

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

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**The Mindyallan Fauna of North-Western  
Queensland**

BY

A. A. ÖPIK

**Volume 1: TEXT**

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Corrigenda

page 2 line 9: for *Bradoriidae* read *Bradoriida*

page 14 line 19: for *ampallatus* read *ampullatus*

page 30, Table 3: "Mindyallan zones of" should be opposite "*Glyptagnostus stolidotus*"

page 31, line 8 from bottom: the word "Cambrian" has been omitted after "Middle".

page 33 (also p. 78 and in References): R. A. Robison's name has been misspelt.

page 47 line 11 from bottom: for (1963) read (1963a)

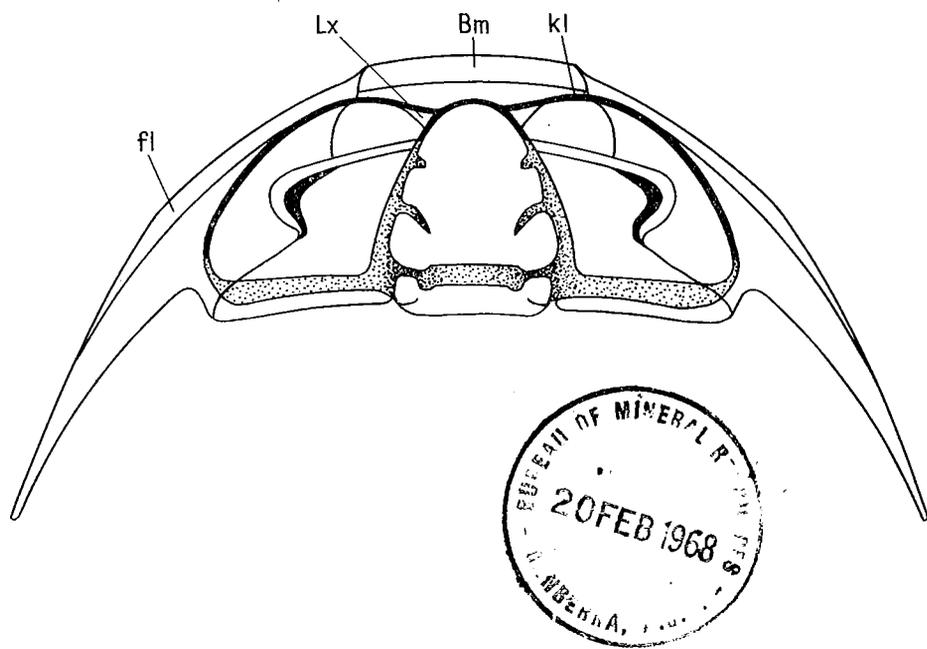
page 238, paragraph 5 line 2: for "first" read "second" and for "second" read "first".

page 372: for *Ajirikina* read "Ajrikina".

page 385: The heading "PTYCHOPARIINA Superfamiliae incertae" is an error: both *Townleyella* and *Liostracinoides* (p. 386) are "PTYCHOPARIINA familiae incertae".

In several text figures, one or two letter symbols in the caption differ slightly from those in the drawing: we do not think they will cause confusion.

At the author's request, Fig. 111 is here reproduced at a larger scale.



COMMONWEALTH OF AUSTRALIA  
DEPARTMENT OF NATIONAL DEVELOPMENT

MINISTER: THE HON. DAVID FAIRBAIRN, D.F.C., M.P.

SECRETARY: R. W. BOSWELL, O.B.E.

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BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS

DIRECTOR: J. M. RAYNER, O.B.E.

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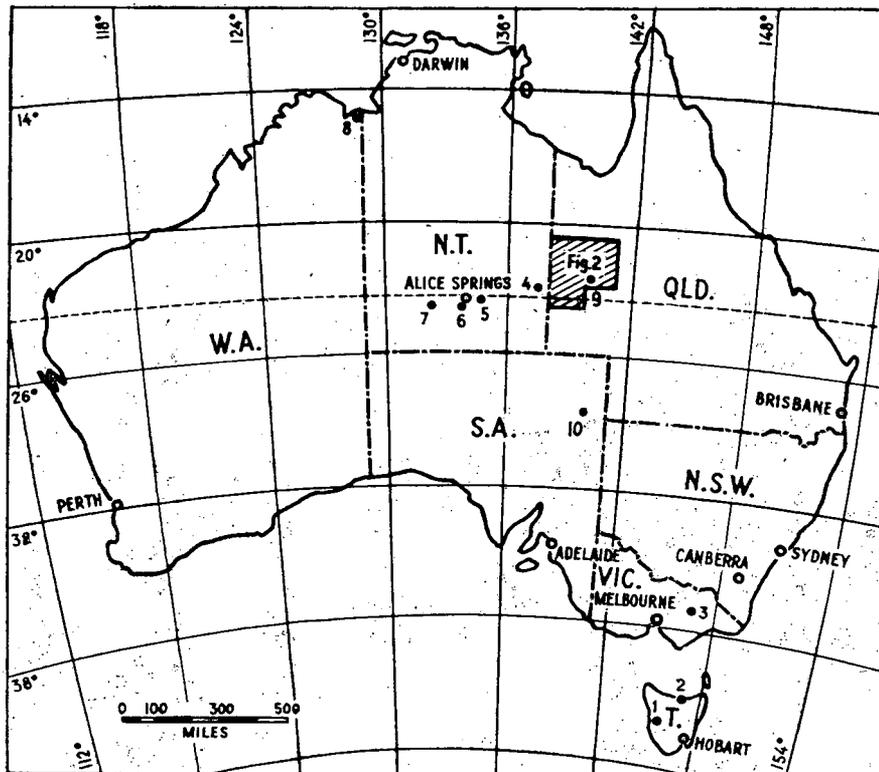


Fig. 1.—Mindyallan fossiliferous sites in Australia: (1) Comet Slate, Barkers' Creek, Dundas, Tas.; (2) Beaconsfield, Tas.; (3) Mt Wellington area, Vic.; (4) Marqua, west of Toko Range, N.T.; (5) Ross River, locality NT 187, N.T.; (6) Waterhouse Range, N.T.; (7) Ellery Creek, N.T.; (8) Skewthorpe Formation, Cambridge Gulf area, W.A.; (9) Queensland (see Text-fig. 2); (10) Gidgealpa No. 1 Well, S.A.

## SUMMARY

### *Stratigraphy*

The initial Upper Cambrian Mindyallan Stage is a succession of three faunal zones: (1) *Erediaspis eretes* zone (below), (2) *Cyclagnostus quasivespa* Zone, and (3) *Glyptagnostus stolidotus* Zone (above). Between the Middle and the Upper Cambrian a Zone of Passage is recognized whose fauna (especially the agnostids) contains several traditional Middle Cambrian genera. Species of such genera are present also throughout the Mindyallan, and one (*Corynexochus plumula*) reached the Idamean. The faunal change from the Mindyallan to the Idamean (above) is abrupt: at the turn of the stages a profound crisis is evident in conditions of continuous sedimentation; this crisis is evident also in east Asia and North America. The temporal distribution of Mindyallan species and genera, and the regional distribution of faunas in Queensland and in Australia, are presented in detail; the correlation of the Mindyallan with the *Agnostus pisiformis* Zone, the Kushanian, and the lower Dresbachian is established. The Cambrian sequence of Queensland in the areas of Mindyallan outcrops, beginning with the *Redlichia* beds and ending with fossiliferous late Upper Cambrian, is also discussed.

Brief notes on geomorphology and geological history accompany the chapters on regional stratigraphy: scarp erosion is the dominant process since the Cretaceous regression; the Middle Cambrian sequence is discontinuous; a wide hiatus and a low-angle unconformity separate the early Upper Cambrian (Mindyallan and Idamean) truncated rocks from the late Upper Cambrian and early Ordovician at the Georgina River; but on the Burke River this hiatus is absent. Faulting and mild folding occurred in the Ordovician along the Smoky Anticline and movements are apparent also in the Lower Cambrian: the *Redlichia* beds (where present) rest partly on the basement and partly on dislocated and mildly folded remnants of lower Cambrian beds.

### *Palaeontology*

The part on palaeontology begins with an epitome of methods and philosophy in systematics. Taxa are subjective aggregates of individuals and of species based on morphology which is objective; species as such are objective aggregates whose unity is evident in palaeontology only from morphological data.

The Mindyallan fauna (besides the described trilobites and bradoriids) consists of phosphatic brachiopods, gastropods, rare nautiloids, conodonts and large numbers of quite diversified sponge spicules.

Items of new and little known morphological features of trilobites, in alphabetic order, are assembled in a separate chapter; they are taken from sundry discussions in the taxonomic text.

*Agnostids*: a suprageneric re-classification of agnostids based on hitherto unused criteria is suggested and discussed; systematics of two prolific families (Diplagnostidae and Agnostidae) is summarized in a chart. Sixty-eight agnostid species are described, forty-one are named new; thirty-five forms are left open, or queried. The nomenclature and system is evident from the list of contents. Fourteen new genera are established. Some Middle Cambrian, as well as Idamean, forms are also described to illustrate aspects of agnostid classification in general.

*Polymerid trilobites*: Eighty-six new named and thirty-five open or queried forms are described. The list of contents gives the summary of the systematics. Notable are the large number of Damesellidae, and the occurrence in the early Upper Cambrian of Asaphidae, Saukiidae, and Dikelocephalinidae. Some Middle Cambrian forms are also described to account for all known Australian Damesellidae and Rhysometopacea (Mapaniidae)—prominent Mindyallan families. For a similar reason the Idamean *Corynexochus plumula* and the Pagodiinae (*Idamea*) are also described.

Finally, two forms of Bradoriidae and two kinds of Problematica are also described.

The descriptions are based on 614 specimens included in the Commonwealth Palaeontological Collection.

## INTRODUCTION

This Bulletin is the third of a series of Bulletins dealing with the palaeontology and stratigraphy of the Cambrian of Queensland, as well as of Australia in general. This Bulletin, dealing with the Mindyallan and its fauna, fills a hitherto blank interval in the Australian Cambrian sequence and supplies amplifying information regarding the geological and biological history of the early Upper Cambrian in general. Originally, the palaeontology of 'the lower chert bed' of the O'Hara Shale was planned as a part of Bulletin 53 (Öpik, 1961), but had to be postponed for technical reasons; subsequently the early Upper Cambrian stratigraphy was presented in Bulletin 64 (Öpik, 1963), and all available information from all geological sources is now included in the present contribution. I wish to emphasize that all Mindyallan comprehensible forms so far collected are described, regardless of their state of preservation, but that some material remains indicating the existence of forms which need further collecting.

Thanks are due again to all persons and institutions already acknowledged in Bulletins 53 and 64; names of others are found on sundry pages of the text and in the Glossary of Taxonomic Names in this Bulletin.

I greatly appreciate the help received from K. A. Townley, the Editor, especially for the fruitful discussions of nomenclature, terminology, and biological problems.

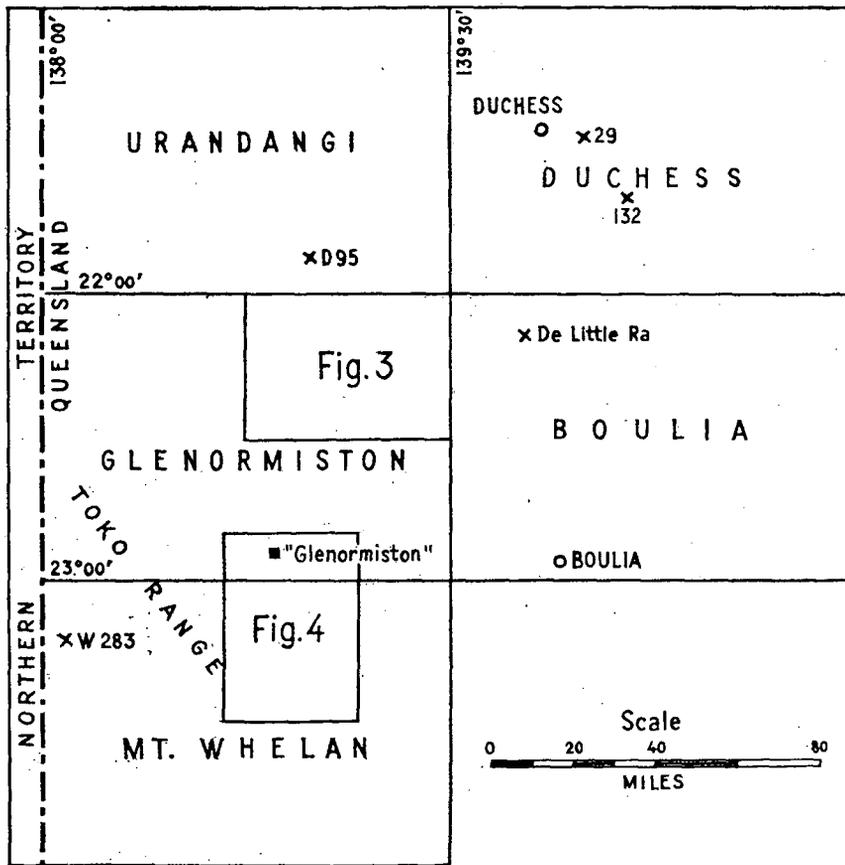


Fig. 12.—Areas and sites of Mindyallan faunas in Queensland; note position of locality W283, on Mt Whelan Sheet.

## STRATIGRAPHY AND REGIONAL DISTRIBUTION

### *The Sequence within the Areas of Mindyallan in Queensland*

The stratigraphy of the Mindyallan Stage and its zones is based on the distribution of trilobite species as shown in the list, p. 41-6. The regional distribution of faunas and zones is discussed in a separate chapter because the sequence is not everywhere complete and gaps occur at various levels. Regional and local data are summarized in the check list of species and again in the list of localities.

The nomenclature and the concepts of the early Upper Cambrian stages and zones have already been discussed (Öpik, 1963), but in an abridged form because at that time published taxonomic names were not available. The concepts and definitions of zones and stages are compiled according to the following three aspects: (1) the character of each zone on its own merits, (2) the distinction from the preceding earlier zone, and (3) the distinction from the subsequent younger zone. Zones are positions in a time scale recognized from their fossil content; each zone, therefore, attains its full meaning and usefulness when its relation to the zones above and below is known. The same applies to stages and other scale divisions of any rank.

Experience so far indicates (Öpik, 1961; 1963) that even in a continuously populated sequence of strata interzonal 'boundaries' cannot be located precisely; the uncertainty between zones encompasses an average interval of half a zone. In a sequence of a number of zones, however, the errors are not cumulative because the interstage, interseries, and intersystem boundaries also are each a junction of two zones in superposition.

In such conditions, however, as are exemplified by the faunal crisis (q.v.) at the turn of the Mindyallan and Idamean stages, theoretically a higher degree of accuracy can be expected in locating a particular zonal boundary in a fossiliferous sequence.

Interzonal 'boundaries' are interpolated by the method of trial-and-error with the objective of narrowing down the span of uncertainty between the zones. In practice this interval of uncertainty may remain inconclusive or may have definable limits, as, for example, in an unfossiliferous sequence sandwiched between two fossiliferous bands. Optimistic extrapolation, however, is unsafe: just as a thermometer gives only its own temperature to be used in reasonable extrapolation so a solitary fossil or a band of fossils define their own age in the first place; extrapolations down or up the sequence become rapidly subjective and inconclusive.

Errors, of course, result from taxonomic misidentifications, from optimistic reliance upon supraspecific taxa and 'evolutionary stages' attributed to undescribed forms, from trust in general aspects of faunas, as well as in significance of numerical predominance of 'older' over 'younger' faunal elements and vice versa, abundance of certain genera and so forth. 'Abundance' especially may be misleading, when applied without a specification regarding the abundant matter itself: abundance may mean frequent occurrence of certain genera and species (abundance of names) each represented by a small, or not defined, number of specimens, or it may mean large numbers of specimens of some or all of the abundant species. Errors of this

TABLE I.—SUMMARY OF STRATIGRAPHY (WESTERN QUEENSLAND)

|   |  |
|---|--|
| Cretaceous  |  |
| Silurian? or Ordovician? (Sandstone at W17a, Text-fig. 4)                                   |  |
| Early Ordovician (Ninmaroo) including late Upper Cambrian (W14, W204 and G332, Text-fig. 4) |  |
| Post-Idamean hiatus and unconformity in the Glenormiston area                               | Continuity of deposition in the Burke River Area (Öpik, 1963) (Chatsworth Limestone)   |
| Early Upper Cambrian  |  |
| Idamean Stage Zones    ....    ....    ....   | <i>Irvingella tropica</i> — <i>Agnostotes inconstans</i> *<br><i>Erixanium sentum</i><br><i>Corynexochus plumula</i><br><i>Glyptagnostus reticulatus</i> — <i>Proceratopyge nectans</i><br><i>Glyptagnostus reticulatus</i> — <i>Olenus ogilviei</i> |
| Mindyallan Stage Zones    ....    ....    ....  | <i>Glyptagnostus stolidotus</i><br><i>Cyclagnostus quasivespa</i><br><i>Erediaspis eretes</i>  |
| Upper Cambrian/Middle Cambrian Passage Zone   | <i>Damesella torosa</i> — <i>Ascionepea janitrix</i>   |
| Middle Cambrian Zones    ....    ....    ....   | <i>Leiopyge laevigata</i> (triple zone)  |
|   | Hiatus**   |
|   | <i>Ptychagnostus punctuosus</i>  |
|   | Hiatus**   |
|   | <i>Redlichia</i> , indet.  |
|   | Hiatus   |
| Lower Cambrian  |  |
| Basement (Precambrian)  |  |

\* Zone absent in the Glenormiston, but present in the Burke River Area, see Table 3 (Post Idamean Hiatus).

\*\* Decreases in the north.

kind, however, cannot compromise the methodical value of geological scales which are constructed to test, and to eliminate, errors in correlation and dating of faunas and sequences.

Errors can be made in dating certain Upper Cambrian collections: for instance, a collection containing only *Hypagnostus*, *Grandagnostus*, and *Ptychagnostus*, and followed above by a find of *Oidalagnostus trispinifer* would indicate 'beyond any shade of doubt' a sequence of the Middle Cambrian, and *Corynexochus plumula*, which is abundant, would impose a similar age on the Georgina Limestone.

Errors of this kind are also recognized, and corrected, in other parts of the world. Borovikov & Kryskov, (1963, p. 173) for example, write: 'placing of sequences in the Middle Cambrian on the basis of some "typical Middle Cambrian forms" is not always correct and reliable'.

### *Middle Cambrian and the Zone of Passage*

The Middle Cambrian as such is not the concern of this Bulletin. Its latest division only—the composite Zone of *Leiopyge laevigata*—is discussed in connexion with the subsequent Zone of Passage, whose fauna grades into the early Upper Cambrian. All aspects of the *Leiopyge laevigata* Zone have been discussed earlier (Öpik, 1961), in describing the fauna of the Devoncourt Limestone of the Selwyn Range. In the Mungerebar area sandstone prevails in the Middle Cambrian; its agnostid fauna differs little from the Devoncourt Limestone, but more polymerid trilobites (Damesellacea and Mapaniidae) are present, some of which are described now. Some agnostids are also described to elucidate aspects of the classification of the Agnostacea, and to illustrate certain genera which pass into the Upper Cambrian.

### *The Middle Cambrian Zone of Leiopyge laevigata*

The Australian fauna of the composite *Leiopyge laevigata* Zone is described in Öpik (1961). The Steamboat Sandstone within the Mungerebar area and to the north (Urandangi Sheet area) is referable to the upper part of the *laevigata* II and the *laevigata* III Zones as regards the agnostid fauna. It contains also several previously undescribed polymerid trilobites, of which a selection is included here.

Some selected trilobites from older Middle Cambrian Zones and from different areas are also included, for reasons that follow below.

1. Some of the fossils from the Steamboat Sandstone are described as well as recorded in the locality lists to facilitate the comparison of the faunas of the *L. laevigata* Zone with the faunas of the Zone of Passage and of the Mindyallan. Furthermore, the Mapaniidae are described to complete the record of the 'Mapania-like trilobites' and to compare these with the Mindyallan Plectriferidae. The species of *Dipentaspis* gen.nov. (and the early Damesellidae, gen. et sp.indet., locality M65) are described for the same stratigraphic reasons, and also for completing the record of the Australian Damesellacea.

2. The Middle Cambrian agnostids (*Linguagnostus* aff. *kjerulfi*, *Dolichoagnostus?* sp.indet., *Diplagnostus crassus* sp.nov., and *Oidalagnostus personatus* sp.nov.) are described for stratigraphic reasons and as material

pertaining to the classification of the Agnostacea. *Goniagnostus spiniger* Westergaard is included because it is a new record in Australia and occurs in the Mungerebar area.

*The Middle Cambrian/Upper Cambrian  
Passage or Transition Zone with Damesella torosa and  
Ascionepea janitrix*

Transition of several Middle Cambrian forms into the Upper Cambrian marks the turn of the epochs; neither an abrupt termination of the Middle Cambrian fauna nor its sudden replacement by an unequivocal Upper Cambrian fauna could be established in the Mungerebar area of Queensland. Hence, the series boundary here is as diffuse as it is elsewhere in the world. For example, the transitional *Oidagnostus trispinifer* occurs in Middle Cambrian sandstone at locality G121, and survived to reach the *C. quasivespa* Zone (locality G131) of the Upper Cambrian sequence. *Hypagnostus*, *Grandagnostus*, *Leiopyge*, *Goniagnostus*, and *Ptychagnostus*, which are regarded as standard Middle Cambrian genera, as well as the polymerid trilobites *Lobocephalina*, *Olenoides*, and *Solenopleura*, have also climbed up well into the Upper Cambrian.

The 'Zone of Passage' itself refers to a fauna that occurs in the span beginning with the last known *Leiopyge laevigata* and ending with the first appearance of *Erediaspis eretes* and its associates. The words 'passage' or 'transition' are used to indicate that the Zone cannot be assigned wholly to the Middle, nor to the Upper Cambrian, but represents the 'boundary' between the two series, or, even simpler, the passage from one epoch to another.

The practice of mapping prefers a two-dimensional boundary, of course, which here should run in an indefinable position within the Zone of Passage. Hence, an approximate boundary on lithological considerations may serve the practice by placing the Steamboat Sandstone in the Middle and the rocks above it in the Upper Cambrian. It will be an unevenly diachronous boundary within the Zone of Passage.

The relationship of the Zone of Passage with the *Leiopyge laevigata* Zone below is not conclusively definable in terms of fossils. By definition, *Leiopyge laevigata* should be regarded as Middle Cambrian, but this definition is applicable strictly only to the Scandinavian sequence, and other sequences whose Middle Cambrian age is evident from the associated fauna (Devoncourt Limestone, Öpik, 1961). In marginal cases an uncritical application of the definition serves little purpose when the associated fauna cannot be placed on its own merit in the Middle Cambrian: the passage fauna appeared in Queensland before, and persisted a while after, the extinction of *Leiopyge laevigata*.

Some nineteen species of trilobites occur in the Zone of Passage—a large number when compared with the relatively small number of specimens and collections. The rocks are friable sandstone, siltstone, and shale (locality G107) of a small total thickness; levelled by erosion and covered by soil, they offer little chance for collecting.

*Damesella torosa* and *Ascionepea janitrix* give their names to the Zone of Passage. The genus *Damesella* occurs in south-eastern Asia late in the Middle and early in the Upper Cambrian and *A. janitrix* belongs to the group of nepeids which attained their maximal development in Mindyallan time.

Other polymerid trilobites confined to the Zone of Passage are *Alomataspis enodis* gen.nov. et sp.nov., Damesellidae gen.nov. et sp.nov., *Lampropeltis nitens* gen.nov. et sp.nov., *Modocia immodulata* sp.nov., and *Rhyssometopus (Rostrifinis) tiro* sp.nov. *Olenoides tranans* is the only bi-zonal species which reached the Zone of *Erediaspis eretes*.

The Middle Cambrian relationship is well expressed in the distribution of the agnostids: *Ptychagnostus fumicola* and *Hypagnostus correctus* are bi-zonal, especially the first-named, which is common through the Steamboat Sandstone; *Leiopyge laevigata* and *L. laevigata armata* are quadrizonal, the fourth zone being the Zone of Passage itself; and *Hypagnostus hippalus* is trizonal.

#### *The Upper Cambrian Mindyallan Stage*

The Mindyallan is the initial stage of the Upper Cambrian Series (and Epoch). The concept and the name were introduced in Öpik (1963) in a simplified form of only two zones—the Zone of *Glyptagnostus stolidotus* (above), and the 'pre-stolidotus' zone (below) (op. cit., p. 8). The concept of the 'pre-stolidotus' Zone, pending the description and naming of the fossils, could not be presented then. The 'pre-stolidotus' Zone is replaced now by two zones, the *Erediaspis eretes* Zone (below) which is the earliest Upper Cambrian Zone, and the *Cyclagnostus quasivespa* Zone (above).

The Zone of *Erediaspis eretes*. (The *eretes* Zone)

*The name:* The name of the zone refers to the tricrepicephalid trilobite *Erediaspis eretes* gen.nov., sp.nov.; *Erediaspis* occurs also in northern Tasmania (unpublished). Some 45 trilobites are known from this zone, including 18 agnostids—a large fauna for a single Cambrian zone.

Confined to the Zone are the agnostids:

*Agnostus* aff. *pisiformis*, *Agnostus artilimbatus*, *Grandagnostus evexus*, *Hypagnostus durus*, and *Ptychagnostus nodibundus*,

whose generic aspect is entirely Middle Cambrian. The majority of the agnostids, however, are alien to the 'standard' Middle Cambrian forms and referred to the genera *Agnostascus*, *Agnostoglossa*, *Hadragnostus*, *Idolagnostus*, *Clavagnostus*, and *Triadaspis*, whose species are bi-zonal (see under the Zone of *Cyclagnostus quasivespa*).

Polymerid trilobites confined to the Zone are:

*Aedotes mutans*, *Aedotes instans*, *Agelagma quadratum*, *Agelagma laticeps*, *Ascionepea anitys*, *Biaverta reineri*, *Cermataspis abundans*, *Erediaspis eretes*, *Ferenepea pilaris*, *Iniotoma iniotoma*, *Interalia serena*, *Meringaspis* sp.nov. *A.*, *Norwoodella? dubitalis*, *Onchonotellus offula*, and *Rhyssometopus neuter*.

These are all new species; and, with the exception of *Norwoodella* and *Onchonetellus*, of new genera. The most abundant species are *Erediaspis eretes*, *Cermataspis abundans*, *Aedotes instans*, and above all the bi-zonal *Rhyssometopus* (*Rostrifinis*) *rostrifinis*.

The bi-zonal polymerids are listed under the Zone of *Cyclagnostus quasivespa*; a single species—*Olenoides tranans*—is common to the Zone of Passage and the *eretes* Zone.

The Zone of *Cyclagnostus quasivespa* (The *quasivespa* Zone)

*The name:* The name *Cyclagnostus quasivespa* Zone can be abbreviated to the name *quasivespa* Zone; the usage of the generic names only cannot be recommended because *Cyclagnostus* is a prospective junior synonym. The occurrence of *Stephanocare richthofeni* is significant in correlation and palaeogeography; but it occurs only in two localities and is confined to a relatively narrow band within the sequence.

More than 40 fossils are recorded in the Zone, of which 18 trilobite species are restricted to it. The following forms can be considered for the purpose of naming the Zone:

*Blackwelderia sabulosa*, *Griphasaphus griphus*, *Palaeadotes* aff. *dissidens*, *Rhyssometopus rhyssometopus*, *Stephanocare richthofeni*, and *Cyclagnostus quasivespa*.

*Blackwelderia sabulosa* and *Cyclagnostus quasivespa* are equally appropriate for naming because they are the best known, and quite abundant; preference, however, is given to *C. quasivespa* because it occurs in the whole sequence and, as an agnostid, has the chance of being found also outside Australia. *Rhyssometopus rhyssometopus* is also rather common, but its identification needs well preserved cranidia; otherwise its distinction from *Rh. princeps* (of the *stolidotus* zone) would remain inconclusive.

*Relationship with, and distinction from, the Zone below (eretes Z.) and the Zone above (stolidotus Z.):* Three or four agnostid species (*Clavagnostus bisectus*, *Idolagnostus dryas*, and probably *Pseudagnostus bulgosus* and *Innitagnostus innitens*) pass through the three Mindyallan Zones and the persistent *Oidagnostus trispinifer*, first recorded in the Middle Cambrian *Leiopyge laevigata* Zone of Sweden, reached Australia in *quasivespa* time.

Some fourteen species of trilobites are common to the *quasivespa* Zone (above) and the *eretes* Zone (below). Among the more abundant bi-zonal species are *Aedotes declivis*, *Meropalla auriculata* and *M. quadrans*, *Plectrifer plectrifer* and *P. mitis*, *Rostrifinis rostrifinis*, *Agnostascus gravis*, *Agnostoglossa bassa*, and *Hadragnostus las*; and collections containing only these bi-zonal species cannot be placed in either zone on their own merit. Consequently continuity of population and deposition as well as environmental stability (within limits) is documented by the large number of the bi-zonal species during the two lower Mindyallan Zones.

The distinction of the *C. quasivespa* Zone from the zone above (*Glyptagnostus stolidotus*) is quite prominent: even small collections and fragmentary material can be interpreted on their own merit. Still, bi-zonal species are *Connagnostus zonatus*, *Ferenepa hispida*, *Palaeadotes italops*, and *Placosema adnatum*, to which the tri-zonal *Clavagnostus bisectus*, *Idolagnostus dryas*, *Innitagnostus innitens*, and

*Pseudagnostus bulgosus* should be added, of course. Of these only *Ferenepea hispida* and *Clavagnostus bisectus* are relatively frequent; but they are not misleading because they are found in association with other, stratigraphically unambiguous, forms. The number of common genera (without common species) is also relatively small as compared with the total number of forms in each of the zones. These genera are *Biaverta*, *Blackwelderia*, *Meringaspis*, *Rhyssometopus*, *Ammagnostus*, and *Xestagnostus*. The relative abruptness of the change of the faunas at the transition from the *quasivespa* to the *stolidotus* Zone reflects a particular depositional event in the Mindyalla area: at this transition a barren dolomite (locality G400) and some dolomitic limestone were deposited, indicating the incidence of a semi-eporitic environment inimical to life. Thus, a large part of the fauna which may have flourished elsewhere was locked out from this particular place. The deposition was not interrupted, but the intervening dolomitic environment acted as a local break in the record of life.

#### The Zone of *Glyptagnostus stolidotus* (*stolidotus* Zone)

The concept of the *stolidotus* Zone has been already discussed (Öpik, 1960, 1961, 1963) and its distinction from the Zone above—the Idamean Zone of *Glyptagnostus reticulatus*—established. The discontinuity between the faunas of these zones is discussed here under the separate heading of the faunal crisis at the turn of the stages. The distinction from the zone below (the *Cyclagnostus quasivespa* Zone) is presented above. The concept of the *G. stolidotus* zone on its own merit refers to its fauna of some 75 species of trilobites. As a whole the fauna is unique in its diversity, but the distribution of the species and genera is uneven: it appears that the Georgina Limestone contains some unique species, but is deficient of several forms found in the 'lower chert bed' of the O'Hara Shale. Common to both formations and occurring in almost every locality are:

*Aulacodigma quasispinale*, *Auritama trilunata*, *Biaverta biaverta*, *Mindycrusta mindycrusta*, *Rhodonaspis longula*, *Rhyssometopus princeps*, *Agnostardis amplinatis*, *Aspidagnostus inquilinus*, *Glyptagnostus stolidotus*, *Xestagnostus legirupa*.

Alone or in combination with others, and even in the absence of *G. stolidotus*, any of these species can be regarded as an index fossil of the *stolidotus* Zone.

Widespread in the Georgina Limestone but absent in the O'Hara Shale are:

*Auritama aurita*, *Blackwelderia gibberina*, *Meteoraspis bidens*, *Palaeadotes dissidens*.

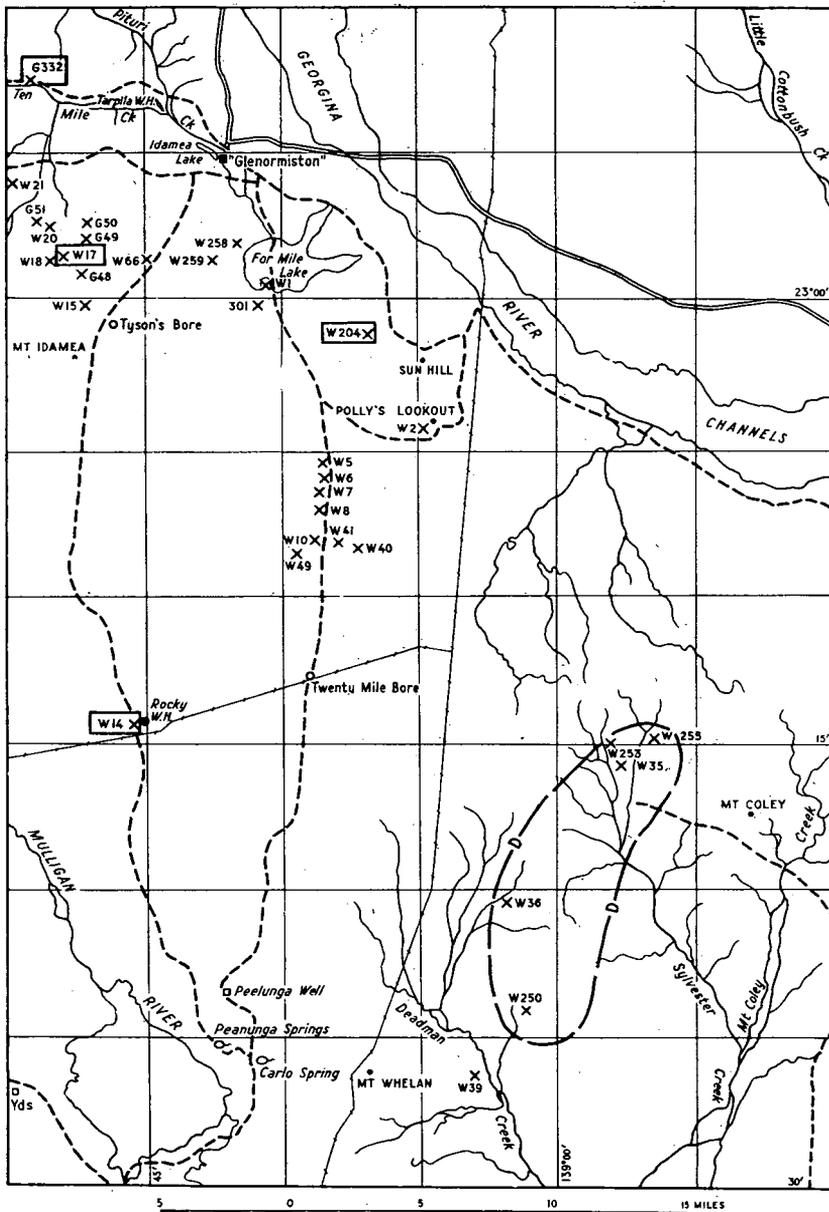
The fauna of the *stolidotus* Zone in the Mindyalla area (Text-fig. 3) is relatively small, and even *Glyptagnostus stolidotus* itself has not been found there as yet. However, the collection from G12 contains *Auritama aurita*, *Meteoraspis bidens*, and *Biaverta biaverta*, and the collection from McCabe Knob *Biaverta biaverta*, *Palaeadotes dissidens*, and *Rhyssometopus princeps*.

#### The Upper Cambrian Idamean Stage

The name of the Idamean and its concept were introduced earlier (Öpik, 1963). Including the new species which are described here, 52 species altogether are described



GLENORMISTON - SYLVESTER CREEK AREA Fig. 4



REFERENCE

- X650 Position of locality
- XW17 Late Upper Cambrian localities
- Area of Middle Cambrian localities
- Cambrian localities
- Main road
- - - Track
- - - Fence

so far from the Idamean sequence. In the Glenormiston area the latest Zone of the Idamean (the Zone of *Irvingella tropica*—*Agnostotes inconstans*) is absent, apparently by non-deposition.

The Idamean, its fauna and some of its fossils, are discussed here as regards their difference from the Mindyallan.

#### The Zone of *Glyptagnostus reticulatus*

The fauna of the Idamean Zone of *Glyptagnostus reticulatus* and *Olenus ogilviei* and the Zone itself have been discussed (in Öpik 1960; 1963). *Aspidagnostus stictus* sp.nov. and *Mindycrusta advena* sp.nov. complete the record of fossils of this zone. They also represent genera (but not species) passing from the Mindyallan into the Idamean.

#### Fossils from other Idamean Zones

The species of the genus *Idamea* Whitehouse are described here to facilitate the comparison with the Mindyallan *Meropalla* gen.nov.; *Blountia georginae* completes the record of the Australian early Upper Cambrian Asaphiscidae; *Corynexochus plumula* is described as an example of an anachronism—a Middle Cambrian trilobite in the Upper Cambrian—and *Peratagnostus* as an example of a late, and effaced, peronopsid. *Pseudagnostus idalis* sp.nov. serves for a comparison with the Mindyallan *Pseudagnostus ampallatus* sp.nov. *Innitagnostus inexpectans* amplifies the previous description (Öpik, 1963) and is compared with the Mindyallan *Innitagnostus immitens*; *Eugonocare* cf. *tesselatum* Whitehouse is briefly discussed as regards an earlier incorrect interpretation.

The Idamean fossils in this paper represent a minor part of a large fauna; but, together with the published material (Whitehouse, 1936–1939; Öpik, 1963) these fossils illustrate a fauna which abruptly replaced the Mindyallan trilobites.

#### REGIONAL DISTRIBUTION OF FAUNAS, ZONES, AND STAGES

The fossils described here come from the following places in Queensland: (1) Mungerebar and Mindyalla areas (Text-fig. 3); (2) Glenormiston and Sylvester Creek areas (Text-fig. 4); (3) Quita Creek area; (4) Selwyn Range, Pomegranate Creek and de Little Range. Furthermore Mindyallan fossils are listed (but none described) from locality NT187, on Ross River, Northern Territory.

The geographical distribution of the Queensland areas is briefly described (with diagrammatic maps) by Öpik (1960). The Selwyn Range localities (D6, D28 and D29) are described in Öpik (1961, p. 119 and 185; map p. 10) and de Little Range in Öpik (1963, p. 17). Data regarding the Sylvester Creek area are found in Öpik (1960, 1961) and a part of the Glenormiston area was described in 1963.

Supplementary information regarding the Mungerebar and Mindyalla, Glenormiston and Sylvester Creek, and Quita areas is given below; the other places are sufficiently described in the literature as indicated above.

The maps (Text-figs 3, 4) were compiled in collaboration with Mr M. A. Reynolds (Bureau of Mineral Resources), who also provided data on the thickness of parts of the Mindyallan sequence.

*The Mungerebar-Mindyalla Area*  
(Map, Text-figure 3)

*Rocks; mode of preservation of fossils; outcrops*

All Middle Cambrian fossils (except for locality G101 and the lower part of the sequence at D114) have been found in sandstone. The fossils of the Zone of Passage were collected in limestone (at locality G9), in siltstone (or shale) with chert pods at G107, and in chert pods at G103.

All Mindyallan fossils of the *eretes* and *quasivespa* zones have been collected from limestone (the Mungerebar Limestone) and its chert pods, layers, and weathered out layers with silicified material. Samples of limestone from most of the localities were etched with acid (by Mr P. Jones, B.M.R.) in a search for conodonts. Phosphatic brachiopods and sponge spicules constitute the main part of the residual; gastropod and trilobite tests, however, are incompletely silicified or disintegrate into fragments; still, one locality (G417) yielded some useful specimens.

Sandstone and dolomite interbeds (Text-figs 9-12) are present in the sequence of the Mungerebar formation, but are barren of fossils. In silty limestone (e.g. loc. G113) the preservation is rather poor.

Fossils of the Zone of *Glyptagnostus stolidorus* are not silicified; they occur in the upper part of the Mungerebar Limestone in light-coloured dolomitic, as well as sandy limestone, and at one locality (McCabe Knob) in siltstone. Some of the fossils which are described here come from weathered-out chert remnants lying on the surface; fossils from transported material, however, have not been described.

Outcrops are numerous, but most of them are very small, representing only a thickness of some few feet of the sequence each. Common (average) outcrops are bare spots within rubble, or sand-covered pediments; an average outcrop is seen in Text-figure 13, taken in the Glenormiston area. An outcrop of some tens of yards square is large. Owing to the low dip of the beds some outcrops are developed as low steps facing watercourses.

Step slopes and scarps are relatively rare (Text-figs 7, 9, and 10), representing each a not quite definable part of the sequence offering little chance for fossil collecting. The thickest (longest) section of about 75 feet was measured at locality G8. At its base, on limestone steps, rather fossiliferous beds are present (Pl. 1) and fossils were found also in higher levels.

To conclude, the sequence had to be pieced together on faunal evidence won from the numerous discontinuous outcrops. No comprehensive section of the Mungerebar Limestone, that is, of the Mindyallan Stage, exists in the area; the reasons for this deficiency are the rather low dip of the strata, the low elevation that prevents a deep dissection by streams, and the morphology in general, which is briefly discussed below.

*Geomorphology*

In general terms the area is a part of the plainlands of Queensland and Northern Territory. The landscape of the area itself, however, is dominated by uplands in the east and north, and a lowland spread to west and south from the uplands. In spite of the small difference in altitudes (a maximum of 500 feet) the contrast of



Fig. 5.—Mungerebar area, northern part; scenery in southern part of the Precambrian inlier, looking south and south-west. Foreground: quartz reef in metamorphic rock; background: *Redlichia* shale, Middle Cambrian Steamboat Sandstone and Cretaceous (flat top on left); skyline: Mungerebar Limestone (Mindyallan) and Steamboat Sandstone. (See Text-fig. 3.)

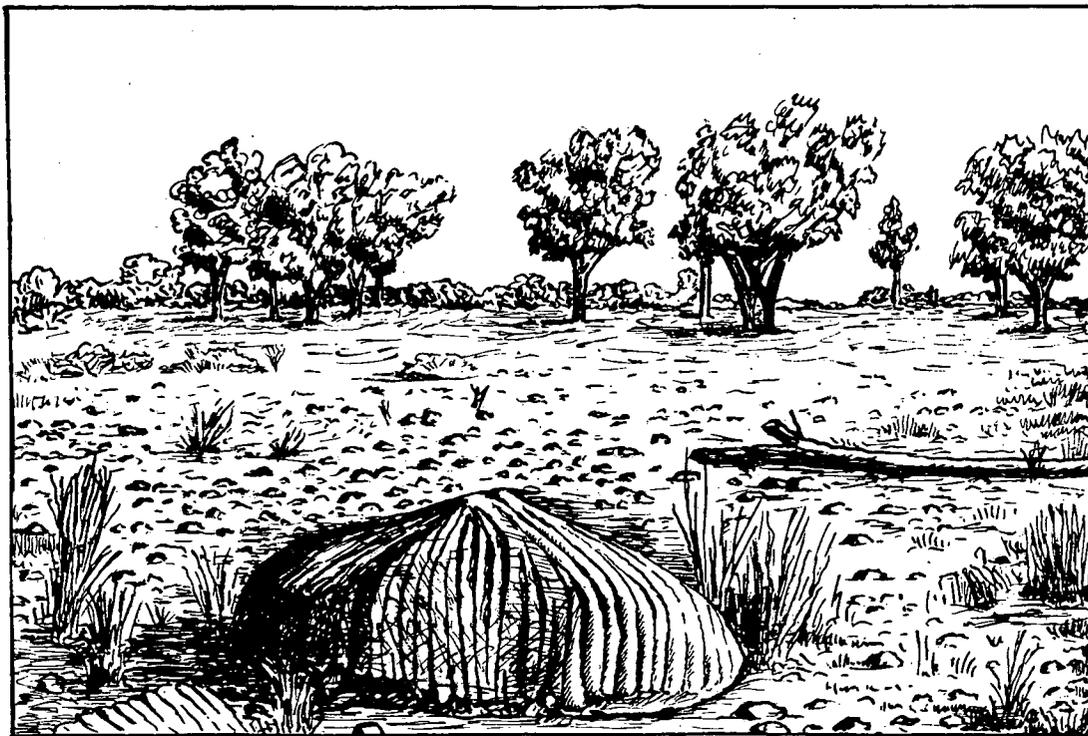


Fig. 6.—Pediplain scenery, vicinity of locality G437, southern part of Mindyalla area. (Text-fig. 3)  
A grooved limestone floater (sandy dolomitic limestone) in foreground; gibber; savannah. (See Text-  
fig. 3.)

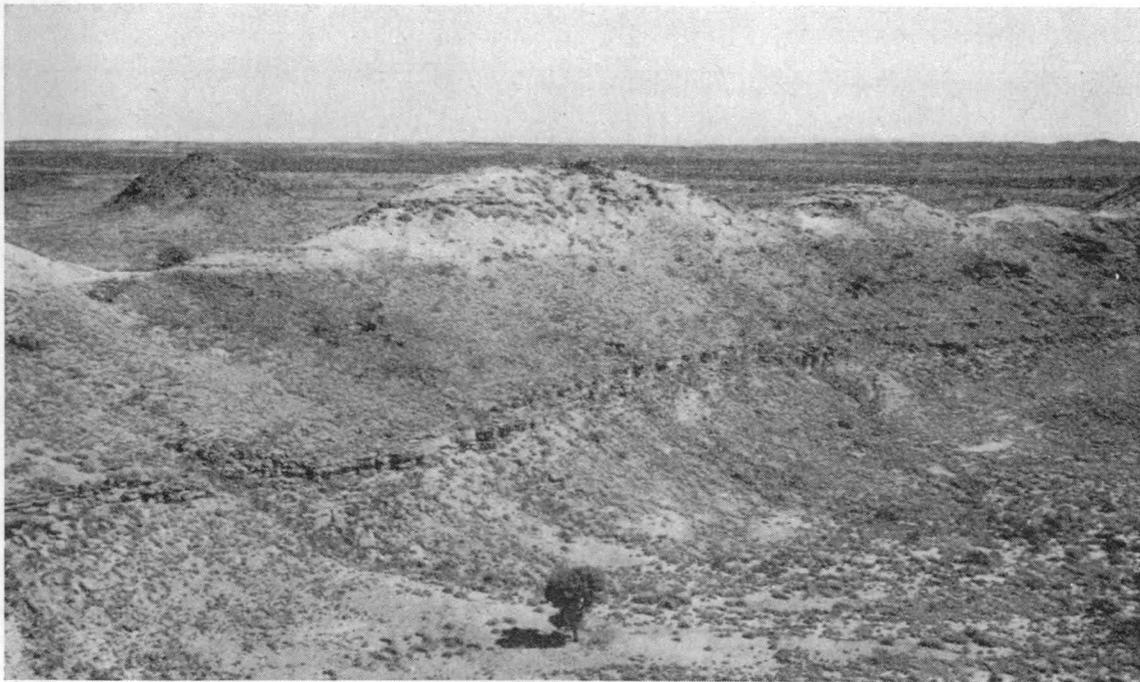


Fig. 7.—Locality G137, Mungerebar area (Text-fig. 3). Outlier of Cretaceous, reduced to a ridge with windgaps, about eighty feet high. Cretaceous/Cambrian contact at the top of the prominent sandstone bed half way up the slope. Skyline: Cretaceous outliers fringing the inlier of Precambrian; background: gentle slope toward Smoky Creek and its tributaries.

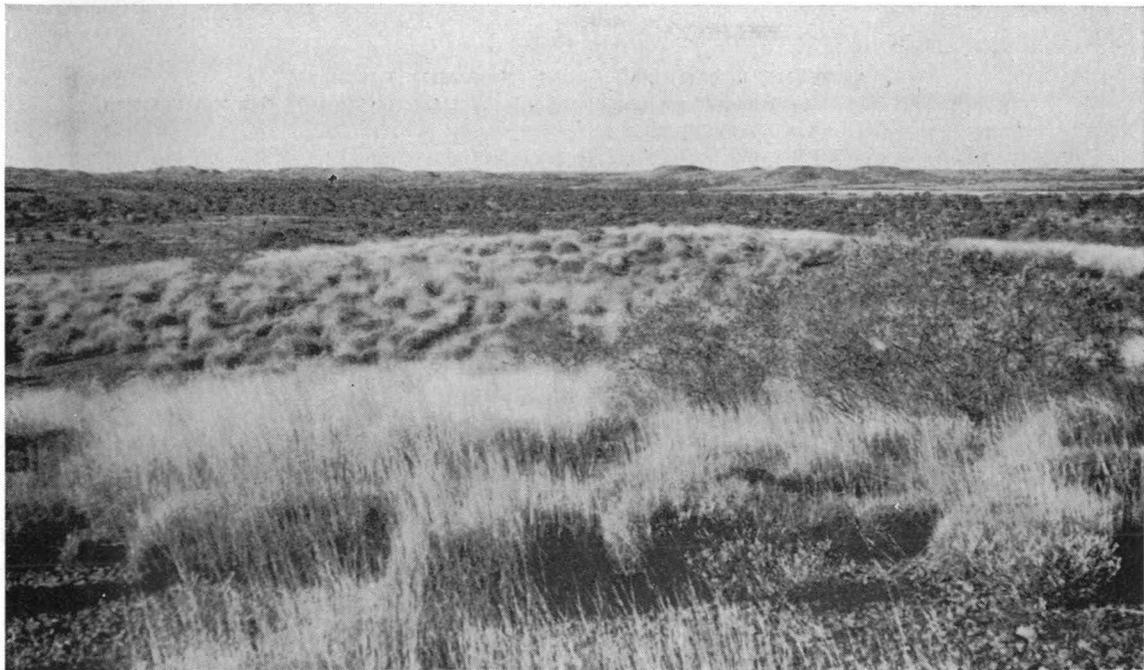
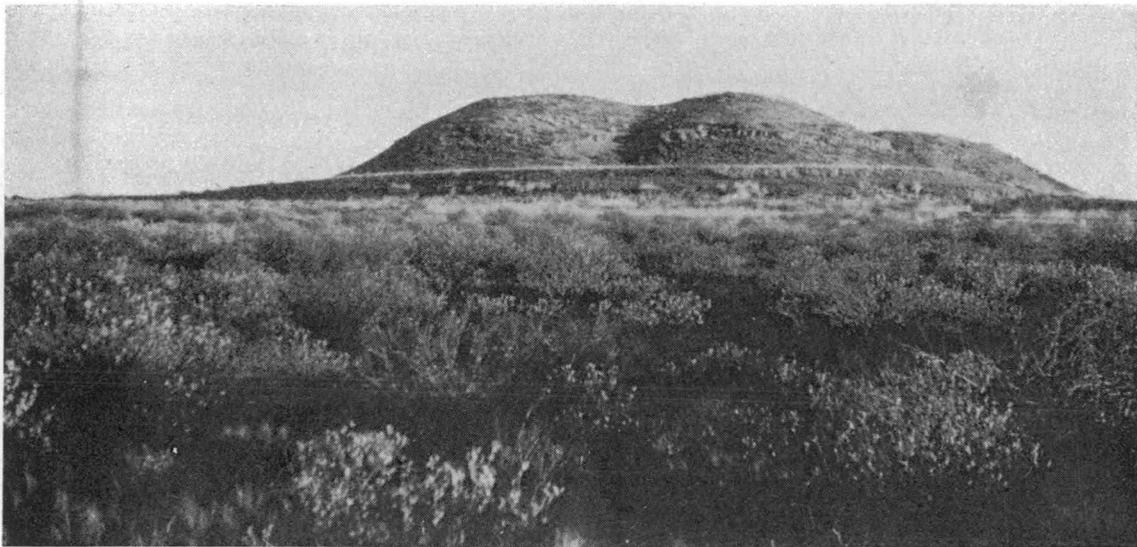


Fig. 8.—Rolling surface of Steamboat Sandstone with spinifex. Looking across the valley of Smoky Creek and tributaries toward the upland (Cretaceous plateau) in the east. Mungerebar area (Text-fig. 3).



**Fig. 9.—**Locality G7, Mungerebar area, (Text-fig. 3). Triple hill of low domes, height above plain about 75 feet. The terrace at the base consists of a single bed (about ten feet) of resistant sandy dolomite (see also Text-figs 11, 12); above follows limestone and marly limestone capped by friable sandstone (Cretaceous). Turkey Bush scrub in foreground.



Fig. 10.—Locality G108, at the heads of Seventeen Mile Creek, Mungerebar area (Text-fig. 3). Syncline in Mungerebar Limestone. For height, note two cars at foot of left hill. Detail in Text-figures 11 and 12.

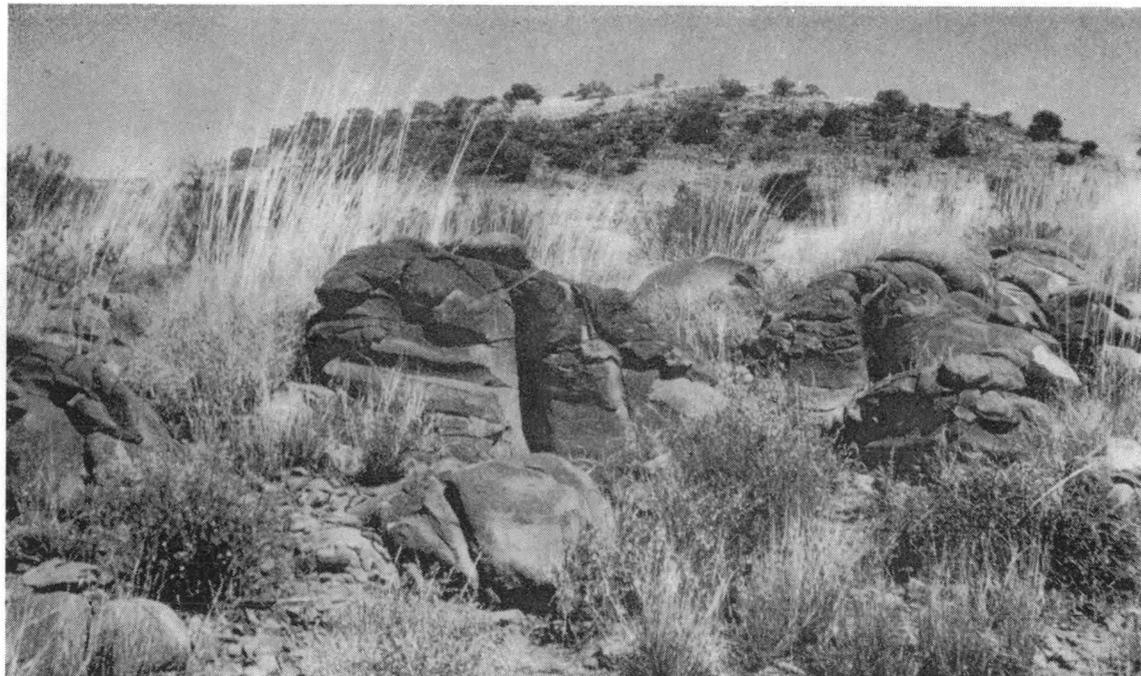


Fig. 11.—Locality G108, detail (see Text-figs 10 and 12; also 9). A bed of sandy massive brown unfossiliferous dolomite.

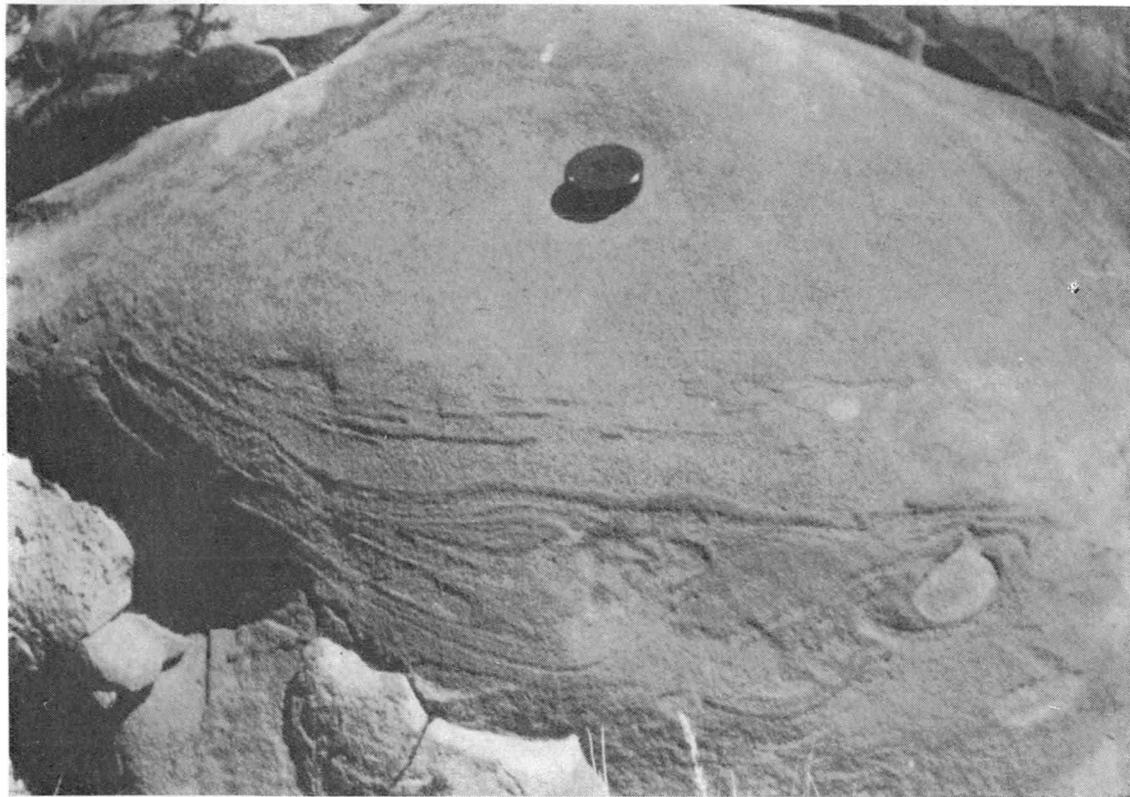


Fig. 12.—Locality G108, detail of Text-figures 10 11 Flowage and slump structures in dolomite.

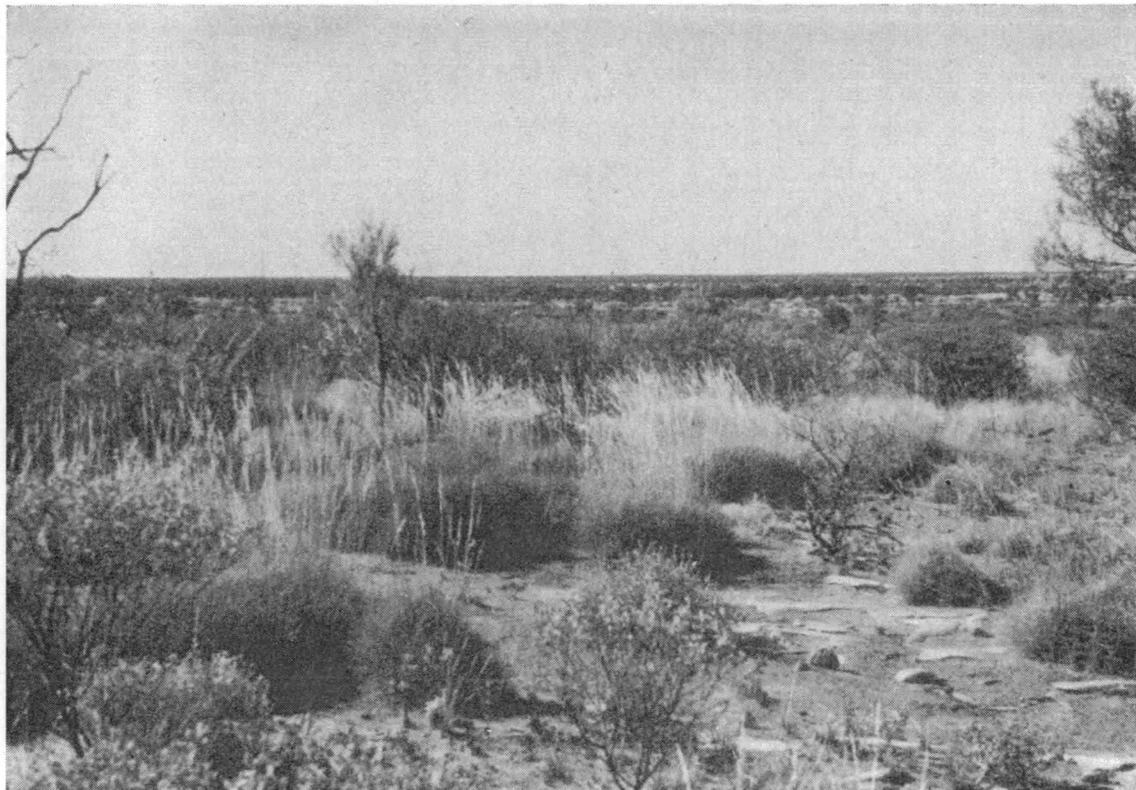


Fig. 13.—Locality W21, Glenormiston area (Text-fig. 4). An average outcrop and fossil locality of Mindyallan rocks; grey sandy limestone in red sand. Skyline: plain on Ninmaroo (Ordovician) limestone.

lowland and upland is well expressed within the area (Text-fig. 8). The plateau of Cretaceous sediments at the heads of Cottonbush Creek is about 950–1000 feet, and in the inlier of the Precambrian in the north summits rise above 1000 feet. From the foot of the uplands the lowland slopes down gently south and south-west to about 500 feet on the bank of the Georgina River.

The inlier of the Precambrian has a rugged surface, is well dissected, and fringed by low hills of the sedimentary mantle (Text-fig. 5). Some of the summits of the inlier (which itself is the southern extremity of the Isa Highlands) are crowned by minor outliers of Cambrian and Cretaceous sediments. Structurally the inlier is the south-plunging core of the Smoky anticline (Öpik, 1960).

The plateau of Cretaceous sediments is fringed by outliers (Text-fig. 7), rapidly decreasing in surface and numbers away from the plateau. The erosion cuts through the Cretaceous-Cambrian contact (the pre-Cretaceous land surface) and some fifty feet down into the Cambrian sediments, irrespective of their lithology (Text-fig. 7), and pediments develop at the foot of the escarpments. This is also seen in the isolated outlier of G7 (Text-fig. 9). The convex slopes of G7 are almost unique in their regularity and exceptional in conditions of slope erosion and pedimentation. The domes or cupola are the result of the gradual decrease of the resistance of the bed upward from the hard, terrace-forming dolomite at the base, through less resistant limestone toward the friable sandstone on top. No streams are present to undercut and destroy the cupola.

The Cottonbush Creek valley has a frame of escarpments of the Cretaceous, but in its floor in the pediments Cambrian limestone is exposed; at locality G12, of about 700 feet altitude, rapids are formed in the creek bed.

The streams draining the lowland arose within the plateau and the hills of the Precambrian inlier and following a south-west direction they join the Georgina River. The Seventeen Mile Creek has, furthermore, left-bank tributaries issued from low hills at localities G107, 108, 133, etc. In these hills the rocks are somewhat deformed and cut by a south-west-trending fault. The buried relief of the basement, which plunges in the same direction, may be an additional reason for the elevated position of the Middle Cambrian sandstone (Text-fig. 8) in these hills, and, to the west, in the interfluvium of the Seventeen Mile Creek and Smoky Creek.

The lowland of the Mungerebar-Mindyalla area can be regarded as a pediplain studded in its central part with bare pediments. In the south, however, the pediments are masked by sand with patches of gibber (Text-fig. 6) and scattered limestone floaters. Farther south the bedrock becomes completely buried under a blanket of sand.

The Ordovician calcareous sequence of the Ninmaroo Formation is not preserved in the Mungerebar-Mindyalla area and the Cretaceous rests on the Cambrian or even on Precambrian rocks. West of the Georgina River, however, the flat-lying Ordovician is dominant; there prevails a plain with a bastion topography (see Öpik, 1961), whose summits rise above 700 feet on the divide between the Pituri Creek and the Georgina River.

The following events are reflected in the landscape of the Mungerebar-Mind-yalla area:

(1) the rise of the Smoky anticline in the Ordovician, followed by the erosion of its sedimentary mantle, including the Ordovician, and the formation of the basement inlier; (2) the Cretaceous marine deposition on the truncated Precambrian and Cambrian rocks; and (3) the subsequent uplift followed by the reduction of the Cretaceous cover.

The erosion is still active, the scarps of the plateau are retreating; its outliers are vanishing, and some of the underlying Cambrian is also eroded away together with the pre-Cretaceous landsurface.

#### *The faunal sequence*

The lines separating the groups of localities on the map (Text-fig. 3) are by no means boundaries of zones; these lines are meant to facilitate the presentation of the distribution of related faunas (the localities shown on the map yielded fossil collections, but many more have been examined from which nothing was collected). The oldest fossils in the area are found at the contact with the basement outcrops, and moving south the belts of the localities become gradually younger in the ascending sequence of zones that are established solely on faunal evidence.

The fossils collected at each site are listed under the heading of 'Description of Localities' in Vol. 2; the faunal content of the zones is listed separately.

#### *The Redlichia fauna: localities G122, G141, G426, and D11*

The age of this *Redlichia* fauna is early Middle Cambrian; it is found in shale and chert resting as erosional residuals partly on the metamorphic basement and partly on erosional residuals of the Riversdale Formation (Noakes et al., 1959; Öpik, 1960), whose age is presumably Lower Cambrian.

#### *Ptychagnostus punctuosus Zone:*

Locality D114. At this site, west of the basement inlier, a limestone topped by a brecciated limestone bed is assigned to the Quita Formation (of the Zone of *Ptychagnostus punctuosus*; see Öpik, 1960). It is absent at the south and east flanks of the Precambrian inlier, but present in the north (see 'Description of localities,' localities D59 and D104).

#### *Ptychagnostus (Goniagnostus) nathorsti Zone:*

Fossils and rocks of this age are absent in the region of the Glenormiston and Urandangi sheets and the Zone is represented by a hiatus. The zone is well represented in the Camooweal area (see 'Description of localities', locality M65).

#### *Leiopyge laevigata Zone:*

Localities G101, G102, G104, G106, G121, G133 and D114; the formation is the Steamboat Sandstone, extending to the north (Urandangi Sheet area). From this northern extension, localities D54, D95 and D96, some agnostids (*Linguagnostus?* *Dolichoagnostus?*, and *Peronopsis*) and polymerids (*Diventaspis* and *Quitacetra*) are also described here.

The *Leiopyge laevigata* Zone is tripartite (see Öpik, 1961); the lowest (*laevigata* I, or *Ptychagnostus cassis*) Zone is absent, as well as the earlier *nathorsti* Zone, and of the *laevigata* II (*Proampyx agra* Zone) only the upper part may be present and not quite discernible from the *laevigata* III (*Holteria arepo*) Zone. For this reason in the description of the fossils the age is given simply as the Zone of *Leiopyge laevigata* (upper part). Some 200–300 feet of the sequence (mostly sandstone) is attributable to the *L. laevigata* Zone.

TABLE 2.—STRATIGRAPHIC SEQUENCE, MUNGEREBAR-MINDYALLA AREA

|                                       |   |
|---------------------------------------|---|
| Cretaceous                            |   |
| Unconformity                          |   |
| Mindyallan Zones of                   | <i>Glyptagnostus stolidotus</i><br><i>Cyclagnostus quasivespa</i><br><i>Erediaspis eretes</i> } 'pre-stolidotus zone' |
| Upper Middle Cambrian Passage zone of | <i>Damesella torosa</i> — <i>Ascionepea janitrix</i>  |
| Middle Cambrian Zones of              | <i>Leiopyge laevigata</i>   |
| Hiatus                                |   |
| <i>Ptychagnostus punctuosus</i>       |   |
| Hiatus                                |   |
| <i>Redlichia</i> beds                 |   |
| Unconformity                          |   |
| Lower Cambrian                        | Riversdale Formation  |
| Unconformity                          |   |
| BASEMENT                              |   |

*The Middle/Upper Cambrian Zone of Passage:*

Localities G9 (lowermost three or four feet at the foot of the escarpment), G103, G107, G116, G427 and G443; and locality D99 (uppermost part of the Steamboat Sandstone, Manganese Ridge, Urandangi Sheet area).

The transition fauna occurs in the uppermost part of the Steamboat Sandstone, in a limestone (G9) and in shale with chert (the G107 outcrop). Most of the examined localities of the Zone of Passage are found in the headwaters area of Seventeen Mile Creek—a place disturbed by faulting. The thickness of the rocks deposited during the time of the transition is estimated at 20–30 feet only.

*Erediaspis eretes* Zone (lowermost Zone of the early Upper Cambrian Mindyallan Stage):

Localities G7, G8, G9 (upper part of the section), G113, G114, G115, G117, G118, G119, G136, G137, G144, G145, G149, G150, G151, G417, G428 and G429. The thickness is about 110 feet (according to M. A. Reynolds, unpublished); some sandstone interbeds are present but yielded no fossils. On the map, Text-figure 3, the *erediaspis* Zone localities are shown between the lines A and B.

*The Cyclagnostus quasivespa* Zone:

Localities G2, G4, G6 and G10; G124, G125, G126, G127, G128, G130, G131, G132, G137, G147 and G153. The greatest measured thickness is 20 feet (M. A. Reynolds); the scattered outcrops make an estimate of the total thickness inconclusive; localities G4, G6, G10 represent, however, a horizon different from the localities G124, G125, G126 and G127, which together belong to a sequence of beds; a third horizon occurs at G153 (with *Stephanocare richtofeni*); all these beds taken together indicate a summary thickness of some 50–60 feet in surface outcrops. On the map, Text-figure 3, the *quasivespa* Zone localities are shown between the lines B and C.

*The Glyptagnostus stolidotus* Zone :

Localities G12, G140, G154, G155a, G161, G407, G408, G409, McCabe Knob, G415, G416, G430 and G437. Of these localities G12 and McCabe Knob yielded most of the fossils; *Acrothele* sp. occurs, however, in all sites, including G140, on the bank of the Georgina River. North of it, at G400, the dolomite with worm burrow (Text-fig. 14) occurs.

The thickness (according to M. A. Reynolds) is at least 75 feet; only the lower part of the zonal sequence is however exposed. On the map, Text-figure 3, the *stolidotus* Zone localities are shown south of line C.

The total thickness of the Mindyallan sequence (including the sediments of the Zone of Passage) is 250–270 feet; this figure is based on fossiliferous surface outcrops, and takes no account of parts that are unfossiliferous, or masked by soil and debris.

## The Glenormiston—Sylvester Creek Area

(Map, Text-fig. 4)

The morphology and the depositional history of the Upper Cambrian sequence of the Glenormiston area have been discussed earlier (Öpik 1963) and brief notes regarding the Sylvester Creek area were published by Öpik (1960).

Most of the fossils are unsilicified and are collected from limestone outcrops. The largest single outcrop, with a section of about 15 feet, is at locality W20, with exceptionally well preserved silicified material on siliceous partings in limestone (see Öpik, 1963, p. 26). An average fossiliferous outcrop of the *stolidotus* zone in the Georgina Limestone is seen in Text-figure 13.

### *The faunal sequence: Middle Cambrian localities*

W2 (in the Glenormiston area); W250, W253, W255, W35 and W36 (all in the Sylvester Creek area). W2 at Sun Hill was discussed by Öpik (1963, p. 16). It refers to the occurrence of *Hypagnostus hippalus* Öpik, 1961, which indicates the *laevigata* II Zone (Zone of *Proampyx agra*). The Middle Cambrian limestone at W2 rests unconformably on Lower Cambrian (Sun Hill Arkose).

The localities at Sylvester Creek are crowded at the headwaters, and two (W36 and W250) occur on the interfluvium of Deadman Creek and Sylvester Creek; there the position of the Middle Cambrian is topographically higher than the Idamean outcrop at W39 (west of Deadman Creek), and the sequence rests, as at W2, unconformably on Lower Cambrian.

The fauna of the Sylvester Creek Middle Cambrian (see Description of the localities, especially W36) indicates the Zone of *Leiopyge laevigata* II. Consequently, earlier Middle Cambrian is absent in the Sylvester Creek area.

### *Zone of Erediaspis eretes* (initial Mindyallan):

Locality W253 (head of Sylvester Creek). Below it the Zone of Passage and the *laevigata* III Zone are missing and a hiatus is indicated (Table 3). The occurrence of the *Erediaspis eretes* Zone fossils at W253 is the only one known in the whole Glenormiston-Sylvester Creek area.

### *Zone of Cyclagnostus quasivespa*—(see under Mungerebar-Mindyallan area):

No fossils of this zone have been found as yet in the Glenormiston-Sylvester Creek area and a hiatus is evident.

### *Zone of Glyptagnostus stolidotus*:

Localities W1, W15, W17, W18, W20, W21, W22, W66, W161, W258, W259, W283, W301, G48, G49, G50 and G51. Of these W283 (Text-fig. 2) is isolated in the Toomba Range west of the Toko Range proper, and the most western occurrence of the Zone in Queensland.

### *The Idamean*:

The Idamean sequence of Zones has been described by Öpik (1963). Some more trilobites are described in this paper from the Zone of *Corynexochus plumula*, localities W39 (*Pseudoagnostus idalis* sp.nov., *Innitagnostus inexpectans* (Kobayashi),

TABLE 3.—STRATIGRAPHIC SEQUENCE, GLENORMISTON-SYLVESTER CREEK AREA

|  |   |
|--|---|
| Cretaceous   |   |
| Unconformity   |   |
| SILURIAN? or ORDOVICIAN? Sandstone, locality W17a, rests on Mindyallan rocks |   |
| Hiatus   |   |
| ORDOVICIAN, early ....   | Ninmaroo Formation  |
| UPPER CAMBRIAN, late (W14, W204, G332<br>—saukiids)                          | rests on Mindyallan and Idamean rocks   |
| Post-Idamean hiatus (unconformity)   |   |
| EARLY UPPER CAMBRIAN   |   |
| Idamean Zones of ....  | <i>Erixanium sentum</i><br><i>Corynexochus plumula</i><br><i>Glyptagnostus reticulatus</i> — <i>Proceratopyge nectans</i> |
| Mindyallan Zones of ....   | <i>Glyptagnostus reticulatus</i> — <i>Olenus ogilviei</i><br><i>Glyptagnostus stolidotus</i>                              |
| Hiatus   |   |
| <i>Erediaspis eretes</i> (Sylvester Creek Area)                              |   |
| Hiatus   |   |
| MIDDLE CAMBRIAN  |   |
| Zone of ....   | <i>Leiopyge laevigata</i> II  |
| Unconformity   |   |
| LOWER CAMBRIAN   | Sun Hill  |

*Corynexochus plumula* Whitehouse), W10, W40 and W41 (*C. plumula*), and W16 (*Idamea venusta* Whitehouse); from the Zone of *Erixanium sentum*, localities W10 (*Peratagnostus nobilis* sp.nov. and *Blountia georginae* sp.nov.), W8 (*Idamea baccata* sp.nov.), and W45 (*Idamea extricans* sp.nov.).

#### *The Post-Idamean unconformity*

According to Öpik (1963, p. 16), on the truncated Georgina Limestone, on Idamean beds in the south and Mindyallan in the north, rests the Ninmaroo Formation, of latest Upper Cambrian and Tremadocian age.

The latest Upper Cambrian fauna was collected at localities G332, W14, and W204. The trilobites comprise: *Tsinania* cf. *ceres* (Walcott), *Pagodia*, *Saukia* (cf. *Saukia? orientalis* Resser & Endo), 'Coreanocephalus', 'Eosaukia' (in terms of Kobayashi, 1957), and a new species of *Parakoldinioidia* Endo; associated are brachiopods tentatively referable to *Billingsella* and *Eoorthis*. In Australia this fauna occurs in the upper part of the Chatsworth Limestone, in Central Australia (Casey & Tomlinson, 1956), and in the Joseph Bonaparte Gulf area in the north-west. Close are also the faunas from the Tarutao Island of Thailand (Kobayashi, 1957), and the Fengshanian (or Yenchou) of China and Korea. A tentative correlation is indicated with the two upper zones of the Fengshanian, which Lu (1960, p. 213) equates to the Trempealeauan—the latest stage of the Upper Cambrian of the United States of America. Consequently, the post-Idamean unconformity on Glenormiston covers the interval of the whole of the Franconian, or of the Changshanian (Daizanian) and lower Fengshanian in terms of Lu.

#### *The hiatus at locality W17:*

At this place a small remnant of a sandstone formation with pelecypods rests in a shallow valley carved in limestone of Mindyallan (*Glyptagnostus stolidotus*) age. These pelecypods are certainly neither Tremadocian (Ninmaroo), nor Cretaceous (verbal communication, Dr J. M. Dickins, B.M.R.); the sandstone is marine and was deposited after the erosion of the Ninmaroo and overlying Ordovician deposits. The collected pelecypods are unfortunately insufficient for a conclusive study; according to Jones (1964), however, a late Silurian sandstone is present in the Toko Range (western part of Glenormiston), and the sandstone at W17a may be its outlier. But an Ordovician ('late Toko' or 'post-Toko') age of these pelecypods remains another possibility.

#### *The Selwyn Range Area*

(For position see map, Text-fig. 2)

The Middle sequence and fauna of the Selwyn Range have been described by Öpik (1961).

In brief the sequence is as follows:

*Leiopyge laevigata* III (Zone of *Holteria arepo* Öpik) terminates the Middle Cambrian Epoch.

The Zone of Passage, the Mindyallan Zone of *Erediaspis eretes*, and the Zone of *Cyclagnostus quasivespa* are not represented by fossils in the Selwyn Range. The latest part of the Devoncourt Limestone and above it the Selwyn Range Limestone

represent sediments of the time of these zones; the Selwyn Range Limestone is diachronous and extends partly into the *G. stolidotus* Zone (op. cit., p. 39), and partly terminates at a diastem.

The *Glyptagnostus stolidotus* Zone: Localities D6, D28, and D29—the 'lower chert bed' of the O'Hara Shale. Fossils are listed in the description of locality D29.

*Idamean*: *Eugonocare* cf. *tesselatum* is described in this paper from locality D6.

#### *The De Little Range Area*

For position, see map, Text-figure 2; some of the fossils are described in Öpik (1961b; 1963)

*Glyptagnostus stolidotus* Zone: all known fossils are listed in the description of localities B525 and B537.

*Glyptagnostus reticulatus* Zone (*Idamean*): all known fossils are listed in the description of localities D126 and B259.

#### *Pomegranate Creek Area*

The Mindyallan and *Idamean* sequence and selected fossils are described in Öpik (1963).

Zone of *Erixanium sentum* (*Idamean*): To the list of fossils for locality D120b (op. cit., p. 9 and 22) is added *Idamea baccata* sp.nov. and *Peratagnostus nobilis* sp.nov.

#### *The Distribution of the Mindyallan Fauna in Australia*

In Tasmania the Comet Slate (Spry & Banks, ed., 1962) contains a fossil band of the Mindyallan *Glyptagnostus stolidotus* Zone; among the common fossils are *Palaeadotes* sp., *Aulacodigma* cf. *quasispinale* and *Agnostardis amplinatis*. Below it Gatehouse (1964) found *Rhysometopus (Rostrifinis)* cf. *rostrifinis*, and at Beaconsfield (op. cit.) *Erediaspis* has been collected. By the way, the chart in Spry & Banks (op. cit., p. 139) shows erroneously the Comet Slate in the *Leiopyge laevigata* Zone. The *Idamean* is represented in Tasmania by *Glyptagnostus reticulatus*.

In Victoria (Thomas & Singleton, 1957, p. 158) the Dolodrook Limestone contains early Upper Cambrian fossils, of which *Tricrepicephalus etheridgei* (Chapman) indicates the Mindyallan, and *Eugonocare* the *Idamean* stage.

Mindyallan trilobites are known in Northern Australia (Text-fig. 1) from several sites. At Marqua a pygidium of *Blackwelderia* was collected. A prolific fauna, apparently of *Glyptagnostus stolidotus* age, occurs at the Ross River (see description of locality NT187), and fossils of similar age are known from the Waterhouse Range near Alice Springs. At Ellery Creek (west of Alice Springs), *Blackwelderia* occurs in a dark limestone. In this belt, from the Toko Range to Ellery Creek, no *Idamean* fossils have been found as yet; the possible reason for absence of fossils (hostile environment of deposition) has been discussed in Öpik (1963, p. 24). Finally, in north-west Australia, in the Cambridge Gulf sequence (Öpik, 1956, p. 53), the Skewthorpe Formation contains a late Middle Cambrian fauna passing upward into the Mindyallan. This is borne out by collections of J. J. Veevers and party in the

Joseph Bonaparte Basin, 1963, which contain Damesellacea related to *Histiomona* gen.nov.; Öpik's (loc. cit.) *Crepicephalus*, however, is neither a *Tricrepicephalus*, nor a middle Dresbachian (Mindyallan), but a Franconian trilobite of Asian affinity.

In South Australia, in the Gidgealpa No. 1 Well, at the depth of some 2 miles, the following trilobites were recovered: *Biaverta biaverta*, *Blackwelderia* cf. *repanda*, *Catillicephala* sp., *Henadoparia integra*, *Leiostracina volens*, Lonchocephalidae (free cheeks), *Meteoraspis* sp., and *Nilegna sigmata*. This collection contains 10 percent of the fauna of the Mindyallan Zone of *Glyptagnostus stolidotus*, but no new forms are present.

#### OVERSEAS CORRELATION AND PALAEOGEOGRAPHIC AFFINITIES

The Mindyallan and Idamean intercontinental correlation was outlined by Öpik (1960; 1963) and is supported by the new palaeontological information.

The Zone of Passage corresponds to the *Bolaspidella* zone as conceived by Palmer (1954; 1962, p. F 10). The concept of the zone, however, is not derived from the genus *Bolaspidella* as such, but from the stratigraphic position of the species *B. burnetensis* (Walcott), *B. prooculis* Palmer, 1954a, and *B. wellswillensis* (Lochman & Duncan).

The genus *Bolaspidella* is based on *B. housensis* (Walcott) (Palmer, 1954b)—a somewhat early Middle Cambrian species.

Robinson (1963, p. 139A) report that the genus *Bolaspidella* in Utah occurs in 'the interval including the *Ptychagnostus atavus* to the *Leioptyge laevigata* zones'. Consequently, it covers the range of six (out of a total of nine) Swedish, and even eight Australian Middle Cambrian Zones.

The *Erediaspis eretes* and *Cyclagnostus quasivespa* Zones together appear equivalent to the American *Cedaria* Zone, and the *Glyptagnostus stolidotus* Zone is the American *Crepicephalus* Zone as well. In passing, the genus *Cedaria* (see Palmer, 1962) is a trizonal or quadrizonal genus reaching into the base of the Idamean (in Australian terms).

The Mindyallan Stage as a whole correlates with the *Cedaria* and the *Crepicephalus* Zones taken together. Not only a temporal correlation but also communicating seaways are evident between North America and Australia; in the Mindyallan time this is testified by the following fossils which occur on both sides of the Pacific Ocean: *Agnostascus*, *Ammagnostus*, *Aspidagnostus*, *Clavagnostus*, *Connagnostus venerabilis*, *Glyptagnostus stolidotus*, *Hadragnostus*, *Oxyagnostus*, *Pseudagnostina*, *Brassicicephalus*, *Catillicephala*, *Henadoparia*, Lonchocephalidae, Menomoniidae, *Meteoraspis*. Further comment is given in the taxonomic description of these forms.

The Damesellacea in Queensland and in China, Korea, and Indochina correlate the Australian Mindyallan and the Kushanian of eastern Asia; the correlation is supported also by *Liostracina*. Open seaways are indicated between these parts of the world in Mindyallan time; these trilobites are practically unknown elsewhere and it appears that Australia maintained its present geographic position in relation to south-eastern Asia since the Cambrian.

In Scandinavia the Upper Cambrian part of the Zone of *Agnostus pisiformis* corresponds to the Mindyallan. This is evident from its position between the early Idamean *Glyptagnostus reticulatus* (above) and *Leiopyge laevigata* (below) rather than from the fossils in the Scandinavian sequence.

The fauna of the *Agnostus pisiformis* Zone is relatively small with its seven species of six genera. *Palaeadotes eremita* (Westergaard), however, supports the correlation with the Mindyallan and is evidence of a communication with China and Australia.

The paucity of the fauna of the *Agnostus pisiformis* Zone in Scandinavia, and its name itself, which refers to a species ranging from the late Middle Cambrian into the early Upper Cambrian (see Öpik, 1961, p. 36), are no reasons to reject its correlation with the Mindyallan and the Kushanian stages. It is, however, apparent that the Scandinavian early Upper Cambrian *A. pisiformis* Zone remains a unit indivisible into 'sub-units' and differs in this respect from the Mindyallan and the Kushanian.

The defence of the Middle Cambrian age of the Kushanian, as for example, by Kobayashi (1933, p. 82-83; also 'Postscript' *ibid.*) is untenable, but has its historical value. '*Ctenosura*' *eremita* in Kobayashi (*op.cit.*) or *Drepanura eremita* Westergaard, 1947, or *Palaeadotes eremita* (Westergaard), is not a 'solitary relict' (Kobayashi, 1956, p. 353), a last survival of a Middle Cambrian trilobite family, but an itinerant of the contemporaneous early Upper Cambrian drepanurids of Australia and China.

According to Chu (1959, p. 81), Y.C. Sun since 1937 regards the Kushanian as the initial Upper Cambrian. A break and conglomerate below the Kushanian *Blackwelderia* Zone is considered the boundary between Middle and Upper Cambrian in Shantung. Assuming the contemporaneity of the *Blackwelderia* Zone of Shantung and the *Cyclagnostus quasivespa* Zone of Queensland one concludes that the Australian *Erediaspis eretes* Zone fauna is absent in China where it is replaced by the above mentioned break.

In South America the Zone of Passage and the Mindyallan are recognizable from forms like *Kootenia cf. incerta* (Rusconi) and *Talbotinella notulata* Öpik, 1963. Furthermore, some of the agnostids described from Argentina by Poulsen (1960) from the *Bolaspidella* Zone may have a possible early Mindyallan age.

As regards the Idamean, and the impossible occurrence of *Glyptagnostus reticulatus* in the Franconian *Elvinia* Zone in Nevada (Lochman & Wilson, 1958; Öpik, 1963, p. 7), Palmer's (1962, p. F9) correction should be noted. The alleged *Glyptagnostus reticulatus* was also subsequently examined jointly by A. R. Palmer and the writer, and both concluded independently that it represents an *Agnostotes* (Öpik, 1963). It occurs in Nevada in a stratigraphic position close to the Australian *A. inconstans*, and postdates *Glyptagnostus reticulatus*.

The marine palaeozoogeography of Mindyallan time is summarized below.

For the agnostids the globe was a relatively small place; the lifetime of an agnostid species was long enough to reach any place; the scarcity or absence of agnostids in particular places and sequences depends on local ecologic conditions which prevented the development of agnostid populations of some duration. Of course, new species could evolve at any place.

Further evidence of the universal aspect of early Upper Cambrian faunas is found in the recent paper of Borovikov & Kryskov (1963) reporting on fossils from

southern Kazakhstan (Chu-Ily Mountains, approx. lat. 43° N., Long. 76° E.), Central Asia. Here in a limestone bed one to three centimetres thick an assemblage of trilobites contains among other forms *Glyptagnostus reticulatus*, *Clavagnostus? lunulosus* Kryskov (= an *Aspidagnostus* related to *A. stictus* sp.nov.), *Tomagnostus tchatertensis* K. (= a species of *Innitagnostus* gen.nov.), *Leiopyge? controversa* K. (a species of *Peratagnostus* gen.nov.), and *Ajrikina bulakensis* K. The genus *Ajrikina* Kryskov is a blind form related to *Aulacodigma* gen.nov., and one zone younger than the two Australian species of *Aulacodigma*.

As regards the Damesellacea, their known province extended from Northern China to Tasmania; migration and migration routes between China and Australia are thus superfluous to describe the distribution of the Damesellacea. North America and Australia were within each other's reach in Mindyallan time, but, nevertheless, both regions preserved their individual faunal aspect.

Faunas of several provinces were commingled in Australia during the Mindyallan; the larger part of the Australian polymerid trilobites, however, is unknown elsewhere (Nepeidae, Auritamidae, Placosematidae, Aulacodigmatidae, Rhyssometopidae, etc.), and in this sense the Queensland Mindyallan fauna represents a zoogeographic province of unknown extent and of a diverse and hitherto unknown fauna of trilobites.

The Idamean fauna of Australia in its palaeozoological aspect is also multi-provincial: Acado-Baltic and Pacific-American, and to a lesser degree Chinese or Korean.

#### THE FAUNAL CRISES AT THE TURN OF THE STAGES; THE ORIGIN OF THE AUSTRALIAN MINDYALLAN FAUNA

The faunal crisis at the turn of Mindyallan and Idamean times in Queensland was briefly described earlier (Öpik, 1963, p. 10 and 33). The crisis manifests itself in the disappearance of the older and abundant Mindyallan fauna within a few feet of strata, followed by the immediate, gapless, arrival of the initial Idamean fauna with *Glyptagnostus reticulatus*. None of the 170 Mindyallan species of agnostids and polymerid trilobites passed across into the Idamean, whose fauna contains some 100 species, of which 52 are already described.

By contrast, the transitional character of the zonal faunas before and after the crisis emphasizes the abruptness of the replacement of faunas at the turn of the stages. The Zone of Passage, with a total of 17 species, and the *Erediaspis eretes* Zone with its 46 species, have four common species; the *quasivespa* Zone (44 species) and the *stolidotus* Zone (81 species) have six species in common. The *quasivespa* and the *eretes* Zones share the relatively large number of seventeen bi-zonal species, though this is less than half of the total of each zone. The faunal composition, therefore, changed relatively rapidly in the Mindyallan succession of zones; but the frequency of bi-zonal and even tri-zonal species still indicates a continuity of the faunal succession within the sequence, and the region as well.

In Queensland, the number of genera common to both the stages is small and the agnostids are visibly prevalent. These genera are: *Aspidagnostus*, *Glyptagnostus*, *Innitagnostus*, *Pseudagnostus*, and *Mindyocrusta*.

The Idamean species of these genera are affiliated with, but not direct descendants of, the Mindyallan forms. For example, the early Idamean *Aspidagnostus stictus* sp.nov. may have evolved from a species of the *A. inquilinus* group, but *inquilinus* itself is not a native of Queensland. The Mindyallan *Glyptagnostus stolidotus* (see Öpik, 1961, p. 430) is not parental to the Idamean *G. reticulatus*; according to Palmer (1962), *G. reticulatus* is closely related to *G. angelini* Resser, which is an American form, and not ubiquitous as are *reticulatus*, and, apparently, *stolidotus*.

*Innitagnostus* is known only from two species, one in each stage, and is not discussed further. The question of *Mindycrusta*, and its only Idamean species *advena* sp.nov., is discussed under that genus: the Idamean *advena* is not a descendant of any of the Mindyallan species, and should be regarded as an immigrant in Queensland.

The forms discussed above expire early in the Idamean, and only *Innitagnostus inexpectans* is trizonal, appearing together with *Glyptagnostus reticulatus* and reaching the Zone of *Corynexochus plumula*.

*Pseudagnostus*, with about forty named species, is the most prolific genus of the Agnostacea; it is of global distribution and ranges through the whole of the Upper Cambrian in Australia and elsewhere. Hence, the extinction of the Mindyallan species of *Pseudagnostus* did not destroy the vitality of the stock itself, leaving intact the sources from which the replacing Idamean species continued to arrive in Queensland after the crisis.

As seen from Table 4, side by side with the Pseudagnostinae (i.e. *Pseudagnostus*) the Agnostinae and the Trinodidae crossed the critical lines and remained prolific and even reached well into the Ordovician.

The remainder of the Agnostacea, however, disappeared within, or at the end of, Mindyallan time, which also was the time of their maximal diversification. Soon after the arrival of the last Glyptagnostidae (*G. reticulatus*, *Agnostotes*) the sources became depleted and the spreading of replacements ceased also.

Polymerid trilobites of long-lived families (Lonchocephalidae and Catillicephalidae) that survived till the end of the Upper Cambrian are present in the Mindyallan fauna; these families have been known hitherto only from North America. Furthermore, the Mindyallan cradles the earliest known species of several families and even superfamilies which hitherto were believed to have evolved much later in the Upper Cambrian and even in early Ordovician time. These are *Lampropeltis nitens* (Plethopeltidae), *Griphasaphus griphus* (Asaphidae), *Nomadinis pristinus* (Dikelokephalinidae), *Lophoholcus asper*, *Saukia? priscilla* (Saukiidae), and *Saratogia? vetusta* (Idahoiidae).

In the Idamean, however, anachronistic forms are still present whose Middle Cambrian ancestors are known. These Idamean forms are *Corynexochus plumula*, *Peratagnostus nobilis*, and the several species of *Proceratopyge*. *Proceratopyge* occurs throughout the Idamean, and its breeding grounds are preserved in the Georgina Limestone. The oldest known *Proceratopyge* is known from the *Leiopyge laevigata* Zone of Sweden.

It seems at first that with the disappearance of the Mindyallan fauna in Queensland the place became vacated and thus ready to receive the replacing Idamean trilobites. This picture is as erroneous as it is simple. Of course, a replacement

is evident because nothing was left of the older populations. But if the Mindyallans (or their progeny) were still present, the Idameans would not be prevented from arrival and from commingling with the existing populations. This is borne out by the fact that the Mindyallan fauna itself was composed largely by an influx from outside, and did not evolve on the spot. Forms like *Auritama*, *Aedotes*, *Meropalla*, *Placosema*, *Aulacodigma*, *Doremataspis*, *Lophoholcus*, *Metopotropis*, *Nomandinis*, *Rhodonaspis*, and many others are of an unknown parentage, and arrivals from as yet unknown places. Others, like *Meteoraspis*, *Olenoides*, and *Brassicicephalus* are well represented in North America but have no Middle Cambrian affiliates in Australia. They were emplaced in the already populated Australian region, replaced nothing, but disappeared at the end of the Mindyallan together with the rest.

A large part of the Mindyallan trilobites occupied the Queensland seaways over a longer interval of time. These are the Damesellacea, the Nepeacea, the Rhyssometopidae and the Plectriferidae. The abundance of the Damesellacea indicates a close and continuous connexion with eastern Asia; the same applies to the Liostracinidae. But the Liostracinidae were of a short duration, and were apparently immigrants in China as well as in Australia. The Nepeacea have a long history in Australia (Öpik, 1963b), but are not quite endemic here. The Plectriferidae are related to the Mapaniidae of the Middle Cambrian, and apparently are natives. The Rhyssometopidae are prolific in Queensland, rare in Tasmania, but unknown elsewhere.

The faunal break described by Lochman & Wilson (1958, p. 332) between the *Crepicephalus* Zone (=Mindyallan) and the *Aphelaspis* Zone (=Idamean) coincides in time with the Mindyallan/Idamean crisis in Australia. According to Palmer (1962, p. F8) below that break 'there is only a gradual evolutionary change from the faunas generally assigned to the older *Cedaria* Zone to those generally assigned to the overlying *Crepicephalus* Zone'; these zones together correspond to the Mindyallan. In Australia no such gradual evolutionary change involving whole faunas of zones is apparent in the Mindyallan.

In China, as first observed by Walcott (1913, p. 53; 1914, p. 66), the Kushanian (=Mindyallan) fauna is also replaced abruptly by the Paishanian (=Idamean) fauna without a single species or genus common to both. According to Kobayashi (1933, p. 63) 'no interruption of sedimentation can be supposed to have occurred between the Middle and Upper Cambrian' (that is, between the Mindyallan and Idamean in our terms), 'but (ibid. p. 83), so far as the Asiatic Cambrian is concerned, the Kushan fauna completely disappears at the end of the Kushan period'.

In Sweden the faunal change should be found at the junction of the *Agnostus pisiformis* (below), and the *Olenus gibbosus* Zone (above). The number of trilobite species in each zone is rather small (about seven in each zone), and one species (*Acrocephalites stenometopus*) is common to both. In this situation the character of the change from one fauna to the next—abrupt or gradual—cannot be ascertained conclusively.

The Kushanian, the *Cedaria-Crepicephalus*, and the *Agnostus pisiformis* Zone faunas of polymerid trilobites are rather different from each other; no common

species, and almost no common genus exists between them. *Agnostus*, however, occurs in Australia also, and *Palaeadotes* (Damesellacea) occurs in China, Australia, and Sweden.

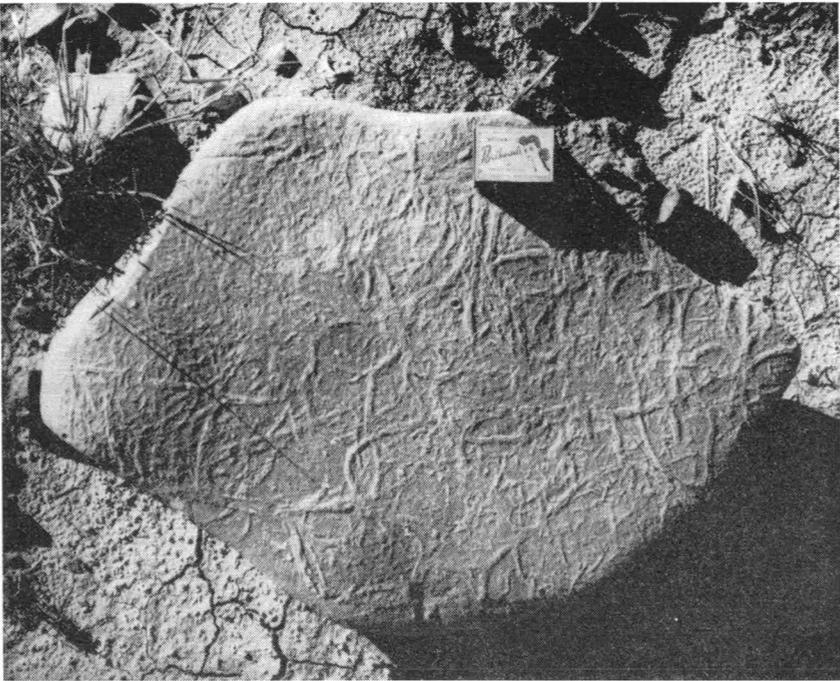
The faunal crisis is widespread and well established. In China and in North America the turn of the Mindyallan to the Idamean has been regarded by several authors as the Middle Cambrian/Upper Cambrian boundary. In China and Korea, for example, the Kushanian, below this boundary, was placed at the top of the Middle Cambrian and correlated erroneously with the *Leiopyge laevigata* zone. In China itself the error has been corrected (Lu, 1954; 1960; see also Öpik, 1960) but as a tradition it still recurs in the literature outside China.

The Upper Cambrian part above the Kushanian carries the name Chaumitien in eastern Asia; Chaumitien with the Kushanian cannot be equated with the Upper Cambrian Series, or Epoch; below it rests the Changhian or Fuchouan, which are not substitute names for the Middle Cambrian because they include the Kushanian as well.

These names, however, are derived from names of rock units (Chaumitien limestone, Kushan formation) and not faunal entities and are therefore unsuitable for general use. All current names of time-rock units in China, including Yenchou and Fengshanian, are derived in a similar manner. Kushanian in the sense of an Upper Cambrian stage is represented by the fauna of the upper part of the Kushan Formation, whose lower part is Middle Cambrian.

The cause of the crisis is obscure. In Australia it was a rather significant event involving some eighty species of trilobites of the final Mindyallan zone—the Zone of *Glyptagnostus stolidotus*—that vanished at the turn of the stages. Simultaneously with Australia the Mindyallan faunas expired in many other places of the World; consequently the cause or causes of the crisis had a fairly universal influence on the marine life of the final Mindyallan time. In marine conditions, however, an overall universal extinction of trilobites is an impossibility, of course. Indeed, in the time of, and in times after, the Idamean, genera of species related to the Mindyallan and earlier trilobites continued to exist and evolve further. Hence, in places inaccessible to our observations (such as oceans) the phyletic continuity was not interrupted; but physical causes of an unknown character acting at once in many disconnected places in the seas of the globe resulted in the extinction of local and even regional faunas. Probably shallow seas and shelves were affected in the first place, but deposition in these seas was not interrupted, at least not in Queensland. Even if deposition were interrupted by a sudden universal regression, the floor of the seas would have emerged for only a rather short interval of time (the turn of the stages)—a fraction of the span of a zone; consequently, the returning sea would have carried with it a large number of species that departed with the regression. It is, however, apparent that most, if not all, species of trilobites endemic to the affected regions disappeared or expired without leaving a progeny. For example, the Damesellacea, whose numerous species populated the seas of Australia and China in Mindyallan time, disappeared completely in the crisis. The agnostids having attained their maximal diversification during the Mindyallan were greatly depleted; selected stocks, however, survived apparently owing to their pelagic mode of life and cosmopolitan distribution.

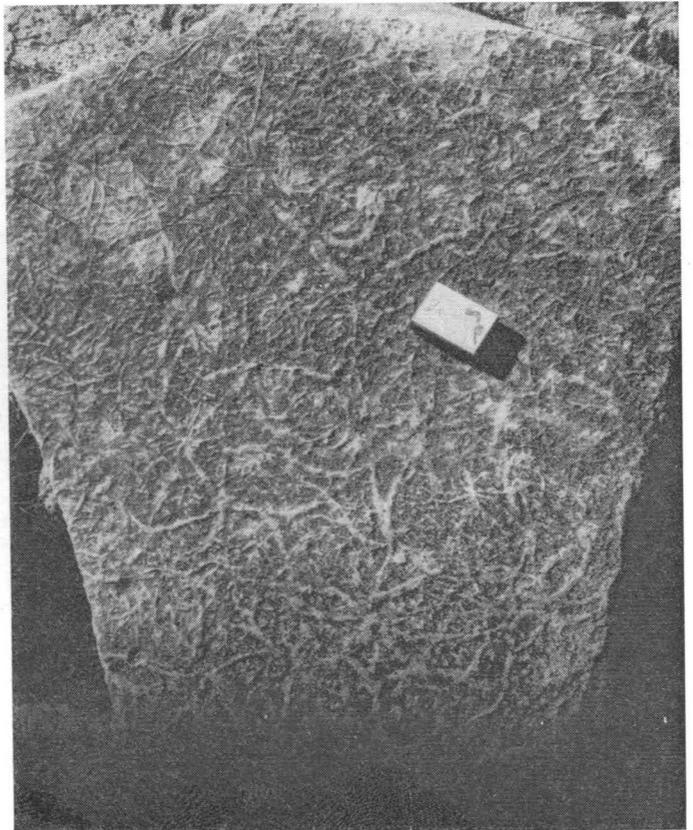
It can be speculated that the life of shallow coastal seas and shelves and the surface waters of the open sea were affected in the first place; but the circulating



**SPECIMEN A**

**Fig. 14.—Burrows No. 2, in dolomite, locality G400, Mungerebar-Mindyalla area (Text-fig. 3). In specimen A, x 0·22, the burrows are relatively coarse; in specimen B, x 0·2, numerous rather thin burrows form an interwoven pattern.**

**SPECIMEN B**



waters of the ocean had a moderating influence on the sudden and transient impact of the 'cause' and the third dimension of the deep offered chances of escape not available in the shallows.

In the history of the Cambrian Period and its life the Mindyallan/Idamean crisis was an important event, but the stratigraphic, applied significance of its physical aspect should not be overestimated. The crisis was real, abrupt as regards the brevity of its own time scale, and geographically universal. But being referable to unknown inorganic causes which left no record in the rocks the event is not demonstrable on its own merit. The inorganic event was no crisis by itself, but its impact induced the biological crisis. Hence, the inorganic happening has little significance in correlation and dating of sequences because it is a phenomenon which itself must be uncovered and dated by biological means. In the case of western Queensland the crisis is dated and correlated on the basis of universal fossil species that lived before (e.g. *Glyptagnostus stolidotus*) and immediately after (*G. reticulatus*) the event. The stages Mindyallan and Idamean, and their distinction from each other, are established solely on biological criteria. Even in the absence of fossils of one of the stages the other, once known, can be safely identified and correlated without supporting evidence. The position of the turn of the stages in a section, however, can be established only on faunal evidence from both the stages in sequence.

No system or series boundary adheres to the turn of the stages, and its significant biological crisis. The nearest in time is the Middle Cambrian-Upper Cambrian transition, which cannot be referred to as an exact 'boundary'; but there is no need to declare the Mindyallan-Idamean boundary a series boundary and thus create another set of Cambrian series.

Faunal breaks occur throughout geological history in marine and in terrestrial conditions; their stratigraphic significance has been recently discussed by Newell (1962).

## REMARKS ON THE STRATIGRAPHIC DISTRIBUTION OF SPECIES

The fossils described here are listed twice:

- (1) in the taxonomic, classificatory order, and
- (2) in order to show the stratigraphic distribution of the species and genera.

1. The classificatory order is given in the contents, and in the descriptive text the taxa are arranged in the same order.

2. The list that follows below (Table 4) illustrates the stratigraphic (zonal) distribution of the fossils; the chosen arrangement of the species names collects the bi-zonal forms into clusters illustrating the faunal continuity within the sequence. Within the zones the arrangement is alphabetic; the alphabetic arrangement, however, prevents the clustering of the two trizonal agnostid species. The overlap of the zonal lists in the bi-zonal clusters does not indicate that the ranges of species are overlapping; the ranges of the species within a zone are unknown and the lists are constructed to indicate the occurrence within the zone in general. The regional as well as local distribution of the fossils is apparent from the description of the localities.

In the list (below) fossils marked with an asterisk (e.g. *\*Discagnostus spectator*) are not described here, but are mentioned in the locality list.

