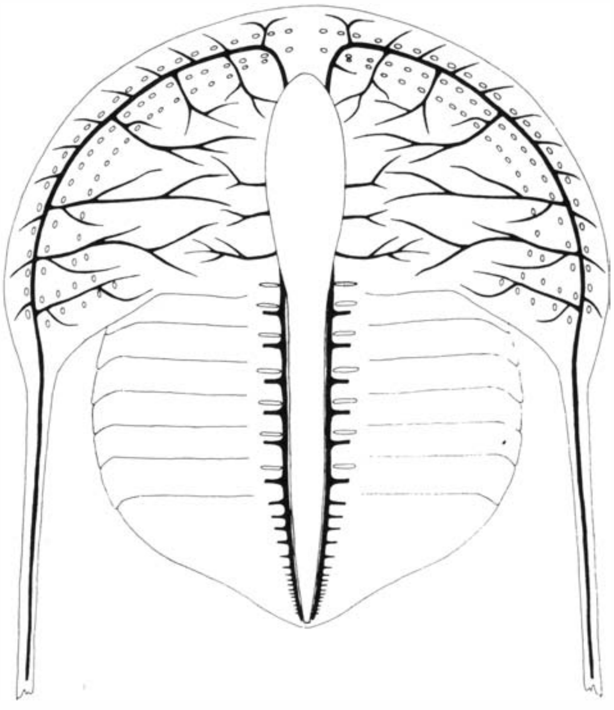

Fig. 6. Schematic reconstruction of the system of venous sinuses of *Cryptolithus.*

gap behind the apodemes and below the 'external dorsal muscles'. This gap opens laterally into the space under the posterior pleural bands. The corresponding positions on the cephalon are behind the occipital apodemes and in the posterior border of the cheeks (see Fig. 5). In *Cryptolithus* the posterior border continues on to the fringe, and beneath it is the site of one of the largest fringe openings as mentioned above (Pl. 2:11). This opening provides entrance to the larger canal that runs around the entire cephalic margin. (In fact, in almost all trilobites there is a marginal canal between the dorsal border and the doublure.)

Limulus has a large marginal artery given off behind the last of the prosomal appendages and after extending out parallel with the posterior margin of the prosoma, runs around its lateral and anterior margins. It seems, then, that the arguments from segmental homology and from analogy with other primitive groups both indicate the presence of a marginal artery in *Cryptolithus*, and probably in all trilobites. Presumably this artery sent branches inwards serving the caecal tissue, the branches passing between the pillars formed by the pits.

There is also a second artery serving the caecal tissue in *Limulus* – the caecal artery. No traces of such an artery are to be found in *Cryptolithus.* Even if it existed, one would not expect to find any indication of it on the exoskeleton since, as in *Limulus,* it presumably would have been buried in the body tissue.

The appendage musculature and other tissues of the glabellar region would have received blood direct from the axial vessels.

It might be suspected that the large space in the fringe over the girder would have contained an artery, but there is no evidence of this. If it did, there would presumably have to be an enlarged connection between it and the posterior part of the marginal artery as in *Limulus,* but there is none. The girder continues laterally down the genal spine.

If the above hypothesis is correct there must be a suitably disposed system of sinuses for the collection of blood in and around the fringe. In *Limulus* there are three longitudinal sinuses, one around the intestine and two on the venter (Gerstaecker, 1866–1879). Into these blood flows *via* a system of collecting sinuses that ramify through the caecal tissues. It is then passed down the length of the animal to the gills, situated beneath the abdomen, and thence back to the elongated heart. Since most of the gills on a trilobite are situated on the thorax and pygidium, one might expect a similar sinus pattern. It is therefore possible that the large canal above the girder acted as the main sinus for the fringe caecal area, passed the blood forwards and then out of the fringe *via* the moderately large spaces between the pits at the front of the glabella. Then it would pass ventrally down the thorax and pygidium. Probably a second main sinus drained the inner parts of the cheeks. This interpretation is more speculative than that dealing with the arteries, simply because the venous sinuses are ventrally placed on merostomes and related organisms (and hence presumably on trilobites also) and do not leave traces on the dorsal exoskeleton.

Musculature

The musculature of a trilobite-like arthropod may be divided into six main groups

a) The dorsal longitudinal muscles (extensors).
b) The external dorsal muscles (extensors).
c) The ventral longitudinal muscles (flexors).
d) The dorso-ventral muscles.
e) The appendage muscles.
f) The muscles for expanding and contracting the oesophagus and the stomach.

These will now be considered *seriatim.*

(a) The dorsal longitudinal muscles are commonly reconstructed as lying against the dorsal surface of the axial region between the apodemes (Hupé, 1953). However, as has been shown above, there is scarcely space for the alimentary and circulatory systems in that position in *Cryptolithus,* and any muscles lying dorsad of these would have to be sheet-like. Such muscles would attach to the front of the articulatory furrow in each segment. There is another site possible – in a longitudinal position through the arch between the apodemal tip and the axial articulating process (Figs. 7, 8). Fibre bundles would pass upwards and backwards from this muscle to the concavity in the front wall of each apodeme described above, and possibly also to the almost vertical wall of the front of the articulating furrow, thus passing around and over the axially placed canals.

This position for the muscles confers several advantages. The muscles do not interfere with any other structures, they are relatively unconfined ventrally, and they are prevented by the arch of the apodemes from rising dorsally when they contract, and thus the length of the lever on which they operate is much greater than if they were placed in the central arch between the apodemes. Hence in this position they have maximal efficiency.

This interpretation offers a location for the anchorage of the dorsal longitudinal muscles in the cephalon and the pygidium. It would be impossible for these muscles to attach to the very restricted occipital doublure because the articulating half ring of the first thoracic segment would prevent it. Insertion on the wall of the glabella is possible in only one place –

LIST OF SYMBOLS USED ON FIGURES

aa	anterior artery of thoracic segment diagrammatically shown	dlm	dorsal longitudinal muscle
ac	alimentary canal	eb	endoskeletal bar
adv	anterior dorso-ventral muscles	edm	external dorsal muscle
ae	axis of enrollment	g	gonads
ahr	articulating half ring	ht	heart
ap	articulating process	nc	nerve cord
apo	apodeme	os	occipital spine
apo oc	apodeme on occipital segment	pdv	posterior dorso-ventral muscles
apo lp	apodeme lp	pyg	pygidium
appm	appendage muscles	vi	ventral integument
ar	axial ring	vlm	ventral longitudinal muscles
cx	coxa	vs	venous sinuses

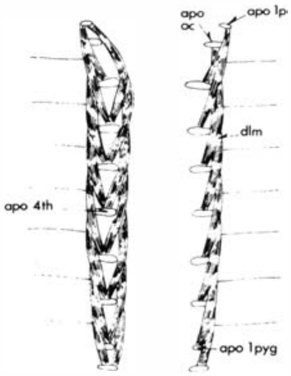

Fig. 7. Schematic diagram of the axial region of *Cryptolithus tesselatus* showing on the right side the dorsal longitudinal muscles in a position in the apodemal arch and their natural atttachment to the apodemes in both cephalon and pygidium. On the left side dorsal longitudinal muscles are also shown in the medial arch, and the less direct insertions onto the cephalic apodemes is clear.

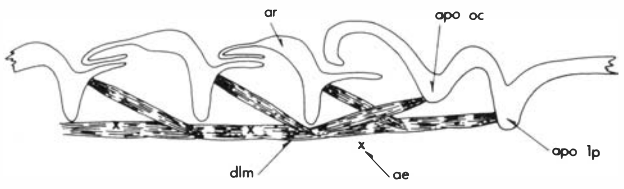

Fig. 8. Schematic diagram of a longitudinal section through the occipital part of the cephalon and the first two thoracic segments, along the line of the arch formed in the ventral edges of the thoracic apodemes. As indicated in the text, part of the dorsal longitudinal muscle may pass through this arch and fibres from it pass postero-dorsally into the upper anterior face of each apodeme. Note that contraction of these muscles will produce outrolling around the axes marked "X", and that they will be capable of exerting a large moment.

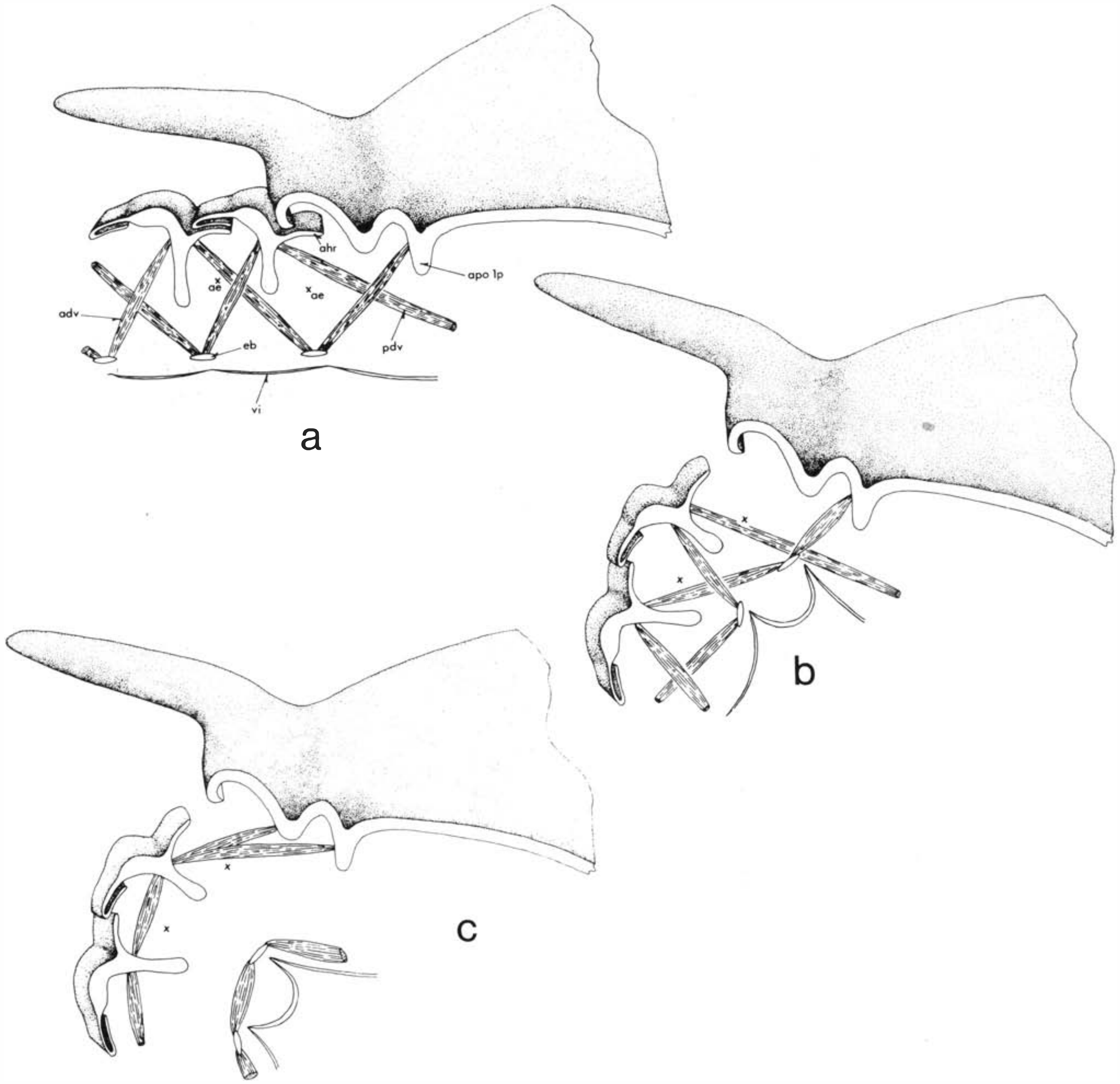

Fig. 9. Schematic longitudinal section (drawn to scale) of the cephalo-thoracic and first thoracic articulations cut through the deepest parts of the thoracic apodemes.

A. The relaxed outrolled position showing the positions of the inferred anterior and posterior dorso-ventral muscles. B. The positions of these segments with the animal in the fully enrolled position. The axes of enrollment (labelled x) have been plotted from the articulatory lines on the segments concerned. Note that if the enrollment is produced by the contraction of the abovementioned muscles, the ventral endoskeletal bars and the ventral integument will be pulled into an impossible position (see text). C. The same position as in (B), but with the enrollment produced by contraction of the ventral longitudinal muscles. Note that this is an effective means of enrollment, obviating the difficulties of (B). The dorsal longitudinal muscles are drawn as though their main body passes on the medial side of the apodemes. An alternative is shown in Fig. 8.

part of the large scar above apodeme lp. However, this scar is similar to those in front of it and hence it is probably the site of attachment of appendage musculature only. The occipital and lp apodemes have ventrad projections that lie on the projected lines of the muscles, and it is suggested that the occipital apodeme anchors an inner group, and lp an outer group of fibres (or their tendons). These attachments would still leave the tips of the apodemes free for the attachment of the appendage muscles and possibly strands from the ventral longitudinal muscles.

A similar account can be given of the attachment of the muscles into the pygidium. The first, second and third segments have progressively weaker apodemes. Most of the fibres would attach to the first which is so shaped as to allow some of the outer fibres to pass to the second and third. It is important to note that on this hypothesis the attachment points in both cephalon and tail are well dorsad of the enrollment fulcra, and hence outroll both parts of the skeleton.

(b) The 'external dorsal muscles' of Hupé may be present in *Cryptolithus*. These seem to be slightly modified areas on the leading edge of the articulating half ring on some specimens. Muscles from these areas would attach along the posterior face of the articulating furrow between the apodemes.

(c and d) The animals could enroll, and therefore they must have had ventral longitudinal muscles and a series of transverse endoskeletal bars or tendons. Much of the enrollment could have been produced by the contraction of the muscles between the bars. However, it is known that in most subclasses of the Crustacea there are dorsoventral trunk muscles connecting the bars with the interior of the dorsal exoskeleton (Hessler, 1964, pp. 38–39, 55). They are usually divided into vertical, and obliquely ascending pairs. The latter types ascend both anteriorly from one segment to the next, and are responsible, in part, for enrolling and outrolling. Their wide distribution suggests that they are primitive.

Their presence in *Cryptolithus* cannot be demonstrated. However, an examination of the skeletal requirements for the efficient operation of such muscles may provide a basis for speculation. (a) They must pass lateral to the axial vessels and hence their attachment to the dorsal exoskeleton (or the dorsal longitudinal muscle) must be at the lateral part of the axial ring. (b) Their points of attachment must be dorsal to the enrollment fulcral axis. (c) In recent crustaceans they commonly attach to infolded bands of exoskeleton, presumably to give a narrow attachment area. The part of a *Cryptolithus* thoracic ring that would satisfy these specifications admirably would be the wide dorsal part of the apodemes.

The presence of suitable attachment sites does not prove the existence of such muscles, but a more powerful argument can be developed from the nature of these sites. It has been shown that the cephalothoracic joint must be able to rotate through 80°+, and the first-second thoracic joint through 40°+. Movements on this scale could not be accomplished by dorsoventral muscles of the type described above. As is shown in Fig. 9B, the endoskeletal bar would be pulled up to an impossible position where it would constrict the alimentary canal and put pressure on the heart. Moreover, the muscle itself would have to undergo something like 50 percent contraction. Similar problems, though not so severe, would occur with the first-second joint. Consequently these segments must be enrolled mainly by the contraction of the ventral longitudinal muscles that must originate anteriorly at a large ventral cephalic bar. There should be no need for the apodemes on the first thoracic segments or the occipital ring to be as expanded dorsally as those on the more posterior segments. That this is the case may be verified by reference to Whittington (1959, Pl. 21: 1–6. and Pl. 2: 4 herein). It has also been confirmed by my observations on other material. Such a verification is strong support for the existence of dorsoventral muscles in the posterior two-thirds of the trunk.

(e) The musculature for the cephalic appendages was extraordinary. In the first place, if the anterior pit was the site of attachment of the antennules, as seems most probable from the appendage bearing specimens described by Beecher and Raymond, there remain five pairs (three pairs of scars and two apodemes) of muscle insertions for postantennular appendages. In adults the two apodemes adjacent to the occipital furrow are identified as the occipital and lp structures by Whittington (1968, Fig. 1). It is true that in younger specimens, the one labelled lp is much further forward, and hence this seems a reasonable interpretation. The large muscle scar medial to it must also be related to the pre-occipital appendage. The most satisfactory interpretation therefore is that lp is divided into two parts – the lateral part, which is apodemal, serves mainly for the attachment of the various longitudinal muscles, and the medial part serves for the attachment of the appendage muscles. Judging from the sizes of all the cephalic muscle scars, the pre-occipital appendages were the largest.

The deep apodemes on the thoracic segments indicate that the muscles that protract and retract the appendage must have been very obliquely inserted and this would have given the

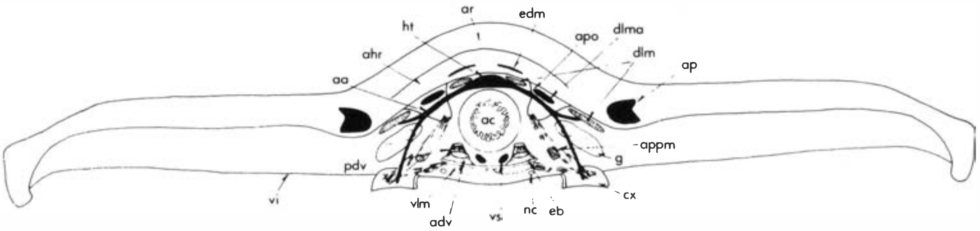

Fig. 10. Anterior view of a single thoracic segment showing an interpretation of the various soft tissues discussed in the text. The arteries in the pleurae are not shown.

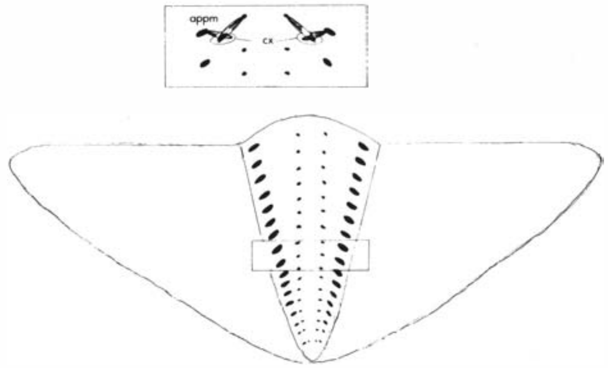

Fig. 11. Schematic diagram showing the positions of the muscle insertions on the pygidium of *C. tesselatus.* The inset shows possible positions of appendage musculature (appm) arranged to show how the coxa (cx) could be rotated.

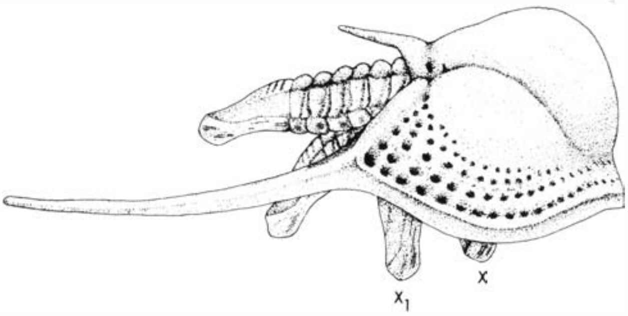

Fig. 12. Lateral view showing how the organism could use the thorax and pygidium as a means of locomotion (see text).

coxae an unusually large capacity to rotate about the vertical axis (see Fig. 10). In addition it is clear that oblique muscles would have been inserted into the coxae from the ventral endoskeletal bars. These also must have produced an important rotational component.

The fact that each pygidial segment has two pairs of muscle insertions, the medial one of each pair lying forward of the lateral one, also suggests a musculature that was adapted to rotating the coxae around a vertical axis. Presumably maximal efficiency would be obtained by the attachment of the protractor to the medial scar.

(f) Eldredge (1971) has drawn attention to the attachment of muscles from the walls of the stomach to the inner surface of the glabella in the Phacopina, and gives an excellent review of the views of previous workers. There would certainly need to be comparable muscles supporting the large stomach in *Cryptolithus,* and it comes as no surprise therefore to find that the diverging ridges on the anterior slope of the inner face of the glabella of *Cryptolithus* (Whittington, 1968 Fig. 1) have a similar disposition to the muscle scars in many phacopines. In the latter the pattern is formed of many small scars, but in *Cryptolithus* the ridges are apparently continuous. The significance of this is not clear, but it may be that there are many small scars placed on a continuous ridge.

Articulatory membranes

The spaces left in the sockets of the axial articulations could have been vacant during life, but it is more likely that they were at least partly occupied by tissues that held the process in the socket. The fulcral processes really articulate so slightly with their opposing sockets that it is almost certain they were held in position by modified arthrodial membranes.

The nervous system

Since the main nerve system of arthropods is ventral, it can only be assumed that trilobites were comparable. So far as I can determine, no trace of the nerves is left on the exoskeleton of *Cryptolithus*. Of course this does not exclude the possibility of the presence of an elaborate chemical and tactile sensory system. Such systems must have existed in view of the reduction of photoreceptors, as has been indicated below.

FUNCTIONAL INTERPRETATION

Plankton, nekton or benthos

Raymond (1920) has briefly discussed earlier views on this question and concluded that *Cryptolithus* was benthic. With this view I am in agreement. *Cryptolithus* produces shallow burrows; the appendages are not well adapted for prolonged swimming; the shape of the head would always force the animal down (see below) if it swam with its ventral side down (though it could have swum on its back as does *Limulus* on occasion); the genal spines would serve as balancing structures on a bottom but are too small to balance the animal if it floated freely; the large glabella, which looks as though it might contain some low density substance to permit flotation for long periods, could equally well be occupied by an enlarged, mud-filled stomach (see above); members of the family are common in shallow and moderately deep water deposits, but they are very rare in open sea, deep water deposits. Some of these arguments seem to me to be conclusive by themselves, but together they provide overwhelming evidence of a benthic existence.

Locomotion

It is clear, both from the study of the appendages and the burrows, that the telopodites of the cephalon and anterior part of the thorax of *Cryptolithus* were able to reach the sediment, and presumably gave the animal an ability to walk. However, in comparison with an active animal of comparable gross shape such as *Limulus,* or other benthonic trilobites such as *Ceraurus* or *Triarthrus,* the limbs of *Cryptolithus* were very short. I see no evidence to support Raymond's view that the telopodites could deliver a powerful thrust, and it is by no means clear that it was an active walker. Even on a flat bottom, the lateral edges of the fringe and the genal spines must have been continually dragging.

The filament bearing branches (exites) of course may have contributed to forward locomotion by a swimming action. However, it should be noticed that propulsive force from the posterior on a cephalon of cryptolithid shape would tilt it towards the bottom. This is the result of two factors. (1) The surfaces of the cephalon exposed to a current from the front are almost all inclined antero- or lateroventrally, thus producing a negative deflection. (2) The centre of gravity of the whole animal, allowing for the fact that the specific gravity of the soft tissues would have been only a little higher than sea water, and that therefore most of the weight of the animal would have been in the exoskeleton and in the detrital material in the stomach, will be well forward in the cephalon. The points at which the propulsive force would be applied were the coxae, which were mainly behind and dorsad to the centre of gravity. Thus a couple would have operated to deflect the cephalon downwards. Hence extensive limb-propelled swimming was impossible.

However, additional forms of propulsion may have been possible. As has been shown above, the dorsal longitudinal muscles were probably strong and had strong insertions into the exoskeleton. Also, although the thorax was capable of a large amount of movement on the first articulation, much less movement was possible on the remainder. Further, the articulatory devices were very strong. Hence the posterior part of the thorax and the pygidium formed a rather rigid sheet. By projecting this downwards and contracting the dorsal longitudinal muscles, the animal could be moved forward as shown in the accompanying figure. This type of locomotion has the added advantage that it would initially raise the cephalon off the substrate, and then allow it to subside as the point of support X, X^1 moved behind the centre of gravity of the whole animal. Naturally there would be some additional propulsion from the swimming and walking action of the limbs. The only resistance to movement would be the friction of the water and the drag of the genal spines.

There is little evidence from the trace fossils available to me to support this hypothesis. There are some V-shaped impressions that could be interpreted as having been made by the tip of the pygidium, but these are not symmetrically placed between drag marks of genal spines or any other markings that could be made by a moving *Cryptolithus.*

The possibility of locomotion by the rapid movement of the posterior part of the thorax and the pygidium up and down from a horizontal position should also be considered. It suffers from the same objection as the hypothesis involving swimming with the aid of the limbs *viz.* the tendency to tilt the head downwards unless it swam on its back. However the shapes of the thorax and pygidium, and the strength of the articulation, are apparently suitable (see discussion on enrollment below), and the necessary musculature is available. Perhaps some limited locomotion of this sort took place, tail propulsion being supplemented by swimming movements of the large exites. There is also some evidence from the trace fossils, in that there are drag marks (see above p. 72) without any appendage tracks between them. However, these would seem to imply swimming in an uninverted position.

Sensing the environment

The antennules just mentioned were obviously sensory, but apart from these the only macroscopic physical sensors to leave a trace on the skeleton were those associated with the median glabellar tubercle. Størmer (1930:85–89) offers cogent reasons for accepting the median tubercle of trinucleids in general as a light sensitive area, and though Whittington (1959:441–2) notes that pits like those figured by Størmer for *Tretaspis seticornis* were not observed in *C. tesselatus,* his Pl. 20:10 does show some pits. These are arranged in a somewhat different way, but there is no reason why they should not have had the same function. Hence, I accept the view that there was a rudimentary light sensitive area in the median tubercle of *Cryptolithus.* There were no lateral eyes. Presumably these animals were dependent largely on chemoreceptors and tactile organs.

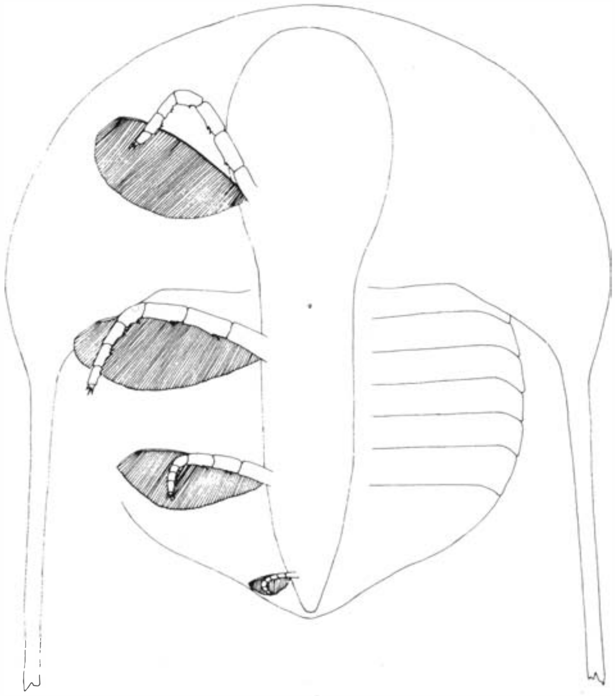

Fig. 13. Schematic diagram to show the relaxed orientation of the appendages at four different points on the skeleton of *Cryptolithus.* There has been no attempt to make the segments of the telopodites the correct size, but the exite filaments are of approximately the observed size and orientation.

Stability and balance

A *Cryptolithus* resting on the sediment surface would be most stable in a current coming from its anterior end. A current from this direction would normally force the head down on to the substrate, but even if it were lifted as a result of flow under the anterior arch, the long genal spines would make it difficult to roll over. A current from its posterior would easily roll it over, and though a current from the side would not make the animal quite so unstable, some water flow under the genal region and pressure against the large side of the cephalon would make it less stable than in currents from the front. This accounts for the 'rheotaxic' orientation noted above.

Feeding and respiration

The picture that has emerged so far is one of an organism without means of sustained locomotion, living on the bottom where it develops shallow burrows, oriented by the current flowing over the sediment on which it lived, and unable to detect more than light and dark with a rudimentary photoreceptor. None of these features suggests a predatory or scavenging mode of feeding (see Størmer, 1930:106, Bergström, 1972:90). Add to this the mud-filled gut of *Onnia ornata,* and the fact that the *Rusophycus cryptolithi* burrows were not successful for concealment or protection (see Osgood, 1970:307), and we have a deposit-feeding animal that burrowed to provide a cloud of particles to ingest. Bergström (1972:90–1) was inclined to this view on other grounds.

The burrows were excavated by both telopodites and exites, and it is clear from traces on the burrow floors that sediment was moved backwards and inwards. However, there are some markings indicating that mud was swept up the back wall of the burrow, but most of them indicate that the particles were moved across the back wall towards the mid-line. In the median space between the telopodites, mud probably went into suspension; particles could have been caught on a setal tract and carried to the mouth, or they could have been pumped towards the mouth by expansion and contraction of the fore-gut. I prefer the former hypothesis since the floor of the burrows between the innermost marks made by the telopodites has fine markings that do not indicate an anteriorly directed flow of water in this region.

This does not preclude the possibility that some filtering of particles took place through the filaments of the exites in the manner postulated by Bergström (1969) and several previous workers. Indeed the vertical wall formed around the thorax and the pygidium by the edges of the pleurae produces an ideal shape for a suction chamber. It is true that the pleural tips on the thorax can be partly explained in terms of an enrollment mechanism, but this explanation cannot be applied to the pygidium. A second line of evidence concerns the disposition of the exite filaments. The lateral walls of the burrows were certainly swept by the ends of the lateral filaments of the cephalic and anterior thoracic exites, but filaments were not restricted to the distal ends of the exites even of these segments. The proximal filaments presumably functioned as filters and/or respiratory surfaces. This implies that the exites on these limbs could swing backwards and forwards (presumably through an angle of about 20–30°) during periods of burrow formation, and then reorient themselves to form suction chambers for feeding and respiring.

The shape and surface markings on the back wall of the burrows imply that the tips of exites on the posterior part of the thorax could swing inwards towards the median line. This would be possible only if the telopodites on the corresponding and the more posterior segments were extended downwards, and the filaments on the exites of the pygidial appendages were held up against the ventral integument. The appendages on the pygidium are so numerous and so crowded, it is clear that the filaments on the exites must have been inclined downwards at a moderate angle before any effective filtering of water through them could take place. This probably accounts for the peculiar configuration of the posterolateral border of the pygidium (Fig. 14). A consequence of this hypothesis is that the movement of sediment and water posterior to the burrow must have been maintained by the telopodites of the pygidium (and possibly the posterior segments of the thorax). As has been shown above, these were not involved in burrow formation, and their segments were strongly compressed, being almost as wide as long in some instances. They were of an ideal shape to keep water in motion and sedimentary particles in suspension if the limbs were able to beat with a fore-and-aft motion.

The dense packing of the limbs on the pygidium, which to date has not received any attention in the literature, can now be explained as an attempt to (1) increase the capacity of the animal to move material from the rear of the burrow and to keep it in suspension, (2) increase the food gathering capacity in a region past which all the detritus removed from the burrow would move, and (3) increase the respiratory surface in a region out of the burrow where the water flow would be greatest.

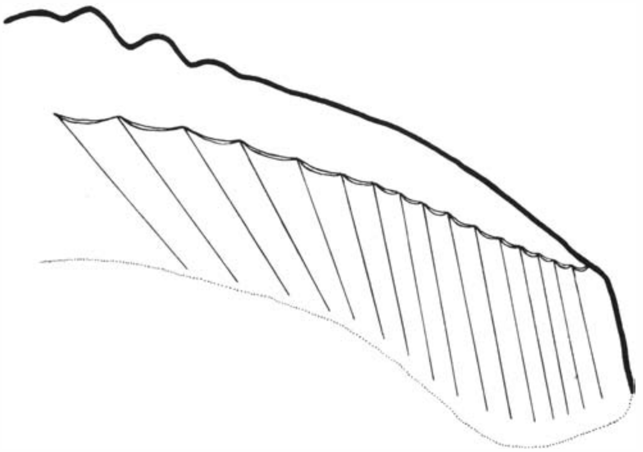

Fig. 14. Schematic diagram of a lateral view of a pygidium showing the angles at which the planes of the filament "combs" of successive exites would have to be suspended in order to permit efficient filtering.

Enrolling and outrolling

It is accepted that *Cryptolithus* exhibited discoidal enrollment (Barrande, 1852, Harrington *in* Moore, 1959). The thorax and pygidium are so short that for the tip of the pygidium to reach the inner lamella, the first two articulations together must be capable of up to 120° + of rotation (Fig. 15). The cephalo-thoracic joint could be rotated through almost a right angle. This explains why the articulatory groove was on the postero-ventral edge of the cephalon, and the articulatory flange of the first segment on its antero-dorsal edge. If they were in their normal position, the joint would become disarticulated on maximum enrollment. It also explains why the thoracic pleural facet of the first segment was moulded to move around the surface of the posterior border, as described above. The next articulation has not been clearly observed. However, those further back have very limited possible movement because of the close fit of the pleural tips. In fact, with the amount of downturn on the segments figured by Whittington (1959, Pl. 21:4–6) it can be shown that probably a maximum of 5°–6° of enrollment was possible at each articulation.

It is clear, therefore, that the animal could not enroll by turning its tail under and then progressively rolling up its thorax. The pygidium and the posterior thoracic segments must have turned down as a rather inflexible unit first, and then been pushed forward into the totally enrolled position by progressively larger movement on the more anterior articulations.

If the cephalo-thoracic joint did rotate through a right angle, a gape would be left between the occipital ring and the articulating half ring of the first segment. This joint is already modified by the inclination of the occipital ring so that it overlaps the axis of the first thoracic segment to an unusual degree, and by the reduction of the articulating half ring. This ring could not be increased in length without altering the position of the occipital and lp apodemes, and this could not be done without altering the globosity of the glabella. Presumably the degree of inflation of the glabella is a feature of primary functional significance. Another point is that if the half ring were increased in length so that no gape appeared when the segment was enrolled

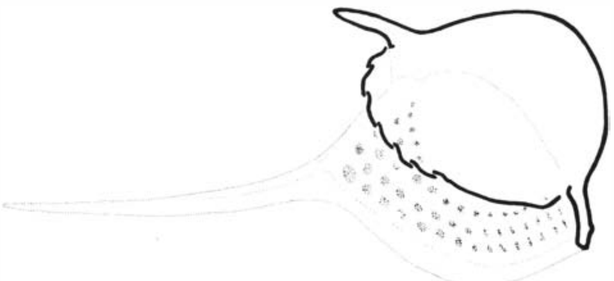

Fig. 15. Reconstructed longitudinal section through an enrolled specimen of *Cryptolithus tesselatus* to show the amount of movement necessary on the first two articulations in order to bring the tip of the pygidium against the inner edge of the fringe.

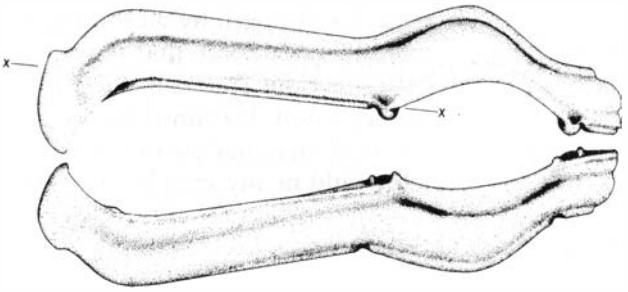

Fig. 16. Oblique views of two consecutive thoracic segments of *Cryptolithus tesselatus* to illustrate the strength of the articulations at both the axial furrow and the fulcrum, and to illustrate that the processes at these positions lie well below the axis of rotation (x-x) of the segments during enrollment.

through 90°, it would have to be strongly arched and the leading edge would project anteroventrally so far as to interfere with the axial vessels (see Fig. 9). The shape adopted seems to be the only one possible. The occipital spines, therefore, would have been developed, at least in part, as a protection for the gape during maximum enrollment.

The fact that the main articulatory processes at the axial furrow lie *below* the pleural articulatory line is probably of some importance. The processes act as short levers and on enrollment describe small arcs up into the socket, thus compressing any tissues they contained (Fig. 16).

The articulations between the segments are stronger than those of most other trilobites. In fact, they seem far stronger than is necessary for simple enrollment. Not only are the processes and sockets strong, but the ridge-and-furrow design of the pleural articulations makes for a junction that will permit vertical movements only. The possibility of dislocation by rotation around a longitudinal horizontal axis is virtually eliminated.

The amount of possible outrolling is limited by the strength of the arthrodial membranes and the other soft tissues, by the large occipital spine which overhangs the first three segments, and by the contact of the tops of the axial rings.

From this evidence, and the evidence of the strength of the extensor muscles given above, it is concluded that the animal was able to unroll rapidly – in fact it could flick its tail out from the enrolled position with sufficient strength to carry it past the horizontal position. This has two important functional consequences. If the animal were rolled over on its dorsal surface, the small limbs would be rather ineffective in righting it, but a sudden flick of the tail could be very effective. In the second place, the possibility of an upward movement of the tail beyond the horizontal does support the hypothesis that some swimming by tail movement was possible.

THE FUNCTION OF THE FRINGE PITS

To date three main functions have been suggested for the fringe pits.

(1) They serve to strengthen the exoskeleton while keeping it light. Størmer (1930:104–5) gives a good summary of this argument.

(2) Together with the long genal spines the fringes provide a light framework on which the animal supports itself on soft muddy bottoms.

(3) They provide a filter to separate fine particles from the surrounding water. These particles are used for feeding (Cisne, 1970, 1973, Seilacher, 1970).

In my view none of these suggestions are satisfactory for the following reasons.

(a) The production of pits in a smooth sheet of material obviously reduces the total mass of the sheet. In trinucleids, however, because both lamellae are deflected into the pits to effect a junction, the surface area of skeletal material is *increased,* and its mass will be the decreased only if the walls of the pits are considerably reduced in thickness. It is difficult to get quantitative information on this matter, but it is clear that in genera such as *Tretaspis* and *Cryptolithus,* although there is a decrease in thickness, this is not enough to produce a decrease in mass. On the contrary, there is probably a slight increase.

(b) The pits undoubtedly strengthen the fringe – they increase the strength by an enormous factor. If this is their primary function, the fringe must be subjected to some force that requires the evolution of such structures. Such a force cannot be hydrostatic since the spaces in the fringe open into an unprotected area under the central part of the cephalon. It cannot be occasional impact that might cause the lamellae to separate around the weak marginal suture. Five or six pits would surely provide against such an eventuality, which would in any case be very rare because the animals inhabited quiet muddy bottoms. Nor can it be the force exerted by a predator. There is no reason to believe that a predator would attack the fringe rather than the relatively unprotected ventral surface of the animal.

There seems to be no known force to which the organism might be subjected that would require such enormous strength. But the 'strength' argument also falters in that it offers no explanation for the existence of the median perforations. Pits with a variety of shapes would provide the same strength without the production of perforations. Why this added complication?

(c) Although it is clear that the animal must have been supported on the sea floor by the genal spines and the margins of the cephalon, only the edge of one part of the fringe was involved while the animal was on the surface of the sediment. Most of the fringe would not be in contact with the sediment unless the animal were half buried. In that circumstance the meshwork only impede burrowing and hence be an evolutionary liability. If it be argued that the above takes no account of irregularities in the sediment surface and that a trinucleid is equipped for sitting on a variety of irregularities, it still remains difficult to explain why it is necessary to have pits in the *upper* lamella of the fringe. It is a well known fact that the doublure of a trilobite is ornamented differently from the border above it, and hence the lower lamella of a trinucleid could presumably be pitted without the upper one being affected. And finally, the existence of the perforations is not explained by this hypothesis.

(d) The filter hypothesis is difficult to accept for several reasons. (1) Water impinging on the animal from the front could pass freely into the space beneath the cephalon *via* the large median arch in the cephalic margin. On the other hand the amount of water that could pass through the capillaries of the fringe would be very small. (2) The capillaries in a cephalon about 7 mm long are in the vicinity of 0.05 mm in diameter, and the bases of the pits are only 0.15–0.20 mm. Even if a continuous water flow could be produced they would soon be clogged and there is apparently no way of clearing them. (3) There is no point in filtering currents from the front in any case, because there is a continual cloud of particles of a variety of sizes produced by the action of the appendages on the sediment inside the fringe. (4) There is no point in filtering currents flowing from the inside to the outside.

The above explanations refer to the functions of support, protection and feeding. Other functions likely to be reflected in the exoskeleton are locomotion, burrowing, respiration, circulation, digestion, excretion and sensory reception. All of these have been considered in the previous discussion and only digestion and circulation have been shown to play some part in controlling the shape of the fringe, but they offer an explanation of neither the junction of upper and lower lamellae in the pits nor the presence of capillary tubes. These two features form part of a highly complex system involving peculiar difficulties for the animal in the deposition of the exoskeleton and in moulting to the extent that a special suture has had to be developed at the bottom of each pit. They are obviously the keys to an interpretation of fringe function.

Another approach is to try to determine if there is any piece of behavioral information that has no satisfactory explanation in terms of the described morphology. There is one such – viz. how does the animal orient itself in bottom currents when its appendages are so ineffective for gripping the sediment?

This is clearly of importance because of instability of the animal in currents from the rear and because of the preferred orientation of specimens in trace fossils. There seem to be two possible ways in which the fringe might function as an orientation device. (a) It might be a sensory array that would give warning of a change in current direction. Minor changes in currents would be detected and give the animal time to adjust its position before it was overwhelmed. (b) It might be a self-correcting structure that automatically adjusted the orientation of the animal in changing currents.

The idea of a sensory array is appealing both because the disposition of the fringe pits is always in a regular pattern and because the poor development or absence of photoreceptors suggests the need for some compensatory device. The operation of such a device must depend on the existence of the capillary tube, and this suggests the presence of a membrane or sensillae to register a flow of water through the capillary. Such a flow would be produced by the production of a negative pressure in the pit in the upper lamella by the flow of a current across it. With a large number of pits in a precise array it should be possible for the animal to detect small changes in current direction and velocity. There seems to be no possibility of a membrane stretched completely or partly across the capillary. It would have to lie in the plane of the sutural contact between the lamellae, and thin sections show no evidence of a slit that could contain it. There could be specialised sensillae in the bases of the pits of both upper and lower lamellae, but these have not been detected.

The possibility that the fringe acted to readjust the animal automatically to changes in current direction has no theoretical or experimental justification at present. Perhaps the best means of testing the hypothesis would be empirical, but this requires very skilful model making.

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EXPLANATION OF PLATES

Plate 1

All photographs are of latex casts taken from specimens of *Rusophycus cryptolithi* Osgood, in the University of Cincinnati Geology Museum, and collected from the Economy Beds, Campell Co., Kentucky. Details may be obtained from Osgood (1970).

Figs. 1–3. Three photographs of UCM37587 (holotype) taken in different lights. Some of the transverse striation on the flanks and in the backs of the burrows is probably the result of compaction emphasising the original bedding of the sediment. This comment applies also to the other figures. Figs. 1 and 3 are X3.0 and Fig. 2 is X2.8. *Figs. 4–5.* Two photographs of another individual on the slab numbered UCM37587, X2.8 and 2.5 respectively. *Figs. 6–7.* Two photographs of UCM37601, X0.70 and 3.0 respectively. Note the current lineations on Fig. 6 and the successive levels of burrowing in Fig. 7. *Fig. 8.* Part of the slab of UCM37587 showing the two burrows figured above, and the strong current lineation. The series of burrows on the left is that interpreted in Fig. 4B. *Fig. 9.* A series of burrows on UCM37567, X2.0. This specimen is interpreted in Fig. 4A.

Plate 2

Figs. 1–13. Cryptolithus tesselatus (Green) from the Lower Martinsburg Shale. Figs. 1–5 are those figured by Whittington 1959, Pl. 21:1–6. All are 8.5 approx. *Figs. 1–3.* Dorsal, ventral and posterior views of probably the fourth and fifth thoracic segments. *Figs. 4–5.* Anterior and ventral views of an isolated first thoracic segment. *Figs. 7–9.* Dorsal, dorso-lateral and lateral views of an almost complete specimen from Locality 12 of Whittington 1956:166. Photographic negative made by Whittington. Fig. 7 is X4.5, and Figs. 8 and 9 are X7 approx. *Figs. 6, 10–13.* Specimens in the Australian National University Collection, Presented by Professor Marshall Kay. *Fig. 6.* Dorsal view of an isolated first thoracic segment, X8.0. *Figs. 10–11.* Ventro-lateral and postero-ventral views of a broken cephalon, X6.5. *Fig. 12.* Ventral view of another cephalon, X6.5. *Fig. 13.* Postero-ventral view of a small cephalon, X6.5.

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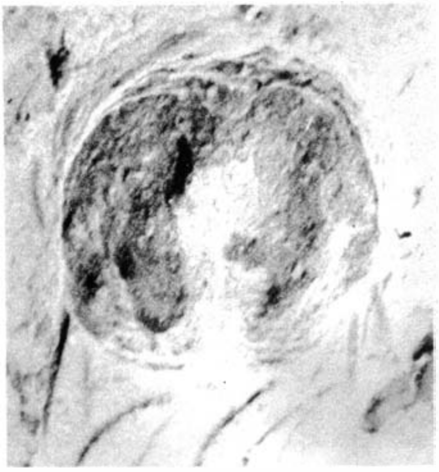

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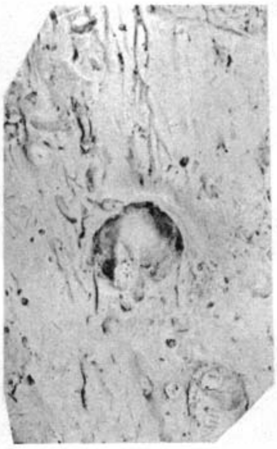

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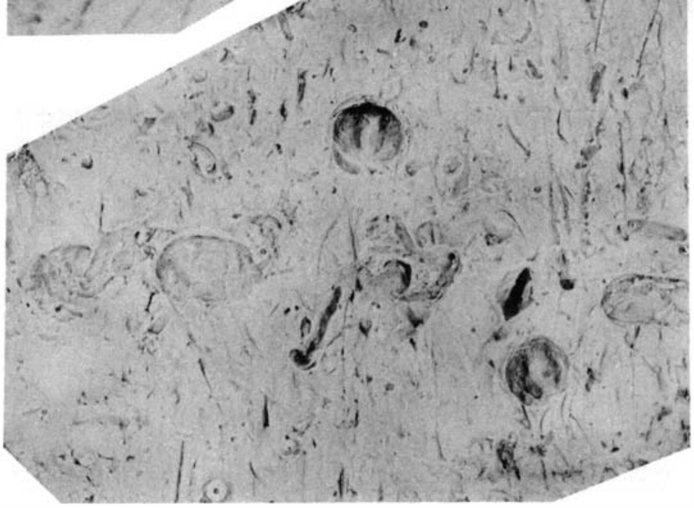

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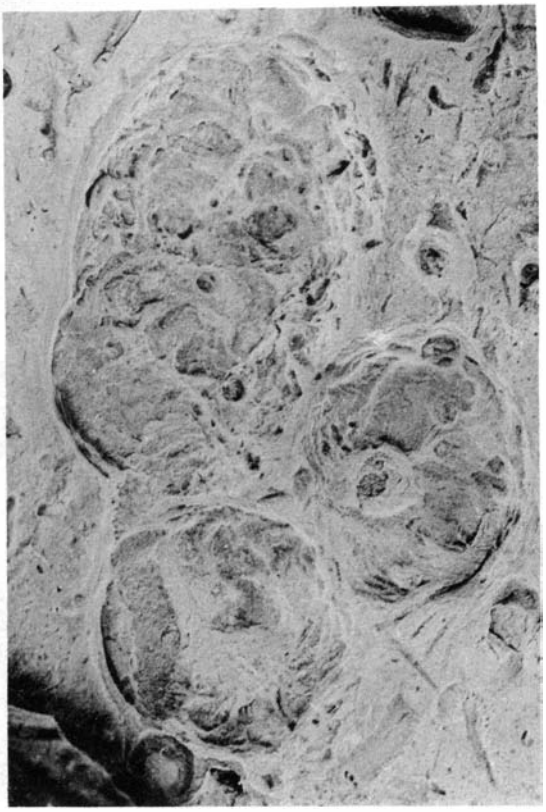

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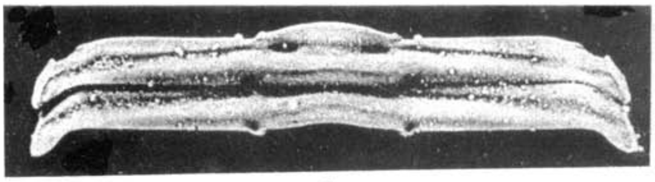
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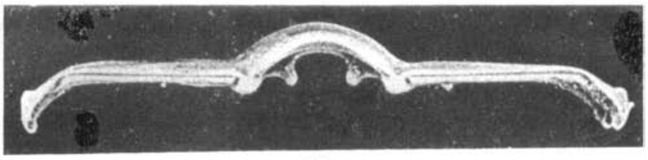
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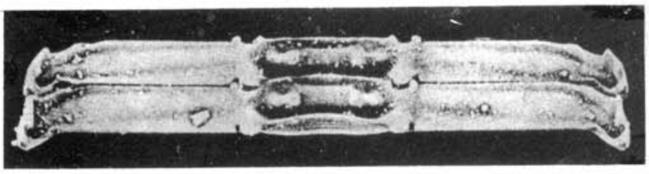
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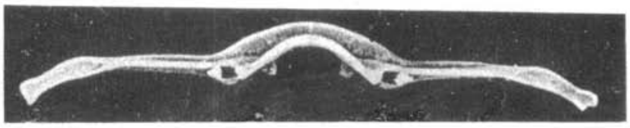
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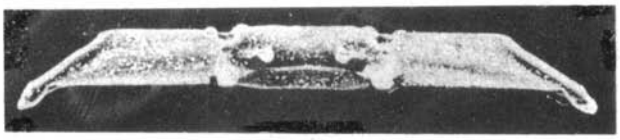
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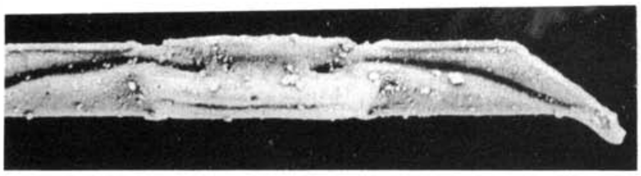
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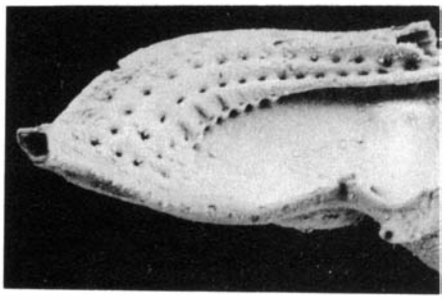
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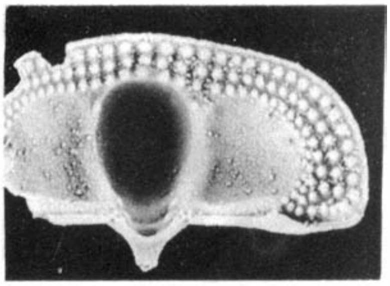
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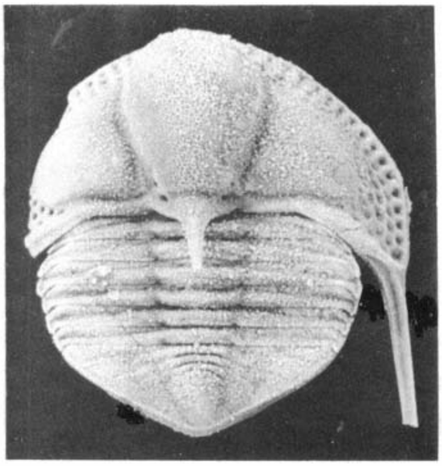
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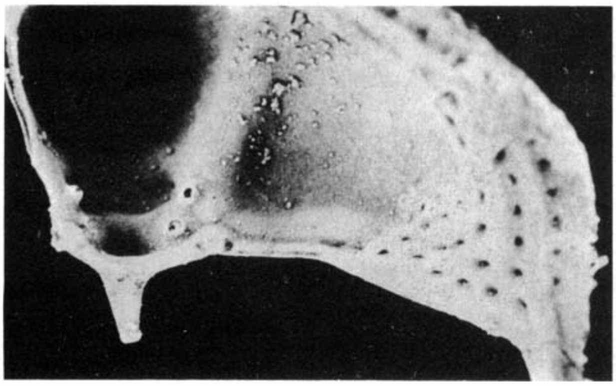
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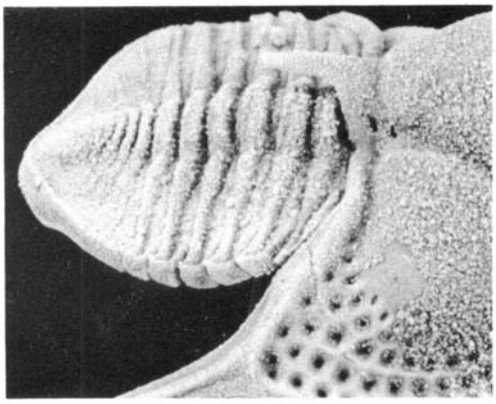
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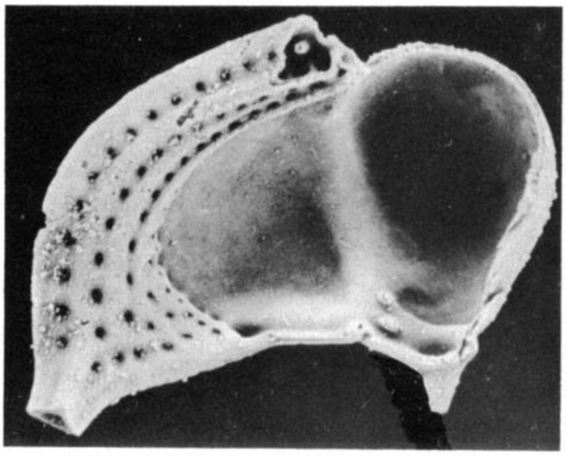
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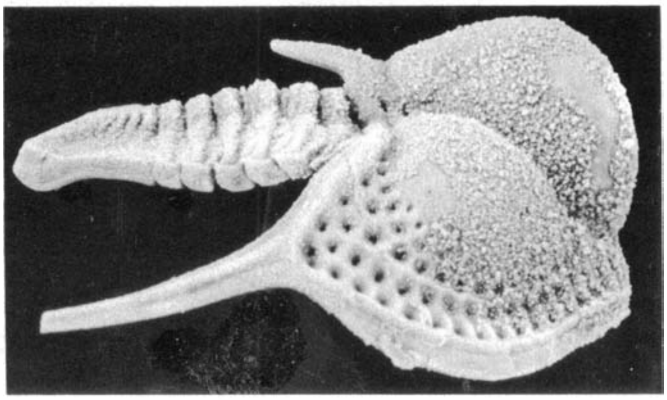

Enrollment and coaptations in some species of the Ordovician trilobite genus *Placoparia*

JEAN-LOUIS HENRY AND EUAN N.K. CLARKSON

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The species *Pl.* (*Placoparia*) *cambriensis*, *Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni*, described by Hammann (1971) from the Spanish Ordovician, are found in Brittany in formations attributed to the Llanvirn and the Llandeilo. The lateral borders of the librigenae of *Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni* bear depressions into which the distal ends of the thoracic pleurae and the tips of the first pair of pygidial ribs come and fit during enrollment. These depressions, or coaptative structures sensu Cuenot (1919), are also to be observed in *Pl.* (*Placoparia*) *zippei* and *Pl.* (*Hawleia*) *grandis*, from the Ordovician of Bohemia. However, in the species *tournemini* and *borni*, additional depressions appear on the anterior cephalic border, and the coaptations evolve towards an increasing complexity. From *Pl.* (*Placoparia*) *cambriensis*, an ancestral form with a wide geographic distribution, two distinct populations seem to have individualised by a process of allopatric speciation; one of these, probably neotenous, is represented by *Pl.* (*Coplacoparia*) *tournemini* (Massif Armoricain and Iberian Peninsula), the other by *Pl.* (*Placoparia*) *zippei* (Bohemia). Geographic isolation may be indirectly responsible for the appearance of new coaptative devices.

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The genus *Placoparia* is common in some Ordovician formations of the Massif Armoricain, but so far no detailed account of the species occurring in Brittany has yet been published. The only recent studies were made by Cavet & Pillet (1964, 1968), who described and figured a *Placoparia* occurring in nodular shales of Llanvirnian age in the synclinorium of Redon-Ancenis, which in 1968 was only provisionally assigned to the species *zippei*.

In 1876, De Tromelin & Lebesconte (pp. 636-637) recognized two species among the specimens found in the Palaeozoic synclines south of Rennes: *Placoparia tourneminei* (Rouault) and *Pl. zippei* (Boeck). which differ essentially in that they have respectively 11 and 12 thoracic segments. Later on, in the thesis he devoted to the Ordovician and the Silurian of the Crozon peninsula, Kerforne (1901:53, 178-179) mentioned one form only: *Placoparia tourneminei;* the author added that he never collected any *Pl. zippei,* "dont l'aire geographique n'est pas assez grande en Bretagne pour qu 'on puisse s'en servir comme fossile caractéristique". Let us add that, what with the lack of good illustrations in the early studies and the loss of part of the material, it is impossible to draw up detailed lists of synonyms.

Now that Hammann (1971a, 1971b, 1971c) has provided a firm systematic basis for the subfamily Placopariinae, it seemed to us pertinent to describe the coaptative devices and the enrollment of the *Placoparia* of Brittany.

TERMINOLOGY AND TECHNIQUES USED

The terminology used in the present paper is that established by Hupé (1953). From rear to front the glabellar furrows are numbered S1, S2, S3, and the corresponding lateral lobes L1, L2, L3. The word coaptation, first introduced by the French biologist Cuénot in 1919, refers to the mechanical adjustment or fitting together of two independent parts of the same animal. The coaptative structures are peculiar morphological devices (cavities, protuberances, notches, furrows etc. . . .) such as for instance interlock in a fully enrolled trilobite.

All the specimens and the latex casts figured here have been slightly whitened with ammonium chloride, and the background in some of the photographs has been partially blocked out with Indian ink. Photographs and drawings are those of the first author.

MATERIAL

The specimens studied are most often small, hardly exceeding 3 or 4 cm in length when complete. All of these come from formations assigned to the Llanvirn and to the Llandeilo. Though frequently distorted in lutites, the *Placoparia* are, however, finely preserved, the ornamentation of the test being perfectly visible on the external moulds.

In the species known from the Ordovician of Brittany, the dorsal exoskeleton is comparatively thick, being about 0.1 mm in individuals whose overall length does not exceed 3 cm. Thus the more delicate coaptative structures of the cephalon are very hard to distinguish, or are even invisible, on internal moulds. Precise determination of the species is therefore possible only in latex replicas obtained from external moulds, except of course when the test itself has been preserved.

The material comprises exoskeletons which are often incomplete and sometimes enrolled, and isolated pygidia and cranidia. Complete cephala with their fixigenae are rather rare. In some cases the hypostoma is preserved "in situ". All the specimens are part of the collections of the Geology Institute in Rennes (IGR). Theu are numbered from IGR N° 1798 to TGR N° 1966. The letter "a" following a sample number indicates an internal mould, the letter"b" an external mould.

THE SPECIES OF THE GENUS *PLACOPARIA* IN BRITTANY AND THEIR VERTICAL DISTRIBUTION

In this paper we have abandoned the stratigraphic nomenclature which students of the Ordovician of the Massif Armoricain have been using for more than a century. This out-of-date nomenclature, which is often misleading, and has become increasingly less useful as research progresses, has been replaced (in all but exceptional cases) by geographical names applying to local lithologically homogeneous units. These units have been known for quite a long time, and besides, they are those referred to on geological maps. They retain, at least for the time being, a deliberately broad meaning so as to avoid an excessive multiplication of names.

The trilobites figured in this paper come from two large geological domains: the Median Armorican synclinorium and the synclinorium of Martigné-Ferchaud (Fig. 1). They have been collected from lutites or from areno-lutites with siliceous nodules, generally known as "schistes à Calymènes". The latter, varying in thickness from about 200 to 400 m, lie over the Armorican Sandstone Formation which probably dates back to the Arenig (Deunff & Chauvel 1970). Let us add that the use of the expression "Armorican Sandstone" for the region of Brittany does not imply, in our meaning, that the lower or the upper limit of this lithological unit is everywhere synchronous.

In the Median synclinorium, the very discontinuous character of the outcrops (there is an almost total lack of continuous sections) justifies the adoption of three different denominations replacing that of "schistes à Calymènes": Postolonnec Formation for the Crozon peninsula in the West, Bas-Couyer Formation in the North of Rennes, for the region of Menez-Belair studied recently by Paris (1971, 1972), and Andouillé Formation for the northern side of the Bassin de Laval in the East. In the Crozon peninsula some quartzites forming broad layers having an overall thickness of about 14 m, appear within the Postolonnec Formation and constitute the Kerarvail Member. South of Rennes, in the synclinorium of Martigné-Ferchaud, we shall refer to the "schistes à Calymènes" under the name of Traveusot Formation. These different lithological units are described in detail and their names defended in a publication which is now in press.

The three species of genus *Placoparia* identified with certainty in the Ordovician of Brittany, namely *Pl.* (*Placoparia*) *cambriensis* Hicks, *Pl.* (*Coplacoparia*) *tournemini* (Rouault), *Pl.* (*Coplacoparia*) *borni* Hammann, have already been described from Spain by Hammann (1971a).

Pl. (*Placoparia*) *cambriensis* has been found in the Lower Llanvirn of the Iberian peninsula; the observations that may be added to Hammann's excellent description need only be minor

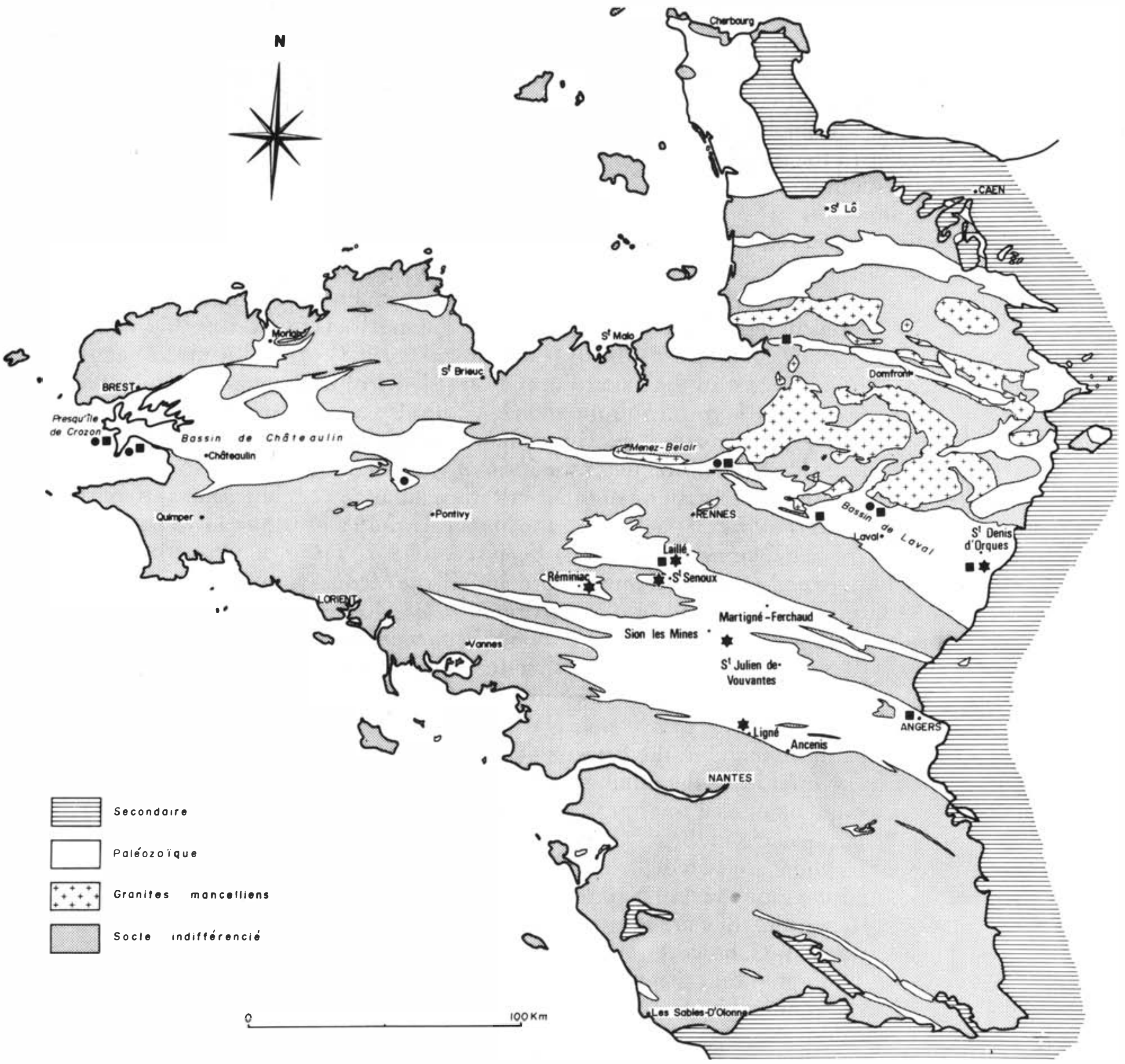

Fig. 1. Geographical distribution, as known at present, of the species *Pl. (Placoparia) cambriensis* (★), *Pl. (Coplacoparia) tournemini* (■) and *Pl. (Coplacoparia) borni* (●) in the Massif Armoricain.

ones. The specimens from the Massif Armoricain are identical with those from Spain, but the few cephala collected near Laillé, in the locality named "cote 85", are remarkably well preserved and make it possible to describe the most minute ornamentation of the exoskeleton. Three distinct elements of surface sculpture are evident. Firstly, all parts of the cephalon are densely perforated with tiny pits; these are largest and most numerous on the regions bordering the cephalic furrows and near the posterior border and near edge of the occipital ring. Secondly, the fixigenae are pitted with about 50 to 60 much larger deep cavities, roughly oval or round in shape. Irregularly distributed, and differing even on the two fixigenae of one single cephalon (Pl. 1:4), these cavities are scattered over a trapezoidal surface separated from the dorsal glabellar furrows and the posterior furrows of the cheeks by a margin ranging from 0.3 to 0.4 mm in breadth. It will be noted that the most distinct cavities lie close against the facial suture, on the external lateral portions of the fixigenae. Three similar cavities are present near the anterior glabellar border, in the plane of symmetry of the cephalon. Thirdly, between the cavities the test carries a fine and dense granulation. The whole cephalon is covered, the furrows excepted, with granules: these are of small size on the occipital ring and on the posterior borders of the cheeks, as well as on the lateral lobes L1, L2, L3, but their dimensions increase on the frontal glabellar lobe (Pl. 1:1; Pl. 3:1). The anterior cephalic border is gently arched and its breadth (sag.) remains more or less uniform over its whole length; the granulation which covers it is identical with that which ornaments the frontal lobe of the glabella. Librigenae have not been found in the material from Brittany, though Hammann (1971a, Pl. 1:9a-b) illustrates a pyritised enrolled specimen with the librigenae in place.

The specimens discovered by Cavet & Pillet (1964) in the nodular shales of Ligné (synclinorium of Redon-Ancenis) are certainly *Pl.* (*Placoparia*) *cambriensis.* The typical ornamentation of the fixigenae, and the presence of 12 thoracic segments and of 3 clear rings on the pygidial axis, make this indisputable. The specimens of the Ordovician shales of Sion-les-Mines (Loire-Atlantique), mentioned by De Tromelin & Lebesconte (1876) as *Placoparia zippei,* must also be assigned to the species *cambriensis.*

In the synclinorium of Martigné-Ferchaud, in Laillé, Saint-Senoux, and Sion-les-Mines, *Pl.* (*Placoparia*) *cambriensis* has been collected at the base of the Traveusot Formation, in black shales containing *Didymograptus* cf. *bifidus.* In addition to this graptolite there occur, in the locality named "cote 85", *Trinodus* sp. and *Pseudosphaerexochus* (*Pateraspis*) sp. *Pl.* (*Placoparia*) *cambriensis* is also present at the same level in the syncline of Réminiac (Quété 1975). Finally, in siliceous nodules from the Ligné region, the species is found together with *Pricyclopyge binodosa* and *Ormathops* cf. *atavus* (Cavet & Pillet 1968). Apart from the genus *Trinodus,* all these trilobites occur in the Šárka Formation (Llanvirn) in Bohemia (Marek 1961; Havlíček & Vaněk 1966). *Ormathops nicholsoni* and *O. alatus* also accompany *Pl.* (*Placoparia*) *cambriensis* and *Pricyclopyge binodosa* in the Hope Shales (Lower Llanvirn) of Shropshire (Whittard 1966; Dean 1967). Though the determination of the *Didymograptus* is uncertain owing to distortion and poor preservation, all other criteria lead us to conclude that the shales containing *Pl.* (*Placoparia*) *cambriensis* belong, in the Massif Armoricain, to the Lower Llanvirn.

In Brittany, the species *cambriensis* has only been recorded, so far, in the Palaeozoic synclines south of Rennes and at the extreme eastern end of the Median synclinorium (region of Saint-Denis-d'Orques : locality called "Butte du Creux").

When Rouault (1847:320, 326) first cited *Calymene tournemini,* he wrote *tournemini,* and not *tourneminei.* Whatever the origin of this specific name may be, and even if there has been an incorrect transliteration, there is no need to amend and modify the name originally given by Rouault. *Pl.* (*Coplacoparia*) *tournemini* is the most common species of this genus in the whole Median synclinorium and in the Palaeozoic synclines south of Rennes. It differs from *Pl.* (*Placoparia*) *cambriensis* in the number both of its thoracic segments (11 instead of 12), and in the clearly individualized rings in the pygidial axis (4 instead of 3). Moreover, the external edges of the librigenae each bear 12 deep cavities, and on the lateral parts of the anterior cephalic border there are two depressions expanding transversely lengthwise; they are a constant feature in all the individuals examined (Pl. 1:6–8). Though the large cavities of the fixigenae remain clearly visible, they are more faintly impressed than those of *Pl.* (*Placoparia*) *cambriensis.* The very small pits, however, are similar in size and distribution to those of that species. Finally, it will be noted that the granules covering the anterior border of the cephalon are smaller, but far more numerous, than those which ornament the frontal glabellar lobe (Pl. 1:8; Pl. 3:4).

The hypostoma has been found "in situ" in several specimens from Traveusot (IGR N° 1873b, Pl. 1:14; IGR N° 1883a–b; IGR N° 1891b, Pl. 1:13). It is oval-shaped; its maximum breadth, measured at the level of the triangular anterior wings, is somewhat greater than its maximum length. The hypostomal suture is a curve, slightly convex towards the front. The median body, strongly curved, has neither an anterior furrow nor distinct maculae, but it displays laterally, half-way down its length, two extremely faint short notches obliquely directed rearwards and inwardly (Pl. 1:14). At the level of these two notches, just where the posterior furrow disappears, the lateral edges of the hypostoma swell into two projecting protuberances. The narrow border constituting the buccal edge carries perhaps one or two pairs of tiny points (?).

In the Crozon Peninsula, *Pl.* (*Coplacoparia*) *tournemini* appears, according to Kerforne (1901:53), above the Kerarvail Member. At about 30 m in thickness under the *Marrolithus bureaui* Zone, this species is still represented by a few specimens only, then it becomes extinct. Its vertical range appears to be identical in both the Bas-Couyer Formation (Menez-Belair) and the Andouillé Formation (Bassin de Laval). To the south of Rennes, *Pl.* (*Coplacoparia*) *tournemini* is present in the middle and upper part of the Traveusot Formation, in micaceous areno-lutites which are of unknown thickness but which overlie black lutites containing *Pl.* (*Placoparia*) *cambriensis.* The areno-lutites of Traveusot en Guichen contain a few *Glyptograptus,* unfortunately incomplete and poorly preserved, which makes their precise determination impossible; these *Glyptograptus* might belong to the species *teretiusculus,* or to a new species (information communicated by V. Jaanusson). Overlying the Traveusot Formation in ascending sequence are the Chatellier Sandstones, about 50 to 60 m thick, then the Shales of Riadan whose trilobite fauna (very similar to that collected from the top of the Postolonnec Formation in the Finistère) shows strong affinities with the fauna known in the Libeň Formation in Bohemia (Middle and Upper Llandeilo, and Lower Caradoc; cf. Williams & al. 1972 : Fig. 2 for

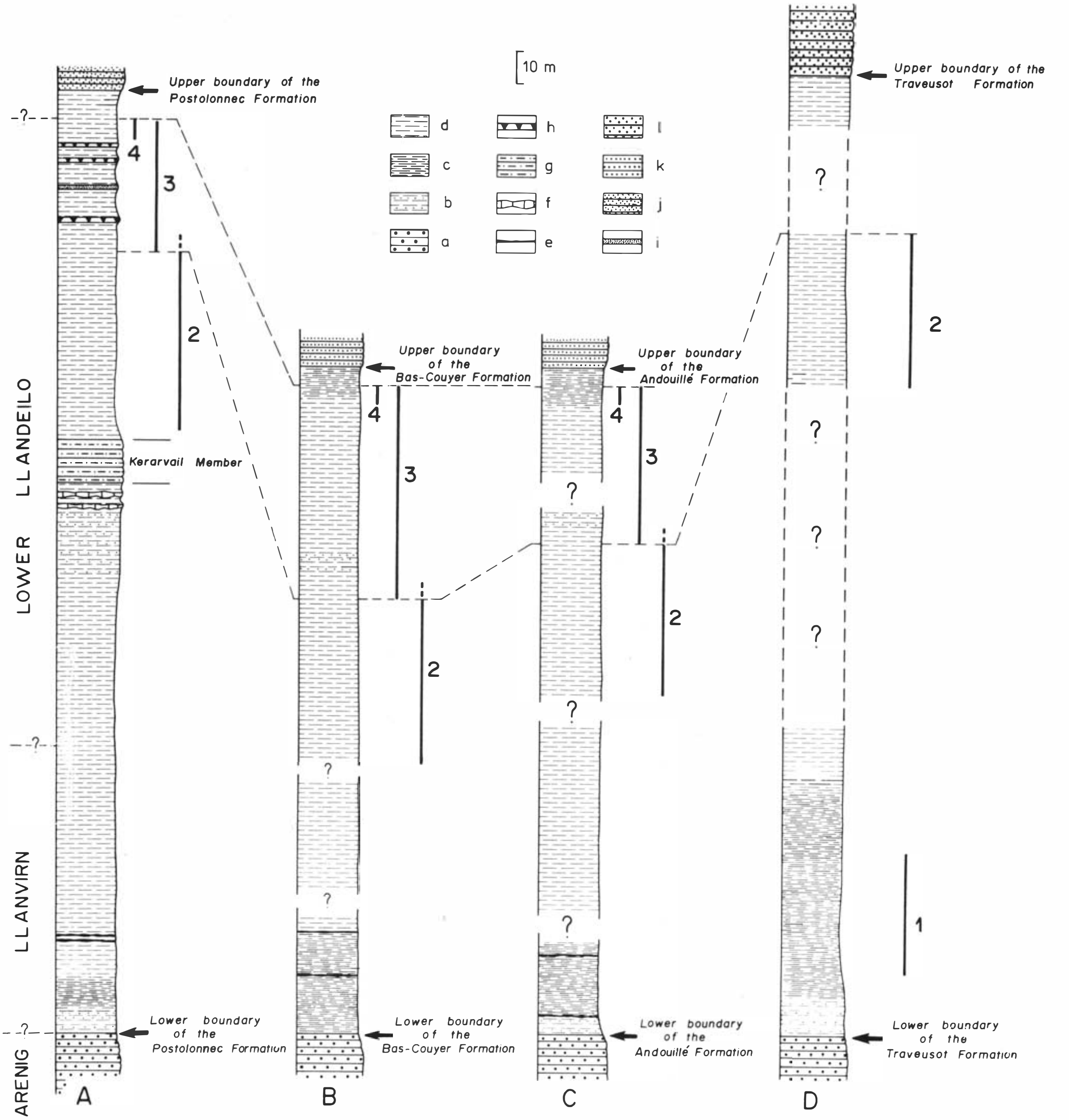

Fig. 2. Vertical distribution, as known at present, of the species *Pl. (Placoparia) cambriensis* (1), *Pl. (Coplacoparia) tournemini* (2), *Pl. (Coplacoparia) borni* (3), *Marrolithus bureaui* (4). A. Postolonnec section, Crozon peninsula. B. Menez-Belair region. C. Bassin de Laval. D. Martigné-Ferchaud synclinorium.
a. Armorican Sandstone Formation (Grès armoricain). b. Sandstone – shale alternations. c. Lutites. d. Areno-lutites. e. Oolitic beds. f. Lenticular beds of calcareous sandstone. g. Kerarvail sandstone. h. Sill. i. Thick sandstone bed. j. Sandstones of the Kermeur Formation. k. Sandstones of the Saint-Germain-sur-Ille Formation. l. Sandstones of the Chatellier Formation.

further information). In the absence of unequivocal criteria and since the sedimentary sequence is apparently conformable, it would seem for the moment that to attribute part of the Formations of Postolonnec (the *Marrolithus bureaui* Zone included) and of Traveusot to the Lower Llandeilo remains the only logical possibility.

In stratigraphic sequence *Pl.* (*Coplacoparia*) *borni* succeeds *Pl.* (*Coplacoparia*) *tournemini*, but this trilobite has never been reported, as far as we know, in the synclinorium of Martigne-Ferchaud. It is well represented, however, throughout the Armorican Median synclinorium, where it is found in association with *N.* (*Neseuretus*) *tristani, Plaesiacomia oehlerti, Crozonaspis struvei, Morgatia hupei*; it is still abundant in the *Marrolithus bureaui* Zone, but then disappears suddenly. One of the remarkable features of *Pl.* (*Coplacoparia*) *borni* is the presence of 4 semicircular depressions on the inner edge of the anterior cephalic border, a border which is covered with extremely close-set granules (Pl. 3:7–8). On the fixigenae the large cavities are barely visible and not numerous, but, as can be observed in the species *tournemini,* a few deep cavities remain on the outer region of the fixigenae. The distribution of the tiny pits remains as in the preceding species.

ENROLLMENT AND COAPTATIVE STRUCTURES

An abundance of well preserved samples, and partially or totally enrolled specimens, has made it possible for us to describe in detail the coaptative devices of *Pl.* (*Coplacoparia*) *tournemini* and of *Pl.* (*Coplacoparia*) *borni,* two species in which the enrollment is exactly alike.

When an individual trilobite enrolled, the rounded distal ends of the thoracic pleurae fitted into well marked cavities, each with a smooth bottom and set in a spiral on the lateral borders of the cheeks. These small depressions, from point ω onwards, have been numbered from 1 to 12 on each border (Pl. 2:6). From rear to front they are first located sub-ventrally, then they gradually become marginal. It is into the two foremost cavities of the librigenae that the blunt tips of the first two ribs of the pygidium come and fit. The tips of the second pair of ribs fit into the lateral depressions of the anterior cephalic border, whereas the tips of the third and fourth pairs of pygidial ribs lock into the preglabellar furrow (Pl. 2:8–10). It will be noted that the posterior border of the fixigenae bears distally a wide and short spine which fits, at the beginning of the enrollment, into a corresponding depression located on the first thoracic pleura (Pl. 2:11–12).

Hammann (1971a, Pl. 1:9a–b) has given two excellent photographs of an enrolled *Pl.* (*Placoparia*) *cambriensis.* Despite appearances, the position of the pygidium in respect to that of the cephalon at the end of the enrollment, does not differ, in that species, from that observed in *Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni*. Indeed, from the lateral view of the specimen figured by Hammann, it may be seen that the distal ends of the thoracic pleurae (from the fifth to the eleventh) are not in contact with the lateral margin of the cheek. Such incompletely enrolled specimens are frequently observed (Barrande 1872, Pl. 8:33; Prantl & Šnajdr 1957, Pl. 1(31):5; Hammann 1971, Pl. 2:13a–b; Pl. 2:7 in the present paper), not only in the genus *Placoparia* but also in *Colpocoryphe* (unpublished). Incomplete enrollment might be explained, in certain cases at least, by a partial relaxation of the musculature after death, together with rapid burial in the sediment.

Pl. (*Placoparia*) *zippei* (Dobrotivá Formation) was also capable of enrollment, as Prantl & Šnajdr (1957, Pl. 2(32):15) have figured the cast of one cheek revealing, on the lateral border, a few depressions which are very similar to those observed on *Pl.* (*Coplacoparia*) *tournemini* and *Pl.* (*Coplacoparia*) *borni.* We have not examined any enrolled individual of *Pl.* (*Placoparia*) *zippei,* but there is no reason to assume that in this species the enrollment differed from that of Ordovician forms from Brittany. The same applies to *Pl.* (*Hawleia*) *grandis* (Libeň and Letná Formations) in which the lateral margins of the cheeks also bear depressions (Barrande 1872, Pl. 8:43–44). The samples of *Pl.* (*Hawleia*) *prantli* (Ashgill of Poland) figured by Kielan (1959, Pl. 23:4–6) are poorly preserved and it is therefore impossible to comment upon the presence or the absence of coaptative structures.

EVOLUTION OF THE GENUS *PLACOPARIA* DURING THE LLANVIRN AND THE LLANDEILO

The most ancient representative of the genus so far known is *Pl. (Placoparia) cambriensis.* The lateral margin of the cheeks belonging to the specimen figured by Hammann (1971a, Pl. 1:9b) seems to reveal very slight depressions in the anterior part. These seem to be present also, and similarly located, on an external mould coming from the Šárka Formation in Bohemia. If the existence of these barely excavated depressions were confirmed by the examination of more abundant material it would reinforce the suggestion that *Pl.* (*Placoparia*) *zippei* and *Pl. (Coplacoparia) tournemini* derived from *Pl. (Placoparia) cambriensis.* Indeed, in the two Llandeilian species the depressions into which the distal ends of the thoracic pleurae interlock are already quite clear. But on the anterior border of *Pl. (Coplacoparia) tournemini* two additional excavations are present. These coaptative structures, like the ones already (described in the case of Ordovician and Silurian t_r)

described in the case of Ordovician and Silurian trilobites (Clarkson & Henry 1973), are remarkably regular features of the adults throughout the whole time range of the species. The same applies to *Pl. (Coplacoparia) borni* in which the cephalon bears, besides the two deepening lateral cavities, four new depressions located on the inner edge of the anterior cephalic border, and not on the outer edge as figured by Hammann (1971a: Fig. 3). It is as though the blunt tips of the pygidial ribs, which come to rest in the preglabellar furrow when enrollment is complete, were imprinted into an exoskeleton which was still soft; yet researches upon the coaptations of contemporary invertebrates have revealed that such mutual moulding of the coapting parts during ontogeny cannot be invoked as an explanation, and that the coaptative devices are genetically inherited (Tétry 1969; Sahuc 1969).

In the Armorican Median synclinorium, *Pl. (Coplacoparia) borni* succeeds *Pl. (Coplacoparia) tournemini* from which it probably derived, but the two trilobites may perhaps have coexisted for a short while, since they are encountered together in the same locality (foundations of the house named "les Atlantes" in Postolonnec). One of the cranidia collected (IGR N° 1851b, Pl. 3:6) shows an interesting peculiarity : although it has most of the characteristics of the species *borni,* the total number of depressions on the anterior border is 4 rather than 6. The two small hollows located immediately on each side of the plane of symmetry are missing. This "absence" originates neither in the distortion it underwent – which is very faint – nor in the preservation – which is excellent since the granulation is perfectly preserved. This specimen could either be representative of an intermediate stage, indicating a gradual transition from *Pl. (Coplacoparia) tournemini* to *Pl. (Coplacoparia) borni,* or else a hybrid, signifying the interfecundity of two distinct populations.

Parallel with the increasing complexity of the coaptative structures throughout time, and perhaps in close connection with this evolution, some characters already observed by Curtis (1961) and by Hammann (1971a) undergo gradual changes. Thus one may observe the decrease in number and size of the small pits on the fixigenae, the increase of the degree of curvature and of the length of the pygidial ribs, the increase of the density of the granules on

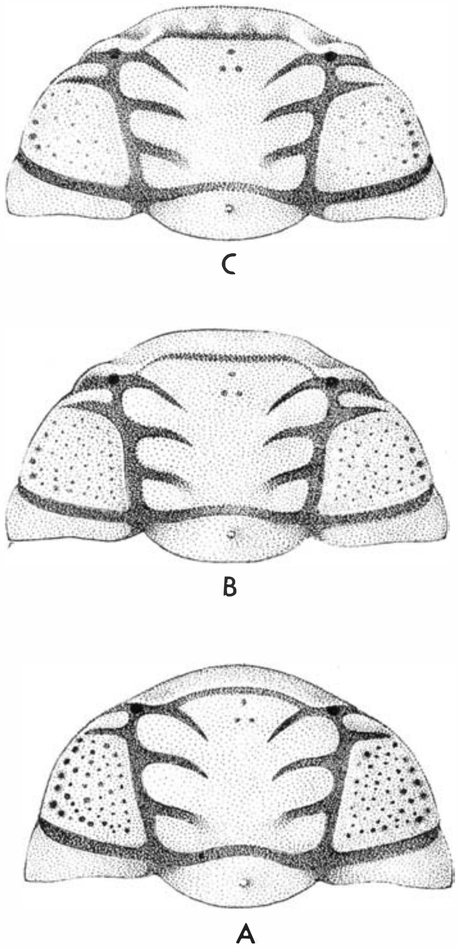

Fig. 3. Pl. (Placoparia) cambriensis (A), *Pl. (Coplacoparia) tournemini* (B), *Pl. (Coplacoparia) borni* (C). Reconstruction of the cranidia.

the anterior cephalic border of the species *tournemini* and *borni*. Along the contact surfaces between two coapting parts, this increase of the granulation has been observed, without any exception, in all the Ordovician trilobites of Brittany having coaptative devices (Clarkson & Henry 1973). In our estimation, this corroborates the ideas of Sahuc (1969) on the direct part played by mechanical rubbing and pressure in the elaboration of the coaptative structures.

In Bohemia, during the Llandeilo and the Caradoc (Dobrotivá Formation, Libeň and Letná Formations), the coaptative devices of *Pl. (Placoparia) zippei* and *Pl. (Hawleia) grandis* do not seem to undergo any improvement. In contrast to what is observed in the species from Brittany, no depressions appear on the anterior border of the cephalon whose granulated ornamentation, at least in the case of *Pl. (Placoparia) zippei,* is not different from that of the glabella. It is difficult to show for the moment, as direct evidence is lacking, that the two species *Pl. (Coplacoparia) tournemini* and *Pl. (Placoparia) zippei,* with their limited geographical distribution, constituted two strictly contemporaneous populations, but it is logical to assume that they are both derived, through allopatric speciation, from *Pl. (Placoparia) cambriensis,* a widely distributed ancestral form, since it is known in Great Britain, in Spain, in Bohemia, and in Brittany. As Devillers (1973:32) puts it: " . . . á partir d'une population ancestrale divergent progressivement des populations entre lesquelles s'établit une barrière, géographique, physiologique ou autre qui, en supprimant les croisements, empêche le brassage génétique. Dans chaque population s'accumulent, peu à peu, des caractères qui vont accentuer sa physionomie particulière et contribueront, avec l'isolement génétique qui progresse, à lui donner le statut d'espèce". Confirmatory evidence from further observations might give additional weight to some of the ideas recently expressed by Eldredge (1971, 1973) regarding allopatric speciation in Palaeozoic invertebrates.

In a paper published recently (Clarkson & Henry 1973), we wrote that the development of of predators (cephalopods) might be an indirect cause of the increasing complexity of the coaptative structures in some of the Ordovician and Silurian trilobites. This suggestion remains reasonable, but, as Hammann (1971a:66) wrote, geographical isolation, leading to particular modes of life in a given region, must not be forgotten. Whereas enrollment is often considered as a defence reaction against predators, it may also be interpreted as a reaction of the animal living in shallow waters liable to rapid variations of ecological factors (temperature, salinity, etc. . . .). In a temporarily isolated palaeogeographical province (Massif Armoricain and Iberian Peninsula), an unfavourable and unstable environment might be indirectly responsible for the appearance of new morphological devices among the representatives of genus *Placoparia.* Such a possibility is not unreasonable since the trilobite faunas known in the Spanish and Armorican Ordovician are poor; they only contain a limited number of genera and species. Moreover, in some fossiliferous localities from Brittany, where the exoskeletons are often complete (Traveusot for instance), the proportion of enrolled individuals is always very high.

The presence of 11 thoracic segments only in *Pl. (Coplacoparia) tournemini* and *Pl. (Coplacoparia) borni,* as compared with the other known species which have 12, remains to be explained. During ontogeny, the posterior elements of the exoskeleton are the last to become differentiated and the growth is directed forwards. This is clear from a number of ontogenetic series, particularly that of *Breviscutellum (Meridioscutellum),* as Feist (1970) has shown. There is no reason to suppose that growth and development in *Placoparia* was any different. Thus to be equivalent to *Pl. (Placoparia) cambriensis,* the pygidium of the *tournemini* and *borni* species would have to release an additional segment towards the thorax, one pair of pleurae then simultaneously originating in the posterior extremity of the pygidium. It may therefore be assumed that *Pl. (Coplacoparia) tournemini* and *Pl. (Coplacoparia) borni* constitute a neotenous line in which there occurs" . . . un retard dans le developpement des structures corporelles relativement à celui des organes reproducteurs" (Hupé 1953:85). To assume that evolution along this line resulted from arrested development, as R. Feist (personal communication) has suggested to us, appears to be the most plausible explanation.

In Brittany, the biozones of the species *cambriensis, tournemini,* and *borni*, such as are illustrated in Fig. 2, certainly could be improved upon, but they are still very useful in an area where the outcrops are scarce and where continuous sections are lacking.

ACKNOWLEDGEMENTS. – We wish to thank Professors and Drs. R. Feist (Montpellier), V. Jaanusson (Stockholm), J.-C. Lefeuvre (Rennes) L. Marek (Praque) and H. Tintant (Dijon), and also the palaeontologists of Brest and Rennes for their advice and assistance.

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EXPLANATION OF PLATES

Plate 1.

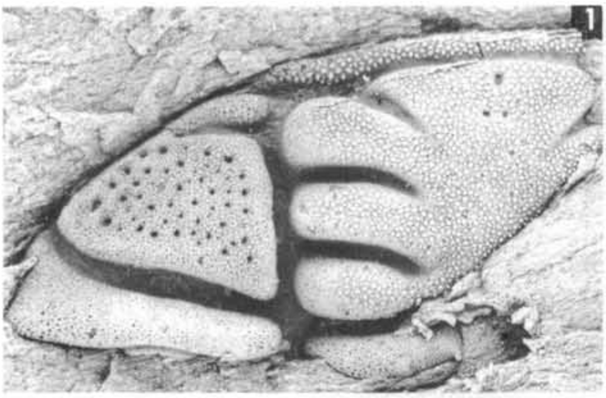
The following figures are based on latex replicas: 1, 3, 5–11, 13–14. *Figs. 1–4. Placoparia (Placoparia) cambriensis* Hicks. *Fig. 1.* Cranidium, dorsal view. IGR N^{O} 1690b. x10. *Figs. 2–3.* Pygidium, dorsal and oblique posterior views. IGR N^{O} 1939a–b. x16.(approx.). *Fig. 4.* Cranidium, dorsal view. IGR N^{O} 1692. x10. All the specimens come from the Traveusot Formation. "Cote 85" near Laillé, Ille-et-Vilaine. *Figs. 5–10. Placoparia (Coplacoparia) tournemini* (Rouault). *Fig. 5.* Cephalon partially shown, in lateral oblique view; note the depressions on the lateral border of the librigena. IGR N^{O} 1894b. x8 (approx.). Traveusot Formation. Traveusot en Guichen, Ille-et-Vilaine. *Fig. 6.* Two cranidia, dorsal view. IGR N^{O} 1854b. x10. Postolonnec Formation. Morgat, Crozon peninsula, Finistère. *Fig. 7.* Incomplete cephalon and three thoracic segments, dorsal view. IGR N° 1823b. x5. Andouille Formation (?). Butte du Creux near Saint-Denis-d'Orques, Sarthe. *Fig. 8.* Cranidium, dorsal view. IGR N^{O} 1852b. x14 (approx.). Postolonnec Formation. Foundations of the house named "les Atlantes", Postolonnec, Crozon peninsula. *Figs. 9–10.* Incomplete pygidium, dorsal and posterior views. IGR N^{O} 1899b. x7. Traveusot Formation. Traveusot en Guichen. *Fig. 11. Placoparia (Coplacoparia)* sp. Hypostoma. IGR N^{O} 1856b. x6. Postolonnec Formation. Morgat, Crozon peninsula. *Figs. 12–14. Placoparia (Coplacoparia) tournemini. Fig. 12.* Hypostoma. IGR N^{O} 1581a. x6. Bas-Couyer Formation. Bas-Couyer en Mélesse, Ille-et-Vilaine. *Figs. 13–14.* Hypostoma "in situ". IGR N^{O} 1891b (Fig. 13) and IGR N^{O} 1873b (Fig. 14). x8. Traveusot Formation. Traveusot en Guichen.

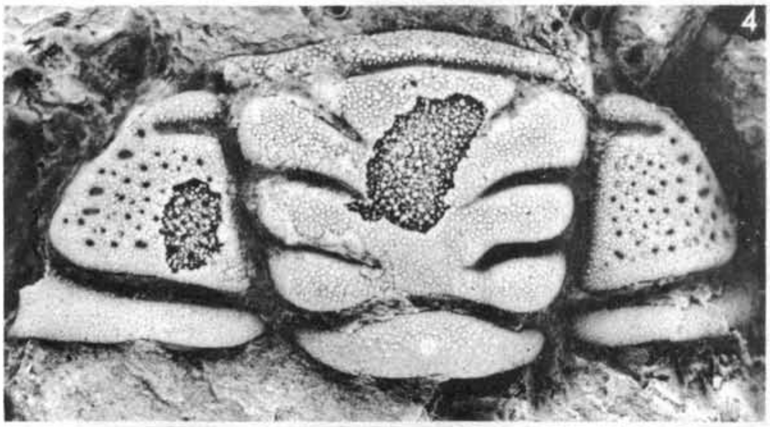
Plate 2.

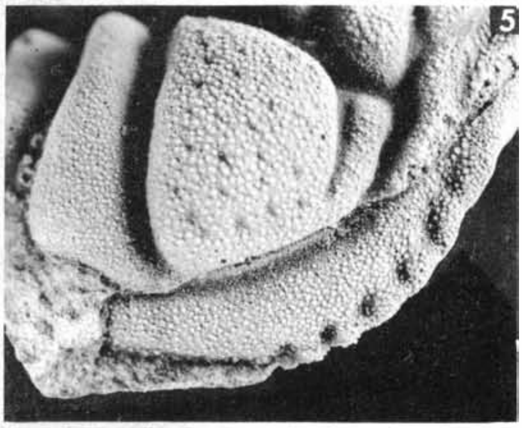
The following figures are based on latex replicas: 2, 6–8, 12. *Figs. 1–5. Placoparia (Coplacoparia) borni* Hammann. *Fig. 1.* Cranidium, dorsal view. IGR N^{O} 1832. x6. Andouillé Formation. Les Monneries, Andouillé, Mayenne. *Fig. 2.* Incomplete cranidium, dorsal view. IGR N^{O} 1853b. x6. Postolonnec Formation. Postolonnec, Crozon peninsula. *Figs. 3–5.* Pygidium in dorsal, posterior and lateral views. IGR N^{O} 1806. x5. Andouillé, Formation (*Marrolithus bureaui* Zone). La Touche, Andouillé, Mayenne. *Figs. 6–8. Placoparia (Coplacoparia) tournemini. Fig. 6.* Incomplete cephalon partially shown, frontal oblique view; note the depressions (from the fifth to the twelfth) on the lateral border of the librigena. IGR N^{O} 1966b. x10. Traveusot Formation. Traveusot en Guichen. *Fig. 7.* Incompletely enrolled specimen, dorsal view. IGR N^{O} 1822b. x4. Andouillé Formation (?). Butte du Creux near Saint-Denis-d'Orques. *Fig. 8.* Incomplete, but fully enrolled specimen, partially shown in dorsal view. IGR N^{O} 5400b. x6 (approx.). Bas-Couyer Formation. Bas-Couyer en Mélesse. *Figs. 9–11. Placoparia (Coplacoparia) borni. Figs. 9–10.* Fully enrolled specimen, lateral and dorsal views. IGR N^{O} 1805a. x3.5 (approx.). *Fig. 11.* Enrolled specimen partially shown, in lateral view, with the distal extremities of five thoracic pleurae fitting into corresponding depressions of the lateral border of the librigena. IGR N^{O} 1818. x10. Andouillé Formation (*Marrolithus bureaui* Zone). La Touche, Andouillé. *Fig. 12. Placoparia (Coplacoparia) tournemini.* Part of an enrolled specimen, lateral view. IGR N^{O} 5400b (see Fig. 8). x10. Bas-Couyer Formation. Bas-Couyer en Mélesse.

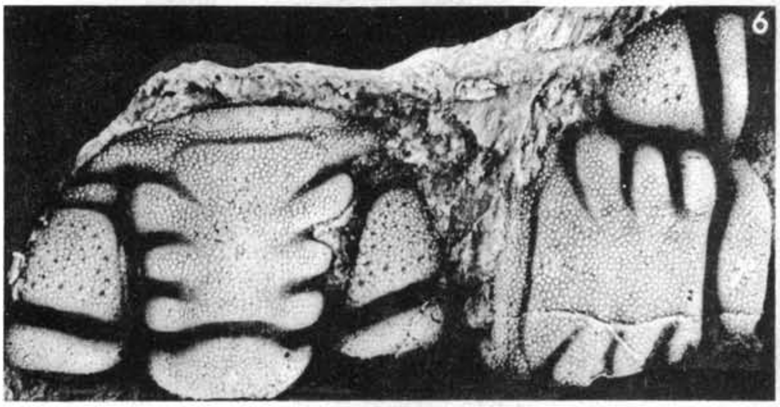
Plate 3.

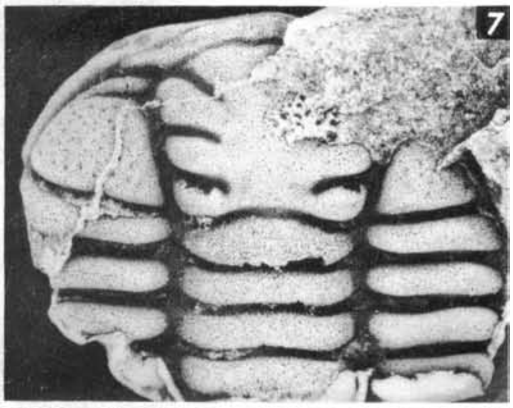
The following figures are based on latex replicas: 1–9. *Figs. 1–3. Placoparia (Placoparia) cambriensis. Fig. 1.* Part of a cranidium showing the anterior cephalic border. IGR N^{O} 1690b (see Pl. 1:1). x15. *Fig. 2.* Fixigena of the same specimen. x15. *Fig. 3.* Incomplete cranidium partially shown; the distortion is very faint. IGR N^{O} 1821b. x15 (approx.). Butte du Creux near Saint-Denis-d'Orques. *Figs. 4–5. Placoparia (Coplacoparia) tournemini. Fig. 4.* Enlargement of part of a cranidium showing the two depressions and the extreme tuberculation on the anterior cephalic border. IGR N^{O} 1852b (see Pl. 1:8). x20. *Fig. 5.* Dorsal oblique view of a fixigena. IGR N^{O} 5400b (see Pl. 2:8, 12). x10. *Fig. 6. Placoparia (Coplacoparia)* cf. *borni.* Enlargement of a cranidium partially shown; the anterior cephalic border bears only four depressions. IGR No 1851b. x15. Foundations of the house named "les Atlantes", Postolonnec, Crozon peninsula. *Figs. 7–10. Placoparia (Coplacoparia) borni. Figs. 7–8.* Two incomplete cranidia partially shown, dorsal views; note the depressions located on the inner edge of the anterior cephalic border. IGR N^{O} 1855b (Fig. 7) and IGR N^{O} 1853b (Fig. 8). x15. Postolonnec Formation. Foundations on the house named "les Atlantes", Postolonnec, Crozon peninsula. *Fig. 9.* Enlargement of a fixigena belonging to the specimen IGR N^{O} 1855b (see Fig. 7). x15. *Fig. 10.* Part of a cranidium in dorsal view showing the six depressions on the anterior cephalic border. IGR N^{O} 1813. x18 (approx.). Andouillé Formation. Les Monneries, Andouillé, Mayenne.

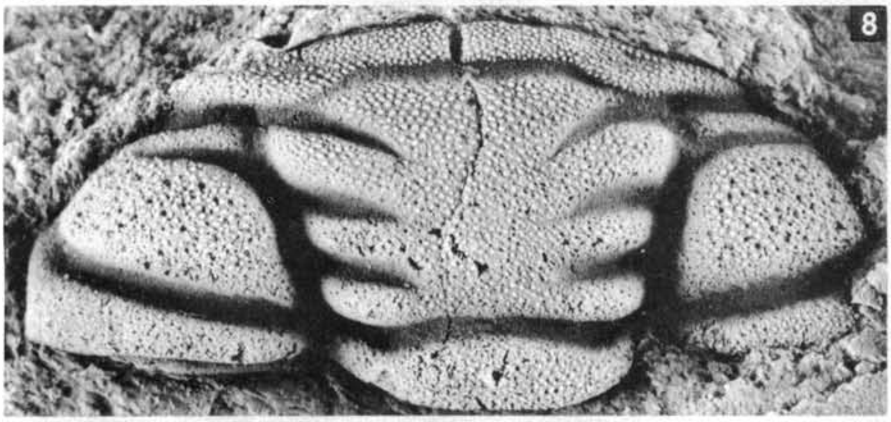


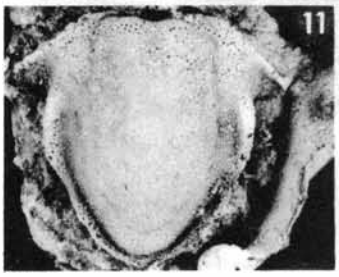


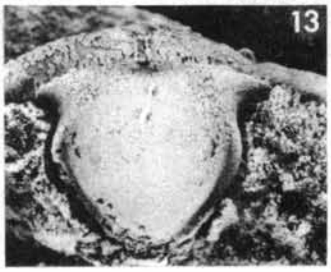












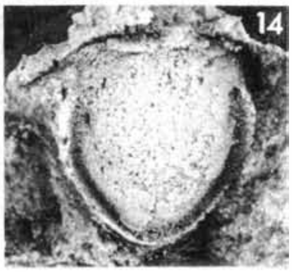


Plate 1.

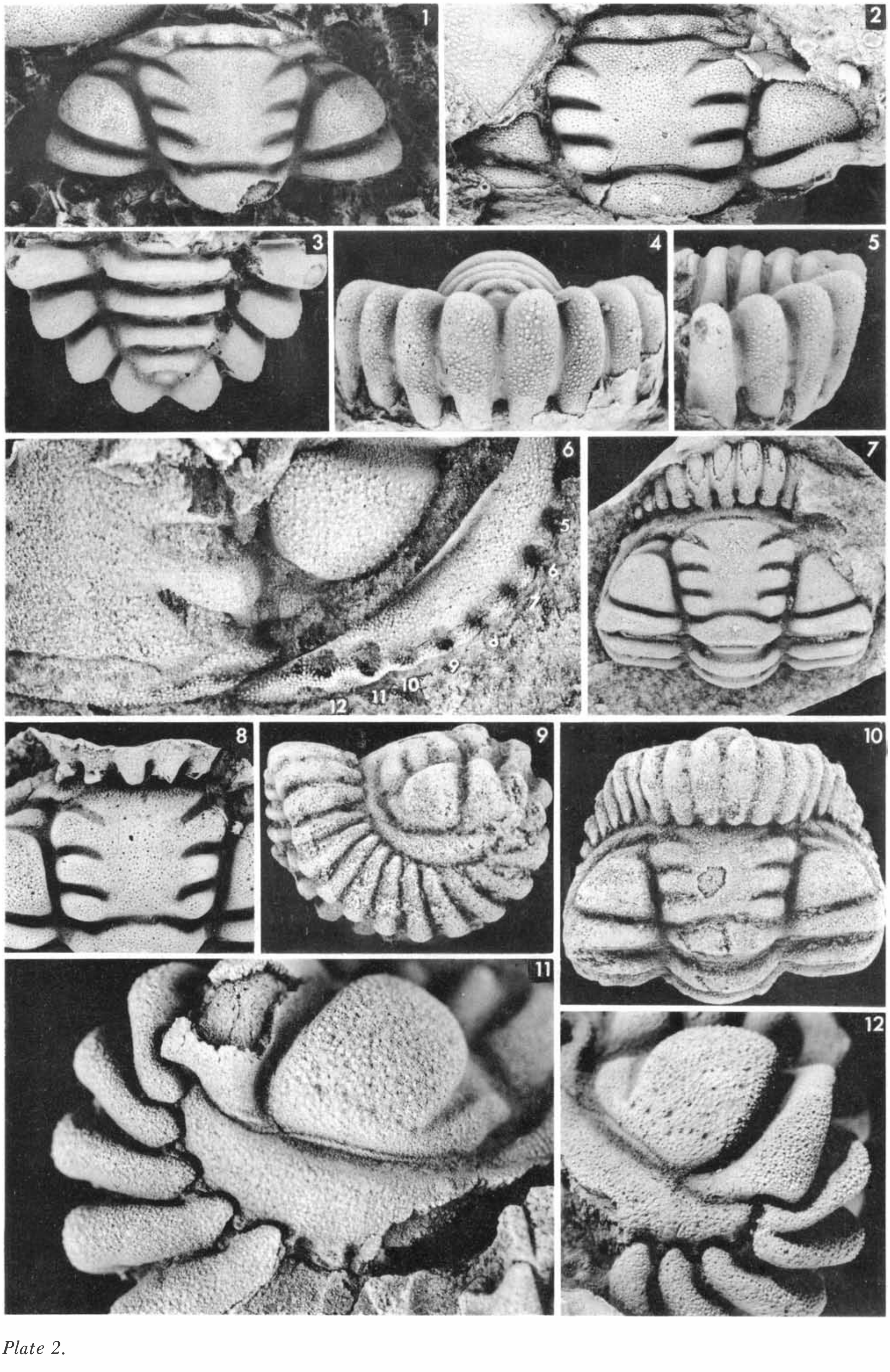


Plate 2.

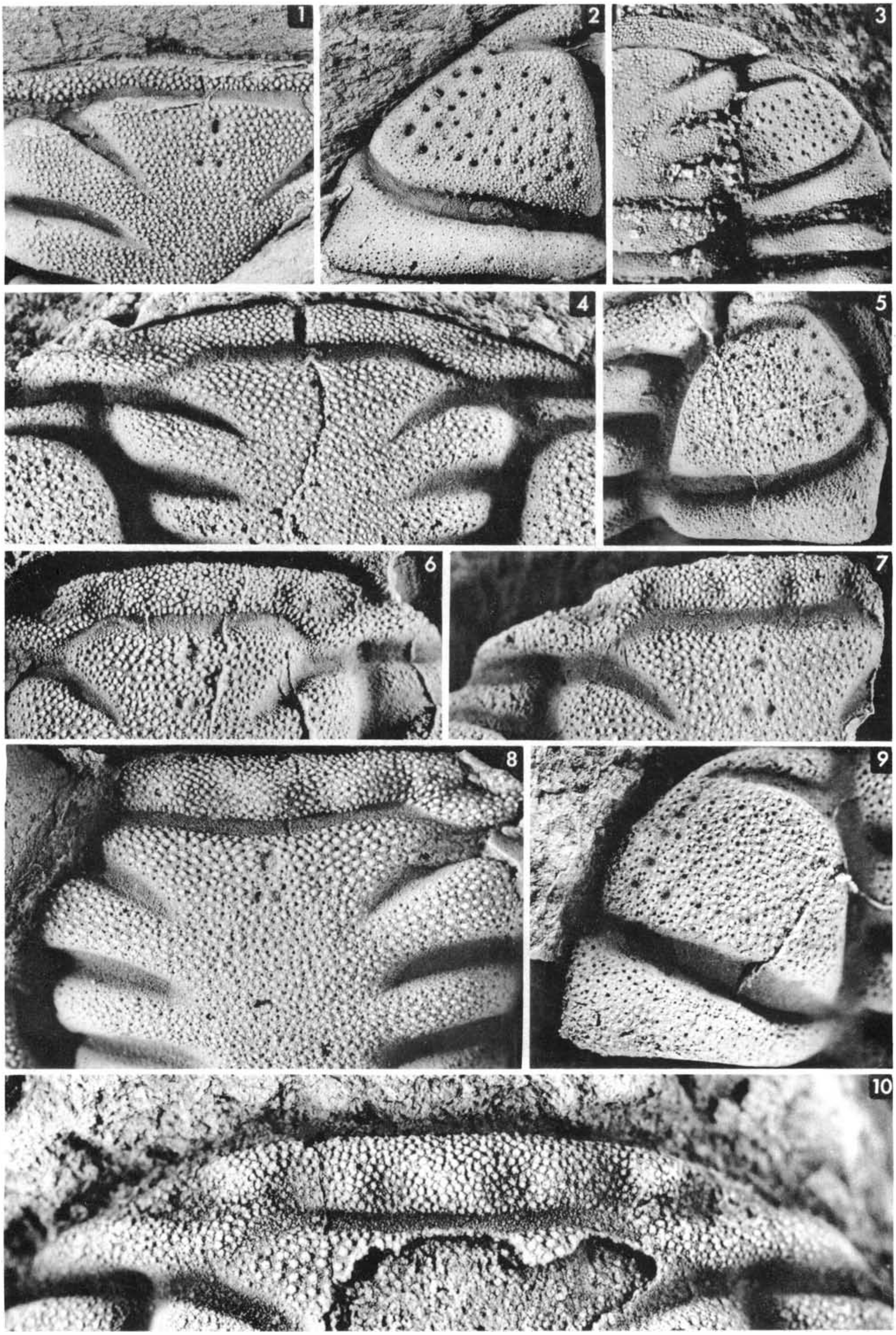


Plate 3.

Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia

HARRY B. WHITTINGTON

Whittington, H.B. 1975 12 15: Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia. *Fossils and Strata,* No. 4, pp. 97 – 136, Pls. 1–25. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

New and old material of *Olenoides serratus* is described. Hypostome was fused with rostral plate, presence of metastome uncertain. Uniramous, multijointed antenna and posterior cercus were each of length three-quarters that of exoskeleton. Individuals of different sizes show 14–16 pairs of biramous appendages. Coxa was large, strongly spinose on ventral and adaxial margins. Inner, leg branch of 6 segments and terminal spines, long spines on proximal podomeres on ventral side. Outer branch arose from dorso-posterior margin of coxa, bilobed, inner lobe bearing some 50 slim filaments which extended back over two following appendages. All specimens show appendages displaced, reconstruction suggests only 3 biramous pairs on cephalon, 7 on thorax, and 4 to 6 on pygidium. Species considered a predator and scavenger, food grasped by spinose leg branches, squeezed by gnathobases and passed forward in midline. Outer branches considered a gill, probably also used in swimming. Gait, trackway, and manner of digging and raking are suggested. No new material of *Kootenia burgessensis* found, Walcott's single specimen shows no clear evidence of anterior rim of shaft of gill branch.

Harry B. Whittington, Sedgwick Museum, Cambridge University, Downing Street, Cambridge, 1st February, 1974.

Walcott figured trilobites with appendages from the Burgess Shale in 1911 and 1912, and gave more detailed descriptions in 1918 and 1921. His illustrations of the material, many heavily retouched, remain almost the only ones available despite the subsequent studies of Raymond (1920) and Størmer (1939, 1951). The discovery of important new material (Plates 17–24) by the Geological Survey of Canada parties in 1966 and 1967 has led to the investigation of all available specimens, including those figured by Walcott (Plates 1–14, 25) and some undescribed ones from his collection (Plates 16, 23:2, 4). The specimens have been flattened as the shale compacted, and present many puzzling features – why does a thin layer of rock separate exoskeleton from appendages and intervene between branches of an appendage? Why is the anterior-posterior face of the coxa and leg branch apparently always parallel to the bedding? Why are appendages apparently always displaced, and well shown on one or other side of the body, but rarely both? These and many other questions are raised by the mode of preservation of any group of specimens (Fig. 2). Some of the deductions made with reference to *Marrella splendens* (Whittington, 1971a, Fig. 24) apply here as to other Burgess Shale fossils, but there are problems peculiar to specimens of *Olenoides serratus*. Some interpretation of what happened to the animal between burial and death and the remains we see now (taphonomy) is an essential preliminary to describing what the specimens show. The original split which produced part and counterpart of a specimen passed ventral to the exoskeleton to reveal the appendages, parts of which adhered to one side or the other. Thus study of both part and counterpart is required, a study not previously undertaken and one which has yielded much new information. I have given a detailed account of each specimen (identified by its catalogue number), with photographs of part and counterpart in most examples. The accompanying Figures 3–24, 31, are camera-lucida drawings, which combine the features of part and counterpart. These figures summarize my conclusions on what a particular specimen shows, and are placed opposite the evidence of the photographs. A final section reviews the findings on morphology of the exoskeleton and appendages, and discusses the reconstruction of the animal and its habits. In providing a new reconstruction I had no wish to portray a dead animal, but have attempted to provide one showing the animal as it may have appeared walking on the sea floor (Figs. 25, 26E). This entails a host of assumptions, not the least of which is to restore the original convexity to a flattened exoskeleton. The convexity I have assumed is greater than in earlier restorations (confined to a cross-section of a thoracic segment, e.g. Walcott, 1921, Fig. 23, Størmer, 1939, Fig. 20), but other species of *Olenoides* appear to be even more convex. It was the attempt at a sagittal section (Fig. 27) that led me to conclude there could have been no more than three pairs of biramous appendages on the cephalon, and not four as previously thought. I do not consider that any specimen shows unequivocally how many there were. My re-investigation has led me to reject Størmer's (1939) view that there was a pre-coxal segment of the appendage, but the nature and position of the coxa-body junction remains unknown, as does the dorsal edge of the coxa. Thus further large assumptions have to be made in the reconstructions, and these and others are discussed in the final sections. Preparation of old and new specimens has revealed the remarkably spinose coxae, and the long ventral spines of the proximal segments of the leg branch. The filaments of the outer branch of the appendage are shown to be far longer than previously supposed, and must have been extended back between leg branch and ventral cuticle. These discoveries lead me to consider *O. serratus* to have been a predator and scavenger, and not a filter feeder, and to regard the outer branch as a gill branch which did not assist in food gathering. Renewed attention has been given in recent years to trace fossils attributed to the activity of trilobites. After assuming a gait for *O. serratus,* I also suggest the trackway that could result (Fig. 28). Sideways raking and the *Cruziana* type of digging are considered to be plausible activities.

In a final section the only known specimen of *Kootenia burgessensis* displaying appendages is redescribed. It is indifferently preserved, and hardly provides sufficient evidence for the conclusions drawn from it by Størmer (1939). Isolated hypostomes and rostral plates, fused together, from the Burgess Shale, were referred by Walcott to *O. serratus,* but probably belong to *K. burgessensis.* The rostral plate and hypostome appear to be similar in the two genera, and fused in both.

A re-investigation of the stratigraphy, palaeontology and palaeoecology of the Burgess Shale, with the co-operation of authorities of the Yoho National Park and the Department of Indian Affairs and Northern Development, was undertaken in 1966 and 1967 by the Geological Survey of Canada. Dr. J.D. Aitken was leader of both parties, accompanied by Dr. W.H. Fritz and by me, in 1967 Dr. D.L. Bruton joined the party. A history of research on the Burgess Shale has been given (Whittington, 1971a), and the geological setting described by Fritz (1971). The Geological Survey of Canada kindly invited me to be Chairman of the palaeobiological work, and I am indebted to the Natural Environment Research Council, London (grant GR3/285) for support of both field and laboratory work by me and by Dr. Bruton. Every facility for work on the Walcott collection in the National Museum of Natural History, Washington, D.C., was afforded by Drs. Porter M. Kier and Richard E. Grant. In discussing the habits of *O. serratus,* and particularly the gait, I have drawn heavily on the work of Dr. S.M. Manton, F.R.S., and am greatly indebted to her for long and detailed discussions of these matters. Her influence on this work will be obvious, but responsibility for suggestions and conclusions is mine. An invitation to attend the NATO Advanced Study Institute provided a forum for presentation of my conclusions, and I tender sincere thanks to the organizers for arranging a most stimulating meeting. My photographs have been enlarged by Mr. David Bursill, and Mr. John Lewis has skilfully converted my pencil drawings into the present Figures.

TERMINOLOGY

Terms used to describe the exoskeleton of the trilobite may be found in Harrington, Moore & Stubblefield (*in* Moore, 1959:O117–O126). The uniramous anterior and posterior appendages of *O. serratus* are referred to as the antenna and the cercus. Various terms have been applied to the biramous appendages, the proximal podomere (or segment) being the coxa, which was attached to the ventral cuticle of the body. The spinose adaxial margin of the coxa is referred to as the gnathobase. The inner branch of the appendage has been termed the endopod(ite) or telopod(ite), but I prefer to call it the leg branch. The outer branch has been termed the exopod(ite) or pre-epipod(ite), but I prefer to use gill branch. These terms follow the usage of Størmer (*in* Moore, 1959, Fig. 5C) and avoid implications of relationships though they assume functions. Podomeres of the leg branch, separated from one another by joints, have been numbered 2 to 7 from the coxa (1) outwards, the terminal spines articulated with podomere 7. The gill branch is divided by a faint line into an inner (proximal) lobe bearing long lamellae, and and outer (distal) lobe fringed with setae. In referring to the direction in which width or length is measured, the terms sagittal (sag.), exsagittal (exsag., parallel to sagittal), and transverse (tr.) are used, abbreviated as indicated. These terms help to avoid ambiguity when describing the exoskeleton, but are difficult to apply to appendages. For example, length of a podomere of the leg branch is measured along the axis of the branch, i.e. in an approximately transverse direction, and is here referred to as axial length.

EXPLANATION OF PLATES 1–25

The photographs have been taken on panchromatic film in ultra-violet radiation, after focussing in ordinary light. The radiation has been directed at 30° to the horizontal, and the direction from which it came is given as west, north-west, et cetera, relative to the margins of the plate. Photographs referred to as reflected were taken in radiation coming from 65° to the horizontal, and the specimen was tilted about 12° so that the maximum reflective effect was directed into the camera. The plates show that each of these two types of photographs reveal particular details more clearly than others, so that all or parts of a specimen may be illustrated by one or both methods. Both part and counterpart of a specimen may be illustrated; for brevity, the counterpart is indicated in the figure explanation, mention of the part is omitted. Further explanation of the locality and horizon is given in the text. Depositories of specimens are USNM, United

States National Museum (now the National Museum of Natural History), Washington, D.C.; GSC, Geological Survey of Canada, Ottawa, Canada; and SM, Sedgwick Museum, Cambridge, England. In the detailed description of a specimen reference is made to earlier illustrations; these are not repeated in the plate explanations.

The items explaining individual figures on the plates are arranged in the following order: depository and catalogue number of specimen, locality if not given in heading, direction of radiation, magnification, comment and/or reference to Figure.

EXPLANATION OF FIGURES 3–24, AND 31.

These figures are camera-lucida drawings of parts or all of particular specimens, intended to explain my interpretation of each. Thin layers of rock separate exoskeleton and appendages, and intervene between branches of an appendage. The appendages are imbricated, and the changes of level between them, between branches of one appendage, and between exoskeleton and appendages, appear as minute scarps. These are indicated by hachures running down the scarp slope from a solid line which runs along the upper edge of the scarp. These scarps have been formed when the rock was split, and by subsequent preparation, and their extent and course reveals the relationships between preserved parts of the animal. They appear on the photographs as light or dark lines, depending on direction of the radiation. As far as possible, Figures have been placed opposite the relevant photographs. The Figures combine evidence from part and counterpart, and in most cases photographs of both are given. Except in Figs. 4, 7, 17, 20, 23, 24 the specimen is viewed from the dorsal, but orientation is indicated by use of prefixes for left and right side. The convention is adopted that the part is the block showing the exoskeleton in dorsal view. The symbols and numbers used on the Figures are as follows:

Symbols

abs = anterior branch of suture
ad = apodeme
alm = anterolateral margin
am = anterior margin
an = antenna
ap = anterior pit
axf = axial furrow
ce = cercus
cox = coxa
cs = connective suture
d = dark area in Fig. 19, suffix indicating dorsal in Fig. 24
do = doublure of exoskeleton
el = eye lobe
er = eye ridge
ex = exoskeleton
fm = supposed frontal rim of gill branch of *K. burgessensis*
fr = fracture in rock
g = suffix indicating gill branch in Figs. 4–24, 31, indicates glabella in Fig. 2
hyp = hypostome
hs = hypostomal suture
il = impressed line (e.g. of connective suture – il cs)
ipl = interpleural boundary of thorax or furrow of pygidium
L = prefix indicating left side
lm = lateral margin
m = macula
mb = middle body of hypostome
mf = median furrow of hypostome
oc = occipital ring
pb = posterior border
pbs = posterior branch of suture
pl = pleura
plf = pleural furrow
pls = pleural spine
pm = posterior margin
py = pygidium, segments numbered 1 py, 2 py, etc.
pys = border spine of pygidium
rp = rostral plate
R = prefix indicating right side
rs = rostral suture
t = thorax, thoracic segments numbered 1t, 2t etc.
wp = anterior wing process of hypostome
wr = wrinkle

Numerals

Roman numerals used to denote series of biramous appendages I to XVI when most anterior is known. Arabic numerals used to denote series of biramous appendages 1 to n when originally most anterior not known, also to denote podomeres 2 to 7 of leg branch. In Figure 20 letters are used in alphabetical order to denote series of appendages, this unique convention is explained in the text. Glabellar furrows numbered 1p and 2p, first and second from posterior.

DESCRIPTIONS OF SPECIMENS OF *OLENOIDES SERRATUS*

Systematics

Olenoides serratus (Rominger, 1887) was redescribed by Rasetti (1951:189–190, Pl. 27:1–3), who gave references to earlier descriptions. Fritz (1971, figs. 5, 6) has shown the stratigraphical range of the species both at the type locality on Mount Stephen and in the Burgess Shale section. Type species of the genus *Olenoides* Meek, 1887, is *Paradoxides? nevadensis* Meek, 1870, redescribed by Palmer (1954:62, Pl. 14:9) and Robison (1964:538, Pl. 83:12, Pl. 84:1, 1971:799–800, Pl. 89:13–15), both these authors discuss the genus and regard *Neolenus* Matthew, 1899, as a junior synonym.

Locality, stratigraphical horizon, numbers of specimens

Middle Cambrian, Stephen Formation, Burgess Shale section, *Pagetia bootes* faunule of *Bathyuriscus – Elrathina* Zone, situated on ridge between Wapta Mountain and Mount Field, at an elevation of approximately 7,500 feet, 3 miles north of Field, southern British Columbia (Fritz, 1971, gives an account of the stratigraphy and setting of the shale).

All but two of the specimens mentioned herein come from what Walcott (1912a:151–153) called the "Phyllopod bed", 7 feet 7 inches thick, in which he excavated his quarry. The

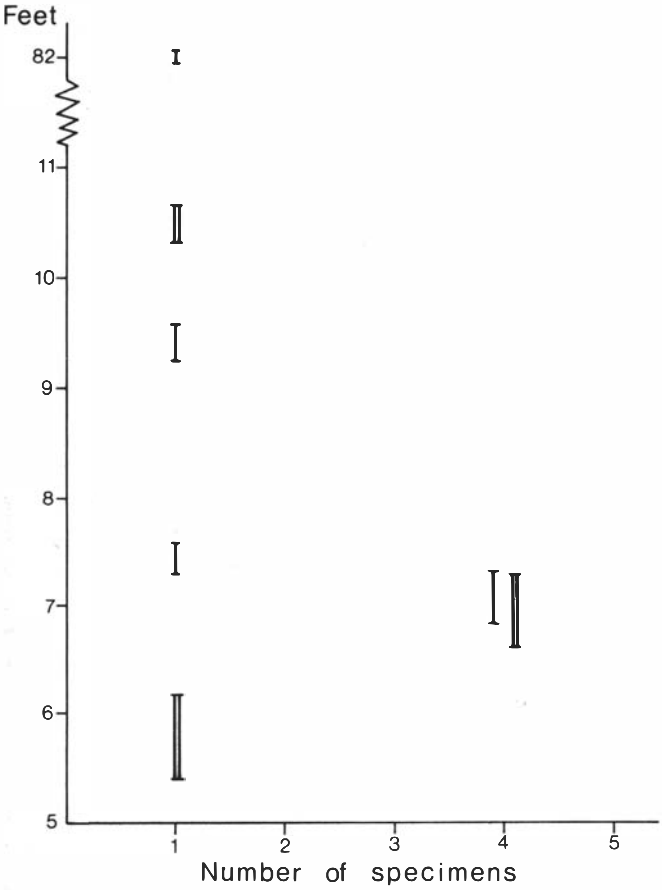


Fig. 1. Numbers of entire specimens with appendages preserved of *Olenoides serratus* collected by the GSC party in 1966 (double vertical bars) and 1967 (single vertical bars). Vertical bars indicate thickness of rock from which specimens came. Level of 5 feet is at base of Phyllopod bed, level of 82 feet is within Raymond quarry (see Whittington, 1971a, for details of levels in quarries).

base of this bed is at level 5 ft in the Geological Survey of Canada party's measured section (Whittington, 1971a, Fig. 3). All Walcott's specimens from this quarry are labelled "35k", with no indication of the exact level from which they came; indeed he states (Walcott, 1918:121) that there is no record of the position of blocks of shale he extracted by blasting. Exceptionally preserved fossils, including rare *O. serratus,* were also obtained from levels 70 feet to 82 feet 8 inches in the GSC section, a level exploited by P.E. Raymond (Whittington, 1971a: 1172, 1174) and so referred to as the Raymond quarry.

Walcott (1921:378) collected 14 specimens with well preserved appendages; these are included in the 15 USNM specimens described below. There are a number of specimens with less well-preserved appendages in the USNM and other collections (SM A 89326 described herein, A5128 in the Oslo collection, Størmer, 1939, Fig. 17) in various museums in the world. Figure 1 summarizes the occurrence of specimens collected by the GSC party. Most of these specimens from the Walcott quarry occur at levels between 6 ft. 7 ins. and 7 ft. 4 ins., at which *Marrella splendens* (Whittington, 1971a, Fig. 5, 1971b, Fig. 1) and *Yohoia tenuis* (Whittington, 1974, Fig. 1) are abundant, but *O. serratus* with appendages is also present in the Raymond quarry, where *M. splendens* is not recorded and *Y. tenuis* is rare. On slabs in the USNM collection *O. serratus* also occurs with *Isoxys* sp., *Canadaspis perfecta, Naraoia compacta* and *Sidneyia inexpectans;* the latter species is relatively common in the Raymond quarry.

Preservation

The exoskeleton is preserved as a thin, black layer, the dark external surface of which preserves the details of granulation (absent in the furrows) and terrace lines on the doublure. The internal surface is smooth, and many specimens show the smooth internal mould with fragments of exoskeleton adhering. The appendages are preserved as an extremely thin, dark film which may be weakly or strongly reflective. A thin layer of rock separates exoskeleton and appendages, and branches of individual appendages. The appendages are imbricated, a rock layer separating one branch from another. It has thus been possible to prepare out individual branches, and to cut through the internal mould of the exoskeleton to expose the appendages below (Pl. 2:1–3).

Of the 15 USNM specimens showing appendages, the entire dorsal exoskeleton is known to be extended parallel to the bedding in 11, and to be straight, without displacement between parts, in 7. The outline of the middle body of the hypostome, impressed into the glabella, shows this plate not to have been rotated or displaced laterally in four of these specimens (e.g. Pl. 1: 2, 3). Of the remaining four specimens having the dorsal exoskeleton preserved parallel to the bedding, two show telescoping of parts (58589, 65520, Fig. 2) and displacement of the hypostome, and two (58588B, 65521, Fig. 2), have the exoskeleton curved, not straight, and the hypostome displaced. Three specimens show a more unusual type of preservation. One (188573, Fig. 2) is lying on its side, the left and right appendages lying close together in the bedding planes, crushed fragments of the exoskeleton across the planes. The axis of 65515 (Fig. 2) was orientated obliquely across the bedding, and it was compacted obliquely to this axis; part of the pygidium lies nearby in the bedding plane. The body of USNM 65514 (Fig. 2) has been bent through 180°, so that when the dorsal face of the pygidium is toward the observer, so is the ventral face of the thorax.

In the samples of 13 specimens showing appendages provided by the GSC collection (Fig. 1), 8 have the dorsal exoskeleton extended straight, parallel to the bedding, without displacement of parts, the hypostome in place approximately in 2. Among the other specimens, one is lying on its side (Pl. 24:1–4), one is poorly preserved but has the body flexed through 180°, and 34692 (Fig. 2, Pl. 17:1–3) is unique in that the appendages are separated from the exoskeleton and only the pygidium lies nearby.

The samples indicate that in about half the specimens with appendages the exoskeleton is extended, parallel to the bedding, and not disarticulated. Slight to complete disarticulation is shown by the remainder, and in a small number the exoskeleton was buried at a steep angle to the bedding. To find the hypostome even approximately in place is relatively rare, and as is shown below, the appendages are never arranged in an approach to a natural position.

Compaction of sediment surrounding the exoskeleton has not only flattened the originally convex exoskeleton, including the hypostome beneath the axial region of the cephalon, but has also resulted in the ridges and furrows of the exoskeleton being impressed on to the appendages beneath. For example, in Plate 2: 1–3 and Plate 5:1, the pleural and interpleural furrows, ridges and border of pygidium may be seen although the rock is split at a level below the exoskeleton.

Fig. 2. Diagrams to explain the attitude in which biramous appendages are preserved relative to the exoskeleton in *Olenoides serratus.* Each specimen is designated by the catalogue number. Position of axial region of dorsal exoskeleton shown by thin solid line when dorsal side toward observer, dashed line when ventral side toward observer, position of middle body of hypostome shown by dashed oval outline. Heavy black line indicates position of leg branch, tick is on ventral side to indicate whether anterior or posterior face of appendages is toward observer, dot at proximal end indicates presence of coxa and position of inner margin of coxa. Thin curved lines adjacent to leg branches indicate attitude and position of gill branches relative to leg branches, when space enclosed by thin line is blank, dorsal face is toward observer, when crossed by thin lines ventral face of gill branch is toward observer. For lettering see Explanation of Figures.

No trace of muscles, ventral membrane or gut (cf. Walcott, 1918:157) appears to be preserved, and in 58588A (Pl. 2:1–3) the inner ends of the right posterior coxae were revealed by excavation to be preserved just beneath the axial rings without any trace of the gut. Thus it appears that only the mineralized exoskeleton and the presumably thick cuticle covering the appendages was preserved. In 34692 (Pl. 17:1, 2) part of the median dark area may perhaps represent the ventral cuticle, but there is no clear evidence for this.

The antennae are preserved diverging forward from the cephalic shield, straight or curved, the cerci subparallel or divergent, projecting straight or gently flexed behind the pygidium. The coxa and leg branch of biramous appendages are always rotated to lie in the bedding planes, anterior or posterior face toward the overlying exoskeleton (Fig. 2). The leg branches are extended straight or gently curved, or flexed through 90° to 180°, the strong flexure being in the distal portion except in 65515. The lamellose gill branches lie between leg branch and exoskeleton, are strongly imbricated, characteristically in a series with the dorsal face toward the ventral surface of the exoskeleton (Fig. 2). The specimens 58588A and B, 58589, show that this is not always the case, for the gill branches may be preserved rotated so that the ventral side faces the ventral surface of the exoskeleton. In such cases the branch is distorted and partially crushed, both orientations may occur in a single specimen (58588A, 34694).

The appendages are never preserved in a symmetrical arrangement about the axis of the exoskeleton, but are invariably displaced. Even in 58588A (Figs. 2, 6), where the arrangement is superficially symmetrical, the entire suite of appendages and the hypostome are displaced to the left, and a backward dispersal is shown since pair VIII of the biramous appendages underlie the last thoracic segment. In many specimens (Fig. 2) the appendages of one side are extended beneath and beyond the pleural regions, while those of the other side are swept into an imbricated group and lie beneath or close to the axis (58588B, 58589, 65519, 34694). In such specimens the hypostome is displaced. However, in 65510 (Pl. 9:1), the exoskeleton is not disarticulated and the hypostome does not appear to be displaced, yet while biramous appendages project beyond the pleural regions on the left side, on the right they do not. The cerci are directed back on the left side, and beside them is a single right leg branch, suggesting that appendages of the right side are imbricated below and adjacent to the axial region. In lateral compressions (Pls. 16, 24) appendages of left and right side have been rotated to lie parallel and close together, projecting vertically down relative to the crushed exoskeleton, while in the oblique longitudinal compression (65515, Figs. 2, 14) each biramous appendage of the left side has been bent into an 'S' curve. The inner, proximal margins of left and right coxae lie close together in this example, as they do in the detached group (34692, Figs. 2, 20). Spreading longitudinally of the appendage series, backward relative to the exoskeleton, has been referred to in 58588A, and is equally evident in 58588B, 58589, 34693, 34694 (Fig. 2). Similar spreading, but in a forward sense, is shown by 58590 and 65520 (Fig. 2).

Taphonomy

The processes that resulted in preservation of the Burgess Shale fossils have been discussed by Whittington (1971a), and the sedimentology by Piper (1972). It appears to be generally true of these fossils that the bodies of the animals were entombed in the sediment at all angles, many approximately parallel to the bedding but others lying on the side or even vertical, and at intermediate angles. Because of this, and because sediment penetrated between body and appendage, and appendage branches, it is envisaged that the animals were trapped alive in a moving cloud of suspended sediment, and buried as it settled out. Burial would have been rapid, but the bodies may not have been transported far nor may the currents have been strong. The way the appendages of one side of *O. serratus* were swept under the body, or the body bent back on itself (65514), or even torn apart (34692), presumably reflects the effects of transportation in rotating the bodies caught in the moving cloud. After the suspension had settled, presumably decay of soft parts and muscles began, and this may account for lack of trace of muscles or gut. Neither the ventral cuticle nor the appendages can have been greatly affected at this stage, however, for the ventral cuticle evidently held the suite of appendages together under the exoskeleton, or together even if it was detached (34692). Compaction of the initial, wet sediment would begin early, and presumably one of the first effects was rotation of coxae and leg branches so that anterior-posterior faces lay parallel to the bedding. Decay of muscles and ligaments at an early stage would have facilitated this rotation of coxae and leg branches. That rotation occurred argues that the cross-section of these parts of the appendages was elongate-oval, the long axis parallel to the anterior-posterior faces. Presumably orientation of gill branches was not affected, that is, rotation of these branches so that they were directed forward or forward-upward took place as a result of turbulence during transportation prior to burial. Most gill branches appear to have retained approximately their presumed natural orientation, dorsal side up, directed backward and imbricated beneath the exoskeleton. Displacement of the hypostome and the appendages relative to one another, and to the dorsal exoskeleton, appears to have resulted in part from the varied obliquity of the angles at which parts of the body were buried relative to the bedding planes, combined with compaction. The axial region of the body had the form of an elongated cone, tapering backward. Compaction of this region may have forced the biramous appendages apart, and in 58588A (Fig. 2) the coxae are most widely separated anteriorly. In many specimens (58588B, 65519, 34694) the proximal margins of the coxae lie well outside the axial furrow, surely not a natural positon. If some of this outward drift of appendages was post-burial, a forcing outward from the axis during compaction, then the curvature of leg branches may have been accentuated, e.g. the distal parts of I to III in 34693 (Fig. 21), or the more gentle curvature of more posterior branches. The spreading out longitudinally of the appendage series may also be an effect of compaction, whereas the backward or forward drift of the whole series may reflect angle of burial, e.g. backward drift reflects compaction after burial of body in a "nose-down" position. The variables in compaction and angle of burial effects are clearly great, as the results show. In certain specimens extended straight in the bedding planes (Fig. 2, 58588A, 58589, 34693, 34694) the biramous appendages of both, or one, side are arranged in a radial, fan-like pattern. As would be expected, the radial pattern is accentuated in specimens in which the body is bent or twisted (Fig. 2, 58588B, 65521, 65514), but in all specimens except 58588A the radial arrangement is shown on one side only. When the body lies on its side (Fig. 2, 188573, see also 34697, Pl. 24), or at a steep angle to the bedding (Fig. 2, 65515), the arrangement is less obviously radial and tends towards subparallel. In 65519 and 65520 (Fig. 2) the arrangement on one or both sides is subparallel to the axis. This discussion indicates that the preserved arrangements of the appendages relative to the exoskeleton are greatly modified from positions in life by processes operating during burial and compaction. The restorations of Walcott (1921, Pl. 94), Raymond (1920, fig. 8) and Størmer (1951, fig. 12), which show the biramous appendages in a markedly radial arrangement, might give the impression that this arrangement was considered a natural one. Both Walcott and Raymond state that they did not consider it so.

USNM 57656

Plate 1 : 1,2, Fig. 5.

☐ 1912a Walcott: 191, Pl. 24 : 1. ☐ 1918 Walcott: Pl. 17 : 1. ☐ 1920 Raymond: 23. ☐ 1921 Walcott: 392. ☐ 1939 Størmer: 193.

Walcott (1912a, 1918) figured this specimen to show the displaced cerci, and in 1921 noted that it was not ”ventral integument” preserved adjacent to their bases, but the coxa and proximal part of the leg branch on each side. These appendages are poorly preserved; there appears to be a fragment of a gill branch on the right, and segmentation of the cerci (Fig. 5) is not as clearly displayed as Walcott's illustrations suggest. The exoskeleton of this specimen is not displaced, and shows the seven thoracic segments and segmentation and border spines of the pygidium. Størmer (1939) referred to this specimen in support of his claim of six fused segments in the pygidium, the terminal lobe behind the fourth axial ring is crushed but shows a shallow furrow dividing it into a larger anterior and a smaller posterior portion. The external surface of the exoskeleton is finely granulated, except in the furrows, and on the left free cheek genal caecae curve outward and backward from the eye lobe. On the right side of the exoskeleton the distal parts of 10 leg branches project outward and backward from beside the thorax and first two segments of the pygidium. Parts of two leg branches are visible on the left side, the anterior exposed where the third and fourth pleurae are broken away. The detached incomplete pair of appendages and cerci (Fig. 5) have presumably been broken from this specimen, and presumably other appendages may have been broken off and others considerably displaced.

USNM 57657

Plate 1 : 3.

☐ 1912a Walcott: 191, Pl. 24 : 1a. ☐ 1916 Walcott, Pl. 9. ☐ 1918 Walcott, Pl. 17 : 2. ☐ 1920 Raymond: 23. ☐ 1939 Størmer: 194.

Both part and counterpart are preserved in large slabs. Besides the divergent cerci emerging from beneath the posterior pygidial border spines, the specimen shows leg branches and antennae. None of the appendages is well preserved, the incomplete antennae curving and forwardly directed, fragments of one or two leg branches curving anterolaterally beside the left cheek and two leg branches outward beneath the genal angle. Parts of the dorsal exoskeleton are not displaced from each other, and the outline of the middle body of the hypostome, flattened beneath the glabella, appears also to be approximately in place. There is nothing remarkable about this specimen in the light of later collections, it was figured early by Walcott to illustrate the discovery of the cerci. Størmer refers to it as showing that the cerci were flexible, but this is far better shown by 188573 (Pl. 16: 1,2).

USNM 58588 A

Plate 2: 1–3, Plate 3: 1, Figs. 3,6

☐ 1913 Walcott, *in* Eastman: 716, Fig. 1376. ☐ 1918 Walcott: 181, 183, Pl. 15 : 1 (part, lower left), Pl. 17 : 3 (counterpart of posterior portion, shown reversed). ☐ 1939 Størmer: 194–196, 199.

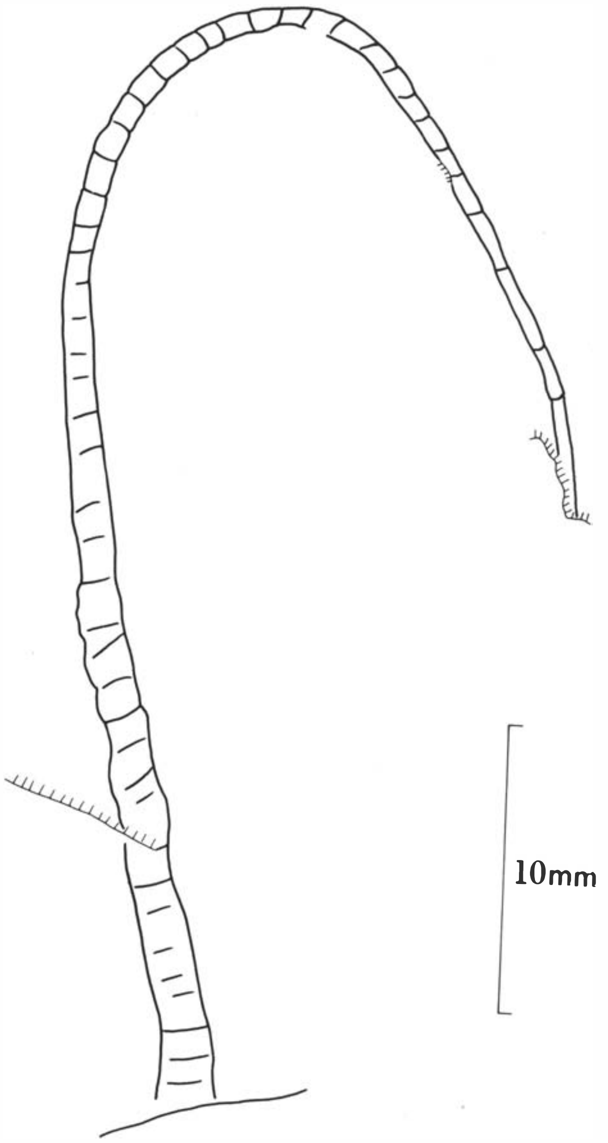


Fig. 3. Olenoides serratus, USNM 58588A, preserved portion of left antenna showing length and segmentation.

This remarkable slab (Walcott, 1918), of which part and counterpart are available, shows two appendage-bearing specimens, each with the horizontal plane approximately parallel to the bedding. One specimen is dorsal side toward the observer, the other ventral side. The larger of the two specimens (sagittal length of exoskeleton 81 mm) is referred to as 58588 A. Walcott wrote little about it, while Størmer used it to determine the length of the antennae (some 60 mm of the left antenna is preserved) and considered that it showed a symmetrical arrangement of the appendages. I have prepared various portions of part and counterpart, and Figure 6 gives my interpretation. There appear to be the antenna, sixteen pairs of biramous appendages, and the cercus on the right side, and the coxae of R VII–XI, L IX, XI have been revealed, as well as ventral spines on leg branches R VIII, IX and L XI. The preserved portion of the left antenna (Fig. 3) shows the gradual narrowing distally, and that the segments become relatively longer. Not all the joints can be seen clearly, and setae are not preserved. Little of the exoskeleton is preserved on the cephalon, for example fragments only adhere to the glabella and outer part of right cheek (Pl. 3:1), and have a granular external surface. Elsewhere the cephalon is preserved as a mould of the internal surface, and on both right and left cheeks a thin layer of rock was removed from this mould to reveal fragments of appendages. Beneath the right half of the cephalon (and adjacent four thoracic segments, Pl. 3:1) areas of long, thin imbricating gill lamellae, and smooth areas showing joints, were revealed. Beneath the right half of the cephalon, and beside the first four axial rings, are portions of I to VI (Fig. 6). Walking leg branches I?, III, IV are proximally directed forward and outward, IV flexed distally, all presumably directed posterior face toward observer. Parts of the smooth inner area of the lobe, and outer area of lamellae, indicate the presence of gill branches I – IV, the lamellae in I directed outward and forward, II and III outward, IV outward and backward. These gill branches lie at the same level as the proximal part of the corresponding leg branch, dorsal surface upward, each branch lying below the one in front of it. Right leg branches V and VI are proximally directed outward, distally flexed back, and the corresponding gill branches lie in front of them, in the same plane; lamellae are directed forward and outward. It is considered that these gill branches exhibit the ventral face, and have been bent forward and down at the coxal junction. In confirmation of this arrangement, gill branch VI lies *above* gill branch V (Fig. 6). On the right side, from the fifth thoracic segment backward, parts of appendages VII–XVI, and the right cercus, are preserved, each coxa and leg branch imbricated so that it lies above the one in front.

Coxae were exposed by removing the thin layer of rock between them and the mould of the inner surface of the axial ring (Pl. 2: 1,3). Coxae VII – XI are subrectangular in outline, the outline of the ventral margin gently convex, proximal edge slightly convex, with a rounded inner, ventral corner. These margins bear closely spaced spines, larger in the mid-part of the ventral region, the two largest, longest spines projecting inward from the inner, ventral angle. The broad basal parts of small and large spines overlap, indicating that they are not a single row, but placed beside each other along the preserved edge of the ventral and inner margins. On VIII and IX the proximal segment (2) of the leg branch shows a group of spines on the ventral margin, the median spine much the stoutest and longest. On VIII the next segment (3) of the leg branches has a similar-sized spine at the distal end of the ventral margin, and smaller spines on the remainder of the margin. More distal segments of VII–XVI are not well preserved, but XI and XVI show the long spines at the distal, ventral edge of segments 5 and 6. The gill branch of VII is represented by a smooth area and some traces of outwardly directed lamellae, and lies anterior to the leg branch, and above leg branch VI. Like those of V and VI, it appears to have been folded downward and forward at the coxal junction, and crushed down over walking leg VI. Elsewhere in this posterior portion only a fragment of gill branch XII has been observed, in presumably a similar attitude to that of VII. The right cercus lies above leg branch XVI, tapers distally, some 37 mm length preserved, the segments becoming longer distally, setae projecting at the proximal joints.

The left side was prepared in a similar manner, and beneath the posterior part of the cheek and pleural regions of the first two thoracic segments are parts of two leg branches and three gill branches. The latter have lamellae of the first two directed outward, those of the third outward and backward, and lie successively one below the other. It is considered that these have been folded down and back, as on the right side, and their position suggests they may be II–IV. The two leg branches curved backward, and their positions suggest they are IV and V, V lying above IV. The ventral spines show that the posterior face is toward the observer, and the large spine at the outer, ventral angle seems to identify segment 3. If so, the coxae must be lying outside the axial furrow, indicating outward displacement. As on the right side, appendage VI has the gill branch ventral face upward, in front of the leg branch, after being bent down and forward. From here posteriorly parts of walking leg branches VII to XVI are preserved, posterior face toward the observer, imbricated and each lying over the one in front. Coxa IX and XI are partially exposed (Pl. 2:3), the ventral and proximal margins spinose, the spines of IX lying below the axial furrow. Ventral spines of segments 2 and 3 of XI are like those of R VIII, and ventral spines are preserved on XIII to XV. Fragments of gill branches VIII to X, XII, appear to be in the folded-forward position, ventral face toward observer. The counterpart shows fragments of gill branches apparently belonging to LXIII to XVI, not shown on Figure 6. These are apparently dorsal face upwards, lying over the leg branch. Walcott's figures (1913, 1918, Pl. 17 : 3) appear to be of this portion of the counterpart, printed reversed to appear like the part, since in the part (Pl. 2 : 1) these gill fragments are not present. The left cercus is less complete than the right, but shows similar features.

Clearly the appendages of this specimen are not arranged symmetrically as Størmer thought, only on the right side does the "axial furrow pass(es) just over the middle of the coxa" (Størmer, 1939 : 195). On the left side the axial furrow passes over the spines on the inner edge of the coxa. The gill branches are folded forward or lie dorsal face upward in a similar way on each side of the body. One cannot from this specimen infer exactly where the coxa lay in life in relation to the axial ring. Further, a line joining the midpoints of coxae IX runs obliquely across the junction between axial rings 1 and 2 of the pygidium. Biramous appendages IX can hardly belong to the first pygidial segment, since this would imply 8 pairs on the pygidium, 7 on the thorax, and 1 on the cephalon. There has thus been considerable backward displacement of the appendages, as well as obliquely outward from the sagittal line. Thus while this specimen supports the view that *O. serratus* had 16 pairs of biramous appendages, it is not decisive as to the number on cephalon or pygidium.

USNM 58588 B

Plate 4: 1–4, Fig. 8.

□ 1912b Walcott: 277, Pl. 45 : 1 (counterpart). □ 1918 Walcott: 181, Pl. 15 : 1 (counterpart, upper right). □ 1921 Walcott: 390–392, Pl. 91 : 1, Pl. 93 : 1, 2 (all of part). □ 1939 Størmer: 193, 196.

Here the smaller of the two specimens (sagittal length of exoskeleton 68 mm) discussed above under 58588A is referred to as 58588B. In 1921 Walcott described this specimen, contending that walking legs 1–6 and 8–16 were visible on the right side. He recognised that the seventh thoracic segment had been pushed partly under the sixth, and considered that one walking leg, number 7 in his series, had been either torn away or was concealed in the rock. The present reconstruction (Fig. 8) is based on part and counterpart, and I have prepared the specimen to show the left and right cerci, the last leg branch on the right (XV) and parts of four leg branches on the left (LXI–XIV). The curvature of the right leg branches, and the ventral spines on III, V–XII, suggest that the posterior side is toward the observer. The irregular elongate fragments of gill branches IVg to IXg are each in front of the corresponding leg branch, and appear to have been crushed down across the axis of the branch. The attitude of leg branches I and II is uncertain, possibly posterior face towards the observer, with lamellae of two gill branches, possibly Ig and IIg, lying on the proximal part of I. The gill branch of XV, however, appears to be dorsal face upwards, and traces of backward and inward directed lamellae are preserved. The coxae of leg branches VIII–XI were prepared by Walcott (1921 : 391) on the part, and show some of the downwardly and inwardly directed spines of the ventral margin. The proximal ends are outside the axial furrow, so that the right appendages appear to have been all displaced to the right, and the position of the antennae corroborates this. On the left side appendages are visible only behind the pygidium, and include the left cercus and portions of four leg branches, imbricated one below the other. Dorsal setae are visible on the lowest two of these branches (XII, XI) suggesting that the posterior face is that toward the observer. The right appendages are imbricated one below the other from the last forwards, and I infer that the left leg branches were similarly imbricated and are arranged fan-wise, the lowest (nearest the sagittal line) being the most anterior. The most posterior has the proximal part of the branch, and a fragment of the gill branch, situated just below and adjacent to the proximal part of the left cercus. This leg branch is similar in size to R XIV, and considerably larger than R XV. I therefore consider the most posterior walking leg visible on the left side to be L XIV, and assume that L XV is concealed, parts of L XIII–XI being preserved to the right. The coxae of L XIV–XI must lie behind the axial termination of the pygidium, those of L XI and XII lying below the proximal part of the right cercus and R XV.

This interpretation indicates that much disturbance of the appendages relative to the exoskeleton has taken place – not only a shift to the right, folding under of some on the left side, but also a relatively backward movement. Walcott (1921 : 434) assumed that there were four pairs of biramous cephalic appendages and five pairs on the pygidium. This cannot be demonstrated unequivocally, since coxa II is opposite the occipital ring. Further, if the total number of right walking legs in this individual is 15 (not 16 as Walcott claimed), then if seven were thoracic and four cephalic, there were only four on the pygidium. Størmer (1939 : 193), while agreeing that an appendage may not be concealed between the present R VI and R VII, considered that one of the cephalic appendages may be concealed. Where the most anterior leg branch is known (Pl. 7 : 1–4, Fig. 10), it appears shorter and slimmer than the second, but perhaps hardly more so than I as compared to II in this specimen.

USNM 58589

Plate 5: 1,2, Plate 6: 1,2, Figure 9.

□ 1912b Walcott: 277, 296, Pl. 45 : 2. □ 1913 Walcott, *in* Eastman, Fig. 1377. □ 1918 Walcott: 128–130, 184, 186, Pl. 18:1, Pl. 20:1. □ 1920 Raymond:24–26, Fig. 2.□ 1921 Walcott:368–369, 381–382, 387–388, 391, Fig. 15, Pl. 91 :2. □ 1939 Størmer: 194–196, Fig. 16. □ 1959 Harrington, *in* Moore, Fig. 56F.

The part was figured by Walcott (1918, Pl. 18, heavily retouched) and portions have been figured by Walcott and by other authors in discussing the structure of the coxae and leg branches of the left side. This specimen was also the basis for Walcott's view that there was a "second and smaller epipodite" (1918: 130) attached to the walking leg. Portions of the external surface of the exoskeleton are preserved in the axial region, right cheek and right pleurae. Other portions of these regions are preserved as an internal mould of the exoskeleton, or this mould has been stripped off to reveal the appendages, as on much of the left pleural region and the posterior part of the right pleural region. The imprint of the furrows and ridges of the pleural regions has been impressed upon the proximal parts of the appendages, as well shown on the left side (Fig. 9, Pl. 5 : 1). Walcott (1921 : 388) prepared parts of this specimen, and I have exposed appendages beneath the mould of the left cheek, my interpretation being summarised in Fig. 9. The axial region is displaced slightly to the right behind the fifth thoracic axial ring, and the seventh axial ring and right pleura pushed under the corresponding parts of the sixth segment. On the left side parts of thirteen biramous appendages are preserved, the leg branches exceptionally well, with fragments of gill branches anteriorly and the coxa of the fifth to eighth appendages partially exposed. Ventral spines on the segments of the leg branches, and the three terminal spines are well displayed. The ventral spines, and dorsal setae on L 2, 3, 6, 7 and 12, show that the posterior face of the walking legs faces the observer. The legs are imbricated so that each goes below the one following, and L13 below the proximal fragment of the left cercus. Gill branches Lg 2–4, 9, 10 are extended horizontally below the pleurae, dorsal face toward observer, lie above the corresponding leg branch and above the following appendage (see appendage L 2 and 3, Fig. 9). The long (transverse) axis of gill branch 2 is directed forward and outward, that of 3 outward, that is, in the same direction as the proximal portion of the leg branch. The lamellae of branches 2–4 are outward and backwardly directed, the outer edge of each lamella lying above the next one outside. Gill branches Lg 5 and 6, however, appear to have been crushed down in an exsagittal direction, over the dorsal margin of the leg branch. Coxae L6 and L8 (Pl. 6:2) show the relative size and distribution of ventral spines, and L8 suggests their presence on the proximal margin. The spinose coxae, and ventral spines of the first two segments of the leg, are similar to those exhibited by 58588A. Raymond (1920, Fig. 2) depicted the coxae and walking legs of L7 and 8, but failed to note the relatively large ventral spines. He also considered the supposed emargination on the distal, ventral part of the margin of coxa L8 (a portion where the margin is broken away) as the socket where the coxa articulated with the apodeme. Consequently Raymond (1920: 25, Fig. 8) considered the spines to be on the dorsal margin of the coxa, an interpretation rejected by Walcott (1921: 381–382). I agree with Walcott, and it is clear from Plates 5,6 that the original form and outline of the appendages have been modified not only by compaction, but by the impression of exoskeletal grooves and furrows upon them. Størmer (1939, Fig. 16) based his drawing of the present L5–8 on Walcott (1921, Fig. 15, Pl. 91 : 2, where the coxae are labelled A–D), and considered that a supposed pre-coxal podomere was probably present. The supposed joint between coxa and pre-coxa ran along a transverse line which I consider is the line of the second interpleural furrow of the pygidium (Fig. 9). The small, triangular portion of coxa L8 lying anterior to this furrow is convex, and running diagonally across the median part of coxa L7 is the impression of the second pleural furrow. I thus consider that the appearance of subdivision of coxa L8 is the result of impressions of grooves and convexities of the exoskeleton upon it, and that there is no evidence of a pre-coxa.

On the right side appendages are far less well preserved. Beneath the fixed cheek are fragments of at least two gill branches (Pl. 5:1). From the fourth thoracic segment posteriorly parts of leg and gill branches are preserved, the leg branches directed posteriorly, imbricated as on the left side. What may be a fragment of the right cercus is visible behind the axial termination. To correspond with the left side, appendages are numbered forward from leg branch R13, which appears to be hindmost. The lobate outer portions of gill branches R5? and 9, fringed with setae, lying above the corresponding leg branch, are incompletely preserved. The fragment of gill branch R5? was interpreted by Walcott (1918: 130) as a "second and smaller epipodite" probably attached to the leg branch. Raymond (1920: 25) and Ulrich, Ruedemann and Bassler (*in* Walcott, 1921: 366, where this specimen is referred to in error as number 58580) believed it to be the outer lobe of a gill branch, an interpretation which Walcott (1921: 369) accepted. The leg branch (R5?) beneath and inside this gill branch fragment shows the two basal segments and their characteristic ventral spines – the large median and smaller spines of segment 2, the large distal and smaller spines of segment 3. The ventral margin of the coxa of this appendage is also poorly preserved.

The appendages of the right side are so poorly preserved, bent back sharply at the joint with the coxa, and showing only fragments of lamellae of other gill branches, that the numbering is arbitrary. It is by no means certain that the hindmost leg branch visible is the last of the series. The displacement of the exoskeleton, and of the appendages outward relative to it on the left side, means that correspondence between appendages and exoskeleton cannot be deduced. If there are 16 pairs of biramous appendages (as in 58588A), then the location of the missing three pairs on the left side is uncertain, particularly how many may have been in front of that here numbered L1.

USNM 65513, 58590, part and counterpart, respectively

Plate 7: 1–4, Figure 10.

☐ 1912b Walcott: 277, Pl. 45 : 3 (58590). ☐ 1918 Walcott: 127–128, Pl. 16 : 1 (65513), 2 (58590). ☐ 1920 Raymond: 30, Fig. 6. ☐ 1921 Walcott: 390. ☐ 1939 Størmer: 194, 196.

Until the information on part and counterpart is combined (Fig. 10), the importance of this specimen is not fully apparent. It shows the left antenna and parts of the first five biramous appendages, followed by parts of imbricated gill branches. Furrows, ridges and broader convexities of the exoskeleton are impressed through the appendages, including part of the anterior margin of the cranidium crossing leg branch I, and (slightly displaced backward) part of the anterolateral margin of the cheek crossing leg branches II and III. The antenna emerges from beneath the anterior border, and shows the short segments and setae at the joints. Leg branches I–IV are slightly flexed, and have the anterior face toward the observer, as evidenced by dorsal setae on segments 4 and 5, and ventral spines on segments 4–6. On 65513 a portion of the spinose, distal ventral edge of the coxa of appendage I is preserved, and below it has been prepared out much of the ventral margin of coxa III (Pl. 7: 1, 3, 4). As Størmer (1939) noted, Walcott's illustration (1918) of this portion of the specimen was retouched. Raymond's (1920) restoration was more accurate, but further preparation has revealed in more detail the length, thickness and direction of these spines; the proximal edge is not preserved. Leg branches II to V appear to be similar in dimensions, but I is markedly shorter. The exact position of the joints proximally is difficult to locate, but it appears that segments 2 and 3 are shorter (tr.) in leg branch I. In 58589 (Fig. 9) the characteristic ventral spines (large median flanked by smaller spines) of segment 2 of the most anterior leg branch exposed are preserved. This branch, labelled "1", is true III or IV. Unfortunately in the present specimen the ventral margins of segments 2 and 3 of leg branches I–IV are concealed or broken, so that how far forward ventral spines are present is not revealed. On 65513 (Pl. 7:4) much of gill branch III is preserved, the edges of the presumed distal lobe broken, so that setae are not preserved. The junction between gill branch and coxa appears as a faint, impressed line; anterior to here there is a slight change in level (which increases outwards) between gill branch and segments 2–4 of the leg branch. This appearance is suggestive of the gill branch being attached to the coxa, but not to proximal segments of the leg branch. Parts of the lamellae of gill branch IV are below and outside those of III. On 58590 (Pl. 7:2) portions of the proximal lobe and lamellae of gill branches I and II are preserved, lying successively above IIIg, and are important as showing the presence and relative size of these branches. The lamellae of all the gill branches of the left side are imbricated so that the outer edge of each lies above the next lamella outwards.

The impression of the axial furrow runs across the proximal parts of appendages I–III. The occipital furrow, 1p furrow, and less clearly 2p, may also be recognised (Fig. 10). The curvature of the antenna, and rotation of the coxae and leg branches, indicate that the appendages are not in their original relation to the exoskeleton. Thus one cannot argue with any conviction from this specimen as to how many biramous appendages belonged to the cephalon.

USNM 58591

Plate 8: 1,2, Figure 11.

☐ 1912b Walcott: 277, Pl. 45 : 4. ☐ 1918 Walcott: 129, Pl. 16 : 3. ☐ 1920 Raymond: 22. ☐ 1939 Størmer: 193.

This specimen is poorly preserved, showing the incomplete cephalon and portions of seven thoracic segments on the part, as internal moulds. Only the right antenna and distal portions of four leg branches project beyond the doublure of the right side of the cephalon. On the right cheek traces of the lamellae of more than one gill branch are directed outward and forward; similar traces are present on and outside the impressions of the thoracic segments. The positions of some of the joints of the antenna and leg branches can be seen (Fig. 11), and the latter have three spines at the termination. Both Walcott (1918) and Raymond (1920) stated that there were four pairs of biramous appendages on the cephalon, without citing a particular specimen as evidence. However, Størmer (1939) used this specimen as his only evidence for such a claim. In no other specimens can the appendages be claimed to be even approximately in their original positions, and I do not consider this poorly-preserved specimen affords clear evidence of four pairs of biramous appendages on the cephalon. Walcott (1912b) drew attention to the three terminal spines of the walking leg in discussing the interpretation of a trace fossil; these spines are better preserved in other specimens.

USNM 65510

Plate 9: 1, Figures 12A,B,C.

□ 1918 Walcott: 126, Pl. 14 : 1. □ 1939 Størmer: 193.

Walcott (1918) commented on the exceptional preservation of the exoskeleton, apart from the crushing of the glabella. It is an internal mould, with fragments of the external surface clinging to the axial region and cephalic border. The seven thoracic segments show the length and direction of the pleural spines, and there are five pairs of border spines on the pygidium, four axial rings and a terminal portion. Størmer (1939) drew attention to the length (sag.) of the terminal portion in arguing that six segments were fused to form the pygidium. In the same paragraph he states that there were five pairs of biramous appendages and the cerci on the pygidium. However, his later reconstruction (Størmer, 1951, Fig. 12) shows six pairs and the cerci on the pygidium. Outside the exoskeleton of the specimen are the left antenna, showing segmentation and setae at some joints (Fig. 12C), the distal parts of eleven leg branches on the left side, the segmented cerci (Fig. 12B), and one walking leg of the right side adjacent to them. Plate 9:1 shows that both cerci are directed backward and to the left, and that no appendages (other than the presumed last leg branch) project from beneath the right side of the exoskeleton. This may be because these appendages have been folded under the body and so are concealed.

The cephalon (Fig. 12A) shows the eye lobe, eye ridge, and course of both branches of the dorsal facial suture. As a result of compaction not only is the glabella crushed but the cheeks are spread out and flattened, with cracks and slight displacement of portions of them. The hypostome has been crushed and pressed against the dorsal exoskeleton, and the line of the connective suture is clearly impressed on each side of the dorsal exoskeleton (Fig. 12A). Since these connective sutures are almost in their correct relative positions, then presumably the impressed lines of the outline of the middle body and posterior margin of the hypostome are also approximately in relative position. The specimen may thus be used as indicating that the hypostome extended back so that the posterior margin lay in about the transverse plane passing through the 1p furrows. The 2p furrow and anterior pit are also visible on each side. This specimen is thus important in attempting to reconstruct the animal.

USNM 65514

Plate 9:2,4, Plate 10:1,2, Figure 13.

□ 1918 Walcott: 128–129, 185, Pl. 19 : 1–3. □ 1920 Raymond: 26–27, Fig. 3. □ 1921 Walcott: 388, Pl. 92 : 6. □ 1939 Størmer: 196–199.

My interpretation (Fig. 13) of the specimen shows the pygidium in dorsal aspect (Pl. 10:2). Fragments of the exoskeleton adhere on the right pleural lobe and at the tip of the axis; the remainder is an impression showing appendages on the left side. In front and to the right of the pygidium parts of impressions of three thoracic segments are preserved in ventral aspect. To the right of them part of the obliquely-oriented cephalic exoskeleton is revealed in section. Left appendages 6–15 are preserved with the anterior face of the leg branch directed dorsally, as inferred from the ventral spines on legs 6 and 7, and the dorsal setae on segments 4 and 5 of leg branches 7 – 10 and 12 – 15. The leg branches are curved concavely back (original dorsal direction), except distally where the last one or two segments are curved in the opposite sense (Pl. 9:2,4). Parts of the gills branches of left appendages 8 – 15 are preserved, those of 8 – 12 flattened in the plane of the rock, the remaining three probably in the same attitude. The gill branches lie above (i.e. dorsal to) the leg branches and overlap each other successively from front to back. The long axis of each gill branch is directed in the same sense as the proximal part of the corresponding leg branch, the appendages thus preserved in a fan-wise arrangement. The lamellae of each branch are directed backward and outward relative to the axis of the branch, and are imbricated so that the outer edge lies below the next lamella outside. The outer lobe of branches 8 – 11 lies above (dorsal to) the adjacent lamellae (Pl. 9: 2).

Parts of right appendages 1 – 7 are preserved adjacent to the thoracic segments. As shown by the attitude of the ventral spines on leg branches 5 – 7, the anterior face is toward the observer, the branches flexed convexly dorsally. The proximal parts of leg branches 5 – 7 overlap each other successively backwards. Fragments of the gill branches are visible, below the corresponding leg branch, crushed across the long axis. The right cercus has been prepared more completely than by Walcott, and the left revealed after the photographs were taken (see Fig. 13). The position of this pair of appendages suggests that left appendages 10 – 15 have been displaced leftwards and probably rotated relative to the axis of the pygidium. Numbering of the appendages is arbitrary, the most anterior seen being called the first, and the assumption made that those numbered L6 and R6 were originally a pair.

The specimen is thus interpreted as that of an individual flexed dorsally through 180°, buried obliquely in the sediment, the rock so split as to reveal part of the left posterior and part of the right anterior portions of the individual. The total number of pairs of appendages cannot be ascertained, and the displacement makes uncertain how many pairs were pygidial. The distance between the proximal part of appendage 11 and the approximate position of the proximal parts of the cerci is about the length of the axial region of the pygidium. If it is assumed that the present positions of appendages 11 – 15, relative to one another, are similar to their relative positions in life, then one might argue, allowing for displacement, that appendage 11 was the anterior of the pygidium. The tenuous nature of this argument is evident.

The specimen shows the relative position of gill branch and leg branch in left appendages 8 – 15, and in 8 – 12 shows the anterior margin of the gill branch lying approximately coincident with the dorsal margin of segments 1 – 3 of the leg branch. In the part (Pl. 10 : 2) these margins are at the same level proximally, but distally the broken anterior edge of the gill branch lies on the leg branch. Hence it is argued that the anterior margin of the gill branch was attached to the dorso-posterior edge of only the first segment (coxa) of the appendage. The difference in level evident between the margin of the gill branch and segments 2 and 3 of the leg branch (Pl. 9:2) suggests that the two branches were not joined beyond the coxa. A gill branch was associated with the last leg branch (15), and this branch was only slightly shorter and slimmer than the preceding one. The faint division between the main portion of the gill branch and the outer lobe, which bore a fringe of fine setae, is shown on appendages 9 – 11. Raymond (1920: 26) referred to a stiffening ridge along the anterior edge of the gill branch, and Størmer (1939: 198, Fig. 20) accepts the presence of a segmented anterior rim, but his evidence was largely derived from interpretation of specimens of *Kootenia.* I see no evidence of such a marginal rim or ridge, but the anterior edge of the gill branch, distal to the coxa, is incomplete where it overlies the leg branch. Walcott (1918: 185) claimed that "epipodites" were shown by this specimen, but later (1921: 388) agreed with Raymond that they were not present.

USNM 65515

Plate 11: 1–3, Figures 14A,B.

□ 1918 Walcott: 130, 160, 186, Pl. 20 : 3,4. □ 1920 Raymond: 28–30, Figs. 4, 5. □ 1921 Ulrich, Ruedemann & Bassler, *in* Walcott: 366–368. □ 1921 Walcott: 369, 371–375, Pl. 92:1–4, Fig. 12. □ 1933 Størmer: 148–149. □ 1939 Størmer: 200–201, Fig. 19.

There has been much controversy about this specimen, which according to Walcott (1921, supported by studies of Ulrich, Ruedemann & Bassler) is the only one which shows a third branch of the appendage, the "epipodite". Its supposed nature and attitude was given by Walcott (1921, Figs. 13, 14, Pl. 94) and he apparently believed (1921: 375) that "epipodites" were present on each appendage. Raymond (1920) considered that the so-called "epipodites" have the exact form of the gill branches of other specimens, and Størmer (1933, 1939) supported him. I concur with them. The part and counterpart of the specimen were shown in retouched illustrations by Walcott (1918, Pl. 20 : 3,4), subsequent illustrations being photographs of portions of the specimens by Walcott (1921) and drawings of portions by Raymond (1920) and Størmer (1939). Figures 14A, B combine features shown by part and counterpart (Pl. 11:1,3), so that portions of six leg branches, with gill branches of the first five, are shown on the left side. The first of these appendages is preserved on the counterpart (Pl. 11:3), the spinose inner and ventral edges of the coxa visible, portions of segments 2–5 of the leg branch, and part of the gill branch. The part (Pl. 11:1, 2) shows similar portions of the succeeding appendage, and less of the next three, the coxae being concealed. Distally the first four leg branches show the setae on the dorsal side of joint four, and so are flexed concavely dorsally. The leg branches are thus thought to have been curved into a reverse "S", and in compaction the upper curve of the "S" has been flattened on itself. Thus the axes of coxae L1 and L2 are directed northeast in Figure 14A, whereas segments 2 and 3 of L1 and L2 are directed southward. In this curving and compaction the outer portion of the gill branch has been flattened out beside the corresponding leg branch. Successive pairs of branches L1–6 are stacked one below the other in this view of the specimen. On the opposite side portions of three leg branches, R1–3, are preserved, directed westward in Figure 14A and stacked one above the other. A fragment of R1 is preserved, together with the coxa and segments 2 and 3 of R2, and a section of the spinose ventral and inner edge of the coxa of R3. This individual is thus viewed as having been oriented approximately vertically in the rock, and flattened from end to end. A portion of the right side of the pygidium is seen on the upper right of the part (Pl. 11:1), apparently bent up during compaction and lying in the plane of the rock. The position of this exoskeletal fragment, below appendages 1–6, suggests that in the drawing anterior is toward the observer. In this event, the appendages on the right of the drawing would be on the left side of the animal, and in this view the anterior face of the leg branch, and bent-up dorsal face of the gill branch, are toward the observer. The coxae of the appendages here called R2 and R3 were recognised by Raymond (as 2 and 3 of his 1920, Fig. 5), and Størmer (1939, Fig. 19) recognised also coxa L2. Neither author used the counterpart (Pl. 11:3) to recognise the coxa of L1, and Størmer did not explain the appearance of the left leg branches as resulting from a sharp flexure (through 180°) of the leg about at the articulation between coxa and podomere 2. Accepting this explanation, the gill branch must have been sharply flexed at about one-third of its axial length, the distal two thirds being flattened beside segments 2–4 of the walking leg. This outer portion of the gill branch is poorly preserved, but the division between the main body and distal lobe is evident. Some of the fine setae at the margin of this lobe are preserved in L2g, and possibly the most proximal part of the lamellae in L3g. In the part the break is along the margin between inner lobe of the gill branch and lamellae, so that in the counterpart the lamellae (if preserved) are concealed beneath the succeeding leg branch. I attribute the wrinkling visible on the inner lobe of L4g to compaction. As in other specimens, I see no basis for claiming the presence of a rim or shaft along the anterior margin of the gill branch, and little evidence is revealed by Walcott's (1921, Pl. 92 : 1,3, 3a) unretouched photographs.

USNM 65519

Plate 12: 1–4, Figure 15.

☐ 1913 Walcott, *in* Eastman, Fig. 1343. ☐ 1918 Walcott: 129, 187, Pl. 21 : 6. ☐ 1920 Raymond: 27. ☐ 1921 Walcott: 388. ☐ 1939 Størmer: 196.

Only portions of the part of this specimen have been illustrated, Raymond (1920) considered it "difficult to study" and Walcott (1921) commented that the walking legs had been crowded forward and displaced. The specimen shows seven thoracic segments and portions of the cephalon and pygidium. The interpretation of the appendages in the axial region and right side (Fig. 15) is based on part and counterpart. Portions of what may be the first three leg branches of the left side have been folded beneath the glabella and right cheek, the anterior side facing the observer. A similar folding may have affected succeeding appendages, for there is no trace of them beside the left pleural region of the thorax or pygidium. On the right side portions of what appear to be appendages 1–7 are preserved. I write "appear" since one cannot excavate to see whether these appendages really are in series without destroying those exposed. While the (hidden) coxa of the first must be situated opposite the anterior part of the glabella, the coxa of the supposed seventh must be opposite axial rings 5–6 of the thorax. Whether or not 1–7 are in a series, there has been displacement and the appendages are not approximately in their natural positions, assuming there was one pair to each thoracic segment and at least three on the cephalon. Displacement has been accompanied by rotation of the coxae and leg branches about the axis, 1–5 clearly showing the anterior face toward the observer, as evidenced by the ventral spines of coxae 2, 4 and 5, and the dorsal setae on 3. On the other hand, 7, and probably 6, exhibit the posterior face, as evidenced by ventral spines on 7. The gill branches have been flattened in the horizontal plane, dorsal surface toward the observer, and are arranged fan-wise with the leg branches. It is considered here that the gill branch was attached proximally along the anterior edge to the dorso-posterior edge of the coxa. This specimen shows that proximally each gill branch of 4, 5 and 6 is at the same level as the coxa and merges with it, the boundary between the two structures disappearing. Distally the boundary becomes increasingly evident, and the gill branch is seen to lie above the leg branch before the outer lobe curves away from it. This appearance supports the view that gill and leg branches were not attached to each other distal to the coxa. The overlapping arrangement and length of the lamellae of portions of the gill branch are well shown by 5, 6 and 7, the outer lobe of 5 showing fine setae on part of the margin. Compaction has resulted in impressions of furrows and ridges of pleurae, and pleural spines, being imprinted upon the appendages.

USNM 65520

Plate 13: 1–4, Figure 16.

☐ 1911 Walcott: 27, Pl. 6: 1, 2. ☐ 1918 Walcott: 128, 130, 188, Pl. 20 : 2, Pl. 22 : 1. ☐ 1920 Raymond: 27–28. ☐ 1921 Walcott: 369, 388–389. ☐ 1939 Størmer: 196, 197, 199.

Walcott illustrated portions of the part and counterpart of this specimen but his photograph of the entire part (1918, Pl. 22: 1) is considerably retouched. My interpretation (Fig. 16) is of part and counterpart of the cephalon and first six segments of the thorax. Raymond (1920) thought that the left cheek had been rotated to bring the eye lobe against the axial furrow. However, impressions of the lateral border and border furrow on the counterpart (Pl. 13: 1), and their relation to the remainder of the cephalon, show that the cheek is not displaced. If thoracic segments are counted forward from the anterior margin of the pygidium, it appears that the second of the seven segments follows the occipital ring (Pl. 13:2). The first has been pushed beneath the occipital ring, and the impression of the left pleural furrow and spine is visible on the counterpart (right side, Pl. 13:1), in a transverse line with the occipital ring. If the impression of the posterior margin of the hypostome has been correctly identified, then it is in advance of the natural position, being in line with the inner ends of the 2p furrows. There has thus been relative displacement of parts of the exoskeleton, and inevitably of appendages also. The appendages on both sides are directed forward. On the left of the occipital ring and glabella are two successive gill branches, the anterior lying above the posterior and showing the distal lobe and marginal setae (Fig. 16). Inside and in front of these gill branches are parts of four leg branches (that numbered III barely visible), stacked one below the other, the anterior at the highest level. These leg branches are flexed inward, and since also the dorsal setae of the fourth(?) segment are preserved on L IV, it is the anterior face that is shown. On the right side parts of leg branches I to VI are preserved, stacked one below the other, proximal portions directed forward, the distal portions flexed sharply inward at the joint between segments 5 and 6. Right branch V shows dorsal setae on segments 4 and 5, the ventral spines on segment 2, and part of the coxa is preserved (Pl. 13: 3,4). The folded gill branch lies immediately behind, proximally in the same plane. Behind appendage five, successively below each other, are parts of leg and gill branch VI, and gill branches VII to IX, the outer lobes of VI, VIII and IX well preserved. The anterior faces of leg branches R I–VI are toward the observer, as are the dorsal faces of the gill branches. Behind this point the appendages of the pleural regions are difficult to interpret, behind the pygidium the posterior faces of two or three leg branches are visible on each side.

The proximal parts of the anterior leg branches are directed forward on the left side, forward to forward and outward on the right side. The gill branches are directed in the same sense as the corresponding leg branch, showing the proximal attachment of the two branches of each appendage. Gill lamellae are directed forward and outward in IV? and V? on the left side, backward and outward in VI to IX on the right. The lamellae are imbricated so that the outer edge of each appears to lie over that next outside it.

On the right margin of the thorax the rock has split below the exoskeleton so that only an impression of the pleurae is visible, and the tips of the pleurae, and pleural spines, are not impressed. A rounded appearance results, as Raymond noted. At these rounded tips are the distal lobes of gill branches VIII and IX, which Walcott (1918) originally interpreted as "epipodites". Raymond (1920) did not accept this view, and Walcott (1921: 369) also abandoned it. Raymond (1920) interpreted leg branches L II and L IV as gill branches, because of the dorsal setae, but noted the articulations. The preserved portion of the most anterior leg branch appears shorter than the succeeding one, this is best shown on the right side, suggested on the left. These leg branches are therefore regarded as the first, and appendages numbered accordingly. The proximal portion of coxa R V is deeply impressed (Pl. 13: 3, Fig. 16) by what appears to be the apodeme of the occipital furrow. Because the first thoracic segment has been pushed below the occipital ring, this apodeme is above that of the first segment. Thus appendage V may have belonged to the first thoracic somite, rather than the occipital, suggesting four biramous pairs on the cephalon. This specimen does not demonstrate this relationship in a convincing manner, and it is argued below that there were three cephalic pairs.

USNM 65521

Plate 14: 1–3, Figures 4,17.

☐ 1918 Walcott: 129, Pl. 23 : 1,2. ☐ 1921 Walcott: 370, 392, Pl. 92 : 5. ☐ 1939 Størmer: 196–199.

An impression of the internal surface of the exoskeleton, upon which are compacted the biramous appendages (mainly of the left side of the animal), and a mould of the middle body of the hypostome, displaced. Thin layers of rock separate the successive appendages from each other. The body is curved, the seven thoracic segments visible, the pygidium displaced, relative to the seventh segment, slightly to the animal's right. Parts of fourteen pairs of left appendages are preserved, the gill branches closest to the exoskeleton, arranged as in an open fan, imbricated, the lamellae lying distally dorsal to the succeeding branch. Thus, as seen in ventral aspect (Fig. 17), the lamellae go below the succeeding appendage. Parts of left leg branches 2, 3, 5–14 are preserved, each arranged in the same relation to the corresponding gill branch.

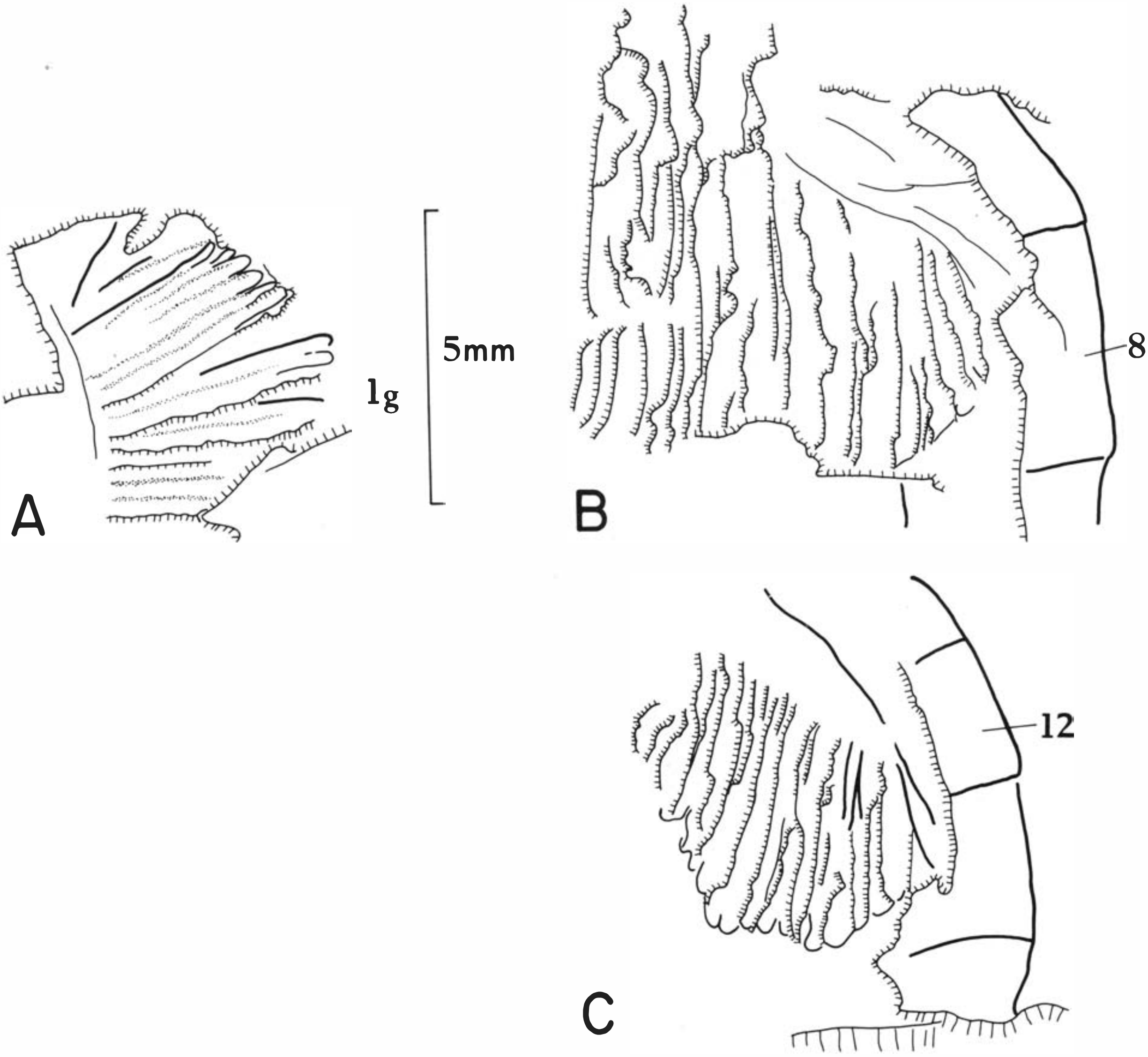


Fig. 4. Olenoides serratus, USNM 65521, portions of gill branches to show imbrication of lamellae and rounded tips. A, branch 1g, compare Pl. 14:1. B, branch 8g, C, branch 12g, compare Pl. 14:3.

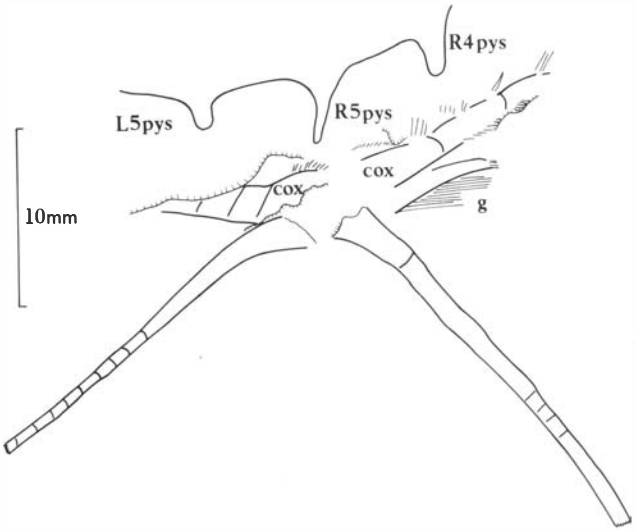
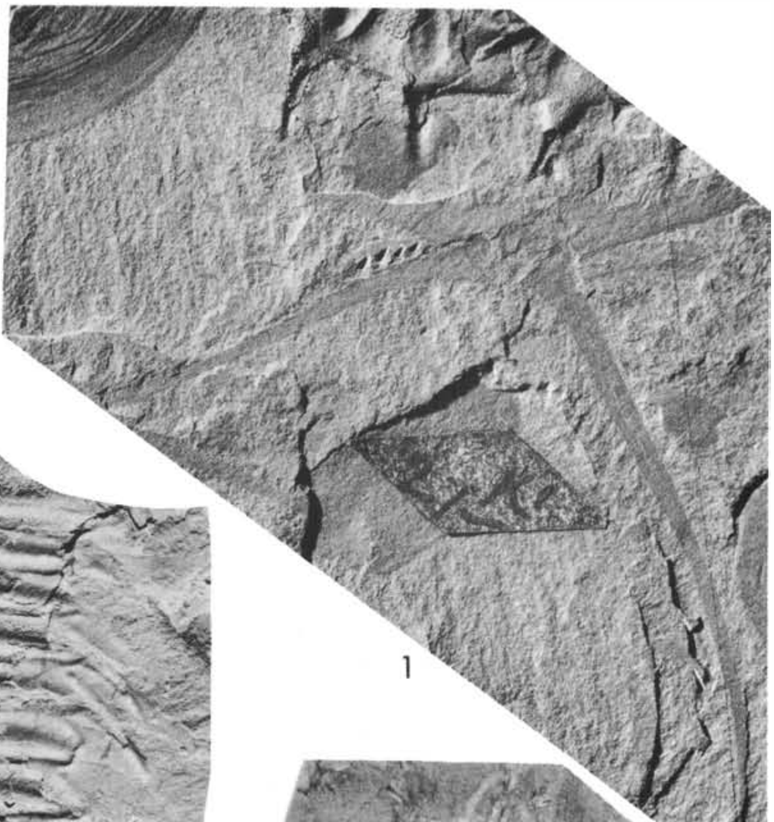


Fig. 5.

Plate 1.

Olenoides serratus (Rominger, 1887), Phyllopod bed, Walcott quarry. 1, USNM 57656, west, x2.5, detail of posterior appendages, see Fig. 5. 2, USNM 57656, north, x1.7. 3, USNM 57657, west, x1.3.



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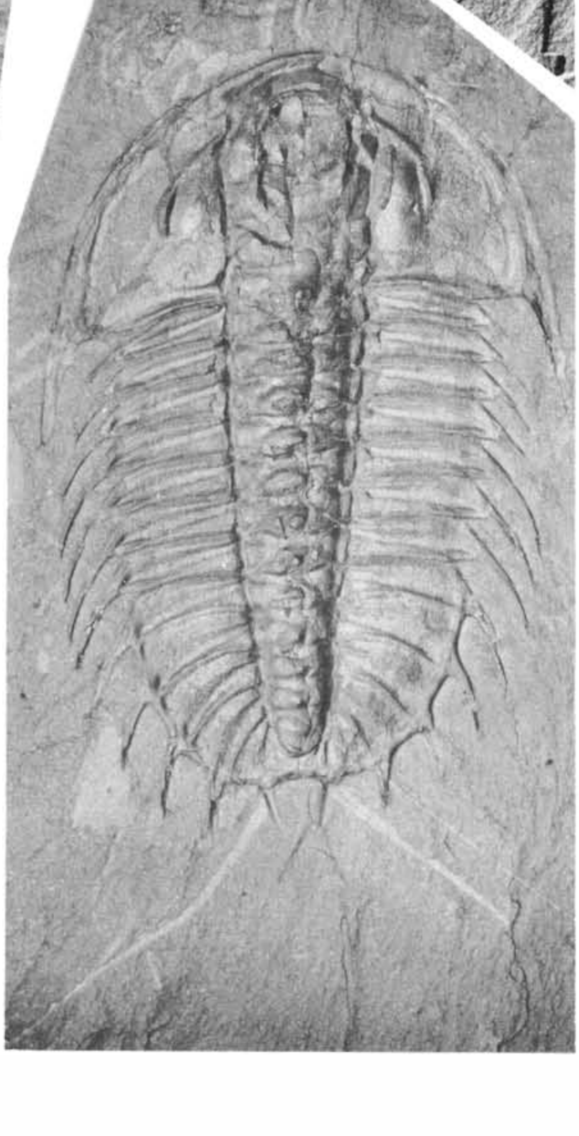

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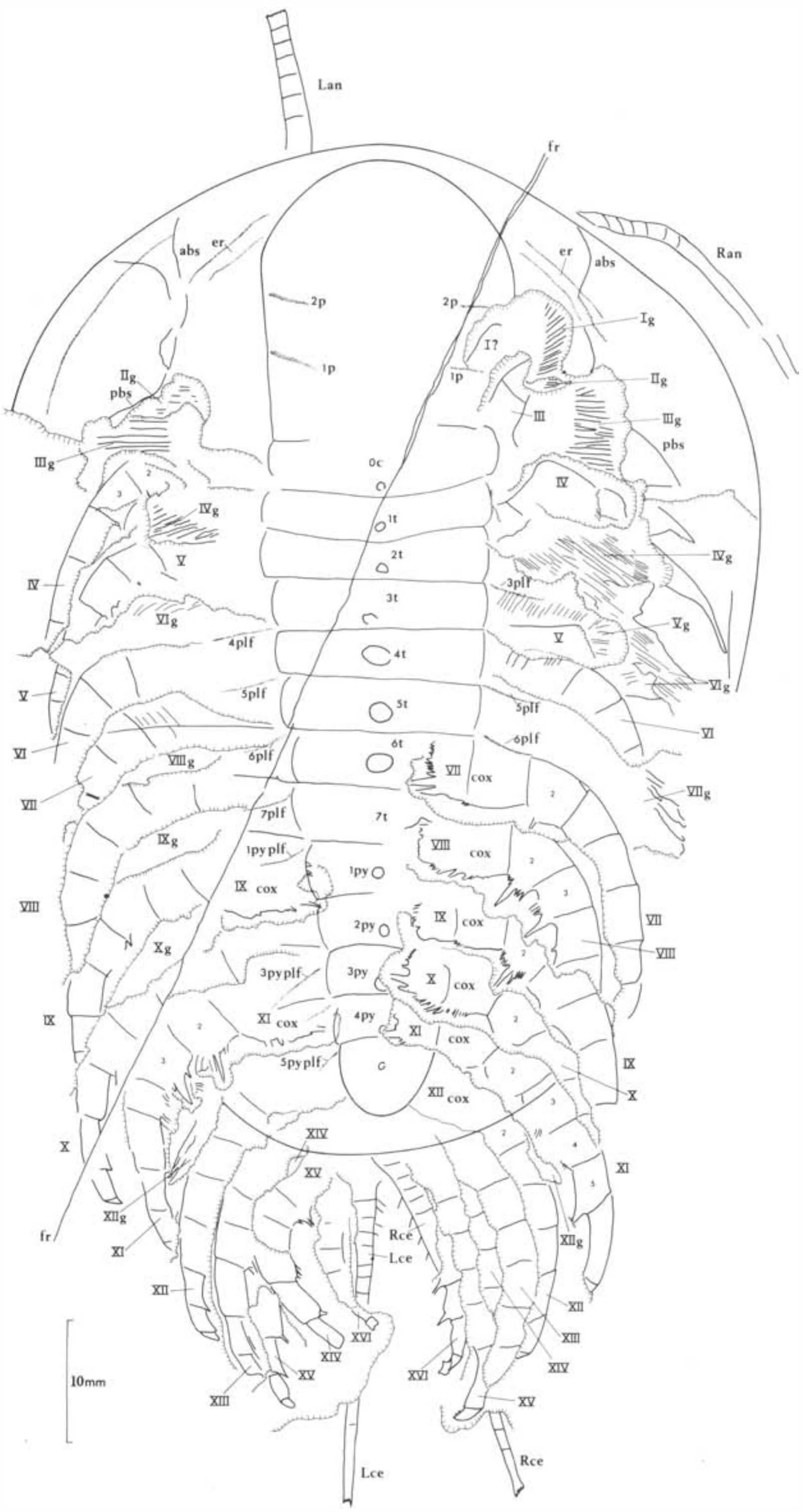

Fig. 6.

Plate 2.

Olenoides serratus (Rominger, 1887). USNM 58588A, Phyllopod bed, Walcott quarry. 1, north, x1.25, see Fig. 6. 2, northeast, x3.3, details of coxae and proximal parts of leg branches R VII to XI. 3, north, x3.3, details of coxae and proximal parts of leg branches R VIII to XI, L IX to XI, see Fig. 6.

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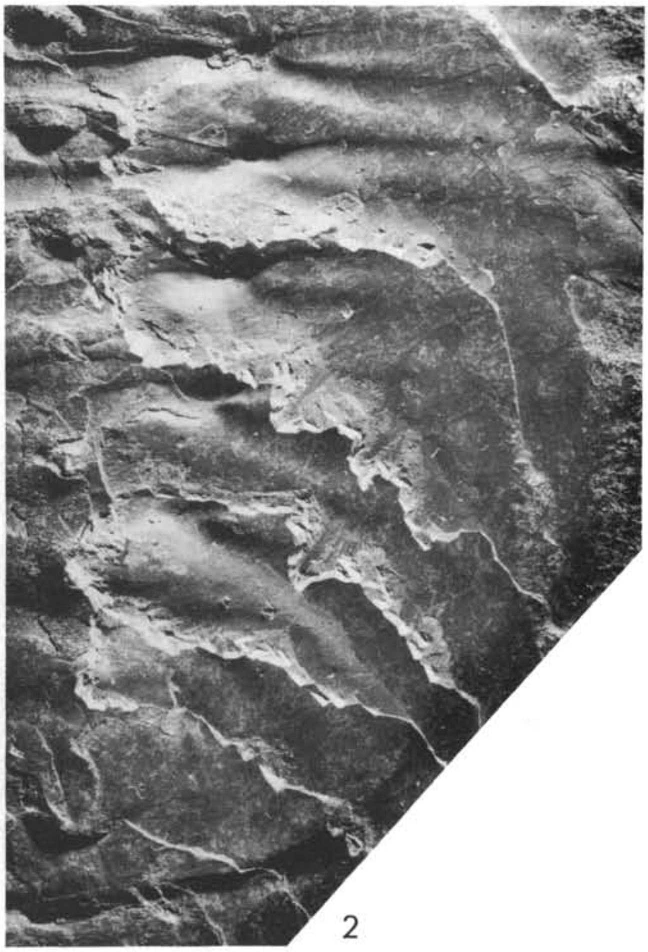

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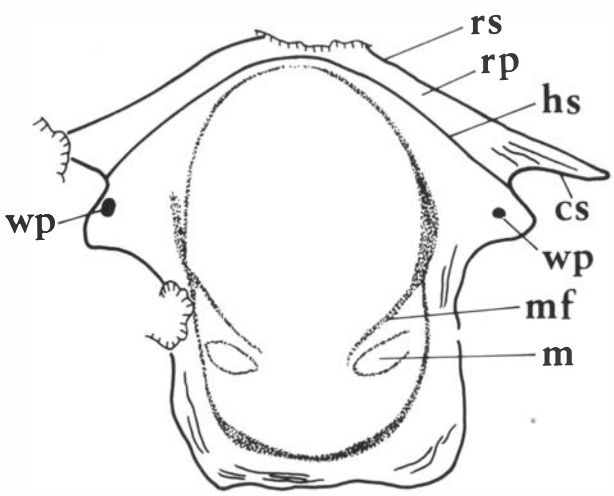
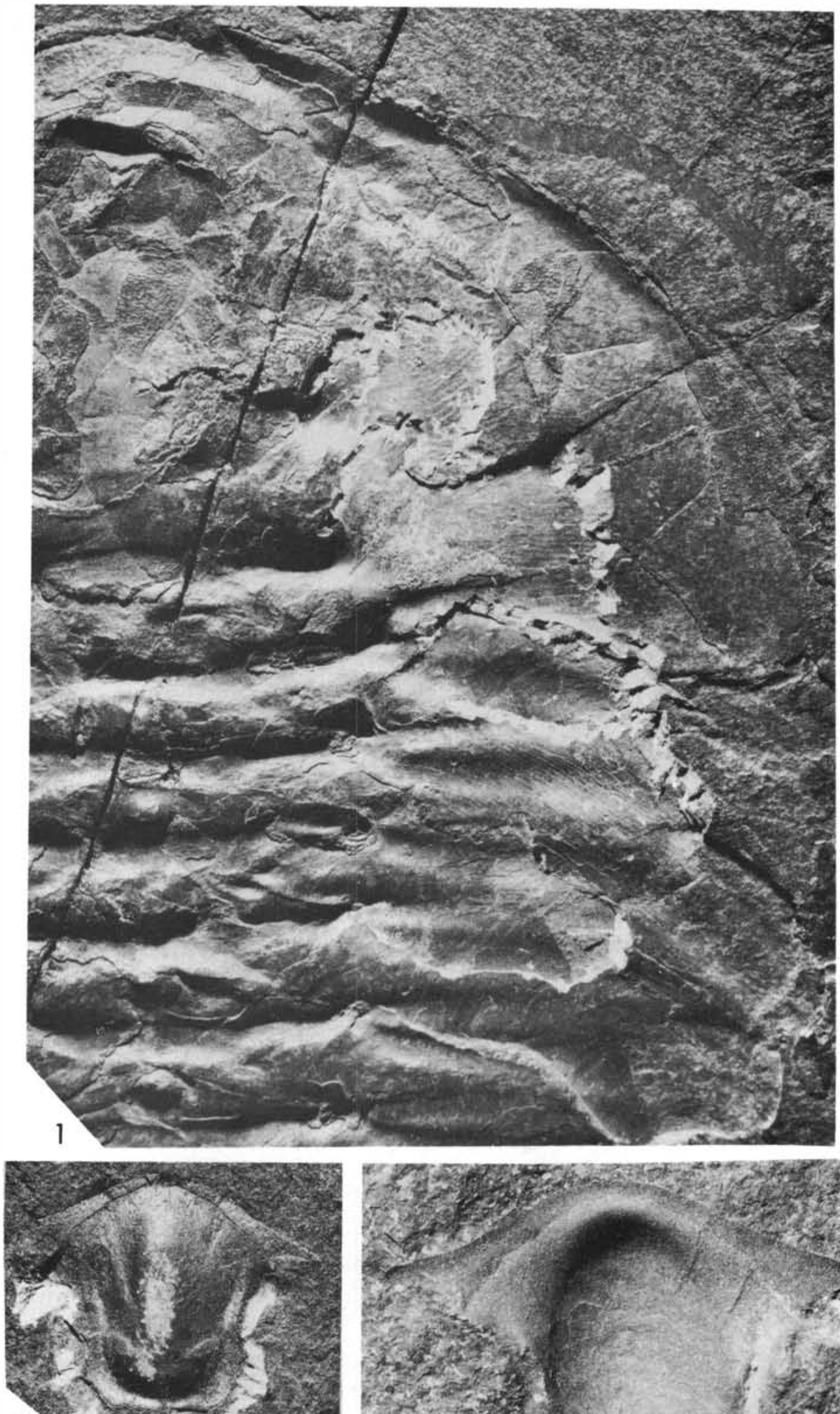


Fig. 7.

Plate 3.

1, *Olenoides serratus* (Rominger, 1887), USNM 58588A, Phyllopod bed, Walcott quarry, north, x3.3, details of appendages RI to VI, see Fig. 6.

2–4, *Kootenia burgessensis* Resser, 1942, Phyllopod bed, Walcott quarry. 2, 3, USNM 65533, north, reflected, x5, see Fig. 7. 4, USNM 188575, northwest, x5.



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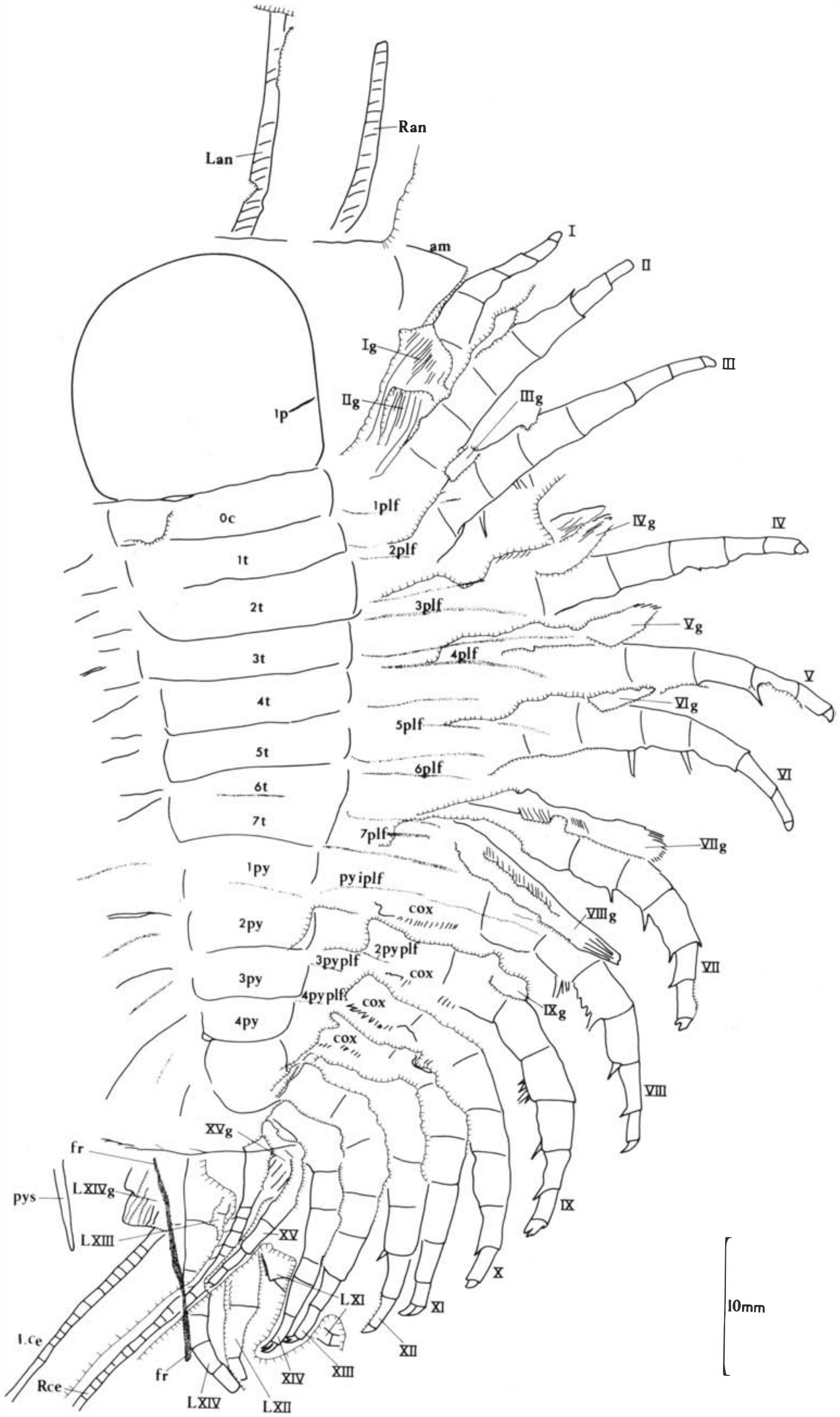
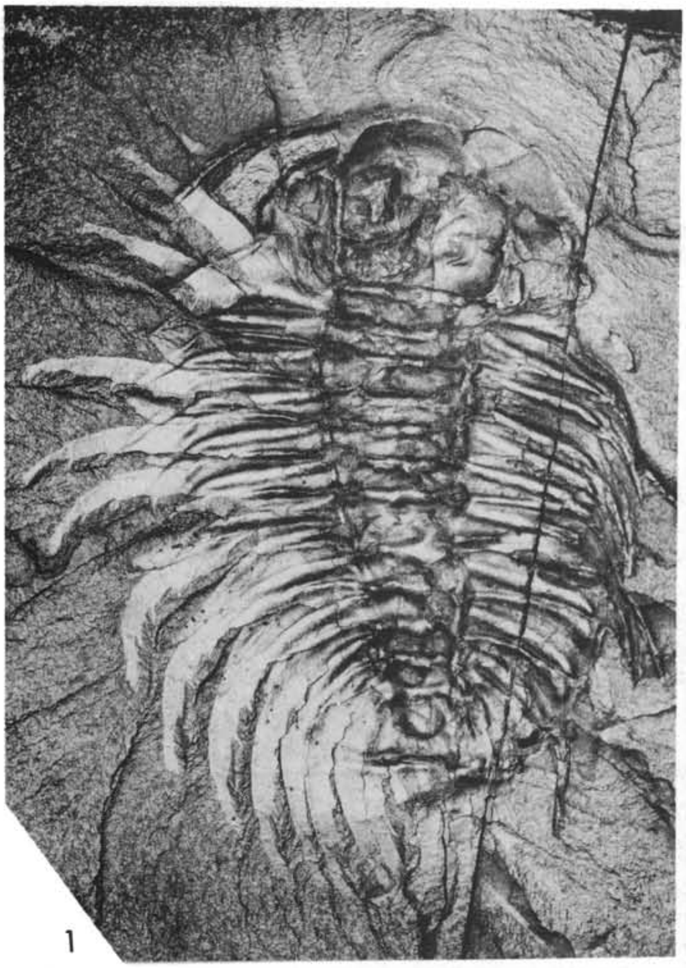


Fig. 8.

Plate 4.

Olenoides serratus (Rominger, 1887), USNM 58588B, Phyllopod bed, Walcott quarry. See Fig. 8. 1, 2, 4, counterpart, reflected, x1.25, north, x2.5, reflected, x1.7, showing leg branch RXV lying ventral to right cercus. 3, reflected, x1.25.



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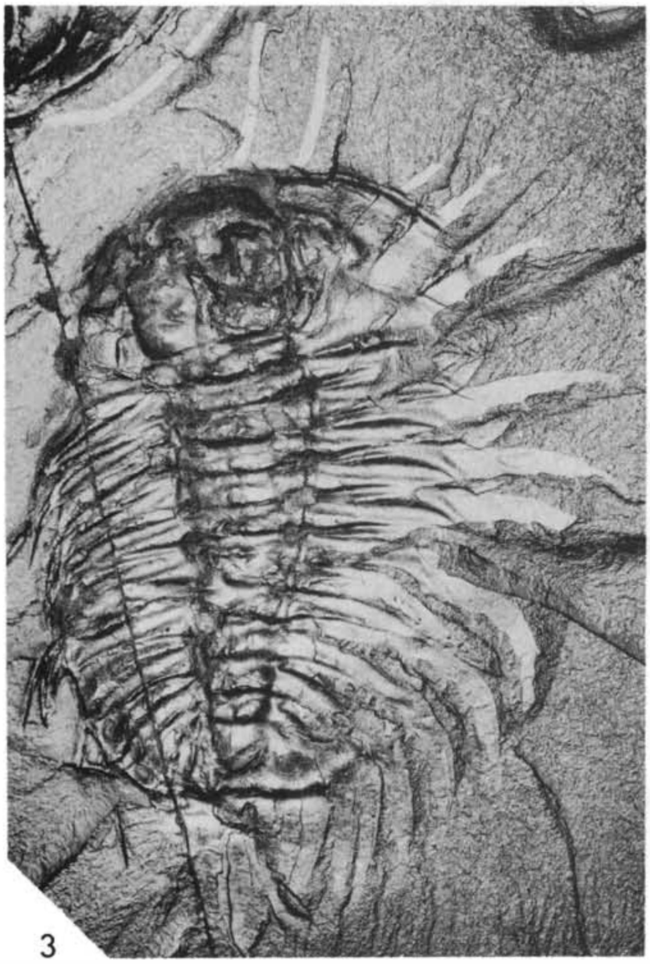

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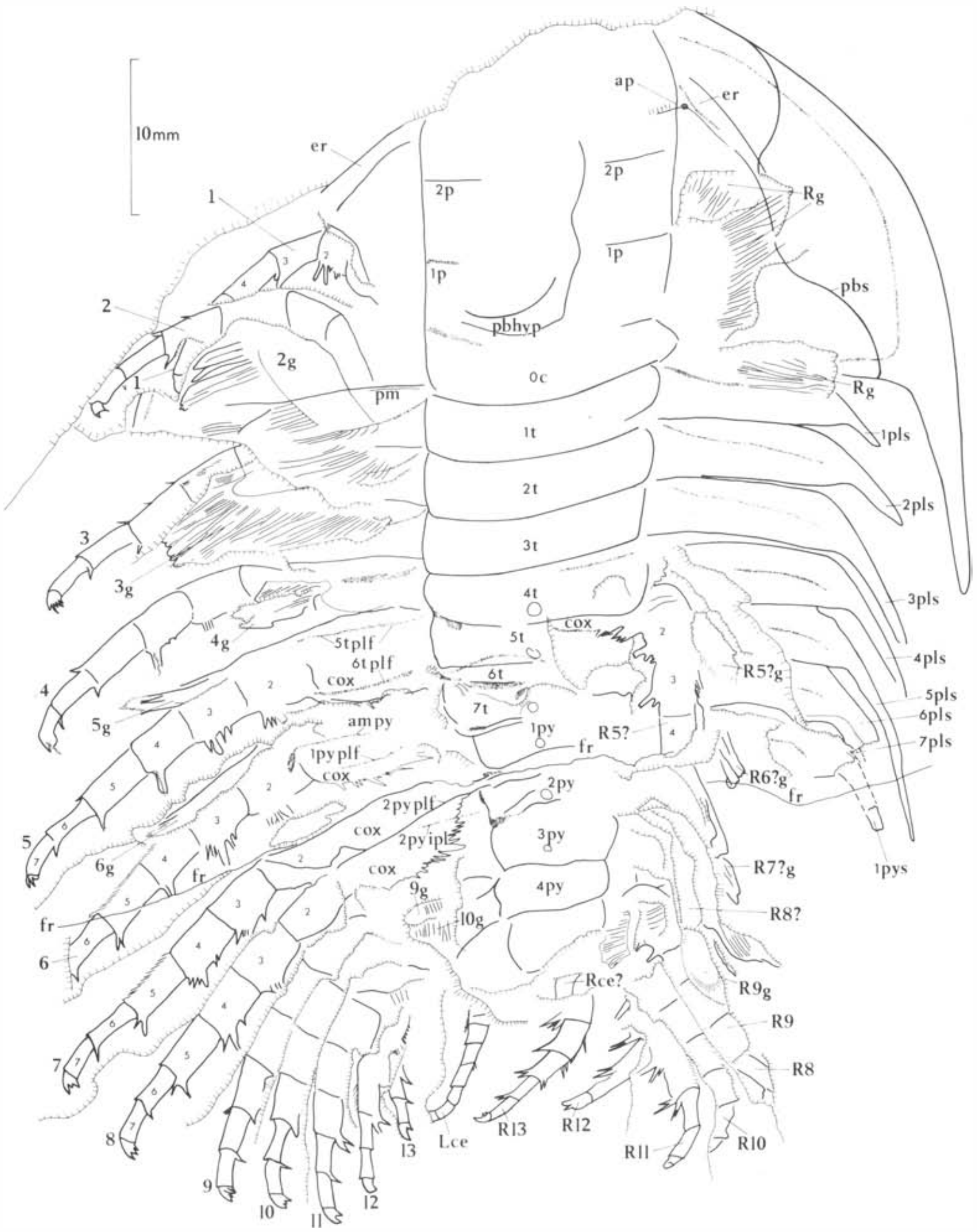
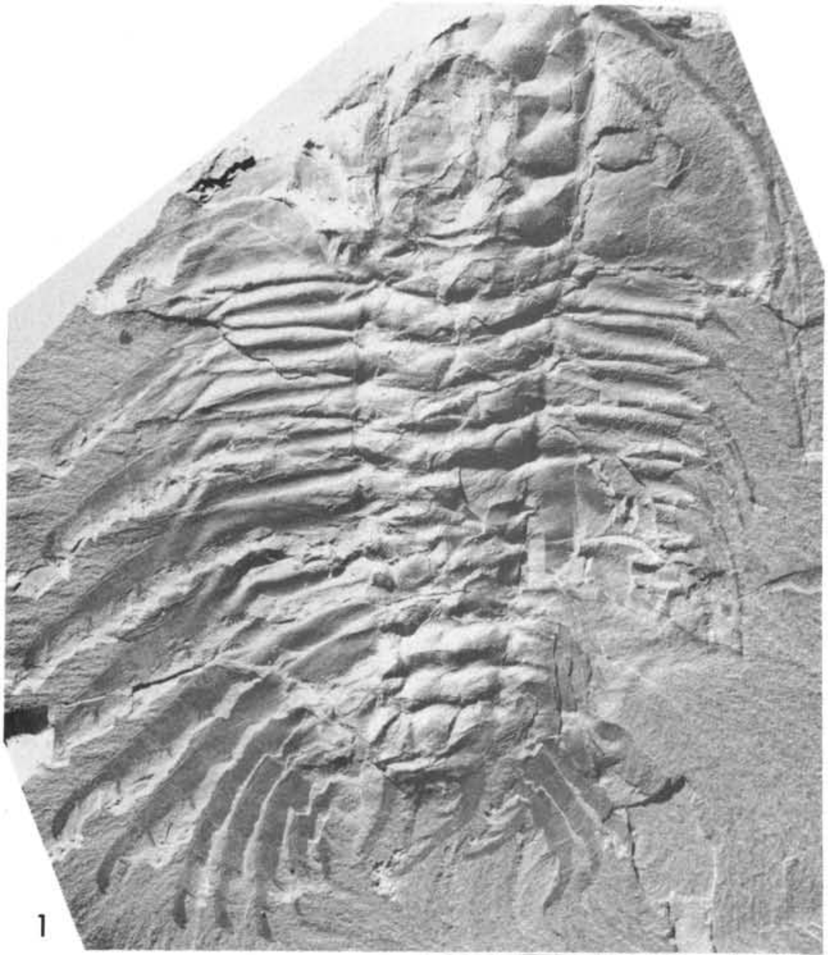


Fig. 9.

Plate 5.

Olenoides serratus (Rominger, 1887), USNM 58589, Phyllopod bed, Walcott quarry. See Fig. 9. 1, 2, north, reflected, x1.7.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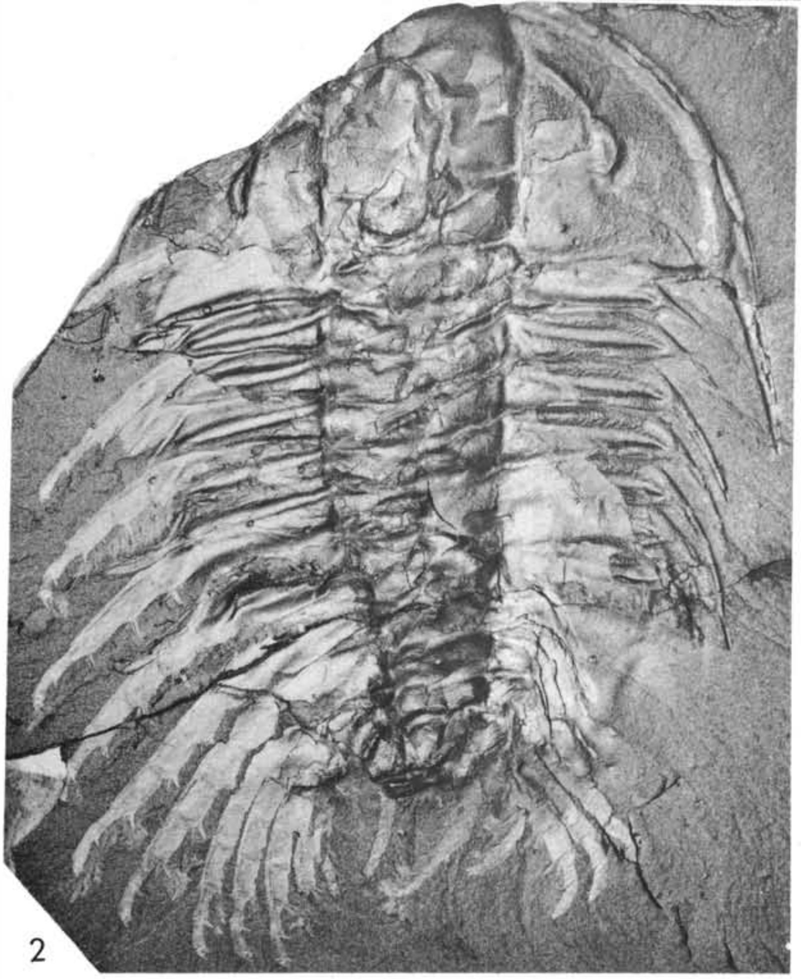
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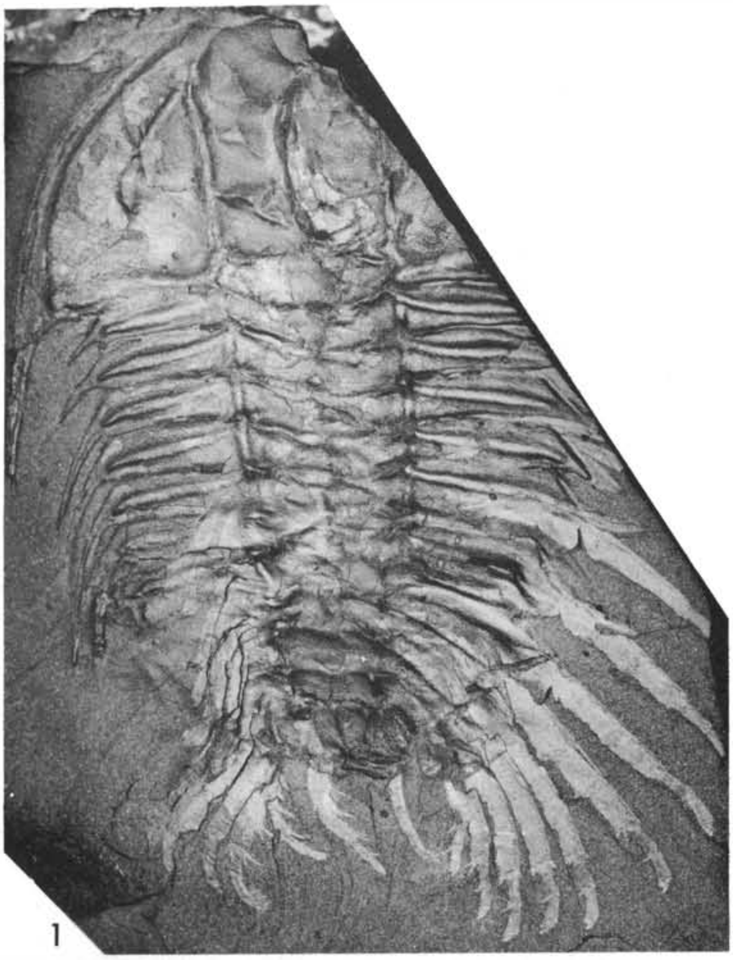
Plate 6.

Olenoides serratus (Rominger, 1887), USNM 58589, Phyllopod bed, Walcott quarry. See Fig. 9. 1, counterpart, reflected, x1.7. 2, reflected, x5, showing details of coxae L 5 to 8.



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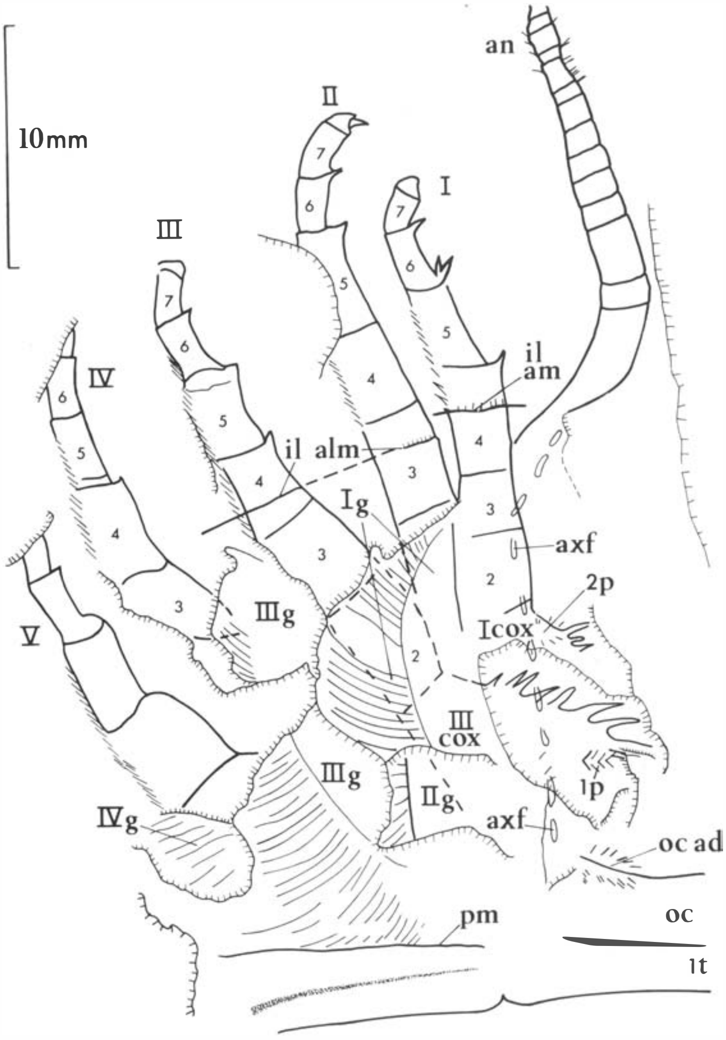

Fig. 10.

Plate 7.

Olenoides serratus (Rominger, 1887), Phyllopod bed, Walcott quarry. See Fig. 10. 1, 3, 4, USNM 65513, northwest, x2.5, reflected, x3.3, northwest, x3.3. 2, counterpart, USNM 58590, north, x3.3.


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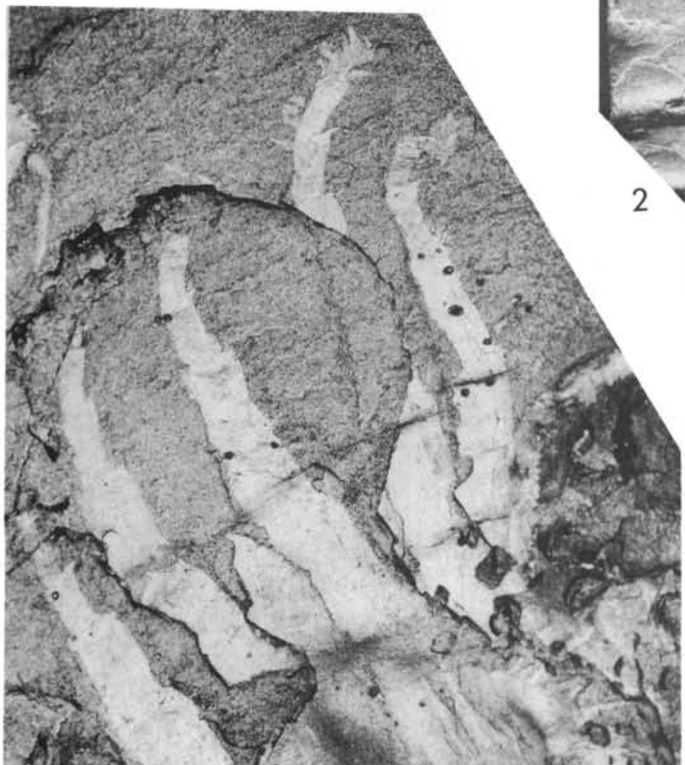
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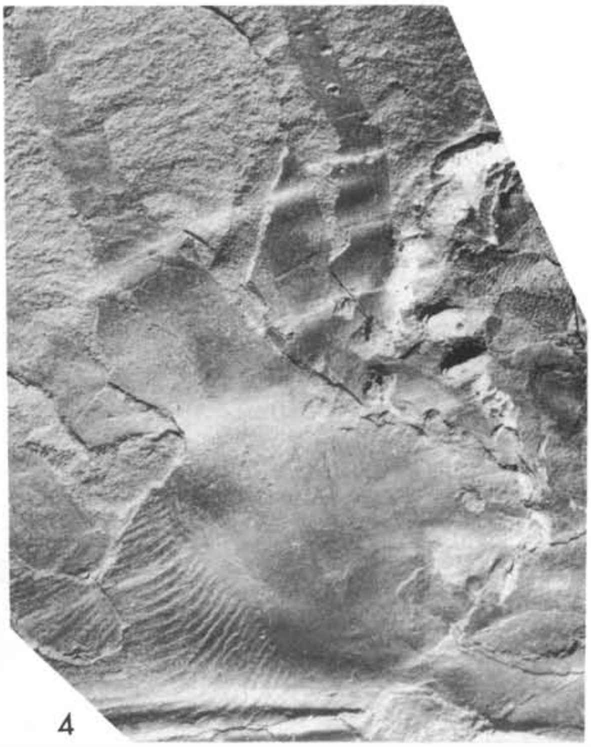
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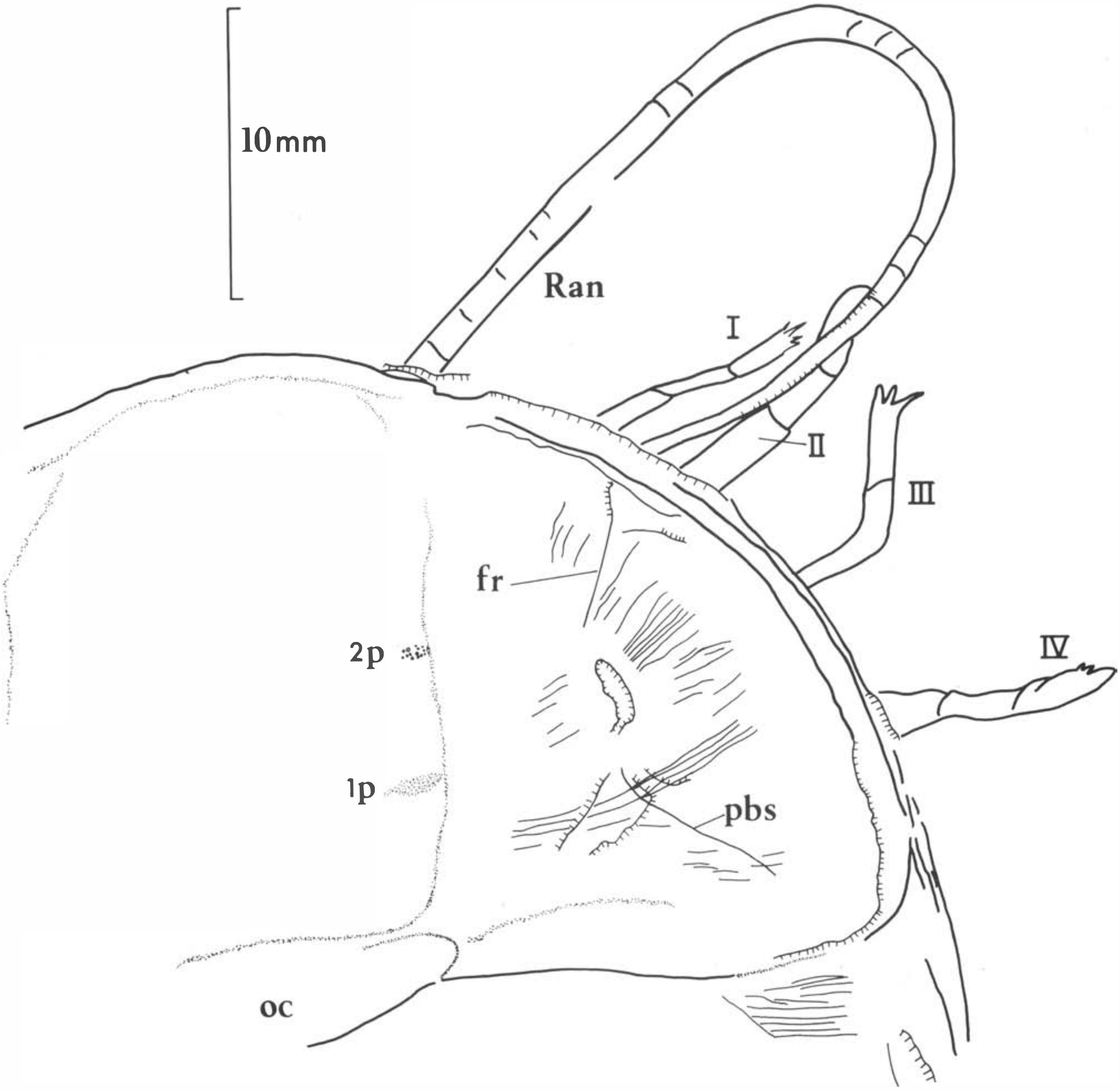

Fig. 11.

