

COMMONWEALTH OF AUSTRALIA  
DEPARTMENT OF NATIONAL DEVELOPMENT  
BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS

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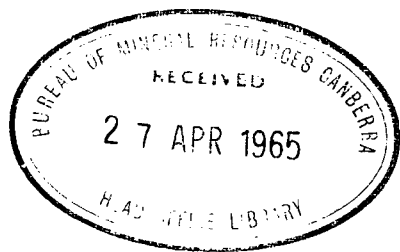
BULLETIN No. 64

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# EARLY UPPER CAMBRIAN FOSSILS FROM QUEENSLAND

BY

A. A. ÖPIK



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*Issued under the Authority of Senator the Hon. Sir William Spooner,  
Minister for National Development*

1963

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COMMONWEALTH OF AUSTRALIA

DEPARTMENT OF NATIONAL DEVELOPMENT

*Minister:* SENATOR THE HON. SIR WILLIAM SPOONER, K.C.M.G., M.M.

*Secretary:* SIR HAROLD RAGGATT, C.B.E.

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BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS

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*This Bulletin was prepared in the Geological Branch*

*Chief Geologist:* N. H. FISHER

*Issued:* 1st July, 1963

PRINTED IN AUSTRALIA BY VARDON PRICE, LTD., ADELAIDE  
PLATES PRINTED BY COTSWOLD COLLOTYPE CO. LTD.,  
WOTTON-UNDER-EDGE, GLOUCS., ENGLAND

#### CORRIGENDA

- p. 37, para. 6, line 5: for *Clavagnostus* (*Aspidagnostus*) read *Aspidagnostus* (*Clavagnostus*).
- p. 40, para. 4, line 8: for "node" read "lobe".
- p. 70, para. 4, line 3: for "short" read "long" (genal spines in *R. longula*).
- p. 82, line 7 from end: for "Text-figure 29" read "Text-figure 28".
- p. 98, para. 2, line 4: for "seven" read "nine".

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## SUMMARY

The early Upper Cambrian sequence of north-western Queensland corresponds in general terms to the Maentwrog and Ffestiniog Stages of Britain, to the *Agnostus pisiformis* and *Olenus* zones of Scandinavia, to the Dresbachian of North America, and to the Kushanian and Paishanian of north-east Asia. The Queensland sequence is divisible into seven zones, six of which are named after trilobite species; the lowermost zone is temporarily called the 'pre-stolidotus' zone in the absence of published names of species. The zones are grouped in two stages: the Mindyallan (below, with two zones), and the Idamean (above, with five zones). The stage division is indicated by a profound change in faunal composition: no species passes from the Mindyallan into the Idamean, and only a few genera are common to both. The uppermost Idamean zone (*Irvingella tropica*-*Agnostotes inconstans*) represents apparently the beginning of the middle Upper Cambrian, having (by correlation) a lower Franconian or lower Daizanian age. In connexion with the zoning the concepts of 'zone' and 'stage' are discussed; these are scale positions distinguished only by different nomenclature: zones have fossil names, and stages are named geographically. The suggested scale of stages and zones serves as a basis for overseas correlation, and for the dating of sequences and faunal collections (localities) within north-western Queensland (Glenormiston, de Little Range, Selwyn Range, and Pomegranate Creek areas), as well as for the presentation of palaeogeographic events and the temporal sequence of environments. Palaeogeographically, the early Upper Cambrian faunal region of Queensland is situated at the junction of a western intracontinental seaway and the eastern sea. The western seaway was dominated by a generally unfossiliferous sandstone-dolomite environment, apparently inimical to life, and the eastern sea by a well-populated limestone environment. Where the two met their influences on the environment fluctuated. Immediately after the end of the Idamean, deposition at the junction of the seas was interrupted by uplift, but in the east (Pomegranate Creek area and Burke River) deposition continued into the Ordovician. Palaeogeographical and lithological considerations supplemented by palaeoecological observations (mode of preservation and embedding of fossils and general faunal aspect) indicate an epicontinental and sheltered marine habitat in Mindyallan and Idamean times in north-western Queensland; this is also the habitat of olenids, as indicated in the discussion of the Superfamily Olenacea.

Of the fifty fossils listed, twenty-five have been previously published by Whitehouse. The list is annotated to show the stage and zonal distribution of the fossils. Suprageneric classification and morphology of agnostids is discussed. Agnostids: Of the twelve listed agnostids, three are new: *Agnostardis amplinatis* gen. nov. et sp. nov., *Agnostotes inconstans* gen. nov. et sp. nov., and *Discagnostus spectator* gen. nov. et sp. nov. (Discagnostidae, fam. nov.). *Discagnostus* is distinguished by two pairs of genal (or ocular) tubercles. Polymerid trilobites: the suprageneric classification of Olenacea is discussed; new forms are: *Olenus ogilviei*, *O. delicatus*, *Asilluchus nanus* gen. nov. et sp. nov., and the subfamily Rhodonaspidinae; *Talbotinella notulata* (Talbotinellidae, fam. nov.). The suprageneric classification of Ptychopariacea (probably a junior synonym of Olenacea) is discussed; the presence of Pterocephaliidae is indicated by ?*Aphelaspis* sp. B; a new family Erixaniidae is erected, with three species of *Erixanium* gen. nov.; Eulomatidae are represented by *Stigmatoa* gen. nov., with four new species; Ptychopariacea familiae incertae is *Hercantyx rudis* gen. nov. et sp. nov. The nomenclature of Telephinacea, Komaspidae (alternative: Ptychopariacea, Elviniidae) is discussed, and *Irvingella tropica* sp. nov. described. Of Ceratopygacea the genus *Proceratopyge* is discussed and *P. lata* Whitehouse and *P. cf. chuhsiensis* Lu described. One species of Beyrichonidae and one of Hydroida (both unnamed) are recorded.

## INTRODUCTION

A selection of early Upper Cambrian trilobites from Queensland is described to lay a basis for zoning of the sequence and to gain knowledge of forms which are, or may become, useful in palaeogeography and in interprovincial correlation. The taxonomy and organization of the same fossils are studied. The zones of the sequence are conveniently grouped in two stages—the Idamean (above) and the Mindyallan (below). The basal Idamean fauna with *Olenus ogilviei*, and the uppermost with *Irvingella tropica*, are presented exhaustively. Lesser attention is paid to the Mindyallan fauna, which is rather large and which is studied separately. The paper is written essentially for readers concerned with the stratigraphy, correlation, and palaeontology of the Upper Cambrian of Australia. Some items of a more general interest, however, are also included. These are a discussion of the concepts of zones and stages and their nomenclature, and some problems of organization and suprageneric classification of trilobites.

The source of material is the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra. The fossils from the Glenormiston area were collected by a party of Bureau geologists led by J. N. Casey, and the writer participated in this enterprise. The fossils from the Selwyn Range and Pomegranate Creek area were collected by the writer. The complete specimens of *Erixanium* illustrated on Plate 9 were collected by Mr R. B. Leslie and party, Frome-Broken Hill Co. Pty Ltd, and kindly released for description by the Management of that Company.

## STRATIGRAPHY AND CORRELATION

### *General overseas correlation*

For general orientation overseas equivalents of the early Upper Cambrian of Queensland are referred to in the first place.

In Britain (Stubblefield, 1956) the names Maentwrog Stage, derived from earlier designations (Maentwrog Beds, Group; Middle *Lingula* Flags), and Ffestiniog Stage are now in use. The Maentwrog Stage possesses species in common with Australia (*Glyptagnostus reticulatus* and *Homagnostus obesus*) and can be roughly correlated with the lower, and the Ffestiniog Stage with the upper half of the Idamean of Queensland.

In Scandinavia the *Agnostus pisiformis* (below) and the *Olenus* zone (above) constitute the early Upper Cambrian sequence. The *A. pisiformis* zone should correspond to our Mindyallan pre-*stolidotus* and *Glyptagnostus stolidotus* zones; *Glyptagnostus reticulatus* (base of the *Olenus* zone) is common to both; the total *Olenus* zone corresponds to the Idamean, but a correlation of the rest of the *Olenus* subzones with the Queensland zones is vague in detail.

In North America, the Dresbachian covers the sequence, and even some fossils are the same in Australia as in North America.

In Korea (Kobayashi, 1956) and in Manchuria (Endo, 1956) the Kushanian, which is attributed to the Middle Cambrian, together with the Paishanian represent

the early Upper Cambrian. The Upper Cambrian age of the Kushanian has been discussed already by Öpik (1960, p. 106, 107).

In China (Lu, 1960, p. 213) the Kushanian and the lower half of the Changshanian together correspond in broad terms to the Queensland sequence.

In Russia no stage names were used before 1960, although early Upper Cambrian faunas are widespread in north-eastern Siberia and in western Siberia (in the region of the Sayan and Altai mountains). In north-eastern Siberia (Savitski, in Tkachenko, 1959) the sequence has been related to the American stage names, including the Dresbachian; but a substantial part, beginning with the zone of *Glyptagnostus reticulatus*, is placed in the Franconian, apparently under the influence of a suggestion by Lochman-Balk & Wilson (1958, p. 333), which is rather confusing from a nomenclatorial point of view. Apparently, the chart by Lochman-Balk & Wilson (loc. cit., p. 334) showing the improbable occurrence of *Glyptagnostus reticulatus* in the Franconian *Elvinia* zone contributed also to the misinterpretations.

The west Siberian early Upper Cambrian sequence is represented in the newly introduced Salairian (below) and Kuyandan stages (new names, Ivshin, 1960). The name Salair has been used, according to Ivshin, previously for a Middle Cambrian sequence that was mistakenly interpreted as Upper Cambrian; but he suggests 'to retain the name Salairian stage by filling it with a new content, and in accordance with it—with a new volume', although an alternative name for the Upper Cambrian unit has been published earlier. No doubt the Siberian early Upper Cambrian sequences and faunas will be capable of intercontinental zonal correlation in future, as can be concluded from the charts and the abundance of *nomina nuda* in the fossil lists.

In Australia, in the absence of appropriate stage names, Öpik (1960) used the name Dresbachian (in its original sense) of the American scale for the early Upper Cambrian sequence, and indicated later (1961b) that such usage is undesirable because the changes in names and concepts that are currently published overseas would result in an uncontrollable instability.

#### *The Sequence of Zones and Stages in Queensland*

The sequence of the early Upper Cambrian zones has been published earlier (Öpik, 1960), but in a tentative form and without naming the zones. Fossil names are now available for most of them and listed below; the enumeration of zones in the following list is the same as in the earlier paper (loc. cit.), to facilitate amplifications and corrections; these numbers, however, should not be regarded as zone symbols.

#### *Idamean Stage*

8. *Irvingella tropica*—*Agnostotes inconstans* Zone.
7. *Erixanium sentum* Zone.
6. *Corynexochus plumula* Zone.
5. *Glyptagnostus reticulatus* Zone with *Proceratopyge nectans*.
4. *Glyptagnostus reticulatus* Zone with *Olenus ogilviei*.

*Mindyallan Stage*

3. *Glyptagnostus stolidotus* Zone.

2. Pre-*stolidotus* Zone.

*Middle Cambrian*

1. *Leiopyge laevigata* (triple) Zone.

Comment:

1. The middle Cambrian *Leiopyge laevigata* Zone has been discussed in detail by Öpik (1961b) and needs no further discussion.

2. The pre-*stolidotus* Zone (lower Mindyallan) remains unnamed for the time being; its fauna is a large one; part has a Middle Cambrian aspect, another part passes into the next zone above, and several characteristic forms can be discerned.

3. The *Glyptagnostus stolidotus* Zone (upper Mindyallan) was so named by Öpik (1961b). The fauna is rather large; besides *Glyptagnostus stolidotus* the following trilobites are now described: *Agnostardis amplinatis*, *Discagnostus spectator*, *Talbotinella notulata*, and *Rhodonaspis longula* Whitehouse, which are all confined to this zone. In the same and in the upper part of the preceding zone representatives of the Catillicephalidae, Norwoodiidae, Menomoniidae, Dameselidae and Raymondinidae have been recorded, including a species of *Meteoraspis*, and *Liostracina*. No species, and only few genera, pass into the next zone above.

4. The fauna of the *Glyptagnostus reticulatus* Zone with *Olenus ogilviei* is small; its third known trilobite is *Agnostus inexpectans* Kobayashi. This zone merges with the next above, and both together can be regarded as a single zone if necessary. The presence of *Liostracina* cannot be confirmed.

5. The fauna of the *Glyptagnostus reticulatus* Zone with *Proceratopyge nectans* Whitehouse is more prolific than the fauna of the lower division, with *O. ogilviei*. *Agnostus inexpectans*, *Aspidagnostus* (*Clavagnostus*) *parmatus* Whitehouse, *Eugonocare* sp., *Blountia*, an aphelaspid, and *Pseudagnosti* are present.

6. The *Corynexochus plumula* Zone has *Agnostus inexpectans* in common with the preceding zone, and *Eugonocare tessellatum* makes in it its first appearance. *Corynexochus plumula* is rather unevenly distributed in the zone, being most abundant in its upper part, and passes into the base of the next zone above. The genus *Corynexochus* was originally described from the Middle Cambrian; it has therefore little stratigraphic value and the zone refers to the species *plumula*.

7. The name *Erixanium sentum* Zone is applied here for the first time. A part of its fauna was described by Whitehouse as the *Eugonocare* stage, and the other part as *Rhodonaspis* stage. *Rhodonaspis longula* itself, however, has not been found in this zone, but occurs much earlier, being common in the *Glyptagnostus stolidotus* Zone. Furthermore, *Eugonocare* as a genus is not confined to this zone: it occurs in the three upper zones of the sequence, and the species *E. tessellatum* belongs to two zones. Hence, the zone had to be referred to a new name. The

following new species from the *E. sentum* zone are now described: *Asilluchus nanus*, *Erixanium sentum*, *E. strabum*, *E. alienum*, *Stigmatoa diloma*, *S. silex*, and *S. tysoni*.

8. The name *Irvingella tropica*—*Agnostotes inconstans* Zone is applied for the first time. The fossils: '*Iddingsia*, *Pterocephalia*, *Parabolina* [= *Asilluchus*] and last *Eugonocare*' which were previously (Öpik, 1956, p. 105) attributed to this zone are not present, but occur immediately below and should be referred to the *Erixanium sentum* Zone (*E. sentum* and *E. strabum* are also present). All determinable fossils that belong to the *I. tropica*—*Agnostotes inconstans* Zone are now described, and the list of species is: *Irvingella tropica*, *Stigmatoa sidonia*, *Olenus delicatus*, *Hercantyx rudis*, *Proceratopyge lata*, *Proceratopyge* cf. *chuhsiensis*, and *Agnostotes inconstans*. All of these (except *Proceratopyge*) make their first appearance in this zone. It should be noted that this fauna is known from a single locality and bed (topmost bed at D120b, Pomegranate Limestone, and area) and could not be located elsewhere on the surface.

The early Upper Cambrian sequence of zones of north-western Queensland can be divided into two stages: 1) The Mindyallan Stage (below) comprising the pre-*stolidotus* and the *Glyptagnostus stolidotus* Zones, and 2) the Idamean Stage (above), consisting of the two *Glyptagnostus reticulatus*, *Corynexochus plumula*, *Erixanium sentum*, and *Irvingella tropica*—*Agnostotes inconstans* Zones.

The name *Mindyallan* refers to the name of the parish Mindyalla (Queensland Four-mile series Sheets 76 and 67) within which numerous fossiliferous outcrops of the Mungerebar Limestone have been recorded. The *Glyptagnostus stolidotus* fauna has been found in the south-west corner of the parish quadrangle at McCabe Knob (latitude 22°19'S., longitude 138°58'E.), sixteen miles north-north-east of Roxborough Downs Station. The sequence at this place consists of siltstone and sandstone above, and white dolomitic and in parts sandy limestone below. Outcrops containing the pre-*stolidotus* fauna occur to the north, and down the sequence.

The name *Idamean* refers to Mount Idamea (locality W16, Text-fig. 1), with a sequence dated as the *Corynexochus plumula* Zone.

The selection of the names of the stages was guided by the following considerations: The Australian Code of Stratigraphic Nomenclature, in Article 40, suggests a geographical nomenclature of stages; consequently (1) the geographical names of stages should be free of any homonymy and synonymy within the whole of the system of the geographical nomenclature in stratigraphy; (2) rock-unit names which are derived from place names are not themselves geographical names and should not be used or borrowed to construct 'patronymic' stage names; the principle that one stratigraphic object should have a unique geographic name, and one such name should adhere to a single object, should be observed—names that have been used for one purpose cannot be used for a different purpose; (3) stages are based on their fossil content (A. Code, Article 38) and are conceptual divisions of the geological scale; and (4) no place is known that

possesses a complete outcrop of either stage; at Mount Idamea—the nominate locality of the Idamean—only a small part of the stage is exposed, and in the Mindyalla quadrangle outcrops are scattered and none of them alone can be regarded as a fixed type locality. The stage names therefore cannot be referred to a 'stratotype' each, but the selected names are code names designating the concepts.

As seen from the discussion of the sequence of environments in early Upper Cambrian time, no lithological boundaries coincide with the 'zone boundaries' and any attempt to accommodate a 'stage boundary' to a lithological (formation) boundary would be futile because such accommodation would involve the span of more than one zone; in the case of the O'Hara Shale, for example, the whole of the early Upper Cambrian would be involved.

The stages can be characterized as follows: The Mindyallan Stage passes downward into the Middle Cambrian *Leiopyge laevigata* Zone with a narrow passage in which the new faunal elements mingle with agnostids of a Middle Cambrian aspect; the fauna of the Stage itself is that of the pre-*stolidotus* and the *Glyptagnostus stolidotus* Zones; the new elements mentioned above consist of several genera of Damesellidae, Norwoodiidae, Agnostacea, and so forth. At the passage from the *G. stolidotus* Zone into the Idamean Stage practically all Mindyallan species disappear; only a few genera survive (*Glyptagnostus*, *Agnostus*, *Pseudagnostus*) in the form of new species. Thus, the passage from the Mindyallan into the Idamean is marked by a most prominent and critical faunal change within the sequence and appears to be unique in its abruptness within the Cambrian of Queensland. In spite of the physical, depositional continuity, very little of the fauna seems to be common to both stages. The older, and more abundant, fauna disappears within a few feet and is followed by a depleted fauna with *Glyptagnostus reticulatus*.

A similar abrupt faunal change, at about the same date, occurs in America 'at the boundary level between the *Crepicephalus* and the *Aphelaspis* faunizones' (Lochman & Wilson, 1958, p. 332) and is apparent even in south-east Asia at the passage from the Kushanian to the Paishanian faunas.

The Idamean Stage is characterized by the fossils listed in its zones: the fauna becomes gradually richer with the advance of time, and culminates in the *Erixanium sentum* Zone. *Glyptagnostus reticulatus* disappears early, but some of the species and all genera associated with it go through the whole of the Idamean sequence. The Idamean fauna as a whole is recognizable at a glance, but its two lowest zones (*G. reticulatus* and *Corynexochus plumula*), especially in less fossiliferous localities, can be identified with certainty only in the presence of their nominate fossils.

#### *Zone and stage concepts*

No difference in principle exists between zones and stages; the only difference that matters is purely nomenclatorial: zones derive their names from fossils and

stages have geographical names. Nothing prevents the giving of geographical names to biological zones, and stages can be named by species, or genera, and by code names of assemblages. For example, the Idamean Stage covers wholly the *Eugonocare* stage of Whitehouse (1939) which, in effect, is the zone of the genus *Eugonocare*, or the zone of *Pseudagnostus vastulus* Whitehouse, and which became split by means of other fossils into four separate zones. No doubt, one of these—the *Erixanium sentum* Zone—will be divided in future, and, if given a geographical name, constitute a separate stage, but remain at the same time the *Erixanium sentum* Zone. Furthermore, the *Glyptagnostus reticulatus* Zone and the *Corynexochus plumula* Zone have *Agnostus inexpectans* Kobayashi in common, and belong therefore into a single species-zone (*Agnostus inexpectans* Zone). It is now apparent that after having established a particular sequence of zones and stages it is not necessary to suppress all other ways of zoning and subdividing the sequence. The practical service of all such subdivisions consists in the dating and correlation of events and sequences; for this purpose alternative divisions offer answers of various degrees of accuracy, according to the quality of the palaeontological collections. So, it is much simpler to say 'within the Zone of *Agnostus inexpectans*' rather than 'somewhere within the *Glyptagnostus reticulatus* and/or *Corynexochus plumula* Zones'. The accuracy of both the phrases is the same, but the first is more definite, especially in the presence of *A. inexpectans* itself.

To conclude, alternative zoning and alternative scales of stages should not be sacrificed in favour of a principle (like uniformity and purity of the scale) which may suppress information of practical value.

It is appropriate at this point to explain what is meant by 'zone' in this paper: a zone is a position in a timescale recognized from its fossils; stratigraphic orientation is its main function, and reliability is its most desired virtue. A zone that is based on determinable species is, therefore, of most value and a scale of species-zones is an ambitious but worthwhile goal.

Even more ambitious is a scale of uniform zones, that is a scale of zones of a single group of fossils: only agnostids, or only graptolites, or only larger foraminifera, and so forth. Such a scale is not attainable always, especially not at the beginning. A mixed scale is easier to construct and may serve well in stratigraphy.

Zones are named after particular species, which indicate the span of each zone and serve as code names for the associated faunas. These associated faunas should be determined and consulted, especially in the absence of the nominate species; but even in the absence of the nominate species the code name of the absentee remains valid.

Zones and scales of zones are established by trial and error and are subject to perpetual revision; clear-cut boundaries between the zones are exceptional: zones usually penetrate one another in large, narrow, or even undefined belts of passage; or may be separated by belts of no contact. The interzonal lines in a scale are not physical boundaries, but lines of convenience; they are, perhaps, comparable with



intervals within which the baton changes from one runner to the next. Zones as such can be, and are usually, classified: the most common sorts of stratigraphic zone are species-zones, biozones, genus-zones, and faunizones. A scale may, and usually does, contain several kinds of zones, which is no evil, as long as the scale and its zones serve the purpose.

A 'teil-zone' is a useful concept. It is not, and cannot be, a division (zone) of a scale because it denotes only a part of a zone with an undefinable position within that zone.

Zones cannot be taken as units of measurement, because they are non-magnitudinal positions within a scale; of course, any zone covers a certain interval of time, but these intervals are not definable as magnitudes and most probably every individual zone of a scale has its own individual magnitude. For this reason, when two different scales (scale A and scale B) are compared (correlated), the assumption that a zone of A is equal to a zone of B would be fallacious. This fallacy will be augmented even more when different principles have been applied in the construction of the scales, and of the zones of each scale as well.

The correlation of the Scandinavian and the American scales of the early Upper Cambrian has been currently discussed in the literature. The problem has been approached mostly with the assumption that a zone of one scale should be equal to a zone of the other scale, in disregard of the totally different principles which have been applied in constructing these scales.

In the Scandinavian scale (Westergaard, 1947) subzone is the term for a species-zone, and corresponds in principle to the concept of zone as used in the present paper. In Sweden, however, the change of terms from subzone to zone would be inconvenient because it would necessitate other changes in the traditional nomenclature. The term zone is used there in the form of "*Olenus* zone", for example, where it designates the whole known range of that genus: the *Olenus* zone contains six consecutive subzones or species zones. In other usages such a set of zones would be a stage, or split in several stages. So, it is apparent that the 'genus zone of *Olenus*' cannot be simply correlated with a 'zone of another genus' of another scale that is constructed on other principles and traditions.

The American scale and its terminology are much more complicated than the Scandinavian scheme. The zones of the American scale according to Lochman-Balk & Wilson (1958) are 'biozones', 'genus-zones', and 'spans' of assemblages of genera (faunizones). 'Assemblage' is also defined: 'the median level where most of the biozones overlap determines the characteristic faunal assemblage'. The names in the scale of the Upper Cambrian charts refer to the faunizones: 'the faunizones are named from one or several of the widespread genera, a) whose biozones fall wholly or largely within the time-rock span covered, or b) whose initial appearance and maximum abundance was during that span', and subzones are widespread subdivisions of a 'standard faunizone'.

It appears that in this scale, species as such have no value at all; genera and assemblages of genera mark the divisions of the scale; most different is the meaning of 'subzone', because a Scandinavian 'subzone' means in translation a 'biozone' and not an American subzone. The names of the Upper Cambrian American zones may become misleading because they are code names of selected genera, and in selecting the name the 'initial appearance and maximum abundance' is considered and not the total range of the name-giving genus. It should be noted also that in the American Upper Cambrian scale good species zones are present but are masked by the names of their respective genera. So, *Crepicephalus*-zone stands for *Tricrepicephalus texanus* zone and *Elvinia* for *Elvinia roemeri*. The 'Elvinia zone' is apparently a faunizone, a biozone (the span of the genus), and a Scandinavian subzone (the span of a species).

No doubt the American scale of zones is the proper instrument for an intra-continental correlation. But North America possesses only a relatively small part of the Cambrian when compared with the global extent of the Cambrian sea; hence, the overall suitability of its scale for intercontinental and universal correlation should be seriously questioned. Intercontinental correlation is, however, progressing by taking advantage of much simpler means. These are the universal species, like *Leipyge laevigata*, *Glyptagnostus reticulatus*, *Lotagnostus trisectus*; they provide for firm 'datum levels' or datum zones and for a correlation by interpolation of matter and events between these levels. Concurrently, the same and similar species determine the stratigraphic value of associated forms and equip them with their own power of datum level markers. Of course, in the absence of the time-marking species widespread genera and assemblages can be considered, but they provide for a lesser accuracy; and even the general aspect of an endemic, or insufficiently described, fauna will be of some use in tentative correlation.

The correlation of the early Upper Cambrian formations of Queensland has been already published (Öpik, 1960) and the formations are related to various positions within the Dresbachian. In this paper the correlation with the newly established zones is discussed under the headings: 'Stratigraphic distribution of localities', and 'The sequence of environments in early Upper Cambrian time'.

The overseas correlation is best presented in relation to the Queensland stages.

The Mindyallan Stage is contemporaneous with the Scandinavian zone of *Agnostus pisiformis*, that is with the Upper Cambrian part of the total span of this species. It is also contemporaneous with the Kushanian of China, or strictly, with the 'Upper Kushanian'; the rock unit, Kushan formation, may be of a Middle Cambrian age in its lower part. In America, probably the upper part of the *Bolaspidella* zone and the *Cedaria* and *Crepicephalus* zones together are the equivalents of the Mindyallan stage.

The Idamean Stage corresponds in time to the Scandinavian *Olenus* zone, not quite accurately to the Paishanian of China and Korea, and to the *Aphelaspis*—*Dunderbergia* zones of North America.

Australia and America have common zone-marking species: *Glyptagnostus reticulatus*, which is universal, *Glyptagnostus stolidotus*, and *Agnostus inexpectans*. The zone of *Irvingella tropica*—*Agnostotes inconstans*, which is included in the Idamean Stage, may be slightly younger than the *Olenus* and *Dunderbergia* zones; it may correspond to the lower part of the Franconian (America) and to a part of the Swedish *Parabolina spinulosa* zone. For a possible correlation with Korea see the description of *Agnostotes inconstans*, and of the genus *Irvingella*.

## REGIONAL DISTRIBUTION OF EARLY UPPER CAMBRIAN ROCKS AND FAUNAS

### *Introduction*

The collections from which the early Upper Cambrian fossils come were made in several separate areas which are briefly described below, under the headings Glenormiston, De Little Range, Selwyn Range, and Pomegranate Creek Area. Brief geomorphological and geological data are given and the fossiliferous localities are related to the sequence of fossil zones. A general locality map of the whole region is omitted because one has been recently published by Öpik (1960, p. 94, 95). The present summary amplifies the too-condensed earlier paper (loc. cit.).

### *Glenormiston*

The map, Text-fig. 1, shows the geographical distribution of the Glenormiston localities from which fossils are described in the present paper. Many more localities have been examined and fossils collected from them. Three localities (W5, W16, and W40), the fossils from which are not yet treated, are also entered in the map to show the position of the best known occurrences of the *Glyptagnostus reticulatus* (W5, W40) and *Corynexochus plumula* (W40, W16) faunas that are mentioned in the text.

The morphology of the Glenormiston area has been discussed briefly by Öpik (1960). It is a plain (a truncated limestone pediment), a prairie with little scrub. The part north of the 23rd parallel is relatively scrubby, with low hills and low-angle cuestas. The surface drainage is undeveloped, consisting of few shallow dry creeks ending in intermittent swamps or lakes only a few feet deep. The present surface is a slightly modified pre-Cretaceous landscape.

The formation of the area is the Georgina Limestone. It is 'a flaggy, grey to blue-grey, sandy limestone with several breccia interbeds' (Öpik, loc. cit., p. 100). This description applies essentially to beds deposited during the *Glyptagnostus reticulatus*, *Corynexochus plumula*, and *Erixanium sentum* Zones. Cross-lamination on a small scale, small flow contortion, and oolitic interbeds are also common in this part of the sequence, but chert and surface silicification are absent.

The lower part of the Georgina Limestone, deposited in the time of *Glyptagnostus stolidotus*, and exposed in outcrops north of the 23rd parallel, is distinct. Dark and rather bituminous beds with scattered small pockets of crystal-



line calcite and chert, and with siliceous shale partings, are here in sequence with light grey non-bituminous varieties and bituminous to non-bituminous aphanitic beds.

The earliest part (late Middle Cambrian, loc. W2), flaggy, grey and sandy, with marly interbeds, is very similar to its time equivalent—the Devoncourt Limestone of the Duchess area—but nevertheless cannot be distinguished readily from the surrounding Georgina Limestone. The structure is relatively simple and mild. A general dip of one to two degrees to the west-south-west, and minor rolls along north-north-west to north-west axes, are apparent. It is the extreme eastern flank of the Toko syncline, or the western flank of an anticline with the Sun Hill Arkose (Lower Cambrian) in its core. The Middle Cambrian limestone (W2) at Polly's Lookout may represent a local culmination and is an erosional inlier. The age of the structures is Ordovician. An older deformation (disconformity 3, in Öpik's chart, 1960; p. 109; columns Sun Hill, Tysons Bore, and Toko Range) is also well documented; the early Upper Cambrian sequence culminates in the Glenormiston area and on its truncated surface rests the Ninmaroo Formation (latest Upper Cambrian and Tremadocian). It is a large break; the Upper Cambrian sequence is much more complete in the Burke River area. The geographical distribution of fossil zones of the Georgina Limestone reflects the structure: the oldest zone is represented in the localities north of the 23rd parallel, and the youngest in the south and south-west, and a general north-west trend is apparent.

The thickness is inconclusive in the absence of a reasonable dissection: most outcrops are pediments, and faces with 10-15 feet of rock are very rare. In outcrops north of the Twenty Mile Bore (personal communication, J. N. Casey) over 100 feet of the Georgina Limestone should be present, and the thickness increases towards the south-west to several hundreds of feet.

#### *Stratigraphic distribution of localities of Glenormiston*

##### *Middle Cambrian*

The late Middle Cambrian *Leiopyge laevigata* Zone is apparent at locality W2, where *Hypagnostus hippalus* Öpik was collected.

##### *Upper Cambrian*

*Mindyallan*: The "pre-*stolidotus*" Zone is not represented on the Glenormiston Sheet; in the vicinity of Glenormiston it is probably concealed under the Ninmaroo Formation; at W2 it should be present above the Middle Cambrian, but no fossil evidence has been collected as yet; even a break is possible here.

The *Glyptagnostus stolidotus* Zone localities are G48, G50, W1, W15, and W20; these represent different beds, but the fauna in them appears to be uniform.

*Idamean*: The *Glyptagnostus reticulatus* Zone localities are W5 and W40; at W40 the next higher zone with *Corynexochus plumula* is also present; the *G. reticulatus* Zone should be traceable to the north-west (Tysons Bore area).

The *Corynexochus plumula* Zone is represented at W40, W16, and W10. At W40 a small fault separates it from beds bearing *Glyptagnostus reticulatus*; at W16 (east face of Mount Idamea) some 15-20 feet belong to this zone; *C. plumula* is abundant in a dark limestone near the top of the sequence. At W10 the top beds of the *C. plumula* Zone are followed above by the *Erixanium sentum* Zone.

The *Erixanium sentum* Zone has been recognized in localities W10 (upper part of the section), W9, W42, W43, W45, W47, and W65/23. At W10 the lowermost part of the *E. sentum* Zone is exposed, and the other localities represent various horizons within the zone. In general terms the fauna is uniform and sub-zonal divisions cannot be established as yet. But the distribution of fossils in these localities indicates a sequence of species and even genera. For example, *Erixanium alienum* is known only at W9, and *E. strabum* at W10; different undescribed genera occur in W65/23, W47, and places that are not yet shown on the map. The clustering of localities north of the Twenty Mile Bore indicates an area of excellent outcrop. It was also the main collecting ground of F. W. Whitehouse (1936, 1939).

#### *De Little Range*

The occurrence of a small inlier of the early Upper Cambrian Pomegranate Limestone at the foot of the De Little Range on Wills Creek, about 5-7 miles south of Buckingham Downs Station, has been already described by Öpik (1956, p. 4 and 14; 1960) and some fossils published by Öpik (1961a). The rock is a grey sandy limestone of alternating hard platy and hard ellipsoidal limestone and laminated, softer marly beds in sequence with aphanitic chert-bearing layers. The lower part belongs in the *Glyptagnostus stolidotus* Zone, and specimens of *Agnostardis amplinatis* are described from it below (Loc. B525, B537). The upper part falls into the *Glyptagnostus reticulatus* Zone (Loc. D126); a cephalon of *Agnostus inexpectans* is described from it in the present paper.

#### *Selwyn Range*

The Selwyn Range localities D6 and D29 yielded material for the description of the Mindyallan *Discagnostus spectator* and *Rhodonaspis longula* and the Idamean *Stigmatia silex*. The formation is the O'Hara Shale, and the localities, including their geographical position and correlation, are described by Öpik (1961b).

#### *Pomegranate Creek Area*

The Pomegranate Creek area (Text-figs. 2-5) is a part of the Burke River outlier (Carter & Öpik, 1963). The occurrence of *Glyptagnostus reticulatus* and *Olenus* aff. *transversus* (now *Olenus ogilviei* sp. nov.) in the area was first mentioned by Öpik (1956, p. 23). Further information, including the occurrence of *Irvingella*, correlation (chart, Bouliia column), and structure, is provided by Öpik (1960).

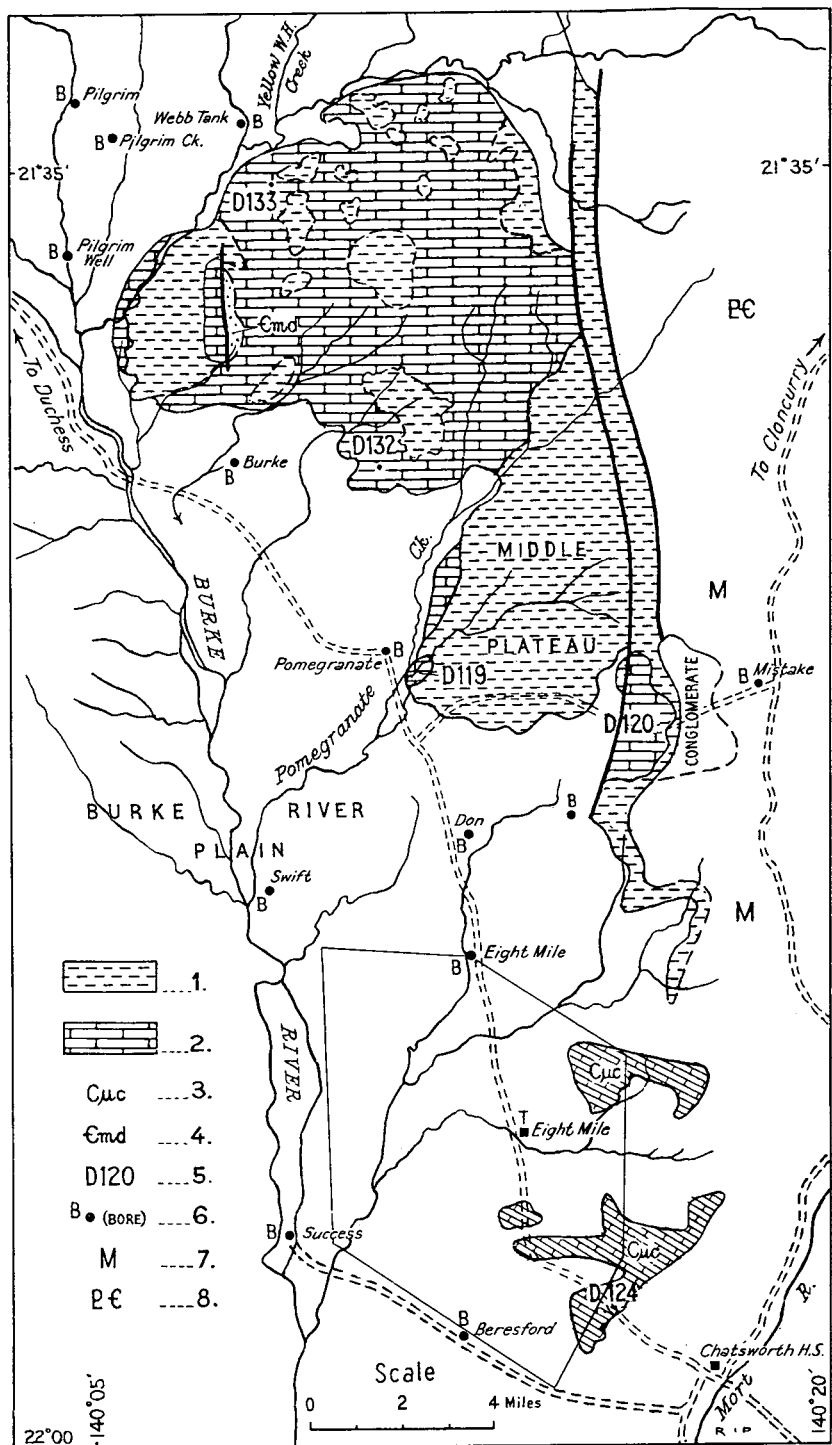


Fig. 2.—Pomegranate Creek area, simplified; adapted from Dutchess 4-mile Sheet. Detail of locality D120 in Text-figs. 3 and 4. 1—O'Hara Shale; 2—Pomegranate Limestone; 3—Cuc.—Chatsworth Limestone (Upper Cambrian, Franconian); 4—Cmd.—Devoncourt Limestone (a small inlier); 5—Localities; 6—Bore (B) and well sites. PC—Precambrian; M—Mesozoic (Lower Cretaceous, including the "conglomerate").