TABLE 4: STRATIGRAPHIC DISTRIBUTION OF SPECIES

|                                       | Late Middle Cambrian | Zone of Passage | Mindyallan             |                              |                               | Idamean |
|---------------------------------------|----------------------|-----------------|------------------------|------------------------------|-------------------------------|---------|
|                                       |                      |                 | Erediaspis eretes Zone | Cyclagnostus quasivespa Zone | Glyptagnostus stolidotus Zone |         |
| AGNOSTIDS                             |                      |                 |                        |                              |                               |         |
| *Diplagnostus cf. planicauda          | X                    |                 |                        |                              |                               |         |
| Diplagnostus crassus                  | X                    |                 |                        |                              |                               |         |
| Dolichoagnostus (?) sp.indet          | X                    |                 |                        |                              |                               |         |
| Linguagnostus aff. kjerulfi           | X                    |                 |                        |                              |                               |         |
| Oidalagnostus personatus              | X                    |                 |                        |                              |                               |         |
| Peronopsis aff. fallax                | X                    |                 |                        |                              |                               |         |
| Ptychagnostus sp.nov.aff. fumicola    | X                    |                 |                        |                              |                               |         |
| Ptychagnostus (Goniagnostus) spiniger | X                    |                 |                        |                              |                               |         |
| *Hypagnostus hippalus                 | X                    | X               |                        |                              |                               |         |
| *Leiopyge laevigata                   | X                    | X               |                        |                              |                               |         |
| *Leiopyge laevigata armata            | X                    | X               |                        |                              |                               |         |
| Oidalagnostus trispinifer             | X                    |                 |                        | X                            |                               |         |
| Ptychagnostus fumicola                | X                    | X               |                        |                              |                               |         |
| Cyclagnostus aff. quasivespa          | X                    |                 |                        |                              |                               |         |
| Hypagnostus correctus....             |                      | X               | X                      |                              |                               |         |
| Triadaspis bigeneris                  |                      | X               | X                      | ?                            |                               |         |
| Agnostascus aff. gravis               |                      |                 | X                      | X                            |                               |         |
| Agnostascus gravis                    |                      |                 | X                      | X                            |                               |         |
| Agnostoglossa bassa                   |                      |                 | X                      | X                            |                               |         |
| Agnostus aff. pisiformis              |                      |                 | X                      |                              |                               |         |
| Agnostus aff. pisiformis subsulcatus  |                      |                 | X                      |                              |                               |         |
| Agnostus artilimbatus                 |                      |                 | X                      |                              |                               |         |
| Clavagnostus bisectus                 |                      |                 | X                      | X                            | X                             |         |
| Cyclagnostus? sp.indet                |                      |                 | X                      |                              |                               |         |
| Grandagnostus evexus                  |                      |                 | X                      |                              |                               |         |
| Hadragnostus las                      |                      |                 | X                      | X                            |                               |         |
| Hypagnostus durus                     |                      |                 | X                      |                              |                               |         |
| Idolagnostus dryas                    |                      |                 | X                      | X                            | X                             |         |
| Innitagnostus innitens ?              |                      |                 | X                      |                              |                               |         |
| Leiopyge cos                          |                      |                 | X                      | X                            |                               |         |
| Ptychagnostus nodibundus              |                      |                 | X                      |                              |                               |         |
| Ammagnostus mitis                     |                      |                 |                        | X                            |                               |         |
| ?Aspidagnostus aff. stictus           |                      |                 |                        | X                            |                               |         |
| Connagnostus zonatus                  |                      |                 |                        | X                            | X                             |         |
| Cyclagnostus quasivespa               |                      |                 |                        | X                            |                               |         |
| Oedorhachis tridens                   |                      |                 |                        | X                            |                               |         |
| Xestagnostus cf. rasilis              |                      |                 |                        | X                            |                               |         |

TABLE 4: STRATIGRAPHIC DISTRIBUTION OF SPECIES—continued

|                                  | Late<br>Middle<br>Cam-<br>brian | Zone<br>of<br>Pas-<br>sage | Mindyallan                        |  |  | Ida-<br>mean |
|----------------------------------|---------------------------------|----------------------------|-----------------------------------|--|--|--------------|
|                                  |                                 |                            | Eredi-<br>aspis<br>eretes<br>Zone | Cycl-<br>gno-<br>stus<br>quasi-<br>vespa<br>Zone | Glypt-<br>agno-<br>stus<br>stoli-<br>dotus<br>Zone |              |
| AGNOSTIDS                        |                                 |                            |                                   |  |  |              |
| Xestagnostus rasilis             |                                 |                            |                                   | X  |  |              |
| Agnostardis amplinatis           |                                 |                            |                                   |  | X  |              |
| Agnostardis cf. amplinatis       |                                 |                            |                                   |  | X  |              |
| Agnostogonus incognitus          |                                 |                            |                                   |  | X  |              |
| Ammagnostus euryaxis             |                                 |                            |                                   |  | X  |              |
| Ammagnostus integriceps          |                                 |                            |                                   |  | X  |              |
| Ammagnostus psammius             |                                 |                            |                                   |  | X  |              |
| Aspidagnostus inquilinus         |                                 |                            |                                   |  | X  |              |
| Connagnostus venerabilis         |                                 |                            |                                   |  | X  |              |
| *Discagnostus spectator          |                                 |                            |                                   |  | X  |              |
| Glyptagnostus lenis              |                                 |                            |                                   |  | X  |              |
| Glyptagnostus stolidotus         |                                 |                            |                                   |  | X  |              |
| Idolagnostus agrestis            |                                 |                            |                                   |  | X  |              |
| Innitagnostus aff. innitens      |                                 |                            |                                   |  | X  |              |
| Innitagnostus innitens           |                                 |                            |                                   |  | X  |              |
| Oxyagnostus apicula              |                                 |                            |                                   |  | X  |              |
| Plurinodus discretus             |                                 |                            |                                   |  | X  |              |
| Plurinodus cf. discretus         |                                 |                            |                                   |  | X  |              |
| Pseudagnostina? aff. vicaria     |                                 |                            |                                   |  | X  |              |
| Pseudagnostina vicaria           |                                 |                            |                                   |  | X  |              |
| Pseudagnostus ampullatus         |                                 |                            |                                   |  | X  |              |
| Pseudagnostus bulgosus           |                                 |                            |                                   |  | X  |              |
| Pseudagnostus mestus             |                                 |                            |                                   |  | X  |              |
| Pseudagnostus sericatus          |                                 |                            |                                   |  | X  |              |
| Ptychagnostus? serus             |                                 |                            |                                   |  | X  |              |
| Xestagnostus aff. legirupa       |                                 |                            |                                   |  | X  |              |
| Xestagnostus legirupa            |                                 |                            |                                   |  | X  |              |
| Aspidagnostus stictus            |                                 |                            |                                   |  |  | X            |
| Glyptagnostus reticulatus        |                                 |                            |                                   |  |  | X            |
| Innitagnostus inexpectans        |                                 |                            |                                   |  |  | X            |
| Peratagnostus nobilis            |                                 |                            |                                   |  |  | X            |
| Pseudagnostus cf. idalis         |                                 |                            |                                   |  |  | X            |
| Pseudagnostus idalis             |                                 |                            |                                   |  |  | X            |
| POLYMERID TRILOBITES             |                                 |                            |                                   |  |  |              |
| Damesellidae, gen. and sp. indet |                                 |                            | X                                 |  |  |              |
| Dipentaspis aff. dipentas        |                                 |                            | X                                 |  |  |              |
| Dipentaspis ratis                |                                 |                            | X                                 |  |  |              |
| Leichneyella sp. B.              |                                 |                            | X                                 |  |  |              |

TABLE 4: STRATIGRAPHIC DISTRIBUTION OF SPECIES—continued

|                                 | Late<br>Middle<br>Cam-<br>brian | Zone<br>of<br>Pas-<br>sage | Mindyallan                        |   |  | Ida-<br>mean |
|---------------------------------|---------------------------------|----------------------------|-----------------------------------|---|--|--------------|
|                                 |                                 |                            | Eredi-<br>aspis<br>eretes<br>Zone | Cycla-<br>gno-<br>stus<br>quasi-<br>vespa<br>Zone | Glypt-<br>agno-<br>stus<br>stoli-<br>dotus<br>Zone |              |
| POLYMERID TRILOBITES            |                                 |                            |                                   |   |  |              |
| Quitulia sp.nov.aff. uncata     | X                               |                            |                                   |   |  |              |
| Quitulia uncata                 | X                               |                            |                                   |   |  |              |
| Quitacetra arenata              | X                               |                            |                                   |   |  |              |
| Dipentaspis dipentas            | X                               | X                          |                                   |   |  |              |
| Alomataspis enodis              |                                 | X                          |                                   |   |  |              |
| Ascionepea janitrix             |                                 | X                          |                                   |   |  |              |
| Damesella torosa                |                                 | X                          |                                   |   |  |              |
| Damesellidae, gen.nov., sp.nov. |                                 | X                          |                                   |   |  |              |
| Kootenia cf. incerta            |                                 | X                          |                                   |   |  |              |
| Lampropeltis nitens             |                                 | X                          |                                   |   |  |              |
| Modocia immodulata              |                                 | X                          |                                   |   |  |              |
| Mapaniidae, gen.nov., sp.nov.   |                                 | X                          |                                   |   |  |              |
| Rh. (Rostrifinis) tiro          |                                 | X                          |                                   |   |  |              |
| Olenoides tranans               |                                 | X                          | X                                 |   |  |              |
| Aedotes instans                 |                                 |                            | X                                 |   |  |              |
| Aedotes mutans                  |                                 |                            | X                                 |   |  |              |
| Agelagma laticeps               |                                 |                            | X                                 |   |  |              |
| Agelagma quadratum              |                                 |                            | X                                 |   |  |              |
| Ascionepea aff. anitys          |                                 |                            | X                                 |   |  |              |
| Ascionepea anitys               |                                 |                            | X                                 |   |  |              |
| Erediaspis eretes               |                                 |                            | X                                 |   |  |              |
| Ferenepea pilaris               |                                 |                            | X                                 |   |  |              |
| Iniotoma iniotoma               |                                 |                            | X                                 |   |  |              |
| Interalia serena                |                                 |                            | X                                 |   |  |              |
| Lonchocephalidae, indet         |                                 |                            | X                                 |   |  |              |
| Norwoodella? dubitalis          |                                 |                            | X                                 |   |  |              |
| Onchonotellus offula            |                                 |                            | X                                 |   |  |              |
| Pygidium No. 1                  |                                 |                            | X                                 |   |  |              |
| Pygidium No. 2                  |                                 |                            | X                                 |   |  |              |
| Pygidium No. 3                  |                                 |                            | X                                 |   |  |              |
| Pygidium No. 4                  |                                 |                            |                                   |   | X  |              |
| Pygidium No. 5                  |                                 |                            |                                   |   | X  |              |
| Rhysometopus neuter             |                                 |                            | X                                 |   |  |              |
| Aedotes declivis                |                                 |                            | X                                 | X   |  |              |
| Cermataspis abundans            |                                 |                            | X                                 | X   |  |              |
| Meringaspis sp.nov. A.          |                                 |                            | X                                 | X   |  |              |
| Meringaspis sp.nov. B.          |                                 |                            | X                                 | X   |  |              |
| Meropalla auriculata            |                                 |                            | X                                 | X   |  |              |
| Meropalla quadrans              |                                 |                            | X                                 | X   |  |              |
| Placosema caelatum              |                                 |                            | X                                 | X   |  |              |

TABLE 4: STRATIGRAPHIC DISTRIBUTION OF SPECIES—*continued*

|                                      | Late<br>Middle<br>Cam-<br>brian | Zone<br>of<br>Pas-<br>sage | Mindyallan                        |  |  | Ida-<br>mean |
|--------------------------------------|---------------------------------|----------------------------|-----------------------------------|--|--|--------------|
|                                      |                                 |                            | Eredi-<br>aspis<br>eretes<br>Zone | Cycl-<br>gno-<br>stus<br>quasi-<br>vespa<br>Zone | Glypt-<br>agno-<br>stus<br>stoli-<br>dotus<br>Zone |              |
|                                      |                                 |                            |                                   |  |  |              |
| POLYMERID TRILOBITES                 |                                 |                            |                                   |  |  |              |
| Plectrifer mitis                     |                                 |                            | X                                 | X  |  |              |
| Plectrifer plectrifer                |                                 |                            | X                                 | X  |  |              |
| Rh. (Rostrifinis) rostrifinis        |                                 |                            | X                                 | X  |  |              |
| Biaverta reineri                     |                                 |                            | X                                 | X  |  |              |
| Blackwelderia sabulosa               |                                 |                            |                                   | X  |  |              |
| Blackwelderia sp.nov. A.             |                                 |                            |                                   | X  |  |              |
| Blackwelderia? sp.nov. B.            |                                 |                            |                                   | X  |  |              |
| Free Cheek No. 2                     |                                 |                            |                                   | X  |  |              |
| Griphasaphus griphus                 |                                 |                            |                                   | X  |  |              |
| Leichneyella? sp.nov. A.             |                                 |                            |                                   | X  |  |              |
| Palaeadotes aff. dissidens           |                                 |                            |                                   | X  |  |              |
| Rhysometopus rhysometopus            |                                 |                            |                                   | X  |  |              |
| Rh. (Rostrifinis) aff. rostrifinis   |                                 |                            |                                   | X  |  |              |
| Rhysometopus rugiceps                |                                 |                            |                                   | X  |  |              |
| Stephanocare richthofeni             |                                 |                            |                                   | X  |  |              |
| Stephanocare sp.nov.                 |                                 |                            |                                   | X  |  |              |
| Tricrepicephalus? indet              |                                 |                            |                                   | X  |  |              |
| Ferenepea hispida                    |                                 |                            |                                   | X  | X  |              |
| Palaeadotes italops                  |                                 |                            |                                   | X  | X  |              |
| Placosema adnatum                    |                                 |                            |                                   | X  | X  |              |
| Acrodirotes fastosa                  |                                 |                            |                                   |  | X  |              |
| Adelogonus solus                     |                                 |                            |                                   |  | X  |              |
| Anopocodia globiceps                 |                                 |                            |                                   |  | X  |              |
| Aulacodigma ilimbatum                |                                 |                            |                                   |  | X  |              |
| Aulacodigma quasispinale             |                                 |                            |                                   |  | X  |              |
| Auritama aurita                      |                                 |                            |                                   |  | X  |              |
| Auritama expansa                     |                                 |                            |                                   |  | X  |              |
| Auritama trilunata                   |                                 |                            |                                   |  | X  |              |
| Avonina? sp.                         |                                 |                            |                                   |  | X  |              |
| Biaverta biaverta                    |                                 |                            |                                   |  | X  |              |
| Blackwelderia gibberina              |                                 |                            |                                   |  | X  |              |
| Blackwelderia repanda                |                                 |                            |                                   |  | X  |              |
| Brassicicephalus sp.indet            |                                 |                            |                                   |  | X  |              |
| Catillicephala sp.indet              |                                 |                            |                                   |  | X  |              |
| Catillicephalidae gen. et. sp.indet. |                                 |                            |                                   |  | X  |              |
| Cyrtoprora intricata                 |                                 |                            |                                   |  | X  |              |
| Dipyrgotes aff. novella              |                                 |                            |                                   |  | X  |              |
| Dipyrgotes novella                   |                                 |                            |                                   |  | X  |              |
| Doremataspis ornata                  |                                 |                            |                                   |  | X  |              |
| Free Cheek No. 1                     |                                 |                            |                                   |  | X  |              |

TABLE 4: STRATIGRAPHIC DISTRIBUTION OF SPECIES—*continued*

|  | Late Middle Cambrian | Zone of Passage | Mindyallan             |                               |                               | Idamean |
|--|----------------------|-----------------|------------------------|-------------------------------|-------------------------------|---------|
|  |                      |                 | Erediaspis eretes Zone | Cyclagnostus quasi-vespa Zone | Glyptagnostus stolidotus Zone |         |
| POLYMERID TRILOBITES                         |                      |                 |                        |                               |                               |         |
| <i>Henadoparia integra</i> ....              |                      |                 |                        |                               | X                             |         |
| <i>Histiomona oculosa</i> ....               |                      |                 |                        |                               | X                             |         |
| <i>Larva</i> gen. et. sp.indet               |                      |                 |                        |                               | X                             |         |
| <i>Leichneyella caseyi</i> ....              |                      |                 |                        |                               | X                             |         |
| <i>Liostracina nolens</i> ....               |                      |                 |                        |                               | X                             |         |
| <i>Liostracina volens</i> ....               |                      |                 |                        |                               | X                             |         |
| <i>Liostracinoides?</i> sp.indet             |                      |                 |                        |                               | X                             |         |
| <i>Lobocephalina pyriceps</i> ....           |                      |                 |                        |                               | X                             |         |
| <i>Lonchocephalus?</i> sp. ....              |                      |                 |                        |                               | X                             |         |
| <i>Lophoholcus asper</i> ....                |                      |                 |                        |                               | X                             |         |
| <i>Lynaspis noakesi</i> ....                 |                      |                 |                        |                               | X                             |         |
| <i>Meringaspis meringaspis</i> ....          |                      |                 |                        |                               | X                             |         |
| <i>Meteoraspis</i> aff. <i>bidens</i>        |                      |                 |                        |                               | X                             |         |
| <i>Meteoraspis bidens</i> ....               |                      |                 |                        |                               | X                             |         |
| <i>Metopotropis travesi</i> ....             |                      |                 |                        |                               | X                             |         |
| <i>Mindycrusta compacta</i> ....             |                      |                 |                        |                               | X                             |         |
| <i>Mindycrusta mindycrusta</i> ....          |                      |                 |                        |                               | X                             |         |
| <i>Mindycrusta notostena</i> ....            |                      |                 |                        |                               | X                             |         |
| <i>Nilegna sigmata</i> ....                  |                      |                 |                        |                               | X                             |         |
| <i>Nomadinis pristinus</i> ....              |                      |                 |                        |                               | X                             |         |
| <i>Olenus?</i> sp.indet                      |                      |                 |                        |                               | X                             |         |
| <i>Palaeadotes dissidens</i> ....            |                      |                 |                        |                               | X                             |         |
| <i>Paracoosia aspis</i> ....                 |                      |                 |                        |                               | X                             |         |
| <i>Peichiashania?</i> <i>lunatula</i>        |                      |                 |                        |                               | X                             |         |
| <i>Peichiashania?</i> <i>pelta</i> ....      |                      |                 |                        |                               | X                             |         |
| <i>Polycyrtaspis flexuosa</i> ....           |                      |                 |                        |                               | X                             |         |
| <i>Rhodonaspis longula</i> ....              |                      |                 |                        |                               | X                             |         |
| <i>Rhysometopus princeps</i> ....            |                      |                 |                        |                               | X                             |         |
| <i>Saratogia?</i> <i>vetusta</i> ....        |                      |                 |                        |                               | X                             |         |
| <i>Saukia?</i> <i>priscilla</i> ....         |                      |                 |                        |                               | X                             |         |
| <i>Solenopleura?</i> <i>erista</i> ....      |                      |                 |                        |                               | X                             |         |
| * <i>Talbotinella notulata</i> ....          |                      |                 |                        |                               | X                             |         |
| <i>Teinistion?</i> <i>amydium</i> ....       |                      |                 |                        |                               | X                             |         |
| <i>Townleyella townleyi</i> ....             |                      |                 |                        |                               | X                             |         |
| <i>Trilobite</i> <i>thorax</i> ....          |                      |                 |                        |                               | X                             |         |
| <i>Blountia georginae</i> ....               |                      |                 |                        |                               |                               | X       |
| <i>Corynexochus plumula</i> ....             |                      |                 |                        |                               |                               | X       |
| <i>Eugonocare</i> cf. <i>tesselatum</i> .... |                      |                 |                        |                               |                               | X       |
| <i>Idamea baccata</i> ....                   |                      |                 |                        |                               |                               | X       |
| <i>Idamea extricans</i> ....                 |                      |                 |                        |                               |                               | X       |

TABLE 4: STRATIGRAPHIC DISTRIBUTION OF SPECIES—*continued*

|                                 | Late<br>Middle<br>Cambrian | Zone<br>of<br>Pas-<br>sage | Mindyallan                        |  |  | Ida-<br>mean |
|---------------------------------|----------------------------|----------------------------|-----------------------------------|--|--|--------------|
|                                 |                            |                            | Eredi-<br>aspis<br>eretes<br>Zone | Cycl-<br>gno-<br>stus<br>quasi-<br>vespa<br>Zone | Glypt-<br>agno-<br>stus<br>stoli-<br>dotus<br>Zone |              |
| <b>POLYMERID TRILOBITES</b>     |                            |                            |                                   |  |  |              |
| Idamea venusta .....            |                            |                            |                                   |  |  | X            |
| Mindycrusta advena .....        |                            |                            |                                   |  |  | X            |
| <b>CRUSTACEA BRADORIIDA</b>     |                            |                            |                                   |  |  |              |
| Aristaluta spicata .....        |                            | X                          |                                   | X  |  |              |
| Svealuta cf. primordialis ..... |                            |                            |                                   |  |  |              |
| <b>PROBLEMATICA</b>             |                            |                            |                                   |  |  |              |
| Castings No. 1 .....            |                            |                            |                                   | X  |  |              |
| Burrows No. 2 .....             |                            |                            |                                   |  | X  |              |

## PART 2: PALAEOONTOLOGY

### *General Composition of the Fauna*

The Mindyallan fauna of Queensland is quite diverse. The trilobites predominate, of course; the collected material is described exhaustively, but it is evident from fragments that further collecting would augment it.

Specimens of inarticulate phosphatic brachiopods are rather abundant. They are present in all collections, and are not mentioned, therefore, in all locality lists. *Acrothele* is mentioned in localities of the *Glyptagnostus stolidotus* Zone of the Mungerebar-Mindyallan area as local evidence for the age of the rocks. Others are '*Acrotreta*', *Paterina*, *Lingulella*, ?*Obolus*, or ?*Dicellomus*. Articulate brachiopods (orthoids, apparently Billingsellidae) are very rare and the obtained specimens are unsuitable for accurate description.

Echinoderms occur only as ossicles.

Conodonts (*Hertzina* ? *bisulcata* Müller) have been observed by Jones (1961) in several samples, particularly from locality G8.

Sponge spicules occur in a great abundance and diversity of forms; among these *Chancelloria* is common.

Crustacea (Bradoriida) are very rare—all collected specimens are described here. New genera of bivalved crustacea (supragenerically new as well) are mentioned in the description of locality G128, and of the Northern Territory locality NT187.

Mollusca are represented by nautiloids, gastropods, and Monoplacophora. The nautiloids are very rare and not well preserved (see locality G409).

Gastropods are represented by several genera of small bilaterally symmetrical and variously ornamented horn-like shells covered by the name of '*Helcionella*' in the locality lists. *Pelagiella* is rare. Furthermore several genera of sinistral gastropods (Mungerebar-Mindyalla localities G119, G124, G126, G127, G128, G153, G417, and most of the localities of the Glenormiston area), referred to as Scaevogyrinae are quite common. In Northern Territory, locality NT 187, even a gastropod limestone is present.

One form of Monoplacophora occurs in the O'Hara Shale ('lower chert bed'), locality D29. Furthermore, a *Stenotheca* occurs in the 'lower chert bed' of the O'Hara Shale, and another in the Idamean sequence.

The mode of preservation of the fossils and palaeoecology are discussed in Öpik (1963).

### *Methods and Philosophy in Taxonomy and Systematics*

Methods and philosophical aspects of systematics are usually discussed in essays illustrated by examples selected from taxonomy for the sake of argument. In taxonomic papers, however, authors rarely discuss such topics, and the interested reader may seek for an answer between the lines. Hence, I like to assist the reader myself with this epitome of the methodological and philosophical background of the present Bulletin, which contains the largest of my taxonomic studies.

The reality of fossils is a fact. The specimens are real and so are their taxonomically exploited characters. Furthermore, each fossil represents a real creature, an individual of a real species. Their fragmentary and incomplete remains are the

only source of the descriptive and comparative morphology and of a taxonomic classification. Lost parts of the fossils cannot be observed; but their reality cannot be denied. The remains in hand provide clues about the lost parts, and aided by comparative anatomy, one ventures to infer the whole and to comprehend the extinction.

The taxonomic categories are categories of the logic of classification. Indefinable each on its own, the categories are definable in relation to each other as ascending or descending steps in the process and system of classification. The number of categories is arbitrary but small, as dictated by common sense.

Taxa are aggregates of individual specimens as well as aggregates of aggregates assigned each to an appropriate category and assembled in consideration of morphological similarities. Hence a genus is a taxon of species, and a family is a family of species, as well as of genera, and so forth. Species and genera, however, cannot be regarded as 'subdivisions' of a family, for example. Infrataxial aggregates like those of subgenera and subfamilies are only semantically 'subdivisions': the nomenclature and the optional status of these categories has no influence on the scientific concept of their taxa. Fundamentally, each supraspecific taxon is a taxon of species, and the number of species in each increases progressively with the rank of the category. A species taxon contains only one species and supraspecific taxa are multi-specific or potentially so. Any species, old or new, should enter particular suprageneric taxa of its class as well; for this purpose, even new suprageneric taxa may become necessary, whose category or categories will be a matter of judgement.

The category assigned to a new taxon is determined by the evaluation of the rank-significance ('category value') of its unifying morphological characters. This is done, for example, by eliminating characters signifying a superior or inferior rank to that of the taxon in question.

Suprageneric taxa established for a single species or a small aggregate of species may not be tested readily by the method of elimination. Comparative morphology and comparative anatomy, however, may indicate the proper mode of action: *Aulacodigma* gen.nov. and Aulacodigmatacea superfam.nov. (q.v.) refer only to two species. Furthermore, concepts of existing taxa should not be violated by inclusion of disparate species. In doubtful cases a convenient form of presentation is a reference to a high ranking taxon followed by a statement of uncertainty regarding the taxa of intermediate categories.

Considerations regarding palaeogeography (provincial segregation), character of the rock, inferred ecology, and stratigraphic data cannot be used in establishing either taxa or their categories. These aspects add nothing to the real morphology of the material, but may be helpful in support of decisions based on morphological evidence.

In palaeontology the purpose of taxonomy may be stated in terms of the following functions:

- (1) The description of fossil remains in terms of taxa of morphological species in a form which serves in subsequent identifications (owing to the unsatisfactory state of preservation a large amount of fossil remains is unsuitable for such treatment); and

(2) The distribution of species-taxa in taxa of supraspecific categories according to morphological criteria evaluated in terms of similarities and dissimilarities, and of their 'category values' (the supraspecific taxa also are established and described in terms suitable for subsequent identification).

These two functions together constitute a logical form of presentation leading to a morphological system of taxa.

The next objective is the interpretation of the morphological criteria in terms of degrees of affiliation of the taxa to each other and in terms of lines of descent and, ultimately, in terms of a phyletic history of a class, for example. This is a task not of taxonomy but of phyletic palaeontology.

Phyletic palaeontology is an interpretative discipline and distinct from taxonomy, which describes and classifies the substance in the first place. Phylogenetic considerations supply no criteria for identification of the actual material, but may provide for constructive criticism of taxonomic classifications and systems. Phylogenetic criticism tests the systems for monophyletic, polyphyletic, and artificially aggregated and segregated taxa and inquires into rules and laws by which phyletically relevant criteria can be separated from less relevant or irrelevant phenomena. Comparative anatomy supplies the concrete data for theoretical designs of 'missing links' and of ancestral forms, and 'taxonomic characters' are examined in terms of anatomy, organization, function, and variability in time. Some aspects of phyletics are also considered in the present paper in discussions of species and other taxa, in expressions like 'affiliation', 'close' or 'remote' relationship, 'familial classification', etc. Examples of phylogenetic reasoning are included in the discussion of effacement ('phyletic simplification') of agnostids as well as of the increase in relief ('complications') in *Ptychagnostus fumicola* and *nodibundus*. The problem of fixation of the number of segments is touched in connexion with agnostids in general. Phyletic criticism is applied in separating the Plethopeltidae from the Proetacea; phyletic histories of the Idahoiidae (*Saratogia? vetusta*), Saukiidae (*Saukia? priscilla*, *Lophoholcus*, *Lobocephalina*), and Dikelokephalinidae (*Nomadinis pristinus*) are discussed. A potential pitfall is illustrated in the discussion of the Asaphiscidae (q.v.): the ascending temporal sequence of the asaphiscid species in Queensland is the reverse of their phyletic succession indicated by their comparative morphology. Phyletic problems and migration are discussed in relation to the early Upper Cambrian faunal crisis. Other topics are the temporal distribution and phylogeny of agnostids, the longevity of the Quadragnostinae (*Peratagnostus*), and anachronisms (*Corynexochus plumula*). In an earlier paper (1961, p. 126) the aspects of primitiveness and specialization were discussed, and in another paper (1963, p. 65) the problem of the restitution of lost characters bears on the phylogeny of olenids. *Discagnostus* (ibid., p. 56) represents a separate phyletic problem regarding the visual organs of miomerid trilobites.

The problem of the objectivity of taxa and of classifications also deserves some comment. Any taxon of any category is a product of logic and has no existence in nature. In this respect even a species-taxon is no exception; but the species as such are, of course, objective aggregates and successions of aggregates of real bions; in palaeontology at least one specimen of a species-taxon belongs to a corresponding objective species; matters of judgement, however, are (1) the identity of a new species when compared with the already known species, and (2) the specific identity of all

specimens attributed to a particular species. The judgement based on the examination of morphology remains valid unless demonstrated to be erroneous, but the hazard of erroneous identifications is no motive for rejecting the principles. A substantial part of palaeontological material attributed or attributable to a morphological species on the evidence of comparative morphology represents an objective species; the homogeneity of the whole material, including the paradigm and all subsequent supplies, remains, however, a subject of criticism and inquiry. The same situation is faced by neontology in determining the specific identity of specimens of extinct generations of living species; for example, *Equus caballus* of A.D. 378 is attributable to *caballus* only on morphological evidence.

In short four aspects of systematics are connoted by the term 'species': (1) a category of taxa; (2) particular taxa of the category species; (3) particular objective biological species; and (4) the general concept of what is a biological species. The modern concept of biological species is an explanatory generalization based on the notion of objective populations of interbreeding individuals. As a concept it holds for a single generation, including reproductive individuals surviving from preceding generations. Extrapolations, however, of the reproductive, specific continuity into the past and future can be contemplated only on the basis of morphology, because the notion of interbreeding of a given population with extinct and unborn generations would be irrational.

The objective homogeneity of a fossil sample is evident in material from a single bedding plane or a single bed of established continuity. Examples of such sites in the Mindyallan have been discussed in the systematic description of the fossils. So, *Nilegna sigmata* was sampled from a single bedding plane and *Auritama aurita* from a single bed of limestone; these samples of a small number of generations represent time spans comparable with the time available in the neozoology of invertebrates. From a palaeozoological angle such samples and time spans are inadequate to encompass the temporal variability of the species. Shortcomings of this kind are shared by the 'single bed species' as described, for example, from 'the lower chert bed' of the O'Hara Shale. Such assemblages, however, are informative in the study of coenoses and of the gross compositions of faunas that are not readily obtainable from fossil remains scattered in a sequence of beds (Öpik, 1961, p. 40, 48; 1963, p. 25-30. See also Plate 1). The material of *Aulacodigma quasispinale* (a species-taxon) collected from two separate sites of no obvious contemporaneity is accepted as representing an objective species on the merit of its morphological homogeneity; *Aspidagnostus inquilinus* from three separate sites represents a species-taxon of two morphologically distinct populations separated from each other by spans of many generations—hence the taxon contains two infraspecific aggregates. Another example is the material of *Centropleura phoenix* (Öpik, 1961, p. 105) which represents a species-taxon of morphological and probably biological homogeneity in spite of its innumerable generations within the span of two zones and some 300 feet of successive beds. To conclude, fossil biological species cannot be recognized by direct observation but are inferable or even detectable by means of morphology, or may remain disguised in the form of species-taxa. A palaeozoological (here trilobite) species-taxon refers to a concept derived from the study of the morphology of small samples of fossil remains taken as representing an objective species.

Genera and suprageneric aggregates (as such, and as taxa) are *res mentis* by design. They refer to composite aggregates made up by judgement in the quest for order. Any particular judgement is replaceable by substitutes; hence, the composition of the aggregates is fluctuating, and the derived concepts (*res mentis*) have no inherent stability. The concepts are plastic, even if the plasticity remains dormant for a while, as for example in a 'well defined genus'. The plasticity of the concepts of suprageneric taxa is shared *arte mentis* by the taxonomic system (in general) and the published versions of particular systems.

So, biological classifications and systems and the 'system of nature' are products of the mind contemplating the objective nature. 'Objective nature' in this connexion means (1) the biological material, (2) the kinematics of changing forms, and (3) the order of nature in general.

The biological (in the present case palaeontological) material consists of the fossil remains and the fact of their morphological diversity. The kinematics refers to the biological events of the change of characters, of organs, of structures, and of the organization of bions as evident from the geological (temporal) sequence of forms and from the fact of the descent from each other of individuals and generations. I think that the objective existence of an order of nature should be accepted a priori and that the order of events is inherent to nature as a principle; the order in biological events is governed in the first place by the irreversibility of the streams of genetic material and of the pageant of life.

In summary, in describing and classifying fossils the following course seems reasonable:

1. The first and fundamental taxonomic objective is the intelligent and intelligible description of the fossil remains. At the present state of palaeontological knowledge the application of a minimal number of three categories ensures an intelligible form of presentation; these categories are (a) species, (b) genus, and (c) the usually obvious class or ordinal category (if such is available or acceptable).

2. The next objective is classification in terms of the family and ordinal categories. Morphological data are generalized with the intention of defining the position of the species in relation to a mostly available system of taxa of its class. This operation may necessitate criticism, and some modification, of the system itself. Indeed, classification is not a game with fixed arbitrary rules; hence, the seemingly 'irregular' reasoning regarding the perspectives of descent and affiliation should be applied wherever possible in the evaluation of the morphological characters and in detection of such characters as have escaped observation earlier. Beyond this auxiliary function the inquiry into the kinematic aspect of life contributes nothing to the substance of taxonomy. Of course, the kinematics are objective and capable of being classified. This is done in terms of phyletics and evolution operating with taxa of any category or even with separate morphological phenomena only.

*The Expanding Knowledge:* The unknown, as in any science, is the challenge in biological palaeontology. The number of published taxa of invertebrates expands, however, at a rate which seems too rapid; the volume of palaeontological knowledge

already published is regarded sometimes as too large by field geologists, stratigraphers, and even authors of geology text books. Even curbing of publication of such taxa and faunas as are 'unnecessary' or 'useless' in stratigraphy has been voiced. Nobody, however, is able to foretell such qualities of particular fossils; all properly described fossils are useful in stratigraphy, correlation, and palaeogeography; determination of fossils in the field in terms of stratigraphically significant genera and species will remain a source of erroneous dating of sequences. Study of properly collected fossils in camera is the only way in assessing their stratigraphic meaning. Not 'palaeontology made easy', but publication of palaeontological monographs revising the already known in the light of advancing knowledge and describing new biological material ensures a concurrent advance in stratigraphy.

### *Morphological Observations*

Observations regarding the morphology and organization of trilobites may remain unnoticed in a text of taxonomic descriptions; hence, an extract from the descriptive part is presented to collect together new or little known data regarding the trilobites in general. The arrangement is alphabetic, in the form of an 'explanation of terms and phrases'—an aid in reading the taxonomic descriptions as well as in locating the explanatory text-figures. The same, alphabetic, form of presentation has been used earlier (Öpik, 1961 and 1963).

*Absence of fulcra:* Pleural fulcra are absent in *Biaverta biaverta*, as concluded from the absence of fulcral sockets and geniculation in the cephalon; in some other menomoniids (*Dresbachia amata* and *Menomonion calymenoides*) no fulcra are recognizable in the thorax. In *Dresbachia* the palpebral lobes are close to the midline and well inside the lines of axial furrows, in a position unsuitable for locating the position of the fulcral lines even if they were present. See under 'fulcral lines', 'fulcra, relative position' and 'spiral coiling'.

*Abbreviated occipital furrow:* In the abbreviated occipital furrow its distal ends are closed by lobules. See under *Iniotoma iniotoma* and *Mindycrusta advena* (Text-fig. 83).

*Accessory furrows (agnostids):* See Text-figure 45; these furrows are interpreted as parietal septa or mesenteries (Öpik, 1963); further discussion under *Pseudagnostus* and its species (q.v.)

*Acrolobe (agnostids):* Text-figure 15.

*Agnostid morphology:* See Öpik, 1963.

*Alae:* Depressed spots flanking the glabellar rear, for example in *Biaverta biaverta*; further discussion under baculae (q.v.).

*Anachronism:* A solitary species postdating the main development and specific diversification of a genus; examples are *Corynexochus plumula* and *Peratagnostus nobilis* (q.v.).

*Anterior knobs:* Small knobs at the anterolateral corners of the glabella (Text-figs 85, 93), of unknown function.

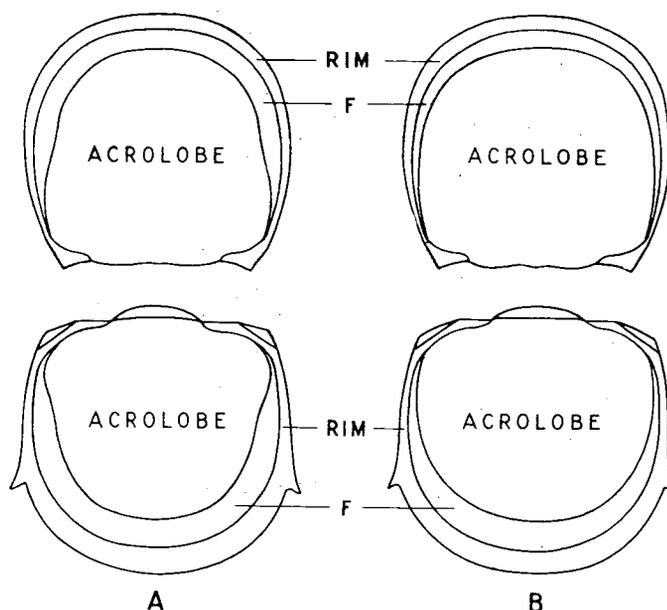


Fig. 15.—The main morphological divisions of the agnostid exoskeleton. The rim and marginal furrow (F) constitute the border enclosing the acrolobes. A.—shields with constricted acrolobes (with concave flanks); B.—with unstricted acrolobes (with flanks convex outward)

*Anterolateral lobes in cranium:* Low triangular lobes flanking the glabellar front of *Blackwelderia sabulosa* (Text-fig. 111), *B. gibberina*, *Dipentaspis*, and *Meropalla*; hitherto known in the Dinesidae.

*Antiplectrum:* A pointed low median elevation behind the pygidial axial terminus—probably a non-segmental extension of the axis (Text-figs 121 and 146).

*Antirostral hood:* A low swelling of the brim reflecting the shape of the rostral shield, Text-figure 93 (*Rhyssometopus*); see also 'frontal boss' and 'plectrum'.

*Articulating device (agnostids):* The articulating device of the agnostid pygidium when complete consists of the articulating half-ring, the articulating furrow, and the recess in the front of the axial lobe. Four kinds are known: (1) the basic, in Quadragnostinae and Ptychagnostinae, (2) the agnostoid, in Agnostinae and Clavagnostidae, (3) the glyptagnostoid, in the Glyptagnostinae, Pseudagnostinae, and Diplagnostinae; and (4) a simple plate in *Xestagnostus*. See also 'concave facets'.

*Axiolobate (agnostids):* Agnostids with the basic unmodified pygidial axial lobe; see also 'modified axiolobate' and 'deuterolobate'.

*Bacculae* (singular—baccula): Swellings flanking the glabellar rear, one on each side; differ by their convexity from alae (q.v.), which are depressed spots. Bacculae and alae are homologous in position, but different in structure. Present in genera of diverse families: *Auritama*, *Metopotropis*, *Nomadinis*; in the Damesellidae (*Blackwelderia gibberina*, *Histiomona*, *Meringaspis*, *Palaeadotes*, *Teinistion*); Liostracinidae

(*Liostracina*, *Lynaspis*, *Doremataspis*), Nepeidae, and *Townleyella*. In *Centropleura* (Öpik, 1961), deep pits are present in the position of bacculae or alae, interpreted as muscle carriers.

*Border (agnostids)*: The border, as distinct from the acrolobe, consists of the rim and the marginal furrow (Text-fig. 15).

*Boss*: See 'frontal boss'.

*Bulge, lateral, of glabella*: A pair of lateral bulges occurs in the Rhyssometopacea (q.v.) defined by the composite second glabellar furrows (Text-figs 93, 101, and 105). These bulges are scars of strong muscles serving a pair of appendages stronger than usual in the trilobite cephalon; a phyletic increase in emphasis of the lateral bulges is apparent in the Rhyssometopacea from *Quititalia* (Middle Cambrian) to *Rhyssometopus* (early and late Mindyallan).

*Caeca, terminal*: See 'terminal caeca'.

*Category value of characters*: see the chapter 'Methods and philosophy'.

*Cephalic recess (agnostids)*: The upward-arched recess in the rear of the cephalon (Robison, 1964), covered in some agnostids by the occipital collar (q.v.).

*Cephalothoracic aperture (agnostids)*: The aperture (Robison, 1964) is formed by the cephalic and the thoracic recesses at the articulating junction of the cephalon with the thorax; the function of the aperture is unknown.

*Cephalic pleural lobe*: This phrase refers originally to that part of the cephalon surrounding the glabella (the axial lobe) (see Öpik, 1961, p. 106); in the present paper (Text-figs 110 and 111) it is used in a somewhat restricted sense, without considering the border; it compares with the cephalic acrolobe of agnostids without the glabella; in terms of Harrington et al. (1959, Text-fig. 31) the present usage refers to the fixigena and librigena together but without the border. See also 'interocular cheek'.

*Circumocular suture* (Text-fig. 52). The assumption prevails that in moulting the visual surface of the trilobite eye remains fused with the free cheek. This is correct as regards the post-Cambrian trilobites. Among Cambrian trilobites, however, the visual surface is retained by the free cheek only in a minority; in the majority the visual surface is liberated as a separate moult unit detached from the palpebral lobe (cranidium) and the free cheek by the circumocular suture. This suture consists (1) of the palpebral suture—the middle part of the facial suture in general, and (2) of the ocular (or genal) suture that separates the visual surface from its base on the free cheek. The ocular suture, apparently, has not been mentioned hitherto in the literature.

The existence of the ocular suture is evident from the following observations: (1) examples of retention of the visual surface by the free cheek are rare, and listed below; (2) free cheeks of most of the Cambrian trilobites are found always without the visual surface; (3) the ocular edge of the free cheek in properly preserved material is clear-cut and differs in no way from the edges of the shields resulting from the opening of the facial sutures; (4) complete tests of opisthoparian trilobites occur mostly without the visual surface, but with hollow 'ocular apertures'; (5) sutureless

trilobites (olenellids) also lose their visual surface—an indication that they also possess the circumocular suture. It is, therefore, fair to assume that the circumocular suture prevalent in early trilobites is a primitive, and the retention of the eye by the free cheek a subsequent, character.

Cambrian examples of the retention of the visual surface by the free cheek are:

(1) *Pagetia significans* (see Öpik, 1963, p. 57);

(2) *Cedaria prolifica* Walcott (Palmer, 1962, p. F 26);

(3) the forms described here: *Rhodonaspis*, *Mindycrusta*, *Auritama*, *Metopotropis*, *Aulacodigma*, *Liostracina*, *Doremataspis*, *Henadoparia*, *Rhyssometopus*, *Rostrifinis*. Except for *Pagetia*, which is Middle Cambrian, all listed trilobites are Upper Cambrian in age. Furthermore, they all have one feature in common: their ventral cephalic structure has departed from the ptychoparioid design, but in various ways: (1) no rostral shield is present, or, (2) the rostral shield is small, or, (3) only a median suture (as in the asaphids) is present.

Moreover, these trilobites are unrelated to each other: they belong to different families, superfamilies, and even orders (*Pagetia*). It appears, therefore, that the loss of the ocular suture and the retention of the cornea of the compound eye by the moult of the free cheek represents a general step in the evolution of the class, and is not a character of a particular phylogenetic lineage.

The circumocular suture, a moulting convenience, cannot be interpreted as having originated from intrasegmental joints.

Coiling: See 'spiral coiling'.

*Collar, occipital (agnostids)*: See 'occipital collar'.

*Collar, pygidial (agnostids)*: See 'zonate pygidium'.

*Concave facets (agnostids)*: The pleural facets of trilobites are presumed to be flat, but their structure has not been studied as yet in detail. In the majority of the Quadragnostinae and Ptychagnostinae which possess the basic form of the articulating device the pygidial facets are flat and the fulcra are geniculate but not pointed; still, moderately concave facets occur sporadically in their subfamilies. In several of the Agnostinae and Diplagnostinae, however, and in the Pseudagnostinae the facets are concave and combined with pointed fulcra; examples (q.v.) are *Cyclagnostus quasivespa*, *Oidalagnostus personatus*, *Pseudagnostus idalis*, and *Xestagnostus legirupa*. In the Glyptagnostinae the facets are flat and the fulcra angulate but not pointed. The concavity of the facets indicates a complication of the mechanics of articulation.

*Constricted acrolobe (agnostids)*: See Text-figure 15.

*Cornea*: See under 'circumocular suture'.

*Cranidial posterolateral spines*: This is a unique peculiarity of *Aulacodigma* (q.v.), Text-figure 143.

*Dent, occipital*: See 'occipital dent'.

*Deuterolobate* (agnostids): A special case of the modified axiolobate structure of the pygidium common to the Pseudagnostinae; the structure of the deuterolobe is discussed in full by Öpik (1963). See also Text-figures 45, 46, and 49.

*Dilated doublure*: See 'doublure of the free cheek'.

*Directional terms for lateral (genal and pleural) spines*:

*Advanced* are spines with an undercut at their rear and displaced forward from the unadvanced position.

*Unadvanced* are spines with the rear margin of the pleura evenly continuous to the tip of the spine.

*Deflected* are spines deflected outward (or downward) from the even curve of the cephalic lateral margin or from the anterior margin of the pleura.

*Undeflected* are spines continuing the even curve of the cephalic flank or of the anterior margin of the pleura.

*Falcate* are undeflected and unadvanced sickle-like sidewise curving spines.

*Retral* are spines directed rearward and parallel to the sagittal direction.

*Dorsal sutures*: See Text-figure 52 and 'circumocular suture'.

*Double ocular ridges*: See 'ocular ridges'.

*Doublure of the free cheek*: The frontal part of the doublure of the free cheeks is dilated in the Rhysosmetopidae (Text-figs 95 and 99) with the effect that its edge contacts the hypostoma in trilobites with a brim. This is a complication of the basic design of trilobites with a brim, in which the doublure and the hypostoma remain disconnected, or connected only by an auxiliary stalk.

*Doublure, pygidial*: See under 'pygidial doublure in *Palaeadotes italops*'.

*En grande tenue*: 'in full dress'; refers to agnostids displaying all their lobes and furrows as distinct from effaced agnostids.

*En grande tenue*: erroneous spelling in Öpik (1961; 1963); see 'en grande tenue'.

*Eyes*: See under 'rudimentary eye' and 'circumocular suture'.

*Facets* (agnostids): See 'concave facets'.

*Flat rim of cranidium*: The vertical flat rim seen in *Meropalla* and *Placosema* (q.v.) occurs also in *Illaeonurus* and *Macellura*; in all these forms this structure may have arisen independently; a similar structure is apparent also in *Idamea* and *Lophoholcus* and even in *Stephanocare*, in which, however, the rim is a bar defined by the fully developed marginal furrow. Hence, the flat rim of *Meropalla* may be only the frontal slope of the otherwise reduced rim.

*Forked ocular ridges*: See 'ocular ridges'.

*Forward produced cephalic front*: See *Blackwelderia sinensis* (Text-fig. 110) and *B. sabulosa* (Text-fig. 111).

*Frontal boss*: The frontal boss is a swelling of the brim in front of the glabella and separated from it by the circumglabellar furrow (the closure of the axial furrows in front of the glabella); its position and prosopon (caecal veins) indicate that it is not a part of the axial lobe of the trilobite but a pleural feature. It has no correspond-

ing sternite and is not underlain by the frontal doublure or the rostral shield; ventrally it was covered by the non-calcified membrane only. The boss begins to develop in an early meraspis stage and is, therefore, a morphogenetically late and, within a given stock, a phylogenetically novel character. Its function is a matter of speculation: the boss may have developed as a secondary ingluvial extension of the stomach or as a fat container. It is homologous neither with the antirostral hood nor with the plectrum (q.v.). Examples here described are *Acrodirotes*, *Ferenepea*, *Ascionepea*, and *Aulacodigma*, representing three diverse superfamilies (see also Shaw, 1962, p. 340).

*Frontal glabellar tubercle (node)*: A small tubercle on the glabellar front is apparent in *Mindycrusta compacta* and was previously observed in *Irvingella tropica*, 1963. Its function is unknown.

*Frontal limit of cephalic pleural lobe*: See 'cephalic pleural lobe'; this phrase is used in cases where the pleural lobes extend forward beyond the glabellar front and the application of the term 'brim' is inappropriate or inconvenient.

*Fulcral lines*: The fulcra are aligned longitudinally on the pleurae of the thorax; these lines are the lines of geniculation and separate the adaxial jointed and articulating part and the free abaxial part of the pleural lobe from each other; the doublure terminates at the fulcra and pleural furrows are often expanded and angulate forward along the fulcral lines. The palpebral lobes are aligned with the cephalic fulcral sockets and, consequently, with the fulcral lines of the thorax; an exception is *Solenopleura? erista* (q.v.); (see also under 'absence of fulcra'). The fulcral lines may be subparallel or converging forward (*Mindycrusta mindycrusta*, Text-fig. 82) or rearward.

*Fulcra, pointed*: See under 'concave facets'; furthermore, in *Corynexochus plumula* (q.v.) the fulcral sockets are swollen externally.

*Fulcra in relation to palpebral lobes*: See 'fulcral lines'.

*Fusion of sutures*: Fused sutures in *Henadoparia* (q.v.) are recognizable from their vestigial lines; see also under 'circumocular suture' (fusion of the ocular suture).

*Gap in zonate pygidium (agnostids)*: See under 'zonate pygidium'.

*Genal spines*: See 'transmarginal spines'.

*Hood*: See 'antirostral hood'.

*Hypostoma*: The hypostoma of *Palaeadotes* (Text-fig. 129) has complicated, apparently tubular lateral notches and two pairs of lateral muscle scars (beside the maculae), which may indicate the possibility of metamerism of the hypostoma.

*Interocular channels*: These are the transverse channels of *Aulacodigma* between the palpebral lobes and the glabella (Text-fig. 143). Bounded by the ocular ridges, the channels are interpreted as a pair of cephalic pleural furrows and the palpebral lobes as tips of the corresponding pair of pleurae.

*Interocular cheek*: The space between the glabella and the palpebral lobe, describable also as the distance of the palpebral lobe from the glabella; it is the 'palpebral area of fixigena' in terms of Harrington et al.

*Interocular swelling*: In some trilobites (for example *Leichneyella* and *Poly-cyrtaspis*) the interocular cheek is swollen and repeats the form of the palpebral lobe.

*Lateral bulge of glabella*: See 'bulge'.

*Marginal furrow (agnostids)*: See Text-figure 15.

*Median glabellar nodes*: Two median glabellar nodes occur sporadically in *Aulacodigma quasispinale* (q.v.) interpretable as rudimentary axial spines.

*Modified axiolobate pygidium (agnostids)*: Modifications of the posterior axial lobe of the pygidium are rather frequent in the Diplagnostidae and Clavagnostidae; so, in *Ammagnostus* the terminal node is shifted forward from its original position; in *Oidalagnostus* the rear axial lobe is expanded, and trapezoidal; in *Aspidagnostus* only the intranotular axis is preserved; in *Glyptagnostus* a caecal bulb invades the median line behind the axial lobe; and the Pseudagnostinae are deuterolobate (q.v.); see also under 'axiolobate'.

*Morphogenesis (morphogeny)*: The term 'ontogeny' as applied in the literature to trilobites refers to the development of the exoskeleton, its parts and structures, as observable on divers instars of different individuals; hence, the fair term is morphogenesis.

*Occipital collar (agnostids)*: In several agnostids a semi-cylindrical projection (the collar) extends from the rear of the cephalon as a cover of the cephalic recess and of the thoracic recess, somewhat protecting from above the apparently exposed viscera which pass from the cephalon into the thorax (Text-fig. 31).

*Occipital dents*: A pair of indentations occurs in the front of the occipital lobe, of unknown function (Text-figs 61 and 87) and incidental in several superfamilies.

*Occipital furrow, abbreviated*: See under 'abbreviated'.

*Ocular ridges*: Simple ocular ridges consist of a single band each; double ocular ridges consist of two bands each; these are parallel and close together; forked ocular ridges start at the glabella as a simple ridge which forks abaxially into two divergent bands; it occurs in the Nepeidae and in the Liostracinidae. See also under 'interocular channels'.

*Ocular suture*: See 'circumocular suture' and Text-figure 52.

*Ontogeny*: See morphogenesis.

*Palpebral suture*: See 'circumocular suture'.

*Paradoublural line*: G. Henningsmoen's term designating an external line or even a faint ridge which reflects externally the edge of the doublure in the cephalon as well as in the pygidium (see also 'tropidium').

*Pathological varicosity (agnostids)*: Observed in the pygidium of *Glyptagnostus stolidotus*, Plate 67, figure 2.

*Peripheral pleural lobe (agnostids)*: That part of the pygidial pleural lobe flanking or even enclosing the deuterolobe in *Pseudagnostus*; the adaxial part of the pleural lobe is incorporated in the deuterolobe.

*Plectrum*: The position of the plectrum is evident in Text-figure 105. It is a known feature usually described as a 'median, posteriorly directed inbend of the marginal furrow' in front of the glabella. The plectrum is a rearward projection

of the rim in front of the glabella, known in several Ptychopariacea, Anomocaracea, in the Plectriferidae and Mapaniidae, and in *Proceratopyge*. Its transverse width is variable; it may be short or, in some forms, it may reach the glabellar front. The plectrum is directly opposed to the rostral shield; its flanks reflect the ventral connective sutures which define laterally the rostral shield. In cases where the rostral shield is fused with the doublure (*Mapania striata*; see Öpik, 1961), the plectrum may be retained as a rudiment. The plectrum and the frontal boss are not homologous structures.

*Polarity of organization (agnostids)* (Öpik, 1961, p. 73): the joint between the two segments of the agnostid thorax is the main tagmatic divisional line; structurally the anterior segment is 'cephalic', the posterior 'pygidial', and the anterior segment lacks the axial articulating device.

*Position of eyes (palpebral lobes)*: The position of the palpebral lobes relative to the centre of the glabella is a useful taxonomic criterion; geometrically it refers to the position of the transverse line connecting the midpoints of the palpebral lobes across the glabella. The numerical data thus obtained for the position of the midpoint are comparable when the examined specimens have equal palpebral lobes in terms of glabellar length. When the lobes are unequal, however, two variables masking each other are involved: the length of the palpebral lobe, and the 'true position of the palpebral lobe'. The true position refers to the cephalon as a whole, as expressed in descriptions like 'central', 'advanced', 'forward', 'in the rear' etc. The known marginal cases are seen in *Dresbachia* (well in front of the glabella) and in *Bronteopsis* (well in the rear). *Bronteopsis* has small eyes whose masking effect on the 'true position' is relatively small.

The following remarks are based on the assumption that within a group of affiliated taxa the length of the palpebral lobe is variable in the caudal but not in the frontal direction. If so, a relative stability of position is attributable to the frontal tip of the palpebral lobe which should be accepted as the 'true position'. This accepted, the position of the anterior palpebral tips varies in relation to the adaxial ends of the ocular ridges, as evident from the phrases 'ocular ridges slanting rearward', or 'horizontal', or 'oblique forward'. The junction of the ocular ridges with the glabella just in front of the fourth pair of glabellar furrows in ptychopariids is also an anatomically meaningful point of reference. This point serves to distinguish a preocular from a postocular glabella (q.v.).

To sum up, some ambiguity results from the employment of the centres of the palpebral lobes in relation to the midpoint of the glabella when describing the position of the eye; meaningful data, however, are obtainable by a reference to the position of the anterior tips of the palpebral lobes. The above discussion of the 'position of the palpebral lobes' represents some thoughts after the completion of the taxonomic part of this paper.

*Posterolateral cranial spine in Aulacodigma*: See 'cranial posterolateral spine'.

*Postocular glabella*: That part of the glabella behind the adaxial ends of the ocular ridges; the 'full set of glabellar furrows of ptychopariids' belongs to the postocular glabella. See also 'preocular glabella'.

*Preocular glabella* (Text-figs 56, 93, and 120): That part of the glabella in front of the adaxial ends of the ocular ridges; not coincident in concept with the 'frontal glabellar lobe'. It is subject to diverse modifications (reduction in various degrees or increase in size, and even hypertropic tumidity). Further comment under *Drepanura*, *Palaeadotes dissidens*, and *P. italops*; see also under 'position of eyes'.

*Principal caecal vein* (Text-fig. 53): The meaning of the term is discussed under *Auritama aurita* (q.v.). The principal caecal vein is a feature common to the Ptychopariida (published examples: *Litocephalus* Palmer, 1960, pl. 8, fig. 16; *Diplapatokephalus* Rasetti, 1943, pl. 19, fig. 7); often it may not be expressed externally at all.

*Ptychoparioid design*: Discussed in Öpik, 1963.

*Pygidial collar*: See under 'zonate pygidium'.

*Pygidial doublure in Palaeadotes italops* (q.v.): *P. italops* is unique in having the doublure of its pygidium divided by a concentric ridge into a smooth and a terraced part.

*Pygidial fulcra (agnostids)*: The pygidial fulcral points in agnostids may be angulate, pointed, and even horned; see under 'concave facets'.

*Relative size of pygidium*: A method of estimating the relative size of the pygidium in the absence of complete specimens is discussed under *Auritama aurita* (q.v.).

*Retention of cornea by moults of free cheeks*: See 'circumocular suture'.

*Rim (agnostids)*: See Text-figure 15.

*Rostellum*: The term 'rostellum' designates a homologue of the rostral shield that is surrounded by the connective sutures. The rostellum has no contact with the hypostoma, or with the ventral membrane connecting the doublure and the hypostoma. A 'rostral shield', however, is cut out of the doublure by the frontal (rostral) part of the facial sutures and their longitudinal branches—the connective sutures, and is connected in the rear with the hypostoma, or with the ventral membrane. It is fair to assume that the rostellum is a shield developed by reduction of a rostral shield, and not an innovation, or a special inherited kind of a rostral shield (see under *Auritama aurita*, *A. trilunata*, and *Griphasaphus griphus*).

*Rostral shield*: The presence of a rostral shield is evident in *Blackwelderia sabulosa* (Damesellidae), a very large shield in *Doremataaspis ornata* (Liostracinidae), a small shield in *R. (Rostrifinis) rostrifinis* (Rhyssometopidae); a rostral shield, however is absent in *Ferenepa hispida* (Nepeidae), in *Mindycrusta mindycrusta* (Asaphiscidae), and, apparently, in *Liostracina*. In these the free cheeks are fused into a unit. It can be concluded that the rostral shield, a fundamental ancestral feature, was subject to modification and loss within the various stocks of trilobites independently and at different times; in this respect the post-Cambrian trilobites retaining the rostral shield are rather conservative, as for example the illaenids, proetids, calymenids, cheirurids, and lichids; in these stocks a phyletic fixation of the rostral shield is evident. In the dalmanitids, however, the fusion of the cheeks was accomplished before Arenigian time and the subsequent phacopids produced no further novel subcephalic structures. Hence, the Phacopida as an order contain only the Phacopacea and the Dalmanitacea, which are distinguished by the absence of a rostral shield through the whole of their known geological record.

*Rudimentary palpebral lobe:* The cranidium (Plate 38, figure 1) of the otherwise blind *Biaverta biaverta* has preserved the rudimentary right palpebral lobe.

*Serpentizing lines:* Weak raised lines flanking the carina of the glabella in the Rhyssometopidae (Text-fig. 93) and in *Plectrifer* (Text-fig. 111), probably fringing the areas of muscle attachments, are observable in well preserved cranidia.

*Simplimarginate pygidium (agnostids):* Simplimarginate are pygidia with the basic, unmodified rim; in this respect they are distinct from the zonate pygidium (q.v.).

*Spiral coiling (or enrolment):* In some Menomoniidae the very long and multi-segmented thorax is capable of coiling into an involute spiral (an extreme form of the 'double enrolment'; Harrington et al., p. 104) of about one complete volution; the absence of fulcra (q.v.) may have facilitated the performance. In the thorax of *Dresbachia* (ibid., p. 0303), which is partly coiled or uncoiled, the rear shows the initial half-volution; in a complete coil the pygidium will be enclosed by the thorax.

*Stalked eyes:* See 'turret eyes'.

*Suture, ocular:* See 'circumocular suture'.

*Terminal node of glabella (agnostids):* A small node in the rear of the glabella occurs in *Hypagnostus correctus*, *Innitagnostus innitens*, in *Aspidagnostus*, *Pseudagnostus*, and *Xestagnostus*; it also occurs sporadically in the Ptychagnostinae (for example, in *Ptychagnostus aculeatus*; Westergaard, 1946, pl. 12, fig. 8). This node is, presumably, a homologue of the glabellar spine of the eodiscids.

*Terminal node of the pygidial axis (agnostids):* The pygidial terminal node basically marks the rear extremity of the axial lobe and the axial viscera; the displaced position of the node is assumed to indicate subsequent anatomical modifications in distribution of the viscera; see under 'modified axiolobate'.

*Terminal caeca (agnostids):* Terminal scrobicules and rugae may cross the marginal furrow and extend to the margin (*Pseudagnostus* cf. *idalis*; *Xestagnostus legirupa*; q.v.).

*Thoracic recess (agnostids):* See cephalothoracic aperture and occipital collar.

*Transmarginal genal spine:* A genal spine is transmarginal if it arises not from the border but from the ocular platform of the free cheek (Text-fig. 93); it occurs in *Rhyssometopus*, *Rostrifinis* and *Aulacodigma* (q.v.). Other examples are *Idahoia simplicitas* Resser (1942, pl. 17, fig. 9), *Leptoplastus* (Henningsmoen, 1957, pl. 15, figs 4, 6) and *Parabolina argentina* (Kayser, Harrington & Leanza (1957).

*Tropidium:* A concentric ridge on the brim of the cephalon not coinciding in position with the edge of the doublure and therefore different from the paradoublural line (q.v.).

*Truncate front of cranidium:* See under *Auritama* and *Griphasaphus*.

*Turret eyes and stalked eyes:* The term 'turret eyes' as particularly applied in the description of *Dipyrgotes novella* gen.nov., sp.nov. refers to damesellid eyes on lofty summits with the test sloping evenly, adaxially, rearward and forward, from the palpebral lobe; only in isolated free cheeks (pl. 49, figs 2 and 3) can a stalked condition

be seen. Stalked eyes (pedunculate eyes, prop eyes) have cylindrical stalks rising above a wider base. Such eyes are fairly common in post-Cambrian trilobites (Asaphidae, *Cybele*, lichids, odontopleurids), but rare in the Cambrian. Stalked eyes are present in *Meringaspis* (Text-fig. 120) and in *Palaeadotes italops*.

*Varicose caecal veins*: Pathological, but not lethal, varicosity of pygidial caecal veins occurs in a pygidium of *Glyptagnostus stolidotus* (q.v.); the fact of abnormal and unilateral varicosity is independent evidence that the rugae represent hollow ducts (Öpik, 1961).

*Vestigial sutures*: Fused, non-functional sutures occur in *Henadoparia integra* (q.v.).

*Vincular pits and sockets*: A vincular function is attributed to ventral pits at the genal angles of the Rhyssometopidae (Text-fig. 95). Vincular sockets (but no vincular furrow) are well developed in the cranial front and in the doublure of the free cheeks of *Stephanocare richthofeni* (q.v.). The vincular sockets of its cranial front are similar to the reconstruction of *Pliomera fisheri* in Harrington et al. (1959, p. 0439).

*Zonate pygidium* (agnostids): In the zonate agnostid pygidium in the rear (between the marginal spines) the rim is duplicated by the pygidial collar—a ridge on the rim or even a fold of the margin of the acrolobe; in the Diplagnostinae, Tomagnostinae, and *Triadaspis* the pygidial collar is continuous; in *Oidalagnostus* and *Aspidagnostus* it is divided by a median gap. See also under 'simplimarginate pygidium'.

# MIOMERID TRILOBITES

## SUPRAGENERIC CLASSIFICATION OF AGNOSTIDS

The fourteen new genera of agnostids here described together with the previously established (Öpik, 1963) *Agnostardis* and *Agnostotes* belong to more than one subfamily of the Agnostacea. The suprageneric classification of these forms can be presented best in the frame of the whole system of agnostids; and the frame in its turn, receiving a substantial influx of new genera, readjusts itself to meet the demand.

The readjustment of the frame has a retroactive effect: in the classification of Öpik (1961, p. 54-55), which involves only a minor part of the system, (a) the familial rank of the Quadragnostidae is changed to the subfamilial Quadragnostinae, and (b) the name Ptychagnostinae replaces the name Glyptagnostinae; and in the classification of Öpik (1963, p. 34) the subfamily Ptychagnostinae, excluded from the Glyptagnostinae, takes its place in the family Agnostidae. This is in agreement with the alternative classification I (op. cit., p. 35). Furthermore, alternative II (ibid.) visualizing a single family, with a new familial concept to cover the diplagnostids, pseudagnostids, and glyptagnostids, is presented in the new classification under the heading of Diplagnostidae.

### *The Adopted Classification of Agnostids:*

Order Miomera Jaekel, 1909

Suborder Agnostina Salter

Superfamily Agnostacea M'Coy

Group A: Small families unrelated to each other, and to the rest:

Family: Trinodidae, Condylopygidae, Discagnostidae, Phalacromidae, Sphaeragnostidae.

Familiae incertae:

*Homagnostoides*

*Blystagnostus*

Group B: Prolific families interrelated with each other:

Family: Agnostidae

Subfamilies: Agnostinae, Quadragnostinae, Ptychagnostinae.

Family: Clavagnostidae

Subfamilies: Clavagnostinae, Aspidagnostinae

Family: Diplagnostidae

Subfamilies: Diplagnostinae, Oidalagnostinae, Tomagnostinae, Glyptagnostinae, Ammagnostinae, Pseudagnostinae.

The distribution of genera among the families is shown in the 'Tabular Classification of Agnostids' (Table 5), which also serves as a guide to the concept of, and interrelation between, the families. The 'Tabular Classification' is discussed at the end of this chapter; it is based on morphological criteria hitherto not considered in systems of agnostids, which are based on the 'classical and traditional set of morphological criteria', presented on the next pages.

### *Brief History of Agnostid Classification:*

The first steps in the problem of a suprageneric classification of agnostids were taken by Jaekel (1909); Raymond (1913) followed suit by replacing Jaekel's irregular nomenclature with formal names. Then, the problem was shelved until Howell (1935-1937) established a number of new families and subfamilies to accommodate the already known, as well as his own new, genera. In the same years Whitehouse (1936) contributed substantially with new concepts and new taxa.

The whole matter of agnostid classification was exhaustively treated by Kobayashi (1939), who revised the existing concepts and nomenclature and amplified the number of taxa once again. Kobayashi's classification is in current use and his monograph remains the main handbook of agnostology. Kobayashi's classification is commendable for the sober application of a small number of family taxa and the preference given to the flexible subfamilial nomenclature. The merits of this, and the disadvantage of an overall family nomenclature employed by Howell (in Harrington et al., 1959) in his latest classification, have been already discussed by Öpik (1963, p. 33).

Recently, however, Kobayashi (1962) departed considerably from his earlier classification and replaced families by superfamilies, raised the Geragnostinae also to a superfamily, and the rest of the subfamilies to independent families. The distribution of genera, however, remained essentially the same as it was in the 1939 classification. A taxonomy oversaturated by nomenclature evolved since Howell initiated the modern study of agnostids; at the same time little was added to the knowledge of agnostid morphology, which is essentially to the credit of Tullberg (1882) and Jaekel.

### *The Classical and Traditional Criteria*

The morphological criteria thus established are classical, traditional, in the specific and generic taxonomy of agnostids. The interpretation of the significance of these criteria and their combinations is subjective, of course, and so is the question of the validity and invalidity of a number of supraspecific taxa. Objective, however, are the determinative keys reflecting the distribution of the morphological characters within the multitude of agnostids. For example, the statement that the preglabellar median furrow is absent in certain agnostids is a fact; but the conclusion would be subjective that all such agnostids are congeneric, or affiliated with each other closer than with the rest.

The classical and traditional set of morphological criteria employed in the systematics of agnostids refers, in brief, to the following items:

A. *Whole exoskeleton.* (1) shape of the shields; (2) presence or absence of borders and size of the border; (3) external ornament visible without whitening. The ornament of agnostids is relatively simple: smooth test prevails; punctate tests occur sporadically (see *Pseudagnostus sericatus* sp.nov.), and granulosity is common among the Ptychagnostinae en grande tenue; rough surfaces occur also in some Pseudagnostinae and in *Trinodus*. Lineate ornaments (apart from *Pseudagnostus araneovelatus* Shaw) are, how-

ever, unknown. Rugosity and scrobiculation reflecting the viscera of the pleural lobes cannot be regarded as 'ornament' (see prosopon, in Öpik, 1961a).

B. *Cephalon*. (4) Subdivision of the glabella; (5) presence or absence of the transverse glabellar furrow; (6) presence or absence, or fading, of the preglabellar median furrow; (7) shape of the glabellar front; (8) structure of the anterior glabellar lobe—sulcate, bilobed, or entire; (9) structure of the basal lobes; (10) position of the median glabellar node.

C. *Pygidium*. (11) Shape and length of the pygidial axial lobe; (12) relative width of pleural lobes; (13) shape of the posterior axial lobe; (14) presence or absence of the postaxial median furrow; (15) number of axial nodes; (16) number of annulations in the anterior part of the axial lobe, and their longitudinal subdivision; (17) shape and length of the median axial node; (18) presence or absence of the marginal spines, including trispinosity.

D. *Emphasis*. (19) Effacement of furrows and lobes in various degrees, and various parts, and overall, or selective as regards the shields; (20) increased emphasis in forms en grande tenue—e.g. depth of furrows, tumidity of lobes, length of spines.

E. *Proportions*. (21) Relative size of parts of the glabella and pygidial axis, and of the axial and pleural lobes.

The number of diagnostic characters referable to these criteria is, of course, much larger; some 130 single characters, for example, have been used in describing the many species of *Pseudagnostus* (Öpik, 1963, p. 49).

As regards genera, only few are based on unique characters, as for example, *Pleuroctenium* and *Pseudagnostus*; most refer to diverse combinations of characters, and the family taxa are defined in the same combinative manner.

The combinative nature of most of the taxa leads to the conclusion that all agnostids within their suborder are relatively close to each other, constituting a single superfamily, the Agnostacea, with a restricted number of interrelated families. Hence, the discontinuities are mild and alternative suprageneric classifications are reasonable and even optional taxa have been suggested (Öpik, 1963, p. 34) in systems based on the classical and traditional set of morphological criteria in agnostid taxonomy.

## THE TABULAR CLASSIFICATION OF AGNOSTIDS

### *Significance of Classificatory Criteria*

Agnostids are lower Palaeozoic arthropods extinct well before the end of the Ordovician Period. Their exoskeletons only can be studied; even their appendages are unknown, and a conclusive comparison with other extinct or living arthropods remains unattainable. Palaeontological intelligence in interpreting the anatomy of agnostids relies therefore on structures and markings which are reflected in the tests, and aims with these deficient means at arranging the multitude of the taxa in a coherent system.

TABULAR CLASSIFICATION OF AGNOSTIDS

| I   | ACROLOBES UNCONSTRICTED        |  |                         | ACROLOBES CONSTRICTED  |  |   | ACROLOBES UNCONSTRICTED      |  |                                |                 |   |   |   |   |             |            |  |                  | ACROLOBES CONSTRICTED  |                                    |  |  |
|-----|--------------------------------|--|-------------------------|--|--|---|------------------------------|--|--------------------------------|-----------------|---|---|---|---|-------------|------------|--|------------------|--|------------------------------------|--|--|
| II  | MODIFIED AXIOLOBATE (B)        |  |                         | DEUTEROLOBATE  | AXIOLOBATE AND MODIFIED AXIOLOBATE (A)       |   |                              |  |                                |                 | AXIOLOBATE  |   |   |   |             |            | MODIFIED AXIOLOBATE (B)                      |                  |  | DEUTEROLOBATE                      |  |  |
| III | SIMPLIMARGINATE                |  |                         |  |  |   | ZONATE                       |  |                                | SIMPLIMARGINATE |   |   |   |   |             |            |  |                  |  |                                    |  |  |
| IV  | GLABELLAR REAR ANGULATE        | GLABELLAR REAR ROUNDED                       | GLABELLAR REAR ANGULATE | GLABELLAR REAR ROUNDED   | GLABELLAR REAR ANGULATE                      |   |                              | GLABELLAR REAR                               |                                |                 |   |   |   | GLABELLAR REAR ANGULATE   |             |            |  |                  |  |                                    |  |  |
|     | 1                              | 2  | 3                       | 4  | 5  | 6   | 7                            | 8  | 9                              | 10              | 11  | 12  | 13  | 14  | 15          | 16         | 17   | 18               | 19   |                                    |  |  |
|     | DIPLAGNOSTIDAE                 |  |                         |  |  |   |                              |  |                                | AGNOSTIDAE      |   |   |   |   |             |            |  |                  | DIPLAGNOSTIDAE   |                                    |  |  |
|     | GLYPTAGNOSTINAE                |  |                         | PSEUDAGNOSTINAE  |  | AMMAGNOSTINAE   |                              | DIPLAGNOSTINAE                               |                                |                 | QUADRAGNOSTINAE   |   | PTYCHAGNOSTINAE   |   | AGNOSTINAE  |            |  | GLYPTAGNOSTINAE  |  | PSEUDAGNOSTINAE                    |  |  |
|     | Corrugatagnostus               | Glyptagnostus<br>Lispagnostus<br>Agnostardis | Agnostotes              | Pseudagnostus<br>Litagnostus<br>Ciceragnostus barlowi<br>Rhaptagnostus<br>Plethagnostus<br>Pseudorhaptagnostus<br>Euplethagnostus<br>Sulcatagnostus<br>Pseudagnostina<br>Oxyagnostus<br>Xestagnostus | Agnostoglossa<br>Ammagnostus<br>Kormagnostus | Connagnostus venerabilis<br>Dolichoagnostus<br>Oidagnostus ? dubius | Connagnostus zonatus         | Linguagnostus<br>Baltagnostus<br>Oedorhachis | OIDALAGNOSTINAE<br>Oidagnostus |                 | Archaeagnostus<br>Eoagnostus<br>Mesopheniscus<br>Peronopsis<br>Diplorrhina<br>Acadagnostus<br>Armagnostus<br>Quadragagnostus<br>Hypagnostus<br>Spinagnostus<br>Cyclopagnostus<br>Cotalagnostus<br>Peratagnostus<br>Pseudoperonopsis<br>Euagnostus<br>Grandagnostus<br>Skryjagnostus<br>Phalagnostus<br>Phoidagnostus bituberculatus<br>"Ciceragnostus" cicer<br>Pseudophalacroma<br>Phalacromina<br>Pseudophalacroma dubium | Pentagnostus<br>Leiopyge<br>Phoidagnostus<br>Triplagnostus<br>Ptychagnostus<br>Doryagnostus<br>Goniagnostus<br>Goniagnostus fumicola<br>Ptychagnostus ? serus<br>Tomagnostella<br>Agnostogonus<br>Delagnostus | Agnostus<br>Innitagnostus<br>Idolagnostus<br>Proagnostus<br>Homagnostus<br>Geragnostus<br>Micragnostus<br>Anglagnostus<br>Hadragnostus<br>Eurudagnostus<br>Rudagnostus<br>Hastagnostus<br>Pseudoperonopsis suninoi<br>Neoagnostus<br>Hyperagnostus<br>Agnostus<br>Homagnostus<br>Acmarhachis<br>Cyclagnostus<br>Geragnostella<br>Trilobagnostus | Agnostus pisiformis<br>Homagnostus sp. indet. Shaw<br>Cyclagnostus quasivespa | Lotagnostus | Agnostates | Glyptagnostus<br>Lispagnostus<br>Agnostardis | Corrugatagnostus | Pseudagnostus<br>Litagnostus<br>Ciceragnostus barlowi<br>Rhaptagnostus<br>Plethagnostus<br>Pseudorhaptagnostus<br>Euplethagnostus<br>Sulcatagnostus<br>Pseudagnostina<br>Oxyagnostus<br>Xestagnostus |                                    |  |  |
|     | CLAVAGNOSTIDAE                 |  |                         |  |  |   |                              |  |                                |                 |   |   |   |   |             |            |  |                  |  |                                    |  |  |
|     | PYGIDIUM RUGOSE (SCROBICULATE) |  |                         | PYGIDIUM SMOOTH  |  |   | SMOOTH and SCROBICULATE      | PYGIDIUM SMOOTH                              |                                |                 |   |   |   | PYGIDIUM RUGOSE (SCROBICULATE)  |             |            |  |                  |  |                                    |  |  |
|     | BORDER NARROW                  |  |                         | BORDER WIDE  |  |   | BORDER WIDE NARROW           | BORDER NARROW                                |                                |                 | BORDER WIDE   |   |   | BORDER NARROW   |             |            |  |                  |  | BORDER WIDE                        |  |  |
|     | ? ARTICULATING DEVICE          |  |                         | GLYPTAGNOSTOID   |  |   | GLYPTAGNOSTOID AND AGNOSTOID | A. D. AGNOSTOID                              |                                |                 | ARTICULATING DEVICE BASIC   |   |   | A. D. AGNOSTOID   |             |            | A. D. BASIC                                  |                  |  | ARTICULATING DEVICE GLYPTAGNOSTOID |  |  |

In systematics, authors are faced with the problem of appraising the significance of morphological characters in terms of their category values: the question of what is 'generic' in characters of a species is ever-recurring. Expressions like 'minute', 'minor', and 'major' characters are popular; such appraisals may mean only that some characters are not visible immediately and others are obvious at a glance or visible even in poorly preserved material.

Characters as such, however, can be classified regarding their category values by elimination. Characters common to an aggregate of taxa are discriminated from characters peculiar to each ingredient taxon of the given aggregate and from such characters as are common to an aggregate of a larger number of taxa. Hence, the qualifications 'significant' and 'insignificant' have only a relative meaning: characters of taxa in a higher category are insignificant as regards the same taxa in a rank below and vice versa. Significant, however, are such characters as are peculiar to a particular taxon, defining it diagnostically and indicating its category. For example, the significant characters of the taxon Agnostacea are common to every one of the species of that superfamily, but are diagnostically insignificant, and of no category value, below that rank.

For the purpose of the present suprageneric classification it is assumed that the characters of the hitherto discovered species are known, and that the generic names refer to the characters regarded as significant generically; it is also reasonable to assume that the validity and invalidity of some of the genera is a matter of subjective judgement.

Hence, the 'Tabular Classification of Agnostids' contains all names of genera attributable to the group B (Prolific families interrelated with each other), including most of the subjective synonyms as well; it is even unnecessary to indicate in the table the mutual synonyms. Several doubtful forms (e.g. *Girvanagnostus*, *Gallagnostus*) remained, however, unplaced but are mentioned in the comment on selected genera.

Summing up (1) the superfamily Agnostacea is the superfamily of known species of agnostids; (2) the agnostid species are aggregated according to their morphological characters and inferred affiliations into genera and families (or subfamilies) of species; (3) the nomenclature is already saturated and can be amplified only as regards new discoveries.

The reclassification here presented deals with the arrangement of genera and suprageneric taxa and with the category ranks of the family aggregates by means of morphological criteria not considered hitherto in the literature.

### *The Criteria*

A survey of published illustrations and descriptions, and of specimens of agnostids in hand and in overseas collections, resulted in the selection of seven independent morphological criteria suitable for classifying the Agnostacea into suprageneric taxa. These criteria are indicated in the Table with the Roman numerals I-VII. The word 'criteria' refers here to morphological features variable in structure, and the structural variants are thought of as 'characters'. This terminology, of course, has only a relative meaning and depends on the rank of the taxonomic

categories. So a family character may serve as a criterion, and its variants as characters in discriminating genera within a family. In compiling the 'Tabular classification' the characters provided by the criteria I-IV were used in the first place, in complete disregard of criteria V-VII; these were kept 'in reserve' to check the first results. The reserve criteria, however, introduced no substantial change in the classification, except for the need to isolate the Agnostinae with scrobiculate pygidia (columns 14, 15) from the rest (see Criterion V below).

Of course, more than seven criteria are available; criterion VIII could be, for example, the relative position of the median glabellar node: in the Pseudagnostinae it is placed in the anterior part of the rear glabellar lobe, but in the rest its position is variable, sometimes even within a genus. The criteria that are discussed below are diagnostically meaningful, especially in combinations, and some may serve, if required, in establishing taxa of such optional categories as, for example, 'sections', 'tribes', or 'clans'. So, no special compartment is allotted in the Table to the number of annulations in the anterior part of the pygidial axial lobe. In the Agnostidae, in all species except those of *Lotagnostus* two annulations are present. In *Lotagnostus* three annulations are discernible, but the third is shorter than the rest. In the Diplagnostidae (including the Clavagnostidae) three annulations are, however, common. A short third annulation is seen in *Xestagnostus* and *Ammagnostus*, and sporadically in *Pseudagnostus*, and three well developed annulations are inherent to *Oidagnostus*, *Triadaspis*, *Aspidagnostus*, *Glyptagnostus*, and *Machairagnostus*. In *Clavagnostus* the three axial annulations are obscured by effacement of the transverse furrows.

Furthermore, in the Condylropygidae the anterior part of the axis is also trilobate.

The number of segments in agnostids is variable, but owing to the scarcity of reliable information it cannot be applied in an overall classification. The cephalon contains five and the thorax two segments—these numbers are fixed. In the pygidium, however, five to eleven segments have been observed. The anterior part of the pygidial axis consists of two or three segments (annulations); the number of pairs of notulae in the posterior pygidial lobe is as follows: in the Quadragnostinae it is four or five pairs; in *Ptychagnostus punctuosus* five pairs; in the Agnostinae *Cyclagnostus* has six and *Idolagnostus* apparently eight pairs; *Glyptagnostus* has five pairs; *Ammagnostus* seven pairs; *Xestagnostus* seven; and in *Pseudagnostus* seven, and rarely nine pairs of notulae are present in the posterior axial lobe of the pygidium. Finally, in an unpublished Australian species of the Ptychagnostinae the pygidial axis contains only five segments. These numbers are meaningful assuming that the pairs of notulae or of muscle scars represent one segment each.

The presence or absence of the preglabellar furrow (=divided or confluent cheeks) may be used to divide the agnostids into two groups; but when applied in this manner it would have the consequence of displacing affiliated species and genera in a most inappropriate manner. This example illustrates the over-estimation of the rank significance of some characters. Other examples of such over-estimated significance refer to the incidence of effacement, shape of the shields, presence or absence of pygidial spines, of the transverse glabellar furrow (the clavagnostids excepted), length of the posterior pygidial axial lobe, and so forth. These criteria,

each taken alone, are of specific, and, combined, may be of generic significance. The number of known as well as of possible combinations, however, cannot be very large, because mutually exclusive characters cannot be combined and because not every kind of cephalon combines with every 'associated' pygidium, as seen in the example of *Aspidagnostus*.

### *The Seven Criteria Explained*

*Criterion I.* The shape of the acrolobes. Acrolobes (Text-fig. 15) are the tumid parts of the agnostid shields enclosed by the border. Two characters excluding each other are evident: (1) constriction of the acrolobes in the middle (the flanks are concave) and (2) unconstricted convex or almost straight flanks. The constriction is well expressed in the Pseudagnostinae, especially in the Mindyallan and Idamean; in some later species of *Pseudagnostus*, however, it may become obscure, or even disappear. In *Ammagnostus* only the pygidia are constricted, and the flanks of the cephalic acrolobes are convex. *Connagnostus zonatus* has constricted acrolobes and is, perhaps, the only constricted form among the zonate Diplagnostinae. Completely out of place is *Pseudophalacroma dubium* (Öpik, 1961, p. 94), which by all other characters belongs to the Agnostidae; the constriction in its pygidium is, however, almost imperceptible. With this exception, all Agnostidae have the acrolobes not constricted, and share this character with the Glyptagnostinae. To conclude, acrolobes are constricted in the Pseudagnostinae, in the Ammagnostinae, and occasionally in the Diplagnostinae. Unconstricted are the Clavagnostidae, the Agnostidae, and the Glyptagnostinae. Consequently, criterion I alone provides for no absolute subdivision of the Agnostacea. It is to be noted that the incidence of constricted acrolobes is confined to the Upper Cambrian Diplagnostidae and the Middle Cambrian Condylopygidae (the group of the 'small families').

*Criterion II.* The structure of the pygidial axis, and particularly of the posterior axial lobe. The characters are (1) axiolobate, (2) modified axiolobate (A), (3) modified axiolobate (B), and (4) deuterolobate structures.

(1) The term 'axiolobate' means that the pygidial axial lobe is the unmodified axial lobe of a trilobite defined by the axial furrows;

(2) 'Modified axiolobate (A)' refers to structures of the axial lobe retaining the apical position of the terminal node, but imitating a deuterolobe (in *Oidalagnostus*), attenuated or drawn out into an ogive (in *Aspidagnostus*) or shortened (in *Linguagnostus*).

(3) 'Modified axiolobate (B)' indicates a forward position of the terminal node (in *Ammagnostus*), as well as invasion of the postaxial median line by a caecum (in *Glyptagnostus*, *Agnostardis*).

The axiolobate (unmodified) structure of the pygidial axial lobe dominates in the Agnostidae; in *Goniagnostus*, however, the pygidial axial rear is modified (*Goniagnostus fumicola* Öpik, 1961, p. 77; 81-83) to some extent; it is probably the result of the process of the accentuation of relief (ibid., p. 76) rather than of a reorganization of the visceral anatomy. Hence, no suprageneric significance is attributed to modifications of this kind.

Modified axiolobate (A) and (B) structures are generally inherent to the Diplagnostidae; but within the Diplagnostinae several forms remain axiolobate (unmodified), as for example *Baltagnostus*, *Oedorhachis*, *Dolichoagnostus*, and *Oidalagnostus? dubius*. *Connagnostus*, however, apparently imitates a deuterolobe and is in this respect similar to *Oidalagnostus*.

(4) The deuterolobate structure has been discussed in detail previously (Öpik, 1963) and once more under *Pseudagnostus ampullatus* sp.nov. and *Xestagnostus legirupa*, gen.nov. et sp.nov., and a recapitulation can be omitted. It is a special case of modification in the structure of the axial lobe. The presence of the deuterolobe in *Pseudagnostina* Palmer and *Oxyagnostus* gen.nov. is morphologically not evident but quite probable in view of their similarity with *Pseudagnostus* in all other aspects. No evidence of the incidence of a deuterolobe exists in the Agnostidae; but the obese posterior pygidial axial lobe of some of the Agnostinae has been occasionally described in the literature as a 'pseudolobe'.

*Criterion III.* The structure of the posterior pygidial border, which may be simplimarginate or zonate.

(1) Simplimarginate are agnostids with a uniform structure of the pygidial border, consisting, when fully developed, of a rim and a marginal furrow. Most of the Agnostacea are simplimarginate.

(2) Zonate are agnostid pygidia in which the border is simple in the flanks, but double in the rear (between the marginal spines). A ridge ('collar') is spanned between the spines and is formed by a fold in the posterior margin of the acrolobe or even along the rim itself. Its anatomical meaning is unknown. The collar is present only in the Diplagnostinae, Tomagnostinae, and Clavagnostinae, but not in all of them. It is absent in *Clavagnostus*, *Dolichoagnostus*, *Oidalagnostus? dubius*, and *Connagnostus venerabilis*, but present in *Connagnostus zonatus*; *Tomagnostus fissus* is simplimarginate (and without marginal spines), but *T. perrugatus* is mostly, but apparently not always, zonate. *Triadaspis*, *Oidalagnostus*, and *Aspidagnostus* are zonate, and the collar is divided by a gap in the two last-mentioned forms.

A ridge is also present on the rim of the pygidial rear in *Peronopsis fallax* (Westergaard, 1946, pl. 2, figs 18-24) and its subspecies, but not along the margin of the acrolobe as seen in *Diplagnostus*. Externally similar, but different in position, the collar of *Diplagnostus* and the ridge of *Peronopsis* may be homologous; this remains, however, inconclusive, and so does the possible derivation of *Diplagnostus* from an early peronopsid.

To sum up, the zonate structure of the pygidial border is confined to the Diplagnostidae, but it cannot be taken as a recognition character of the whole family because it is present in two and absent in three subfamilies.

*Criterion IV.* The shape of the glabellar rear. Two characters are considered: (1) angulate, and (2) rounded.

These terms are self-explanatory. The angulate rear occurs only within the Diplagnostidae, but not in all of them; it is rounded in *Tomagnostus*, in the Ammagnostinae and Glyptagnostinae; in *Diplagnostus* it is angulate in some species and

rounded in others, as for example in *Diplagnostus crassus*. Forms with a broad, almost truncate glabellar rear (*Lispagnostus*, *Glyptagnostus*, and *Diplagnostus crassus* sp.nov.) belong to the 'rounded' group.

Among the Diplagnostidae the angulate glabellar rear is most prominent in the Pseudagnostinae. In the Agnostidae the glabellar rear is rounded; forms with an angulate glabellar rear which have hitherto been included in the Agnostidae (*Agnostus caduceus* Barrande) should be revised as regards their familial classification.

*Criterion V.* Scrobiculate (rugose) pleural lobes. All agnostids (Öpik, 1961a) have ramified cephalic caeca, which, however, are not always reflected externally by rugae or scrobicules. Among agnostids with strongly developed cephalic caeca some have also rugose scrobiculate pygidial lobes, and in others these lobes are smooth; furthermore in forms with both shields rugose the degree of expression of the rugae and scrobicules is about the same in the pleural lobes of both shields. Consequently, in forms combining rugose cephalic caeca with smooth pygidia the pygidia have no ramified caeca. Hence, criterion V allows for two characters: (1) smooth pygidia without ramified caeca, and (2) rugose pygidia with ramified glands. The first character (smooth pygidia) remains inconclusive because most of the Agnostidae have not yet been scrutinized for vestiges of pygidial rugae; all known Ptychagnostinae have smooth pygidia—by contrast with the often strongly rugose cephalic caeca.

The second character (rugose or scrobiculate pygidial pleural lobes), however, is certainly conclusive.

Rugose pygidia are observed in the Diplagnostidae (*Oidalagnostus*), Clavagnostidae (*Aspidagnostus*), in Pseudagnostinae, Glyptagnostinae, and in *Corrugatagnostus*, and are probable in *Ammagnostus*. *Lispagnostus* is a glyptagnostid with smooth (not rugose) cheeks and its pygidium is unknown; but its close similarity with *Glyptagnostus* indicates that it should have deep-seated glands that are not reflected externally. There is no subfamily within the Diplagnostidae without forms having rugose pygidia, and in two subfamilies (Glyptagnostinae and Pseudagnostinae) rugose pygidia are dominant.

To sum up, the Diplagnostidae are characterized by a high frequency of forms with visibly rugose pygidia; an estimated 60-70 percent of its species are known to belong to this group.

In the family Agnostidae rugose pygidia have not yet been observed among the Quadragnostinae and Ptychagnostinae; but in the Agnostinae rugose pygidia are known in four forms (Table 5, columns 14 and 15): *Agnostus pisiformis*; *Homagnostus* sp.indet. Shaw, 1951; *Cyclagnostus quasivespa* sp.nov.; and *Lotagnostus*.

*Agnostus pisiformis* (in Henningsmoen, 1958) may have in some specimens minutely scrobiculate pygidial pleural lobes. The possibility of absence of major caecal trunks and bifurcations has been already discussed (Öpik, 1963, p. 35).

The *Homagnostus* of Shaw (1951, p. 110), has a large number of primary rugae and is comparable in that respect with *Lotagnostus*.

*Cyclagnostus quasivespa* sp.nov. (Text-fig. 28) has a faintly visible but regular system of pygidial glands and recalls *Glyptagnostus*. In passing, the cephalons of *C. quasivespa* and of the glyptagnostid *Agnostardis amplinatis* are similar in design and differ only in few and inconspicuous characters. Nevertheless these three

forms are retained in the subfamily Agnostinae, not only because *Agnostus pisiformis* gives its name to the subfamily, but also on general morphological considerations.

*Lotagnostus* (discussed in Öpik, 1963), however, is placed tentatively, but not conclusively, in the Agnostinae; it is probably affiliated with *Agnostotes*, which in its turn shares characters with *Glyptagnostus* and *Pseudagnostus*.

Summing up, in the Agnostidae a small minority of species have rugose pygidial pleural lobes; these forms provide one of the links between the Glyptagnostinae (Diplagnostidae) and the Agnostinae (Agnostidae) which confirm the interrelationship of these families. A similar interrelationship is discussed below (Criterion VI).

*Criterion VI:* The size (width) of the border.

For the purpose of this discussion (Text-fig. 15) the border, when fully developed, consists of the rim and the marginal furrow. Some twenty structural characters of the border (for example rim convex, flat, wide, narrow, etc.) and their combinations have been exploited in specific, generic, and familial categories of taxa; of these only two characters, (1) wide border and (2) narrow border, are employed in the 'Tabular classification'.

Some of the characters of the border are quite reliable. For example, the Ptychagnostinae possess a distinctive narrow and relatively flat border. Furthermore, the border is a rather unstable feature: hypertrophic (especially in pygidia), diminutive, obsolete in both or in one of the shields, it provides for generic and specific characters in a number of effaced forms.

The meaning of what is a wide and what a narrow border should be examined statistically; but not enough measurements (preferably of all satisfactorily preserved species) are available; so the characters are based on estimated size in relation to the size of the acrolobes, or shields.

Narrow and wide bordered forms are present in the Diplagnostidae, as well as in the Agnostidae; in the Agnostidae, the Quadragnostinae have wide borders and recall the Diplagnostinae, Pseudagnostinae, and Ammagnostinae. The border is narrow in the Agnostinae and the Glyptagnostinae, as well as in *Lotagnostus*—one feature more (beside the rugose pygidia) to suggest their affiliation as discussed under criterion V.

*Ammagnostus* is peculiar with its wide *Pseudagnostus*-like pygidial, and narrow (*Glyptagnostus*- or *Ptychagnostus*-like) cephalic border. This is unusual among forms en grande tenue, but not among the effaced agnostid forms, in which unequal borders are common.

*Criterion VII:* The structure of the pygidial articulating device. The following three types of articulating device are considered as characters: (1) The glyptagnostoid (2) the agnostoid, and (3) the peronopsid, basic device.

(1) The glyptagnostoid device (Öpik, 1961a; 1963) is illustrated here by examples of *Pseudagnostus*. It is inherent to the Glyptagnostinae and Pseudagnostinae and occurs also in *Agnostascus* and several others; it is less pronounced in *Diplagnostus* and *Linguagnostus*, which possess a relatively low half-ring. It is, however, absent in the Agnostidae.

(2) The agnostoid device, exemplified by *Cyclagnostus quasivespa* sp.nov. is common to all Agnostinae (*Lotagnostus* excluded). In *Aspidagnostus* (see *A. inquilinus*) the articulating device is a variation of the agnostoid kind.

(3) The basic, or ordinary peronopsid, device is represented here in *Hypagnostus correctus* sp.nov. and *Peratagnostus nobilis* gen.nov. et sp.nov. It prevails among the Quadragnostinae and the Ptychagnostinae and is also present in *Lotagnostus*.

The structure of the articulating device is, however, unknown in many agnostids and cannot be studied sufficiently from published illustrations: hitherto it has been a neglected feature.

Exceptional in its simplicity is the articulating device of *Xestagnostus legirupa* gen.nov. et sp.nov., especially in comparison with *Pseudagnostus*.

Of the criteria discussed, the shapes of the acrollobes and of the border refer to the whole exoskeleton, four criteria to the structure of the pygidium, and only one (the shape of the glabellar rear) to the cephalon. The significance of the characters of the cephalon in the classification of the prolific families is, consequently, small; the cephalon is conservative in its structure and relatively undiversified. It is more diversified in the group of the 'small families'; in the Condylopygidae the anterior glabellar lobe is modified, and in the Trinodidae the glabella is abbreviated as it is in the Clavagnostidae, among the 'prolific families'; the Discagnostidae are also based on cephalic characters.

Familial significance has been attributed in the literature also to the frontal glabellar sulcus and its corollary the bilobation of the frontal glabellar lobe, as seen for example in *Diplagnostus crassus* sp.nov. This structure, variously expressed, is present also in *Glyptagnostus*, *Agnostotes*, in some of the species of *Pseudagnostus*, in *Tomagnostus*, and in the Diplagnostinae; but also in some of the peronopsids and in *Ptychagnostus*. Though externally weak, it reflects a fundamental feature of agnostid anatomy, as indicated in Öpik (1961a).

#### *Temporal Distribution and Phylogeny of Agnostids*

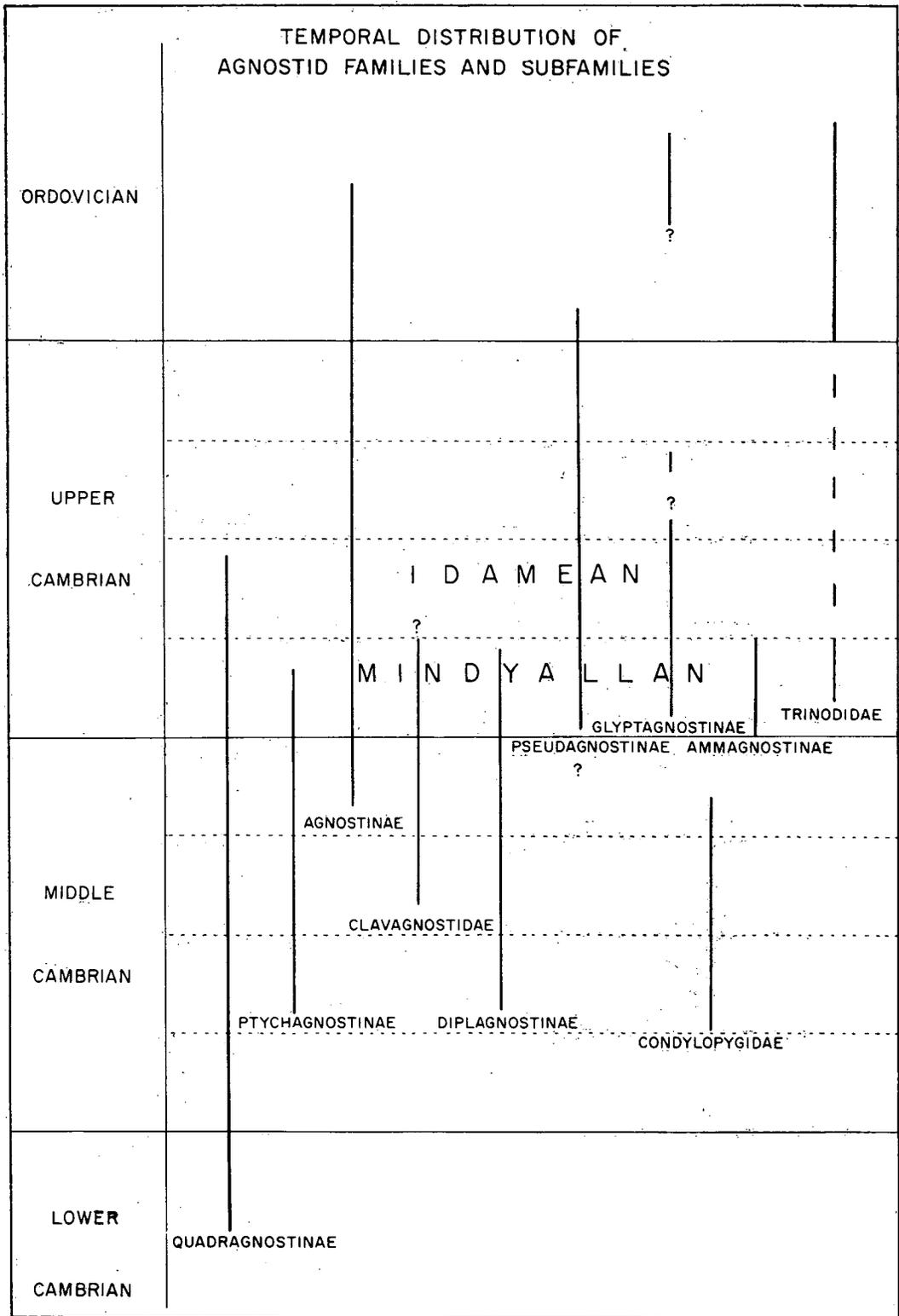
The temporal distribution of agnostid species and genera is known, and has been presented already by Kobayashi (1939) in an illustrated form; some amplifications, of course, should be added.

Table 6, the 'Temporal distribution of agnostid suprageneric divisions', complements the 'Tabular classification', which is constructed on morphological criteria in the first place.

The Clavagnostidae, the Quadragnostinae (with *Peratagnostus nobilis*), and the Ptychagnostinae (with *Goniagnostus nodibundus* and *Ptychagnostus? serus*) have reached well into the Upper Cambrian; these subfamilies were hitherto known only from the Middle Cambrian.

The Agnostinae arose in the Middle Cambrian from the peronopsids, but no definite transitional forms have been recorded as yet. *Agnostus pisiformis* itself is hardly ancestral to the other forms of its subfamily, because these are forms *en grande tenue* as compared with *pisiformis*, which lost earlier the transverse furrows in the pygidial axis—a structure common to all peronopsids.

TEMPORAL DISTRIBUTION OF  
AGNOSTID FAMILIES AND SUBFAMILIES



Bureau of Mineral Resources, Geology and Geophysics. July, 1964.

The Ptychagnostinae, on available evidence, cannot be derived from the known Quadragnostinae; in *Pentagnostus* the deficient preglabellar median furrow reminds one of a peronopsid; but for this very reason *Pentagnostus* cannot be assumed ancestral to the ptychagnostids, neither to the gradually effacing stock (*Triplagnostus-Leiopyge*) nor to the stock en grande tenue whose relief increased with advancing time (see Öpik 1961, p. 76); in this subfamily the preglabellar furrow is a persistent feature.

The Diplagnostidae also are not confined to the Middle Cambrian as assumed previously; on the contrary, the number of genera was greatest in the Mindyallan. It is a fair assumption, as discussed under Criterion III, that *Diplagnostus* arose from a form close to *Peronopsis*. The Clavagnostidae are linked with the Diplagnostinae via *Oidalagnostus-Triadaspis-Aspidagnostus*; but the known record of the clavagnostids and of *Oidalagnostus* is insufficient for grasping the phyletic aspect of the apparently haphazard incidence of simplimarginate and zonate pygidia as well as of the zonate pygidia with the median gap within this group of affiliated forms.

Of the small families only the Condylopygidae and the Trinodidae are included in the table of temporal distribution. The Condylopygidae are unrelated to others as regards the cephalic features, but their wide border, constricted acrolobes, and triannulated pygidial axis may indicate some affiliation with the diplagnostids. Notable is the relative antiquity of the Condylopygidae: in Sweden *Condylopyge regia* pre-dates all other agnostids by a zone. The Trinodidae are shown to indicate their relative antiquity (the Mindyallan *Plurinodus*); hitherto they were known only in the Ordovician.

The agnostids in general attained their maximal diversification in the Mindyallan, followed by a rapid extinction of a number of genera and subfamilies in a faunal crisis which is discussed in the first part of this paper.

The phylogenetic relationship of species within each subfamily is apparent in general terms, but details remain obscure, or disputable, because of the incompleteness of the record. The great mobility and ubiquity of the genera and of many species indicate the necessity of studying the phylogeny and evolution of agnostids in global terms, because local and regional developments are masked by the influx of visitors and departure of endemic forms.

#### *The Structure of the Table 'The Tabular Classification of Agnostids'*

The arrangement of the names of genera in each of the columns follows no particular order, either of affiliation or of temporal sequence; synonyms are more or less close together, and the effaced forms are collected into clusters. The temporal sequence of families and subfamilies is already shown in a separate table and discussed above. No vertical lines between the columns are used, except for the double line separating the Diplagnostidae from the Quadragnostinae; this partition, however, is left open at the top to indicate that the diplagnostids may have arisen from *Peronopsis*-like forms.

Columns 1-4 or 16-19 are repeated on the left and right sides of the Table, but in a different arrangement, so as to demonstrate the tie of the Pseudagnostinae

and the Glyptagnostinae with the Diplagnostinae on the left, and with the Agnostinae on the right side of the Table. In other words, the two-dimensional Table can be transformed into a cylinder with columns 1-4 overlapping columns 16-19.

The columns in the Table can be re-arranged, of course, according to changes in the arrangement of the master criteria and their characters; any rearrangement however, will maintain the Agnostidae as a unit different from the Diplagnostidae, wherever they are placed in the Table or the cylinder.

Brief diagnoses for each column, and groups of columns (subfamilies and families), can be compiled by reading the criteria and characters above and below the columns. Note, in column 8, that criteria V-VII refer to the incidence of characters excluding each other and the position of *Diplagnostus* (which should belong to column 8), whose species can have an angulate or a rounded glabellar rear, as well as a narrow or wide border. Three columns are needed to separate the apparently controversial characters of column 8 from each other.

The condensed form of column 8 is, however, convenient in illustrating in a vertical (here also temporal) sequence the chain of the zonate genera *Diplagnostus-Linguagnostus-Oedorhachis*, followed by the trispinose *Oidalagnostus-Triadaspis-Aspidagnostus*, which are zonate and two of which are provided with a median gap in the pygidial collar.

#### *Comment on Selected Genera and Species*

*Ammagnostus* gen.nov. (column 5) is placed with the axiobate forms; it may belong, however, in the modified axiobate (B) group as indicated by the position of its terminal node. The Ammagnostinae are assumed to have smooth pleural lobes, in the absence of evidence to the contrary; most probably they have deep-seated ramified caeca in the pygidium.

*Machairagnostus* Harrington & Leanza, following the current classification, is placed in column 4 with the Pseudagnostinae because of its accessory pygidial furrows. Its border, however, is narrow, the pygidial axis has three annulations and the glabella reminds one of *Aspidagnostus*; hence, it should be regarded as a genus of the Diplagnostidae incertae subfamiliae or of the Clavagnostidae?

*Peronopsis* Corda, 1847 (column 11). The type species as accepted is *Battus integer* Beyrich, 1845. Snajdr (1956, pl. 3, fig. 2) selected a neotype for this species. *P. integra* is simplimarginate (not zonate), with an evenly convex pygidial border; its cheeks are smooth (not rugose). Kobayashi's (1939) illustration of *P. integra* is that of Barrande; according to Snajdr (op. cit.) it represents *Diplorrhina triplicata* Hawle & Corda (subjective synonym: *Mesopheniscus cuneifer* H. & C.).

*Diplorrhina* itself is based on another species (*sirius* H. & C.) and probably is a synonym of *Peronopsis*. Accepting for the time being the synonymy of *triplicata* and *cuneifer*, *Mesopheniscus cuneifer* is the valid name for the quasi *integra* in Kobayashi's interpretation as well as for the *integra* in Harrington et al. (1959, p. 0185, fig. 126-4). *Mesopheniscus cuneifer* with its angulate glabellar rear and rugose cheeks is a distinctive species generically different from *Peronopsis*. *Peronopsis integra* is co-familial with the Peronopsinae (=Quadragnostinae) but *Mesopheniscus*

*cuneifer* may be a diplagnostid. It is to be noted that the current concept of what is *Peronopsis* is traditionally illustrated not by its type (*Peronopsis integra*) but by another agnostid.

*Pseudoperonopsis* Harrington (column 11) is based on *Peronopsis sallesi* (see Harrington & Leanza, 1957, p. 75), which is related to the group of *P. fallax* (Linnarsson) and possesses a zonate pygidium. Hence, *Pseudoperonopsis* may represent a subgenus, or a subjective synonym of *Peronopsis*; *P. fallax*, of which two syntypes (Westergaard, 1946) and no lectotype are available, differs also from *P. integra* by the ridge (collar) on the posterior pygidial border (it is possibly zonate). *Pseudoperonopsis suninoi* Harrington & Leanza, 1957, 1957 (column 13) may represent a separate genus of the Agnostinae and is not related to the *fallax* group of forms.

*Corrugatagnostus* Kobayashi, 1939 (columns 1 and 18). *Corrugatagnostus* is regarded in the literature as a genus of the Geragnostidae Howell (= Agnostinae in our terms) solely because of its short pygidial axis. Whittard's (1955) material leads to a different interpretation: (1) the pygidium is rugose; (2) converging notular lines mark the end of the rather small posterior axial lobe; (3) in *C. morea* a postaxial bulb is present; (4) the articulating device is glyptagnostoid; and (5) the glabellar rear is angulate. Hence *Corrugatagnostus* belongs to the Glyptagnostinae and is distinguished by the angulate rear, straight rugae, and trilobate glabella. A wide temporal gap separates the Ordovician *Corrugatagnostus* from the early Upper Cambrian *Glyptagnostus*, but this is apparently a gap in the record rather than an indication of a mimetic repetition of glyptagnostoid characters in another, unrelated stock.

*Girvanagnostus* Kobayashi (not included in the 'Tabular classification') may be related to *Corrugatagnostus*, but its classification is still inconclusive. The faint radial lines on its pleural lobes and cheeks are the only justification of a definite generic name. The type (Reed, 1903, pl. 1, figs 2-4) is too incomplete to justify the reconstruction showing the glabellar rear rounded and the genal spines arising from the lateral rim (see Reed's reconstruction in Harrington et al., 1959, p. 0176).

*Ciceragnostus barlowi* (columns 4 and 19) and '*Ciceragnostus*' *cicer* (column 11) are neither congeneric nor co-familial, and quite different in age (see Öpik, 1961, p. 53, 92).

*Agnostascus* gen.nov. (column 6) combines a *Pseudagnostus* cephalon with an axiolobate (not deuterolobate) pygidium. It may belong to a separate diplagnostid subfamily distinct from the Diplagnostinae.

*Diplagnostus* Whitehouse contains species some of which have an angulate and some a rounded glabellar rear, some a narrow and some a wide border; its articulating half-ring is less prominent than in the subsequent Diplagnostidae. In the related *Linguagnostus grönwalli* the pygidial acrolobe is constricted. Consequently, within this group some familial characters are unstable.

*Phoidagnostus* Whitehouse 1936 (column 12) is a ptychagnostid and a synonym of *Leiopyge* (Öpik, 1961, p. 54); '*Phoidagnostus*' *bituberculatus*, however, belongs to the Quadragnostinae. No generic name is available for *bituberculatus* (Angelin); *Phalagnostus* Howell is a possibility, but needs confirmation.

*Pseudophalacroma* Pokrovskaja (column 11) is a genus of the Quadragnostinae; *Pseudophalacroma dubium* (Whitehouse) (Öpik, 1961) is the only species of the Agnostidae having constricted acrolobes; the constriction is, however, almost imperceptible.

*Oidalagnostus? dubius* Westergaard (column 6) is, of course, not an *Oidalagnostus*; it belongs probably to *Dolichoagnostus* Pokrovskaja, but its cephalon is unknown and the generic position remains therefore inconclusive.