Plate 8.

Olenoides serratus (Rominger, 1887), USNM 58591, Phyllopod bed, Walcott quarry. See Fig. 11. 1, reflected, x2.5. 2, southwest, x2.5.


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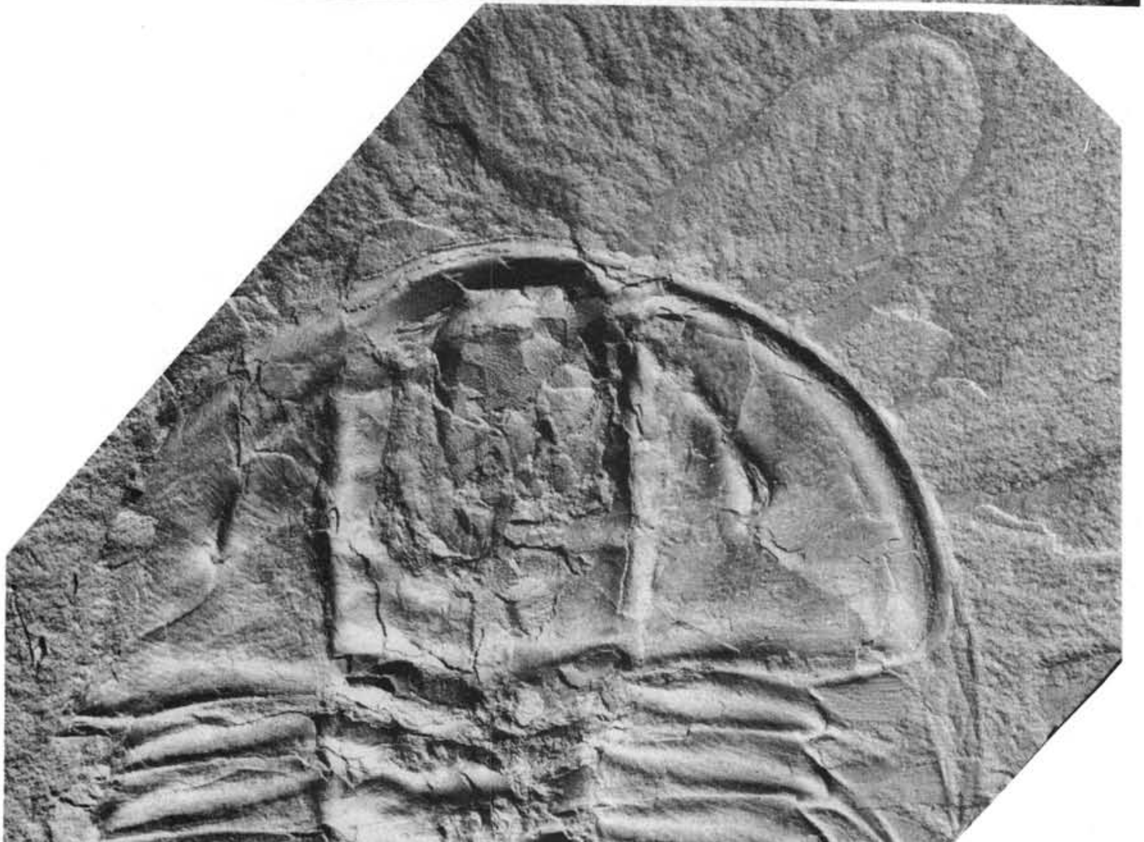
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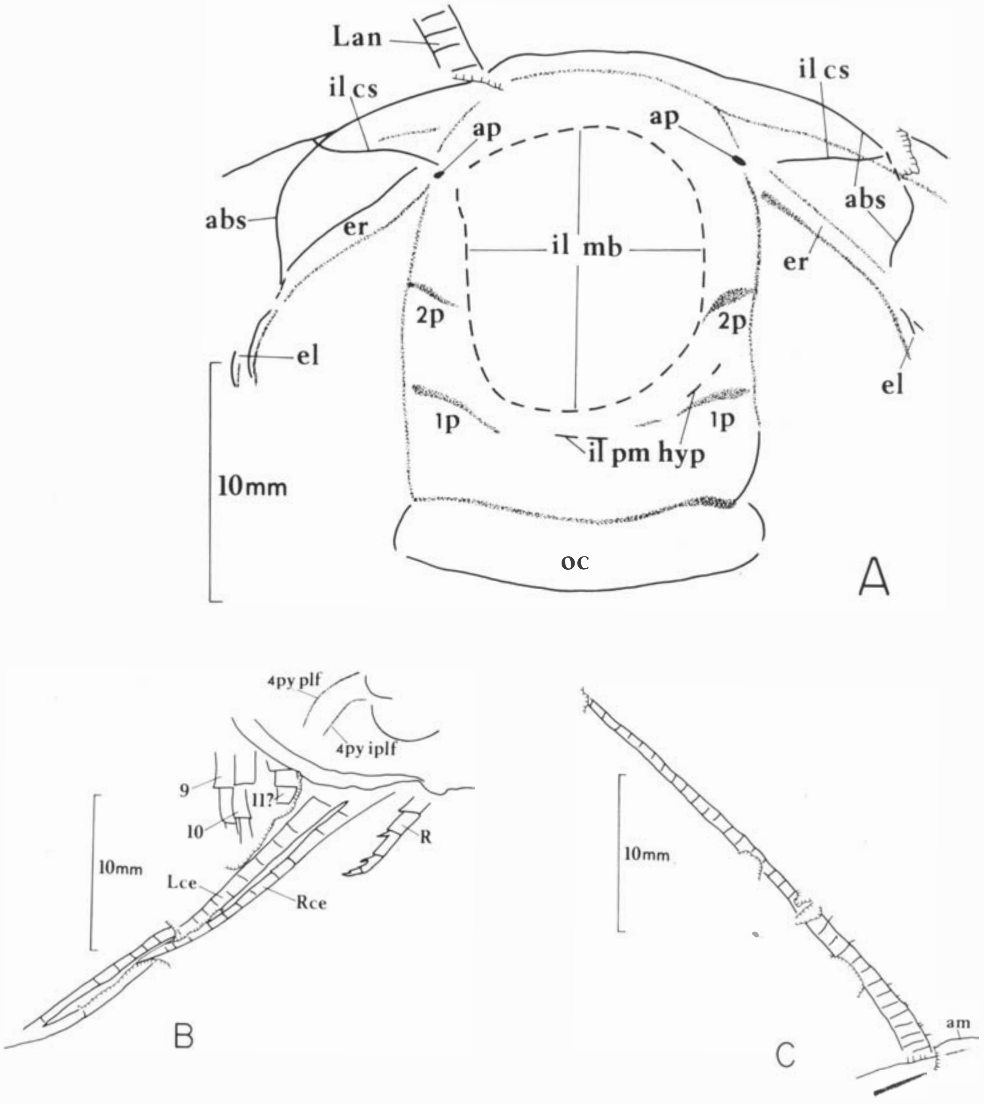
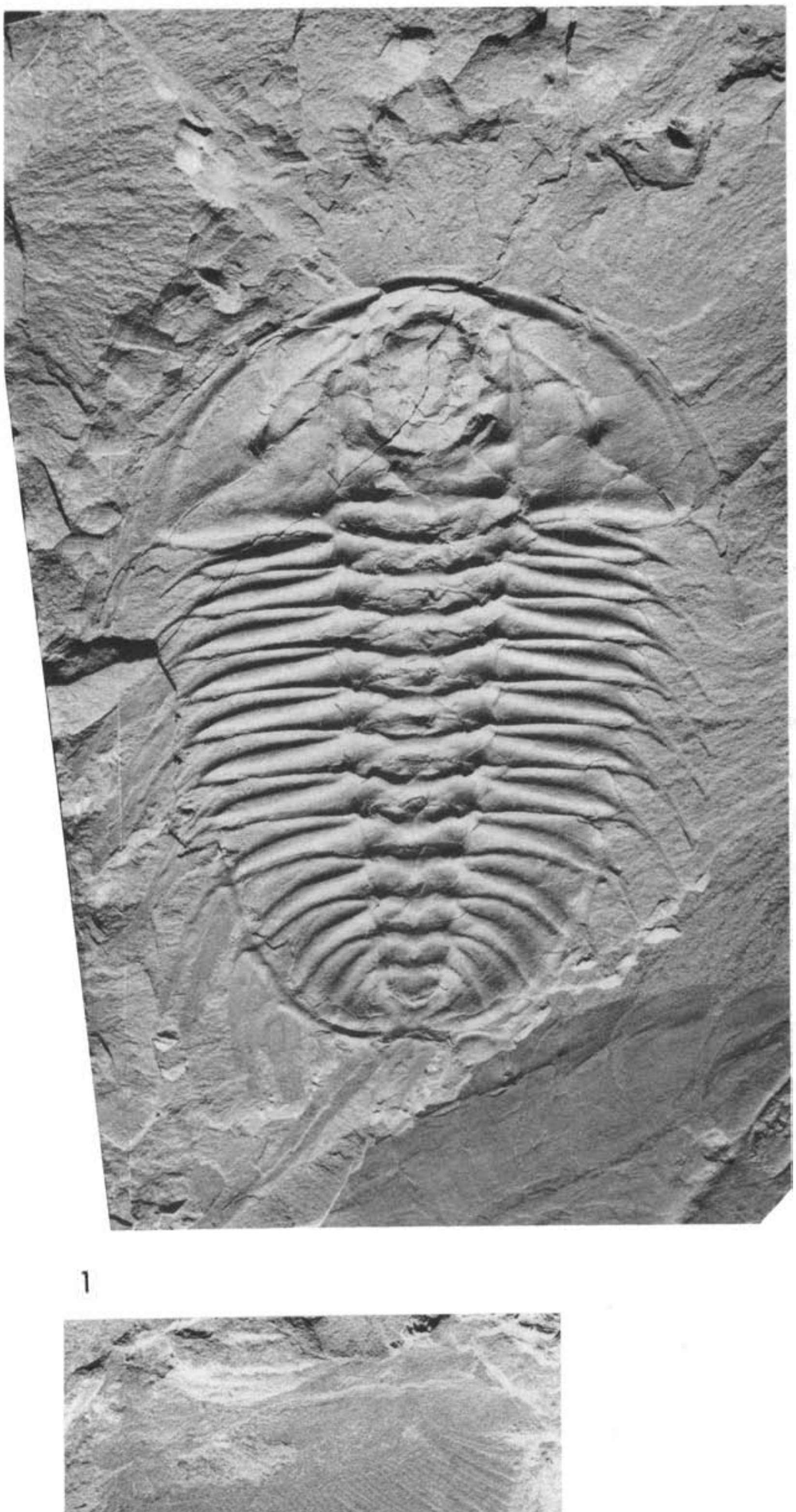


Fig. 12.

Plate 9.

Olenoides serratus (Rominger, 1887), Phyllopod bed, Walcott quarry. 1, USNM 65510, north, x1.7, see Figs. 12A, B, C. 2, 4, USNM 65514, counterpart, north, reflected, x1.7, see Fig. 13. 3, USNM 188574, north, x3.3, incomplete isolated appendage.



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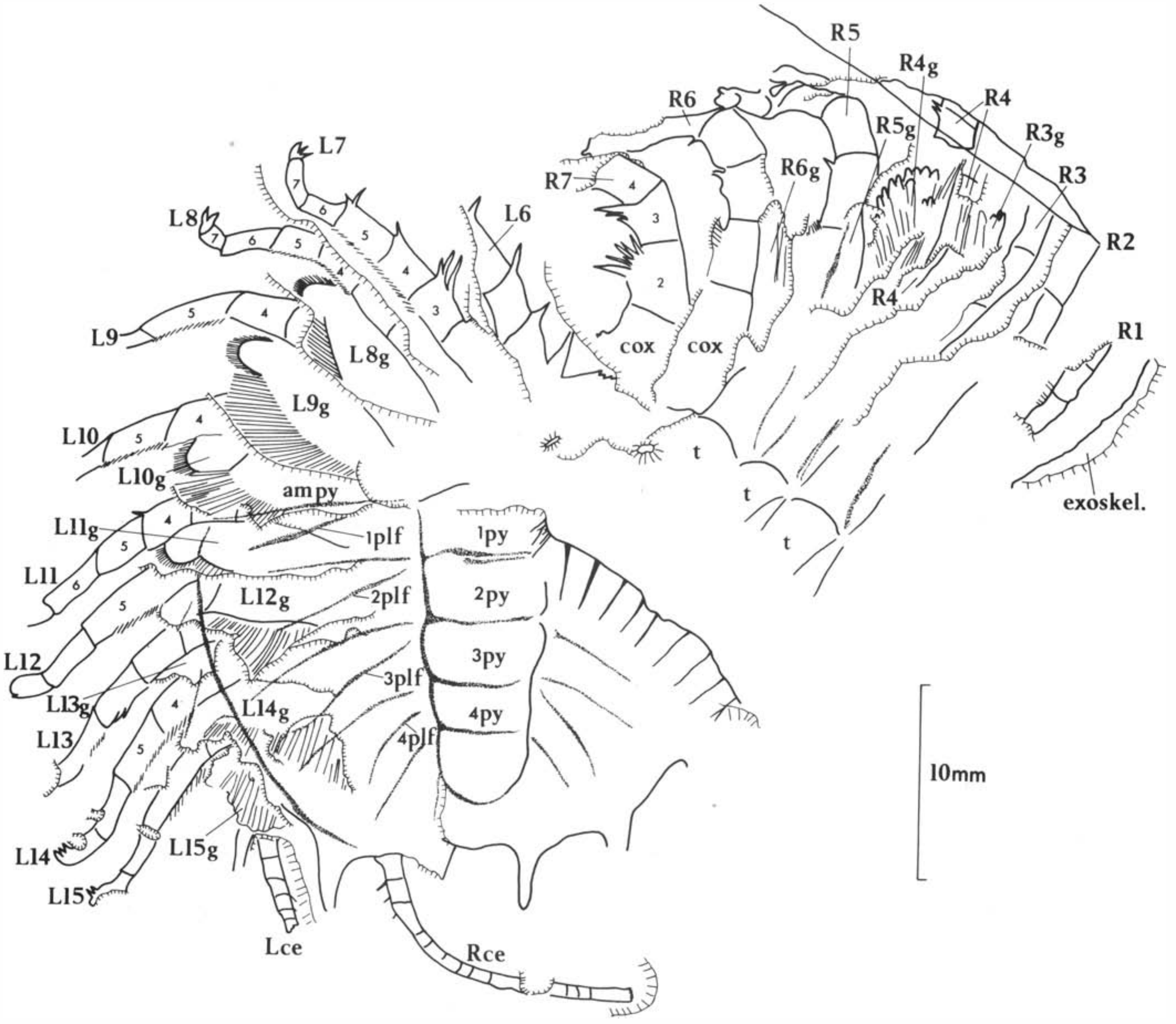
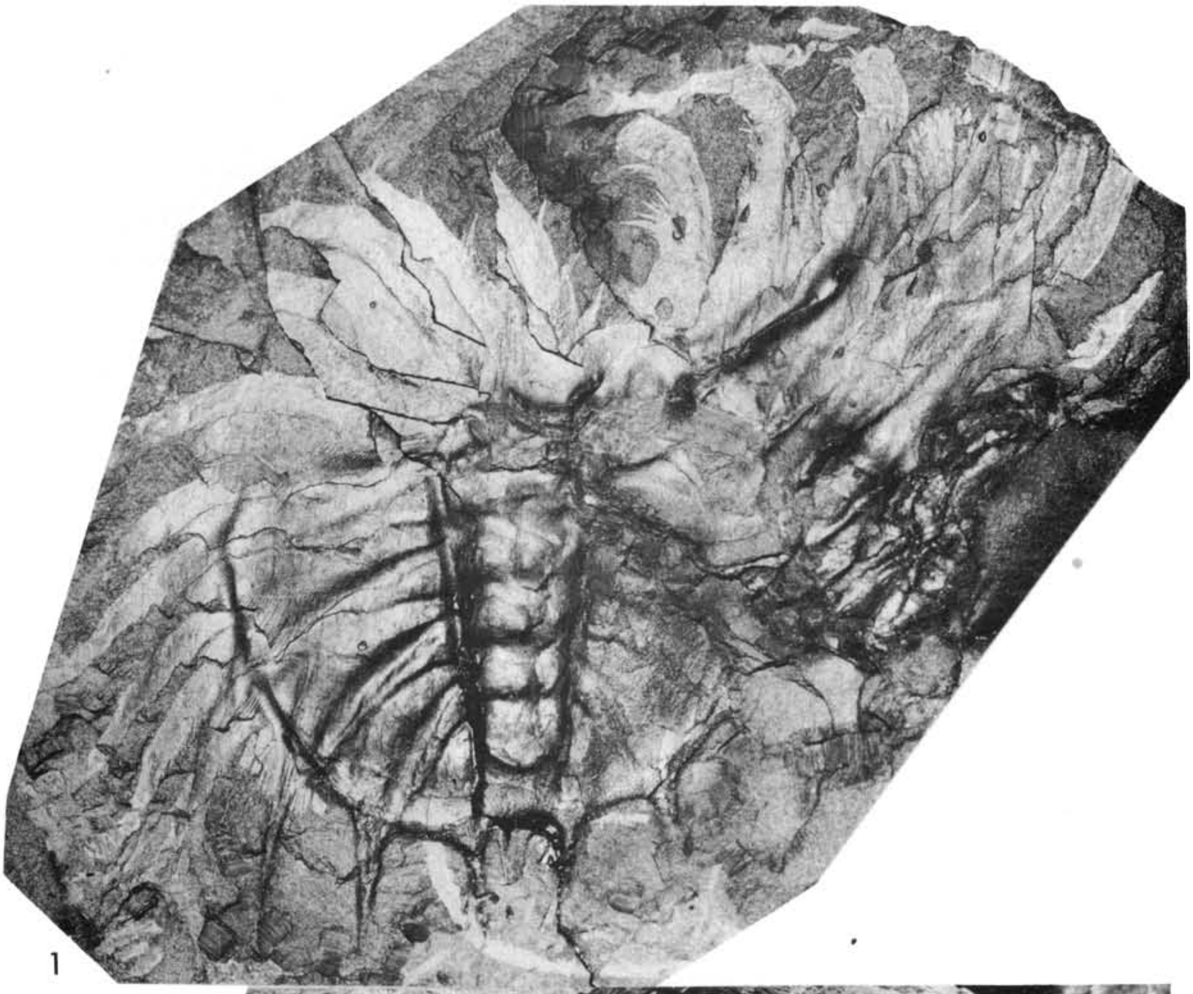


Fig. 13.

Plate 10.

Olenoides serratus (Rominger, 1887), USNM 65514, Phyllopod bed, Walcott quarry. See Fig. 13. 1, reflected, x2.5. 2, northeast, x2.5. Photographs made before excavation of left cercus.



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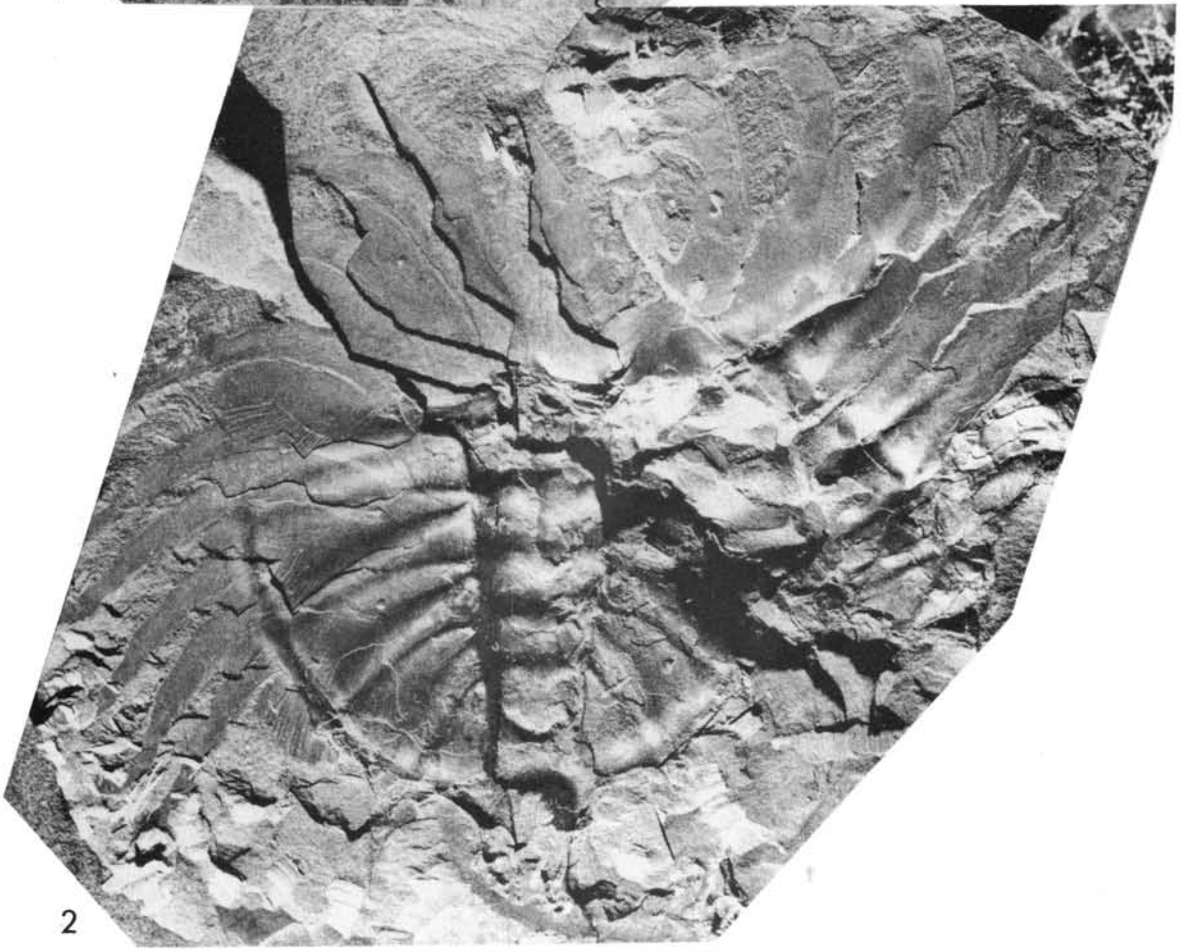

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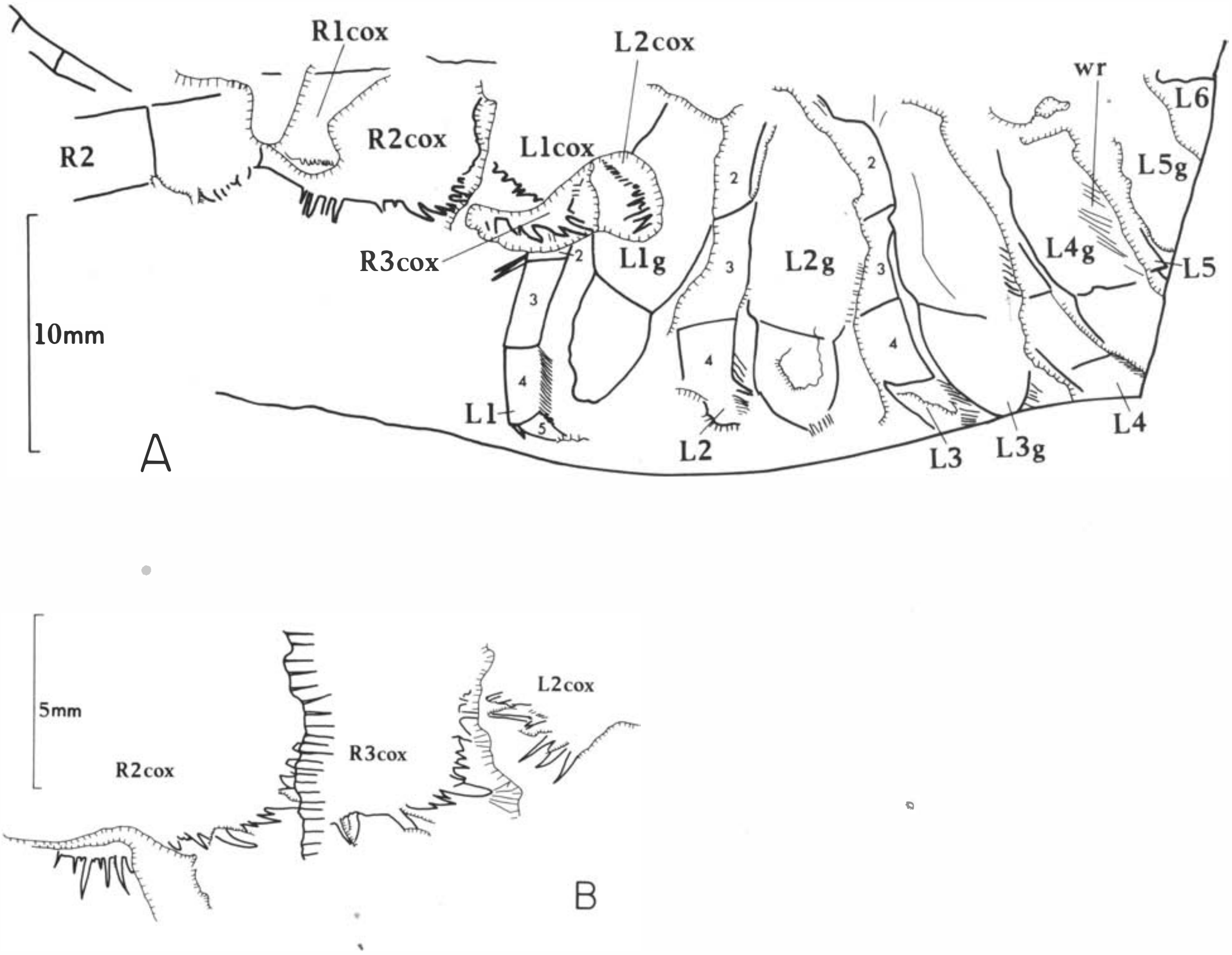

Fig. 14.

Plate 11.

Olenoides serratus (Rominger, 1887), USNM 65515, Phyllopod bed, Walcott quarry. 1, west, x2.5, see Fig. 14A. 2, reflected, x5, see Fig. 14B. 3, counterpart, reflected, x2.5, showing appendage L1, see Fig. 14A.

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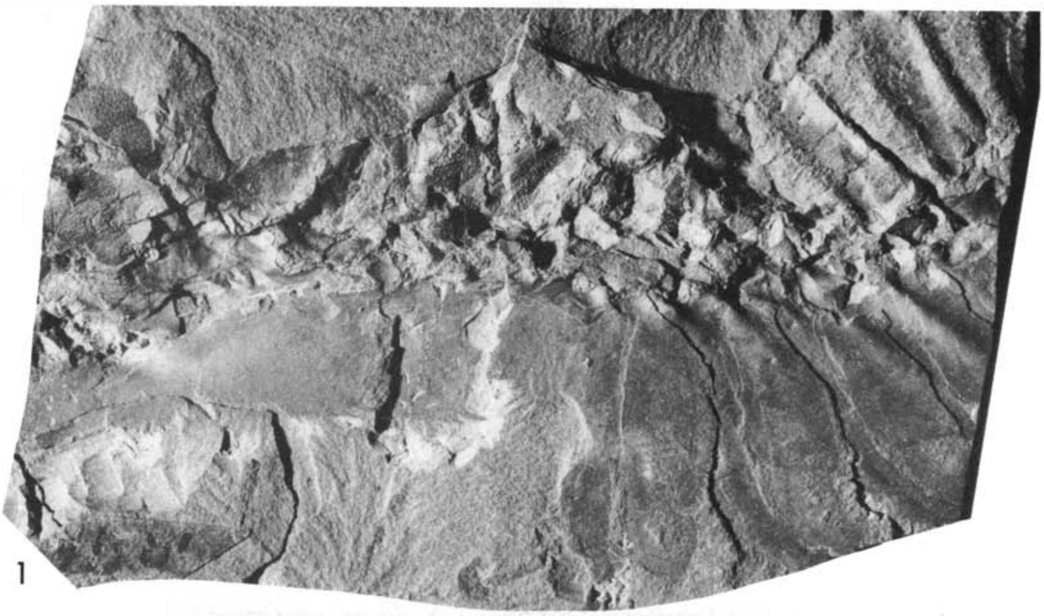

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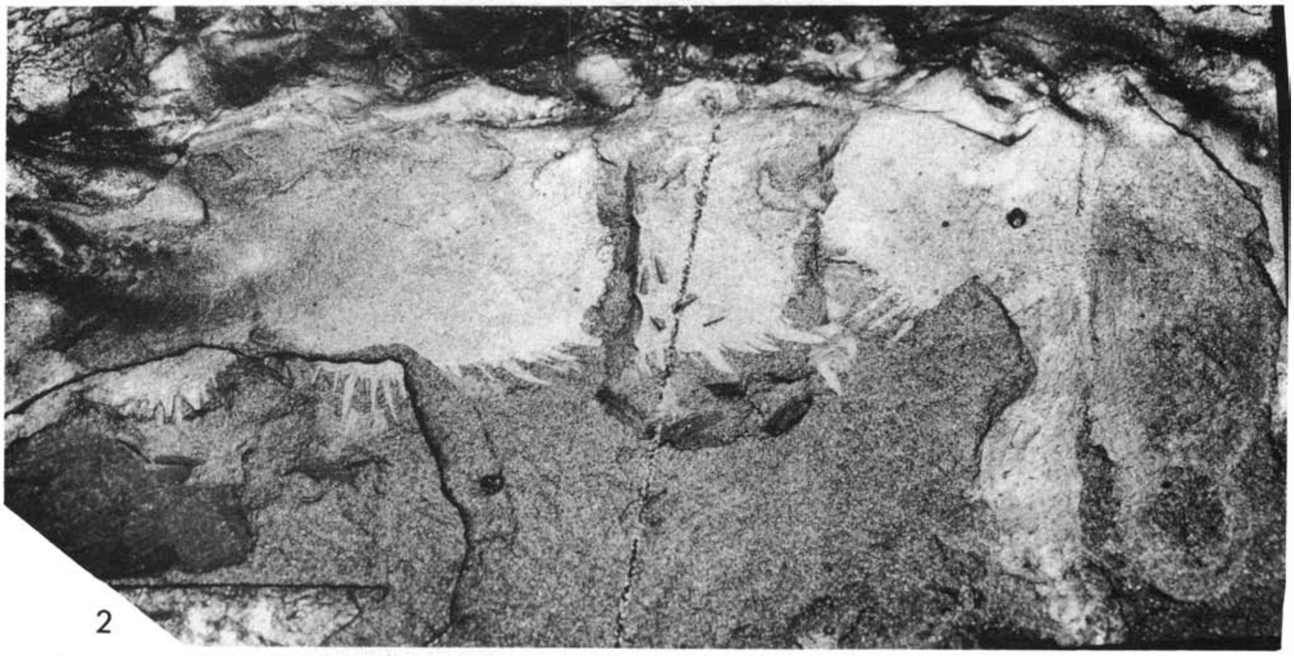

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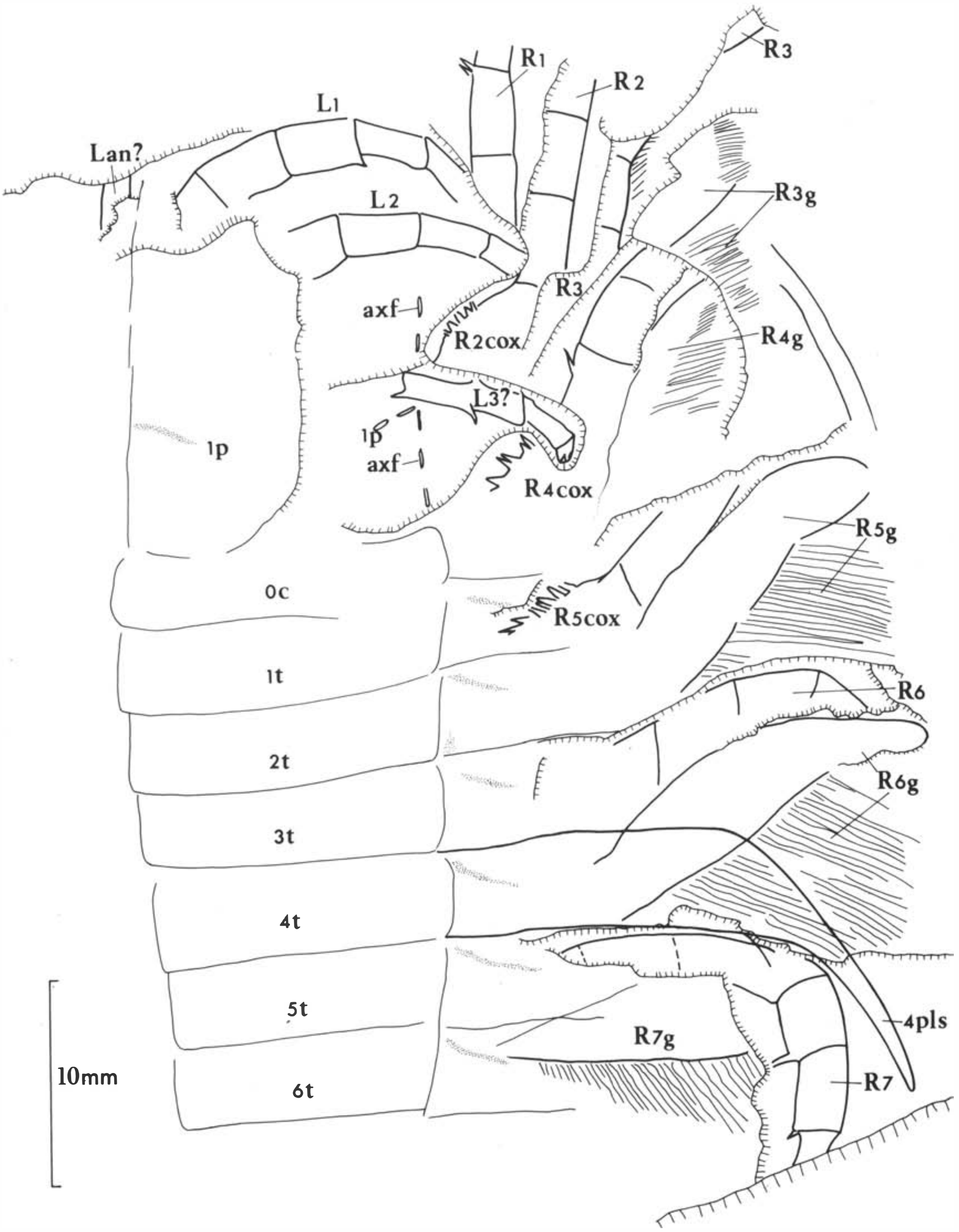
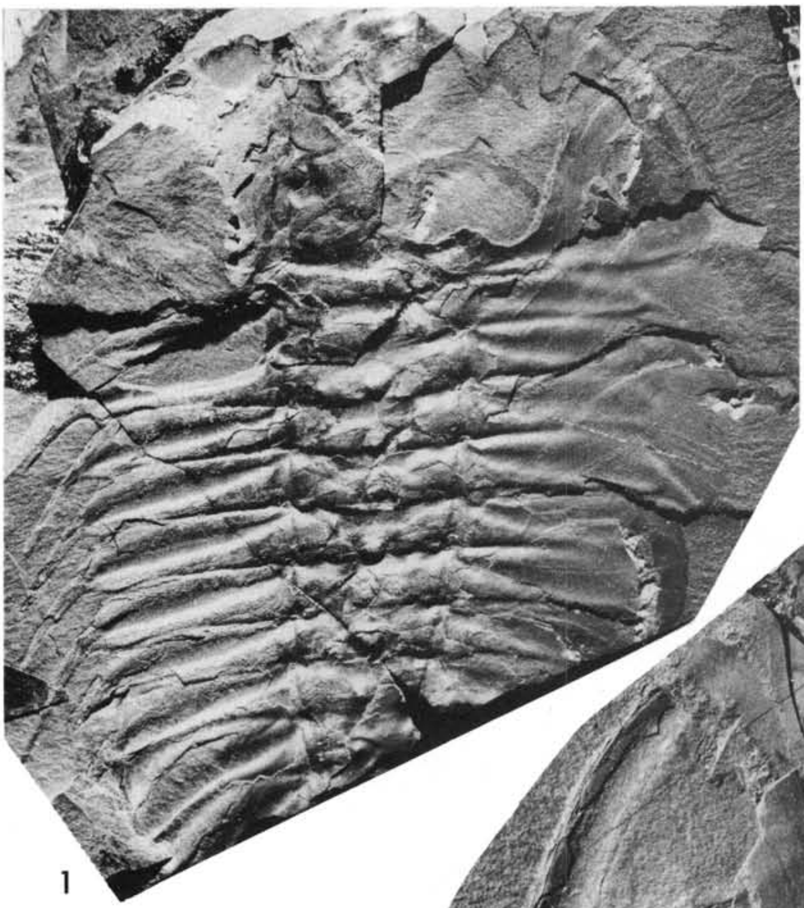


Fig. 15.

Plate 12.

Olenoides serratus (Rominger, 1887), USNM 65519, Phyllopod bed, Walcott quarry. See Fig. 15. 1, 3, north, reflected, x1.7. 2, counterpart, northwest, x2.5. 4, northwest, x2.5, details of right appendages 5 and 6.



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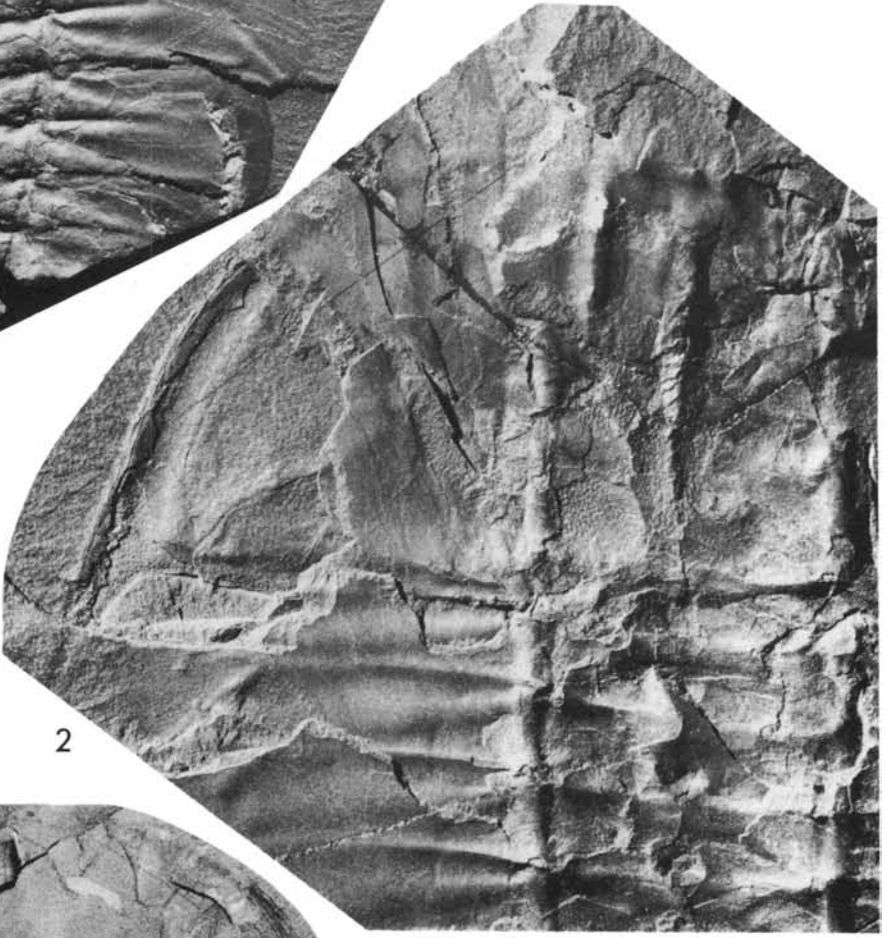

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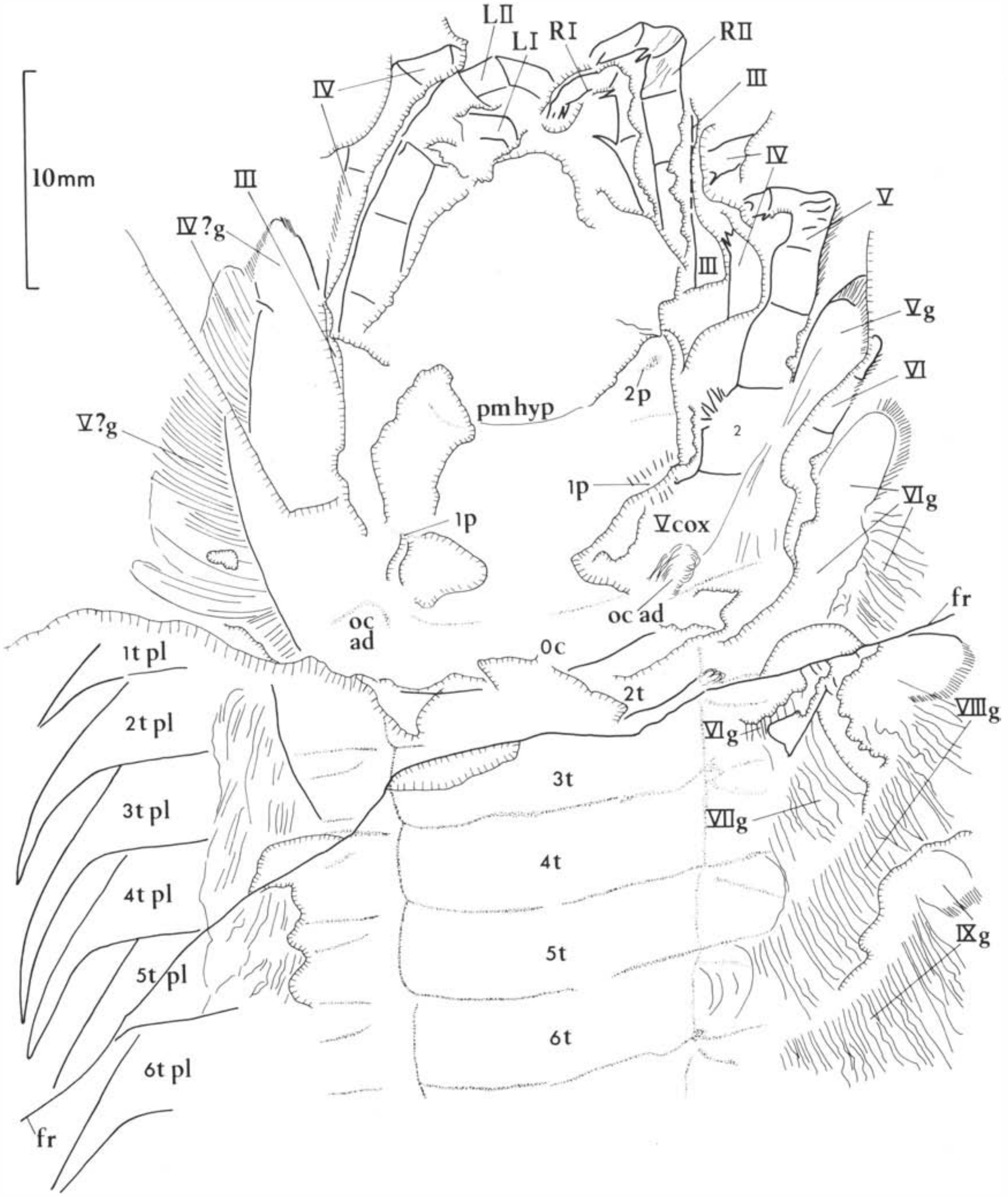
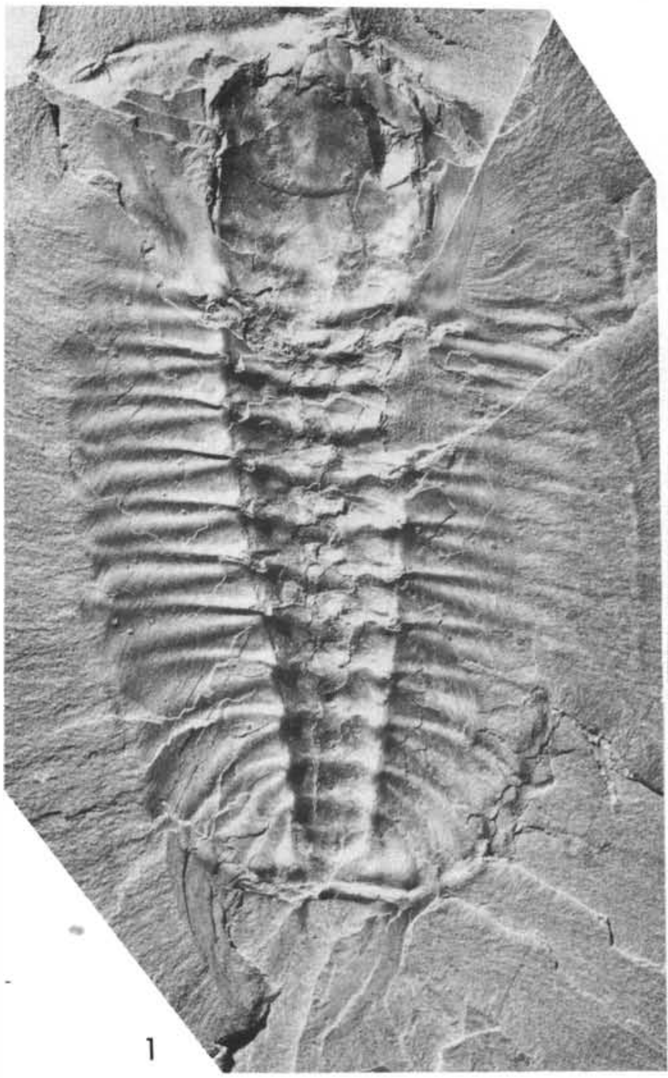


Fig. 16.

Plate 13.

Olenoides serratus (Rominger, 1887), USNM 65520, Phyllopod bed, Walcott quarry. See Fig. 16. 1, counterpart, north, x1.7. 2, 3, 4, north, x1.7, west, x2.5, reflected, x2.5.



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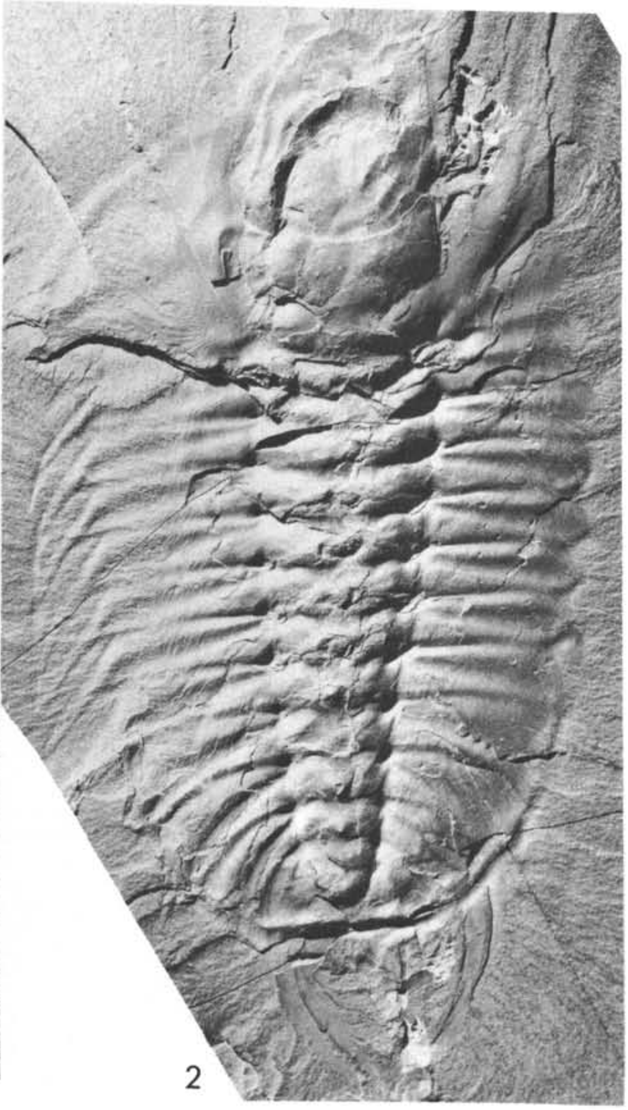

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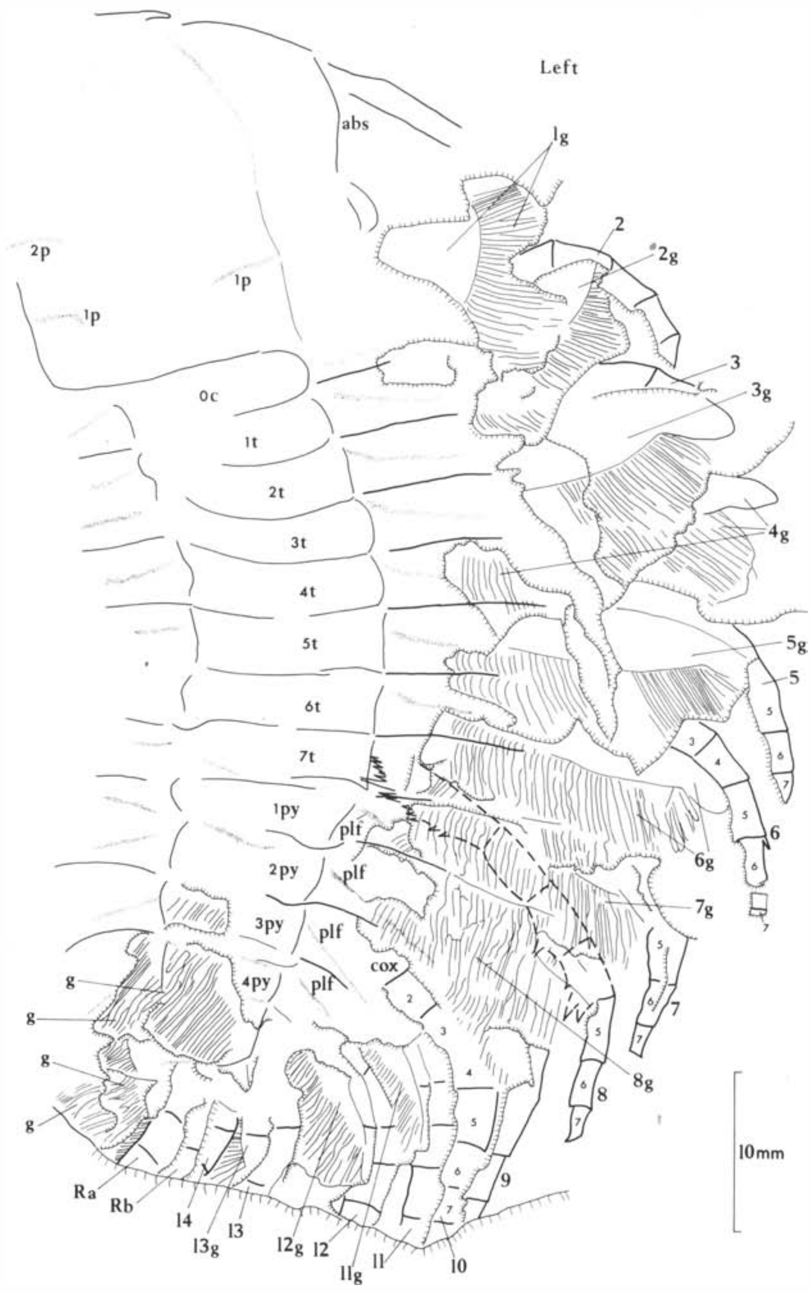
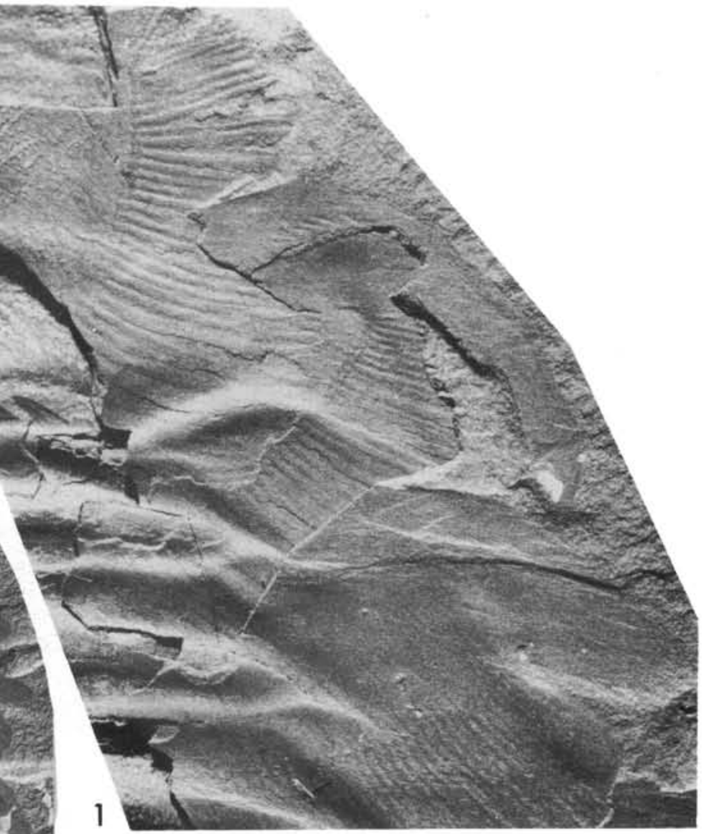


Fig. 17.

Plate 14.

Olenoides serratus (Rominger, 1887), USNM 65521, Phyllopod bed, Walcott quarry. See Figs. 4, 17. 1, north, x5, showing appendages L 1 to 3, see Fig. 4A. 2, northwest, x1.7, see Fig. 17, in which coxa and leg branch 8 are restored in outline. 3, west, x5, showing appendages L 8 to 14 and right appendages, see Figs. 17, 4B, 4C.



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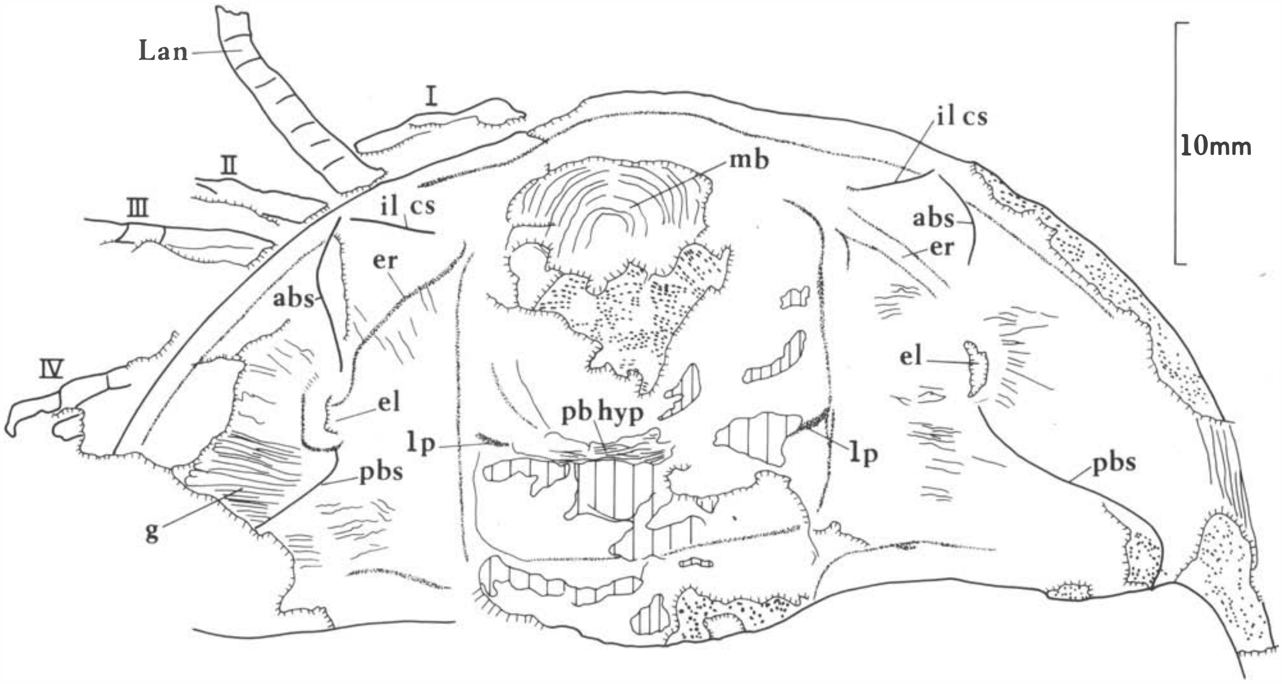
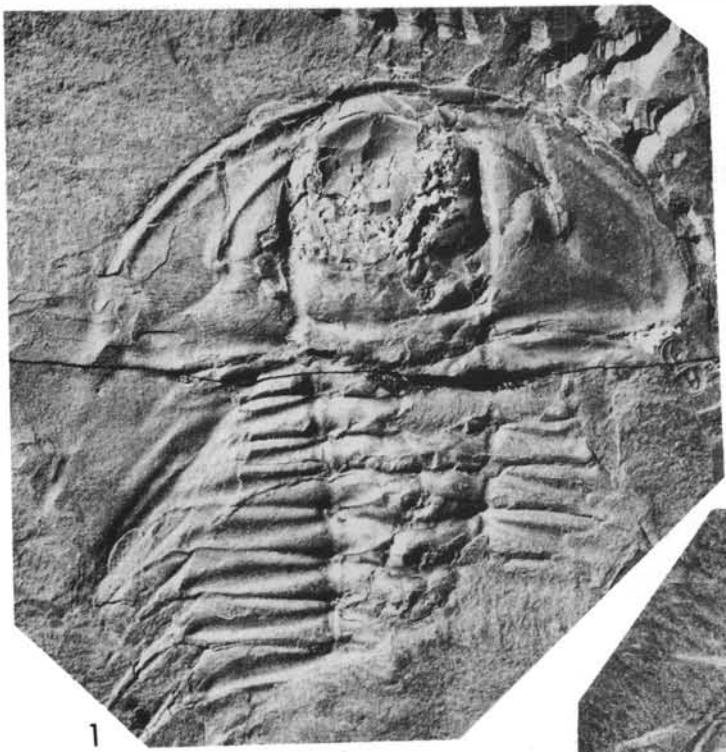


Fig. 18.

Plate 15.

Olenoides serratus (Rominger, 1887), USNM 188572, Phyllopod bed, Walcott quarry. See Fig. 18, in which highly reflective areas are shown by vertical lines, and granulation indicated on fragments of external surface. 1, 2, northwest, reflected, x1.7. 3, northwest, x3.7.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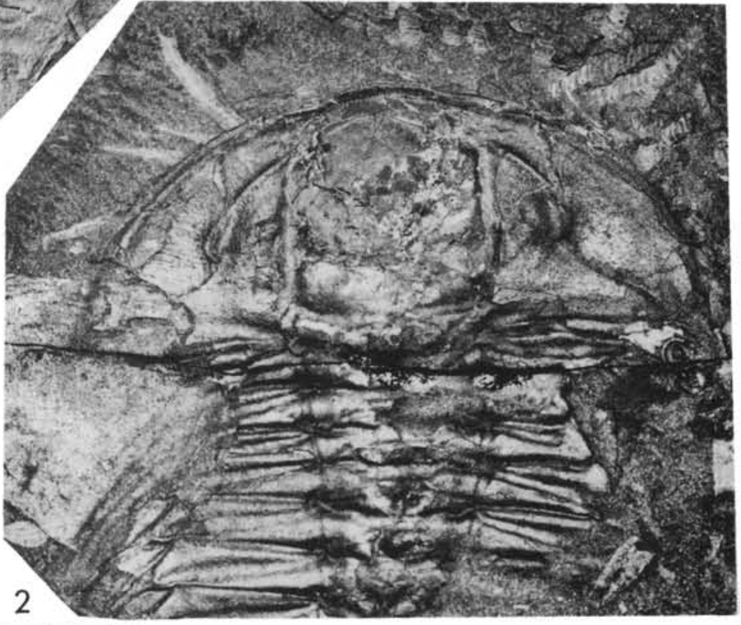
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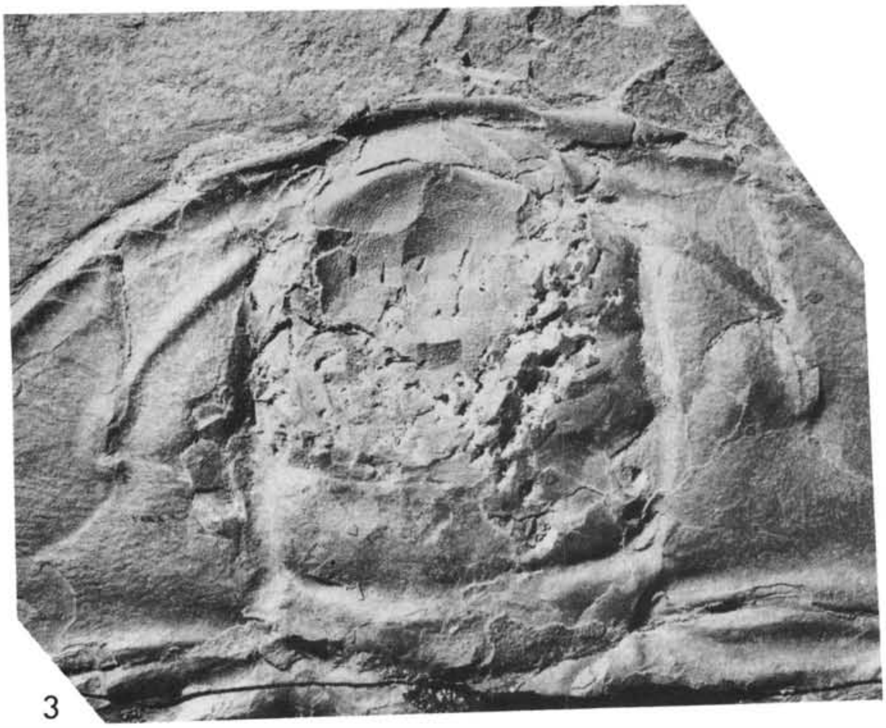
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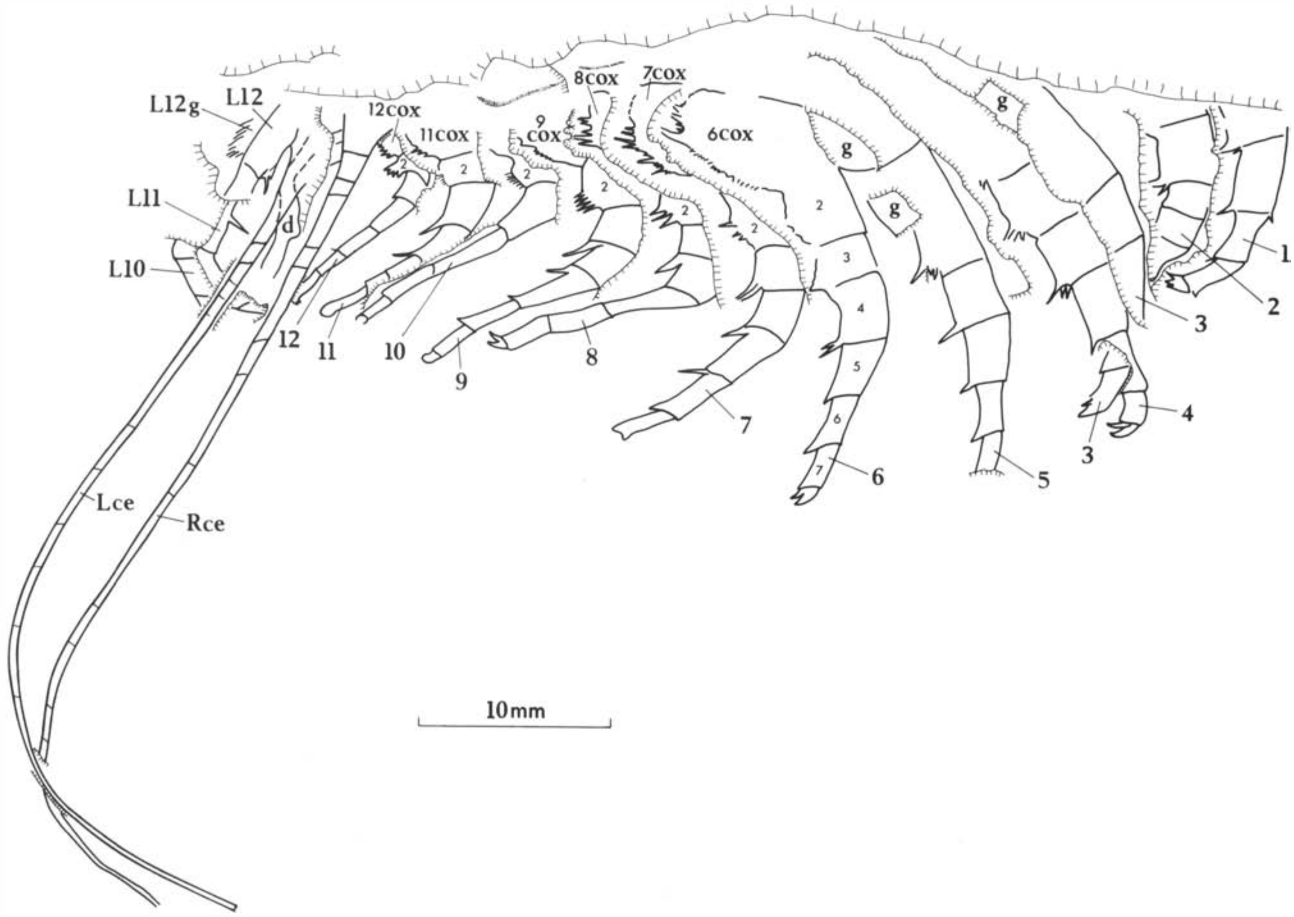
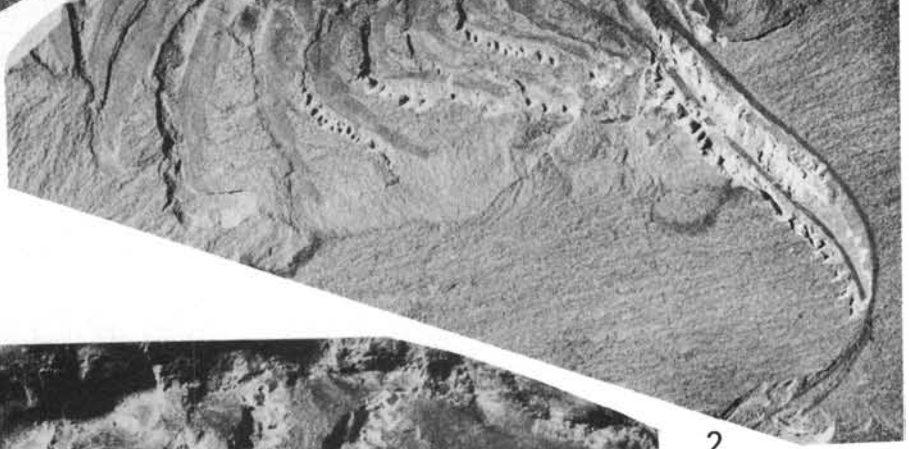


Fig. 19.

Plate 16.

Olenoides serratus (Rominger, 1887), USNM 188573, Phyllopod bed, Walcott quarry. See Fig. 19. 1, east, x1.7. 2, counterpart, west, x1.7. 3, northwest, x5, showing coxae and leg branches 6 to 12 and base right cercus. 4, counterpart, northwest, x5, showing leg branches 8 to 12, base cerci, and left appendage 12.

1



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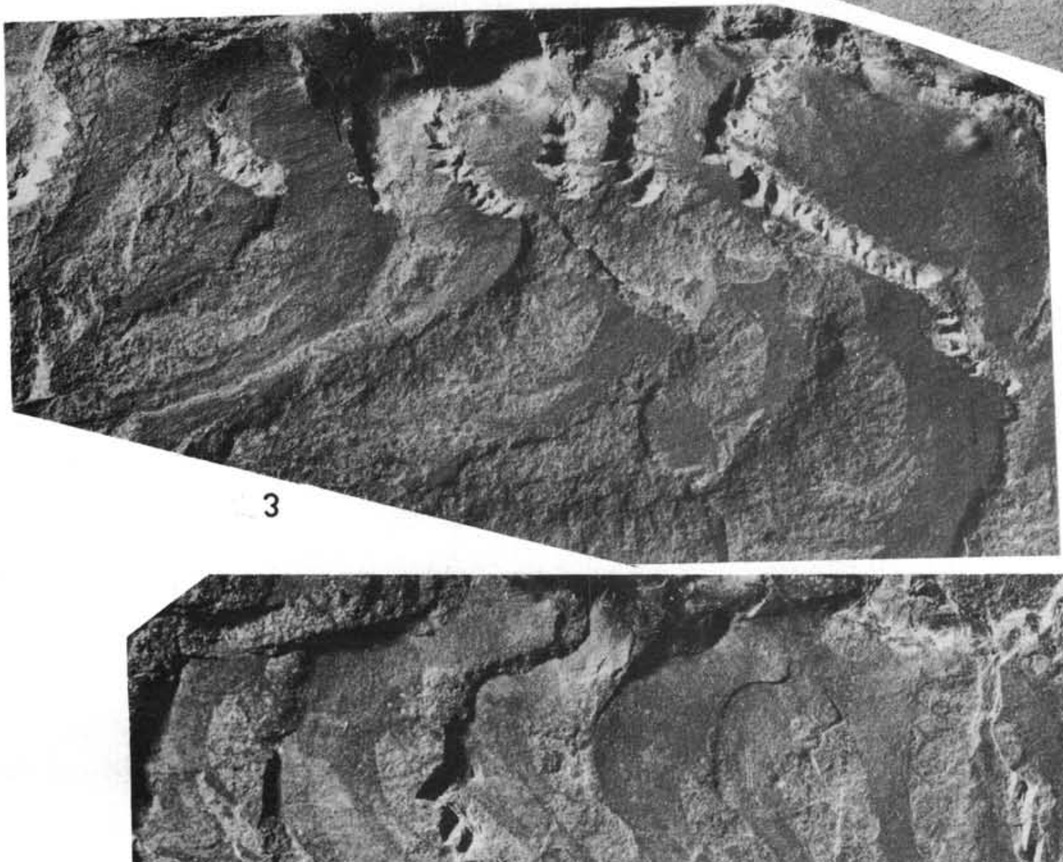

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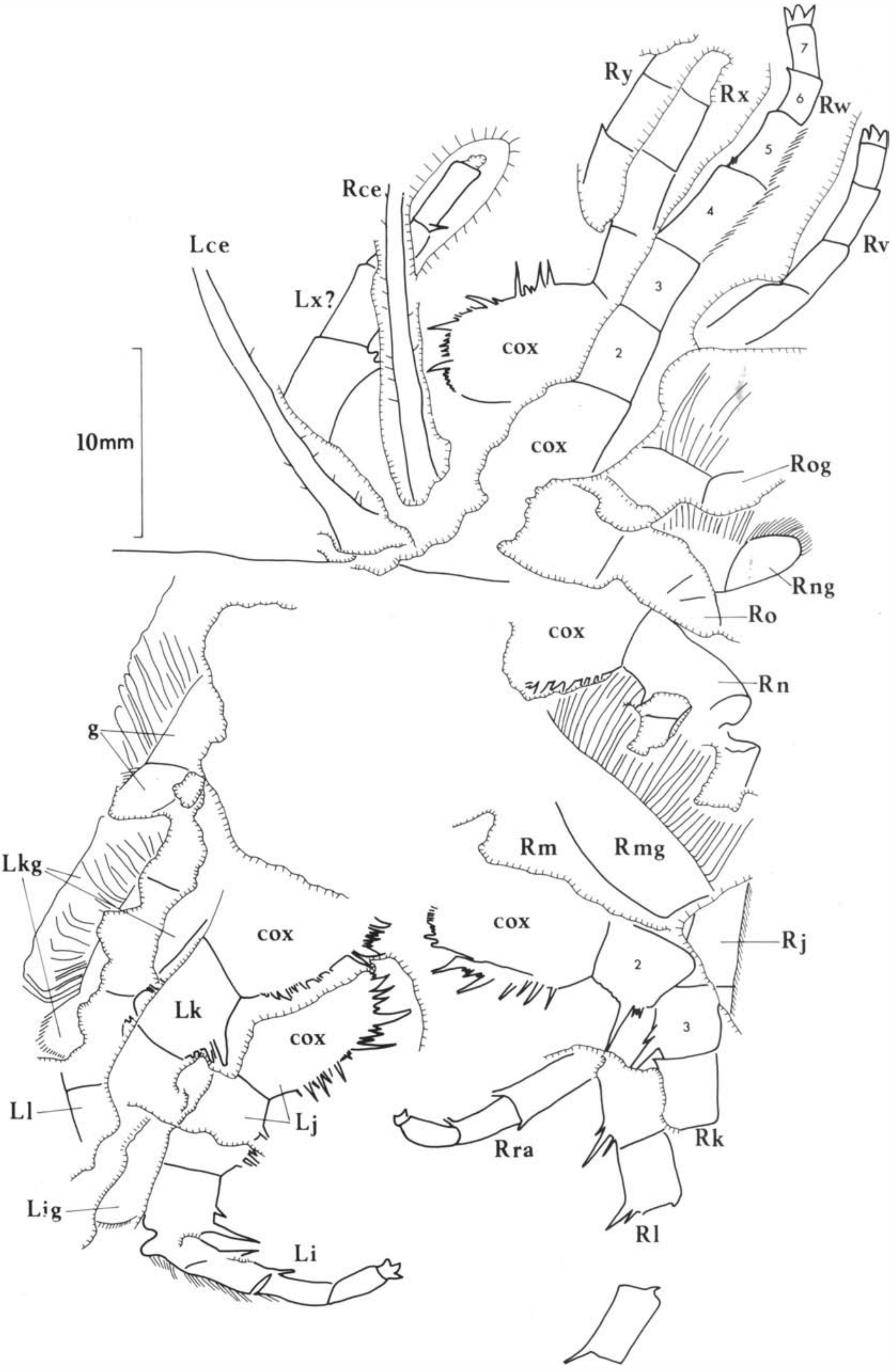
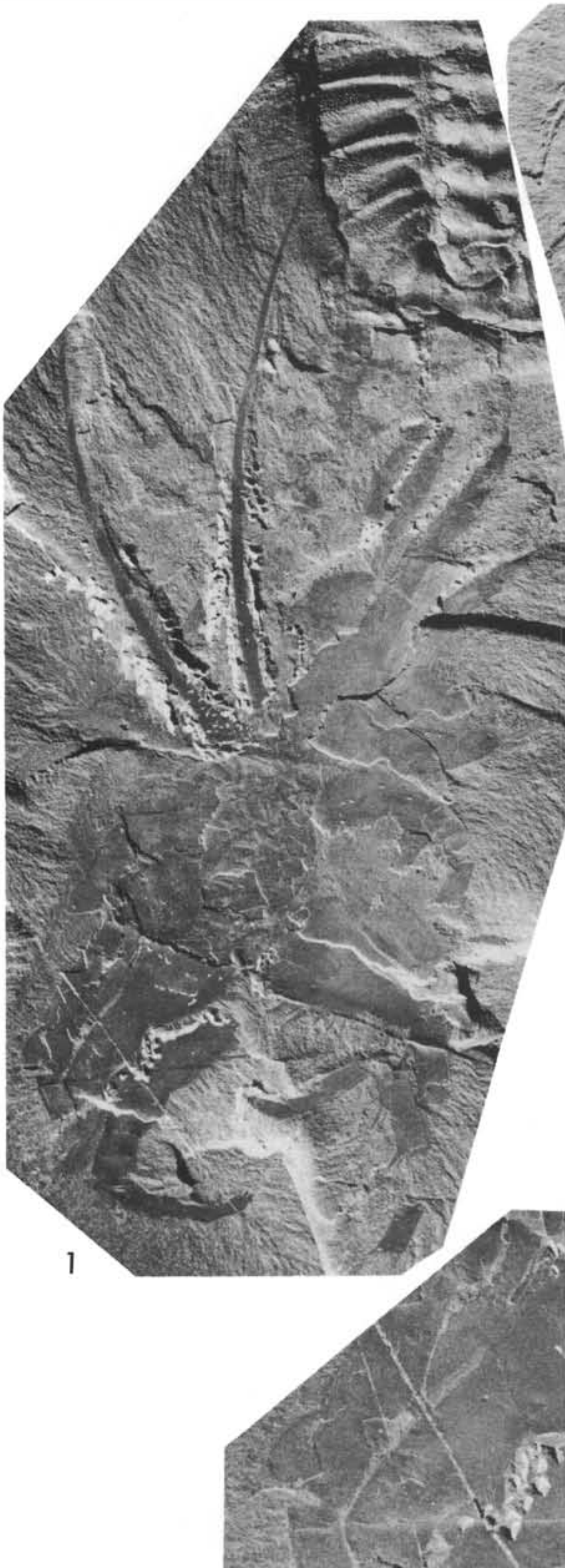


Fig. 20.

Plate 17.

Olenoides serratus (Rominger, 1887), GSC 34692, Walcott quarry, level 6ft. 10ins. to 7ft. 2ins. See Fig. 20.
1, counterpart, northeast, x1.7. 2, north, x1.7. 3, counterpart, southwest, x3.3.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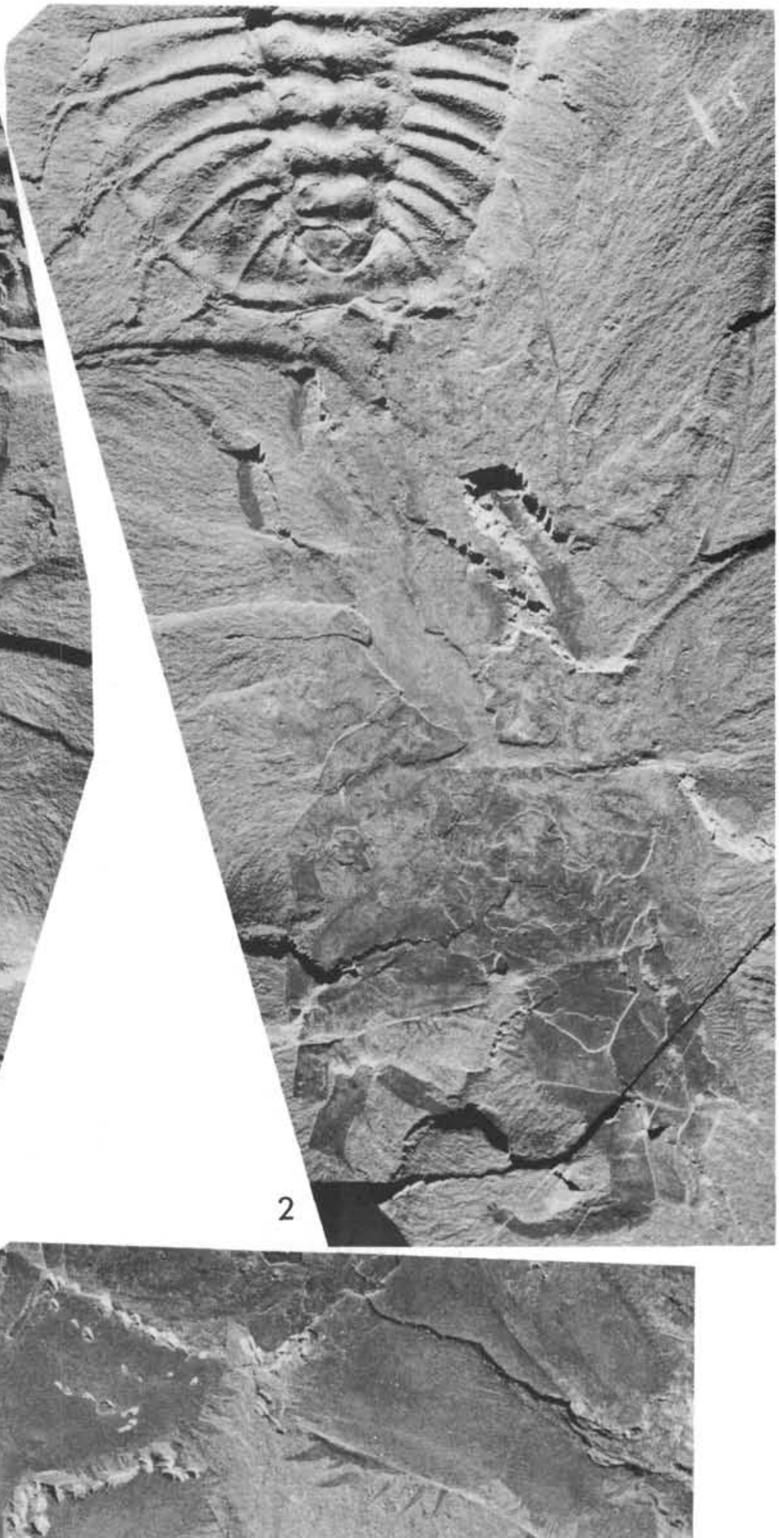
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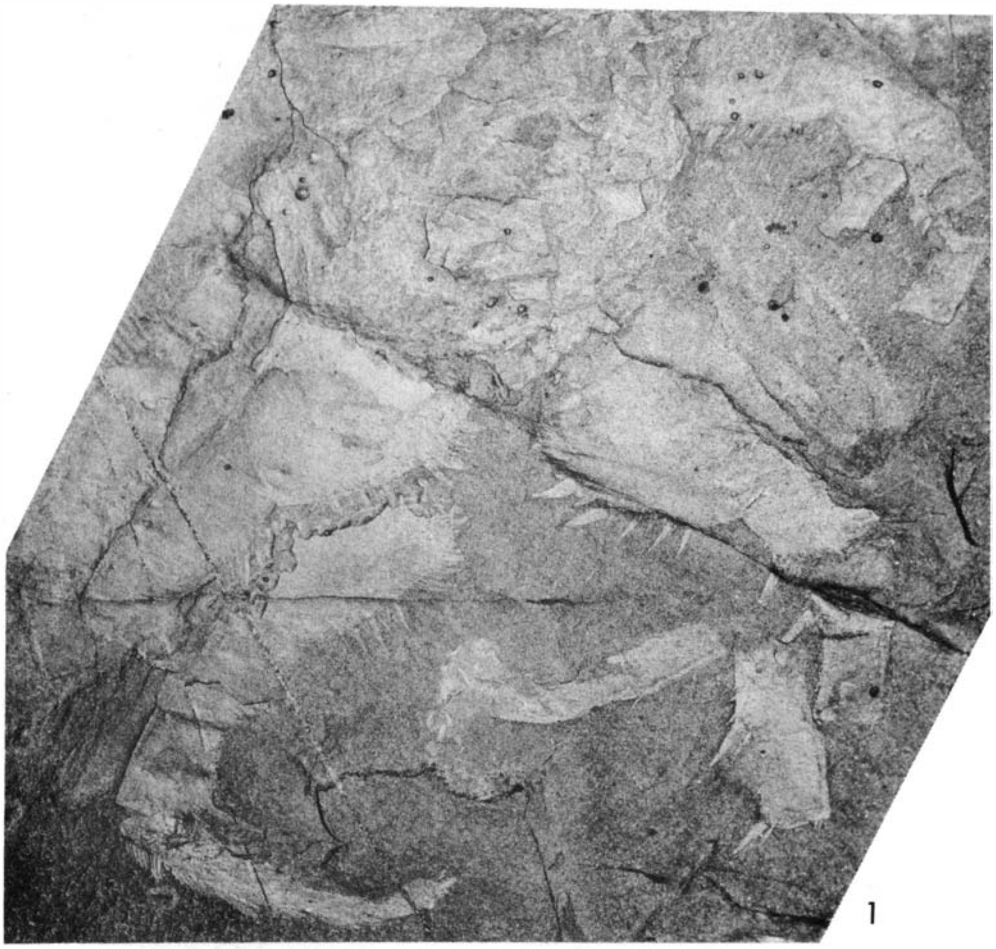
3

Plate 18.

Olenoides serratus (Rominger, 1887), GSC 34692, Walcott quarry, level 6ft. 10ins. to 7ft. 2ins. See Fig. 20.
1, counterpart, reflected, x3.3, compare Pl. 17:3. 2, reflected, x3.3, showing left leg branch x?, right leg branches v to y and coxa Rx (inverted relative to Fig. 20).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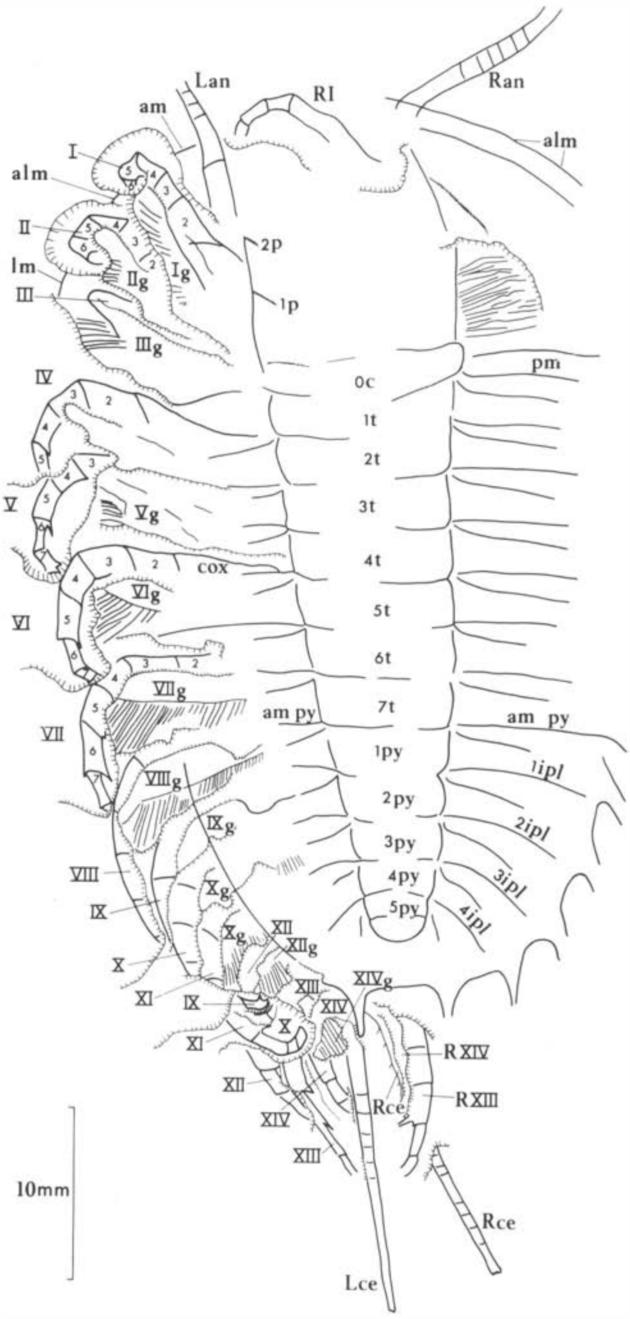
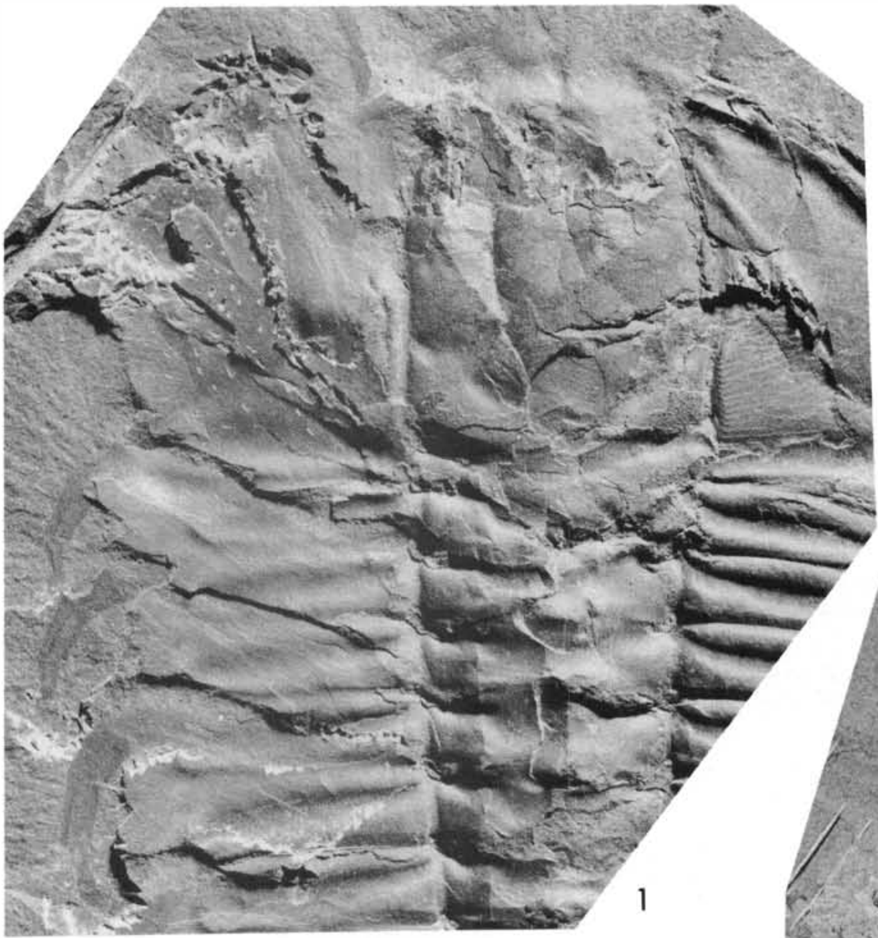


Fig. 21.

Plate 19.

Olenoides serratus (Rominger, 1887), GSC 34693, Walcott quarry, level 10ft. 4 ins. to 10 ft. 8 ins. See Fig. 21. 1, northeast, x3.3, details of anterior portion. 2, northwest, x3.3, detail of posterior portion. 3, reflected, x1.7.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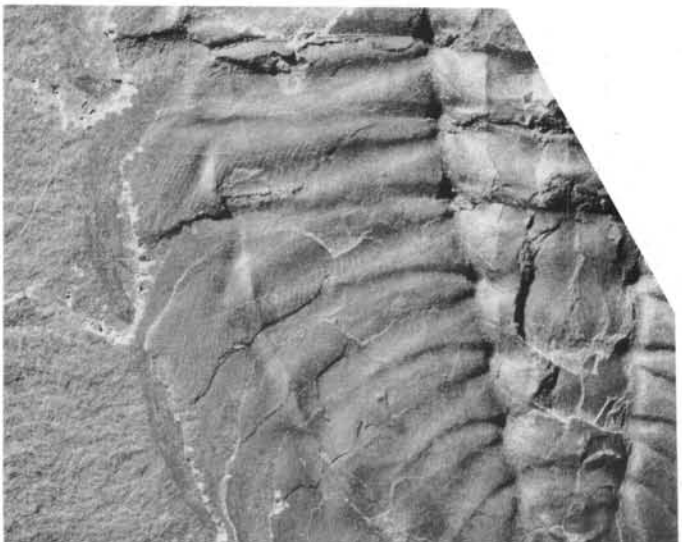
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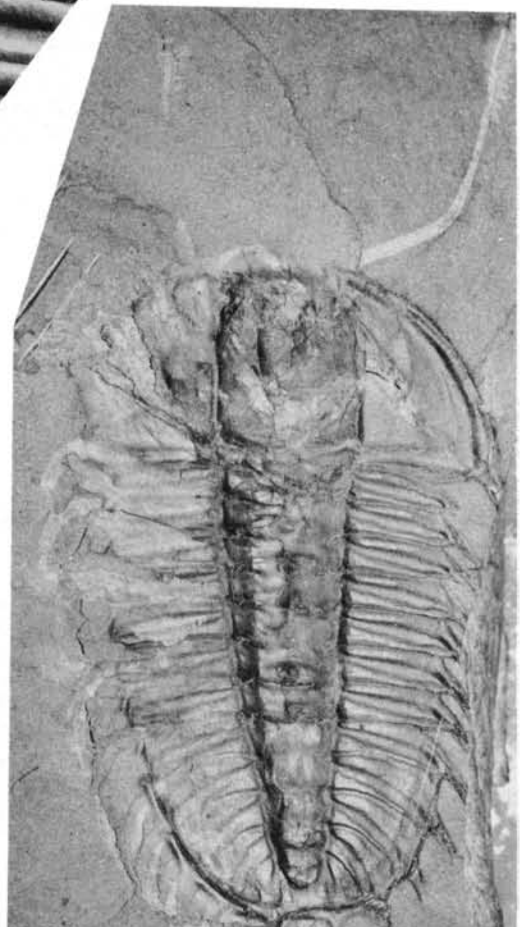
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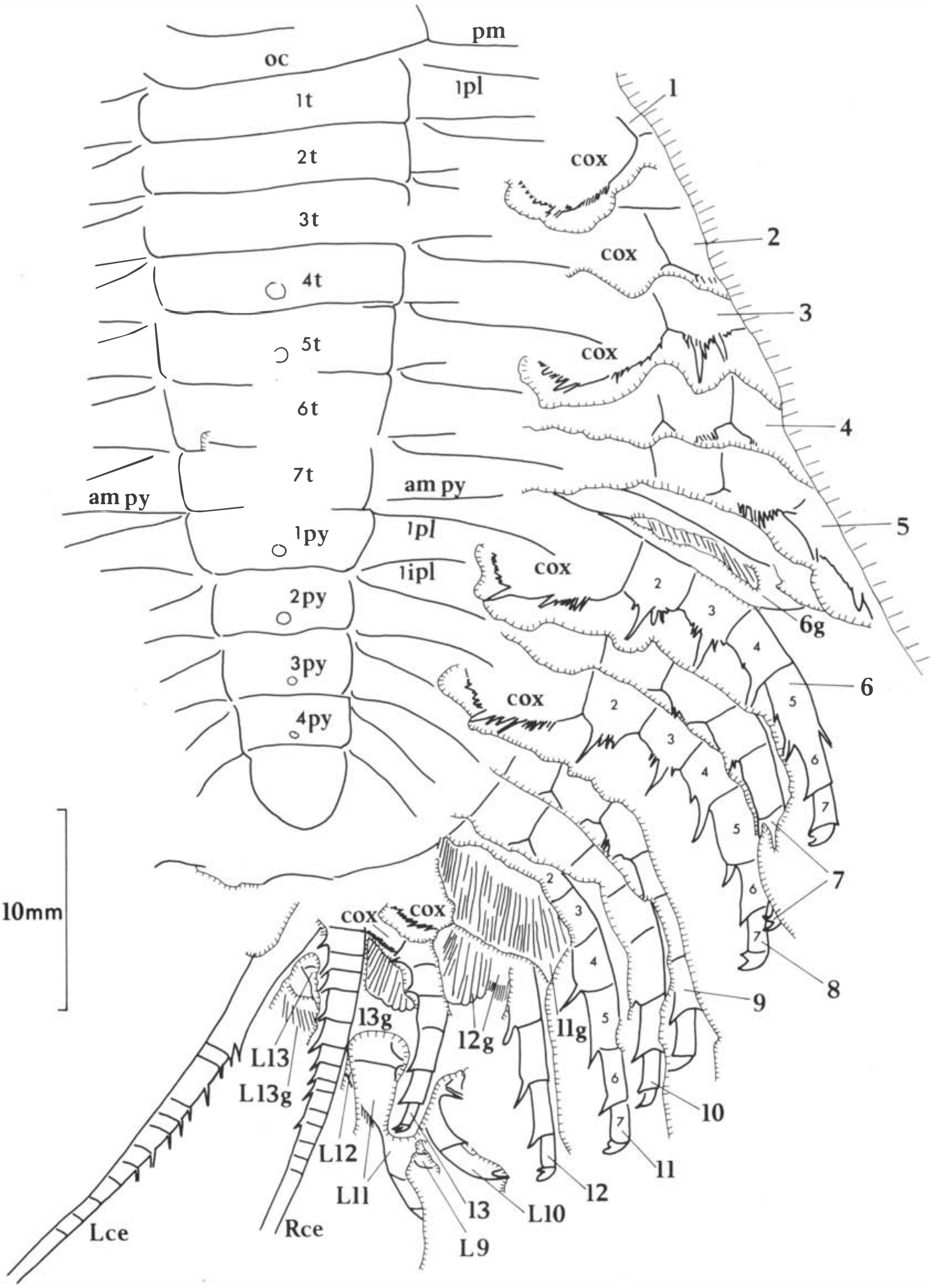


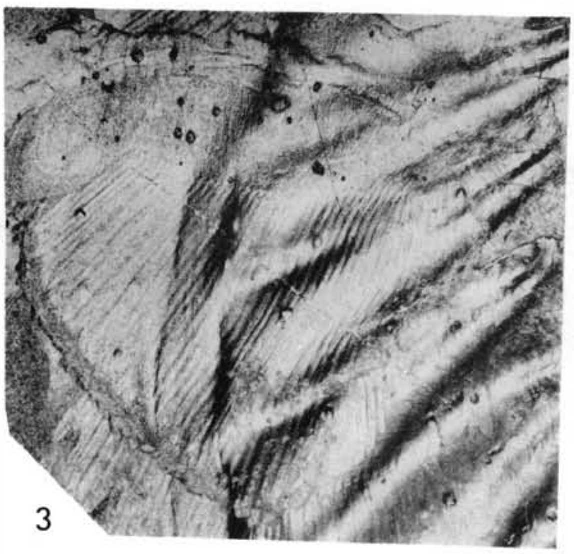
Fig. 22.

Plate 20.

Olenoides serratus (Rominger, 1887). 1, 2, 4, GSC 34694, Walcott quarry, level 6ft. 7.5ins. to 7 ft. 3.5ins., see Fig. 22, 1, northeast, x3.3, 2, reflected, x3.3, 4, northwest, x1.7. 3, GSC 34695, Walcott quarry, level 6ft. 11ins. to 7ft. 0ins., reflected, x3.3, see Fig. 23 and Plate 23:1.

1

2



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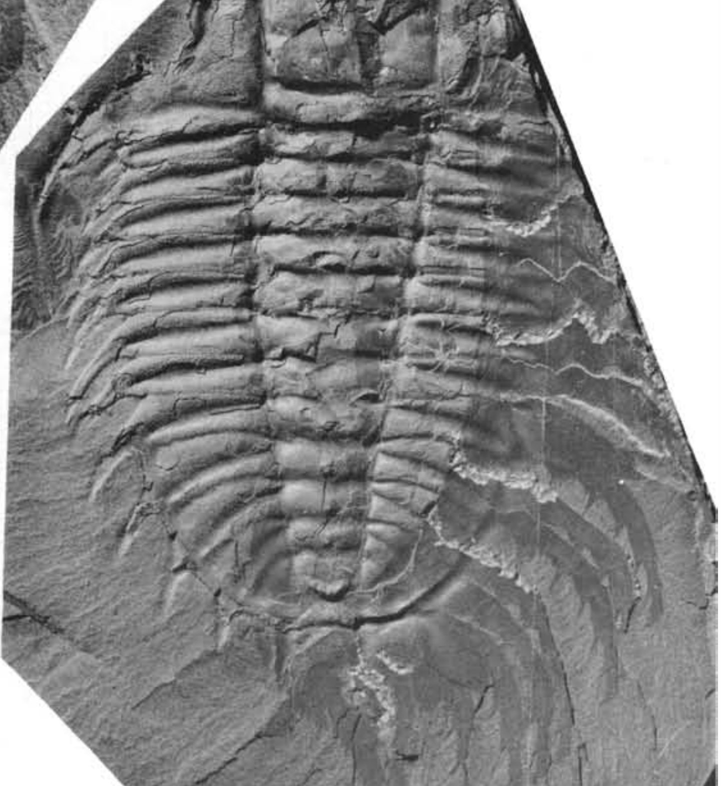
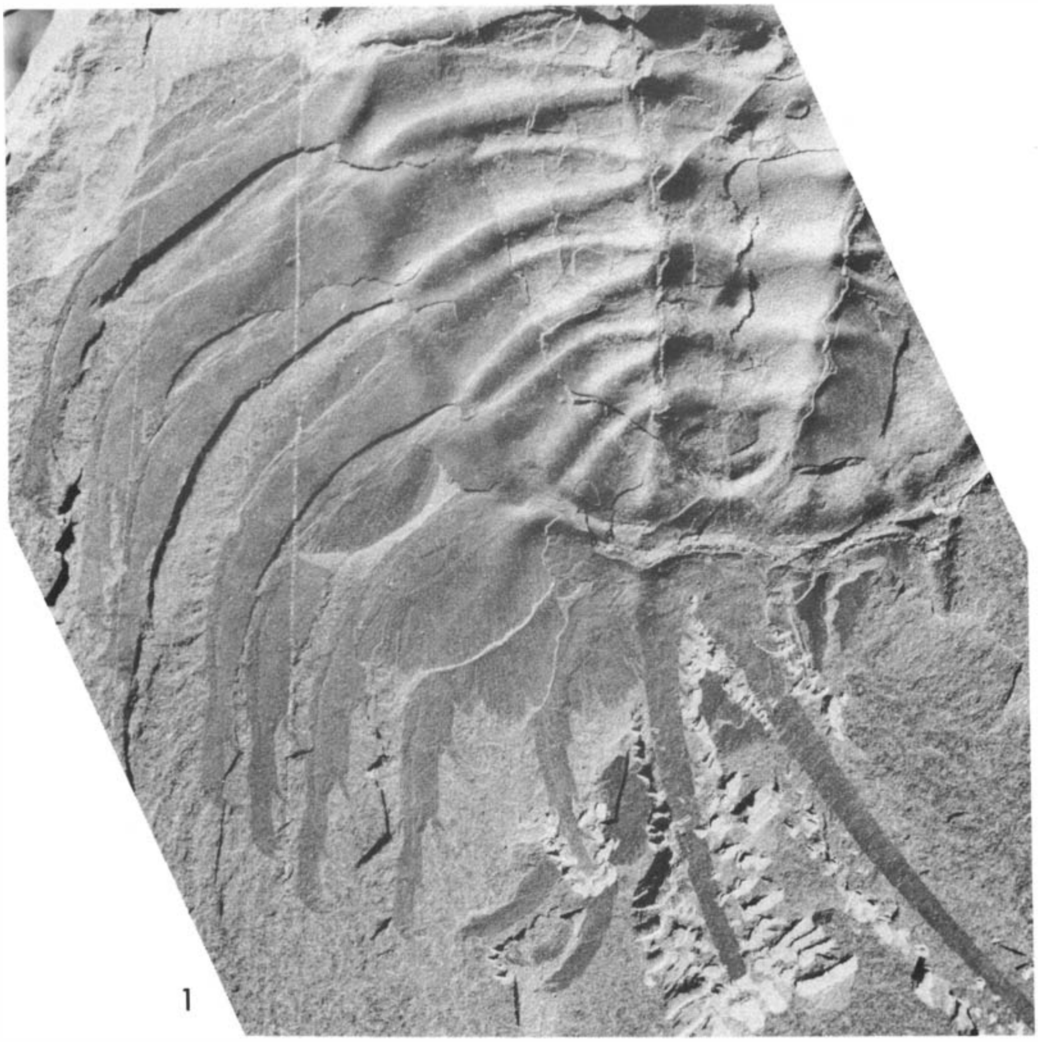


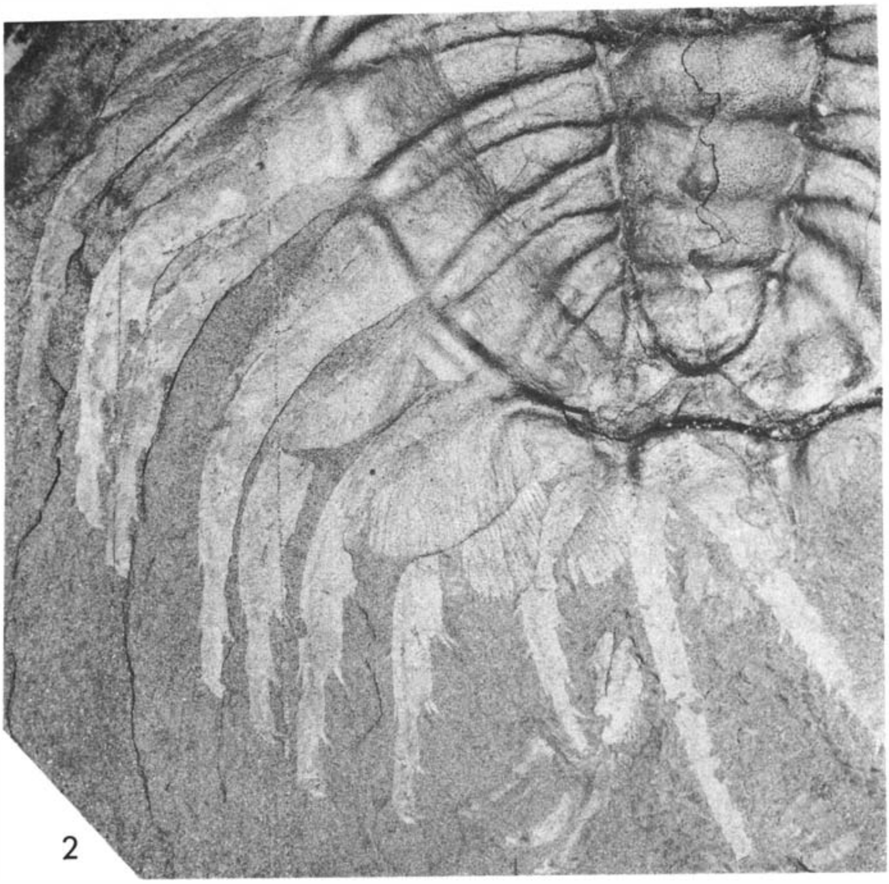
4

Plate 21.

Olenoides serratus (Rominger, 1887), GSC 34694, Walcott quarry, level 6ft. 7.5ins. to 7 ft. 3.5ins. See Fig. 22.
1, 2, counterpart, northwest, reflected, x3.3.



1



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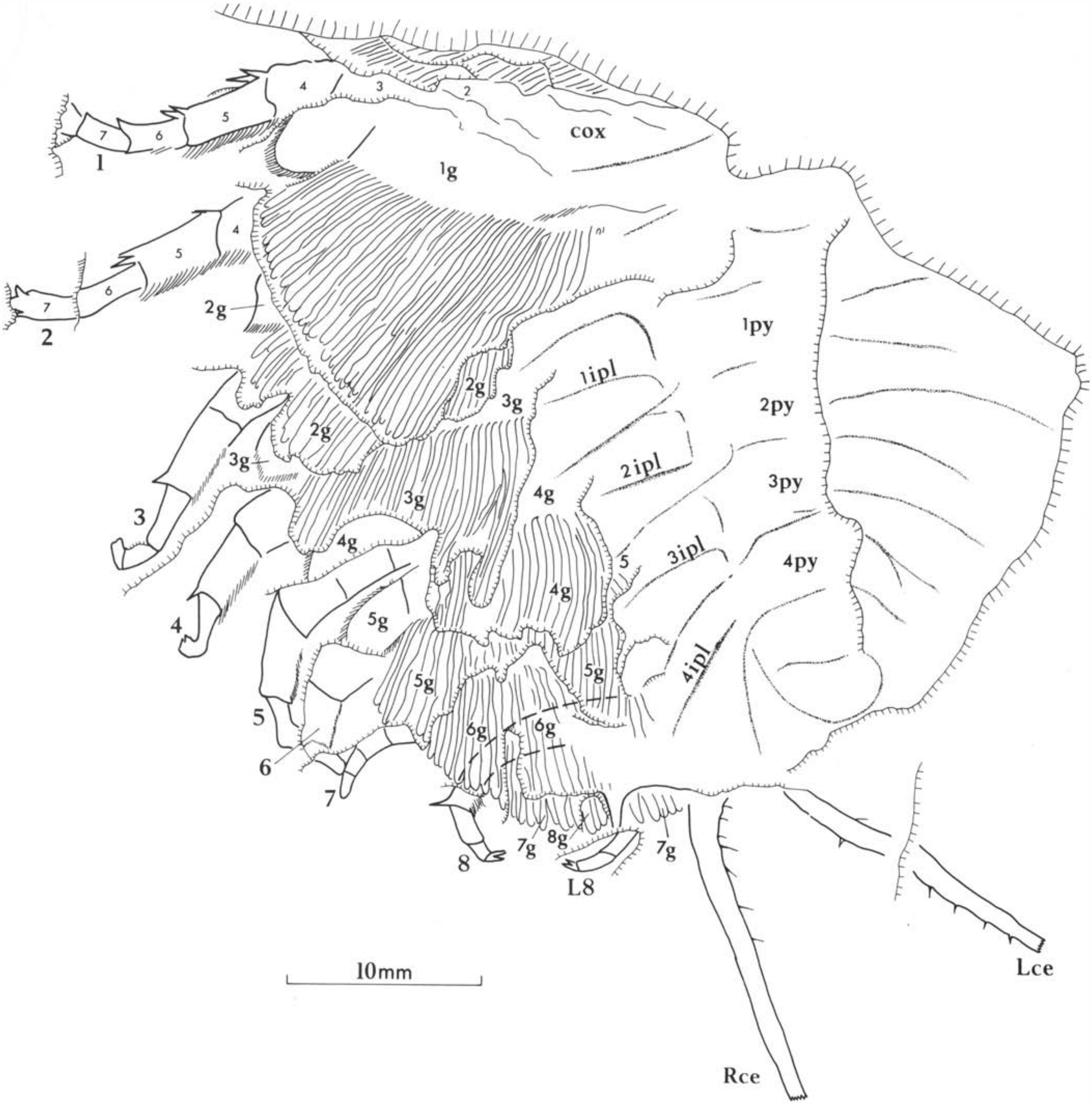
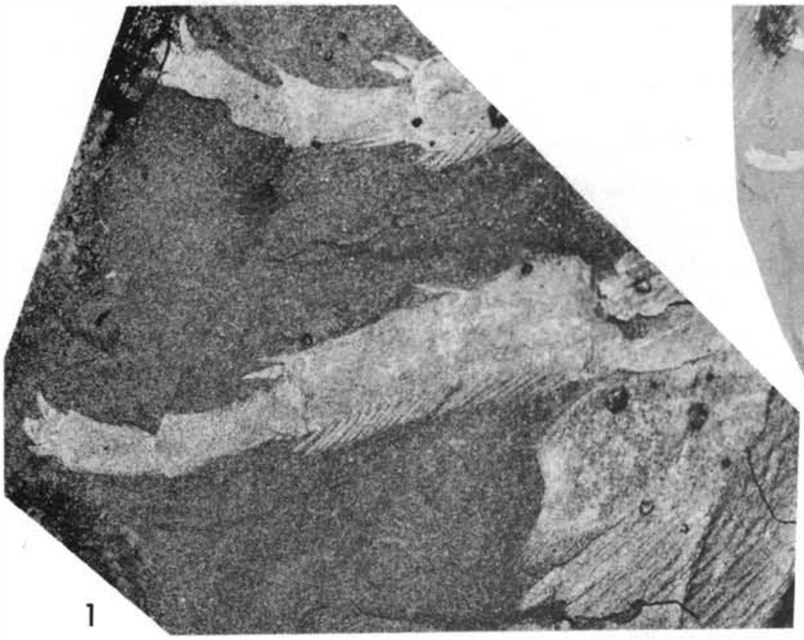


Fig. 23.

Plate 22.

Olenoides serratus (Rominger, 1887), GSC 34695, Walcott quarry, level 6ft. 11ins. to 7ft. 0ins. See Fig. 23. 1, 4 counterpart, reflected, x5. 2, 3, counterpart, reflected, northeast, x1.7, before excavation of lamellae of 1g (see Pl. 23:1).



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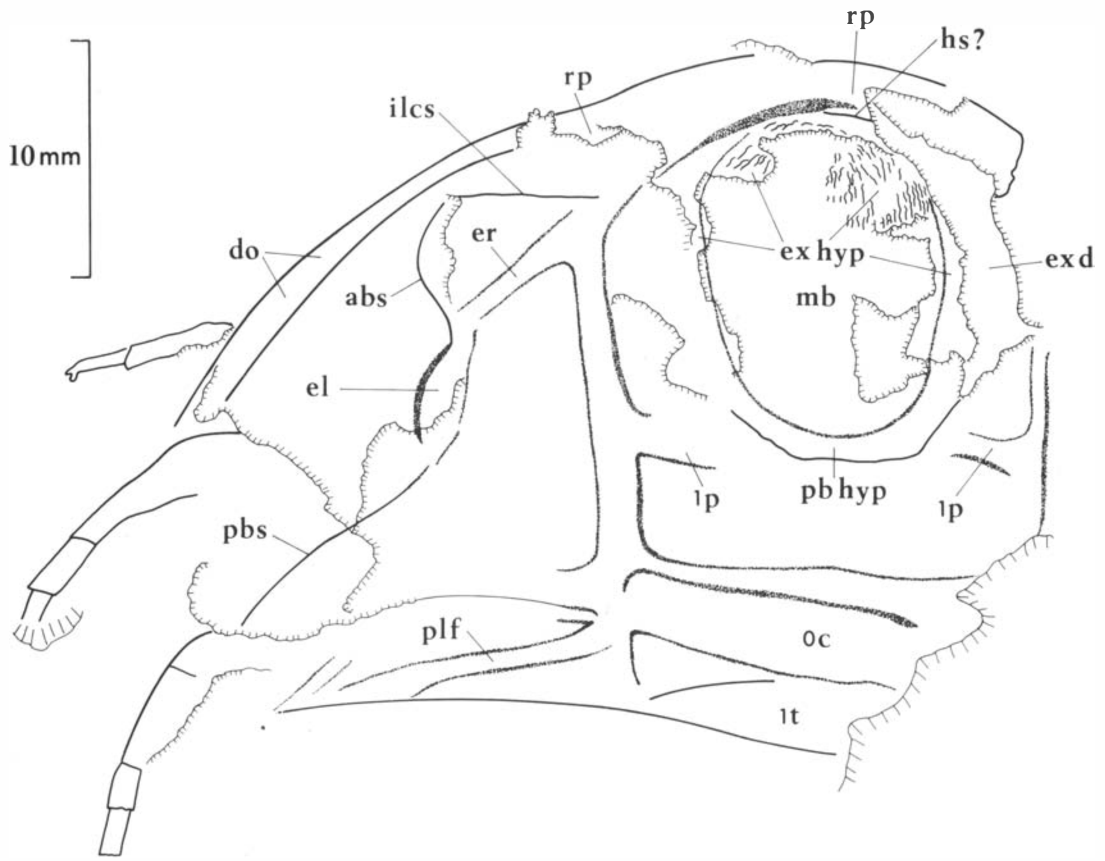


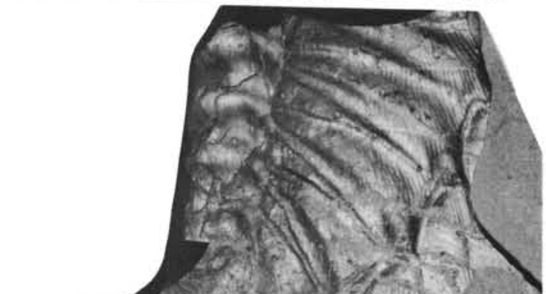
Fig. 24.

Plate 23.

Olenoides serratus (Rominger, 1887). 1, 3, GSC 34695, Walcott quarry, level 6ft. 11ins. to 7ft. 0ins, 1, counterpart, west, x5, showing lamellae of 1g, see Fig. 23, 3, reflected, x1.7, showing leg branches R7, R8, and L8, see Fig. 23. 2, 4, SM A 89326, Phyllopod bed, Walcott quarry, 2, west, x1.7, 4, reflected, x2.5, see Fig. 24.


1


2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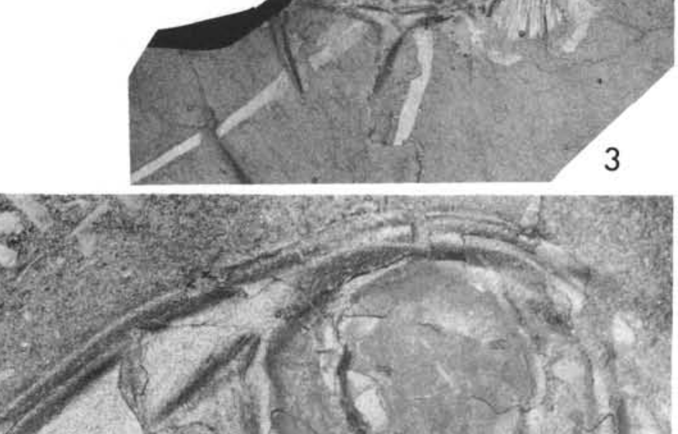
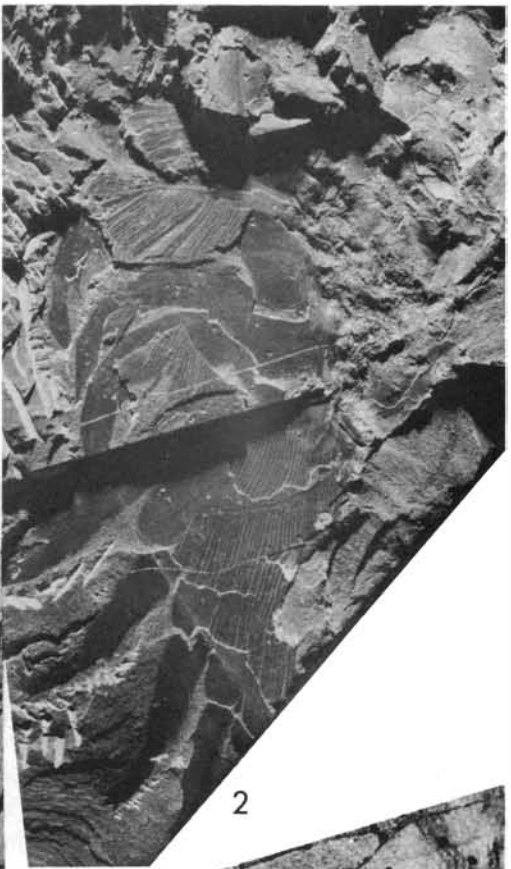

4

Plate 24.

Olenoides serratus (Rominger, 1887), GSC 34697, Walcott quarry, level 6ft. 11ins. to 7ft. 2ins.. 1, 2, north, x3.3, x1.7, showing details of appendages and entire specimen. 3, 4, reflected, x5.0, x3.3.

1



2

3

4

This arrangement is that the leg branch is flexed to curve backward, and lies ventral to (i.e. nearer the observer) the anterior part of the inner and outer lobes of the gill branch (Pl. 14: 1,3). The preciseness of this arrangement, well displayed in appendages 2,3,5–9,11–13, reflects the attachment of the two branches. This attachment must be proximal, presumably of the gill branch to the coxa, and distally segments 4–7 of the leg branch lie ventral to (i.e. nearer the observer) the outer part of the inner lobe and outer lobe of the gill branch. Ventral spines and dorsal setae are not preserved on the leg branches, but the direction of flexure implies that the anterior face is toward the observer (i.e. ventrally directed). This implies in turn that the leg branches have been rotated through about 90° to lie close to the ventral surface of the gill branches. Presumably this rotation was approximately along the line of attachment between the two branches, i.e. along the upper, posterior edge of the coxa, and the coxa was also rotated. Only in appendage L10 (Pl. 14:3) is a portion of the coxa preserved. In Fig. 17 a restoration of the coxa and leg branch L8 is outlined, based on the similar sized appendage in 58589. This restoration implies that segment 4 of the leg branch was situated in life below the outer lobe of the gill branch (as also shown by 58588B and 58589). This relationship is also suggested by appendages L5 and 6 (Pl. 14:2) of this specimen. Accepting this relationship, then appendages L5, 6 and 8 show that lamellae of the gill branch are present proximally as far as at least the outer two-thirds of the coxa. Størmer suggested that these lamellae extended inward "practically to the axial furrows" (1939: 197) of this specimen, and concluded that the gill branch ("preepipodite") was attached not to segment 2 (the basal of the leg branch) but to the proximal portion of the coxa. This latter claim appears exaggerated, but this specimen does show the relative positions and size of the two branches, and that the gill branch lay beside at least the outer two-thirds of the coxa. The regular fan form arrangement of the appendages confirms the attachment between the two branches. Distally the difference in level and relative position between segments 3–5 of the leg and gill branch in appendages L2, 3, 5, 6, indicates that the attachment was proximal to segment 3. Evidence from specimens 65514, 65519, and 65520, combines to suggest that the attachment was between the outer two-thirds of the coxa and the basal part of the inner lobe of the gill branch.

In this specimen the curvature imposed on the body has imbricated the right pleurae, and the pygidium is also slightly displaced. The restoration of coxa and leg branch L8 shows that appendages of the left side are displaced outward relative to the exoskeleton. Behind the pygidium there is a large change of level beside leg branch L14 (Fig. 17, Pl. 14:3). To the left of this step, and below and adjacent to the axis of the pygidium, are parts of the right appendages. There are portions of two leg branches (Ra and b) and of at least four gill branches. It will be seen that the lamellae of these right gill branches are directed approximately parallel to those of the corresponding left appendages, and not inward and backward as a symmetrical arrangement would require. I explain this as meaning that these gill branches have been folded under through 180° so that they lie beneath the axis, dorsal surface toward the observer, the long axis directed inward and backward, the lamellae at right angles, outward and backward. Whether or not the leg branch fragments have been similarly folded over is uncertain, but the dorsal setae of segments 4 and 5 appear to be visible on Ra, suggesting a symmetrical arrangement of these two branches. A folding over of more anterior right appendages, beneath the axis and the appendages of the left side, would explain the absence of appendages preserved beneath the right pleurae of the thorax and anterior part of the pygidium.

Størmer cited this specimen as showing a "frontal marginal rim" (1939: 198) of the gill branch. As explained above, I interpret appendages L3, 5 and 6, as showing the distal part of the leg branch lying beneath (i.e. ventral to) the anterior margin of the gill branch and so concealing it. The anterior margin is thus not displayed, and whether or not a marginal rim exists on the inner lobe cannot be seen. The distal lobe of L3 and 4 is exposed and shows no sign of such a rim. The gill branches show not only the length (exs.) of the lamellae – extending back above the leg branch of the succeeding appendage – but also their arrangement (Fig. 4, Pl. 14:1,3). Each lamella is rounded at the tip, and on the left side successive lamellae are seen to be imbricated so that the outer edge is dorsal to the lamella external to it. Plate 14:3 shows the ventral side of gill branches L 8–13, and the broken edges of the lamellae form a series of scarps facing the sagittal line. In the distal part of gill branch L 1 (Fig. 4A), this imbrication appears to be reversed. Further, the gill branches of the right side (Pl. 14: 3), which it is argued above may be folded under to show the dorsal side, have the "scarp" faces of individual lamellae facing away from the sagittal line, i.e. are imbricated so that the outer edge of each lamella is below the one next to it. One interpretation is that flat lamellae could be rotated to be imbricated either way. A second interpretation is that the lamellae were originally oval in cross section, and by compaction have been flattened and imbricated in either sense.

USNM 188572

Plate 15: 1–3, Figure 18.

☐ 1949 Størmer, *in* Grassé: 176, Fig. 11D. ☐ 1951 Størmer: 128, Fig. 7. ☐ 1959 Harrington, *in* Moore: O56, Fig. 41.

Størmer (1951) gave a drawing of the cephalon of this specimen, claiming that it showed the postoral plate or metastome. His 1949 illustration was only of the part he considered to represent the "labium" or metastome. The specimen shows the cephalon, parts of the seven thoracic segments, and the left anterior portion of the pygidium, preserved as a mould of the internal surface of the exoskeleton. Fig. 18 indicates the features displayed by the cephalon, and that some fragments of the exoskeleton adhere to it and reveal the granulate external surface. The glabella is crushed, parts of both branches of the dorsal suture, eye ridges, and impressions of connective sutures are preserved. The latter suggest that the hypostome was approximately in place, and portions of the middle body and posterior border are visible, including granulation and terrace lines on these regions. On the left side, outside the cephalic border, part of an antenna and distal portions of four leg branches are poorly preserved. On the left cheek, outside and behind the eye lobe, outwardly directed lamellae of a gill branch are visible. These traces of appendages are more strongly reflective than adjacent areas of the exoskeleton (Pl. 15: 1,2). On the glabella are areas which reflect with different intensities, those which reflect more strongly are shown in Fig. 18 by vertical ruling. In low angle radiation (Pl. 15: 3) some of these latter areas appear darker, their boundaries vaguely defined and irregular, except for the curving strip lying near the mid-length of right glabellar lobe 2p. These reflective areas are on the internal mould of the glabella, and might, as Størmer (1951) claimed, be fragments of appendages. Their size, irregular outline and positions make any interpretation dubious. The quadrangular area which Størmer outlined (1951, Fig. 7) as the metastome is just recognisable in low angle radiation (Pl. 15: 3), and less clearly so in reflected radiation (Pl. 15: 2). The triangular central area which Størmer showed is barely discernible, and the outline of the supposed plate itself by no means clear. I conclude that this specimen, as the only evidence of the metastome in *O. serratus,* is not convincing.

USNM 188573

Plate 16: 1–4, Figure 19.

Twelve appendages of the right side, the cerci, and three appendages of the left side are incompletely preserved as counterparts approximately parallel to the bedding. On the broken edge of the block may be seen fragments of the exoskeleton, the external surface facing in a direction which is towards the top in Figure 19. These fragments lie across the bedding, in surfaces which are beyond and below the edge shown in the figure. The animal was thus buried lying obliquely on its side. During the process of burial the coxae and leg branches of the right side were imbricated so that each passes marginally below the one following, swung round to lie in exsagittal planes, the leg branches curved to face convexly forward, the posterior side facing outward. The right cercus lies over the left cercus, but passes marginally below the coxa of right appendage 12. Left appendages 10 to 12 are curved to face in the opposite direction, and imbricated in the same sense. Since both cerci are visible, and three left as well as twelve right biramous appendages, burial of the animal was not exactly on its side, but obliquely as described above.

Coxae 6–9, 11, 12 have been partially excavated and show the relative size and spinose ventral and inner margins (Pl. 16: 3). A large spine is present on the inner, ventral corner of coxae 6–9, other spines varying in size and also partially overlapping proximally. This overlap indicates that they were not arranged in a single line on a sharp edge, but over the surface of a convex margin. A prominent group of long spines was present on the mid-ventral side of segment 2 of the leg branch, and groups of spines, diminishing in size distally, at the distal ends of segments 3 – 6. Up to three short, broad-based spines, overlapping at their bases and evidently movable, terminate the leg branch. Fragments of gill branches lie upon leg branches 3 and 5, and beside L 12, the latter showing lamellae. The cerci are broad-based, taper rapidly, then gradually, segments are short proximally, with spines at the joints, distally apparently much longer. Running below and between the cerci proximally is a narrow strip, appearing dark in low angle illumination but highly reflective. The position of the strip suggests that it may represent contents of the gut squeezed out posteriorly.

USNM 188574

Pl. 9:3.

The specimen shows an almost complete, isolated gill branch, the posterior margin of the inner lobe bearing about 50 lamellae. These lamellae are imbricated so that each passes beneath that next inside it, shortest distally and with tips bluntly rounded. The lamellae become progressively longer inwards, the appearance that they shorten in the innermost portion may be because they are incomplete or hidden by matrix. The maximum length of the lamellae is about two-thirds the axial width of the inner lobe. A distinct line separates inner and outer lobe, the latter broken around the margins and thus not showing marginal setae. Adjacent to the anterior margins of the two lobes, crumpled and lying at a slightly lower level, is an irregular dark strip that shows no clear subdivisions. I regard this strip as a poorly preserved portion of the leg branch, broken at each end. Since it lies at a lower level than the lobes of the gill branch, the change in level being least proximally and at a maximum distally, one may assume that the photograph shows the dorsal side of the gill branch, in the usual relation to the leg branch. In form the gill branch is typical of *O. serratus* and is so assigned. Another fragment, the distal parts of the two branches of an appendage, typical in form though crumpled, was figured by Walcott (1931, Pl. 13:1) and assigned to *O. serratus* by Størmer (1939:199). A third, less complete specimen was obtained by the GSC party from level 8 ft 7 ins to 8 ft 10 ins in the Walcott quarry. Thus broken portions of appendages of *O. serratus* do occur rarely in the Burgess Shale.

GSC 34692

Plate 17: 1–3, Plate 18: 1, 2, Figure 20.

This unique specimen, on a bedding plane with *Marrella splendens,* shows an isolated pygidium split so that some of the external surface is revealed (Pl. 17: 1,2). Behind it are a group of appendages, not associated with the exoskeleton, and showing the coxae exceptionally well. The specimen may be part of a disrupted animal, or part of a fresh moult in which the sclerotized cuticle of the appendages, presumably held together by the ventral cuticle, has separated from the mineralized exoskeleton. Numbering of these appendages presents a special problem since they are not in a single series. A unique convention of lettering has therefore been adopted in Figure 20, which is a ventral view, i.e. as seen in the counterpart, Plate 17: 1,3. The outline, particularly of the broad base, and the setae along the margins, suggest that it is the cerci that curve back to the right of the pygidium. Imbricated successively above the cerci are four pairs of appendages (Rv to Ry and Lx?) showing in ventral view the anterior face of the coxa and leg branch. The gill branches are not visible, since they were on the posterior side of the appendage and so are concealed in the rock. The coxa of appendage Rx has been excavated to reveal the spinose ventral and inner margins (Pl. 18: 2, inverted relative to Fig. 20). Three larger spines are directed ventrally in the mid-ventral region, another large spine is directed inward and ventrally from the inner part of the ventral margin, and two large spines are directed inward from the proximal margin. Between these large spines are many smaller spines, which overlap at their bases, suggesting that they were originally directed slightly forward or backward as well as outward. Small spines continue to the most dorsal part of the proximal margin.

A further group of imbricated appendages lies adjacent to those described. In ventral view (Fig. 20) the leg branches are preserved with the posterior face toward the observer. That nearest on the right side is labelled Rj, a fragment of the leg, visible on the part (Pl. 17:2). Those successively below it are labelled Rk to Ro, Rra being a fragment whose position in the series is uncertain. Rm and Rl both underlie Rk (Pl. 17: 1,3), and may be parts of one appendage but I consider this unlikely. Gill branches labelled Rmg, Rng, and Rog, are preserved extended in the same plane as the leg branch. The spinose ventral and inner margins of coxa Rk (Pl. 17: 3, Pl. 18:1) are well shown despite a fold running parallel to, and inside, the ventral margin. The long ventral spines of segments 2 and 3 of leg branch Rk are also clearly shown. On the left side four appendages are preserved and labelled Li to l on the assumption that Lk and Rk, being on the same level (Pl. 17:3), belonged to the same somite. Large and small spines on the ventral and inner margins of coxae Lj and Lk are evident, and with those of coxa Rk give an impression of the opposition of the gnathobases in life (Pl. 18:1). Fragments of gill branches, similarly extended to those of the right side, are also preserved.

This specimen thus show parts of at least eleven pairs of biramous appendages and the cerci. Too little of Ry is preserved to indicate whether or not it is the last appendage, but differences in level imply that it cannot be more than 1 or 2 from the last. It is uncertain whether Li represents the pair that originally lay next to the Rv pair, and the coxae and leg branches of the two groups of appendages have not only been rotated but their serial alignment modified. If Ry was the penultimate biramous appendage, and none is missing between Rv and Li, then appendages j and k are 7th and 8th in front of the cerci, i.e. they belonged to the middle part of the thorax. The large size and spinosity of the coxae in the posterior half of the animal's appendages is notable, and accords with the evidence from other specimens.

GSC 34693

Plate 19: 1–3, Figure 21.

The entire exoskeleton is extended in the bedding plane, and shows the antennae, fourteen biramous appendages on the left side, the cerci, the presumed first, and the last two, leg branches of the right side. A fragment of the lamellae of a gill branch is revealed beneath the right fixed cheek, and the right margin of the block cuts off the tips of some of the pleural spines and the first pygidial border spine. It is presumed, from the attitude of the labelled right branches, and the fragments revealed where axial rings are broken away, that the biramous appendages of the right side were folded beneath the axial and inner right pleural region. No attempt has been made to excavate them.

On the left side the antenna is preserved (Pl. 19:1) beneath the cephalic exoskeleton to a point almost in line (tr.) with the anterior margin of the eye lobe. The antenna broadens proximally, where it lies at a level above that of the proximal part of the succeeding appendage. The biramous appendages are disposed in a fan-wise arrangement, each gill branch lying dorsal to the leg branch and overlapping its successor. The posterior side of the leg branch faces dorsally and each branch passes below its successor, XIV going beneath the left cercus (Pl. 19:2), though gill branch XIV overlaps the left cercus. The cercus in thus preserved in an attitude corresponding to that of the leg branches. The latter are flexed distally, most strongly anteriorly, where in I and II segments 4 and 5, and 5 and 6, are flexed almost at right angles to each other, without disruption being apparent (Pl. 19: 1). In III the flexure is so sharp that the distal two or three segments are apparently hidden beneath the proximal segments and gill branch. In IV to VIII the flexure is less than 90° between each of segments 2 – 7, so that the branch curves through between approximately 100 – 180°. Excavation has shown (Pl. 19:2) how leg branches IX to XI curve beneath each other below the gill branches. Curvature is less in XII to XIV. The preservation is such that proximally gill and leg branch were pressed closely one above the other, and it has not proved possible to remove the gill branch to reveal the coxa completely. The portion of the coxa visible in VI indicates displacement of the appendages behind the cephalon to the left of the sagittal line, as does the position of the cerci. The antenna, and possibly left appendages I to III, appear not far removed from their original positions. If one assumes they originally belonged to the cephalon (III being the occipital appendage), then presumably IV to X each belonged to a thoracic segment. Backward displacement during burial is evident, since coxal IV is opposite the second axial ring of the thorax, and coxa X opposite pygidial axial rings 2 and 3. The above assumptions mean that XI to XIV belonged to pygidial segments 1 to 4, and the cerci perhaps to pygidial segment 5. These assumptions are based on the earlier assumption that I to XIV is a complete series of biramous appendages, and the present preparation suggests that this is reasonable.

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Plate 20: 1,2,4, Plate 21: 1,2, Figure 22.

The dorsal exoskeleton (Pl. 20: 4) is extended in the bedding plane, and appendages project from beneath it on the right side and posteriorly. The hypostome is displaced back and to the right, the posterior border lying beneath the right half of the occipital furrow. The rock slab terminates in a joint which runs diagonally across the cephalon on the right side just outside the eye lobe, so that anterolaterally appendages and exoskeleton are not seen. No appendages project from beneath the left side, apparently because they have been folded under the axis and right side. This is deduced from the position of the five posterior walking legs on the left side, which are imbricated and project posteriorly below the cerci and appendage R 13. The left cercus is not so folded, and extends backward and outward on the left side. On the right side parts of 13 biramous appendages are preserved, principally the leg branches, in dorsal view posterior face towards observer, imbricated so that each goes below the one following. Coxae 1,3,6,7, have been excavated (Pl. 20: 1,2) to show the spinose ventral and inner margins, large spines being present in the mid-ventral and inner ventral regions. Coxae 12 and 13 have also been excavated, and while smaller show the spinose ventral margin. The leg branches, and ventral spines of segments 2 – 6, are revealed in 6 and 8, and appear to be similarly developed on the other leg branches, including 13 (Pl. 21: 1,2). Gill branches 11 – 13 are imbricated dorsal to the leg branches, each going above the one following, and 12 g shows the outer lobe. Gill branches 11 to 13 extend inward close the margin of the pygidium (Pl. 21: 1,2) and thus must extend inward for much of the length of the coxa. Gill branch 6 g is also visible (Pl. 20:1), crushed in the exsagittal direction and lying in front of the leg branch, and the counterpart shows parts of gill branches 5 and 8, lying dorsal to the leg branches. The cerci are broad proximally and taper rapidly initially, more gradually distally. Stout spines project from the joints on one side (Pl. 21:2), which appears to be the ventral side, distally the spines are slimmer and seemingly less frequently developed.

GSC 34695

Plate 20:3, Plate 22: 1–4, Plate 23: 1,3, Figure 23.

Eight biramous appendages of the right side, the cerci, and left leg branch 8 are preserved beneath and outside the last three thoracic segments and the pygidium. Fragments of three more anterior gill branches are preserved on the counterpart (Pl. 22: 2,3) but not numbered, and leg branches R 7, 8 and L8 are best seen on the part (Pl. 23: 3). Figure 23 is a ventral view and the gill branches are immediately beneath the exoskeleton, overlapping so that each lies dorsal to the one following (Pl. 22: 3). The outer lobes of gill branches 1 to 5 are partly visible, and show the marginal setae (Pl. 22: 1,4). These setae overlie dorsally the adjacent lamellae of the inner lobe (Pl. 23: 1). Each lamella is long and narrow (tr.), and their length is such that they extend above the second leg branch following (Pl. 23: 1). The slat-like lamellae are compacted upon each other, the inner edge lying dorsal to its neighbour so that across their width they slope downward and outward. The tip of each lamella is rounded and bears four or five fine hairs (Pl. 22:4). Leg branches R 1–8 are preserved with the posterior side facing ventrally, and are extended in an "S" curve, concave posteriorly over much of the length, becoming convex distally. The concave curvature increases progressively backward, so that leg branch 8 is curved backward through more than 90° (Pl. 23:3). The proximal portions of appendages 7 and 8 have been excavated in the part, and the spinose margin of the coxa is visible in 7. The distal portions of the leg branches are well preserved, and show the groups of spines on the ventral side at the joints, and the setae along the dorsal margins of segments 4 and 5 (Pl. 22: 1,4). The distal portion of a leg branch that has been excavated outside the right cercus (Pl. 23:3) is considered to have the posterior face directed dorsally, and to belong to the left side, having been bent under the right appendages. The cerci shows marginal spines on both sides, and widen rapidly proximally but cannot be traced inside the pygidial border.

This specimen is notable for the exceptional preservation of the appendages, and, judging from the positions of coxae 7 and 8, shows that the gill branches extend far in towards the inner edge of the coxa. This is also well shown by appendage R 1 (Pl. 23: 1, Fig. 23), for the outer lobe of the gill branch is beside segment 4 of the leg branch, and the lamella extend far inward. The proximal part of the appendage is crumpled and poorly preserved, but inner lobe of gill branch is seen to merge into the coxa.

GSC 34697

Plate 24: 1–4.

In this specimen crumpled fragments of the exoskeleton, with the external surface facing the observer, lie partly above and partly beside biramous appendages (Pl. 24: 2). Anteriorly, portions of six appendages of the left side have the leg branches curved convexly forward, rotated so that the posterior side faces the observer, each branch imbricated to pass below that following. The gill branches lie dorsal to the leg branches, and are imbricated so that each lies above the one following (Pl. 24: 1). Behind these appendages, and on a slightly lower level, are four biramous appendages of the right side, folded through 180° at the axial region and extended below those of the left side. The distal parts of the leg branches are curved convexly backward, and have been rotated so that the posterior side faces the observer. The gill branches are extended and pass below the one following, i.e. are ventral face toward the observer, an opposite arrangement to the gill branches of the left side (Pl. 24: 1). The preservation of the appendages is exceptionally fine, and the marginal setae of the outer lobe of the gill branch, and hairs at the tips of the lamellae (Pl. 24: 3) are clearly displayed. The distal four segments of the right leg branches (Pl. 24: 1,4) show the dorsal setae on segments 4 and 5, the ventral spines at the joints, and the three blunt, broad-based, triangular spines at the termination. The lamellae of the main lobe of the gill branches on the left side are imbricated so that the outer edge is over the adjacent lamella, i.e. across its width the lamella slopes inward and downward. On the appendages of the right side this slope is reversed, the outer edge lying *under* the adjacent lamella. In these right gill branches the outermost lamellae lie beneath (above in ventral view, Pl. 24: 1) the edge of the outer lobe with the marginal setae.

SM A 89326

Plate 23: 2,4, Figure 24.

Isolated hypostomes from the Burgess Shale, originally referred to this species by Walcott, are now thought more likely to belong to *Kootenia burgessensis* (see below). Part of the outline and in some cases the approximate position of the hypostome is shown in a number of specimens preserved from the dorsal side (57656, 58588A, B, 58589, 65510, 65520). Only the present specimen, discovered among a collection sent from the U.S. National Museum to University College, London, shows the hypostome from the ventral side, incompletely preserved, crushed down approximately in position. The convex middle body, outlined by broad, shallow furrows, is widest at a point about one-quarter the length (sag.), the straight sides converging back to the rounded posterior portion. The highest point appears to be about central. Crushing has obscured any middle furrow and subdivision of the body. The anterior wing and lateral border are not preserved, but posteriorly a section of the gently convex border runs transversely behind the middle body, and turns posterolaterally to run forward and outward at 45° to the sagittal line, for a length similar to that of the transverse section. Judging by the lateral border furrow, the lateral border appears to be directed backward and very slightly inward. The anterior limit of the hypostome is difficult to see, but medially it may lie on the posterior slope of the anterior border furrow, at the line presumed to represent the hypostomal suture (Fig. 24). The exoskeleton is preserved in this specimen, as in others, as a thin black layer, reflective on the smooth inner surface. Such a layer lines the cheek and glabella of this specimen, a sharp edge denoting where it is broken. The layer also clings to the hypostome, and anteriorly shows the raised, anastomosing ridges of the external surface. On the left side (right in Pl. 23: 2,4) the broken edge runs along the slope of the lateral border, matrix intervening between it and the smooth, inner side of the dorsal exoskeleton. Along the posterior and posterolateral borders of the hypostome two exoskeletal layers (outer and doublure) may be observed compacted together. Beneath the lateral border of the cheek part of the doublure exoskeleton appears to be present (Fig. 24), and fragments of an exoskeletal layer, partly obscured by matrix, cling to the anterior border. It is possible that portions of the rostral plate are represented, especially anteriorly to the hypostome adjacent to the supposed hypostomal suture. A line impressed on the inner surface of the dorsal exoskeleton is interpreted (compare Figs. 12A, 18) as the connective suture, by analogy with the hypostome of *Kootenia burgessensis* (Pl. 3: 2,3,4, Fig. 7). Thus, following Rasetti (1952: 889), the hypostomes and rostral plates of *Kootenia* and *Olenoides* are considered to have been similar, and possibly fused, though in *K. burgessensis* the hypostomal suture is clearly preserved. The imperfectly preserved rostral plate and hypostome of *O. serratus* differ from those of *K. burgessensis* in the more gently rounded anterior margin (line of the rostral suture), the shorter, median transverse section of the posterior border and longer, obliquely directed posterolateral portion. The external surface of the middle body in *O. serratus* bears fine tubercles connected by low, anastomosing ridges arranged concentrically (Figs. 18, 24), whereas that of *K. burgessensis* may be smooth. Dr. W.H. Fritz kindly investigated material of *O. serratus* in the GSC and American Museum of Natural History collections, which suggests that there may have been a small anterior wing behind the sharply pointed distal part of the rostral plate, i.e. a structure similar to that in *K. burgessensis* (Fig. 7).

Only one other hypostome of a species of *Olenoides* has been described (Fritz, 1968, Pl. 43 : 23), and it appears to be similar to that of *O. serratus*, and shows a small anterior wing. The rostral plate may be missing from Fritz's specimen.

MORPHOLOGY AND MODE OF LIFE OF *OLENOIDES SERRATUS*

Form and convexity of exoskeleton

The Burgess Shale material is all flattened, but parts of unflattened exoskeletons of other Middle Cambrian species have been described by Rasetti (1948b: 336–339, Pl. 51, Pl. 52 : 9–15), Robison (1964, 537–539, Pl. 83 : 12, Pl. 84 : 1–9, 11, 14, 17), and Fritz (1968: 199–201, Pl. 39 : 1–8, Pl. 43 : 20–23). I have also examined material of *Olenoides curticei* Walcott, preserved uncrushed in nodules from the Conasauga Formation, Middle Cambrian, Alabama, in the U.S. National Museum. On this evidence I have assumed the form and convexity shown in the restorations (Figs. 25, 26). Particularly critical is the convexity of the cephalon (including the hypostome). The anterior and lateral views by Fritz (1968, Pl. 39 : 2,3, Pl. 43 : 21, 22) do not suggest that the anterior border is arched transversely more than gently, if at all, and the Alabama material is similar in this respect. These assumptions determine the angle at which the hypostome is placed (Fig. 27), and thus the way in which the anatomy of the cephalon is restored. Convexity and form of thoracic segments and pygidium, and directions of pleural and border spines, are based on the Alabama material and Fritz, 1968, Pl. 39 : 4,5. The convexity of the thorax is considerably greater than assumed by Walcott (1918, Pl. 34 : 3, 1921, Fig. 13), Raymond (1920, Fig. 7) and Størmer (1939, Fig. 20), because of the greater convexity given to the axial ring, and because the inner part of the pleura must have been horizontal to act as a hinge between segments.

Hypostome

An isolated specimen (65533) referred to this species by Walcott (1918) seems to belong to *Kootenia burgessensis* (Pl. 3: 2,3). The only available specimen from the Burgess Shale (Pl. 23: 2,4) showing the hypostome incompletely has been described above, and reasons given for assuming the presence of a rostral plate. On this basis these parts are shown in the restorations, the angle at which they are placed being determined by assumptions on convexity of the dorsal exoskeleton. In crushed specimens (Pl. 9: 1) the posterior margin of the hypostome lies approximately in a transverse line with the 2p glabellar furrows, and the restoration places it in an appropriate position.

Metastome

This supposed ventral plate, not shown by Walcott (1918, Pl. 31, 1921, Pl. 94), was portrayed by Raymond (1920: 30, Fig. 8) ”without any evidence for its former presence”. Walcott (1921: 393) thought that this ”may be misleading”. Størmer (1951: 128, Fig. 7) described USNM 188572 (Pl. 15: 1–3) in which he believed the metastome or postoral plate was visible. I do not find this specimen convincing as evidence of such a plate, and so omit it in my restorations.

Antenna

The antenna is broadest proximally (Pl. 7: 2, Pl. 19: 1), distally the width only one-fifth that proximally, the maximum length preserved (Fig. 3) being three-quarters that of the exoskeleton (sag.). Segments are short and broad proximally, progressively lengthening so that the length is at least four times the width. Minute setae are preserved rarely along the side of the flattened antenna. Only in one specimen (Pl. 19:1) is the proximal part preserved inside the cephalic margin, as far back as a point in front of the line of lateral glabellar furrow 2p. There seems no reason to doubt that the antenna was inserted in the ventral membrane approximately in the vertical plane passing through the axial furrow, at a point lying a short distance behind the anterior wing of the hypostome. As has been argued elsewhere (Whittington & Evitt, 1954: 20), muscles at the base of the antenna may have been attached to the anterior boss (ventral surface of the anterior pit).

Coxa

There has been much discussion of this basal segment of the appendages, Walcott (1918: 127, 129, 1921: 381–2) describing the spines and refuting Raymond's (1920: 24–25) contention that the spines were on the dorsal margin and that the coxa articulated distally with the invagination of the dorsal exoskeleton along the axial furrow. Størmer (1939: 194–196) did not consider the spines to be any stronger than those of the leg branch, and suggested that a precoxal segment was possibly present. Preparation and reinterpretation of earlier specimens (Pl. 2:2,3, Pl. 6: 2, Pl. 11: 2), together with study of additional specimens (Pl. 16: 3, Pl. 18: 1,2, Pl. 20: 1,2), has given much additional information. When flattened the axial length of coxa of II to XII is two or three times the depth, the length being equivalent to approximately half the width (tr.) of the axial ring with which it is associated. The length is more than twice that of any segment of the leg branch. The spines of the ventral and inner side are relatively much larger than was thought (Pl. 11: 2, Pl. 18: 1,2). Three long, slim spines were directed downward from the outer, ventral margin, two large, curved scimitar-like spines situated near the inner, ventral angle, and a large spine midway along the proximal edge. Between these large spines are many smaller spines, their bases overlapping in the flattened specimens, indicating that they were closely spaced along the convex margin. The size and arrangement of the spines was, as to be expected, variable, but the larger ones are situated as indicated, particularly at or near the inner, ventral angle. All the coxae were spinose from the first (Pl. 7: 1,3,4) to the last (Pl. 16: 3, Pl. 20: 1). That of the first appendage is incompletely known, but may be relatively shorter than the next known, that of the third appendage (Pl. 7). The original of Plate 16 suggests that the coxae of the last four appendages are progressively reduced in relative size, but retain the spinosity.

As the photographs show, the proximal parts of the appendages had the ridges and grooves of the dorsal exoskeleton impressed upon them during compaction. As explained above in describing 58589 (Pl. 6: 2), it is this effect that led Størmer (1939: 194, Fig. 16) to interpret a triangular, convexly upfolded part of the coxa as a precoxa. I do not consider there is any evidence from other specimens to support this view.

As a result of preservation the coxae are imbricated, and while it has proved possible to excavate ventral and inner margins, the dorsal margin is poorly preserved or concealed. Thus the shape of this margin is uncertain, and the coxa is not seen in its natural position relative to the rest of the body.

Walking leg

The leg branch is articulated to the outer end of the coxa and consists of six podomeres (numbered 2–7 in the Figures), the last bearing three terminal spines (Pl. 24: 1,4). Segments 2 to 5 are approximately equal in length, the distal two progressively shorter and slimmer. Preparation has shown (Pl. 2: 2,3, Pl. 6:2, Pl. 10:1, Pl. 20:1,2) that the major ventral spines, median on segment 2, distal on segments 3–5, are much longer and stouter than previously thought, and that on segments 2–4 they are flanked by a group of shorter, slimmer spines. Spines are absent on the dorsal side, but on segments 4 and 5 this surface bears many fine setae (Pl. 22: 1, Pl. 24: 4). In specimens in which the curvature of the leg branch is convex dorsad (Pl. 2: 1,2, Pl. 20: 1,2) the outline of podomeres 2 and 3, in relation to each other and the coxa, shows the dorsal margins aligned across the joints, and the ventral margins meeting at approximately the same level. The nature of the joint between coxa and 2, and between 2 and 3, is uncertain. It may be a pivot joint (Manton, 1958: 496, Fig. 4a, *in* Moore, 1969, Figs. 1,2), but the podomeres are preserved flexed down (ventrally) relative to each other, not flexed upward. The joints between podomeres 3–4, 4–5, 5–6, and 6–7 may, on the other hand, be hinge joints (Manton, 1958: 496, Fig. 4a, *in* Moore, 1969, Figs. 1,2). The dorsal margins across these joints are aligned, whereas on the ventral side there is a marked 'step', where the slimmer proximal part of the podomere fits inside the base of the ventral spine of the preceding podomere (Pl. 5: 1,2, Pl. 21: 2, Pl. 22: 1, Pl. 24: 4). In the reconstructions the presence of these hinge and pivot joints is assumed, and their positions are indicated in Figure 29, right side.

The originals of Plate 4 and Plate 7 suggest that there is a progressive increase in length of the coxa and leg branch of appendages I–III, and 65520 (Pl. 13) supports this view. The relative increase in length may be predominantly in the coxa and segments 2 and 3 of the leg branch,

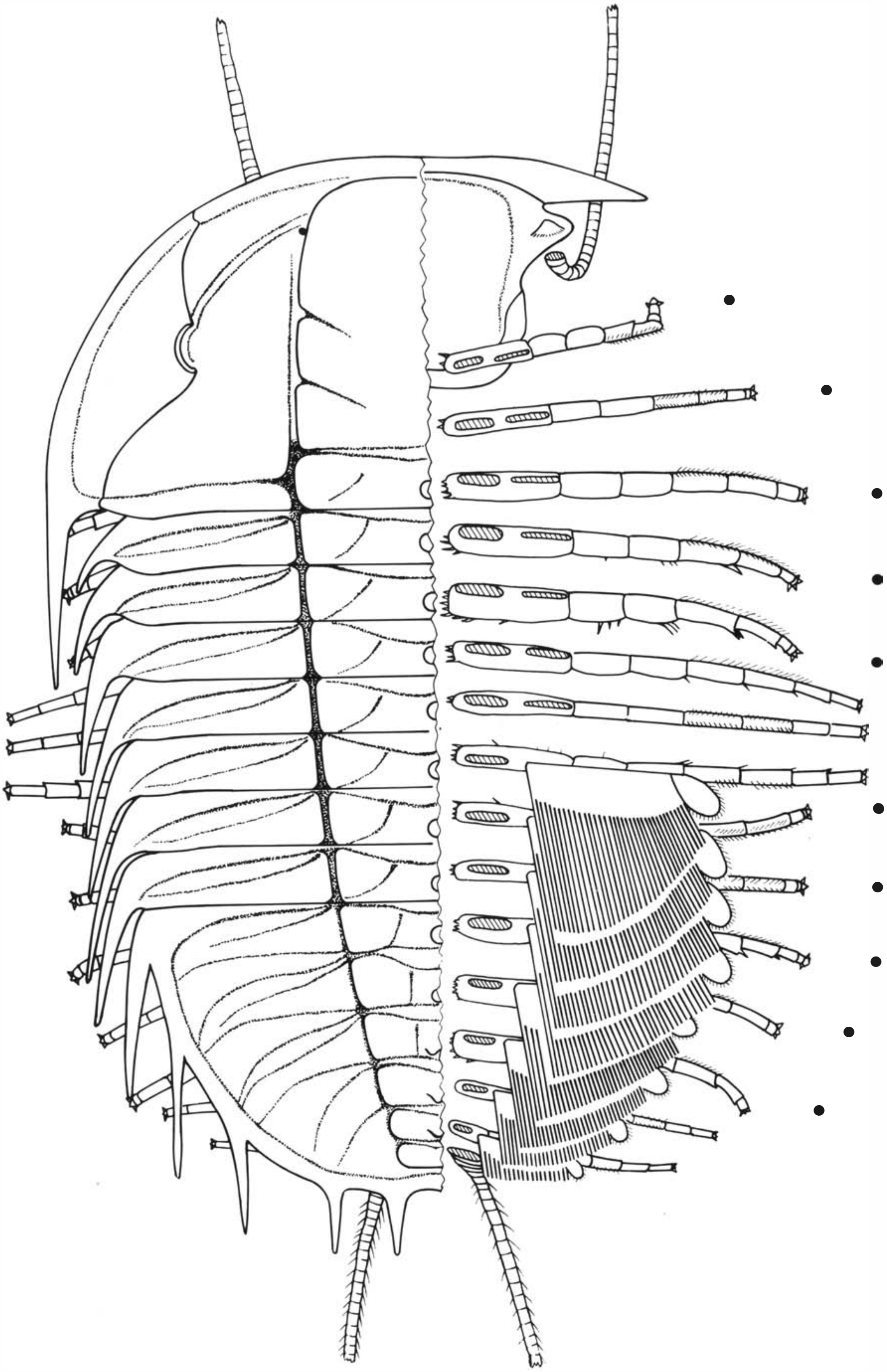


Fig. 25. Olenoides serratus, reconstruction of animal in dorsal view, right half of dorsal exoskeleton and ventral cuticle removed to show appendages and inner view of exoskeleton of rostral plate and hypostome. Antennae and cerci incomplete, gill branches of appendages I to VII removed and area of attachment to leg branch is diagonally shaded. Biramous appendages shown in 'still' position in the course of a particular gait (see text), solid circles in transverse line with tips of leg branches which are stepping on sea floor, other leg branches in recovery phase. Diagonal shading shows area of insertion in ventral cuticle of antenna, coxae and cercus.

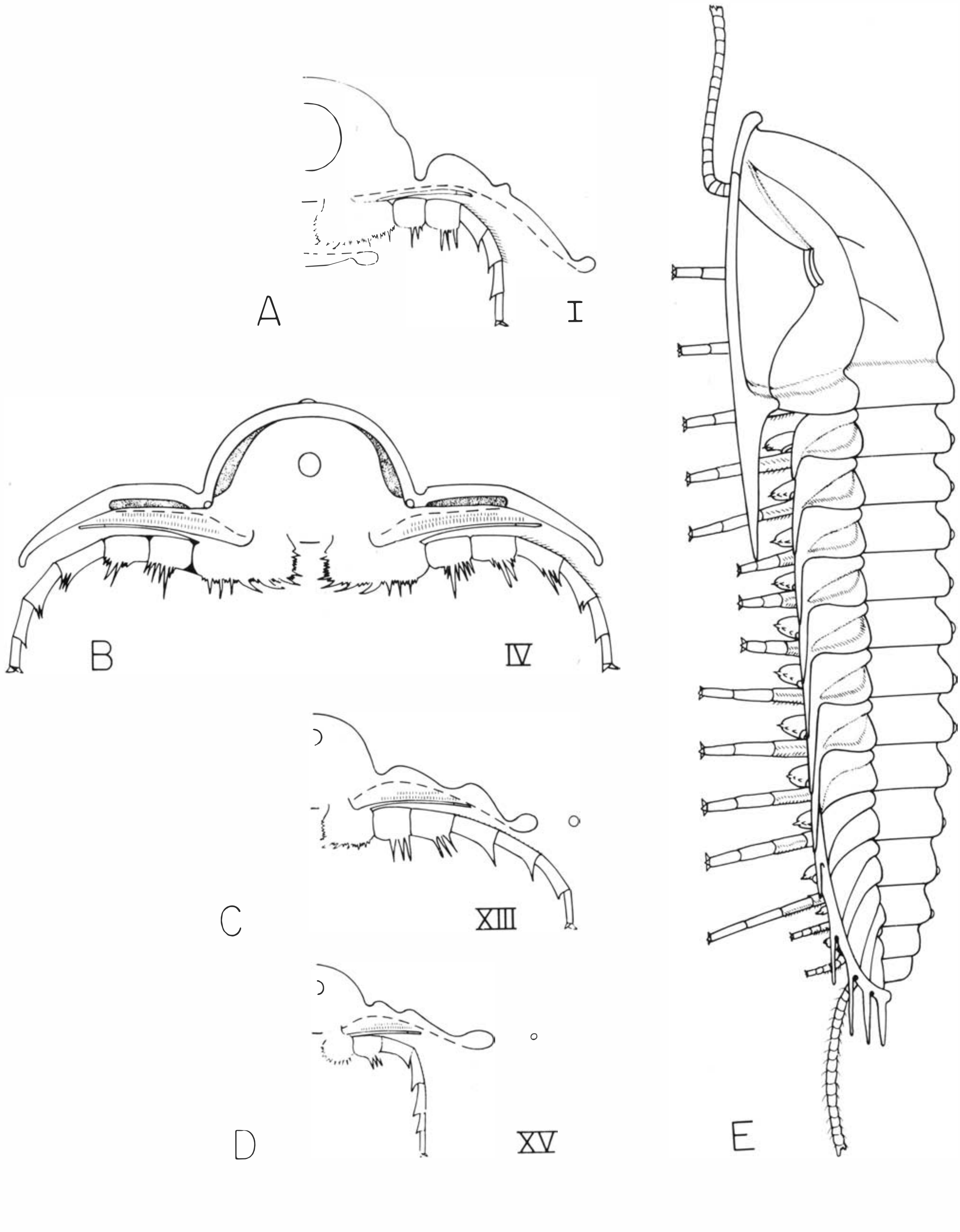


Fig. 26. Olenoides serratus. A, B, C, D, cross sections of animal at appendage I, IV, XIII and XV respectively, viewed from the posterior, compare Fig. 25. Each section shows the exoskeleton, as a cross section in A, C and D, as a posterior view of the first thoracic segment in B, and the ventral cuticle as a heavy dashed line. The coxa and leg branch is seen from the posterior, in the course of a step when in the transverse plane. The gill branch is shown in section (passing through the inner and outer lobes), and filaments of the next two anterior branches are shown in section between it and the ventral cuticle. E, left lateral view of animal, in 'still' position of gait show in Fig. 25, antenna and cercus incomplete.

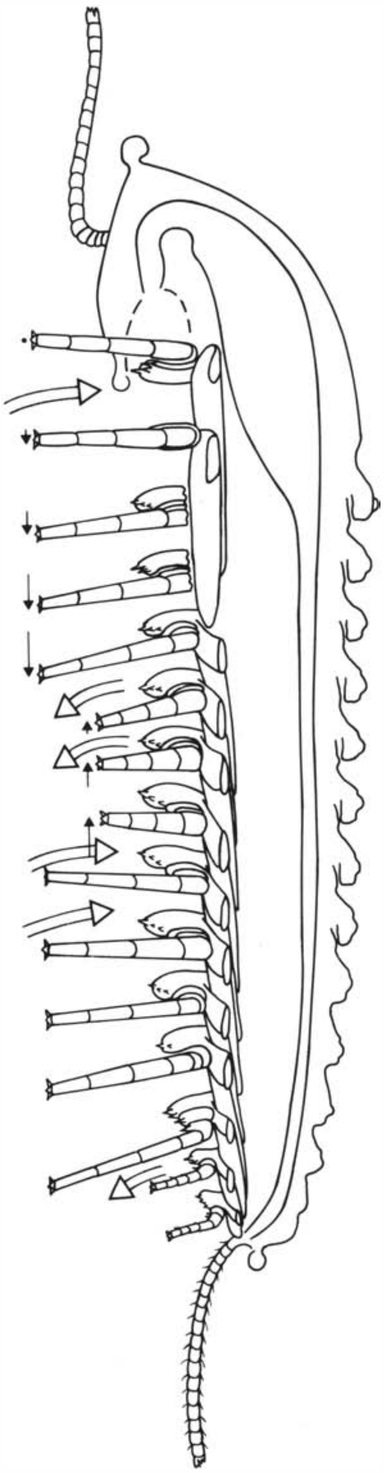


Fig. 27. Olenoides serratus. Left lateral view of left appendages in 'still' position of gait shown in Figs. 25, 26E, combined with sagittal section showing gut. Beneath tips of leg branches I to VIII (in same metachronal wave) are arrows showing direction and amount of swing (promotor and remotor) leg branch has passed through, dot under I indicates beginning of remotor stroke. Outline only of tips of filaments of gill branches shown, appendages III and IV partly cut away. Arrows with double shafts indicate directions of water currents caused by approach or separation of coxae and leg branches.

but the evidence is inadequate. Coxa and leg branch of appendages III–XI of 58588B (Pl. 4) are similar in length, as are IV to XII or XIII in the largest specimen, 58588A (Pl. 2). Coxa and leg branch of the last three or four appendages are progressively shorter (Pl. 5, Pl. 16, Pl. 21) and the original of Plate 16 shows that the reduction is particularly great in the coxa and podomeres 2 and 3 of the leg branch.

Outer (gill) branch

This branch (Pl. 9: 2,4, Pl. 10, Pl. 14, Pl. 22, Pl. 24) lies on the dorsal side of the appendage and consists of a proximal lobe, of width about one-third the axial length, and a much smaller, ovate distal lobe. A faint diagonal line separates the two lobes, and the outer and posterior margins of the distal lobe bear close-spaced, fine setae. From the posterior margin on the proximal lobe lamellae, preserved as flat, imbricated strips, extended backwards and outwards. The maximum length of these lamellae (Pl. 23: 1) was slightly less than the axial length of the proximal lobe, the longest situated close to the inner edge of the branch, the length reduced progressively outward. The distal lamellae were less than one-third the length of the longest, and extended outward and backward beneath the inner edge of the distal lobe. The lamellae may be imbricated in either sense, for example in Plate 24: 1, upper part of figure, appendages of the left side show the posterior face of the leg branches curving beneath the outer branches. The lamellae of these latter branches are imbricated so that each goes below the next inside. In the lower part of the figure are appendages of the right side, the outer branches exposed from the under (ventral) surface, and each lamella overlaps the one inside it, sloping outward and downward (ventrally). Figures 4, 17 show that on 8g and 12g the scarp slope faces inwards, i.e. each lamella slopes below (ventral to) the one inside it. Thus the arrangement, while similar over one side of a specimen, may be symmetrical or opposite on the two sides. The lamellae may have had the form of long, narrow thin slats, and during compaction been rotated to imbricate in either sense. The tip of a lamella appears rounded, and bore four or five fine hairs (Pl. 24: 3). Some 50 lamellae are present on the proximal lobe, each of the order of 0.3 mm in width.

Størmer (1939: 198) considered that there was a "frontal marginal rim" along the anterior margin of the outer branch, but his evidence was mainly drawn from the specimen of *Kootenia burgessensis* (Fig. 31, Pl. 25: 1–4) described below. In such specimens of *O. serratus* as 65521 (Pl. 14), the anterior margin of the lobe of the outer branch is concealed by the leg branch e.g. in appendages 2, 3, 5 & 6 (the specimen is exposed from the ventral side). In 65514 (Pl. 9 : 2,4, Pl. 10) the imbrication of the outer branches again conceals this margin. In appendage 1 of 34695 (Pl. 23 : 1) this margin is exposed but hard to define – proximally there is a faint, irregular line separating inner lobe of outer branch and what must be the coxa. Traced outward this line becomes a distinct step between the outer portion of the gill branch and podomeres 2, 3 & 4 of the leg branch. This specimen shows no sign of an anterior rim on the gill branch, and suggests that the gill branch was attached only proximally and to the outer part of the coxa. Plate 14 and Figure 17 also show in appendages 5–8 how far inward the gill branch extended, at least to the outer half of the coxa. These specimens also show that the inner lobe of the gill branch did not narrow so markedly proximally as Walcott (1921, Figs. 13, 14) thought. Thus I do not consider that the gill branch can have arisen from a narrow base at the coxa-podomere 2 junction as Raymond (1920, Figs. 7,8) and Walcott (1921, Figs. 13, 14) portrayed, nor does there appear to be a pre-coxal segment from which it arose (Størmer, 1939, Fig. 20). I suggest (Figs. 25, 26 A–D) that the gill branch was attached along the inner part of the anterior margin to the dorso-posterior side of the coxa. Such an attachment would tend to keep the longitudinal axis of coxa and gill branch aligned during preservation, and such an alignment is characteristic (e.g. Pls. 10, 14, 22, 24).

Gill branches were present on all the appendages from I (Pl. 7:2) to the most posterior (Pls. 10, 19, 21, 22), the last two or three having progressively shorter (exs.) filaments so that in life they did not project beyond the margin of the pygidium. The outer lobe is developed on the posterior gill branches (Fig. 22). The length of the filaments (Pl. 23: 1) was such that they extended back over the two following appendages (and probably reached the third), and thus over parts of two succeeding gill branches. In life they lay in the narrow space between the ventral cuticle of the pleural regions and the leg branches. As pointed out in discussing preservation, in most specimens the gill branches are in this position but in some cases (Fig. 2) the gill branches have been rotated (with the leg branch?) and are crushed down along the exsagittal direction and lie over and in front of the anterior margin of the leg branch (e.g. 6g in Fig. 22, Pl. 20: 1, 2). Both orientations of gill branches may be present in parts of the same specimen (e.g. Fig. 9, Pl. 5: 1, 2). The unusual orientations are further evidence for the type of junction between gill branch and coxa suggested above, and the interpretation of 65515 (Figs. 2, 14) implies that the two branches of each left appendage were held in relation to each other and bent through 180°.

In his final restoration Walcott (1921:368–9, 393, Figs. 13, 14, Pl. 94:1) retained a third branch of the appendage, the 'epipodite'. Størmer (1933:148–149, 1939:200–1) gave reasons for not accepting the reality of this third branch, and, as explained above in discussing specimen number 65515, I concur with this view. No new evidence for an additional branch has come to light.

Cercus

Length when incomplete is some seven-eighths of the length (sag.) of the exoskeleton (Pl. 16: 1, 2), so that length appears to have approximated to that of the axis. Proximally the cercus was broad, subtriangular in outline, the width at the base equal to, or greater than, the length of the adjacent coxa of the last biramous appendage (Pl. 16: 3, 4, Pl. 21: 1, 2). The proximal one-quarter of the length of the cercus tapered rapidly, the segments wider than long. Beyond this proximal portion the cercus tapered gradually, the segments becoming progressively longer. The margins bore thorn-like setae at the joints of the proximal portion, slimmer setae were present but less numerous for about half the length.

The basal portions of the cerci are preserved between the last pair of biramous appendages, and in many examples (Pl. 2: 1, Pl. 4: 2, Pl. 19: 2, Pl. 21: 1, 2) are imbricated in series with the leg branches. The outer margin of the cercus lies above the adjacent leg branch, as the anterior margin of each leg branch lies over the preceding branch. Exactly how and where the cerci were attached is uncertain, but the serial arrangement of the basal portion with the coxae of the last pair of appendages is apparent in the fragmentary specimen (Pl. 1:1) as well as others. In the reconstruction (Fig. 25) it is suggested that the cerci were attached to the telson, flanking the anal opening.

Number and arrangement of biramous appendages

Walcott (1918: 126–131, Pl. 31, 1921: 374, Pl. 94) considered that there were four pairs of biramous appendages on the cephalon, one pair on each of the seven thoracic segments, and five on the pygidium, a total of 16 pairs. Raymond (1920: 21–23, Fig. 8) showed the same numbers of pairs. Størmer (1939: 193) likewise accepted the 16 pairs of biramous appendages, in the same arrangement, but showed 17 pairs (6 on the pygidium) in his restoration (1951, Fig. 12). Only three specimens appear to me to show all the biramous appendages, and the size and numbers of pairs are:

58588A (Fig. 6), sagittal length 81 mm, 16 pairs.
58588B (Fig. 8), sagittal length 68 mm, 15 pairs.
34693 (Fig. 21), sagittal length 52 mm, 14 pairs.

These specimens suggest that, while the number of pairs on cephalon and thorax presumably remained constant, new pairs were added posteriorly as size increased. If, for example, there were three pairs on the cephalon and seven on the thorax, there were 4,5 and 6 pairs on the pygidium as size increased. In these three specimens, the axial length of coxa plus walking leg branch of the last pair is about half that of pair VI (in the anterior thoracic region where appendages are largest). This contrast in size is very different from that obtaining in *Triarthrus* (Raymond, 1920, Fig. 10) or *Cryptolithus* (Raymond, 1920, Fig. 20). In these forms axial length of coxa plus leg branch of the last paired appendage is one-tenth that of the larger pairs in the anterior region of the thorax, i.e. the progressive reduction in size backward is much greater. As many specimens of *O. serratus* show, including 57656 (Fig. 5), the last pair of appendages was relatively large and there was no diminutive series in front of the telson. This implies that if additional pairs of appendages were being added to the holaspid trilobite, growth of each additional pair was rapid, unlike the progressive growth apparent in the Ordovician species.

Størmer (1939: 193) cited 58591 (Pl. 8) as evidence of four pairs of biramous appendages on the cephalon. This poorly preserved specimen, showing distal parts of four leg branches outside the cephalic margin, does not give decisive evidence. Three additional specimens (Pls. 7, 12, 13) show the cephalic appendages more completely, but in these as in other specimens there has been considerable displacement of appendages during preservation. If one assumes that the occipital somite and the two in front (1p and 2p, which are of similar sagittal length to the occipital) each bore a pair of biramous appendages, then it does not appear possible, after making assumptions as to convexity of cephalon, position of hypostome, foregut and stomach, to reconstruct the cephalon (Figs. 25, 27) with more than three pairs of biramous cephalic appendages. This conclusion is at variance with that of Walcott, Raymond and Størmer, who all assumed four cephalic pairs. The fourth pair could only be inserted (as by these authors) by having the three anterior pairs beneath two segments indicated on the exoskeleton by the 1p and 2p glabellar furrows. It will be observed (Figs. 26A, 27) that in the present reconstruction the cephalic convexity must be approximately as here assumed to allow space for the coxae of the anterior appendages between the hypostome and the rest of the cephalon.

It is reasonable to assume also that each thoracic segment bore one pair of biramous appendages, though no specimen shows such an arrangement because of displacement. As noted above, if there are 10 pairs on cephalon and thorax, the pygidium bore apparently 4, 5 or 6 pairs as size increased.

Coxa-body junction

The ventral cuticle is not preserved in any specimen, except perhaps as the dark area adaxial to coxae Rk, Rm and Rn in 34692 (Fig. 20, Pl. 17: 1, 2, Pl. 18: 1). That the ventral cuticle is not (or very rarely) preserved, and appendages are always displaced, suggests that the ventral cuticle was thinner (less heavily sclerotised) than that covering the appendages. Further, the dorsal side of the coxa is not preserved in any specimen, so that the nature of the coxa-body junction is unknown, nor is its position on either the body or the coxa known. Presumably there was no articulation at the junction, and whether coxal movement was restricted in any direction is uncertain. I have argued above that the gill branch was attached to the postero-dorsal wall of the outer part of the coxa. If this is correct, then it was the inner, dorsal surface of the coxa that was joined to the body wall (Figs. 25, 26A–D). Walcott (1921:382–386, Fig. 13) discussed this junction, believing it to be between the outer, dorsal edge of the coxa and the body wall. He also suggested extrinsic muscles attached to the dorsal exoskeleton adjacent to the axial furrows. Raymond (1920: 24–25, Fig. 2) thought there was an articulation between the coxa and the inner side of the exoskeleton at the axial furrow. I agree with Walcott (1921: 381–382) that 58589 (Pl. 6:2) does not afford evidence for such a structure. Størmer (1939: 218, Fig. 20) believed the junction was situated below the lateral quarter of the axial ring and in the anterior half of the segment. The junction was with a short pre-coxal segment, which was joined to the upper, inner edge of the coxa. I do not consider that 58589, or any other specimen, affords evidence of a pre-coxal segment.

Størmer's interpretation resulted in a wide separation of the adaxial margins of the coxae, here shown to be strongly spinose and considered to be gnathobases. Walcott's solution to the problem does bring the inner ends of the coxae closer together, and I have done the same by placing the junction relatively close to the midline (at about the midlength of the segments, Figs. 25, 26A–D) to bring the gnathobases in opposition.

Enrollment

The increased depth of the axial furrow at the anterior and posterior margins of each thoracic segment suggests the presence of axial articulating process and socket (cf. Bergström, 1973: 22). The margins of the segments between axial furrow and fulcrum are straight and transverse, and the anterior margin appears to bear a flange which fits beneath the posterior margin of the segment in front. Articulating half rings and facets were present on thoracic segments and pygidium. Thus the exoskeleton structures associated with enrollment were present in *O. serratus,* but no enrolled specimen is known. Perhaps it enrolled partly, or even as closely as the related *Bonnia* (Rasetti, 1948a, Pl. 4: 22–24), i.e. with the posterior border of the pygidium brought into contact with the anterior cephalic border. Particularly in the latter case, the reconstructions (Figs. 26, 27) suggest that the ventral cuticle must have been sufficiently flexible to allow some retraction of the coxae beneath the axis to bring the appendages up within the arch formed by the pleural regions.

Gait

The mode of preservation suggests that the holaspid *O. serratus* was benthonic in habit. In the reconstruction (Figs. 25, 26E) I have shown the animal in one position of a possible gait, based upon studies of arthropod locomotory mechanisms by Manton (1952–1973). Joints between the exoskeleton of cephalon, thoracic segments and pygidium were hingelines which did not permit lateral movement, i.e. in walking the body was kept straight, and locomotion was principally by action of legs II to XII or XIII, all of similar size. It is suggested that each pair of legs moved in unison, in a promotor-remotor swing about an approximately horizontal, transverse axis at the coxa-body junction (Manton, 1958, Fig. 3e). The swing of the leg would have been implemented by extrinsic muscles arising from the proximal coxal margin and inserting within

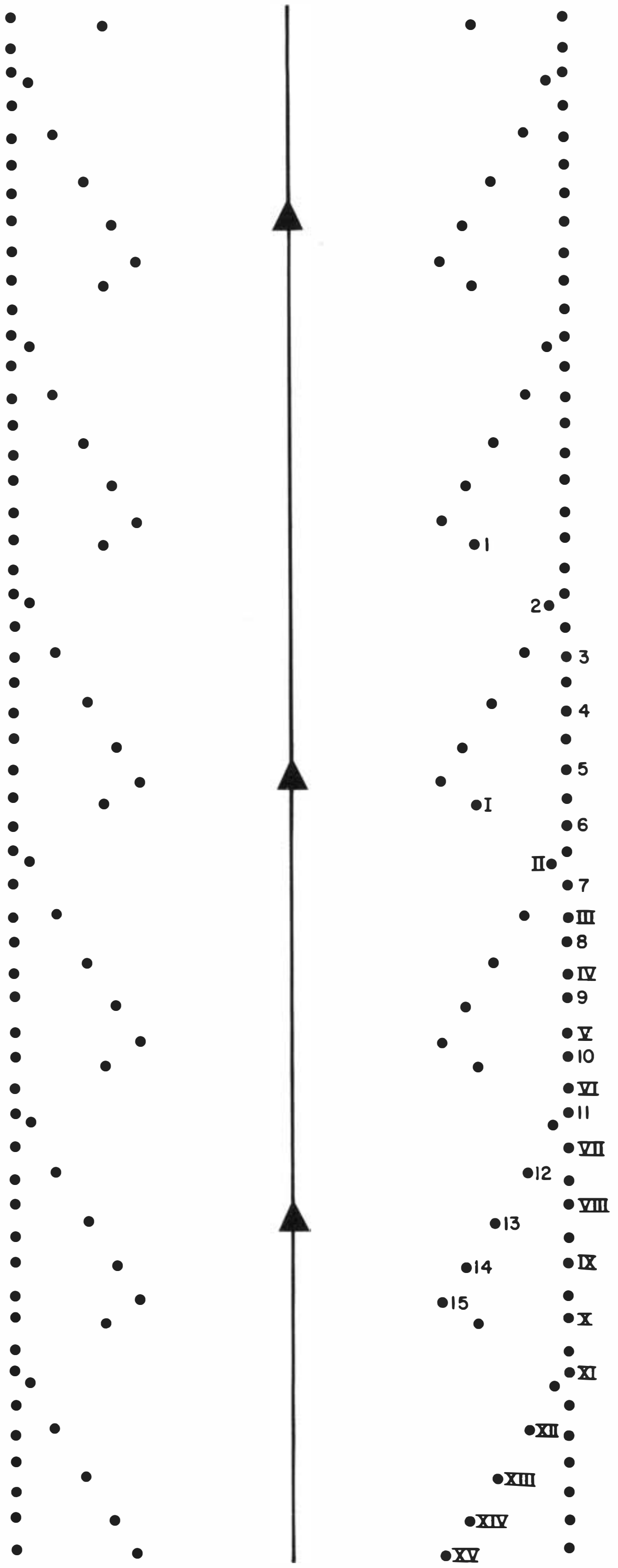


Fig. 28. Olenoides serratus. Trackway (each footprint indicated by solid circle) made by animal when walking in the manner shown in Figs. 25, 26E. Direction indicated along median line, footprints of appendages I to XV of first pace by roman numerals, of second pace by arabic numerals. Stride is distance between repetition of any two footprints, e.g. III to 3. See text for discussion of gait.

the body. The probable nature of the joints of the walking leg (coxa to 1, 1 to 2 being pivot joints, the remainder hinge joints) suggests a 'hanging stance' (Manton, 1952: 97, Fig. 2), the leg in a curve convex upward, which keeps the centre of gravity low and promotes stability. This stance may have been facilitated by the axis of swing at coxa-body being directed slightly upward and outward rather than exactly horizontal. In the cross-sections (Fig. 26A–D) each leg is portrayed in the vertical position, part-way through the span of the promotor-remotor swing. It is suggested that the leg musculature may have been like that of a millepede as illustrated by Manton (1958, Figs. 4a, 17), antagonistic levator and depressor muscles would be present in podomeres 2 and 3, separated by pivot joints (Manton, 1958: 504) from each other and the coxa. Flexor muscles only would be present in podomeres 4–7, separated from each other and 3 by hinge joints (Manton, 1958: 504) along the dorsal margin. During the earlier part of the propulsive phase the flexor muscles would produce some of the propulsive force, but in the latter part the leg is extending and the depressors produce the thrust (Manton, 1958:505–6, 508–9, Fig. 3a). In the forward, recovery swing the leg would have been lifted by the antagonistic levator muscles of podomeres 2 and 3, extended by hydrostatic pressure, and swung forward with the tip much farther from the body than in the propulsive phase (Manton, 1952). Having made these assumptions, one may go on to suggest a particular gait. An approximately horizontal axis of swing of the coxa favours slow movements close to the ground (Manton, 1958:496), and for the slow movement portrayed here a relative duration of forward and backward strokes of 3 to 5 is selected. Each metachronal wave includes eight legs, five on the ground at one time, and three in the recovery phase. A leg is put on the ground one-eighth of a pace before the one in front, a phase difference of 0.125. An angle of swing of the legs of 16° is selected, 4° in front of the transverse plane and 12° behind, a swing which means that the tips of the legs do not cross over each other at the maximum angles. Consideration of gaits of animals with a series of legs of equal length is given by Manton (1952: 108–113, Fig. 5, 1954: 328–336, Fig. 5, 1973, Figs. 7–9). A gait similar to that proposed is shown for *Polydesmus* (Manton, 1952, Fig. 5) and in Figure 5n (Manton, 1954), where the angle of swing is greater than proposed for *O. serratus.* In such a gait, where the phase difference is less than 0.5, the metachronal wave moves forward (Manton, 1952: 103). As shown in lateral view (Fig. 26E) the body is well supported in such a gait, even when the three pairs of cephalic legs are momentarily all in the recovery phase and the cephalon supported by the longitudinal muscles. The track made in this gait is shown in Fig. 28, where allowance is made for the shorter anterior and posterior legs and posterior segments. This track is unlike that portrayed by Seilacher (1959, Fig. 2b) for a supposed *Olenoides*-like trilobite from the Lower Cambrian. The repeated series of footprints in a straight line on each side, the lines converging back, could only be made by simultaneous stepping of legs III–XV, i.e. a jump with all these pairs moving simultaneously in the propulsive backstroke. Such a 'jump' might be used by *O. serratus* to launch itself off the bottom in order to glide in a current or to begin swimming, but such a track is not that made by walking in the manner suggested here.

Digging and raking

The *Cruziana* type of trail (Crimes, 1970: 49–53, Birkenmajer & Bruton 1971: 313–318) is regarded as typical of the activity of Cambrian trilobites, searching in the bottom sediments for food. Fig. 29 shows on the left the apparent maximum flexure possible of the walking leg of *O. serratus.* Pairs of legs, flexing inward in combination with a remotor swing of the coxae, could have produced the 'V'-shaped scratches (the V pointing backward) in the floor of the shallow, double longitudinal trough of *Cruziana.* Possibly the successive pairs of legs flexed and extended alternately, and the backward swing would push the animal forward. The cephalon may have been inclined slightly upward and forward, keeping the antennae free, the digging being done by leg branches III to XII or XIII. The inward movement of the tips of the appendages, and the ventral spines, would have aided in trapping food and pushing it toward the coxae in the mid-line. Bergström (1973: 54) has discussed the association between *Cruziana* trails and other burrows which end at the junction of the two trails, and interpreted these as the record of an arthropod catching its prey.

Birkenmajer & Bruton (1971, Fig. 13) have portrayed a trilobite making a *Cruziana* type trail by ploughing or even burrowing in sediment. In sagittal section (Fig. 27) the cephalon of *O. serratus* is seen to be bluntly tapered forward, with a tubular edge, a form not well suited to ploughing. Further, the apparent thinness and flexibility of the ventral cuticle means that to transfer a push from the legs to the cephalic exoskeleton puts a strain on extrinsic muscles of the coxae (cf. Raymond, 1920: 74). Hence I question that ploughing or burrowing in a resistant medium was a possible activity for *O. serratus,* but perhaps it could plough to a limited depth in wet sediment.

Sideways raking (Seilacher, 1955: 346–355, Crimes, 1970: 57–59) is another activity deduced from tracks and ascribed to trilobites. Figure 29 shows on the right a leg in a raking attitude, on the extreme left is a leg flexed and pushed into the sediment. Further flexure of the left leg would enable the tip of the right leg to be raked over the surface.

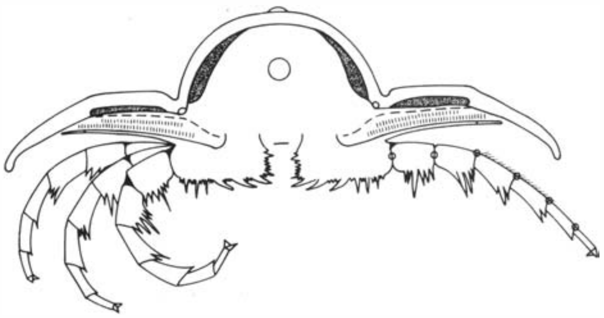


Fig. 29. Olenoides serratus. Posterior view of first thoracic segment and cross section of body and gill branches (compare Fig. 26B). Left coxa and leg branch in posterior view, leg branch in three positions of increasing flexure, possibly as used in *Cruziana*-type digging. Right coxa and leg branch extended with tip on sea bottom, possibly as used in raking. Positions of pivot and hinge joints between podomeres indicated by heavy circles.

The present investigation has revealed the rows of setae along the dorsal margins of segments 4 and 5 of the leg branch (Pl. 22: 1, Pl. 24: 4). Presuming that these setae were sensory in function, they could have aided in indicating leg branch position in walking, digging and raking (Figs. 26A–D, 29).

Swimming

As noted above, a backward push by a series of legs in unison may have served to lift *O. serratus* off the bottom. It may have progressed in a series of such jumps, taking advantage of suitable currents for drifting. The walking legs, though flattened in the axial plane, would hardly have aided in swimming since they could not be 'feathered' during the recovery swing. If, as suggested in Fig. 30, the axis of swing of the coxa remained approximately transverse, but directed somewhat downward, and the coxa and walking leg were swung back into a 'trailing' position, there would be a greater space between the leg branch and the ventral cuticle. It is suggested that within this space the gill branch might have been flexed up and down, the axis of its attachment to the coxa directed transversely. If the gill branches moved in this manner in a metachronal rhythm (similar to that which may have occurred when the animal was walking, see below), water would have been squeezed out backward as successive lobes of the gill branches moved up against the ventral cuticle of the pleural region. Water would have been drawn inwards as the branches moved down and away. Possibly the outer lobe was pressed against, and withdrawn from, the ventral surface and aided in directing such currents. This does not appear to have been a strong swimming mechanism, but the size and consequent overlapping arrangement of the gill branches must have meant that their movements were confined within the space between leg branch and ventral cuticle of the pleural region. Both Størmer (1939: 223–227, Fig. 28) and Bergström (1969: 407–408, 410, Fig. 4) have suggested similar movements of the outer branches, mainly with reference to filter-feeding, though Bergström notes the possible propulsive effects of the water currents.

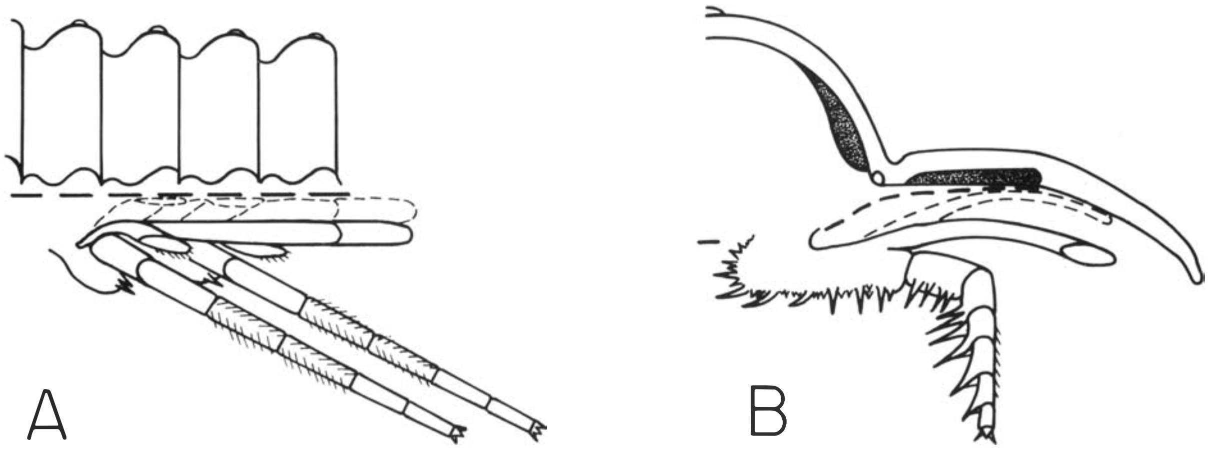


Fig. 30. Olenoides serratus. Possible positions of appendages when swimming. Axis of swing of coxa changed to outward and slightly downward in transverse plane, coxa swung back and leg branch in 'trailing' position. Up and down positions of gill branches suggested by dashed and solid outlines, heavy dashed line is ventral cuticle. A, left lateral view, showing left appendages of first two thoracic segments, exoskeleton cut through inner part of pleura. B, posterior view of first thoracic segment and appendage, lobes of gill branch only shown.

Respiration

Figure 27 suggests water currents sucked into the interlimb space as the leg branches move away from each other, or expelled as the interlimb space contracts, during walking. In addition, the axis of the coxa-gill branch junction was parallel to, and just below, the axis of swing of the coxa. Consequently, as the coxa swung forward in the recovery phase, the gill branch would be drawn away from the ventral surface of the pleural region, and driven towards it as the coxa swung back. Such movements of the gill and leg branches would have served to force water between the gill filaments and promoted aeration. The postulated swimming mechanism would promote such aeration more strongly. It is assumed herein that the outer branches of the appendages, bearing many long (much longer than has previously been supposed), thin filaments, the branches strongly overlapping and extended back close beneath the pleural regions, were gill structures. Bergström (1969: 403–404, 410–411) has argued that the filaments were not suited to such a function, and that so far unknown gill-structures were situated on the ventral cuticle of the pleural regions.

Manner of feeding

The entire series of coxae in *O. serratus* have been shown to be relatively large and strongly spinose on the inner and ventral margins. As preserved in most specimens this inner margin is far from the sagittal line (Fig. 2). This is not considered to be the natural position, which may be more nearly represented in exceptional preservations (Pl. 11, Fig. 14, Pl. 17, Fig. 20). In Figs. 25, 26 I have placed the inner margins of the coxae relatively close together because I interpret these margins as gnathobases which served to squeeze food and pass it forward to the mouth. This armoury of gnathobases, flanking a median groove, extended along the body from the mid-length of the pygidium to the mid-length of the cephalon. The coxa of *O. serratus* did not have the dorso-lateral extension which articulates with the doublure of the exoskeleton, as in *Limulus* (Manton, 1964: 29, Figs. 14–17, *in* Moore, 1969, Fig. 7), so it cannot be assumed that the food-grinding mechanism of this trilobite was as powerful or efficient as that of *Limulus.* It is also clear that the method of moving food forward in the two animals was different. In the dorsal reconstruction (Fig. 25), the axis of swing of the coxae of the first three and last three appendages is not drawn transverse, but in a slightly radial arrangement to suggest the fanning of legs seen in living arthropods (Manton, 1952, Figs. 2, 3). In appendages IV to XII the axis of swing of the coxa is not drawn directly transverse, but outward and backward at 5° to the transverse plane. Such an inclination would bring the large, spinose gnathobases of these appendages closer together as they swung back, enabling them to seize and crush food. In the forward swing the gnathobases would separate, so releasing the crushed mass to be seized by the next pair in front (compare drawing of coxae of an iuliform millepede by Manton, 1958, Figs. 7 a–c). Such a mechanism, perhaps aided by adduction of the coxae and a shift forward of the gnathobase edge at the end of the backstroke, may have operated during walking or during the *Cruziana* type digging to carry food forward along the midline. After release by the anterior gnathobases a bolus of food could have been drawn in to the gut by peristaltic action of the oesophagus and driven along the gut cavity. It is not intended to suggest that food could only be squeezed and moved forward while the animal was walking or digging. While at rest adductor-abductor movements of coxae, possibly combined with a forward shift of gnathobases, may have been more readily achieved.

A remarkable feature of the limb of *O. serratus* is the armoury of fixed spines on the distal, ventral side of the coxa and on the ventral side of podomeres 2–5 of the leg branch (Figs. 26 A–D, 29). It recalls the similar spines on the coxa and leg branch of *Phacops* (Seilacher, 1962: 220–221, Fig. 1). The spinose appendages were present along the length of the body, the spines longest on the proximal segments of the leg branch. Their function must have been to grip prey. In Fig. 29, left side, a possible maximum flexure of the leg branch is suggested. In this figure the axis of promotor-remotor swing of the coxa is in the transverse plane, directed outward and slightly upward. If this angle could have been changed to outward and downward, as suggested in Fig. 30B, but perhaps to a greater extent, prey could have been gripped between the leg branches for squeezing and shredding by the coxae. *O. serratus* is thus considered to have been a benthonic predator on small and soft-bodied animals as well as a scavenger, gathering food by its digging and raking activities, and pushing it into the midline using the leg branches and their armoury of ventral spines. The importance of intrinsic limb musculature in all its activities is evident.

Størmer (1939: 222–227, 1951: 132–134) did not have clear evidence of gnathobases, and both he and Bergström (1969: 404–408) emphasized the importance of filter-feeding in trilobites, the filter being the lamellae of the outer branch. Both were aware of the problem of how food particles trapped by the filaments could have been scraped off and carried to the mouth. I have preferred to emphasize the function of the gnathobases and ventral spines of the leg branches of *O. serratus* in food catching and transport along the midline, and to regard the outer branches as primarily used in respiration and swimming.

DESCRIPTIONS OF SPECIMENS OF *KOOTENIA BURGESSENSIS*

USNM 65512

Plate 25: 1–4, Figures 31A, B.

☐ 1918 *Kootenia dawsoni* Walcott (part): 131–132, Pl. 14:3. ☐ 1920 *Kootenia dawsoni,* Raymond: 46. ☐ 1933 *Kootenia dawsoni,* Størmer: 147–148, Figs. 1a, 2b. ☐ 1939 *Kootenia dawsoni,* Størmer: 192, 193, 196–199, Fig. 18. ☐ 1942 *Kootenia burgessensis* Resser: 27. ☐ 1951 *Kootenia burgessensis,* Rasetti: 189.

The right half of this specimen is preserved as counterparts, the biramous appendages best preserved below and outside the outer parts of the thoracic segments, the ridges and furrows of which have been impressed upon them. The total number of appendages cannot be determined, and neither antennae nor cerci (if present) are preserved. Parts of apparently the lamellae of three gill branches are preserved beneath the posterolateral part of the cheek and first thoracic segment. The next four appendages (4–7) are the best preserved, the leg branches curved outward and backward, only partially exposed, the position of the joints difficult to discern. The gill branch lies dorsal to the leg branch, and consisted of a larger inner portion, subrectangular in outline, and a tongue-shaped outer portion. The posterior margin of the inner portion bore imbricated lamellae, each lamella long and slim, rounded at the tip (7g, Fig. 31B). The lamellae are imbricated in this specimen so that each overlaps the lamella inside it. The margin of the outer portion bore slim setae (5g, 7g, Pl. 25: 4, Fig. 31B). The posterior margins of the inner and outer lobes of the gill branch curve and meet at an oblique angle, but there is no line between the two portions (Pl. 25: 4). Størmer (1939, Fig. 18) gave a drawing of the two gill branches here labelled 5g and 6g (Pl. 25: 4, Fig. 31B). He showed several lines traversing the inner lobes and the outer lobe of 6g, interpreting them as possibly indicating segmentation (1939: 198). Further, Størmer (1933: 148, 1939: 198) considered that there was a distinct frontal rim along the anterior margin of the gill branch, divided into numerous 'segments'. The gill branches in this specimen have been compacted against the pleurae so that ridges and furrows, including the ridge at the outer edge, are impressed on them. The preserved anterior edges of gill branches 4g to 7g are at a slight change in level (Fig. 31B), and may not represent the original edge. In the photographs (Pl. 25:1, 4) some traces may be seen of the structures interpreted by Størmer as the frontal rim, and these are indicated by the letters 'fm' in Figure 31B. The lines crossing the gill branch are not as evident as Størmer's figure 18 suggests, and there are what I interpret as wrinkles resulting from compaction on gill branch 6g. I do not consider that there is sound evidence for a segmented frontal rim on the gill branch or subdivisions of the gill branch, that Størmer (1939, Fig. 20) shows in his reconstruction of *O. serratus,* based largely on evidence he drew from this specimen of *K. burgessensis.* I prefer to consider the gill branch in both species to have consisted of a larger inner, presumably plate-shaped portion bearing lamellae, and a smaller, tongue-like outer portion bearing marginal setae and to show no divisions or supposed segments.

Behind appendage 7 portions of appendages 8–11 can be seen (Fig. 31A), but behind here it is not possible to be sure of details.

USNM 65533

Plate 3:2, 3, Figure 7.

□ 1918 *Neolenus serratus,* Walcott, Pl. 36:3. □ 1942 *Kootenia burgessensis* Resser: 27. □ 1951 *Kootenia burgessensis* Rasetti: 189.

USNM 65533 shows the exoskeleton in relief, the middle body smooth, but terrace lines are visible on the posterior and lateral borders. A second specimen (Pl. 3:4) is a mould of the inner surface of the exoskeleton viewed from the interior and consequently concave. Both specimens show the deep, narrow groove separating hypostome from rostral plate (Fig. 7), the line of the hypostomal suture. Rasetti concluded that hypostome and rostral plate were fused in *Kootenia, Olenoides* and other genera, and illustrated this in *Olenoides curticei* (1952: 889–890, Pl. 1:3). The present two specimens show the course of the connective suture, and its junction at an acute angle with the anterior edge of the anterior wing of the hypostome. This is unlike Rasetti's drawing in which the triangular distal part of the rostral plate, and the anterior wing of the hypostome, are fused into a single triangular projection, and in which no trace of the hypostomal suture is shown. The middle body is divided by a shallow middle furrow, and on the posterior lobe, beside this furrow, is the ovate, slightly raised macula. The deep pit in the anterior wing indicates the position of the wing process on the inner surface.

No reasons for assigning this isolated hypostome to *O. serratus* were given by Walcott, but presumably he used it for his restoration (1918, Pl. 31), as may have Raymond (1920, Fig. 8) and Størmer (1951, Fig. 12). The first two of these authors show the hypostome separated from the anterior doublure by a line, presumably a suture, but no connective sutures. Størmer shows hypostome and doublure fused and no ventral sutures. Isolated hypostomes of species of *Kootenia* have been illustrated by Rasetti (1948b, Pl. 49: 6, 8) and Fritz (1968, Pl. 40: 6). In all the examples mentioned the anterior outline of fused hypostome and rostral plate is bluntly and obliquely angulate, and the distal part of the rostral plate and anterior wing are fused to form an outwardly-directed, triangular projection. The specimens illustrated here are similar in outline and form, but differ in showing the position of the hypostomal suture by a narrow groove, and in that distal part of rostral plate and anterior wing are not completely fused into a single structure. These differences may be in preservation, for a trace of the hypostomal suture may be visible on the left (right in the figure) side of Fritz's example. I conclude that these isolated hypostomes may belong to *K. burgessensis* rather than *O. serratus,* and reasons for this conclusion are given above in discussing SM A 89326.

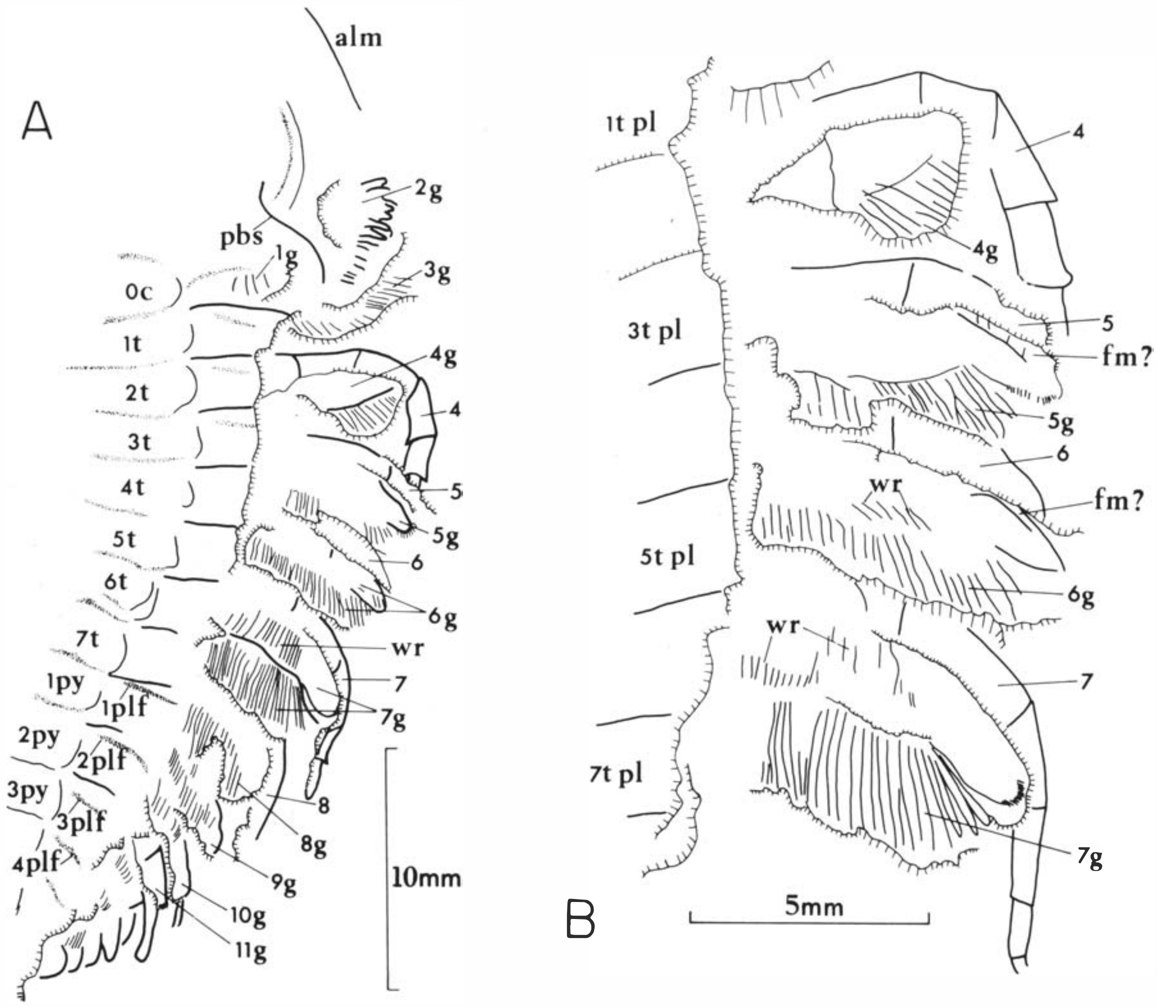
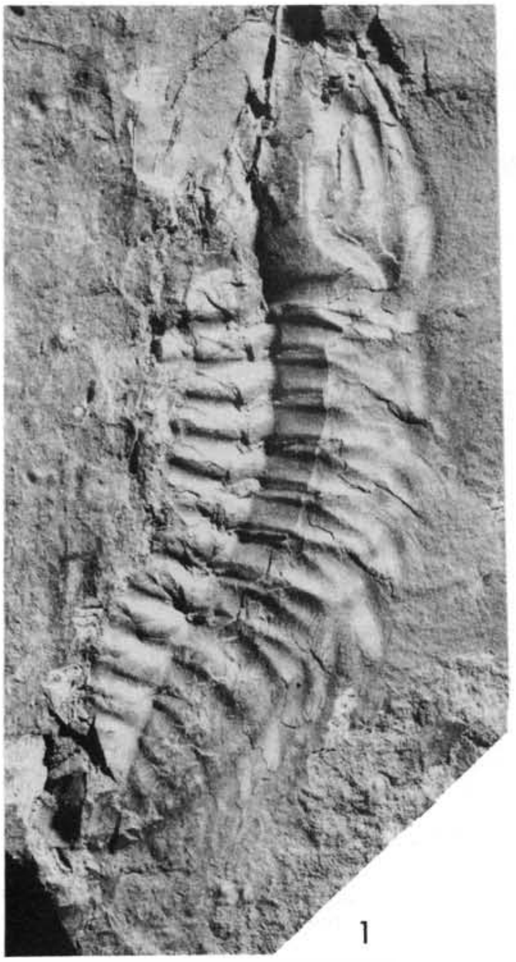


Fig. 31.

Plate 25.

Kootenia burgessensis Resser, 1942, USNM 65512, Phyllopod bed, Walcott quarry. 1, 3, north, reflected, x2.5, see Figure 31A. 2, counterpart, north, x2.5, see Figure 31A. 4, north, x5, see Figure 31B.



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Microstructure and composition of the trilobite exoskeleton

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Representatives of the major orders of trilobites have been studied by polarized light and electron microscopy as well as electron probe, X-ray diffraction and amino acid analysis. Data were collected with respect to crystallography-mineralogy, layering-lamination, pore canals, and organic matrices. A C-axis preferred orientation of microcrystalline calcite is characteristic. Layering, lamination, pore canals, and a pseudopleochroism vary in appearance and distribution. Phosphate layers occur in two species. Decalcified cuticles reveal a structurally preserved, biochemically degraded meshwork of organic material. The trilobite exoskeletal microstructure compares more favorably with that of calcified ostracodes than with the typical, generalized arthropod cuticle.

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By comparison with other invertebrate groups that are common in the fossil record the microstructure and composition of the trilobite cuticle has received very little attention. With the exception of a recent study by Dalingwater (1973) there have been no extensive papers published on this subject to date. Cayeux (1916) figured a section of *Trinucleus goldfussi* showing a thin external fibrous layer and a "lamellar" inner layer. Størmer (1930) described a few well-preserved specimens in which evidence of layering and laminations could be seen. Rome (1936) also observed laminations in some specimens of *Phacops* and Kielen (1954) illustrated a specimen with a pigmented layer. Pore canals are also frequently mentioned and while the composition of the exoskeleton is generally considered calcitic there have been scattered but persistent reports of phosphate in the trilobites (von Zittel, 1887; Richter, 1933; Rhodes & Bloxam, 1971). Primarily because of these few observations the currently held textbook conception of the trilobite cuticle is that of a calcareous-phosphatic structure with pore canals and a layered and laminated microarchitecture which is in general directly comparable with that of the typical extant cuticle (Harrington, 1959). In extant arthropods the external skeleton or cuticle is secreted by the epidermal cells forming the inner part of the body wall and it is commonly composed of several layers consisting primarily of microfibrils of chitin associated with protein. It usually contains pore canals and is stiffened and hardened over most of the body surface by a process of tanning and in the case of many crustaceans by the deposition of calcium salts (Richards, 1951).

The present study is aimed at examining representative, well-preserved trilobite exoskeletons with a view towards comparison, both compositionally and microstructurally, with that of extant arthropods as well as among the trilobites themselves.

MATERIALS AND METHODS

The majority of the specimens examined in this study were obtained from the collections of the National Museum of Natural History and the United States Geological Survey housed at the Smithsonian Institution, Washington, D. C. Additional specimens were made available by Dr. Ewa Tomczykowa, Instytut Geologiczny, Warsaw, Poland. The taxonomic and locality data for all of the species studied are listed in Appendix I. The selection of material was limited to well-preserved specimens that were neither museum types nor exceptional or one-of-a-kind specimens from rare localities. This left a minimum to work with and although an attempt was made to select a standard region of the cuticle for comparison, more often than not only fragments of cuticle were available for sectioning. Accordingly, the coverage is necessarily spotty geographically, stratigraphically, anatomically and taxonomically for the twenty species studied.

The trilobite material was embedded, where necessary, in epoxy resin and sectioned for polarized light microscopy according to methods similar to and modified from those developed by Nye *et al.* (1972). Mineralogical and chemical determinations were made on selected material by Debye-Scherrer powder X-ray diffraction methods and electron probe microanalysis. Transmission electron microscopy of the calcified cuticle was accomplished using either the single- or double-stage replica techniques on polished and etched surfaces as well as on untreated surfaces. The organic matrix from within selected exoskeletal fragments was isolated by means of Na-EDTA decalcification at pH 8. Aliquots were used for amino acid analysis by high-sensitivity ion-exchange chromatography or for subsequent epoxy embedding and ultramicrotomy.

RESULTS

The most characteristic and consistent feature of the trilobite exoskeleton is its mineralogy and crystallography. In agreement with Sorby (1879) and Cayeux (1916) all of our specimens which represent well-preserved, primary cuticle material (*i.e.*, not impressions or silicified material, etc.) are constructed of calcite crystals which have a C-axis preferred orientation more or less perpendicular to the skeletal surface. This is a statistical preferred orientation of the crystals as regards their crystallographic C-axis and is best observed on *thin* thin-sections in cross-polarized light where it manifests itself as a zone of darkness (optical extinction) through the cuticle wall perpendicular to its surface (Pl. 1). Such a high degree of crystallographic preferred orientation is not, except for the ostracodes, common among extant calcified arthropod cuticles (Dudich, 1931) where a more irregular, mosaic pattern is often seen. We have been able to detect two general types of optical extinction within the trilobites studied. The first is a homogeneous extinction (Pl. 1: 3, 5, 6) and the other is a patchy extinction (Pl. 2: 1, 2). In the former the zone of darkness between crossed polars is rather uniformly dark within the major layer. In the latter there appear to be irregular patches of uniform darkness separated by areas less dark. The two types grade into one another in many instances and all species have one or the other or both.

From a morphological point of view the electron microscope is capable of providing the best information on the calcite crystals. Here we have found that in some of the cuticles examined the calcite exhibits a crudely layered aspect parallel or subparallel to the surface (Pl. 2: 5, 6). The individual crystals are difficult to define with certainty but appear to be irregularly shaped and plate-like so that in plan view (Pl. 2: 1–4) a sutured, mosaic pattern can be discerned. This type of pattern was seen in *Phacops, Isotelus* and *Agnostus* and it compares with that observed in some ostracodes (Pl. 2:3) as well as in some salcareous foraminifera (Towe & Cifelli, 1967), both groups of which can also have a C-axis preferred orientation.

As expected in fossil material of Paleozoic age, the calcite composition is not magnesian. Whether or not there was any magnesium in solid solution in the original trilobite cuticle cannot be stated with any reliability from our data since magnesian calcites rapidly lose their magnesium with diagenesis. Some magnesium was likely to have been present as this is a common constituent of extant calcified arthropod cuticles (Vinogradov, 1953).

As stated in the introduction, it is a commonly held generalization regarding the trilobites that a certain proportion of calcium phosphate is present in the cuticle mixed with the calcium carbonate. Our evidence does not support this generalization although we did find at least two specimens with discrete outer layers composed of calcium phosphate. Our attention was drawn to these specimens (an *Ellipsocephalus* from Sweden and a *Calymene* from Poland) because of the presence of a thin, pink covering layer. In thin-section these layers behave quite differently as compared to the rest of the cuticle (Pl. 3). They are yellow-brown in color which in polarized light becomes a dark gray appearing almost isotropic due to the very low birefringence. The layers are uniform in thickness (~ 20 μm), clearly follow the surface of the calcite below, and are penetrated by pores, all of which argue in favor of a primary origin for the layer itself but not necessarily for its phosphatic composition. Samples of the outer layer in both species were carefully scraped from the surface and analyzed by powder X-ray diffraction. Plate 4: 6–8 shows that in both species the mineral is a member of the apatite group, comparing favorably with an apatite standard.

The distribution of the phosphatic material in *Calymene* was studied by means of electron probe analysis on a polished, transverse section. Traverses across the cuticle were made for calcium and phosphorus and these were compared with an apatite standards as well as with traverses across a specimen of *Isotelus* similarly prepared. The results are given in Plate 3: 1–3. It can be seen that the phosphorus content (dashed line) is essentially negligible throughout all of the cuticle in *Isotelus* as well as the bulk of the cuticle in *Calymene,* rising sharply only at the location of the outer, pink layer in the latter. We attempted to compare these data with those from extant arthropod material and although there have been several chemical analyses of various crustaceans reporting phosphorus (Clarke & Wheeler, 1922; Lowenstam, 1972; Vinogradov, 1953; Bøggild, 1930) we were unable to locate any specific information regarding its mineralogy and distribution within the cuticle itself. Accordingly, therefore, we undertook to examine a known phosphorus accumulating crustacean, the crab. Electron probe analysis (Pl. 4: 1, 2) of both Recent and fossil crabs (*Cancer* sp., Late Miocene) shows that phosphorus, while present throughout the cuticle, is in both instances more concentrated toward the outermost exocuticular portion. Powder X-ray diffraction analysis (Pl. 4: 3–8) shows that the phosphorus-rich outer portions in both the Recent and fossil crab contain calcite but only in the fossil material is the phosphate in the form of a crystalline apatite. It is amorphous to X-rays in the Recent crab. The point of comparison with the trilobites is that in both cases the phosphorus is concentrated toward the exterior of the cuticle. But in the trilobites the phosphate mineral is not admixed with calcite. If this apatite layer in the trilobites is indeed a primary layer there is the possibility that, like the crab, in the living condition the phosphorus accumulated in an amorphous condition.

Although the calcite mineralogy and crystallography of the trilobite cuticle is consistent throughout the group, few other microstructural features that we investigated were so uniformly present. The presence of an organic matrix preserved within the calcite exoskeleton is something we observed with regularity where it was feasible to do so and inasmuch as calcification in general is a process intimately related to an organic precursor this was an expected and predictable result for reasonably well-preserved specimens.

If pieces of trilobite cuticle freed from the rock matrix are placed in a solution of ethylenediaminetetracetic acid (EDTA) at pH > 7.0 and left undisturbed the calcitic material will be gently and completely dissolved, usually within 24 hours. The organic matrix (and pyrite) left after decalcification retains the shape of the original fragment (Pl. 5: 1, 2) but is exceptionally fragile and delicate, subject to breakage with the slightest agitation. Plate 5: 1 shows a fragment from *Phacops rana* including a portion of the eye. The organic matrix mimics the original fragment even to its presence within the original calcitic lenses of the eye. In the light microscope the organic matrix of the trilobites is brownish in color and generally amorphous in structure. In the electron microscope, however, a delicate meshwork is seen in ultrathin-sectioned material (Pl. 5: 4). There are openings and spaces that are in reasonable agreement with the size of the "crystals" as illustrated in Plate 2. In platinum-shadowed preparations (Pl. 5: 3) the network appears to be more granular in aspect. Bate and East (1972) have figured a similar organic matrix meshwork from within the ostracode carapace.

With the help and guidance of Dr. P. Edgar Hare (Geophysical Laboratory, Washington, D. C.) we attempted to obtain data on the amino acid composition of the isolated organic matrix by means of high-sensitivity ion-exchange chromatography. Utilizing extreme care to avoid contamination (Hare, 1964), we were unable to detect any meaningful amino acids at a sensitivity of 10^{-9} moles. The amino-sugar glucosamine which is the basic building-block of chitin (sensu stricto) was especially searched for but not found. It is apparent from these data that the organic matrix of the trilobites has been, like that from other older fossil material, diagenetically altered to a non-proteinaceous, carbonaceous material. The absence of glucosamine in particular does not mean that the original material was not chitinous but only that it is not now chitinous in a biochemical sense.

In the introduction we raised the point that the trilobite cuticle is generally regarded as being layered and laminated in a fashion similar to that of the typical extant arthropod. Our data, summarized in Table I, fail to support this generalization and we find that in this microstructural aspect there is wide variation.

Layering was distinguished by changes in either mineralogy, mineralogical microstructure, or pigmentation. Lamination, on the other hand, is a generally finer-scaled repetitive feature within a layer and usually related to organic substances within this layer. The crudely laminated aspect of the crystals making up the cuticle alluded to earlier (Pl. 1: 3, 4; Pl. 2. 5, 6) is not here considered as true lamination. Almost half of the trilobite species included in this study lack any evidence of layering or lamination. In the others no more than two layers could be distinguished and in each case the outermost layer was always the thinner. Three types of outer layers could be discerned: (1) a prismatic layer, (2) a pigmented layer, and (3) a phosphatic layer. The prismatic layer is the most common and is so named because it is constructed of elongated blocks roughly perpendicular to the cuticle surface (Pl. 1). These prisms are larger than the crystals of the underlying microcrystalline layer. In most instances they form an outer layer up to 20 or 30 μm in thickness. The pigmented layer, also very thin, is a dark, brownish layer which is generally microcrystalline helping to distinguish it from the prismatic layer which is itself occasionally pigmented. The phosphatic layer has been described above. It is worth emphasizing here that because of the thinness of these layers in many instances the outer layer will be found to have been worn away from some portions of the calcite cuticle. Thus it is difficult to make any definite statements about the distribution of the outer layer on the exoskeleton as a whole. The taxonomic distribution of these various outer layers is given in Table I.

The layered and lamellar microstructure of many living arthropods, especially among the insects, has been studied intensively by a number of workers including Bouligand (1965), Neville (1965), and Locke (1964). In particular, Neville (1965) has shown that daily growth patterns are visible in the cuticle of a number of insects where non-lamellate day layers having fibrils oriented in a preferred direction alternate with lamellate night layers having helicoidally oriented microfibrils.

Based on the paleontological literature as well as on the generalized structure of living arthropod endocuticle we expected to find abundant lamination in the trilobites. Contrary to this expectation we found little evidence for lamination and nothing directly comparable with the laminations often described in Recent arthropods. With respect to the ostracodes Bate and East (1972) concluded that the structural matrix of the carapace is also quite different and unlike that present in insects and decapod Crustacea.

All of the laminations we observed in the trilobites were confined to the principal layer. That is, we never recognized, unequivocally, any lamination in the thin, outer layer. All of the laminations seen could be related to the presence of dark, brownish organic pigmentation within the principal layer. Such laminations were found in all six examined specimens of *Phacops rana* from New York and in two species of *Isotelus*, one from New York and one from Vermont. On the other hand, *Phacops logani* from Tennessee exhibited no lamellae whatever. If a fragment of laminated *Phacops rana* cuticle is etched briefly in EDTA the lamellae will stand out in relief to some extent (Pl. 6: 1). Such material was replicated for electron microscopy and the results (Pl. 6: 2) show that there is no essential difference in the texture of the calcitic material forming the lamellae from that of the rest of the cuticle. Only a slight furrowing (arrows) can be seen. Etched material of the non-laminated *Flexicalymene* showed a similar structure but without furrowing. These data support the contention that the lamination is due to variation in the organic concentration within the cuticle rather than in some basic variation in the nature of the calcite crystals.

Whether or not the laminations are controlled by taxonomy, ecology, diagenesis or a combination thereof remains to be determined. The evidence based on our data favors taxonomy as the major influence. This, we argue, is the likely case because: (1) All specimens of *Phacops rana* from the Moscow Formation (Windom Member) near Buffalo, New York show laminations as do those of *Phacops accipitrinus* from Gotland figured by Rome (1936). However, those of *Phacops logani* from the Linden Group in Tennessee do not. (2) Specimens of *Isotelus gigas* from the Trenton Limestone in New York display laminations but specimens of *Odontopleura trentonensis* from this same locality do not. (3) *Isotelus platymarginatus* from the Upper Chazy Valcour Limestone in Vermont also have laminae while the specimens of *Bumastus subglobosus* from there do not.

Accordingly, if laminations were a general feature of the Trilobita, being well-preserved only under unusual diagenetic conditions, we would expect all trilobites from one such locality to show them and this is not the case. The same line of reasoning should hold for the laminations if they were primarily controlled by environment. Until further work can be done, a genetic control appears to be the major factor in their distribution.

In thin-sections of certain trilobites (see Table 1) ordered accumulations of some of the brownish organic material within the cuticle exhibit a phenomenon known as pseudopleochroism. The brownish color of the organic substance varies in its intensity in plane-polarized light depending on the orientation of the thin-section with respect to the polarizers. The maximum intensity (deepest brown coloration) corresponds or coincides with the position of maximum extinction of the calcite in the cuticle (under crossed polars) when this direction (C-axis) is perpendicular to the vibration direction of the lower polar (Pl. 7: 1, 3). Conversely, the weakest brown coloration is 90° to this position when the calcite extinction (C-axis) is parallel to the vibration direction of the lower polar (Pl. 7: 2, 4). In optical parlance: E, weak; O, strong. This phenomenon has been described by Hudson (1962) in the unrecrystallized mollusk shells from the Middle Jurassic Great Estuarine Series of Western Scotland. As noted by Hudson there may be a correspondence between microscopic organic inclusions and the absorption-pleochroism; such inclusions in this case having an index of refraction near the E-ray of calcite at 1.486. The biological significance of this phenomenon is unknown but it is of interest to note that the brownish organic material in the laminations of *Phacops rana* does not exhibit pseudopleochroism while the organic material within the eye lenses does (Pl. 7: 3). Neither the Recent nor fossil crab sections with brownish material exhibit the phenomenon. We conclude that two types of organic material may have been present – one which in association with the calcite of the cuticle gives rise either intrinsically or diagenetically to a pseudopleochroism and one which does not.

"Pore canals are widely but not universally found in arthropod cuticles" (Richards, 1951: 182). This statement concerning extant arthropods applies similarly to the trilobites (see Table 1) with the proviso that we are using the term "pore canal" to include all primary duct-like processes actually observed in the cuticles studied. That is, we do not here include secondary borings nor do we distinguish semantically between different types on the basis of presumed functional differences.

The pore canals observable in trilobite cuticles have a considerable size range as well as mode of preservation. Some pores are 75 μm or more in diameter while others are very narrow being 2–3 μm in diameter. The pore canals can be observed as true openings in the cuticle, or filled secondarily with calcite, pyrite or organic material. When the fine pores are filled with calcite they are best observed in thin section with cross-polarized light since the crystallographic orientation of the calcite fillings is commonly different from the C-axis preferred orientation of the cuticle itself. In most of the trilobite cuticles that have pore canals the canals are usually of one size range but we noted the presence of two distinct size populations (bimodal) in some species. *Calymene,* for example, has in addition to the narrow pore canals about 3–4 μm wide another set of pores 20–30 μm in diameter. *Odontocephalus* also has two sets of pore canals with the very large population easily visible and averaging 70–80 μm in diameter. Some of these varations are illustrated in Plate 8.

The pore canals of many living arthropods are twisted or helical in structure and the lamellar nature of the cuticle in sections produces a parabolic pattern. Bouligand (1965) has proposed a model demonstrating that this parabolic pattern could be due to an optical illusion created by sectioning obliquely through a stack of single sheets, each having its component fibers arranged in parallel. This stack, similar to plywood, is arranged such that each sheet is rotated slightly creating a twisted structure. As a result of this rotation the pore canals can also be apparently twisted or helicoidal (Neville, 1969). The parabolic pattern has been reported by Neville & Berg (1971) in the cuticle of a Jurassic fossil lobster (*Eryma stricklandii*) and twisted pore canals have been observed by Rolfe (1962) in ceratiocaridid Crustacea from the Middle Silurian. The parabolic pattern has been observed in Recent crab and crayfish cuticles and we have observed it in a fossil crab along with evidence of twisted pore canals (Pl. 9: 1, 2) where the pitch of the helical pores is in register with the light-dark laminations. Bate and East (1972) did not find evidence of parabolic structure in any calcified ostracodes and only indistinctly in uncalcified species. Harding (1964) figured one twisted pore canal in a calcified ostracodes cuticle but other photos figured by him of the same species do not appear to have twisted canals.

If twisted pore canals were observable in trilobites this would be evidence in support of the viewpoint that the trilobite cuticle is directly comparable with the generalized typical arthropod cuticle and would further indicate that a comparable lamellar structure must have been present originally, its absence now being therefore due to some diagenetic change. But in all of the trilobite material studied here only one vague instance provided any real evidence for helical pore canals (Pl. 8: 5). Observations of this material in the electron microscope (Pl. 8: 6) did not support the vague light microscopic image.

In addition to twisted or helical pore canals, the microstructure of some extant arthropod surface tubercles in polarized light is characteristic. As Bouligand (1965, 1971) has illustrated, such tubercles tend to exhibit a spiral pattern when sectioned tangentially. Our data on the crab cuticle confirm this general pattern (Pl. 9: 4, 5). However, the pattern for the tubercles in *Phacops rana* is completely different and, as with the helical pore canal data, lends no support to the comparison between the trilobite cuticle and that of the typical arthropod. As shown in Plate 9: 3 the cross-polarized light view of the tangentially sectioned tubercles is one of a dark cross or pseudo-optic axis figure. This figure is similar to that displayed by the corneal lens covering in phacopid eyes (Towe, 1973) produced by the radial distribution of the crystallographic C-axes in the cuticle. A similar pattern has been observed in the "eye spots" of some ostracode carapaces and we have noted its presence also on the nodes of *Agnostus pisiformis.* Whether or not these crystallographically oriented tubercles and nodes functioned as light sensors similar to the phacopid eyes themselves or to the ostracode "eye spots" is not known, but the possibility exists. This could be especially true for *Agnostus* where the calcified cuticle is unusually thin and transparent.