The morphology of the area is relatively simple. The depositional Burke River Plain, with deep soil, alluvial deposits, and flat-lying Tertiary limestone, is the dominant feature. Within the Plain in the south-east several pediments of truncated Upper Cambrian limestone (Cuc) represent remnants of the pre-Cretaceous landsurface; in the north low plateaux of Upper Cambrian sediments, with escarpments facing west, rise above the Burke River Plain. The northern plateau (Text-fig. 5) is clustered with mesas of O'Hara Shale standing above transitory rubble-covered limestone pediments which are in the process of dissection by modern drainage. The altitude of the pediment at locality D133 is about 1,000 feet. The middle plateau (O'Hara Shale with a lateritic surface) is relatively little dissected by Pomegranate Creek, with limestone pediments at its

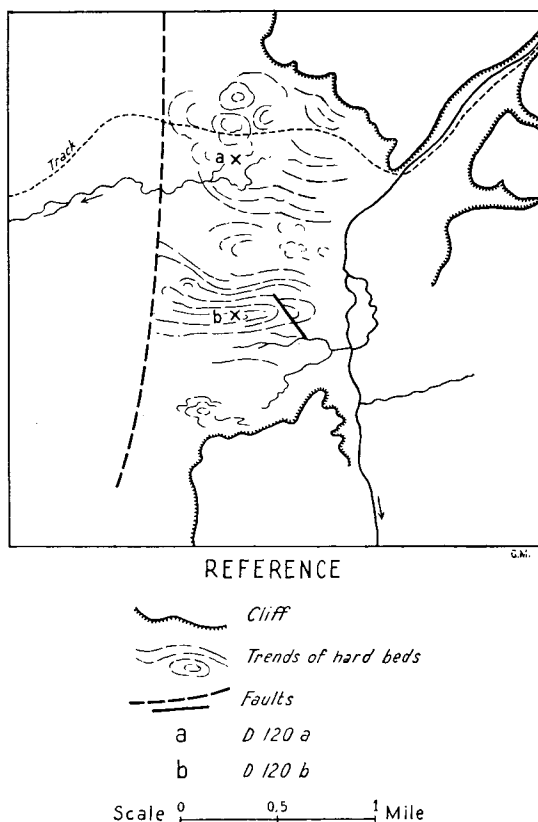


Fig. 3.—Detail of locality D120, Pomegranate Creek area (Text-fig. 2). Adapted from air photograph.

western escarpment. Its altitude is also about 1,000 feet, indicating a lesser altitude for the surface of the limestone, and a broad and shallow basin (syncline).

The D120 outcrop (Text-figs. 3, 4) is a broad erosional recess of the escarpment of the O'Hara Shale. The floor of the recess is a slightly uneven, rubble-covered limestone pediment.



The Upper Cambrian formations of the area are the Pomegranate Limestone, the O'Hara Shale, and the Chatsworth Limestone. The Pomegranate Limestone is a sequence of hard sandy bituminous and dark limestone (ellipsoidal at D120a), interbedded with softer marly beds and intraformational breccias. Light-coloured aphanitic limestone with chert and light-coloured well-laminated silty beds are also present. The visible thickness is about sixty feet, but the base is not exposed.

The contact of the Pomegranate Limestone with the O'Hara Shale is diachronous and climbs in a southerly direction: in the north at locality D133 it is only slightly above the limestone beds with *Glyptagnostus stolidotus*, at locality D132 the contact is above the zone with *Corynexochus plumula*, at locality D119 above *Erixanium sentum*, and at D120b about 15 to 20 feet above the beds with

*Irvingella tropica* and *Agnostotes inconstans*.

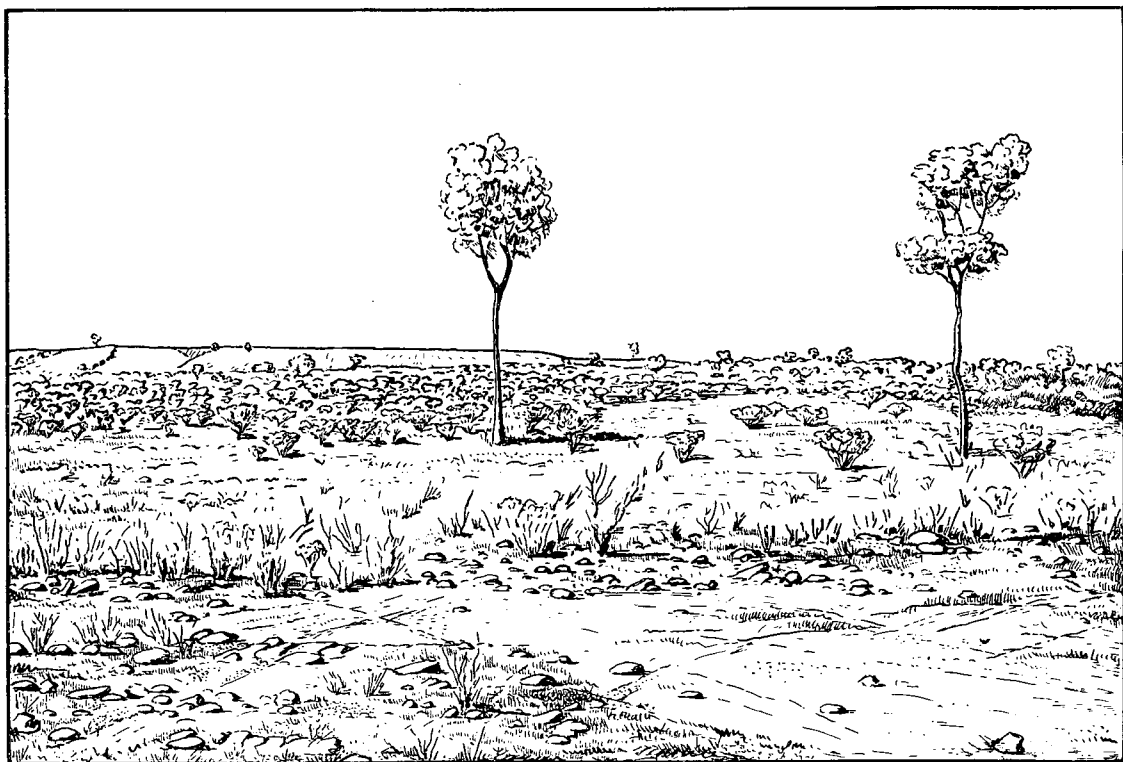


Fig. 4.—Locality D120a (see Text-fig. 3), looking east. Skyline: scarp of southern extension of the Middle plateau (O'Hara Shale); middle: limestone pediment with soil and rubble, and turkey bush scrub; foreground: weathered outcrop of Pomegranate Limestone with *Olenus ogilvei*, *Glyptagnostus reticulatus* and *Agnostus inexpectans*. Ellipsoids of hard limestone scattered on decomposed marly bed.

The O'Hara Shale, of which 100-150 feet is present, is a sequence of well-laminated pink and red shale and siltstone with sandstone and chert interbeds. Its contact with the Chatsworth Limestone is not exposed.

The Chatsworth Limestone within the area consists of light-coloured, non-bituminous fine-grained and sandy grey beds in sequence with coarse-grained calcite beds, and the calcite is mixed brown and colourless. The distribution of fossil fragments shows grading on a small scale, and current lamination is also present. Best outcrops occur around locality D124. North of it another pediment is present with bituminous interbeds and ripple marks, but without fossils. The age of the Chatsworth Limestone is middle to late Upper Cambrian; that part exposed in the Pomegranate Creek area has a Franconian age.

The general structure is that of a mildly deformed sunkland. Within the Pomegranate Limestone small rolls (folds) and faults are common, and the middle plateau is a broad syncline. The Chatsworth Limestone within the area is gently folded along west-north-west axes. The total thickness of early Upper Cambrian and Middle Cambrian rocks in the area exceeds 1300 feet (penetrated in the Pilgrim Creek Bore west of Locality D133).



Fig. 5—Locality D133 (see Text-fig. 2), looking south-east. Dissected escarpment of red O'Hara Shale; rubble-covered limestone pediment; Pomegranate Limestone contains here *Glyptagnostus stolidotus*.

#### *Stratigraphic distribution of localities in the Pomegranate Creek area* *Middle Cambrian*

The late Middle Cambrian *Leiopyge laevigata* Zone is indicated by a cephalon of *Diplagnostus* cf. *planicauda vestgothicus* found (courtesy Mr D. Taylor) at the east side of the fault, south of locality D133. Apparently the Devoncourt Limestone (Cmd) has reached the surface here by the drag of a small fault.

#### *Upper Cambrian*

*Mindyallan*: The rocks of the pre-*stolidotus* Zone in the whole area of the Burke River outlier are unfossiliferous (Öpik, 1961b); they should be present above the

Devoncourt Limestone at the fault south of locality D133. The *Glyptagnostus stolidotus* Zone (with *G. stolidotus*) has been recorded in bituminous limestone at locality D133; above it, and below the O'Hara Shale, a bed of aphanitic limestone may belong to the next, *G. reticulatus*, Zone.

*Idamean*: The *Glyptagnostus reticulatus* Zone is well represented at locality D120a. The nominate species is associated here with *Olenus ogilviei* and *Agnostus inexpectans*. These beds represent the lower part of the Zone; the upper part of the Zone (*Glyptagnostus reticulatus* associated with *Proceratopyge nectans*) is not well represented, but its presence is indicated in intraformational breccias above the *Olenus*-bearing bed. The *Corynexochus plumula* Zone is represented at locality D132; *C. plumula* has not been found, however, at this place. The *Erixanium sentum* zone is well represented at localities D119 (complete specimens of *E. sentum*) and D120b (below the bed with *Irvingella*); furthermore beds of this age underlie the O'Hara Shale in the middle plateau and may extend toward locality D133 as well. The *Agnostotes inconstans*—*Irvingella tropica* Zone has been recorded at a single locality—D120b, on top of a low rise, and above an intraformational breccia and a slumped bed with the fauna of the *Erixanium sentum* Zone. The limestone fragments in the breccia contain *Glyptagnostus reticulatus* and *Proceratopyge*. The slumped bed extends into the matrix of the breccia.

The sequence of zones described above could not be established with certainty from the information obtained in the Pomegranate Creek area, but became apparent with the aid of the Georgina Limestone sequence on Glenormiston. In the Pomegranate Creek area the sequence is obscured by the erratic occurrence of fossiliferous beds, numerous intraformational breccias, and absence of vertical sections. Further complications result from the diachronous relationship of the Pomegranate Limestone with the O'Hara Shale, which could be established and considered only in connexion with the zoning.

It should be noted that the *Agnostotes inconstans*—*Irvingella tropica* Zone is not present on Glenormiston, where sedimentation ceased at the end of *Erixanium sentum* time, but continued in the Burke River region, including the Pomegranate Creek area.

The next higher and younger fauna above the Pomegranate Limestone is found at locality D124 in the Chatsworth Limestone in a rather different lithology. The formations are separated by an intervening and unfossiliferous sequence of an undefinable thickness (some hundreds of feet). The age of the fauna at D124 is according to Öpik (1960, p. 105) lower Franconian or Daizanian, and the *Agnostotes inconstans*—*Irvingella tropica* Zone is basal Franconian: consequently, if a break is present, it is intra-Franconian; the possible break, however, together with the intervening barren sequence may represent a substantial part of that stage, and the qualification 'lower' is therefore questionable.

## PALAEOGEOGRAPHY

The general distribution of land and sea in Upper Cambrian time in Australia has been indicated by Öpik (1956, p. 258). Some details are added now regarding the early Upper Cambrian of Queensland. It is apparent that the Georgina Limestone was deposited at the junction of two seas, the intracontinental seaway in the west, and the eastern sea. Sandstone and dolomite, frequently with calcareous algae, were deposited in the intracontinental seaway, and in places saline beds, now with halite pseudomorphs, indicate evaporitic conditions. Apparently aridity of the air and intense evaporation, along with the intake of marine water by currents, defined the hydrological regime in this seaway, which was confined by lands in the south and north. In the deposits of the junction (Georgina and Mungerebar Limestones), however, calcareous algae are absent, sandy limestone prevails, and the fauna is diversified and abundant. Still, in the Mungerebar sequence, almost barren dolomitic limestone is interbedded and pseudomorphs, apparently of gypsum, occur on some partings in limestone and as inclusions in chert. In the east, in the Burke River Outlier, the general picture is similar to the Georgina River area in early Upper Cambrian time.

A general instability, however, is apparent in the epicontinental area of the junction of the seaways, and in the east is indicated by numerous breaks in the lower Palaeozoic sequence (Öpik, 1960, correlation chart) and rather frequent occurrence of intraformational breccias. These breccias indicate a persistently recurrent seismic activity. The intraformational breccias originated in places where, presumably, selective consolidation hardened some of the limestone beds above or between layers of water-impregnated plastic sediment. Tremors shattered the hard beds, but the plastic mass intruded the layers of fragments; voids remained, of course, and became filled with precipitated calcite. Furthermore, the number of formations in the region is relatively large, and several of them are local and deposited in short intervals of time. This mosaic of rock units, as seen in the maps and in charts, reflects changes in elevation and drainage of the land, and in the configuration of its shores, as well as fluctuations of the marine currents. The stretch of water, however, affected by these events was relatively small, smaller even than the present Timor Sea. Large lowlands were close by, and islands may have existed in the Sun Hill and Sylvester Creek areas (see Öpik, 1960, map, p. 95), and possibly in places that are now concealed under the Cretaceous deposits. The sea was shallow and relatively sheltered, but not everywhere and not at any time equally aerated in its depth, as can be concluded from the unequal distribution of the organic matter in the sequence.

During early Upper Cambrian time communication was maintained with other seas of the globe, as testified by the presence of species and genera of trilobites that are already known in the Baltic, North America, south-eastern Asia, and Argentina, or even distributed universally. The small thickness and mild deformation of the early Upper Cambrian sequence in the Georgina region are noteworthy as compared with the thicknesses and degree of deformation in the west and in the Burke River belt. Furthermore, at the end of the early Upper Cambrian the

Glenormiston area (west and east of the Georgina River) was uplifted and communication between the intracontinental western seaway and the eastern sea was interrupted at this place for almost the whole of the remaining larger part of the Upper Cambrian Epoch. In the late Upper Cambrian marine communication was restored, as seen from a pre-Tremadocian fauna collected in basal beds of the Ninmaroo Formation in the Glenormiston area.

#### THE SEQUENCE OF ENVIRONMENTS IN EARLY UPPER CAMBRIAN TIME

It is convenient to relate depositional environments to formations when these formations are deposited in a strict superpositional order. When, however, a region is viewed which possesses numerous formations in diachronous as well as synchronous relationships, a comprehensive picture is more conveniently attained with the aid of a time scale, as seen in the brief notes below concerning the early Upper Cambrian of Queensland.

The time scale (the sequence of stages and zones) has been already discussed above, and the chart of formations has been published (Öpik, 1960).

##### *End of Middle Cambrian*

At the conclusion of the Middle Cambrian (*Holteria arepo* or *laevigata* III Zone; see Öpik, 1961b) the Devoncourt Limestone and its equivalents were deposited in fully marine conditions in sparsely populated seaways whose sediments have been recorded in the Selwyn Range, and from there south-west to the Glenormiston area, and west to and beyond the Toko Range. Only in the Quita-Mungerebar area were calcareous sandstone with dolomite and limestone interbeds deposited (the rather fossiliferous Steamboat Sandstone) interfingering laterally with the early part of the Mungerebar Limestone. The Steamboat indicates agitated shallow water and abundance of food, whereas in the Mungerebar Limestone at the end of the Middle Cambrian conditions were similar to the Devoncourt Limestone.

##### *Early Upper Cambrian*

Mindyallan faunas (faunas of the pre-*stolidotus* and early *stolidotus* Zones) have been found in Queensland in the Mungerebar Limestone and in diverse formations in several localities in Northern Territory as far as Ellery Creek, about one hundred miles west of Alice Springs. During the same time in Queensland, in the Selwyn Range, aphanitic limestone was deposited in a restricted area in almost evaporitic conditions inimical to life. Barren dolomite interbeds are also present in the Mungerebar Limestone in sequence with barren sandstone and sandy grey limestone; but its bituminous and siliceous interbeds are very fossiliferous, and the fauna is diversified. It can be concluded that in pre-*stolidotus* time discontinuous outposts of the sandstone-dolomite regime of the intracontinental seaway had their greatest extent to the east.

During the time of *Glyptagnostus stolidotus* the influence of the intracontinental seaway retreated westward. In the Selwyn Range O'Hara Shale in sequence with chert and sandstone contains a very fossiliferous bed near its base (localities D6 and D29); at the same time in the Pomegranate Creek area bituminous limestone was deposited. In the De Little Range grey ellipsoidal and marly beds recall conditions seen in the late Middle Cambrian (Devoncourt Limestone) with fossils scattered in the rock and not concentrated in bands. The *stolidotus*-fauna is well represented in the Mungerebar Limestone, which, however, contains an extensive development of dolomitic limestone and aphanitic limestone, as for example at McCabe Knob. In such beds fossils are rare. Around Glenormiston bituminous limestone with chert is conspicuous in sequence with detrital coquinoïd bands and even aphanitic beds; the sequence is fossiliferous throughout and beds with complete trilobites are also present. Fossils of the *G. stolidotus* Zone have been recorded in scattered localities as far west as the Western MacDonnell Ranges in oolitic rocks, but the fauna is depleted; remarkable because of this early age is a oolitic gastropod limestone in the Ross River section.

No fossils of the *Glyptagnostus reticulatus*, *Corynexochus plumula*, and *Erixanium sentum* Zones are known in the Northern Territory: in Idamean time the life-inimical environment apparently became well-established there, although breaks of non-deposition cannot be ruled out definitely. On Glenormiston, however, in the Georgina Limestone, signs of the influence of the regime of the intracontinental seaway are small and confined to interbeds of aphanitic and nodular dolomitic limestone in the west of the area. Diversified marine life populated that part of the Idamean sea. In the Pomegranate Creek area quiet or sheltered conditions prevailed during *Glyptagnostus reticulatus* time, as testified by the preservation of *Olenus ogilviei*, and continued apparently into *Erixanium sentum* time. Of course, numerous intraformational breccias indicate an increase in seismic and tectonic activity. In *Irvingella tropica*—*Agnostotes inconstans* time the sea receded from the junction of the seaways and the intracontinental seaway became isolated for almost the whole of the remaining Upper Cambrian time, as indicated above; but in the east, in the Pomegranate Creek area, sedimentation persisted after the end of the early Upper Cambrian. To conclude, the sequence of the early Upper Cambrian environments indicates co-related geographic fluctuations between marine and well-populated, and inhospitable or even life-inimical facies.

## PALAEOECOLOGICAL OBSERVATIONS

Palaeoecology means extrapolation from ecology, which studies by direct observation existing life and its environments. Palaeoecology becomes rather speculative when applied to remote periods in attempts to explain the habits of completely extinct forms of life. The deduced habits of the extinct animals must be interpreted in terms of their physical environment, and the deduced habits are taken as clues regarding the physical data. Reasoning in circles becomes inevitable when the speculation is carried beyond the broad environmental divisions, which themselves are models by trial and error.

From the discussion of the palaeogeography and of the sequence of environments of the early Upper Cambrian of Queensland one concludes that the physical environment was marine, and within it unfossiliferous and fossiliferous strata were deposited. The unfossiliferous strata are laid down in conditions inimical to life. Toxic, atrophic, or particular physico-chemical, conditions and partial isolation can be assumed to have prevailed in the intracontinental seaway; these reasons, however, are headings for problems which, in the absence of life, are not ecological but physical, inorganic. A special problem is given by barren beds which do not differ lithologically from fossiliferous ones in the same sequence. The reverse formulation of the problem—why in generally barren or almost barren sequences scattered fossiliferous bands occur—provides for no complete answer, and some examples from the Cambrian of Queensland have been discussed earlier (Öpik, 1961b).

The palaeoecological observations that are discussed below refer to fossiliferous beds in the first place. The early Upper Cambrian of Queensland bears a diversified and abundant fauna. Considering its Cambrian age it can be regarded as being rich indeed. The total number of known forms described by Whitehouse and supplemented in the present paper is about fifty. It is, however, a selection only: the large trilobite fauna of the pre-*stolidotus* Zone has not been touched as yet, nor has the greater part of the *stolidotus* fauna; about half of the trilobites in the collections from the *Erixanium sentum* Zone should be known by now; the total number of species in the early Upper Cambrian sequence is estimated at about 220-250 species. Brachiopods, gastropods, sponges, and conodonts should increase the figure substantially. It is a fauna that lived in normal marine euphotic conditions.

Four localities (W20, D120a, D119, and W47) from which fossils are now described have yielded complete specimens of trilobites, and in each case the reasons for the exceptional preservation are different from the others.

At W20, in a sequence of grey impure limestone and bituminous limestone with chert and with shale partings, complete specimens of six species of diverse genera have been recovered. All these specimens occur on thin shale partings within a limestone only a few feet thick and the embedding is dorsum up, as well as dorsum down. Some of them are undisturbed exuviae and others, with all parts present, are bodies of dead animals. In limestone below and above the partings the same forms occur as dismembered shields. It is apparent (1) that the depth of water remained unchanged for the time interval of the few feet of the sediment; (2) the mode of embedding (stable—dorsum up, and unstable—dorsum down) indicates quiet water; (3) the shale partings, a fracture of an inch thick, represent each a sudden and brief cessation of carbonate precipitation; (4) in the limestone the distribution of sand and fossil fragments discloses in places a mild cross-lamination, and, consequently, mildly agitated water. It can be concluded that a recurrent decrease in surface evaporation, or even increased intake of fresh water by abundant rain, may have stopped the precipitation of lime without stopping the

settling of the impurities (shale); the glueing effect of the shale-to-be protected some of the exuviae and dead bodies from being dismembered by the motion of the water. It should be noted that most of the fossils on the partings are still dismembered exuviae. Generally speaking, ecologically no substantial changes are recorded on the shale partings when compared with the fossil content of the enclosing limestone beds. The limestone is bituminous, but the diversity of its fossils indicates an absence of an anaerobic regime in the bottom water, though anaerobic conditions in the sediment itself can be assumed.

At locality D120a (Text-figs. 2 and 3) a fauna of the *Glyptagnostus reticulatus* Zone occurs. Only three trilobites, *Glyptagnostus reticulatus*, *Agnostus inexpectans*, and *Olenus ogilviei*, are present. The agnostid species are universal, and so is the genus *Olenus*. The universality indicates a pelagic mode of life, and at the same site benthonic forms are absent. It stands to reason, however, that pelagic animals—the dwellers of the surface waters—are not confined to places without benthonic life and are not influenced by a Euxinic or any other regime at depth.

*Olenus ogilviei* occurs mostly as complete specimens with the free cheeks in their original position, representing dead bodies and not exuviae. In the absence of motion and predators on the bottom of the sea the bodies remained undismembered and were embedded as whole tests. The Pomegranate Limestone is bituminous, and apparently the contact of the anaerobic bottom water and the oxygen-bearing water remained above the floor of the sea. From a bedding plane in a thin marly interbed a piece (CPC 4307) was recovered with about a dozen complete specimens of *Olenus ogilviei*—perhaps a swarm that perished at once. Presumably, for reasons unknown, the swarm ventured to the floor of the sea at an exceptionally poisonous place and perished there. It appears that at this particular place (D120a) and time the subsidence of the trough was relatively rapid and was not compensated for by deposition; a local closed depression ensued, stagnant without sufficient circulation.

Recently Henningsmoen (1957, p. 62-66, and 79-82) has suggested that the Scandinavian olenid sea was 'rather shallow and the bottom waters were stagnant apparently right up to the shore line', and this is borne out by the large amount of organic matter in the sediment. He also assumes that Olenidae were, probably, adapted to stagnant water and that they were 'capable of sojourning on the foul bottom'. It appears, however, that the 'enormous numbers' of olenids found in certain beds represent swarms that perished because they were incapable of escaping from the water that reached from time to time lethal levels of stagnation.

At locality D119, in the Pomegranate Limestone, in a single bed, numerous specimens of *Erixanium sentum* have been found. The rock is an almost non-bituminous, laminated and fissile, light grey impure sandy and marly limestone, an interbed in a sequence of black (bituminous) and non-bituminous aphanitic limestone below the O'Hara Shale. In this bed (Pl. 9) the specimens of *Erixanium* are complete; even the hypostomata are in their proper position, or only slightly displaced. This preservation indicates that these fossils are dead bodies and not



exuviae. They rest in equal numbers dorsum-up and dorsum-down, indicating motionless water; the swarm consists of adult individuals of diverse size.

It appears that the whole swarm died quickly and at once on the floor of the sea, or near it. The dorsum-up specimens died probably on the floor, whereas the dorsum-down ones died floating above the ground and settled on it in a free fall with the convex side down.

Another explanation is also possible that requires no assumption of a swarm consisting of adults of different age groups. It is possible that single specimens were trapped when crossing accidentally and at different times an extremely poisonous place, and died instantly before reaching the healthier waters. The rock is, however, non-bituminous, and without pyrite, and there is no apparent reason to assume anaerobic conditions similar to locality D120a. Furthermore, a bed of bituminous limestone in the same sequence contains brachiopods and fragments of cystids which are benthonic.

At locality W47 in the Georgina Limestone (grey and blue-grey, sandy) all beds are fossiliferous; a very fossiliferous band of ellipsoidal limestone coincides with a bedding plane with a coquinoid layer of dismembered parts of trilobites. Complete specimens of *Proceratopyge*, with their free cheeks preserved, are also present in the coquinoid. It appears that these complete specimens arrived and settled to die on the bedding plane after the formation of the coquinoid, when the motion of water ceased for a short while. Rapid burial prevented the subsequent dismembering of these stray specimens of *Proceratopyge*. Complete specimens are also found in the ellipsoids some inches above the accumulation of fragments. No special significance can be attributed to this mode of preservation of complete trilobite tests because the abundance of fossils should include for some of them the chance of preservation as undisturbed exuviae and even dead bodies. The general mode of preservation indicates the absence of transport, whose action would totally prevent the preservation of complete tests.

The trilobites in the Georgina Limestone are generally dismembered; broken fragments are relatively rare, but worn rounded fragments are totally absent. Fragments have not been sorted by size or by shape, and free cheeks, cranidia, and pygidia of one or several species are found in close association together. It appears that there was time available for dismembering of the exuviae, but that they were not transported from the moulting sites: the distribution of fossils and the mode of their embedding reflects the true biocoenoses that existed in early Upper Cambrian time.

#### LIST OF EARLY UPPER CAMBRIAN FOSSILS OF QUEENSLAND

This list contains only the names of published fossils; names which have been only mentioned in stratigraphic papers are not included. The abbreviated annotations should be read as follows: W. = Whitehouse (1936, 1939); Ö. = Öpik (this paper); asterisk (\*) in front of a name indicates fossils which are re-described in the present paper; revised stratigraphic data are given in brackets [ ]; M. stands for

Mindyallan Stage; Id.—for Idamean Stage; the numbers 2 to 8 indicate zones as listed earlier; query (?) indicates inconclusive stratigraphic position of fossils for which new information is not yet available.

#### *Agnostids*

- Agnostardis amplinatis* Ö. [M., 3].  
*Agnostotes inconstans* Ö. [Id., 8].  
*Agnostus inexpectans* Kobayashi; Ö. [Id., 4, 5, 6].  
*Aspidagnostus parvatus* W. [Id., ?4].  
*Discagnostus spectator* Ö. [M, 3].  
*Glyptagnostus reticulatus* (Angelin), Ö. [Id., 4, 5].  
*Glyptagnostus stolidotus* Ö. [M., 3].  
\**Glyptagnostus toreuma* W. [Id., 5, = *reticulatus*].  
*Homagnostus* cf. *obesus* (Belt), W. [Id., 7].  
*Pseudagnostus* cf. *cyclopyge* (Tullberg), W. [Id., 5].  
*Pseudagnostus nuperus* W. [M? Id.].  
*Pseudagnostus vastulus* W. [Id., 5, 6, 7; 8?].

#### *Polymerid trilobites*

- ?*Aphelaspis* sp. B, Ö. [Id., 8].  
*Asilluchus nanus* Ö. [Id., 7].  
*Charchaia erugata* W. [Id., 7].  
*Charchaia* spp. W. [Id., 7].  
*Corynexochus plumula* W. [Id., 6, rare in lower 7].  
*Elrathiella plebeia* W. [M?].  
*Elrathiella* sp., W. [?].  
*Ellipsocephalus* (?) sp., W. [Id., 7].  
*Erixanium alienum* Ö. [Id., 7].  
*Erixanium sentum* Ö. [Id., 7].  
*Erixanium strabum* Ö. [Id., 7 lower].  
*Eugonocare propinquum* W. [Id., 7].  
*Eugonocare tessellatum* W. [Id., 5, 6, 7].  
*Eugonocare* sp. indet., W. [Id., 5].  
*Hercantyx rudis* Ö. [Id., 8].  
*Idamea superstes* W. [Id., 6?].  
*Idamea venusta* [Id., 6, 7].  
*Irvingella tropica* Ö. [Id., 8].  
*Olenus ogilviei* Ö. [Id., 4].  
?*Olenus* sp. A, Ö. [Id., 7].  
*Olenus* sp., W. [Id., 5].  
*Proceratopyge* cf. *chuhsiensis* Lu; Ö. [Id., 8].  
\**Proceratopyge lata* W. [Id., 7, 8].  
*Proceratopyge nectans* W. [Id., 5].  
*Proceratopyge polita* W. [Id., 7?].

*Proceratopyge rutellum* W. [Id., 7].  
*Protemnites elegans* W. [?].  
 \**Rhodonaspis longula* W. [M., 3].  
*Rhodonaspis prosecta* W. [?].  
*Rhodonaspis* sp. W. [?].  
*Stigmatoa diloma* Ö. [Id., 7].  
*Stigmatoa sidonia* Ö. [Id., 8].  
*Stigmatoa silex* Ö. [Id., 6? or 7?].  
*Stigmatoa tysoni* Ö. [Id., 7].  
*Talbotinella notulata* Ö. [M., 3].  
*Trilobite* sp. C, Ö. [Id., 8].  
                     *Crustacea Bradoriida*  
*Beyrichonidae?* sp. D, Ö. [Id., 8].  
                     *Hydroida*  
*Hydroida*, sp. indet., Ö. [Id., 4].

## AGNOSTID TRILOBITES

Collections from the early Upper Cambrian of north-western Queensland contain an abundance of agnostids with some described and many undescribed species and even genera. A small selection from this material is described here, to present some forms of an obvious stratigraphic interest, as for example *Agnostus inexpectans* Kobayashi, and taxonomic significance. Furthermore, the material is exploited to study the morphology and organization of agnostids and to elucidate aspects of their suprageneric classification. Special attention is paid to the genera of the Glyptagnostidae, of which, however, some are reserved for future study.

### *Morphology and terminology*

The morphology, terminology, and organization of agnostids have been already discussed in two papers (Öpik, 1961a; 1961b) and the discussion is continued here. In the diagrammatic Text-figures 6-13 the annotations (lettering) are the same as applied previously; to facilitate the reading of the narrative text, an explanation of terms is given here in alphabetical order.

The explanation of terms that follows refers to new and old concepts, but is incomplete, supplementing the previous papers, and especially the 'Comments and Explanatory Notes' in Öpik (1961a). A summary of agnostid terminology with letter symbols of a uniform system to be used in any explanatory diagram of agnostids can be visualized, but is as yet premature: the suitability of some of the terms can be questioned; probably a diversification in the terminology and concepts is needed, and new terms will be requested in the course of the study. No concise and agreed terminology of agnostids exists in the literature—an advantage in the sense that a uniform and organized approach is as yet not impossible.

*Accessory furrows:* A pair of diagonal furrows in the pygidium of *Pseudagnostus* arising at the posterolateral corners of the second axial lobe and directed abaxially and rearward. These furrows are not axial furrows but major scrobicules (parietal septa of pygidial alimentary glands); see under *Pseudagnostus* cf. *vastulus*.

*Articulating device*: A phrase to denote the combination of the articulating half-ring, articulating furrow, and axial recess in agnostids. In the glyptagnostid articulating device the half-ring is a narrow arched ridge, and the furrow is a wide elliptical depression; in the more common articulating device the half-ring is a segment of a circle and the furrow is narrow.

*Articulating furrow*: See *Articulating device*.

*Articulating half-ring*: See *Articulating device*.

*Axial bar*: The convex floor of the articulating furrow in the form of a median segment of a cylinder, between the muscle spots. It is in line with the axial node and the intranotular axis.

*Axial furrows*: The meaning of the term is well established; it denotes the primary and fundamental furrows dividing the trilobite body into an axial lobe and a pair of pleural lobes. The qualifying adjective 'axial' may be misleading, because axially arranged furrows may be present that are not the 'axial furrows'. In all trilobites apodemes (appendiferi) and muscle attachments are placed adaxially from the axial furrows. An alternative term is 'dorsal furrows'. See *notular furrow* and *accessory furrows*.

*Caeca, reticulate*: Reticulation of caeca is indicated by confluent external rugae and short disconnected scrobicules.

*Deuterolobe*: A deuterolobe is a composite pygidial lobe consisting of confluent pleural and axial elements; the deuterolobe (pseudolobe) of *Pseudagnostus* is a usually tumid lobe in the rear of the pygidium, surrounded by the marginal furrow, the accessory furrows, and the second axial lobe. Externally uniform, it comprises the posterior part of the axis and of the pleural lobes. Howell in Harrington et al. (1959) regards it as the rear lobe of the pygidial axis. See *Endlobe*.

*Diverticular duct*: A major intestinal appendage, or a duct leading from or into an ingluvial sac. It may be represented externally as a ruga or as an interruption of a furrow (scrobicule). In *Pseudagnostus* cf. *vastulus* the accessory furrows (scrobicules) are interrupted by a pair of such ducts.

*Endlobe*: Jaekel in 1909 applied the term 'Endlobus' in the diagnosis of his new genus *Pseudagnostus*; for the same structure Kobayashi (1939) suggested the word pseudolobe; see *Deuterolobe*.

*Extranotular axis*: The two longitudinal parts of the axial lobe situated between the axial furrows and the notular lines. In the absence of axial furrows the extranotular parts of the axial lobe may be mistaken for parts of the pleural lobes, and the notular lines regarded as the 'true axial furrows'.

*Facet*: Agnostids with facets on the pygidium have been known since Barrande, but the distribution of facets among the genera and species has not been explored, and their taxonomic value is unknown.

*Fulcral point and geniculation*: These can be distinguished in unflattened specimens, and belong to the fundamentals of the organization of trilobites.

*Genal tubercles*: An objective designation of two pairs of lateral reniform tubercles on the cheeks of *Discagnostus*; they are interpretable as ocular tubercles.

*Intranotular axis*: The main, median part of the pygidial axial lobe between the notular lines, or between the two lines of notulae (muscle scars or muscle spots). The notular lines and the extranotular axis belong also to the axial lobe. Other terms are 'elliptical ring' (Troedsson, 1937), and 'lancetoid field' (Ivshin, 1956; Rosova, 1960).

*Muscle scars*: Relatively large, but shallow, parietal depressions in the trilobite test that served as muscle attachments. They are designated muscle spots when visible as coloration of the test, or when distinguished by their degree of translucency from other parts of the test. See *Notula*.

*Notula, -ae*: Small but well defined subcircular muscle-scars (or appendiferi) which may occur as external or parietal pits, and may be included in an area occupied by a muscle scar. Muscle scars are much larger than notulae, and sometimes composite. Notulae, like muscle scars, never occur in the axial furrows; they are clearly separated, and placed adaxially, from them. See *notular line*, *notular furrow*, *muscle scars*.