*Agnostus pisiformis* (Henningsmoen, 1958), *Homagnostus* sp.indet. Shaw, 1951, and *Cyclagnostus quasivespa* sp.nov. are as yet the only known species of Agnostinae (and Agnostidae) with scrobiculate or rugose pleural lobes of the pygidium. In *A. pisiformis* scrobicules are known only from few specimens; the *Homagnostus* is represented by a unique pygidium; from these examples it would be speculative to conclude that all species of *Agnostus* and *Homagnostus* have pygidial ramified caeca. *Cyclagnostus quasivespa*, however, has rugae in the pygidium. These are even more conspicuous in *Lotagnostus* (column 15); it has already been mentioned that the cephalon of *Cyclagnostus quasivespa* and the glyptagnostid *Agnostardis* (column 17) are very similar indeed, and that *Agnostotes* (column 16) bears similarities with *Lotagnostus*, *Glyptagnostus*, and *Pseudagnostus*. The sequence of forms from left to right (from column 14 to 19) can be interpreted, therefore, as a chain of forms linked together by morphological similarities. The sequence on the left side, and going left from the Pseudagnostinae (column 4), indicates a linkage of the Pseudagnostinae with the Glyptagnostinae via *Agnostotes*.

*Lotagnostus* Whitehouse, 1936 (column 15) has been discussed in some detail by Öpik (1961, p. 53, 54). It has been assigned to the Glyptagnostinae as well as to the Agnostidae; morphologically the nearest family is Agnostidae (Agnostinae).

*Leiagnostus* Jaekel, *Gallagnostus* Howell, and *Gallagnostoides* Kobayashi. These genera and the family Leiagnostidae are not included in the 'Tabular Classification'. They are most probably Agnostidae, but their almost perfectly effaced exoskeletons defy any further interpretation. The family Leiagnostidae Jaekel, 1909, may cause nomenclatural difficulties if *Leiagnostus* is included in a family of a later date.

*Baltagnostus* Lochman 1944 (column 8) is zonate, has an angulate glabellar rear, and is distinguished by its unmodified axiolobate pygidium. It cannot be placed, however, in a column of forms with constricted acrolobes and should have a separate column for itself. *Baltagnostus eurypyx* Robison, 1964, has a rather obscure pygidial collar (Robison, pl. 80, fig. 16).

*Pentagnostus* Lermontova, 1940 (column 12), is listed in the Spinagnostidae (=Quadragnostinae, but without *Spinagnostus*; see Öpik, 1961) in Harrington et al. (1959); it is considered a synonym of *Peronopsis* in Tchernysheva et al. (1960). The *Peronopsis*-like characters of *Pentagnostus* are (1) the incomplete preglabellar median furrow, and (2) the relatively blunt front of the anterior glabellar lobe. The narrow and relatively flat border, the trilobate pygidial axis with transcurrent furrows, and the forward projecting front of the anterior glabellar lobe indicate, however, an affiliation with the Ptychagnostinae. *Pentagnostus* is an early Middle

Cambrian form and reminiscent of *Ptychagnostus* (*Triplagnostus*) *praecurrens* Westergaard, in which the glabellar front is also not quite pointed; furthermore in *P. praecurrens* as in *Pentagnostus* marginal spines are absent.

*Pentagnostus* is common in Australia (Northern Territory) in association with *Xystridura*.

*Euagnostus* Whitehouse, 1936, is monotypic and placed here tentatively in the Quadragnostinae because the holotype of *E. opimus* is an imperfect pygidium which recalls a *Hypagnostus*; the associated cephalon, however, may belong to a species related to *Ptychagnostus convexus* Westergaard or *P. stenorrhachis* Grönwall. It is still not impossible that the holotype pygidium and the cephalon are conspecific.

*Utagnostus* Robinson, 1964, is not included in the Tabular classification. Its angulate glabellar rear, wide border, and trispinosity of the pygidium indicate a genus of the Diplagnostidae.

*Homagnostus* Howell, 1935. *Homagnostus* and *Aagnostus* are rather close to each other. *Homagnostus obesus* has a well developed preglabellar median furrow (Henningsmoen, 1958, pl. 5, figs 13 and 15); in the much younger *H. tumidosus* (Hall & Whitfield) this furrow is obsolete or almost so.

#### *Comparison with Current Classifications*

The current classifications of agnostids are Howell's (in Harrington et al. 1959) and Kobayashi's (1939-1962); the classification of Pokrovskaja in Tchernysheva et al. (1960) is a simplified working version of the two combined.

In our classification the standard nomenclature of the families and subfamilies (except for the new Oidagnostinae and Ammagnostinae) has been employed (see Öpik, 1961, p. 52), because the number of such legitimate names is rather large, and the selection of names is guided by the type genera. The concepts of the suprageneric taxa, however, are new although their headings are the old and valid names.

The re-arrangements of genera and family taxa is briefly outlined below.

The Quadragnostinae (in our classification) include the Cyclopagnostidae, Hypagnostinae, most of the Phalacromidae (except for *Phalacroma*), *Cotalagnostus* ('Leiopyginae'), and Archaeagnostinae; *Spinagnostus* (with a true genal spine) and Spinagnostidae are included, but the family name still stands for reasons given by Öpik (1961).

The Ptychagnostinae include Triplagnostinae and Leiopyginae.

The Agnostinae include Geragnostidae, Micragnostidae, Hastagnostidae; but the Clavagnostidae are regarded as a separate family on even terms with the Diplagnostidae.

The Pseudagnostinae received *Litagnostus* ('Phalacromidae') and *Ciceragnostus*. The Diplagnostidae include Pseudagnostinae and Glyptagnostinae; these names (Whitehouse, 1936) are equal as regards priority; the subjective preference is given here to the Diplagnostidae, which contain *Diplagnostus*, the geologically oldest known genus of the family.

In our classification the number of family taxa has been reduced, and the names of some superfamilies and families are reduced to subfamilies. This change in rank, of course, is a subjective procedure not affecting the legitimate status of the suppressed taxa. But equally subjective is the employment of high ranks saturated with family and subfamily names.

#### *Concepts of Suprageneric Taxa of Agnostids*

The concepts of the suprageneric taxa of agnostids are assembled together below to facilitate their comparison with each other. These are amended, or even new, concepts, based essentially on characters of forms en grande tenue. Effaced forms are deprived of some of the obvious characters and cannot serve therefore in construction of comprehensive concepts. The distribution of the effaced forms among the subfamilies and families, however, is guided by the fundamental concepts serving as keys for the interpretation of vestigial characters.

#### Order Miomera Jaekel, 1909

The suborder Isopygia Gürich, 1907, refers to the taxa of agnostids and eodiscids, but its concept and rank are not identical with the modern concept of the order of the same taxa; furthermore, the older subordinal name Agnostina (in modernized spelling) Salter, 1864, is used in the current literature.

Jaekel (1909) introduced the concept and the name of the order Miomera; this name is also currently used (Whitehouse, 1936; Hupé, 1953; Tchernysheva et al., 1960) and needs no substitutes. Agnostida Kobayashi, 1935, is a junior synonym, but the authorship of the concept of this order remains with Jaekel and cannot be attributed to Kobayashi (see Kobayashi, 1939, p. 73, 74; Harrington et al., 1959, p. 0172).

Admittedly, no rules govern the taxonomic nomenclature above the superfamily rank; hence, neither the creation of new names nor adherence to an already established name is illegal. New names are necessary to denote new concepts or modified forms of existing concepts as well as emphasize a particular aspect of a known ordinal taxon; reasons of this kind, however, are not evident in the case of the agnostids.

#### Suborder Agnostina Salter, 1864

#### Superfamily Agnostacea McCoy, 1849

The superfamily concept coincides with the concept of the suborder.

Agnostacea are trilobites with two segments in the thorax and with the cephalon and pygidium equal in size. The articulation between the cephalon and the thorax hinges only on the pleural fulcra at the geniculation points; there is neither an axial articulating device nor a cephalic articulating doublure. The anterior segment of the thorax is the replica of the cephalic rear, and the posterior the replica of the pygidial front; hence in the agnostid exoskeleton the main tagmatic divisional line is the articulating joint between the two segments of the thorax—resulting in a polarity of the organization. The border fringing the shields consists of a rim and a marginal furrow and surrounds the tumid acrollobes which contain the viscera. The glabella

is completely surrounded by the pleural lobes, which contain ramified caeca. Basal lobes flank the glabellar rear, and the frontal glabellar lobe is isolated by the transverse glabellar furrow—a fused, vestigial intersegmented joint. The pygidial axis consists of a posterior lobe and an anterior part of two or of three annulations. No segmentation is apparent on the pleural lobes of both the shields. The cephalic (genal) spines arise from the fulcral points (geniculation) at the posterior border. The constant number of two segments in the thorax may be regarded as a fixation of the number of metamers; the cephalon is formed of five original segments; the pygidium, however, may contain five to nine and even eleven segments, the total being twelve to eighteen segments. The test is smooth, or granulose, or punctate, but ornamental lines are unknown. The cephalothoracic aperture is unique. Agnostacea are sutureless, blind and eyeless, except for *Discagnostus*, which probably possesses two pairs of lateral eyes.

#### Family Agnostidae McCoy, 1849

Agnostidae are Agnostacea with unconstricted acrolobes, an axiolobate and simplimarginate pygidium, rounded glabellar rear, and no ramified caeca in the pygidium (except for a few Upper Cambrian forms, column 14 and 15 in the 'Tabular Classification').

The subfamily Agnostinae is distinguished by a narrow border, rounded glabellar front, and well annulated anterior part of the pygidial axis. The articulating device is agnostoid.

The subfamily Ptychagnostinae is distinguished by a narrow border with a relatively flat rim, pointed to subangulate glabellar front, pointed pygidial axial lobe, well annulated anterior part of the axis, frequent occurrence of cephalic rugae and granular ornament, occasional occurrence of a frontal sulcus and of a median spine on the second segment of the thorax; the articulating device is basic.

The subfamily Quadragnostinae is distinguished by a wide border, blunt to rounded glabellar front, blunt rear of the pygidial axis, undeveloped annulation of the anterior part of the pygidial axis, and predominance of species with confluent cheeks (or absence of the preglabellar median furrow); the articulating device is basic.

#### Family Diplagnostidae Whitehouse, 1936

Diplagnostidae are Agnostacea with a glyptagnostoid articulating device, frequent occurrence of forms with pygidial rugae, frequent modifications of the pygidial axis, frequent occurrence of three annulations in the anterior part of the pygidial axis and of constricted acrolobes, of zonate posterior margin, angulate glabellar rear, and sulcate or even bilobed anterior glabellar lobe.

Diplagnostidae are a very diversified family of a relatively large number of genera; except for the prolific *Pseudagnostus* the number of species in each genus is relatively small. The subfamilies are based on the combinations of the familial characters; that is, not all these characters occur together in every subfamily.

Diplagnostinae are Diplagnostidae with a zonate pygidium without rugae, angulate or rounded glabellar rear sulcate anterior glabellar lobe and wide border.

As an appendix four forms with a simplimarginate pygidium and constricted acrolobes are included; *Agnostascus* gen.nov., *Connagnostus venerabilis* sp.nov., *Dolichoagnostus* Pokrovskaja, and *Oidalagnostus? dubius* Westergaard. These forms are even more conveniently referred direct to the family rather than to a definite subfamily of the Diplagnostidae.

Oidalagnostinae subf.nov. are Diplagnostidae with a zonate and rugose pygidium, triannulated anterior part of the pygidial axis, and enlarged posterior pygidial lobe. In the known species the pygidial margin is trispinose and the collar has a median gap.

Tomagnostinae Kobayashi are Diplagnostidae with a zonate pygidium without rugae, with a narrow border, a narrow pygidial axis, a rounded glabellar rear, and a sulcate anterior glabellar lobe; the articulating device is basic, of a kind not seen in other diplagnostids. The family classification of the Tomagnostinae, however, allows for several equally inconclusive solutions and represents a problem of phyletics (Öpik, 1963, p. 34).

Ammagnostinae subf.nov. is described separately on p. 137.

Pseudagnostinae Whitehouse are simplimarginate Diplagnostidae with a deutero-lobate and rugose pygidium, wide border, constricted acrolobes, and angulate glabellar rear (for a detailed description see also Öpik, 1963, p. 48-58).

Glyptagnostinae Whitehouse are simplimarginate Diplagnostidae with a narrow border, rugose pygidium, with the median line behind the pygidial axis invaded by a caecum, and a rounded glabellar rear. *Agnostotes* Öpik, 1963, lacks the invading caecum, but in other characters is referable to the Glyptagnostinae.

#### Family Clavagnostidae Howell, 1937

Clavagnostidae are Agnostacea with an abbreviated glabella lacking the transverse glabellar furrow, with a narrow border, long, narrow, and drawn out posterior pygidial lobe, and with three annulations in the anterior part of the pygidial axis.

Clavagnostinae are simplimarginate Clavagnostidae with effaced transverse axial furrows, a smooth (not rugose) pygidium, and rounded as well as angulate glabellar rear.

Aspidagnostinae are zonate Clavagnostidae en grande tenue with well developed transverse pygidial axial furrows, scrobiculate pygidium, and acutely angulate glabellar rear; in the known species the pygidial margin is trispinose. In *Aspidagnostus* the pygidial collar has a median gap.

#### Family Trinodidae Raymond

This family is discussed on p. 170.

#### Family Discagnostidae

See Öpik (1963, p. 54).

#### Family Sphaeragnostidae Kobayashi, 1939

See Kobayashi (1939); Harrington et al. (1959).

### Family Phalacromidae Hawle & Corda, 1847

The family Phalacromidae contains only one genus—*Phalacroma* Hawle & Corda, and a single species, *Ph. bibullatum* (Barrande). It refers to a semi-effaced form with the cephalic axial furrows exposed only in the rear and bypassing, apparently, the basal lobes abaxially (which are obliterated); with a very broad, expanding pygidial axis well defined by axial furrows and reaching the border; the border, relatively narrow in the pygidium, is almost imperceptible in the cephalon.

As employed in the literature the name 'Phalacromidae' refers to effaced agnostids of diverse subfamilies (Pseudagnostinae, Quadragnostinae, Ptychagnostinae, Agnostinae).

### Family Condylropygidae Raymond, 1913

Condylropygidae are Agnostacea with constricted acrolobes, truncate glabellar rear, diminutive basal lobes, expanded anterior glabellar lobe, and triannulated anterior part of the pygidial axis. The expanded anterior lobe of the glabella may be a cephalic 'deuterolobe'.

### Family AGNOSTIDAE McCoy

#### Subfamily QUADRAGNOSTINAE Howell, 1935

#### Genus PERONOPSIS Hawle & Corda, 1847

#### PERONOPSIS aff. FALLAX (Linnarsson)

(Pl. 54, fig. 1)

The pygidium Pl. 57, fig. 1, CPC 5799, in sandstone, is 3.6 mm long. It belongs to a species reminiscent of *Peronopsis fallax* (Linnarsson), but is distinguished from the latter by its relatively wide, almost parallel-sided axis with a rounded rear, and by the absence of the collar-like ridge on the posterior rim.

*Occurrence and Age:* Steamboat Sandstone, locality D95, associated with *Linguagnostus* aff. *kjerulfi* and *Quitacetra arenata* sp.nov. Its age is late Middle Cambrian, the Zone of *Leiopyge laevigata*.

#### Genus HYPAGNOSTUS Jaekel, 1909

The generic characters and the familial classification of *Hypagnostus* have been recently discussed by Öpik (1961).

The subfamily Hypagnostinae Ivshin, 1953, which also includes according to Pokrovskaja (1960) the genera *Eoagnostus* and *Kormagnostus*, is obviously heterogeneous, and its nominate genus *Hypagnostus* is itself polyphyletic, containing forms derived from several lineages of peronopsids.

*Hypagnostus* has been regarded hitherto as a Middle Cambrian genus; this view must be changed, however, because the Australian new species and the species described by Kryskov (1963) are early Upper Cambrian.

HYPAGNOSTUS CORRECTUS sp.nov.

(Pl. 52, figs 1-4; Text-fig. 16)

*Hypagnostus* cf. *brevifrons*, Öpik (1961, p. 47), refers to the specimens described here as *H. correctus* sp.nov.

*Material*: The illustrated material consists of two pygidia and three cephalae.

*Holotype*: The pygidium, Plate 52, fig. 1, CPC 5776, locality G9, is selected holotype; the selection of a cephalon is inappropriate because of its close similarity with *Hypagnostus brevifrons* (Angelin).

*Diagnosis*: *Hypagnostus correctus* sp.nov. is a species with a suboval cephalic margin, a short and oval glabella, a pointed pygidial axis without transverse furrows not reaching the marginal furrow but having a terminal node; it is distinguished by the presence of a small node on the glabellar rear and a well impressed posterior median furrow.

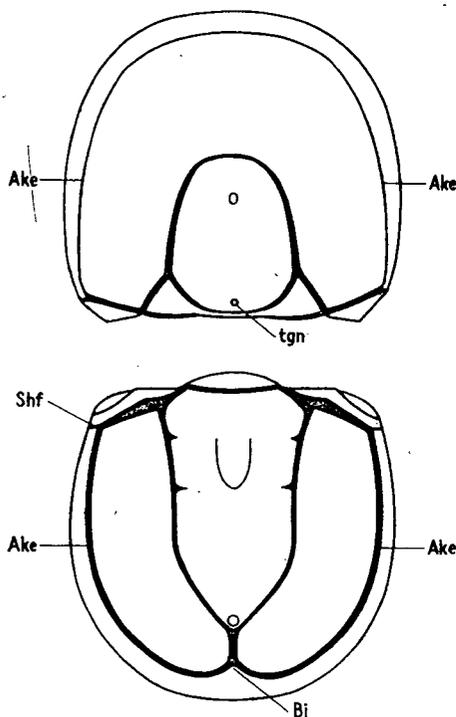


Fig. 16.—*Hypagnostus correctus* sp.nov., diagram from Plate 52, figs 1 and 2a, 2b. Ake—flanks of acrolobes (convex outward); tgn—glabellar rear (rounded), with node; Bi—median salient of pygidial border; Shf—shoulder furrow (crossing rim).

*Differential diagnosis*: The structure of the cephalon, especially the short oval glabella, and the undivided pygidial axis indicate a close affiliation with *H. brevifrons* (Angelin); but in *brevifrons* the pygidial axial lobe is shorter, a postaxial median furrow is absent, and no node is present on the glabellar rear.

*Supplementary description*: The test is smooth and caecal rugae are not apparent; in the cephalon a vestige of the preglabellar median furrow occurs sporadically, and in some specimens (Pl. 52, fig. 3) the anterior glabellar lobe is outlined as a low swelling; this structure is important because it indicates that the anterior part

of the stomach is not reduced, as seen also in *H. parvifrons* (Westergaard, 1946, pl. 4, fig. 31). The posterior glabellar lobe is half the cephalon in length, but variable within small limits. The median glabellar node is placed well forward, as seen also in *H. brevifrons*.

In the pygidium the axis is 0.7 the shield's length, pointed, constricted at the median node; its anterior transverse furrows are obsolete. In the rear the rim invades the flaring tip of the postaxial median furrow. The rim is flat and slopes outward, and the junction of the marginal and shoulder furrows is angulate. The fulcral points are close to the axis and the facets are slightly concave. The articulating half-ring, as in all peronopsids, including all species of *Hypagnostus*, is low, short, and convex, and the articulating furrow is narrow. Marginal spines are absent.

*Comment on illustrated specimens:*

The holotype pygidium is 4.2 mm long.

The cephalon, Plate 52, figs 2a, 2b, CPC 5777, locality G9, is 4.2 mm long, as long as the holotype pygidium with which it is closely associated.

The cephalon, Plate 52, fig. 3, CPC 5778, locality G103, 5.1 mm long, shows the outline of the anterior glabellar lobe.

The cephalon Plate 52, fig. 4, CPC 5779, locality G131, is 2.8 mm long. The glabella is carinate. It is the youngest known specimen of the species.

*Occurrence and Age:* *Hypagnostus correctus* sp.nov. occurs frequently in the Mungerebar Limestone, at localities G9 and G103 (the Zone of Middle Cambrian-Upper Cambrian passage); G427 (Zone of *Erediaspis eretes*); and G131 (Zone of *Cyclagnostus quasivespa*).

HYPAGNOSTUS DURUS sp.nov.

(Pl. 52, figs 5-6; Text-fig. 17)

*Material:* Three cephalons and one pygidium are illustrated, selected from a large number of examined specimens.

*Holotype:* The cephalon Plate 52, fig. 5 (the cephalon on the left), CPC 5781, locality G119 is selected holotype because it is the best preserved specimen.

*Diagnosis:* *Hypagnostus durus* sp.nov. is a species en grande tenue with an angulate and trilobate glabella provided with a subcentral median node, and a pygidium having a well subdivided pointed axis with a relatively large second annulation, a postaxial median furrow, and marginal pygidial spines.

The species is distinguished by the combination of characters indicated in the diagnosis that occur in other species of *Hypagnostus* in different combinations.

*Differential diagnosis:* Pygidial spines are known only in two species—in *Spinagnostus franklinensis* Howell, 1935, and *Hypagnostus denticulatus* Westergaard, 1946. In *S. franklinensis* the pygidial axial annulations are obscure, the axial tip is rounded and reaches the marginal furrow. In *H. denticulatus* the pygidium recalls *H. durus*, but the postaxial furrow is absent and the second annulation is relatively short. The glabella of *denticulatus* has a rounded front, as seen in *H. correctus* sp.nov. and *H. brevifrons*. It appears that *H. durus* is not closely affiliated with such forms. *H. sulcifer integer* (Wallerius), however, is close: its cephalon

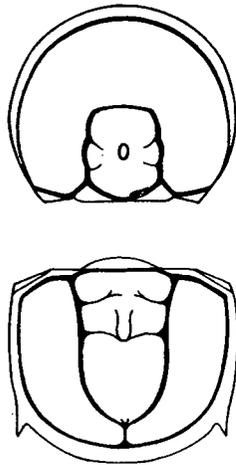


Fig. 17.—*Hypagnostus durus* sp.nov., combined from Plate 56, figs 5 and 6.

(Westergaard, 1946, pl. 6, fig. 18) has also a subangulate glabella with a subcentral node, but differs in having a straight cephalic margin. The pygidium of *sulcifer integer* is unknown, but in *sulcifer sulcifer* itself marginal spines are absent, and both subspecies, according to Westergaard, are connected by intermediate forms. *H. sulcifer* has a well divided pygidial axis and a postaxial median furrow. The *sulcifer* group of forms occurs in Sweden in the Zone of *Leiopyge laevigata*, upper part, which precedes the Australian Zone of *Erediaspis eretes*, in which is *H. durus* sp.nov.

*Description:* The margin of the cephalon is evenly rounded, the rim is narrow and slightly convex, and the marginal furrow narrow. No scrobicules or rugae are present on the cheeks. The glabella is slightly less than half the length of the shield and about one third of its width.

The front of the glabella is truncate to angulate and the rear rounded. Two pairs of lateral glabellar furrows are indicated, converging toward the subcentral median node; the middle glabellar lobes are expanded laterally. The basal lobes are short, triangular, and connected by a narrow band behind the glabella.

The pygidial axis is trilobate; the relatively large middle annulation bears a low median node; the posterior lobe is pointed and bears a small terminal node. The postaxial furrow, faint in the middle, is flaring in the rear, joining the marginal furrow.

*Comment on illustrated specimens* (All specimens are silicified):

The holotype cephalon is 2.2 mm long; the test is preserved, the top of the node is worn off. The largest associated cephalon (CPC 5780) is 2.5 mm and the small 1.2 mm long. The matrix is chert.

The pygidium, Plate 52, fig. 6, CPC 5782, locality G417, is 2.7 mm long; the marginal spines are partly concealed by unremovable silica; the postaxial node is partly masked by chlorammonia.

*Occurrence and Age:* *Hypagnostus durus* sp.nov. is found in the Mungerebar Limestone in most of its localities; it is abundant at G8, G119, G150, and G417. Its age is the Mindyallan Zone of *Erediaspis eretes*.

Genus GRANDAGNOSTUS Howell, 1935

The genus *Grandagnostus* has been recently discussed by Öpik (1961, p. 54) and further comment is unnecessary.

*Grandagnostus evexus* sp.nov., which is described here, is the only known Upper Cambrian species of the genus.

GRANDAGNOSTUS EVEXUS sp.nov.

(Pl. 52, figs 7-9)

*Material:* Two cephalon and three pygidia are illustrated, selected from a large number (over one hundred) of examined specimens. Only silicified shields are available.

*Holotype:* The cephalon plate 52, fig. 7, CPC 5783, locality G417, is selected as holotype because its border and posterior margin are well preserved.

*Diagnosis:* *G. evexus* sp.nov. is a species with a subovate cephalon provided with a border, distinguished by the absence of a cephalic median node.

*Differential diagnosis:* In all known species of *Grandagnostus*, with or without a cephalic border, the cephalon bears a median node. Furthermore, *G. imitans* Öpik (1961) has preserved the vestige of the pygidial axis and *G. marginatus* (Brögger), which has a subovate cephalon, is distinct by its very wide pygidial border. According to Westergaard (1946, p. 95) its cephalic node is very weak.

*Description:* The cephalon is as wide as long, subovate in plan and somewhat truncate in the rear. The border is narrow and convex, the spines are small, depressed, and defined by the posterior marginal furrows. The glabellar rear is faintly outlined, and the basal lobes are weak swellings at the cephalic margin.

In the pygidium the rim is convex and the marginal furrow is a deep channel. As in all effaced agnostids the shoulder furrows are distinct. In the axial lobe only the quite prominent terminal node and the rather weak circular median node are discernible.

*Comment on illustrated specimens:*

The holotype cephalon is 3.0 mm long. Its test is preserved.

The pygidium, Plate 52, fig. 8, CPC 5784, locality G417, is 3.0 mm long; the median node is almost indiscernible.

The pygidium, Plate 52, fig. 9, CPC 5785, locality G417, is 2.2 mm long. Its border is intact.

*Occurrence and Age:* *Grandagnostus evexus* occurs in the Mungerebar Limestone at G8, G119, G147, G145, G150, G417, and in many other localities. Its age is the Mindyallan Zone of *Erediaspis eretes*.

Genus PERATAGNOSTUS nov.

*Peratagnostus* is monotypical, and its type is *P. nobilis* sp.nov.

*Diagnosis:* *Peratagnostus* refers to effaced quadragnostid (=peronopsid) species distinguished by the absence of the cephalic rim and marginal furrow, but having a narrow and flat downsloping border in the pygidium.

It can be also described as an effaced *Hypagnostus* with a terminal pygidial node and a vestigial anterior glabellar lobe distinguished by the absence of the cephalic border.

*Differential diagnosis:* The affiliation of *Peratagnostus* with the quadragnostids and with the various species of *Hypagnostus* is discussed below in connexion with its familial classification. Furthermore, as in *Peratagnostus*, the cephalic border is missing also in *Grandagnostus*, *Phalagnostus*, *Ciceragnostus*, and *Skryiagnostus*; these genera have been discussed earlier (Öpik, 1961) and refer to forms with a rather wide pygidial border and a different mode of effacement. '*Ciceragnostus*' *cicer* also lacks a cephalic border, but is not congeneric with the type of *Ciceragnostus* and the only species of its genus (*Ciceragnostus barlowi*).

The Tremadocian *Ciceragnostus barlowi* (Belt) is, according to Öpik (op. cit.), probably an effaced derivative of *Pseudagnostus*. Finally, '*Phoidagnostus*' *bituberculatus* (Angelin), although without a cephalic border, and without a generic name, has a *Grandagnostus*- or *Phalagnostus*-like pygidial structure and cannot be included therefore in *Peratagnostus*.

*Familial classification:* *Peratagnostus nobilis* belongs to the subfamily Quadragnostinae Howell, 1935 (=Peronopsidae Westergaard, 1936) because it is close to such species as *Hypagnostus truncatus* (Brögger), *H. exsculptus* (Angelin), and *H. hippalus* Öpik. All these forms (including *Peronopsis pusilla* (Tullberg)) possess similar cephalic caecal glands whose pattern is unknown in other agnostids. The pygidia of the mentioned species of *Hypagnostus* have a terminal axial node (see Öpik, 1961, p. 61), which is also present in *P. nobilis*. The pygidium, especially the pygidial axis, of *P. nobilis* is similar to *Hypagnostus nepos* (Brögger) (Westergaard, 1946, pl. 5, fig. 9), to *H. exsculptus* (ibid., pl. 6, fig. 5), and to *H. sulcifer* (ibid., fig. 13). In the latter a postaxial median furrow occurs sporadically, and the vestige of that furrow is also observable in *P. nobilis*. *P. nobilis* is even closer to *Hypagnostus correctus* sp.nov.: both share a similar pygidial axis (vestigial in *nobilis*), a postaxial median furrow, and a flat sloping pygidial rim.

A temporal gap of about four to five zones separates *P. nobilis* from the Middle Cambrian *Hypagnostus*, and it is therefore impossible to name a specific parental form even if it is by chance a described species. Forms like *H. (Tomagnostella) exsculptus* also cannot be considered because of the complete loss of the anterior glabellar lobe (Öpik, 1961a, p. 417), which is still present in *P. nobilis*. Therefore, the ancestors of *Peratagnostus* are agnostids (peronopsids) en grande tenue whose progeny retained the anterior part of the stomach (the anterior glabellar lobe) during all phases of external effacement. Examples of such conservative forms are *Hypagnostus parvifrons* (Westergaard, op. cit., pl. 4, fig. 31), and the Australian late Middle Cambrian and early Upper Cambrian *Hypagnostus correctus* sp.nov. (Pl. 52, fig. 3).

#### PERATAGNOSTUS NOBILIS sp.nov.

(Pl. 52, figs 10 and 11a, b, c; Pl. 53, figs 1-11; Text-fig. 18).

*Material:* Six pygidia and seven cephalae are selected from a large number of specimens to illustrate and describe *P. nobilis*.

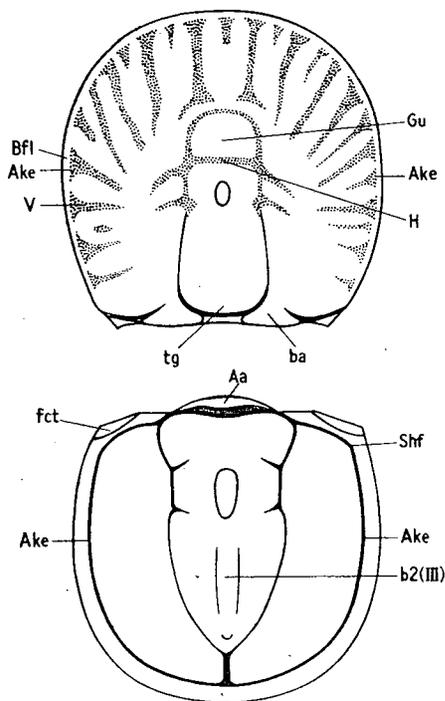


Fig. 18.—*Peratagnostus nobilis* gen. nov. sp. nov., diagram, combined from Plates 52 and 53. Ake—flanks of acrolobes (convex outward). Cephalon: ba—basal lobe; Bfl—marginal flange (border); Gu—frontal glabellar lobe (vestigial); H—transverse glabellar furrow (vestigial); Tg—rear of glabella (rounded). Pygidium: Aa—articulating half-ring; b2(III) intranotular axis; fct—facet; Shf—shoulder furrow (not crossing rim, but confluent with marginal furrow). V—cephalic scrobicule.

**Holotype:** The pygidium, Plate 52, figs 11a, b, c, CPC 5787, locality D120b, is selected as the holotype; it is the best preserved specimen and shows all vestigial features leading to the familial interpretation of the species.

**Diagnosis:** The diagnosis of the species *Peratagnostus nobilis* coincides with the generic diagnosis. Previously the species has been referred to as *Litagnostus* (Öpik, 1956, p. 33).

**Variability:** In the comment on the illustrated specimens the variability is described: it refers to the outline (subcircular to elliptical), and the variable expression of the rugae, scrobicules, basal lobes, and axial furrows.

**Description:** The cephalon is evenly convex, subglobose, with an upward arched rear margin which is straight between, but geniculate outside, the spines. The summit of the cephalon lies just behind the median node, the slope forward is gentle, but rearward it is steeper and strongly arched. The outline is variable, almost circular to elongate elliptical, and specimens are present that are equidimensional or slightly wider, or narrower than the length. A border is absent, but a marginal narrow flange may be present, probably the remnant of the rim. The glabella is indicated only by vestigial swellings and the anterior glabellar lobe may be also visible in some specimens. The rear of the glabella, however, is well developed, separated from the basal lobes and the connective band by a U-shaped furrow. The basal lobes are tumid, and mostly ill defined in front; the posterolateral marginal furrows are distinct; the spines are depressed, short, and inconspicuous. In the margin of the connective band a semicircular notch (the cephalic recess; Robison, 1964) represents

the passage connecting the cephalic and the thoracic part of the viscera. The median node, placed behind the midpoint, is elongate and prominent. Coarse peripheral rugae are present, especially in smaller specimens, but well developed scrobicules have been observed only in a few shields.

The pygidium is longitudinally less convex than the cephalon; its subtriangular transverse section is about as high as the cephalon. The elongate and prominent median node placed on the second axial annulation is the summit of the shield. The outline, not counting the articulating half-ring, is slightly variable, elongate elliptical to almost circular, and about equidimensional. Marginal spines are absent. The rim is relatively narrow, slightly convex or almost flat, and slopes steeply, following the general arc of the shield. The marginal furrow, narrow and deep, is continuous with the shoulder furrow, which, in turn, does not cut the rim. The fulcral points, placed close to the axial lobe, are acute and the facets concave. The articulating device is basic: the axial recess is shallow, the articulating furrow narrow and provided with a pair of pits at its flanks; the half-ring is low and short and has a convex rear margin. The axial furrows are developed only in their foremost part; otherwise they are only vestigial lines delineating the axial lobe, which is constricted at the median node and pointed in the rear. The axial lobe is long, but does not reach the border; the terminal node is prominent and placed slightly forward from the tip of the axis. The posterior axial lobe is somewhat carinate; a vestige of the postaxial median furrow is observable in several specimens.

The test is thin, smooth, and shiny.

*Comment on illustrated specimens:*

All specimens, except for the last mentioned, are collected from a single limestone bed ('a sandy, bituminous, slumped limestone band' of the Pomegranate Limestone; Öpik, 1956, p. 33).

The holotype pygidium is 3.0 mm long. The axial lobe is visible and in the rear view the vestigial postaxial median furrow is apparent. Note the slope of the rim coincident with the slope of the pleural lobes.

The pygidium, Plate 52, fig. 10, CPC 5786, is also 3.0 mm long. The rear of the axial lobe is indistinct, but the foremost parts of the axial furrows are wide and relatively deep.

The pygidium, Plate 53, fig. 1, CPC 5788, is 2.7 mm long; it is decorticated; against expectation the internal cast is devoid of vestiges of furrows and the axis is indicated only by a swelling.

The pygidium, Plate 53, fig. 2, CPC 5789, is 1.8 mm long and illustrated for its small size. It is proportionally wider than the larger pygidia; the axial lobe is pointed and the terminal node prominent.

The pygidium, Plate 53, fig. 3, CPC 5790, is 2.2 mm long; the margin is evenly curved, the outline (without the articulating half-ring) is almost circular.

The pygidium, Plate 53, fig. 4, CPC 5791, is 2.9 mm long. The vestiges of furrows are almost invisible.

The cephalon, Plate 53, figs 5a, b, c, CPC 5792, is 2.9 mm long and equal in length to the preceding pygidium. The stereoscopic pair shows vague outlines of the glabella, its well defined rear, the basal lobes, the connective band, the left spine, and a marginal flange; rugae are absent; the outline is subcircular.

The cephalon, Plate 53, figs 6a, b, c, CPC 5793, is 2.8 mm long. The outline is somewhat elliptical, rugae are barely indicated and the glabella is almost indiscernible. Note the 'hanging' flanks in the rear view.

The cephalon, Plate 53, fig. 7, CPC 5794, is also 2.7 mm long. There is a flange, but the rugae are weak. The pit in front of the median node may be accidental; but it may represent the rudimentary junction of the circumglabellar and median preglabellar furrows.

The cephalon, Plate 53, fig. 8, CPC 5795, is 2.7 mm long; the outline is subelliptical, a marginal flange is present, and the rugae are distinct.

The cephalon, Plate 53, figs 9a, b, c, CPC 5796, is small—1.9 mm long; the flange is prominent, the rugae are weak, and the outline is circular. The rear of the glabella is straight.

The cephalon, Plate 53, fig. 10, CPC 5797, is 1.7 mm long and is the smallest illustrated. The flange is distinct, the basal lobes are defined all around and the rugae and scrobicules are prominent, and not vestigial. The median scrobicule may represent the median preglabellar furrow, and its forked rear the remnant of the circumglabellar furrow.

The cephalon, Plate 53, fig. 11, CPC 5798, locality W10, is 4.3 mm long and the largest collected. Rugae are present; the transverse depression just in front of the median node may be the vestige of the transverse glabellar furrow.

*Occurrence and age:* *Peratagnostus nobilis* is found in the Pomegranate Limestone at localities D119 and D120b, and in the Georgina Limestone at the localities W8, W9, W10, and W45; its age is the Idamean Zone of *Erixanium sentum*.

#### Subfamily PTYCHAGNOSTINAE Kobayashi, 1939

(=Leiopyginae Harrington, 1939, in Kobayashi, 1939)

Temple (1962, p. 341) indicates that the name Leiopyginae, a synonym of Ptychagnostinae (Öpik, 1963, p. 38) erroneously attributed to Kobayashi, 1939, should be referred to as Leiopyginae Harrington, 1938; according to Temple, it was originally published without a diagnosis; Kobayashi, 1939, produced the diagnosis by which the name became valid (Leiopyginae Harrington, not Kobayashi, in Kobayashi, 1939). If this date (1939) is accepted, the names Ptychagnostinae and Leiopyginae are published simultaneously with the preference given by Öpik (1963) to the first.

The matter of the validity of the date (1938 or 1939) depends on a forthcoming decision of the International Commission on Zoological Nomenclature.

#### Genus PTYCHAGNOSTUS Jaekel, 1909

Subgenus GONIAGNOSTUS Howell, 1935

#### PTYCHAGNOSTUS (GONIAGNOSTUS) SPINIGER (Westergaard, 1931)

*Ptychagnostus (Goniagnostus) spiniger* (established by Westergaard, 1931) as a subspecies of *Aagnostus nathorsti*, was finally described and illustrated by him in 1946 (p. 82, pl. 12, figs 18, 19). The test is smooth, the pygidial spines are very long and the axial lobe narrow; otherwise it is reminiscent of *Ptychagnostus (Goniagnostus) nathorsti* and *P. fumicola*.

Within the Glenormiston Sheet area it occurs in the sandstone at locality G106.

*Occurrence and Age:* In Australia *Ptychagnostus spiniger* occurs in the Steamboat Sandstone at localities G106 and D96 (Urandangi area), and in limestone at locality T87 (Öpik, 1961, p. 48). In Sweden it occurs in the 'Zone of *Leiopyge laevigata*, basal layer', in Australia it is present in the upper part of the *L. laevigata* II and in the *laevigata* III Zones.

PTYCHAGNOSTUS (GONIAGNOSTUS) FUMICOLA Öpik, 1961

(Pl. 57, figs 1, 2)

Two separate forms were originally included in *Ptychagnostus (Goniagnostus) fumicola*: (1) The type material of *P. fumicola* from locality G9 and (2) a pygidium from the Devoncourt Limestone, which is described separately below as *Ptychagnostus* sp.nov. aff. *fumicola*. Furthermore, a third species related to *fumicola* occurs in the Mungerebar Limestone, and is described as *Ptychagnostus (Goniagnostus) nodibundus* sp.nov.

The oldest form is *P. sp.nov. aff. fumicola*, followed upward by *fumicola* itself, and finally *P. nodibundus*. In this sequence of forms the size of the pygidial ornamental granules increases with the advance of time.

As regards *Ptychagnostus fumicola* itself, the illustrated large pygidium Plate 57, figure 2, CPC 5840, locality G9, possesses a well developed postaxial median furrow which is not evident in the previously described specimen (Öpik, 1961, plate 20, fig. 14). Hence, the presence or absence of that furrow cannot be regarded as specifically significant in *P. fumicola*. The illustrated pygidium is 4.9 mm long and belongs to the original collection from G9. Its age was originally (Öpik, op. cit. p. 83) given as the Zone of *Ptychagnostus cassis*, based on the misinterpretation of *Hypagnostus correctus* sp.nov. (q.v.), whose specimens from locality G9 were erroneously attributed to *Hypagnostus brevifrons* (Angelin). More to the point, however, is the age given as *laevigata III* Zone (ibid, p. 47). So, *P. (Goniagnostus) fumicola* is definitely younger than *Ptychagnostus* sp.nov. aff. *fumicola* and two zones younger than *Hypagnostus brevifrons*.

*Occurrence and Age:* *Ptychagnostus (Goniagnostus) fumicola* is widespread in the Steamboat Sandstone of the Urandangi area on the Quita Creek and in the Mungerebar area (Text-fig. 3) at localities G103, G104, G121, and D114—in the Middle Cambrian Zone of *Leiopyge laevigata*; and at localities G103 and G9 it occurs also in the Middle-Upper Cambrian zone of passage.

PTYCHAGNOSTUS (GONIAGNOSTUS) sp.nov. aff. FUMICOLA

The fragmentary pygidium described by Öpik (1961, p. 83, pl. 21, fig. 2) from the Devoncourt Limestone, and the Middle Cambrian Zone of *Ptychagnostus cassis*, as belonging to *P. fumicola* represents a different species. It differs from *fumicola* by its much finer granulation and the confluence of the granules into a vermiculate pattern. Because the specimen itself is incomplete the specific nomenclature remains open.

*Occurrence and Age:* The specimen was found (Öpik, 1961) in the Devoncourt Limestone, at locality D15; its age is the Middle Cambrian Zone of *Proampyx agra* (*Leiopyge laevigata* II). It is one zone older than the first appearance of *P. fumicola*.

PTYCHAGNOSTUS (GONIAGNOSTUS) NODIBUNDUS sp.nov.

(Pl. 1; Pl. 57, figs 3, 4)

*Material:* Illustrated are one cephalon and one pygidium, selected from a small number of less well preserved specimens.

*Holotype:* The pygidium, Plate 57, fig. 3, CPC 5841, locality G417, is selected as the holotype because the pygidial ornament is the essential specific character; it is 2.5 mm long.

*Diagnosis:* *Ptychagnostus (Goniagnostus) nodibundus* sp.nov. is distinguished by the rather coarse granulation of the pygidial flanks; the granules are rounded blisters.

*Differential diagnosis:* *P. nodibundus* is close to *P. fumicola*, which, however, has much smaller, and more than four times as many, granules.

The cephalon Plate 1 and Plate 57, fig. 4, CPC 5842, is 2.9 mm long. It differs from *P. fumicola* (1961, Text-fig. 28) in having convex glabella flanks and a narrower glabellar rear. It should be noted that in *fumicola* as well as in *nodibundus* the cephalon is only minutely granulose and rather different from the pygidium as regards the ornament.

*Occurrence and age:* *Ptychagnostus (Goniagnostus) nodibundus* comes from the Mungerebar Limestone, localities G8 and G417. Its age is the Mindyallan Zone of *Erediaspis eretes*. It is the youngest (Upper Cambrian) species of the *fumicola* sequence of forms.

PTYCHAGNOSTUS? SERUS sp.nov.

(Pl. 57, fig. 7; Text-fig. 19)

*Material:* Only one cephalon—the holotype, CPC 5845, is illustrated and described.

*Generic classification:* The generic classification (*Ptychagnostus?*) is queried because the pygidium of this species is unknown and a new genus cannot be established for the same reason. The general aspect of the cephalon is that of a *Ptychagnostus* with a very large frontal glabellar lobe. *P. punctuosus* is the nearest species: it has also a granulose test, its basal lobes have the tendency to extend forward, the frontal lobe has the same shape, and in some of its specimens a median sulcus is present on the glabellar tip.

*Diagnosis:* *Ptychagnostus? serus* is a species with a granulose test, flat cephalic rim, short spines, and a low and semielliptical frontal glabellar lobe distinguished by the absence of a preglabellar median furrow, by the rearward position of the transverse glabellar furrow (well behind the middle), very long frontal glabellar lobe (about 0.36–0.37 of cephalic length), a relatively short and constricted posterior lobe whose median part is oval and tumid, and whose flanks are the greatly extended low basal lobes, and a pair of lobes at the anterolateral corners.

*Differential diagnosis:* Differences from *Ptychagnostus punctuosus* are indicated in the discussion of the generic classification of *P.? serus*; the distinguishing characters mentioned in the diagnosis are sufficient to prevent any confusion with other agnostids.

*Remarks:* The holotype cephalon is about 1.2 mm (1.17 mm) long. It is slightly wider than long, with an evenly rounded margin. The convexity is moderate, but the posterior part of the glabella rises well above the cheeks. Scrobicules are absent. On the frontal glabellar lobe a pair of lines extends from the short median sulcus as far as the transverse furrow—a feature well developed also in *Glyptagnostus*.

*Occurrence and age:* The holotype of *P. ? serus* was found in the O'Hara Shale ('lower chert bed'), and another cephalon in the Georgina Limestone, locality W20—both in the Zone of *Glyptagnostus stolidotus*; fragmentary cephalons have been observed in the Mungerebar Limestone, locality G417, in the Zone of *Erediaspis eretes*; consequently, the age should be the whole Mindyallan, although *serus* has not yet been recorded in its middle Zone of *Cyclagnostus quasivespa*.

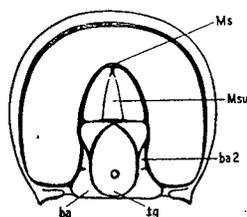


Fig. 19.—*Ptychagnostus?serus* sp. nov., from Plate 57, fig. 7. ba—basal lobe; ba2—anterior part of basal lobe; Ms—frontal sulcus, Msu—depressed extension of frontal sulcus; Tg—rear of glabella (rounded).

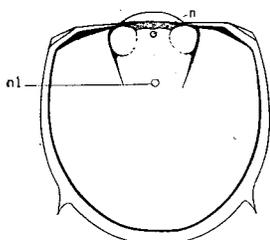


Fig. 20.—*Leiopyge cos* sp. nov., from Plate 57, fig. 5; n1—axial node; n—axial node on anterior annulation.

## Genus LEIOPYGE Hawle and Corda, 1847

### LEIOPYGE COS sp. nov.

(Pl. 57, figs 5 and 6; Text-fig. 20)

*Material:* A cephalon and a pygidium are selected for description from a limestone bed with silicified fossils.

*Holotype:* The pygidium, Plate 57, fig. 5, CPC 5843, is selected as the holotype.

*Diagnosis:* *Leiopyge cos* sp. nov. is distinguished by well developed posterior section of the cephalic axial furrows and rather distinct but relatively small basal lobes, short pygidial marginal spines, and two median nodes on the pygidial axial lobe; the additional node is placed on the anterior axial annulation.

*Differential diagnosis:* The marginal pygidial spines of *L. cos* are shared by *Leiopyge laevigata armata* (Linnarsson), but *armata* has only one node, on the second axial annulation; furthermore, the cephalic spines of *armata* are long (short in *cos*, as observed on specimens not illustrated).

*Leiopyge calva* Robison, 1964, lacks the axial nodes and marginal spines in the pygidium that are present in *L. cos*.

*Remarks:* The holotype pygidium is 3.3 mm long, and somewhat fragmentary; the short axial furrows are quite deep, the axial nodes are faint, and the anterior axial annulation is relatively broad and tripartite.

The cephalon, Plate 57, fig. 6, CPC 5844, is 1.5 mm long (as preserved). The glabellar rear is broad, the glabellar node prominent, and the basal lobes are small.

The genus *Leiopyge*, and its species *laevigata* and *laevigata armata*, have been discussed by Öpik (1961); these forms are essentially Middle Cambrian; in the Mungerebar area *L. laevigata* occurs at localities G102, G103, G104, G106, and G107; *L. laevigata armata* occurs at G103. The occurrences at G103 and G107 are the latest known for these forms, representing the Middle Cambrian-Upper Cambrian Zone of passage.

*Occurrence and age:* *Leiopyge cos* sp.nov. occurs in the Mungerebar Limestone, localities G131, G150, and G417. The described specimens came from locality G131—Mindyallan Zone of *Cyclagnostus quasivespa*; in G150 and G417 it is a Zone older—the Zone of *Erediaspis eretes*.

#### Genus AGNOSTOGONUS gen.nov.

The type species of *Agnostogonus* is *A. incognitus* sp.nov.

*Diagnosis:* *Agnostogonus* refers to effaced species in which in the cephalon the basal lobes and the rear part of the glabellar furrows and in the pygidium only the anterior part of the axial lobe comprising two annulations are indicated; it is distinguished from other similarly effaced forms in having a convex rim of equal width in the cephalon and pygidium, and no tumidity of the basal lobes and of the glabellar rear.

*Differential diagnosis:* Among the effaced agnostids only *Gallagnostus* Howell, 1935, possesses a rim of equal width in the cephalon and the pygidium, but otherwise it is completely featureless and therefore not comparable with *A. incognitus*. The Tremadocian *Ciceragnostus barlowi* (Belt) (the only species of the genus) lacks a cephalic border, and, furthermore, its type material is insufficiently preserved. The Middle Cambrian *Agnostus cicer* Tullberg (see Westergaard, 1946,) is similar to *A. incognitus* as regards the degree of effacement of the lobes and furrows, but possesses no cephalic border.

*Pseudophalacroma* Pokrovskaja, 1958 (see Öpik, 1961, p. 91) is comparable also as regards the degree of effacement, but is distinct because its cephalic and pygidial borders are rather unequal in width.

The early Ordovician effaced agnostid pygidia (*Agnostid*, gen. and sp. indetermined) described by Rasetti (1954, p. 582, pl. 61, figs 13, 14) recall *Agnostogonus incognitus* as regards size, shape, absence of spines, and the structure of the articulating device. They possess, however, a terminal axial node and faint outlines of the axial lobe, and are consequently less effaced than the much older *Agnostogonus*. The border in Rasetti's specimens is twice as wide as in *Agnostogonus* and much wider than in *Lotagnostus*, which, according to Rasetti, is comparable with his specimens as regards the pattern of the pygidial furrows. In passing, the structure of the border is a fair criterion in generic classification of effaced agnostids.

The following features of *Agnostogonus incognitus* have a bearing on its familial classification: (1) the articulating device is basic, peronopsid or ptychagnostid, and excludes *Diplagnostus*, *Pseudagnostus*, *Glyptagnostus*, and *Agnostus* from the kinship; (2) the oval shape of the shields combined with the broad pygidial axis is suggestive of some exceptional ptychagnostids, e.g. *Ptychagnostus (Triplagnostus) elegans laevissimus* Westergaard (1946, p. 74, pl. 10, figs 21, 22), which is attributed to the evolutionary series of *Leiopyge laevigata*; (3) the structure of the border, however, is not ptychagnostid, but bears some similarity with certain forms of the peronopsid *Cotalagnostus lens*; but in the *lens* group the border is unstable; and (4) no clues as regards the shape of the glabella and the posterior axial lobe of the pygidium are available.

On these features, *Agnostogonus* could be placed in the Ptychagnostinae or the Quadragnostinae (peronopsids). Preference could be given to the Ptychagnostinae because of the oval shape of the shields and the absence of the pygidial spines in *Agnostogonus*; the peronopsids en grande tenue have mostly 'subquadrate' shields and pygidial spines. One notes, however, that the effaced peronopsids (*Hypagnostus*, *Cotalagnostus*, *Grandagnostus*) also have no pygidial spines, and the familial affiliation remains therefore open for doubt and inquiry.

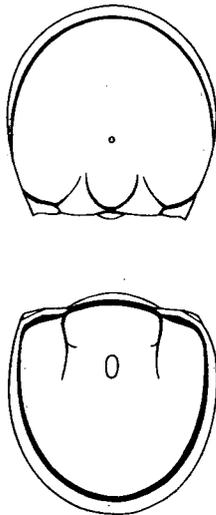


Fig. 21.—*Agnostogonus incognitus* gen.nov., sp.nov. From Plate 57, figs 8, 9.

AGNOSTOGONUS INCOGNITUS sp.nov.

(Pl. 57, figs 8, 9; Text-fig. 21)

**Material:** The illustrated and described material consists of one cephalon and one pygidium. Nine pygidia and five cephalata have been examined altogether.

**Holotype:** The cephalon, Plate 57, fig. 8, CPC 5846 is selected as the holotype because in effaced agnostids the structure of the cephalic border taxonomically is quite distinctive.

**Diagnosis:** The diagnosis and differential diagnosis of the species *Agnostogonus incognitus* are the same as of the genus.

*Description:* The holotype cephalon and the pygidium Plate 57, fig. 9, CPC 5847, are equal in length (3.2 mm) and width; the total length of an exoskeleton was between 8 and 9 mm—a usual size for an agnostid.

The cephalon is suboval, with an evenly curved and forward arched margin; it is strongly and rather evenly convex, with the summit in the posterior half; at the flanks it is rather steep, overhanging partly the marginal furrow, and in the rear bulging over the furrow and the rim. No lobes or swellings rise above the vaulted surface of the cephalon. A tiny median node placed behind the cephalic midpoint is discernible in decorticated specimens.

The cephalic rim is of medium width, convex, and defined by a relatively deep marginal furrow which undercuts the periphery of the cheeks; this condition occurs in several other agnostids and is concurrent with the lateral bulging of the cheeks. The posterolateral marginal furrows are distinct, oblique, and mark off the spines. The spines are swollen, and short, and rise steeply upwards.

The furrows delineating the basal lobes and the rear of the glabella are faint; only the posterior part of the glabella is indicated: it is rounded and coincides with the general curvature of the shield. The basal lobes, connected by a narrow connective band behind the glabellar rear, are relatively large, triangular, and almost imperceptibly swollen, and their frontal tips are not enclosed by furrows.

The pygidium is suboval to subelliptical, slightly less convex than the cephalon, and bulging less along the flanks; its summit is placed at or just behind the median node. The structure of the border is the same as in the cephalon, but the marginal furrow is not concealed by the pleural flanks. The margin is evenly rounded, and strongly arched retrally; marginal spines are absent.

The articulating half-ring is rather short, convex, and separated by a narrow furrow from the front of the axial lobe, which has no recess.

The axial lobe is rather wide, about half the width of the pygidium; only the two anterior annulations are defined laterally, by shallow but distinct axial furrows; no transverse furrows are present, but the second annulation is constricted. It bears a low elongate median node. The rear part of the axis is completely effaced.

*Occurrence and age:* *Agnostogonus incognitus* sp.nov. has been found only in the O'Hara Shale ('lower chert bed') at localities D6 and D29; the age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Subfamily AGNOSTINAE McCoy

#### Genus AGNOSTUS Brogniart

#### AGNOSTUS aff. AGNOSTUS PISIFORMIS Linnaeus, 1758

(Pl. 57, figs 12, 13)

The concept of the species *Agnostus pisiformis* has been revised recently by Westergaard (1922; 1946) and Henningsmoen (1958). The species is known in great detail, especially by the work of Henningsmoen, who applied whitening on his specimens. Better preserved material than has yet been found would therefore be needed to identify the species in Australia, which is rather remote from Sweden and Norway. Furthermore, *A. pisiformis* is variable, but it cannot be established whether or not the Australian form coincides with any of the variants of *pisiformis*.

The illustrated specimens come from the Mungerebar Limestone, locality G417. The cephalon, Plate 57, fig. 13, CPC 5851 is 3.5 mm long. Conformably with the definition of the genus, and the species *pisiformis*, the marginal furrow is deep, the rim is elevated, the preglabellar median furrow is present, the rear of the glabella is rounded, and its posterior lobe bears an inconspicuous subcentral node; but, compared with *pisiformis*, the glabella is wider and the preglabellar area is shorter in our specimen.

The pygidium, Plate 57, fig. 12, CPC 5850, is 2.0 mm long. As in *A. pisiformis*, a postaxial median furrow is absent, the axis is indistinctly subdivided, slender, pointed and not reaching the marginal furrow. Lateral spines are present: the left spine is preserved but hidden by silica of the matrix. Its rear margin is, however, damaged. It differs from *pisiformis* by its longer and less prominent median node.

*Occurrence and age:* *Agnostus* aff. *pisiformis* is relatively common in the Mungerebar Limestone; its age is the Mindyallan Zone of *Erediaspis eretes*.

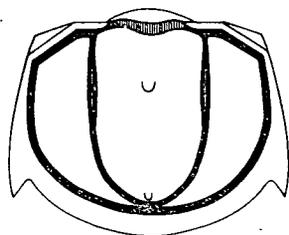


Fig. 22.—*Agnostus artilimbatus* sp.nov., from Plate 57, fig. 11.

AGNOSTUS ARTILIMBATUS sp.nov.

(Pl. 57, figs 10, 11; Text-fig. 22)

*Material:* One cephalon, the holotype, CPC 5848, locality G417, is illustrated (fig. 10), selected from several less well preserved specimens; an example of the associated pygidium is also described.

*Diagnosis:* *Agnostus artilimbatus* is a species related to *Agnostus pisiformis*, from which it is distinguished by its narrow cephalic rim, very narrow marginal furrow, and the small size of the rounded glabellar node.

*Differential diagnosis:* No species of *Agnostus* is known to have a border as narrow as *A. artilimbatus*; in *A. pisiformis* as illustrated by Henningsmoen (1958) the rim and the marginal furrow are wider, and the rim is elevated. Furthermore, the anterior glabellar lobe in *A. artilimbatus* is somewhat shorter than in *pisiformis*.

*Description:* The holotype cephalon is 2.5 mm long; the border is narrow and relatively flat, and the test is probably minutely granulose—though this may be merely a reflection of the granulosity of the silica.

The associated pygidium, Plate 57, fig. 11, CPC 5849, is 1.7 mm long; it is selected from several less well preserved specimens. The flanks diverge rearward, and carry triangular spines creating the impression of a *Peronopsis* pygidium. The articulating device, however, is that of an *Agnostus* or *Homagnostus*. The shape of the axial lobe is about the same as in *Agnostus pisiformis*, as illustrated by Henningsmoen (1958, pl. 5, fig. 2), but in our form (1) transverse furrows are absent, (2) the

median node is very low, and (3) the axis is longer, touching with its tip the marginal furrow. The current diagnosis of the genus *Agnostus* indicates, however, that the pygidial axial lobe should be shorter, not reaching the border, that the pleural lobes are confluent in the rear, and that no postaxial median furrow is present.

Neither pygidia of another kind to suit the holotype cephalon, nor other cephalons to match the particular pygidium are present and it is, therefore, probable that both described shields are conspecific. If this can be proven *Agnostus artilimbatus* may represent a separate genus of Agnostinae (or a subgenus of *Agnostus*) distinguished by the flat and narrow cephalic border and the effaced pygidial axis reaching the marginal furrow.

*Occurrence and age:* *Agnostus artilimbatus* sp.nov. occurs in the Mungerebar Limestone; the illustrated specimens have been etched out of limestone from locality G417; the form (cephala and pygidia) occurs also at localities G8 and G119. The age is the Mindyallan Zone of *Erediaspis eretes*.

AGNOSTUS? sp. aff. AGNOSTUS PISIFORMIS SUBSULCATUS Westergaard, 1946  
(Pl. 58, fig. 1)

Only one cephalon, CPC 5852, locality G119, was found. It is 2.9 mm long, its border is relatively narrow, the glabella is parallel sided and slender (about 0.26 of shield's width), its frontal lobe is large, its rear rounded, and its posterior lobe carries an almost imperceptible central node. No preglabellar median furrow is present.

Species of the genus *Agnostus* are assumed to possess a preglabellar median furrow; but in one species—*A. pisiformis subsulcatus* Westergaard (1946, pl. 16, fig. 4)—this furrow is absent, or almost so. Consequently, the identification of the genus *Agnostus* cannot depend on the preglabellar median furrow. Our specimen differs from *A. pisiformis subsulcatus* by the large size of the anterior glabellar lobe and the narrowness of its glabella. *A. subsulcatus* is also older (*Leiopyge laevigata* Zone).

*Occurrence and age:* The cephalon was found in the Mungerebar Limestone, locality G119; its age is the Mindyallan Zone of *Erediaspis eretes*.

#### Genus INNITAGNOSTUS nov.

*Diagnosis:* The species of the genus *Innitagnostus* are distinguished by a laterally notched glabella with angulate recesses to fit the basal lobes, and by a pygidium in which the anterior axial annulation is tripartite and the axial tip bears a terminal node.

The type of the genus is *Innitagnostus innitens* sp.nov.; other species are *A. inexpectans* Kobayashi, *Agnostus neglectus* Westergaard, and *Tomagnostus tchatertensis* Kryskov, 1963. The last-named species is distinguished by its strongly scrobiculate cephalon and the well developed frontal glabellar sulcus. It occurs in the early Upper Cambrian of Kazakhstan.

*Differential diagnosis:* In *Agnostus* (*Agnostus*) and related groups (*Homagnostus*, *Geragnostus*, *Micragnostus*) the glabella has neither lateral notches nor angulate recesses at the base.

The cephalon of *Innitagnostus* imitates to some degree *Diplagnostus* (see *D. crassus* sp.nov.), and, in the absence of a published suitable generic name, one species was placed in *Tomagnostus* (*T. tchatertensis* Kryskov).

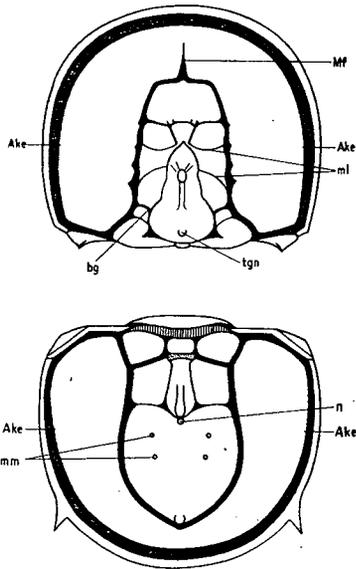


Fig. 23.—*Innitagnostus innitens* gen.nov., sp.nov., from Plate 58, figs 2–4. Ake—unconstricted acrolobes with flanks convex outward; Cephalon: bg—basal corner; Mf—preglabellar median furrow (incomplete); ml—margins (lines) of muscle spots; Tgn—node on rounded glabellar rear. Pygidium: mm—notulae; n—accessory median node.

INNITAGNOSTUS INNITENS gen.nov. et sp.nov.

(Pl. 8, fig. 5; Pl. 58, figs 2–4; Text-fig. 23)

*Material:* The illustrated material consists of one cephalon and two pygidia from the Pomegranate Limestone at Wills Creek, which yielded nine cephalons and eight pygidia; and some rather poorly preserved specimens from the O'Hara Shale ('lower chert bed').

*Holotype:* The cephalon Plate 58, fig. 2, CPC 5853, locality B537, is selected as the holotype because of its excellent state of preservation; the characteristic surface granulation is, however, stronger developed in the pygidia, which are, therefore, equally important in the identification of the species.

*Diagnosis:* *Innitagnostus innitens* sp.nov. is a species with a narrow cephalic and pygidial border, with an elongate subcentral node on its posterior glabellar lobe, and with a tripartite anterior annulation of the pygidial axial lobe; distinguished by the shallowness of the preglabellar furrow, which does not reach the marginal furrow, by the pyriform shape of the median part of the posterior glabellar lobe, by relatively large and complicated basal lobes, and by the granularity of the test, especially in the pygidium.

*Differential diagnosis:* *Innitagnostus innitens* is comparable with *A. inexpectans* Kobayashi (see Öpik, 1963) in having a similar narrow border and a tripartition of the first axial annulation; but in *inexpectans* the glabellar node is absent, the posterior glabellar lobe is broad and plump, the median preglabellar furrow is well defined, the basal lobes are small and the test is smooth. *Agnostus pisiformis* has a glabellar

node, but is rather different in other details of the cephalon and pygidium (compare Henningsmoen, 1958, pl. 5). In *Agnostus neglectus* Westergaard, 1964, the pygidial relief and the length of its axis are about the same as in *Innitagnostus innitens*, but its test is smooth, the cephalic preglabellar median furrow is deep and complete, and the border is wider than in other species. Finally, *Cyclagnostus quasivespa* sp.nov. differs by its long pygidial axis, short axial node, different arrangement of the glabellar lobes and minutely pitted surface; but the incomplete preglabellar median furrow and the sporadic appearance of two pairs of notulae in the pygidium are common to *quasivespa* and *innitens*.

In passing, in *neglectus* and in *tchatertensis* three pairs of notulae have been observed.

*Description:* In both shields the rim and the marginal furrows are narrow and distinct. The cephalon is moderately convex and the glabellar rear rises well above the cheeks. No rugae or scrobicules are present. As in *inexpectans*, the glabella is 0.7 of the cephalic length, and the frontal lobe pentagonal; the transverse glabellar furrow in *innitens* is shallow and almost disappears at the flanks. The numerous lateral glabellar lobules seen in *I. inexpectans* are absent here; two pairs of low and relatively large and oblique lateral lobes are present in *innitens* instead, and the median part of the glabella is pyriform, tumid in the rear, narrow in front, almost carinate, and carries an elongate subcentral node. There is also a tiny node near its posterior margin. The basal lobes are large, swollen, and somewhat composite, and placed in rectangular recesses of the glabellar rear, which is rounded and slopes down steeply. The cephalic spines are relatively short and provided with extenuated tips.

In the pygidium the posterior axial lobe is relatively narrow, and pointed; the terminal node is weak; the median axial node is pointed and its tip is almost in touch with the test, concealing a tiny node—an unusual feature in agnostids. The lateral spines are small and divergent; the articulating device consists of an upward arched half-ring and a narrow articulating furrow, as seen also in *Agnostus pisiformis*, *Homagnostus*, and *Cyclagnostus quasivespa* sp.nov. The test is minutely granulose.

*Variability:* The posterior axial lobe of the pygidium is variable; it can be as wide as long, or slightly wider.

*Comment on illustrated specimens:*

The holotype cephalon is 2.3 mm long; it is slightly fractured in front but otherwise intact. Note the weak median preglabellar furrow, the shallowness of the transverse furrow, the swollen basal lobes, and the extenuated tip of the left spine. Details of its relief are shown in Text-figure 23.

The pygidium, Plate 58, fig. 4, CPC 5855, locality B537 is 2.0 mm long; it is associated with the holotype. Its frontal part is damaged, but the granulation is well preserved; the tip of the median axial node is broken, exposing the otherwise hidden tiny node.

The pygidium, Plate 58, fig. 3, CPC 5854, locality B525, is 2.5 mm long. Its anterior axial annulation and the articulating device are preserved; on the axis two pairs of weak notulae are indicated; the top of the median node is intact. The posterior axial lobe is slightly wider than in the previous specimen.

The cephalon, Plate 8, fig. 5, CPC 5417, locality D29, associated with a cranidium of *Townleyella townleyi*, is 1.9 mm long; its preglabellar median furrow is obscure; the median part of the glabella is ill preserved; the test is granulose.

*Occurrence and age:* *Innitagnostus innitens* has been found in the Pomegranate Limestone at localities B525 and B537, and in the O'Hara Shale ('lower chert bed') at localities D6, D28, and D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

INNITAGNOSTUS INNITENS?

(Pl. 58, fig. 6)

A fragmentary pygidium, locality G8, assignable to the genus *Innitagnostus* is illustrated in the right-hand lower corner of figure 6 in Plate 58. The structure of the axial lobe and the articulating half-ring are rather similar to *I. innitens* and even a terminal node is present. Fragments of cephalae are also observable, supporting the presence of *Innitagnostus* in the *Erediaspis eretes* Zone, but the material is insufficient for a conclusive identification; these forms have, apparently, a smooth test and a glabella less tumid than *I. innitens*.

*Occurrence and age:* Mungerebar Limestone, localities G8, G119, and G417; the age is the Mindyallan *Erediaspis eretes* Zone. The form is, therefore, older than the type material of *Innitagnostus innitens*.

INNITAGNOSTUS aff. INNITENS

(Pl. 58, fig. 5)

The complete specimen CPC 5856, in grey limestone, 2.2 mm long, is very small, its cephalon and pygidium each being about 1.0 mm long. The thorax with its two segments is, however, fully developed. The test is granulose, the preglabellar furrow is short, not reaching the marginal furrow, and the border narrow—all as in *Innitagnostus innitens* sp. nov.

The pygidial axis, however, is relatively short and tapering, and its rear lobe is not expanded as in *I. innitens*. A terminal node is present. Specimens of *Innitagnostus innitens* of a similar size are, however, not available, a conclusive comparison cannot be made, and the species name is therefore reserved.

It should be noted that in this specimen the pygidial axis compares with *Hastagnostus angustus* Howell (1937, pl. 3, fig. 4).

*Occurrence and age:* *Innitagnostus* aff. *innitens* was found in the Georgina Limestone at locality W20; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

INNITAGNOSTUS INEXPECTANS (Kobayashi, 1938)

(Pl. 63, fig. 2)

The species *A. inexpectans* has been recently revised by Palmer (1962). Öpik (1963) described Australian specimens from the Zone of *Glyptagnostus reticulatus* and indicated that it is also present stratigraphically higher—in the Zone of *Corynexochus plumula*.

The illustrated cephalon from that zone, locality W39, CPC 5912, is 3.0 mm long. On the cheeks rugae are indicated, but the test is smooth. The lateral lobules seen in the previously described older Australian specimens are absent here but close similarity is apparent with the American cephalae described by Palmer.

The pygidia associated with the described cephalon differ in no way from the earlier described pygidium (Öpik, op.cit.).

In passing, the reconstruction of the thorax of *I. inexpectans* in Öpik (1963, p. 36) is confused: the triangular pleural tip of the rear segment belongs to the anterior, and the forward swinging tip of the anterior belongs to the posterior segment.

*Occurrence and age:* *Innitagnostus inexpectans* occurs in Australia in the Georgina Limestone and in the Pomegranate Limestone, in the lower part of the Idamean (*Glyptagnostus reticulatus* and *Corynexochus plumula* Zones). In America (U.S.A. and British Columbia) it occurs in the *Glyptagnostus reticulatus* zone.

#### Genus HADRAGNOSTUS nov.

The type species of *Hadragnostus* is *H. las*, sp.nov.

*Diagnosis:* The name *Hadragnostus* refers to Agnostinae with a preglabellar median furrow and a rather large pygidial axis which touches the marginal furrow and carries a terminal node distinguished by its long glabella and short preglabellar area and by the absence of distinct annulations and transverse furrows in the pygidial axis.

*Differential diagnosis:* The nearest genus is *Homagnostus* Howell, 1935, as regards the size of the pygidial axis. But in *Homagnostus* the pygidial axis is well annulated and does not reach the marginal furrow, and its cephalic preglabellar median furrow is narrow and unstable, whereas in *Hadragnostus* this furrow is rather wide and prominent.

*Proagnostus modestus* Lochman, 1944, is also probably a *Hadragnostus*; it is however, based on very small specimens (about one mm long) which cannot be readily compared with *H. las*.

The pygidial structure of *Hadragnostus* is reminiscent of *Agnostascus* gen.nov., but in *Agnostascus* the acrolobes are constricted, the pygidial pleural lobes are relatively narrow and the rear of the glabella is angulate.

In *Agnostus artilimbatus* sp.nov. the pygidial axis is as long as in *H. las*, but narrower, and the glabella is relatively short; moreover, *A. artilimbatus* is an aberrant species of its genus and cannot serve to accommodate even more aberrant forms in the genus *Agnostus*.

The broad and square shape of the pygidium of *Hadragnostus* is not unlike a *Peronopsis*, but in *Peronopsis* no terminal node is present, the axial lobe and the glabella are shorter, and a preglabellar median furrow is absent.

#### HADRAGNOSTUS LAS sp.nov.

(Pl. 58, figs 6-10; Text-fig. 24)

*Material:* Two cephalata and three pygidia are selected for illustration from a large number of specimens which are mostly fragmentary or are partly covered by silica.

*Holotype:* The pygidium, Plate 58, fig. 8, CPC 5861, is selected as the holotype because it is the best preserved specimen.

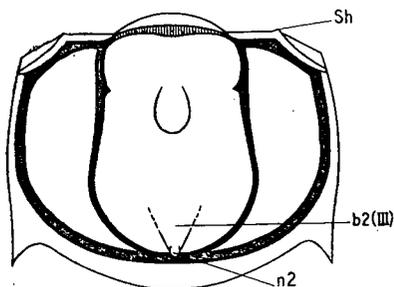


Fig. 24.—*Hadragnostus las* gen.nov., sp.nov., from Plate 58, fig. 8. b2 (III)—intranotular axis; n2—terminal node; Sh—fulcral point.

**Diagnosis:** The generic diagnosis serves as the diagnosis of the species.

**Description:** Both shields have a similar shape and are quite broad, the length being about 0.75 of width.

The border is narrow, consisting of an elevated narrow rim and a slightly wider marginal furrow—a structure seen in *Aagnostus pisiformis*. The acrolobes are not constricted, and the flanks of the cheeks and of the pygidial pleural lobes are convex. Scrobicules and rugae are absent.

The cephalon in plan is well rounded, wider than long, and widest across its middle. The frontal margin is straight or may have even a shallow rearward recess, though this needs verifying by supporting observations. The cheeks are tumid and divided in front by a rather wide preglabellar median furrow, whose width, however, is variable. The glabella is long, about 0.8 of shield length, which is unusual, because in most of the agnostids it is about 0.7. Its width in the middle is, however, moderate, about 0.25–0.27 of the shield. The anterior glabellar lobe is triangular, subangular in front, and the transverse glabellar furrow is straight and distinct. The posterior lobe expands and rises rearward, and is evenly rounded in the rear. There is no glabellar median node. The basal lobes are triangular, tumid, and connected in the rear by a narrow connective band. The axial furrows are deep.

In the pygidium the lateral margins are slightly convex; the marginal spines are relatively large, broad, and placed well behind, level with the rear of the axial lobe. The fulcral points are angulate and the facets are slightly concave. The articulating device is simple, with a very shallow recess in the front of the axis and a narrow articulating furrow. The axial lobe carries a rounded and prominent node, apparently on its second annulation, but transverse furrows are absent. The axial lobe is slightly constricted at the level of the node, but expands slightly in the rear and attains about 0.5 of shield width. In not flattened specimens (the holotype) the rear of the axis is swollen and slopes down steeply; the posterior lobe appears only slightly longer than the two anterior annulations. The terminal node is prominent, directed rearward, and arises from a weakly swollen base which is probably the end of the otherwise not discernible intransotular axis.

*Comment on illustrated specimens:*

The holotype pygidium is 2.0 mm long; its lateral spines are preserved, the left shoulder exposed, but the articulating half-ring is covered by silica. The terminal node is distinct.

The pygidium, Plate 58, fig. 10, CPC 5863, locality G417, is 1.8 mm long; it is slightly flattened, but shows the articulating half-ring.

The pygidium, Plate 58, fig. 9, CPC 5862, locality G8, is 2.0 mm long; the termina. node carries some extra silica.

The cephalon, Plate 58, fig. 6, CPC 5857, locality G8, is 2.5 mm long; the anterior glabellar lobe is triangular, the preglabellar median furrow wide and no median node is apparent.

The cephalon, Plate 58, fig. 7, CPC 5860, locality G429, is 2.3 mm long. It is partly immersed in chert. Note the connective band, the short preglabellar area with the extraordinary wide preglabellar median furrow; the frontal margin has a recess which may not be accidental.

*Occurrence and age:* *Hadragnostus las* is abundant, and occurs in the Mungerebar Limestone in almost all places; the illustrated material comes from G8, G417, and G429; other localities are G7, G119, G114, and G150; its age at these localities is the Mindyallan zone of *Erediaspis eretes*; at locality G124 it is found in the Zone of *Cyclagnostus quasivespa*.

#### Genus IDOLAGNOSTUS nov.

The type species of *Idolagnostus* is *I. agrestis* sp.nov.

*Diagnosis:* *Idolagnostus* refers to Agnostinae en grande tenue distinguished by a completely trilobate glabella with a diminutive anterior, and tumid posterior lobe, and by a large oval and pointed posterior pygidial axial lobe which touches the marginal furrow and coincides with the general curvature of the shield.

*Differential diagnosis:* Agnostids with a trilobate glabella are not rare, as for example, some species of *Pseudagnostus*, *Agnostardis amplinatis*, *Cyclagnostus quasivespa*, and *Neoagnostus* Kobayashi. In all these forms the anterior glabellar lobe is normal in size and the furrows dividing the posterior glabellar lobe are not quite transcurrent. These furrows are, however, transcurrent in *Trilobagnostus innocens* (Clarke, 1924, pl. 1, figs 7, 7a; also Rasetti, 1944, p. 234), which, however, is distinct by its large triangular anterior glabellar lobe and short and narrow pygidial axis.

The familial classification of *Idolagnostus* (Agnostidae, Agnostinae) is borne out by the pygidial structure: the main differences from *Agnostus* are the longer pygidial axis, which recalls *Cyclagnostus*, and the depressed posterior axial lobe.

*Idolagnostus* represents probably a separate subfamily of the Agnostidae; this, however, is reserved because the generic concept of *Idolagnostus* imposes no substantial changes on the concept of the subfamily Agnostinae.

Two species of *Idolagnostus* are present in the Mindyallan of Queensland:

1. *Idolagnostus agrestis* sp.nov., from the late Mindyallan Zone of *Glyptagnostus stolidotus*; and
2. *Idolagnostus dryas* sp.nov., from the Mindyallan in general.

#### IDOLAGNOSTUS AGRESTIS sp.nov.

(Pl. 59, figs 9, 10; Pl. 60, figs 1, 2; Pl. 63, fig. 10; Text-figs 25, 26)

*Material:* Two cephalata and three pygidia are illustrated; observations made on other specimens are incorporated in Text-figure 25A and 25B. All these specimens are selected from an abundance of material (*I. agrestis* is the most common agnostid in the 'lower chert bed' of the O'Hara Shale).

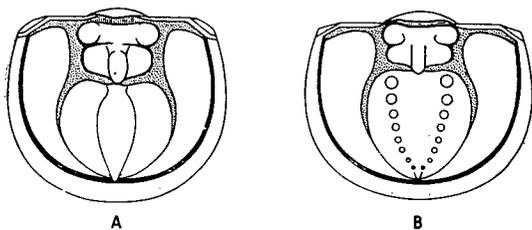


Fig. 25.—*Idolagnostus agrestis* gen.nov., sp.nov. A.—pygidium showing intranotular axis; B.—pygidium showing notulae.

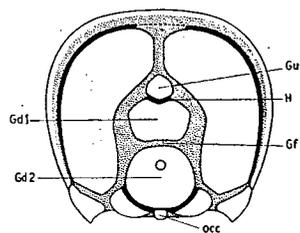


Fig. 26.—*Idolagnostus agrestis* gen.nov., sp.nov., from Plate 60, fig. 1. Gd1—anterior part of rear glabellar lobe; Gd2—posterior part of rear glabellar lobe; Gf—transverse furrow of rear glabellar lobe; Gn—frontal lobe of glabella; H—transverse glabellar furrow; occ—occipital collar.

*Holotype*: The cephalon Plate 60, fig. 2, CPC 5766, locality D29, is selected as holotype; preference is given to a cephalon because of its diagnostic features, and because the pygidium of the second species (*Idolagnostus dryas* sp.nov.) is unknown.

*Diagnosis*: The diagnosis of *I. agrestis* is essentially the same as of the genus; the differential diagnosis is given with *I. dryas* sp.nov.

*Description*: Shields 1.2–1.5 mm long are most common; the largest, which are rare, may reach 2.0 mm. Small shields, down to 1.0 mm, are also present and are not otherwise different from the larger specimens; consequently all observed specimens belong to mature individuals. *I. agrestis* is therefore a small agnostid which rarely attained the length of 5.0 mm. Equal abundance and similar size of cephala and pygidia, and the similar structure of their furrows, indicate that they are conspecific. The examination of the external moulds indicates that the furrows externally are less wide and less deep than on the casts, but remain rather distinct.

The cephalon is as wide as long, suboval, with a moderately arched frontal margin and rearward converging flanks. The rim is relatively flat, and the marginal furrow is shallow and diffuse. The cephalic spines are relatively large, triangular, thickened and directed rearward and upward. The cheeks are moderately tumid, without scalloped edges, but traces of marginal rugae have been observed. Furthermore, scrobicular pits may occur in some specimens (Pl. 60, fig. 1). The axial furrows and the preglabellar median furrow are V-shaped in section. The glabella is trilobate: the anterior glabellar lobe is unusually small, subcircular and swollen; the second lobe is angulate, subhexagonal, large and relatively flat, separated in front by the rearward convex transverse furrow, which is quite deep. The posterior lobe is large, subcircular and semiglobose, elevated above the shield, and bears a rounded node on its anterior slope. The basal lobes are tumid, reniform, relatively short and wide; the semicylindrical occipital collar is short and narrow.

The pygidium is wider than long, with an evenly curved margin and without marginal spines. The rim, as wide as in the cephalon, is slightly convex, and the marginal furrow distinct; the laterally bulging pleural lobes overhang the adaxial part of the furrow. The facets are small and, apparently, slightly concave. In the articulating device the furrow is narrow, the half-ring only little arched, and the recess in the front of the axis is shallow.

The axial furrows are deep and wide, but change to mere lines at the posterior half of the rear axial lobe. The second annulation of the axis is constricted and bears a long node with an almost vertical tip; the second transverse axial furrow is broad and transcurrent; the posterior axial lobe is wide, suboval, pointed at the rear and contacts the marginal furrow; it coincides completely with the transverse, and longitudinal arc of the shield. A terminal node is present. In some specimens an intranotular axis is indicated (Text-fig. 25A) and in others (Text-fig. 25B) notulae are observable.

*Comment on illustrated specimens:* (All specimens are from locality D29).

The holotype cephalon is 1.5 mm long. The test is missing but the specimen is otherwise complete.

The cephalon, Plate 60, fig. 1, CPC 5874, is 1.6 mm long. The pits on the cheeks may be scrobicules, but this is not quite certain. Note the prominent triangular spines. Text-figure 26 is essentially based on this specimen.

The pygidium, Plate 59, fig. 9, CPC 6872, is 1.2 mm long. It has preserved its convexity and its rear slopes down steeply.

The pygidium, Plate 59, fig. 10, CPC 5873, (associated with a cranidium of *Liostracina volens* sp.nov.) is 1.1 mm long. The axial furrows are quite distinct and enclose the axial lobe completely.

The pygidium, Plate 63, fig. 10, CPC 5921, is 0.5 mm long; its posterior axial lobe is relatively narrow.

*Occurrence and Age:* *Idolagnostus agrestis* sp.nov. occurs abundantly in the O'Hara Shale ('lower chert bed') at localities D6 and D29: It occurs also in the Georgina Limestone, at locality W20. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### IDOLAGNOSTUS DRYAS sp.nov.

(Pl. 60, figs 3-5; Text-fig. 27)

*Material:* Three cephalons are illustrated, selected from a large number of specimens.

*Holotype:* The cephalon, Plate 60, fig. 3, CPC 5875, locality G119 is selected as the holotype because it has retained its test.

*Diagnosis:* *Idolagnostus dryas* sp.nov. is distinguished by its subrectangular cephalon, pointed anterior glabellar lobe and a relatively narrow posterior glabellar lobe which is slightly narrower than the middle part of the glabella; the cephalic furrows are relatively narrow.

*Differential diagnosis:* In *Idolagnostus agrestis* sp.nov. (the type species of the genus) the cephalon is more rounded, the posterior glabellar lobe is wider than the middle lobe, and the furrows are wider and deeper; furthermore, in *agrestis* the cephalic spines are about twice the size of the spines of *dryas*.

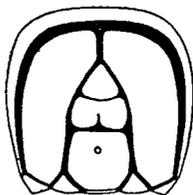


Fig. 27.—*Idolagnostus dryas* sp.nov., from Plate 60, fig. 4.

*Variability:* *I. dryas* is mainly found in the Mungerebar Limestone (Zone of *Erediaspis eretes*); in this material the convexity of the lateral margin varies somewhat. In the higher zone of *Glyptagnostus stolidus* two cephalons have been found which also belong to *I. dryas*. The cephalon Plate 60, fig. 5, CPC 5877, locality D29, is 1.6 mm long; it has the correct subrectangular outline, its posterior glabellar lobe is relatively narrow, the spines are small; but its frontal glabellar lobe is not quite pointed and the furrows are deep—as in *I. agrestis* sp.nov. which is rather abundant in the same bed. Presumably *Idolagnostus dryas* disappeared simultaneously with its junior derivative *I. agrestis*.

*Description:* The diagnosis, the differential diagnosis, and the discussion of the variability, together with the diagnosis of the genus, contain most of the relevant descriptive data.

The holotype is 1.4 mm long; its test is smooth and shiny; the basal lobes are rather small, and the middle glabellar lobe is divided by an incomplete longitudinal furrow into two parts.

The cephalon Plate 60, fig. 4, CPC 5876, locality G429, is also 1.4 mm long. Its test is missing; the flanks are almost parallel, the spines are small, and so are the tumid basal lobes.

*Occurrence and age:* *Idolagnostus dryas* sp.nov. is abundant in the Mungerebar Limestone, at localities G8, G119, G417, and occurs also at G429; at these localities its age is the Zone of *Erediaspis eretes*; it is also recorded from localities G10(?), G124, G127, and G131, in the Zone of *Cyclagnostus quasivespa*. It is rare in the O'Hara Shale ('lower chert bed'), at locality D29, in the Zone of *Glyptagnostus stolidus*. Consequently, *I. dryas* ranges through the total span of the Mindyallan stage.

#### Genus CYCLAGNOSTUS Lermontova, 1940

The Mindyallan agnostid described here as *Cyclagnostus quasivespa* of the subfamily Agnostinae is of some importance in the problems of the agnostid supra-generic classification because it shares with the Glyptagnostinae the scrobiculate structure of the pygidium. *C. quasivespa* is affiliated to a group of forms believed to possess a deuterolobe and placed, therefore, in current classifications in the Pseudagnostinae (q.v.)

A review of the hitherto published information regarding these forms shows, in summary, that: (1) they possess no deuterolobe and have no place in the Pseudagnostinae; (2) *Cyclagnostus quasivespa* sp.nov. is related either to *Acmarhachis* Resser or to *Cyclagnostus* Lermontova, but is closer to *Cyclagnostus*.

Palmer (1962, p. F-19) gives the following synonymy pertaining to *Cyclagnostus*: *Acmahachis* Resser, 1938; *Oedarhachis* Resser, 1938; and *Cyclagnostus* Lermontova, 1940 of the family Pseudagnostidae Whitehouse, 1936. This classification presumes that the posterior axial lobe in the pygidium of these forms is a deuterolobe (pseudo-lobe), homologous with the deuterolobe of *Pseudagnostus*. I think, however, that *Oedorhachis* is a valid genus of the Diplagnostidae (Öpik, 1961, p. 53, 69), and that *Cyclagnostus* and *Acmahachis* belong to the Agnostinae, because inter alia they are axiolobate and not deuterolobate.

Two species as revised by Palmer (op.cit.) belong to *Acmahachis*: *A. typicalis* Resser and *A. acuta* (Kobayashi). In these the pygidial border is wide (wider than in *Cyclagnostus*) and the tumid posterior pygidial lobe definitely contacts the marginal furrow—a combination of characters acceptable as being of generic significance within the Agnostidae. No pseudolobe (=deuterolobe) is present, however, and the forms also possess an articulating device comparable with *Agnostus* and quite different from *Pseudagnostus*.

*Acmahachis acuta* illustrated by Rasetti (1961, p. 109, pl. 23, figs 1-8) is apparently nearer to *typicalis* than to *acuta*, but is distinguished by a very large and prominent pygidial axis.

The genus *Cyclagnostus* is based on *C. elegans* Lermontova, which hitherto was the only known species of its genus. *Agnostus australiensis* Chapman, 1911, based on three specimens from Victoria, may include *Cyclagnostus*-like pygidia; this cannot be decided, however, without a revision of the Victorian material. A third, unnamed species can be included in the genus; it is described by Shaw (1952) from Vermont and attributed to the genus *Acmahachis* Resser, 1938.

Lermontova compared *Cyclagnostus elegans* with *Agnostus*, *Homagnostus*, and the Pseudagnostidae: 'It is apparently an intermediate form between *Agnostus* and *Homagnostus* on one hand, and the family Pseudagnostidae on the other' (op. cit., p. 127; translation A. A. Öpik). Earlier, Kobayashi (1939) had placed *Agnostus australiensis* Chapman (spelled 'australis' by Kobayashi) in the Ptychagnostinae.

Here *Cyclagnostus* is included in the family Agnostidae, for the following reasons: (1) *Cyclagnostus quasivespa* sp.nov. is classified in the first place; (2) *C. quasivespa* does not seem to be closely affiliated to *Pseudagnostus*; (3) some characters suggest a comparison with the Glyptagnostinae *Agnostardis* and *Glyptagnostus stolidotus*; (4) the cephalic and the pygidial acrolobes are not constricted, but have convex flanks; and (5) most conclusive is a comparison with *Agnostus* and *Homagnostus*.

*Cyclagnostus quasivespa* sp.nov. has a well defined pygidial axial lobe, no accessory furrows, and no deuterolobe, and is in this sense primitive and conservative when compared with the complicated *Pseudagnostus*. Their disparity is also expressed in the cephalic structure: *Pseudagnostus* has an angulate glabellar rear and mostly a forward placed median node; but in *quasivespa* the glabellar rear is rounded and the node is placed centrally—conditions seen in *Glyptagnostus stolidotus* and in *Agnostardis amplinatis*, but also in the Agnostinae, Quadragnostinae, and Ptychagnostinae.

The rugosity of the pygidial pleural lobes in the glyptagnostids as well as in *C. quasivespa* gives further reasons to compare these forms with each other. Pygidial

caeca (scrobicules, rugae), however, are also present in *Agnostus pisiformis* (Henningsmoen, 1958, pl. 5, figs 7 and 8) and in *Homagnostus* sp.indet. Shaw (1951, pl. 24, fig. 8); consequently, pygidial caeca are not exclusively a glyptagnostid feature, being also present in the Agnostidae.

Moreover, the articulating device of *Cyclagnostus quasivespa* (pl. 59, figs 1 and 5) is identical with that of *Agnostus pisiformis* (Henningsmoen, op. cit., pl. 5, fig. 2) and *Homagnostus tumidosus*, as illustrated (but not described) by Bell & Ellinwood (1962, pl. 51, figs 2 and 3). The pygidial axis of *C. quasivespa* is closely comparable with the axis of *Agnostus* and *Homagnostus*, but not with the complicated axial lobe of *Glyptagnostus*. Thus, it is most probable that *C. quasivespa* belongs to the Agnostidae and Agnostinae and that it can be placed neither in the Pseudagnostinae nor in the Glyptagnostinae.

The application of the name *Cyclagnostus* Lermontova, 1945, and not of the senior name *Acmahachis* Resser, 1938, for the species *quasivespa* sp.nov. presumes that these are not synonyms and represent a separate genus each. The original type material of *Cyclagnostus elegans* Lermontova and of *Acmahachis typicalis* Resser, however, are insufficiently described and leave open the question of their synonymy. But it appears that *quasivespa* sp.nov. is quite close to *Cyclagnostus elegans* and less close to *Acmahachis typicalis* Resser (1938, pl. 10, figs 4 and 5) and should be placed therefore, for the time being, in *Cyclagnostus*.

The concept of *Cyclagnostus* can be summarized briefly as follows: species of the subfamily Agnostinae equipped with pygidial pleural caeca, with a narrow border, with a rounded (not angulate) rear of the glabella, distinguished by the tumidity of the posterior third of the glabella, and by the large, wide, tumid, pointed and subovate posterior pygidial axial lobe which extends to the marginal furrow or almost so.

#### CYCLAGNOSTUS QUASIVESPA sp.nov.

(Pl. 59, figs 1-7; Text-fig. 28)

*Material:* Two cephalae and five pygidia are illustrated and described; they come from a single locality (G131), and limestone bed, and are selected from a larger number of specimens; supporting information was obtained from the limestone at locality G10, and from silicified material from several other localities.

*Holotype:* The specific uniformity of the material is evident; pygidia and cephalae therefore are equally suitable for selection; the pygidium Plate 59, fig. 1, CPC 5864, showing most of the details is selected as the holotype.

*Diagnosis:* *Cyclagnostus quasivespa* sp.nov. is distinguished by its relatively long and subpentagonal anterior glabellar lobe, short (incomplete) preglabellar median furrow and attenuated and pointed cephalic spines; and in the pygidium by the axial lobe not quite touching the marginal furrow and the clear tripartition of the anterior axial annulation.

*Differential diagnosis:* In *Cyclagnostus elegans* Lermontova the tip of the pygidial axial lobe contacts 'the very margin (=rim) of the pygidium' (Lermontova, op.cit., p. 127) and the anterior glabellar lobe is rounded and relatively broad. Also, on the pygidial posterior axial lobe a rather weak and narrow intranotular axis is indicated.

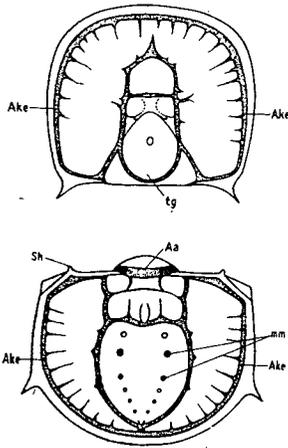


Fig. 28.—*Cyclagnostus quasivespa* sp.nov., combined from Plate 59, figs 1-7. Ake—unstricted acrolobes (flanks convex outward); Tg—glabellar rear (rounded). Pygidium: Aa—articulating device; mm—notulae (two pairs as pits); Sh—fulcrum, pointed.

In the holotype of *Acmarrhachis typicalis* (Resser, 1938, pl. 10, fig. 5), the intranotular axis is distinct and swollen and defined by notular furrows in a manner reminiscent of *Lotagnostus*, and the tip of the axial lobe extends to the marginal furrow. According to Palmer (1962) the last mentioned character is of generic significance. From this discussion a potential synonymy of *Cyclagnostus* and *Acmarrhachis* can be assumed; but the three forms *typicalis*, *elegans*, and *quasivespa* remain a separate species each.

**Description:** *C. quasivespa* is a relatively small to medium sized agnostid en grande tenue, attaining the length of about 8.0 mm. Its furrows are deep, lobes tumid, and pleural lobes rugose. The rugae are, however, low, and discernible mainly along the fringe, and in the scalloped adaxial flanks of the pleural lobes. Scrobicules of any kind are absent. The rim in both shields is rather narrow, convex, and elevated, and the narrow marginal furrows are deep.

The cephalon, slightly wider than long, appears subrectangular, with moderately convex to subparallel flanks, a slightly forward arched front, and strongly curved anterolateral margins. The cephalic spines are deflected sidewise, extenuated, and extended into sharp points. The preglabellar median furrow is deep, but fades out half way from the border.

The glabella, 0.7 of the length, and about 0.3 of the width of the cephalon; is relatively slender; the transverse glabellar furrow is straight and distinct, and deepened subaxially. The anterior glabellar lobe is moderately convex, pentagonal, with an angulate front, and about 0.3 of glabellar length. The posterior lobe is divided in two parts by a pair of broad and oblique lateral notches extending to the midline as shallow furrows and meeting at an almost right angle; the anterior part consists of a pair of tumid lobules. The posterior oval part, pointed in front and rounded in the rear, rises well above the level of the cephalon and bears a subcentral small node.

The basal lobes are triangular, almost equilateral, tumid but low, and connected in the cephalic rear by a connective band.

The pygidium is visibly wider than long; its length without the articulating device is about 0.75 of its width. The margin bears a pair of deflected, extenuated, and pointed spines, and similar but smaller spines directed upward and forward are

placed on the fulcral points. The articulating device is relatively narrow (transversely) and comprises a broad and prominent articulating half-ring arched forward and upward, a deep articulating furrow with deep abaxially placed pits, and a moderate median recess of the front of the axial lobe.

The articulating half-ring is quite different from the narrow half-ring of *Glyptagnostus*, but is identical with the device of *Aagnostus pisiformis* and *Homagnostus*.

The pygidial axis is very long, but its tip equipped with a small terminal node fails to reach the border by the rim's width. A distinct postaxial furrow is present. The axis is constricted at the second annulation to about 0.33 of the pygidial width and the posterior lobe is almost half as wide (0.45) as the pygidium. The axis is divided by two transcurrent furrows; the anterior annulation is short and tripartite; the second annulation is twice as long as the first tripartite, and its median part carries a broad node with a superimposed point. The posterior lobe of the axis is oval, pointed in the rear, and tumid; the intranotular axis is indicated by a low, almost imperceptible, swelling; it is bordered by about six pairs of rarely visible shallow and small notulae converging at the terminal node. In some specimens (e.g. in Plate 59, fig. 3) two pairs of the notulae may be rather conspicuous (compare *Innitagnostus innitens*). The axial lobe in its shape can be compared with the body of an insect.

The test is smooth to the naked eye; in stronger magnification (more than x 20) the test appears densely pitted or reticulate; the pits are shallow.

*Comment on illustrated specimens:*

All specimens come from locality G131.

The holotype pygidium, a mould of the external surface in limestone, is 2.3 mm long. The marginal spines, the pointed fulcra, the median and terminal nodes, and the articulating device are all preserved.

The pygidium, Plate 59, fig. 3, CPC 5866, is 3.0 mm long; two pairs of notulae on the posterior lobe are developed as pits. Weak rugae cover the pleural lobes.

The pygidium, Plate 59, fig. 2, CPC 5865, is 2.2 mm long. It is not flattened as seen in the rear view. Rugae are present.

The pygidium, Plate 59, fig. 4, CPC 5867 is 2.9 mm long. Its articulating device is intact and the preserved right fulcral point has preserved its spine.

The cephalon, Plate 59, fig. 6, CPC 5869, is 2.9 mm long. The extenuated and pointed spine on the right is preserved. Note the tumidity of the glabellar rear.

The cephalon, Plate 59, fig. 7, CPC 5870, is 3.0 mm long. The cheeks are rugose and densely and minutely ornamented by shallow punctae and granules.

The pygidium, Plate 59, fig. 5, CPC 5868, is 3.0 mm long. Its posterior axial lobe is relatively wide; the two pairs of the notulae are rather weak.

*Occurrence and age:* *Cyclagnostus quasivespa* sp.nov. comes from the Mungerebar Limestone localities G6, G10, G124, G130, G131 (the described material), G137(?), and G147; its age is Mindyallan, the Zone of *Cyclagnostus quasivespa*.

CYCLAGNOSTUS? sp.indet.

In the Mungerebar Limestone, at localities G8, G119, G417, and G429, assigned to the Zone of *Erediaspis eretes*, occurs a form which resembles in some aspects *Cyclagnostus quasivespa* sp.nov.

The queried material is too fragmentary for a description; but in these specimens the rear part of the glabella and the posterior axial lobe of the pygidium are less tumid than in *quasivespa*.

CYCLAGNOSTUS sp.aff. QUASIVESPA

(Pl. 59, fig. 8)

The illustrated pygidium, CPC 5871, is 3·7 mm long. It differs from *quasivespa* by its less expanded posterior axial lobe, by the absence of any trace of the postaxial median furrow, and by the less pronounced axial annulations. Two pairs of weakly impressed notulae are present in the same position as in *Cyclagnostus quasivespa* (Plate 59, fig. 3.)

*Occurrence and age:* The specimen was found in the Mungerebar Limestone at locality G9, together with *Hypagnostus correctus* and *Ptychagnostus fumicola*. Its age is the Middle Cambrian/Upper Cambrian Zone of passage.

Genus PROAGNOSTUS Butts, 1926

No agnostids referable to *Proagnostus* are described here; the genus must be discussed, however, because this name has been applied in the literature to diverse forms which are affiliated with several Mindyallan genera.

The generic name *Proagnostus* is applicable only to its type species—*P. bulbus* Butts, of which only one specimen (the holotype) is known. In the literature, however, the name has been applied to forms which can be distributed among our new genera *Ammagnostus*, *Agnostascus*, *Connagnostus*, and *Hadragnostus*.

According to Palmer (1962, p. F 13) the description (diagnosis) of *Proagnostus* was first published by Shimer & Shrock, 1944, which year should be accepted as the date of the validation of the name and the concept of *P. bulbus* Butts. Before then, illustrations, but no descriptions nor references to published description, had been published.

The holotype of *P. bulbus* Butts (in Shimer & Shrock, op.cit., and in Resser, 1938, pl. 10, fig. 21) belongs to the family Agnostidae and resembles a *Homagnostus* distinguished by a faint but complete preglabellar median furrow. Consequently Howell in Harrington et al. (1959) with good reason regards *Proagnostus* as a synonym of *Homagnostus* Howell, 1935. But Howell dates *Proagnostus* with the year 1926, thus acknowledging its priority and simultaneously suppressing it in favour of its junior synonym *Homagnostus*. When, however, the date of the validation of the name *Proagnostus* is accepted as 1944 *Homagnostus* should prevail.

Palmer (op.cit) published an extended description of *Proagnostus* essentially based on the holotype, and maintains the independence of the genus from *Homagnostus*. At this point further comment is reserved.

A second specimen (Resser, op.cit., pl. 10, fig. 17) has been also traditionally quoted as *Proagnostus bulbus* Butts. This specimen is not conspecific with *bulbus*, and belongs to another subfamily or even family because (1) its acrolobes are constricted; with concave flanks of the cheeks and the pygidial pleural lobes, (2) the rear

of the glabella is angulate, (3) the median nodes are long and elongate, and (4) the glabellar node has a forward position as in *Pseudagnostus*. These are characteristics of *Agnostascus* gen.nov. (q.v.).

*Proagnostus centrensis* Resser, 1938, was selected by Lochman (1944) as the type of her new genus *Baltagnostus*; this genus is distinguished by its *Diplagnostus*-like pygidial collar and is accepted here in the Diplagnostidae. *Proagnostus modestus* Lochman, 1944, however, is neither a *Proagnostus*, a *Baltagnostus*, nor a *Homagnostus*, but appears congeneric with *Hadragnostus las* gen. et sp.nov. (q.v.)

*Baltagnostus beltensis* Lochman, 1944, quoted by her (op.cit., p. 164) as 'n.gen. nov.sp.', belongs probably to *Ammagnostus* gen.nov. if the forward position of what appears the terminal node and the distribution of notulae in the holotype pygidium (Lochman, op.cit., pl. 10. fig. 3) are inherent and not accidental features. If, however, the node is truly terminal the generic name *Kormagnostus* should be favoured as suggested by Palmer (1954, p. 718).

Finally, Palmer (1962, p. 14) applied the name *Proagnostus*? to agnostids related to *Connagnostus venerabilis* gen.nov., sp. nov., but also indicated the probability that his material represented a new genus.

#### Family CLAVAGNOSTIDAE Howell, 1937

The following genera belong to the family Clavagnostidae:

1. *Clavagnostus* Howell, 1937, with *C. repandus* (Westergaard) as its type. This is a form with a forward arched (not angular) cephalic front and without a preglabellar median furrow. A median pygidial marginal spine is absent.

2. *Clavagnostus sulcatus* Westergaard, 1946, which has been assumed congeneric with *C. repandus*, has an angular (pointed) cephalic front and a preglabellar median furrow—characters indicating a close affiliation with *Aspidagnostus* Whitehouse, 1936. According to Westergaard (1946, p. 57) the pygidium of *sulcatus* resembles *Tomorhachis spinosa* Resser, 1938, whose cephalon, however, is unknown. Consequently, *Tomorhachis* cannot be an unquestionable synonym of *Clavagnostus*, but can be interpreted as a subgenus of the latter, or even a separate genus of the family. Of course, the cephalon of *Tomorhachis* should be identified before introducing a new generic (or subgeneric) name for *C. sulcatus*.

3. *Stigmagnostus* Poulsen, 1960, refers to *Tomagnostus canotensis* Rusconi, 1951 (Poulsen, op.cit., p. 15). It appears that Poulsen's specimen (op.cit., pl. 1, fig. 12) is not a pygidium, but a cephalon of a clavagnostid; the pitted cheeks recall *Aspidagnostus*, but the cephalic front is arched (not angular) as in *Clavagnostus*. The cephalon attributed by Poulsen (op.cit., pl. 1, fig. 11) to *Stigmagnostus* belongs possibly to an *Oedorhachis*, or *Oidalagnostus*, or a *Baltagnostus*-like agnostid.

4. *Aspidagnostus* Whitehouse, 1936, is the first named genus of the family. Öpik's (1956, p. 21) statement that 'the cephalon of "*Aspidagnostus*" is a *Clavagnostus* Howell'—is erroneous: the name *Aspidagnostus* has the

nomenclature priority, and *Clavagnostus* can be regarded as its subjective junior synonym. It all depends on the taxonomic significance attributable to the presence or absence of an unpaired pygidial spine, a pointed cephalic front and zonate pygidium.

5. *Triadaspis* gen.nov. whose only known species (*T. bigenerus* sp.nov.) possesses characters of *Aspidagnostus* and *Oidalagnostus*.

*Rhaptagnostus acutifrons* Troedsson, 1937, was placed by Kobayashi (1939, p. 164) (under the name of 'acutus') in *Aspidagnostus*; it should, however, remain in the Pseudagnostinae.

## Subfamily CLAVAGNOSTINAE Howell

### Genus CLAVAGNOSTUS Howell, 1937

#### CLAVAGNOSTUS BISECTUS sp.nov.

(Pl. 55, figs 6-9)

**Material:** The illustrated material consists of two cephala from the O'Hara Shale, one cephalon from the Georgina Limestone, and one pygidium from the Mungerebar Limestone. The specific identity of the pygidium can be questioned because it comes from beds older than the holotype. Cephala (although fragmentary) associated with the pygidium are, however, not separable morphologically from the specimens of the O'Hara Shale; moreover, the pygidium and the cephalata belong to the same group of *Clavagnostus sulcatus*.

**Holotype:** The largest cephalon, Plate 55, fig. 8, CPC 5820, from the O'Hara Shale ('lower chert bed'), locality D29, is selected as the holotype because of its size.

**Diagnosis:** *Clavagnostus bisectus* is a species of the *C. sulcatus* group (cephalon with a preglabellar median furrow, and pygidial axis pointed in the rear) distinguished by the forward arched (but not angulate as in *C. sulcatus*) cephalic front, rounded to subangulate (but not pointed) glabellar front, forward placed (not central) glabellar node, and relatively long anterior part of the pygidial axial lobe. The pygidium is simplimarginate.

**Differential diagnosis:** *C. sulcatus* Westergaard, 1946, is the nearest species; its distinguishing characters are indicated in parenthesis in the diagnosis above.

**General classification:** In discussing the genus *Clavagnostus* the possibility is indicated that the *C. sulcatus* group of species may represent a subgenus of, or a genus distinct from, *Clavagnostus* Howell, and that *Tomorhachis* Reisser is the name reserved for this group. No decision, however, can be made because the cephalon of *T. spinosa* Reisser, 1938, is unknown and the taxonomic significance of its pygidial characters cannot be evaluated with certainty.

**Description:** The cephalon is semielliptical, as long as wide, strongly convex, with cheeks overhanging the border in the rear. The rim is narrow, and the marginal furrow is narrow and deep; the frontal margin is evenly arched forward, without any angularity. The preglabellar median furrow is narrow and deep, but slightly flaring in front. The glabella in larger specimens is half the length of the shield, but in smaller it is somewhat longer. It tapers to about half its posterior width

and is subangulate to rounded in front. The median node is long, very low, and placed on the anterior half of the glabella; on small specimens the node is obscure and may be even missing. The basal lobes are small and tumid and the spines are relatively short.

In the pygidium the spines are placed at about the posterolateral angles. The anterior part of the axial lobe is longer than half the shield, and the posterior is rather short, with a pointed tip not quite reaching the marginal furrow. In the anterior lobe only the first annulation is indicated by weak lateral notches, and the axial node is very small and low.

The test is smooth.

*Comment on illustrated specimens:*

The holotype cephalon, in friable silica, is 1.9 mm long. The right spine has lost its tip. The node (crest) on the anterior half of the glabella is distinct. The glabella is half as long as the shield.

The cephalon, Plate 55, fig. 7, CPC 5819, locality D29, in friable silica, is 1.6 mm long, and smaller than the holotype; its glabella is 0.55 the shield length.

The cephalon, Plate 55, fig. 6, CPC 5818, locality W1, in limestone (a calcite pod), is 1.3 mm long and smaller than the other specimens; its glabella is 0.65 of shield length; the glabellar node is indistinguishable, and the glabellar front is angulate.

The pygidium, Plate 55, fig. 9, CPC 5821, locality G417, silicified and etched out from limestone, is 1.9 mm long; its lateral spines are broken.

*Occurrence and age:* *Clavagnostus bisectus* sp.nov. occurs in the O'Hara Shale ('lower chert bed') at locality D29 and in the Georgina Limestone at locality W1—in the Zone of *Glyptagnostus stolidotus*; it occurs also in the Mungerebar Limestone at localities G417 and G429 in the Zone of *Erediaspis eretes*; consequently its known age is Mindyallan.