While many of the trilobites have pore canals a number of the cuticle fragments studied show no evidence at all of any pore canals (Table 1). Most extant arthropods have some evidence of pore canals although certain areas of the cuticle may lack them (Richards, 1951). The trilobites, therefore, would have to be considered unique if a substantial number of their representatives lacked these structures. However, this finding may be biased in several ways and thus may be more apparent than real. Firstly, the fragments studied in some instances may represent portions of the cuticle that lacked pore canals while other portions of the exoskeleton not studied in fact contained these structures. Secondly, the pore canals could have been totally obliterated by diagenesis. The total obliteration of larger pore canals (> 10 μm) appears unlikely but in the case of narrow canals it is a possibility. As stated above, the pore canals are preserved in several ways, being filled with calcite, organic material or iron minerals. To obliterate pore canals completely without recrystallization or solution-reprecipitation of the cuticle, it is necessary to fill them with calcite in crystallographic optical continuity with the cuticle itself and therefore with the same C-axis preferred orientation. If the calcite filling is grown at any other orientation then it will be readily detected from the cuticle in cross-polarized light. For example, such is the case in our specimen of *Odontocephalus* (Pl. 8: 2). Pore canals filled with pyrite or organic material are seen best without polarized light but it can be noted that in cross-polarized light such canals when incompletely filled often disappear when traced forward (see

TABLE 1.

Specimen (No.)	Region sectioned	Outer layer	Laminations	Pore canals	Pseudo-pleochroism
Paradoxides (2)	Cephalon	p	+ i	N, i	+
Olenoides (2)	Pygidium	p	—	—	+
Ellipsocephalus (2)	Cephalon	A	—	N	—
Olenellus (2)	Cephalon	pr	—	—	—
Agnostus (6)	Whole	—	—	N	—
Isotelus (N.Y.) (4)	Pygidium and pleural fragment	p, pr	+	N	+
Isotelus (Vt.) (2)	Pleural fragment	p, pr	+	N	+
Cryptolithus (10)	Cephalon	—	+ i	—	—
Tretaspis (1)	Cephalon fragment	—	—	—	—
Bumastus (3)	Cephalon	pr, i	—	i	+ i
Proetus (2)	Cephalon	—	—	N, i	—
Odontopleura (2)	Whole	—	—	—	+ i
Diacalymene (2)	Pygidium	—	—	W	+
Calymene (1)	Cephalon	A	—	N, W	—
Flexicalymene (10)	Whole	pr	—	N—W	—
Acastopyge (1)	Cephalon	—	+ i	N	—
Odontocephalus (2)	Cephalon	—	—	N, W	—
Scutellum (1)	Pygidium	pr	—	—	—
Phacops (N.Y.) (11)	Whole	pr	+	N—W	E
Phacops (Tenn.) (3)	Pleural fragment	pr	—	N	E

+	present	p	pigmented	i	indistinct
—	absent	A	apatite	N	narrow (> 10 μm)
pr	prismatic	E	eye lenses only	W	wide

for example Pl. 8: 3). Thus in the absence of the opaque filling the canals might not be seen at all. The narrower the pores, the greater this possibility.

Størmer (1930) figured "minute tubulae or canaliculae" in the cuticles of some Scandinavian trinucleids where they were preserved as radiating lines of pyrite grains. This feature is conspicuous in *Tretaspis seticornis* but only in the sections containing pyrite. The other sections of *T. seticornis* figured from the same locality do not show pore canals nor do the other trinucleids figured by Størmer. Our trinucleid specimens (*T. clarkii* and *Cryptolithus tesselatus*) failed to show pore canals, although the "stay lines" also mentioned by Størmer are visible.

We conclude from these data that the diagenetic obliteration of narrow pore canals through calcite filling in optical continuity with the cuticle can be a common occurrence and that trilobites appearing to lack pore canals need to be carefully evaluated from this point of view. Therefore, in Table 1 we list those specimens in which we were unable to see evidence of narrow pore canals but this does not necessarily imply that these species were in fact lacking them in life. Only a careful evaluation of many thin-sections of the same species from different localities can clarify these data.

SUMMARY AND CONCLUSIONS

Twenty species of trilobites ranging from Cambrian through Devonian in age have been studied with regard to microstructure and composition. Only the mineralogy and crystallography of the principal layer is consistent throughout all of the specimens studied. All other features were found to vary. The data can be summarized as follows:

(1) MINERALOGY. – The highly calcified principal layer of all twenty species is composed of calcium carbonate in the form of calcite. Two species were found with an outer layer composed exclusively of apatite (calcium phosphate).

(2) CRYSTALLOGRAPHY. – The calcite of all twenty species is statistically oriented with the C-axis of the component crystals more or less perpendicular to the cuticle surface. The ultrastructural morphology of the component crystals is plate-like parallel or subparallel to the cuticle surface and the boundaries of the crystals are sutured and irregular, rarely with straight edges or primary crystal faces.

(3) LAYERING. – Twelve of twenty species have a principal layer as well as a thinner outer layer which can be prismatic in structure, pigmented, or composed of apatite. The remaining eight species have only the principal layer.

(4) LAMINATIONS. – Fine-scale lamellae related to the distribution of organic material occur within the principal layer in six out of twenty species. Parabolic structure was not observed.

(5) PSEUDOPLEOCHROISM. – This optical phenomenon related to the preservation of organic material in the calcitic cuticle could be observed in seven of twenty principal layers and only in the schizochroal eye lenses of two phacopids.

(6) PORE CANALS. – Fourteen out of twenty species show evidence of some type of pore canal structure preserved in the cuticle. Two of these have two types of pore canals with two distinct size ranges. None of the pore canals is distinctly twisted or helical.

(7) ORGANIC MATRIX. – Structurally well preserved organic material isolated from selected cuticles shows a fine reticulated meshwork ultrastructure but is devoid of original biochemical constituent amino acids.

From the data given in this report, and as summarized above, we conclude that trilobite exoskeletal microstructure and composition do not compare as favorably with that of a typical generalized arthropod cuticle as has been thought. That is to say, the three-fold division of the typical arthropod cuticle into an outer epicuticle, a middle exocuticle and an inner laminated endocuticle is not found in the majority of trilobites. This does not mean, however, that the trilobites lacked the three-fold division in life since the epicuticle in extant arthropods is generally a thin, non-chitinous and uncalcified layer and is unlikely to have been preserved except under unusual circumstances. It is possible therefore that the outer thin layer observed in many trilobites represents the exocuticle and the inner or principal layer corresponds to the endocuticle; the epicuticle being lost with the other soft tissues in fossilization.

The fine endocuticular lamellae commonly observed in extant arthropods (especially insects) are generally lacking among the trilobites. These laminations are not universally found in arthropod endocuticle as the work of Bate & East (1972) and Harding (1964) shows in some calcified ostracode carapaces. The presence or absence of lamellae in trilobites may be due to genetic factors or to fossil preservation but the absence of parabolic structures (and helical pore canals) indicates that those lamellae that are found are not the same as those normally observed in the typical extant arthropod endocuticle.

Narrow pore canals, often observed in trilobite cuticles, are apparently subject to the vagaries of fossilization and we believe that their absence in a given specimen may be due to diagenetic obliteration. Only by checking several specimens from different localities can it be established whether or not a given species lacked small pore canals in life. The larger wide pore canals, less likely because of their size to be obliterated, may have functioned differently from the narrow ones and as with extant arthropods could have been ducts containing a sensory apparatus – an uncertain conclusion.

The structurally preserved but biochemically destroyed organic matrix isolatable from trilobite cuticle is in keeping with the pattern of preservation found in other older fossil material. The reticulate meshwork observed in the electron microscope compares favorably with a similar pattern seen in decalcified ostracode cuticle (Bate & East, 1972). The absence of biochemical evidence for chitin does not mean that the trilobite cuticle lacked this material but only that it is not now chitinous. It is highly probable that at least some chitin and protein was present in the living trilobite cuticle simply by analogy with extant arthropods.

The crystallography, mineralogy and high degree of calcification of the trilobites also compares favorably with that of many (but not all) ostracodes where the carapace too has a pronounced C-axis preferred orientation, is calcitic and is highly calcified (Sohn, 1958). The trilobite cuticle is not phosphatic. Although two species were found with distinct outer phosphatic layers showing evidence to indicate they could be primary, the distribution of the phosphate is completely separate from the carbonate and this is not typical for many extant calcareous-phosphatic arthropod cuticles. In spite of some evidence to support the primary nature of these outer phosphatic layers it is not certain and until this can be confirmed with other specimens the significance of this finding is not clear.

The trilobites studied range in age from Cambrian through Devonian and represent six orders. No clear pattern or correlation with either geologic age or with systematic position could be discerned from the data and it appears that most of the microstructural and compositional features in one species or another can be dated from the Cambrian, but the data are too limited to draw any firm conclusions in this respect.

Throughout this work we have emphasized the lack of correspondence between the microstructural and compositional details of the trilobite cuticle and that of the typical arthropod (insects and decapod Crustacea). At the same time, we have pointed out several similarities with the calcified ostracode carapace. It is our conclusion that no other group of arthropods living today compares in as many ways as favorably with the trilobites in this respect as do the calcified ostracodes. A phylogenetic relationship between these two groups of arthropods is not, on the basis of shell structure and composition, out of the realm of possibility.

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APPENDIX

Each specimen in this study has been assigned a USNM catalog number here listed under its name. A second number in parentheses is the older USNM number of the suite of specimens from which the individual was taken in those instances where such a number existed.

Specimen	*Locality*	*Age*
Paradoxides oelandicus 203467	Borgholm, Öland, Sweden	Middle Cambrian
Olenoides neolenus 203468	Antelope Springs, House Range, Utah	Middle Cambrian
Ellipsocephalus polytomus 203469 (23928)	Borgholm, Öland, Sweden	Middle Cambrian
Olenellus logani 203470 (137537)	Forteau Bay, Labrador, Canada	Middle Cambrian
Agnostus pisiformis 203471 (23905)	Tomta Närke, Sweden	Middle Cambrian
Cryptolithus tesselatus 203472 (72057)	Cold Brook, Poland, New York	Middle Ordovician
Isotelus gigas 203473-75	Grays Brook, Russia, New York	Middle Ordovician
Isotelus platymarginatus 203476	Isle la Motte, Vermont	Middle Ordovician
Tretaspis clarkei 203477	Whitehead, Mont Joli, Perce, Quebec	Late Ordovician
Bumastus subglobosus 203478 (72225)	Isle la Motte, Vermont	Middle Ordovician
Odontopleura trentonensis 203479	Grays Brook, Russia, New York	Middle Ordovician
Flexicalymene meeki 203480 (40926)	Waynesville, Ohio	Middle Ordovician
Proetus signatus 203481	Potok, Poland	Late Silurian
Diacalymene diademata 203482	Mielnik, Poland	Middle-Upper Silurian
Calymene cf. beyeri 203483	Radoszewo, Poland	Late Silurian
Acastopyge shergoldi 203484	Karwia, Poland	Late Silurian
Odontocephalus selenurus 203485 (79160)	Union Springs, New York	Early Devonian
Goldius palifer (Scutellum) 203486 (72519)	Koneprusy, Bohemia	Early Devonian

Specimen	*Locality*	*Age*
Phacops rana 203487-92	Buffalo, New York	Middle Devonian
Phacops logani 203493-94 (27849)	Big Sandy River, Benton County, Tennessee	Early Devonian
Unidentified phacopid 203495	Decatursville, Tennessee	Silurian
Cancer sp.	Virginia Beach, Virginia	Recent
Cancer sp.	Chuckatuck, Virginia	Late Miocene

EXPLANATIONS OF PLATES

Plate 1

Fig. 1. Isotelus gigas (203473) viewed in cross-polarized light to show a typical "patchy" extinction of the calcite cuticle. Note also the outer prismatic layer. Cross section of a portion of a cephalon. X325.

Fig. 2. Isotelus gigas (203475) cross section of a pleural fragment, also with patchy extinction. The step-like surfaces of the prismatic layer are cross sections of terrace lines (arrow). X175, cross-polarized light.

Fig. 3. Flexicalymene meeki (203480) pygidium viewed in cross-polarized light to show the zones of extinction. This is an example of the more homogeneous extinction of the microcrystalline calcite which is crudely layered. These are not true laminations. The prismatic layer has a somewhat different extinction pattern and larger crystals. X260.

Fig. 4. The same section as in Fig. 3 but viewed with ordinary light. The prismatic layer (PR) is visible as well as portions of some pyrite-filled pores (arrows). X260.

Fig. 5. Flexicalymene meeki (203480) a thoracic segment showing the extinction zones and the outer prismatic layer (left side of cuticle). X140.

Fig. 6. Phacops rana showing patchy and homogeneous extinction. X140.

Plate 2

Figs. 1–4. Electron micrographs of replicas of the surface of three trilobites and an ostracode showing the similar plate-like, sutured appearance of the surfaces. The sutured plates of the ostracode are smaller.

Fig. 1. Agnostus pisiformis (203471) X8,900 (unetched). Fig. 2. *Isotelus gigas* (203471) X4,400. Fig. 3. Unidentified marine ostracode X28,000 (unetched). Fig.4. *Phacops rana* (203489) X4,900. Figs. 5 & 6. Electron micrographs of carbon-platinum replicas of cross sections of different specimens of *Phacops rana* showing the typical arrangement of crystals in the cuticle. There is a rough shingle-like orientation parallel to the cuticle surface. X5,300.

Plate 3

Fig. 1. Electron probe scanning profile across a section of *Calymene* sp. (203482) showing the distribution of P (dashed) and Ca (solid).

Fig. 2. A similar electron probe scanning profile of *Isotelus gigas* (203473) for comparison.

Fig. 3. A back-scattered electron photograph of the same cross section of *Calymene* as in Fig. 1 showing the sharp distribution of phosphorus at the outer edge (C – cuticle, M – plastic embedding medium).

Fig. 4. Photomicrograph of a section of *Calymene* sp. (203482) showing the apatite layer on the exterior which corresponds to the region of high phosphorus concentration in Figs. 1 and 3. X240.

Fig. 5. Cross section of *Isotelus gigas* (203473) such as was scanned in Fig. 2. Although the section is laminated and has a pigmented prismatic outer layer (PR), no region contains phosphorus. The wide surface pits are characteristic of this species.

Plate 4

Figs. 1 and 2. Electron probe scanning profiles showing the distribution of P (Kα) and Ca (Kα) in a cross section of fossil (Fig. 1) and Recent crabs (Fig. 2). The graph of Fig. 1 begins at approximately the middle of the cuticle and extends to the exterior while that of Fig. 2 scans the entire cuticle thickness. In both cases the amount of P tends to increase in the outer third of the cuticle. The dip in Ca in Fig. 2 represents a less calcified area rich in organic material.

Fig. 3–8. Powder X-ray diffraction patterns. Fig. 3. Sample from the upper surface of a Recent crab (same specimen used in Fig. 2), calcite. Fig. 4. Calcite standard. Fig. 5. Upper surface of a fossil crab; mixture of calcite and apatite. Fig. 6. Apatite standard. Figs. 7 and 8. Samples of the pink outer layer of *Ellipsocephalus polytomus* (203469) and *Calymene* (203482) respectively. Both are apatite.

Plate 5

Fig. 1. A fragment of a schizochroal eye from *Phacops rana.*

Fig. 2. The same fragment as in Fig. 1 after complete decalcification in EDTA showing the residual organic material and some pyrite.

Fig. 3. Electron micrograph of organic material such as in Fig. 2, which was air-dried and shadowed with platinum-carbon. X32,000.

*Fig. 4.*Electron micrograph of phacopid organic matrix which has been embedded and sectioned showing the delicate meshwork. X9,400.

Plate 6

Fig. 1. A section of *Phacops rana* (203489) cuticle lightly etched and coated with platinum-carbon, viewed in reflected light. Note the lamina which have etched differentially. X260.

Fig. 2. Electron micrograph of the replica in Fig. 1 showing the slight furrowing (arrows) indicating the direction of the laminae. X6,000.

Figs. 3–6. The various appearance of laminae within the same specimen and in different specimens from the same locality. Fig. 3. *Phacops rana* (203491). X120. Fig. 4. *Phacops rana* (203489). X260. Fig. 5. *Phacops rana* (203489). X230. Fig. 6. *Phacops rana* (203489). X100.

Plate 7

Figs. 1 and 2. A section of *Isotelus gigas* (203472) to show the effect of the pseudopleochroic material when viewed at right angles in plane polarized light. The vibration direction is east-west. X185.

Figs. 3 and 4. A calcite lens of a phacopid eye which also contains pseudopleochroic material. There is however no pseudopleochroism in any other region of this specimen (unidentified, 203495). X185.

Plate 8

Fig. 1. Section of *Odontocephalus selenurus* (203485) showing two of the many very large pore canals present in the pygidium. X185.

Fig. 2. Another area in the same section of *Odontocephalus* viewed in cross polarized light to bring out the narrow pores also present in the cuticle (an oblique view of a large pore can be seen at the left). X260.

Fig. 3. Flexicalymene meeki (203480) showing some of the many pore canals discontinuously filled with pyrite. X145.

Fig. 4. Calymene sp. (203482), one of the large pores present in the cuticle. Compare with the small pore from the same specimen, Plate 3, Fig. 4 (arrow). X200.

Fig. 5. Photomicrograph of a possibly twisted pore from a phacopid cuticle (203495). X720.

Fig. 6. Electron micrograph of a replica of a pore from the same section as in Fig. 5, indicating that the pore is not helicoidal. X3,900.

Plate 9

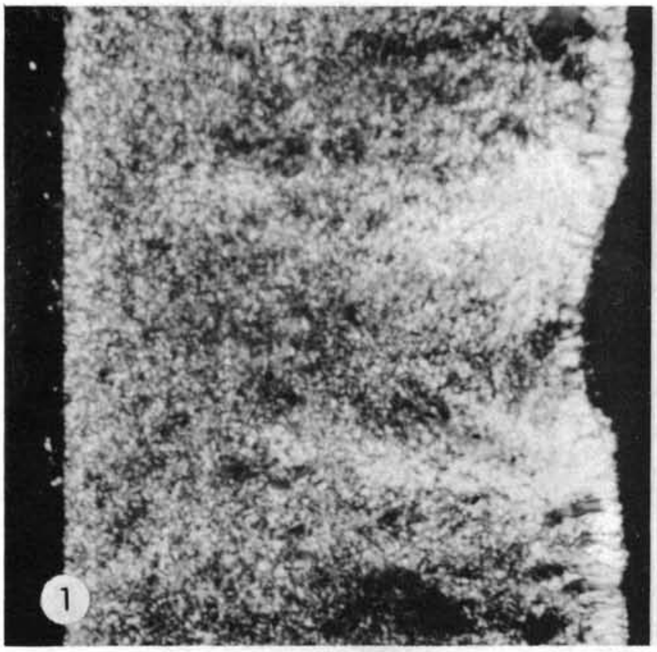
Fig. 1. A large twisted pore in the cuticle of a fossil crab. X1,000.

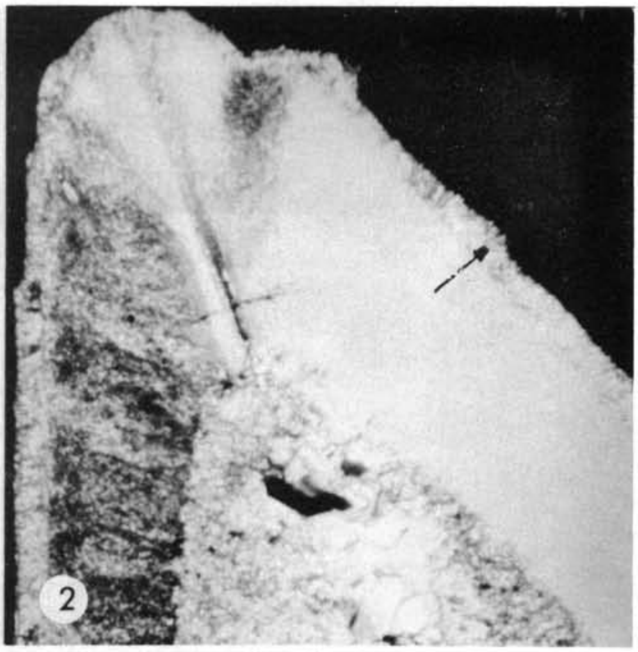
Fig. 2. An oblique section of fossil crab cuticle showing the parabolic pattern indicative of twisted layers. X570.

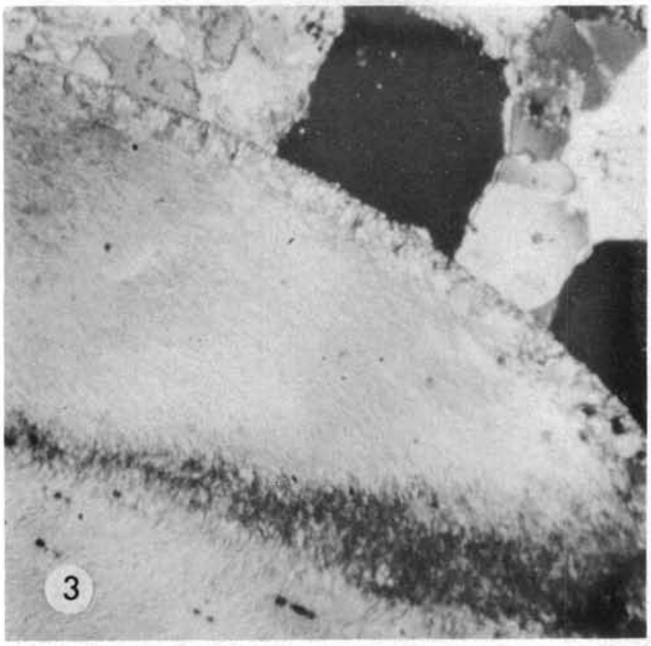
Fig. 3. A tangential section in polarized light of tubercles on the cephalon of *Phacops rana* indicating a radial C-axis orientation of the calcite crystals in each. X140.

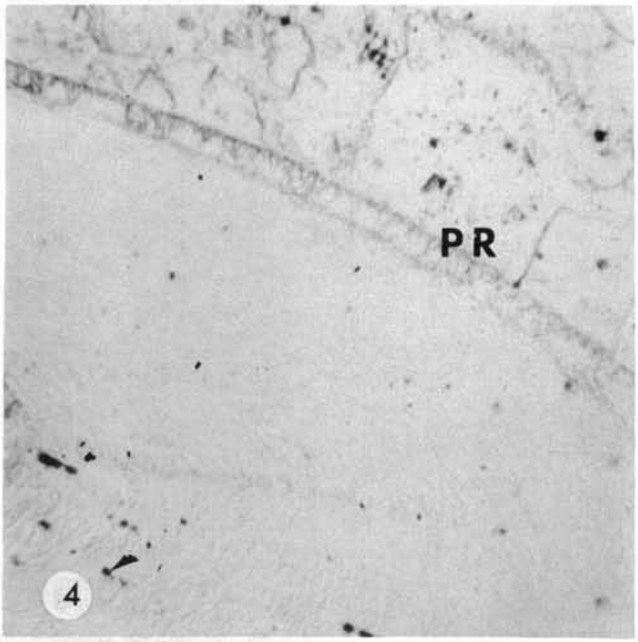
Fig. 4. A tangential section of a tubercle of a fossil crab showing the spiral pattern characteristic of this type of cuticle architecture. X350.

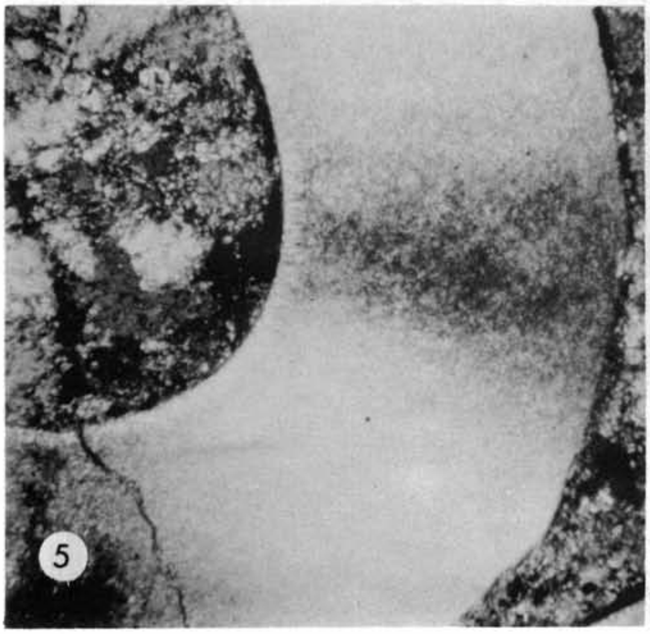
Fig. 5. The same section as in Fig. 4 viewed with polarized light. Contrast this to the trilobite tubercle pattern seen in Fig. 3. X350.











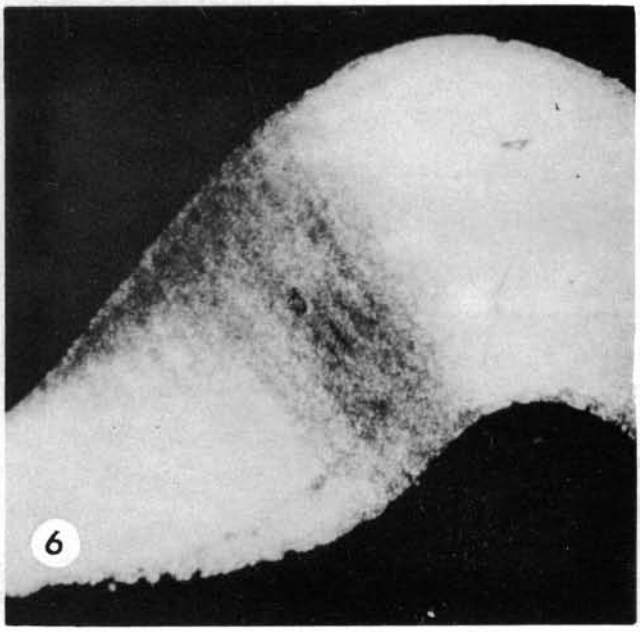
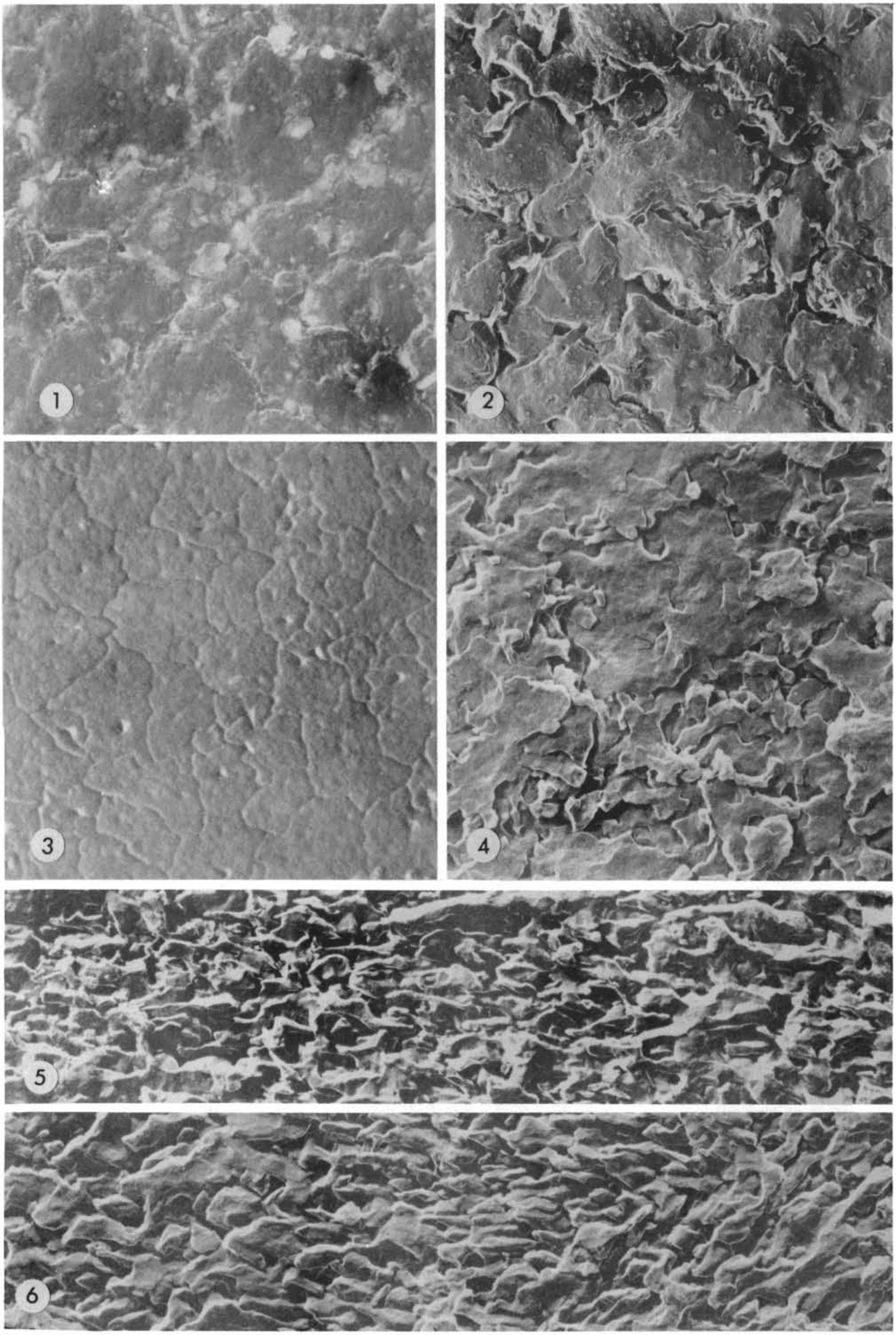


Plate 1.



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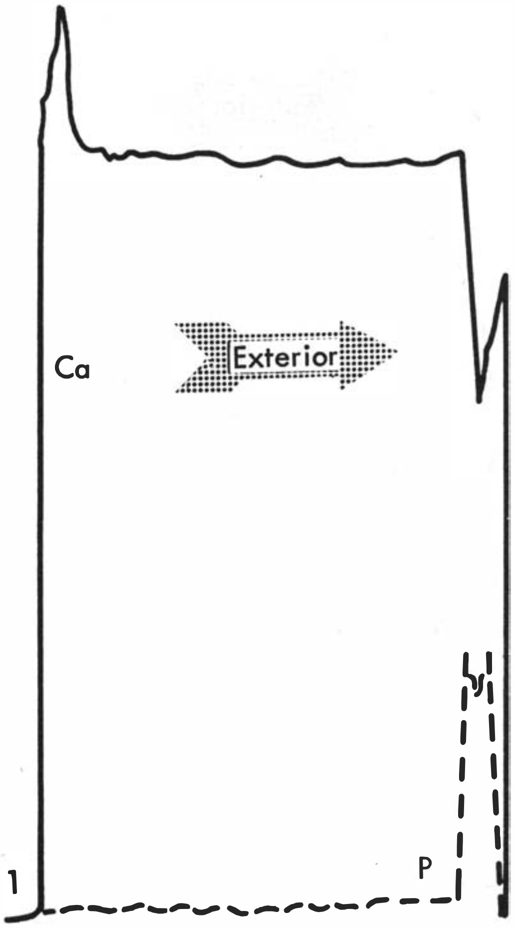

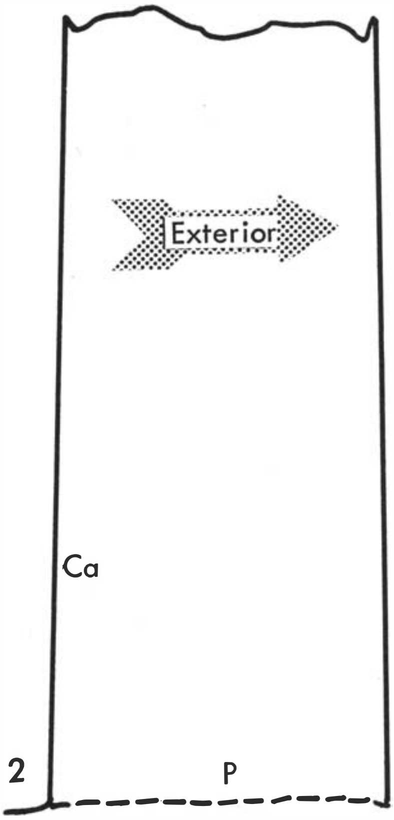

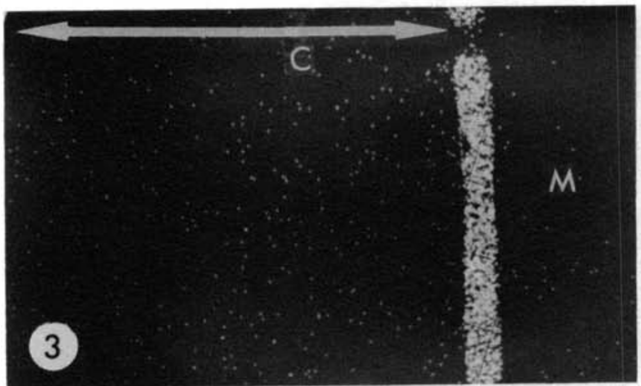

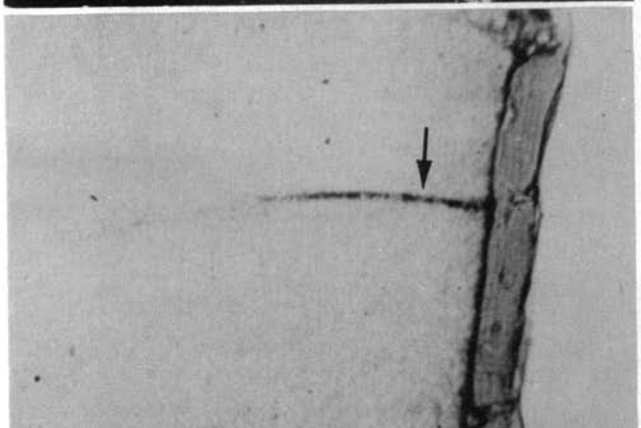

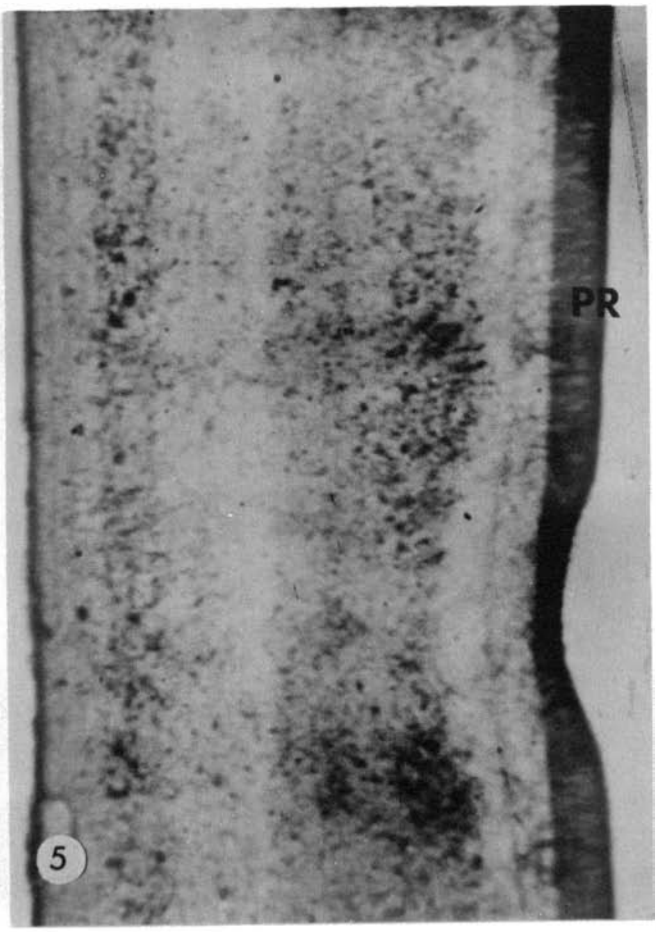

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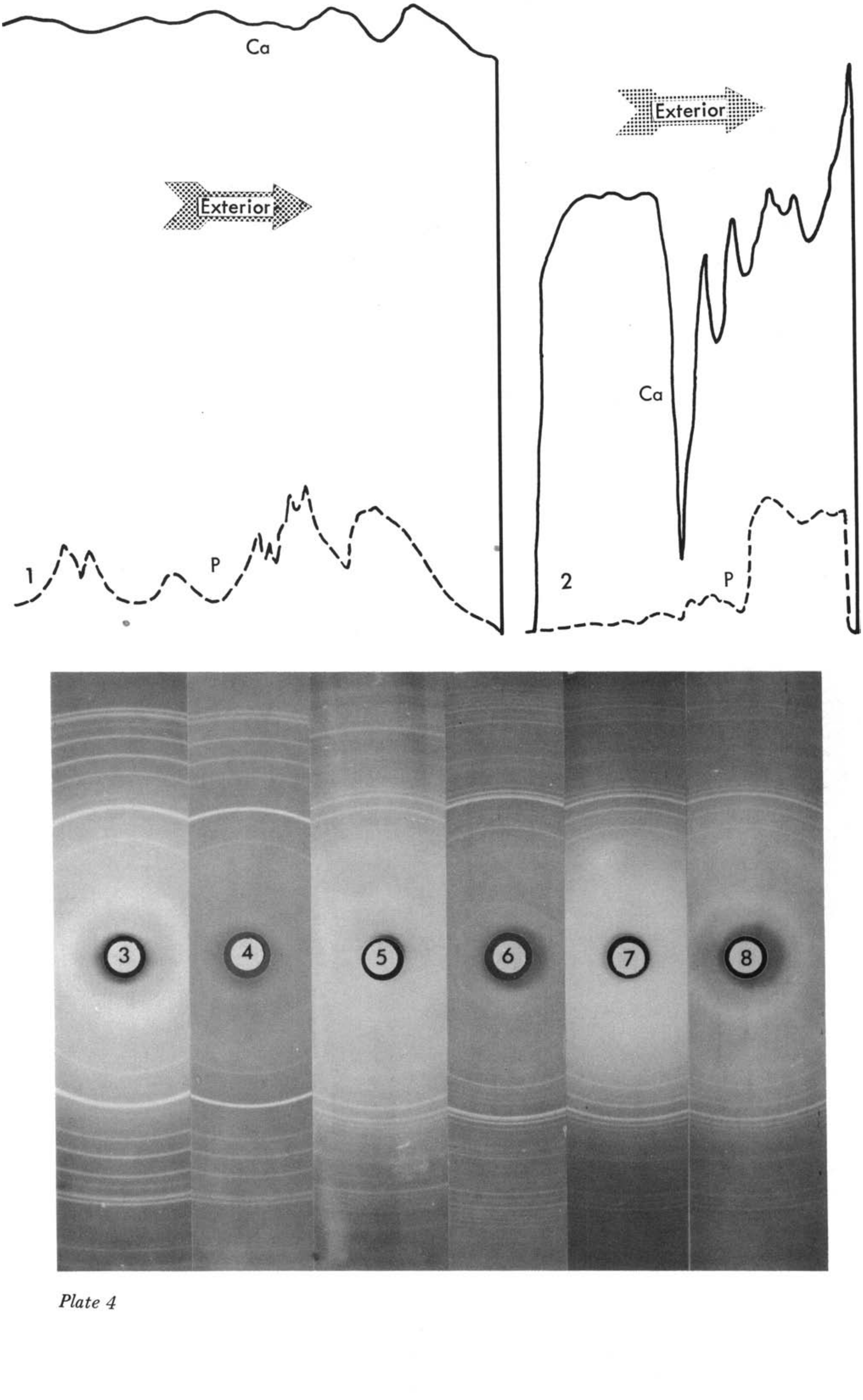

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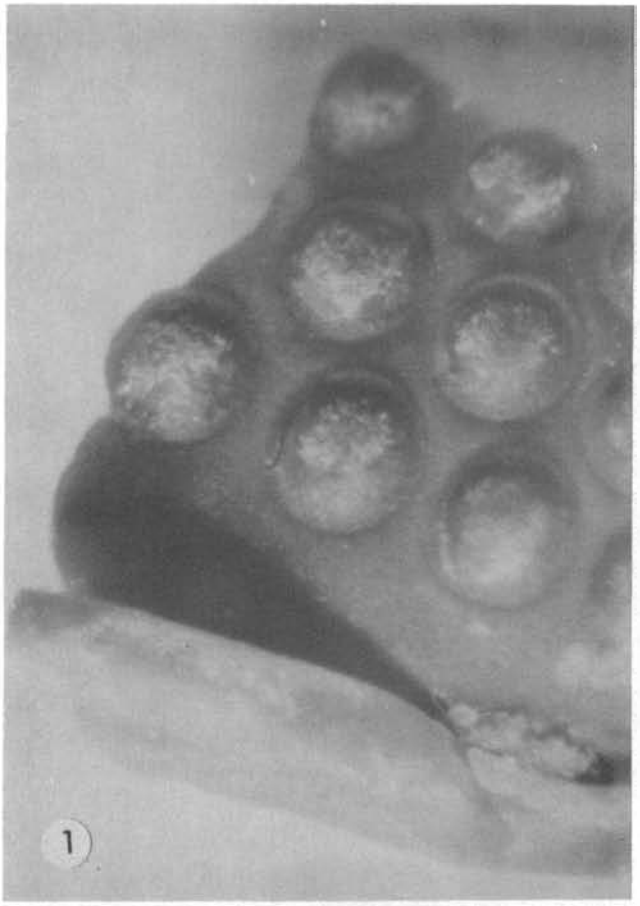
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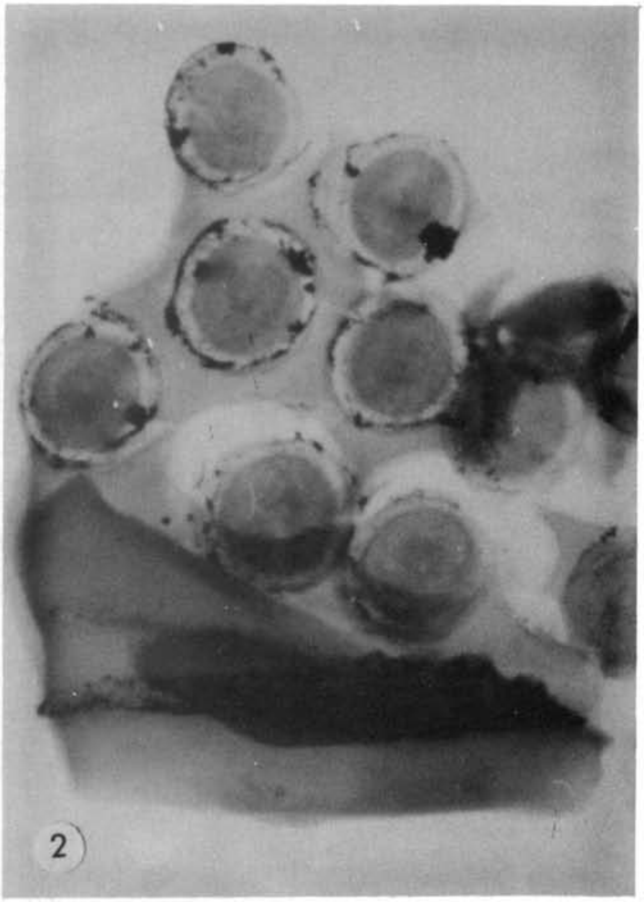
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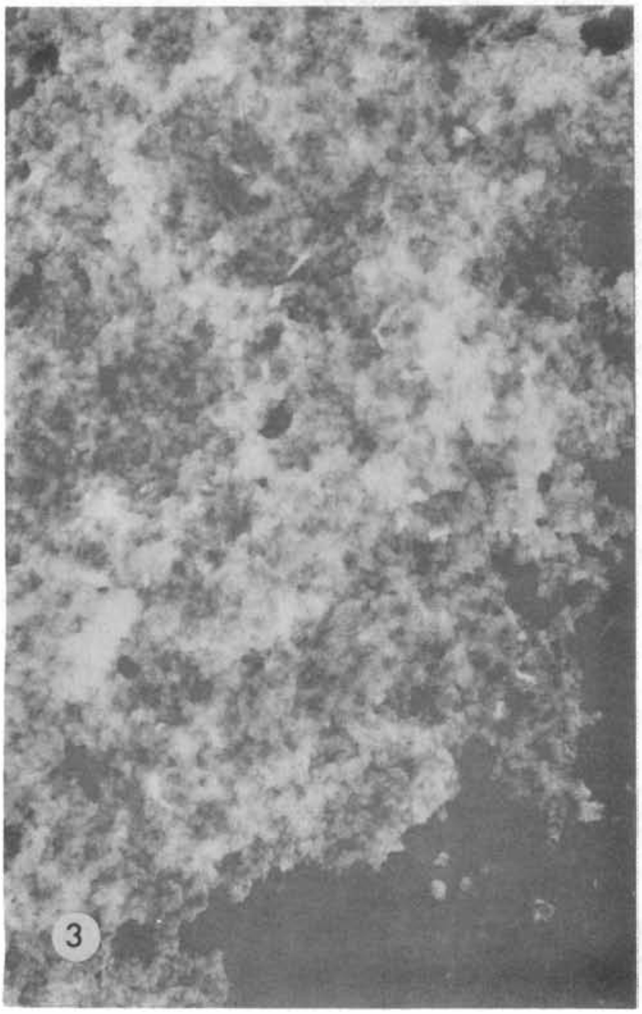
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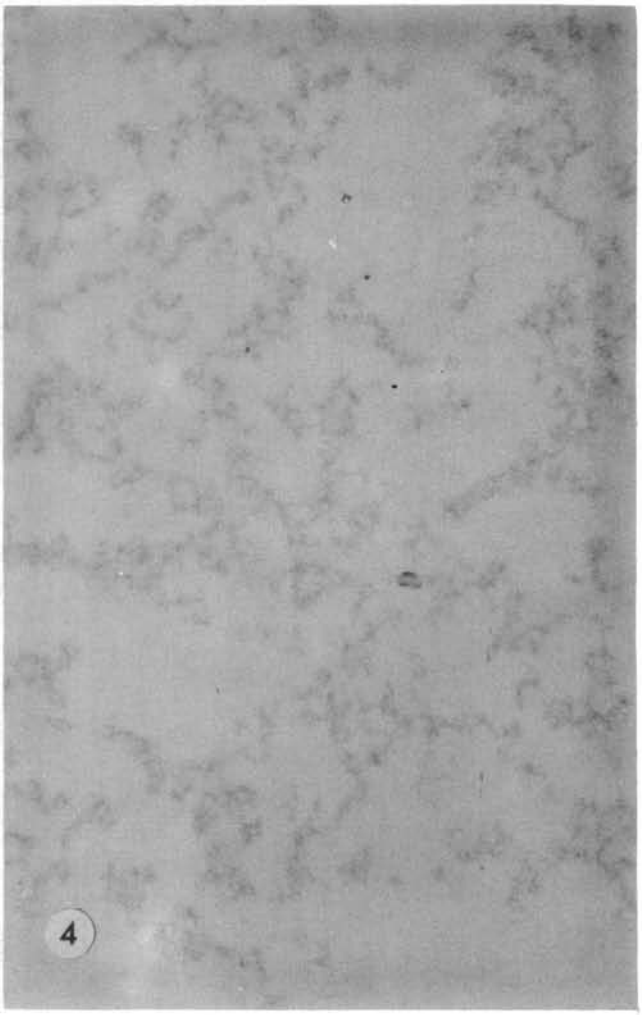
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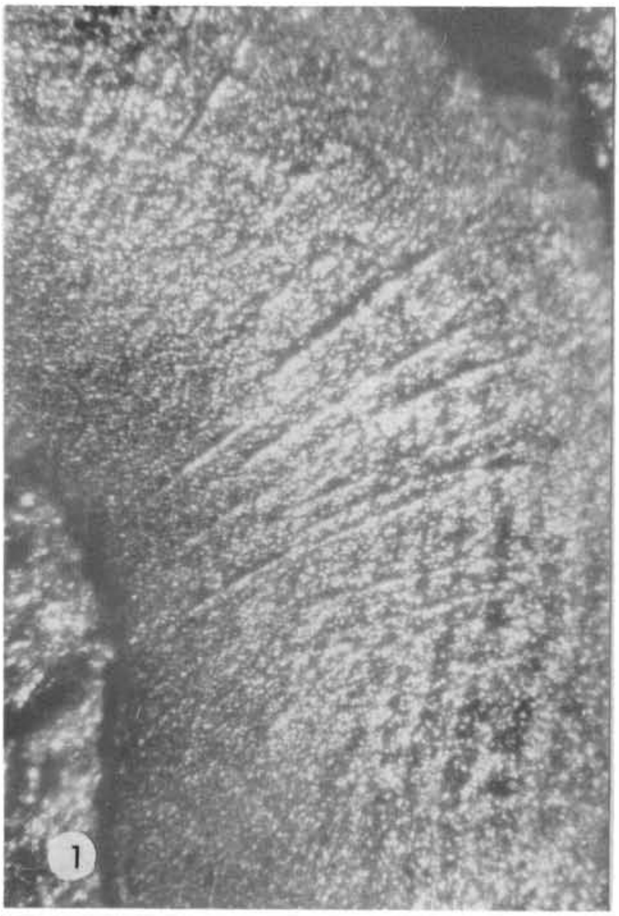
Plate 5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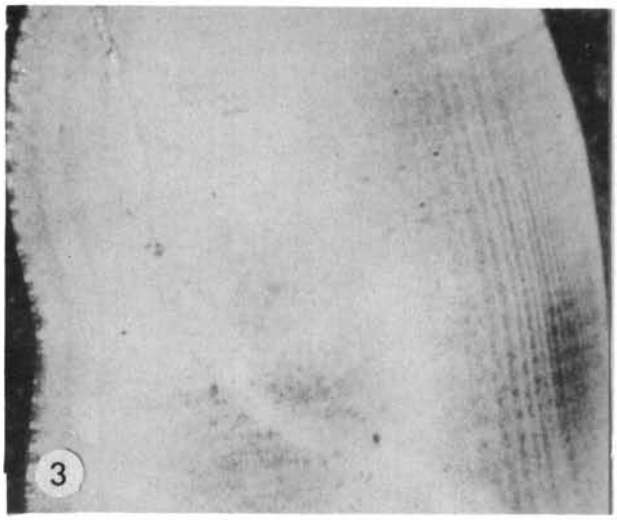
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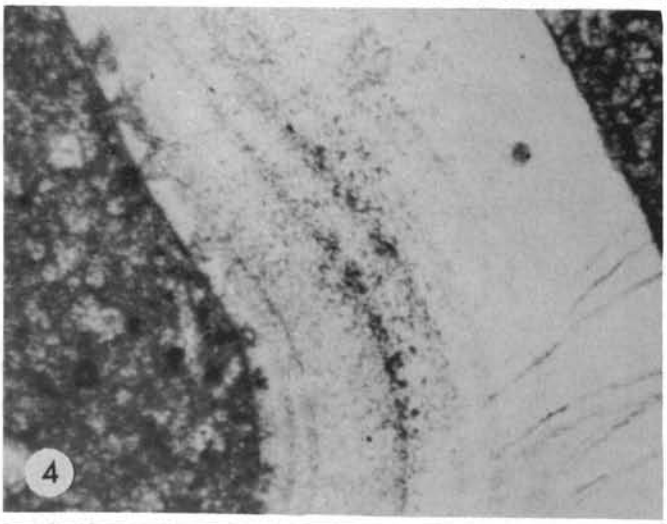
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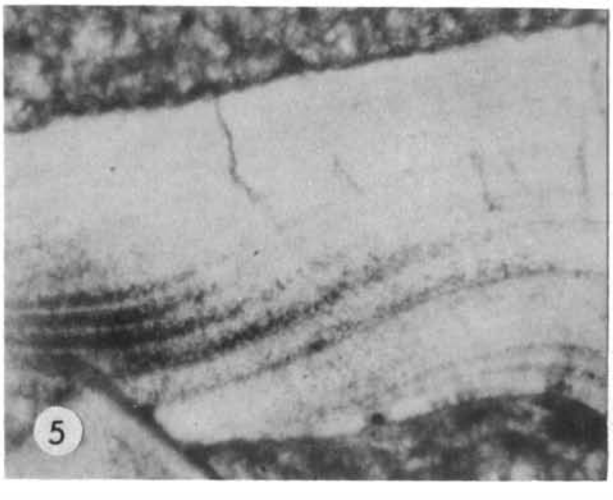
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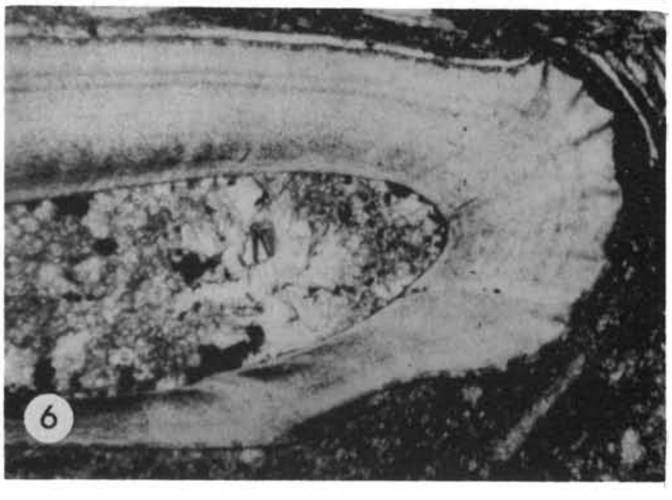
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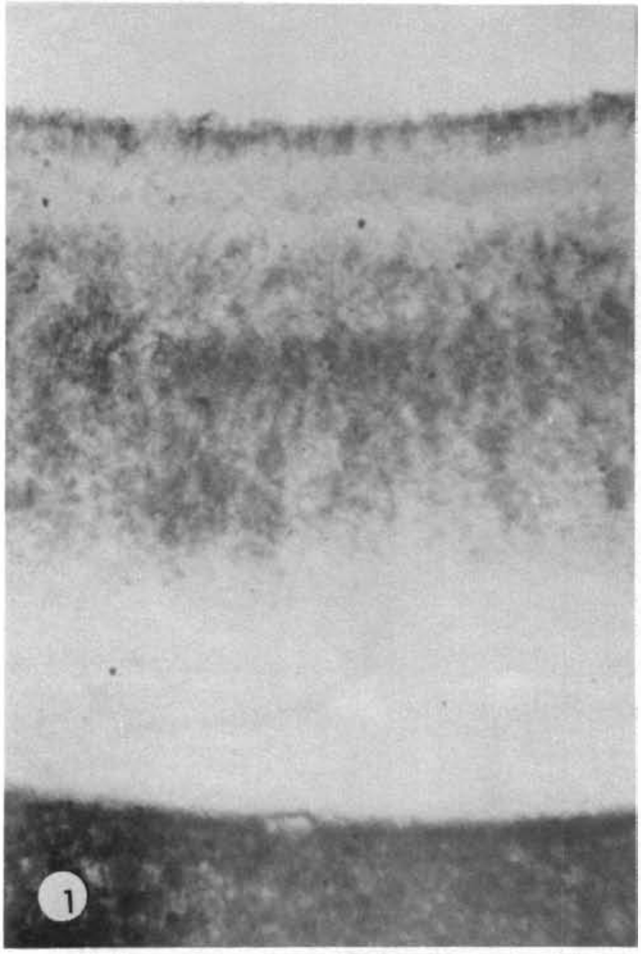
Plate 6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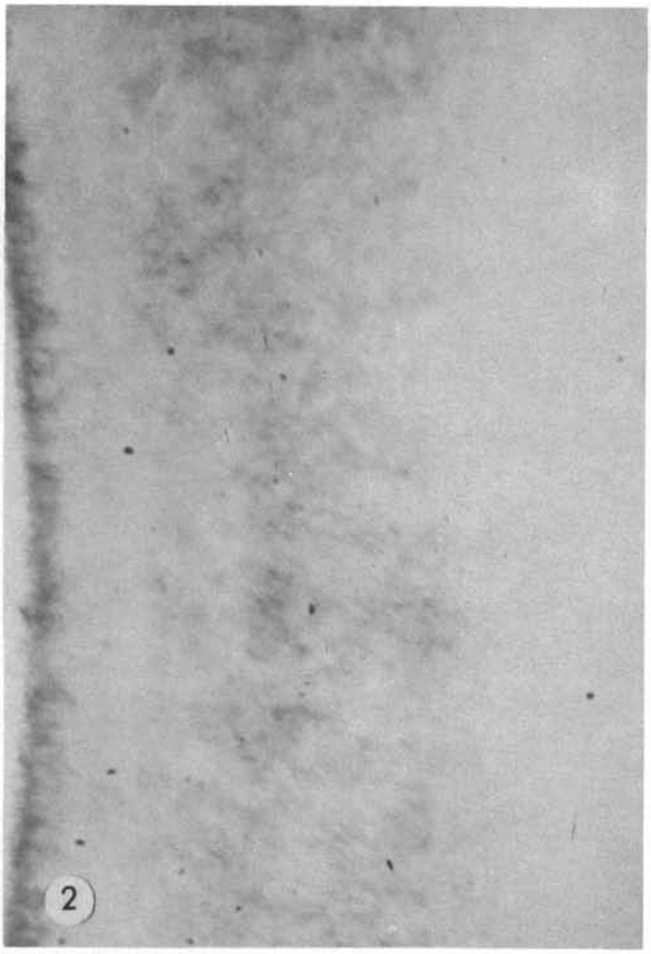
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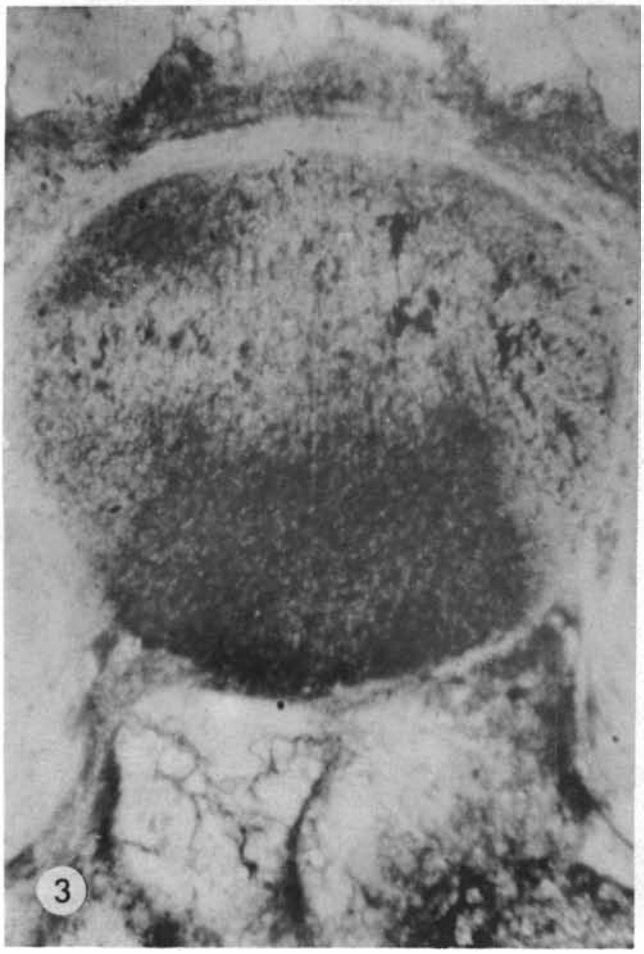
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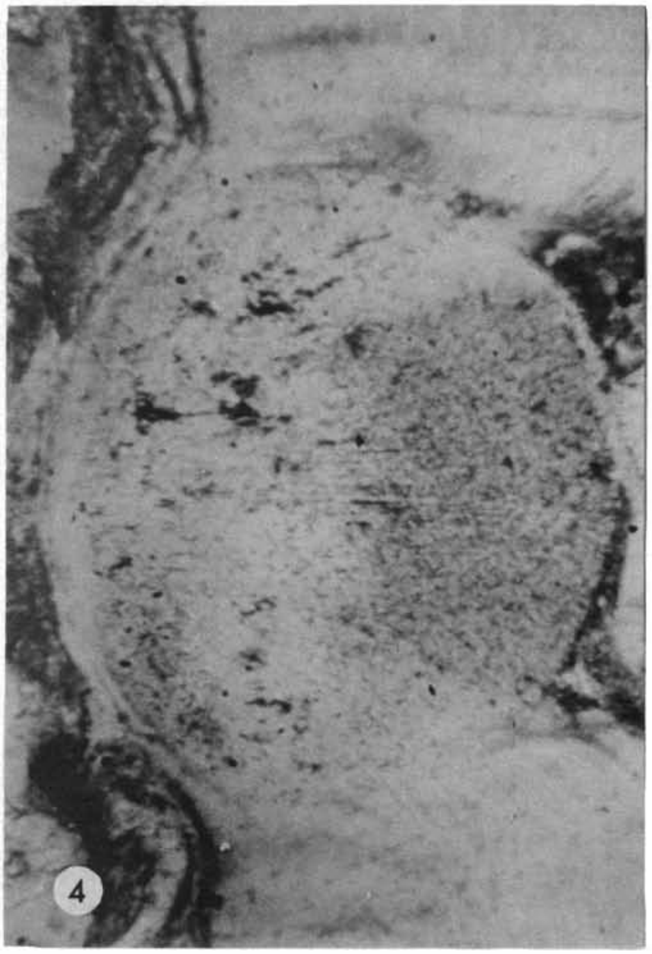
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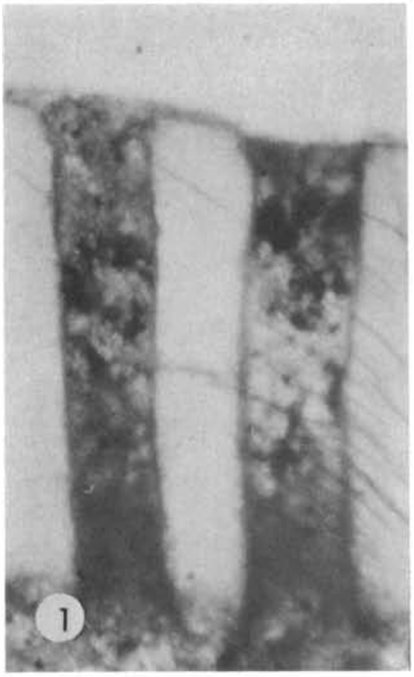
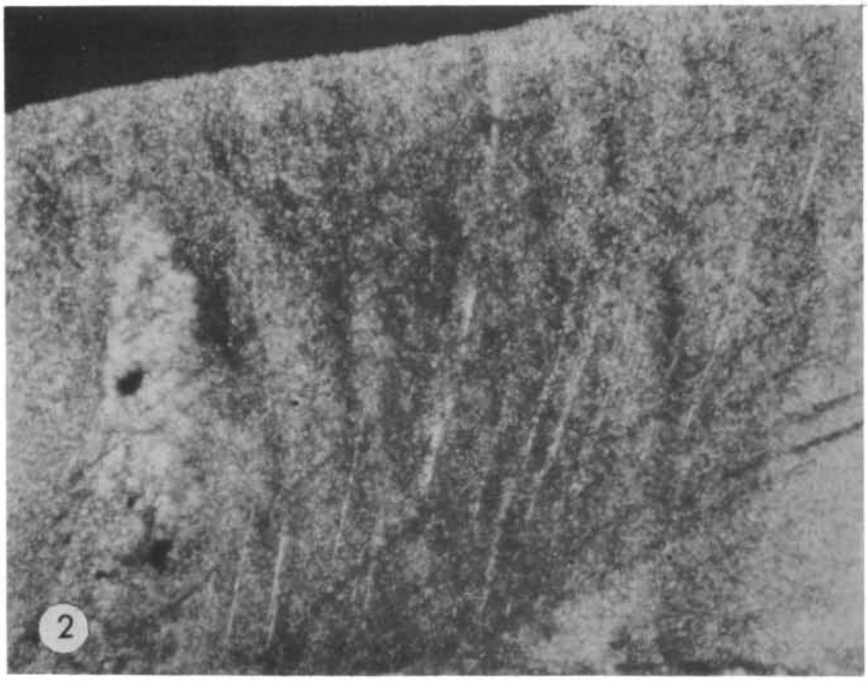
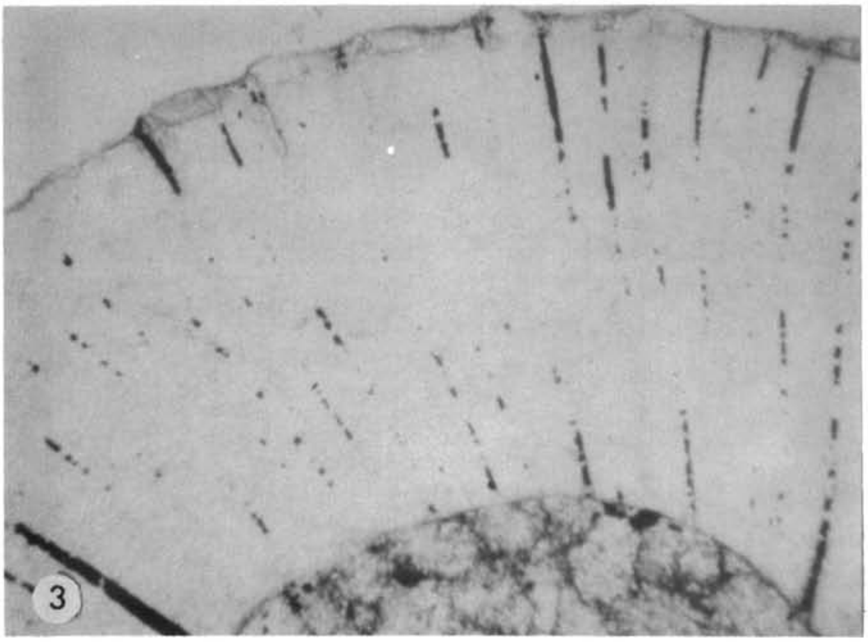
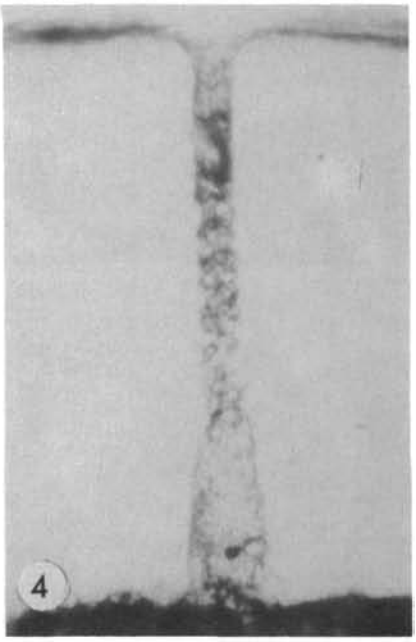
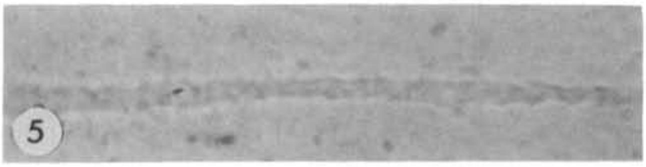
Plate 7











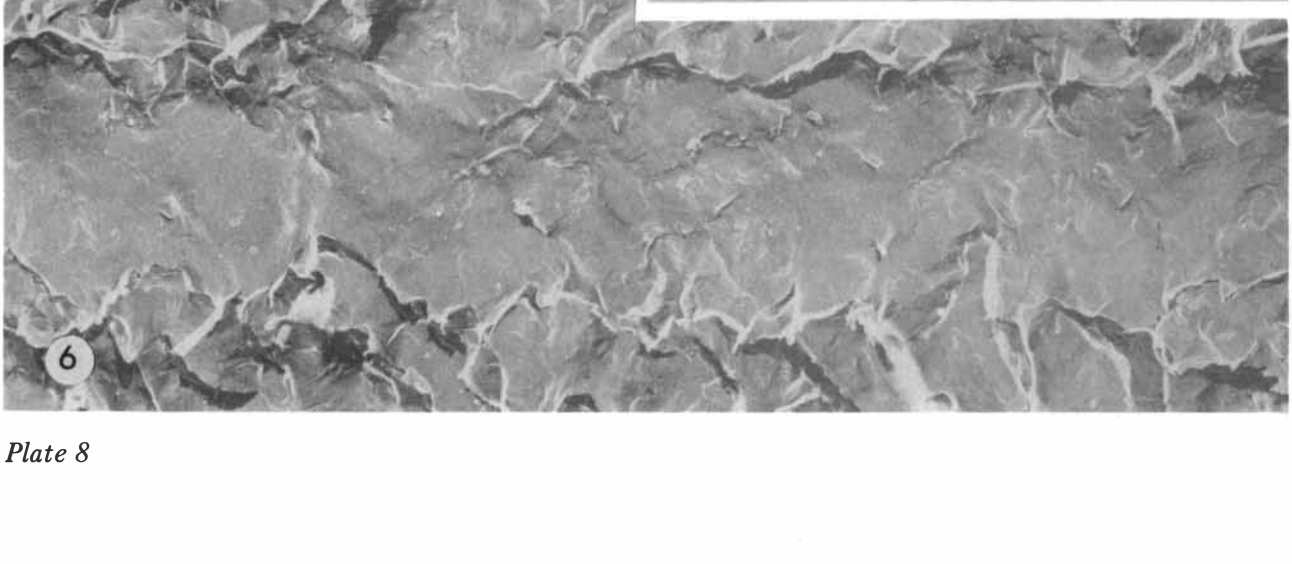
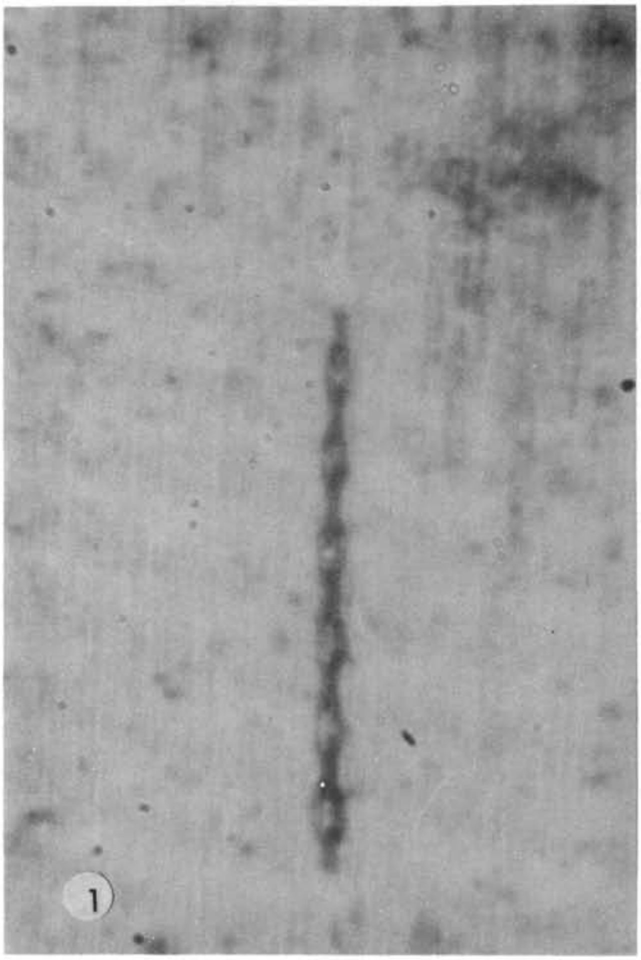
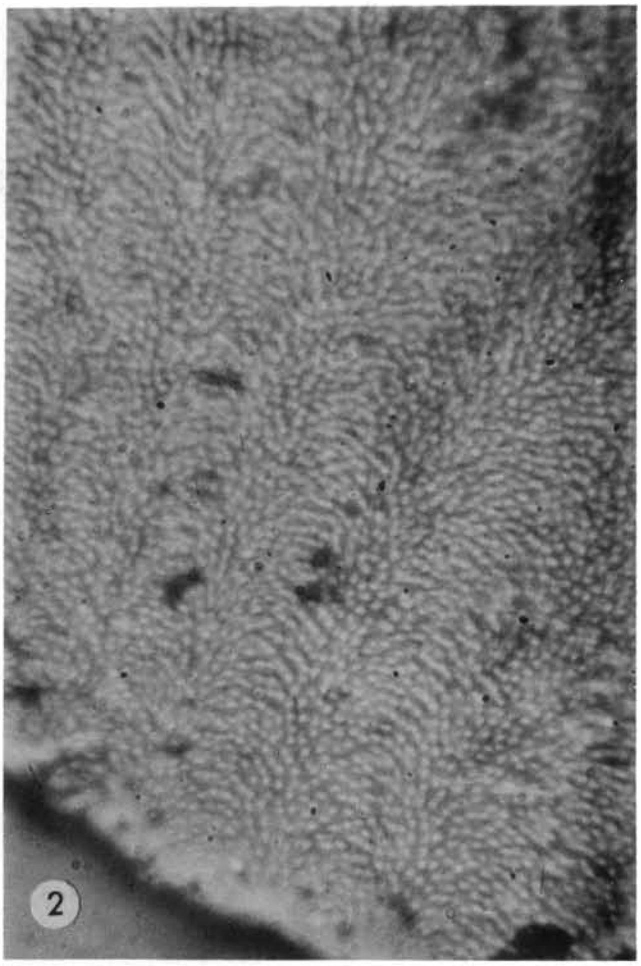
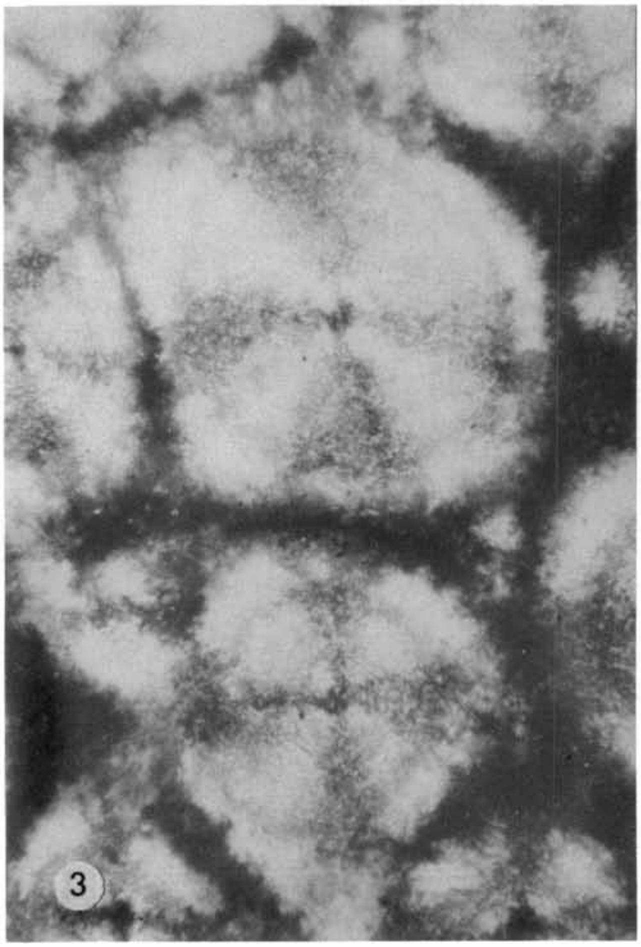
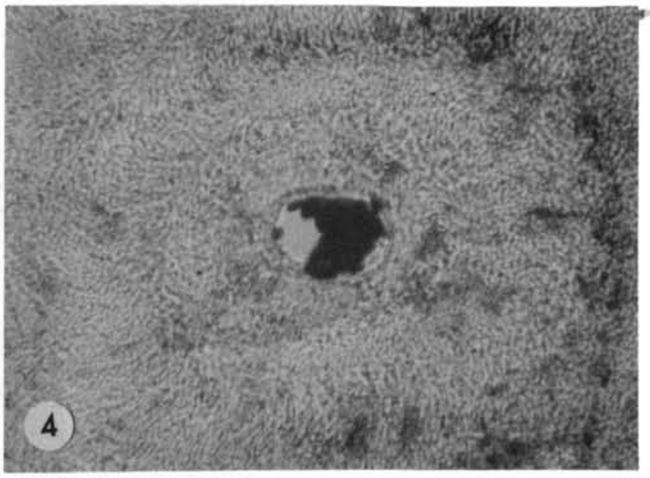


Plate 8









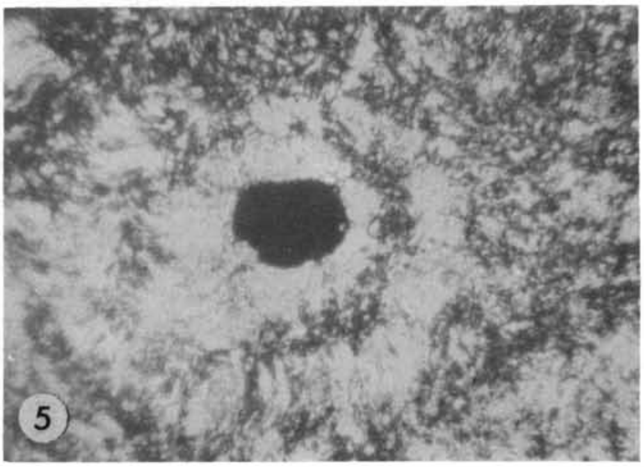


Plate 9

Secondary microstructures in trilobite cuticles

JOHN E. DALINGWATER

Dalingwater, J.E. 1975 07 15: Secondary microstructures in trilobite cuticles. *Fossils and Strata.* No. 4. pp. 151–154. Pl. 1. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

Descriptions are given of a variety of secondary microstructures in trilobite cuticles, possibly due to the action of boring organisms, which were encountered whilst studying primary microstructure. The majority of these borings are considered to result from fungal activity.

J.E. Dalingwater, Department of Zoology, The University, Manchester M13 9PL, England, 15th August, 1973

During a study of primary microstructure of the trilobite cuticle (Dalingwater 1973), various secondary structures were encountered. Only those structures which can possibly be referred to the action of epizoic, saprophytic or parastic organisms are considered here, as it is useful to be able to distinguish these from primary microstructures. Størmer (1931), in a paper discussing boring organisms in trilobite 'shells', reviewed the early literature, while Rolfe (1962) summarised subsequent work on borings in fossil arthropod cuticles. Other important and relevant contributions are Hessland's (1949) study of the action of 'penetrative and enveloping algae', Størmer's (1963) detailed account of the micro-organisms associated with the cuticle of a fossil scorpion, Bromley's (1970) extensive general review of borings as trace fossils, and Taylor's (1971) description of thallophyte borings in decapod and brachiopod shells from the Lower Cretaceous of Alexander Island.

This topic seems complex, as do most considerations of traces of animal or plant activities, rather than of the organisms themselves, but a few general considerations can briefly be outlined:

(1) Borings in cuticles may be the result of:

(a) penetration during the life of the 'host' commencing from either the inner or outer margin of the cuticle.

(b) penetration immediately after ecdysis or the death of the animal, which may also commence from either the inner or outer margin.

(c) penetration some time after ecdysis or the death of the 'host', in which case it may proceed preferentially from one margin, because of chemical or physical differences between inner and outer margins (or, for example, if the cuticle was partly buried in sediment).

(2) Different species, even organisms belonging to different phyla, may produce similar borings under similar conditions. Alternatively, the same species may produce different types of borings in different conditions (at different stages in its life cycle, in different types of shell, or in different regions of the same shell). It is therefore difficult to apply Linnaean nomenclature to borings.

(3) Organisms recorded as responsible for borings in fossil shells are algae, fungi, bryozoans, cirripedes, sponges, and worms. Of these, only fungi have been recorded as decomposing chitin (Richards 1951). Other chitinoclastic groups are bacteria (Campbell and Williams 1951) and actinomycetes (Waksman 1959), most decomposition of chitin in nature being attributed to the former group.

Only larger borings which penetrate the cuticle are described here. The cuticle/matrix boundary in many slices is indistinct, possibly the result of activity of endolithic algae – this aspect will be discussed in a later paper. It is possible that the outermost layer isolated on decalcification of the cuticle of *Asaphus raniceps* Dalman with E.D.T.A. (Dalingwater 1973) is not primary but the result of endolithic algal activity.

I am most grateful to Dr. B. Taylor, Dr. G. Taylor and Dr. J. Miller for help and advice during the course of the work, and to Mr. B. Atherton for photographic services. Part of the study was carried out during the tenure of an S.R.C. Studentship.

MATERIAL AND METHODS

Thin-sections prepared for a study of primary microstructure were re-examined for traces of the activity of boring organisms. The majority of these thin-sections are of the lower *'Raniceps'* limestone, Haget, Öland, Sweden, and most of the borings are in trilobite cuticles from that locality. In the descriptions that follow the material is from the lower *'Raniceps'* limestone unless otherwise indicated. Details of borings can best be seen in fairly thick slices (30 μ or more thick) but these are difficult to photograph satisfactorily, so some slices were re-ground. Preliminary studies of etched blocks and etched slices with the Scanning Electron Microscope have not yet yielded useful results. All preparations are stored in the Department of Zoology, University of Manchester, England.

DESCRIPTIONS OF THE BORINGS

SLICE Öl. 0.8.1. – Includes a tangential perpendicular section (Tan.P.S.) of a pygidium, possibly of an illaenid. The inner margin of the cuticle is almost completely filled with a dark mass of pyrite impregnated tubes which penetrate into and occasionally almost through the cuticle, including fine tubes 1–3 μ in diameter filled with pyrite, wider tubes 6–8 μ in diameter less heavily impregnated with pyrite, and larger club-shaped structures (Pl. 1:1). Branching of tubes is rare. A similar range of structures is seen on the inner margin of a transverse perpendicular section (T.P.S.) of a thoracic segment possibly belonging to *Asaphus raniceps* Dalman *(Slice Öl. A. 11b.2,* Pl. 1:2).

SLICE Öl. 0.36.2. – Longitudinal perpendicular section (L.P.S.) of the thoracic axis of *A. raniceps.* Fine tubes (1–2 μ in diameter) are concentrated on the outer edge of the cuticle, while wider tubes (8–10 μ in diameter), which sometimes branch dichotomously, penetrate into the cuticle (Pl. 1:3). Both types of tube are accentuated by pyrite impregnation. A somewhat similar series of tubes penetrate the cuticle of an unidentified species (*Slice Öl. 0.110.1*).

SLICE Öl. 0.45.3. – Tan. P.S. across the edge of the cephalon of *Ampyx nasutus* Dalman. Twisted ribbon-like structures 2–4 μ wide extend along the cuticle near its outer edge, but sometimes extend deep into the cuticle (Pl. 1:4). It is difficult to perceive any detail in the ribbons, which have a distinct orange colouration. They seem to be related to the endolithic algal borings at the cuticle/matrix boundary. Similar orange ribbon-like sturctures are just visible in the outer region of the cuticle in an L.P.S. of a pygidium, probably of *A. raniceps* *(Slice Öl. 0.6.1)*.

SLICE Öl. 0.102.1. – Tan.P.S. of a fragment of cuticle, possibly belonging to *A. raniceps.* The cuticle contains masses of pyrite impregnated thread-like structures, some forming circular masses, others elongate skeins (Pl. 1:5). Individual threads, where distinguishable, are about 1 μ wide, and the majority are irregularly thickened by small nodose swellings. Somewhat similar structures are present in the outer area of the cephalic doublure in an L.P.S. of *A. raniceps* (*Slice Öl.A. 18.2*).

SLICE Öl. A. 27.1. – L.P.S. through the pleural region of a thorax, probably of *A. raniceps.* Straight, unbranched, pyrite impregnated tubes 2–4 μ in diameter penetrate the cuticle and its surrounding matrix, particularly shell fragments (Pl. 1:6). Apparent concentration of tubes within shell particles may be because they are readily visibly in these areas, their pyrite impregnation affording good contrast with calcite.

SLICE Öl. B.e. 1b.2. – Tan.P.S. of the pygidium of *Boedaspis ensifer* Whittington and Bohlin, Expansus Limestone, Haget, Öland. In all sections of this cuticle, fine tubes 2–4 μ in diameter extend along the inner margin of the cuticle and pass across the cuticle at various angles. The appearance of these tubes is fragmentary, possibly due to patchy impregnation with pyrite (Pl. 1:7).

SLICE Dy. E. 7.1. – L.P.S. through the posterior edge of the cranidium of *Encrinurus punctatus* Wahlenberg, Wenlockian, Dudley, Worcs., England. Both edges of the cuticle are heavily impregnated with pyrite, but the central area is clear. In this area primary fine and wider perpendicular canals are accentuated by pyrite and show Rolfe's (1962) 'Christmas-tree effect', possibly due to growth of pyrite along laminae. In the posterior part of the section tubes, 1–4 μ in diameter, similar in appearance to the fine perpendicular canals, are disposed at various angles to the perpendicular (Pl. 1:8); these are considered secondary. Some tubes branch, although much apparent branching may be due to individual tubes crossing.

DISCUSSION

Most of the structures described above can probably be attributed to the action of some type of boring organism. Their occurrence is 'casual' Størmer (1931) and for this reason it is difficult to make a planned study in isolation from, for example, a study of primary microstructure.

Most boring systems occur in only one cuticle in a block, indicating that incorporation of the cuticle within the sediment probably took place after transport from a localised environment where the action of boring organisms was prevalent. Only one example (*Slice Öl. A. 27.1)* is described in which post-lithification penetration of a cuticle has certainly occurred.

Insufficient examples are described to make firm conclusions as to preference of establishment on the inner or outer edges of the cuticle. There would seem to be physical differences between the edges and centre of cuticles and, if the trilobite cuticle resembled that of other arthropods, physical and chemical differences between inner and outer edges of exuviae or complete cuticles.

Again, insufficient material is described to make possible a detailed classification of different types. Each boring system described has unique features, and to complicate matters further, might well be the result of the activities of a number of different types of organism. However, certain similarities between types have already been noted in the descriptions and the following groupings are suggested:

(1) Structures forming a mat on both edges of the cuticle and penetrating inwards from both sides (*Slice Dy. E. 7.1*).

(2) Structure forming a mass on one edge of the cuticle with various structures penetrating inwards (*Slices Öl. O. 8.1* and *Öl. A. 11b.2)*.

(3) More or less straight tubes, which rarely branch, penetrating the cuticle (*Slices Öl. O. 36.2* and *Öl. O. 110.1*), or both cuticle and matrix (*Slice Öl. A. 27.1*).

(4) Irregular ribbon-like material forming skeins which generally extend along the cuticle (*Slices Öl. O. 45.3* and *Öl. O. 6.1*).

(5) Irregular thread-like masses, forming aggregations towards the centre of the cuticle (*Slices Öl. A. 102.1* and *Öl. O. 18.2*).

It is extremely difficult to assign responsibility for the borings to particular groups. None resemble the borings described by Størmer (1931) from trilobite cuticles, but those described from *Slice Dy. E. 7.1* show a strong resemblance to those figured by Hessland (1949). For the reasons outlined by Taylor (1971) discussion of responsibility for the described borings can be limited to the Algae, Fungi and Actinomycetes. Dr. G. Taylor (Botany Department, Manchester University, pers. comm.) considered that the borings are too large to be referable to the Actinomycetes. Bromley (1965) outlined various criteria to distinguish algal and fungal borings, indicating that no one of his criteria can be regarded as diagnostic, yet a group of features taken together can add weight to an interpretation. Fungal borings are generally finer than those of algae (1–2 μ as opposed to 6–15 μ); their diameter is more or less constant; false ramification is characteristic of algae; angle of branching is more constant in fungi; and finally, the articles in fungi tend to be more or less straight or gently curved, whilst those of algae are sometimes very irregular. On these criteria borings in Slices *Öl. O. 8.1, Öl. A. 11b.2, Öl. O. 36.2, Öl. O. 110.1, Öl. O. 27.1,* and *Öl. B.e. 1b.2* can possibly be referred to the action of fungi. In contrast, borings in Slices *Öl. O. 45.3, Öl. O. 6.1* and *Öl. O. 102.1* are referred to the algae. In particular, there seems a strong resemblance between the borings in the latter slice and those of the green endolithic alga *Gomontia polyrhiza* from a Recent oyster shell, figured by Bathurst (1971).

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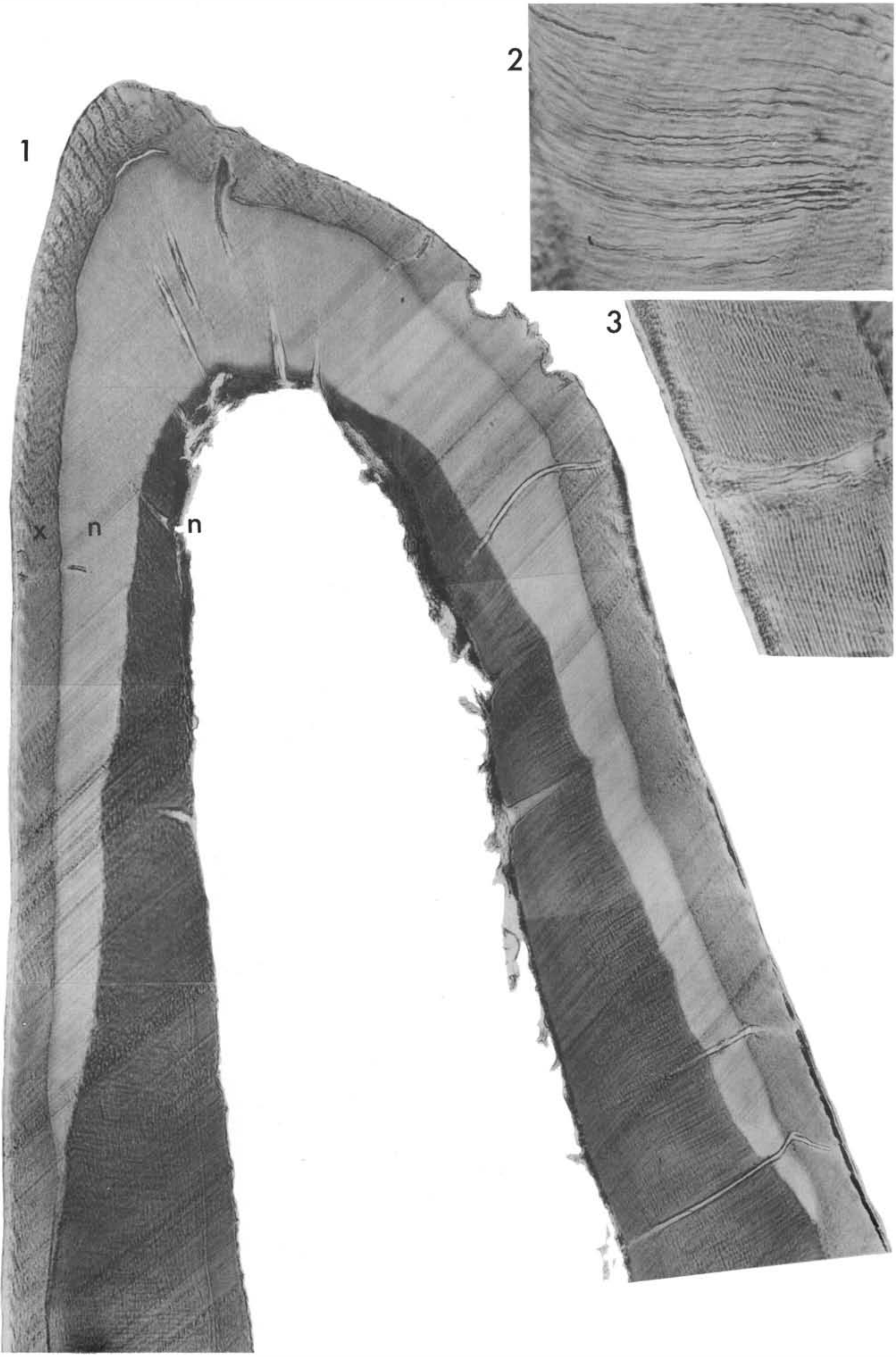
Plate 1

Fig. 1. Slice Öl. O. 8.1. X125. Fig. 2. Slice Öl. A. 11b.2. X150. Fig. 3. Slice Öl. O. 36.2. X120. Fig. 4. Slice Öl. O. 45.3. X100. Fig. 5. Slice Öl. O. 102.1. X180. Fig. 6. Slice Öl. A. 27.1. X40. Fig. 7. Slice Öl. B.e. 1b.2. X170. Fig. 8. Slice Dy. E. 7.1. X125.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Structure and function of trilobite terrace lines

JOHN MILLER

Miller, J. 1975 07 15: Structure and function of trilobite terrace lines. *Fossils and Strata,* No. 4, pp. 155–178. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

Terrace lines are escarpment-like ridges on the outer surface of trilobite cuticle. The ridges are consistently associated with canals opening tangentially into pits below the ridge crests. Accessory canals pass vertically through the cuticle to open into pits between the ridge crests. It is suggested that these features together form a terrace ridge system, and the position, orientation and behaviour of this system on the trilobite exoskeleton is discussed. Possession of a terrace system is regarded as a characteristic trilobite feature; the ridges apparently originated on the doublure and then variously migrated onto the dorsal surface, were modified, or were lost completely in different taxa. Note is made of possible terrace ridges in eurypterids. Possible terrace functions in strengthening, sediment-guiding and mechanoreception are examined. It is concluded that the terrace system was a current monitoring apparatus. The palaeozoological and palaeoecological consequences of such a function are discussed.

John Miller, Grant Institute of Geology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW, Scotland, 10th October, 1973.

Most formal descriptions of trilobites make brief reference to the form and distribution of sculptural features on the dorsal exoskeleton. However, there have been no systematic attempts to provide accurate, detailed and quantified anatomical descriptions of these cuticular structures, nor has their distribution over the exoskeleton been carefully mapped. Only a few workers have tried to interpret trilobite sculpture in functional terms or to evaluate any possible significance in relation to the animal's mode of life. Most have simply described 'ornament' in loosely-defined terms such as 'granules', 'pustules', 'tubercles', 'striae', etc.

Work on fossil cuticle sculpture has been hampered by a lack of information on parallel structures in modern arthropods. Many of the relief features on extant cuticles are assumed to be sensorial. There are a number of anatomical descriptions of such organs, but very little of the definitive physiological evidence which is required to conclusively establish functions. Very generalised accounts of sensorial distribution over arthropod bodies have been given, but again there are few descriptions detailed enough to allow of comparisons with fossils.

Working both with trilobites and some modern arthropods, Miller (1972, 1974) discussed possible and probable functions for a variety of cuticular relief features, and introduced the technique of making detailed maps of sculptural distribution over the exoskeleton. Using this approach, it was possible to demonstrate a number of consistent relationships between the types and densities of relief features with their position on the exoskeleton. This work owes much to the elaboration of cuticle structure and composition by Dalingwater (1969, 1973), and Teigler & Towe (this volume). Dalingwater himself described a variety of pustules, pits and tubercles as seen in thin-section; however, his study did not extend to correlations between sections and surface appearance, or to detailed consideration of position on the body.

The so-called 'terrace lines', elongate cuticular ridges, are probably the commonest sculptural features of trilobites apart from pits – and less attention has perhaps been accorded to terraced sculpture than to pustules, spines and 'tubercles'. This paper is an account of the structure of terrace lines and an attempt to consider their possible palaeozoological significance. The intention is not to provide an exhaustive account (for such would require an examination of most trilobites) but to present an example of approaches and techniques useful in studies of sculpture generally. It is hoped to stimulate interest and further investigation in the subject.

Abbreviations for specimen repositories are as follows: BM – British Museum (Natural History), London; PMO – Paleontologisk Museum, Oslo; GrI – Grant Institute of Geology, Edinburgh; MM – Manchester Museum, England. Thin-sections in the care of Dr. J.E. Dalingwater, Dept. of Zoology, University of Manchester are given a JED prefix. All other material is in the writer's personal collection.

I wish to thank Dr. E.N.K. Clarkson for reading the manuscript and offering encouraging discussion. Dr. D. Ball, Manchester University, initiated me into the joys of playing with water and offered much helpful instruction in hydrodynamics. Prof. G. Henningsmoen, Oslo, drew my attention to the problem of terrace lines and kindly showed me the results of some interesting experiments he had performed. I am most grateful to Dr. J.E. Dalingwater for supplying material and loaning thin-sections, as well as for much discussion. Other material was examined at or loaned from various institutions noted above and I am most grateful for their co-operation. R. Brown of the Grant Institute of Geology expertly prepared some of the thin-sections. Dr. C.D. Waterston (Royal Scottish Museum) kindly advised on the eurypterids with 'terrace lines'. Financial support from the Natural Environment Research Council of Great Britain is gratefully acknowledged, as are the facilities provided by the Grant Institute, Edinburgh.

APPROACHES AND TECHNIQUES

Studies of trilobite sculpture ideally require a suite of well-preserved specimens which include complete dorsal exoskeletons as well as identifiable fragments partially embedded in matrix. The cuticles should have as little diagenetic alteration as possible (see below). Generally, the best material is found in dark impure limestones where the trilobites are mid- or dark-brown with a glossy outer surface. White or very pale cuticles from very pure limestones are generally unsatisfactory for all but the coarsest details. Clearly, material such as described above is available only with comparative rareity, so investigations must be based on less complete or less well-preserved specimens.

The first stage in investigation is a thorough examination of exoskeletal surfaces using a zoom binocular microscope and a variety of lighting conditions. Light coatings of ammonium chloride are often helpful in increasing contrast. All sculptural features are described, their positions on the exoskeleton noted, and estimates or measurements of density and dimensions made. A calibrated square-grid eyepiece insert and an eyepiece micrometer are used for these quantitative parameters. In the case of asymmetric features such as terrace ridges etc., an orientation with respect to the body sagittal axis is also recorded. Following this general examination which is used to prepare a sculpture map, cuticle fragments may be removed for Scanning Electron Microscope (SEM) examination after preparation in the usual way (see Miller, 1974). Finally, a series of thin-sections are made, preferably of matrix-embedded specimens. Where these are not available, the less satisfactory method of embedding in artificial resins may be used to facilitate sectioning without undue damage to the cuticle. Porous matrices require vacuum impregnation with resin. Thin slices are first cut, then these are ground and highly polished on one side using Aloxite powders, removing the shatter-zone produced by cutting. Epoxy resins are used to mount the lower prepared surface on a glass slide, then the upper face of the slice is similarly polished down to the required thickness. Slides are normally left uncovered and thinly smeared with non-drying immersion oil, prior to examination. This has the advantage that adjustments in thickness can quickly be made later if required.

Study of thin-sections is an essential complement to surface observations. A number of superficially similar surface features, especially those of the 'tubercle' or 'pustule' type, each have a fundamentally different underlying organisation only revealed in section (Miller, 1972). Furthermore, erosion, wear or extraction damage frequently affects surface relief, and sections of matrix-embedded cuticle allow a view of the structures before most of this damage takes place.

The final interpretative stage, both of thin-sections and SEM observations, requires some knowledge of changes produced in cuticles by diagenetic processes. This question of preservation is discussed in detail by Miller (1972; in preparation), and a short account will suffice here. The main factors involved may broadly be categorised as biological, mechanical, recrystallization, solution and replacement. Since trilobite cuticles were originally largely calcite in composition (Dalingwater, 1973; Teigler & Towe, this volume), they were particularly prone to diagenetic alteration, beginning immediately after exuvial casting or death of the animal. By far the commonest process affecting the exoskeleton is the biological one of micritisation. Boring algal or fungal threads invade the cuticle, forming matted galleries. Micrite is precipitated after the galleries are vacated (Bathurst, 1966), and this results in formation of a dense micrite envelope as a replacement of original cuticle. Frequently the replacement affects only the outer surface and removes all traces of the prismatic layer, but considerable thicknesses of the principal layer may also be involved. In thin-section, the micrite envelope is recognised by its fine-grained character, lack of internal structure, and darker appearance compared to the rest of the cuticle and its smooth outer boundary. The interface between the micrite envelope and the unaffected cuticle is hazy and vague. Sometimes fine individual bored canals can be seen at this interface. In SEM preparations, micritic envelopes produce very smooth surfaces with subdued relief, in which only very small micrite or microspar grains can be seen. Because of this smoothing effect, micritised material is unsuitable for detailed sculptural studies. Other types of borings are more obvious; examples are given by Størmer (1931) and Dalingwater (this volume). It is important to distinguished between pits and canals of primary origin and such structures produced secondarily by boring activity.

Mechanical damage to cuticles, including pre-sedimentation abrasion and later compactional fracture, is usually easy to recognise in thin-sections. Stripping of the outer (prismatic) cuticle layer is not always easy to determine in surface view alone. The stripping often occurs in specimen extraction or development, and may seriously affect the surface expression of sculpture. This is particularly so with pits, for the wide mouths of some canals are developed as socket-pits exclusively in the prismatic layer. Outer layer stripping is also common on terrace ridges, as described on p. 207.

The effects on cuticles of complex solution-recrystallization-replacement processes can be very difficult to unravel. Where sufficiently intense, these processes can obliterate any primary cuticle fabrics. Recrystallization and solution together are mainly responsible for this destruction; some forms of replacement, particularly that of syngenetic framboidal pyrite, can actually enhance detail by depicting canals, laminae and tubercle infillings. Quartz replacements, although providing spectacular specimens when etched out in full relief, are unsatisfactory for sculpture studies. Fine detail, apart from larger canals and 'tubercles' is lacking, and surfaces present a similar smooth aspect to micritic envelopes, despite the larger quartz grain size. Possibly, in these cases, quartz replacement has been based on the mould of a rather insoluble micritic envelope, as described by Boyd & Newell (1972).

Any or all effects of the processes outlined above can be found within a single trilobite specimen, or even within one thin-section. The effects are highly localised, so that within a few hundred microns 'length' of cuticle in a slide, the quality of preservation may vary from excellent to very poor. For this reason, having selected good material, it is important to make as many preparations of it as possible.

Several other factors must be taken into account before interpretation. Surface SEM studies can be carried out on museum material, which often looks attractively glossy and well-preserved. Frequently this gloss may be some kind of varnish, or even perspiration-etched polish produced deliberately by handling; these methods of presenting specimens were much favoured by earlier collectors. Finally, interpretation of thin-sections requires careful consideration of the three-dimensional arrangement of sectioned structures, and also account of the exact plane and thickness of the section in that three-dimensional context. This is discussed more fully below (p. 206).

STRUCTURE OF TERRACE LINES

Basic structure

Terraced sculpture is an extremely common form of surface relief in trilobites. Several groups, however, appear to be lacking in terraces, notably the large group of agnostids, as well as calymenids, harpids and possibly cheirurids. In other taxa they may be weakly developed on the doublure and absent from the dorsal exoskeletal surface. Because of the relative lack of note

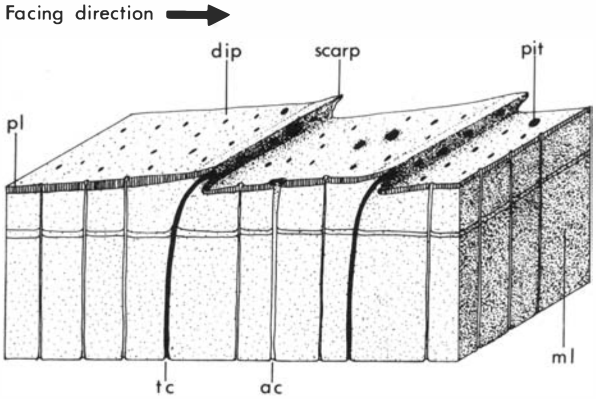

Fig. 1. Schematic diagram showing construction and terminology of terrace system. A few horizontal laminae of the cuticle are shown diagramatically to illustrate their upward deflection in the vicinity of a canal. ac – accessory canal. ml – main layer of cuticle. pl – prismatic layer of cuticle. tc – terrace canal.

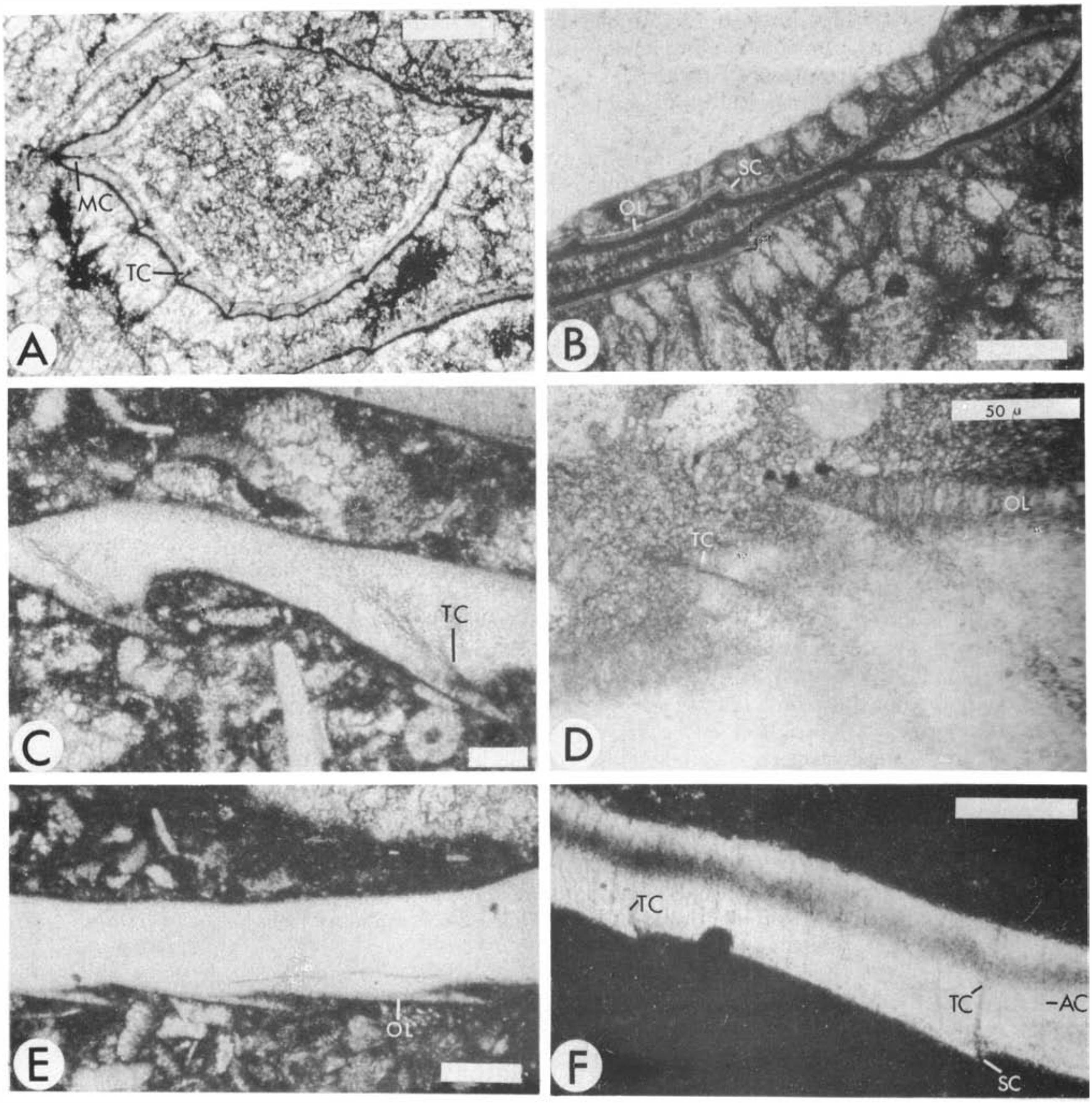

Fig. 2. Thin-sections of trilobite cuticles under plane polarised light. A. Transverse section of left genal spine of *Paradoxides* sp., Upper Cambrian, Newfoundland. Note the terrace canals (TC) and the outward facing terrace ridges. Marginal canals (MC) are seen in the section opening on a high lateral ridge on the inner and outer margins of the librigena. B. Section across the margin of the librigena of *Anopolenus* sp., Upper Cambrian, Newfoundland. Note the thick, pellucid outer or prismatic layer (OL) and the dark principal layer. The outer layer is continuous over the terrace scarps (scarp face – SC). C. Tangential section across terrace ridges of the librigenal doublure of *Asaphus raniceps* Dalman, lower 'Raniceps' limestone, Haget, Öland. Note the angled terrace canals (TC) and the diffuse appearance in their proximal portions caused by lamellar deflection. JED 01 0.96.1. D. Detail of two dorsal surface terrace ridges and canals (TC) on the librigena of *Asaphus raniceps* (same slide as C. above). Note the termination of the prismatic layer (OL) at the terrace scarp. E. Section across the cephalic doublure of *Asaphus raniceps* showing the acutely extended scarps composed only of prismatic layer (OL). Same slide as C. above. F. Section across pygidial doublure of *Bumastus* sp., Wenlock Limestone, Dudley, England. Note the distally curving terrace canals (TC) opening at the scarps (SC). Vertical accessory canals (AC) are also visible. JED B.lb.l. All scale bars represent 320 microns except where otherwise stated.

previously paid to terraces, it is not possible at present to provide a full account of their distribution in the Trilobita. Further information would be most welcome, especially on Cambrian groups.

In all the material so far examined in detail, there is considerable uniformity in basic terrace construction, so that a generalised model can conveniently be presented (Fig. 1). The terracing is formed by slight expansions in cuticle thickness expressed in a linear way on the outer

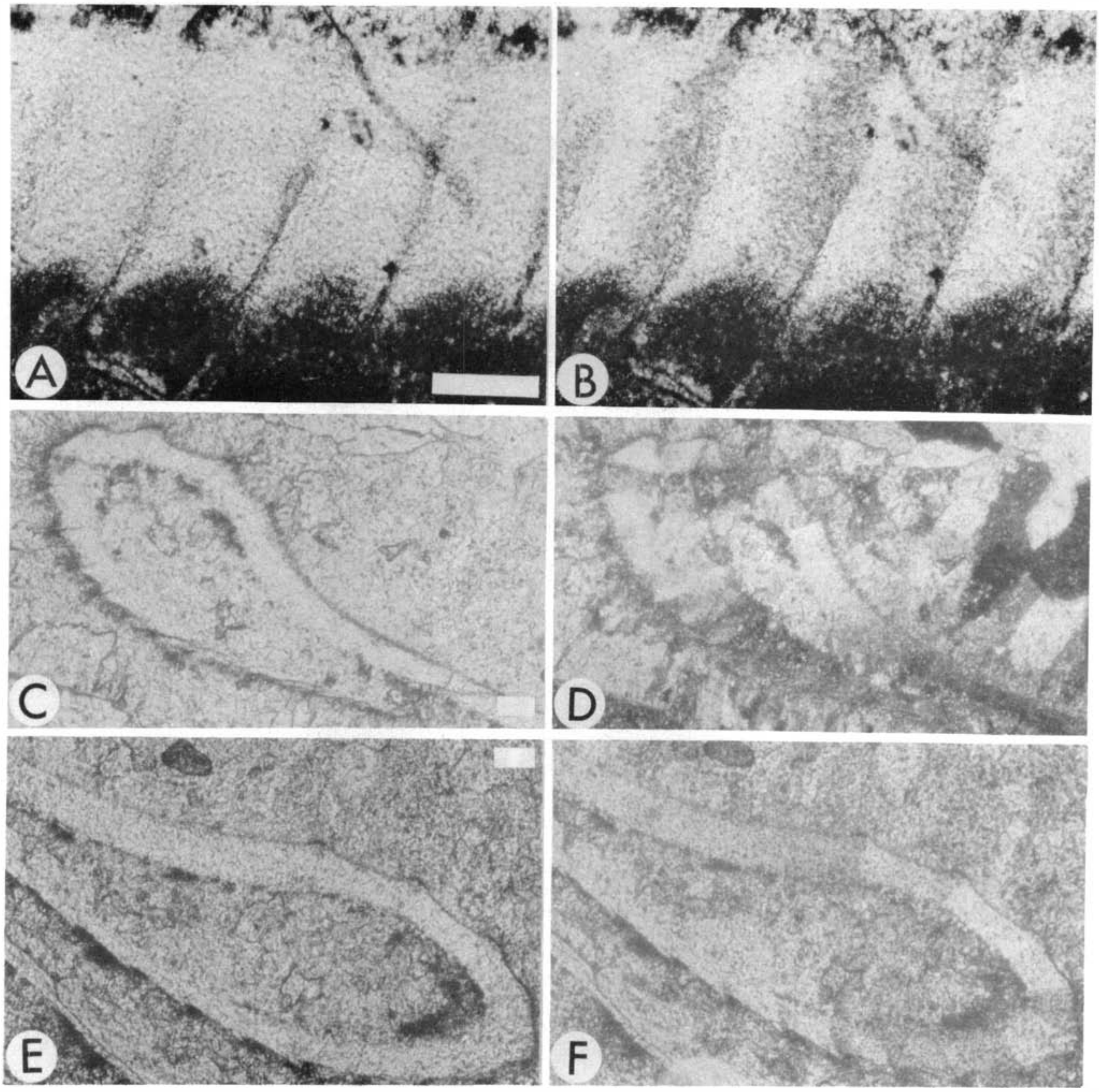

Fig. 3. Thin-sections of trilobite cuticles. Scale bar represents 100 microns. A. Slightly oblique section of pleural tip of *Illaenus aduncus* Jaanusson, lower 'Raniceps' limestone, Haget, Öland. Note the evenly-spaced terrace scarps with angled terrace canals opening out on to them. Plane polarised light. JED IIa – 1. B. As above, crossed polars. Note the extinction stripes adjacent to the terrace canals. C. Section transversely through the librigenal doublure of *Archegonus (Phillibole) twistonensis* (Reed), Lower Carboniferous, Twiston, N. England. Despite considerable recrystallization in a pure limestone, the terrace canals are still visible. Note the sharper, more asymmetric ridges of the doublure compared to those on the dorsal surface. Plane polarised light. D. As C., crossed polars. Note the extinction stripes but the difficulty in distinguishing recrystallized cuticle from highly recrystallized matrix. E. Transverse section of pygidial doublure of *Archegonus (Phillibole) twistonensis* (Reed), showing obliteration of primary cuticle features, including terrace canals, by recrystallization. Plane polarized light. F. As E., crossed polars. Note the extinction stripes related to the former position of the terrace canals.

surface of the cuticle only, the expansions abruptly returning to, or just below, average cuticle level. Ridges are thus formed, and Whittington (1965) noted their asymmetric profile, describing a long gentle slope and a short steep slope (Whittington, 1965:386). These ridges resemble miniature escarpments and it is convenient to use the topographical terms 'dip' and 'scarp' to describe gentle slopes and steep faces respectively (Fig. 1). Mostly, the thin outer or prismatic layer of the cuticle is continuous over the dip slope, but is interrupted at the ridge crest and is absent from the scarp (Figs. 1, 2D–E, 5). This is visible both in thin-section and SEM preparations and is therefore not an artifact produced by extraction from the matrix. The absence of the prismatic

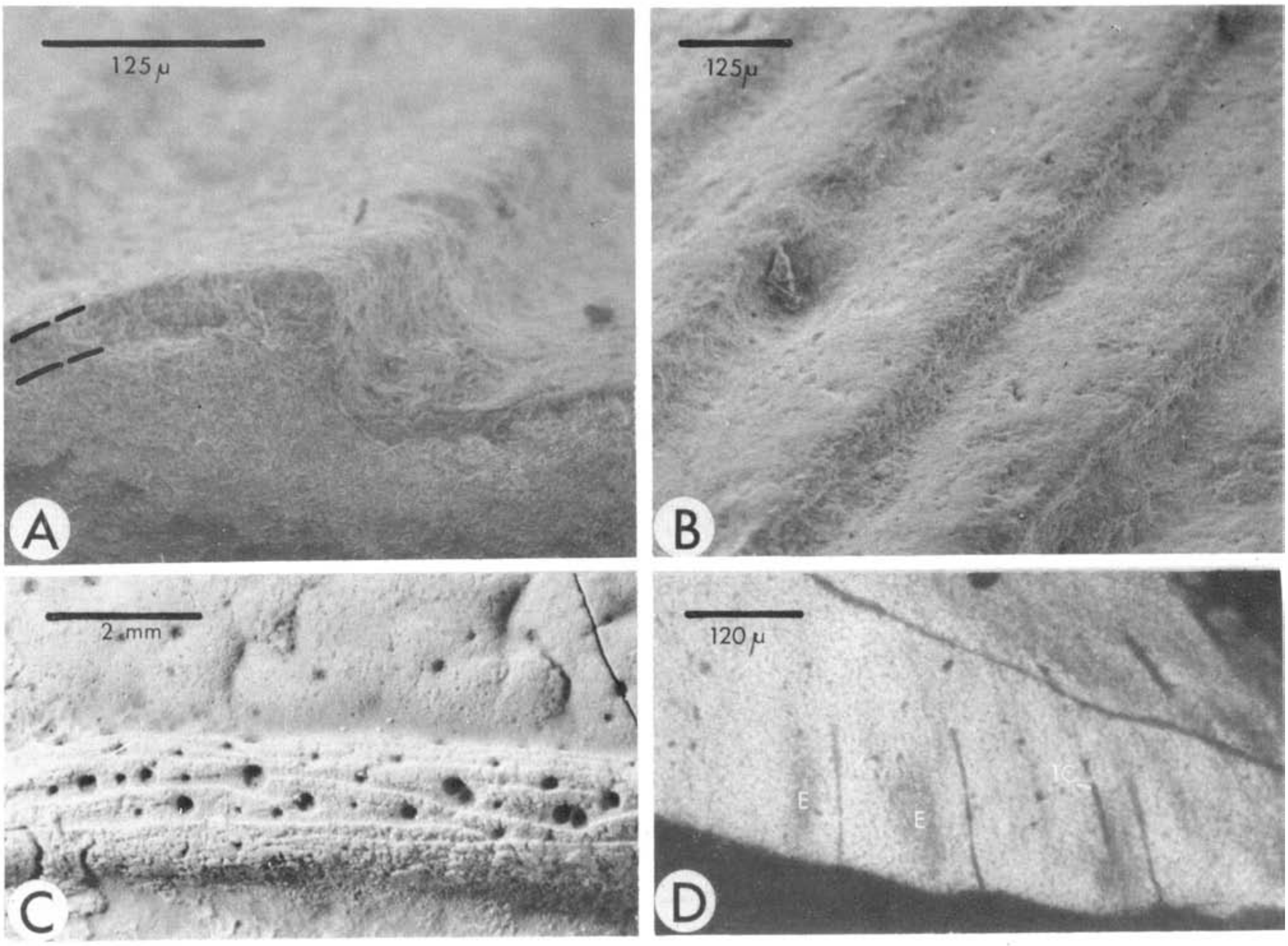

Fig. 4. A. Scanning electron micrograph of oblique view on fracture cutting across a terrace ridge of *Phacops rana* ssp., Eifelian, Spanish Sahara. Cuticle from BM In 56877. Note the prismatic layer of coarser crystalline calcite (dashed on left) halting at the terrace scarp. B. SEM photograph, oblique view along terraces of the pygidial doublure, same specimen as A. Note the right-angled scarps with a large accessory pit opening on the terrace scarp, with abundant very small accessory pits on the dip slopes. C. Frontal view of the anterior cephalic border, *Phacops rana* ssp., Eifelian, Spanish Sahara, BM In 57166, showing large socketed accessory pits with the small canal openings oat the base of the pits. Note also the smaller accessory pits. D. Thin-section of the pygidial doublure of *Phacops rana* ssp. Eifelian, Spanish Sahara, BM In 57167e, showing large accessory canals and diffuse extinction stripes (E) in the position of the terrace canals, only one of which (TC) lies in the plane of section. The terrace relief has been reduced by weathering prior to resin-embedding.

layer from the scarp face itself is apparently unique; no sculptural feature other than terrace ridges are so far known to lack the prismatic layer. In the Cambrian *Paradoxides* (Paradoxidinae) and *Anopolenus* (Centropleurinae), however, the prismatic layer is very thick and is continuous over the terraces (Fig. 2B). Examination of more Cambrian trilobites is required before it can be determined if this feature is of taxonomic or stratigraphic value.

Other features consistently associated with the terrace ridges are canals arising from the inner cuticle boundary and curving distally to open tangentially in a small pit on the scarp, often just below the crest. These terrace canals are usually 30—60 µ across, although sometimes larger canals 100 µ across open into socket-pits on the scarp (Fig. 4B). The terrace canals and pits are always angled in the same direction as the scarp faces.

It should be noted that even in well-preserved material, the exact outline of each canal may not be visible in all sections of terraces. As the canals are so narrow, the chances of sectioning one on the longitudinal axis of its lumen are very small. In any case, although it is not difficult to obtain sections more or less normal to terrace ridges, it is extremely difficult to avoid making the section at least slightly oblique to the cuticle thickness. Thus, in any one section, particularly with tangential canals such as the terrace canals, it may not be possible to trace the full passage of the canal through the cuticle. Only its distal or proximal parts will be visible, giving a false impression that the canal does not continue through the whole cuticle thickness. If the outlines of the canal itself are not seen, commonly there will be a less distinct angled zone with different optical density to the rest of the cuticle. Close examination of this at high magnification will often reveal that the zone results from upward deflection of fine cuticle laminae. This is the

'Christmas tree' effect described by Rolfe (1962) and Dalingwater (1969; 1973) from fossil crustaceans and trilobites. The deflections are well-known in modern arthropod cuticles, where they result from passage of canals upwards through the laminae. Since the zone of deflection has a larger cross-section than the canal itself, the effect is frequently encountered and may reliably be used as indication of a canal not exactly in the plane of section.

In cuticles which have suffered some degree of recrystallization and thus destruction of their primary fabric, canals as such may not be preserved anywhere in the cuticle. It is often still possible to detect the sites of obliterated canals, at least the larger ones, as recrystallization and grain enlargement were apparently controlled by primary features such as canals (Miller, 1972; in preparation). Viewed with crossed polars, 'extinction stripes' corresponding to the sites and orientations of primary canals may be visible. In sections of terraces, the extinction stripes are always angled in the same direction as the scarps, though not neccessarily at the same angle as the scarp wall (Fig. 2C—D, Fig. 3B, D, F). Where cuticles are well-preserved but with little optical contrast, the phenomenon of pseudopleochroism (Hudson, 1962) may be useful. Rotation of the lower stage polarizer without the analyzer in place will often give a position with markedly increased contrast for primary features.

In surface view, the pit openings both of angled terrace canals and accessory canals are visible in very well-preserved cases (Figs. 4, 5), sometimes without the aid of SEM. The terrace canal pits themselves are most difficult to see directly, owing to the fracturing of the terrace scarp and its partial removal in extraction from the matrix. The pits are normally distinguishable from artifacts and surface damage by their smooth and symmetrical shape. Accessory pits, of size groups 10—15 μ, 50—100 μ and 100—250 μ across occur on dip slopes (Fig. 1, Figs. 4, 5A). The accessory pits are as characteristic of terraced sculpture as the true terrace canals. Other features I have seen associated with terraces are very short U-shaped ridges or scales which sometimes occur in *Paradoxides* (Fig. 9); possibly these are modified terraces. In some scutelluids, the terrace ridges are associated with granules; however, granular and terraced sculpture are normally mutually exclusive.

Other types of ridge-systems occur on trilobites. Often these are coarse reticular systems, as on many trinucleids, but the ridges are symmetric in profile, although they do bear large vertical canals opening on the ridge crest (Miller, 1972). Much finer but similarly symmetric ridges occur on the dorsal exoskeleton of many proetids. They follow the so-called Bertillon pattern said to be characteristic of terraced systems (see below), but apart from their lack of typical profile, these proetid ridge systems are too fine for true terraces. The normal terrace ridges in proetids are restricted to the doublure and margins of the exoskeleton.

Variation in structure

Obviously many further descriptions are required before the full extent of constructional variation in terraces becomes apparent. In material so far examined, morphological variation mainly concerns scarp angles as well as ridge spacing, facing and course.

A primary distinction is apparent between doublure terraces and those developed on the dorsal surface of the exoskeleton. With few exceptions, doublure ridges are very long, gently curved and have a low anastomosis frequency. They have a higher relief and steeper, more overhanging scarps compared to dorsal ridges. The dorsal ridges are shorter, vary more in course, have higher anastomosis frequencies but usually lower relief and are much less asymmetric in profile. Examples of terrace changes in passing from dorsal to doublure side are given in Figs. 2D—E, 3A, 6. Despite these differences, both dorsal and doublure terraces retain the basic construction of the model outlined above, and thus Jaanusson (1959) and Whittington (1965) were correct in referring both dorsal and doublure types to the terrace system.

Terrace scarp profiles may be obtuse, right-angled or acute (Fig. 7), either in different trilobites or in different sites on an individual. The dip slope may be evenly inclined, but often has a break in slope just in advance of the crest, producing a chamfered appearance (Fig. 7D, Fig. 9, Fig. 11B). Combination of a dip slope chamfer with an obtuse scarp can provide difficulty in determination of the facing direction of the ridges. It should be re-emphasised that these profiles are those as seen in thin-section and not in hand specimen, where extraction from the matrix causes ridge damage such that the terrace 'lines' we see are not the true terrace ridges.

An unusual feature of terrace construction occurs in the doublure ridges of *Asaphus raniceps* Dalman (Fig. 5A—B), as well as *Homotelus bromidensis* Esker and *Isotelus gigas* de Kay. The bases of the scarps are here buttressed by short crested cuticle folds at right angles to the ridges. I have not so far observed this feature in any other trilobites, and it may well have some taxonomic significance.

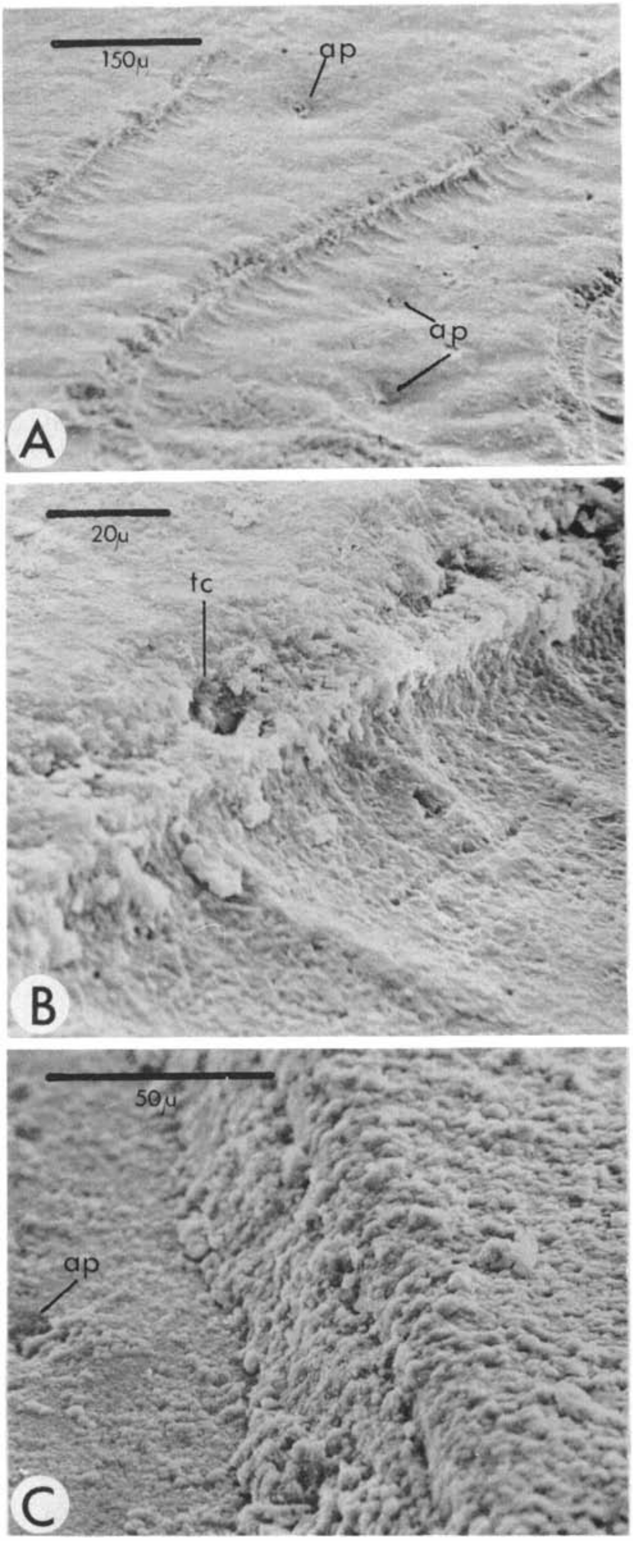

Fig. 5. All scanning electron micrographs. A – B. Cephalic doublure of *Asaphus raniceps* Dalman, lower 'Raniceps' limestone, Haget, Öland. A. Oblique view on to the terrace field, showing ridges broken back in their extraction from the matrix, but with buttress-like folds on the dip slopes close to the scarps. Note the accessory pits (ap). B. Close view of above. Note the section of the broken-across terrace canal (tc). C. *Homotelus bromidensis* Esker, Bromide formation, Ohio. Oblique view along a terrace ridge of the pygidial doublure showing the break-back line and a distinct prismatic layer wall on the scarp.

Terrace ridge length and curvature vary between the extremes of the long, gently arched type (Fig. 8A) and the very short serrate type (Fig. 8C). High anastomosis rates produce strongly curved ridges interlocked to form a reticulate or scale-like pattern (Fig. 8B). Although a basic plan pattern of terraces is probably characterised taxonomically at species level, such structural variation as outlined above may occur over the exoskeleton of an individual, where it is clearly related to position on the body. This position-related variation is discussed further below.

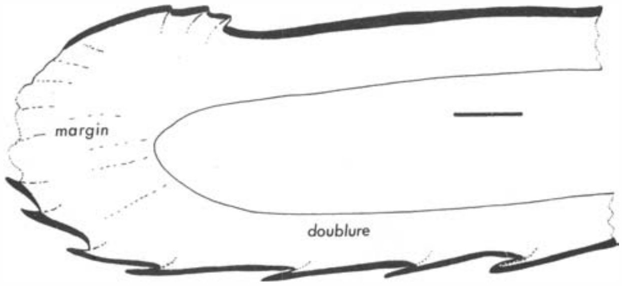

Fig. 6. Shadowgraph drawing of section across the librigenal margin of *Asaphus raniceps* Dalman, lower 'Raniceps' limestone, Haget, Öland, JED 01. 0.96.1. Note the change in terrace profile passing from the doublure to the dorsal surface. The prismatic layer is black. Scale bar – 320 microns.

Fig. 7. Schematic profiles of terrace ridges encountered in trilobites. A. Simple, obtuse, e.g. *Homotelus bromidensis* Esker. B. Chamfered, obtuse, e.g. *Paradoxides* sp. (locally on exoskeleton). C. Right-angled or vertical, e.g. *Phacops rana* ssp. D. Acute or overhanging, e.g. *Asaphus raniceps* Dalman doublure.

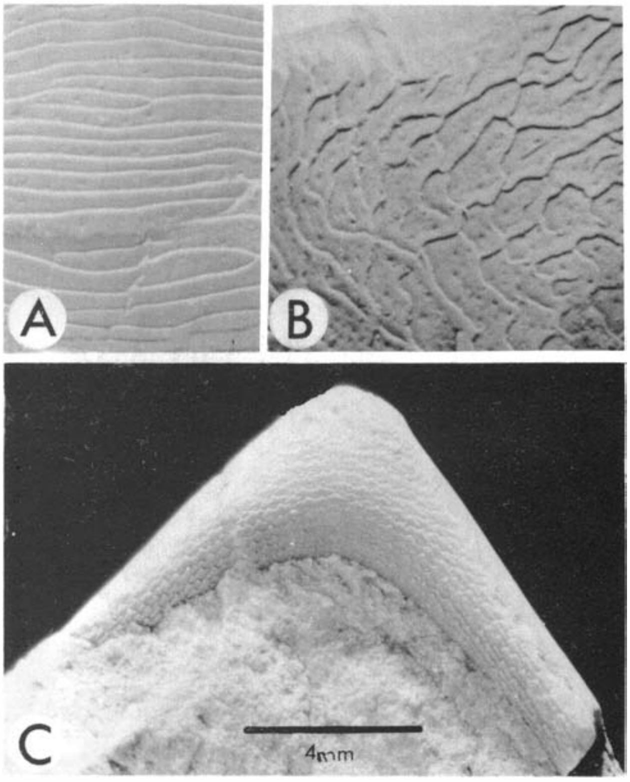

Fig. 8. A – B Terrace ridges of *Paralejurus brongniarti* Barrande, Devonian, Tetin, Bohemia. BM It 1596. A. Terrace ridges of the rostrum, note the forward-facing even, sub-concentric habit, and the associated accessory pits. x3. B. Anastomosing reticule-like terraces of the librigena, same specimen, also with accessory pits. x3. C. Doublure of the pygidial tip, *Trimerus (Trimerus) delphinocephalus* Green, Wenlock Limestone, Dudley, England. MM L 9949. Note the short serrated terrace ridges facing posteriorly.

DISTRIBUTION AND ORIENTATION OF TERRACE RIDGES

In all the trilobites I have examined so far, doublure terrace ridges invariably face peripherally (Fig. 20A). Thus ridges on the cephalic doublure face forwards and outwards, those on the thorax laterally (often obliquely), and those on the pygidium backwards and outwards. A cautionary note is required in this connection. Facing directions of terrace ridge impressions preserved on the matrix mould of the doublure are in the opposite sense to those of the true ridges preserved on the cuticle. Care should be taken not to confuse cuticle and mould in a number of difficult cases, especially where the cuticle is very thin and of the same colour as the matrix.

The antero-peripheral ridge facing of the doublure is continued on to the rostrum and hypostome (where these are present and not otherwise sculptured). Here, however, there are disturbances in the simple sub-concentric ridge patterning. These perturbations are also found where terraces extend on to the dorsal surface of the exoskeleton, and the course of terraces appears to follow a number of general 'rules' as follows:

(1) Terrace ridges change course in response to changes in surface or edge curvature of the exoskeleton (e.g. Figs. 9, 10, 13C, 18).

(2) Terraces do not continue across or into deep furrows (Figs. 9, 10).

(3) Terraces tend to swing so as to run tangentially to deep hollows or furrows (Figs. 9, 10, 19).

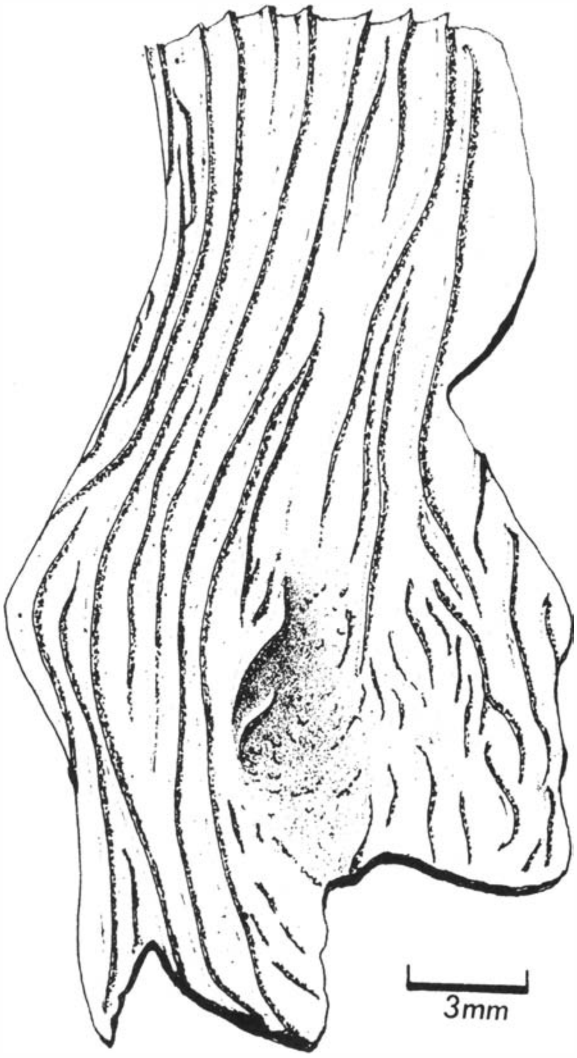

Fig. 9. Camera lucida drawing, ventral surface of fragment from *Paradoxides* sp. hypostome. Upper Cambrian Newfoundland. Where the terrace ridges diverge to follow the curvature of the hypostome, note the intercalation of new ridges to maintain a rather constant spacing. The macula hollow near the bottom of the figure is mostly skirted by terraces, but those which approach the margins of the hollow increase markedly in relief as they do so. There are small granules scattered on the floor of the macula.

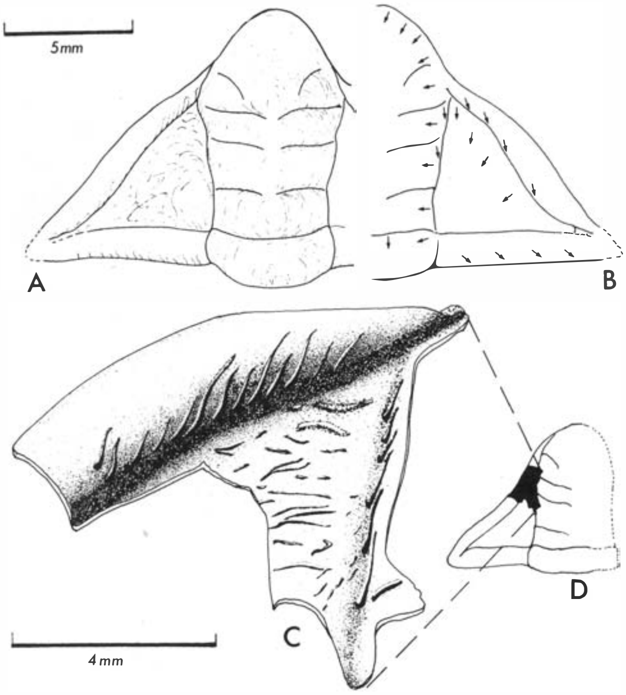

Fig. 10. Anopolenus sp., Upper Cambrian, Newfoundland (exact locality unknown). A. Schematic diagram of cranidium showing the pattern of terrace ridges. B. Arrows indicating the varied facing directions of the cranidial terraces. C. Camera lucida drawing of oblique view on the area of cranidium indicated on D. Note the increase in terrace ridge relief close to the furrows, and the change in terrace orientation on the gently inflated fixigenal field.

(4) Terrace ridges avoid muscle scars by deflecting around them. This applies also to hypostomal maculae. Dalingwater (1969, 1973) has described the cuticular structures of some maculae which strongly indicate that maculae also represent muscle scars. An example of deflection around a macula is given in Fig. 9. Further examples are found illustrated in Whittington (1965), Pl. 26:6,8; Pl. 27:10; Pl. 29:2; Pl. 40:12; Pl. 43:3.

(5) Where not fractured badly in extraction from the matrix, terrace ridges are normally seen to increase markedly in relief as they approach a furrow or hollow (e.g. Figs. 9, 10).

Examination of a variety of trilobites suggests that the spacing between successive terrace ridges, where these are reasonably parallel, remains rather even and often constant over the exoskeleton. I have made measurements of spacing on trilobites ranging from juvenile proetids only a few mm long to paradoxidids and megistaspids up to 25 cm long. Terrace separations range between 60 μ and 1000 μ. These figures are for average ridge separation between parallel terraces on several parts of the exoskeleton. Obviously there are places where these distances are exceeded, but these are comparatively rare and very local. Apparently there is rather strict control over terrace formation such that ridges are evenly-spaced and are not normally separated by more than just over a millimetre. It is remarkable that within such a great range of body sizes there is such a small range in terrace separation. The mechanism by which such even spacing is maintained involves interpolation of a new ridge between others caused to diverge by their 'reaction' to a change in surface curvature (illustrated in Fig. 9).

There is unfortunately little information available concerning terrace pattern and construction changes in ontogeny. In *Paladin eichwaldi shunnerensis* (King), an Upper Carboniferous proetid, a complete meraspis stage 1 (Fig. 11A) has no terrace ridges on the dorsal surface, but is covered with a fine mesh of raised ridges in reticular pattern. In marked contrast, the early holaspid assumes the adult sculpture of granules, pits and a terrace field on the librigena (Fig. 11B) as well as on the doublure. Though the meraspis doublure is not visible, it too may lack terraces as well as the genal margin. A developmental series of *Paladin eichwaldi shunnerensis* from a single population has provided a range of librigenae upon which terrace separation could be measured (Fig. 12). Some increase in terrace spacing with size is apparent, but the rate of terrace separation increase is very small in comparison to the rate of librigenal size expansion. Particularly interesting is the high proportion of individuals with average separations of about 100 μ regardless of size. The 100 μ spacing is also the dominant one for the doublure terraces of *Paladin eichwaldi shunnerensis.*

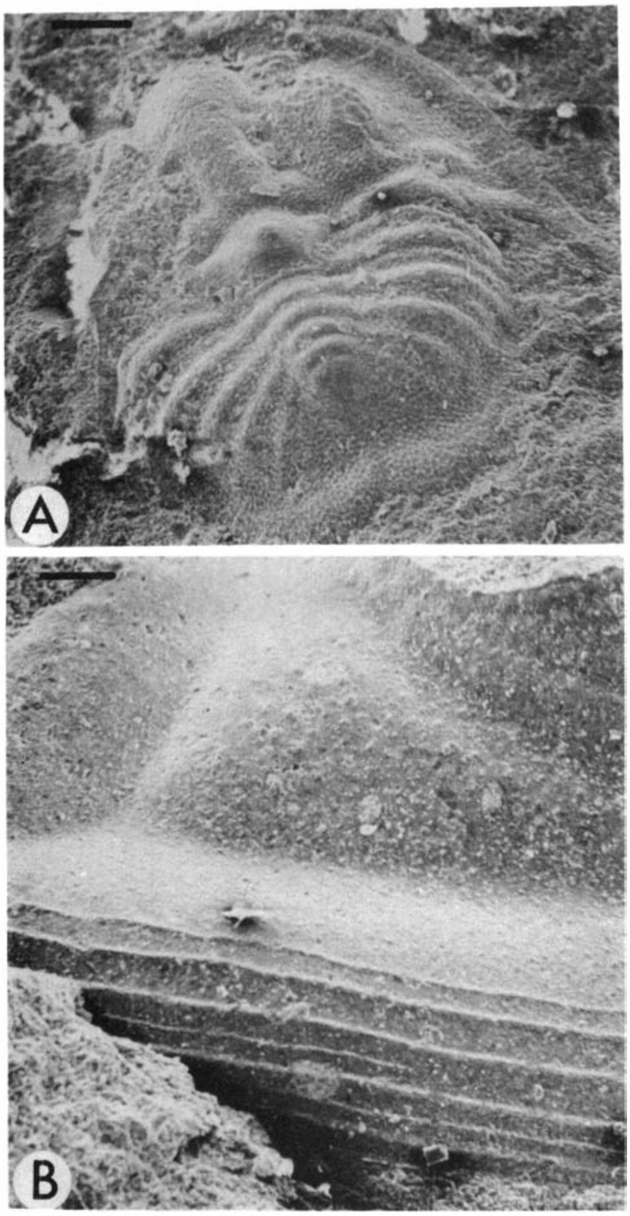

Fig. 11. Scanning electron micrographs of *Paladin eichwaldi shunnerensis* (King), Namurian (Upper Carboniferous), Shunner Fell, Yorkshire, England. GrI 40, 176. A. Dorsal view of entire meraspis 1, note the complete cover of a fine reticule of ridges but lack of true terraces from the librigenal margin. B. Lateral view of the librigena from an early holaspis. Note the well-defined terrace field and granulated sculpture below the eye.

Although a good deal more data on such ontogenetic changes is required, even the limited example above suggests that terrace formation is under some kind of genetic control, and that an 'optimum' or characteristic spacing is acquired fairly early in the life-history. The possible significance of such control is discussed in following sections on terrace function.

In summary, terrace 'lines' are truly ridges of varied but always asymmetric profile, they show consistent variation in spatial distribution and structure which is position-related, and there are indications of some inherent controls over ridge spacing. The ridges are accompanied by terrace canals and accessory canals, and this whole morphological complex can justifiably be termed the 'terrace system'.

TERRACE RIDGES IN OTHER ARTHROPODS

To my knowledge, terrace systems or even terrace ridges themselves have not been reported from extant arthropods. Some similar structures, however, occur in the Eurypterida. Størmer (1955:P24) referred to ridges on hughmilleriid eurypterids as 'terrace lines'. I have examined *Nanohughmilleria conica* (Laurie) from the Pentland Hills, Scotland. The cuticle itself is fragmentary and poorly-preserved, but when removed reveals excellent detailed moulds of the ex-

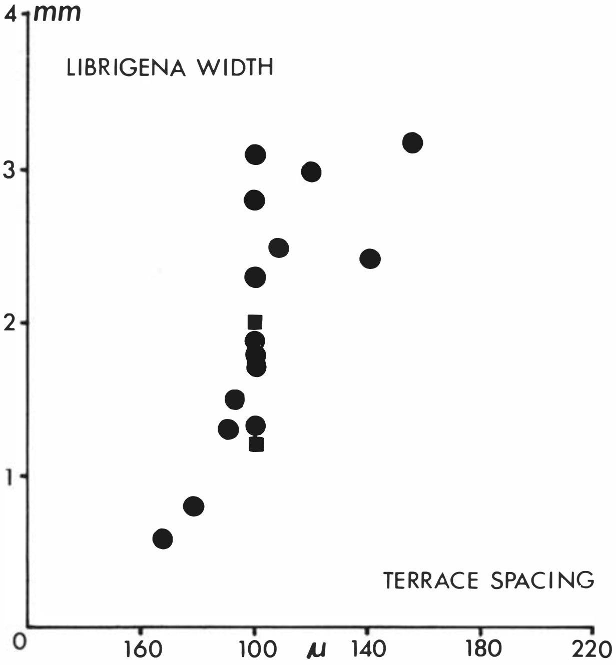

Fig. 12. Scatter diagram of terrace spacing against librigenal width for *Paladin eichwaldi shunnerensis* (King), Namurian (Upper Carboniferous), Shunner Fell, Yorkshire, England. Dots — one specimen. Squares — two specimens.

terior cuticle surface. The prosomal doublure bears sub-parallel concentric ridges with a scarp slope and a dip slope of low relief (30—50 μ; Fig. 13A). The scarps on the mould face inwards, thus the true ridges faced forwards and peripherally, exactly as on a trilobite cephalic doublure. Ridge spacing ranges from 200—1000 μ for a prosoma 3·3 cm long (RSM 1885.26.73S). The ridges become more sinuous and increase in anastomosis frequency on the genal part of the doublure. Passing inwards across the width of the doublure, the ridges become shorter and more curved, eventually assuming a scale-like appearance, but the outward facing is consistently maintained. At the inner part of the doublure in the midline region, there is a field of deep circular hollows in the matrix, which are almost certainly moulds of setae originally projecting from the cuticle (Fig. 13A).

Similar ridges are present also on the outer parts of the pre-abdominal tergites, where they are mostly straight, coursing parallel to the longitudinal body axis and facing outwards (Fig. 13B). Towards the anterior margins of each tergite, the ridges swing outwards and converge (Fig. 13B), probably reflecting an original flexure of the tergite in this region. The tergite ridge spacing ranges between 500 μ and 1100 μ. The disposition of the ridges is similar to that of *Illaenus sarsi* Jaanusson thoracic pleurae (Fig. 13C), amongst many other trilobites.

It will be noted from the above description that hughmilleriid and trilobite terrace ridges have many features in common, especially their basic structure, spacing, attitude and pattern. Until a well-preserved cuticle has been examined, however, it will not be possible to determine whether eurypterids also possessed a complement of terrace and accessory canals and thus bore fully-developed terrace systems. Should this prove to be so, it would underline the functional significance of the terrace system, in that it must have evolved independently in trilobites and some eurypterids.

Størmer (1955) considered the eurypterid ridges as 'integumental folds', following Schultz (1937) who sought to homologise cuticular folds (by definition involving both depressions and ridges) on *Limulus* and other extant merostomes, with trilobite terraces. There are no morphological or other similarities between the folds and terraces to make such a comparison valid.

FUNCTIONS OF TERRACE SYSTEMS

The consistent association of terrace ridges with angled canals and accessory canals demands that the terrace ridges be considered only as parts of an integrated system, rather than in isolation, and thus a functional explanation must operate in terms of the system and not just concern the ridges. Bearing in mind the close relationships demonstrated between the disposition of terrace ridges and the configuration of their bearing surfaces, the different degrees of terrace develop-

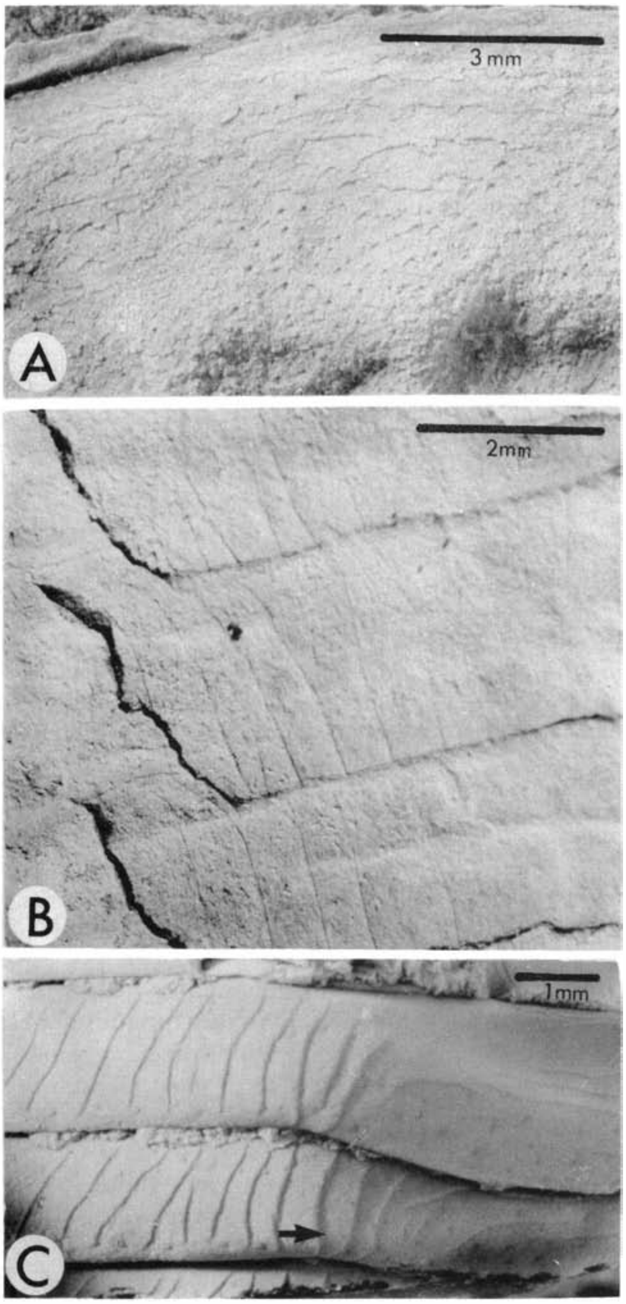

Fig. 13. A. Dorsal view of the external mould **from the** prosomal doublure of the eurypterid *Nanohughmilleria conica* Laurie, Silurian, Gutterford Burn, **Pentland Hills**, Scotland. RSM 1897.32.85. Some cuticle remains on the ridge moulds and thus detracts from their smooth sub-concentric appearance. Note the dense fields of pits, bottom centre, which are in the midline and posterior margin of the doublure. B. Same specimen, dorsal view near the extremites of the thoracic tergites. Note the 'terrace' ridges and their even spacing. C. Dorsal view of the pleural area of some thorax segments of *Illaenus sarsi* Jaanusson, Middle Ordovician, Oslo region. Note the outward facing terrace ridges and the change in terrace orientation at the break in slope indicated by the arrow. Large accessory pits can also be seen.

ment in some taxa and their complete absence in others, there are strong suggestions that terraces had some adaptational significance. Terraces are paralleled in this respect by other types of trilobite sculpture, including pits of various sizes and shapes, domes, pseudotubercles and tubercles (Miller, 1972; 1974). These sculptural features also demonstrate changes in density, size, type and orientation at breaks in slope, and they form distinct fields on specific areas of the exoskeleton, as in extant arthropods. Best (1961) has shown that 'tubercle' inheritance in *Encrinurus* populations were controlled by simple Mendelian laws and followed the Hardy-Weinberg equilibrium. This implies that selection played some considerable part in maintaining these structures. Comparing many trilobite sculptural features with those of modern arthropods (Miller, 1972; 1974), I have concluded that most of them performed a sensory function. Independent evidence for such a sensory function is obtained from the common occurrence of specialized pits and tubercles as proprioceptive organs in enrollment (coaptative devices of Clarkson & Henry, 1973; Miller, 1974). Other such structures are intimately associated with known visual organs (Clarkson, this volume; Miller, 1973) and must have formed accessory senses complementing vision. The following sections provide some discussion of possible functions for terrace ridge systems.

Strengthening function

Very few authors have specifically commented on the properties of terrace lines. Whittington (1962) expressed the earlier consensus view that terraces were used to strengthen the exoskeleton in the manner of corrugations on iron sheets. Unfortunately, terrace ridges are absent from the Agnostida, where the cuticle is extremely thin (10—20 μ) and generally poorly-developed in the Olenidae (cuticle rarely exceeds 100 μ in thickness). Normal cuticle thicknesses range between 300—1000 μ in most other trilobites. Furthermore, terrace systems are developed to varying degrees in closely-related trilobites with the same cuticle thickness. In many cases, terrace ridges are restricted to the doublure and there is no reason to suppose that this region bears significantly more mechanical stress than some other areas of the exoskeleton.

The form of terraces is not the same as that of corrugated iron, as the ridges usually involve only a few percent of the total cuticle thickness. Whittington (1965: 386) later correctly described terraces as asymmetric ridges developed only on the external cuticle surface. Plotting terrace relief against total cuticle thickness for a number of trilobites (Fig. 14) shows no consistent relationship between these parameters as would be expected if strengthening were a significant function of terrace ridges. Some support may have been afforded by high-relief terrace ridges to very thin cuticles and elongated tubular structures such as some genal spines (Fig. 2A).

Finally, the strengthening function hypothesis does not account for the presence of the terrace and accessory canals, nor for the detailed relationships of terrace pattern to surface topography.

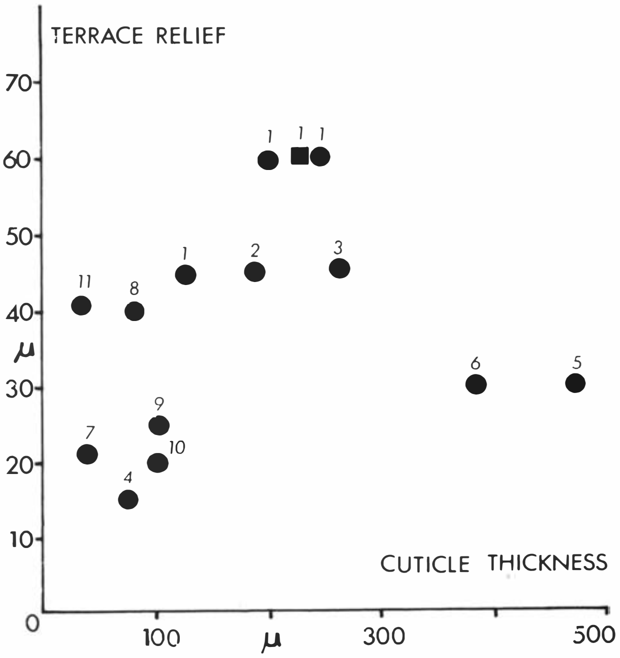

Fig. 14. Scatter diagram showing plot of terrace relief against cuticle for a variety of trilobites. Dots — one observation, squares — two observations. 1. *Asaphus raniceps.* 2. *Illaenus aduncus.* 3. *Bumastus* sp. 4. *Homotelus bromidensis.* 5. *Phacops rana* ssp. 6. *Phacops rana crassituberculata.* 7. *Anopolenus* sp. 8. *Archegonus (Phillibole) twistonensis.* 9. *Breviscutellum paliferum.* 10. *Onnia cobboldi.* 11. *Paradoxides davidis.*

Sediment guide function

Prof. G. Henningsmoen has kindly showed me the results of moving a replica of *Eobronteus laticauda* (Wahlenberg), PMO 80263, forwards through fine sand in a tray. The particles generally moved across and not along the very well-developed dorsal terrace system of this trilobite. Nevertheless, the possibility of terraces exerting some control over sediment passage or removal of surplus sediment from the exoskeleton deserves examination. The hypothesis does not, however, stand up to close scrutiny and must be rejected for the following reasons:

(1) The suggested flow-lines of sediment across the body in forward movement are not controlled by the ridge courses but by the exoskeletal morphology.

(2) Even allowing for the breakage of ridge crests which is prevalent on trilobites extracted from the matrix, the maximum terrace relief is probably little over 100 μ, which is very small to have any consistent guiding effect on sedimentary particles in the wide range of environments apparently inhabited by trilobites.

(3) The functions of the terrace and accessory canals are not explained.

(4) Trilobites known to have had a burrowing habit from direct trace fossil evidence may have weakly developed terrace ridges or none at all (e.g. *Cryptolithus* and *Flexicalymene,* Osgood, 1970).

(5) The highly overhanging scarps (Fig. 2E) of many terraces, especially on the doublure, would be most inefficient as particle guides; they would considerably increase drag effects in or on the substrate, large particles would not 'fit' and small particles would rapidly clog the guides unless some cleaning mechanism were available.

(6) There is no explanation for the different ridge profiles, or indeed for the asymmetry of terrace ridges – symmetrical ridges would be able to guide particles on both sides and thus be more efficient than terraces.

Mechanoreceptor function

Miller (1974) has shown that most pits and associated canals of trilobite exoskeletons were most likely the sites of former setae. The form of the pits is in many cases identical to the setal pits of modern arthropods, and the pits and canals of trilobites fall into size groups corresponding with those of the extant animals. For descriptive purposes, very small setae 10 μ – c. 250 μ across are referred to as microtrichs, larger ones as macrotrichs. The terrace canals and pits, therefore, are interpreted as the sites of microtrichs projecting at an angle from the scarp wall and pointed in the same direction as the scarp facing. The accessory canals are believed to have been the seats of other microtrichs emerging vertically from the dip slopes. Occasionally, macrotrichs must also have been accessory hairs, to judge from the size of some pits.

Arthropod setae perform a great variety of functions (Fish, 1972), depending on their location on the exoskeleton. Those situated on the dorsal exoskeleton and doublure, as in the case of trilobite terraces, would mainly have been concerned with tactile responses and possibly chemoreception (Thomas, 1971). However, considering the terrace setae simply as tactile mechanoreceptors does not fully explain the system as a whole, especially the presence of the ridges. Sensory fields simply comprised of dense concentrations of setae (represented by pits and canals) are elsewhere common features in trilobites (Miller, 1972; 1974). The close relationships of terrace ridge pattern to ridge topography suggests a possible relationship between the terrace system and water flow patterns over trilobite bodies.

When a fluid flow is set up over a surface, there is a film of motionless fluid in contact with the surface, above which is a boundary layer where the speed of flow changes from zero at the surface to a velocity unimpeded by viscous forces at the outside edge of the boundary layer (Shapiro, 1961). That part of the boundary layer in which viscous forces play a major role in controlling flow rate is known as the viscous sub-layer.

Properties of the boundary layer are related to the Reynolds Number, such that:

Reynolds Number = Speed x Size x Density/Viscosity.

At speeds likely to be occasioned by trilobites moving through water, flow within the boundary layer would be laminar (i.e. non-turbulent), the Reynolds Number would be rather small so the boundary layer would be relatively thick. Above the boundary layer, flow may often be turbulent – erratic both in speed and in direction. The effects discussed above are the same if the surface is at rest with respect to a moving fluid or is itself in motion.

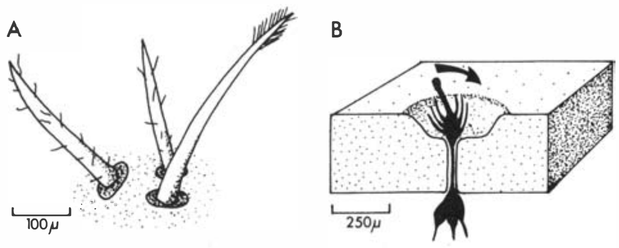

Fig. 15. Diagrams showing the structure of current receptors in extant crustaceans. A. Hair p an of *Procambarus* (after Mellon, 1963, Fig. 2). The 'active' seta has a fan of setules distally. Note innervated accessory hairs. B. Hair peg organ of *Homarus* (after Laverack, 1962, Fig. 2). Arr ner of setal deflection by current from the left. Note situation in a cuticular hollow.

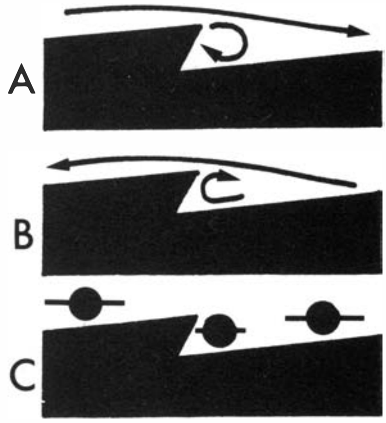

Fig. 16. A–B. Terrace ridge profiles showing idealised effect of the ridge in causing flow separations in a fluid boundary layer moving normal to the crests. In practice, viscous forces probably prevent these flow patterns from realisation. C. Condition with the currents parallel to the ridge crest.

The boundary layer properties, of flow rather consistent in speed and direction, are obviously those most suitable for efficient monitoring of current strength and vector by an animal. Current-sensing is one of the most important capabilities of aquatic animals; the viscous properties of the dense medium are exploited to provide information on the animal's speed and direction, and to monitor those fluctuations in the fluid environment which threaten stability. Two organs in recent Crustacea have been identified as current detectors. These are the hair peg organs of the lobster *Homarus* (Laverack, 1962) and hair pit receptors of the crayfish *Procambarus* (Mellon, 1963). These organs, like most other arthropod exoreceptors, are modified setae. They are contained in small pits (Fig. 15). Their trichs are 300–1000 μ long in *Procambarus* and 300 μ in *Homarus.* They would thus be within a laminar boundary flow over the exoskeleton under normal conditions of movement or currents.

We may now consider the effect of such boundary flows on trilobite terrace systems. There is every reason to believe that the terrace scarp crests will normally have been well within the laminar layer at flow rates likely for trilobites. However, it is not certain how thick the viscous sub-layer would have been. On theoretical grounds, it may have been thicker than the terrace relief (Dr. D. Ball, personal communication). Regrettably there is no experimental proof that this is so in modern arthropods. However, with some certainty, we can expect that flows across terrace ridges would generally be in the same sense as main flows but of lower velocity. Considering boundary layer flows with respect to terrace ridges, the following effects may be noted:

(1) Flows normal or oblique to the terrace scarps might separate off the crests producing separation bubbles in the trough adjacent to the crest (Fig. 16A, B). Very little is known in detail about the hydrodynamics of viscous sub-layer flow; in view of the very small scale involved it is likely that large viscous forces would not allow these effects. There will, however, probably be zones of slow flow in these troughs.

(2) The least resistance to flows (i.e. the lowest drag) impinging normally or obliquely to ridges would be with the terrace scarps facing downstream (compare Fig. 16A with 16B).

(3) Flows parallel to the terrace scarp will move with low drag in the direction of the ridges (Fig. 16C).

(4) Differences in ridge relief and profile would produce varied flow velocities, drag effects and patterns of trough slow flow zones, but it is not possible to predict these theoretically in view of the lack of knowledge about detailed behaviour of viscous-controlled flows.

Angled setae in modern arthropods have a flexibility limited to the plane of their inclination (see Fig. 18B). The angled terrace setae, if suitably compliant, would be in an ideal position for their deflection by currents flowing normal or obliquely to the ridges, as shown in Fig. 17. Modern crustacean current receptors are bi-directional owing to their bipolar innervation. In *Procambarus* the hair pit organs of the carapace are oriented to detect only currents flowing in either direction along the longitudinal body axis (Mellon, 1963). In the case of the trilobite, there are potentially four main directions at which current flows might cause setal deflection.

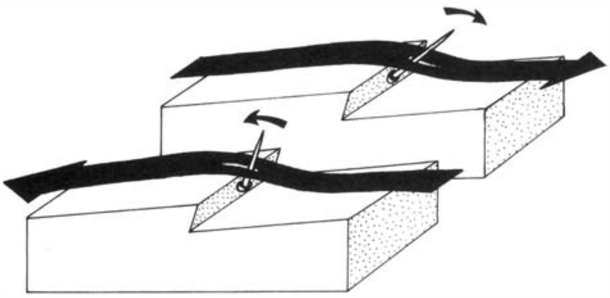

Fig. 17. Schematic diagram showing mechanism for deflection of proposed terrace crest microtrichs by currents moving obliquely or normal to the terrace scarps.

These are the forward and backward flows normal to the ridges and forward and backward flows parallel to the ridges. To sense all these directions, the terrace setae would need at least 4-polar innervation (i.e. would have four nerve cell transducers of the setal deflection into electric impulses). This arrangement would need intricate nervous filtering in the central nervous system to interpret the flow directions, especially those which would commonly occur between the four nominal polar directions. Instead, the angled emergence of the terrace setae with their implied limited flexibility suggests that they deflected only in response to flows normal or oblique to the ridges. In this much simpler case, only the bipolar innervations found in the recent current receptors would be required.

If deflections of the sensillae are thus limited to a plane normal to the terrace ridges, it remains to consider the function of those terraces which course parallel to flow when this is along the body antero-posterior axis. There are two possible explanations here:

(1) No terraces are perfectly straight, and this curvature will mean that for most points along the ridges the nominally parallel flows will meet them tangentially and thus have at least a small component to deflect the terrace microtrichs in their preferred vertical plane. Possibly, though, in a number of cases, this small component may not be above the threshold value for stimulation of the nerve cells associated with the microtrichs.

(2) Trilobites had the ability to move sideways and obliquely as well as forwards as we know from trace fossil evidence (e.g. Seilacher, 1955; Crimes, 1970; Miller, 1972). Furthermore, current in natural environments can impinge upon an animal from any direction. Lateral or oblique currents and movement would thus cause flows across the antero-posteriorly orientated terrace ridges in question, appropriately stimulating the microtrichs. Thus the generally concentric pattern of terrace ridges, especially on the dorsal surface, offers a potentially useful method of detecting flow or movement directions, and could have been a mediating factor in producing the appropriate rheotactic response in the animal. The longitudinal terraces are especially characteristic of long genal spines, and these would form the leading edge of the body in lateral movement or to lateral currents.

Perhaps the nearest approach to the trilobite terrace system in a modern arthropod is found in the small freshwater isopod crustacean *Asellus.* The dorsal exoskeleton of this animal is equipped with short crescentic rows of angled microtrichs with a common ridge-like base (Fig. 18). There are also angled macrotrichs with their flexibility restricted by a basal semilunate flap (Fig. 18). Everywhere on the body, the microtrich crescents face outwards, recalling the trilobite

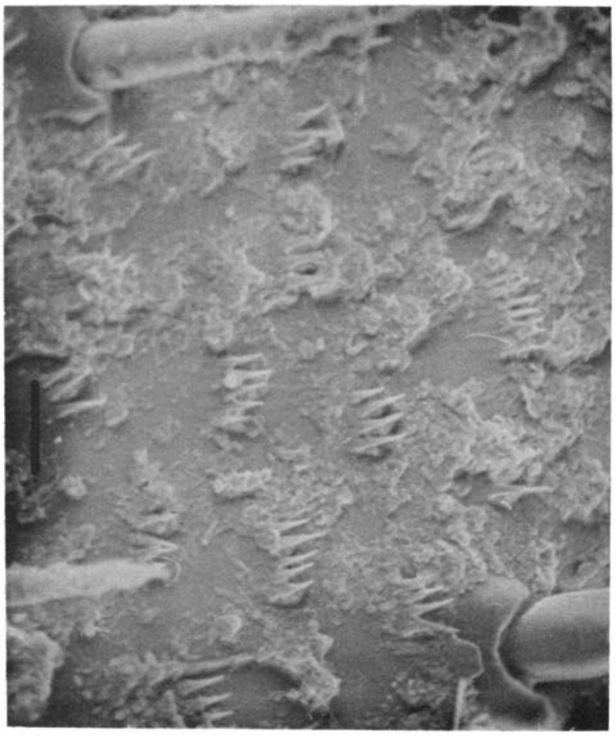

Fig. 18. Scanning electron micrograph of dorsal view of the telson of the extant isopod **crustacean** *Asellus aquaticus* L. Note the crescentic rows of microtrich setae and the angled macrotrichs (top left, lower right) with semi-lunate base flaps, all the setae facing in the same direction. Scale bar 4 microns.

doublure terraces, and were supposed by Needham (1942), although without experimental evidence, to act as current detectors.

The presence of accessory micro- and macrotrichs along with current detectors is to be expected, and occurs in modern crustaceans (note the two non-innervated accessory hairs of the *Procambarus* organ, Fig. 15A). These setae would provide a screen to keep sediment from clogging the ridges and possibly may have had an active cleaning role, since many setae of modern arthropods are mobile and are used in this way. If they were innervated, the trilobite accessory setae could have added tactile information about sediment passage over the exoskeleton, but most likely they would not have sufficient compliance to register the water flows, as is the case in the modern arthropods. The current-detecting setae are specially modified for their purpose. The dense concentrations of accessory pits at the anterior of *Eobronteus* (Fig. 19A) and *Nanohughmilleria* (Fig. 13A) suggest such a tactile function.

To complete the model for the current-monitoring function of the terrace system, it remains to enquire if the terrace microtrichs as proposed would indeed be compliant enough to detect the low flow velocities of the viscous sub-layer. This does not seem a serious problem, however, since the modern current receptors are significantly of great sensitivity, and they would certainly operate well within the boundary layer. In *Homarus,* for example, Laverack (1962) reports a threshold current velocity for the hair peg organs of only 0·23 cm/sec. In trilobites, the angled terrace trichs appear of comparable size to the modern current receptors, although of course it is impossible to determine their exact morphology. They may have been some form of pit organs as in Crustacea, but perhaps were more likely simple setae, possibly with tufts of fine setules to increase their drag effectiveness, although this may not have been neccessary in viscous flows.

In order to test further the current sensing hypothesis, I have performed some more experiments with the extended *Eobronteus laticauda* Wahlenberg specimen previously used by Prof. Henningsmoen, as described above. The trilobite exists as an excellently-detailed external mould, from which an accurate heavy rubber mould was prepared for me at the Paleontologisk Museum, Oslo. The replica was embedded in fine sand with the body horizontal and head upstream at the bottom of a 180 x 12 x 12 cm glass flume tank. Water was circulated by means of a peristaltic pump regulated to provide flow rates of 3—5 cm/sec. at the centre of the tank occupied by the model. Once set up, the tank was allowed to run undisturbed for at least two hours before the start of the experiment to allow steady-state conditions to be established.

Small quantities of a water soluble dye were injected by means of a fine hypodermic syringe into the laminar boundary layer near the front of the model. Flow patterns across the exo-

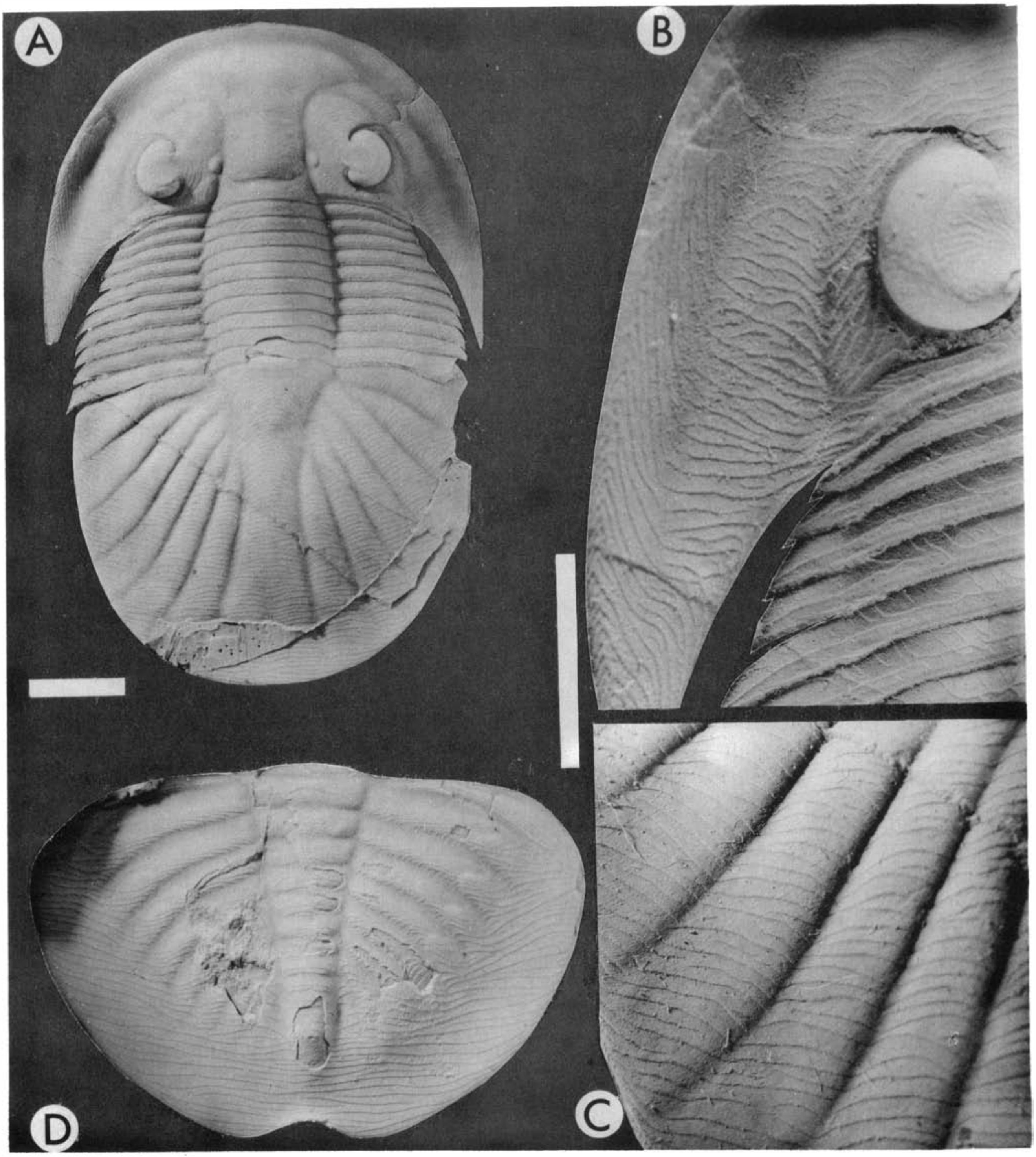

Fig. 19. A – C. Rubber mould of *Eobronteus laticauda* (Wahlenberg), Upper Ordovician, Stage 5a, Modum, near Oslo. PMO 80263. All scales 1 cm. A. Dorsal view of complete specimen showing course of terrace ridged and disposition of dorsal terrace system. B. Details of librigenal area, note deflections of terraces into the shallow furrows and the deflections over the crest of the border. C. Detail of terrace disposition on the pygidium. Note the outward and backward facing of the ridges. E. Pygidium of *Ogygiocaris dilatata* Sars, Stage $4a\alpha_{3-4}$, Muggerudkleiva, Øvre Sandsvær, Norway. PMO 70518. Note the similar disposition of the terrace system to the *Eobronteus* pygidium above, but more marked deflection of the ridges towards, and their absence from, the much deeper pleural furrows.

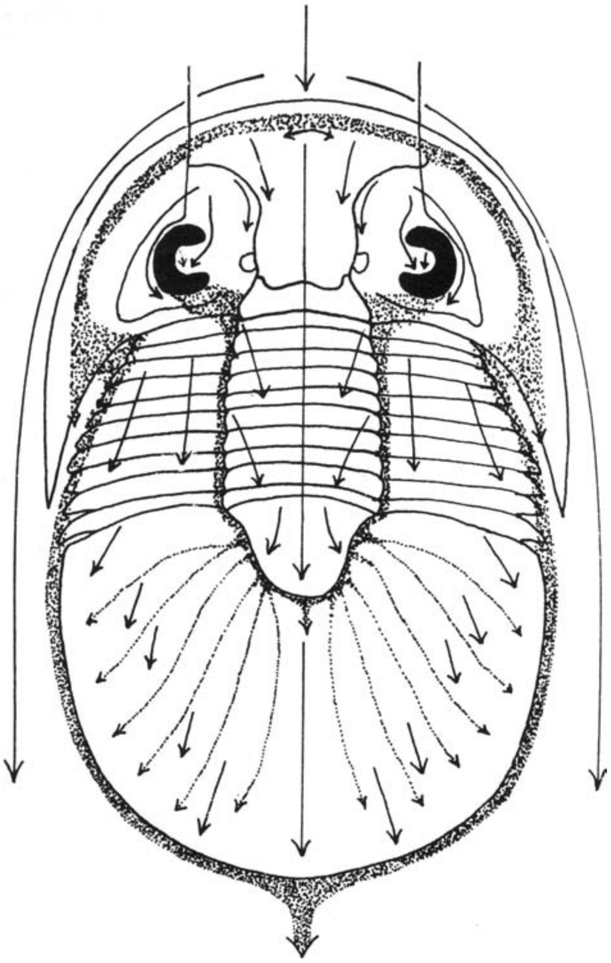

Fig. 20. Sketch of boundary layer flow trends produced experimentally with an anterior-posterior current flow over a mould of *Eobronteus laticauda* PMO 80263. Dotted areas indicate slow flow zones.

skeleton were observed using the dye streamers; these are presented diagramatically in Fig. 20. Flow separation occurred around the front of the cephalon to form streams moving rapidly down the lateral margins of the exoskeleton. These lateral flows reunited behind the pygidium. Other rather fast flows swept backwards across the cheeks and glabella with separations and higher velocities around the eyes. It may be noted in connection with this behaviour of ocular flows that strips of terrace field part way around the eye at the base of the eye socle are common in many trilobite groups. The steep anteriormost face of the eyes produced vertical separations with some turbulence a little way above the eyes, but the boundary layer flow across the palpebral lobes was directed posteriorly.

The most striking feature of the flow pattern was the existence of slow-flow zones set up in the axial furrows. Dye persisted for some minutes in these furrows, being slowly drawn backwards from a pool behind the palpebral lobes and eyes (Fig. 20), finally draining across the pygidium down the rib furrows, following the confluence of the flows from the two dorsal furrows at the rhachis termination (Fig. 20). The rest of the boundary layer sheet showed faster flows posteriorly over the raised portions of the pygidial ribs. A further slow-flow zone was established in the shallow border furrow of the cephalon; the water from this drained from the genae backwards against the pleural segment tips and pygidial border.

At no time during the experiment was any impression gained that the terrace ridges themselves were guiding the boundary layer flows. The terrace ridges, although of somewhat reduced relief owing to crest breakage, were well within the boundary layer, and the flow patterns of the boundary layer sheet were undoubtedly a product of the exoskeletal morphology.

Comparing the experimental flow patterns (Fig. 20) with the terrace pattern (Fig. 19), there are evidently close connections. The tendency of terrace ridges to run tangentially into furrows has been noted already; the experimental evidence shows that such furrows are the sites of slow-flow zones within the boundary layer sheet. It is tempting to suggest that this orientation and the accompanying increase in terrace relief combine to offset the much-reduced flow velocity in the furrows which may fall below the threshold for stimulation of the proposed terrace microtrichs. In very deep furrows, for example apodemal furrows, there would be dead water or at most extremely slow flows which would be useless for current detection purposes. This could explain the failure of terraces to continue across the deep furrows.

Responses of terrace course patterns on the *Eobronteus* to the flow patterns are remarkably exact. Note the abrupt backward deflection of terrace ridges at the crest of the raised cephalic border (Fig. 19B), where this border separates two slow-flow zones (Fig. 20), so that the terraces meet the flows at right angles or obliquely and face downstream. The general pattern, especially for the fast-flow areas, is for the currents to meet the terraces either normally or obliquely with a downstream facing, as predicted by the rheo-sensing model.

Obviously much further work on experimental testing of the current-monitoring model is required, using different trilobites and currents impinging from different directions. However, at this stage there seems enough support for the model from both experimental and comparative morphological viewpoints to examine some further implications. What advantage does a rather complex ridge-borne system of sensillae have over the simple scattered pit system of some modern arthropods? Is it possible to explain the even terrace space and the apparent restriction on ridge-spacing?

With regard to the ridge system and the tendency to even ridge separation in parallel terrace zones, it might be suggested that such an arrangement offers a convenient method of detecting not just flow directions but also flow velocities – or rather changes in flow velocities. Such changes would induce 'waves' of terrace microtrich stimulation along successive ridge crests along the direction of flow. This effect is reminiscent of the occlusion of successive ommatidia by a moving object, postulated by Clarkson (1966) as a method of detecting movement with the trilobite schizochroal eye. Both the eye and the terrace systems embody the two essentials for successful operation of this function, namely a linear strip succession of sensillae and an even spacing of the strips. Apart from the doublure ridges discussed below, the zones of parallel terraces are situated mainly on or close to the exoskeletal borders. The margins of modern aquatic arthropods are similarly equipped with 'early warning' sensillae. The terrace ridge system is thus seen as a convenient method of ensuring simultaneous stimulation of a linear series of current transducers, which in trilobites may have been used as a detector for changes in current speed.

The reason for the restricted range in ridge separation (and the preferred ridge separations characteristic of certain taxa) is more difficult to explain. Presumably some common and therefore external factor arbitrates the separation range, rather than this resulting from some inherent phyletic character (note the close similarities of the probable eurypterid terrace system to that of trilobites). Possibly the hydrodynamics of the boundary layer are again involved. The Reynolds Number (p. 216) includes consideration of both size and speed of the moving body as well as viscosity of the medium. Since the viscosity remains a constant in an aquatic medium for practical purposes, the size and speed of trilobites would materially affect the properties of their boundary layer flows. For very small trilobites or juveniles to possess terrace ridges allometrically scaled down from the adult condition would be pointless, as the viscous forces would be so high as to prevent their operation. This may explain why, for example, the tiny meraspis of *Paladin eichwaldi shunnerensis* described on p. 211 apparently has no terrace system. Development of the ridges can certainly begin early in ontogeny, but only at some critical size-weight ratio could the terrace system become fully functional. Larger trilobites, with their greater power:weight ratio would be capable of much greater movement speeds, apart from having boundary layers in which viscous forces have less of a limiting effect on the terrace functions envisaged. The upper limit of the ridge spacing may be a function of both nervous integration problems and a 'compromise' separation which is optimum for detecting flow speed changes of magnitudes normally encountered, but this is merely speculative.

The discussion so far has mainly been concerned with the dorsal terrace system. The doublure, however, is far more commonly terraced than the dorsal surface of the exoskeleton. In highly vaulted trilobites, the doublure is often held at a steep angle to the substrate, and being thus deeply recessed within the exoskeletal cavity is somewhat sheltered from external currents. In all cases, however, currents generated locally by metachronal limb movements in this cavity will dominate and interfere with any external flows. The limb-beats of modern aquatic arthropods set up a continuous current pattern over the ventral surface, which may be variously specialised for feeding, propulsion or gill ventilation. The limb-generated currents follow patterns determined by the nature of the limbs and the topography of the ventral surface, following the rules of hydrodynamics. Knowledge of the anatomy of some trilobite limbs enables us to use the modern analogues in reconstruction of trilobite ventral currents. Fig. 21B shows a generalised current pattern as deduced by Cannon & Manton (1926), Bergström (1969, 1973) and Miller (1972). This may be compared with the terrace course and facing on the doublure (Fig. 21A). The relationships of the doublure terraces to the proposed ventral flow pattern are similar to those discussed above for dorsal terrace systems and flows. Currents pass over the terraces at right-angles or obliquely, the ridges are orientated to face downstream to the anterior mid-line

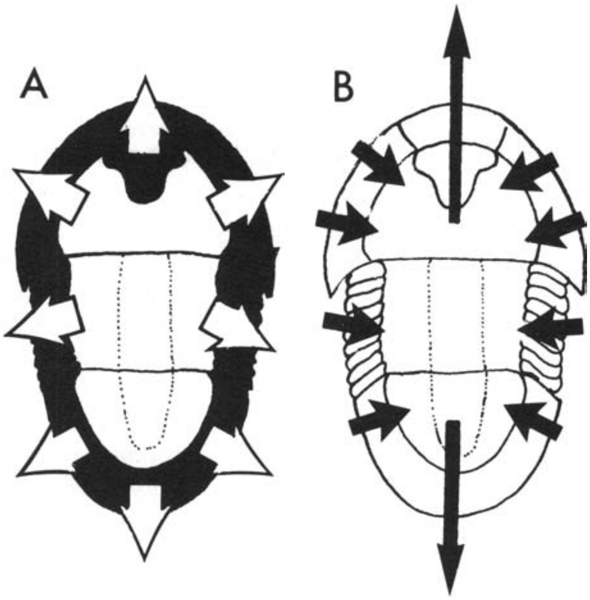

Fig. 21. Generalised view of a trilobite in ventral aspect, showing: A. Facing direction of doublure terrace ridges. B. Courses of reconstructed feeding – propulsory – ventilatory currents generated by appendage activity.

current which presumably emerged through the anterior arch when not deflected into the mouth by the hypostome for feeding purposes. The ridges also face downstream to the posterior 'propulsive' backwash, similarly offering low drag. The laterally ingoing currents, however, cross with the terrace ridges facing upstream. This could merely be the result of continuation of the ridges concentrically around the doublure, or it may offer a method of differentiation between ingoing and outgoing flows by the terrace setal deflection.

It will be noted that doublure terraces have particularly high relief and asymmetry, as well as being very evenly-spaced. This might suggest that their efficiency in monitoring current strength and direction was high, and therefore that the terrace function and doublure function are closely connected. Modern crustaceans are equipped with hair pits and other sensillae on the appendages themselves and can thus monitor limb movements and concomitant water disturbances directly. The crustaceans, however, do not possess the laterally expanded trilobitoid dorsal shield and doublure, which offers an ideal site for steady-state active current monitoring. The doublure system would complement the sensillae borne on the trilobite appendages. In view of the wider distribution of a doublure terrace system in trilobites, and its greater degree of morphological development, it is possible that the terrace system had its origins on the doublure, later migrating dorsally for rheotactic purposes connected with specific habitats. At present, there is no direct evidence bearing upon the origin of terrace systems or their evolution. One may speculate that the development may have proceeded from an arrangement of setal pits or seta-bearing 'tubercles' in rows to exploit the flow-rate measuring possibility of this configuration, subsequently resulting in the fusion of such sensillar rows into ridges. Work in progress in collaboration with R. Feist on evolutionary studies of scutelluids may offer some information on this problem.

CONCLUSION AND IMPLICATIONS OF THIS STUDY

In this type of functional analysis, it is always important to avoid circular arguments, but still to recognise that much of the evidence is linked. It is difficult to escape the anatomical evidence that the terrace system was involved in some sensory function. The construction, size, scale and pattern of terraced systems, and the relations of these patterns to surface topography in a consistent way preclude merely a tactile function. Instead, these features are considered to relate to hydrodynamic conditions within the laminar boundary layer set up whenever water moved over the exoskeleton, with rows of angled microtrichs for detecting changes in direction and speed of water movements. This system, especially where well-developed on the dorsal surface as well as the doublure, would have been potentially of great flexibility, capable of supplying detailed information about external flow conditions, the animal's movements and its feeding-respiratory currents. It would not be surprising if the terrace development were linked in many ways with the animal's mode of life, so that study of terrace systems along with other trilobite sensory fields could offer a tool of some value in determination of specific life-modes. Of course, this hypothesis of the terraces as current-monitors cannot be directly tested, but from abundant trace fossil evidence, there is no doubt that trilobites exhibited rheotactic behaviour and therefore must have possessed some sort of current-detecting devices.

A number of aspects of trilobite terrace systems remain for study: the manner of terrace ridge secretion, their origin and evolution, the reasons for their absence in some trilobite groups and the nature of compensatory organs in these groups, the extent of terrace pattern variations between individuals of the same species. These problems are common to all forms of trilobite sculpture and also apply equally to modern arthropods. The morphological investigatory techniques perforce developed by palaeontologists can be very powerful when applied to modern animals, especially when supplement is made with physiological work. It is hoped that future work along these lines will be attempted in connection with arthropod sensillae; for example, the relationships of extant arthropod sensillae to physical characteristics of the environment such as fluid boundary layers have hardly been considered. Until such work is completed, it will hardly be possible to interpret many features of trilobite morphology with great confidence.

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Moulting in trilobites

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Moulting in trilobites is insufficiently understood. Configurations of trilobite exoskeletons that may be exuviae, assumed examples of abnormal moulting, cephalic morphology, and moulting in recent marine arthropods are used as evidence for deducing modes of ecdysis in trilobites. Apparently most or all exuviating trilobites generally emerged forwards. In trilobites with sutures certain sutures (and occasionally the neck joint) opened to form the main ecdysial opening, whereas other sutures may have had other functions. In trilobites without sutures the ecdysial opening had to be formed in a different way. In both cases thoracic joints could become disarticulated. Various aspects of the moulting are discussed, not least its bearing on cephalic morphology. Specimens of *Isotelus* with fused median suture are reported.

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Moulting in trilobites deserves attention for the following reasons.

(1) Knowledge of mode of moulting adds to our knowledge of general trilobite biology.

(2) Demonstration of mode of moulting may aid in understanding location of sutures and morphology of exoskeleton in general.

(3) Recognition of exuviae lying where they were shed would be important, because they, besided being body fossils, are also in a way trace fossils, showing where, how, and in which direction the trilobite moved out of its old exoskeleton. Being in situ, such exuviae would be of palaeogeographic, palaeoecologic, and palaeo-environmental implication (indicating, for example, low-energy environment).

(4) Recognition of exuviae lying where shed might eventually be used to indicate orientation of host layers.

(5) Too little is known about moulting in trilobites, and additional observations are badly needed.

GENERAL REMARKS ON MOULTING

Arthropods generally moult and shed their integument several times. These are critical times for the animal, both because it is practically defenceless at and just after ecdysis, and because of the danger that it will hurt itself during exuviation. Few aspects of arthropod physiology are as important as moulting, which in fact dominates the life of an arthropod (Passano 1960:473).

The term "moulting" is used in a rather broad sense in modern literature on recent arthropods, where it may include "all of the processes of preparation for withdrawal from the old integument, ecdysis and postecdysis, increase in linear size, as well as subsequent tissue growth" (Passano 1960:473). Casting of the old exoskeleton, exuviation, takes place during exdysis, which may also comprise swelling of the animal by uptake of water.

MOULTING IN RECENT MARINE ARTHROPODS

Before discussing moulting in trilobites, it may be useful to recapitulate a little of what is known about moulting in recent marine arthropods (mainly decapods), treated in greater detail by Passano (1960).

Fig. 1 illustrates the time span from one exdysis (E) to the next. This intermoult cycle may be divided into 5 stages, A–E (and subdivisions). The proportions between the various stages vary somewhat from species to species. Some of the events characterizing the stages are given below, especially those of direct interest to the palaeontologist.

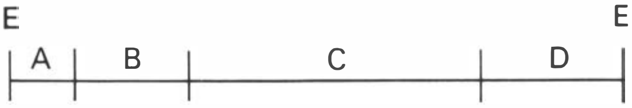

Fig. 1. Ecdysial stages from ecdysis (E) to ecdysis. See text.

The hard stage (C) is the "normal", intermoult stage with both fully developed exoskeleton and full activity level of the animal. It may last no longer than 20% of the intermoult cycle in some forms.

In the *proecdysial stage (D)*, also a "hard-shell" stage, similar in appearance to stage C, the ecdysis is prepared for in various ways. Among other changes, the animal ceases to feed and oxygen uptake increases markedly. The inner layer of the old cuticle is softened or dissolved, liberating it from the epidermis, and pre-exuvial layers of new, elastic exoskeleton are formed. Resorption of organic and inorganic matter in the exoskeleton makes the old exoskeleton (the exuvium) brittle (thus the crab *Carcinus* resorbs 79% of the organic matter and 13% of the inorganic matter in the carapace). A lobster manages to withdraw its large chela through a relatively small tubular space because decalcification takes place in certain areas such as at the bases of chelipeds, thus softening the 'bottle necks'. Specific resorption occurs along the exdysial sutures, resulting in opening of the sutures at the very end of stage D. By then, the animal has retreated to as safe a place as its environment permits.

Ecdysis (stage E) can be divided into the passive phase and the active phase in decapods. In the passive phase (which may last between 2 and 8 hours in *Cancer*), nearly all movements of the animal cease, but water is swallowed, increasing the hydrostatic pressure in the digestive tract lumen, and the blood volume doubles. The animal swells, pushing apart the old exoskeleton at the ecdysial sutures. The passive phase is succeeded by the exuviation, spasm-like movements of the animal (cf. Richter 1937:424), and active withdrawal from the old exoskeleton. This may last a few seconds, or half an hour or more, but if abnormally prolonged, it usually ends in death. The mucilaginous layer may lubricate the animal's withdrawal from the old exuvium. The whole of the integument (including that of appendages) is cast, and so is the lining of the digestive tract, remaining attached to the rest of the exuvium at mouth and anus (it breaks or is entirely resorbed in the cardiac region).

There are two "postecdysial stages", *the soft stage (A)* and *paper shell stage (B).* The soft-skinned animal in stage A immediately recommences to take up water; this time to swell in order to expand its new, elastic exoskeleton before it stiffens at the close of stage A and in stage B, when also endocuticle secretion begins. Feeding starts again at the close of stage B, which is succeeded by the hard stage C.

TRILOBITE EXUVIAE AND MOULTING

Growth stages have long been described in trilobites, showing that trilobites moulted. Little has been published on *how* they moulted, although this undoubtedly affected exoskeletal morphology. Thus it must have been vital to the animal to ensure a smooth and easy exuviation.

RECOGNITION OF TRILOBITE EXUVIAE

It is now generally accepted that trilobite exuviae could become fossilized, although this was earlier doubted (cf. discussion by Richter 1937:422). It appears that exuviae are less attractive to scavengers and stand an even better chance of being preserved than do remains of dead animals.

Størmer (1934:56) describes how he once kept a large aquarium with several specimens of *Limulus* as well as a number of shrimps and crabs. The *Limulus* specimens died, and their bodies were immediately attacked by crustaceans. The ventral soft parts were removed, and the more solid dorsal test was partly torn to pieces along the margins. The *Limulus*-exuviae in the same aquarium were left untouched.

The chances of finding exuviae should, then, be greater than finding remains of dead animals, and even more so because each trilobite normally produced several exuviae (and but one dead animal).

Most trilobite remains found are totally isolated parts of the exoskeleton, frequently transported and sorted. The discussion above suggests that most of them are exuvial remains, but it does not seem possible at present to distinguish these from exoskeletal parts of dead trilobites, unless their structure is different, as suggested by Balashova (1955:33).

The chances of distinguishing exuviae from exoskeletons of dead animals is greater when it comes to more or less complete specimens or dismembered specimens with all or most exoskeletal parts preserved. Such preservations are rarer, but may be common locally.

Complete specimens showing no fissures between exoskeletal plates may represent dead animals, especially if they are found in life attitude or are tightly enrolled (particularly if interlocked, cf. e.g. Clarkson & Henry 1973).

A specimen with "open" sutures or one which is more or less dismembered may represent the remains of:

(1) A dead trilobite, dismembered or with sutures opened at its site of death or after post-mortem transport, or

(2) an exuvium, as shed by the trilobite (undisturbed exuvium) or disturbed post-ecdysially.

It seems probable that decomposition, attacks by scavengers, and other causes may have led to an opening of sutures in dead animals and dismembering of its exoskeleton in such a way as to simulate undisturbed exuviae (cf. Richter 1920:201).

As to displacement of exoskeletal parts, it may be recalled that exuviae are hardly attacked by scavengers. *The animal most likely to displace exuvial units is the exuviating trilobite itself,* although other animals might do so more or less accidentally. As to displacement by currents, this is not very likely when detached parts of a single individual and of different sizes and hydrodynamic properties occur associated. Generally it is evident when currents have had a transporting effect.

Certain types of configurations of exoskeletal parts are more common than could be expected if their arrangements were due to chance displacement by scavengers or other animals, not to mention displacement by currents.

Criteria used for recognizing exuviae:

(1) Presence of ecdysial lines (generally cephalic sutures) showing evidence of having been opened.

(2) Displacement of exoskeletal parts (exuvial units), attributable to movements of the soft trilobite emerging from its old integument.

(3) Marked tendency for a certain type of configuration (with variations) of exoskeletal parts of a certain species or group.

(4) Evidence of abnormal exuviation.

(5) Evidence of quiet bottom conditions.

(6) Lack of evidence indicating a dead trilobite (such as life attitude and locked enrolled test).

Criteria 2–4 indicate strongly that the exoskeletal parts are exuvial parts preserved where they were shed (undisturbed exuviae).

Even if it should be impossible to prove that any one specimen represents an exuvium, the frequency of certain exoskeletal configurations or constellations, their agreement with inferred ecdysial openings, and other circumstances may disclose with a high degree of possibility how exuviation took place in a given species.

EXUVIAL UNITS AND ECDYSIAL LINES

It is generally accepted that cephalic sutures played a role during ecdysis (cf. e.g. Hupé 1953a:120, 1953b:69, Harrington 1959:O58, O111). In addition to sutures, joints are lines of weakness (separating parts of the mineralized exoskeleton) and as such are potential ecdysial lines. Apparently single exoskeletal plates as well as several plates together could be shed as *exuvial units.* The following terms are used for some composite integumental units:

Axial shield (Henningsmoen 1957): cranidium + thorax + pygidium.

Genicranidium (pl. *-ia*): main part of cephalon delimited by marginal or submarginal suture (= genicranium Henningsmoen 1959).

Lower cephalic unit: the cephalic integument with exception of cranidium or genicranidium (= *upper cephalic unit*).

Thoracopygon (pl. *-a*): thorax + pygidium.

The maximum number of sutures and exoskeletal plates in the trilobite head appears to have been the ancestral condition in many, if not all, trilobite groups. The maximum number of sutures appears to be seven: 2 facial sutures + 1 rostral suture (or 1 "grande suture" + 2 connective sutures), 1 hypostomal suture, and 2 ocular sutures. A circumocular suture (Öpik 1967:54) is present in most Cambrian trilobites, whereas the visual surface is fused with the free cheek in most post-Cambrian forms. Disregarding a metastome, the resulting maximum number of exoskeletal plates in the head is also seven: 1 cranidium, 2 visual surfaces, 1 rostral plate, 2 free cheeks, and 1 hypostome.

Sutures are lines of weakness in the exoskeleton, and as such are likely to yield to pressure. It is therefore not surprising that a general trend in trilobite evolution was the reduction of the number of sutures and thus of exoskeletal parts. Disregarding a metastoma, the minimum number of exoskeletal plates known in the head is apparently two, as in some phacopids, where the entire cephalon is separated from the hypostome by the hypostomal suture. In agnostid families and eodiscids the hypostome is an isolated plate which was probably connected to the cephalon by a soft integument. Olenellids with ankylozed hypostomal suture have two main plates, the cephalon and the rostri-hypostomal unit, but according to Öpik (1967:55) they have two additional small plates, the visual surfaces.

THE ECDYSIAL LINES AND THE ECDYSIAL OPENING

When moulting, most or perhaps all trilobites apparently withdrew from their old exoskeleton through an opening in front. To withdraw from the post-cephalic integument was relatively simple. Difficulties lay in the head, with its vital and delicate organs like eyes, mouth, and digestive tract, and where an ecdysial opening had to be formed. This demanded special provisions; the sutures are regarded as such.

One may distinguish between two kinds of cephalic sutures according to function, i.e. (1) the *ecdysial gape suture* providing for the main ecdysial opening, and (2) *auxiliary sutures* facilitating ecdysis in other ways (e.g. facilitating ecdysis of certain organs). It should be borne in mind, however, that the ecdysial gape suture in many trilobites could serve more than its main function.

The ecdysial gape suture

The ecdysial gape suture, dependent on type of cephalic sutures, could be either the facial sutures (together with rostral suture where present) or the marginal or submarginal suture. By the opening of these, the upper cephalic unit formed the upper 'jaw' of the ecdysial gape. It was the cranidium in trilobites with facial sutures, and the cephalon (strictly genicranidium) in trilobites with marginal or submarginal sutures. In both cases the lower 'jaw' (the lower cephalic unit) was the remaining part of the cephalic integument. It is not known whether the lower unit generally remained attached posteriorly by the soft integument, or was completely detached. In both cases, however, the soft trilobite withdrew between the lower and upper cephalic unit. During exuviation the *neck joint,* between the cranidium or genicranidium and thorax, apparently opened easily. The upper cephalic unit was no longer a hinged lid but was shed separately, leaving a correspondingly large ecdysial opening formed both by the facial sutures (± rostral suture) and the neck joint. This may possibly have been the rule in some trilobites. Occasionally, the whole cephalic integument may have been split from the post-cephalic integument, leaving a large post-cephalic ecdysial opening. Even so, the ecdysial gape suture may have opened to facilitate exuviation of the head.

ANTERIOR PASSAGEWAY. – To allow the soft trilobite to emerge forwards through an anterior opening below the cranidium (or genicranidium), the latter could not be bent under in front to form an exoskeletal 'pocket' (Fig. 2). If such a hindrance was present, the cranidium or genicranidium, generally together with the attached thoracopygon, would be dragged along with the advancing soft trilobite. It is significant that such a pocket is generally avoided by the location of the anterior sutures. In a few trilobites with a distinct anterodorsal pocket, the mode of ecdysis had to be changed. Thus in those phacopids where the cephalon is a single shield with the doublure bent under in front, the cephalon had to be thrown away before the animal could emerge (Salterian mode of moulting).

Most trilobites, however, had no anterodorsal pocket. This is, of course, the case in trilobites with marginal suture and in trilobites where the suture is marginal in front but becomes dorsal (facial) for a shorter or longer stretch laterally or posterolaterally, as in entomaspidids and some harpidids, trinucleids, dionidids, and raphiophorids. In olenellids, with their ventral-intramarginal suture, the anterior part of the suture is close to the margin, closer than it appears in some schematic reconstructions. In forms with facial suture, the cranidium does not generally form a pocket at the anterior margin because of the location of the facial or rostral and facial sutures. Exceptions can be forms with an inflated and anteriorly protruding glabella, where, however, the pocket is wide and open. Nevertheless, even in these trilobites a pocket is commonly avoided. Thus in forms with rostral plate, the rostral suture may be placed far forwards, as in *Staurocephalus* and *Paralejurus*. The median and facial sutures are extended all the way to the tip of the extremely long but broadbased anterior process of the cranidium in forms like *Ectenaspis* and *Megistaspidella*, and the rostral suture extends to the front of the tongue-shaped anterior process of *Lichas platyrhinus* (cf. Hupé 1953, Fig. 200).

Anterior pockets and low barriers do exist in the lower cephalic unit. If the exuviating trilobite first released itself from the lower cephalic unit, as suggested by exoskeletal configurations of assumed exuviae, a low barrier in front would not be a great obstacle to a forward movement. Nevertheless, anterior pockets and barriers appear to be avoided. Thus the anterior-most part of the facial sutures tends to lie close to the margin in various

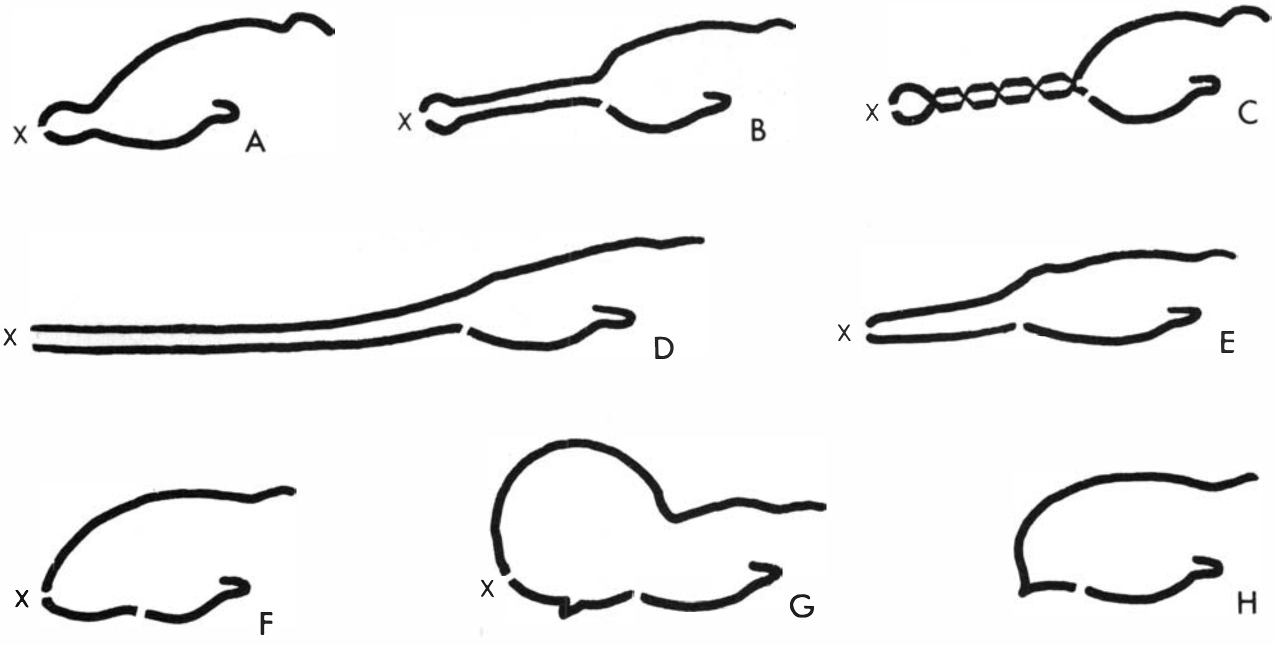

Fig. 2. Schematic sagittal sections (not to scale) of trilobite cephala with (A–G) or without (H) anterior suture (at x) splitting the anterior exoskeletal "pocket". A, with rostri-hypostomal plate and without preglabellar field sagitally. *B*, with brim. *C*, with brim and connective pillars between upper and lower lamella. *D* with long, anterior spine *(Megistaspidella)*. *E*, with tongue-shaped anterior process *(Lichas celorhin)*. *G*, with protruding anteriorly inflated glabella *(Staurocephalus)*. *H*, without anterior suture.

groups, possibly to reduce the pockets formed by the anterior parts of the free cheeks and their doublures. Anyhow, narrow librigenal pockets do exist. Since the soft trilobite apparently did manage to emerge forwards in forms with fused free cheeks and between these and the cranidium, it seems probable that they could do so also in forms with median or connective sutures, even if the lower cephalic unit was not completely detached. If complete shields of trilobites with median or connective sutures (and opened facial sutures) represent post-ecdysially "closed" exuviae (Fig. 3), as may be common in trilobites with the harpid mode of moulting – the soft trilobite could undoubtedly emerge forwards through the ecdysial gape in spite of small anterior pockets formed by the free cheeks.

According to Öpik (1958:28), the facial sutures of *Redlichia* would have been adequate for moulting, but for a trap consisting of a row of spines on the ventral surface of the cranidium, interlocking with a row of spines on the dorsal side of the line of fusion between rostral plate and hypostome (Fig. 4). The row of spines on the ventral surface of the

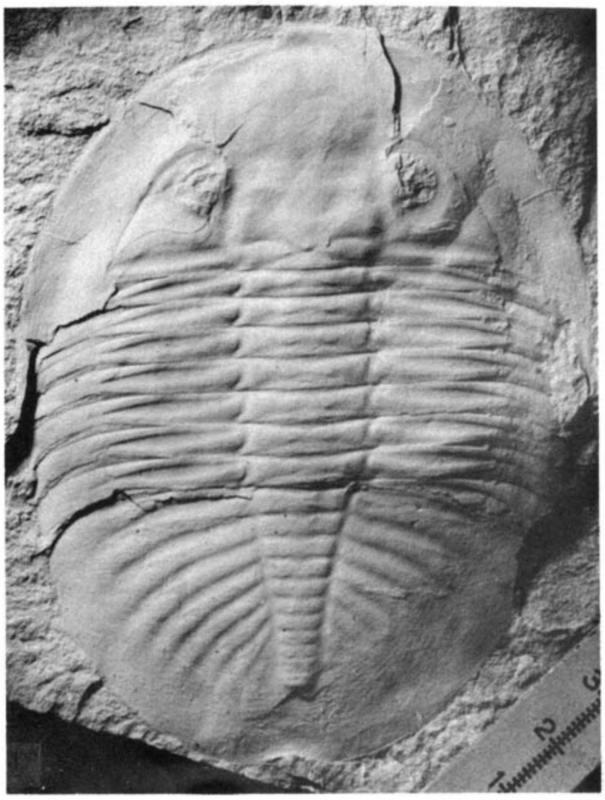

Fig. 3. Almost complete shield of an asaphid *(Ogygiocaris)* with opened facial sutures. Cranidium slightly displaced forwards in relation to free cheeks, as seen anteriorly and by "double facial sutures". *Collapsed exoskelton of dead animal or exuvium?* Either is possible. Slight telescoping of pygidium beneath thorax (most of 8th segment missing) may indicate exuvial origin, but when not more pronounced than here, the telescoping could possibly be ascribed to collapse of exoskeleton. From Henningsmoen (1960, Pl. 1:1). Size indicated by centimetre scale.

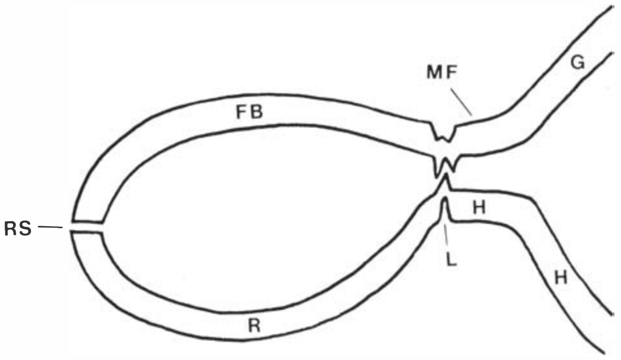

Fig. 4. Schematic sagittal section through anterior part of cephalon of *Redlichia* (ca. x 15). FB = anterior border of cranidium. G = glabella, L = interlocking spines and sockets of dorsal and ventral exoskeleton, MF = marginal furrow, R,H = fused rostral plate (R) and hypostome (H). The anterior border and rostral plate form an exoskeletal closet, the cranidium and rostri-hypostomal plate form a larger exoskeletal pocket. Both had to be opened to allow the soft trilobite to emerge forwards. After Öpik (1958, Fig. 6).

cranidium is reflected by a row of pits along the marginal furrow. Öpik maintained, with obvious correctness, that moulting required an extra provision, in this case the rostral suture, otherwise the soft parts of the trilobite could not have been withdrawn from the closet formed by the anterior border of the cranidium and the rostral plate. However, the rostral suture must have been present also because of the much larger pocket otherwise formed by the cranidium and rostri-hypostomal plate.

As a general rule, an anterior exoskeletal pocket is avoided (especially on the cranidium or genicranidium) by the location of the marginal, submarginal, rostral, or facial sutures. This, too, indicates that the exuviating trilobite emerged forwards through an ecdysial opening formed when the sutures opened.

MARGINAL, SUBMARGINAL, ROSTRAL, AND FACIAL SUTURES. – Trilobites with a *marginal* or *submarginal suture* apparently had a simple ecdysial gape suture. Exceptions are trilobites like harpids and trinucleids with a brim where exoskeletal pillars connect the dorsal and ventral test. The pillars "nailed" the flesh to the exoskeleton, and a special provision was required – the *interlamellar suture* (cf. p. 190), which split each of the pillars into a ventral and a dorsal part.

Trilobites with *facial sutures* had an ecdysial gape suture that generally also served to facilitate the ecdysis of the visual surfaces, and had a more varied pattern of cephalic sutures. It has long been accepted that the course of the facial sutures were affected by the location of the eyes. However, the facial sutures (and the *rostral suture* where present) were also strongly affected by their function as ecdysial gape suture. Thus a submarginal course of the anterior-most part of the facial sutures may have been developed to avoid an exoskeletal pocket in front (cf. p. 183). The necessary width of the ecdysial gape likewise affected the facial sutures, and no doubt the advantage of having a clean, not rugged gape suture. In order to serve its functions, the course of the facial sutures was undoubtedly modified by the topography of the cephalon. This deserves further studies.

It seems, for instance, that the preocular parts of the facial sutures tend to diverge strongly mainly in trilobites with rather flat genal regions, whereas they tend to be subparallel or even convergent in trilobites with more strongly vaulted cephalon, except where the glabella is so wide in front that they have to diverge so as not to cross the glabella. Incidentally, an ecdysial gape suture across the glabella would result in a lower cephalic unit with a pronounced anterior pocket.

The different courses of the preocular (and postocular) sutures furthermore reflect another function of the facial sutures, namely to facilitate withdrawal from the free cheeks.

Thus the ecdysial gape suture had to be located so as to allow withdrawal both from the lower and upper cephalic unit, and from the post-cephalic integument, and generally also to facilitate ecdysis of the eyes. Where the rostral plate is fused with the hypostome, the rostral suture (and connective sutures) may have functioned like a hypostomal suture.

Auxiliary sutures

HYPOSTOMAL SUTURE. – With the exception discussed below, the hypostomal suture is always present when the hypostome and cephalic doublure are in contact. This indicates that it had a special function, the most obvious being that it facilitated ecdysis of the vulnerable mouth region. By the hypostomal suture being opened, the hypostome could be released from the soft trilobite in a simple manner. As suggested by Whittington (1959:395), the hypostomal suture may not be a homologous (but analogous) structure from trilobite to trilobite. This, too, indicates its importance. It is not known whether the hypostome was generally shed as a separate unit or as part of the lower unit.

Where the hypostomal suture is ankylozed, the hypostome is fused with the rostral plate.

Fusion of hypostome and rostral plate seems to have happened in trilobites where the glabella on the dorsal side, and thus the hypostome on the ventral side, lie close to the anterior margin, leaving little space for the rostral plate medially.

Fused hypostome and rostral plate might be regarded as an "enlarged hypostome", where the rostral and connective sutures took charge of the function of the hypostomal suture (a rostri-hypostomal plate is never fused with the cranidium).

MEDIAN AND CONNECTIVE SUTURES. — As proposed by Rasetti (1958:889), the connective sutures may not have been used in ecdysis like the facial sutures, and the same may be true of the median suture. They do not seem necessary in forming the main ecdysial opening, but their opening would no doubt facilitate shedding of the free cheeks and visual surface, even as parts of an exuvial unit (lower cephalic unit). Another possible function of the median and connective sutures may be suggested; they cut the edge of the anterior doublure, and this may well be where splitting of cephalic sutures was initiated. In the recent Natantia, the splitting of the median ecdysial line starts at the posterior edge of the carapace and proceeds forwards (Schäfer 1962:482), and the animal withdraws from the exuvium behind the carapace. Since trilobites apparently emerged forwards, it seems most likely that the sutures started to split anteriorly.

In evolutionary series where the rostral plate was abandoned, the connective sutures generally came gradually closer to each other, especially in the middle, and finally met to form a median suture — at least in some lineages through a stage both with median suture and a small rostral plate (the rostellum, cf. Öpik 1967:60) before the rostral suture disappeared. In *Panderia,* however, Bruton (1968, Fig. 2) has shown that the relatively widely spaced connective sutures disappeared (without joining to form a median suture), and that the rostral suture became part of the facial sutures. The facial sutures may have become non-functional (Dr. David Bruton, personal communication, 1973), and thus did not need the connective sutures. It is not known whether *Panderia* showed the Salterian mode of moulting. In some specimens, however, the cephalon is detached from and somewhat displaced in relation to the thoracopygon (Bruton 1968, Pl. 11:8—10). This suggests that the cranidium and fused free cheeks were shed as a single unit, in which case also the neck joint became an ecdysial line.

Where both median and connective sutures are missing, there seems to be a tendency in some groups to develop proparian facial sutures (as in most Cheirurina).

ROSTRAL PLATE. — This ancestral feature in trilobites (Öpik 1967:60) may be present as a consequence of the rostral and connective sutures, rather than of its own status, but although the rostral plate was reduced in size and was finally lost in several evolutionary series, a small (often ridiculously small) rostral plate was kept for a while as if, so to speak, there was a certain reluctance to dispose of it entirely; this suggests that it served some purpose. If the initial splitting of cephalic sutures started in front, the rostral plate may have had a triggering function by being more easily pushed outwards than the other larger plates of the cephalic shield. Even a very small size would be compatible with this, and its location between sutures would be more important than its shape. Where the rostral plate was reduced to a small, triangular plate (rostellum) ”connected” with the doublural edge by a median suture, it could still have served the same purpose.

Generally, the rostral plate is merely a part of the doublure, except for modifications due to an attached or fused hypostome. It extends on to the dorsal surface where the rostral suture is dorsal-intramarginal (e.g. in homalonotids). The large and wide (tr.) rostral plate in, for example, several illaenids and thysanopeltids is a result of a considerably inflated glabella or cephalon ”pushing” the facial and connective sutures apart. In forms with protruding, inflated glabella (e.g. *Staurocephalus*), the rostral plate, ”encroaches” onto the ventral surface of the glabella , reflecting the forward and upward shift of the rostral suture (for ecdysial purposes).

CIRCUMOCULAR SUTURE. — Among many Cambrian and some post-Cambrian trilobites, the visual surface is shed as a separate moult unit, thanks to the circumocular suture (Öpik 1967:54), both in trilobites without facial sutures (e.g. olenellids) and with facial sutures. The circumocular suture consists of two parts, referred to by Öpik as the palpebral suture (generally a part of the facial suture) and the ocular or genal suture (between visual surface and free cheek). In some Cambrian and most post-Cambrian trilobites the visual surface and free cheek are fused, and the palpebral suture is located below the palpebral ”lid” in such a way that a slight sideways removal of the free cheeks (e.g. by the opening of the median or connective sutures) would liberate the visual surfaces.

Rare specimens show deformation of the exoskeleton (cf. Harrington 1959:O107–O110). Öpik (1961:130) described two specimens of *Centropleura sonax* where minor scars in the cranidium were healed, and "seemingly were no hindrance to successful moulting afterwards". In other cases, pathologically deformed exoskeletons may have affected the

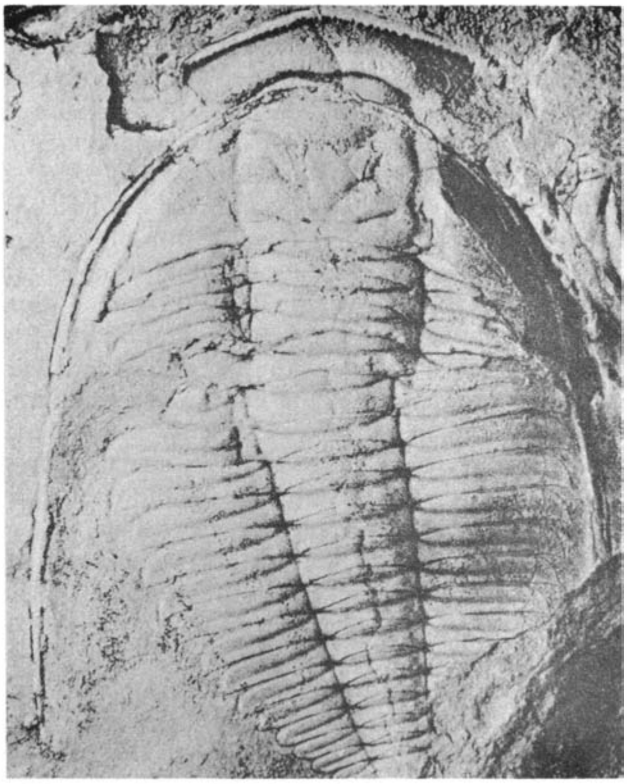

Fig. 5. Harrington's configuration in an olenid *(Parabolinella),* showing also "entangling" of the free cheeks (partly beneath, partly on top of axial shield). Thorax broken at deformed segments. X1.6. From Harrington & Leanza (1957, Fig. 38:8).

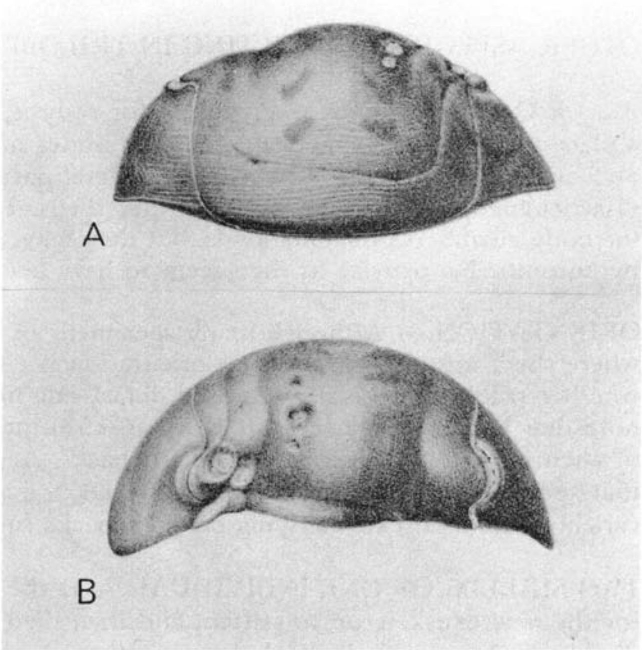

Fig. 6. Anterior and dorsal view of deformed cephalon of *Illaenus wahlenbergi* (Eichwald 1825) apparently showing impressions corresponding to the edges at the rostral and left facial suture of the cranidium of the preceding moult. X1. From Holm (1886, Pl. 2:2).

exuviation. Thus a specimen of *Parabolinella argentinensis* figured by Harrington & Leanza (1957, Fig. 38:8) shows two considerably shortened (tr.) pleurae on its left side (Fig. 5). The dorsal shield is broken in front of these, and the posterior part of the thoracopygon lies at an angle to the anterior part, possibly reflecting difficulties during exuviation. Three abnormal pleurae on the right side of a specimen of a shumardiid were inferred by Stubblefield (1959:O109, Footnote 1) to denote an injury to the right macropleural spine in a preceding moult. Several instances of regeneration of eye lenses are known, probably due to injuries during moulting (Harrington 1959:O107).

If the soft trilobite encountered difficulties in releasing itself from parts of the exoskeleton, this could result in abnormal exuviations, including perhaps, telescoping of parts of the dorsal shield. A probable example (Fig. 6) of deformation caused by overdue retention of parts of the last exuvium is a cranidium of *Illaenus wahlenbergi,* described and figured (as *I. revaliensis*) by Holm (1886:92, Pl. 2:2), who pointed out that some depressions were apparently made while the test was still soft. A depressed line on the cranidium appears like an extra left facial suture plus rostral suture, and may be impressions of the corresponding edges of the preceding, smaller cranidium. An occipital furrow-like line may be the impression of the posterior cranidial edge. No impression is seen corresponding to the right-side edge of the exuviated cranidium, but a faint impression on the right free cheek may correspond to the lateral border of the exuviated free cheek, indicating that this was not separated from the exuviated cranidium. The impressions of the finally shed cranidium and free cheek are slightly rotated to the right in relation to the present cephalon, which has an unduly large left free cheek. This strongly suggests that the soft trilobite, at first not able to free itself from its old cephalon dorsally, later managed to shed its left free cheek (which, however, also seems to have left some impressions on the present left free cheek), and finally to shed the cranidium and right free cheek. The cause of the overdue retention may be indicated by depressions on the left side of the glabella and on the left fixed cheek near the eye.

Non-opening of ecdysial sutures could result in abnormal exuviation. This is probably demonstrated by a specimen of *Ogygiocaris sarsi sarsi* figured by Henningsmoen (1960, Pl. 4:1–2), where the left facial suture may not have been opened. This would force the exuviating animal to emerge more to the right, and not straight forwards. It is rather suggestive that the thoracic segments behind the cephalon are somewhat rotated, so that their axis is in accordance with this direction.

Although abnormal moulting was undoubtedly rare, the huge number of trilobite exuviae shed indicates that many more examples demonstrating this can be recognized. So far, they seem to indicate that cephalic sutures normally opened to allow the soft trilobite to emerge forwards.

OTHER ASPECTS OF MOULTING IN TRILOBITES

PLACE OF MOULTING. – Preparing for ecdysis, recent marine arthropods hide in as safe a place as their environment permits. Trilobites may have hidden between sea-weeds, in pockets and caves in reefs (where exoskeletal parts may be common, although generally disarticulated), in burrows, and in empty shells. Trilobite fragments are not infrequent in the body chambers of cephalopods, but they may, of course, have been brought there by currents. No exuviae as shed seem to have been described from body chambers.

ORIENTATION. – Although many specimens of trilobites have been interpreted as exuviae where shed, information on their orientation is extremely scarce. We still do not know whether trilobites generally moulted dorsal side up or down, or both. It is interesting to note that Walcott as early as in 1875 (p. 159) mentioned that 1.110 out of 1.160 specimens of cheirurids were found lying on their backs. Agassiz (1878:75–76) quoted this and added that specimens of *Limulus* that he observed in a glass jar both rested on the bottom and invariably cast their exuviae lying on their backs (quoted in Walcott 1910:241).

TWO SHIELDS OF ONE INDIVIDUAL. – If the trilobite rested long enough after ecdysis for the new exoskeleton to stiffen, and then died, there is a possibility of finding two shields of the same individual close together. A specimen of *Hanchungolithus primitivus* figured by Dean (1966, Pl. 5:9) might possibly be an example of this. If so, it again indicates forward movement of the exuviating trilobite, since the larger specimen lies in front of the smaller.

SOFT STAGE AND PAPER SHELL STAGE. – If trilobites in these ecdysial stages by chance become fossilized, one may expect to find wrinkled and otherwise deformed specimens, that might easily be mistaken for new species.

FREQUENCY OF MOULTING. – This is not known in trilobites, nor in most species of recent crustaceans. Schäfer (1962:482) gives the following information on the frequency of moulting in lobster (*Homarus*): First year 9 moults, second year 5 moults, third year 3 moults, apparently 2 moults in each of the following years, and from then on one moult in a year in the male lobster. Chance finds of trilobite exuviae in varved sedimentary rocks might give us some indication of moults per year in trilobites.

LAST MOULT. – It is not known whether trilobites ceased to moult after having reached a certain size or not. Both cases are known in recent arthropods. Occasional huge specimens of a trilobite species may indicate that at least some trilobites moulted until they died.

MODES OF MOULTING IN TRILOBITES

THE SALTERIAN MODE OF MOULTING (cf. p. 192). – This type is known with certainly to occur normally only within phacopids which possess only a hypostomal suture. The neck joint broke open and the cephalon was shed as a single unit. The Salterian mode of moulting is apparently the exception rather than the rule, contrary to statements by Richter (1937:423), but in accordance with statements by Maksimova (1955:207) that the neck joint was not of such importance in ecdysis as believed by Richter.