*Notular furrows*: The longitudinal ('axial') furrows developed between the notulae; or, in the absence of external manifestation of the notulae, occupying the position of the notular lines. These furrows, or the notular lines, are intra-axial and divide the axial lobe into a median (intranotular) and a pair of extranotular parts. In the pygidium of *Lotagnostus* the axis is tripartite, which is effected by deep axial and notular furrows.

*Notular lines*: The two longitudinal lines of notulae converging at the terminal node in the pygidial axial lobe. The notular lines, the notulae, and the notular furrows lie within the axial lobe and cannot be regarded as the limits of that lobe; the limits are the axial furrows.

*Pseudofurrows*: A term that has been used in the literature as a replacement of the phrase 'accessory furrows' of *Pseudagnostus*. The origin of the term has not been explained; it obviously does not carry the meaning it purports to have—'false furrows'—but could be a contraction of some phrase like 'pseudoaxial furrows' or 'furrows characteristic for the pygidium of *Pseudagnostus*'. In the absence of appropriate terms 'pseudofurrows' is a sufficiently intelligible term, but 'accessory furrows' is preferable. The pseudo-furrows are a particular pair of scrobicules in *Pseudagnostus*, but can be identified also in several other glyptagnostids. See also *True axial furrows*.

*Pseudolobe*: The meaning is explained under *deuterolobe*. The literal translation is 'false lobe' but originally it was meant as an allusion to *Pseudagnostus*, or the brief form of the phrase 'false axial lobe'; it is, however, morphologically a regular lobe and contains the axial lobe as well. See also *Endlobe* and *True axial lobe*.

*Scalloped, scallops*: These words are used in their vernacular meaning, to avoid the already abused terms 'lobate' and 'lobes', which are used to designate regular structures in trilobites, and in derived terms (pseudolobe, bilobed, bilobate, etc.). The term scalloped is used here to indicate that edges of some of the furrows are, against expectations, not straight but 'lobate'.

*Shoulders*: In the agnostid pygidium the anterior border of the pleural lobes, separated by the shoulder or anteromarginal furrows, and geniculated at the fulcral points.

*Shoulder furrows*: Furrows separating the shoulders from the rest of the pleural lobes in an agnostid pygidium. They are possibly, but not certainly, homologous to the anterior pygidial pleural furrows in polymerid trilobites. In most agnostids the shoulder furrows form a unit with the marginal furrow, but in some they extend straight to the margin. They are never effaced, not even in *Delagnostus*, which has the most effaced pygidium.

*True axial furrows, axial lobe, axis*: The designation 'true' has been used in the literature to emphasize the distinction from the 'false' pseudofurrows and pseudolobe; it is less needed if the 'pseudo' terms are replaced by accessory furrows and deuterolobe, which are also 'true', and not 'false', but in their own manner.

### *Suprageneric classification*

Of the genera described in this paper only *Agnostus* is represented in the Middle Cambrian; it appeared first in the latest zones of the Middle Cambrian, and the Agnostinae, persisting into the Ordovician, underwent a considerable diversification. It is apparent that the passage from the Middle Cambrian to the Upper Cambrian is readily recognizable in the change in composition of the agnostid faunas, and the agnostid stock itself passed through a crisis which is reflected in the rapid extinction of old, and diversification of new, genera. In Queensland the most critical time was the passage from the Mindyallan to the Idamean.

On a suprageneric level, however, a continuity is evident between the Upper Cambrian and Middle Cambrian agnostids. This continuity should not be concealed under the veil of family and higher ranking categories, and can be revealed with the aid of a reasonable application of subfamilial nomenclature.

The system of agnostids proposed by Howell in Harrington et al. (1959) has dispensed with the subfamilial categories and resorts to an overall family nomenclature. This procedure has the merit of an apparent simplicity, because the families stand as disconnected equals and are separated by large gaps that are inevitable between categories of high denomination. Nevertheless, even some of the genera can be transferred from one family to another without inflicting changes in the family concepts, which is an indication that many of the interfamilial gaps are in reality quite narrow. A more flexible system can be achieved with the application of subfamilial categories, which also would remain equals within a large family but with the effect that intrafamilial re-arrangements would not necessarily involve the whole system of the agnostids.

The preserved record of agnostids is still incomplete and cannot be translated into an overall and unambiguous phylogenetic arrangement, although this is possible within some of the subfamilies. Hence, the continuity of the Upper and Middle Cambrian agnostids is evident, but definite phylogenetic trends that should be based on sequences of species and genera cannot be constructed as yet. The discussions that follow below under the headings of the genera indicate that the glyptagnostids and pseudagnostids, being morphologically related among themselves, are similarly related to the ptychagnostids and diplagnostids respectively.

At this point any deductions regarding the affiliation of the taxa can be omitted and consideration given to the particular characters instead. For example, an articulating device similar to that of *Glyptagnostus* and *Pseudagnostus* is present in the Middle Cambrian *Diplagnostus*, beginning with its first appearance in Australia, but is unknown in the ptychagnostids and peronopsids; an excessively wide border occurs in diplagnostids, and in all species of *Pseudagnostus*; in the Middle Cambrian rugose pygidial flanks are known only in the diplagnostid *Oidalagnostus*, but not in the ptychagnostids, and are characteristic for the Upper Cambrian glyptagnostids and pseudagnostids. Any assumption as regards a monophyletic or polyphyletic origin of these characters will remain speculative;

the Middle Cambrian ptychagnostids and diplagnostids are contemporaneous, and distinct as regards the above mentioned as well as other characters, offering no answer to the puzzle of *Glyptagnostus*, which shares characters with *Diplagnostus* and *Ptychagnostus*.

For the completeness of this review the Middle Cambrian *Tomagnostus* should be also mentioned. Its morphology is well known (Westergaard, 1946); it has been placed in Diplagnostidae, in Peronopsidae, and in Agnostidae (subfam. Tomagnostinae Kobayashi), and the various classifications are not the result of an imperfect preservation, but of differences in evaluation of characters. It can be left with the Diplagnostidae, because it has the collar-like duplication of the posterior pygidial border, but its border is narrow, its axial lobe is ptychagnostid, and so are the cephalic rugae and the ordinary articulating device. *Tomagnostus* remains remote in time from the Upper Cambrian *Glyptagnostus*, but can be interpreted in two different ways: either 1) that characters of *Tomagnostus* which are assumed to be of a familial significance are, in effect, minor, and can occur in combination with others, independently in different stocks; or 2) that *Tomagnostus* possesses an incomplete set of 'ancestral' characters, whereas other agnostids retained only single items of the set, and that the fundamental diversification of the agnostids antedates the appearance of *Tomagnostus*.

Unattainable as yet is a final and unambiguous suprageneric classification of agnostids that would reflect at once the morphological diversification and the deducible or deduced phylogenetic relationships of the genera. But the morphology provides for some objectivity, and leads to systems which can be used as patterns for an organized and intelligent presentation of observations, and even interpretations. Such a system may include optional categories, or may be replaced, according to the treated material, by corollaries, but without nomenclatorial contradictions and simultaneous synonyms.

Agnostids described and mentioned in the present paper are classified as follows:

Superfamily Agnostacea (Agnostidea) of the Suborder Agnostina Salter.

Family Diplagnostidae (mentioned).

Family Agnostidae.

Subfamily Agnostinae (*Agnostus inexpectans*).

Family Glyptagnostidae.

Subfamily Ptychagnostinae (mentioned).

Subfamily Glyptagnostinae (*Glyptagnostus*, *Agnostardis*, *Agnostotes*, *Pseudagnostus*).

Subfamily Pseudagnostinae (optional).

Family Discagnostidae fam. nov.

This classification represents a continuation of the classification of Middle Cambrian agnostids (Öpik, 1961b, p. 54), but with some rearrangements: the Glyptagnostidae Whitehouse, 1936, are restored in their original familial rank and

include the subfamily Ptychagnostinae Kobayashi, 1939, not acknowledged previously. Furthermore, the independence of the Pseudagnostidae is not accepted, because they can be treated conveniently as a subfamily of the Glyptagnostidae, or even simply included in the Glyptagnostinae.

Alternative classification I: The Ptychagnostinae can be transferred to the Agnostidae; the concept of this family will remain unchanged, but the Glyptagnostidae will include only genera with rugose pygidia.

Alternative classification II: The Diplagnostidae, Pseudagnostidae, and Glyptagnostidae can be regarded as subfamilies of a large family; a new familial concept must be compiled, for the purpose of which a material restudy of *Diplagnostus*, *Linguagnostus*, *Oidalagnostus*, *Oedorhachis*, *Baltagnostus*, *Proagnostus*, and *Tomagnostus* is needed.

Alternative classification III: All families and subfamilies that are mentioned above become subfamilies of the Agnostidae. This classification is in contrast with the Howell's in which only family names are employed. Alternative III serves all practical needs in describing new species of known genera referable 'to the nearest subfamily', which in turn, is in no need of a family reference. Furthermore, rearrangements in the phylogenetic order of the subfamilies can be undertaken without introducing 'phylogenetic taxa' of higher rank, and the criterion of the presence or absence of pygidial caeca will remain a subject of further inquiry. The presence of rugae is certainly observable, but their absence is not yet a definite proof that ramified deep-seated caeca were absent in the pygidium altogether. Even the structure of the pygidial flanks of *Agnostus pisiformis* itself is open to query: Henningsmoen (1958, p. 181, pl. 5, figs. 7, 8) illustrates two pygidia of *A. pisiformis* with 'reticulate or pitted' pleural lobes that may indicate the presence of a caecal system without major trunks and without regular bifurcation, and different from *Glyptagnostus*.

Family AGNOSTIDAE Salter

Subfamily AGNOSTINAE

Genus AGNOSTUS Brongniart

AGNOSTUS INEXPECTANS Kobayashi, 1938

(Pl. 2, figs. 10-13; Text-fig. 6.)

A. R. Palmer (personal communication) has revised the original material of *A. inexpectans*, established its presence in Nevada and Alabama, and recognized it in our material. Thus, *Agnostus inexpectans* becomes an important species in the intercontinental correlation of the early Upper Cambrian and in its palaeogeography.

Previously the Australian specimens (Öpik, 1956, p. 23) were referred to as *Homagnostus* because of the relatively wide pygidial axis with a tripartite anterior lobe. In *Agnostus pisiformis*, which is the type, and the only properly known, species of its genus, the axis is relatively narrow and the tripartition is obscure. Henningsmoen (1958, pl. 5, fig. 2), however, has illustrated a pygidium with a wider axis similar to *inexpectans*, but without any tripartition. I concur with Henningsmoen in regarding *Homagnostus* as a subgenus of *Agnostus*.



*Description:* The border in both shields is convex and narrow, the marginal furrows are deep narrow channels. The pleural lobes are slightly convex and almost smooth. Faint radiating wrinkles, however, are present along the outer slope of the cheeks in the cephalon. The convexity of the shields including the axial lobes

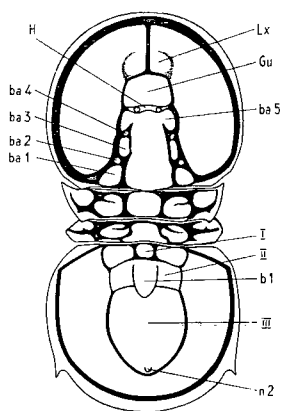


Fig. 6.—*Agnostus inexpectans*, diagram from Pl. 2, fig. 10-13. Cephalon: ba1—basal lobes; ba2—ba5—lateral lobes; Gu—anterior glabellar lobe; H—transverse glabellar furrow with muscle scars; Lx—lateral preglabellar lobes. Pygidium: I—anterior axial segment (tripartite); II—middle axial segment; III—posterior axial lobe; b1—axial node; n2—terminal axial node.

cannot be accurately established in our specimen, which is flattened. The glabella is elevated above the cheeks and its height rises evenly toward the rear. The pygidial axis is highest about the middle of its posterior lobe.

The frontal lobe of the glabella is pentagonal, and angular in front. The posterior portion of the glabella is flanked by five pairs of lateral lobes; the posterior, basal, lobes are triangular to pentagonal; in front of them is a pair of small rounded depressed lobes; a pair of elongate almost rectangular lobes follow (ba 3), which are separated from the glabella by narrow and shallow longitudinal furrows; the lobes of the fourth pair are again rounded, small, and depressed. The anterior pair of lobes (ba 5) remains connected with the glabella. The described lateral glabellar lobes are less well developed in other specimens from the Georgina Limestone.

The transverse furrow is relatively deep, with a distinct floor and a pair of muscle spots. This furrow has the appearance of an articulating intersegmental furrow and its floor is, probably, the vestige of the articulating half-ring.

A peculiarity is a pair of large but very flat lobes (Lx) in front of the glabella, on both sides of the posterior end of the median preglabellar furrow. These lobes are not seen in all specimens. Similar indistinct lobes occur sporadically also in *Agnostus pisiformis*, as illustrated, for example, by Henningsmoen (1958, pl. 5, fig. 5). Similar lateral glabellar lobes and the 'preglabellar' lobes are discernible in many specimens of *Glyptagnostus reticulatus* (Angelin).

In the pygidium the anterior segment of the axis (I) is tripartite; the middle segment (II) bears a stout node (b 1) that becomes posteriorly a blunt spine. The posterior axial lobe (III), which consists of several segments, is suboval and bluntly pointed in the rear. A terminal node forms the tip of the pygidial axis.

The cephalic (genal) spines are short and slightly curved; the pygidium bears a pair of short marginal spines.

The two segments of the thorax show no specific characters of significance, especially because in most of the related species the thorax is unknown. *Agnostus pisiformis*, *Agnostus (Homagnostus) obesus* and *A. inexpectans* have almost identical segments. As usual in agnostids (see Öpik, 1961a, b), the anterior segment of the thorax displays a perfect 'occipital similarity': the median node corresponds to the glabella, the lateral nodes are the basal lobes; the pleural furrow is the posterior section of the cephalic marginal furrow, in front of which is a portion of the cheek, and in the rear the marginal spine. It can be seen from Text-figure 6 that the posterior segment displays a 'pygidial similarity' and repeats the structure of the anterior segment of the pygidium.

*Comment on illustrated material:* The large specimen Plate 2, figures 10-12 (CPC 4260), locality D120a, is 6.6 mm. long and the only known complete specimen of *A. inexpectans*; the small lateral glabellar lobes are well visible, although they cannot be distinguished in other Australian specimens. The cephalon Plate 2, figure 13 (CPC 4261), locality D126 (De Little Range), is 2.4 mm long; the median part of its glabella, and its two pairs of larger lateral lobes are rather prominent, but the two pairs of smaller lobes are not discernible.

To conclude, *A. inexpectans* is a species with a subangular, pentagonal anterior glabellar lobe and with four pairs of isolated lateral glabellar lobes that are alternately large and small; the small lobes may be absent, or inconspicuous. The pygidial axis is relatively long and bluntly pointed, and its anterior segment is tripartite.

*Occurrence and age:* *Agnostus inexpectans* occurs in the Pomegranate Limestone at locality D120a (see Text-figs. 2 and 3) in association with *Glyptagnostus reticulatus* and *Olenus ogilviei*, and at locality D126 on Wills Creek, at the foot of the De Little Range, in association with *Glyptagnostus reticulatus*, *Eugonocare* sp., *Clavagnostus (Aspidagnostus)*, and *Blountia*. The age of these finds is early Upper Cambrian (Idamean), Zone of *Glyptagnostus reticulatus*. *A. inexpectans* is also fairly common in the Georgina Limestone, where it is associated with *Glyptagnostus reticulatus* and extends upwards into the Zone with *Corynexochus plumula*.

Family GLYPTAGNOSTIDAE Whitehouse, 1936  
(Synonym: Hastagnostidae Howell, 1937.)

*Glyptagnostus* Whitehouse, 1936, is the type genus of the family, and its organization was discussed in some detail by Öpik (1961a). The familial nomenclature was emended by Öpik (1961b). A. R. Palmer (pers. comm., not yet published) is describing the American glyptagnostids.

Within the family two groups of genera can be distinguished:

1) The group whose species have non-scröbiculate pygidia. It contains seven genera (this number is subjective), four of which already have been used to derive subfamilial names. Of these genera *Hastagnostus* Howell should be transferred to the Agnostinae (see Öpik, 1961b) and the rest could be referred to one of the three following subfamily names (Kobayashi, 1939): Leiopyginae, Triplagnostinae, and Ptychagnostinae. *Culipagnostus* Rusconi (see Harrington et al., 1959) has been excluded already by Poulsen (1960), and identified as a *Clavagnostus*.

2) The group that contains forms in which caecal scröbiculation has been established in the pygidia. These are *Glyptagnostus* Whitehouse, *Lotagnostus* Whitehouse, *Pseudagnostus* Jaekel, and the new genera *Agnostardis* and *Agnostotes*. These constitute the subfamily Glyptagnostinae.

A subfamily name for the first group is needed and it should be selected from the three synonyms (Leiopyginae, Triplagnostinae and Ptychagnostinae) which were published simultaneously. I select the name Ptychagnostinae Kobayashi, 1939, because no doubt exists as regards the validity and meaning of its type genus *Ptychagnostus*, when compared with the controversy as regards *Leiopyge* and *Triplagnostus*; hence, this nomenclature problem need not be solved by the application of page priority. The invocation of the page priority was suggested earlier (Öpik, 1961b) as a possibility, but a binding decision was reserved.

When a further splitting of the Glyptagnostinae becomes desirable, two groups of genera are already indicated: 1) *Glyptagnostus* and *Agnostardis*, which are distinguished by the invasion of the pygidial axial area by caeca, and 2) *Pseudagnostus*, *Agnostotes*, and *Lotagnostus*, in which the pygidial axis remains morphologically or only anatomically intact; in this group *Lotagnostus* is the most conservative form, and *Agnostotes* remains intermediate between the other two and *Glyptagnostus*. It is even possible to assign these five genera to a separate subfamily each, but without any particular gain in taxonomy.

*Pseudagnostus* has been regarded hitherto as representing an independent family, or subfamily; this familial taxon (Pseudagnostidae or Pseudagnostinae) is regarded here as a subjective synonym of the Glyptagnostinae, but the name can be retained without any difficulty to designate forms with a morphologically developed deuterolobe. Further detail study of late Middle Cambrian and Upper Cambrian agnostids may necessitate, of course, modifications in the familial taxonomy of the glyptagnostids.

#### Genus GLYPTAGNOSTUS Whitehouse, 1936

##### GLYPTAGNOSTUS RETICULATUS (Angelin)

(Plate 2, figs. 6-9; Text-fig. 7.)

The taxonomy and organization of *Glyptagnostus reticulatus* have been discussed recently by Öpik (1961a) on the basis of Australian uncompressed specimens in limestone. The new material of flattened specimens facilitates a comparison with Australian (Tasmanian) and overseas occurrences in shale.

The cephalon, Plate 2, figure 6 (CPC 4257), differs little from the lectotype (Westergaard, 1947, pl. 1, fig. 2) of the species. The only difference seems to be the apparent absence of the median preglabellar furrow in our specimen. However, a median partitional line in front of the glabella, wriggling between the blisters, is still in the position of the equally wriggly furrow in the lectotype.

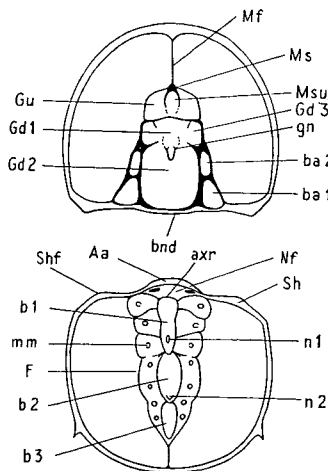


Fig. 7.—*Glyptagnostus reticulatus*. diagram from Pl. 2, figs. 6 and 7. Cephalon: ba1—basal lobe; ba2—lateral glabellar lobe (probably the same as ba3 in Text-fig. 6); Gd1—anterior part, and Gd2—rear part of posterior lobe of glabella; Gn—glabellar node; Gu—anterior glabellar lobe; Mf—preglabellar median furrow; Ms—frontal sulcus; Msu—depressed extension of frontal sulcus. Pygidium: Aa—articulating half-ring; axr—axial recess; b1—anterior bulb; b2—middle bulb; b3—posterior bulb; F—dorsal (axial) furrow; mm—notulae (muscle spots); n1—tip of axial spine (node); n2—terminal axial node; Nf—articulating furrow; Sh—shoulder, geniculate; Shf—shoulder furrow. Aa, Nf, and axr together form the articulating device.

The pygidia Plate 2, figures 7-8 (CPC 4258) and 9 (CPC 4259) served as the basis of the explanatory diagram, Text-figure 7, which was also used in a previous paper (Öpik, 1961a). The illustrated pygidia differ in no way from Swedish specimens (Westergaard, 1947). The blisters are a specific character of *G. reticulatus*, and are omitted in the diagram, which is intended to illustrate the generic concept.

**Occurrence and age:** The illustrated specimens are a selection from abundant material from the Pomegranate Limestone, locality D120a (Text-figs. 2 and 3). The age is early Upper Cambrian (Idamean), the Zone of *Glyptagnostus reticulatus* and *Olenus ogilviei*. *G. reticulatus* is a universal species.

#### Genus AGNOSTARDIS nov.

*Type of the genus: Agnostardis amplinatis* sp. nov.

**Family relationship:** The characters of the family Glyptagnostidae (Glyptagnostinae) are not immediately apparent in *Agnostardis*: the cephalon is weakly scrobiculate, but the scrobiculation of the pygidium, which is one of the main criteria of the Glyptagnostinae, is obscure. However, in some of the better preserved pygidia (Pl. 3, fig. 8) terminal third-order caeca are visible; the flanks

of another specimen (Pl. 3, fig. 7) are irregularly pitted; and in the specimen Plate 3, figure 6, a delicate rugose, or even reticulate, pattern is perceptible, similar to that of *Glyptagnostus reticulatus*, but is so weak that it cannot be readily photographed. Consequently, the rugae of *Agnostardis amplinatis* are effaced, or simply not properly reflected in the test. Its cephalic marginal furrow is wide, but not wide enough to suggest a resemblance to *Pseudagnostus*. The glabellar node is small, and slightly behind the centre of the posterior glabellar lobe, as in *Glyptagnostus stolidotus*, and in a position unknown in *Pseudagnostus*. In the pygidium (compare Text-figs. 8, 7, and 13) the articulating furrow is wide, the articulating half-ring is narrow, and the articulating recess is prominent; the short axis has three segments and a conspicuous terminal node; behind the axis the posterior bulb is well developed, similar to that of *Glyptagnostus reticulatus*; this bulb is asymmetrical and in some specimens (Pl. 3, fig. 1) is connected with the left pygidial flank, as described in *G. stolidotus* (Öpik, 1961a).

To conclude, the nearest genus is *Glyptagnostus*, and *G. stolidotus* is, probably, the nearest species.

*Diagnosis:* *Agnostardis* is a genus of the Glyptagnostinae with a trilobate glabella, short triangular and trilobate pygidial axis, and a narrow elongate posterior bulb interpreted as a caecal ruga of the left alimentary gland invading the median line. In the type species (*A. amplinatis*) the rugae and scrobicules are obscure, but a latent reticulation in the manner of *G. reticulatus* is suggested.

*Machairagnostus* Harrington & Leanza, 1957, bears some resemblance to *Agnostardis*, but this is superficial. *Machairagnostus* has a short trilobate pygidial axis not extending rearward beyond the axial node; it possesses a long intranotular axis as seen from the position of the terminal node at its tip, which is seen in the photographs (loc. cit., figs. 7, 3-5). I concur with Harrington & Leanza in regarding *Machairagnostus* as a genus of the Pseudagnostinae distinguished by the complete trilobation of the anterior section of the pygidial axis and rather reduced anterior glabellar node. In *Pseudagnostus* (see Text-fig. 13) the vestigial third lobe of the reduced pygidial axis is also present in several species.

The Ordovician genera *Trinodus* and *Corrugatagnostus* remind one of *Agnostardis* in having the pygidial axis short and trilobate; of these two, *Corrugatagnostus* has even a trilobate glabella and scrobiculate pygidium, but no close relationship of the two is apparent.

AGNOSTARDIS AMPLINATIS sp. nov.

(Pl. 3, figs. 1-8; Text-figs. 8, 9.)

*Material:* Eight specimens (three cephalae, four pygidia, and one complete) are selected for description; they represent all kinds of preservation, ranging from flattened specimens to specimens in full relief, decorticated and with the test intact. More than a hundred specimens were examined.

*Holotype:* The pygidium CPC 4270, Plate 3, figure 8 (locality B525), is selected as the holotype because of its large size and the clarity of the diagnostic characters.

*Diagnosis:* A separate specific diagnosis is superfluous; *Agnostardis* is a monotypical genus, and the specific diagnosis coincides with that of the genus.

*Description (general)*: *Agnostardis amplinatis* is an agnostid en grande tenure, with all its furrows and lobes developed; only its cephalic caecal rugae are weak and the pygidial ones are almost imperceptible. The adult was between 8 and 9 mm. long, and half as wide as long. The cephalon is slightly shorter than the

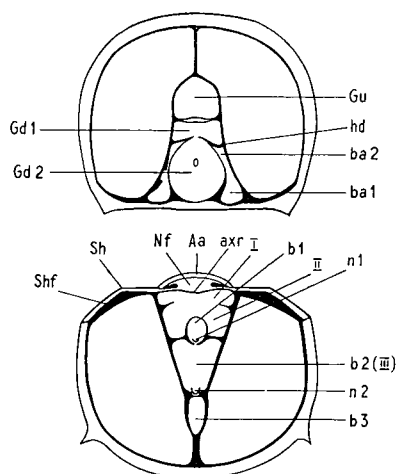


Fig. 8.—*Agnostardis amplinatis*, diagram combined from several specimens, Pl. 3. Cephalon: ba1—basal lobe; ba2—lateral glabellar lobe (composite); Gd1—anterior part, and Gd2—rear part, of posterior lobe of glabella; Gu—anterior glabellar lobe; hd—posterior transverse furrow. Pygidium: Aa—articulating half-ring; axr—axial recess; b1—axial node; b2 (=III)—middle axial segment (=middle bulb of Text-fig. 7); b3—posterior bulb; n1—tip of axial spine (node); n2—terminal axial node; Nf—articulating furrow; Sh—shoulder (geniculate); Shf—shoulder furrow; I—anterior axial segment; II—middle axial segment; III—posterior axial lobe (composite).

pygidium, moderately convex and evenly sloping forward down from its summit in the posterior part of the glabella. The structure of the cephalon, especially the pointed anterior glabellar lobe, recalls a simplified *Ptychagnostus* or even an *Agnostus*, but its bipartite (bilobed) posterior glabellar lobe is the most easily observable peculiarity.

The pygidium is the larger shield, and twice as convex as the cephalon, with the summit on the axial node, and the front of the axis vertical and high; the pleural lobes are tumid; the shoulders are angular and prominent, the border narrow, and all furrows, including the postaxial furrow, rather distinct. The axis is elongate-triangular and relatively short, followed in the rear by the narrow posterior bulb. The axial lobe as a whole has the appearance of a torch whose handle is the posterior bulb. Some variability is apparent in the form of the glabellar node, which may be elongate or circular, and in the width of the glabella and in minor features of the basal lobes.

*Comment on illustrated specimens.* The complete specimen Plate 3, figure 1 (CPC 4263), a flattened external mould in siliceous shale, locality W20, shows the combination of the characteristic pygidium with the same kind of cephalon as seen in Figures 2, 4, and 5. The pygidium is slightly larger than the head. The tip of the posterior (b3) bulb joins the left pleural lobe as described in *Glyptagnostus stolidotus* (Öpik, 1961a). The holotype pygidium is 3.8 mm. long;

it is wider than long (without the articulating half-ring), the ratio being about  $3/4$ . The articulating half-ring is a narrow arc, the articulating furrow is wide, with muscle pits in the corners. The shoulders are prominent; the border is narrow and slightly convex and possesses the usual pair of spines, which are slightly deflected sideways. The pleural lobes are tumid and an indistinct rugosity is indicated. In the pygidial axis the anterior furrows are short lateral indentations and the anterior lateral lobes are distinct. The second axial furrow is transcurrent and circumvenes the prominent but blunt axial node, which belongs to the middle axial annulation. The posterior axial lobe (b2) is triangular and undivided but for a pair of almost imperceptible lateral indentations which may indicate the original presence of two annulations in b2; its tip bears a quite prominent terminal node (n2). The posterior bulb (b3) is a low but well defined 'arrow point' with its tip joining the left pleural lobe. The postaxial furrow is deep and straight.

The pygidium Plate 3, figure 6 (CPC 4268), locality G50, supplements the holotype; it is 3.0 mm. long, with a length/width ratio of about  $5/6$ . It is less wide than the slightly flattened holotype. This pygidium has preserved its test over a core of coarse calcite. It is very tumid with the highest tip on the node: its height/length ratio is about  $1/2$ . The axis is elevated above the pleurae, but the posterior bulb (b3) is depressed very slightly below the level of the pleural lobes.

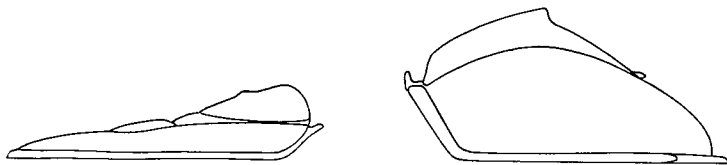


Fig. 9.—*Agnostardis amplinatis*, lateral view of cephalon, Pl. 3, fig. 5, and of pygidium, Pl. 3, fig. 6.

The anterior slope of the axis towards the articulating furrow is vertical and relatively high and has a rearward recess, a structure seen also in *Glyptagnostus* and *Agnostotes*. In the two pygidia described above the flanks converge slightly rearward. Under a strong magnification ( $\times 50$ ) the test is minutely and densely pitted. The small pygidium Plate 3, figure 7 (CPC 4269), locality B537, is about 2.1 mm. long (as preserved). It has abaxially convex flanks and a quite prominent terminal node, and its posterior bulb is small owing to the immaturity of the specimen. It is decorticated and its furrows are therefore particularly deep, and the rugae and scrobicular pits, although weak, are accentuated as compared with the other specimens. The large pygidium, Plate 3, figure 4 (CPC 4266) locality W20, is 3.5 mm. long. It is flattened in siliceous shale (chert), but otherwise has preserved the essential characters of *Agnostardis*. This mode of preservation is also usual in the lower O'Hara fauna at localities D6 and D29. The cephalon Plate 3, figure 2 (CPC 4264), in chert, is associated with CPC 4266 at locality W20. It is 2.4 mm. long. Owing to decortication its glabellar node is prominent; its glabellar flanks are parallel, and not slightly converging as in other specimens. The cephalon Plate 3, figure 5 (CPC 4267), in limestone, locality W1, is 3.4 mm. long, and slightly wider, the length/width ratio being  $4/5$ . The border is narrow and almost flat, the marginal furrow narrow and deep. The cheeks are moderately

convex and covered with radiating rugae of a rather low relief, the axial furrows are deep, the preglabellar furrow and the transverse furrow are shallow but distinct. The glabella is about  $3/4$  of the length of the cephalon, and about one-quarter of its width. It is trilobate, because its posterior lobe is divided in two unequal parts by a pair of oblique lateral furrows which meet in the middle. The frontal lobe is relatively long, with an obtusely angular tip. The rear part of the posterior lobe is egg-shaped and rises towards the rear; an elongate node is placed in the posterior third of the glabella. The basal lobes are small, triangular and tumid. The left lobe is longer than the right one, and two deep pits are present in the dorsal furrow that are absent on the right; no other specimen possesses such pits. The connective band is narrow and has an upward arched edge.

The cephalon Plate 3, figure 3 (CPC 4265) in limestone, locality B537, is 3.1 mm. long and has a relatively narrow glabella (about  $1/5$  of the cephalon), and the glabellar node is not elongate but rounded.

*Occurrence and age:* The origin of the illustrated specimens is indicated in their description by locality numbers. *Agnostardis amplinatis* occurs in the O'Hara Shale ('lower O'Hara fauna'); in the Pomegranate Limestone at locality D133 (see Text-figs. 2 and 3), and in Wills Creek at the foot of De Little Range; and in the upper part of the Mungerebar Limestone, and the lower part of the Georgina Limestone: its age is invariably the Mindyallan Zone of *Glyptagnostus stolidotus*. *A. amplinatis* is a common species of that Zone.

#### Genus AGNOSTOTES nov.

*Type species:* *Agnostotes inconstans* sp. nov.

*Diagnosis:* *Agnostotes* is a genus of the family Glyptagnostidae distinguished by a combination of characters of *Glyptagnostus* and *Pseudagnostus*; glyptagnostid characters are the narrow borders and marginal furrows, the overall scrobiculation of the pygidial pleural lobes, and the depressed sulcus of the frontal glabellar lobe; pseudagnostid are the absence of the posterior sections of the pygidial axial furrows, the presence in the pygidial axis of only two anterior lobes, and the sporadic development of accessory furrows (major scrobicules) on the pygidial flanks.

*Differential diagnosis:* *Agnostotes* cannot be confused with *Agnostardis* gen. nov. because of the striking difference in the cephalic and pygidial structure. In known species of *Glyptagnostus* the pygidial axial furrows are complete and the tip of the axis is invaded by a caecum; nevertheless, *Agnostotes* and *Glyptagnostus* have the following characters in common: 1) the border and the marginal furrow are narrow; 2) the frontal glabellar lobe has a median sulcus of a similar structure; 3) in the pygidium the notular furrows and the intranotular axis are indicated; and 4) the articulating device is identical in both genera. These common characters are assumed to indicate that *Agnostotes* and *Glyptagnostus* are related on a subfamilial level. *Lotagnostus* differs from *Agnostotes* as follows: 1) the pygidial axial furrows are complete in *Lotagnostus*; 2) its articulating furrow is narrow, 'normal'; and 3) it has about twice as many first-order pygidial caeca (14-16 pairs) as *Agnostotes* (about 6-7 pairs). *Lotagnostus* and *Agnostotes* are



similar in having notular furrows, with or without notulae, and in both the tip of the pygidial axis is not invaded by a caecum. The last-named character is significant only in relation to *Glyptagnostus* and *Agnostardis*; otherwise it is not indicative of a close affiliation of *Agnostotes* and *Lotagnostus* because they share it with all other agnostids. *Pseudagnostus* and *Agnostotes* are similar in the absence of the posterior sections of the pygidial axial furrows and the retention of the two anterior axial lobes; furthermore, in several species of *Pseudagnostus* the lines of notulae, and even an internotular axis, are indicated, and in *Agnostotes* the anterior diverticular scrobicules may attain the appearance of the accessory furrows which are believed to be diagnostic of *Pseudagnostus*. But in *Agnostotes* no deutero-lobe is developed behind these scrobicules, and its pleural lobes are scrobiculate all over.

*Overseas occurrence:* *Agnostus* (*Ptychagnostus*?) *orientalis* Kobayashi (1935, p. 105, pl. XIV, figs. 11-12), is a pygidium of an *Agnostotes* erroneously described as a cephalon of a *Ptychagnostus*. *Agnostotes orientalis* has deep notular furrows with six or seven notulae; the holotype, which is the only described specimen, is too fragmentary for a proper specific identification and comparison. It is associated with a cephalon of another agnostid whose wide border suggests a *Pseudagnostus*. Its age is given as the Middle Cambrian 'Olenoides zone of Neietsu', Korea; it is, however, most probably upper Dresbachian (see under *Irvingella*).

#### AGNOSTOTES INCONSTANS sp. nov.

(Pl. 3, figs. 9-14; Pl. 4, fig. 13; Text-figs. 10-12.)

*Material:* Four specimens—one cephalon and three pygidia—are selected for description, from a total of eight available specimens. The described material was all found in the same bed—in the limestone matrix of an intraformational breccia of the Pomegranate Limestone, locality D120b (Text-figs. 2 and 3).

*Holotype:* The large pygidium, Plate 3, figure 11, CPC 4272, is selected as the holotype because of its size.

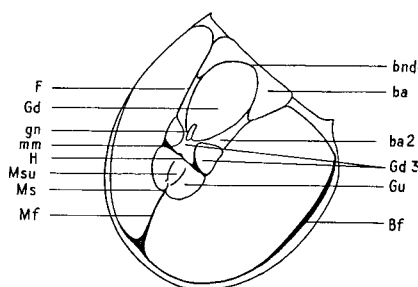


Fig. 10.—*Agnostotes inconstans*, diagram of cephalon Pl. 3, figs. 13, 14. ba—basal lobe; ba2—lateral glabella lobe (composite); Bf—marginal furrow; bnd—connective band; F—axial furrow; Gd1— anterior part (tripartite) and Gd2—rear part of posterior glabella lobe; gn—glabella node; Gu— anterior glabella lobe; H—transverse glabella furrow; Mf—preglabellar median furrow; mm— muscle spots; Ms—frontal sulcus; Msu—depressed extension of frontal sulcus.

*Diagnosis:* A separate specific diagnosis is superfluous because *Agnostotes* is a monotypical genus, and the specific diagnosis coincides with the generic.