### Subfamily ASPIDAGNOSTINAE Pokrovskaja, 1960

#### Genus ASPIDAGNOSTUS Whitehouse, 1936

The type species of *Aspidagnostus* is *A. parmatus* Whitehouse, 1936. The holotype is a cephalon (Whitehouse, 1936, pl. 9, fig. 5) distinguished by the following features: (1) the glabella widens forward, (2) the glabellar front is rounded (not pointed), (3) the glabella carries a long node, (4) the glabella lacks a transverse, transcurrent furrow, (5) the preglabellar median furrow is present (as in *Clavagnostus sulcatus*), (6) the cephalic front is not arched, but angular as in *C. sulcatus*, and (7) the cheeks are scrobiculate (blistered).

According to Whitehouse, basal (accessory) lobes are absent in *Aspidagnostus parmatus*; but the holotype cephalon (judging from the illustration) is fragmentary and its occipital part is insufficiently preserved; consequently the presence or absence of the basal lobes cannot be established with certainty. Basal lobes are shown in the reconstruction of *A. parmatus* in Harrington et al., (1959, p. 173), but its cephalic front is arched (and not angular as seen in the original illustration).

The affiliation of *Clavagnostus* (1937) and *Aspidagnostus* (1936) passed unnoticed (1) because *C. sulcatus*, which is an 'intermediate' form, became known only in 1946, (2) because the pygidium attributed by association to *Aspidagnostus parmatus* by

Whitehouse (1936, pl. 9, fig. 6) is not clavagnostid; such pygidia (e.g. *Pseudagnostus leptoplastorum* Westergaard, 1944) have been found later without being associated with *Aspidagnostus*, or clavagnostid cephalo. The correct pygidium is evident from *Aspidagnostus rugosus* Palmer (1962, pl. 1, figs 24–30), which is related to *A. parmatius* Whitehouse (scrobiculate cheeks and bluntly rounded, forward expanding glabella); it possesses a clavagnostid pygidium.

The subfamily Aspidagnostinae Pokrovskaja, 1960, was established bona fide—in acceptance of the original generic diagnosis (Whitehouse, 1936), which refers to the ‘associated pygidium’ as well.

*The concept of Aspidagnostus:* The concept of the genus is conveniently presented in two parts; first its familial (clavagnostid), and secondly its generic characters.

Familial characters of *Aspidagnostus* are (1) a relatively long glabella, whose transverse furrow is absent or vestigial. Kobayashi’s (1939) idea that in the clavagnostids the frontal lobe is not obsolete but confluent with the posterior lobe finds support in *A. inquilinus* sp.nov. (Text-fig. 31), in which the division into a frontal and a posterior glabellar lobe is indicated by a vestigial transverse partition. Hence, the intersegmental transverse furrow has disappeared and the glabella is completely fused—an advanced stage in cephalization, unique in Cambrian agnostids. (2) A relatively wide posterior cephalic border carrying the tumid base of the spines. In other agnostids the spines arise from the margin of the border. In all agnostids, however, including the Clavagnostidae, the cephalic spines are placed at the fulcral geniculations and not on the genal angles. (3) The pygidial axis is long and pointed and carries a pair of elongate pits behind its middle.

The genus *Aspidagnostus* is distinguished by the following characters: (4) the cephalic front is angular in all species; (5) the basal lobes are composite; (6) the glabella is fundamentally trilobate and crossed in its rear by a second transverse furrow; (7) the pygidium is trispinose; (8) the pygidial rear between the lateral spines consists of a depressed flange and an elevated collar (the pygidium is zonate); (9) the collar is crossed by a deep median gap which is flanked by a pair of knobs; the pygidial axis is quadrilobate (segmented) and bears a strong terminal node on the third lobe; and (11) the pygidium as well as the cephalon have branching caeca, but the scrobiculation may be latent.

The median ogive of the cephalic front and the posterior pygidial spine are not correlated features (*C. sulcatus* has an ogive but no median pygidial spine; *Oidagnostus* possesses a median pygidial spine but no frontal angulation).

The narrow but prominent occipital collar (occ. in Text-figs 29–31) of *Aspidagnostus* is, probably, not diagnostic generically, being apparently overlooked in many other agnostids.

In the articulating device the half-ring is arched rearward. It is distinct from *Glyptagnostus* and *Pseudagnostus*, and from the device of *Aagnostus*, *Peronopsis*, and other Middle Cambrian forms.

The zonate pygidial rear of *Aspidagnostus* between the lateral spines, consisting of the depressed marginal flange and the elevated collar divided by the median gap, is rather different from *Clavagnostus*, but very close to *Oidagnostus personatus*

sp.nov. Furthermore, in *Aspidagnostus* and *Oidalagnostus* the axial lobe is quadrilobate and the margin trispinose—consequently pygidia of *Aspidagnostus* and *Oidalagnostus* are of a fundamentally similar design. In the pygidia they differ only in having one a trigonal and the other a tumid trapezoidal posterior lobe. This similarity of the pygidia is too close to be accidental and an affiliation should be considered; but the disparity of the cephala is against such a possibility. It can be speculated, however, that *Clavagnostus* and *Aspidagnostus* arose together from an unknown diplagnostid, but *Aspidagnostus* underwent changes that obliterated completely the original diplagnostid cephalic design. In *Oidalagnostus*, however, the diplagnostid cephalon remained unchanged.

Another intermediate form is *Triadaspis bigeneris* gen.nov. et sp.nov. It can be interpreted as an *Aspidagnostus* with an unreduced posterior axial lobe of the pygidium, or a simplified *Oidalagnostus* with a pointed axis and undivided median crest. The similarity of *Aspidagnostus*, *Oidalagnostus*, and *Triadaspis* invokes the notion that the agnostid families are objectively much closer to each other than appears from the multitude of their familial taxa.

#### ASPIDAGNOSTUS PARMATUS Whitehouse, 1936

*Aspidagnostus parmatus* Whitehouse (1936, p. 105, pl. 9, fig. 5; not the pygidium, fig. 6) as well as its subsequent interpretations, are discussed under the heading of the genus *Aspidagnostus*. In brief, the species is characterized by its scrobiculate cheeks ('traversed by irregular radial furrows') and forward expanded glabella ('contracted at the base'), which probably is bluntly rounded in front; the frontal margin is angulate.

The usage of the specific name *parmatus* should be restricted for the time being to the holotype only (1) because its state of preservation and the original illustration are insufficient for detailed comparison, and (2) because its stratigraphic position remains speculative (Idamean or Mindyallan).

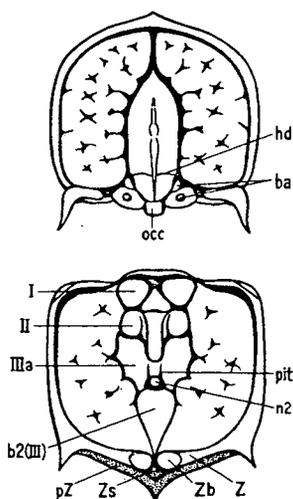


Fig. 29.—*Aspidagnostus stictus* sp.nov., cephalon combined from Plate 55, figs 10 and 15; pygidium from Plate 55, fig. 11. ba—basal lobe (double, and with a central node); hd—posterior transverse furrow; I—anterior, II—middle, and IIIa—posterior axial annulation; b2 (III)—intranotular axis; n2—terminal node; pit—*Clavagnostus* pit (a pair of pits); Z—pygidial collar (the pygidium is zonate); Zb—knob on collar; Zs—median gap (between the knobs); pZ—depressed margin behind collar.

According to Whitehouse (1939, p. 268) *Aspidagnostus parmatus* was found in association with *Idamea superstes* Whitehouse at a locality which, I think, should be in the vicinity of Mount Idamea—our locality W16. If so, *A. parmatus* is possibly not younger than the Idamean *Corynexochus plumula*, and apparently not older than the *Glyptagnostus stolidotus* Zone (upper part), that is, late Mindyallan.

ASPIDAGNOSTUS sp.indet.

Worn cephalo of an *Aspidagnostus* with pitted cheeks occur sporadically in the Mungerebar Limestone, as for example, at locality G153 (specimen CPC 6740) and, probably, G119. These specimens are insufficiently preserved to warrant illustration and further description, although they are not referable to any of the described species. It is even possible that they are the cephalo of *Triadaspis bigeneris*, which is based on pygidia only.

ASPIDAGNOSTUS STICTUS sp.nov.

(Pl. 55, figs 10–15; Text-fig. 29)

*Material:* Three cephalo and three pygidia are selected from about fifteen specimens of two kinds of preservation: (1) a cephalo and a pygidium from locality B259 are relatively little flattened, and not corroded, and are embedded in a grey fine-grained limestone, and (2) two cephalo and two pygidia come from locality D126, where all specimens are visibly flattened and most have a corroded test; the matrix is a grey laminated sandy and marly limestone.

*Holotype:* Most of the holotypes of the species of *Aspidagnostus* are cephalo; only one species (*A. rugosus* Palmer) is based on a pygidium. Hence, a cephalo—Plate 55, fig. 10, CPC 5822, locality B259—is selected as the holotype of *A. stictus*.

*Diagnosis:* *Aspidagnostus stictus* sp.nov. is a species with a relatively long and pointed glabella, acute glabellar tip, and sparsely pitted and scrobiculate, as well as minutely granulate, test.

*Differential diagnosis:* In *Aspidagnostus parmatus* Whitehouse and *A. rugosus* Palmer the test is scrobiculate, but in a different manner; but in these species the glabella is obtuse and short. *Clavagnostus? lunulosus* Kryskov (1963, p. 276, Pl. 1, figs 16, 17) is also an *Aspidagnostus* (L. N. Kryskov, personal communication). It is close to *A. stictus* and of the same age (associated with *Glyptagnostus reticulatus*), but is distinguished by its rectangular glabellar tip and slightly wider glabella, and its test is apparently smooth. The illustrations, however, are too small for further comparison.

*Description:* The cephalo is slightly wider than long, with a narrow rim and narrow marginal furrow. The median preglabellar furrow is deep and connects with the marginal furrow; the front is angular, forming a low ogive. The spines, arising from their tumid bases, turn abruptly rearward. The cheeks are moderately convex, sloping outward and toward the glabella, and are sparsely pitted, having about ten pits each arranged in two irregular concentric rows. Short shallow straight scrobicules connect some of the pits with the axial furrows and occur also along the periphery of the cheeks. The axial furrows are deep and narrow. The margin of the cheeks at the axial furrows is scalloped. The glabella is relatively

long, about 0.7 of the cephalic length, and narrow, about 0.25–0.27 of its width. It is oval, with almost straight flanks, bluntly rounded rear, and a trigonal front with a prick-like point. The posterior quarter of the glabella is separated from the rest by a shallow transverse furrow; a long narrow carina thickened in its middle into a small node extends from the rear over three-quarters of the glabella. The basal lobes are composite; an anterior, rather small pair of lobes nesting in the glabellar flanks is followed rearward by a pair of large triangular lobes each bearing a small tubercle. Extending from the glabellar rear and flanked by the adaxial corners of the basal lobes, the semicylindrical occipital collar extends beyond the marginal line.

The pygidium is zonate. It is also slightly wider than long (without the median spine). The rim is convex, narrow in front, and wide in the rear. Between the lateral spines it possesses a depressed flange which bears the median spine. Above the flange the collar is divided in the middle by the median gap which extends into the base of the spine; and the adaxial ends of the collar are thickened into a pair of elevated knobs flanking the gap. The pleural lobes are moderately convex, sparsely and somewhat irregularly pitted, and scalloped along the axial furrows by short scrobicules; two pairs of these pits opposite the third axial lobe are stronger than others, and occur also in *A. inquilinus* sp.nov. The articulating device consists of the articulating half-ring, which is arched rearward, and a curved articulating furrow combined with an articulating recess in the front of the axial lobe.

The axial lobe is long, reaching the border, and consists of four lobes; these comprise together more than four metamers. The posterior lobe, elongate, triangular, depressed, and pointed, is placed behind the terminal node, separated from the rest by a deep transverse furrow, and represents apparently the intranotular axis. The terminal node is rather conspicuous and flanked by a pair of elongate pits (the 'clavagnostid pits'). The three anterior lobes are tripartite, divided by a long axial node which reaches to the middle of the third lobe. The second lobe is rather narrow, the first and third are equally wide.

The test is minutely granulose.

*Comment on illustrated specimens:*

The holotype cephalon, locality B259, is 2.3 mm long, and slightly wider than long; the illustrated internal cast is borderless, but the border is preserved in its counterpart. The external granulation is visible, mostly along the furrows.

The pygidium, Plate 55, fig. 11 CPC 5923, associated with the holotype, is 2.0 mm long and slightly wider than long; its test is preserved; it is granulose, but the pits are weak; the posterior part of the axial lobe is damaged.

The next four specimens are from locality D126.

The cephalon, Plate 55, fig. 15, CPC 5827 is 2.3 mm long. The pits and scrobicules and the central glabellar node are distinct.

The cephalon, Plate 55, fig. 14, CPC 5826 is 2.3 mm long; it is complete with the frontal ogive, but the test is corroded.

The pygidium, Plate 55, fig. 12, CPC 5824, is 2.5 mm long; the posterior median marginal spine is preserved.

The pygidium, Plate 55, fig. 13, CPC 5825, is 1.9 mm long—the smallest specimen in the collection. The test is corroded.

*Occurrence and age:* *Aspidagnostus stictus* sp.nov. has been found only in the Pomegranate Limestone at Wills Creek, at the foot of the De Little Range at localities D126 and B259. Its age is the Idamean Zone of *Glyptagnostus reticulatus* (lower part).

ASPIDAGNOSTUS INQUILINUS sp.nov.

(Pl. 41, fig. 11; Pl. 45, fig. 1; Pl. 56, figs 1–10; Text-figs 31–33)

*Material:* The illustrated material consists of seven cephalata and five pygidia selected from a large number of specimens. The selection was made to present (1) three different kinds of preservation—in calcite pods in limestone, in marly limestone, and in shale, and (2) three geographical occurrences (Glenormiston, De Little Range, and Selwyn Range areas)—Glenormiston is 120 miles from Selwyn and the De Little Range is halfway between them. The length of all examined specimens lies in the range 2.0–3.5 mm; consequently only mature individuals are present.

The material from Glenormiston (locality W1) and from the Selwyn Range area (D29), each embedded in a single bed, can be regarded as samples of two geographically separate populations; the absence of shields smaller than 2.0 mm, even two separate sojourning swarms of adults can be assumed that left behind their exuviae. At the De Little Range *Aspidagnostus inquilinus* is rather rare and no swarm is apparent. At Glenormiston scattered fragments occur in several more localities and beds.

All recorded occurrences are referable to a single zone (*Glyptagnostus stolidotus*) but their time relationship within the limits of that zone cannot be estimated. *A. inquilinus* cannot be regarded as being an indigenous Queensland species.

*Holotype:* The cephalon plate 56, fig. 1, CPC 5828, locality W1, is selected as the holotype because it shows the most common shape of the glabella.

*Diagnosis:* *Aspidagnostus inquilinus* sp.nov. is a species with (1) a pentagonal cephalon, (2) a smooth test, (3) obscure cephalic and pygidial scrobiculation, (4) double basal lobes, and (5) pointed glabella distinguished by its oval shape.

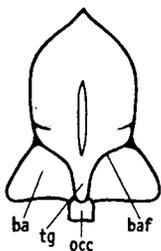


Fig. 30.—*Aspidagnostus laevis* Palmer, outline of glabella and basal lobes, adapted from Palmer (1962, Pl. 1, fig. 22) to show attenuated glabellar rear and simple basal lobes (compare *A. inquilinus* sp.nov., Text-fig. 31). ba—basal lobes; baf—basal furrow (between glabella and basal lobe); occ—occipital collar; tg—drawn-out rear of glabella.

*Differential diagnosis:* *A. laevis* Palmer from Nevada has an extenuated glabellar rear (Text-fig. 30) and apparently simple basal lobes, but otherwise appears to be close to *inquilinus*; the Australian *A. stictus* sp.nov. has a similar oval and pointed glabella and double basal lobes, but differs in having a granulose test, cheeks and pygidial pleurae pitted, and a relatively long glabella; it is younger than *inquilinus* and *laevis*, which both are of about the same age.

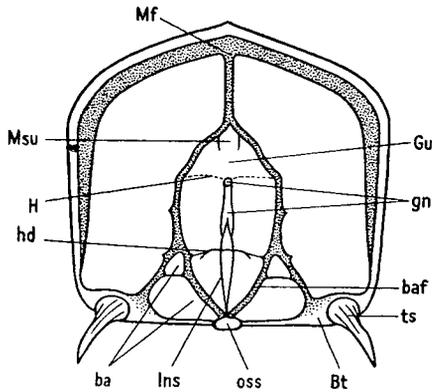


Fig. 31.—*Aspidagnostus inquilinus* sp.nov., from Plate 56, fig. 7. ba—basal lobes; baf—basal furrow; Bt—posterior border; gn—median node; Gu—frontal lobe of glabella; H—transverse glabellar furrow; hd—posterior transverse furrow; lns—posterior lines; Mf—preglabellar median furrow (connects marginal furrow; see Text-fig. 32); Msu—tip of glabella flanked by furrows; occ—occipital collar; ts—cephalic spine (with striae).

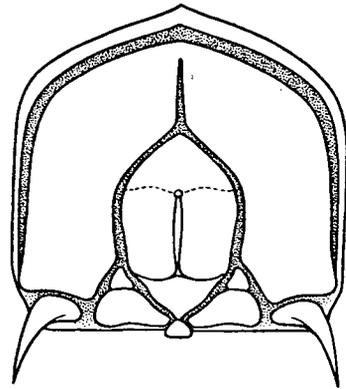


Fig. 32.—*Aspidagnostus inquilinus* sp.nov., after Plate 56, figs 1, 2. The median preglabellar furrow is disconnected from the marginal furrow (see Text-fig. 31).

*Description:* The cephalon is pentagonal and as wide as long; its lateral margins are parallel in unflattened specimens; about opposite the middle of the preglabellar area the margins curve adaxially and meet at an obtuse angle (of about  $138^{\circ}$ – $140^{\circ}$ ) in the middle, as a slightly expressed frontal ogive; the tip itself is curved downward. The marginal furrow is rather deep, relatively wide in front, but narrows rearward; the flanks of the cheeks, however, are not parallel to the lateral margin, but converge visibly forward.

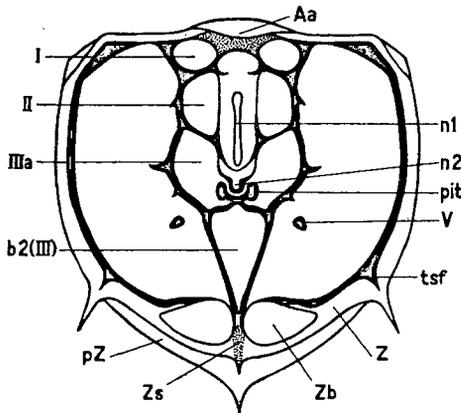


Fig. 33.—*Aspidagnostus inquilinus* sp.nov., pygidium from Plate 56, fig. 5. I—anterior, II—middle, and IIIa—posterior axial annulation; Aa—articulating device; b2 (III)—intra-nodular axis; n1—median node; n2—terminal node; pit—'Clavagnostus' pit (a pair of pits); tsf—furrow at base of spine; V—scrobicule (scrobicular pit); Z—pygidial collar (the pygidium is zonate); Zb—knob on collar; Zs—median gap (between knobs); pZ—depressed margin behind collar.

The posterior margin is straight, the posterior border wide and flat—a peculiarity of *Aspidagnostus*. It carries the broad and tumid bases of the spines, and the spines are relatively long, slender, and directed almost rearward. In one specimen (Pl. 56,

fig. 7) the spines are longitudinally striate. In the middle a small semicylindrical occipital collar protrudes rearward beyond the margin.

The median preglabellar furrow is deep and narrow; it may be connected to the marginal furrow, or fade out shortly before reaching it.

The cheeks are moderately arched upward and at the posterior lateral corners expand laterally and become tumid. Owing to this tumidity the cephalic acrolobe appears somewhat constricted. Rugae or scrobicules are absent in most of the specimens, but the edge of the cheeks along the axial furrows is scalloped—a sign of deep-seated caecal glands.

The basal lobes are triangular, large, tumid, and composite, with an anterior pair of small lobules separated by distinct but shallow transverse furrows. The flanks of the basal lobes against the glabella are concave (convex in *Aspidagnostus laevis* Palmer, Text-fig. 30). The adaxial tips of the lobes are close to each other, but remain separated by the hour-glass junction of the occipital collar and the glabellar rear. Between the adaxial tips of the lobes and the base of the spines the floor of the posterior border is flat.

The axial furrows are deep and narrow and nowhere crossed by diverticular ducts, which, therefore, are deep-seated.

The glabella is moderately convex and elevated above the cheeks, but coincides with the transverse and longitudinal arcs of the acrolobe; the anterior part of the median crest is the summit of the cephalon. The glabella is oval, pointed in front and rear, but its flanks are convex (compare *A. laevis*, Text-fig. 30). In Text-figure 32 the commonly visible glabellar features are shown—which should be considered taxonomically in the first place; in Text-figure 31, however, such features are explained as cannot be exploited taxonomically because they are mostly undetectable in other specimens.

The glabella is commonly 0·6 of cephalic length, but shorter glabellae (0·58) may occur; the width/length ratio is variable between 0·5 (peeled material, mostly De Little Range and Selwyn Range specimens), and 0·55–0·6. The glabella is widest about the middle of its anterior half; it is trilobate, as indicated by two vestigial transverse partitions (furrows). The anterior partition is the transverse glabellar furrow (H)—a fundamental feature of all agnostids. The frontal lobe is triangular, with sharp point which may be swollen and accentuated by a pair of feeble longitudinal short furrows comparable with the frontal sulcus of *Glyptagnostus*. The posterior transverse furrow (hd) is a transverse depression between the anterior tips of the basal lobes, distinguishable in all specimens of *A. inquilinus* and even of *A. stictus*; it is a feature of generic significance, being absent in other agnostids. The posterior glabellar lobe is also triangular and pointed. The middle glabellar lobe bears a narrow, low, but conspicuous crest; in its front a tiny node is always visible; in the rear the crest forks and continues as a pair of delicate lines (posterior lines) which meet at the rear tip of the glabella.

The pygidium is zonate; it is as wide as long (the median spine included), with a well rounded outline; its lateral margins are convex (in the cephalon they are straight). The acrolobe is evenly and gently arched, unconstricted, and has the node on the second axial annulation as its summit. The posterior, triangular part of the axis remains, however, depressed below the level of the pleural lobes.

The rim is convex and widens rearward; the marginal furrow is deep and narrow. The lateral spines are usually slender, slightly curved, and deflected sidewise. The posterior margin between the lateral spines passes in two sigmoidal curves into the median spine; the base of all the three spines is furrowed.

The posterior flange (a part of the rim) is thickened in the middle and defined by a furrow; laterally it passes into a depressed step. The collar is prominent, connected with the marginal spines and crossed in the middle by the postaxial median gap; the parts of the collar flanking the gap are swollen into a pair of prominent oval knobs.

The pleural lobes are scalloped along the axial furrows, but only one pair of short scrobicules is usually present. A pair of isolated scrobicular pits is placed behind the third annulation in line with the anterior section of the axial furrows.

The shoulders are steeply geniculate and narrow, the fulcral points rounded, and facets are quite small.

The articulating half-ring is lip shaped, arched upward and rearward, and the articulating furrow is narrow; an articulating recess in the front of the axis is indicated.

The axial lobe is elaborate, almost baroque in appearance. It is long, extending into the median gap of the collar; it has a constricted second and laterally expanded third annulation with rounded and rearward-converging flanks. The anterior three annulations are tripartite, the long median node being the dividing middle part. It bears a narrow crest, and a node in the middle of the second annulation, and a point is also present on the rear end of the crest; from here rearward the annulated part of the axis is depressed, and the whole structure ends in a prominent terminal node flanked by a pair of deep pits.

The first axial annulation is relatively short and wide, and its lateral parts are well rounded and oval; the lateral parts of the second annulation are elongate and combined with the much longer dividing node form the figure of a cross with stout bars. The third annulation is the longest and its lateral parts are swollen; it is the widest part of the axial lobe, as wide as 0.33 of the shield on the same level.

The three anterior axial annulations constitute a unit separated from the posterior lobe by a deep transverse furrow.

The posterior (fourth) axial lobe is triangular and pointed; it is laterally defined by rather deep furrows. These furrows have the position of notular lines of forms like *Agnostotes* and *Pseudagnostus*, or even *Oidalagnostus*, and are regarded, therefore, as notular furrows; consequently in the posterior part of the axial lobe only the intranotular axis is developed; the posterior sections of the axial furrows are obsolete and the extranotular parts of the axial lobe are confluent with the pleural lobes.

*Comment on illustrated specimens:*

A. Specimens from the Georgina Limestone, locality W1. The matrix is dark grey bituminous limestone with irregular pods of relatively coarse calcite.

The holotype cephalon, Plate 56, fig. 1, CPC 5828, is 3.0 mm long; a large part of the test is preserved, the left spine is broken; the frontal rim is flattened and a faint flange indicates the presence of a narrow doublure.

The cephalon, Plate 56, fig. 3, CPC 5830, is 2.7 mm long; holes on the right cheek are referable to tips of calcite crystals. The occipital collar is well visible; the preglabellar furrow connects the marginal furrow; the frontal tip is curved downward; the cheeks are scalloped along the axial furrows.

The cephalon, Plate 56, fig. 2, CPC 5829, is 3.0 mm long; the basal lobes and the posterolateral corners of the cheeks are rather tumid, the median preglabellar furrow is short and the glabellar front is less acute than in the other specimens; some details invisible in the photograph are shown in Text-figure 32.

The pygidium, Plate 56, fig. 4, CPC 5831, is 3.0 mm long (without the median spine); the posterior flange is laterally indistinct, apparently owing to the mode of preservation of the test; the pleural lobes are scalloped along the axial furrow; the lateral spine is relatively small.

The pygidium, Plate 56, fig. 5, CPC 5832, is 3.0 mm long (to the tip of the median spine). The main scrobicules (Text-fig. 33, V) are distinct. The lateral spines are slender.

B. Specimens from the De Little Range, Pomegranate Limestone, locality B537. The matrix is a grey sandy and slightly marly limestone and the fossils are in some of its layers flattened by compaction.

The cephalon, Plate 56, fig. 7, CPC 5834, is 3.5 mm long; it is somewhat flattened. The spines are longitudinally striate; the median preglabellar furrow joins the marginal furrow; the cheeks are scalloped along the axial furrow. Some delicate details (Text-fig. 31) which remain invisible in the rest of the specimens, are exceptionally well preserved: they are anatomically important, but cannot be exploited taxonomically.

The pygidium, Plate 56, fig. 6, CPC 5833, is about 2.2 mm long; it is flattened and decorticated and the posterior flange is distinct; the lateral spine is relatively long and robust.

C. Specimens from the Selwyn Range area (O'Hara Shale, 'lower chert bed'). The matrix is silica: hard chert with unflattened fossils, and shale with variously flattened fossils.

The cephalon, Plate 56, fig. 10, CPC 5837, locality D6, is 2.5 mm long; the matrix is chert; the preglabellar median furrow is long; the roughness of the surface is the reflection of the granularity of the silica replacing the test.

The cephalon, Plate 45, fig. 1, CPC 5714, locality D28, in a shale lamina in chert, is 3.0 mm long; it is completely flattened and dilated in the rear, showing the rim not concealed by the overhanging cheeks.

The pygidium, Plate 41, fig. 11, CPC 5687, locality D29, is about 2.0 mm long; its test is preserved, but flattened in friable matrix. The surface features (lobes and furrows on the axis) are inconspicuous owing to the flattening.

The pygidium, Plate 56, fig. 8, CPC 5835, locality D29, in friable silica, is 2.0 mm long. The test is replaced by granular silica, which produces a false granulation and lessens the relief of the axial lobe. The posterior flange is well developed and the posterior spine is intact; the median gap extends into the base of the spine.

The cephalon, Plate 56, fig. 9, CPC 5836, locality D6, is 3.0 mm long. It is very close to the holotype as regards its size, shape of the glabella and the incompleteness of the median furrow, which is disconnected from the marginal furrow; and its cheeks are weakly rugose. This is the only O'Hara specimen in which the median furrow does not reach the marginal furrow.

*Variability:* The comments above indicate that in the cephalon the length of the median preglabellar furrow, the shape of the glabella (its apical angle), and the degree of the tumidity of the basal lobes and posterolateral corners of the cheeks are subject to variations. In the pygidium the length of the lateral spines is almost an individual feature and the posterior flange is not equally distinct abaxially. In the Glenormiston area cephalons with a short median preglabellar furrow prevail, and in all of the De Little Range and in most of Selwyn Range specimens this furrow is long, reaching the marginal furrow. From the Selwyn Range only one exception is known (Pl. 56, fig. 10) in which the median furrow contacts the marginal furrow.

It is possible that the short and the long furrowed groups represent populations each of a slightly different age (within the limits of the zone to which they are confined), but it is impossible to say which, if either, is the older group. These variations are, however, somewhat erratic to warrant a subspecific nomenclature. Furthermore, in the 'lower chert bed' the inferior preservation prevents a comparison of the details, and of the emphasis of characters, although specimens are abundant. The subdued relief of the pygidial axial lobe in the O'Hara specimens, attributed to the mode of preservation, may be a distinctive feature within this particular population; this, however, cannot be checked unless limestone specimens of the same population are collected.

*Occurrence and age:* *Aspidagnostus inquilinus* sp.nov. occurs in the Georgina Limestone at localities W1, W15, W20, G48, G50; in the Pomegranate Limestone at Wills Creek at localities B537 and B535; and in the O'Hara Shale at localities D6, D28, and D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Genus TRIADASPIS nov.

*Triadaspis* is monotypical and its type species is *T. bigeneris* sp.nov.

*Diagnosis:* *Triadaspis* refers to Clavagnostidae with a quadrilobate and trifid pygidial axis and a trispinose margin with a submarginal gapless collar between the lateral spines, distinguished by having its median axial node developed as a crest over the three axial annulations and having a pointed and fully defined posterior axial lobe and axial furrows.

*Differential diagnosis:* *Triadaspis* is affiliated with *Aspidagnostus* Whitehouse, from which it differs by its fully defined posterior axial lobe and the absence of the median gap in the collar. It is also morphologically intermediate between *Aspidagnostus* and *Oidalagnostus* as discussed under these genera.

*Triadaspis* is placed in the Clavagnostidae because of its similarity with the Clavagnostid *Aspidagnostus* and because it possesses the *Clavagnostus*-like pair of pits at the end of its third axial annulation.

The cephalon of *Triadaspis bigeneris* is unknown, but it is suspected that the cephalon mentioned under the heading of *Aspidagnostus* sp.indet. may be its cephalon.

#### TRIADASPIS BIGENERIS sp.nov.

(Pl. 54, Fig. 6 ; Text-fig. 34)

*Material:* Only three pygidia have been observed, and the best preserved is illustrated.

*Holotype:* The illustrated pygidium, Plate 56, figure 6, CPC 5804, locality G417, is the holotype.

*Diagnosis:* The diagnosis of the genus serves as the diagnosis of the species *T. bigeneris*.

*Description:* The holotype pygidium, silicified and etched from limestone, is 2.3 mm long. It is almost complete, but its right anterolateral corner is concealed under an irremovable fragment of a cephalon of another agnostid.

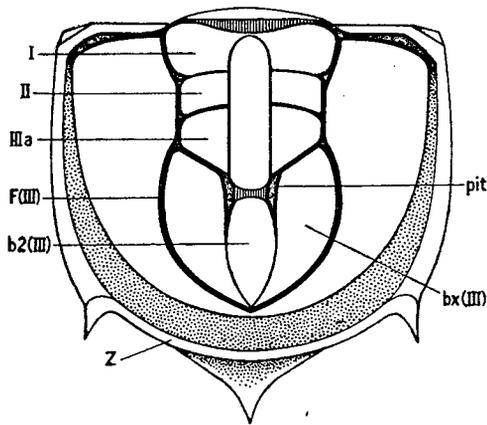


Fig. 34.—*Triadaspis bigeneris* gen.nov., sp.nov., from Plate 54, fig. 6. I—anterior, II—middle, IIIa—posterior axial annulation; b2(III)—intranotular axis; bx(III)—extranotular axis; F(III)—axial furrow; pit—‘*Clavagnostus*’ pit (a pair of pits); Z—pygidial collar (without gap; the pygidium is zonate). Compare Text-figures 33 and 39.

The shield without its median spine is wider than long, semielliptical, with subparallel flanks and an evenly curved rear margin. The rim and the marginal furrow are expanding rearward, and the border is widest at the lateral spines. A low submarginal collar is present between the lateral spines and the median spine is depressed below the level of the border.

The pygidial axis is constricted at the second and third annulation; in the posterior pygidial lobe the intranotular axis is well defined by continuous notular furrows which start at the subcentral and elongate ‘*Clavagnostus*’ pits; these are placed at the rear end of the long axial node (crest). In front of the axial lobe a distinct recess is apparent, the articulating furrow is narrow, and the articulating half-ring inconspicuous.

*Occurrence and age:* *Triadaspis bigeneris* sp.nov. is a rare species of the Mungerebar Limestone, found at localities G119 and G417. Its age is the Mindyallan Zone of *Erediaspis eretes*. It is probably present also at G103 (in the Zone of passage) and at G153 (in the zone of *Cyclagnostus quasivespa*).

Family DIPLAGNOSTIDAE Whitehouse, 1936

Subfamily DIPLAGNOSTINAE

Genus DIPLAGNOSTUS Jaekel, 1909

DIPLAGNOSTUS CRASSUS sp.nov.

(Pl. 54, Fig. 4)

*Material:* Only the holotype cephalon, CPC 5802, is available.

*Diagnosis:* *Diplagnostus crassus* sp.nov. is a species with a very convex cephalon, scrobiculate cheeks, an incomplete preglabellar median furrow, and a wavy transverse glabellar furrow; distinguished by its broadly rounded glabellar rear without lateral angular indentations to receive the basal lobes.

*Differential diagnosis:* In all other species of *Diplagnostus* the rear of the glabella is angulate and the basal lobes are nesting in angulate indentations. Furthermore, *D. humilis* (Whitehouse) has no scrobicules and its preglabellar median furrow is

complete; some specimens of *D. planicauda* (Angelin) have scrobiculate cheeks (Westergaard, 1946, pl. 8, fig. 22), but its median preglabellar furrow is complete and its basal lobes are nesting in the recesses at the glabellar rear; *D. planicauda bilobatus* Kobayashi (Westergaard, op. cit.) has an incomplete or even absent preglabellar furrow, but its cheeks are without scrobicules; finally, *D. planicauda vestgothicus* (Wallerius) (Öpik, 1961) has scrobiculate cheeks, but its median preglabellar furrow is complete and the glabellar rear is sharply angulate.

The species of *Diplagnostus* with the glabellar rear angulate are reminiscent of *Pseudagnostus*; but *D. crassus* with its broadly rounded glabellar rear recalls *Glyptagnostus*, e.g. *G. (Lispagnostus) lenis* sp.nov.

*Description:* The holotype is 2.3 mm long, and about 1.2 mm high in the middle, indicating a strong convexity of the shield. The scrobicules on the cheeks are combined with pits. The anterior glabellar lobe is bilobate, divided into two elliptical parts by the median sulcus, which is expanded rearward in the manner seen in *Glyptagnostus*. The posterior glabellar lobe is carinate, with a tiny sub-central node and a pair of lateral oblique furrows (as in *Pseudagnostus*).

The glabellar rear bears a small pointed tubercle as seen in *Diplagnostus* (Westergaard, 1946, pl. 8, figs 15, 20, 25), but also in *Xestagnostus legirupa* sp.nov., in some species of *Pseudagnostus*, in *Innitagnostus innitens* sp.nov., and in *Hypagnostus correctus* sp.nov.

The Middle Cambrian *Diplagnostus crassus* sp.nov. (no species of *Diplagnostus* occurs in the Upper Cambrian) is described here to facilitate the comparison of its cephalon with the cephalata of *Pseudagnostus* and *Glyptagnostus*.

*Occurrence and age:* The cephalon of *Diplagnostus crassus* comes from locality W36 (map, Text-fig. 4; 'Devoncourt' limestone; see Öpik, 1961, p. 47), where it is associated with *Oidalagnostus personatus* sp.nov. Its age is the Middle Cambrian Zone of *Proampyx agra*, or *Leiopyge laevigata* II.

#### Genus LINGUAGNOSTUS Kobayashi, 1939

LINGUAGNOSTUS sp.nov. aff. KJERULFI (Brögger)

(Pl. 54, Fig. 2)

The illustrated cephalon, CPC 5800, in sandstone, is 4.6 mm long. The wide concave border, the boat-shaped glabella with the angulate and pointed rear, and the absence of a preglabellar median furrow indicate a species of *Linguagnostus*. It is, however, distinguished by its relatively short glabella and basal lobes from *L. kjerulfi* (Brögger) (Westergaard, 1946, pl. 8, fig. 31 and pl. 9, fig. 1) and represents a new species. Its pygidium is, however, unknown, and the final description is therefore reserved. Further comment is given under *Dolichoagnostus?* sp.nov. (q.v.).

*Occurrence and age:* Steamboat Sandstone, locality D95; the age is late Middle Cambrian, the zone of *Leiopyge laevigata*.

#### Genus OEDORHACHIS Resser, 1938

Palmer (1962, p. F-19) regards *Oedorhachis* Resser as a synonym of *Acmarrhachis* Resser; both genera were published with the same date (October 31, 1938). *Acmarrhachis* has a page priority and is based on immature specimens, whereas *Oedorhachis*

refers to mature specimens. Consequently, in case of a synonymy *Oedorhachis* may prevail over *Acmarrhachis*. The synonymy itself, however, cannot be accepted because the genera belong to different families.

OEDORHACHIS? TRIDENS sp.nov.

(Pl. 54, Fig. 5, Text-fig. 35)

*Material:* Only one pygidium, the holotype, CPC 5803, is available.

*Diagnosis:* *O.?* *tridens* is distinguished by its median posterior marginal spine and by the absence of a collar between the lateral spines.

*Differential diagnosis:* The type species of the genus, *Oedorhachis typicalis* (Resser, 1938, p. 50, pl. 10, fig. 16) shows no indication of a median spine, but in *O. ulbrichi* Resser (*ibid.*, fig. 29) the rear of the pygidium is angulate—a sign of a potential median spine.

The presence of a posterior collar in the pygidium of *Oedorhachis typicalis* indicates its affiliation with the Diplagnostidae, but a collar is not necessarily present in every species of that family (Öpik, 1961, p. 69).

The genus *Oedorhachis* is also briefly discussed under the heading of *Dolichoagnostus*.

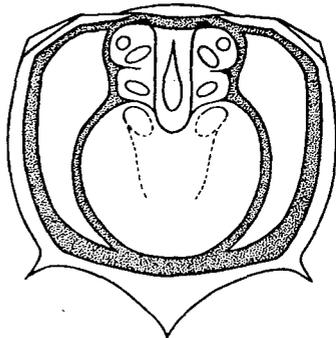


Fig. 35.—*Oedorhachis? tridens* sp.nov.,  
from Plate 54, fig. 5.

*Description:* The holotype pygidium is 6.0 mm long, indicating a relatively large specimen, about 15 mm long. The posterior median spine has a rather stout base and the margin underneath (not seen in the illustration) is vertical.

*Occurrence and age:* *O.?* *tridens* has been found in the Mungerebar Limestone at locality G10; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

Genus CONNAGNOSTUS nov.

The type species of *Connagnostus* is *C. venerabilis* sp.nov.

*Diagnosis:* Agnostids en grande tenue, as well as semi-effaced forms, with a subangulate rear of the glabella, a narrow, long, forward-placed glabellar node, evenly arched cephalic front, a wide border (including the rim and the marginal furrow), and constricted acrolobes; distinguished by the external absence of the

preglabellar median furrow and the rather wide and long pygidial axial lobe with almost parallel flanks; in maturity the axial lobe is in contact with the marginal furrow and its posterior lobe may be expanded laterally; in small, immature pygidia the axial lobe is short and has slightly converging flanks.

The phrase 'external absence of the preglabellar median furrow' is explained below in the description of the cephalon of *C. venerabilis*, plate 54, figure 14.

The type species (*C. venerabilis* nov.) is simplimarginate, but another species (*C. ? zonatus* nov.) has a zonate pygidium and is, therefore, only tentatively attributed to *Connagnostus*.

*Differential diagnosis*: The diagnostic characters of *Connagnostus* refer, in brief, to a form with constricted acrolobes and a long pygidial axis without a deutero-lobe; the deutero-lobate genera (e.g. *Pseudagnostus*) are thus excluded from further comparison.

*Agnostascus* gen.nov. is somewhat similar to *Connagnostus* in its glabellar node and long pygidial axis, but the narrow border, rather acute glabellar rear, deep preglabellar median furrow, and pyriform pygidial axis of *Agnostascus* are rather distinctive. Less different are the *Ammagnostinae*; but in *Connagnostus* the forward-placed glabellar node and the pygidial axis with its parallel flanks prevent a confusion with *Ammagnostus*. Nevertheless, a comparison of the pygidia of *Ammagnostus* (Pl. 55, fig. 3) and *Connagnostus* (Pl. 55, fig. 2) indicates a possible subfamilial affiliation.

Among the genera with constricted acrolobes, however, the nearest to *Connagnostus* is *Dolichoagnostus* Pokrovskaja, including *Oidalagnostus ? dubius* Westergaard, which belong to the *Diplagnostidae*; *Connagnostus ? zonatus* sp.nov. has retained even the *diplagnostid* pygidial collar, and the general aspect of *Connagnostus* suggests a simplified version of *Oidalagnostus*. Hence, it is quite probable that *Connagnostus* is more closely affiliated with the *Diplagnostidae* than with the other familial groups of agnostids.

In passing, the immature pygidium of *Connagnostus venerabilis* (Pl. 54, fig. 13) is reminiscent of a collarless *Diplagnostus*, or even a *Peronopsis* (e.g. *P. fallax*, Westergaard, 1946, pl. 3, fig. 2) evoking once more the notion of an affiliation of the *diplagnostids* and *peronopsids*.

The provision in the diagnosis for semi-effaced forms refers to the 'Agnostid, genus and species undetermined' of Palmer (1962, p. F-14, pl. 1, figs 31-33). In this form the transverse glabellar furrow is absent and in the pygidium only the anterior portion of the axis is defined by lateral furrows. It represents, presumably, a subgenus of *Connagnostus*. Palmer himself indicated that this agnostid is related to his *Proagnostus ?* sp. and indicated that the latter may represent a new genus. This *Proagnostus ?* (Palmer, op.cit., pl. 1, figs 17-19 and 23) is very close to, if not identical with, *Connagnostus venerabilis* sp.nov. According to Palmer, *Proagnostus ?* sp. is associated with *Glyptagnostus reticulatus*. Palmer's chart for Woodstock, Alabama (op.cit. p. F-4) indicates, however, the association with *Glyptagnostus stolidotus*, which is also the age of *C. venerabilis* in Australia.

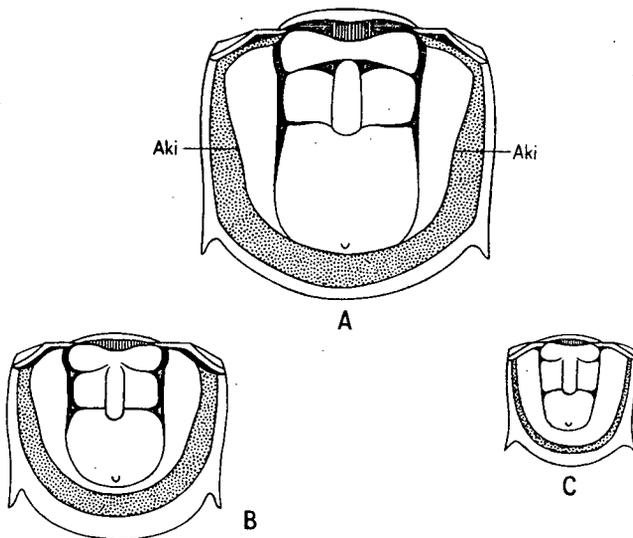


Fig. 36.—*Connagnostus venerabilis* gen.nov., sp.nov; three pygidia, same magnification, from Plate 54. A—from fig. 11, B—from fig. 12, C—from fig. 13. Aki—constricted acrolobe (flanks concave)

CONNAGNOSTUS VENERABILIS sp.nov.

(Pl. 54, Figs 11–14; Pl. 55, Figs 1, 2; Text-fig. 36)

*Material:* Six specimens (one cephalon and five pygidia) are illustrated. The illustrated cephalon is exceptionally well preserved; the structure of the glabellar rear as described below is observable on a deformed cephalon, CPC 6738, from the O'Hara Shale, locality D29; it is not illustrated. Palmer's observation (1962, p. F-14) that 'for some undetermined reason the matrix adheres to the cheek areas of both the cephalon and pygidia' applies also to some of our material. In *C. venerabilis* the test of mature specimens is rather thin and of a leathery or parchment-like appearance and is often irregularly creased. Only in pods of calcite is the preservation satisfactory. Latent scrobiculation of the cheeks may be one reason for the adherence of the matrix.

*Holotype:* The pygidium, Plate 54, figures 11a, 11b, CPC 5809, is selected as the holotype; it is complete although it consists of two pieces.

A specific diagnosis is unnecessary because it is the same as the diagnosis of the genus.

*Description:* In cephalon preserving their high convexity the border appears narrow because part of the marginal furrow is concealed by the overhanging bulges of the cheeks. The anterior glabellar lobe is almost semicircular, and 0.25 of glabellar length. The posterior glabellar lobe is slightly constricted in the middle and the basal lobes are tumid and triangular; they are connected behind the glabella by the vertically sloping connective band; the glabellar rear ends in a small point observable in flattened specimens and is angulate. This angulation is masked by the tumidity of the cephalic rear which forces the converging axial furrows to slope down (and rearward). The whole shield is strongly convex.

In the mature pygidium the axial lobe is in contact with the marginal furrow which causes the obliteration of the closure of the axial furrows at the rear of the lobe. In young specimens the axis is short, well rounded, to somewhat angulate in the rear; a terminal node is present. Two anterior axial annulations are well defined by transverse furrows; the anterior annulation is wider than the rest, and constricted in the middle by the articulating recess and the anterior extension of the axial node, which itself rests on the second annulation. The pleural lobes are very narrow as compared with the axis. The rim is wide, and so is the marginal furrow; the marginal spines are placed well in rear, at the level of the closure of the marginal furrow, and of the rear of the axial lobe of mature specimens.

The articulating half-ring is large and convex, and the deep articulating furrow has a pair of pits (notulae) at its flanks. The fulcral points are close to the axis and facets are present.

*Morphogenesis:* the growth of the axial lobe of the pygidium is illustrated in Text-figure 35. It refers essentially to the increase of the posterior axial lobe in length and width. The pygidium from Alabama (*Proagnostus?* sp. Palmer, 1962, pl. 1, fig. 19), about 2.2 mm long, has the axis short, and corresponds well with the pygidium Plate 54, figure 12, which is of about the same size and has a similar short axis completely surrounded by the furrow. In *Pseudagnostus* (Palmer, 1955) and in *Ammagnostus* (see under *A. mitis* sp.nov.) the axial lobe is long even in early immature instars.

*Occurrence of Connagnostus venerabilis in Alabama:* *Proagnostus?* sp. (Palmer, 1962, p. F-14) from Woodstock, Alabama, differs from the Australian *C. venerabilis* in having a somewhat longer anterior glabellar lobe and possibly a wider cephalic marginal furrow. It appears, however, that this furrow is better exposed in the cephalon from Alabama owing to flattening. The Australian and Alabaman pygidia, however, are identical.

*Comment on illustrated specimens:*

The following four specimens come from the Georgina Limestone, locality W1.

The cephalon, Plate 54, fig. 14, CPC 6812, is 3.5 mm long. The glabellar rear is crushed, but its angulate shape is recognizable. Some of the test is preserved. A preglabellar median furrow is absent; but on the testless front of this cephalon a small notch in front of the glabella, and an almost imperceptible depression extending forward from the notch, indicate a vestigial internal preglabellar mesentery.

The holotype pygidium, Plate 54, figs 11a, 11b, is 3.2 mm long. Calcite crystals disfigured the posterior axial lobe; muscle spots are present, a pair on each of the two anterior annulations.

The pygidium, Plate 54, fig. 12, CPC 5810, in a calcite pod, is 2.3 mm long. It is almost mature, but the axial lobe is still short, not quite reaching the marginal furrow. Muscle spots are visible.

The immature pygidium, Plate 54, fig. 13, CPC 5811, is 1.3 mm long. The axial lobe is short, and tapers rearward.

The next two specimens came from the O'Hara Shale (lower chert bed), locality D29.

The pygidium, Plate 55, fig. 1, CPC 5813, in friable silica, is 2.7 mm long. Its articulating half-ring is preserved.

The pygidium, Plate 55, fig. 2, CPC 5814, in hard silica, is 3.0 mm long; its abraded surface is usual in specimens of *Connagnostus*.

*Occurrence and age:* *Connagnostus venerabilis* sp.nov. occurs in the Georgina Limestone at localities W1 and W20 and in the O'Hara Shale ('lower chert bed'), locality D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*. It occurs also in the Conasauga Formation of Alabama in the same zone.

CONNAGNOSTUS? ZONATUS sp.nov.

(Pl. 55, Fig. 5)

*Material:* Only three pygidia have been found as yet.

*Holotype:* The illustrated pygidium CPC 5817, locality G137, in a chert of the Mungerebar Limestone, is the holotype. It is 4.2 mm long.

*Diagnosis:* *Connagnostus zonatus* sp.nov. is distinguished by its gapless sub-marginal *Diplagnostus*-like collar between the marginal spines and by having three annulations in the anterior portion of its pygidium.

*Differential diagnosis:* The collar and the three anterior axial annulations prevent any possibility of confusion with *C. venerabilis*, which is simplimarginate and has only two annulations.

*Generic classification:* *Connagnostus? zonatus* is placed in this genus only provisionally; it is, perhaps, a form intermediate between *Connagnostus venerabilis* and *Oidalagnostus*, or even a 'simplified' *Oidalagnostus*.

*Description:* Most of the border consists of the rather wide marginal furrow, and the spines are placed well in the rear, on the level of the end of the axial lobe. The pleural lobes are very narrow, without scrobicules, and strongly constricted in the middle. The articulating furrow is narrow, but the articulating half-ring is large and extends into the recess in the front of the axial lobe. The axial lobe itself is long, extending to the marginal furrow. The anterior axial annulations are defined by shallow but distinct transverse furrows; the anterior annulation is tripartite, wider than the rest, and tumid at the flanks. The axial node is pyriform and stretched over the two posterior annulations. The posterior axial lobe, as long as the three anterior annulations, is slightly expanded and bears a transverse depression similar to *Dolichoagnostus* and *Oedorhachis*.

*Occurrence and age:* The holotype and another pygidium come from the Mungerebar Limestone, locality G137, in the Zone of *Cyclagnostus quasivespa*; one pygidium was found in the siltstone at McCabe Knob (near locality G409) low in the Zone of *Glyptagnostus stolidotus*.

GENUS DOLICHOAGNOSTUS Pokrovskaja, 1958

The type species of *Dolichoagnostus* is *D. admirabilis* Pokrovskaja (1958, pl. 3, figs 1-3); its pygidia, as illustrated, appear simplimarginate, but the upturned rear margin has the appearance of a collar connecting the marginal spines and the depressed rim behind it may be covered by the matrix; hence, a zonate structure can be suspected. *Oidalagnostus? dubius* Westergaard, 1946, is a simplimarginate species of the same or a related genus, distinguished by a median pygidial spine

from *admirabilis*, which is angulate in the rear. Close to *Dolichoagnostus* is *Oedorhachis* Resser, 1938, which is distinct in having the *Diplagnostus* collar in its pygidium. Furthermore, in *D. admirabilis* the absence of the transverse glabellar furrow is regarded by its author as a generic character; it is at least of specific significance.

*Dolichoagnostus*, *Oedorhachis*, *Linguagnostus*, and most of the *Diplagnostus* forms have a rather similar (conservative) cephalon with an acute glabellar rear; this structural similarity prevents a safe generic identification when the species is unknown and pygidia are absent. Characters like the presence or absence of a frontal glabellar sulcus, a median preglabellar furrow, a transverse glabellar furrow, etc., are guides leading to the identification of the species, but may be misleading as regards the genus.

DOLICHOAGNOSTUS? sp.nov.

(Pl. 54, Fig. 3; Text-fig. 37)

The illustrated pygidium CPC 5801, in friable red sandstone, is 2.5 mm long. The axial lobe reaches the margin, is expanded in the rear, and bears a depression behind the median node. There are two distinct annulations in the anterior portion

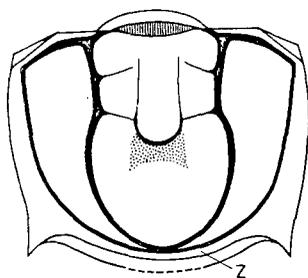


Fig. 37.—*Dolichoagnostus?* sp. nov., from Plate 54, fig. 3. Z—pygidial collar (without gap; pygidium zonate).

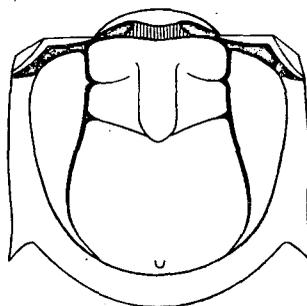


Fig. 38.—*Agnostascus gravis* gen. nov., sp.nov. from Plate 61, figs 4a, 4b.

of the axis; a third annulation is indicated by the posterior end of the axial node which extends well beyond the second annulation and the second transverse furrow. The posterior margin is worn and it is therefore unknown whether it was angulate or not; but the border is apparently zonate, although the collar is also worn off almost completely; furthermore, similar but even more fragmentary pygidia are present having the zonate structure of the posterior border more or less well preserved.

In view of the difficulty of identifying the genus of an unknown species (see ante), the possibility remains that this particular pygidium may belong to the cephalon described as *Linguagnostus* sp.nov. aff. *kjerulfi*.

*Occurrence and age:* Steamboat Sandstone, locality D95; the age is late Middle Cambrian, the Zone of *Leiopyge laevigata*.

#### Subfamily OIDALAGNOSTINAE nov.

The characters of the subfamily Oidalagnostinae of the Diplagnostidae are (1) the zonate and scrobiculate pygidium, (2) the median gap in the pygidial collar (reminiscent of *Aspidagnostus*), (3) the triannulated anterior part of the pygidial axis, and (4) the enlarged posterior pygidial axial lobe. The subfamily type is *Oidalagnostus* Westergaard, 1946, based on the species *trispinifer*.

#### Genus OIDALAGNOSTUS Westergaard, 1946

The occurrence of *Oidalagnostus* in the Middle Cambrian of Australia (Queensland) has been mentioned by Öpik (1962, p. 36, 48); this form is described here as *O. personatus* sp.nov. Another form occurs in the Upper Cambrian Mindyallan Zone of *Cyclagnostus quasivespa* and is classified as *O. trispinifer* Westergaard, which was originally found in Sweden in the upper part of the Zone of *Leiopyge laevigata*. Thus *O. trispinifer* covers the range of several zones and transgresses the Middle Cambrian–Upper Cambrian boundary.

*Oidalagnostus* is a diplagnostid with a scrobiculate pygidium, with an expanded and tumid posterior axial lobe, with 'lateral bosses' flanking the two posterior axial lobes, and with a trispinose pygidial margin.

The posterior pygidial axial lobe has been regarded as a 'pseudolobe' by Westergaard; this lobe, however, is laterally defined by the straight extension of the axial furrows and not by the accessory scrobicules of *Pseudagnostus* (see Öpik, 1963). Westergaard (1946, p. 65, pl. 9, fig. 6) interpreted a pair of lines (grooves) carrying two pairs of notulae in the middle of the posterior lobe as representing the axial furrows. The furrows, however, are not the axial furrows (see Öpik, 1963), but the notular lines, and placed well adaxially from the axial furrows.

*Oidalagnostus* is placed in the Diplagnostidae because of its rather distinct pygidial collar; it differs, however, from other diplagnostids (1) by its expanded and tumid posterior axial lobe of the pygidium, (2) by the pygidial scrobiculation (in *Diplagnostus* only the cephalon is scrobiculate), and (3) by having three annulations in the anterior part of the pygidial axis.

The pygidial structure of *Oidalagnostus* (see under *O. personatus* sp.nov.) bears many similarities with *Aspidagnostus* (q.v.).

#### OIDALAGNOSTUS TRISPINIFER Westergaard, 1946

(Pl. 54, Fig. 10)

The illustrated pygidium, CPC 5808, is 4.4 mm long (as preserved); the matrix is crystalline calcite—a calcite pod in bituminous limestone (Mungerebar Limestone; locality G 131).

The lateral bosses flanking the third axial annulation and the posterior (expanded) axial lobe are well defined and arrayed diagonally on lines directed toward the lateral spines. *O. personatus* sp.nov. has only one pair of bosses which are arranged longitudinally.

*Occurrence and age:* In Australia *O. trispinifer* occurs in the Mungerebar Limestone at locality G131, in the Mindyallan Zone of *Cyclagnostus quasivespa*; in Tasmania it occurs in the Zone of *Glyptagnostus stolidotus*; it is found also in the

Steamboat Sandstone (localities G121 and G133), where its age is the topmost Middle Cambrian zone of *Leiopyge laevigata* III; this corresponds, according to Öpik (1961, p. 38), to the upper part of the *Leiopyge laevigata* zone of Sweden, from which *O. trispinifer* was described originally.

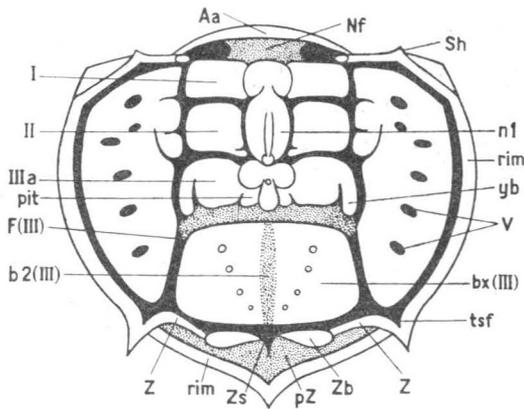


Fig. 39.—*Oidalagnostus personatus* sp. nov., A: A complete cephalon, CPC 6726, loc. W36, x 12; B: Diagram of pygidium, from Plate 54, fig. 8. I—anterior, II—middle, III—posterior axial annulation; Aa—articulating half-ring; b2(III)—intranotular axis; bx(III) extranotular axis; F(III)—axial furrow; n1—median node; pit—the '*Clavagnostus* pits', rim—rim; Sh—fulcral point (pointed); tsf—furrow at base of spine; yb—lateral boss of third annulation; V—scrobicule (pit); Z—pygidial collar (the pygidium is zonate); Zb—knob on collar; Zs—gap between knobs; pZ—depressed margin (with rim) behind collar. Compare Text-figures 33, 34.

OIDALAGNOSTUS PERSONATUS sp.nov.

(Pl. 54, Figs 7-9; Text-fig. 39)

*Introduction:* *Oidalagnostus personatus* sp.nov. is a Middle Cambrian species, and about one zone older than the earliest known occurrence of *O. trispinifer*. Previously (Öpik, 1962, p. 36 and 48) it was referred to as *Oidalagnostus* sp. (cf. *trispinifer*). *O. personatus* is not present in the Mindyallan, but is described here for completeness of the record, and to clarify the stratigraphic distribution of *Oidalagnostus*.

*Material:* One almost complete and another fragmentary cephalon and two pygidia are described, selected from about six specimens. The matrix is a dark and smelly bituminous sandy limestone.

*Holotype:* The best preserved pygidium (a mould) Plate 54, fig. 8, CPC 5806, is selected as the holotype because the holotype of *O. trispinifer* is also a pygidium (Westergaard, 1946, pl. 9, fig. 6).

*Diagnosis:* *Oidalagnostus personatus* is distinguished in the cephalon by its parabolic frontal glabellar lobe and vestigial preglabellar median furrow; and in the pygidium by having only one pair of lateral bosses (at the third axial annulation) which are longitudinal, and by the deep median gap dividing the 'collar' in two separate parts.

*Differential diagnosis:* In *O. trispinifer* Westergaard the frontal glabellar lobe is subangular and bluntly rounded, the preglabellar median furrow is quite distinct, the pygidial axis is flanked by two pairs of diagonally arranged bosses, and the 'collar', though having a median gap, is not completely divided as in *O. personatus*.

*Aspidagnostus* (Text-fig. 33), as described in this paper, cannot be confused with *O. personatus*, but the structure of their pygidial rear is the same: (1) the margin is trispinose, (2) the margin between the lateral spines is a depressed flange, (3) the 'collar' is split in the middle and carries a pair of knobs, (4) the pygidial axis itself is quadrilobate, and (5) the pygidia are scrobiculate.

*Description:* the fragmentary cephalon Plate 54, fig. 9, CPC 5807, is 3.5 mm long, indicating a total length of about 6 mm; the complete cephalon, CPC 6726, Text-figure 39A, is 4.5 mm long. The frontal margin is evenly rounded, and arched forward more than in *O. trispinifer*. The rim is elevated and convex and the marginal furrow is rather wide and deep. The cheeks are pitted; the preglabellar median furrow is represented by a short median scrobicule. The frontal lobe of the glabella is small, parabolic to subtriangular, and bears a faint median sulcus at its tip. The transverse glabellar furrow forms a retral inbend.

The glabellar node is a narrow crest; the posterior glabellar lobe is constricted in the middle and divided into two subequal parts by a transverse depression just behind the node; the glabellar rear, slightly swollen, is defined by a pair of weak longitudinal lines.

The holotype pygidium (Plate 54, fig. 8) is 4.0 mm long. The lateral rim is wide and convex, the marginal furrow deep. The posterior flange (between the lateral spines) is depressed and bears a narrow elevated border with a median spine, which is apparently bent down. The knobs on the collar are elongate (transversely) and rather prominent; laterally the collar swings abruptly toward the marginal spines.

The pleural lobes are pitted, and, along the periphery, scrobiculate. The geniculation at the fulcra is rather strong, the shoulder furrows are deep, and the shoulders prominent, with pointed tips.

The axial lobe has a distinct 'face'—the face of a bearded mask. It differs from the face in the pygidium of *O. trispinifer* which has the diagonally arranged lateral bosses which are absent in *O. personatus*.

Two faint tubercles can be distinguished on the median node, and on the third axial annulation a short median protuberance is flanked by a pair of pits comparable with the pits in *Aspidagnostus*. The posterior lobe is trapezoidal and not suboval as in *O. trispinifer*; it has a narrow, almost imperceptible median depression, and bears at least three pairs of notulae seen on another (not illustrated) specimen.

The articulating device consists of a broad recess, a wide articulating furrow with a pair of pits and a rather narrow upward-arched articulating half-ring. A somewhat similar device occurs in some species of *Diplagnostus*; it differs from *Glyptagnostus* and *Pseudagnostus* only by the narrowness of its half-ring.

The fragmentary pygidium, Plate 54, Figure 7, CPC 5805 is 4.0 mm. long as preserved. Its shoulder tip is strongly pointed and the marginal furrow extends into the base of the lateral spine.

*Occurrence and age:* *Oidagnostus personatus* comes from locality W36 (Map, Text-fig. 4). The age is the Middle Cambrian Zone of *Proampyx agra*, or the *Leipyge laevigata* II zone.

#### Subfamily AMMAGNOSTINAE nov.

*Diagnosis:* Ammagnostinae (of the family Diplagnostidae) are simplimarginate agnostids with constricted acrolobes and wide border in both shields or only in the pygidium, with a centrally placed glabellar node, and a rounded glabellar rear having a long pyriform pygidial axial lobe contacting the marginal furrow.

*Differential diagnosis:* The Ammagnostinae are based on a combination of characters; no characters are unique. The wide border and constricted acrolobes indicate an affiliation with the Pseudagnostinae, from which they differ in having a rounded glabellar rear, subcentrally placed glabellar node, and no deuterolobe. Some similarity with the Glyptagnostinae may be assumed, as discussed under the heading of the genus *Ammagnostus*.

The following genera constitute the subfamily Ammagnostinae: (1) *Ammagnostus* gen.nov., (2) *Agnostoglossa* gen.nov., and (3) *Kormagnostus* Resser, 1938.

*Kormagnostus* is discussed below, under *Ammagnostus*.

The known species of the Ammagnostinae, including most of the species of *Kormagnostus*, are Mindyallan in age.

#### Genus AMMAGNOSTUS nov.

The type species of *Ammagnostus* is *A. psammius* sp.nov.

*Diagnosis:* *Ammagnostus* refers to species with (1) a cephalon en grande tenue and a pygidium semi-effaced in various degrees, (2) no preglabellar median furrow, scrobicules, or rugae, (3) a narrow cephalic and rather wide pygidial border, and

(4) widely spaced pygidial axial furrows which meet in the rear at the marginal furrow. The pygidial acrolobe is constricted but the cephalon is not. In the known species the test is granulose.

*Differential diagnosis:* *Ammagnostus* can be compared with *Glyptagnostus* because the distribution of notulae and the terminal node in its pygidium are the same (Öpik, 1963, p. 39). The reasoning is based on the two following assumptions: (1) that the terminal node (n2 in Text-figs 40, 41, 43) marks the rear of the visceral axial lobe, and (2) that the notulae (mm) are the apodemes of the appendages. It is evident that in *Ammagnostus* and *Glyptagnostus* the notulae (pygidial appendages) retain their original segmental arrangement, but the rear of the axial lobe (in its visceral, anatomical sense) is placed forward between the fourth, or the third pair of appendages counting from the rear of the shield. The axial furrows, however, retain their position in relation to the lines of notulae; consequently, behind the terminal node these furrows are somewhat rudimentary because there are no viscera to be supported by these parietal mesenteries. It is concluded that the visceral axial lobes in *Ammagnostus* and *Glyptagnostus* became modified and contracted in a similar manner. In agnostids without such modifications the notular lines and the axial furrows converge at the terminal node in the rear of the axial lobe.

*Ammagnostus* differs from *Glyptagnostus* in the absence of scrobicules and rugae, in its wide pygidial border, and in the expanded posterior axial lobe, that is, the wide spacing of the pygidial axial furrows.

The presence in the anterior part of the pygidial axis in *Ammagnostus* of a third, narrow annulation (Text-fig. 40) is reminiscent of *Lotagnostus trisectus* (Westergaard, 1922, pl. 1, fig. 12), but this is the only similarity between the two.

*Kormagnostus* Resser appears affiliated on a subfamilial level with *Ammagnostus*. Common to both are (1) the absence of the preglabellar median furrow, (2) the constriction of the pygidial acrolobe and its absence in the cephalon, (3) the straight and deep transverse glabellar furrow, (4) the rounded glabellar rear, (5) the long and wide pygidial axis and narrow pygidial pleural lobes, and (6) the wide pygidial border. *Kormagnostus*, however, is distinguished by its wide cephalic border (which is narrow in *Ammagnostus*), and by the effacement of the anterior glabellar lobe, which is also weak in *Ammagnostus*; furthermore, the pygidial axis in *Kormagnostus* is rather obese and its tip bears the terminal node. In current classifications *Kormagnostus* is placed with the peronopsids because of the effacement of its anterior glabellar lobe, reminiscent of the peronopsid *Hypagnostus*, which itself is polyphyletic. Ivshin included *Kormagnostus* in his subfamily Hypagnostinae and regarded the effacement of the frontal lobe as a unifying suprageneric character. The whole structure of *Kormagnostus*, however, prevents its inclusion in the peronopsids.

Lochman & Hu (1960, p. 805 and p. 823) describe the pygidial axial lobe of *Kormagnostus simplex* Resser (and of *Baltagnostus wyomingensis*, which is not a *Baltagnostus*) in terms of a pseudolobe, but without any supporting reason. *Kormagnostus* appears first in the late Middle Cambrian (*K. antiquus* Rasetti, 1948) and cannot be derived, therefore, from the subsequent *Ammagnostus* or *Agnostoglossa*, which themselves are less modified than *Kormagnostus*; still, a common ancestor

of these genera should be postulated. Robison (1964, p. 519) suggests *Homagnostus* as the ancestor of *Kormagnostus*; his Middle Cambrian '*Homagnostus*' *incertus* is, however, a *Peronopsis* with an obese pygidial axial lobe.

*Ammagnostus* is compared with *Agnostoglossa* under the heading of the latter.

The morphogenesis of *Ammagnostus* (as distinct from *Connagnostus*) is apparent in *Ammagnostus mitis* sp.nov. (q.v.).

The following new species of *Ammagnostus* are described here:

Zone of *Cyclagnostus quasivespa*

1. *Ammagnostus mitis* sp. nov.

Zone of *Glyptagnostus stolidotus*

2. *Ammagnostus psammius* sp.nov.
3. *Ammagnostus integriceps* sp.nov.
4. *Ammagnostus euryaxis* sp. nov.

The American early Dresbachian (= Mindyallan) *Baltagnostus beltensis* Lochman, 1944, is probably also an *Ammagnostus* (see the discussion of *Proagnostus*).

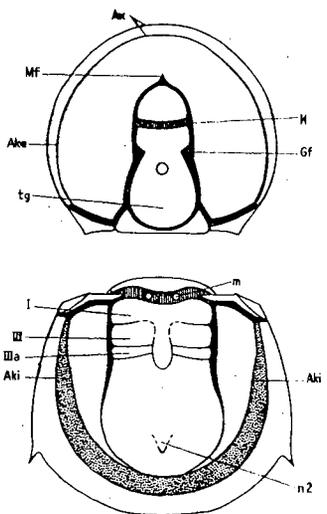


Fig. 40.—*Ammagnostus psammius* gen.nov., sp.nov. Cephalon from Plate 66, fig. 1; pygidium same Plate, fig. 3. Cephalon: Ake—acrolobe unconstricted (flanks convex); Ax—truncate front of rim and acrolobe; Gf—lateral glabellar furrow; H—transverse glabellar furrow; Mf—median preglabellar furrow (relic); tg—glabellar rear, rounded. Pygidium: I—anterior, II—middle, III—posterior axial annulation; Aki—acrolobe constricted (flanks concave); m—notulae in articulating furrow; n2—terminal node.

AMMAGNOSTUS PSAMMIUS sp.nov.

(Pl. 55, Fig. 3; Pl. 66, Figs 1–4; Text-fig. 40)

*Material:* Two cephalons and four pygidia, all silicified, and in chert, are illustrated.

*Holotype:* The pygidium Plate 66, fig. 3, CPC 5937, is selected as the holotype because its test is preserved in detail.

*Diagnosis:* *Ammagnostus psammius* sp.nov. is a species en grande tenue with a strongly constricted pygidial acrolobe distinguished by (1) the rather wide cheeks and a narrow glabella, (2) the truncate frontal margin and the truncate front of the acrolobe, (3) laterally constricted and notched glabella, (4) the truncate rear margin

of the pygidium, (5) well developed pygidial axial furrows closing behind the sub-angulate rear of the pygidial axis, and (6) having the terminal node in the middle of the rear half of the posterior axial lobe. The pygidial border consists of an elevated rim and a wide marginal furrow.

The differential diagnosis is given under *Ammagnostus integriceps*.

Complete specimens of *A. psammius* are unknown, but the conspecific character of these cephalata and pygidia is apparent from the truncation of the cephalic front and of the pygidial rear and from the observed occurrence of such shields in close association; their generic identity is borne out by the similar granular ornament. Since the pygidial acrolobe is constricted but the cephalic is not, the pygidium cannot be matched with the cephalon as is possible, for example, in *Pseudagnostus*, *Agnostascus*, and *Agnostoglossa*.

*Description:* The margin of the cephalon is convex at the flanks and somewhat parabolic in front, and reminiscent of *Glyptagnostus reticulatus*; but the frontal margin and the front of the acrolobe are truncate—a rare feature hitherto known only in some species of *Hypagnostus*. The rim is narrow and almost flat and the marginal furrow is rather weak. The cheeks are slightly convex and slope roofwise down from the midline. A preglabellar median furrow is absent except for a short notch in front of the glabella.

The glabella is relatively short (0.6 of cephalic length) and narrow (0.23 of cephalon in the middle), slender, bluntly rounded in the rear and angulate in front. The anterior glabellar lobe is defined by shallow furrows; it is low, subpentagonal and 0.3 of glabellar length.

The transverse glabellar furrow is wide and deep and almost straight, or slightly sagging like *Kormagnostus*. The posterior glabellar lobe expands rearward, and is laterally notched in its anterior half; the small median circular node is placed subcentrally, in front of the midpoint. The basal lobes are small, triangular and apparently divided, with isolated anterior tips. The spines are triangular, and the connective band behind the glabella is well developed. The whole cephalon is slightly wider than long, and moderately convex.

The pygidium is also slightly wider than long, and its marginal outline (except for the spines) is congruent with the margin of the cephalon. Broader pygidia occur also (Pl. 66, fig. 4), but are rare, and cephalata with matching margins are unknown. The border is very wide (in contrast to the narrow and flat cephalic border), is widest at the spines, and consists of a convex rim and a wide and shallow furrow, which are about equal in width. The marginal spines are small, directed rearward, and placed on the level of the terminal node (which itself is placed forward from the tip). The facets are concave and the fulcral points are relatively close to the axis. The articulating recess in the axial front is quite pronounced, the articulating furrow bears a pair of elevated notulae, and the half-ring is arched rearward. The articulating device compared with *Aspidagnostus* and *Kormagnostus* (see comment on the holotype), but not with *Glyptagnostus* and *Pseudagnostus*.

The pygidial acrolobe is constricted (more than in the other species), tapers rearward, and the pleural lobes are rather narrow. The axial furrows are distinct, but, because of the length of the axial lobe, they appear to merge with the marginal furrow at the axial tip.

The axial lobe is long, reaches the marginal furrow, and is about as wide as half the shield. The posterior lobe is expanded and bears the terminal node in the middle of its posterior half. Notulae are present and arranged in lines converging at the axial tip and bypassing the terminal node. The anterior section of the axial lobe is almost parallel-sided. The anterior annulation is weakly tripartite, narrow (longitudinally) in the middle, and has tumid and expanded flanks. The second annulation is twice the length of the first, and carries the long median node which extends rearward as a blunt low spine. In the holotype and in some other well preserved specimens a third narrow annulation is discernible, comparable with *Xestagnostus* and *Lotagnostus*. Muscle spots are also discernible on the annulations.

Rugae and scrobicules are absent on the cephalon as well as on the pygidium, and the test is densely and minutely granulose.

*Comment on illustrated specimens* (All material comes from the O'Hara Shale, 'lower chert bed').

The cephalon, Plate 66, fig. 1, CPC 5935, in chert, locality D29, is 2.5 mm long; the dense granulation is preserved, the left spine is partly missing; note the truncated front.

The cephalon, Plate 66, fig. 2, CPC 5936, in chert, locality D29, is 2.7 mm long. The right posterolateral corner is missing. The basal lobe is, probably, divided.

The pygidium, Plate 55, fig. 3, CPC 5815, locality D29, is 3.0 mm long. The silicified test is preserved, and is densely granulose. Some of the notulae are visible as elevated grains of silica filling the notular pits.

The holotype pygidium, Plate 66, fig. 3, in chert, locality D6, is 3.2 mm long. Preserved are the articulating half-ring (comparable with *Kormagnostus simplex* Palmer, 1954, pl. 76, fig. 12), a pair of notulae in the articulating furrow, close to the midline (also visible in *Kormagnostus*, but less close), the three anterior annulations with muscle spots, the terminal node and the granulation. Note the truncated rear margin of the pygidium.

The pygidium, Plate 66, fig. 4, CPC 5938, in chert, locality D6, is 2.5 mm long. It is an external mould with a less pronounced relief of lobes and furrows as compared with the holotype. It is also broad, wider than the holotype.

*Occurrence and age*: *Ammagnostus psammius* comes from the O'Hara Shale ('lower chert bed'), localities D6 and D29; its age is the zone of *Glyptagnostus stolidotus*.

#### AMMAGNOSTUS INTEGRICEPS sp.nov.

(Plate 66, figs 5-8; Text fig. 41)

*Material*: One cephalon and three pygidia are selected for illustration and description.

*Holotype*: The pygidium Plate 66, figures 6a, 6b, CPC 5940, is selected as the holotype because its external mould and the test are preserved. A pygidium is selected because the types of all species of *Ammagnostus* are pygidia.

*Diagnosis*: *Ammagnostus integriceps* sp.nov. is a species with a slightly effaced pygidium and feebly constricted pygidial acrolobe distinguished by the relatively narrow cheeks and a wide glabella, by the arched frontal margin and slightly truncated front of the acrolobe, straight glabellar flanks, rounded rear margin of the pygidium, fading out of the pygidial axial furrows in the rear, rounded rear of the pygidial axis, and the location of the terminal node at the centre of the posterior axial lobe.

*Differential diagnosis* : *A. integriceps* differs from *A. psammius* in all characters of the diagnosis; and by its flat pygidial border, which in *psammius* has a convex rim and a distinct marginal furrow. The border is flat also in *A. euryaxis* and *A. mitis*, whose difference from *integriceps* is discussed under their headings.

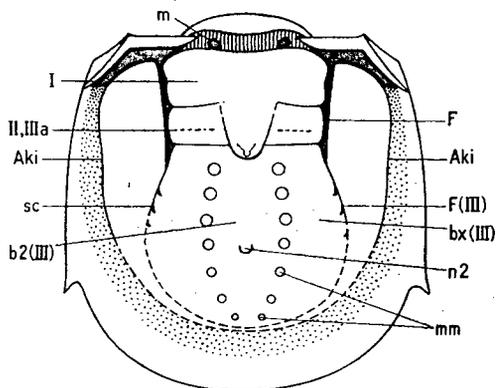


Fig. 41.—*Ammagnostus integriceps* sp. nov., from Plate 66, figs 7, 8. I—anterior, II, IIIa—middle and posterior axial annulations, confluent. Aki—acrolobe constricted; b2 (III)—intranotular axis; bx (III)—extranotular axis; F—anterior section and F (III) posterior section of axial furrows; m—notulae in articulating furrow; mm—notulae behind terminal node; N2—terminal node; sc—scalloped flank of axial lobe.

*Description* : The margin of the cephalon is moderately convex at the flanks (visibly less than in *A. psammius*), the frontal margin is about semicircular, without the frontal truncation seen in *A. psammius*; though the front of the acrolobe in *integriceps* is straight, truncate. The cheeks are slightly tumid in the rear, and no trace of a dividing preglabellar median furrow is present. The border is narrow and a shallow marginal furrow is present.

The glabella, about 0.65–0.67 of cephalon's length and 0.3 its width in the middle, is visibly longer and wider than in *A. psammius*. It is indeed, wider than the cheek, especially in the rear. The posterior glabellar lobe expands and gains in tumidity rearward, has no lateral indentations and bears a tiny subcentral node. The basal lobes are small and simple and the strong connective band is vertical and cannot be seen from above. The whole cephalon is as wide as long and, because of the prominent posterior glabellar lobe, quite convex.

The pygidium is also as wide as long, or slightly wider, not counting the articulating half-ring. The margin is evenly rounded; and the small marginal spines are placed relatively forward—somewhat behind the level of the terminal node. The border is wide, flat or slightly convex, and the marginal furrow, when present, is rather shallow. The facets are concave and the fulcra are pointed, as seen in the holotype. The articulating recess is relatively shallow, the articulating furrow is narrow, and the half-ring, elevated and arched, is almost straight transversely; the articulating device as a whole compares well with *Agnostus*, *Kormagnostus*, and *Cyclagnostus*.

The pygidial acrolobe is weakly constricted. The axial furrows are shallow in the front and fade out rearward and do not close around the axial lobe. The anterior annulations are indicated and the posterior lobe evenly rounded in the

rear, bears its terminal node almost in, or slightly behind, the middle. Notulae are visible in Plate 66, figure 7, in a pair of lines converging at the rear tip of the axial lobe.

The test of both shields is densely and minutely granulose.

*Comment on illustrated specimens* (All specimens come from locality D29, O'Hara Shale ('lower chert bed').

The cephalon, Plate 66, fig. 5, CPC 5939, is 2.5 mm long; note the plump posterior glabellar lobe, its subcentrally placed tiny median node, and the minutely granulose ornament.

The holotype pygidium, Plate 66, figs 6a, 6b, is 2.5 mm long; its test is preserved and seen in fig. 6b; the external mould (cast in rubber) fortified by acetone glue lost some detail of its surface.

The pygidium, Plate 66, fig. 8, CPC 6712, is 3.2 mm long. Its silicified test is broken along the margin and the doublure is exposed.

The pygidium, Plate 66, fig. 7, CPC 6711, is 3.0 mm long. The flank of the posterior axial lobe is apparently scalloped, suggesting that the pleural lobes probably contain deep-seated caeca.

*Occurrence and age:* *Ammagnostus integriceps* sp.nov. occurs in the O'Hara Shale ('lower chert bed') at localities D6 and D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*; it is also recorded from the same zone at McCabe Knob, Mungerebar (map, Text-fig. 3).

AMMAGNOSTUS EURYAXIS sp.nov.

(Pl. 66, fig. 9; Text-fig. 42)

*Material:* Only pygidia are known, and are rather rare. One specimen, CPC 6713, locality D29, is illustrated and is the holotype. It is 3.2 mm long and the test is silicified.

*Diagnosis:* *Ammagnostus euryaxis* is a species with a flat pygidial rim without a marginal furrow and with the terminal node placed in the middle of the posterior half of the rear lobe of the pygidial axis; distinguished by the continuous axial furrows closing in the rear, and by the shape of the pygidial axial lobe, which expands almost evenly and slightly rearward.

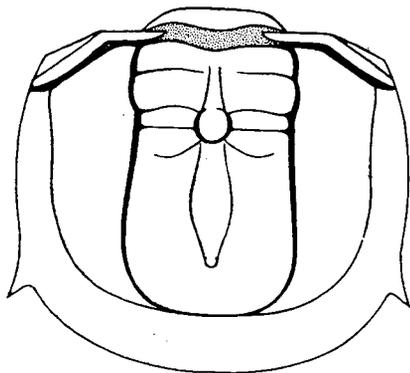


Fig. 42.—*Ammagnostus euryaxis* sp.nov., from Plate 66, fig. 9.

*Differential diagnosis:* In *A. psammius* and *integriceps* the anterior part of the axial lobe is visibly narrower than the expanded posterior lobe, and the axis therefore does not evenly expand rearward; in *integriceps* the axial furrows fade out rearward, but are continuous in *euryaxis*. The terminal node is similarly placed in

*psammius* and *euryaxis*—the only specific character they have in common—but is different in *integriceps* and the terminal node also has a different position.

**Occurrence and age:** *Ammagnostus euryaxis* sp.nov. occurs in the O'Hara Shale ('lower chert bed') locality D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

AMMAGNOSTUS MITIS sp.nov.

(Pl. 66, figs 10, 11; Text-fig. 43)

**Material:** Only two pygidia, both in limestone, are available; one is an immature specimen.

**Holotype:** The large, mature pygidium CPC 6714, Plate 66, figure 10 is the holotype; it is 3.1 mm long.

**Diagnosis:** *Ammagnostus mitis* sp.nov. is a species with a semi-effaced pygidium with a rather low axial lobe having only vestiges of axial annulations, almost parallel axial furrows and a flat rim; distinguished by the position of the terminal node in the middle of the posterior half of the rear lobe of the axis. *A. mitis* is the oldest, and most effaced, species of the genus.

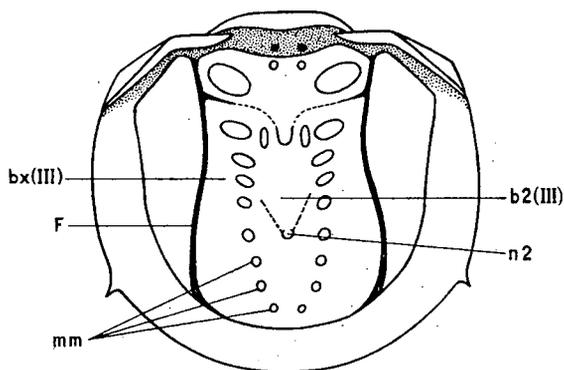


Fig. 43.—*Ammagnostus mitis* sp.nov., from Plate 66, fig. 10. Muscle spots and notulae indicated. F—axial furrow; b2 (III)—intranotular axis; bx (III)—extranotular axis; mm— notulae behind terminal node; n2— terminal node.

**Differential diagnosis:** *A. mitis* resembles *integriceps* as regards the position of the terminal node and the flat border, but in *integriceps* the posterior pygidial lobe is much more expanded; in *A. euryaxis* the pygidium is less effaced than in *mitis*, has in the anterior part of the axis three distinct annulations, and its median node is stronger.

**Comment:** The articulating device in the holotype of *A. mitis* is well preserved and resembles *A. psammius* and *Kormagnostus*; the marginal spines are very small and the test is granulose.

**Morphogenesis:** The small pygidium, CPC 6715, Plate 66, figure 11, is 1.3 mm long and belongs to an immature specimen. It is less effaced than the holotype, has a tumid axial lobe and a relatively wide border. The axial lobe is long, reaching the border and indicating a manner of growth different from *Connagnostus venerabilis* sp.nov.: in the latter the axial lobe is short in small specimens and touches the border only in fully grown specimens.

*Occurrence and age:* The two specimens of *Ammagnostus mitis* are found in Mungerebar Limestone at locality G10; the age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

Genus AGNOSTOGLOSSA nov.

*Agnostoglossa* is a monotypical genus, with *A. bassa* sp.nov. as the type.

*Diagnosis:* *Agnostoglossa* refers to agnostids of a low relief with a long and fused pygidial axis rounded in the rear and contacting the marginal furrow, and with a wide border in both shields; distinguished by the constricted acrollobes of the cephalon, as well as of the pygidium.

*Differential diagnosis:* The constriction of the acrollobes is unknown in peronopsids, but suggests a comparison with *Pseudagnostus*, in which the border is also wide. But the rounded rear of the glabella, the subcentral position of its node, the transverse (and not forward-directed) lateral furrows of the posterior glabellar lobe, the absence of a preglabellar median furrow, and in the pygidium the absence of a deutero-lobe as well as the simple articulating device, constitute a combination of characters alien to *Pseudagnostus*. *Agnostascus* gen.nov. is similar in the size and outline of its pygidial axis, but it has a different articulating device and its cephalon is quite different with its angulate glabellar rear, and well developed preglabellar median furrow. *Agnostoglossa* is quite close to *Ammagnostus* gen.nov. Common to both are: (1) the absence of the preglabellar median furrow, (2) the subcentral position of the glabellar node, (3) the rounded glabellar rear, (4) the long pyriform pygidial axis, and (5) the constriction of the pygidial acrollobe. In *Agnostoglossa*, however, the transverse glabellar furrow is V-shaped (straight in *Ammagnostus*), the cephalic border is wide (narrow in *Ammagnostus*), the cephalic acrollobe is constricted (unconstricted in *Ammagnostus*) and the terminal node is placed in the rear and not advanced forward as in *Ammagnostus*.

AGNOSTOGLOSSA BASSA sp.nov.

(Pl. 60, figs 6-14; Text-fig. 44)

*Material:* *Agnostoglossa bassa* is a common species; all specimens are, however, silicified and more or less fragmentary. Four pygidia and five cephalae, selected from the better preserved material, are illustrated.

*Holotype:* The pygidium Plate 60, figure 6, CPC 5878, locality G150, is selected the holotype because of its almost complete state of preservation and because of the durability of its matrix (solid chert).

The specific diagnosis is the same as that of the genus *Agnostoglossa*.

*Description:* The border in both shields is relatively wide, with a shallow marginal furrow and ill defined rim. In the pygidium the border appears even unusually wide because the acrollobe is separated from the border only by a gentle change in the angle of the slope.

The marginal pygidial spines are very small and have a relatively forward position. The axial furrows are defined along the flanks of the axial lobe, but their closure in the rear is rather diffuse. The axial node is elongate but very low. The doublure is wide, probably the widest known in agnostids. The articulating device consists

of a low articulating half-ring and a narrow furrow, as commonly seen in peronopsids. A terminal (subterminal) node is present, but it is seldom preserved. The flanks of the pygidial acrolobe are concave and the lobe itself is therefore constricted; the pygidial acrolobe is congruent with the equally constricted cephalic acrolobe.

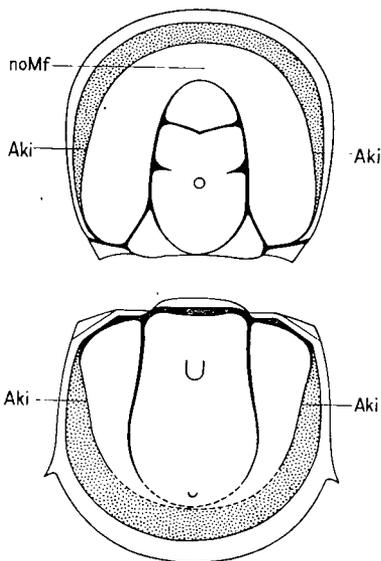


Fig. 44—*Agnostoglossa bassa* gen.nov., sp.nov., combined from Plate 60, figs 6, 7, 9, 12. Aki—acrolobes constricted; noMf—cheek confluent, preglabellar median furrow absent.

In the cephalon the acrolobe is defined clearer against the border than in the pygidium. The cheeks are moderately tumid and, in the absence of a preglabellar median furrow, confluent in front. The glabella, 0.7 of cephalic length and about 0.34–0.35 of its width, is defined by shallow axial furrows and stands low above the level of the cheeks. The anterior lobe is well rounded; the V-shaped transverse glabellar furrow is shallow; the transverse lateral furrows of the posterior glabellar lobe are short but distinct, and the subcentral node is very small and often obliterated; it may be, however, accentuated by subsequent silicification. The basal lobes are relatively large and connected in the rear by a narrow connective band.

*Comment on illustrated specimens:*

The holotype pygidium is 3.9 mm long. Its test is preserved; the middle part of the articulating half-ring is free of silica. A terminal node is present but obscured by the abrasion of the test.

The next three specimens come from locality G8.

The pygidium, Plate 60, fig. 7, CPC 5879, is 4.0 mm long; the right facet and shoulder are preserved; the articulating half-ring is exposed but is disfigured by silicification.

The cephalon, Plate 60, fig. 8, CPC 5880, is 3.2 mm long. The rounded rear of the glabella, the basal lobes, and the right spine are intact.

The fragmentary cephalon, Plate 60, fig. 9, CPC 5881, is 3.7 mm long. The lateral transverse furrows of the rear lobe of the glabella are distinct.

The following five specimens come from locality G417.

The pygidium, Plate 60, fig. 11, CPC 5883, is 3.0 mm long; secondary silica accentuates its median node; the wide doublure is partly exposed.

The cephalon, Plate 60, fig. 12, CPC 5884, is 2·3 mm long; its glabella and frontal part of the border are well preserved; the specimen is, however, mislaid.

The cephalon, Plate 60, fig. 10, CPC 5882, is 2·7 mm long. The glabellar furrows are well visible.

The cephalon, Plate 60, fig. 13, CPC 5885, is 3·2 mm long; it shows the inconspicuous median glabellar node.

The pygidium, Plate 60, fig. 14, CPC 5886, is 3·7 mm long; it shows the inconspicuous axial node and a part of the doublure; two vestigial axial annulations are indicated; parts of the margin have crumbled away.

*Occurrence and age:* *Agnostoglossa bassa* sp.nov. is a common species of the Mungerebar Limestone, especially at localities G8, G114, G119, G417, G429; the holotype comes from G150; at these localities its age is the Mindyallan Zone of *Erediaspis eretes*: it occurs also at G124 and G127 in the Zone of *Cyclagnostus quasivespa*, and at McCabe Knob—low in the Zone of *Glyptagnostus stolidotus*.

#### Family DIPLAGNOSTIDAE, subfamiliae suae

##### Genus AGNOSTASCUS gen.nov.

The type of *Agnostascus* is *A. gravis* sp.nov.

*Diagnosis:* The name *Agnostascus* refers to axiolobate agnostids with an angulate glabellar rear, forward-placed glabellar node, and distinct preglabellar median furrow, combined with a pygidium possessing a pseudagnostid articulating device and a wide and plump pygidial axis without a deuterolobe, whose posterior lobe is only slightly expanded and contacts the marginal furrow with its well rounded and wide rear; the acrolobes in both shields are constricted, the marginal spines are placed well in the rear, the rim is narrow, and so is the marginal furrow.

*Differential diagnosis:* The cephalon of *Agnostascus* is like that of *Pseudagnostus*, but is different in having a quite narrow border. The pygidium, however, is rather different from *Pseudagnostus* with an axial lobe reminiscent of *Ammagnostus* and lacking the deuterolobe. The combination of a cephalon and pygidium with a narrow border seen in *Agnostascus* is by itself already a striking diagnostic character of the genus. The combination is, however, correct, as can be concluded from the complete specimen (Resser, 1938, pl. 10, fig. 17) attributed to *Proagnostus bulbus*, and belonging neither to this species nor genus, but to *Agnostascus*, as discussed under the heading of the genus *Proagnostus* (q.v.).

*Subfamilial classification:* The characters of *Agnostascus* indicate its intermediate position between the Pseudagnostinae (the cephalon and the articulating device) and the Ammagnostinae (the pygidial axial lobe). Hence, *Agnostascus* may represent a subfamily of its own (subfamilia sua) with a reserved name. It cannot be placed in a known subfamily; consequently it is not 'subfamiliae incertae.'

##### AGNOSTASCUS GRAVIS sp.nov.

(Pl. 61, figs 1-4; Text-fig. 38)

*Material:* One cephalon and three pygidia, all silicified, are selected for description and illustration. *A. gravis* is a relatively common form, but most of the material is fragmentary.

*Holotype:* The cephalon, Plate 61, figure 1, CPC 5890, locality G119, is selected the holotype in preference to a pygidium, most of which are fragmentary.

*Diagnosis:* The generic diagnosis serves as the diagnosis of the species *A. gravis*.

*Description:* The cephalon is strongly convex; the rim and the marginal furrow are quite narrow. The frontal lobe of the glabella is large (0.3 of glabella length) and the transverse glabellar furrow straight and shallow. The median glabellar node is elongate, prominent, and placed on the anterior half of the posterior glabellar lobe, whose lateral furrows are indistinct. The basal lobes are tumid and connected in the rear by a narrow connective band.

In the pygidium the two anterior annulations of the axial lobe are defined by indistinct transverse furrows, and are as wide as half the shield. The median node is inconspicuous, and extends from the rear of the first to beyond the rear of the second annulation. The fulcral points are angulate and the facets concave. The marginal spines are flat and triangular, with tips almost level with the rear of the pygidial axis. The posterior lobe of the pygidial axis is quite tumid and slightly overhangs in the rear the marginal furrow. The terminal node is rather small.

*Comment on illustrated specimens:*

The holotype cephalon is 3.6 mm long. It is slightly flattened, the right spine is missing, and the left is covered by unremovable silica. Note the connective band, heart-shaped rear of the glabella, the large anterior lobe, and the narrow border.

The pygidium, Plate 61, fig. 4, CPC 5893, locality G119, is 3.6 mm long. The articulating half-ring is exposed.

The pygidium, Plate 61, fig. 2, CPC 5891, locality G417, is 3.2 mm long; its rim is flat.

The pygidium, Plate 61, fig. 3, CPC 5892, locality G417, is about 3.0 mm long. Its terminal node and the right fulcral point (shoulder) are preserved.

*Occurrence and age:* *Agnostascus gravis* sp.nov. occurs in the Mungerebar Limestone and is common at localities G8, G119, G150, and G417. Its age is the Mindyallan Zone of *Erediaspis eretes*; it is also recorded from localities G124 and G127 in the Zone of *Cyclagnostus quasivespa*.

AGNOSTASCUS sp.nov. aff. GRAVIS

(Pl. 61, figs 5, 6)

Only pygidia are available, and these are quite rare. Cephalata of this form have not been found as yet and a specific name is therefore reserved. All specimens are silicified.

The pygidia of this form are distinguished from *A. gravis* sp.nov. by their distinct annulation of the anterior part of the axis, the strongly developed axial node, and deep marginal furrow; the pygidial rim is prominent and convex, and the marginal spines are placed even more in the rear than in *A. gravis*.

*Comment on illustrated specimens:*

The pygidium, Plate 61, fig. 6, CPC 5895, locality G8, is 2.0 mm long. The terminal node is prominent and the annulations of the axis distinct. The right spine is exposed, but fragmentary.

The pygidium, Plate 61, fig. 5, CPC 5894, locality G417, is 4.0 mm long. Its border is well preserved; but in the articulating device the half-ring has crumbled away.

· *Occurrence and age:* *Agnostascus* aff. *gravis* sp.nov. occurs in the Mungerebar Limestone, at localities G8, G119, G150 and G417; its age is the Mindyallan Zone of *Erediaspis eretes*.

#### Subfamily PSEUDAGNOSTINAE Whitehouse, 1936

The characters of the subfamily Pseudagnostinae are evident from the 'Tabular Classification of Agnostids', and are also formulated under the heading 'Concepts of suprageneric taxa of agnostids' (q.v.).

#### Genus PSEUDAGNOSTUS Jaekel, 1909

The characters of *Pseudagnostus* and its organization have been recently discussed (Öpik, 1963, p. 48-53); consequently, a repetition of its diagnosis is unnecessary. The statement that *Pseudagnostus* is distinguished '... by reticulating pygidial caeca in the anterolateral parts of the pleural lobes' (op. cit. p. 48) must however be amplified: it should be replaced by: '(1) by reticulate and radiating caeca in the pleural lobes outside the deuterolobe (P in Text-fig. 45) and (2) by caeca radiating from the vestigial axial furrows within the parts of the pleural lobes which are included in the deuterolobe (PIII in Text-fig. 45)—as observed in *Pseudagnostus ampullatus* sp.nov.'

Smooth species of *Pseudagnostus*, without externally developed caecal rugae, exist. Hence, neither the rugosity nor its absence provides infallible 'characters of identification' of genera. But, once established in some of the species, the caecal pattern disclosed a fundamental peculiarity of the anatomy of *Pseudagnostus* in general which must be considered in the taxonomic diagnosis as well.

The accessory pygidial furrows in *Pseudagnostus* deserve comment. In many species these furrows are 'diagonal' to the deuterolobe. But, as seen in *P. ampullatus*, these furrows (parietal mesenteries) may extend rearward and surround the deuterolobe completely. They had apparently a mechanical function, adding in rigidity to the pygidium. The axial furrows which served the same mechanical purpose were permanently lost, and the device of the accessory furrows became instrumental instead.

A phylogeny of the species of *Pseudagnostus* cannot be contemplated (1) because the morphology of most of them is insufficiently known, and (2) because it is unknown how many species remain to be discovered. A general phyletic trend, however, is apparent, leading from species en grande tenue toward forms with a complete effacement of furrows and lobes. This final state may have been reached at various times, and independently in diverse lineages.

The temporal sequence of forms: *Pseudagnostus ampullatus* sp.nov. (with peripheral parts of the pleural lobes enclosing the deuterolobe), followed by *P. idalis* sp.nov. (with the posterior tips of the pleural lobes reduced, but extending rearward beyond the spines), and subsequently by *P. vastulus* and the majority of species (pleural lobes restricted to the anterolateral areas), may indicate a phylogenetic expansion of the deuterolobe and the suppression and reduction of the accessory furrows in its rear. This idea is supported by the observation that the accessory (diagonal) furrows are reduced, or even effaced completely, in late species.

The basic assumption is that the accessory furrows originally existed as a 'circum-axial' continuous intrapleural mesenterial septum. This is, of course, speculative; equally speculative is the assumption that the continuous mesentery evolved from a pair of short diagonal mesenteries located at the rear of the second axial annulation and that the reduction through the expansion of the deutero-lobe resulted in the restoration of the initial state of 'short diagonal accessory furrows'.

No evidence, however, exists that the three species—*ampullatus*, *idalis* and *vastulus*—are links of a single line of descent; they may equally well illustrate gradational changes in anatomy that occurred independently in diverse lineages and in different geographical sites.

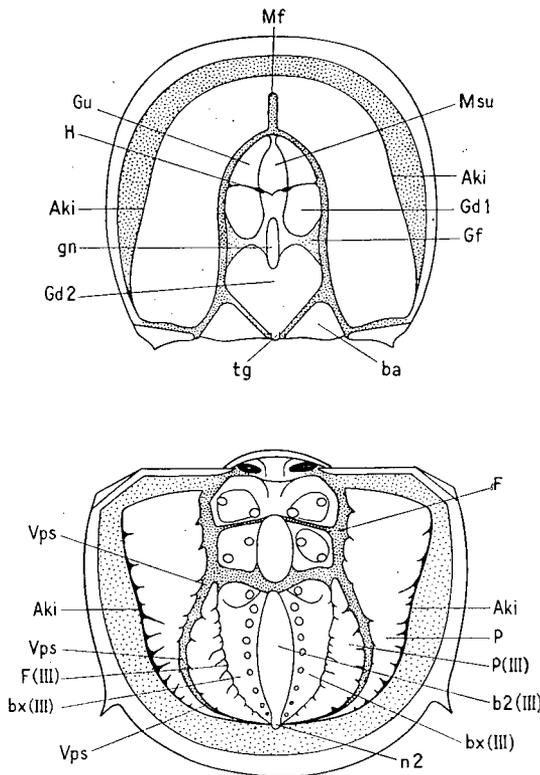


Fig. 45.—*Pseudagnostus ampullatus* sp. nov., from Plate 61, figs 10 and 7 (pygidium). Aki—acrolobes constricted (flanks concave). Cephalon: ba—basal lobes; Gd1—anterior part, and Gd2—posterior part of rear glabellar lobe; Gf—lateral glabellar furrow; gn—glabellar node; Gu—frontal lobe of glabella; H—Transverse glabellar furrow; Mf—preglabellar median furrow (not connecting marginal furrow); Msu—depressed extension of frontal sulcus (sulcus vestigial); tg—glabellar rear, angulate and pointed. Pygidium: b2 (III)—intranotular axis; bx (III)—extranotular axis; F—axial furrow; F (III)—posterior section of axial furrow, vestigial (included in the deutero-lobe composed of b2 (III) + bx (III) + F (III) + P (III)); n2—terminal node; P—peripheral pleural lobe, scalloped and rugose; P (III)—part of pleural lobe included in deutero-lobe; Vps—accessory furrows (major mesenteries) enclosing the deutero-lobe. See also Öpik (1963, p. 51, Text-fig. 13).

PSEUDAGNOSTUS AMPULLATUS sp.nov.

(Pl. 61, figs 7–11; Text-fig. 45)

*Material*: About 20 specimens have been examined; five (two cephalata and three pygidia) are illustrated.

*Holotype*: The best preserved pygidium, Plate 61, figure 7, CPC 5896, locality B525, is selected as the holotype. Preference is given to a pygidium because agnostid pygidia are more diversified than the conservative cephalata.

The pygidium is wider than long, with a curving margin tapering evenly rearward; as in the cephalon, its acrolobe is constricted in the middle. The border is rather wide (wider than in the cephalon) and the marginal furrow is a broad channel. The deuterolobe is oval to subcircular, slopes evenly rearward, and is well defined all round.

*Comment on illustrated specimens:*

The holotype pygidium is 3.0 mm long. The test is missing and the internal cast has preserved the delicate imprints of rugae and vestigial lines: caecal rugae are seen on the left pleural lobe, and on the pleural part of the deuterolobe. On the latter the rugae radiate outward, all starting at the line of the otherwise obsolete axial furrow.

The pygidium, Plate 61, fig. 9, CPC 5898, locality B537, is 3.3 mm long; its rear margin is damaged; the articulating device is well preserved; notulae and raised notular lines are indicated and the internotular axis is depressed.

The pygidium, Plate 61, fig. 8, CPC 5897, locality B525, is 2.5 mm long. The posterior ends of the pleural lobes meet in the rear.

The cephalon, Plate 61, fig. 10, CPC 5899, locality B525, is 2.9 mm long; its counterpart is also preserved. On the frontal glabellar lobe the depressed median extension of the sulcus is indicated, as in *Glyptagnostus*, by a pair of converging lines; the sulcus itself is, however, absent.

The cephalon, Plate 61, fig. 11, CPC 5900, locality B537, is 3.2 mm long; the angulate glabellar rear is equipped with a point; the pair of small muscle spots in the transverse furrow are distinct.

*Occurrence and age:* *Pseudagnostus ampullatus* sp.nov. comes from the Pomegranate Limestone at Wills Creek, from localities B525 and B537; fragments are also present in the O'Hara Shale ('lower chert bed') at locality D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

PSEUDAGNOSTUS SERICATUS sp.nov.

(Pl. 62, fig. 7)

*Material:* Only one cephalon, the holotype, CPC 5907, in limestone, has been found.

*Diagnosis:* *Pseudagnostus sericatus* sp.nov. is a species en grande tenue with a short and narrow glabella, a deep channel-like marginal furrow, and a narrow and elevated rim; distinguished by the minutely and densely punctate test.

*Differential diagnosis:* No *Pseudagnostus* has been described hitherto as having a punctate test. *P. araneavelatus* Shaw, 1951, has a surface ornament, but it consists of a 'fine web of inosculating ridges'.

*Description:* The cephalon is large, 5.0 mm long, and slightly wider, subelliptical (truncate in the rear), and with an evenly curved margin. The rim is narrow and high, and the marginal furrow is a deep channel with vertical slopes and a relatively flat floor. The preglabellar median furrow, deep and narrow, connects with the marginal furrow. The cheeks are moderately inflated and bear delicate marginal scrobicules and rugae extending on to the floor of the marginal furrow. The glabella is short (0.6 of shield length) and narrow (0.26 of shield width) and its rear is angulate. The anterior lobe is short (0.25 of glabella) but well defined; the V-shaped transverse glabellar furrow is distinct. The posterior lobe has parallel flanks and carries an elongate node on its anterior half. The basal lobes are tumid, triangular, and relatively small.

*Diagnosis:* *Pseudagnostus ampullatus* sp.nov. is a species en grande tenue whose pygidial deuterolobe is enclosed by the peripheral parts of the pleural lobes and the accessory furrows meeting in the rear; distinguished by a short, incomplete preglabellar median furrow, a long and subcentral glabellar node, small basal lobes, and low tumidity of the deuterolobe.

*Differential diagnosis:* The most conspicuous feature of *P. ampullatus* is the enclosure of the pygidial deuterolobe by the peripheral pleural lobes and the accessory furrows. Only one previously described species shows this structure: *Pseudagnostus canadensis* (Billings), as illustrated by Rasetti (1944, pl. 36, figs 9, 12 and 13). But *canadensis* has an extremely tumid deuterolobe, no transverse glabellar furrow, and divergent pygidial flanks with a rapidly expanding border, and is quite distinct. In all other known species of *Pseudagnostus* the rear part of the deuterolobe is in contact with the marginal furrow, the pleural lobes are eliminated in the rear and do not extend beyond the transverse line across the spines. As already mentioned the accessory furrows in *P. ampullatus* are evenly curved and meet at the rear; they should be similar in *P. canadensis*. In all other species these furrows are straight, or almost so, reaching the marginal furrow at the level of the spines, or more commonly fading out before reaching the marginal furrow.

Other characters mentioned in the diagnosis are specifically significant in combination. These characters are (1) the short preglabellar median furrow; in about four other species of the genus this furrow fades out before reaching the marginal furrow as concluded from published illustrations; (2) the subcentral position and the large size of the glabellar node; and (3) the relatively flat deuterolobe—in other species it is more tumid than in *ampullatus*.

*Pseudagnostus* cf. *vastulus* Whitehouse (Öpik, 1963, text-fig. 13) is a species en grande tenue with greatly reduced pleural lobes not reaching even the lateral spines; its deuterolobe is larger and more tumid than in *P. ampullatus*. The relative proportions of the cephalon and its glabella are the same in both species; but morphology differs as follows: in *P. cf. vastulus* (1) the preglabellar median furrow is connected with the marginal furrow, (2) the basal lobes are larger, (3) the glabellar node is reduced in the rear and appears therefore placed more forward, and the lateral (Gt) furrows are more conspicuous than in *P. ampullatus*.

*Description:* Descriptive data are contained in the diagnosis, in the differential diagnosis, in the comment on the illustrated specimens, and in Text-figure 45; some amplifications are given below.

The cephalon is semielliptical, as long as wide, with an evenly curved and somewhat forward tapering margin; on the flanks the border widens forward rapidly, the flanks of the cheeks are constricted, tapering forward, and the acrolobe is consequently pyriform. The frontal glabellar lobe is subtriangular and depressed and bears a pair of faint lines converging forward. The posterior glabellar lobe is slightly constricted in the middle, but its lateral furrows are shallow. The angulate glabellar rear slopes gently and bears a rearward-directed marginal tubercle or point. The preglabellar median furrow, broad and deep, fades out before reaching the marginal furrow.