THE SUTURAL GAPE MODES OF MOULTING. – In the numerous trilobites with sutures traversing the cephalon, combined evidence from exoskeletal configurations and isolated composite exoskeletal units (cf. p. 193), possible examples of abnormal moulting, and cephalic morphology (not the least the location of anterior sutures) strongly indicates that the soft trilobite generally emerged forwards through an ecdysial gape formed by the opening of the sutures. This agrees with the ideas of Henriksen (1926), and Richter (1920) postulated the same for harpids and trinucleids. However, Richter (1937:423, 429) apparently believed that the opening in most other trilobites was formed more or less as in the Salterian mode of moulting, and much the same was proposed for trinucleids, aulacopleurids, and ptychopariids by Přibyl & Vaněk (1969). From the discussion below it appears that all trilobites with more sutures than only a hypostomal suture have modes of moulting of the same general type, where an ecdysial gape is produced between the cranidium or genicranidium (upper cephalic unit) and the lower cephalic unit. This apparently applies to the *Harpes, Ductina,* and olenid mode of moulting, as well as mode of moulting in olenellids (perhaps excepting the *Fallotaspis* type) and in trilobites with median or connective sutures. These modes, here referred to as the sutural gape modes of moulting, are distinguished from each other by the number and types of cephalic sutures rather than by the mode of withdrawal from the exuvium.

There are transitional types between the Salterian mode and sutural gape modes of moulting. Thus occasionally trilobites with ecdysial gape suture could become disarticulated at the neck joint during ecdysis, and this may have been the rule in a few forms. In all trilobites other dorsal joints could occasionally become disarticulated.

Recalling that exuviae of recent crustaceans and *Limulus* commonly close postecdysially, it is tempting to suggest that complete trilobite shields with opened sutures are not necessarily remains of dead animals, but also may be exuviae where the ecdysial gape closed again after ecdysis.

Below follows a discussion of evidence for mode of moulting from exoskeletal configurations, isolated composite exoskeletal units, and location of anterior sutures in various trilobites, grouped according to development of cephalic sutures.

Trilobites with marginal or submarginal suture

MARGINAL-INTERMELLAR SUTURE. *HARPES* MODE OF MOULTING. – The *Harpes* mode of moulting (named here) was first described in detail by Richter (1920:200–203). The suture along the cephalic margin of *Harpes* and other harpids was not in itself suf-

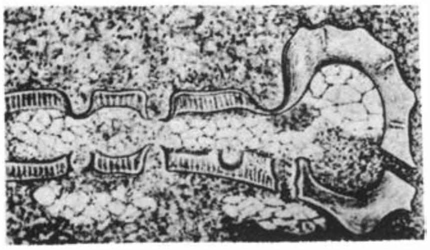

Fig. 7. Opened marginal-interlamellar suture in anterior part of harpid fringe. Upper lamella above. X14. From Richter (1920, Pl. 17:12a).

ficient to allow the animal to withdraw from the exuvium. Each of the exoskeletal pillars connecting the lower and upper lamella of the pitted fringe had to be split (Richter 1920:201–202), thus separating the two lamellae (Fig. 7) along what may be referred to as the *interlamellar suture,* which really is a set of numerous small sutures. The lower and upper lamella are separated by from a millimetre to several centimetres of matrix in many complete exoskeletons of harpids, interpreted by Richter (1920:201) as undisturbed exuviae in which the lower lamella was attached by soft integument only. Isolated lower lamellae and isolated dorsal exoskeletons without a lower lamella were regarded as possible exuvial units, as well as disarticulated shields.

It is hard to prove whether any one specimen really represents an exuvium in harpids, since possible exuviae do not show configurations particularly ascribable to movements of the exuviating trilobite. Nevertheless, it seems most reasonable to assume with Richter that the intricate suture of *Harpes* had its main and probably only function in ecdysis. When the suture opened, an exuvial gape was formed through which the soft trilobite moved forwards out of its exuvium. This type of withdrawal is known in *Limulus,* in some crustaceans such as *Triops,* and in eurypterids (see Henriksen 1932). Apparently the ecdysial opening tended to close again after exuviation in *Harpes,* as it commonly does in *Limulus* and several other recent arthropods. However, in some cases the lower part of the cephalic integument together with the lower lamella became entirely detached – perhaps by the spasm-like movements of the exuviating trilobite. Even one or more joints in the dorsal exoskeleton could be broken. As in other trilobites, the construction of the exoskeleton would allow bending up and down rather than sidewise wriggling.

In addition to harpids, trinucleids and dionidids with pitted fringe no doubt shed their exuviae in a similar manner (cf. Richter 1920:200). Trinucleids and dionidids have the same type of marginal-interlamellar suture, with one interesting exception; the marginal suture becomes dorsal across the base of the genal spines, where such are present. The genal spines in trinucleids do not need a splitting suture distally to the dorsal suture, where they are not pitted as in *Harpes* and do not have exoskeletal pillars connecting the ventral and dorsal sides (Richter 1920:201).

MARGINAL SUTURE. *DUCTINA* MODE OF MOULTING. – The blind phacopid *Ductina ductifrons* (R. & E. Richter 1923) has a functional, strictly marginal suture between the cephalic doublure and the dorsal cephalon. According to R. & Emma Richter (1926:209), the marginal suture opened to form the ecdysial opening through which the soft trilobite moved out forwards, leaving behind it the dorsal cephalon connected with the thorax and a displaced cephalic doublure. This "*Ductina* mode of moulting" (Richter, Richter & Struve 1959:O462) has been discussed further by Maksimova (1955), Osmólska (1963), and Alberti (1972).

A characteristic configuration of exuvial parts (Fig. 8B) shows the cephalic doublure displaced below the dorsal shield, commonly so as to lie beneath the posterior portion of the glabella (Maksimova 1955, Pls. 15–17; Osmólska 1963, Pls. 1,2,4). This constellation, here called *Maksimova's configuration,* apparently represents exuvial remains, as may also isolated cephalic doublures and dorsal shields lacking cephalic doublures. The relatively small displacement of the cephalic doublure in Maksimova's configuration may indicate that it was still attached posteriorly by the soft ventral integument. Apparently the hypostome could retain its position in relation to the cephalic doublure.

Apart from in *Ductina,* the *Ductina* mode of moulting is known in early stages of other blind phacopid genera such as *Dianops* and *Trimerocephalus,* where, however, the late holaspids are without functional cephalic suture and display the Salterian mode of moulting, as first pointed out by Maksimova (1955), and supported by Osmólska (1963) and Alberti

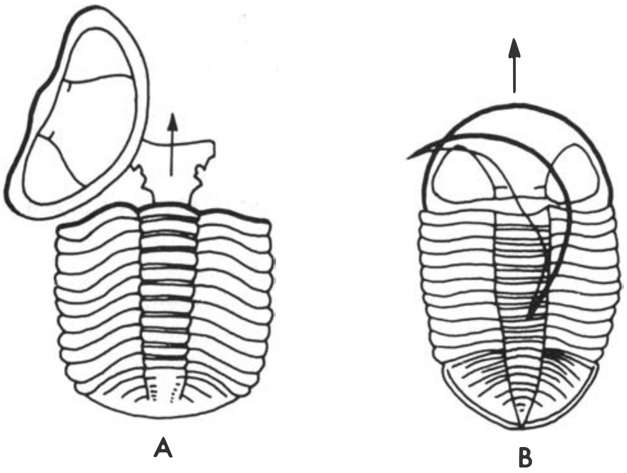

Fig. 8. Phacopids showing Salter's configuration (A) with cranidium turned upside down, and Maksimova's configuration (B), but with lower cephalic unit obliquely oriented instead of athwart as is generally the case. Arrows indicate direction of exuviating trilobite. After Maksimova (1955, Fig. 39).

(1972). The functional suture in *Dianops* (degrees 3—10) is not entirely marginal, but is dorsal-intramarginal antero-laterally, delimiting a pair of narrow free cheeks. Morphologically, these degrees of *Dianops* are transitional between phacopids with entirely marginal suture and phacopids with typical facial sutures. The *Ductina* mode of ecdysis is further reported in the eye-bearing phacopid *Cryphops* (Osmólska 1963:510), but at what growth stage is not certain.

VENTRAL-INTRAMARGINAL CEPHALIC SUTURE. — Olenellids have a ventral-intramarginal suture (the perrostral suture) separating the crescent-shaped rostral plate (± attached or fused hypostome) from the remaining part of the cephalon (= genicranidium).

A specimen of *Wanneria walcottana,* figured by Resser & Howell (1938, Pl. 10:9), shows the rostral plate with hypostome displaced sideways in relation to the dorsal shield (Fig. 9:2). Hupé (1953a:122, Fig. 18:2; 1953b:69, Fig. 48:2) believed this specimen to be an exuvium. Compatible with this, isolated rostral plates with hypostoma have been reported in various species (cf. e.g. Walcott 1910) and are not uncommon in material of *Holmia kjerulfi* in the collections of the Palaeontological Museum in Oslo.

It appears that the perrostral suture functioned as an ecdysial suture, and that the soft trilobite emerged forwards from its old exoskeleton, first releasing itself from the lower cephalic unit that could become (or generally was?) detached from the genicranidium. Occasionally the neck joint opened.

A peculiar configuration of exoskeletal parts in *Fallotaspis* (Fig. 9:1) shows the rostral

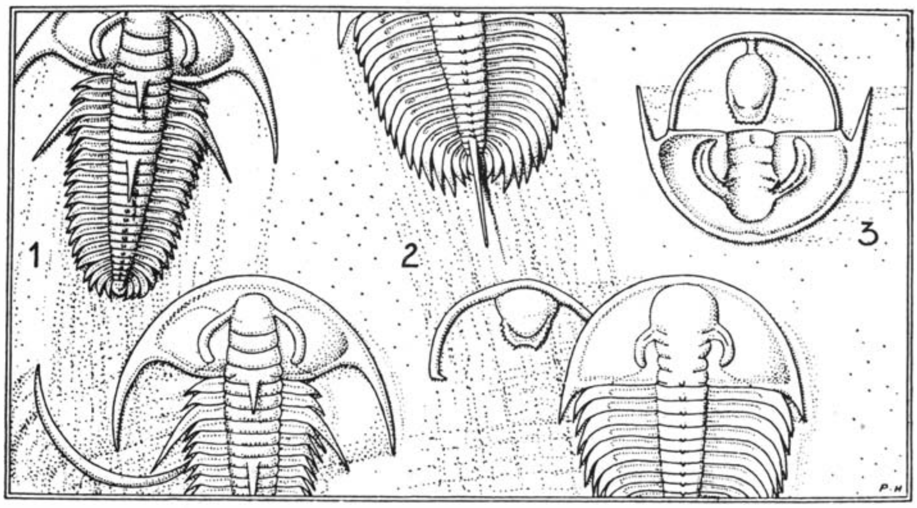

Fig. 9. Possible exuviation in olenellids. 1. *Fallotaspis longispina* Hupé 1952. 2. *Wanneria walcottana* (Wanner 1901), 3. *Paedumias transitans* Walcott 1910. From Hupé (1953a, Fig. 18).

plate detached from the cephalon, displaced backwards and more or less sideways, and overturned in relation to the dorsal shield. (Hupé (1953a:122, 1953b:70) regarded this configuration as most probably representing exuviae. The exact position of the rostral plate varies somewhat from specimen to specimen (cf. Hupé 1953a; Pl. 1:1,8,9).

Hupé suggested that the exuviating trilobite either emerged through an opening formed at the perrostral suture, or, more likely, through a larger opening formed by the detachment of the rostral plate. In the latter case, he visualized the emerging trilobite moving over and dragging along the detached rostral plate before shedding the dorsal shield. According to him, the dragging could result in further displacement of the rostral plate, even to the extent that it was rotated 180°. The lateral displacement is ascribed to other causes, such as currents.

Although it is not clear how exuviation took place in *Fallotaspis,* it seems reasonable to assume with Hupé that the unusual configuration of exoskeletal parts in some specimens represent exuviae more or less in the position they were shed. It may aptly be referred to as *Hupé's configuration.*

Another unusual preservation is represented by a small (1.5 cm long) cephalon of *Paedeumias transitans* (figured by Walcott 1910, Pl. 34:16 and refigured by Resser & Howell 1938, Pl. 9:6) and regarded by Hupé (1953a:121, Fig. 18:3; 1953b:69, Fig. 48:3) as a possible cephalic exuvium. The cephalon is preserved with the rostral plate (bearing the stalked hypostome) still attached posteriorly, but rotated 180° in relation to the cephalon (Fig. 9:3). Harrington (1959:O114) found it difficult to imagine how this could have happened during ecdysis, except, perhaps, incidentally in small specimens. Apparently only one such specimen has been reported, and it may or may not represent an exuvium. If it is an exuvium the configuration may have been caused by a mode of moulting similar to that in *Fallotaspis.*

Trilobites without cephalic sutures

AGNOSTIDA WITHOUT SUTURES. – Agnostina are not known to have cephalic sutures and the cephalon, including doublure, is in one piece. Within the Eodiscina, the same is true for the Eodiscidae, while the Pagetiidae have facial sutures of proparian type. Where known, the hypostome in Agnostina is an isolated exoskeletal plate which is unattached to other exoskeletal plates (Robison 1972). Among Eodiscina, the hypostome is known in *Pagetia,* where it apparently is not attached to the doublure (Öpik 1952:272).

Hughes (1969:60) suggested that specimens of *Geragnostus mccoyi* showing rotation of cephalon and thorax in relation to the pygidium were exuviae, and that the complete or nearly complete specimens showing no rotation were from individuals that died. It seems quite likely that the specimens with pygidium slightly displaced, and at an angle to the remaining dorsal shield, do represent exuviae. Similar configurations are also known in other agnostids, as in *Tomagnostus fissus* (cf. Westergård 1946, Pl. 7:29). The specimen figured by Hughes (1969, Pl. 1:3) also appears to have the cephalon slightly displaced in relation to the thorax, while another specimen figured by him (Pl. 1:5) consists of only a combined pygidium and thorax, and may represent part of an exuvium. A specimen of *Ptychagnostus atavus,* figured by Westergård (1946, Pl. 11:23), shows the cephalon detached from, and at a slight angle to a combined thorax and pygidium. Probably any one of the dorsal joints could become disarticulated during exuviation.

Complete and unbroken dorsal shields may represent dead animals, but since they are rather common, and since exuviation in Agnostina may have been rather simple, it is quite possible that many or even most of them are exuviae.

SALTERIAN MODE OF MOULTING. – A characteristic constellation of exoskeletal parts shows the cephalon lying upside-down and back foremost in front of the thoracopygon. Richter (1937) discussed it in detail, termed it the "Salter'sche Einbettung", and explained it as a result of the shedding procedure. The configuration occurs in phacopids, but is restricted to forms with non-functional facial sutures. For this reason, and because it is restricted only to adults in some species, the term "Salterian mode of moulting" (Richter, Richter & Struve 1959:O462) seems preferable to "Phacopid mode of moulting" (Harrington 1959:O111). The configuration itself may be referred to as *Salter's configuration* (Figs. 5, 8A). The angle and distance between cephalon and thorax vary from specimen to specimen (cf. Richter 1937, Figs. 2,2; Maksimova 1955, Pls. 17,18; Osmólska 1963, Pls. 3,4), and the cephalon may even lie right-side up (Maksimova 1955, Pl. 17:8). The hypostome may be present in front of the thorax (Richter 1937, Fig. 3; Maksimova 1955, Pl. 14:8) or not.

According to Richter (1937:428–429), Salter's configuration occurs most commonly in blind species, less commonly in species with small eyes, and rarely in species with eyes of normal size. In this he saw that ecdysis went more smoothly in small-eyed and especially blind forms, so that the exuviae were more liable to be preserved as they were shed. Configurations resembling the Salterian configuration are known in trilobites with typical facial sutures (cf. below).

To free itself of the old exoskeleton, the trilobite had no cephalic sutures to open and instead split open the joint between cephalon and thorax. This was done probably by the animal buckling itself upward and shedding the cephalon, which easily became turned upside down with back-edge foremost. The hypostome may have been shed as a separate unit, or it remained part of the lower cephalic integument, comprising also the soft integument. In the latter case, the cephalon must have been split off both from the thorax and from the lower cephalic integument.

Schäfer (1951) observed that both dead animal and exuviae of recent Brachyura could become imbedded with the carapace turned 180° in relation to the thorax as a result of currents, and with the two parts connected by soft tissue. He referred to this as "Salter'sche Einbettung" (cf. also Bishop 1972), indicating that currents might also have caused the configuration described by Richter in phacopids. However, Rabien (1956:38) maintains that Schäfer's specimens do not show the same configuration of exoskeletal parts as described by Richter. Rabien strongly supported Richter's explanation of the "Salter'sche Einbettung" in phacopids as due to the movements of the trilobite during exuviation. This appears even more probable since it has been shown that in some species this preservation is restricted to late holaspids, whereas earlier instars show the *Ductina* mode of moulting. However, Schäfer's observations deserve serious attention when discussing exoskeletal configurations of trilobites.

Trilobites with facial sutures

Configurations of exoskeletal parts of olenids interpreted as exuviae were described by Henningsmoen (1957:70), and the possible mode of moulting discussed. This has later been referred to as the "Olenid mode of molting" by Harrington (1959:O112). It was suggested that the facial sutures opened and that the soft trilobite emerged forwards, leaving the exuvial parts in various configurations. The free cheeks and hypostome may lie more or less in normal position to each other even when displaced, suggesting that they were held together by soft integument (Henningsmoen 1957:72) in a lower cephalic unit.

Although the free cheeks are fused in some olenids, as in *Parabolina* (cf. Henningsmoen 1957:91), Palmer (1962:F–35) reported that cranidia and free cheeks of the very early olenid *Olenus gibbosus* show that it had a small rostral plate. It is thus possible that other olenids had a rostral plate, or perhaps a median suture. The free cheeks of *Acerocare ecorne* may not have been fused. If they were (as considered a possibility by Henningsmoen 1957:72), their narrow connection easily broke, since they generally are slightly rotated in relation to each other even when lying in pairs.

A characteristic preservation shows the exoskeleton split in two main parts (exuvial units?); axial shield (cranidium + thorax + pygidium) and paired free cheeks (± hypostome). They may lie close together or more or less removed from each other. In some cases the free cheeks are

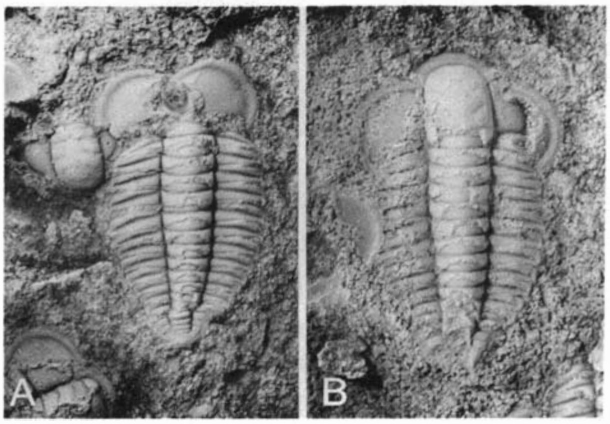

Fig. 10. Olenids (*Acerocare*) showing Harrington's configuration (B) and shield with detached cranidium (A). X1.8. From Henningsmoen (1957, Pl. 30:5,6).

displaced backwards below the axial shield. This condition was reported by Harrington (1959:O114) also in non-olenid trilobite specimens, and may be referred to as *Harrington's configuration* (Figs. 5,10). Viewed from the dorsal side the detached free cheeks may lie below the axial shield, and in some specimens one or both free cheeks may be partly above or partly below the axial shield, thus being "entangled" with it.

The free cheeks of a dead trilobite could also become detached and displaced when the soft parts decomposed, and especially if attacked by scavengers. Possibly free cheeks may have had a tendency to slip backwards in relation to the cranidium, and perhaps even become entangled with it, when the empty exoskeleton of a dead animal or an exuvium collapsed on the sea floor. However, the consistency of Harrington's configuration suggests that it can be most readily explained by the forward movement of the soft trilobite during exuviation whereby the trilobite released itself from the lower cephalic unit before shedding the axial shield.

The common occurence of axial shields in all groups of trilobites with facial sutures may well reflect that they were shed as exuvial units, the lower cephalic unit having been shed separately (Fig. 11).

In some specimens (Fig. 10A) the cranidium is displaced or even missing, while the free cheeks (± rostral plate, ± hypostome) are preserved more or less in normal position in front of the thorax. Such specimens may represent cases where the cranidium, but not the lower cephalic unit, became detached during exuviation, the opening of the neck joint perhaps being caused by spasm-like movements of the animal.

A fairly common constellation consists only of thoracopygon and a displaced cranidium (Fig. 12). Rarely, the cranidium may even lie upside down in relation to the thoracopygon, resembling Salter's configuration in forms without sutures. A good example shown by Lehman (1960) was interpreted as due to feeble currents or a crawling animal. It might as well be the result of exuviation. Much the same applies to disarticulated axial shields in general. The resulting parts may be preserved separated, as if pulled apart, or lie telescoped under each other. Telescoped shields are best explained as the result of the forward movement of the exuviating trilobite itself during times when it got stuck to areas of the exuvium.

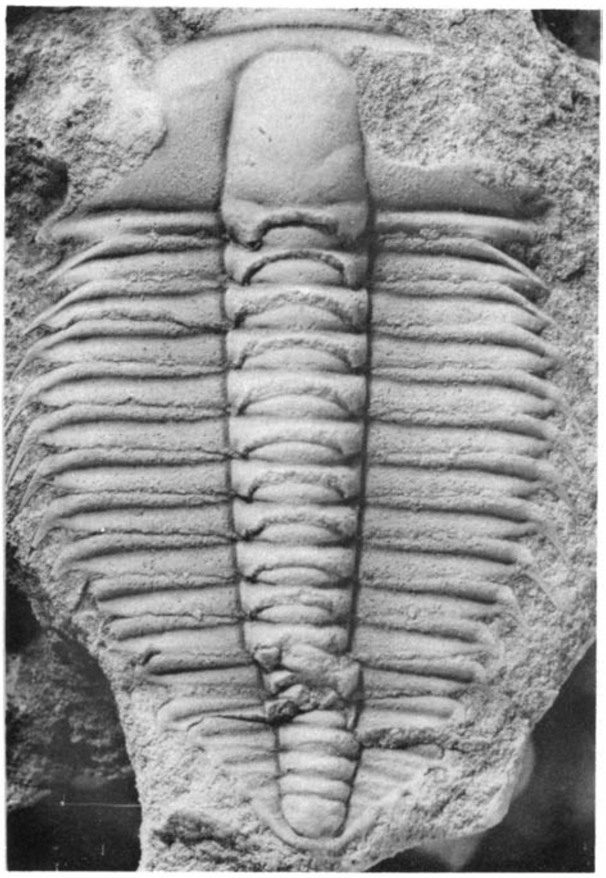

Fig. 11. Axial shield (cranidium damaged) of an olenid (*Leptoplastus*). Breaks posteriorly may have been caused by axial spine of 11th segment, after deposition or during ecdysis, – in the latter case the breaks and slight telescoping posteriorly may indicate minor difficulties encountered during exuvation. X5. From Henningsmoen (1957, Pl. 15:7).

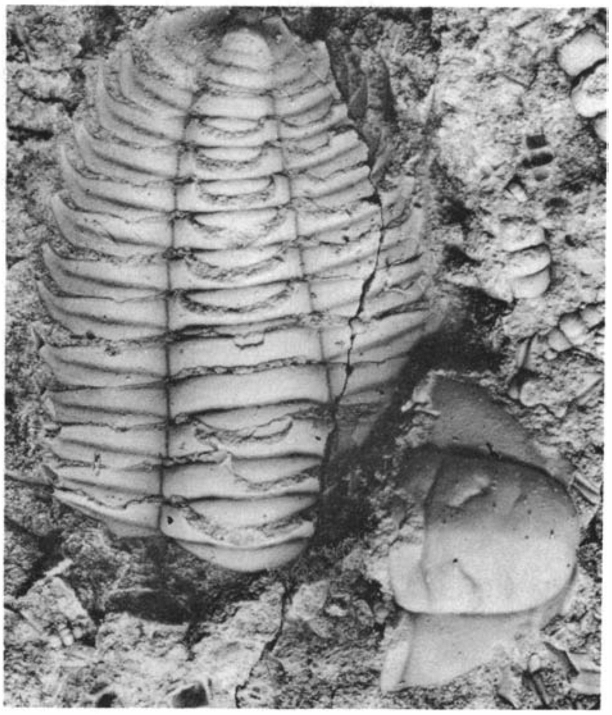

Fig. 12. Thoracopygon (slightly telescoped in parts) and relatively displaced cranidium of an olenid (*Protopeltura*). X5.7. If they are exuvial units, the lower cephalic unit (with free cheeks) was shed at another stage of the exuviation (probably earlier). From Henningsmoen (1957, Pl.24:10).

MODE OF MOULTING IN TRILOBITES WITH FACIAL SUTURES. – Evidence discussed below, as well as above under "Abnormal moulting" and "The ecdysial lines and the ecdysial opening" suggest that generally trilobites with facial sutures moulted more or less in the same manner as olenids, by opening the facial (± rostral) sutures and emerging forwards. To which degree the lower cephalic unit, including the free cheeks, became entirely detached is not known, but the unit was probably released earlier from the soft trilobite than the axial shield, Occasionally (or perhaps as a rule in certain forms such as in *Telephina spinigera* mentioned below), the neck joint also opened and the cranidium was shed in a manner similar to that of the cephalon in trilobites with the Salterian mode of moulting.

Přibyl & Vaněk (1969:125) introduced the term "ecdysis of the aulacopleurid mode" for the mode of moulting in aulacopleurid and ptychopariid trilobites. According to their brief description it consisted in the opening of two joints in the exoskeleton, one between cephalon and thorax, and one in the middle of thorax, resulting in a tripartition of the exoskeleton during exuviation. However, even in aulacopleurids and ptychopariids, the "grande suture" easily split open (cf. Prantl & Přibyl 1950, Pl. 5:12–13; Šnajdr 1958, Pl. 38:10–11, Pl. 40:2). In all probability the "grande suture" also opened to form an anterior ecdysial opening in these groups, as also indicated by the common occurrence of axial shields. Dorsal joints might, or might not open during moulting, just as in other trilobites.

TRILOBITES WITH FUSED FREE CHEEKS. – Harrington's configuration, with free cheeks displaced backwards, is apparently more common in trilobites with fused free cheeks than in other trilobites. A specimen of the olenid *Parabolinella argentinensis*, figured by Harrington & Leanza (1957, Fig. 38:8) and refigured herein (Fig. 5), shows Harrington's configuration and is significant because its exuvial nature is supported by evidence of abnormal moulting. A specimen of the proetid *Phyllaspis? expansa*, figured by Alberti (1969, Pl. 29:5), shows both Harrington's configuration and a telescoped shield.

The free cheeks are also commonly displaced in other directions; the main point is that the facial sutures opened, indicating that the soft trilobite emerged forwards. Specimens and published illustrations indicate the same mode of moulting in other trilobites with fused free cheeks. This mode was suggested by Öpik (1967:236) for the asaphiscid *Blountia (Mindycrusta) mindycrusta*.

A specimen of *Isotelus gigas* (Fig. 13) is remarkable because it could well be an exuvium with the ecdysial gape still open (at least partly) – apparently kept open by a chance "card house" constellation of cranidium and free cheeks.

This 18.5 cm long specimen (PMO A31036) and another about 4 cm long damaged specimen (PMO A31037) of *Isotelus gigas* Dekay, 1824, with doublure exposed, show the free cheeks fused. The specimens were collected by C.D. Walcott in Trenton Limestone at the type locality, Trenton Falls, Oneida County, New York, and are preserved in the Palaeontological Museum, Oslo. The figured specimen shows traces of an ankylozed median suture in the anterior part of the doublure only. Dr. Valdar Jaanusson, Stockholm, Sweden, has observed fused free cheeks in other specimens (personal communication 1973). At least other isotelid species have a functional median suture, e.g. *I. harrisi* Raymond, 1905 (cf. Shaw 1968, Pl. 22:2). The median suture evidently could become ankylozed in asaphids as e.g. in dikelocephalids.

A mode similar to the Salterian mode of moulting was suggested by Glaessner (1948) for a specimen of *Telephina spinigera* figured by Fischer (1946:567). The fused free cheeks with the large visual surfaces lie slightly displaced in front of the articulated thoracopygon, whereas the detached cranidium lies further forward, upside down and back foremost.

TRILOBITES WITH CONNECTIVE SUTURES. – Detached free cheeks in some cases show but slight displacement along the opened connective sutures and may occur together with the rostral or rostri-hypostomal plate. Possibly the exoskeletal parts were held together by soft integument. The unit is present in a specimen of *Redlichia idonea* figured by Öpik (1958, Pl. 4). The cranidium is displaced sideways, and the three thoracic segments behind the free cheeks are overturned, whereas the succeeding segments lie in normal orientation in relation to the free cheeks. This unusual constellation of the thoracic segments can best be explained by the movements of the exuviating trilobite, but seems hard to explain in other ways. Accepting Öpik's

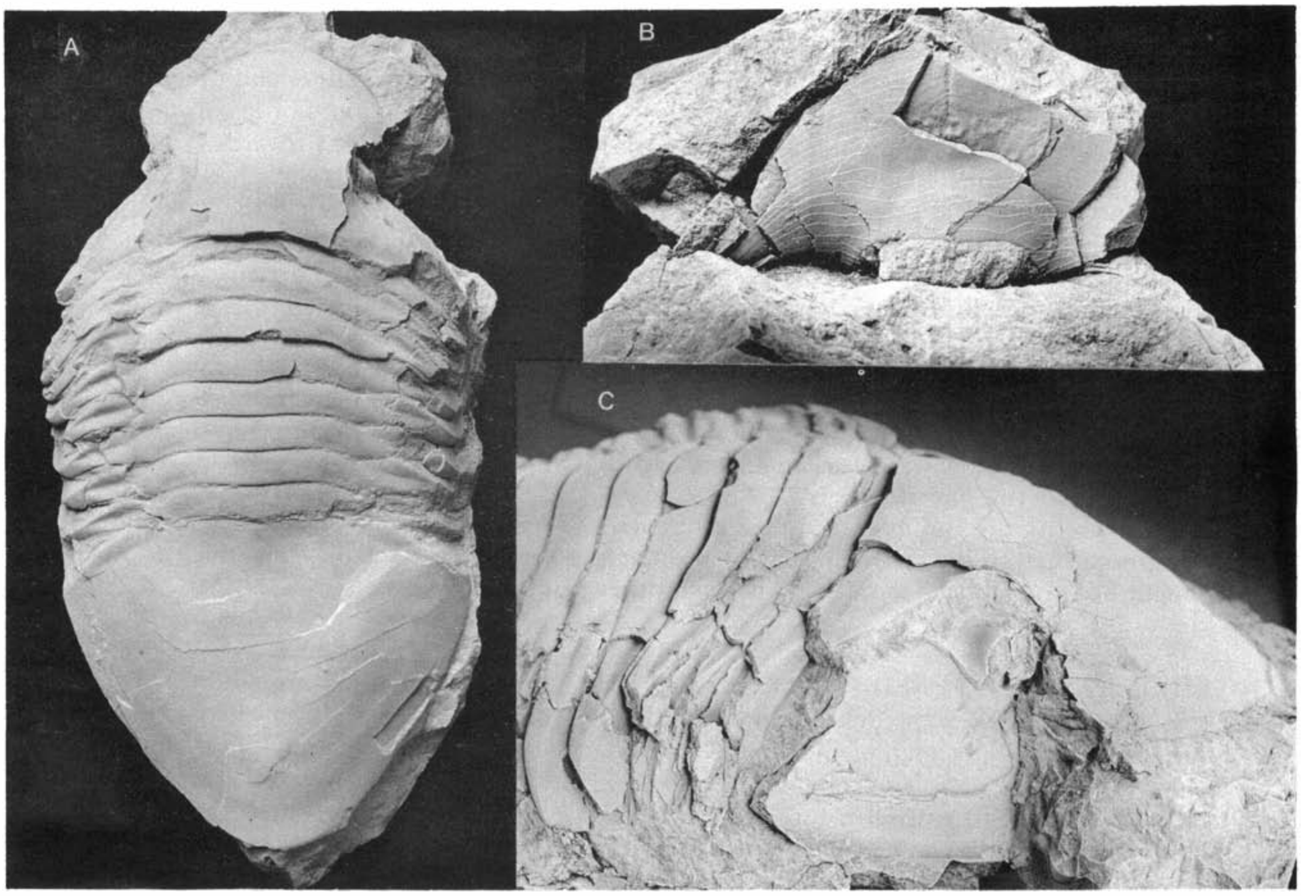

Fig. 13. A specimen (PMO No. A31037) of *Isotelus gigas* Dekay 1824 from the type locality, with open facial sutures, possibly the ecdysial gape left open (partly) after exuviation. A–D, dorsal view (cranidium foreshortened as it is slightly bent down in relation to thorax) (X0.56). B, ventral view of exposed part of cephalic doublure (X1.1); C, oblique view showing tilted right-hand free check (X1.1). Note trace of fused median suture in B.

view that the specimen is an exuvium, it seems clear that the rostral and facial sutures ("la grande suture") opened to form the ecdysial opening, and that even the neck joint opened. Detached units of free cheeks and rostri-hypostomal plate were reported in oryctocephalids by Rasetti (1952:889). To him this suggested that the connective sutures were either in a state of partial symphysis, or were not used in ecdysis like the facial sutures. The second explanation seems reasonable for at least most trilobites with connective sutures, since the rostral or rostri-hypostomal plate may occur isolated (even in oryctocephalids), showing that the connective sutures are not even partially ankylozed.

TRILOBITES WITH MEDIAN SUTURE. – The free cheeks are commonly displaced (generally assymetrically), showing that the median and facial sutures opened easily. Axial shields are common. It may be difficult to prove that any one specimen is an exuvium and does not represent a dead animal, but there may be indications like telescoped shields and signs of abnormal moulting.

CONCLUSIONS

(1) Too little is known about moulting in trilobites. More respect should be paid to this aspect of trilobite biology, also because it is important in understanding location of sutures and general morphology of exoskeleton, and because exuviae where shed are fossils preserved in situ (with all implications thereof).

(2) Apparently most, perhaps all exuviating trilobites emerged forwards out of their old exoskeleton (in accordance with the views of e.g. Henriksen 1926), as evidenced by exoskeletal configurations regarded as exuviae where shed, complex parts of the shield regarded as exuvial units, possible examples of abnormal moulting, and general exoskeletal morphology.

(3) The same features suggest that in most, perhaps all trilobites with marginal, submarginal, "grande suture" (rostral + facial sutures), or joined facial sutures, these sutures normally opened to form the main ecdysial opening (in contradiction to views expressed by Richter 1937 and Přibyl & Vaněk 1969).

(4) The upper "jaw" (genicranidium or cranidium) of this exdysial gape could become detached from the thoracopygon, but commonly was not.

(5) It is not known whether the lower "jaw" (free cheeks ± rostral plate ± hypostome, possibly held together by soft integument) was normally entirely detached (and if so, in one or more parts), or remained attached posteriorly by soft integument. Apparently both could happen.

(6) Anterior exoskeletal pockets were generally avoided (by a transverse anterior suture, e.g. the rostral suture) so as not to block the passageway of the exuviating trilobite.

(7) The ecdysial gape suture was located so as to allow withdrawal of the soft trilobite from the cephalon and post-cephalic integument, and in some cases to serve additional functions (e.g. facilitate ecdysis of visual surfaces).

(8) Auxiliary sutures, not partaking in forming the main ecdysial opening, were opened for other reasons. The hypostomal suture apparently facilitated ecdysis of the mouth region – a function that may have been added to the function of the rostral and connective sutures in trilobites with a rostri-hypostomal plate. The circumocular sutures allowed separate shedding of the eye surfaces (Öpik 1967). The median and connective sutures may have facilitated withdrawal from the old free cheeks (± visual surfaces) and may have initiated splitting of the dorsal cephalic sutures.

(9) The function of the rostral plate is uncertain. The rostral plate may be present more as a consequence of the rostral and connective sutures than of its own status, but it may have had a triggering effect in connection with the initial opening of the sutures.

(10) As well known, phacopid trilobites with entire cephalon (no sutures) shed the cephalon in one piece (Salterian mode of moulting). Apart from Agnostina and Eodiscidae, apparently all other trilobites normally opened cephalic sutures to exuviate (here called the sutural gape modes of moulting).

(11) During exuviation, dorsal joints occasionally could become disarticulated, and the resulting parts be pulled apart or telescoped more or less under each other.

(12) Certain exoskeletal configurations and certain composite exoskeletal units may be indicative of exuviae (Fig. 14).

(13) Entire trilobite exoskeletons with opened sutures may be post-ecdysially closed exuviae and not necessarily the remains of dead animals (as suggested for harpids by Richter in 1920).

(14) At least some specimens of *Isotelus* had fused free cheeks, demonstrating that the median suture could become ankylozed in asaphids.

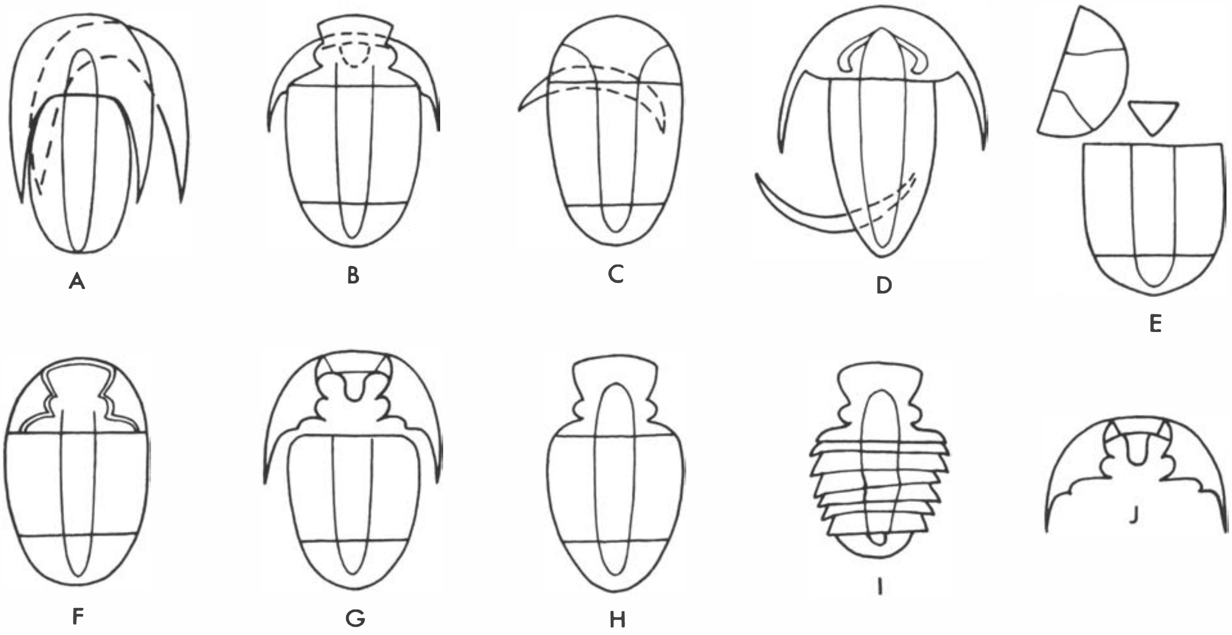

Fig. 14. Schematic illustrations (not to scale) of some exoskeletal units and configurations of units indicative of exuviae. A. Displaced lower lamella in trilobite with marginal-interlamellar suture (commonly the lower lamella is much less displaced). B. Harrington's configuration. C. Maksimova's configuration. D. Hupé's configuration. E. Salter's configuration. F. Complete shield with opened sutures (exuvium?). G. Shield with missing cranidium. H. Axial shield. I. Telescoped (shortened) axial shield. J. Exoskeletal parts of lower cephalic unit (in trilobite with facial sutures and rostral plate).

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Fine morphological characters of some Upper Palaeozoic trilobites

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Thin sections of the integument of some Devonian and Carboniferous trilobites have been investigated by means of light microscopy. Observations on pore canals, cephalic tubercles, external pitting of the integument, doublural terrace lines, the organization of the marginal region of the caparace, as well as the results of examination of some fine morphological characters in different ontogenetic stages are reported. An attempt is made to identify phacopine species in thin sections.

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Thin sections of the trilobite integument have been studied mainly by means of light microscopy. The material for investigation came mostly from the Fammenian limestone of Poland. It represents the phacopine species: *Phacops granulatus* (Munster, 1840), *Trimerocephalus mastophtalmus* (Richter, 1856), *T. caecus* (Gürich, 1896) and *Dianops anophthalmus?* (Frech, 1892) as well as the cyrtosymboline species *Cyrtosymbole pusilla* (Gürich, 1896), *C. franconica primitiva* Osmólska, 1962, *C. franconica nova* Osmólska, 1962, *Waribole conifera* Richter & Richter, 1926. The integuments of the Middle Devonian phacopine trilobite *Pedinopariops sobolewi* (Kielan, 1954) as well as of some Carboniferous proetid species: *Phillibole* sp., *Cummingella carringtonensis tuberculigenata* Osmólska, 1970, *Griffithides claviger halinae* Osmólska, 1970, *Paladin eichwaldi shunnerensis* (King, 1914), *P. trigonopyge* Osmólska, 1968 have also been sectioned for a comparison. Integuments of all the trilobites mentioned above are composed of microcristalline calcite. Prismatic structure has been observed only in some phacopines and is restricted there to the very thin outermost layer; lamination of the integument was found in one species (*T. caecus*), but occurs only in the top parts of the glabellar tubercles; the layering has not been generally noticed, but in several cases, the thin, outermost portion is darkened, which may be secondary.

Most of the observations were made on the sections of the integument of phacopine trilobites, which are usually 120–500 μ thick (for the cephala and pygidia 10–20 mm long). The integuments of the cyrtosymboline trilobites are very thin and their thickness ranges between 10–60 μ, the average being 45 μ (for the cephala and pygidia 3–6 mm long).

CEPHALIC TUBERCLES IN THE PHACOPINES

Thin sections of the cephala of the phacopine trilobites revealed that the structure of the glabellar tubercles (or granules) varies significantly even between closely related species. In *T. caecus,* the tubercles are relatively large, rounded (although some smaller and pointed granules are also found among them), and are each thoroughly pierced by a very broad duct (Pl. 1:2, 9). Some oblique sections, which crossed the tubercle peripherally to the main duct, expose the laminated structure of the top portion of the tubercle (Pl. 1:3,5), with the laminae spaced well apart. The tubercles in *T. caecus,* when sectioned tangentially, show the presence of dark patches arranged roughly radially around the opening of the main duct (Pl. 1:6); they may correspond to the thinner, laminated portions.

The structure of the glabellar tubercle changes during the ontogenetic growth in *T. caecus*; the tubercles on the integument of the adolescent specimens are hollow (Pl. 1:1), becoming solid and completely mineralized later. This agrees with the present author's earlier observations (Osmólska 1963) on the ontogenetic growth of *T. dianopsoides.* The internal moulds of the young cephala bear in this species the conical tubercles which become lower and then almost obsolete on the moulds of the adult cephala.

The glabellar tubercles of the closely related species *T. mastophthalmus* never show any lamination, apart from being smaller, conical, and pierced by a thin duct (Pl. 1:15–17).

The broad duct piercing the glabellar tubercles has never been noticed in *P.granulatus,* although the general form of the tubercles resembles this in *T. caecus.* Instead, the examination of the integument within the tubercle revealed the presence of a bunch of thin, numerous canals, which diverge dorsad so that they are all perpendicular to the external surface of the integument (Pl. 1:11). They do not seem to reach the inner surface of the integument (Pl. 1:13), and definitely do not reach the external surface either. They seem to end at the hollow zone present under the top of the tubercle. This zone is visible in *P.granulatus* on all the tubercles sectioned centrally. It is irregular in shape and on some specimens shows traces of the activity of boring microorganisms. There exists some doubt as to whether the hollow zone corresponds to the interlaminar zone, such as found in *T.caecus,* or whether it is due to secondary changes.

Rome (1936), who examined the thin sections of the integument of the closely related species *Phacops accipitrinus,* noticed the presence of a depression on the top of each glabellar tubercle, which is absent in *P. granulatus.* Otherwise, the structure of the glabellar tubercles is closely comparable in both species, the *piliers* of Rome corresponding most probably to the thin canals. Although Rome did not mention the presence of the broad canal piercing the tubercle, such a structure seems to be present, at least in young specimens, in *P.accipitrinus* from the Famennian of Morocco (Alberti 1972:32).

CANALS

The undoubted helical pore canals of other arthropods have never been observed on the trilobite integument, for which the state of preservation or the inadequacy of microscopic technique may be responsible. Two size groups of canals were noticed by the present author on the thin sections examined – the very thin canals, which are less than 2 μ in diameter, and the broad ones which range between 10–30 μ in diameter. Both the thin and the large canals are normal to the external surface of the integument. The thin canals are usually arranged densely and parallel. On some specimens examined they are restricted to certain regions of the carapace, very often where the integument is folded or bent. For example, they are present along the margins of the cephala (Pl. 1:10) and pygidia, across the convex portions of the axial rings and pleurae, on the occipital ring, etc., that is to say the places which may be subjected to the abrasion. For this reason, the thin canals (or at least some of them) may represent the ducts of the tegumental glands rather than those of the nerves, as reported in some decapod crustaceans (Dennell 1960:461). However the possibility cannot be excluded that some of the densely arranged canals of about 1 μ in diameter (other than those of the restricted distribution) may be the true pore canals, whose helical structure, if preserved, will be recognized in the future by using the electron microscope technique.

Numerous thin canals have been found in some cases (*P.granulatus*) within the large glabellar tubercles (cf. above). Generally, the canals of this size are most clearly visible in the middle portion of the integument. Their external and internal outlets are very rarely visible (Pl. 1:20).

Earlier studies of the trilobite integument (Cayeux 1913; Størmer 1930; Balashova 1948, 1955; Kielan 1954) noticed that broad canals often pierce the integument along the margins of the cephala and pygidia, as well as the region around the eyes. They were usually interpreted as setal ducts, which seems reasonable, as they are known to play this role in the integument of living arthropods. The canals representing the sensory ducts were also found on the thin sections of integuments examined by the present author. They pierce the margin of the cephalon above the vincular furrow in *P.sobolewi, P.granulatus* (Pl. 1:10), and *T.caecus* (Pl. 1:4), in the latter species being also present on the dorsal surface of the cephalic border, close to the margin of the carapace. There were not noticed, however, above the vincular furrow in *T.mastophthalmus.* In some species the broad ducts pierce the cephalic tubercles in, for example, the Middle Devonian *Proetus granulosus* (in this species the main, broad duct is surrounded by the sparsely spaced, comparatively thinner canals), as well as in *T.caecus* (Pl. 1:2, 9), *T.mastophthalmus* (Pl. 1:15–17), and *Dianops anaphthalmus*? (Pl. 1:18). The ducts piercing the glabellar tubercles in *T.caecus* have unusually broad lumen (Pl. 1:9), much broader than the lumen of the marginal sensory ducts. They can be noticed even on the surface of the internal mould of the cephalon (Richter & Richter 1926, Pl. 10:84). The internal outlets of these ducts in *T.caecus* are usually placed on the small elevation of the internal surface of the exoskeleton. The external outlets are broadened, funnel-like, which may indicate that they were connected with some movable, pedunculate setal element similar to that reported in some decapod crustaceans (Dennell 1960:454; Fig. 1).

The large duct piercing one of the glabellar tubercles in *T.caecus* (Pl. 1:2) is filled with the transparent, amber coloured substance (very dark on the photograph), which might constitute the sclerotized cuticular lining around the setal peduncle.

Contrary to the setal ducts in *T.caecus,* these piercing the glabellar tubercles in *T.mastophthalmus* are much thinner. As a rule, they do not reach the internal surface of the integument (Pl. 1:15—17). In some tubercles there is a suggestion that the ducts break up inwards into several thin branches. Similarly thin setal ducts pierce the scarce, conical tubercles in *D.anophthalmus* (Pl. 1:18), but they always reach the internal boundary of the integument.

The thin integuments of the cyrtosymbolines allowed the present author to observe the canals of one size group only, namely those which are connected with the ornamental elements of the cephalon, and probably also these of the marginal regions of the carapaces (cf. below). They seem to correspond to the sensory ducts of the thick-shelled trilobites, although they are much thinner (1—2 μ in diameter) than the latter (Pl. 2:10).

EXTERNAL PITTING

The examination of the thin sections of the phacopine integuments revealed the presence of fine, relatively shallow pits, which are more or less evenly distributed on the entire external surface of the integument, sometimes also including the doublure (hypostomata were not examined). The pits mentioned lead to the tiny cavities measuring 12—15 μ in diameter and 10—18 μ in depth. Their absolute sizes differ only slightly in all specimens investigated (Pl. 1:7, 14, 17—20), and have little relation to the thickness of the integument, or to the size of the individual. As far as one could see from the light microscope, they are not connected with any visible canals, except, perhaps, in *P.sobolewi,* where some of them are prolonged internally by very thin canals (Pl. 1:20). They vary in shape between the examined phacopine species, being ampule-like, narrowed externally, or cup-like, broadly open externally.

The sections of the integument of the immature individuals of *T.caecus* prove that the pits are relatively larger on the thin integuments of the adolescent animals than those on the integuments of the full-grown ones (Pl. 1:1, 8). This seems to indicate that they might be functionally important during larval life, but it is difficult at present to conclude which role they played.

STRUCTURE OF THE MARGINAL REGION OF THE CYRTOSYMBOLINE CARAPACES

The calcified integument of all trilobites is marginally folded downwards and inwards forming the so-called "doublure". The same element is found on the shell of the ostracodes where it has been named "duplicature" or "infold", as was recently proposed by Kronicker (1969). In all the non-cyrtosymboline trilobites the marginal portion of the cephalic and pygidial carapaces have the shepherd's crook shape in the cross-section (Horowitz & Potter 1971:68). The external margin of these trilobites is more or less blunt; the thickness of the integument measured across the margin usually only slightly exceeds the thickness of the dorsal exoskeleton. By contrast, in the representatives of the Cyrtosymbolianae, which occur in the Upper Devonian and Lower Carboniferous, the margin of the carapace, especially of the pygidium, is sharp. This is due to the strong flattening of the thin cyrtosymboline carapace, with the doublure close, and on the pygidium generally parallel to the dorsal exoskeleton. The thickness of the integument measured across the margin is usually double that of the dorsal exoskeleton. When the cyrtosymboline pygidia are sectioned they always expose a distinct, straight line which marks the boundary between the dorsal exoskeleton and the doublure (Pl. 2:3-7). This feature has so far been noticed exclusively in the cyrtosymbolines among other trilobites. But the same character has been reported in some groups of ostracodes. The dark line present in the sectioned ostracodes on the boundary between the outer lamella and the infold was named "line of concrescence" by some authors. After Harding (1964) proved that the line was not due to the fusion of these two elements, Kronicker (1969) introduced a new term "axial line" (and "axial zone" respectively) for this feature in the ostracodes. The reason is still unknown for the occurence of the axial line in ostracodes. The continuity of the entire integument (whether mineralized or soft) which was stressed by Harding (1964:10) for the ostracodes, should also be true for the trilobites. Thus it is highly probable that the infold of the ostracodes is homologous to the doublure of the trilobites, and consequently the line marking the boundary between the dorsal exoskeleton and the doublure in the cyrtosymbolines may correspond to the axial line of the ostracodes. That is why the latter term is also accepted in this paper. Apart from being more strongly pronounced, the axial line of the cyrtosymbolines differs from that in ostracodes in its straight course, the entire axial plane (= axial zone) being flat and horizontal. The pygidial doublure can be very easily separated from the dorsal exoskeleton in the cyrtosymbolines, by breaking along the axial zone, which means that here the resistance of the exoskeleton is weakened. The surface of the axial zone of the pygidium of *W.conifera*, obtained by this method, was examined using the scanning electron microscope. Examination revealed the presence of very closely spaced dark lines crossing the entire axial zone between the external and internal surfaces of the pygidial integument (Pl. 2:8, 9). They may correspond to the marginal sensory ducts of other trilobites (= marginal pore canals of the ostracodes). However, as far as could be discerned from the examination of the external margin of the pygidium, they do not open outwards. If this is true, their sensory function should be doubted. Until further studies on the axial zone of the cyrtosymbolines are carried out, the question of their function must remain unsolved.

A slightly different organization of the cyrtosymboline carapace is seen around the cephala. The cross sections cutting the lateral cephalic border show a kind of "intercalation" between the dorsal carapace and the doublure (Pl. 2:1, 2). This intercalating unit is wedged between the two most peripheral terrace lines – one on the lateral border and the other on the doublure. The unit shows in polarized light the extinction opposite to those of the neighbouring portions of the margin. It still remains unclear which of the two boundaries of the intercalating unit corresponds to the axial line and which (if any) conducts the marginal sensory duct.

TERRACE LINES

The term "terrace lines" has been adopted both for the ornamental elevated ridges covering the external surface of the dorsal exoskeleton of some trilobites, and for the ridges or lists which are very often present ventrally along the cephalic and pygidial doublures, and dorsally along the borders. In the present author's opinion the term should be limited to one of these structures only, because they differ significantly in their construction and possibly also in the role they played. The "ornamental terrace lines" are more or less irregularly spaced, exposing often the undulating pattern. The "doublural terrace lines" (this term is used below) are regular, uniformly spaced, and concentrically arranged, resembling in their pattern the growth lines of the pelecypods. The thin sections through the marginal portions of the carapaces of some trilobites revealed that the doublural terrace lines are variable, though the differences are not easily noticed in the superficial observation. The sectioned phacopines did not have any terrace lines. The typical doublural terrace line, such as those present in the cyrtosymbolines and some other proetids, constitutes an elevated, sharp ridge, which is inclined towards the periphery, the steeper and shorter slope being this distal one. When cross-sectioned, each of these ridges shows a medial crevice, directed obliquely towards the inner surface of the integument (Pl. 2:11-13). It is, generally, broader externally and narrows on its way inwards. The ridge slope, which is lateral to the crevice, consists of slightly darker (thinner?) calcite, which makes it less clearly visible (Pl. 2:12). The crevices very rarely reach the inner surface of the integument, since they are usually very short. The portions of the doublure marked off by the neighbouring crevices seem to represent different structural units, which expose distinctly opposite extinctions when looked at in the polarized light. The crevices cannot be interpreted as a series of canals arranged along the doublural terrace line, because they are present on each of many sections cutting the same specimen. It suggests that they form a continuous slit along the doublural terrace line. In some species (*C. carringtonensis tuberculigenata*: Pl. 2:11, *P. eichwaldi shunnerensis,* and *G. claviger halinae*: Pl. 2:12) the crevices along the marginal region of the pygidia are penetrated by the marginal sensory canals or the ducts of the tegumental glands. The doublural terrace lines on the pygidium of the Upper Carboniferous species *P. trigonopyge* differ from those described above. They are represented by the short crevices only, while the ridges are absent (Pl. 2:13). Some of these crevices may collect tegumental ducts, which are very numerous in this species, especially in the marginal zone, but as a rule, the direction of the crevices does not coincide with that of the ducts.

IDENTIFICATION OF THE PHACOPINE TRILOBITES IN THIN SECTIONS

Although the material of the phacopine integuments examined by the present author was not very extensive, it shows that species belonging to Phacopinae can probably be determined in thin sections. This is possible because of the variability in the form and distribution of the external pitting of the exoskeleton (p. 203), as well as in such features as the shape, size, and density of the distribution of the tubercles and the size and structure of the setal or tegumental ducts. The thickness of the exoskeleton is also of some importance in specific determination, but it changes during individual growth.

This method of trilobite identification can be useful for microfacial analysis or for stratigraphic purposes, whenever the trilobite material is too scanty and fragmentary for macromorphological identification, as is often the case with material from bore cores.

The present author, after examining a large amount of sectioned material, is convinced that not only the phacopines but also the cyrtosymbolines can be identified in thin sections. However, the thinness of their integuments requires high magnification power and consequently thinner sections, which may be difficult for practical purposes.

The specific assignment of *Dianops anophthalmus* is provided here with a question mark, because the specimen was not determined specifically prior to its sectioning. However, its assignment to this species is highly probable, because it comes from the beds (Upper Famennian, Dzikowiec, Lower Silesia) in which only two phacopine species were recorded (Richter & Richter 1926), namely *D. anophthalmus* and *P. granulatus.* The latter species cannot be taken into account, as the microstructure of its integument is completely different.

TABLE 1

	Phacops granulatus	*Trimerocephalus caecus*	*Trimerocephalus mastophthalmus*	*Dianops anophthalmus*
External pitting:				
shape	ampulla-shaped	cup-like	cup-like	cup-like
distribution	very dense, present on doublure	dense, absent on doublure	scarce, absent on doublure	dense
Glabellar tubercles:				
shape	large, rounded	large, rounded laminated at top and small conical	small, conical	small, conical
distribution	dense	dense	dense	extremely scarce
Thin canals	numerous across cephalic margin; in bunches within tubercles	occasionally noticed	?	?
Broad canals:				
marginal	scanty	numerous	?	?
piercing tubercles	absent	extremely broad, reaching inner surface	very thin, rarely reaching inner surface	thin, reaching inner surface
Average thickness of integument	420-450 μ	150-180 μ	130 μ	120 μ

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EXPLANATIONS OF PLATES

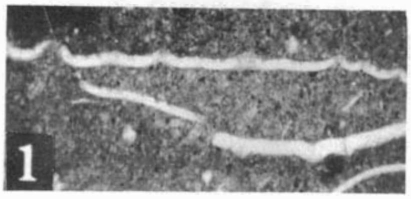
All specimens are housed in the Palaeozoological Institute of the Polish Academy of Sciences, Warszawa, for which the abbreviation ZPAL is used.

Plate 1

Thin cross-sections of phacopine integuments. Fig. 1. Above: *Trimerocephalus caecus* (Gurich). Section of glabellar integument of adolescent specimen. Tubercles and pits visible. Below: *Cyrtosymbole pusilla* (Gurich). Section of glabellar integument (upside down). ZPAL Tr. IV/1. X50. *Fig. 2. T. caecus.* Section crossing glabellar tubercle centrally. Setal duct, broadened externally and internally, exposed. Two dark spots, visible on both sides of the duct, represent iron oxide particles. Calcareous element above the tubercle is due, most probably, to accidental association. ZPAL Tr. IV/1. X50. *Fig. 3. T. caecus.* Section crossing glabellar tubercle obliquely. Centre: Lamination, pitting and lumen of setal duct visible. Left, below: Internal outlet of setal duct exposed. ZPAL. Tr. IV/1. X50. *Fig. 4. T. caecus.* Section of cephalic margin, above vincular furrow. Several marginal sensory canals crossed. Pitting in vincular furrow absent. ZPAL. Tr. IV/1. X50. *Fig. 5. T. caecus.* Section crossing glabellar tubercle obliquely. Lamination and lumen of setal duct exposed. ZPAL. Tr. IV/1a. X95. *Fig. 6. T. caecus.* Tangential section of glabellar integument. Larger, star-like spots correspond to openings of setal ducts, small ones represent pits. ZPAL Tr. IV/1. X90. *Fig. 7. T. caecus.* Section of top portion of glabellar tubercle. Same as on Fig. 3. X100. *Fig. 8. T. caecus.* Section of integument of adolescent specimen. Details of pitting visible. ZPAL Tr. IV/1. X120. *Fig. 9. T. caecus.* Section of integument crossing glabellar tubercle centrally. Very broad setal duct exposed. ZPAL Tr. IV/1a. X95. *Fig. 10. Phacops granulatus* (Münster). Section of cephalic margin, above vincular furrow. A marginal sensory duct partly crossed, as well as numerous thin ducts of tegumental glands. ZPAL Tr. IV/5. X28. *Fig. 11. P. granulatus.* Section crossing glabellar tubercles. Bunch of thin canals within tubercle diverging externally, exposed. Dark, arched space at top of tubercle corresponds to hollow zone. Pitting obscured by particles of iron oxide. ZPAL Tr. IV/5. X25. *Fig. 12. P. granulatus.* Section of cephalic integument with pitting visible. ZPAL Tr. IV/5. X50. *Fig. 13. P. granulatus.* Section of glabellar tubercle. Same as on Fig. 11. X50. *Fig. 14. P. granulatus.* Section of cephalic integument. Details of pitting visible. Same as on Fig. 12. X120. *Fig. 15. T. mastophthalmus* (Richter). Section of cephalic integument. ZPAL Tr. IV/2. X50. *Fig. 16. T. mastophthalmus.* Section of glabellar integument. Tubercles exposed, pierced by setal ducts not reaching internal surface. ZPAL Tr. IV/2. X50.*Fig. 17. T. mastophthalmus.* Section of glabellar integument. Details of pitting and setal ducts visible. Same as on Fig. 16. X120. *Fig. 18. Dianops anophthalmus* (Frech) ? Section of cephalic integument. Details of pitting, tubercles and setal ducts visible. ZPAL Tr. IV/3. X120. *Fig. 19. Pedinopariops sobolewi* (Kielan). Section of pygidial integument; doublure. Details of pitting visible. ZPAL Tr. IV/6. X90. *Fig. 20. P. sobolewi.* Section of pygidial integument. Darkening of pitted layer visible. Thin, dark canals exposed, possibly connected with pits. Light, round spots accidental. ZPAL Tr. IV/6. X90.

Plate 2

Figs.: 1-7, 10-13. Thin cross-sections of proetid integuments. *Figs. 8-9.* Scanning electron micrographs. *Fig. 1. Cyrtosymbole pusilla* (Gürich). Section of marginal portion of librigena. Intercalating unit, axial line and doublural terrace lines exposed. ZPAL Tr. IV/7. X50. *Fig. 2. C. franconica primitiva* Osmólska. Section of marginal portion of librigena. Intercalating unit, axial line and doublural terrace lines exposed. ZPAL Tr. IV/7. X50. *Fig. 3. C. franconica nova* Osmólska. Section of posterior part of pygidium. Marginal portion of pygidium obliquely crossed. Axial line visible. ZPAL Tr. IV/8. X50. *Fig. 4. C. franconica nova.* Section of posterior part of pygidium. Axial line visible. Same specimen as on Fig. 3. X50. *Fig. 5. Waribole* sp. Section of marginal portion of pygidium. Axial line visible. ZPAL Tr. IV/5. X50. *Fig. 6. C. franconica nova.* Section of marginal portion of two pygidia. The upper one obliquely crossed. ZPAL Tr. IV/10. X50. *Fig. 7. Waribole conifera* (Richter & Richter, Section of marginal portion of pygidium. Axial line visible. ZPAL Tr. IV/11. X50. *Fig. 8.* Scanning electron micrograph of pygidial integument of *W. conifera* broken along axial zone. Closely spaced lines visible on the left side, possibly representing marginal sensory ducts. ZPAL Tr. IV/12. X180. *Fig. 9. W. conifera.* Same as on Fig. 8. Two dark lines crossing axial zone visible. X2000. *Fig. 10. C. franconica nova.* Section of glabellar integument crossing ornamental ridges. Dark, vertical lines probably represent setal ducts. ZPAL Tr. IV/9. X170. *Fig. 11. Cummingella carringtonensis tuberculigenata* Osmólska. Section of marginal portion of pygidium. Doublural terrace lines and marginal sensory ducts visible. ZPAL Tr. IV/13. X50. *Fig. 12. Griffithides claviger halinae* Osmólska. Section of marginal portion of pygidium. Structure of doublural terrace lines and marginal sensory ducts visible. ZPAL Tr. IV/14. X50. *Fig. 13. Paladin trigonopyge* Osmólska. Section of marginal portion of pygidium. Structure of doublural terrace lines and numerous thin integumental (?) ducts visible. ZPAL Tr. IV/15. X50.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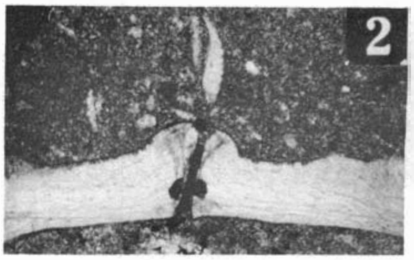
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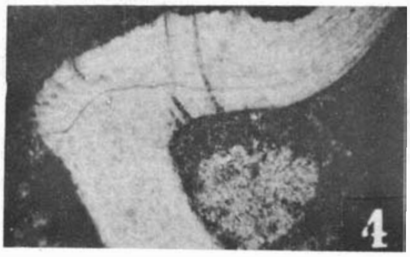
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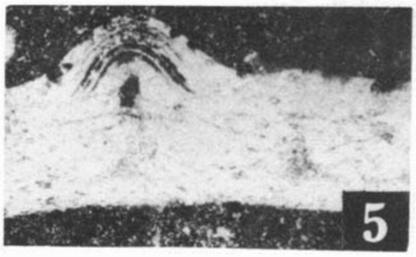
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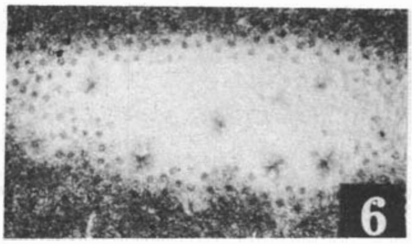
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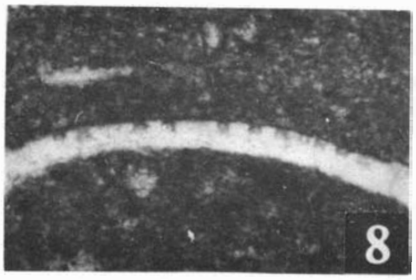
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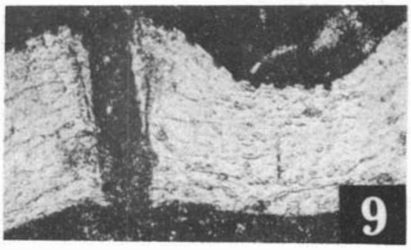
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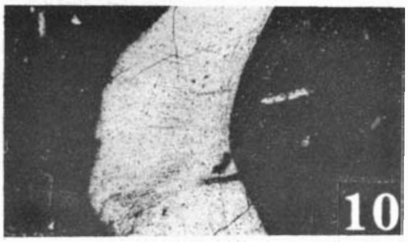
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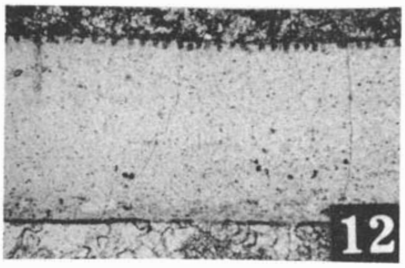
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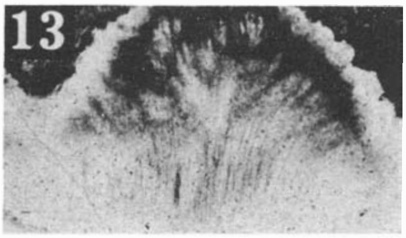
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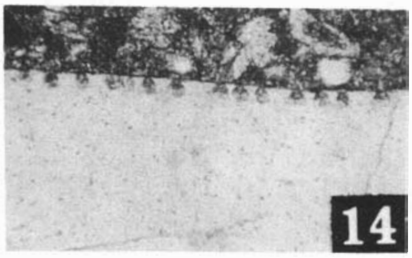
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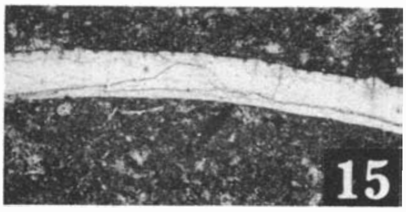
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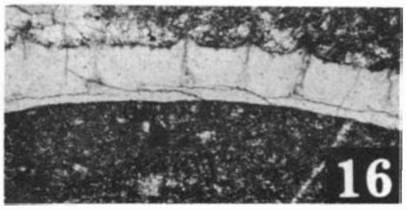
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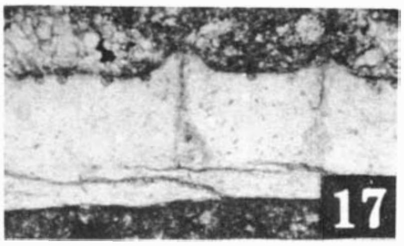
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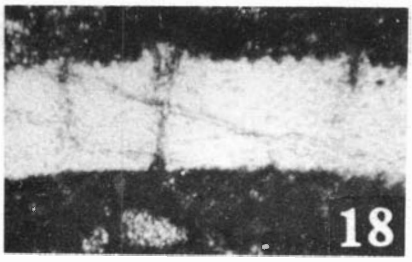
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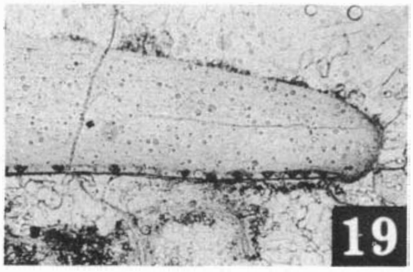
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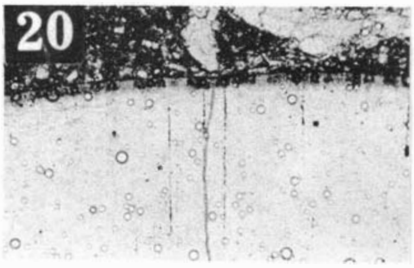
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Plate 1


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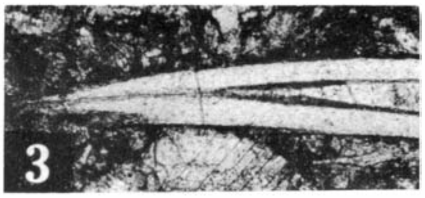
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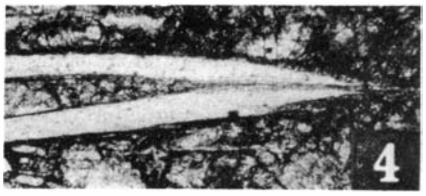
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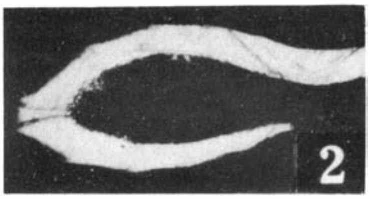
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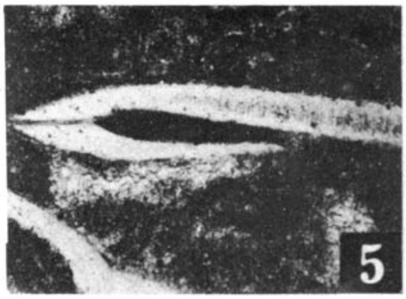
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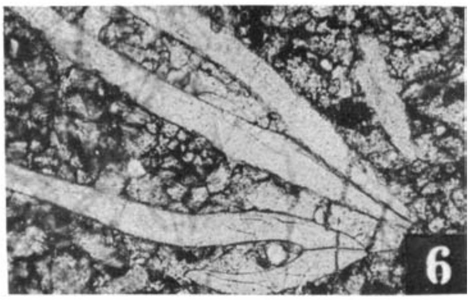
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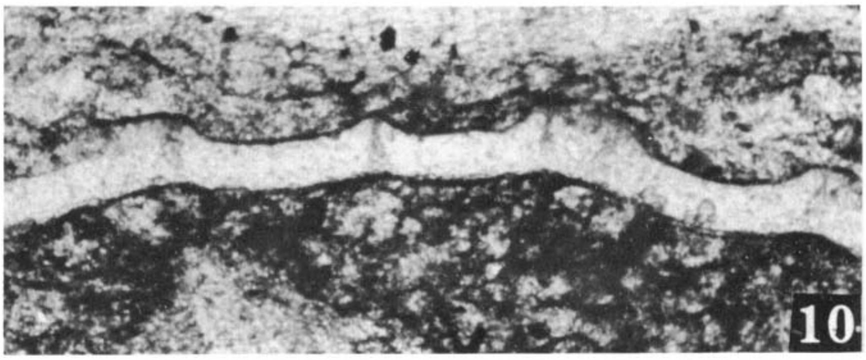
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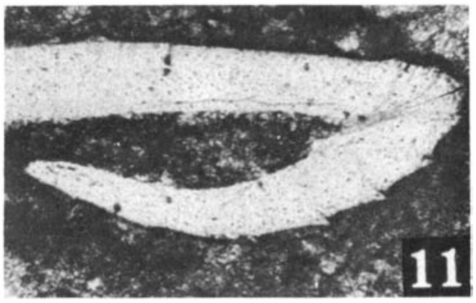
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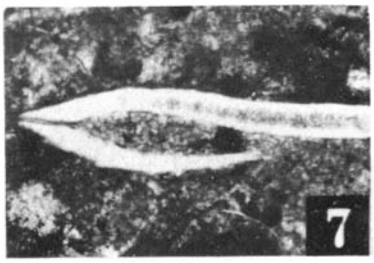
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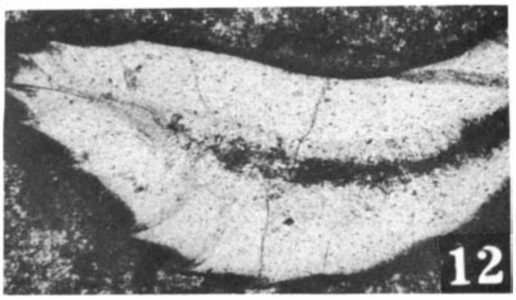
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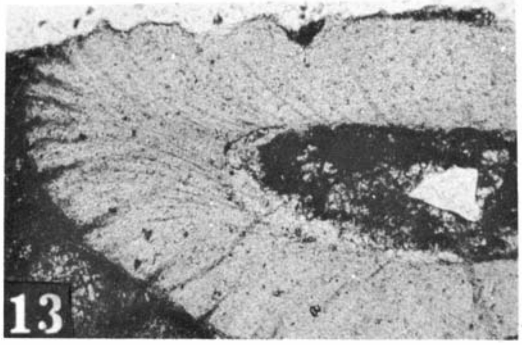
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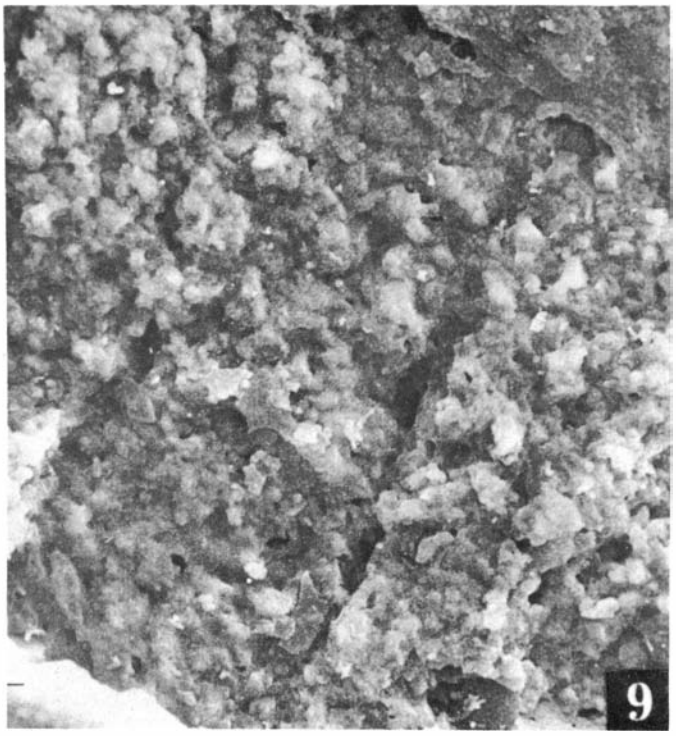
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Plate 2

Evolutionary processes leading to the trilobite suborder Phacopina

VALDAR JAANUSSON

Jaanusson, V. 1975 07 15: Evolutionary processes leading to the trilobite suborder Phacopina. *Fossils and Strata,* No. 4, pp. 209–218. Oslo ISSN 0300–9491. ISBN 82-00-04963-9.

A new Ordovician genus, *Gyrometopus* (fam. Diaphanometopidae, subfam. Gyrometopinae nov.), is established and the type species *Nileus? lineatus* Angelin, 1854, redescribed. The origin of the Phacopina was associated with at least two morphological discontinuities: fixation of the number of thoracic segments and fusion of free cheeks. The characters of *Gyrometopus* (number of thoracic segments, general morphology of the cephalon and pygidium, structure of the thoracic pleurae) agree with those of the Phacopina except that the genus possesses a functional rostral shield. Thus *Gyrometopus* fulfills most of the requirements of an immediate ancestor of members of the Phacopina but has not bridged one of the morphological discontinuities. The evolutionary processes associated with bridging morphological discontinuities are discussed.

Valdar Jaanusson, Paleozoologiska sektionen, Naturhistoriska Riksmuseet, S-104 05 Stockholm 50, 26th August, 1973.

Examination of material of a species, described by Angelin (1854) as *Nileus? lineatus,* showed that the main characters of this species are relatively close to what can be postulated to have been those of an immediate ancestor of members of the suborder Phacopina (as defined in Harrington *et al*., 1959). This has resulted in a study of some probable main evolutionary processes that pertain to the origin of the suborder.

Nileus? lineatus belongs to a new, and at present monotypic genus, described herein. The morphology of the type species is treated in some detail as it plays a central part in the evolutionary arguments put forward.

GYROMETOPUS N. GEN.

TYPE SPECIES.– *Nileus? lineatus* Angelin, 1854.

DIAGNOSIS. –Glabella flattened, slightly expanded anteriorly, with three pairs of faint, narrow lateral glabellar furrows. Rostral plate triangular, with convex sides; connective sutures unite before reaching the inner margin of doublure and continue in a short median suture. 11 thoracic segments, pleural furrows narrow, distinct, continue on the broad articulating facet. Pygidial margin entire, pygidial pleurae with well-defined narrow pleural and interpleural furrows on two first segments.

GYROMETOPUS LINEATUS (ANGELIN, 1854)

Figs. 1-4, 5A-B.

SYNONYMY.– ☐ 1854 *Nileus? lineatus* n.sp. – Angelin: 60, Pl. 33:12, 12a. ☐ 1893 *Trilobit* mit *Phacops* verwandt *n.gen. et n.sp.* – Wiman: 71. ☐ 1906 *Diaphanometopus lineatus* A. – Wiman: 291-292, Pl. 29:16-20. ☐ 1908 *Diaphanometopus lineatus* A. – Wiman: 89, Pl. 7:8. ☐ 1956 *Diaphanometopus lineatus* (Dalman) – Tjernvik: 135, 279.

HOLOTYPE (by monotypy).– Cranidium, RM No. Ar. 15368, figured by Angelin, 1854, Pl. 33:12, 12a. Västergötland, Oltorp. Zone of *Megistaspis planilimbata.*

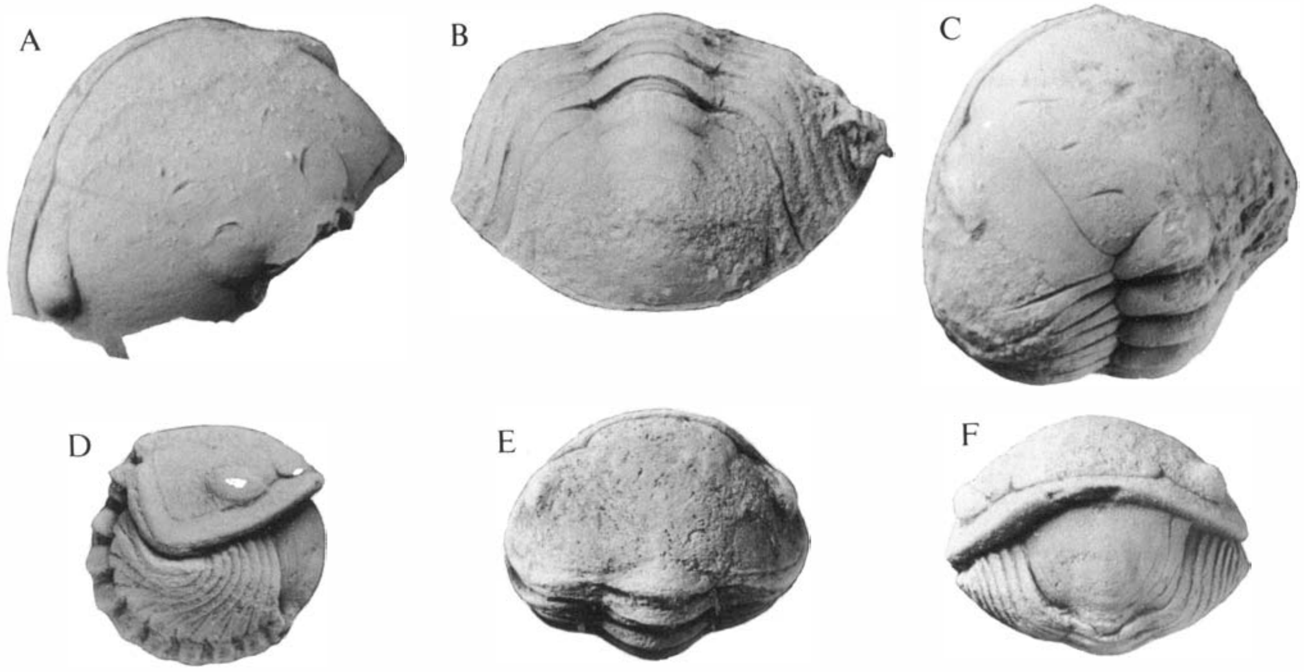

Fig. 1. Gyrometopus lineatus (Angelin). Närke, Lanna, Hunneberg Stage, zone of *Megistaspis planilimbata*, collected by J. G. Andersson. Magnification x4. A. Cephalon, Ar. 13142; B. Pygidium of the same specimen; C. Cephalon of a complete, enrolled specimen, Ar. 47938; D–E. Complete enrolled specimen in three different views, Ar. 47939 (previously figured by Wiman, 1906, Pl. 29:16–18).

CEPHALON.– Cephalon semicircular in outline, moderately convex. Glabella defined by distinct narrow furrows all around, flattened, not protruding from the general convexity of the cephalon; broadest anteriorly between the points where rhachial furrows meet anterior border furrow and narrowest posteriorly between the points where rhachial furrows join occipital furrow; width of the frontal lobe somewhat greater than length of glabella. Three pairs of faint, narrow, curved lateral glabellar furrows with slightly raised posterior margin. Rhachial furrows, and thus also the sides of glabella, have a distinctly sigmoidal curvature; they are distinct, narrow, and comparatively shallow. The point where rhachial, preglabellar, and anterior border furrows meet is distinctly deeper than the bottom of the furrows and may represent fossula. Occipital furrow similar to rhachial furrows, weakest in the middle; occipital ring somewhat more convex than glabella.

Genae regularly convex; cephalon surrounded by a well-defined border defined by narrow border furrows. Cephalic border flattened, narrowest in front of glabella; posterior cephalic border narrowest close to the rhachial furrow, increasing in width laterally. Genal angles broadly rounded.

Eyes fairly small; length somewhat greater than the exsagittal distance between anterior end of eye and anterior cephalic margin, about equal to exsagittal distance between posterior end of the eye and posterior border furrow; situated fairly close to the anterior cephalic margin. Palpebral lobes narrow, moderately convex, defined mesially by a distinct furrow which originates at the middle of the posterior end of the eye, surrounds palpebral lobe posteriorly and mesially, and continues in an antero-median direction towards a point which is situated somewhat posterior to the junction of the rhachial and preglabellar furrows, disappearing gradually some distance before reaching that point. The furrow clearly corresponds to the posterior furrow defining an eye ridge in forms with an eye ridge.

Only a few of the available specimens have the visual surface preserved well enough for observation of details of the surface. Visual surface moderately convex (Fig. 3); the specimen Ar. 13134 has 145 lenses, arranged in 21 rows. Individual lenses with a fairly strongly convex outer surface, the outline is circular, and the lenses are separated from each other by moderately thick sclerotic walls. In specimens where weathering has exposed a deeper section through the visual surface, the lenses have a hexagonal outline, though the intervening sclerotic walls are thicker than in forms with typical holochroal eyes. Owing to the scarsity of suitably preserved material, no thin sections through the eye have been prepared and the relation of corneal covering to the visual surface is unknown. The hexagonal outline of deep sections through the lenses suggests that eyes in *Gyrometopus* are advanced holochroal with biconvex lenses, but this is difficult to prove without information on corneal covering.

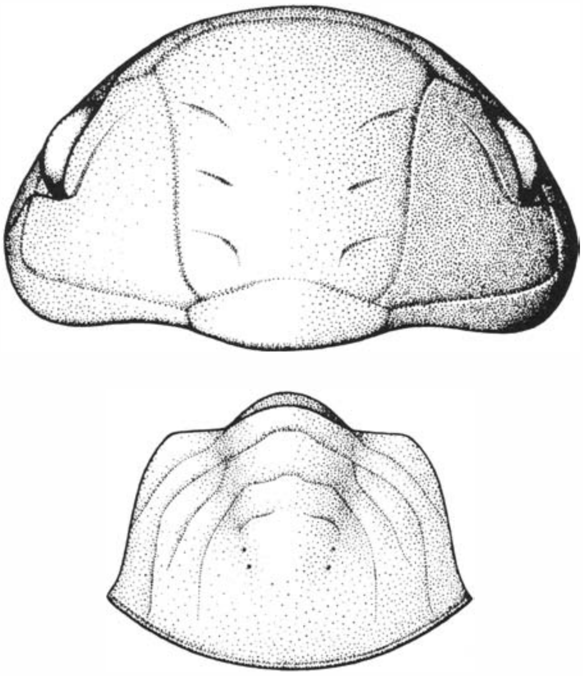

Fig. 2. Gyrometopus lineatus (Angelin). Reconstruction of the cephalon and pygidium. The articulating facets of the pygidium have been omitted since none of the available specimens shows the anterior margin of the facet clearly. Magnification ca. x8.

Anterior section of facial suture runs from the eye almost straight to anterior border furrow and crosses the border in anteromedian direction. Posterior section runs almost straight to cephalic border, curves abruptly in posterolateral direction, and continues nearly straight to the external cephalic margin (Fig. 2).

Genae covered with shallow scattered pits and glabella with small scattered granules, both faint and visible only on well-preserved specimens.

VENTRAL CEPHALIC SUTURES.– Ventral surface of the cephalic doublure flattened in the middle and faintly convex laterally. Rostral plate triangular with distinctly convex sides (Fig. 4); length about half the width. Connecting sutures unite at the posterior end of the rostral plate and continue in a very short but distinct median suture (Fig. 4). Surface of rostral plate and doublure finely granulate. The posterolateral edge of the librigenae flattened and lightly projecting ventrally. Labral plate unknown.

THORAX.– Thorax consists of 11 segments. Rhachis moderately convex, articulating furrow distinct, articulating half-ring about half the length of the rhachial ring, flattened in longitudinal and moderately convex in transverse direction. Rhachial furrow well-defined, narrow. Upon each tergite the anterior section of the furrow runs straight in anteromedian direction from

Fig. 3. Gyrometopus lineatus (Angelin). The visual surface of the eye in one of the specimens where the surface is best preserved. Ar. 13143, magnification x32. Närke, Lanna.

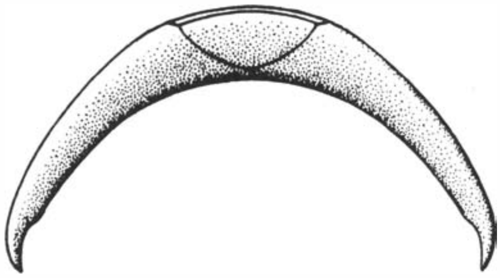

Fig. 4. Gyrometopus lineatus (Angelin). Diagrammatic drawing of the ventral cephalic sutures based on the specimen Ar. 13133 (previously figured by Wiman, 1906, Pl. 20, fig. 19).

the inner end of the pleural furrow to the anterior margin of the tergite, while the posterior section runs straight in posteromedian direction from the inner end of the pleural furrow to the posterior margin of the tergite. Anterior and posterior sections meet at a distinct angle so that the course of thoracic rhachial furrow describes a zig-zag line (Fig. 5B). Posterior section somewhat longer and shallower than anterior section. Width (*tr.*) of the inner portion of the pleurae (from rhachial furrow to fulcrum) of fourth and fifth segments slightly less than half the width of the corresponding rhachial ring. Pleural furrows narrow, distinct, resembling rhachial furrows. Articulating facet long, about twice the length of the inner part of the pleura of the first thoracic segments, distinctly concave, with granulate surface. The pleural furrow continues upon the articulating facet roughly parallel to the anterior margin of the facet and becomes gradually obsolete first close to the lateral termination of the pleura. Pleural doublure unknown.

PYGIDIUM.– Pygidium (Figs. 1B, 2) moderately convex, about 2/3 the length of the cephalon, external margin rounded, entire. Rhachis convex, poorly defined, rhachial furrow faint. Rhachis evidently consists of five poorly defined rings and a terminal piece; anterior three rings defined by shallow ring furrows, indistinct in the middle, and posterior rings by two pairs of shallow pits (Fig. 2). When immersed in some liquid, the pits are distinctly darker than the surrounding test; similar dark spots are visible on the lateral extremities of the three anterior ring furrows. Pygidial pleural and interpleural furrows of almost equal distinctness, narrow, and resembling thoracic pleural furrows. Foremost interpleural furrow entire, extending from the rhachis to the external pygidial margin; second interpleural furrow weak, extending only over a third of the width of the pleural region; interpleural and pleural furrows of the posterior segments obsolete. Details of articulating facet unclear except that, as on thoracic pleurae, the pleural furrow continues on the facet. Pygidial doublure unknown.

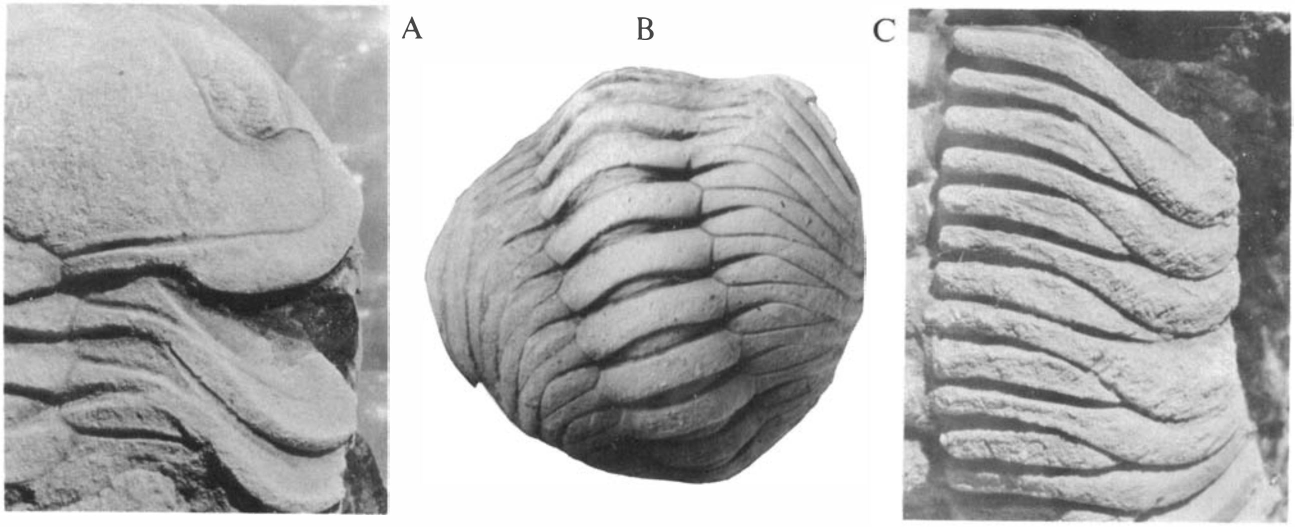

Fig. 5. A and B. *Gyrometopus lineatus* (Angelin). A. Pleura of the first thoracic segment and the adjoining parts of the carapace; note the continuation of the pleural furrow on the articulating facet; Ar. 13133, magnification x9, Närke, Lanna, collected by J. G. Andersson. B. Thorax of an enrolled specimen; Ar. 47940, Närke, Yxhult, collected by J. G. Andersson, magnification x4. C. *Pterygometopus sclerops* (Dalman), anterior part of the thoracic pleurae; note the continuation of the pleural furrow on the articulating facet; Ar. 18035, Östergötland, Västanå, Kunda Stage, zone of *Asaphus expansus;* magnification x7.

OCCURRENCE. Lower Ordovician (Ontikan) Hunneberg Stage, zone of *Megistaspis planilimbata*. Västergötland: Oltorp, Stenbrottet (Orreholmen); Närke: Lanna, Yxhult; erratics from the South Bothnian area (cf. Wiman, 1908, Pl. 7, fig. 8).

REMARKS ON THE MORPHOLOGY OF THORACIC PLEURAE

In taxonomic and phylogenetic considerations relatively little attention has hitherto been paid to the thoracic structures. For the purpose of this paper, the mutual relations between the articulating facet and pleural furrow are of some importance and must be briefly considered.

In many trilobites which possess an articulating facet as well as a pleural furrow, the outer portion of the pleural furrow runs behind the facet in lateral direction until it becomes obsolete. Such type of pleural furrow, here termed the *postfacetal* type, occurs in the asaphids, nileids, bathyurids, cyclopygids, holotrachelids, and a number of other trilobites.

In most representatives of the suborder Phacopina the relation between the facet and the pleural furrow is different. Here, the outer portion of the pleural furrow crosses the posterior margin of the articulating facet and continues as a narrow, distinct furrow on the articulating facet (Fig. 5C). This type of pleural furrow is termed here the *epifacetal* type. The epifacetal pleural furrow occurs also in encrinurids (at least in the Encrinurinae and Cybelinae, cf. Öpik, 1937, Pl. 21:4), calymenaceans (cf. Campbell, 1967, Pl. 11:1, 2), many proetids (cf. Whittington & Campbell, 1967, Pl. 2:7, 14, 15), and otarionids. This is the type of pleural furrow also in *Gyrometopus* (Fig. 5A).

The functional significance of these differences is not clear. At any rate, the epifacetal position of the outer part of the pleural furrow has nothing to do with enrollment. The type of pleural furrow tends to be constant within large groups of trilobites, at subfamily to superfamily level, and may have a considerable taxonomic importance.

Within the suborder Phacopina a remarkable change from one type to the other has taken place during the evolution of the group. All pterygometopids and phacopaceans seem to have the epifacetal type of pleural furrow. So do also several dalmanitids (such as *Ormathops,* personal observations) and at least most forms classified by Struve (in Harrington *et al.*, 1959) as the subfamily Acastinae (*Kloucekia, Acaste* etc.). On the other hand, in the Silurian and Devonian Dalmanitinae the pleural furrow is distinctly postfacetal (cf. Campbell, 1967, Pl. 17:13; Whittington & Campbell, 1967, Pl. 14:11 etc.). The transition from one type to the other may have taken place via forms in which the articulating facet became obliterated (*Mucronaspis* seems to be fairly close to this condition, the non-facetal type). When during evolution the articulating facet was developed anew, it did not incorporate the pleural furrow any more. Thus the transition from epifacetal to postfacetal pleural furrow represents an interesting evolutionary problem that should be studied carefully.

AFFINITIES OF *GYROMETOPUS*

Gyrometopus lineatus was included in *Diaphanometopus* by Wiman (1906, 1908) and Tjernvik (1956). The only known specimen of *Diaphanometopus volborthi* Schmidt, 1881 – the type species of this monotypic genus – cannot be found in the collections of the CNIGR Museum in Leningrad (Dr. I. M. Kolobova, personal communication). It has 12 thoracic segments, anteriorly slightly tapering glabella, a trace of an additional lateral glabellar furrow in front of S 3, and a different course of ventral cephalic sutures (Schmidt, 1881, Pl. 12:28d) suggesting a wide rostral shield (however, Schmidt could not observe a rostral suture). Moreover, the pygidial pleurae are extended by pleural spines (the length of which is unknown since in the holotype they are broken off close to the base), and the pygidial rhachis seems to have one segment less than in *Gyrometopus* (which in this case implies that the total number of segments in the thorax and pygidium is the same in both genera). *Diaphanometopus* is thus clearly different from *G. lineatus.* Schmidt (1881) suggested affinities with *Amphion* (=*Pliomera*), Öpik (1937) included *Diaphanometopus* tentatively in the Pliomeridae, and Jaanusson (in Harrington *et al.*, 1959) classified the genus as a monotypic subfamily of the family Pliomeridae. Whittington (1961) found that ”*Diaphanometopus* is perhaps more pilekiid than pliomerid in appearance”, but that its relationships are uncertain. Pilekiinae were included by Harrington (in Harrington *et al.*, 1959) in the Pliomeridae, but were excluded from that family by Whittington (1961), who considered them to be either a separate family (as suggested by Sdzuy, 1955) or a subfamily of the Cheiruridae. Lane (1971) stated that *Diaphanometopus* forms a monotypic subfamily within the Pliomeridae and classified pilekiids as a subfamily of the Cheiruridae. Thus *Diaphanometopus* is a further genus that is difficult to classify. However, there is scarcely any doubt that it belongs to the Cheiruracea.

The writer agrees with Whittington that *Diaphanometopus* probably has affinities with the pilekiids. The pygidium agrees with the general pattern of that of the pilekiids except that the terminal piece too is produced into a spine. *Diaphanometopus* also has well-defined pleural furrows on the thorax as well as on the first two segments of the pygidium. However, in those pilekiids in which thoracic segments are known, the pleural furrow mostly runs in the middle of the pleura, no articulating facet seems to be developed, and the outer part of the pleura protrudes as a spine (Sdzuy, 1955, Pl. 8:28). In *Diaphanometopus* details of the morphology of the outer part of the thoracic pleura are unknown because the holotype is enrolled. However, the tight arrangement of the outer parts of pleurae when enrolled, similar to that in pterygometopids, suggests that an articulating facet may be developed. Moreover, the manner in which the posterior margin of a thoracic segment overlies the pleural furrow of the following segment strongly suggests that, if an articulating facet is developed, the pleural furrow continues on the facet, that is to say, is of epifacetal type. The features of the thorax, the lack of an eye ridge, and the presence of a median pygidial spine, distinguish *Diaphanometopus* clearly from the pilekiids. Still, it is probable that the genus is an offshoot of early pilekiids. It is clearly younger (Volkhov or Kunda Stage, i.e. *D. hirundo* or *D. bifidus* zone) than any known pilekiid.

If *Diaphanometopus* has the construction of the thoracic pleurae like that of *Gyrometopus,* these two genera may be related. Further similarities include the position of the eyes (not unlike that of the pilekiids), shape of the cephalic border, and the presence of pleural furrows on the pygidium. If these two genera are related, *Gyrometopus* may also have had its roots somewhere within pilekiid-like ancestors from which it may have developed via forms not too unlike *Diaphanometopus.* In this connection it is interesting to note that *Gyrometopus* still has a trace of an eye ridge. Differences between the two genera in ventral cephalic sutures and pygidium are, however, pronounced, and suggest distinction at least at subfamily level.

If in *Gyrometopus* the ventral cephalic sutures were unknown, the genus could easily be classified with the suborder Phacopina. The general features of the cephalon and the course of lateral glabellar furrows are not unlike those of certain dalmanitaceans, such as *Ormathops, Baniaspis,* or *Prodalmanitina.* The number of thoracic segments agrees with that of the suborder Phacopina, and the thoracic pleurae have the same morphology as that of the early members of the Phacopina. The pygidium has a general appearance not unlike that of many members of the suborder. The structure of the eyes may not be schizochroal in *Gyrometopus,* but the general appearance is not much different from that type. However, according to current criteria, the presence of a functional rostral shield would put *Gyrometopus* in a suborder other than the Phacopina.

The suborder Phacopina has undoubtedly been derived from ancestors which possessed a functional rostral shield and biconvex holochroal ocelli. *Gyrometopus* fulfills the requirements of such an immediate ancestor to a high degree. It itself has certainly not been on the direct line of ancestry towards the Phacopina (among others, it is only slightly older than the earliest known true members of Phacopina – *Pterygometopus* from the *D. extensus* zone of Montagne Noir and Morocco), but it may belong to the same group of subfamily or family category which includes the ancestors of the Phacopina. No better alternative for possible immediate ancestors for Phacopina is known. Bergström's (1973) suggestion that Phacopacea (incl. Dalmanitacea) may have been derived from the Middle Cambrian edelsteinaspidids is interesting but not convincing. It is mainly based on a rough similarity in the morphology of the pygidium. Otherwise the organization of edelsteinaspids is still far removed from that of Phacopina. In edelsteinaspidids no articulating facets seem to be developed and the visual surface is probably surrounded by sutures. The ventral cephalic sutures of edelsteinaspidids are unknown. Suvorova (1964) suggested that this family belongs to the order Corynexochida the members of which normally have a fused hypostomal suture. If the ventral cephalic sutures in edelsteinaspidids turn out to be of this type, then the derivation of the suborder Phacopina from this family is scarcely probable.

If the ancestors of Phacopina resemble *Gyrometopus* and this genus is related to *Diaphanometopus,* then the ancestors of Phacopina may ultimately be traced back to pilekiid-like forms. In this case the question arises whether or not the suborder is of too high taxonomic level for separation of Cheiruracea and Phacopacea (incl. Dalmanitacea).

The classification of *Gyrometopus* is at present uncertain on account of unsatisfactory knowledge of the morphology of *Diaphanometopus.* If the latter genus has the same morphology of the thoracic pleurae as *Gyrometopus,* then the appropriate classification would be to include *Gyrometopus* as the subfamily Gyrometopinae (with the characters of the genus) in the family

Diaphanometopidae of the superfamily Cheiruracea. This is considered at present to be the most likely alternative. The family can be characterized as cheiruriaceans with small eyes placed far forwards, only traces of eye ridges (*Gyrometopus*), rostral plate either wide and probably of ptychopariid type (*Diaphanometopus*), or triangular and associated with a short median suture (*Gyrometopus*), 11 to 12 thoracic segments bearing well-developed pleural articulating facets, well-defined thoracic pleural furrows of epifacetal type, pygidial rhachis with four to five segments and a terminal piece, anterior pygidial pleurae with pleural furrows, and pygidial margin either entire (*Gyrometopus*) or extended into spines (*Diaphanometopus*). The family would differ from the other cheiruriaceans by this combination of characters, but first of all by the construction of thoracic pleurae. The encrinurids too have well-developed pleural articulating facets and an epifacial type of pleural furrows but differ in many important respects, not at least as regards the morphology of the pygidium.

EVOLUTIONARY PROCESSES IN THE EXOSKELETON PERTAINING TO THE ORIGIN OF THE SUBORDER PHACOPINA

The suborder Phacopina is a large group, comprising some 85 described genera, with the earliest known representatives in the lower Arenigian beds and latest species in the uppermost Devonian. During the whole life-span, the group is characterized by a well-defined set of constant exoskeletal characters.

The suborder is defined to include proparian trilobites with fused free cheeks, constantly 11 segments in the thorax, and schizochroal eyes (Struve, in Harrington *et al.*, 1959). It is interesting to note that two of these characters, possibly all three, are associated with a morphological discontinuity during evolution. A morphological discontinuity implies a change in the morphology from one condition to the other in one step because intermediate stages are not possible functionally. The free cheeks can be either fused and form one unit at moulting or separated by suture or sutures. The number of thoracic segments can only be a whole number.

The functional importance of these two characters has not been particularly great. The reason why they form constant characters for a large group probably is that, in addition to their functional role, they were controlled by pleiotropic or other correlative factors in the organization of the organism.

The development of ventral cephalic sutures tends to be constant within a group of related trilobites of family or superfamily category. The primitive condition obviously was the presence of a functional rostral plate (the ptychopariid type, Rasetti, 1952) from which the other common types of ventral cephalic sutures were derived. The process involved was either reduction of the rostral plate until free cheeks were separated by a median suture (the asaphid type), ultimately followed along some lineages by fusion of free cheeks (the levisellid type), or fusion of the rostral plate to free cheeks without the intervening stage of a median suture (resulting again in the levisellid type). In some groups fusion of the rostral plate and the labral plate (used here for "hypostome") also took place. The number of possible arrangements is limited and the same process has demonstrably been repeated in several unrelated or remotedly related groups. However, after having bridged the morphological discontinuity from one type to the other, the arrangement of the ventral cephalic sutures tended to become stable.

There are some examples of change of the type of ventral cephalic sutures within an otherwise homogenous group. Cyclopygids include forms with a median suture as well as those with fused free cheeks. Whittington (1954) reported that *Brachyaspis rectifrons,* the type species of *Brachyaspis*, has fused free cheeks – hence it is not an asaphid but a nileid. Among closely similar species, "*Asaphus" laevigatus* Angelin (from the red Jonstorp Formation of Västergötland, Sweden) lacks a median suture and isolated free cheeks occur fused (personal observations), whereas in *"Isotelus" robustus* (Pirgu Stage, Estonia) Schmidt (1901) reported the presence of a median suture. Since other characters of *Brachyaspis laevigatus* (including those of the labral plate) agree with the asaphids, this group of asaphid species obviously includes forms with a median suture as well as those with fused free cheeks. A specimen (Riksmuseum Ar. 47937) from Cincinnati, Ohio, identified as *Isotelus gigas* (probably from the Eden Shale) lacks any trace of a median suture, suggesting that *Isotelus* too may include species with fused free cheeks. Bruton (1968) described the presence of a functional rostral plate in early species of the illaenid genus *Panderia* and fused free cheeks in the late species of the genus. In this case the levisellid type of ventral cephalic sutures was derived by fusing the rostral plate with the free cheeks. Other examples of variation in the type of ventral cephalic sutures are known, but in some instances the homogeneity of the group may be uncertain.

In complete late protaspides of all groups of trilobites in which this ontogenetic stage is known, the ventral cephalic sutures are basically the same as in holaspides. In the protaspides of the phacopids, for instance, the free cheeks are fused (Whittington, 1956) (the structure in meraspides of *Phacops,* termed "rostral shield" by Alberti, 1972, represents fused free cheeks or "librigenal plate" of Henningsmoen, 1959). In early protaspides of the asaphids and remopleuridids (Evitt, 1961) the ventral cephalic sutures differ from those of late protaspides and subsequent ontogenetic stages (free cheeks and labral plate are fused). The significance of this difference is not clear, not least because well-preserved specimens of this ontogenetic stage are known in very few trilobites so far. The condition in the early protaspides may reflect a "recapitulation" of a primitive condition in early ancestors or it may have been a larval adaptation. At which stage of the ontogenetic development a sudden change in the ventral cephalic sutures was introduced, when evolution proceeded, is an important question which at present is difficult to answer. Ontogenetic studies of *Isotelus gigas* (of which suitable material might be available) are of great interest in this respect.

In many large families of Cambrian polymerous trilobites the number of thoracic segments varies within wide limits (Redlichiidae 11 to 17, Paradoxididae 13 to 22, Oryctocephalidae 5 to 18, Ptychopariidae 12 to 17, Conocoryphidae 7 to 25, Solenopleuridae 11 to 17, Olenidae 9 to 19 segments etc.). Since the Upper Cambrian, the number of thoracic segments becomes narrowly restricted in several large groups of trilobites (Cyclopygidae 5 to 6, Illaenidae, Proetidae and Odontopleuridae 8 to 10, Calymenidae 12 to 13 segments etc.) or fixed (Scutellidae 10, Asaphidae 8, Trinucleidae 6 etc.). The tendency towards restriction in the number of thoracic segments within a group as evolution proceeds conforms to Rosa's (1899) "rule" of progressive reduction of variability and similar "rules" by several other authors (for a critical review, see Remane, 1956:199-204). The "rule" can be described as a generalization subject to exceptions and expressed as "reduction of adaptability with increase in specialization" (Simpson, 1944). The process is probably associated with increase in morphogenetic correlative ties within the general framework of the developmental system of the organisms when specialization increases.

In the suborder Phacopina the number of thoracic segments is fixed to 11. Lespérance & Bourque (1971) recorded 12 thoracic segments in two species, but later corrected the number to 11 (Lespérance & Bourque, 1973). However, there is a notable exception. Maximova (1957) reported 10 segments in a species of *Isalaux,* known only from a single specimen. Another species of *Isalaux* has 11 segments (Frederickson & Pollack, 1952). Ten segments were reported also in the single complete specimen of a species of *Isalaux* (*Isalauxina*) (Maximova, 1962). Presumably in these cases the evolution within Phacopina was able to break through the established morphogenetic pattern of 11 segments.

Change in the number of thoracic segments is a process affecting the transition between the meraspid and holaspid stages in the composition of thorax and pygidium. Increase in the number of thoracic segments implies that during the moulting from the latest meraspid to the earliest holaspid a further segment is released to the thorax along the zone of growth. The increase may be caused either by addition of one segment to the total set of segments in thorax and pygidium, or by transfer of one pygidial segment to the thorax. Decrease in the number of thoracic segments is due either to retainment of a previous thoracic segment in the pygidium or to loss of a segment. Unimportant as such change may seem to be, the constancy in the number of thoracic segments in several major groups of trilobites indicates that the change was often difficult within the general framework of the particular developmental and functional system of the organism.

How the change from holochroal to schizochroal eyes took place cannot yet be reconstructed in detail. The principal difference between these two types of eyes is that the holochroal eyes have a thin pellucid cornea which extends continuously over the whole visual surface, whereas in schizochroal eyes each lens has its own corneal covering. Undoubted schizochroal eyes have at present been described only from the suborder Phacopina. Whittington & Evitt (1953) reported schizochroal eyes also from some cheirurids but their material is silicified and does not allow the examination of critical details. The change from holochroal to schizochroal eyes involves splitting up a continuous corneal covering and this seems to include a moment of morphological descontinuity. However, details of this process are not yet clear.

Thus the origin of some of the most distinctive characters of the suborder Phacopina could not have taken place continuously by a gradual or microdiscontinuous process, but has proceeded over at least two separate morphological discontinuities where functionally no intermediate stages are possible. A morphological discontinuity can only be bridged by a succession of consecutive populations in which the morphologies on either side of the discontinuity coexisted as genetic polymorphs (Jaanusson, 1973). One of the discontinuities had to be bridged by a succession of populations which included a morph with either a functional rostral shield or a median suture as well as a morph in which free cheeks were fused. In other words, in one of the morphs the free cheeks separated during the moulting, whereas in the other morph they were shed in one piece. Ultimately the morph with fused free cheeks became fixed in the population. The other of the discontinuities was surmounted by a succession of populations in which a morph with 11 segments coexisted with a morph with a different number of thoracic segments (either 10 or 12). Such populations in which major morphological discontinuities are bridged have been termed "dithyrial populations" (Jaanusson, 1973).

If *Gyrometopus* belonged to a group which was in the evolutionary lineage leading to normal Phacopina, it would have already bridged one of the discontinuities – the fixation of the number of thoracic segments to 11. Bridging of this discontinuity may have taken place still earlier, in the possible pilekiid ancestors of diaphanometopids where 11 is the common number of thoracic segments. The other discontinuity would not yet be surmounted in gyrometopus-like forms, because *Gyrometopus* still has a functional rostral shield. Experience from a study of some other groups of invertebrates suggests that, during the evolution of a group, bridging of several major morphological discontinuities seldom, if ever, takes place simultaneously within one succession of populations (Jaanusson, 1973). Ordinarily one discontinuity after another is bridged through separate "dithyrial populations", which can even belong to different taxa of various categories. If *Gyrometopus* is related to the immediate ancestors of the suborder Phacopina, it may constitute an example in this respect.

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Species diversity among agnostoid trilobites

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Most species of the suborder Agnostina are non-intergrading and best fit an allopatric model of speciation. Continued allopatry of some species is indicated by the existence of temporally correlative biofacies. Abrupt introduction of morphologically distinct agnostoid species into many areas suggests that migration often resulted in sympatry of other species. To avoid competitive elimination, sympatric agnostoids probably followed a variety of adaptive pathways. Evidence of two strategies, depth segregation and character displacement with respect to size, is presented. Size displacement apparently increased from the late Early Cambrian until the middle Middle Cambrian, at which time size ratios stabilized at about 1.3. Attainment of apparent optimum size displacement coincides with the beginning of a period of marked increase in agnostoid diversity, which reached a maximum during the late Middle and early Late Cambrian.

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Diversity among agnostoid trilobites reached a maximum during the late Middle and early Late Cambrian when more than 200 species made their appearance. Multiple closely related species commonly are present in a single stratum, and paleoecologic evidence usually indicates that a given agnostoid assemblage lived in the area where the specimens accumulated and were buried. The purposes of this paper are to examine the general nature of speciation among agnostoids, to consider possible adaptive pathways, and to investigate possible techniques by which closely related agnostoid species may have coexisted without competitive elimination.

New or revised descriptions of some of the taxa referred to in this paper are being prepared for separate publication. Several of the agnostoid collections are from the Wheeler Formation of western Utah, and new information requires revision of the concept and biostratigraphy of that formation. Instead of being 94 m (307 feet) thick in the Drum Mountains as previously reported (Robison, 1964:1001), the Wheeler Formation in that area actually is 302 m (990 feet) thick. Depending on the locality in western Utah, the boundary between the *Bathyuriscus-Elrathina* and *Bolaspidella* Assemblage Zones is located from 27 to 61 m (90 to 200 feet) above the base of the Wheeler Formation.

Because of a major hiatus between the Lower and Middle Cambrian in most of northwestern Europe, in this paper the traditional North American rather than the Scandinavian concept of the Middle Cambrian is used. For purposes of discussion, an informal tripartite subdivision of the Middle Cambrian also is used. The lower Middle Cambrian commences with a mostly undescribed "pre-*Albertella*" fauna, and it succeeds olenellid-bearing strata. The middle Middle Cambrian commences with the *Bathyuriscus-Elrathina* Zone, and the upper Middle Cambrian commences with the *Bolaspidella* zone. Occurrences of agnostoids show the boundary between the *Bathyuriscus-Elrathina* and *Bolaspidella* Zones of North America correlates closely with the boundary between the *Ptychagnostus gibbus* and *Ptychagnostus atavus* Zones as defined in Sweden (Westergård, 1946).

AGNOSTOID CHARACTERISTICS

The Agnostina of Moore (1959:172-186) includes relatively small trilobites with a restricted size range. The maximum observed holaspid or adult length is about 20 mm, but length in most species does not exceed 10 mm. The cephalon and pygidium are similar in outline and nearly equal in size, eyes are absent from the dorsal exoskeleton, the hypostoma and cephalothoracic hinge line are unique among trilobites, and the thorax invariably has only two segments in the

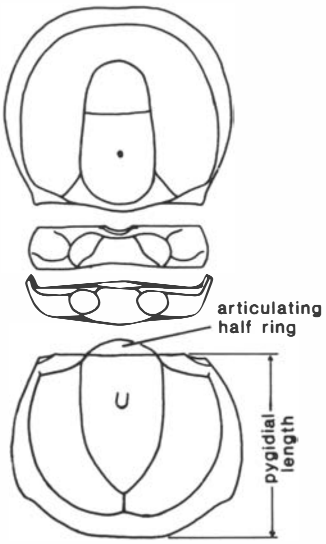

Fig. 1. Dorsal view of the disarticulated cephalon, thoracic segments, and pygidium of the agnostoid trilobite *Peronopsis interstricta* (White). As used in this study, the measure of pygidial length does not include the articulating half ring.

holaspid period (see Fig. 1). Enrollment was an important agnostoid function, which is indicated by a number of specialized exoskeletal structures (Robison, 1972b), and during ontogeny a constant size relationship between the cephalon and pygidium apparently was maintained in response to the method of enrollment.

AGNOSTOID SPECIATION AND COMPETITION

From an extensive study of Middle Cambrian agnostoids in western North America I have found a conspicuous lack of intergradation in species-specific characters, and I also have found little or no change in those characters throughout the observed stratigraphic ranges of most species. This general morphologic stability suggests that substitution or addition of agnostoid species mostly resulted from migration rather than gradual evolution *in situ.* Such a pattern is consistent with a model of allopatric speciation (Eldredge, 1971; Eldredge & Gould, 1972), which is predicated on the concept that new species arise by relatively rapid development of species-specific characters in peripheral isolates, and that stability of species-specific characters is the norm, except when two species become sympatric for the first time.

When closely related species become sympatric, morphologic differences tend to be accentuated in response to pressures of competition (Brown & Wilson, 1956). Extensive study of competition theory has led to formulation of the Principle of Competitive Exclusion, which states that in equilibrium communities no two species occupy the same niche (Hutchinson, 1965:27). Hundreds of examples of neontological exclusion have been cited, and Mayr (1963:69-88) has reviewed many of them. A few apparent exceptions to the principle have been reported (*e.g.,* Ayala, 1969, 1972), but the great frequency of demonstrable exclusion establishes it as a major factor in evolutionary divergence. Similar patterns of exclusion are shown by Cambrian agnostoid trilobites, and they indicate the operation of competitive exclusion since early in the history of metazoans.

Modern animals have been found to avoid competition by both spatial and nonspatial segregation. Spatial strategies tend to be more conspicuous and mostly involve geographic separation, but among marine faunas they also may involve depth stratification. Non-spatial strategies tend to be more subtle and commonly involve isolating mechanisms such as time, diet, or foraging techniques (*e.g.,* Diamond, 1973:767). Those strategies amenable to analysis in the fossil record are considered here.

SPATIAL SEGREGATION OF AGNOSTOIDS

GEOGRAPHIC.– From several lines of evidence I (Robison, 1972b) have concluded that most agnostoid trilobites probably were pelagic inhabitants of open oceans. Such an inferred mode of life is supported by the wide geographic distribution of many genera and species. Nevertheless, various types of geographic segregation of some agnostoids can be observed.

Segregation of certain genera occurs on different geographic scales. On an intercontinental scale the condylopygids and phalacromids are common in western Europe and parts of maritime Canada (components of a single early Paleozoic tectonic plate), but are unknown from most of North America. In an opposite pattern, *Baltagnostus* and *Spinagnostus* (=*Kormagnostus*) are common in most of North America, but are absent in western Europe and related maritime Canada. Within North America, *Baltagnostus* and *Spinagnostus* normally are found in biofacies shoreward from those with cosmopolitan agnostoids such as *Ptychagnostus* and *Hypagnostus*. Similar biofacies patterns have been described for Middle Cambrian agnostoid communities in Tasmania (Jago, 1972). Among modern marine faunas comparable distribution patterns can be found in most pelagic groups.

Some species are futher segregated within regional biofacies. For example, 10 agnostoid species have been found in the *Ptychagnostus gibbus* Zone in Nevada and Utah, and most have similar geographic ranges within the region. However, an observed maximum of six, and usually no more than four species are present in any single stratum, and combinations of species are variable from one stratum to another. The same type of segregation occurs in collections from the same zone in Sweden and Norway.

Partial geographic segregation is displayed by *Ptychagnostus gibbus* and *P. intermedius* in Nevada and Utah. Both species are similar in maximum size and commonly are found together in the same stratum, but in any given stratum almost always one species is abundant and the other is rare (*e.g.,* Table 1-D). This suggests the possibility that the respective competitive superiority of the two species may have shifted with environmental conditions or with population densities (*cf.* Mayr, 1970:49).

The segregation patterns cited for agnostoids are similar to those described for modern animals, and it appears likely that similar adaptive pathways were followed during Cambrian as in modern times. Direct competition for resources probably was more important as a factor in local exclusion, whereas opportunistic adaptation to different resources may have been more significant in segregation on regional and larger scales.

VERTICAL.— Although inconclusive, some evidence suggests the possibility that certain agnostoid species may have achieved habitat segregation by living in different depths of water. In Nevada, Utah, and Sweden; faunas typical of the lower part of the *Ptychagnostus gibbus* Zone are found in a succession of transgressive marine strata. In these strata *Peronopsis fallax* consistently makes its first appearance lower in the section than does *Ptychagnostus gibbus*. However, once *Ptychagnostus gibbus* appears, the two species commonly are associated in successively higher strata. In a transgressive sequence, such an occurrence pattern would result if *Peronopsis fallax* lived in shallow depths and *Ptychagnostus gibbus* lived at greater depths. Also, the same pattern would develop if *Peronopsis fallax* was adapted for life in additional and more shoreward habitats than those favored by *Ptychagnostus gibbus*. The fact that the same pattern is found in different rock types and at widely separated localities seems to favor the depth control alternative. Further comment on this pattern is given in the following section.

NON-SPATIAL SEGREGATION OF AGNOSTOIDS

The phenomenon known as character displacement (Brown & Wilson, 1956) develops when the ranges of two or more closely related species overlap geographically. Differences between the species are accentuated in the zone of sympatry, but remain less in the parts of their ranges outside that zone. One of the most common characters displaced is size. From studies of such diverse groups as mammals, birds, and aquatic insects, Hutchinson (1959:152-154, 1965:55-60) has shown that moderate differences in size are sufficient to cause obligate feeding on different sizes of food. Where closely related species are sympatric he found the size ratios of larger to smaller species to range from 1.1 to 1.4 with the mean ratio being 1.28. Several other studies have produced similar observations. For example, in a recent study of New Guinea birds Diamond (1973:767) used body weight as a measure of displacement, and found that among congeners sorted by size

> "the ratio between the weights of the larger bird and the smaller bird is on the average 1.90; is never less than 1.33 and never more than 2.73. Species with similar habits and with a weight ratio less than 1.33 are too similar to coexist locally (that is, to share territories) and must segregate spatially."

The cube root of 1.90 equals 1.25, which compares closely with the linear average size ratio of 1.28 calculated by Hutchinson.

Although character displacement with respect to size has been described in many modern faunas, it has received little attention in the study of fossils. A few authors have mentioned the possibility of character displacement in fossils, but usually specific examples have not been cited. Eldredge (1972:93-102) has discussed an apparent case of character displacement in *Phacops rana* and *P. iowensis,* and he states in a recent letter (September, 1973) that the maximum cephalic length ratio for these two species is 1.37. Except for that example, and those mentioned in a preliminary abstract (Robison, 1973) concerning this study, I know of no other specific discussions of size displacement in fossils. From the analysis of several agnostoid trilobite assemblages, I have found that where two or more species occur together they commonly show maximum size ratios remarkably close to the average of 1.28 reported by Hutchinson.

PROCEDURES. — Because size displacement has been demonstrated to correlate with differences in size of food, it is desirable to measure the the trophic apparatus. In the calcified exoskeleton of agnostoids that apparatus consists only of the hypostoma, which because of its fragile nature is seldom preserved. In fact, only recently have a few such sclerites been discovered and described (Robison, 1972a). Thus, rare and poor preservation make the agnostoid hypostoma an unsuitable subject for biometric analysis.

A second option is cephalic length, which is a measure used by Hutchinson (1959:153) in his study of size displacement in mammals. Again, a problem exists with agnostoids because the exoskeleton commonly is found disarticulated, and in that condition it is difficult to determine the species identity of some cephala. On the other hand, disarticulated pygidia usually can be identified with ease. Fortunately, because of the special method of enrollment, a constant length ratio is maintained between the cephalon and pygidium during ontogeny. For these reasons, pygidial length (Fig. 1) is the measure selected for size analysis of agnostoid trilobites. The articulating half ring is not included in the measure of pygidial length because it is covered by the posterior thoracic segment of articulated specimens, and not uncommonly is broken on disarticulated specimens.

AGNOSTOID SIZE DISPLACEMENT. — From 19 collections analyzed, data from seven are presented in Table 1 to illustrate observed maximum pygidial length (hereafter abbreviated *mpl)* ratios for sympatric agnostoid trilobite species. The collections were selected from different stratigraphic intervals ranging in age from late Early to late Middle Cambrian. An attempt was made to select representative assemblages, as well as to illustrate as many kinds of size patterns as possible. Also, in order to facilitate recognition of possible phyletic trends, the collections (A to G) are ordered in relative stratigraphic position.

Collection A from the upper *Olenellus* Zone of late Early Cambrian age contains the oldest recorded assemblage with multiple species of agnostoid trilobites. The numbers of specimens are from Rasetti & Theokritoff (1967), and I have obtained length measurements from published illustrations. According to Theokritoff (1972, written communication), all specimens of *Peronopsis evansi* and *Eoagnostus acrorhachis* came from a single limestone boulder. The sample of about 13 pygidia is too small to be statistically reliable. However, the observed mpl ratio of 1.09 is low, and this may reflect insignificant or only minor displacement of size in the oldest known assemblage of agnostoid trilobites.

Collection B from the lower *Glossopleura* Zone of early Middle Cambrian age contains 26 silicified pygidia of *Peronopsis brighamensis* and *P. bonnerensis,* which were extracted with acid from a single piece of limestone. The mpl ratio is 1.15, but again is based on a small sample. Another collection (UU-100) from the same formation and from a similar stratigraphic interval at Wellsville Mountain in northern Utah has yielded 12 pygidia of the same two species. They have an mpl ratio of 1.19, which is close to that calculated for the specimens from Idaho, and therefore suggests that the ratios may be meaningful.

Ratios for the three species in collection C have been calculated from maximum pygidial lengths recorded by Westergård (1936), which to my knowledge is the only published study to provide such measurements for multiple agnostoid species from a limited area and from a thin stratigraphic interval. It is not clear from Westergård's account whether or not the specimens came from a single bed, but they apparently did come from a stratigraphic interval probably no more than five meters thick. Although the statistical validity of the sample is unknown, the ratios of 1.35 and 1.39 suggest that size displacement had evolved to a degree comparable to that observed in modern communities with closely related sympatric species.

Collection D from the upper *Bathyuriscus-Elrathina* Zone of middle Middle Cambrian age

Table 1. Lists of agnostoid trilobite species from selected collections. Data includes total number of specimens of each species in the collection (N), percentage of each species in the collection (%), maximum pygidial length (mpl) measured in mm, and ratios of maximum pygidial length (ratios). University of Utah collections are designated by numbers preceded by the letters UU.

G. Upper *Bolaspidella* Zone (upper *Lejopyge calva* Subzone) from top bed of member A, Emigrant Springs Limestone at Patterson Pass, Schell Creek Range, Nevada (UU-154).

	N	%	mpl	ratios	
Utagnostus trispinulus Robison	2	<1	2.0		
				1.25	
Ptychagnostus n. sp.	2	<1	2.5		1.30
				1.04	
Baltagnostus eurypyx Robison	50±	10±	2.6		
				1.35	
Hypagnostus n. sp.	50±	10±	3.5		1.54
				1.14	
Lejopyge calva Robison	400±	80±	4.0		

F. Lower *Bolaspidella* Zone (middle *Bathyuriscus fimbriatus* Subzone) from 50 feet below top of Wheeler Shale, near Swasey Spring, House Range, Utah (UU-114).

	N	%	mpl	ratios	
Ptychagnostus atavus (Tullberg)	481	68	2.7		
				1.04	
Peronopsis fallax ferox (Tullberg)	15	2	2.8		
				1.07	1.26
Hypagnostus parvifrons (Linnarsson)	9	1	3.0		
				1.13	
Baltagnostus eurypyx Robison	74	11	3.4		
				1.29	
Peronopsis interstricta (White)	126	18	4.4		

E. Lower *Bolaspidella* Zone (lower *Bathyuriscus fimbriatus* Subzone) from 200 feet above base of Wheeler Shale, Drum Mountains, Utah (UU-520).

	N	%	mpl	ratios	
Peronopsis? n. sp.	75	48	2.5		
				1.08	
Ptychagnostus gibbus n. subsp.	9	6	2.7		
				1.04	1.32
Peronopsis fallax fallax (Linnarsson)	9	6	2.8		
				1.18	
Peronopsis segmenta Robison	34	22	3.3		
				1.30	
Peronopsis interstricta (White)	29	18	4.3		

D. Upper *Bathyuriscus-Elrathina* Zone from 154 feet above base of Wheeler Shale, Drum Mountains, Utah (UU-250).

	N	%	mpl	ratios
Ptychagnostus intermedius (Tullberg)	5	2	2.3	
				1.13
Ptychagnostus gibbus n. subsp.	43	17	2.6	
				1.00
Peronopsis fallax fallax (Linnarsson)	44	18	2.6	
				1.27
Peronopsis interstricta (White)	157	63	3.3	

C. Upper *Paradoxides oelandicus* Stage (*P. pinus* Zone), Öland, Sweden (Westergård, 1936).

	N	%	mpl	ratios
Condylopyge carinata Westergård	?	?	3.3	1.39
Peronopsis fallax fallax (Linnarsson)	?	?	4.6	1.35
Ptychagnostus praecurrens (Westergård)	?	?	6.2	

B. Lower *Glossopleura* Zone from 50 feet above base of Spence Shale, Two Mile Canyon near Malad, Idaho (UU-142).

	N	%	mpl	ratio
Peronopsis bonnerensis (Resser)	13	45	2.6	1.15
Peronopsis brighamensis (Resser)	16	55	3.0	

A. Upper *Olenellus* Zone from Taconic Mountains, New York (Theokritoff locality 58–11; Rasetti & Theokritoff, 1967).

	N	%	mpl	ratio
Peronopsis evansi Rasetti & Theokrit.	3	23±	2.3	1.09
Eoagnostus acrorhachis Rasetti & Theo.	<10	77±	2.5	

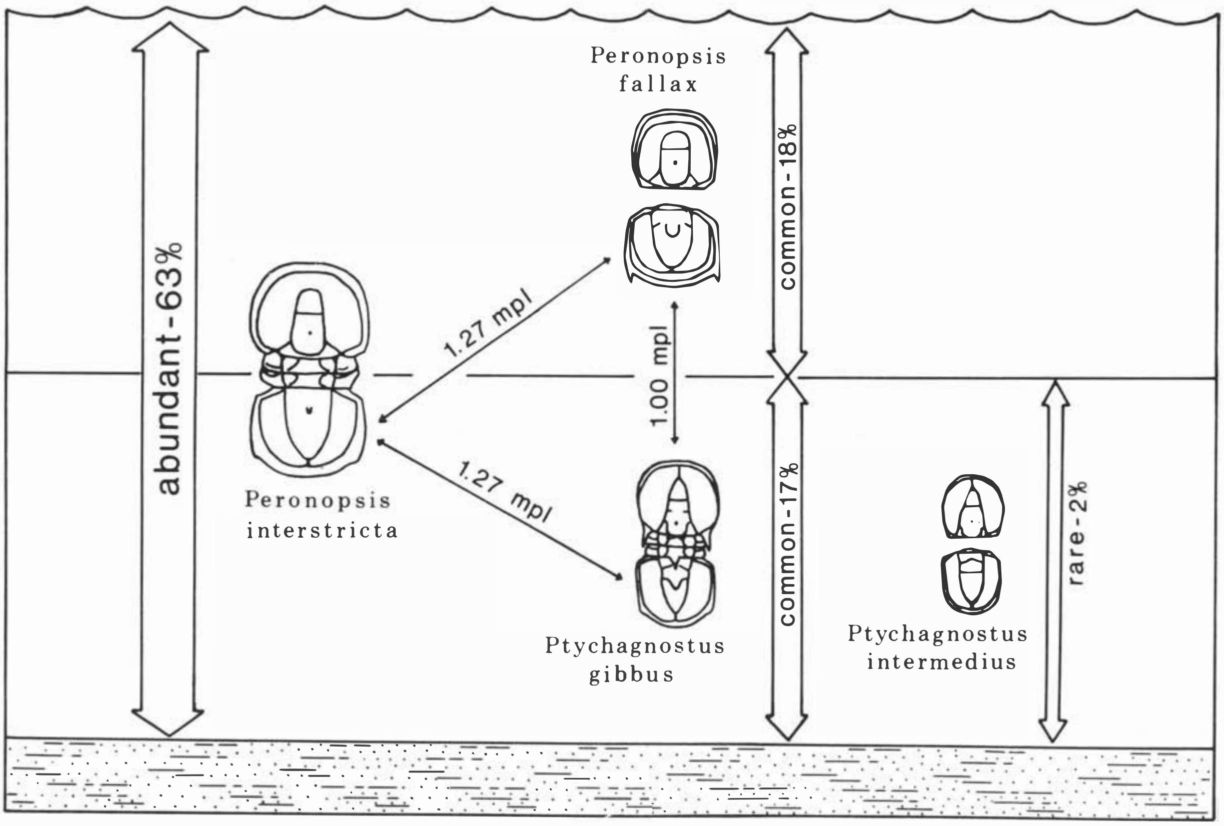

Fig. 2. Suggested model of inferred depth stratification, relative abundance, and maximum lengths (mpl) of agnostoid trilobites in collection UU-250. *Peronopsis interstricta* is inferred to have lived throughout the water column, whereas *Peronopsis fallax* is inferred to have lived in shallow water, and *Ptychagnostus gibbus* and *Ptychagnostus intermedius* are inferred to have lived in deeper water. *P. intermedius* may have been an immigrant from a peripheral biotope, and not a normal member of this particular agnostoid community.

is only slightly younger than collection C. It includes 249 silicified pygidia, which were extracted with acid from a single piece of limestone, and the sample is large enough to be statistically reliable. The collection illustrates a different pattern of sizes by having two common species, *Peronopsis fallax* and *Ptychagnostus gibbus,* with the same maximum pygidial lengths. Thus, each of those species has an identical mpl ratio of 1.27 with *Peronopsis interstricta,* which is the only abundant species in the collection. The same three species also are similarly abundant and have practically identical mpl ratios in collections UU-251 and 253 from beds one and six feet higher at the same locality. This stratigraphic repetition indicates an equilibrium in size displacement and stability in community structure rather than initial sympatric congregation without size displacement.

It was suggested in the preceding section of this paper that *Peronopsis fallax* probably lived in a shallow depth zone and *Ptychagnostus gibbus* probably lived in a deeper depth zone. A suggested model to explain inferred relationships for collection D is illustrated by Figure 2. In this model *Peronopsis fallax* and *Ptychagnostus gibbus* utilized food resources of the same size, but avoided direct competition by adapting to different depth zones. *Peronopsis interstricta* was not influenced by depth restrictions and coexisted with both *Peronopsis fallax* and *Ptychagnostus gibbus*, but avoided competition by utilizing food resources of different size as indicated by the numerical displacement of maximum exoskeletal size.

Ptychagnostus intermedius is a rare component of collection D, and its abundance relative to that of *P. gibbus* is discussed in a previous section concerning geographic segregation.

Collections E and F exhibit species diversity typical of that observed in several late Middle Cambrian agnostoid trilobite assemblages, and equilibrium in size displacement appears to have been achieved among those species that comprise more than about 10 percent of the specimens in each collection. Collection E contains 156 silicified pygidia that were extracted with acid from a single piece of limestone. Collection F contains 705 articulated specimens that came from weathered shale. Three species each comprise more than 10 percent of the population in both collections, and when arranged according to increasing maximum size, the mpl ratios all fall within a range from 1.26 to 1.32. The average for those ratios is practically identical to the average of 1.28 recorded by Hutchinson (1959:152) for modern communities with closely related sympatric species that take food of different sizes. Therefore, I suggest that the regular occurrence of similar mpl ratios probably indicates that the common agnostoid species in collections E and F also avoided competition by taking food of different sizes. Species comprising less than 10 percent of the agnostoid specimens in collections E and F possibly filled more restricted niches, or may represent immigrants from more favorable peripheral biotopes.

Collection G is interpreted here to be an example of mixed agnostoid communities in which optimum size displacement was not established between some species. The collection is late Middle Cambrian in age and came from the top bed of member A of the Emigrant Springs Limestone at Patterson Pass, Nevada. The uppermost beds of member A consist of biosparite, whereas the lowest beds of member B consist of laminated calcareous mudstone with biomicrite lenses. The lithologic change from member A to member B represents an abrupt decrease in energy regime, probably as a result of increased water depth. It further represents an apparent change from outer shelf-edge to basinal marine environments. In the lower 10 feet of member B the agnostoid fauna also changes from the composition indicated for collection G to a compostion of 95 to 100 percent *Lejopyge calva.* Therefore, I suggest that collection G contains mixed elements of a shallow shelf-edge community and a normally more seaward and deeper basinal community. These probably correspond to Jago's (1972:98–120) Tasmanian agnostoid communities (1) and (2). *Baltagnostus eurypyx* and a new species of *Hypagnostus* appear to be the dominant species of the adjacent shelf-edge community. They show an mpl ratio of 1.35, which is near the apparent optimum in size displacement, and I suggest they avoided competition by that means. On the other hand, *L. calva* appears to be the only common species in the open ocean community at this particular locality. The mpl ratios between *L. calva* and associated common agnostoid species in collection G are 1.14 and 1.54, which are well outside the uniform range of 1.26 to 1.32 observed in collections E and F. In regards to this interpretation of biofacies, it is notable that *Baltagnostus* as an inferred shelf inhabitant is known only for North America and questionably from South America, whereas *Lejopyge* as an inferred inhabitant of open oceans is cosmopolitan.

In conclusion, size displacement among agnostoid trilobites usually is most evident between those species comprising more than approximately 10 percent of each assemblage, and in assemblages that are middle Middle Cambrian or younger in age. From the limited number of collections analyzed, size displacement appears to have been an important technique for the nonspatial segregation of some agnostoid trilobites, and thereby likely contributed to increased diversity. Beginning in the late Early Cambrian, size displacement appears to have been negligible, but increased until the middle Middle Cambrian, at which time ratios tended to stabilize near an apparent optimum of about 1.3. Concomitant with that attainment of apparent optimum size displacement is the beginning of a period of marked increase in diversity in numbers of species per single stratum, as well as increase in total numbers of species per unit time. Prior to the middle Middle Cambrian no more than two agnostoid species have been reported from any single stratum, whereas throughout the upper half of the Middle Cambrian it is not uncommon to find as many as six agnostoid species in a single stratum. Furthermore, a total of not more than a dozen agnostoid species have been described from the interval prior to the middle Middle Cambrian, whereas more than a hundred agnostoid species have been described from the latter half of the Middle Cambrian.

The limited data in Table 1 suggest possible fruitful subjects for further investigation. One such subject involves niche partitioning. Agnostoid trilobites probably arose by neoteny as indicated by the holaspid retention of juvenile characters such as small size, few thoracic segments, and an isopygous condition. In accord with that probability, figures in Table 1 show that the oldest known agnostoid species were small in relative maximum size. Subsequent niche partitioning usually was achieved by the addition of new species at the upper end of the size scale. In general, this pattern supports the thesis by Stanley (1973) that new taxa tend to arise at small relative body size and niches requiring larger body size tend to be filled subsequently by niche partioning so that vacant regions of a group's maximum potential adaptive zone are progressively invaded. Another subject for further investigation involves geographic size difference in the same species. Most cosmopolitan agnostoid species tend to have larger maximum sizes in Scandinavia than they do in western North America. This empirical knowledge is based on direct field investigation as well as study of numerous museum collections, and is exemplified by measurements given for *Peronopsis fallax fallax* in collections C, D, and E. Nevertheless, similar size displacement patterns are developed in both regions. Because marked differences in rock matrices probably reflect significantly different Cambrian environments in Scandinavia and western North America (cf., Robison, 1972b, p. 34–35), I suggest that geographic difference in maximum size for the same species most likely was caused by phenotypic rather than genotypic factors.

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Proetida – a new order of trilobites

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A new order of trilobites – the Proetida – is proposed to include the families Aulacopleuridae, Bathyuridae, Brachymetopidae, Celmidae, Dimeropygidae, Glaphuridae, Otarionidae and Proetidae, based on study of a wide range of material of these families. This is believed to be a more natural grouping of these families than that currently adopted. The supposed relationships of these trilobites are based on a comparison of morphological features and ontogenies; new discoveries of early species are consistent with this conclusion. The families are considered to have been derived from various species of the subfamily Hystricurinae, probably during the Tremadoc, from which evolution may have subsequently proceeded along relatively independent lines. Parallelism of morphological features in different groups of the Proetida indicate the repeated adoption of similar life habits.

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During the course of studying early Ordovician faunas from Spitsbergen and Ireland (R.A.F.) and Lower Palaeozoic Proetidae and Otarionidae (R.M.O.), we were led independently to re-examine critically the systematic position used in the *Treatise* (Part O) of the trilobite families Aulacopleuridae, Bathyuridae, Celmidae, Dimeropygidae, Glaphuridae, Otarionidae and Proetidae, and the subfamily Hystricurinae. We now believe that together these families constitute a major natural group of the Trilobita – the order Proetida. In this paper we summarise the evidence for such a reorganisation, which is based on examination of a wide variety of species of the group, and briefly consider some aspects of its evolution. Various interrelationships between some of the families named above have been postulated periodically over the last twenty years. Whittington & Evitt (1954: 35–36), for example, noted similarities between dimeropygids, the otarionid-proetid group and hystricurines, and these comments were reiterated by Whittington (1966: 707, 709). Information relevant to classification is derived from three sources:

(1) Consideration of comparative morphology

(2) Discovery of some new early representatives of particular families

(3) Knowledge of ontogenies

Our conclusions are based on as many lines of evidence as possible in a phylogenetic model, and are not consistent with a "single character" classification. The morphology of the Phillipsinellidae seems to us to place that family outside the Proetida as here defined, and we have not studied sufficient material to be able to evaluate the systematic position of the Lecanopygidae and Plethopeltidae. We can find no evidence to suggest close relationships between the Proetida, as defined here, and the illaenid-thysanopeltid group, which are included together in a high-level taxon in the *Treatise* and in the classification of Bergström (1973: 41).

PROPOSED RELATIONSHIPS OF PROETIDA

It is believed that early representatives of the families included in the Proetida were derived from a plexus of early to Middle Canadian (Tremadoc) Hystricurinae which were widespread across the North American craton, the USSR and China during this period. There are also indications that the geographical range of the subfamily may be greater than the literature indicates at the moment: for example, "Proetid gen. et sp. indet." from southern France (Dean 1961, Pl. 15: 1,7), *Tasmanaspis* from Tasmania (Kobayashi 1940, Pl. XI: 3,4) and *Protarchaegonus* from Bavaria (Sdzuy 1955, Pl. 7: 2–7) may possibly be hystricurines. Various hystricurines are considered to be close enough to early representatives of the families discussed below to be their most likely ancestors.

DIMEROPYGIDAE

Early species of the family Dimeropygidae referable to the genus *Ischyrotoma* Raymond are found in the Arenig of North America (Ross 1951, Pl. 35:18,23–28; Hintze 1953, Pl. 19: 1–10). Characteristic features of these early species are the convex, transversely narrow anterior border, and the slightly converging anterior branches of the facial sutures. In anterior view (Ross 1951, Pl. 35: 23) the cranidium shows a distinctive X-shaped junction between the downward and forward-curving axial furrows and the upward arched anterior border furrow. Large free cheeks lack genal spines, or they are much reduced, but on immature free cheeks (Ross 1953, Pl. 63: 24) they are still prominent. It is believed that *Ischyrotoma* was derived from a hystricurine merely by reduction of the genal spines. The most likely species to be near the origin of the genus are found in *Pseudohystricurus* Ross, a genus which occurs in beds underlying those with *Ischyrotoma* in Utah and may also occur in Kazakhstan (Lisogor 1961, Pl. 1: 15–17). Cranidia of this genus, and particularly *Pseudohystricurus* sp. of Ross (1951, Pl. 16: 26,27,31), show similar structure, with a closely comparable anterior profile. Unfortunately free cheeks and pygidia are not described for *Pseudohystricurus,* but probable hystricurine pygidia with steeply sloping posterior margins not unlike those of *Ischyrotoma* species are present among unassigned pygidia (Ross 1951, Pl. 19: 13) from the same beds as *Pseudohystricurus.* Ross (1953: 638) has also noted the similarity of paired tubercles on small *Ischyrotoma* to those on hystricurines at a similar stage of development. There can be little doubt that species ancestral to *Dimeropyge* are to be found in *Ischyrotoma* (Ross 1951: 123). Other Middle Ordovician dimeropygid genera which are relevant to the problem of the classification of the Glaphuridae are discussed below.

BATHYURIDAE

Early species of the family Bathyuridae in the Lower Ordovician of Utah and Nevada belong to the genera *Licnocephala* Ross, 1951 and *Peltabellia* Whittington & Ross, 1953, the appearance of the latter genus preceding that of the former. In contemporaneous deposits over the Siberian Platform the genus *Biolgina* Maksimova, 1955 is widespread, some species of which (e.g. Rozova 1968, Pl. 17: 4–8) are very similar to *Peltabellia* and probably closely related. *Peltabellia* thus probably represents a genus close to the ancestral bathyurid and *Peltabellia* sp. B of Hintze (1953: 175, Pl. 9: 8,11,12) from Canadian, zone G, is the earliest known representative of the family. Cranidia of the hystricurine *Psalikilopsis cuspicaudata* Ross (1953, Pl. 63: 3–5,8,9) are similar to *Peltabellia* sp. B and *P. peltabella* Ross, 1951 in size and positon of eyes, in having a convex, steeply downsloping preglabellar field, transversely arched anterior border and in having divergent, anteriorly inward-curving anterior branches of the facial suture. The pygidium of *P. cuspicaudata* differs from that of *Peltabellia* sp. B in having a steeply downturned posterior border which carries a short terminal spine; however it does resemble that of another early bathyurid, *Goniotelina brevus* Hintze (1953, Pl. 26: 8) in these features. Early bathyurids with long terminal spines on the pygidium (Hintze 1953, Pl. 26: 1–6,14; Ross 1951, Pl. 14: 16–22, 25) may be directly compared with hystricurines such as *Pseudohystricurus orbus* Ross (1953, Pl. 63: 10–11, 13–20, 23). This species has a nasute border on the cranidium, characteristic also of early *Goniotelina* species, while the free cheek is closely similar to that of *Goniotelina williamsi* Ross (1951, Pl. 14: 16–22,25) in having a long, gently curved genal spine which does not continue the line of curvature of the lateral border of the cheek, but is kinked abaxially. The border of the free cheek of *P. orbus* carries a sculpture of parallel raised lines which is typical of *Goniotelina* and *Acidiphorus* species, but unusual among hystricurines. The pygidium of *P. orbus* (Ross 1953, Pl. 63: 13,14; Hintze 1953, Pl. 20: 16) tapers posteriorly with the axis continued into a long spine and is closely similar to that of *Goniotelina williamsi* (Ross 1951, Pl. 14: 16–17). The principal difference between *P. orbus* and the early *Acidiphorus* species is in the greater curvature of the palpebral lobes of the latter which restricts the postocular fixed cheek to a narrow (exsag.) strip.

The second major morphological type of bathyurid with a flat, wide pygidium, broad anterior border to the cranidium and blade-like genal spines, typified by *Bathyurellus,* is already represented in early bathyurid faunas by species of *Licnocephala* (Ross 1951, Pl. 28: 12–14; 1953, Pl. 64: 1–29; Hintze 1953, Pl. 10: 1–5). It is conceivable that *Licnocephala* was derived from a *Peltabellia*-like ancestor; the pygidium of *P. peltabella* has a wide border onto which the pygidial pleural ribs do not continue, similar in this respect to *Licnocephala* species, and the free cheek of *P. peltabella* is transversely wide with a tendency towards flattening out of the postero-lateral border (Ross 1951, Pl. 17:7,13). The preglabellar field of *Peltabellia* is relatively wide (sag.), like that of *Licnocephala* and *Bathyurellus,* but unlike that of *Goniotelina* and *Acidiphorus.* It seems possible that the *Acidiphorus/Goniotelina* type of bathyurid may have had an origin in the Hystricurinae independent of that of the *Licnocephala/Bathyurellus* type, the former arising from a species close to *Pseudohystricurus orbus* Ross, the latter (via *Peltabellia)* possibly from *Psalikilopsis.* If this view is substantiated the separation of the *Goniotelina*-type bathyurids from *Licnocephala/Bathyurellus*-type bathyurids into two subfamilies (Bathyurinae and Bathyurellinae respectively) as proposed by Hupé (1953: 198) will be justified.

PROETIDAE

Owens (1970, 1973a, 1973b) has redescribed north European Ordovician and Silurian Proetidae, and has recognised two major groups within the family as conceived in the *Treatise.* These groups, centred on *Proetus* and on *Decoroproetus,* appear to be two natural phyletic units, and on present evidence (Owens 1973b: 79–85) appear to have quite independent origins. The *Proetus* group is here termed 'Proetidae A', and the *Decoroproetus* group 'Proetidae B'.

PROETIDAE A. – The earliest species belonging to this group is *Cyphoproetus facetus* Tripp, 1954 (Owens 1973b, Pl. 5: 10–12; Pl. 6: 1) from the Caradoc of the Girvan district. *Proetus* has its earliest representatives in the Ashgill (Owens 1973b: 84) and might be derived from *Cyphoproetus* simply by effacement of the deep 1P glabellar furrows. It has been suggested (Owens 1973b: 85) that the proetids belonging to Proetidae A possibly have their origins in the Otarionidae in the earlier Ordovician. A cranidium which is almost intermediate between *Otarion* and *Cyphoproetus* has been figured by Whittington (1965, Pl. 19: 13,14,18) from the Table Head Formation (Llanvirn) of western Newfoundland. This specimen resembles both *Cyphoproetus* and *Otarion* in glabellar characters, and has a short (sag.) convex preglabellar field. *Otarion* has a rather longer (sag.) convex preglabellar field than this specimen, while *Cyphoproctus* typically has a short (sag.) preglabellar field, which is commonly straight in profile. Unfortunately this cranidium is too incomplete for detailed comparison, and the position of the palpebral lobe is unknown, but suggests that Proetidae A might have become separated from the Otarionidae early in the Ordovician. Bergström (1973:41–42) placed the Proetidae and Otarionidae in different orders – the Illaenida and Ptychopariida respectively. A major reason for this classification was because he claimed that Proetidae and Otarionidae exhibited different kinds of enrollment – sphaeroidal and spiral respectively. (For definitions of these, see Bergström 1973: 15). However, on examination of hundreds of enrolled specimens of *Otarion elegantulum* (Lovén, 1845) at the Naturhistoriska Riksmuseet, Stockholm in July 1973 we discovered that both types of enrollment were to be found in the sample, so in *Otarion,* the spiral enrollment would appear to be only a degree of sphaeroidal enrollment rather than a separate and distinct type. This character does not, therefore, preclude a close relationship between the Proetidae and Otarionidae, as Bergström would claim.

PROETIDAE B. – There is now evidence to suggest that Proetidae B were already well established by the late Arenig. Fortey has found cranidia and pygidia of a *Decoroproetus*-like species in the Arenig Tourmakeady Limestone of western Ireland (Fig. 1, D, E, F) and Mr. L. Karis (S.G.U. Stockholm) [verbal communication, July 1973] has found similar cranidia in the Kunda Formation (Arenig-Llanvirn) of Jämtland, Sweden, while Ross (1972, Pl. 16: 16) has figured a *Decoroproetus* pygidium (as 'proetid pygidium') from beds of Llanvirn age in Nevada. *Paraplethopeltis? generectus* Hintze (1953, Pl. 7: 6–9) (which we consider to be a hystricurine), from the Lower Canadian of Utah, is strikingly similar to these early Proetidae B in many ways. The moderately inflated, unfurrowed glabella, the weakly convex, declined preglabellar field and the smooth dorsal surface are all features in common with the Tourmakeady cranidia, the principal difference being the larger palpebral lobe of the latter. The type of free cheek and the small, triangular rostral plate are also like those of *Decoroproetus* species. The length-breadth proportions and number and type of axial rings and pleural ribs are all similar to *Decoroproetus,*

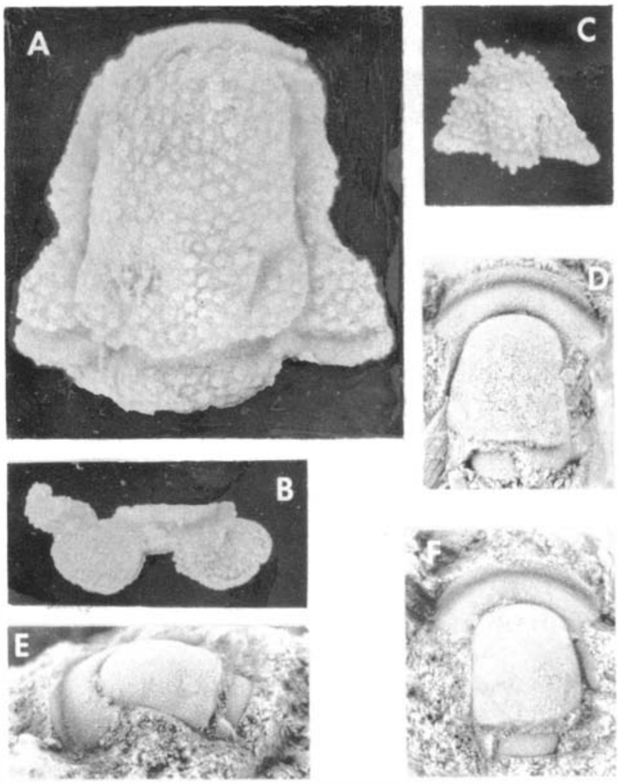

Fig. 1. A, B. *Celmus* sp. Silicified cranidium and pygidium in dorsal view (x10) BM It 12853, 12854. C. *Glaphurus* sp. Immature silicified cranidium, dorsal view (x15) BM It 12855. D,E,F. *Decoroproetus?* sp. D, cranidium, dorsal view (x8) BM It 12856. E.F. cranidium in oblique lateral and dorsal views (x8) BM It 12854. All specimens from the Tourmakeady Limestone (Arenig), Gardiner & Reynolds' Loc. 58, Co. Galway, Western Ireland. Specimens in the collections of the British Museum (Natural History).

although the characteristic 'imbricate' pygidial pleural rib profile (Owens 1973b: 5, Fig. 2) is not fully developed.

The similarities between *Decoroproetus,* early Ordovician *Decoroproetus*-like species and *Paraplethopeltis? generectus* suggest a close link between Proetidae B and hystricurines. Other early species evidently belonging to Proetidae B are not easy to connect directly with the possible hystricurine-*Decoroproetus* line. *Phaselops sepositus* Whittington (1963, Pl. 4: 11–13; Pl. 5: 1–6) from the Whiterock (Llanvirn) of Newfoundland may represent a specialised reef-dwelling offshoot. One of the cranidia figured by Ogienko (*in* Abdullaev, Ogienko, & Semenova 1972, Pl. 55: 10) as *Hystricurus secundus* Ogienko does not belong to *Hystricurus,* but the glabella shape and deep 1P and 2P furrows are reminiscent of *Xenocybe micrommata* Owens (1973a, Fig. 14: G,H,J) from the Ashgill of Norway, which is a probable member of Proetidae B, but it differs from this species in its granulose surface sculpture (that of *X. micrommata* is striated). *'Phaseolops?* sp. ind.' Whittington (1965, Pl. 19: 1–5) from the Table Head Formation (Llanvirn) of Newfoundland also bears a general resemblance to the cranidium figured by Ogienko, but has a smooth dorsal exoskeleton, and the occipital ring is narrowed laterally. Much more information on these early species is required to be able to assess their affinities in more detail.

OTARIONIDAE AND AULACOPLEURIDAE

We agree with Bergström (1973: 42) that these two families are synonymous; the overall cephalic and pygidial morphology of *Aulacopleura* and *Otarion* is very similar, and the only major differences between the two genera are the greater number of thoracic segments, lack of the thoracic axial spine, and the presence of well developed eye ridges in the former. The obvious close relationship between the two genera makes a separation at familial level quite artificial.

Like proetids, aulacopleurids occur only in small numbers in the early Ordovician, but *Otarion*-like species are already present in the Arenig of the Montagne Noire, southern France (Dean 1966, Pl. 19: 11,13,14) and in the Arenig and early Llanvirn of Spitsbergen, western Ireland and Nevada, and *Otarion spinicaudatum* Shaw (1968, Pl. 4: 2–6,9–12,16–19) occurs in beds of Llandeilo age in New York State.

Several hystricurines show striking similarities to aulacopleurids. Most similar to *Otarion* is *Hystricurus paragenalatus* Ross (1951, Pl. 8: 14–16; Hintze 1953, Pl. 6: 12–14) from the Lower Canadian, zone B, of Utah. This species has a preglabellar field, weak 1P glabellar furrows (see Hintze 1953, Pl. 6: 14a–b), incurved lateral margin at the base of the genal spine and a granulose sculpture. Hintze (1953, Pl. 6: 23–26) figures pygidia (which are not assigned to a described species) from the same horizon and locality as cephala of *H. paragenelatus,* and these, which are transverse with a small number of axial rings and pleural ribs and a weak border, are very similar to the pygidium of *Otarion* (cf. *Otarion* pygidia figured by Whittington & Campbell 1967, Pl. 8: 1–12,16–20,22–26). There can be little doubt that *H. paragenelatus* and the associated pygidia are closely related to *Otarion.* Less closely related hystricurines, but also very similar to *Otarion* in general aspect, include *Hystricurus genalatus* Ross (1951, Pl. 8: 1--13; Hintze 1953, Pl. 6: 1–6) from zones B–C of Utah, which has a small, triangular rostral plate like *Otarion,* but lacks 1P furrows and does not have an incurved lateral cephalic margin at the base of the genal spine, and *Parahystricurus pustulosus* Ross (1951, Pl. 12: 17–32) from Middle Canadian, zone F of Utah (which lacks 1P furrows). Such species, as well as *H. paragenalatus* are probably members of the hystricurine plexus from which *Otarion* arose. On present evidence, other Ordovician aulacopleurids such as *Panarchaeogonus* appear to be derived from *Otarion* species in Llanvirn/Llandeilo times (*O. spinicaudatum* Shaw, 1968 has moderate cephalic vaulting, a triangulate glabella and a *Panarchaeogonus*-like transitory pygidium, and might belong to the ancestral stock of *Panarchaeogonus*) rather than directly from hystricurines.

BRACHYMETOPIDAE

This is the only family within the Proetida to have originated in post-early Ordovician times. Its earliest members are species of *Cordania* in the early Lower Devonian (Whittington, 1960), and the youngest are known from the late Carboniferous. The general aspect of the cephalon of *Cordania* (e.g. *C. falcata* Whittington 1960, Pl. 51: 8,11,14–18) is *Otarion*-like, but the rostral plate is much wider (trans.) and the thorax has less segments (nine opposed to eleven) and the pygidium is longer with more axial rings and pleural ribs. *Cordania* might have arisen from the aulacopleurids by the release of less segments from the pygidium during ontogeny, thus producing the longer pygidium and smaller number of thoracic segments, and by the increase in width of the rostral plate and thickening of the genal spine. In broad morphology, brachymetopids also resemble members of the subfamily Warburgellinae Owens, 1973b (Proetidae B) which became extinct in the early Devonian, so there is also the possibility that they might be related to them. In later brachymetopid genera – e.g. *Australosutura* (Amos, Campbell & Goldring 1960, Pl. 39: 10,11) the rostral plate widens laterally to occupy a major part of the cephalic doublure, thus departing from the typical small triangulate rostral plate found in most Proetida. *Brachymetopus* also has a rostral plate like that of *Australosutura,* and the facial sutures become ankylosed, although the eyes are not reduced.

GENERA OF PROBLEMATICAL AFFINITIES

GLAPHURIDAE, CELMIDAE. – The systematic position of the family Glaphuridae has presented a persistent problem. Ulrich (1930: 8) placed *Glaphurus* in the Telephinidae, and the glaphurids continued to be classified close to the telephinids in Hupé's (1953: 200) classification and in the *Treatise.* Jaanusson (1956: 39) questioned the supposed telephinid-glaphurid relationship, pointing out that the small eyes and broad fixed cheeks of *Glaphurus* make a relationship to *Telephina* unlikely; this view was supported by Whittington (1963: 53). Whittington disagreed, however, with Jaanusson's suggestion that the Glaphuridae might be related to the Upper Cambrian family Catillicephalidae, as this group of trilobites has median or connective sutures on the doublure which are lacking in *Glaphurus;* the large prominent glabella reaching the anterior border of the cranidium of catillicephalids also makes a relationship with *Glaphurus* unlikely. Nor is Henningsmoen's (1951: 200) suggestion that the Glaphuridae might be related to the Odontopleuridae borne out by present knowledge of these two groups: despite a similar exoskeletal spinosity, the hypostomata and pygidia of the two groups are quite different (Shaw 1968, Pl. 7: 12,15,16), and glaphurids lack the inflated glabellar lobes characteristic of the Odontopleuridae.

We consider that the Glaphuridae belong within the Proetida, although differing in a number of features from other members of the order, and that the family is closely related to certain Dimeropygidae and to *Celmus*.

The genus *Ischyrophyma* Whittington, 1963 is a dimeropygid with relatively deep glabellar furrows, the posterior pair strongly backward curving and on some species (e.g. *I. deserta* (Billings) – see Dean 1970, Pl. 1: 8) with inner ends isolated within the glabella. Whittington (1963: 49) points out the similarity of cephalic structure of *Ischyrophyma* and *Celmus* and attention may also be drawn to the similarity of the *Celmus* hypostoma (Jaanusson 1956, Fig. 2C) to that of *Ischyrophyma marmorea* Dean (Dean 1970: 8, Pl. 2: 10); examination of material of *Celmus granulatus* shows that these similarities extend as far as closely similar surface sculpture on the borders of the free cheeks of both genera. However, *Celmus* possesses a curious single-segment pygidium unlike that of a early Dimeropygidae such as *Ischyrotoma,* and apparently also that of *Ischyrophyma* (Dean 1970, Pl. 2: 2). Jaanusson (1956) placed *Celmus* in a separate family Celmidae. New silicified material of a species, probably best referred to *Celmus,* from the Tourmakeady Limestone, western Ireland, is shown on Fig. 1, A, B. The cranidial similarity of this species to *Ischyrophyma* is apparent in the sharply backward-deflected and distally deepened 1P lateral glabellar furrows, position of the eye lobe, form of the facial suture and surface sculpture. The minute single segment pygidium possesses a pair of flanges similar to those on the pygidium of *C. granulatus* (Jaanusson 1956, Pl. 1: 7; Fig. 2D) and characteristic of *Celmus.* The origin of this unique pygidium may be understood if it is derived from that of a normal dimeropygid by release of anterior pygidial segments into the thorax. The pygidia of *Ischyrotoma* species (Hintze 1953, Pl. 19: 4,7,10) show a pair of prominent tubercles at the tip of the pygidial axis similar to those on the *Celmus* pygidium; release of two pygidial segments into the thorax from such a species as *Ischyrotoma ovata* (Hintze) would leave the terminal piece as a pygidium with a resemblance to that of *Celmus.* Given the other strong similarities between *Celmus* and the Dimeropygidae, it would seem very probable that the peculiar *Celmus* pygidium was connected with a comparable structure on the earliest dimeropygids; no other early Ordovician trilobite known to us has such a pair of nodes at the tip of the axis.

A similar relationship seems to pertain between *Glaphurus* and *Glaphurina* (Shaw 1968, Pl. 7: 18,12,15; Pl. 8: 3,10; Pl. 9: 3). *Glaphurus pustulatus* (Walcott) has ten thoracic segments

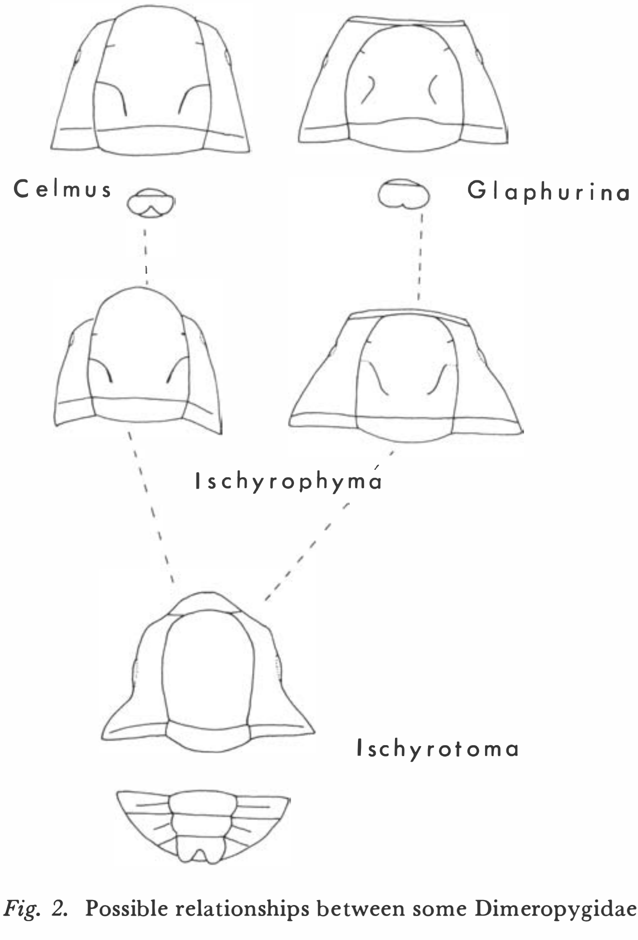

Fig. 2. Possible relationships between some Dimeropygidae, Glaphuridae, and *Celmus.*

and three pygidial segments, whereas *Glaphurina lamottensis* Ulrich has twelve thoracic segments and the pygidium reduced to a single segment. The hypostoma attributed by Shaw (1968, Pl. 7: 16) to *Glaphurus* is similar to that of both *Celmus* and *Ischyrophyma*. Dean (1970: 5) indicates that the posterior lateral glabellar lobes of *Ischyrophyma marmorea* are bicomposite, which Jaanusson (1956: 39) states is also true of *Glaphurina.* The well preserved cranidium figured by Tjernvik (1956, Pl. 10: 20–21) as *Glaphurina? insolita,* from the early Arenig of Sweden may be more correctly referred to *Ischyrophyma* (Dean 1970:8) but resembles the cranidium of *Glaphurina lamottensis* Ulrich in its general proportions, form of facial suture and size and position of the eye lobe (see also *Celmus? longifrons* Poulsen 1965, Pl. 6: 7–9). A similar cranidium has been described from the Middle Ordovician of Tien-Shan as *Glaphurina quadricornuta* Abdullaev (*in* Abdullaev, Ogienko & Semenova 1972:238, Pl. 55:12), and another similar species occurs in the Middle Ordovician of Kazakhstan, described as *Glaphurina dulanensis* by Chugaeva (1958, Pl. 8: 13–15).

Glaphurus lacks median or connective sutures (Whittington 1963, Pl. 8: 14); i.e. the free cheeks are fused to form a single unit connected by a relatively narrow strip of median doublure. While this is unlike most Proetida, the subfamily Mesotaphraspidinae Jaanusson (1956: 47) of the Dimeropygidae (including the genera *Mesotaphraspis, Chomatopyge* and possibly *Toernquistia*) shows exactly the same modification of the sutures. The rostral plate on such dimeropygids as *Ischyrotoma twenhofeli* Raymond (Whittington 1963, Pl. 7: 13) is extremely narrow (trans.) and it may be suggested that in the Mesotaphraspidinae and Glaphuridae, perhaps in response to a need to strengthen the anterior border of the cephalon, this narrow rostral plate was "lost" by ankylosis of the connective sutures. The similarity of early *Glaphurus* growth stages to those of other Proetida is discussed below.

The Glaphuridae, Dimeropygidae and *Celmus* thus seem to form a closely inter-related group. The differences between *Ischyrophyma* and *Glaphurina* cited by Dean (1970: 8) may be sufficient to justify the retention of the Glaphuridae as a separate family. It is to be anticipated that further discoveries in Tremadoc and Arenig strata will help to provide more definite phyletic links; Fig. 2 is an attempt to show possible connections between known genera. There is evidence to suggest that glaphurids were a distinct group as early as the Tremadoc (e.g. *Glaphurus alimbeticus* Balashova, 1961), and the possibility of a separate origin for the glaphurid-*Ischyrophyma-Celmus* group from the hystricurines cannot be eliminated.

PROBLEMATICAL PROETIDS. – Besides those genera of uncertain affinities mentioned above (under Proetidae B), there is a small number of genera which are apparently proetids, which are difficult to relate to any established subfamilies. These include *Rorringtonia* Whittard (see Owens 1973b, Pl. 15:7–10) and *Analocaspis* Owens (1970:Fig. 8:A–H) from the Caradoc, *Parvigena* Owens (1973a: Fig. 14: K–N) from the Ashgill, and *Pseudoproetus* Poulsen (1934, Pl. 3: 1–4) from the Llandovery. Of these, *Parvigena* might be a specialised "smoothed out" (morphological type (3), see below) proetid, but its pygidium is unknown, while the others all share certain characters in common – a forward-tapering, furrowed glabella, small eyes and pygidial pleural ribs with parallel, narrow pleural and interpleural furrows of similar depth – which suggest that they may all be related. *Protarchaegonus* Sdzuy (1955, Pl. 7: 2–7) from the Tremadoc of Bavaria, Germany, which may be a hystricurine, shows glabellar and pygidial characters which are quite similar to *Analocaspis,* but there are no known similar trilobites in the intervening Arenig to Llandeilo.

Owens (1974) considers that the aberrant genus *Scharyia* (range Ashgill to high Middle Devonian) is probably related to *Panarchaeogonus* (see above, under Otarionidae and Aulacopleuridae).

HYSTRICURINAE. – Hystricurines can be accommodated within the concept of the Proetida. If the phyletic links described here are substantiated, separation of the Hystricurinae from the Proetida would seem to be excessively arbitrary, and there would seem to be no reason for excluding them from the order.

ONTOGENY

Similarities between early growth stages of the families under discussion have been noted by several authors. Whittington & Campbell (1967: 450,460) discussed the close similarity of

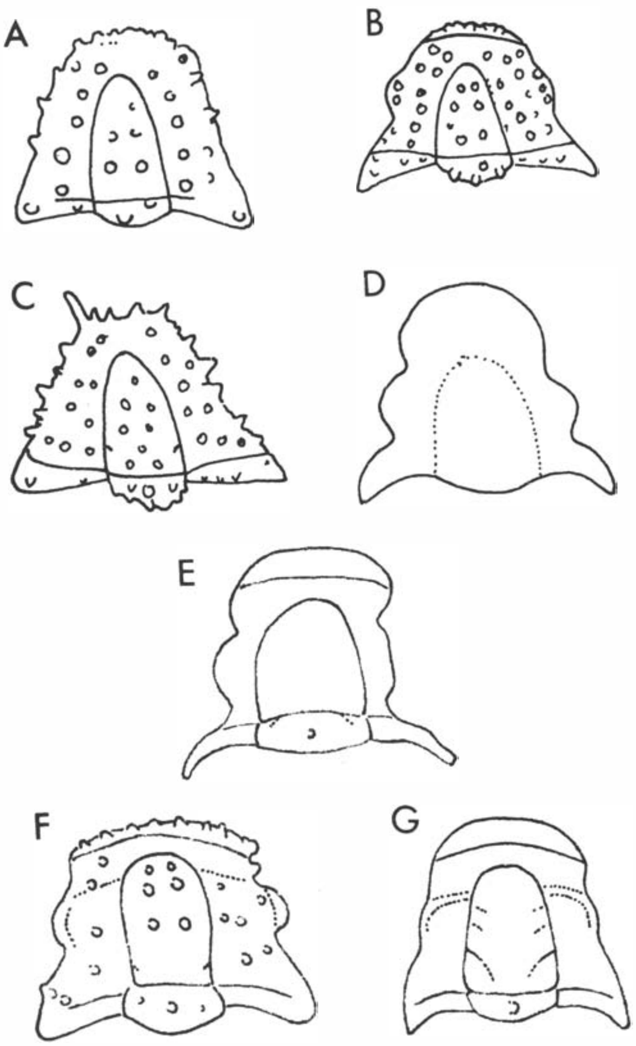

Fig. 3. Schematic outline drawings, early ontogenetic stages of some Proetida. A. *Ischyrotoma caudanodosa* (Ross) (after Ross 1953). B. *Parahystricurus fraudator* Ross (after Ross 1951). C. *Glaphurus* sp. (this paper, Fig. 1). D. *Licnocephala cavigladius* (Hintze) (after Ross 1953) *E. Proetus pluteus* Whittington & Campbell (after Whittington & Campbell 1967) F. *Otarion dabrowni* Chatterton (after Chatterton 1971). G. *Proetus talenti* Chatterton (after Chatterton 1971).

meraspide *Otarion* and *Dimeropyge* and considered Otarionidae and Dimeropygidae to be related. Chatterton (1971: 72), in a discussion of the ontogeny of *Otarion (Otarion) dabrowni* from the Devonian of New South Wales, further extended these comparisons to include *Hystricurus* species figured by Ross (1951, Pl. 9: 17–19) and Hintze (1953, Pl. 6: 23–26). Chatterton postulated a common origin in the Hystricurinae for the Dimeropygidae, Otarionidae and Proetidae. Immature cranidia of the Middle Ordovician species "*Phaseolops*" *conus* Hu (1971, Pl. 23: 10–12), which is an aulacopleurid, are similar to those of the Devonian Otarionidae figured by Chatterton. Chatterton also (1971: 64) noted a resemblance between early *Proetus* growth stages and those of the bathyurid *Licnocephala cavigladius* Hintze (Ross 1953, Pl. 64: 8,14). A comparison may also be drawn between small cranidia of *Proetus pluteus* Whittington & Campbell (1967, Pl. 1: 21) and those of *Bathyurellus nitidus* Billings (Whittington 1963, Pl. 11: 8-10). A meraspis cranidium of *Glaphurus* sp. from the Tourmakeady Limestone (Arenig), western Ireland, figured on Fig. 1,C shows marked similarities to early growth stages of *Dimeropyge virginiensis* (Whittington & Evitt 1954, Pl. 3: 24,28) in the trapezoidal outline of the cranidium, size and position of the palpebral lobes, fusiform glabella and distinct preglabellar field. 1P glabellar furrows are developed on this small *Glaphurus* as on *Proetus talenti* Chatterton (1971, Pl. 14: 1a–b,2a–b) and *Otarion spinicaudatum* Shaw (1968, Pl. 4: 3). The immature *Dimeropyge* and *Glaphurus* cranidia are themselves closely comparable to small specimens of *Parahystricurus fraudator* Ross (1951, Pl. 12: 4).

Available ontogenetic information thus supports a phyletic relationship between hystricurines, aulacopleurids, proetids, bathyurids, dimeropygids and glaphurids. Because of their spinosity and smaller eyes small growth stages of Dimeropygidae and Hustricurinae tend to resemble one another more closely than those of the larger-cyed, smooth Bathyuridae and Proetidae. Proetida appear to bear opisthoparian sutures throughout all stages of ontogeny.

DIAGNOSIS

Members of the order Proetida possess a combination of the following characters:

(1) Medially transversely narrow rostral plate which generally tapers backwards (except cases outlined above). This feature in particular suggests that the Bathyuridae are related to the Proetidae rather than to the Illaenidae, which have broad rostral plates. Examples of rostral plates of Proetida are figured for Bathyuridae (Whittington 1963, Pl. 11: 15; Pl. 14: 8), Hystricurinae (Hintze 1953, Pl. 6: 1c), Dimeropygidae (Whittington 1963, Pl. 7: 13), Aulacopleuridae (Whittington & Campbell 1967, Pl. 6: 9), Proetidae (Owens 1973b, Pl. 3: 9; Pl. 15: 3) and Brachymetopidae (Amos, Campbell & Goldring 1960, Pl. 39: 10,11).

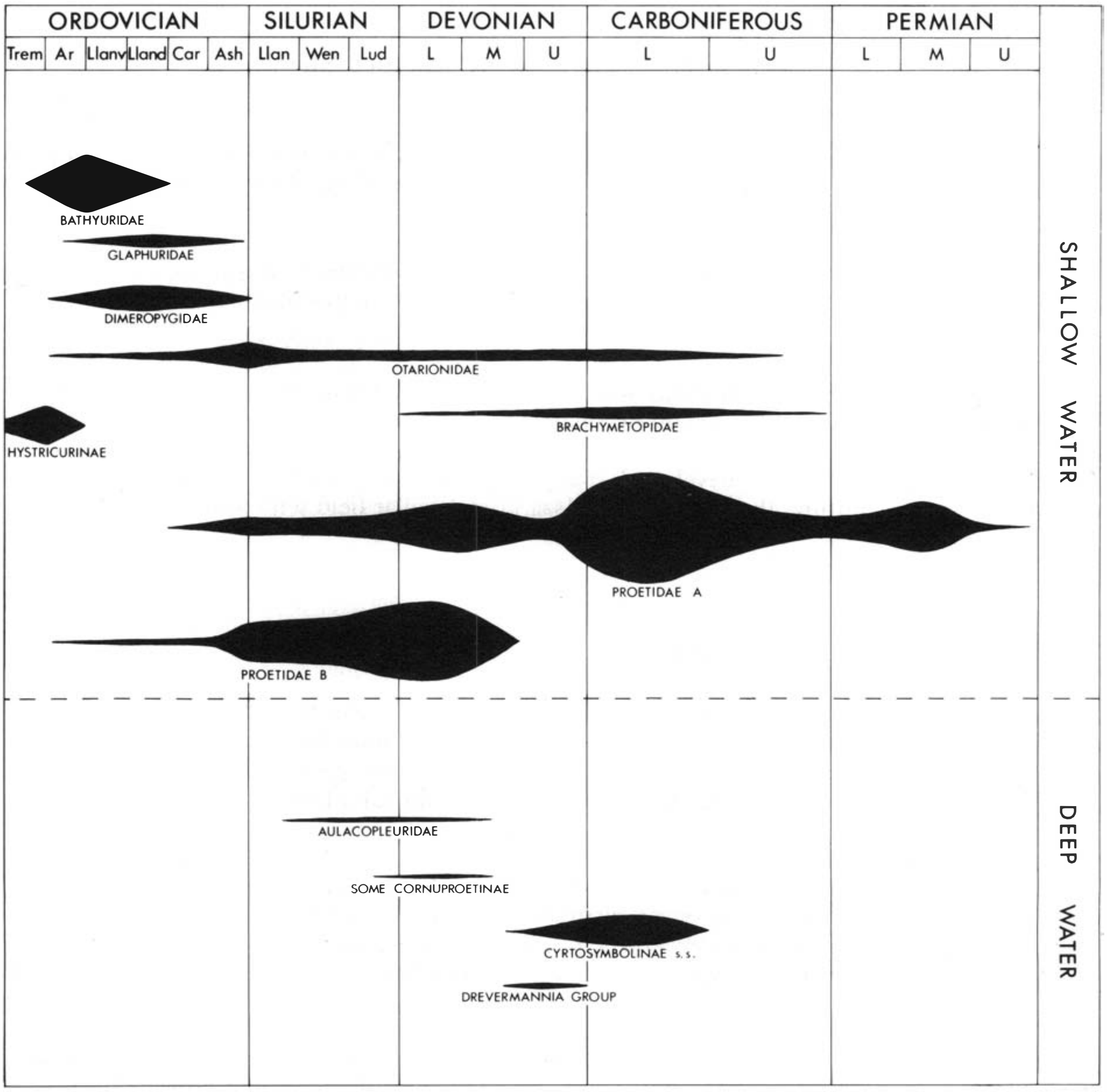

Fig. 4. Outline geological history of Proetida, showing relative number of genera of principal groups, and appearance of the order in the deep water environment.

(2) Glabella well defined, commonly with a characteristic vaulted profile in anterior view. The front margin of the glabella is rounded on the mid-line, usually strongly so, coming almost to a point medially on many genera (*Bathyurellus, Mesotaphraspis,* some cyrtosymbolines s.l.).

(3) Glabellar furrows or muscle impressions (which are usually visible on well preserved material) with following characteristic form: 1P is invariably most strongly developed (longest and deepest), backward-curving; 2P, 3P and 4P are progressively smaller anteriorly, and may not themselves curve backwards.

(4) The occipital ring is normally well defined (exception: *Benthamaspis* (Bathyuridae)).

(5) Genal spines well developed – commonly blade-like – on most species, but may be reduced on some Silurian and later Proetidae, and a few Dimeropygidae.

(6) Eyes with semicircular outline, holochroal, medially or backwardly positioned, and usually of moderate size, although some species with small and some with large eyes are known, and in the Devonian some blind forms appear.

(7) Posterior sections of facial suture diverge at a moderate to high angle, anterior branches usually divergent, may be subparallel. (Exceptions: species with reduced eyes or blind; *Scharyia* with a cedariiform posterior branch).

(8) Doublure of convex species usually recurved steeply beneath the border of the free cheek to form a lateral cephalic "tube".

(9) Thorax usually with 8–10 segments, but may be as few as 6 or as many as 22. Width of pleurae equal to or exceeding that of axis, thoracic segments in contact along their length; pleural furrows diagonal.

(10) Pygidium with strong pleural furrows and margin usually entire. (Exceptions, e.g. *Pseudoolenoides* (Bathyuridae) and *Phaetonellus* (Proetidae) develop spinose pygidial margins). Doublure with strong terrace lines.

(11) Hypostoma longer (sag.) than wide with elongate, oval middle body and one pair of relatively posteriorly situated middle furrows, borders narrow.

(12) Preglabellar field variously developed; species with short preglabellar field tend to have a granulose surface sculpture; those with a long (sag.) preglabellar field tend to have a surface sculpture of fine terrace lines.

EVOLUTIONARY TRENDS AMONG THE PROETIDA

The range of morphological diversity among the trilobites here considered to constitute the order Proetida may be summarised in terms of a few "end member" morphotypes which were attained many times in the evolution of the group. Similar morphological types were produced in the early Ordovician by the Bathyuridae that were attained in the later Ordovician to the end of the Palaeozoic by the Proetidae.

(1) *Bathyurus-Proetus* type. More convex trilobites with preglabellar field short or absent, strongly furrowed pygidium with convex pleural fields, "rolled" anterior border to the cranidium close to the glabella. Examples are *Proetus* and other Proetinae; *Bathyurus, Goniotelus* and Bathyuridae of the subfamily Bathyurinae Hupé 1953; *Dimeropyge, Ischyrotoma* from the Dimeropygidae.

(2) *Bathyurellus-Tropidocoryphe* type. Trilobites with a broad, gently downsloping preglabellar field, anterior border developed as a more or less horizontal plane. Pygidium typically of low convexity with sigmoidal pleural furrows and commonly relatively flattened border. Doublure wide and flat. Examples are *Decoroproetus, Tropidocoryphe* from Proetidae B and *Bathyurellus* and *Uromystrum* from the Bathyuridae. This morphological type commonly has surface sculpture of fine terrace lines.

(3) Species with large or relatively large eyes and relative obliteration of glabellar and axial furrows, "smoothed out" species. Relatively rare, but include the bathyurid *Benthamaspis,* the aulacopleurid *Isbergia* and the possible proetid *Parvigena.*

(4) *Aulacopleura* type. There is a multiplication of thoracic segments, which become narrow (sag., exsag.). Preglabellar field broad and pleural areas relatively wide compared with morphological types 1–3.

We consider many Proetida to have lived in shallow water, sometimes in "reef" environments. The morphological types 1–3 outlined above are believed to have been adaptations to particular ecological niches in the shallow water environment, niches which were occupied by different groups from the Ordovician to the Permian. Such ecological replacement is not far from the biomere concept of Palmer (1965). Proetida are found in greatest abundance in limestones, but are not confined to that lithology.

We believe that the *Aulacopleura* type, with its multiplication of thoracic segments and hence of thoracic appendages and "gill branches", may have been connected with a mode of life in deeper water, perhaps under relatively deoxygenated conditions giving them a superficial resemblance to olenids which have a comparable mode of life and which occur in similar lithologies. This resemblance has led to the classification of *Aulacopleura* with the olenids (Hupé 1953: 207). *Aulacopleura* is found for example in deeper water facies of the Liteň Formation, Prague district, Czechoslovakia (Horný, Prantl & Vaněk, 1958), and is widespread elsewhere in Europe in similar facies – e.g. Holy Cross Mountains, Poland, (Tomczykowa 1957), Dalarne, Sweden (Törnquist, 1884). We consider that this overall flattened morphological type is unlikely to have been a vigorous swimmer.

GEOLOGICAL HISTORY

During the early Ordovician (Tremadoc-Arenig) the Bathyuridae rapidly diversified to display a wide range of morphological types (1–3 above) and are abundant as fossils in the shallow water limestones across North America and northeastern USSR. During this period the Proetidae and Aulacopleuridae remained a relatively insignificant part of the fauna. During mid-Ordovician times (Llanvirn-Llandeilo) the Bathyuridae slowly declined and there was a corresponding gradual increase in the diversity of the Proetidae and Aulacopleuridae, some of which have a close overall resemblance in size and in gross morphology to the earlier Bathyuridae (e.g. *Tropidocoryphe* to *Bathyurellus*). In the late Ashgill (e.g. in the Boda Limestone reefs) there was a great increase in diversity of proetids, particularly Proetidae B. Throughout the Ordovician the Dimeropygidae (and Aulacopleuridae from the Caradoc onwards) remained a constant but never dominant element of shallow water faunas. Proetida appear to be almost confined in the Ordovician to areas outside the *Selenopeltis* Province; i.e. if the interpretation of Whittington & Hughes (1972) is correct, they evidently eschewed cold water regions. Throughout the Ordovician, Proetida seem to be found only in shallower water deposits.

In the Silurian, the rate of diversification of Proetidae B gradually increased and that of the Aulacopleuridae remained more or less constant, but *Aulacopleura* (Morphological type 4) was the first representative of the order to colonise a deep water environment, in which it appears to have remained until its extinction in the mid-Devonian. In the later Silurian there was an increase in the rate of diversification of Proetidae A, when many important Devonian lines were established in shallow water environments, particularly in reefs such as those developed in Gotland.

The Devonian marked a further expansion in the importance of the Proetida, and the order became a major constituent of trilobite faunas for the first time since the early Ordovician, and along with the Phacopida dominated Devonian trilobite faunas. Proetida presumably filled niches vacated by other trilobites declining at the end of the Silurian. This is accompanied by major speciation and by the further development of many minor modifications of morphological types 1 and 2 above, and many different lines in both Proetidae A and B achieved similar basic morphology, particularly of type 1, by convergent evolution (e.g. Cornuproetinae and Eremiprotinae among Proetidae B and Proetinae among Proetidae A). In the later Devonian and in the earlier Carboniferous two major groups of Proetida occur (Prentice 1967, p. 209): the deeper water was colonised by thin-shelled small-eyed or blind forms (mostly members of the polyphyletic Cyrtosymbolinae, some at least belonging to Proetidae A), while thicker-shelled, commonly granulose, larger-eyed forms (all Proetidae A) occupied the shallow water environment.

The Proetida are the only trilobites to survive into the Carboniferous and Permian, where they are represented by Proetidae A (in shallow and deep water), Aulacopleuridae and Brachymetopidae (in shallow water only). Proetidae A are represented by the polyphyletic 'phillipsiids', which were probably derived by several lines from the Proetinae and Schizoproetinae, and by cyrtosymbolines. many members of which were probably derived from the Dechenellinae. The deep water genera all became extinct by mid-Carboniferous times, while the shallow water genera, which underwent diversification in the early Carboniferous, and apparently again in the late Carboniferous and early Permian (Hahn & Hahn 1967, Chamberlain 1969) persisted, sometimes in abundance, and particularly in reef environments, until the end of the Permian. Some genera, such as *Paladin,* may have replaced Phacopida in certain niches, as there is some parallel development in expansion and inflation of the frontal lobe of the glabella and in "basisolution" (Richter, Richter & Struve *in* Moore 1959, p. O383) of the posterior part of the glabella.

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Gill structures in the Lower Devonian eurypterid *Tarsopterella scotica*

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Waterston, C.D. 1975 07 15. Gill structures in the Lower Devonian eurypterid *Tarsopterella scotica. Fossils and Strata.* No. 4, pp. 241–254, Pls. 1–2. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

The lectotype, from the Gedinnian of Angus, Scotland, has been prepared to show the ventral structures of the abdomen. Surface features of the gill tracts, the ventral body wall, the skin forming the roof of the gill chambers anterior and posterior to the gill tracts and that forming the anterior and posterior surfaces of the hinge of the plate-like abdominal appendages are described and illustrated and a tentative reconstruction of the gill chambers is given. The significance of these findings is discussed in the light of recent literature on eurypterid gill anatomy and they are found to support the general interpretation suggested by P.F. Moore and substantiated by L.J. Wills that eurypterid gill tracts are specialisations of the ventral body wall. A revised description of the general anatomy of this species will appear elsewhere.

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The respiratory organs of eurypterids were first recognised by H. Woodward in *Erettopterus* (1868: 294; 1869: 66–8) and later in *Slimonia* (1871: 115–6). Hall (1859) having established the true position of the eurypterid operculum, and the homology with the operculum in *Xiphosurus* having been recognised (Woodward 1869: 61; 1871: 114), Woodward looked for evidence of eurypterid gills in an analagous position to those of the King Crab, dorsal to the operculum. His evidence from *Erettopterus* left him in little doubt "that the normal place of attachment (of the gills) would be under the thoracic plate or operculum" (1869: 66). The "branchiae" were attached, he thought, in single or double rows to the ventral surface of the body by their anterior margins, the rounded leaf-like lateral and posterior borders being freely bathed with water. In *Slimonia* he recognised the existence of abdominal appendages with which gills were also associated on segments posterior to the operculum, but he believed them to be of similar form to the operculum, bearing genitalia, and more or less covered on the ventral side by the operculum.

M. Laurie (1893: 514–5) made a further study of *Slimonia* and rejected Woodward's idea of several plates similar to the genital operculum lying one on top of another and recognised for the first time that paired plate-like ventral appendages were borne on the mesosomatic segments. He concluded that at least one, and probably more "branchial lamellae" were carried on the inner or dorsal side of each of these abdominal appendages. Laurie seemed to make an exception of the first gill, however, for not having found any trace of gills on detached genital plates, he considered that the gill structures sometimes seen through the operculum must be attached to the soft skin of the body on the second mesosomatic somite.

A milestone was reached in the understanding of the eurypterid gill when G. Holm's classic monograph on *"Eurypterus fischeri" (= Eurypterus tetragonophthalmus* (Fischer)) was published in 1898. He demonstrated that the two sides of the gill tract were different and that what he termed the *"Kiemenplatten"*, which he correlated with Woodward's "branchiae" and Laurie's "branchial lamellae", were therefore part of the skin and not free lamellae as previously supposed. He pointed to the inconsistency of Laurie's conclusions but in part agreed with him in supposing that the gill structures were borne on the mesosomal appendages believing that the *Kiemenplatten* were spongy thickenings of the dorsal skin of these appendages. While he did not think that the *Kiemenplatten* were themselves free lamellae he believed that they would form the attachments for such lamellae. Holm extended his study of the gills of *Eurypterus* and *Erettopterus* and had made many important discoveries but his death occurred before publication of his work. It is fortunate that some of the illustrations which he had prepared have since been published by Professor Wills (Wills, 1965, posthumous Plate 1—5). Holm's interpretation has been adopted by many authors who have described gills in other genera (e.g. Clarke and Ruedemann 1912 in *Paracarcinosoma scorpionis* and *Onychopterella kokomoensis*, Størmer 1934, 1944 and 1955 in *Hughmilleria norvegica* and *Mixopterus kiaeri*).

P.F. Moore (1941) re-examined one of the *Slimonia* specimens studied by Laurie and concluded that the gills are not borne on the genital operculum or abdominal plates, but occur dorsal to them as highly vascular areas of the body wall. He further argued that analogies with living animals (Xiphosurans, Scorpions and Pedipalpids) suggest that on a segment specialised for reproduction, as is the eurypterid operculum, the respiratory apparatus would be atrophied and he concluded that the first gill in eurypterids, which is covered by the operculum, is therefore likely to be in the body wall of the second mesosomatic segment.

The last major work on eurypterid gills was the detailed description of *"Eurypterus fischeri"* by L.J. Wills (1965) for which he used Holm's unpublished plates and preparations and new acid preparations in embedding resin made by himself. Wills supplemented Holm's findings but added a great deal of new information and, in particular, established the form of the gill chamber describing the different appearances of the cuticle in its various parts. He produced convincing evidence for the gill tract being a specialisation of the ventral body wall. He followed Moore in the opinion that the genital segment of no present day chelicerate carries a gill or lungbook, but believed that the operculum in the eurypterid included the ventral elements of the first two mesosomal segments. He concluded, therefore, that the smaller-than-usual gill pouches which he found associated with the operculum were developed on the second, or postgenital segment, of the mesosoma. (Wills 1965: 129). This interpretation was not accepted by Størmer & Kjellesvig-Waering (1969: 203) who claimed that lungs do occur in the genital segment of the recent arachnids Uropygi, Amblypygi and Aranaea and inferred that the first gill of eurypterids is developed on the first mesosomal segment. Were this the case it would show that the operculum in eurypterids was in a more primitive condition than had been supposed by Moore and Wills since it had retained its respiratory function as well as being specialised for reproduction.

It is clear that no settled conclusions have yet been reached as to the nature and position of the gills in eurypterids and any additional evidence will be of value in bringing us nearer to a true understanding of this aspect of eurypterid anatomy. The writer was interested, therefore, when in the course of re-describing the Scottish Devonian eurypterids, new evidence became available to him on the gill anatomy of the large and rare form, *Tarsopterella scotica*.

THE MATERIAL

Stylonurus scoticus was described by Woodward (1865, p. 484; 1872, p. 126), *Stylonurus armatus* Page (1867: 230) being a junior synonym. Clarke and Ruedemann (1912: 287) erected a new subgenus *Tarsopterus* to accommodate Woodward's species but this name was preoccupied by an amphibian and Størmer (1951: 421) made *S. scoticus* the type species of a new genus *Tarsopterella* which was referred "with considerable misgivings" to the Dolichopteridae by Kjellesvig-Waering (1966: 176).

The species was described from two specimens found in 1863 by James Powrie in an Old Red Sandstone quarry "in Montroman Muir, near the Forfar and Montrose Pike". It is likely that this locality is Balgavies Quarry (Grid No. 537519), Angus, which falls within the Arbuthnott Group of the Lower Old Red Sandstone (Gedinnian) Region of the Midland Valley of Scotland in the sense of Armstrong and Paterson (1970). One of the syntypes was an almost complete individual, lacking much of the prosomal appendages (Woodward 1872, Pl. XXIII), which is now in the Royal Scottish Museum numbered 1891.92.103. The other was a dorsal shield of the prosoma (Woodward 1872, Pl. XXII) of which the part was in Lady Kinnaird's cabinet and is now in the Royal Scottish Museum (Kinnaird 70), while the counterpart is in the British Museum (Nat. Hist.). Of these the more complete specimen R.S.M. 1891.92.103 is here designated lectotype.

The lectotype existed in three parts, the dorsal surface of the prosoma and abdomen being displayed on one slab, while the post-abdomen and telson were preserved on an adjacent block from which the natural cast of the last five body segments could be detached. Because of the importance of the specimen it was most desirable to reveal such ventral structures as could be exposed in a way consistent whith the conservation of the type. Taking advantage of a natural parting in the matrix, the block containing the anterior part of the body was split in such a way that the dorsal shield of the prosoma and the anterior tergites could be preserved separately. On the remaining block many of the ventral structures were revealed in dorsal aspect including the remarkably preserved gill structures which are here described.

DESCRIPTION OF THE GILL STRUCTURES

Removal of the dorsal shield of the lectotype revealed, in addition to parts of the prosomal appendages, some of the ventral structures of the first three mesosomal segments and in particular the gills, gill pouches, ventral body wall and parts of the plate-like mesosomal appendages (*Blattfüsse*) of the animal, the details of which have been admirably preserved in the fine sediment. The view of the gill chambers is comparable to that of *Eurypterus tetragonophthalmus* illustrated by Holm (1898, Pl. 10: 9). The structures are complex and difficult to interpret because many types of surface are exposed. Most are natural moulds of the ventral surface of the ventral cuticle of the body wall. Others have been formed by the *Blattfüsse* and their doublures while, here and there, the cuticle itself has been preserved. These surfaces have been distorted due to compression of markedly three-dimensional structures and the segments have been telescoped, probably during ecdysis, resulting often in one surface having been superimposed upon another. For simplicity of presentation each type of surface is described with an indication of the interpretation put upon it in the light of Wills (1965) but the main discussion of how these surfaces are related to one another, together with the consequent interpretation of the anatomy of the gills and gill pouches of which they form parts, follows the descriptive section.

Seven types of surface have been recognised and their distribution is illustrated in Fig. 1. They are described as follows: (1) Gill tract, (2) Median skin of ventral body wall, (3) Microfolds, (4) Macrofolds, (5) Posterior granular skin, (6) Anterior granular skin, (7) The variously ornamented ventral surfaces of the ventral plates – operculum, *Blattfusse* etc.

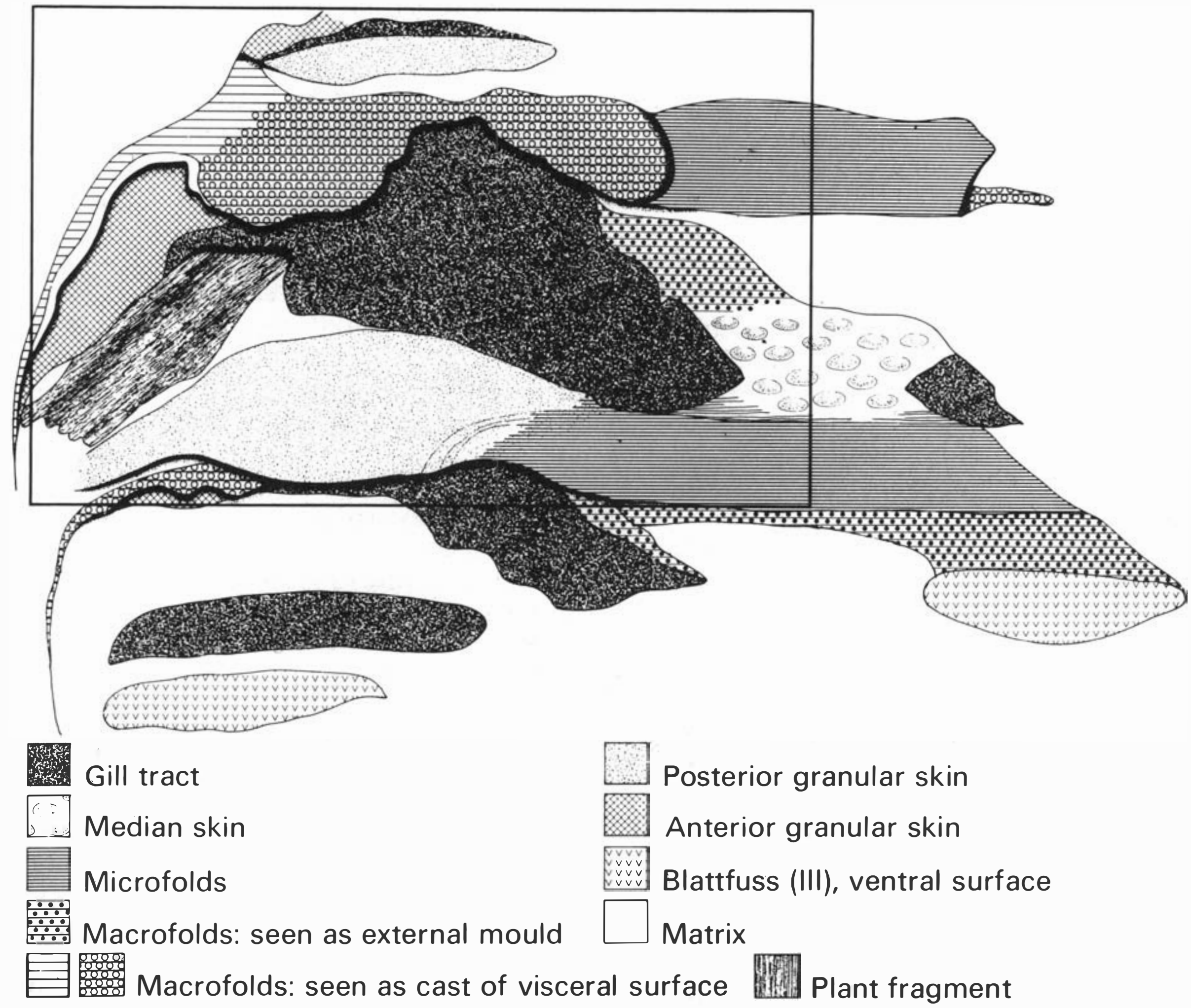

Fig. 1. Diagram to illustrate the distribution of the various types of cutiular surfaces as exhibited on the ventral surface of the mesosomal segments of the lectotype of *Tarsopterella scotica* (Woodward) R.S.M. 1891. 92. 103. See also Pl. 1: 1, the area of which is indicated by the rectangle on the diagram.

The gill tract

The characteristic surfaces of the gill tracts (Pl. 1: 1, Pl. 2: 4,5) are seen on the left and right sides of the second, and left side of the first, third and fourth mesosomal segments. The most complete is that of the left side of the second mesosomal segment of which the anterior and medial parts are complete but the post-lateral portion has been broken away. This tract is 90 mm wide and, when complete, must have been some 35 mm in maximum length. The segment measures 137 mm from the mid-line to the left lateral margin so that the gill tracts must have occupied about two thirds of its total width. The tracts are therefore much broader than long, the greatest length being in the lateral part of the tract. The inner margins are extended towards the median line of the animal in a well-defined and broadly hastate prolongation so that the overall shape of the tracts is sub-triangular. This differs from the oval or elliptical form more usual in eurypterids but is reminiscent of *Mixopterus* (Størmer 1934, Fig. 38, Pls. 5 and 7) in which the gill tracts are wedge shaped having the thin end of the wedge pointing towards the mid-line of the animal. The tract of the first mesosomal segment is incomplete anteriorly but appears to have been much smaller than that of the succeeding tract described above, and is likely to have been less than half the width of the tract of the second segment. That of the third mesosomal segment is very incomplete, only that portion nearest the mid-line being present, the left tract of the fourth segment appears to be fairly complete and is lath-shaped measuring 72 mm in width but only 17 mm in maximum length.

The most conspicuous feature of the gill tracts is the branching plexus of grooves which is quite sharply defined from the spongy tissue making up the bulk of the tract. From a large trunk groove, situated within the anterior margin of the gill tract, a series of five or six major branches passes postero-medially and divides into small ramifying members to every part of the tract. The walls of the major grooves are pitted but the chitinous spinules which cover the ventral surface of the spongy tissue are sparse or lacking (Pl. 2: 4,5). The dendritic pattern of grooves has been noted by all previous workers (e.g. Holm 1898: 40, Pl. 11: 5) and is clearly equivalent to the "valleys" of Wills who noted (1965: 119—20, Pl. 6: 1, 2, Pl. 7) that on the "inner" or dorsal surface of the tract the "valleys" are represented by strips of dimpled, but otherwise featureless skin. From his reconstruction of Holm's section across a gill tract (Wills 1965, Pl. 6: 3 and 4) it is clear that the "valleys" appear as such from the ventral side of the tract. On the dorsal side, however, they also appear as depressions between the masses of spongy tissue which overlie the "ridges" of the ventral surface. What is seen in *Tarsopterella* appears to be a natural cast of the dorsal surface of the gill tract and a mould of the exposed surface made in rubber latex (Pl. 2:5) shows the probable appearance of the blood vessels lying in the dorsal grooves of the valley system. These were papillate, the largest papillae being on the ventral crests of the vessels.

While the dendritic grooves are seen as a natural cast of the dorsal surface of the gill tract, the intricacies of the spongy surface between the grooves are such that a clean cast has not been formed, but the spongy mass has been broken apart to reveal it at different depths through the thickness of the tract. That the spongy appearance is due to small outgrowths and invaginations of the cuticle is shown by the presence of broken sections of cuticle intimately associated with and distributed throughout the mass. When examined microscopically under alcohol (Pl. 2: 4) the black cuticle is seen to be disposed in a network of polygons and circles having a diameter in the order of 0.02 mm, the walls of which have a beaded appearance. This reticulate pattern is almost certainly formed by transverse sections of spinules (Wills 1965: 119) which, by analogy with Wills' material would be expected to be borne in large numbers on the ventral side of the ridges between the "valleys". The beaded appearance of the chitin wall is probably due to sectioning through the minute polygonal patterning with which the gill tract and the basal parts of the spinules were covered in the Oesal material (Wills 1965: 119, Pl. 6: 8: noted also by Holm in *Eurypterus* in posthumous Plate 3: 5 and 6, and in *Erettopterus* posthumous Plate 1: 7—11). That the reticulate patterns seen in the spongy mass of the *T. scotica* gills is not itself this minute polygonal patterning is evident from the fact that in areas where the tract has been sectioned to a more ventral level, the continuation of the reticulate chitin ventrally into the solid apices of the spinules can be seen. The order of size of the patterning in *T. scotica* is similar to that of the diameter of the spinules of *Eurypterus* and of a larger size than the minute polygonal patterning of the gill tract and spinules in *Eurypterus.* If Wills (1965: 122) was correct in believing that the spinules performed a physiological function in the oxygenation of the blood, their size would probably be dictated by this function and it would not be expected that in larger gill tracts, such as that of *T. scotica,* they would necessarily be larger but rather that they would be more numerous. Towards the margins of the gill tracts the spinules appear to become orientated laterally, so that in the marginal areas the structures have been sectioned longitudinally instead of transversely as elsewhere.

The ventral body wall of the median region

The surface of the ventral body wall (Pl. 1: 2, 3) is displayed in its simplest form in the median region between the gill tracts and is well seen on the second mesosomal segment, where the features are preserved as a natural mould of the ventral surface. The change in character of the cuticle from the thin cuticle of the median region to the specialised spongy cuticle of the gill tracts on either side is very sharp, giving clear margins to the tracts (Pl. 1: 2). A cast of the median skin reveals the true ventral appearance of the cuticle at this point and macroscopically it appears to be smooth with small scattered squamae. Under the microscope, however, the squamate areas are seen to be formed of groups of sharply defined small pustules of differing size. The granulation in regions between the squamae is subdued. As the surface is traced posteriorly the squamate appearance is lost, the granulation becomes finer and intense lattice folds or microfolds are developed.

Microfolds

Such folds (Pl. 1. Figs. 1, 4; Pl. 2. Fig. 7) are developed in the median region and are well seen in the lectotype associated with the joints between the first and second mesosomal segments, and the second and third segments (Pl. 1: 1). They are formed of tightly folded thin cuticle, the crests of the folds being about 1 mm apart. These folds occupy belts up to 20 mm from anterior to posterior in the median region and extend laterally to a maximum width of some 120 mm. The axes of the folds run transversely across the animal and as they pass laterally they curve slightly towards the posterior. The belts taper off laterally and the anterior folds which persist into the gill chambers are seen to pass behind the gill tracts and grade into, and die out in, the posterior granular skin (see below). To the naked eye the cuticle of the microfolds appears to be smooth but under the microscope it is seen to be ornamented with a very regular pattern of fine striae which run parallel to the axes of the folds (Pl. 1: 4), an ornament which distinguishes them from every other surface in the lectotype. There are about 15 striae within 1 mm of cuticle. Similar striae have been described from a nepeonic type B median abdominal appendage of *Slimonia* (Waterston 1960: 255, Pl. 43: 1) and may prove to be a more common surface feature of thin and otherwise smooth eurypterid cuticles than has been realised up to the present. Striations of a similar kind are found on thin and otherwise unornamented cuticles in other arthropod groups. The microsculpture of insect and arachnid cuticles is of this order of size (J. Millot 1949: 283, Fig. 63) and varies from sub-parallel sinuous striae, as in the Araneae, to complex patterns found in many insects. Such microsculpture is found to have taxonomic significance among modern insects and arachnids and it would be of interest to discover whether advanced eurypterid groups developed more complex patterns than the simple striae observed in *Slimonia* and *Tarsopterella.*

As the striate cuticle is traced anteriorly it is gradually replaced by the fine granular ornament described above. On the right side of the second abdominal segment of the lectotype the microfolds may be traced posteriorly and are seen to pass into coarse lattice folds or macrofolds.

Macrofolds

Folds of this type (Pl. 1: 1; Pl. 2: 1, 2) are interposed between the microfolds and the outer, or ventral, cuticle of the *Blattfuss.* They grade into microfolds anteriorly and medially and are attached posteriorly to the forward margin of the *Blattfuss.* The attachment to the *Blattfuss* is well seen on the right side of the lectotype where macrofolds forming the most posterior surface of the second abdominal segment join the anterior margin of the *Blattfuss* of the third segment. Here the macrofolds are in the same plane as the succeeding *Blattfuss* and are seen as a natural mould of the ventral or outer surface. The true position of the macrofolds, however, is better appreciated from the macrofold surface associated with the *Blattfuss* of the post-opercular segment where, in the broken right side, it is seen to pass antero-ventrally under the microfolds at the posterior of the first abdominal appendage. On the left side of the same segment they reappear in a similar posture from beneath the microfolds of the first abdominal appendages, which occupy a median position, where these folds have been broken away to expose them. The macrofolds extend to the left lateral margin of the segment passing, for the most part, in front of the gill tract of the second mesosomal segment. They obscure this gill tract in part, however, where they now occupy a position dorsal to it. Macrofolds can also be seen in a lateral position on the left side of the specimen where they occupy a position ventral to the posterior granular skin of the second mesosomal segment and dorsal to the anterior granular skin of the third mesosomal segment. Only in the exceptional case of the third abdominal segment on the right side is the attachment of the macrofolds to the *Blattfuss* seen since in all other cases the *Blattfüsse* are obscured by structures lying dorsal to them.

Macrofolds are fairly regular and strongly developed and, like the microfolds, their axes run transversely across the specimen. The fold crests are some 2 mm apart, about twice the distance separating the crests of the microfolds. In its greatest development the macrofold surface measures 20 mm from anterior to posterior and in width it apparently coincides with that of the *Blattfuss* with which it is associated. Details of the sculpture of the outer or ventral surface are best seen in the negative, where a natural mould of this surface has been preserved (Pl. 2: 2). It has pustules of two orders of size, the smaller giving an overall granular appearance while the larger are developed along the crests of the folds. In the negative the pits formed by the larger pustules contain the cuticle of one, or sometimes two, bristles embedded in the matrix showing that they formed bristle bases. Where the surface has been folded back upon itself, as in the area lying anterior to the left gill tract of the second abdominal segment a natural cast of the visceral surface of the cuticle is exposed, covered here and there by small patches of the cuticle itself. This cast surface (Pl. 2: 1) shows the bristle bases clustered on the fold crests but their appearance is less clear-cut than in the natural mould. Macrofolds in these positions are interpreted as the anterior skin of the movable hinge of the *Blattfüsse.*

Surfaces very similar to macrofolds are developed in the median region of the second and third abdominal segments immediately anterior to the hastate prolongation of the gill tracts (Pl. 1: 2). They are seen as natural moulds of the ventral surface and are less regular in their folding than elsewhere.

Posterior granular skin

Surfaces of this type (Pl. 1: 1, Pl. 2: 7) are preserved posterior to the gill tracts on the left side in the first and second mesosomal segments. In the second segment the surface is seen to grade medially into microfolds while medially also the anterior margin of the surface abuts the gill tract. As the surface is traced laterally it assumes an antero-ventral inclination which carries it ventral to the posterior part of the gill tract. The posterior granular skin associated with the first mesosomal segment lies dorsal to the macrofolds but has been broken away posteriorly from its associated surfaces. Medially it appears to have graded into the microfolds, while anteriorly it abuts the gill tract of the first mesosomal segment. In its greatest development behind the second gill tract it measures 28 mm from anterior to posterior and over 90 mm in width.

The surfaces are preserved as natural moulds of the outer surface of the cuticle. This mould has a rather spongy appearance having an ornament of circular pits of differing radius and depth, which entirely covers the surface. In life the surface of the cuticle must have had an ornament of rounded granules of differing size but of the same order of magnitude, the size distributions being random over the whole surface. All, except perhaps the smallest granules, formed hair bases since the chitin of the hairs remains embedded in the matrix.

The posterior granular skin is interpreted as forming the roof of the gill chamber posterior to the gill tract.

Anterior granular skin

This type of surface (Pl. 2: 6) closely resembles the posterior granular skin in having an ornament of rounded granules of differing size randomly distributed over the whole surface, but it differs in having a number of very large bristle bases sparsely distributed over the surface. Like the posterior granular skin it is preserved as a natural mould of the ventral surface and the chitin of the hairs and bristles is preserved embedded in the matrix. The rather crumpled state of the granular skins might suggest that they were formed of thin cuticle. The anterior granular skin occurs anterior to the gill tracts and is seen in this position in the lectotype in the first three mesosomal segments. Evidence from the second segment would suggest that this type of surface also extended laterally from the gill tract and appears to unite with the left lateral extremity of a tergite and may be formed in part by the lateral doublure of the tergite. As mentioned above, the anterior granular skin does not extend into the medial region since the ventral body wall is skinned by folded cuticle reminiscent of the macrofold surfaces anterior to the hastate medial extension of the gill tracts. The anterior granular skin is interpreted as forming the roof of the gill chamber anterior and lateral to the gill tract.

The ventral surface of the Blattfüsse

The character of the ventral surface (Pl. 2: 3) of the plate-like abdominal appendages is seen in the natural mould of the *Blattfuss* of the third mesosomal segment on the right side and on the mould of a detached appendage, perhaps of the fourth segment, on the left side. The ornament consists of "pterygotoid scales" which are more numerous and obtuse anteriorly and become larger, sparser and more acute posteriorly. The nature of the posterior margin of the *Blattfuss* is not know.

INTERPRETATION OF THE STRUCTURES

The surfaces described above are found in association with one another on the left side of the lectotype in the first three mesosomal segments. Unfortunately the structures of the fourth mesosomal segment have become dissociated and those on the right side of all the visible segments are very incomplete. Fig. 2 shows in schematic form the relationships of the various surfaces exhibited by the specimen. While, because of distortion or loss, the relationships of all the surfaces to one another are not seen in any one mesosomal segment, the relationship of one surface to

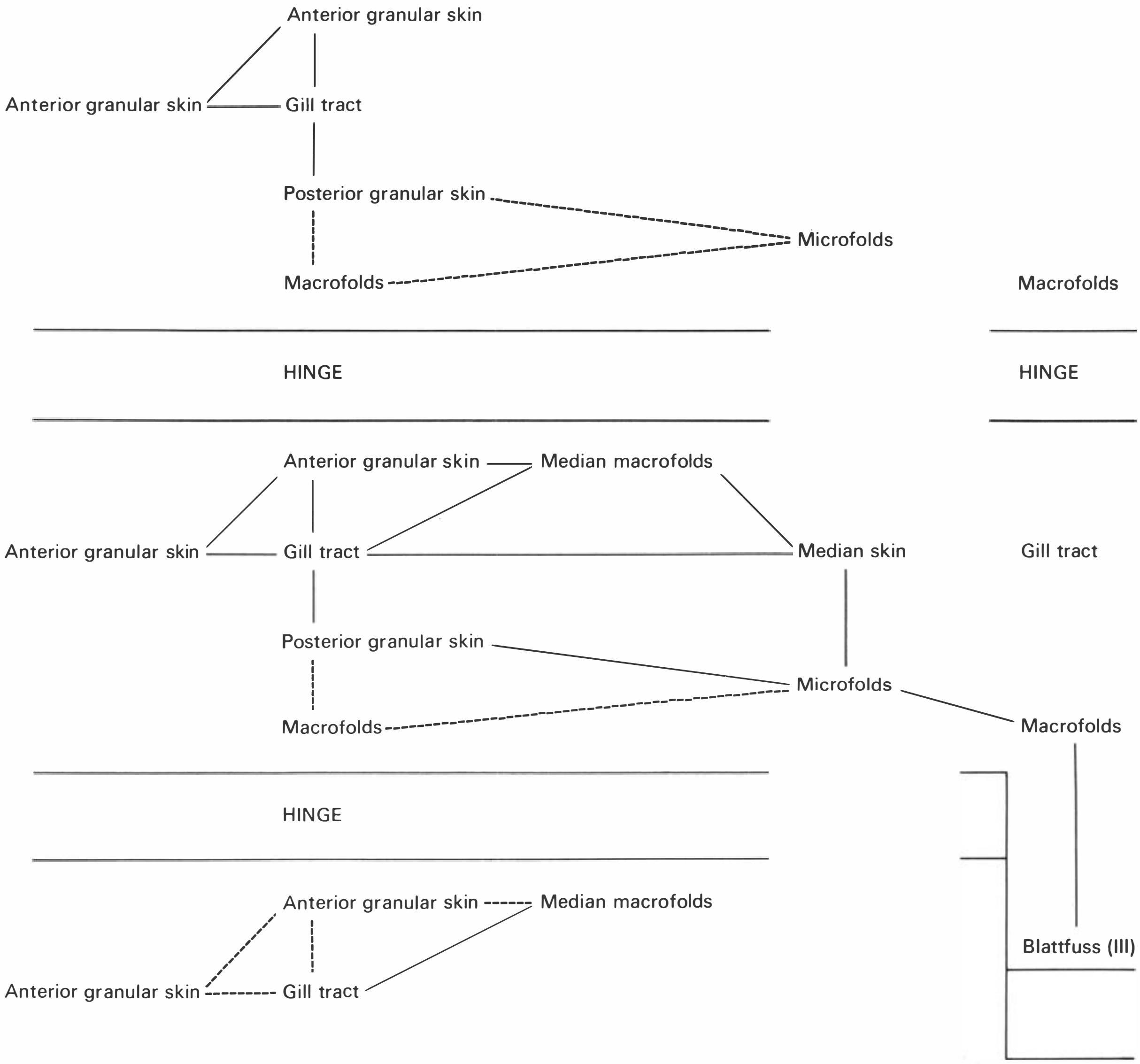

Fig. 2. Diagram illustrating the relationships of the surfaces exhibited on the ventral side of *Tarsopterella scotica* (Woodward) R.S.M. 1891.92.103. Solid lines connect surfaces which can be seen to pass into one another and broken lines indicate those which, by direct examination are thought to do so or, by analogy, with associations proved in other parts of the specimen, it is inferred must do so.

another can be established at one or more points in the specimen and thus a complete picture of the structures can be built up.

That the outer or ventral surfaces of the *Blattfüsse* are attached at their anterior margins to the macrofolds is established in the right *Blattfuss* covering the third mesosomal segment where structures which would lie dorsal to the *Blattfuss* (gill tract and associated roof of the gill chamber) have been removed. In this case the *Blattfuss* has been displaced posteriorly thus pulling the attached macrofolds on the second segment into the same plane as itself and both surfaces are seen as natural moulds of the outer or ventral surface. The normal posture of the macrofolds is seen in the broken section on the right side of the first mesosomal segment and on the left side of the same segment where it is seen to pass anteroventrally for some distance before, as may be supposed, turning sharply backwards upon itself just anterior to its junction with the *Blattfuss* covering the second mesosomal segment which is not exposed. The macrofold surface must have skinned the anterior surface of the hinge bar from which the *Blattfuss* is articulated and floored the posterior portion of the gill chamber of the preceding segment (c.f. Wills 1965: 115–6).

The macrofolds associated with the *Blattfuss* of the right side covering the third mesosomal segment, which must have formed the posterior portion of the gill chamber of the second mesosomal segment, are seen to pass anteriorly into tight microfolds which cross the median region of the animal. In the preceding segment where the macrofolds assume an anteroventral posture the microfolds lie dorsal to them. The macrofold surface at this point passes backwards and upwards as the anterior skin of the hinge until it joins the ventral body wall where it folds over upon itself and passes anteriorly as microfolds on the ventral body wall.

In the median region of the second mesosomal segment microfolds pass anteriorly into smooth cuticle of the ventral body wall which in turn develops the granular squamate ornament as it is traced anteriorly. Laterally, on the left side of the second segment microfolds are clearly seen to pass into the posterior granular skin which lies posterior to the gill tract of the second segment. The hastate extension of the gill tract into the median region of the second segment is less disturbed in its relationships with neighbouring surfaces than is the main portion of the tract, and is seen to have well-defined boundaries with the squamate median ventral cuticle and that part of the posterior granular skin nearest the mid-line. In this region it is clear that the gill tract, the median squamate cuticle, and the posterior granular skin all occupy one plane and are specialisations of the ventral body wall.

From the relationships described in the second segment it is clear that the posterior granular skin forms part of the ventral body wall in a position anterior to the hinge and posterior to the gill tract. It has also been shown that macrofolds, which form the anterior skin of the hinge, pass anteriorly through microfolds into the posterior granular skin. The posterior granular skin of *Tarsopterella* thus occupies an equivalent position to the skin forming the roof of the gill pouch posterior to the tract in *Eurypterus* which Wills (1965: 115–6) showed was the anterior extension of the doublure of the *Blattfuss* which formed the anterior skin of the hinge. In *Tarsopterella,* however, this skin shows a characteristic granular ornament and probably carried a felt of fine hairs on its ventral side, unlike the equivalent in *Eurypterus* which is described as thin and devoid of ornament (Wills 1965: 114). As the granular skin is traced laterally in the left gill chamber of the second mesosomal segment it is found to extend for some distance antero-ventrally under the gill tract. Since both these surfaces represent specialisation of the ventral body wall it is clear that such a position must be abnormal and appears to have resulted from telescoping of the gill chamber to form a fold between the tract and the posterior roof of the chamber. It would be expected that such a disturbance would be greatest where the gill chamber is largest and most three-dimensional. In the first mesosomal segment, where the gill tract is greatly reduced in size, the junction of the posterior granular skin with the tract is not disturbed and the granular skin is seen to pass anteriorly into the gill tract along the whole of the exposed width. Unfortunately the posterior granular skin of this segment has become isolated from the adjacent folded cuticle by breakage but it is clear that, as in the second mesosomal segment, it must have passed medially into microfolds.

The relationships of the surfaces anterior to the gill tracts are more disturbed because of dislocation and collapse of the hinges. In the first and second mesosomal segments, however, the junction of the gill tract with the anterior granular skin can be seen and the evidence of the second segment would suggest that this surface with the large bristle bases is most strongly developed antero-laterally and laterally to the gill tract. Wills (1965: 116) showed that the skin forming the body wall anterior to the tract in *Eurypterus* also skinned the posterior wall of the hinge. He believed that in *Eurypterus* the "lattice-folds" (described Wills 1965: 113) occured on this surface skinning the posterior of the hinge. If, as seems likely, the "lattice-folds" of Wills are equivalent to what has been termed the macrofolds in the present paper, then we must conclude that either the present account differs from that of Wills in its interpretation of similar evidence or that the anatomy of *Eurypterus* differs from that of *Tarsopterella* since the macrofolds are here regarded as forming the anterior skin of the hinge. Only in the medial part of *Tarsopterella* anterior to the hastate prolongation of the gill tracts do surfaces similar to the macrofolds occur posterior to the hinge. As described above (p. 000), the opinion that in *Tarsopterella* the macrofolds skin the anterior surface of the hinge is based upon the evidence provided by the attachment of macrofolds to the right *Blattfuss* of the third abdominal segment, and to a consideration of the aspect and disposition of the macrofold surfaces which are consistent with the interpretation adopted. In *Tarsopterella* it would appear probable that the posterior surface of the hinge was skinned, at least in part, by bristle-bearing skin similar to that forming the roof of the gill pouch anterior to the gill tract.

Many types of bristle with many different functions occur in arthropods and of particular relevance are those described from other eurypterids as in *Eurypterus* (Holm 1898: 10, Pl. 7: 4), *Rhenopterus* (Størmer 1936: 31–2, Pl. 9: 4–5), *Erettopterus* (Tobien 1937, Pl. 20) and in a Scottish Carboniferous form (Waterston 1957, Pl. 3: 8). Others have been described from the Cyrtoctenida (Størmer & Waterston 1968, Fig. 5, Pl. 6: 14) while fossil scorpions have yielded bristles of many forms the evidence for which has been reviewed in connection with his description of *Gigantoscorpio willsi* by Størmer (1963: 25–31). Most of the bristles associated with the anterior granular skin are attached to a rounded knob-like projection of the integument and, from the works cited, it is evident that they were not movable setae but fixed spines possibly acting as water filters. It is also possible, however, that setae with a tactile function were also present.

THE STRUCTURE AND FUNCTION OF THE GILL CHAMBERS

The reconstruction (Fig. 3) is an attempt to show the probable relationship in life of the various del structures associated with the gills and gill chambers of *Tarsopterella scotica.* More reliance can be placed upon the relative positions of the surfaces than on the actual proportions of the gill chambers for which evidence is incomplete. While the relative size of the surfaces on the ventral body wall is known, the ventral extent of such structures as the hinge or the gill tract in life are not known and the depths of the gill chambers must therefore be conjectural. Enough is known, however, to permit some discussion of the structure and function of the gill chambers.

The interpretation of the structures of the gill chambers, and in particular the recognition of the gill tracts as a specialisation of the ventral body wall, have so far been based entirely on the relationships of the various body surfaces exhibited by the specimen. An important piece of confirmatory evidence lies in the fact that a portion of plant stem has been lodged within the gill pouch on the left side of the second mesosomal segment having entered the chamber post-laterally. It is seen to have passed ventrally beneath the gill tract but must lie dorsal to the associated *Blattfuss* (see Fig. 1, Pl. 1: 1).

The reconstruction may suggest the function of the bristles clustered on the crests of the macrofolds. The chitin of the macrofold surface, forming the anterior skin of the hinge, folds sharply forwards at the base of the hinge bar to continue anteriorly as the microfolds of the ventral body surface. The function of the microfolds was clearly to accommodate the extension or contraction of the abdominal segments in response to movements of the longitudinal muscles. Part of the function of the macrofold bristles must have been to prevent unwanted matter from becoming lodged within the acute fold anterior to the base of the hinge. I am grateful to Dr. J. Miller of the Grant Institute of Geology, Edinburgh, for bringing to my notice the possibility that bristles so arranged in association with an extensible surface, formed in this case by the microfolds, may also serve a sensory function in monitoring the degree of extension of the microfolds.

T. scotica was an animal approximately one metre in length and it would be reasonable to suppose that the oxygen requirements of an eurypterid of such a size, however passive its mode of life, would be greater than could be provided by simple diffusion through the gill tracts. Some mechanism would therefore be required to create a current of water over the gill tracts to increase the available dissolved oxygen. That such currents did pass through the gill chambers in a controlled fashion is suggested by the asymmetrical distribution of structures such as the occurrence of the large bristles on the anterior granular skin in front of and lateral to the gill tract but not behind or medial to it, and also by the broadly triangular plan of the gill tract itself having the broadest part laterally and the narrowest part medially. The presence of the bristles – fixed spines and possibly setae – associated with the anterior granular skin in the antero-lateral position with their probable filtering and tactile function, would strongly suggest that they guarded the gill tract from unwanted matter, which would in turn suggest that water-currents approached the gill tracts from the antero-lateral direction and, having passed over the surface of the tract, the spent water would be expelled posteriorly.