*Description (general):* *Agnostotes inconstans* is a semi-effaced agnostid with shallow furrows and lobes in low relief. Posterior portions of its pygidial axial furrows have disappeared completely, and secondary notular furrows are erratic and probably *in statu nascendi*. In spite of the effacement its cephalic and pygidial rugae and scrobicules are distinct; the scrobicules are short, disconnected, and in the pygidium are arranged in circumaxial girdles. A postaxial pygidial furrow is absent, but in the cephalon the preglabellar median furrow, the median glabellar sulcus, and all main lobes of the glabella (the frontal, the posterior, and basal) are present. Both shields are conspicuously tumid, but the pygidium is visibly higher than the cephalon; the slope in the cephalon is almost vertical along the

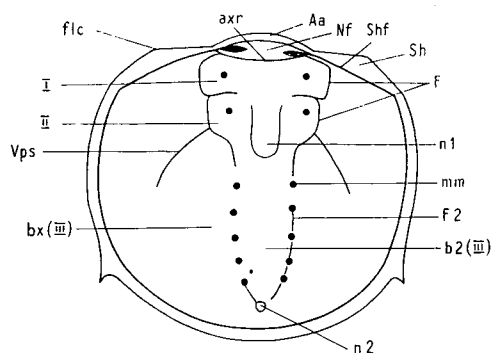


Fig. 11.—*Agnostotes inconstans*, diagram of pygidium. Aa—articulating half-ring; axr—axial recess; bx (III)—extranotular axis (undefined laterally); b2 (III)—intranotular axis; F—axial (dorsal) furrow; F2—notular furrow; mm—notulae; flc—fulcral point (geniculation of shoulder); n1—axial node; n2—terminal axial node; Nf—articulating furrow; Sh—shoulder; Shf—shoulder furrow; Vps—accessory furrow, pseudofurrow, anterior diverticular scrobicule (mesentery).

margin. The shields are evenly rounded in outline, the pygidium bears the usual marginal spines, and the cephalic posterolateral spines are relatively large, triangular and pointed. It is a relatively large agnostid which may have reached 15 mm. in length. The variability of the pygidial structure is striking; the four illustrated pygidia could be regarded as representing four different species if they were found in different localities and beds. But even in one and the same specimen the characters of the left and right half are as strikingly different as they are in different specimens. Hence these pygidia are individual variants of a morphologically unstable species. The effacement of the external relief is a general



Fig. 12. *Agnostotes inconstans*, lateral view of cephalon, Pl. 3, figs. 13, 14, and of pygidium, Pl. 3, fig. 11.

process in agnostids, and *Agnostotes inconstans* is apparently rapidly progressing towards complete effacement. Further progress of the effacement should result in almost featureless forms of a pseudagnostid appearance retaining the vestige of the two anterior pygidial axial segments and a sporadic manifestation of the notular

furrows, or notular lines: these cannot disappear completely because the muscles themselves should persist. Presumably the characteristic narrow arched articulating half-ring combined with the wide articulating furrow and the axial recess may remain unchanged as a functional, mechanical device inherited from the initial glyptagnostids. The presence of this glyptagnostid articulating device, of course, cannot be taken as proof that all such effaced agnostids of a pseudagnostid design are derived from *Agnostotes* only.

*Comment on illustrated specimens:* The holotype pygidium Plate 3, figure 11, is 5.5 mm. long, and slightly wider, the ratio being 7/9 (without the articulating half-ring). The articulating half-ring is a narrow arc and the articulating furrow an elliptical depression with a pair of deep muscle pits in its corners. The shoulders are angular and prominent; the border is narrow, its spines are minute and slightly deflected, and the marginal furrow is also narrow and distinct. The pleural lobes slope outward in an even curve that flattens gradually towards the border; in the rear, however, the slope is very steep behind the terminal node. The surface is scrobiculate; the scrobicules are discontinuous, indicating that the caeca formed a reticulating system of ducts. The scrobicules are arranged in three circumaxial girdles, and between the axis and the girdle of the first-order caeca a pair of wide crescentic main trunks is indicated by absence of scrobicules. Seven or eight pairs of first-order caeca are present, and numerous third-order caeca are indicated by marginal scrobicular pits.

The terminal node is a sharp point in the proximity of the marginal furrow, indicating that the axis is long and almost reaches that furrow. But morphologically, as a feature of relief, only the two anterior axial lobes are developed, representing the visible part of the axis. A pair of short and shallow disconnected furrows separates the lobes; the anterior lobe is visibly wider than the posterior one, and the axial furrows are shallow, with a tendency toward a complete effacement. The axial node extends over the whole length of the posterior lobe, and beyond it rearward, and culminates as a blunt tubercle. The lobes bear each a pair of notulae of inequal depth. The described structure of the axis is pseudagnostoid. Behind the bilobed axis follow five pairs of notulae in two lines converging towards the terminal node; the intranotular axis is slightly convex, the notular lines are depressed, and parts of them are distinct furrows: secondary axial notular furrows are apparent. The test is smooth.

The pygidium Plate 3, figures 9-10 (CPC 4271), is 3.9 mm. long, and differs from the holotype in several ways: 1) its intranotular axis is somewhat carinate; 2) the notular furrows are deep, but remain incomplete; 3) the notulae are almost absent; 4) weak accessory furrows are present, but inequal in length and in an asymmetrical position; the right furrow interferes with scrobicules. The pygidium Plate 3, figure 12 (CPC 4273), is 3.5 mm. long, and displays also some peculiarities: 1) the axis is carinate; 2) the notular furrows are shallow, but continuous; 3) the notulae are absent; 4) the left accessory furrow is long, whereas the right one is indicated by a short, almost pitlike scrobicule.

The pygidium Plate 4, figure 13 (CPC 4281), is about 5 mm. long and 6 mm. wide. No notulae are developed, the notular axis is indicated, the scrobicules are shallow but arranged in three quite regular girdles. About 55 third-order marginal rugae are discernible.

To sum up, the axial part of the pygidium suggests a comparison with *Pseudagnostus*, and especially with forms designated as *Rhaptagnostus*, in which the lines of notulae and the intranotular axis are visibly expressed. It is, however, important to note the similarity with *Glyptagnostus stolidotus* (Öpik, 1961a) as well; 1) *G. stolidotus* has well developed notulae, notular furrows, and an intranotular axis; 2) the sporadic accessory furrows of *Agnostotes* correspond to the anterior scrobicules (=caecal mesenteries) of the main diverticula (op. cit., D in text fig. 16); and 3) the structure of the anterior two lobes of the pygidial axis is the same in *G. stolidotus* and in *Agnostotes*. The difference is only in degree: *G. stolidotus* is a species en grande tenure, whereas *Agnostotes* is relatively effaced. Of course, *Glyptagnostus stolidotus* and *Agnostotes* differ greatly in the structure of the posterior part of the pygidial axis.

The cephalon, Plate 3, figures 13 and 14, and Text-figure 10 (CPC 4274), is 4.3 mm. long and 5.2 mm. wide, the length/width ratio being 5/6. In outline it is evenly curved, and widest in the posterior third. The border is very narrow, and almost flat, the marginal furrow is distinct, but shallow and narrow. The spines are triangular, upturned, curved, and pointed. The cheeks are slightly tumid and almost vertical along the margin. The surface is scrobiculate, the scrobicules are short lines and pits, the rugae are tumid and form a confluent, reticulate system. The arcuate scrobicules are present, and the anterior caecal diverticula, arising at the rear flanks of the frontal glabellar lobe, are rather distinct. The preglabellar furrow, and all the furrows on and around the glabella, are shallow, indicating a moderate degree of effacement.

The glabella is relatively large, slightly more than 2/3 of the length, and 2/7 of the width of the cephalon. The posterior lobe is convex, but the anterior glabellar lobe is flat and depressed almost to the level of the cheeks. The basal lobes are long, triangular, and connected by the connective band along the posterior margin of the cephalon. An elongate node is seen on the anterior quarter of the posterior glabellar lobe. In spite of the low relief a number of details are discernible; they are presented in Text-figure 10. The rear part of the posterior glabellar lobe (Gd 2) is an elliptical dome with the node on its anterior tip and rising above the depressed glabellar flanks (ba 2); in front of it there is a tripartite portion (Gd 1) with the median part elevated above the level of the lateral lobules.

The transverse glabellar furrow (H) is shallow in the middle, but deepened abaxially, with muscle scars (mm.). The anterior glabellar lobe (Gu) is relatively short, subpentagonal, and provided with a median sulcus (Ms) and its depressed extension (Msu), and exhibits a structure previously known only in *Glyptagnostus* (see Öpik, 1961a).

*Occurrence and age:* *Agnostotes inconstans* has been found only in the Pomegranate Limestone, in its highest fossiliferous bed, locality D120b (see Text-fig. 3).

Its age is Upper Cambrian (Idamean), about the passage between the early and middle part of the series—about the lower Franconian in American terms.

#### Genus PSEUDAGNOSTUS Jaekel, 1909

The genus *Pseudagnostus* is discussed to clarify its relationship with *Glyptagnostus* and its allies. The familial relationship and the diagnostic characters are discussed first on the basis of published material; this is followed by a description of the organization of an Australian *Pseudagnostus*.

Whitehouse (1936) established the family Pseudagnostidae as a separate family, which is also acknowledged by Howell in Harrington et al. (1959). Kobayashi (1939), however, regarded it as a subfamily of the Agnostidae, and so did Shaw (1951) and Palmer (1960).

*Pseudagnostus cyclopyge* (Tullberg), 1880, is recognized as the type species of the genus. It is not known in great detail, and has not been studied since Tullberg's original contribution.

The most exhaustively described *Pseudagnostus* is *Agnostus koerferi* Monke, 1903, from the early Upper Cambrian of China. It is correctly compared with the subsequent type of the genus—*Agnostus cyclopyge* Tullberg; Monke succeeded also in describing its cephalic and pygidial doublure and the pygidial articulating device. The doublure is as wide as the border and the articulating device has the same structure as seen in *Pseudagnostus vastulus* (Text-fig. 13). The species is distinguished by the absence of the preglabellar median furrow in adult specimens, although it is present in immaturity. According to Walcott (1913) *koerferi* is a synonym of the earlier *Agnostus douvillei* Bergeron, 1899. Monke's species is based on numerous syntypes, and no lectotype has been designated as yet. It is probable that on the superb limestone plate (Monke, loc. cit., pl. 9) more than one species is present, and the synonymy with *douvillei* should, therefore, be examined once more.

The concept of *Pseudagnostus* that results from our survey can be summarized as follows:

*Pseudagnostus* is a genus of the family Glyptagnostidae (with caeca in the pygidium and with a glyptagnostid articulating device, but also with some characters of Diplagnostidae) distinguished by wide borders and wide marginal furrows in the cephalon and pygidium, by reticulating pygidial caeca in the anterolateral parts of the pleural lobes, by the pygidial axis reduced to the two anterior annulations, and the posterior portion of the axis fused with the pleural lobes to form a composite deuterolobe. The cephalon has a conservative structure, with a trilobate glabella in which the frontal lobe and the lateral lobes behind it are combined with the glabellar node in a clover leaf design; its basal lobes are simple and in the majority of species the median preglabellar furrow is present.

Cephalae and pygidia of *Pseudagnostus* cannot be confused with any other Upper Cambrian agnostid. In *Agnostotes* gen. nov. the absence of the posterior sections of the axial furrows, the erratic appearance of the accessory furrows,

and the presence of only two anterior axial annulations may be misleading; but in *Agnostotes* the borders and marginal furrows are rather narrow, the pygidial pleural lobes are scrobiculate all over, and are consequently not fused with the axis, and no deuterolobe is present.

About thirty-two species have been attributed to *Pseudagnostus*; the most complete list, with twenty-eight species, was published by Ivshin (1956). These numbers are subjective, of course, because synonyms may be present on the specific level and subjective generic synonyms exist also. I have made a survey of the published species, reading their descriptions and examining the published illustrations, with the result that about 130 single characters are applicable to describe the *Pseudagnosti*. These characters are affirmative or negative statements as regards some of the features, and counts, proportions, shapes, and evaluations of the degree of effacement as regards others.

The following summary of the generic characters of *Pseudagnostus* is made with reference to the data provided by the survey.

1. The great majority of the species surveyed are Upper Cambrian; one is probably Middle Cambrian (*Pseudagnostus* (*Sulcatagnostus*) *securiger*); the Tremadocian *Ciceragnostus barlowi* (Belt) may be a late, and almost effaced *Pseudagnostus*.
2. In all species of which the pygidium is known it possesses the deuterolobe, and in many species the accessory furrows are present. These, however, vary in length and are subjected to effacement.
3. In all species two anterior pygidial axial lobes (axial annulations), or their vestiges, are present; these lobes are often confluent by the effacement of the dividing furrows or furrow (when transcurrent). These two lobes are flanked by axial furrows. A third lobe is sometimes indicated in the form of a pair of low elevations.
4. In all species the axial furrows behind the bilobed axis are externally obsolete, and the only external morphological expression of the posterior part of the axis is its tip, which is indicated by the terminal node. The axis and the pleural lobes are confluent and form the deuterolobe (item 2, above).
5. In all species the pygidial and cephalic marginal furrows and the borders are wide; but in some peronopsids and diplagnostids these can be also as wide, or even wider (e.g. *Linguagnostus*, of the Diplagnostidae). Completely effaced agnostids with a narrow cephalic and wide pygidial border cannot be taken into consideration.
6. In all species the basal lobes are simple.
7. About 80 per cent. of the species have a preglabellar median furrow reaching the border; in about 10 per cent. (four species) the furrow is shallow and fades out before reaching the border; 10 per cent. of the species (three species) have no preglabellar furrow; this may or may not be attributed to partial effacement.

8. The glabellar node in most species lies in the middle of the anterior part of the posterior lobe; in six species it is behind that position.

9. Rugose (or scrobiculate) cheeks can be seen in four or five species; presumably all species had dendritic cephalic caeca which belong to the general anatomy of agnostids.

10. In the pygidium rugae are visible in three species, and confined to the anterolateral flanks in front of the accessory furrows; no rugae have been detected as yet on the flanks of the deuterolobe. This may indicate a particular distribution of caeca, confined to the anterolateral flanks, which apparently contain the pleurae of the two preserved anterior axial lobes. In one species the surface of the deuterolobe is minutely pitted or scrobiculate (Lochman & Hu, 1959, p. 412, text-fig. 1). The presence of rugae in the pygidium suggests a relationship with the glyptagnostids.

11. Notulae, notular lines, and even the intranotular axis are visible in several species and a similarity with *Glyptagnostus* is thus indicated.

12. The articulating device has been described in a single species by Monke (1903); its structure (Text-fig. 13) is glyptagnostid; this is valid for all undescribed Australian forms, but its validity should be checked on other described species. Among Middle Cambrian agnostids, as seen in undescribed Australian specimens, *Diplagnostus* has an articulating device resembling that of *Pseudagnostus*.

13. As regards the external relief, species en grande tenue, semi-effaced in various degrees, and almost completely effaced can be recognized. The effacement affects the furrows (most commonly the accessory furrows), whereas the lobes are more persistent. The absence of the posterior sections of the pygidial axial furrows combined with the presence of the deuterolobe must be regarded not as a result of external effacement but as a fundamental feature of the anatomy of *Pseudagnostus*.

#### PSEUDAGNOSTUS cf. VASTULUS Whitehouse, 1936

(Text-fig. 13.)

The Text-figure is made from a cephalon and pygidium that are side by side in a piece of Pomegranate Limestone (CPC 4302) from locality D120b (see Text-figure 3); the horizon is the *Erixanium sentum* Zone, and immediately above it at the same locality follow beds with *Agnostotes inconstans* and *Irvingella tropica*.

My aim is to describe the organization of a *Pseudagnostus*, and not the species *vastulus*. It is, indeed, difficult to ascertain the specific identity of our specimens, which greatly differ in their preservation from the type material of *vastulus*. Nevertheless, *P. vastulus* is suggested for the following reasons: (1) *P. nuperus*, the second species described by Whitehouse, is also probably present, and could

be identified as being distinct from our specimens of *vastulus*; (2) the illustrated cephalon has a constricted glabella, which is a character of *vastulus*; and (3) the mode of occurrence indicates that the cephalon and pygidium both belong to the same species.

The cephalon is 5.2 mm. and the pygidium 6 mm. long; being of different size these shields belong apparently to two different specimens, unless in this species the cephalon is smaller than the pygidium; if so, they could be interpreted as parts of an individual. The geological age of our specimens and of the types of *vastulus* is the same.

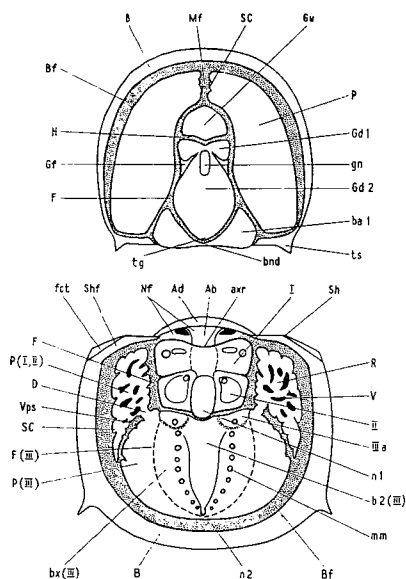


Fig. 13. *Pseudagnostus vastulus*, cephalon and pygidium, CPC 4302. Cephalon: ba1—basal lobe; bnd—connective band; F—axial furrow; Gd1— anterior part, and Gd2—rear part, of posterior lobe of glabella; Gf—lateral glabellar furrow; gn— glabellar node; H—transverse glabellar furrow; Mf—preglabellar median furrow; P—cheek (pleural lobe); sc—scallop; tg—rear tip of glabella; ts— cephalic spine. Pygidium: Aa—articulating half- ring; Ab—axial bar; axr—axial recess; B— border; Bf—marginal furrow; b2 (III)—intranotular axis; bx (III)—extranotular axis; D—diverticular duct; F—axial furrow; F (III)—posterior part of axial furrow (vestigial); fct—facet; mm—notula; n1—axial node; n2—terminal axial node; Nf— articulating furrow; P (I, II)—pleural lobe (anterior part); P (III)—pleural lobe (rear part); R—rugae, reticulate; sc—scallop; Sh—shoulder with fulcral tip and geniculation; Shf—shoulder furrow; V— scrobicule; Vps—accessory furrow (major scrobicule pseudofurrow); I—anterior axial segment (tripartite); II—middle axial segment (tripartite); IIIa—vestigial axial lobe of third segment; III— posterior axial lobe (composite). Articulating device is composed of Aa, Ab, axr, and Nf; deutero-lobe (pseudolobe, endlobe) contains the elements P(III), bx (III), and b2(III).

The illustrated cephalon has preserved its test, but its right flank is damaged, and restored in the diagram. The pygidium is decorticated, which is an advantage, because the relief of the cast is stronger than of the exterior, and therefore, much more informative regarding vestigial characters.

The cephalon exhibits the clover-leaf combination of lobes in the anterior part of the glabella and the wide border and marginal furrow; the border narrows rearward, as is the rule in all agnostids. The preglabellar furrow is deep and scalloped by genal caeca. The transverse glabellar furrow is shallow and cusped. The cheeks are tumid, and so are the large but simple basal lobes, and the posterior part of the glabella. In the rear the glabella is angulate, which is common in *Pseudagnostus* and in some diplagnostids.

The pygidium is readily explained with reference to the explanation of terms given on pp. 30-32, but some elucidating notes are still necessary. The pair of muscle spots in the articulating furrow are closer to the midline than in



*Glyptagnostus*, and the floor of the furrow (the articulating bar) is convex upward; the articulating facets are exceptionally well developed; the lateral scrobicules (accessory furrows) are crossed each by a major caecal diverticulum (Vps) at their adaxial ends, and the furrows have scalloped flanks; the diverticula connect the anterolateral reticulate caecal glands (R) with the flanks of the deuterolobe; the deuterolobe is moderately tumid; on its parietal surface (internal cast) the vestigial axial furrows are faintly indicated, but the pleural lobes and the extra-notular axis are otherwise completely confluent, and the curvature does not change during the passage from the pleural to the axial area; the notular lines carry nine pairs of notulae, a number that is known from other species; the intranotular axis is slightly elevated along the midline, but its flanks are somewhat depressed, and its tip bears the terminal node. Kobayashi's suggestions that the accessory furrows do not represent the axial furrows, and that the deuterolobe (pseudolobe) has a composite structure, have been subsequently supported by Palmer's (1955) studies. Further improvements on Kobayashi's and Palmer's results are the observations (1) that the notular lines are not the 'true axial furrows'; (2) that the axial furrows became obsolete in their original position; and, finally, (3) that the diagonal accessory furrows are not 'axial', nor 'pseudo-axial', but are regular major pleural scrobicules. In other words, the accessory furrows are parietal septa between the anterolateral reticulate caeca and the flanks of the deuterolobe. These septa were mesenteries, or carried mesenteries, and had only a mechanical function. Their size, or even their external absence, was not significant, as long as they adequately supported the internal alimentary apparatus. Considering the proximity of the accessory furrows to the original axial furrows or to their vestiges, as well as to the marginal furrow, one should expect that the accessory furrows could merge with one or another of the pre-existing furrows in some species of *Pseudagnostus*.

The anatomy of the deuterolobe is obscure and remains a subject of speculation. Externally the lobe is smooth, without rugae, and may have contained a pair of large ingluvial sacs with a scalloped periphery: the edges of the accessory furrows and even of the deuterolobe are wavy or even scalloped also. These scallops, however, may represent the distal ends of deep-seated caeca that are not reflected by rugae in the test of the deuterolobe. The first explanation (ingluvial sacs) is preferable, because no specimen of a *Pseudagnostus* was known with rugae on the deuterolobe. An exception, however, is a specimen of *Pseudagnostus prolongus* (Hall & Whitfield), recently described by Lochman & Chung-Hung Hu (1959, text-fig. 1). In its pygidium the flanks of the deuterolobe are minutely pitted (scrobiculate) in a manner indicating the presence of reticulate caecal glands in their pleural parts. The adaxial limits of the pitted areas are situated about half way between the accessory furrows and the intranotular axis, and in a position where the axial furrows or their vestiges should be expected. Thus, the accessory furrows lie within the pitted flanks, that is, within the pleural lobes, and cannot, therefore, be homologous with the axial furrows. As regards the presence of reticulate caeca the possibility remains that the pits (scrobicules) held the ingluvial sacs suspended without dividing them into a reticulate system of ducts.

Recently Rosova (1960) correctly observed that the intranotular axis (the 'lancetoid field' in her terms) represents only the median part of the posterior axial lobe of the *Pseudagnostus* pygidium, but insisted that the accessory furrows are the true ('primary') axial furrows. This means that they should be homologous with the fundamental axial furrows of trilobites in general. The accessory furrows, of course, are not meant to be secondary 'axial' furrows, but 'primary diagonal furrows', and Rosova herself (loc. cit., p. 11) succeeds in demonstrating their primary nature, but in this case the terms 'primary' and 'axial' cannot be equated. Furthermore, Palmer's (1955) material indicates the presence of true axial furrows in early stages of *Pseudagnostus* and a gradual development of the diagonal accessory furrows; in later stages the axial furrows disappear, but an intranotular axis gains in relief.

The pygidial muscle scars of *Pseudagnostus* cf. *vastulus* have the same distribution as in *P. communis*, described by Palmer (1955, pl. 20, fig. 14). These scars in *P. vastulus* are shallow parietal depressions, and the presence of them on three metamers indicates a trilobation of the anterior part of the axis. The two posterior metamers have also each a pair of notulae included in the muscle scars. Thus, the scars and the notulae may have been functionally different: it can be speculated that the scars held the muscles and the notulae were the apodems of the appendages. In some of the peeled cephalae of cf. *vastulus* muscle scars comparable with those of *P. communis* are also observable; they are petaloid with points converging toward the glabellar node, and apparently composite.

#### Genus LOTAGNOSTUS Whitehouse, 1936

A brief review of the genus *Lotagnostus* is needed to facilitate the comparison with other genera of the Glyptagnostidae. *Lotagnostus* was established by Whitehouse (1936, p. 101) for 'the group of *Aagnostus trisectus* Salter (1864, p. 10, pl. 1, fig. 11), a specimen figured by Westergaard (1922, pl. 1, fig. 12) being taken as the genoholotype'. This nomenclatorial procedure indicates that the concept of the genus is based on a Swedish specimen (a pygidium from Andrarum), but the nomenclature of *Lotagnostus trisectus* still adheres to the specimen described by Salter from Britain. The holotype is a solitary pygidium for which even the term 'lectotype' is superfluous. Salter's and Westergaard's specimens are congeneric, but their specific identity is not obvious, because, according to Matthew (1903, p. 221), none of the British specimens has 'any trace of a tubercle at the extremity of the mid-lobe of the pygidium'. This tubercle—the terminal axial node—is well developed in the Cape Breton specimens described by Matthew, and in Westergaard's specimen.

The type specimen of *Lotagnostus trisectus* (Salter) has a trifid ('trisepte') pygidial axis which is the fundamental character of the genus. The axis is defined all around by the axial furrows, and its rear lobe is divided into three longitudinal parts by the notular furrows. No muscle scars (notulae) are present in the British, Scandinavian, and Cape Breton specimens. But these pits are

present, for example, in a pygidium of a *Lotagnostus* illustrated by Rasetti (1945, pl. 60, fig. 1), and are indicated in *Lotagnostus americanus* (Billings), in Rasetti (1944, pl. 36, fig. 2).

Kobayashi (1939) included in *Lotagnostus* the species *Agnostus hedini* Troedsson, 1937. According to Troedsson (loc. cit. p. 20) its 'posterior axial lobe is quite undivided', without any trisection; it should remain, therefore, in *Agnostus*. *A. hedini* has, of course, a terminal axial node, but such a node occurs also in some species of *Agnostus*, *Homagnostus*, and several more genera. Furthermore, the pygidial flanks of *A. hedini* are non-scröblicate and, therefore, not indicative of *Lotagnostus*. The glabella of *A. hedini* can be compared with that of *Lotagnostus trisectus*, but also with other genera, including *Agnostus* itself. The tripartition of the anterior axial lobes of the pygidium also is not indicative when the posterior lobe shows no trisection.

The characters of the genus *Lotagnostus* are as follows: 1) The pygidium and the cephalon both are scröblicate, as in other glyptagnostids, but the pygidium has twice as many first-order caeca as *Glyptagnostus*; 2) the pygidial axis is trifid, with well defined axial and notular furrows, and with a conspicuous intranotular axis; 3) the articulating device is ordinary, and not glyptagnostoid; 4) in the cephalon the scröblication is ptychagnostid or glyptagnostid; all furrows and lobes are developed, and the basal lobes are simple; its conspicuous scröblication prevents a confusion with *Agnostus* and the position of the node in the middle of the posterior glabellar lobe serves to distinguish *Lotagnostus* from *Pseudagnostus*. The cephalic border and marginal furrow are wide in *Pseudagnostus*, but narrow in *Lotagnostus*. The species of *Lotagnostus* are forms en grande tenue, with an accentuated relief, but effacement of furrows occurs also, as seen in *Lotagnostus obscurus* Palmer (1955).

*Lotagnostus* and *Agnostotes* gen. nov. have similar narrow borders and marginal furrows, but differ in several other characters which eliminate any possibility of confusion.

*Acmarrhachis* Resser is probably related to *Lotagnostus* in having well developed pygidial axial and notular furrows, and a distinct intranotular axis, but undescribed forms exist which can be interpreted as being intermediate between *Acmarrhachis* and *Pseudagnostus*. Some uncertainty remains regarding the affiliation of *Lotagnostus* to the remainder of the Glyptagnostidae because of the different structure of the articulating device in *Lotagnostus*.

#### Family DISCAGNOSTIDAE nov.

The family Discagnostidae is established to include agnostids (*Discagnostus*) with two pairs of genal tubercles and a striated cephalic border. The family is related to the family Agnostidae; some similarity with *Ptychagnostus* (*Goniagnostus*) is indicated below, in the description of the only genus and species of the family.

Genus DISCAGNOSTUS nov.

DISCAGNOSTUS SPECTATOR, sp. nov.

(Pl. 2, figs. 15, 16; Text-fig. 14.)

*Material*: One cephalon (CPC 4262), the holotype, has been found, of which the internal cast and part of the external mould were recovered. The rock consists of fine-grained silica, in parts porous, and relatively friable. The specimen had to be fortified by impregnation with dilute acetone glue to prevent it from breaking up.

*Measurements*: 1.56 mm. long and 1.62 mm. wide.

*Diagnosis*: *Discagnostus spectator* gen. nov., sp. nov., is an agnostid *en grande tenure* distinguished by a very short glabella, a densely and minutely striated cephalic border, and by two pairs of uniform lateral genal (ocular) tubercles.

*Description*: The cheeks are moderately scrobiculate, with a pennate arrangement of caecal rugae; the scrobicules are broad and shallow, distinct on the parietal surface, but not indicated externally. A single pair of diverticula is present,

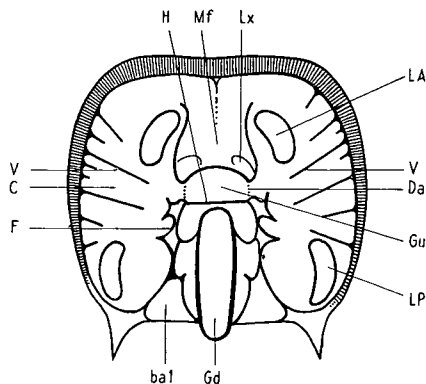


Fig. 14. *Discagnostus spectator*, diagram of cephalon. bal—basal lobe; C—caecum (ruga); Dd—anterior diverticular duct; F—axial furrow; Gd—posterior glabella lobe; Gu—anterior (frontal) glabella lobe; H—transverse glabella furrow; LA—anterior genal (ocular) tubercle; LP—posterior genal (ocular) tubercle; Lx—lateral prelabellar lobe; Mf—preglabellar median furrow; V—scrobicules.

connected with the flanks of the anterior glabella lobe. The axial furrow is distinct, but shallow. The prelabellar area between the anterior genal tubercles is depressed and a vestigial prelabellar median furrow is indicated. This depressed prelabellar area is laterally limited by the steep edges of the alimentary rugae. The cheeks are convex, even tumid, and sloping outward, as well as toward the axial furrows. The glabella is relatively short (about 0.6 of the total length) and has a strong relief. Its anterior lobe is small and semiglobose, the transverse furrow is distinct and evenly deep. The median part of the posterior glabella lobe is a narrow elevated crest evenly rising rearward, culminating at its posterior end and overhanging the posterior border; the flanks of the glabella are depressed, with two pairs of low lobes and large but low subtriangular basal lobes. The postero-lateral spines are relatively large, as is seen on the right spine, which is free, but still surrounded by matrix.

The genal tubercles are of about equal size, reniform, and rise abruptly from the surface of the cheeks. No trace of sutures could be detected. The abaxial base

of the anterior tubercles coincides with the position of the arcuate scrobicules of *Ptychagnostus* and *Tomagnostus*, whereas the posterior tubercles are placed on the posterolateral ends of the genal glands. Ocular ridges are absent. The test is minutely granulated. The border is minutely striate and the striae reach the margin. A similar striation of the pygidial border occurs in the Middle Cambrian *Blystagnostus* (Öpik, 1961b). In *Pagetia* and *Opsidiscus* the border is also striate, but the striae (impressed lines) are less numerous, and do not reach the margin.

*Comparison:* No agnostid is known as yet that has genal tubercles; if these tubercles are eyes or vestigial eyes, *Discagnostus* is unique in having two pairs of cephalic eyes. The minute striation of the border recalls *Opsidiscus* Westergaard and *Pagetia* Walcott, but in the organization of the cephalon *Discagnostus* is an agnostid and not a pagetiid trilobite. It is related to *Ptychagnostus*, especially to species with pennate scrobicules (*Ptychagnostus atavus*, *punctuosus*, and *lundgreni*; vide Westergaard, 1946). The rearward-overhanging glabella recalls some undescribed Australian species of *Ptychagnostus* (*Goniagnostus*); but no *Ptychagnostus* has the anterior glabellar lobe as short as *Discagnostus*.

*Interpretation of the genal tubercles:* The genal tubercles of *Discagnostus* have the shape of trilobite eyes, and are, probably, ocular tubercles. They are upward expansions of the genal glands, and therefore similar to the palpebral lobes of trilobites (Öpik, 1961a). Furthermore, the posterior genal (ocular) tubercles have the same position as the cephalic eyes of *Pagetia*, which are true schizochroal eyes as described below.

The presence or absence of ocelli in the genal tubercles of *Discagnostus* cannot be established owing to the smallness of the object, its imperfect preservation, and the character of the rock. Absence of visual surfaces, however, would be no proof that these organs had no original ocular function, in view of the known modifications of eyes in trilobites. If *Discagnostus* were an 'ordinary' trilobite or an *Opsidiscus*-like pagetiid its genal tubercles could be regarded without much difficulty as lateral cephalic eyes. The presence of more than one pair of eyes, the possibility of which is indicated in *Papyriaspis* (Öpik 1961a), would support Raw's idea of an original multiple number of eyes in trilobites. In agnostids, however, the problem is much more complicated. Thus, the view prevails that agnostids, which are all blind, are derived from sighted ancestors. Accepting this, the two following possibilities should be considered: (1) a stock of agnostids related to *Ptychagnostus* existed that preserved the eyes, but escaped detection because of the small size of the individuals; (2) lateral eyes homologous with the eyes of other trilobites were lost by all agnostids, but in *Discagnostus* another set of eyes became subsequently developed. This would mean that at least three pairs of eyes are inherent in agnostids.

Another school of thought claims that agnostids, being all blind, never had eyes. If this is accepted *Discagnostus* represents a novel but phylogenetically late development. It is, however, unknown whether the ocular tubercles of *Discagnostus* are eyes *in statu nascendi*, or whether they are in a process of degeneration. The degeneration of eyes in trilobites is an established fact and occurs independently

in several lineages, but this is no reason to assume that agnostids followed a similar development.

For comparison, and to indicate the possible structure of the lateral eye of *Discagnostus*, a free cheek of *Pagetia significans* (Etheridge Jr.) with the preserved visual surface is illustrated in Text-figure 15. This specimen, together with several more free cheeks, isolated as well as in situ (CPC 4308, 4309, 4310), comes from the Alexandria beds, about 3 miles north-west of Alexandria Station, Northern Territory, locality N25B; the rock is an extremely fine-grained hard siliceous shale which is slightly porous through leaching; its age is the Middle Cambrian Zone with *Xystridura browni* (Etheridge Jr.); the tests of trilobites are not preserved, but the casts and moulds reflect minute details of the fossils.

The illustrated free cheek is an internal cast. The eye is schizochroal, with about 25 widely spaced ocelli. In eyes of larger specimens up to fifty ocelli are present, and in smaller specimens 11-12 have been counted. *Pagetia significans* occurs in several other localities, but without the preserved visual surface which is quite common in specimens from locality N25B.

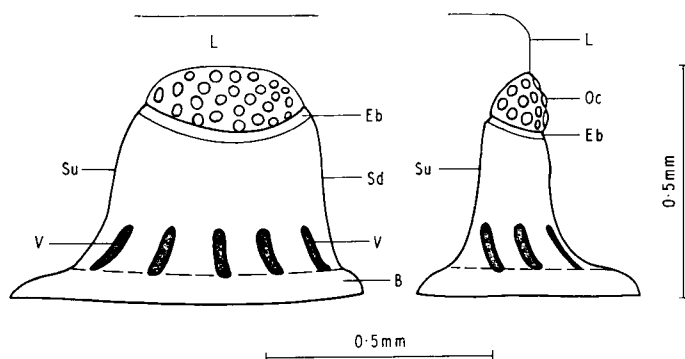


Fig. 15. *Pagetia significans* (Etheridge), left free cheek with visual surface of eye; lateral view (on left), frontal view (on right), from specimens CPC 4308, 4309, 4310. B—border; Eb—base of eye; L—palpebral lobe; Oc—visual surface with ocelli; Su—anterior facial suture; Sd—posterior facial suture; V—marginal scrobicules.

**Occurrence and age:** *Discagnostus* was found in the O'Hara Shale, in a chert layer near its base, at locality D29, in the Selwyn Range, Queensland. Its age is Upper Cambrian (Mindyallan), the second zone (*Glyptagnostus stolidotus* Zone) above the base of the Series. It belongs to the 'lower O'Hara fauna' (Öpik, 1956, 1960), and is associated with *Glyptagnostus stolidotus*, *Rhodonaspis longula*, *Agnostardis amplinatis*, and other trilobites.

## POLYMERID TRILOBITES

Superfamily OLENACEA Burmeister

Family OLENIDAE Burmeister, 1843

The taxonomy of the Olenidae has been discussed profoundly by Henningsmoen (1957), but without a reference to the superfamily. In an earlier paper (1951) he placed the Olenidae in the Conocoryphacea Swinnerton, 1915, which name, however, is attributable to Angelin, 1854. Furthermore, Conocoryphacea can be regarded with good reasons as being the senior synonym of the subsequent Ptychopariacea Matthew, 1887. According to Harrington et al. (1959)

Conocoryphacea and Ptychopariacea are valid taxa of equal rank—a subjective solution which usefully shelves the problem of nomenclatorial priority and maintains the usage of Ptychopariacea as a heading of a major concept in trilobite taxonomy. The original priority, however, belongs to the names Olenidae and Olenacea Burmeister 1843, and only because of common usage (popularity) does the name Ptychopariacea prevail in the literature, including the present paper.