The test is thin and shiny, but densely, evenly, and minutely punctate all over. The combination of the shiny surface and the dense punctation results in a silky lustre.

*Occurrence and age:* The holotype pygidium of *Pseudagnostus sericatus* sp.nov. was found in the Georgina Limestone (dark grey bituminous) at locality W15; fragments are also recorded from W20. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

PSEUDAGNOSTUS IDALIS sp.nov.

(Pl. 62, figs 8, 9; Pl. 63, figs 1 and 3)

*Material:* Specimens from limestone only are available; the selection is made from locality W39 (Georgina Limestone) and D132 (Pomegranate Limestone), both from the Idamean Zone of *Corynexochus plumula*. The matrix is dark grey laminated bituminous limestone and most of the specimens are flattened in various degrees. Two cephalae and three pygidia are illustrated.

*Holotype:* The pygidium, Plate 62, figure 8, CPC 5908, locality W39, is selected as the holotype because of its large size and because the posterior ends of the accessory furrows are well visible. It is, however, flattened and the accessory furrows are, therefore, unnaturally straight.

*Diagnosis:* *Pseudagnostus idalis* sp.nov. is a species en grande tenue with a complete preglabellar median furrow and the pygidial accessory furrows extending rearward beyond the marginal spines but not joining in the rear.

*Differential diagnosis:* In *P. ampullatus* sp.nov. the preglabellar median furrow is shorter and the accessory furrows enclose the deuterolobe all round in the rear. In *P. vastulus* the preglabellar median furrow is complete, but the accessory furrows do not reach the level of the marginal spines. Furthermore, in other species of *Pseudagnostus* en grande tenue (as indicated in the differential diagnosis of *P. ampullatus* sp.nov.) the accessory furrows and the tips of the anterolateral pleural lobes are not extended beyond the spines. Finally, *P. nuperus* Whitehouse (which occurs also in the Georgina Limestone) is insufficiently known and is unsuitable for a conclusive comparison.

*Description:* The cephalic border is about 0.18 of the cranial length and most of it consists of the wide channel-like marginal furrow. The cephalic acrolobe is only slightly constricted. The glabella is relatively short, about 0.63 of cephalic length, its rear is angulate, but the flanks of the angulate part are convex and not straight as in *P. ampullatus*.

In the pygidium as in the cephalon the acrolobe is only slightly constricted and the accessory furrows by-pass the level of the spines for a short distance; the deuterolobe is oval owing to the relatively small divergence of the slightly curved accessory furrows. The articulating device is large and strong and the fulcral tips are pointed. The pygidial border is not quite 0.2, and the deuterolobe 0.6 of the pygidial length without the articulating device.

*Comment on illustrated specimens:*

The holotype pygidium, locality W39, is 4.2 mm long. Its deuterolobe is collapsed and only the adaxial flank of the right pleural lobe has somewhat preserved the original curvature of the accessory furrow. The rear tips of the pleural lobes extend beyond the marginal spines; both sides of the accessory furrows are scalloped; the fulcrum is pointed.

The cephalon, Plate 63, fig. 1, CPC 5911, locality W39, is 3.7 mm long; the rear part of the glabella is crushed and has lost therefore its original angulate form.

The cephalon and the pygidium, Plate 62, fig. 9, CPC 5909, 5910, locality W39, are unequal in length, but belong probably to a single exuvia. The cephalon is 3.7 mm and the pygidium 4.1 mm long. The pygidium is longer because its rear border is wider than the frontal border of the cephalon; the acrolobes of the cephalon and of the pygidium are congruous and equal in size, suggesting that both shields, as indicated above, are parts of a single exuvia. In the pygidium the accessory furrows appear to diverge more than in the holotype, and the crushed test obliterates their distal parts.

The pygidium, Plate 63, fig. 3, CPC 5913, locality D132, is 3.5 mm long. The fulcra are pointed; the accessory furrows diverge less than in the previous specimen, but about the same as in the holotype.

*Occurrence and age:* *Pseudagnostus idalis* is found in the Georgina Limestone (locality W39) and in the Pomegranate Limestone (locality D132), but also in several other places; the age is the Idamean Zone of *Corynexochus plumula*. But the species first appears probably at the end of the *Glyptagnostus reticulatus* Zone (below) and may have reached the base of the *Erixanium sentum* Zone (above).

PSEUDAGNOSTUS cf. IDALIS sp.nov.

(Pl. 63, fig. 4)

The illustrated cephalon, CPC 5914, 4.7 mm long, is associated with specimens of *Pseudagnostus idalis* from locality D132. It is distinguished from the cephalon attributed to *P. idalis* by its extremely wide frontal border, which is wider than in *idalis*, being half the length of the preglabellar area. Furthermore, its basal lobes are relatively long and extenuated forward. The frontal glabellar lobe is peculiar in having a rectangular outline, but this may be the result of deformation by compression. Otherwise it is similar to *idalis* in proportions and in the structure of the complete and flaring preglabellar median furrow.

For comparison, the cephalic rim in *Pseudagnostus idalis* is 0.4 of the length of the preglabellar area; but in other cephalon, somewhat smaller values have been also observed; in *P. cf. idalis*, however, the rim is 0.45 of the preglabellar area. It should be noted that measurements of this area on flattened specimens are inaccurate because the limits of the marginal furrow are not well recognizable.

Informative and therefore important is the glandular pattern of *P. cf. idalis*. The cheeks are scrobiculate, the scrobicules are delicate lines, separating relatively low and wide rugae; these multiply by consecutive branching, extend into the floor of the marginal furrow, and continue across the rim to the margin. The same caecal pattern is observable also in *Xestagnostus legirupa* sp.nov., and less clearly in *Pseudagnostus sericatus*. Anatomically essential is the fact that in agnostids the terminal caeca extend to the margin and are not confined only to the acrolobes.

*Occurrence and age:* The cephalon of *Pseudagnostus cf. idalis* was found in the Pomegranate Limestone at locality D123; its age is the Idamean Zone of *Corynexochus plumula*.

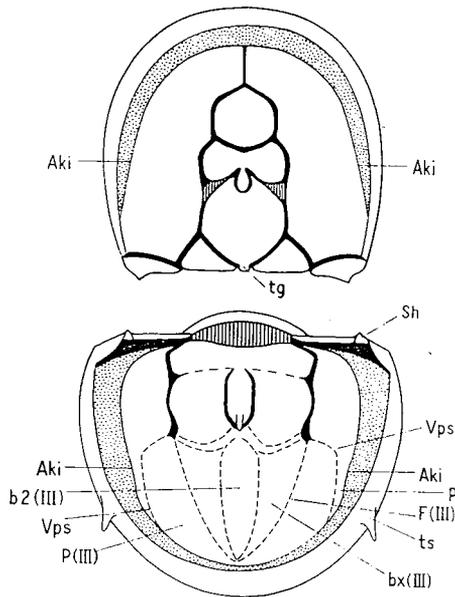


Fig. 46.—*Pseudagnostus mestus* sp.nov., from Plate 62, figs 5, 6. Aki—acrolobe constricted, flanks concave; tg—glabellar rear, angulate and pointed. Pygidium: b2 (III)—intranotular axis; bx (III)—extranotular axis; F (III)—axial furrow, vestigial, included in the deuterolobe; P—peripheral pleural lobe; P (III)—part of pleural lobe included in the deuterolobe; Sh—fulcral point with spine; Ts—marginal spine, arising from the rim; Vps—slope of deuterolobe.

PSEUDAGNOSTUS MESTUS sp.nov.

(Pl. 62, figs 5, 6; Text-fig. 46)

*Material:* The material available consists of the holotype pygidium, Plate 62, figure 6, CPC 5906, and a cephalon, CPC 5905, which presumably belongs to *mestus* sp.nov.

*Diagnosis:* *Pseudagnostus mestus* sp.nov. is a semi-effaced species without accessory furrows and with almost completely effaced transverse axial furrows; distinguished by its rather wide axial lobe, narrow anterolateral parts of the peripheral pleural lobes, deeply concave facets, and strongly pointed fulcra.

The characters indicated in the diagnosis are so peculiar that a differential diagnosis seems unnecessary.

The characters of the cephalon are not included because it is not quite certain whether it is the cephalon of *mestus*, or of another form whose pygidium is unknown.

*Description:* The holotype pygidium is 2.9 mm long; the relief of the internal cast (not illustrated) and of the external surface are the same, indicating a thin test. It is elongate semielliptical, with an evenly curved margin. The lateral spines are small, deflected, and arise from the surface of the rim slightly off the margin. The border is very wide; left and right borders together occupy about 0.25 of the width of the shield. The marginal furrow is shallow, wide in front and narrow in the rear. The facets are relatively large, deeply concave, and the fulcra are produced into strong points. The axis and the deuterolobe are rather tumid, and elevated above the anterolateral part of the pleural lobes; these are also tumid, very narrow (about 0.3 of the axis), and continue to the line of the spines as elongate and very narrow strips; at these strips the pleural flanks are slightly constricted.

The anterior part of the axial lobe is rather wide, about 0.5 of the shield, and laterally defined by distinct axial furrows, but the transverse furrows are almost obsolete and the two annulations are recognized from their tumidity only. The axial node, extending over the full length of the second annulation, and even slightly beyond it rearward, is distinct; it is relatively low but bears a knob on its tip. The accessory furrows are absent, but their position is nevertheless rather conspicuous owing to the change of slope from the tumid deutero-lobe to the depressed pleural lobes. The anterolateral flanks of the deutero-lobe are subangulate; within the deutero-lobe the intranotular axis, the extranotular axis (left and right), and the pleural parts of the lobe are distinguishable because they form separate swellings (Text-fig. 46). A terminal node is absent. The articulating device (crushed in the middle) is large, with a prominent arched half-ring, and a wide articulating furrow; but the recess in the front of the axial lobe is moderate only. Notulae and caecal rugae are absent.

The cephalon Plate 62, figure 5, is 2.5 mm long; it is attributed to *mestus* because (1) its border is rather wide, (2) the outline of its acrolobe is the same as of the pygidium, (3) no other pygidia are present which could be connected with this cephalon, and (4) the cephalon itself is diagnostically distinct from other species of *Pseudagnostus*. Some uncertainty however remains as regards the specific classification of this cephalon because the pygidium and cephalon are both unique, and are associated with thousands of fossils which cannot be all described exhaustively: the chance remains that the cephalon represents a separate species whose pygidium is as yet unknown.

The cephalon is distinguished by the faint but complete preglabellar furrow, the rather large subcircular and slightly pointed anterior glabellar lobe, the swollen and upturned spines, the rather wide border and forward tapering acrolobe. The cast and its counterpart are preserved and both are exploited in Text-figure 46.

*Occurrence and age:* *Pseudagnostus mestus* sp.nov. comes from the O'Hara Shale ('lower chert bed'), locality D29; fragments are also recorded from the Georgina Limestone, locality G49. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### PSEUDAGNOSTUS BULGOSUS sp.nov.

(Pl. 38, fig. 8; Pl. 62, figs 1-4; Text-fig. 47)

*Material:* The illustrated and described material consists of one cephalon and four pygidia.

*Holotype:* The pygidium Plate 62, figure 1, CPC 5901, locality D28, is selected as holotype because it has retained most of its test; preference is given to a pygidium because cephalae of *Pseudagnostus* are less diversified than pygidia; moreover, complete specimens are absent and the association of the pygidia and cephalae cannot be proven conclusively.

*Diagnosis:* *Pseudagnostus bulgosus* sp.nov. is a species en grande tenue with strongly convex shields and prominent lobes; distinguished by the absence of both the preglabellar median furrow and the pygidial spines and by its deep straight accessory furrows, which are connected with the marginal furrow. This diagnosis refers to the pygidium in the first place.

*Differential diagnosis:* *Pseudagnostina vicaria* sp.nov. also lacks the median furrow and pygidial spines, but its pygidium is effaced and the outline of the cephalon is different. *Pseudagnostus (Plethagnostus) clarki* Kobayashi, 1935, also has neither a preglabellar median furrow nor pygidial spines. It is, however, quite effaced, 'without any particular prominence of the axial lobe', and its pygidial axial lobe is short (about 0.4 of the deuterolobe; in *bulgosus* it is 0.7). Close to *bulgosus* is the pygidium in Lochman (1940, pl. 2, fig. 38), from Missouri, attributed to *Pseudagnostus messleri* (Resser, 1938); it has, however, marginal spines. The original material of *messleri* is, unfortunately, inadequate for comparison.

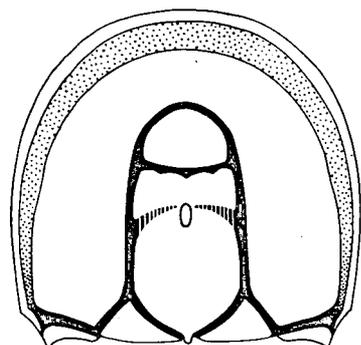
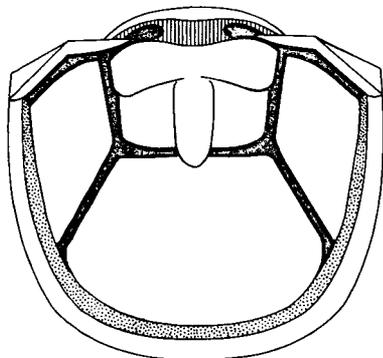


Fig. 47.—*Pseudagnostus bulgosus* sp.nov., from Plate 62, fig. 4 and figs 1 and 2.



*Description:* The cephalon is semielliptical to parabolic, very convex, and the constriction of its acrolobes is almost imperceptible. The furrows and lobes are distinct, but the preglabellar median furrow is absent. The marginal furrow is rather wide, the rim convex and elevated, the spines short and pointed. The anterior glabellar lobe is evenly rounded, but may be also subangular in front. The glabellar rear is angulate, and the lateral furrows of its posterior lobe are weak. The glabellar node is relatively small in most of the specimens, but in larger cephalata it is relatively long and extends well forward.

The pygidium is also very convex, with a relatively flat border and fulcral points close to the axial furrows. Marginal spines are absent. The anterior part of the axial lobe is large and prominent, and the tip of the median node is extended into

a short and rearward-directed spine. The accessory furrows are deep and straight and connected with the marginal furrow. The deuterolobe is prominent, surrounded in the rear by the marginal furrow, and bears an inconspicuous terminal node. The anterolateral parts of the pleural lobes are relatively small and well defined, reaching in the rear to about the middle transverse line across the deuterolobe. The articulating device is relatively large, with a spacious furrow and forward-arched half-ring, but remains depressed below the level of the axial lobe.

*Comment on illustrated specimens:*

The holotype pygidium, silicified, on a bedding plane of chert, is 2.5 mm long; its test is mostly preserved; the lobes and furrows are, nevertheless, quite distinct.

The exfoliated fragmentary pygidium, Plate 62, fig. 2, CPC 5902, locality D29, in chert, is 2.2 mm long. It is not flattened as seen in the lateral view.

The small pygidium, Plate 62, fig. 3, CPC 5903, locality D29, in chert, is 1.5 mm long. It is rather tumid but otherwise differs little from the larger specimens.

The pygidium, Plate 38, fig. 8, CPC 5656, locality D29, associated with *Biaverta biaverta* in friable silica, is 2.0 mm long. The flanks of the deuterolobe and the pleural lobes along the accessory furrows are scalloped.

The cephalon, Plate 62, fig. 4, CPC 5904 in silica, locality D29, is 2.6 mm long; it is deformed (askew to right).

*Occurrence and age:* *Pseudagnostus bulgosus* sp.nov. occurs in the O'Hara Shale ('lower chert bed') at localities D6, D28, and D29, and in the Georgina Limestone at locality W1; it is a rare fossil. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*. It is recorded also in the Mungerebar Limestone, locality G417, in the Zone of *Erediaspis eretes*.

#### Genus PSEUDAGNOSTINA Palmer, 1962

The genus *Pseudagnostina* is based on *P. contracta* Palmer, from the *Glyptagnostus stolidotus* bearing beds of Alabama and Nevada.

The characters of *Pseudagnostina* are (1) the subrectangular, not parabolic or semielliptical, cephalon, (2) the absence of the preglabellar median furrow, (3) the small subcentral glabellar node, (4) the absence of accessory furrows, and (5) the external absence of the deuterolobe, or of a tumidity interpretable as such a lobe.

#### PSEUDAGNOSTINA VICARIA sp.nov.

(Pl. 55, fig. 4; Pl. 63, figs 8, 9)

*Material:* Two cephalata and one pygidium are illustrated which are sufficiently preserved for description; it is a rare form and its shields are mostly fragmentary. The cephalata and the pygidium are conspecific because of their general similarity with the shields of *Pseudagnostina contracta* Palmer (1962, pl. 2, figs 18-20, 23-25).

*Holotype:* The pygidium, Plate 63, figure 8, CPC 5918, locality D29, in chert, is selected as the holotype because a pygidium is also the type of *P. contracta* Palmer.

*Diagnosis:* *Pseudagnostina vicaria* is a species with a relatively slender glabella (about 0.25 of the shield width) and narrow pygidial axis (less than 0.4 of pygidial width), and without pygidial marginal spines.

*Differential diagnosis:* In the only other known species (*P. contracta* Palmer) the glabella (about 0.28–0.29), and the pygidial axis (almost 0.5) are wider than in *vicaria*, and pygidial spines are present. *Agnostus* (= *Pseudagnostus*) *douvillei* Bergeron, as described by Monke (1903), Walcott (1913), and Resser & Endo (1937), is also possibly a *Pseudagnostina* with pygidial spines, distinguished by its small subcircular frontal glabellar lobe.

*Description:* The diagnosis of the species and the discussion of the characters of *Pseudagnostina* provide a general description, which needs, however, some amplification.

The holotype pygidium is 3.3 mm long. Its articulating device consisting of an axial recess, an elliptical articulating furrow and an upward and forward arched half-ring is pseudagnostoid. The two anterior axial annulations are almost confluent; the axial node has two median tips, and some of the notulae are distinct knobs (not pits). Pygidial spines are absent; this is inconclusive here because the margin is damaged, but other specimens with an unbroken margin, and without spines, are available also.

The cephalon, Plate 63, figure 9, CPC 5919, is 2.6 mm long. The rim, together with the rather shallow marginal furrow, is wide in front and narrows rearward. The circumglabellar furrow is shallow, and the glabellar rear angulate (as in *Pseudagnostus*).

The cephalon, Plate 55, figure 4, CPC 5816 is 2.5 mm long; its glabellar node is prominent and the border appears venulose.

*Occurrence and age:* *Pseudagnostina vicaria* is a rare fossil in the O'Hara Shale ('lower chert bed') at localities D6 and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*, and it is contemporaneous with *P. contracta* Palmer from Alabama and Nevada.

PSEUDAGNOSTINA? sp.indet. (aff. VICARIA sp.nov.)

(Pl. 63, fig. 10)

Only one pygidium, CPC 5920, has been found. It is 2.5 mm long, apparently flattened, and its articulating half-ring is missing. Like *Pseudagnostina vicaria* sp.nov. it possesses no marginal spines, the posterior part of the axial lobe is confluent with the pleural, and a terminal node is indicated in the rear, at the marginal furrow. It differs, however, from *vicaria* by the larger size of the anterior part of the axis and the relatively narrow border, especially in the rear.

*Occurrence and age:* The pygidium comes from the O'Hara Shale ('lower chert bed'), locality D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Genus OXYAGNOSTUS gen.nov.

The type species of *Oxyagnostus* is *O. apicula* sp.nov.

*Diagnosis:* the name *Oxyagnostus* refers to forms with constricted acrolobes of both shields, with a wide and convex rim and a deep and relatively narrow marginal furrow, and with rugose pygidial pleural lobes; it lacks a preglabellar median furrow, but its glabellar node is placed forward and the glabellar rear is angulate; in

the pygidium the posterior axial lobe is subpentagonal and long, reaches the marginal furrow, and is defined all round, but a deuterolobe is externally not apparent; its spines arise from the surface of the rim and not from the margin, and the pygidial rim widens in the rear.

*Differential diagnosis:* The general aspect of *Oxyagnostus* suggests a close similarity with *Pseudagnostus*, from which it differs by having (1) narrow marginal furrows, and (2) a subpentagonal pygidial axial lobe which is completely enclosed by furrows. These furrows may be the axial furrows, or, if a deuterolobe is present, the accessory furrows. Furthermore, the absence of the preglabellar median furrow, and the widening of the rim in the rear, distinguish *Oxyagnostus* from most of the species of *Pseudagnostus*.

*Acmahachis?* sp. Palmer (1962, p. F-20, pl. 2, figs 9, 10) is also an *Oxyagnostus*. In *Oxyagnostus* the pygidial axis in plan is reminiscent of *Acmahachis*, but other characters mentioned in the diagnosis cannot be confused.

OXYAGNOSTUS APICULA sp.nov.

(Pl. 63, figs 5-7; Text-fig. 48)

*Material:* The material consists of two cephalae and four pygidia, of which one cephalon and two pygidia are illustrated.

*Holotype:* The largest pygidium, Plate 63, figure 6, CPC 5916, locality B525, in limestone, is selected as the holotype.

The diagnosis of the genus is also that of the species.

*Acmahachis?* sp. described by Palmer from Alabama (1962, pl. 2, figs 9 and 10) is also a species of *Oxyagnostus*; it may even belong to *apicula* sp.nov., although its glabella is somewhat shorter.

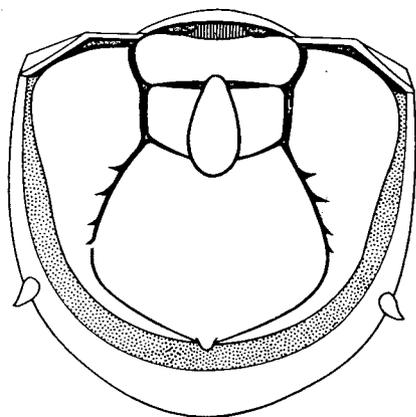


Fig. 48.—*Oxyagnostus apicula* gen.nov., sp.nov., from Plate 63, fig. 6.

*Description:* The holotype pygidium is 2.5 mm long; the second pygidium, Plate 65, figure 5, CPC 5915, locality B537, is 2.2 mm. Beside the difference in size the smaller specimen has a narrower, more slender axial lobe. The pygidium is longer than wide, semielliptical, with an evenly curved margin and a pair of tiny

spines arising from the surface of the rim. The border is convex and wide and widens rearward; the marginal furrow is distinct but narrower than the rim (in *Pseudagnostus* the marginal furrow is wider than the rim). The pleural lobes are moderately tumid; the edges against the axis are scalloped, indicating the presence of ramified caeca. The articulating device is inconspicuous as compared with *Pseudagnostus*: the half-ring is low and slightly retroverted, as, for example in *Aspidagnostus* (but not in *Pseudagnostus*), the articulating furrow is shallow, and the axial recess short.

The axial lobe is long, reaching with its prominent terminal node slightly over the marginal furrow; it is elevated above the pleurae, and moderately tumid but not swollen in the rear; it is strongly constricted at the second annulation, which is about 0.62 of the posterior lobe. The anterior annulation is visibly wider. The second annulation carries a prominent oval node protruding well rearward over the transverse furrow. The posterior lobe is subpentagonal and widest in its posterior half, where its straight flanks turn quite abruptly to meet at the acute posterior tip. Neither an intranotular axis nor notulae are visible, and no deutero-lobe is apparent.

The cephalon, Plate 63, figure 7, CPC 5917, locality B525, is 2.6 mm long. It is laterally distorted and the shield appears therefore somewhat narrow. The rim is relatively narrow and convex, the marginal furrow is narrow and deep, and quite distinct from *Pseudagnostus*. A preglabellar median furrow is absent. The basal lobes are small and triangular. The glabella, about 0.72 of the cephalic length, has parallel flanks and an angulate rear (as in *Pseudagnostus*); the frontal lobe is relatively large. The posterior lobe has no lateral indentations and its node is long.

*Occurrence and age:* *Oxyagnostus apicula* comes from the Pomegranate Limestone at Wills Creek, from localities B525 (two specimens) and B537 (two specimens); it is also recorded from the O'Hara Shale, locality D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*. It is probably present also in Alabama, in rocks of the same age.

#### Genus XESTAGNOSTUS nov.

The type of the genus is *Xestagnostus legirupa* sp.nov.

The known species of *Xestagnostus* have a relatively thick test with externally almost completely effaced furrows and lobes. On the internal surface of the test, however, the original relief is retained and imprinted on the casts as delicate furrows around the lobes; muscle spots and notulae are also exceptionally well developed. The shields are moderately and rather evenly convex and only the median nodes rise externally, and on the casts, above the arcs of the shields.

*Concept:* *Xestagnostus* comprises externally effaced agnostids with constricted acrolobes, with scrobiculate pleural lobes in the cephalon and pygidium, and with an almost flat border in both shields; it lacks externally a preglabellar median furrow and the rear of the glabella is angulate and pointed. In the pygidium only the rectangular anterior part of the axis, with two large and a third small annulations, is indicated; the posterior axial lobe and the axial furrows are obsolete, but the lines of notulae converging at the terminal node indicate a long axial lobe which touches

the border; accessory furrows are absent, but in the type species a low tumid deuterolobe is present, defined by its slope against the depressed peripheral parts of the pleural lobes; along the flanks of the deuterolobe the test of the lobe itself and of the pleurae is scrobiculate; within the deuterolobe the adaxial ends of the scrobicules mark the position of the otherwise effaced axial furrows. In the type species the facets are concave, the fulcral points carry short, forward-inclined spines, and the articulating device consists of an elliptical depressed plate.

*Summary of the diagnosis:* *Xestagnostus* is in general organized as a *Pseudagnostus* (deuterolobate, simplimarginate, and with constricted acrolobes), but is distinguished by its simple articulating device (the simplest known), rectangular anterior part of the pygidial axial lobe, and the total absence of the accessory furrows (=diagonal parietal mesenterial septa). This diagnosis is based essentially on *X. legirupa*, which is the type of the genus.

Three other species are assigned here to *Xestagnostus*: (1) *X. rasilis* sp.nov., (2) *Xestagnostus* cf. *rasilis*, known from a single pygidium, and (3) *Xestagnostus* sp.aff. *legirupa*, known from a single cephalon. The two unnamed forms, lacking sufficient material, cannot be diagnosed. *Xestagnostus rasilis* however, is a diagnostic species, whose peculiarities are (1) the absence of spines on the fulcral points, (2) the absence of an externally expressed, tumid deuterolobe, and (3) the feebly convex (not flat) articulating half-ring. These characters may be of a generic significance, but can be regarded also as specific only, because in all other aspects the organization of *rasilis* differs little from *legirupa*. Furthermore, *rasilis* is the older species, apparently retaining some of the characters that became subsequently modified in *X. legirupa*.

*Differential diagnosis:* Characters indicated in the summary of the diagnosis (above) are sufficient to separate *Xestagnostus* from, and prevent a confusion with, *Pseudagnostus* and the other genera of the Pseudagnostinae.

The simple articulating device of *Xestagnostus legirupa* is unique. As a rule, all Pseudagnostinae are distinguished by the elaborate glyptagnostid articulating device, but *Xestagnostus* breaks the 'family rule' in a most emphatic manner. Nevertheless, a separate subfamily for *Xestagnostus* seems unnecessary because in all other structures it conforms to the concept of the Pseudagnostinae.

So, *Xestagnostus legirupa*, presumably an offshoot of an early *Pseudagnostus*, acquired a structural simplification which could be expected to occur only to a phyletically mature stock; but, remarkably enough, it broke the 'family rule' rather early, at a time when the pseudagnostids and the glyptagnostids were passing through the formative period of their phyletic history.

*Previous record in the literature:* Previously, specimens of *Xestagnostus* from the O'Hara Shale that retain the test (which is almost featureless) were interpreted as *Litagnostus* Rasetti (Öpik, 1956, p. 22), and fragmentary peeled specimens from the Georgina Limestone (Öpik, 1960, p. 106) as *Lctagnostus* Whitenhouse, which also possesses delicate rugae and a narrow third annulation in the pygidial axis.

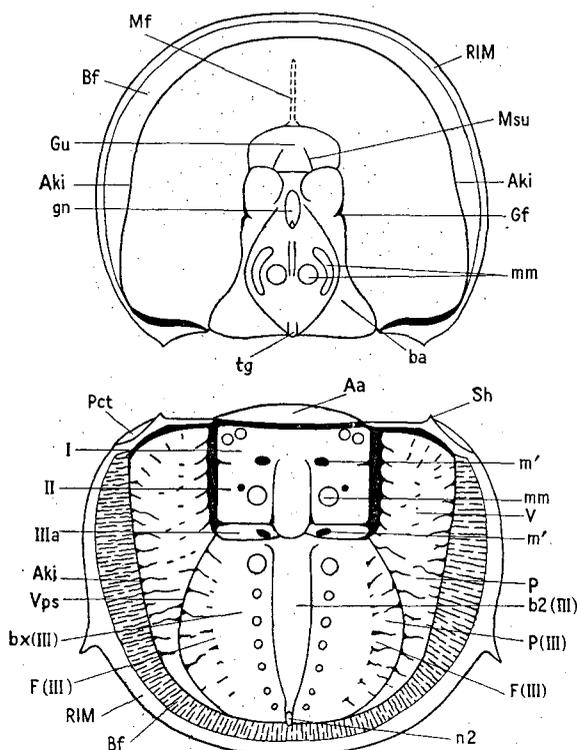


Fig. 49.—*Xestagnostus legirupa* gen.nov., sp.nov., from Plate 64; cephalon combined from figs 4, 5 (scrobicules are omitted); pygidium combined from figs 1, 2. Aki—acrolobes constricted, flanks concave. Cephalon: ba—basal lobe; Bf—marginal furrow; Gf—lateral glabellar furrow; gn—glabellar node; Gu—frontal glabellar lobe; Mf—preglabellar median furrow (vestigial); mm—muscle spots; Msu—vestigial extension of frontal sulcus; tg—glabellar rear, angulate and pointed. Pygidium: I—anterior; II—middle, IIIa—posterior annulation; Aa—articulating half-ring; Bf—marginal furrow (with terminal rugae); b2 (III)—intra-notular axis; bx (III)—extra-notular axis; F (III)—posterior part of axial furrow, vestigial, included in deuterolobe; fct—facet (concave); m—notulae in anterior part of axial lobe; mm—muscle spots (some indistinct); n2—terminal node; P—peripheral pleural lobe; P(III)—part of pleural lobe included in deuterolobe; RIM—rim of border; Sh—fulcral point, with spine; V—scrobicules; Vps—slope of deuterolobe.

*XESTAGNOSTUS LEGIRUPA* sp.nov.

(Pl. 64, figs 1-5; Pl. 65, figs 1-3; Text-fig. 49)

*Material:* The illustrated and described material consists of five cephalons and three pygidia, from the Georgina Limestone, locally G50, and from the O'Hara Shale ('lower chert bed'), locality D29. These sites are dissimilar in lithology and separated by about 150 miles. Nevertheless, the material is morphologically homogeneous, and cannot be regarded as representing two separate populations.

*Holotype:* The pygidium, Plate 64, figure 1, CPC 5922, locality G50, is selected as the holotype because it has retained a part of the test and shows at once the external and internal features of the shield. A pygidium is selected in preference to a cephalon because it displays most of the significant characters.

*Diagnosis:* *Xestagnostus legirupa* sp.nov. is distinguished by its external effacement, as well as by the retention of the features of relief on the inside surface of the shields; its articulating half-ring is a flat plate, the fulcral points are horned (extended

into short spines), the anterior part of the pygidial axial lobe is rectangular and consists of three annulations of which the posterior is rather short (longitudinally); the pygidial border is very wide on the flanks, but narrow in the rear; both shields are scrobiculate and the acrolobes are constricted.

Supplementary diagnostic characters, and differential diagnosis, are given in the discussion of the genus.

*Description:* The cephalon is moderately and evenly convex, with an evenly rounded margin; it is wider than long, the proportion being around 0.8–0.85. The border has a narrow and low rim, and the floor of the wide marginal furrow is slightly concave, almost flat. The glabella coincides with the convexity of the shield, and is about 0.25 its width, and about 0.62 its length, and is therefore short.

The rear of the glabella is angulate and bears a prominent node, and an elongate node is placed on the anterior half of the rear glabellar lobe. The anterior glabellar lobe is short, transverse, and flat, and in front of it the median preglabellar furrow is weakly indicated. Muscle scars, in contrast to the general effacement, are well developed in a pattern seen in *X. rasilis* (Pl. 65, fig. 4). The basal lobes are triangular and long, but ill defined in front. The posterolateral furrows are deep, and the spines short. The test is scrobiculate, and the distal rugae extend across the floor of the marginal furrow. The cephalic acrolobe is constricted rather weakly.

The pygidium is also of a low convexity, wider than long, the proportion being about 0.8. The margin is evenly rounded, the marginal spines are small, deflected and placed well forward. The border, narrow at the shoulders, widens rapidly on the flanks, but decreases again in the rear. Its rim is narrow and elevated and the marginal furrow is wide and shallow. The fulcral points are produced into short and forward-directed spines, and the facets are relatively strongly concave. The articulating half-ring is a simple transverse-elliptical plate. The anterior part of the axial lobe, wider than long, is a rectangle of three annulations and flanked by weak axial furrows; the second annulation carries an elevated stout node; the third annulation is a narrow band well defined by shallow furrows. Muscle scars are discernible on the anterior part of the axis and two pairs of deep pits (notulae) are placed at the anterior and rear ends of the median node.

The posterior, suboval, lobe of the axis is in contact with the rear part of the marginal furrow and carries a terminal node; there are no axial furrows, but their position is marked by a pair of rearward converging lines (F (III), Text-fig. 49) of scrobicular pits; the median part of the lobe between the lines of notulae is a shallow blade-like depression with angulate margins. Outside the vestigial axial lobe the pleural part of the deutero-lobe, and the peripheral pleural lobe (P) are delicately scrobiculate and pitted; accessory furrows are totally absent; the flanks of the deutero-lobe are expressed as a change in slope and as lines of disconnected ends of scrobicules. The distal rugae cross the floor of the marginal furrow.

The axial notulae are developed as pits, and seven pairs of them are discernible. The test is thick and smooth.

*Comment on illustrated material:*

The following five specimens come from the Georgina Limestone, locality G50; the matrix is dark grey bituminous limestone.

The holotype pygidium, Plate 64, fig. 1, is 6.0 mm long. The external surface of the test is effaced, but the partly exposed cast shows muscle scars, notulae, and scrobicules; the test is thick; the articulating half-ring, the left facet, the horned fulcral points, the right marginal spine, the border, which is narrow in the rear, and the externally tiny terminal node are preserved.

The decorticated pygidium, Plate 64, fig. 2, CPC 5923, is 6.0 mm long. It shows all features indicated in the diagram, Text-figure 49.

The decorticated cephalon, Plate 64, fig. 5, CPC 5926, is 4.0 mm long. In addition to the features shown in Text-figure 49 scrobicules are also visible. The terminal scrobicules extend across the marginal furrow almost to the margin.

The decorticated cephalon, Plate 64, fig. 4, CPC 5925, is 6.0 mm long. Muscle scars, the node on the rear of the glabella, the vestige of the preglabellar median furrow, and the scrobicules in the marginal furrow are visible.

The decorticated cephalon, Plate 64, fig. 3, CPC 5924, is 4.0 mm long. The vestiges of the preglabellar median furrow and of the right arcuate scrobicule are distinct.

The following three specimens come from the O'Hara Shale ('lower chert bed'), locality D29. The matrix is friable silica, hard siliceous shale, solid chert.

The cephalon, Plate 65, fig. 1, CPC 5927, is 5.7 mm long; the test is preserved; outlines of the glabella, the basal lobes and the transverse glabellar furrow are discernible. The preglabellar median furrow is indicated.

The fragmentary cephalon, Plate 65, fig. 3, CPC 5929, is 5.4 mm long. Note the angulate glabellar rear with the node, muscle scars and the distinct basal lobes.

The pygidium, Plate 65, fig. 2, CPC 5928, is 4.6 mm long. The articulating half-ring, the horned fulcral points, and the terminal node are well preserved.

*Occurrence and age:* *Xestagnostus legirupa* sp.nov. is found in the Georgina Limestone at localities W2, W15, W18, W20, W48, G50, and W301, and in the O'Hara Shale ('lower chert bed') at localities D6, D28, and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### XESTAGNOSTUS aff. LEGIRUPA

(Pl. 65, fig. 8)

The illustrated large cephalon, CPC 5934, is 5.0 mm long; it is distinguished by its parabolic, forward-arched frontal margin and circular glabellar node from the cephala assigned to *X. legirupa*.

The test is almost intact, showing weak outlines of the glabella and the basal lobes; the border is almost flat. The tumid spines are well preserved.

This specimen may belong not to *Xestagnostus* but to an early species of *Litagnostus* Rasetti, 1944.

*Occurrence and age:* The cephalon was found in the Georgina Limestone, locality G50; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### XESTAGNOSTUS RASILIS sp.nov.

(Pl. 65, figs 4-6)

*Material:* Two cephalo and one pygidium are illustrated, constituting the material suitable for description.

*Holotype:* The pygidium, Plate 65, figure 6, CPC 5932, is selected as the holotype to facilitate the comparison with *X. legirupa* sp.nov., whose type is also a pygidium.

*Diagnosis:* *Xestagnostus rasilis* sp.nov. is distinguished by its forward-arched cephalic front, equidimensional shields, relatively narrow border, complete effacement of furrows, even on the internal surface, absence of marginal pygidial spines, and a slightly convex, not flat, articulating half-ring.

*Differential diagnosis:* The characters indicated in the diagnosis are sufficient to distinguish *X. rasilis* sp.nov. from *X. legirupa* sp.nov.

*Description:* The holotype pygidium is 5.0 mm long. It is almost as long as wide, the ratio being about 0.9. The anterior part of the axial lobe is rectangular, but only weakly defined; the axial node is short and rounded. The border is flat and narrow. Selective silicification of the specimen developed all muscle spots and notulae, whose distribution is the same as in *X. legirupa*.

The cephalon, Plate 65, figure 4, CPC 5930, is also 5.0 mm long, with a length/width ratio of about 0.9. A median node is not discernible; the glabellar rear is angulate. The glabellar muscle scars are graphically developed by silicification. Muscle scars are placed on the basal lobes, and a pair of scars and a single median scar on the glabellar rear. The lateral glabellar scars are composite, and the position of the median glabellar node is also marked by a white spot.

Rugae are rather weak, but are present on the cephalon and the pygidium.

The test is, apparently, densely punctate.

The small cephalon Plate 65, figure 5, CPC 5931, is 2.8 mm long; basal lobes and the median node are visible; the glabella is somewhat outlined by accidental fractures which seemingly coincide with the axial furrows.

*Occurrence and age:* All illustrated specimens are associated in a single piece of limestone, locality G10, Mungerebar Limestone. The age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

#### XESTAGNOSTUS cf. RASILIS

(Pl. 65, fig. 7)

The illustrated, and only available, pygidium, CPC 5933, is 6.0 mm long. It is distinguished from *X. rasilis* sp.nov. by the absence of the median axial node whose position is indicated by the silicification mark; the rear margin of the pygidium is slightly angulate.

The arrangement of the muscle spots and notulae is the same as in *X. rasilis*; note the pair of small notulae in the articulating furrow, which are present also in *X. rasilis* (Pl. 65, fig. 6) and the bilobed rear of the spot that represents the axial node.

*Occurrence and age:* The pygidium was found in the Mungerebar Limestone at locality G10; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

#### Subfamily GLYPTAGNOSTINAE Whitehouse, 1936

Genus AGNOSTARDIS Öpik, 1963

AGNOSTARDIS AMPLINATIS Öpik, 1963

(Pl. 67, figs 6, 7)

The complete specimen, Plate 67, figure 6, CPC 6722, flattened in limestone (Georgina Limestone, locality W20) and 3.6 mm long, confirms that in *Agnostardis* the pygidium is visibly wider than the cephalon. The postaxial median furrow is

quite deep. In the large pygidium, Plate 67, figure 7, CPC 6723, 3·3 mm long, Georgina Limestone, locality W1, this furrow is shallow and the axial annulations are indistinct. Pygidia of *A. amplinatis* are also seen in Plate 33, figures 2 and 3, and a cephalon in Plate 45, figure 1.

As originally stated, *Agnostardis amplinatis* occurs in the Georgina Limestone and in the O'Hara Shale ('lower chert bed'), in the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### AGNOSTARDIS cf. AMPLINATIS Öpik, 1963

(Pl. 67, fig. 8)

The illustrated cephalon, CPC 6725, is quite large—4·5 mm long; it is flattened and somewhat fragmentary. The narrow glabella, the subpentagonal anterior glabellar lobe, and the rounded rear of the glabella indicate a close similarity with *A. amplinatis*. But the elongate and forward-placed glabellar node is not consistent with *amplinatis*, in which this node is small and placed behind the glabellar midpoint; and the rugosity of the cheeks is stronger than in the earlier described specimens.

*Occurrence and age:* The cephalon was found in the O'Hara Shale ('lower chert bed') at locality D29; its age is the Zone of *Glyptagnostus stolidotus*.

#### Genus GLYPTAGNOSTUS Whitehouse, 1936

##### Subgenus GLYPTAGNOSTUS (GLYPTAGNOSTUS) Whitehouse, 1936

The genus *Glyptagnostus* and its two Australian species were revised by Öpik (1961); supplementary data can be found in Öpik (1963); Palmer (1962) produced an exhaustive account on *Glyptagnostus* and associated trilobites in the United States; Kobayashi (1962) confirmed once more the occurrence of *G. reticulatus* in Korea, and, finally, Pokrovskaja (in Tchernysheva, 1960) illustrated a cephalon and a pygidium of the same species from Siberia (Yakutia).

In the present paper a new species and subgenus *Glyptagnostus (Lispagnostus) lenis* is described; furthermore, material is published regarding the morphogenesis of the pygidium of *Glyptagnostus*—to substantiate an earlier statement (Öpik, 1961, p. 433).

#### GLYPTAGNOSTUS RETICULATUS (Angelin)

(Pl. 67, fig. 3a)

The illustrated small pygidium, CPC 6719, locality D126, in limestone, is 1·2 mm long. It differs little from larger and mature specimens because (1) the posterior bulb is already indicated, (2) the caeca show an incipient blistering and (3) their terminal ends are bifurcate. Even at this size the holaspid stage with two segments in the thorax has been attained; it cannot be confused with *G. stolidotus* even in such small specimens because the blisters characteristic of *reticulatus* are present.

GLYPTAGNOSTUS STOLIDOTUS Öpik, 1961

(Pl. 67, figs 1-5)

*Material:* The holotype cephalon, Plate 67, figure 1, is once more illustrated to supplement the two pygidia, figures 4, 5; an immature (fig. 3) and a pathological pygidium are also described.

*Morphogenesis:* Relatively large specimens of *G. stolidotus* have been published as yet, 4.8-6.1 mm long, by Öpik, and about 5.0 mm by Palmer, 1962.

The smallest available specimen is the pygidium, Plate 67, figure 3, CPC 6718, locality B525. It is 1.0 mm long. It retains the second segment of the thorax and resents, therefore a meraspis whose total length was about 2.0 mm. Behind the acute tip of the axial lobe the postaxial furrow is distinct and deep; a caecal bulb is absent behind the axial lobe. Consequently, this caecal bulb develops after the liberation of the second and last segment from the pygidium, that is, at the beginning of the holaspis stage of the morphogenesis. In *Glyptagnostus reticulatus* a similar situation has been reached earlier (Pl. 67, fig. 3a).

In the immature pygidium of *G. stolidotus* five pairs of rugae are present, of which the two anterior show an incipient bifurcation. These rugae are arranged segmentally, but their connexion with the axial annulations is not evident because the rugae (caeca) even at this early morphogenetic stage arise from a pair of major trunks flanking the axial lobe. The axis itself is narrow and pointed and reminiscent of *Ptychagnostus*. Of course, such similarity alone is not evidence that *Glyptagnostus stolidotus* arose from a *Ptychagnostus* or a species of the Agnostidae.

The pygidium, Plate 67, figure 4, CPC 6720, locality B537, is 1.9 mm long. The posterior median rugae are developed and bifurcated, and incipient rugae of the next order are also present. The pygidium, Plate 67, figure 5, CPC 6721, locality D126, is 2.5 mm long. The postaxial caecal bulb is well developed and the third order rugae have gained in size. The posterior bulb in the pygidium of *Glyptagnostus stolidotus* is therefore an acquisition of the early holaspis.

*Pathology:* The pathological pygidium, Plate 67, figure 2, CPC 6717, Georgina Limestone, locality W1, is 3.0 mm long. The right side is almost normal, except for the uneven and unequal expression of the scrobicules. On the left side, however, the main caecal trunk is hypertrophic or varicose, and connected abnormally with the posterior lobe of the axis; whereas the distal rugae are reduced in size and completely disarrayed. The posterior bulb is also unusually large (varicose), but retains its connexion with the gland of the left pleural lobe.

The specimen is an exuvia, not the animal itself; consequently the monstrosity was inflicted before, or at the time of, moulting and the deformed animal was alive and able to produce its new test: it was not a lethal disease. This unique pygidium is also the best available evidence of rugae being the prosopon of glandular ducts in the pygidium of an agnostid, because varicosity develops in ducts.

All illustrated material comes from rocks deposited during the Mindyallan Zone of *Glyptagnostus stolidotus*.

Subgenus LISPAGNOSTUS subgen.nov.

The type species of *Lispagnostus* is *L. lenis* sp.nov. whose diagnosis serves as the diagnosis of the subgenus.

In brief, *Lispagnostus* is close to *Glyptagnostus reticulatus*, from which it is distinguished by the absence of rugae and scrobicules and by a semi-effaced appearance of the cephalon.

GLYPTAGNOSTUS (LISPAGNOSTUS) LENIS sp.nov.

(Pl. 66, fig. 12; Text-fig. 50)

*Material:* One cephalon, the holotype, CPC 6716, 2.5 mm long from the Georgina Limestone, locality W15.

*Diagnosis:* *Glyptagnostus (Lispagnostus) lenis* sp.nov. is a species with a subelliptical cephalon without a preglabellar median furrow, with a weakly outlined and almost vestigial anterior glabellar lobe, with a circular and centrally placed glabellar node, fused lateral glabellar lobes, and non-rugose test.

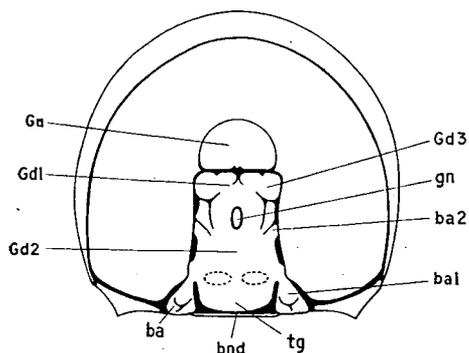


Fig. 50.—*Glyptagnostus (Lispagnostus) lenis* sp.nov., from Plate 66, fig. 12. ba1—basal lobe; ba2—lateral glabellar lobe; bnd—connective band; Gd1—anterior part and Gd 2—posterior part of rear lobe of glabella; Gd 3—lateral lobe; gn—median node; tg—glabellar rear (obtuse). Compare *Glyptagnostus reticulatus* (Öpik, 1963, p. 39, Text-fig. 7).

*Description:* The rim is almost flat and the marginal furrow narrow. The anterior glabellar lobe is flat and surrounded by almost vestigial furrows. The transverse glabellar furrow is straight and distinct. The lateral glabellar lobe (ba2) is confluent with the glabella. The basal lobes are tumid, triangular, and rectangular in the rear, as in *Glyptagnostus reticulatus*.

The test in the holotype is roughened by corrosion, but the intact parts are smooth and minutely punctate. Latent radiating rugae are, apparently, present and the corrosion of the test was governed by their pattern. On the rear of the glabella a pair of impressed muscle spots is present.

A species of *Glyptagnostus* without scrobicules and rugae is a paradox, a contradiction in terms; external absence of rugae, however, is no indication of the absence of caecal glands, which may be deep-seated and not reflected externally (Öpik, 1961).

*Glyptagnostus lenis* is affiliated with the contemporaneous *Glyptagnostus stolidotus*, in which, however, the glabellar node is placed behind the centre and the outline of the cephalon is different. Closer is *Glyptagnostus reticulatus*, which postdates *G. lenis* by the span of a zone.

The phylogenetic relationship of the earlier and effaced *Glyptagnostus lenis* and the subsequent *G. reticulatus* en grande tenue is obscure. *G. reticulatus* arrives in Australia after the extinction of the Mindyallan fauna, which includes *G. lenis*; *lenis* is also a visitor here, representing an offshoot from the unknown ancestral lineage of *G. reticulatus*.

*Occurrence and age:* The holotype cephalon of *Glyptagnostus (Lispagnostus) lenis* was found in the Georgina Limestone at locality W15; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Family TRINODIDAE Howell, 1935

##### Genus PLURINODUS nov.

The type of *Plurinodus* is *P. discretus* sp.nov.

*Diagnosis:* *Plurinodus* gen.nov. is distinguished by having (1) the posterior pygidial axial lobe completely effaced, (2) the anterior part of the pygidial axial lobe trilobate, (3) deep and wide axial furrows, which are present only in the anterior part of the pygidium, (4) the terminal node in contact with the marginal furrow, and (5) notulae arranged in lines converging at the terminal node.

*Familial nomenclature and classification:* The family name Trinodidae Howell, 1935, was placed in the synonymy of Geragnostidae Howell, 1935, by Kobayashi (1939) and by Howell in Harrington et al. (1959). This synonymy is, of course, subjective. The Trinodidae are retained here as a separate family because (1) the Geragnostidae are regarded as a synonym of the Agnostinae, (2) the organization of *Trinodus* is rather different from the Agnostidae, and (3) the early Upper Cambrian *Plurinodus* gen.nov. is much older than the earliest known *Geragnostus* and, for morphological reasons, cannot be ancestral to *Geragnostus* and its allies.

*Differential diagnosis:* The pygidium of *Plurinodus* resembles closely *Trinodus* M'Coy, which also has a trilobate and short axis; in *Trinodus*, however, the terminal node (known for certain only in *T. mobergi* Tjernvik, 1956, text-fig. 28) is placed at the tip of the third annulation. The same may be present also in *T. tardus* (see Whittington, 1950, pl. 68, fig. 4). In detail *Trinodus* is more elaborate than *Plurinodus*, as seen in the description of *T. elspethi* (Raymond) by Cooper (1953, p. 7, pl. 1, figs 1-12): *elspethi* has a rather prominent and distinctive ornament, a rather wide rim (border) in both shields, a long and high pygidial axial node, excavated facets, and pygidial spines arising not from the margin but developed as folds of the rim.

The pygidial structure of *Trinodus* is close to *Plurinodus*; hence, *Trinodus* may have evolved from *Plurinodus* through the reduction of all vestiges of the posterior axial lobe and the forward shift of the terminal node from the marginal position.

##### PLURINODUS DISCRETUS sp.nov.

(Pl. 60, figs 15-17; Text-fig. 51)

*Material:* Three pygidia are illustrated, selected from a large number of examined specimens.

*Holotype:* The largest available pygidium, Plate 60, figure 17, CPC 5889, locality D29, is selected as the holotype.

**Diagnosis:** The specific diagnosis is the same as the diagnosis of the genus.

The pygidia of *P. discretus* are common and have a size range from 1.3 to 2.0 mm in length; the most common size is around 1.5 mm. All specimens are presumably mature and belong to a small form. Cephalae, however, attributable with certainty to *discretus* have not been identified as yet, though the cephalae described below as cf. *discretus* may belong to this species.

**Description:** *P. discretus* is a small agnostid whose complete shields may have attained the length of about 5 mm.

The pygidium is broad (its length is 0.8 of width) with slightly rearward-diverging flanks and an evenly rounded posterior margin. Its acrolobe has convex flanks somewhat converging rearward. The lateral spines are short and arise from the rim slightly off its margin. The marginal furrow is a wide channel separated from the narrow rim by a change in slope, but from the acrolobe by a rather abrupt edge. The pleural lobes are moderately convex and narrow (about 0.5 of the axis). The

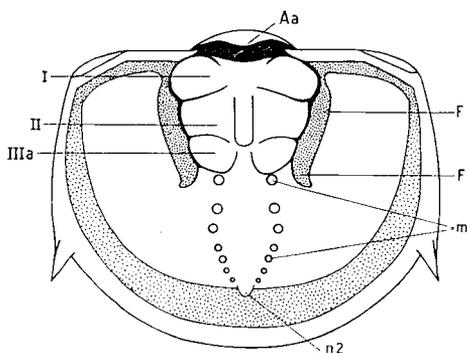


Fig. 51.—*Plurinodus discretus* gen.nov., sp.nov., from Pl. 60, figs 15–17. I—anterior, II—middle, IIIa—posterior annulation of the axial lobe; Aa—articulating device; F—axial furrow; m—notulae; n2—terminal node.

axial furrows are wide and deep; the trapezoidal axial lobe consists of three annulations separated by shallow transverse furrows, and the second annulation carries a short and low node. The posterior annulation is bilobed in the rear by the slightly depressed intranotular axis reaching from the median node to the terminal node. The notulae are elevated knobs (not pits), rapidly decreasing in size rearward. The articulating device recalls *Agnostus*, but also *Trinodus*, and the facets are slightly concave.

**Comment on illustrated specimens:**

The holotype pygidium, locality D29, a cast in friable silica, is 1.7 mm long. The notulae and the terminal node are well visible. The left furrow appears shorter than the right—an effect of illumination.

The pygidium, Plate 60, fig. 15, CPC 5887, locality D6, a cast in rather hard chert, is 1.5 mm long.

The pygidium, Plate 60, fig. 16, CPC 5888, locality D6, in hard silica (associated with a pygidium of *Agnostogonus* sp.nov.) is 2.0 mm long. It is an external mould, showing a relief similar to the relief of internal casts.

**Occurrence and age:** *Plurinodus discretus* sp.nov. has been found only in the O'Hara Shale ('lower chert bed') at localities D6 and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

PLURINODUS cf. DISCRETUS?  
(Pl. 51, fig. 4; Pl. 60, fig. 18)

Only two cephalons of this kind, in friable silica, have been found as yet. Both are rather small; the illustrated cephalon, CPC 5765, is 0.6 mm long.

The shield is strongly convex, its rim is relatively narrow, the basal lobes are small and tumid; the glabella, about 0.5 the shield's length, is swollen, tapers evenly forward, is rounded in front, and bears a subcentral node. The furrow around the glabella is well defined and evenly deep; a transverse glabellar furrow and a preglabellar median furrow are absent.

The cephalon is quite similar to *Trinodus* and may belong, therefore, to the pygidia described as *Plurinodus discretus* sp.nov. Another possibility is a *Clavagnostus* without a preglabellar median furrow; but the glabellar front is too blunt for a *Clavagnostus*. The glabella is also too long and too much tapering for a *Hypagnostus*.

*Occurrence and age:* O'Hara Shale ('lower chert bed'), locality D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

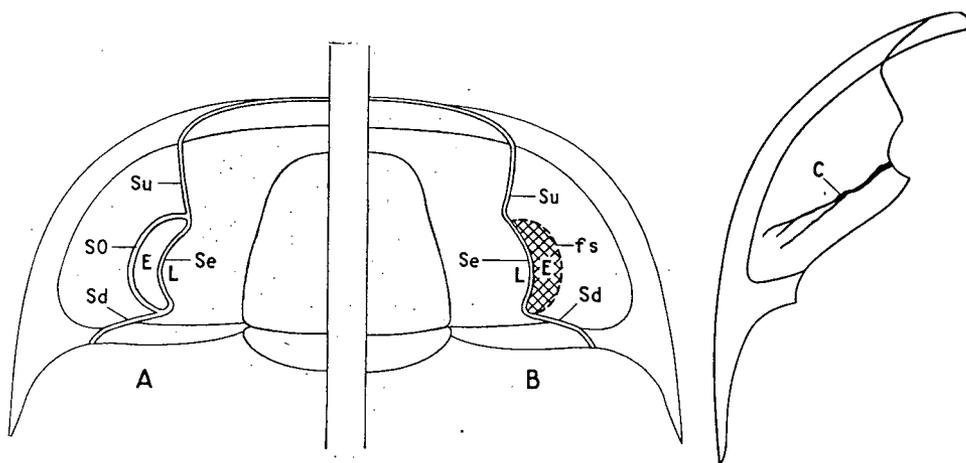


Fig. 52.—Dorsal sutures in an opisthoparian trilobite. A—ocular suture functional; B—ocular suture fused; the eye is retained by the moult of the free cheek. Su—anterior suture; Sd—posterior suture; Se—palpebral suture; SO—functional ocular suture; fs—fused (non-functional) ocular suture; SO and Se together constitute the circumocular suture; E—cornea (visual surface) of the eye, liberated in A and retained by the free cheek in B; L—palpebral lobe. The sutures are shown open to indicate the start of moulting.

Fig. 53.—Free cheek of a trilobite with a developed principal caecal vein (C).

## POLYMERID TRILOBITES

The heading 'Polymerid trilobites' is short for 'polymerid orders of trilobites'. The order, and the ordinal name *Polymera* Jaekel, are currently used (Hupé, 1955; Tchernysheva, 1960) and cannot be regarded as obsolete; when this order is accepted the orders in the classification of Harrington et al. (1959) will change their status in favour of a subordinal nomenclature involving the existing suborders as well. Trilobite classification need not be revised wholesale immediately, however, and the material in hand is described in acceptance of several orders of polymerid trilobites.

Order CORYNEXOCHIDA Kobayashi, 1935

Family DORYPYGIDAE Kobayashi, 1935

Genus KOOTENIA Walcott, 1888

KOOTENIA? cf. INCERTA (Rusconi) Leanza, 1947

(Pl. 2, fig. 7; Text-fig. 54)

*Material:* One pygidium, CPC 5367, in sandstone, has been found so far. It is 12.3 mm long and therefore relatively large.

*Description:* The pygidium is semielliptical, almost as long as wide, strongly convex, with a prominent axial lobe and sloping flanks. The border bears four pairs of marginal spines, the pleural lobes are divided into four pairs of ribs, and the axial lobe consists of four annulations and a rounded terminus which reaches the border. The pleural lobes are rather narrow, and the axis is wide—as wide as half the shield, and twice a pleural lobe.

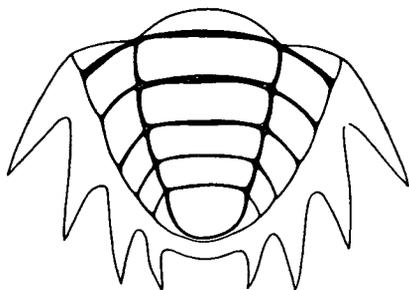


Fig. 54.—*Kootenia?* cf. *incerta* (Rusconi), from Plate 2, fig. 7.

*Comparison:* *Kootenia incerta* (Rusconi) as illustrated and described by Leanza (1947, pl. 1, fig. 16) from South America appears identical as regards the shape of the shield, the marginal spines, and the size of the lobes; the state of preservation of Leanza's specimen prevents, however, a conclusive comparison of the numbers of spines, ribs, and annulations.

The generic classification is queried because cranidia are unknown and the plump and large pygidial axis is quite different from any of the known species of *Kootenia*.

*Occurrence and age:* The pygidium of *Kootenia* cf. *incerta* comes from the Steamboat Sandstone, locality D99; it is associated with *Rhyssometopus* (*Rostrifinis*) *tiro*, sp.nov. Its age is the Zone of the Middle Cambrian-Upper Cambrian Passage.

Genus OLENOIDES Meek, 1877

OLENOIDES TRANANS sp.nov.

(Pl. 2, fig. 8; Text-fig. 55)

*Material:* The material consists of the two illustrated pygidia.

*Holotype:* The pygidium Plate 2, figure 8, CPC 5368, locality G417, is well enough preserved and is selected therefore as the holotype; it is 9·0 mm long.

The second pygidium, Text-figure 55, CPC 6727, locality G107, is 13·0 mm long; it is fragmentary, but shows the specifically significant long posterior spines.

*Diagnosis:* *Olenoides tranans* sp.nov. is a species with a narrow pygidial border, five pairs of pygidial marginal spines, relatively narrow pleural lobes, four axial annulations, and a relatively long terminus; distinguished by the exceptional length of the posterior spines.

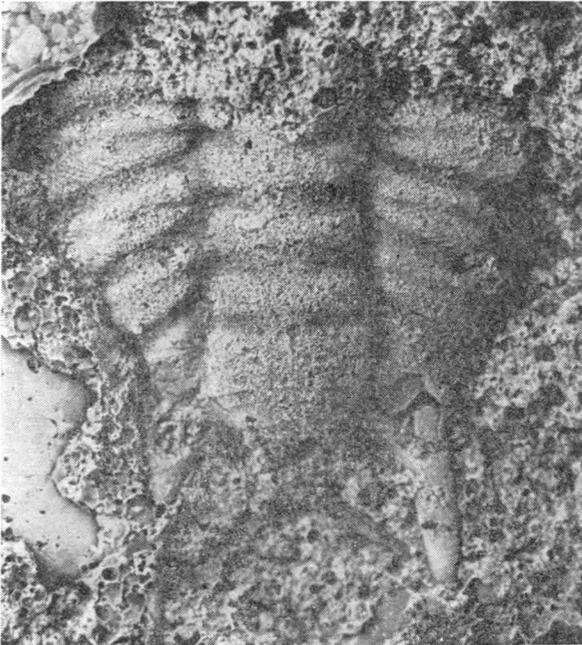


Fig. 55.—*Olenoides tranans* sp. nov., rubber cast of CPC 6727, x 3·5; locality G107, Zone of Middle Cambrian-Upper Cambrian Passage.

In all known species of *Olenoides* the pygidial marginal spines are evenly long. Long posterior pygidial spines occur, as a rule, in *Dorypyge* Dames, but in this genus the pygidial pleurae are well fused. In *Olenoides*, however, the interpleural grooves are rather distinct, as seen also in *O. tranans*.

All hitherto known species of *Olenoides* are Middle Cambrian; it appears, therefore, that *O. tranans*, found in the Middle Cambrian-Upper Cambrian passage (locality G107) and in the lowermost Upper Cambrian Zone (locality G417), is one of the last species of its kind. It is the only species of *Olenoides* found in Australia.

*Occurrence and age:* *Olenoides tranans* has been found in the Mungerebar Limestone at locality G107 (the zone of passage between the Middle and Upper Cambrian), and at G115 and G417 in the Mindyallan Zone of *Erediaspis eretes*.

Family DOLICHOMETOPIDAE Walcott, 1916

Genus ALOMATASPIS nov.

*Alomataspis* is monotypical, with *A. enodis* sp.nov. as its type species.

The familial affiliation (Corynexochidae, subfamily Dolichometopinae) is evident and is in no need of further proof.

*Diagnosis:* *Alomataspis* is distinguished by its long, concave and rimless frontal area combined with a long slightly tapering glabella and rather indistinct glabellar furrows; the preocular part of the glabella is relatively short.

*Differential diagnosis:* In all known species of the Dolichometopinae the frontal area is much shorter than in *Alomataspis*; most species have a convex rim (border) and a definite marginal furrow, or an upturned cranial margin, and a forward expanded or clavate glabella. Only *Amphoton* (*Amphotonella*) *alceste* (Walcott), Kobayashi, 1942, is assumed to have a tapering glabella, but possesses a distinct border (rim) and the usual short frontal area. Furthermore, in all known forms the preocular part of the glabella is much longer than in *Alomataspis*.

The Dolichometopidae of Australia and south-eastern Asia have been reviewed by Öpik (1961).

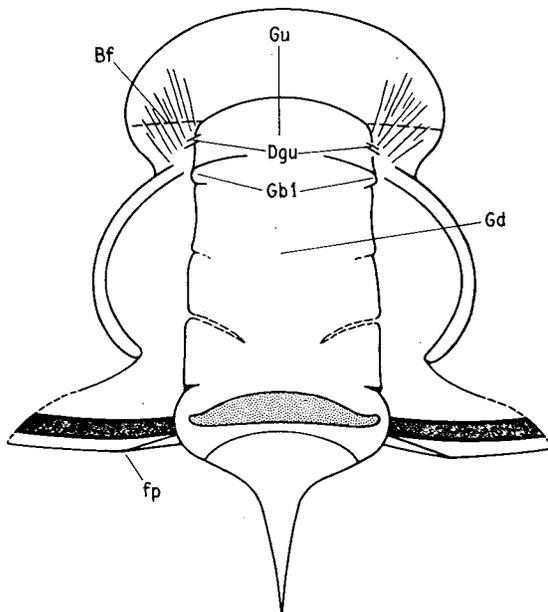


Fig. 56.—*Alomataspis enodis* gen. nov., sp.nov., from Plate 2, fig. 5. Bf—vestige of marginal furrow; Dgu—preocular glabellar diverticulum, crossing the axial furrows; fp—fulcrum (point of geniculation); Gb1—lateral anterior bulges; Gd—postocular part of glabella; Gu—preocular part of glabella.

ALOMATASPIS ENODIS sp.nov.

(Pl. 2, figs 5, 6; Text-fig. 56)

*Material:* The illustrated material consists of a cranium in chert exposing the inside surface of the test; it is the holotype, CPC 5365. A pygidium is also described which probably belongs to *A. enodis*.

A specific diagnosis is unnecessary because the generic diagnosis refers to characters by which *A. enodis* is distinguished from all known species of the Dolichometopinae.

*Description:* The cranium, including the preserved part of the occipital spine, is 17 mm long and about 14 mm long without the spine, indicating a total length of 35–40 mm. The cranium is moderately arched transversely and longitudinally, indicating a relatively low convexity of the cephalon.

The anterior sutures are convex outward, evenly curved, and marginal in front; a rim is absent, the brim is transverse elliptical, concave, and relatively long—about 0.25 of the glabellar length. Vestigial marginal furrows are faintly indicated in front of the eyes, and joining the axial furrow at the anterolateral corners of the glabella. The posterior sutures are relatively straight, the posterolateral limbs are triangular, visibly swollen and narrower (transversely) than the occipital lobe. Their marginal furrows are deep, the posterior border is narrow and strongly geniculate at the prominent fulcra, which are close to the glabella.

The interocular cheeks, as wide as 0.5 of the glabella, are slightly tumid; the palpebral lobes are long (0.6 of glabella), arcuate, very narrow but well defined by shallow palpebral furrows. The eyes are placed only slightly behind the glabellar midpoint, that is, more forward than in other dolichometopids with large eyes. Owing to the large size of the palpebral lobes the pre-ocular part of the glabella is relatively short. The ocular ridges are distinct and slanting, and confluent with the palpebral lobes. Ill-defined branching veins radiate from the adaxial ends of the ocular ridges. In front of the ridges a pair of minute diverticula issued from the glabella cross the axial furrows.

The occipital furrow is broad and shallow and arched forward in the middle; laterally the furrow fades out before reaching the axial furrows and the occipital lobe bulges laterally. Most of the occipital lobe is occupied by the broad base of the axial spine, which is directed up and rearward.

The axial furrows are deepened and well defined throughout, with shallow pits at the ends of the ocular ridges.

The glabella is subcarinate, tapers slightly, is relatively long and narrow, its width being about 0.6 of length; the front is rounded, and the flanks are faintly constricted in its anterior half.

Four pairs of glabellar furrows are indicated; they are rather faint on the internal and, presumably, obsolete on the external surface. Relatively strong are the anterior furrows combined with a pair of laterally bulging lobes—a structure more distinct in the Dorypygidae (e.g. in *Olenoides*, *Dorypyge*, and *Bonnia*) than in the dolichometopids.

The test is apparently smooth.

The pygidium, Plate 2, fig. 6, CPC 5366 is 3.0 mm long. It was found at the same locality as the cranidium, but in another piece of chert and is not, therefore, the 'associated' pygidium. It is, however, the pygidium of a dolichometopid which cannot be assigned to a known genus, and so is the holotype cranidium; presumably only one dolichometopid species is present, represented by a cranidium and a pygidium; it is unlikely that these shields belong to two separate species.

The dolichometopid characters of the pygidium are (1) the elevated, slightly tapering, and well annulated axial lobe, with a steep and rounded terminus almost contacting the margin; and (2) the angulate flanks of the annulations extending into the pleural furrows (although not developed into cushions). There are three annulations in the axis, and three pairs of pleurae, with pleural furrows and interpleural grooves almost reaching the margin. The border is very narrow, as in *Fuchouia*, indicating a very narrow doublure. The excavated ill defined marginal furrow is the distinguishing character of this form. It can be compared with *Glossopleura* Poulsen, whose pygidium, however, contains more segments, with *Polypleuraspis* Rasetti, which has a multisegmented and triangular pygidium, and with *Athabaskia* Raymond, in which the pygidial furrows also extend to the margin, but whose border is much wider and whose axial lobe consists of six annulations.

*Occurrence and age:* The two shields of *Alomataspis enodis* come from locality G103; from the top of the Steamboat Sandstone passing into the Mungerebar Limestone; their age is the zone of Middle Cambrian-Upper Cambrian passage.

#### Family CORYNEXOCHIDAE Angelin

##### Genus CORYNEXOCHUS Angelin, 1854

The history of the genus *Corynexochus* has been discussed by Whitehouse (1939); subsequently Westergaard (1948) revised the Scandinavian material, including the type species, *C. spinulosus* Angelin. Walcott (1916b) redescribed exhaustively the four species then known; a British species (*cambrensis*) was added to the list by Nicholas (1916; see also Lake, 1934), and Whitehouse (1939) described the sixth—*C. plumula*. Two Siberian species were described by Lermontova (1940; Tschernysheva, 1960). The latest review of *Corynexochus* and its species is found in Suvorova (1964). This paper, however, became available after the completion of the present contribution and cannot be considered therefore further. According to Suvorova, *Corynexochus*, containing not less than sixteen species, is a relatively large genus. Fifteen species belong to the upper half of the Middle Cambrian and one (*C. plumula*) is early Upper Cambrian.

*Corynexochus* is generally a rare, inconspicuous, and small trilobite and is, therefore, an insignificant faunal constituent. Only the Upper Cambrian Australian *C. plumula* can be regarded as being frequent to abundant and therefore an aid in stratigraphy.

The suprageneric classification of *Corynexochus* stands in need of comment. No doubt the Corynexochinae are a distinctive subfamily of the Order Corynexochida, but a family Dolichometopidae as distinct from the Corynexochidae appears a somewhat artificial division. Kobayashi's (1942) classification recognizes, however, the

family *Corynexochidae* Angelin and its two subfamilies—the *Corynexochinae* and *Dolichometopinae*. The problem of the suprageneric classification of *Corynexochus* has been also discussed by Rasetti (1951, p. 139) from a wider aspect, including the *Zacanthoididae* as well.

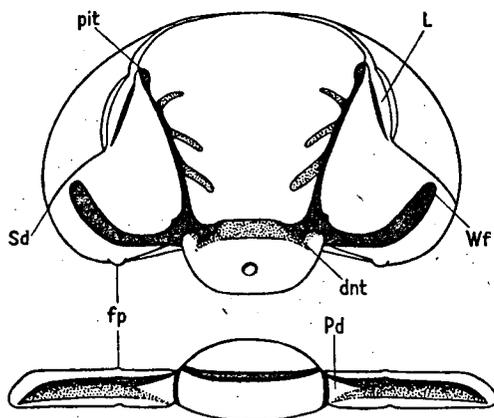


Fig. 57.—*Corynexochus plumula*, cephalon and a segment of the thorax. Cephalon combined from Plate 3. dnt—occipital dent; fp—fulcrum (pointed); L—palpebral lobe; Pd—opisthopleural cushion; pit—anterolateral pit; Sd—posterior suture cutting margin in an advanced (quasi-proparian) position; Wf—advanced blind end of posterolateral marginal furrow.

CORYNEXOCHUS PLUMULA Whitehouse, 1939

(Pl. 3, figs 1–11; Text-fig. 57)

*Corynexochus plumula* has been adequately described by Whitehouse (1939, p. 234, pl. 24, figs 8–10); the new material extends the knowledge of the species as well as the organization of the genus. Stratigraphic significance has been attributed to *C. plumula* by Öpik in applying its name to a zone of the Idamean Stage and the species is, therefore, in need of a revised description. Its Upper Cambrian age is noteworthy, because the traditional belief prevails that *Corynexochus* is a reliable Middle Cambrian genus. Whitehouse (op. cit., p. 267) placed *C. plumula* originally at the base of the Upper Cambrian, that is, immediately above the *Leiopyge laevigata* zone, which in Sweden contains *C. spinulosus*. In reality in Queensland *Corynexochus plumula* occurs in the fifth zone above the top of the Middle Cambrian and a *Corynexochus* (cf. *plumula*) passes even into the basal part of the *Erixanium sentum* Zone at three localities. No *Corynexochus* however has been found as yet within the interval of the Mindyallan stage or of the two lowermost Idamean zones with *Glyptagnostus reticulatus*. The phyletic continuity of *Corynexochus* from the Middle Cambrian into the Idamean is nevertheless obvious; consequently *C. plumula* appeared abruptly in Queensland as an anachronistic invader from elsewhere.

Doubt, however, may be expressed on the generic classification of the species *plumula*. But the specific characters of *plumula* (deeper pits, straighter palpebral lobes, and posterolateral limbs advanced more than in the other species) indicate differences in emphasis only and cannot serve to compile either a generic or a sub-generic diagnosis different from *Corynexochus* Angelin.

**Diagnosis (amplified):** *Corynexochus plumula* Whitehouse is an impunctate species with erratically and weakly granulose cheeks and pleurae and densely pitted parietal surface of the glabella; with (in plan) straight palpebral furrows and the

palpebral lobes placed close to the glabella and touching the anterolateral pits which are rather deep; with strongly forward curved posterolateral margins and deep posterolateral furrows whose blind ends are on the level of the posterior glabellar furrows; and with spineless free cheeks without borders and without marginal furrows.

*Differential diagnosis:* In the other known species, which are all Middle Cambrian, the posterolateral margin curves forward in a much lesser degree, the posterolateral furrow reaches the posterior suture, the palpebral lobes are curved, and their anterior tips do not reach the pits or the axial furrows. Furthermore, *Corynexochus spinulosus* (the type) and *C. bornholmiensis* Grönwall are punctate, and *C. minor* (Walcott) is granulate. *C. delagei* Miquel, 1905 (see Walcott, 1916b) has a smooth test, but only slightly advanced posterolateral margins; the same applies to *C. cambrensis* Nicholas, 1916 (see Lake, 1934), which is a species with ocular ridges. The Siberian species are established after *plumula*; they have large palpebral lobes, and *C. perforatus* Lermontova, 1940, is also distinguished by its occipital spine.

Pygidial characters are not included in the diagnosis because of their variability (see below). In other species whose pygidia are known, the discernible number of axial annulations is up to four, and of pleural ribs two to three, as in *C. plumula*, though *delagei* may have even five or six annulations; the pygidia are, however, much less known than in *C. plumula* and details cannot be compared.

*Description:* The cephalon, the hypostoma, the pygidium and isolated segments of the thorax are known. By analogy with *C. minor*, which is completely known, *C. plumula* is visualized as a small, compact, and streamlined trilobite without spines, strongly convex, with abruptly geniculate pleurae, a relatively large head, with about seven segments in the thorax, and a pygidium of about half the length of the thorax, or of the cephalon. The fulcral points are prominent and somewhat tubercular.

The cephalon is transverse elliptical and strongly arched transversely. Along the margin it is ornamented by terraced lines, especially on the downsloping glabellar front. The anterior sutures converge in even curves, meeting in front; they remain marginal in front and separated from the glabella by a narrow thread-like frontal border. The posterior sutures diverge in even curves and cut the lateral margin at the level of the posterior glabellar lobes. Hence, the condition is proparian, either genuine or not, camouflaged by the absence of a controlling genal spine.

The cheeks are inflated, tumid; the palpebral lobes are oblique, elongate, and narrow.

The occipital lobe is rather long, arched, and cusped, bears a pair of denticles and sometimes a node; the occipital furrow is broad, straight and distinct.

The axial furrows are deeply sunk between the glabella and the cheeks, with a pair of deep anterolateral pits at the tips of the palpebral lobes. These pits notch the glabellar flanks, and are therefore not homologous with the fossulae of the ptychoparioids.

The glabellar flanks are slightly to visibly concave; the glabella expands forward (clavate) and is most dilated in front of the pits; the ratio of aft to fore is variable between 0.5 and 0.6. It is arched transversely, horizontal on the crest, and tumid

and sloping steeply down in front. A median low carina occurs in some specimens. Up to three pairs of broad glabellar furrows may be present, but the anterior two pairs are seldom visible, and even the posterior remains often indiscernible. The parietal surface of the glabella, except for the median line, is densely covered with small and shallow pits that indicate a potential granulated surface; in several specimens a granulation is apparent on the cheeks.

The hypostoma is elongate and tumid and ornamented by a transverse network of delicate lines, but the maculae are smooth. The rostral shield is convex, arched forward, and ornamented by terraced lines. The hypostoma and the rostral shield are fused completely, a condition regarded by Rasetti as a rule in all *Corynexochidae*—though, at least in some of the Middle Cambrian dolichometopids of Australia attributed to *Amphoton*, *Fuchouia*, and *Sunia*, these shields, where known, are not fused.

The segments of the thorax (Text-fig. 57) have a very large and convex articulating half-ring; the pleural furrow is deep and long, reaching almost to the pleural tip; the pleurae bear facets and are obliquely truncate, with rounded tips. Some of the specimens possess an obscure granulation on the pleurae, and axial nodes are absent. As in most of the *Corynexochidae* a triangular opisthopleural cushion can be seen in the adaxial part of the pleural furrow.

The pygidium is somewhat variable. It is semicircular to subtriangular, the axial furrows are deep, the pleural lobes convex and sloping outward to a vertical position; there is neither border nor marginal furrow, but the pleural furrows and ribs do not reach the margin. The anterolateral corners are acute and slightly drawn out, as for example in some pygidia of *C. spinulosus* Angelin, or *Amphoton bensoni* (Öpik, 1961, pl. 11, figs 5 and 6). The pygidial axis is arched transversely, moderately tapered, and long, the fulcral points are prominent, and the articulating half-ring is long and convex. In all observed pygidia the test is smooth except for terraced lines along the margin.

*Variability:* Several characters of *C. plumula* are rather variable. In the cranidium glabellar furrows may be absent, or developed in various degrees of emphasis, as may the occipital node. The pygidium may be subcircular or sub-triangular, and its length/width ratio varies between 0.5 and 0.6. One to four axial annulations and one to three pleural ribs are present, in several diverse combinations from specimens having one pair of pleural ribs combined with four annulations to specimens with three ribs and one annulation. The external relief and the relief of the cast differ in emphasis but not in numbers of ribs and annulations.

Such variability of the pygidial relief is usually regarded as a sign of a specific inhomogeneity; but in the case of *Corynexochus plumula* this is rather improbable; if taxonomically applied a considerable quantity of ill-defined, or not properly definable, 'species' will result. The localities of W10, W40, and W41 yield large numbers of specimens and within each of these collections the same variability is apparent. Each locality represents, presumably, an identical population, or sites within a single population. In the absence of complete specimens a correlation of cranidia and pygidia cannot be established; the material is abundant (especially

in W10) but mostly fragmentary and variously distorted; silicified material is absent; and the variability of *Corynexochus plumula* cannot be treated quantitatively.

*Comment on illustrated specimens:*

Three cranidia, two hypostomata, and six pygidia are illustrated and briefly described below, in the order of increase in size; all these specimens are selected from beds below the zone of *Erixanium sentum* and above *Glyptagnostus reticulatus*, that is, from the *Corynexochus plumula* Zone. As already mentioned *Corynexochus* passes also into the lower part of the *Erixanium sentum* Zone, where it is rather rare and fragmentary; no specimens from the *sentum* Zone have been illustrated, because the fragments so far obtained allow for no definite specific identification and should be referred to as *C. cf. plumula*.

The small cranidium, Plate 3, fig. 1, CPC 5369, locality W10, is 1.8 mm long. The test is intact and smooth; no glabellar furrows can be seen, but the occipital node is prominent.

The relatively large cranidium, Plate 3, fig. 2, CPC 5370, locality W41, is 3.3 mm long. It shows the narrow thread-like preglabellar border, the straight edge of the palpebral lobe, the straight palpebral furrow running into the pit, the expansion of the glabella in front of the pit, short and shallow glabellar furrows, a prominent occipital node, and the prominent fulcral tubercle. Associated with this cranidium in the same piece of limestone is:

The cranidium, Plate 3, fig. 4, CPC 5372T, is 3.4 mm long. Its occipital node is obscure, three pairs of glabellar furrows and the granulosity of the fixed cheek are discernible. In lateral view the blind end of the posterolateral furrow is well visible.

The hypostoma, Plate 3, fig. 5, CPC 5373, locality W10, is 1.4 mm long. The rostral shield is fragmented, but the hypostoma itself is complete, with intact posterior border. Its structure is the same as in *Corynexochus minor* (Walcott, 1916a, pl. 36, fig. 7, and 1916b, pl. 55, fig. 6).

The hypostoma, Plate 3, fig. 3, CPC 5371, locality W40, is 2.1 mm long and represents a large specimen. The rostral shield is covered with coarse terraced lines, and the hypostoma has a minutely reticulate ornament. The line between the two kinds of the ornament is the line of fusion of the shields.

The pygidium, Plate 3, fig. 6, CPC 5374, locality W39, is 2.0 mm long. The test is intact; the fulcral points are prominent, facets distinct, and the anterolateral angles acute and slightly attenuated; two pairs of pleural ribs and one complete axial annulation are present. The border along the margin is vertical. It is subcircular; the length (without the articulating half-ring) is about 0.5 of the width.

The pygidium, Plate 3, fig. 7, CPC 5375, locality W10, is 2.4 mm long. It is slightly elongate; its length is 0.55 of the width.

The pygidium, Plate 3, fig. 8, CPC 5376, locality W41, is 2.5 mm long. It is subtriangular; its length is 0.6 of the width. Its test is intact. The axis shows three annulations and is sunk between the pleural lobes.

The pygidium, Plate 3, fig. 11, CPC 5379, locality W41, is 2.9 mm long. Its relief is strong: the pleural furrows are deep externally (on the left); three pairs of pleural ribs are present; the posterior ribs are small but prominent knobs, and the decorticated axis consists of four annulations and a short terminus.

The pygidium, Plate 3, fig. 10, CPC 5378, locality W40, is 3.3 mm long. It is crushed and its left side is decorticated. Externally, and on the cast, three axial annulations and three pairs of pleural ribs are present.

The pygidium, Plate 3, fig. 9, CPC 5377, locality W40, is 3.5 mm long. Four axial annulations but only one pair of pleural ribs are indicated.

*Occurrence and age:* *C. plumula* is common and in places abundant in the Georgina Limestone; it has been found at localities W10 (lower part, very abundant), W16, W39, W40, W41 (abundant), W51, and W57. It is also probably present in the Pomegranate Limestone. Its age is Idamean, the Zone of *Corynexochus plumula*.

Order PTYCHOPARIIDA Swinnerton, 1915  
Suborder PTYCHOPARIINA Richter, 1933  
Superfamily ELLIPSOCEPHALACEA Matthew, 1887  
Family PLETHOPELTIDAE Raymond, 1925  
Genus LAMPROPELTIS nov.

The type, and only known, species of *Lampropeltis* is *L. nitens* sp.nov.

*Diagnosis:* *Lampropeltis* is distinguished by its relatively large palpebral lobes, well developed axial furrows, strong occipital spine, relatively blunt front of the tapering glabella, relatively short frontal area, and the presence of ocular ridges.

It is affiliated with *Plethopeltis* Raymond and *Paraplethopeltis* Bridge & Cloud; but it differs from these genera by its larger palpebral lobes, and from *Plethopeltis* by the externally well impressed axial furrows.

*Paraplethopeltis obesa*, the type species of its genus (Bridge & Cloud, 1947, p. 557; footnote, p. 553), is known only from 'chert impressions of under surface of the test' and the external character of its furrows is, therefore, unknown.

The plethopeltid characters of *Lampropeltis* are the rimless frontal border, the down sloping front, narrow interocular cheeks, long (longitudinally) triangular posterolateral limbs, obsolescent glabellar furrows, and the large, only slightly tapering glabella.

Harrington et al. (1959) included the Plethopeltidae in the superfamily Proetacea. A temporal gap, however, separates the effaced and greatly modified plethopeltids from the subsequent proetids, which are not effaced at all and which cannot be derived therefore direct from the plethopeltids.

Hupé (1955) has assumed an affiliation of the plethopeltids with the agraulids—a classification that can be readily accepted.

*Lampropeltis* is the oldest known genus of its family, retaining externally the ocular ridges and deep axial furrows that are unknown in the subsequent forms.

LAMPROPELTIS NITENS sp.nov.  
(Pl. 16, fig. 11; Text-fig. 58)

*Material:* A single cranidium, 2.5 mm long (without spine), the holotype, Plate 16, figure 11, CPC 5493, on the surface of a chert biscuit, locality G103.

The specific diagnosis coincides with the generic diagnosis.

*Description:* The cranidium is strongly arched transversely and longitudinally, with a steep front, and less steep posterolateral limbs. The anterior sutures are straight and slightly divergent, the posterior ones are slightly sinuous, diverge at an acute angle (about 70 degrees in plan) and delineate relatively long (longitudinally) and narrow triangular posterolateral limbs. The posterior marginal furrows are distinct. The cranial front, a downsloping brim, lacks a rim, and is slightly less than one sixth of the length of the cranidium; the margin is arched up and forward. The interocular cheeks are narrow (about 0.25 of the glabella), and slightly convex. The occipital lobe, long in the middle, and crescentic in shape, bears a spine near its margin. The occipital furrow is obsolete, but its position is indicated by the steep slope of the rear of the glabella.

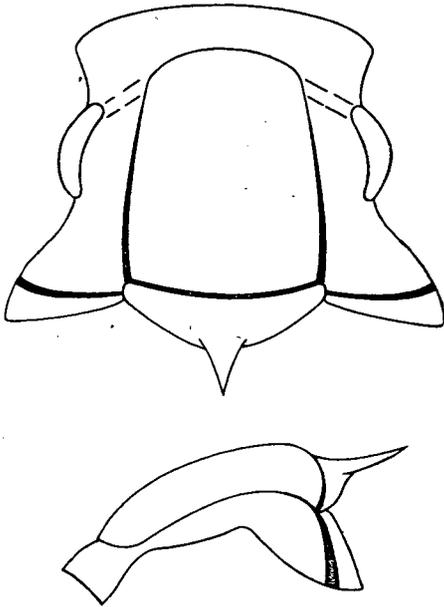


Fig. 58.—*Lampropeltis nitens* gen.nov., sp.nov.,  
from Plate 16, figs 11a, b.

The axial furrows are deep along the flanks of the glabella and less deep in its front. The glabella is prominent, slightly longer than wide: its width in the rear is about 0·8 of the length. It tapers slightly to a bluntly rounded front. Its flanks are not quite straight, being visibly convex in the posterior half. Glabellar furrows are absent, but their position is indicated by two pairs of dark spots.

The palpebral lobes are relatively long (about 0·4 of glabellar length), upturned and slightly curved, and situated in front of the posterior half of the glabella. Palpebral ridges are rather weak and broad. The test is smooth and shiny.

*Occurrence and age:* The cranidium of *Lampropeltis nitens* was found in a chert biscuit at locality G103, from the local topmost silty bed of the Steamboat Sandstone. The age is the Zone of the Middle Cambrian-Upper Cambrian passage.

#### Superfamily PTYCHOPARIACEA Matthew, 1887

##### Family SOLENOPLEURIDÆ Angelin, 1854

*Diagnosis* (revised): Solenopleuridae are Ptychopariacea distinguished by relatively deep axial furrows, a conical, tapering glabella which is rounded in front, and by the strong convexity of the shield.

*Comparison:* Solenopleuridae are close to *Ptychoparia* and the Ptychopariidae in the number of segments in the thorax (not over fourteen). Most of the Ptychopariacea are less convex and have a slightly longer glabella which can be more or less subtruncate in front. Many solenopleurids have an irregularly granulose test and rounded pleural tips, but these characters are as variable as in several forms of Ptychopariidae.

Only one subfamily—the Solenopleurinae— can be included in the family with certainty; the other subfamilies (Hystricurinae, Saoinae and Acrocephalitinae)

placed by Harrington et al. (1959) in the Solenopleuridae and the Solenopleuracea may be of different affiliations. The Hystricurinae are separated from the solenopleurids by a wide temporal gap.

As regards other families included in the Solenopleuracea, the Agraulidae have been already placed with the ellipsocephalids (Öpik, 1961); the affiliation of the Dokimocephalidae and Kingstoniidae among themselves and with the solenopleurids cannot be substantiated on morphological grounds; the Lonchocephalidae and the Catillicephalidae constitute a separate superfamily which includes also *Avonina*.

It should be noted that the names Solenopleuridae and Solenopleuracea (1854) antedate the names Ptychopariidae and Ptychopariacea (1887). Hence the nomenclatural priority belongs to the Solenopleuracea. Furthermore, it has been indicated (Öpik, 1961) that the name Ptychopariacea is a synonym of the still older name Olenacea Burmeister, 1843. The name Ptychopariacea should be therefore regarded as a junior synonym of Olenacea and Solenopleuracea (as well as of Conocoryphaea); it can be preserved only by the suspension of the rule of priority.

#### *Discussion of some genera of solenopleurids:*

*Solenopleurella* Poulsen cannot be retained in the subfamily Solenopleurinae; it has an almost rectangular glabella reaching the rim and small posterolateral limbs, and belongs, apparently, to the Namanoiidae Lermontova.

*Asthenopsis* Whitehouse, however, can be regarded as a solenopleurid, as well as a ptychopariid, genus, and can be described even as a *Ptychoparia* with deflected genal spines.

Snajdr (1958) restricted the genus *Solenopleura* Angelin to a single species—*S. canaliculata* Angelin—and established the genus *Jincella* for the rest of the Scandinavian and one Bohemian species. *Jincella* includes also *Solenopleura brachymetopa* Angelin, which was placed by Whitehouse, and not without reason, in *Asthenopsis*. Snajdr, however, did not indicate the difference of *Jincella* from *Asthenopsis*, which is of a specific significance. Hence, *Jincella* is apparently a synonym of *Asthenopsis*.

*Parasolenopleura* Westergaard, 1953, is probably a junior subjective synonym of *Solenopleurina* Ruzicka, 1938 (see Snajdr, 1958).

*Modocia* Walcott, 1924, and *Ithyektyphus* Shaw, 1956 (see Lochman & Hu, 1960) are also Solenopleuridae, and even Solenopleurinae, which have lost some of the original familial convexity, but retained the granular ornament, as for example in *Modocia weedi* and *centralis* (see Lochman & Duncan, 1944).

Kobayashi (1960) reviewed the latest acquisitions of the Solenopleuridae and also separated the acrocephalitids and agraulids from them. Some reservation is, however, needed regarding forms with very small posterolateral limbs as in *Menocephalites*, that are inconsistent with the concept of the Ptychopariacea.

The regional distribution may have influenced to some extent the classification of ptychopariids and solenopleurids. In America the only *Solenopleura* known is the deformed material in the Acado-Baltic Province, and first preference is given there to the names Ptychopariidae and Marjumiidae; in Scandinavia *Solenopleura* is dominant, no other ptychopariids are associated with them, and *Solenopleura* dominates in the nomenclature.

Subfamily SOLENOPLEURINAE Angelin

Genus NILEGNA nov.

*Diagnosis:* Solenopleurinae with falcate pleurae and serrate flanks of the thorax; distinguished by having twelve segments, a very small pygidium, and sigmoid palpebral lobes.

*Type species:* *Nilegna sigmata* sp.nov.

*Differential diagnosis:* In other genera of the Solenopleurinae the pleurae are rounded, the number of segments in the thorax is fourteen (exceptionally thirteen), and the palpebral lobes are crescentic in shape.

NILEGNA SIGMATA sp.nov.

(Pl. 4, figs 2-8; Pl. 5, fig. 8; Text-fig. 59)

*Material:* Eight specimens are illustrated and described, selected from a single locality (W20) and bed. Only one specimen (pl. 4, fig. 3) is in limestone and has preserved its test; all others are silicified and decorticated.

The holotype is the cranidium Plate 4, figure 2, CPC 5381; it is selected because it is the least deformed specimen.

The diagnosis of the genus serves as a specific diagnosis because the genus is monotypical.

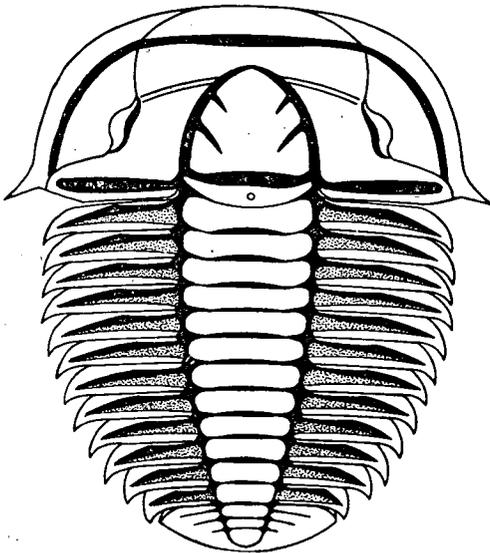


Fig. 59.—*Nilegna sigmata* gen.nov., sp.nov., combined from Plate 4.

*Description:* *Nilegna sigmata* is a small trilobite which may have reached the length of about 12-14 mm. The shield is oval and widest along the posterior margin of the cephalon; it is as wide as the length of the cephalon plus ten segments of the thorax; the cephalon is large and as long as seven segments, but the pygidium is relatively small, having the length of about 1.5 of an anterior segment. The cephalon is moderately convex for a solenopleurid, with tumid cheeks, and a slightly

convex downsloping brim; the rim is relatively wide and convex and so is the border of the free cheeks; the genal spines are diminutive, slightly advanced and strongly deflected. The eyes are relatively large (as long as half the glabella), elevated, far apart, and placed opposite the glabellar midpoint. The interocular cheek, including the palpebral lobes, is as wide as three-quarters of the glabella on the same level. The palpebral furrow is deep and narrow, the palpebral lobe sigmoidal and swollen (Pl. 4, fig. 6). The ocular ridges are low but distinct, slanting, and slightly curved.

The anterior sutures are slightly convex abaxially, subparallel within the brim, and converge on the border almost to the midline, where they become marginal. The posterior sutures diverge strongly and intercept the posterior margin almost at the base of the genal spine. The posterolateral limbs are large and subtriangular. The pleurooccipital furrow is deep and wide, but becomes abruptly shallow or even obsolete at the tip of the posterolateral limb, as seen in the holotype and in the complete specimen Plate 4, figure 1.

The free cheek is about as wide as the interocular cheek, and evenly convex; its surface is densely but weakly venulose.

The occipital lobe is convex, relatively short, and bears a small tubercle; the occipital furrow is straight, deep, and rather wide.

The cephalic axial furrows are very deep and wide along the flanks of the glabella, but shallow in front of it.

The glabella is wider than long (the ratio is about 7 : 6), with convex flanks, subtriangular, and tapers rapidly; its convexity is relatively low, rising only slightly above the cheeks. Two pairs of oblique and slightly curved glabellar furrows are present.

The cranial ornament consists of coarse pustules with a minute granulation in between; on the brim the granulation is arranged in radial lines and the frontal slope of the rim bears terraced lines; the palpebral lobes are smooth. The ornament of the rest is unknown.

The thorax consists of twelve segments and is wider than long, with a ratio of about 5 : 4 in the less compressed specimen Plate 4, figure 5. The axis is almost as wide as the pleural lobe, convex, and the axial furrows are deep. The pleural lobe is abruptly geniculate along the fulcral line, which runs slightly abaxially from the pleural midline: the free (outer) parts of the pleurae are, consequently, slightly longer than their adaxial hinged parts. The pleural furrows are wide and relatively deep, but their width decreases abaxially from the fulcra. The free pleurae are provided with articulating facets and have short falcate pointed tips; the flanks of the thorax are serrate.

The pygidium is relatively short and wide and has no border. The axis tapers; it consists of two complete annulations and a terminus, and two pairs of weak pleural ribs are present.

The doublure is narrow; a simple, *Ptychoparia*-like rostral shield is probably present: it is indicated in Plate 4, figure 5, in which the doublure of the free cheek does not reach the midline of the cephalon.

*Variability:* The relative length of the frontal area and its parts (the brim and the rim) varies slightly, but the variability is of an individual significance only.

*Comment on illustrated specimens:*

Complete test, 7.0 mm long, CPC 5385, Plate 4, fig. 6. It is imperfectly preserved, without the free cheeks, with most of the glabella lost, and the pygidium displaced. All twelve segments are present and some of the short falcate tips are preserved as moulds and show the narrow doublure.

Complete test, 8.8 mm long, CPC 5384, Plate 4, fig. 5. Parts of the cheeks, of the brim, glabella and anterior part of the axis are lost, and the pygidium is worn; the free cheeks are in situ, showing the doublure and the cast of the tiny deflected spine; the doublure of the cheek appears to be clean-cut in front, indicating a narrow rostral shield which itself is not preserved. Casts of the falcate pleural tips are preserved on the left side of the thorax and the fulcral line is distinct.

Isolated fragmentary pygidium, 1.2 mm long, CPC 5383, Plate 4, fig. 4. The pygidium is relatively flat, lacking the usual solenopleurid convexity; the axis is long, almost to the border, tapering, and with two annulations and a terminus; two pairs of pleural ribs are indicated.

Decorticated cranidium, the holotype, 4.5 mm long, CPC 5381, Plate 4, fig. 2. Traces of granulation and terraced lines are indicated on the brim; broad glabellar furrows are visible on the right side; note the abrupt shallowing of the otherwise deep and wide marginal furrow at the tip of the posterolateral limb. The occipital lobe is only partly preserved. The total length of the trilobite was about 14 mm.

A cranidium in limestone, 2.5 mm long, CPC 5382, Plate 4, fig. 3. The glabella is fractured on the left side and laterally deformed and appears therefore less conical than in the other specimens. The test is intact, its ornament consists of coarse pustules and minute granules which are radiating on the brim. The convex rim is granulose and bears terraced lines; the ocular ridges are indicated by absence of pustules; two pairs of oblique glabellar furrows are well visible, the occipital node is prominent. The right palpebral lobe is sigmoidal and smooth, and the palpebral furrow narrow and deep.

Isolated decorticated free cheek, 4.5 mm long, CPC 5387, Plate 4, fig. 8. The minute deflected, 'solenopleurid' genal spine is well preserved; obscure caecal veins are also present.

Isolated decorticated free cheek, 4.2 mm long, CPC 5386, Plate 4, fig. 7. The genal spine is preserved as a cast only.

Isolated cranidium, 4.5 mm long, associated with *Meteoraspis* cranidia, CPC 5396, Plate 5, fig. 8. Its ornamental granules are preserved and are the same as in the specimen Plate 4, figure 3.

*Occurrence and age:* The examined material has been collected at locality W20, where *Nilegna sigmata* is abundant; but it is absent in all other localities. Its age is Mindyallan, the Zone of *Glyptagnostus stolidotus*.

Genus SOLENOPLEURA Angelin, 1854

SOLENOPLEURA? ERISTA sp.nov.

(Pl. 4, figs 1 a, b, c; Text-fig. 60)

*Material:* Only one cranidium, the holotype, CPC 5380, has been found as yet. It is fragmentary, but the internal cast as well as the external mould are available.

*Diagnosis:* *Solenopleura? erista* sp.nov. is a species without glabellar furrows and with a minutely granulose test; distinguished by the effacement of the marginal furrow in front of the glabella, very wide interocular cheeks (almost as wide as the glabella), forward placed palpebral lobes (opposite the middle of the anterior half of the glabella), and fulcral points placed close to the axial furrows, at a distance of about half of the occipital width.

*Differential diagnosis:* In *S. ? erista* the interocular cheeks are as wide as, or even slightly wider than, in *Solenopleura canaliculata* (Angelin), which is the type of its genus. It is, however, less tumid, possesses glabellar furrows, and the frontal marginal furrow is continuous.

From the numerous species of *Solenoparia* Kobayashi, *S. ? erista* differs by the characters mentioned in its diagnosis.

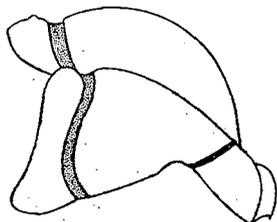


Fig. 60.—*Solenopleura? erista* sp. nov., lateral view of cranidium, Plate 4, fig. 1.

*Familial and generic classification:* No question arises as regards the familial and subfamilial classification of *S. ? erista* because the genus nearest to it is the Middle Cambrian *Solenopleura*. But *S. ? erista* may represent another genus related to *Solenopleura* because in *erista* (1) the glabella lacks the furrows, (2) the frontal marginal furrow is partly effaced, and (3) the fulcral points are placed much closer to the glabella than the palpebral lobes. As a rule, in opisthoparian trilobites the palpebral lobes and the fulcral points coincide in their exsagittal position.

*Description:* The holotype cranidium is 3.8 mm long; it is extremely tumid and the glabella is especially so. The palpebral lobes are small, about 0.2–0.25 of glabellar length; the ocular ridges are curved, low and double. The anterior sutures converge forward, and the frontal area is relatively short—slightly more than 0.2 of glabellar length. The axial furrows are very deep and narrow and surround the glabella; the glabella is about as wide as long, well rounded and oval, tapering somewhat forward.

*Occurrence and age:* *Solenopleura? erista* comes from the O'Hara Shale ('lower chert bed'), locality D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Genus MODOCIA Walcott, 1924

#### MODOCIA? IMMODULATA sp.nov.

(Pl. 4, fig. 9; Text-fig. 61)

*Material:* The material consists of a single complete specimen, the holotype, CPC 5388; it is an external mould in friable siliceous (or silicified?) silstone or shale. The specimen is 18.7 mm long. The pleural tips on the left and a part of the left free cheek are missing; the right free cheek is displaced adaxially, just concealing the palpebral lobe. The preserved parts allow for a fair reconstruction of the cephalon (Text-fig. 61), in which, however, the course of the anterior sutures is probably not quite accurate. The test appears to be smooth, but some parts of the thorax have preserved low rounded granules.

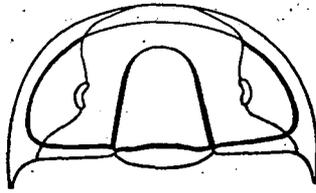


Fig. 61.—*Modocia? immodulata* sp.nov., reconstructed from Pl. 4, fig. 9.

*Generic classification:* The structure of the cranidium, the small eyes, the tapering and well rounded glabella and the size and form of the pygidium indicate a close affiliation with the genera *Armonia* Walcott and *Modocia* Walcott.

According to Palmer (1954, p. 763), the thorax of *Modocia* is unknown. Lochman-Balk in Harrington et al. (1959) added *Armonia* to the list of its synonyms and illustrates *Armonia elongata* (Walcott), as an example of a *Modocia* with fourteen segments in the thorax. Because in *immodulata* the number is only twelve its generic classification is queried here.

*Diagnosis:* *Modocia? immodulata* is a species without glabellar furrows, and without ocular ridges, distinguished by its brim being slightly longer than the rim, and by its subtriangular pygidium with weak pleural furrows. The thorax consists of twelve segments.

*Differential diagnosis:* No species of *Modocia* are close enough to *M.? immodulata* to necessitate a comparison.

*Description:* The body is oval; the semicircular cephalon is as long as eight segments of the thorax and the pygidium is three to four segments long. The axial and pleural furrows are well impressed and the marginal furrows in the cephalon are distinct. The original convexity cannot be established, but apparently the relief was moderate, less tumid than in *Solenopleura*. The fulcra in the thorax are distinct and the fulcral line remains slightly abaxially from the midline of the pleurae, whose free ends were originally geniculated downward. The pleurae are equipped with well developed facets. The cephalon is of a distinct ptychoparioid design, with a tapering glabella, a brim, and a slightly narrower rim in front of it. The border (the cranidial rim and the border of the free cheeks) is elevated but only moderately convex. The anterior sutures are slightly divergent, and probably subparallel in an uncompressed state; within the rim the sutures remain dorsal for about one-third of the anterior width of the cranidium. The posterior sutures are greatly divergent, delineating large triangular posterolateral limbs, cutting the posterior margin close to the genal angles. The free cheek, rhomboidal in outline, bears a short undeflected spine. The palpebral lobes (and the eyes) are small, about one-quarter of glabellar length, opposite the middle of the glabella, and at a distance of about one-half of the glabellar width. Ocular ridges are absent. The occipital lobe is relatively short, the occipital furrow distinct and widened in the middle. An occipital node is absent. The axial furrows are distinct and deep, and enclose the front of the glabella. The glabella is as wide (at base) as long, tapering, and well rounded in front. Glabellar furrows are absent. In the thorax, which consists of twelve segments, the axis is slender and narrow, about 0.25 of the thorax in its anterior part, but remains wider than the pleural lobe part between the fulcral line and the axial

furrow. The flanks of the axial lobe are slightly concave, with the effect that the tapering of the axis decreases rearward and the axial furrows of the pygidium acquire finally, a subparallel course.

The pygidium is relatively large, subtriangular, with straight lateral and rounded rear margins. Its width is more than twice the length (in the compressed state). A narrow border and about three pairs of weak pleural ribs are present. The border is accentuated by compression and the reflexion of the narrow doublure. The pygidial axis is long, with subparallel flanks, about (or over) one-quarter of the width of the pygidium (flattened), and consists of three annulations and a bluntly rounded terminus.

*Occurrence and age:* *Modocia? immodulata* was found at locality G107, in a siltstone or shale topping the Steamboat Sandstone; its age is the Zone of the Middle Cambrian-Upper Cambrian passage.

#### Family TRICREPICEPHALIDAE Palmer, 1954

Tricrepicephalidae are a well known but small family of Ptychopariacea, of three or four known genera. In addition to these, the new genus *Erediaspis* is described below.

A previously described Australian tricrepicephalid is *Tricrepicephalus etheridgei* (Chapman, 1911), from the Upper Cambrian of Victoria.

#### Genus EREDIASPIS nov.

The type species of *Erediaspis* is *E. eretes* sp.nov.; the genus is monotypical.

*Diagnosis:* *Erediaspis* is a tricrepicephalid with pygidial spines arising from the posterior part of the pleural lobes and with a steeply downsloping pygidial periphery; distinguished (1) by its five annulations of pygidial axis, (2) by parallel interpleural grooves and pleural furrows, (3) by rather narrow propleura and wide opisthopleura; furthermore, its cephalon has (4) a convex, relatively narrow yoke shaped rim, (5) small eyes, (6) wide interocular cheeks, (7) indistinct and erratic pits in the marginal furrow, and (8) deflected genal spines.

*Familial classification:* The family reference (Tricrepicephalidae) is borne out by the pygidial structure, by the markings (pits) in the cranidial marginal furrow, deep axial furrows and the shape of the glabella; the nearest, but still rather distinct, genus is *Tricrepicephalus* itself, in which the pygidial spines arise also from the pleural lobes and the pygidial periphery slopes steeply. A posterior view of a *Tricrepicephalus* pygidium has been published by Lochman (1941, p. 324), showing the steep slope behind the terminus, and the same is evident from Walcott (1916, pl. 30, figs 1 and 1a). Comparing Walcott's figure 1a (inner side of a pygidium of *Tricrepicephalus*) with our specimens Plate 7, figures 1 and 2, the similarity in structure becomes apparent. But a significant difference remains: the pygidium of *Erediaspis* with its five segments is much more caudalized than that of the later *Tricrepicephalus*, which has only three axial annulations. The high convexity of the cranidium, however, and convex flanks of the glabella recall a *Meteoraspis* rather than a *Tricrepicephalus*.

It should be noted that the cephalic structure of *Erediaspis* is close to solenopleurids (*Solenopleura*, *Modocia*) which are discussed in connexion with the genus *Nilegna*. The general design of the cephalon is similar to that of the Ptychopariidae.

*Erediaspis* is the oldest known genus of the Tricrepecephalidae.

EREDIASPIS ERETES sp.nov.

(Pl. 6, figs 1-4; Pl. 7, figs 1-5; Text-figs 62-64)

*Material*: Eleven specimens (cranidia, free cheeks, and pygidia) are selected for description; many specimens have been studied. All specimens are silicified, or buried to some extent in silica. The rock is limestone with siliceous partitions, and chert pods.