The simple beating of the *Blattfüsse* would not produce the controlled flow through the gill chamber which the morphology indicates and which analogy with modern gill-breathers suggests must have been present. It would rather have caused turbulence which, in the sandy or muddy environment of the lakes and rivers of the Scottish Gedinnian which was the habitat of *Tarsopterella,* would have produced the harmful effect of introducing grit and dirt into the gill chambers. From the reconstruction it is apparent that there are a number of mechanisms which could have contributed to the control of water flow over the gills. Movement of the *Blattfuss* to open the gill chamber, or to close it by adpressing the appendage against the succeeding one which it overlapped, could have been accomplished by muscle action in the hinge and appendage in association with the action of the macrofold integument of the hinge. Since the *Blattfüsse* are abdominal appendages modified to a plate-like form their musculature must have been analagous to that of other arthropod abdominal appendages. In *Limulus* the abdominal appendages are controlled by at least five groups of muscles, the branchio-thoracics (Milne Edwards 1873), the external branchials, the anterior and posterior entapophysio-branchials and pre-entapophysial-branchials (Benham 1885). As both Holm (1898) and Wills (1965) have noted the "lattice-folds" or macrofolds have to do with movement of the *Blattfuss* but whether the role of this robust integument was purely passive as a hinge flexing as a result of muscle action, or whether it had an elasticity which supplemented or even replaced the action of certain muscle groups in either raising or lowering the *Blattfuss*, we do not know. The volume of the gill chamber could have been controlled by lengthening or shortening of the abdomen in response to movement of the longitudinal muscles and such movements would have been accommodated in the ventral body

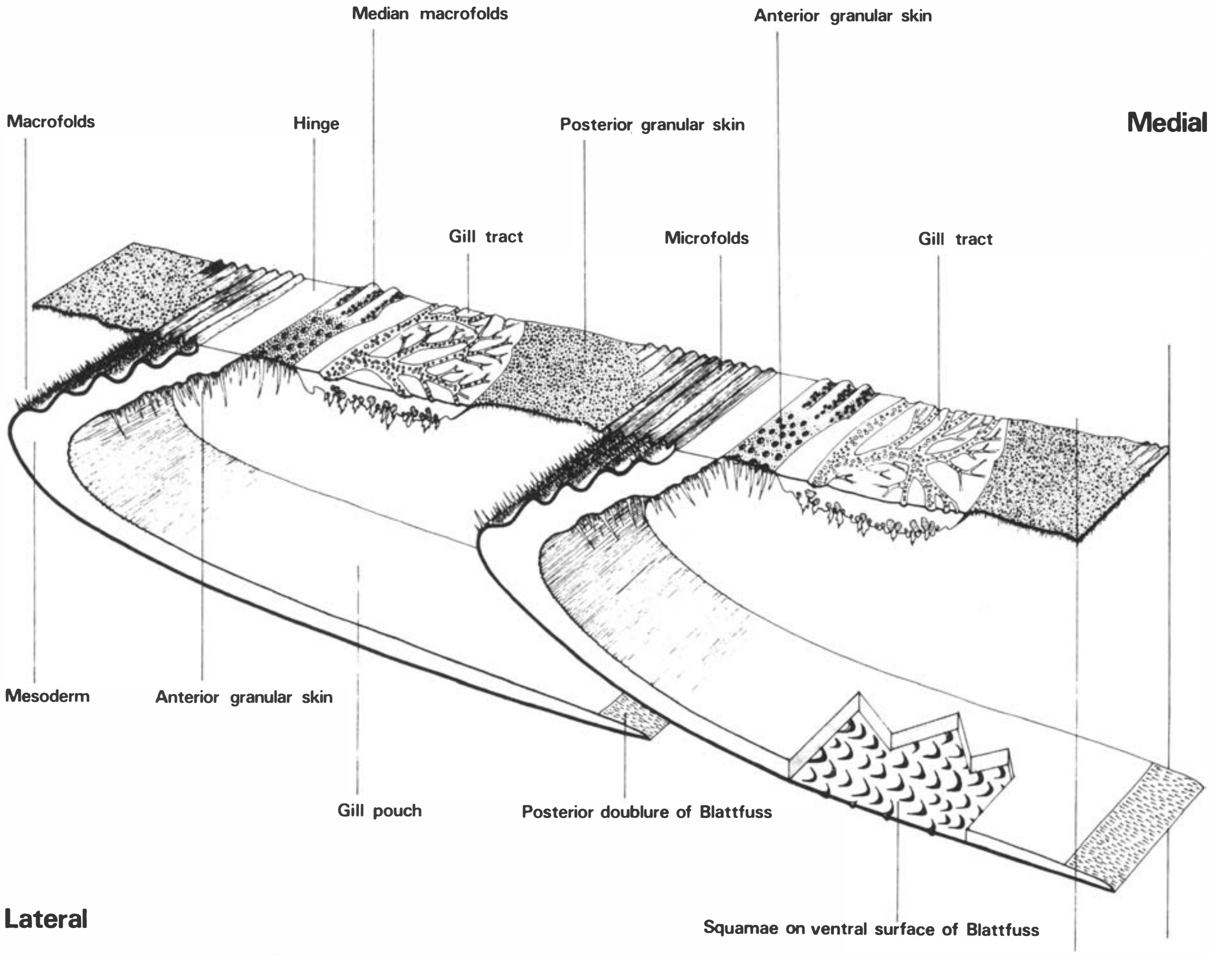

Fig. 3. Sectioned reconstruction of the post-opercular gill chambers of *Tarsopterella scotica* (Woodward). The upper surface shown in the diagram represents the dorsal view of the ventral body wall as seen in the lectotype. For the sake of clarity the lateral arching of the roof of the gill chamber has not been indicated although it is most probable that in life the roof of the chambers would be domed.

wall by expansion and contraction of the microfolds. Another way in which the volume of the gill chamber could have been altered would have been by swinging the hinge bar forward or backward and so altering the angle formed between the ventral body wall, the hinge and the *Blattfuss* and thus effectively altering the length of the anterior wall of the gill chamber. Any suggestion as to how the gill chamber functioned in life must of course be speculative but the writer believes that a current of water in the required direction could have been achieved. By closing the gill chamber posteriorly by pressing the *Blattfuss* against that of the succeeding segment, and by swinging the hinge posteriorly and so increasing the volume of the chamber, water would be inhaled laterally. By then opening the gill chamber posteriorly by a downward movement of the *Blattfuss* and by decreasing the volume of the chamber by swinging the hinge anteriorly and possibly also contracting the length of the segment, the spent water would be expelled. The forward swinging of the hinge would juxtapose the anterior part of the *Blattfuss* to the roof of the gill chamber and thus close the lateral openings and force the water backwards through the posterior gape. Such a movement of the gill chambers of each segment in turn could be achieved by the metachronal rythm of the abdomen even when the animal was otherwise at rest.

RESPIRATORY STRUCTURES IN EURYPTERIDS, SCORPIONS AND XIPHOSURANS

The present work on *Tarsopterella* confirms the findings of Moore (1941) on *Slimonia* and Wills (1965) on *Eurypterus* that eurypterid gill tracts are specialisations of the ventral body wall (see also Wills 1964 for his deductions on the gill pouches of *Adelophthalmus).* Morphologically the eurypterid gill is thus comparable with the respiratory structures in scorpions rather than those of xiphosurans. The lung sacs of modern scorpions occur in the four abdominal segments succeeding the pectine and open by way of spiracles placed in relation to each segment in a very similar position to the eurypterid gill. Pocock (1901: 306, 1911: 15) claimed that *Palaeophonus* was an aquatic animal and that the overlapping ventral plates in lobostern scorpions probably concealed gills. (Wills (1925: 95) followed Pocock's view and later (Wills 1960: 329–30) concluded that in the Carboniferous there were two races of scorpions. One, mostly but not entirely, with lobate sternites was aquatic breathing by gills in gill pouches lying above deeply overlapping sternites, the second comprised terrestrial animals with short orthostern sternites. *Mazoniscorpio,* however, showed some characters of each race. Størmer's work on *Gigantoscorpio* (1963: 120–4) confirmed the view of Pocock and Wills and summing up the evidence he concluded that Silurian and probably Devonian scorpions and some Carboniferous scorpions led an aquatic life and that probably the aquatic forms breathed by gills like the merostomes and further that although the nature of the respiratory organs is not known in lobostern scorpions it is likely that they were gills as in eurypterids. If these assumptions are correct it is clear that the gills of eurypterids and the gills of lobostern scorpions must be homologous structures.

Many years ago Lankester (1881) demonstrated the homology between the book-gills of *Limulus* and the lung-books of scorpions. Embryological studies have confirmed his results by showing that the lung-lamellae of the scorpionids, pedipalpids and areneids are formed as folds at the posterior basal surface of the embryonic limb (Kästner 1940, see also Dawydoff 1949: 365–366). Størmer (1944: 59 and 125, 1963: 99–100, 110–114) has reviewed the embryological evidence and discussed the phylogenetic significance of the structures of the ventral abdominal plates as found in trilobites, aglaspids, xiphosurans, eurypterids and scorpions and concluded that during evolution of the Chelicerata there was a gradual transition from free appendages to fixed ventral plates and that in the mesosomal appendages there was a successive simplification and reduction of the primary structures. In this morphological succession he saw the eurypterids as intermediate in structure between the Xiphosura and Scorpionida. Our present knowledge of *Eurypterus tetragonophthalmus* and *Tarsopterella scotica,* while confirming this general conclusion, would suggest that the gill structures of eurypterids are closer to the scorpions than to the xiphosurans in that, in the post-embryonic condition, the gill tracts, placed on the ventral body wall, have become entirely separated from the associated plate-like abdominal appendage. Just as the gill-books of the scorpions are known to be part of the embryonic limb, so it is likely that the embryonic limbs of eurypterids gave rise both to the gill tracts and to the *Blattfüsse* anterior to them.

The gill chambers of eurypterids appear to have been suited to protect the damp gill tracts from desiccation and thus to have permitted the animal to crawl on dry land for limited periods.

This may also have been true of the lobostern scorpions but for effective land life the invagination of the gills to form lung sacs is clearly of enormous adaptive advantage. While this was accomplished in scorpions there is no evidence that a similar adaptation was achieved in eurypterids which must have severely limited the possible adaptive response of the surviving swamp-dwelling eurypterids of the Carboniferous to the onset of the arid conditions of the Permo-Triassic.

It has been suggested in the present paper that water flowed over eurypterid gills in a controlled manner entering the gill chamber laterally and leaving it posteriorly. This control must have been achieved by the functioning of the gill pouches of each abdominal segment independently. It cannot be supposed that aeration of the gills would be very efficient even if this independent functioning was in some way co-ordinated, since five pairs of water currents must have been generated (Fig. 4A). A much more efficient way of creating the desired flow of water over the gills has been developed in the xiphosurans where the gill appendages work together to create a flow of water through what may be thought of as a single gill chamber. Firstly the jointed nature of the biramous gill appendages allows them to be moved in such a way as to beat the water in a desired direction, and by the co-ordinated beating of the five pairs of branchial appendages such a strong backwardly-directed current can be generated that the modern King Crab can use it for propulsion. Secondly, the anchylosis of the abdominal segments in the King Crab permits the formation of a beautifully streamlined deep ventral cavity in the abdominal buckler into which the gill appendages are set. In addition to providing protection to the gill appendages the shaped walls of the cavity promote water flow over the dorsally placed gill lamellae. The cavity gapes antero-laterally and water can enter it on each side by way of the laterally open joint between the prosoma and the abdomen. Posteriorly it narrows and the water is expelled near the base of the telson (Fig. 4B). The presence of the biramous gill appendage with its power to create water currents, and of the anchylosed abdominal buckler shaped to control the direction of these currents are xiphosuran characters which are in striking contrast to the gill structures of eurypterids and probably also of those of aquatic scorpions. One may speculate that the need for a more effective flow of water over the gills may have been one of the adaptive pressures which led to the anchylosis of the abdominal segments in groups of Xiphosura from the Palaeozoic onwards.

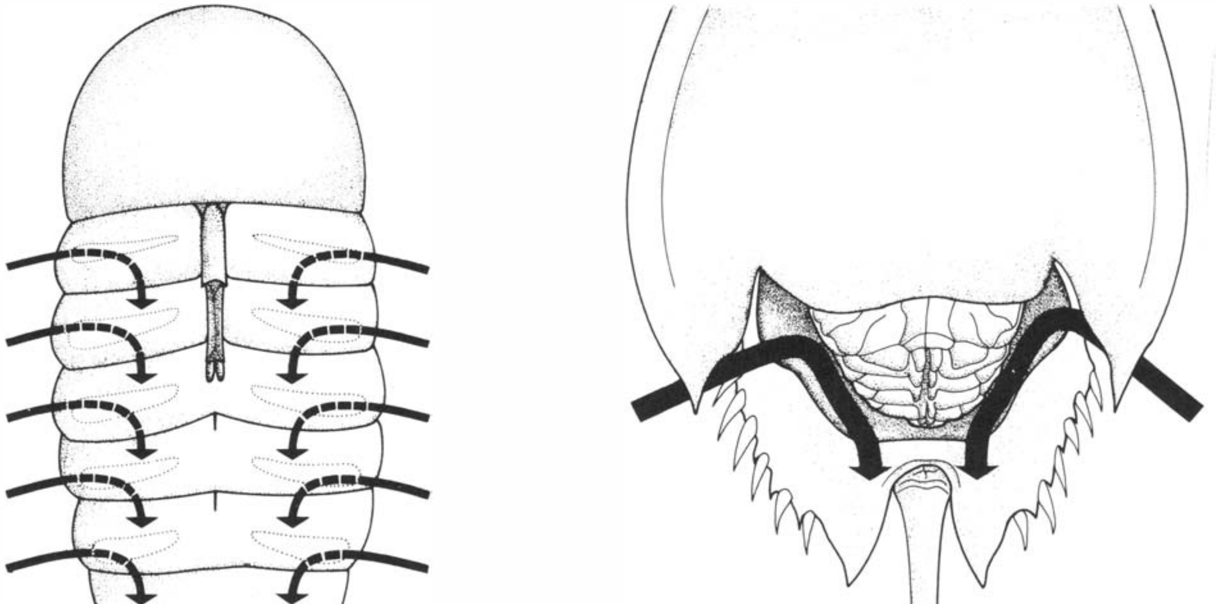

Fig. 4. A. Direction of water-currents passing through the gill chambers of an eurypterid as postulated in the present paper. B. Direction of water currents passing through the composite gill chamber formed by the anchylosed abdominal segments of *Limulus*.

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EXPLANATION OF PLATES

All illustrations are of the lectotype of *Tarsopterella scotica* (Woodward) from the Arbuthnott Group, Lower Old Red Sandstone (Gedinnian) of Angus, Scotland. Royal Scottish Museum 1891.92.103.

Plate 1

Fig. 1. Dorsal view of the gill chamber on the left side of the second mesosomal segment showing gill tract (centre), microfolds (bottom right and top right), posterior granular skin (lower left) and macrofolds (upper centre) X1.2. Compare with text Fig. 1. *Fig. 2.* Detail of dorsal view of the hastate median extension of the gill tract on the left side of the second mesosomal segment, showing the junction with the cuticle of the ventral body wall of the median region and the median macrofolds (top left) X3. *Fig. 3.* Squamae of cuticle of ventral body wall enlarged from Fig. 2. to show the concentration of larger granules at the squamae X7.5. *Fig. 4.* Detail of the cuticle of the microfolds at the postero-median region of the first mesosomal segment showing, in the upper portion of the figure, the fine parallel transverse striae X16.

Plate 2

Fig. 1. Natural mould of the "visceral" surface of the cuticle of the macrofolds anterior to the gill tract on the left side of the second mesosomal segment, showing the concentration of the larger pustules on the crests of the folds X10. *Fig. 2.* Natural mould of the exterior surface of the macrofolds anterior to the *Blattfuss* on the right side of the third mesosomal segment. The larger pustules or bristle bases are seen to be concentrated at the crests of the folds which are here seen in the negative X10. *Fig. 3.* Natural mould of the exterior surface of the *Blattfuss* on the right side of the third mesosomal segment to show the ornamentation of small crescentic squamae of varying size X10. *Fig. 4.* Dorsal view of part of the gill tract on the left side of the second mesosomal segment photographed under alcohol. The darker tone of the "spongy" tissue is due to the sectioned chitin of the spicules, while the "valley" on which the spicules are sparse or absent, shows in a lighter tone. The anterior trunk groove from which the branch is given off is situated at the top of the picture X6. *Fig. 5.* Latex cast of the gill tract on the left side of the second mesosomal segment showing pustules along the trunk groove (top) and along two major branches X6. *Fig. 6.* Natural mould of the exterior surface of the anterior granular skin on the left side of the second mesosomal segment, showing large bristle bases. The contact of the anterior granular skin with the anterior border of the gill tract is shown (bottom right) X10. *Fig. 7.* Natural mould of exterior surface of the posterior granular skin on the left side of the second mesosomal segment, succeeded posteriorly by microfolds X10.

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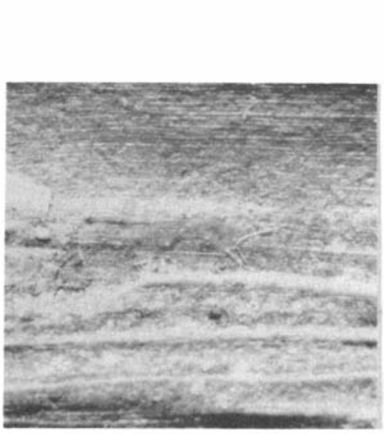

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Plate 1


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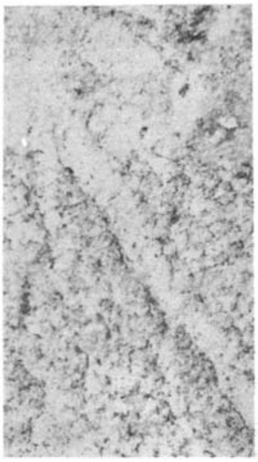
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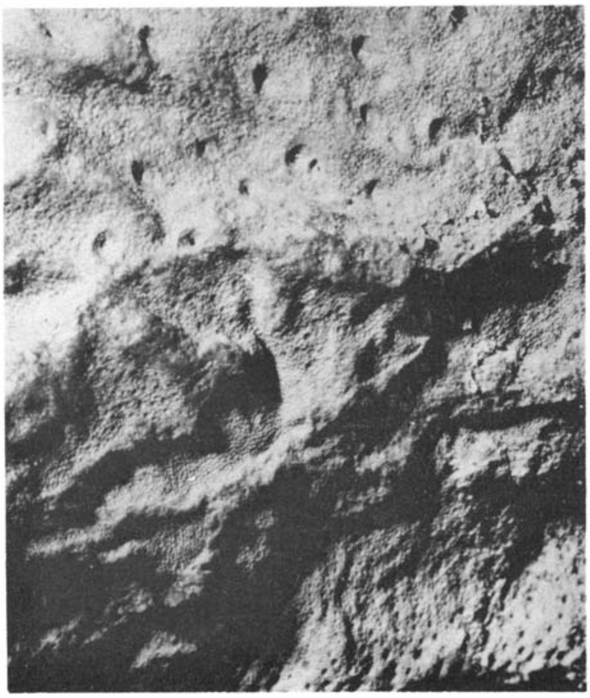
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Plate 2

The trail of a large Silurian eurypterid

NILS-MARTIN HANKEN and LEIF STØRMER

Hanken, N.-M. & Størmer, L. 1975 07 15: The trail of a large Silurian eurypterid. *Fossils and Strata*, No. 4, pp. 255–270, Pl. 1–3. Oslo. ISSN 0300-9491. ISBN 82-00-04963-9.

The Upper Silurian red beds of Ringerike, Norway, have yielded a well preserved trail which probably belongs to the large eurypterid *Mixopterus kiaeri*, known from equivalent beds in the same area. Life-size models both of the eurypterid and of its trail have been prepared in order to study the functions of the appendages, particularly in relation to the animal's gait.

N.-M. Hanken and L. Størmer, Institutt for Geologi, Postboks 1047, Blindern, Oslo 3, Norway, 1st October 1973.

In the following discussion the term track is limited to a single imprint of one appendage, while the term trail is used for a sequence of tracks formed by one individual (comp. Caster 1938). Arthropod trails occur occasionally in fine-grained, usually argillaceous sand- and siltstones. Only in a very few cases, however, has it been possible to determine the animal that made the impressions in the sediment. Trails which are supposed to have been formed by merostomes have occasionally been referred to as *"Merostomichnites"* (Fig. 2).

The trail described in the present paper was found by Hanken and Dr. J. Miller in 1971. It is unique in the sense that it may, with considerable certainty, be assigned to one particular eurypterid species, *Mixopterus kiaeri* Størmer.

In order to be able to study in detail the relations between the eurypterid and its trail as well as the general mode of life of the animal, a life-size model has been made (Pl. 2:7, Pl. 3:1–3). The rather complicated model was prepared by Hanken in collaboration with Dr. Størmer, and valuable technical assistance was rendered by Mr. A. Jensen.

The morphology of *Mixopterus kiaeri* is not known in detail. In assessing the structures and positions of the various appendages, it has therefore been useful to consider the corresponding structures in the genera *Lanarkopterus* and *Carcinosoma* which belong to the same superfamily Mixopteroidea.

The model is based on the holotype of *M. kiaeri* (H. 2044 of *Univ. Paleont. Museum*, Oslo, coll.). This specimen, however, is evidently somewhat larger than the one that made the trail. When making a reconstruction of the trail it therefore had to be slightly enlarged to fit the model. The reconstructed trail can be seen on Pl. 3:1. In the model we have chosen to illustrate the tail in the raised position not straight, and the anterior appendages (II-III) somewhat convergent.

The interpretation of the track structures, and their relation to a life-size model of *Mixopterus kiaeri* on its trail, has been discussed with several paleontologists. We wish in particular to express our thanks to Professor A. Heintz, Oslo, Cand. Real. B. Christiansen, Oslo, and Dr. J. Miller, Edinburgh, for valuable advice. Thanks are also due to Dr. W. Struve who kindly showed Dr. Størmer a trail described by Richter (1954) which shows certain features in common with the present one. We are also indebted to Mr. Aage Jensen, Paleontological Museum, Oslo, for valuable assistance in making the model, and to Mrs. Kari Ruud Öztürk and Mr. O. Brynildsrud, for making the drawings and photographs respectively. Dr. D. Worsley has kindly corrected the manuscript.

GEOLOGICAL SETTING

The Silurian of Ringerike, about 30 km NW of Oslo, is well exposed in the western flank of a broad syncline (Fig. 1). In his comprehensive and important paper *Das Obersilur im Kristianiagebiete* Kiær (1908) describes in detail the main Silurian section which he divided into stages 6–9, corresponding largely to the Llandoverian (6–7) and the Wenlockian (8–9). The marine sequence is succeeded by red beds, the Ringerike Sandstone Formation (assigned to stage 10) which Kiær assumed to be of Devonian age. However, with our present knowledge of the red bed faunas, the age of these continental deposits is more likely to be Ludlovian, with the basal

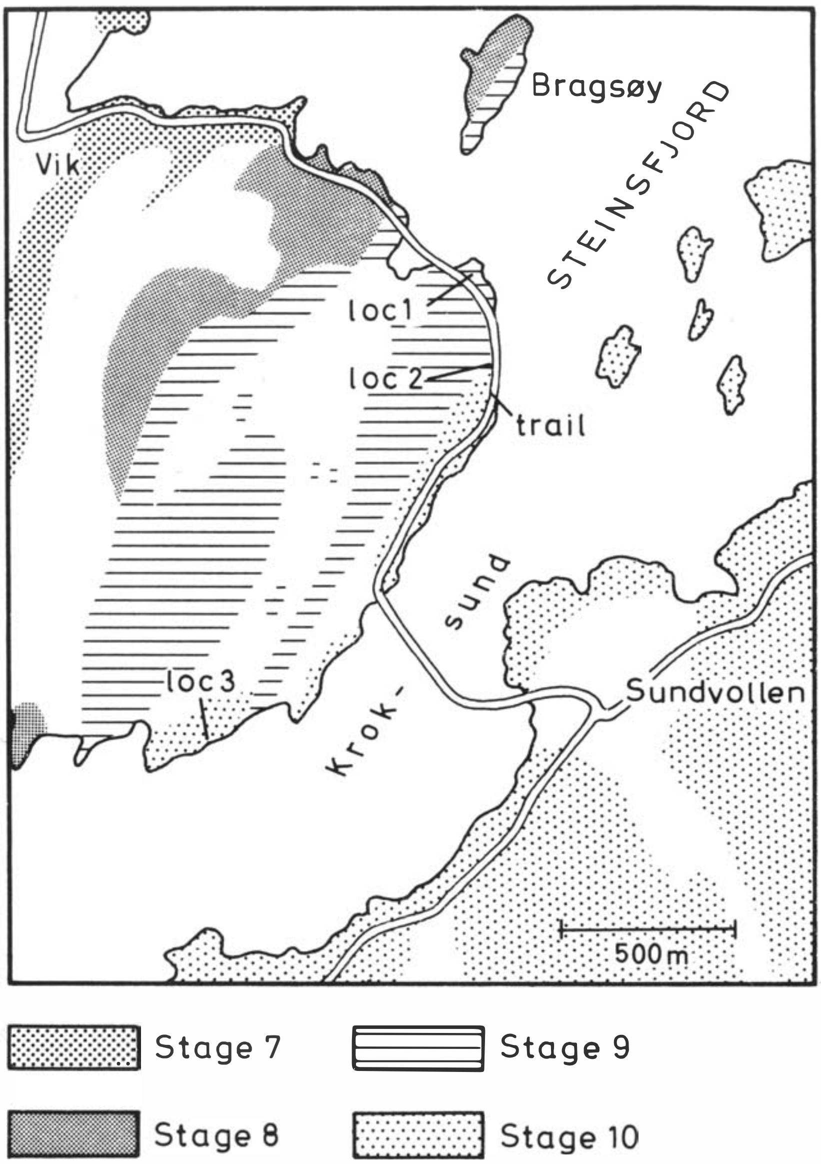

Fig. 1. Eurypterid localities at Kroksund, Ringerike showing the distribution of the Llandoverian (stage 7), Wenlockian (stage 8 and most of stage 9), Ludlovian (upper part of stage 9 and stage 10). Loc. 1 = Northern Nes, loc. 2 = Southern Nes, and loc. 3 = Rudstangen. The occurrence of the trail is marked just south of loc. 2 (modified after Kiær 1908 and Heintz 1969).

part being of late Wenlockian age. The uppermost marine beds (9g of Kiær), which are well exposed by the main road (E 68) along the shore of Kroksund, have a meager fauna of ostracodes, brachiopods, and bryozoans. Isolated bryozoans persist 1—2 m up into the overlying red beds.

Eurypterids have been found in the marine sequence, but they are most common in the continental deposits. Three different merostome faunas can be distinguished at three separate localities (Fig. 1).

LOCALITY 1. — At Northern Nes intermittent dark mudstones in shales and limestones of 9d contain the eurypterids *Baltoeurypterus tetragonophthalmus ("Eurypterus fischeri"), B.? latus,* and a small specimen of *Mixopterus* sp. (Størmer 1933, 1938), together with the alga *Chaetocladus capillatus* (Høeg & Kiær 1926).

LOCALITY 2. — A little further south by the main Kroksund-Vik road, another eurypterid locality was discovered in 1953 by Dr. R. Denison, Chicago. The following eurypterids have been preliminarily identified in dark grey shales: *Baltoeurypterus tetragonophthalmus, Nanahughmilleria* sp., *Pterygotus* sp., and fragments of large specimens of *Mixopterus* sp. (Størmer 1954). Ostracoderms occur in the more arenaceous beds; both these and the eurypterids are closely related to the K_1 —K_2 faunas of Estonia (Heintz 1969). The succeeding lower part of the red beds contains numerous animal trails in addition to mud cracks and ripple marks. Although these tracks are mostly diffuse and difficult to determine, the large well preserved trail described

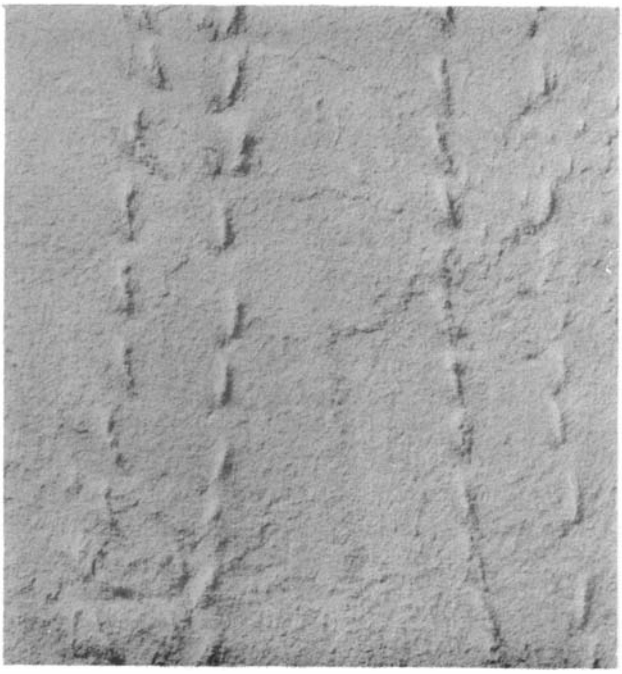

Fig. 2. Merostomichnites sp. trail. From Rudstangen. J. Kiær coll. x2.

below, was found by Hanken and Miller 10 m above the base of the red beds. Several diffuse trails at the same level might be of the same kind. Another large trail, not yet described, had previously been found a little farther up in the section.

LOCALITY 3. – This famous locality was discovered by Kiær (1911) at Rudstangen. The fossiliferous horizons belong to the lowermost part of the red beds, although the precise stratigraphic position is not certain. The fauna contains ostracoderms (Kiær 1924, Heintz 1939), crustaceans (Størmer 1935), and merostomes (Størmer 1934). The eurypterids are *Nanahughmilleria norvegica* (common), *Pterygotus holmi, Brachyopterella pentagonalis, Stylonurella ruedemanni, Stylonuroides dolichopteroides* and *Mixopterus kiaeri.* The xiphosurans are *Bunodes* sp. and *Kiaeria limuloides. Pterygotus, Mixopterus* and *Kiaeria* are the only large forms which occur in this fauna. Numerous trails of *Merostomichnites* type occur immediately below and above the fossiliferous beds at Rudstangen (Fig. 2).

Comparison with other faunas (Kjellesvig-Waering 1961) suggests that the lower eurypterid fauna (loc. 1) with *Baltoeurypterus* might have been largely marine while the uppermost one with *Nanahughmilleria* (loc. 3) belonged to a more brackish water environment. The middle fauna (loc. 2) which contains both species probably lived in a transitional environment. The large *Mixopterus* specimens probably belonging to *M. kiaeri* occur in the two upper faunas.

The Rudstangen fauna was primarily regarded as Downtonian (Størmer 1934). The occurrence of eurypterids identical with, or at least closely related to *Nanahughmilleria norvegica,* in the presumed Lower Downtonian beds of Stonehaven, Scotland, was one of the main reasons for this age determination. The Lower Downtonian age of the Stonehaven beds is based on its vertebrate fauna (Westoll 1951: 6,26 and Cocks et. al. 1971:118). The occurrence of *Baltoeurypterus* together with *Nanahughmilleria* and ostracoderms similar to those in K_1 (Kaarema formation) of Estonia (Størmer 1938 and Heintz 1969:24–25) indicate, however, that the eurypterid faunas belong to the Ludlovian and possibly appeared already in the Wenlockian. Recent studies by Basset & Rickards (1971) and Bockelie (1973:321) suggest that the whole of stage 9 is of Wenlockian age. The probable occurrence of *Nanahughmilleria norvegica* in the Stonehaven beds may suggest that also these deposits may be older than the Downtonian, possibly Lower Ludlovian as the Rudstangen fossils.

DESCRIPTION OF THE TRAIL

The trail occurs in a red, argillaceous siltstone. The preserved part of the trail (Pls. 1,2:1-4, Figs. 3–4) is 520 mm long and the width varies from 160 mm – 170 mm. The trail has three pairs of tracks on either side of a broad median groove. For the sake of identification the paired impressions are designated A, B, C, and numbered from 1 to 12. The A, B, C tracks on the left side have odd numbers and the C, B, A tracks on the right side have even numbers. Each number refers to one transverse band or axis, e.g. C_8, B_8, and A_8.

The median groove is called the m-track. Other tracks which may not belong to the main trail are named the X-, Y-, O_1-, O_2-, O_3- and n-tracks.

THE A-TRACKS. – (Pl. 1,2:1,2, Figs. 3, 4). These tracks are the largest and most significant. They form the straight lateral border of the trail. A_6 and A_8 are the best preserved impressions (Pl. 2:2, Fig. 4). The tracks are hook-shaped with a convex, longitudinally directed steep lateral wall. Posteriorly the wall changes its direction from longitudinal to transverse and even slightly anteromedian. The outer wall of the main furrow becomes steeper posteriorly so that its transverse part is vertical. The inner wall of the longitudinal part of the track is rather steep near its bottom but flattens out upwards.

These A-tracks are characterised by distinct *mounds* or elevations behind the median portions of the transverse parts of the main furrows (Pl. 2:2, Fig. 4). Each mound forms a median continuation of a transverse flat ridge or inflated surface behind the transverse furrow. The inflated surface has a steep anterior and a very moderate posterior slope.

In addition to the main furrow and mound, well preserved A-tracks and their surroundings show numerous *accessory grooves and ridges* (these structures are well demonstrated in A_6, A_8, and A_{10} (Pl. 2:2, Fig. 4). Concentric grooves and ridges occur around the posterior side of the mound, and are evidently wrinkles formed by the compaction of the mounds. In A_8 the concentric wrinkles are crossed by three radial grooves. Since these radial grooves distinctly cross the concentric ridges the former must be younger. Posteriorly the three grooves diverge slightly and fade out. Similar grooves, but more faint and close set, are present or indicated in A_6 and A_{10}. However in these cases there are two set of grooves, one more lateral than the other. In addition

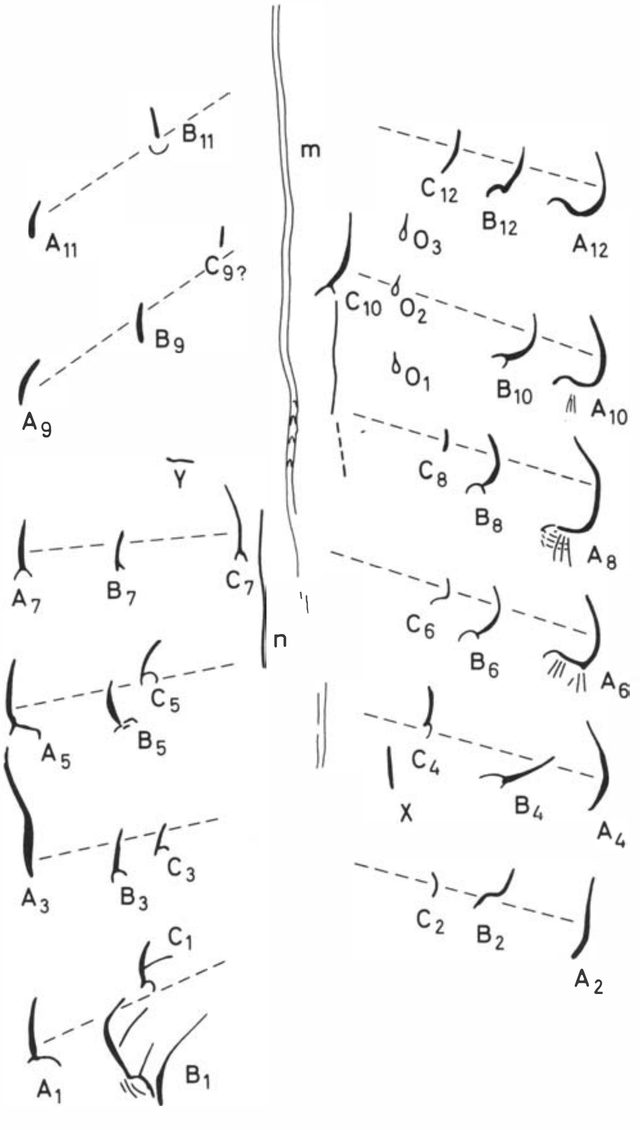

Fig. 3. Trail with designations. Stippled lines indicate bands of three tracks. x0,5.

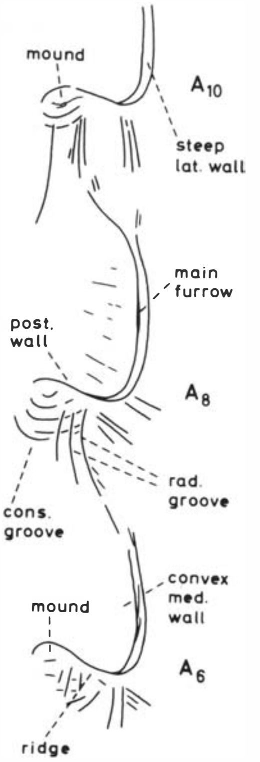

Fig. 4. Details of A-tracks on the right side of the trail. x1.2.

occur more diagonal grooves directed towards the bend of the main furrow. Very faint parallel grooves are suggested on the smooth area inside the main furrow of A_8.

In some cases, e.g. in A_4, A_6, and A_8 the main furrow continues almost to the furrow in front. From being longitudinal the furrow attains an anteromedian direction towards the mound in front.

THE B-TRACKS (Pls. 1,2:1). – The imprints are with a few exceptions smaller than the A-tracks. The B-tracks have a sigmoid shape, the transverse continuation of the main furrow is practically missing. The generally convex longitudinal furrow abuts posteriorly to a mound similar to that of the A-track but without a lateral flat ridge. The mound is demonstrated in B_1, B_3 –B_6 and B_8 –B_{10}. In B_1 concentric grooves and ridges are also indicated on the mound (Pl. 2:1, Fig. 3).

Unlike the corresponding furrow in the A-track the B-track furrows are almost symmetrical in cross section, this is well seen in B_1, B_3 and B_5. B_2 and B_4 differ from the rest of the B-tracks in that the direction of the curved furrow is nearly transverse, indicating a twisting of the distal portion of the appendage.

B_1 (Pl. 2:1) is bigger than the other B-tracks, its length equalling that of the A-tracks. Unique for this B-track is the presence of four slightly curved grooves running posterolaterally to the track which they reach at about a right angle. The concave side of the grooves faces posteromedially. The posterior groove abuts the mound and extends for a short distance. The other grooves meet the furrow in the middle and at both ends.

THE C-TRACKS. – These tracks (Pl. 1, Fig. 3) are smaller than the others, C_1 and C_3 to C_5 are fairly well preserved. Particularly C_5 shows the convex to sigmoidal furrow with the mound at the posterior end. It has an anteromedian position in relation to B_5. As in the B-tracks the furrow has equally sloping sides. The position and direction of the C-tracks varies to some extent. In C_7 and C_{10} which have an unusual median position the main furrow is prolonged into a faint groove. In the first case the groove extends forward from the furrow, in the second case it leads into the furrow from behind. In C_{10} only the posterior half of this groove seems to be real, the anterior part resembles other "lines" which occur several places, and evidently represent borders between slightly different levels of the rock. The mound of C_{10} is cut off. C_1 is placed in front of the corresponding B-track (Pl. 2:1), and this track also has a concave groove leading into the main furrow.

Although the A, B, C-tracks are arranged in transverse bands slightly converging forwards, a considerable variation of this pattern exists (Fig. 3). The A_1, B_1, C_1 tracks form a triangle rather than a line. In this case, however, the walking legs were kept in an oblique position so that the lateral spines touched the ground. Smaller deviations are found in A_5, B_5, C_5. Differences are also seen in the position of the B- and C-tracks in relation to the median line. C_7 and C_{10} have a marked median position; the longitudinal furrow forming a continuation of these tracks probably results from a vertical position of the legs so that the tip of the appendage was apt to touch the ground even when it normally should be lifted up. The direction of the main furrow of all the tracks is usually longitudinal, but more transverse furrows are seen in B_2, B_4, and B_{10}. The bands of the A-, B-, C-tracks (stippled lines in Fig. 3) alternate on opposite sides. If C_9 and B_{11} belong to A_9 and A_{11} bands respectively, the direction of these bands deviate from the other bands. Since the direction of the m-tracks is fairly constant the change in direction of the bands can hardly indicate a turn of the trail.

THE X- AND Y-TRACKS (Pl. 1, Fig. 3). – These additional tracks situated near C_4 and C_7 do not seem to have any direct relation to the other tracks. The X-track is straight with a longitudinal direction while the other is straight and transverse. Both lack the mound behind.

THE O_1 – O_3 - TRACKS (fig. 3). – These small tracks occurring between C_8 and C_{12} evidently belong to one side of a trail of a small arthropod walking along the same trail. The longitudinal furrows have a distinct mound at one end.

THE m-TRACK (Pl. 1,2:3,4). – The median groove forming this track occurs mainly in the anterior half of the trail. The distance from the groove to the lateral margins of the trail varies from 80–88 mm to the right border and 74–84 mm to the left border. A slight undulation is expressed in the course of the groove. In plan the suggested saddles and lobes succeed each other with a wave-length which largely equals the distance between the transverse ABC bands. The groove or furrow has a fairly constant width of 2 mm. The sides of the shallow groove are relatively steep while the bottom is slightly concave. Of interest are indications of parabolic impressions along the bottom of the groove (Pl. 2:3,4).

THE n-TRACK (Pl. 1, Fig. 3). – This faint longitudinal groove possibly belongs to the track, in which case it might have been formed by a lateral spine of a walking leg.

PRELIMINARY INTERPRETATION OF STRUCTURES

Before we try to identify the arthropod that made the trail it is necessary to interpret the structures which made it. Judging from the good preservation of some parts of the trail it is obvious that each type of track was made by a specific appendage. This implies that the three pairs of tracks were made by three pairs of appendages, presumably legs.

The A-tracks have a deep longitudinal furrow with a steep lateral wall and a median wall that flattens out in the upper part. This indicates that the distal portion of the appendage which made this imprint was broad and flat. The hook-shaped track, of which the transverse portion is a wall abutting a flat area rather than a distal wall of a furrow, probably indicates that the flat appendage had a rounded distal outline. These features show that *the appendage was broad and flattened and had a rounded distal outline, and that these features fit well a paddle-like appendage, which could have been a swimming leg.*

The B- and C-tracks resemble the A-track but are not hook-shaped, and the inner wall of the furrow does not flatten out to the same degree. This indicates that the appendage making the tracks was pointed, perhaps a broad, somewhat flat spine. Imprints of lateral spines occur in one band (B_1, C_1). The structures show that the *appendages which made the B- and C-tracks could have been walking legs with one distal and at least one pair of lateral spines.*

The median m-track might have been formed by a tail-spine of the metasoma, but since the track is relatively broad and shallow, it is unlikely to have been produced by a pointed tail or spine. The track must have been made by a blunt fairly long appendage which occasionally reached the ground. Its median position and shape would seem to indicate an appendage or structure protruding from the underside of the animal, which could be a genital appendage.

WHAT KIND OF ANIMAL MADE THE TRAIL?

When we try to identify the animal which made this trail the following conditions have to be fulfilled: (1) Only three pairs of legs took part in the gait of the arthropod, the last pair being of the swimming leg type, the others of the spiniferous walking leg type. (2) A long genital appendage was present.

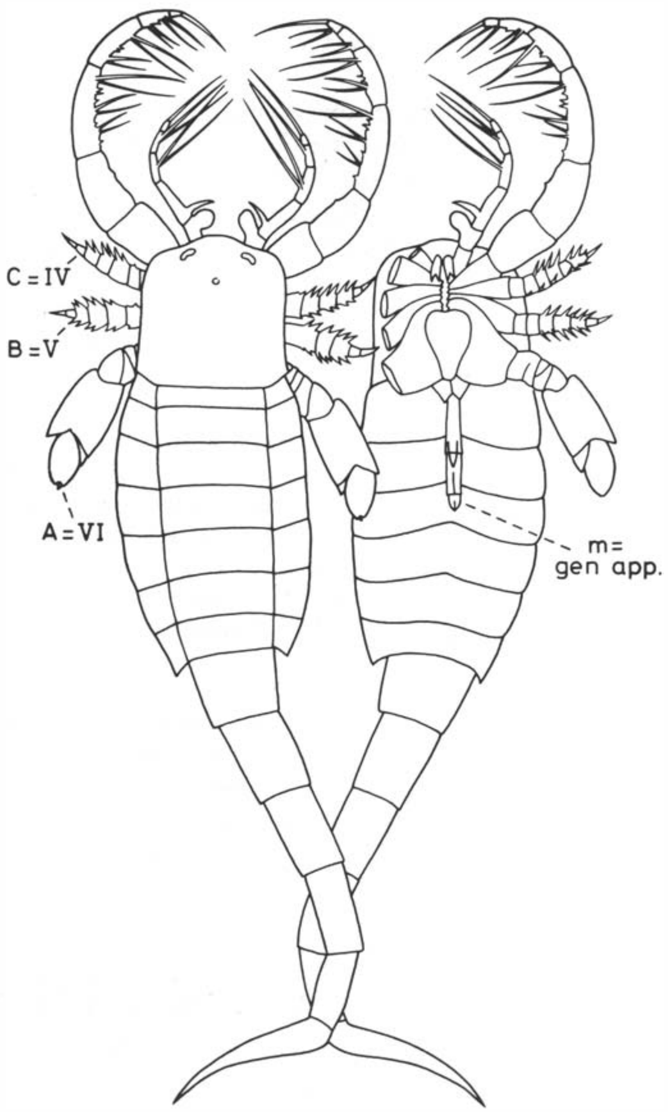

***Fig.** 5. Mixopterus kiaeri* Størmer. Reconstruction of dorsal and ventral surface. A, B, C, m refer to track. About x0.2.

Swimming legs constituting the last prosomal limbs (VI) occur in eurypterids, and have as an exception been described in a xiphosuran (Størmer 1972). However, a long median appendage is unknown in members of the latter group, which also have more than three pairs of walking legs taking part in the gait (Caster 1938). It is therefore very probable that *the trail was made by a large eurypterid.*

As mentioned above (p. 257) the large eurypterids present in the same beds are *Pterygotus holmi* and *Mixopterus kiaeri. Pterygotus* with its slender spineless walking legs and short genital appendage could not have produced the present track. *Mixopterus* on the other hand corresponds very well with the form we are looking for. This eurypterid (Fig. 5, Størmer 1934, Fig. 13, 14) is of the right size, the two first pairs of legs (II, III) are highly specialized and are not used for walking. The two succeeding pairs (IV—V) are typical spiniferous walking legs, and the last legs (VI) form a pair of characteristic swimming legs. *Mixopterus* also has a long ventro-medially placed genital appendage of Type A (regarded by Størmer & Kjellesvig-Waering, 1969, as belonging to a male). The terminal joint is not preserved in Norwegian specimens but since the related *Lanarkopterus* (Ritchie 1968) has a blunt termination this might also have been the case in *Mixopterus.* Even if a bifurcate termination should be found in fossil specimens of *Mixopterus* the two spines might have been held close together when the animal was alive.

The great morphological correspondence, as well as the common occurrence, makes it very probable that the present trail was made by the eurypterid Mixopterus kiaeri Størmer.

MODE OF FORMATION AND PREDIAGENETIC PRESERVATION OF TRAIL

In a study of Upper Carboniferous limulid tracks in North Cornwall, Goldring & Seilacher (1971:434), assume that "Optimal conditions for the preservation of the tracks occurred when silt and clay sediment was deposited from low velocity currents, sufficient to maintain adequate oxygenation of the bottom waters but insufficient to extensively scour the substrate". Limulid trails are regarded as being formed in an offshore environment preferably a brackish or freshwater lagoon.

The *Mixopterus*-trail is preserved in a red argillaceous silt which presumably was deposited in a well oxygenated environment. Desiccation polygons in the beds immediately above and below those containing the trail suggest shallow water and emergence. The trail therefore was probably formed in the intertidal zone (if the environment was marine or estuarine) or the trail may have been formed on or near the shore of a lake. In the present trail the mounds formed by the push of the paddles have concentric wrinkles on their surface. Such compaction wrinkles could hardly have been formed and preserved in a soft mud. The wrinkles show that the thin layer of mud on the top of the silt was very cohesive and preserved the tracks in full relief.

A dragging of the genital appendage along the bottom is hardly present in aquatic invertebrates, and this indicates that the body was weighed upon, and that additional weight could have been due to the specimen of *Mixopterus kiaeri* being either partly emerged or above the water when it made the trail. In these cases the tail was probably held in a raised position to keep the balance as mentioned below.

Some of the individual tracks, particularly the A-tracks, are deep and well preserved. A_6, A_8, and A_{10} on the right side are hook-shaped while A_9 and A_{11} on the left side are only slightly convex and lack the transverse portion forming the rear wall. The reason for this is probably that the latter are *undertracks* (Goldring & Seilacher 1971). Other undertracks may be seen in B_9 and B_{11}, and the B- and C-tracks on the right side of the trail where the sediment has obviously been removed.

THE MOVEMENT OF THE THREE PAIRS OF LEGS IN *MIXOPTERUS*

The mound or terminal elevation of the end of each track-furrow is the result of a push and compaction of the silt by one of the legs. Usually the mounds are formed at the rear end of the tracks (Fig. 6D), but, in certain cases they may also be formed in front (Fig. 6B). The latter case may occur either when the leg is thrust forward into the sediment, or when the leg is withdrawn from the track furrow as demonstrated by Goldring & Seilacher in *Limulus* (1971:426).

When we began the studies of the trail we were inclined to believe that the mounds were formed in front of the tracks. The main reason for this assumption is the presence of three radial furrows crossing the concentric wrinkles on the mound A_8 (Pl. 2:2, Fig. 4). The furrows were thought to have been made by the three-pointed tip of the swimming leg dragged over the mound. However, this explanation would imply very complicated and improbable movements of the swimming leg, and the radial furrows which occur at one track only might be explained merely as tension grooves or wrinkles formed on the skin of a moist surface (comp. accessory grooves and ridges in A_6 and A_{10} in Fig. 4).

However, further studies of the trail and movements of the swimming leg indicate that the

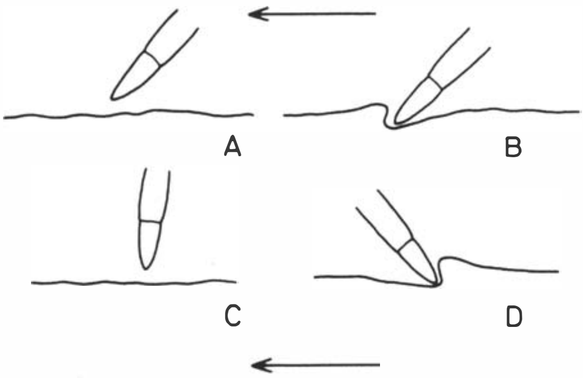

Fig. 6. The direction of movement in relation to the mound formed in front or behind the track.

mounds or terminal elevations were formed at the rear end of the track. This conforms with Caster's (1938) studies of Paleozoic and Recent Xiphosura. Similar mounds are indicated in the Lower Cambrian *Diplichnites* and the Upper Devonian *Kouphichnium* (Häntzchel 1962, Figs. 121:1, 124:2). The same is the case with the Lower Devonian *Palmichnium* discussed below (Figs. 11B, 12B).

The presumed movements of the swimming leg are demonstrated in Fig. 7. In the first phase (1) the swimming leg touched the ground in a nearly transverse position with the proximal portion of the leg practically horizontal, while the distal portion comprising the paddle was inclined to face laterally. The distal portion of the paddle made the deep lateral furrow, and it was in this position that the forward push started. The push continued into the next phase (2) in which the appendage, due to the forward movement of the body, became more outstretched and the paddle less inclined. The paddle produced a push backwards and formed the posterior wall and the mound and ridge behind. A transverse furrow would not be formed by the moderately inclined paddle. In the third phase (3) the appendage is fully extended. The previous inclination evidently took place at the "knee" formed by the tibia (this specialized joint is well demonstrated in *Carcinosoma,* Clarke & Ruedemann 1912, Figs. 57, 58). In the last phase (4) the posterolaterally extended leg is lifted slightly from the ground and carried forward to attain the original nearly transverse position in the first phase. In Fig. 7 the distances and corresponding time intervals between the succeeding phases are assumed to be equal, but we do not know the actual length of the time intervals. The duration of the protraction and retraction (time off and on the ground) is unknown. The forward continuations of some of the A-tracks (A_4, A_6, A_8) might indicate that the swimming legs were not lifted much above the ground,

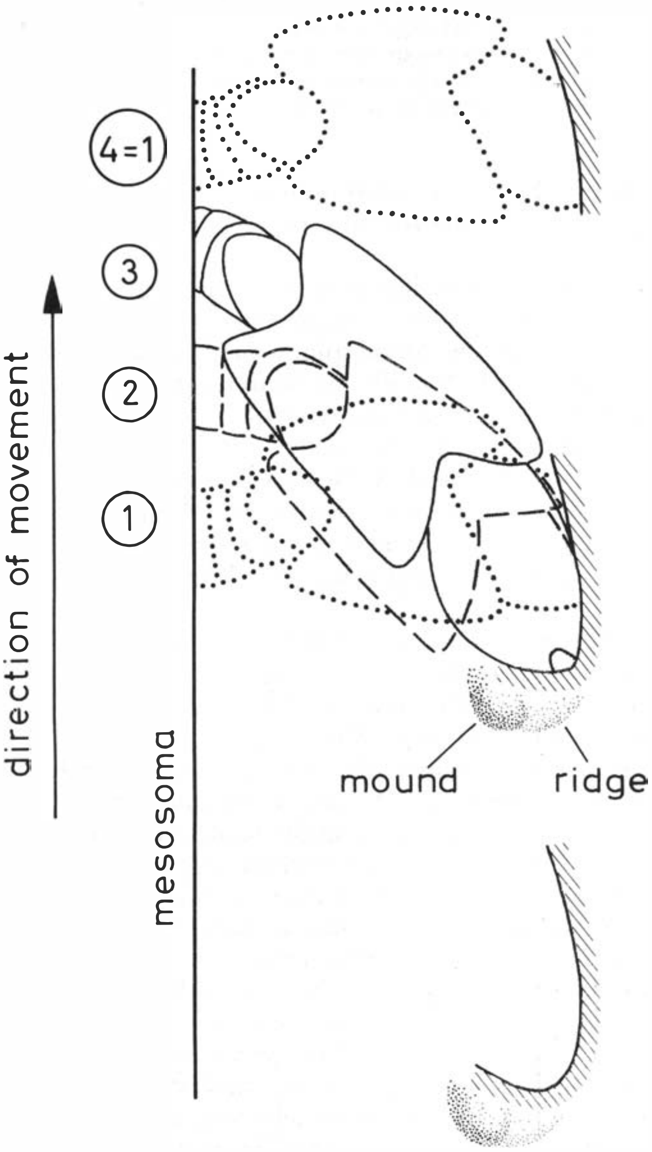

Fig. 7. Four phases in the movement of the swimming leg (VI). The second phase is shaded in order to distinguish this leg from that of the first and third phase.

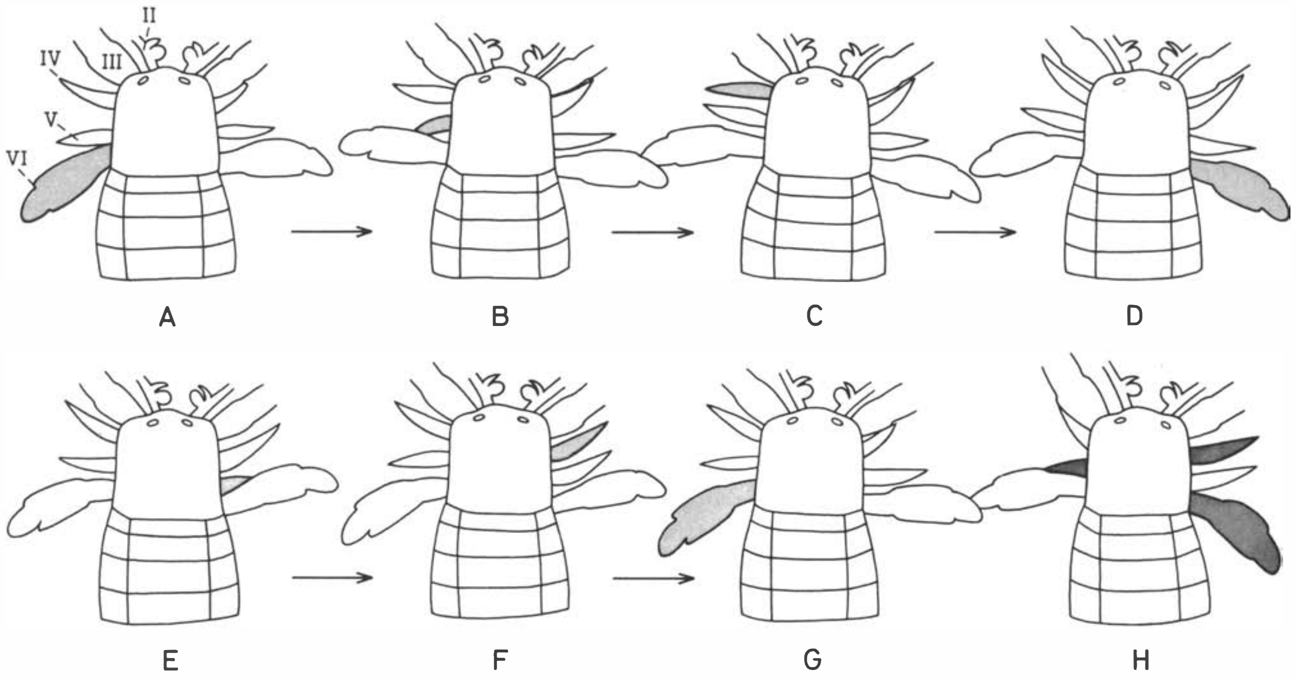

Fig. 8A-G. Probable slow gait of *Mixopterus kiaeri* when making the present trail. The seven phases illustrate one cycle of movements of the left swimming leg. The foot leaving the ground within one phase is shaded, those not shaded rest on the ground. The lifting of the swimming leg (VI) is succeeded by the next leg in front (V), and then the first walking leg (IV) is lifted. The limbs are drawn in an outstretched position. Particularly the two walking legs had a more vertical position during the gait. Fig. 8H suggests a more rapid gait when the animal was fully emerged. In this case, like in most insects, three legs (shaded) rested on the ground at the same time (two on one side and one on the other alternatively). In other cases the swimming legs might have been kept as flappers above the ground, and only two pairs of legs were engaged in the walking.

and that the time of protraction was correspondingly short. This interpretation of the structures presents a simple and apparently reasonable explanation for the features displayed in the fossil trail.

The two walking legs (IV and V) made the B- and C-tracks. The first leg seems to be slightly bigger than the second. Both had normally a more vertical position than the swimming leg. In a few cases the legs had a more outstretched position so that the lateral spines touched the ground and produced the impression demonstrated in B_1 and C_1 (Pl. 2:1, Fig. 3). With regard to the walking legs the strongest weight must have been placed on the second walking leg which therefore should have made the deepest and biggest impression, i.e. the B-track.

The median furrow or m-track, which we interpret as caused by the dragging along the ground of the genital appendage, indicates an undulation with a wave-length corresponding to the distances between succeeding A-tracks. The undulation of the median track evidently has something to do with the gait of the animal, and may suggest a slight swinging of the body during locomotion.

In order to interpret the movements of the three pairs of legs in *Mixopterus* it might be useful to consider the mode of movement in the Hexapoda which have the same number of walking legs. As pointed out by Hughes (1952), Chapman (1969), Manton (1972) and others, a hexapod always has at least 3 legs on the ground at the same time. These legs are arranged as a tripod around the point of gravity of the insect. Each leg alternates with the contralateral leg of the same body segment (except in swimming and jumping). The pattern of gait and the number of legs touching the ground simultaneously depend, however, on the relative duration both of protraction (the time when the legs are above the ground), and of retraction (the time when the legs are placed on the ground). When the ratio is 1:1 the gait pattern is the simple one where one leg on one side and two legs on the other are in protraction and retraction alternatively. Changes in this pattern occur when the speed changes. At a slow gait five legs might touch the ground at the same time. From what it said above there are reasons to believe that the speed was low when the trail was made. The pattern of the slow gait of an insect demonstrated by Champman (1969, Fig. 79) has been used in preparing an illustration of the probable gait of *Mixopterus kiaeri* when it made its trail (Fig. 8A–G). This pattern of gait was hardly typical of this eurypterid walking on the sea bottom. At normal speed the pattern might have been the simple one, two to one on either side, as mentioned above for most insects (Fig. 8H). It is probable, however, that in certain cases the swimming legs were held as balancing or swimming flappers above the ground, and did not make any tracks in the sediment.

MODE OF LIFE OF *MIXOPTERUS*

In the water the eurypterid was able to swim, and to walk on the bottom. It was hardly a good swimmer and kept near the bottom. It is not likely that it swam on its back like the Xiphosura or the more stream-lined eurypterids (Størmer 1934:62). During swimming the prosomal legs (IV–V) were probably directed backwards, producing smaller lateral strokes (Fig. 9A) while the

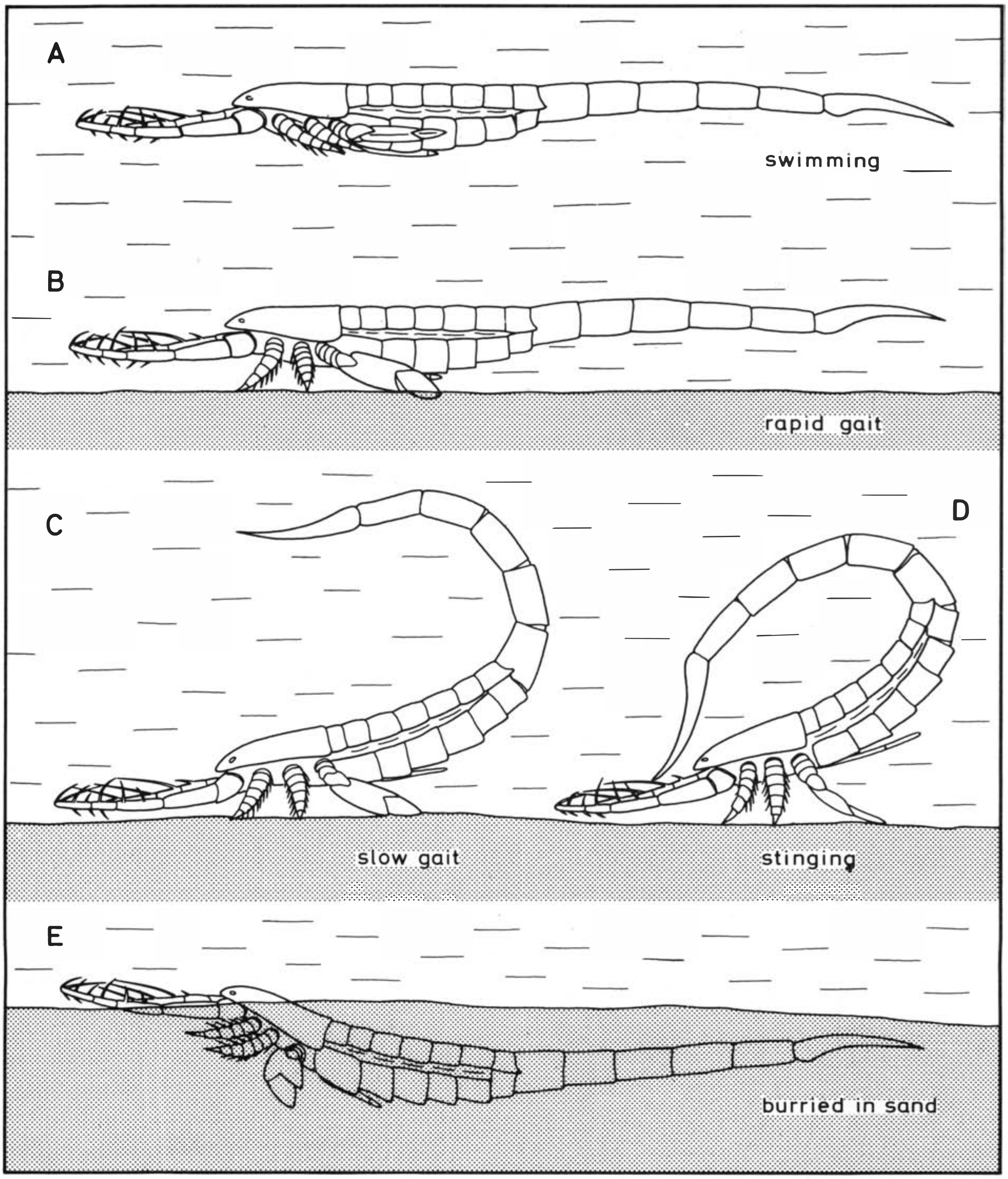

Fig. 9. Body-positions of *Mixopterus*, lateral view. A. During swimming the opisthosoma was probably extended, and the prosomal appendages directed mainly backwards and sidewards. The postlaterally directed paddle was moved slightly up and down. B. The body was probably also extended when the eurypterid walked rather fast on the bottom. C. The raised opisthosoma would give a better balance, especially if the body was partly or completely out of the water. D. The stinging of the prey was probably accomplished as in recent scorpions. E. In looking for prey, *Mixopterus kiaeri* might have been buried in the sand, except for the "cage" formed by the anterior appendages (II, III), and the anterior portion of the prosoma.

swimming legs were used as flaps moving in a vertical plane. A forward propulsion by rapid strokes of the ventral plates (Størmer 1934:62) might have been possible but was hardly characteristic of this form.

When walking on the bottom the common insect method was probably frequently used (Fig. 9B). The long outstretched abdomen would be largely counterbalanced by the two heavy specialized frontal appendages (II, III) which were kept above the bottom. *Mixopterus kiaeri* was evidently able to raise its tail (Fig. 9C, Pl. 2:7 and Pl. 3:1–3). The outspread appendages provided a good foothold and stable base for the body. While walking on land, the raised tail

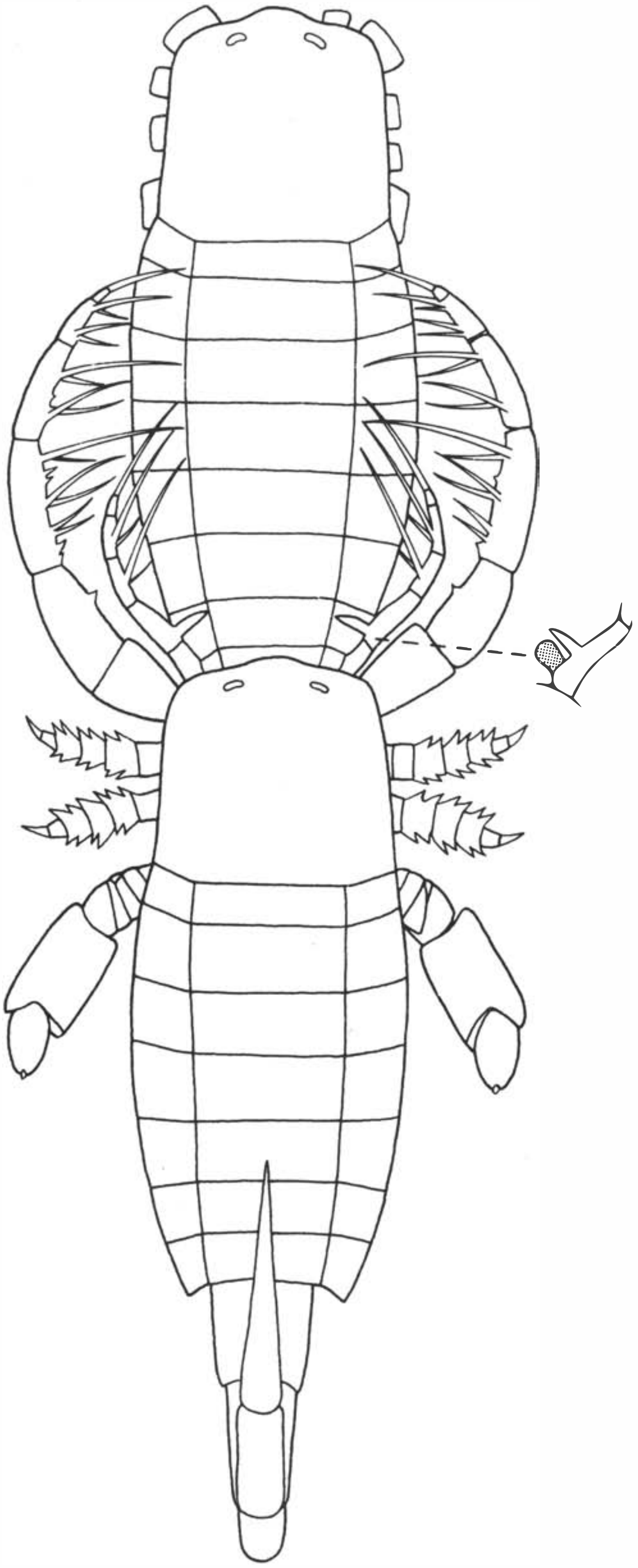

Fig. 10. Possible position of female and male of *Mixopterus kiaeri* during mating. A part of the clasping organ is shown to the right. Also in this fig. the legs are drawn in an outstretched position.

would facilitate the balance of the body. In the water when the weight of the body was small, this was less important. An overhead thrust and push of the tail would enable the telson spine to sting prey held between the front legs (Fig. 9D). Whether the spine was poisonous or not is not known. In waiting for prey it seems reasonable to assume that *Mixopterus* buried itself in the silt or sand; the swimming legs in particular were well-fitted for digging. Only the frontal legs and frontal portion of the prosoma with the eyes were kept above the sediment (Fig. 9E). When a prey approached the outstretched frontal appendages could be clasped together forming a catching organ or cage. The stiff and flat spines (except the pretarsus) of two pairs of appendages (II, III) where not movable.

The structure of the present trail suggests that *Mixopterus* was able to walk on land. Because of the weight of this large arthropod, the locomotion above the water must have been difficult. With moist gills well concealed above the ventral plates, the respiration would present no problems.

The method of mating of *Mixopterus* might have been somewhat similar to that of the horseshoe crabs. The presumed clasping organ on appendage II consists of a flat round lobe with a scimitar-shaped flat spine behind and resembles the clasping organ in *Limulus* (Størmer & Kjellesvig-Waering 1969). The organ in the eurypterid male could attach itself to the lateral corners of the last prosomal segment (Fig. 10). At the same time the pleurae of the anterior portion of the mesosoma might have been held between the spines of the frontal appendages. The long genital appendage of the male might have been directed, on one side of the tail of the female, to the point where the eggs were placed by the female (Størmer 1973:145).

RELATED TRAILS

In trying to find related structures we have to look for trails which have three tracks arranged along a more or less transverse axis on either side of the median line.

A Permian trail described as *Paleohelcura* by Gilmore (Häntzschel 1962: Fig. 128, 4a, b) shows three tracks along alternating, anterolateral directed axes on either side of a median furrow probably made by a pointed telson.

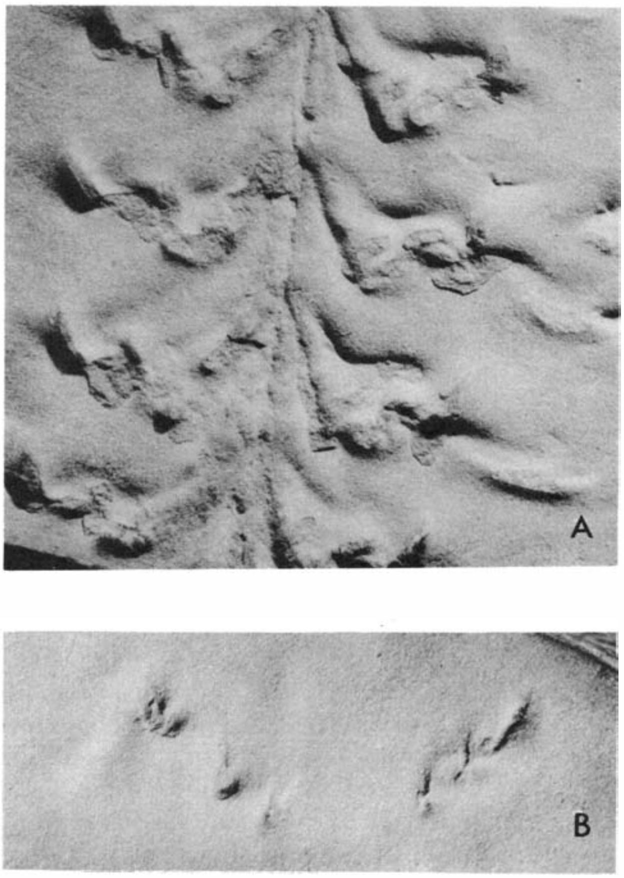

Fig. 11. Palmichnium palmatum Richter, a trail from the Lower Devonian of Germany. Above detail of trail with median impressions of coxae. Below tracks where the coxae did not touch the ground. The inner "C-tracks" on the right side shows a small mound at the end of the furrow.

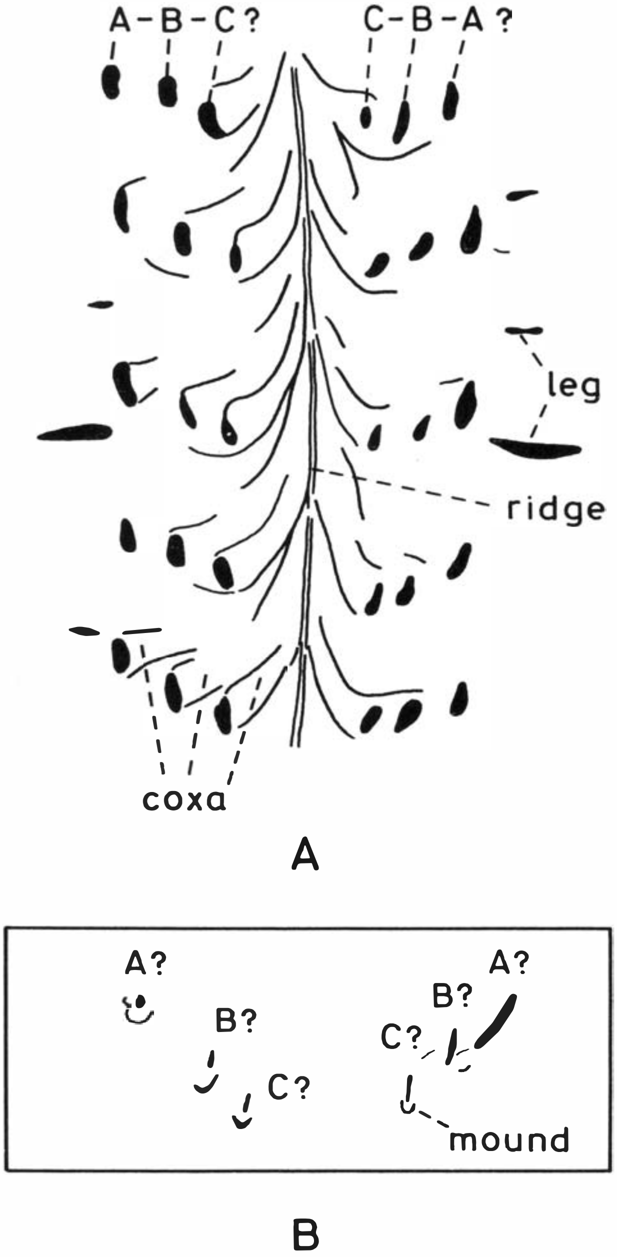

Fig. 12. The same trail. Above a partly diagrammatic drawing of the trail. Below a drawing of the other tracks in Fig. 11.

More details are demonstrated in a well preserved Lower Devonian trail from the Rhein area, Germany, described by Richter (1954). The palmbranch-like trail was said to have been about 10 m long when collected, and the distance between the "A"-tracks is 11 cm against 16 cm in our trail. The trail (Figs. 11, 12) which was named *Palmichnium palmatum,* was interpreted as the trail of an eurypterid. Instead of a median furrow the trail has a median ridge which is interpreted as representing the mud pressed up between opposing limbs.

During a visit to the Forschungsinstitut Senckenberg, Frankfurt am Main, Størmer had the opportunity to study the type specimen, and Dr. Struve very kindly made some new photographs of the trail. In addition to the main trail illustrated by Richter, there are a few single groups of tracks which lack the median lobes close to the median line (Figs. 11B, 12B). The axis of the three tracks on either side have anterolateral directions forming an angle of about 45° to the median line. In the main trail this angle varies, and may approach 90°, i.e. a transverse direction of the axis. It is interesting to notice that the pits or short furrows (Figs. 11B and 12B) have a little mound at one end just as in limulids and in *Mixopterus.* This indicates that the direction of movement of the trail was the opposite of that suggested in Richter's illustrations. The forward divergence of the track axis differs from that in *Mixopterus,* but such a difference may be found in one and the same animal, e.g. in the Thysanura (Manton 1972, Figs. 8G, H).

The three tracks on the more or less transverse axis may probably be interpreted as ABC-CBA tracks. The club-shaped median structures probably represent the imprints of the coxae. In eurypterids these wedge-shaped joints are usually transversely directed except for the two posterior coxae which have a more posterolateral orientation. The median portion of the coxal imprints have a certain resemblence to the triangular median lobes in the coxae of scorpions. However, in Lower Devonian time the lobes were not developed to such a degree (Størmer 1970). A transverse furrow lateral to the A-track (leg, Fig. 12A) may represent the lateral margin of a proximal joint of a bent anterior appendage such as the large appendage (III) in *Mixopterus.*

The difference between the simple and the more complicated tracks (Figs. 11A, B, 12A), is evidently due to the weight of the animal when it made the tracks. In the latter case the heavy body was pressed down so that also the coxae left imprints in the mud. When the main trail was made the tide may have gone out so that the arthropod had to drag itself on a wet subaerial surface. When the simple tracks were made, however, the water may still have been present. But how could the arthropod drag itself along on the surface and at the same time leave good impressions of the individual coxae? The evident reason for this is the animal lifted itself on the three pairs of legs, which were able to lift the body off the ground. In the next moment, however, the body fell down making imprints of the coxae in the mud before it again was lifted by the legs. The lack of alternation of the axis or bands of tracks on either side supports the assumption of a simultaneous lifting action of the six legs. The strong median prolongation of the coxal tracks might be due to a certain forward drag of the anterior portion of the coxae during the formation of their tracks.

A close identification of the arthropod that made this trail is hardly possible, it might have been an eurypterid, although not necessarily a member of the Mixopteroidea.

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EXPLANATIONS OF THE PLATES

Plate 1

The trail. From Silurian siltsone, 10 m above the transition from green to red sediments in the roadside (E 68) profile, Kroksund-Vik, Ringerike. A drawing of the trail is shown in Fig. 3. x3/4. Specimen belonging to the collections of the Paleontological Museum, University of Oslo (PMO 93913).

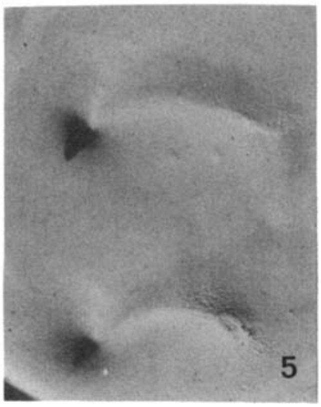
Plate 2

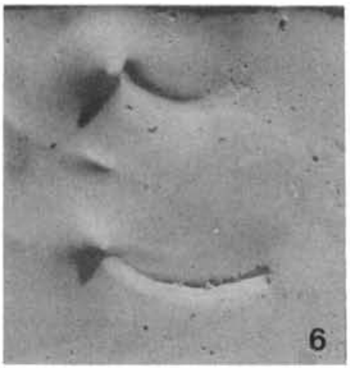
Fig. 1. Details of tracks B_1 and C_1. x1,5. *Fig. 2.* Details of tracks A_8 and A_{10}. Compare Fig. 4. x1.5. *Fig. 3.* The median groove or m-track. x1.7. *Fig. 4.* Detail of the m-track. Rounded areas at the bottom of the groove. x2. *Figs. 5-6.* Artificial tracks in plaster. The tracks were made by a blunt and flat stick pushed from right to left. A distinct mound is formed at the distal point of the furrow. *Fig. 7.* A model of *Mixopterus kiaeri* in anterodorsal view. The trail below is not well demonstrated.

Plate 3

Figs. 1-3. A model of *Mixopterus kiaeri.* x1/3. *Fig. 1.* Dorsal view of the model. The tracks formed by the appendages are indicated. *Fig. 2.* Ventral view showing the chelicerae, coxae, metastoma and the genital appendage. *Fig. 3.* Lateral view.

Plate 1





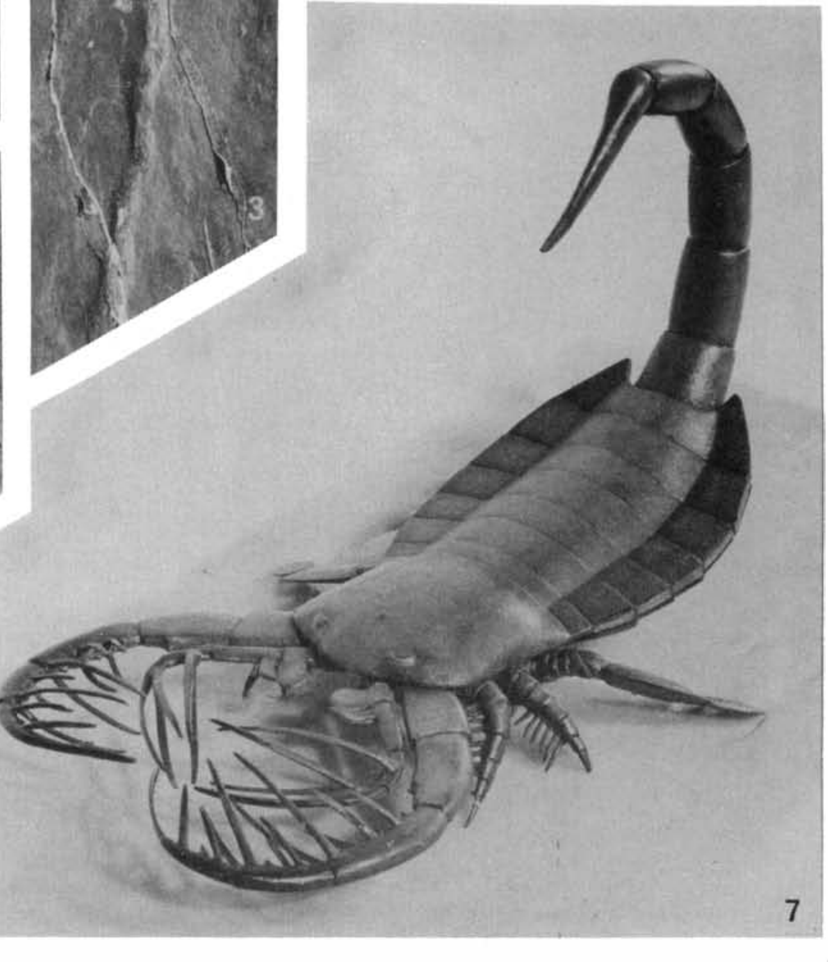


Plate 2

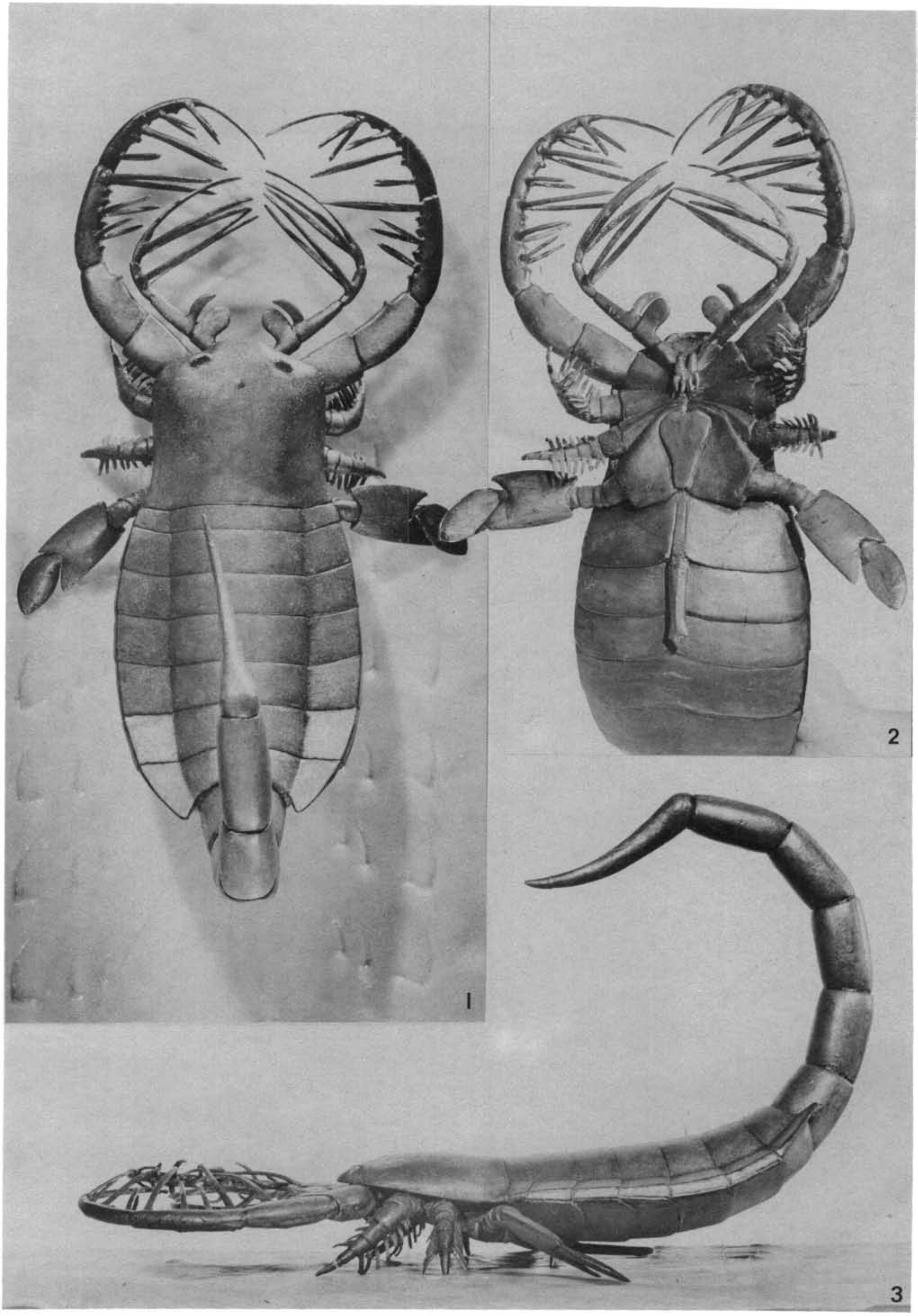


Plate 3

Further observations on eurypterid cuticles

JOHN E. DALINGWATER

Dalingwater, J.E. 1975 7 15: Further observations on eurypterid cuticles. *Fossils and Strata*, No. 4, pp. 271–279, Pls. 1–4. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9

The cuticles of *Eurypterus tetragonophthalmus* Fischer, 1839 (*Eurypterus fischeri*) from the Upper Silurian, Rootziküll, Ösel (Rootsikula, Saaremaa). Estonia, and of *Mycterops* (?) *blairi* Waterston, 1968 from the Namurian of Scotland, have been studied by light and scanning electron microscopy, and a comparative study of the cuticle of *Limulus polyphemus* (Linnaeus) has also been made. The eurypterid cuticles so far studied have a major laminate outer layer and one or more inner non-laminate layers, and resemble the cuticle of *Limulus* more closely than that of any scorpion so far described. The laminar ultrastructure of *M.* (?) *blairi* is comparable with that of extant arthropod cuticles. All eurypterid cuticles so far described are probably now composed largely of silica.

J.E. Dalingwater, Department of Zoology, The University, Manchester M13 9PL, England, 15th August 1973.

In a previous paper (Dalingwater 1973) a small restricted area of the cuticle of one species of eurypterid (*Pterygotus (P.) ludensis* Salter) was described. Many problems remained unresolved, among these: how does the cuticle vary from one area of the exoskeleton to another; are the cuticles of different eurypterid species similar; how do the cuticles of eurypterids compare with those of other chelicerates; and finally, how does the ultrastructure of the laminae relate to that of extant arthropod cuticles.

The eurypterid collections of the British Museum (Natural History), the Royal Scottish Museum, and the Manchester Museum were examined to obtain material for further study. A preliminary study of the cuticle of *Limulus polyphemus* (Linnaeus) has been made using light and scanning electron microscopy, and is reported here. Studies to elucidate laminar ultrastructure, particularly of decapod crustacean cuticles, are in progress under the direction of Professor R. Dennell (see Dennell 1973, 1974, and Dalingwater in press). The main conclusions from these studies of relevance here are that the laminae of decapods are discrete entities with laminar membranes, possibly giving rise to oblique arcing sheets of fibres which cross the interlaminae; also that pore canals with contained filaments and/or membranous linings, traverse the cuticle perpendicularly. These conclusions contrast with the model proposed and elaborated by Bouligand (1965, 1971, 1972), in which the cuticle of *Carcinus* is composed of successive more or less horizontal sheets of parallel fibres, with each sheet orientated at a slight angle from the preceeding sheet, the angular deviation proceeding in a constant direction. In this model laminae are artefacts, resulting from sectioning sheets of fibres parallel to the plane of the section, and the parabolic arcs seen in angled sections are also artefacts.

I am most grateful to Professor L.J. Wills and Dr. C.D. Waterston for their help and advice during the course of the work; to Professor R. Dennell, Dr. E.N.K. Clarkson, and Dr. J. Miller for their critical reading of the manuscript; to Mr. L. Lockey and Mr. B. Atherton for photographic services; and to the S.E.M. Unit, Department of Textile Technology, U.M.I.S.T. for S.E.M. facilities.

MATERIAL AND METHODS

The following eurypterid material was selected for study:
Eurypterus tetragonophthalmus Fischer, 1839: a fragment of limestone which on development revealed part of a small telson with a maximum width of 10 mm (B.M.N.H. In 61369), one nearly complete small specimen (B.M.N.H. I 2772), a series of whole mounts of small specimens, separate tagma, separate body segments, and various appendages, prepared by Holm (B.M.N.H. I 3406, slides 1–32). All material from the Upper Silurian Limestone, Rootziküll, Isle of Ösel (Rootsiküla, Saaremaa), Estonia.

Mycterops (?) *blairi* Waterston, 1968: fragments of large opisthosomal segments probably belonging to this species (Waterston pers. comm. 1973) from the No. 2 Ironstone, Loanhead – Scottish Limestone Coal Group – Namurian (R.S.M. 1886.90.58, 1886.90.59). Also a fragment of cuticle possibly belonging to this species (Waterston pers. comm. 1973) probably from the Burdiehouse Limestone – Viséan (R.S.M. 1973.13). Specimens prefixed B.M.N.H. and R.S.M. were kindly lent by the Trustees of the British Museum (Natural History) and of the Royal Scottish Museum, respectively.

The cuticle of *Eurypterus tetragonophthalmus* was chosen for study because of the range of well-preserved material available, and that of *Mycterops* (?) *blairi* because its thickness made it particularly suitable for studies of laminar ultrastructure. Small fragments of cuticle were removed from the hand specimens and examined by the methods described previously (Dalingwater 1973). All preparations are stored with their parent specimens. Those of Holm's slides mounted in Canada balsam were examined and photographed in transmitted light.

Small specimens of *Limulus polyphemus* (Linnaeus) preserved in alcohol were obtained from the collections of the Zoology Department, University of Manchester, and dried exuviae were purchased from Woods Hole Oceanographic Institute. For light microscopy both sets of material were washed in de-ionised water, then soaked in insect saline for a few days prior to sectioning with a freezing microtome. Sections were stained with Mallory's Triple Stain and mounted in Canada balsam. For scanning electron microscopy both sets of material were washed, air dried at room temperature for a few days, mounted on stubs, and coated with gold or gold/palladium prior to examination with a Cambridge Instruments Stereoscan Mark 2.

THE CUTICLE OF *LIMULUS POLYPHEMUS* (LINNAEUS)

As the limulids are the only extant group of merostomes, some knowledge of their cuticle structure seems an essential pre-requisite for a comparative study of eurypterid cuticles. Scorpion cuticles have been studied by many workers, notably Kennaugh (1959) and Malek (1964), but the limulid cuticle has been strangely neglected. Lafon (1943) gave a brief account of the histology of the cuticle of *Limulus polyphemus* (Linnaeus) distinguishing an outer epicuticle, a laminate exocuticle, and an apparently non-laminate endocuticle. Kennaugh (1968) indicated that the epicuticle described by Lafon is either a tanned cuticulin layer or a hyaline exocuticle, and that a paraffin layer of epicuticle lies outside this layer. Neville, Thomas & Zelazny (1969), in a paper largely concerned with pore canal shape, distinguished a lamellate exocuticle and non-lamellate pre- and post-ecdysial endocuticular layers. Richter (1969) examined exuviae with the scanning electron microscope (S.E.M.) and noted differences in appearance between natural and experimental fracture surfaces, both effectively representing perpendicular sections of the cuticle. However, his discussion was handicapped by limited knowledge of both the previous literature on *Limulus* cuticle in particular, and laminar ultrastructure in general.

There seems to be no previous description of the distribution of the various cuticular layers in different areas of the exoskeleton, nor a comparison of complete and exuvial cuticles. In addition, Richter's (1969) observations clearly need expanding.

Perpendicular sections were made across the lateral edge of the carapace, of the thin cuticle on the underside of the head-shield, and of the telson. The distribution of the various layers of the complete cuticle and their staining reactions in Mallory's Triple Stain are indicated in Pl. 1:1 and Fig. 2. The terminology used by Neville, Thomas & Zelazny (1969) is retained here for convenience, although their observation that the post-ecdysial endocuticle is non-lamellate is incorrect.

Examination of exuvial cuticles indicates that the post-ecdysial endocuticle is dissolved away prior to ecdysis. Staining reactions of exuvial cuticles are similar to those of complete cuticles, though sometimes a thin blue-staining zone is evident at the inner edge of the cuticle. In addition, in a few sections of the telson of large exuviae, laminae are apparent in the central area of the pre-ecdysial endocuticle. In these sections also, the pre-ecdysial endocuticle is subdivided into two layers, the inner layer comprising about one-fifth of the overall thickness of the pre-ecdysial endocuticle.

S.E.M. investigations confirm Richter's (1969) observation that the non-lamellate pre-ecdysial endocuticle appears to have a roughly laminate appearance at the natural moulting break around the margin of the head-shield. This contrasts strongly with its appearance in induced fractures, when perpendicular elements, particularly pore canals, predominate (Pl.

2:1,2). The appearance of the exocuticle also differs in natural and induced breaks, but in contrast to Richter's (1969) observation, fine horizontal elements are seen in natural breaks (Pl. 2:3). Each unit, however, is considerably narrower than the laminae observed in induced breaks (Pl. 2:4). This last observation might be considered supporting evidence for Bouligand's helicoidal model, but initial examination of angled breaks across the lamellate exocuticle seems to indicate that the laminae are real structures (Pl. 2:5), possibly with fibres passing across laminar units (Pl. 2:6). Helicoidal arrays of flat sheets of fibres with laminae as artefacts are not evident. Furthermore, the appearance of the pre-ecdysial endocuticle in natural breaks does not seem entirely in accordance with the preferred orientation system proposed for it by Neville, Thomas & Zelazny (1969).

Clearly, further work is needed for a complete evaluation of the *Limulus* cuticle, preferably on fresh material using light, transmission, and scanning electron microscopy. These preliminary observations are presented here as a basis for comparison with eurypterid cuticles.

THE CUTICLE OF *EURYPTERUS TETRAGONOPTHALMUS* FISCHER

S.E.M. Observations. – The area of the cuticle of *Eurypterus tetragonophthalmus* Fischer studied in detail with the S.E.M. was that of the ventral surface of the telson (Specimen B.M. N.H. In 61369, see Fig. 1). Some vertical breaks, giving effectively perpendicular sections of the central ventral carinae, indicate that the structure of the cuticle in this region is very similar to that described for the carinae of *Pterygotus* (*P.*) *ludensis* Salter (Dalingwater 1973) in possessing: a thin inner apparently non-laminate layer, a main laminate layer with laminar units progressively becoming narrower towards the outer edge of the cuticle (from approx. 1–0.5 μ), and an outer layer in which perpendicular elements predominate (Pl. 3:1). In addition, perpendicular canal-like elements are often prominent in the inner part of the laminate layer (Pl. 3:2). The overall thickness of the cuticle is about 50 μ. The cuticle of the lateral carinae is thinner (about 30 μ thick) and has a somewhat similar appearance to that of the central ventral carinae. However, in addition to a thin non-laminate layer inside the major laminate layer, in several preparations a further (?) inner non-laminate layer is evident, particularly at the apex of the carina. In this layer perpendicular canals are extremely prominent (Pl. 3:3). Some vertical breaks of the central ventral carinae have a somewhat different appearance to that described

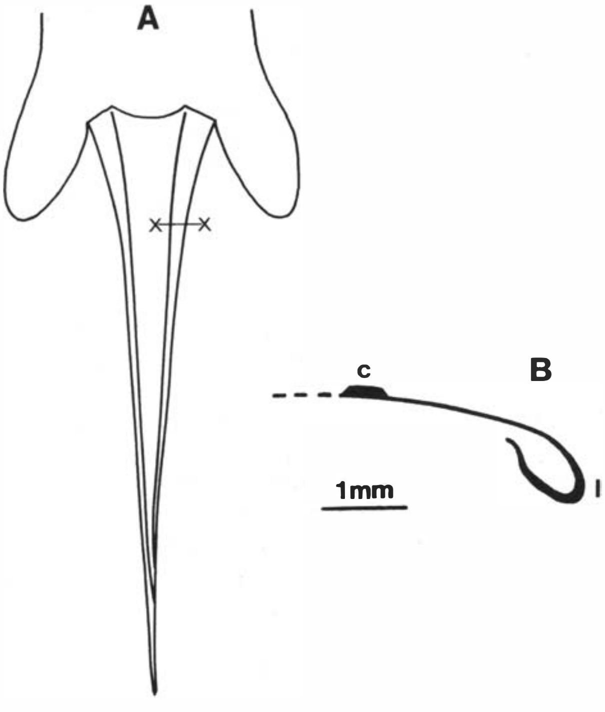


Fig. 1 A. Ventral view of the telson of *Eurypterus tetragonophthalmus* Fischer, after Holm (1898), with position of section B indicated. X1.5. B. Reconstruction of a perpendicular section across part of the telson of *E. tetragonophthalmus* (B.M.N.H. In 61369). Thickness of the cuticle exaggerated. c-left central ventral carina. l-left lateral carina.

above. The overall thickness is about 35 μ, and an outer laminate layer and two inner non-laminate layers are present (Pl. 3:4). The general aspect is similar to that of the lateral carinae, except that individual laminae are wider. The two aspects of the thicker cuticle of the central ventral carinae are repeated in perpendicular breaks of small pieces of cuticle from the thickened posterior margin of the prosoma of specimen B.M.N.H. I 2772. Many small fragments of the thin "body" cuticle of *E. tetragonopthalmus* were examined, but little detail could be determined in most fragments. The average thickness is about 10 μ, and in some specimens a laminate layer with fine laminae and prominent perpendicular elements can be seen. A thin inner non-laminate layer may also be present.

Light microscope observations. – S.E.M. observations were confirmed and complemented by examination of Holm's preparations (B.M.N.H. I 3406, 1–32) with the light microscope. Most areas of the cuticle appear to be extremely thin, and are covered by a roughly polygonal network, described by several previous authors, notably Wills (1965). In some areas the cuticle seems to consist of this network alone. In most areas of the cuticle, minute circular pores open at the surface. These are particularly prominent in slightly thicker areas of the cuticle and are clearly the openings of fine canals which, if the microscope is slowly focussed down through the thickness of the cuticle, appear to rotate somewhat around a central point and therefore probably follow a helical pathway through the cuticle. In places, the cuticle retains the impressions of tiny calcite rhombs as described by Eisenack (1956). The most significant areas for the present study are the edges of thick areas of the exoskeleton, where the cuticle folds over, and therefore effectively perpendicular sections of the cuticle can be examined. The cuticle of the gnathobasic teeth of the third appendage (B.M.N.H. I 3406, slide 12; Pl. 3:5) is 40-80 μ thick with the maximum thickness at the tips of the teeth. The total thickness of the cuticle appears to be laminate. Laminar units are about 1.5 μ thick at the inner edge of the cuticle, progressively becoming narrower towards the outside of the cuticle. Extremely fine perpendicular canals can just be perceived, packed closely together, and are more noticeable as they traverse the laminae. Their diameter is impossible to measure accurately but is of the order of 0.1 μ. In addition, wider perpendicular or near perpendicular canals are prominent at the tips of the gnathobasic teeth. These taper from about 2 μ in diameter of about 1 μ towards the outer edge of the cuticle. "Sections" through teeth, probably at the base of the fourth appendage, are similar but in addition, large goblet-shaped setal sockets are present (Pl. 3:6). A tangential view of the cuticle in this area reveals the perforations of the fine canals described above. "Sections" of the tarsal spines of the fourth appendage (B.M.N.H. I 3406, slide 19) show the usual laminate layer, but inside this layer, fine canals appear to pass tangentially across a non-laminate layer, and are particularly prominent immediately below the laminate layer. In the laminate layer itself, fine perpendicular canals can just be perceived while larger canals are prominent. Above the laminate layer there appears to be a thin yellow translucent layer about 1 μ thick (Pl. 3:7). A condyle at the base of a swimming foot (B.M.N.H. I 3406, slide16) is the only area of cuticle on Holm's slides so thick that is not translucent. However, laminae in the cuticle of the smaller teeth at the base of this limb are picked out with some darker material and can be seen extremely clearly.

Composition. – No detailed analyses were made of the cuticle, but the fracture patterns observed with the S.E.M. and in reflected light are very similar to those of the cuticle of *Pterygotus* (*P.*) *ludensis,* which on analysis was found to consist largely of silica (Dalingwater 1973). Two interesting notes are attached inside the box containing Holm's slides. The first, dated 24/2/1905, is a request from the Director of the B.M.N.H. to arrange for a Mr. Prior to test a fragment of Holm's eurypterid preparations and to inform him whether the material was still chitin or whether it was mainly siliceous. The reply dated 27/2/05 and initialled G.J.P. was: "The fragment on heating blackens and burns (organic matter), but leaves a skeleton of silica retaining the shape of the fragment". An addition to the reply in another hand: "Undissolved by ether and alcohol, and by strong alkalis. Acted on by strong nitric acid. Polarised light shows minute specks of silica". Rosenheim (1905) mentioned Prior's preliminary analysis and reported that his own analyses of the cuticle of *Pterygotus osiliensis* indicated the presence of chitin (although his tests actually only indicated the presence of a reducing substance in an aqueous solution prepared after prolonged treatment with concentrated hydrochloric acid and subsequent evaporation). The only observations that can be added here are that after prolonged treatment with hot concentrated nitric acid, fragments of the cuticle of *E. tetragonophthalmus* appear more flexible and change colour from chestnut-brown to red. Extraction and analysis of amino-acids from the cuticle, using thin-layer chromatography, proved unrewarding.

THE CUTICLE OF *MYCTEROPS* (?) *BLAIRI* WATERSTON

The cuticle of *Mycterops* (?) *blairi* Waterston (specimens R.S.M. 1886.90.58, 1886.90.59) was selected for a study of laminar ultrastructure because the cuticle is comparatively extremely thick (about 300 μ). Therefore angled breaks can readily be made, which effectively widen the laminar units and enable comparisons to be made with extant cuticles, where sections cut at pre-determined angles from the horizontal have proved invaluable in interpretation of laminar ultrastructure (although it must be noted that different authors have made entirely different interpretations of the patterns observed in angled sections or breaks).

S.E.M. Observations. – An inner non-laminate layer, about 200 μ thick, merges upwards into a further non-laminate median layer about 20 μ thick with a rough texture and traversed by perpendicular elements. The laminate outer layer of the cuticle is about 80 μ thick, with laminar units gradually widening towards the centre of the layer from about 0.5 to 1.5 μ wide, and then narrowing again to about 1 μ wide towards the outer edge of the cuticle (Pl. 4:1). Fracture patterns in vertical breaks are similar to those previously described from other eurypterid cuticles and again suggest a composition largely of silica. One fractured preparation reveals a small area of cuticle passing around an angle of about 70°, with the laminar units retaining their integrity around the angle (Pl. 4:3). The significance of this observation is discussed later.

Laminar ultrastructure. – In vertical breaks the appearance of laminar units shows some variation, possibly the result of differences in the precing angle of breakage, or perhaps due to slight differences in the process of breaking. Generally the laminae are clearly apparent with perpendicular elements, about 0.2 μ wide, traversing the inter-laminae. These perpendicular elements appear as solid structures between the laminae, but where continuity of fine perpendicular elements is apparent across several laminae, the elements appear to be canals. Larger perpendicular canals, 2 μ and more wide, are occasionally present.

In one perpendicular break preparation, a small area of the laminate layer deviates from the perpendicular, and the appearance of the laminar units in this region is surprisingly reminiscent of those of *Limulus,* with the suggestion of fibres forming rough chevrons in some inter-laminae. In breaks of about 45° from the horizontal across the laminate layer, arcs of fibrous material can be seen crossing the inter-laminae, with occasional holes possibly representing perpendicular canals (Pl. 4:4). Breaks of about 30° from the horizontal are somewhat different: arcs in the inter-laminae are less clear, but the laminae themselves have a feathered aspect (Pl. 4:5). Areas of the laminate zone broken at angles of around 10° from the horizontal suggest that the laminae themselves contain or consist of fibres arranged in gentle horizontal arcs (Pl. 4:6), these arcs meeting to form elongate chevrons.

Inner laminate layers. – Because of the difficulties in precise identification of specimen R.S.M. 1973.13 no detailed formal description is given here. The overall pattern is similar to that described above for R.S.M. 1886.90.58 and 1886.90.59 except that the non-laminate zone is considerably narrower. The exceptional feature of this cuticle is, however, the presence of one, or in some areas of the "section" two, *inner* laminate layers (Pl. 4:2). The persistent laminate layer is about 10 μ thick with narrow laminar units (0.5 μ), whereas the second innermost laminate layer is slightly narrower overall but with relatively wide (1.5 μ) laminar units. The development of this second laminate layer corresponds with the position of the large ornamental scales.

DISCUSSION

Some preliminary conclusions on the general structure of the eurypterid cuticle. – From the observations reported here and in a previous study (Dalingwater 1973) some preliminary remarks may now be made on the general structure of the eurypterid cuticle. The cuticles examined consist of: a major laminate outer layer, with the narrowest laminar units towards the outer edge of the cuticle, one or more non-laminate inner layers, and in one case (R.S.M. 1973.13) an innermost laminate zone. The outer areas of both the laminate and outer non-laminate layers are characterised by the accentuation of perpendicular elements, which in the latter layer are almost certainly fine perpendicular canals resembling the pore canals of extant arthropod cuticles. The outer part of the cuticle was previously described (Dalingwater 1973) as a separate layer in which perpendicular elements, possibly fractures, predominate. However, this may merely represent part of the main laminate layer (for laminae, though faint, still persist) in which perpendicular canals are accentuated and which is liable to fracture along these natural lines of weakness. Light microscope observations of *E. tetragonophthalmus* cuticle indicate that there may be a further thin outer layer outside the main laminate layer, not apparent under the S.E.M. because of "flaring" as the beam strikes the edge of the specimen. This, however, may be an artefact at the edge of the cuticle.

The "body cuticle" of *E. tetragonophthalmus, of P. ludensis,* and of other Silurian eurypterid species whose cuticles have been examined but not yet formally described, is extremely thin. However, in the few preparations of these thinner areas of the cuticle of *E. tetragonophthalmus* in which detail can be perceived, the organisation seems to conform to the pattern outlined above. In contrast, the "body cuticle" of *M.* (?) *blairi* is extremely thick in comparison with that of Silurian eurypterids, even that of such large species as *Pterygotus osiliensis.*

The observations made here and previously can be reconciled within a common framework if two assumptions are made:

(1) That the non-laminate layers described from the carinal cuticle of *P. ludensis,* from the thicker central ventral carinal areas of *E. tetragonophthalmus,* and the outer non-laminate layer of *M.* (?) *blairi* cuticle, are equivalent to the inner of the two non-laminate layers described from the lateral carinae and the thinner central ventral carinal areas of *E. tetragonophthalmus.* The outer non-laminate layers in these latter two cases may merely be part of the laminate zone in which laminae are not apparent.

(2) That the cuticles of both examples of *M.* (?) *blairi* studied are complete, whereas the rest of the cuticles described here and previously are exuviae. Størmer (1955) suggested that most eurypterid cuticles are in fact exuviae. If this is the case, then the line of ecdysis is probably between the two non-laminate layers in *M.* (?) *blairi,* and in an equivalent position in the other cuticles studied.

Fig. 2 is a comparison of the various eurypterid cuticles, *Limulus* cuticle and a scorpion cuticle, based on the thesis that the above assumptions are correct.

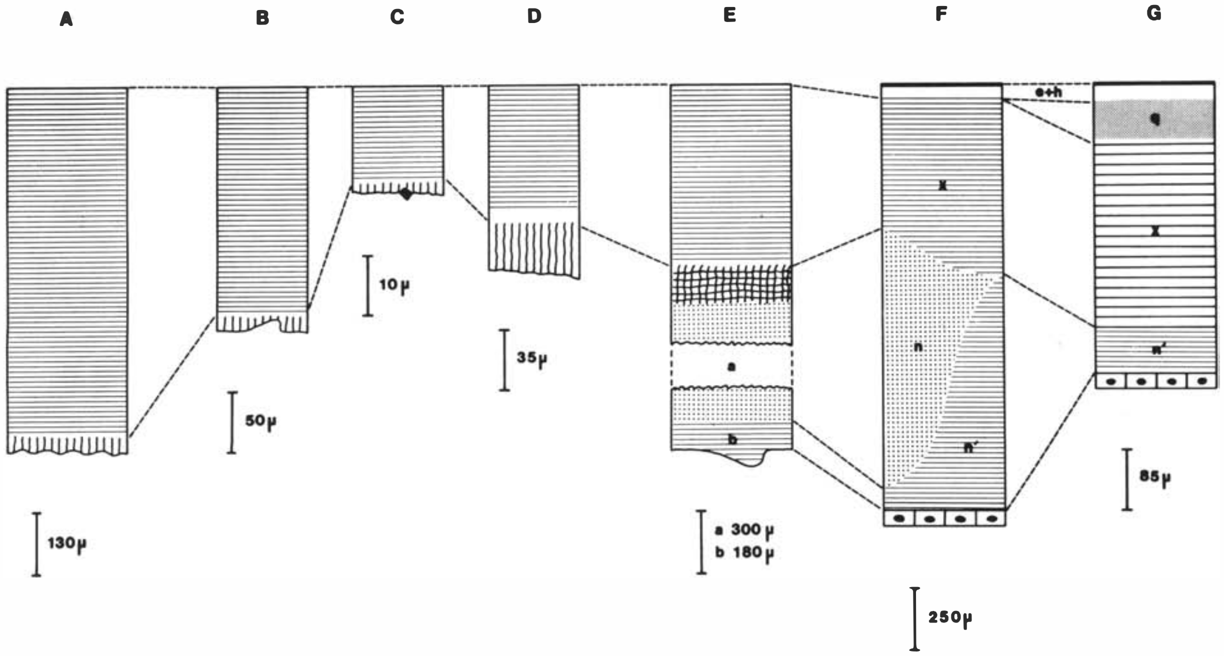


Fig. 2. Comparison of eurypterid, limulid, and scorpion cuticles: simplified and stylised diagram. A. *Pterygotus (P.) ludensis* Salter carinal cuticle, after Dalingwater 1973. B, C, D. *Eurypterus tetragonophthalmus* Fischer central ventral carinal, body, and lateral carinal cuticle, respectively. E. *Mycterops* (?) *blairi* Waterston cuticle. a. R.S.M. 1886.90.58, 59. b. R.S.M. 1973.13. F. *Limulus polyphemus* (Linnaeus) cuticle. G. *Pandinus imperator* (Koch) cuticle, after Kennaugh 1959. Approximate thickness of a perpendicular section through each cuticle indicated. Key to shading: horizontal lines – laminate layers; vertical lines – layers in which perpendicular elements predominate; dots – apparently non-laminate layers; cells – epidermis. Key to symbols: e + h – epicuticle + hyaline exocuticle, q - quinone tanned exocuticle, x– exocuticle, n – pre-ecdysial endocuticle; n' – post-ecdysial endocuticle.

Comparison of eurypterid cuticles with those of extant arthropods. – Recent studies by the present author on extant cuticles, particularly that of *Limulus,* have facilitated comparison of eurypterid cuticles with those of extant arthropods. Eurypterid cuticles so far studied seem to resemble *Limulus* cuticle more closely than the cuticle of any scorpion so far described. Wills (1965) noted that he and previous authors had found differences in the nature of the cuticle between eurypterids and fossil xiphosurans, yet these may be attributable solely to differences in preservation. It is hoped that some fossil xiphosurans (and also some fossil aquatic scorpions) with well-preserved cuticles will soon become available for study.

Eurypterid cuticles resemble that of *Limulus* in the presence of a thick laminate outer layer with narrow laminae; particularly in the presence of a non-laminate zone, which has not been described from any scorpion cuticle; and in one specimen (R.S.M. 1973.13), in the presence of an inner laminate zone. The fine perpendicular canals described from eurypterid cuticles resemble the pore canals of *Limulus,* particularly in their prominence and accentuation at the outer edges of both laminate and non-laminate zones (see Pl. 1:2, 3) Pore canals and laminar units are somewhat larger in *Limulus* than in the eurypterid cuticles studied, about 0.5-1.0 μ in diameter and 2-3 μ wide respectively. Perpendicular canals of greater diameter are not often seen in eurypterid cuticles examined under the S.E.M., but examination of Holm's slides by light microscopy indicates that larger canals are common in some areas of the cuticle, particularly at the tips of limb processes. In the cuticle of *Carcinus,* tegumental ducts are prominent at the tips of the limbs, and Dennell (1960) has suggested that they are associated with the extensive phenolic tanning of these regions. In *E. tetragonophthalmus* and *P. ludensis,* increase in thickness of the thicker areas of the cuticle is largely the result of thickening of the laminate layer, whereas in *Limulus* the laminate zone is of consistent thickness at, for example, the edge of the carapace, and increase in thickness in this region results from the development of the non-laminate pre-ecdysial endocuticle. In addition, non-laminate zones are present in all regions of all eurypterid cuticles studied, whereas in *Limulus* the non-laminate pre-ecdysial endocuticle is developed only in certain areas of the cuticle, such as the edge of the carapace and the telson. It is difficult to indicate a line of ecdysis for eurypterid cuticles in general, but it probably occurs within the non-laminate zone contrasting with its position in *Limulus.*

In the absence of chemical criteria, it is impossible to relate with confidence the various layers described from eurypterid cuticles to the defined layers of extant arthropod cuticles. But if a close similarity between eurypterid and xiphosuran cuticles is assumed, then the thin outermost layer seen with the light microscope may be related to the hyaline exocuticle, the outer laminate zone to the exocuticle, part of the non-laminate zone to the pre-ecdysial endocuticle, and the inner laminate zone to the post-ecdysial endocuticle of *Limulus.*

Laminar ultrastructure. – Further details of eurypterid laminar ultrastructure were provided from studying the cuticle of *M.* (?) *blairi.* In addition, details described from *P. ludensis* (Dalingwater 1973) can now be interpreted in the light of recent S.E.M. studies of extant cuticles undertaken by the present author.

The laminar units of the *M.* (?) *blairi* cuticle seem discrete rather than the result of sectioning helicoidally arranged sheets of fibres, since the laminae maintain their integrity around a substantial angle (Pl. 4:3). If the laminae are to be explained in terms of Bouligand's (1965) model, a discontinuity amounting to a displacement of nearly half the inter-laminar interval is to be expected. Perpendicular elements which appear as solid structures in the interlaminae in both *M.* (?) *blairi* and *P. ludensis* are possibly pore canal linings, whereas fine canal-like elements which continue across several laminae probably represent the pore canals themselves. Observations from low angle breaks of *Mycterops* (?) cuticle indicate that the laminae themselves contain or are composed of fibres which form gently curving arcs in the horizontal plane, similar to those observed in decapod crustacean cuticles. Sheets of fibres probably arise from and arc between laminae, the feathery appearance of the laminae in 30° breaks is remarkably similar to that described from *Carcinus* cuticle by Dennell (1973). Rough chevrons seen in almost perpendicular breaks (e.g. of *P. ludensis* cuticle, Fig. 3A, Dalingwater 1973) may be the result of near horizontal fibres in the laminae meeting fibres passing across interlaminae at a substantial angle.

Composition of eurypterid cuticles. – All thicker areas of eurypterid cuticles so far examined are probably now composed largely of silica, and this may also be true of thinner regions. The extent and nature of any organic material still present remains undetermined.

TERMINOLOGY

Cuticle. The material secreted at the outer surface of arthropod epidermal cells, solidifying there to form the exoskeleton (after Richards 1951).

Epicuticle. The outer portion of the cuticle, negative to chitin tests (Richards 1951).

Procuticle. The major part of the cuticle, positive to chitin tests.

Exocuticle. The outer portion of the procuticle which becomes hardened and darkened (Richards 1951).

Endocuticle. The seemingly unaltered inner portion of the procuticle (after Richards 1951).

Lamellate. Term applied to areas of cuticle which are considered to have helicoidally oriented layers of microfibrils and in which laminae are seen as artefacts (Bouligand, Neville model).

Laminate. Term applied to areas of cuticle which are laminated, that is, which are considered to consist of real laminae (narrow zones which appear as dark lines under the light microscope) separated by wider inter-laminae (Richards, Dennell view of laminae).

Pre-ecdysial. Portion of the new cuticle formed below the old cuticle before ecdysis of the old cuticle.

Post-ecdysial. Portion of the new cuticle formed after ecdysis. In *Limulus* the post-ecdysial endocuticle is dissolved prior to ecdysis.

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EXPLANATION OF PLATES

Plate 1

The cuticle of *Limulus polyphemus* (Linnaeus)-light micrographs. Sections cut at 12 μ and stained with Mallory's Triple Stain. *Fig. 1.* Montage from a perpendicular section across the postero-lateral edge of the carapace. Staining reactions: epicuticle (very thin dark outermost layer) – dark blue; hyaline exocuticle (thin clear layer just inside the epicuticle) – unstained; exocuticle (x) – red; pre-ecdysial endocuticle (n) – pink; post-ecdysial endocuticle (n') – light blue. The exocuticle and post-ecdysial endocuticle are both clearly laminate whereas the general aspect of the pre-ecdysial endocuticle is non-laminate. Setal and tegumental ducts are prominent in this region of the cuticle. Fragments of epidermal cells adhere to the inner surface of the cuticle. Knife marks pass tangentially across the section; these are difficult to avoid when cutting hard material on the freezing microtome. Note that the pre-ecdysial endocuticle is only developed at the margin of the carapace and fades out dorsally and ventrally. X120. *Fig. 2.* Accentuation of pore canals at the outer edge of the pre-ecdysial endocuticle. In this region the pore canals seem to widen and their linings or possibly contained filaments take up stain readily. At the endocuticle/exocuticle boundary the pore canals appear to be sharply deflected. From a perpendicular T.S. of the telson. X750. *Fig. 3.* Accentuation of pore canals at the outer edge of the exocuticle. The outermost epicuticle (seen as a dark line) and the clear unstained hyaline exocuticle are more readily seen here than in Pl. 1:1. From a section in the same series as that in Pl. 1:1. X500.

Plate 2

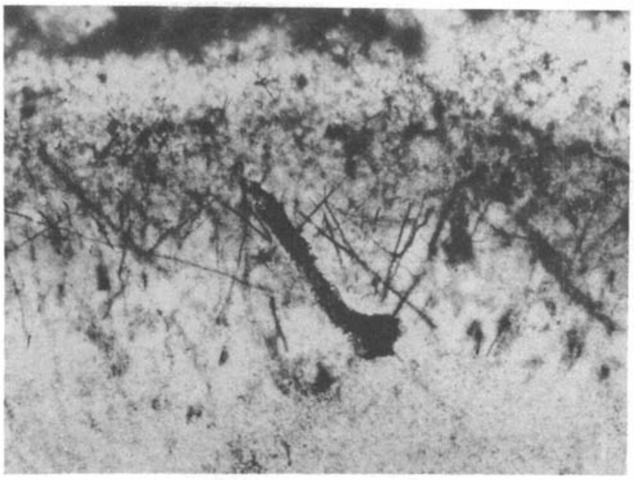
Scanning electron micrographs of the cuticle of *Limulus polyphemus* (Linnaeus) – anterior edge of the carapace of an exuvium. *Fig. 1.* Pre-ecdysial endocuticle – natural break. X2200. *Fig. 2.* Pre-ecdysial endocuticle – artificial break X1050. *Fig. 3.* Exocuticle – natural break. X950. *Fig. 4.* Exocuticle – artificial break. X1050. *Fig. 5.* Exocuticle – artificial break at 30° from the horizontal: the laminae appear discrete. X950. *Fig. 6.* Exocuticle – artificial break at about 10° from the horizontal. The laminae are less discrete but fibres appear to follow arced pathways in the perpendicular plane. X900.

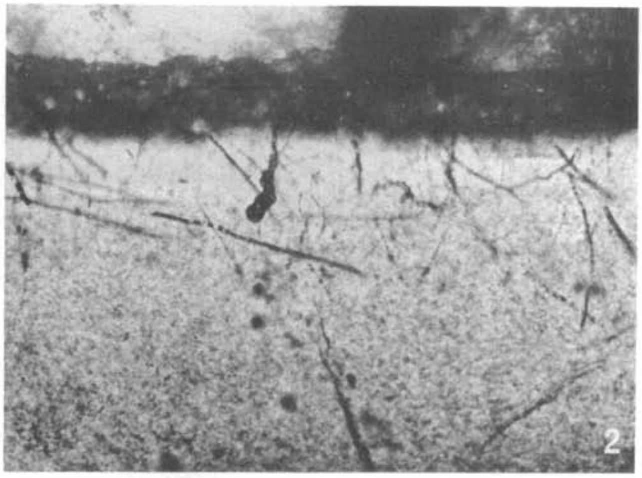
Plate 3

The cuticle of *Eurypterus tetragonophthalmus* Fischer. *Figs. 1-4.* Scanning electron micrographs. *Figs. 5-7.* Light micrographs. *Fig. 1.* Perpendicular break of the central ventral carinal cuticle – complete "section". X1 750. *Fig. 2.* Detail of Pl. 3:1 – a perpendicular canal from the inner part of the laminate layer. X8750. *Fig. 3.* Fine vertical canals in the non-laminate layer of the lateral carina. X4800. *Fig. 4.* Second aspect of the central ventral carinal cuticle. X1750. All preparations from specimen B.M.N.H. In 61369. *Fig. 5.* The cuticle at the tip of a gnathobasic tooth of the third appendage. Laminae and wider perpendicular canals clearly apparent, finer perpendicular canals just visible. X480. *Fig. 6.* "Section" of a tooth at the base of the fourth appendage. Goblet-shaped setal sockets are seen in perpendicular and surface views. Perforations of fine canals are also present, particularly around the point marked "x". X280. *Fig. 7.* "Section" of a tarsal spine of the fourth appendage showing possible thin clear outermost layer, also accentuation of fine canals just inside the laminate layer. X540. From B.M.N.H. I 3406, slides 12, 12, 19 respectively.

Plate 4

Scanning electron micrographs of the cuticle of *Mycterops* (?) *blairi* Waterston. *Fig. 1.* Perpendicular break of the outer region of the cuticle, the major part of the inner non-laminate layer not shown. Preparation from R.S.M. 1886.90.58. X500. *Fig. 2.* Perpendicular break preparation from R.S.M. 1973.13. Complete thickness of the cuticle. The persistent inner laminate layer can be seen at the bottom right of the picture – out of focus, as this layer has broken to form a forwardly projecting shelf at this point. X500. Inset left (2:) – detail of the inner laminate zone with both layers present. The persistent layer is not clearly laminate in this micrograph, but laminae are apparent in the innermost laminate layer. X1100. *Figs. 3-6.* Details of laminar ultrastructure – preparations from R.S.M. 1886.90.58,59. *Fig. 3.* Laminae pass around a substantial angle at a fracture and maintain their integrity. X1700. *Fig. 4.* The appearance of laminar units in a break of 45° from the horizontal . X4400. *Fig. 5.* Feathery aspect of the laminae in a break of 30° from the horizontal. X4200. *Fig. 6.* The laminae themselves, viewed from below, seem composed of fibres forming rough horizontal arcs which join to form elongate chevrons – a break of about 10° from the horizontal. X4750.





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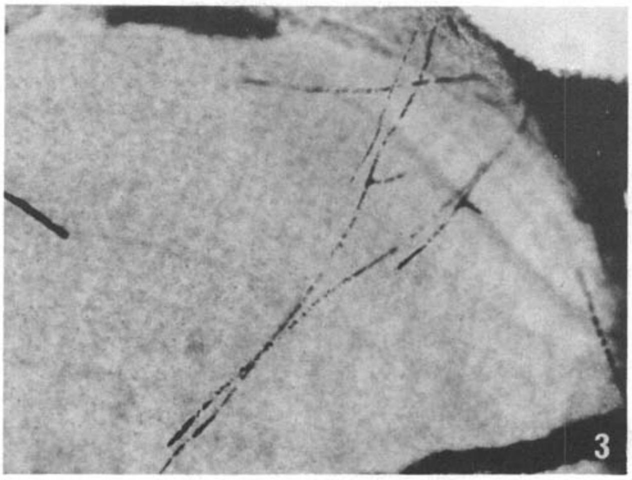

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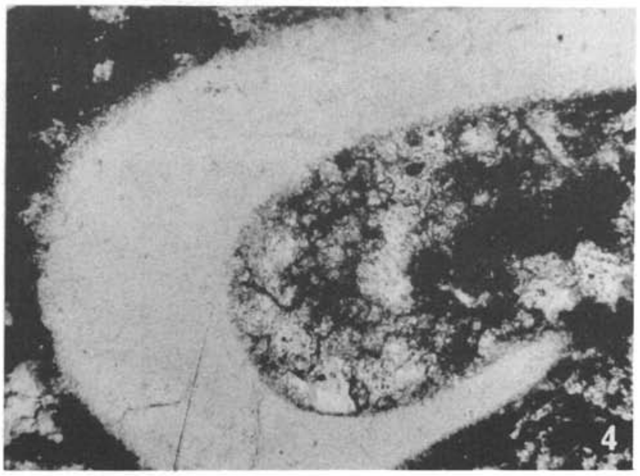

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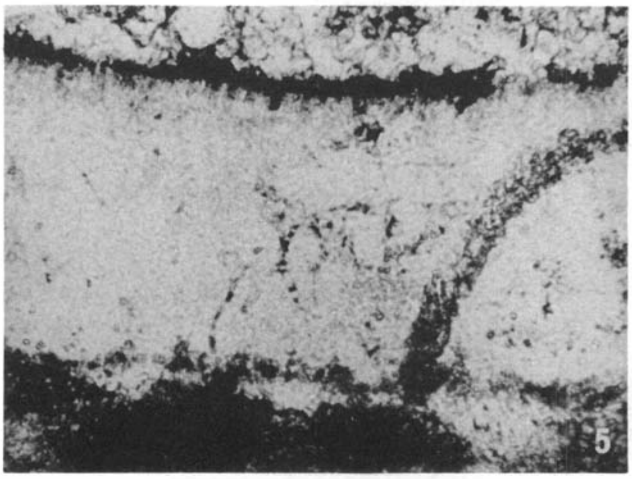

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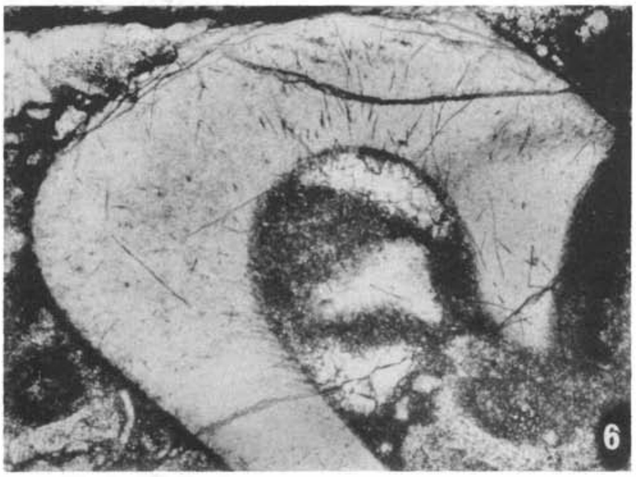

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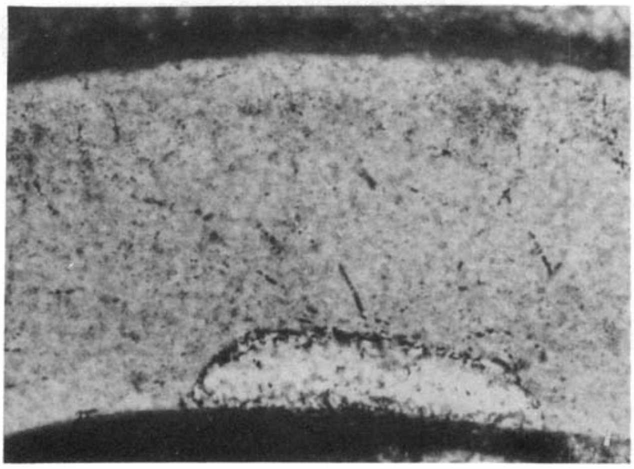

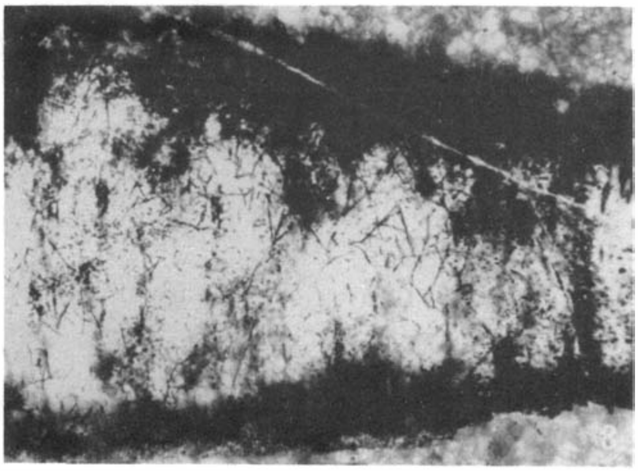

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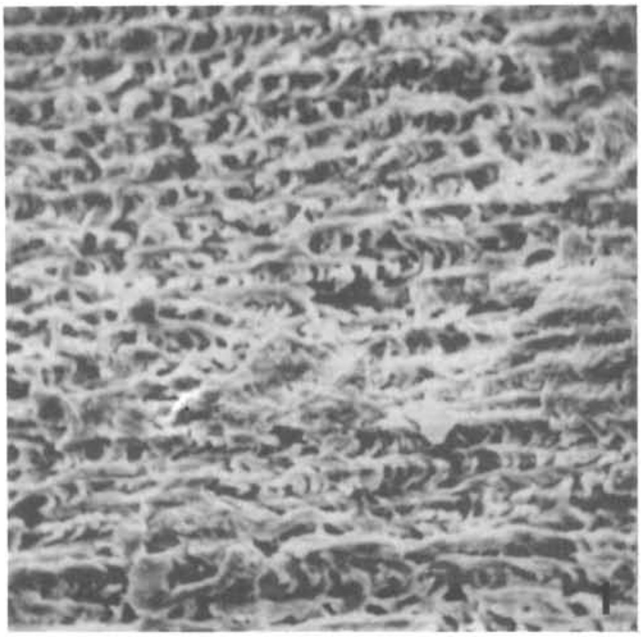
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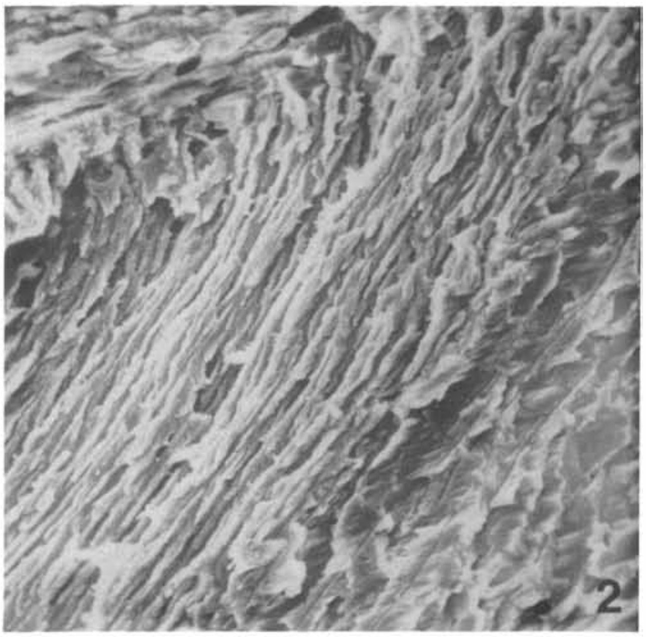
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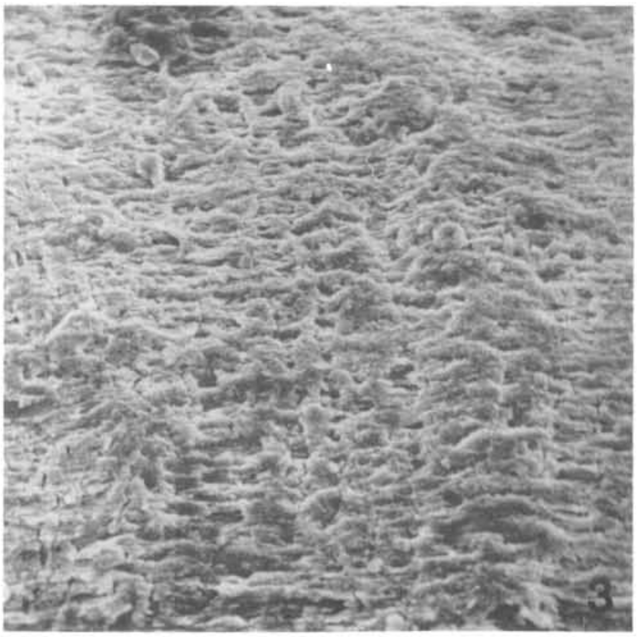
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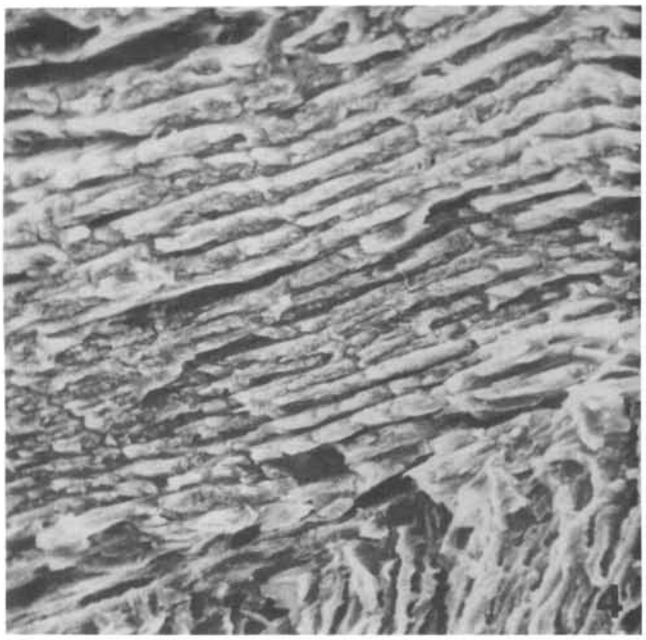
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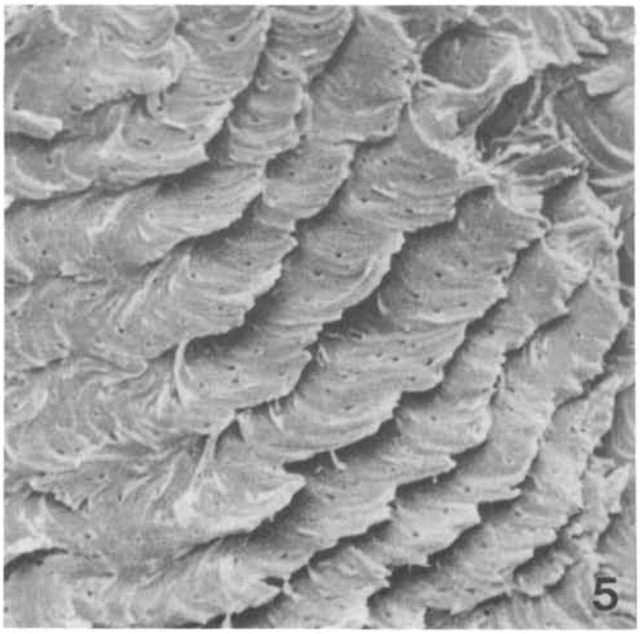
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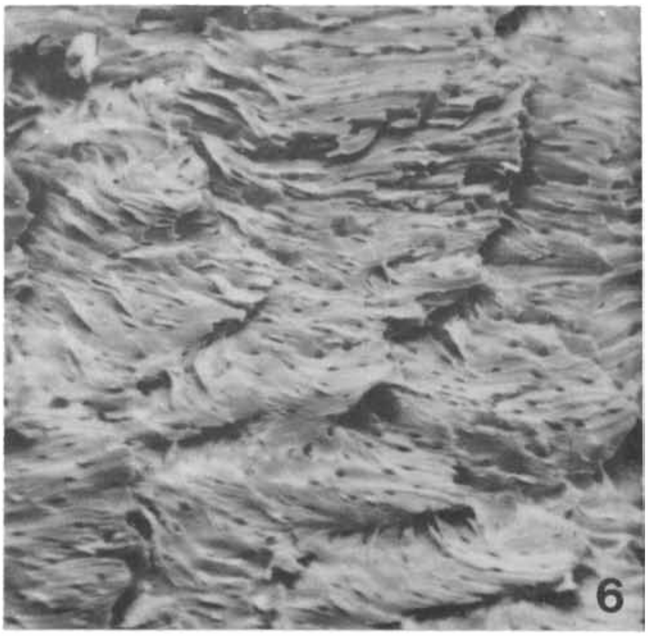
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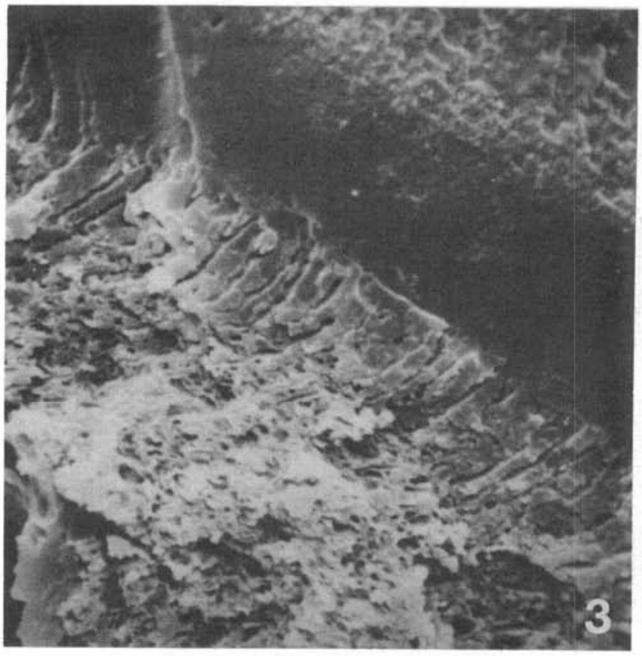
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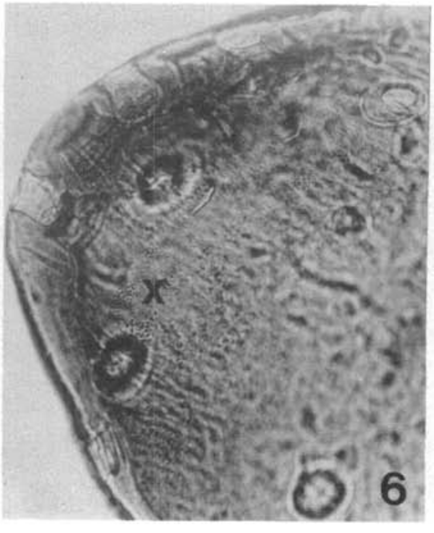

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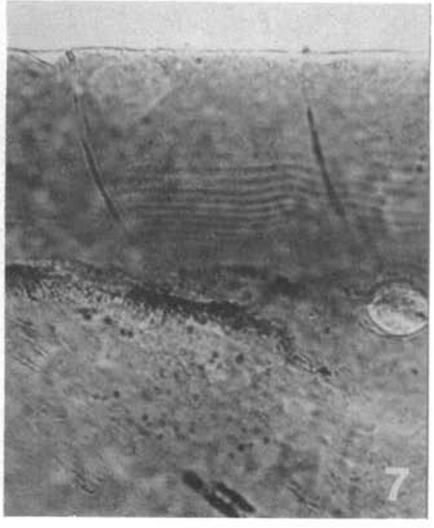
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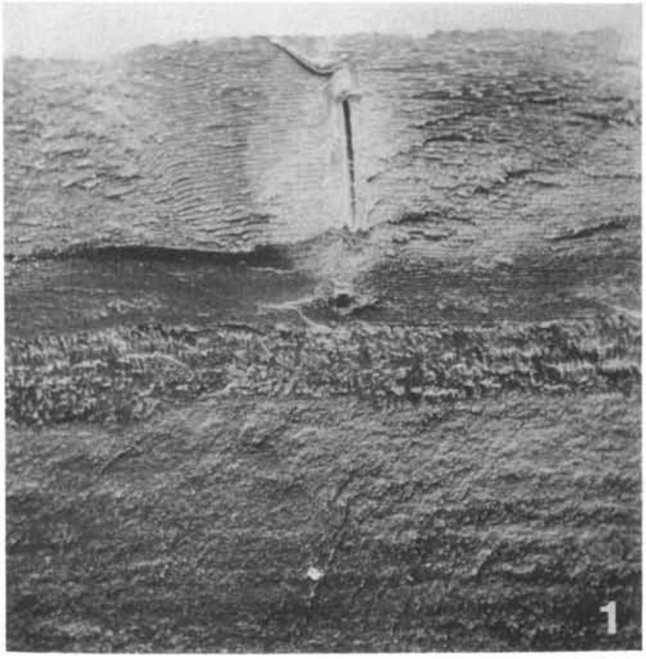
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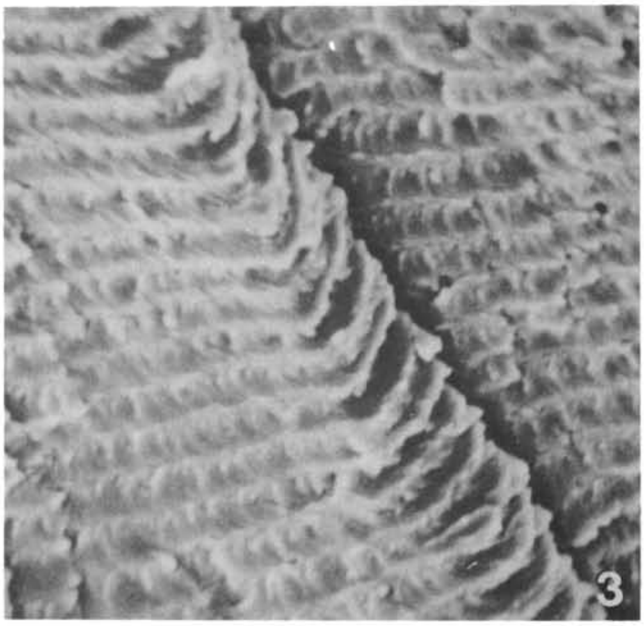
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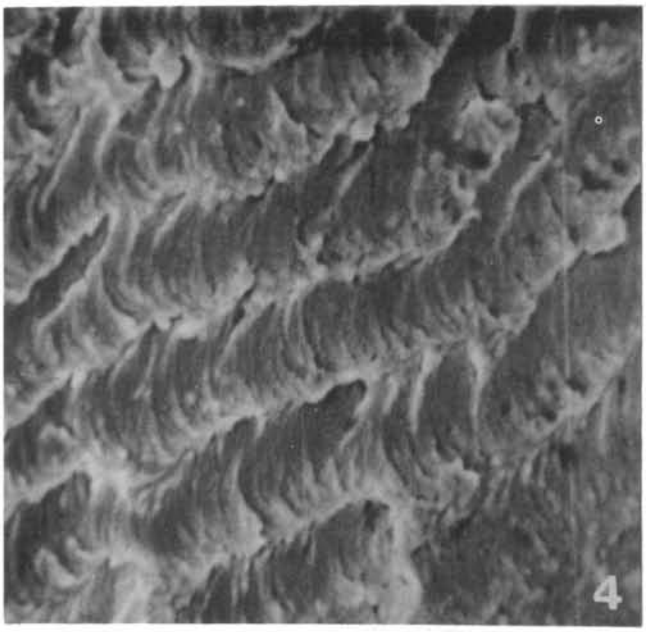
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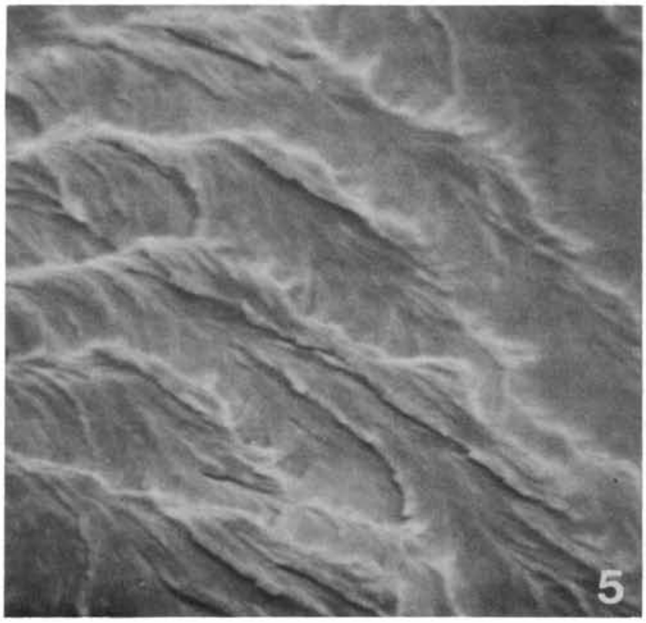
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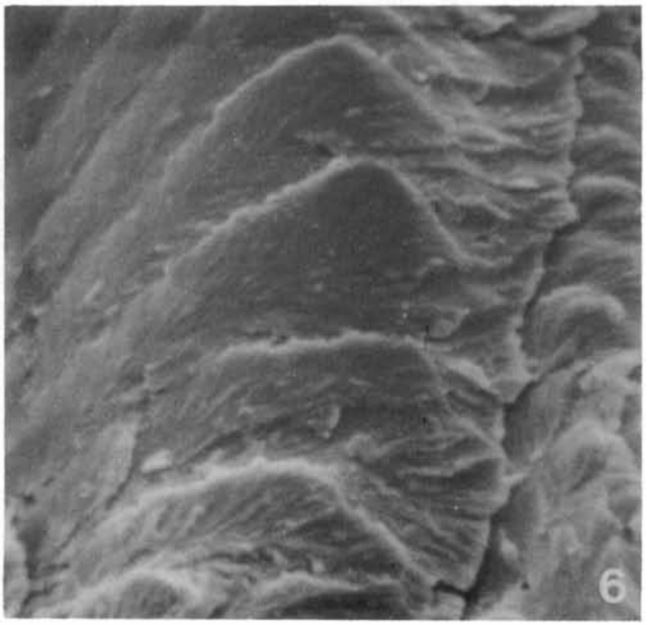
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Plate 4

Swimming and burrowing in *Limulus* and *Mesolimulus*

DANIEL C. FISHER

Fisher, D.C. 1975 07 15: Swimming and burrowing in *Limulus* and *Mesolimulus*. *Fossils and Strata,* No. 4, pp. 281–290. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

In the swimming of *Limulus polyphemus,* the development of an unstable, recirculating vortex within the prosomal vault is an important factor determining swimming orientation, swimming speed, and stroking rate of appendages. Experimental evaluation of the characteristics of vortex formation in *Mesolimulus walchi* gives us a good estimate of its swimming orientation, speed, and stroking rate. The highly vaulted prosoma of *Limulus,* which limits its speed as a swimmer, contributes to its proficiency as a burrower. Similarly, the mechanics of the femoral-patellar joint indicate greater swimming abilities for *Mesolimulus* and greater burrowing abilities for *Limulus.* The morphology of each species represents a compromise between the conflicting requirements imposed by swimming and burrowing.

Daniel C. Fisher, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A., 1st June, 1973. Present address: Dept. of Geological Sciences, University of Rochester, Rochester, New York 14627 U.S.A.

The swimming and burrowing of Recent horseshoe crabs is of special interest to those of us concerned with the ethology of fossil merostomes and trilobitomorphs. As Eldredge (1970) has pointed out, the very general similarities in form between these groups tempt us into studies of comparative functional morphology. In making such comparisons, however, it is extremely important that we do not simply note specific correlations between form and behavior, but rather that we go on to understand the precise, physical reasons for these correlations. This approach leads us to focus directly on the physical basis of the relationship between form and movement.

The following analysis of swimming and burrowing is very limited in its goals. It will consider only a few aspects of each activity, and only a few sorts of evidence supporting an interpretation of each. It should, however, have some intrinsically interesting results and also show something of the power of techniques that directly investigate the physical consequences of ethological and morphological patterns. The adaptive relationship between form and movement constitutes one of the most fruitful approaches to the reconstruction of the behavior of fossil animals. In an extended sense, movement is really only another dimension of morphology; one may thus speak of the shape of movement. However, movement, with its peculiar evanescence, places the burden of its documentation on static form. It is with this, then, that we must begin.

STATIC MORPHOLOGY OF *LIMULUS POLYPHEMUS* AND *MESOLIMULUS WALCHI*

The morphology of the Recent *Limulus polyphemus* is well enough known to require little more than a mention of the features which will be compared in our two species. The morphological knowledge of the Jurassic *Mesolimulus walchi* is based on study of material from the Solnhofen limestone, some of which has been prepared by a specially developed acid technique. This work is part of a larger scale investigation of the morphology and evolution of horseshoe crabs which is in preparation by the author. Pertinent morphological details are presented in Fig. 1. Of importance for the following discussion are the difference in prosomal width and height, the different angular relationships of podomeres when withdrawn into the prosomal vault, and the difference in the robustness of podomeres.

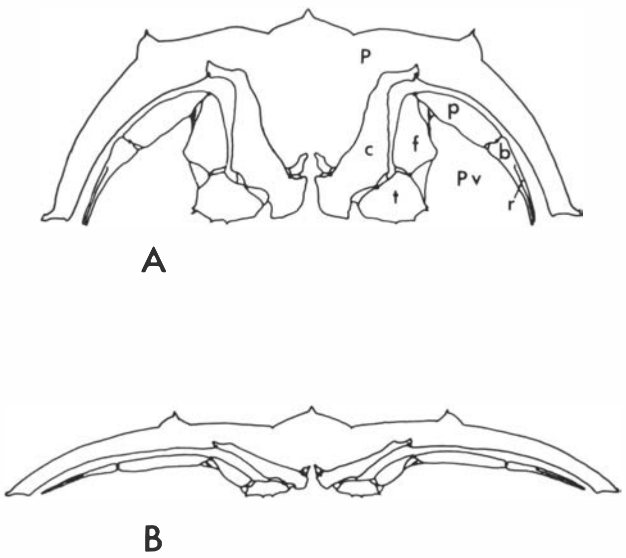

Fig. 1. Transverse cross sections of *L. polyphemus* (A) and *M. walchi* (reconstructed) (B), through the lateral compound eyes, and perpendicular to a plane defined by the post-ophthalmic branches of the ophthalmic ridges. The plane of the appendages has been rotated somewhat to lie in this transverse plane of the body. Both are drawn to the same scale and represent animals 4.5 cm in prosomal length. P, body cavity of prosomal carapace; Pv, prosomal vault; c, coxa; t, trochanter; f, femur; p, patella; b, tibia; r, tarsus.

SWIMMING

Swimming is probably the most complex of the activities in the behavioral repertoire of *L. polyphemus*. A full understanding of the precision and coordination of swimming movements and the several phases of swimming behavior would involve a number of different sorts of physical analyses. However, at present, I wish to consider only three facets of swimming behavior: (1) orientation of the body relative to the horizontal, (2) swimming speed, and (3) stroking rate of the appendages. I shall refer to these as Θ, v, and f_s respectively. I will deal with these factors only in the context of unaccelereated swimming in a horizontal direction, well above the surface of the sediment, and below the surface of the water. Furthermore, I will limit the discussion of investigative techniques to experiments involving visualization of the pattern of fluid flow about a swimming horseshoe crab, especially in the region of the ventral prosomal vault.

The basic motions of horizontal swimming in *L. polyphemus* have been described, with various degrees of accuracy, by numerous authors. The most recent descriptions are by Vosatka (1970), Knudsen (1973), and Fisher (1971). The following analysis, however, rests on only a few simple observations, based on work with individuals one to five centimeters in prosomal length (Fisher, 1971).

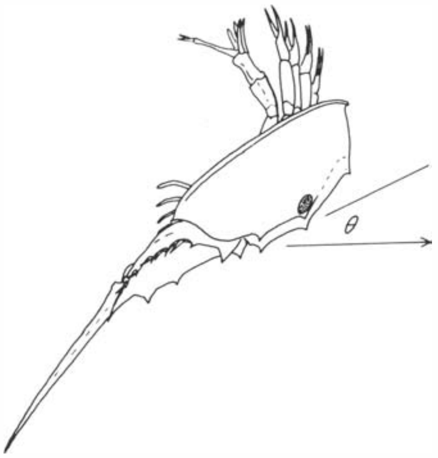

Fig. 2. A swimming horseshoe crab. Movement is in a horizontal direction, as indicated by the arrow. Swimming orientation (Θ) is defined as the angle, measured in a vertical longitudinal plane, between the post-ophthalmic branches of the ophthalmic ridges and the direction of movement. The prosomal appendages have just begun their power stroke.

(1) a. During unaccelerated horizontal swimming the body moves in a generally anterior direction, with the ventral surface uppermost.
    b. The body is inclined in such a way that a plane described by the post-ophthalmic branches of the ophthalmic ridges lies at 20°–30° to the horizontal, measured in the direction of motion (Fig. 2).

(2) Swimming speed usually ranges between 10 and 15 cm sec^{-1}.

(3) a. Swimming is powered by the motions of the prosomal and opisthosomal appendages, which consist of power and recovery phases of a stroking cycle.
    b. This cycle has a frequency of 2.0–2.4 sec^{-1}.

(4) The opisthosomal appendages and the sixth prosomal appendages stroke in a metachronal rhythm, the wave of activation passing anteriorly. Prosomal appendages 2–5 move in phase with one another, and begin their stroking cycle immediately after the sixth prosomal appendages.

(5) During their power stroke, the prosomal appendages extend ventrally and move posteriorly. During their recovery stroke, they withdraw into the prosomal vault and move anteriorly, their distal elements approximated to the ventral surface of the prosoma.

We would now like to investigate the quantitative aspects of the foregoing description of swimming, in order to understand the specific values of Θ, v, and f_s that are observed in *L. polyphemus* and to reconstruct values of each of these factors for *M. walchi.*

The qualitative aspects of a similar description of swimming movements for *M. walchi,* and the rather basic assumption that *M. walchi* swam at all, will be dealt with in detail elsewhere (Fisher, in preparation). Briefly, the argument is as follows.

Despite the differences in shape between *L. polyphemus* and *M. walchi,* it can be shown that their carapaces have a similar relative spatial distribution of centers of mass-buoyancy and lift (as determined for any swimming position). These observations, coupled with data from the measurement of the forces acting on a swimming horseshoe crab, indicate that if *M. walchi* swam, it also swam on its back – i.e. item (1) a. applies to *M. walchi.* Similarly, anatomical and energetic-mechanical considerations of appendage movement allow the transposition of items (3) a. and (4). Furthermore, the best interpretion of such anatomical details as the course and development of the ophthalmic ridges of *M. walchi* (also based on force measurement data not given here) involves the assumption of swimming in *M. walchi.* This line of reasoning, together with evidence from trace fossils and details of preservation, supports the assumption that *M. walchi* swam and that its *general* manner of swimming was similar to that exhibited by *L. polyphemus.*

Materials and methods

It is standard practice, in studies of fluid mechanics, to simulate the conditions of an object moving through a quiescent fluid, by setting up the dynamically equivalent situation of a stationary object immersed in a flowing fluid. For this study, models of horseshoe crabs were mounted in a flume which supplied a non-turbulent flow, whose velocity could be regulated between 0 and 70 cm sec^{-1}, through a test section measuring 45 cm by 45 cm. The flume was built, and is maintained by, the Division of Engineering and Applied Physics, Harvard University.

Models of *L. polyphemus* were made by sealing the anterior exuviation suture of dried molts. Prosomal and opisthosomal appendages were removed and the resulting openings into the body cavity were plugged. For *M. walchi,* a reconstruction of the carapace (without appendages) was sculpted in wax, molded in silicone rubber, and cast in polyester resin. Both models have a prosomal length of 4.5 cm.

The removal of appendages from the models was originally done in order to study how the carapace itself would tend to influence the development of flow patterns. It later became clear that the motion of the appendages during swimming was such as to reinforce the patterns set up by carapace shape, not obliterate them. Unless a mechanism were developed for accurate animation of model appendages, their motionless presence on a model would constitute more of a distortion of the 'real' situation than their absence.

We must next raise the question of how accurately a model reproduces the control of flow patterns that the real carapace would exercise. In morphological detail, the models are probably excellent representations of the real animals. The molt of *L. polyphemus* gives us as near perfect a model, in this respect, as could be desired. In fact, flow visualization experiments on plastic models representing progressively more simplified abstractions of the carapace morphology of *L. polyphemus* show that it is its general shape, rather than minute surface details, which is significant for explaining the flow patterns that will be dealt with here.

Some attempts to model organisms for hydrodynamic study are confounded because of the difficulty of reproducing the elastic and textural properties of biological surfaces. For the present study, this problem is of minimal importance. For our purposes, the smooth, stiff, chitinous exoskeleton is effectively simulated by rigid plastics.

The models were supported in the flume on the end of a brass rod, one quarter inch in diameter, mounted on the ventral surface of the model. The rod was held in a brace which could be rotated about the animal's center of mass (Fig. 3). This varied the orientation of the model relative to the direction of fluid movement, without displacing the model within the test section. The similarity of the flow patterns, using this method of support, to those developed using other methods (not involving structures within the prosomal vault) indicates that the presence of the rod does not significantly affect flow patterns within the prosomal vault.

In order to trace the patterns of flow about the models, hydrogen bubbles were generated upstream of the models through the electrolysis of the flume water. The electrodes were fine wires mounted paradiametrically across a plexiglass hoop. In most cases, the cathode was platinum and the anode copper, resulting in a single linear source of H_2 bubbles.

The results of bubble tracking are obviously most significant when the terminal velocity of bubble ascension is very much less than the velocity of fluid flow. In these experiments terminal ascension velocity of the bubbles was usually 5–10% of the flow velocity. As bubbles were generated from a linear source, a planar sheet of bubbles was propagated downstream. In the presence of an object suspended in the flow, this sheet was deformed in a manner closely approximating streamline deformation around the object, thus giving a visible record of flow patterns.

Flow patterns developed for each of the models, at specified orientations and flow velocities, were recorded on 3" x 5" Polaroid film and on 16 mm cine film. Frame by frame analysis of the cine film provided a means for measuring the periodic structure of these patterns.

Results

The flow patterns illustrated by these experiments are caused solely by the interaction of carapace morphology and the moving fluid medium. The details of the flow pattern which are most informative concerning the aspects of swimming that we have chosen to analyse

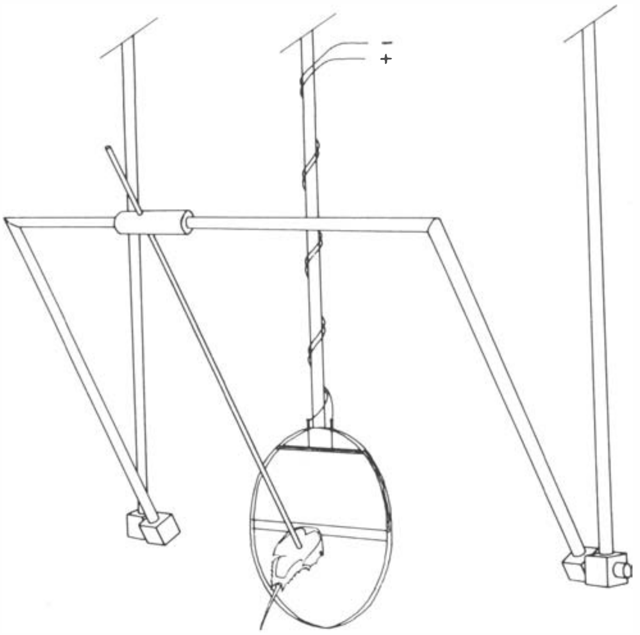

Fig. 3. Model mount and electrode for flow visualization experiments. The tops of the vertical supports were attached rigidly to the top of the flume channel. Direction of flow is from right background to left foreground.

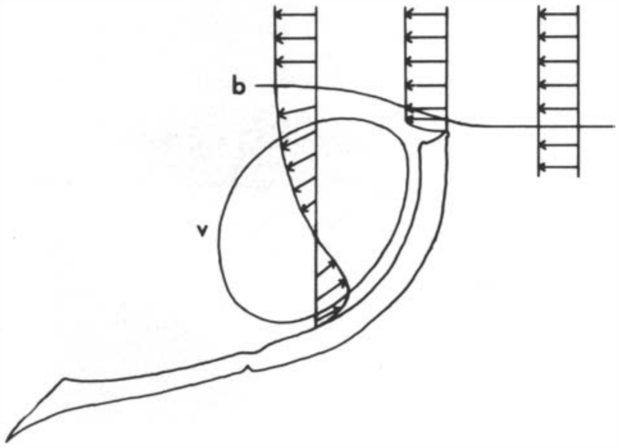

Fig. 4. Flow pattern near the prosoma (shown in longitudinal section through the interophthalmic region) of a swimming *Limulus polyphemus.* Vectors on the velocity profiles indicate direction and magnitude of the flow velocity at their origins on a vertical baseline. The curve b represents a streamline which, above the prosoma, marks the upper extent of the boundary layer. The curve v represents the locus of points with a velocity equal in magnitude to the maximum flow velocity in the anteriorly moving portion of the vortex. v may be taken as the size and shape of the fully developed vortex.

(orientation, speed, and stroking rate) are those concerning flow in the prosomal vault and in the wake behind it.

When fluid approaches the anterior prosomal margin, it either moves over the dorsal surface of the carapace or passes ventrally across the prosomal doublure. Fluid moving along this ventral path experiences an abrupt discontinuity in surface conformation, resulting in a flow separation at this margin. (The physics of flow separation are discussed in any fluid dynamics text. What concerns us here is only the resulting pattern of flow.) This fluid is deflected further ventrally in a smooth arc and then passes back into the wake. The space between this deflected flow and the ventral surface of the prosoma is occupied by a recirculating vortex which, when intact within the prosomal vault, has a roughly crescentoid shape. The 'dorsal' portion of this vortex is appressed to the ventral surface of the prosoma and the 'ventral' portion of the vortex grades into the body of deflected flow, occasionally incorporating some of this flow into its own recirculation (Fig. 4).

Another important feature demonstrated by the flow visualization experiments is that the vortex formed in the prosomal vault is not continually present or active there. Rather, vortices are periodically formed and shed into the wake behind the horseshoe crab. This may be expressed as a strong periodicity in the energy distribution of fluid moving in the separated region. This periodicity is superimposed on the more randomly variable energy distribution of turbulent flow in the wake (the unstable range of vortex shedding, in Roshko's terminology, 1954). This allows the period of individual formation-shedding cycles to vary somewhat, but does not obscure the strong periodic structure of the wake (Figs. 5 and 6).

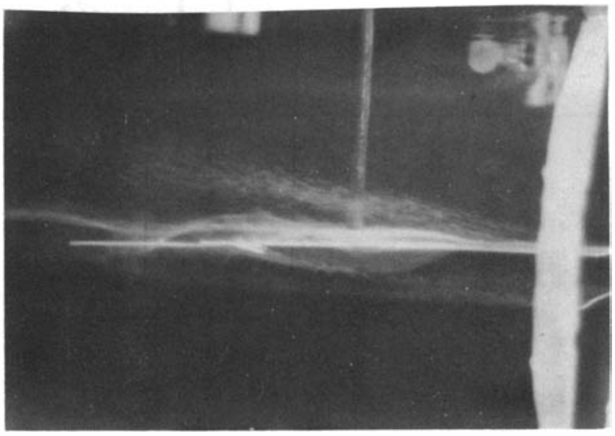

Fig. 5. A single frame of the 16 mm cine film of flow visualization using a model of *M. walchi.* Bubbles moving below the model are O_2, formed at a platinum anode. H_2 bubbles formed at the cathode are of a small and a large (due to particulate matter in the water) size class. The former are useful for tracing flow patterns, while the latter rise conspicuously. A vortex has just been shed, and the deflection in bubble paths which is seen just posterior to the opisthosoma represents a portion of its recirculating flow.

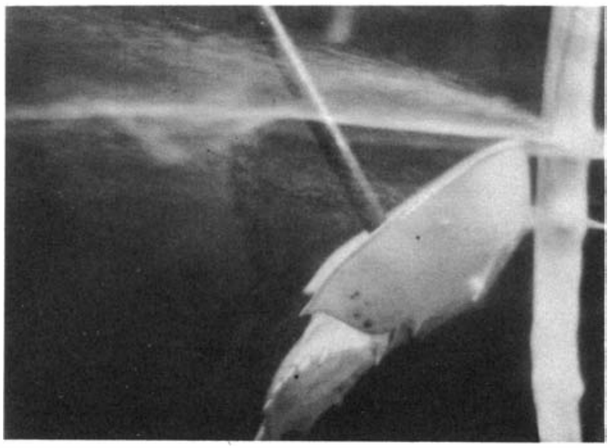

Fig. 6. A single frame of the 16 mm cine film of flow visualization using a model of *L. polyphemus* (details as for Fig. 5).

Vortex formation and shedding in and from the prosomal vault is characteristic of any generally horseshoe crab-like shape, at any of the orientations or flow velocities under consideration. However, a closer look at these flow patterns shows that the precise size and shape of the vortex is dependent on the orientation of the model and the velocity of the fluid. This dependency is illustrated in Figs. 7 and 8, matrices of orientation-velocity variation for each model. Dependency is mappable on a finer scale than the divisions of this matrix might suggest. However, the most unambiguous significance can be assigned to variation of this scale.

Now, of what importance to a swimming horseshoe crab is the formation of a vortex of a particular size and shape? One aspect of efficient swimming is efficient production of thrust. This, in turn, requires efficient appendage functioning in both power and recovery phases of the stroking cycle. It is during the recovery stroke that the vortex comes most directly into play. Efficient recovery means reduction of the drag forces acting on the appendages during recovery movements, since these forces would be oriented opposite to the direction of motion. One important way in which horseshoe crabs effect this drag reduction is to reduce the velocity

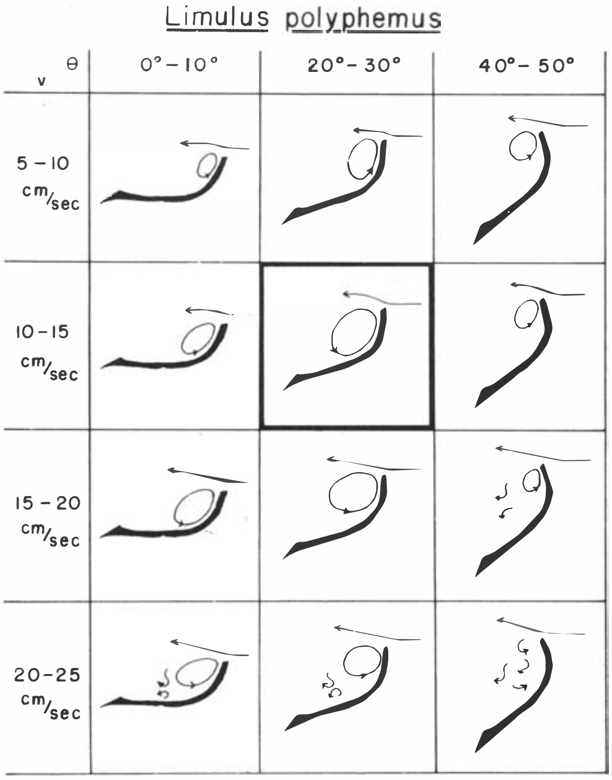

Fig. 7. Matrix showing variation in vortex size and shape corresponding to different values of Θ and v for *L. polyphemus.* The heavily framed square indicates the value of Θ and v which results in the most efficient recovery stroke for the prosomal appendages. Flow is indicated by arrows which correspond to curves b and v in Fig. 4.

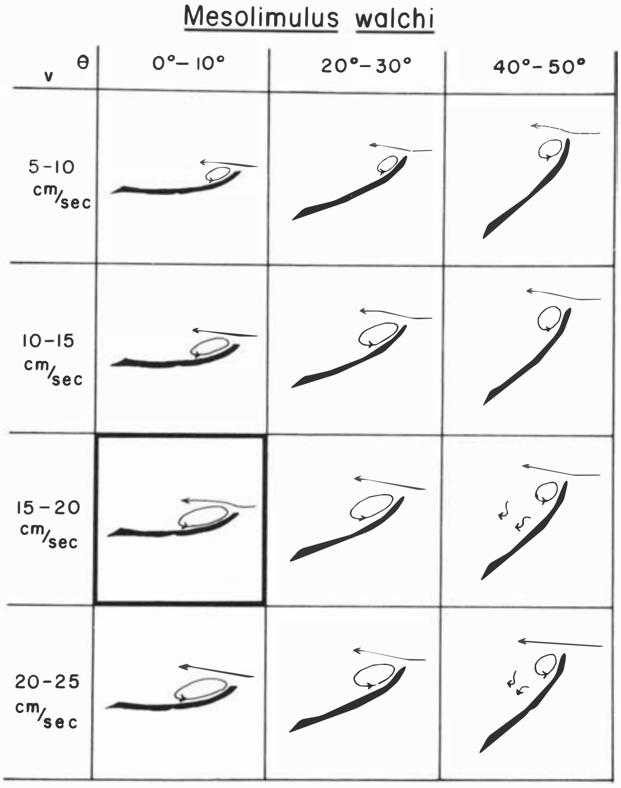

Fig. 8. Matrix showing variation in vortex size and shape corresponding to different values of Θ and v for *M. walchi* (details as for Fig. 7).

of prosomal appendages relative to their surrounding fluid during the recovery, and one important method for doing this is to execute the recovery stroke via the 'dorsal' anteriorly moving portion of the prosomal vortex. Therefore, the vortex arrangement which would be most auspicious for efficient recovery stroking would be one in which there was a coherent backflow extending from the posteriormost portion of the excursion range of the prosomal appendages, forward to the anteriormost portion of their excursion – the edge of the prosomal doublure. This configuration is best obtained, for the models, under the conditions represented by the heavily framed squares of Figs. 7 and 8. These same conditions therefore constitute our prediction of Θ and v values for the swimming animals.

Indeed, for *L. polyphemus* these conditions of orientation and flow velocity are just those under which horizontal swimming occurs. This behavioral observation constitutes convenient and encouraging corroboration of our predictions of Θ and v based on the experiments. However, the predictions can be made just as strongly in the absence of observed values for these characters.

The coincidence of the path of movement of the prosomal appendages with the flow patterns observed on the *L. polyphemus* models, and the coincidence of observed values of Θ and v with the range of those values predicted from flow visualization, argue that flow patterns are an important control of swimming orientation and speed. In reality, there are other physical relationships which share in this control. The most important of these is the dependence of lift and drag forces on Θ and v. In the final analysis, though, these other controls simply serve to locate the actual values of Θ and v within the range prescribed by flow patterns.

As noted above, and as shown in Fig. 8, the values of Θ and v which result in the most 'helpful' vortex configuration for *M. walchi* are 0°–10° and 15–20 cm sec^{-1}. These results give us an experimental estimate of these characters for this fossil species.

Vortex shedding frequency (f_V) is dependent on the same variables as vortex shape and size. Thus, for the optimum conditions specified above, each model has a characteristic f_V.

In order for the relative velocities of prosomal appendages and their surrounding fluid to be minimized during their recovery stroke, it is obvious that the prosomal vortex must be intact and in place during recovery execution. If this relationship is to be preserved throughout consecutive stroking cycles, stroking frequency (f_S) must equal f_V and vortex shedding must occur during the power phase of the stroking cycle.

This is not to say that stroking is absolutely constrained to coincide with vortex shedding as observed in the legless models. The energy input of appendage motion is great enough to overcome the periodic energy distribution associated with the vortex. In fact, within certain limits, stroking frequency is probably able to control the actual rate of vortex shedding in the swimming animal. This is why there is no problem in coordinating phases of these two cycles, once their periods are equal. The point is simply this: when vortex shedding and stroking are coordinated, there is a savings of appendage energy which would otherwise be invested in setting up a periodic distribution of current energy different from that distribution which is potentially (i.e. independent of appendage motion) in force.

For the *L. polyphemus* model, the measured f_V is about 2 sec^{-1}. This corresponds closely to the f_S noted above, lending support to the hypothesis of control that has been set forth. This hypothesis would also argue that the measured f_V for the *M. walchi* model (1.7 sec^{-1}) indicates for that species a normal f_S during horizontal swimming of 1.7 sec^{-1}. Again, we have an experimental determination of a swimming character for a fossil species that is independent of our knowledge of the value of that character in the Recent species.

To summarize this look at swimming, experiments involving the visualization of flow patterns around models of swimming horseshoe crabs allow one to explain or reconstruct swimming orientation, swimming speed, and stroking rate. *M. walchi* swam at a smaller angle to the horizontal, swam faster, and swam with a lower stroking rate than *L. polyphemus.* The full significance of the values for each of these characters will take form only in the light of other investigations on the swimming of horseshoe crabs. However, even at this point, the differences between *M. walchi* and *L. polyphemus* suggest greater swimming ability and endurance for the former.

If the carapace morphology of *M. walchi* is more specialized for swimming, what is the reason for the more highly vaulted carapace of *L. polyphemus*? Part of the answer becomes clear when we look at the burrowing behavior of horseshoe crabs.

BURROWING

The discussion of swimming has involved a consideration of the direct interaction between the dome-like prosoma of a horseshoe crab and the external environment; here, let us look at a more indirect interaction. During burrowing, the ventral surface of the prosoma and the substrate define a closed space, the prosomal vault, within which the prosomal appendages operate. The ventral surface of the prosoma corresponds precisely to the surface form of an abstract three-dimensional body defined as the locus of all appendage positions. This relationship means that during burrowing, the limb elements of *M. walchi* cannot obtain the acute angulation of those of *L. polyphemus* (see Fig. 1).

During burrowing, part of the first phase of propulsive movements of the prosomal appendages consists of flexion at the femoral-patellar articulation. This flexion takes place about an axis defined by two points of articulation on the dorsal surface of the joint. It is accomplished largely by muscles in the femur which insert on an arcuate sclerite embedded in the ventral arthrodial membrane of this joint (Ward, 1969). As can be seen in Fig. 9, the moment arm of these muscles acting about the femoral-patellar articulation is greatest when the angle between the femur and patella is small. When the length of this moment arm is maximized (holding other variables constant), so is the force which can be generated, at the distal end of the appendage, against the substrate. Thus, the prosoma of *L. polyphemus* allows greater force production, in this respect, than that of *M. walchi.*

We may also look at the shape of podomeres themselves. The femur and patella of *L. polyphemus* are much deeper dorso-ventrally and of greater cross-sectional area than those of *M. walchi.* Besides being able to accommodate a larger muscle mass, this means that at any possible limb orientation the arcuate sclerite is located farther from the femoral-patellar articulation in *L. polyphemus.* Again, this represents an increase in the moment which can be developed for flexion at this joint. These observations are only brief examples of the sort of differences that exist between the mechanical system of burrowing in *L. polyphemus* and *M. walchi.* Other indications of specializations for burrowing behavior in *L. polyphemus* have been noted by Eldredge (1970) and will be dealt with further elsewhere.

Before leaving the matter of appendage morphology, it is important to note that the joint mechanics of *M. walchi* are not without their advantages. The shorter moment arm of muscles acting at its femoral-patellar joint means that for a given rate of displacement of the muscle insertion, the appendage tip will move at a greater linear velocity. This is important because flexion at the femoral-patellar joint also occurs during the power stroke of the swimming cycle of the prosomal appendages, and because the propulsive force generated by the appendage varies as the square of its linear velocity. In general, the appendages of *M. walchi* are 'designed' for quick action against relatively small forces of resistance, while those of *L. polyphemus* are 'designed' for more powerful action against larger resistance. These alternate strategies may be interpreted as specializations for swimming and burrowing respectively.

CONCLUSIONS

A hydrodynamic and mechanical analysis of swimming and burrowing in horseshoe crabs can help to explain and reconstruct precise details of their morphology and behavior. This discussion has dealt with only a few aspects of each of these activities. Many activities (e.g. walking, scuttling, feeding, enrolling, righting) have not even been mentioned. However, further work on these and other activities supports the specific determinations made here, the importance of swimming and burrowing to each of the species considered, and the general view of relative swimming and burrowing proficiencies.

It is interesting that each morphological character discussed (general prosomal shape, appendage angulation, and appendage robustness) is influenced, in each species, by conflicting selective pressures that are related to the divergent mechanical requirements of two important activities. The state of any one of these morphological characters thus reflects a compromise representative of the relative importance of the activities. Certainly there are instances of morphological change, in the evolution of horseshoe crabs, that are related to real innovations in their behavioral repertoire. However, at least some of the differences between *M. walchi* and *L. polyphemus* seem rather to be the result of a shift in the balance of importance between two mechanically competing activities – swimming and burrowing.

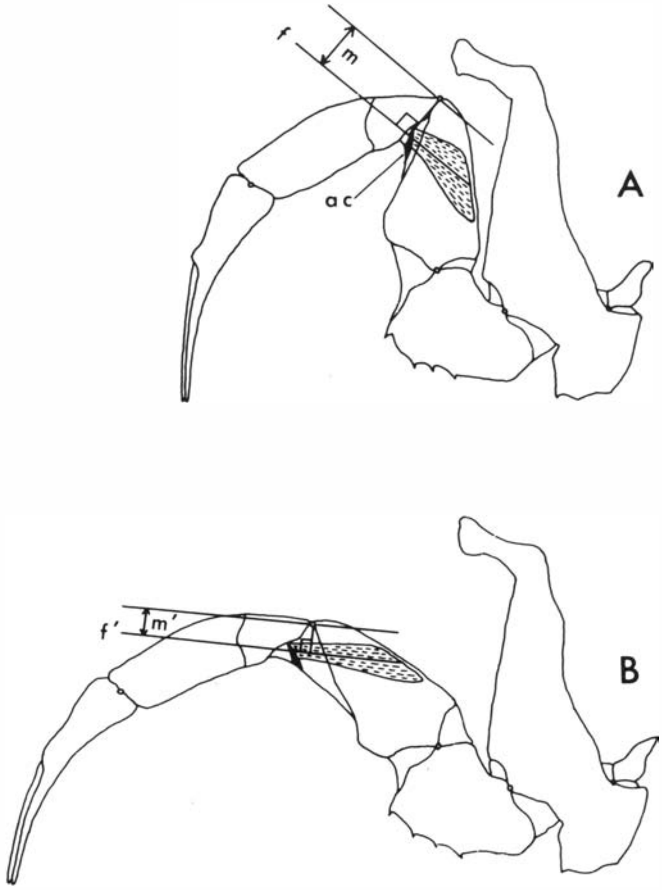

Fig. 9. Moment of a femoral-patellar flexor (muscle represented by dashed lines). Axes or points of articulation are shown as small circles. f, line of force production, or line of muscle action in a flexed position (A); f', line of muscle action in a more extended position (B); m, moment arm of muscle acting in the flexed position (A); m', moment arm for the more extended position (B); ac, arcuate sclerite.

ACKNOWLEDGEMENTS. – Part of this work was completed during tenure of a National Science Foundation Graduate Fellowship. I am particularly grateful to Richard I. Land and D. James Baker for advice and equipment pertaining to technical aspects of the experimentation. I have also appreciated discussions of the material presented here with Niles Eldredge, Stephen J. Gould, Thomas A. McMahon, Jane A. Peterson, and Leif Størmer.

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Functional morphology and evolution of xiphosurids

JAN BERGSTRÖM

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Aspects of the morphology, evolution and systematics of the Xiphosurida are treated. The ancestral forms lacked specialization for ploughing, and their chilaria were evidently developed as prosomal walking legs. The corresponding tergite (of the pregenital segment) was probably separate from the main prosomal shield in the early xiphosurids as well as in the eurypterids. From this stem two main groups seem to have evolved. One consists of the synziphosurids, large-eyed eurypterid-like hunters with striking opisthosomal tagmosis. The other consists of the burrowing and ploughing xiphosurids, in which the opisthosomal tergites were subject to progressive fusion ending with a single opisthothoracic tergal shield in the Late Palaeozoic. The last prosomal appendages evolved into the chilaria, if this did not happen earlier, and the corresponding free tergite disappeared. Probably in Carboniferous time the limulines came into existence through a sudden displacement of the prosomal/opisthosomal boundary.

Jan Bergström, Department of Historical Geology and Palaeontology, University of Lund, Sölvegatan 13, S-223 62 Lund, 1st August 1973.

The Xiphosura may be considered to constitute a subclass or class of chelicerate arthropods. The delimitation has been discussed in the past, but no general agreement seems to exist. Generally, the xiphosurids are included with the aglaspidids and eurypterids in the Merostomata. However, as generally understood, this taxon probably represents an evolutionary grade rather than a phylogenetic unit. The differences between xiphosurans and eurypterids are clear enough to make the taxonomic distinction quite easy. The differences between the xiphosurans and the aglaspidids are still more profound, but are hardly appreciated accordingly in the general literature. The aglaspidids differ from xiphosurans and all other known chelicerates in having a phosphatized exoskeleton. The aglaspidids are also unique in lacking distinct tagmosis ventrally. This means that prosomal and opisthosomal appendages are all uniformly built, except for the chelicerae (Raasch 1939). Moreover, the aglaspidid appendages are bifid like those of the trilobites, although the detailed morphology is poorly known (Repina & Okuneva 1969). There is said to be six pairs of prosomal appendages (Raasch 1939), a number also found in terrestrial chelicerates, while the original postantennal number appears to be seven in the xiphosurans (see below). The strabopids appear to differ from the aglaspidids in having a calcified exoskeleton and probably fewer prosomal appendages, features which do not indicate close xiphosuran affinities (Bergström 1971).

Synziphosurids and chasmataspidids have a eurypterid-like body, but an analysis of prosomal characters indicates that they may be true xiphosurans. The poor preservation of their exoskeleton is a xiphosurid character which also serves to distinguish them from the eurypterids (cf. Wills 1965).

Discussions on xiphosurid phylogeny have generally avoided any functional aspects (e.g. Størmer 1952). On the other hand, when the function has been taken into consideration, the palaeontological evidence has been misinterpreted (Tiegs & Manton 1958:313). Herein an attempt is made to see the connection between function and morphology and to draw phylogenetic conclusions from the result.

The study was performed at the Department of Historical Geology and Palaeontology in Lund with the aid of its facilities kindly put at my disposal by Professor Gerhard Regnéll. I am very grateful for the loan of xiphosuran material from the Swedish Museum of Natural History and the Swedish Geological Survey in Stockholm, The British Museum (Nat. Hist.) in London, the Geological Institute in Cambridge, and Professor Paul Tasch of Wichita, Kansas. I was also kindly permitted to study the collections at the Palaeontological Museum in Oslo. In the work I have been aided greatly by discussions and information, and in this respect I would like to thank particularly Dr. Niles Eldredge of New York, Professor Robert R. Hessler of La Jolla, Calif., Prof. Leif Størmer of Oslo, Dr. Valdar Jaanusson of Stockholm, Drs. Charles Waterston and John Miller of Edinburgh, and Dr. Daniel C. Fisher of Cambridge, Mass.

Mrs. Siri Bergström finished the drawings and Mr. Sven Stridsberg made the photographs, except for some exposures. Language correction was performed by Mr. Brian Holland. Grants from Kungliga Fysiografiska Sällskapet and Matematisk-naturvetenskapliga fakulteten, Lund, and Naturvetenskapliga Forskningsrådet, Stockholm, facilitated the study. I am grateful to the above institutions and persons, and still others, for all kinds of assistance.

THE XIPHOSURIDS

Early representatives

Among the early xiphosurans formerly recognized as constituting the Synziphosurina two general types may be distinguished. One of them is particularly characterized by a marked opisthosomal tagmosis resulting in the formation of a broad preabdomen and a narrow postabdomen. This type is found in the Limuloididae, type family of the Synziphosurina. The other type has an opisthosoma without strongly marked tagmosis and is therefore more similar to the true xiphosurids (cf. Bergström 1968:500—501). It is possible that these comparatively unspecialized xiphosurans belong to an ancestral group which may have given rise to later xiphosurids as well as to the synziphosurids and perhaps the chasmataspidids.

The ancestral xiphosuran group hinted at may include genera like *Eolimulus* and *Drabovaspis* of Cambrian to Ordovician age. *Eolimulus* and *Drabovaspis* are not particularly similar to one another but both have a low relief of the prosoma (cf. Bergström 1968, Fig. 6E, F), indicating that they did not plough the sediment in a limulid-like manner. The paired eyes seem to have been comparatively large in both of them. The late Early Cambrian (or perhaps Middle Cambrian) *Eolimulus* is fairly similar to the approximately contemporary supposed eurypterid *Kodymirus* (cf. Chlupáč & Havlíček 1965:9; Bergström 1968:502) and the common ancestor may have been fairly close to these forms. Unfortunately the opisthosoma is not known with certainty in any of the two xiphosurans, although *Triopus* has been suggested to represent the opisthosoma of *Drabovaspis* (Bergström 1968:492; Fig. 3; Chlupáč in a personal communication has indicated other possible combinations with undescribed forms).

Evolutionary trends in the Palaeozoic

In the Palaeozoic there are a number of xiphosurids with morphological features intermediate between those of the two xiphosurids treated above and extant limulids. The oldest of the intermediate genera are *Archeolimulus* from the Middle Ordovician and *Pseudoniscus* from the Late Silurian. *Neolimulus* may be a junior synonym of *Pseudoniscus*. The ophthalmic and interophthalmic ridges are more distinctly developed than in the xiphosurids discussed above, in which they may even be entirely absent.

ARCHEOLIMULUS. – Unfortunately this old genus is known only from isolated prosomal shields of *A. hanusi* while the opisthosoma is unknown. The prosoma is strongly arched and

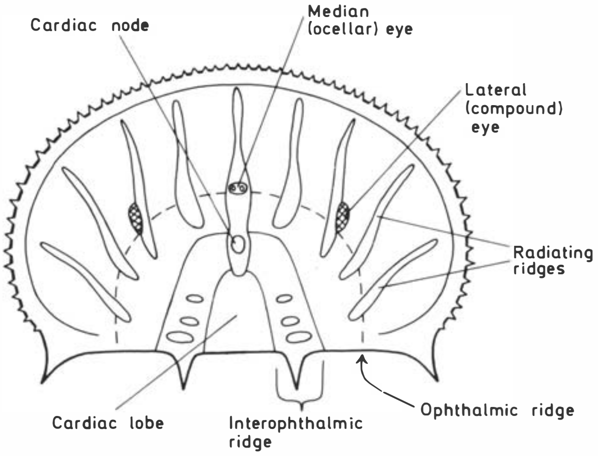

Fig. 1. Diagrammatic drawing of the prosoma of *Limuloides limuloides* (Woodward) to show various xiphosuran and synziphosurid characters.

more elongate than in later xiphosurids. The cardiac lobe is exceptionally narrow, bordered by straight parallel interophthalmic ridges. The ophthalmic ridges are well developed only close to the lateral eyes, the position of which is marked by an elevated node. A small median node slightly behind the lateral eyes evidently indicates the position of the median eye.

Although the proportions of the prosoma differ appreciably from those of later xiphosurid prosomas, the detailed features are remarkably similar. The strong arching with a steeply sloping anterior surface is also reminiscent of that of later forms (cf. Chlupáč 1965, Pl. 4; Bergström 1968, compare Fig. 6G with 6H). This morphology may indicate that *A. hanusi* ploughed its way through the sediment in the same way as probably most later xiphosurids.

PSEUDONISCUS, NEOLIMULUS. – In the Late Silurian *Pseudoniscus* and the probably congeneric *Neolimulus,* the prosoma had attained a shape roughly like that of modern limulids. The interophthalmic ridges differ from those of *Archeolimulus* in diverging backwards. The ophthalmic ridge is more laterally positioned than in any other xiphosurids and has been mistaken for an ecdysial suture in *P. aculeatus* (cf. Schmidt 1883:41, *Gesichtslinien*) and in *P. roosevelti* Clarke and *P. clarkei* Ruedemann (cf. Ruedemann 1918:106–107; Pl. 33:6–9). Small lateral eyes at the ophthalmic ridges were observed by Ruedemann (1918) in both *P. roosevelti* and *P. clarkei.* The correctness of the observation has been doubted, but there is no reason to suppose that these forms were blind.

Most interesting are the finds of opisthosomata in some cases. The typical opisthosomal segmental tergites lack tagmosis and number nine in those cases where the number is complete, that is in specimens of *P. aculeatus, P. roosevelti* and the Scottish specimen I. 14724 (British Museum, Nat. Hist.; labelled 'cf. *Pseudoniscus aculeatus*' but possibly belonging to *N. falcatus* Woodward). The tergites are all free. The tail spine is known from the Scottish specimen referred to above and from *P. aculeatus.* It is comparatively short and provided with a blunt median edge. The opisthosoma is convex with fairly steeply sloping sides as excellently seen in a specimen figured by Ruedemann (1918, Pl. 33:6). There is no horizontal hinge-line (cf. Bergström 1973:14). The rhachis is not only highly convex but also exceptionally wide in front. This feature is particularly evident in flattened specimens like the type specimen of *Neolimulus falcatus* Woodward.

BELINURUS, NEOBELINUROPSIS. – Species of *Belinurus* have a prosoma of comparatively modern appearance. It may be strongly arched, although diagenetic flattening commonly obscures this feature. The doublure has a flattened marginal shelf similar to that of *Limulus.* On the dorsal side the ophthalmic ridges are distinctly developed and much closer together than in *Pseudoniscus.* The cardiac area is delimited by inter-ophthalmic furrows, while the interophthalmic ridges are weakly developed or absent. The ophthalmic ridge is straight behind the paired eye. Generally the ophthalmic ridge does not seem to be extended into a spine posteriorly. In posterior view the prosomal arching is similar to that of many trilobites, as *e.g.* seen in the holotype of *Belinurus koenigianus* Woodward, 1872. The vaulted cardiac lobe is morphologically analogous to the arched rhachis of a trilobite. Laterally there is a horizontal strip ending in a fulcral point beyond which the "cheek" slopes uniformly outwards-downwards. In contrast to the condition in *Pseudoniscus,* a horizontal hinge-line is thus formed to ensure a rigid articulation.

The opisthosomal exoskeleton may consist of five articulated segmental tergites and a posterior tergal shield with three pairs of pleural spines, as in *B. koenigianus.* The tail spine generally is keeled and long. The horizontal articulating hinge-line is found along the opisthosoma but the length decreases backwards. In *B. koenigianus* the anterior side of each tergite has a weakly defined fulcral node, which apparently fits into a socket on the under side of the next anterior tergite, a condition well known from many trilobites (cf. Bergström 1973). The pleural spine flattens out distally to become horizontal.

The Late Devonian *Neobelinuropsis rossicus* (Tschernyschew, 1933) shows considerable similarities with species of *Belinurus* and may be phylogenetically intermediate between *Pseudoniscus* and *Belinurus.* The cardiac lobe is more wedge-shape than in *Belinurus* and in that respect reminds one of that of *Pseudoniscus.* According to descriptions there are eight movably articulated opisthosomal tergites, corresponding in number with the pleural spines in *B. koenigianus.* The main difference between *Neobelinuropsis* and *Belinurus* seems to be the progressive fusion of posterior tergites in the latter genus.

As pointed out to me by Dr. Eldredge, and further elaborated by him in a separate contribution, some species generally included in *Belinurus* (or *Koenigiella* Raymond, 1944) have an opisthosomal rhachis that is markedly wider than the cardiac lobe. The same condition is found in *Pseudoniscus* and *Neolimulus,* whereas most *Belinurus* species and later xiphosurids have an opisthosomal rhachis and a cardiac lobe of corresponding width. Eldredge regards the different morphology as characteristic of two evolutionary sister groups. However, it is evident from the *Eolimulus-Archeolimulus-Pseudoniscus-Belinurus* suite that the cardiac lobe was subject to a gradual widening throughout the Palaeozoic, the narrow condition being primitive. Therefore, instead of constituting a sister group of the *Belinurus* group, the considerably older *Pseudoniscus* and its allies might have been in part truly ancestral to the former. If a sister group to the *Belinurus* group is to be searched for, *Koenigiella* may, for instance, fit better than the pseudoniscids.

As in the synziphosurids treated below, there may be a microtergite on the boundary between the prosoma and opisthosoma. This microtergite is probably confined to the rhachial ring and seems to be fused to the succeeding tergite in *Belinurus koenigianus* (Pl. 1:4).

EUPROOPS. – The prosoma of this mainly Late Carboniferous genus is generally similar to that of *Belinurus*. However, the ophthalmic ridge distinctly curves inward behind the paired eye and may be prolonged into a spine that extends backwards from the posterior margin of the prosoma. For instance, this 'intergenal' spine is found in *Euproops rotundatus* (Prestwich), *E. amiae* Woodward, and *E.? anthrax* (Prestwich). In *E.? anthrax* there is also a median spine projecting backwards from the cardiac lobe. The interophthalmic ridge may be distinct or more or less obscure. The posterior profile of the prosoma is like that of *Belinurus*. On each side of the arched cardiac lobe is a straight horizontal hinge-line.

The opisthosoma differs from that of *Belinurus* in having an entirely fused tergal cover and the outline is generally more rounded. The number of pleural spines as far as I know is constantly seven, i.e. one less than in *Belinurus*. In the rhachis the anterior five segments (corresponding to the free tergite segments in *Belinurus*) are individually distinct. Behind the fifth segment the remainder of the rachis forms an elevated boss. The prosoma is appreciably arched, but the more or less fused pleural spines form a flattened horizontal brim around the vaulted shield. The tail spine varies in length but seems to be consistently styliform.

Enrollment and folding up

It is possible that all or most Early Palaeozoic xiphosurids were able to enroll like most trilobites. However, *Pseudoniscus* is the oldest genus in which the enrollment has been seen. The ability to enroll was clearly demonstrated by a specimen of *P. roosevelti* Clarke figured by Ruedemann (1918, Pl. 33:6; cf. Bergström 1973, Fig. 6A, B). The enrollment was obviously of a sphaeroidal type (cf. Bergström 1973:14).

No doubt the ability to enroll was shared by many or all species of *Belinurus*. A case with an enrolled *B. arcuatus* Baily was noticed by Woodward (1878:242). The horizontal flattening of the pleural spines of *B. koenigianus* mentioned above evidently allows the spines to abut against the flattened prosomal doublure when the animal was wholly enrolled.

Enrolling necessitates the presence of more than two body tergites besides a tail spine, and as the opisthosomal tergite cover is fused into one shield in the euproopids, it is clear that true enrollment did not occur in these forms. The presence of only one articulation in the tergite cover would perhaps lead the observer to the conclusion that species of euproopids were unable to fold up in any way to protect the venter. However, one specimen of *Euproops? anthrax* (Prestwich), preserved in an Upper Carboniferous limestone nodule from Shropshire and kept in the British Museum of Natural History, is actually preserved with the prosomal and opisthosomal shields folded up to one another (Pl. 1:6). This condition appears to explain the rounded shape of the opisthosoma and the horizontal flattening of the opisthosomal spines in euproopids. Obviously the bases of the spines fitted tightly against the marginally flattened doublure of the prosoma, whereas the tips of the spines formed a protective girdle around the folded up animal except along the articulation side. The latter side was protected by the three spines projecting from the posterior margin of the prosoma. Another morphological feature is obviously connected with the folding ability in *E.? anthrax*, namely the strong arching of the opisthosoma. This arching is probably due to the need of space for the appendages when the tergal shields were folded up.

E.? anthrax seems to be so different from *E. amiae* and *E. rotundatus* as to merit the erection of a new genus, but this is not done here. The differences do not influence the conclusion that *Euproops* did fold up. The morphological characters with functional importance in the folding, such as the vaulted and rounded opisthosoma with a flattened spine border and a lowered level of articulation between prosoma and opisthosoma indicate that probably all known members of *Euproops* were able to fold up in the same manner as *E.? anthrax.*

The folding up has also been observed in a species of *Pringlia* (Pl. 1:4). The figured specimen shows the marked convexity of the opisthosoma and the development of a horizontal hinge-line. The opisthosomal border is flattened but lacks the spines characteristic of *Euproops.* The hinge-line and the narrow rhachis with its vestigial and probably fused pregenital (?) microtergite (discovered in euproopaceans first by Dr. D. Fisher, personal communication) is also well exhibited by a specimen of *Pringlia birtwelli* (Woodward) (Pl. 1:11).

Creation of the modern limulids

In many respects Mesozoic and Cenozoic limulaceans are close to *Belinurus* and *Euproops,* but still there are consistent differences. The most obvious limulacean characteristic is the fused trapezoidal opisthosoma with its movable lateral spines, without counterpart in other xiphosurids. However, what seems to be really fundamentally different is the articulation between the prosoma and the opisthosoma, although it is functionally very similar in *Euproops* and limulaceans. In *Belinurus* and *Euproops* there tends to be a noticeable difference dorsally between five anterior tergite segments in the opisthosoma and the succeeding ones. In *Belinurus* some three tergal segments behind the anterior ones may form a fused tergal shield which commonly has a pronounced rhachial node. In *Euproops* and its allies the opisthosomal tergites in front of the tail spine form a completely fused shield, but still the rhachis has five distinct tergal segments in front of a pronounced posterior boss. At least the anterior five rhachial segments have direct counterparts in the pleural area. In limulaceans the segmentation of the rhachis is directly comparable with that of the Palaeozoic forms. Five rhachial segments are more or less distinctly visible in front of a uniform posterior part, which may have one or two nodes, one of which is at the anterior end. Surprisingly enough, the anterior five rhachial segments more or less correspond to six pleural spines. The most anterior of these spines is set off from the others by a flexure line. Moreover, this spine is elevated over the others and in level with the prosomal roof, and it lacks connection with the opisthosomal rhachis. Actually, in position and morphology, it looks very much like the paired spines on the posterior margin of the prosoma in species of *Euproops* and its allies. In addition, we know from the embryological development (Iwanoff 1933) that this spine is actually formed by somite VI (cheliceral somite counted as I), of which the rhachial portions are entirely confined to the prosoma.

The number of opisthosomal spines is identical in euproopids and limulids if the elevated spine is not counted. However, if the elevated spine is regarded to have a counterpart in the euproopid opisthosoma, there arises the difficulty of explaining how the limulids could have developed one segment more than in their probable forebears, and how it is possible that the rhachial rings seem to correspond one by one.

I find no way to avoid the conclusion that the articulation typical to modern limulids is unlike that of Palaeozoic xiphosurids in general with regard to the somites involved. There is no indication whatsoever of the presence of somite VI in the opisthosomal tergum of belinurids or euproopids, and somite VII is obviously represented only by a microtergite. On the contrary, the chilaria (as also the metastoma of eurypterids), which probably belong to somite VII, no doubt have their position under the main prosomal shield where the position is known, and they may even be developed as prosomal walking legs in *Weinbergina* (see below). To my mind these circumstances strongly speak in favour of two conclusions. First, the articulation between prosoma and opisthosoma in limulaceans has a secondary position with regard to the segmentation of the animal. Second, the xiphosurans, like probably the eurypterids, basically have their junction between prosoma and opisthosoma between somites VII and VIII (or within VII), that is behind the pregenital segment rather than in front of it as in typical terrestrial chelicerates.

It seems probable that the limulaceans arose from the generally similar euproopaceans through a change in the position of the articulation between the tergal shields. This change must have been momentaneous and evidently represents a major event in the evolution of the xiphosurids. I regard the change and the resulting difference reason enough to differentiate the limulaceans from the older xiphosurids as a distinct suborder.

Apparently the change in the articulation brought with it a considerable change in the folding up mechanism with a loss of the typical sphaeroidal folding up. At the same time the opisthosoma may have received its trapezoidal shape (through loss of margin to margin fit in folding up) and its marginal movable spines. The mode of formation of the movable spines is unknown. It might be argued that the spines represent the tips of the euproopacean pleural

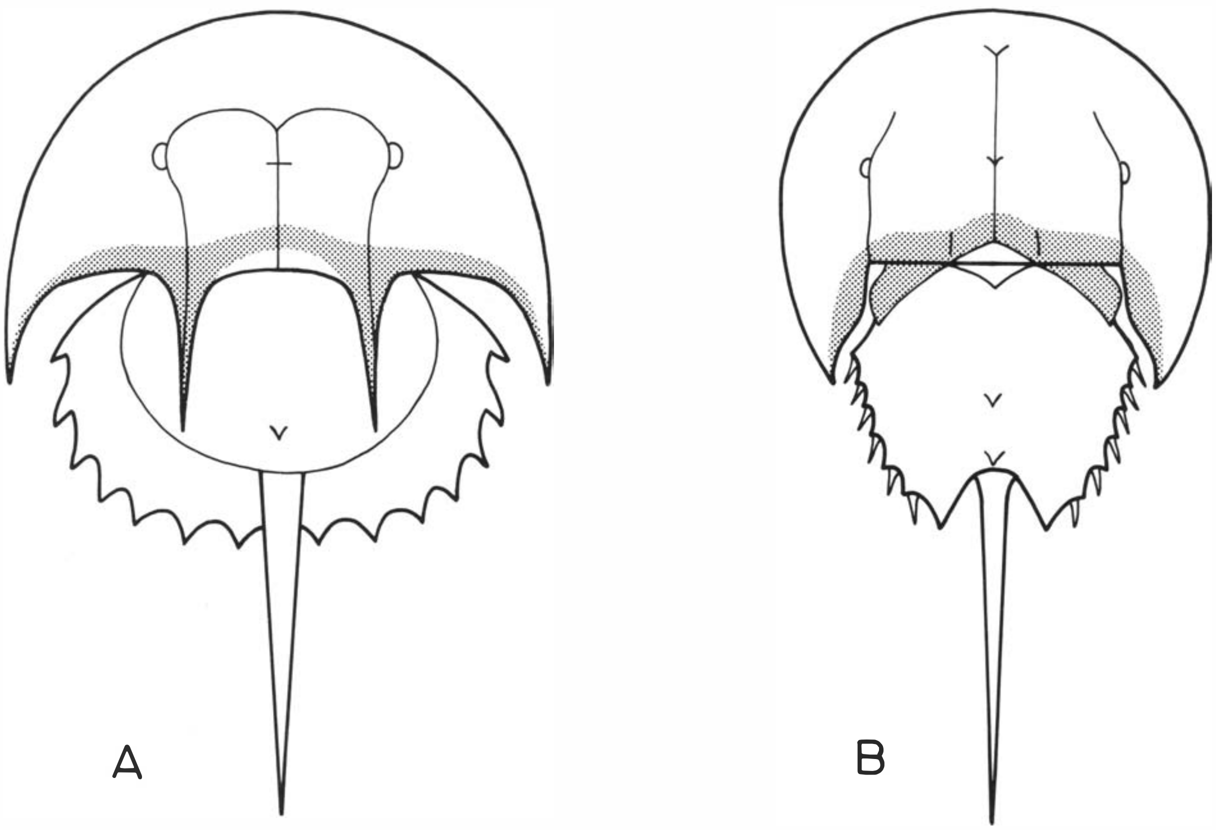

Fig. 2. Comparison between A, the belinurine *Euproops rotundatus* (Prestwich) and B, the limuline *Limulus polyphemus* (Linné). The presumed extent of somite 6 (with last walking leg) is shown by stippling. The true opisthosoma has seven pleural spines in both forms, but in *Limulus* an extra pleural lobe with unique morphology obviously has been formed through the transformation of the "intergenal" spines of *Euproops*. The "intergenal" spine, probably belonging to somite 6, was apparently separated from the prosomal shield through a joint and fused to the opisthosomal shield through a revolutionary ontogenetic change, which in one step produced the limulines. The concentric line in the opisthosoma of *Euproops* marks the inner limit of the flattened border, which fits the prosomal doublure in the folded up animal. No similar coaptational feature is found in *Limulus.* Redrawn after Størmer 1955.

spines, which became articulated like the 'intergenal' spine of the prosomal posterior border. The similarity in the position of the articulation with respect to the extent of the various segments may indicate that the articulations are serially homologous throughout.

The classification of the limulaceans has recently been discussed by Riek & Gill (1971). It may be remarked that the oldest limulacean known is probably the unnamed species described by Dix & Jones (1932) from the Upper Carboniferous of Wales. The species may belong to *Paleolimulus.*

EURYPTERID-LIKE XIPHOSURANS

Under this heading the synziphosurids (Synziphosurina as restricted by Bergström 1968 with the weinberginids added in accordance with Eldredge) and chasmataspidids are treated. In addition, the odd diploaspidids and heteroaspidids are discussed. They are all characterized by an opisthosoma divided into two distinct tagmata, apart from the tail spine or plate.

There is no doubt that the synziphosurids are closely related to the xiphosurids. The relationships of *Chasmataspis* are somewhat more difficult to interpret. A few but diagnostic features indicate that *Chasmataspis* belongs to the Xiphosura and not to the Eurypterida. These are:

(1) The ornament consists of rounded tubercles, not of scales.

(2) There is a marginal prosomal rim, not seen in eurypterids.

(3) At least some of the walking appendages appear to be chelate.

(4) The poor preservation of the integument (cf. Wills 1965:140).
Other characters, besides being of ziphosurid type, particularly indicate synziphosurid affinities.

(5) Strong opisthosomal tagmosis. The trend may be inherited form common pregenitors and may be connected with a particular mode of life. The tagmosis is dissimilar in detail, but this is also the case within the synziphosurid and eurypterid groups.

(6) The presence of a large ocellar node approximately between the compound eyes.

(7) Comparatively large compound eyes (cf. below).

(8) Absence of a median prosomal keel (cardiac ridge), typical for the xiphosurids.

(9) Radiating rays on the prosoma, consisting of ridges or patterned fields in the synziphosurids and tuberculated fields in *Chasmataspis.*

(10) A spiny margin of the prosoma in *Chasmataspis* and the synziphosurid *Limuloides.*

The listed characters corroborate the view of Bergström (1968) on the comparatively close relationship between synziphosurids and chasmataspidids. On the other hand the many differences in opisthosomal tagmosis and sclerite arrangement show that neither group is directly derived from the other. The differences that exist, after all, may justify a separation into two orders in accordance with Størmer (1972).

The affinities of the other chelicerates treated are discussed below.

A few words should be said about the relationships within the family Bunodidae. Unpublished research indicates that the genus *Bunodes* has been used in the past to designate Estonian synziphosurids preserved in lithographic limestone, while *Limuloides* has been used for British and Australian synziphosurids preserved in shale, regardless of the relationships. Some of the British forms undoubtedly belong to *Bunodes,* while others may belong to new genera. The type species of *Limuloides* and *Bunodes* are generically distinct, but so similar that Limuloididae may be considered as a junior synonym of Bunodidae.

Opisthosomal tagmosis

BUNODES, LIMULOIDES. – The appendages are unknown and the extent of the mesosoma and metasoma therefore can only be subject of speculation. This is unfortunate as the extent of meso- and metasoma is much more important for the discussion of relationships than is the delimitation between the broad preabdomen and the narrow postabdomen.

The two bunodid genera are identical with regard to opisthosomal tagmosis. The wide preabdomen includes six normally developed tergites, each with a horizontal hinge-line and a broad pleural spine distal to the fulcrum. The postabdomen has three tergites in front of the slender tail spine. The postabdominal tergites lack the hinge-line and the pleural spine. There may also be ornamental differences between pre- and postabdomen. This is the case in *Bunodes lunula* Eichwald (with junior synonyms *B. rugosus* Nieszkowski and *B. schrenki* Nieszkowski), in which the preabdominal tergites have a pattern of circles of varying size, while the postabdomen is smooth (e.g. specimen I. 2774(g) in British Museum, Natural History). The postabdominal sclerites bend down laterally but are terminated without bending inward. Therefore they are not ring-shaped like the postabdominal sclerites of the eurypterids.

It was noted above that the intertergal articulation of the preabdomen differs from that in the postabdomen by the presence of a horizontal hinge-line. The articulation between the last preabdominal tergite and the first postabdominal tergite is of the postabdominal type. The last preabdominal tergite is functionally adapted to this condition in lacking a hinge-line on the posterior side, where the tergal extremities are bent down to accommodate the first postabdominal tergite. This duality in the morphology of the last preabdominal tergite is therefore a functional necessity and must not be interpreted as the result of a fusion of two segments, as has previously been done (e.g. Størmer 1955:P16).

WEINBERGINA. – There are ten articulated "normal" tergites in the opisthosoma, seven of which belong to the preabdomen. The flattened condition of the material makes it difficult to reconstruct the original shape. However, new material from Bolivia shows that the construction of the opisthosoma of the weinberginids is very similar to that of the bunodids. (Eldredge, personal communication). Lehmann (1956) has shown the existence of plate-like abdominal appendages. However, the detailed structure and the number of appendages is not known.

There is a long and slightly curved tail spine, which may have acted as a ski.

CHASMATASPIS. – The Ordovician freshwater (?) merostome *Chasmataspis laurencii* Caster & Brooks, 1956, conforms with the synziphosurids in having a broad preabdomen and a narrow postabdomen. In detail, however, the arrangement is quite dissimilar. The chasmataspidid preabdomen is encased in a rigid armour of tergites belonging to three segments and a large sternite. The sternite is entire except for a pair of transverse slits which may have served as openings of gill chambers. The sternite may represent altered appendages. There are no other external opisthosomal appendages.

There are nine postabdominal segments, each with a ring-shaped exoskeleton consisting of a dorsal tergite and a ventral sternite, forming a small pleural fold at the junction. The last segment carries a fairly long tail spine.

DIPLOASPIS, HETEROASPIS. – An opisthosomal tagmosis similar to that of *Chasmataspis* is found in a few merostomes of problematic affinities described under the generic names *Diploaspis, Heteroaspis* and *Borchgrevingkium* (cf. Størmer 1972). The best known species is *Diploaspis casteri* Størmer, 1972, from the Lower Devonian. In this species there is a large preabdominal tergite and a slightly smaller sternite. The preabdomen is followed by a postabdomen with probably nine segments and a tiny rounded telson. The postabdominal segments appear to carry ring-shaped sclerites (cf. Størmer 1972, Pl. 2:3 and Fig. 10, in which the curvature of the sclerites indicates that the exposed parts are ventral). If the entire set of opisthosomal segments is 12, the number thought to be primitive for chelicerates, the preabdomen may include three segments. A plate-shaped tail is found also in pterygotids (cf. Størmer 1972:6) as well as in the poorly known xiphosurid *Moravurus rehori* Pribyl, 1967, but in both cases the tail sclerite is keeled and probably derived from a tail spine of more normal merostome type. The tail sclerite of *Diploaspis* looks entirely primitive.

A tail spine is found in *Borchgrevinkium,* but this merostome is not necessarily closely related to *Diploaspis.* The state of preservation of *Heteroaspis novojilovi* Størmer, 1972 (cf. Størmer 1972, Pl. 5:1c, d) may indicate xiphosuran rather than eurypterid affinities (cf. Wills 1965:140, referring to Holm and Størmer). The fragmentary remains of the Silurian *Kiaeria limuloides* Størmer, 1934, are said to represent the preabdomen but may be postabdominal. They are associated with probable xiphosurid trails made by a large (about 20 cm wide) animal. Preabdominal modifications similar to those in *Diploaspis* and *Heteroaspis* (at least dorsally) are found in some eurypterids (cf. Størmer 1972:2, 12).

Prosomal characters

BUNODES, LIMULOIDES. – The blindness of the bunodids is generally accepted, though erroneous. I had the occasion to study Woodward's material of bunodids on a visit to British Museum in January 1970. This study revealed the presence of exceptionally large paired eyes in *Bunodes* n. sp. 1 and somewhat smaller eyes in other species of *Limuloides* and *Bunodes.* In *B.* n. sp. 1 they are actually so large and bulging that they were cut off when the specimens were split out from the rock and the specimens were not later prepared. The paired eyes are situated on a pair of radiating ridges. The eye node is one of a series of nodes which together form a curved structure apparently corresponding to the ophthalmic ridge of other xiphosurans. A median node may represent a median eye. The presence of a median eye is evident in *Bunodes lunula* Eichwald, in which there are distinctly two ocelli in the median eye (British Museum specimen No. I. 2774).

The bunodids have a flattened cardiac lobe surrounded by interophthalmic ridges. The nodes constituting the ophthalmic ridge separate a central area with low convexity from a more or less steeply sloping margin. The nodes are situated on nine ridges which cross the ophthalmic ridge and approach the marginal rim. The median ocelli mentioned above are situated on the median ridge, and the compound eye on the lateral side of the second pair (from in front) of ridges. The posterior margin may be provided with strong spines, which may have protected the prosomal-opisthosomal boundary in the enrolled animal (enrollment capacity deduced from experiments with paper models). The marginal rim is provided with fine spines in *Limuloides,* a good indication that the animals were no active burrowers.

Eldredge (personal communication) identified a tiny sclerite directly beneath the posterior border of the prosoma in *Bunodes lunula* and *Limuloides limuloides* (Woodward). It is not evident from the material if this tergite is fused or articulated with the next following tergite. It is difficult to tell if this tergite represents an entire somatic segment or only part of one. There is also no evidence that it belongs to the opisthosoma. The arthropod head (including the prosoma) is a functional unit, and the delimitation backward is decided by the appendage morphology. I find it quite likely that the small tergite belongs to the chilarial (pregenital) segment, the succeeding large tergite representing the genital segment. As the chilaria obviously belong to the head, functionally speaking, this would also be the case with the small tergite.

WEINBERGINA. – The prosomal shield of *Weinbergina opitzi* Richter & Richter, 1929, is flattened in slightly different ways in the three hitherto described specimens (Richter & Richter 1929; Lehmann 1956). The folding over of the margin, the manner of wrinkling and the absence of large-scale ornamentation together indicate that the shield was fairly evenly vaulted prior to flattening. In contrast to conditions in extant xiphosurids the ventral margin is formed as an edge and not as a flat surface facing ventrally (cf. Richter & Richter 1929:197). Nothing is said about the existence of any doublure in the descriptions. However, a line parallel to the border in one of the radiographs (Lehmann 1956, Pl. 2:5) may mark the edge of a doublure.

Lehmann (1956:75; Fig. 3) remarks that 13 pyrite grains arranged in two arched lines may mark the position of a compound eye. This supposition seems to be verified by the observation of a long eye beneath an ophthalmic ridge in a new Bolivian weinberginid (Eldredge, personal communication). Eldredge also reports the presence of a small tergite at the posterior border of the prosoma in the Bolivian species, similar to that of the bunodids.

According to Lehmann (1956) there are six pairs of prosomal walking legs in *Weinbergina opitzi,* as compared with five pairs in all other xiphosurids in which the appendages are known. All of these are provided with spurs indicating that the animal lived on a very soft bottom. Lehmann reports possible traces of chelicerae in one specimen, but he does not regard the existence as proved.

There are at least three possibilities to account for the large number of walking legs. First, the prosoma in *Weinbergina* may have included one segment more than in extant xiphosurids. Second, the appendages corresponding to the chelicerae may have been developed as ordinary walking legs. Third, the appendages of the seventh (pregenital) segment may have been developed as walking legs situated in the prosoma. The first two possibilities appear to be too unlikely to be seriously considered. In addition, the last pair of walking legs occupied the normal position of the chilaria, leaving no space for separate chilaria. *Weinbergina* therefore appears to be the only chelicerate known, excepting probably the aglaspidids, in which the appendages of the seventh segment are still developed as walking legs. In the development of the pregenital appendages, *Weinbergina* is still closest to modern xiphosurids, in which the chilaria have considerable similarity to the coxae of the walking legs and may fairly easily be accepted as reduced appendages. In eurypterids the metastoma may be a radically altered remnant of the appendages of the pregenital segment (cf. e.g. Størmer 1963, Fig. 44; Wills 1965) and in adult scorpions the pregenital segment is completely aborted. The condition in *Weinbergina,* if correctly interpreted, indicates that the pregenital segment morphologically and functionally was included in the prosomal tagma, except for the separate tergite. This means that *Weinbergina* obviously had one prosomal segment more than is generally accepted as normal for the chelicerates. However, the morphology and position of the chilaria in xiphosurids and the metastoma in eurypterids indicates that the longer prosoma may be characteristic for the xiphosuran and eurypterid chelicerates in general. According to Raasch (1939:12), the aglaspidids differ from the xiphosurans and eurypterids in having the shorter prosomal segment number characteristic of terrestrial chelicerates.

The lack of a ventral flat border on the prosoma and the corresponding lack of rigidity (cf. Richter & Richter 1929:197) indicates that *Weinbergina* did not push its way through the superficial sediment in the manner typical for extant xiphosurans. This conclusion is corroborated by the extraordinary length of the walking legs, which made them protrude outside the prosomal shield in the fossilized specimens and probably also in life. The prosomal shield was obviously held elevated over the substratum, the margin not touching the bottom. The development of spurs on all walking legs, making them brush-like, has been taken as an indication of a considerable shoveling capacity (cf. Richter & Richter, 1929:203-204). However, the distal podomeres of the legs seem to have been turned outward approximately in the horizontal plane (Lehmann 1956, Pl. 2:6; Figs. 1, 2). This outward bend is not found in extant xiphosurans, nor is it found in any fossil representatives other than *Weinbergina.* In connection with the probable life attitude of the prosomal shield as deduced above, this more or less horizontal posture indicates that the spur-bearing distal podomeres were used in the soft sediment similar to a snow-shoe in deep snow. Seilacher (1962:224) and Seilacher & Hemleben (1966, Fig. 2) have shown that different arthropods in the Hunsrück Shale used the snow-shoe principle and that trails of burrowing arthropods are absent. (Still, it would seem dangerous to conclude that *Weinbergina* was unable to burrow). A possible merostome walking trail (cf. Seilacher & Hemleben 1966, Fig. 2d) is apparently only similar to *Weinbergina* in showing the presence of six pairs of walking legs. The last two pairs of imprints are much larger than the anterior four pairs. It is noteworthy that Lehmann (1956:69) stressed a morphological difference in *Weinbergina* between the two last pairs on the one hand and the anterior four pairs on the other, the former being notably stronger. The correspondence may be more than incidental.

CHASMATASPIS. – The arrangement of the eyes is similar to that in the bunodids although the tubercle probably carrying the median eye is situated further back.

The number of appendages is not known, but systematically arranged rows of tubercles and depressions on the dorsal exterior may indicate a detailed similarity with extant xiphosurids. Walking appendages are known to be chelate (Caster & Brooks 1956:168; Fig. A1; Pl. 13:5) like those of xiphosurids but unlike those of other chelicerates. Gnathobasic masticatory legs were developed.

DIPLOASPIS, HETEROASPIS. – In dorsal aspect the Devonian *Diploaspis casteri* Størmer shows none of the ridges or furrows characteristic of xiphosurans inclusive of the synziphosurids and chasmataspidids, and the narrow margin found in those groups also has no counterpart (cf. Størmer 1972). In addition, *Diploaspis* is supposed to be blind, a condition probably not found in any xiphosuran known until now. However, it is true that it may be difficult to recognize the eyes, and I am not entirely convinced that eyes are not present in *Diploaspis*, e.g. in the paired wrinkles seen in one of the specimens figured by Størmer (1972, Pl. 1:1b).

The paddle-shaped swimming legs are superficially similar to those of some eurypterids, but were obviously independently evolved, and do not prove anything with regard to relationships (cf. Størmer 1972). More important may be the non-chelate character of the walking legs, a character separating *Diploaspis* from all xiphosurids and chasmataspidids in which the walking legs are sufficiently well known.

The paired eyes of *Heteroaspis novojilovi* Størmer, 1972 have an anterior position not seen in any undoubted xiphosuran and no other prosomal characters particularly indicate xiphosuran affinities.

EVOLUTION AND CLASSIFICATION

The xiphosurans constitute a well defined group of chelicerates with close affinities to the scorpionomorphs (eurypterids and scorpions), which may form a sister group. The earliest known representative (*Eolimulus*) is probably of late Early Cambrian age. It is therefore unlikely that the ancestors of the xiphosurans will ever be found in the fossil record. However, the Early or Middle Cambrian supposed eurypterid (cf. Bergström 1968:502) *Kodymirus* may be fairly close to *Eolimulus*, indicating a possibly Early Cambrian common ancestry of xiphosurans and eurypterids. The features in common may have included a similarly shaped prosoma with chelicerae and six additional pairs of non-chelate walking appendages (compared with five pairs in other chelicerates), 11 or 12 opisthosomal segments, and a keeled styliform telson. Easily identifiable remains of the keeled telson, in cases with segmental material added to, are found in all typical xiphosurans and eurypterids, and the scorpions differ only in the lack of a keel. However, no trace of a keeled styliform telson is found in *Diploaspis* or terrestrial chelicerates (arachnid grade) other than scorpions, and it is possible that two early lines of divergence are traced here. *Diploaspis*, dissimilar to xiphosurans and still less similar to eurypterids, may therefore represent the merostome grade of the arachnid main line(s), otherways completely unknown. A styliform telson is also found in the aglaspidids, argued to be only distantly related to the xiphosurans and probably a sister group to all other known chelicerates. However, the aglaspidid telson is not typically keeled and may even be shaped in other ways, as in *Beckwithia*, and it seems probable that the aglaspidid tail spine evolved independently.

The Cambrian *Eolimulus* and the Ordovician *Drabovaspis* reveal the absence of typical xiphosurid pushing specializations in the morphology of their prosomata, which are of low relief.

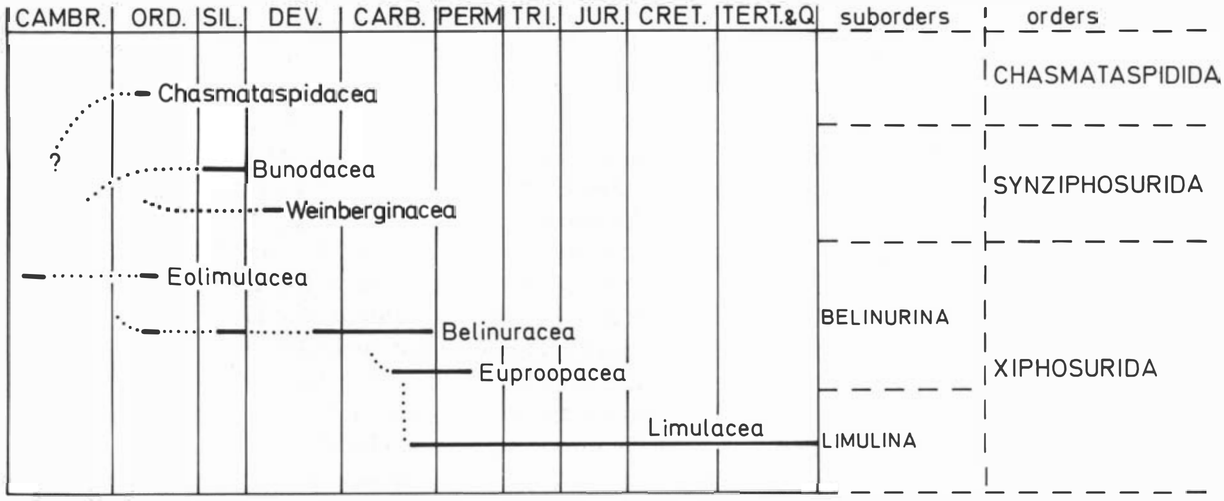

Fig. 3. Diagram showing the systematics and evolutionary lines as suggested in the text. The position of the chasmataspidids is particularly questionable.

These xiphosurids may represent an archaic group of xiphosurans devoid of the specializations characteristic of the derived later xiphosurids, synziphosurids, and chasmataspidids. It is interesting to see that features like the differently shaped ophthalmic ridge of synziphosurids and late xiphosurids are foreshadowed by a somewhat intermediate structure already in *Eolimulus* and *Drabovaspis.* These archaic xiphosurans may be contained in a superfamily *Eolimulacea* within the suborder Belinurina.

The Ordovician *Archeolimulus,* found associated with *Drabovaspis,* shares features with later xiphosurids which may indicate that this early form had already acquired the pushing habits characteristic of later xiphosurids. The advanced features include a strongly arched prosoma with well developed (strengthening?) ridges. The prosoma is not horse-shoe-shaped but rather elongate, a feature which may mean that *Archeolimulus* differed from later xiphosurid in its moving pattern in one respect or another. The burrowing and pushing habits appear to have been preserved throughout the later history of the xiphosurids, possibly with isolated exceptions like *Euproops? anthrax* with long slender appendages and spines, and possibly surface-dwelling habits.

The Palaeozoic evolution is dominated by a trend towards a fusion of the opisthosomal tergites with a beginning in the rear (contrary to the opinion of Tiegs & Manton 1958:313). One of the reasons for the fusion to begin in the posterior end may be that the early xiphosurids were able to enroll and "tried" to preserve this ability be keeping the anterior tergites free. The fusion is associated with a loss of posterior segments. Xiphosurids on this organizational level may be included in the superfamily Belinuracea and include forms referable to *Archeolimulus,* Pseudoniscidae, Belinuridae, Elleriidae, Moravuridae, and possibly Kiaeridae. The three last families are poorly known and may be more or less aberrant. Moravuridae is characterized by a transformation of the tail spine to a small rounded but still keeled plate, which is probably free.

Euproops and its allies represent a further evolutionary step with regard to the fusion of opisthosomatic tergites. The entire opisthosoma in front of the tail spine is encased in a single tergal shield formed by the fusion of the segmental tergites. By adjusting the articulation between prosoma and opisthosoma the animals were still able to flap the shields together despite the fact that the entire bending had to be performed in a single articulation. This is an almost incredible case of enrollment perfection, and it appears unlikely that this folding up ability evolved more than once. Therefore the Euproopidae and Liomesaspididae may be united in the Euproopacea, which together with the Eolimulacea and Belinuracea constitute the suborder Belinurina.

In one evolutionary line within the Euproopacea the ontogenetic development of the articulation between the prosomal and opisthosomal shields was disturbed, possibly formed too early, with a revolutionary result. An individual came into existence, in which the articulation was not consequently behind or through the chilarial (seventh, if cheliceral is counted as first) segment, but behind the seventh axially and through the sixth segment laterally. The sudden change meant that the mechanism regulating the folding up was disturbed and the typical sphaeroidal folding up with the shield margins abutting edge to edge was abandoned. This was the birth of a last xiphosurid group of high dignity, the suborder Limulina. The oldest known representative appears to be an unnamed form from the Late Carboniferous.