Henningsmoen (1957, p. 95) in quoting Rasetti (1951, p. 202) indicates that it is impossible to formulate a set of diagnostic features of Olenidae. More precisely, it is impossible to diagnose the distinction between the Olenacea and Ptychopariacea because these superfamilies are morphologically and, therefore, objectively inseparable one from another. It is even difficult to construct a diagnosis of the family Olenidae in relation to the rest of the Ptychopariacea, as seen from the following: Olenidae are delicate, refined Ptychopariacea with a thin test, and a consistently very narrow cephalic border, with large triangular posterolateral limbs, transverse (horizontal) or slightly slanting ocular ridges, but without any uniformity in the shape of the glabella, in the number and character of glabellar furrows, size and position of the eyes, number of segments in the thorax, structure of the thorax, and shape of the pygidium.

This lack of uniformity means a considerable morphological diversity which is successfully exploited in establishing the multitude of good diagnostic genera and species of olenids.

An olenid genus may be recognizable at a glance, but not from its 'familial characters'. The olenids are recognizable immediately because their genera are well established and studied, being illustrated in all textbooks and included in all syllabuses of invertebrate palaeontology. In effect, the genera, or a particular genus, are identified, but not the family as such; and an unknown genus is called an 'olenid' when it appears to be similar to another genus which is already listed and accepted as being an olenid. In other words, the name Olenidae is the heading of a particular 'roll' of ptychopariacean genera as regards the procedure of 'recognition at a glance'. Further comment on the distinction between Olenacea and Ptychopariacea (Papyriaspidae) has been given by Öpik (1961b).

The present status of Olenacea and Olenidae can be summarized as follows: (1) the Olenidae remain a family and include the Oleninae, Leptoplastinae, Pelturinae, Triarthrinae (optional; Henningsmoen includes it in the Oleninae) and Rhodonaspidinae (nov.), which is left in the Olenidae after the removal of the Papyriaspidae(-inae); (2) the Hypermecaspidinae Harrington & Leanza (described as a family of the Olenacea) should be included on account of its *Parabolinella*-like glabella, and in spite of its otherwise non-olenidian characters; finally, (3) the Talbotinellinae (nov.), which, if the Olenacea is retained as a superfamily, may represent a separate family within that superfamily.

Whitehouse (1939) first recorded the occurrence of Olenidae and *Olenus* in Australia. Subsequently Öpik (1956, p. 23) mentioned *Olenus* aff. *transversus*, which is described here as *Olenus ogilviei* sp. nov., but other records (loc. cit.

p. 22, 23) are inconclusive. These refer to numerous small cranidia of a trilobite which may belong to immature instars of *Eugonocare* and which are very similar to adults of *Olenus*.

The character of the habitat of olenids in Australia is discussed above on p. 27. The mode of life of the olenids has been discussed recently in general by Wilson (1957), Lochman-Balk & Wilson (1958), and Henningsmoen (1957). Contrary to the assumptions of the first-named authors, the main bulk of olenid species is found in epicontinental and not in geosynclinal deposits. The known habitat of the olenids is the epicontinental sea and their mode of life was the same as that of agnostids. Olenids were floaters, often in swarms; they spread over the waters of the globe when caught accidentally by the surface currents and travelled with them, regardless of the future geotectonic classification of the ground below; they settled and proliferated in places of abundant food, and developed populations in quiet waters off the lanes of dominant currents.

Subfamily OLENINAE  
Genus OLENUS Dalman  
OLENUS OGILVIEI sp. nov.

(Pl. 1; Pl. 2, figs. 2-5; Text-fig. 16.)

*Material*: Nine specimens, of which five are complete, are selected for description, and illustrated. About fifty specimens were examined; the rock is a dark grey bituminous limestone.

*Selection of the holotype*: The largest specimen (CBC 4248, Pl. 2, figs. 1-4, a complete specimen) is selected; it shows all diagnostic characters, including details of the pygidium.

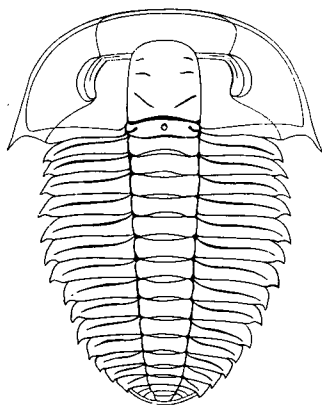


Fig. 16. *Olenus ogilviei*, reconstruction of holotype, Pl. 1.

*Diagnosis*: *Olenus ogilviei* is a species with fourteen segments in the thorax and a non-spinose transverse pygidium; it is distinguished by its relatively large eyes and the small size of its pygidium, which is as long as one segment of the thorax and provided with two axial annulations and a terminus.



*Differential diagnosis:* Only the three British species (Lake, 1908) have fourteen segments in the thorax, as in *Olenus ogilviei*. Of these *Olenus micrurus* Salter has a pygidium with a pair of spines and with only one annulation in its axis; *O. cataractus* Salter is distinguished by a wide axial lobe (as wide as a pleural lobe), and a spinose pygidium with three axial annulations; and, finally, *O. mundus* Lake has even a wider axial lobe (wider than the pleural lobe), which is provided with median tubercles.

*Olenus asiaticus* Kobayashi (1944) is geographically the nearest to Australia. It was found in southern Korea about 60 degrees north of the Australian occurrence. It is a true *Olenus*, 'apparently closest to *O. gibbosus*' according to Henningsmoen (1957, p. 100). In *O. asiaticus* the frontal area (brim + rim) is longer than half the glabella or glabella and occipital lobe taken together and is, therefore, much longer than in *O. ogilviei*; and the palpebral lobes of *asiaticus* are shorter than those of *ogilviei*.

Scandinavian species (Westergaard, 1922; Henningsmoen, 1957) with triangular pygidia (*O. gibbosus*, *truncatus*, *attenuatus*, *wahlenbergi*) are all different from *O. ogilviei*, which has a short transverse pygidium. *O. rotundatus*, *scanicus*, and *dentatus* have rounded pygidia provided with marginal spines that are absent in *O. ogilviei*; furthermore the pygidial axis in these species is relatively wide and has more annulations than *O. ogilviei*.

*Olenus transversus* Linnarsson (in Westergaard, 1922) and *Olenus alpha* Henningsmoen (1957, p. 100) have transverse pygidia comparable with the pygidium of *O. ogilviei*. Still, the pygidium of *O. alpha* (Henningsmoen, pl. 9, fig. 6) has a narrower axial terminus and *transversus* has a fairly large pygidium with three or even four (Westergaard, loc. cit., pl. 3, fig. 17) annulations in its axis. These differences are small and, perhaps specifically insignificant if considered alone. But in *O. alpha* the palpebral lobes are relatively small, 'about one-third of that of cephalic axis' (in *ogilviei* it is about half) and the posterolateral limbs are comparatively long, narrow, and large. The test of the cranidium of *O. alpha* is smooth but that of *ogilviei* is venulose.

*O. transversus* has also smaller palpebral lobes than *ogilviei*, a larger pygidium, and is true to its name *transversus*, being very wide in the beam. According to Westergaard, p. 195, the width of the body is nearly four-fifths of its length (the width equals the length of the pygidium, the thorax and the occipital lobe taken together), whereas full-grown specimens of *ogilviei* with fourteen segments are only as wide as thirteen segments of the thorax.

*O. wahlenbergi* Westergaard has large palpebral lobes and a short brim resembling *O. ogilviei*; but *wahlenbergi* has, as mentioned already, a triangular pygidium and 15-16 segments in the thorax.

*External habit:* *Olenus ogilviei* with its maximal length of 10 mm. is a small trilobite, even for a species of a genus whose size is between 10 and 30 mm. The cephalon is broad and moderately convex, with a delicate border and short

deflected genal spines; the oval thorax is widest at its fifth segment and has serrate margins; the axial lobe is narrow and slender, the pleural lobes are wide and distinctly but gently geniculate along the midline of each lobe; the pleural tips are short and slightly advanced rearward directed spines; the pygidium is small.

*Description:* *Olenus* is, perhaps, the best known Upper Cambrian genus of trilobites. Several of its species are known from complete shields. Because ample information is available in the literature a full description of the new species is omitted and only brief notes are given instead.

The pygidium is very small, even for an *Olenus*. It is as long as an anterior segment of the thorax, whereas in the related *O. transversus* (Westergaard, 1922, pl. 3, fig. 11) it is twice as long. It has an axis of two annulations and a very short terminus, and relatively flat pleural lobes with two pairs of weak ribs and a delicate narrow border. In several specimens the pygidial axis has a median depression that may represent the trace of an axial spine of the thirteenth segment which has not been preserved. If such a spine exists it may indicate some relationship with the olenid *Leptoplastus*.

The thorax in largest (adult) specimens consists of fourteen segments. British species have the same number, but Scandinavian species whose thorax is preserved have thirteen, fifteen, or even sixteen.

The cephalon is more than twice as long as wide and as long as six segments of the thorax, which is usual in other species also. The genal spines are short and slightly deflected. The border of the free cheek is delicate and narrow. The frontal border (rim) of the cranidium is slightly upturned; the brim is relatively short. The palpebral lobes are long (half, or slightly more than half, of the glabella), flat and horizontal and connected with the ocular ridges. The connexion itself is, however, depressed. The ocular ridges are elevated, relatively wide, and bear indistinct ocular strigae that extend into the palpebral lobes: consequently the ocular ridges are double. Three pairs of glabellar furrows are present. In immature specimens these furrows are distinct and even transcurrent, but in adults the anterior furrows are feeble, and the posterior ones are disconnected.

The surface of the cephalon is (except for the smooth glabella) venulose and reticulate; the posterior genal margins bear a distinct diverticular vein each; two pairs of similar veins are present on each pleura of the thorax, one in front, the other in the rear of the pleural furrow. The veins are wavy and delicately ramified and reticulate (see Öpik, 1961a).

The surface of the test shows a false granulation, produced by the reflection of the fine sand grains in the matrix.

*Comment on illustrated material:* All the illustrated specimens, as well as the whole material, were collected at locality D120a (Text-figs. 2 and 3) in limestone beds totalling 2-3 feet in thickness; they can be regarded as representing a population. The holotype (Pl. 1, figs. 1-4) is 7.6 mm. long; the posterior part of the

glabella is damaged and the right free cheek is missing. The delicate border, short and deflected genal spine, ornament, and pleural veins are well preserved; the pleural spines of the anterior segments of the thorax are deflected, but in the posterior segments they are directed rearward. The pygidial axial terminus is very short.

The specimen Plate 1, figure 8 (CPC 4251) is 7.4 mm. long, and has the posterior part of the glabella intact; on the occipital lobe small lateral lobules are indicated; the free cheeks are flattened, but remain in their original position, and even the visual surface of the eye is indicated, but the test is corroded and details are not preserved; the ocular ridges are double.

The specimen Plate 1, figures 6-7 (CPC 4250), is 6.8 mm. long and has apparently preserved its original convexity; the geniculation is distinct; the test is partly corroded and the false granulation well visible.

The fragmentary specimen Plate 1, figure 5, (CPC 4249) is the largest and may have been about 10 mm. long. The geniculation is distinct and the free cheeks have preserved their convexity.

The immature specimen Plate 1, figure 9 (CPC 4252), is 4.1 mm. long. Its glabellar furrows are well impressed laterally and transcurrent in the middle; an occipital node is present. The thorax contains twelve free segments.

A specimen (CPC 4303, not illustrated), 5.8 mm. long, has thirteen free segments in the thorax; the fourteenth is also present, but not quite separated from the pygidium. Consequently *Olenus ogilviei* reached maturity with a size of about 6 mm.

On Plate 2, figures 2-5, three isolated cranidia are illustrated. The specimen Figure 2 (CPC 4254) is 2.2 mm. long; it has preserved the tumidity of the cheeks, and has a distinct occipital node. The specimen Figure 3 (CPC 4255) is 3.0 mm. long, and has the first segment of the thorax attached. The glabellar furrows are broad and the left palpebral lobe is slightly larger than the right. The specimen Figures 4, 5 (CPC 4256) is 3.1 mm. long and has preserved its original convexity, and displays in frontal view the upward arc of the border that is only rarely seen in flattened trilobites.

*Occurrence and age:* *Olenus ogilviei* has been found as yet only in the Pomegranate Limestone at locality D120a (see Text-figs. 2 and 3), where it is quite common. It is associated with *Glyptagnostus reticulatus*, and is contemporaneous with *Olenus gibbosus* and *O. transversus* of the Scandinavian Upper Cambrian sequence. Its age in Australian terms is the basal Idamean Zone of *Glyptagnostus reticulatus* and *Olenus ogilviei*.

OLENUS DELICATUS sp. nov.

(Pl. 4, fig. 12; Text-fig. 17.)

*Material:* Only one cranidium, the holotype, CPC 4284, has been found as yet. It is 2 mm. long.

**Diagnosis:** *Olenus delicatus* is a species with a square glabella, medium sized eyes, granulose surface, and four pairs of glabellar furrows distinguished by its wide interocular cheeks that are as wide as half the glabella.

**Differential diagnosis:** *Olenus granulosus* Palmer (1960) has a cranidium of about the same size, with an overall granulose surface and apparently also with four pairs of glabellar furrows which are arranged as in *O. delicatus*. *O. granulosus* however has a much stronger occipital node, much narrower fixed cheeks ('slightly more than one-fourth of basal glabellar width', whereas in *O. delicatus* it is one-half), slanting ocular ridges, smaller eyes, and radial arrangement of granules on the brim. No other species of *Olenus* is known to have four pairs of glabellar furrows. In its cranidial proportions *O. delicatus* appears to be quite similar to *O. dentatus* Westergaard, 1922, which, however, has only three pairs of glabellar furrows and no granulation.

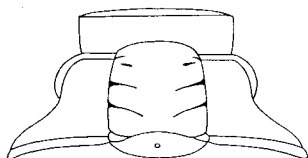


Fig. 17. *Olenus delicatus*, reconstruction of holotype, Pl. 4, fig. 12.

**Description:** The somewhat square glabella, as in most of the species of *Olenus*, is as long as wide; the occipital ring is as wide as the posterolateral limb and bears a node; the rim is very short and delicate, the brim is one-sixth of the length of the cephalon. The palpebral lobes are of medium size and are connected with the ocular ridges. The glabellar furrows are relatively short; the two posterior and the anterior furrows are connected with the axial furrows, whereas the furrows of the third pair do not reach the axial furrows.

**Generic relationship:** If the concept of the genus *Olenus* remained restricted to species with only three pairs of glabellar furrows, then *O. delicatus* should be removed from it. The fourth, anterior pair of the furrows is, however, quite weak and may have escaped detection in other species, and its presence or absence should not be regarded as a character of an absolute generic significance. Furthermore, in all other aspects the species *delicatus* remains a regular *Olenus*. The significance of the presence of four glabellar furrows is discussed in more detail below, under ?*Olenus* sp. A.

As seen from its age (below), *Olenus delicatus* is, probably, one of the youngest known species of its genus. Nevertheless, it is conservative in retaining the ancestral four pairs of glabellar furrows.

**Occurrence and age:** *Olenus delicatus* was found in a grey laminated limestone at locality D120b, which is the highest known fossiliferous bed in the Pomegranate Limestone. The age is the Upper Cambrian (Idamean) Zone with *Agnostotes inconstans* and *Irvingella tropica*.

?OLENUS sp. A

(aff. *Parabolina? quadrisulcata* Henningsmoen, 1957)

(Pl. 2, fig. 1; Text-fig. 18.)

**Material:** One fragmentary cranidium (CPC 4253) in dark grey limestone, associated with fragments of *Pseudagnostus*, *Proceratopyge* and *Eugonocare*.

**Nomenclature:** The occipital lobe is not preserved and the species name is left open, therefore, although the species is evidently new. A definite generic name cannot be applied either for the following reasons: (1) ?*Olenus* sp. A. is related to *Olenus* (?) sp., Westergaard (1922, plate 6, fig. 25) of which only one cranidium is known; (2) Henningsmoen (1957, p. 128) assigned Westergaard's specimen to a new species *Parabolina? quadrisulcata*; this new species cannot be questioned, but the application of the generic name *Parabolina* is as doubtful as *Olenus* (?) in Westergaard's interpretation; (3) The Swedish *quadrisulcata* and the Australian specimen belong to the subfamily Oleninae.

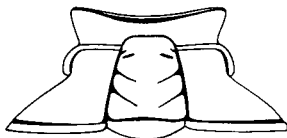


Fig. 18. ?*Olenus* sp. A, reconstruction of specimen Pl. 2, fig. 1. Presence or absence of occipital node unknown.

**Description:** The fragment of the cranidium is 4 mm. long (as preserved). The glabella is tapering, slightly longer than wide, and subtruncated in front; four distinct pairs of glabellar furrows are present, of which the third pair does not reach the axial furrows. The frontal margin recedes rearward in the middle, and the anterior border is delicate and upturned. The brim is relatively large, expanding anterolaterally, and the anterior sutures are straight and divergent. The palpebral lobes are small, and opposite the third glabellar lobes, and the interocular cheeks are only slightly narrower than the glabella on the same level. The ocular ridges are strong, confluent with the palpebral lobes, and slant adaxially. The glabella is smooth, the brim venulose to reticulate, and the cheeks reticulate.

*Parabolina? quadrisulcata* differs from our specimen in having converging anterior sutures, but the resemblance is, nevertheless, close: both have four pairs of glabellar furrows in a similar arrangement, receding frontal margin, large posterolateral limbs, small eyes in similar position, and a conical glabella; the ornament is also identical.

Apparently congeneric with ?*Olenus* sp. A. is a trilobite whose cranidium has been assigned by Kindle & Whittington (1959, fig. 3b) to *Ulrichaspis*; it is specifically distinct from ?*Olenus* sp. A in having a relatively long brim. Both ?*Olenus* sp. A and the '*Ulrichaspis*' of Kindle & Whittington are rather different from *Ulrichaspis* Rasetti, 1945, which has only two pairs of furrows, and palpebral lobes 'situated somewhat in advance of the anterior end of the glabella'.

**Significance of four pairs of glabellar furrows:** The observation that the early olenids (*Olenus*, *Parabolina*) have three, and the late (*Parabolinella*) four, pairs

of glabellar furrows deserves special attention. According to Henningsmoen (loc. cit.) *Parabolina? quadrisulcata* 'is the earliest known olenid with four distinct pairs of glabellar furrows': ?*Olenus* sp. A and *Olenus delicatus* sp. nov. are of about the same age as *quadrisulcata*. Four pairs of glabellar furrows with the third pair not reaching the axial furrows represent the 'full set' of furrows of early ptychopariids (Öpik, 1961b; description of *Papyriaspis*). It is a primitive and fundamental character; once lost its recurrence is doubtful: the early Upper Cambrian *Oleni* with a lesser number of furrows are themselves modified derivatives from earlier bearers of a 'full set', and cannot be regarded as ancestors of the late species with four pairs of glabellar furrows. It appears that all Olenidae with the 'full set' represent the main stock, whereas the Scandinavian *Oleni* with a reduced number of glabellar furrows represent one of its lateral off-shoots; and *Olenus delicatus* is a conservative species of this off-shoot. In Henningsmoen's interpretation (Chart 6; p. 17; 82), however, *Olenus* is regarded as the ancestral form.

Of course, the possibility of a repeated re-occurrence of the 'full set' by a reversal of the process of effacement in late forms cannot be definitely denied: it depends on the function of the glabellar furrows. The external absence of a pair of glabellar furrows may not mean that organs supported by the furrows became obsolete; if so, the re-appearance of furrows may be only a mechanical accommodation by a development of totally new furrows, the place of which is predetermined by the fixed position of the organs, and not by the furrows which were present and lost in the ancestors.

*Occurrence and age:* The specimen was found in the Pomegranate Limestone at locality D119, in a bed of dark grey bituminous limestone above the beds with the complete specimens of *Erixanium sentum*; its age is the upper part of the Idamean *Erixanium sentum* Zone.

#### Genus ASILLUCHUS nov.

*Diagnosis:* *Asilluchus* is a genus of the Oleninae with a distinct but short brim, divergent anterior sutures, small eyes, long and narrow trapezoidal posterolateral limbs, only slightly divergent posterior sutures, and five pairs of glabellar furrows; distinguished by its long glabella with furrows that join the axial furrows. The genus is monotypical, with *Asilluchus nanus* sp. nov. as the type.

*Asilluchus* possesses a combination of characters that are already known in *Plicatolina* Shaw, *Westergaardites* Troedsson, and *Parabolina* Salter, but this particular combination, as a whole, is unknown in any of these genera, and is accompanied in *Asilluchus* by a relatively long glabella not seen in other genera of the Oleninae.

*Asilluchus* is included in the Oleninae, being comparable with several genera of that subfamily, as listed by Henningsmoen (1957); but the subfamily Triarthrinae, when accepted, is also a possibility, because it contains the 'nearest genus'—*Plicatolina*.

The Tremadocian *Plicatolina* Shaw (1951) has wider, triangular fixed cheeks, its posterior sutures are convex, its glabella has a frontal notch, and only four pairs of furrows not reaching the axial furrows. The main difference between these genera is the convexity of the posterior suture in *Plicatolina* and the triangular shape of its posterolateral limbs; in *Asilluchus* these sutures are sinuose, and the posterolateral limbs are trapezoidal.

Shaw (loc. cit., p. 104) indicated that the immature specimen of *Parabolinella evansi* Kobayashi (1938, pl. 16, fig. 14) is similar 'in the advanced position of the eyes and the manifold lobation of the glabella' to *Plicatolina*. It appears, however, that this specimen is not related to '*Parabolinella*' *evansi*, but is a cranidium of a mature *Asilluchus*, and contemporaneous with *A. nanus*.

*Asilluchus* (early Upper Cambrian) and *Plicatolina* (Tremadocian) are closely related genera and represent a lineage ranging through the whole of the Upper Cambrian into the Lower Ordovician; this lineage is parallel with the lineages of *Olenus* and other Oleninae and cannot be derived even from the earliest known olenid genera, including *Olenus* itself.

*Westergaardites* Troedsson (1937) has narrow posterolateral limbs similar to those of *Asilluchus*, but is distinguished by the absence of a brim, and by its expanded glabella. Incidentally, the pleurae of the thorax of *Westergaardites* and of *Centropleura* have the same structure.

*Asilluchus* differs from *Parabolina* in having divergent preocular sutures, a relatively long (and narrow) glabella and five pairs of glabellar furrows. From *Parabolinella* it differs in its relatively large glabella, very short brim, and the simplicity of the glabellar furrows, which all join the axial furrows.

The presence of five pairs of glabellar furrows in *Asilluchus* and in *Parabolinella* deserves some more comment. According to Henningsmoen (op. cit., p. 138) in *Parabolinella rugosa* Brögger 'apart from the four pairs of glabellar furrows, there are also two pairs of faint furrows between the occipital furrow and S 1' (the

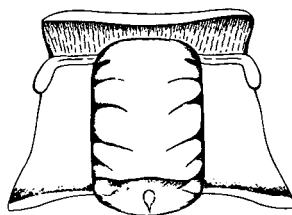


Fig. 19. *Asilluchus nanus*, holotype cranidium (Pl. 6, fig. 8), reconstructed with the aid of internal cast and associated specimens.

posterior pair of glabellar furrows). Henningsmoen's illustration (pl. 12, fig. 9) suggests, however, only one, but bifurcate, pair of short intervening furrows. *Parabolina heres* Brögger, as illustrated by Westergaard (pl. 7, figs. 17 and 30) displays also these intervening glabellar furrows. Finally, *Acerocare ecorne* has externally 'four pairs of faint glabellar furrows', but five pairs of parietal glabellar muscle spots (Henningsmoen, loc. cit., p. 92). To conclude, the number of

glabellar furrows is variable and usually less than five, or even less than four; but *Asilluchus*, *Parabolina*, and *Parabolinella*, by analogy with *Acerocare*, should have also six pairs of parietal muscle spots (one occipital and five glabellar) that correspond to the maximal possible number of furrows. Thus, the fifth pair of furrows is by itself not an extraordinary character, but its presence or absence is still of taxonomic value.

ASILLUCHUS NANUS sp. nov.

(Pl. 6, fig. 8; Text-figs. 19, 20.)

**Material:** Six cranidia, all in limestone, were examined; all are fragmentary, but together they provided information for the reconstruction in Text-figures 19 and 20.

**Holotype** is the illustrated specimen Plate 6, figure 8, CPC 4294, 2.5 mm. long.

*Asilluchus nanus* is a small trilobite with cranidia not exceeding 2.5 mm. in length. This small size might be interpreted as larval; but olenids of this size are usually mature, and no larger trilobites are known which could represent the adult stage of *Asilluchus*. Several examples of small mature olenids are known. For instance, Westergaard (1922, pl. 6, fig. 19) illustrates a mature specimen of *Parabolina spinulosa* whose cranidium is less than 2 mm. long, and in the mature specimens of *Olenus ogilviei* the cephalae are of a similar size.

The diagnosis of *A. nanus* coincides with the generic diagnosis.

**Remarks:** The two text-figures indicate a certain variability: 1) the glabella varies in shape, between almost parallel-sided and slightly tapering; 2) the brim can be quite large, as seen in the holotype, or relatively short (Text-fig. 20); 3) in the holotype the rim is upturned and recedes rearward, but in other specimens, probably owing to flattening, it is straight.

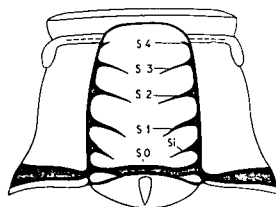


Fig. 20. *Asilluchus nanus*, reconstruction of cranidium CPC 4305, Georgina Limestone, locality W10. SO—occipital furrow; S1—first (posterior), S2—second, S3—third, S4—fourth (anterior) glabellar furrows; these furrows constitute the full set of glabellar furrows of ptychopariids and of most of the olenids. Si—intervening glabellar furrows of *Asilluchus* and some other olenids.

The ocular ridges are horizontal, prominent and faintly duplicated; they pass without interruption into the very small reniform palpebral lobes and form with them a structure shaped like a golf club. The interocular cheek is about as wide as half the glabella, and the rest of the cheek (the posterolateral limb) is not much wider, except for a slight widening in its rear part. The position of the eyes opposite the anterior glabellar lobes is most striking, and not seen in any other olenid. The occipital segment has a pair of lateral lobules, and the occipital lobe bears a triangular, elongate, and prominent node.



*Occurrence and age:* The holotype and most of the specimens were found in the Pomegranate Limestone at locality D120b (see Text-fig. 3); one cranidium (CPC 4305) was found in the Georgina Limestone, locality W10. The age is the early Upper Cambrian (Idamean) Zone of *Erixanium sentum*.

Subfamily RHODONASPIDINAE nov.

*Diagnosis:* Rhodonaspidinae are multisegmented Olenidae distinguished by large eyes, divergent anterior sutures, elongate parallel-sided glabella, and a *Parabolina*-like spinose pygidium.

The subfamily is monotypical. Reasons for including *Rhodonaspis* in Olenidae have been discussed previously by Öpik (1961).

Genus RHODONASPIS Whitehouse, 1939

RHODONASPIS LONGULA Whitehouse

(Pl. 6, figs. 1-7; Pl. 7, figs. 1-2; Text-figs. 21, 22.)

*Rhodonaspis longula*, the type species of the genus, is based on a single and almost complete specimen (Whitehouse, 1939, pl. 23, fig. 9). The reconstruction of this specimen (op. cit., p. 220) is, however, incorrect: in it 1) the postero-lateral limbs are too short, 2) the anterior sutures are shown to be convex abaxially, and 3) the cranidial front is too narrow. As seen from the illustration (op. cit., pl. 23, fig. 9) of the type specimen these parts are damaged and allow of no accurate reconstruction. Reasons are given below for considering our material to be conspecific with *Rhodonaspis longula*.

Crania such as those illustrated on Plate 6 have been found in many localities of early Upper Cambrian (Mindyallan) rocks of north-western Queensland, in various states of preservation, but they appeared to be different from the type specimen of *Rhodonaspis longula* because the course of the anterior sutures in them is divergent, and rather different from that shown in the reconstruction of Whitehouse. The presence of *Rh. longula*, however, was evident from associated pygidia, as illustrated in Plate 6, figures 5-7, which are identical with the pygidium of the holotype.

Similar pygidia are also seen in the two incomplete thoraces, Plate 7, figures 1-2; these thoraces are identical with the thorax of the holotype of *Rh. longula* in Whitehouse (1939, pl. 23, fig. 9). Finally, close comparison of the occipital (posterior) part of the cranidia (Pl. 6) with the anterior segment of the thorax (Pl. 7, fig. 1) and with the same parts of the specimen of Whitehouse indicates that all these specimens should be regarded as conspecific.

*Mode of preservation:* The cranidium Plate 6, figure 3, and the thoraces occur on thin siliceous shale partings in limestone; they are weathered and the test is not preserved. The testless cranidium Plate 6, figure 4, is in hard chert. The specimens Plate 6, figures 1, 2, 5, and 6 are in limestone, and partly flattened, but the test is preserved. The type specimen of Whitehouse is a mould in chert.

*Remarks:* The doublure, as can be seen in Plate 7, figures 1-2, is extremely narrow. Its narrowness is also apparent from the extent of the pleural furrows reaching into the base of the spines. Olenidae also have a narrow doublure (Henningsmoen, 1957, p. 95).

The pleural furrows are oblique, as required by the diagnosis of Olenidae, but obliquity of these furrows is a common character in trilobites (see Öpik, 1961b). The long, backward-directed pleural spines are similar to those of the olenid *Parabolina*. However, a segment of the thorax of *Rhodonaspis* differs from *Parabolina* in having wider, channel-like pleural furrows and a relatively narrow axial lobe (about one-fifth of the total width in the anterior part of the thorax). The thorax of *Rhodonaspis* is multisegmented, with 19 segments, but not reaching the maximum number of 21-22 observed in Olenidae.

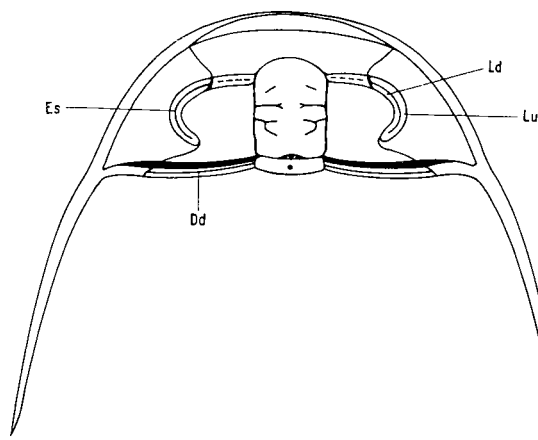


Fig. 21. *Rhodonaspis longula*, diagram of cranium, Pl. 6, fig. 2. Es—ocular striga; Dd—opisthopleural vein; Ld—inner (shorter) arc of palpebral lobe; Lu—outer arc of palpebral lobe.

The pygidium of *Rhodonaspis* is small, about one-eleventh of the total length of the body, and its size is, therefore, 'olenid'. The structure of the pygidium of *Rhodonaspis* is the same as that of *Parabolina heres* (vide Westergaard, pl. 7, fig. 27); the only differences are the wider and longer pleural furrows and the overlap of anterior pleurae over the second pair in *Rh. longula* and a small deviation in proportions. The pygidium has four pairs of pleurae with spines and four annulations and a terminus in its axis. An exception is the large specimen Plate 7, figure 2, which has five annulations and five pairs of marginal spines. In this specimen the anterior segment of the pygidium is, perhaps, a semi-detached or semi-anchylosed segment, and a part of the thorax.

Presumably *Rhodonaspis* and *Parabolina* share a pygidium with a conservative design persisting in olenids through the whole of Upper Cambrian and Tremadocian times. If so, *Parabolina* is not derived phylogenetically from a late *Olenus* (see Henningsmoen, 1957, p. 303) but represents a separate trend. Thus, the *Olenus*—and the *Parabolina*—trends were already separate in the early Upper Cambrian time. *Rhodonaspis*, however, in spite of its conservative pygidium, cannot be regarded as the direct ancestor of *Parabolina*.

The cranium of *Rh. longula* is distinguished by its very large palpebral lobes and short and wide (transversely) posterolateral limbs. These are correlate characters, however, because large palpebral lobes naturally will reduce the length of the posterolateral limbs. The ends of the posterolateral limbs are not rounded, but pointed, as seen in some species of *Olenus*. The glabella is parallel-sided, rounded in front and relatively long, with a width to length ratio of 2:3; but in olenids it is 1:1; thus *Rhodonaspis* has a 'stretched' glabella of an *Olenus*. The ocular ridges are prominent and 'horizontal' and separated from the palpebral lobes by a depression.

As seen in Plate 6, figures 2 and 3, and Text-figure 21, the palpebral lobes are double, with a palpebral striga as a dividing line. The outer lobe is the longest and almost touching the ocular ridge, whereas the adaxial lobe is shorter, with a depression separating it from the ocular ridge. It appears that the ocular ridge itself is also double, being divided in two by a line, which can be taken as the vestige of the striga.

The brim, one-sixth of the total length of the cephalon, is well developed, as is common in *Oleni*, and the rim is also narrow and delicate. But the front is curved; this is uncommon in olenids, most of which have an almost straight anterior cranial margin. Only the Tremadocian *Beltella* can be compared in this sense with *Rhodonaspis*. The brim is minutely venulose and the cheeks reticulate. A peculiarity of the cranium of *Rhodonaspis* is the course of the anterior sutures. They are slightly sinuous or almost straight and diverge at an angle of slightly more than 90 degrees. Only in late olenids (*Parabolinella*, *Beltella*) are these sutures also strongly divergent.

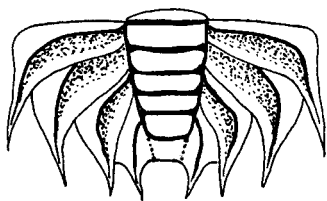


Fig. 22—*Rhodonaspis longula*, diagram of pygidium, Pl. 6, fig. 5.

*External habit:* *Rhodonaspis longula* is a small trilobite that may have been 30 to 40 mm. long; its cephalon is broad, much wider than the anterior part of the thorax, with short genal spines, wide brim and cheeks, parallel-sided long glabella, with interocular cheeks as wide as the glabella, and very large arcuate eyes. The ocular ridges are distinct, horizontal, and separated from the palpebral lobes, which consist of a shorter adaxial and a longer abaxial arc. The occipital lobe has a low node, and the glabella bears three pairs of furrows, of which the posterior ones are trifid. The cephalic border is narrow, the glabella is smooth, the brim is weakly venulose, and the cheeks reticulate.

The thorax is lanceolate, tapering evenly rearward; it consists of nineteen segments, with a narrow axial lobe; the pleural lobes are geniculate about their

midlines; the pleural furrows are broad channels which almost reach the pleural tips; these tips are extended into spines deflected sideways, which increase in length rearward; in the rear they are as long as three segments. The pygidium is small, as long as about two anterior segments, with an axis of four annulations and a terminus reaching the border; its pleural lobes are little fused, with four pairs of furrowed pleurae with rearward directed spines. No external border is present.

*Comment on illustrated material:* The cranium in limestone, Plate 6, figure 1, CPC 4288, locality W15, is 10 mm. long and belongs to a specimen more than 40 mm. long. Its test is shiny, the veins on the brim and reticulation on the cheek are barely visible.

The cranium in limestone, Plate 6, figure 2, CPC 4289, locality W20, shows the double palpebral lobes with the shorter adaxial arc, and the pointed postero-lateral limbs provided with the opisthopleural vein on its border; the frontal marginal furrow is rather deep and the rim elevated above it.

The cranium, Plate 6, figure 3, CPC 4290, locality W20, is 7.3 mm. long; the matrix is a siliceous (chert) parting in limestone. The specimen is worn by weathering.

The cranium, Plate 6, figure 4, CPC 4291, locality D29 ('the lower chert bed' of O'Hara Shale) is an internal cast in hard chert. The glabellar furrows are deep and the veins on the brim are much clearer than in specimens retaining the test.

The pygidium in limestone, Plate 6, figure 5, a rubber cast of CPC 4292, locality G48, is 3.7 mm. long, and belongs to a specimen of almost 40 mm. The pleural furrows extend into the spines, and are broad and deep; the anterior pleurae have conspicuous propleural and opisthopleural veins; the second pair of pleurae is partly concealed under the anterior pleurae.

The small pygidium in limestone, Plate 6, figure 6-7, CPC 4293, locality W15, is 1.8 mm. long, of a specimen about 20 mm. long. Its axis is rather strong, with a pointed terminus reaching the margin.

The thorax and pygidium, in a siliceous parting in limestone, Plate 7, fig. 1, CPC 4296, locality W20, are 12.5 mm. long together; the thorax is almost complete, with sixteen segments out of nineteen, and some of the pleural spines are exposed. It was a specimen 15-16 mm. long.

The fragmentary thorax with the pygidium, Plate 7, figure 2, CPC 4297, locality W20, is 10.6 mm. long. Nine segments are preserved; the narrow doublure is exposed; the pygidial axis has exceptionally five annulations, and five pairs of marginal spines are present.