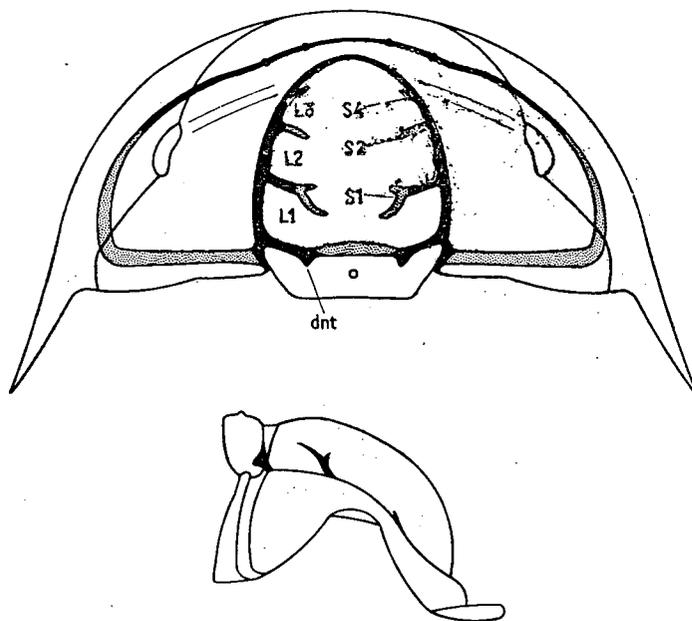


Fig. 62.—*Erediaspis eretes* gen.nov., sp.nov., combined from Plate 6, figs 1 and 3. dnt—occipital dent; S1, S2, S4—glabella furrows; L1, L2, L3—glabella lobes; vestigial pits are indicated in the frontal marginal furrow.



Fig. 63.—*Erediaspis eretes*, silicified cheek, CPC 6728, x 4, lateral view.

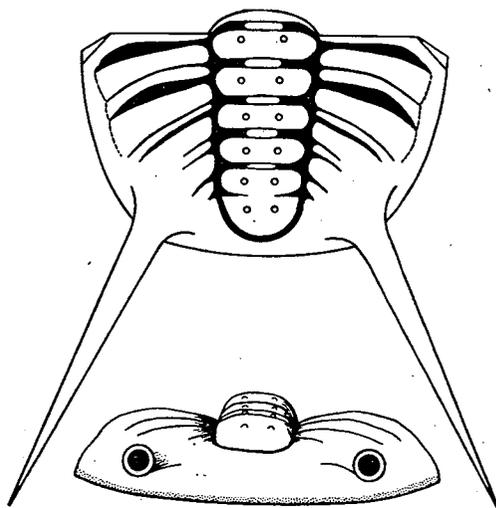


Fig. 64.—*Erediaspis eretes* gen.nov., sp.nov., pygidium combined from Plate 7, figs 1-5; rear view from specimen CPC 6729.

*Holotype*: The best preserved cranidium, Plate 6, figure 1, CPC 5400, locality G119, is selected, although its originally granulose ornament is obliterated. A specific diagnosis is superfluous because it coincides with the generic diagnosis.

*Description*: *The cephalon*: The cephalon is semielliptical, slightly more than twice as wide as long, and strongly convex, the convexity being almost two-thirds of the length. The glabella is elevated above the tumid cheeks, which slope outward; the free cheeks follow the slope and are also slightly tumid. The genal spines are relatively short, deflected, and slightly advanced.

The cranidium is subtrapezoidal; the anterior sutures are relatively straight and converging, intercepting the frontal margin opposite the rear flanks of the glabella; the posterior sutures are straight, divergent, and subparallel at the rear margin; they cut the margin close to the genal angles, crossing the lateral, not the posterolateral, marginal furrow. The posterior border widens abaxially from the fulcrum. The posterolateral limbs are large and triangular owing to the forward position of the eyes and the straight course of the posterior sutures. The palpebral lobes are rather small (about 0.3 of glabellar length), oblique, with elevated edges, but remain below the level of the cheeks; the palpebral furrow is barely indicated. The interocular cheek is wide, about 0.6 of the glabella at the level of the eyes. The ocular ridge is straight, slanting, and ill-defined. The rim is relatively wide (sagittally, about 0.12 of cranidial length), shaped as a yoke or the bar of a balance, and almost flat; the rim has a doublure of about a quarter of its width (longitudinal); consequently the sutures meet in a submarginal position. The frontal marginal furrow is deep and narrow, but may have a shallow median part in the position where a plectrum is developed in some other trilobites. In

the furrow small spots occur sporadically, comparable in position with the tricepcephalid markings (see under *Meteoraspis*). The brim is steep and convex and overhangs somewhat the marginal furrow; it is about as wide as the rim, but in the photographic projection appears shorter.

The occipital lobe is elaborate: rectilinear in the middle, it turns abruptly forward and outward and bears two occipital dents on its frontal margin. A low occipital node is also present.

The occipital furrow is wide and shallow but still distinct in the middle, and deep and narrow on the flanks, where it is overshadowed by the bulging glabellar lobes.

The axial furrows between the glabella and the cheeks are wide and deeply sunk, but shallow around the front, and may be almost obsolete at the tip of the glabella. The glabella is as wide as long, with convex flanks, tapering, and almost angular at its tip. Three pairs of glabellar furrows are present: the posterior (S1) furrows are forked, with an oblique and angular posterior branch; the S2 furrows are simple, short and slightly oblique; the S3 are not discernible; the S4 are, however, evident. The posterior glabellar lobes are tumid, the L2 lobes slightly swollen, and the glabella is slightly constricted at their level. The L3 lobes are inconspicuous and so is the small and relatively low frontal lobe.

The cephalic ornament consists of coarse rounded granules with a dense minute granulation in between.

*The pygidium:* The pygidium is distinguished by its strong relief; it is almost twice as wide as long; small pygidia are semicircular, and larger ones are semicircular in relation to the centre of the first (transverse axial) furrow. The pygidial axis is relatively narrow (variable, around 0.27 of shield width), with almost subparallel flanks, and reaches the border. A rounded terminus and five, rarely six, annulations are present. The axis is convex, with almost vertical flanks, elevated above, and at the same time sunk between, the pleurae. The axial furrows are deep and wide. The border is indicated only by change of slope; it is steep, and near vertical in the rear of the pygidium. The pleural lobes are convex, sloping adaxially and outward. Three pairs of anterior pleurae are divided by narrow and deep interpleural grooves reaching the border; the pleural furrows are very wide and deep showing sporadically the geniculation and even the position of the fulcral points. Notable is the 'horizontality' of the pleural furrows, which do not run diagonally but are parallel to the interpleural grooves. Such structure is very rare indeed; among the proparian trilobites transverse furrows occur in the cyrtometopids, but in the opisthoparia such furrows are unknown. The pleurae are divided by the pleural furrows into a narrower propleuron, and a wider and more conspicuous opisthopleuron. Short furrows not reaching the border indicate two more, but undeveloped, pairs of pleural ribs in the posterior of the pygidium. A pair of diverging spines arises from the rear part of the pleural lobes. They appear straight in plan, but in fact curve upward. The doublure of the pygidium is narrow and vertical, and bears terraced lines.

The ornament of the pygidium also consists of rounded granules with minute granulation in between. Each axial annulation bears a pair of pustules.

The thorax is unknown, but fragments of segments have short falcate pleural tips and the pleurae are divided also by transverse and deep pleural furrows into a narrow and low propleuron, and a wide and elevated opisthopleuron.

As a guess, the thorax of *Erediaspis eretes* consisted of ten or eleven segments, and the length of the pygidium (without spines) was two-thirds of the cephalon.

*Comment on illustrated material:*

The holotype cranidium, Plate 6, fig. 1, CPC 5400, locality G119, is 10.5 mm long and 18.5 mm wide along its posterior margin. It is undeformed, preserving the convexity, which is illustrated in Plate 6, figure 3. The flanks of the cranidium (the sutures) are rectilinear in plan, emphasizing the trapezoidal shape; in the marginal furrow on the right two 'tricrepicephalid' spots are visible, whereas on the left the furrow is too narrow to show its floor. The pair of occipital dents on the anterior border of the occipital lobe are rather distinct.

The fragmentary free cheek Plate 6, fig. 2, CPC 5401, locality G149, shows the concentric arrangement of the granulation and the course of the posterior suture cutting the marginal furrow of the cheek (and not the posterolateral marginal furrow). The advanced position of the genal spine is also indicated. The free cheek Text-fig. 63, CPC 6728, locality G119, is almost complete, showing the short genal spine.

The cranidium, Plate 6, fig. 3a, b, CPC 5402, locality 41625, 10.5 mm long, is partly buried in silica; it shows the ornament, the profile, and the posterior suture cutting the lateral marginal furrow.

The pygidium, Plate 7, fig. 5, CPC 5408, locality G119, is 8.2 mm long; its left side is missing, but for the purpose of description it can be regarded as being complete because even the articulating half-ring is preserved. A sixth axial annulation is indicated; note the absence of the fulcral geniculation on the pleurae and the distinct border. The ornamental coarse granules are not preserved and the abraded fine granulation is indicated by punctation.

The pygidium, Plate 7, fig. 4, CPC 5407, locality G119, is 6.5 mm long. It is complete but buried partly in silica. The fulcral geniculation is indicated in the second pleurae; only five axial annulations are developed; the ornament is partly preserved and on the anterior axial annulations paired tubercles are visible.

The pygidium, Plate 7, fig. 1, CPC 5404, locality G149, is 6.2 mm long and 10.0 mm wide; the parietal surface of the intact test is exposed. The narrow doublure bears terraced lines; the ornament, the paired axial tubercles, and the appendifers along the axial furrows are well preserved; five axial annulations are present. The spines arise above the doublure. Compare Walcott (1916, pl. 30, fig. 1a).

The pygidium, Plate 7, fig. 2a, b, CPC 5405, locality G149, is about 3.2 mm long (without the articulating half-ring). The furrows on the pleurae, and the fulcral geniculation are rather distinct. The posterior view illustrates the vertical rear border and the high position of the spines above the margin. The pustules are destroyed and replaced by punctae.

The fragmentary pygidium, Plate 7, fig. 3, CPC 5406, locality G119, is 3.2 mm long; it is sub-triangular, with straight flanks, and the posterior pleural furrows are rather indistinct. The largest known pygidium (CPC 6731, locality G119, not illustrated) is about 24 mm long, with spines over 30 mm long.

The cranidium, Plate 6, fig. 4, CPC 5403, locality G417, is 6.1 mm long; it is etched from limestone.

*Occurrence and age:* *Erediaspis eretes* occurs in the older part of the Mungerebar Limestone; the described material was collected at localities G119 and G149. Relatively well preserved silicified specimens have been etched out from the limestone of locality G417. Other localities are G8, G151, and G429b. Its age is the Mindyallan Zone of *Erediaspis eretes*.

Genus TRICREPICEPHALUS Kobayashi, 1935

TRICREPICEPHALUS? sp.

(Pl. 5, fig. 9; Text-fig. 65)

The material consists of a single fragmentary pygidium, CPC 5399. The left pleural lobe and the axial lobe are preserved; the right side and a part of the posterior margin are missing. Nevertheless, it could be reconstructed (Text-fig. 65).

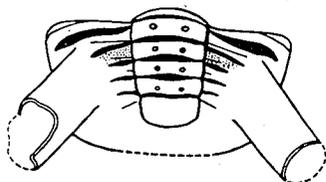


Fig. 65.—*Tricrepecephalus?* sp.,  
from Plate 5, fig. 9.

The fragment is 6.3 mm long. The downsloping periphery and the strong spines arising from the pleural lobes indicate a species of the family Tricrepecephalidae; the generic assignment is, however, questioned because no cranidia are available to support the evidence provided by the pygidium.

The fragment represents apparently a new species having four axial annulations, whereas the known species of *Tricrepecephalus* have three annulations

*Erediaspis* gen.nov. is improbable because it possesses five annulations and its pygidial spines arise nearer to the posterior margin.

*Occurrence and age:* The fragment was found in the Mungerebar Limestone, in limestone of locality G131; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

Genus METEORASPIS Resser, 1935

The type of *Meteoraspis* is *Ptychoparia metra* Walcott, 1890; according to Lochman (1938b) this species is based on a poorly preserved cranidium, which is illustrated by Lochman (1938a), but not re-described. Palmer (1954) illustrated a cranidium and a pygidium of *Meteoraspis metra* and compiled a generic diagnosis in terms that are broad enough to accommodate all known species of the genus. It is important to note that the pygidium of *M. metra* has no border and its pleural lobes have no trace of ribs or furrows. Lochman (1938b), and later Lochman in Harrington et al. (1953) based the diagnosis of *Meteoraspis* on *M. borealis* Lochman, 1938, and indicated that the species of the genus should have a pygidial border, interpleural grooves and pleural furrows, and only two pits in the cranidial marginal furrow. This is apparently a narrow definition applicable only to species like *borealis* and *bidens*, but not to the group of *M. metra*.

METEORASPIS BIDENS sp.nov.

(Pl. 5, figs 4-8; Text-fig. 66)

*Material:* Four cranidia and two pygidia are selected for description from abundant but less well preserved material. They are silicified, but one cranidium and one pygidium have retained the test and are otherwise intact; non-silicified specimens

in limestone have been also examined. Non-flattened as well as flattened specimens are described—an advantage in comparing the modes of preservation in limestone and in shale.

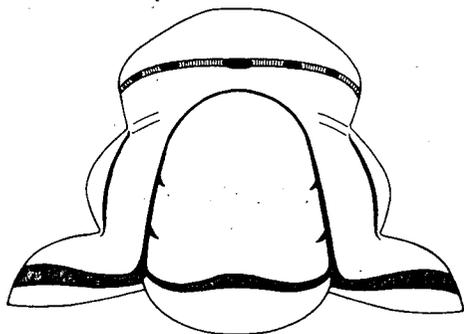


Fig. 66.—*Meteoraspis bidens* sp.nov. combined from Plate 5, figs 4 and 8.

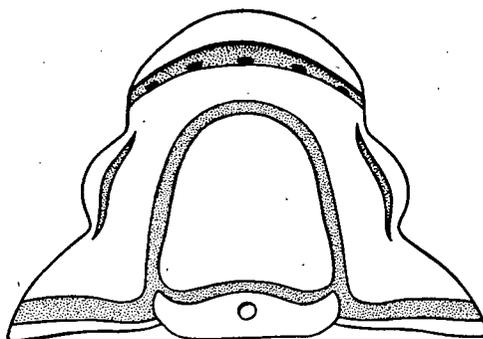


Fig. 67.—*Meteoraspis* aff. *bidens*, from Plate 5, fig. 2.

*Holotype* is the pygidium CPC 5393, Plate 5, figure 5, from locality W17; it is selected because it displays the essential diagnostic characters of the species.

*Diagnosis:* *Meteoraspis bidens* sp.nov. is a species with a cranidium of a tricrepecephalid appearance having (1) a relatively long and moderately convex rim, (2) three to five pits in the marginal furrow (3) pleural pygidial ribs (4) a pygidial axis not reaching the margin, (5) a smooth test, and (6) a pygidial border; distinguished by its short (longitudinally) occipital lobe, long palpebral lobes, rather short and flattened triangular pygidial spines, and rearward converging flanks of the pygidium.

*Differential diagnosis:* *Meteoraspis borealis* Lochman, 1938, has a pygidium somewhat resembling the pygidium of *M. bidens*. A pygidium of *M. borealis* illustrated by Rasetti (1946, pl. 70, fig. 4) has, however, a longer terminus reaching the margin and less fused pleurae. Furthermore, the test of *borealis* is granulose (smooth in *bidens*), the cranidial rim is much narrower and rather convex, and the marginal furrow bears only two pits. *Tricrepecephalus nuperus* Resser, 1938, which is a *Meteoraspis* by its pygidium (see Palmer, 1954, p. 754) has three pits in the frontal furrow and a relatively large and moderately convex brim, but, compared with *M. bidens*, its occipital lobe is longer, the pleural lobe of the pygidium is rather narrow, without ribs and without a border, and the spines are long. One notes that the cranidia of *Meteoraspis bidens* and *M. nuperus* resemble *Tricrepecephalus* rather than *Meteoraspis*. In all species of *Meteoraspis*, as far as could be gathered from the literature, the pygidial flanks are parallel, and not converging as seen in *M. bidens*, and the pygidium has no border (except for *M. borealis*). Completely borderless pygidia have been also attributed to *M. borealis* by Kindle (1948).

*Description:* The whole trilobite may have attained the length of about 40 mm. It had a narrow and strongly convex body, with strongly geniculate pleurae and posterolateral limbs, and rather steeply downsloping free cheeks.

The cranidium is about as long as wide and evenly convex; the anterior sutures are slightly divergent or even subparallel in undeformed, and straight and divergent in flattened specimens. The posterior sutures run parallel to the posterior border and then curve evenly rearward to cut the posterior margin in a distance of about three-quarters of the width of the occipital lobe in compressed specimens. The posterior limbs are broad and spatulate. The interocular cheek is narrow, being slightly less than a third of the glabellar width on the mid-level of the palpebral lobes.

The palpebral lobes are slightly oblique, narrow and long, somewhat longer than half the glabella, and the palpebral furrows are shallow but distinct. Weak ocular ridges occur in some specimens and are strongly slanting. The rim is subtriangular, gently convex, and about twice the length of the brim; the frontal area (brim and rim together) is about one-quarter of the cranidial length. The marginal furrow is relatively straight, narrow, and distinct, and possesses three to five tri-crepicephalid pits.

The occipital lobe is about one-fifth of the glabellar length, and bears a weak node, and the occipital furrow is wide in the middle and narrows toward the flanks. The axial furrows are sunk down deeply, but the circumglabellar furrow is less deep in front of the ocular ridges. The glabella, as long as wide at its base, has convex flanks, tapers evenly, and has a rounded front, but remains somewhat angular at its tip. Two pairs of rather weak and short glabellar furrows, or even lateral notches, are indicated.

The pygidium is smooth; it has rearward-converging flanks, a pair of short and relatively flat triangular spines arising from the margin and involving the doublure, and a gently curved posterior margin; a relatively wide border is indicated, which is unique in *Meteoraspis*. The pleural lobes show two or three pairs of ribs, divided by the pleural furrows; the pygidial axis rises high above the pleural lobes, is parallel-sided, touches the border, and contains three annulations and a short rounded terminus; the axis is slightly wider, or almost as wide as a pleural lobe. The doublure is narrow—as wide as the border—and bears about 10–12 terraced lines. The pygidium is strongly convex, having a height of about half its width.

*Comment on illustrated material:*

Silicified undeformed cranidium, 6.0 mm long, CPC 5392, Plate 5, fig. 4, locality W66, in a current-laminated coquinoid of trilobite fragments (silicified) in limestone matrix. The surface is smooth, two pairs of short vestigial glabellar furrows are indicated; the ocular ridges are very weak; the frontal marginal furrow is narrow and shows three crepicephalid pits; the palpebral lobes are long and narrow; the occipital lobe bears a low node; the posterolateral limbs are strongly geniculate and the anterolateral corners slope down steeply. The anterior sutures are parallel.

Decorticated crushed cranidium, 13.3 mm long, locality W20, CPC 5395, Plate 5, fig. 7, siliceous shale parting in limestone. The three crepicephalid pits in the marginal furrow have retained remnants of the silicified test; the anterior sutures, owing to flattening, are divergent; because of flattening the large and usually down-bent posterolateral limbs are visible in plan; the glabellar furrows are represented by two pairs of weak lateral notches.

Two decorticated, partly flattened cranidia, locality W20, CPC 5397 and 5398, Plate 5, fig. 8. The larger cranidium is 12.5 mm long. The anterior sutures are almost parallel owing to a lesser degree of flattening; the crepicephalid pits in the marginal furrow have retained the silicified test; in the smaller (opposing) specimen the left ocular ridge is indicated.

The holotype—a silicified undeformed pygidium (test), in limestone, locality W17, CPC 5393 Plate 5, figs 5a, b, c. The pygidium is 6.5 mm long and 10.2 mm wide. The test is smooth; pleural ribs and furrows are present; in the anterior pleura the pleural furrow is distinct and the interpleural groove is indicated; the pygidium displays a border, which is exceptional in *Meteoraspis*; note the great convexity amounting to half the width of the shield.

Decorticated flattened and crushed pygidium, 7.0 mm long, in siliceous shale parting of limestone; locality W20, CPC 5394, Plate 5, fig. 6. The pleural ribs are distinct and the doublure with terraced lines is exposed; the terminus, owing to crushing, appears pointed.

*Age and Occurrence:* *Meteoraspis bidens* is a species confined to the *Glyptagnostus stolidotus* Zone. In the Georgina Limestone it has been found at localities W17, W20, W66, W301, and W1, and in the Mungerebar Limestone at G12; fragments of pygidia have been observed in the O'Hara Shale, locality D29.

METEORASPIS aff. BIDENS  
(Pl. 5, figs 1-3; Text-fig. 67)

*Material:* The illustrated three cranidia are selected from a small number of fragmentary specimens.

Open specific nomenclature is employed because pygidia are absent and no conclusive comparison can be made on the cranidia alone. The cranidia represent nevertheless a species distinct from *Meteoraspis bidens* because: (1) the test is minutely granulose, but in *bidens* it is smooth; (2) the posterolateral limbs are triangular, in *bidens* spatulate; (3) five shallow pits are present in the marginal furrow, but *bidens* has three deep and two weak pits; (4) the glabellar front is evenly and strongly arched, whereas in *bidens* the frontal margin is subangulate; (5) the rim is shorter and the brim long than in *bidens*.

*Comment on illustrated specimens:*

The cranidium, Plate 5, fig. 2, CPC 5390, locality D29, in hard matrix, is 2.2 mm long. It is completely decorticated and all furrows are wide and deep, indicating a thick test, especially in the furrows. An occipital subcentral node is present.

The cranidium, Plate 5, fig. 1, CPC 5389, locality D28, in chert, is 3.0 mm long. The test is preserved, and the furrows are therefore narrow; the granulation is visible on the rim and brim and on parts of the glabella.

The immature cranidium, Plate 5, fig. 3, CPC 5391, is 1.3 mm long. It differs from the adult specimens in having wider interocular cheeks and no pits in the marginal furrow.

*Occurrence and age:* *Meteoraspis bidens* occurs only in the O'Hara Shale ('lower chert bed'), at localities D6, D28, and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Family ACROCEPHALITIDAE Hupé, 1955

In the discussion of the family Solenopleuridae in this paper it is suggested that the acrocephalitids may not be affiliated with *Solenopleura*, and should be regarded as a family of the Ptychopariacea instead. The name Acrocephalitidae in its turn may be a subjective synonym of the Dokimocephalidae Kobayashi, 1935, but also a standing subfamily of the latter (Kobayashi, 1960, p. 383). *Acrocephalites*

and *Dokimocephalus* are similar in having a frontal cusp and an angular forward-protruding cranial rim. The presence of a cusp alone should not be overestimated taxonomically because it occurs in many unrelated genera (*Proampyx*, *Rostrifinis* gen. nov., *Nasocephalus*, *Hapalopleura*, several dalmanitids).

The family Acrocephalitidae (Acrocephalitinae Hupé, 1953) as conceived in Harrington et al., (1959) is composite; it contains four groups of forms, which are discussed below. The family itself is based on *Acrocephalites* Wallerius, 1895, of which *Acantholenus* Matthew, 1898, is probably a junior synonym.

#### Group A.

*Acrocephalites stenometopus* (Angelin); *A. stenometopus agnostorum* Westergaard, 1948; *A. stenometopus olenorum* Westergaard, 1948; *Acantholenus spiniger* Matthew, 1898; *A. militans* Lermontova (vide Tchernysheva et al. 1960); *A. mirabilis, weberi, intermedius, and regularis* Lermontova, 1940.

These species are closely related to each other, having a cusp, a forward-produced angular rim, and a semiglobose preglabellar boss.

#### Group B.

*Acrocephalina* Troedsson, 1937, *Aldanaspis* Lermontova, 1904, and ?*Acrocephalites minimalis* Sivov, 1955. These are Acrocephalitidae with incomplete or obsolete cranial marginal furrow. *Acrocephalites vigilans* Walcott & Resser, 1924, also may belong to this group. Frederickson (1949, p. 350) included *A. vigilans* in his new genus *Deckera*; but this cannot be accepted. Even the familial position of *Deckera* is inconclusive; it has been placed in the Solenopleuridae, in the Dokimocephalidae, and recalls a damesellid as well.

#### Group C.

This group includes genera without a cusp, but with a forward-produced angular rim and a preglabellar boss. The genera are *Kujandaspis*, *Kuyandina*? and *Acrocephalaspis* all by Ivshin, 1956, and *Rawlinsella* Shaw, 1956.

#### Group D.

Genera like *Pesaia* Walcott & Resser, *Paracrocephalites* Poulsen, *Cliffia* Wilson, *Kassinus* and 'Tatulaspis' Ivshin, 1956 (possibly its correct name is *Tollaspellus* Ivshin, 1953, according to Ivshin, 1956, footnote, p. 72) are doubtful acrocephalitids and may belong to different families.

*Acrodirotes* gen.nov., as seen from the following discussion, belongs to the Acrocephalitidae but cannot be placed in any of the groups above because it combines a forward arched cranial border with a preglabellar boss, but lacks the angularity of the cranial front; somewhat similar is *Acrocephalites*(?) *rarus* Westergaard (1922, p. 123). The structure of the occipital lobe of *Acrodirotes* is the same as in *Acrocephalina armata* Troedsson, 1937 (pl. 3, fig. 18), but the glabella is quite near to *Acrocephalites* itself. *Acrocephalites stenometopus* (Angelin) as illustrated by Westergaard (1948, pl. 2, figs 9 and 13) has the same granulose ornament, a boss, and a subtruncate glabella with three pairs of furrows, forked in the posterior pair, and *A. stenometopus agnostorum* (ibid., fig. 14) shows the transverse ocular ridges.

*Acrodirotes* resembles the Lonchocephalidae *Weeksina* Resser and *Talbotina* Lochman in the position of the eyes; but this character is too common, and, therefore, no reason to include *Acrodirotes* in the Catillicephalacea.

Genus ACRODIROTES nov.

*Acrodirotes* is a monotypical genus, with *A. fastosa* sp.nov. as its type species. The generic diagnosis coincides with the diagnosis of the type species.

A differential diagnosis in relation to the genera of the Acrocephalididae is contained in the discussion of that family.

It is possible, although rather uncertain, that the type specimen of *Elathriella plebeia* Whitehouse (1939, p. 207, pl. 22, fig. 8) represents a species of *Acrodirotes*: *E. plebeia* has also a granulose test and long palpebral lobes ('more than one-third the length of the cranidium'), placed close to the glabellar middle. Its ocular ridges are, however, narrow and slanting, a boss is apparently absent, and it is, therefore, specifically distinct.

ACRODIROTES FASTOSA sp.nov.

(Pl. 7, figs 6-8; Text-fig. 68)

*Material*: Illustrated and described are three cranidia, all in bituminous limestone, selected from a larger number of specimens.

*Holotype*: The specimen Plate 7, figure 7, CPC 5410, Georgina Limestone, locality G50, 1.8 mm long, is selected as the holotype.

In the following diagnosis characters are listed the combination of which refers to the genus *Acrodirotes* in the first place; it is also a specific diagnosis as regards everyone of the hitherto described species included in the family of the Acrocephalididae.

*Diagnosis*: *Acrodirotes fastosa* is a small trilobite (less than 10 mm long, and a cephalon reaching 2.5 mm) of a ptychoparioid design, having a granulose test, deep furrows, a tapering subtruncate and somewhat depressed glabella about as wide as long; divergent anterior sutures and spatulate posterolateral limbs; long palpebral lobes (0.7 of glabellar length) placed close to and opposite the glabellar middle, and palpebral furrows interrupted in the middle; a high and upward-arched occipital lobe; a forward-arched cranidial margin; and a circular preglabellar boss separated from the glabella by a deep furrow.

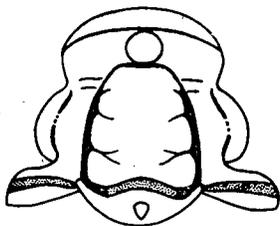


Fig. 68.—*Acrodirotes fastosa* gen. nov., sp.nov., reconstructed from Plate 7, figs 6-8.

*Description*: *A. fastosa* is a small trilobite, with a cranidium not exceeding 2.5 mm in length. The cranidium is subtrapezoidal, with well developed furrows and lobes. The anterior sutures are divergent and almost straight within the brim,

then continue within the border obliquely and in an even curve, to reach the margin a short, but not definable, distance from the midline. The posterior sutures diverge diametrically first and then turn abruptly rearward, delineating spatulate posterolateral limbs. These are geniculate at the prominent fulcra and slope down steeply. The posterior marginal furrows are wide and deep and their adaxial ends of the rear border are pointed. The palpebral lobes are bean-shaped, swollen, and long (0.7 of the glabellar length), and placed opposite the middle of the glabella at a distance of about 0.3 of its width. The interocular cheek is swollen, slopes steeply adaxially, rearward, and forward, and culminates at the middle of the palpebral lobe; at this point the palpebral furrow is almost obsolete, but deepens markedly rearward and forward. The ocular ridges are transverse (not slanting) and broad but inconspicuous. The rim and the brim are about equal in length, together about 0.5 of the glabella and 0.25 of the cranidium in plan. The frontal margin is strongly arched forward, the rim is convex and bears transverse terraced lines. The marginal furrow is deep on the flanks but shallow in the middle opposite the preglabellar boss. The brim is moderately convex, down-sloping, and bears radiating caecal veins. The centre of the brim is occupied by a low circular boss separated from the glabella by a rather deep but short furrow which is the median part of the circumglabellar furrow.

The occipital lobe is convex, wide in the middle, with extenuated and forward-curved flanks that by-pass the posterolateral marginal furrows and almost interrupt the axial furrows. The occipital node is prominent and rises well above the cranial level. The occipital furrow is rather deep at the flanks, and shallow but distinct in the middle.

The axial furrows are very deep to about the ocular ridges, shallow at the anterolateral corners of the glabella, and deep again at its front.

The glabella has slightly convex, almost straight flanks, tapers forward to about 0.7 of its posterior width, and is as long as, or slightly longer than, wide. It is arched longitudinally, somewhat depressed on the top, but steeply sloping on the flanks, and a weak median carina is also apparent. The glabellar front is truncate, but its corners are rounded. Three pairs of glabellar furrows are present, and the posterior ones are forked. The posterior and the middle glabellar lobes are slightly swollen. The surface is granulose.

*Comment on illustrated specimens:*

The three illustrated cranidia originate from locality G50, Georgina Limestone. The two first described specimens are together on a single piece of rock.

The cranidium, Plate 7, fig. 6, CPC 5409, is 1.5 mm long; its left posterolateral limb and the right palpebral lobe are preserved.

The holotype cranidium, Plate 7, fig. 7, CPC 5410, is 1.8 mm long; both posterolateral limbs and the right palpebral lobe are preserved; note the extenuated flank of the occipital lobe and the forked posterior glabellar furrows.

The cranidium, Plate 7, fig. 8, CPC 5411 is 2.2 mm long; it is almost complete and displays in lateral view the rather high occipital lobe.

*Occurrence and age:* *Acrodirotes fastosa* has been found in the Georgina Limestone at localities G48, G49, G50, W1, W15, and W20; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Family OLENIDAE Burmeister, 1843

OLENIDAE, gen. et sp.indet.

(Text-fig. 69)

The Text-figure has been prepared from a fragmentary cranium, CPC 6730, in limestone. The specimen is 1.5 mm long; apparently immature, its generic and specific identity cannot be ascertained. The forward position of the small

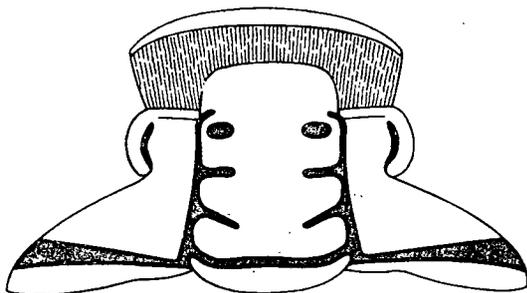


Fig. 69.—*Olenidae*, gen.indet., sp.indet.,  
from specimen CPC 6730.

palpebral lobes and divergent anterior sutures as well as the long glabella indicate a possible affiliation with *Parabolina* rather than with *Olenus*. The test is minutely granulose all over. The glabellar furrows represent the 'full set' of ptychopariids.

*Occurrence and age:* The cranium comes from the Pomegranate Limestone of the De Little Range, locality B537; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*. It is, therefore, one of the oldest known olenids.

Subfamily RHODONASPIDINAE Öpik, 1963

RHODONASPIS LONGULA Whitehouse, 1939

(Pl. 51, fig. 10)

The free cheek CPC 5772, locality W20, is 20 mm long; this specimen was used in the reconstruction of the cephalon of *Rhodonaspis longula* in Öpik (1963, p. 69). The cheek has retained the visual surface of the eye.

*Rhodonaspis longula* localities are: D6, D28, and D29, in the O'Hara Shale; W1, W15, W20, G48, G79, G50, W205, W258, in the Georgina Limestone; B525, in the Pomegranate Creek limestone on Wills Creek.

Family PTEROCEPHALIIDAE Kobayashi, 1935

Subfamily APHELASPIDINAE Palmer, 1960

Genus EUGONOCARE Whitehouse, 1939

*Proaulacopleura* Kobayashi, 1936, is probably the senior synonym of *Eugonocare* Whitehouse, 1939. This synonymy can be concluded from Palmer's (1962, pl. 4, figs 23, 26 and 31) revision of *Proaulacopleura*. According to Palmer (op.cit.) *Proaulacopleura* itself is a subjective synonym of the senior *Aphelaspis* Resser, 1935.

Furthermore, *Olenaspella* Wilson, 1956 (as revised by Palmer) and *Eugonocare* are very close to each other, especially regarding the structure of the cranial rim; it is narrow, elevated and defined by a deep and abrupt marginal furrow. *Olenaspella*, however, is distinguished by its spinose pygidium. A similar structure of the rim, rather unlike that of *Aphelaspis*, is also apparent in *Proaulacopleura*. Hence, the latter genus together with *Eugonocare* should not be included in *Aphelaspis*.

The published information regarding *Eugonocare* is, however, insufficient to decide upon its potential synonymy with *Proaulacopleura*.

Species of *Eugonocare* are Idamean in age and occur in Queensland in the Georgina Limestone, the Pomegranate Limestone, and the O'Hara Shale. According to Thomas & Singleton (1956, p. 158), an undefined species of *Eugonocare* occurs in Victoria, in the Dolodrook Limestone.

#### EUGONOCARE cf. TESSELATUM Whitehouse, 1939

(Pl. 8, fig. 2)

Whitehouse described two species of *Eugonocare*—*tesselatum* and *propinquum*, which have distinctive pygidia and inseparable cranidia; the cranidia here illustrated are immature and no pygidia are available—hence the specific identification of our material remains inconclusive.

The immature specimens illustrate the misleading similarity of *Eugonocare* with adult olenids, as already corrected (Öpik, 1963, p. 59). Palmer (1962, p. F-32; F-35) also refers to the similarity of the Aphelaspidae with Olenidae and *Olenus*; furthermore, generic names like *Olenus* and *Parabolinella* have been applied, and later replaced by *Proaulacopleura* and *Olenaspella*, which also are derived from names of olenids.

The specimens are 2 mm long and are preserved in a fine-grained sandstone as external moulds.

*Occurrence and age:* *Eugonocare* is an Idamean genus, common in the Georgina Limestone. The illustrated specimens, however, come from the Idamean part of the O'Hara Shale, locality D6, Selwyn Range; the sandstone interbed with *Eugonocare* and other Idamean fossils is about 70 feet above the Mindyallan 'lower chert bed' in the same section.

#### PTYCHOPARIINA FAMILIAE INCERTAE

Genus ADELOGONUS nov.

*Adelogonus* is a monotypical genus, with *A. solus* as the type species.

*Adelogonus* is distinguished by the combination of the following characters: (1) large triangular posterolateral limbs, (2) narrow interocular cheeks (about 0.3 of glabellar width), (3) narrow palpebral lobes of a medium size (0.4 of glabellar length) placed opposite the glabellar midpoint, (4) narrow, well-defined, and slightly upturned rim, (5) distinct but short brim, (6) forward projected cephalic pleural lobes defined by a pair of shallow convex furrows (frontal limits of the cephalic pleural lobes), (7) forked ends of the occipital furrow not reaching the axial furrows, and (8) strongly tapering glabella with concave flanks in its anterior half, angular and bluntly rounded in front.

*Familial classification:* Some similarity with *Chuangia* Walcott suggests a comparison with the Leiostegiacea; but this remains inconclusive because of the peculiar structure of the frontal area, the rather large posterolateral limbs, and the strongly tapering glabella of *Adelogonus*. Equally inconclusive is a comparison with the Damesellacea because the pygidium of *Adelogonus* is unknown. The nearest genus, however, is *Chelidonocephalus* King, 1937, of which two interpretations have been published: in the first, in Harrington et al. (1959, p. 0241), it is placed in the Alokistocaretidae, and in the second (Kobayashi, 1962) in the Asaphiscidae. *Adelogonus* differs from *Chelidonocephalus* in having a much shorter frontal area, and larger posterolateral limbs; furthermore *Chelidonocephalus* lacks palpebral furrows, which are present in *Adelogonus*. The genera are co-familial.

ADELOGONUS SOLUS sp.nov.

(Pl. 8, fig. 3; Text-fig. 70)

*Material:* The material consists of the illustrated cranidium (the holotype), CPC 5415.

*Diagnosis:* The diagnostic characters are given in the description of the genus; a differential diagnosis is superfluous because of the isolated position of *A. solus* within the suborder Ptychopariina.

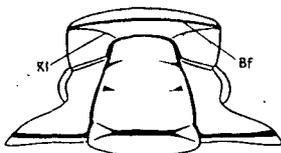


Fig. 70.—*Adelogonus solus* gen. nov., sp.nov., from Plate 8, fig. 3. Bf—marginal frontal furrow; Kl—frontal limit of cephalic pleural lobe.

*Description:* The holotype cranidium is 6.0 mm long and, therefore, relatively large. The ocular ridges are distinct, two pairs of glabellar furrows are indicated, and the test is minutely and densely granulose.

*Occurrence and age:* The cranidium of *A. solus* comes from the O'Hara Shale ('lower chert bed'), locality D29; its age is the Zone of *Glyptagnostus stolidotus*.

Genus CERMATASPIS nov.

The type species of *Cermataspis* is *C.abundans* sp.nov.

*Diagnosis:* *Cermataspis* gen.nov. is a trilobite of a ptychopariacean design distinguished by relatively small blade-like posterolateral limbs, divergent anterior sutures cutting the rim in even curves without perceptible points of interception of the margin, convex brim defined by a broad marginal furrow, long palpebral lobes close to the glabella, and a strongly tapering glabella with two pairs of lateral furrows.

*Differential diagnosis:* *Cermataspis* may be related to *Acrodirotes* gen.nov., but lacks the frontal boss of the latter; if these genera are really affiliated *Cermataspis* also should be placed in the Acrocephalitidae.

CERMATASPIS ABUNDANS sp.nov.

(Pl. 7, fig 9; Pl. 8, figs. 1 and 6; Text-fig. 71)

*Material:* Silicified cranidia of *C. abundans* occur in almost all sites of the Mungerebar Limestone (Zone of *Erediaspis eretes*); three cranidia are illustrated.

*Diagnosis:* The specific diagnosis is the same as that of the genus.

*Holotype:* Is the cranidium, Plate 8, figure 1, CPC 5413.

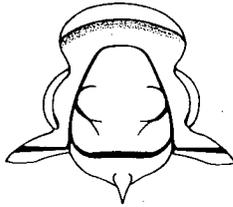


Fig. 71.—*Cermataspis abundans* gen.nov., sp.nov., from Plate 8, figs 1 and 9.

*Supplementary description:* The interocular cheek is narrow (about 0.25 of glabella), the palpebral lobes, placed opposite the glabellar midpoint, are of about 0.5–0.53 of glabellar length; the frontal area, about 0.35 of glabellar length, slopes gently forward. The axial furrows are deep and surround the evenly rounded glabellar front. The occipital spine is submarginal.

*Comment on illustrated specimens:*

The holotype cranidium, locality G417, is 3.0 mm long; the glabella is somewhat pyriform.

The cranidium, Plate 8, fig. 6, locality G417, CPC 5419 is 3.2 mm long. The rim is relatively long (longitudinally) and the marginal frontal furrow rather conspicuous because of the coarse granularity of the silica.

The fragmentary cranidium, Plate 7, fig. 9, locality G8, CPC 5412, is 2.0 mm long. It shows the posterolateral limb.

*Occurrence and age:* *Cermataspis abundans* gen.nov., sp.nov., is very common in the Mungerebar Limestone, in the Mindyallan *Erediaspis eretes* Zone (localities G8, G119, G130, G417, and G429); it is rare in the Zone of *Cyclagnostus quasi-vespa* (locality G128).

Superfamily CATILLICEPHALACEA Raymond, 1938

As mentioned already in the discussion of the Solenopleuridae, the families Catillicephalidae and Lonchocephalidae cannot be placed in the Solenopleuracea, which is a synonym of Ptychopariacea. At the same time the Lonchocephalidae and the Catillicephalidae are closely related to each other and represent a taxon of a higher rank.

The following system is adopted here :—

Superfamily: Catillicephalacea.

Families: Catillicephalidae; Lonchocephalidae, with the subfamilies Lonchocephalinae and Avonininae.

Within this system the Avonininae, if necessary, can be regarded as an independent family Avoninidae; furthermore, the system can be modified as follows: the superfamily Catillicephalacea could be considered to contain a single Family—Catillicephalidae, consisting of three subfamilies (Catillicephalinae, Lonchocephalinae, and Avonininae).

Described here are the following:—

Lonchocephalidae: *Lonchocephalus* sp.nov.; *Interalia serena* gen.nov. sp.nov.; *Agelagma quadratum* gen.nov. and sp.nov.; *Agelagma laticeps* sp.nov.; *Avonina* sp.nov. (subf. Avonininae); ?Lonchocephalidae, gen.nov. et sp.nov.

Catillicephalidae: *Catillicephala* sp.indet.; Catillicephalidae, gen.nov. et sp.nov.; *Onchonotellus offula* sp.nov.

### Family CATILLICEPHALIDAE Raymond, 1938

#### Genus CATILLICEPHALA Raymond, 1938

CATILLICEPHALA sp.indet.

(Pl. 9, fig. 8)

The illustrated cranidium, CPC 5427, is 2.2 mm long; it is a mould in friable silica. Enough of it is preserved to recognize its generic identity, but the fragment is insufficient for specific identification.

*Occurrence and age:* Fragmentary cranidia of this *Catillicephala*, including the illustrated specimen, occur in the O'Hara Shale ('lower chert bed') at locality D29. The age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Genus ONCHONOTELLUS Lermontova, 1956

The generic name *Onchonotellus* Lermontova, 1951, refers to *Solenopleura subcincta* Lermontova, but only conditionally: 'in case—if the discovery of complete shields of the given species would demonstrate its substantial difference from *Solenopleura* s. str. the new generic name *Onchonotellus* gen.nov. could be proposed for it' (Lermontova, 1951, p. 25 transl. A.A.Ö.). So Lermontova coined a new word but not a new taxonomic name.

Ivshin (1956, p. 26) applied the word '*Onchonotellus*' as a taxonomic name; he is, therefore, the publishing agent, and the full reading should be: *Onchonotellus* Lermontova, 1956 (in Ivshin, 1956, p. 26). This is, however, disputable because Lermontova's provision regarding the discovery of complete shields of *Solenopleura subcincta* was not observed by Ivshin and the name therefore in its taxonomic meaning should not be credited to Lermontova at all. Hence Ivshin, 1956, may be the legitimate 'taxonomic' author of the name *Onchonotellus*. The problem of authorship and date cannot be legally and finally solved yet; it is therefore, convenient to resort to 'custom and usage' as introduced by Ivshin, in regarding Lermontova, 1956 (not 1951!) as the nomenclatural author of *Onchonotellus*. Ivshin (op. cit.) and Tchernysheva et al. (1960, p. 119) included *Onchonotellus* in the family

Solenopleuridae—a classification incompatible with their own concept of that family. More suitable is the family Catillicephalidae Raymond, the concept of which remains unchanged when *Onchonotellus* is included.

*Diagnosis* (emend.): *Onchonotellus* is a genus of the Catillicephalidae without glabellar furrows and with relatively wide interocular cheeks; distinguished by its well developed prominent roll-like cephalic rim and barrel-like glabella.

ONCHONOTELLUS OFFULA sp.nov.

(Pl. 9, fig. 7)

*Material*: The illustrated holotype cranidium, CPC 5426, locality G429, is 2.1 mm long; it is silicified.

*Diagnosis*: *Onchonotellus offula* sp.nov. is distinguished by its very narrow (sagittally) rim and the position of the palpebral lobes in front of the glabellar midpoint.

*Differential diagnosis*: In the described species (*subcincta* Lermontova, 1951, plate 5, figure 5; and *abnormis* Ivshin, 1956) the rim is thicker and the palpebral lobes are opposite the glabellar midpoint. Both these forms are also Upper Cambrian, but are younger than *O. offula*.

In passing, *O. abnormis* has in its thorax a wide axial lobe and nine segments—a good number for Catillicephalidae but too small for a solenopleurid. The Middle Cambrian *Catillicephalites marginatus* Rasetti (1963; especially pl. 70, fig. 5) also has a strong and narrow rim, but its palpebral lobes are larger, and closer than in *O. offula* to the glabella.

*Description*: The anterior sutures converge strongly and cut the rim obliquely. The posterior sutures are relatively straight, delineating the triangular down-sloping posterolateral limbs. The abaxial ends of the posterior marginal furrow are curved forward, the posterior border widens rapidly and the fulcral points are angulate and prominent. The palpebral lobes are small (about 0.15 of glabellar length) and oblique.

The axial furrows are rather deep; less deep but still distinct is the occipital furrow. The crescentic occipital lobe bears a node near its margin. The ovate, barrel-like glabella, slightly longer than wide, is very tumid and elevated above the down-sloping pleural lobes.

*Occurrence and age*: *Onchonotellus offula* occurs in the Mungerebar Limestone at localities G429 and G417 (fragments). Its age is the Mindyallan Zone of *Erediaspis eretes*.

CATILLICEPHALIDAE, gen.nov. et sp.nov.

(Pl. 9, fig. 5)

Only one fragmentary cranidium CPC 5424, a mould in limestone, is available. It is peculiar in having a very narrow (transversely) occipital lobe and fixed cheeks intruding between the glabella and that lobe. It appears that the posterior border

is not connected with the axial furrow at the flanks of the occipital lobe. Two pairs of glabellar furrows are apparent. The palpebral lobe is narrow, rather oblique, close to the glabella and placed opposite its anterior half.

*Occurrence and age:* The illustrated specimen comes from the Georgina Limestone, locality W15; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Family LONCHOCEPHALIDAE Hupé, 1953

Subfamily LONCHOCEPHALINAE

Genus LONCHOCEPHALUS Owen, 1852

LONCHOCEPHALUS sp.nov.

(Pl. 10, fig. 12)

The illustrated silicified cranidium, CPC 5439, is 2.3 mm long to the tip of the occipital spine, and 1.5 mm without the spine. It is distinguished by its strongly forward-arched front, rapidly tapering glabella, tumid posterior glabellar lobes, straight and deep middle glabellar furrows, rather weak ocular ridges which are masked by the whitening, and by the relatively wide interocular cheeks. None of the species of *Lonchocephalus* listed by Rasetti (1959, p. 601) appear sufficiently close to warrant further comparison.

*Occurrence and age:* The illustrated cranidium comes from the Georgina Limestone, locality G49. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Genus INTERALIA nov.

The genus *Interalia* is monotypical, with *I. serena* as the type.

*Diagnosis:* *Interalia* refers to Lonchocephalidae having a parallel-sided glabella, a down-sloping rimless frontal border, glabellar furrows not connected with the axial furrows, and a rather convex cephalon.

*Differential diagnosis:* A rimless and narrowing frontal border is present also in *Amiaspis* Lochman, 1944, in which the palpebral lobes are also placed forward; but *Amiaspis* is distinguished by its suboval and tapering glabella from *Interalia*, whose glabella is parallel-sided. The parallel-sided glabella of *Interalia* is rather similar to *Welleraspis* Kobayashi; but *Welleraspis* has a narrow brim and a well developed rim, and its palpebral lobes are placed about opposite the glabellar middle. It appears that *Interalia* is intermediate between *Amiaspis* and *Welleraspis*, and can be regarded, if necessary, as a subgenus of either of these genera.

*Interalia* is about one zone older than *Amiaspis* and the earliest known species of *Welleraspis*; but being rimless it cannot be regarded as the ancestor of these forms.

INTERALIA SERENA sp.nov.

(Pl. 10, figs 6, 7)

*Material:* Two cranidia, representing the better preserved material, are illustrated; all available specimens are silicified.

*Holotype:* The cranidium, Plate 10, figure 7, CPC 5434, locality G119, is almost complete and is therefore selected as the holotype.

*Diagnosis:* The generic diagnosis serves as the diagnosis of the species *I. serena*.

*Description:* As usual in the Lonchocephalidae, *Interalia serena* is a small trilobite; all examined cranidia are small, but belong to mature specimens.

The cranidium is very convex, with a prominent glabella, steeply down-sloping ('hanging') posterolateral limbs, and down-sloping slightly convex frontal border. The posterolateral limbs are large, triangular, with a posterior swing; their border is very narrow, almost pointed adaxially and widens in the opposite direction. The tips of the posterolateral limbs are rounded but the end of the furrow does not turn forward. The posterior sutures are relatively straight, running down and rearward.

The glabella is parallel-sided, tumid, and slightly longer than wide, with a rounded, steeply down-sloping front. Two pairs of glabellar furrows are discernible; the anterior furrows are shallow elongate pits, and the posterior are curved rearward. Neither of the furrows is connected with the axial furrows.

The test is smooth, but the frontal border appears to be delicately venulose in some specimens.

The anterior sutures, also almost straight, converge forward and cut the margin about opposite the glabellar corners; the frontal margin is only slightly arched forward; a marginal furrow and a rim are absent. The frontal area is trapezoidal and narrows rapidly forward.

The palpebral lobes are small, about 0.23 of glabellar length, rather oblique, and placed opposite the middle of the anterior half of the glabella; the interocular cheek is narrow, slightly less than 0.25 of glabellar width; the ocular ridges are distinct. The occipital lobe is depressed below the rear of the glabella and extended into a spine. The axial furrows are deep and surround the glabella along its flanks and front.

*Comment on illustrated specimens:*

The holotype cranidium is 3.4 mm long, including the spine; the glabella is 2.0 mm long. The front and the right palpebral lobe are well preserved.

The cranidium, Plate 10, fig. 6, CPC 5433, locality G417, is 3.3 mm long as preserved. The test along the margin has crumbled away.

*Occurrence and age:* *Interalia serena* sp.nov. comes from the Mungerebar Limestone, localities G119 and G417. Its age is the Mindyallan Zone of *Erediaspis eretes*.

Genus AGELAGMA nov.

The type of *Agelagma* is *Agelagma quadratum* sp.nov.

*Diagnosis:* *Agelagma* gen.nov. refers to Lonchocephalidae with a well developed brim and rim, without occipital spine, with relatively wide interocular cheeks and the glabellar furrows developed as pits. The cranidial front is straight.

*Differential diagnosis:* *Glaphyraspis* Resser and *Glyptometopus* Rasetti are somewhat comparable with *Agelagma* because of the absence of an occipital spine and the relative forward position of the eyes. In *Glyptometopus* as recently revised by Rasetti (1961) the front is arched forward, but in *G. ovata* Rasetti (op.cit.) it is straight, almost as straight as in *Agelagma*. In *Glyptometopus*, however, the glabellar furrows are furrows connecting the axial furrow and not isolated pits, and the interocular cheeks are less wide than in *Agelagma*.

Shallow pits are present in *Interalia* gen.nov., but it has an occipital spine, its interocular cheeks are narrow and the frontal area has a structure different from *Agelagma*.

Two new species are assigned to the genus: *Agelagma quadratum* and *Agelagma laticeps*.

AGELAGMA QUADRATUM sp.nov.

(Pl. 10, figs 1-3; Text-fig. 72)

*Material:* Three crania are illustrated selected from a number of less well-preserved materials. All specimens are silicified.

*Holotype:* The cranium, CPC 5429, Plate 10, figure 2, is selected as holotype; its occipital lobe is incomplete. It is 1.7mm long.

*Diagnosis:* *Agelagma quadratum* is distinguished by its parallel-sided glabella and wide interocular cheeks.

The differential diagnosis is given under *A. laticeps* sp.nov.

*Description:* The anterior sutures converge strongly, cutting evenly, in a gentle curve, the brim and the rim; the posterior sutures are relatively straight and delineate triangular, steeply downsloping, posterolateral limbs. The rather tumid interocular cheeks are wide in the rear (more than half the glabella) and narrower in the front (0.35 the glabella), owing to the rather oblique set of the palpebral lobes, which are placed well in front of the glabellar midpoint. The ocular ridges are strong and arched forward; the palpebral lobes are narrow crescents about 0.4 of glabellar length. The frontal area consists of an elevated and rearward expanded rim and a moderately convex brim. The occipital lobe is relatively large, triangular, and bears a small node. The occipital and axial furrows are rather deep; the glabella is parallel-sided, with a bluntly rounded front. Two pairs of glabellar furrows are present: the anterior furrows are deep rounded pits and the posterior are deep pits connected with the axial furrows. The test is granulose.

*Comment on illustrated specimens:*

The cranium, Plate 10, fig. 1, CPC 5428, locality G114, is 1.7 mm long. The test is missing, but otherwise it is complete.

The holotype cranium (a silicified test) locality G417, shows the structure of the frontal area and some of the original granulation.

The cranium Plate 10, fig. 3, CPC 5430, location G417, has its occipital lobe preserved; the glabella is somewhat deformed and not quite parallel-sided. It is 2.0 mm long.

*Occurrence and age:* *Agelagma quadratum* occurs in the Mungerebar Limestone, at localities G114 and G417; its age is the Mindyallan Zone of *Erediaspis eretes*.

AGELAGMA LATICEPS sp. nov.

(Pl. 10, figs 4 and 5; Text-fig. 73)

*Material:* Only the two illustrated specimens are available.

*Holotype:* The cranium Plate 10, figure 5 and Plate 46, figure 5, CPC 5432, is selected as the holotype; it is fragmentary but allows for a complete reconstruction (Text-fig. 73).

*Diagnosis:* *Agelagma laticeps* sp.nov. is distinguished by its forward expanding glabella, relatively narrow interocular cheeks, small palpebral lobes and crescentic occipital lobe.

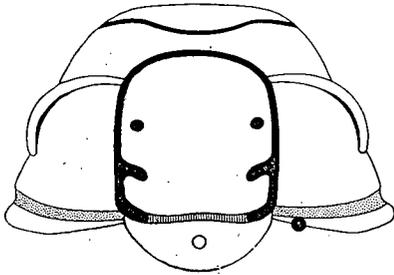


Fig. 72.—*Agelagma quadratum*, gen.nov., sp.nov., combined from Plate 10, figs 1 and 2.

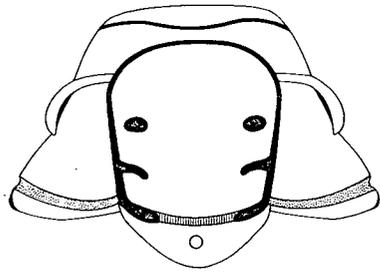


Fig. 73.—*Agelagma laticeps* sp.nov., combined from Plate 10, figs 4, 5.

*Differential diagnosis:* *A. laticeps* differs from the type species of the genus (*Agelagma quadratum*) by all the characters mentioned in the diagnosis. The shape of the glabella recalls *Pemphigaspis* Hall, which also has pit-like glabellar furrows in one species (*P. inexpectans* Lochman; see Palmer, 1951), but possesses a different, reduced frontal area.

*Description:* The palpebral lobes are about 0.3 of the glabellar length, the interocular cheek is narrow, 0.2 in front, and 0.4 in its rear as compared with the width of the glabella. The posterior glabellar furrows are elongate deep pits. The test is granulose.

*Comment on illustrated specimen:*

The holotype cranidium, locality G119, is 2.4 mm long. The fragmentary cranidium Plate 10, fig. 4, CPC 5431, locality G145, belongs to a larger specimen, probably about 3.0 mm in length. It preserves some of the granulations of the test.

*Occurrence and age:* *Agelagma laticeps* sp.nov. comes from the Mungerebar Limestone, localities G119 and G145; its age is Mindyallan, the Zones of *Erediaspis eretes* (at G119) and *Cyclagnostus quasivespa* (at G145).

Subfamily AVONININAE Lochman 1963

Genus AVONINA Lochman, 1936

AVONINA sp.nov.

(Pl. 9, fig. 6)

*Material:* Only the illustrated specimen, CPC 5425, has been found as yet. It is complete, but its glabella is crushed, preventing a conclusive comparison with *Avonina bizarria* Lochman, the type, and hitherto only known, species of the genus; it occurs in the Bonnetterre Dolomite of Missouri.

*Comparison with Avonina bizarria:* In *A. bizarria* no occipital spine exists; in our specimen, however, a rather strong occipital spine is present. It is also probable that in the new species the glabella is pyriform, whereas in *A. bizarria* (Lochman, op. cit., Pl. 9, figs 22–26) the glabella has subparallel flanks.

*A. bizarria* and *Avonina* sp.nov. have several characters in common: (1) the tumid glabella without furrows, (2) the course of the sutures, (3) the position of the palpebral lobes, (4) the rimless brim, and (5) the spines, which may or may not be genal spines. These spines without a free cheek are insufficient to decide whether *Avonina* is a proparian or an opisthoparian trilobite, though the former is more likely.

The pygidium and the thorax are preserved in *Avonina* sp.nov. The pygidium is triangular, with three pairs of pleurae and three axial annulations. The pygidial border is vertical with its upper margin angulate. It resembles *Lonchocephalus*, *Glaphyraspis*, and *Terranovella*; but its plump and parallel-sided axial lobe reminds one of the pygidium of a catillicephalid. The thorax consists of seven segments with broad pleural furrows and with an axial spine on the fifth segment.

*Familial classification:* The cephalic brim, and the structure of the thorax and the pygidium suggest the family Lonchocephalidae; the presence of genal (?) spines does not seem sufficient reason for maintaining a separate family (Avoninidae), but a subfamily Avonininae Lochman of the Lonchocephalidae seems acceptable.

*Occurrence and age:* *Avonina* sp.nov. was found in the Georgina Limestone at locality W20; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### ?LONCHOCEPHALIDAE gen.nov. et sp. nov.

(Pl. 10, fig. 8)

The illustrated fragmentary silicified cranidium, CPC 5435, is rather large for a lonchocephalid: with the spine the fragment is about 40 mm long. The glabella is elliptical and very tumid, and has three pairs of shallow and short lateral furrows. The occipital lobe, apparently almost confluent with the glabella, bears a curved long spine. The depressed fixed cheeks are wide and moderately convex. The glabella is granulose, but the cheeks are coarsely pustulose.

*Occurrence and age:* The fragment was found in the Mungerebar Limestone, near locality G119; its age is the Mindyallan Zone of *Erediaspis eretes*.

#### Superfamily ANOMOCARACEA Poulsen, 1927

##### Family AURITAMIDAE nov.

##### Subfamily AURITAMINAE

*Diagnosis:* Auritamidae are Anomocaracea with a long parallel-sided glabella and a relatively small pygidium; in the type genus (*Auritama* nov.) the pygidium is provided with marginal spines.

*Differential diagnosis:* the Anomocaridae are distinguished by their large pygidia—they are isopygous; but as the ventral cephalic structure of the Anomocaridae is unknown they cannot be fully compared.

The Auritamidae and the Anomocaridae are affiliated at the superfamilial level because (1) both families include forms with bacculae, (2) *Anomocaroides* Lermontova (Anomocaridae) has a parallel-sided glabella reminiscent of *Auritama*, and (3) the eyes are large in all Anomocaracea.

The subfamily Auritaminae contains *Auritama aurita* sp.nov., *A. trilunata* sp.nov., and *A. expansa* sp.nov.

*Metopotropis* gen.nov. is regarded as subfamiliae incertae because its pygidium is unknown; *Peichiashania* Chang, however, whose two Australian new species (*lunulata* and *pelta*) are rather close to *Auritama*, is tentatively retained in the Auritaminae; their pygidia are unknown as yet.

The following overseas genera belong to the Auritamidae: (1) *Westergaardella*, Kobayashi, 1962, based on *Conocephalina olenorum* Westergaard, 1922; it is distinguished by a rather small and non-spinose pygidium; (2) *Chondranomocare* Poletaeva, *Pseudanomocarina* Tchernysheva, and *Shoriella* Sivov (see Tchernysheva et al., 1960).

These forms cannot be placed in the subfamily Auritaminae; but whether they represent one or more subfamilies is not yet clear.

Closest to *Auritama* is the early Upper Cambrian *Westergaardella olenorum* (Westergaard, 1922) whose adult cranidia can be compared with immature specimens of *A. trilunata*: both have a relatively long brim. In *W. olenorum* the long arcuate palpebral lobes (0.8 of glabellar length) placed in the rear of, and close to, the glabella, the subcylindrical, long, and furrowless glabella, the divergent anterior sutures, and the structure of the doublure of the free cheeks, possibly indicating the presence of a median suture, are characters of the Auritamidae.

#### Genus AURITAMA nov.

The type of the genus is *Auritama aurita* sp.nov.

Two other species, *A. trilunata* sp.nov. and *A. expansa* sp.nov., are described. In selecting the type of the genus preference was given to *A. aurita* because a sample of cranidia, free cheeks, and pygidia of this species was obtained from a few square feet of a limestone bed about three inches thick at locality W18 in the Georgina Limestone; no other allied trilobites are present, so that the associated pygidia are certainly conspecific with the cephalic remains.

*Diagnosis:* *Auritama* gen.nov. refers to species of the Auritamidae distinguished by pygidia with marginal spines.

This rather condensed diagnosis needs further comment. The species of the genus *Auritama* have the following characters in common: (1) a semicircular cephalon of low convexity; (2) a wide and flat marginal border; (3) a long straight-sided glabella with a long preocular part (about 0.3 of glabellar length); (4) arcuate palpebral lobes, large (0.7 to 0.8 of glabellar length), opposite the posterior two-thirds of the glabella, with the tips close to the glabella; (5) divergent anterior sutures which, within the border, are arcuate and converge to the midline; (6) bacculae; (7) a subcephalic frontal median suture; (8) a pygidium having a tapering long

axis of four to five annulations; (9) two to three pleural ribs; (10) a broad and depressed pygidial border fringed by nine or ten rearward-directed flat marginal spines; (11) a rather wide pygidial doublure; (12) falcate pleural tips in the thorax; (13) distinct and long pleural furrows which are angular in longitudinal section; (14) well elevated propleural crests or propleural caecal veins, which are also developed in the anterior part of the pygidium; (15) facets in the thorax and the pygidium; and (16) retention of the cornea by moults of the free cheeks.

The pygidium is relatively small, estimated as between 0.3 and 0.4 of the cephalic length. The estimate is based on the combined occurrence of cranidia and pygidia of *A. trilunata* showing the proportions given above, and on the fact that the pygidia have only two to three pleural ribs. All trilobites with a small number of pygidial pleural ribs totally filling the space of the pygidial pleural lobes have relatively small pygidia. Such pygidia cannot be large because the pleural ribs can be no wider, and are usually narrower, than the segments of the thorax. For example, seven to nine pygidial ribs occur in anomocarids whose pygidium and cephalon are of equal length and whose pygidium is as long as seven segments of the thorax; hence, the pygidium of *Auritama* with its three ribs is less than half the cephalon.

The truncation of the cranidial front may not be diagnostic because it occurs in other families as well, but it is, nevertheless, an important character of *Auritama*. The truncated part represents the marginal rostral suture which is present in *A. trilunata*, in *A. expansa*, and in early instars of *A. aurita*.

The structure of the free cheeks of *A. trilunata*, doublures of which have rounded corners, indicates the presence of a rather small triangular plate, the rostellum. The rostellum is a reduced remnant of a rostral shield enclosed by sutures. It is a vanishing feature, as seen in *A. aurita*, where in larger cranidia the front is not truncated but evenly rounded. Furthermore, the rostellum is not functional, because its presence or absence does not affect the mechanics of moulting. Its sporadic presence or absence in *A. aurita* and persistence in *A. trilunata* is of some specific significance, of course. *Auritama* is an early example of how a rostral shield, after being reduced to a rostellum, disappears, and is replaced by a median subcephalic suture. Examples of geologically later repetitions of a similar process are probably represented by the Pterocephaliidae and Housiidae, as can be concluded from Palmer's (1960) diagrams. A rostellum is probably present also in *Griphasaphus* gen.nov. and may be taken as a plausible explanation of the origin of the median subcephalic suture of asaphids.

*Auritama* can be compared in several characters with asaphids, as for example with *Griphasaphus griphus* sp.nov. These characters are (a) the long subcylindrical glabella with a long preocular part, (b) wide border (c) strongly arcuate anterior sutures, and (d) the median subcephalic suture. A lesser, vague, similarity appears to be present with *Proceratopyge*. Among the Pterocephaliidae, *Sigmocheilus serratus* Palmer (1960, p. 89) has a pygidium resembling *Auritama*; but the cranidial features of *Sigmocheilus* (short glabella, small subcentral eyes, subparallel anterior sutures) are rather different and even a superfamilial affiliation therefore seems improbable.

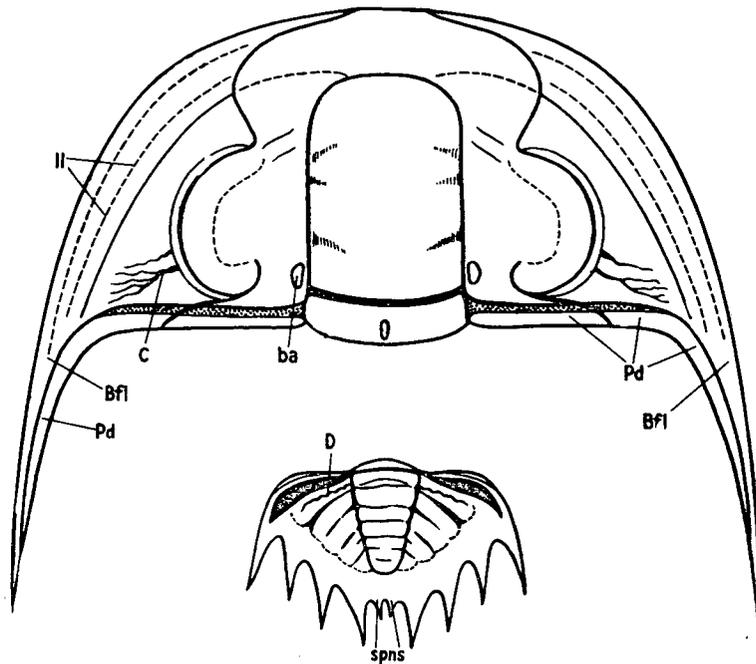


Fig. 74.—*Auritama aurita* gen.nov., sp.nov., combined from Plate 13, figs 9x12, and Plate 14, figs 1, 2—ba—baccula (—ae); Bfl—flange of genal spine and border; C—principal genal vein; D—pygidial caecal vein; Il—lines on border; Pd—posterolateral (pleuro-occipital) border, extends on the spine; spns—paired terminal spines.

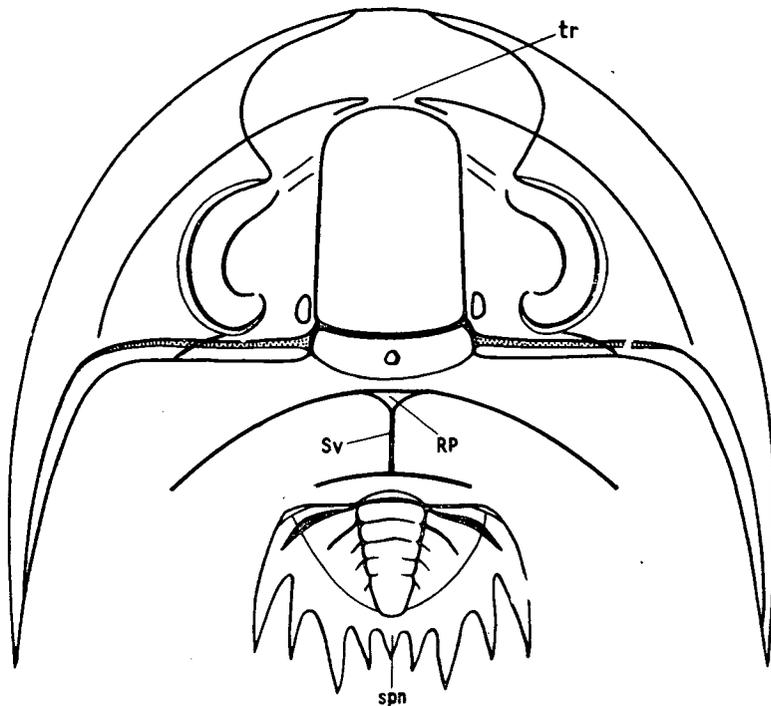


Fig. 75.—*Auritama trilunata* sp.nov. combined from Plate 14, fig. 6, and Plate 15, figs 1, 2, 5, 7 and 8. RP—rostellum; spn—solitary terminal spine; Sv—ventral median suture; tr—plectrum.

AURITAMA AURITA, sp.nov.

(Pl. 13, figs 9-13; Pl. 14, figs 1 and 2; Text-fig. 74)

*Material:* Numerous cranidia, pygidia, and other parts found in a thin bed of limestone at locality W18. Selected for description and illustration are four cranidia, one free cheek, one segment of the thorax and two pygidia.

*Holotype:* The cranidium, Plate 13, figure 12, CPC 5467, is selected as the holotype in preference to the largest available (Pl. 13, fig. 10), which is distorted; the two other cranidia are of the same proportions as the holotype and provide for supplementary observations.

*Diagnosis:* *Auritama aurita*, the type of its genus, is distinguished by the effacement of the palpebral furrows and the cranidial marginal furrow, by the reduction of the brim, by the length of the anterior border (no more than 0.35 of the glabellar length), by its strictly parallel-sided glabella, by its elongate occipital node, by the absence of the frontal truncation of the cranidium in older specimens, and by a pygidium with ten marginal spines of which the first eight are subequal in length, and a pygidial axis with five to six annulations.

*Description:* The cephalon is semicircular, and somewhat lunate considering the rearward swept genal spines. The convexity is low, marked by a peripheral slope of the shield toward the border, which is almost flat and sloping at a low angle outward. The glabella rises slightly above the level of the horizontal palpebral lobes; the interocular cheeks slope gently in adaxial direction. The eyes are low, and the cornea is quite convex (convex outward in radial section). The test is thick and smooth, without any ornament.

The free cheek is distinct by its flat and forward expanding border and the absence of an incised marginal furrow, which is replaced by an angular change of slope. The border bears a pair of faint peripheral lines. The outer edge of the genal spine is as flat as the border, whereas its adaxial edge is convex and thick and inseparable from the posterolateral border. The cornea of the eye is rather low and has a low base. About two wiggly caecal veins arise at the eye toward the corner of the cheek. These are the principal genal veins (Text-fig. 53) of opisthoparian trilobites. Besides the usual venulosity of the cheeks (which incidentally is absent in *A. aurita*), similar principal veins occur in many genera of diverse families of ptychoparioids. The principal genal veins are seen, for example, in *Litocephalus* (Palmer, 1960, pl. 8, fig. 16), in *Diplapotokephalus* (Rasetti, 1943, pl. 19, fig. 7), but also in some dolichometopids.

The cranidium is cruciform, wider than long across the palpebral lobes and between the posterolateral tips, but narrower in the front. Its width in the front is 1.4 (variable between 1.36 and 1.45) of glabellar length and 0.9 of cephalic length; across the palpebral lobes it is about 1.1 of the length of the cephalon. In terms of the glabellar length the frontal border is around 0.3 to 0.35 (0.4 to 0.5 in *A. trilunata*) and the palpebral lobe consistently 0.7 long. The interocular cheek together with the palpebral lobe varies between 0.75 and 0.9 of glabellar width.

The anterior sutures diverge first, then, within the border, swing adaxially, reaching the margin near the midline. In younger specimens, the frontal margin between the ends of the dorsal sutures is straight and the cranidial front truncate,

indicating the marginal position of the rostral suture. In older specimens, however, no truncation is apparent, the curves of the sutures continue to the midline, and a marginal rostral suture cannot be distinguished; hence the rostellum may have also disappeared in older specimens. The posterior sutures diverge greatly and delineate rather narrow (sagittally) and small posterolateral limbs.

The rim is flat, crescentic, the marginal furrow and plectrum are absent or vestigial, and there is practically no brim in front of the glabella. The posterior tips of the large and flat palpebral lobes are thickened, uplifted 'ear lobes'; the palpebral furrow is vestigial in younger, and absent in older specimens; the ocular ridges are wide and low. The axial furrows are straight and relatively deep, and the circum-glabellar furrow in smaller specimens is deepened in the middle.

The occipital furrow is distinct and evenly deep, the occipital lobe widens rearward, being along its rear wider than the glabella; it bears an elongate median node. The glabella is parallel-sided and not tapering as in *A. trilunata*, long, as wide as 0.7 of its length, with a long preocular part of 0.3 to 0.35 of the total length of the glabella. Three pairs of obscure glabellar furrows are present; the posterior furrows are oblique and stronger than the others. The bacculae are small, inconspicuous, close to the glabella, and placed just in front of the ends of the occipital furrow.

The segments of the thorax have falcate pleural tips, and distinct long pleural furrows angular in longitudinal (sagittal) section; the propleuron is elevated with a rather distinct caecal vein on its crest, but the opisthopleuron is flat and depressed, and bears a weak vein near its posterior margin.

The pygidium is subtriangular, as long as about 0.6 of its width, with rounded, faceted anterolateral corners; the margin bears five pairs of retral spines; the anterior four pairs of spines are subequal in length, decreasing only slightly and evenly in size; the posterior spines are rather short and close together. The border is wide and slightly concave, but a marginal furrow is absent. The pleural lobes are moderately convex, provided with about three pairs of broad ribs and pleural furrows which become rather indistinct toward the rear. The anterior pleural furrow is wide and angular in section, the foremost propleuron rises high with a caecal vein on its crest, and another, weaker vein may be present on the next pleural rib. The pygidial axis is about as wide as a pleural lobe, elevated, evenly tapering to a rounded point, and consists of five to six inconspicuous annulations and a terminus. In specimens with a narrower border (Pl. 14, fig. 1) the axis has six, and with a wider border (Pl. 13, fig. 13) five, annulations. The axial furrows are distinct and relatively deep, but the transverse furrows on the axis are shallow, but transcurrent. Chevron terraced lines on the anterior spines of the pygidium are the only ornament; the test is otherwise smooth.

*Comment on illustrated specimens:*

The cranium, Plate 13, fig. 9, CPC 5464, is 6.0 mm long, and the smallest available; its frontal border and the palpebral lobes are damaged. The glabella has a weak keel, three pairs of rather shallow lateral furrows (which are better visible in illumination from the rear), distinct ocular ridges, barely indicated palpebral furrows, and small bacculae.

The cranium, Plate 13, fig. 11, CPC 5466, is 6.5 mm long, and consists of translucent calcite, showing the traces of the plectrum and the frontal and palpebral furrows, which are on the cast

stronger than on the surface. The glabellar front owing to accidental distortion is much more rounded than in the other specimens. The frontal truncation is well visible in this specimen.

The holotype cranidium, Plate 13, fig. 12, CPC 5467, is 7.1 mm long; its thick opaque test is almost devoid of traces of the frontal and palpebral furrows and only the posterior glabellar furrows are indicated. The frontal truncation is barely visible.

The cranidium, Plate 13, fig. 10, CPC 5465, is 8.5 mm long; its frontal border is relatively short; the frontal furrow and the posterior glabellar furrows are indicated; the posterior tips of the palpebral lobes ('ear lobes') are rather prominent; this cranidium represents, apparently, a mature instar in which the frontal truncation has disappeared completely.

The free cheek, Plate 14, fig. 2, CPC 5470, is 12.5 mm long; note the flat abaxial border of the spine and the posterolateral border that extends along the adaxial edge of the spine; veins at the base of the eye and two weak lines on the flat border are also visible; the lateral marginal furrow is intercepted by the posterolateral furrow which extends into the genal spine.

The segment of the thorax, Plate 14, fig. 2, has a pleura 4.6 mm wide (traversely); the total width is estimated at about 13 mm. The anterior vein forms the crest of the propleuron, and a faint vein also runs along the depressed opisthopleuron.

The pygidium, Plate 14, fig. 1, CPC 5469, is 5.4 mm long and about 8.8 mm wide without spines. Caecal veins and chevron terraced lines on the anterior spine are distinct; the border is narrower than in the other pygidium.

The pygidium, Plate 13, fig. 13, CPC 5468, is relatively small, about 3.5 mm long; the border is wide, and the flanks of the axis are slightly concave.

*Occurrence and age:* *Auritama aurita* sp.nov. has been found in the Georgina Limestone at localities W17, W18, W259, and in the Mungerebar Limestone at G12; its age is the Zone of *Glyptagnostus stolidotus*.

#### AURITAMA TRILUNATA sp.nov.

(Pl. 14, figs 3-6; Pl. 15, figs 1-11; Pl. 16, fig. 3; Pl. 56, fig. 10; Text-fig. 75)

*Material:* Nine cranidia, two free cheeks, and six pygidia are illustrated. Most of the specimens are selected from abundant material found in the O'Hara Shale ('lower chert bed'); these specimens are more or less flattened but preserve the silicified test. Two cranidia are selected from the Georgina Limestone, in which the species is relatively rare.

*Holotype:* The cranidium Plate 14, figure 4, CPC 5472, from the O'Hara Shale, locality D29, is selected as the holotype because its matrix is hard and durable, whereas most of the other specimens have a rather friable matrix.

*Diagnosis:* *Auritama trilunata* is a species with well incised palpebral and cranidial marginal furrows, with a distinct brim, especially in younger specimens, with sigmoid sutures within the rim, with a long anterior border (of 0.45 to 0.5 of glabellar length), with a tapering glabella, and a rounded occipital node; the frontal truncation of its cranidium is retained in maturity; the pygidial axis possesses three to four annulations and there are nine marginal spines of unequal size, the first and the third being the largest.

*Differential diagnosis:* *A. trilunata* differs from the type of the genus, *A. aurita*, by all the characters included in the diagnosis. Further differences are discussed under *A. expansa* sp.nov.

*Description:* The cephalon is lunate, with rearward swept genal spines which are wider than in *A. aurita*. The convexity is low, the border is flat, and the glabella (Pl. 14, fig. 3b) and the cranidium slope down in an even curve toward the border.

The palpebral lobes are flat, horizontal, and slightly below the level of the glabella. The visual surface of the eye is low and convex outward. The test is relatively thin, smooth (without ornament), and the relief of the external and internal surfaces appear to be the same. In the free cheek the border is evenly wide, an incised marginal furrow is absent, and its adaxial thick edge is the extension of the posterolateral cephalic border. Internally the cheek is minutely and densely venulose, but the principal genal caecal veins are missing.

As in *A. aurita*, the cranium is cruciform, and of similar proportions, except for the length of the frontal border, which is 0.4 to 0.5 of the glabellar length (0.3 to 0.35 in *aurita*). The anterior sutures are divergent at first, but within the rim turn in a sigmoidal curve toward the margin, intercepting it near the midline; between the points of interception the margin is straight, truncated. Particulars of the subcephalic frontal structure are given in Text-figure 75 and are discussed in the description of the cranidia, Plate 15, figures 5 and 6. The rostellum is retained in maturity. The rim is rather large and flat and separated from the brim by the incised marginal furrow, which is interrupted in the middle by a broad plectrum. In large specimens the brim in front of the glabella is rather short, but in young cranidia it is as long as the rim. The posterior sutures diverge greatly, delineating small, rather narrow and almost pointed posterolateral limbs.

The palpebral furrow is distinct, the rear tips of the arcuate palpebral lobes are elevated ('ear lobes'); the ocular ridges are broad and low. The axial furrows are straight shallow valleys between the glabella and adaxially sloping interocular cheeks; the circumglabellar furrow is deep in the middle, having a paraglabellar band at its front. The occipital furrow is narrow, distinct, and the occipital lobe carries a small rounded median node. The glabella tapers forward, to 0.85-0.9 of its posterior width; up to three pairs of rather weak, almost imperceptible, glabellar furrows can be seen. The baculae are small, reniform, and placed close to the glabella at its base.

The pygidium is similar to *A. aurita* in its subtriangular outline, and wide concave border. But it possesses only nine spines (four and half pairs), of which the anterior and the third pair are large, but the posterior, unpaired spine is rather small. The axial lobe of the pygidium contains only three to four annulations and a long terminus. The test is smooth, except for chevrons of terraced lines on the pygidial spines.

*Comment on illustrated specimens:*

The specimens whose locality is not mentioned in the following description come from the 'lower chert bed', about 3-4 inches thick, of the O'Hara Shale, locality D29, within ten to fifteen square feet of outcrop.

The holotype cranium, Plate 14, fig. 4, CPC 5472, is 6.6 mm long. Most of its test is preserved; the matrix is hard porous siliceous shale.

The cranium, Plate 14, fig. 3, CPC 5471, is 5.5 mm long; the test is preserved, the matrix is porous silica. The glabella (here carinate) tapers very little, being in front 0.95 of the posterior width; the palpebral lobes, 0.85 of glabellar length, are the largest known in *A. trilunata*; its profile (fig. 3b) is characteristic for all species of *Auritama*.

The cranium, Plate 14, fig. 5, CPC 5473, is 4.4 mm long, an external mould in friable silica. It is rather wide across the palpebral lobes; the minute granulation appears to be the reflection of the granular matrix.

The cranidium, Plate 15, fig. 3, CPC 5477, is 4·3 mm long; the matrix is a pod of rather friable silica in chert. A young specimen, it has a relatively long (longitudinally) brim.

The cranidium, Plate 16, fig. 3, CPC 5487, is 4·0 mm long; the matrix is friable silica. The frontal marginal furrow is pitted, the test is smooth.

The free cheek, Plate 15, fig. 1, CPC 5475, locality D28, flattened in chert, is 10·0 mm long from tip to tip. The anterolateral corner of the doublure is rounded, indicating the contact with the rostellum; the cheek (internal cast) is minutely venulose; the cornea is partly buried in the matrix.

The free cheek, Plate 15, fig. 2, CPC 5476, is 7·8 mm long, the matrix is friable silica. A part of the doublure covered with terraced lines is preserved; it is clean cut by the median suture, and its rounded anterolateral corner indicates the contact with the rostellum. The cornea is preserved. The posterior margin continues all along the adaxial edge of the genal spine.

The pygidium, Plate 14, fig. 6, CPC 5476, locality D6, in porous chert, is 7·9 mm long. It is unusually large, corresponding to a cephalon of about two centimeters. The test and the mould of the posterior unpaired spine are preserved.

The pygidium, Plate 15, fig. 10, CPC 5484, in friable silica, is 3·5 mm long. The test is preserved; the anterior pleural furrow extends into the base of the spine.

The pygidium, Plate 15, fig. 8, CPC 5482, is 3·5 mm long; its test, even the wide doublure, is preserved.

The cranidium, Plate 15, fig. 5, CPC 5479, Georgina Limestone (bituminous limestone), locality G50, is 9·8 mm long. It retains its test and is not flattened. Note the bacculae, the right posterolateral limb, the ocular ridges, the circumglabellar furrow deepened in the middle, and the tapering glabella. The front is truncated and bent down; the frontal part of the plectrum is depressed.

The cranidium, Plate 15, fig. 6, CPC 5480, Georgina Limestone (chert in bituminous limestone), locality G49, is 8·5 mm long. It is the only available exfoliated cranidium of *A. trilunata*. Bacculae, three pairs of weak glabellar furrows, and the depressed front of the plectrum are apparent. Faint veins are present in front of the ocular ridges. The truncated front is clean cut by the rostral suture—a front doublure is absent; combined with the structure (rounded corners and sagittally clean cut edges) of the doublure of the free cheeks, the triangular space occupied by the rostellum and the median suture (Text-fig. 75) are evident.

The pygidium, Plate 15, fig. 7, CPC 5481, locality D29, in friable chert, is 4·7 mm long; only the anterior pair of pleural ribs is indicated; the median spine is broken; the left facet and the terraced lines (chevrons) are well preserved.

The small pygidium, Plate 15, fig. 9, CPC 5483, locality D6, is 2·4 mm long (without median spine). Two pairs of pleural ribs and the border are distinct; the spines are slender.

The cranidium, Plate 56, fig. 10, CPC 5838, locality D6, in hard chert, is immature; it is 2·5 mm long, with a long brim and a rather narrow glabella (width/length = 0·6).

The smallest illustrated cranidium, Plate 15, fig. 4, CPC 5478, in chert, locality D6, is 2·0 mm long; it has a relatively long brim and a short rim. Compare the slightly larger, and more advanced cranidium Plate 56, figure 10.

*Occurrence and age:* *Auritama trilunata* has been found in the O'Hara Shale ("lower chert bed") at localities D6, D28, and D29; in the Mungerebar Limestone at locality G12; and in the Georgina Limestone at localities G48, G49, G50, G51, W1, W15, W20, and W21. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### AURITAMA EXPANSA sp.nov.

(Pl. 16, fig. 6)

*Material:* Only the illustrated holotype, CPC 5490, from the Georgina Limestone, locality G48. It is 4·2 mm long.

*Description (and diagnosis):* The new species *Auritama expansa* has a distinct brim, and a long frontal border of 0.45 of glabellar length, and externally well expressed palpebral and frontal furrows; it recalls, therefore, *Auritama trilunata*; it differs, however, from *trilunata*, as well as from *aurita*, in the following features: (1) the glabella expands forward and has slightly concave flanks; (2) three pairs of glabellar furrows are present; the posterior furrows are transcurrent; (3) the palpebral lobes are 0.8 of the glabellar length (longer than in the other species), and broad; (4) in the front the width of the shield is 1.6 of glabellar length, more than in the other species, in which it is 1.4 to 1.45; and (5) the interocular cheeks together with the palpebral lobes are as wide as 1.2 of glabellar width, whereas in the others it varies from 0.75 to 0.9. The test is smooth.

*Occurrence and age:* Only one cranidium has been found, in the Georgina Limestone, locality G48. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Genus PEICHIASHANIA Chang, 1957

The genus *Peichiashania* is nomenclaturally valid, but its concept is in need of clarification. Chang established the genus by reference to the type species—*Eymekops rectangularis* Endo, 1937. Endo's description of this species (Endo, op.cit., p. 334) is rather brief—only a differential diagnosis in relation to other species of *Eymekops* is given. He mentions a 'relatively rectangular glabella', but the illustrated type (op.cit., pl. 68, fig. 21) has a pyriform glabella, being in its anterior third 0.75 of its width in the rear.

Subsequently, Chang (1959, p. 223) briefly mentioned the differences of *Peichiashania* and *Eymekops*, and illustrated (op.cit., p. 202, fig. 22) a cranidium of *rectangularis* with a slightly tapering, but not pyriform, glabella. Finally, Kobayashi (1960, p. 372; text-fig. 6e) produced a diagram of Endo's specimen, but with straight glabellar flanks.

The two new Mindyallan species (*lunatula* and *pelta*) are placed in *Peichiashania* because of their similarity to *rectangularis* as presented in the diagrams of Chang and of Kobayashi.

The specific differential diagnosis is as follows:

*P. rectangularis* (Endo) is distinguished from the Australian forms by (1) its 'finely pitted test', (2) the pyriform shape of the glabella seen in its illustration, (3) wider interocular cheeks, and (4) slightly more divergent anterior sutures.

*Familial classification:* *Eymekops* Resser & Endo is a genus of the Anomocarellidae Hupé (1955), as well as of the Anomocaridae (Harrington et al., 1959), or of the 'group of *Anomocarella* and its affiliates' (Öpik, 1961, p. 165). *Peichiashania rectangularis*, however, is not a member of this group. According to Kobayashi (1960) it is a genus of his family Pagodiidae, as well as of the subfamily Ordosiinae Lu (1954), which is placed by Lu in the Leiostegiidae.

The classification with the family Auritamidae is apparent from the following diagnosis.

*Generic diagnosis:* *Peichiashania* refers to species of the Auritamidae without bacculae, distinguished by narrow palpebral lobes placed close to the glabella.

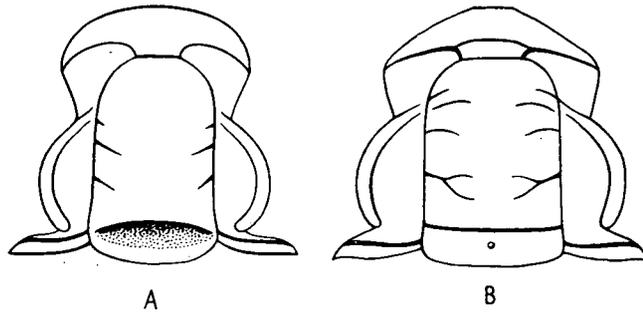


Fig. 76.—A. *Peichiashania? lunatula* sp.nov., from Plate 16, fig. 8;  
B. *Peichiashania? pelta* sp.nov., from Plate 16, fig. 7.

It is notable that in *P.? pelta* sp.nov. the cranidial front is similarly truncate to *Auritama aurita* sp.nov.

The diagnosis is applicable to the Australian species and to the diagrams of Chang and Kobayashi; but its application to the type specimen of the generic type (*Eymekops rectangularis* Endo) is inconclusive, and the generic classification is therefore queried.

PEICHIASHANIA? LUNATULA sp.nov.  
(Pl. 16, fig. 8; Text-fig. 76A)

*Material:* Only one cranidium is sufficiently preserved for description.

*Holotype:* The illustrated cranidium, CPC 5492, is the holotype; it is 7.2mm long, moderately flattened, in friable silica, O'Hara Shale ('lower chert bed'), locality D29.

*Diagnosis:* *P.? lunatula* is distinguished by a relatively long cranidium, evenly arched cranidial front, elliptical occipital lobe, and palpebral lobes placed relatively close to the glabella; the plectrum completely interrupts the marginal furrow.

The differences from *P. rectangularis* are given in the discussion of the genus, and from *P.? pelta* in the description of that species.

*Description:* The cranidium is longer than wide, its length being about 7/6 of the width across the palpebral lobes. The posterior sutures are strongly divergent, delineating small blade-like posterolateral limbs.

The anterior sutures are almost straight, divergent at an angle of about 20 degrees to the midline, and converge within the border in an even arc.

The palpebral lobes, defined by distinct palpebral furrows, are arcuate, rather narrow, placed opposite the posterior part of the glabella; they are about 0.75 of glabellar length, with posterior tips reaching beyond the glabellar rear; the anterior tips are very close to the axial furrow, the distance being about 0.12–0.13 of the glabellar width only. The ocular ridges are barely indicated. The interocular cheeks are slightly swollen and about one-third of glabellar width. The cranidial front is about 0.33 of glabellar length, with a flat lunate rim and a broad plectrum which interrupts the marginal furrow and reaches the glabellar front but remains separated from it by the deepened transverse part of the circumglabellar furrow.

The occipital furrow is broad, well marked by the abrupt glabellar rear, but diffuse in the rear; it is wide in the middle, and obscure at the flanks, not quite reaching the axial furrows. The occipital lobe is elliptical in outline.

The axial furrows are distinct but shallow.

The glabella is parallel-sided, slightly expanded in the rear, evenly rounded in its front, but subtruncate opposite the plectrum; it is a long glabella, as wide as about 0·8 of its length. Three pairs of almost imperceptible glabellar furrows are present.

The test is minutely granulose.

*Occurrence and age:* *P. ? lunulata* is rare in the O'Hara Shale, and fragments occur also in the Georgina Limestone at locality W1. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

PEICHIASHANIA? PELTA sp.nov.

(Pl. 16, fig. 7; Text-fig. 76B)

*Material:* A single cranidium is illustrated; it is the holotype, CPC 5491, 4·8 mm long and not flattened; the matrix is relatively firm silica, O'Hara Shale ('lower chert bed'), locality D29.

*Diagnosis:* *P. ? pelta* is distinguished by a cranidium as long as wide having an angular (not evenly arcuate) cranidial front, an evenly wide occipital lobe, transcurrent marginal frontal furrow, and distinct glabellar furrows.

The characters listed in the diagnosis serve to distinguish *P. ? pelta* from *lunatula*.

*Description:* The cranidium is moderately convex, as long as wide across the palpebral lobes. The posterior sutures diverge less than in *P. ? lunatula* and the small posterolateral limbs are triangular.

The anterior sutures diverge at about 18° to the midline, converge within the border in almost straight lines and cut the margin near the midline; hence, the cranidial front is straight, subtruncate, as seen also in *Auritama*.

The palpebral lobes are arcuate and long (0·75 of glabella as in *P. ? lunatula*), but the posterior tips are on the level of the glabellar rear, and the anterior tips are farther apart, the distance being about 0·2 of glabellar width. The ocular ridges are quite distinct.

The interocular cheek is slightly larger than in *P. ? lunatula*—about 0·4 of glabellar width.

The cranidial front, about 0·3 of glabellar length, is flat, with a flat rim, and a broad low plectrum which is separated from the rim by the continuous marginal furrow.

The occipital lobe is evenly wide, not tapering sideways.

The glabella is parallel sided, relatively long, about 0·8 of its length, as in *P. ? lunatula*. Four pairs of weak but distinct glabellar furrows are present.

The test is minutely granulose.

*Occurrence and age:* *P. ? pelta* was found in the O'Hara Shale ('lower chert bed'), locality D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

## AURITAMIDAE SUBFAMILIAE INCERTAE

### Genus METOPOTROPIS nov.

The type of the genus *Metopotropis* is *M. travesi* sp.nov.; it is a monotypical genus.

*Diagnosis:* *Metopotropis* refers to Auritamidae with a parallel-sided glabella flanked by bacculae and having the free cheeks provided with a broad and flat border, and retaining the ocular cornea; distinguished from *Auritama* by its relatively short palpebral lobes, by the absence of a plectrum, by its evenly arched and not truncated cranial front, and by its rather long excavated frontal area equipped with a tropidium. The absence of the plectrum and of the cranial truncation in *Metopotropis* may indicate that it possesses a ventral structure somewhat different from *Auritama*.

Beside the type, another, undescribed, species occurs in a Mindyallan gastropod limestone, locality NT187 on the Ross River east of Alice Springs.

*Metopotropis* recalls the genera *Anomocarina* and *Anomocaroides* of the family Anomocaridae Poulsen. These forms are also bacculate, and bear tropidia, but are distinguished by their rather small protolateral limbs, tapering glabella with a well rounded front, and a node on the rear of the glabella.

### METOPOTROPIS TRAVESI sp.nov.

(Pl. 16, figs 9 a, b-10; Text-fig. 77)

*Material:* The material consists of a single dismembered cephalon, of which the cranidium and one of the free cheeks (CPC 5494) are illustrated.

*Holotype:* The holotype is the illustrated cranidium, CPC 5495, 2.7 mm long.

*Diagnosis:* The diagnostic characters of the species are the same as of the genus.

*Description:* The anterior sutures diverge greatly within the brim, swing abruptly in the rim and cut the anterior margin about opposite the anterior tips of the palpebral lobes; the posterior sutures, diverging first, turn rearward and cut the posterior margin at the genal angle. The flat border of the free cheek extends into the similar flat, broad, and almost falcate genal spine. The subocular part of the free cheek is relatively narrow and slopes steeply, and the visual surface (the cornea) is large. The eye is holochroal and the ocelli are extremely small. The crescentic palpebral lobes, placed opposite the glabellar midpoint, are about half the glabella in length. The interocular cheek, 0.3 of glabellar width, slopes gently adaxially. The slanting ocular ridges are prominent, tumid and even bulbous—an unusual feature in trilobites.

The cranial frontal area is elliptical, rather wide and long—0.6 of glabellar length; since the marginal furrow is not clear, the rim is almost undiscernible. The brim is concave and carries in its posterior part the swollen bow-shaped tropidium and a shallow median depression between the tropidium and the front of the glabella. Radiating caecal lines cover the brim; the upturned margin of the rim is ornamented by relatively coarse terraced lines extending across the sutures on to the border of the free cheeks.

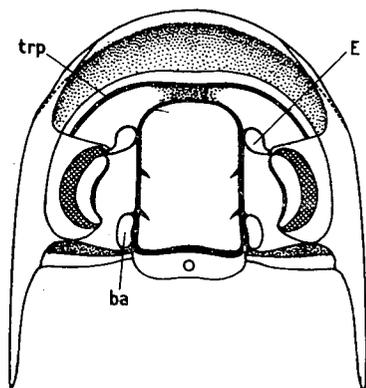


Fig. 77.—*Metopotropis travesi* gen.nov., sp.nov., combined from Plate 16, figs 9, 10. ba—baccula (—ae); E—ocular ridge; trp—tropidium.

The occipital lobe is short and bears a barely visible node; the occipital furrow is straight and deep; the axial furrows are deep V-shaped valleys between the glabella and the cheeks. The elongate bacculae are separated from the glabellar rear by the axial furrows. The glabella is parallel-sided, has its front bluntly rounded, and is rather strongly arched transversely, rising above the level of the palpebral lobes. Two pairs of short and shallow glabellar furrows are indicated.

The test is smooth (except for the venulose caecal lines of the frontal area).

The whole cephalon is strongly convex; its flanks are parallel or almost so, to about the level of the palpebral ridges; in front of the ridges the margin is concave; the frontal margin is evenly arched in plan.

*Occurrence and age:* *Metopotropis travesi* gen.nov., sp.nov. was found in the Georgina Limestone at locality G48; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

## ANOMOCARACEA FAMILIAE INCERTAE

### Genus PARACOOSIA Kobayashi, 1936

The genus *Paracoosia* is discussed in connexion with *Leichneyella* gen.nov.

#### PARACOOSIA ASPIS sp.nov.

(Pl. 31, figs 3a, 3b)

*Material:* Only one pygidium, the illustrated holotype, CPC 5599, 3.3 mm long, has been found; it is probably the best preserved pygidium of a *Paracoosia*.

*Diagnosis:* *Paracoosia aspis* sp.nov. is distinguished by the length of its pygidial axis (as long as 0.6 of pygidial length) and by having six annulations, six pairs of pleural ribs, and long pleural furrows almost reaching the margin.

*Differential diagnosis:* In the two previously known species of *Paracoosia* (*deprati* Mansuy and *asiatica* Mansuy) the pygidial axis is shorter (0.5 of total length), and as seen in Mansuy's illustrations, it has only five annulations and four to five pleural ribs. Furthermore, in these species the pleural furrows peter out immediately after crossing the paradoublural line and do not extend to the margin.

*Occurrence and age:* *P. aspis* was found in the O'Hara Shale ('lower chert bed'), at locality D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

### Genus LEICHNEYELLA nov.

The type of the genus is *L. caseyi* sp.nov. The characters of the genus are, in the first place, based on those of its type species. *Leichneyella* can be compared with *Coosia* Walcott as regards the cranial design, but it is different in having widely divergent anterior sutures and large eyes, and a narrow rim defined by a rather distinct marginal cranial furrow. In *Coosia* the rim is wide and ill-defined. Even closer is *Paracoosia* Kobayashi, the two species of which (*deprati* and *asiatica*) have been described by Mansuy (1915, 1916) from Tonkin (northern Indo-China). *Paracoosia*, however, has no rim at all and its interocular cheeks are wider than in *Leichneyella*.

*Leichneyella* is somewhat similar to the Middle Cambrian *Grönwallia? angermanensis* Westergaard, 1953 (p. 34, pl. 8, fig. 1): *G.? angermanensis* has also a very large brim and large palpebral lobes placed close to the glabella, but it has no rim, its glabella is subquadrangular, and the occipital lobe is extended into a large spine with a broad base.

The familial classification of *Leichneyella* is inconclusive. It is placed here in the Anomocaracea in agreement with Hupé (1955, p. 189), who included in the anomocarids *Coosia*, as well as *Paracoosia*. Applying the classification of Harrington et al. (1959), an arbitrary choice between the Coosellidae (Marjumiacea), which includes *Coosia*, and Anomocaracea with *Paracoosia*, is possible. On the other hand, following the earlier classification by Kobayashi (1936) and accepting a mutual affiliation of *Paracoosia* and *Leichneyella*, the latter could be placed in the Dikelocephalacea.

Incidentally, the specific name *Paracoosia asiatica* (Mansuy) was replaced by *P. mansuyi* Kobayashi, 1936 on grounds of a subjective homonymy: Kobayashi assumed that *Pterocephalus asiaticus* Walcott (1905; 1913, pl. 14, figs 5-5b) is also a *Paracoosia*, and for this reason regarded *asiatica* Mansuy as the junior homonym of Walcott's name. The examination of Walcott's as well as Kobayashi's (op.cit., pl. 21, fig. 8) illustrations of *Pterocephalus asiaticus* Walcott reveals that this form represents a separate genus with the following characters: (a) the glabella is sub-pentagonal, as wide as long, and with a truncated front; (b) baculae are present, and are relatively large and tumid; (c) the distance of the anterior tips of the palpebral lobes from the glabella is about 0.7 to 0.8 of its width; (d) the pygidial border is denticulate; and (e) the pleural furrows reach the margin of the pygidium. These characters exclude any affiliation with *Paracoosia* and *Pterocephalia*; hence, the reference '*Pterocephalus*' *asiaticus* is, therefore, preferable.

In *Paracoosia deprati* and *asiatica* (Mansuy) the pygidial structure is rather different from the Dikelocephalacea. *Paracoosia* is early Upper Cambrian in age, but has a fused pygidium without interpleural grooves, whereas in the late and latest Upper Cambrian Dikelocephalidae the pygidium is relatively primitive, with well-developed pleural furrows and interpleural grooves, and it cannot be derived, therefore, from the older but much more advanced *Paracoosia*; the structure of the pygidium of *Paracoosia* is, however, close to the Anomocaracea.

To complete the comparison *Dikelocephalites* Sun (1935, p. 36) deserves also some comment. *D. flabelliformis* Sun has also a large frontal area (0.83 of glabella,

and 0.4 of cranidial length); it is much less than in *Leichneyella* (1.8), but the cranidia have a similar aspect. *Dikelocephalites*, however, has no rim, its glabella is subtruncate, the palpebral lobes are small and remote from the glabella, and the anterior suture is 'distinctly intramarginal' (Sun, op.cit., p. 37). In spite of the dorsal position of the suture the affiliation of *Dikelocephalites* with the Dikelocephalidae, as assumed by Sun, is not evident; but, being close to *Paracoosia*, it shares with the latter the chance of being an anomocarid. Equally inconclusive is its affiliation with *Pterocephalia* (see Lochman, 1956, p. 459; Palmer, 1960, p. 84) and the Pterocephaliidae.

Notable is the morphological analogy of *Leichneyella* with the Devonian Tropidocoryphinae. Taken alone, and without any other evidence of its age, *Leichneyella* could be mistaken for a genus of the Proetidae, having an Upper Silurian to Middle Devonian aspect.

The species of *Leichneyella* here described are: *Leichneyella casei* gen.nov., sp.nov., *Leichneyella* sp.A, *Leichneyella* sp.B.

LEICHNEYELLA CASEYI sp.nov.

(Pl. 31, figs 1a, b; Text-fig. 78)

*Material:* The material consists of the holotype cranidium, CPC 5597, embedded in chert. It is 5.9 mm long, and not flattened. The test is not preserved, but is represented by the external mould (rubber cast) which is identical with the internal cast.

*Diagnosis:* The genus *Leichneyella* is monotypical, and the diagnosis of the species *L. caseyi* sp.nov. is, therefore, the same as of the genus. The relevant characters are: (1) the greatly divergent anterior sutures cut the rim in straight lines and abruptly intercept the margin at a distance slightly less than half way from the midpoint to the cranidial corners; (2) The frontal area is extremely long (1.8 of glabellar length), provided with a narrow, flat rim and a distinct marginal

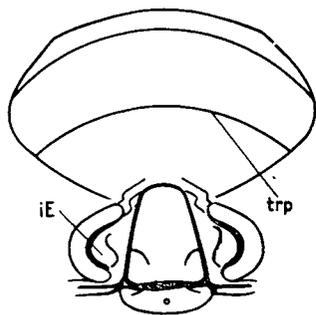


Fig. 78.—*Leichneyella caseyi* gen. nov., sp.nov., from Plate 31, fig. 1. iE—interocular swelling; trp—tropidium.

furrow; (3) A tropidium is half way between the margin and the glabella; (4) The brim is convex in the rear and concave in front of the tropidium; the brim is rather wide (1.7 of its length); (5) the posterior sutures diverge diametrically and the posterolateral limbs are narrow blades; (6) the occipital lobe bears a tiny node and narrows only little toward the flanks; (7) the palpebral lobes are broad, strongly arcuate, and very large—0.8 of glabellar length; (8) the interocular cheeks

are 0.5 of glabellar width, and bear a crescentic swelling each parallel to, and imitating, the palpebral lobes; (9) the ocular ridges are nodulose and join the glabella at its front—a most unusual feature; (10) the glabella is conical and longer than wide; and (11) a pair of vestigial (posterior) glabellar furrows is present.

The brim is venulose, the test is smooth, except for delicate marginal terraced lines on the rim.

To sum up, the conical glabella, the very large arcuate palpebral lobes placed close to the glabella, the wide and long concave-convex brim with the tropidium, and the narrow border are the characteristic features of *Leichneyella caseyi*. Its design reminds one of *Pterocephalia*, which, however, has smaller eyes farther from the glabella, no rim, and a rather different shape of the glabella.

*Occurrence and age:* The described specimen of *Leichneyella caseyi* was found in the O'Hara Shale ('lower chert bed') at locality D6. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

LEICHNEYELLA? sp.A.

(Pl. 31, fig. 2; Text-fig. 79)

The illustrated cranidium, CPC 5598, 10.0 mm long, is partly masked by silica and cannot be sufficiently described. It belongs to *Leichneyella* because of its conical glabella, large palpebral lobes close to the glabella, large brim with a narrow marginal rim and strongly divergent and convex anterior sutures. It differs, however, from *L. caseyi* in having a much shorter frontal area (0.85 of glabellar length), which is shorter than the glabella.

*Occurrence and age:* The only available fragment was found at locality G127; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

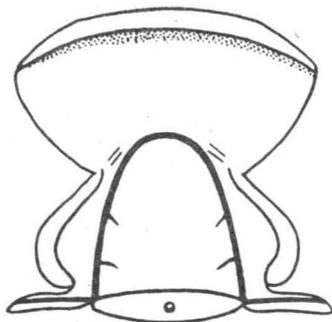


Fig. 79.—*Leichneyella?* sp. A., from Plate 31, fig. 2.

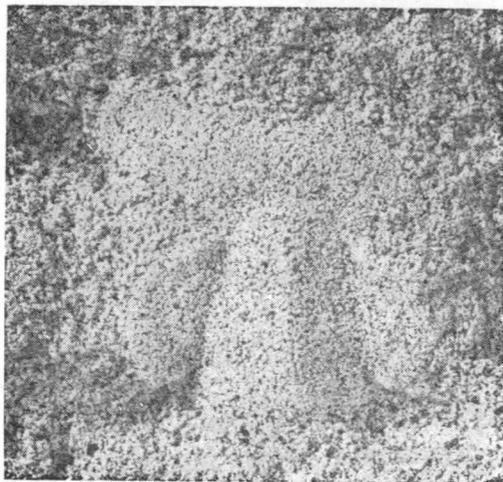


Fig. 80.—*Leichneyella?* sp. B, CPC 6732, x 6.

LEICHNEYELLA? sp.B.

(Text-fig. 80)

The illustrated cranidium, CPC 6732, a cast in friable sandstone, was originally about 12 mm long. Its rim is preserved at the left corner of the frontal area and curvature of its margin suggests a somewhat parabolic curvature of the front. It appears that the brim was longer than the glabella, but less long than in *Leichneyella caseyi* sp.nov.

*Occurrence and age:* *Leichneyella?* sp.B comes from the Steamboat Sandstone, locality D95; its age is Middle Cambrian, the Zone of *Leiopyge laevigata*.

Superfamily ASAPHISCACEA Raymond

Family ASAPHISCIDAE Raymond, 1924

The families Asaphiscidae, Anomocarellidae, and Anomocaridae cannot be convincingly separated from each other in an attempt to place every known genus of this group with certainty in one or another family. Hence, the number of genera to be classified as Asaphiscidae will remain for the time being a subjective matter (see Öpik, 1961, p. 164).

Harrington et al. (1959) include twenty-one genera and subgenera in the Asaphiscidae; Chang (1959) increased the number by three more, Poulsen (1960) by one, and two new genera are described here. Of these twenty-seven genera nine are either doubtful, or not asaphiscids. Tchernysheva et al. (1960) included fourteen generic names in the Asaphiscidae, but five of these were placed in different families by Harrington et al. Tchernysheva's classification of the Asaphiscidae is a modification of Hupé's (1955).