Already previous to this event adjustments apparently took place in the prosomal-opisthosomal boundary region. According to Eldredge (personal communication) *Pseudoniscus* as well as the synziphosurids had a small tergite at the posterior border of the main prosomal shield. The small size may indicate that this tergite covers only part of a somital segment, the rest of which may be concealed under the main shield, but this is just one possibility. A similar small tergite has been observed in *Belinurus* and a possible remnant in the euproopacean *Pringlia*. This tergite has not been identified in any later xiphosurids but it is possible that it is at least partly homologous to the steep posterior slope of the prosoma in limulaceans. If so, it seems to represent (part of) the seventh (pregenital, chilarial) segment, the last prosomal segment as argued herein (cf. Störmer 1963, Fig. 44). The probably articulated state of the tergite in *Pseudoniscus, Belinurus* and the synziphosurids tells us nothing about its prosomal or opisthosomal character. Similar articulated or free tergites are found in the prosoma of the Schizomida, Palpigradida, Solifugae, and Acarida among terrestrial chelicerates.

If correctly interpreted, the Devonian synziphosurid *Weinbergina* represents an archaic condition in which the chilarial segment (VII) still has well developed walking legs of prosomal type. The probability of the interpretation is strengthened by the circumstance that the two posterior appendage pairs both have a morphology characteristic of only the last pair in xiphosurids and by the find of walking trails made by an arthropod with six pairs of walking appendages of which the two posterior pairs are stronger. The long appendages extending outside the prosomal margin and the lack of a flat horizontal shelf on the prosomal doublure together with the sedimentary facies indicate that *Weinbergina* had habits somewhat different from those of *Limulus*. Spurs were present on all legs and may have acted as snow-shoes.

As argued above, the synziphosurids and the chasmataspidids have several features in common. This means that they may be closely related, but the differences may be large enough for an acceptance of a separation on the order level, as argued by Størmer (1972). In comparison with the xiphosurids the two groups have a slender opisthosoma and a comparatively small prosoma with large eyes, features indicating an agile life on the bottom. Small spines on the prosomal border in some species indicate that at least those species were not great burrowers. The synziphosurids and chasmataspidids probably paralleled the eurypterids not only in appearance but also partly in habits. Their ancestry is probably to be found among early xiphosurids, although there is a possibility that the chasmataspidids are somewhat more distantly related.

The position of *Heteroaspis, Borchgrevinkium* and similar forms is difficult to figure out at present. They may be xiphosurids as proposed by Størmer (1972) but more material is urgently needed before the problem is solved.

An attempt towards a classification is made below.

Subclass XIPHOSURA Latreille, 1802 (emended Bergström 1968)
Order XIPHOSURIDA Latreille, 1802
  Suborder BELINURINA n. subord.
  Xiphosurids with prosomal-opisthosomal boundary behind chilarial (pregenital) segment; this segment possibly with small articulated tergite; prosoma strongly convex except in some early representatives; ophthalmic ridge developed at least posteriorly; opisthosomal tergal cover articulated or fused, without lateral movable spines; with sphaeroidal enrolling or folding up ability.

Superfamily Eolimulacea Bergström, 1968 (*nom. transl.* herein, *ex* Eolimulidae Bergström, 1968)
Xiphosurida with short and moderately convex prosoma; ophthalmic ridge more or less well developed posteriorly, not present anteriorly; interophthalmic ridge missing; compound eye nodes comparatively large. Opisthosoma not known with certainty.
  Eolimulidae Bergström, 1968
    Eolimulus Bergström, 1968
  Family not erected
    Drabovaspis Chlupac, 1963

Superfamily Belinuracea Zittel & Eastman, 1913 (*nom. transl.* Raymond 1944 *ex* Belinuridae Zittel & Eastman). Emended herein.
Xiphosurids with ophthalmic and interophthalmic ridges; with or without horizontal hinge-line between articulated tergites; tergite cover of opisthosoma with articulated sclerites at least anteriorly, fusion apparently proceeding forwards from the posterior end; with sphaeroidal enrollment.
  Archeolimulidae Chlupac, 1963
    Archeolimulus Chlupac
  Pseudoniscidae Packard, 1886 (=Neolimulidae Packard, 1886)
    Pseudoniscus Nieszkowski, 1859
    Neolimulus Woodward, 1886 (may be a junior synonym of *Pseudoniscus*)

Belinuridae Zittel & Eastman, 1913
Belinurus König, 1820
Neobelinuropsis Eller, 1938
Koenigiella Raymond, 1944
Moravuridae Pribyl, 1967
Moravurus Pribyl, 1967
Elleriidae Raymond, 1944
Elleria Raymond, 1944
?Kiaeridae Størmer, 1952
Kiaeria Størmer, 1934

Superfamily Euproopacea Eller, 1938 (*nom. transl.* Raymond 1944 *ex* Euproopidae Eller, 1938)
Xiphosurids with or without ophthalmic and interophthalmic ridges; opisthosomal exoskeleton completely fused; articulation between prosomal and opisthosomal shields lowered, without a free microtergite, with horizontal hinge-line allowing the shields to fold up sphaeroidally.
Euproopidae Eller, 1938
Euproops Meek, 1867
Liomesaspididae Raymond, 1944
Liomesaspis Raymond, 1944
Pringlia Raymond, 1944 (=*Anacontium* Raymond, 1944)
Prolimulus Fritsch, 1899

Suborder LIMULINA Richter & Richter, 1929 (emended herein)
Small to large forms; interophthalmic ridges lacking; ophthalmic ridges tend to obliterate in front of paired eyes. Secondary segmentation between prosomal and opisthosomal shields, articulation situated approximately behind segment VII (cheliceral counted as I) axially and through segment VI laterally; spine of segment VI obviously fused to opisthosomal tergite shield. Fused opisthosomal exoskeleton more or less trapezoidal, with low convexity and movable lateral spines. If folding up, the opisthosoma fits inside the prosomal ventral border.

Superfamily Limulacea Zittel, 1885 (*nom. transl.* Raymond 1944, *ex* Limulidae Zittel, 1885)
Paleolimulidae Raymond, 1944
Paleolimulus Dunbar, 1923
Limulitella Størmer, 1952
Austrolimulidae Riek, 1968
Austrolimulus Riek, 1968
Heterolimulidae Boada & Villalta, 1966
Heterolimulus Boada & Villalta, 1966
Limulidae Zittel, 1885 (=Mesolimulidae Størmer, 1952)
Mesolimulus Størmer, 1952
Psammolimulus Lange, 1923
Victalimulus Riek & Gill, 1971
Limulus Müller, 1785
Tachypleus Leach, 1819
Carcinoscorpius Pocock, 1902

Order SYNZIPHOSURIDA Packard, 1886 (*nom. transl.* Bergström 1968, *ex* Synziphosura Packard, 1886; emended herein).
Xiphosurans with comparatively small prosoma carrying fairly large eyes; ophthalmic ridge short or consisting of line of nodes along a geniculation separating a flattened central area from a peripheral slope; opisthosoma divided into wide preabdomen with six or seven articulated tergites and narrow postabdomen with three articulated tergites and tail spine; additional small tergite at the prosomal-opisthosomal boundary may belong to prosomal (chilarial) segment.

Superfamily Bunodacea Packard, 1886 (*nom. transl.* herein, *ex* Bunodidae Packard, 1886)
Synziphosurids with comparatively small prosoma characterized by a pattern of radiating ridges; compound eyes of globular shape; ophthalmic ridge discontinuous, consisting of a row of nodes at the intersection between nine radiating ridges and a semicircular prosomal geniculation; preabdomen with six well developed tergites.
Bunodidae Packard, 1886 (=Limuloididae Størmer, 1952)
Bunodes Eichwald, 1859
Limuloides Størmer, 1952

Superfamily Weinberginacea Richter & Richter, 1929 (*nom. transl.* herein, *ex* Weinberginidae Richter & Richter, 1929)
Synziphosurids without strong radiating ridges; compound eye extended along distinct ophthalmic ridge, as long as the eye; preabdomen with seven well developed tergites; all legs with long spurs; chilaria probably developed as walking legs similar to those of the segment next in front.
Weinberginidae Richter & Richter, 1929
Weinbergina Richter & Richter, 1929

Order CHASMATASPIDIDA Caster & Brooks, 1956
Xiphosurans with weakly defined or non-existent prosomal morphological features such as radiating ridges, ophthalmic ridge or line, interophthalmic ridge and cardiac lobe; opisthosoma divided into preabdomen with three segments and postabdomen with nine segments and caudal spine; preabdomen with fused tergites and sternites, apparently without appendages (sternite may represent appendages); postabdomen with tergites and sternites arranged as rings, without appendages.

Superfamily Chasmataspidacea Caster & Brooks, 1956 (*nom. transl.* herein, *ex* Chasmataspidae Caster & Brooks, 1956)
  Chasmataspididae Caster & Brooks, 1956
    Chasmataspis Caster & Brooks, 1956

Incertae sedis, Chasmataspidida?
  Heteroaspididae Størmer, 1972

Incertae sedis
    Bembicosoma Laurie, 1899
    Bunodella Matthew, 1889
    Belinuropsis Matthew, 1909
    Bunaia Clarke, 1919
    Cyamocephalus Currie, 1927
    Pincombella Chapman, 1932

Rejected from the Xiphosura
    Bifarius Tasch, 1961 (insect)
    Cyclocephalus Tasch, 1961 (insect)
    Diploaspis Størmer, 1972 (and Diploaspididae) (chelicerate of new type)
    Elmocephalus Tasch, 1963 (crustacean?)
    Hypatocephala Tasch, 1961 (insect)
    Permolimulinella Tasch, 1963 (insect)
    Strongylocephalus Tasch, 1961 (insect)

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ADDENDUM

Since the manuscript was delivered two papers dealing with xiphosurid morphology, evolution, and systematics have been published, one by Eldredge (1974) the other by Eldredge & Plotnick (1974). The Devonian weinberginid *Legrandella* from Bolivia was described, and based on new material *Cyamocephalus* was referred to the Pseudoniscidae, as was with hesitation *Bunaia.* The ideas on the evolution and systematics are quite different from those advocated by me, but no facts presented have caused any change in my views presented above. My results are based on a consideration of the inherited or derived state of features of the ventral morphology and of functional adaptations, in addition to the dorsal morphology mainly considered by Eldredge (1974).

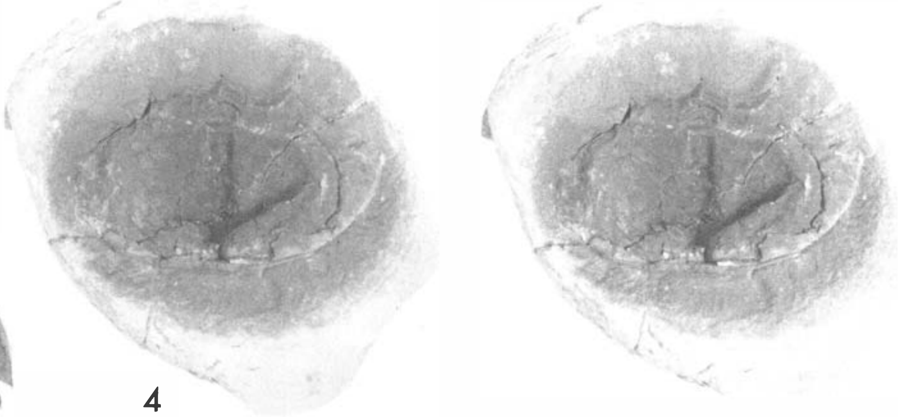
Eldredge, N. 1974: Revision of the suborder Synziphosurina (Chelicerata, Merostomata), with remarks on merostome phylogeny. *Amer. Mus. Novitates 2543.* 41 pp. New York, N.Y.

Eldredge, N. & Plotnick, R.E. 1974: Revision of the pseudoniscine merostome genus *Cyamocephalus* Currie. *Amer. Mus. Novitates 2557.* 10 pp. New York, N.Y.

EXPLANATION OF PLATE 1

Fig. 1. Type specimen of *Eolimulus alatus* (Moberg), a prosoma. Probably upper part of Lower Cambrian, Ekerum, Öland, Sweden. Plastic cast of natural mould, coated with ammonium chloride. Swedish Geological Survey, Ser. C:125, Fig. 14. X2.25. *Fig. 2.* Type specimen of *Neolimulus falcatus* Woodward. Upper Silurian, Lesmahagow, Lanarkshire. Plastic cast coated with ammonium chloride. Notice narrow cardiac region, distally positioned ophthalmic ridges, and wide opisthosomal rhachis. BM (British Museum) In. 44122. X3.75. *Fig. 3.* Cf. *Pseudoniscus aculeatus* according to label. Upper Silurian, Dunside, Logan Water, Scotland. Plastic cast coated with ammonium chloride. Notice similarity with specimen in previous figure. A short keeled tail spine is present. BM In. 14724. X2.8. *Fig. 4. Pringlia* sp. Upper Carboniferous, Britain. Folded up individual. Stereo pair with individual copies interchanged and light from lower right to give a positive impression. The opisthosomal shield is surrounded by the prosomal border. The prosomal shield is provided with three posterior spines which are directed upward in the figure. Notice horizontal hinge-line. Sedgwick Musem, Cambridge. E. 16940a. X1.5. *Fig. 5.* Type specimen of *Belinurus koenigianus* Woodward. Upper Carboniferous, Dudley, Britain. Actual specimen, without coating. An advanced feature is that the posterior part of the cardiac lobe and the anterior end of the opisthosomal rhachis correspond in width. The opisthosoma has segmental tergites in front and a fused shield posteriorly. Notice the small wedge-shaped tergite in the rhachis at the posterior end of the prosoma. Notice also the development of a horizontal hinge-line. British Museum. X2.4. *Fig. 6. Euproops? anthrax* (Prestwich). Upper Carboniferous, Shropshire, Britain. Actual specimen, without coating. Opisthosoma of folded up specimen with three prosomal spines pointing upward in the figure. BMJ. 2753 British Museum. X1.5. *Fig. 7.* Type specimen of *Limuloides limuloides* (Woodward). Upper Silurian, Leintwardine, Herefordshire. Actual specimen, without coating. The microtergite at the posterior end of the prosoma is not visible. British Geological Survey, No. 32393. X1.95. *Fig. 8. Bunodes lunula* Eichwald, in "*B. schrenki*" state of embedding, *i.e.* with the prosoma tilting slightly forward to give a concave posterior profile. Upper Silurian, Ösel, Estonia. Actual specimen, without coating. Notice the median eye with two ocelli and the integumental ornament nicely prepared by weathering. BM I. 2774. X2.15. *Figs. 9, 10.* Anterior and anterodorsal views of *Bunodes* n. sp. 1. Upper Silurian, Stephenton, Britain. Plastic cast of natural mould, coated with ammonium chloride. Notice the line of nodes on the geniculation more or less constituting the ophthalmic ridge. The large second lateral nodes obviously are paired eyes, although no lenses have been seen. BM In. 48425. X3.2 and X2.75, respectively. *Fig. 11. Pringlia birtwelli* (Woodward). Upper Carboniferous, Britain. Actual specimen, without coating. Notice steep posterior wall of prosoma, horizontal hinge-line, and the wedge-shaped rhachial feature at the prosomal/opisthosomal boundary. Sedgwick Museum, Cambridge, E. 16917.a. X4.85.


1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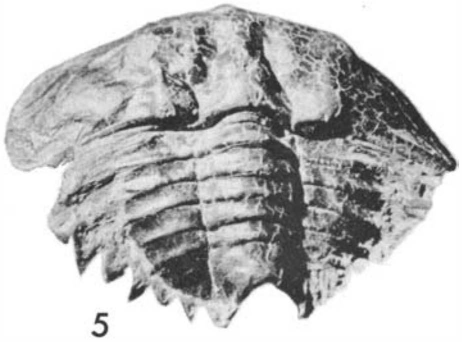
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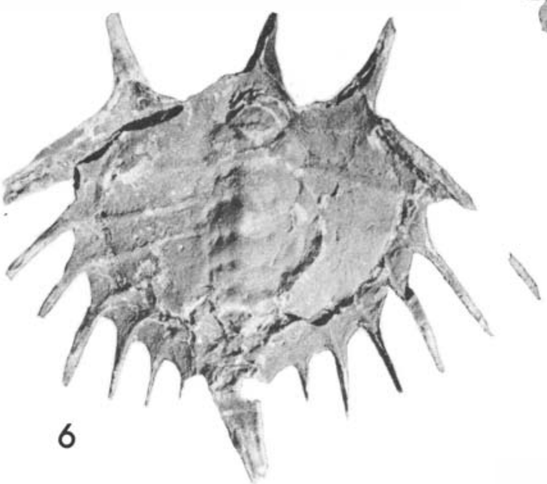
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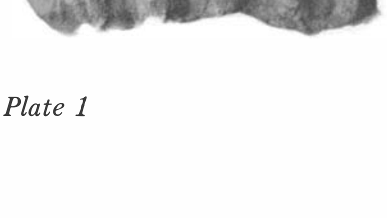
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11

Plate 1

Early Paleozoic trilobites, sedimentary facies, lithospheric plates, and ocean currents

REUBEN JAMES ROSS, Jr.

Ross, R.J. Jr. 1975 07 15: Early Paleozoic trilobites, sedimentary facies, lithospheric plates, and ocean currents. *Fossils and Strata,* No. 4, pp. 307–329. Oslo ISSN 0300–9491. ISBN 82-00-04963-9.

Examination of the known occurrence of Cambrian and particularly Ordovician trilobites has determined that: (1) Faunas of continents and platforms that have remained in a single latitudinal zone, particularly in a warm climate, show most strongly the effects of local environment. Concentric geographic changes in faunal composition and diversity result, as in North America. (2). Faunas of continents that passed rapidly through inclement climatic zones bear the print of climatic rather than local environmental variants. Faunas may be arranged in broad latitudinal bands, and apparent standing diversities may change stratigraphically within each continental shelf area, as in western Gondwana (Andean area). (3). Inferred patterns of warm oceanic currents relative to latitude and to changing continental obstructions are compatible with distribution of pelagic trilobites. (4). Tethyan trilobite distribution during the Ordovician shows reversals in migration related to (a) movement of Moroccan and Algerian Gondwana into warmer climate, (b) removal of Antarctic and Australian Gondwana from its obstructing position across the equatorial current, (c) westward movement of Baltoscandia and (d) eastward movement of North America.

Reuben James Ross, Jr. U.S. Geological Survey, Denver, Colorado 80225, 1st August, 1973.

This paper is about Cambrian and Ordovician trilobite distributions when effects of warm oceanic currents are inferred.

Portrayal of continents or cratonic plates (Figs. 6–9) is deliberately crude. Modern outlines are roughly preserved for purposes of recognition although early Paleozoic shapes were clearly different; fold belts have been added to the borders of many plates and some, like North America, have acquired large pieces of western Europe, Africa (Florida), and South America (Southern Mexico, Oaxaca) since Ordovician time. It was assumed that 0° longitude passed through western Algeria at the close of the Devonian and all other longitude was worked backward from that position. The paper on Phanerozoic World Maps by Smith, Briden, & Drewry (1973) became available after this manuscript was completed.

Preliminary assembling of data on the positions of continents for this paper early revealed that the "Bullard Fit" is not applicable until Devonian time at the earliest and then only partly so, that the cratonic plates were all constantly moving relative to each other and to the magnetic poles, and that because paleomagnetic information is scarce and only latitudinal in its constraints, the biogeographic data have the best chance of indicating relative longitude.

I am greatly indebted to Warren Hamilton for many discussions about possible plate movements and positions, to Robert J. Hite for data on evaporite distributions, and to A.R. Palmer & M.E. Taylor about additions to the paper.

Much painstaking work has been done in recent years on the distribution of trilobites by Whittington (1966, 1973), Dean (1967), Whittington & Hughes (1972, 1973), and Palmer (1960, 1969, 1972). Palmer has dealt mostly with Cambrian trilobites but the others have worked primarily on the Ordovician. All these authors rely on a broad and thorough knowledge of trilobites and accept the general concepts of the new plate tectonics. It is probable that no authors better qualified to write on the subject of trilobite biogeography could be found. Rather than reviewing every detail of their papers, I propose that we use them as starting points for further discussion.

Palmer (1960, 1969, 1972:310–311) has repeatedly championed the belief that lithologic facies concentrically arranged on and around the North American platform were closely related to distribution of Cambrian faunas. In this belief he is supported by Wilson (1957), Lochman-

Balk & Wilson (1958), and North (1971). It has been suggested by Ross & Ingham (1970) that the same scheme may apply to part of the Ordovician deposits around North America. In 1972, however, Palmer (p. 313, Fig. 3) noted that the scheme of restricted shelf environment surrounded by "shelf-margin-open sea" environment could not be applied to Gondwana, although it seemed to fit the Siberian platform and some of the component parts of Gondwana.

Whittington (1966:697–698), in his classic compilation of Ordovician faunas, concluded that they fell into two main geographic groupings: a northern region composed of

North America and Arctic Islands
Greenland
western Ireland and Scotland
Spitsbergen
Russian platform (Baltoscandia)
U.S.S.R.

a southern region composed of

Argentina and Bolivia, in South America
Central Britain
Normandy and Brittany in France
Central Europe and Mediterranean area
Himalayas
China and southeast Asia
Australia and New Zealand

Although Whittington (1966, Figs. 1, 2, 16) plotted these two regions on a projection showing the continents in their present positions, the paleoequators for three continents indicate that the author was concerned about a different earlier alignment. Whittington's two regions are valid and have been the basis for most subsequent speculation on Ordovician trilobite distribution.

In apparent disagreement with Palmer, Whittington (1966: 698, 717, 724) concluded that "there is no unequivocal correlation between trilobite faunas and rock type and/or tectonic environment; rather, similar faunas occur in quite different rock sequences". This point of view was subsequently tempered by Whittington & Hughes (1972:264–271) in their analysis of the trilobites of the platform and continental-slope environments.

Dean (1967:13) has pointed to the crux of the matter in discussing Ordovician Tethyan faunas; he noted that Trinucleacean, Calymanacean, and Asaphacean trilobites are "numerically dominant constituents of the mudstone faunas, although members of all three superfamilies are found elsewhere in rocks varying from limestones to sandstones, and even ashes".

Following the example of Lane (1972:337–339), one may compare Warburg's (1925) study of the trilobites of the reefy Leptaena Limestone of Late Ordovician age, Whittington's (1963) treatise on Middle Ordovician trilobites from the reeflike limestone at Lower Head, Newfoundland, Ross's (1972) discussion of a similar limestone in Nevada, and Lane's (1972) paper dealing with the Silurian of northeast Greenland. Lane (1972: 337–339) has called attention to the similar trilobites that populated these and other similar limestone bodies from Ordovician into Devonian time. Although I (Ross, 1972:16) agree with Lane's conclusions, in searching for facies control of fossils in the carbonate mound at Meiklejohn Peak, Nevada, I, like Dean (1967:13), could find few if any genera that were limited in occurrence to a single lithologic facies, a point already noted by Whittington (1966:724–725, Table 6) concerning the Swedish Boda Limestone.

Although the relationship between lithologic facies and trilobite biofacies may be indirect, it does exist. Taylor (1973) has shown undeniable evidence that North American latest Cambrian and Earliest Ordovician trilobites were organized into two main biofacies; one of these preferred shallow-water carbonate bottoms whereas the other was associated with "shelf-edge and/or basinal sedimentary environments".

Sylvester-Bradley (1971:11–13) has reminded us of the possible complexities of facies control, and has suggested the resurrection of Caster's (1934:19, Fig. 2) magnafacies and parvafacies. To do this we must first decide which are the "magnas" and which the "parvas" of trilobite biogeography.

FRAMEWORK OF PHYSICAL GEOGRAPHY

As a basis for discussion of trilobite paleobiogeography, evidence for the physical geography of the Paleozoic is presented here. Much of this "evidence" is still in a formative stage, and much is inference, all seasoned with a sprinkling of conjecture. Paleomagnetic information continues to become more readily available although its merits may be questioned. Evaporites as indicators of hot climates are useful, with limitations. Finally, the trilobites themselves might be more useful in speculations about paleogeography if we were not simultaneously attempting to interpret their distribution in terms of paleogeography.

Paleomagnetic evidence

For purposes of this paper, I assume that the paleomagnetic poles virtually coincide with the axis of rotation of the earth. If that assumption eventually proves to be invalid we may still use the data to estimate relative positions of one or more continents, but we may not use them to estimate longitudinal position.

Gilluly (oral. commun., Mar. 8, 1973) noted that the north and south magnetic poles are currently moving independently and at quite different rates; furthermore a line joining the two magnetic poles misses the center of the earth by several hundred kilometers. This information is not particularly comforting.

Reliable paleomagnetic information concerning the positions of Ordovician continents is scarce. The oldest Paleozoic fixes for North America are Silurian (Roy, Opdyke, & Irving, 1967; McElhinny & Briden, 1971:414), and these indicate that the equator passed through northernmost Hudson Bay from east to west. As a result almost all of the United States and Canada lay well within latitudes 20° N. and 20° S. To take up the position required by the "Bullard fit" in the Carboniferous the entire continent would have rotated clockwise less than 45° with Hudson Bay remaining on the equator.

Park, Irving & Donaldson (1973:867–868, Fig. 9) have shown the "track" of the north (?) pole relative to North America during the Precambrian. Their map suggests that North America in the late Precambrian moved south so that the eastern one-third of the present continent lay south of the equator 675 mybp.

The Baltoscandic platform was in such a position that Oslo was on the Tropic of Capricorn in the Cambrian, at 15° N. by Early Ordovician time, at 10° S. by Early Silurian time, and at 8° N. in the Late Devonian (Hamilton, 1970:1). In other words, the platform remained on the equator throughout most of early Paleozoic time. This is important when we consider the relative positions of the Norwegian and North American coasts in the Ordovician and Silurian.

Jaanusson (1972:12–15) has suggested, on the basis of carbonate petrology, that Baltoscandia lay in a temperate region until Late Ordovician time when bahamitic limestone was first widespread. Furthermore Lindström (1972a, 1972b) considered that this region was in arctic or subarctic environments in the Early Cambrian on the basis of sedimentary structures and in the Early Ordovician based on surface texture of sand grains. Lindström's supposedly supporting paleomagnetic information applies to North Africa, but probably should not be used for northern Europe. The interpretations of both these authors serve to warn us that my inference concerning latitudinal positions of tectonic plates based on currently available paleomagnetic data may be premature.

The Siberian platform in late Precambrian time may have been bisected by the Tropic of Cancer and then moved southward to straddle the Equator by Early Ordovician time; or it may have lain across the Tropic of Capricorn in late Precambrian time moving north to the Equator in the Early Ordovician. Thereafter it moved northward to 45° N. in the Devonian (Hamilton, 1970, Fig. 1).

Korea and North China, according to data presented by Smith, Briden, & Drewry (1973:10, Table 1), was in the Cambrian at lat. 35° S. or 40° N., a rather wide range of possibility that precludes a position at the equator. Unfortunately, no polar wandering curve is available for Korea and no decision can be reached concerning these two alternatives.

If McElhinny & Briden (1971:411–412) are correct, Gondwana moved rapidly northward in the Late Ordovician and Silurian. As a result, although the south pole lay in Morocco in the Cambrian and Ordovician it is believed to have been in southernmost Africa by Late Silurian time. In other words, Africa moved very rapidly northward about 3,900 miles (6,275 km) in about 45 million years. That requires moving at about 13 cm per year or about three times as fast as the Mid-Atlantic ridge is spreading today and about the same speed as the Pacific is currently spreading. I therefore suggest that the Late Ordovician-earliest Silurian pole lay in Gabon or south of Salvador, Brazil. This requires movement of 6 cm/yr., still 1.5 times that at the present mid-Atlantic ridge. If the south pole was near Johannesburg by Late Silurian time the Morocco-Bohemia coast would have lain between lats. 20° and 30° S.

Three observations (McElhinny & Briden, 1971:410, Table 2) on the Girvan lavas, Borrowdale volcanics, and Builth volcanics are in general accord and indicate that Great Britain was at lat. 20° N. or 23° S. in the Ordovician; the latter seems to be the more reasonable assumption and places Britian as much as 40° south of Oslo. The indication is that Britain and Scandinavia were not in their presently close positions until after the Ordovician.

Europe south of the Russian platform in the Ordovician seems to have been allied faunally and lithologically to Africa, not to the Baltic (Spjeldnaes, 1961, 1967; Dean, 1967). It seems possible that south and west Europe were a part of the Morocco-Tunis border of Gondwana at least as early as Ordovician time and probably throughout the Paleozoic, and did not join the Russian platform until the Late Silurian or Devonian at the earliest.

McKerrow & Ziegler (1972) have presented a far more sophisticated estimate of the early Paleozoic positions of the circum-Atlantic continents than I am venturing here. They expressed the belief that "Europe south of the Hercynian belt probably lay closer to Algeria, Tunisia and Libya than do the Baltic Shield". For a variety of reasons they concluded that "central Europe did not collide with the Baltic Shield until the Upper Carboniferous".

Several continental or smaller platforms, such as North America, Siberia, and Baltoscandia may have moved great distances but remained mostly in the tropical latitudes.

Much of western Gondwana traversed 90° of latitude from the Cambrian to the end of the Silurian; but eastern Gondwana, that is, Australia-India, seems to have behaved much like a pivot. The longitude of Australia remained little changed while its latitude did not shift out of the tropics until the Late Silurian to lie between 20° and 40° S.

These inferences with regard to Australia (Figs. 6–9) have been confirmed in a recent paper by Embleton (1973).

Unfortunately, to date, paleomagnetism gives us no hint on the position of the Kolyma platform or any of the small platforms comprising Tibet, South China, and Indochina.

Evidence from evaporites

The distribution of halite deposits has been summarized by Hite (1968:311), who noted that such evaporites are found in strata of every period of the Paleozoic. Hite has plotted probable equatorial positions for each continent without regard to plate tectonics. However, if these occurrences are plotted taking plate tectonics and Gondwana into consideration, they may be interpreted as very nice support for the theory of continental drift.

Hite (1968:311, Figs. 1–7) lists the evaporites by period.

Cambrian: Canada, between Great Bear and Great Slave Lakes; Australia, in Northern Territory; Siberian platform over a vast area; and Indian platform, in the Salt Ranges of Pakistan.

Ordovician: Canada, in MacKenzie Basin and Norman Wells area of the Northwest Territories, and Thailand (Hite, oral commun., March 12, 1973).

Silurian: Canada, in Ontario; and USA, in Michigan, Ohio, New York, Pennsylvania, and West Virginia. Possibly northern Australia (Hite, oral commun., March 29, 1973).

Devonian: Russian platform, in Pripiat Depression and Treva Basin; and USA, in Williston basin of North Dakota and adjoining Saskatchewan, Canada.

If we assume that deposits of salt formed close to the horse latitudes we find that there is much agreement between the implied latitudinal positions and paleomagnetic information, and paleobiogeographic implications (Figs. 6–9).

However, in the western USA we are aware of the Great Salt Lake which can hardly be considered an indicator of equatorial latitude, although it surely exists because of an arid climate. It is not, of course, populated by marine organisms.

MORPHOLOGIC EVIDENCE

We can only guess at trilobite life habits. Which genera seem to have been pelagic, which benthic? How much of each benthic genus' life may have been pelagic? Were trilobites with big eyes, like *Telephina* or *Cyclopyge,* pelagic? Their distribution suggests that they were. But an even wider distribution of various genera of olenid trilobites suggests that they must have been pelagic, and olenids had very small eyes. Furthermore, widespread agnostids and raphiophorids were blind. Ontogenies of asaphids and of remopleuridids, for instance, include little ball-shaped protaspids which seem ill-suited for any self-propelled locomotion and better adapted for floating; they may have rested within some sort of egg case which lay on the bottom or formed part of a floating raft. Distribution of *Asaphellus, Ogygiocaris, Leiostegium,* and most remopleuridids suggest that they were pelagic for some part of, if not all, their lives.

Which genera lived in cold water, which in warm water? Which in deep water, which in shallow? It is difficult to believe that spiniferous Silurian *Odontopleura* or Devonian *Gaspelichas* could have been burrowers. It is much more reasonable to suppose that smooth, streamlined *Isotelus* and *Nileus* were burrowers. But out of the geologic context, we would have no reason to believe that any trilobites burrowed.

In truth, our best estimates of habits are based, not only on the animals' skeletons, but particularly on their geologic distribution, that is, their distribution in time, in space, and in lithologic type.

Dissimilarity index and hazards to travel

Cloud (1961:165) found that the most widely distributed modern marine organisms are:

(1) Actively nektic animals.

(2) Planktic animals or those capable of attaching to floating objects.

(3) Organisms with great larval dispersion and reproductive adaptability.

(4) Species of shallow, warm, or temperate marine waters with long-lasting planktic larval stages (to drift across the deep-water barriers).

(5) Deep-water and cold-water species having abbreviated larval life (maturing quickly) or viviparous reproduction, and able to move with deep currents.

Although we have no means of distinguishing them, it seems reasonable to believe that some trilobites satisfied at least the first four of these characteristics.

Cloud (1961:167) further noted that a pelagic larva caught in a current like the Gulf Stream could travel as little as 700 km in one week or as far as 4,000 km in three weeks. Such a trip might not be beneficial because it could end in a hostile environment, but it illustrates the possibilities of faunal dispersion.

Cisnē (1973) has estimated that the larval stage of the olenid *Triarthrus eatoni* lasted for 10 weeks. If *Triarthrus* is typical of all olenids the wide distribution of similar trilobites may be readily understood.

Robertson (1964) has reported on the dispersal of larvae of the benthic gastropod *Philippia krebsii* from the West Indies via the Gulf Stream to points as far distant as the Canary Islands. The length of larval stage is estimated at close to three months.

Whittington (1973:17) stated that the widespread Ordovician trilobite genera *Geragnostus, Lonchodomas,* and *Carolinites* were able to cross wide oceans either because of their prolonged larval stages or because their adult stages lived near the water surface and were able to drift across the oceans.

Whittington & Hughes in 1972 attempted to treat Ordovician trilobite distribution by series statistically, their purpose being to equate the dissimilarities between geographic assemblages with relative distances separating these assemblages. At the outset, presumably for statistical reasons, they (p. 238) eliminated from consideration any described fauna of fewer than 10 taxa. Because there are only eight genera reported in the Llandeilan rocks of China an exception was made, but compassion was lacking in the case of the five genera in the Caradocian of Argentina, as an example. Bits of evidence which may eventually prove significant were excluded from the statistical analysis. For that reason Whittington's 1966 paper, although it antedated the new plate tectonics, will remain as an indispensible reference.

The genera least likely to indicate relative proximity of two land areas are those with the greatest potential for travelling, in this case in marine waters, from one to the other. That potential belongs to the pelagic forms, whether they be swimmers or floaters for part or all of their lives. The statistical comparison used by Whittington & Hughes (1972, Figs. 1, 2, 4, 5, 7, 8, 10, 11) makes no effort to discriminate between pelagic and benthic or endemic genera, and in fact it advocates the opposite course (p. 269). However, if a large fauna from the restricted shelf environment, much of which may have been truly endemic, is artifically mixed with the outer shelf-open ocean fauna, a high percentage of which was probably pelagic, the resulting comparison will be biased. The direction of bias will depend on relative sizes of each of the two habitat faunas from each of the two continents, subcontinents, or platforms being compared, as well as on the hazards to pelagic genera attempting travel between them. The subjective measure of distance being sought is actually only relative to this last factor – hazards to pelagic travel. The greater the distance the greater the potential hazards.

Common occurrence of benthic, rather than pelagic genera, is more likely to indicate proximity of two land areas, but the two areas would have had to be connected by a shallow shelf. If, however, the life cycle of these genera included a planktic or nektic stage they temporarily became pelagic. In the fossil record they probably successfully masquerade in that guise.

Benthic genera without any effectively pelagic stage of development will probably appear paleontologically as 'endemics' if their homeland is surrounded by deep water or other barriers to migration.

The mere existence of a pelagic stage does not overcome the barriers erected by other factors, such as temperature, which may render a pelagic genus "endemic" to a hemisphere or to a particular climatic zone.

No wonder that Whittington & Hughes (1972:269) forewent any attempt to separate pelagic from other genera in their analysis of Ordovician biogeography! And yet the distinction is worth attempting and might be the subject of further discussion at this symposium.

Chugaeva (1972) has attempted to separate Ordovician trilobites into an American-Siberian realm, a Baltic realm, and a Paleo-Tethyan realm in which widespread and endemic genera are separated. Although I would modify some of the details, her approach to the problem has merit, as has Ormiston's (1972) division of Devonian trilobites into communities and provinces.

Faunal diversity and Ardovician climate of western North America

It is reasonable to assume that North America lay largely in the tropics throughout the early Paleozoic and that the equator ran from southern Nevada through Great Slave Lake (Whittington, 1966, Fig. 1) or from Oklahoma through Hudson Bay (Whittington & Hughes, 1972, Fig. 3). As already noted the paleomagnetic information for the Late Silurian indicates that the equator passed through Hudson Bay from east to west. Fischer (1960) concluded that tropical faunas diversify more rapidly than those in temperate zones and that faunas of the tropics represent more stable highly evolved lineages. If Fischer was correct we should be able to examine the diversity of trilobites in western North America and to get some hint of the direction in which the equator lay.

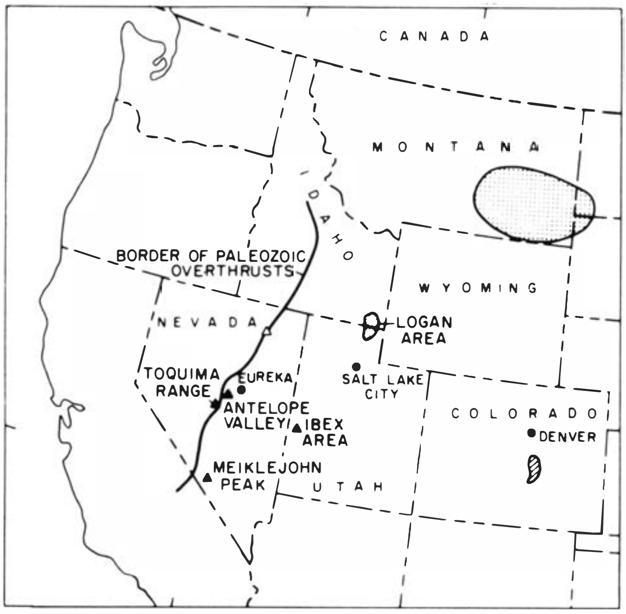

Fig. 1. Selected Ordovician fossil localities in the western United States. Antelope Valley is flanked on the east by the Antelope Range and on the west by the Monitor Range. Eastern carbonates are exposed locally in windows (fensters) in northern Toquima Range west of the east edge of the belt of overthrusts (Ross, 1958, McKee & Ross, 1969).

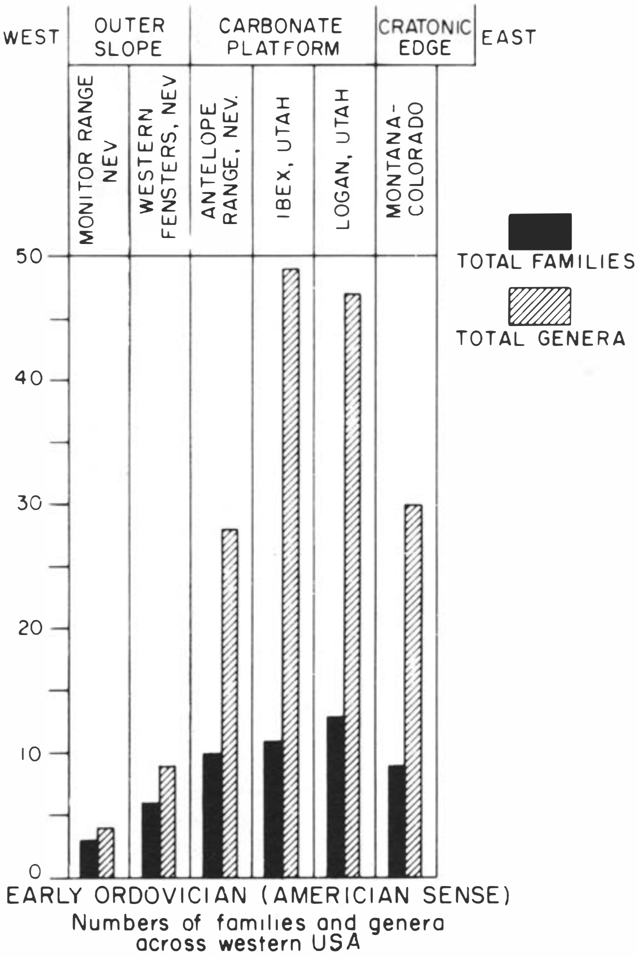

Fig. 2. Graph showing numbers of Early Ordovician trilobite families and genera by environment of deposition across western States at localities shown in Fig. 1. Derived from Table 1.

Early Ordovician (Canadian) trilobites (Fig. 1, Table 1 and Fig. 2) toward the center of the continental platform are not well known, but we can take faunas from Montana to Colorado as representative of the platform; in that area 30 genera represent 9 families (Ross, 1957; Berg & Ross, 1959; Lochmann, 1965, 1966).

Westward in the miogeosynclinal area near Logan, Utah, 44 genera represent 14 families (Ross, 1951), and in the Ibex area to the southwest, 12 families are represented by 47 genera (Hintze, 1952). Still farther west in the Antelope Range, Nevada, 28 genera represent 11 families (Ross, 1970:31–32). In two fenster areas west of the edge of overthrusting (Fig. 1) (Ross, 1958; McKee & Ross, 1969) Lower Ordovician strata represent a facies intermediate between that of the Antelope Range and that of the Monitor Range. In these two localities, 9 genera represent 5 families. In the most westerly range in which we find Canadian strata exposed, the Monitor Range, Nevada, only 4 genera represent 3 families. Diversity increases toward the middle of the carbonate platform and then decreases toward the outer slope of the continent (Table 1 and Fig. 2).

No strata which are confidently placed in the Llanvirnian (Table 2 and Fig. 4) are present in the Montana-Colorado region. However, near Logan, Utah, in beds of Llanvirnian age we found 6 genera in 4 families; at Ibex, Utah, 13 genera in 6 families; in Antelope Valley, Nevada, we found five genera in four families. All of these areas are within the carbonate platform.

The Toquima Range on the other hand includes at least three stratigraphic sequences in thrust relationship and all three in a facies beyond the main carbonate platform. In the Mill Canyon sequence (of Kay & Crawford, 1964) at Ikes Canyon (Ross, 1970:21–27) there are 17 genera in 12 families of trilobites. This sequence is at the lip of the outer slope and not truly in the platform; unfortunately, Whittington and Hughes (1972:367, Table 9, 10) included several genera from this locality (Whittington in Kay, 1962:1424–1425) in their compilation of the platform fauna.

In the June Canyon sequence (of Kay & Crawford, 1964), collections include 15 genera in 13 families; lithologically, the facies corresponds to the platy limestone of Whittington & Hughes (1972, Table 9, column 4). In the next more westerly sequence, graptolite shales include no trilobites.

Table 1. Occurrences of Early Ordovician families and genera at selected localities in western United States and, for comparison, in the Andean area of South America. Summarized in Figs. 2 and 3.

Family	Genus	Monitor Range	Meiklejohn Peak	Antelope Range	Nevada Test Site	Pahranagat Range	Ibex, Utah	Logan, Utah	Montana-Colorado	S. Mexico	Colombia	Bolivia	Argentina
Agnostidae	*Geragnostus*	x		x		x				x	x		x
	Trinodus		x		x								x
Olenidae	*Parabolinella*	x		x					x	x			x
	Hypermecaspis	x		x									x
	Paenebeltella			x				x					
	Bienvillia			x						x			
	Pyraustocranium							x					
Shumardiidae	*Shumardia*			x		x				x			x
Hystricuridae	*Hystricurus*			x		x	x	x	x				
	Hillyardina			x			x	x					
	Amblycranium						x	x					
	Parahystricurus						x	x					
	Psalikilus						x	x	x				
	Psalikilopsis							x					
	Pachycranium							x					
	Nyaya							x					
	Glabretina							x	x				
Komaspidae	*Goniophrys*			x			x	x					
	Carolinites					x	x	x					
	Benthamaspis						x						
Raphiophoriidae	*Ampyx*		x		x								
Leiostegiidae	*Leiostegium*			x		x	x	x	x				x
	Evansaspis						x		x				
	Perischodory								x				
	Manitouella								x				
Remopleurididae	*Pseudokainella*	x					x				x	x	x
	Apatokephalus		x	x			x		x				x
	Kainella			x		x	x		x		x		x
	Eorobergia			x									
	Remopleuridiella						x	x					
	Menoparia						x	x					
	Macropyge							x					
	Scinocephalus							x					
Asaphidae	*Lachnostoma*		x		x	x	x	x					
	Ptyocephalus		x	x	x	x	x	x	x				
	Protopresbynileus		x	x	x		x						
	Aulacoparia		x	x			x		x				
	Bellefontia		x				x	x	x				
	Symphysurina		x		x		x	x	x				
	Xenostegium		x		x		x	x	x				
	Isoteloides			x		?	x	x					
	Presbynileus			x	x	x	x		x				
	Hunnebergia			x									
	Trigonocerca			x	x	x	x	x					
	Megistaspis (*Ekeraspis*)			x		x							
	Asaphellus			x		x		x	x	x			x
	Niobella			x							x		
	Varvia			x									
	Parabellefontia				x		x						
	Megalaspides					x							
	Aulacoparina						x						
	Stenorhachis						x						
	Trigonocercella						x						
	Niobe							?					
	Kobayashia							x					

Cont. next page

Family	Genus	Monitor Range	Meiklejohn Peak	Antelope Range	Nevada Test Site	Pahranagat Range	Ibex, Utah	Logan, Utah	Montana-Colorado	S. Mexico	Colombia	Bolivia	Argentina
	Ogygiocaris								x				x
	Notopeltis								x				x
	Megistaspis Megistaspis								x				x
	Kayseraspis								x				x
	Basiliella								x				x
Taihungshaniidae	*Asaphellina*							x					
Nileidae	*"Barrandia"*						x						
Thysanopeltidae													
Illaenidae													
Bathyuridae	*Goniotelina*					x	x	x					
	Peltabellia					?	x	x	x				
	Bolbocephalus					?							
	Jeffersonia					x							
	Licnocephala						x	x	x				
	Bathyurellus						x	x					
	Oculomagnus							x	x				
	Gonioteloides								x				
Lecanopygidae	*Strigigenalis*							x	x				
	Reubenella								x				
Plethopeltidae	*Paraplethopeltis*						x						
Dimeropygiidae	*Ischyrotoma*		x	x		x	x	x					
	Pseudohystricurus			x			x	x					
Harpididae													
Entomaspididae	*Hypothetica*							x					
Pliomeridae													
	Pseudocybele			x	x	x	x	x					
	Rossaspis			x			x	x	x				
	Hintzeia				x		x	x					
	Protopliomerops					x							x
	Pseudomera					x		?					
	Leiostrototropis					x							
	Cybelopsis						x						
	Pilekia						x						
	Parapilekia						x						
	Tesselacauda						x	x					
	Kanoshia						x						
	Protopliomerella						x	x					
Encrinuridae													
Calymenidae													
Plerygometopidae													
Lichidae													
Odontopleuridae	*Diacanthaspis*					x							
Uncertain	*Clelandia*				x		x	x					
	Pseudoclelandia						x	x	x				
	Hyperbolochilus						x	x					
Total Families		3	5	10	5	11	11	13	9				
	Total Genera	4	11	28	13	24	49	47	30				

Table 2. Distribution of trilobite genera in Llanvirnian (*Orthidiella* and *Anomalorthis* zones) strata of Utah and Nevada. Summarized in figures 4 and 5.

		Outer Detrital		West Transition		East Carbonate Olatform			
Family	Genus	Toquima Range June Sequence	Toquima Range Mill Sequence	Meiklejohn Peak reef cover	Meiklejohn Peak reef	Nevada Test Site	Antelope Valley	Ibex, Utah	Logan, Utah
Olenidae	New genus (= Spitsbergen)	x	x						
	Hypermecaspis								
Agnostidae	*Geragnostus*	x							
	Trinodus			x	x	x			
Shumardiidae	*Shumardia*			x					
Komaspidae	*Carolinites*		x	x	x	x		x	
	Goniophrys		x						
	Carrickia			x					
Raphiophoridae									
Telephinidae	*Telephina*	x							
Glaphurinidae	*Glaphiurus*				x				
Remopleuridae	*Remopleurides*	x	x	x		x			
Asaphidae	*Basilicus*		x						
	Niobe	x	x						
	Isotelus (= *Stegnopsis*)			x					
Nileidae	*Nileus*	x	x	x	x	x	x		
	Peraspis	x	x		x				
Thysanopeltidae	*Perischoclonus*		x						
Illaenidae	*Illaenus*	x	x	x	x		x	x	
	Harpillaenus				x				
Bathyuridae	*Eleutherocentrus*							x	x
	Pseudoolenoides							x	x
	Uromystrum							x	
	Goniotelina							x	
	Bathyurellus				x	x			x
	Barrandia							x	
	Bathyurus						x		
	Raymondaspis	x							
	Raymondites				x				
	Acidiphorus								x
Dimeropygidae	*Ischyrotoma*		x						
	Ischyrophyma			x					
	Pseudohystricurus			x					
Harpidae	*Selenoharpes*			x	x				
Endymionidae	*Endymionia*	x			x				
Cheiruridae	*Kawina*			x	x			x	
	Xystocrania		x		x				
	Cydonocephalus		x						
	Lehua				x				
	Heliomera				x				
	Ceraurus?			x					
Pliomeridae	*Cybelopsis*							x	x
	Parapilekia							x	
	Pseudomera	x	x	x			x	x	x
	Kanoshia							x	
	Ectenonotus	x	x	x	x	x		x	
	Pliomerops			x	x				
	Perissopliomera						x		
Encrinuridae	*Miracybele*	x	x	x		x			
Calyminidae	*Protocalymene*	x	x	x		x			
Pterigometopidae	*Callyptaulax*			x					
Lichidae	*Apatolichas*				x				
Odontopleuridae	*Diacanthaspis*					x			
Proetidae	*Phaseolops*	x							
Dikelokephalinidae									
Trinucleidae									
Total Families		14	12	15	11	9	4	6	4
Total Genera		15	17	20	17	9	5	13	6

For the Llanvirnian, diversity would seem to increase outward from the carbonate platform onto the outer detrital belt (or slope) before dropping off suddenly.

Although they do not behave in the same way the numbers of genera in Early Ordovician and early Middle Ordovician faunas differ according to the geographic position and to the kind of rock in which they are found. Furthermore the composition of the trilobite faunas by family is related to these same factors. The numbers of genera per family per geographic locality are plotted in Figs. 3, 4, and 5.

In the Early Ordovician (Fig. 3) agnostids, olenids, and remopleurids occur in all of the tabulated habitats. The carbonate platform was preferred by hystricurids, leiostegiids, asaphids, bathyurids, and pliomerids. Although the leiostegiids have more genera in the area of cratonic onlap they are represented on the outer slope, and are one of the families with a genus common to Argentina.

All four genera of the Monitor Range outermost slope assemblage occur in Argentina. Five of the six asaphid genera ranging as far as Argentina come from the Montana localities; the sixth is ubiquitous *Asaphellus*.

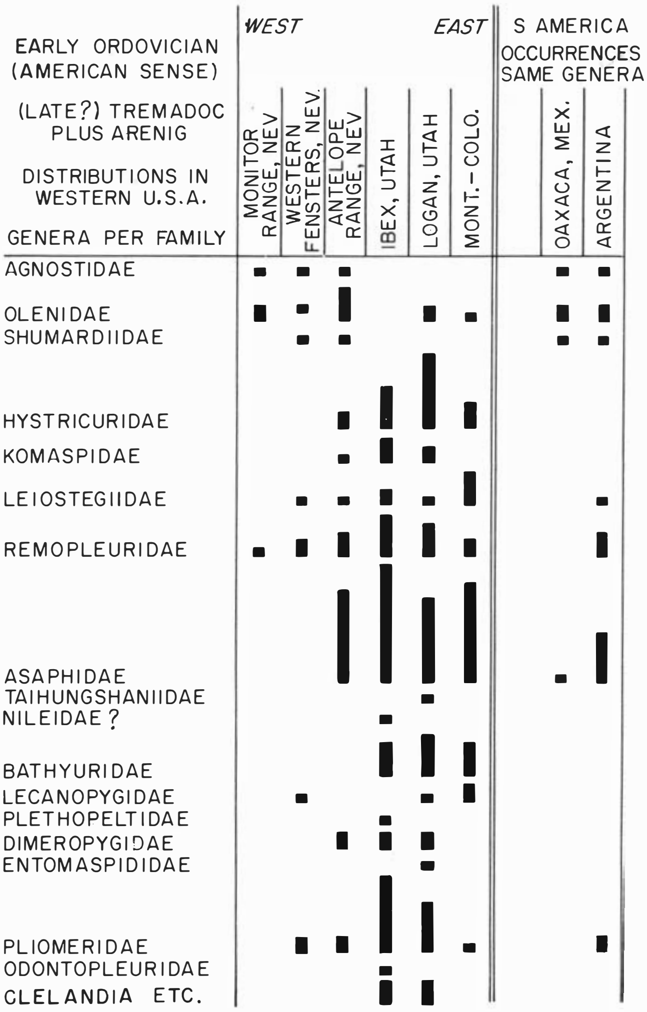

Fig. 3. **Numbers of Early Ordovician trilobite genera per family by environment of deposition across western States at localities shown in Fig. 1. Derived from Table 1.**

The early Middle Ordovician (Llanvirnian) (Figs. 4 and 5) tabulation shows clearly that the bathyurids preferred to live over the carbonate platform. Pliomerids as a family had no marked preference. Considering that some were already travellers in the Early Ordovician it should probably be no surprise to find asaphids forsaking the carbonate platform for the outer slope. Olenids, telephinids, thysanopeltids, dimeropygids, endymionids?, and proetids seem to have been better adapted to life over the muddy bottom of the outer slope. Although the preference is not pronounced in every family, glaphurinids, illaenids, harpids, endymionids(?), cheirurids, and lichids are generically more numerous in the transitional carbonate mudmound (reef) facies.

It is therefore certain that some factor must have affected both the conditions under which the bottom sediments were deposited and the trilobites that lived on or above the bottom.

What the differences in diversity indicate can be debated.

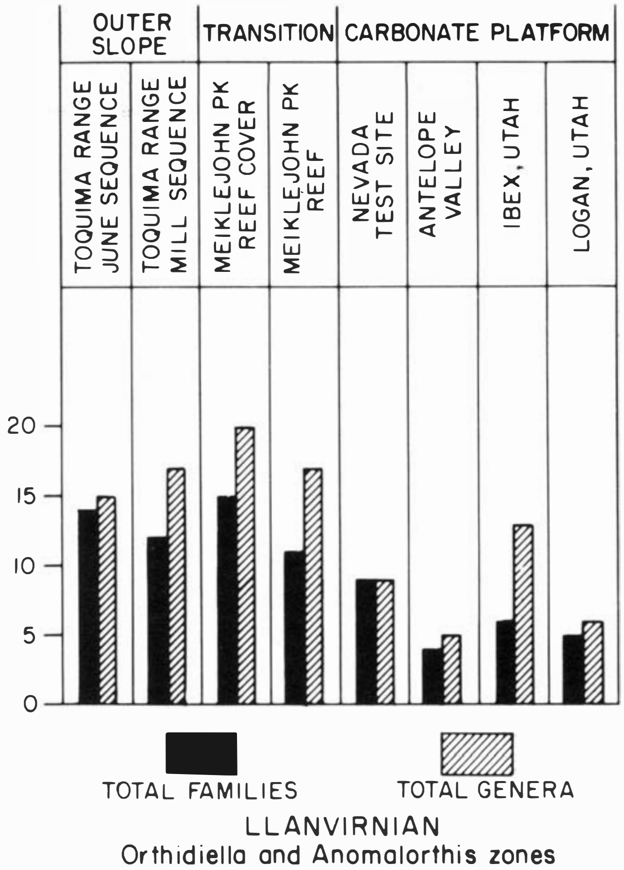

Fig. 4. Graph showing numbers of early Middle Ordovician trilobites by environment of deposition across Utah and Nevada at localities shown in Fig. 1. Derived from Table 2.

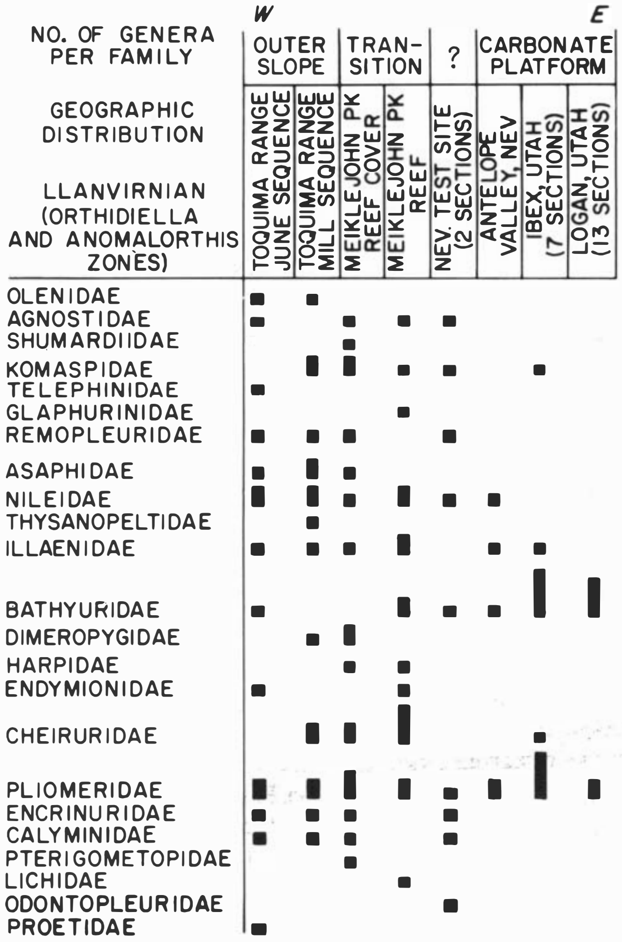

Fig. 5. Numbers of early Middle Ordovician trilobite genera per family by environment of deposition across Utah and Nevada at localities shown in Fig. 1. Derived from Table 2.

The findings of Whittington & Hughes (1972, Table 9) agree with these (when their column 1, platform, is corrected) except that their findings are in the opposite direction — on the east side of the continent. Therefore, diversity of trilobite faunas in North America was not directly related to the equator and must have had some other environmental control.

Cloud (1961:167) has noted that many pelagic microorganisms seldom found in shallow water live in deep water near the bottom of the photic zone where phytoplankton can find abundant upwelling food and zooplankton can live comfortably on the phytoplankton. A similar situation may have existed along the western margin of North America, and may be exemplified by the Llanvirnian localities in the Toquima Range; graptolites are the obvious pelagic element of the fauna which includes trilobites and brachiopods. Clearly (Table 1 and 2), the Bathyuridae characterize the carbonate platform, not the outer slope; virtually all the other families of trilobites were as much or more at home on the slope than in the platform and were probably pelagic.

However, Hessler & Sanders (1967) showed that benthonic diversity (number of species) in the deep sea is as great as, or greater than, in shallow water and is independent of food supply.

Sanders (1968:254, 257) has concluded that time and stability are required for high diversification of a fauna. Therefore, equatorial regions have more diverse faunas not because the water is warm but because tropical regions are less affected by climatic change than the higher latitudes and are thus more stable. Valentine (1968:273) has favored nearly the opposite viewpoint.

From the facts presented here I suggest that:

(1) In the lower part of the Ordovician, faunal control is empirically related to lithologic belts as noted by Palmer for the Cambrian, (2) because North America spent most of its early Paleozoic history in the same low temperate or tropical zones its fauna became well adjusted to a charitable and uniform climate, (3) it is the stamp of environmental differences within that broad climate that is made most obvious by faunal distributions as we see them.

CAMBRIAN BIOGEOGRAPHY

Palmer (1972) has reviewed the biogeography of Cambrian trilobite faunas and has concluded that faunal distributions are best explained by a combination of facies and climatic (latitudinal) control. His case for two main facies groups is convincing: one facies composed in part of endemic genera living on a restricted cratonic shelf, usually in carbonates; the other inhabiting the shelf margins and the open sea, composed of widespread pelagic genera.

He concluded further that there were four distinct restricted shelf areas: (1) North America, (2) Siberia, (3) China-Australia, and (4) Central Europe. Bordering each of these areas was an outer marginal belt usually of dark thin-bedded muddy limestone or shale containing a pelagic fauna of paradoxidids, olenids, and agnostids.

No amount of rearrangement of continental platforms seems to satisfy all the distributional problems encountered for Cambrian trilobites. In 1968, Palmer found that Early Cambrian trilobites of Alaska were closely related to those of Siberia, but that Late Cambrian forms, which belong in his open-ocean faunas (Palmer, oral commun., June 6, 1973), are like those of Korea, eastern China, and Australia. Palmer & Gatehouse (1972:D4—D6) reported that Early Cambrian trilobites from Mount Spann in Antarctica were closely related to those of southern Siberia, that early Middle Cambrian forms were Australian in affinity, and that Late Middle Cambrian trilobites were related to forms in eastern Asia, China, Australia, and eastern Siberia. All the Antarctic faunas are restricted platform assemblages (Palmer, oral commun., June 6, 1973). Palmer (1972) emphasized that Antarctic faunas have nothing in common with those from Andean Argentina and that the Argentine faunas are North American in aspect. Furthermore, the Bolivian-Venezuelan faunas have much in common with those of North Africa and southwestern Europe.

The arrangement of continental plates shown in Figs. 6A—D satisfies most paleomagnetic data now available and most of the latitudinal and faunal requirements noted by Palmer (1968, 1972). Siberia is placed close to Antarctica to allow for the similarity of their restricted shelf faunas, although purely geologic considerations might favor a position for Siberia closer to the present northeast coast of Australia or adjacent to Antarctica in the Ross Sea. Palmer (oral commun., June 6, 1973) objects to the first two positions because the Cambrian shelf faunas of Australia have nothing in common with Siberia, but are related to those of China.

Because the south pole is believed to have been west of Morocco, Palmer (1972) suggested that the various restricted shelf faunas may have been arranged latitudinally. The faunas of the Asiatic areas would have been in the tropics or in the northern hemisphere, the American faunas in the middle latitudes, and the central European faunas in the high Antarctic latitudes (Palmer, 1972, Fig. 3).

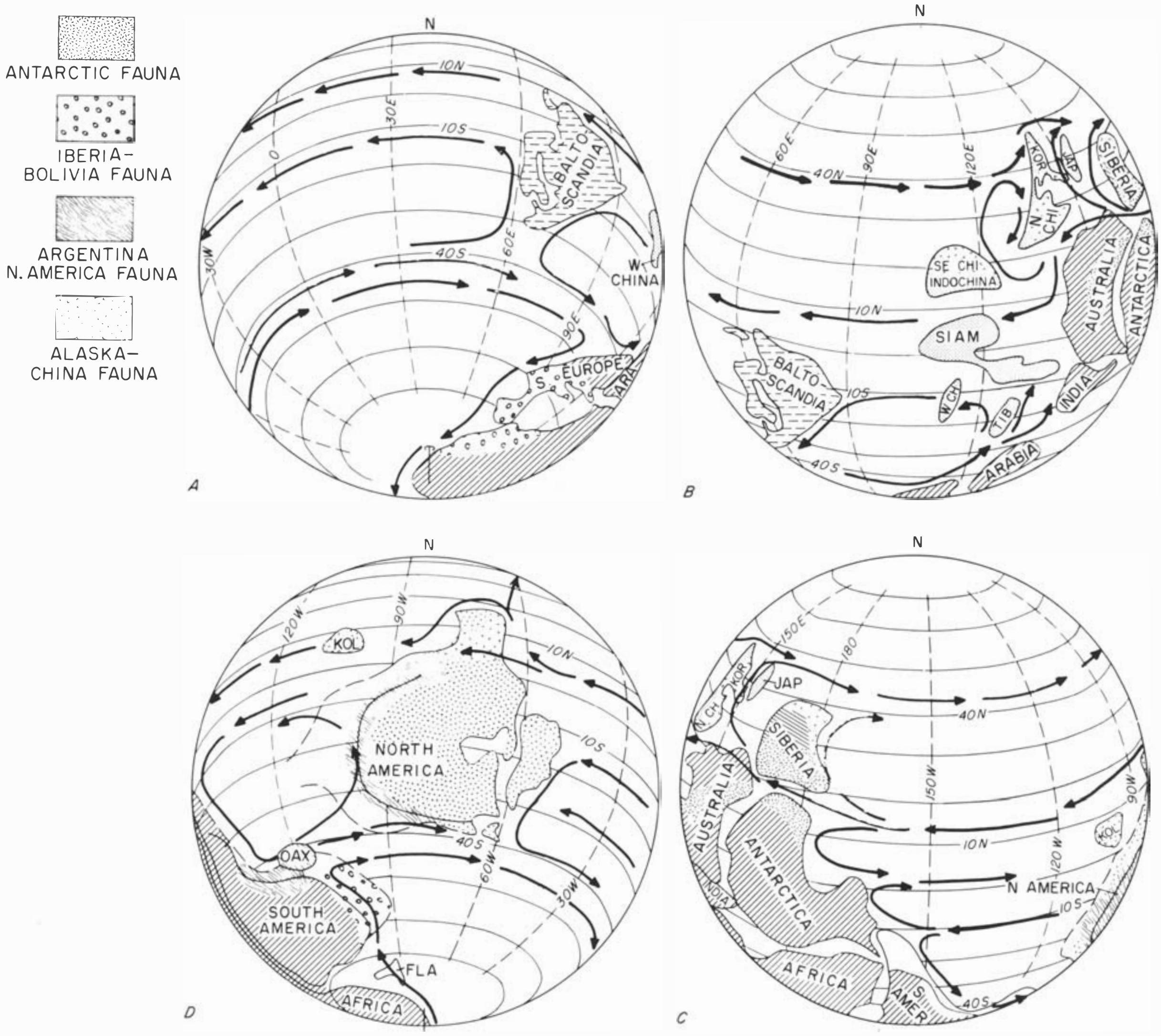

Fig. 6. Hypothetical positions of continental plates in the Cambrian. South equatorial current deflected into three separate counterclockwise gyres shown in A, B, D. Clockwise counter current shown south of 40° S. Lat. in A, D.

The scarcity or lack of carbonates in the Cambrian and most of the Ordovician in southwestern and central Europe is compatible with a cold-water environment.

Whittington (1973:16–17, Fig. 3), like Palmer, has noted that the distribution of Early Ordovician trilobites around Gondwana may be related to latitudinal belts around a South Pole in Morocco.

The westward-flowing north equatorial current (Figs. 6D and 6C) could have carried such forms as are in common from the Alaskan coast to Siberia, Australia, Korea, and China. It is probable that most of the volume of this current after flowing against the coasts and over the shelves of these Australasian areas would have been deflected in northward clockwise gyres to return eastward close to the 40th parallel (the early Paleozoic Roaring Forties) along which route there seem to have been no other hospitable shores (Figs. 6A, B). Potential immigrants caught in this current would have had to circle the earth or perish.

The southern equatorial current (Figs. 6C, D) would have swung southward in a counterclockwise gyre along the then east coast of Argentina. This current, like the modern Gulf Stream, would have warmed the coast and carried North American genera to the Andean region. In fact, this 'Andean Stream' probably split close to 40°S. lat., part curling north along the west coast of North America to be recirculated back along the Argentina coast, and the other fellowing the present east coast of north America to mix with waters of another gyre deflected southward by the other east coast of north America. We would expect the Cambrian faunas of south central and western United States, in particular, to closely resemble those of Argentina, and this, Dr. Palmer assures me, they do.

Similarly, another gyre should have operated between Baltoscandia and North America (Figs. 6A, D); the northern limit of this gyre would also have been controlled by the south equatorial current and the southern limit by the east-flowing current close to the 40° S. parallel.

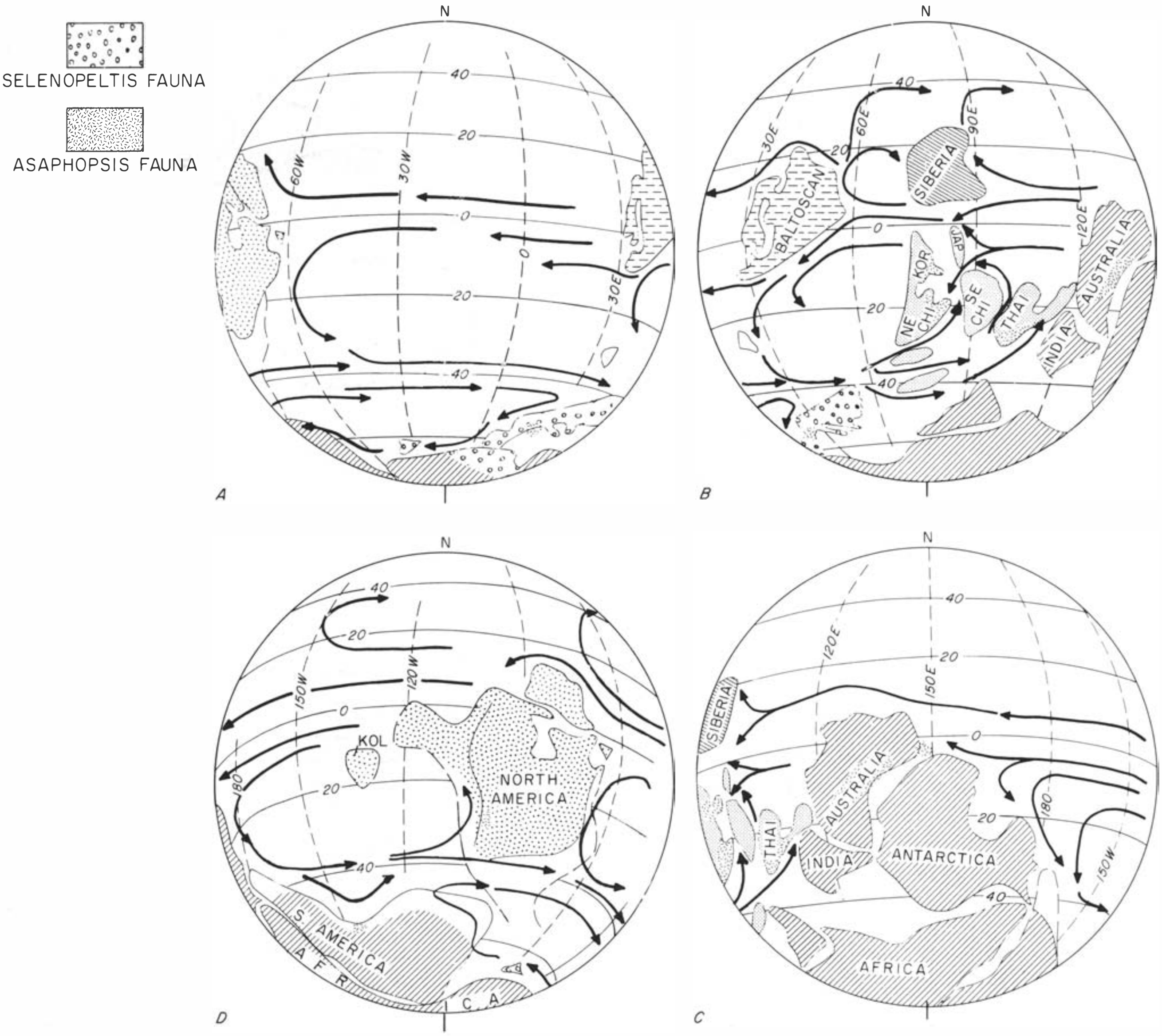

Fig. 7. **Hypothetical Middle Ordovician distribution of continental plates. South equatorial currents deflected into separate gyres. Clockwise current south of 40° S. Lat. nurtures *Selenopeltis* fauna (A, D).**

A third similar gyre should have operated east of Baltoscandia and west of the Australian coast of Gondwana (Fig. 6B).

Although there would have been some mixing of waters of these gyres and, therefore, of pelagic faunas, the gyres may have been the fundamental cause of geographic provincialism. Palmer (1968: B17) has commented that the outer shelf-open ocean trilobites found on the present west side of North America are like those of Asia and Australia, whereas those on the present east side of North America resemble forms from Europe.

All these counterclockwise gyres operated south of the equatorial belt and probably no farther south than 40° S. Palmer (1972) considered the trilobites of the Andean region from Bolivia to Venezuela, of Morocco, and of southwestern and central Europe, to have been Antarctic. The distribution of these trilobites also seems to have been determined by a gyre which resembled the modern combined Alaska, Oyashio, and Subarctic currents of the Pacific (Munk, 1955, Fig. 1). This clockwise Cambrian gyre probably flowed eastward from the Bolivian coast (Fig. 6A, D) close to parallel 35° S., turned southwest through southwest Europe to Morocco and Florida, and back to Bolivia via Venezuela and Colombia. This should indeed have supported a cold-water fauna. The only chance for emigrant genera to escape was by crawling slowly along the coast westward into Argentina or eastward into the Middle East, or by taking the ocean trip eastward with hopes of straying into the more northerly current. I would expect to see some evidence of westward migration along the coast from central Europe to Africa and Bolivia. Dean (1967) has called attention to such a migration in the Early Ordovician.

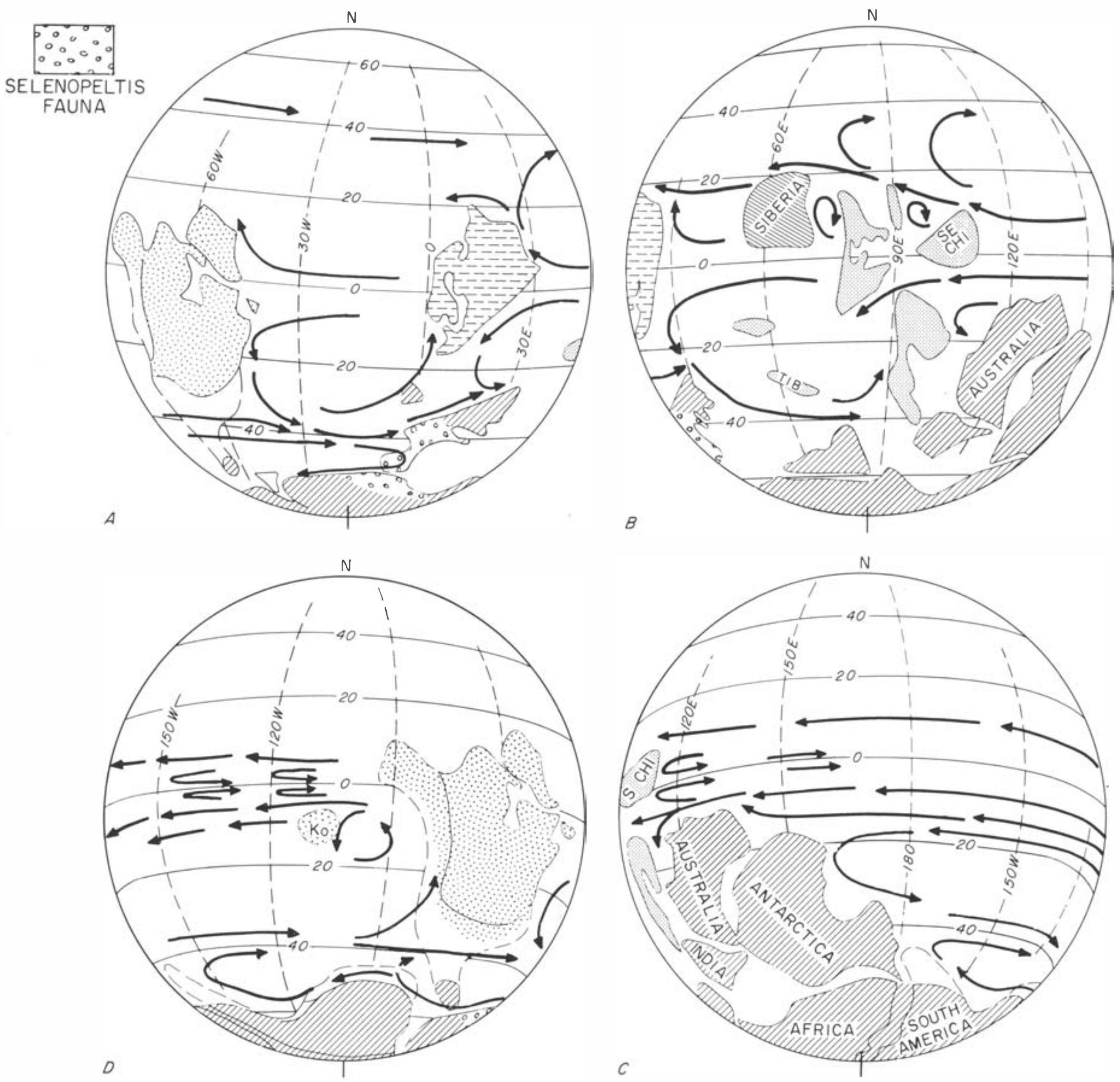

Fig. 8. Late Ordovician removal of Australian and Antarctic portions of Gondwana from obstructing position across equator permits increased sweep of equatorial current shown in B. South America coast completely south of 40° S. Lat. shown in D. *Selenopeltis* fauna restricted as clockwise gyre is constricted (A, D).

EARLY PALEOZOIC OCEANIC CIRCULATION

We find a pattern established in the Cambrian of three separate counterclockwise oceanic gyres south of the equator(?) and north of latitude 40° S., each separated from the others by a continental plate. South of lat. 40° S. there was a single clockwise gyre in which a cold water fauna could have been almost as closely confined as if the gyre had been entirely landlocked.

The northern hemisphere was almost devoid of land areas; oceanic circulation should have been virtually unrestricted. Lacking a polar land area like modern Antarctica or a landlocked polar ocean like the modern Arctic Ocean, no ice could form. As a result, no steep latitudinal climatic gradient would have existed in the northern hemisphere. It is, therefore, probable that a pelagic or nektonic organism would have had a better chance of surviving a long ocean voyage in the northern than in the southern hemisphere in Cambrian and Ordovician time.

These contrasting patterns between northern and southern hemisphere continued through Middle Ordovician time.

SINGLE AND MULTICLIMATE LANDMASSES

North America, the Siberian platform, and the Russian (Baltoscandia) platform are each believed to have remained in a single latitudinal zone throughout the early Paleozoic. Therefore, the climates of these areas should have been stable and warm. Such pelagic faunas as were present should have

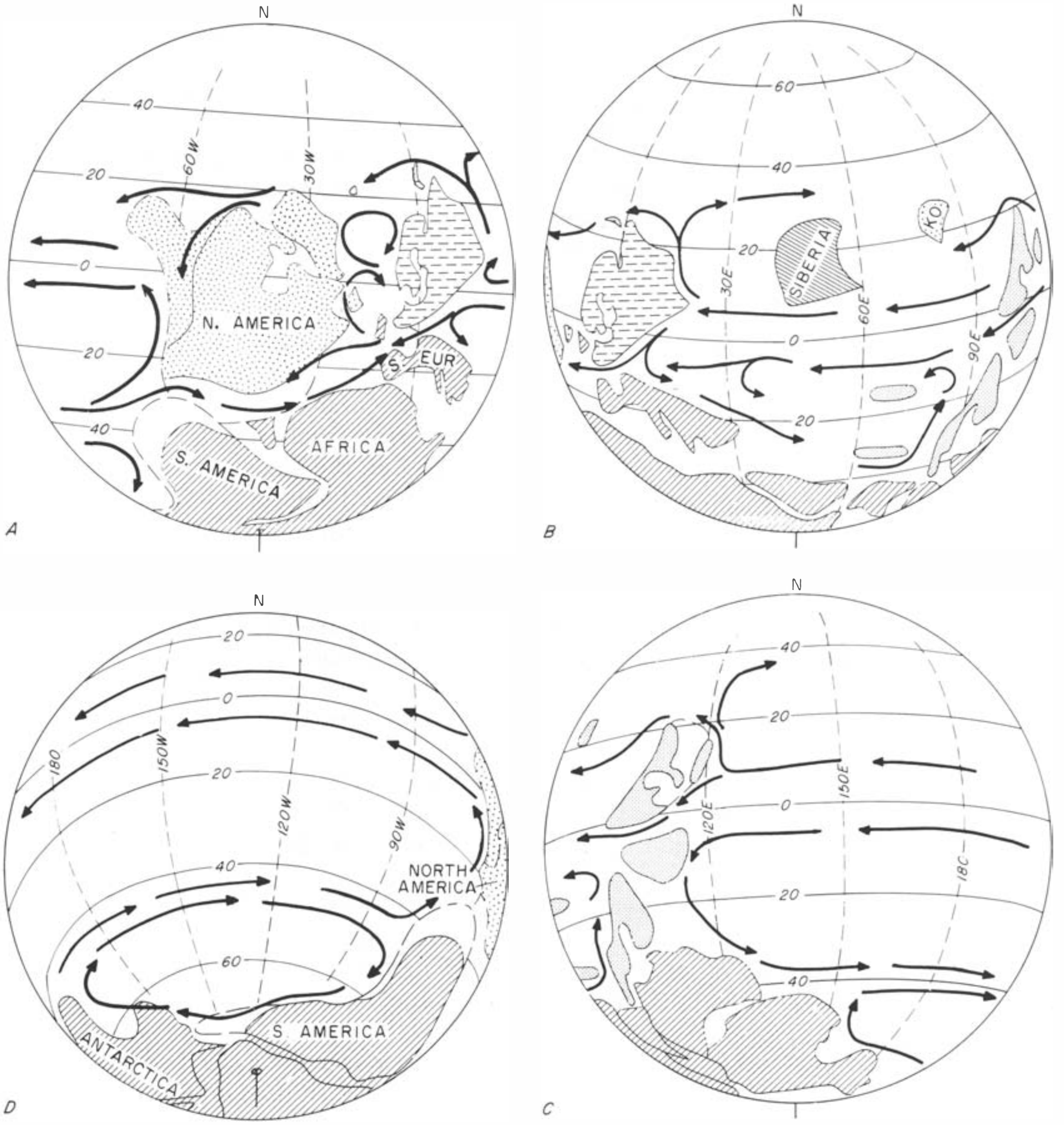

Fig. 9. Hypothetical Late Silurian positions of continental plates. Clockwise gyre (south of 40° S. Lat.) north of Antarctic-South American-S. African coast of Gondwana and in position to nurture Malvenokaffric fauna of Early Devonian as shown in D.

been widely distributed to all these platforms; in fact, the high degree of similarity between Ordovician faunas of the Cherskyii Mountains along the west side of the Kolyma platform (northeast USSR) (Ross & Ingham, 1970:402–403) and those of the North American "Toquima-Table Head Faunal Realm" is probably attributable more to the pelagic nature of the fauna than to proximity on a contiguous shelf required by similarity of a benthic fauna.

Inasmuch as each of these single climate platforms experienced a relatively uniform climate for a very long time, the greatest influence on diversification of faunas should have been exercised by local variants, such as salinity, depth, turbidity, restricted circulating; and the nature of the sea floor (Craig, 1961:211; Sanders, 1968:251). There was ample opportunity for the development of the carbonate platforms which fostered the restricted shelf faunas as opposed to the outer shelf-open ocean faunas of the Cambrian (Palmer, 1972) and Ordovician of North America.

In contrast to the stability of North America, the Siberian Platform, and the Russian Platform, the evidence already presented suggests that the continent of Gondwana traversed 90° of latitude in the early Paleozoic. As the central part of Gondwana moved through the south polar region, the climates of western Africa and South America must have been constantly changing. The west coast of Argentina in the Cambrian would have been at 40° S. (Fig. 6D), moved southward past 60° S. by Late Ordovician time (Fig. 8D), passed 70° S. by Late Silurian time (Fig. 9D), and reached a more northerly position in the Devonian. It is small wonder that Ordovician carbonate rocks are small in volume north of the province of La Riojas and that there is evidence of glacial deposition in the Caradocian rocks of the Precordillera.

The most striking change in trilobite diversity in the northern Eastern Cordillera of Argentina (Harrington & Leanza, 1957:22–39) is temporal. Total genera in the Early Tremadocian number 37, in the Late Tremadocian, 28, in the Arenigian, 15, and in the Caradocian, 5. The decrease coincides with the drift of northern Argentina closer to the South Pole.

Harrington & Leanza (1957: 43, 51) reported that some of the Tremadocian shales yielded thousands of complete trilobites, particularly olenids, belonging to a few species; in the Arenigian some near-shore deposits contain countless specimens of the asaphid *Kayseraspis*, whereas others farther offshore yield abundant *Thysanopyge.* Craig (1961:211) noted that cold water assemblages commonly contain few species but great numbers of individuals of a few species.

Palmer (1972:313, Fig. 3) concluded that trilobite distributions in the Cambrian of Gondwana seemed to be controlled by latitudinal, presumably climatic, belts. Similarly, climatic change has placed the strongest stamp on Ordovician faunas.

Gondwana, unlike North America, was in the early Paleozoic a multiclimate continent. As noted above, the geometry of the globe and the shape of the supercontinent caused the east corner to behave as a pivot. Therefore, Australia remained across or close to the equator until Late Silurian time. According to Hamilton (oral commun., March 1973) the Malay Peninsula and Siam (Thailand) were probably linked geologically with eastern Australia prior to the Jurassic; possibly all of Indochina, China, Korea, and Japan acted as a unit in Paleozoic time, rather than as separate small plates shown crudely in Figs. 6–9. There is some suggestion that faunas of a probable pelagic or outer shelf nature occur at the margins of some of these plates. In any case it seems likely that southeast Asia, like Australia, remained in the equatorial zone throughout the early Paleozoic, and that each should have developed a carbonate platform bounded by a seaward outer detrital belt, as in North America. Ordovician limestone is present in the interior of the Australian continent with thick sequences of graptolite shales in the eastern ranges.

It is obvious that two extremes are exemplified by the Andean region on the west coast of Gondwana where changing climate dominates biogeography, and by Australia where local environments may have determined trilobite distributions within a warm single climate area similar to North America.

Tethys stretched between these two extremes along the north margin of Gondwana so that its west end lay at the South Pole (Fig. 6A) and its east across the equator in the Cambrian (Fig. 6B). In the latest Ordovician, Morocco lay at 50° S. (Fig. 8A) and northeastern Australia at 10° S. (Fig. 8B, C). And by the close of the Silurian both Morocco and northeastern Australia were at approximately 30° S. (Fig. 9A, C).

As a result, we might expect a thermal gradient from cold to warm along the Tethyan realm from west to east in the earliest Paleozoic, a uniform temperature toward the end of the Silurian, and a reversal from the Devonian onward.

Spjeldnaes (1967) showed that the Ordovician strata of Spain, Portugal, and Morocco were related geologically and were probably laid down in a shallow marginal sea. Shales and mudstones are unaccompanied by limestone and probably represent littoral and tidal flat deposits. In this western area, Middle Ordovician faunas are characterized by great numbers of specimens of a few species. These beds resemble those of Argentina of the same age and were probably deposited in cold water (Spjeldnaes, 1961).

As Emerson (1956:394) noted, cold water organisms which live in shallow water in high latitudes are found living closer to the equator in progressively deeper water. We might, therefore, expect to find that Cambrian and Ordovician faunas of western and central Europe migrated along the coast toward Australia; the reverse would be less likely.

GYRES AND MIGRATIONS

Dean (1967) has emphasized the dynamic nature of Ordovician trilobite faunas of the Tethyan area, citing numerous examples of generic migration. *Taihungshania* and associated genera, including *Asaphopsis* and its close relatives, occur in France in the Arenigian and seem to have moved eastward to persist in the Llanvirnian in China, Korea, Tasmania, and New Zealand. The next younger *Bathycheilus* fauna, including *Neseuretus* and *Selenopeltis,* is present in the Arenigian of France, Iberia, and Morocco. Elements of this fauna arrived in southern China in Llanvirnian time. Dean further noted that many species appear in the Llanvirnian of England, Wales, and Iberia that occur later in Bohemia or more easterly points, and that lichids, illaenids, and nileids appearing in southern China add to that fauna a Scandinavian element.

At this time the westward flow of the equatorial current should have been obstructed by Baltoscandia (Fig. 7B), and farther west by North America (Fig. 7A or 7D). The southern part of the current should have been deflected southward in counterclockwise gyres, so that warm eastward-flowing water washed the north coast of Gondwana (Fig. 7A, B); these currents would have resembled the North Pacific and North Atlantic Drift currents of the modern oceans. As shown in Figs. 7A, B;9A, B the "Tethyan Drift" probably did not have much warming effect on the Moroccan coast until Late Ordovician or Silurian time, although it impinged on central Europe as early as Cambrian time (Fig. 6A, B).

Dean (1967, Figs. 2, 4; written commun., June 1973) showed that Baltoscandian trilobites appeared in southeast Asia in the Arenigian or Llanvirnian, in southern Turkey in the Late Arenigian and in the Anglo-Welsh area in the Caradocian; this implies that Baltoscandia was moving westward along an equatorial path north of Gondwana. Furthermore the seeming lack of American elements in Tethys at this time would suggest that North America was still too far to the west or southwest to deflect a warm water gyre toward northern Gondwana (Fig. 7A). However, we should note that the illaenid, lichid, and nileid trilobites which purport to be Baltoscandian in this case are the kinds of trilobites that are particularly abundant in the outer shelf open-ocean pelagic environment around North America at this same time.

As already noted, the drift of the prevailing current should have been adequate to effect the eastward migration of trilobites along the Tethyan coast of Gondwana (east of Iberia) into warmer waters north of lat. 40° S. (Fig. 7B).

On the other hand, the clockwise gyre south of lat. 40° S. (Figs. 6A, D; 7A, D) would have assisted the migration of genera from western Europe to Morocco and Florida and to South America as far as Bolivia but not as far as Argentina. By Ashgillian time (Figs. 8A, D), this southern gyre had probably extended as far as the Argentine coast. Throughout its Ordovician existence its waters nurtured the *Selenopeltis* fauna of Whittington & Hughes (1972).

By Late Silurian time the old gyre ceased to function (Fig. 9A, B) in the area west of Iberia because the Gondwana coast had moved north of lat. 40° S. Instead, the gyre seems to have been in full operation along the South American and Antarctic coasts (Fig. 9D) and may have influenced provincial faunas of Silurian-Devonian age in South America. In fact, Dr. Alan Ormiston (oral commun., July 5, 1973) stated that the distribution of the Devonian Malvinokaffric province of Boucot, Johnson & Talent (1969:27) might be closely related to such a current.

Whittington & Hughes (1973:238) proposed that the *Asaphopsis* fauna of Argentina indicated a warmer climate and therefore a lower latitude than the *Selenopeltis* fauna. As we have seen, the *Selenopeltis* fauna continued to exist as long as it remained in the cold waters of the clockwise gyre as far north as lat. 40° S. (Fig. 8A). The *Asaphopsis* fauna of Argentina probably survived south of lat. 40° S. only as long as the warm stream of the counterclockwise gyre could reach it along the Andean coast (Fig. 7D). The survival of one and the end of the other depended not only on latitude but also on the behavior of tectonic plates and oceanic currents. The distribution of the *Asaphopsis* fauna may be somewhat more widespread than visualized by Whittington & Hughes (1972, 1973). Closely related *Asaphopsoides,* until recently (Hupé, 1953) assigned to *Asaphopsis,* is associated in southern France with *Taihungshania* and *Asaphelina. Asaphelina* is present in Arenigian strata of northern Utah (Ross, 1952).

The Early and early Middle Ordovician trilobites of the Andean area show several affinities with the Tethyan area, not limited to the common occurrence of *Asaphopsis.* As an example, 11 of 16 Llanvirnian genera have distribution outside of South America. *Bathyuriscops (=Proetiella)* is known only in Khazakstan but its synonym *Annamitella* is widespread (Ross & Ingham, 1970). *Asaphopsis* is widespread in Australia, Korea, China and, possibly, France. *Carolinites, Lonchodomas, Pliomera, Cyrtometopus* and *Encrinurus* are widespread genera. *Synhomolanotus* is Tethyan. *Parabasilicus* and *Dolerobasilicus* are Korean, although poorly known and therefore of questionable value. *Nanillaenus* is North American although it is questionable whether the Argentine specimens (Harrington & Leanza, 1957:193, Fig. 10 1) are correctly assigned thereto.

OPENING OF THE EQUATORIAL FLOODGATES

As already noted above, in the Cambrian and Early Ordovician the equatorial current should have been deflected by Antarctica so that a southward counterclockwise gyre flowed along the Andean coast; this gyre split so that a part washed the present west coast of North America while a part flowed into the west end of the Tethyan realm. However, by late Middle and Late Ordovician time the drift of Gondwana removed the Antarctic and Australian coasts from the main stream of the equatorial current, and the warm southward gyre along the Andean coast was greatly reduced. The reduction of this ameliorating warm current may have been as effective in reducing the Caradocian trilobite population of Argentina to five genera as the approach to the polar region.

The withdrawal of Antarctica and Australia from positions obstructing the westward flow of the equatorial current must have happened gradually and must have affected more than the

Andean coast. Dean (1967, Fig. 4) and Whittington (1966:725–726) have shown that the earlier eastward trend in Tethyan migration is mixed in Caradocian time with some westward movements of genera from China to Asia Minor and from Europe to North America. This change may coincide with the interplay between the increasing westward sweep of the equatorial current past eastern Gondwana and the eastward flow of the "Tethyan Drift" generated by the southern counterclockwise gyre. The result is difficult to portray inasmuch as we have no firm information on the relative positions of component platforms of Tibet, China, Korea and Thailand (Fig. 8B).

Whittington (1966), Dean (1967), Whittington & Hughes (1972, 1973) have commented on the breakdown of provincialism in Late Caradocian and Ashgillian faunas throughout the world. This breakdown is illustrated particularly by the spread of the *Hirnantia* fauna (Dean, 1967, Fig. 5) and the occurrence of the "remopleuridid" fauna (Whittington & Hughes, 1972, Fig. 12).

The Copenhagen and Hanson Creek Formations of central Nevada (with *Remopleurides, Hypodicranotus, Robergia,* and *Robergiella,* the olenid *Triarthrus,* the komaspidid *Carrickia, Nileus, Toernquistia, Cryptolithoides,* the raphiophorids *Lonchodomas, Ampyxina,* and *Raymondella,* the cheirurids *Ceraurinella, Ceraurus,* and *Sphaerocoryphe,* the encrinurid *Cybeloides,* a calymenid (possibly *Platycoryphe), Calyptaulax, Amphilichas, Miraspis, Primaspis,* and several illaenids including *Thaleops)* provide examples of formations containing such remopleuridid assemblages.

The improved flow of the equatorial current around the platforms of southeast Asia, the continued northerly movement of the northwest coast of Gondwana, and the increased deflection of the equatorial current by North America, which was approaching Baltoscandia and Gondwana from the west, improved the chances of dispersal.

Whittington (1966:716–717, 728–729) has shown that certain agnostids, raphiophorids, alsataspidids, shumardidids, olenids, telephinids, kompaspids, and nileids are widespread in the Ordovician and although he has not done so I suggest that these genera were pelagic in habit and more easily disseminated than their benthic relatives. To Whittington's list asaphids such as *Asaphellus* and several remopleurid genera should probably be added. There is some indication that dimeropygids, leiostegiids, hystricurids, some encrinurids, dalmanitinids, and pliomerids were pelagic to a certain degree.

Obviously not every genus of each of these families was pelagic; within the Remopleurididae, *Scinocephalus* and *Menoparia* seem to be restricted to North America, for instance.

On the other hand, most trinucleids and calymenids seem to have been benthic unless certain genera took up a pelagic habit in the late Middle Ordovician. Only then do they seem to have made the passage from the Gondwana coast to the North American coast.

The removal of barriers to dispersal of benthic trilobites has been cited as the reason for the decreased provincialism (Whittington & Hughes, 1972:263), but it seems equally likely that improved circulation of favorable currents aided the dispersal of pelagic trilobites. Berry & Boucot (1973) have recently proposed that the removal of water from the oceans by Late Ordovician-Early Silurian glaciation resulted in a restriction of the oceans. Such restriction should have had a far more drastic effect on the benthonic genera than on the outer margin and pelagic forms, but it might also have put formerly deep bottoms within the reach of benthonic genera. Was the Caradoc-Ashgill remopleurid fauna widespread because it was pelagic or benthonic? Was the improved distribution of graptolites at precisely the same time because graptolites were pelagic or benthic?

CONCLUSIONS AND ECONOMIC IMPORTANCE

The combined evidence of paleomagnetism, occurrence of evaporites, and distribution of trilobite faunas suggest that the landmasses of the earth have been in constant movement relative to the poles and relative to each other. In attempting to visualize paleobiogeography it is advisable to take into account not only the particular area under immediate scrutiny but also the effects upon oceanic circulation of plate movements on the opposite side of the globe.

In examining the known occurrences of Cambrian and particularly Ordovician trilobites, it has been found that:

(1) Faunas of continents and platforms that have remained in a single latitudinal or climatic zone, particularly in a warm climate, for long periods of time are well adjusted to a uniform climate but show most strongly the effects of local environment. The trilobites related to the inner detrital, carbonate platform, and outer detrital belts of Palmer (1972) in Cambrian (and Ordovician) North America are examples. Centrifugal changes in faunal composition and diversity result.

(2) The faunas of continents which passed rapidly through climatic zones, particularly through inclement zones, bear the print of climatic rather than local environmental variants. Faunas may

be arranged in broad latitudinal bands, and diversities may change stratigraphically within each band as in western Gondwana (Andean area).

(3) Inferred patterns of warm oceanic currents relative to latitude and changing continental obstructions are compatible with distribution of pelagic trilobites.

(4) Tethyan trilobite distribution during the Ordovician shows a reversal in migration related to movement of Moroccan and Algerian Gondwana into a warmer climate, removal of Antarctic and Australian Gondwana from its obstructing position across the equatorial current, westward movement of Baltoscandia, and eastward movement of North America.

The search of mineral and fuel deposits should not neglect the use of paleobiogeography to assist in inferring ancient physical geography. Deposits of one continent may once have been continuous with or closely related to those of a formerly juxtaposed land. Evaporites, a source of fertilizer and an associate of close to 50% of the world's petroleum, are related in origin to a continent's former position close to the equator. Inasmuch as a large share of oil reserves are related either to evaporites or to limestone/dolomite terrain the greatest chance of successful exploration may lie in platforms that have been close to the equator in their geologic history or so affected by oceanic currents as to maintain a warm climate for long periods of time. It seems reasonable to expect that oil and evaporites of early Paleozoic age will be found in Antarctica, for instance. Furthermore, the lands that have spent the longest geologic time in the equatorial zone may have the greatest potential for petroleum production.

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Early Ordovician trilobite communities

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From a numerical abundance study of the distribution of trilobites through the Valhallfonna Formation (Arenig-Llanvirn), Ny Friesland, Spitsbergen, three major types of early Ordovician trilobite communities are distinguished, each with a characteristic suite of genera. These are termed the olenid, nileid and illaenid-cheirurid communities. Their occurrence is related to a shallow to deep water environmental gradient, across which individual genera had different tolerance ranges. A fourth group of trilobites was independent of bottom conditions and is considered to represent a pelagic community.

Within the limits of available data on relative abundances, comparisons with contemporary faunas suggests that the community types may have been widespread in early Ordovician times. The shallow water illaenid-cheirurid community and deep water olenid community have a relatively long geological history compared with the nileid community. It is necessary to take community types into account before making generalisations about early Ordovician faunal provinces; the olenid community, for example, may have been independent of provincial boundaries.

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This paper presents an analysis of the numerical distribution of trilobite remains through the Valhallfonna Formation, of early Ordovician (Arenig-Llanvirn) age. The Valhallfonna Formation consists of several hundred metres of highly fossiliferous limestones and subordinate shales exposed in a number of sections in north Ny Freisland, Spitsbergen (Fortey & Bruton, 1973). The complete exposure of this Formation makes it ideal for bed by bed collecting, while the abundance of fossils makes it comparatively easy to obtain large samples. While collecting the section for the first time in 1967 (Cambridge University Expedition) it became apparent that the distributions of fossils through the section were related to the enclosing rock type, and it was with a view to clarifying these relationships that the present study was made. Most of the data is based on the 1967 collections, although certain parts of the section which were inadequately sampled then were collected in detail in the 1971 expedition, organised by the Paleontologisk Museum, Oslo, and the Norsk Polarinstitutt.

Few detailed studies have been made which attempt to discover which genera of trilobites lived together to form a natural community. Comments on possible relations of trilobites to sediment type, environment or to each other are in general scattered through systematic descriptions, or the environment is considered as an explanation of particular morphological features, such as blindness (Erben, 1961; Clarkson, 1967). This study is a preliminary attempt to suggest ways in which trilobite communities may be recognised, with some comments on their palaeogeographic interpretation.

As indicated below the Spitsbergen sections are unusual in the variety of assemblages present in a single geographic area. Confirmation or otherwise of the community types recognised there is to be anticipated as other sections are investigated in a similar way.

Many of the trilobites in the Spitsbergen sections are referable to new genera. Those belonging to the family Olenidae have recently been described (Fortey, 1974a). A number of others of which the distribution is discussed below are referred provisionally to the genus of their closest relatives in the present account with the designation "aff."

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SAMPLING METHODS

Most of the Valhallfonna Formation was collected bed by bed in 1967, and almost every horizon collected yielded numerous macrofossils. An analysis follows of the numerical variation in the kind and numbers of the fossils obtained through the section. Only the lower 75 m of the Profilbekken Member were analysed as fossils are relatively rare above that in the section. It is recognised that it is virtually impossible to obtain a completely unbiased sample which reflects the initial population of the fossils in the rock. This might only be possible where silicification of all hard parts of all groups of organisms has occurred, when the residues remaining after acid digestion of equal weights of rock might be compared. In the Valhallfonna Formation silicification appears to have been highly selective, some groups of organisms (such as Orthacean brachiopods) being frequently found replaced by silica, others (such as gastropods) very rarely, and so solution techniques are not of general use in establishing relative abundances of different groups. Solution of limestones remains the best method of extracting inarticulate brachiopods. The method used to determine relative abundances remains inevitably subjective. Approximately equal thicknesses of the section were collected each day, and the total number of fossils exposed on the broken surfaces of the fragments of rock obtained per collecting unit has been taken as a *relative* measure of their abundance. The rock is usually so fossiliferous that biased collecting for one particular species is difficult – many more are associated on the same rock fragment. Furthermore, as will be seen, the changes in relative abundance are so marked that collecting bias probably makes little difference to the general conclusions. The data are presented in the form of block diagrams, each block representing the yield of specimens of the taxon concerned on the rock surfaces from an approximate two metre unit of the section. Such values are more precise than subjective terms such as "relatively common" or "uncommon", the usage of which will vary from worker to worker.

Trial samples from a single intensively collected bed indicate that a count of 100 fossils is sufficient to give an accurate idea of the relative abundances of the most abundant genera present. The table just below shows the percentage of different genera from a series of samples from the same bed. For each sample the first 100 fossils recognised were used to give the percentages shown. It will be seen that the proportions in each sample are closely similar, with Nileidae exceeding aff. *Ampyxina,* and these two groups together comprising about 60% of the fauna. Lingulid brachiopods comprise between 9-15% of the remainder. *Ampyx, Carolinites, Raymondaspis, Miracybele* and *Shumardia* are all present in approximately equal proportions. Other trilobites (*Parapilekia,* remopleuridids) are present only as occasional rarities.

	Sample 1	Sample 2	Sample 3	Sample 4
Nileids	35	30	36	32
aff. *Ampyxina*	21	26	20	26
Lingulid	11	15	9	11
Raymondaspis	12	8	5	5
Ampyx	4	4	7	8
Carolinites	5	6	7	6
Miracybele	7	7	5	5
Shumardia	3	1	8	4
Parapilekia	1	–	–	–
Remopleuridids	1	–	1	–
Acrotretid	–	–	2	2
Murchisoniid gastropod	–	2	–	1
Monoplacophora	–	1	–	–

The numbers of all groups of macrofossils other than trilobites were counted, although I am not qualified to analyse them all at the generic taxonomic level. In particular the ostracodes when present are abundant and appear to be diverse, but no attempt has been made to subdivide them into genera.

TYPES OF ASSEMBLAGES

One of the major problems in palaeoecological work it that of how the assemblages of fossils in the rocks reflect the living population, in, on and above the sediment surface that is acting as collecting area for the organic remains. Fossil assemblages that exactly reflect the living population are very rare, perhaps being limited to the catastrophic over-whelming of the whole biota by such mechanisms as an ash shower, or a "poisoning" plankton bloom. More usually the sediment surface collects those animals and plants with hard parts that have died, been brought in by currents, or reworked. Martinsson (1955:12-17) has discussed the particular problems of arthropod assemblages, in which the adult exoskeletons are mixed with the moults of earlier growth stages. The problem as here considered consists in recognising *autochthonous* and *allochthonous* assemblages. Autochthonous assemblages reflect the initial population of animals on or above the sediment surface, that is the fossil remains are of a community (or communities) which have not been moved from their original place of deposition. An allochthonous assemblage shows evidence of transport of the fossil remains, and may or may not be a living association of animals.

Evidence of autochthonous assemblages comes from a number of sources:

(1) Where trilobite exoskeletons are found still articulated, this is taken as evidence of lack of disturbance of the remains, and indicates autochthoneity. Articulated remains include either complete dorsal exoskeletons, or exoskeletons lacking free cheeks, or in some other arrangement probably representing undisturbed moults (Fortey, 1974a, Pl. 12:1). Preservation of exuviae *in situ* – which lack soft parts and are presumably easily dissociated – is positive evidence that the trilobite concerned lived where the remains accumulated, and that the fossilisable material was not transported. Bohlin (1955) has indicated the possibility of transport of complete exoskeletons in suspension to give an allochthonous assemblage. An assemblage so derived is characterised by a spherical random orientation of the organic clasts, or even size grading (Dr. J. Bird, personal communication 1970). No beds with these distinctive characters have been found in the Valhallfonna Formation.

(2) Where fossils of great fragility are preserved they are believed to be autochthonous. The fused free cheeks of olenids, for example, connected by a narrow strip of thin ventral doublure, would not withstand transport after deposition. The same might be said of delicate large dichograptids such as *Sigmagraptus.*

(3) Meraspid to late holaspid trilobite growth stages differ greatly in size. Where they occur together in the same bed of rock it is considered probable that the trilobites were living in the area around the sediment surface. Current sorting or transport is likely to remove at least some sizes.

(4) Where lingulid brachiopods are found orientated vertically with respect to the bedding in life position this indicates a lack of reworking consistent with an autochthonous assemblage. High articulation indices for brachiopods (Boucot 1953) are also indicative of autochthonous assemblages. *Disarticulation* per se does not indicate allochthoneity. Sea bottom scavengers and burrowers will normally tend to disassociate articulated remains accumulated *in situ,* and so a perfectly autochthonous assemblage may contain isolated brachiopod valves. Evidence of the activities of the disturbing organisms is seen in the form of bioturbation, rarely silicifed burrow infillings.

(5) Parts of the section consist predominantly of flaggy limestones with very fine scale undisturbed laminations, which in thin sections are seen to be marked by thin carbonaceous layers. The lack of disturbance of laminae, and the complete absence of any scour structures or intraformational conglomerates in these parts of the succession, are believed to indicate sediment accumulation under quiet bottom conditions. Such conditions favour the preservation of autochthonous assemblages.

It is more difficult to prove allochthoneity, as the converse of the criteria cited above are not to be regarded as positive evidence for transport of fossil material. Allochthonous assemblages are indicated:

(1) Where the fossils are concentrated into thin bands, disarticulated, sorted and especially where robust shells are broken. Breakage of thin shelled organisms, such as olenid trilobites, must be interpreted with caution, especially where the compaction of the rock has produced flattened specimens.

(2) Current action is indicated by lineation of elongated fossils, especially orthoceracone nautiloids.

(3) Where the faunal content of one bed differs markedly from that of a considerable thickness of adjacent strata, allochthoneity of the fauna of that bed is more probable. A rapid and

short lived environmental change may produce the same effect and other criteria are required to prove allochthoneity.

(4) Current activity is probably indicated also by beds of intraformational conglomerates.

Diagenetic changes are of importance in some parts of the succession, particularly in the Profilbekken Member. Changes that have been observed include: (1) recrystallisation of calcite to give a coarse sparry mosaic, (2) dolomitisation in irregular patches or as scattered rhombs visible in thin section, (3) redistribution of pyrite as irregular veins. These changes are most noticeable where the original texture of the rock was 'open', as in the intraformational conglomerates and bioclastic limestones. The question arises how these changes may affect the yield of fossils compared with unaltered beds. Generally the originally aragonitic gastropods have been most affected by recrystallisation, trilobites, brachiopods, ostracodes and other calcite shelled fossils hardly at all. Although considerably recrystallised, the rock still breaks around rather than through these gastropods, and it is unlikely that many have been so extensively altered as to be unrecognisable. Diagenetic bias is not considered to be important.

RELATIVE ABUNDANCE CHARTS FOR THE VALHALLFONNA FORMATION

Benthic genera

To indicate the variety of bottom living animals, the number of genera of trilobites, brachiopods, gastropods, sponges and echinoderms for each unit were counted and plotted stratigraphically. It will be seen that there are two parts of the section with low benthic diversity: at the bottom and towards the top of the Olenidsletta Member – and two parts with high diversity – one between the two parts with low diversity, the other through the top part of the section. The number of genera present in the benthic 'low' is generally three or four, rarely greater. The trilobites dominate the fauna. The number of genera in the benthic 'highs' varies considerably, averaging twelve, but at certain horizons rising to over twenty, that is the benthic diversity is three to five times that of the parts of the section with low diversity. Many kinds of organisms besides trilobites are important. There is a transition in numbers of genera between the benthically restricted parts of the section succeeding high diversity parts, this being marked by a transition in the composition of the faunas. A comparison with the stratigraphic section on Fig. 1. shows the associated sedimentary and fossil criteria used to determine environmental details.

If the ostracodes had been divided generically, this would have raised the peaks in the benthically diverse parts of the section still further, as the ostracodes are largely confined to those parts of the section (Fig. 1).

Olenid trilobites

Trilobites of the new olenid subfamily Balnibarbiinae (Fortey 1974a) are confined to and abundant in two parts of the section (Fig. 2), the bottom 75 m of the Olenidsletta Member, and between 106 m and 145 m. Note that this distribution is closely similar to that of the parts of the section with low benthic diversity. The range of this particular group of trilobites is shown as stippling on the abundance chart, and it will be seen that the distribution and abundances of other trilobites are related either positively or negatively to that of these olenids.

The peculiar olenids *Anaximander, Psilocara*, and *Svalbardites* are confined to the balnibarbiinid bearing parts of the section, where they are abundant at some horizons. Trilobites of the olenid subfamily Hypermecaspidinae are similarly confined to the Olenidae-bearing part of the section. Of the olenids only the Triarthrinae extend into the parts of the section with numerous Nileidae.

Non-olenid genera

(a) Nileid trilobites (Fig. 2) have a mutually exclusive distribution with the olenid genera mentioned above, and are abundant in those parts of the section in which the diverse olenid fauna is absent. Through certain parts of the section (About 100 m the base of the Olenidsletta Member for example) nileid-bearing and balnibarbiinid-bearing beds intermingle. Many other

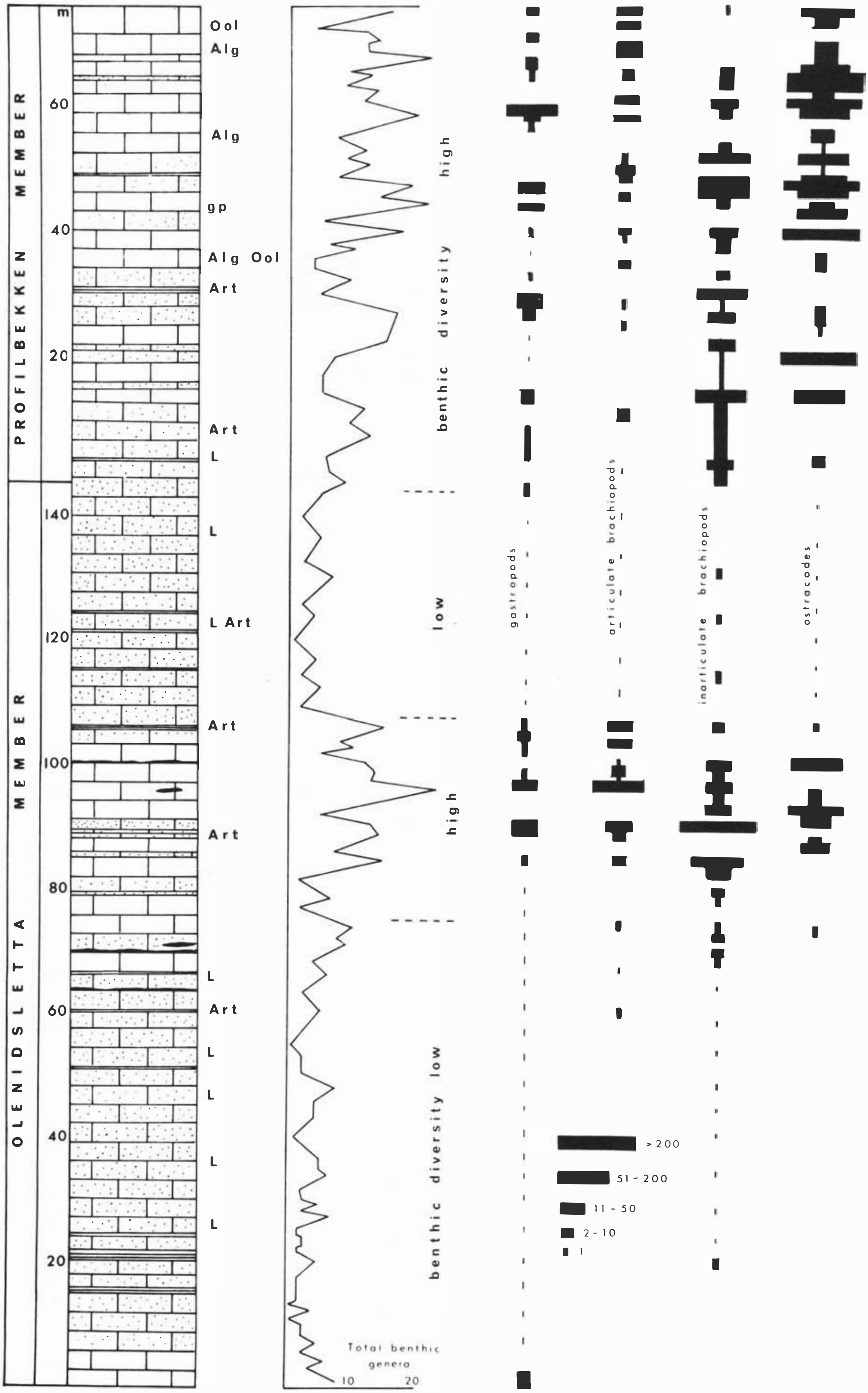

Fig. 1. The Valhallfonna Formation. Diagram to show the principal lithological characteristics plotted against the diversity of benthic genera, and the distribution of some non-trilobite groups showing their restriction to the parts of the section with high benthic diversity (compare with the distribution of olenid trilobites, Fig. 2). KEY. *block:* lighter coloured, often more coarsely crystalline limestone; *stippled block:* black, generally fine grained limestone; *horizontal rule:* shales; *black:* chert layers; *Ool:* ooliths present; *Alg:* algae of *Girvanella* type; *gp:* lingulids in growth position; *Art*: articulated remains of trilobites numerous; *L:* presence of undisturbed laminae on a fine scale.

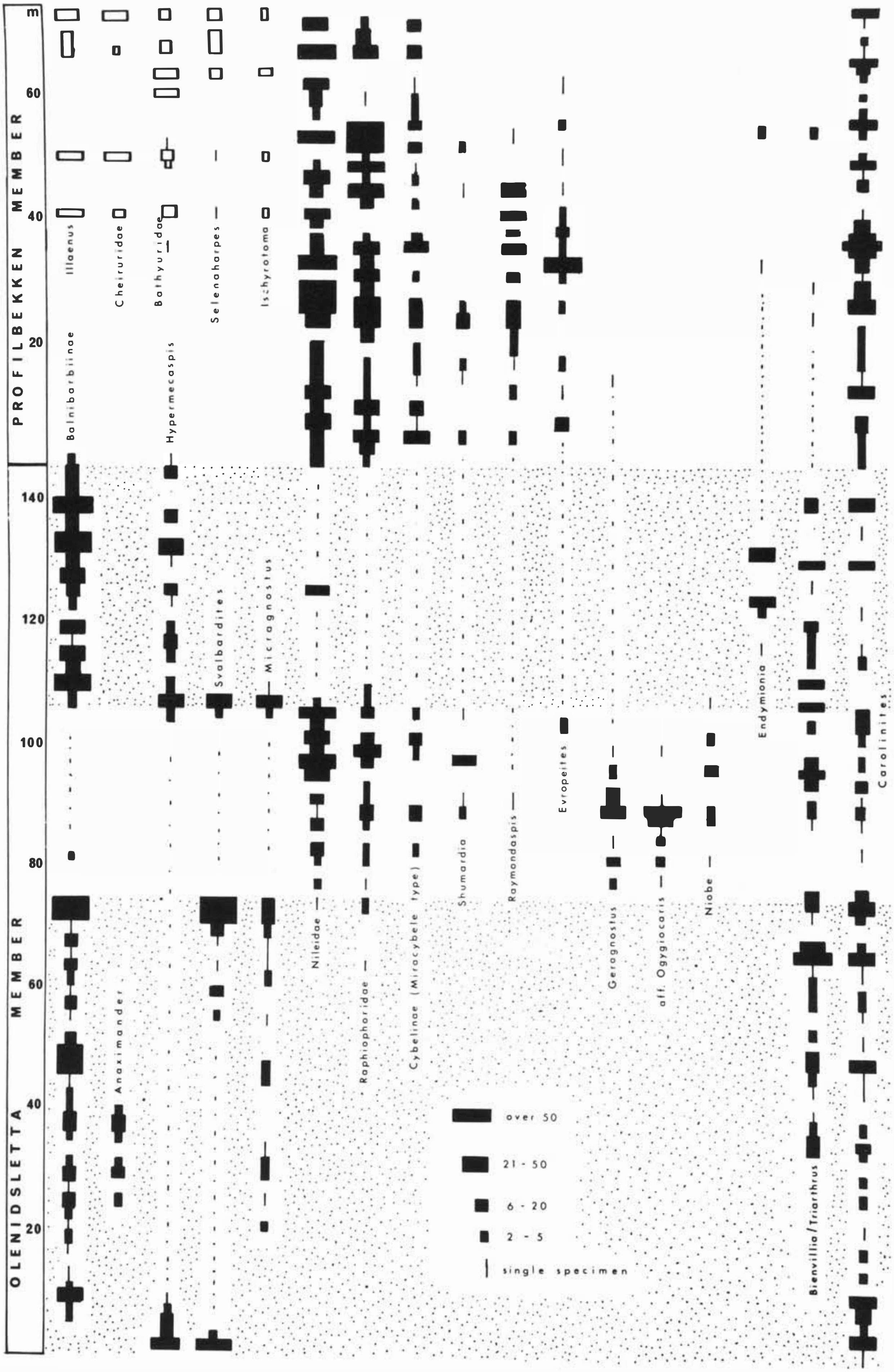

Fig. 2. Chart showing the relative abundance distributions of trilobites through the Valhallfonna Formation. Parts of the section characterised by olenid-dominated assemblages are stippled areas. Characteristic elements of the illaenid-cheirurid community open rectangles top left; tolerant genera on right.

groups of organisms considered have either the olenid pattern of distribution (0–75 m, 106–145 m of the Olenidsletta Member) or that of the nileids (75–106 m of the Olenidsletta Member, and the lower 70 m of the Profilbekken Member).

(b) Cybelinid trilobites have a distribution closely comparable to that of the nileids. Raphiophorid trilobites again follow the nileid distribution pattern, being most abundant in the nileid-bearing parts of the section, but extending marginally into the olenid-bearing beds as a rare component of the fauna. The peculiar raphiophorid *Endymionia* is almost confined to the upper olenid bearing part of the section. Of the agnostid trilobites *Micragnostus* is associated with the olenids, *Geragnostus* with the lower non-olenid part of the section. Ogygiocarinid trilobites are confined to the earlier nileid bearing part of the section; *Niobe* and *Megalaspides* are similarly limited. Similarly *Shumardia* occurs sporadically in the non-olenid parts of the section, and is probably confined thereto. Stygininae (*Raymondaspis*) and the pliomerid *Pliomeroides* (*Evropeites*) are similarly distributed.

(c) *Illaenidae, Cheiruridae.* Illaenids and cheirurids appear at localised horizons only above the lower 40 m of the Profilbekken Member; where they occur they do so in abundance Only at the very top of the section studied do they become the dominant element in the fauna. Associated with the trilobites of these families are Bathyuridae of *Bathyurellus* type, and rather rare but confined to this association are *Selenoharpes* and Dimeropygidae (*Ischyrotoma, Ischyrophyma*). None of these genera occur lower in the Valhallfonna Formation, although Bathyuridae, Illaenidae and Cheiruridae are dominant elements in the fauna of the underlying Nordporten Member of the Kirtonryggen Formation.

Non-trilobite groups

Non-trilobite groups (Fig. 1) show distributions comparable to those of most of the non-olenid trilobites considered above. Gastropods and ostracodes are confined to the non-olenid parts of the section, the latter attaining enormous abundances at some horizons, hundreds of specimens occurring on a single surface. The dropping off in numbers in the olenid bearing parts of the section is very striking, scarcely a single specimen occurring in the lower 75 m of the section. Brachiopods are similarly most abundant in the non-olenid bearing parts of the section. Inarticulate brachipods (lingulids *sensu lato* and acrotretids) have a distribution comparable to that of the raphiophorid trilobites, their range overlapping marginally with that of the balnibarbiinids. Their maximum abundances are in the non-olenid bearing parts of the section.

ASSEMBLAGE TYPES IN THE ORDOVICIAN OF SPITSBERGEN

It is clear from the distribution of the trilobites and other fossils that there are three assemblage types:

(1) A major distinction may be drawn between the olenid-dominated assemblage, and those in which diverse olenid faunas are absent. The olenid assemblage is found in the bottom 75 m of the Olenidsletta Member, and re-appears between 106–145 m from the base of that Member. Apart from the presence of characteristic olenid genera the olenid assemblage includes *Micragnostus,* is typified by a low diversity of benthic genera of all taxa, with brachiopods, ostracodes and gastropods very rare or absent.

(2) Between 75 m and 102 m from the base of the Olenidsletta Member, and again through the greater part of the Profilbekken Member, the assemblage type is dominated by trilobites of the families Nileidae, (*Nileus* and *Peraspis*) and Raphiophoridae (*Ampyx,* aff. *Ampyxina, Mendolaspis*). Cybelinid trilobites (of *Micracybele* type), *Shumardia* and Stygininae (*Raymondaspis* and allied forms) and *Ectenonotus* are characteristic. Asaphidae of the genera *Niobe,* aff. *Ogygiocaris* and *Megalaspides* are confined to this assemblage type.

(3) In the upper part of the Profilbekken Member a third assemblage type appears in the section, usually as thin, winnowed horizons. The characteristic trilobites, which make their first appearance in the Valhallfonna Formation here, are Illaenidae (*Illaenus*), Cheiruridae (*Kawina, Ceraurinella*), Bathyuridae (*Acidiphorus, Bathyurellus, Uromystrum*), Dimeropygidae (*Ischyrotoma, Ischyrophyma*) and *Selenoharpes.*

INTERPRETATION OF ASSEMBLAGE TYPES

The olenid assemblage

The olenid assemblage is found in black, graptolitic limestones and shales (Fig. 1, Fig. 7:1), in which laminations are preserved undisturbed. Interbedded cherts may be associated with the dark limestones. Benthic variety is low. Articulated skeletal remains of trilobites are relatively numerous, and growth series are frequent (e.g. Fortey 1974a, Pl. 12:1, Pl. 11:1–11). Delicate remains of olenid trilobites are preserved without breakage (Fortey 1974a, Pl. 15:2) and large dichograptid stripes are common.

These characters indicate an autochthonous assemblage as defined above, that is the organisms found fossil probably reflect a living community of animals – the *olenid community.* Numbers of individuals are generally lower than in non-olenid assemblages, although certain bedding planes may be crowded with the remains of olenids.

The only benthos found in any abundance are trilobites. Sessile benthos is absent. Perfectly preserved laminations indicate a complete absence of infauna in the sediment, possibly due to deoxygenation beneath the sediment surface. All sedimentary features, and the occurrence of the fossil remains, point to quiet water bottom conditions. An assemblage characterised by olenid trilobites is well known and widely distributed in Upper Cambrian and Tremadoc times (Wilson 1957; Henningsmoen 1957), and the associated lithologies are closely similar to those of the appropriate parts of the Valhallfonna Formation. The olenid community occupied a well-defined and persistent ecological niche, the occurences in the Valhallfonna Formation representing its extension into the Ordovician. The still bottom waters may also have been low in oxygen, conditions to which the olenids were particularly adapted (see Henningsmoen 1957: 61–62; Størmer 1939:220) and to which they were largely confined. There is a complete absence of any evidence of shallow water conditions, in contrast to other parts of the Valhallfonna Formation, and this is regarded as indicating the strong probability of accumulation of the olenids at a considerable depth. The common occurrence of graptolites in the olenid bearing parts of the section testifies to an abundance of plankton in the surface waters, and complete connection with the open sea.

The nileid assemblage

Many but not all of the beds yielding this assemblage contain evidence of its autochthoneity on the criteria listed above. Trilobites occur in all growth stages, and particularly in the nileid-bearing part of the Olenidsletta Member there are horizons at which articulated remains are common, and on a few bedding planes trilobite remains are completely articulated. A fragment of one such bedding plane (Fig. 7) includes those dorsal exoskeletons of nileids which lack free cheeks, this mode of occurence being particularly common among nileids, and quite probably the result of moulting. At several horizons in the Profilbekken Member lingulids occur in position of growth (e.g. 42 m from base of Member), and from 48 m from the base of the Profilbekken Member several complete specimens of monaxon sponges have been found, which dissociate into separate spicules after death and would be easily redistributed by the slightest current. The nileid-bearing parts of the section are thus considered to include the fossils of a generic association that is a natural community – the *nileid community.*

Dark flaggy limestones with occasional shales are the characteristic lithologies (Fig. 7) although black, well laminated limestones and 'stinkstones' typical of the olenid-bearing rocks are generally absent. Laminae are frequently destroyed by burrowing benthonic animals, which may have also often aided the disarticulation of the trilobite remains. Such bioturbation and the presence of lingulid burrows indicates that the bottom was at least in places soft and muddy. The variety of benthos is much greater than in the olenid community and there is nothing to suggest deoxygenation of the bottom waters. Several of the characteristically abundant elements of the nileid community (particularly some raphiophorid trilobites and inarticulate brachiopods, notably acrotretids) intermix with reduced abundances with the olenid assemblage, so that a mixed assemblage does exist, although impersistent in the Valhallfonna Formation. Positive evidence of current activity is generally lacking, and the autochthonous beds indicate that the bottom waters were quiet.

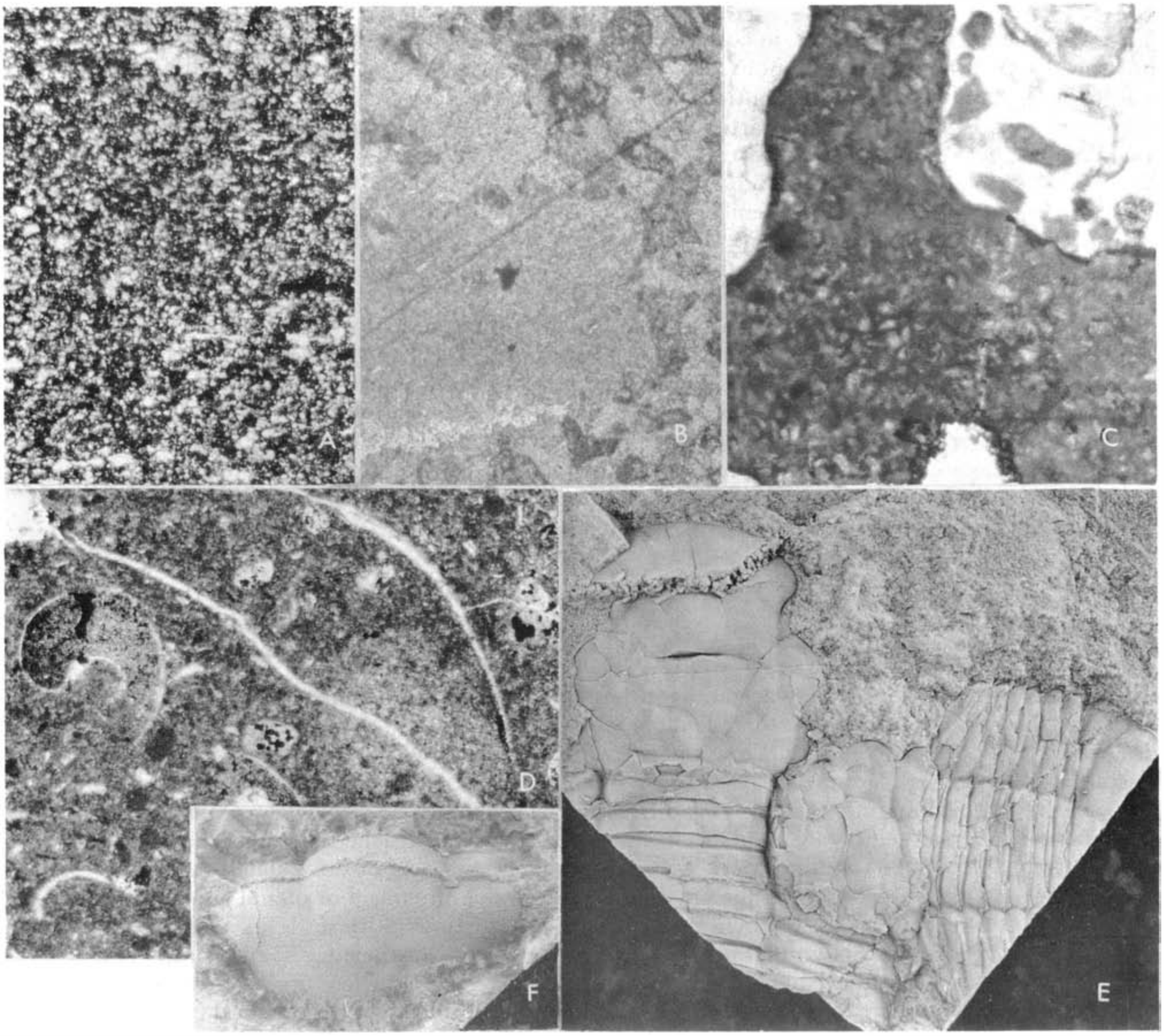

Fig. 7. A. Section through typically black, conchoidally-fracturing limestone of the olenid community (x30) showing abundant disseminated pyrite. B. Section through recrystallised pellet-limestone of the illaenid-cheirurid community (x30). C. Nodule of *Girvanella* in sparry calcite, illaenid-cheirurid community (x30). D. Section through dark brown, micritic limestone typical of the nileid community (x35), showing sections through gastropods and other small fossils. E. Dorsal exoskeletons of nileid trilobites lacking free cheeks (x4), believed to represent moults, and demonstrating the autochthonous nature of the nileid community. Olenidsletta Member about 80 m from base. SMA 84301. F. Broken cranidium of an *Illaenus* sp. from an allochthonous layer in the Profilbekken Member (x3), 62 m from base. SMA 84352.

The illaenid-cheirurid assemblage

The illaenid-cheirurid assemblage, in contrast to the olenid and nileid communities, generally shows evidence of being allochthonous. The thin bands occurring in the upper part of the Profilbekken Member at intervals contrast faunally with the intervening nileid assemblages, and are composed of completely disarticulated material, often with examples of stout illaenid cranidia being broken (Fig. 7:F) occurring in thin irregular lenses, with randomly orientated material. Associated orthocone nautiloids are in strong current orientation. In the top part of the section the illaenid-cheirurid assemblage is associated with intraformational conglomerates, with clasts consisting largely of *Girvanella*-type algal nodules (Fig. 7:C). The limestones in this part of the section are of much purer, lighter coloured type than those containing the nileid community (Fig. 7:C).

The presence of algal structures and the associated lithological types would seem to indicate a shallow water origin for the illaenid-cheirurid assemblage. It is suggested that the remains of an illaenid-cheirurid community was swept as an allochthon from a shallow water – perhaps reef – environment, into the nileid environment by strong currents generated periodically during storms. Transport of material was sufficiently violent to result in breakage of robust shells, yet sufficiently rapid not to result in abrasion of the surface sculpture of the illaenid cranidia. Illaenid-cheirurid assemblages do not occur as allochthonous lenses within the olenid bearing parts of the section.

Palaeogeography

One palaeogeographic model may account for the relationships between the assemblages (Fig. 3). The environment occupied by the nileid community is considered to have occupied an intermediate depth between the shallow water environment from which the illaenid-cheirurid assemblage was derived, and the deep water environment where the specialised olenid community lived, the three communities occupying different parts of the Early Ordovician continental shelf. Periodically flushed organic remains from the shallow water reached the nileid environment but not the olenid. The limestones and shales of the major part of the Valhallfonna Formation were deposited either in the environments in which the nileid or olenid communities lived, their alternation possibly being the result of changes in relative sea level.

Richards (1956) has shown that in the North Atlantic towards the edge of the continental shelf (centering on about the 100 m depth contour) there is a region where the oxygen content of the water just above the bottom is much lower than that at shallower depths on the shelf.

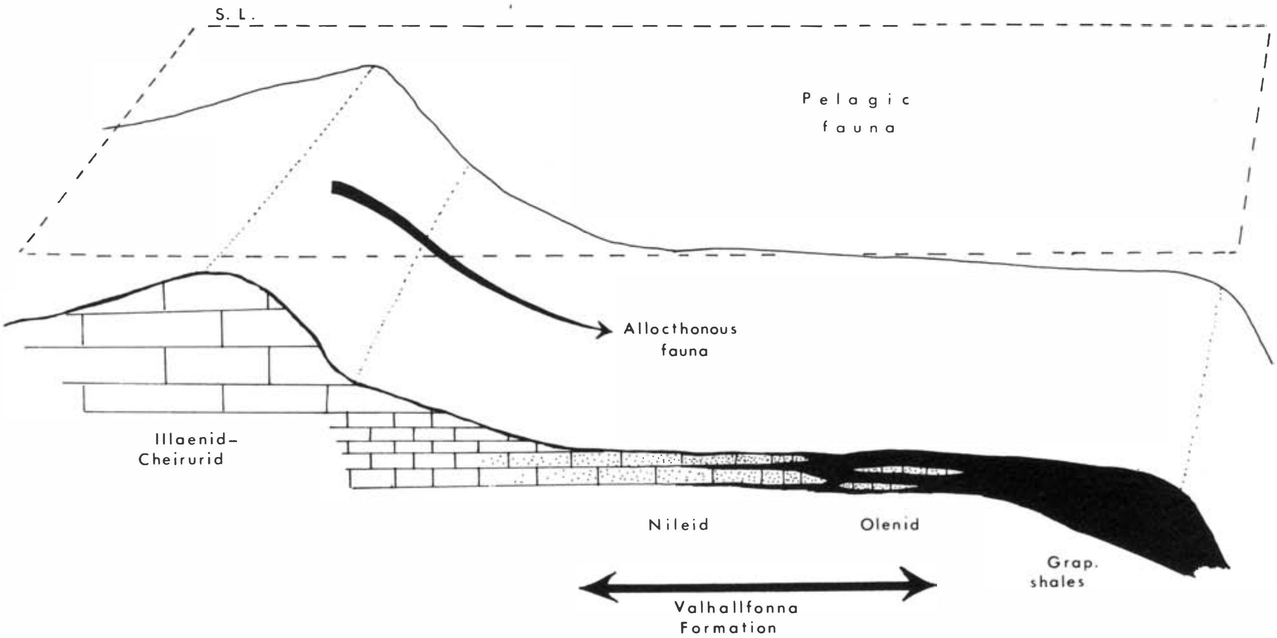

Fig. 3. Palaeogeographic model showing disposition of community types across an early Ordovician shelf sea. The Valhallfonna Formation accumulated in the region shown, where it could receive allochthonous material from the illaenid-cheirurid environment. Lithologies graded from massive "white" limestones on left, through platy black limestones to graptolitic shales on right.

This forms a belt of low oxygenation running parallel to the shelf edge and, less rigourously, parallel to the land edge. The same region is characterised by a higher organic content in the sediment. This is a striking parallel with the inferred conditions for the olenid community. In the Cambrian Wilson (1957) has noted the tendency for olenid-bearing strata to parallel major geosynclines, which may be regarded as the sites of former continent edges. Bulman (1964) has also remarked that the dark, shaly sediments bearing abundant graptolites, such as those occuring at intervals through the Olenidsletta Member, are characterised by an unusually high organic content. The olenid environment is regarded as having occupied an outer region of the continental shelf. Nearer shore there was the better oxygenated, soft bottomed, quiet water nileid environment, with a transition between this and the olenid environment in which a somewhat mixed assemblage could occur. The illaenid-cheirurid community is represented by allochthonous material, possibly derived from fringing reefs. The admixture of the various assemblage types in the same vertical succession is a particularly fortuitous feature of the Spitsbergen succession, and accounts in part for the exceptional richness of the total fauna.

ENVIRONMENTAL TOLERANCE RANGES OF TRILOBITES

The concept of a community as applied to trilobites needs some clarification. In studies of recent marine benthos some workers emphasise the existence of discrete types of bottom communities of wide geographic distribution and constant generic composition (e.g. Thorsen 1957, 1966); other workers have shown that some communities are the product of a fortuitous series of overlapping tolerance ranges of particular species along an environmental gradient (see, for example Hughes & Thomas, 1971, Figs. 12–15), and that the definition of community types is at best arbitrary. The palaeogeographic model proposed to account for the illaenid-cheirurid, nileid, and olenid communities is based on an environmental gradient, and it is necessary to examine the discreteness of the proposed community types. A study of critical "transition beds" between nileid and olenid communities shows that the ranges of genera typifying these communities overlap in a complex way (Fig. 4). Samples were taken at about 20 cm intervals through this part of the section and relative numbers obtained by breaking up approximately 1 kg blocks and counting all fossil fragments. The overlap, with the gradual, but irregular decline of nileid community genera upwards in the section with a concomitant increase in olenid community genera, demonstrates that it is correct to regard the distribution of numbers of particular trilobites as being controlled by changes along the environmental gradient, and the communities here defined as relatively stable end members of a spectrum of individual tolerance ranges of trilobites. To define such end members in terms of the most abundant genera in the fauna seems to be in accordance with findings on recent marine communities, for example Sanders (1960, Table 4) has shown that a mere 6 species out of more than 70 for the *Nephthys incisa – Nucula proxima* community comprise almost 90% of the numbers of individuals in the community.

The fact that the trilobites so far considered have different ranges related to different bottom conditions (indicated by different facies) along the environmental gradient implies that they were benthic. Certain trilobites are restricted in their ranges to one small interval of one general environmental type (e.g. within the olenid environment the peculiar olenid *Anaximander* is restricted to a small thickness of the earlier olenid-bearing part of the section; *Mendolaspis* to the earlier nileid community). Such trilobites were presumably adapted to a particular critical set of conditions, and were not able to tolerate even minor changes, let alone shifts from one major environment type to another. Elucidation of these critical conditions may be impossible, and will certainly require geochemical and other techniques beyond the scope of the crude approach used here. Such trilobites may also be predicted to be of sporadic geographic occurrence because of the low chance of finding many localities in exactly the right facies. *Anaximander* is so far unique to Spitsbergen, for example, while *Mendolaspis* is known otherwise only from Argentina.

Tolerant genera will be expected to have a more general distribution. *Nileus,* for example, is widespread in North America, Scandinavia and Russia (e.g. Männil, 1960; Balashova 1966; Bursky, 1970), with 'outliers' of the genus in Poland (Bednarczyk, 1962) and Morocco (Destombes, 1970).

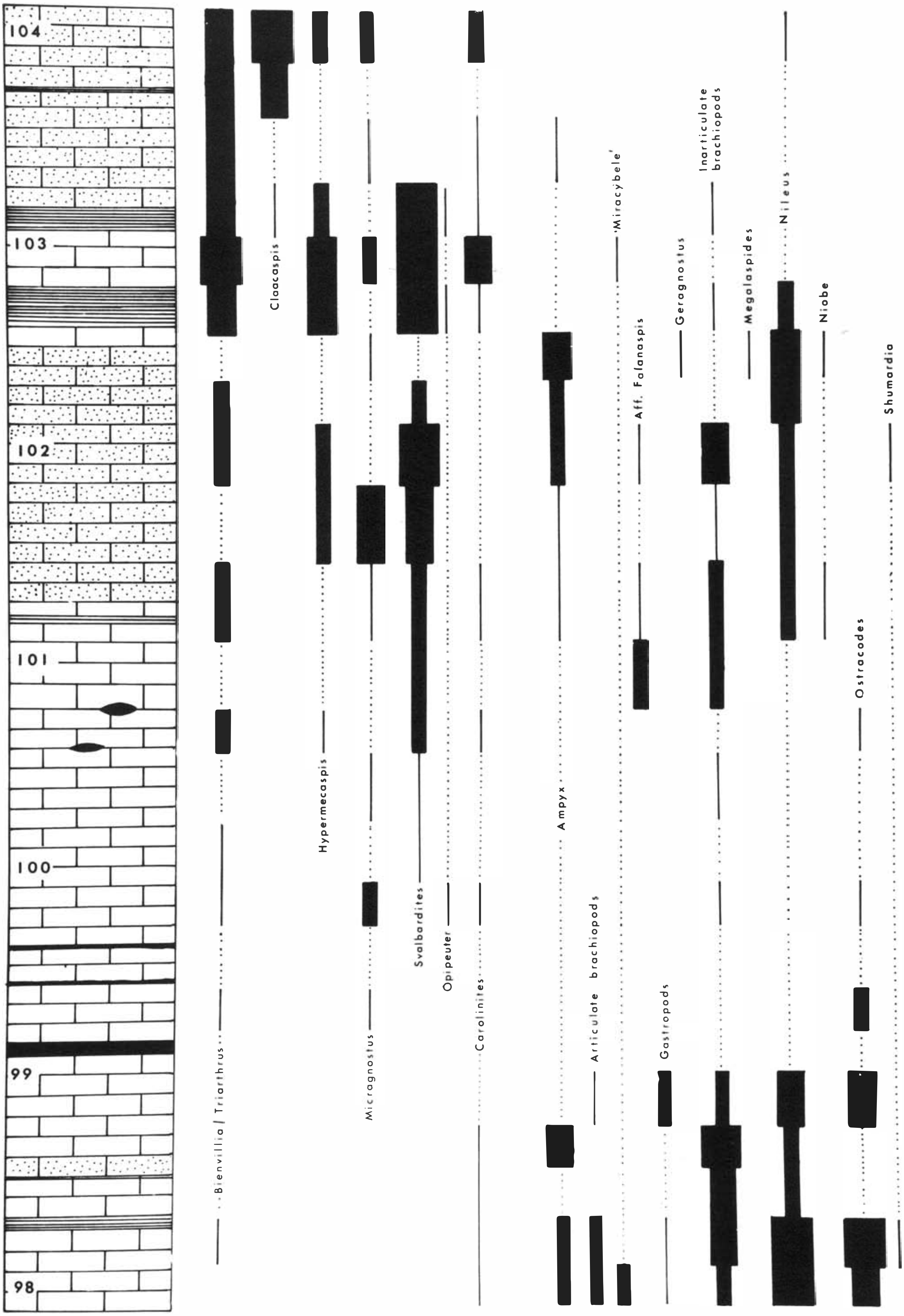

Fig. 4. Detailed analysis of abundance changes of fossils through 6 m of the Olenidsletta Member showing the gradational change from nileid community type below to olenid community above. Olenid community element elements on left, nileid community elements on right. Lithological characters represented as on Fig. 1.

Pelagic community

The stratigraphic distribution diagram showing the relative abundance through the section of *Carolinites* is shown on Fig. 2. It is present throughout the section, attaining equal abundances in those parts of the section with olenid and non-olenid communities alike. Thus the occurrence of *Carolinites* is independent of community type (and of the enclosing rock type), that is, its occurrence is not related to the bottom conditions. For this there seem two possible explanations. Either *Carolinites* was remarkably tolerant, being able to survive equally well in deoxygenated, deep waters in which the specialised olenids were the dominant benthic animals, as well as in better oxygenated water with many other types of benthos, or *Carolinites* was a pelagic trilobite living in the surface waters, in which case the nature of the sea bottom was irrelevant. The latter explanation is the most probable as it is unlikely that any benthic organism could be equally adapted to the widely different conditions of the olenid and non-olenid environments. The very wide geographical distribution of the genus also supports the same conclusion; it is found in Siberia, Estonia, Greenland, Newfoundland, Utah and Nevada, Arctic Canada, Ireland, Argentina, Turkey and Australia as well as Spitsbergen. One species, *C. genacinaca* Ross, is recorded from Utah and Nevada, Greenland, Spitsbergen, North Arctic Urals, Western Siberia. Stubblefield (1950) suggested that the geographic dispersion of *Carolinites* may have been rapid in relation to its evolution. In view of the present analysis it seems that a swimming or free floating habit of the mature animal is beyond much doubt.

The morphology of *Carolinites* is consistent with such a conclusion. The enormous globular eye commanded a view forwards, upwards, sideways, backwards, and if the orientation of the eye was as I believe, downwards as well. This last adaptation would scarcely be pertinent to a benthic animal. The eyes project laterally beyond the level of the thorax and pygidium, so that the backward view was unimpeded. The free cheeks are reduced except for large genal spines hanging down below the level of the rest of the exoskeleton. The all round vision is most likely to be an adaptation to cope with the greater vulnerability of a surface living trilobite with the delicate ventral surface exposed. The relatively thick cuticle may also have afforded some protection from predators, and acted as a support for powerful musculature needed in swimming and is in remarkable contrast to the extremely thin shelled ("safe") olenids with which they are found in death assemblage. The combination of detailed abundance distribution studies of a single section, palaeogeographic distribution, and morphological information provides a powerful method of establishing the probable life habits of trilobites.

Aff. *Telephina* occurs along with *Carolinites* in the lower part of the section, and is found in equal abundance in the lower nileid assemblages. The morphological similarity to *Carolinites* is considerable, sharing with that genus the large eyes commanding a wide field of view, and long downward directed genal spines. It is probable that aff. *Telephina* was also free-swimming or planktonic. The bizarre genus *Opipeuter* Fortey, 1974 also shows many morphological similarities to *Carolinites* and aff. *Telephina* and a pelagic mode of life for this trilobite has been argued elsewhere (Fortey, 1974). Although its occurrences are too few for quantitative treatment, it is widely distributed throughout the Olenidsletta Member, in beds with both olenid and nileid communities, and in western Ireland occurs with an illaenid-cheirurid community in the Tourmakeady Limestone, thus exhibiting the same degree of tolerance as *Carolinites.* These surface living trilobites, together with the graptolites, constitute a fourth, *pelagic community*. The remains of this community will accumulate with those of the originally bottom living communities whenever conditions are suitable.

Triarthrines. The olenid subfamily Triarthrinae has a distribution pattern which contrasts with other members of the same family, being an important component of the fauna almost throughout the Olenidsletta Member, and occurring also, though very rarely, in the Profilbekken Member. It is not found associated with illaenid-cheirurid assemblages. Its fairly complete distribution through the section might suggest that it is also planktonic or free swimming. There is no feature of the morphology of *Triarthrus* or *Bienvillia* which obviously supports such a suggestion, both being quite similar in general features to the restricted olenid *Cloacaspis.* The alternative explanation – that triarthrines were tolerant and able to live both in olenid and nileid environments – seems to be more acceptable for this reason, although such negative evidence can scarcely be regarded as conclusive.

Convergent evolution

The individual benthonic trilobite species within a single community were specialised for different modes of life, but what these particular functions were cannot proceed beyond speculation at the moment. It is significant that all three assemblages contain taxonomically unrelated trilobites which are convergent in gross morphology. For example a morphological type characterised by isopygous or nearly isopygous trilobites of fairly low convexity, broad cephalic borders with genal spines, and large crescentic eyes, is represented in the olenid community by *Hypermecaspis,* in the nileid community by asaphids and such nileids as *Peraspis,* and in the illaenid-cheirurid community by the bathyurid *Bathyurellus.* Similarly, a "smoothed out" morphological type is present among the olenids (*Psilocara*), represented by *Nileus* itself in the nileid community, and by *Illaenus* in the illaenid-cheirurid community. These similar morphological types were probably adapted to a particular mode of life within their respective environments. The unique admixture of the different communities in the Spitsbergen section accounts for the exceptional diversity of the fauna, although, conceivably, the same type of ecological niches were occupied by similar morphological types in the different environments.

COMPARISON WITH CONTEMPORARY FAUNAS IN OTHER AREAS

Comparisons with other areas are hampered by a lack of comparable data, but in some cases sufficient details are given to enable a reasonably objective comparison with the Spitsbergen data. In present day oceans similar generic assemblages may be found with a wide geographical spread if there are comparable bottom conditions (accepting the view of Thorsen, 1957). We might reasonably expect the assemblages outlined above to be found in broadly contemporaneous deposits accumulated under similar environmental conditions.

Newfoundland

Whittington (1963) has described an assemblage from a single enormous boulder in the Cow Head Breccia at Lower Head. The enclosing lithology is a pure, white limestone, and contains a high proportion of articulated material (e.g. Whittington 1963, Pl. 36), and probably is an autochthonous assemblage. The total abundances given show that illaenids, cheirurids, and *Bathyurellus*-type bathyurids and lichids are especially prominent, while there are no olenids, raphiophorids, or cybelinids, and *Nileus* is represented by one specimen compared with hundreds of illaenids. This would seem to be the illaenid-cheirurid assemblage *par excellence,* with lichids as an additional element (this family may also be characteristic of this assemblage). The whole boulder is itself allochthonous, that is, has been transported into an environment where graptolitic shales accumulated (Whittington 1968:53).

The Table Head Formation (Whittington & Kindle 1963; Whittington 1965) contains a fauna with many trilobite genera in common with those found in the Profilbekken Member of the Valhallfonna Formation. The Lower Table Head Formation contains Illaenidae, Bathyuridae and *Pseudomera* (Pliomeridae) most prominent in light-coloured limestones and dolomites with lime sands. This seems to be closest to the illaenid-cheirurid type of association, although, as Whittington remarks, it is a relatively impoverished fauna. The Middle Table Head Formation contains a much more varied fauna, and 70 per cent of the genera present in the Profilbekken Member of the Valhallfonna Formation are present also in this part of the Table Head – a great resemblance which might lead us to expect comparable community types: an autochthonous nileid community with largely allochthonous illaenid-cheirurid assemblage. The upper part of the Middle Table Head becomes more shaly, and it is from this part of the section that the illustrated articulated material comes, consisting particularly of abundant and varied raphiophorids, *Triarthrus,* such nileids as *Peraspis,* and asaphids, an autochthonous assemblage of the nileid type. Illaenids are abundant at some horizons, associated with rarer cheirurids, particularly (Whittington, personal communication) in one thin band of lime sand. They are represented only by disarticulated material. This mode of occurrence is what would be expected from the study of the Profilbekken Member of the Valhallfonna Formation, these thin abundantly fossiliferous bands probably being allochthonously emplaced assemblages originating from the environment of the illaenid-cheirurid community. Thus the Newfoundland Ordovician assemblages appear to be similar to those occurring in Spitsbergen. The olenid assemblage is not present in Newfoundland, although the presence of *Endymionia* and rare hypermecaspidinids may indicate faunas transitional in type between nileid and olenid communities. A probable nileid community is present further to the south in Maine (Whittington in Neuman, 1964).

Recent palaeogeographic interpretations of this part of the Caledonian geosyncline (Rodgers 1968) have postulated the previous existence of an extensive carbonate – accumulating shelf or bank, beyond which dark limestones, limestone-shales, and shales were deposited. Dewey (1969) has further suggested that this facies disposition might be related to the continental shelf at the edge of a 'Proto-Atlantic Ocean'. Such an interpretation may be consistent with our environmental conclusions, the illaenid-cheirurid community originally living on the relatively shallow bank (Lower Head), the nileid community living in the deeper waters beyond, into which material from the bank may be periodically flushed to give an exceptionally rich death assemblage (Middle Table Head). Allochthonous blocks of shelf limestone, perhaps emplaced by periodic gravity sliding (Bird & Rasetti 1968), accumulated in beds among the deep water graptolite shales (Cow Head Group).

This interpretation agrees with the environmental and faunal types recognised by Whittington & Hughes (1972:267), with the illaenid-cheirurid communities living on "platform" and reef environments, nileid communities in "slope" environments, particularly associated with platy limestones and black shales.

Ross & Ingham (1970) have recently charted the distribution of faunas with generic assemblages of trilobites comparable to that of the Table Head Formation. Broadly interpreted "Table Head type" faunas occur in scattered outcrops around the perimeter of the North American-Canadian-Greenland craton, again suggesting a relationship with a former continental margin (Ross & Ingham 1970), although similar faunas are quite widespread also in Siberia. Detailed comparisons with the Spitsbergen assemblages are not possible until more details regarding stratigraphic occurrence and relative numbers are available. However, the similarity to the Middle Table Head Formation (and the Profilbekken Member of the Valhallfonna Formation) suggests that the nileid and/or the illaenid-cheirurid communities may have been widespread in North America and Canada during early middle Ordovician times.

Tourmakeady Limestone, western Ireland

The Tourmakeady Limestone, of late Arenig age (e.g. Skevington 1971:80), has yielded a silicified fauna with many brachiopods, trilobites and bryozoa. The percentage abundances of the trilobites, based on 572 specimens, is as follows:

	%
Illaenidae (*Illaenus*)	22.8
Cheiruridae (aff. *Sphaerexochus*)	15.0
(*Ceraurinella*)	1.6
(*Kawina*)	3.0
Dimeropygidae (*Ischyrophyma*)	16.2
(*Ischyrotoma*)	4.2
Bathyuridae	5.6
Glaphuridae (*Glaphurus*)	5.2
Otarionidae	5.2
Nileidae (*Nileus*)	3.3
Geragnostidae (*Trinodus*)	3.1
Proetidae (*Decoroproetus*)	2.6
Odontopleurida	1.6
Isocolidae (aff. *Isocolus*)	1.2
Raphiophoridae (*Ampyx*)	0.2

Pelagic trilobites:

	%
Telephina	6.6
Opipeuter	2.6

It will be seen that the four typical families of the illaenid-cheirurid community (Illaenidae, Cheiruridae, Dimeropygidae, and Bathyuridae) contribute almost 70% of the fossil remains, and the fauna is undoubtedly of that type. Elements of the nileid community (Nileidae and Raphiophoridae) together constitute only 3.5% of the fauna. Other families appearing here, which are rare or absent in Spitsbergen (Glaphuridae, Otarionidae, Proetidae, Isocolidae) may also prove to be characteristic of the illaenid-cheirurid community. The fauna occurs in white or pink relatively pure limestones which form a breccia, probably allochthonous, interbedded with volcanic ashes and graptolitic shales. The limestone may have been derived as fringing-reef debris from a volcanic island at the edge of the western proto-Atlantic continent. The pelagic community is present in both Spitsbergen and western Ireland, indeed, the species of *Opipeuter* is common to both areas (Fortey, 1974), *Carolinites* has not yet been found in the silicified fauna, but occurs in the same general area (Stubblefield, 1950; J.B. Archer, personal communication 1971). Note that on the basis of graptolite correlations the illaenid-cheirurid Tourmakeady fauna is approximately the *time* equivalent of the lower nileid and upper olenid phases in the Spitsbergen sections.

Nevada, western United States

Field demonstrations under the guidance of Dr. R.J. Ross in 1972 suggested to me that the complete range of community types may be present also in Ordovician outcrops in Nevada. Until details of relative abundances are available from sections there an objective comparison with Spitsbergen is not possible, but the following comments are probably valid generalisations. The bioherm at Meiklejohn Peak contains an early Llanvirn (Whiterock) illaenid-cheirurid association, with species of Illaenidae, Cheiruridae (including *Kawina*) and Bathyuridae (*Bathyurellus*) dominating the fauna in numbers and variety (Ross 1972). *Glaphurus, Selenoharpes* and *Apatolichas* are also associated with the bioherm. In the limestones flanking the bioherm, mostly well-bedded, dark and fine grained, I have collected abundant *Nileus, Triarthrus* and lingulid brachiopods; Ross (1972:12–13) also records *Miracybele, Shumardia* and *Ectenonotus* as well as the ubiquitous *Carolinites.* The presence of the nileid community is indicated, and is consistent with the interpretation that "the flanking beds were deposited in deeper water than the biohermal mudbanks" (Ross, 1972:8). Species associated with the bioherm, but found also within the flanking beds as allochthonous assemblages, were due to "periodic showers of animal remains swept from the top of the mudbanks". Ross's interpretation of the Meiklejohn bioherm and associated facies is remarkably similar to the interpretation of the assemblages of the Profilbekken Member of the Valhallfonna Formation in Spitsbergen.

It may be suggested also that a progressive change from nileid to illaenid-cheirurid communities probably occurred during the deposition of the Whiterock Antelope Valley Limestone in the Ikes Canyon section, Toquima Range (Ross 1970, Pl. 20). The "slabby bedded unit" at the base of the section contains abundant articulated specimens of *Peraspis,* together with *Miracybele* and *Triarthrus* and seems to represent an autochthonous nileid community. Higher in the lower member of the Antelope Valley Limestone *Nileus* itself, *Niobe, Ampyx* and *Ectenonotus* of the same community type are numerous, together with the calymenid *Protocalymene*. Higher beds are characterised by the appearance of *Illaenus* and numerous Cheiruridae (*Kawina, Xystocrania*), disarticulated, and possibly representing flushed-in elements of the illaenid-cheirurid community.

The olenid community may be present futher to the west in the Arenig Al Rose Formation, Inyo Mountains, California (Ross, 1967, Pl. 11). The Basin Range area of the western United States would be ideal for an extension of studies on trilobite communities, both because of the fossiliferous nature of the sediments there and their complete exposure. The distribution of these community types may well prove relevant to the problems of correlation between shifting facies in the Ordovician of this region (e.g. Ross, 1970:46–52).

Scandinavia

The Tremadoc of this area is typified by widespread development of the olenid environment (Henningsmoen 1957). The olenid-bearing parts of the Spitsbergen section represent the continuation of this environment into the early Ordovician, this being accompanied by a renewed period of evolution of these trilobites detailed elsewhere (Fortey, 1974a). These Arenig episodes of the olenid environment are as so far known unique to Spitsbergen, olenids (apart from *Triarthrus*) being a generally rare component of contemporary faunas. In the Early Ordovician of Sweden (Tjernvik 1956) Olenidae are represented by rare *Saltaspis* and *Triarthrus* specimens. Nileid trilobites and Raphiophoridae are prominent, the former represented by many undescribed species (Tjernvik, written communication 1971). The Swedish assemblages are thus well represented by the diagnostic families of the nileid community, a resemblance which is strengthened by the occurrence there of *Raymondaspis, Pliomeroides* (*Evropeites*) and and a cybelinid close to the Spitsbergen forms (Tjernvik, written communication 1971) as well as the asaphids *Niobe* and *Megalaspides*. A typical nileid community has been described also from the Arenig of Norway (Skjeseth 1952). From the island of Bornholm, Poulsen (1965) has described a trilobite fauna of similar type, material of which I was able to examine at Copenhagen through the kindness of Dr. Poulsen, and from which the predominance of *Nileus* and raphiophorid trilobites was apparent, with the addition of a *Cyclopyge* species. It is tempting to assume that *Cyclopyge,* with its enormously developed eyes like those of *Carolinites,* was similarly adapted to life in the surface waters. The nileid assemblage is probably also present in Estonia (Männil 1963), from which region *Carolinites* is also recorded (Balashova 1961).

It is clear that assemblages of a type close to the nileid community of Spitsbergen are widespread over Scandinavia in the early Ordovician. The possible eastward extension of occurrences of this assemblage cannot be documented with certainty due to lack of data on the relative abundances of the trilobites concerned. It may be significant that particularly rich raphiophorid faunas have been described from Kazakhstan (e.g. Chugaeva 1958), while as far East as the Ch'i lien Mountains, Northern China, a fauna with raphiophorids and nileids prominent occurs (Chang & Fan 1960). It seems possible that this community (and environment) type was particularly widespread in the early Ordovician.

PERSISTENCE OF COMMUNITY TYPES

That the *olenid community* was persistent has already been pointed out, lasting from the Upper Cambrian at least until the Llanvirn and associated with a similar rock (and environment) type. During this considerable period of time successive genera and species of the different subfamilies evolved, perhaps the last major group of the family to evolve being the Balnibarbiinae Fortey 1974a. Persistence of a broad group of trilobites in a particular environment in no way implies evolutionary inactivity. An olenid community of Llanvirn age is present in black shales from the Madre de Dios in Peru, species similar to those figured by Bulman (1931) from Bolivia being present there. Percentage composition of this fauna, based on 106 specimens, is shown in the following table, from which the dominance of *Triarthrus* and *Hypermecaspis* in the fauna, and its low diversity will be apparent.

	%
Triarthrus	78
Hypermecaspis	14
Asaphidae	5
Trinucleidae	2
Lingulid	1

The olenid community does not seem to have survived beyond the Middle Ordovician, the same ecological niches presumably being occupied thereafter by different trilobite groups. It might be tentatively suggested that the Liberty Hall facies of the Athens Shale of Virginia, which is of lithological type reminiscent of the olenid-bearing sediments, may contain the successor of the olenid community, including *Robergia* and Dionidiidae (Cooper 1953) as well as the last known new olenid genus to evolve – *Porterfieldia* Cooper.

Recognition of illaenid-cheirurid and nileid communities is difficult due to the lack of data on relative abundances of trilobite faunas, and the relation of the faunas to the enclosing rock type. A possible early *nileid community* is present in the late Tremadocian Ceratopyge Limestone of Scandinavia in which nileids (*Symphysurus*), raphiophorids (*'Ampyx'*), niobinids, the pliomerid *Evropeites,* and *Shumardia,* recall the nileid community of the Valhallfonna Formation, although Cambrian elements such as *Ceratopyge,* which do not persist into the later Ordovician, are also prominent. Lower Ordovician samples of the nileid community have been considered above, and are widespread. I cannot identify the assemblage beyond the Middle Ordovician. This may be due to evolution and generic turnover of faunas adapted to this environment being relatively rapid. The nileid community may have acted as a source for genera which later invaded shallower water environments (Whittington & Hughes 1972:266).

The *illaenid-cheirurid community,* once established, appears to have been remarkably stable. From its early occurrence in the Arenig Tourmakeady Limestone, faunas dominated by similar groups of trilobites are present in the Llanvirn (Lower Head, Newfoundland; Meiklejohn bioherm, Nevada; upper part of the Valhallfonna Formation, Spitsbergen), Llandeilo (Chazy Group of New York, Shaw, 1968), and Ashgill (Boda Limestone of Dalarna, Sweden; Chair of Kildare Limestone, Eire). Lane (1972:338) notes these similarities, and the occurrence of such faunas in pure, white limestones, and extends the stratigraphic range of the illaenid-cheirurid fauna into the Silurian of Greenland and even into the Devonian of Czechoslovakia and Devon, England. Stability of familial composition of these faunas is extraordinarily constant throughout this long period of time, and even some genera such as *Selenoharpes* persist from the early Ordovician to late Silurian. Once adapted to this environment the trilobites of the illaenid-cheirurid community were evidently well-equipped to survive. In later Ordovician and subsequent occurrences of the community Scutelluidae of *Scutellum* type become a prominent component of the faunas. It is interesting to observe the resemblance in gross morphology between these scutelluids and the *Bathyurellus*-type Bathyuridae which are characteristic of the earlier Ordovician illaenid-cheirurid community, and it may be suggested that similarly adapted scutelluids arose during the later Ordovician to fill the ecological niche formerly occupied by these Bathyuridae.

COMMUNITY TYPES AND FAUNAL PROVINCES

The possibility of trilobite communities existing at the same time in relatively close proximity and having few or no genera in common poses interesting questions regarding the faunal provinces of the early Ordovician:

(1) To what extent may 'provincial' differences be accounted for simply by differences in facies and community types?

(2) To what extent may particular community types be independent of provincial differences?

Whittington & Hughes (1972:262) indicate that trilobite provinciality was at its maximum in the Arenig-Llanvirn, that is, during the period of deposition of the Valhallfonna Formation, and distinguish four major provinces on the basis of trilobite distributions – the Asaphid, Bathyurid, Asaphopsis and Selenopeltis Provinces (Whittington & Hughes, 1972, Fig. 1–3). These provinces are believed to have occupied "shallow-waters around a single continental block; the oceans that separated these blocks in the early Ordovician were barriers to migration so that evolution was independent in each province" (Whittington & Hughes, 1972:236).

Palaeogeographic reconstructions based on geophysical evidence (Whittington & Hughes 1973, Fig. 1). and on trilobite distributions (Whittington and Hughes, 1972, Fig. 3) both place Spitsbergen as part of the Bathyurid province in an equatorial position in the early Ordovician, as part of a continent including Greenland and North America. This placement is in accordance with most of the stratigraphic information from the lower Palaeozoic successions in Ny Friesland (Fortey & Bruton, 1973). However, from analysis of the fauna of the Valhallfonna Formation it is clear that:

(1) The fauna of the upper part of the Profilbekken Member, where the illaenid-cheirurid and nileid communities are in close proximity, contains a fauna generically very close to that of the Middle Table Head Formation, Western Newfoundland and typical of the Bathyurid Province (Fortey & Bruton, 1973).

(2) The nileid community of the Olenidsletta Member, however, contains a fauna of which almost every genus may be matched in the Asaphid Province faunas of Whittington & Hughes (1972, Fig. 2).

(3) As discussed above, the olenid community has a counterpart in the Llanvirn of Peru and Bolivia, an area which is included in the Asaphopsis province of Whittington and Hughes. Further similarities to South America are the occurrence of *Mendolaspis, Micragnostus* and *Tropidopyge* in Spitsbergen. No connection is suggested with the fauna of the Selenopeltis Province, which remained distinct until the end of the Ordovician, and was probably adapted to the cool waters surrounding the Ordovician pole.

The Spitsbergen sections thus contain faunas suggestive of connections with three of the four early Ordovician faunal provinces, an occurrence indicating that the oceans of the time may not have been as effective barriers to migration as Whittington and Hughes considered. The following model may account for the inter-provincial connections in Spitsbergen (Fig. 5).

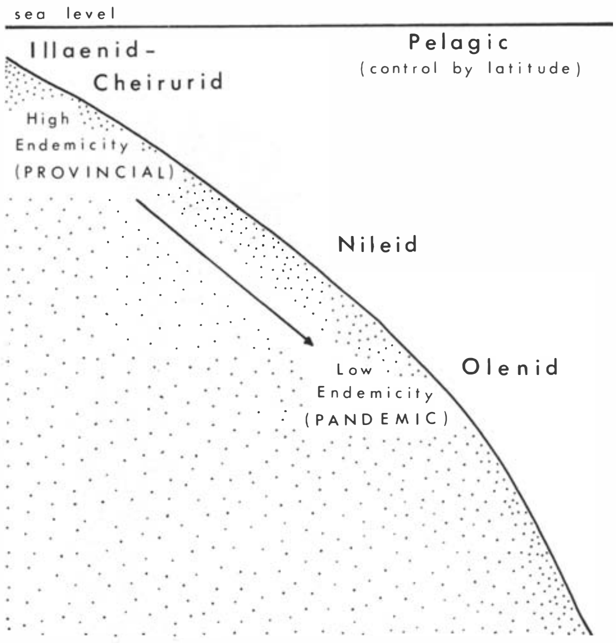

Fig. 5. Diagram showing the influence of community type on trilobite distributions.

(1) The olenid community was adapted to a peculiar set of environmental conditions probably in deep water, and may therefore have been independent of factors such as temperature or turbulence of importance in determining the composition of shallower water faunas. It is suggested that the olenid community could establish itself wherever suitable bottom conditions pertained, essentially independent of the faunal provinces. Because of its environmental requirements, olenid communities may be expected to occur most frequently in the marginal areas of continental shelves (cf. Wilson, 1957). Because of its low generic diversity its presence may not be detected in analyses which limit acceptable data to faunas with more than eight or ten taxa (Whittington & Hughes 1972:238). Although at present the olenid community is known from the Arenig-Llanvirn of Spitsbergen and South America its discovery elsewhere is to be anticipated, when rocks of the right facies are discovered. It may be noted here that certain bathyal species of present oceans are remarkable for the breadth of their distribution (e.g. Knudsen, 1967:325). The olenid community may also prove to be independent of palaeolatitude, occurring near the Ordovician equator in Spitsbergen and in higher latitudes in S. America.

(2) The faunas of the nileid community, particularly towards the lower end of the environmental gradient, while more dependent than olenids on surface conditions as limiting factors on their distribution, may still be independent enough to occur over a wide geographic range. In the case of Spitsbergen, which is believed not to have been geographically very far removed from the Asaphid "province" faunas of the Baltic and Pay Khoya (Whittington & Hughes, 1973, Figs. 1,2, but note that Jaanusson, 1972, presents evidence to suggest a temperate, rather than tropical, climatic zone for Baltoscandia at this time), colonisation of a suitable bottom type across the "Proto-Atlantic" ocean may have been relatively easy. Temperature differences incurred by the extension of a fauna towards the equator may have been accomodated by a down-shelf migration, i.e. a fauna at the high latitude extreme of its range may occur in a shallower environment than at the equator. It will be interesting to see whether other Asaphid province faunal elements are discovered in the nileid communities (described above) elsewhere in the North American block.

(3) Trilobites at the shallow water end of the environmental gradient are closely adapted to the surface temperature conditions and other stresses of high energy environments, which will lead to evolution of species and genera with a high degree of endemicity. Faunal provinces will be areas over which this sort of fauna is widely distributed; this may be expected in the fossil record because such faunas will occur over platform areas likely to escape tectonism, although they may also occur around volcanic islands. The palaeoequatorial Bathyurid province faunas widespread across platform north America, Greenland and northeast USSR and including the shallow water parts of the Spitsbergen sequence are of this type.

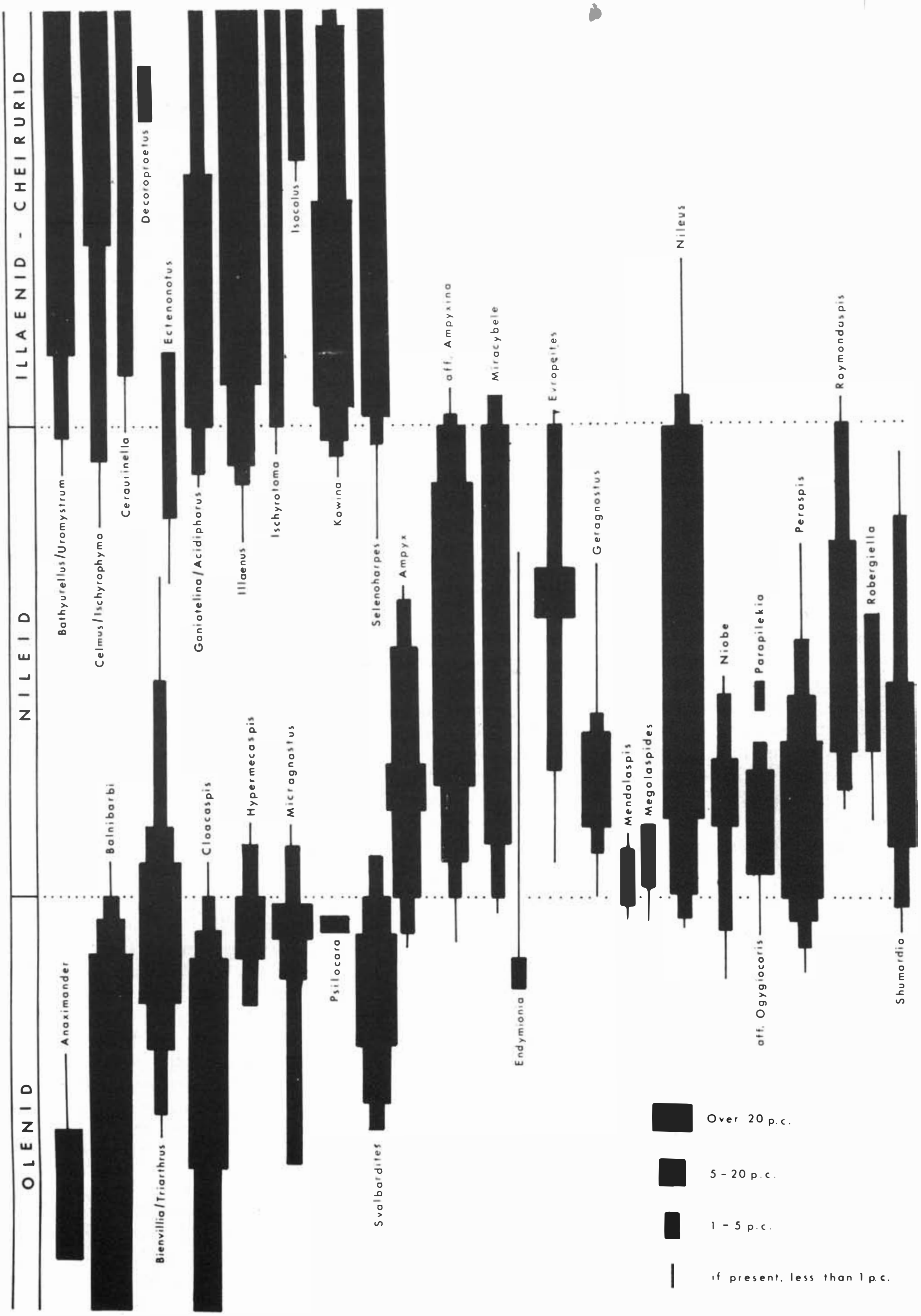

Fig. 6. Summary. Diagram to show the tolerance ranges and expected relative (%) abundances of early Ordovician trilobites across the shallow to deep water environmental gradient. Nileid community elements on right, illaenid-cheirurid and olenid community elements on left.

To arrive at the causes of early Ordovician trilobite distributions it therefore seems necessary to consider the community type as well as the gross generic composition over a given area. Provinces will be discerned from shallow water faunas which respond particularly to ambient temperature which may prove of greater importance in determining provinciality than geographic separation *per se.* Deep water faunas with particular habitat requirements are likely to be cosmopolitan. Distribution patterns of individual genera will be due to a complex interaction between community type, individual tolerance ranges and barriers to dispersal, including such imponderables as current patterns and the life span of the pelagic larvae. Elucidation of such problems has hardly begun.

SUMMARY

Fig. 6 is an attempt to chart the ranges of individual genera across the shelf-slope environmental gradient, expressing their occurrence as *potential* relative abundances within faunas and indicating their tolerance ranges. The diagram is based on the Arenig-Llanvirn of the Spitsbergen section, with some additions from my study of the Tourmakeady Limestone, for which reasonably accurate relative abundances are known. It is hoped that this diagram will be useful as a basis for the interpretation of contemporary faunas with common faunal elements, although its usefulness will be greatly extended when other sections are studied in similar detail.

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Cambrian and Ordovician correlation and trilobite distribution in Turkey

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Known Cambrian outcrops in Turkey are confined to the south, especially the Taurus Mountains, where late Lower and Middle Cambrian limestones contain trilobites of western European and Mediterranean type. Middle Cambrian strata in the Amanos Mountains and near Derik also include shales in which eastern North American elements are present. A Tremadoc fauna near Saimbeyli is of western European type. In much of the central Taurus thick Ordovician flysch deposits are found, the highest beds near Beyşehir containing Mediterranean-type trilobites and succeeded by limestones with a Baltic fauna related to others farther east. Arenig shales with *Taihungshania* near Saimbeyli link corresponding deposits in southern France and southwestern China. The easternmost fauna, that of the Bedinan Formation, is mainly of Bohemian type but some elements are related to faunas in Afghanistan, Burma, and China.

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The recognition of Cambrian and Ordovician rocks and faunas, both shelly and graptolitic, in Turkey is a relatively recent development. Publication of the 1:800.000 geological map by Maden Tetkik ve Arama (M.T.A.) in 1942-45 marked an important advance not only because it provided the first comprehensive geological coverage available for the whole country, but also because it focused attention on numerous areas of older rocks which would repay further investigation. In the absence of fossil evidence to the contrary, many of these areas were shown as Devonian at a time when little detailed stratigraphic collecting had been done, and in some instances the rocks are known now to be of Cambrian or Ordovician age. The work was carried a stage further in M.T.A.'s 1:500.000 geological map, now completed but not yet published in full.

Earlier work on the geological structure of Turkey was reviewed by Ketin (1966), who demonstrated the subdivision of the country into four tectonic units, from north to south as follows: Pontids, Anatolids, Taurids and Border Folds region. Cambrian and/or Ordovician rocks have been recorded to some degree from all these units, which form a convenient basis for the following account, but most of the known outcrops occur in the Taurids. The description and notes now presented do not attempt to give a comprehensive account of Turkish Cambro-Ordovician trilobite faunas, but are intended as an assessment of the present state of knowledge, and any conclusions may be liable to modification in the light of new discoveries. Many of the conclusions are based essentially on sections and material examined by the writer in the course of field seasons during 1965 and 1968, together with specimens collected before then and since by various friends from Ankara and Université de Paris-Sud. Some of the areas described are sited in out of the way parts of the country but all those shown in the figures can be localized with reference to place-names in Fig. 1. Further collecting of some of the faunas is now in progress, and they will be described in future publications. I am much indebted to M. Olivier Monod, Dr. R.J. Ross, Jr., and Prof. H.B. Whittington who kindly acted as critical readers of the manuscript.

DISTRIBUTION OF KNOWN CAMBRO-ORDOVICIAN OUTCROPS IN TURKEY

Pontids Region

The westernmost Ordovician outcrops in Turkey occur in the vicinity, and by the east side, of the Bosphorus north-northeast of Istanbul, and little is known of their precise age. The only systematic descriptions of Ordovician fossils were given by Sayar (1964) who described a new species, *Exoconularia istanbulensis,* and listed other conulariids that she considered to indicate a Middle Ordovician age. Sayar's material came from fossiliferous, chamositic oolite beds interbedded with shales which formed part of an "Arkose Horizon", underlain by a "Conglomerate Horizon" of "? Lower Ordovician" age and overlain by a "Main Quartzite Horizon" of "? Upper Ordovician" age. She pointed out that Ordovician conulariids occur in oolitic ironstone beds over a wide area of Europe, including Thuringia, Bohemia and Normandy. The Bohemian and western French affinities were emphasized further after comparison with Czech faunas described by Bouček (1928), the stratigraphical distribution and nomenclature of which can now be brought up-to-date with the help of faunal lists published by Havliček & Vaněk (1966: 52–57). The ranges of the species listed by Sayar are as follows: *Archaeoconularia fecunda* (Barrande), Dobrotiva Formation to Bohdalec Formation, *Exoconularia exquisita bohemica* (Barrande), Zahořany Formation only, *Metaconularia consobrina* (Barrande), Dobrotiva Formation to Zahořany Formation. In modern stratigraphic terms, these formations are now considered to range from Llandeilo Series to the upper half of the Caradoc Series. Asaphid remains have also been reported by Yalçinlar (1955), but no descriptions of these or other trilobites have been published. Judging from the evidence of the recorded conulariids one may expect to find further evidence of an easterly extension of the Bohemian faunas, perhaps forming a link with those of the Bedinan area in southeastern Turkey (see Anatolids Region, p. 000), but the evidence so far is too meagre to evaluate.

On the Asiatic side of the Sea of Marmara, south-east of Istanbul, Haas (1968, pp. 63–66) established a number of new stratigraphic terms for the Palaeozoic sequence there. The oldest subdivision, termed Bithynian Series, was in turn divided as follows:

	AIII	Yayalar – Schichten
Bithynian Series 1000 m	AII	Ayazma – Schichten
	AI	Kurtköy – Schichten

The Kurtköy – Schichten were shown resting discordantly on Precambrian rocks and described as comprising arkoses, tonschiefer and conglomerates to which Haas ascribed a Lower? to Middle Ordovician age. Commenting on the chamosite-oolite horizon of Çengelköy from which Sayar had described conulariids (see above), Haas noted that asaphid remains had been found in the same strata by both Yalçinlar and Erben, but no faunal list was given. The Ayazma – Schichten, apparently unfossiliferous, were assigned to the highest Ordovician and lowest Silurian, followed by the Yayalar – Schichten of Llandovery age.

30 km northwest of Izmit, a town situated 80 km east of Istanbul, lies a quarry from which Ordovician fossils were recorded by Yalçinlar (1959). The evidence for the age of the argillaceous and sandy schists exposed there is somewhat confusing. Dendroid graptolites and conulariids were described by Yalcinlar as occurring together, but the former were said to include a form comparable with the Tremadoc subspecies *Dictyonema flabelliforme sociale* (Salter), whilst the latter were listed merely as *"Conularia niagarensis* et *Archaeoconularia"*, suggesting a much younger horizon. It may be that the rocks represent an easterly extension of those of the Bosphorus region, but the faunal evidence requires reexamination.

Ordovician sediments have been recorded also from the Zonguldak area, on the Black Sea coast some 250 km east of Istanbul by Kamen-Kaye (1971: 112–113). It was implied that the rocks correspond to those of the Istanbul area and contain a higher proportion of sandstone as they are traced eastwards, but no faunal evidence of age was given.

In a recent review Brinkmann (1971: 175) grouped the Ordovician rocks of northwestern Anatolia and the Istanbul region as a series of mostly continental-type deposits skirting the southern margin of a so-called Pontic Land, a term used earlier by F. Frech, which ran roughly E – W forming the northern boundary of the Tethys geosyncline in Turkey. The chamosite-oolite beds with conulariids of the Bosphorus region were interpreted by him as a thin marine development at the top of these continental strata.

Anatolids Region

Little published information is available on the Cambro – Ordovician rocks of this region. In the vicinity of the Babadağ, about 20 km west of Denizli (Fig. 1), Yalçinlar (1963) described briefly a series of folded schists and crystalline limestones from which the dendroid graptolites *Dictyonema* and *Acanthograptus*? (identified by O.M.B. Bulman) were recorded. The rocks, which overlay crystalline schists of uncertain age, were said to be overlain by graptolitic strata of Lower Silurian age, but the account is not clear; the only mention of Silurian fossils is with reference to the above genera, and may in fact refer only to their possible range. Whatever their age, and an early Ordovician horizon seems likely, these Lower Palaeozoic strata are then succeeded by unconformable beds of Carboniferous and Permian age.

Just off the Aegean coast of Turkey, and about 200 km southwest of Denizli, lies the Greek island of Kos, where Ordovician rocks represent the westernmost outcrops of the Anatolian region. Brinkmann (1971: 175) noted the Ordovician rocks of southern Anatolia and Kos as comprising "marine siltstones and sandstones with a brachiopod fauna of Bohemian type". Such an observation implies that the strata on Kos may represent the Seydişehir Formation of the Taurids, but no further details were given.

Taurids Region

The southern half of Turkey is dominated by the Taurus (or Toros) Mountains, which separate the Anatolian Plateau from the Mediterranean Sea. The Taurus range is of variable width and for the most part follows the Mediterranean coastline in a sinuous course which finds its easterly extension in the Zagros Mountains of Iran. Most of the mountains are composed of Mesozoic and Tertiary formations but inliers of Palaeozoic, including Cambrian and Ordovician, rocks occur at intervals (see Fig. 1) and are described here in order from west to east.

The area south-east of Beyşehir (Fig. 3), between Konya and Antalya, contains a succession of Cambrian and Ordovician rocks and faunas that is at least one of the best-developed in Turkey, and so far is the most completely documented. The first discovery of Ordovician fossils there was made by Olivier Monod, whose initial paper (1967) on the subject demonstrated the presence of a thick succession (more than 1000 m) of flysch-like sediments known as the Seydişehir Formation, in the upper portion of which shelly fossils of Mediterranean-Bohemian type occur with occasional graptolites of Lower Arenig age. In the meantime unpublished work by Haude and Kelter (since reviewed by Haude, 1969) on part of the Sultan Dağ massif, northwest of Beyşehir, showed the presence there of Middle Cambrian fossils, and subsequently Cambrian faunas were found near Beyşehir by Monod, in strata now termed Çal Tepe Formation

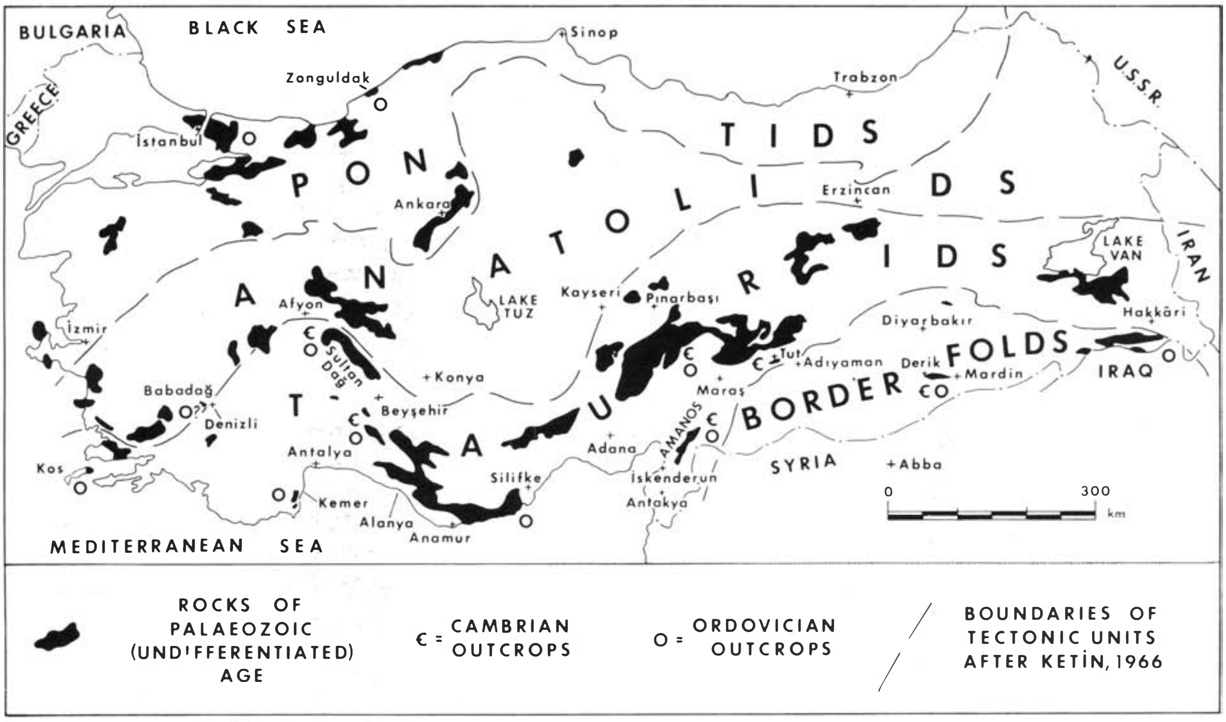

Fig. 1. Outline map of Turkey showing the division of the country into various major tectonic units according to Ketin (1966). The black areas denoting Palaeozoic (undifferentiated) rocks are based on the work of Erentöz (1966) with modifications and additions by the writer. Each area shown in Figs. 3—8 contains at least one place-name from Fig. 1.

(Dean & Monod, 1970) after the large hill of that name. The complete lithostratigraphic succession is as follows:

Sobova Formation	Grey Shale member	c. 20 m
	Limestone member	0 to 10 m
Seydişehir Formation		> 1000 m
Çal Tepe Formation	Red, nodular limestone member	40 m
	Light-grey Limestone member	10 m
	Black Limestone member	30 m
	Dolomite member	> 50 m
	(Base of formation not seen)	

No traces of organisms have been found in the Dolomite Member, but the Black Limestone Member at the Çal Tepe itself comprises the oldest fossiliferous rocks known so far from Turkey. To date the fossils include only sporadic and fragmentary trilobites which are still under investigation, whilst slightly higher in the succession, the lower part of the succeeding Light-grey Limestone Member has yielded Lower Cambrian trilobites, again uncommon but including fragmentary protolenids. The Lower/Middle Cambrian boundary, believed to lie within this member, is now being investigated further, and although the more characteristic Middle Cambrian strata, with their abundant paradoxidids, agnostids, solenopleurids and corynexochids, are conspicuous in the field, it is not yet known whether a continuous faunal succession exists. The Red Nodular Limestone Member, the highest of the three composing the Çal Tepe Formation, marks a change in lithology and is poorly fossiliferous, with only two known levels, one of them in the topmost beds. These levels together contain corynexochids, paradoxidids and solenopleurids, and are of Middle Cambrian age, as are overlying shales mapped by Monod as the lowest member of the Seydişehir Formation, the highest beds of which are Lower Ordovician (Arenig Series) (Dean & Monod, 1970) no evidence of Upper Cambrian yet having been found.

The remainder of the large thickness of Seydişehir Formation has yielded fossils only in the upper half. Graptolites 100 m below the summit indicate the *Didymograptus extensus* Zone, the lower zone of the Arenig Series, and are accompanied by occasional trilobites (*Geragnostus, Neseuretus* and asaphids), bivalves (*Redonia*), gastropods and brachiopods. In the highest strata are concretions in which the cephalopods *Bactroceras, Proterovaginoceras* and *Protocycloceras* suggest a possibly Upper Arenig horizon (Collins *in* Monod, 1967: 83). Evidence for this suggestion, though not conclusive, receives some support from the appearance in the same beds of the trilobite *Symphysurus,* a genus that becomes more abundant in the succeeding Sobova Fm., which is definitely of Upper Arenig age. The Sobova Formation (Dean & Monod, 1970) marks a change in facies to pink and grey detrital limestones, and the line of junction with the underlying Seydişehir Formation, though not seen, is probably conformable, at least at the type section in the Sobova Valley, southeast of Beyşehir, in view of the Upper Arenig age of the trilobites from the limestones there. The fauna includes a few cosmopolitan or Tethyan elements but the majority of the genera exhibit affinities with corresponding Baltic faunas (Dean, 1973) and are discussed later (p. 367). Elsewhere in the area, the relationships of the Sobova Formation and underlying strata are not always clear, and at some localities limestones of uncertain position have been found to contain Arenig trilobites and conodonts older than those at the type section.

The level within the Seydişehir Formation at which the Cambrian – Ordovician boundary should be drawn is not known, and no trace has yet been found of Tremadoc or Upper Cambrian faunas. Prof. Klaus Sdzuy (personal communication) kindly informs me that he has identified evidence, as yet unpublished, of the former and possibly of the latter in material collected by H. Haude & D. Kelter from the vicinity of the Sultan Dağ, a region where the two latter workers found also Middle Cambrian fossils (Haude, 1969). Further investigation of the Çal Tepe and Seydişehir Formations is continuing and the above conclusions may eventually require modification.

A northerly extension of the Seydisehir Formation is suggested by a single generically indeterminate asaphid pygidium collected in the summer of 1966 during mapping of the area "at the northern edge of the Sultan Dag" by the late M. Marcel Gutnic who informed me (personal communication, 1970) that the specimen and other, indeterminate fossil fragments occurred in slightly metamorphosed shales very similar to the rocks of the Seydişehir Formation. This is presumably "la faune récoltée au Nord-Ouest de Sagirköy (25 km au Nord-Ouest de Yalvac)" noted by Gutnic *in* Monod (1967: 88). Also from the vicinity of the Sultan

Dağ is a record by Yalcinlar (1959a) of shales with dendroid graptolites, including *Dendrograptus* and a *Dictyonema* said to be very like *D. flabelliforme* (Eichwald), at two places south of Akşehir (Fig. 2).

An extension of Cambrian strata northwestwards into the region between Seydişehir and Eğridir (see Fig. 3) has been described by Dumont (1972) who gave the following succession:

Middle Trias	Limestones and quartzites
	UNCONFORMITY
	9. Shales
	8. Black dolomite
	7. Nodular limestone with trilobites
	6. Diabases
Kocaosman Formation, 310 m shown	5. Black limestone
	4. Sandy shales
	3. Thick black dolomite
	2. Silty limestone and quartzite
Sarıcıcek Formation	1. Grey-green schists. 2000 m visible

Bed 7 yielded the only fossils found in the area, and these were kindly sent to me by M. Dumont. They proved to be poorly preserved and fragmentary trilobites, but included *Paradoxides* (s. 1) and *Corynexochus,* indicating a Middle Cambrian age. Dumont noted that diabases are unknown from the Çal Tepe Formation and pointed out that his succession could be more closely correlated with Haude's as yet unpublished sequence in the Sultan Dağ region.

A curiously isolated occurrence of an Ordovician shelly fauna was discovered in 1969 by M. Jean Marcoux while mapping the area near Kemer, south-west of Antalya (Fig. 1). M. Marcoux sent me part of a small, fossiliferous concretion containing fragments of trilobites that I identified as *Placoparia* sp. These were later cited in an account of the regional structural geology by Brunn *et al.* (1972: 238), where the Ordovician strata in question were stated to comprise scattered outcrops of dark shales which "are tectonically crushed between the Tahtalı Dağ and the Alakir Çay units", the two latter denoting structural units of the Antalya Nappes in this complex portion of the Taurus. Since then additional collecting by M. Marcoux has produced

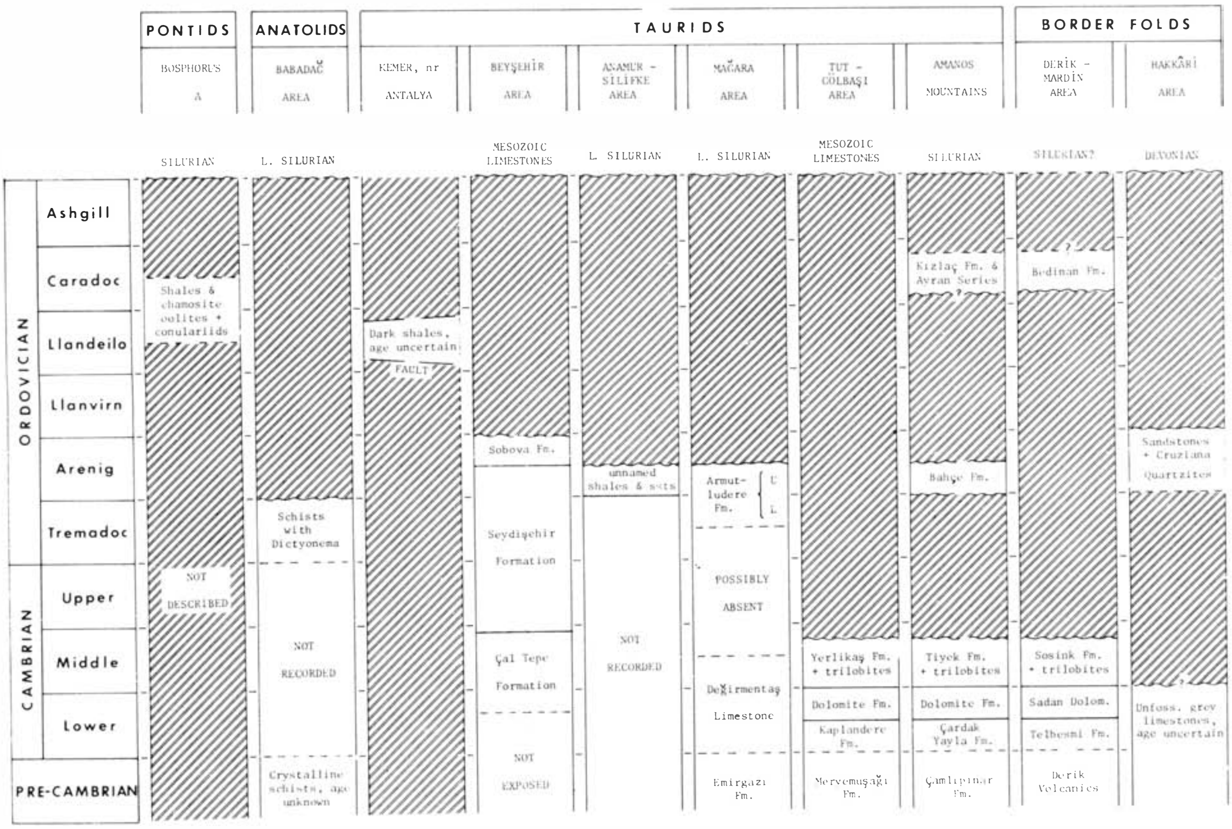

Fig. 2. Correlation chart summarizing principal successions of Cambrian and Ordovician rocks in Turkey.

a few fragments of cyclopygids and a poorly-preserved illaenid, and further structural studies show that the Lower Palaeozoic formations of the Kemer region lie at the base of the Permian to Mesozoic limestones in the Tahtalı Dağ unit of the Antalya Nappes. Studies of this material are not yet complete but the trilobites exhibit Bohemian affinities and are probably younger than those of the Seydişehir and Sobova Formations. No comparable strata are yet known from the remainder of Turkey and the beds at Kemer are certainly quite distinct from any recorded in the sections at Beyşehir or in the Anamur – Silifke area (see later). However, they lie within a tectonically complex region – the so-called "Courbure d'Isparta" – where nappes are abundant, and so may have been transported to their present position from a location farther south.

Both Cambrian and Ordovician rocks and fossils have been reported from the coastal portion of the Taurids lying between Anamur and Silifke, some 200 km south-east of Beyşehir. No fossils have yet been described or illustrated, but Erentöz (1966: 3, 4) noted Ordovician sandstones and schists overlying shiny, yellow schists of supposed Ordovician age, as well as Cambrian (undifferentiated) strata and trilobites. The records were not elaborated and the only published account deals with the coastal section in the vicinity of the Bay of Ovacık, west of Silifke (see Fig. 4), where Lower Ordovician strata, the faunas of which are as yet poorly known, crop out. Yalçinlar (1964) gave the following generalized succession for the pre-Devonian strata there, in ascending order: (a). Sandy shales with inarticulate brachiopods and "méduses" (Cambrian), (b) marbles and sandy limestones with cephalopods, and shales

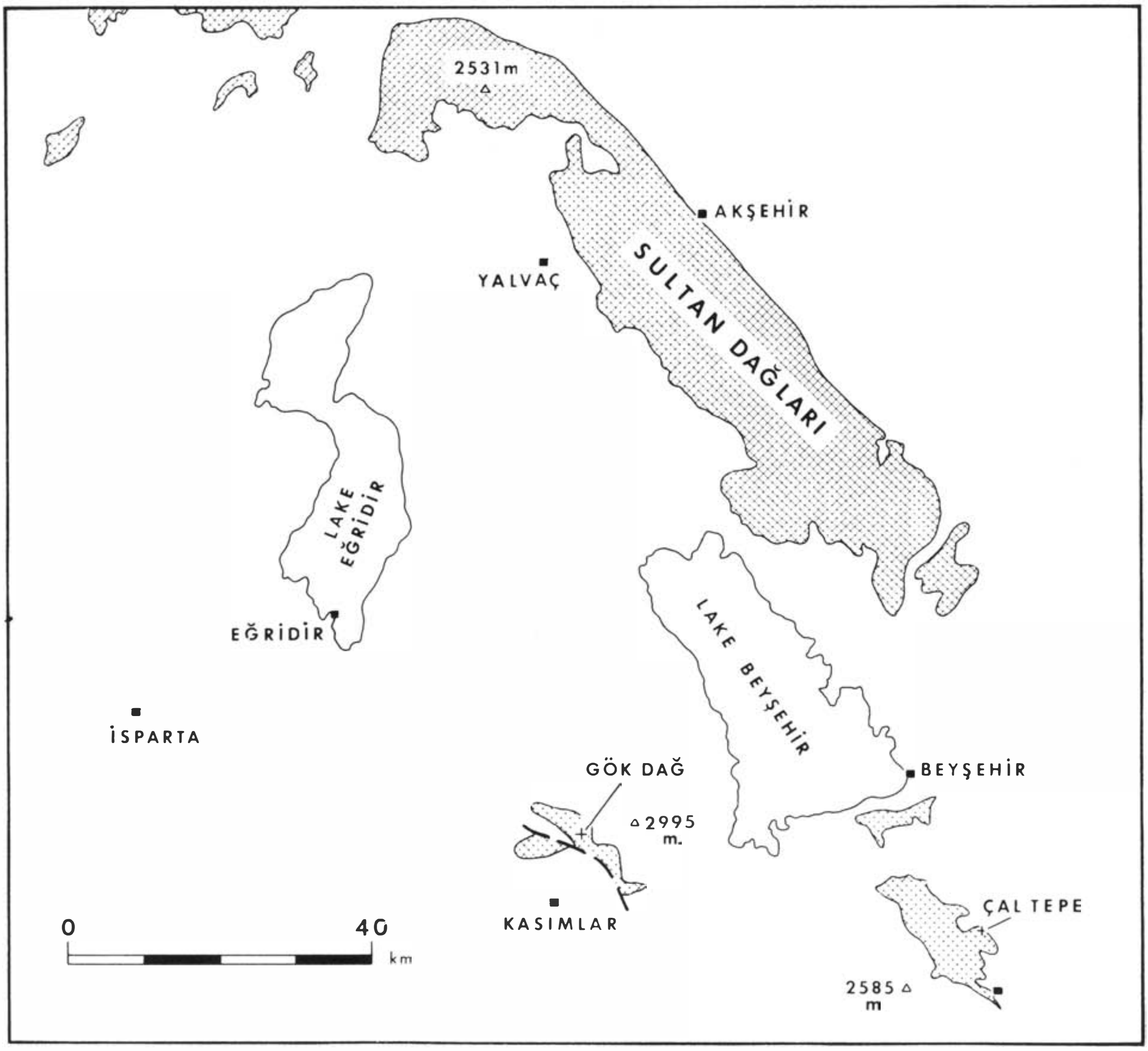

Fig. 3. Sketch-map showing localities and Palaeozoic (undifferentiated, including Cambrian and Ordovician) outcrops in the region near Beyşehir and Eğridir, southwestern Turkey.

and sandstones with brachiopods (Lower Palaeozoic), (c) conglomerates and sandstones (Cambro-Ordovician), (d) shales and sandstones with graptolites and brachiopods (Lower Silurian), (e) graptolitic shales (Lower Gotlandian), (f) shales and sandstones with *Orthoceras* and brachiopods (Silurian), (g) siliceous schists with interbedded black limestones (Silurian). The account is somewhat confused and, while claiming the first discovery of Cambrian and Ordovician beds in this region, stated (p. 7) that the Cambrian is overlain discordantly by conglomerates, sandstones and a thick graptolitic series, all of Silurian age. A dark sandstone with lingulid and obolid brachiopods between the Silurian strata and Cambrian shales with inarticulate brachiopods was stated to be a Cambro-Ordovician formation.

A subsequent paper (Yalçinlar, 1965: 3–13) gave the following section for the same area, in ascending order from south-east to north-west as follows: (1) Shaly sandstones, cream and rose-coloured, with inarticulate brachiopods ("Lower Ordovician (probably Upper Cambrian)"), (2) creamy yellowish shales with trilobites, graptolites and *Acrothele,* (3) yellowish, clayey shales with trilobites, (4) sandy shales with trilobites, graptolites, cone-in-cone and "phycoides", (5) rose-coloured sandstones with cephalopods and brachiopods, interbedded with pink, nodular limestones (Ordovician), (6) conglomerates and hard, whitish sandstones lying discordantly on "Lower Palaeozoic" beds, (7) greyish, sandy shales with trilobites, graptolites and brachiopods (Silurian), (8) grey shales with Lower Silurian graptolites, (9) clayey shales and sandstones with cephalopods and siliceous concretions (Lower Silurian), (10) "probablement lydites" interstratified with black shales forming abrupt cliff by sea, (11) blackish shales, siliceous sandstones and greyish, reefy limestones (Silurian). Conglomerates and sandstones at the base of the Silurian were said to rest with angular disconcordance on Cambro-Ordovician rocks.

In an attempt to clarify these accounts the Ovacık area was visited briefly in 1968. The lowest strata seen were silty, micaceous, brown-grey shales and subsidiary bands of hard siltstone which yielded only small numbers of poorly-preserved fossils, including indeterminate asaphid trilobites and *Didymograptus* of extensiform type, so one may suggest a lower Arenig age for these strata and a correlation with part of the Seydişehir Fm. The silty shales, which coincide probably with the two lowest subdivisions (a. & b. above) of Yalçinlar's 1964 account, were

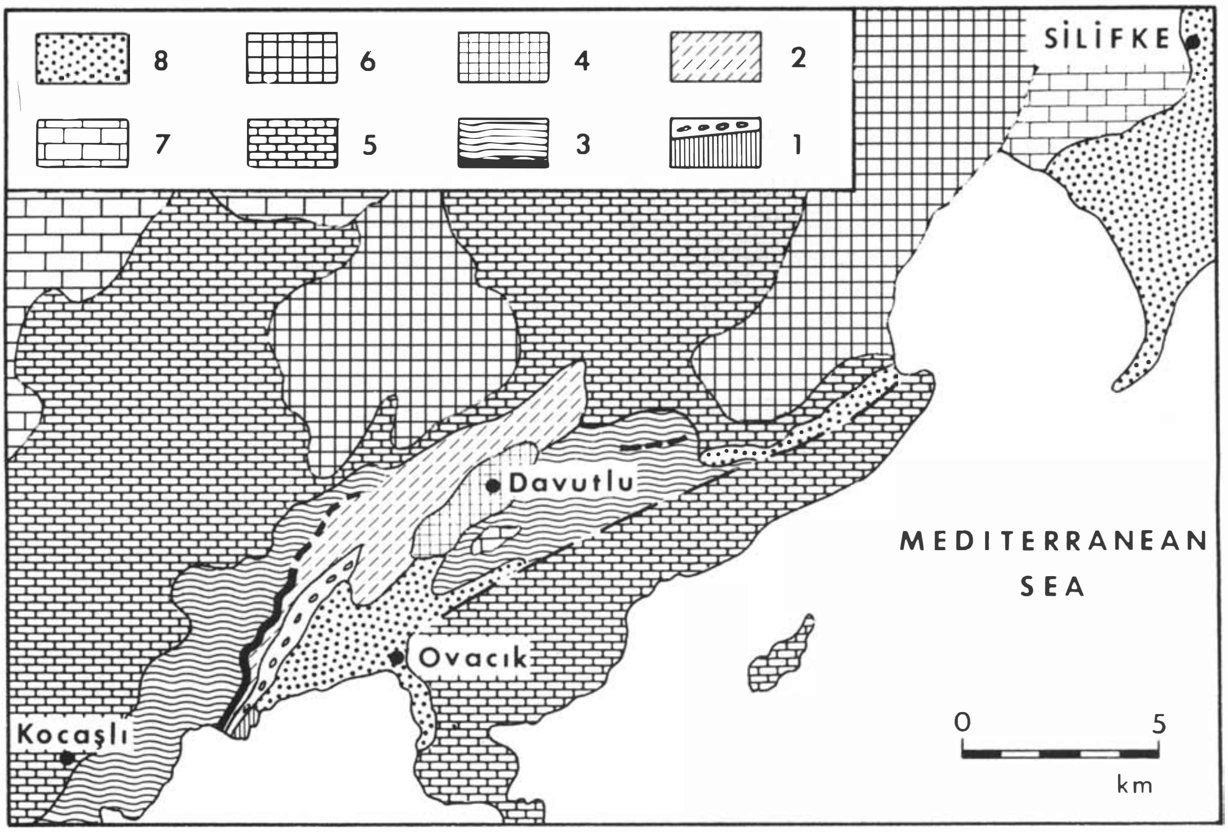

Fig. 4. Sketch-map, after Yalçinlar, 1964, of the Ovacik area, west of Silifke on the south coast. Key: (1) Cambrian(?) & Ordovician shales and conglomerates, (2) Lower Silurian shales and sandstones, (3) Silurian shales and sandstones with black graptolitic shales at base, (4) Lower Palaeozoic limestones, shales and sandstones, (5) Devonian limestones and shales, (6) Upper Cretaceous limestones, (7) Miocene limestones and sandstones, (8) Quaternary and Recent alluvium and beach deposits.

succeeded in turn by massive, yellow-weathering sandstones with bands of conglomerate, followed by almost unfossiliferous, grey-brown, silty shales which were separated by a hard siltstone bed (40 cm) from a conspicuous group of black, pyritous shales about 10 m thick. This last subdivision, which bears a close lithological resemblance to parts of the Skelgill Beds of Northern England, yielded graptolites identified by Dr. P. Toghill as *Monograptus denticulatus* Törnquist, *M. limatulus* Törnquist, *M. lobiferus* (McCoy), *Rastrites peregrinus* (Barrande), *R. capillaris* Lapworth, *Diversograptus* sp. and *Climacograptus* sp., and considered by him to indicate the *convolutus* Zone of the Llandovery Series. Lack of time prevented detailed sampling of these shales, which closely resemble strata that range in age from the *convolutus* Zone to the *sedgwickii* Zone of the Llandovery Series in the Saimbeyli district, 250 km farther east in the Taurus Mountains, where overlying shales with siliceous concretions containing *Encrinurus* sp. and cephalopods invite comparison with subdivision 9 of Yalçinlar's 1965 succession. It is likely that beds of Llandovery age rest with marked unconformity upon Arenig strata in the Ovacık district, and that the sandstones and conglomerates noted above represent the local base of the Silurian.

Among the lower Ordovician fossils described from the Taurus region is the trace fossil *Phycodes circinatum* (Rheinhardt Richter, 1850), illustrated from "Hadjin" by Fuchs (1902: 330, Fig. 2) and recorded also from "Armud-dalen (Bakyr Dagh)" by Broili (1911: 24). M. Olivier Monod informs me that it is fairly common in the upper part of the Seydişehir Formation. The "species" is widespread in the Mediterranean – Bohemian province, and is known now to occur also in the Mytton Flags (Lower Arenig Series) of the Shelve Inlier in the Anglo-Welsh Borders. All the known records are from early Ordovician strata. Recently it was collected by Mr. Necdet Özgül from an unspecified locality north of Alanya, and the rocks in question are probably the local equivalents of the upper Armutludere Fm. or part of the Seydişehir Fm.

Large outcrops of Cambrian and Ordovician strata are found in the Saimbeyli region of the Taurus Mountains, between Pınarbaşı and Feke (Figs. 1, 5), but apart from M.T.A.'s

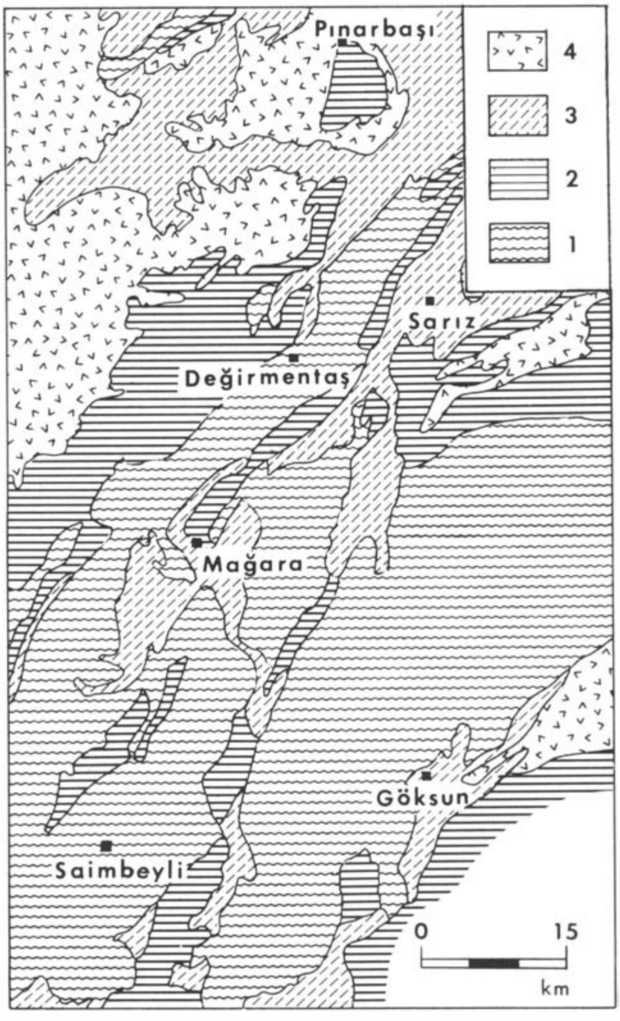

Fig. 5. Sketch-map showing place-name in the Pınarbaşı – Saimbeyli area of the Taurids, south central Turkey. Geological boundaries generalized from MTA's map of 1961. Key: (1) Undifferentiated Palaeozoic, (2) Mesozoic, including Cretaceous ophiolites, (3) Tertiary – Recent sediments, (4) undifferentiated igneous rocks.

1:500.000 map, which shows the general geological features, the only detailed published account of the Cambro-Ordovician stratigraphy covers the rather isolated mountain area around Tufanbeyli, a village north of Saimbeyli (see Özgul, Metin & Dean, 1973). The succession there commences with metamorphic rocks of the Emirgazi Formation at least 100 m thick, assigned to the Pre-Cambrian and probably representing the oldest-known rocks in the eastern Taurus. Next comes the Değirmentaş Formation, grey and pink limestones 110 m thick which contain no fossils but bear a remarkable lithological similarity to the Çal Tepe Formation so that a Lower – Middle Cambrian age has been postulated for them. The limestones are succeeded by the lower member of the Armutludere Formation, comprising grey-green schists, at least some of which are of Tremadoc age having yielded the trilobite *Macropyge taurina* Dean and eocrinoids. The upper member of the Armutludere Formation follows the lower with apparent conformity and is made up of hard, brown-grey shales in which a sparse fauna of trilobites (asaphids, *Symphysurus*) and graptolites *(Didymograptus, Tetragraptus)* indicates an Arenig age. The precise nature of the Cambro-Ordovician boundary in this area is imperfectly understood and although the junction between the Değirmentaş Fm. and the Armutludere Fm. appears to be conformable, there is a sharp lithological change. Bearing in mind that the youngest limestones of the type Çal Tepe Formation, with which the Değirmentaş Formation is correlated lithologically, range no higher than Middle Cambrian (see earlier) and are succeeded by Middle Cambrian shales, then obviously one cannot rule out the possibility of a disconformity at Armutludere. No Upper Cambrian fossils have yet been found there, though Necdet Özgül has reported inarticulate brachiopods said to be of that age elsewhere in the region.

The asaphacean trilobite *Taihungshania* has been found only rarely in the Seydişehir Formation of the type area. Its precise horizon there is not known, but may be lower than that of the highest strata of the Seydeşehir Formation, which are probably latest Lower Arenig or earliest Upper Arenig in age. The genus has been found in some abundance 370 km farther east, in the Taurus mountains south of Saimbeyli, where several specimens were collected by Dr. Cahide Kırağlı and the writer in 1968. The strata are greenish-brown shales which weather regressively and bear a remarkably close lithological resemblance to coeval strata in the Montagne Noire, southwestern France. They have not yet been shown in detail on any published geological map but may correspond to part of the upper member of the Armutludere Formation of the Tufanbeyli district. To the west of the road to Feke and Adana at a point 4.7 km south of Saimbeyli, *Taihungshania miqueli* (Bergeron) was found accompanied by rare *Niobella* cf. *fourneti* (Bergeron) and *"Ampyx"* cf. *villebruni* Thoral, an assemblage found in the Montagne Noire as well as Morocco (Dean, 1966: 281, 328).

An interesting new discovery was made in 1972 when Mrs. Ayca Baysal-Salanci, working in the Saimbeyli region, collected what proved to be fragments of dalmanitid trilobites about 25 km south of the town of Mağara (Fig. 5). The occurrence is being investigated further as it involves a trilobite group previously reported in Turkey from the Ordovician only in the Amanos Mountains and the Bedinan area (see later, p. 368).

The Cambrian rocks of the Amanos Mountains, just east of the north-eastern corner of the Mediterranean (Fig. 1), occupy a position just north-west of the line separating the Taurids and the Border Folds region according to Ketin (1966). They are thus analogous in position to the outcrops of the Gölbaşı – Adiyaman area (see later) and, like them, are sited south of a conspicuous line of overthrusting from the north. The stratigraphic succession proposed by Ketin (1966a: 83) is as follows:

C_3.	Tiyek Formation 250–750 m	White quartzites & interbedded shales calcareous & micaceous shales & siltstones thin, nodular 1sts & shales with trilobites
C_2.	Dolomite Formation 100–150 m	Brown to black dolomites & dolomitic 1sts. coarsely crystalline, dark dolomitic 1st.
C_1.	Çardak Yayla – Calaktepe Formation 280 m	Quartzites with thin, interbedded shales conglomeratic arkoses and quartzites
Slight disconformity		
C_e.	Çamlıpınar Formation > 1500 m	Greenish-grey phyllitic shales, siltstones, sandstones and greywackes

An earlier account of the Lower Palaeozoic rocks of the Amanos (Dean & Krummenacher, 1961) utilized a succession of five unnamed formations (lettered A to E), of which Formation D corresponds to Ketin's Tiyek Fm. and yielded trilobites described as *Pardailhania* cf. *barthouxi* (Mansuy). The latter were claimed to indicate both a Middle Cambrian age and affinities with corresponding faunas in Morocco and eastern Canada, conclusions upheld more recently by Sdzuy (1967a: 112–114) who placed the material in synonymy with what he termed *Badulesia tenera* (Hartt), a species described originally from the Fossil Brook Formation of New Brunswick.

The geology of the Amanos region (Fig. 7) was shown on the Hatay sheet of the 1:500.000 geological map of Turkey published by M.T.A. in 1962. The map in Yalçinlar's (1965: 13–18, Fig. 3) account of the area is virtually the same as M.T.A.'s, but some of the rocks shown originally as Cambrian were held to be of Carboniferous age, and an area of Ordovician strata was indicated near Bahçe. The latter strata, as yet unnamed, correspond to "Formation E" in the section described by Dean & Krummenacher (1961: 73, Fig. 2) and comprise 115 metres of sandstones and sandy shales which rest disconformably on Tiyek Fm. These apparently flysch-like deposits, bearing a general resemblance to the Seydişehir Formation, have proved virtually unfossiliferous, and yielded only a single specimen of an Ordovician trilobite, *Dalmanitina* sp. (R. Richer *in* Dubertret, 1953). Yalçinlar's (1965: 17) record of *"Dictyonema?"* suggests the possible presence of Tremadoc strata, but the evidence of age listed so far is scanty.

Since the above publications, Schwan (1972) has reviewed the results of recent studies in the Amanos, which show the mountain region separated from the Arabian Shield by the so-called Kara Su Graben. Near-shore deposits containing "a few Lower to Middle Cambrian trilobites" and beds of Arenig age with *Cruziana* were reported from the southern Amanos, whilst 1000 m or so of Ordovician quartzites, siltstones and shales with trilobites, brachiopods and molluscs were said to occur in the central Amanos. These flysch-like deposits recall those of the Seydişehir Fm. of the western Taurus but the degree of correspondence between the two is not yet known. A stratigraphic table introduced several new formational names, one of which, the "Ayran Series" in the central Amanos, was stated to be of Caradoc age, but no faunal data were given.

Situated just inside the southern boundary of the Taurus according to Ketin (1966) are

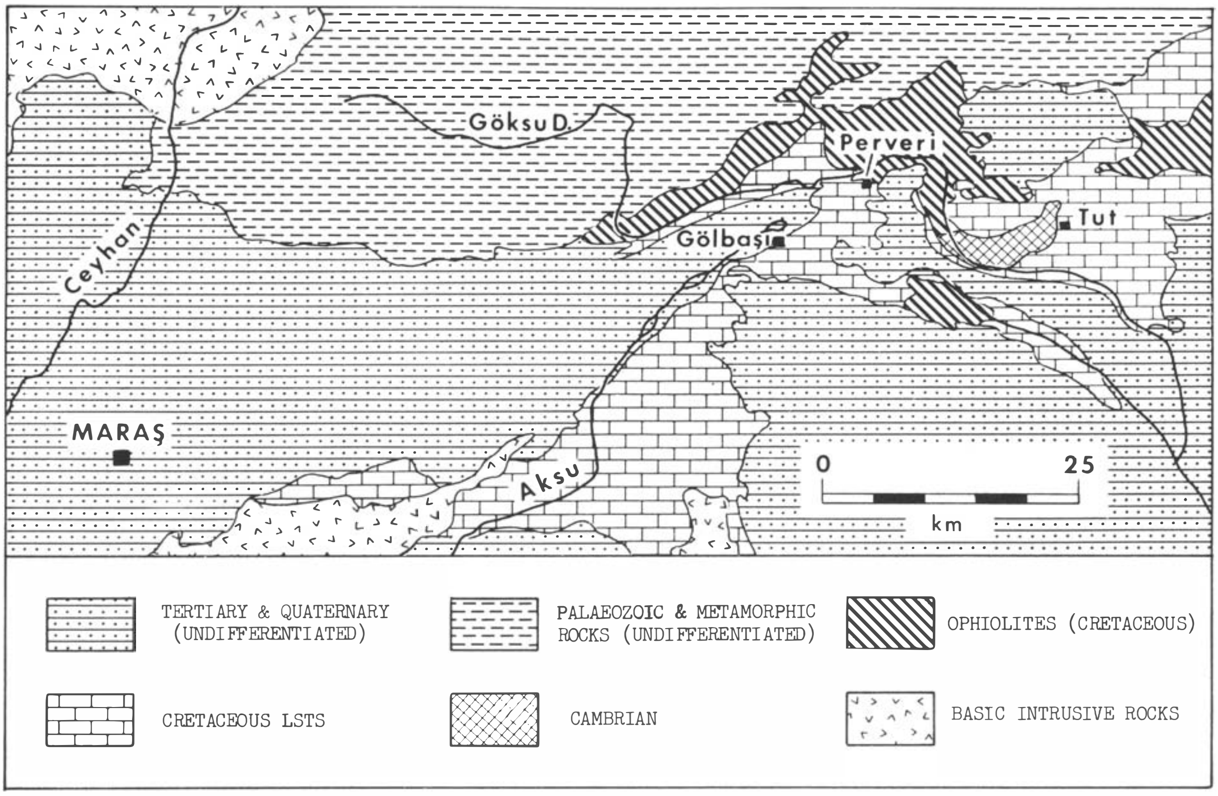

Fig. 6. Sketch-map showing location of some of the fossiliferous Cambrian outcrops in the area near Gölbaşı, northeast of Maraş, south central Turkey. Geological boundaries from MTA's map of 1962 with addition of the Cambrian outcrop west of Tut, after Ketin (1966a).

the Cambrian outcrops of the Gölbaşı – Adıyaman area, situated in the mountains some 75 km east-north of Maraş (Fig. 1). The Cambrian rocks were not indicated on the 1962 edition of the Hatay Sheet of the geological map of Turkey, but their approximate location was documented by Ketin (1966: 80) who described a group of small outcrops elongated east-northeast and centred on the Penbeğli – Tut area, east of Gölbaşı (Fig. 6). Ketin's lithostratigraphic succession is as follows:

Mardin Limestone (U. Jurassic-L. Cretaceous)

Unconformity

C_3.	Yerlikaş Formation 70–270 m	Thin bedded siltstones and calcareous shales with trilobites
C_2.	Dolomite Formation 116 m	Well-bedded dolomites and dolomitic limestones
C_1.	Kaplandere Formation 100 m	Diabase layer (25 m) Purple quartzitic sandstones Conglomeratic and cross-bedded sandstones
	Meryemuşağı Formation 225 m	Diabase sill Purple sandstones and siltstones Dark-green siltstones and shales Glauconitic, green sandstones and greywackes Dark shales

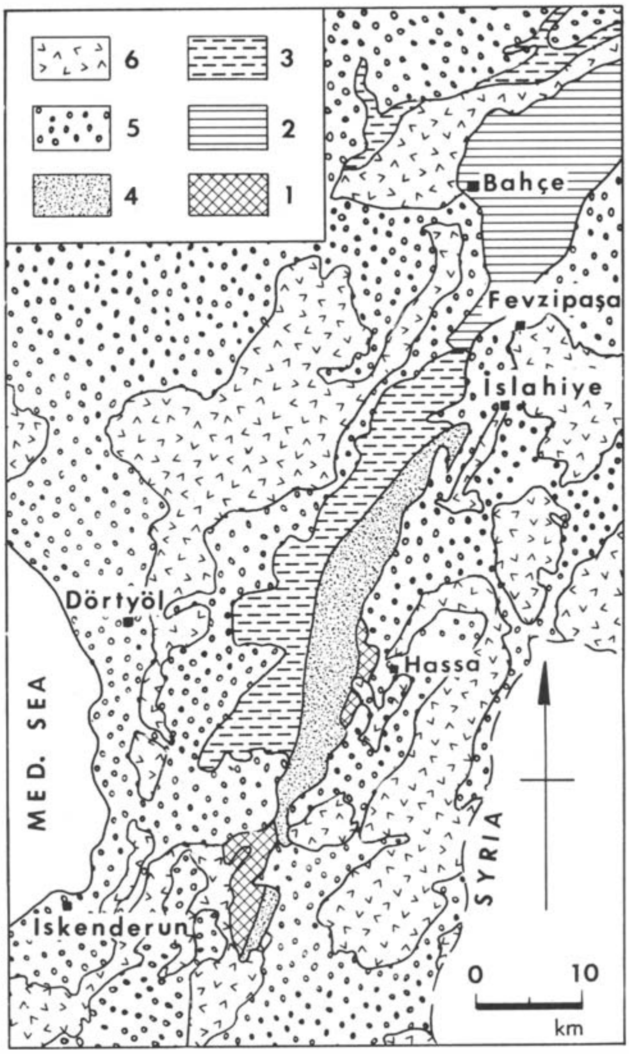

Fig. 7. Generalized geological map of the Amanos Mountains, near Iskenderun, southernmost central Turkey. Geological boundaries after MTA's map of 1962 with minor emendations of Ordovician and Carboniferous strata after Yalçinlar (1965). Key: (1) Cambrian, (2) Ordovician, (3) Undifferentiated Ordovician & Silurian, (4) Carboniferous, (5) Mesozoic – Recent, (6) Basic igneous rocks.

Access to the Kaplandere section, located in the mountains west of Tut, is not particularly easy and in summer 1968 Dr. Necip Tolun kindly accompanied me there. Fossils were found only in the Yerlikaş Formation and included several examples of *Paradoxides* (s. 1.) preserved in both flaggy limestone beds and, to a lesser degree, silty shales. Limestone beds became progressively less common in the higher beds of the formation where brown-weathering shales and siltstones were often heavily micaceous with ripple-marks and worm-burrows. Pink and grey limestones in the lower part of the Yerlikaş Formation were found also in the section near Kuçuk Perveri, a village east of Gölbaşı, though nodular beds were less well developed whilst thicker beds of grey, crystalline limestone were more in evidence, succeeded by sandy, micaceous shales and siltstone bands very like those at Kaplandere. Fossils found in the limestones included the trilobites *Paradoxides* (s.l.) and *Solenopleuropsis.* No evidence of Upper Cambrian or Ordovician strata has been found in the Penbeğli — Tut area.