*Occurrence and Age:* According to Whitehouse (1939, p. 220) the type specimen of *Rhodonaspis longula* was found 'about two miles south of Tyson's Bore on Glenormiston', but the place has not yet been found again. *Rh. longula* has been found, however, in almost all localities of the lower part of the Georgina Lime-

stone, the upper part of the Mungerebar Limestone, and in the lowermost part of the O'Hara Shale (localities D6, D28 and D29; Öpik, 1961a); it is a common species of the early Upper Cambrian (Mindyallan) Zone of *Glyptagnostus stolidotus*, and is confined to that Zone.

#### Family TALBOTINELLIDAE nov.

*Diagnosis:* Talbotinellidae are Olenacea with an extremely conical glabella and large posterolateral limbs.

It is possible to include *Talbotinella* in the Family Olenidae, together with the genus *Parabolinites* Henningsmoen, as a separate subfamily Talbotinellinae; if so, the 'extremely conical glabella' should be regarded only as a generic character.

#### Genus TALBOTINELLA Poulsen, 1960

*Talbotinella* according to its author is a genus of the family Lonchocephalidae (Solenopleuracea) being comparable with the lonchocephalid *Talbotina* Lochman. The affiliation of these genera is, however, rather general and remains inconclusive even on a superfamilial level. *Talbotina*, for example (Harrington et al. 1959, p. 0279), 'may be synonymous with *Weeksina*' and both are once more illustrated (op. cit., p. 0307) in association with Marjumiacea from which they differ very little indeed. Hence, the classification of *Talbotina* is controversial, and remains a problem with many possible solutions.

When *Talbotinella* is classified with *Talbotina* it remains without a conclusive familial status. It is, however, possible to place *Talbotinella* at the head of a separate family of Olenacea, and reserve the classification of *Talbotina* as a separate problem.

The synonymy of Olenacea and Ptychopariacea is apparent from our discussion of their superfamilial concepts, and *Talbotinella* can be therefore regarded as a ptychopariacean as well. Nevertheless *Talbotinella* and Talbotinellidae are closest to the Olenidae, within which they could be accommodated as a separate subfamily.

The suggested classification of *Talbotinella* remains, of course, subjective because it depends on the emphasis on characters which are regarded as being significant in olenids. For example, the occurrence of a pair of glabellar furrows intervening between the occipital (So) furrow and the S1 glabellar furrows (see under *Asilluchus*) should be regarded as an olenid character, and the erratic occurrence of such furrows is evident from the diagnosis of *Talbotinella* (Poulsen, loc. cit., p. 23). These furrows are absent in the Australian *Talbotinella notulata*. It should be noted here that Poulsen annotates the glabellar furrows beginning from the front, whereas in this paper it is reversed, beginning with the posterior (S1) pair of furrows. The first furrows in Poulsen's annotation are the S3 pair, and the S4 pair of furrows is absent in the Argentinian species.

The olenacean relationship of *Talbotinella* emerges from a comparison with the olenids *Parabolinella*, *Protopeltura*, and *Parabolinites*.

The following similarities to *Parabolinella* are apparent: 1) several of its species have divergent anterior sutures; 2) the S1 furrows have the same trifid shape as seen in *Talbotinella*; 3) the intervening glabellar furrows occur in some species of *Parabolinella* and in Argentinian species of *Talbotinella*.

In *Protopeltura* Brögger the cranidium is of the same character as in *Talbotinella*, but the glabella is less conical and the anterior sutures are convergent.

*Parabolinites* Henningsmoen is similar in the structure of the cranidium and has a similar position of the eyes, a similar course of the sutures, and also large posterolateral limbs. Its glabella has a well rounded front, but, compared with *Talbotinella*, is less conical and has a lesser number of glabellar furrows. Its pygidium (Westergaard, 1922, pl. 8, figs. 6 and 7) differs from that of *Talbotinella* in minor details only and both have a 'flat rim' (Westergaard, op. cit., p. 199). *Talbotinella* was described originally from the uppermost Middle Cambrian *Bolaspidella* zone of Argentina (Mendoza) (Poulsen, 1960).

**TALBOTINELLA NOTULATA sp. nov.**

(Pl. 6, fig. 9; Text-figs. 23, 24)

**Material:** Only one cranidium, the holotype (CPC 4295), is sufficiently preserved. A chip containing parts of the glabella and the occipital ring is lost, but the remaining part allows of a fair reconstruction. The holotype is 8 mm. long.

**Diagnosis:** *Talbotinella notulata* is a species without an occipital spine, with strongly divergent anterior sutures (at about 60 degrees), with relatively forward

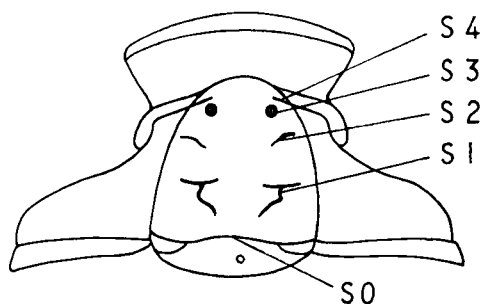


Fig. 23. *Talbotinella notulata*, reconstruction of holotype cranidium, Pl. 6, fig. 9. See Text-fig. 24. SO—occipital furrow; S1—first, S2— second, S3—third, and S4—fourth glabellar furrows.

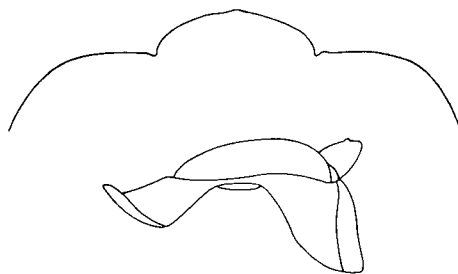


Fig. 24. *Talbotinella notulata*, transverse section (rear part of cranidium) and lateral view of holotype (see Text-fig. 23).

placed eyes (opposite the second glabellar furrows) which are close to the glabella (about half of the length of the palpebral lobes), with the base of the glabella wider than its length, with large posterolateral limbs, and a smooth test.

Among the known species only *T. rusconii* Poulsen has no occipital spine, but its glabella is much narrower (longer) and the anterior sutures are only slightly divergent, or almost parallel.

*Generic position:* *Talbotinella* Poulsen is a distinctive genus and the species *notulata* is identifiable at a glance as a *Talbotinella*. It deviates from the generic diagnosis by the presence of the anterior glabellar furrows and by the greater divergence of the anterior sutures; but these characters, having a specific significance, cannot change the generic position of *notulata*.

*Description:* The cranidium is hourglass shaped, the lower part being the larger. It is rather convex, with the glabella elevated, and with downsloping convex posterolateral limbs, and a relatively flat downsloping brim. The eyes are close to the glabella, the interocular cheek (including the palpebral lobes) being slightly less than a third of the width of the glabella between the eyes. The eyes are opposite the second (S2) pair of the glabellar furrows. The palpebral lobes are small, convex, reniform, and confluent with the prominent and slanting ocular ridges. The posterolateral limbs are large, with a strongly sinuous sutural edge and almost vertical at the tips. The anterior facial sutures are divergent and nearly straight within the brim. Within the marginal furrow the sutures turn inward, cut the rim in a gentle curve and, most probably, meet on the margin. The rim is narrow, slightly convex and not elevated. The anterior margin is evenly curved, whereas in the olenids it is almost straight. A curved front occurs, however, in the olenid *Beltella* and in some species of *Parabolinella* and *Parabolina*, as, for example, in *Parabolina jemtlandica* Westergaard (1922, pl. 7, fig. 35). The brim is long, about a quarter of the glabella, which is usual, e.g. in *Parabolinella*. The glabella is conical and tapers more than in any other olenid. It is wide at its base, with slightly convex sides and an evenly rounded front, and surrounded by a well marked axial furrow of an even depth.

Four pairs of glabellar furrows are present, as seen in the early ptychopariids and late olenids (*Parabolinella*, *Plicatolina*; see also under ?*Olenus* sp. A). The posterior (S1) furrows are deep, trifid, and geniculate (as in *Parabolinella limitis* Brögger) and do not reach the axial furrows. The furrows of the second (S2) pair are moderately impressed, oblique, curved, short, and not connected with the axial furrows either. The third (S3) furrows are a pair of isolated rounded pits on the level of the anterior ends of the palpebral lobes. Such pits occur in the youngest (Ordovician) olenid *Triarthrus* (Henningsmoen, 1957, pl. 11, fig. 10) and in *Westergaardites* Troedsson (ibid., p. 153). The anterior (S4) furrows are connected with the axial furrow. They are short, faint and directed obliquely backward and outward. The occipital furrow is furcate at its ends, with a pair of lateral elongate occipital lobules. The occipital lobe bears a weak node. The surface of the brim is delicately venulose, the rest of the cranidium is apparently smooth.

*Occurrence and age:* The holotype was found in the Georgina Limestone at locality G50. Its age is the early Upper Cambrian (Mindyallan) Zone of *Glyptagnostus stolidotus*.

#### Superfamily PTYCHOPARIACEA Matthew, 1887

The superfamily Ptychopariacea can be defined on its own merit, but its differential diagnosis in respect of the Olenacea, as discussed above, cannot be established. The retention of these two synonyms is possible only on subjective considerations, or under the assumption that a distinction will be finally discovered and formulated. Neither of the two names can be suppressed because neither can be regarded as an exhumed, forgotten or obsolete name whose re-establishment would upset the current usage. The name Olenacea especially cannot be suppressed, although twice as many genera are listed under the Ptychopariacea as under the Olenacea in Harrington et. al. (1959), and the numerical predominance of the former may increase greatly with the inclusion of the pterocephaliid and solenopleurid genera. Using the priority name Olenacea and adding to it the Ptychopariacea would produce a very large superfamily. So it can be argued that it is too large a superfamily and should be split; but this argument is irrelevant from a scientific point of view, and, furthermore, the existing families and subfamilies satisfy the need for reasonably small units. The fact that the ptychoparioids are a most prolific and diversified stock of trilobite species and genera is rather notable and should not be masked and sacrificed in favour of artificial subdivisions.

To conclude, the name Ptychopariacea is regarded here as a synonym of Olenacea, but is retained as a heading of reference which preserves the contact with the current taxonomic literature, and especially with the fundamental concept of the ptychoparioid organization or design.

#### Family PTEROCEPHALIIDAE Kobayashi, 1935

The concept of the Pterocephaliidae has been recently revised by Palmer (1960). Harrington et al. (1959) included them in the superfamily Dikelocephalacea, but dispersed some of them under different taxa, placing *Olenaspella* in the Illaenuracea, *Proaulacopleura* in the Papyriaspidae (Olenacea), but retaining the related *Eugonocare* together with *Aphelaspis* in the pterocephaliids. All these genera belong to the subfamily Aphelaspinae Palmer, 1960, affiliated with the Ptychopariacea. Their connexion with the Dikelocephalacea is only of a subordinal character.

#### Subfamily APHELASPIDINAE Palmer, 1960

Two cranidia are described below as ?*Aphelaspis* sp. B; open nomenclature is necessary because the aphelaspids are now a well known group and the identification of their genera needs more information than is provided by our fragmentary material. The queried generic designation ?*Aphelaspis* indicates the nearest genus within the subfamily.



?APHELASPIS sp. B.

(Pl. 4, figs. 14 and 15; Text-fig. 25.)

*Material*: Two small cranidia on a piece of limestone that contains also the cranidia of *Hercantyx* and *Olenus delicatus*, and the pygidium of *Irvingella*.

*Remarks*: Palmer's (1954) diagnosis of *Aphelaspis*—'cranidium with glabella straight-sided, usually truncate anteriorly; frontal area consisting of distinct brim and border but lacking well defined marginal furrow'—is applicable to these specimens. Furthermore the position of the palpebral lobes and the course of the sutures are the same as in *Aphelaspis*.

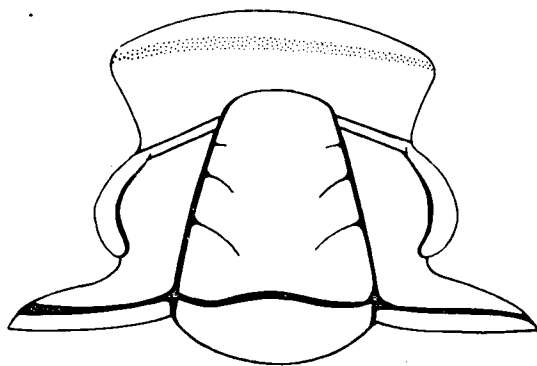


Fig. 25. ?*Aphelaspis* sp. B. reconstruction with aid of counterpart of cranidium Pl. 4, fig. 14.

The relatively large palpebral lobes, the large occipital lobe, and the minute granulation of the surface are specific characters if compared with the known species of *Aphelaspis*. The species however cannot be named because the specimens are insufficiently preserved.

*Stratigraphic significance*: The occurrence of an *Aphelaspis*-like trilobite in Queensland is no reason for a correlation with the American *Aphelaspis* zone, which refers to the species *A. walcotti* and the fauna associated with it. *Aphelaspis walcotti* is about one or two zones older.

*Comment on illustrated material*: The cranidium, Plate 4, figure 14, CPC 4286, is 2.6 mm. long; its counterpart is also preserved and was used in drawing Text-figure 25. The other specimen (CPC 4285) is 1.9 mm. long; its glabella has a slightly more rounded front and abaxially convex flanks.

*Aphelaspis brachyaspis* Palmer appears to be an affiliated species: it also has a rather narrow rim, a distinct marginal furrow, slanting ocular ridges, but its glabella and occipital lobe are shorter than in the Australian form.

*Occurrence and age*: Found only in the Pomegranate Limestone at locality D120b; the age is the early Upper Cambrian (Idamean) Zone of *Agnostotes inconstans* and *Irvingella tropica*.

#### Family ERIXANIIDAE nov.

*Diagnosis:* Erixaniidae are Ptychopariacea with a short pygidial axis, narrow pygidial border and doublure, a subrectangular glabella, a very large brim, a narrow rim, large eyes, and a large rostral shield; in the type genus the thorax has twelve segments.

This diagnosis is based essentially on a particular combination of ptychoparioid characters; the structure of the pygidium is however unique and the small number of segments in the thorax is exceptional and rare: *Annamitia* has eleven, and only the blind Ptychopariacea and Olenidae may have even less.

The family Erixaniidae is monotypical, and all known material is included in the genus *Erixanium*. The familial name is introduced here as a taxonomic necessity, because the concept of any other family of the Ptychopariacea would be greatly changed and expanded with the inclusion of *Erixanium*.

The superfamilial classification (Ptychopariacea) is immediately evident from the external habit and the ventral cephalic structure of *Erixanium*. Its small number of twelve segments in the thorax is even less than in the Ptychopariidae (thirteen to fourteen segments), and much smaller than in the multisegmented Papyriaspidae, including *Alokistocare* and its allies (see Öpik, 1961b). As regards the number of segments in the thorax and the structure of the pleurae (rearward-swept long spines) *Erixanium* is comparable with some of the Pterocephaliidae (Ptychopariacea), especially with *Litocephalus* Resser (see Palmer, 1956; 1960). But *Litocephalus* has a long ('normal') pygidial axis, no defined pygidial border, a very wide pygidial doublure, small and forward placed eyes; and the Pterocephaliidae in general have only a median subcranial suture and not the large rostral shield of *Erixanium*.

#### Genus ERIXANIUM nov.

*Type species:* *Erixanium sentum* sp. nov.

*Generic diagnosis:* *Erixanium* (and Erixaniidae) are Ptychopariacea distinguished by having twelve segments in the thorax and a small pygidium with a short axis, wide pleural lobes, narrow border and doublure, and subparallel anterior flanks. Furthermore, the following combination of characters (which occur in other genera of Ptychopariacea in different combinations) appears to be inherent to *Erixanium*: 1) a very large and relatively flat brim with divergent straight sutures and a narrow rim; 2) large arcuate palpebral lobes half or more as long as the glabella and placed behind its middle; 3) relatively wide interocular cheeks, which may be even as wide as the glabella itself; 4) an exceptionally narrow (longitudinally) occipital lobe; 5) a low subrectangular to rectangular glabella, with three to four pairs of furrows; 6) pleurae of the thorax extended into long and rearward-directed spines; 7) wide (transversely) rostral shield not contacting the hypostoma.

Three Idamean species, all new, are described below: *E. sentum*, *E. strabum*, and *E. alienum*.

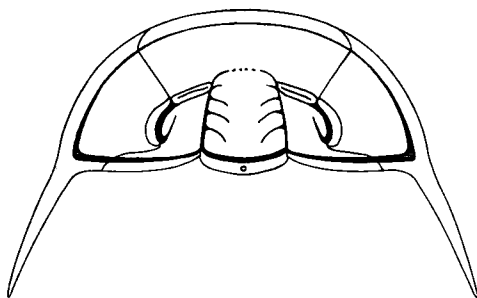


Fig. 26. *Erixanium sentum*, diagram of dorsal side of cephalon, composite, from specimens Pl. 8 and 9. See Text-fig. 27.

The genus *Erixanium* is also represented in the Dunderberg shale in Nevada, as seen from Palmer (1960, pl. 11, figs. 1-3 and 5, 6), by forms which are apparently not conspecific with the Australian species, although they are of the same geological age.

*ERIXANIUM SENTUM* sp. nov.

(Pl. 8, figs. 1-4, 7 and 8; Pl. 9; Text-figs. 26, 27.)

*Material:* Six selected specimens (four cranidia and two pygidia on Plate 8) from the Georgina Limestone, and the complete specimens, one cranidium, and one isolated hypostoma (on Plate 9) from the Pomegranate Limestone.

Holotype is the pygidium, CPC 578, Plate 8, figure 1, previously published by Öpik (1961a, pl. 69, fig. 2).

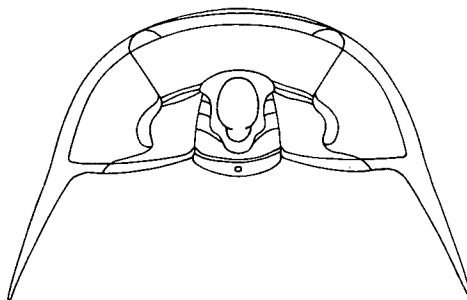


Fig. 27. *Erixanium sentum*, diagram of ventral side of cephalon, composite from specimens Pls. 8 and 9.

*The cephalon:* The cephalon is slightly wider than a semicircle, and relatively large. It is as long as nine anterior segments of the thorax, and about 0.36 of its total length. The marginal furrow is distinct, the border is narrow, less than one-tenth of the cephalic length (variable between 0.07 and 0.09). The genal spine is slender, slightly deflected, and five to seven segments long. The free cheek is fairly large—at the level of the eyes, about as wide as the rear of the glabella. The posterior sutures diverge greatly; the anterior sutures diverge at an angle of about 72-73 degrees, the angle with the midline being about 36 degrees. The rearward extensions of the anterior sutures meet at about the middle of the second segment of the thorax.

The brim is almost flat, and long, as long as half the glabella. The interocular cheeks slope adaxially, and (including the palpebral lobes) are as wide as three-quarters to four-fifths of the glabella. The posterolateral limbs are short and wide (transversely), almost triangular, and their marginal furrow is wide and deep.

The palpebral lobes are long (slightly longer than half the glabella), arcuate, elevated, and separated by the distinct palpebral furrow from the interocular cheek. This furrow is deepest at its ends. The ocular ridges are wide, distinct, and slanting, forming together an angle of about 125 degrees. They are separated from the palpebral ridges by a depression each. In some specimens (e.g. Pl. 8, fig. 2) shallow ocular strigae are indicated, dividing the ocular ridges into an anterior and a posterior band each: these ridges are, consequently, double.

The dorsal furrows and the preglabellar furrow are distinct and of an even depth. In the cranidium Plate 9, figure 3, the median part of the preglabellar furrow is exceptionally shallow. The glabella is relatively short, slightly longer than wide, subangular, and bluntly rounded in front. It tapers slightly, the ratio of the width being around 4 (front) to 5 (rear). The glabella is only slightly convex, and broadly carinate. The glabellar furrows are variable in depth: in Plate 8, figure 3 they are shallow, but more commonly they are quite distinct. In the best preserved specimens four pairs of them can be seen (Text-fig. 26, and Pl. 8, fig. 2); they curve gently rearward; the anterior furrows are very small. All the furrows join the axial furrows.

The occipital lobe is narrow and low, and bears a low node. The occipital furrow is transcurrent, deep, but narrower than the occipital lobe.

The caeca are represented by veins on the brim, anastomotic veins on the free cheeks, and reticulate veins on the interocular cheeks and the posterolateral limbs. A caecal vein is present on each of the posterior cranial margins. The brim and the cheeks are minutely pitted in the interspaces between the veins; but the thorax is minutely granulose.

The shape of the cranidium is 'ptychoparioid'. It is widest in the rear, between the tips of the posterolateral limbs, and less wide between the anterolateral corners, the ratio being 4:3. Between the palpebral lobes the cranidium is variable around 0.9 of the frontal width. The difference in width between the anterior and the posterior ends of the palpebral lobes illustrates the set of the eyes: this ratio is about 1.1, which indicates that the eyes are not quite parallel, but set at a small angle (about 5 degrees) to the midline.

*The thorax:* The thorax has 12 segments, with narrow, deep, oblique pleural furrows. The thorax tapers rather rapidly, especially because the anterior pleural spines are divergent and the posterior ones gradually acquire a straight rearward direction. Depending on the specimen, and considering the spines as well, the ratio of fore and aft is variable between 4/1.7 and 5/1.7. The pleural lobe, however (without spines) is about 14/11 of the axis in the front, and about 5.5/6.5 in the rear; when the outer edge of the spine is included it is about 1/1.

Consequently, the pleural lobes and the thorax are more tapering than the axis. The axis is moderately convex, and the axial furrows are distinct. The pleural tips are long spines (as long as six segments) deflected sideways in anterior, and parallel to the axis in posterior, segments. The posterior spines become gradually shorter and the tips of the posterior five pairs of spines are in line with the posterior edge of the pygidium. Opisthopleural and propleural veins are discernible in proper illumination. The usual point-and-socket arrangement along the dorsal furrows provides for the articulation, but pleural fulcra could not be detected and are probably weak.

*Size:* The complete specimens Plate 9, figure 1, show that the lengths of the pygidium (without the articulating half ring), cephalon, and the whole body are about in the ratio 1:2:6, which can be used for estimation of an upper size limit of the trilobite. So, the large holotype pygidium Plate 8, figure 1, which is 8 mm. long (with the articulating half ring), corresponds to a specimen 45 mm. long and represents the largest known. The smallest complete specimen (CPC 3847, not illustrated) with the full number of twelve segments in the thorax is an adult 6 mm. long; specimens 15-20 mm. long are more frequent. Consequently *Erixanium sentum* is a small trilobite.

*The pygidium:* The pygidium is relatively small, between 0.17 and 0.18 of the total length, and slightly less than five anterior segments long. It is slightly wider than long; the ratio varies between 1.2 and 1.35. The anterior flanks are sub-parallel, and the remaining margin has an elliptical curvature. The border is narrow, and convex in its anterior part, but flattens in the rear. The axis is short, with a rounded rear without a terminus, convex anteriorly, and depressed in the rear. It is short—half the total length of the pygidium in Plate 8, figure 1, and slightly longer in other specimens. Five axial annulations are present; the inter-segmental axial ('articulating') furrows are usually transcurrent, but in Plate 8, figure 1 the posterior pair is interrupted by an axial carina. Three pairs of pleurae are present, but in Plate 8, figure 4 four pairs are indicated. The posterior, pleural portion of the pygidium bears a low sub-globose boss with a terminal prong reaching the margin at a small recess in the border. The caecal veins of the pygidium have been already described (Öpik, 1961a).

*Ventral structure:* The doublure is narrow in the pygidium and the cephalon; in the thorax, on account of the long spines, it is wider, but extends adaxially only little from the base of the pleural spines. The edge of the doublure of the pleurae has a sinus opposite the end of the pleural furrow.

In the cephalon (Text-fig. 27) a rostral shield is present, cut out of the frontal doublure by the ventral extensions of the facial sutures and the rostral suture. The rostral suture is slightly submarginal. The hypostoma is free; it was connected with the rostral plate only by the ventral membrane, without a connective stalk or any other sclerite. This condition is the result of the narrowness of the doublure and the large size of the brim, and should be expected in any trilobite with a similar cephalic structure. No hypostomal suture is present, of course; it develops

only when the hypostoma comes in touch with the doublure in trilobites with a short brim or without a brim, or when the growth of the brim becomes arrested at an early stage of the morphogenesis.

*The hypostoma:* The hypostoma is about as wide as long, and about three-quarters as long as the glabella, reaching with its tip beyond the posterior glabellar furrows. The median lobe is strongly convex, pyriform, and surrounded by a deep furrow and narrow border; the tip is extended into a tongue-like flat process.

*Comment on illustrated material:* The holotype pygidium (Pl. 8, fig. 1), 8 mm. long and 10.3 mm. wide, is exceptionally well preserved and shows even minute details of the caecal system. The smaller (6 mm. long; CPC 3844, locality W65/23, Pl. 8, fig. 4), has four pairs of pleurae and less angular flanks than the holotype.

The holotype pygidium and the cranidia on Plate 8 are all from the locality W42, and belong to the same population. The cranidium Plate 8, figure 2, CPC 3842, is 6 mm. long; its four pairs of glabellar furrows are well impressed, and the carina is prominent. The cranidium Plate 8, figure 3, CPC 3841, is relatively large (9 mm. long), but has weakly developed furrows and a narrow carina. The cranidium Plate 8, figures 7-8, CPC 3843, 6 mm. long, is distinguished by broad glabellar furrows. These cranidia indicate a variability in the development of the glabellar furrows unrelated to the size of the specimens.

The specimens on Plate 9 occur on a single bedding plane at locality D119. Frome Broken Hill Pty Ltd, collecting number 41614, by Mr R. Leslie and party, 1958) on Pomegranate Creek. Of the specimens Figures 1 and 2 (CPC 3846) the larger is 14.2 mm. long. The hypostoma has impressed itself on the glabella, and the displaced rostral shield on the brim; the narrow pygidial doublure is exposed. A small overturned specimen has preserved its hypostoma. The large cranidium (11.2 mm. long), Figure 3, CPC 3850, has a weak circumglabellar furrow and a glabella somewhat more conical than the other specimens. The hypostoma Figure 4, CPC 3849, is about 2.2 mm. long. Figure 5 (CPC 3848) is a part of the bedding plane displaying the dorsum-up and dorsum-down mode of embedding.

*Occurrence and age:* *Erixanium sentum* occurs in the Georgina Limestone and in the Pomegranate Limestone in the early Upper Cambrian (Idamean) Zone that carries the name of this species. It is common at W42 (Georgina Limestone) and D119 (Pomegranate Limestone).

#### ERIXANIUM STRABUM sp. nov.

(Pl. 8, figs. 5, 6.)

*Material:* Only two specimens, the holotype cranidium (CPC 3840) and the pygidium (CPC 3845), are well enough preserved, and suitable for description; they came from the same limestone bed, and within a few square yards of its surface.

The cranium is 7 mm. and the pygidium 3.1 mm. long; they belong to two different specimens, of unequal size (the pygidium indicates a relatively large specimen).

*Diagnosis (and differential diagnosis):* *Erixanium strabum* is known only from its cranium and pygidium: free cheeks, the thorax, and the hypostoma are unknown. The subparallel flanks of the pygidium indicate that the thorax had long backward-directed pleural spines.

In the cranium the frontal area is relatively short, the brim being one-third of the glabellar length (one half in *sentum*); the interocular cheeks, including the palpebral lobes, are half as wide as the glabella ( $\frac{3}{4}$  to  $\frac{4}{5}$  in *sentum*); the palpebral lobes are wide, about  $\frac{1}{3}$  of the glabella (in *sentum* they are narrow, about  $\frac{1}{7}$  to  $\frac{1}{8}$ ); the occipital furrow is wide, wider even than the narrow occipital lobe; the glabellar furrows are distinct; and the posterior pair connect with the occipital furrow isolating the posterior lobes; a carina is absent, but the glabella in its middle (between the adaxial ends of the furrows) is an elevated ridge; the anterior sutures diverge at an angle of about 80 degrees (in *sentum* 72 degrees) and their extensions meet on the occipital node (in *sentum* on about the second segment of the thorax); the ocular ridges are strongly slanting, with an angle of 104 degrees (125 degrees in *sentum*). The pygidium is rounded, with four to five pairs of backward-swept pleurae; its axis is pointed (blunt in *sentum*), and annulated in its anterior half (in *sentum* the whole axis is annulated), with three transcurrent furrows, and with 2-3 pairs of feebly-indicated lateral short furrows in the terminal part; no boss, but a postaxial median carina is present.

*Occurrence and age:* The illustrated specimens are from the Georgina Limestone, locality W10, south of Glenormiston, Queensland. The age is lower Upper Cambrian (Idamean). *Erixanium strabum* is associated with fragments of *Corynexochus plumula* Whitehouse, which is very abundant lower down. Above it follows the limestone with *E. sentum*; so it belongs in a low horizon in the *Erixanium sentum*, or even the passage from the *Corynexochus plumula* Zone.

Identifiable fragments occur also in the Pomegranate Limestone in association with *E. sentum*, at locality D120b.

ERIXANIUM ALIENUM sp. nov.

(Text-figs. 28 and 29.)

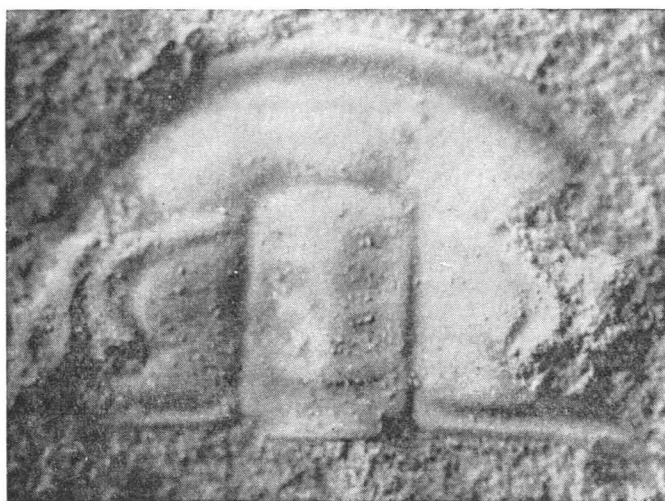
*Material:* Two pygidia and several cranidia, all in limestone, have been examined.

*Selection of the holotype:* The cranium, CPC 4299, Text-figure 29, is selected because it can be identified at a glance.

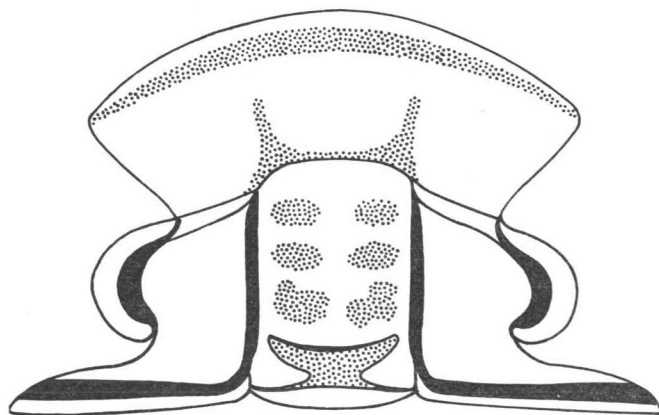
*Diagnosis:* *Erixanium alienum* is a species with an elongate subpentagonal pygidium with seven annulations in its axis; the four anterior axial furrows are transcurrent, the three posterior ones are discontinuous. The associated cranium has a parallel-sided glabella as wide as the interocular cheek (with the palpebral lobe); the glabellar furrows are developed as shallow depressions not reaching the

axial furrows; the occipital furrow is a wide depression not reaching the axial furrow and contains a pair of large lateral lobuli; the occipital lobe is extremely narrow (longitudinally).

*Differential diagnosis:* *E. alienum* differs from the two other species by its longer pygidium with a larger number of axial annulations; its glabella is distinguished



a



b

**Fig. 28.** *Erixanium alienum*, (a) Rubber cast of cranidium CPC 4299, x 12. (b) reconstruction of cranidium.

by its parallel flanks and its furrows, which do not reach the axial furrows: in other described species the glabellas are tapering and the furrows connect the axial furrows. The cranidial proportions are also distinctive; especially large is the interocular cheek, which is narrower in *E. sentum* and *strabum*. Among the material described by Palmer (1960) from the Dunderberg shale (Nevada) and



referred to as 'genus and species undet.', the pygidium, plate 11, figure 3 ('genus and species undetermined 3') resembles that of *E. alienum* in all aspects, except for the number of axial annulations, which are said to be eight, and not seven as in *E. alienum*. No cranidia have been mentioned in association with the pygidium of 'species 3'. One of the cranidia ('genus and species undetermined 1', op. cit., pl. 11, fig. 2) resembles *E. alienum* in having similar broad glabellar furrows 'that are isolated from the dorsal furrows', but 'species 1' has a tapering glabella and much narrower interocular cheeks.

*Description:* The pygidium CPC 4304 is 2.9 mm. wide and belongs to a specimen about 14 mm. long. It is about as long as wide. Its postaxial portion is laterally compressed and bears an elongate boss; the boss is damaged, but seen in another, larger specimen (CPC 4406, not illustrated). The narrow anterior portion of the pygidium has subparallel flanges, indicating that the thorax also had long rearward-directed spines.

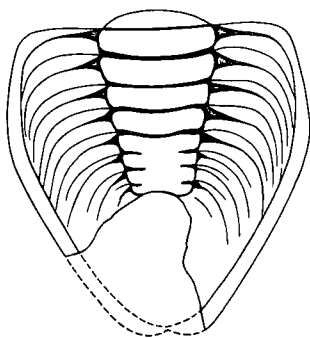


Fig. 29. *Erixanium alienum*, pygidium.

The holotype cranidium (Text-fig. 28a, b, CPC 4299) is 4.4 mm. long. It is slightly longer than in the other species, with a length/width ratio of slightly over 4/3. The frontal area (brim + rim) is very long, slightly more than one-third of the total length. The frontal marginal furrow is distinct but shallow, the rim is gently convex and upturned. In front of the glabella the brim is swollen, indicating an incipient boss, which is laterally defined by a pair of low depressions. Three pairs of glabellar furrows (depressions) are present, separated by a low median carina, as seen also in *E. sentum*. The occipital lobe is rather short, apparently as long as its doublure, and an occipital node is absent. The brim is covered with fine radiating lines, but the test is otherwise smooth and shiny.

*Occurrence and age:* *Erixanium alienum* has been found in the Georgina Limestone at a single locality (W9), where it is relatively common; its age is the Idamean *Erixanium sentum* Zone.

#### Family EULOMATIDAE Kobayashi, 1955

The name was originally proposed in the form of Eulominae (Eulomidae); the Greek word 'loma', genitive 'lomatos' implies, however, the form of the familial name as above.

The familial category is used here because *Euloma* and its allies cannot be accommodated in the family Ptychopariidae (Eulomatinae of the family Ptychopariidae) without substantially changing the concept of that family, but it is possible to interpret the Eulomatidae as a family of the superfamily Ptychopariacea.

Sdzuy (1955, p. 18) reviewed the various interpretations of the familial position of *Euloma*: Solenopleuridae, Pharostomidae, Calymenidae, Richardsonellidae, Aulacopleuridae, Olenidae, and familiae incertae have been suggested since the genus was established more than a century ago by Angelin (1854). Rasetti (1954) included *Euloma* and the new genus *Pareuloma* in the family Ptychopariidae. The main difficulty was, and still is, the absence of intermediate forms between the Middle Cambrian and the Ordovician (Tremadocian and Arenigian) *Euloma*.

The family Eulomatidae can be described as consisting of trilobites of a ptychoparioid design with deep cranial and glabellar furrows and pits in the marginal cranial furrow; in early forms (*Stigmatocera*) the glabellar furrows are straight and the glabellar lobes not swollen, whereas in the Ordovician forms the posterior glabellar furrows curve rearward and the lobes show a tendency to develop into swollen cushions. The Eulomatidae are a small but well diversified family, but *Euloma* itself, and especially *E. ornatum*, is relatively conservative in having preserved its resemblance to *Stigmatocera*. A brief review of genera attributed to the Eulomatidae is needed to substantiate the definition (or diagnosis) of the family.

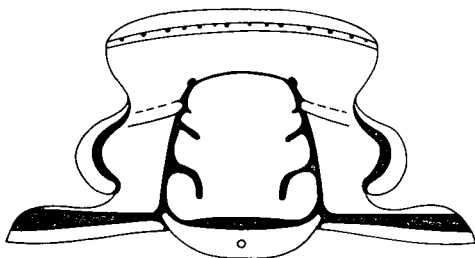


Fig. 30. *Euloma ornatum* Angelin, adapted from Tjernvik (1956, pl. 11, fig. 4).