The disparity of the current classifications casts doubt on the concept of the Asaphiscacea itself and prevents a phylogenetic arrangement of the asaphiscid genera. Furthermore, asaphiscids are widespread over the globe: they are known in the Appalachians, the Rocky Mountains, in Argentina, in the Arctic, and in the Siberian, Manchurian, and Cathayan regions of Asia, as well as in Australia. Intra-regional diversification, no doubt, occurred in these seas, but also in places covered by the present oceans; at the same time the evolving forms spread beyond the limits of their native habitats, masking elsewhere the trends to a degree which prevents the palaeontologist from a conclusive study of the phylogeny of the species of the Asaphiscidae. This situation can be illustrated by the Australian forms, which are arranged below in their stratigraphic order. In the discussion that follows it is concluded that the probable phylogenetic order indicated by the morphological evidence is the reverse of the temporal sequence of forms.

The oldest species (1) *I. iniotoma* has an occipital structure similar to 2, 3, 4, and 5, but is otherwise rather distinct and cannot be regarded as being ancestral to any one of the rest, and will not be considered, therefore, further.

Species (2) and (3) are contemporaneous and concurrent. *M. mindycrusta* is the more effaced form and could be regarded as a derivative of *compacta* when their contemporaneity is overlooked; but neither can be taken for an ancestor of the species 4, 5, and 6, because these are related among themselves and are less effaced

STRATIGRAPHIC ORDER OF SPECIES OF ASAPHISCIDAE  
IN QUEENSLAND

|   |                                       |
|---|---------------------------------------|
| 6. <i>Blountia georginae</i> sp.nov. ....                       | <i>Erixanium sentum</i> Zone          |
|   | <i>Corynexochus plumula</i> Zone      |
| 5. <i>Blountia (Mindycrusta) advena</i> sp.nov. ....            | <i>Glyptagnostus reticulatus</i> Zone |
| 4. <i>B. (Mindycrusta) notostena</i> sp.nov. ....               | <i>Glyptagnostus stolidotus</i> Zone  |
| 3. <i>B. (Mindycrusta) mindycrusta</i> subgen. nov.,<br>sp.nov. |                                       |
| 2. <i>B. compacta</i> sp.nov.                                   |                                       |
| 1. <i>Iniotoma iniotoma</i> gen.nov., sp.nov.. ....             | <i>Erediaspis eretes</i> Zone         |

than the earlier forms. Nevertheless 4, 5, and 6 represent no direct phylogenetic line, because the latest species, (6) *B. georginae*, possesses the least fused pygidium and should be regarded as the most primitive in this group of species. Its predecessor in time, (5) *Mindycrusta advena*, shows an incipient fusion of the pygidium with interpleural grooves replaced by raised lines; and in the earliest species (*notostena*) the pleural lobes are almost completely fused. If the stratigraphic sequence of the species were the reverse of what it actually is a true phylogenetic lineage could be assumed.

The superpositional and temporal order of the asaphiscids as above has been established on geological evidence. In the absence of independent geological criteria, however, the phylogeny, if relied upon, would enforce the conclusion that the strata containing the more primitive *Blountia georginae* are the oldest and lowermost in the sequence, followed above by *Mindycrusta advena* and topped by *Mindycrusta compacta*. In other words a geological misinterpretation may result when the 'degree of maturity' of species and genera and phylogenetic considerations alone are used in solving stratigraphical problems.

Therefore, the Queensland species of Asaphiscidae, which cover the span of almost five early Upper Cambrian zones, cannot be interpreted as a phylogenetic lineage that evolved in the Georgina region. Each species is an independent invader from somewhere else, and the more advanced forms are the first to arrive; the less advanced followed, and the last of them (*B. georginae*) was a primitive and conservative form, almost 'behind its time', displaying characters of ancestral significance.

### ASAPHISCIDAE SUBFAMILIAE INCERTAE

#### Genus INIOTOMA nov.

The type species of *Iniotoma* is *I. iniotoma* sp.nov.

*Diagnosis:* Asaphiscidae with an abbreviated occipital furrow whose ends are closed by lobules; distinguished by relatively large eyes placed only slightly in front of the glabellar midpoint, bluntly rounded glabellar front, a convex and narrow rim, and small posterolateral limbs.

The structure of the occipital furrow of *Iniotoma* suggests an affiliation with *Blountiella* Resser and *Blountia* (*Mindycrusta*), but is in itself no reason to place *iniotoma* in one of these genera of the Blountiinae, which all have small and forward placed eyes.

*Lecanopleura* Raymond, 1937, externally reminds one of *Iniotoma*, but differs from it as follows: (1) eyes are small, (2) anterior sutures diverge strongly, and (3) the occipital furrow is transcurrent to the axial furrows, and may be interrupted or continuous in the middle. According to Raymond (1937, p. 1111) in *Lecanopleura interrupta* 'the nuchal furrow is not continuous across the glabella, nor does it join the furrows on the fixed cheeks'. The illustration (op.cit., pl. 3, fig. 1) reveals that the ends of the occipital and the marginal furrow do not meet and are by-passing one another, but also that the occipital furrow is not abbreviated but reaches the axial furrow. The same structure is apparent in Rasetti's (1946, pl. 69, figs 35-38) specimens of *Lecanopleura*(?).

Some resemblance to *Iniotoma* can be seen in *Dunderbergella* Howell (Harrington et al., 1959, p. 0291), which has also small posterolateral limbs, a slightly tapering glabella, and a narrow rim, but is distinguished by its narrow occipital lobe, transcurrent occipital furrow (Howell, 1944, p. 17), and plump glabella. Among the many species included in *Proasaphiscus* by Resser & Endo *P. offula* (R. & E., 1937, p. 267, pl. 46, fig. 30) recalls *iniotoma* in the shape of the glabella and the occipital lobe, but has larger palpebral lobes, distinct glabellar furrows, and a transcurrent occipital furrow. Chang (1959, p. 208) refers to it as *Szeaspis*(?) *offula*.

#### INIOTOMA INIOTOMA sp.nov.

(Pl. 11, figs 1-3; Text-fig. 81)

*Material:* Only cranidia have been found as yet; all are silicified. The three illustrated cranidia supplement one another and are selected from about fifteen, mostly fragmentary, specimens.

*Holotype:* The cranidium, Plate 11, figs 2a, b, CPC 5441 from the Mungerebar Limestone, locality G119, is selected as the holotype; it is fragmentary, but shows the posterolateral limb, which is incomplete or inaccessible in the other specimens.

The diagnosis of the species *iniotoma* coincides with the diagnosis of the genus.

It is possible, but not certain, that the unidentified Pygidium No. 2 (q.v.) belongs to *Iniotoma iniotoma*; if so, *Iniotoma* should be excluded from the Asaphiscidae.

*Description:* The cranidium, trapezoidal in outline, has a strongly forward-arched anterior margin; it is arched transversely, slopes forward, and the glabella, including the occipital lobe, is raised above the level of the cheeks. The anterior sutures are relatively short, straight, and divergent, turning within the rim rather abruptly toward the midline, and change into a submarginal course about half way between the midline and the anterolateral corners; they delineate a rather narrow submarginal doublure. The posterior sutures diverge at about a right angle and cut the posterior border in an even curve. The posterolateral limbs are relatively narrow (transversely) and long, triangular, and downsloping steeply from the fulcra, which are rather close (about 0.25 of glabellar width from the axial furrow). The posterior marginal furrow is relatively deep, the posterior border narrow and convex.

The frontal area is as long as 0.35 of glabella and 0.2 of the total length of the cephalon; the rim is convex, elevated, and overhanging in front; the marginal furrow is broad and ill-defined; the brim is slightly convex, longer than the rim, and slopes at a low angle.

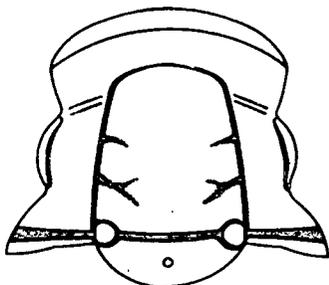


Fig. 81.—*Iniotoma iniotoma* gen. nov., sp.nov., from Plate 11, figs 1 and 3.

The occipital lobe is relatively long (0.25 of the glabella), triangular, and angular in the rear, and bears an obscure median node. The occipital furrow is straight, relatively deep, and abbreviated to about three-quarters of the glabellar width; its ends are replaced (or filled) with a pair of rounded tumid lobules: in the majority of trilobites, however, the ends of the occipital furrow are deeply sunk inward and produced into appendiferi.

The interocular cheek is tumid, 0.3 of glabellar width, and elevated above the palpebral lobes. These are long (0.4 of glabellar length) narrow, gently arched, subangular in the middle and placed in front of the glabellar midpoint. The palpebral furrow is distinct but shallow. Vestigial ocular ridges occur in some of the specimens.

The axial furrows are deep and narrow, but shallow in front of the glabella. The glabellar flanks are slightly convex in the rear, but constricted in the anterior third; the glabellar front is bluntly rounded to subtruncate, but not angular. The glabella tapers moderately to about 0.75 (opposite the ends of palpebral ridges) of its width in the rear. It is weakly carinate and the examination of a number of specimens reveals the presence of two pairs of rather shallow glabellar furrows of which the posterior furrows are forked.

*Comment on illustrated specimens:*

The holotype cranidium, Plate 11, fig. 2, CPC 5441, locality G119, is 4.6 mm long; the right side is complete, glabellar furrows are indicated, and the convex rim is seen in lateral view. The ocular ridges are obscure. The glabella is weakly carinate.

The cranidium, Plate 11, fig. 1, CPC 5440, locality G119, is 5.0 mm long. The lobules at the ends of the occipital furrow and the angularity of the occipital lobe are distinct. The test is rough through silicification.

The cranidium, Plate 11, fig. 3, CPC 5442, locality G150, is 8.0 mm long. The lobules are prominent; the rim remains in the matrix.

*Occurrence and age:* *Iniotoma iniotoma* sp.nov. occurs in the Mungerebar Limestone at localities G8, G119, G150, G417, and G429; its age is the Mindyallan Zone of *Erediaspis eretes*.

## Subfamily BLOUNTIINAE Lochman, 1944

### Genus BLOUNTIA Walcott, 1916

Between twenty-five and thirty species have been included in *Blountia* since the genus was established by Walcott. The total number of the species is variable; it depends on subjective synonyms and the generic classification of some of the species, which involves the closely affiliated genera *Maryvillia* Walcott, 1916, *Homodictya* Raymond, 1937, and *Blountiella* Resser, 1938: the three genera together contain fewer species than *Blountia*. According to Harrington et al. (1959) all these genera constitute the subfamily Blountiinae Lochman, 1944. Originally, Lochman established a separate family (Blountiidae), which was regarded by Rasetti (1956, p. 1269) as a synonym of the Asaphiscidae (Asaphiscina) Raymond, 1924. In the Blountiinae the eyes are small and placed anterior to the centre of the glabella (Harrington et al., p. 0292), and not opposite or slightly behind the centre (*ibid.*, p. 0290) as in the Asaphiscinae.

Four of the five new species of *Blountia* that are described below are similar in having an 'abbreviated' occipital furrow not connected with the axial furrows; it is assumed, therefore, that these species are affiliated among themselves and different from species with a transcurrent occipital furrow. It should be noted that in several species of *Blountia* the occipital furrow is abbreviated as well. For instance, '*Blountia* sp. Tenn; specimen clearly showing 9 thoracic segments' (Harrington et al., *op.cit.*, p. 0293, fig. 3c) shows the abbreviated occipital furrow; so does *Blountiella alemon* (Walcott, 1916), Resser (1938, pl. 12, fig. 35). (*B. alemon* is the type of *Blountiella*, originally described as *Blountia? alemon* by Walcott.) Also, Tash (1951, p. 285) notes that in *B. prolifica* the occipital furrow is 'defined along midpart only', and the same may apply to *Coosella convexa magnalimbata* Tash (*ibid.*, p. 290). *Blountia mimula*, however, lacks an occipital furrow: it is the type of *Blountia* and its holotype is a complete specimen (Walcott, 1916b, pl. 61, fig. 4) with seven segments, 7 mm long; according to Walcott (*op.cit.*, p. 396) it is an adult specimen. The holotype was re-figured photographically by Resser (1938, pl. 12, fig. 18), but without supplementary notes. Rasetti (1946, p. 446, pl. 67, figs 6-7) illustrates two cranidia and a pygidium as cf. *mimula* with the remark that 'in such a prolific genus as *Blountia* it is difficult to be certain of specific identity'.

The holotype of *B. mimula* is the only hitherto described complete specimen of a *Blountia*, as well as of the Blountiinae. Lochman (1944, p. 52 and 53) is of the opinion that the holotype of *mimula* is an immature specimen, but this cannot be demonstrated. A diagram of another unnamed specimen with nine segments is given in Harrington et al. (*op.cit.*, p. 0293). This specimen is less than 5 mm (about 4.6) long and, consequently, smaller than *mimula* with its seven segments. Comparing these it becomes apparent that the holotype of *mimula* cannot be regarded as an immature specimen with an incomplete number of segments.

As regards the concept of the genus *Blountia*, *B. mimula* should be considered in the first place because the structure of the segments of its thorax is most peculiar for an asaphiscid. The illustration in Resser (*op.cit.*), a photograph prepared with a coating of chlorammonia, indicates that the pleurae are flat and pleural furrows are absent. According to Walcott (*op.cit.*, p. 396), however, pleural furrows

are present, but are very shallow, and in his illustration they are drawn as faint and rather narrow lines. Hence, I assume that the apparent absence of pleural furrows or their vestigial character in *B. mimula* must be included in the diagnosis of *Blountia*, or of the subgenus *B.(Blountia)*.

The absence of the occipital furrow in *B. mimula* is a specific character, but in combination with others it may be also of a subgeneric value because the rest of the American species have a more or less well-defined occipital furrow. The abbreviated occipital furrow is also a character of supraspecific significance.

In the majority of the species assigned to *Blountia* the structure of the pleurae is unknown, and their generic classification cannot be regarded, therefore, as conclusive. Hence, the following taxonomic procedure is adopted: (1) All species whose thorax is unknown and listed as belonging to *Blountia* are referable to that genus without any subgeneric designation; (2) the full reference of the species *mimula* is *Blountia* (subgenus *Blountia*) *mimula*.

*Diagnosis (revised)*: *Blountia* is a genus of the Asaphiscidae with small eyes placed anterior to the glabellar midpoint, with unfurrowed pleurae (or, probably, with vestigial pleural furrows) in the typical subgenus, and with a subtriangular pygidium possessing a relatively narrow border.

Furthermore, in most of the species the posterior sutures are evenly arched, the posteriolateral limbs are large, subtriangular, and pointed at the tips, and the occipital lobe is conspicuously narrow (longitudinally).

#### Subgenus BLOUNTIA (MINDYCRUSTA) subgen.nov.

Type species of *Mindycrusta* is *B. (Mindycrusta) mindycrusta* sp.nov.

In the diagnosis that follows the differential diagnosis is given in parenthesis. Familial characters are omitted, and the subfamilial name Blountiinae can be replaced by the phrase 'asaphiscids with small eyes placed anterior to the glabellar midpoint'.

*Diagnosis*: The species of *Blountia (Mindycrusta)* are Blountiinae with slightly sinuous posterior sutures (in *B. (Blountia)* these are evenly arched) and rounded tips of the posterolateral limbs (these are mostly acute in *B. (B.)*, but rounded in *Maryvillia*), with abbreviated occipital furrow, and with a relatively long occipital lobe (short in *Blountia*); with seven segments in the thorax in the type species (as in *B. mimula*) bearing deep and distinct pleural furrows (as in *Asaphiscus*, but not *B. mimula*, which lacks pleural furrows); and with a large pygidium as long as 0.8 of the cephalon (as in *Asaphiscus*; in *B. mimula* it is only 0.65 of the cephalon) provided with a distinct but narrow border about 0.13 of pygidial length (in *Blountia* and *Asaphiscus* it is over 0.2).

Summing up, the subgenus *Mindycrusta* refers to species of *Blountia* having (1) well-defined, *Asaphiscus*-like pleural furrows, (2) an abbreviated occipital furrow which may be also obsolete, and (3) a narrow pygidial border.

The ventral cephalic structure of *Mindycrusta* (cheeks fused into a unit, and no rostral shield), and the retention of the cornea in moults of the free cheek, cannot be evaluated taxonomically in the absence of relevant information regarding the rest of the Asaphiscidae.

BLOUNTIA (MINDYCRUSTA) MINDYCRUSTA sp. nov.

Pl. 11, figs 4-10; Pl. 12, figs 1-3; Text-fig. 82)

*Material:* Described and illustrated are eleven specimens: two complete tests, one isolated cranidium, two free cheeks, two pygidia connected with the thoraces and four isolated pygidia. The selection was made to illustrate all available modes of preservation: complete and dismembered parts, silicified and not silicified, flattened and undeformed, and with, as well as without, the test.

The material from locality W20 represents a population in a single bed, or even on a single bedding plane; the age of the specimens from G50 may be somewhat different from W20, but the difference is an undefinable small fraction of the *G. stolidotus* Zone. The specimens from locality D29 represent a separate site of the same population, apparently contemporaneous or penecontemporaneous with the sites W20 and G50.

*Holotype:* The complete specimen Plate 11, figure 4, CPC 5443, locality W20, is selected as the holotype because it provides data regarding the proportions of the tagmata, the ventral structure, and the ornament (veins on the free cheeks); it is, however, worn and flattened and must be supplemented, therefore, by specimens that retain the original convexity.

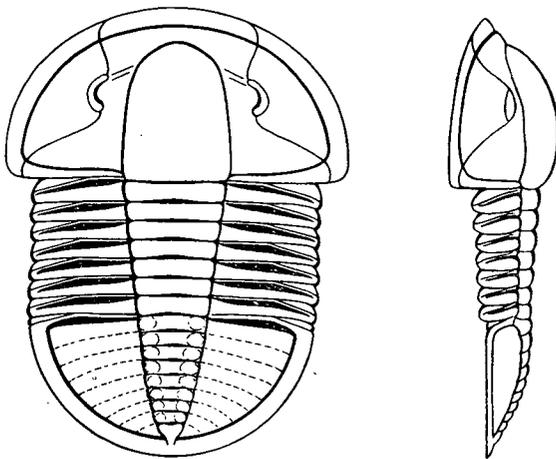


Fig. 82.—*Mindycrusta mindycrusta* gen.nov., sp.nov., combined from Plate 11, figs 4, 7 and 9, and Plate 12, figs 2a, b. Top view flattened in plane.

*Diagnosis:* *B. (Mindycrusta) mindycrusta* is a species with sinuous posterior sutures and rounded posterolateral cranial tips, and with a moderately tapering glabella having a subangular frontal lobe; distinguished by the absence of the occipital furrow, effaced pygidial pleural lobes, and a relatively narrow pygidial axis with straight or even concave flanks.

*General Habit:* *Mindycrusta mindycrusta* is a small trilobite reaching the length of about 30 mm. The body is broad elliptical with subparallel flanks and evenly curved semicircular cephalic and pygidial margins. The thorax consists of seven segments. The cephalon, thorax, and pygidium differ little in their length, the proportions being 10 : 7 : 8: consequently *M. mindycrusta* can be described as an

almost isotagmatic trilobite. The cephalon is strongly vaulted and spacious, with a tumid and relatively long glabella and down-sloping cheeks. In transverse section the glabella rises only a little above the arc of the whole cephalon. The thorax is less convex and its convexity decreases rearward, as seen from the fulcral lines, which diverge to the rear, and shortening of the free pleurae in the same direction; the pygidium, as compared with the cephalon, is relatively flat; it appears (Text-fig. 82), therefore, that the cephalon and the anterior segments of the thorax contained muscles more powerful than the posterior part. The smooth test without spines, combined with the strong convexity of the body, indicates a streamlined and agile animal. The isotagmatic body and well-developed pleural and pygidial facets indicate an excellent ability for coiling. In its external appearance, especially its vaulted cephalon, *M. mindycrusta* is comparable with the illaenids, which R. Richter also regarded as agile swimmers. Notable also is the similarity with the affiliated asaphiscid *Blainia paula* Walcott (1916b, pl. 62, fig. 2a).

*M. mindycrusta* was apparently as agile in the water above the sea floor as it was on the floor itself.

The moulting habits of *M. mindycrusta* are evident from several exuviae. The moulting occurred on the sea floor and was apparently a rapid process owing to the narrowness of the doublure, efficiency of the sutures, and absence of spines. In the holotype, Plate 11, figure 4, the cheek unit was pushed to one side and the animal left its exuvia by crawling forward without displacing the rest of the exoskeleton. Even simpler was the event in Plate 11, figure 6: the sutures opened and the animal dragged the cranidium forward for a short distance only. In others the thorax with the pygidium was abandoned first, but the cephalic integument was carried for a while and dropped some distance away.

Specimens also occur in an incompletely coiled (or uncoiled) state with the cephalon connected with, but bent under, the thorax: these are, apparently, dead bodies.

*Description:* The cephalon is semicircular and strongly arched, with convex slopes. The anterior sutures are straight and moderately divergent; they cut the rim in short curves and, remaining marginal, meet in the middle. The posterior sutures are slightly sinuous, and cut the posterior cephalic border in short and slightly convex-outward curves almost at the genal angles. The free cheeks are roughly triangular; genal spines are absent; the border is almost flat, the marginal furrow distinct but shallow. The cornea of the eye (the eye) is low, convex in vertical section, slopes outward, and stands on a low base. The eye is apparently holochroal. The ocular platform is venulose.

The posterolateral limbs are large, triangular, with rounded tips; the marginal furrow is shallow. The fulcral point is close to the glabella, at a distance of about one-quarter to one-fifth of its width; this distance increases rearward consistently in the thorax.

The cranial margin is arched forward only slightly but remains horizontal; the frontal area slopes down, but the slope of the rim is less than that of the brim; both are only slightly convex. The rim is about as wide (longitudinally) as, or somewhat wider than, the brim. In the frontal furrow, along the rear edge of the rim,

irregularly distributed shallow pits are present. Four of these are deeper and placed symmetrically to the midline as seen in Plate 12, figure 2.

The palpebral lobes are small, about 0.2–0.25 of the glabella, oblique, and placed opposite the rear of the anterior half of the glabella.

The ocular ridges are slanting; they are rather faint and mostly not discernible at all. The interocular cheek slopes gently abaxially, is somewhat convex, and about as wide as 0.25–0.3 of the glabella.

The occipital furrow is obsolete and the occipital lobe is vaguely discernible from the glabella by its almost imperceptible tumidity in uncompressed specimens.

The axial furrows are distinct but shallow, and surround the glabella evenly; in the furrow shallow pits can be seen one at each ocular ridge.

The glabella is relatively long; together with the occipital lobe, which is inseparable, the width/length ratio is variable around 0.7. It tapers forward, and the ratio of the frontal width (at the ends of ocular ridges) to the marginal width in the rear is variable between 0.8 and 0.85.

The glabellar flanks are slightly convex and somewhat angulate at the tips of the ocular ridges; the glabellar front is subangulate also. Three pairs of almost obsolete glabellar furrows appear to be present in Plate 12, figure 2. In the same specimen minute granulation is seen in the occipital part, but the rest is smooth.

In the thorax the axial lobe tapers evenly rearward, but the pleural flanks remain parallel; as the fulcral lines diverge rearward the free pleurae decrease and the hinged parts of the pleurae increase in length (transversely). The facets are large, the pleural furrows are oblique, deep, long, and angulate at the fulcral points.

The pygidium is subcircular, relatively flat, with tumid pleural lobes and a low axis. The axis is arched transversely and becomes rather low in the rear. It is long, and reaches the border, and at its tip a low antiplectrum cuts across the marginal furrow. The flanks of the axis are straight to slightly concave, and there are seven to eight annulations and a minute triangular terminus. Each annulation bears a pair of large and low muscle scars. In the front the axis is about 0.25 of the pygidial width. The fulcra are placed far apart, more than half way abaxially from the axial furrow; the facets are depressed, bound in the rear by a high step of the test which served as a firm stop for the segmental pleura in uncoiling. Pleural ribs and furrows are almost obsolete, but in some specimens (Plate 11, figure 9) up to five pairs of flat ribs can be seen in low-angle illumination. The border is narrow (about 0.13 of pygidial length), slopes outward, and is defined by a shallow furrow.

On the ventral side the doublure is narrow and bears terraced lines; in the cephalon the doublure is continuous and a rostral shield is absent.

*Comment on illustrated specimens:*

The first seven described specimens were collected at locality W20, in a single bed of the Georgina Limestone.

The complete specimen (the holotype), Plate 11, fig. 4, CPC 5443, silicified, and flattened on a shale lamina, is 15.6 mm long. It is worn, but displays all essential parts, including the rim and most of the right palpebral lobe. The cheek unit is displaced to the left in the process of moulting and the right cheek is overridden by the cranidium. A rostral shield is absent; a splinter of the doublure is displaced upward, but should not be mistaken for the

rostral shield (1) because it is not in a sagittal position and (2) because its flanking fractures are uneven. A fragment of another fossil occupies the approximate position of the hypostoma. The left fulcral line of the thorax is rather distinct, and the free cheeks are venulose.

The complete specimen, Plate 11, fig. 6, CPC 5445, is 10·7 mm long; it is relatively small, but mature, having the same number of segments as the much larger holotype. A rostral shield is absent, the frontal doublure is fractured, and the central part of the hypostoma is preserved. During moulting the cranium was dragged forward but the cheek unit remained in its position relative to the thorax.

The thorax and pygidium, Plate 11, fig. 5, CPC 5444, are together 9·0 mm long. The articulating doublures of the axial lobe are exposed.

The silicified pygidium, Plate 11, fig. 10, CPC 5449, is 9·2 mm long. The inside of the doublure is exposed and the muscle spots on the axial annulations are distinct.

The silicified pygidium, Plate 11, fig. 9, CPC 5448, is 8·0 mm long; its test is intact and the pleural ribs are indicated.

The pygidium, Plate 11, fig. 7, CPC 5446, non-silicified, in bituminous limestone, is 6·7 mm long; its test is intact. Note the depressed facets separated by elevated ridges from the rest of the pleural lobes.

The free cheek, Plate 12, fig. 1, CPC 5450, in limestone is 11·0 mm long; it is venulose and the cornea of the eye is retained and bears the imprints of the ocelli.

The two specimens described next come from the Georgina Limestone, locality G50.

The cranium, Plate 12, fig. 2, CPC 5451 is 6·4 mm long. An occipital furrow is absent or vestigial; the sinuosity of the posterior suture and the roundness of the posterolateral tip is apparent.

The pygidium with a part of the thorax, Plate 12, fig. 3, CPC 5452, are together 5·0 mm and the pygidium alone is 3·2 mm long. The narrow axis of the pygidium and the smoothness of the pleural lobes indicate *M. mindycrusta*?

The pygidium, Plate 11, fig. 8, CPC 5447, O'Hara Shale, locality D29, is 7 mm long. It is decorticated, showing the terraced lines of the doublure; the posterior pleural ribs are obsolete, or almost so.

*Occurrence and age:* *B. (Mindycrusta) mindycrusta* occurs in the Georgina Limestone at localities W1, W15, W20, G48, G49, G50, and W301; and in the O'Hara Shale ('lower chert bed') at localities D6, D28, and D29; its age is the Zone of *Glyptagnostus stolidotus*.

#### BLOUNTIA (MINDYCRUSTA) COMPACTA sp.nov.

(Pl. 12, figs 4-6)

*Material:* Two cranidia and one pygidium, all in limestone, are preserved sufficiently to warrant a description; in smaller fragments the species cannot be identified safely.

*Holotype:* The cranium Plate 12, figure 4, CPC 5453, is selected as holotype.

*Generic classification:* The thorax of *M. compacta* is unknown and the question regarding the presence of pleural furrows cannot be answered. Other characters (the sinuosity of the posterior sutures, rounded posterolateral tips, as well as the general aspect), however, indicate a species of *Mindycrusta*.

*Diagnosis:* *B. (Mindycrusta) compacta* is a species with convex glabellar flanks and rapidly tapering glabella possessing an occipital furrow which is abbreviated and shallow, and an occipital node; in the pygidium the pleural ribs are indicated and the pygidial axis is relatively wide and has convex flanks.

It is closely related to the type of the subgenus, *M. mindycrusta*, from which it differs in characters indicated in the diagnosis.

*Description:* The cranium is strongly vaulted, but the glabella rises relatively little above the transverse profile of the cheeks. The anterior sutures cut the frontal margin about half way to the midline. The posterior sutures diverge, are sinuous and cut the posterior border in an outward convex, almost cedariform curve. The brim and the rim are of about equal width, downsloping, and separated by a distinct marginal furrow; in the furrow, the specimen Plate 12, figure 5, possesses small, irregularly-spaced knobs instead of pits and the rim recedes in the middle and forms a somewhat incipient plectrum. The occipital furrow is shallow, narrow, and abbreviated, and replaced on its flanks by large but low lobules. The occipital lobe is inconspicuous and coincides with the glabellar profile; it bears a weak median node and is as long as about 0.22 of the glabella. (In *Blountia* the occipital furrow is transcurrent and the occipital lobe is narrower and depressed down in a step in relation to the glabella, as can be seen for example in *B. nixonensis* Lochman (Palmer, 1954, pl. 79, fig. 4).) The interocular cheeks are horizontal and as wide as about 0.2 to 0.25 of the glabella. The palpebral lobes are small (0.3 of glabellar length), oblique, curved in the posterior half, and defined by shallow palpebral furrows; they are placed opposite the anterior half of the glabella. Vestigial ocular ridges are present. The glabellar flanks are visibly convex, the glabella tapers rapidly (opposite the tips of ocular ridges it is 0.6 of the maximal width in the rear) and has a subangular front. Three pairs of vestigial glabellar furrows can be seen; the glabellar front bears a tiny tubercle of the kind seen in *Irvingella tropica* (Öpik, 1963). Presumably such a tubercle will be found in several more ptychoparioids. The brim is venulose, and the posterior limit of the veins marks the vestigial ocular ridges. The test is smooth or, probably, minutely, almost imperceptibly, granulose.

The pygidium is semicircular; its relatively flat axial lobe is about 0.27 of pygidial width; there are eight axial annulations and six pairs of flat pleural ribs; the flanks of the axis are convex outward. The border is flat, depressed, and as wide as about 0.15 of pygidial length. The pygidial cast is densely punctate (the inner surface is pustulose)—a feature known in some other species of *Blountia*. The pygidium of *B. (Mindycrusta) compacta* compares well with *Blountia carlotta* Lochman (see Lochman & Hu, 1961, pl. 28, fig. 34) as regards the relief of the pleural ribs, their number, and the number of axial annulations; but in *carlotta* the axial lobe is broader and the border is wider (about 0.22 of pygidial length).

*Comment on illustrated specimens:*

All illustrated specimens were found in the Georgina Limestone at locality G50, in one and the same piece of rock.

The holotype cranium, Plate 12, fig. 4, CPC 5453, is 7 mm long (chord between the margins of the test). The illustration (fig. 4a) is made in a horizontal attitude (palpebral lobes about horizontal); in this projection the specimen is about 6.7 mm long. Because of this attitude, the glabella, especially its steeply sloping front, appears to be relatively short.

The cranium, Plate 12, fig. 5, CPC 5454, is 10.5 mm long; it is illustrated in various attitudes, to facilitate a comparison with *M. mindycrusta*, which has a less tapering glabella. The brim is venulose; vestigial ocular ridges and glabellar furrows are indicated; the knobs in the marginal furrow are prominent and the tumid lobules at the ends of the abbreviated occipital furrow are distinct. In front view the small node of the glabellar tip is visible.

The pygidium, Plate 12, fig. 6, CPC 5455, is 5.0 mm wide and 4.7 mm long without the articulating half-ring; the punctuation of the cast of the pleural lobes and the border is visible; the test is thick.

*Occurrence and age:* *B. (Mindycrusta) compacta* was found in the Georgina Limestone at locality G50; it is probably present also at W1, W15 and G48. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

BLOUNTIA (MINDYCRUSTA) NOTOSTENA sp.nov.

(Pl. 13, figs 1, 2)

*Material:* One cranidium and one pygidium have been found associated in the same piece of rock; they differ in size and belong to two separate individuals.

*Holotype:* The pygidium, Plate 13, fig. 2, CPC 5457, is selected as the holotype because it is specifically more distinctive than the cranidium.

*Diagnosis:* *B. (Mindycrusta) notostena* is a species with a subangular glabellar front, and with a distinct but wavy occipital furrow; distinguished by relatively narrow palpebral lobes, by a prominent occipital node, and a pygidium with effaced pleural lobes, a rather narrow and convex border, a well defined marginal furrow, and a slender and narrow pygidial axis.

*Differential diagnosis:* The cranidial characters are discussed below, in relation to *M. compacta*; the wavy occipital furrow suggests a comparison with *B. (M.) advena* sp.nov., in which this furrow is, however, shallow in the middle.

The pygidium is unique as regards the convexity of the border, the character of the marginal furrow, and the narrowness of the axis and the border.

*Description:* The cranidium, Plate 13, fig. 1, CPC 5456, is 2.7 mm long, but lacks the posterolateral limbs. Its general aspect is the same as in *M. compacta*, from which it differs as follows: (1) The occipital node is prominent (in *compacta* vestigial); (2) the abbreviated occipital furrow is distinct and wavy (vestigial in *compacta*); (3) the glabella tapers to about 0.7 of its maximal posterior width (0.6 in *compacta*), and (4) the palpebral lobes are narrow, evenly curved, and well defined by palpebral furrows (in *compacta* they are broad, asymmetrical, and the palpebral furrows are vestigial).

The apparent duplication of the occipital lobe seen in the illustration is produced by the imprint of the articulating doublure.

Similar to *compacta* are the slightly convex brim, pits in the marginal furrow, veins on the brim, the size (0.3 of glabellar length) and position of the palpebral lobes, the width (0.22 of glabella) of the interocular cheeks, the angularity of the glabellar front, the vestigial glabellar furrows (the posterior furrows are also forked), and the smoothness of the test. The ocular ridges are flat and broad and somewhat better defined than in *compacta*.

The holotype pygidium, Plate 13, fig. 2, CPC 5457, is 4.0 mm long. It is semi-circular; the pleural lobes are slightly tumid and effaced, except for the anterior pleural furrows, which only rarely become obsolete in trilobites. The fulcra are far apart, the facets well defined. The border is convex and very narrow (0.1 of pygidial length), and the marginal furrow is distinct and deep. The axial lobe is also rather

narrow (0.2 of pygidial width), straight-sided, slender and evenly tapering; it terminates in a conspicuous antiplectrum which merges with the border interrupting the marginal furrow. The left and the right limb of the marginal furrow turn forward and join the axial furrows along the flanks of the antiplectrum. The axial lobe consists of seven complete and one incomplete annulations and a rather small terminus. The test is smooth.

*Occurrence and age:* The described specimens of *B. (Mindycrusta) notostena* come from the Pomegranate Limestone, locality B537, on Wills Creek; the age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

BLOUNTIA (MINDYCRUSTA) ADVENA sp.nov.

(Pl. 13, figs 3–8; Text-fig. 83)

*Material:* Five cranidia and one pygidium are described and illustrated. The cranidia are selected to present various degrees of flattening which accentuates some characters and obliterates others; the pygidium is the only one found as yet.

*Holotype:* The cranidium, Plate 13, fig. 3, CPC 5458, locality B259, is selected as the holotype because of its exceptional preservation.

*Previous record:* Öpik (1956, p. 23) mentioned the occurrence of ‘an *Elvinia*?-like trilobite’ in the Upper Cambrian on Wills Creek; the comparison with *Elvinia* was suggested by flattened specimens like Plate 13, fig. 8, in which the posterior glabellar furrows are transcurrent owing to accidental deformation.

*Generic classification:* The general aspect of the cranidium and the pygidium indicates an asaphiscid of the subfamily Blountiinae; even a form intermediate between *Blountia* and *Maryvillia* could be assumed. The abbreviated occipital furrow, however, combined with the small and forward placed palpebral lobes indicates a close affiliation with *Mindycrusta compacta*. So, *advena* is interpreted as a species of *Mindycrusta* of a rather low degree of effacement of furrows in the cranidium and the pygidium.

*Diagnosis:* *Blountia (Mindycrusta) advena* is a species with a moderately convex cephalon, a relatively short frontal area, an abbreviated occipital furrow, a smooth test, and fully developed pygidial relief; distinguished by (1) very narrow interocular

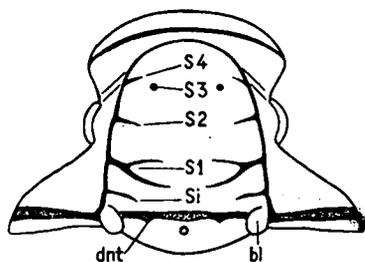


Fig. 83.—*Mindycrusta advena* sp.nov., from Plate 13, fig. 3. dnt—occipital dent; S1—first (posterior), S2—second (‘middle’), S3—third and S4—anterior glabellar furrows; Si—intervening glabellar furrow; Bl—occipital (lateral) lobule.

cheeks (up to 0.13 of glabella), (2) evenly rounded (not angular) glabellar front, (3) deep and wavy lateral sections of the occipital furrow, (4) the presence of a fifth intervening pair of glabellar furrows in addition to the ‘full set’ of four pairs, and (5) raised interpleural ridges (replacing interpleural grooves) in the pygidium.

*Differential diagnosis:* *M. mindycrusta*, *compacta*, and *notostena* have fused pygidia, wider interocular cheeks, and subangular glabellar fronts; *M. mindycrusta* has no occipital furrow, in *compacta* this furrow is faint and of even depth, and in *notostena* it is more distinct, but still evenly deep. *Blountia georginae* has a different cranial structure, but its pygidium recalls *advena*, except for the presence of interpleural grooves instead of ridges.

*Description:* The cephalon is vaulted, sloping forward in an even arc; the brim deviates only slightly from the sagittal curve of the glabella, but the rim changes to a shallower slope and is only slightly convex. The interocular cheeks are slightly tumid and sloping towards the palpebral lobes; the posterolateral limbs are convex and moderately geniculate at the fulcra; the glabella, in transverse section, rises relatively little out of the arc of the cephalon. In *M. advena* the cephalon is less tumid than in *M. mindycrusta* or *M. compacta* or most of the species of *Blountia*.

In the cephalon the anterior sutures are first straight and divergent, then turn within the rim abruptly toward the midline, and reach the margin at an undefinable distance from the middle. The cranial margin is arched strongly forward; and the rim is visibly longer than the brim, both together being about 0.16–0.17 of cephalic and about 0.25 of glabellar length. Both are only slightly convex, but the brim has the steeper slope.

The posterior sutures are only slightly sinuous, curving evenly rearward and cutting the posterior border at an almost right angle. The posterolateral limbs are large, triangular, and subangulate at the tips. The fulcral points are close to the axial lobe, at a distance of about 0.15 of the width (transversely) of the occipital lobe.

The posterior marginal furrow is distinct and relatively wide. The frontal marginal furrow is distinct but shallow. The interocular cheek is rather narrow, about 0.12 to 0.13 of glabella; the palpebral lobes are small, between 0.25 and 0.3 of glabellar length and placed in front of the midpoint of the glabella. The ocular ridges are distinct and strongly slanting, and the palpebral furrows are also distinct.

The occipital lobe, about 0.25 of glabellar length, is slightly convex and bears a distinct occipital node. The occipital furrow (Text-fig. 83) has a peculiar structure: it is abbreviated, as in *M. compacta* and in *Iniotoma iniotoma*, with ends closed by a pair of tumid lobules; the middle part of the furrow is shallow and wide; laterally it is deep and narrow, but wavy in the rear. It appears that the lateral 'deep' of the occipital furrow functioned as apodems for a relatively complicated set of ligaments and muscles.

The axial furrows are narrow and relatively deep, sunk in a shallow valley between the cheeks and the glabella; less deep, but still distinct, is the circumglabellar furrow in front of the ocular ridges.

The glabella is only slightly longer than wide, with slightly convex flanks, well rounded in front (without any of the angularity seen in other species of *Mindycrusta*), suboval and tapering, being at the ends of the ocular ridges about 0.75 of its width in the rear.

In exceptionally well preserved material (Pl. 13, figs 3a, b) four pairs of glabellar furrows can be distinguished, arranged as the 'full set' (Öpik, 1961, p. 179); the S 3

furrows are pits and the S 1 furrows are forked. In addition to the 'full set' a fifth pair of furrows (Si) is apparent behind the forked posterior glabellar furrows. Such intervening glabellar furrows occur in some of the Olenidae (see Öpik, 1963).

The test is smooth except for the rather weak and erratic veins in front of the ocular ridges.

The pygidium is elongate (not semicircular as in *M. mindycrusta* and *compacta*), its length being about 0.7 of the width; in its rear a shallow marginal recess is present. The border is relatively flat and narrow and the marginal furrow is distinct; it is scalloped by the ends of the pleural ribs, especially in the anterior part, and somewhat crossed by the pleural furrows. Six pairs of flat but distinct pleurae with oblique and broad pleural furrows are apparent, separated by interpleural ridges (not grooves). The axial lobe, almost 0.3 pygidial width, has straight flanks, about eight distinct annulations, and a tiny terminus reaching with its antiplectrum into the border, and almost to the margin. The test is smooth.

*Comment on illustrated specimens:*

The holotype cranidium, Plate 13, fig. 3, CPC 5458, locality B259, is 7.5 mm long. The matrix is grey phanocrystalline fine-grained sandy limestone; the specimen is undeformed. The test is shiny and displays the delicate and shallow glabellar furrows in a perfection rarely seen in trilobites of low relief. There are four pairs of standard glabellar furrows, and a fifth (Si) pair intervening between the occipital lobe and the forked S 1 furrows (Text-fig. 83). The ocular ridges and the palpebral furrows are distinct.

The next five specimens come from locality D126. The matrix is a grey laminated sandy and lutitic limestone.

The cranidium, Plate 13, fig. 5, CPC 5460, is 8.5 mm long. It is slightly flattened, the palpebral furrows are somewhat diffuse, and the glabellar furrows are vaguely discernible; note the structure of the occipital furrow.

The cranidium, Plate 13, fig. 7, CPC 5462, is 9.6 mm long. In the collapsed glabella the posterior glabellar furrows are almost transcurrent.

The cranidium, Plate 13, fig. 8, CPC 5463, is 11.0 mm long and the largest available. It is flattened, the posterior branches of the forked S 1 furrows became transcurrent, producing an *Elvinia* or *Bernia*-like pattern.

The cranial fragment, Plate 13, fig. 6, CPC 5461, is 5.3 mm long as preserved. The glabellar furrows, including the intervening furrow, and the palpebral lobe and furrow, are distinct; the posterior suture is relatively straight, but the tip of the posterolateral line is rounded.

The pygidium, Plate 13, fig. 4, CPC 5459, is 8.7 mm long and 12.8 mm wide. The thin test is preserved. Its well developed external relief and, therefore, a low degree of fusion and effacement are apparent; the furrowed pleurae are separated by interpleural ridges.

*Occurrence and age:* *Blountia (Mindycrusta) advena* has been found only in the Pomegranate Limestone in the inlier at Wills Creek, localities D126 and B259; its age is the Idamean Zone of *Glyptagnostus reticulatus* (lower part).

BLOUNTIA (?MINDYCRUSTA) GEORGINAE sp.nov.

(Pl. 10, figs 10 and 11)

*Material:* One pygidium and one cranidium are illustrated and described; a second pygidium has been found at the same locality (W10) a bit lower down in the sequence (in beds of the Zone of *Corynexochus plumula*).

*Holotype:* The pygidium Plate 10, fig. 10, CPC 5437, is selected as the holotype; the cranidium associated with the pygidium in the same piece of limestone is fragmentary and, therefore, less suitable to serve as a holotype.

*Diagnosis:* *Blountia* (?*Mindycrusta*) *georginae* is a species with a subangular frontal lobe of the glabella and with a wide frontal area; distinguished by the position of the palpebral lobes opposite the glabellar midpoint, by an almost transcurrent occipital furrow which is rather shallow at the abaxial ends, and by an unfused pygidium with well developed interpleural grooves.

*Differential diagnosis:* The nearest species is, apparently, *B. (M.) advena*; but it differs by its pygidial interpleural ridges. *M. advena* has also narrower interocular cheeks, eyes placed more forward, a narrower frontal area, and an occipital furrow abbreviated by lobules. Other species are distinct by their fused pygidia, narrow frontal area, forward placed eyes, and abbreviated occipital furrow.

*Subgeneric classification:* The assignment to the subgenus *Mindycrusta* is questioned because the occipital furrow is almost transcurrent and not visibly abbreviated; furthermore, the position of the palpebral lobes in *georginae* opposite the glabellar midpoint is unusual in the Blountiinae, but characteristic in the Asaphiscinae.

*Description:* The cranidium Plate 10, fig. 11, CPC 5438, is 8.0 mm long. The cranidial margin is strongly arched forward; the anterior sutures are strongly divergent; within the rim they remain dorsal for a relatively long distance, but the point at which they intercept the margin cannot be clearly established. The frontal area is 0.3 of glabellar, and 0.2 of cephalic length, and therefore longer than in the other species; the rim is gently convex and almost double the length of the brim.

The frontal cranidial area is relatively wide, about 2.2 of the width of the glabella in its rear; it is much wider than in *advena* and the others, where it is only about 1.2. The occipital lobe is relatively short (0.23 of glabella) and a node is absent. The occipital furrow is straight, shallow and wide in the middle, with rather shallow ends connecting the axial furrows; but half way between the midline and the abaxial ends the furrow is deepened in a manner seen in *advena*. The palpebral lobes are small (0.3 of glabellar length) and placed almost opposite the glabellar midpoint.

The interocular cheek is slightly tumid and 0.27 the width of the glabella, and consequently, much wider than in *advena*. The axial furrows are relatively deep throughout. The glabella is longer than wide, with convex flanks which are almost parallel behind the palpebral lobes, and the glabellar front is subangular, as in *M. mindycrusta* and *M. compacta*. The brim is delicately venulose, numerous small knobs are present in the frontal marginal furrow, but otherwise the test is smooth.

The holotype pygidium (Pl. 10, fig. 10) is 6.3 mm long, and 10.5 mm wide, and, therefore, elongate (as in *advena*) and not sub-semicircular as in the earlier species of *Mindycrusta*. The border is narrow and flat, defined by a shallow marginal furrow. Seven pairs of flat pleurae are marked off by interpleural grooves (not ridges, as in *advena*) and are channelled by oblique and relatively wide pleural furrows; the grooves and furrows in the anterior part of the pygidium cross the marginal furrow; in the posterior part, however, they stop at the furrow. The pygidial axial lobe, 0.23 of pygidial width, consists of eight annulations, and a small terminus;

the somewhat bulbous antiplectrum almost reaches the margin and interrupts the marginal furrow in a manner seen in *B. (M.) notostena* sp.nov. Pygidia with well developed interpleural grooves and pleural furrows are rare among the Blountiinae and unknown in the Asaphiscinae. A pygidium of this kind, with well developed furrows and grooves, has been described by Lochman (Lochman & Duncan, 1944, pl. 11, fig. 34) as *Blountia* cf. *carlotta*. In a pygidium of *B. carlotta* Lochman (Lochman & Hu, 1961, pl. 28, fig. 43) the pleural furrows and grooves also cross the marginal furrow in a manner seen in *B. (?M.) georginae*. *B. carlotta* has, however, a much broader pygidial axis and a wider border.

*Occurrence and age:* *Blountia* (?*Mindycrusta*) *georginae* has been found in the Georgina Limestone at locality W10, at two Idamean levels. The described specimens belong to the lower part of the Idamean *Erixanium sentum* Zone; another pygidium was identified about ten feet below, in beds of the *Corynexochus plumula* Zone.

### Superfamily DIKELOCEPHALACEA Miller, 1889

#### Family IDAHOIIDAE Lochman, 1956

The genera *Idahoia* Walcott, *Saratogia* Walcott, 1916, *Meeria* Frederickson, and *Wilbernia* Walcott constitute the core of the Idahoiidae; they are named in order of decreasing probability as regards their familial affiliation. Harrington et al. (1959) include three more genera in the Idahoiidae: *Bellaspidella* Rasetti, *Comanchia* Frederickson, and *Pseudosaratogia* Wilson. *Bellaspidella* and *Comanchia* cannot be placed in a definite family, and their affiliation with the Dikelocephalacea is doubtful. *Pseudosaratogia*, however, is probably affiliated with the Elviniidae (Palmer, 1960, p. 101). Hupé (1955) included *Idahoia* and *Saratogia* in his family Parasolenopleuridae; Tchernysheva et al. (1960, p. 109) placed *Idahoia* (with a query) in the family Liostracidae Angelin (= Andrarinidae Raymond; see Harrington et al., 1959), and *Wilbernia* (op. cit., p. 97) in the Asaphiscidae, following Hupé's (1955) classification. These diverse classifications, being subjective, reflect the scarcity of information regarding the organization of the involved forms.

#### Genus SARATOGIA Walcott, 1916

Only one species—*Saratogia calcifera* (Walcott)—remained till recently in the genus. Walcott (1916a, p. 196) lists eight species, most of which were transferred into *Idahoia* (Bell et al., 1952); some are placed in *Aphelaspis* (*Clevelandella* Resser, 1938); the Chinese species *Saratogia tellus* (Walcott, 1913) belongs, apparently to *Annamitia* Mansuy.

*Saratogia calcifera* is known from cranidia, free cheeks, and pygidia, and has been adequately described by Walcott; diagrams are published by Harrington et al. (1959) and Hupé (1955.)

Lochman & Hu (1959) recently revised the generic concept of *Saratogia*, and its relation to *Idahoia*, and described a new species, *S. fria*.

Bell & Ellinwood (1962) included in the genus also *Minkella americana* and *Idahoia (Meeria) modesta*, both of Lochman & Hu (op. cit.). All these species

differ clearly from *S. vetusta* sp. nov. and a comparison is, therefore, omitted. Finally Grant (1962, p. 988) comments on the difference of *Saratogia* from *Idahoia* and derives *Saratogia* from *Psalaspis* (op. cit., p. 983) but without convincing evidence.

SARATOGIA? VETUSTA sp. nov.

(Pl. 30, fig. 4; Text-fig. 84)

*Material:* Only the illustrated holotype cranidium, CPC 5593, has been found; it is 3.5 mm long, silicified, partly corroded, but not flattened.

*Diagnosis:* *Saratogia? vetusta* is a species of the family Idahoiidae related to *Saratogia calcifera* (Walcott); distinguished by its large frontal area, narrow rim, broad marginal furrow, relatively great width across the palpebral lobes and the position of these lobes slightly behind the glabellar midpoint.

The description (below) includes also the differential diagnosis in relation to *Saratogia calcifera* (Walcott).

*Generic classification:* *Saratogia? vetusta* fits the diagnosis of the family Idahoiidae (Lochman, 1956, p. 459); the nearest genus is *Saratogia*, the diagnosis of which remains substantially unchanged with the inclusion of the new species *vetusta*. Nevertheless, the generic classification is queried because (1) the free cheek and the pygidium are as yet unknown, and (2) *vetusta* is much older than *Saratogia calcifera* and the hitherto known Idahoiidae, which are middle to late Upper Cambrian. In passing, Lochman, (1956) believes that the Idahoiidae arose 'sometime during the late Dresbachian' (that is, in the Idamean). The early Dresbachian *Saratogia vetusta* sp. nov., however, indicates that the Idahoiidae and the Dikelocephalacea are older than the Idamean, and are not natives of North America, as presumed in the phylogenetic hypothesis of Lochman. Of course, the degree of the affiliation of the Idahoiidae, including *Saratogia* and *S. vetusta*, with the Dikelocephalidae is itself a matter of further inquiry.

*Description:* The anterior sutures are slightly sinuate and moderately divergent; within the rim they converge in even curves and intercept the margin at undefinable points more than half way from the anterolateral corners towards the midline. The posterior sutures diverge strongly and delineate long (transversely) and narrow

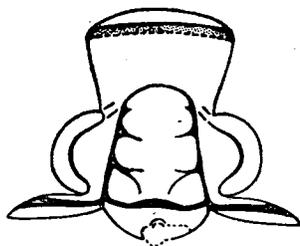


Fig. 84.—*Saratogia? vetusta* sp. nov., from Plate 30, fig. 4.

blade-like posterolateral limbs. The frontal area is rather long, slightly longer than in *Saratogia calcifera*, approaching the size seen in *Idahoia*. It is as long as 0.6 of the glabella, 0.5 of glabella and occipital lobe together and about 0.3 of the cranidium. It is as narrow as in *S. calcifera*, about 1.1 of glabellar length. The rim is

short, convex, and upturned, and separated from the brim by the broad, concave marginal furrow, which is even less defined than in *S. calcifera*. The frontal width of the cranidium is 0.7 of the width across the palpebral lobes, in *S. calcifera* it is about 0.8. The brim slopes gently forward and is delicately venulose. The palpebral lobes are placed slightly behind the glabellar midpoint, are broad, arcuate, and as long as about 0.65 of the glabella and consequently about as large as in *S. calcifera*. The ocular ridges are faint. The interocular cheeks are slightly wider than 0.3 of glabellar width, tumid, adaxially sloping, and bear faint radiating veins. The cusps of the palpebral lobes are rather close to the axial furrows.

The glabella is truncate, conical, tapering, and slightly longer than wide. Three pairs of glabellar furrows are present, as strong as, and similarly arranged to, *S. calcifera*; the posterior furrows are forked (compare *S. calcifera*, Walcott, 1912, pl. 43, fig. 8).

In the illustrated specimen the occipital lobe is fragmentary; a remnant of an occipital node, or even an occipital spine is still apparent.

The test is minutely granulose.

*Occurrence and age:* *Saratogia? vetusta* sp.nov. comes from the Georgina Limestone, locality W20; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Family CONOKEPHALINIDAE Hupé, 1955

The following three genera belong to the family Conocephalinidae:

(1) *Conocephalina* Brögger; *C. ornata* is its type, and the only known species. After Brögger's original publication (1878, pl. 3, figs 5-7) no new material has been published; the diagram in Harrington et al. (1959, p. 0237) of *C. ornata* is utterly misleading. Compare also the photograph of *ornata* in Kobayashi (1962, pl. 9, fig. 18).

(2) *Wuhuia* Kobayashi, based on *Conocephalina belus* Walcott, which is the only certain species of the genus.

(3) *Lobocephalina* Ruzicka, based on *Lobocephalina emmrichi* (Barrande) revised by Snajdr (1957).

All modern authors include *Conocephalina* and *Lobocephalina* in the same family (or subfamily), but disagree regarding other genera; ten genera are involved, but these will not be discussed further.

A somewhat similar disagreement exists regarding the superfamilial classification of the Conocephalinidae. According to Harrington et al. (op. cit.) it is a subfamily of the Ptychopariidae—a rather speculative interpretation. The large eyes close to the glabella and the shape of the glabella suggest, however, an affiliation with the Saukiidae; furthermore, *Wuhuia belus*, according to Lochman (1956), may be 'a late *Conaspis* species' and Lochman postulates 'that the line of descent of the Saukiidae began with one of the variants of *Conaspis perseus*'. The origin of the Saukiidae, however, pre-dates the arrival of *Conaspis* and *Wuhuia*, but not of the Conocephalinidae in general, which are Middle Cambrian as well. The Saukiidae and the Conocephalinidae are regarded, therefore, as independent families of a common descent, and superfamily.

It should be noted that *Conocephalina ornata* is known insufficiently to serve as a familial 'yardstick', and that the reasoning is based, therefore, on the well known *Lobocephalina emmrichi* (Barrande).

*Lobocephalina pyriceps* sp.nov. represents the Conocephalinidae in the Mindyallan of Australia.

#### Genus LOBOCEPHALINA Ruzicka, 1939

Snajdr (1957) surveyed all Bohemian species hitherto attributed to the genera *Conocephalina* and *Lobocephalina* and placed all of them in the synonymy of *Conocephalina emmrichi* (Barrande). The diversity of species, according to Snajdr, is not taxonomic but accidental, being referable to tectonic deformation.

The synonymy of *Lobocephalina* and *Conocephalina* Brögger, 1886, suggested by Snajdr in 1957 is subjective, and based on the then inadequate information regarding the type of *Conocephalina ornata* (Brögger).

The disparity of *emmrichi* and *ornata*—the almost straight-sided glabella of the first, and the pyriform glabella of the second species—is relevant. The pyriform shape of the glabella of *emmrichi* is recognizable even in Barrande's original material, including the lectotype (Snajdr, op. cit.), although it is not evident in the traditional textbook illustrations of *Conocephalites emmrichi* Barrande (1852, pl. 11, fig. 4). Kobayashi (1962, p. 76, pl. 9, fig. 18) described and illustrated a plaster cast of *Conocephalina ornata*, which, combined with Brögger's (1878) and Snajdr's data, leads to the conclusion that *Conocephalina* and *Lobocephalina* are separate genera, as summarized below.

1. *Conocephalina ornata* is distinguished by a broad slightly tapering glabella, and denticulate pygidial margin.
2. *Lobocephalina emmrichi* is distinguished by a pyriform glabella, and pygidium without marginal spines.

One notes, however, that the available information regarding the original material of *C. ornata* is still incomplete.

#### LOBOCEPHALINA PYRICEPS sp.nov.

(Pl. 30, figs 1-3; Text-fig. 85)

*Material:* Three cranidia are illustrated, selected from a number of similar specimens.

*Holotype:* The cranidium Plate 30, figure 1, CPC 5590, is the holotype; it is 4.0 mm long (chord); its test is preserved, but somewhat corroded on the glabella. The glabellar furrows in the illustration are obscure, but are clearly visible in a reverse illumination (from the rear) and shown in Text-figure 85; the photograph figure 3a is taken with the palpebral lobes horizontal, and the glabella appears in a shortened projection, the brim reduced and partly concealed by the frontal glabellar lobe. The chordal length of the cranidium, including the brim, is seen in the lateral, and the plectrum in frontal, view.

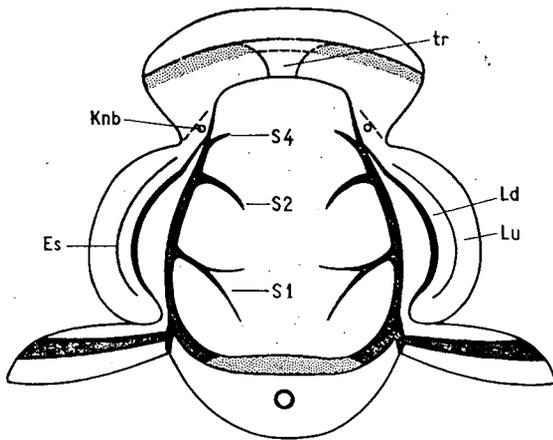


Fig. 85.—*Lobocephalina pyriceps* sp. nov., from Plate 30, fig. 1. Es—ocular striga; Knb—anterior knob; Ld—inner and Lu—outer palpebral lobe; S1, S2, and S4—posterior, middle, and anterior glabellar furrows; tr—plectrum.

**Diagnosis:** *Lobocephalina pyriceps* is distinguished by its (1) pyriform glabella, which is rather tumid in the rear, (2) large palpebral lobes, whose cusps are almost in touch with the axial furrows, (3) diminutive interocular cheeks, (4) diffuse frontal marginal furrow, and (5) plectrum.

**Differential diagnosis:** The Middle Cambrian *Lobocephalina emmrichi* (Barrande) (see Snajdr, 1957) has a less tumid cranidium, a more distinct frontal marginal furrow, wider interocular cheeks, and cusps of the palpebral lobes clearly separated from the axial furrows.

**Generic classification:** *L. pyriceps* possesses essential cranial characters of *Lobocephalina*, that is, a pyriform glabella, large eyes close to the glabella, three pairs of glabellar furrows, and long and narrow posterolateral limbs. Other parts of *L. pyriceps* are, however, unknown and the characters of the cranidium alone are considered. It can be, therefore, speculated that the similarity with *Lobocephalina emmrichi* is familial and that *pyriceps* represents a separate genus of the Conocephalinidae, or even an early form of the Richardsonellidae.

**Description:** The anterior sutures are sinuate and generally divergent but subparallel for a short distance within the posterior part of the rim; farther on they converge in a gentle curve and intercept the margin half way from the cranial corners to the midline. In the middle the suture is marginal and a frontal doublure is absent. The posterior sutures diverge diametrically, defining narrow (longitudinally) blade-like long posterolateral limbs. The posterolateral furrows are distinct. The frontal area is of a medium size, about 0.23 of glabellar length; the rim is somewhat convex in the front, flattens rearward and is about as wide as the brim which is slightly concave; the rim slopes forward and bears a low plectrum. The marginal furrow is shallow and diffuse.

The palpebral lobes are flat, placed rather close to, and opposite the posterior two-thirds of, the glabella with cusps touching the axial furrows. In plan, when the palpebral lobes are in a horizontal attitude, their posterior tips are in line with the glabellar rear. The palpebral lobes are 0.65 of chordal glabellar length and 0.8 of its horizontal projection. The palpebral furrows are distinct but shallow, and

the interocular cheeks diminutive crescents about 0·15 of glabellar width. Strongly slanting ocular ridges are present and remain inseparable from the palpebral lobes. The occipital furrow is distinct and deepened at the ends. The occipital lobe is strongly arched and relatively long, and bears a median node.

The axial furrows are deep, and accentuated in the middle by the tumidity of the interocular cheeks and the steep slopes of the glabellar flanks.

The glabella is strongly arched sagittally and transversely, and rather tumid; the rear rises above the occipital lobe. In the rear the flanks of the glabella are convex, but in the anterior third, concave; the glabellar front is somewhat subtruncate; the posterior glabellar margin curves forward in the middle. The glabella is thus pyriform and tapers forward. Three pairs of glabellar furrows are present, and the posterior furrows are forked. The test is minutely granulose.

The palpebral lobes are divided in two unequal bands by a shallow ocular striga, and a pair of knobs is present just in front of the ocular ridges.

*Comment on illustrated specimens:*

The cranium, Plate 30, fig. 2, CPC 5591, is 5·0 mm long; the frontal area is flattened and shows the divergent anterior sutures. The cranium, Plate 30, fig. 3, CPC 5592, 4·0 mm long, shows the minute granulosity of the test.

*Occurrence and age:* *Lobocephalina pyriceps* is relatively common in the O'Hara Shale ('lower chert bed') at localities D6, D28 and D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Family SAUKIIDAE Ulrich & Resser, 1933

Genus SAUKIA Walcott, 1914

SAUKIA? PRISCILLA sp.nov.

(Pl. 30, figs 5-7)

*Material:* Only pygidia are available: (1) the holotype, Plate 30, figure 7, CPC 5596, Georgina Limestone, locality W1; it is 2·5 mm long, and undeformed; (2) several flattened and fragmentary pygidia in the O'Hara Shale ('lower chert bed'); the fragment, Plate 30, figure 6, CPC 5595, locality D6, is 4·3 mm and the third, Plate 30, figure 5, CPC 5594, locality D29, is 3·1 mm long; this specimen retains its minutely granulose test, but is somewhat deformed laterally.

*Introductory remarks:* As seen from the heading, the Saukiidae are regarded as a family of the Dikelocephalacea as envisaged originally by Ulrich & Resser, 1933. *Saukia? priscilla* sp.nov. is placed in the Saukiidae on morphological grounds, but its generic classification is queried for two reasons: (1) the new species could be placed also without difficulty in the genus *Tellerina* Ulrich & Resser, 1933, which can be conveniently taken as a subgenus of *Saukia* Walcott, 1914, and (2) *priscilla* sp.nov. may represent a separate new genus of the Saukiidae which, however, cannot be established on pygidia alone.

*Differential diagnosis:* The characters indicated in the diagnosis serve to distinguish *S.? priscilla* from all such species of *Saukia* and *Tellerina* as have a gap between the ends of the pleural furrows and the interpleural grooves; species without the gap need not be considered further.

*Description:* The pygidium is transverse, semielliptical, widest about the middle, with a length of about 0.7 of its width. The margin bears no spines, but is subangular in the rear. A marginal furrow is absent, but a flattened border is defined by the distal ends of the pleural ribs. The pleural lobes are sloping outward; the slope is gentle inside, but increases visibly outside the paradoublure line, which coincides with the fulcral geniculation. The pleural furrows and the interpleural grooves are well impressed, and nine pairs of them are present altogether, corresponding to five pairs of pleurae. The interpleural grooves are well incised and broader at the geniculation, but are shallow for a short distance from the axis, indicating, presumably, the advance of the process of fusion. The pleural furrows are relatively narrow but distinct; the propleura are much narrower, and less prominent than the opisthopleura, which are broad and swollen.

The distal ends of the interpleural grooves and pleural furrow approach each other, but gaps remain open between the furrows. The axial lobe is relatively narrow (0.3 of the maximal width), convex and elevated; it is slightly longer than half the pygidium, tapering to a small rounded terminus and having five annulations decreasing in size toward the rear. *Saukia* and *Tellerina* also have five annulations and five pairs of pleurae. Behind the terminus a low, extenuated antipleurum extends almost to the margin.

*Occurrence and age:* The formations and localities are indicated above; the age of *Saukia? priscilla* is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Genus LOPHOLCUS nov.

*Lopholcus* is a monotypical genus, with *L. asper* sp. nov. as its type species.

The new genus is placed here in the family Saukiidae (as discussed below) although it may represent a separate subfamily within the Saukiids.

*Diagnosis:* *Lopholcus* gen. nov. is a genus of Saukiidae Ulrich & Resser distinguished by its accentuated cephalic relief, parallel-sided glabella with laterally expanded posterior glabellar lobes, curved and rearward directed posterior glabellar furrows which are not connected across the glabella, and a pygidium with a large axial lobe reaching the border.

The differential diagnosis in relation to the Saukiidae and the ptychaspidid *Keithiella* Rasetti is included in the discussion of the familial classification of *Lopholcus*.

*Familial classification:* *Lopholcus* can be regarded as of *suae familiae* affiliated with the Saukiidae Ulrich & Resser, 1935; when this is accepted, it is fair to assume that *Lopholcus* and the Saukiidae arose from common ancestors not later than in the Mindyallan, that is, in the earliest Upper Cambrian (early Dresbachian) time.

*Lopholcus* differs from the Saukiids by its strong cephalic relief and the disconnected posterior glabellar furrows, which are transcurrent in the Saukiids. The cranidial design of *Lopholcus* is, however, the same as in *Prosaukia*, *Saukia*, *Calvinella* etc., as seen from the size, structure, and position of the palpebral lobes, the long and subrectangular glabella, the structure of the rim and the frontal border furrow, the convex-outward anterior sutures, and the granulose and lineate ornament. Furthermore, a cephalic relief as strong as in *Lopholcus* is present in *Keithiella*

Rasetti, 1944. In *Keithiella maior* Rasetti (1945, pl. 61, figs 6, 7) the rim is also an elevated ridge, the border furrow is deep and deviates forward on the flanks, as in *Lophoholcus*. *Keithiella* is, nevertheless, distinguished from *Lophoholcus* by its transcurent glabellar furrow, smaller palpebral lobes, and laterally expanded glabella. It appears that *Keithiella* itself belongs to the Saukiidae rather than to the Ptychaspididae Raymond, 1924. This is, however, of minor significance in view of the close affiliation of the families.

The cranium of the saukiid from China in Chu (1959, pl. 7, fig. 14) also belongs to *Lophoholcus*.

LOPHOHOLCUS ASPER sp.nov.

(Pl. 31, figs 4-6; Pl. 32, figs 1-4; Pl. 33, fig. 1; Text-fig. 86)

*Material*: Six crania and one pygidium are illustrated. A free cheek is also described, which probably belongs to *L. asper*. The crania are relatively common but most of them are fragmentary or deformed.

*Holotype*: The cranium Plate 32, fig. 1, CPC 5603 is selected as the holotype because of its large size and absence of deformation; the palpebral lobes and posterolateral limbs are incomplete, but can be seen in the other illustrated specimens.

The generic diagnosis serves as the diagnosis of the species *L. asper*.

*Description*: Crania ranging in length from 1.5 mm to 6 mm have been examined; within these limits no perceptible differences have been observed, and the small specimens are therefore regarded as already mature.

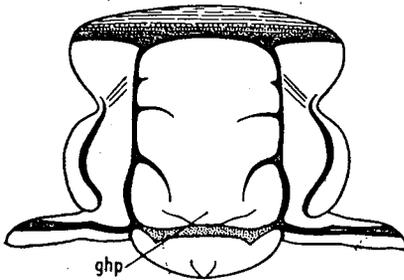


Fig. 86.—*Lophoholcus asper* gen.nov., sp.nov., combined from Plate 31, fig. 4; Plate 32, fig. 1; Plate 33, fig. 1. ghp—tumid rear of glabella ('hump').

The outline of the cranium is subrectangular. The posterolateral limbs are narrow and, when flattened, almost as long (transversely) as the occipital lobe. The posterior sutures diverge greatly and are almost straight. The fulcral points are placed about the middle of the posterolateral limbs. The posterolateral furrow is very deep and in some specimens the palpebral furrow appears to be connected with it. The anterior sutures are convex outward, then, within the rim, turn adaxially and reach the margin about opposite the corners of the glabella. A brim is absent; the rim is very prominent, steep in the front and somewhat retroverted, overhanging the marginal furrow, and covered by relatively coarse lines. The palpebral lobes are long, variable, about 0.5-0.54 of glabellar length, and are well defined by the palpebral furrows, which even by-pass the tips of the lobes. The interocular cheeks, 0.3 of glabellar width, are moderately convex and slope down into the axial furrows. The

distance of the anterior palpebral tips is about 0.25 of glabellar width and the mid-points of the palpebral lobes are opposite the midpoint of the posterior 0.6 of the glabella. The ocular ridges are slanting but rather weak and not always discernible; the ridges appear, nevertheless, double.

The occipital lobe, 0.3 of glabellar length, is straight in front and slopes forward; it bears a submarginal conical prominent node and weak occipital dents.

The axial furrow is deep all around the glabella. The glabella has parallel flanks, but is slightly expanded in the rear; its front is well rounded at the corners and weakly arched forward; longitudinally the glabella is well arched, especially in its anterior part which slopes rather steeply; transversely it slopes like a gable roof down from a rounded or even subangulate crest. The rear of the glabella is well marked by its vertical edge; the part between the posterior glabellar furrows rises like a somewhat tumid hump. Three pairs of glabellar furrows are present. The posterior furrows are curved rearward, defining a pair of laterally expanded lobes, and the anterior furrows are short, weak, and oblique.

The pygidium is vaulted, with a prominent broad almost parallel-sided axis which reaches the border; four annulations are present, and the terminus is rounded. Three pairs of pleural furrows are distinct, but only two pairs of interpleural grooves are developed. The foremost pleurae are well defined and indicate falcate pleural tips; they belong, apparently, to the last and not yet separated segment of the thorax.

The surface of the test is granulose.

The free cheek, Plate 31, figure 5, probably belongs to *Lophoholcus asper* because (1) its border gains in convexity and prominence anteriorly in accordance with the prominent cranial rim; (2) the position of the ocular aperture and its length correspond to the palpebral lobe; and (3) the edge of the anterior suture fits the cranium. The cheek is distinguished by a subocular step which fades out at the anterior suture and before reaching the posterior furrow; the surface is granulose and venulose.

*Comment on illustrated specimens:*

All specimens, except for the free cheek, come from locality D29; the matrix is friable silica.

The holotype is 5.0 mm long; it is not deformed. Subsequently (as seen in the lateral view) it lost its occipital spine. The ornament is less distinct than in the other specimens.

The cranium, Plate 31, fig. 4, CPC 5600, is 4.6 mm long. Note the 'hump' of the tumid glabellar rear. The ornament is distinct, the third glabellar furrows are indicated, and so is the ocular ridge. The rim is deformed and pressed against the front of the glabella, as seen in the lateral view.

The cranium, Plate 33, fig. 1, CPC 5611, is 3.5 mm long; a transverse fracture takes the place of the anterior glabellar furrow; the rim is slightly flattened.

The cranium, Plate 32, fig. 3, CPC 5606, (frontal view only) is 1.8 mm long. It is a small specimen, but its proportions are the same as in the holotype.

The fragmentary cranium, Plate 32, fig. 4, CPC 5607, is 6.0 mm long. It shows the extent of the posterolateral limbs, and the lineate frontal ornament. The associated free cheeks belong to *Auritama*.

The cranium, Plate 32, fig. 2, CPC 5604, is 6.0 mm long; owing to some flattening, it shows clearly the three pairs of glabellar furrows; the left palpebral lobe, the line of the anterior suture and the granulose ornament are preserved.

The pygidium, Plate 31, fig. 6, CPC 5602, is 2.3 mm long and about 4.2 mm wide. The granulation is well preserved. Note the anterior interpleural partition which defines a falcate but still fused pleura.

The free cheek, Plate 31, fig. 5, CPC 5601, locality D6, is 2.3 mm long.

*Occurrence and age:* *Lophoholcus asper* sp.nov. is known only from the O'Hara Shale ('lower chert bed') localities D6, D28, and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Family DIKELOKEPHALINIDAE Kobayashi, 1936

The Dikelokephalinidae was originally established as a subfamily of the family Dikelocephalidae Miller, 1889. In his latest classification Kobayashi (1962, p. 132) applies higher taxonomic categories, but retains the Dikelokephalinidae in the superfamily Dikelocephalacea of his suborder Dikelocephalida. Lochman (1956, p. 453) considers that 'the Dikelokephalinidae Kobayashi, 1936, is a separate family in no way related to the Dikelocephalidae,' but it 'gave rise to the dominant Asaphoidae of the Lower and Middle Ordovician', and in Harrington et al. (1919) the Dikelokephalinidae are classified as Asaphina. This classification, however, has no morphological support and Kobayashi's view should be favoured instead. In the early Upper Cambrian (Mindyallan) the Asaphidae (*Griphasaphus* gen.nov.) and the Dikelokephalinidae (*Nomadinis* gen.nov.) are already present, and the one cannot, therefore, be derived from the other. The much younger *Dikelocephalus*, however, can be regarded as a modified dikelocephalinid in which the alae (or bacculae) became suppressed externally.

The Mindyallan form is *Nomadinis pristinus* gen.nov., sp.nov.

#### Genus NOMADINIS nov.

The type species of *Nomadinis* is *N. pristinus* sp.nov.; the genus is monotypical.

*Diagnosis:* *Nomadinis* is a dikelocephalinid with cranidial outlines recalling a *Dikelocephalus* or *Asaphopsis* with bacculae (convex alae); distinguished by its well-marked paradiplural lines, very large palpebral lobes, strongly indented occipital lobe, a short triangular pygidial axis of three annulations, and delicate ornamental lines on the interocular cheeks, palpebral lobes, and pygidial pleurae.

*Comparison:* Paradiplural lines are also present in *Dikelocephalina furca* (Salter; see Lake, 1917, pl. 14, fig. 11) and a weakly indented occipital lobe in *Asaphopsis nakamurai* Kobayashi (1936, pl. 20, figs 19, 20). These forms, however, have small palpebral lobes, alae (not bacculae), and also different pygidia. *Leimitzia* Sdzuy, 1955, is similar to *Nomadinis* in having bacculae (not alae) but is rather distinct in having a well-defined rim. Indeed, the cranidial front of *Leimitzia*, consisting of a rim and brim, is not an asaphid character.

*D. asiatica* Kobayashi, 1934, however, possesses bacculae ('semi-circular callosity on each side of base of glabella', op. cit., 563).

Reminiscent of *Nomadinis* are two pygidia assigned by Chu (1959, pl. 7, figs 3 and 4) to Damesellidae.

NOMADINIS PRISTINUS sp. nov.

(Pl. 32, figs 5-7, Pl. 33, figs 2 and 3, Text-fig. 87)

*Material:* The available material consists of two cranidia and three fragmentary pygidia, of which one is not illustrated.

*Holotype:* The cranidium Plate 33, figure 2, CPC 5612, from locality D29 of the O'Hara Shale ('lower chert bed'), in friable silica, is the best preserved specimen and is, therefore, selected as the holotype.

*Diagnosis and differential diagnosis:* These are the same as for the genus *Nomad-  
inis*.

The pygidia have the same ornament as the cranidium and are therefore considered conspecific; furthermore, there is no other trilobite present to which such pygidia could be assigned.

*Description:* The cranidium is broad and relatively flat. The anterior sutures have an elliptical course and remain dorsal; the posterior sutures diverge strongly, but the extent of the posterolateral limbs cannot be established. The brim is relatively flat, somewhat upturned at the margin, and slightly longer than half the

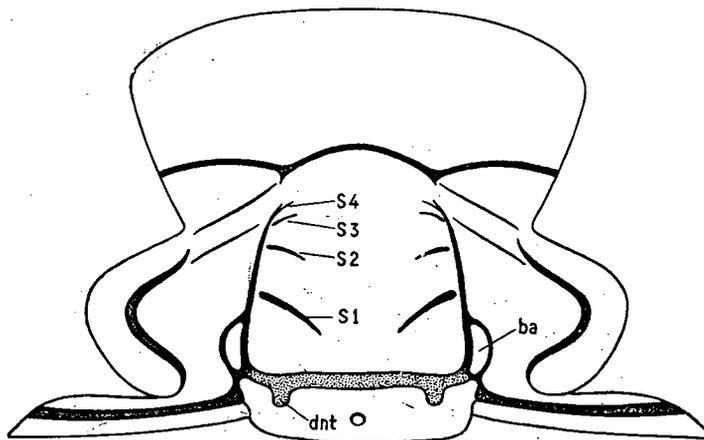


Fig. 87.—*Nomadinis pristinus* gen.nov., sp.nov., from Plate 33, fig. 2. ba—baccula (—ae); dnt—occipital dent; S1-S4—glabellar furrows.

glabella; there is no rim, and no marginal furrow, but the brim is defined in the rear by forward-arched paradoublural lines which coincide with the circumglabellar furrow. The interocular cheek is relatively wide, as wide as half the glabella. The palpebral lobes are broad, well-defined by palpebral furrows, arcuate and rather long, about 0.75 of glabellar length. They are placed well in the rear, with their posterior tips level with the midline of the occipital lobe. The palpebral ridges are slanting and broad, and join the frontal glabellar lobe almost completely, interrupting the axial furrows. The occipital lobe is relatively long, with forward curving ends and an obscure median node; the occipital dents separate the lateral cusps from the median part of the lobe. The occipital furrow is broad, but not well-defined in the rear. The bacculae are tumid, elongate, and placed close to the posterior glabellar lobes. The glabella, as long as wide at the base, tapers moderately,

has slightly convex flanks and a bluntly rounded front. Four pairs of glabellar furrows are present, not quite reaching the axial furrows; the S3 and S4 furrows are short, shallow, and close to the ocular ridge and to each other. The cranial ornament, as far as preserved, consists of a fine reticulation in front of the ocular ridges, and dense delicate lines on the interocular cheeks and palpebral lobes in a pennate arrangement (directed outward and rearward). The pygidium is rather wide, with an indistinct and somewhat concave border, with two or even three pairs of expanding pleural ribs and two pairs of pleural furrows. The axial lobe is conical, rather short (less than half the pygidial length), and consists of three annulations and a short terminus; a long and narrow antiplectrum behind the terminus extends, apparently, almost to the margin. The pygidial margin is incompletely known, but one or more pairs of spines were present. The pygidial ornament, especially on the border, consists of delicate, more or less transversely arranged, wavy lines. This kind of ornament occurs also in *Hungioides* Kobayashi (see Richter, 1954), and in *Hungaia* Walcott (see Rasetti, 1944, pl. 37, figs 3, 6 and 7); of these two genera *Hungioides* belongs to the Dikelocephalinidae, but the affiliation of *Hungaia* and the Hungaiidae remains a matter of contention. The pygidia of *Nomadinis* and *Hungaia* are somewhat similar (the short axis, long antiplectrum, and lineate ornament), the cranidia are rimless, and the glabellar furrows remain separate from the axial furrows, but the designs are otherwise different, and the two genera may not be closely affiliated.

*Comment on illustrated specimens:*

The holotype cranidium is 5.7 mm long; a part of its frontal border is missing; the ornamental lines are preserved on the interocular cheeks and on the palpebral lobe; the glabellar furrows do not reach the axial furrows. The associated agnostid pygidium belongs to *Agnostardis amplinatis*.

The cranidium, Plate 32, fig. 5, CPC 5608, locality D29, is only 2.2 mm long; it is slightly deformed laterally; the frontal margin is upturned.

The fragmentary pygidium, Plate 32, fig. 6, CPC 5609, locality D29, is 6.0 mm long (as preserved); its right lateral margin is intact, and the base of its right spine is partly preserved; ornamental lines are also preserved in parts.

The pygidium Plate 32, fig. 7, and Plate 33, figs 3a and 3b, CPC 5610, locality W1, in bituminous limestone, is 5.0 mm long (as preserved). The delicate ornamental lines are well visible on the rubber cast. A pygidium of *Agnostardis amplinatis* is associated.

*Occurrence and age:* *Nomadinis pristinus* is a rare fossil of the O'Hara Shale ('lower chert bed'), locality D29, and of the Georgina Limestone, locality W1; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Superfamily LEIOSTEGIACEA

Family LEIOSTEGIIDAE Bradley, 1925

Subfamily PAGODIINAE Kobayashi, 1935

The Pagodiinae are represented in the early Upper Cambrian of Australia by nine species of three genera as follows:

Idamean: *Pagodia (Idamea) venusta* Whitehouse, *P. (I.) baccata* sp.nov., *P. (I.) extricans* sp.nov., and *P. (I.) superstes* Whitehouse.

Mindyallan: *Meropalla quadrans* gen.nov., sp.nov., and *M. auriculata* sp.nov.; *Aedotes instans* gen.nov., sp.nov., *A. mutans* sp.nov., and *A. declivis* sp.nov.

The concepts of the genera *Pagodia* Walcott and *Idamea* Whitehouse are clarified below, under the headings of these generic names. *Pagodia* and the Pagodiinae cannot be retained in the Marjumiacea (see Harrington et al., 1959); their place is in the Leiostegiacea; this rearrangement is obvious and needs no further comment.

#### Genus PAGODIA Walcott, 1905

*Summary:* The characters of the genus *Pagodia*, and especially its type species *P. lotos* Walcott, are discussed and compared with *Chuangia*, *Ch. tawenkouensis*, *Eochuangia*, *Chuangioides*, and *Idamea*.

Walcott (1913) described several species of *Pagodia*, including its late Upper Cambrian type species *Pagodia lotos* (Walcott, op. cit., p. 162, pl. 15, figs 12, 12a). Subsequent commentators (Kobayashi, Hupé, and Harrington et al.), however, based their views regarding *Pagodia* not on *P. lotos* (known from fragmentary specimens) but on *P. buda* Resser & Endo, 1937.

*Pagodia lotos* has (1) a forward-arched cranidial margin, (2) a prominent elevated and relatively narrow ridge-like rim, (3) the rim separated from the glabellar front by the deep marginal furrow, (4) no brim, (5) a pitted internal cast of the glabella, (6) no ocular ridges, and (7) two pairs of weak glabellar furrows. The pygidium, as illustrated by Walcott, has (8) four axial annulations and a terminus (Walcott's text, however, reads that the axial lobe is 'divided by three transverse furrows into three rings and a terminus'), (9) interpleural grooves, (10) a slightly concave upsloping border, and (11) no marginal furrow.

The species of *Idamea* described below are close to *Pagodia lotos*; both have a similar structure of the cranidial rim. *Pagodia buda*, however, is distinguished by its elongate glabella from *lotos* and *Idamea*. The cranidium in Harrington et al. (op. cit., p. 0311, fig. 231-8a) referred to as *P. lotos* belongs to some other trilobite.

*Pagodia duliuijiangensis* Chien (1961, p. 124, pl. 3, fig. 11) has the correct, *lotos*-like, cranidial structure; its genal spines are undeflected; the specimen is complete with ten segments and a pygidium as large as 0.6 of the cephalon. The pygidium has a relatively wide depressed border.

The pygidia assigned to various published species of *Pagodia* lack a uniformity of structure—an advantage in specific taxonomy, but a possible source of generic misinterpretations. For example, '*Chuangia*' *tawenkouensis* Sun (Sun, 1935, p. 23, pl. 1, figs 18-14; Lu, 1957, pl. 145, figs 3 and 4) has a *Pagodia*-like cranidial rim, but its pygidium is reminiscent of *Chuangia batia*. *P. tawenkouensis* has no brim and its rim is like *Idamea*—an elevated angulate ridge with strong terraced lines on its front. Similar is '*Chuangia*' *kawadai* Kobayashi (1933, pl. 11, figs 1-3).

The type of *Chuangia* Walcott is *Chuangia batia* Walcott (1913, pl. 17, figs 20-20d; Endo and Resser, 1937, pl. 53, figs 17-22). *Chuangia* has a short brim and a relatively flat rim and differs in these characters from *Pagodia lotos*, *P. buda*, *Idamea*, '*Chuangia*' *tawenkouensis*, etc.

Regarding the stratigraphic distribution of the species of *Pagodia* opinions are divided. Kobayashi (1957; 1960) includes in *Pagodia* only the late Upper Cambrian species and suggests that Endo's Paishanian (= *Idamean*) species (in Endo & Resser,

1937) should be placed elsewhere. Three of Endo's species—*perquadrata*, *laohuensis* and *trisulcata*—however, conform with the characters of *Pagodia* as discussed above.

It appears that three somewhat intergrading groups are represented:

1. *Chuangia* Walcott, with a brim and a depressed rim;
2. *Pagodia* Walcott, without a brim and with a ridged or bar-like rim and relatively narrow interocular cheeks;
3. The '*Chuangia*' *tawenkouensis* group, with a relatively wide cranidium, and interocular cheeks, but with a *Pagodia*-like rim; the pygidia of this group have no defined border. The third group is, probably, close to *Idamea* Whitehouse.

Some 'intermediate' forms like *Chuangia nitida* Walcott and *transversalis* Kobayashi cannot be placed convincingly in any one of the groups above. A refined re-study of the Asian collections is needed to disentangle all classificatory aspects of *Pagodia*, *Chuangia*, and related genera.

*Eochuangia* Kobayashi, 1935, is distinct, with its terminal axial pygidial spine, and stands apart from the three groups. Its cephalon, however, is reminiscent of *Idamea baccata* in the structure of the rim, including the terraced lines on its front, and the deflected genal spine. In passing, a similar spine belongs to *Chuangia batia* (Resser & Endo, pl. 53). Till lately (Harrington et al., 1959, p. 0315) *Eochuangia* was assumed to be a Middle Cambrian trilobite. The list of fossils from the *Eochuangia* Zone of Kobayashi (1962, pp. 8 and 9), however, indicates a post-Kushanian or even a late Paishanian (late Idamean) age (see under '*Olenoides* Zone of Neietsu', Öpik, 1963).

*Pagodia* has been twice recorded in Australia: (1) by Tomlinson in Casey & Tomlinson (1956, 1957, pp. 65 and 71) as *Pagodia* cf. *buda* Resser & Endo, and (2) (ibid, p. 71, Öpik's personal communication) as *Pagodia*. The first is a late Upper Cambrian form represented by several cranidia and pygidia; it is similar to *P. buda* in all aspects, including the ornament; the cranidial rim is angulate on its crest. The second refers to *Pagodia (Idamea) baccata* sp.nov. and its associates (see also Kobayashi, 1957, p. 372; 1960, p. 367).

#### Genus IDAMEA Whitehouse, 1939

*Idamea* is regarded here as a subgenus of *Pagodia*: *Pagodia (Idamea)* (Whitehouse), amended.

The diagnosis of the subgenus can be based neither on the original nor on the supplementary specimens of *Idamea venusta* Whitehouse, because they are insufficient for a conclusive comparison with *Pagodia* and '*Chuangia*' *tawenkouensis* Sun (see under the heading of *Pagodia*). It is assumed, however, that *Pagodia (Idamea) baccata* sp.nov. and *P. (Idamea) extricans* sp.nov. are affiliated generically and subgenerically with *Idamea venusta* and can be legitimately used in the present survey as a basis of a diagnosis.

*Diagnosis*: *Idamea* refers to *Pagodiinae* with a ridged or bar-like rim and somewhat wide interocular cheeks; distinguished by (1) the position of the eyes slightly behind the glabellar midpoint, (2) deflected genal spines, and (3) a pygidium without

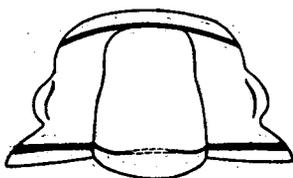


Fig. 88.—*Idamea venusta* Whitehouse, 1939. Diagram from Whitehouse, Pl. 24, fig. 4.

a depressed border and with relatively widely spaced fulcral points. These characters occur in *Pagodia*, *Chuangia*, and *Eochuangia* in different combinations (see under the heading of the genus *Pagodia*).

*Comment:* The characters of the genus *Idamea* and its two species (*venusta*, which is the type, and *superstes*) of Whitehouse are uncertain. The second species, *Idamea superstes* Whitehouse, refers to a single cranidium which is fragmentary, or partly covered by matrix: its specific identity remains, therefore, inconclusive, and will not be discussed further. Whitehouse established *Idamea* on second thoughts for trilobites which he originally attributed to *Pagodia*. He states that in *Idamea* (1) the fixed cheeks are narrower than in *Pagodia*, (2) the occipital ring widens centrally, (3) glabellar furrows are absent, (4) the palpebral lobes are slightly behind the central point, and (5) ocular ridges are absent. All these characters, and their combination, with the possible exception of item 4, correspond to the concept of the genus *Pagodia* Walcott. Furthermore, the illustrated cranidia of *Idamea venusta* are so silicified that any statements regarding the absence or presence of glabellar furrows and ocular ridges and of fine ornament must be inconclusive. The occipital lobe is short in exfoliated specimens of *Pagodia*, but wide in specimens which have their thick test preserved. *Pagodia lotos* (the type of the genus) and associated forms (Walcott, 1913, pl. 15, figs 10–12) are described from exfoliated specimens which display only the rather narrow internal cast of the occipital lobe. The holotype cranidium of *Idamea venusta* (Whitehouse, op. cit., pl. 24, fig. 4) and the second specimen (*ibid.*, fig. 5) are insufficient to substantiate the concept of the genus. From these two, but essentially from the second, I prepared the diagram, Text-figure 88. It appears that the glabella tapers slightly and is somewhat constricted; the interocular cheeks between the anterior tips of the palpebral lobes are half as wide as the glabella; the palpebral lobes are, indeed, slightly behind the glabellar midpoint, and of medium size (larger than, for instance, in *Pagodia buda*). The position of the palpebral lobes and the shape of the glabella compare well with *Pagodia damesi* Kobayashi (1933, pl. 11, fig. 4), but *damesi* is pustulose and has glabellar furrows.

The pygidium associated with *Idamea venusta* (Whitehouse, op. cit., pl. 24, fig. 6) is hardly a pygidium of a pagodiid or leiostegiid trilobite; but I cannot assign it to any of the described or undescribed trilobites of the Georgina Limestone. Seeing, however, that the cranidium of *I. venusta* (Text-fig. 88; pl. 18, fig. 6) has the same organization and proportions as *Pagodia* (*Idamea*) *extricans* sp.nov., I assume that their pygidia should also be similar.

Walcott (1913, p. 172–177) described under the provisional name of *Menocephalus* Owen a group of species distinguished by a granulate, ‘baccate’ ornament. In reference to these forms, Whitehouse (1939, p. 232) compared *Menocephalus*

*acis* Walcott with *Idamea*, and Kobayashi (1960, p. 366) included *Menocephalus? depressus* in *Pagodia*. These forms may belong to the Pagodiinae, but the material is too fragmentary for a conclusive comparison.

According to Whitehouse, *I. venusta* was collected at a place fourteen miles south of Glenormiston, and *I. superstes* in the vicinity of Tyson's Bore, apparently at Mt Idamea, within the outcrop area of rocks of the *Corynexochus plumula* Zone.

PAGODIA (IDAMEA) VENUSTA (Whitehouse, 1939)

(Pl. 18, fig. 6; Text-fig. 88)

*Material*: Two cranidia, of which the larger and better preserved specimen (CPC 5509) is illustrated.

The characters of *P. venusta* have been discussed. Some differences are still apparent in the glabella: Text-figure 88 shows it slightly constricted, whereas in our specimen it appears to have straight flanks, which may be the result of accidental distortion; in the second cranidium, not illustrated and fragmentary but otherwise undistorted, the glabella is constricted. Furthermore, glabellar furrows are according to Whitehouse absent in *I. venusta*, which, presumably, is the result of an extreme silicification of the type of material. An occipital node is absent, but the occipital lobe carries a particle of unremovable silica. The illustrated specimen is a silicified test developed from the matrix (sandy limestone) by acid, drill, and needle.

The cranidium is 7.5 mm long (from edge to edge), and about 6.4 mm in horizontal projection. In the front it is 7.4 mm, and between the tips of the posterolateral limbs 11.0 mm wide. It is convex, arched longitudinally and sloping evenly forward, with slightly tumid cheeks and downsloping geniculate posterolateral limbs. The anterior sutures are convergent and almost straight in front of the eyes as well as within the border. The posterior sutures diverge widely and delineate medium-sized triangular posterolateral limbs, which in horizontal projection are about 0.7 of the width (transversely) of the occipital lobe. The palpebral lobes are elongate and narrow, about 0.4 of glabellar length, slightly behind its midpoint; the interocular cheek is about 0.5 of glabellar width. The rim is a forward-arched narrow and elevated bar with downward geniculate ends, a convex anterior slope, and a subangular crest; the bar is slightly inclined rearward, overhanging the rather deep and narrow marginal furrow in the middle. The occipital lobe is crescentic, with cusps projected slightly forward; the occipital furrow is almost straight, shallow in the middle and deepened abaxially. The axial furrows are distinct but shallow, the glabella, reaching the marginal furrow, tapers to about 0.7 of its posterior width, and is as long as wide at its base. Two or three pairs of rather indistinct lateral depressions may represent the glabellar furrows. The foremost furrows are short oblique depressions in the frontal part of the glabella, connected with the axial furrows. The test is smooth; the rim bears regular terraced lines.

The frontal margin is clear-cut indicating the presence of a marginal suture cutting off the subfrontal doublure—apparently the rostral shield.

*Occurrence and age:* The described cranium was found at locality W16, at the foot of Mount Idamea, in the Georgina Limestone; its age is the Idamean *Corynexochus plumula* Zone.

PAGODIA (IDAMEA) EXTRICANS sp.nov.

(Pl. 18, figs 4, 5)

*Material:* The material studied consists of four crania and one pygidium in a single hand-specimen of limestone; one cranium and the pygidium are illustrated. The counterpart of the pygidium is also available; its external surface is ornamented similarly to the cephalon, leaving no doubt of the specific association of the shields.

*Holotype:* The cranium Plate 18, figure 4, CPC 5507, is selected because it facilitates the comparison with *I. venusta*, which is known only from crania.

*Diagnosis:* *Pagodia (Idamea) extricans* is a species with externally developed glabellar furrows and ocular ridges; distinguished by its punctate test and relatively long palpebral lobes, which are placed opposite the midpoint of the posterior half of the glabella.

*Differential diagnosis:* *Idamea venusta* has almost the same cranial proportions, but lacks external ocular ridges and is impunctate; *Pagodia (Idamea) baccata* sp.nov. has a slightly longer glabella; it is not only punctate, but also granulose.

The disparity of *extricans* and *baccata* is obvious; less obvious is the difference between the better preserved *extricans* sp.nov. and *venusta* Whitehouse because the latter is known only from silicified specimens which are insufficient for a reliable comparison; morphological differences, however, are present; and the ages are also different.

*Description:* The holotype cranium is 4.7 mm long and 6.5 mm wide between the edges of the palpebral lobes. The palpebral lobes are relatively long, about 0.45 of glabellar length; the interocular cheek between anterior palpebral tips and glabella is as wide as 0.5 of the glabella on the same level; the palpebral lobes are placed well to the rear—almost opposite the midpoint of the posterior half of the glabella. The anterior sutures converge slightly, and are somewhat convex or almost straight. The rim is a forward-arched bar with steep slopes and a subangular crest, with delicate terraced lenses on its front. The glabella is as long as wide, constricted in its anterior third, tapers forward to about 0.8 of its width at base, and bears three pairs of weak glabellar furrows.

The ocular ridges are straight, broad, and slanting swells with undefined borders. The palpebral furrows are shallow and straight. The test is rather thick and punctate and not granulose.

The exfoliated pygidium Plate 18, figure 5, CPC 5508, is 9.8 mm wide and 6.1 mm long, including the articulating half-ring; without the ring it is 5.8 mm long. Its outline is sub-semicircular; the ill defined border is relatively wide, slightly concave and slopes downward. A weak marginal furrow, or rather a paradoublur line, is apparent. Three pairs of low pleural ribs are present, but interpleural grooves are absent; the pleural lobes are minutely venulose. At the fulcrum the pygidium is abruptly geniculate, and the fulcral points are far apart, the distance being 0.8 of the anterior width of the pygidium. The down-bent corners bear facets. The

axis is well elevated above the convex pleural lobes and is surrounded by the deep axial furrows. In front the axis is as wide as the pleura; it tapers moderately to about 0.7 of its anterior width and reaches the border; it is divided into three distinct and a fourth weak annulations, and a rounded terminus. The anterior transverse furrow is rather deep, the others become shallower toward the terminus. Externally the test is minutely punctate and the furrows are less distinct than on the internal cast.

*Occurrence and age:* *Pagodia (Idamea) extricans* was found in the Georgina Limestone at locality W45; its age is the Idamean Zone of *Erixanium sentum*.

PAGODIA (IDAMEA) BACCATA sp.nov.

(Pl. 17, figs 1-8; Pl. 18, figs 1-3; Text-fig. 89)

The test of *P. (Idamea) baccata* is rather thick, with the effect that the well developed internal relief is only weakly reflected on its external surface; for the same reason the internal casts of the cephalic border and of the occipital lobe are much narrower and the marginal furrows are much wider on the cast than on the surface of the test, but the granulation is not reflected internally. Hence, the external and decorticated appearances of the trilobite are rather different and should be considered in its description and identification.

*Material:* Illustrated and described are: one cranium from the Georgina Limestone (locality W8), two cranidia from the Pomegranate Limestone (locality D119) and three cranidia, three pygidia, one free cheek, and one rostral shield, eleven specimens altogether, from the Pomegranate Limestone locality D120b; *P. (I.) baccata* is most abundant at locality D120b in a dark, almost black, current-laminated limestone. Altogether about fifty cranidia, twelve pygidia, four free cheeks, and two rostral shields have been examined.

*Holotype:* The cranium Plate 17, figure 1, CPC 5496, locality D126b, is selected as holotype; it has preserved the test, but is slightly deformed in the front, which is straight and not arched; the associated exfoliated cranium supplements the holotype. Attempts to obtain the external and internal casts of the same cranium failed. The selected holotype cranium and the associated pygidium possess the same baccate ornament and belong together.

*Diagnosis:* *Pagodia (Idamea) baccata* is a species having (1) a very thick test, (2) a relatively long glabella which is longer than wide, (3) deflected and advanced genal spines, (4) a wide pygidial border and a border furrow, (5) externally simple and internally double ocular ridges, (6) no distinct external glabellar furrows but four pairs of glabellar furrows on its cast, (7) a punctate and granulose test, and (8) well developed terraced lines on the cephalic border.

Double eye ridges and four pairs of glabellar furrows are expected to be present in other species of *Pagodia* and related genera; they are visible in *P. (Idamea) baccata* owing to the exquisite preservation of its internal casts.

*Differential diagnosis:* *P. (Idamea) venusta* Whitehouse has a smooth test, and in *extricans* sp.nov. the test is punctate but not granulose; furthermore, *baccata* and *extricans* differ in the structure of the pygidial axis, which is narrower and shorter,

and more strongly annulated, in *baccata* than in *extricans*. '*Chuangia*' *kawadai* Kobayashi and '*Ch.*' *tawenkouensis* Sun (see under the discussion of the genus *Pagodia*) and its affiliates that are possibly related to *Idamea* have a smooth test. The later Upper Cambrian species of *Pagodia*, several of which have a granulose test, have smaller eyes, a more elongate glabella, and a shorter distance between the pygidial fulcral points. Of the early Upper Cambrian (Paishanian, and, in Australian terms, Idamean) species described by Endo (1937) from Manchuria, *P. perquadrata* is, probably, quite near to *baccata* but is distinguished by its shorter glabella, dense granulation, and stronger occipital node.

The pygidia of *P. (Idamea) baccata* are very similar to the early Upper Cambrian *Chuangioides punctatus* Chu (see Kobayashi, 1960, fig. 3i); the difference consists in the ornament: *baccata* is granulose and *punctatus* is punctate.

*Description:* The cephalon is broad, semielliptical, sloping strongly forward and sideways; the pleural lobes are tumid with eyes on summits slightly below the level of the glabella. The free cheeks are moderately tumid and provided with relatively short, slightly advanced, and widely divergent deflected genal spines. The

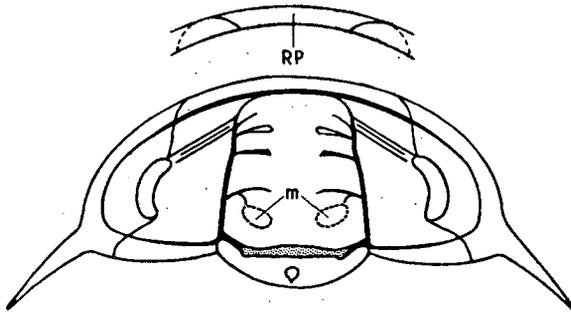


Fig. 89.—*Idamea baccata* sp. nov., combined from Plate 17, figs 1, 2, 3, and 8 (rostral shield), and Plate 18, fig. 1 (free cheek). Frontal ventral doubleure with rostral shield (R.P.); m—muscle spots.

marginal furrow is rather deep and narrow within the cranidium, but becomes shallower when passing into the free cheek, and almost disappears at the base of the spine. The marginal border—the cranidial rim and the genal border—are elevated as a bar with a subangular crest and a slightly convex outward slope which bears sharp terraced lines. The crest disappears before reaching the genal spine. The cranidium is subtrapezoidal in outline. The cranidial rim (bar) is arched forward and upward, but a lateral geniculation as seen in *venusta* is absent. The anterior sutures are straight and slightly converging, cut the frontal border at an abrupt angle, and remain marginal, meeting in the front. The posterior sutures diverge strongly and delineate triangular and abruptly geniculate posterolateral limbs. The posterolateral marginal furrow is externally narrow and deep, but on the internal cast it is a broad channel and the marginal border is a narrow ridge. The palpebral lobes are long (about 0.4 of glabellar length) and upturned; they are placed opposite the cephalic centre, or slightly behind the midpoint of the glabella; the interocular cheek between the tips of the palpebral lobe is as wide as about half the glabella on the test and slightly wider on the cast. The palpebral furrows are narrow externally, but wide channels on the cast. The ocular ridges are slanting broad swells, and

internally are double, consisting of two distinct and narrow elevated lines. The occipital lobe is crescentic, relatively flat and short, and the occipital furrow narrow and deep; on the cast, however this furrow is a broad channel and the occipital lobe is reduced to half of its external length (longitudinally); a small, elongate occipital node is present at the posterior margin. The axial furrows externally are narrow and deeply incised and merge in front with the marginal furrow; on the cast, however, they are deep and broad and with convex slopes indicating that the test in the furrow was rather thick and solid. The glabella tapers forward to about 0.8 of its posterior width; externally its front is truncate, but internally it is broadly rounded; the flanks of the glabella are slightly concave in the anterior third, more on the cast, and less on the surface. The glabella has a low subangular keel which is well expressed on the cast, but externally very low, marked only by a dark line. Dark spots indicate externally the position of the glabellar furrows, but on the cast the furrows are distinct, and four pairs of them are present: the posterior (S1) furrows are trifold, and their posterior branches are connected with large oval muscle spots occupying the centres of the posterior lobes; the second (S2) furrows are simple; the third (S3) furrows, which are distinct on the cast, are represented externally by a pair of elongate spots not reaching the axial furrows, and the anterior (S4) furrows are short oblique depressions at the adaxial ends of the ocular ridges. It appears that *P. (Idamea) baccata* possesses the full set of four glabellar furrows of a ptychopariid (see Öpik, 1961, p. 159). The ornament consists of scattered rounded granules in an approximate symmetrical arrangement; the granules are rather weakly reflected on the internal cast; furthermore, the test is minutely punctate, and so is the cast, indicating that the parietal surface is sparsely and minutely pustulose.

The rostral shield (Text-fig. 89) is a piece of the doublure cut out by the marginal rostral suture and the connective sutures, which are the ventral extension of the even curve of the marginal section of the anterior sutures, cutting obliquely, adaxially and downward through the marginal border and its doublure. This is a rather general arrangement seen in ptychopariids, in *Redlichia*, *Centroleura*, and many other trilobites of diverse stocks.

The pygidium is sub-semicircular, and when decorticated almost a half of a circle. The border is wide, slightly convex, and down sloping, and marked by an external faint, but distinct, furrow from the ribbed part of the pleural lobes. Three pairs of pleural ribs are present externally and on the cast, separated by broad and shallow pleural furrows; interpleural grooves however are absent. At the fulcra the pygidium is abruptly geniculate, and the fulcra are far apart for about 0.85 of the width of the pygidium. At the corners facets are present. The axis is well elevated above the pleural lobes, and the axial furrow, distinct on the surface, is wide on the cast. In front the axis is narrow, narrower than the pleural lobe, and narrower than the distance between the axis and the fulcrum. The axis reaches the marginal furrow, is relatively short, about 0.7 of the pygidial length, tapers gently, and consists externally and internally of four annulations and a rounded, short terminus; its internal relief is the strongest. The internal cast is minutely and sparsely punctate;

the external ornament consists of granules arranged in lines on the ribs and in concentric girdles on the border. The axial annulations carry two symmetrically placed knobs each. The doublure slopes more steeply than the border, and the ventral margin of the pygidium is flat.

*Comment on illustrated material:*

The holotype cranium is 4.2 mm long; its preservation, as compared with all associated specimens, is exceptional. The rock is petroliferous and a film of oil may have intervened between the matrix of calcite and the recrystallized test. The front appears straight, because it is deformed (pressed against the glabella) and because the illustration was made with the front rotated upward; in a normal position (that is with the palpebral lobes in horizontal attitude) the front is still arched forward. The ocular ridges are well visible; the glabellar furrows are almost imperceptible, but the distribution of the smooth muscle spots is well expressed. The median carina is barely indicated, but in the actual specimen it is a dark line. The axial, occipital, and posterolateral furrows are deep and narrow.

The decorticated cranium associated with the holotype, Plate 17, fig. 2, CPC 5497, is 4.5 mm long. The test is preserved on the rim, but covered by irremovable calcite matrix. The furrows are broad, especially the posterolateral furrow, which reaches the posterior tip of the palpebral lobe; the median carina, the right palpebral lobe, the double ocular ridge, the glabellar furrows, the punctation, and low casts of the external granulation are distinct.

The decorticated cranium Plate 17, fig. 3, CPC 5498, Pomegranate Limestone, locality D120b, is 4.5 mm long. Calcite adheres to the rim and cannot be removed. The ocular ridges are double. In lateral view the correct position of the rim is evident; in the holotype it is pressed against the front of the glabella.

The free cheek, Plate 18, fig. 1, CPC 5504, Pomegranate Limestone, locality D120b, is decorticated but preserves part of its test on the border, showing the terraced lines. It is 4.5 mm long as preserved.

The rostral shield, Plate 17, fig. 8, CPC 5503, Pomegranate Limestone, locality D120b, is 6.0 mm long; it is illustrated from its convex ventral side; it is arched forward and upward, but subsequently somewhat twisted; some matrix covers one of its inside lateral edges, creating the impression of asymmetry; regular terraced lines are present.

The cranium, Plate 18, fig. 2, CPC 5505, Pomegranate Limestone, locality D119, is 5.2 mm wide; it is embedded in a pod of coarse calcite and decorticated.

The cranium, Plate 18, fig. 3, CPC 5506, Pomegranate Limestone, locality D119, in calcite, is 4.6 mm long. It is assigned to *P. (Idamea) baccata* because of the similarity in ornament; but this assignment is tentative, because the anterior sutures here are parallel and the rim has a rather sharp crest and a relatively low slope forward; it represents, possibly, another species related e.g. to *Chuangia kawadai* Kobayashi. The ocular ridges are double.

The cranium, Plate 17, fig. 4, CPC 5499, Georgina Limestone, locality W8, is 3.5 mm wide between the edges of the palpebral lobes. The crest of the rim (which bears the terraced lines) is subangular, the ocular ridges are distinct, and the granulation is somewhat less dense than in the holotype.

The pygidium, Plate 17, fig. 7, CPC 5502, Pomegranate Limestone, is 1.8 mm long and 3.2 mm wide. The axis is decorticated, the pleurae have preserved the test; the pleural ribs and the border are distinct.

The pygidium, Plate 17, fig. 6, CPC 5501, Pomegranate Limestone, locality D120b, is 1.9 mm long and 3.3 mm wide; on the cast interpleural grooves are indicated, and the cast itself is punctate.