Border Folds Region

The principal outcrops of Cambrian and Ordovician rocks here form a relatively small but important inlier some 22 km long and up to 5 km wide between Derik and Mardin, near the Syrian border in southeastern Turkey (Fig. 1). These older strata have a moderate regional dip slightly east of south and the inlier is elongated approximately east-west, bounded on the north and northeast by Cretaceous strata, and on the south and west by large spreads of Quaternary volcanics. The oldest rocks of the inlier crop out in the vicinity of Derik, a small town built for the most part on a steep hillside formed by a conspicuous escarpment of white Cretaceous limestones. Immediately and unconformably beneath these limestones is a much older volcanic sequence, the so-called Derik Volcanics, to which a Precambrian or early Cambrian age has been variously ascribed.

The first account of the local geology was given by Tolun & Ternek (1952), who discovered Middle Cambrian trilobites, identified by Stubblefield, and subsequently Tolun (1960: 235—236) established a sequence of eight stratal subdivisions, in ascending order as follows: (1) Felsitic porphyry cut by dykes; (2) Red-brown sandstones with some lava flows, 110 m, (3) Red and green sandstones and conglomerates, 55 m; (4) Black to grey, bedded limestones, 60 m, (5) Green shales, with sandstones and conglomerates, 45 m; (6) Pink and white, well-bedded quartz sandstones, 450 m; (7) Compact limestones and dolomites, 190 m; (8) Schistose sandstones, argillites, and glauconitic sandstones 750 m. The Middle Cambrian trilobites listed earlier were said to occur in subdivision (8). No formal stratigraphic names were introduced at that point by Tolun, but in the same year Kellogg (1960), whose work forms the basis of the sketch-map in Fig. 8, produced the first systematic geological account and map of the area. Kellogg erected the following succession of local lithostratigraphic names: Derik Volcanics (Precambrian?) 488 m+; Telbesmi Formation (Lower? Cambrian) 584 m; Sadan Dolomite 243 m; Sosink Formation 1057 m. Since then various other authors have proposed minor refinements of the stratigraphic nomenclature but none of these accounts was accompanied by a map, and Kellogg's work is followed here as it formed the basis of the writer's own field collecting in the Derik region. Studies on the Cambrian rocks and faunas there are not yet complete, but suggest that the lowest fossiliferous beds comprise limestone horizons in the lowest portion of Kellogg's Sosink Formation, no fossils having been recovered from the underlying Sadan Dolomite as interpreted by him. The fossiliferous, generally flaggy limestone beds are concentrated mainly in the lowest 250 metres of the Sosink Formation and contain trilobite remains which occur sporadically and almost invariably as disarticulated, broken fragments accompanied by small numbers of inarticulate brachiopods. The trilobites consist of paradoxidids (including *Eccaparadoxides*), agnostids (*Peronopsis*), dorypygids (*Dorypyge*) and solenopleurids (*Solenopleuropsis*) together with other, as yet unidentified forms. The thin limestone beds are separated by sandstones which become more dominant higher in the sequence, where massive, cross-bedded strata are common. 560 m below the top of the Sosink Formation there occurs at least one horizon of grey-green shales, from which the ptychopariid(?) *Holasaphus mesopotamicus* Dean (1972) has been described, together with *Peronopsis*, both trilobites indicating a Middle Cambrian age.

The Sosink Fm. is followed by the Bedinan Formation, named for a village 20 km east-southeast of Derik where regressively-weathering Ordovician shales and siltstones floor a valley between marked features of both Cretaceous and Tertiary limestones. An abundant trilobite fauna (see p. 369) indicates an approximately middle Caradoc age and the base of the Bedinan Formation was shown by Kellogg (1960) to rest disconformably on the Sosink Formation, though sometimes obscured by minor faulting. There is no faunal evidence for Ordovician strata

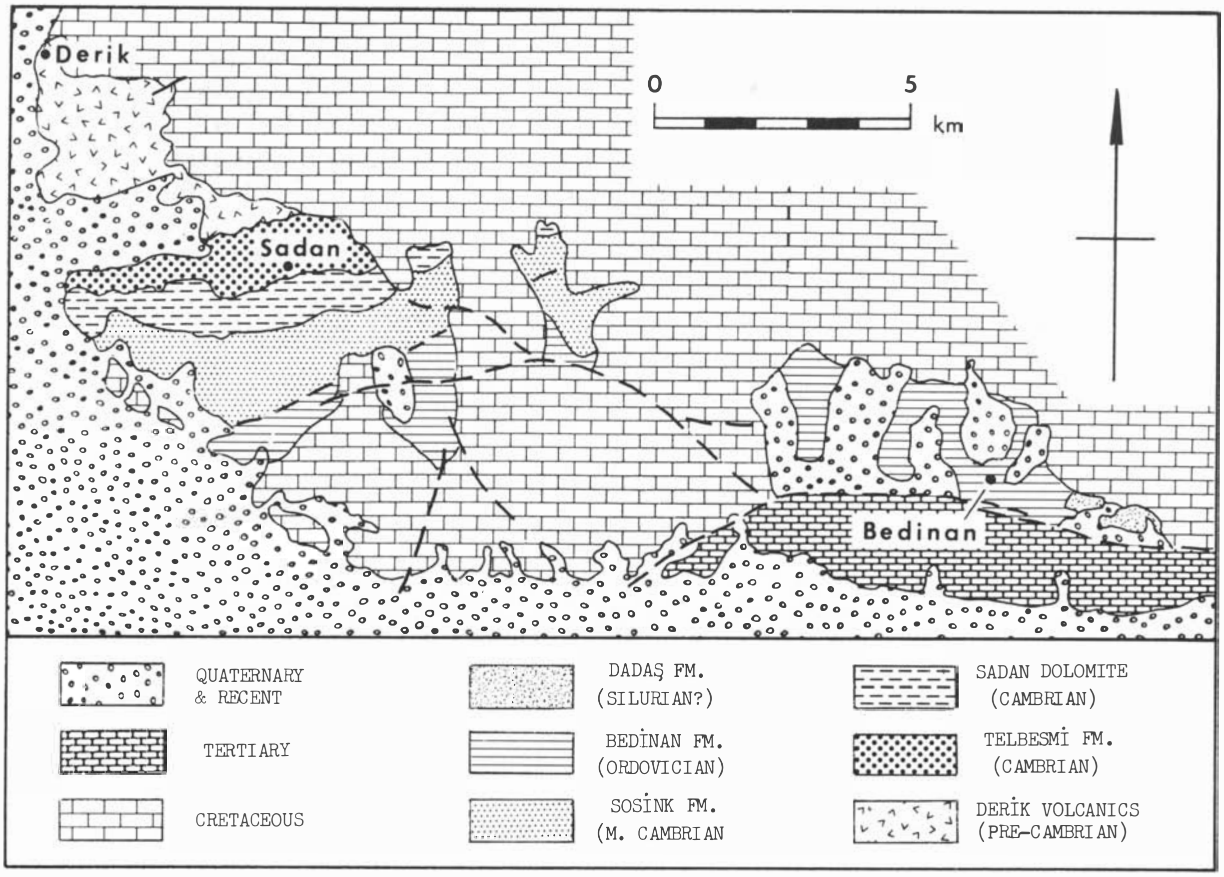

Fig. 8. Geological map of part of the area between Derik and Mardin in south-eastern Turkey. Geological boundaries after Kellogg (1960).

older than middle Caradoc in the Bedinan Formation, nor is there any for Upper Cambrian in the Sosink Formation, the topmost 560 metres of which have yielded no fossils and comprise deposits of shallow-water type including massive, cross-bedded sandstones. The Bedinan Formation also becomes sandier in its higher beds and passes upwards into a series of flaggy and massive, often current-bedded sandstones (Dean, 1967: 88).

Kellogg (1960) regarded these arenaceous strata as "Middle? or Upper? Ordovician", succeeded by the Dadaş Formation, comprising sandstones and shales of "Lower Silurian?" age. On the other hand Schmidt (1965) equated the Bedinan Fm. questionably with the whole of the Ordovician and Silurian, succeeded by a Dadaş Formation of Devonian age. Whatever the merits of these two alternatives, there is as yet no faunal evidence for either, nor can one accept Haude's (1969: 714) correlation table, in which the Bedinan Formation is equated with the whole of the Ordovician and succeeds, though the nature of the boundary is questioned, a Koruk Formation that corresponds to the Upper and most of the Middle Cambrian.

The present interpretation is shown in Fig. 2 and may be summarized as follows. The base of the Cambrian near Derik is conjectural and has not yet been defined faunally, so that it is not known whether the Derik Volcanics are of truly Precambrian or early Cambrian age. Fossils show that the lower half of the Sosink Formation belongs to the Middle Cambrian, and the unfossiliferous upper half may also be of that age. The trilobites of the Bedinian Formation indicate only a middle Caradoc age, so that the disconformity between the Bedinan and Sosink Fms. is a large-scale one and there is no evidence of Upper Cambrian strata, nor of Ordovician strata in the range Tremadoc to early Caradoc Series. The top of the Bedinan Formation may involve yet another disconformity and there is no evidence yet of late Caradoc or Ashgill strata.

Almost 300 km east of Mardin, Altınlı (1966: 54) recorded rocks of Cambrian? age (no formational name used) from the area south of Hakkâri, in the south-eastern corner of Turkey. The rocks were said to comprise thick limestones conformable with overlying "Silurian" [= Ordovician] quartzites – the Giri Formation. The latter was described as being nearly 1000 m thick with subsidiary, lenticular limestones, marls, slates, tuffs and siltstones. The quartzites may show ripple-marks and flow-casts together with the trace fossil *Cruziana,* and Altınlı noted the occurrence of possibly analogous quartzites with *Cruziana* of presumed Ordovician age in Iraq.

RELATIONSHIPS TO OTHER REGIONS

Referring to the regional setting of the Lower Palaeozoic rocks, Kamen-Kaye (1971, Fig. 1) showed most of Turkey as part of a "Turkish–Iranian hinterland", with the southeastern portion of the country, including apparently the Amanos Mountains and the Derik – Mardin district, belonging to a "Middle East folded belt" which extended along the border of Turkey with Syria and Iraq and then veered southeast to run along the northeast coast of the Arabian Gulf. A slightly earlier interpretation by Wolfart (1967) showed that the majority of the Cambro-Ordovician outcrops fall within the limits of his Mobile Shelf, sited between the Nubian – Arabian Platform to the south and the geosynclinal area of southern Russia. Flügel (1971a: 211) has postulated three sedimentary cycles within the Palaeozoic sediments of the Mobile Shelf; the first of these included rocks from Precambrian to Silurian in age but, as noted elsewhere in the present paper, the succession is apparently less continuous than was assumed by Flügel.

Cambrian faunas

Lower Cambrian trilobites are known so far from only part of the Çal Tepe Formation near Beyşehir but as limestone outcrops of similar lithological type are known to extend eastwards along the Taurus at least as far as the Saimbeyli district, where they may be affected by low-grade metamorphism, it is possible that the appropriate faunas may eventually be found to be more widespread. The older Cambrian trilobites of the Beyşehir area are still being collected prior to description but they have been found only in the Black Limestone member and the lower part of the Grey Limestone member of the Çal Tepe Formation (see earlier). Most of the material is fragmentary but includes probable protolenids, suggesting that their affinities lie with late Lower Cambrian faunas elsewhere in the Mediterranean region and western Europe. Middle Cambrian trilobites from the higher parts of the Çal Tepe Formation, as well as those from limestones in the Gölbaşı and Derik – Mardin regions farther east, indicate affinities with the Iberian Peninsula, western Mediterranean, Bohemia and Sardinia (Rasetti, 1972), whilst shale faunas from the Amanos Mountains and the Derik area include, respectively, *Badulesia* and *Holasaphus,* both of which occur in the Middle Cambrian of eastern Canada. The Çal Tepe limestone facies either dies out or has not yet been recognized in the Taurus Mountains east of the Saimbeyli district. It may possibly be represented by part of the Dolomite Formation (Ketin, 1966a: 83) in the Tut – Penbeğli area, east of Gölbaşı (see earlier), where the appropriate strata are succeeded by silty shales of the Yerlikaş Formation, with paradoxidids and other Middle Cambrian trilobites of Mediterranean – Bohemian type, but no Lower Cambrian trilobites have yet been discovered there.

The conspicuous reddish or grey-green, often fine-grained, muddy limestones in the late Lower Cambrian and early Middle Cambrian of the Taurus generally resemble other developments which can be traced over large distances both in the Mediterranean region and beyond. Examples are to be found in southwestern France, the Iberian Peninsula, the Welsh Borderland, eastern Newfoundland and Massachusetts, and contain some of the "predominantly restricted shelf faunas" indicated by Palmer (1972). Within this region protolenids are well represented, a group which, although widely distributed elsewhere in Asia, is apparently not found immediately east of Turkey.

Lithologically the Cambrian rocks of the Tut district and the Amanos are better grouped with those of the adjacent Border Folds Unit than with sequences farther west in the Taurids, and Flügel (1971: 63) has pointed out that Ketin's tectonic units are, in fact, a post-Palaeozoic feature. As far as can be judged from the rather small illustrations, these areas lie slightly within or immediately northwest of the northern margin of the Arabian Shield as interpreted by McKenzie (1970) and McKenzie, Davies & Dolmar (1970). Ketin (1966a: Pl.1) demonstrated the correlation of the sequences within southeastern Turkey but his further attempt to equate them in detail with Cambrian strata in Iran was questioned by Ruttner *et al.* (1968: 33) who accepted only a remote resemblance between the two regions.

A revision of late Lower Cambrian trilobites from the Dead Sea area, some 700 km to the south, by Parnes (1971) emphasized their western Mediterranean, especially Moroccan, affinities. Faunas of this type have not been found farther east, but Sdzuy (1967) demonstrated their extension into southeastern Siberia and other parts of Asia by way of what he considered to be a branch of the Tethys sea. Sdzuy pointed out also that Middle Cambrian trilobite faunas of Mediterranean type apparently did not extend farther east than Turkey. Such an eastern limit would coincide at least approximately with the western limit of Upper Cambrian trilobites of Asiatic type, and one might infer that the two regions were separated by some sort of barrier. On the other hand Upper Cambrian strata have not yet been proved in eastern Turkey, whilst a hint of Mediterranean affinities may be found in the Middle Cambrian trilobites from Tadzhikistan (Lermontova, 1951, Markovsky, 1959: 59), which include *Dorypyge, Corynexochina, Solenopleura, Bailiella* and *Paradoxides?.*

Ordovician faunas

Strata in three areas of Turkey can be assigned with varying degrees of confidence to the Tremadoc Series. The only fossils so far described come from the Taurus Mountains north of Saimbeyli (Özgül, Metin & Dean, 1973), where a slaty argillite sequence, the lower member of the Armutludere Fm. has yielded *Macropyge taurina* Dean, *Symphysurus* and undetermined eocrinoids. The close resemblance of *M. taurina* to *M. sica* Sdzuy (1955: 26) from the Upper Tremadoc of Bavaria suggests a close link with western European faunas, presumably by way of the Sultan Dağ region (see Sdzuy, this paper, p. 356). The pygidia of both *M. taurina* and *M. sica* show a close resemblance to that of the type species, *M. chermi* Stubblefield (*in* Stubblefield & Bulman, 1927) from the Anglo-Welsh Tremadoc, and the further extension of these faunas is indicated by the record of *M.* cf. *chermi* from the Altai region of Russia (Poletaeva *in* Petrunina *et al.,* 1960: 421, Pl. 0–19: 15). Tremadoc faunas, though not yet confirmed in the region of the Taurus between the Sultan Dağ and Saimbeyli, may be expected to occur there, whilst the eastwards extension of the same faunal province is suggested by the presence of *Macropyge* in Afghanistan where Wolfart (1970) has described *M. brevicaudata* in association with, inter al., *Saukia* and *Pilekia.* It would thus appear that in Afghanistan one finds an overlap of the western European type of Tremadoc fauna with elements of more typically North American aspect. A further indication of North American affinities may be found in what Wolfart (1970: 37) described as a new leiostegiid subgenus *Pagodia (Wittekindtia),* a trilobite regarded here as being indistinguishable from *Leiostegium* sensu stricto, a genus that is widespread in the early Ordovician of both eastern and western North America, particularly in carbonate rocks, and is recorded also from argillaceous strata in Argentina (Harrington, 1938: 181, Harrington & Leanza, 1957: 81). *Saukia* and *Pilekia* in the faunas described by Wolfart also suggest North American and Asiatic affinities, whilst an unnamed cranidium (1970, Pl. 9: 1) resembles that of *Euloma* and may represent an additional European element.

No Tremadoc trilobites have been recorded in Turkey west of the Sultan Dağ and the only strata that may possibly be assigned to the series are graptolitic, though their age is not well established.

The Lower Arenig trilobites of the Seydişehir Fm. near Beyşehir occur in only the upper portion of that subdivision but include *Geragnostus,* the calymenaceans *Colpocoryphe* and *Neseuretus,* and asaphids. Such an assemblage is difficult to correlate precisely but is typical of the cold-water faunas that range through much of the Ordovician in the Mediterranean – Bohemian region, northwest Africa, southwestern Europe and the Anglo-Welsh area (Spjeldnaes, 1961: 66). Thence they extend for remarkably long distances to both east (at least as far as southern China) and west (by way of eastern Newfoundland and Florida, which at that time formed part of Gondwanaland, into the Andean region of South America). In southwestern France flysch deposits of Lower Arenig age in the Montagne Noire were shown (Dean, 1967a: 18) to contain three distinct trilobite faunas, in ascending order as follows: *Taihungshania* fauna, *Bathycheilus* fauna and *Hanchungolithus* fauna. A single specimen of *Taihungshania* sp. from an as yet unascertained horizon within the upper half of the Seydişehir Formation (Dean, 1971:19), though inconclusive, suggests that the lowest of the three faunas may be present. Much better evidence for the *Taihungshania* fauna occurs in the Saimbeyli region (see p. 361) where a representative sample of *T. miqueli* and associated genera closely matches material from the western Mediterranean region. The discovery of *T. miqueli* in the Taurus is not unexpected as it forms a link between France and south-western China where Sheng (1958:192–7) reported *T. miqueli* and other species of the genus, but it does offer a noteworthy example of the remarkably constant lithologies and faunas that may be developed over considerable horizontal distances. The Arenig trilobite faunas known so far from the Anamur – Silifke and Mağara districts of the Taurus, like their enclosing strata, show little variety and appear to correspond to part of the Seydişehir Formation.

Near Beyşehir the limestone member of the Sobova Formation marks a conspicuous change in lithology from most of the underlying Seydişehir Formation, and the change from flysch-like sediments to pinkish-grey limestones and calcarenites is accompanied by a corresponding change in fauna from one of Mediterranean type to one in which Baltic elements predominate (Dean.

1973). One might suspect that the faunal change is simply a reflection of the facies change, but this may be an oversimplification as the highest beds of the Seydişehir Formation are marked by a slightly more varied fauna in which the nileid trilobite *Symphysurus* appears, prior to its becoming moderately abundant (though represented by a different species) in the Sobova Formation. *Symphysurus* and *Carolinites* are widespread, almost cosmopolitan genera but others in the type Sobova Formation are best known from the Baltic region and Scandinavia, where they occur most typically in carbonate deposits, though some extend to eastern and western North America; they include *Agerina, Metopolichas, Nileus, Niobe* and *Panderia.* The abundance of Baltoscandian elements at the Sobova Valley tends to overshadow the fact that certain contemporaneous Bohemian genera, rare even in their type area, are present; these include *Pseudopetigurus* and *Protostygina,* and indicate that the Bohemian Basin and south-western Turkey were linked during at least later Arenig times.

Geographically the Sobova faunas are important in that they provide a link between the early Ordovician of the Baltic region and northeast Poland (Bednarczyk, 1968) and the less wellknown faunas from the Middle East and Asia. In the central Elburz Mountains of northern Iran, Gansser & Huber (1962:612–616) recognized a dolomitic and shaly Lower Hezarchal Formation overlain unconformably by quartzites with *Cruziana,* the Upper Hezarchal Fm., which were followed conformably in turn by the Lashkerak Formation, comprising silty shales followed by red silty and nodular limestones that graded into fossiliferous, red, nodular, calcareous marls. The fauna of the last-named strata included trilobites of Baltic type – *Asaphus, Illaenus* and *Panderia?* – and the overall succession recalls that of the Seydişehir and Sobova Formations. The quartzites with *Cruziana* may represent analogous beds in the Amanos Mts. and Hakkâri region of south and southeastern Turkey (see earlier) and were said by Gansser & Huber to resemble material from the Khabour Fm. of northern Iraq.

The Shirgesht Fm. of eastern Iran (Ruttner *et al.,* 1968:22, 33–37) was said to span the Cambro-Ordovician boundary, and fossiliferous limestones 166 m thick in the middle of the formation contain Ordovician trilobites. Genera listed include *Illaenus, Megalaspides* and *Symphysurus,* indicating affinities with early Ordovician Baltic faunas, but the rest are inconclusive and include the essentially North American *Hystricurus,* and the trinucleids *Marrolithus?* and *Ningkianolithus* which, if confirmed, would suggest a later age and affinities with Tethyan faunas to both east and west.

Farther east, in the Karakoram Range, Ordovician trilobites described by Gortani (1934) are of Baltic type and exhibit affinities also with the Upper Arenig fauna found in limestones of the Sobova Formation in the Beyşehir region of the Taurus (Dean, 1973).

The composition of the Ordovician faunas in Yunnan, southwestern China, has been discussed elsewhere (Dean, 1967a:33–34), and suggests affinities with those at Sobova and in other regions of the Middle East. Baltic elements such as asaphids, illaenids, and lichids occur, as does the cystoid *Sinocystis loczyi* Reed, a species with which material from the Iranian fauna of the Elburz Range was compared (Gansser & Huber, 1962:616).

Midway between the Middle East and Yunnan is the central Himalayan region of Spiti, where trilobites and other fossil groups were described from a number of strata by Reed who commented (1912:166) on the "striking American stamp of the whole succession of faunas" and claimed that "the European elements were almost entirely excluded from the marine basin in which these beds were deposited". However, the trilobites, the age of which is uncertain, include asaphids, illaenids and lichids that could be used as evidence of Baltic Lower Ordovician affinities, whilst Reed's illustrations of *Calymene nivalis* Salter show a typical *Neseuretus* s.s., suggesting Tethyan affinities.

At this point attention is drawn to two Turkish Ordovician faunas that are known, so far, from only restricted areas of the Taurids. First, the single much-quoted, but still unillustrated specimen from the Amanos region. Cited originally as "un *Dalmanitina* ordovician, voisin de *D. solitaria* Barr. et *D. incerta* Deslongchamp" (R. & E. Richter *in* Dubertret, 1936:1174), it has been listed more recently by Flügel (1964:13) as *Dalmanitina (Chattiaspis) kegeli* R. & E. Richter, 1927. *Chattiaspis,* now regarded as a genus, was founded on *D. kegeli* from the Andreasteich Quartzite of Germany by Struve (1958:198), and if the latter species is truly present in the Amanos (I have not seen the specimen), it indicates central European affinities, though its age is uncertain and may be post-Arenig. At present it is not known whether the Ordovician strata of the Amanos, which rest disconformably on Middle Cambrian beds (Dean & Krummenacher, 1961), are analogues to those of the Seydişehir Formation or whether they are at least partly younger.

The second fauna is that found by Jean Marcoux near Kemer, by the southwestern coast of Turkey (see p. 357), where *Placoparia,* an illaenid and a cyclopygid occur rarely in a small area of dark mudstones with siliceous concretions. The affinities clearly lie with Bulgaria, Bohemia, and southwestern Europe though the age is not yet satisfactorily established, but a tentative assignment to the Llandeilo Series, or possibly a somewhat older or younger horizon, is not unreasonable. No comparable fauna is known elsewhere in the country.

The trilobites of the Bedinan Formation were shown to exhibit marked Bohemian affinities, and a generalized correlation with the Černín and Chlustina Beds of that area was proposed. No evidence of older Ordovician strata is known from the Derik – Mardin area, where the Bedinan Fm. rests unconformably on Cambrian beds, so that if early Ordovician rocks corresponding to those of the Amanos and Hakkâri regions should be present at depth, they must have been overlapped or overstepped. The Bedinan trilobites show only rare specific identity with Bohemian forms and a few have been differentiated as subspecies, suggesting some degree of separation of the two regions. The trinucleids, as is so often the case, flourished in the muddy environment. One of the most informative trilobites in the Bedinan fauna is the calymenid (synhomalonotinid) *Neseuretus (Neseuretinus) turcicus* Dean which, whether one regards it as a genus or subgenus, probably represented the last stage in the evolution of the long-lived *Neseuretus,* whose career began in the early Arenig and whose distribution was confined to an elongated "strip" of sea extending from southern China through the Mediterranean region and southwestern Europe to South America. So far the distribution of *N. (Neseuretinus)* appears to be distinctive, involving only Turkey and regions farther east, where *Calymene birmanica* Reed, 1906 from Burma and China is assigned to the subgenus (Dean, 1967: 92, 117).

Southwest of Bedinan, at Abba in north Syria (Fig. 1), a deep borehole passed through 2300 m of Mesozoic and Tertiary rocks, 460 m of probably Permian rocks, and was finally terminated without reaching the base of a series of grey-black micaceous shales at least 308 m thick (Sudbury, 1957). The latter beds yielded a new species of graptolite, *Diplograptus spinulosus* Sudbury, together with brachiopods, machaeridians and trilobites identified by Stubblefield as *Colpocoryphe arago* (Rouault) and *Pseudobasilicus* cf. *nobilis* (Barrande); a Llandeilo age was postulated, apparently on the trilobites rather than the graptolitic evidence. Since then Tolun (1960:236) has noted the resemblance of the strata now termed Bedinan Formation to rocks in wells in north Syria, and the two sequences may well belong to the same lithostratigraphic group. *Colpocoryphe arago* (Rouault) is a specific name nowadays confined to the type specimen (lost) of a north French species and the genus ranges from Arenig to Ashgill Series. *Asaphus nobilis* Barrande was made the type of *Opsimasaphus (Nobiliasaphus),* by Přibyl & Vaněk (1965), based on material from Bohemia where *O. (N.) nobilis nobilis* (Barrande) ranges through most of the Caradoc Series, namely the Vinice, Zahořany and Bohdalec Fms. according to Havlíček & Vaněk (1966:52–58) who recorded *O. (N.) nobilis repulsus* Přibyl & Vaněk from only the Dobrotiva Formation of Llandeilo age. There seems to be a case for regarding at least some of these Syrian strata as being of Caradoc age, and even if the Llandeilo evidence is confirmed, it comes from the lowest 30 metres, so that the remainder of the sequence could extend into the Caradoc Series or even higher.

More recently a link between the Bedinan and eastern Asiatic occurrences has been provided by Wolfart's (1970) paper on Afghanistan Ordovician faunas, though his conclusions differ from those presented here. The calymenacean *Pharostoma malestana* Wolfart (1970:82, Pl. 17:2–7) was founded on an incomplete cranidium, the holotype, which differs little if at all from that of *N. (Neseuretinus) turcicus.* Likewise the paratype pygidia, one of which (1970, Pl. 17:7a–c) appears to be a pathological specimen, agree in all essentials with *Neseuretus* but not with *Prionocheilus* [= *Pharostoma*]. The supposed librigena assigned to his species by Wolfart (pl. 17:2) does not resemble any described for *Prionocheilus,* which generally show a comb-like row of distinctive small spines directed ventrally. Wolfart's specimen is probably better interpreted as part of the posterior margin og a pygidial doublure (not a calymenid) which shows some of the free points of the pleural ribs.

Further support for this suggestion may be derived from Pillet & de Lapparent (1969) who described what was stated to be a single Ordovician fauna from two adjacent localities near the "Col de Kherskhan", east central Afghanistan. The trilobites were said to include *Diacalymene birmanica* (Reed, 1915), *Cryptolithus* sp., a cyclopygid eye and fragmentary asaphid pygidia and a hypostoma. The asaphids and cyclopygid are inconclusive, though suggestive of Bohemian and Mediterranean faunas, whilst the specimens of *Cryptolithus* may, perhaps, be compared with *C.? bedinanensis* Dean (1967:104) of Caradoc age in Turkey. Pillet & de Lapparent's calymenid material, though distorted, shows the long, convex preglabellar field of *Neseuretus (Neseuretinus)*; this feature is not found in *Diacalymene,* which lacks a preglabellar field but possesses a thick, reflexed anterior border and has the 2p glabellar lobes almost in contact with the corresponding swollen portion of the fixigenae. The pygidia from the Col de Kherskhan are of generalized calymenid type and the axis has a funnel-shaped outline, a feature seen often in *Neseuretus* (s.l.) but not in *Diacalymene.*

Earlier reviews of Ordovician trilobite distribution in the Mediterranean and adjacent regions (Whittington, 1966, Dean, 1967a) took account only of present-day geography, whilst a more recent account (Whittington & Hughes, 1972) sought to explain Ordovician palaeogeography in terms of trilobite faunal provinces and plate tectonics. A few comments are now given with reference to the Tethyan region, which coincides largely with Whittington & Hughes' interpretation of the "Selenopeltis Province", a term introduced earlier by Whittington (1966). The latter province in Arenig – Llanvirn times was shown to cover southern Europe and Iberia, terminating to the east in Turkey (beyond which point south-east Asia was regarded as having undergone considerable clockwise rotation) and to the west in Florida. Such an interpretation does not take account of the records of *Neseuretus* and *Taihungshania* in Yunnan, southwestern China, and the present account prefers to regard the southern French, southern Turkish and Yunnan early Ordovician faunas as being of cold-water type, forming parts of an elongated continuous province, though both versions must be regarded as provisional. In South America *Neseuretus* occurs in Argentina and Bolivia (Harrington & Leanza, 1957:221), and recently Prof. A.J. Boucot sent me specimens collected by him in Peru, where the specimens occur in dark-grey mudstones very similar to rocks found commonly in the Mediterranean region, suggesting that Tethyan faunas continued around the margin of Gondwanaland as far as Argentina, where they must have passed into the Asaphopsis province of Whittington & Hughes. Although it is generally true (Whittington, 1966:698) that Ordovician trilobites show no unequivocal restriction to a particular rock type, this is not always the case at generic level. The widespread Tethyan genera *Neseuretus* and *Colpocoryphe* may represent calymenaceans which became adapted to a cold-water environment very early in the Ordovician, as neither has yet been satisfactorily documented from carbonate deposits of warm-water type. The same may also be true of certain asaphaceans such as *Taihungshania,* though generic similarities may be obscured by difficulties of comparing specimens from platform limestones with compressed material in shales and mudstones.

The Baltic region in the Arenig-Llanvirn is shown by Whittington & Hughes (1972:245, Fig. 3) as separated from southern Europe by a "mid-European sea" which, according to them, "was the barrier to faunal migrations between the provinces". Such an interpretation omits the Baltic faunas of the Sobova Fm. which immediately succeed the Tethyan faunas of the Seydişehir Fm. (see earlier). The relatively sharp lithological change from Seydişehir to Sobova Formations must have involved, inter al., a rise in water temperature and was more than a local phenomenon, as is suggested by the Lashkerak Formation of Iran. These early Ordovician faunas of Baltic type in Turkey and Iran may have been linked with those of the Karakorum and south-east Asia, as noted earlier, but the relationships are not clear and the occurrences are not shown on Whittington & Hughes' reconstruction.

All the palaeogeographic maps proposed by Whittington & Hughes for the various Ordovician series show the Arabian Shield and a large neighbouring area of Iran connected firmly to Africa, thus forming part of Gondwanaland and being separated from southern Europe by a Proto-Tethys sea. This is difficult to reconcile with the distribution of Iranian rocks and trilobites noted earlier, which seem to form a link between Turkey and regions farther east. It also takes no account of the appreciable succession of fossiliferous Llandeilo or Caradoc strata in the subsurface of north Syria (see earlier) which must surely be linked closely with the Bedinan Formation in southeastern Turkey. Still farther south, in Jordan, Wolfart's (*in*Bender, 1968:56) faunal list from the "Nautiloideen-Sandsteine", said to be of Llandovery age, includes three representatives of the homalonotid *Brongniartella, B. benderi, B.* aff. *platynota* (Dalman) and *B.* aff. *edgelli* (Salter). The first of these is a *nomen nudum* whilst the other two are likened to species from, respectively, the Ashgill Series of Scandinavia and western Europe, and the Caradoc Series of South Shropshire. Nowhere else is *Brongniartella* recorded from post-Ordovician strata, but the affinities of the genus lie mainly with European faunas, and it occurs also in the Caradoc Series (Bedinan Fm.) of southeastern Turkey (Dean, 1967:118). At the western end of the Mediterranean, the close relationship, even at specific level, of Arenig trilobites in southwestern France (Dean, 1966) and the Anti-Atlas of Morocco (Destombes, 1972:27, 28) indicates the close proximity of the two areas and argues against their being separated by a barrier in the form of the Proto-Tethys.

Cowie's (1971, Figs. 2, 4) reconstruction of Lower Cambrian faunal provinces prior to the break-up of Gondwanaland showed the western end of the Mediterranean with the Iberian Peninsula in appropriately close proximity to both eastern Newfoundland and north-west Africa, a position equally suitable to account for the distribution of similar Lower Ordovician trilobites in France and Morocco (see earlier). At the other end of the Mediterranean, shown as part of the site of a "Tethys Sea" which widens considerably eastwards, Cowie included as part of Gondwanaland that portion of Arabia southwest of a line joining the Arabian Gulf with the southeastern Mediterranean coast (approximately Wolfart's (1972) boundary of Arabian Shield and adjacent Mobile Shelf), and grouped all areas to the north of this line with the region along the north side of a "Tethys Sea". If such a situation were to hold good for part of the Ordovician (by no means a foregone conclusion), then one could group the Turkish Cambrian and Ordovician rocks together with those of Syria, Jordan and Israel as shelf-type deposits along the northern edge of the "Tethys Sea". This explains the faunal links with the western Mediterranean and Afghanistan, but does not account satisfactorily for the southern edge of the same sea and is difficult to reconcile with Rigo de Righi & Cortesini's (1964:1913) assertion that the Derik – Mardin area's Lower Palaeozoic clastics represent detritus derived from a southerly source, the Arabian Shield.

The close correspondence of faunas to both north and south of the Mediterranean at its western end renders it difficult to accept Whittington & Hughes' concept of a wide Ordovician Proto-Tethys, separating Gondwanaland from Laurasia and acting as a barrier to trilobite migration. At the eastern end of the Mediterranean it is similarly difficult to visualize a Tethyan barrier of equal or greater dimensions separating the Mobile Shelf of the Arabian Shield from the Taurus and associated regions. The evidence seems rather to favour a continuous shelf area linking the two and acting as a repository for a few thousands of metres (the published thickness of 3200 m for the Cambrian of the Derik district (Beer, 1966) includes volcanics which may be at least in part Precambrian) of mostly shallow-water sediments in which disconformities or faunal breaks of sometimes regional extent may be discerned but which was insufficiently deep to act as an authenticated barrier to faunal migration.

ADDENDUM

Since the final draft of this paper was completed, a recent account of the mountainous Sultan Dağ region by Haude (1972) has become available to me. It contains two faunal lists made up of trilobites identified by K. Sdzuy. The first, from the Flaserkalk and of Middle Cambrian age, contains paradoxidids, solenopleurids and corynexochids typical of the Mediterranean – Bohemian region and corresponds broadly to that from the high portion of the Çal Tepe Formation (Dean & Monod, 1970). The second list, from the Kuruderebaşı-Schiefer, is of Tremadoc age and Bohemian – Bavarian type and includes *Macropyge.* It corresponds to the fauna noted by Prof. Sdzuy earlier in the present paper.

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Ordovician trilobite assemblages of Kazakhstan

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In the Ordovician of Kazakhstan facies control seems to have played an important role in the distribution of trilobite assemblages on the sea-floor. Several facies zones, mainly controlled by the depth of the sea and distance from the coast, can be distinguished, each containing a distinctive assemblage of trilobites.

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The relationship between extant and extinct marine faunal assemblages and the depositional environment appears to be well known and has been considered by several writers. The author (Apollonov, 1968) has briefly discussed the problem and treated the Ordovician zonal trilobite assemblages of Kazakhstan separately for carbonate and terrigenous sequences. New data indicate that in the Ordovician succession of Kazakhstan with its variety of facies types the relationship between trilobite assemblages and type of sediment is more complicated than previously thought.

This contribution is intended as a brief review of the relation of Ordovician trilobite assemblages to types of lithofacies in Kazakhstan.

The Tremadocian trilobites of Kazakhstan are still poorly studied. They are mainly known from faunal lists in Borukaev (1955) and Nikitin (1972), and from the monograph 'Geology of USSR', Vol. 20, Central Kazakhstan (1972). The collections from Kendyktas and Kirgiz Alatau have been described by Lisogor (1961, 1962); those from the Maly Karatau Range are being studied by G.H. Ergaliev, and those from northeastern Kazakhstan and the Chingiz Range by N.K. Ivshin and the author.

At present four different lithofacies are known to contain Tremadocian faunas:

(1) Grey, yellow, and white thick-bedded algal limestones and dolomites, with abundant

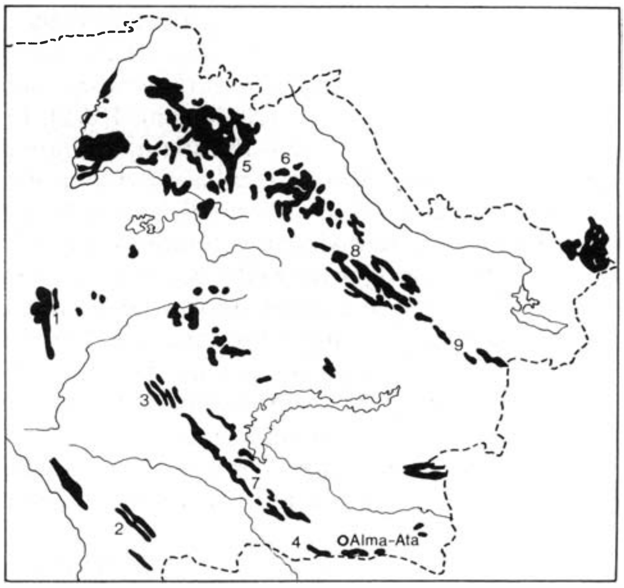

Fig. 1. Distribution of Ordovician rocks (black) in Kazakhstan. *1.* Ulutau Range. *2.* Karatau Range. *3.* Betpak-Dala Desert. *4.* Kendyktas Mountain. *5.* Selety River. *6.* The district of Olenty and Shiderty Rivers. *7.* Chu-Ili Mountains. *8.* Chingiz Range. *9.* Tarbagatay Range.

gastropods and cephalopods but without trilobites, form a thick formation in the Maly Karatau Range. These deposits resemble the Lower Ordovician (Canadian) carbonate sequence of North America and the Arctic regions. They seem to have been formed in a shallow, warm sea.

(2) Black to dark grey thin-bedded limestones containing *Niobe, Euloma, Rhadinopleura, Geragnostus, Macropyge, Hysterolenus, Harpides,* and other trilobites form a formation in the Aksay block in the northeastern Maly Karatau Range. They were probably deposited in a relatively deep, open sea, the bottom of which may have corresponded to the slope of the Maly Karatau massif.

In the Ulutau Range similar limestones with *Rhadinopleura* and *Ceratopyge* alternate with graptolitic shales. Limestone beds of this general type in the Akzhar River district, northeastern Kazakhstan, have yielded *Niobe, Asaphellus, Apatokephalus, Parabolinella, Harpides,* and *Harpes* (s.l.) (Apollonov *et al.,* 1963). From similar limestones in a tufaceous-terrigenous formation of the Kirgiz Range, Lisogor (1972) recorded *Geragnostus, Leiagnostus, Trinodus, Pseudagnostus, Shumardia, Harpides, Niobe, Rhadinopleura,* and other trilobites. Both the assemblage with *Harpides, Bicornipyge,* and *Hysterolenus* from siltstones in Kendyktas (Lisogor, 1961) and that with *Bienvillia* and *Hysterolenus* (found together with *Dictyonema ex gr. flabelliforme*) in the Satpak Stage of the district of Olenty-Shiderty Rivers were probably deposited in an open sea area with similar palaeogeographic conditions.

(3) Pink to white, usually detrital (calcarenitic) limestones, frequently abounding in skeletal remains, contain a rich trilobite assemblage including *Niobe, Euloma, Harpides, Loganopeltis, Ceratopyge,* and the brachiopods *Clarkella, Nanorthis,* and *Tritoechia.* This assemblage characterizes shallow-water carbonate deposits in northeastern Kazakhstan (the district of Olenty-Shiderty Rivers). A similar assemblage has been encountered in the Chingiz Range (in the vicinity of the Mamat Hill) and in the Kendyktas Mountains of southern Kazakhstan.

(4) Dark graptolitic shale of Tremadocian age in the Ulutau and Djebagly Mountains appears to have been deposited in deeper water than any of the other Tremadocian deposits known in Kazakhstan. No trilobites have been found in this shale.

The trilobites mentioned belong to the Upper Tremadocian except for those from Satpak (Lower Tremadocian according to N.K. Ivshin). G.H. Ergaliev has discovered a Lower Tremadocian trilobite assemblage in the Maly Karatau Range, but its taxonomic content is as yet not clear.

The known Arenigian trilobite fauna of Kazakhstan is small and poorly studied. Arenigian deposits are usually represented by thin-bedded siltstones with graptolites. Rare cyclopygids and *Shumardia* have been found in these sediments in the district of Akzhar River and in the Betpak Dala Desert. The other type of Arenigian deposits is represented by thick-bedded, mostly grey limestones. In the Maly Karatau Range, beds of Arenigian age form a part of the thick Tamdy limestone-dolomite succession of Cambrian and Ordovician age. *Hystricurus, Bathyuriscops,* and numerous illaenids have been found there by Weber (1948) and K.A. Lisogor. In other districts limestones with extremely rare trilobites occur as lenses and beds within terrigenous and volcanic formations. From limestones lenses of the Naiman Formation in the Chingiz Range, *Pliomerops* has been identified by N.K. Ivshin, who also recorded *Tesselecauda, Apatokephalus,* and some new genera from strongly arenaceous limestones of the Saryshoky Formation in the same range. In limestones at the base of the Akzhal Formation in Chu-Ili Mountains, the author found *Carolinites, Bumastides, Bathyuriscops,* and *Pliomerops,* genera common in the younger deposits of Karakanian age (Nedovizin, 1961). From limestones within volcanogenous deposits of Bolgozha Formation, Chu-Ili Mountains, numerous poorly preserved asaphids have been collected, but only *Kayseraspis* has been identified so far.

The Karakan Stage of Kazakhstan can be roughly correlated with the Llanvirnian of the British sequence. Karakanian trilobites in Kazakhstan are abundant and have been described by Weber (1948), Lisogor (in Keller & Lisogor, 1954), Chugaeva (1958), and the author. Thin-bedded silts and fine-grained sands were deposited in Kazakhstan over extensive areas both during the Arenigian and the Karakanian. In other areas, however, rather varied facies conditions stimulated the development of a diverse Karakanian trilobite fauna.

In the Karakan Stage of Kazakhstan, the following main types of lithofacies with associated trilobite assemblages can be distinguished:

(1) Greenish calcareous sandstone containing undescribed asaphids, *Lonchodomas, Eorobergia,* and articulate brachiopods is known from a single locality at Anderkenyn-Akchoku, Chu-Ili Mountains.

(2) Grey and white, massive, coarsely crystalline, rarely aphanitic limestones contain a characteristic assemblage of trilobites including *Bathyuriscops, Bumastides, 'Pseudosphaerexochus', Ectenonotus, Pseudomera, Colobinion, Cybelurus, Amphilichas,* and numerous illaenids. These deposits are particularly well represented in the Betpak-Dala Desert and Chu-Ili Mountains.

Trilobites belonging to this assemblage have also been found in several districts of northern and northeastern Kazakhstan (Ishim, Akzhar, Shiderty River, Chingiz and Tien-Shan Ranges). From the top of the Tamdy Limestone Group of the Maly Karatau Range, probably of Llanvirnian or Late Arenigian age, Weber (1948) described *Hystricurus, Apatokephalus (=Eorobergia), Lyralichas, Glaphurina, 'Pseudosphaerexochus',* and *Illaenus.* Trilobites are associated with articulate and inarticulate brachiopods, nautiloids, gastropods, ostracodes, crinoids, and rare conularids.

(3) Yellowish or greenish, often nodular, argillaceous limestones are occasionally developed at the base or top of the limestones of Karakanian type. Such limestones also form isolated beds or lenses within clastic deposits. In this rock, numerous articulate brachiopods (with characteristic *Aporthophyla kazakhstanica*) and trilobites (undescribed asaphids and illaenids) are not uncommon. Such limestones have been recorded from many localities in the Anderkenyn-Akchoku district, Chu-Ili Mountains.

(4) Greenish siltstones and fine-grained, thin-bedded sandstones of Karakanian age with *Ampyxinella, Lisogorites, Telephina, Bulbaspis, Mendolaspis, Raphiophorus, Shumardia, Selenoharpes, Trinodus, Endymionia, Niobe, 'Symphysurus',* and new raphiophorid and remopleuridid genera are known from Chu-Ili Mountains.

Black, thin-bedded limestone, with *Endymionia, Lonchodomas,* and graptolites, discovered near the Kiik railway station, northwestern Balkhash region, was probably deposited in closely related conditions.

(5) Graptolitic shales with rare cyclopygids are developed in the Betpak-Dala Desert and Selety district. The trilobites and graptolites are associated with rare inarticulate brachiopods.

The Tselinograd and Erkebidaik Stages of Kazakhstan correspond roughly to the Llandeilian and Early Caradocian of the British sequence. Trilobites of this age have been found at some localities of the Ishim district (the villages of Kuprijanovka and Stavropolskoe), Stepnyak district (Lidievka village), and from the Chingiz Range. Some of the trilobites have been described by Koroleva (1961, 1964, 1967).

In the Ishim and Stepnyak districts, trilobites are known exclusively from greenish siltstones and thin-bedded, fine-grained sandstones. These beds are characterized by an assemblage including *Ampyxinella, Telephina, Trigonoaspis,* a new genus related to *Robergia,* and a new raphiophorid genus with three thoracic segments. The assemblage is associated with graptolites and small inarticulate brachiopods. In some districts, with finer grained sediments, rich in graptolites, the trilobites are represented mainly by cyclopygids, agnostids, *Shumardia, Dionide, Dindymene,* and other small forms with a very thin carapace.

Tselinogradian and Erkebidaikian trilobites are also known at some levels in the Bestamak Limestone, exposed along the Chagan River, Chingiz Range (Nikitin, 1960, 1972). Here a transgressive sequence begins with a bed of arkosic conglomerate (*a*), succeeded by calcareous arkose (*b*), and limestone (*c*) with rare *Basilicus*-like asaphids and large, flat articulate brachiopods. The sequence continues with an unfossiliferous algal limestone (*d*), more than 150 m thick, followed by a yellowish argillaceous limestone (*e*), 10 to 15 m thick and containing numerous asaphids, illaenids, and brachiopods. The top of the limestone formation is formed by a member (*f*) consisting of black and dark grey limestones, coarse-grained and thick-bedded (individual beds 10 to 15 cm) at the base merging upwards to fine-grained, thin-bedded (individual beds 1 to 2 cm) limestone at the top. The limestone formation is succeeded by black graptolitic shales (*g*).

The thick-bedded limestones (lower part of the division *f*) have yielded numerous trilobites (more than 21 genera), including *Illaenus, Sphaerexochus sp., Lonchodomas, Remopleurides,* and *Hadromeros.* These genera normally characterize carbonate mound (bioherm?) deposits. *Telephina, Nileus,* and other genera occur in carbonate mound deposits as well as in siltstones, where they are mostly accompanied by graptolites. *Ampyxinella, Trigonaspis,* a new genus related to *Robergia,* and a new raphiophorid genus with three thoracic segments are rare in limestones but numerous in siltstones. The fauna of the limestone includes also nautiloids, hyolithids, rare gastropods, and crinoids. Numerous spiculae and inarticulate brachiopods were obtained by dissolving the limestone. L.E. Popov has discovered unique Radiolaria which are being described by B.M. Nazarov (MS).

In the uppermost, thin-bedded portion of the limestone sequence (upper part of the division *f*) numerous graptolites appear. The deposition of these beds probably took place in a deeper water than that of the thick-bedded lower part of the member. The assemblage of trilobites changes markedly. Small forms and two endemic raphiophorid genera (one with three thoracic segments is characteristic for siltstones of the Karakan, Tselinograd, and Erkebidaik Stages) strongly predominate. *Telephina, Ampyxinella,* and odontopleurids become abundant. Higher up in the sequence (division *g*), in the graptolitic shales with *Nemagraptus* *gracilis,* 10 to 15 m above the top of the limestone formation, trilobites are represented by rare *Telephina* and a new genus related to *Robergia.*

In argillaceous limestones, Tselinogradian and Erkebidaikian trilobites are known from localities near Kupriyanovka village, Ishim River, near Lake Amanbaysor, and at the base of the Lidievka sequence, Stepnyak district. Large *Basilicus*-like and *Asaphus*-like asaphids, illaenids, and other forms are characteristic here. These faunules are so far undescribed.

The Anderkenyn and Dulankara Stages of Kazakhstan are rough equivalents to the Middle and Upper Caradocian of the British classification. Rocks of Anderkenian and Dulankaran age, with distinctive assemblages of trilobites partly described by Weber (1948) and Chugaeva (1958), occur in some districts of the Chu-Ili Mountains (Dulankara, Anderkenyn-Akchoku, Sarytuma, Buldukbai-Akchoku). Similar assemblages are known in other districts of northern, northeastern, eastern, and southern Kazakhstan. Trilobites of this age are among the most widespread in the territory of Kazakhstan. The following lithofacies types with associated trilobites assemblages can be distinguished.

(1) Coarse-grained sandstones, containing only one trilobite, *Isotelus romanovsky,* as well as pelecypods, gastropods and remains of seaweeds, have been distinguished at the base of the Anderken Formation in a few localities in the Chu-Ili Mountains.

(2) Medium- to fine-grained sandstones with *Basilicus* and other asaphids, *Lonchodomas, Dulanaspis,* and other trilobites are known at the base of the Anderken Formation and contemporaneous deposits in a few regions of Kazakhstan (Apollonov, 1968). In the Chu-Ili Mountains they overlie the beds with *Isotelus romanovsky.* These beds have also yielded occasional articulate brachiopods.

(3) Medium- to coarse-grained sandstones with *Isotelus, Dulanaspis, Pliomerina,* and *Remopleurides,* in places associated with accumulations of large articulate brachiopods, are characteristic in many sections of the Dulankara Formation in Chu-Ili Mountains (Chugaeva, 1958) and in contemporaneous deposits of the Chingiz Range and Dzhebagly Mountains. In many cases these beds directly overlie conglomerates.

(4) Yellow or greenish argillaceous limestones with numerous brachiopods and trilobites occur frequently at the base and upon the top of carbonate mounds (bioherms?) or as separate lenses or beds. The limestone contains characteristic asaphids (*Isotelus, Homotelus, Parabasilicus,* and others), *Remopleurides, Illaenus, Pliomerina,* and other genera associated with bryozoans, crinoids, and ostracodes.

(5) Light (pink, white, grey) coarsely crystalline limestones form thick (up to 800 m) carbonate mounds, possibly of biohermal origin. They are common in many regions of Kazakhstan, particularly in volcanic areas. In the limestone, trilobites are varied and in places numerous, such as *Illaenus, Stenopareia, Bumastus, Sphaerexochus, Holotrachelus, Amphilichas,* and others. Scutellids (*'Bronteus'*), *Hadromeros,* and *Pliomerina* are common. The trilobites are associated with numerous articulate brachiopods, crinoids, nautiloids, and tabulate corals. In thick limestone sequences of northeastern Kazakhstan, the lowest part of the succession may be represented by dark, massive limestones, often abounding in pyrite, with abnormal assemblages consisting exclusively of small *Pliomerina* and illaenids, associated with small gastropods and pelecypods.

(6) Siltstones and fine-grained sandstones with *Ampyxinella, Telephina, Cyclopyge, Symphysops, Birmanites,* raphiophorids, and endemic remopleuridids related to *Bobergia.* This assemblage is associated with graptolites, occasionally numerous, and rare nautiloids. Articulate brachiopods are rare and represented mainly by small, flat plectambonitaceans with a very thin shell. This assemblage is known from the Dulankara Formation of the Chu-Ili Mountains.

Ashgillian trilobites from Kazakhstan were first recorded by Apollonov (1968). Lower and Middle Ashgillian deposits contain mainly graptolites, and trilobites are comparatively rare. Almost all sufficiently well-preserved Ashgillian trilobites of Kazakhstan have been described by the author (Apollonov, 1974). A few characteristic assemblages can be distinguished.

(1) An assemblage, which includes *Ampyxinella, Microparia, Tretaspis,* and *Remopleurides* has been discovered in black graptolitic shales near Akdombak Hill, Chingiz Range. Graptolites are numerous.

(2) More than 20 species of the genera *Trinodus, Telephina, Remopleurides, Cyclopyge, Microparia, Psilacella, Symphysops, Warburgaspis, Phillipsinella, Hadromeros, Hammatocnemis, Cyphoniscus, Panderia, Stenopareia,* and others have been found in yellowish and pink, sandy, organodetritic (calcarenitic) limestones at Zharyk near the Shiderty River. Elements of this assemblage (*Ovalocephalus, Hammatocnemis*) are known in the Stepnyak district in sandstones and argillaceous limestones. A related assemblage with *Symphysops* and others is represented in light grey fine-grained sandstones of the Tarbagatay Range.

(3) Various poorly preserved trilobites *'Cybele', Pliomerina, Remopleurides, Opsimasaphus, Isotelus, Homotelus, Holotrachelus, Illaenus, Bumastus, Encrinurus, Dicranopeltis,*

Hadromeros, 'Bronteus', and others) are known from argillaceous limestones and calcareous shale exposed near Tolen and Bakanas Rivers close to Akdombak Hill, Chingiz Range. Tabulate corals and brachiopods have also been found in limestones. The discovery of the pentameracean brachiopod *Holorhynchus* at this level is important. The shales contain graptolites.

(4) *Illaenus, Bumastus, Pliomerina,* and *Hadromeros* occur in a carbonate mound (biohermal?) near the town of Maykain, but they are comparatively rare. The trilobites are associated with numerous tabulate corals and brachiopods, including *Holorhynchus.*

(5) Rare odontopleurids have been found in the Chokpar Shales north of Dulankara, Chu-Ili Mointains, together with numerous graptolites, mainly *Rectograptus.*

Three Upper Ashgillian trilobite assemblages, related to distinctive lithofacies, can be distinguished.

(1) *Dalmanitina* (represented by two species) and *Platycoryphe* have been found in a few localities in the Chu-Ili Mountains. The rock is a black, bedded aphanitic limestone and argillaceous limestone. The associated fauna consists of rare articulate brachiopods and comparatively numerous graptolites, including *Glyptograptus persculptus.* In the Chu-Ili Mountains and in a few districts of the Chingiz Range (Mizek, Akdombak), *Dalmanitina* has been found also in siltstones and fine-grained sandstones, occasionally accompanied by *Otarion* and rare odontopleurids. Fine-grained sandstones in the Chu-Ili Mountains have yielded various brachiopods, including *Hirnantia.*

(2) *Warburgaspis* and illaenids occur in arenaceous organodetritic (calcarenitic) limestones together with varied and very numerous shelly organisms, such as brachiopods, nautiloids, gastropods, and crinoids. This limestone replaces the *Dalmanitina* Limestone spatially or is interbedded with it in the Chu-Ili Mountains.

(3) *Holotrachelus,* lichids, and illaenids have been reported by Chugaeva (1958) from a carbonate mound, possibly biohermic (Ul'kuntas Limestone). In this limestone tabulate corals predominate.

A comparison of various indicators of depositional environment in Ordovician sediments with those of recent shelf deposits (Nalivkin, 1956) makes it possible to draw some conclusions as regards the depositional conditions of various facial zones in the shelf region of an idealized Middle and Late Ordovician basin of Palaeokazakhstan. It also gives some clues as to the environment in which trilobites lived.

The reconstruction is based on analysis of numerous Ordovician transgressive sequences in certain regions of Kazakhstan. In each sequence a regularity in the succession of distinctive types of sediment can be observed. The base of a sequence is normally formed by conglomerates and gravelites. These are succeeded by sandstones, siltstones, and limestones. The limestones are argillaceous to a varying degree at the base and on the top. Above the limestones follows a sequence of siltstones and argillites. The rule of Golovkinsky—Walther permits the assumption that within a transgressive sequence various types of sediment were deposited roughly in the same order also relative to the coast.

The zone of pebbles was formed at or close to the beach. The sand zone probably reached down to some tens of meters. According to Nalivkin (1956 : 231), in normal marine basins the depth of deposition of the sand zone rarely exceeds 28 m. In Kazakhstan this zone is characerized by asaphids. In shallowest water, forms with a heavy carapace of *Isotelus romanovsky* type are common, associated with pelecypods and gastropods. In the deeper part of the sand

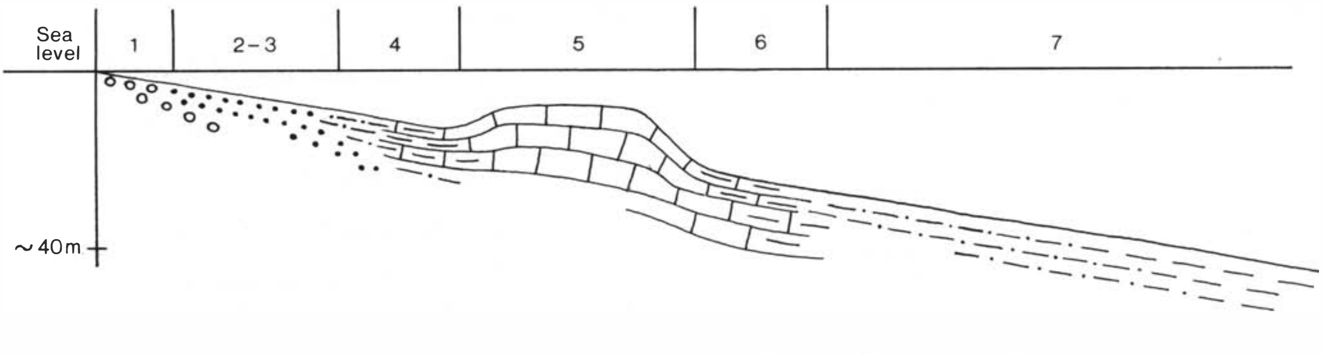

Fig. 2. Tentative reconstruction of facies belts in the Ordovician sea of Palaeokazakhstan relative to the coast and the depth of the sea. *1.* The zone of pebbles. *2–3* (1–3). The zone of sand. *4.* (4). Argillaceous carbonate mud. *5.* (5). Carbonate mound (bioherm?). *6.* Argillaceous carbonate mud like that of *4.* *7* (6). Silt, carbonate mud and clay. Numbers in brackets correspond to the Anderkenian and Dulankaran facies belts described in the text (p. 8–11).

zone large *Basilicus* and other asaphids occur, accompanied by *Dulanaspis, Lonchodomas,* and rare articulate brachiopods. In the sand zone also sand banks were developed with accumulations of transported trilobite and brachiopod remains. Farther from the coast, calcareous silt and argillaceous carbonate mud were deposited. Ordovician sediments deposited in this zone are represented by calcareous siltstone and argillaceous limestone. Asaphids, illaenids, raphiophorids, and numerous articulate brachiopods characterize this zone.

Still farther from the coast carbonate mounds (bioherms?) were formed. The depth of deposition of the mounds was probably some few to some tens of metres and may have been comparable to that of shallow-water sand zone or the zone of argillaceous carbonate mud. The fauna is diverse and rich, and is associated with calcareous algae. Convex trilobites are especially characteristic.

The zone of silt and/or argillaceous carbonate mud either continues seawards from the zone of carbonate mounds or follows directly the zone of sand. The assemblage with *Ampyxinella, Telephina, Trigonaspis,* endemic remopleuridids, and raphiophorids probably existed in the deepest part of the zone, possibly at a depth up to 40 m.

In still deeper parts of the basin (up to hundreds of metres) pure clays were deposited. Rare cyclopygids and *Telephina* were the only trilobites who inhabited this bottom. They are found associated with graptolites, which alone are present in sediments deposited in still greater depths.

The material presented seems to testify that facies control played an important role in distribution of trilobite assemblages on the sea-bottom. This permits the introduction of the concept of *arenophilous* (existed mainly on sand bottoms), *calcarophilous* (confined mostly to carbonate banks and mounds, including bioherms and reefs), and *argillophilous* (existed mainly on silty, muddy and clay bottoms) forms and communities, keeping in mind the intermediate forms and communities also existed.

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Adaptive radiation, trilobite paleoecology, and extinction, Ptychaspidid Biomere, Late Cambrian of Oklahoma

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Adaptive radiation, consolidation, and intraniche evolution – specialization are the three stages in the development of a stable shelf community of trilobites during the latest Cambrian in Oklahoma. Each stage is recognized by the morphologic variability and stratigraphic ranges of the trilobites. Shallow burrowing, bottom crawling, and epiphytic modes of life are interpreted from morphological characteristics of these trilobites. The encroachment of cool polar water onto the North American cratonic shelf populated by diverse but specialized trilobites is suggested as a possible event that triggered a fourth evolutionary pulse and ultimately the abrupt mass extinction of these trilobites.

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Late Cambrian non-agnostid trilobites of the North American cratonic shelf existed within a framework of mega-evolutionary biostratigraphic units called biomeres (Palmer, 1965a). Each biomere is characterized by its abrupt, non-evolutionary boundaries, its unique family assemblage, and by the four stages of evolution experienced by the trilobites (Stitt, 1971a). The objectives of this paper are to:

(1) Review briefly the characteristics of biomeres.

(2) Discuss the evolution and development of the trilobite community of the Ptychaspidid Biomere.

(3) Suggest some generalized living habits for these trilobites based mostly on considerations of their cephalon morphology.

(4) Explore a possible cause for the abrupt extinction of the trilobites of the Ptychaspidid Biomere.

BIOMERES

The characteristics of biomeres, as summarized by Palmer (1965a) and as observed personally in the field, are as follows (see also Fig. 1):

(1) Each biomere is bounded at its base and top by abrupt, non-evolutionary extinctions of the entire non-agnostid trilobite fauna (see for example Stitt, 1971b, Pl. 12).

(2) The replacement trilobites are unrelated (at the family level) to those just extinguished.

(3) There is little or no mixing of adjacent faunas at biomere boundaries.

(4) The boundaries are probably diachronous (Palmer, 1965a).

(5) These abrupt faunal changes are not related to unconformities or drastic lithologic changes. In my experience it is impossible to locate these horizons on lithologic grounds.

(6) Other phyla present (e.g. brachiopods, conodonts) are not similarly affected.

(7) Trilobites at the bases of these biomeres look alike [compare *Aphelaspis* (base of the Pterocephaliid Biomere, Palmer, 1965b) with *Parabolinoides* (base of the Ptychaspidid Biomere, Longacre, 1970, Stitt, 1971b) and both of those genera with *Plethopeltis* (base of an unnamed Ordovician biomere, Stitt, 1971b)].

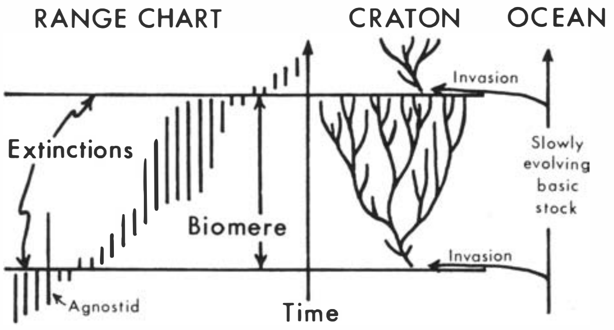

Fig. 1. Diagrammatic summary of biomere characteristics and interpretation, including appearance on range charts (left) and in evolutionary lineages (right).

Palmer (1965a: 150 and Fig. 1; 1965b: 4 and Fig. 2) suggested that periodically members of a slowing evolving stock of oceanic trilobites migrated onto the cratonic shelf. The previously existing cratonic fauna was probably extinguished by whatever (climatic?) factors favored this migration. The invading trilobites then remained on the cratonic shelf areas and evolved into a diversified trilobite assemblage that was later eliminated itself and the cycle started again. This pattern has repeated at least three and perhaps as many as five times during the Cambrian.

PTYCHASPIDID BIOMERE

Within both the Ptychaspidid and Pterocephaliid Biomeres, there are three recognizable stages of evolution (Stitt, 1971a) in the development of the trilobite community from a fauna of low diversity to one of high diversity. There is a concluding stage of 'evolutionary desperation' just before complete extinction of the trilobites of each biomere. I want now to take a close look at each of these evolutionary stages, and will use for illustration the Ptychaspidid Biomere as developed in Oklahoma.

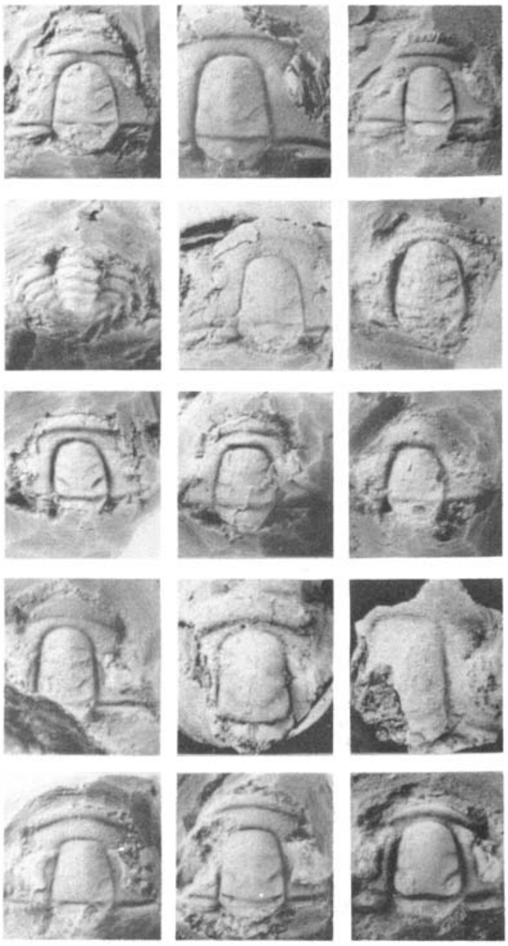

Fig. 2. Range chart and trilobites of Stage 1. Trilobites of *Parabolina spinulosa* Zone (lower left hand corner) from Henningsmoen (1957).

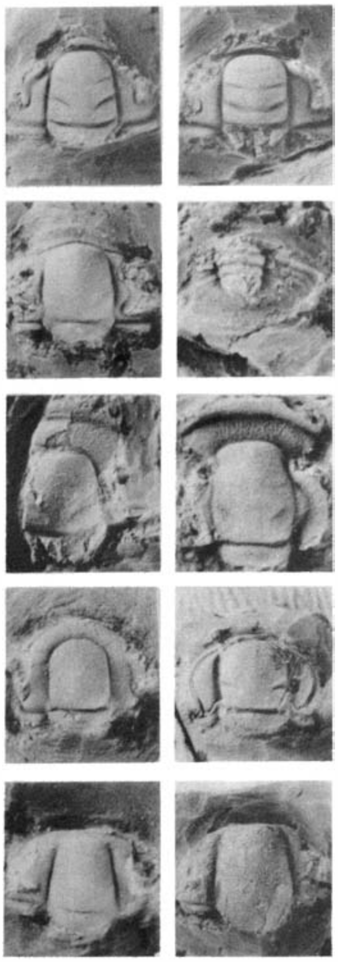

Fig. 3. Range chart and trilobites of Stage 2.

Stage one

At the base of the Ptychaspidid Biomere (defined by Longacre, 1970), there is an initial stage of adaptive radiation that occurs during the *Taenicephalus* Zone and the *Idahoia lirae* Subzone (Stitt, 1971b: 9-10, Pls. 2, 3, 9, 11, 12). Species of trilobites occurring in this interval are characterized by their short stratigraphic ranges (Fig. 2), their marked intraspecific morphologic variability and even the relative plasticity and apparent gradation between genera (see for example the gradation between *Parabolinoides contractus* and *Orgymaspis llanoensis* documented by Longacre, 1970, Pl. 1, Figs. 2-16). Overall, these trilobites are rather "average looking", and there is not much diversity in cranidial shape (Fig. 2). Faunal diversity is low, with seldom more than two or three species present in any one bed.

This stage has most of the characteristics given by Simpson (1953, p. 228-229) for an adaptive radiation, even including the taxonomic headaches common when trying to classify the trilobites of this stage. This radiation is probably stimulated by the opportunities present on the cratonic shelf for these formerly oceanic trilobites – new food sources, water depths, light, substrate, etc. Morphotypes that were not well suited to this environment quickly perished, and those that were initially fairly well adapted continued to evolve rapidly as successive populations sought the best combination of morphologic characters to utilize this new environment.

Stage two

Stage one is gradually succeeded by Stage two, which occurs during the *Saratogia* Zone (above the *I. lirae* Subzone) in Oklahoma (Stitt, 1971b: 10, Pls. 3, 9, 10, 12). Species of trilobites in this evolutionary stage have slightly longer stratigraphic ranges (Fig. 3) and less intraspecific morphologic variation than in Stage 1. There is, however, an increase in the diversity of cranidial shapes (Fig. 3).

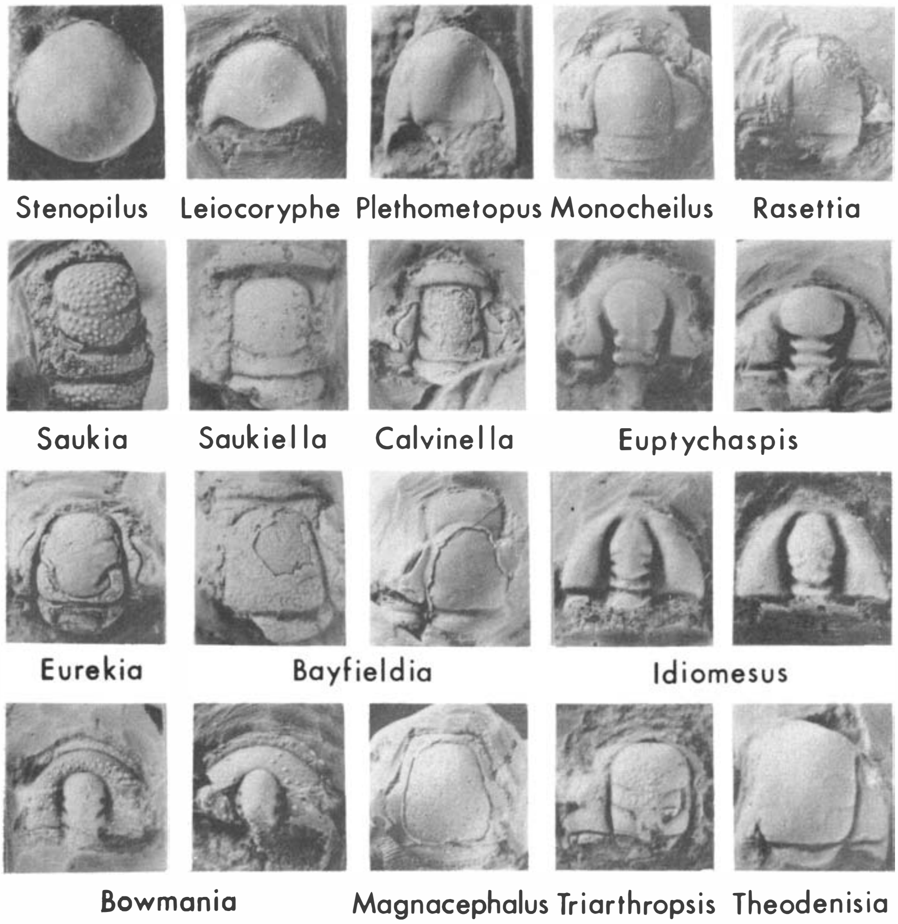

Fig. 4. Representative genera of Stage 3.

Stage two is what Simpson (1953: 229) calls the consolidation or weeding out phase of adaptive radiation. Species of a few genera have attained some sort of stability and equilibrium with the environment. These species become abundant (thick lines on Fig. 3), and other species, less well adapted, are slowly eliminated. The increase in diversity of cranidial morphologies evident in Stage two is an indication that the trilobite population has begun to establish distinct ecologic niches in the environment, and those forms best suited to particular niches are the ones that become abundant in the population.

Stage three

The third evolutionary stage occurs in the *Saukia* Zone (below the *Corbinia apopsis* Subzone) in the Ptychaspid Biomere in Oklahoma (Stitt, 1971b: 11-12, Pls. 4-7, 9, 10, 12). Characteristics of this stage are (1) species with very long stratigraphic ranges, (2) high species diversity, (3) less intraspecific variation, especially when compared with stage one. Genera are very easy to identify in this stage. Commonly several species in the same genus succeed each other stratigraphically, with little or no overlap in range. Overall, there is a marked diversity in cranidial sizes and shapes (see Fig. 4).

With its high species diversity, marked cranidial variability, and long ranges, this stage represents the stable shelf community of trilobites, with most if not all ecologic niches filled. This corresponds to Simpson's (1953: 230-232) intrazonal evolution, in which the main adaptive zones (niches) are now established, and subsequent evolution occurs only within each main niche, and there is little interaction between species and genera adapted to basically different niches. This is evidenced by the fact that most of the evolutionary changes within Stage three are transformations, and examples of speciation are rather rare. Abundant genera within which transformations occur include *Stenopilus, Plethometopus, Rasettia, Saukiella, Eurekia,* and *Bayfieldia.* Only in *Euptychaspis* among the abundant genera is there speciation, resulting in three species that are contemporaneous for a long period of time. This suggests that the species and genera present at or near the beginning of Stage three are very well adapted to their particular ecologic niches, and dominate them in such a way that further niche splitting is difficult to accomplish. The main thrust of evolution through Stage three seems to be directed toward relatively minor morphologic adjustments of basically sound, ecologically well adapted organisms.

This well adjusted trilobite community of increasingly specialized trilobites persisted for a long period of time with relatively little change. During this time, natural selection would favor those qualities that enabled the trilobites to increase their proficiency within their chosen niche. There would be little selection for genetic or physiological flexibility in what must have been a fairly constant environment. Then some major (climatic?) change occurred in the cratonic shelf environment, and the trilobite community, with its loss of genetic polymorphism, found itself unable to adjust or respond rapidly to this change. The result was the extinction of most of the established species, genera and families at or near the end of Stage three, and the onset of Stage four.

Stage four

Stage four occurs in the *Corbinia apopsis* Subzone in the Ptychaspidid Biomere in Oklahoma (Stitt, 1971b: 12, Pls. 5, 7, 9, 10, 12). Characteristics of this stage are (1) species with very short stratigraphic ranges (see Fig. 5), (2) coquinoid abundances of species that are clearly members of the established families of the biomere, (3) presence of other species not clearly related to the established families of biomere, and (4) a few members of the family Olenidae, a trilobite family usually found in extracratonic faunas.

Stage four is a stage of what might be called 'evolutionary desperation', in which the established families of the biomere attempted to adjust to whatever environmental changes were causing the rapid extinction of the trilobite shelf community. With the craton rapidly becoming depopulated, some species (e.g. *Corbinia apopsis*) of the established families were no longer restrained in their population numbers by the pressure of other trilobites, and became very abundant. The well known *Irvingella major* coquina at the very top of the underlying Pterocephaliid Biomere is another example of this. Species that can only questioningly be related to the established families may represent aberrant evolutionary offshoots, more-or-less desperate attempts to survive whatever was causing the extinctions. The olenids (such as *Leiobienvillia*) which make their only appearance among the cratonic shelf trilobites at this time, may be the first migrants from the open oceanic replacement fauna. All of these different species fail to survive very long, and are replaced by unrelated trilobites as the cycle starts again.

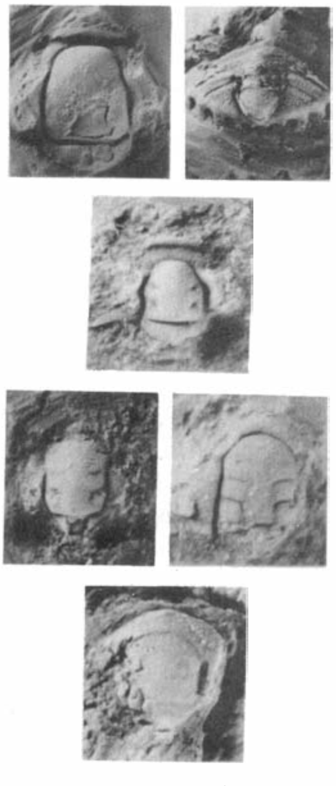

Fig. 5. Range chart and trilobites of Stage 4.

In the discussion of these four evolutionary stages, I have roughly equated length of stratigraphic range with duration of time. As argued earlier (Stitt, 1971a: 181), this four-stage pattern of evolution can be seen in the range charts of the Ptychaspid Biomere in Texas (Longacre, 1970) as well as in my work in Oklahoma, and also in the range chart presented for the Pterocephaliid Biomere in Nevada by Palmer (1965b). These three areas have different total thicknesses of rock for the intervals under consideration, and probably had different rates of sedimentation at different times and at different places in these three separate areas. That the four evolutionary stages with their particular characteristics can be easily identified in each area is evidence of the significance of this evolutionary pattern.

PALEOECOLOGY

Attempts to reconstruct the living habits of the trilobites of the Ptychaspidid Biomere are hampered by the complete disarticulation of almost all preserved carapaces. I have prepared slightly more than 8000 specimens, and only one specimen (of *Stenopilus pronus*) is nearly complete, and it lacks the librigenae. Nonetheless, I think valuable clues concerning the general mode of existence can be gleaned from considerations of the morphology of the cranidium, librigenae, and pygidium, which are known through association for most species of the Ptychaspidid Biomere.

Shallow burrowing trilobites

Species of *Stenopilus* (Stitt, 1971b: 36-37, Pl. 6: 1-7) and *Plethometopus* (Stitt, 1971b: 33-35, Pl. 6: 10-18) seem to me to have specialized morphological features that would make them well adapted for a life of shallow burrowing in the substrate. These features include a smooth, nonpustulose, moderately convex cranidium in which the glabella is either obsolete or at most barely visible. The eyes are very small, and the librigenae continue the smooth, streamlined profile of the cranidium. The pygidium is short and steep, with a prominent axial region. The thorax, when preserved intact, has a prominent axis (rhachis) and, on *Stenopilus,* the pygidium, instead of lying flat behind the thorax, actually is tucked up against the thorax so that its upper surface makes a slope of about 45 degrees to the horizontal. With this orientation, the pygidium of *Stenopilus* may have been used as a buttress to help the trilobite push down into the substrate. Or, alternately, Bergstöm (1973: 44) has suggested that *Stenopilus* may have burrowed tail first, in which case the tail would function as a shovel to scoop sediment away and draw the trilobite down into the substrate.

Specimens of these two genera, and especially *Stenopilus,* are quite abundantly preserved, something I would expect for an animal that spent much of its time somewhat immersed in the substrate.

Bottom crawling trilobites

Species of *Saukia, Saukiella,* and *Calvinella* (Stitt, 1971b: 44-45, Pl. 4: 15-17; Pl. 6: 8, 9), and *Bayfieldia* and *Eurekia* (Stitt, 1971b: 41-42, Pl. 5: 6-10, 13-15) seem to me to have morphological characteristics that would make them adapted to a life of crawling around on the sea floor. Important features include their rather large size, generally thick, usually granular to pustulose carapace, cranidium with a prominent glabella set off by deep axial furrows, medium to large sized eyes, large convex librigenae with long genal spines. Carapaces of this type should be able to withstand buffetting by waves, currents, and particles on the sea floor, and also provide a measure of protection from possible predators. The long genal spines and broad thorax and pygidium should add stability (see Ulrich & Resser, 1933, Pl. 29: 16-17 for complete specimens of *Saukia*) and prevent trilobites from being easily overturned.

Specimens of these several genera are preserved in intermediate numbers, almost always disarticulated and in some cases fragmented, as though the carapaces had been washing around on the sea floor awhile before burial.

Epiphytic trilobites

The small but perfectly formed trilobites of the family Catillicephalidae (especially species of *Triarthropsis, Theodenisia* and *Acheilops*) may have been adapted for life on whatever vegetation (probably algal) was growing on the sea floor or floating in the water. These very small, lightweight trilobites (see Stitt, 1971b: 15-17, Pl. 7: 1-6) resemble bottom crawling trilobites with their prominent axial regions and frequent granular ornament, but differ principally in their tiny size. They look very similar to the small arthropods that live today on various marine vascular plants and attached and floating algae, and I envision much the same habitat for these Cambrian trilobites. Their distribution is very sporatic, but frequently they are moderately numerous when preserved in a particular bed, as though this was a place where perhaps a plant stood where they grazed and molted, or perhaps a locality where a piece of floating algae loaded with epiphytes came to rest.

Swimming trilobites

I did not find any trilobites that I would interpret as spending most of their time swimming in the water. That is not to say that the trilobites I have already mentioned couldn't swim, for I imagine most of them could, at least a little. But for a trilobite to be predominantly a swimmer, I would expect to find it with some of the streamlining of the burrowing trilobites, but with large, marginally located eyes and a large, broad tail, perhaps with a wide doublure, that would aid in propulsion and gliding. No real candidates are present in my collections.

Perhaps this is not surprising, because if most trilobites scavenged or fed on organic debris, almost all of their food would be located on the sea floor at and just below the sediment-water interface, not up in the water. Hence, it would seem more reasonable that most of the trilobites would be adapted to life on, in, or near the sea floor, not swimming in the overlying water.

POSSIBLE CAUSE OF EXTINCTION

What factor or factors might have caused the abrupt faunal extinctions that characterize the boundaries of biomeres? Although a wide range of possibilities exists, from a trilobite disease, virus or plague to magnetic reversals or an extraterrestrial or cosmic event, I would like to explore one possibility that has been mentioned by several authors – namely, the possible effects of a marked decline in the temperature of sea water.

Certain facts are available that must be included in any attempt to explain these faunal discontinuities. Palmer (1962: 8, 9) demonstrated that the abrupt change in faunas at the base of the Pterocephaliid Biomere did not happen everywhere simultaneously, but is a time-transgressive phenomenon. He observed (p. 9) that the oldest *Aphelaspis* fauna at the base of the Pterocephaliid Biomere is found in Nevada and Alabama, and the youngest fauna immediately underlying the Pterocephaliid Biomere is found on the continental interior. He suggested (1965a: 150) that the migration of the invading fauna of the *Aphelaspis* zone began at the continental margins and progressed onto the craton.

A second critical fact is that the faunal changes at biomere boundaries take place in the major non-agnostid trilobite families (Palmer, 1965a: 150, also observe that *Pseudagnostus communis* ranges across the Pterocephaliid-Ptychaspid Biomere boundary, Stitt, 1971b, Pls. 11, 12). Robison (1972) believes that agnostid trilobites were pelagic, either possibly swimming by clapping the cephalon and pygidium together like recent pectinid pelecypods, or perhaps more likely, merely floating at or near the surface of the ocean. Non-agnostid trilobites were probably mostly benthic. Therefore, any factor or factors used to explain the extinction of the cratonic shelf trilobites must act differently on benthic and pelagic (planktic?) organisms.

Another important observation is that the faunal changes at the boundaries are not related to lithologic changes (Palmer, 1965a: 150). Furthermore, in numerous sections where biomere boundaries can be pinned down to as little as a few inches (Palmer, 1965a: 150), no evidence of erosion or interruption in sedimentation at these horizons has been detected. The sharpness of the change is clearly not related to erosion or nonpreservation of part of the rock record. Also the lack of significant mixing of the faunas at the biomere boundaries (Palmer, 1965a: 150) probably eliminates a forcible replacement, such as cannibalization of the original fauna by the invading fauna.

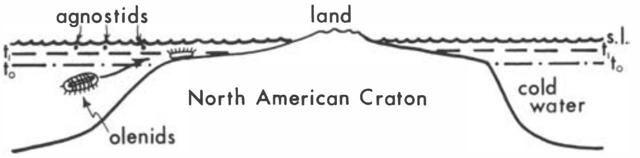

Fig. 6. Diagrammatic representation of possible extinction and replacement mechanisms at biomere boundaries.

It should also be observed that other phyla (notably the brachiopods and conodonts) are apparently unaffected by the factors causing the change in the trilobites (Winston & Nicholls, 1967: 71; Derby, Lane & Norford, 1972, Fig. 3). A possible exception occurs in the acrotretid brachiopods, where the same genus, *Angulotreta,* occurs at the base of the Pterocephaliid and Ptychaspidid Biomeres (Bell & Ellinwood, 1962: 408).

To be explained, then, is a gradual migration of ultimately bottom-dwelling trilobites from the ocean and/or continental slope onto the cratonic shelf, where they replaced an already well-established benthonic trilobite fauna. Their migration was instigated by factors that did not necessarily affect planktonic trilobites or other phyla, and that left no recognizable imprint on the sedimentary environments existing during the migrations.

What factors might be suggested? At the moment I know of no independent evidence that would point to any particular factor or factors. Detailed geochemical studies of trace element distribution or oxygen isotopes across biomere boundaries probably offer the best hope. Such studies must be done with particles in the rock that we can be reasonably sure were there in their present form during the critical time (this excludes secondary cements, for instance). Trilobite carapaces, brachiopod shells, or conodonts may be best, because the fibrous nature of their calcite seen in thin section suggests that they have not been recrystallized. The use of animal skeletal parts for trace element studies would assume that different organisms did not preferentially concentrate different trace elements in their skeletons; use of all available faunal elements below and above the boundaries might help solve this problem.

Rothwell (1968: 547) suggested that temperature may be one of a complex of factors that affected similar migrations of Oligocene-Miocene Foraminifera. Lochman & Duncan (1944: 32), Palmer (1965b: 6), and myself (Stitt, 1971a: 181) have suggested that a decline in water temperature would be one possible way to kill the trilobites without interrupting sedimentation. Ross (elsewhere in this volume) suggested that during the Late Cambrian North America lay astride of the equator. If he is correct, and if Bretsky et al. (1973) are correct in believing that taxa that live in predictable tropical environments are more susceptible to extinction through sudden changes in their environment than organisms that live in more variable environments, then perhaps the following paragraphs parallel what may have happened.

In all probability the water covering the craton during the Late Cambrian was shallower than that in the oceanic areas (Fig. 6). The temperature of surface water in both areas would be about the same, but bottom water on the craton would be warmer than that in the depths of the ocean. So then during most of the time, the interface between warmer water and colder water might be approximated by the line t_0 in Fig. 6. Now if the climate cooled down, either through glaciation or some other mechanism, cold, dense polar water would migrate along the sea floor down from the polar regions toward the equator. When these cold water currents reached the North American craton, they would surge up the continental slopes and penetrate onto the shelf, starting at the margins and continuing toward the shores. This would eventually raise the warm water – cold water interface to level t_1 (Fig. 6).

Such a rapid change in water temperature might kill the benthic cratonic trilobites that were adapted to warm water, starting with those at the cratonic margins. Such a temperature change, coupled with incipient depopulation at the cratonic margins, might have instigated a migration of oceanic trilobites that were used to cold water onto the craton that would occur just after the gradual but progressive extinction of cratonic trilobites. In this fashion a change in faunas would occur that was slow enough to have been diachronous, drastic enough to prevent mixing of the two faunas, and yet resulted in replacement of the cratonic trilobites by a completely different group. That trilobites at the base of the Pterocephaliid Biomere look like those at the base of the Ptychaspidid and Ordovician Biomeres suggests repeated invasions from the same slowly evolving oceanic stock (Palmer, 1965a: 150).

The change in water temperature and its effects on benthic trilobites as outlined above might not affect pelagic agnostid trilobites, especially if they floated near the surface of the ocean. Surface water temperatures fluctuate from day to night and from season to season, and organisms floating in or near the surface of the water either have a tolerance for temperature changes or else migrate frequently to maintain conditions favorable to their survival. This is at least one way to explain the observation that species of agnostid trilobites survived the mass extincion of species of non-agnostid trilobites.

Benthic tropical trilobites, used to the more stable, constant temperatures of bottom water, probably did not need, and therefore may not have had, a wide tolerance to changes in water temperatures. They would be more affected, and perhaps would be unable to survive a marked change in the overall temperature of the water.

At some later time after the extinction of all of the original non-agnostid cratonic trilobites and their gradual replacement by the oceanic fauna, the water began to warm and to return to the temperature that existed before the cooling. Because migration of the oceanic trilobites occurred gradually, there was time for a certain amount of evolution within this group as they moved onto the craton. As conditions returned to normal, they had evolved far enough that instead of migrating back to the ocean, they remained on the cratonic shelves and continued to evolve to meet what were for them new conditions of water temperature and depth, salinity, light, food supply, and a host of other environmental factors.

It is interesting to note that *Parabolina spinulosa* and *Parabolina brevispina* (lower left hand corner, Fig. 2), the olenid trilobites that lived in the nearby oceanic areas during the time of extinction at the base of the Ptychaspidid Biomere, are both very similar in appearance to and probably the ancestors of *Parabolinoides contractus* (right hand side of Fig. 2, top row, center and right hand pictures and pygidium, left hand picture of row two), the first abundant species at the base of the Ptychaspidid Biomere.

Henningsmoen (1957) suggested that olenids spend considerable time swimming in the open ocean water, venturing to the stagnant and probably cold sea floor for brief periods to feed on the organic rich detritus. He found no apparent reason for their restriction to oceanic areas floored by probably stagnant conditions, and suggested that perhaps competition from more specialized cratonic forms drove them to this less-than-choice environment. If this was true, then perhaps the sudden depopulation of the craton released them from this pressure, and the more adventurous species spread onto the craton. Species of olenids make their appearances on the craton only during Stage 4 (as the old fauna dies out), and forms apparently closely related to olenids are the first to become established again during Stage 1 of the next biomere.

The preceding is probably an oversimplification of what really happened, but it is at least one reasonable explanation that is consistent with the facts available at this time.

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Siegenian trilobite zoogeography in Arctic North America

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Siegenian trilobites (*Toquimaella* Zone through *Eognathodus sulcatus Zone*) in Arctic North America display provincial affinities which are transitional between the Old World Province, represented by Gedinnian trilobites, and the provincial diversification characteristic of Emsian trilobites in this region. An Old World suite consisting of *Denemarkia, Prodrevermannia, Eremiproetus, Erbenaspis, Coniproetus, Crotalocephalus,* and others, is associated with various endemic forms, including progenitors to some subsequent Emsian endemics. Excepting the presence of *Cheirurus* in Alaska, no Phacopida are known. Trilobites suggest a zoogeographic history in this area characterized by a progressive decline in cosmopolitanism after Gedinnian time. Some speculations concerning possible causes are advanced.

Allen R. Ormiston, Amoco Production Co., Research Center, Tulsa, Oklahoma, 1st September, 1973.

As shown on Fig. 1, a large number of Siegenian trilobite localities has been employed in this synthesis. In Alaska, trilobites of this age are known from the Salmontrout River and Linear Ridge localities (Fig. 1, Loc. G), and from Three-Mile Creek slightly to the southwest, as well as from Prince of Wales Island (Fig. 1, Loc. B) in southeastern Alaska. Marine Siegenian rocks are not yet known from northernmost Alaska, that is in the Brooks Range and areas to the north. The oldest Devonian rocks known in this area are littoral marine sandstones of late Emsian or Eifelian age in the southern part of the Demarcation Point Quad, Alaska. It is known that the Barrow Arch was probably of Devonian age, and it is possible that no marine Siegenian rocks were

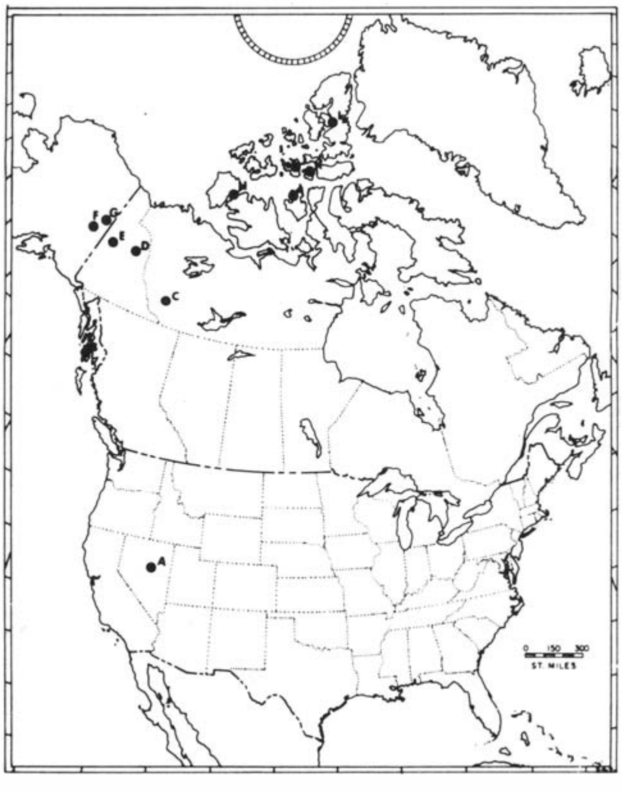

Fig. 1. Siegenian trilobite localities, western North America.

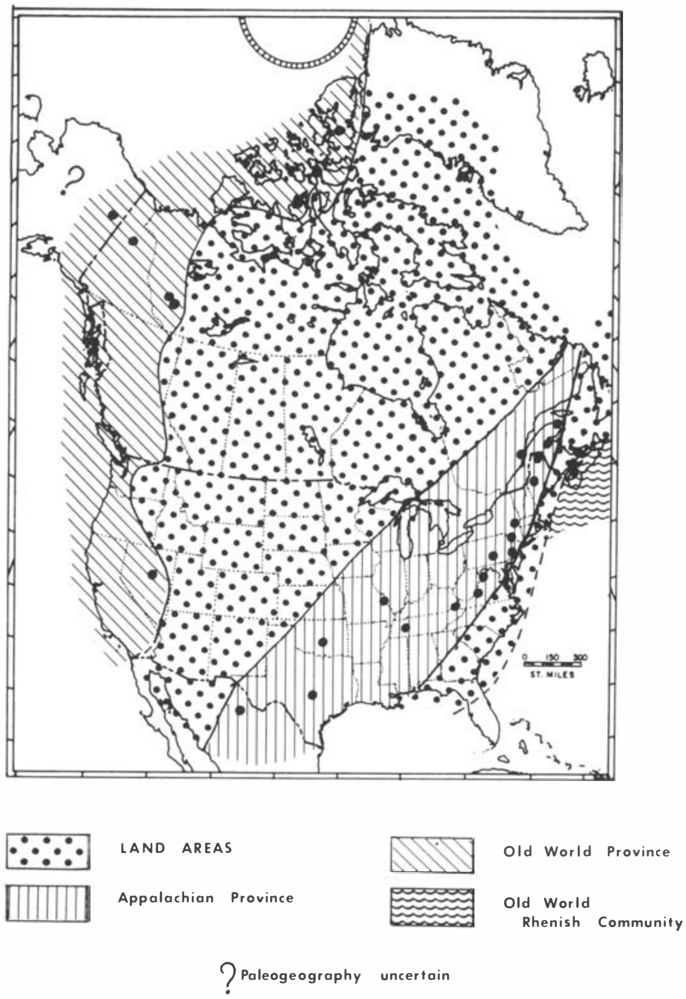

Fig. 2. Gedinnian paleogeography.

deposited in northernmost Alaska. In the Canadian Arctic Islands, Siegenian trilobite collections have been made on (Fig. 1, Locs. H-L) Prince of Wales, Princess Royal, Ellesmere, Cornwallis, and Bathurst Islands. In the Yukon Territory, collections have been obtained (Fig. 1, Locs. E, F, D) from Royal Creek, Ogilvie River, and the Hart River. In the Northwest Territories (Fig. 1, Loc. C), Siegenian trilobites are available from the vicinity of the Root River. Noteworthy among the above-mentioned localities are three which provide important, reasonably continuous Successions of Lower Devonian trilobites at Royal Creek, Yukon Territory; Salmontrout River, Alaska; and Prince of Wales Island, Canada. Of further importance are Siegenian localities in central Nevada (Fig. 1, Loc. A), from where trilobites have been described by Haas (1969) and collected by myself.

The collections on which this paper is based have been made by myself in the Canadian Arctic, Alaska, and Nevada, by the Geological Survey of Canada in the Canadian Arctic, by the Shell Oil Company Ltd. in the Yukon, and by the U.S. Geological Survey in southeastern Alaska.

BIOSTRATIGRAPHY

Since any meaningful zoogeographic synthesis requires a reliable time framework, it is appropriate to describe briefly the biostratigraphic basis for this paper. Work done in Alaska and western Canada by myself on megafossils and my colleague H. R. Lane on conodonts in the past several years is the source of my biostratigraphic information. For the purposes of this paper, I am using the term "Siegenian" in the sense of the interval occupied by the *Toquimaella* Zone (equals *Quadrithyris* and *Spirigerina* Zones of Johnson and Lenz) through *Eognathodus sulcatus* Zone. The important Siegenian index *Spirigerina* occurs in this interval, and the upper part of this interval partly overlaps the lower range of *Monograptus yukonensis.* Elements of this faunal assemblage can readily be recognized from Nevada through the Arctic Islands. In

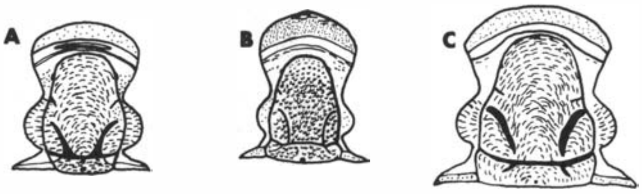

Fig. 3. Allopatric subspecies of the early Gedinnian *Warburgella rugulosa* A. *Warburgella rugulosa rugosa,* Europe; B. *Warburgella rugulosa eureka,* Nevada; and C. *Warburgella rugulosa canadensis,* Alaska and Canada, all x8.

terms of international correlation, I subscribe to the arguments of Strusz et al. (1972:428) in considering the Siegenian to equate with the uppermost Lochkovian and part of the Pragian.

The sequence of megafossil and conodont faunas in the Lower Devonian of east central Alaska has been described by Lane & Ormiston (1973), who showed that, in contrast to the conclusions of Strusz et al. (1972:437), *Eognathodus sulcatus* (early forms, *sensu* Klapper, 1969) appears with megafossil elements of the *Spirigerina* Zone (equals *Toquimaella* Zone of this paper). Thus, the range zone of *Eognathodus sulcatus* is employed in this paper as essentially corresponding to the duration of the Siegenian. Conodont faunas are also known with the important trilobite successions at Royal Creek (Klapper, 1969) and with the succession at Prince of Wales Island, Canada (Ormiston, 1969). I suggest, therefore, that the interval designated Siegenian in this paper is at least being consistently identified, even though, because of difficulties in correlating with the clastic type Siegenian, it may ultimately prove not to correspond precisely to the Siegenian stage.

GEDINNIAN PALEOGEOGRAPHY

As shown on Fig. 2, North American trilobite faunas of the earliest Devonian are clearly separated into two large provinces, the Appalachian on the east and a western province which proves to have close affinity with Old World trilobites. Within this western Old World Province, geographic variation (Fig. 3) is expressed only at the level of allopatric subspecies of *Warburgella rugulosa.* The subspecies *canadensis* occurs throughout the arctic regions, while the subspecies *eureka* existed in central Nevada. Other subspecies are found in Europe. Similar sorts of otarionids occur throughout western North America and an as yet undetermined tropidocoryphinid is known together with *Warburgella rugulosa* in Nevada. The uniqueness of the Gedinnian Appalachian Province has been documented elsewhere, but it is of interest to note the presence (Pl. 1) in Nova Scotia of *Acastella* aff. *herberti elsana* characteristic of the Rhenish Community, which suggests to me juxtaposition of North America and Europe at this time. I have earlier suggested (Ormiston, 1972) that the Old World aspect of western North America trilobites can only be explained by easy communication at this time between Europe and North America, and have further proposed that the high arctic served as a primary entry way for European faunas into western North America. We will see in our discussion of Siegenian trilobites that it continued to function in this way at that time, but that some restriction of access, as shown by the development of endemics in the arctic part of western North America and by the dilution of the Old World fauna at the southern end of the western seaway in Nevada by Appalachian elements, had already begun in Siegenian time.

SIEGENIAN PALEOGEOGRAPHY

As shown on Fig. 4, the distribution of Siegenian provinces is a slightly modified version of Gedinnian distributions. However, the trilobite faunas of arctic North America were no longer purely Old World in aspect, as some endemic elements appear probably in very latest Gedinnian time and begin to diversify in the Siegenian. Among the important endemic or partly endemic stocks of Siegenian trilobites (Pl. 2) are the forms *Schizoproetoides* sp. *A,* which is probably ancestral to the younger *Schizoproetoides richteri* and the *Ganinella* stock which persisted into the Emsian and Eifelian in western Canada and may have migrated into western North America from Siberia where early species of *Ganinella* have been documented by Yolkin, 1968. Another stock of possible Siberian origin is the *Lacunoporaspis* stock which first appears in North America in the Siegenian beds of the Canadian Arctic Islands, and persists into rocks at least as

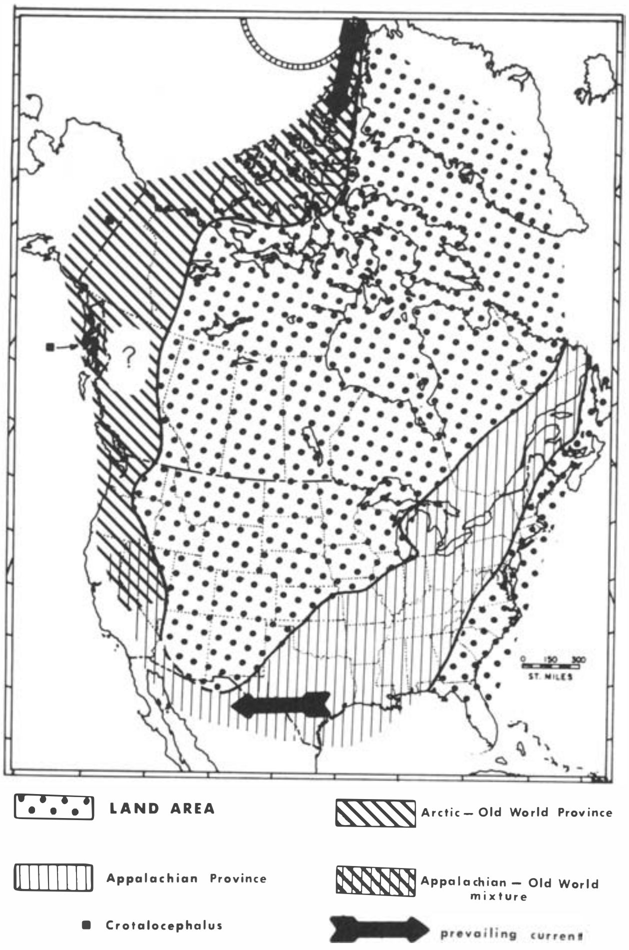

Fig. 4. Siegenian paleogeography.

young as upper Emsian. *Proetus* (*Coniproetus*) appears in the late Gedinnian of the Yukon and may give rise to a form which I have described as *Basidechenella laticaudata,* and an undescribed species here designated *B. inflecta* (*nomen nudem*). On the basis of these forms, I had earlier (1967) speculated that the dechenellids had descended from *Proetus.* It is at least certain that dechenellids undergo a striking radiation in Emsian and Middle Devonian rocks in the Arctic Islands.

Nevertheless, as shown on Plates 3 through 5, much of the Siegenian trilobite fauna of the high arctic continues to consist of Old World sorts of genera, proving the continued operation of the high arctic immigration route. Among the genera of Old World type known in the area are *Coniproetus, Maurotarion, Prodrevermannia,* (the last-named represented by the species *sverdrupi* (Tolmachoff, 1926) both in the Arctic Islands and in Alaska), *Denemarkia, Eremiproetus, Otarionella, Ceratarges* (*Ceratolichas* of Ormiston, 1972), and in Alaska two occurrences of *Crotalocephalus,* the only phacopid specimens known to me in the entire Lower Devonian of the high arctic. *Cheirurus* does not appear in any younger Devonian samples I have examined anywhere in Alaska, nor in any samples elsewhere in the Arctic. Possibly these samples represent a brief and unsuccessful incursion by phacopids into a realm which, for reasons puzzling to me, was inimical to phacopids. Thus, the high arctic during Siegenian time contained a basically Old World sort of trilobite fauna significantly modified by the appearance of some endemic forms, among them possible precursors to the dechenellid radiation of the Emsian and Eifelian, and some invaders from Siberia.

Siegenian rocks of central Nevada contain trilobites documented by Haas (1969) supplemented by my collections, representing an admixture of Appalachian elements, such as species of *Phacops, Dalmanites, Leonaspis,* and *Odontochile,* with Old World genera such as *Decoroproetus, Koneprusia,* and *Cheirurus.* This mixture suggests to me a substantial dilution of southward-migrating Old World forms in the western province by Appalachian forms (Fig. 3) which had turned the southern limit of the landmass separating these two major provinces during Siegenian time. The Siegenian *Cheirurus* of Nevada (Ormiston, 1972, Pl. 1:17) does not belong to the subgenus *Crotalocephalus* and possibly represents an indigenous holdover from the Silurian *Cheirurus* (*Cheirurus*). It therefore has a different zoogeographic significance from the *Crotalocephalus* of Alaska which was a European immigrant. The abundance of Old World forms in the high arctic makes understandable the suggestion by Erben (*in* Boucot, Johnson & Talent, 1969) that Siegenian trilobites at Royal Creek were of Uralian (i.e. Old World) type. But this is only partly true as closer study shows the appearance already in Siegenian time of several lineages which radiated during the Emsian and Eifelian to produce the even greater zoogeographic differentiation of those times.

EMSIAN AND EIFELIAN PALEOGEOGRAPHY

As shown in Fig. 5, provincialism among the North American trilobite faunas is most pronounced during Emsian through Eifelian time. At least four biogeographic subdivisions can be recognized: (1) Appalachian Province, (2) Cordilleran Subprovince, (3) Canadian/Siberian Subprovince, distinguished by the endemic genera *Fuscinipyge, Humeia* (distinctive proetid previously identified as *Odontocephalus* by some authors; in reality no phacopids are known anywhere in western Canada from Emsian or Eifelian rocks), *Reticuloharpes, Lacunoporaspis,* and numerous endemic species of *Dechenella;* (4) a Uralian subprovince occupied the Arctic Islands and was especially distinguished by the absence of any phacopids and the presence of *Weberopeltis, Harpes, Kielania, Ancyropyge,* and others.

I suggest that the stage for this zoogeographic differentiation was set in the Siegenian by the development of endemic lines, the incursion of some new lines from Siberia, and, in the case of the appearance of the Cordilleran subprovince, this endemism may have arisen through evolutionary changes induced by niche competition between interlopers from the Appalachian Province and southward migrators from the modified Old World Province of the Siegenian.

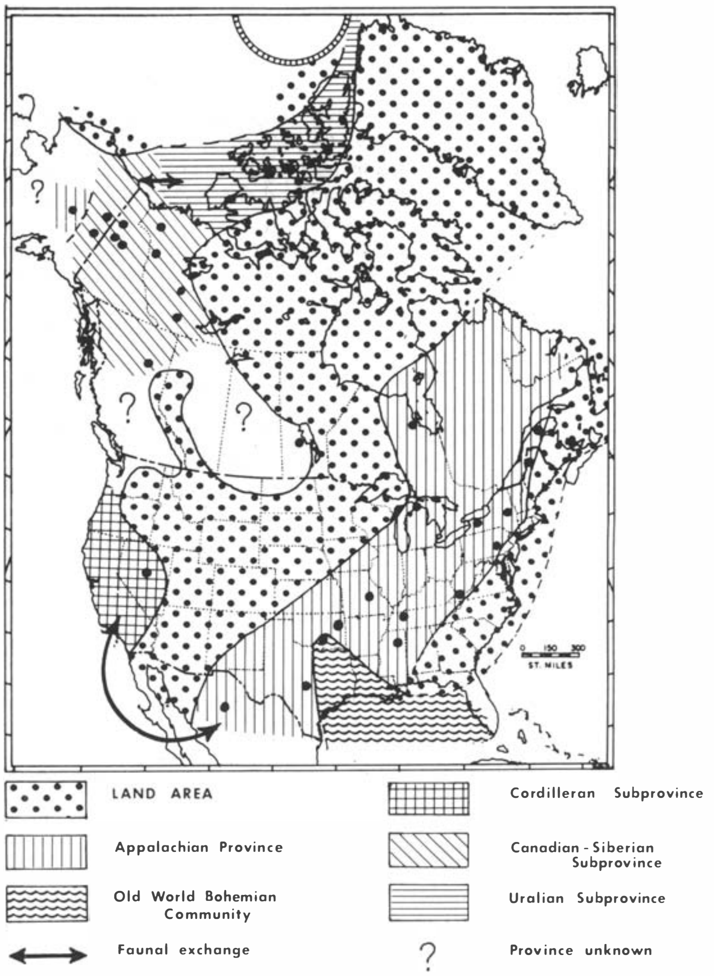

Fig. 5. Emsian-Eifelian paleogeography.

POSSIBLE CAUSES

Trilobites show a progressive decline in cosmopolitanism throughout western North America after Gedinnian time. As shown by the nature of the Siegenian trilobite assemblages, this decline did not begin abruptly, and I would propose that it is either an expression of a progressive narrowing of the area of access via the Arctic Islands from Europe into western North America through Hercynian movements in the high arctic which preceded the widespread development of land areas in the Late Devonian or, alternatively, the beginning of physical separation through drift of previously juxtaposed Canadian and Soviet Arctic seaways.

The absence of Phacopids in northern North America during the Lower Devonian (excepting *Crotalocephalus* in Alaska) seems to require a different sort of explanation. The distributions of organisms can be a result of either internal or external limitations – the former involving the life habits, larval history, and environmental requirements of the organisms themselves, the latter the distribution of landmasses, currents, etc. It would appear to me that the absence of the Phacopids must somehow relate to biologic requirements of Phacopids themselves which could not be met in the arctic areas.

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EXPLANATIONS OF PLATES

Plate 1

Trilobites from three provinces, Gedinnian of North America. *Figs. 1-6. Acastella* aff. *A. heberti elsana* R. & Emma Richter, 1954. 1. dorsal view of internal mold of cranidium, x5. 2,5. Dorsal view of internal mold (note lateral denticles) and latex cast of one pygidium, x7. 3. Dorsal view of internal mold of pygidium showing lateral denticles, x5. 4, 6. Dorsal view of internal mold of pygidium, x5 and x7. All are from near the base of the Torbrook Formation, Spinney Brook, Nova Scotia, collected by L. Jensen. *Figs. 7-8. Acastella* sp., dorsal and anterior views of internal mold of cranidium, x3, from a higher stratigraphic level in the Torbrook Formation, Spinney Brook, Nova Scotia, collected by L. Jensen. *Fig. 9-10. Corycephalus dentatus* (Barrett, 1876) 9. Dorsal view of partly exfoliated cephalon, x2. 10. Dorsal view of latex cast of pygidium, x2. 4. Both are from the New Scotland Formation, Port Jervis, New York and represent a typical Appalachian Prouvince genus. *Figs. 11-12. Warburgella rugulosa eureka* Alberti, Haas & Ormiston, 1973, dorsal and anterior views of paratype cranidium, USMN 173724, x10, Birch Creek section II at 608' above base, Roberts Mountains, Nevada. *Figs. 13-16.* Unidentified tropidocoryphinid genus. 13-14. Dorsal and lateral views of cranidium, x8. 15. Dorsal view of latex cast of same cranidium x8. 16. dorsal view of internal mold of pygidium x8. All are from same horizon and section as preceding, Roberts Mountains, Nevada.

Plate 2

Arctic lineages arising in the Siegenian. The figures are arranged in a presumed phylogenetic sequence (bottom to top of plate) within each of three genera: *Ganinella* (Figs. 1-4), *Lacunoporaspis* (Figs. 5-10), and *Schizoproetoides* (Figs. 11-15). *Figs. 1-2. Ganinella* cf. *G. schebalinoensis* Yolkin, 1968. 1. Dorsal view of cranidium, x5, GSC locality, C-158, Eifelian, Hume Formation, Lat. 65°24'N, Long. 131°21'W, N.W.T. 2. Dorsal view of cranidium, x4, GSC locality C-159, Eifelian, Hume Formation, same coordinates. *Figs. 3-4. Ganinella* n.sp. 3. Dorsal view of cranidium, x8. 4. Dorsal view of pygidium x4, Amoco 6795-1, Nelsen's Bluff, Alaska. *Figs. 5-6. Lacunoporaspis* n.sp. cf. *L. norrisi* Ormiston, 1971. 5. Dorsal view of cranidium, x2. 5. 6. Dorsal view of pygidium, x2. 5, both from Ogilvie Formation, Lat. 65°23'N, Long. 140°49'W, Yukon Territory. *Figs. 7-8. Lacunoporaspis norrisi* Ormiston, 1967. 7. Dorsal view of holotype cranidium, GSC 24255, x4, GSC locality, 47331, Michelle Formation, Lat. 65°23'N, Long. 137°07'W, Yukon Territory. 8. Dorsal view of several pygidia, hypotype GSC 24260, x2, GSC locality 54177, Michelle Formation, Lat. 65°29'N, Long. 139°09'W, Yukon Territory. *Figs. 9-10. Lacunoporaspis* n.sp. 9. Dorsal view of cranidium x3. 10. Dorsal view of pygidium x4, both from GSC locality C-8256, western Prince of Wales Island, District of Franklin. *Figs. 11-12. Schizoproetoides richteri* (Tolmachoff, 1926). 11. Dorsal view of cranidium, hypotype GSC 18217, x2. 12. Dorsal view of pygidium, hypotype GSC 18220, both from Blue Fiord Formation, Svendsen Peninsula, Ellesmere Island. *Fig. 13. Schizoproetoides macnairi* (Ormiston, 1967), dorsal view of cranidium, x3, GSC locality C-8243, western Prince of Wales Island. *Figs. 14-15. Schizoproetoides* sp. A. 14. Dorsal view of cranidium, x3, Salmontrout Limestone, Linear Ridge, Alaska. 15. Dorsal view of pygidium, x1.5, Shell Canada 20922, Prongs Creek Formation, Royal Creek area, Yukon Territory.

Plate 3

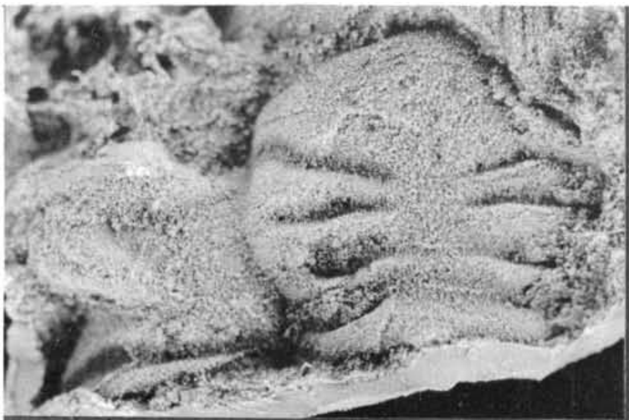
Lower Devonian trilobites from Alaska. *Fig. 1. Koneprusia* sp., oblique view of pygidium, USNM 163592, x8, USGS collection 6492-SD, McCann Hill Chert, type section, Eagle D-1 Quad. *Fig. 2. Acanthopyge* (*Nitidulopyge*) sp., dorsal view of cranidium x6, USGS collection 6492-SD. *Fig. 3. Ceratarges* n. sp., dorsal view of cranidium, x5, Amoco 6217-1, Three Mile Creek. *Figs. 4-5, 7. Ganinella* n.sp., dorsal and anterior views of cranidium x4. 7. Dorsal view of pygidium, x4, Nelsen Bluff, Lat. 66°30'N, Long. 142°40'W. *Fig. 6. Astycoryphe* aff. *A. cimelia* Ormiston, 1967, dorsal view of pygidium, x3, USGS collection 6492-SD. *Figs. 8-9. Cheirurus* (*Crotalocephalus*) sp., dorsal and lateral views of cranidium, x2.5, USGS collection 73ACN32, Kassan Island, Craig B-1 Quad. *Figs. 10, 16, 24. Otarionella* sp. 10. Dorsal view of cranidium, x5. 16. Dorsal view of cheek showing lateral spines, x10. 24. Dorsal view of pygidium x5, Amoco 6217-1, Three Mile Creek, Lat. 65° 33 N, Long. 142°50'W. *Fig. 11. Eremiproetus* cf. *E. tozeri* (Ormiston, 1967), dorsal view of cranidium, x10, Amoco 6217-1, Three Mile Creek. *Figs. 12-15. Prodrevermannia sverdrupi* (Tolmachoff, 1926). 12. Dorsal view of cranidium. x10. 13. Dorsal view of cranidium, x5. 14. Dorsal view of latex cast of pygidium, x10, Amoco 6217-1. Three Mile Creek. *Figs. 17-23. Denemarkia* n. sp. 17. Dorsal view of cranidium, x10. 18-19. Dorsal and lateral views of cranidium x10. 20. Dorsal view of cranidium, x3. 21. Dorsal view of cheek x3. 22. Dorsal view of pygidium x10, all from 5 feet above base of type Salmontrout Limestone, Lat. 67°10'N, Long. 141°40'W. 23. Dorsal view of pygidium x10, Deacon Rock, Lat. 66°59'N, Long. 143°00'W. *Fig. 25. Maurotarion* sp., dorsal view of cephalon, x5, USGS collection 72AE106, Keete Inlet, Craig A-2 Quad. *Figs. 26-27.* Dorsal views of pygidium and free cheek of *Proetus* sp. A, both x3, 5' above base of type Salmontrout Limestone. *Fig. 28. Schizoproetoides* sp. A, dorsal view of cranidium, x4, Salmontrout Limestone, Linear Ridge, Lat. 66°55'N, Long. 141°26'W. *Fig. 29. Cyphaspides* sp., dorsal view of pygidium x8, from Pridoli strata in Road River Formation, Linear Ridge. *Figs. 30-32. Warburgella rugulosa canadensis* Ormiston, 1967. 30. Dorsal view of cranidium x8. 31. Dorsal view of pygidium x8, 32. Dorsal view of pygidium x7, all from base of Salmontrout Limestone, Linear Ridge. *Fig. 33. Proetus* cf. *P. affinis Boucek, 1934, dorsal view* of pygidium x8, base of Salmontrout Limestone, Linear Ridge.

Plate 4

Lower Devonian trilobites, Canadian Arctic Islands. *Figs. 1, 5. Eremiproetus tozeri* Ormiston, 1967. 1. Dorsal view of paratype cranidium, GSC 18143, x2. 6. 5. Dorsal view of paratype pygidium, GSC 18143/2, x5.3. Princess Royal Islands. *Fig. 2. Astycoryphe* sp., dorsal view of pygidium x8, GSC Loc. C-2692, Lowther Island. *Fig. 3. Dechenella paragranulata* Ormiston, 1967, dorsal view of paratype pygidium, GSC 18181, x6, Twilight Creek (Eifelian horizon but species is also known from the Emsian), Bathurst Island. *Fig. 4. Kielania triabsidata* Ormiston, 1971, lateral view of paratype cephalon, GSC 25528, x1. 5, from GSC Loc. C-2682, Lowther Island. *Fig. 6. Ceratarges* n. sp., dorsal view of latex replica of pygidium, x1. 5., GSC Loc. C-8228, western Prince of Wales Island. *Fig. 7. Schizoproetoides macnairi* (Ormiston, 1967), dorsal view of cranidium, x3, GSC Loc. C-8243, western Prince of Wales Island. *Fig. 8. Prodrevermannia sverdrupi* (Tolmachoff, 1926), dorsal view of holotype cranidium, PMO A28846, x6, Goose Fiord, Ellesmere Island. *Figs. 9-11. Lacunoporaspis* n. sp. 9. Dorsal view of cranidium, X4. 10. Dorsal view of cranidium, x3. 11. Dorsal view of pygigium x3, all from GSC Loc. C-8256, western Prince of Wales Island. *Figs. 12-15. Basidechenella laticaudata* Ormiston, 1967. 12. Dorsal view of cranidium, x4. 13, 14. Dorsal and lateral views of pygidium, x4. 15. Dorsal view of pygidium, x4, all from GSC Loc. 8234, Lat. 73°20′N, Long. 100°07′W, western Prince of Wales Island. *Figs. 16, 18-19. Maurotarion* n. sp. 16. Latex replica of articulated specimen, x5, GSC Loc. C-8804. 18. Dorsal view of pygidium, x8, 19. Dorsal view of cranidium, x5, both from GSC Loc. C-8231, western Prince of Wales Island. *Fig. 17. Basidechenella inflecta* n. sp., dorsal view of specimen lacking only right free cheek, x3, GSC Loc. C-8225, Prince of Wales Island. *Figs. 20-21,* 25. *Proetus* cf. *P. affinis* Bouček, 1934. 20. Dorsal view of cranidium, x3. 21. Dorsal view of free cheek, x3. 25. Dorsal view of pygidium, x3, all from GSC Loc. C-8231, western Prince of Wales Island. *Figs. 22-24. Warburgella rugulosa canadensis* Ormiston, 1967. 22. Dorsal view of nearly complete specimen, x5, GSC Loc. C-11438. 23. Dorsal view of paratype cranidium, GSC 18136, x5. 3. 24. Dorsal view of pygidium, GSC 18139, x6, all from Read Bay Formation, Cape Washington, Baillie Hamilton Island.

Plate 5

Lower Devonian trilobites from the Yukon. *Figs. 1-2. Lacunoporaspis* n. sp. cf. *L. norrisi* Ormiston, 1971. 1. Dorsal view of cranidium, x3. 2. Dorsal view of pygidium, x2. 6, both from Ogilvie Formation, Lat. 65°23′N, Long. 140°49′W. *Figs. 3-4. Dechenella* n. sp.. 3. Dorsal view of cranidium, x2. 4. Dorsal view of pygidium, x2,, GSC Loc. 54900, Ogilvie Formation, Lat. 66°02′N, Long. 139°05′W. *Fig. 5. Koneprusia* sp., dorsal view of cranidium, x3, 960′ above base of Ogilvie Formation, Lat. 65°36,N, Long. 136°45′W. *Fig. 6. Spiniscutellum* n. sp., dorsal view of cranidium, x5, Shell Canada 21055, Prongs Creek Formation, Royal Creek area. *Figs. 7-8. Ceratarges* n. sp.. 7. Dorsal view of pygidium x3. 8. Dorsal view of cranidium x3, both 0 to 80′ above base Michelle Formation, Nahoni Range, Lat. 65°29′N, Long. 139°10′W. *Figs. 9-12. Erbenaspis* n. sp. 9-11. Dorsal and lateral views of cranidium and of latex cast of external mold of cranidium, x8. 12. Dorsal view of pygidium, x10, all from Shell Canada 20514. ?Ogilvie Formation, 850′ below top, Royal Creek area, Lat. 64°55′N, Long. 135°10′W. *Fig. 13. Ganinella* n. sp., dorsal view of cranidium, x4, Shell Canada 20950, Prongs Creek Formation, Royal Creek area. *Fig. 14. Cornuproetus* cf. *C. haentzscheli* Alberti, 1967, dorsal view of cranidium, x5, Michelle Formation, Lat. 65°40′N, Long. 137°08′W. *Fig. 15. Proetus* sp. A., dorsal view of pygidium, x3, Shell Canada 21051, Prongs Creek Formation, Royal Creek area. *Figs. 16-21. Schizoproetoides* sp. A. 16. Dorsal view of cranidium, x3, Shell Canada 20867. 17. Dorsal view of cranidium in sample with *Spirigerina supramarginalis,* x5, Shell Canada 20923. 18. Dorsal view of cranidium, x3, Shell Canada 20555, all from Prongs Creek Formation, Royal Creek area. 19. Dorsal view of pygidium, GSC 24280, x2, from Michelle Formation, GSC Loc. 54092, 20. dorsal view of pygidium, x1. 5. 21. Dorsal view of cheek x1. 5. both from Shell Canada 20922, Prongs Creek Formation, Royal Creek area. *Fig. 22. Proetus* (*Coniproetus*) sp., dorsal view of pygidium, x4, Shell Canada 20555, Prongs Creek Formation, Royal Creek area. *Fig. 23. Prodrevermannia*? sp., dorsal view of cheek x3, Shell Canada 20818, Prongs Creek Formation, Royal Creek area. *Figs. 24-25. Basidechenella inflecta* n. sp., 24. dorsal view of cranidium, x4. 25. Dorsal view of pygidium, x4, both from Shell Canada 19059, Prongs Creek Formation, Royal Creek area. *Fig. 26. Basidechenella laticaudata* Ormiston, 1967. dorsal view of pygidium, x3, Shell Canada 20922, Prongs Creek Formation, Royal Creek area. *Figs. 27-28. Warburgella rugulosa canadensis* Ormiston, 1967. 27. Dorsal view of cranidium, GSC 29076, x10. 28. Dorsal view of pygidium, GSC 29088, x10, both from Delorme Formation, 550′ below top, South Canyon Range, Lat. 62°30′N, Long. 125°01′W., *Fig. 29. Otarion* sp., dorsal view of cranidium, x5, Shell Canada 19055, Road River Formation, Royal Creek area.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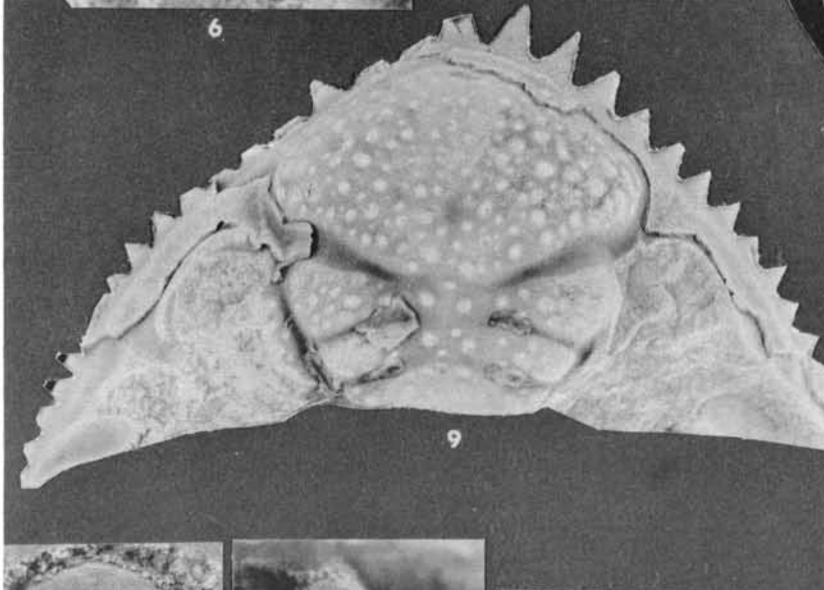
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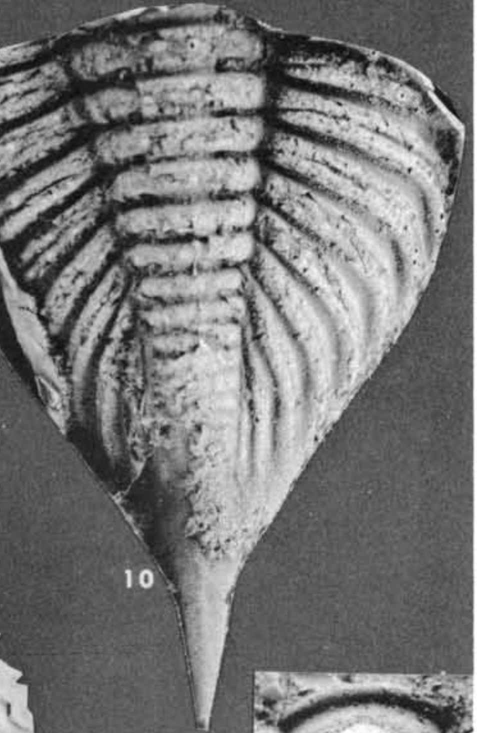
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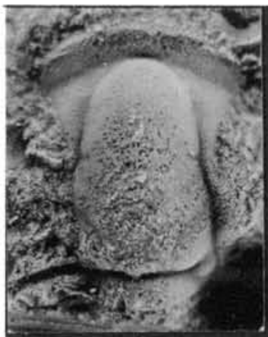
Plate 1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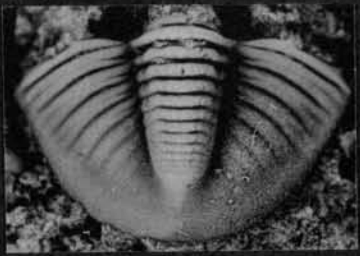
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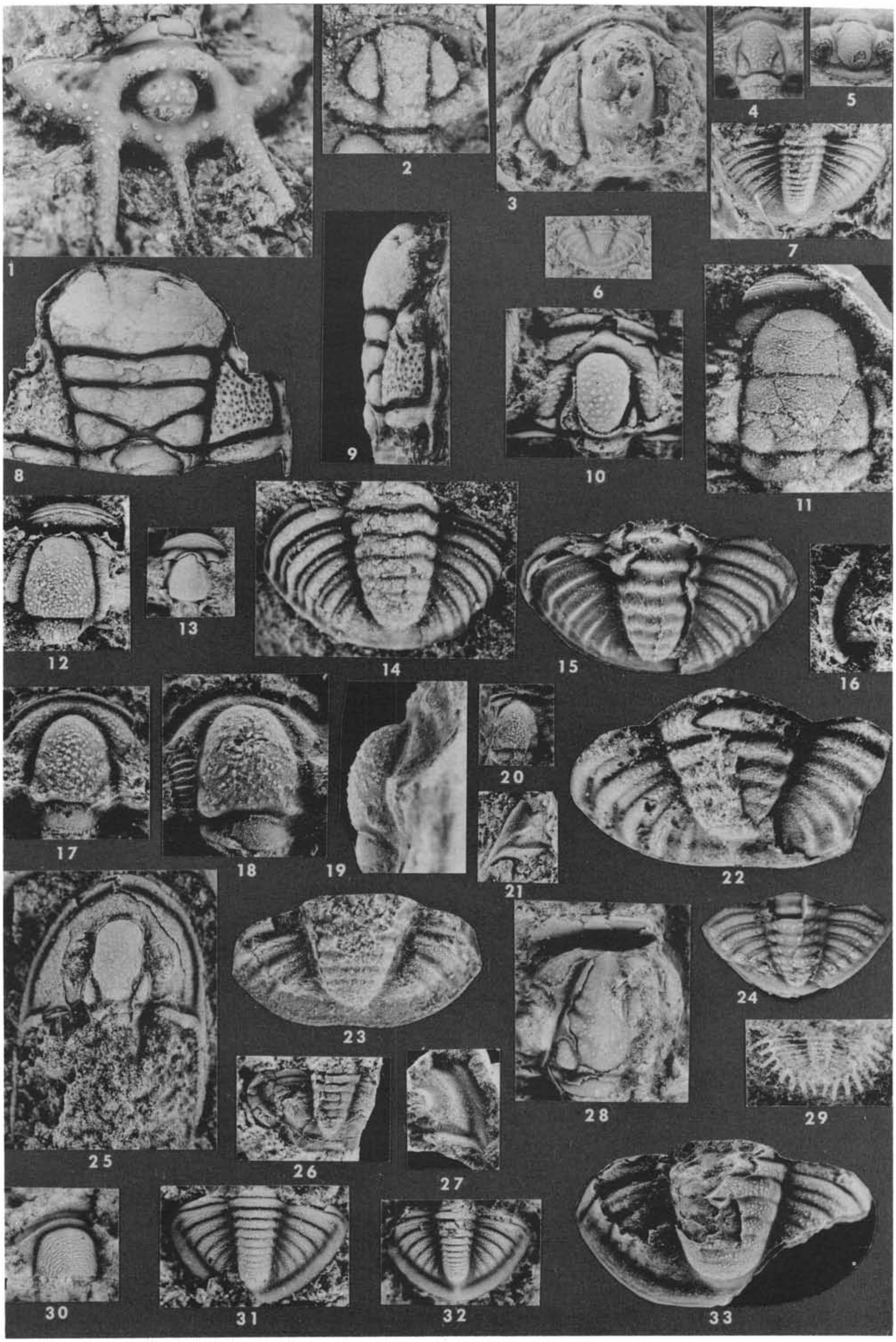
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Plate 3


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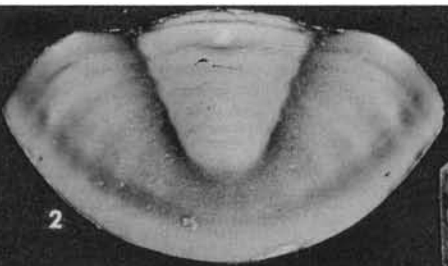
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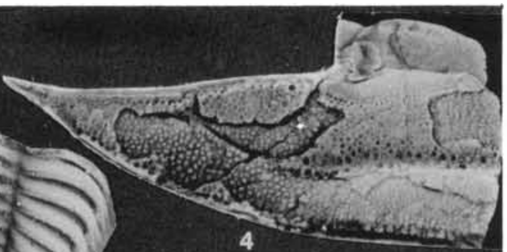
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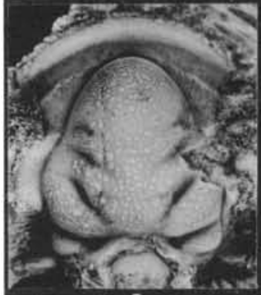
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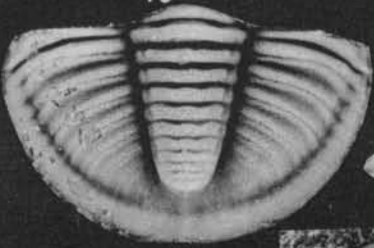
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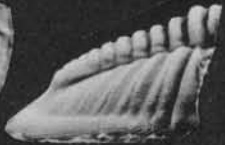
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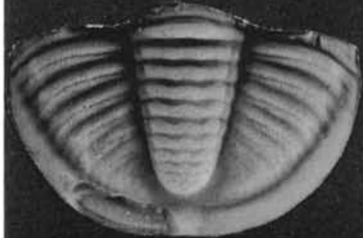
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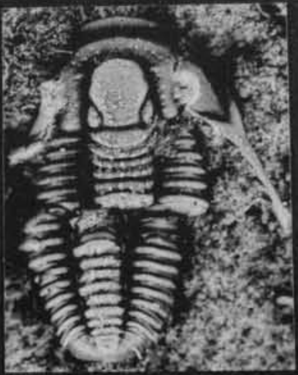
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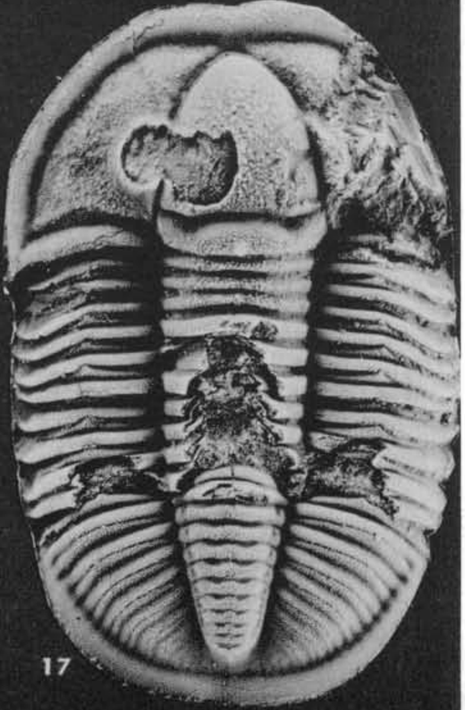
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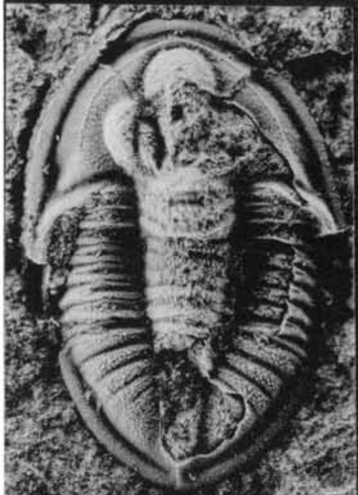
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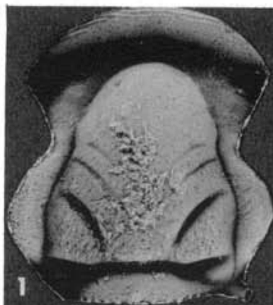
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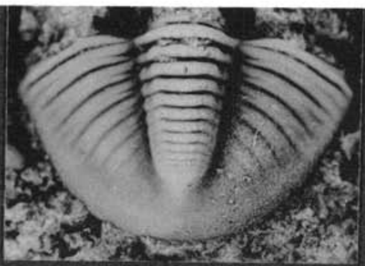
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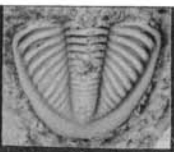
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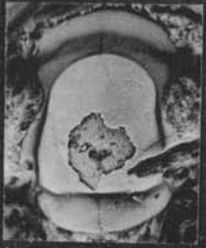
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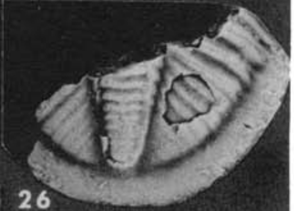
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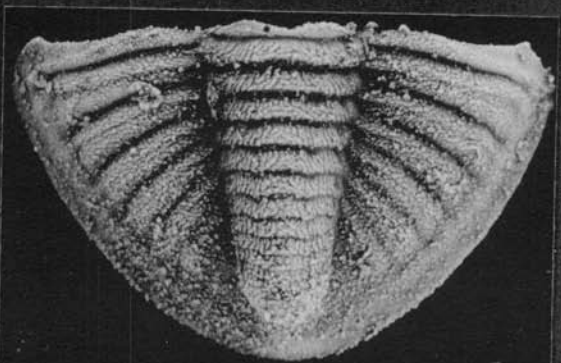
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Plate 5

The distribution of phacopid trilobites in space and time

IVO CHLUPÁČ

Chlupáč, I. 1975 07 15: The distribution of phacopid trilobites in space and time. *Fossils and Strata,* No. 4, pp. 399–408. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

The richest representation and radiation of phacopid trilobites during their entire development (early Silurian – late Devonian) is within the shallow-water, mostly carbonatic facies in the inferred tropical to subtropical palaeoclimatic zone. The greatest diversity in species and genera is indicated in the geosynclinal regions (e.g. the Bohemian magnafacies of the Palaeotethyan region). Provincialism is manifest, especially in the Lower Devonian. In the Silurian, and Middle and Upper Devonian, there is strong evidence of migration (especially Europe-North Africa and Europe -Central and S.E.-Asia). The influence of environment is markedly expressed in the concentration of phacopids with reduced eyes in pelagic muddy facies and phacopids with well developed eyes in the epicontinental shallow-water facies. The development of phacopids in time is characterized by their sudden appearance at the beginning of the Silurian, a certain crisis in the uppermost Silurian, an acme of development in the early Middle Devonian, and total extinction at the Devonian/Carboniferous boundary. The changes in phacopid evolution, especially during the Late Devonian, reflect the events (possibly climatic, magnetic, or extra-terrestrial) which also affected other animal groups.

I. Chlupáč, Ústřední Ústav Geologický, Malostranské náměsti 19, Praha 1, Czechoslovakia, 1st August, 1973.

The trilobites of the family Phacopidae Hawle & Corda are an important component of Silurian and Devonian trilobite faunas. Because of their abundant occurrence and world-wide distribution they provide suitable material for palaeobiogeographical studies.

The objective of this paper is to summarize the existing knowledge of the distribution of phacopid trilobites from their appearance at the Ordovician/Silurian boundary, until their extinction at the Devonian/Carboniferous boundary. The impulse to this work was given by the revision of phacopid trilobites from the Silurian and Devonian of Czechoslovakia, and by comparative study of phacopids from other regions.

The submitted report is based on generic and subgeneric levels. The principal taxonomic difficulty is that a large number of species have so far been cited in the literature under the collective generic name *Phacops,* although they represent different genera and subgenera, which often show diverse stratigraphical range of occurrence and distribution. The paper of Campbell (1967) and some more recent works appreciably contributed to the refinement of the phacopid classification. Most genera and subgenera discussed are defined in the Treatise (Harrington et al. 1959); genera and subgenera erected more recently have been described by G. Alberti (1970), Maksimova (1955, 1968), Přibyl & Vaněk (1971), Struve (1972) and the author (1971, 1972). Knowledge about phacopids has been further augmented, especially by the studies of H. Alberti (1965, 1968), Haas (1968), Struve (1970), Eldredge (1972, 1973), Sherwin (1972), etc. The genera and species of questionable validity, and those which the author considers to be invalid, are not discussed (this applies also to the five subgenera of *Phacops* established by Struve, 1972, which are based on features of specific rather than subgeneric value). *Bouleia* Kozłowski and *Dereimsia* Kozłowski are excluded from the family *Phacopidae,* in agreement with Eldredge (1972). The following genera and subgenera are discussed:

Acernaspis Campbell 1967, *Ananaspis* Campbell 1967, *Cryphops* Richter & Richter 1926, *Denckmannites* Wedekind 1914, *Dianops* Richter & Richter 1923, *Dienstina* Richter & Richter 1931, *Ductina* Richter & Richter 1931, *Eocryphops* Richter & Richter 1931, *Eophacops* Delo 1935, *Lochkovella* Chlupáč 1972, *Murphycops* Lespérance 1968, *Nephranops* Richter &

Richter 1926, *Phacopidella* Reed 1905, *Phacops* (*Phacops*) Emmrich 1839, *Phacops* (*Chotecops*) Chlupáč 1971, *Phacops* (*Prokops*) Chlupáč 1971, *Phacops* (*Paciphacops*) Maksimova 1972, *Phacops* (*Boeckops*) Chlupáč 1972, *Plagiolaria* Kegel 1952, *Reedops* Richter & Richter 1925, *Signatops* Přibyl & Vaněk 1971, *Struveaspis* Alberti 1966, *Trimerocephalus* McCoy 1849.

The distribution of seas in the Silurian and Devonian has been reconstructed mainly according to the works published in the Internat. Symposium on Devonian System, Calgary 1967, Atlas of Palaeobiogeography (Hallam, 1973) and some other works, e.g. Boucot, Berry & Johnson (1968), Walter (1972), etc. It should be emphasized that all reconstructions are but approximate and strongly extrapolated. For the sake of objectivity, the occurrences of phacopids are plotted in the maps on continents as they are distributed today, although the author is convinced that the theory of continental drift, postulating a close *approchement* of continents on the southern hemisphere into the incompletely divided Pangaea, is correct.

SILURIAN

The first unquestionable representatives of the family *Phacopidae* appear near the Ordovician/Silurian boundary. The oldest well known genus is *Acernaspis,* widely distributed in the Llandoverian. The occurrences of *Acernaspis* are concentrated mainly in the shallow-water carbonate facies; they are traceable from eastern North America (Anticosti, Nova Scotia) across the British Isles to the Baltic Region (abundant e.g. in Estonia, see Männil 1970). These phacopids are also widely distributed in similar facies of the Siberian platform and are known from the Arctic region (New Siberian Islands). The occurrences of *Acernaspis* furnish evidence of migration through shallow seas between eastern North America, northern Europe, and Siberia, i.e. in a relatively continuous belt belonging to the warm zone (benthos rich carbonate facies). The absence of *Acernaspis* in southern Europe and northern Africa may be explained by a less favourable living environment in the mudstone facies or by palaeoclimatic conditions (cooler zone of the Silurian southern hemisphere, see the interpretation of mudstone graptolite-

Fig. 1. Distribution of phacopid trilobites in Lower Silurian (Llandoverian – Wenlockian). Ac = Acernaspis, An = Ananaspis, E = Eophacops, M = Murphycops, Pd = Phacopidella. Supposed land areas stippled.

Fig. 2. Distribution of phacopid trilobites in Upper Silurian (Ludlovian — Přídolian). An = Ananaspis, E = Eophacops, D = Denckmannites, L = Lochkovella. Land areas stippled.

bearing facies in Berry & Boucot 1967). The finds of *Acernaspis* in south-eastern Australia suggest that the distribution was greater than is inferable from the occurrences known so far.

In the *late Early Silurian,* in the Wenlockian, and at the beginning of the Late Silurian (early Ludlovian), the genus *Eophacops* shows a conspicuously wide distribution. Its representatives, like those of *Acernaspis,* are confined to shallow-water carbonate facies; they are known to occur chiefly in the U.S.A. (Illinois, Ohio, Indiana, Tennessee), England, Czechoslovakia (Barrandian), Germany, and north-western Africa (Morocco). The occurrences recorded from Asia (Maksimova 1962 et seq.) belong mostly to *Acernaspis.* Compared with the occurrences of *Acernaspis,* those of *Eophacops* are pronouncedly shifted southwards. This very likely reflects the extension of shallow-water carbonate facies at the expense of mudstone facies, consistent with the continental drift tendency during the Silurian (it can also be interpreted by the migration of the greater part of continents into the warm climatic zone).

The *Upper Silurian,* in particular the Ludlovian, is distinguished by a wide distribution of the genus *Ananaspis,* which is known from North America, the British Isles, Central Europe (Barrandian, Carnic Alps), North Africa (Morocco), and Central Asia (Kazakhstan). The probable representatives from south-eastern Australia (New South Wales, see Sherwin 1972) complement the picture of the wide distribution of *Ananaspis* along the Palaeotethys. The relation of *Ananaspis* to shallow-water carbonate facies and its principal distribution areas is analogous to that of *Eophacops.* Additionally, some remarkable genera of a strongly restricted distribution belong to the Silurian — for example, *Phacopidella,* of phylogenic significance and with some primitive dalmanitid features, which is so far known only from the Wenlockian of Czechoslovakia (Barrandian area), and *Denckmannites* from the Ludlovian of the same area, which provides a good example of eye-reduction depending on the living environment in the facies of the cephalopod limestone.

In the Silurian, the *Reedops* branch of phacopids also appears. It is represented by *Lochkovella,* known from the Upper Silurian of Europe (Carnic Alps) and reaching the maximum development in early Lower Devonian within the Palaeotethys (occurrences in Spain, North Africa, Thuringia, Barrandian, USSR, New South Wales).

The distribution of Silurian phacopids does not show any marked provincialism. This agrees with the observations made on other animal groups (cf. Boucot 1970; Holland 1971).

Yet, the relationship with the shallow water environment of the warm climatic zone is clear. Towards the end of the Silurian (in the Přídolian) a conspicuous decrease in phacopid fauna has been established, which can reflect the palaeogeographical changes or other factors, such as palaeoclimatic changes, changes of magnetic field, etc.

LOWER DEVONIAN

The Lower Devonian is characterized by a distinct differentiation of palaeobiogeographical provinces (cf. Boucot, Johnson & Talent 1967, 1969; House 1971) and by spectacular facies differences within marine regions (cf. Erben 1962, etc.). As to the phacopid trilobites, they experienced an extensive development and rich radiation.

The richest development is observable in the *Bohemian magnafacies* of the *Old World Province,* where most of the Lower Devonian genera and subgenera occur. Here are representatives of the genus *Phacops* linked with the Silurian genus *Ananaspis, Phacops (Boeckops), Phacops (Prokops), Lochkovella,* and *Reedops,* which reached its maximum development, and is especially abundant. Apart from the classical Barrandian area, the phacopid faunas of this composition have been found mainly in North Africa (Morocco), in the Bohemian magnafacies of the European Variscan geosyncline (France, southern and eastern parts of the Rheinisches Schiefergebirge, the Harz, Moravia), in Turkey (Bithynia, cf. Haas 1968), Central Asia (Kazakhstan, cf. Maksimova 1968), and probably also in south-eastern Asia and Australia. The migration possibilities within the Old World Province and with the Pacific region (Cordilleran Subprovince) of North America are demonstrated by the presence of *Reedops* in Nevada (Haas 1969), while the find of *Reedops* in Oklahoma (Ormiston 1968) indicates the possibility of migration into the Appalachian Province when a suitable facies is present. These two occurrences are accompanied by other trilobites of Bohemian type.

The typical *Rhenish magnafacies* of the Old World Province with prevailing clastic sedimentation is relatively poor in phacopids. This is most probably caused by unfavourable environment (strong supply of terrigenous sandy material).

Fig. 3. Distribution of phacopid trilobites in Lower Devonian (Lochkovian – Zlíchovian). Pp = Phacops (Phacops), Pa = Phacops (Paciphacops), Pr = Phacops (Prokops), B = Phacops (Boeckops), L = Lochkovella, R = Reedops. Supposed land areas stippled.

The Appalachian Province of North America is distinguished by a rich development of *Phacops* (*Paciphacops*), which is represented mainly by the *Phacops logani* Group. *Phacops* (*Paciphacops*) is also locally abundant in South America, even in the Malvinokaffric (Austral) Province, characteristic of the cold climatic zone in the Lower Devonian. The occurrences of *Phacops* (*Paciphacops*) in Central Asia and in the Far East (Maksimova 1972) point to the possibility of migration between the Appalachian and Old World Provinces. The phacopids included in *Phacops* (*Paciphacops*) are obviously less environment- and climate-controlled than, for example, *Reedops.*

Comparison of the distribution of Lower Devonian phacopids with the position of continents reconstructed from palaeomagnetic data and with palaeoclimatic conditions (Chlupáč & Krs 1967) shows that the phacopid faunas richest in genera and species were concentrated in the warm palaeoequatorial zone comprising most of the Old World Province and the Appalachian Province. The rather cold water phacopid faunas of South America (Malvinokaffric Province) are poor in genera and species, although the number of specimens is locally large (e.g. in Bolivia, cf. Wolfart 1968).

MIDDLE DEVONIAN

Assessment of phacopid occurrences in the Lower/Middle Devonian boundary interval is difficult because the Lower/Middle Devonian boundary is conceived differently by individual (German, French, Czechoslovak, and Soviet) geological schools. If this boundary were identified with the upper boundary of the Zlíchovian, as the case in the Bohemian magnafacies often is, the beginning of the Middle Devonian would be distinguished by a high differentiation of phacopid genera and subgenera: *Phacops* (*Chotecops*), *Eocryphops, Struveaspis* and *Ductina* would make their first appearance, and *Phacops* (*Phacops*), *Phacops* (*Paciphacops*), *Plagiolaria,* and the last representatives of *Reedops* and *Phacops* (*Boeckops*) would survive from the Lower Devonian. Most of these phacopids occur in the carbonate and pelitic facies of the Bohemian magnafacies of Europe, and North Africa. Remarkable are phacopids with reduced eyes (*Eocryphops,*

Fig. 4. Distribution of phacopid trilobites in Middle Devonian (Eifelian s. lat. – Givetian). Pp = Phacops (Phacops), Pa = Phacops (Paciphacops), Pch = Phacops (Chotecops), B = Phacops (Boeckops), R = Reedops, Ec = Eocryphops, Pl = Plagiolaria, S = Struveaspis, Du = Ductina. Supposed land areas stippled.

Plagiolaria, some species of *Struveaspis,* possibly also *Reedops*) or blind ones (*Ductina*), which occur mainly in the mudstone or cephalopod micritic limestone facies of pelagic environment in Europe and North Africa (Rheinisches Schiefergebirge, Harz, Barrandian, Moravia, Morocco) and south-eastern Asia (north Viet Nam, Thailand, see Maksimova 1965; Kobayashi & Hamada 1968). The relationship between these occurrences and the pelagic, often deeper-water geosynclinal facies provides evidence for the influence of the environment on eye-reduction (cf. Clarkson 1967); the same effect can be postulated even for the Lower Devonian, but phacopids from the shaly pelagic facies of this epoch are little known.

The *Middle Devonian* is characterized by a wide distribution of *Phacops* (*Phacops*), which is represented abundantly in the shallow-water platform and even geosynclinal facies of Europe, North Africa, West, Central and East Asia, and North America. It documents the rather cosmopolitan character of most Middle Devonian faunas, marked e.g. in brachiopods (Boucot, Johnson, & Talent 1967, et seq.). *Phacops* (*Chotecops*) is not so widespread; it is known from Europe (Barrandian, Rheinisches Schiefergebirge, Harz, Moravia, France, South England), Asia Minor (Bithynia) and North Africa. *Phacops* (*Chotecops*) tends to occur in impure limestone, mixed pelitic-carbonate to mudstone facies. Some differences in the distribution of phacopids (see e.g. Burton 1972) can be easily explained by environmental control rather than by geographical barriers, etc.

In North America, mainly in the Appalachian Province, the evolution of *Phacops* (*Paciphacops*), equal here to the *cristata* Group of phacopids, persists to the early Middle Devonian, during which it extends to Central Asia (Kazakhstan) as well. The Upper Eifelian and Givetian of North America are distinguished by an abundant development of *Phacops* (*Phacops*), comprising numerous species of the *Phacops rana* Group and *Phacops* (*P.*) *iowensis* Group (cf. Eldredge 1972).

Remarkable is the lack of phacopids in the Arctic region of Canada, where the facies development is very near the Bohemian magnafacies (elsewhere rich in phacopids). The character of trilobite faunas is also similar to that of the Bohemian type (cf. Ormiston 1967). This feature can be regarded as a manifestation of provincialism and interpreted in terms of geographic isolation or palaeoclimatic conditions.

During the *late Middle Devonian* (*Givetian*) the generic diversity of phacopids generally decreases (cf. Fig. 6). However, imperfect knowledge of the trilobite faunas from the geosynclinal carbonate and mudstone pelagic facies may be partly the cause.

UPPER DEVONIAN

Characteristic of the Upper Devonian Epoch is the extinction of many trilobite families and higher groups; calymenids, calmonids, homalonotids and cheirurids die out near the Middle/Upper Devonian boundary, and scutelluids, harpids, dalmanitids and odontopleurids become extinct during the Frasnian or near the Frasnian/Famennian boundary. This boundary is especially prominent, and represents a sudden break in the evolution of Devonian faunas and their environment on a global scale (extinction of reefs, extension of pelagic facies, etc.). Extra-terrestrial effects are considered as possible causes of this change by some authors (McLaren 1971). However, the evolution of the family Phacopidae was affected, but not interrupted by these events, so that it continued throughout the Upper Devonian until the Devonian Carboniferous boundary.

The evolution of *Phacops* (*Phacops*) and *Phacops* (*Chotecops*) persists during the *Frasnian,* although the number of known species is smaller than in the Middle Devonian (they are known from Europe, North Africa, Central and East Asia and North America). The development of *Cryphops* with reduced eyes decreases in the late Frasnian. *Cryphops* finds are concentrated in the pelagic facies of the Old World Province (England, Rheinisches Schifergebirge, Harz, Thuringia, Carnic Alps, Moravia, Ural Mts., Asia Minor, North Africa, Kweichow in China).

The development of *Phacops* (*Phacops*) and *Phacops (Chotecops)* continues in the *late Upper Devonian (Famennian),* and some species are of a wide geographical distribution – *Phacops (P.) granulatus* (Münster) is recorded from many European regions (south-western England, Rheinisches Schiefergebirge, Harz, Thuringia, Góry Swietokrzyskie in Poland, Silesia, Moravia and Spain), from the South Ural region, Kirgizia, China (Great Chingan) and North-Africa (Morocco, Sahara). One of the youngest phacopids, *Phacops* (subg.?) *accipitrinus* (Phillips) from the *Wocklumeria* Zone, is also widely distributed; it tends to have a greater concentration in shallow-water facies influenced by current activity. Occurrences of this species are known from England, Rhineland, Belgium, northern France, Moravia, North Africa, U.S.S.R. and Afghanistan.

Fig. 5. Distribution of phacopid trilobites in Upper Devonian (Frasnian – Famennian). Pp = Phacops (Phacops), Pch = Phacops (Chotecops), C = Cryphops, D = Dianops, Di = Dienstina, Du = Ductina, N = Nephranops, T = Trimerocephalus.

Characteristic of the *Famennian* is the rich development of phacopids with reduced eyes *(Nephranops, Dienstina),* or phacopids completely blind *(Trimerocephalus, Dianops, Ductina).* As in the Middle Devonian, the phacopids with reduced eyes are concentrated in the facies, which is of rather pelagic, both shaly and impure, limestone character. They can be distinguished from so-called *Clymenia* Limestones, where they are accompanied occasionally by phacopids with well developed eyes (Maksimova 1955; Chlupáč 1966). The occurrences of these phacopids have been established in the Old World Province, mainly in geosynclinal areas: European Variscan geosyncline (southern England, northern France, Rhineland, Harz, Saxony – Thuringia, Frankenwald, Poland, Silesia, Moravia, Carnic Alps, North Africa, Asia Minor, Ural region, Kazakhstan).

The distribution of phacopids during the Famennian, as that of goniatites (House 1971, 1973), suggests the possibility of migration, especially within the Old World Province between Europe, North Africa and Central and South-East Asia, i.e. within the Palaeozoic Tethys. The dependence of some phacopids (in particular with reduced eyes) on pelagic environment explains their absence from the areas of the former Appalachian Province of North America. It is so far difficult to decide whether the lack of these forms, e.g. in the Cordilleran region, Alaska, and in eastern Australia, is the result of provincialism or of insufficient investigation.

The sudden and complete extinction of phacopids near the *Devonian/Carboniferous boundary* is striking. It is extremely remarkable because during the Famennian a relatively rich radiation of phacopids takes place, and at the Devonian/Carboniferous boundary both phacopids of older branches (*Phacops* and its subgenera) and genera appearing as late as in the Famennian die out. The complete extinction of phacopids is approximately synchronous with the extinction of clymeniid cephalopods. It is one of the most important events that justifies the drawing of the upper boundary of the Devonian at the upper boundary of the *Wocklumeria* Zone. On the other hand, it is remarkable that e.g. the development of small cyrtosymbolid trilobites, which in the Famennian are common associates of phacopids, continues from the Famennian into the Lower Carboniferous without substantial changes, and many genera and subgenera of cyrtosymbolids overreach this boundary (cf. Chlupáč 1966 et al.). The sudden extinction of phacopids and clymenids at the end of the Famennian is difficult to explain; it may be tentatively accounted for by the change of geomagnetic field, which is most important to the evolution in general, as pointed out by Crain (1971).

CONCLUSIONS

The main distribution of the trilobites of the fam. *Phacopidae* falls in the *Silurian* in a shallow-water environment (mainly carbonatic facies), where it does not show any marked provincialism and is probably controlled by palaeoclimatic factors. This is also evidenced by the close affinity of phacopids of the Old World and North America, and by synchronous changes in their evolution. The uppermost Silurian (Přídolian) is distinguished by the decrease in phacopids, and reflects a certain crisis in their evolution.

In the *Lower Devonian,* the family shows an extensive development, and phacopids display a distinct provincialism (e.g. marked differences between the phacopids of the Old World Province and the Appalachian Province). The phacopid associations richest in genera and species occur in the Palaeozoic Tethydian region, mainly in the Bohemian magnafacies, and genera-poor associations extend into the Malvinokaffric Province (cool zone in the Devonian). The Rhenish magnafacies is relatively poor in phacopids (probably unfavourable environment in areas of clastic sedimentation).

In the *Middle* and *Upper Devonian* the rich development of phacopids continues in the Old World Province. The phacopids of these epochs attest to the possibility of migration, in particular between Europe and North Africa and between Europe, Central and Southeast Asia. The associations richest in genera are assembled in geosynclinal facies. In North America, a strikingly lower diversity in generic representation has been observed. Although the distribution of phacopids (esp. those with reduced eyes) is environmentally controlled, the lack of phacopids

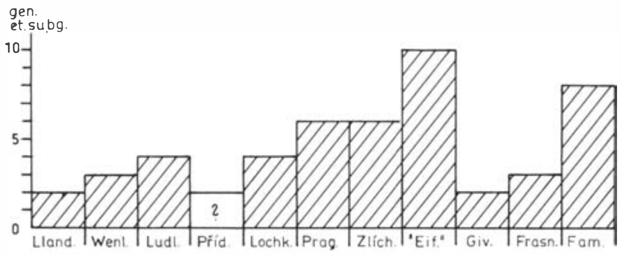

Fig. 6. Representation of genera and subgenera of phacopid trilobites during Silurian and Devonian.

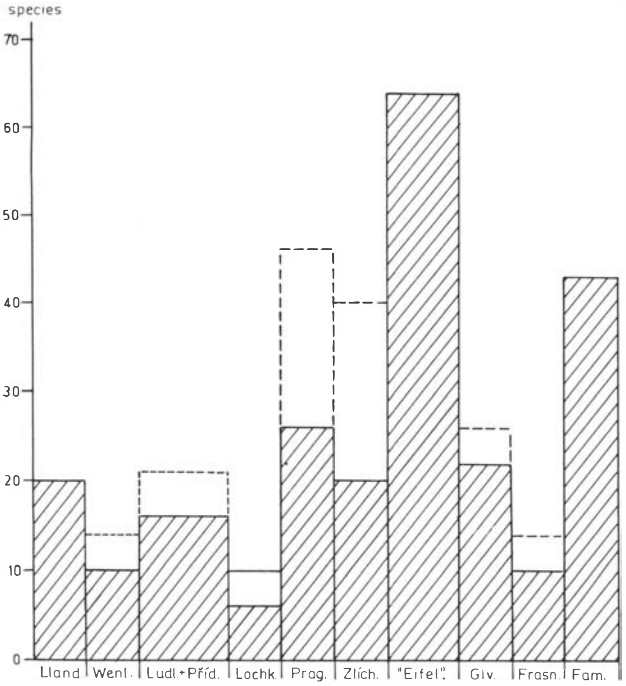

Fig. 7. Representation of species of phacopid trilobites during Silurian and Devonian (as of 1972, empty parts of columns = occurrences of species not precisely dated with regard to stage).

in the Canadian Arctic Islands cannot be explained in these terms, and some other factors causing a certain provincialism should be considered (palaeoclimatic factors, geographic barriers, etc.).

During the *Upper Devonian* (esp. Famennian) there is a striking development of phacopids with reduced eyes, synchronous with the extension of areas of pelagic facies. The changes in the phacopid faunas in the Upper Devonian occur at the same levels as the changes documented in other animal groups (e.g. cephalopods and brachiopods) and mirror the events affecting the character of the marine associations the world over. They can be explained, for example, by climatic changes, changes in the Earth's magnetic field, or in the case of the changes at the Frasnian-Famennian boundary, even by extraterrestrial agents. The extinction of the whole family at the Devonian/Carboniferous boundary is one of the important criteria for drawing this boundary at the upper limit of the *Wocklumeria* Zone.

The diagram of stratigraphic representation of genera and subgenera of phacopids (Fig. 6) reflects a gently progressive development during the Lower and Upper Silurian, a retreat of phacopids in the uppermost Silurian and an increasing diversity during Lower Devonian up to the maximum diversity gradient reached in the early Middle Devonian. The larger diversity in the uppermost Devonian (Famennian) is caused mainly by the development of phacopids with reduced eyes under environmental control. The diagram of species diversity (Fig. 7) shows most features common to Fig. 6. It should be noted, however, that the exact stratigraphical occurrence of many species with regard to the stage division is not sufficiently known, and numbers of species recorded from respective stages are rather approximate.

The areas of wide distribution and radiation of phacopid trilobites during their entire development from the beginning of the Silurian until the end of the Devonian are consistent with the alleged course of the warm periequatorial zone in Silurian-Devonian time, interpreted from the palaeomagnetic, lithologic, and palaeontologic data. Hence, they are in full agreement with the concept and trend of the continental drift during the Silurian and Devonian.

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Homalonotinae in Upper Silurian and lowermost Devonian biostratigraphy and palaeogeography

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Tomczykowa, Ewa 1975 07 15: Homalonotinae in Upper Silurian and lowermost Devonian biostratigraphy and palaeogeography. *Fossils and Strata,* No. 4, pp. 409–414. Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

The stratigraphical and palaeogeographical importance of Homalonotinae is discussed. The Homalonotinae are a very characteristic group of trilobites with a very limited stratigraphical range. Their importance is particularly well demonstrated in the Upper Silurian and lowermost Devonian deposits in Poland. Their wide geographical distribution in the Lower Devonian deposits can considerably facilitate the correlations between different areas of sedimentation and reflects zoogeographic connections. The occurrence of Homalonotinae in Upper Silurian and Lower Devonian sediments in Europe helps us to reconstruct the extent and migration of benthic faunas within the Rhenish facies.

Томчикова, Е.: Homalonotinae как биостратиграфический и палеогеографический показатель в верхах силура и низах девона. В статье рассмотрено стратиграфическое и палеогеографическое значение Homalonotinae. Они представляют весьма характерную группу трилобитов, распространенных в очень узком стратиграфическом интервале. Особенно важную роль играют Homalonotinae в верхнем силуре и нижнем девоне Польши. Их широкое геогражическое распространение в отложениях нижнего девона может в значительной степени облегчить корреляцию между отдельными областями седиментации и выявление зоогеографических связей. Распространение Homalonotinae в верхнесилурийских и нижнедевонских отложениях Европы способствует определению границ распространения и миграции бентонной фауны в пределах рейнской фации.

The abundant Homalonotinae in the Upper Silurian and Lower Devonian of Poland have been referred to nine species of five genera.

They give evidence for important conclusions as to the evolution, biostratigraphy, and palaeogeography of this group of trilobites. The present author has collected an ample material for comparative studies, particularly moulds of most holotypes of the type species. The total number of known and described species of Homalonotinae does not exceed 70, about 30 being synonyms.

So far only 13 species have been described from the Silurian. The remaining species are Lower Devonian. It appears that the vertical ranges of the individual species of Homalonotinae were short-lived. Thus, in possession of sufficient material, we can observe not only their evolution, but can also subdivide deposits in which they occur. The Homalonotinae are a group of very progressive trilobites, whose stratigraphical range slightly exceeds the Llandoverian-Emsian interval.

STRATIGRAPHICAL OCCURRENCE OF THE HOMALONOTINAE

The first Homalonotinae appear in the Llandoverian, and then they develop fairly intensely in the Wenlockian and Ludlovian. Their main development, however, is related to the Lower Devonian, at the end of which they disappear.

Only some species are of biostratigraphical importance in the Silurian; nevertheless *Trimerus delphinocephalus* Green enabled the correlation of the Wenlockian deposits of England and of North America to be defined accurately. *Homalonotus knighti* König, described for the first time from the Upper Ludlovian of Great Britain, also determined the Upper Ludlovian in North America (McLearn 1924), and in Poland both in the Góry Świętokrzyskie and in the eastern part of the Peri-Baltic area (Tomczykowa 1971).

The Post-Ludlovian–Pre-Gedinnian deposits have so far been little examined, hence the

Table 1. Upper Silurian and Lower Devonian in Poland.

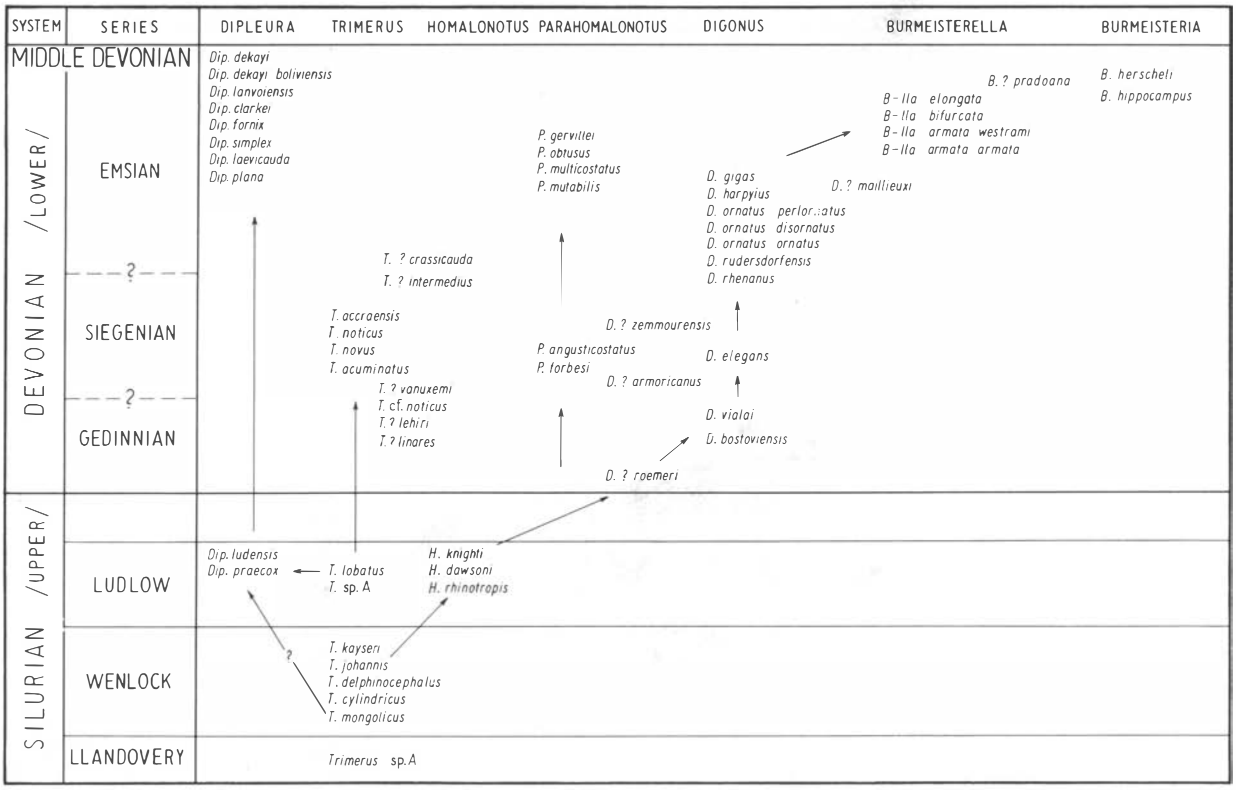
SYSTEM	SERIES	STAGES		GRAPTOLITE ZONES	TRILOBITE OCCURRENCE
DEVONIAN /LOWER/	EMSIAN			OLD RED /predominantly/	
	SIEGENIAN	Ciepielów Beds	Upper	Rare graptolite remnants	Eurypterids and fishes Tentaculitids, bivalves, brachiopods
			Lower		*Parahomalonotus angusticostatus* *Digonus elegans* *Trimerus novus* *Parahomalonotus forbesi* *Acastella rouaulti*
	GEDINNIAN	Bostów Beds	Upper		*Digonus vialai* *Digonus bostoviensis* *Phacopina* n. sp. *Podolites rugulosus*
			Lower		*Acastava* n. sp. *Podolites rugulosus rhenanus* *Acastella tiro* *Acastella elsana*
SILURIAN /UPPER/	PODLASIAN	Podlasie Beds	Upper	*Monograptus angustidens* *Pristiograptus transgrediens* *Pristiograptus perbrevis* *Pristiograptus admirabilis* *Monograptus bouceki–M. perneri*	*Acastella* n. sp. *Acastella spinosa podolica* *Calymene tuberculata* *Acastopyge shergoldi* *Calymene tentaculata*
			Lower	*Pristiograptus samsonowiczi* *Pristiograptus chelmiensis* *Pristiograptus bugensius* *Monograptus ultimus*	*Acaste podolica* *Calymene beyeri* *Acaste dayiana* *Acastella prima*
	LUDLOW	Siedlce Beds	Upper	*Monograptus* n. sp. *Monograptus formosus* *Monograptus* n. sp.	*Homalonotus knighti* *Acastella spinosa* *Dipleura praecox* *Trimerus lobatus*
			Middle	*Monoclimacis haupti* *Monoclimacis tomczyki* *Pristiograptus dubius frequens*	Trilobites yet not discovered
			Lower	*Neocucullograptus kozlowskii* *Neocucullograptus auriculatus* *Bohemograptus cornutus* *Bohemograptus praecornutus* *Bohemograptus bohemicus*	
		Lower		*Saetograptus leintwardinensis*	*Spathacalymene linguata*

fauna occurring in them is not known satisfactorily. In Poland, the Podlasian deposits (Table 1) are developed in clay lithofacies (Tomczyk 1970) and comprise nine graptolite zones. Trilobites of the following genera occur in the shallow-neritic facies, in which five ostracode-trilobite zones have been recently distinguished (Tomczykowa & Witwicka 1974): *Calymene, Proetus, Leonaspis,* as well as the stratigraphically very important *Acaste, Acastella,* and *Acastopyge*. So far, Homalonotinae have not been found in these deposits either in Poland, or in Podolia.

The Homalonotinae present very valuable biostratigraphical evidence in the Lower Devonian of Rhenish facies, beginning mainly with the Upper Gedinnian. In the Lower Gedinnian in Poland, as within the entire zone of the Rhenish facies, trilobites including *Acastella* prevail. *Digonus? roemeri* (Koninck), thought to be a Lower Gedinnian species, is very difficult to identify, since its holotype is missing, and a neotype has so far not been determined. Specimens that are referred by Richter & Richter (1954) and Balashova (1968) to *Homalonotus (Digonus) roemeri* seem to be doubtful.

In Poland, deposits characterized by an uninterrupted marine sedimentation occur and their faunas have been investigated thoroughly (Tomczykowa & Tomczyk 1970), from the Ludlovian up to the Siegenian inclusive (Table 1). The representatives of Homalonotinae appear in the Upper Ludlovian, and then reappear in the Upper Gedinnian. Along with numerous Acastavinae, *Digonus bostoviensis* Tomczykowa and *D. vialai* (Gosselet) also occur. Higher up, as early as in the Siegenian deposits, the specimens of Homalonotinae are very abundant. There occur here one after another: *Parahomalonotus forbesi* (Rouault) known from Brittany; then *Trimerus novus* Tomczykowa, in some measure resembling *Trimerus acuminatus* (Tromelin & Lebesconte) from Brittany, and later *Digonus elegans* Tomczykowa and *Parahomalonotus angusticostatus* Tomczykowa (Table 1).

Table 2. Stratigraphical ranges of some Homalonotinae.



The Upper Gedinnian and the Lower Siegenian are best represented by Homalonotinae from Poland and Brittany. The higher members of the Siegenian and the Emsian, along with *Homalonitinae* occurring in them, are better known from the area of Germany. The following representatives are found, probably in the Middle and Upper Siegenian: *Trimerus? intermedius* (Viëtor) and numerous species of the genus *Digonus,* such as: *D. rhenanus* (Koch), *D. rudersdorfensis* Richter & Richter, and a group of *D. ornatus* (Table 2). At the decline of the Siegenian, maybe already in the Emsian, the uninterruptedly occurring species of the genera *Digonus* and *Trimerus,* like *T.? crassicauda* (Sandberger) and *D. gigas* (Roemer), are accompanied by the representatives of the genera *Burmeisterella, Parahomalonotus,* and *Dipleura* (Table 2). Unfortunately, their precise stratigraphical dependence has not been explained.

Numerous species of Homalonotinae described from the Lower Devonian of Germany (Roemer 1843–1870, Sandberger 1856, Koch 1883, Kegel 1913, Viëtor 1919, Richter & Richter 1932, 1954) have also been described or reported from Belgium (Asselberghs 1946; Maillieux 1940) and from France (Peneau 1928; Renaud 1942; Pillet 1961). From the point of view of detailed stratigraphy, their occurrence is also unsatisfactorily known. It seems, however, that most species are already referred to the Emsian deposits. Some species of Homalonotiae are more wide-spread, like *Digonus gigas* (Roemer) known to occur in the Świętokrzyskie Góry (Czarnocki 1936), the Sudetes Mts., Rhineland (Koch 1883), Ardennes (Asselberghs 1946), and Spain. In Great Britain only *Burmeisterella elongata* (Salter) and *B. bifurcata* Reed appear in the Emsian (Table 2). In Turkey, within the Bithynia area (Haas 1968), are found *Dipleura fornix* Haas and *Parahomalonotus gervillei* (Verneuil), which probably also appear in Roumania (Iordan 1967).

The Homalonotinae, known to occur in other continents, are not abundant, and do not have any biostratigraphical significance. They are very important, however, in the correlation and discussion on the extent of the sedimentary basin and on its neritic facies. Most Homalonotinae that belong to the Lower Devonian of South Africa and South America, mainly of Bolivia, Brazil, and Uruguay, are found probably in the Emsian deposits, like the same or related species in Europe.

PALAEOGEOGRAPHICAL IMPORTANCE OF HOMALONOTINAE

On the basis of the distribution of the Homalonotinae, one can investigate in Europe the extent of the northern neritic zone, which in the Devonian is called the zone of Rhenish facies. This zone came into being already in the Upper Ludlovian, running from the Šwietokrzyskie Góry through North Poland, Gotland Island and Scania, westwards as far as the northern area of France (Artois) and Great Britain (Wales). From there it was connected with the province of the north Appalachians (Maine, Nova Scotia). The deeper basin extended in Europe southwards from this Upper Silurian northern neritic zone. The south neritic zone of this basin is proved by the Upper Silurian sediments and their fauna in the Barrandian area (Chlupâč 1960).

In the light of the latest theory of plate tectonics, the distribution of the benthic fauna in the Proto-Atlantic Ocean proves a free migration within a shallowing zone before the advancing continental collision (McKerrow & Ziegler 1972). A complete shallowing within the area of Great Britain at the decline of the Silurian was probably the final act of the marine sedimentation as proved by the Downtonian deposits, and by the lack of the Gedinnian and Siegenian marine deposits.

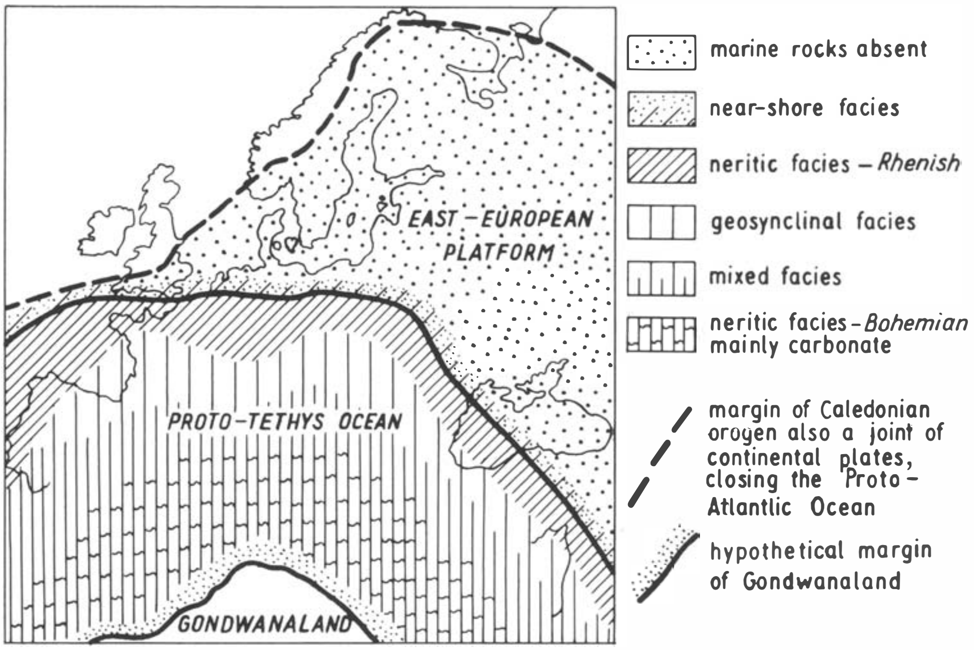


Fig. 1. Tentative facies map of the Gedinnian-Siegenian (Early Devonian) in the Proto-Tethys region.

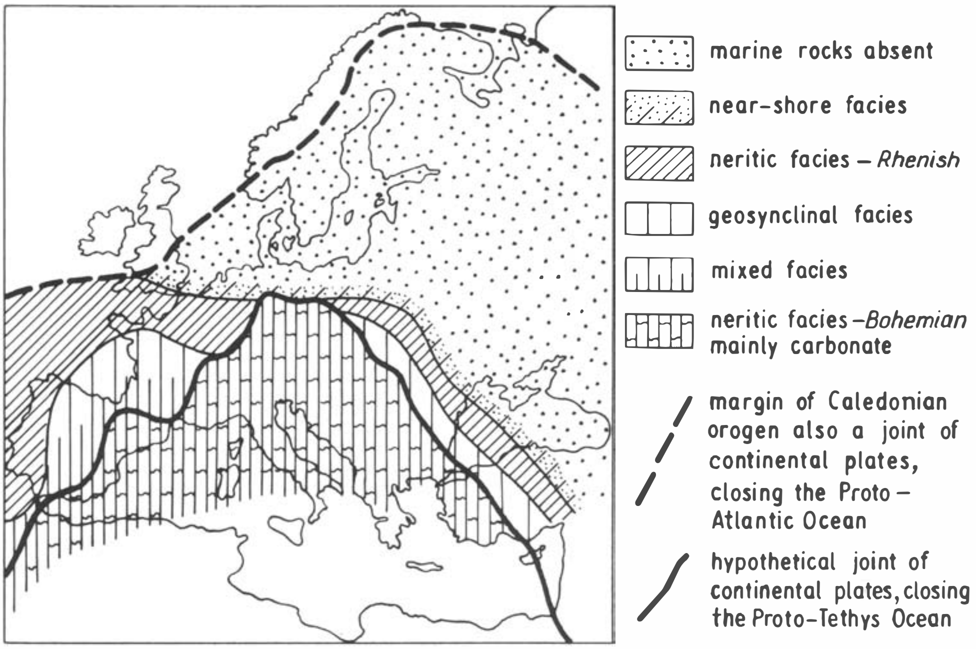


Fig. 2. Reconstruction of areas with preserved Gedinnian-Siegenian marine sedimentary rocks after the closing of the Proto-Tethys, probably due to the collision of continental plates.

In Poland, in the Podlasian (Table 1), the neritic zone persisted in the Peri-Baltic area; its partial relations to the Downtonian are evidenced by the research of ostracodes and trilobites (Tomczykowa and Witwicka 1974). In the Świętokrzyskie Góry, marine sedimentation seems to be deeper with sporadic faunal entrances. It may well be that the Upper Silurian deep basin migrated southwards from the Świętokrzyskie Góry, being an obstacle for benthic fauna migration, previously interpreted by the author as emergence.

At the decline of the Silurian and at the beginning of the Devonian in Europe, the northern neritic zone was displaced distinctly southwards. In Poland, a shallow basin with a rich benthic fauna, typical of the Rhenish facies, developed in the northern part of the Świętokrzyskie Góry, and more to the north (Tomczyk 1968, 1970; Tomczykowa & Tomczyk 1970). In the east it was connected with the area of Podolia, and in the west with the Rhineland, Ardennes, and Artois, further west with Brittany, and in the south with the Anti-Atlas in Morocco. Perhaps this basin at the Gedinnian or at the Siegenian had a branch which extended in a southern direction as far as Mauretania and Ghana. From here single species of Homalonotinae are known as *D.? zemmourensis* Pillet and *Trimerus accraensis* (Saul). It is also possible that this basin was connected with South America, where the oldest Lower Devonian Homalonotinae are represented by such species as *T.? linares* (Salter), *Trimerus noticus* (Clarke), and *T.* cf. *noticus,* known from Uruguay, Bolivia, and Brazil (Berry & Boucot 1972).

However, the determination of the extent of the basin and of its neritic zones must be supported by a precise biostratigraphical correlation based mainly on the benthic fauna. Determination of complete stages during the palaeobiogeographical consideration with respect to the Old World Province (Johnson & Dasch 1972; Johnson & Boucot 1973) is unsatisfactory today. The Old World province with its two facies, which have been called for a long time the Rhenish and Bohemian (Fig. 1), are still underestimated, particularly regarding the Gedinnian and Siegenian. Undoubtedly they make two, completely separate neritic zones, which at present are accidentally juxtaposed (Fig. 2). It seems that a gradual restriction of the Proto-Atlantic Ocean (McKerrow & Ziegler 1972) could have corresponded with the contemporaneous retreat of the Proto-Tethys Ocean, of which the Barrandien constituted the opposite neritic zone (Fig. 1). Such a retreat might have begun at the close of the Lower Ludlovian, when the so-called Cracow Phase of Caledonian movements occured in Poland (Lydka, Siedlecki & Tomczyk 1963). Since that time, the benthic fauna have developed between Poland and Barrandien in a quite different way. The difference is evidenced by a benthich fauna, including trilobites, not only Homalonotinae, but also Acastavinae, which do not occur in the Bohemian facies.

Unfortunately, the deposits of the uppermost Silurian, Gedinnian, and Siegenian, as well as their extent and fauna within the area of Europe, have so far not been investigated satisfactorily. A close time-correlation between the Lochkovian interval and the Gedinnian and Siegenian still remains debatable. Detailed additional studies of Homalonotinae from the Gedinnian and Siegenian deposits of the Rhineland and Ardennes, where no doubt a migration of benthic fauna took place between the area of Poland and Brittany, could explain numerous questions related not only to the detailed biostratigraphy, but also to the range of the northern neritic zone of this very important basin that closes the sedimentation of the Lower Palaeozoic of Central Europe.

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Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia

CHRISTOPHER P. HUGHES

Hughes, C.P. 1975 07 15: Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia. *Fossils and Strata,* No. 4, pp. 415–435, Pls 1– 13, Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

Previously studied specimens and additional material of *Burgessia bella* from old and new collections have been prepared, and new photographs accompanied by explanatory line drawings are given together with reconstructions in various aspects. The carapace is roughly circular, invaginated posteriorly, and extends back above the trunk leaving only the long unsegmented posterior spine uncovered. The carapace is gently convex sagitally and transversely. No cephalic doublure or ventral plates are present. The body is segmented and appears to have been subcircular in cross-section, with no pleurae. The mouth is ventral. Four appendage-bearing somites lie within the cephalon and the remaining eight in the trunk. A large kidney-shaped gut-caecal system occupies the lateral portion of the carapace, being connected by a wide diverticulum to the alimentary canal at the posterior cephalic somite. The so-called eyes are reinterpreted as attachment areas for muscles connecting the anterior end of the body to the carapace. The anterior cephalic appendages consist of a pair of multijointed uniramous antenna, the second, third and fourth are biramous, consisting of a jointed walking-leg and a whip-like flagellum. All the trunk appendages, except the last, are biramous and consist of a coxa with telopod composed of six segments and terminal claws, and a small lateral, leaf-like gill branch presumed to be attached to the coxa. The posterior appendage is believed uniramous consisting simply of a backwardly curved spike. The telson consists of an anal segment lacking lateral appendages, and a long, tapering unsegmented caudal spine jointed at the base to the anal segment. Dark stains are occasionally associated with specimens and are presumed to represent organic matter squeezed out of the body during compaction. The carapace ranges from four to seventeen mm in maximum width, the size-frequency histogram being unimodal except that the smallest three specimens are somewhat detached. The occurrence within the Phyllopod bed closely matches that of *Waptia, Marrella,* and *Yohoia.*

Christopher P. Hughes, Sedgwick Museum, Downing Street, Cambridge CB2 3EQ, England, 1st August, 1973.

A re-investigation of the stratigraphy, palaeontology and palaeoecology of the Burgess Shale was begun in 1966 by the Geological Survey of Canada, with the kind cooperation of the authorities of the Yoho National Park and the Department of Indian and Northern Affairs. Ottawa. Field work was undertaken in 1966 and 1967 (Aitken, Fritz & Whittington 1967, Aitken & Fritz 1968). The author was kindly invited to join the palaeontological investigation by Whittington in 1967. The paper, one of a series devoted to the systematic redescription of the fauna and flora of the Burgess Shale, is concerned with the third most common non-trilobite arthropod, *Burgessia bella.* Although abundant, this species has attracted less attention since Walcott's original descriptions (Walcott 1912, 1931) than some other species, Simonetta (1970) being the only author to give a redescription based on a reappraisal of the original collections. As in the restudy of other forms (Bruton in preparation, Whittington 1971b, 1974, 1975) preparation of previously described specimens together with detailed study of much additional material has revealed new information. Also it is shown that specimens do not lie precisely parallel to the bedding surface, but that different parts of an individual lie at slightly different levels within the rock.

The photographs used herein have been taken using ultraviolet radiation both at high and low incident angles (Whittington 1971b: 1, 2). All previously figured material is refigured, many with accompanying explanatory camera lucida drawings. Since the drawings were made using a variety of lighting conditions, in some instances they show details not at all clear on particular photographs – any doubts of interpretation may thus only be resolved by examination of the relevant specimen.

Throughout this work I have been greatly aided by discussions with Professor H.B. Whittington and Dr. D.L. Bruton, who together with Drs. W.T. Dean and W.H. Fritz have critically read the manuscript. I am also indebted to Dr. S.M. Manton, F.R.S., for much useful discussion, particularly concerning the function of the appendages. Drs. Porter M. Kier and Richard E. Grant, United States National Museum (USNM), gave every facility for study of the Walcott collections. The figures were prepared by Mr. John Lewis and photographs enlarged by Mr. David Bursill. To all these persons I give my thanks. I am also particularly grateful to the organisers and sponsors of the NATO advanced study institute held in Oslo in July 1973 for the invitation to present the results of this study. Financial support for this study was provided by Natural Environment Research Council grant GR3/285 awarded to H.B. Whittington.

Preservation

Whittington (1971a: 1180 – 1189) has discussed the general nature of the preservation of the Burgess Shale fossils, with specific reference to *Marrella* (see also Whittington 1971b: 19 – 20), and Piper (1972) has postulated a sedimentary model for the deposition of the Burgess Shale. Both the palaeontological and sedimentological evidence suggest that preservation was due to the live entombment in a moving cloud of sediment, presumably in the terminal regions of a turbidity flow, where current velocity and turbulence would be relatively low. The preservation of *Burgessia* supports this, in that, like all other forms so far restudied, the specimens are preserved as a thin, dark apparently carbonaceous film, with individual specimens being preserved at all angles to the bedding plane (Pl. 1: 1, 4, 9), although when the specimen is preserved very obliquely to the bedding, problems of identification arise (Pl. 13: 1). Many specimens are twisted to some extent, and in particular the carapace is commonly pulled forward from over the trunk (Pl. 3: 8, Pl. 4: 1) and in extreme cases nearly pulled completely free of the remainder of the animal (Pl. 7: 1, 2), this presumably reflects the effects of transportation for at least a short distance within the entombing sediment cloud.

Compaction has been considerable, and one effect has been to rotate the walking-legs so that the anterior-posterior surfaces lie parallel to the bedding (this has also been demonstrated in *Olenoides* (Whittington 1975) and is almost certainly the case in other forms). The gill branches, however, appear to have retained their approximate life-attitude in specimens preserved approximately parallel to the bedding, which is to be expected. Gill branches have not been identified in obliquely preserved specimens where they may have been rotated, or possibly more likely crumpled due to their fragile nature.

Virtually no decomposition of the specimens has taken place and the ventral cuticle appears to have been intact during transportation and compaction since in not one specimen are the appendages displaced relative to the body or each other.

In his redescription of *Yohoia,* Whittington (1974) has shown that the preservation of *Yohoia*, and by inference, that of many other Burgess Shale fossils, is such that part and counterpart specimens are not directly comparable with those of more common types of preservation, which might, for example, show the outer surface of the exoskeleton and a mould of the outer surface, or if the shell has been dissolved away, moulds of the internal and external surfaces. Rather he showed that in *Yohoia* the split has occurred within the exoskeleton and not along either the inner or outer surface. The situation is further complicated by the fact that the surface along which the rock splits jumps from one level to another on which different portions of the specimen are preserved. Though it is more difficult to be certain that this is the case in *Burgessia* since the carapace is smooth, there is no reason to suspect that it is any different. The full nature and significance of this type of preservation is not fully understood at present. Since it is impossible to say in a particular specimen whether one is seeing the inside, outside, or some internal surface of the exoskeleton, counterpart specimens preserved in lateral or oblique views are simply referred to as lateral or oblique; the prefixes left and right or dorsal and ventral are not used. In parallel preserved specimens, if the carapace is nearer the exposed surface than the appendages, then the specimen is referred to as being a dorsal view, whereas if the reverse is the case, then it is referred to as a ventral view. Since in oblique preservation the carapace becomes wrinkled, the terms forward and backward as applied to *Marrella* by Whittington are not employed.

Terminology

As advocated by Whittington (1971b) descriptive terms such as 'walking-leg' and 'gill branch' have been used in preference to terms such as 'exopodite' and 'endopodite', since they have the advantage of not being the same as applied in either the trilobite or crustacean literature, and so carry no implication of possible phylogenetic relations. However, there are certain terms used in arthropod studies that can be usefully employed, and in general such terms are used as defined by Moore & McCormick (*in* Moore 1969: 90 – 103), e.g. 'segment' for an individual component of a limb, connected by a movable 'joint' with the adjoining segment. A few terms (see below) are not used strictly acccording to their definitions, either because they are defined in terms of specifically modern arthropod morphological terms, or because sufficient details of morphology are not known in *Burgessia.* A few terms are used in a restricted sense. Terms relating to the gut-caecal system are based on those of Öpik (1961). Terms relating to the attitude of the specimens within the rock have been discussed above (*Preservation*).

Antennae: Anterior pair of uniramous, multisegmented appendages.

Carapace: This term is restricted to the dorsal, slightly sclerotized surface of cephalic cuticle. The unsclerotized cuticle forming the underside of the fold of cephalic exoskeleton is not included.

Endite: Ventrally positioned lobe of coxa or of any walking-leg segment.

Flagellum: Slender, outer branch of post-antennal cephalic appendage. Not known whether it is multisegmented.

Explanation of symbols on Plates and Figures.
a = antenna
ad = anterior diverticulum
al = anterior lobe of gut
al c = alimentary canal
an = anus
ap = appendage (branch not specified); suffix denotes somite number following antenna
c = caecum
ca = carapace
cl = claws
cn = caecal node
co = coxa
coe = coxal endite
d = diverticulum
ds = dark stain
e = endite
fl = flagellum
g = gill branch, suffix denotes trunk somite number
hj = hinge joint
j = joint
icn = intercaecal node
l = prefix indicating left side
m = mouth
ma = muscle attachment area
mc = margin of unsclerotized cuticle
ms = muscle strands
ob = outer branch of cephalic appendages, suffix denotes somite number following antenna
pd = posterior diverticulum
pj = pivot joint
r = prefix indicating right side
s = segment
se = seta
t = telson
w = walking-leg, suffix denotes somite number following antenna
1–11 = suffixes denoting the number of the appendage numbering from the first post-antennal biramous appendage, except for the gill branches which are numbered from the first trunk somite.

Hachures show break in slope, the solid line at the upper edge of the break, the hachures directed downslope from this line.

GENUS *BURGESSIA* WALCOTT, 1912

SYSTEMATIC ATTRIBUTION. – Family Burgessiidae Walcott, 1912. [*nom. corr.* Størmer 1959 (*ex* Burgessidae Walcott, 1912)].

TYPE SPECIES. – *Burgessia bella* Walcott, 1912 by original designation.

DIAGNOSIS. – Subcircular carapace extending back over trunk with wide invagination posteriorly, no compound eye, no well-developed sclerotized labrum. One pair of antennae with twenty to thirty segments, three post-antennal biramous cephalic appendages with inner branch a walking-leg, outer branch a flagellum. Trunk of eight segments without pleurae, each, except the last, with a pair of biramous appendages, inner branch a walking-leg, outer branch a gill-branch, eighth somite with short uniramous appendages. Telson of anal segment, without lateral appendages, and long unsegmented, single, caudal spine. Large gut-caecal system fills most of carapace, connected to alimentary canal at posterior cephalic somite by a large diverticulum.

GEOLOGICAL HORIZON. – Middle Cambrian, Stephen Formation, Burgess Shale section, *Bathyuriscus – Elrathina* Zone, British Columbia.

BURGESSIA BELLA WALCOTT, 1912

Plates 1 – 13, Figs. 1 – 35

SYNONYMY. – □ 1912 Walcott: 177–180, Pl. 27: 1–3; Pl. 30: 3. (*non* Pl. 30: 4 which is *Waptia fieldensis*). □ 1920 Raymond: 108–109. □ 1925 Fedotov: 385, 386, 389. □ 1928 Henriksen: 11–13. □ 1930 Beurlen: 501. □ 1931 Walcott: 15–20, Figs. 3–5, Pl. 15: 4–7; Pl. 16; Pl. 17; Pl. 18: 1. □ 1932 Richter: 855, 866, Fig. 44B. □ 1939 Størmer: 232, 236, 237, Fig. 30c. □ 1944 Størmer: 98, 99, Figs. 19, 1–4, 25. □ 1949 Størmer *in* Grassé: 204, Fig. 30. □ 1958 Tiegs & Manton: 291–293, 313, 316, Fig. 6C. □ 1959 Størmer *in* Moore: O32, Fig. 21, 1–5. □ 1970 Simonetta: 41, 42, Pl. 28: 1–3, 5–10; Pl. 29; Pl. 30: 1–3; Pl. 32: 1–4.

LECTOTYPE. – USNM 57676, Pl. 1: 2, 3, 8, Figs. 11, 12; original of Walcott 1912, Pl. 27: 1, designated herein. Also figured Richter 1932, Fig. 44B; Simonetta 1970, Pl. 28: 1.

OTHER MATERIAL. – USNM 57677 – 57678, 57680 (erroneously recorded as USNM 57679 by Walcott 1912, explanation Pl. 30: 3), originals of Walcott 1912, Pl. 27: 2, 3; Pl. 30: 3, and Simonetta 1970, Pl. 28: 2, 5, 3 respectively: USNM 83947 a–o, originals of Walcott 1931, Pl. 15: 4–7; Pl. 16: 1–6; Pl. 17: 1–4; Pl. 18: 1: USNM 83947h is also original of Størmer *in* Grassé 1949, Fig. 30: USNM 114243, 155623, 155624, 155626, 155630, 155632, 155661, 155665, 155667, 155669, 155676, 155680 (erroneously recorded as USNM 155678 by Simonetta 1970, explanation Pl. 28: 6), originals of Simonetta 1970, Pl. 28: 10; Pl. 30: 1, 3; Pl. 28: 9; Pl. 32: 1; Pl. 28: 8; Pl. 30: 2 (erroneously recorded as USNM 155661 by Simonetta 1970, explanation Pl. 30: 2, counterpart specimens are numbered 114240 and 155678 in USNM collections); Pl. 32: 4 (erroneously recorded as Fig. 7 by Simonetta 1970, explanation Pl. 32), 2; Pl. 28: 7; Pl. 32: 3; Pl. 28: 6 respectively. USNM 155625, 155627–155629, 155631, 155633, 155634, 155664, 155666, 155668,155670–155675, 155677, 155679, studied but not figured by Simonetta. Major additional collections in USNM and GSC, both including material figured and measured herein. Fifty-four additional specimens collected by P.E. Raymond are present in the Museum of Comparative Zoology, Harvard University (Rolfe 1962: 6).

LOCALITY, STRATIGRAPHICAL HORIZON, NUMBERS OF SPECIMENS, SIZE. – Middle Cambrian, Stephen Formation, Burgess Shale section, *Pagetia bootes* faunule of *Bathyuriscus – Elrathina* Zone, situated on the ridge between Wapta Mountain and Mount Field at an elevation of approximately 2,300 m (7,500 ft), longitude 116°28’30”, latitude 51°26’50”, 4.8 km (3 miles) north of Field, southern British Columbia (see Fritz (1971) for geology and stratigraphy and Piper (1972) for a description of the sediments).

Burgessia bella occurs only in the lower half of that part of the Burgess Shale referred to as the ’Phyllopod bed’ by Walcott (1912). The base of this bed 2.3 m (7’7”) thick corresponds approximately with the 5 ft level on the scale used to record levels at which fossils were obtained in 1966 and 1967 (see Whittington 1971a, Fig. 3). Fig. 1 shows the numbers of specimens collected from the various levels in the 1966 and 1967 collections. In both collections the bulk of specimens come from around the 7 ft level, 21 specimens from an 8 inch band (6'7½" to 7'3½") in 1966 (84% of total in collection) and 21 from a 6 inch band (6'10" to 7'4") in 1967 (60% of total in collection from the main quarry). There are about 1800 specimens in the U.S. National Museum, although this figure almost certainly includes some unidentified counterparts. All specimens collected by Walcott are labelled '35k', i.e. the 'Phyllopod bed' in the Walcott quarry, but there is no indication from which particular layer individual specimens came. Fig. 1, however, suggests that there are relatively few layers in the 'Phyllopod bed' in which *Burgessia* occurs, and comparison with Whittington (1971a, fig. 5) indicates that these may well correspond to the main *Marrella*-bearing levels. From the new collections it is known that *Marrella* occurs in the same bedding surface as *Burgessia* as do the following genera: *Canadia, Elrathina, Ottoia, Ptychagnostus, Scenella, Selkirkia, Waptia* and *Yohoia.* Walcott (1912: 152–153) also recorded *Amiskwia, Miskoia, Molaria, Mollisonia, Naraoia, Opabinia, Pikaia, Wiwaxia* and *Yohoia (= Plenocaris) plena* with *Burgessia* from his bed 12 (only 1½" thick) at the base of the phyllopod bed.

Measurements of maximum carapace width were made to the nearest 0.5 mm on 154 specimens in which the carapace was preserved more or less symmetrically. The width ranged from 4.0 to 16.5 mm (Fig. 2), though no specimen less than 7.0 mm wide was observed showing more than the outline of the carapace and digestive system. This range is in good accord with Walcott's (1931:17) figures for length, excluding the caudal spine, and those of Simonetta (1970:41). Width measurements were used since this allowed a greater number of specimens to be measured. The smallest identified specimen (Pl. 9: 1) is of the order of 3 mm wide. The significance of the gap in the size-frequency curve between 4.5 and 7.0 mm is uncertain. Its presence might invite the interpretation that the small individuals represent an early instar. The fact that no

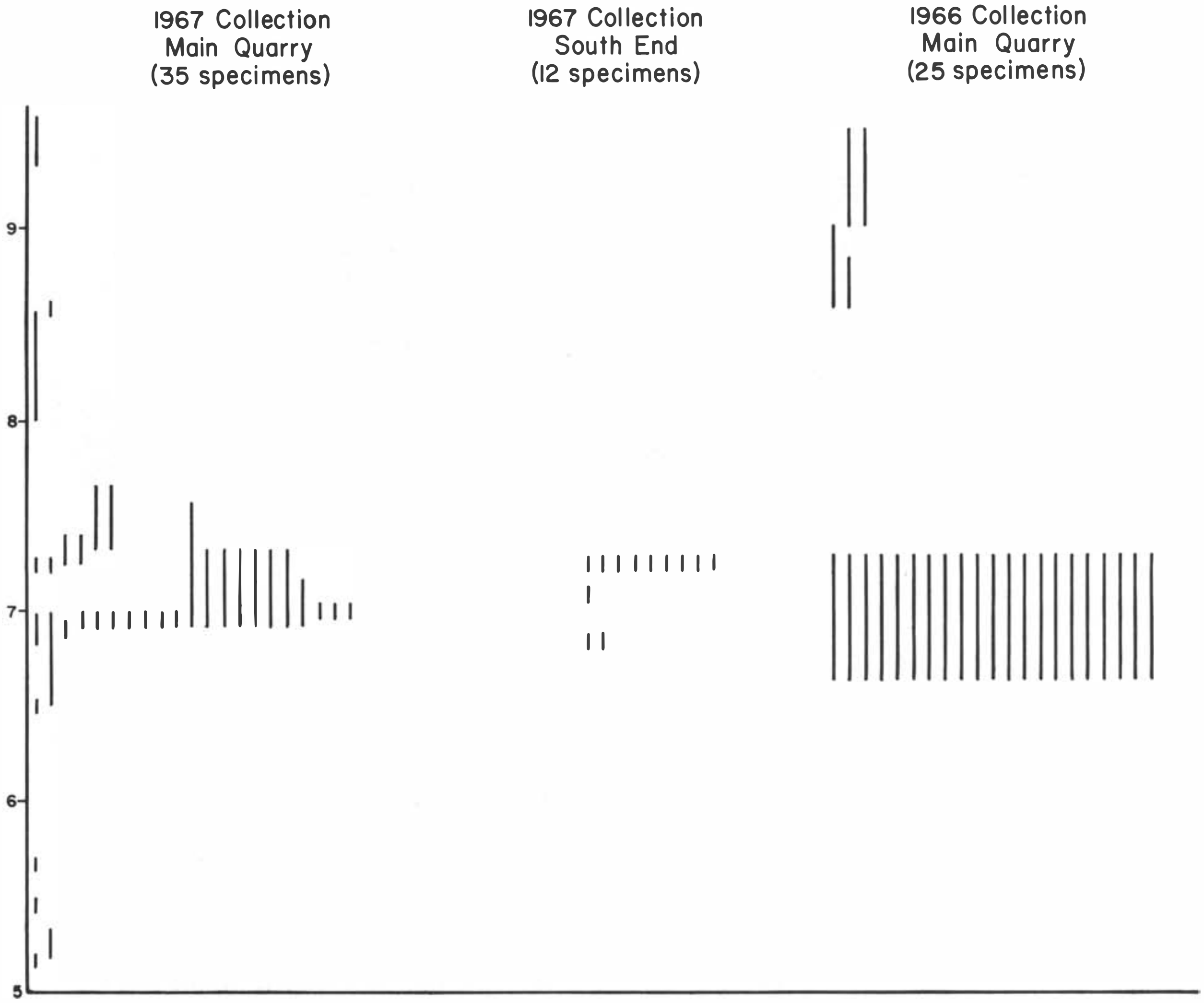

Fig. 1. Distribution within the Phyllopod bed of *Burgessia bella* from the 1966 and 1967 Geological Survey of Canada collections. Each line represents one specimen.

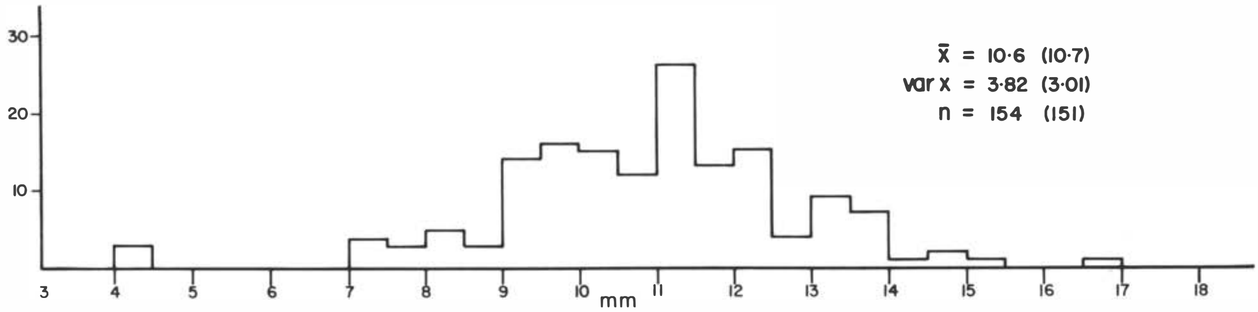

Fig. 2. Size-frequency histogram for 154 specimens of *Burgessia bella.* Size measured as the maximum carapace width. Summary statistics in brackets based on the sample less the three smallest specimens.

trace of appendages or caudal spine has been seen in these small specimens might even suggest that they represent a late larval stage, though the absence of such details in so tiny and fragile specimens could easily be attributed to the preservation, and in fact some larger specimens show little else other than the carapace. The details of the carapace, body and digestive system are, as far as can be determined, the same as in larger specimens. Specimens in the collections made in 1966 and 1967 are not sufficiently abundant to investigate the changes in size-frequency distributions in different levels in the succession as in *Marrella splendens* (Whittington 1971a: 1193—1196).

DETAILED DESCRIPTION

Carapace

The carapace is subcircular, elongate sagittally with a wide relatively large posterior invagination. Although entirely flattened in the majority of specimens, a few obliquely and laterally preserved specimens give some indication of an original convexity (Pl. 1: 9, 10, Pl. 6: 3, 4), the transverse convexity being by far the greater. Many laterally compressed specimens show how easily the carapace could become wrinkled and distorted (Pl. 3: 4, 8, Pl. 4: 1, Pl. 6: 2), this, coupled with the fact that the details of the underlying digestive organs are clearly seen, suggests that the carapace was extremely thin and only weakly sclerotized. Most laterally compressed specimens indicate that many of the somites are free, since the carapace is clearly above and separate from them (Pl. 1: 4—7, 9, 10, Pl. 4: 1, 3). It is inconceivable that the diverticulum (see *Digestive system*) of the fourth appendage-bearing somite should be unenclosed like 'aircraft wing struts', and this, together with the specialisation of the anterior four pairs of appendages (see *Antenna* and *Post-antennal cephalic appendages*) is believed to be strong grounds for considering these anterior somites to form the cephalic region and the dorsal cuticle to form a true carapace extending back over the trunk as a fold of the cephalic cuticle.

Unsclerotized cuticle

Very little is seen of this, the only direct evidence being seen in specimens such as USNM 83947c (Pl. 2: 3) and USNM 83947m (Pl. 5: 4). When these are viewed in high angle illumination they show a silvery line 'cutting-off' a small region of the carapace (mc on Fig. 15). This has in the past been interpreted as the anterior margin of a labrum (Walcott 1931: 17; Pl. 15: 6; Pl. 17: 3). However, since such lines may be present in other quadrants of the carapace (Pl. 9: 3, Pl. 10: 7, where it is present around about two-thirds of the margin), this interpretation is believed to be in error (see also *Labrum*). This silvery line is here thought to be the outer edge of the unsclerotized cuticle forming the underside of the carapace, where it has pulled away from the rim of the weakly sclerotized dorsal carapace upon compaction, since assuming the ventral surface to be approximately flat, the flattening of the gently convex carapace on compaction would cause the unsclerotized cuticle either to stretch or pull away from the rim at some point. If this is correct, then there is no ventral doublure to the carapace, as suggested by Walcott (1931: 17), because there was no ventral sclerotization.

Body

Walcott (1912, 1931) made very little mention of the form of the body, apart from stating it to be segmented. In his reconstruction (1931, Fig. 5) he showed this clearly and also indicated that the alimentary canal tapered rapidly in the anterior portion and that in the trunk it occupied approximately one third of the width of the body. Simonetta (1970) believed all the trunk segments (which included three now believed to be cephalic) to possess small pleural lobes, though he gave no indication as to which specimen(s) showed this. In the present study I have found no convincing evidence for the presence of any pleural structures, and it is believed that the trunk body region tapered posteriorly and was segmented. It might be argued that the slightly 'stepped' outline of the trunk region in USNM 83947c (Pl. 2: 3) is due to small pleurae: however, it is believed equally possible that this is simply a result of the compaction of an annulated body. In cross-section the body is though most likely to have been oval.

Labrum

Walcott (1912: 178) originally believed the labrum to be a small narrow plate covering the central portion of the stomach anteriorly and that it was the cause of the apparent bifid anterior of the stomach. At this time he clearly did not fully realise the significance of the mode of preservation in determining whether a specimen was exposed in dorsal or ventral aspect, since he believed USNM 57676 (Pl. 1: 2) and USNM 57677 (Pl. 1: 1) to be seen in dorsal and ventral aspect respectively. However, as may be seen from Plate 1, they are both preserved in dorsal view. In his subsequent redescription (1931: 17, Fig. 3) he considered the labrum to be a much larger structure covering the entire width of the gut and extending back to cover the anterior part of the mouth, which he believed lay between the first pair of cephalic walking-legs (his mandibles). As has been shown above, the feature considered by Walcott to be the anterior edge of the labrum is now thought to be the torn-away edge of the ventral cuticle. No evidence has been found for the pair of short lateral furrows shown on the labrum by Walcott (1931, Fig. 3) and claimed by him to be present on USNM 83947m (Pl. 5: 1, 3, 4; Pl. 6: 1). Any wrinkling on this region of this specimen and also on GSC 35455 (Pl. 10: 5, 8) is thought to be explained by the compaction of the downturned, rearward facing anterior portion of the anterior end of the gut with the mouth at its termination (see *Digestive system*). The general highly reflective region, interpreted by Walcott as representing the main body of the labrum, is thought to be the result of compaction of the filled anterior region of the gut. The apparent lack of evidence for a labrum in many specimens was explained by Walcott as being due to it being very thin, readily distorted and rarely preserved. In view of the general completeness of specimens in all other respects (see *Completeness of specimens*) it is thought unlikely that if it were developed it should be preserved in so few specimens. Simonetta (1970, Pl. 30: 3, Pl. 32: 3) considered the labrum to be even bigger than that described by Walcott, claiming that there was a wide triangular labrum (his epistomium) along the margins of which the antennae were inserted. Restudy of these specimens does not substantiate this (Pl. 7: 6, 7; Pl. 7: 3, 5 respectively).

Eyes

Walcott (1912: 178; 1931: 17) considered a pair of eyes was present, represented by the small highly reflective spots seen on each side of the dorsal median axis near to the anterior margin in many specimens when viewed with high angle illumination (Pl. 4: 5; Pl. 9: 3, 7; Pl. 10: 5). These spots are now thought to represent muscle attachment areas for muscles supporting the anterior end of the body from the dorsal carapace (see *Musculature*). Simonetta (1970, Pl. 29: 1a, 1d) shows two large oval regions, ?presumably representing eyes, on the lateral portions of the carapace. However, he makes no reference to these in the text or plate explanations, and no structure on which they may have been based has been detected in the present study.

Antenna

This is clearly seen in the majority of specimens and consists of a uniramous appendage tapering distally, which projects in front of the carapace and is variously outwardly curved and clearly flexible. In some specimens the curvature is such that the distal portion lies beneath the anterolateral part of the carapace (Pl. 7: 3; Pl. 10: 3). A few specimens clearly show, particularly when viewed with high angle illumination, that the antenna is attached to the body just posterior to the anterior lobes of the gut (Pl. 2: 3; Pl. 9: 5, 8). Several other specimens, while not being conclusive in themselves, clearly support this interpretation (Pl. 7: 4, 6, Pl. 9: 3, Pl. 10: 1). No specimen shows any structure that could be interpreted as a second branch to the antenna (see also *Post-antennal cephalic appendages).* The length of the antenna is generally about equal to that of the carapace (Pl. 2: 3; Pl. 4: 2; Pl. 9: 5, 8).

Previous descriptions and reconstructions of *Burgessia* have indicated that the antenna consists of many segments, but no specimens have been figured in support of this, nor has any statement been made regarding the number of segments present. Walcott, in his reconstruction (1931, Fig. 3) showed seventeen segments, whereas Simonetta (1970, Pl. 29: 1c) showed about eighty-five. Specimens USNM 204715 and 204718 (Pl. 13: 2, 4, 5) do, however, show some segmentation of the antenna. USNM 204715 shows ten segments clearly over about two-thirds of the visible portion. Although this specimen is a little distorted, it is believed that this structure must be the antenna despite its unusually straight attitude. The associated fossil at about its mid-point is a small specimen of *Marrella splendens.* In USNM 204718 there can be no doubt of the identity of the antenna, but in this instance the segmentation is not so clearly preserved. However, the length of the segments discernible suggests that the total number of segments present is probably between twenty and thirty. The disparity in the number of segments between the two specimens may, in part at least, be due to more of the proximal portion being hidden beneath the carapace in USNM 204715, but the segments visible are apparently relatively much shorter in specimen USNM 204718, and so there may be some variation between individuals, or the preservation may be such as not to reveal all the joints present. Neither of these specimens shows any trace of the presence of setae at the joints as are known in *Marrella, Waptia,* and some other genera.

In his original description, Walcott (1912: 178) stated that some specimens showed a second pair of antenna-like appendages. His description is, however, ambiguous. He stated (: 178) that the specimen figured by him on Pl. 27: 2 (this paper Pl. 1: 1) showed slender antennae (labelled a' on his Plate). He then stated,'Others show a second shorter, smaller pair that is nearer the median line and probably represents the antennules.' Then in describing the specimen illustrated on Pl. 27: 3 (this paper Pl. 2: 6, 9), he stated,'A flattened specimen of the underside of the head shows the basal joints of the first five pairs of appendages. An antenna may be traced to the second joint.' In this case he labelled it a" on his plate. Raymond (1920) accepted the two pairs with the smaller as the antennules. From Walcott's description it might be concluded that his a" referred to the antennules. However, Henricksen (1928: 12) considered Walcott intended a" (A_2 of Henricksen) to be the antennae with a smaller pair being the antennules, and Henricksen considered that by comparison with the development of these structures in *Apus* (=*Triops*) that the terms should be interchanged. Fedotov (1925: 385) was not convinced of the presence of antennules. Walcott's later, fuller description and reconstruction (1931: 15—20) makes no reference to antennules and presumably he was of the opinion then that his earlier interpretation was in error and that the apparent differences were caused by differences in the incident angle of illumination and/or preservation in slightly different attitudes within the rock, the view also held by the present author. Simonetta (1970: 41) made no specific reference to the possible existence of antennules, although he did hint at the possibility that some small appendages might be hidden beneath an 'epistome'. No structure has been found in the present study that is interpreted as an antennule. The varying length and position of emergence of the antenna from beneath the carapace is believed to be accounted for simply by a difference in direction of compaction of the specimen, which thus affects the relative positions of the carapace and the cephalic and subcarapace structures. Further, since it is believed that no labrum or 'epistome' was developed, it is felt that there is little possibility of any pairs of appendages being hidden by any ventral skeletal structure as suggested by Simonetta.

Post-antennal cephalic appendages

Originally Walcott (1912: 178) believed there to be three pairs of post-antennal appendages anterior to the diverticulae, and these he termed cephalic appendages. Since he initially believed there to be antennules as well as antennae to be developed, this made a total of five pairs of cephalic appendages. This was accepted by Raymond (1920), Fedotov (1925), and Henriksen (1928), although, as mentioned above, Fedotov was not entirely convinced over the presence of antennules. The only change made by Walcott in his later paper (1931: 17) was to delete the antennules, thus reducing the number of cephalic appendages to four. Størmer (1944: 133, Fig. 25) tentatively suggested, mainly on theoretical grounds, that there might be a fourth pair of post-antennal cephalic appendages. The most recent reconstruction (Simonetta 1970: 41, Pl. 30) suggests that the cephalon was abnormally short and contained no post-antennal appendages.

The present study shows that Walcott's original conclusion that there were three pairs of post-antennal cephalic appendages was correct. In 1912 Walcott gave no details of the structure of these cephalic appendages, although he did note that distally they were very slender and one at least ended in two fine filaments. It is thought likely that he was in fact referring to the outer branches of these appendages which are developed as flagella (see Simonetta 1970: 41, and below). Rather strangely Walcott (1931), having concluded that there were ten pairs of walking-legs, retained the three post-antennal cephalic appendages, the structure of which he knew very little about, and placed all ten walking-legs in the post-cephalic region, thus increasing the number of trunk somites above his 1912 figure of eight. He apparently ignored the possibility that the more anterior of the walking-legs might be cephalic appendages. Walcott's 1931 interpretation was accepted by subsequent authors without much question until Simonetta (1970) found no evidence of any post-antennal appendages and again considered all the walking-legs to belong in the post-cephalic region.

As has already been discussed the cephalon is believed to extend back to include the somite from which the diverticulae arise. Evidence of the presence of some cephalic appendages is to be found in numerous specimens (Pl. 2: 6, 9; Pl. 9: 3, 7; Pl. 11: 2, 5, 6, 7) and suggests the presence of three pairs of appendages anterior to the diverticulae, the anterior one being the antennae. At least one of these (Pl. 11: 2, 7) suggests that there is also a pair of appendages attached to the somite bearing the diverticulae. This is confirmed by a unique specimen (USNM 204716, Pl. 9: 8) which when viewed with high angle incident light, clearly has an appendage base beneath the diverticulum, with a further three in front. This is supported further by specimens such as USNM 204703 (Pl. 9: 4, 6) which clearly show no obvious break in the spacing of appendages from the cephalic to trunk regions.

There can be little doubt from the evidence of specimens such as those illustrated (Pl. 11: 2, 5, 6, 7; Pl. 12: 7, 9) that these cephalic appendages are the three most anterior walking-legs, and not as Walcott believed some entirely separate type of appendage. Unfortunately no known specimen shows any detail of the structure of these appendages. Although numerous specimens (Pl. 3: 4, 5, 8, 9; Pl. 4: 1–4; Pl. 5: 6, 7; Pl. 6: 2, 5; Pl. 8: 8; Pl. 11: 2, 7) suggest that there is little or no difference between the cephalic walking-legs and those of the trunk, only two specimens show their structure in any detail. In one (Pl. 11: 3) it is difficult to determine to which somite the legs belong, although it is almost certain that some of the cephalic legs are visible, and distally at least they appear to have the same form as more posteriorly positioned legs. The second specimen (Pl. 5: 2, 5), from which most of the known detail of the trunk walking-legs is derived, shows only the distal part of the third cephalic walking-leg. Again there appears to be little difference from the distal part of subsequent walking-legs. Thus, since contrary evidence is lacking, it is presumed that the detailed structure of the cephalic walking-legs is similar to those of the trunk region (see below), although it is possible, if not probable, that structures, such as the large cuspidate endite on segment one (Fig. 3), concerned with feeding or grasping (see *Function of appendages*) may well be modified on the cephalic appendages due to their proximity to the mouth.

A relatively small number of specimens show another set of cephalic appendages, namely fine flagella. These are probably the structure that Walcott (1912) thought were the distal ends of the cephalic appendages, which he believed to be uniramous. The form of these structures is best seen in USNM 155624 (Pl. 7: 4, 6, 7) where there are clearly three flagella developed, the second and third looking as if they possibly fuse together just outside the carapace margin. Other specimens (Pl. 3: 2, Pl. 7: 3, 5) also show the presence of a flagellum, but in both instances only one is visible. Apart from Walcott's possible reference to these structures, Simonetta was the first to make any reference to them. He considered them to be the outer branches of the first two walking-legs (considered by him to belong to the trunk), though rather oddly in light of specimen USNM 155624, interpreting the more anterior one to bifurcate distally. While accepting that the bifurcate nature of one of the flagella is a possible interpretation, it is preferred to consider that there are three separate structures each being the outer branch of one of the three post-antennal cephalic appendages and to consider the apparent bifurcation in USNM 155624 the result of an accident of preservation in which two flagella are crossed. A further possibility might be that one or more of the flagella represent a uniramous, biramous or even triramous antennule. This can, however, be discounted since USNM 83947c (Pl. 2: 3, 7, Fig. 15) shows a single flagellum joining the basal portion of an appendage immediately posterior to the antenna in a position that has already been shown to be occupied by the anterior most walking-leg. It is not known whether the flagella are segmented or not.

Trunk appendages

The anterior seven trunk somites, that is all but the most posterior of the appendage-bearing somites, each bear a pair of biramous appendages, the inner branch being a walking-leg and the outer a gill. This broadly agrees with previous authors' interpretations (e.g. Walcott 1931, Fig. 3; Simonetta 1970, Pl. 29: 1c). The most fundamental difference in the present interpretation is in regard to the total number of biramous trunk appendages. This arises to some extent as a consequence of the recognition that the three most anterior pairs of walking-legs are cephalic appendages.

Several specimens (Pl. 3: 4, 5; Pl. 8: 8; Pl. 9: 6) clearly show ten pairs of walking-legs (excluding the posterior-most short appendage). Others, however, (Pl. 4: 1 – 4; Pl. 5: 6, 7; Pl. 8: 5) show fewer, commonly eight or nine. It is considered that those specimens with less than ten pairs of walking-legs visible may be explained by preservational differences, and that all individuals had a total of ten walking-legs, seven of which belonged to the trunk. The segmentation of the trunk offers little evidence, for although there is clearly one walking-leg to each segment (Pl. 4: 1, 3; Pl. 13: 6, 7), no specimen shows the body segmentation sufficiently clearly to be able to count the number of segments with any certainty, though specimens such as USNM 83947h (Pl. 4: 5, 6) indicate that a total of eight segments would be likely in the trunk.

It is clear from the majority of specimens showing the legs, that there is a progressive diminution in size posteriorly (Pl. 3: 1, 4, 5; Pl. 4: 2, 4; Pl. 6: 2, 5). It is also apparent that the more distal segments of each appendage are more slender than the proximal ones (Pl. 4: 2, 4, Pl. 6: 2, 5; Pl. 13: 6, 7). Very few specimens show any detail of the segments and joints (Pl. 4: 2, 4; Pl. 5: 2, 5; Pl. 6: 8, Fig. 24; Pl. 11: 1, 3) and only two of these show any detailed information regarding the structure of the walking-legs. In USNM 83947i (Pl. 5: 2, 5) the seventh, eighth and ninth walking-legs are particularly well preserved, although even in this specimen certain important features cannot be discerned. The specimen is exposed from the ventral side and the legs have been rotated on compaction through 90°, so that the segments are seen in anterior view. Proximally there appears to be a basal segment (coxopodite of Walcott 1931: 18) to which he believed the outer branch (exopodite) was attached, although he admitted that he had very little direct evidence for this. Simonetta (1970: 41, Pl. 29: 1e) also considered this segment to represent the coxa, but in addition believed a short precoxa was developed, possibly immovably jointed to the body, from which the outer branch arose. As may be seen from Pl. 5: 2, no details are visible of the proximal end of the presumed coxa, nor are they on any other specimen. Thus from the available evidence it is impossible to deduce the presence of a pre-coxa, and Simonetta's interpretation remains purely conjectural. The place of attachment of the outer branch is discussed more fully below, but is believed to be to the coxa. In the reconstruction given here (Fig. 3), it will be noted that in addition to the endital swelling clearly visible on the underside of the distal portion of the coxa, a dorsal flange-like structure is proposed to join the segment to the body. No specimen shows any detail of the coxa-body joint, but this flange-like extension is postulated in order to make a more feasible arrangement for the musculature which, without such an extension, would be very inefficient, or surprisingly complex. Such functional arguments may explain Simonetta's postulated pre-coxa. The walking branches of the seventh and eighth post-antennal somites (fourth and fifth trunk appendages) consists of six segments and some terminal claws, and, in the absence of contrary evidence (see above) it is presumed that the other walking-legs are of similar construction.

The first segment of inner branches 7 – 9 (fourth – sixth trunk appendages) (Pl. 5: 2) has a very pronounced cuspidate endite particularly clearly seen on the eighth appendage. The second segment, best seen on the seventh walking-leg, has a smaller endite surmounted by a pair of bristles or setae. Segments three and four appear basically similar to one another, being subcylindrical, expanding slightly distally with at least one strong seta present at the joint between them (Pl. 11: 3). The fifth and sixth segments are basically similar to the third and fourth, but are considerably slimmer, a seta is present at the joint between them, and between the fourth and fifth segments. Two or three terminal claws to the sixth segment are just discernible in two specimens (USNM 83947j (Pl. 5: 6), USNM 204719 (Pl. 11: 1, 3)). The type of joint between segments varies and is thought to be of the pivot type (Manton *in* Moore 1969, Figs. 1,

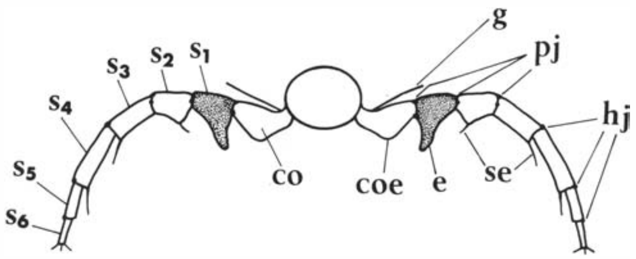

Fig. 3. Diagram showing the basic structure of the trunk appendages of *Burgessia bella* in probable life-attitude. First segment of walking-leg stippled showing strong cuspidate endite which acted as a 'pincer' with the coxal endite.