The nominate genus *Euloma* (see Tjernvik, 1956) has very large eyes opposite the midpoint of the glabella: in the type species (*E. laeve* Angelin) the eyes are as long as the glabella; the frontal furrow of the cranidium has pits on its anterior (rearward facing) slope; the posterolateral limbs are long (transversely) narrow straps; all furrows are deep, posterior glabellar furrows are curved rearward, and the glabella lobes are swollen; the pygidium has facets, three pairs of ribs and furrows, and a thick border with terraced lines, and is not therefore of a 'generalized ptychopariid' structure. Facets are also present in *E. ornatum* (see Moberg & Segerberg, 1906, pl. 4, fig. 44). *Proteuloma* Sdzuy (1958) was originally established as a subgenus of *Euloma*. It is related to *Euloma* in having pits in the

marginal cranial furrow, and the position of the eyes and character of the glabellar lobes and furrows are also similar; but it is distinguished by its much smaller eyes, short (transversely) posterolateral limbs and a more arched cranial front. Its pygidium is small (about one-twelfth of the total length), and of a 'ptychoparioid' appearance. As seen from Lake (1940) the segments of the thorax have facets. *Euloma* and *Proteuloma* have advanced genal spines. In *Pareuloma* (Rasetti, op. cit., p. 584-585) the 'end of posterior limb is rounded, marginal furrow turning slightly forward', indicating the possibility that its genal spine was also advanced.

*Pareuloma* Rasetti has very small eyes opposite the glabellar front (and not opposite its midpoint), but long (transversely) posterolateral limbs, pits in the marginal furrow, and a *Euloma*-like glabella; the pygidium is incompletely fused—the interpleural grooves are preserved—and its 'marginal furrow and border are indistinct'. In *P. impunctata* Rasetti the cranial marginal furrow is shallow (almost effaced) and without pits. In *Euloma*, *Proteuloma*, and *Pareuloma* the frontal part of the glabella (the part in front of the ocular ridges) is rather short, only slightly rounded, or even truncate.

All three genera are early Ordovician in age; their independent generic status is well justified, but they remain unified as regards the following characters: 1) their general aspect is ptychoparioid; 2) they share a similar structure of the glabella and glabellar furrows; 3) the cranial furrows are deep; 4) they have a marginal cranial furrow with pits. These pits are absent in *Pareuloma impunctata*; but the stock has a long history at the end of which, in the course of specific diversification, the most stable character (the pits) became obliterated in one of its offshoots.

The new genus *Stigmatoa* is early Upper Cambrian; it differs from the Ordovician genera by its straight glabellar furrows, by less prominent glabellar lobes, and more rounded glabellar front; but in other characters (size and position of the eyes, presence of pits in the marginal furrow, strap-like posterolateral limbs, and ptychoparioid design) it is very close to *Euloma* itself, especially to *E. ornatum* Angelin. The type species of *Stigmatoa* (*S. diloma*) has also advanced genal spines, but this 'advance' is less abrupt than in the Ordovician forms.

For completeness, *Eulomina* Ruzicka, 1931, and *Eulomella* Kobayashi, 1955, should be mentioned. In Harrington et al. (1959) these genera are mentioned under the heading 'Order and Family Uncertain'. But *Eulomina mitratum* is a ptychoparioid trilobite with a short and rapidly tapering glabella, with eyes opposite the mid point, and large posterolateral limbs. The shape of the glabella prevents its inclusion in the Eulomatidae, but otherwise it appears to be a form of the superfamily Ptychopariacea. *Eulomella mckayensis* is represented by a fragment; it is a ptychoparioid with pits in the cranial marginal furrow, and it can be included in the Eulomatidae provisionally, without modifying the concept of the family.

The pits in the marginal furrow are assumed to be a significant character of the Eulomatidae. Pits of a similar kind occur also in other trilobites, as for example Redlichiidae, Richardsonellidae, and Loganellidae. Such pits are functional, as described in *Redlichia* (Öpik, 1958), and are accompanied by 'counterpits' in the cephalic doublure. Another kind of pits in the marginal furrow occurs in trilobites with strong genal caeca, as depressed interspaces between the elevated terminal ends of caeca (*Papyriaspis*; Öpik, 1961b), and has no 'counterpits' on the doublure. When the number of pits in the marginal doublure is visibly smaller than the number of caeca, functional pits are indicated, as is seen in *Redlichia* and *Euloma*; but when the pits are numerous the count may remain inconclusive, and even a coincidence of the 'functional pits' with the 'caecal interspace pits' should be expected, and the decision will depend on the presence or absence of the 'counterpits' on the doublure. *Levisella oweni* (Billings) (Rasetti in Harrington et al., 1959, p. 0333) is an illuminating example of numerous caecal veins, and numerous pits and counterpits.

The ventral doublure of the Eulomatidae is unknown, but the number of pits is small and the pits are interpreted therefore as 'functional pits'. If this interpretation is erroneous and the pits are 'interspace pits', then the difference between the families Ptychopariidae and Eulomatidae will be smaller than it appears to be now.

#### Genus STIGMATOA nov.

*Type Species: Stigmatoa diloma* sp. nov.

*Diagnosis:* *Stigmatoa* is a genus of the family Eulomatidae with large eyes, straight glabellar furrows, inconspicuous glabellar lobes, evenly tapering glabella with a rounded and relatively long front, with the string of marginal pits interrupted in the midline, and with a strong occipital spine. The genus is based on cranidial characters.

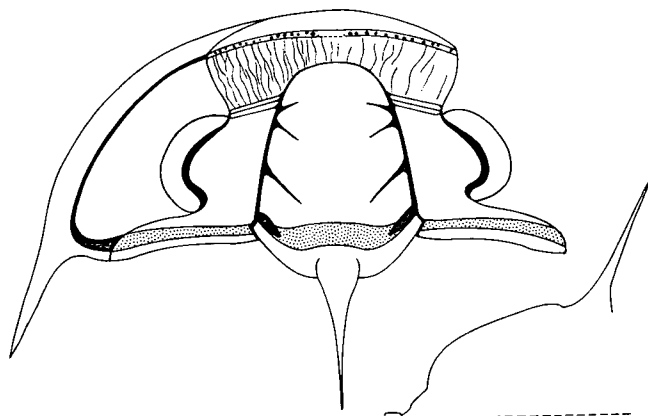


Fig. 31. *Stigmatoa diloma*, composite diagram of cephalon and profile. Cranidium: holotype, Pl 4, fig. 2; free cheek: specimen CPC 4306; occipital spine: cranidium CPC 4301.

*Comparison:* The nearest genus is *Euloma* Angelin; the type, *E. laeve*, has very large eyes with forward slanting ocular ridges and two pairs of glabellar lobes, and is unique, but *E. ornatum* Angelin (see Tjernvik, 1956) with its rearward slanting

ocular ridges and slightly smaller eyes and three pairs of glabellar furrows (Text-fig. 30) appears to be the nearest species. But its posterior glabellar furrows are curved, the glabellar lobes are swollen, the string of its marginal pits is continuous, and no prominent occipital spine, but only a low node, is present.

The familial affinity of *Stigmatia* with *Euloma* and *Pareuloma* may explain the recurrence of minor characters of specific significance in diverse species of these genera. Thus, the punctate ornament of *Stigmatia sillex* is the same as in *Pareuloma monile* (see Lake, 1940, pl. 43) and *geinitzi* (Sdzuy, 1958, pl. 3, fig. 4); *S. diloma* and *Euloma* aff. *filacovi* (Sdzuy, op. cit., fig. 2) have the same 'cambric' ornament; the border is flat in *E. laeve*, and convex in *E. ornatum* (Tjernvik, 1956), and the flatness or convexity of the border serves to distinguish the species of *Stigmatia*



Fig. 32. *Stigmatia diloma* sp. nov., pygidium, x 14. Georgina Limestone, Frome-Broken Hill Co. Pty. Ltd., collection, locality 41639, Glenormiston Station, about 4 to 5 miles north of the Twenty Mile Bore.

as well. Such characters cannot be included in generic and familial diagnoses because by themselves they indicate the specific diversity that prevails within the family. But these characters nevertheless are recurrent in diverse combinations within the family and support therefore, the concept of the familial unity.

*Annamitia* Mansuy (1916) is probably related to *Stigmatia*. *Annamitia*, however, has smaller posterolateral limbs; but it should be checked as regards the possible presence of pits in the marginal furrow. It is an early Upper Cambrian form, and associated with the 'Upper Kushan' fauna which traditionally and erroneously is regarded as Middle Cambrian (see Öpik, 1961b).

*Eugonocare* (?) sp. (Lu, 1956, p. 376, pl. 1, figs. 3-4) from the Upper Cambrian of China appears to be a *Stigmatia*, and closely related to *S. diloma*.

Four new species of *Stigmatia* are described below: *diloma*, *sidonia*, *sillex*, and *tysoni*. This taxonomy is based on cranial characters, and should be valid, if the

following assumptions are accepted: (a) that the cranial rim cannot be flat in some and convex in other specimens of a single species; (b) that the distance of the palpebral lobes from the glabella is stable within a species; (c) that a punctate glabella, and a glabella with a 'cambric' ornament, belong to diverse species; and (d) that diverse combinations of these characters belong to diverse species. These criteria were applied to classify the available material and it became apparent that the distribution of these minor and not immediately evident characters supports the initial assumptions. Furthermore, when only one of the four assumptions is regarded as invalid a taxonomic classification of the material becomes inconclusive, because any character, and any combination of characters, should be present in any species.

STIGMATOA DILOMA sp. nov.

(Pl. 4, fig. 2; Text-figs. 31, 32.)

*Material*: Two cranidia (CPC 4276, 4301) and one free cheek (CPC 4306) were selected for the description. The cranidium CPC 4301 is not illustrated but served for the reconstruction of the occipital spine; the free cheek is incorporated in the reconstruction Text-figure 31.

*Holotype*: The cranidium Plate 4, figure 2 (CPC 4276) is designated as the holotype because it is the best-preserved specimen.

*Diagnosis*: *Stigmatoa diloma* is a species with a flat rim distinguished by its cambric ornament of the glabella, wide interocular cheeks (wider than half the glabella), slender conical glabella, moderately diverging anterior sutures and a strong occipital spine.

*Differential diagnosis*: *Stigmatoa silex* has also a flat rim and a strong occipital spine, but its glabella is punctate, its interocular cheek is narrow (less than half the glabella), the glabella is broad, and the anterior sutures are widely divergent. *Stigmatoa sidonia* is quite similar to *diloma*, but differs by its convex rim and short occipital spine.

*Description*: The aspect of the cephalon is ptychoparioid, but of a particular appearance created by the following traits: the outer edge of the marginal furrow, the adaxial edges of the palpebral furrows, and the anterior edge of the occipital furrow are abrupt and angular, the interocular cheeks and large palpebral lobes are flat and sloping adaxially, and the axial furrows are straight.

The free cheek is relatively large, slightly convex, and has a relatively short, advanced, and slightly deflected genal spine. The posterior margin of the cheek is about as wide (transversely) as the base of the spine.

The frontal marginal furrow is wide and deep, with about twenty-four pits; the row of pits is interrupted in the middle by a low, plectrum-like structure: consequently, two rows of pits, one on the left, another on the right, are present. No pits are present in the marginal furrow of the free cheek. The rim is slightly shorter than the brim.

The cranidium is 8.6 mm. long without the spine and visibly wider between the eyes than in front; it is, however, widest in the rear owing to the narrow (transversely) and long posterolateral limbs. The palpebral lobes are very large (two-thirds of glabellar length), broad and flat, and situated opposite the midpoint of the glabella. The ocular ridges are slightly slanting, prominent, and divided by a narrow, thread-like crest into two bands each. The glabella is as long as wide (at its base), with straight flanks, and an evenly rounded front, and with a thread-like median carina. Three pairs of glabellar furrows are present, decreasing rapidly in size forwards. The furrows are straight and oblique, the anterior furrows being deflected forward, the posterior ones rearward. The occipital lobe is wide, arched rearward, and narrowing abaxially, and bears a long, almost erect spine that arises from the posterior border. The occipital furrow is rather deep and wide in the middle, but narrows outward; its abaxial ends are deepened and similar to the posterior glabellar furrows. The axial furrows are deep, but the circumglabellar furrow is rather shallow. The brim and the free cheek bear faint, even indistinct, radiating caecal veins. The ornament is quite minute: the cheeks, the brim, the border, posterolateral limbs, and palpebral lobes are minutely and densely punctate, whereas the surface of the glabella is densely covered with low elongate granules separated by pits comparable with a delicate cambric texture.

A pygidium of *Stigmatopora diloma*, obtained too late for inclusion in Plate 4, is illustrated in Text-figure 32. It is 4.5 mm. long and 7.8 mm. wide. It possesses the same ornament as the cranidium but with an emphasis on the punctuation; the parietal surface is smooth. A border furrow is absent, but the border is concave. Three pairs of rather broad, concave pleural furrows are present, separated by the crests of the fused interpleural partitions which within the border are swept abruptly rearward and reach the margin. Caecal veins are apparent also on the pleural lobes. The axis, as wide as one-third of the pygidium, is prominent, tapers slightly, and reaches the border. It bears two complete and a third incomplete annulation and a short, broad, and bluntly rounded terminus.

*Occurrence and age:* Georgina Limestone, locality W47 (the described cranidia) and locality W45 (the free cheek); fragments are present in other localities as well, and in the Pomegranate Limestone. The age is early Upper Cambrian (Idamean), the Zone of *Erixanium sentum*.

STIGMATOIA SILEX sp. nov.

(Pl. 4, fig. 4; Text-fig. 33.)

*Material:* Only one cranidium (the holotype, CPC 4278) is available. It is an external mould in fractured chert; the specimen lost some of its parts after being damaged in a fire.

*Diagnosis:* *S. silex* is a species with a flat rim distinguished by its punctate test, narrow interocular cheeks (less than half the glabellar width), a stout glabella which is wider at its base than its length, and greatly divergent anterior sutures.

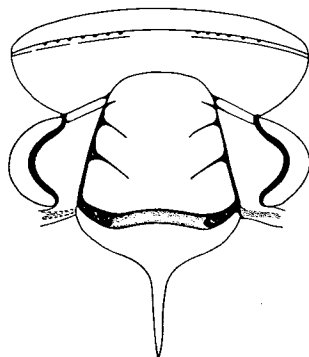


Fig. 33. *Stigmatocera silex*, reconstruction of holotype cranidium, Pl. 4, fig. 4.

The differential diagnosis is given under *Stigmatocera diloma*.

*Comment:* The cranidium is 6 mm. long without the spine; apparently between the eyes it is as wide as its front; the rim is short, about half as long as the brim; the interocular cheeks are slightly convex, and not flat; the glabellar furrows and the ocular ridges are less pronounced than in *S. diloma*; the test is punctate, except for the spine, which is smooth; the punctae are relatively coarse, and granulation or a cambic texture is absent; pits are present in the marginal furrow, but cannot be counted.

*Occurrence and age:* The specimen was found at locality D6, Duchess Sheet area, in a chert interbed in O'Hara Shale, about 70 feet above the local base of the formation. Fragments are also present in the Pomegranate Limestone. The age is early Upper Cambrian, the Zone of *Erixanum sentum*, probably lower part of that zone.

STIGMATOCERA SIDONIA sp. nov.

(Pl. 4, fig. 1; Text-fig. 34.)

*Material:* Only one cranidium (the holotype, CPC 4275) is available; it is embedded in limestone, exposing its parietal surface; but parts of the test are missing, so that the external surface and its ornament can be examined. The specimen is flattened.

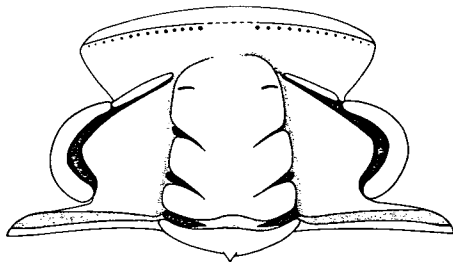


Fig. 34. *Stigmatocera sidonia*, reconstruction of holotype cranidium, Pl. 4, fig. 1.



*Diagnosis:* *Stigmatóa sidonia* is a species with a convex rim distinguished by its short occipital spine and minutely punctate test.

For differential diagnosis see under *Stigmatóa diloma* and *S. tysoni*.

*Comment:* The cranium is 6.9 mm. long. As in *S. diloma*, the interocular cheeks are wide (more than half the glabella) and the palpebral lobes are similarly long; but the narrow convex rim is distinctive, and so is the ornament, which lacks the cambric pattern. The punctae are much smaller and more numerous than in *E. silex*. The number of pits in the marginal furrow is about 26-28.

*Occurrence and age:* The illustrated cranium was found in the Pomegranate Limestone, locality D120b (Text-fig. 3), in a limestone in association with *Agnostotes inconstans* and *Irvingella tropica*. Its age is Upper Cambrian (Idamean), Zone of *Agnostotes inconstans* and *Irvingella tropica*. It is the youngest known species of the genus.

STIGMATOEA TYSONI sp. nov.

(Pl. 4, fig. 3.)

*Material:* Only two crania are available; the holotype is the illustrated specimen, CPC 4277. It is an internal cast, but its counterpart permits the study of the ornament.

*Diagnosis:* *Stigmatóa tysoni* is a species with a convex rim distinguished by its narrow interocular cheeks which are less than half the glabellar width, and an occipital node in addition to a slender marginal occipital spine. The rim is longer (sagittally) than the brim.

*Differential diagnosis:* The ornament of *S. tysoni* is similar to *S. diloma*, the convexity of the rim is shared with *S. sidonia*, and the relative narrowness of the interocular cheeks recalls *S. silex*. From *S. diloma* it differs by its narrow interocular cheeks, its convex rim which is longer than the brim, slender occipital spine and the additional node. From *S. sidonia* it differs in a similar manner except for the convexity of the rim. From *S. silex* it differs by the convexity and size of the rim and the ornament of the glabella, which is punctate in *silex*. Furthermore, *S. tysoni* has a lesser number of pits in its marginal furrow than *S. diloma* and *sidonia*, but as the number of pits in *S. silex* is unknown, this character is not included in the diagnosis.

*Comment:* The cranium is 7.2 mm. long without the spine; its front is 6.5 mm. wide and narrower than the cranium between the eyes; the interocular cheeks are moderately tumid; the glabella is as long as its width at the base; the internal surface is smooth, as it is in all other species of *Stigmatóa*, but the external surface of the glabella bears a minute cambric ornament and the other parts of it are minutely punctate; caecal veins are absent, and in the marginal furrow only twenty pits are present; the plectrum is distinct and has about five shallow grooves impressed on the internal cast.

The aspect of the cranidium of *S. tysoni* when compared with *S. diloma* is distinguished by lesser angularity of the edges, and mild tumidity of the cheeks and the rim.

*Occurrence and age:* *S. tysoni* has been found only at locality W45, in the Georgina Limestone. The age is early Upper Cambrian (Idamean), the Zone of *Erixanium sentum* (probably upper part of that zone).

#### PTYCHOPARIACEA FAMILIAE INCERTAE

##### Genus *HERCANTYX* nov.

*Type species:* *Hercantyx rudis* sp. nov.

The genus *Hercantyx*, as seen from its cranidium, belongs to Ptychopariacea; but it cannot be attributed to a known family, even by comparison with a known genus.

*Diagnosis:* *Hercantyx* is distinguished from other Ptychopariacea by the following characters: 1) the cranidium is subtrapezoidal; 2) the anterior border is straight, prominent, and almost vertical; 3) the anterior sutures are straight, divergent, and cut the margin opposite the anterolateral corners of the glabella; 4) the palpebral lobes are very large (longer than half the glabella), arcuate and elevated,

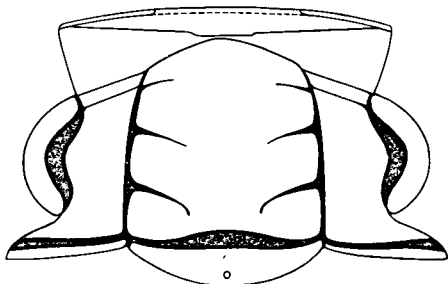


Fig. 35. *Hercantyx rudis*, reconstruction of holotype cranidium, Pl. 4, fig. 16.

and placed opposite, or slightly behind, the glabellar midpoint, and opposite the second glabellar lobes; the palpebral furrows are deep and wide; 5) the ocular ridges are wide and slanting; 6) the interocular cheeks are as wide as half the glabella, with a strong adaxial slope; 7) the posterolateral limbs are small and triangular; 8) the glabella is tumid, as wide as long and reaching the anterior border; slightly tapering, it is subangular in front and has an elongate pentagonal outline; 9) three pairs of glabellar furrows are present, the posterior furrows are long and curved, and the glabellar lobes are swollen; 10) the occipital ring is prominent, relatively short, and bears a node; 11) the surface is densely granulated.

It is possible that *Hercantyx* is an aberrant form of the Damesellidae, and related to *Stephanocare*. But it also appears to show some similarity to the solenopleurid *Psalikilus* Ross, with the Eurekiidae, and with *Bellaspidea minor* Rasetti (1945, pl. 60, figs. 23 and 24). *Bellaspidea minor* has large eyes and a steep frontal border, but it has a brim, a more elongate glabella, and only two pairs of glabellar furrows. Furthermore, *Bellaspidea* is placed in the family Idahoiidae

(Harrington et al., 1959), which is impossible for *Hercantyx*, and not quite convincing for *Bellaspidea* itself. *Bellaspidea* is much younger than *Hercantyx*. *Quebecaspis* Rasetti (1944, p. 254, plate 39, figs. 44, 45), a genus of the family Lonchocephalidae, is similar in having a large glabella with three pairs of glabellar furrows, but it has an ordinary convex border, small eyes, and convergent anterior sutures.

HERCANTYX RUDIS sp. nov.

(Pl. 4, fig. 16; Text-fig. 35.)

*Material*: A single cranidium has been found in a piece of limestone together with the pygidium of *Irvingella tropica*, *Olenus delicatus*, and ?*Aphelaspis* sp. B.

*Holotype* is the illustrated cranidium (CPC 4287), 2.5 mm. long.

A separate specific diagnosis is unnecessary, because it would coincide with the generic diagnosis.

*Comment on the illustrated specimen*: It is a fragmentary cranidium: the right palpebral lobe and a part of the left posterolateral limb are missing. The relief is rather strong and all furrows are distinct. On the upturned border the free margin and the cranidial face of the sutures are visible from above. A broad, low, and short plectrum connects the front of the glabella with the base of the anterior border.

*Occurrence and age*: The specimen was found on a piece of Pomegranate Limestone, locality D120b (see Text-figs. 2 and 3), in association with *Olenus delicatus*, *Irvingella tropica*, and ?*Aphelaspis* sp. B; its age is the early Upper Cambrian (Idamean) Zone of *Agnostotes inconstans* and *Irvingella tropica*.

Superfamily TELEPHINACEA Marek, 1952

Family KOMASPIDIDAE Kobayashi, 1935

Sive

Superfamily PTYCHOPARIACEA Matthew, 1887

Family ELVINIIDAE Kobayashi, 1935

The new species *Irvingella tropica* which is described below needs a familial classification. The heading above indicates that this classification is ambiguous and subjective and involves two equally valid alternatives.

The first alternative presumes that the genera *Komaspis* Kobayashi and *Irvingella* Ulrich & Resser are ancestors of several late genera including *Carolinites* and *Goniophrys* (Komaspidae), *Telephina* (Telephinidae), and *Glaphurus* (Glaphuridae), which together represent a modified ptychoparioid stock. Harrington et al. (1959) include also the Elviniidae in the 'Komaspidae' (here: Telephinacea). The second alternative, adopted by Palmer (1960), refers to the close morphological similarity between *Irvingella* and *Elvinia*, and prefers the family name Elviniidae, suppressing its contemporaneous synonym

Komaspididae. Phylogenetic deductions of the first alternative cannot be substantiated because *Irvingella* is separated from the other komaspidids (telephinids) by a wide temporal gap without intermediate links. Palmer's classification is meritorious in two ways: 1) it is essentially based on morphology, and 2) it is conveniently applicable for the trilobites of the early half of the Upper Cambrian without involving the progeny, which did not exist then.

In the first alternative, which reflects the classification adopted by Henningsmoen in Harrington et al. (1959), a change in nomenclature is here introduced by substituting the name Telephinacea Marek 1952 in place of 'Komaspidacea', which is attributed to Kobayashi against his intention. Kobayashi (1954, p. 30) himself accepted the name 'Telephacea' Stubblefield, which is quoted by Henningsmoen (loc. cit., p. 0294) as Telephidaceae in the synonymy of Komaspidacea; the correct quotation, however, is: 'Superfamily Telephaceae Angelin, 1852; Ulrich 1930'; in Stubblefield (1950, p. 344). It refers, however, to the name Telephidae Angelin, 1854 (op. cit., p. 0297) which is quoted by Kobayashi (op. cit., p. 31) as a family of Telephacea. Hence, the valid superfamily name is Telephinacea Marek, 1952, transcribed from Telephinidae Marek (see Harrington et al., p. 0297). Komaspidacea Henningsmoen 1959 quasi Kobayashi, is a synonym of Telephinacea Marek.

#### Genus IRVINGELLA Ulrich & Resser, 1924

The Australian *Irvingella tropica* is a species of the subgenus *Parairvingella* Kobayashi, 1938, which is established for forms with a distinct brim. *Komaspis* Kobayashi, 1935, also possesses a brim, and Kobayashi (1954) regards *Parairvingella* as a subgenus of *Komaspis*. It is quite possible that *Parairvingella* and *Komaspis* are synonyms, and that *Komaspis* has the priority. *Komaspis* (see Harrington et al., 1959, p. 0295) is believed to be a 'Middle Cambrian (Taizuiian)' genus, and, therefore, an ancestral trilobite (Kobayashi, 1954, p. 29). Its age is, however, Upper Cambrian, and most probably Upper Paishanian. The 'Middle Cambrian age' of *Komaspis* refers to the obsolete 'so-called *Olenoides* zone' (Kobayashi, 1956, p. 356), which is a name applied to a sequence of Middle Cambrian and early Upper Cambrian faunas. According to Kobayashi (1954, p. 26) *Komaspis* 'marks off a distinct zone between the *Olenoides* and *Olenus* zones in South Korea'—an improvement, but still an overestimation of age. In brief, the 'Yokusen orogenic zone', and the Machari formation (with *Komaspis*) in southern Korea are 'complicated by imbrication' that obviously obscures the correct sequence of faunas. *Komaspis* is also associated with *Ptychagnostus orientalis*, which is an *Agnostotes*, and its age is late Dresbachian or early Franconian, and certainly not Middle Cambrian.

It should be noted also that the published specimens of *Komaspis* are insufficiently preserved to warrant a conclusive description. Several diagrammatic interpretations of it have been published, but each of them represents a different trilobite. Consequently, the substitution of the older name *Komaspis* for the name *Parairvingella* should be postponed for a while.

IRVINGELLA TROPICA sp. nov.

(Pl. 4, figs. 5-8; Text-fig. 36.)

*Material*: Two cranidia and one pygidium have been recovered; they are the only specimens of *Irvingella* found as yet in Australia.

*Holotype*: The cranidium, Plate 4, figures 5-7, CPC 4279, is selected as the holotype. It is 8.4 mm. long. One more fragmentary cranidium (CPC 4300) is available, but not illustrated.

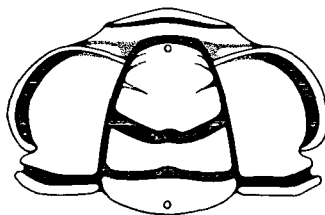


Fig. 36. *Irvingella tropica*, reconstruction of holotype cranidium, Pl. 4, figs. 5-7.

*Differential diagnosis*: *Irvingella tropica* is a species of the group with developed brim and rim (*Parairvingella*, or *Komaspis*, or both) distinguished by its strongly tapering glabella, by the presence of a glabellar frontal node, large fixed cheeks, and large posterolateral limbs. Besides the transcurrent posterior glabellar furrow three more disconnected pairs are present, discernible on the internal cast.

*Differential diagnosis*: *Komaspis typa* Kobayashi and K. (?*Parairvingella*) *convexa* Kobayashi are insufficiently known, but they appear to have much narrower fixed cheeks than *I. tropica*. The remaining five species of this group (*angustilimbata* Kobayashi, *arctica* Walcott & Resser, *eurekensis* Resser, *intermedia* Resser, and *suecica marginata* Westergaard) have a less tapering, almost subparallel-sided glabella and smaller cheeks. *Parairvingella hamburgensis*, which has a tapering glabella, is an *Elvinia* according to Palmer (1960).

*Description*: The test is thick, externally smooth (except the reticulation on the cheeks), without ornament; but on the cast minute punctation is indicated. The glabella is conical, almost twice as wide in the rear as in the front at the level of the ocular ridges. The occipital and the transcurrent posterior glabellar furrows are wide and deep. The second and third furrows are short and of uneven depth, the right ones being the deeper. A fourth pair of furrows is indicated, directed outward and rearward toward the ocular ridges. No other species of *Irvingella* is known to have four pairs of glabellar furrows, owing perhaps to the imperfect preservation. The occipital lobe bears a small node—an exceptional character in the genus. Unusual for a trilobite also, is the solitary frontal node, suggesting a comparison with the much younger *Symphysops* Raymond (Cyclopygacea), whose pygidium also is not unlike the pygidium of an *Irvingella*. The axial furrows are deep and wide, and the preglabellar furrow is accentuated. The brim is short (about one-sixth of the glabella) and convex; the rim is convex, slightly upturned and angular in the middle. The interocular cheeks

are gently tumid and covered with reticulate veins. The ocular ridges are weak (strong for an *Irvingella*), directed outward and joining the narrow and very large palpebral lobes. The palpebral furrows are deep wide channels. The posterolateral marginal furrow is deep and wide; the posterolateral limbs are large (almost half of the cranidial length), advanced, and abruptly deflected downward. Presumably all furrows are externally less deep than on the exfoliated internal cast.

The pygidium (Pl. 4, Fig. 8, CPC 4283) is 2 mm. long. It is subtriangular, with a narrow elevated border and flat pleural lobes that bear vestiges of two pairs of pleural furrows. The axis is elevated, almost bulbous, with two annulations and a short blunt terminus which is connected with the border by a median rise. The posterior margin has a shallow sinus. It is a true *Irvingella* pygidium, comparable with that of *I. media* and distinguished only by its slightly longer axis.

*Generic and familial position:* The taxonomic position of *Irvingella tropica* can be summarized as follows: it is a species with a well developed brim and can be placed, therefore, in the subgenus *Parairvingella* Kobayashi, 1938—if such a subgenus is necessary. It differs from the known species of *I. (Parairvingella)* in having a strongly tapering glabella. Species with a brim and a tapering glabella belong to *Komaspis* Kobayashi, 1935, if the reconstruction of *Komaspis typa* as suggested by Kobayashi (1954, pl. 6, fig. 10) is accepted. If so, *I. tropica* is a species of *Komaspis*, which should be regarded as a subgenus of *Irvingella* and a senior synonym of *Parairvingella*. *Komaspis* is, however, inadequately known and the concept of the genus is too vague to be applied for species other than *K. typa* itself.

*Occurrence and age:* *Irvingella tropica* has been found in the Pomegranate Limestone at locality D120b (see Text-figs. 2 and 3); it is the only known occurrence of *Irvingella* in Australia. Its age is the early Upper Cambrian (Idamean) Zone of *Agnostotes inconstans* and *Irvingella tropica*.

Superfamily CERATOPYGACEA  
Family CERATOPYGIDAE Linnarsson  
Genus PROCERATOPYGE Wallerius

About eighteen species of *Proceratopyge* have been described as yet; these include two species (*rotundum* and *triangularis*) which Kobayashi placed in the subgenus *Kogenium*, 1935. The pygidia of *Kogenium* cannot be distinguished from those of *Proceratopyge*, but the cranidium assigned to them seems to belong to a different, but otherwise not determinable, family.

Troedsson (1937) distributed the then known species between two genera: *Proceratopyge*, without ocular ridges, and *Lopnorites*, with ocular ridges. Westergaard (1947) indicated, however, that the type of *Proceratopyge* (*P. conifrons*) also possesses ocular ridges and that *Lopnorites* is therefore a synonym of *Proceratopyge*. Kobayashi (1956) regards *Lopnorites* as a subgenus of *Proceratopyge* distinguished by its subcylindrical glabella, and Lu (1956) accepts

this procedure. If this character is valid, *Lopnorites* should include forms with large eyes and strap-like posterolateral limbs, as well as species with small eyes and triangular and large posterolateral limbs. Hence, subdivisions based on the character of the glabella are unsatisfactory; it is, perhaps, possible to divide the genus into two groups by other means: a group with a plectrum (as in the type of the genus—*P. conifrons*) and another with plectral lines only. These characters will be useful in a diagnostic key of species, but they cannot as yet be visualized as having a subgeneric significance.

It is, however, possible to preserve *Lopnorites* as a subgenus of *Proceratopyge* when pygidial characters are considered: *Lopnorites rectispinatus* (the type species) has a large triangular pygidium with six axial annulations, *L. fragilis* Troedsson has seven annulations, and *L. grabaui* Troedsson has nine or ten. Species with five or less annulations in the pygidial axis are referable to *Proceratopyge* (*Proceratopyge*), and its type (*P. conifrons*) has only three annulations. The application of these criteria may be difficult in forms with a partial effacement of the external axial annulation, unless decorticated specimens are available. Most of the known species of *Proceratopyge* (and *Lopnorites*) occur in the lower third of the Upper Cambrian. Two species (*P. conifrons* and *P. (Lopnorites) magnicauda*) are known from the uppermost Middle Cambrian in Sweden. The species attributed to *Kogenium* Kobayashi and dated as the Middle Cambrian 'so called *Olenoides* zone' may be also of an Upper Cambrian age (see under *Agnostotes*, and *Irvingella tropica*).

PROCERATOPYGE LATA Whitehouse, 1939  
(Pl. 4, figs. 9, 10; Pl. 5, figs. CC, EF, GF.)

*Material*: Three cranidia and one pygidium are illustrated; the pygidium, Figure 9, is associated with the cranidia, Plate 5 (CPC 4281), and the cranidium, Figure 10, (CPC 4282) was found separately, slightly higher in the sequence.

The pygidium is 6.5 mm. wide, semicircular, twice as wide as long, with an evenly rounded margin and straight rearward directed spines; besides the usual well-developed anterior pleurae the flanks bear three pairs of ribs; the pygidial axis is long and slender, with three distinct annulations and a long terminus. A narrow concave border is indicated and the edge of the doublure is projected on the surface as a concentric ridge. Whitehouse (1939, pl. 25, fig. 13) illustrated a pygidium associated with *Proceratopyge lata* but assigned it to *P. rutellum*. It is also semicircular, but has a wider border with a shallow sinus and four annulations, or five segments including the terminus. *Proceratopyge (Lopnorites) rectispinata* (Troedsson, 1937, pl. 2, fig. 2) has also three annulations in the pygidial axis (the type specimen has six), but it is subtriangular and not rounded. In all other described species the pygidium is longer or shorter than in our specimen, and the axis is plump.

The illustrated cranidia are assigned to *P. lata* because its holotype (and the only published specimen) has also a short frontal area and a similar position of the

eyes, and the interocular cheeks including palpebral lobes are in both about half the width of the glabella on the same level. The palpebral lobes are relatively large and strongly arcuate, the ocular ridges are distinct. The form of the glabellar front varies: it is rounded in Plate 4, figure 10 and subtruncate in the other specimens. No uniformity is apparent in the glabellar furrows; in Plate 4, figure 10 only the posterior pair is developed; in another specimen (Plate 5, F-E) three pairs of weak furrows can be seen; but in the third (Plate 5, fig. FG) the posterior and the anterior furrows are deeply impressed whereas the second pair is feeble—a most peculiar arrangement unknown hitherto in trilobites.

On the brim a pair of diverging plectral lines arises at the anterolateral corners of the glabella and terminates at the corners of the cranidium. Such lines are present in all Australian specimens of *Proceratopyge* so far inspected, and in the Manchurian *P. liaotungensis* Kobayashi. These lines are weak or even obliterated in less well preserved forms, as for example in the Swedish Upper Cambrian, and the Tien-shan specimens described by Troedsson.

*Occurrence and age:* Our specimens come from the Pomegranate Limestone, locality D120b, from the early Upper Cambrian (Idamean) Zone of *Irvingella tropica* and *Agnostotes inconstans*. *P. lata* is also common in the Georgina Limestone above the Zone with *Glyptagnostus reticulatus*, and in the Pomegranate Limestone in the *Erixanium sentum* zone.

PROCERATOPYGE cf. CHUHSIENSIS Lu, 1956

(Pl. 5, fig. AA; Text-fig. 37.)

*Material:* Only one cranidium (CPC 4281) is available. It is described here for completeness of the record of the fauna associated with *Irvingella tropica*, *Olenus delicatus*, and *Agnostotes inconstans*. As indicated below, this form is related to *Proceratopyge rutellum* Whitehouse and *P. polita* Whitehouse from the Georgina Limestone. Additional material of these forms is now available and may yield in future more information as regards the specific identity of the cranidium in question.

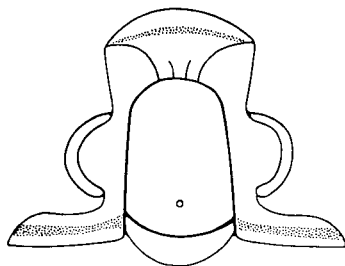


Fig. 37. *Proceratopyge* cf. *chuhsiensis*, diagram of cranidium, Pl. 5, fig. A.

*Proceratopyge* (*Lopnorites*) *chuhsiensis* Lu belongs to the same group of forms, and is selected for reference because of its informative illustrations and description. *Generic relationship:* The plectral lines on the brim, the glabellar node, and the general character of the cranidium indicate a species of *Proceratopyge*.



*Description:* The specimen is 2.5 mm. long. The glabella is subcylindrical, with a rounded front and without glabellar furrows. The occipital furrow is distinct and arched rearward. The frontal limb (brim and rim) is relatively long, about two-sevenths of the length of the cephalon; the rim is convex, the marginal furrow indistinct; the plectral lines are weak and these terminate at the anterolateral corners of the cranidium. The palpebral lobes are large, opposite the centre of the glabella, and about one-half of the glabellar width from it. The posterolateral limbs are narrow straps with a shallow anterior sinus. The glabellar node is small and low.

*Comparison:* *Proceratopyge chuhsiensis* Lu (1956, pl. 1, fig. 1) has a pair of glabellar furrows, but is similar in all other aspects. *P. polita* Whitehouse has no glabellar furrows but no rim, and its posterolateral limbs are unknown. *P. rutellum* has three pairs of faint glabellar furrows and the anterior ends of the palpebral lobes are very close to the glabella. *Proceratopyge asiatica* Ivshin, 1956, belongs to the same group. It has a subcylindrical glabella without glabellar furrows, a narrow frontal rim and strap-like posterolateral limbs; but the ends of the palpebral lobes are very close to the glabella. All these forms have a subcylindrical glabella; the remaining described species of *Proceratopyge* have a tapering glabella and are, therefore, quite distinctive.

*Occurrence and age:* The cranidium was found in the Pomegranate Limestone, locality D120b, in the early Upper Cambrian (Idamean) Zone of, and associated with, *Irvingella tropica* and *Agnostotes inconstans*.

#### INCERTAE SEDIS

#### TRILOBITE sp. C.

(Pl. 5, fig. B; Text-fig. 38.)

The illustrated pygidium (CPC 4281) is very small, about 2 mm. long. Its long axis has five complete and two incomplete annulations and a short terminus; broad convex pleural lobes carry five pleural ribs, and a relatively wide concave border. It cannot be assigned to any of the genera known in the Upper Cambrian of Queensland, and belongs, perhaps, to an early asaphid or to a late anomocarid trilobite.

*Occurrence and age:* Pomegranate Limestone, locality D120b, the early Upper Cambrian (Idamean) Zone of *Agnostotes inconstans* and *Irvingella tropica*.

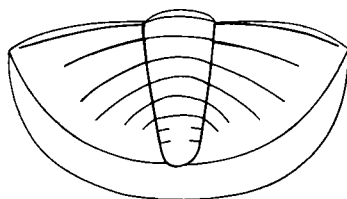


Fig. 38. Diagram of pygidium of trilobite sp. C, Pl. 5, fig. B.

## CRUSTACEA

### BRADORIIDA Raymond

Fam. ?BEYRICHONIDAE Ulrich & Bassler, gen. indet., sp. D

(Pl. 4, fig. 11; Text-fig. 39.)

A single left valve (CPC 4280), about 2.5 mm. long, has been found. It is very tumid, with a rounded anterior extremity and an obtuse posterodorsal angle. It has no border, and apparently no doublure, nor a gap. The test is smooth, without any ornament. Shallow furrows (Text-fig. 39) divide the valve into three lobes that coincide with the general convexity of the valve; only the anterior lobe rises slightly higher. The anterior and posterior furrows meet in a shallow depression, and continue downward as a third, very weak furrow which fades out rapidly.

This fossil cannot be assigned to a known genus of Bradoriida; externally it resembles *Beyrichona rotundata* Matthew (Ulrich & Bassler, 1931, pl. 6, fig. 12) and is, therefore, provisionally referred to the family Beyrichonidae.

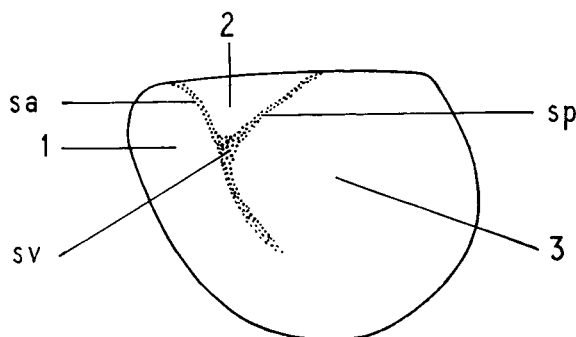


Fig. 39. Beyrichonidae, gen. indet., sp. D, diagram of left valve, Pl. 4, fig. 11. sa—anterior furrow; sp—posterior furrow; sv—shallow depression; 1—anterior lobe; 2—middle lobe; 3—posterior lobe.

It is described because no Australian Upper Cambrian Bradoriida were previously known, and because the great majority of all described Bradoriida are Lower or Middle Cambrian in age.

*Occurrence:* The specimen is preserved on the piece of limestone, Plate 5, from locality D120b, upper bed; its age is the Upper Cambrian (Idamean) *Agnostotes inconstans* and *Irvingella tropica* Zone of Queensland.

## HYDROIIDA

Gen. et sp. indet.

(Pl. 7, fig. 3; Text-fig. 40.)

The fossils are fragments of either a dendroid or a hydroid; but a definite identification is impossible.

The material consists of a cluster of conical thecae on a bedding plane (CPC 4298); the limestone split evenly because thin films or blots of 'oily?' organic matter served as parting and appear to accompany the cluster of thecae. The limestone itself contains small thin irregular flakes of light brown organic matter and some pyrite. The thecae are about 0.4-0.5 mm. long, of friable black

carbonaceous matter without any growth-lines. They are hollow and filled with calcite. One of the thecae ('a' in Text-fig. 40) is attached to torn fragments of two or three other cones; another specimen (b) consists, probably, of two joined thecae and a third specimen (c) has preserved its nema or a part of the stem. Thus it appears that the cluster consists of fragments of a single rhabdosome.

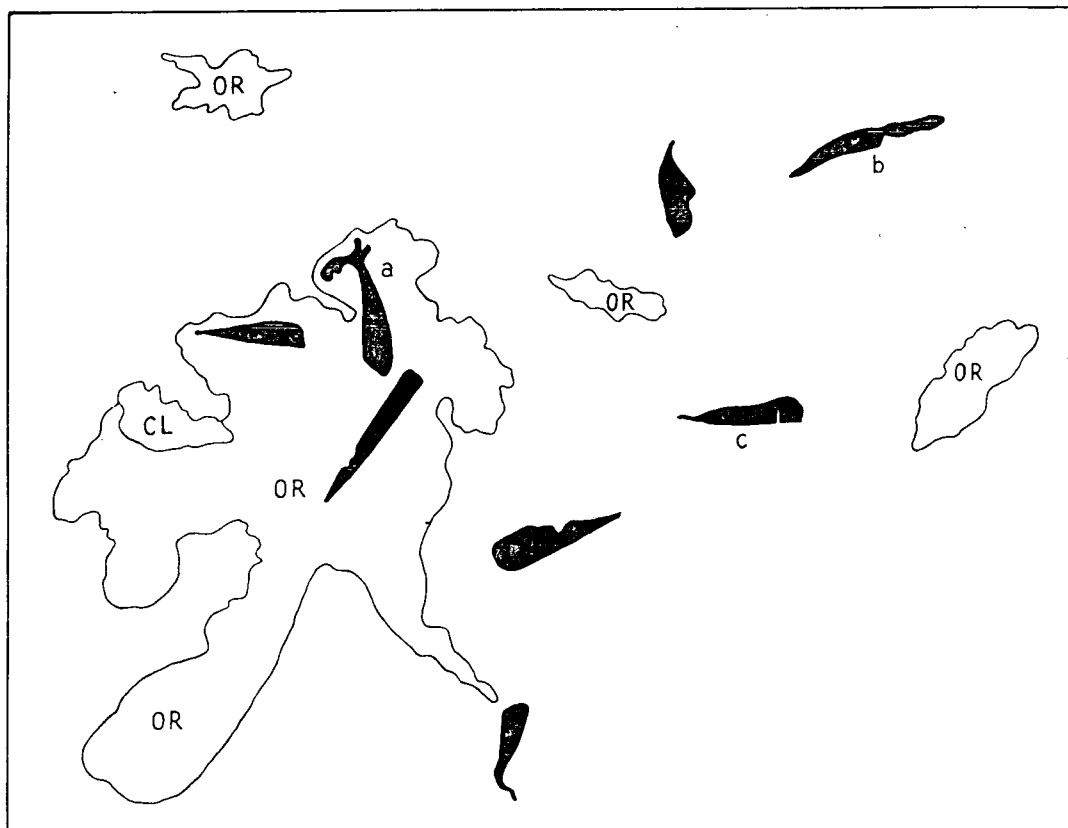


Fig. 40—Hydroida, gen. et sp. indet., diagram of Pl. 7, fig. 3. a—theca with torn fragments at its proximal end; b—probably two joined thecae; c—theca with nema, or fragment of stem; CL—calcite; OR—films of organic (oily?) matter.

The specimen seems to be somewhat similar to *Haplograptus wisconsinensis* Ruedemann (1933, p. 324, pl. 52); but the thecae in *H. wisconsinensis* are larger, and this species is also younger (Trempealeauan).

The cones scattered on the bedding plane can be interpreted also as fragments of a hydroid, comparable with *Archaeolafoea* Chapman or *Sphenoecium* Chapman & Thomas, 1936. These forms are, however, Middle Cambrian.

*Occurrence and age:* The specimen has been found in the Pomegranate Limestone, in Upper Cambrian beds with *Glyptagnostus reticulatus* and *Olenus ogilviei*, at locality D120a, sixteen miles north of Chatsworth. It is as yet the only find of hydroids (dendroids?) in the Cambrian rocks of Queensland. Such a rarity is noteworthy when compared with the abundance and taxonomic variety of hydroids in the Middle Cambrian of Victoria and Tasmania.

## GLOSSARY

(Explanation of new names of fossils)

*Agnostardis*: Fem.; combined *Agnostus*, and *ardis* (Greek) 'arrow point'; alludes to the pointed postaxial bulb of the pygidium.

*Agnostotes*: Fem., Greek, 'having the quality of *Agnostus*'.

*alienum* (*Erixanium*): Lat., 'strange'.

*amplinatis* (*Agnostardis*): Lat., 'ample rump', alludes to the large size of its pygidium.

*Asilluchus*: Masc., Greek, 'yoke bearer', alluding to the horizontal ocular ridges with palpebral lobes.

*delicatus* (*Olenus*): Lat., 'delicate'; alludes to the phrase 'Olenidae are delicate Ptychopariacea'.

*diloma* (*Stigmatosa*): Greek, 'double band, fringe'; alludes to the two rows of pits (a right and a left) of the cranidial front.

*Discagnostus*: Masc., Greek; combined from the generic names *Eodiscus* and *Agnostus*.

*Erixanium*: Neuter, Greek; 'a very comb', alludes to the long spines of the thorax.

*Hercantyx*: Fem., Greek, 'fence rim', alludes to the vertical frontal rim.

*inconstans* (*Agnostotes*): Lat., alludes to the variability of the species.

*nanus* (*Asilluchus*): Lat., 'tiny'.

*notulata* (*Talbotinella*): Lat., 'marked' (with a pair of pits on the glabella).

*ogilviei* (*Olenus*): After Ch. Ogilvie, the discoverer of Upper Cambrian fossils in the Georgina region.

*rudis* (*Hercantyx*): Lat., 'rough', having a rough surface of the cranidium.

*sentum* (*Erixanium*): Lat., 'thorny', because of the spinose pleurae.

*sidonia* (*Stigmatosa*): Lat., Greek, 'pomegranate', alludes to Pomegranate Creek Limestone, and area.

*silex* (*Stigmatosa*): Lat., 'flint', preserved in chert.

*spectator* (*Discagnostus*): Lat., alludes to the ocular tubercles.

*Stigmatosa*: Fem., Greek, 'with stitched hem or border', alluding to the frontal pits.

*strabum* (*Erixanium*): Lat., 'squinting', having oblique palpebral lobes.

*tropica* (*Irvingella*): Lat., alludes to the occurrence within the tropics.

*tysoni* (*Stigmatosa*): After James Tyson, pioneer on Glenormiston Station.

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## PLATES

PLATE 1

*Olenus ogilviei* sp. nov.

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Figs. 1-4.—Holotype, CPC 4248; fig. 1—x 7; figs. 3 and 4—x 22; fig. 2, rubber cast of holotype, x 5.5.

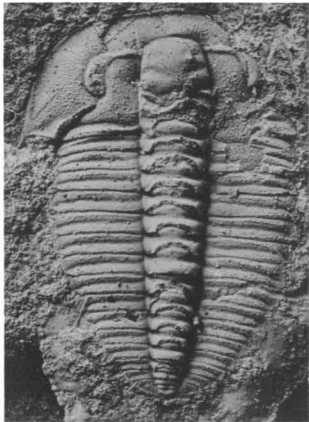
Fig. 5.—Fragmentary specimen, CPC 4249, x 5.5.

Figs. 6-7.—A non-flattened specimen, CPC 4250, two views, x 5.5.

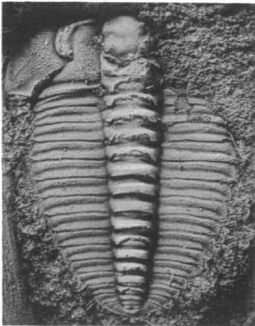
Fig. 8.—A complete specimen, CPC 4251, x 5.5.

Fig. 9.—An immature specimen, CPC 4242, x 11.

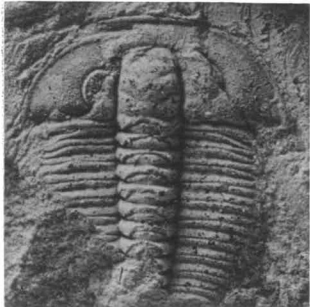
Pomegranate Limestone, locality D120a.



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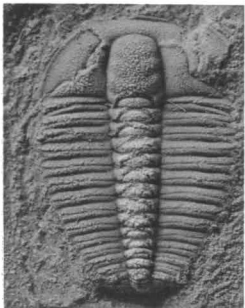
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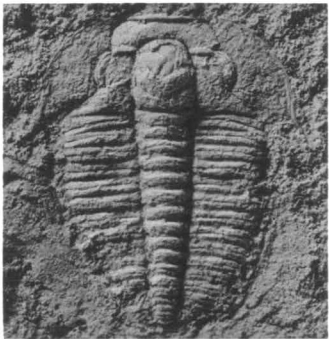
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## PLATE 2

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| <p style="text-align: center;">? <i>Olenus</i> sp. <i>A.</i></p> <p>Fig. 1.—Fragmentary cranidium, CPC 4253, x 2.<br/>Pomegranate Limestone, locality D119.</p>  | <p>Page 64</p> |
| <p style="text-align: center;"><i>Olenus ogilviei</i> sp. nov.</p> <p>Three cranidia, about x 5.<br/>Fig. 2.—A cranidium, CPC 4254.<br/>Fig. 3.—A cranidium with first segment of the thorax, CPC 4255.<br/>Figs. 4, 5.—Two views of a large uncompressed cranidium, CPC 4256.<br/>Pomegranate Limestone, locality D120a.</p>            | <p>Page 59</p> |
| <p style="text-align: center;"><i>Glyptagnostus reticulatus</i> (Angelin)</p> <p>Fig. 6.—A large flattened cephalon, CPC 4257, x 3.<br/>Figs. 7 &amp; 8.—A pygidium, CPC 4258; fig. 7 is the rubber cast, x 4.5; fig. 8, the mould, x 3.4.<br/>Fig. 9.—A small pygidium, CPC 4259, x 3.2.<br/>Pomegranate Limestone, locality D120a.</p> | <p>Page 38</p> |
| <p style="text-align: center;"><i>Agnostus inexpectans</i> Kobayashi</p> <p>Figs. 10-12.—A complete specimen, CPC 4260; fig. 11, x 4.2; fig. 10, a rubber cast, x 6; fig. 12, x 10.<br/>Pomegranate Limestone, locality D120a.<br/>Fig. 13.—A cephalon, CPC 4261, x 7.5.<br/>Pomegranate Limestone, De Little Range, locality D126.</p>  | <p>Page 35</p> |
| <p style="text-align: center;"><i>Discagnostus spectator</i> gen. nov. et sp. nov.</p> <p>Figs. 15 &amp; 16.—Stereopairs of internal cast (fig. 15) and rubber cast (fig. 16) of external mould of holotype cephalon, CPC 4262, x 18.<br/>O'Hara Shale, locality D29, Selwyn Range.</p>  | <p>Page 55</p> |



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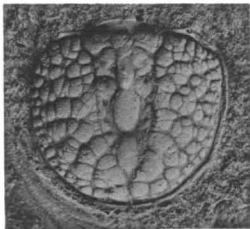
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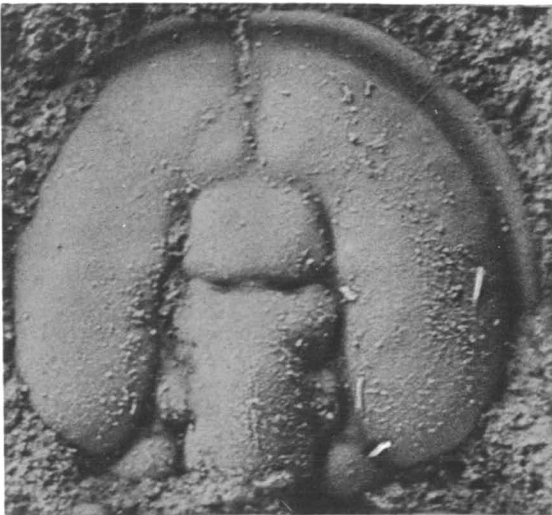
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# PLATE 3

- Agnostardis amplinatis* gen. nov. et sp. nov. .... Page 40
- Fig. 1.—Rubber cast of complete specimen, CPC 4263, x 7.
- Fig. 2.—Cephalon in chert, CPC 4264, x 7.4.
- Fig. 4. Pygidium in chert, CPC 4266, x 7.4.  
Georgina Limestone, locality W20.
- Fig. 3.—Cephalon, CPC 4265, x 7.  
Pomegranate Limestone, De Little Range, locality B537.
- Fig. 5.—Cephalon, CPC 4267, x 7.  
Georgina Limestone, locality W1.
- Fig. 6.—Pygidium in calcite, CPC 4268, x 7.  
Georgina Limestone, locality G50.
- Fig. 7.—Small pygidium, CPC 4269, x 7.  
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- Fig. 8.—Holotype pygidium, CPC 4270, x 7.  
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- Figs. 9 & 10.—A pygidium, CPC 4271, with notular furrows and accessory furrows, x 7, and x 15.
- Fig. 11.—Holotype pygidium, CPC 4272, with notulae, x 8.
- Fig. 12.—A pygidium, CPC 4273, with continuous notular furrows, x 8.
- Figs. 13 & 14.—Cephalon, CPC 4274, x 7.  
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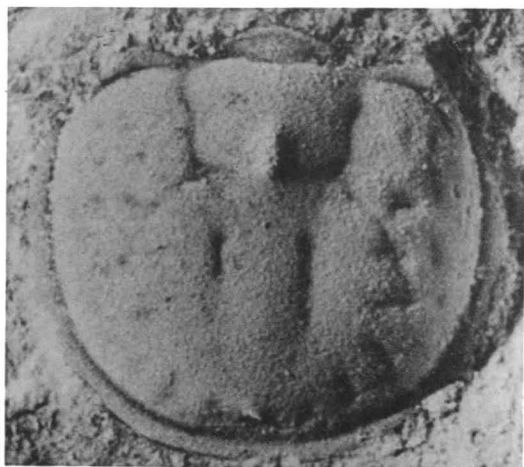
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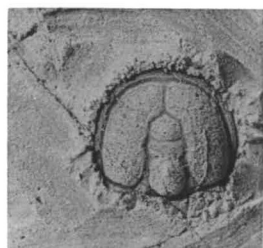
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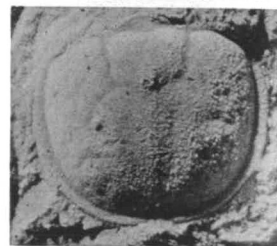
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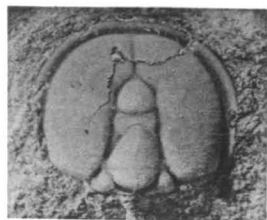
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# PLATE 4

	<i>Stigmatoa sidonia</i> sp. nov. ....	Page 91
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Pomegranate Limestone, locality D120b.		
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	<i>Stigmatoa tysoni</i> sp. nov. ....	Page 92
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	Beyrichonidae, gen. & sp. indet. ....	Page 101
Fig. 11.—A left valve, CPC 4280, x 9.		
	<i>Olenus delicatus</i> sp. nov. ....	Page 62
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Fig. 15.—Cranidium, CPC 4286, x 12.		
	<i>Hercantyx rudis</i> gen. nov. & sp. nov. ....	Page 94
Fig. 16.—Holotype cranidium, CPC 4287, x 12.		
Pomegranate Limestone, locality D120b.		





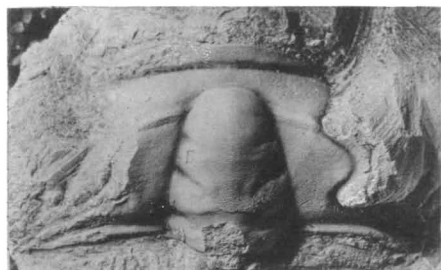
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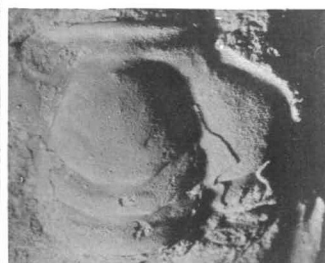
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# PLATE 5

magn. x 8.

Fig. A-A.—*Proceratopyge* cf. *chuhsiensis* Lu ..... Page 99

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Fig. C-C.—Hypostoma.

Figs. D-D, F-E, and F-G.—Cranidia.

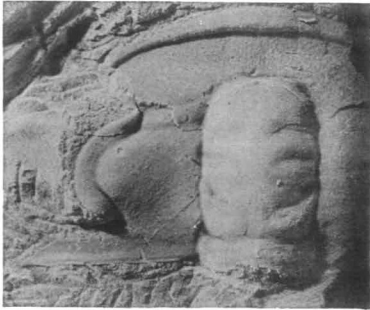
A calcite lamina, CPC 4281, Pomegranate Limestone, locality D120b.

(The specimens Plate 4, figs. 9, 11, and 13 are on the same piece of rock.)

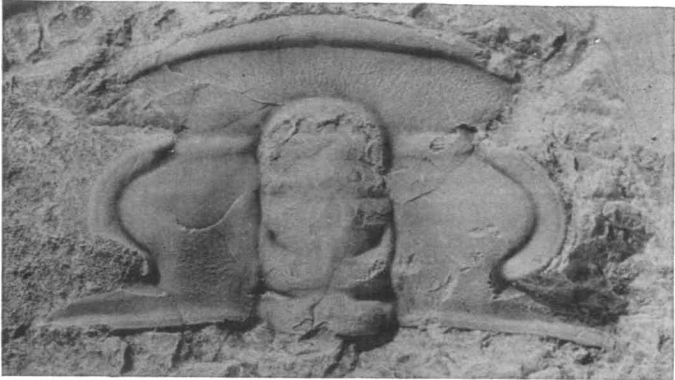


# PLATE 6

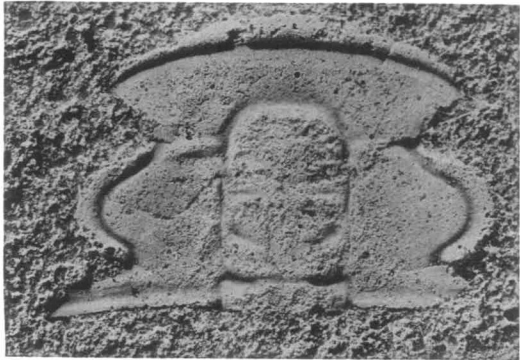
- |   |   |         |
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|   | <i>Rhodonaspis longula</i> Whitehouse           | Page 68 |
| Fig. 1.—Cranidium, CPC 4288, in limestone, x 3.5.             |   |         |
| Georgina Limestone, locality W15.                             |   |         |
| Fig. 2.—Cranidium, CPC 4289, in limestone, flattened, x 5.    |   |         |
| Fig. 3.—Cranidium, CPC 4290, in shale parting, x 5.5.         |   |         |
| Georgina Limestone, locality W20.                             |   |         |
| Fig. 4.—Cranidium, CPC 4291, in chert, x 4.                   |   |         |
| O'Hara Shale, locality D29.                                   |   |         |
| Fig. 5.—Pygidium, rubber cast of CPC 4292, in limestone, x 8. |   |         |
| Figs. 6 & 7.—Small pygidium, CPC 4293, x 10 and x 20.         |   |         |
| Georgina Limestone, locality W15.                             |   |         |
|   | <i>Asilluchus nanus</i> , gen. nov. et sp. nov. | Page 67 |
| Fig. 8.—Rubber cast of holotype cranidium, CPC 4294, x 12.    |   |         |
| Pomegranate Limestone, locality D120b.                        |   |         |
|   | <i>Talbotinella notulata</i> , sp. nov.         | Page 73 |
| Fig. 9.—Holotype cranidium, CPC 4295, x 4.                    |   |         |
| Georgina Limestone, locality G50.                             |   |         |



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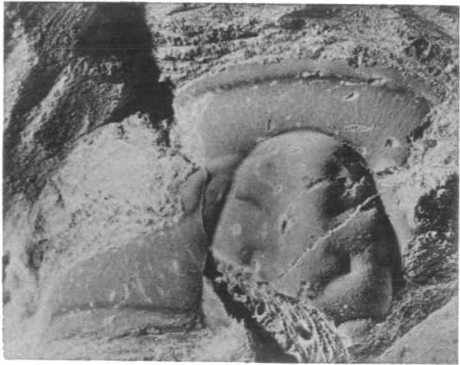
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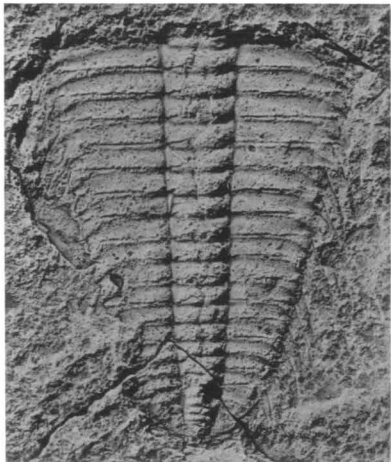
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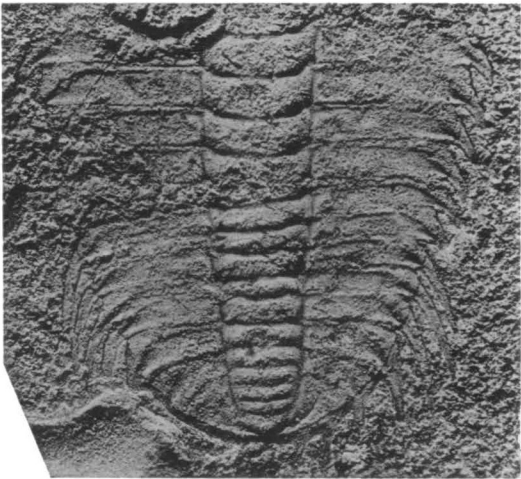
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# PLATE 7

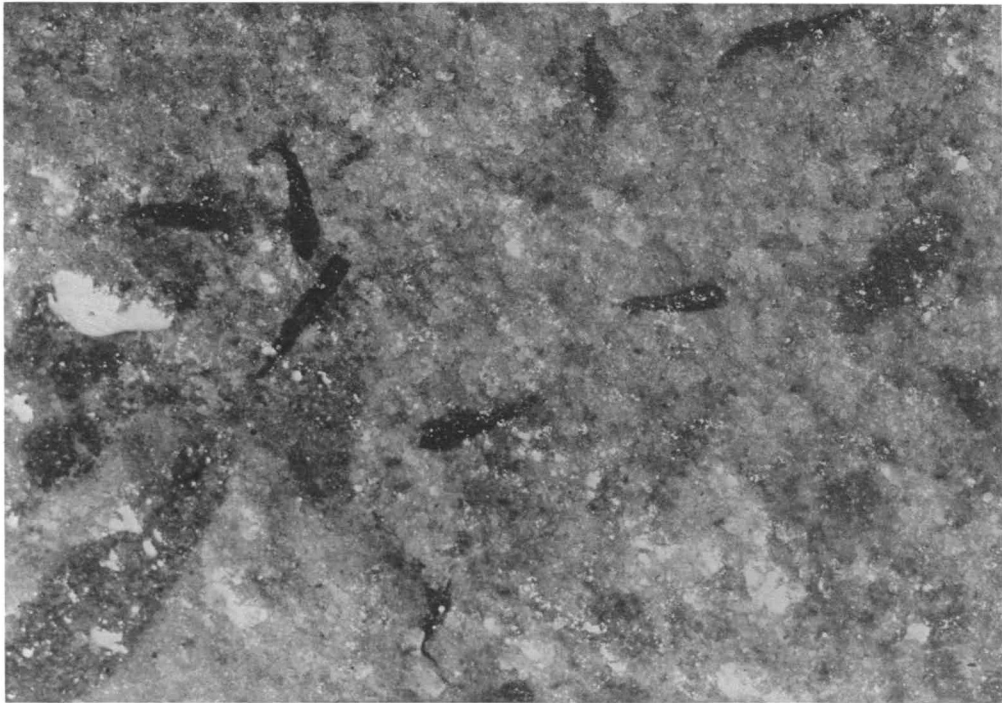
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|----------|---|-------|-------|----------|
|          | <i>Rhodonaspis longula</i> Whitehouse                                 | ..... | ..... | Page 68  |
| Fig. 1.— | Almost complete thorax with pygidium, CPC 4296, x 5.                  |       |       |          |
| Fig. 2.— | Part of thorax with pygidium, CPC 4297, x 5.4.                        |       |       |          |
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|          | Hyroida, gen. & sp. indet.  | ..... | ..... | Page 101 |
| Fig. 3.— | Fragments of thecae or a bedding plane, CPC 4298, x 8.                |       |       |          |
|          | Pomegranate Limestone, locality D120a.                                |       |       |          |



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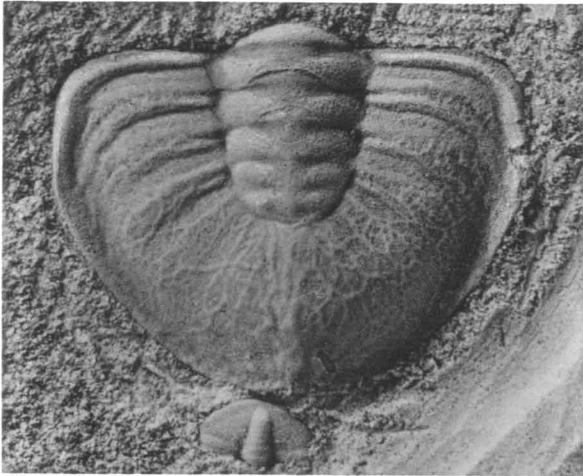


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# PLATE 8

	<i>Erixanium sentum</i> gen. nov. et sp. nov.	.....	.....	Page 78
Fig. 1.—	Holotype pygidium, CPC 578, x 6.			
Fig. 2.—	Cranidium, CPC 3842, x 7.			
Fig. 3.—	Cranidium, CPC 3841, x 4.			
	Georgina Limestone, locality W42.			
Fig. 4.—	Rubber cast of a pygidium, CPC 3844, x 4.			
	Georgina Limestone, locality W65/23.			
	<i>Erixanium strabum</i> sp. nov.	.....	.....	Page 81
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Fig. 6.—	Holotype cranidium, CPC 3840, x 4.			
	Georgina Limestone, locality W10.			
	<i>Erixanium sentum</i> sp. nov.	.....	.....	Page 78
Figs. 7 & 8.—	A cranidium, CPC 3843, and its rubber cast, x 4.			
	Georgina Limestone, locality W42.			





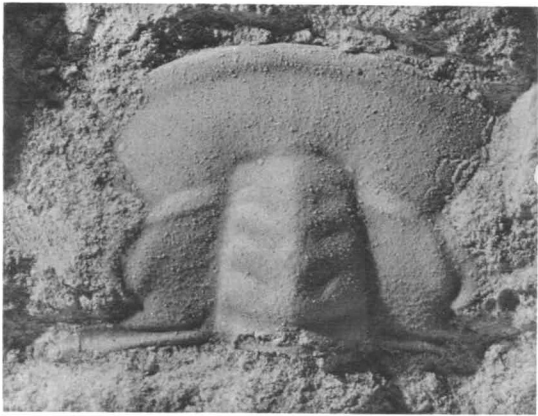
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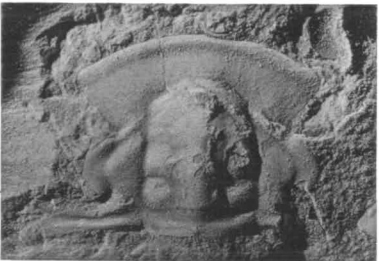
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PLATE 9

*Erixanium sentum* sp. nov. .... Page 78

Fig. 1.—Two complete specimens, CPC 3846, x 4.

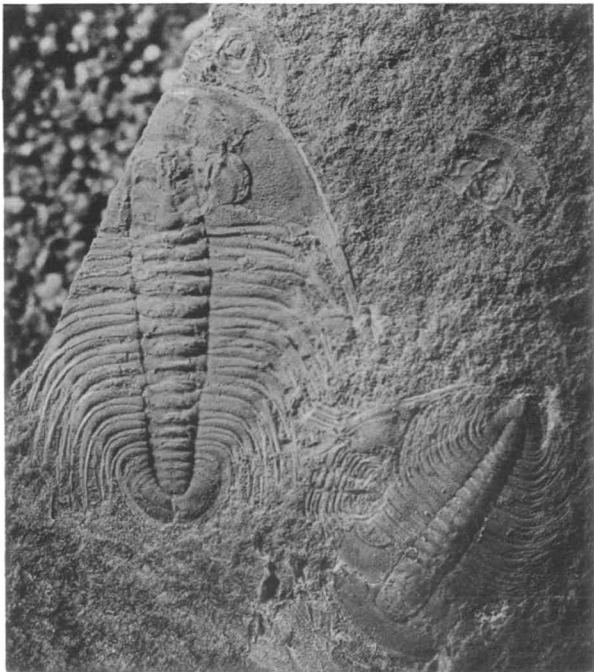
Fig. 2.—Detail of fig. 1, x 8.

Fig. 3.—Large cranidium, CPC 3850, x 4.

Fig. 4.—Hypostoma, CPC 3849, x 12.

Fig. 5.—Part of a bedding plane with numerous complete specimens, CPC 3848, embedded  
dorsum up and dorsum down, x 4.

Pomegranate Limestone, locality D119, collected by Mr. R. B. Leslie.



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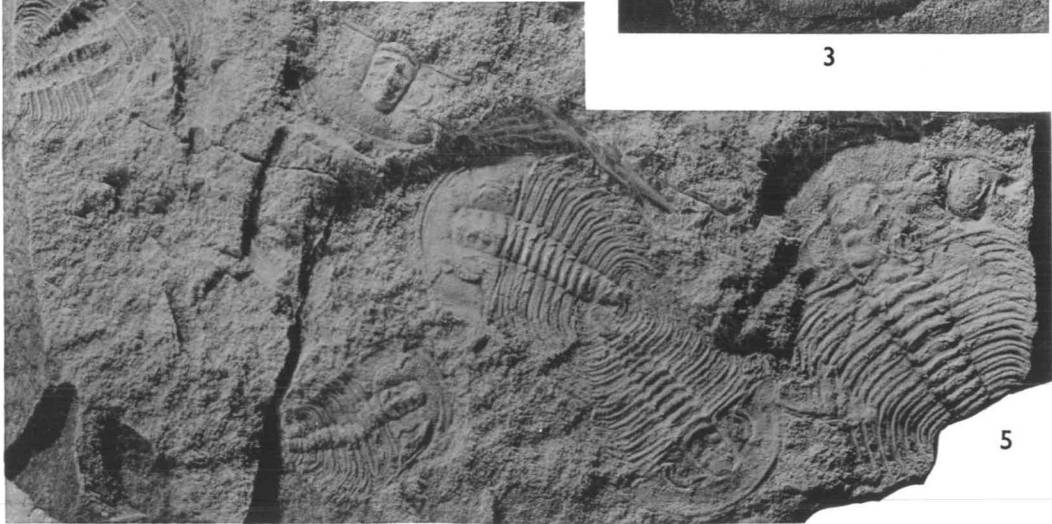
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