2) between the coxa and first, first and second and second and third segments and a hinge joint between the fourth and fifth and more distal segments. The type of joint between the third and fourth segments is more uncertain, but is possibly more likely to be of pivot type. The evidence for this interpretation is seen in the specimens figured on Pl. 5: 2, 5; Pl. 11: 1, 3 where the segments pivot-jointed are both the same depth at the joint, whereas in those hinge-jointed the distal depth of the more proximal segment is greater than that of the proximal depth of the more distal segment, which dorsally is in line with the previous segment, but ventrally fits within the segment.

This interpretation of the walking-leg differs from those of Walcott (1931) and Simonetta (1970) in a number of features. Although the original of Pl. 5: 2 was figured by Walcott (1931, Pl. 16: 5), his reconstruction (Fig. 3) shows progressively more segments with an endite expansion on the more posteriorly placed legs, with the inner five segments being so expanded on the last four pairs. The evidence of Pl. 5: 2 does not support this. It is possible that Walcott considered specimens such as the original of his Pl. 16: 1 (herein Pl. 3: 4, 5, 7, 9) as indicating the higher number of expanded segments. Walcott's photograph is considerably retouched, but even so shows no evidence for more than two or three expanded segments. Restudy of the specimen suggests that this is to be explained by the rather indifferent preservation. Walcott himself was not entirely consistent, for although the orientation of his diagramatic outline of a trunk limb (1931, Fig. 4) is not entirely clear, the outline shows no expansion of any of the segments – all joints are of the hinge type, with two setae present at each. As has been shown above the present study clearly indicates that the inner joints are almost certainly of pivot type. No trace has been found for any dorsally positioned setae and ventrally placed ones have only been seen at the joints between the third and fourth, fourth and fifth, and fifth and sixth segments (Pl. 11: 1, 3). Simonetta's reconstruction of the walking-leg (1970: 29) is considerably different. As already mentioned he introduced a pre-coxa, but he also reduced the number of distal segments by one. Further he showed the coxa and first segment (his throcanter) to have multiple rows of strong spines along their inner surface. No evidence for such spines has been found; on the contrary Pl. 5: 2 clearly shows there are no spines. Simonetta also reconstructed the joint between segments two and three (his femur and patella) as a 'knee-joint'. By analogy with modern arthropods it is believed that if this were the case then the cuticle would have been very much thickened at the joint, this would then appear in the fossil as the most prominent joint. Since this is not the case it is thought unlikely that a knee-joint was developed here or at any other point along the walking-leg, and that the attitude of the leg was more as shown in Fig. 3.

The outer, gill, branch of the trunk appendages is rarely well-preserved and is best seen in specimen USNM 83947n (Pl. 6: 6, 8). This specimen is exposed from the ventral side and it is the underside of the left gill-branches that is visible. These are oval in outline, and each one is overlapped (in dorsal aspect) by the next most anterior one. They are positioned dorsal to the walking branch (see below) and in this specimen the left walking-legs will be preserved within the matrix of the counterpart (which has not been recognised). As with the walking-legs there is gradual diminution in size to the posterior. No jointing or filamentous structure within the lobe has been detected, and contrary to Walcott's statement (1931: 18, and explanation Pl. 14: 4) no indication of any fringing setae have been seen. Traces of seven gill branches are seen (Pl. 6: 6) which supports the evidence for seven trunk walking-legs. Other specimens showing traces of the gill branches (Pl. 8: 4, Pl. 10: 1) show no indication of any being present in the cephalic region. Because the specimens in which the gill branches are clearly visible are preserved in such a way that the leg branches are not seen, it is difficult to prove the relationships between the two branches. However, in USNM 83947f (Pl. 4: 2, 4) there is a structure which it is believed can only be part of a gill branch, lying dorsal to the walking-legs. Specimen USNM 114242 (Pl. 10: 1, 2), which is exposed from the dorsal side, also suggests that the gill branch is dorsal to the walking-legs. Walcott figured a specimen (1931, Pl. 16: 6) which he believed indicated that there was an anterior support to the gill branch (his exopodite) which extended beyond the lobe and terminated in two minute spines. Størmer (1944) commented on this specimen and believed Walcott's interpretation to be correct. This specimen (Pl. 5: 6, 7) is laterally compressed and seen from the left side. The proximal portion of the left walking-legs have broken away, revealing the proximal portions of the right-side appendages. The anterior edge of these right-side appendages appears prolonged and is clearly the structure interpreted by Walcott and Størmer as the anterior support for the gill branch. It is thought more likely, however, that this is part of the right walking-leg and that it continues into the sediment beneath the left walking-legs. Whether or not the broad basal portion exposed is a single structure is not certain. As shown in Fig. 21, the posterior part of the basal region is at a slightly higher level within the matrix than the anterior part, although as can be seen in Pl. 5: 7 this change in level is very small. Since the gill branch is believed to be dorsal to the walking-leg, in a laterally compressed specimen seen from the left side, the right gills should be at a lower level than the right walking-legs. It is thought that this specimen may be explained in one of two ways. Either the walking-legs were rotated on compaction and buckled so that the ventral portions were pressed upwards, or on compaction portions of the gill branches were pushed up between the dorsal portions of the walking-legs. Whichever is correct, it does not affect the interpretation of the supposed anterior supports to the gill branches of Walcott being part of the right walking-legs. The point of attachment of the gill branch is not seen in any specimen. Pl. 6: 6, however, clearly shows the proximal portion of the gill to be very close to the body, and even allowing for some lateral extension of the body on compaction, the gill must have been attached very near the proximal end of the appendages, presumably to the coxa.

The posterior trunk appendage appears to be little more than a short uniramous spike-like structure (Pl. 4: 1—4, Pl. 5: 2, 5, Pl. 7: 8, Pl. 8: 1, 5) which may represent a reduced walking-leg. Walcott (1931: 18) stated that one specimen showed a modified 'exopodite' consisting of a central axis with seven sharp spines projecting from the posterior side and a terminal spine at the posterior, although he considered that this structure might possibly be a walking-leg, the 'spines' being part of the expanded portions of the inner segments of the leg that he believed were developed. However, since he showed it as a modified appendage in his reconstruction he clearly favoured the first explanation. Oddly he made no reference to this structure on any of the plate explanations, though restudy of his collections indicates that he was referring to the structure seen in specimen USNM 83947e (Walcott 1931, Pl. 16: 1, herein Pl. 3: 4, 5, 7, 9). It is clear that some kind of apparently spinose structure is present (Pl. 3: 7) though its details are not well-preserved. As no other specimen shows any indication of a second spike-like branch to the posterior trunk appendage, it is thought unlikely that this structure represents any such second branch. Similarly Walcott's suggestion that the 'spines' are the expanded parts of the inner segments of the walking-legs can be discounted since it is now known that only the first two segments of the walking branch bear expansions on the ventral side. If the appendage on this eighth trunk somite does represent a reduced walking branch, then the six or seven spine-like extensions might be homologous to the setae known to occur at least at some of the joints of more anteriorly placed walking-legs. Alternatively it is possible that this structure does not belong to the specimen at all, for it could be argued that since all other trunk appendages of both left and right sides are preserved 'below' the body, it would be unlikely that the posterior appendage, whether left or right, should be preserved in such a different attitude. However, other specimens both of *Burgessia* and other genera show that such twisting of specimens is quite possible. Simonetta (1970) was unequivocal in considering this posterior-most appendage to be a specialised, reduced, walking-leg, lacking any outer branch, and he made no reference to Walcott's biramous interpretation.

Telson

The trunk terminates in a short segment with no lateral appendages, interpreted by Walcott (1931: 18) as the anal segment, and a long caudal spine. This terminal segment and spine are considered to form a telson. The one specimen that shows the terminal segment most clearly (Pl. 9: 2) shows neither the alimentary canal nor the posterior appendages, and so it is difficult to be certain of the relationships between these various structures. However, the evidence afforded by USNM 204717 (Pl. 9: 2) as to the size of the segment, and by USNM 155680 (Pl. 7: 8, 10) as to the position of the last lateral appendage in relation to the point of flexure at the base of the caudal spine, strongly suggests that the last trunk appendage belongs to the somite immediately to the anterior and not to the terminal segment. Walcott described an anal plate on this segment (1931: 18, Figs. 3, 5, Pl. 17: 3), rather curiously showing it on both his ventral and dorsal reconstructions. Despite his assertion in the plate explanation that the anal plate was 'clearly indicated', his illustration does not support this. Restudy of the specimen, Pl. 5: 1, 3, 4, Pl. 6: 1, shows that the shield-shaped structure referred to by Walcott as the anal plate appears to be the faint impression of the rounded posterior of the alimentary canal within the terminal segment. If this interpretation is correct, this is the only specimen that shows the alimentary canal definitely within the terminal segment. Some specimens show a thread-like structure apparently extending posteriorly from the end of the alimentary canal, particularly well seen in USNM 83947d (Pl. 2: 8) and USNM 83947c (Pl. 2: 3). This could be a short anal passage, but other specimens e.g. USNM 155680 (Pl. 7: 8), USNM 83947h (Pl. 4: 5) also show a thread-like structure which continues back through the terminal segment and along the centre of the caudal spine. This is seen best when the specimen is viewed with high incident angle illumination, and is thought to represent some fluid-bearing vessel (Whittington 1971b: 15) that lies along the axis of the body either dorsal or ventral to the gut, and which only becomes visible in the flattened specimen behind the termination of the alimentary canal. Thus although Walcott's large anal plate cannot be substantiated, it is thought that the anus lies within the terminal segment.

Walcott believed the caudal spine (his telson) to be segmented with at least thirty segments (1912: 178, 1931: 15). This was not questioned by subsequent workers until Simonetta (1970: 41) considered it to be an unsegmented conical spine. The present study supports Simonetta's interpretation. The great majority of specimens show no sign of any segmentation of the spine. Although Walcott does not specifically identify the specimen showing at least thirty segments, it seems likely from his illustrations that the figure of thirty may have been based in part at least on specimens USNM 57677 and USNM 57680 (1912, Pl. 27: 2; Pl. 30: 3). However, both these photographs have been considerably retouched (Pl. 27: 2 even appears to show setae present at the joints), and it can be seen (Pl. 1: 1, 4–7) that neither of these specimens shows any sign of segmentation. A few specimens, notably USNM 83947a (Pl. 3: 1, 8) and USNM 83947d (Pl. 2: 1, 5, 8), show some changes in direction along the spine that might be interpreted as joints. However, since they show no definite joint structure nor any regularity in position, it is preferred to consider them as *post-mortem* fractures. One specimen USNM 204712 (Pl. 12: 1, 8, Fig. 31) does show what could possibly be joints, if there are, then there would appear to be of the order of twelve rather than thirty segments. However, as can be seen from the illustration, the indications of joints are extremely tenuous and I am not convinced that they represent original structures.

Digestive system

Walcott (1912: 179, Pl. 27: 1, 2, 1931: 18–19, Fig. 5, Pl. 16: 4) described the mouth as being ventral, presumably opening into a gullet and passing into a stomach apparently divided, with a straight intestine extending from the rear of the stomach along the axis of the animal terminating in the telson. He considered the large kidney-shaped caecal system present, branching off from the fifth somite, to be an hepatic organ. This interpretation was accepted by subsequent authors including Simonetta (1970), with only small modifications in terminology, and the present study has revealed only a few further minor modifications. Relatively recent work by Öpik (1961), Bergström (1973) and Shergold (this volume) on agnostids has indicated that they possess a digestive system not unlike that of *Burgessia*. As stated above (*Terminology*) the terms employed here are based on those of Öpik (1961).

It is difficult to imagine the mouth being anywhere but on the ventral side, but the positive evidence for its position is very little. Walcott and Simonetta both believed a relatively large labrum to be present and presumed the mouth was positioned immediately to the rear of this. However, as shown above (*Labrum*), this view is no longer considered correct. GSC 35455 (Pl. 10: 5), which is seen in ventral aspect, shows, in high angle illumination, a distinct lobe-like structure at the anterior end of the body which is interpreted as the outline of a downturned, rearward facing portion of the digestive tract, presumably with the mouth at the posterior. Other specimens (e.g. USNM 204702, Pl. 10: 1) show the outline of a similar lobe which has been compacted to be at a slight angle to the main portion of the alimentary canal. Further specimens GSC 35461 (Pl. 12: 9) and USNM 83947m (Pl. 5: 1) show the impres-

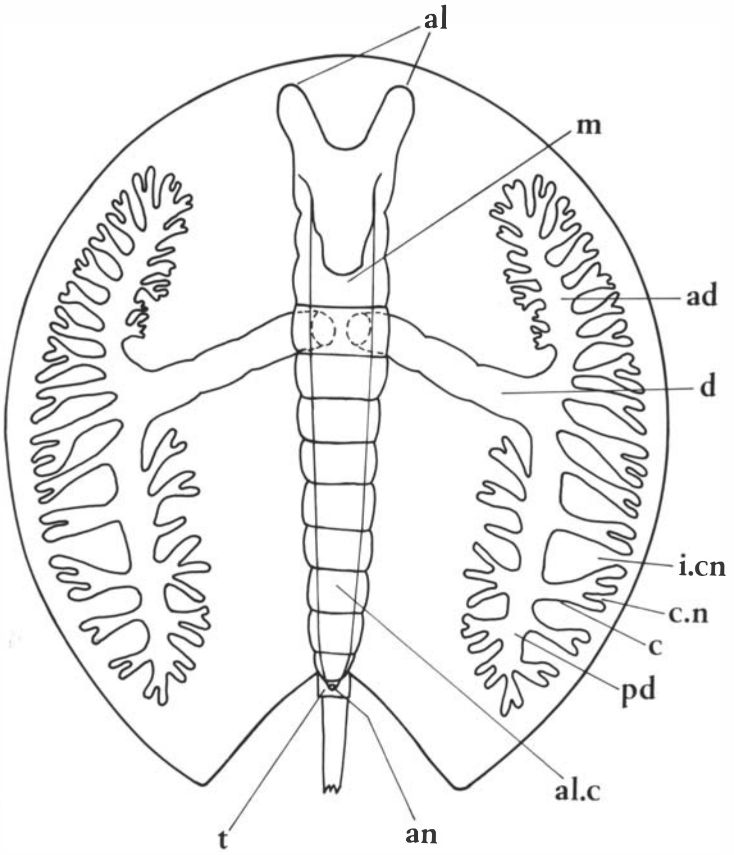

Fig. 4. Ventral reconstruction of digestive system of *Burgessia bella.*

sion of the ventral surface of the gut and also show indications of some lobe-like structure. In Walcott's reconstruction (1931, Fig. 5) a third 'anterior central lobe of stomach' is shown. This is thought to have been based on such specimens as USNM 57677 (Pl. 1: 1) where there is some indication of a third central lobe anteriorly (originally thought by Walcott (1912) to represent the labrum). However, this and similar specimens are believed to be explained by the rearward facing anterior portion of the gut having been pushed forwards by oblique compaction. It should be noted (Pl. 1: 1) that there are other signs that the carapace has been pushed posteriorly and slightly obliquely with respect to the remainder of the animal, in that no appendages are visible behind the carapace, and the right antenna, as far as can be seen, appears as if it joins the body far forward on the anterior gut lobe (cf. Pl. 9: 8). The frontal part of these anterior gut lobes is thought to have been the point of attachment for muscles from the fore end of the body to the carapace (see *Musculature*), and the lobes themselves may have housed some kind of digestive gland. The diverticulum leading to the lateral gut-caecal system arises from the gut at the posterior-most cephalic somite which also bears the fourth pair of lateral appendages. It is a moderately large tube and occasionally shows some signs of annulation (Pl. 1: 2). Distally it bifurcates, one branch directed anteriorly, the other posteriorly. Numerous short caecal tubes branch off these both internally and externally, commonly dividing once or even twice to give a bifid or trifid caecum (Pl. 4: 5). The caecae to the anterior of the diverticulum tend to be closer packed than those to the posterior, particularly on the inner side of the anterior diverticulum. Those on the posterior diverticulum tend to have much deeper caecal nodes and larger intercaecal nodes (Pl. 4: 5, 6, Fig. 4). Whether or not this organ served as a digestive organ or simply as a storage organ is not known, and for this reason it is preferred to consider it simply as a gut-caecal system rather than as an hepatic or hepatopancreatic organ as it has been termed in the past. In *Burgessia* this is a cephalic organ; hepatic or hepatopancreatic organs are more typically organs of the post-cephalic region in arthropods. The posterior portion of the gut, occupying the trunk region, tapers slightly posteriorly and appears to be bluntly rounded at its extremity on the telson. In many specimens the entire digestive system is not flattened to the same extent as the remainder of the animal due to it having been filled at the time of burial with sediment-rich fluid. In many specimens in which the gut is so preserved, it appears as if it entirely fills the body cavity. However, it is clear that other organs, such as the heart, circulatory system, muscles and nervous system must have been present, and it is thought that the gut must have spread out on compaction so as to appear to more or less fill the body cavity. Nevertheless it is believed that the gut must originally have occupied a large proportion of the body cavity in both the cephalic and trunk regions.

Musculature

With one exception, there is no trace of the musculature system. As has been mentioned above (*Eyes*), Walcott interpreted as eyes the two small highly reflective spots present on each side of the dorsal median axis. The present study confirms the presence of these spots on many specimens (e.g. Pl. 2: 6; Pl. 4: 5; Pl. 9: 3, 7). In some other specimens (Pl. 9: 8; Pl. 10: 5) the spots appear to be superimposed on top of the anterior ends of the anterior gut lobes. Since the relative position of the carapace with reference to the remainder of the animal varies according to the direction of compaction, this evidence is not inconsistent with Walcott's interpretation of these as eyes, presumably set on the dorsal surface of the carapace. A unique specimen, believed to be of *Burgessia* (GSC 35459, Pl. 7: 1, 2) has the carapace torn almost entirely free from the remainder of the specimen. However, there are a number of strands of organic material joining the carapace to the anterior portion of the body where two highly reflective spots are present, thus the silvery spots appear to be located beneath rather than on the dorsal carapace and are therefore presumably not eyes. It is thought that these strands represent muscles originally attached to the underside of the carapace and the frontal end of the anterior gut lobes, and that the highly reflective spots mark the attachment areas and not eyes. A possible alternative explanation of this unique specimen is that the strands represent the torn remains of the diverticulae. There is no evidence, however, that they extend far enough back to this to be a reasonable possibility.

Dark stain

Whittington (1971a: 1180–1190, Figs. 6a, c, 7, 9, 16, 1971b: 16) showed that a dark organic stain was almost always associated with specimens of *Marrella.* A similar, though smaller stain is present associated with only a few specimens of *Burgessia* (Pl. 4: 4; Pl. 7: 5; Pl. 10: 3). No chemical analyses have been made of the stain associated with *Burgessia,* but it is assumed to be of the same nature as those associated with *Marrella* and is thought to represent squeezed out organic matter.

Completeness of specimens

The figured specimens show that the vast majority of specimens are demonstrably complete individuals with all the appendages preserved in their entirety and are not exuviae. Others (e.g. Pl. 2: 6, 9) presumably have the missing portions present on the counterpart specimen. A few specimens (Pl. 7: 9; Pl. 9: 1) appear only to have the carapace and digestive organs visible, although the appendages may well be present within the matrix. The absence of the caudal spine may well be real or a function of the difficulty of preparation of some specimens, particularly the very small ones. No specimens show any clear evidence of predation and few of decomposition. The preservation of some (Pl. 7: 1, 2; Pl. 10: 1, 2) suggests that some decay may have taken place before or immediately after entombment. However, a moulted carapace of *Burgessia,* with no trace of the digestive organs, would be very difficult to recognise.

Function of appendages

There is little doubt that the uniramous antenna were tactile organs. The three cephalic flagella show no trace of fringing setae that might suggest a natory function, and it is believed that they also were tactile appendages, as are the antennules in many malacostracans and the triramous appendage in *Triops.* The cephalic and trunk walking-legs are believed to have functioned both as locomotory organs and as food gatherers, all ten walking-legs being able to reach the ground (Fig. 9). Since the cross-section of the body is relatively small compared to the size of the limbs, there was apparently little space within the body for any efficient extrinsic limb musculature to be developed. However, the large size, especially of the proximal segments of the walking-leg and of the coxa, would allow ample space for a well-developed intrinsic musculature to be present which could allow a relatively slow gait. Such a musculature would enable the leg to be used propulsively both on flexure and by extension, and in common with many modern arthropods (Manton 1952, 1954, 1958) it is thought likely that in the more anterior appendages the propulsive stage was during flexure and in the more posterior during extension. This gives rise to a certain amount of fanning out of the appendages which is suggested in some specimens (Pl. 5: 2, 6) and is depicted in the reconstruction (Figs. 6, 9). The form of the proximal segments of the walking-leg and that of the coxa, particularly the large endital processes on the coxa and first segment (Fig. 3), suggests a gripping or crushing function, since on curling the leg up these two endites provide the 'jaws' of a very effective pincer (Fig. 5). Not only do these segments form an effective gripping or crushing mechanism, but by allowing a certain amount of dorso-ventral movement at the coxa-body joint, known to be possible in some modern hexapods (Manton 1972), then the pincer can be brought more or less into the mid-line (Fig. 5). By a simple process of slight rotation of the limbs and a successive gripping and releasing by the pincer, captured food could be brought into the mid-line and passed forwards to the mouth. It is particularly unfortunate that no knowledge is available of any modifications of the basal joints in the mouth region.

The gill branches are thought to be simply oxygen exchange organs. Bergström (1969) threw doubt on the previous interpretations that the gill branches in trilobites were respiratory, considering that the bulk of oxygen exchange took place through the ventral cuticle. He made no specific reference, however, to the function of the gill branches in the non-trilobite arthropods of the Burgess Shale. Whittington (this volume) has rejected Bergström's view and reaffirms that respiration in the trilobites was effected by the outer, or gill, branch of the biramous appendages. The gill branches in *Burgessia* overlap each other slightly and are believed to be able to come in contact, or very nearly so, with the underside of the carapace. It is considered that metachronal beating of the appendages would produce sufficient water currents to ensure an adequate oxygen supply in much the same way as has been described by Cannon (1933) and Sanders (1963) for branchiopods and cephalocarids, respectively.

The function of the posterior-most, probably uniramous appendage is uncertain. If it represents a degenerate walking-leg then it might have little or no function.

Mode of life

Very little comment has been made in the past regarding the possible mode of life of *Burgessia.* Walcott (1931: 20) suggested that the functions of the limbs of *Burgessia* were similar to those of *Marrella,* and he concluded (:35) that *Marrella* was free-swimming. Little further comment appears to have been made until Størmer (*in* Moore 1959: 027) stated that *Burgessia* with its broad carapace was likely to be a planktonic form. The only other remark appears to have been by Bergström (1973: 6) and concerned the diet of *Burgessia:* he suggested that *Burgessia* ingested fluid food.

As has already been discussed, the preservation and relationship between the specimens of *Burgessia* and the sediment indicate that it must have lived on or near the bottom, and was thus able to become caught up in the entombing sediment cloud. The detailed morphology of the appendages suggests that it would be feasible for *Burgessia* to walk, albeit rather slowly, on the sea bottom using the antennae and cephalic flagella as tactile organs, sweeping across and through the soft sediment. Whether or not *Burgessia* could swim is more uncertain. As mentioned above it seems unlikely that the flagella could have been natory in function. Also it seems unlikely

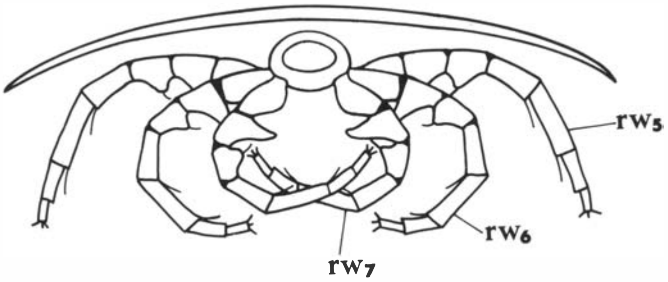

Fig. 5. Diagramatic cross-section of walking-legs 5 to 7 of *Burgessia bella* showing possible attitudes of legs to encircle food.

that it could use the walking-legs in swimming since it is improbable that they could be 'feathered' sufficiently on the return strokes. Whether or not metachronal beating of the gill branches would be sufficient to effect a swimming motion is debatable. As discussed above it is thought unlikely that any musculature was developed allowing swift motion of the appendages. Manton, in a series of papers (e.g. Manton 1952, 1954, 1958, 1972), has discussed the various gaits to be found in modern arthropods, and it would seem possible that *Burgessia* walked with left and right walking-legs in phase and with six pairs of legs on the ground at any given time. This would give a gait comprising two metachronal waves, each with five pairs of legs. Whittington (this volume) has described very fully the possible gait of *Olenoides* and the general style of gait in *Burgessia* is believed to be the same, i.e. each pair of legs moved in unison in a promotor-remotor swing about an approximately transverse axis at the coxa-body junction. One major difference in *Burgessia,* however, is caused by the progressive diminution of the length of leg posteriorly.

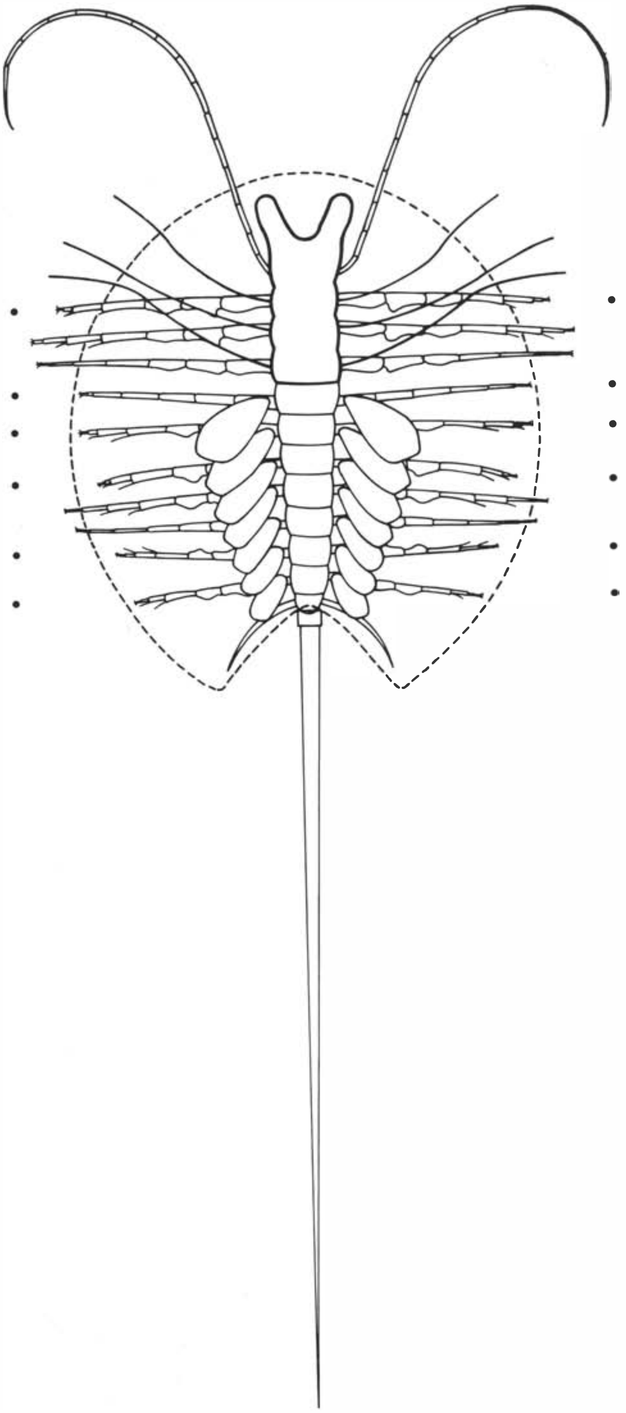

Fig. 6. Dorsal reconstruction of *Burgessia bella* with carapace and gut-caecal system removed to show appendages. Margin of carapace shown dotted. Gait assumed is with six pairs of legs on the ground (indicated by °) and four pairs off at any time (see text), giving two metachronal waves.

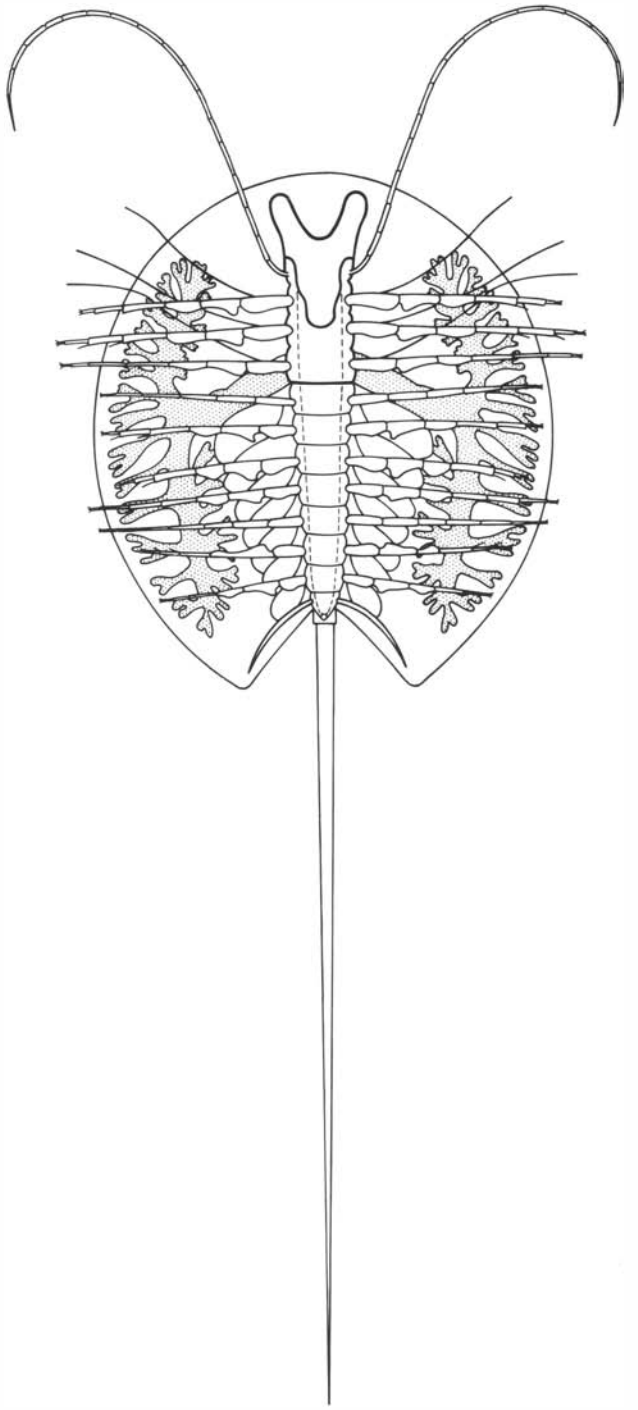

Fig. 7. Ventral reconstruction of *Burgessia bella.* Gait same as for Fig. 6, gut-caecal system stippled.

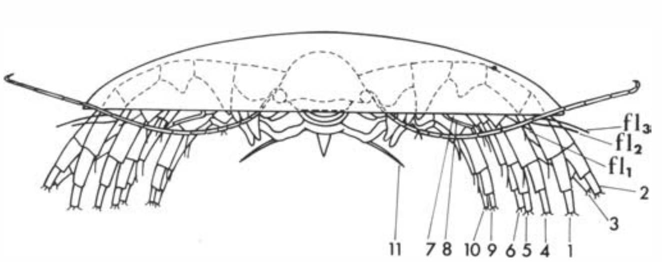

Fig. 8. Anterior reconstruction of *Burgessia bella.* Gait as for Fig. 6. Outline of first walking-leg and gut shown dotted.

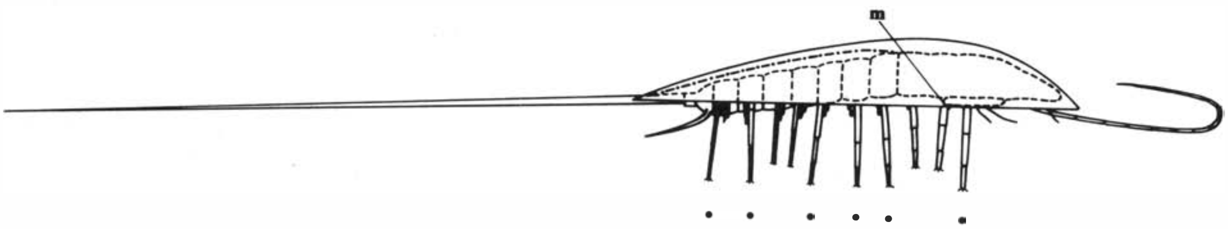

Fig. 9. Lateral reconstruction of *Burgessia bella.* Gait as for Fig. 6. Legs on ground indicated by ◦ , underside of carapace as seen in longitudinal section indicated by —·—. Cephalic region of body shown in heavy dashes, m — mouth.

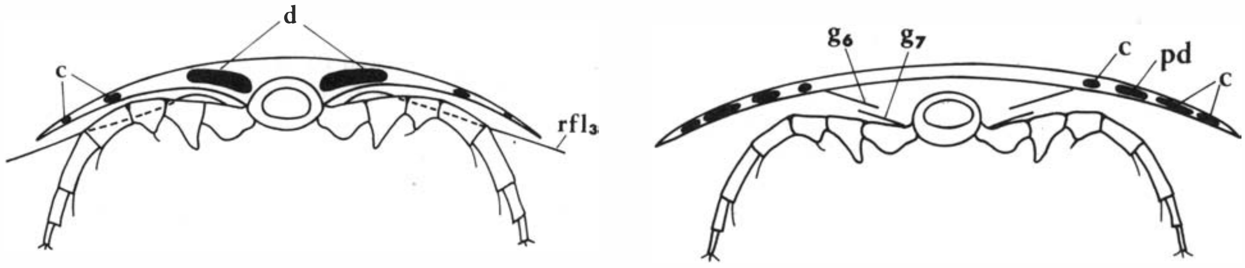

Fig. 10. Cross-sectional reconstructions of *Burgessia bella.* A — anterior of diverticulum, B — posterior of diverticulum (somite 7).

Symbols used on Figures are explained under *Terminology.*

In order to keep the stride length the same, the swing of legs must decrease anteriorly. An angle of swing of the posterior-most leg of 16° was taken, reducing to 12° for the anterior-most leg. As mentioned above it is believed the propulsive stage of the legs was mainly during flexure anteriorly and during extension posteriorly; accordingly the swing of the leg has been taken as 4° in front of the transverse plane and 12° behind for the posterior-most leg, changing progressively to 9° forwards and 3° back for the first walking-leg.

It is postulated that *Burgessia* walked slowly on the sea-bottom, walking on all ten pairs of legs. It is also possible that it could have moved with the leading edge of the carapace buried shallowly in the soft substrate. In this attitude only the anterior few pairs of legs could have been in contact with the ground, unless there was a large amount of flexing at the cephalon-trunk junction (Fig. 9). It is also possible that the long caudal spine dug into the substrate to help give a more positive forward motion, though its extreme length might argue against this.

Over-all shape might suggest some comparison with *Limulus,* indicating a possible inverted swimming attitude. However, the detailed morphology of the appendages of *Limulus* and its method of propulsion clearly show there to be no analogy with *Burgessia.* A more meaningful comparison is believed possible with many diplopods (Manton 1952, 1954). One feature of *Burgessia* is the wide carapace which virtually covers the long appendages, which is a feature commonly found in various diplopods as an adaption to a shallow burrowing habit, since the carapace gives protection to the propulsive appendages.

The detailed morphology of the appendages argues against *Burgessia* being a fluid feeder, although as Bergström (1973) correctly states the food must have been in a fluid state on reaching the gut-caecal system. Since nothing is known of any masticulatory apparatus, it is possible that whatever food *Burgessia* grasped with its walking-legs was simply held against the mouth and externally digested, being sucked into the alimentary canal by muscular contractions. If this is correct, then the anterior gut lobes may have functioned as digestive glands providing the necessary digestive fluids.

Affinities

Many of the authors who have considered the affinities of *Burgessia* have stressed the similarity with some notostracan branchiopods. Walcott (1912: 179—180) believed the best living branchiopods to compare with *Burgessia* were the Apodidae (= Triopsidae). He admitted, however, that the possession of eight pairs of thoracic (= trunk) appendages and the absence of abdominal segments with appendages in *Burgessia* distinguished it from apodids and were more characteristic of the Phyllocarida. Crampton (1919: 155) believed that *Burgessia,* with its resemblance to the recent notostracan *Lepidurus,* indicated what the first arthropods were like. Raymond

(1920) dissented in part, believing *Burgessia* to be both more primitive and more specialised than *Apus* (= *Triops*), pointing out that although the carapace and lack of limbs posteriorly were *Apus*-like, the form of the trunk appendages was more comparable with those of the trilobites. Raymond also believed that of the other Burgess Shale genera a closer comparison could be made with *Marrella.* However, he considered *Burgessia* a notostracan (1920: 109), but placed *Marrella* in the order Marrellina in a new subclass Haplopoda (1920: 148–149).

The present investigation has supported the interpretation of the trunk limbs as being trilobitan in *Burgessia,* i.e. having a six-segmented leg branch and a lobe-shaped outer branch from the coxa. Whittington (1971b) has shown that the walking-leg of *Marrella* may be different from that of *Burgessia* in having only five, and not six segments plus a coxa. Fedotov (1925: 385, 386), having rejected the two specimens figured by Walcott (1912, Pl. 30: 3, 4) as not belonging to *Burgessia,* unequivocally considered *Burgessia* to be a notostracan. He commented, however, that if the two rejected specimens were subsequently shown to belong to *Burgessia* (which they have), then, since these had segmented trunk appendages, it would be necessary to acknowledge that the appendages of the Cambrian notostracans were jointed, not unjointed as in recent genera. Henriksen (1928) followed the general concensus and considered *Burgessia* to have definite notostracan affinities, holding the opinion, contrary to Fedotov, that the early notostracan branchiopods had jointed appendages and that the unjointed condition in modern forms is a specialised condition. Walcott (1931) inferred that he still held that *Burgessia* was most closely related to the branchiopods. Raymond (1935) erected the order Pseudonotostraca in which he placed *Burgessia* together with *Waptia* and *Protocaris.* Størmer (1939: 236, 237), believing he had substantiated Walcott's suggestion that there was an anterior support to the gill branches, suggested there was a close resemblance between *Burgessia* and *Leanchoilia, Neolenus* (= *Olenoides*) and *Opabinia.* The present study, however, does not support this interpretation of the gill branch. Subsequently, Størmer (1944: 98, 99), having briefly reviewed the morphology and previous opinions as to the affinities of *Burgessia,* concluded that the large carapace and lack of trilobation pointed towards the Crustacea. On the other hand the trilobitan limb (here substantiated), the labrum (no longer believed to exist), the styliform caudal spine (thought by Størmer to be a segmented telson), and intestinal caecal system, strongly suggested to Størmer affinities with the Trilobita, merostome-like Cambrian arthropods, as well as to the Chelicerata. In his formal classification (1944: 133–136), he considered *Burgessia* to belong within the new Class Pseudocrustacea, which he placed in a new subphylum Trilobitomorpha. In 1959 (Størmer *in* Moore) he clearly still held much the same views on the affinities of *Burgessia,* although he made some modifications in the names of the higher taxonomic ranks, erecting a new class Trilobitoidea with Burgessida as an order within the subclass Pseudonotostraca. In a recent discussion of the phylogeny of the arthropods (Manton 1973) no attempt is made to place the Burgess Shale forms within what is, and must be, a framework based on extant forms. Simonetta (1973, pers. comm.) believes *Burgessia* to stand somewhat alone within the Burgess Shale fauna, possibly a 'proto-notostracan' and a possible ancestor to at least some crustaceans.

Various authors have commented on the similarities between *Burgessia* and *Naraoia,* especially the gut-caecal system and appendages (Walcott 1912, 1931, Størmer 1944). However, full assessment of these must await the redescription of *Naraoia.* Other occurrences of unusual fossil arthropods in the lower Palaeozoic rocks offer little help in deciding possible affinities of *Burgessia. Douglasocaris* Caster and Brooks, 1956 from the Ordovician of Tennessee, thought possibly to be a notostracan branchiopod (Rolfe *in* Moore 1969: R330), shows some superficial similarity; close comparison, however, reveals there to be little affinity between the two forms. The only other form exhibiting any similarity is *Cheloniellon* Broili, 1933 from the Devonian of Germany. Again detailed examination reveals no close similarity, any resemblance being thought to be most likely accounted for by convergent adaption to a similar mode of life. Sharov (1965, 1966) apparently accepted Walcott's ascertion that the appendages of *Burgessia* were trilobite-like, and considered *Burgessia* to be derived from the trilobite by the reduction in trunk pleurae accompanied by the backward growth of the head shield to cover the trunk segments.

Since the current restudy of all the Burgess Shale arthropods is revealing that the detailed morphology of these forms is not as previously thought, the present author considers further discussion of the affinities of *Burgessia* as premature; such discussion must await the completion of the redescription of all the arthropods within the fauna. What is apparent from this restudy is that *Burgessia* did possess a mixture of characters, e.g. carapace, trilobitan appendages (but no trilobitan labrum), an intestinal cephalic caecal system, antennae, styliform caudal spine, many of which are to be found in modern arthropods of various groups. Thus it is clearly possible that *Burgessia's* affinities are within an early arthropodan stock which gave rise, either directly or indirectly, to many of the major extant arthropod taxa.

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Plates 1 – 13

EXPLANATIONS OF PLATES 1–13 AND FIGURES 11–35

The photographs were taken on panchromatic film with ultraviolet radiation. The radiation was directed at 30° to the horizontal and the direction from which it was from is stated as west, north, etc., relative to the margins of the plate. Photographs referred to as reflected were taken with the incident radiation at 60° to the horizontal, and the specimen tilted slightly at about 10° so that the maximum reflective effect was directed into the camera. The orientation of the specimen relative to the bedding is given as dorsal, oblique, etc., the full explanation of the terms being given under *Preservation.*

Figures 11–35 are camera-lucida drawings showing parts of the animals present in a specimen and their relative levels within the rock. All or part of the specimen may be shown, and where counterparts are known some details from both may be incorporated in the drawing.

Symbols on the Plates and Figures are explained under *Terminology.* Depositories of specimens are USNM, United States National Museum, Washington, D.C., and GSC, Geological Survey of Canada, Ottawa.

The items explaining individual figures on the plates are arranged in the following order: depository and specimen number, orientation of specimen, direction of incident radiation, magnification, reference to previous illustration, comment and/or reference to Figure, locality and horizon in terms discussed in the text.

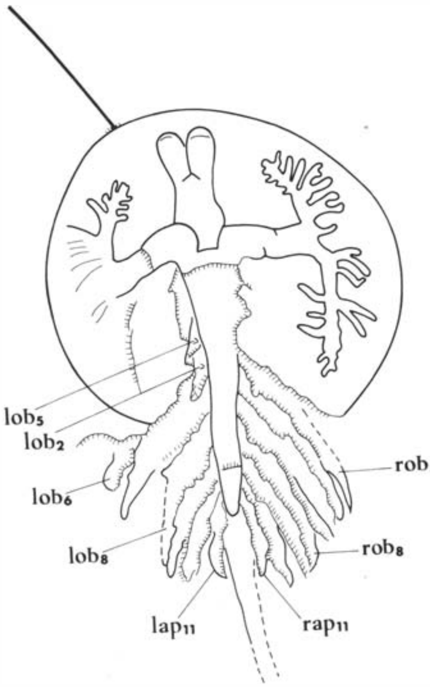

Fig. 11.

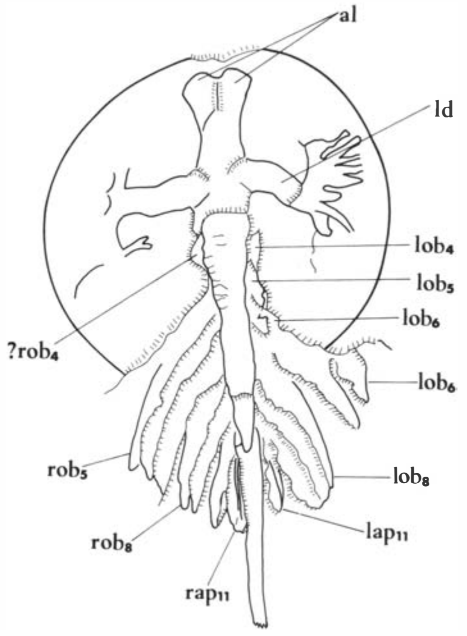

Fig. 12.

Plate 1

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Fig. 1. USNM 57677, dorsal, west. X5, original of Walcott 1912, Pl. 27: 2; Simonetta 1970, Pl. 28: 2. *Figs. 2, 3, 8.* USNM 57676, part and counterpart 2. Dorsal, northwest, X5, see Fig. 11. 3. Ventral, northwest, X5, see Fig. 12, 8. Ventral, reflected, X5, original of Walcott 1912, Pl. 27: 1, Simonetta 1970, Pl. 28: 1a, b. *Figs. 4–7.* USNM 57680, part and counterpart. 4. Lateral, west, X3. 5. Lateral, west, X3. 6, 7. reflected, X3, original of Walcott 1912, Pl. 30: 3, Simonetta 1970, Pl. 28: 3a, b. *Figs. 9, 10.* USNM 155667, oblique. 9. Reflected, X5. 10. West, X5, original of Simonetta 1970, Pl. 32: 2.

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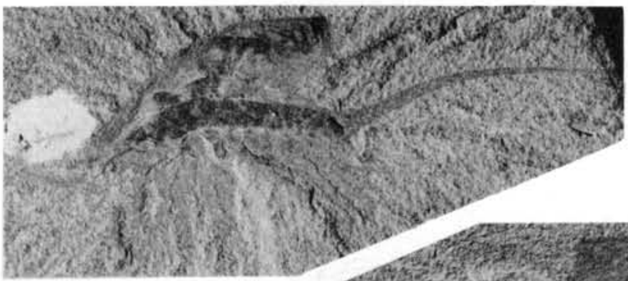

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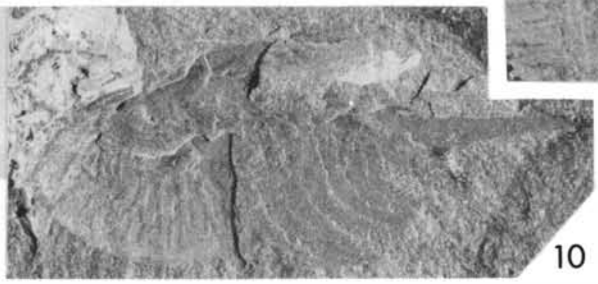

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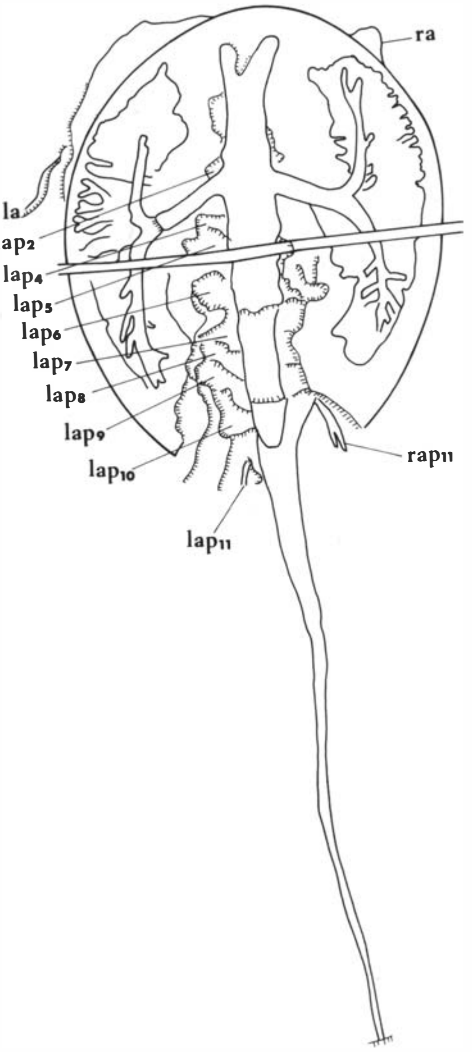


Fig. 13.

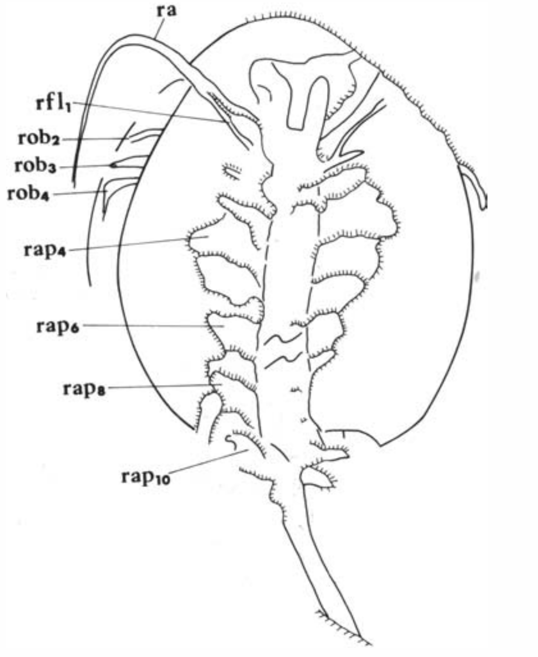


Fig. 14.

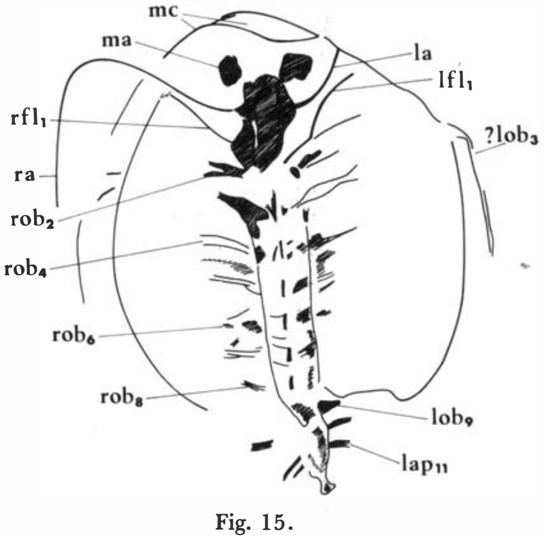
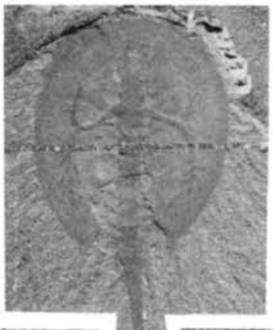


Fig. 15.

Plate 2

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 5, 8. USNM 83947d, dorsal. 1. North, X2½. 5. North, X10. 8. Reflected, X2½; original of Walcott 1931, Pl. 15: 7. Shows fractures in caudal spine, see Fig. 13. *Figs. 2, 4, 10.* USNM 83947b, dorsal. 2. Northwest, X2½. 4. North, X10. 10. Reflected, X2½; original of Walcott 1931, Pl. 15: 5. *Figs. 3, 7.* USNM 83947c, ventral. 3. Reflected, X5. 7. North, X5; original of Walcott 1931, Pl. 15: 6. See Fig. 15. *Figs. 6, 9.* USNM 57678, ventral. 6. Reflected, X5. 9. North, X5; original of Walcott 1912, Pl. 27: 3, Simonetta 1970, Pl. 28: 5. See Fig. 14.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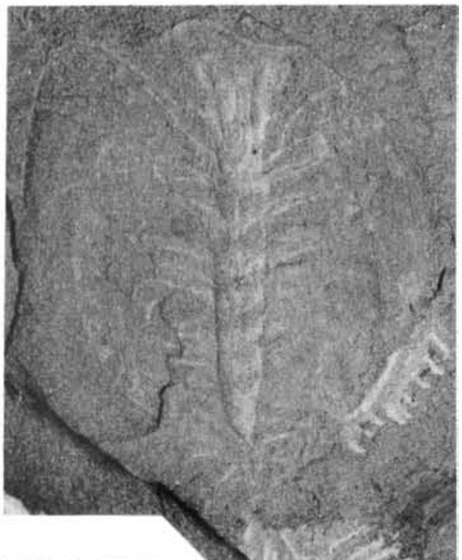
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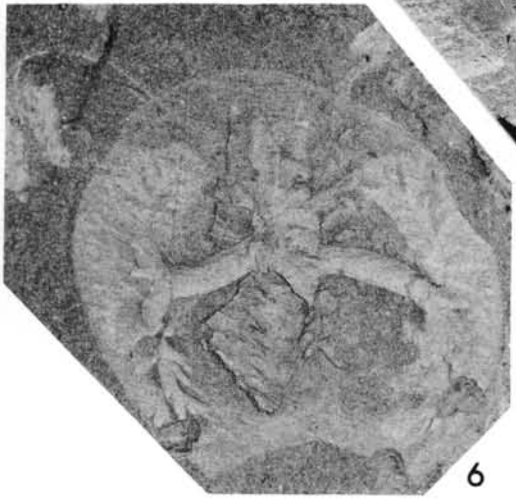
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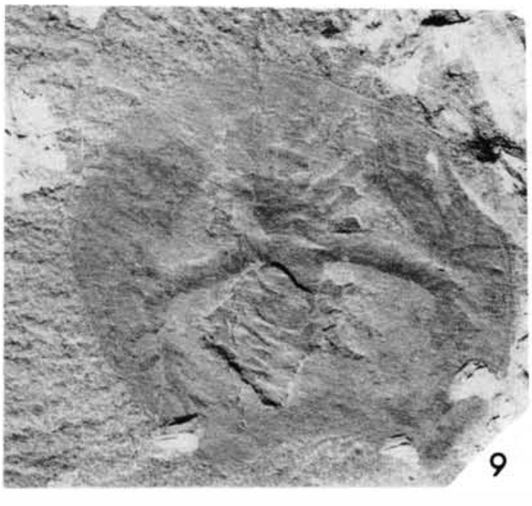
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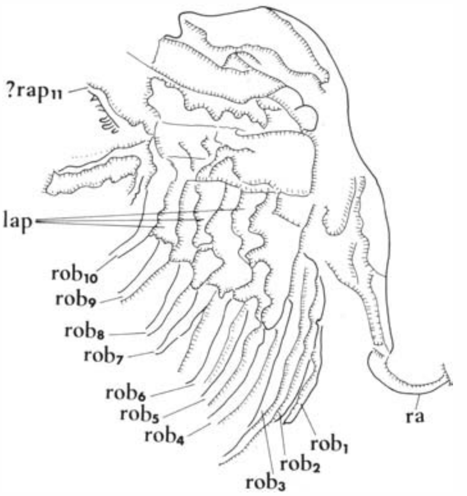


Fig. 16.

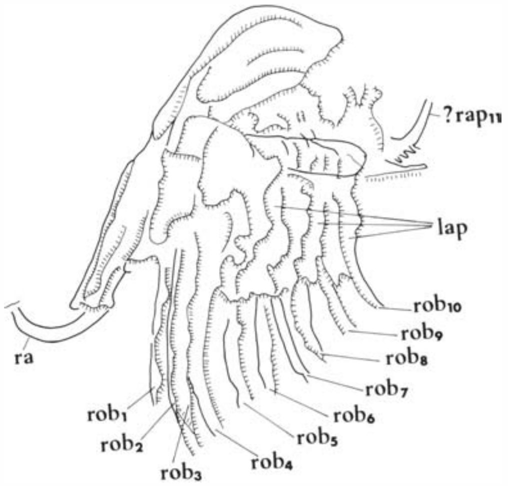


Fig. 17.

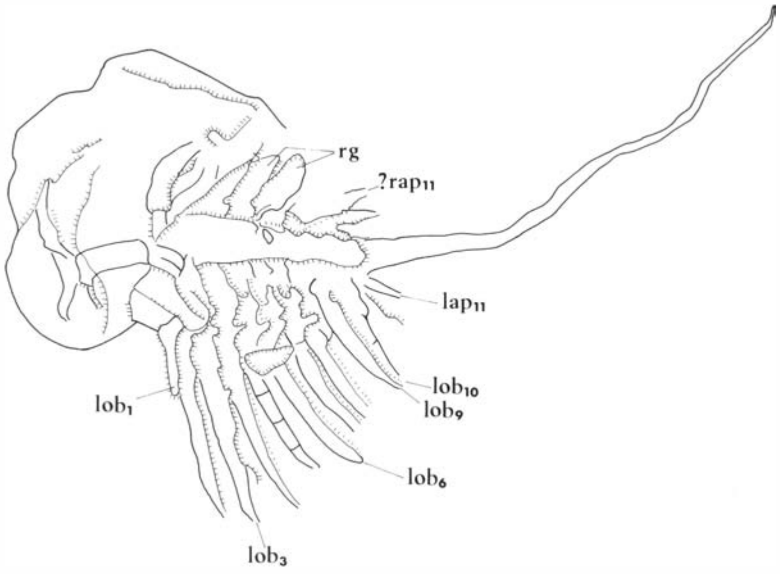
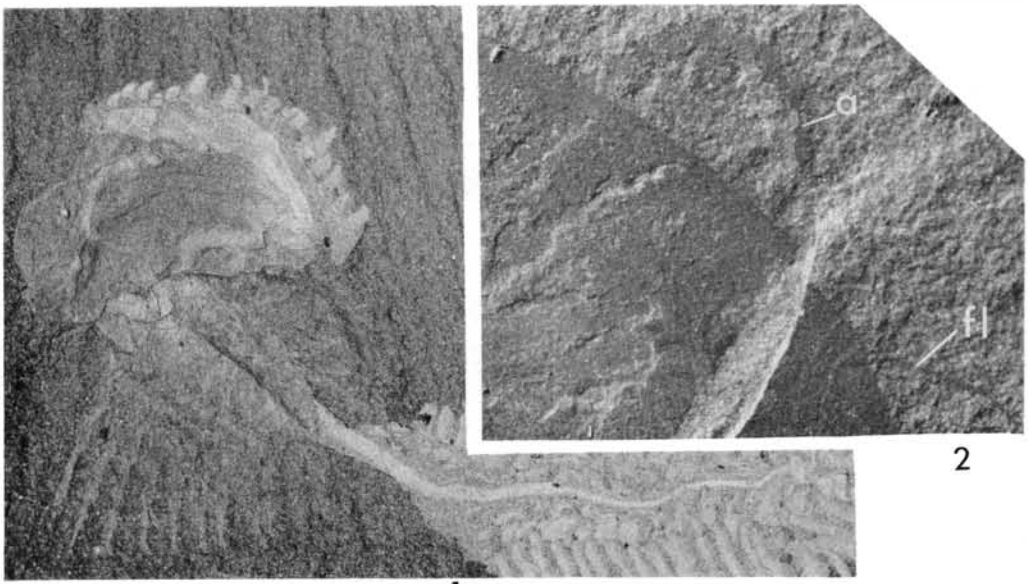


Fig. 18.

Plate 3

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 8. USNM 83947a, oblique. 1. Reflected, X5. 8. South, X5; original of Walcott 1931, Pl. 15: 4. See Fig. 18. *Fig. 2.* USNM 83947b, dorsal, northwest, X10. Shows one flagellum (fl). See Pl. 2: 2. *Figs. 3, 6.* USNM 155632, dorsal. 3. Reflected, X2½ 6. North, X2½, original of Simonetta 1970, Pl. 28: 8. *Figs. 4, 5, 7, 9.* USNM 83947e, part and counterpart, oblique. 4, 5. North X5, 7, 9. Reflected, X5, original of Walcott 1931, Pl. 16: 1. See Figs. 16, 17.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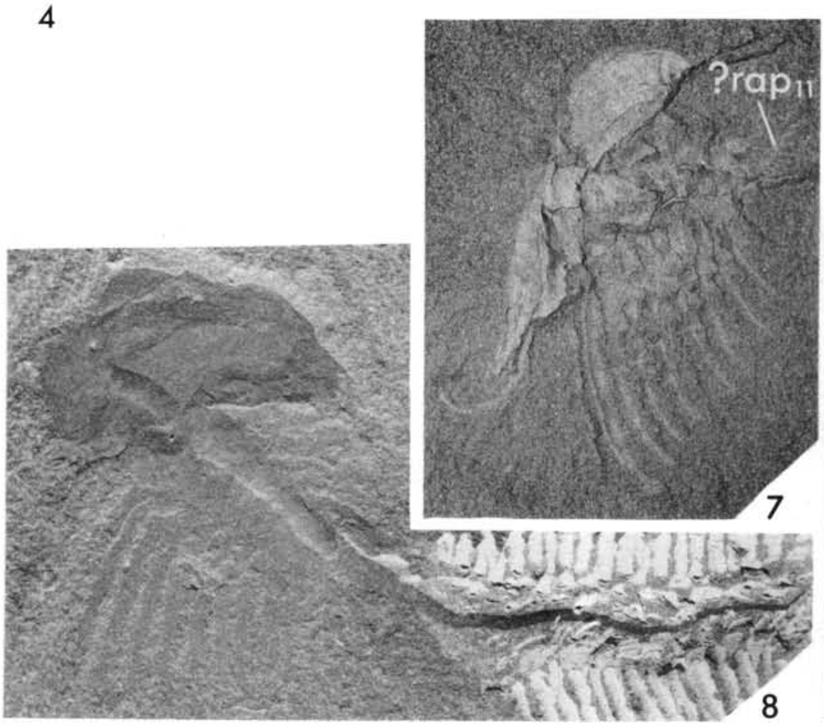

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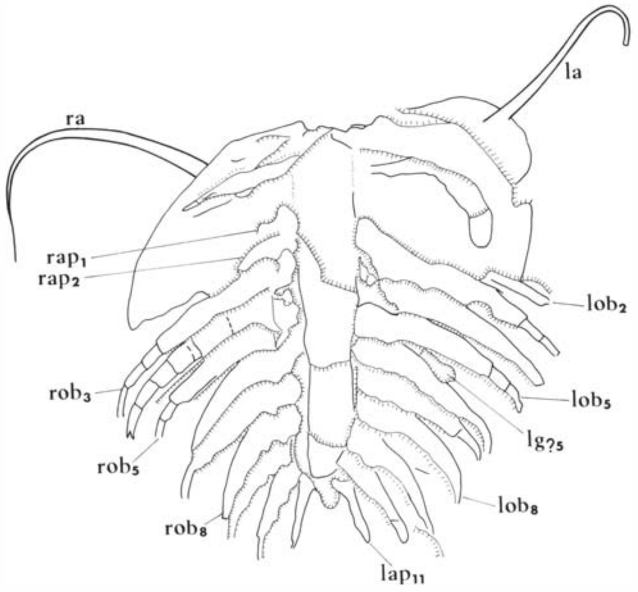
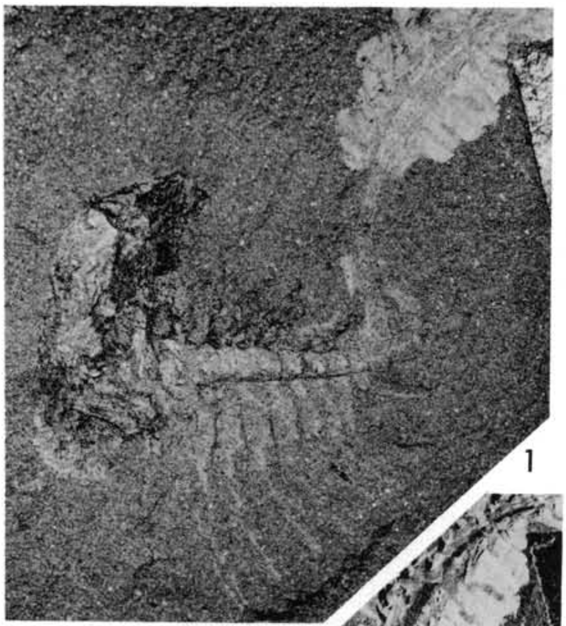


Fig. 19.

Plate 4

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 3. USNM 83947g, oblique lateral. 1. Reflected, X5. 3. West, X5; original of Walcott, 1931, Pl. 16: 3. *Figs. 2, 4.* USNM 83947f, ventral. 2. Reflected, X5. 4. North, X5; original of Walcott 1931, Pl. 16: 2. See Fig. 19. *Figs. 5, 6.* USNM 83947h, dorsal. 5. Reflected, X5. 6. Northwest, X5; original of Walcott 1931, Pl. 16: 4.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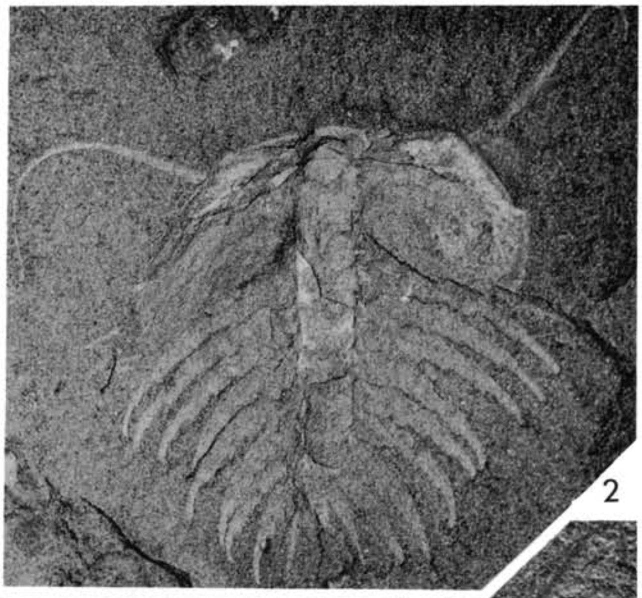
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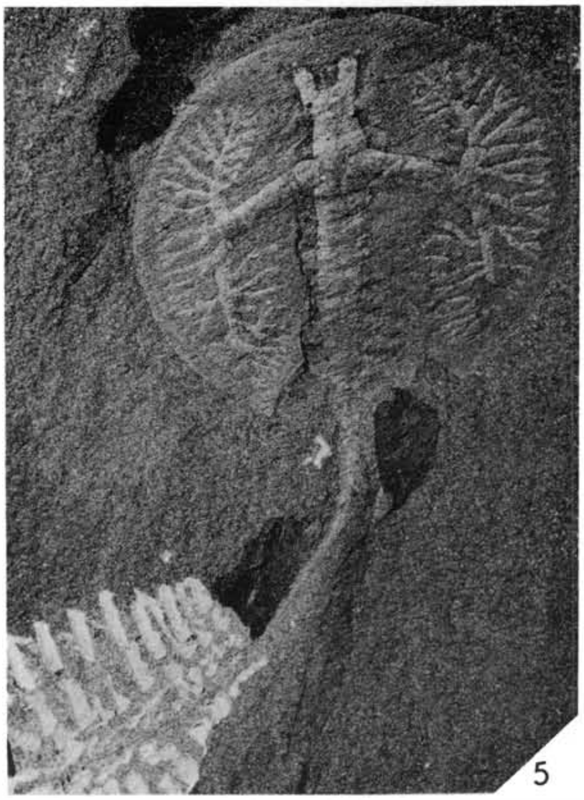
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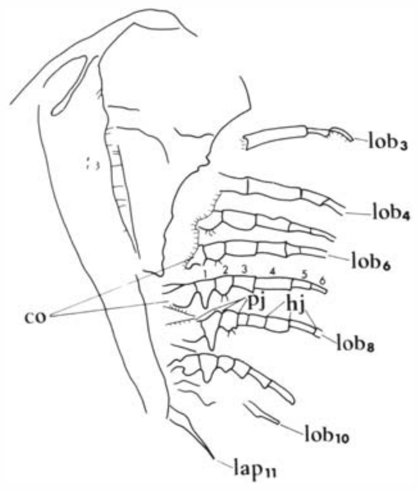

Fig. 20.

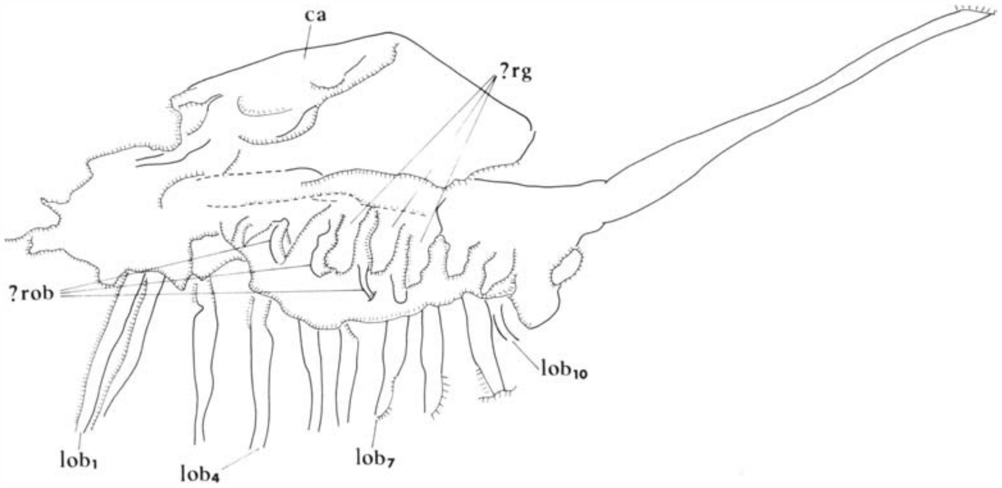

Fig. 21.

Plate 5

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 3, 4. USNM 83947m, part and counterpart. 1, 3. Ventral. 1. Northwest, X5. 3. Reflected, X5. 4. Dorsal, reflected, X5; original of Walcott 1931, Pl. 17: 3. See Pl. 6: 1. *Figs. 2, 5.* USNM 83947i, dorsal. 2. Reflected, X10. 5. South, X5; original of Walcott 1931, Pl. 16: 5. Shows details of walking-legs. See Fig. 20. *Figs. 6, 7.* USNM 83947j, lateral. 6. Reflected, X5. 7. North, X2½; original of Walcott 1931, Pl. 16: 6. See Fig. 21.


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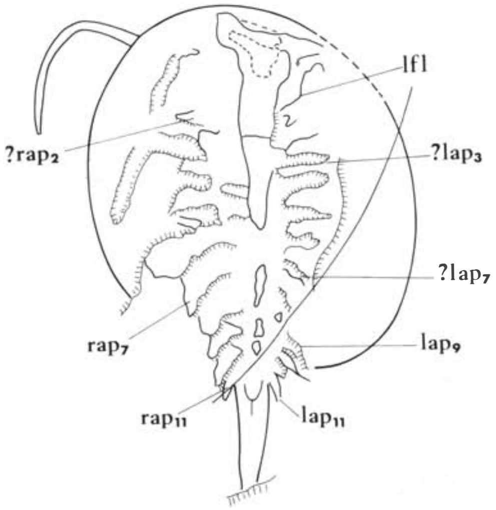

Fig. 22.

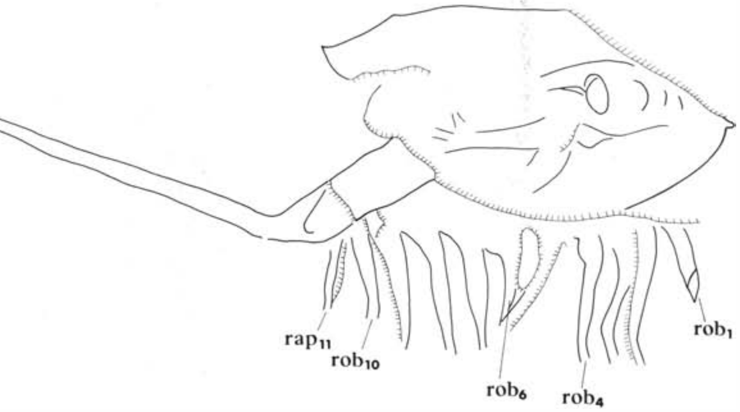

Fig. 23.

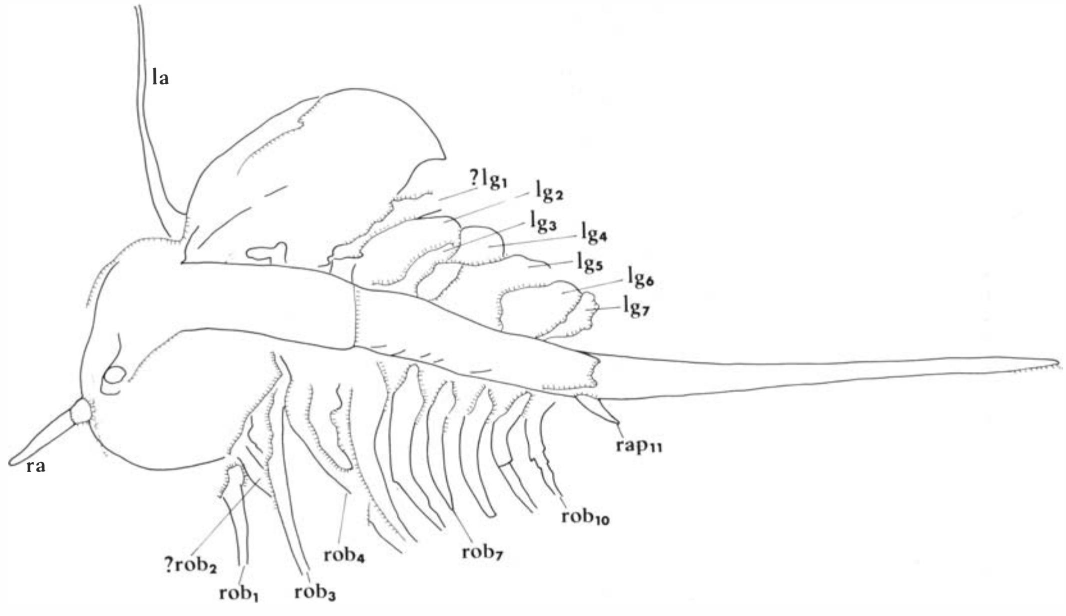

Fig. 24.

Plate 6

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Fig. 1. USNM 83947m, ventral, north, X5; original of Walcott 1931, Pl. 17: 3. See Pl. 5: 1, 3, 4. and Fig. 22. *Fig. 2, 5.* USNM 83947k, lateral. 2. Reflected, X5. 5. West, X5; original of Walcott 1931, Pl. 17: 1. *Figs. 3, 4.* USNM 839471, lateral. 3. West, X2½. 4. Reflected, X2½; original of Walcott 1931, Pl. 17: 2. *Figs. 6, 8.* USNM 83947n, ventral, west. 6. X10. 8. X2½; original of Walcott 1931, Pl. 17: 4. Shows details of gill branches. See Fig. 24. *Figs. 7, 9.* USNM 83947o, lateral. 7. North, X5. 9. Reflected, X5; original of Walcott 1931, Pl. 18: 1. See Fig. 23.


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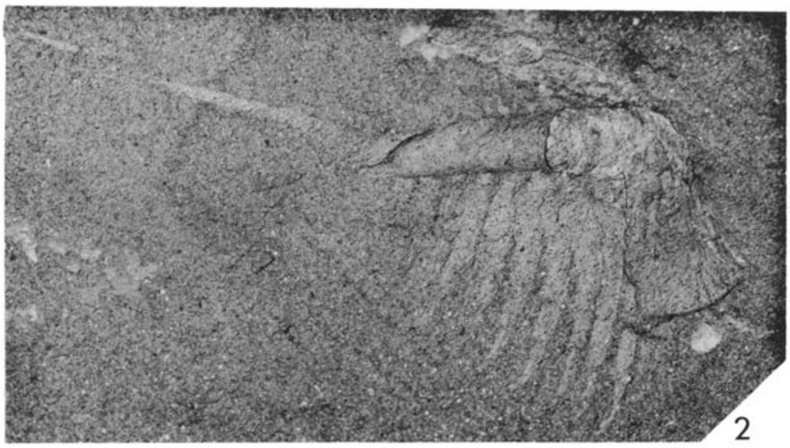
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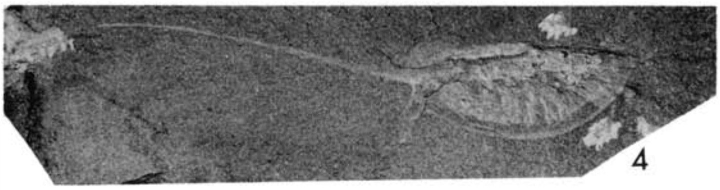
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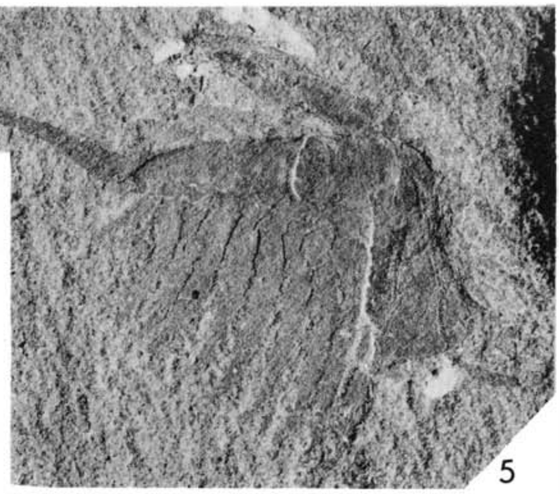
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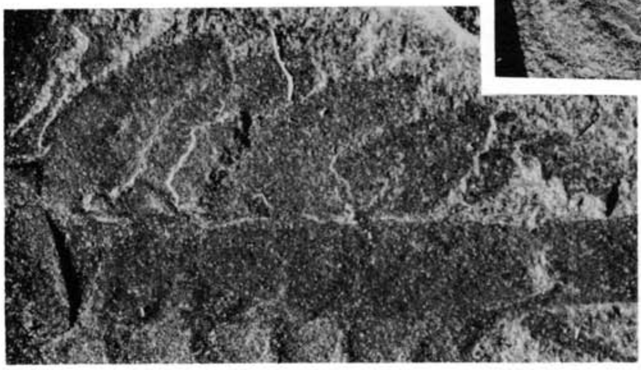
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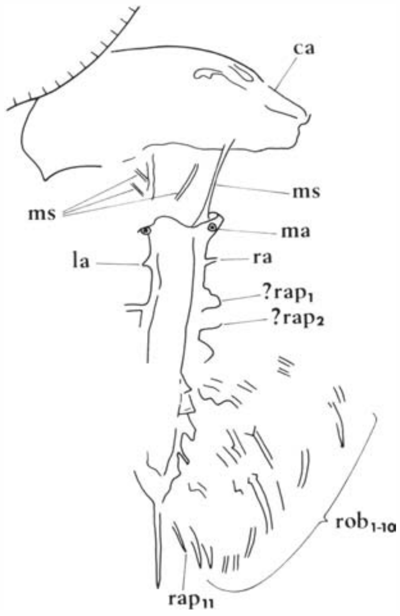

Fig. 25.

Plate 7

Burgessia bella Walcott, 1912.

Figs. 1, 2. GSC 35459, dorsal. 1. Northwest, X5. 2. Reflected, X5. See Fig. 25. Walcott quarry, level 6'7½" to 7'3½". *Figs. 3, 5.* USNM 155676, dorsal. 3. Reflected, X5. 5. Northwest, X5; original of Simonetta 1970, Pl. 32: 3. Phyllopod bed, Walcott quarry. *Figs. 4, 6, 7.* USNM 155624, ventral. 4. West, X10. 6. West, X2½. 7. Reflected, X2½; original of Simonetta 1970, Pl. 30: 3. Phyllopod bed, Walcott quarry. *Figs. 8, 10.* USNM 155680, oblique. 8. Northeast, X5. 10. Reflected, X5; original of Simonetta 1970, Pl. 28: 6. Phyllopod bed, Walcott quarry. *Fig. 9.* USNM 155630, dorsal, reflected, X5; original of Simonetta 1970, Pl. 32: 1. Phyllopod bed, Walcott quarry.


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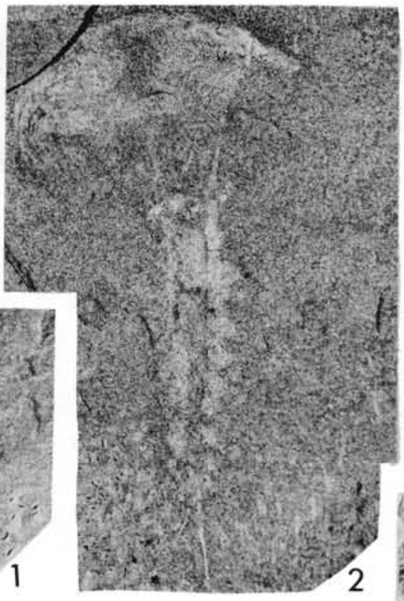
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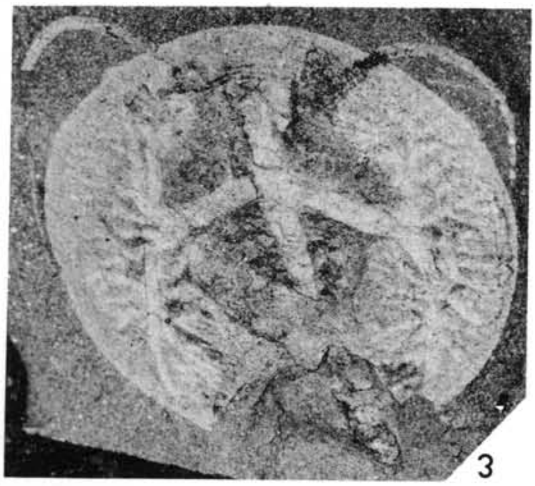
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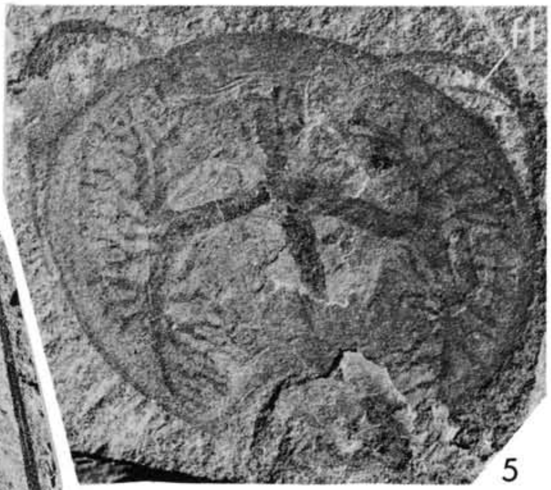

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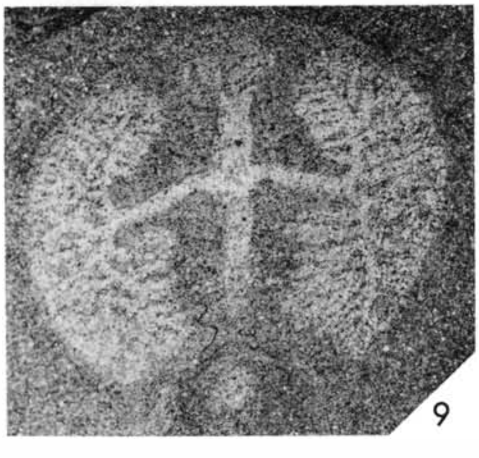
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Plate 8

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 5. USNM 155623, oblique lateral. 1. Northwest, X4. 5. Reflected, X4; original of Simonetta 1970, Pl. 30: 1. *Figs. 2, 7.* USNM 114243, part and counterpart. 2. Oblique lateral, north, X4. 6. Oblique lateral, west, X4; originals of Simonetta 1970, pl. 28: 10a, b. *Figs. 3, 4.* USNM 155626, oblique lateral. 3. Southwest, X4. 4. Reflected, X4; original of Simonetta 1970, Pl. 28: 9. *Fig. 6.* USNM 155665, ventral, north, X10; original of Simonetta 1970, Pl. 32: 4. *Fig. 8.* USNM 114240, lateral, northeast, X5; original of Simonetta 1970, Pl. 30: 2.

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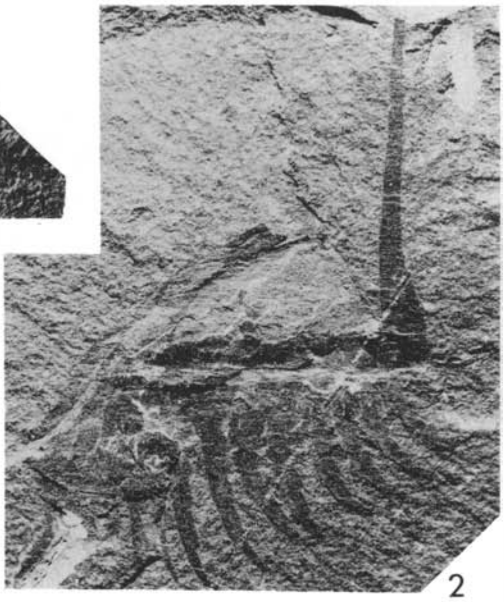

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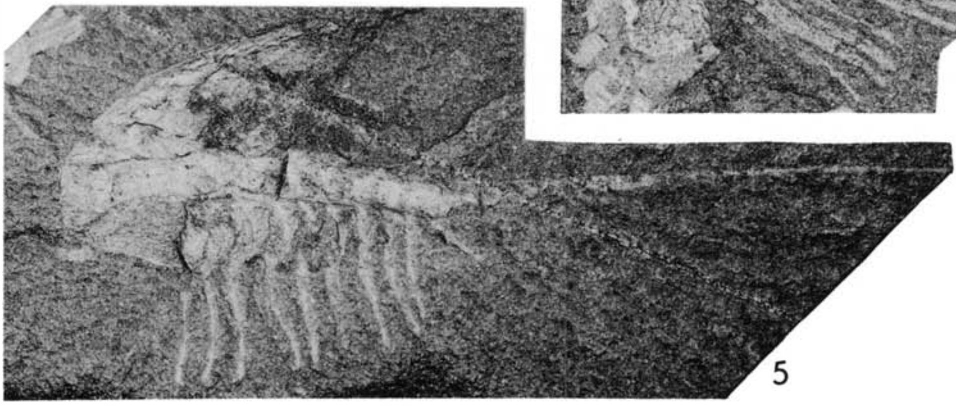

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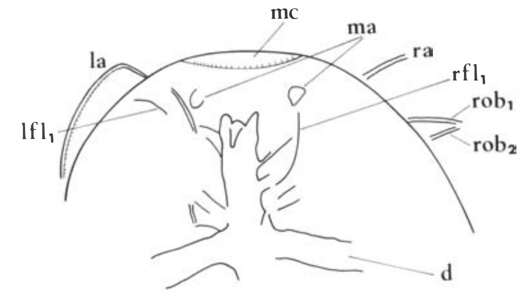

Fig. 26.

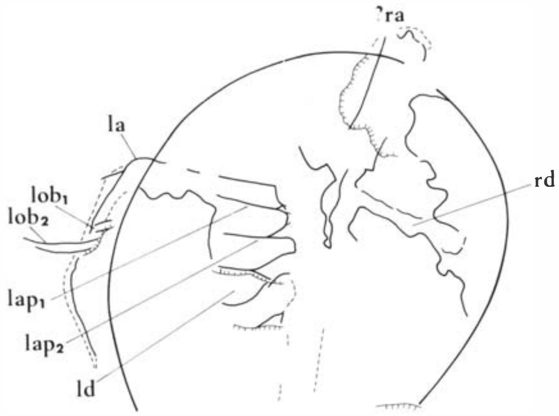

Fig. 27.

Plate 9

Burgessia bella Walcott, 1912

Fig. 1. USNM 204711, dorsal, south, X10. Smallest identified specimen. Phyllopod bed, Walcott quarry. *Fig. 2.* USNM 204717, dorsal, reflected, X5. Phyllopod bed, Walcott quarry. *Fig. 3.* USNM 204709, dorsal, reflected, X5. Phyllopod bed, Walcott quarry. See Fig. 26. *Figs. 4, 6.*-USNM 204703, ventral. 4. Reflected, X5. 6. North, X5. Phyllopod bed, Walcott quarry. *Fig. 5.* GSC 35457, dorsal, reflected, X5. Walcott quarry, level 8'7". See Fig. 27. *Fig. 7.* USNM 204707, dorsal, reflected, X5. Phyllopod bed, Walcott quarry. *Fig. 8.* USNM 204716, dorsal, reflected, X5. Phyllopod bed, Walcott quarry.

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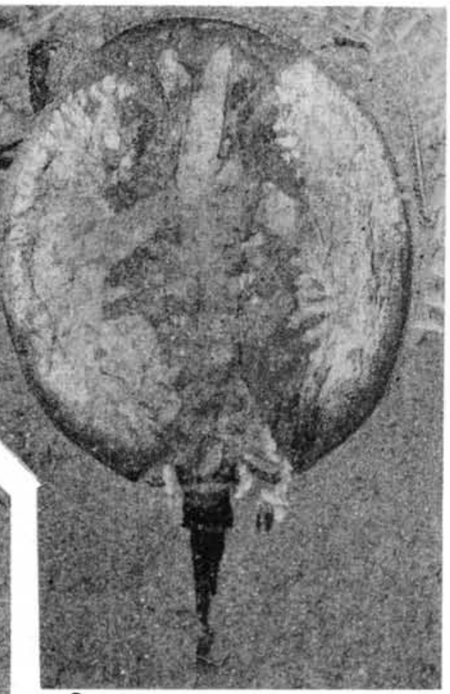

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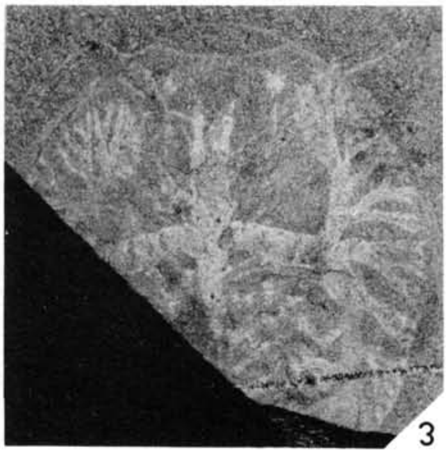

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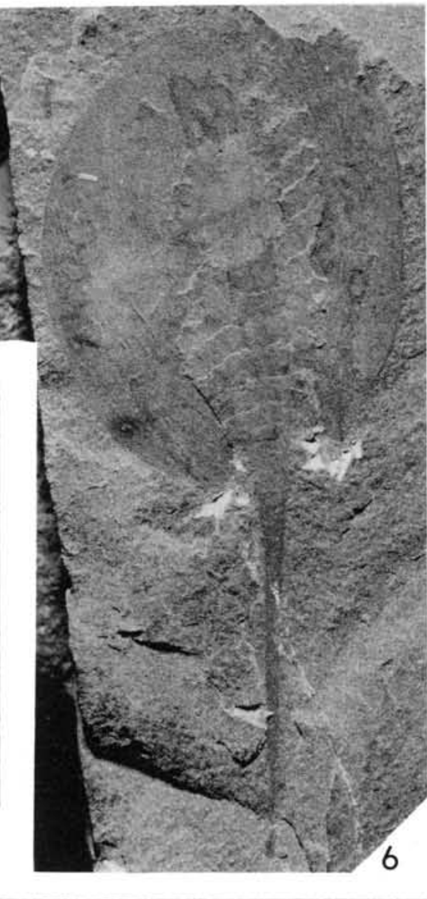

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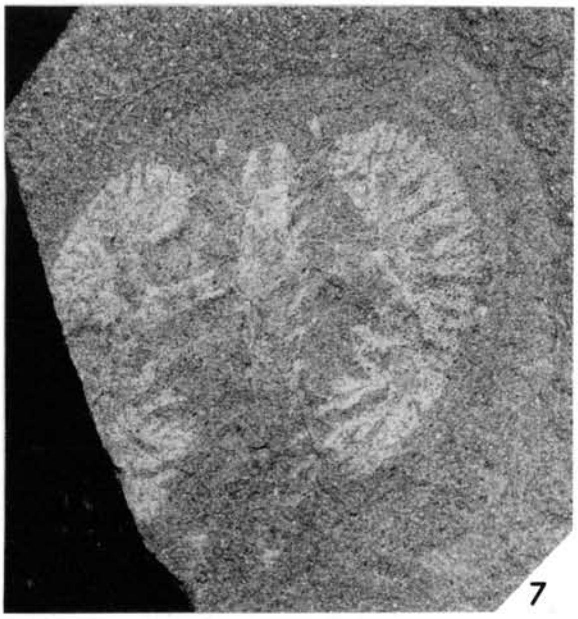

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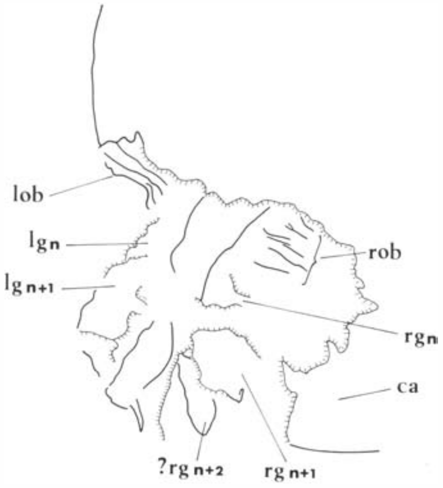
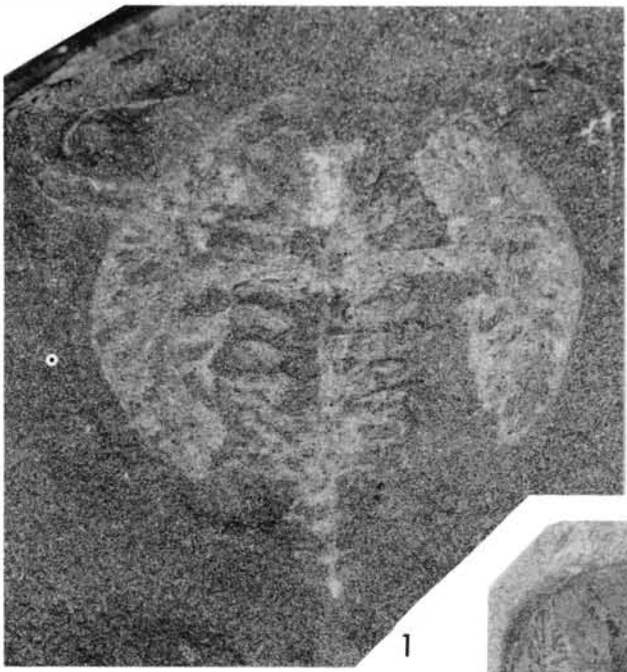


Fig. 28.

Plate 10

Burgessia bella Walcott, 1912

Figs. 1, 2. USNM 114242, dorsal. 1. Reflected, X5. 2. West. X5. Shows gill branches. Phyllopod bed, Walcott quarry. *Fig. 3.* GSC 35454, dorsal, west, X5. Walcott quarry, level 7'0". *Figs. 4, 7.* USNM 204710, dorsal. 4. North, X5. 7. Reflected, X5. Shows unsclerotized cuticle pulled away from margin posteriorly and right laterally. Phyllopod bed, Walcott quarry. *Figs. 5, 8.* GSC 35455, ventral. 5. Reflected, X5. 8. Northwest, X5. Shows position of mouth. Walcott quarry, level 6'11" to 7'4". *Fig. 6.* USNM 204713, dorsal, west, X5. Phyllopod bed, Walcott quarry. See Fig. 28.



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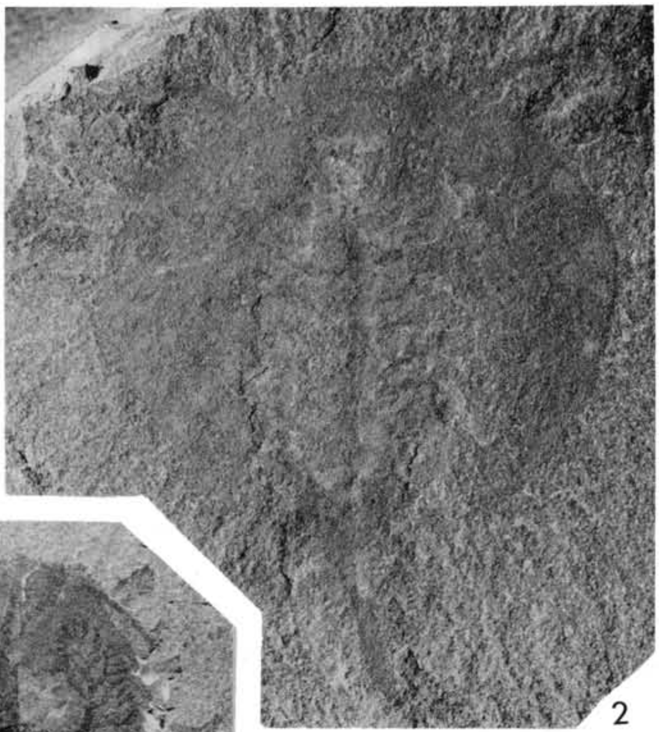

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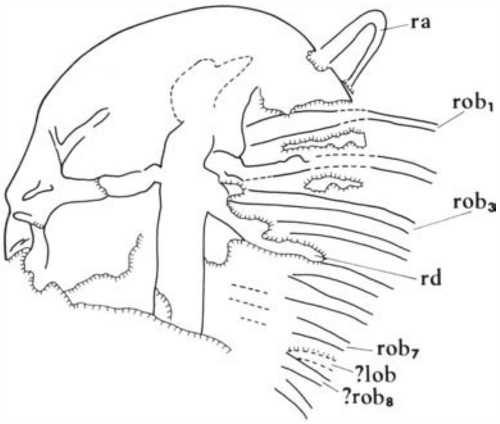

Fig. 29.

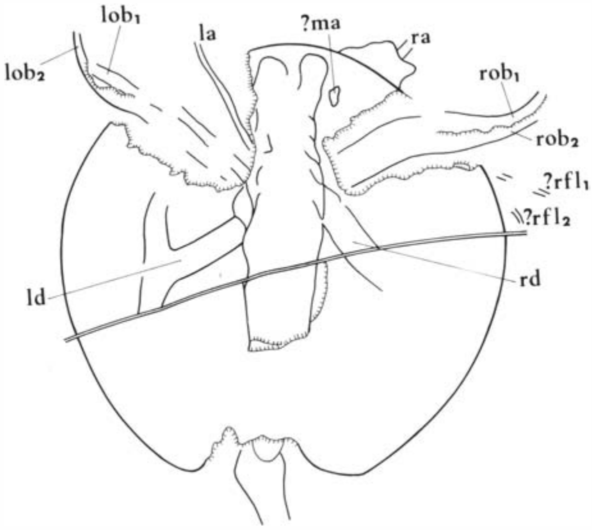

Fig. 30.

Plate 11

Burgessia bella Walcott, 1912

Figs. 1, 3. USNM 204719, oblique. 1. North, X10. 3. Northwest, X5. Shows detail of walking-legs. Phyllopod bed, Walcott quarry. *Figs. 2, 7.* GSC 35458, dorsal. 2. Reflected, X5. 7. Northwest, X5. Shows position of walking-legs beneath carapace. See Fig. 29. Walcott quarry, level 5’1” to 5’6”. *Fig. 4.* GSC 35460, ventral, north, X5. Walcott quarry level 6’7” to 7’3½”. *Figs. 5.* GSC 35463, dorsal, north, X5. Shows two walking-legs anterior to the diverticulum. Walcott quarry, level 6’11” to 7’0”. See Fig. 30. *Fig. 6.* USNM 204706, dorsal, west, X5. Phyllopod bed, Walcott quarry. *Fig. 8.* USNM 204705, dorsal, west, X5. Shows gill branches posteriorly. Phyllopod bed, Walcott quarry.

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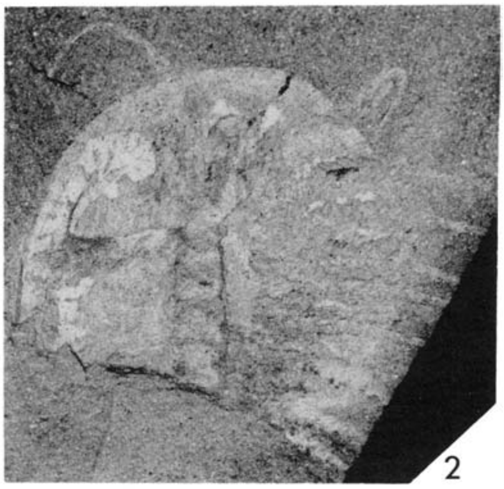

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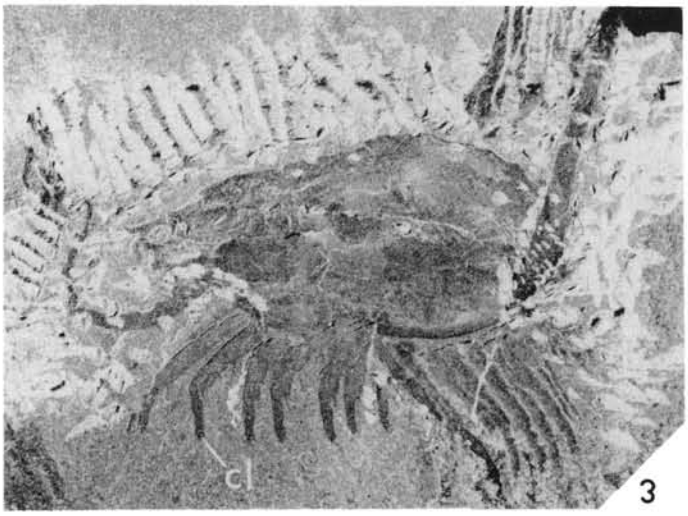

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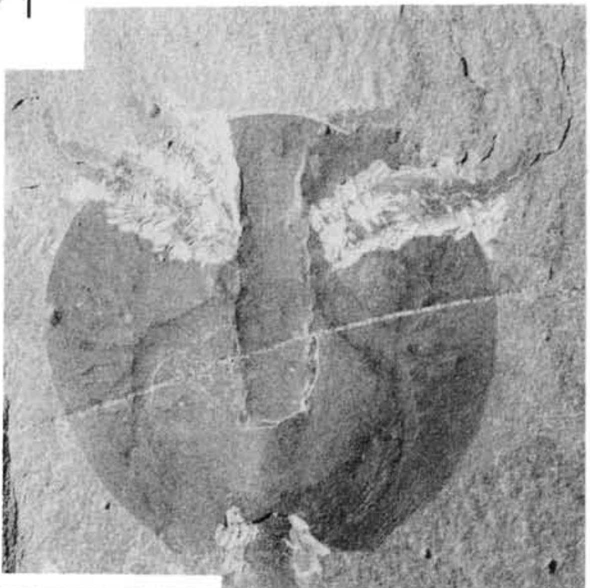

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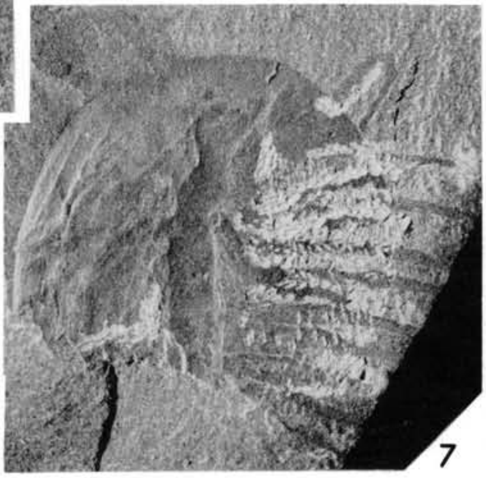

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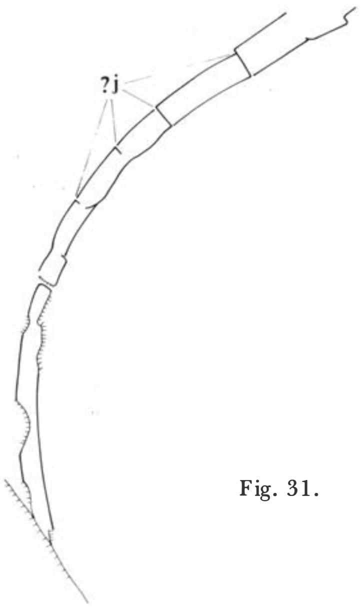

Fig. 31.

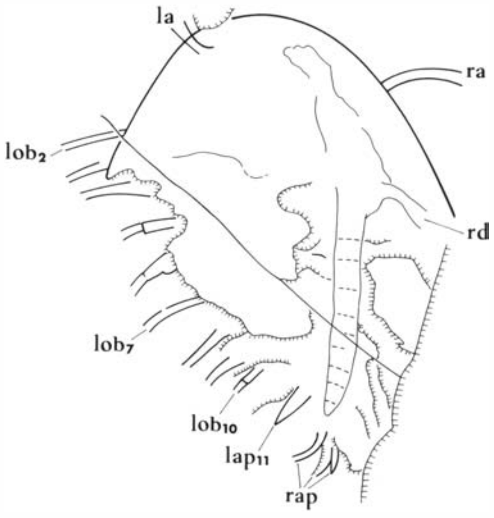

Fig. 32.

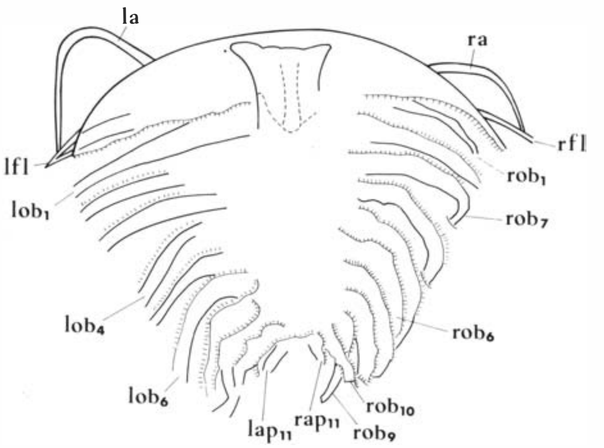

Fig. 33.

Plate 12

Burgessia bella Walcott, 1912

Figs. 1, 8. USNM 204712, ventral. 1. Northwest, X5. 8. Reflected, X5. Shows possible segmentation of caudal spine. See Fig. 31. Phyllopod bed, Walcott quarry. *Figs. 2, 3.* GSC 35456, ventral. 2. North, X5. 3. Reflected, X5. Walcott quarry, level 6'11" to 7'0". *Fig. 4.* USNM 204714, oblique, west, X5. Phyllopod bed, Walcott quarry. *Fig. 5.* USNM 204708, oblique, northwest, X5. Phyllopod bed, Walcott quarry. *Fig. 6.* GSC 35453, ventral, west, X5. Walcott quarry level 7'3". *Fig. 7.* GSC 35462, dorsal, northwest, X5. Walcott quarry, level 6'7" to 7'3½". See Fig. 32. *Fig. 9.* GSC 35461, dorsal, northwest, X5. See Fig. 33. Walcott quarry, level 6'7½" to 7'3½".

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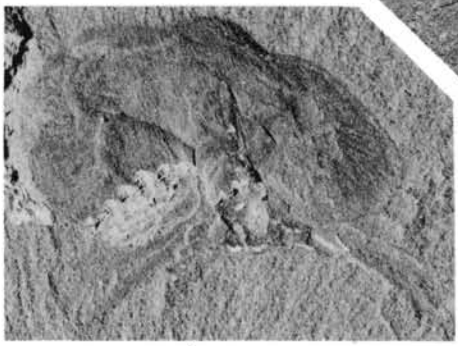

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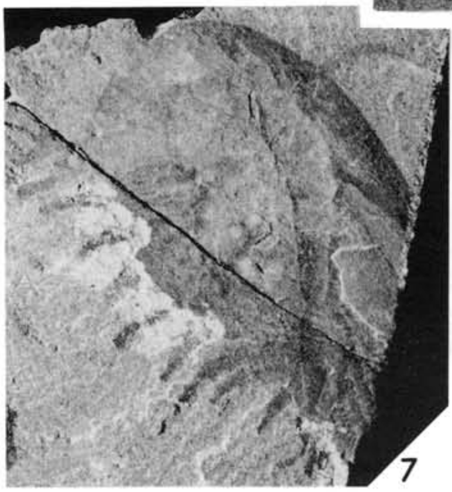

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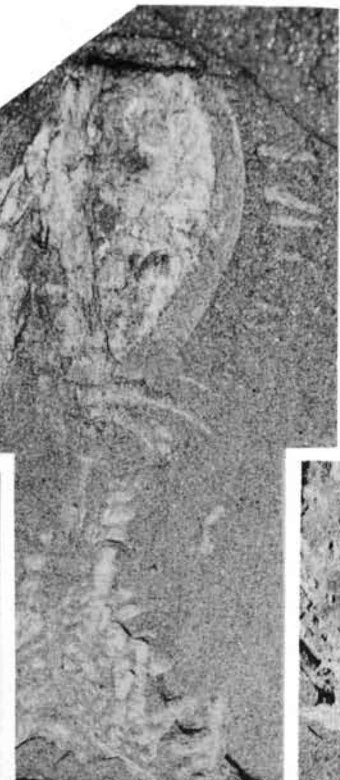

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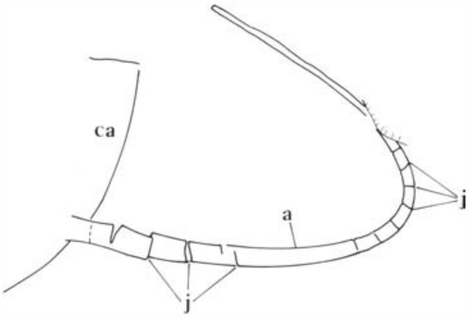

Fig. 34.

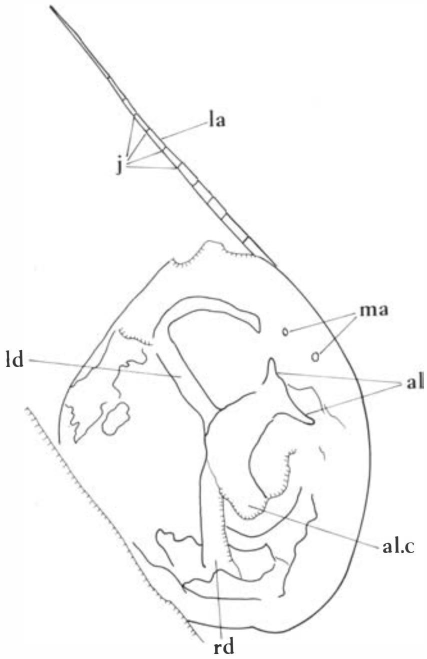

Fig. 35.

Plate 13

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 3. USNM 204704, oblique lateral. 1. West, X10. 3. Reflected, X5. *Figs. 2, 5.* USNM 204715, dorsal, 2. Northwest, X5. 5. Reflected, X5. Shows segmentation of antenna. See Fig. 34. *Fig. 4.* USNM 204718, oblique, reflected, X5. Shows segmentation of antenna. See Fig. 35. *Figs. 6, 7.* USNM 155669, ventral. 6. West, X5. 7. Reflected, X5; original of Simonetta 1970, Pl. 28: 7.

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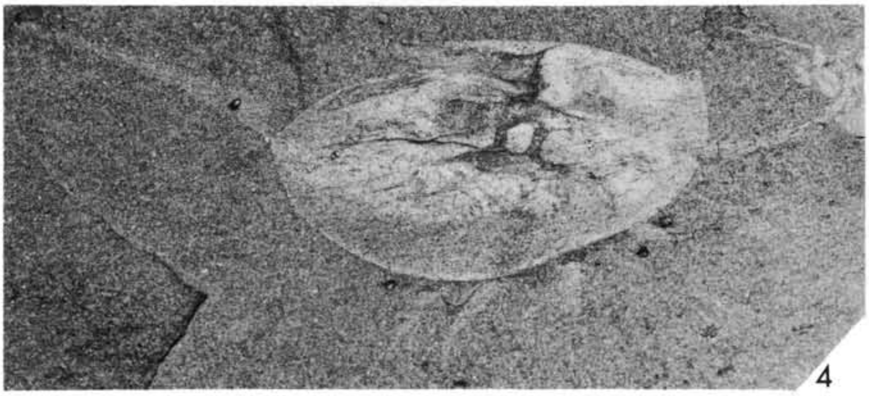

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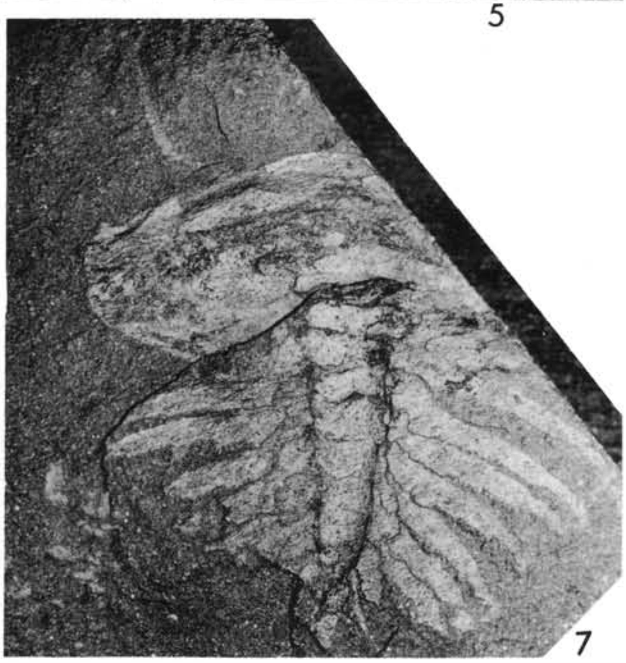

7

A trilobitomorph origin for the Crustacea

ROBERT R. HESSLER AND WILLIAM A. NEWMAN

Hessler, R. R., & Newman, W. A. 1975 07 15: A trilobitomorph origin for the Crustacea. *Fossils and Strata,* No. 4, pp. 437-459. Oslo ISSN 0300-9491. ISBN 82-00-04963-9.

In recent years, it has been strongly argued that the Arthropoda are polyphyletic, with the origin of the crustaceans being independent of the other two major arthropodan lines. We disagree with the latter conclusion. The topic can be meaningfully discussed only in terms of the similarity of primitive crustaceans to possible progenitors. From a suite of crustacean characters, primarily those seen in the Cephalocarida and in primitive Malacostraca and Branchiopoda, one can reconstruct a hypothetical primitive crustacean. Its fundamental similarity to the Trilobitomorpha far outweighs the list of valid differences. Thus, the present argument suggests that the Arthropoda has had at most a diphyletic origin: a terrestrial line running from Onychophora through Myriapoda to Insecta, and a marine radiation, with Trilobitomorpha giving rise to both Crustacea and Chelicerata.

Robert R. Hessler and William A. Newman, Scripps Institution of Oceanography, La Jolla, California 92037, 1st August, 1973.

It is not difficult to recognize an arthropod. This phylum possesses diagnostic features that are among the most distinct and simply determined in the animal kingdom. One would not think to question the phyletic unity of this clear-cut taxon, yet in the last few years this unity has not only been restudied,but rejected by some of the phylum's most accomplished students.

The primary building blocks of the Arthropoda are the five great classes Trilobitomorpha, Chelicerata, Crustacea, Myriapoda, and Insecta. In addition to these are several taxonomically minor groups, the Onychophora, Tardigrada, Pentostomida, and Pantopoda, whose precise relationship to or within the "euarthropods" is still undecided.

The affinities of some of these taxa are no longer seriously in doubt. The myriapods are thought to have given rise to the insects, although the details of this relationship are unclear (Manton, *in* Brooks et al., 1969). The trilobitomorph origin of the chelicerates seems well established (Størmer, 1944). Other alliances are not so uniformly accepted.

The gulf which deserves most serious attention is that which isolates the Myriapoda-Insecta line from the rest of the arthropods, as proposed by Tiegs (1947) and Tiegs & Manton (1958). Those authors trace that lineage back to an onychophoran ancestor, which they regard as a primitive arthropod rather than a separate phylum. In their view, there is no evidence that this onychophoran can be related to any other arthropod group, including the trilobites, which they regard as the other arthropodan stem form. Tiegs & Manton suggest that these two primitive arthropods are derived from separate annelid ancestors. Thus, the Arthropoda has a polyphyletic origin. Manton (1972) formally designated the onychophoran-myriapod-insect line as the phylum Uniramia, but gives the rest of the arthropod taxa no parallel designation.

The conception of the position of the Crustacea has fluctuated considerably. Because of their common possession of antennae and mandibles, it was long thought that crustaceans and insects had strong affinity. The lucid work of Snodgrass (1938, 1950, 1956, 1958) is the best documentation of this school of thought, which graced the relationship with the formal appellation, Mandibulata. Manton's (1963, 1964) extensive study of the arthropodan jaw destroyed this conception. The onychophoran-myriapod-insect jaw is derived from the whole limb, in contrast to the crustacean jaw which is derived from just the base of the limb. The strong similarity of the jaws of advanced insects and crustaceans is simply the result of convergent evolution. The documentation of this point is a critical factor supporting Tiegs & Manton's diphyletic hypothesis.

The bond between crustaceans and trilobitomorphs has had an equally venerable acceptance. The history of this idea is well reviewed by Størmer (1939, 1944, 1951) and for the most part will not be repeated here. The discovery that trilobites had filamentous antennae and biramous postoral appendages (Walcott, 1881; Beecher, 1893) was the most compelling proof of trilobitomorph-crustacean affinity. For some this relationship displaced the possibility of trilobitomorph-chelicerate kinship, yet in the main, a trilobite origin for both crustaceans and chelicerates seemed most reasonable (Raymond, 1920, 1935; Tiegs, 1947).

In an extensive series of papers, Størmer (1933, 1939, 1942, 1944) gives strong support to trilobitomorph-chelicerate affinity, but rejects any phyletic union of these groups with the crustaceans. In his view the biramous limb is not at all the same in crustaceans and trilobitomorphs. In the former, the exite is an exopod, arising from the basis, while in the latter it is a pre-epipod arising from a small segment proximal to the coxa. Nor is the structure of the exite the same in the two groups. Størmer regards these differences as unbridgeable. In addition to this the trilobitomorph cephalon included four postoral primary somites (in the sense of Ivanov, 1933) in contrast to two in crustaceans. Crustaceans lack the tendency toward trilobation of the dorsal shield, have a cephalic shield only secondarily, do not display a styliform telson, and do not have strongly developed intestinal diverticula.

On the other hand, in Størmer's view, chelicerates showed good correspondence with trilobitomorphs in these same areas. As a result of these and other considerations, Størmer (1944: O148) concludes: "To the present author a polyphyletic origin of the Arthropoda seems to be most in accordance with the fossil record. Finally we may conclude that the Arachnomorpha [Trilobitomorpha plus Chelicerata] appear to constitute a distinct major group of the Arthropoda, a phylum which may have evolved directly from a special group of polychaete annelids."

Considerable disagreement with his views on the isolation of crustaceans (Heegaard, 1945; Linder, 1945; Tiegs, 1947; Vandel, 1949) caused Størmer (1951, and *in* Harrington et al., 1959) to retrench and allow that the affinity of crustaceans may still be an open question.

Størmer's ideas find strong support in the works of Manton (1963, 1964, 1969). While Manton's primary concern was with the independent origin of the onychophoran-myriapod-insect line, she frequently considered the origin of the other classes and concluded that there is no demonstrable arthropodan bridge between the crustaceans and the trilobite-chelicerate line. In addition to accepting Størmer's arguments about the fundamental limb differences, Manton raises several issues of her own. The function of gnathobases in crustaceans and xiphosurans is fundamentally different. The crustacean limb is sternal in origin, while that of the xiphosuran and probably the trilobite arose from a flexible pleural region. Since the primitive crustacean probably did not have a compound eye, this organ must be convergently evolved in the two lines. The head shield of trilobites and merostomes has more in common than with that of the crustaceans. Manton (*in* Brooks et al., 1969: R53) concludes, "Thus, as far as the evidence at present available goes, a supposed polyphyletic evolution of Arthropoda seems inescapable in the sense that the Onychophora-Myriapoda-Insecta and the Crustacea have evolved independently from each other and from the Merostomata and Trilobita."

Few investigators have addressed themselves to Manton's arguments for a triphyletic origin of the arthropods, so it is difficult to assess the degree to which these ideas have found acceptance. One gets the impression that the independent origin of the Uniramia has been received with general favor, although the concept of the Mandibulata lingers surprisingly in the texts (Barnes, 1968; Kaestner, 1968; Meglitsch, 1972). Anderson (1969) documents the gulf between Crustacea and the Uniramia on embryological grounds. We are in tentative accord with this conclusion that crustaceans are not closely related to the onychophoran-myriapod-insect line (Fig. 12).

The lack of published disagreement to recent arguments regarding the independence of crustaceans from the trilobitomorph-chelicerate line implies by default the validity of this idea. In our minds, this is an unsatisfactory conclusion. We feel that much new evidence, such as the functional morphology of the Cephalocarida (Sanders, 1963a, 1963b), has been overlooked, and that much of the old evidence has been improperly handled. Furthermore, we think that the philosophical ground rules within which the question of polyphyly should be treated have often been ignored.

It is within this framework that the present essay considers the origin of the crustaceans.

THE PRIMITIVE CRUSTACEAN

A discussion of the origin of crustaceans would not be meaningful unless a primitive crustacean were used in the comparisons. The derivative features of advanced forms are of small concern. Therefore it is crucial to ask what the primitive crustacean looked like.

The fossil record gives seemingly little insight, mainly because those fossil forms which do

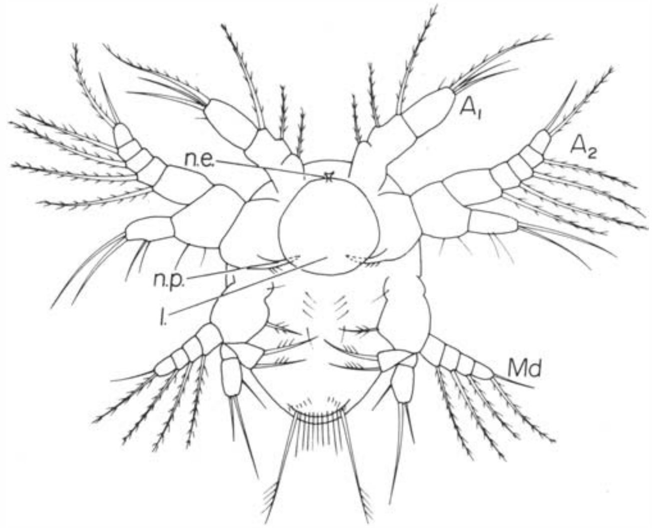

Fig. 1. Nauplius of the copepod *Cyclops bicuspidatus,* from Gurney, 1933. Note that the mandible at this early stage lacks jaws and that it is the basal endite (n.p.) of the second antenna that serves to pass food into the mouth. Symbols: A_1, first antenna; A_2, second antenna; Md, mandible; l, labrum; n.e., naupliar eye; n.p., naupliar process.

not belong to extant taxa are so problematical that there is real question about their true affinities. This is usually a function of poor preservation of critical features. In this category we place the Cycloidea, Bostrichopodida, *Oxyuropoda, Marria,* and *Mimetaster* (Brooks et al., 1969). Furthermore, none of these forms displays clearly features giving insight into primitive crustacean morphology that are not better documented in living forms. Schram (1971) places *Oxyuropoda* in the Euthycarcinoidea, and Birenheide (1971) documents placement of *Mimetaster* in the Trilobitoidea.

The Lower Triassic Euthycarcinoidea is considered by some to be the only extinct crustacean class (Moore, *in* Brooks et al., 1969). The inclusion of up to four thoracic segments under a single tergite is unique within the Crustacea and is surely a specialization. The cephalon seems to have the typical crustacean complement of a pair of first antennae, second antennae, and mandibles. Eyes are sessile. Preservation is not sufficient to allow judgement concerning the form of the first maxilla and second maxilla. All the thoracic limbs seem to be uniramous and completely alike. The abdomen is apparently limbless. The existence of this advanced class in the Mesozoic tells us nothing of the origin of the Crustacea. Schram (1971) suggests that this group actually belongs to the Trilobitomorpha.

Of the eight extant crustacean classes, five have fossil records (Brooks et al., 1969). Copepod remains are first found in the Miocene. Cirripeds date back to the Upper Silurian. The oldest branchiopods are Lower Devonian. Ostracode valves date from the Cambrian. The earliest malacostracan, a phyllocarid, is from the Cambrian; eumalacostracans first appear in the Middle Devonian. These patchy records (Benson et al., 1961; Brooks et al., 1969) document an early Paleozoic or Precambrian origin and Middle Paleozoic radiation of the Crustacea. Unfortunately the Cephalocarida is known only from the Recent, although its morphology has a Lower Paleozoic cast. The radiation into the basic extant classes had been completed by the Devonian, with only the date of origin of the maxillopodan classes Mystacocarida, Copepoda, and Branchiura being in serious doubt.

With the few exceptions to be discussed later, poor preservation of fossil crustaceans prevents us from recognizing significant primitive features which are not displayed in living forms. The primitive features seen on living animals to be discussed below are well established in the carcinological literature and may be found in Calman (1909), Brooks et al. (1969), or Kaestner (1970).

All have a nauplius or metanauplius larva in at least some representatives (Fig. 1). That is, the earliest free-living stage is one in which the cephalon bears as few as three pairs of appendages: preoral, uniramous first antennae, and postoral, biramous second antennae and mandibles. The last may be uniramous in the aberrant ostracods and branchiurans. In metanauplii, rudimentary first maxillae may be present. Where present, the photoreceptor is a median naupliar eye. The mouth is covered by the posteriorly directed labrum, except in the ostracodes and branchiurans. These two exceptions are of no fundamental importance, since the former, although free-living, are highly specialized, and the latter are wholly parasitic. The naupliar trunk is undivided or of only a few segments.

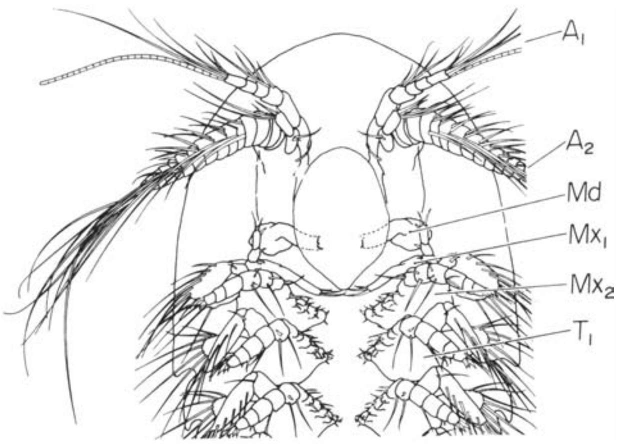

Fig. 2. Anterior end of the cephalocarid *Hutchinsoniella macracantha*, ventral view. Symbols: $A_{1\&2}$, first and second antennae; Md, mandible; $Mx_{1\&2}$, first and second maxillae; T_1, first thoracopod.

The cephalon of the adult bears five pairs of appendages (Fig. 2): the preoral first antennae and second antennae, and the postoral mandibles, first maxillae, and second maxillae. It is important to note that while the second antennae are embryologically postoral, they have migrated to an essentially preoral position in the adult. In ostracods the presence of second maxillae has been controversial, but we agree with Kaestner (1970) that the interruption in the developmental addition of limbs has been given undue importance, and consider the first so-called walking limb the second maxilla (Hartmann, 1966, 1967). In many classes, thoracic segments may be fused to the cephalon, with their limbs becoming trophic in function.

In at least the most primitive members of each class, the telson bears a pair of uniramous appendages called the caudal furca (Fig. 3).

The basic postoral limb is multiramous. A biramous limb is most common (Fig. 4). Here the single exite, the exopod, arises from the second segment of the protopod, the basis. (In thoracopods 6–8 of the hoplocarid malacostracans, the exopod arises from the third segment of the protopod. Hansen (1925) used this as evidence for existence of a precoxa. However, it may actually be that the three-segmented condition is a result of subsequent subdivision of the basis.) Such a limb is characteristic of second antennae and mandibles, and may be found among various postmandibular limbs of all the maxillopodan classes including the ostracods. A biramous limb is also characteristic of the malacostracan abdominal appendage.

In the thoracopods of the cephalocarids, branchiopods, and primitive malacostracans, there are additional lateral rami (Fig. 5). Most characteristic is the epipod, arising from the first limb segment, the coxa. This ramus does not stem from the proximal coxal portion of the protopod in cephalocarids, but distally, near the exopod. Therefore, it has been called the pseudepipod. However, it is so similar to the undoubted epipod of leptostracans that it seems reasonable to conclude its present position in cephalocarids has resulted from a secondary shift. Branchiopods may have one or two additional exites.

The cirripeds, copepods, branchiurans, and mystacocarids are often claimed to be a phylogenetic unit within the Crustacea called the Maxillopoda (Dahl, 1956b; Siewing, 1963; Newman, Zullo, and Withers *in* Brooks et al., 1969). It has been suggested that the ostracodes may belong to this lineage, as a reduction of the general plan (Dahl, 1956b). If so, the extensive specialization resulting in the Maxillopoda was at least an ancient feature of crustacean evolution, dating to the early Paleozoic. It suggests a bifurcation which left on the other hand three classes (Malacostraca, Cephalocarida, and Branchiopoda) that are not only primitive in many ways, but similar to each other in a number of features not shared with the Maxillopoda. Because of the general similarity of these three subclasses (Figs. 3, 5) particularly with regard to their common primitive feeding method, which relies on the thoracic limbs (Sanders, 1963a), we give them the collective name Thoracopoda, a term equivalent in rank to the Maxillopoda.

It has been frequently argued that the Malacostraca occupy an isolated position within the Crustacea (Cannon, 1927; Dahl, 1963; Manton, 1934; discussion following Siewing, 1963). This line of reasoning emphasizes embryological differences in the form of the nervous system and compound eye, the fixed position of the gonopores, differences in the gut, and the presence of abdominal appendages. Corollary to this point of view is the conclusion that the Phyllocarida are an early secondary specialization (Cannon, 1927; Manton, 1964; for contrast, Siewing, 1963). In our view this idea puts undue emphasis on the caridoid facies (Calman, 1909). The lepto-

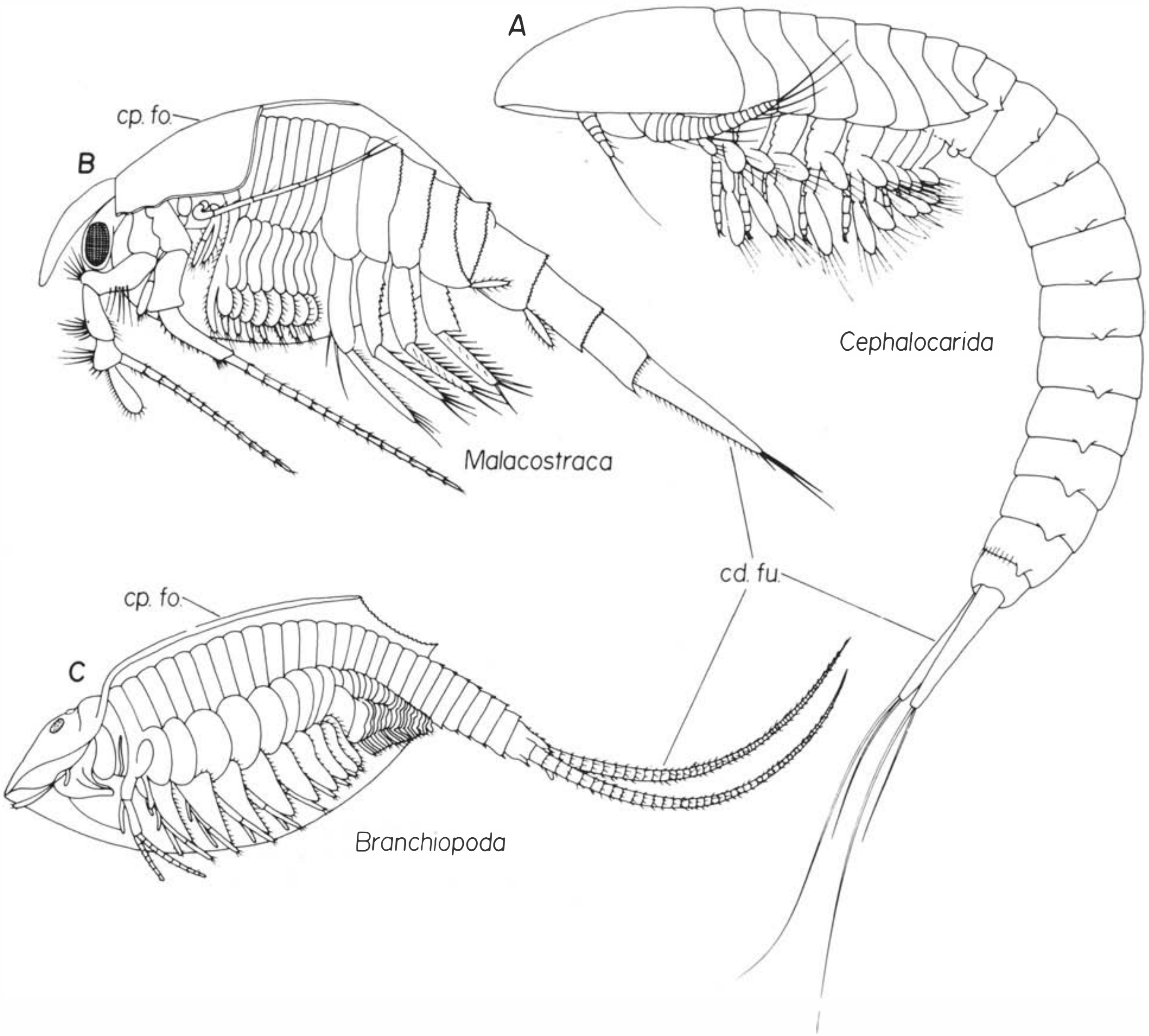

Fig. 3. Three primitive crustaceans in lateral view: A. The cephalocarid *Hutchinsoniella macracantha*. B. The leptostracan malacostracan *Nebalia bipes* (after Calman, 1909). C. The notostracan branchiopod *Lepidurus glacialis* (after Calman, 1909). In B and C portions of the carapace fold have been removed to show structures beneath. Symbols: cp.fo., carapace fold; cd.fu., caudal furca.

stracan phyllocaridans are too similar in form and function to the cephalocarids (Sanders, 1963a; Hessler, 1964) for this to be simply convergence. Furthermore it ignores the antecedence of phyllocarids to eumalacostracans in the fossil record (Rolfe, *in* Brooks et al., 1969).

The body form of maxillopodans (including ostracodes) is so modified that there is little to tell us what the primitive crustacean was like. In the Ostracoda, the profoundly abbreviated trunk, the strong serial specialization of the limbs, and the advanced development of the carapace fold into valves label this group as morphologically progressive in spite of its ancient age. Similarly, the majority of the Cirripedia are so altered as a result of their evolution to a sedentary mode of life, that few primitive features remain. Even the free-living Ascothoracica are advanced crustaceans, although as the most primitive order they merit special attention by those studying the origin of Maxillopoda. The Branchiura are apparently related to the cirripeds and the copepods, but are quite specialized for the benefit of their ectoparasitic mode of life. The free-living Copepoda are well known for their relatively primitive head appendages, but the abbreviation of the trunk, with its distinct subdivision into thorax and limbless abdomen is a maxillopodan condition which is quite derived. This combination of characters has always lent special appeal to the idea that the basic copepodan form, and therefore in part, the basic maxillopodan form is a result of neoteny in a malacostracan ancestor (Gurney, 1942). The argument of neoteny can be applied to the Mystacocarida as well. The seemingly primitive cephalic appendages (particularly second antenna and mandible) then, would be simply the retention of basic naupliar or metanaupliar morphology.

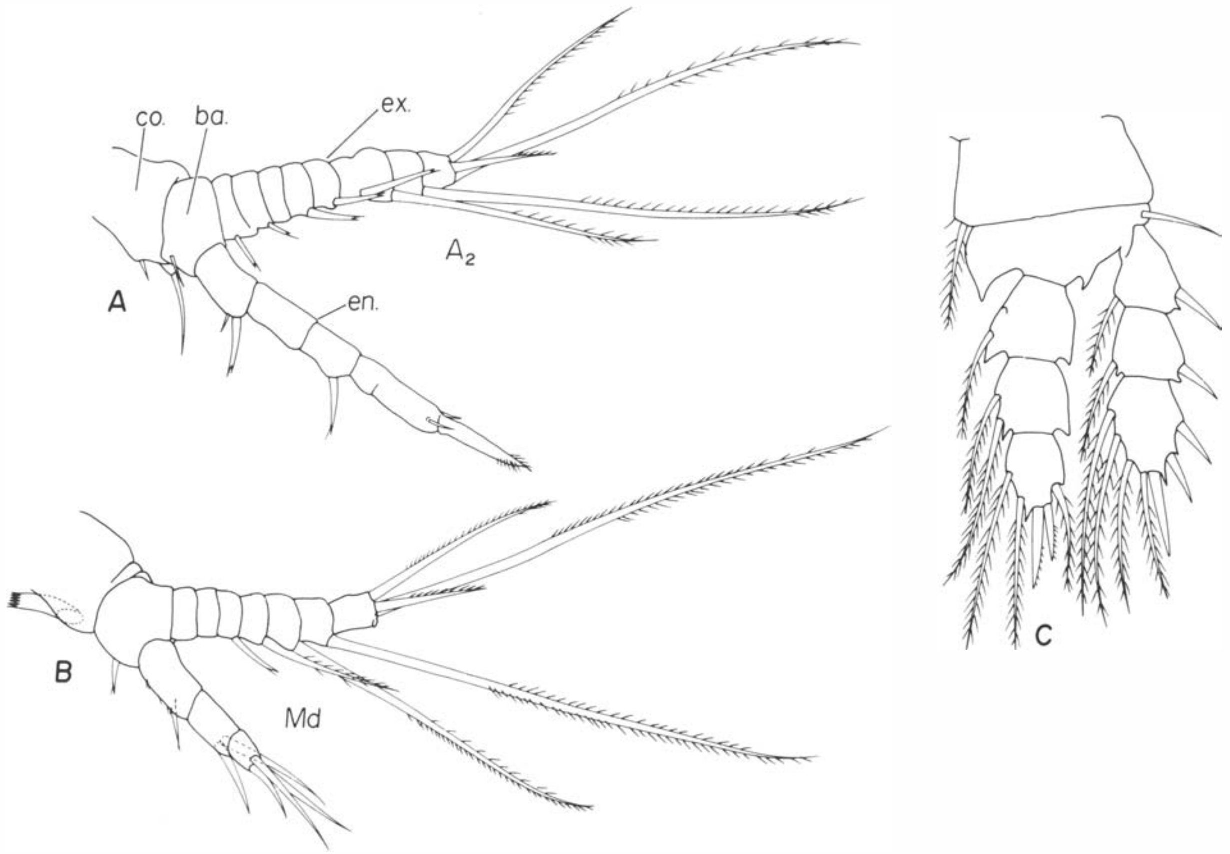

Fig. 4. Biramous crustacean appendages. A, B. Second antenna and mandible of the mystacocarid *Derocheilocaris ingens* (after Hessler, 1969). C. Fourth urosomal limb of the copepod *Cyclops bisetosus* (after Gurney, 1933). Note the high degree of similarity of A and B, and their essential likeness to the naupliar appendages shown in Fig. 1. Symbols: ba., basis; co., coxa; en., endopod; ex., exopod.

Of the Thoracopoda, the Cephalocarida (Figs. 2, 3, 5) is especially primitive and is sufficiently generalized to reflect much of the precursor condition for the other classes, particularly the branchiopods and malacostracans (Sanders, 1957, 1963a, b). That is, it is most richly endowed with features we are compelled to ascribe to the urcrustacean. Lack of photoreceptors, abdominal limbs, and perhaps carapace is apparently secondary.

Cephalocarids possess a large number of trunk segments, twenty in number. This trait characterizes the malacostracans and branchiopods as well, the former having 15 segments, the latter, up to 42. Most branchiopods have a much smaller number of segments, but in the Notostraca supernumerary trunk segments (and limbs which exceed the number of segments) are secondarily derived. That the precursor should have more segments than derivative forms is generally accepted, although the condition of the notostracan branchiopods is an exception (Calman, 1909). The tendency is well shown in the vertebrates, in the annelid-arthropod line, in the myriapod-insect line, and in the trilobitomorph-chelicerate line.

The cephalocaridan trunk displays a high degree of serial homology. Other than the division into thorax and abdomen, all the segments are alike. Most significantly, the limbs are also essentially alike, except for the eighth thoracic and genital appendage, both of which are greatly reduced, in part for reproductive purposes. Even the postoral cephalic appendages share in the basic thoracic plan, the second maxilla being almost exactly the same (Fig. 2). The first maxilla, mandible, and second antenna are very different in the adult, but have larval morphologies that clearly indicate derivation from the thoracic plan (Sanders, 1963a; Hessler, 1964).

The primitive malacostracans and branchiopods similarly display a high degree of serial homology (Fig. 3), although in neither is the similarity of head appendages to those of the trunk so clearly expressed. As with the cephalocarid, the malacostracan trunk is clearly divided into thorax and abdomen, but the malacostracan may be more primitive in that all of its pretelsonic abdominal segments (except the seventh, as seen in the Leptostraca) bear appendages, albeit

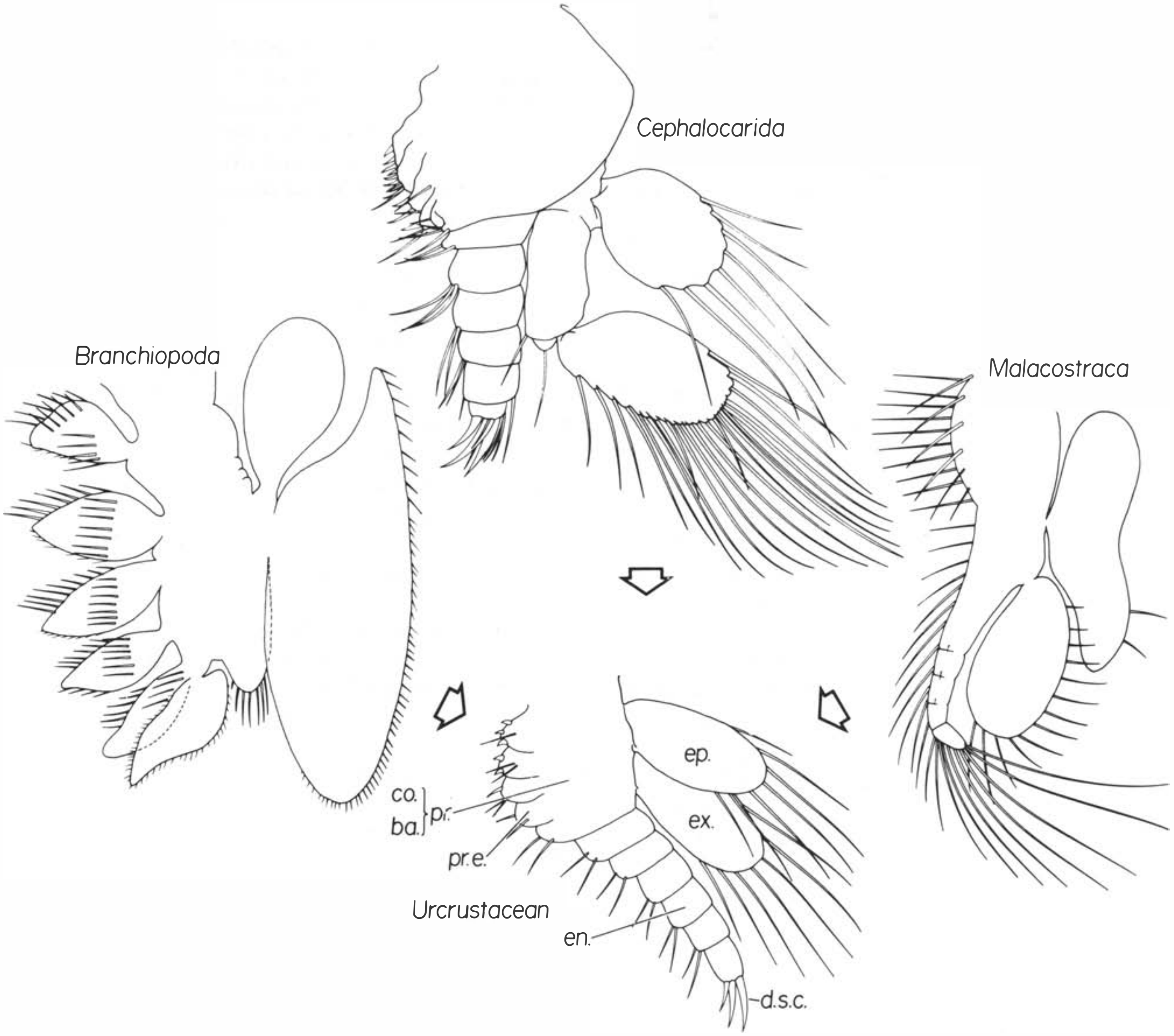

Fig. 5. Derivation of the urcrustacean trunk limb morphology from that of a notostracan branchiopod, *Triops cancriformis* (after Lankester), a cephalocarid, *Hutchinsoniella macracantha* (after Hessler), and a leptostracan malacostracan, *Nebalia bipes* (after Claus). Symbols: ba., basis; co., coxa; d.s.c., distal setal claws; en., endopod; ep., epipod; ex., exopod; pr., protopod. pr.e., protopodal endites.

ones that differ markedly from those of the thorax. The division into thorax and limbless abdomen is well expressed in the notostracans, anostracans, and most primitive diplostracans.

That a high degree of serial homology in metameric animals is a primitive trait hardly needs defense. Serial homology is illustrated by the trilobites and onychophorans, which are the oldest and most primitive known arthropods, by annelids, in the evolution of the vertebrates, and apparently even in primitive molluscs.

Did the urcrustaceans have a carapace? There are two alternative views. (1) (preferred by Newman): The most primitive malacostracans (Phyllocarida, Hoplocarida, and caridoid eumalacostracans), branchiopods (Notostraca and Conchostraca), Cirripedia, Ostracoda and Branchiura display a carapace fold which develops as an extension of the posterior margin of the segment of the second maxilla (commonly called the maxillary segment) (Fig. 3). Where the carapace is bivalved (Phyllocarida, Conchostraca, Cirripedia, Ostracoda), it is flexed by a carapace adductor muscle located in the maxillary region posteroventral to the esophagus (Hessler, 1964). On this basis it is reasonable to conclude that the urcrustacean possessed a well developed carapace enveloping a large portion of the trunk. (2) (Preferred by Hessler): In the Cephalocarida (Figs. 2, 3) there is no carapace fold of the cephalon; each thoracic segment possesses pleurae which are flexed by a pair of segmentally arranged adductor muscles (Hessler, 1964). The cephalic shield possesses three pairs of muscles which are homologs to those of the thoracic somites: those of the mandibular, first maxillary and second maxillary segments. The latter two pairs are combined into a single major pleural adductor presumably homologous (all or in part) to the carapace adductor muscle in other classes. If this condition is primitive, as suggested by Hessler, then the urcrustacean had no carapace fold, and the carapace fold of other Crustacea must be secondarily and polyphyletically derived. At present we do not have sufficient knowledge to determine which of these hypotheses for the carapace is correct.

Sanders (1963a) documented the essential similarity of feeding function of the thoracic limbs in branchiopods, leptostracan malacostracans, and cephalocarids, with the situation in the last being most basic of the three. By means of the metachronal beating of the trunk limbs, food is concentrated midventrally. Through action of the protopodal endites, food is moved forward to the mouth. In connection with this function, all three taxa have limbs which are largely foliaceous, for more efficient maintenance of currents. In all, the protopod and exites are quite flattened. In the leptostracans, the endopod is also flattened, but it is probably derived from a more stenopodial form (Calman, 1909), as seen in the cephalocarids. The cephalocaridan mixopodial limb form (Sanders, 1963a) is the most primitive trunk limb morphology known in the crustaceans and can therefore be tentatively ascribed to the urcrustacean (Fig. 5). This stands in contrast to hypotheses which favor a biramous stenopodial limb (e.g. Siewing, 1963).

Cephalocarids and mystacocarids lack eyes. This is related, of course, to the subsurface habitat. Compound eyes are found in all the other classes except for the copepods. Considering primitive forms, they are stalked in malacostracans, and in anostracan and conchostracan branchiopods. They are sessile and trilobitan-like in notostracans but this is a secondary invagination of stalks beneath the carapace. This may also be the case in the branchiurans (Calman, 1909). In ostracodes and the cypridid larvae of cirripeds, they lie beneath the bivalved carapace. In the former the ommatidia appear to be supported on a short, narrow pedicle, but in the latter they are not distinctly elevated above the body surface. In the non-malacostracans then, there is the suggestion that the compound eye is basically stalked but the stalked nature becomes suppressed with an anterior elaboration of the carapace. It would follow that the urcrustacean probably had stalked compound eyes (Fig. 6).

Both the heart and nerve cord of primitive crustaceans (Fig. 7) reflect the high degree of serial homology seen in the external morphology. A tube-like dorsal heart runs the length of the thorax and bears a pair of afferent ostia in each segment. The heart is enclosed in a portion of the haemocoel set off by the pericardial septum. This condition is seen in cephalocarids, less advanced branchiopods and malacostracans. In the last, the heart may extend into the abdomen, probably in relation to the presence of abdominal limbs, but the number of ostial pairs there is usually reduced.

The ventral nerve cord consists of a pair of longitudinal tracts (Fig. 7). In each segment they are connected by two commissures and are invested by paired ganglia. The commissures for the postoral cephalic appendages run posterior to the esophagus, and the ganglia for the postoral segments are discernible from each other.

The gut is tube-like, but with a pair of digestive glands emptying into the midgut at its junction with the foregut (Fig. 7). The foregut curves up from the mouth and then passes posteriorly (Dahl, 1956a); otherwise, the gut is straight. In malacostracans, ostracodes and cirripeds there may be a stomach, but this we regard as a secondary elaboration. The presence of digestive caeca in cephalocarids, branchiopods, malacostracans, and cirripeds suggests that these are fundamental structures.

Excretory and reproductive glands are the last coelomic remnants. The former are located at the bases of the second antennae and/or the second maxillae (Fig. 7). Sanders reports both to be functional in the adult cephalocarid, although the maxillary gland is much the larger.

The features discussed above are, in our opinion, reasonably ascribed to the primitive or urcrustacean. To summarize, the urcrustacean appeared as follows (Figs. 5–7): The cephalon bore first antennae, second antennae, mandibles, and two pairs of maxillae. The second antennae, while essentially postoral, had lost feeding function in the adult and had gained sensory capabilities. Their job of directing food under the labrum was taken over by the mandibles and first maxillae, the extent of whose alteration for this purpose is conjectural. The second maxillae, although attached to the cephalon, retained thoracic functions. The trunk was many-segmented, with most of the segments bearing limbs. All postantennal segments exhibited a high degree of serial homology in regard to morphology and functions of body shape, limbs, heart, gut, and nerve cord. Postoral limbs were multiramous mixopodia, with flattened protopod, foliaceous epipod and exopod, and stenopodial endopod. Metachronal activity of postoral limbs resulted in concentration of food along the ventral midline, which in turn was passed forward to the mouth by protopodal endites. These same limbs also participated in locomotion and respiration. The mouth was directed posteriorly and was floored by a posteriorly directed labrum. If a carapace fold was not developed, all thoracic segments would have had well developed pleurae. The compound eyes were stalked. The first free-living stage was a nauplius larva.

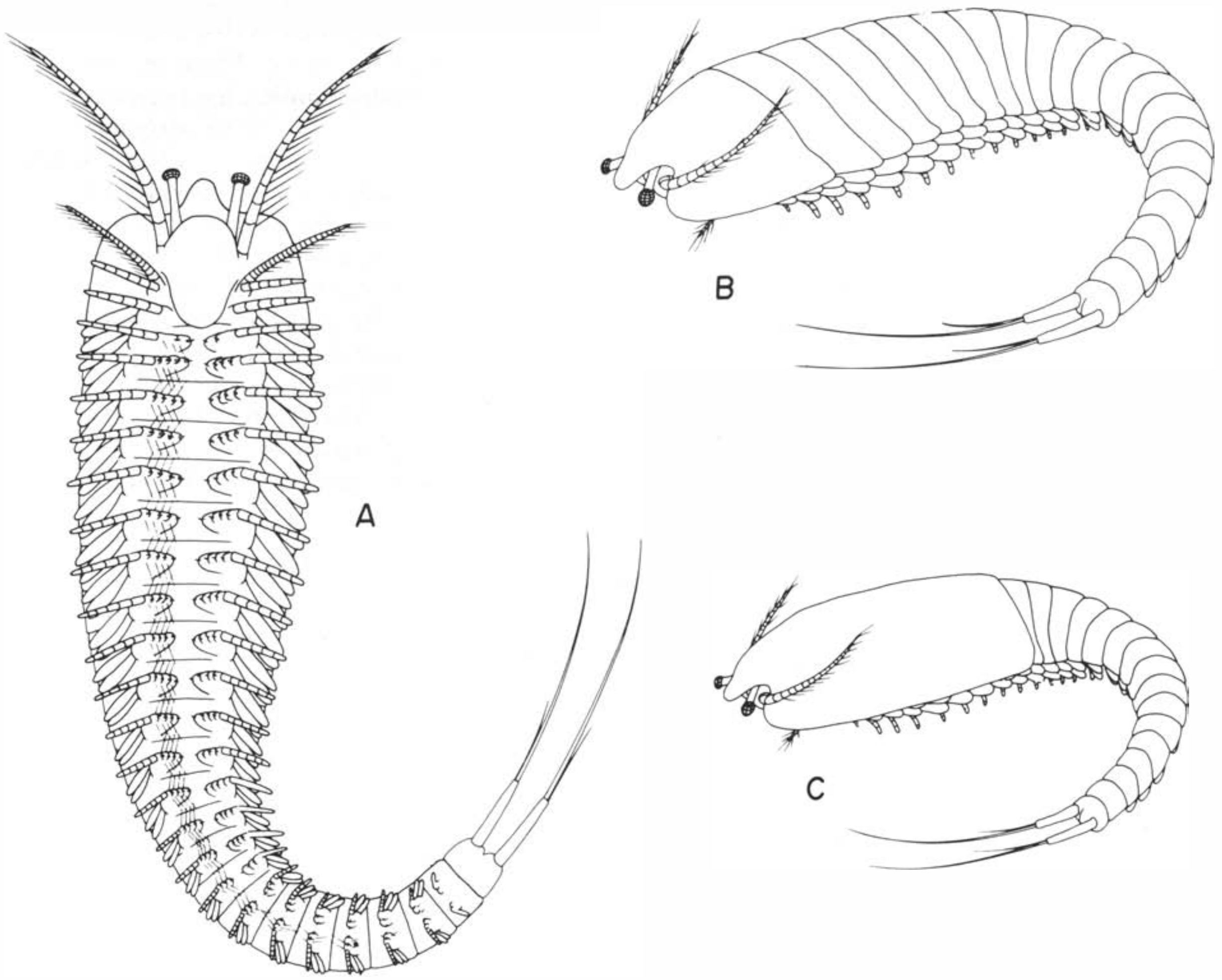

Fig. 6. The urcrustacean. A. Ventral view. B. Oblique dorsal view showing the hypothetical condition where a carapce fold is absent, and each anterior trunk segment possesses pleurae. C. The urcrustacean as it would look if a carapace fold covered the anterior portion of the trunk.

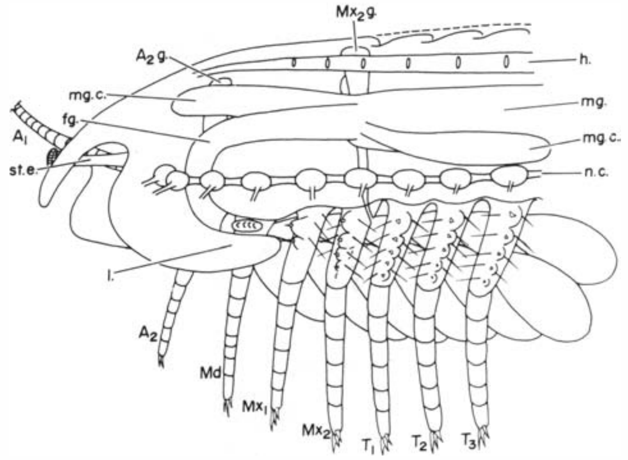

Fig. 7. The urcrustacean. Midsagittal section through the cephalon and the first three thoracic segments. Neither the musculature nor the reproductive organs are included. The dashed line above the thorax represents the position of a possible carapace fold. Symbols: $A_{1\&2}$, first and second antennae; Md, mandible; $Mx_{1\&2}$, first and second maxillae; T_{1-3}, first three thoracopods; A_2g., antennal gland; fg., foregut; h., heart; l., labrum; mg., midgut; mg.c., midgut caecum; Mx_2g., maxillary gland; n.c., nerve cord; st.e., stalked compound eye.

With this hypothetical urcrustacean in mind, we may now attempt to deduce what its progenitor might have been like. There are but two possibilities – either the urcrustacean descended directly from the Annelida, or it evolved from a pre-existing arthropod stock. There are no appropriate annelids, living or fossil, for one to use as models in understanding the derivation of urcrustaceans as envisaged here. Furthermore the urcrustacean discussed above, although generalized, is clearly a fully developed arthropod. At its inception the urcrustacean had jointed appendages, a midventral feeding mechanism formed by the limb bases, and well developed limb mouthparts. These features preclude a direct annelid derivation – there must have been some intermediate arthropod form. Among the arthropods, the Triolobitomorpha (*sensu* Størmer, *in* Harrington et al., 1959), while differing from the crustaceans on a number of counts, bear many similarities, and it is therefore necessary to look critically at the possibility that it is from within this group that the antecedents of the Crustacea are to be found.

The general facies of the urcrustacean body, with or without carapace fold, is well represented among the Trilobitomorpha. The condition of the most primitive trilobites, the Olenellidae, is quite similar (Fig. 8). Here the development of an axis with pleural expansions is characteristic of the cephalon and much of the trunk, although the strong development of the trilobite axial

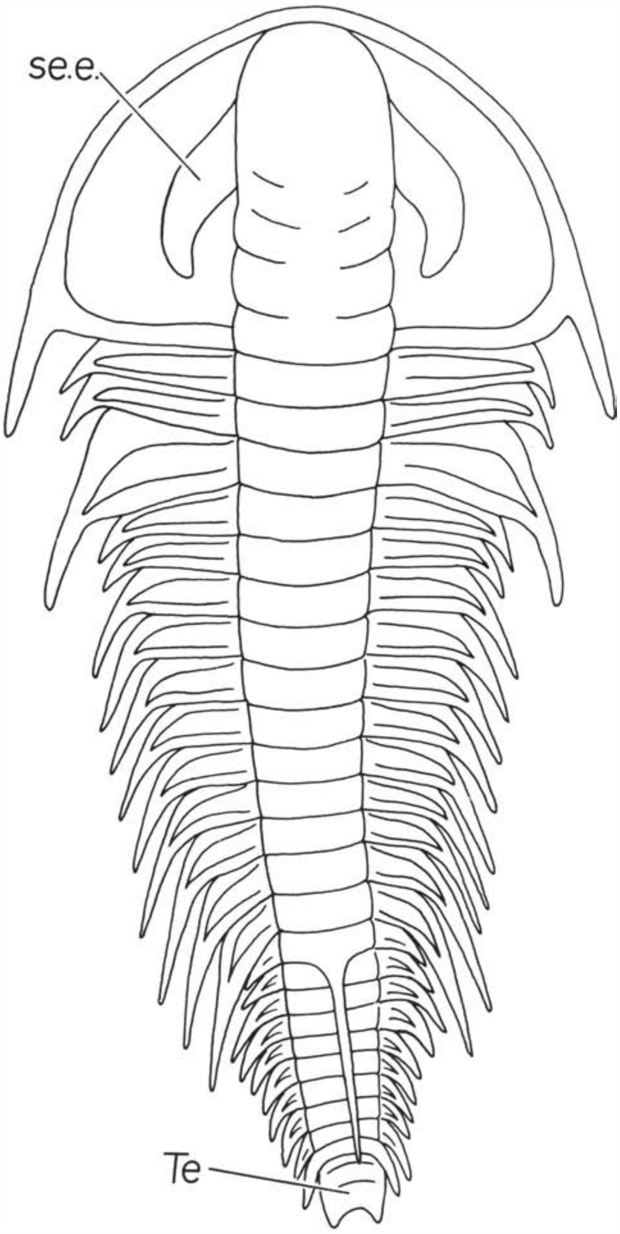

Fig. 8. The Lower Cambrian trilobite *Olenellus vermontana* (after Walcott, 1917). Symbols: Te, telson; se.e., sessile compound eye.

furrows would not have been a feature of the progenitor of the urcrustacean. Interestingly, the olenellid trunk terminates in a few segments that lack extensive pleurae, much as in a crustacean abdomen. There is no pygidium.

Within the Trilobitomorpha the mouth is posteriorly directed because it is covered ventrally by a posteriorly directed labrum (= hypostome) (Fig. 9). The gut is a straight tube, but with midgut diverticula.

branched appendages. The latter are basically like the appendages of the thorax, thus forming a repetitious series that changes little from end to end. The telson bears a caudal furca (Fig. 9).

In the basic trilobitomorph type, best represented by the Trilobita but also most common among trilobitoideans, food must be gathered by the postoral cephalic-trunk limb series by means of metachronal activities. It is then passed forward to the mouth along the ventral midline between the limbs, most often via manipulation of the basal endites.

The arguments for the above attributes of the urcrustacean have already been made in the

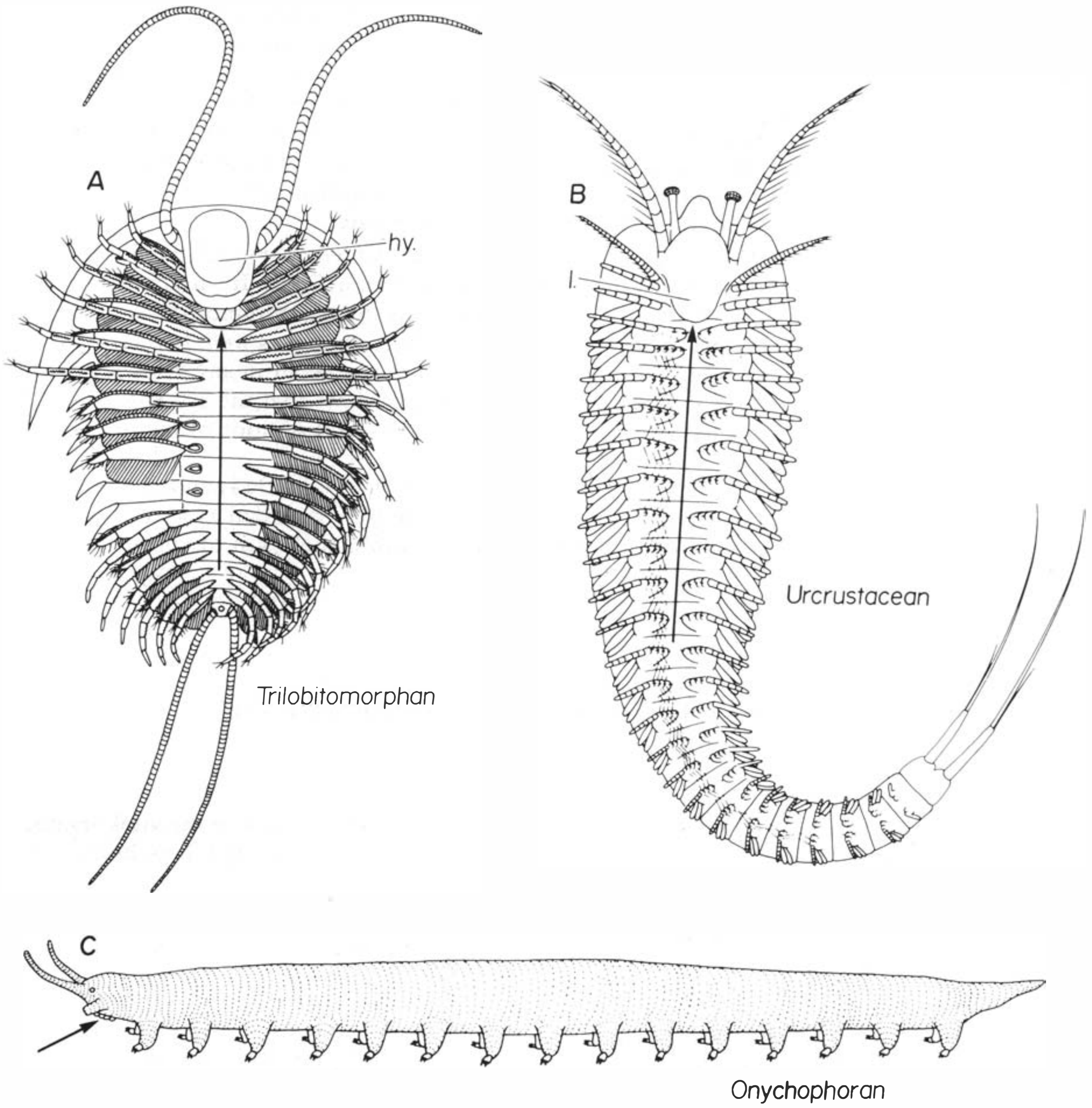

Fig. 9. Comparison of the urcrustacean to a trilobitomorph, *Olenoides serratus* (after Harrington, 1959), and an onychophoran, *Peripatoides novae-zealandiae* (after Snodgrass, 1938). The arrow shows the direction of food travelling to the mouth. Symbols: hy., hypostome; l., labrum.

section on the morphology of the primitive crustacean. The trophic features with which we endow the trilobitomorph progenitor still need clarification. Our belief in the possibility of gnathobasic manipulation will be taken up in the section on Jaw Structures (p. 453). The dorsolateral food channel suggested for trilobites by Bergström (1969) can hardly apply in pleuraeless types like *Marrella* (Whittington, 1971). Only midventral transport between the limbs (Stürmer & Bergström, 1973) satisfies all known morphologies. It also avoids the awkward problem of efficient transfer from epipods to the mouth.

That food must have been gathered by postoral limbs is simply based on the posteriorly directed orientation of the mouth and the absence of anteriorly directed trophic structures. The use of a long series of such limbs rather than just those of the cephalon is suggested by the lack of serial differentiation, a condition which would surely not have evolved if there were any marked partitioning of limb function. The likelihood of a metachronal activity is based on the almost universal existence of such behavior when movement of a long series of similar structures is involved. Many Burgess Shale trilobitoids have some cephalic appendages which are clearly developed for approaching and handling food directly from the front. Assuming the Trilobitomorpha are not in themselves polypheletic, it is reasonable to conclude that this presumably predacious morphology is derived from the more generalized type seen best in the trilobites. Thus, we regard posteriorly conducted trunk limb feeding as being basic within the Trilobitomorpha.

The strength of these similarities is heightened by comparison with the primitive attributes of the onychophoran-myriapod line (Fig. 9). Here there is no trilobation in the broad sense. There is no labrum, and the mouth is directed forward. The gut lacks diverticula, at least primitively. The postoral limbs are uniramous and lack endites. Only those few appendages that are specifically cephalized are used in feeding, and the food is approached from the front.

Onychophoran-myriapod features which are common with those of the trilobitomorph-crustacean are the first antennae and possible caudal cerci. The value of these features as indices of affinity are of course thus diminished. Similarly, metachronal activity within a long series of similar trunk limbs is no more than a functional necessity.

Even considering these deletions, the suite of similarities which characterize trilobitomorphs and crustaceans stands as compelling indications of their affinity. It should be emphasized that the mode of postoral feeding with which we endow the trilobitomorph-crustacean is unique to that arthropodan branch, which includes the chelicerate line as well. It is not only absent in the onychophoran-myriapod-hexapod line, but does not occur in any known annelid or minor vermiform phylum, and it is from annelidan-like ancestors that the arthropods are generally considered to have evolved. In view of the uniqueness of this mode of life, its presence surely conveys the likelihood of a common phyletic bond.

However, as already indicated, both Størmer (1933, 1939, 1942, 1944) and Manton (*in* Brooks et al., 1969) have noted differences which at the time they regarded as so profound as to render any similarity between crustaceans and trilobitomorphs the result of convergence.

THE ARGUMENTS AGAINST CRUSTACEAN-TRILOBITOMORPH AFFINITY

Trilobation

Trilobation involves the division of the body into an axial portion containing the vital organs, and a pair of lateral outgrowths, the pleurae, which cover the limbs and which may house the glandular tissue (reproductive, digestive, and/or excretory).

Størmer (1944, 1951) lists trilobation of the tergum as being a feature of significant similarity between trilobites, xiphosurans, and many trilobitoideans. He points out that this morphology is not characteristic of the Crustacea.

The validity of this statement is unchallenged regarding the homology of trilobation in trilobites and xiphosurans, particularly the aglaspids. However, while this feature may be atypical of crustaceans, it is at least characteristic of the most primitve known forms, the cephalocarids, whose cephalon and thoracic segments are each supplied with extensive pleurae. That the elaboration of pleurae does not result in dorsally expressed trilobation is of minor importance; the required parts are present. Many trilobitoideans (*Sidneyia, Burgessia, Waptia, Marrella, Yohoia)* lack an axial furrow, or even lack pleurae (Fig. 10A).

If, on the other hand, the urcrustacean possessed a carapace, with the cephalocaridan con-

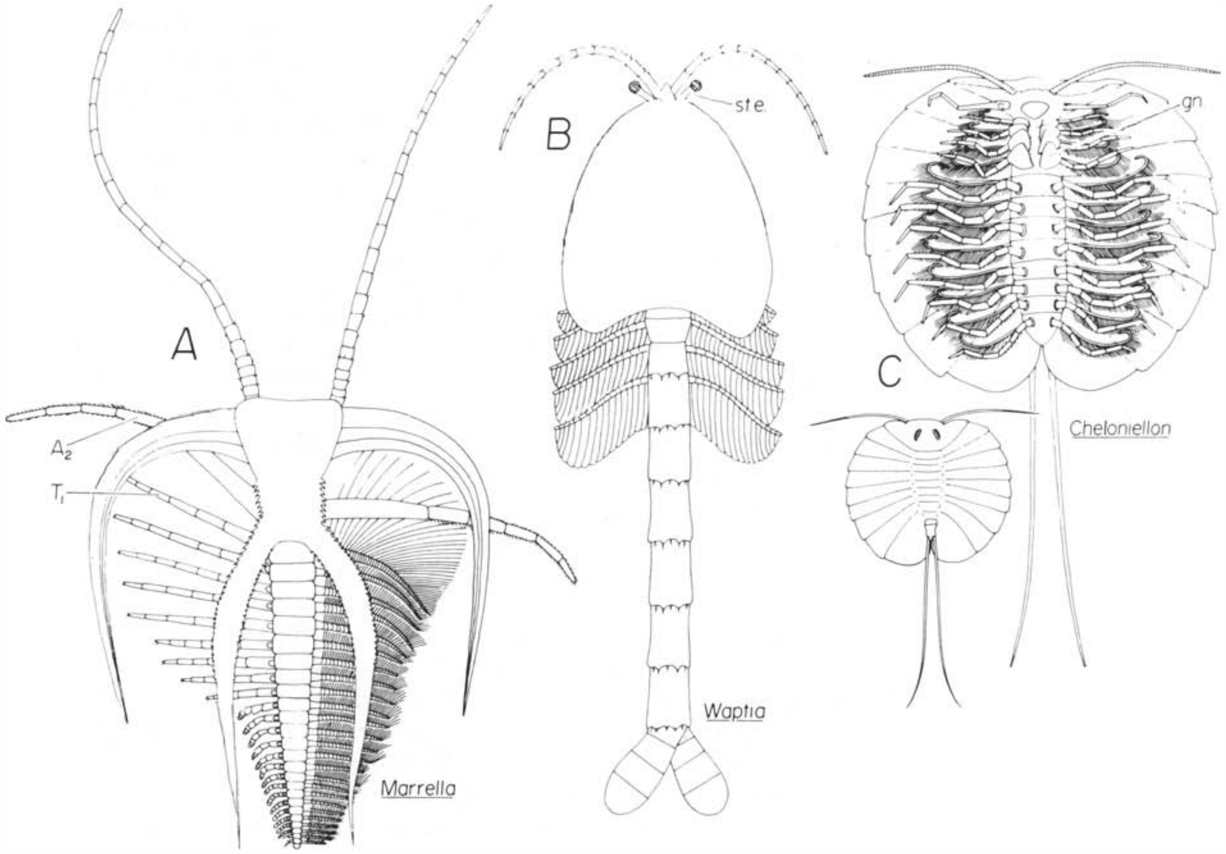

Fig. 10. Three of the Trilobitoidea, to illustrate some of the range of morphologies within the Trilobitomorpha. A. *Marrella splendens* (after Whittington, 1971). B. *Waptia fieldiensis* (after Störmer, 1944). C. *Cheloniellon calmani* (after Størmer, 1944). Symbols: A_2, second antenna; T_1, first trunk appendage; gn., gnathic basal endite; st.e., stalked compound eye.

dition being secondary, then the crustacean ancestor may have been related to one of the more derived carapace-bearing trilobitomorphs, the "pseudocrustaceans" of the Burgess Shale. One such form, *Waptia,* possessed other crustacean features, such as second antennae and stalked eyes (Fig. 10B). Thus, the presence of pleurae versus a carapace fold in the urcrustacean bears mainly on where within the trilobitomorph radiation the crustacean could have appeared.

Postoral cephalic somites in larva and adult

It has been generally agreed that the basic number of postoral cephalic appendages, and therefore the number of postoral somites in trilobites was four (Raymond, 1920; Walcott, 1921; Snodgrass, 1938; Størmer, 1951, *in* Harrington et al., 1959). The presence of only three in *Phacops* and *Asteropyge* (Stürmer & Bergström, 1973) is considered a secondary reduction (Bergström, 1973). The cephalon of the protaspis, the earliest known larva of the trilobite, usually consists of five discernable somites, as indicated by transverse furrows in the axial cuticle (Størmer, 1942; Whittington, *in* Harrington et al., 1959). The developmental fate of these somites in combination with the evidence from adult limb counts suggests that the basic number of postoral somites in the protaspis was also four.

The fact that the adult crustacean also possesses four postoral cephalic somites is a strong argument for affinity between these two groups. However, Størmer (1944) considered the basic number in crustaceans to be two because of the number of naupliar appendages and because in at least one crustacean *(Hemimysis)* the primary, nonteloblastic mesoderm includes only two postoral somites.

It is true that the nauplius has only two pairs of postoral appendages, the second antennae and mandibles. However the mesoderm of the two maxillary segments is already present in the nauplius, as shown in cirripeds and branchiopods (Anderson, 1965, 1967). In the cirriped *Ibla*

(Anderson, 1965) and the malacostracan *Leander* (Sollaud, 1923), the maxillary mesoderm is probably primary, that is, not of teloblastic origin, but in the malacostracan *Hemimysis lamornae* it is a product of the mesodermal teloblast (Manton, 1928). In the branchipods *Limnadia* and *Artemia* even some of the anterior thoracic somites seem to differentiate from nonteloblastic mesoderm (Anderson, 1967). This variation shows that the number of somites appearing before activation of the mesodermal teloblast is not of great phylogenetic significance.

Regardless of its embryogenesis, the naupliar cephalon does possess the mesoderm of the full complement of four postoral cephalic segments. Thus, the difference between protaspis and nauplius is not the number of cephalic segments, but only the degree to which they are developed. The evidence that all the protaspid postoral cephalic segments are well differentiated seems adequate, but there is still no information on whether all these segments bore limbs at this early stage. It may well have been less than the adult number, as is the case in the nauplius. On the other hand, it has also been suggested (Sollaud, 1923; Gurney, 1942) that the nauplius is a derivative specialization of a precursor larva that had more cephalic limbs, such as the protaspis.

As Manton (1964) has shown, Snodgrass (1938) was in error in considering the basic anostracan head to have only one postoral segment. The cervical groove in branchipods is not an external expression of the junction of the maxillary region with a primitive cephalon that carried only two postoral segments, but is merely a structural bar which aids the functioning of the mandible. No adult crustacean gives cause to suspect that the basic cephalon ever included anything fewer than four postoral segments.

In the final analysis, these arguments about the similarity between cephalic somite counts in crustaceans and trilobites may largely be irrelevant. What is important is the similarity between crustaceans and trilobitomorphs as a whole, not simply the trilobites *sensu stricto.* The trilobitomorphs show a great range in the number of postoral cephalic somites. For example, there is one in *Marrella* (Whittington, 1971), three in *Leanchoilia* (Simonetta, 1970; Bruton, in prep.), and five in *Emeraldella* (Simonetta, 1964; Bruton, herein). Finally, Cisne (1973 and in prep.), has found that *Triarthrus*, representing the basic trilobitan stock, has only three postoral cephalic limbs, not four as it was always thought. Thus, even the basic count for trilobites needs to be reconsidered.

Compound eye

Manton (1963), in enumerating the major arthropodan structures which are thought to be convergently evolved, notes that the compound eyes in those crustacean classes that have them (malacostracans, cirripeds, ostracods, branchiurans, and branchiopods) are not exactly the same, and that copepods show no evidence of having ever lost them. She concludes that the urcrustacean lacked compound eyes, which therefore evolved more than once within the superclass.

If neoteny is the organizing principle around which the origin of copepods is centered (Gurney, 1942), one would expect that the eyes as well as the body plan might be involved. That is, copepods retain the larval eye, the compound eye common to the maxillopodan ancestor simply having been lost through neoteny. The evidence for copepods then does not seem sufficient to justify Manton's conclusion.

More serious is the question of difference between compound eyes in crustaceans (Dahl, 1963, and the following discussion; Elofsson & Dahl, 1969). These need not indicate independent evolution, but rather lead one to question what kind of compound eye might have been present in the ancestor.

The malacostracan eye, with chiasmata and medulla interna in addition to the structures seen in the branchipod eye, is the more highly evolved. It is claimed that the gulf between the two types is deep, but the leptostracans give some hint of intermediacy (Elofsson & Dahl, 1969). Here the medulla interna is not developed, but a projection of the medulla terminalis may be its equivalent. This is highly suggestive in view of the fact that the medulla interna of eumalascostracans is embryologically derived from the medulla terminalis. While these considerations do nothing to reveal the origin of chiasmata, they at least show us that the unbridgeability of evolutionary gaps is often more apparent than real.

Preoral limbs

The number of antennae has been considered a feature which distinguishes crustaceans from trilobitomorphs; the former has two preoral pairs, and the latter has but one. A few crustaceans have less than two pairs, but this has come about through reduction and is of no importance here. On the other hand, certain of the Trilobitomorpha (e.g. *Marrella)* have an additional pair of appendages resembling antennae, but these are postoral in position (Størmer, *in* Harrington et al., 1959). Actually, then, two pairs of antennae may appear in the Trilobitomorpha as well as in Crustacea (Fig. 10A). The only distinction between the two is the postoral position of the second antenna in the former group.

In the fundamental crustacean larva, the nauplius, the second antennae are also postoral in position (Fig. 1). In addition, they have a part for part correspondence with the following pair of appendages, the mandibles, and are not antenniform at all. In those nauplii that feed they are provided with gnathobasic endites (Fig. 1), as may be the mandibles, and both pairs of appendages are utilized in pushing food under the labrum to the mouth, as well as in locomotion. As ontogeny progresses the naupliar postoral antennae, while retaining their nervous connections with the postoral tritocerebrum, shift forward to a preoral position. Here, having become antennular in function, they are no longer involved in feeding, and the mandibles become the first postoral appendages.

What is the significance of the naupliar condition? While we do not know the appendages of the trilobite protaspis, they must have been present for locomotion and feeding, and there is no reason to suspect they were arranged much differently than in the adult. Since the nauplius has the primary head appendages of the trilobite, the naupliar arrangement must also be comparable to that of the protaspis. Thus, the ontogenetic postoral to preoral shift of the second antennae must certainly represent a recapitulation of crustacean evolution.

Postoral limbs

Of all the features that have been used to separate the crustaceans from the trilobitomorphs, most important are the differences between their biramous postoral limbs. The trilobitan limb consists of a main ambulatory shaft, the telopod, with an exite arising from the proximal segment. Størmer (1939, 1944, *in* Harrington et al., 1959) claims the point of origin of the exite

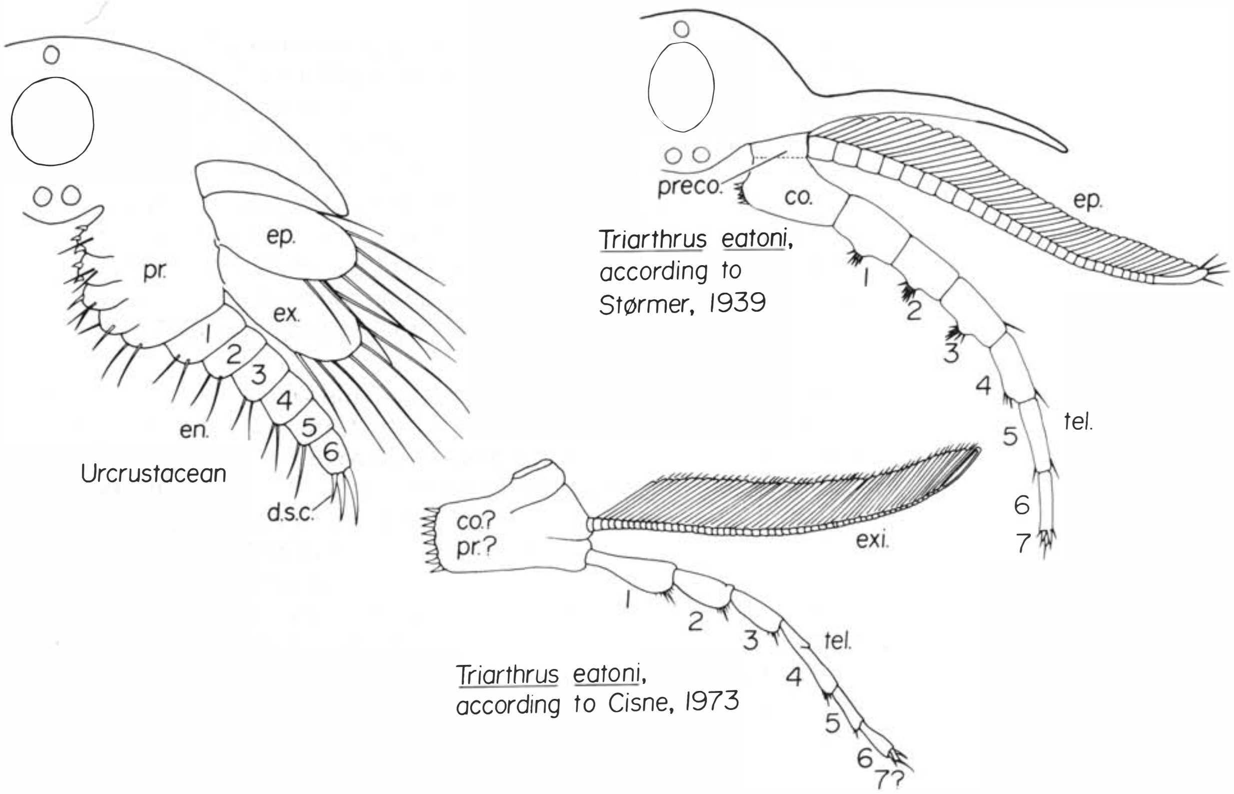

Fig. 11. Comparison of the urcrustacean trunk limb to two interpretations of the trilobitomorph limb as seen on the trilobite *Triarthrus eatoni*. The numbers count the segments of the inner ramus (endopod/telopod). Each limb is labelled according to the appropriate author. We suggest a possible homology between the distal claws of the urcrustacean and the seventh telopodal segment of *Triarthrus*. Symbols: co., coxa; d.s.c., distal setal claws; en., endopod; ep., epipod; ex., exopod; exi., exite; pr., protopod; preco., precoxa; tel., telopod.

is a small ring proximal to the large coxa. He called this segment the precoxa and therefore labelled the exite the pre-epipod (Fig. 11). Størmer does not document the existence of an articulation between precoxa and coxa. Furthermore, the presence of a precoxa is strongly claimed only in *Ceraurus*; its existence is only suggested for *Neolenus, Triarthrus,* and *Cryptolithus.* The validity of an independent precoxa has been questioned by Garstang (1940), Calman (1939), Snodgrass (1956), and Sanders (1957). Recently, Cisne (1973 and herein) has restudied the limb of *Triarthrus eatoni.* He finds no precoxa and interprets the epipod as inserting midway along the outer edge of the coxa, not proximally. Thus, there is little reason to consider this structure characteristic of the trilobitomorph limb. Rejecting the precoxa as being ill-proven, we subscribe to the idea that the exite arose from the coxa. Thus, the exite should be considered an epipod.

It is the crux of Størmer's argument that, whether pre-epipod or epipod, the exite cannot be homologous to the crustacean exopod because the latter arises from the second segment of the limb, the basis. In all discussions of the possibility of independent origin of the Crustacea and Trilobitomorpha, this has been a prime consideration.

Calman (1939) and Sanders (1957) minimize this difference by suggesting that the basal segment in the trilobitan limb is a protopod or sympod composed of combined coxa and basis. In this context the exite could be considered an exopod as in the crustaceans. Calman points to the not uncommon occurrence of such a condition in crustaceans. Størmer (1944) counters Calman by disbelieving that a protopod would be reduced to so small a segment as is the trilobitan precoxa, and by pointing to Hansen's (1925, 1930) claim that the primitive crustacean limb base consisted of three segments (precoxa, coxa, basis), not one (protopod). Størmer goes on to point out that the structure he is calling a coxa would be an ischium in Calman's interpretation. Not only would this be unusually large for an ischium, but it would give the primitive endopod eight segments, two more than in any known crustacean. However, Calman's wording leads us to believe that he doubted the validity of the precoxa as an independent segment at all. Thus he would not have accepted the statements Størmer regarded as corollary to his view.

Sanders (1957) emphasizes that the cephalocarid thoracic limb (Fig. 5) has an undivided protopod and therefore conforms to the trilobitan condition. This interpretation minimizes the distal origin of the exites from the cephalocarid protopod in contrast to the proximal origin in trilobites, and suggests that it is a question of relative growth patterns causing the position of the exite to shift.

However, while the cephalocarid thoracic protopod is not sharply demarked into coxa and basis, there is a line of preferential bending which subdivides it into nearly equal distal and proximal portions. This zone is expressed by indistinct furrows in the cuticle (Sanders, 1957) and by the limb musculature (Hessler, 1964). In the activity of the animal, the limb is usually flexed along this zone, and in preserved specimens, the protopod is often bent. Thus the protopod of thoracic appendages and the second maxilla is divisible into coxa and basis, with the basis bearing both exopod and "pseudepipod". In the second antenna, mandible, and first maxilla the coxa and basis are distinct and articulated segments. Here the single exite is on the basis. One must conclude that if the ancestor of the crustacean had an undivided protopod, it was at a grade of development more primitive than that of the Cephalocarida. The trilobitomorphs fill this category.

There is some evidence regarding the question of whether the position of the exite can shift as Sanders suggests. The thoracic limb most similar to that of the cephalocarid is seen on the Leptostraca (Fig. 5). They both have foliaceous exites and a multisegmented endopod. The similarity in the function of their limbs plus the many similarities between these taxa in other respects makes certain the basic homology in these thoracic limb structures. However, in the leptostracan protopod, which is faintly but unequivocally divided into coxa and basis, the proximal exite stems from the coxa and is therefore a true epipod. Because this ramus is apparently a homolog of the cephalocaridan pseudepipod, it follows that the "pseudepipod" has secondarily migrated distally. Similarly, the mandibular palp is known to have shifted onto the labrum in thoracican cirripeds, and branchiae have shifted onto the body wall in decapods. Thus, Sanders' hypothesis that the different position of the exite in trilobites and crustaceans is only a function of differential growth is reasonable.

Yet another possible way in which trilobitan and crustacean limbs may be related emphasizes the crustacean epipod. The presence of this exite in cephalocarids, malacostracans, and branchipods suggests the presence of an epipod on the urcrustacean limb. If so, then the homologization with the trilobitan epipod is direct. Complications with this hypthesis are twofold. First, the complete lack of an epipod in the Maxillopoda may mean that this exite is not primitive, but a specialization of the thoracopodan line. Second, if primitive, it means the basic crustacean limb was multiramous, a situation unknown in trilobitomorphs. It is our view that the maxillopodan condition is derived, as are so many other maxillopodan features. Thus, we must contend with the problem of the multiramous limb.

The trilobitan telopod (= inner ramus distal to the coxa) is claimed to consist of a constant seven segments (Størmer, 1939). Størmer finds a similar or easily derived segment count in chelicerates, but notes that in crustaceans the endopod has generally five segments, one fewer than in trilobitomorphs if one takes the segment distal to the trilobitan coxa to be the basis. Sanders (1957) stated that the cephalocarid endopod also had seven segments, but this assumed the second of the three distal claws was a segment, which proves not to be the case (Hessler, *in* Brooks et al., 1969). Whittington (1971) reports six segments in the trilobitomorph *Marrella,* because he considers the distal claw to be merely a seta, as in the cephalocaridan situation. If the distal segment of the trilobitomorph limb (pretarsus) did prove in general to be only a seta, and if the most proximal segment ("coxa") was homologous to the crustacean protopod, then the trilobitomorph telopod would have the same six segments seen in the cephalocarid endopod (Fig. 11). Manton (1969) minimizes the phylogenetic significance of segment number in the endopod/telopod, stressing the ready response of limbs to changing functional needs. The variability of endopodal segment number between crustacean classes illustrates this point, although the rather constant composition of the eumalacostracan thoracic endopod shows that the need for change may be balanced by a basic conservatism.

Størmer (1931, 1944, *in* Harrington et al., 1959), followed by Manton (*in* Brooks et al., 1969), emphasizes the uniqueness of the flattened filaments of the trilobitan epipod which have no easy counterpart in the Crustacea. However, not all trilobitomorphs have this structure. The foliaceous epipod of *Molaria* and *Emeraldella* (Simonetta, 1964) is fringed with setae in a manner most reminiscent of the cephalocaridan condition (see addendum).

Jaw structures

Størmer (1939, 1944, 1951) has made much of his interpretation that trilobites lack any sort of jaw structure. He claims that the postoral cephalic appendages are essentially like the postcephalic limbs, and the limb origins are so far lateral that the medial edges of the coxae could not meet at the ventral midline. This would contrast strongly with the Crustacea, where the presence of a mandible is characteristic and where primitively trunk limbs pass food forward to the mouth through manipulation by opposing protopodal endites.

The supposed absence of mandibular structures in trilobites is no impediment to phylogenetic relationship to the Crustacea. What is important is that trilobitomorphs in general must have carried food forward via gnathobases along the midline (Bergström, 1973) and had a capacity to form jaws.

Cisne (1973 and herein) reconstructs *Triarthrus eatoni* as having well developed enditic lobes on all the postoral limbs (Fig. 11), and those of the cephalon even show slight modification as mouthparts. This stands in strong contrast to Størmer's (1939) interpretation. It agrees with that of Raymond (1920), who ascribes enditic lobes to trilobites in general. Simonetta (1962, 1963) reconstructs the limbs of *Marrella* and *Sidneyia* as having enditic processes on the coxa, although Whittington (1971) disagrees regarding the former. As the morphology of the other trilobitomorphs becomes better known, other examples may emerge.

The capacity to form jaws is demonstrated by the xiphosurans, on which they are well developed (Manton, 1964). Here, all the prosomal appendages are capable of close midline interaction. If the xiphosurans are derived from the trilobitomorphs, it must follow that either some trilobitomorph developed the capacity for gnathobasic mastication, or that trilobitomorphs in general already had this capacity. Furthermore, the trilobitomorph *Cheloniellon* (Fig. 10C) gives direct evidence that some trilobitomorphs had evolved jaws. Here, the first four pairs of postoral limbs have well developed gnathobases. Stürmer and Bergström (1973) endow the trilobite *Phacops* sp. with more than one pair of strong gnathobasic jaws.

In her elegant study of mandibular mechanisms, Manton (1964) has decisively shown the lack of homology between the crustacean and hexapod mandibles, thus deriving critical evidence for the artificiality of the taxon Mandibulata. At the same time she shows that there are fundamental differences between the biting mechanisms of xiphosurans and crustaceans, in spite of the fact that in both cases the coxa of the limb is the structure involved. In crustaceans, biting is supposedly achieved through modification of the promotor-remotor movements of the precursor ambulatory limb. Opposite to this is the condition of *Limulus,* where biting results from direct transverse movements totally divorced from ambulatory behavior. Manton (1964:100) concluded that "this, and the associated morphology, must surely mean that the merostome and crustacean gnathobases have been independently acquired as a parallel evolution not indicative of affinity".

While we will not argue about the great differences between xiphosuran and crustacean mandibular mechanisms, we do not see that this constitutes evidence for the independent and totally separate origin of the Crustacea. There is no question that the chelicerates and crustaceans are not directly related, but this does not preclude the possiblity of a common ancestral stock which used gnathobases in feeding. Fossil evidence indicates a rather direct lineage from trilobites or related trilobitoids to xiphosurans via the aglaspids (Størmer, 1944). Manton (1964: 100) states, "if a common basis for the limulid and crustacean gnathobasic mechanisms had ever existed, it could only be sought for in a small arthropod possessing no basal articulations to its limbs, an undifferentiated link by arthrodial membrane permitting a variety of slow movements by promotor, remotor, and abductor muscles." There is no solid information on trilobite musculature, but there is every reason to believe her criteria for the cuticle are satisfied quite well by trilobitomorphs. The ventral integument is very rarely preserved, and then only faintly (Størmer, 1939). It must have been very thin and flexible. Such a cuticle floored not only the axial lobe, but the medial half of the pleurae as well. This encompasses the entire area that gave rise to the limbs. Thus there is every reason to believe that the trilobitomorph's limbs were flexibly attached to the body (Cisne, 1973). With this type of flexible limb attachment in mind, the fact that trunk limb endites do not meet at the midline in reconstructions of some fossil forms (Stürmer & Bergström, 1973; Simonetta, 1962; Størmer, 1939) does not preclude their ability to interact as a result of dynamic muscular control in the living animal. In view of the complete lack of contrary evidence, there is no reason why the Trilobitomorpha could not have given rise to both types of mandibular motion.

The pleural origin of limbs in xiphosurans (Manton, 1969) has no bearing on the issue at hand, since as far as we know, the origin of the trilobite's limbs was ventral or only moderately ventrolateral.

Digestive tract

The digestive system of the Chelicerata is characterized by extensive and highly ramified pairs of digestive diverticula stemming from the midgut. Dendritic impressions of internal soft parts on the pleurae of trilobites have been interpreted as digestive diverticula (Jaekel, 1901, Öpik, 1961). In *Burgessia* and *Naraoia* the glands themselves have left fossil imprints. From this, Størmer (1944) and others conclude that the gut of chelicerates and trilobitomorphs is basically the same.

Størmer further points out that as a characteristic feature, highly ramified diverticula are limited to those taxa, perhaps in conjunction with the lack of true jaws. In his view, while similar structures may be found in parasitic copepods and ascothoracians, they are the exception in crustaceans. This feature, then, would join the list of differences. Sanders (1957) agrees with Størmer's functional interpretation, and on those grounds regards the difference as trivial in view of the unquestioned evolution of the crustacean mandible from a nonmandibulate ancestor. However, xiphosurans are not truly jawless. They triturate food with their coxae and in contrast to nonmerostome chelicerates, swallow large chunks which are further reduced by a gastric mill.

A point of some significance that is lost in these discussions is that a pair or more of midgut diverticula is actually characteristic of crustaceans, being typical of branchiopods, cirripeds, malacostracans, and cephalocarids. This stands in contrast to the Onychophora and basal Myriapoda, where they are lacking. Thus, the presence of midgut digestive diverticula is a feature that relates crustaceans and trilobitomorphs rather than separates them; they differ only in the degree of ramification.

Telson

As one last potential difference between trilobitomorphs and crustaceans, we note Størmer's (1944) comment that while the styliform telson is characteristic of trilobitomorphs, it is not of crustaceans. That this structure is not of great significance is seen from its absence in the trilobitomorphs *Sidneyia, Marrella, Waptia, Cheloniellon, Yohoia,* and others (Fig. 10).

Burgess Shale and other trilobitomorphs

The diverse arthropodan fauna of the Middle Cambrian Burgess Shale has always played an important part in considerations of crustacean and trilobite phylogeny. Prior to Størmer's studies, it was generally agreed that many of the Burgess Shale genera were crustaceans because of their close similarity to crustacean facies. *Hymenocaris (=Canadaspis)* looked like a phyllocarid; *Waptia* is strikingly like a natantian decapod; *Burgessia* resembles notostracan branchiopods, while *Leanchoilia* and *Opabinia* resemble anostracans; *Marrella* has a generally crustacean appearance, even bearing what may be called a second antenna.

Størmer (1944) studied the limbs of these genera and concluded that they were basically like those of trilobites. In view of the seemingly unbridgeable differences that separated the trilobite and crustacean limbs, he concluded that the similarities in body form were convergently evolved. Tiegs and Manton (1958) are reluctant to discredit the remarkable resemblances as being simply convergence. But later Manton (*in* Brooks et al., 1969), agreeing with Størmer on the limb issue and concluding an independent origin of the Crustacea, must have regarded crustacean similarities in the Burgess Shale fauna as convergence.

The real significance of the Burgess Shale and Devonian "pseudocrustaceans" is not in whether they establish firm linkages between trilobites and crustaceans, but in the fact that they demonstrate a portion of the range of morphology that trilobitomorphs were capable of attaining. The trilobite facies was only a small stereotyped part of this great range. The trilobitomorphs encompassed a large number of the body forms also seen in crustaceans today. They showed that the trilobitan postoral limbs were not rigidly confined to a single morphology, but differed from group to group and even along the length of a single animal. As seen in previous pages, this taxon displays a range in the number of postoral cephalic somites, the development of a carapace or pleurae, and in the form of the telson and compound eye. In each case, this range easily encompasses the primitive crustacean morphology and offers cause to suspect affinity.

It should not surprise us that the fossil record had not yielded taxa actually on the stem line of the crustaceans. The urcrustacean was probably small and ill-suited to fossilization (Tiegs & Manton, 1958; Sanders, 1957). The preservation of the Burgess Shale fauna was an extraordinarily rare event, and it is likely that it gives us only a fraction of the taxa that actually lived in the Cambrian.

CONCLUSIONS

Of the reasons which have been offered in defense of independent origin of trilobitomorphs and crustaceans, only the following seem to present real or potential support for this view. The basic crustacean limb is not just biramous, but actually multiramous. There is no substantial evidence to show that the trilobitomorph epipod is homologous with the crustacean exopod, although the crustacean epipod may fill this gap.

As evidence for a common origin of the two taxa there is a common general appearance which included trilobation, the same organization of mouth and digestive tract, and a common mode of feeding conducted by a series of serially similar postoral cephalic and trunk appendages which are branched and which possess enditic processes.

As our knowledge of arthropods has improved we have come to perceive with increasing clarity the phylogenetic pathways that led to the variety of morphologies alive today. As part of this we are increasingly aware of the fact that complex structures have evolved more than once, in a parallel or even convergent fashion. The compound eye, tracheae, malpighian tubules, and the mandible are among the more important examples of clear convergence (Manton, *in* Brooks et al., 1969).

In the face of such remarkable examples, it is not surprising that the uniqueness of the very suite of characters that defines the phylum is questioned. The result has been the increasingly accepted view that the onychophoran-myriapod-hexapod line has evolved from an annelidan ancestor completely independently of the other superclasses (Tiegs & Manton, 1958). The essence of this is expressed by Manton (*in* Brooks et al., 1969:R35): "In view of the strong probability of a parallel evolution of uniramous legs and of more than one type of biramous leg, as well as several types of jaws and compound eyes, and a variety of respiratory and excretory organs, we may ask what surety have we that surface sclerites and a hemocoel have been evolved once only in metamerically segmented animals?"

While we would not question the fact of convergence in many of the examples mentioned above, we are concerned about the philosophical implications inherent in the above quotation. Does this attitude not lead to phylogenetic anarchy? How can one ever decide that two taxa are related if one is always willing to invoke convergence? In short, how does one falsify the hypothesis of polyphyly? Fortunately, Manton *in* Brooks et al., 1969: R 106) suggests workable guidelines: "Where similarities exist which can reasonably be accounted for by convergence, such similarities cannot be considered to represent sound evidence of affinity *in the face of much contrary evidence"* (italics ours). The critical issue becomes the nature of the features that preclude affinity and the degree of assurance that such differences cannot be bridged.

Is there, then, strong reason for concluding that those features that make the urcrustacean and trilobitomorphs look so very much alike are actually convergent similarities? Most of the differences which have been emphasized in the past are in our opinion either nonsequitors, in error, based on supposed attributes of trilobitomorphs that are insufficiently known, or are easily bridged. All but the morphology of the limb seem to fall into one or more of these categories.

Even features of the limb do not drive us without recourse toward independent origin. So little is really known about limb structure in the diverse Cambrian trilobitomorph fauna. Such glimpses into the true potential for adaptive radiation as the evolution of a series of gnathobasic jaws in *Cheloniellon* undermine arguments that attribute a narrow, inflexible suite of characteristics to the trilobitomorph stock. In view of the availability of two reasonable hypotheses for the relationship between the trilobitomorph epipod and crustacean exites, the apparent differences in the exites of these two taxa do not seem to fulfill the criterion of "much contrary evidence".

In short, we believe that trilobitomorphs and crustaceans share so many features in common, both in terms of characteristics of the phylum and aspects not found in other arthropodan taxa that the only reasonable conclusion is that they stem from a common arthropod stock: The differences between the two taxa do not seem to carry the weight necessary to force us to define separate phyla at the arthropodan grade of evolution. This is not to say that as presently known they are not different. Crustaceans are not trilobitomorphs; the two taxa do have diagnostic features, as do all taxa in our present Linnean classification. But as in most cases, the ability to distinguish related taxa is dependent upon the poor quality of the fossil record and the lack of relict living intermediates. The wonder is that there are as many primitive or generalized forms living as there are.

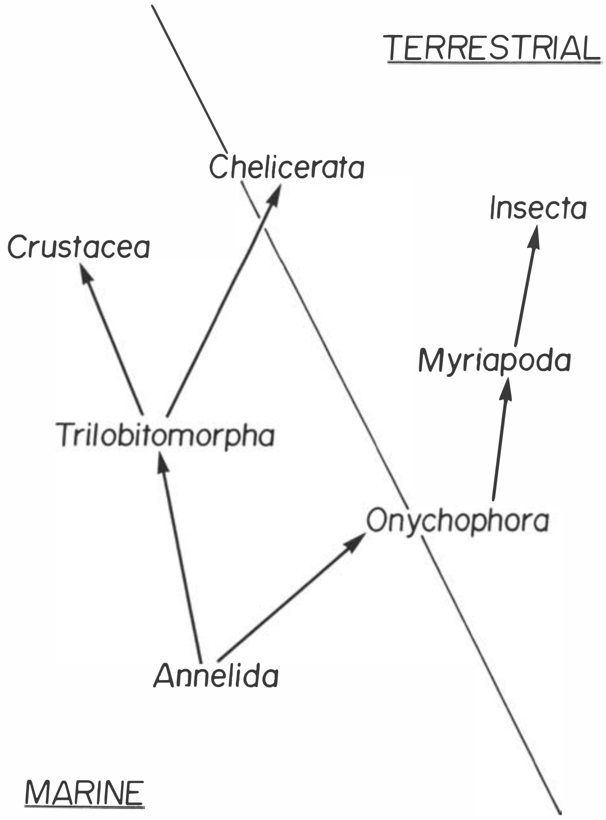

Fig. 12. A phylogeny of the Arthropoda, combining the diphyletic hypothesis of Tiegs & Manton (1958) with the evolution of the Trilobitomorpha, Chelicerata, and Crustacea as suggested herein. Only major features are shown. The Pantopoda, Tardigrada, and Pentostomida are not considered.

ADDENDUM

This paper was written on the basis of information available prior to the symposium on trilobites and merostomes held in Oslo, July 1–8, 1973. During the course of this meeting there emerged additional data which enhance the likelihood of trilobitomorph-crustacean affinity.

Whittington (herein) redescribed the limbs of the trilobite *Olenoides (= Neolenus) serratus* from the Burgess Shale. The presence of only three pairs of postoral cephalic limbs further increases the possibility that this, and not four, is the basic number in the Trilobita. The inner ramus of the trunk limbs comprised only six segments beyond the coxa/protopod, Størmer's pretarsus being interpreted as merely a distal claw-seta as in *Marrella.* There is no precoxa. The coxa/protopod had well developed enditic spines, making the animal well suited for midventral transport of food toward the mouth.

During an informal evening discussion on Burgess Shale trilobitomorphs. Simonetta drew attention to a somewhat damaged, isolated appendage he ascribed to *Leanchoilia* (Simonetta, 1970, Pl. XXV:3a,b). Bruton suggested, and Simonetta concurred, that this appendage more probably belonged to *Emeraldella.* In the formal sessions, Bruton (in prep.) described the limb. It is a triramous mixopodium having a flattened coxa/protopod, ambulatory inner ramus, and two large, foliaceous outer rami. Thus, it corresponds to a startling degree to the urcrustacean limb postulated herein.

This is not to say that *Emeraldella* must be regarded as a close relation to the urcrustacean line. Among the obvious differences are its five postoral cephalic limbs and its styliform telson. Nevertheless, it does once again demonstrate that features attributed to the urcrustacean fall well within the spectrum of trilobitomorph morphologies. In particular, it dispels the important argument that the limb of crustaceans and trilobitomorphs are basically different.

It might be argued that the question which now emerges is whether the Trilobitomorpha is in itself polyphyletic. On the basis of present knowledge, we regard such speculation as without foundation and unnecessarily complex. More reasonable is the suggestion that the Trilobitomorpha as seen in the Burgess Shale were representatives of an explosive early Paleozoic radiation. Most of the lineages were short-lived. A few, as seen in the Hunsrück Shale (illustrated by Stürmer and Bergström at the meeting) lasted until the last half of the Paleozoic, and perhaps even into the Mesozoic (e.g. *Euthycarcinus).* Only three lines were truly successful (Fig. 12). These were the enormous, sustained radiations that comprise the Trilobita, Chelicerata, and Crustacea.

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Standardisation of trilobite orientation and measurement

JOHN T. TEMPLE

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Results are reported of discussion on the standardisation of trilobite orientation and measurement at the Oslo meeting on *Evolution and Morphology of the Trilobita, Trilobitoidea and Merostomata,* 1-8 July 1973. Standard orientations for both measurement and illustration are defined for cephala and cranidia, hypostomes, free cheeks, thoracic segments, and pygidia. Shaw's 1957 measurement notation is recommended for adoption. The discussion document circulated before the meeting, which includes supplementation of Shaw's notation, is reprinted.

J.T. Temple, Birkbeck College, 7/15 Gresse Street, London W1P 1PA, 29th August, 1973.

Inclusion of a discussion on the measurement of trilobites in the programme of the Oslo meeting on *Evolution and Morphology of the Trilobita, Trilobitoidea and Merostomata* was proposed by Temple on 17th October 1972 and accepted by D.L. Bruton on behalf of the Organising Committee. A document for discussion at the meeting was produced by Temple (with the help of comments on an initial draft by A.W.A. Rushton, C.J. Stubblefield and R.P. Tripp) and circulated on 15th January 1973. This discussion document was circulated to all trilobite workers listed in Nos. 1 and 2 of *Trilobite News* as well as to a small number of workers not so listed: approximately 175 copies were despatched. The discussion document is reprinted below in Appendix 1, the original accompanying illustrations being re-drawn and re-numbered for the present version.

Comments on the draft document, which had been requested by 1st May, 1973, were received from 22 persons; of these, 11 indicated that they would accept a majority decision of the Oslo meeting and apply it in their future work, one indicated qualified acceptance of a majority decision, while 4 indicated that they would not be prepared to accept a majority decision. Some omissions from the discussion document were pointed out – orientation and measurement of free cheeks, depth of cephalon and pygidium, thickness of cuticle. The comments were duplicated and made available to members at the beginning of the Oslo meeting.

Discussion on the standardisation of measurements had been scheduled for 16.00 hrs. on 6th July, 1973 (the last discussion day of the meeting) but was not reached until about 17.30 on that day. It soon became clear that the time then available for discussion was insufficient, and it was agreed to reconvene the meeting at 20.30 that evening. At the evening session the following were present:

H. Alberti (Germany), K.S.W. Campbell (Australia), N. Eldredge (USA), J.K. Ingham (Britain), V. Jaanusson (Sweden), P.A. Jell (Australia), P.J. Lespérance (Canada), K.J. McNamara (Britain), L. Marek (Czechoslovakia), B.S. Norford (Canada), Halszka Osmólska (Poland), D.R. Schwimmer (USA), J.T. Temple (Britain), A.T. Thomas (Britain), Ewa Tomczykowa (Poland), and H.B. Whittington (Britain).

A chairman was not formally elected but Temple acted as unofficial coordinator of the discussion.

The following decisions regarding orientation and measurement were reached. It was recognised that exceptions to them might well arise in individual groups of trilobites, but in these cases authors would be expected to state explicitly what alternative orientation and measurement procedure they were adopting.

(1). For isolated parts of the exoskeleton (i.e. cephala, cranidia, free cheeks, hypostomes, thoracic segments, pygidia) a single-orientation method with definition of an arbitrary horizontal plane is preferred to a multiple-orientation method.

(2) For the cephalon and cranidium the horizontal plane is that defined by the sagittal cranidial length, which is interpreted in forms with overhanging anterior cranidial margins as the maximised sagittal cranidial length. (Agreement was not reached – voting 4-4 – as to whether the maximised sagittal cranidial length should be defined posteriorly for this purpose by the posterior margin of the occipital ring or by the base of the occipital furrow, but it was recognised that the difference in orientation in the two cases would be slight).

(3) For dissociated free cheeks the horizontal plane is that which maximises the visible exterior surface. [Note by Temple: it would make easier the definition and measurement of free cheek and genal spine lengths (m) – see Appendix 2 – if this plane were additionally constrained to pass through the points α and ω, as indeed it would probably do in many cases].

(4) For the hypostome the horizontal plane is that defined by the sagittal length, i.e. by the line joining the mid-points of the anterior and posterior margins of the hypostome (voting 8-3).

(5) For individual thoracic segments the horizontal plane is that defined by the bases of the rachial furrows at the front and back of the segment.

(6) For the pygidium the horizontal plane is that defined by the sagittal pygidial length, i.e. by the line joining the mid-point of the articulating furrow to the mid-point of the posterior margin of the pygidium.

(7) These standard orientations apply to both measurement and illustration (voting 8-4).

(8) Measurements should be made on external surfaces.

(9) A standard notation of measurements should be based on Shaw's 1957 system as amended along the lines of the discussion document (voting 11-2).

(10) No system of "basic" measurements is recommended.

It was impracticable in the time available to attempt detailed discussion of individual measurements. Definitions of some of the measurements omitted from the discussion document were subsequently drafted by Temple on the basis of the comments received. These additional measurements are presented in Appendix 2 below.

APPENDIX 1: PROPOSED STANDARDISATION OF TRILOBITE MEASUREMENTS

The publication of measurements of trilobites as part of systematic descriptions and studies is becoming increasingly common, and it is clearly highly desirable that measurements should be standardised so that published data may be used for comparative statistical and numerical taxonomic studies.

The standardisation of measurements will be discussed at the forthcoming meeting on the *Evolution and Morphology of the Trilobita, Trilobitoidea and Merostomata* to be held in Oslo on 1-8 July 1973, and it is hoped that as a result of these discussions agreement can be reached on a scheme of standard measurements. The following notes have been prepared as a basis for discussion at the Oslo meeting. Comments on them are invited, both from those attending the meeting and from those unable to attend. Such comments will be duplicated and circulated at the meeting provided they are received before 1st May, 1973. Whether you wish to comment or not, it would be useful if you would state whether you would be prepared to accept a majority decision of the Oslo meeting on this subject and to apply it in your future work.

In a pioneer publication, Shaw (1957) discussed methods of measurement and defined a comprehensive set of measurements for most parts of the trilobite exoskeleton. As Shaw pointed out, a decision must first be made on the orientation to be adopted:

"It is basic to any system of measurement that a standard orientation of the trilobite be used. Two approaches can be used: (1) Take all measurements normal to the surface (or the chord of a convex feature) being measured, or (2) orient the trilobite one way for all measures. The first method has the advantage of giving true size on sloping parts, but has the serious disadvantage of requiring repeated manipulation of the specimen. The second method requires only one orientation of the specimen and has the very real advantage of giving measurements that can be compared with those taken from photographs. Also, measurements from a single orientation more closely approximate the visual impression of the specimen. The single-orientation method is used throughout this article with one exception, which is noted explicitly" (1957:193-4). Subsequent authors who have discussed this question (Bruton, 1965:342; Hughes, 1969:50; Temple, 1969:201) have followed Shaw in adopting the single-orientation method, and to the advantages listed by Shaw may be added that of suitability for automatic character recognition and measurement if such become feasible in the future. It must, however, be recognised that in practice single-orientation is difficult with large specimens which are too big for the field of view of the normal binocular microscope: such specimens lend themselves more readily to measurement by calipers, and the latter method (unless used on an image on a screen) measures each structure as its own normal projection. On balance, though, the advantages of single-orientation seem far to outweigh its disadvantages.

If single-orientation is adopted, the problem arises of defining a "horizontal" plane perpendicular to which measurements are to be projected. For cephala and cranidia three possibilities have been suggested, each of which has disadvantages:

(1) Place the palpebral lobe (or its chord, where the lobe is curved) horizontal (Shaw, 1957:194; Owens, 1970:311). An equivalent but more precise definition of this orientation is that of Eldredge (1972:61) who placed the dorsal margin of the visual surface horizontal.
Disadvantage: The palpebral lobes are absent in some trilobite families, and in others are too small to define a plane accurately.

(2) Place vertical the plane passing through the posterior margin of the occipital or axial ring (this orientation was defined originally for purposes of illustration by Whittington & Evitt, 1954:11, and has been applied to measurement by Bruton, 1965:342).
Disadvantage: The exact orientation of this vertical plane is uncertain in many cases, while in some families this projection foreshortens excessively the anterior part of the glabella and makes measuring difficult because of the difference in level between the anterior and posterior ends of the cephalon.

(3) Place horizontal the normal projection of the sagittal cranidial length, i.e. the straight line joining the mid-point of the anterior margin of the cranidium to the mid-point of the posterior margin of the occipital ring (Temple, 1969:201; Ingham, 1970:32). The "anterior margin of the cranidium" in this context is either the rostral suture (if this is on the dorsal surface) or the anterior margin of the cephalon (if the rostral suture is on the ventral surface).
Disadvantage: The presence of an axial occipital spine may make the sagittal cranidial length difficult to define.

Orientation of the hypostome has apparently not been explicitly discussed in the literature, but Temple (1969:208, 213, 219, 227) has projected measurements at right angles to the normally projected sagittal length of the hypostome.

For thoracic segments there is, as Shaw remarked, little problem: "they may be oriented with the dorsal furrow (or its chord, where the furrow is convex) horizontal" (Shaw 1957:194).

For pygidia the horizontal plane may be:

(1) That defined by "the plane determined by the ventral margin of the border, where the border rolls under to form the doublure (Shaw, 1957:194). This definition is not unambiguous, and was interpreted by Temple (1969:201) to mean the plane defined by the lateral and posterior pygidial margins. Even so, the plane is not always definable.

(2) The plane defined by the normal projection of the sagittal pygidial length (i.e. mid-point of articulating furrow to mid-point of posterior margin) (Temple, 1969:201). This definition can apply to cases where the plane in (1) is not definable but, like the corresponding cranidial definition, it becomes difficult to define in the presence of a terminal axial spine.

(3) The plane defined by the rachial furrows (Owens, 1970:311).

(4) The plane defined by the surface of the first axial (rachial) ring (Eldredge, 1972:61).

Once a decision has been reached on orientation, there remains the question of defining the individual measurements. Here the simplest procedure is to use Shaw's definitions and symbols as a basis. If the orientation adopted is different from Shaw's projection on to the plane defined by the palpebral lobes it will be advisable to distinguish the new symbols typographically from Shaw's, e.g. by the use of lower case letters in place of Shaw's capitals.

Although some additional measurements and symbols are suggested below to supplement Shaw's, no attempt is made to produce an exhaustive list of all possible measurements — others will need to be defined from time to time for particular families. On the other hand adoption of Shaw's scheme does not imply that all of Shaw's measurements are considered necessary or even useful. A list is therefore given of the basic recommended measurements (this list differs from that given by Shaw, 1957:202-3).

Experience suggests that Shaw's symbols for the cephalon need supplementing by the addition of measurements relating to the positions of the lateral glabellar furrows. These can be inserted into Shaw's scheme without duplication of symbols as follows (see Fig. 1A):

b_5 = anterior end of glabella to distal end of S_3 (exsag.)
b_{32} = distal end of S_3 to distal end of S_2 (exsag.)
b_{21} = distal end of S_2 to distal end of S_1 (exsag.)
b_{10} = distal end of S_1 to distal end of occipital furrow (exsag.)
k_{00} = transverse separation of distal ends of occipital furrow
k_{10} = maximum width of glabella opposite L_1
k_{11} = transverse separation of distal ends of S_1
k_{21} = maximum width of glabella opposite L_2
k_{22} = transverse separation of distal ends of S_2
k_{32} = maximum width of glabella opposite L_3
k_{33} = transverse separation of distal ends of S_3
k_5 = maximum width of frontal lobe of glabella

Notes:

(1) b_{32}, b_{21} and b_{10} can be combined to give e.g. b_{30}, b_{20} for the lengths of various lobes taken together.

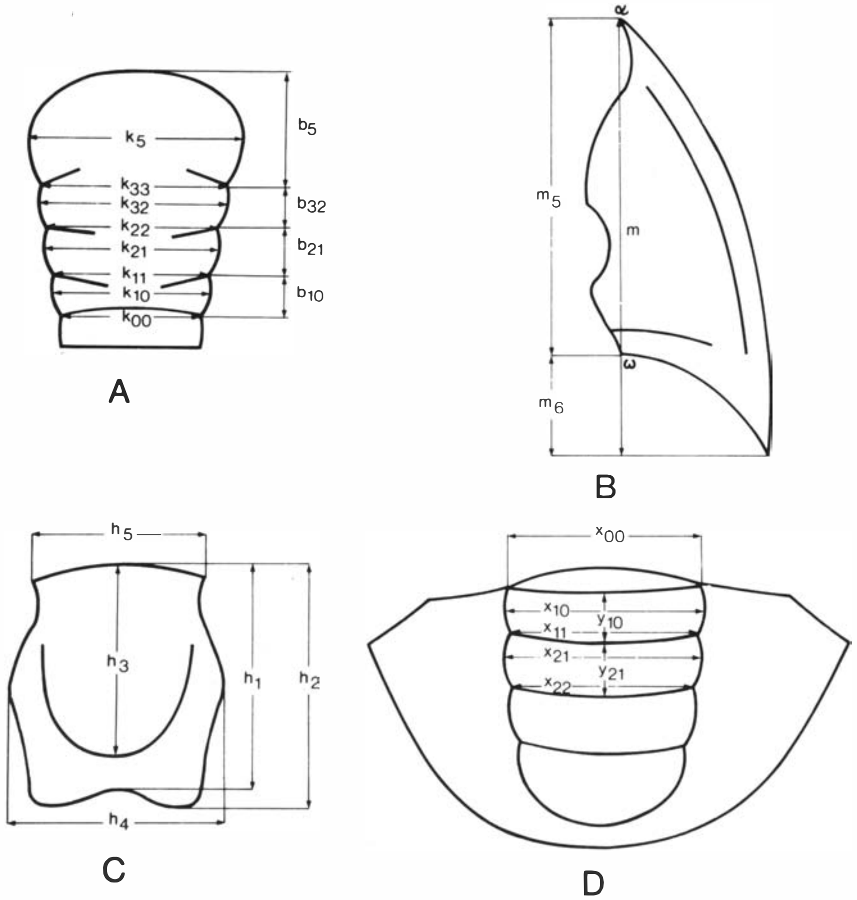

Fig. 1. Proposed additional measurements for glabella, free cheek, hypostome, pygidial rachis.

(2) In many cases some or all of k_{10}, k_{21}, k_{32} and k_5 will coincide with k_{00}, k_{11}, k_{22} or k_{33}.

(3) The width of the glabella is measured in each case from the deepest points of the rachial furrows.

(4) When glabellar lobes overhang the rachial furrows, glabellar widths measured across the outermost parts of the lobes (rather than to the bases of the furrows) may be distinguished by a prime, e.g. k'_{10}.

(5) When a glabellar furrow does not reach the rachial furrow its "distal end" is the point where the continuation of the glabellar furrow along its length meets the rachial furrow.

Shaw did not designate measurements for the hypostome, and unfortunately he used H as the sagittal width of the pre-glabellar area (recte pre-glabellar field). If the latter measurement is re-designated f_2 (this and x_{10} – see below – are the only changes proposed in Shaw's symbols), then h becomes available for hypostomes, and the following are proposed (see Fig. 1C):

h_1 = sagittal length of hypostome
h_2 = overall length (between planes tangent to anteriormost and posteriormost points of hypostome)
h_3 = middle body sagittal length (anterior margin of hypostome to posterior end of middle body)
h_4 = maximum width of hypostome
h_5 = width of hypostome across anterior wings

For thoracic segments an additional measurement is proposed:

q_2 = sagittal length (="width" of Shaw's q_1) of thoracic segment excluding articulating half ring, measured from articulating furrow to posterior margin of rachial ring.

By analogy with the proposed notation for the lengths and widths of glabellar lobes, the following pygidial measurements are proposed (1st ring furrow is taken as that behind the 1st rachial ring; see Fig. 1D):

x_{00} = transverse separation of rachial furrows at ends of articulating furrow
x_{10} = transverse separation of rachial furrows at position of maximum width (tr.) of 1st rachial ring (= Shaw's X)
x_{11} = transverse separation of rachial furrows at ends of 1st ring furrow
x_{21} = transverse separation of rachial furrows at position of maximum width (tr.) of 2nd rachial ring
etc.
y_{10} = articulating furrow to 1st ring furrow (sag.)
y_{21} = 1st ring furrow to 2nd ring furrow (sag.)
etc.

Notes:

(1) y_{10}, y_{21}, etc. can be combined to give the length of several rings as e.g. y_{20},etc.

(2) In many cases, due to the tapering of the pygidial rachis x_{10}, x_{21}, x_{32}, etc. coincide respectively with x_{00}, x_{11}, x_{22},etc.

A further pygidial measurement is proposed, namely w_{21}, w_{22}, etc. for the transverse separation of the tips of the first, second, etc. (counted from the front) pairs of pygidial marginal spines in multi-spinose pygidia.

Slight changes in the wording of some of Shaw's definitions are proposed as follows (they do not alter the sense of any of the measurements):

Pre-occipital glabellar length [re-named] (B) measured from the deepest point in the occipital furrow to the deepest point in the pre-glabellar furrow, in the sagittal plane.

Sagittal width of the pre-glabellar field (H) is re-designated f_2.

Posterior facial suture width [re-named] (J_1) is measured between two exsagittal planes touching the distal ends of the dorsal posterior facial sutures [re-defined to take account of proparian forms].

Maximum pre-occipital glabellar width [re-named] (K_2).

Transverse length of axial lobe (R_1) measured between exsagittal planes through the deepest parts of the rachial furrows.

Transverse pleural length (R_2) measured between exsagittal planes tangent to the outer tip of the pleura and through the deepest part of the rachial furrow.

It is proposed that the following should be considered *basic measurements* which should all be measured when available.

cephalon:	b, c, d_5, e, f_2, g, g_1 (from these a, a_1, a_2, b can be calculated if necessary); i, j, j_1, j_2, k, k_2
hypostome:	h_1, h_3, h_5
pygidium:	w, x_{00}, y_1, z_1

These basic measurements, together with the newly proposed measurements are shown in Figs. A-E: (Note: The Figures from the discussion document are here redrawn as Figs. 1A, C and D, that of the proposed basic measurements being omitted.)

As regards the technique of measurement, it is proposed that measurements should wherever possible be made on testiferous specimens or external moulds (or artificial casts therefrom), and only exceptionally on internal moulds; that measurements should not be made on distorted or strongly flattened specimens; that measurements on furrows be made at their bases (i.e. their deepest points when viewed in the projection adopted). Measurements on the bases of furrows are in practice affected by the direction of incident light, and as it is impracticable to standardise this because of differences of convexity etc., consideration should be given to the desirability of making all measurements on external moulds or artificial external casts of testiferous specimens. Measurement by micrometer eye-piece (preferably with a rectangular grid or with intersecting scales at right angles) is convenient but is subject to errors of calibration and parallax, although the latter error can be minimised by utilising only the central part (preferably less than half-diameter) of the field of view. Measurement by accurately calibrated travelling microscope is preferable. If a single-orientation method is adopted accuracy of specimen orientation is clearly important. It is recommended that specimens to be measured should be mounted on a platform which can be fixed relative to the viewing microscope and can be rotated on a horizontal axis for profile viewing. For cranidia with large eyes, the palpebral view is probably the easiest to set up accurately by viewing in profile or otherwise. Setting up specimens with the sagittal cranidial length horizontal can be done by viewing in profile, by getting both ends of the cranidium in focus simultaneously, or by maximising the projected sagittal cranidial length.

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APPENDIX 2: ADDITIONAL PROPOSED MEASUREMENTS

Dissociated opisthoparian free cheeks (see Fig. 1B)

m = total length of free cheek and genal spine measured along line from α through ω to projection of tip of genal spine on to this line (redefined after Pabian & Fagerstrom 1968).

m_5 = length of free cheek from α to ω.

m_6 = length of genal spine (measured along continuation of line from α to ω) from ω to projection of tip of genal spine.

Depth of cranidium and pygidium

n_1 = sagittal cranidial depth measured as perpendicular distance between horizontal reference plane (as decision 2 above, but defined posteriorly by posterior margin of occipital ring) and parallel line in sagittal plane tangent to highest point of glabella.

n_2 = sagittal pygidial depth measured as perpendicular distance between horizontal reference plane (as decision 6 above) and parallel line in sagittal plane tangent to highest point of pygidial rachis.

Thickness of cuticle

To be measured along sagittal line at mid-length of glabella.

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Future authors in *Fossils and Strata* should be aware of the fact that the present issue represents a first effort to apply an inexpensive typescript base for the text. The text in most forthcoming numbers is expected to be photo-composed, and even when a typescript base is used the making-up of text and figures will be considerably more sophisticated than in the present issue. Authors should therefore rather take Nos. 5–8 as examples when planning text, illustration sizes, and tables.

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