The large pygidium Plate 17, fig. 5, CPC 5500, Pomegranate Limestone, locality D120b, is 4.0 mm long and 7.8 mm wide; it is completely decorticated, exposing the mould of the ventral side of the doublure.

*Occurrence and age:* *Pagodia (Idamea) baccata* is common in the Pomegranate Limestone at localities D119 and D120b, in the Idamean *Erixanium sentum* Zone; one cranium was found in the Georgina Limestone at locality W8 in the lowermost part of the same zone.

LEIOSTEGIIDAE, SUBFAMILIAE INCERTAE

Genus AEDOTES nov.

The type of the genus *Aedotes* is *A. instans* sp.nov.

*Familial classification:* The parallel-sided to slightly constricted and relatively long glabella, the absence of a brim, and the position of the palpebral lobes indicate the family Leiostegiidae. Among the leiostegiids two genera—*Pagodia* Walcott and *Prochuangia* Kobayashi—can be compared with *Aedotes*. *Prochuangia* is considered by Harrington et al. (1959, p. 0319) to be a genus of the Kaolishaniidae, but Kobayashi (1960, p. 361) regards it as a leiostegiid, and this should be accepted. From both these genera *Aedotes* differs by its slightly convex or even flat rim and the triangular shape of the occipital lobe, with a submarginal spine or a subcentral node.

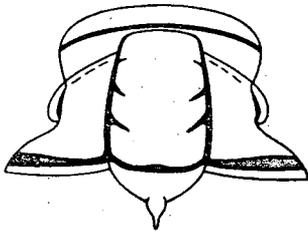


Fig. 90.—*Aedotes instans* gen.nov., sp. nov., combined from Plate 21, figs 3, 4.

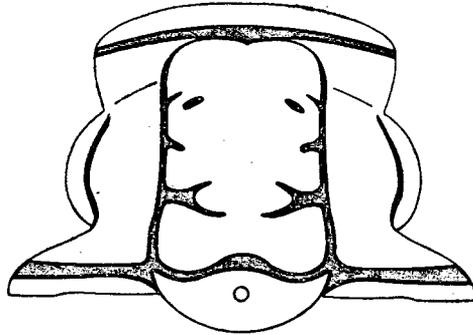


Fig. 91.—*Aedotes mutans*, sp.nov., combined from Plate 21, figs 5 and 6.

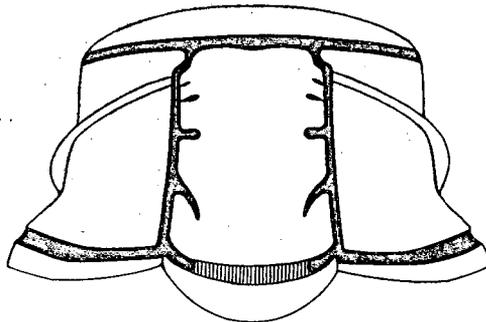


Fig. 92.—*Aedotes declivis* sp.nov., from Plate 21, figs 1 and 2.

*Diagnosis:* *Aedotes* gen.nov. refers to brimless leiostegiids with a long and more or less parallel-sided glabella, with eyes placed opposite the glabellar middle, and distinguished by a long subtriangular occipital lobe and a flat or moderately convex rim without any angularity, and without a vertical or steep margin.

Three species are attributed to *Aedotes*: *A. instans* sp.nov., *A. mutans* sp.nov., and *A. declivis* sp.nov.

AEDOTES INSTANS sp.nov.

(Pl. 21, figs 3, 4; Text-fig. 90)

*Material:* Two cranidia selected from a large number of specimens are illustrated.

*Holotype:* The cranidium Plate 21, fig. 3, CPC 5523, locality G8, is the holotype.

*Diagnosis:* *Aedotes instans* is distinguished by its slightly convex rim, relatively small palpebral lobes, and an occipital spine placed at the occipital margin.

The differential diagnosis is given under *Aedotes mutans* sp.nov.

*Description:* The holotype cranidium is 2.0 mm long; the largest specimens may have reached 3.0 mm. The cranidium is somewhat rectangular if the posterolateral limbs and the weakly forward arched frontal margin are disregarded. The posterior sutures diverge in even curves; the posterolateral limbs are triangular and moderately geniculate. The anterior sutures are almost straight and slightly divergent, but converge within the rim and remain marginal in the front. The rim is convex, subhorizontal and defined in the rear by the shallow but distinct marginal furrow. The interocular cheeks, 0.5 of glabellar width, have a pronounced adaxial slope indicating a relatively prominent elevation of the eyes. The palpebral lobes are small, about 0.3 of glabellar length and placed opposite its middle. The ocular ridges are weak and erratic, and even not quite discernible in some specimens. The occipital lobe, subtriangular to lunate, bears an upward and rearward directed curved submarginal spine. The occipital furrow is distinct and evenly deep. The axial furrows are narrow and deep at the flanks, but relatively shallow around the glabellar front. The glabella is moderately arched longitudinally and its flanks are straight; it tapers slightly to a broad subtruncate front, about 0.9 of posterior width. Three pairs of rather shallow glabellar furrows are indicated.

The test is smooth.

The specimen Plate 21, fig. 4, CPC 5524, locality G8, is 2.0 mm long; the spine is broken, but the right palpebral lobe and the posterolateral limb are intact.

*Occurrence and age:* *Aedotes instans* sp.nov. is found only in the Mungerebar Limestone in most of the localities, as for example in G8, G119, G417, G427. Its age is the Mindyallan Zone of *Erediaspis eretes*.

AEDOTES MUTANS sp.nov.

(Pl. 21, figs 5, 6; Text-fig. 91)

*Material:* Two cranidia are illustrated, selected from about ten specimens.

*Holotype:* The cranidium Plate 21, fig. 5, CPC 5525, is selected as the holotype because of its large size and satisfactory preservation.

*Diagnosis:* *Aedotes mutans* sp.nov. is distinguished by its large palpebral lobes and its subcentral occipital node. Furthermore, the glabella may be constricted in the middle, or almost parallel sided, and in some specimens four pairs of glabellar furrows are discernible.

*Differential diagnosis:* In *Aedotes instans* sp.nov. the palpebral lobes are small (0.3 of glabella against 0.5 in *mutans*) and a submarginal occipital spine (and not a subcentral node) is present. The difference from *Aedotes declivis* sp.nov. is indicated under the latter.

*Description:* The holotype cranium is 2.0 mm long; the border is only little convex, the frontal marginal furrow is wide, the interocular cheek, 0.4 of glabellar width, is slightly inflated, the palpebral lobe is long, only little curved and placed with its middle just behind the glabellar midpoint.

The cranium Plate 21, fig. 6, CPC 5526, is 1.5 mm long; four pairs of glabellar furrows are discernible; the third pair is not connected with the axial furrow, and the posterior furrows are apparently forked; the abaxial ends of the two posterior glabellar furrows are deep notches. The rear of the glabella is arched forward, and a strongly slanting ocular ridge is indicated.

*Occurrence and age:* *Aedotes mutans* is found in the Mungerebar Limestone; the illustrated specimens come from locality G8; other localities are G119, G149 and G417. Its age is the Mindyallan Zone of *Erediaspis eretes*.

#### AEDOTES DECLIVIS sp.nov.

(Pl. 21, figs 1, 2; Pl. 61, fig. 4b; Text-fig. 92)

*Material:* Two crania are illustrated, selected from several more fragmentary specimens. All specimens are silicified.

*Holotype:* The cranium Plate 21, fig. 1, CPC 5521, locality G8, is selected as the holotype because of its better preservation.

*Diagnosis:* *Aedotes declivis* sp.nov. is a species with relatively small palpebral lobes and concave flanks of the glabella; distinguished by its wide interocular cheeks, well developed ocular ridges, steep and flat slope of the glabellar front, and a longitudinally strongly arched cephalon.

*Differential diagnosis:* The palpebral lobes in *A. instans* and in *A. declivis* are of similar size, but in *declivis* the interocular cheek is wider, 0.7 of glabellar width against 0.5 in *instans*. Furthermore, *declivis* lacks an occipital spine. *Aedotes mutans* and *A. declivis* are similar in having concave glabellar flanks (these are straight in *instans*), but in *mutans* the palpebral lobes are longer (0.5 against 0.3 of *declivis*) and the interocular cheek is narrow (0.4 against 0.7 of *declivis*). *A. instans* and *A. mutans* have a less arched cephalon, and their anterior sutures are divergent, but convergent in *declivis*.

Some similarity is apparent between *Pagodia (Idamea) baccata* sp.nov. (Text-fig. 89) and *Aedotes declivis* sp.nov. (Text-fig. 92), indicating that these forms are affiliated on a familial level.

*Description:* The holotype cranium is not quite 2.0 mm (1.8–1.9 mm) long. The ocular ridges are worn but distinct. The two posterior glabellar furrows are deep and short, the third pair is represented by weak pits, and a fourth pair is present at the ends of the ocular ridges. The anterolateral corners of the glabella are dented, in the position of the anterior pits of *Leiostegium*. The front of the glabella recedes slightly rearward, and slopes down steeply forming a somewhat triangular face.

The cranium Plate 21, fig. 2, CPC 5522, locality G119, is also about 1.8 mm long and partly immersed in silica. It illustrates the steep slopes of the cephalon and shows the four glabellar furrows, the frontal recess, and the flat front of the glabella.

*Occurrence and age:* *Aedotes declivis* sp.nov. occurs in the Mungerebar Limestone, at localities G8, G119, G151 and G417, in the Mindyallan Zone of *Erediaspis eretes*: it is also recorded at G127 (Zone of *Cyclagnostus quasivespa*).

#### Genus MEROPALLA nov.

The type of the genus is *Meropalla quadrans* sp.nov.

*Diagnosis:* The genus *Meropalla* includes species having (1) a rather convex cephalon, (2) small eyes which are placed opposite the posterior part of the glabella, (3) interocular cheeks as wide as half the glabella, (4) a long and tapering glabella reaching the marginal furrow, and (5) a rather narrow frontal rim consisting of a steeply sloping almost vertical flat face.

The type of the genus has a relatively large convex pygidium with effaced furrows and without any indication of a border. Two species, *quadrans* sp.nov. and *auriculata* sp.nov., are included in the genus.

*Meropalla* is placed here in the family Leiostrigiidae because of its similarity with such early leiostrigiids as *Pagodia*, *Idamea*, and *Eochuangia*. It is, however, distinct in having an extremely narrow, flat, and vertical frontal rim, and eyes placed far in the rear, opposite the posterior part of the glabella, like *Leiostrigium* itself. *Meropalla*, although the earliest known leiostrigiid, cannot be regarded as ancestral to any of the known members of the family; it possesses a modified frontal border from which the frontal bars and rims of the subsequent forms cannot be derived.

*Macellura* Resser (Illaenuridae) bears some resemblance with *Meropalla* as regards the convexity of the cranidium and the structure of its front; the eyes of *Macellura* are, however, subcentral and closer to the glabella than in *Meropalla*.

#### MEROPALLA QUADRANS sp.nov.

(Pl. 1; Pl. 18, fig. 7; Pl. 19, figs 1-3)

*Material:* The illustrated and described material consists of three cranidia, one pygidium, and one free cheek, all silicified, in siliceous laminae in limestone. Cranidia are relatively common, but only one pygidium (associated with the holotype cranidium) has been found so far.

*Holotype:* The largest cranidium Plate 18, fig. 7, CPC 5510, locality G127, is selected because of its satisfactory preservation.

*Diagnosis:* *Meropalla quadrans* sp.nov. is a species with a smooth test lacking the ocular ridges, relatively small and depressed (not uplifted) palpebral lobes and a keen (not rounded) edge of the cranial rim.

The differential diagnosis is given under *Meropalla auriculata* sp.nov.

*Description:* The cephalon is rather convex, approaching a quadrant of a globe; the test is smooth, without any trace of granulation or punctation. The free cheek, trapezoidal in outline, is moderately convex, slopes down steeply, bears a small deflected and slightly advanced genal spine, and a narrow convex border separated by a distinct marginal furrow. The outline of the free cheek can be seen, Plate 19, figure 3, and also in the lateral view of the holotype cranidium, Plate 18. The anterior sutures are moderately convex and converging, and cut the anterior border rather

abruptly; the sutures continue, and meet on the cranial margin, which, therefore, has no doublure attached to it. The posterior sutures diverge in almost opposite directions, delineating rather short and narrow posterolateral limbs, geniculating downwards. The posterior marginal furrow is distinct and narrow. The interocular cheeks are slightly convex, rising above the level of the palpebral lobes, but remaining lower than the glabella; they are as wide as 0.5 of the glabella measured between the anterior tips of the palpebral lobes. The palpebral lobes are small, about 0.23 of the chordal length of the glabella, horizontal, and placed far in the rear, opposite the posterior fifth of the glabella. Ocular ridges are absent, and the palpebral furrows are almost straight and shallow. The frontal rim is a flat, slightly forward and upward arched crescentic piece or plate, whose keen edge rises above the very narrow marginal furrow. The flat face of the border bears terraced lines.

The occipital lobe is inconspicuous and bears a low median node which may be missing in smaller specimens. Abaxially the occipital lobe in larger specimens is connected with a pair of large lateral lobules separated from the posterior glabellar lobes by a pair of transverse furrows; in smaller specimens these lobules and furrows are less prominent than in the holotype. The axial furrows are wide and distinct along the glabellar flanks but shallow at its front. The glabella is weakly constricted in its anterior third, reaches the front furrow, tapers forward to about 0.65 of its rear width and bears two pairs of rather shallow lateral furrows. An indistinct keel is apparent, with a tiny median node on the midline level of the palpebral lobes.

The pygidium associated with the holotype is sub-semicircular in outline, strongly convex, even subglobose. The flanks are convex, with a steeply sloping periphery. Three pairs of rather low and broad pleural ribs are indicated. The geniculation at the fulcrum is abrupt and the anterolateral corners bear depressed and pronounced narrow facets. The anterolateral furrow, as deep as usual in effaced trilobites, fades out adaxially, but persists abaxially to the margin. The axial furrows are weak, indicated only by a change in slope. The axis is slightly elevated, long, tapering, and divided into five rather weak annulations and a terminus.

*Comment on illustrated specimens:*

The holotype cranium, Plate 18, fig. 7, CPC 5510, locality G127, is 9.4 mm long (the length of the sagittal chord); in horizontal projection (horizontal palpebral lobes) it is about 7.8 mm in front of the eyes it is 11.7 mm wide.

The pygidium, Plate 19, fig. 1, CPC 5511, locality G127, is 7.8 mm long and estimated 13.0 mm wide. The holes in the right side of the axis may correspond to muscle spots or to low swells on the annulations.

The free cheek, Plate 19, fig. 3, CPC 5513, locality G8, is 2.4 mm high from the eye to the margin below it. The small deflected and slightly advanced genal spine is preserved.

The fragmentary cranium, Plate 1, CPC 5360, locality G8, is 6.0 mm long; its frontal border is buried in silica; its occipital furrow is distinct and the lobules are smaller than in the holotype.

The flattened and fragmentary cranium, Plate 19, fig. 2, CPC 5512, locality G149, is 8.5 mm long and 7.2 mm wide in front. Note the rearward position of the palpebral lobes and the shape of the frontal border, which is different in different attitudes.

*Occurrence and age:* *Meropalla quadrans* has been found in the Upper Cambrian (Mindyallan) part of the Mungerebar Limestone at localities G8, G119, G127, G130, G149, and G417; its age is the Mindyallan Zones of *Erediaspis eretes* and *Cyclagnostus quasivespa* (at G127 and G130).

MEROPALLA AURICULATA sp.nov.

(Pl. 1; Pl. 19, figs 4, 5)

*Material:* Only cranidia have been found. Two of these are illustrated and described.

*Holotype:* The cranidium Plate 1, and Plate 19, figure 4, CPC 5514, locality G8, is selected as the holotype because it is the largest and best preserved specimen. It is 8.6 mm long (sagittal chord) and 10.4 mm wide in front of the palpebral lobes, and 10.1 mm at its frontal margin. The second cranidium Plate 19, fig. 5, CPC 5515, locality G119, is 5.6 mm long, and 6.9 mm wide in front of the palpebral lobes. It supplements the holotype, having preserved the pustulose ornament and showing the double ocular ridges.

*Diagnosis:* *Meropalla auriculata* is a species with a pustulose test, externally expressed ocular ridges, relatively large and ear-like uplifted palpebral lobes, and with a straight and low frontal border which has a rounded crest and is geniculated at its flanks.

*Differential diagnosis:* The diagnosis lists the main characters that separate *M. auriculata* from *M. quadrans*; several more distinctive characters are evident from the description that follows below; it appears that *M. auriculata* is not closely related to *quadrans*; but in the absence of the pygidium *auriculata* cannot be regarded as representing a separate genus or subgenus.

*Description:* The cranidium is convex, strongly arched sagittally and sloping forward in an even curve; the test is ornamented by scattered coarse pustules. The free cheek, indicated by its outline in Plate 19, figure 5c, is trapezoidal and slopes steeply. The anterior sutures are convex, converge only slightly toward the front, and cut the margin abruptly for a short distance toward the midline; they remain marginal, and meet in the middle, indicating the absence of an attached subcephalic doublure. The posterior sutures diverge strongly and delineate small subtriangular posterolateral limbs. The posterior marginal furrow is distinct and narrow. The interocular cheeks slope adaxially and are as wide as about 0.6 of the glabella at the anterior tips of the palpebral lobes. The palpebral lobes are relatively large, about 0.3 of the length of the glabellar chord, and placed far in the rear, opposite the posterior quarter of the glabella. These lobes are not horizontal, but are ear-like, uplifted, and slope adaxially, and their tips are on the level with the top of the glabella. The ocular ridges are double, consisting of two straight low swells each. The palpebral furrows are curved and rather shallow but distinct. The frontal border is straight in the middle, but geniculated down opposite the anterolateral corners of the glabella. The rim is a rather narrow low bar with a rounded (not keen) crest and a flat face ornamented by terraced lines. The frontal marginal furrow is shallow but distinct.

The occipital lobe is prominent; it has no median node and its lateral lobules are barely indicated. The occipital furrow is deep and narrow. The axial furrows are shallow valleys between the glabella and the pleural lobes. The glabella tapers evenly to about 0.75 of its rear width, reaches the marginal furrow, has a subtruncate front, and bears two pairs of broad and shallow lateral furrows; it is well arched

transversely, but a keel is absent. A pair of low triangular lobes are present at the anterolateral corners of the glabella, similar to *Blackwelderia sabulosa* sp.nov. (Text-fig. 111).

*Occurrence and age:* *Meropalla auriculata* has been found in the Mungerebar Limestone at localities G8, G119, and G417, in the Mindyallan Zone of *Erediaspis eretes*; and at G130 in the Zone of *Cyclagnostus quasivespa*.

#### Superfamily RHYSSOMETOPACEA nov.

The subordinal classification of the Rhyssometopacea is not immediately evident: the Rhyssometopacea are placed here in the Ptychopariina, and therefore in the order Ptychopariida which contains several genera with a plectrum. However, in the rhyssometopid *Plectrifer plectrifer* gen.nov. et sp.nov. the bispinose pygidium, the plectrate front, and the occurrence of a glabellar node (if this is accepted) may indicate some affiliation with the superfamily Ceratopygacea (Asaphina). It is, perhaps, also significant that the ceratopygids and the rhyssometopid *Rh. (Rostrifinis)* have a relatively small and about equal number of segments in the thorax. In passing, I think that the assumed affiliation of the Ceratopygacea with the asaphids, if challenged, will be difficult to defend.

In the Rhyssometopacea the large palpebral lobes, the long glabella which almost reaches the rim, the small number of segments in the thorax, and the character of the pygidium are also reminiscent of the Dolichometopidae of the order Corynexochida. The Corynexochida, however, possess a rather different ventral cephalic structure—a transversely wide rostral shield which in many species is fused with the hypostoma.

Among the superfamilies of the Ptychopariina the Remopleuridacea also have a relatively small number of segments in the thorax, large eyes close to the glabella, and laterally expanded glabella which can be compared with the laterally bulging glabella of *Rhyssometopus*. This comparison fails, however, as regards all other features; furthermore, the Remopleuridacea are much younger than *Rhyssometopus* and no intermediate forms, either in time or in morphology, are apparent.

Some similarity exists between *Rhyssometopus (Rostrifinis)* subgen.nov. and the Middle Cambrian *Agraulos anceps* Westergaard: *anceps* is cusped, has a subrectangular glabella and relatively large eyes, which however, are remote from the glabella. The presence of a frontal cusp, however, is incidental in diverse superfamilies, and may not be present in all genera of a single family, and should not be considered therefore as a unifying character on a higher taxonomic level. Still, if *A. anceps* and *Rostrifinis* are somehow affiliated, the *Rhyssometopacea* should be connected with the ellipsocephalids: *Agraulos anceps* is probably a species of *Proampyx*, which is a genus of the Agraulinae of the family Ellipsocephalidae according to Öpik (1961, p. 142). To conclude, the rhyssometopids have little in common with the Corynexochida (Dolichometopidae) and the ptychoparioids Ellipsocephalacea and Remopleuridacea; they are also remote from, or only remotely affiliated with, the Ceratopygacea, although *Plectrifer* and even *Mapania* (in its cranidium; see Öpik, 1961, p. 166) possess characters reminiscent of *Proceratopyge*. Hence, the superfamily Rhyssometopacea of the suborder Ptychopariina becomes a necessity.

The three following families are included in the Rhyssometopacea: Rhyssometopidae, fam. nov., Plectriferidae, fam. nov., and Mapaniidae Chang, 1963.

The diagnosis of a superfamily refers to characters which are common to all its subordinate taxa; the concept of the superfamily however, remains incomplete without a reference to the particular characters of its components; hence, the concept of the Rhyssometopacea is also composite, as presented here.

*The concept of Rhyssometopacea, nov.*

Diagnosis of the family Mapaniidae: The Mapaniidae are Rhyssometopacea distinguished by a relatively large pygidium, marginal (not transmarginal) genal spines, and a short brim with a plectrum; the type genus is *Mapania* Resser & Endo. The Mapaniidae appear remote from *Rhyssometopus*; but considering the intermediate position of the Plectriferidae there is reason enough to include the Mapaniidae in the Rhyssometopacea.

Diagnosis of the family Plectriferidae: Plectriferidae are Rhyssometopacea with marginal (not transmarginal) genal spines, with a plectrum and reduced brim; distinguished by large arcuate palpebral lobes, and a relatively small pygidium with a pair of spines. The type is *Plectrifer*, gen.nov.

Diagnosis of the family Rhyssometopidae: The Rhyssometopidae are Rhyssometopacea with large palpebral lobes and relatively small pygidia; distinguished by—(1) transmarginal genal spines, (2) dilated frontal parts of the free cheeks, (3) the transverse wrinkle on the brim, (4) the antirostral hood, and (5) the absence of pygidial spines. The type is *Rhyssometopus* gen.nov.

Diagnosis of the superfamily Rhyssometopacea: Rhyssometopacea are Ptychopariina with (1) a relatively small number of segments in the thorax (about 9–10), (2) a narrow doublure, (3) a relatively long glabella with subparallel flanks, (4) lateral bulges on glabellar flanks, and (5) a narrow rostral shield reflected externally as an antirostral hood or as a plectrum. In some of the species a median glabellar node occurs sporadically.

The type family is Rhyssometopidae, and the type genus *Rhyssometopus*.

To conclude, the whole concept of the superfamily Rhyssometopacea, and not only its own diagnosis, provides criteria for a comparison with other superfamilies of the Ptychopariina. Of course, the concepts of the families, in their turn, include the characters of their genera and species.

The morphology is discussed in detail under *Rhyssometopus (Rostrifinis) rostrifinis*, of which a complete specimen has been found.

#### Family RHYSSOMETOPIDAE nov.

##### Genus RHYSSOMETOPUS nov.

The type species of *Rhyssometopus* is *Rh. (Rhyssometopus) rhyssometopus* subgen. nov. et sp.nov.

The diagnostic characters of the genus are: (1) transmarginal deflected genal spines inseparable from the ocular platform and interrupting the marginal cephalic furrow; (2) long arcuate palpebral lobes placed close to the glabella, and variable between 0.6 and 0.85 of glabellar length; (3) a long cranial frontal area which

may be arched forward, or truncate, or cuspidate; it may be undivided, or divided into a brim and rim of variable length; (4) a transverse wrinkle on the brim close to the glabella; (5) a relatively long glabella (longer than wide), which is moderately arched, and low; (6) an elongate hexagonal or subtruncate and slightly tapering glabella; (7) obsolete or weakly indicated glabellar furrows; there are four pairs of them combined with muscle spots, and a fifth pair of spots in the glabellar rear; (8) a pair of lateral glabellar bulges; (9) a subcranial apical doublure; (10) a relatively narrow (transversely) rostral shield in contact with the hypostoma, and flanked by the dilated ends of the doublure of the free cheeks; (11) an antirostral hood; (12) nine segments in the thorax; (13) long or very long pleural spines; (14) deep and broad pleural furrows reaching into the pleural spines; (15) a pygidium of about four segments, well fused, but with distinct broad pleural furrows; (16) a distinct but narrow pygidial border; (17) a rather prominent pygidial axial lobe with parallel or slightly converging flanks, which is long (reaching the border) and provided with three to four annulations and a rounded and steep terminus; and (18) pointed median tip of the pygidial rear margin.

Two subgenera have been recognized within *Rhyssometopus*:

Subgenus *Rhyssometopus (Rhyssometopus)*: Its species have a truncate or forward-arched, non-cuspidate front and large or very large palpebral lobes about 0.7–0.85 of glabellar length. The type is *Rh. (Rh.) rhyssometopus* sp.nov.

Subgenus *Rhyssometopus (Rostrifinis)* subgen. nov.: its species are distinguished by a cuspidate front and palpebral lobes about 0.55–0.7 of glabellar length. The type is *Rh. (Rostrifinis) rostrifinis* sp.nov.

One species, *Rh. neuter* sp.nov., cannot be placed in either subgenus; it may be sui generis, but this cannot be established owing to the scarcity of the material.

The subgenera are based on the combination of two criteria—the structure of the frontal margin and the size of the palpebral lobes. Pygidial characters are not included in the subgeneric, and only little referred to in the specific diagnoses, because in all species of *Rhyssometopus* the pygidia are rather similar, and of no subgeneric significance.

#### RHYSSOMETOPUS (RHYSSOMETOPUS) RHYSSOMETOPUS sp.nov.

(Pl. 25, figs 1–4; Pl. 33, fig. 4; Pl. 46, fig. 3, Text-figs 93–95)

*Material*: The illustrated material consists of one cranidium, two pygidia, one free cheek, and one segment of the thorax; one more fragmentary cranidium CPC 6739, locality G153) is included in the type material; it was specially prepared to examine the ornament. Fourteen cranidia and four pygidia have been examined altogether.

*Holotype*: The cranidium, Plate 25, fig. 1, CPC 5552, is selected as the holotype because of its excellent preservation.

*Diagnosis*: *Rhyssometopus (Rh.) rhyssometopus* is a species with an elongate hexagonal (not subtruncate conical) glabella and a granulose test; distinguished by

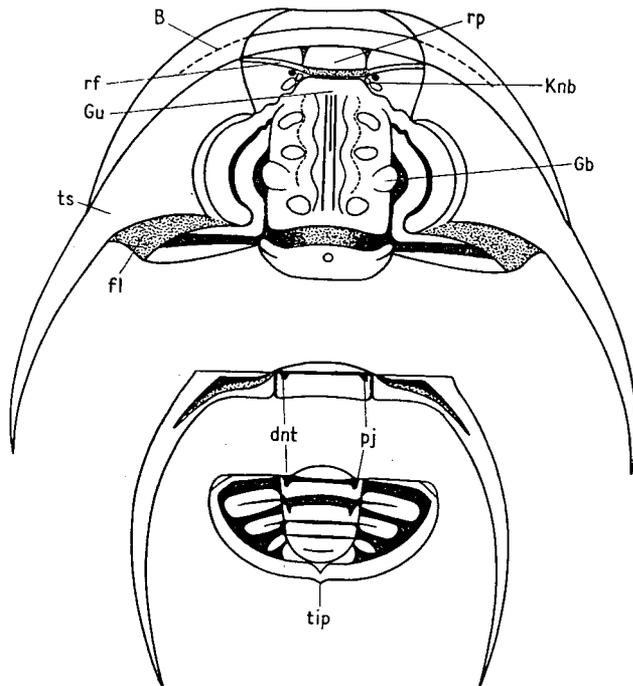


Fig. 93.—*Rhyssometopus rhyssometopus* gen.nov., sp.nov., combined from Plate 25 and segment of thorax CPC 6733. B—dilated part of border, upturned; fl—depressed flange; Gb—lateral bulge of glabella; Gu—preocular part of glabella; Knb—anterior knobs and pit; rf—frontal wrinkle; rp—antirostral hood; ts—transmarginal genal spine; dnt—longitudinal dent on axial lobe; pj—annular projection; tip=tip of pygidium. Other features see Text-figure 101.

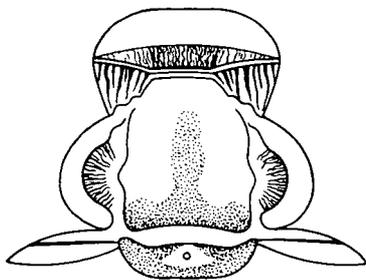


Fig. 94.—*Rhyssometopus rhyssometopus* sp.nov.—distribution of granules and caecal veins, from specimen CPC 6739, locality G153

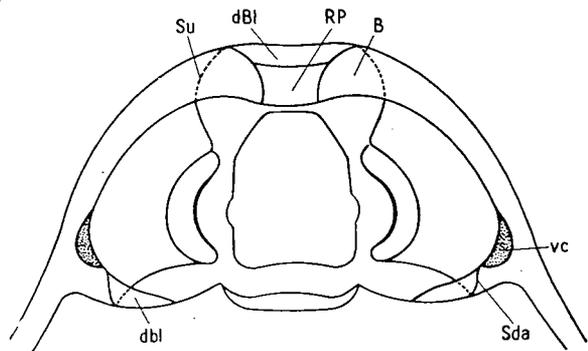


Fig. 95.—*Rhyssometopus rhyssometopus* sp.nov., cephalon in ventral view. B—dilated doublure of free cheek; dBl—frontal doublure; dbl—doublure of posterolateral limb; RP—rostral shield; Sda—ventral posterior suture; Su— anterior suture (dorsal); vc—vincular pit.

its straight, or even rearward receding front, long rim, large palpebral lobes (about 0.75 of glabellar length), and the restriction of the granulation to the occipital lobe, the glabellar rear and the elevated features of the pygidium.

*Differential diagnosis:* See under *Rh. (Rh.) princeps* sp.nov. and *Rh. (Rh.) rugiceps* sp.nov.

*Description:* The cephalon is transversely semielliptical, and moderately convex; the relief of the furrows (except for the glabellar furrows) and lobes is distinct; the free cheeks are tumid, and the glabella is low and relatively little arched. The free cheek is large, and provided with a curved and advanced transmarginal spine which is as long as the cephalon, and arises from the ocular platform. The lateral border is relatively flat in the rear, and expands forward, where its marginal part turns upward to coincide with the upturned cranial rim. The base of the eye is low, rather convex transversely, and undercut at the base by a deep furrow. The free cheek shows no posterior marginal furrow and the area behind the ocular platform is depressed. The ocular platform is delicately venulose. The anterior sutures are straight and divergent; within the rim they turn abruptly toward the midline in a rather broad curve and cut the margin half-way between the midline and the cranial corners. The posterior sutures diverge diametrically and reach the margin in an even curve delineating blade-like posterolateral limbs.

The palpebral lobes are relatively flat, broad, arcuate, and long (0.75 of glabellar length); their cusps almost touch the axial furrows; the palpebral furrows are distinct and the interocular cheeks are small (0.23 of glabellar width) and slope adaxially; delicate radial veins can be seen on the interocular cheeks. The palpebral lobes are placed opposite the posterior part of the glabella and their posterior tips are level with the glabellar rear.

The anterior cusps of the palpebral lobes pass into the somewhat nodose ocular ridges, which, interrupting the axial furrows, join the frontal glabellar lobe; in front of the junctions a pair of low knobs is apparent similar to the anterior knobs seen in *Lobocephalina pyriceps* sp.nov.; just in front of each knob a shallow pit is present.

The cranial margin is straight or even recedes slightly rearward. The cranial front is relatively wide, between 1.4 and 1.45 of glabellar width, and moderately long (0.4 of glabellar length). It is divided equally into a rim and a brim, separated by an angular change of slope in the position of a marginal furrow. The rim is flat, slightly upturned, and its margin is folded over, passing into the subcephalic doublure. The brim is also almost flat and slopes forward. The quadrangular low antirostral hood is defined laterally by faint lines, apparently reflecting the flanks of the rostral shield and the position of the connective sutures. The antirostral hood is delicately venulose. The rear of the rectangle is defined by a transverse wrinkle whose lateral limbs are curved and swept forward, and toward the anterolateral corners of the cranidium. These curved limbs of the wrinkle coincide with the position of the edges of the doublure of the free cheeks. At the anterior tips of the palpebral lobes and the ocular ridges coarse veins arise (four or five on each side), reaching the limbs of the wrinkles; these veins are distinct on the internal cast.

The occipital furrow is almost straight, wide, and bears a pair of muscle spots at its ends. The occipital lobe is relatively short, arched transversely, but otherwise flat, and bears a tiny median node. The occipital lobe and furrow together are relatively long (as long as in *Rh. rugiceps*), and longer than in *Rh. princeps*. The axial furrows are deep on the flanks, but shallow at the anterolateral part of the glabella; the furrow in front of the glabella, however, is rather deep.

The glabella is relatively short and broad, its width being 0.9 of its length; The slightly forward-arched glabellar rear is abrupt and angular, but its front is straight, truncate. The glabella tapers slightly to the anterior ends of the palpebral lobes, then with an angular turn its flanks, remaining straight, converge toward the anterolateral corners, which also are angular. The glabella, as a whole, is elongate hexagonal, as in *Rh. (Rostrifinis) rostrifinis* sp.nov.

A pair of distinct lateral bulges of the glabellar flanks are placed opposite the palpebral lobes, and separated from the interocular cheeks by the axial furrows; they are tumid and defined by shallow furrows; and from them faint veins radiate toward the palpebral lobes. Such bulges are present in all species of *Rhyssometopus*. Glabellar furrows are absent, replaced by three pairs of slightly depressed muscle spots, the fourth pair being represented by the tumid bulges. Adaxially the muscle spots are defined by a pair of slightly elevated serpentizing ridges flanking the relatively broad and low carina. The carina itself is double, divided in its frontal part by a longitudinal furrow. The ventral structure of the cephalon (Text-fig. 95) is the same as in *R. rostrifinis* (Text-fig. 99), with an apical doublure, vincular depressions at the genal angles, and expanding anterior parts of the free cheeks. The rostral shield, however, is trapezoidal and different from *rostrifinis*. Its rear edge is close to the glabellar front, that is, in contact with the hypostoma. The hypostoma, apparently, was not fused to, but separated by a suture from, the rostral shield.

The ornament (Text-fig. 94) consists of minute pustules on the occipital lobe, the rear and median part of the glabella, and, probably, on the genal spines; other parts of the cephalon are smooth. On the occipital lobe the area around the node is also smooth, and on the glabellar rear the pustules are transversely arranged. Relatively coarse terraced lines are present along the cephalic margin, including the genal spines.

In the segments of the thorax (Text-fig. 93) the pleural furrows are deep and wide, reaching into the pleural spines, which are rather long and curved, and directed rearward, at least in the posterior half of the thorax, as seen also in *Rh. princeps* sp.nov.

The pygidium of *Rh. rhyssometopus* has a well developed relief. It is slightly shorter than half the width, and broadly semielliptical, almost semicircular; it is also geniculate at the fulcra near the anterolateral corners, which bear small facets. In the rear the margin is arched slightly upward, and bears a tiny downsloping tip. The border is moderately wide, slightly concave (almost flat) on the flanks, and convex in the rear. The marginal furrow of the pygidium is broad and shallow, but the border is well defined by the ends of the pleural ribs. Three pairs of pleural furrows are present, and a fourth is indicated at the terminus. The pleural furrows are broad, deep, smooth channels. The pleural ribs (four pairs are present, the fourth being vestigial) are broad elevated swells lacking the knobs seen in *R. rostrifinis*

sp.nov. On the anterior rib a narrow interpleural groove is incised, and on the second the interpleural partition is indicated by an obscure crest. The pleural lobes as a whole are horizontal in the ribbed, and slope gently toward the border in the peripheral, part. The axial furrows are distinct, but become shallow around the terminus. The axial lobe, as wide as the anterior pleural rib, is elevated, and strongly arched transversely, and almost semicylindrical. It tapers slightly, and reaches the border, sloping towards it vertically in the rear. Three prominent complete and a fourth incomplete annulations and a short terminus are present. The anterior transverse furrow is broad, exposing the non-functional articulating half-ring of the second segment, and the posterior furrow is defined only in the middle, not on the flanks, of the axis. The two anterior annulations bear rather distinct anterolateral annular projections; the tips of the anterior projections merge with the pleural margin; and each projection itself is defined by a longitudinal dent.

The pygidial test is granulose, but the distribution of the ornament is selective: it is present on the elevated median part of the axial annulations, including the terminus, and on the crests of the two anterior pleural ribs. All furrows, the border, the flanks of the axis, and the posterior, fused, part of the pleural lobe are smooth. The rear slope of the articulating half-ring is minutely granulose. Relatively coarse terraced lines adorn the margin.

*Comment on illustrated material:*

All specimens were collected in the Mungerebar Limestone; one pygidium, as indicated below, comes from locality G125, and the rest from locality G153; the matrix (light grey, slightly pink, almost aphanitic limestone with chert laminae and granular silica) is the same in both localities, and so are the associated fossils. The collection, presumably, belongs to a single bed. Furthermore, the cranidium Plate 46, fig. 3, CPC 5719, locality G124, may belong here but is too solidified for a definite identification.

The holotype cranidium, Plate 25, fig. 1, CPC 5552, is 7.0 mm long. It is not flattened, and complete with posterolateral limbs. The granulose ornament is minute, visible in the middle of the posterior part of the glabella and occipital lobe.

The pygidium, Plate 25, fig. 3, CPC 5554, is 4.0 mm long; the border is concave, the first interpleural groove is present, and the annular projections at the anterolateral corners of the two anterior annulations visible.

The pygidium, Plate 25, fig. 4, and Plate 33, fig. 4, CPC 5555, locality G125 (associated with cranidia of *Griphasaphus griphus*), is 3.4 mm long and 7.4 mm wide. The border is concave on the flanks, but slightly convex in the rear; the annular projections are distinct.

The isolated segment of the thorax, CPC 6733, incorporated in Text-figure 93, is 6.5 mm wide (transversely). The left spine is missing in the original, but restored in the diagram.

The silicified free cheek, Plate 25, fig. 2, CPC 5553, is 11.3 mm long (as preserved); the ocular part is broken and the base of the spine collapsed, creating the impression of a continuous marginal furrow; the widened and angular subcephalic doublure is exposed. It is associated with a fragment of *Stephanocare*.

*Occurrence and age:* *Rh. (Rhyssometopus) rhyssometopus* has been found in the Mungerebar Limestone, at localities G124, G125, G126, G127, G128, G132, and G153. Its age is the Mindyallan Zone of *Cyclagnostus quasivespa*. It has been recorded also at G417, in the Zone of *Erediaspis eretes*.

RHYSSOMETOPUS (RHYSSOMETOPUS) PRINCEPS sp.nov.

(Pl. 26, figs 1-9; Pl. 27, figs 1-3; Pl. 51, fig. 10; Text-figs 96, 97)

*Material:* The described material comes from two collections—(1) a single bed of the Georgina Limestone locality W20—three cranidia, one defective coiled complete specimen, four free cheeks and three pygidia; these are selected from a large number of specimens which are mostly fragmentary or partly immersed in the siliceous matrix: (2) O'Hara Shale ('lower chert bed'), locality D29—two cranidia and two pygidia.

*Holotype:* The cranidium Plate 26, fig. 1, CPC 5560, is selected as the holotype because it retained most of its test and is undeformed.

*Diagnosis:* *Rhyssometopus (Rh.) princeps* is a species with a slightly tapering (not elongate hexagonal) subtruncate glabella, and evenly granulose test; distinguished by its forward arched front, narrow rim, very large palpebral lobes (about 0.85 of glabellar length), and distally widening pygidial ribs.

*Differential Diagnosis:* The characters mentioned in the diagnosis are distinctive, preventing any confusion with other species of the subgenus; in the description that follows, *princeps* is compared with *rhyssometopus* and the differences between them indicated.

*Description:* The cephalon is semicircular and moderately convex, with a well developed relief and curving slopes. The glabella is depressed slightly below the level of the palpebral lobes, and forms with the brim a more or less even arch. The

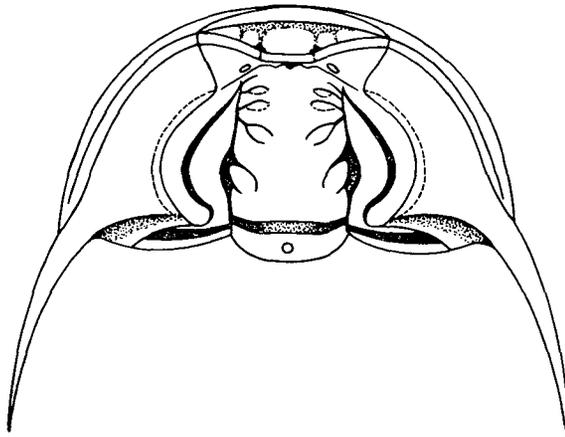


Fig. 96.—*Rhyssometopus princeps* sp.nov., combined from Plate 26, figs 1 and 3, and Plate 27, fig. 1.

free cheek is large, with a moderately tumid ocular platform, and a slightly advanced (less than in *Rh. rhyssometopus*), curved, and relatively short transmarginal genal spine which is confluent with the ocular platform. The lateral border is defined by a weak marginal furrow and has a flange produced by a peripheral depression (almost a furrow). A posterior marginal furrow is absent, as in all species of *Rhyssometopus*, but there is a depressed flange behind the ocular platform. The cheek is conspicuously venulose, more than in *Rh. rhyssometopus*.

The anterior sutures diverge relatively strongly and, converging within the rim, intercept the margin opposite the anterolateral corners of the glabella. The posterior sutures diverge diametrically, curving evenly toward the margin, and delineating small blade-like posterolateral limbs.

The palpebral lobes are very large, as long as 0.85 of glabellar length, and longer than in any other species of the genus; their posterior tips are level with the front slope of the occipital lobe. The interocular cheeks, 0.27 of glabellar width, are slightly swollen and slope adaxially. The ocular ridges are distinct, confluent with the palpebral lobes, and merge with the glabella at its anterolateral angles; in front of them is a pair of small, low knobs.

The cranial margin is arched forward (straight in *Rh. rhyssometopus*) and the front of the cephalon is evenly curved. The cranial front between its anterolateral corners is wide, between 1.4 and 1.5 of glabellar width, and relatively short, about 0.35 of glabellar length, and consequently shorter but wider than in *Rh. rhyssometopus*. The rim is less than half the length of the brim, slightly upturned, and the border furrow is concave and not angular as in *Rh. rhyssometopus*. The central part of the brim carries a low, transversely elongate antirostral hood, which in some specimens (Pl. 26, figs 2, 3) may be developed as a low quadrangular swelling. The wrinkle on the brim is always distinct, but varies in relief, and is divided into three segments by the furrows flanking the antirostral hood. The expansion of the lateral segments of the wrinkle into elevated nodes (or bosses) seen in Plate 26, figure 3, is unique.

The occipital lobe and furrow together are shorter than in *Rh. rhyssometopus*, relative to the length of the cephalon. The occipital furrow in *Rh. princeps* is moderately wide and deep, and almost straight; the occipital lobe is flat longitudinally and bears a small node.

The axial furrows are distinct and more or less evenly deep around the front and at the flanks of the glabella.

The glabella is moderately long, as wide as 0.8 of its length (0.9 in *Rh. rhyssometopus*), more or less evenly and slightly tapering, subtruncate in front, with rounded anterolateral corners. It lacks the angularity in front of the palpebral lobes, and the elongate hexagonal shape seen in *Rh. rostrifinis* and *rhyssometopus*, but can be compared with *Rh. (Rostrifinis) tiro* and *Rh. rugiceps* as regards the glabellar outline.

The lateral bulges of the glabellar flanks are distinct but inconspicuous and are defined by glabellar furrows. Four pairs of glabellar furrows can be distinguished on an intact test, but usually they are rather shallow or even obliterated; on the internal cast they are combined with muscle spots similar to *Rh. rhyssometopus*.

The glabella is weakly carinate, but lacks the longitudinal serpentines of *Rh. rhyssometopus*. In exceptional preservation (Pl. 26, fig. 3) the glabellar front is wavy and bears a tiny median node at its margin.

The palpebral lobes, the rim, and the muscle spots are smooth; the rest of the surface is evenly, densely, and minutely granulose, and on the interocular cheeks and the anterolateral limbs the granules are arranged in radiating lines. Terraced lines can be seen along the margin of the cephalon.

The ventral structure is the same as in *Rh. rhyssometopus* (Text-fig. 95).

The segments of the thorax (Pl. 26, fig. 4) have long, rearward-directed pleural spines, and the pleural furrows are wide and long, reaching into the recurved base of the spines; apparently all segments have the same structure of the pleurae and, consequently, no macropleural segments are present.

The pygidium of *Rh. princeps* is semicircular to transverse semielliptical (in flattened specimens). It resembles closely *Rh. rhyssometopus*, but (1) in its axis the fourth annulation is well defined, (2) the pleural ribs widen distally and are somewhat bilobed, (3) the axial lobe tapers visibly, and (4) the test is minutely granulose, over all, including the pleural furrows.

The pygidial border is moderately wide, the border furrow wide, concave, and shallow, and the pleural lobes are moderately convex. Three pairs of pleural furrows and ribs are present; on the first two ribs interpleural partitions are indicated by raised lines. The axis is as wide as the pleural lobe, elevated high, strongly arched transversely, and reaches the border in an almost vertical slope.

*Comment on illustrated specimens:*

(a) Specimens from locality W20, from a single bed of limestone, or its siliceous bedding plane—a shale lamina.

The holotype cranium, Plate 26, fig. 1, CPC 5560, in bituminous dark limestone, is 5.0 mm long. It is undistorted, but has lost a part of its test. The palpebral lobes and the rim are smooth, lacking the minute granulosity of the rest. The junction of the left ocular ridge with the frontal lobe is visible. The posterior tips of the palpebral lobes are level with the occipital furrow; a part of the doublure of the occipital lobe is exposed. The antirostral hood is slightly swollen.

The cranium, Plate 26, fig. 2, CPC 5561, is 5.2 mm long. It is flattened, and dilated in the rear; the glabella appears, therefore, more tapering than in the holotype. The posterolateral limbs are exposed, the carina and the wrinkle on the brim are accentuated; the edges of the palpebral lobes are worn off. The antirostral hood is relatively prominent and trapezoidal.

The cranium, Plate 26, fig. 3, CPC 5562, flattened and crushed in limestone, is 7.5 mm long. The left side is decorticated, an advantage in comparing the parietal and external features; the low-angle illumination accentuates the relief, especially of the antirostral hood, including the median preglabellar node and the veins in the preglabellar furrow.

The fragment of a coiled complete test, Plate 26, fig. 4, CPC 5563, is 3.0 mm long; five posterior segments and the frontal part of the cranium are present; the rest is worn off; the associated free cheek, Plate 26, fig. 5, probably belongs to it. The pleurae terminate in long spines; the pleural furrows are wide and extend into the spine.

The free cheek, Plate 26, fig. 5, CPC 5564 (associated with the coiled specimen, fig. 4), is 5.0 mm long including the spine; the spine is deflected, transmarginal, and the cheek is venulose.

The free cheek, Plate 51, fig. 10, associated with the free cheek of *Rhodonaspis longula*, is 6 mm long, including the spine.

The free cheek, Plate 27, fig. 1, CPC 5569, in dark bituminous limestone, is 6.5 mm long without the spine. It is associated with two crania (not illustrated). Note the flange on the border and the course of the posterior suture.

The free cheek, Plate 26, fig. 6, CPC 5565, is 9.0 mm long as preserved (without the spine); it belongs to a relatively large specimen. The shallow furrow defining the flange extends along the whole length of the border.

The pygidium, Plate 26, fig. 7, CPC 5566, in dark bituminous limestone, is 4.9 mm long; the right pleural lobe is missing. The deep furrow on the anterior rib is accidental. The interpleural crests (not grooves) are weak but distinct.

The pygidium, Plate 26, fig. 8, CPC 5567, in limestone, is 4.3 mm long; it is crushed and decorticated, showing the smooth (not granulose) internal cast; the annular projections on the anterolateral corners of the axial rings are distinct.

The pygidium, Plate 26, fig. 9, CPC 5568, is 2.0 mm long; it is silicified and flattened; it is a small pygidium, still showing the four axial annulations.

(b) Specimens from the O'Hara Shale ('lower chert bed'), locality D29, all in friable matrix. All specimens in this bed are relatively small.

The fragmentary cranium, Text-figure 97, CPC 6734, is 3.1 mm long. The palpebral lobe, 0.9 of glabella length, is exceptionally large; its posterior tip is on the level of the occipital node. The antirostral hood is faintly indicated.

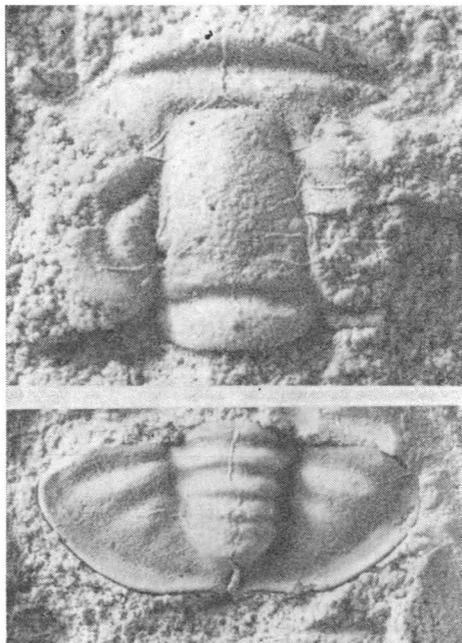


Fig. 97.—*Rhyssometopus princeps* sp.nov., O'Hara Shale ('lower chert bed'); cranium CPC 6734, x 14; pygidium CPC 6734a, x 8.

The cranium, Plate 27, fig. 3, CPC 5571, is 2.2 mm long; the glabella is parallel-sided and almost rectangular.

The pygidium, Plate 27, fig. 2, CPC 5570, is 2.1 mm long. It is somewhat flattened and the axial lobe is relatively narrow.

The pygidium, Text-figure 97, CPC 6734a, is 3.0 mm long; it shows the left facet and the median tip on the rear margin.

*Occurrence and age:* *Rh. (Rhyssometopus) princeps* is a common species; it occurs in the lower part of the Georgina Limestone at locality W20, and also at W1, W15, W17, G48, G49, G50, W66, W258, W301; it is also common in the O'Hara Shale ('lower chert bed') at localities D6 and D29; in the Mungerebar Limestone it is present at McKabe Knob.

Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

RHYSSOMETOPUS (RHYSSOMETOPUS) RUGICEPS sp.nov.

(Pl. 25, figs 5-8)

*Material:* The described and illustrated material consists of two cranidia and two pygidia found in a single piece of limestone; no other *Rhyssometopus* is associated with these specimens. About 20 cranidia and 15 pygidia were included in the collections from two sites (G10 and G131); most of these are fragmentary.

*Holotype:* The cranidium Plate 25, fig. 5, CPC 5556, locality G10, is selected as the holotype, being the better preserved specimen.

*Diagnosis:* *Rh. (Rhyssometopus) rugiceps* is a species with a subtruncate (not elongate hexagonal), tapering, and relatively long glabella and an overall minutely granulose cranial and pygidial test, and large palpebral lobes (0.70 of glabellar length); distinguished by its short cranial front (0.25 of glabellar length), and the shortness of the brim, which is shorter than the rim. Its antirostral hood is rather inconspicuous.

*Differential Diagnosis:* *Rh. rugiceps* combines the glabellar shape and the characters of the granulation of *Rh. princeps*, and the length of the occipital lobe and furrow taken together and relatively short palpebral lobes of *Rh. rhyssometopus*, with a rather small frontal area and short brim. In *princeps* the palpebral lobes are much longer (0.85 of glabellar length), the occipital structure is smaller, and the rim narrow, whereas in *Rh. rhyssometopus* the glabella is elongate hexagonal, the rim and the brim are about equal, and the granulation is restricted to the cranial rear and elevated part of the pygidium.

*Rh. rugiceps* varies in the width of the palpebral lobes and the form of the cranial front, which may be straight as well as angular.

*Description:* The palpebral lobes are large, between 0.7 and 0.73 of glabellar length, and somewhat variable in width, but remain broad and almost flat. Their posterior tips reach the rear of the glabella. The interocular cheeks, 0.25 to 0.3 of glabellar width, and variable depending on the width of the palpebral lobes, are slightly swollen and slope adaxially down from the palpebral edge. The palpebral lobes merge with the ocular ridges, which are rather oblique, reaching the anterolateral corners of the glabella.

The cranial margin is slightly arched, subtruncate in the middle, but may be also subangular (Pl. 25, fig. 6), as if attempting rather unsuccessfully to produce a frontal cusp. The cranial front between the anterolateral corners is relatively narrow, about 1.3 of glabellar width, and the frontal area conspicuously short, 0.25 of glabellar length. The rim is twice the length of the brim; the marginal furrow is a concave to subangular depression in the middle, but somewhat better defined on the flanks, of the frontal area. The antirostral hood is defined laterally by lines and the slightly elevated median segment of the wrinkle.

The occipital lobe and furrow together are visibly longer (longitudinally) than the frontal area, and the occipital furrow is rather wide and well defined by the sharp edge of the glabellar rear. The occipital structure compares well with *Rh. rhyssometopus* but not with *princeps*. The same applies to the preglabellar furrow, which is deep and straight, separating the antirostral hood and the median part of the wrinkle from the truncate to subtruncate frontal lobe of the glabella.

The glabella is relatively long (having a width/length ratio of 0.75 to 0.8), truncate conical (but not elongate hexagonal), tapering to about 0.75 of its posterior width. The lateral bulges are inconspicuous, and together with these, four pairs of glabellar furrows combined with five pairs of muscle spots are present in the same arrangement as seen in *R. rhyssometopus* and *princeps*. The glabella is weakly carinate, the carina is double and flanked by almost imperceptible serpentizing ridges.

The test is minutely granulose, including the marginal terraced lines. The glabella, the furrows, and the muscle spots are smooth. Delicate veins are present in front of the ocular ridges.

The undistorted pygidium is semicircular, its border is flat and narrow, the marginal furrow is distinct, the peripheral and unfurrowed part of the pleural lobes slopes down abruptly from the terminal ends of the ribs; four pairs of pleural furrows and three of ribs are well expressed, and the fourth pair of ribs is diminutive. The axial lobe is as wide as the pleural (in plan), high, and reaches the border. Three complete annulations, a fourth rather incomplete annulation, and a short rounded and steep terminus are present. The test, including the marginal terraced lines, is densely granulose.

The ventral cephalic structure, in the absence of the free cheeks with preserved doublure, cannot be restored. The short brim, however, indicates an equally short rostral shield, and the presence of an apical doublure is evident.

*Comment on illustrated specimen:*

All specimens have been recovered from a single piece of limestone, locality G10.

The holotype cranidium, Plate 25, fig. 5, CPC 5556, is 5.2 mm long; the front is straight, the double carina and the serpentizing lines are discernible; the glabellar furrows are distinct on the internal cast, and the palpebral lobe is relatively narrow.

The cranidium, Plate 25, fig. 6, CPC 5557, is 6 mm long. The front is subangular, and the palpebral lobe relatively wide.

The pygidium, Plate 25, fig. 8, CPC 5559, is 3.4 mm long; note the narrowness of the border.

The pygidium, Plate 25, fig. 7, CPC 5558, is 2.1 mm long; it is flattened and somewhat dilated.

*Occurrence and age:* *Rh. (Rhyssometopus) rugiceps* is a rare fossil of the Mungerebar Limestone found at localities G10 and G131. Its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

RHYSSOMETOPUS NEUTER sp.nov.

(Pl. 27, fig. 7)

*Material:* Only the holotype cranidium, 8mm long, CPC 5575, is illustrated, but several more fragmentary cranidia have been collected.

*Subgeneric Classification:* *Neuter* cannot be regarded as a species of *Rh. (Rostrifinis)* because it lacks the frontal cusp; neither is it a *Rh. (Rhyssometopus)* because the frontal area is not divided into a brim and a rim, the wrinkle is straight, and its ends are not swept forward; furthermore, the glabellar furrows are distinct.

The description below contains the diagnosis and the differential diagnosis.

*Description:* The parabolic cranial margin protrudes forward, is subangular (rounded) in the middle, and upturned; but it is not pointed—a structure not seen in other species of *Rhyssometopus*. The frontal area, 0.4 of glabellar length, is evenly concave, and lacks a marginal furrow; the wrinkle is transverse and straight. The palpebral lobes are moderately arcuate, 0.7 of glabellar length (longer than in *R. rostrifinis* where it is 0.55 to 0.6); the interocular cheeks, 0.2 of glabellar width, are convex and slope rather steeply toward the axial furrows. The glabella is relatively long, subtruncate and slightly tapering, with well rounded anterolateral corners, and bears four pairs of relatively distinct glabellar furrows; its flanks are straight and the lateral bulges are barely indicated.

The test is preserved, but corroded; nevertheless, minute granulation is visible on the glabella and in its middle a pair of longitudinal serpentine lines are indicated, as seen in *Rh. (Rhyssometopus) rhyssometopus* and *rugiceps*.

*Occurrence and age:* *Rh. neuter* has been found in the Mungerebar Limestone at localities G119, G149 and G150; its age is the Mindyallan Zone of *Erediaspiresetes*.

#### Subgenus RHYSSOMETOPUS (ROSTRIFINIS) nov.

The type of the subgenus *Rostrifinis* is *Rh. rostrifinis* sp. nov.

The characters of the subgenus are given under the genus *Rhyssometopus*.

The following species belong to *Rostrifinis*—(1) *Rostrifinis rostrifinis* sp. nov., (2) *R. tiro* sp. nov., and (3) *R. aff. rostrifinis*.

A separate generic rank appears inappropriate because the cuspidate frontal margin of the cephalon is the sole reliable character of this group of species; when it is not preserved the material must be referred to as *Rhyssometopus* unless the specific identity is known beforehand.

#### RHYSSOMETOPUS (ROSTRIFINIS) ROSTRIFINIS sp. nov.

(Pl. 27, fig. 9; Pl. 28; Pl. 29, figs 1–8; Pl. 58, fig. 6, Text-figs 98 and 99)

*Material:* Abundant material of cranidia, free cheeks, and pygidia is present in the collections. For description and illustration thirteen specimens—four cranidia, three free cheeks, and five pygidia—have been selected; the thirteenth specimen is a unique complete shield.

*Holotype:* The cranidium Plate 28, figure 3, CPC 5580, locality G8 is selected as the holotype because (a) it is complete, (b) its frontal apical ventral doublure is accessible for observation, and (c) during the removal of the matrix by acid and needle the ornament was observable. The associated cranidium supplements the holotype (for example, showing the preglabellar pits and the left palpebral lobe), and so does the isolated cranidium (Pl. 28, fig. 1) which is rather friable and therefore less suitable as a holotype. The complete specimen, though rather informative in a generic and familial sense, would be insufficient as regards specific detail.

*Diagnosis:* *Rh. (Rostrifinis) rostrifinis* is a species with (1) a long and upturned frontal cusp, (2) an elongate hexagonal glabella, (3) rather narrow interocular

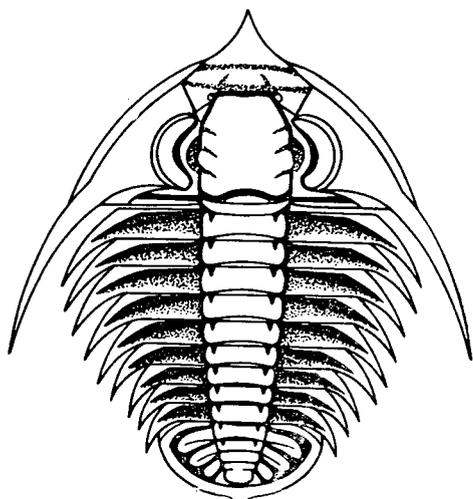


Fig. 98.—*Rhyssometopus (Rostrifinis) rostrifinis* subgen.nov., sp.nov., combined from Plate 28 and Plate 29, figs 1, 3, 4, and 8.

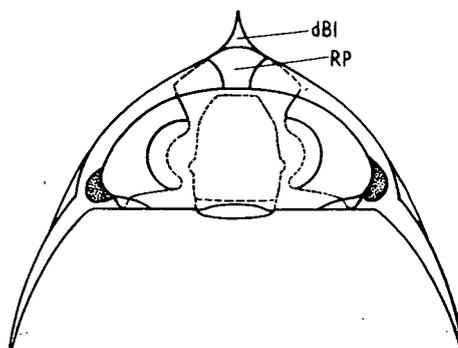


Fig. 99.—*Rhyssometopus (Rostrifinis) rostrifinis* sp.nov., cephalon in ventral view, combined from Plate 29, figs 2 and 4. dBl—doublure of frontal cusp; RP—rostral shield.

cheeks (0.2 of glabellar width), (4) large palpebral lobes (about 0.7 of glabellar length) placed with their posterior tips on level with the glabellar rear, and (5) a short triangular cusp on the posterior pygidial margin.

Also, its ventral cephalic structure, especially the shape of the rostral shield, and the thorax, are characteristic, as described below; these cannot be included in the specific diagnosis because of lack of comparable detail in other species.

The differential diagnosis is given with the next species, *Rostrifinis tiro* sp.nov.

*External Habit:* (Text-fig. 98): *Rhyssometopus rostrifinis* is a small trilobite which may have reached 2.5–3.0 cm in length. The cephalon is relatively large (as long as about seven segments of the thorax); the pygidium, 0.4 of the cuspidate cephalon, and 0.5 without the cusp, is medium, or, for a Cambrian trilobite, even large. The proportions of the tagmata are 1 (cephalon): 1.2 (thorax): 0.4 (pygidium). The body is oval, tapering rearward and widest in the rear of the cephalon, with a width/length ratio of about 0.7, or slightly less, depending on the actual slope of the free cheeks, which cannot be established exactly. The convexity is moderate, but the relief of furrows and lobes, except for the glabellar lobes, is well developed. The cephalon is subtriangular and tricuspidate (divergent trans-marginal genal spines and the upturned frontal cusp), and with large arcuate eyes close to the low glabella. The thorax consists of nine segments, decreasing rearward, with long pleural spines but the pygidium has no marginal spines; it has a well developed relief with peculiar knobs or knuckles (almost short vertical spines) on the ends of the pleural ribs and a short projection of the border behind the axis.

*Description:* The free cheek is relatively large, moderately convex and gently sloping outward. A narrow and flat lateral border peters out at the base of the genal spine; a marginal furrow is missing and a change of slope marks the limit of the border. The genal spines are long (about half the length of the thorax) evenly

curved and deflected. The dorsal side of the spines is flat and broad and the outer edge overhangs slightly the narrower and convex ventral side. The genal spine is transmarginal, inseparable from the ocular platform and disrupting the connexion of the lateral and posterolateral border. The only sign of a posterolateral marginal furrow in the free cheek is a broad triangular depression bounded by the even curve of the spine and stretching to the posterior tip of the eye (Pl. 29, fig. 4). The cornea is retained by the free cheek; it is low, convex, and separated at the base by a deep furrow. The anterior sutures are straight and divergent in front of the eyes; within the border they turn abruptly toward the midline, but remain straight and dorsal to the base of the frontal cusp, where they pass into the ventral rostral and the connective sutures. The posterior sutures diverge diametrically first, then curve toward the margin to cut it about half-way between the lateral margin and the occipital lobe. The posterolateral limbs are narrow (longitudinally) and pointed, and bear distinct marginal furrows which do not cross the suture.

The palpebral lobes are long, about 0.7 of glabellar length, arcuate, wide, almost flat and horizontal, with tips close to the axial furrow, and the rear tips level with the glabellar rear. The anterior cusps of the palpebral lobes extend into the very short and slanting ocular ridges; the palpebral furrows are distinct and join the axial furrows at the ocular ridges. The interocular cheek, about 0.2 of glabellar width, slopes adaxially. Most of it is occupied by a crescentic ridge parallel to the palpebral lobe, and covered by faint veins which radiate abaxially.

The cranial front is somewhat diamond-shaped, and varies between 1.2 and 1.4 of glabellar width. It is not divided into a brim and a rim, but a straight and convex transverse fold (the wrinkle) stands out in front of the glabella, between the lateral corners; delicate veins arise from the ocular ridges and peter out at the fold. Anterior to the transverse wrinkle, in a concave curve, rises the frontal cusp with an attenuated pointed tip. The antirostral hood is inconspicuous, indicated by faint lateral lines. The cranial front is as long as 0.65 of the glabella and slightly more than 0.3 of the cephalon.

The occipital lobe is relatively short, arched transversely, but flat and low in profile. The occipital furrow is wide in the middle, with angular edges and with slightly deepened muscle scars in its flanks. The axial furrows are distinct, and a pair of pits can be seen at the anterolateral corners of the glabella.

The glabella is as wide as 0.8 of its length, relatively low, and only slightly arched. It is angular, elongate hexagonal, with parallel flanks behind the ocular ridges; the preocular part of the glabella has straight converging flanks and a straight, transversely truncated front provided with an almost imperceptible recess in the middle. The angularity of the anterior part of the glabella is rather abrupt and curves are absent. The same shape of the glabella is seen in *Rh. rhyssometopus* sp. nov. Opposite the middle of the palpebral lobes the glabella is slightly constricted by a lateral depression, and behind it expanded as a pair of lateral bulges. The same structure is even more conspicuous in other species of *Rhyssometopus*. Three pairs of rather weak glabellar furrows can be seen in some specimens, and a faint median carina is also usually present.

In the thorax the pleural furrows are wide and long, and the pleural spines are long, pointed, and falcate in the anterior, and directed rearward in the posterior

segments. The axial lobes bear at each of the anterolateral corners an annular projection pointing forward (see Text-fig. 93). The pygidium is semielliptical to semi-circular (when not flattened) in outline, with geniculated, faceted anterolateral extremities and slightly arched rear. The border is narrow, slightly convex, almost flat, and defined by a distinct marginal furrow. Three pairs of elevated pleural ribs are separated by broad, channel-like pleural furrows, and a fourth pair of diminutive ribs may be seen flanking the axial terminus in larger specimens. The interpleural grooves are fused and represented by crests on the pleural ribs; the distal, abaxial ends of these crests develop into raised knobs or knuckles, or even into vertical projections in larger specimens (Pl. 58, fig. 6). The axial lobe has straight flanks, tapers slightly, is elevated above the pleural lobes, and is as wide as a pleural lobe without border. In smaller specimens three complete and one incomplete annulations are present, but in larger all four pygidial annulations are complete. In two anterior annulations anterolateral annular projections are present. The terminus is short, well rounded, and reaches the border, and a low antiplectrum behind the terminus may even reach the margin. The terminal part of the margin itself bears a short and broad projection—a terminal pygidial tip or cusp; it is stronger than in other species of *Rhyssometopus*.

The ventral structure of the cephalon (Text-fig. 99) is complicated. The doublure is narrow and rather convex in the rear, but widens toward the front; at the base of each genal spine it bears a vincular depression, to accommodate the tips of some of the pleural spines in a coiled state. An hourglass-shaped rostral shield is also present, separated by the rostral suture from the apical (subcuspal) doublure. The rear of the rostral shield is depressed apparently to accommodate the pygidial terminal cusp. The rostral shield reaches the glabella, and was consequently connected with the hypostoma.

The test is smooth.

*Comment on illustrated specimens:*

All specimens described below were collected in the Mungerebar Limestone; they are silicified and retain the test.

The isolated cranidium, Plate 28, figs 1a, 1b, CPC 5578, locality G417, is 6.2 mm long; its surface is rough with irremovable silica, but shows the glabellar furrows; on the ventral side the apical doublure indicates the position of the rostral suture. A sponge spicule (*Chancelloria*) adheres to the specimen.

The next five specimens are all from a single bed and bedding plane, locality G8.

The holotype cranidium, Plate 28, fig 3, CPC 5580, is 8.2 mm long. A pygidium about 3.5 mm long should correspond to this cranidium. The fossils rest on and adhere to a layer of silica, exposed by etching from under the limestone matrix. Agnostids and sponge spicules including *Chancelloria* cover the layer of silica.

The cranidium, Plate 28, fig. 2, CPC 5579, associated with the holotype is 7.5 mm long; it is partly immersed in silica. Its anterolateral corners are less angular than those of the holotype.

The free cheek, Plate 29, fig. 1, CPC 5581, is 10 mm long (as preserved); note the flat dorsal side of the genal spine.

The free cheek, Plate 29, fig. 3, CPC 5583, is 11.6 mm long from tip to tip. Note the narrow and flat lateral border petering out rearward and the confluence of the transmarginal genal spine with the ocular platform.

The free cheek, Plate 29, fig. 2, CPC 5582, is 12.2 mm. long from tip to tip. Note the widening of the anterior part of the doublure and the vincular depression at the genal angle. Ventrally the genal spine is not broad and flat but narrow and rounded and the doublure at the base of the spine is an elevated crest; the margin of the flat dorsal surface is seen in the shadow just above the base of the spine.

The four pygidia described below occur on a bedding plane, locality G119. They are associated with numerous cranidia.

The pygidium, Plate 29, fig. 5, CPC 5586, is 2.5 mm long; its pleural ribs (interpleural crests) are relatively low, the axis contains three complete and one incipient posterior annulation. The median terminal cusp of the margin is distinct. The forward-pointing annular projections is preserved on the left side of the anterior axial annulus.

The pygidium, Plate 29, fig. 7, CPC 5588, is 2.5 mm long; it is worn and has lost the posterior marginal cusp. It is associated with a pygidium of *Erediaspis eretes* sp.nov.

The pygidium, Plate 29, fig. 4, CPC 5584, is 4.1 mm long, and should correspond to a cephalon about 10 mm long. The fourth axial annulation is complete, the posterior marginal cusp is well preserved, and the distal ends of the pleural ribs (interpleural crests) are elevated knobs. Associated are cranidia of the same species and an immature damesellid cranidium.

The fragmentary pygidium, Plate 29, fig. 6, CPC 5587, is 4.5 mm long. The interpleural knobs are distinct and the terminal marginal cusp slopes down. The first and second axial annulations show the forward-pointing annular projections.

The pygidium, Plate 29, fig. 8, CPC 5589, locality G114d, is 3.3 mm long; it is a latex cast. The 'knuckles' are exceptionally undeveloped; the posterior marginal cusp is rather small. All other pygidia show the external surface of the test.

The cranidium, Plate 27, fig. 9, CPC 5577, locality G119, is 7.3 mm long (as preserved). It is silicified and fragmentary. It is illustrated to show that even with a broken front, and in the absence of evidence of the presence or absence of the frontal cusp, the species *rostrifinis* can be identified from other characters; but the identification of the subgenus *Rostrifinis* as such depends on the evidence of the cusp. In the given example the subgeneric identity is not evident but is deduced from the specific characters (elongate hexagonal glabella, straight frontal wrinkle, and length of the palpebral lobe, which is 0.7 of the glabellar length).

The pygidium, Plate 58, figure 6, CPC 5858, (associated with *Hadragnostus*) is 3.0 mm long. The knobs on the pleural ribs are exceptionally strong—almost spines.

The fragmentary, but nevertheless complete exoskeleton, Plate 29, figs 4a, b, CPC 5585, collection 41625 (Frome Broken Hill Pty Ltd) is 9.5 mm long. It is silicified and is exposed from the internal side. Note the rostral shield and the expanded frontal part of the doublure of the fixed cheek. Text-figures 98 and 99 are based essentially on this specimen.

*Occurrence and age:* *Rh. (Rostrifinis) rostrifinis* occurs in the Mungerebar Limestone in almost all localities. Its age is the Mindyallan Zone of *Erediaspis eretes*; fragments have been also found in the Zone of *Cyclagnostus quasivespa* and even in the earlier part of the *Glyptagnostus stolidotus* Zone (one fragment at G12).

#### RHYSSOMETOPUS (ROSTRIFINIS) TIRO sp.nov.

(Pl. 27, figs 4-6; Text-fig. 100)

*Material:* The available material consists of two cranidia and one free cheek, which are illustrated. The matrix is friable red sandstone; the cranidia are decorticated, the free cheek is an external mould. Taken alone, these specimens appear insufficient for a taxonomic treatment on a specific level; however, the comparison with *R. (Rostrifinis) rostrifinis* reveals definite diagnostic characters recognizable in each of the cranidia of *tiro*, which also supplement one another, warranting the reconstruction, Text-figure 100.

*Holotype:* The cranidium Plate 27, fig. 4, CPC 5572, locality D99, is selected as the holotype because it shows the posterolateral limbs, the frontal area, and the palpebral lobe more clearly than the other specimen.

*Diagnosis:* *Rh. (Rostrifinis) tiro* is a species with a short frontal cusp distinguished by a wide cranial front (1.7 of glabellar width), relatively large posterolateral limbs, moderately arched palpebral lobes not reaching the glabellar rear, straight glabellar flanks, and long genal spines which are twice the length of the cephalon.

*Differential diagnosis:* In the description below reference is made regarding the different characters of *R. rostrifinis*.

*Subgeneric classification:* *Rostrifinis tiro* possesses an extenuated frontal cusp and cannot be placed, therefore, in *Rh. (Rhyssometopus)*, which is distinguished by the absence of a cusp. The frontal part of the glabella in *tiro* lacks the angularity seen in *Rostrifinis rostrifinis* and recalls *Rhyssometopus princeps*.

*Description:* In the free cheek the genal spine is twice the length of the cephalon, curved, and extended, apparently, beyond the posterior margin of the pygidium. The spines are transmarginal and deflected as in *R. rostrifinis*, but in the latter they are much shorter (as long as the cephalon). The anterior sutures have the same course as in *R. rostrifinis* but diverge more strongly, which results in a relatively wide front of almost 1.7 of glabellar width (in *rostrifinis* it is 1.4 or even less). The posterior sutures are the same in both species, but in *tiro* the posterolateral limbs are larger (longer longitudinally) owing to the more forward placing of the posterior tips of the palpebral lobes. The cranial front is as long as about 0.55–0.6 of the glabella (0.65 in *rostrifinis*), provided with a broad straight fold (wrinkle); the brim is concave in front of the wrinkle, and extends into the short upturned extenuated

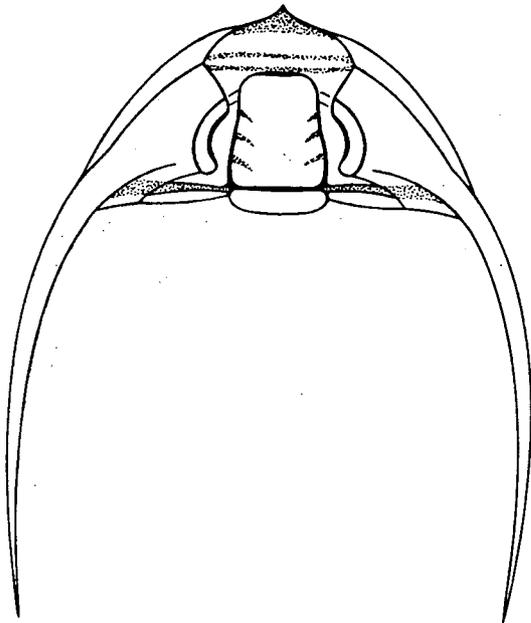


Fig. 100.—*Rhyssometopus (Rostrifinis) tiro* sp.nov., combined from Plate 27, figs 4–6.

cusps. The cusp is much shorter than in *rostrifinis*. The palpebral lobes are moderately arcuate, about 0.55 of the glabellar length, and their posterior tips are not on the level of the glabellar rear but placed more forward. The interocular cheek is 0.25 of glabellar width (0.2 in *rostrifinis*) and the cusps of the palpebral lobes are less close to the axial furrows than in *rostrifinis*. The glabella is longer than wide (width/length = 0.8 as in *rostrifinis*), subtruncate, but not narrowing abruptly in front of the palpebral lobes. The glabella is arched longitudinally and three pairs of rather weak glabellar furrows can be seen in oblique light.

*Comment on illustrated specimens:*

All three specimens come from a single piece of sandstone from locality D99.

The holotype cranium, Plate 27, fig. 4, is 9.0 mm long; the left side of the glabella is distinct; the tip of the frontal cusp broke off in the course of manipulations.

The cranium, Plate 27, fig. 5, CPC 5573, is 7.5 mm long; the glabella is undistorted, the left palpebral lobe and the anterolateral corners of the frontal area are preserved.

The free cheek, Plate 27, fig. 6, CPC 5574, is 28 mm long from tip to tip; the anterior part (with the doublure) is missing.

*Occurrence and age:* *Rhyssometopus (Rostrifinis) tiro* has been found only in the Steamboat Sandstone at locality D99. Its age is the Middle Cambrian/Upper Cambrian Zone of passage.

#### RHYSSOMETOPUS (ROSTRIFINIS) aff. ROSTRIFINIS

(Pl. 27, fig. 8)

The illustrated fragment of a cranium, CPC 5576, is silicified, and 6 mm long (as preserved).

It belongs to the subgenus *Rostrifinis* as seen from the extenuated cusp, which is, however, rather short; the cusp is complete (not broken) and the apical doublure is also partly exposed. The subangular shape of the glabella recalls *rostrifinis*, but the glabellar furrows are distinct, the lateral limbs of the frontal wrinkle are swept forward, and the frontal area and the cusp are relatively short for this species.

*Occurrence and age:* Mungerebar Limestone, localities G125 and G131; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

#### Family PLECTRIFERIDAE nov.

##### Genus PLECTRIFER nov.

The type species of the genus (and the family) is *P. plectrifer* sp.nov.; *P. mitis* sp.nov. is another species of the genus.

The diagnosis of the genus coincides with the diagnosis of the family Plectriferidae (p. 273).

##### PLECTRIFER PLECTRIFER sp.nov.

(Pl. 23, figs 3 & 4; Pl. 24, figs 1-4; Text-figs 101-102)

*Material:* Four cranidia, one free cheek, and two pygidia are illustrated and described; the material is somewhat fragmentary; in all specimens the test is exceptionally well preserved, displaying minute features seldom seen in Cambrian trilobites. Silicified specimens are common in many localities of the Mungerebar Limestone (*Erediaspis eretes* Zone).

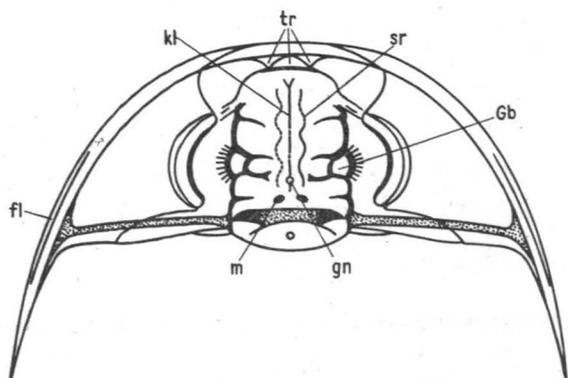


Fig. 101.—*Plectrifer plectrifer* gen.nov., sp.nov., combined from Plates 23 and 24. fl—flange; Gb—lateral glabella bulge; gn—glabella node; kl—carina; m—muscle spots; sr—serpentine lines; tr—plectrum (tripartite); other features see Text-fig. 93.

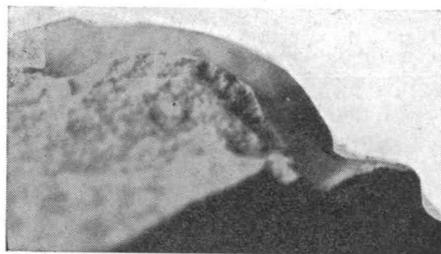


Fig. 102.—*Plectrifer plectrifer* sp.nov., Lateral view of cranidium, Plate 24, fig. 1, x 7·5.

*Holotype*: The cranidium Plate 23, figs 3a, b, c, CPC 5540, is selected as the holotype; it is the best preserved specimen.

*Diagnosis*: *Plectrifer plectrifer* is a species with a relatively short anterior border (less than 0·2 of glabella length) almost parallel-sided glabella (tapering to about 0·9 of its posterior width), relatively large palpebral lobes (0·62–0·7 of glabella length), and a narrow and straight posterior pygidial margin, and emphasized relief of pleural ribs which carry elongate knuckles.

The differential diagnosis is given under *Plectrifer mitis* sp.nov.

*Description*: The cephalon is broadly transverse semielliptical, or even lunate when the divergent genal spines are also considered; the convexity is moderate, and the glabella coincides with the general arc of the cephalon. The free cheek is relatively large, slightly tumid, and provided with marginal furrows and a narrow border; the anterior part of the border is flat, but the posterior part carries an inconspicuous longitudinal ridge extending into the genal spine. The lateral marginal furrow, as usual, is confluent with the posterolateral marginal furrow; but the posterolateral margin at the genal spine is crossed by a branch of the lateral furrow with the effect that the genal spine remains the extension of the lateral border only; its tie with the posterior border is thus disrupted. The posterior border of the free cheek is relatively long (transversely), almost as long as the posterolateral limb. The caecal veins in the proximity of the eye are relatively coarse, but change distally into a dense and delicate irregular radiating pattern.

The anterior sutures are moderately divergent, sinuate, and convex outward; within the rim they converge as almost straight lines and intercept the margin at points about 0·6 of the distance from the cranidial corners toward the midline. In the middle the suture is, apparently, marginal. The posterior sutures diverge almost diametrically and cut the margin in even curves, half way between the axial furrows and the flanks, delineating pointed blade-like posterolateral limbs as long transversely as 0·9 to 0·95 of the occipital lobe.

The frontal area is short, up to 0·18 of glabellar length; the marginal furrow is narrow and distinct on the sides, but shallow at the plectrum; furthermore, the furrows defining the flanks of the plectrum merge with the marginal furrow; but it can be also said that the plectrum divides the marginal furrow into two lateral parts swinging rearward at the plectral flanks. The rim is gently convex, bears faint transverse terraced lines, and is in front of the glabella about as wide as the brim. The plectrum is tripartite; its middle part is a triangle pointing forward, and the lateral parts are also triangles, pointing rearward.

The palpebral lobes are large (0·62–0·7 of glabellar length), arcuate, narrow, placed with posterior tips on the level of the glabellar rear, and at a distance of 0·25 to 0·3 of glabellar width from the axial furrows; the eyes are, therefore farther apart than in *Rhyssometopus* and *Rostrifinis*. The ocular ridges are double, narrow and slanting; interrupting the axial furrows they join the glabella. Delicate veins arise from the ocular ridges and the anterolateral glabellar flanks.

The interocular cheeks, about 0·3 of glabellar width, are relatively flat, sub-horizontal to sloping slightly adaxially.

The structure of the occipital lobe and furrow is the same as in the *Rhyssometopinae*, but of a lesser relief: the glabellar rear is abrupt, the occipital furrow is wide but ill defined in the rear; it tends to fade out laterally and has a pair of variable (deep to indistinct) appendiferi (pits). The occipital lobe is arched transversely, but otherwise flat, and provided with a pair of inconspicuous lateral lobules and a small median node. The occipital lobe and furrow together are 0·3 of glabellar length and slightly less than in *Rhyssometopus* and *Rostrifinis* where they are about 0·35.

The axial furrows are narrow and relatively deep, and very deep between the glabellar front and the corners of the plectrum. A pair of pits is placed at the posterolateral corners of the plectrum, and pits occur also at the adaxial ends of the ocular ridges. The glabella is slightly longer than wide, the width being variable around 0·8 of its length; it tapers also to 0·9 (at the adaxial ends of the ocular ridges) of its rear width. The preocular part of the glabella has rounded anterolateral corners, and a subtruncate broad front, comparable in shape with *Rhyssometopus princeps* and *Rh. rugiceps* but not with the other species that have an elongate hexagonal glabella. The carina is distinct, wavy and simple (not double), comparable with the ridge of a low gable roof in transverse section (Pl. 24, fig. 1b). Parallel to the carina a pair of serpentizing elevated lines are sometimes visible, marking the adaxial sides of the muscle spots like *Rhyssometopus rhyssometopus*. The glabellar flanks are straight except for the pair of distinct lateral bulges on the mid-level of the palpebral lobes; at the bulges the axial furrows are widened and weak radiating veins can be seen on the interocular cheek; the same structure is more conspicuous in *Rh. rhyssometopus*. Glabellar muscle spots and furrows are present; the furrows are rather shallow, and, therefore, somewhat erratic, and may be present alone, or combined with the spots; or the furrows are suppressed and the spots prevail (Pl. 23, fig. 3, second specimen). The glabellar furrows at the bulges are composite, and notable is the presence of a pair of intervening furrows on the posterior glabellar lobes; on the same transverse level, between the intervening furrows, a pair of muscle spots or even pits can be seen in some specimens. It appears (Text-fig. 101) that altogether five

pairs of lateral furrows are present if the furrows in front of and behind the bulge are separate features. In one specimen (Pl. 23, fig. 4) a weak but distinct median tubercle is present in the middle of the rear half of the glabella.

The test is minutely punctate.

The pygidia attributed to *Plectrifer plectrifer* (as well as the cranidia) are associated with pygidia and cranidia attributed to *P. mitis*; in the absence of a complete specimen cranidia and pygidia cannot be indisputably matched. I assumed that (1) the punctuation in the cranidium and the pygidium should be similar, (2) the narrow rear border of the pygidium should correspond to cranidia with the narrower frontal area, and (3) that the species represented by more cranidia in the sample should also be represented by more pygidia. The sample itself contains two species, *plectrifer* and *mitis*, and cranidia and pygidia attributed to the second species are both rare. It is notable, also, that two kinds of pygidia can be distinguished from each other; consequently if the assignment of the pygidia, against all expectations, turns out erroneous, the validity of the species will not be affected.

The pygidium is as long as half or slightly more than half the cephalon: this is indicated (1) by the relatively small numbers of four axial annulations, and (2) by the comparison of lengths of the available pygidia (around 3.0 mm) with the length of the associated cranidia between 5.4 and 6.1 mm.

The pygidium, as long as 0.45 to 0.5 of its width, is subrectangular (without the spines); its posterior margin is straight, and the flanks are subparallel. A border furrow is absent, but the outward-sloping border is well defined by the abrupt terminations of the pleural ribs. At the anterolateral angles and behind the terminus the border is very narrow, but expands greatly at the base of the spines; the posterolateral marginal spines, directed rearward and slightly upward, are about 0.3 of the pygidium; the rear margin at the adaxial base of the spine is slightly concave in some specimens. The pleural lobes of the pygidium are divided into two pairs of rather convex and broad and a third posterior and indistinct pair of ribs; the pleural furrows are rather deep. The distal ends of the pleural ribs are developed into elongate knuckles, somewhat similar to *Rostrifinis rostrifinis*. The anterior interpleural grooves are indicated. The axis is slightly narrower than a pleural lobe, has convex flanks, and tapers to a narrow rounded terminus which reaches the border. Four axial annulations are present, each carrying a pair of inconspicuous tubercles; furthermore a pair of low lobules (apparently representing an undeveloped annulation) are discernible at the anterolateral corners of the terminus. The test is punctate and caecal veins are present on the pleurae and on the base of the spines.

*Comment on illustrated specimens:*

All specimens have been collected in a single bed of limestone at locality G131.

The holotype cranidium, Plate 23, fig. 3, CPC 5540, is 7.0 mm long; it served essentially as the model for Text-figure 101. In frontal illumination the glabellar furrows and the junction of the ocular ridges with the glabella are well visible. In lateral light the carina and its flanking serpentizing lines are apparent. In the associated cranidium (fragmentary and partly covered by the matrix) the glabellar furrows are obscure, but the muscle spots and the punctuation of the test are well expressed.

The cranidium, Plate 24, fig. 1, CPC 5543, is 6.1 mm long; the glabellar furrows and muscle spots are weakly indicated; a posterolateral limb and a palpebral lobe are preserved,

but the plectrum is subdued. The frontal glabellar lobe appears angular because of the prominence of the carina; the roof-like transverse slope of the glabella is seen in the frontal view.

The fragmentary cranidium, Plate 23, fig. 4, CPC 5542, is 5.4 mm long; the glabella appears relatively slender because a part of its left flank is missing; the plectrum is also less distinct than in the holotype. A median node is indicated in the middle of the posterior half of the glabella.

The free cheek, Plate 24, fig. 2, CPC 5544, is 13 mm long from tip to tip; note the angular ridge extending from the border into the genal spine. The veins at the base of the eye are relatively coarse, but otherwise fine and densely interwoven.

The pygidium, Plate 24, fig. 3, CPC 5545, is 3.0 mm long. The interpleural ridges are inconspicuous; the knuckles on the two anterior pairs of ribs are rounded, the test is punctate; note the contrast between the deep pleural furrows and the shallow transverse furrows of the axis.

The pygidium, Plate 24, fig. 4, CPC 5546, is 3.0 mm long. The articulating half-ring of the second annulation is showing, and the anterior interpleural groove on the right is partly open. On the axis each annulation bears a pair of weak nodes, the knuckles on the ribs are elongate, and the narrow doublure is exposed on the left.

*Occurrence and age:* *Plectrifer plectrifer* occurs in the Mungerebar Limestone at localities G131 (the illustrated specimens), G8, G10, G119, G417, and probably in several others. Its age is the Mindyallan Zones of *Erediaspis eretes* and *Cyclag-nostus quasivespa* (G10 and G131).

#### PLECTRIFER MITIS sp.nov.

(Pl. 24, figs 5-9)

*Material:* The concept of the species *P. mitis* is based essentially on the illustrated limestone material consisting of one cranidium, one free cheek, and three pygidia; more specimens are available from the same sample. Silicified cranidia and pygidia (of which one is illustrated) occur in several localities, but less well preserved than the specimens in limestone.

The described specimens of *P. mitis* occur together with *Plectrifer plectrifer*: the reasons for associating pygidia with cranidia have been given under *P. plectrifer*.

*Holotype:* The cranidium Plate 24, fig. 5, CPC 5547, locality G131 is selected as holotype because of its satisfactory preservation and because *P. plectrifer* is also typified by a cranidium.

*Diagnosis:* *Plectrifer mitis* is a species with (1) a relatively long frontal area of glabellar length, (2) a long tapering glabella whose width at the rear is about 0.7 of length, and at the level of the adaxial ends of the ocular ridges is 0.8 of its rear width, (3) palpebral lobes of about 0.55 to 0.6 of glabellar length, (4) the lateral border of the free cheek convex (without a supplementary ridge); the pygidium is distinguished by (5) a relatively wide border, and rounded (not straight) posterior margin which is truncated only for a short distance, and (6) three distinct and one indistinct pair of fused pygidial pleural ribs, with a relatively low relief and a pair of low nodes on the anterior pleural ribs.

*Differential diagnosis:* *Plectrifer mitis* differs from the type of the genus (*P. plectrifer*) in all characters mentioned in the diagnosis. *P. plectrifer* has a shorter

and less tapering glabella, a shorter frontal area, a flat border with a ridge in its free cheek, and a less fused pygidium with a straight rear margin and a rather strong relief of the pleural lobes.

*Description:* The holotype cranidium is 7.2 mm long; it is carinate, the brim is relatively long, and the glabellar furrows are relatively clear (well discernible). The right posterolateral limb (as long transversely as the occipital lobe), and the left palpebral lobe are preserved.

The free cheek Plate 24, fig. 6, CPC 5548 locality G131, is 11.0 mm long (from tip to tip). It is assumed to belong to *P. mitis* because the relatively large distance from the anterior tip of the eye to the border along the suture indicates a cranidium with a relatively long cranial front, longer than in *P. plectrifer*. The border of the free cheek is convex, without a ridge, and the strong and reticulate pattern of its caecal veins is quite distinctive.

The pygidium Plate 24, fig. 7, CPC 5549, locality G131, is 3.7 mm long. In addition to the brief description in the diagnosis, the minute punctation and delicate caecal veins on the pleural lobes, terraced lines on the spine, and the length of the spines (over half the shield's length) are noteworthy.

The fragmentary pygidium Plate 24, fig. 8, CPC 5550, is 3.5 mm long (as preserved); its border is defined somewhat less than in Plate 24, fig. 7.

The silicified and worn pygidium Plate 24, fig. 9, CPC 5551, locality G429, is 2.5 mm long. The relatively wide border, the rearward arched posterior margin, the long spine, and the low relief of the pleural ribs indicate *P. mitis*.

*Occurrence and age:* *Plectrifer mitis* occurs sparsely in the Mungerebar Limestone, as for example, at localities G8, G10, G119, G131, G417, and G429b. Its age is the Mindyallan Zones of *Cyclagnostus quasivespa* (G10 and G131) and *Erediaspis eretes*.

#### Family MAPANIIDAE Chang, 1963

The family Mapaniidae, according to Chang, includes only two genera—*Mapania* Endo & Resser and *Mapanopsis* Chang. Chang, however, has restricted his classification of trilobites to Chinese forms and his diagnosis of the Mapaniidae is an abstract of characters of *Mapania striata* Resser & Endo, 1937.

The concept of the family Mapaniidae that follows amplifies Chang's (1963, p. 486) concept; it was, however, compiled independently. Of course, *Mapania striata* is the first described form, but details of its organization are still a matter of contention; even the latest reconstructions of the cranidium of *Mapania*—in Harrington et al. (1959), by Kobayashi, 1960, p. 392, and by Öpik, 1961, p. 161—represent a different trilobite species each.

*Diagnosis:* Mapaniidae of the superfamily Rhyssometopacea are distinguished by (1) a relatively long glabella, with a width/length ratio around 0.75, (2) a well developed plectrum, (3) narrow interocular cheeks (0.5 of glabella, or less), (4) large arcuate palpebral lobes, about 0.5 of glabellar length in a subcentral position, (5) straight anterior sutures slightly divergent within the brim, (6) large free cheeks, and posterior sutures cutting the margin at some distance from the genal angles, (7) a large pygidium of five to seven segments, (8) a long pygidial axial lobe reaching

the marginal furrow, (9) narrow pygidial doublure and border; and (10) composite second glabellar furrows (in *Mapania*) and lateral glabellar bulges (in *Quitacetra* and *Quititalia*). Furthermore, in the genera *Quitacetra*, *Quititalia* and *Mapania* the pygidial margin in the rear is sinuate and arched upward.

*Differential diagnosis:* The plectrum in the cranidium suggests a comparison with *Anomocarella* (Anomocaracea, or Anomocarellidae, or Asaphiscidae); but a plectrum occurs in a number of genera of diverse superfamilies and, taken alone, is inconclusive as regards the mutual affiliation of all plectrate species. The cranial designs of a Mapaniid (*Mapania*; see Öpik, 1961, p. 166) and of *Proceratopyge* are quite similar, except for the glabellar node in the latter. The cephalic structure compares well with the Plectriferidae nov. (Rhyssometopacea nov.). The pygidial structure compares with bathyuriscids, a similarity augmented by the anterolateral spines in *Quititalia*; the bathyuriscid character of the pygidia was first indicated by Dr A. R. Palmer (verbal communication).

To sum up, the Mapaniidae are distinguished by the combination of rhyssometopid characters in the cephalon with a pygidium which morphologically imitates a bathyuriscid.

Previous and diverse classifications are based on *Mapania striata* Resser & Endo, 1935 (first published and correctly attributed to Resser & Endo by Kobayashi, 1935; subsequently described by Resser & Endo, 1937; erroneously attributed to Kobayashi in Harrington et al., 1959, p. 0288).

The familial classification of *Mapania* (*M. striata*) has never been satisfactory. Ptychopariidae and Anomocarellidae (see Öpik, 1961, p. 164) have been suggested previously. Kobayashi (1960, p. 392) placed *Mapania* in his new subfamily Liopariinae (?family Asaphiscidae)—a rather heterogeneous taxon obscured by nomenclatural misinterpretations as shown below.

1. The genus *Lioparia* Lorenz (1906, p. 92), the type of Liopariinae, was originally established as '*Lioparia blautoeides*, nov.gen. et nov.spec., Lorenz'; consequently *blautoeides* is the type species of *Lioparia*; the type specimen (the lectotype) is the cephalon in Lorenz (op.cit., pl. 6, fig. 3), which, according to Lorenz, bears the main character of that genus. Consequently, no other specimen can serve as a lectotype. The cephalon of *Lioparia blautoeides* is distinguished by the pointed glabellar front and a preglabellar median furrow.

2. Kobayashi (1935) thought, however, that *Anomocare latelimbatum* Dames should be the type species of *Lioparia*; but Lorenz mentions no other species than *blautoeides*; his remark (p. 92): 'The species of this genus v. Richthofen brought from Saimaki in Manchuria is not identical with that of mine because of the different form of the glabella' disqualifies *latelimbatum* from typifying *Lioparia*. The pygidium (*ibid*, pl. 6, fig. 1) that Lorenz attributed to *blautoeides* may be regarded as *latelimbatum* Dames—a subjective interpretation, of course. Finally, Lorenz (*ibid*., p. 99, pl. 5, fig. 19) described a fragmentary cranidium as '*Lioparia latelimbata*, Dames spec.' which is obviously different from *L. blautoeides* and cannot qualify, therefore as the type of the genus.

3. *Pseudoliostracina* Kobayashi, 1938, is an objective (and invalid) synonym of *Lioparia* Lorenz, 1906, being based on the lectotype of the type species of the latter—*L. blautoeides*.

4. *Liaoyangaspis* Chang, 1959, is probably a subjective synonym of *Lioparia*; its type is *Asaphiscus bassleri* Resser & Endo.

5. *Yokusenina* Kobayashi, 1935, currently regarded as a synonym of *Lioparia*, is a valid genus; it has nothing in common with *Lioparia*; the generic status of *Anomocare latelimbatum* has no influence on the status of the name *Yokusenina*.

6. The subfamily name Liopariinae Kobayashi, 1960, is valid and refers to two genera only: *Lioparia* and *Liaoyangaspis*, whose affiliation with the Asaphiscidae is quite improbable.

The following forms are included in the Mapaniidae: *Mapania* Endo & Resser, 1935; *Quitacetra* gen.nov.; *Quititalia* gen.nov.; furthermore the three species *Mapania synophrys*, *M. faceta*, and *M. dicella*, described by Öpik (1961), which may belong to *Mapania* or another related genus; the available material is, however, insufficient for further study.

*Luia* Chang, and *Poshauia* Chang, as discussed by Öpik (1961, p. 164, 165), can be placed in the Mapaniidae, but in their pygidia the rear margin is neither sinuate nor arched.

Finally, reminiscent of Mapaniidae is *Szeaspis reticulatus* Chang (1959, pl. 3) in having the anterior sutures within the brim concave, as seen also in *Quitacetra arenata* sp.nov. and *Quititalia uncata* sp.nov.

#### Genus QUITACETRA nov.

The type species of *Quitacetra* is *Q. arenata* sp.nov. As described, the genus is monotypical, but related undescribed species are apparent in the Middle Cambrian of Queensland.

*Diagnosis:* *Quitacetra* gen.nov. refers to species of the Mapaniidae with well developed brim, rim, and plectrum, concave sutures within the rim, and a large trapezoidal pygidium; distinguished by its glabella with subparallel flanks and truncate front, eyes behind the glabellar midpoint, obliteration of the glabellar furrows, and a relatively well fused pygidium without interpleural grooves and of about seven segments indicated by the number of the axial annulations.

*Differential diagnosis:* *Quitacetra* differs from *Quititalia* gen.nov. by its well developed frontal area, wider interocular cheeks and large fused pygidium lacking anterolateral spines.

*Mapania* Resser & Endo, 1935, has also a well developed frontal area, but is distinct in having more forward placed eyes, a tapering glabella, distinct glabellar furrows, and in the pygidium well developed interpleural grooves.

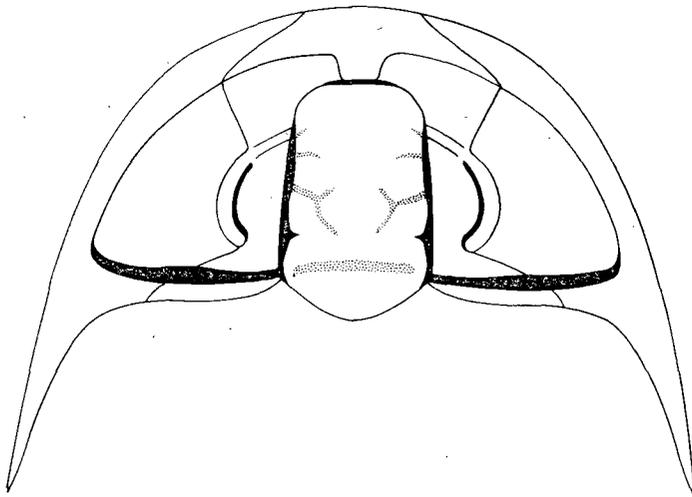


Fig. 103.—*Quitacetra arenata* gen.nov., sp.nov., combined from Plate 21, figs 7, 8, and Plate 23, figs 4 and 5.



Fig. 104.—*Quitacetra arenata* sp.nov., pygidium, same as in Plate 22, fig. 4, x 2, showing left margin and less contrast.

QUITACETRA ARENATA sp.nov.

(Pl. 21, figs 7, 8; Pl. 22, figs 1-5; Text-figs 103, 104)

*Material:* Six specimens—three cranidia, one free cheek, and two pygidia—all in friable sandstone, are selected from a number of specimens for description; on Plate 21, figure 7, two more pygidia are illustrated.

*Holotype:* The cranidium Plate 21, figures 7, 8, CPC 5527, is selected as the holotype because of its preservation and its association with cranidia of the same species. The matrix is sandstone.

*Diagnosis:* The specific diagnosis is essentially the same as that of the genus *Quitacetra*; the triangular and relatively large occipital lobe of *Q. arenata* is, apparently, a further distinguishing character of the species.

*Description:* The cranidium, free cheeks, pygidium, and isolated segments of the thorax, which have short falcate tips, are known. The large pygidium with about seven segments and about 0.7-0.8 of the cephalon in length suggests that the thorax should have about 10 segments and subparallel flanks.

The anterior sutures within the brim are almost straight and diverge at a low angle; within the rim they turn abruptly adaxially and connect with the margin opposite the anterolateral corners of the glabella; before reaching the margin the sutures become concave and the cranidial front attains a short forward projection. The posterior sutures are almost straight and the posterolateral limbs triangular and slightly less wide than the occipital lobe. The posterolateral furrows are shallow and the posterior border narrow and elevated.

The palpebral lobes, placed well behind the centre of the glabella, and half the glabella in length, are arcuate, narrow, and defined by a shallow palpebral furrow; the ocular ridges are slanting and inconspicuous. The interocular cheeks, 0.4 of glabellar width, slope gently toward the midline. The frontal area, about 0.23 of cephalic length, slopes gently forward; the brim and the rim are about equal in length. The plectrum and the almost flat rim together are quite prominent and merge into a structure shaped like a double-pointed miner's pick. The marginal furrow, interrupted by the plectrum in the middle and itself shallow, is accentuated by the steep rear edge of the elevated rim.

The axial furrows are sharp and their deep frontal closure separates the glabella from the plectrum. The glabella is relatively long, or narrow, its width being 0.7 of the length; the frontal lobe is blunt, even truncate, and tapers in front of the ocular ridges. The flanks of the glabella are straight, except for the lateral gentle bulges opposite the palpebral lobes. Three pairs of glabellar furrows are weakly developed and the posterior furrows are trifid or even composite; these furrows, connected with the lateral bulges, repeat the structure seen in *Rhysometopus* and *Plectrifer*. The occipital furrow is effaced and remains disconnected from the axial furrows. The visibility of these furrows depends on the degree of whitening and the angle of illumination: they are visible in Plate 21, figure 7, but obscure in figure 8. The free cheek is large, wide, with a moderately tumid ocular platform and a narrow and flat border lined with a very narrow doublure which has an angulate edge. The border widens consistently but slightly forward. The genal spine, about 0.6 of cephalic length, is flat and falcate and arises from the margin. The posterolateral marginal furrow is relatively shallow; faint radiating veins can be seen on the ocular platform in better preserved specimens. Fragments of frontal parts show the ventral doublure not reaching the cephalic midline, suggesting that a small rostral shield, not larger than the plectrum, should be present.

The pygidium is relatively large, almost trapezoidal, with only slightly convex and rearward-converging flanks; its rounded rear has a short sinus and an upward arch in the midline. The pygidium is relatively wide, having a width/length ratio of about 0.65. The border is flat and narrow, defined by a feeble marginal furrow and a very narrow doublure with terraced lines. The pleural lobes are flat, but, outside the fulcral lines, slope toward the border; about five pairs of rather shallow pleural furrows and four broad ribs in between are discernible. Interpleural grooves are absent. The facets are small, undeveloped, and the fulcra are far apart, 0.75 of shield's width from each other. The axial lobe is narrow (0.23 of shield's width), tapering slender, long (reaching, with a short antiplectrum, the border) and with six to seven annulations and a short elevated terminus.

*Comment on illustrated specimens:*

All specimens come from the Steamboat Sandstone, locality D95.

The holotype cranidium, Plate 21, figs 7, 8, is 13.2 mm, and the associated pygidium (left lower corner in fig. 7) is 10.0 mm long; a larger pygidium and fragments of free cheeks are also illustrated. The occipital margin is broken.

The cranidium, Plate 22, fig. 3, CPC 5530, is also 13.2 mm long; the occipital margin is preserved; the occipital lobe is triangular; the right posterolateral limb is almost intact.

In the fragment of a large cranidium, Plate 22, fig. 4, CPC 5531 (the fragment is 12.0 mm long), the straight posterior suture and the triangular posterolateral limb are well preserved.

The free cheek, Plate 22, fig. 5, CPC 5532, is 3.2 mm long from tip to tip; the always faint radiating veins cannot be distinguished in this specimen.

The pygidium, Plate 22, fig. 2 and Text-figure 104, CPC 5529, is 17.5 mm long; the test is missing, and the narrow doublure exposed.

The pygidium, Plate 22, fig. 1, CPC 5528, is 18.6 mm long; the test is weakly silicified; note the narrow border and the marginal furrow.

*Occurrence and age:* *Quitacetra arenata* sp.nov. is common in the Steamboat Sandstone, and occurs at localities D54, D74, D95, D96, Urandangi 1 : 250,000 Sheet area, and D114, G102, G104, G121, Glenormiston Sheet area; its age is the

two uppermost Middle Cambrian Zones of *Leiopyge laevigata* (Zones of *Proampyx agra* and *Holteria arepo*), and the Zone of the Middle/Upper Cambrian passage.

Genus QUITALIA nov.

The type species of *Quititalia* is *Q. uncata* sp.nov.

**Diagnosis:** *Quititalia* gen.nov. refers to species of the Mapaniidae having concave sutures within the rim, and distinguished by its reduced brim, short plectrum, narrow interocular cheeks, the presence of a median occipital spine, and by a subcircular pygidium preserving the interpleural grooves, crested axial annulations, and incipient or weakly developed anterolateral marginal spines.

**Differential diagnosis:** The differential diagnosis is given under *Quitacetra*. From *Mapania*, *Quititalia* differs in all characters included in the diagnosis.

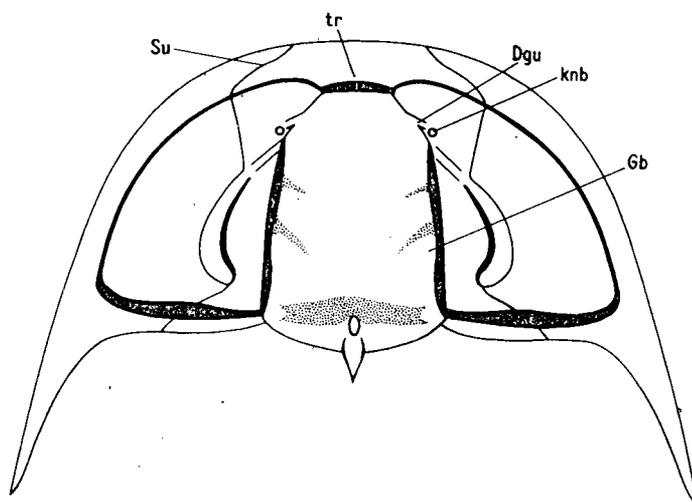


Fig. 105.—*Quititalia uncata* gen.nov., sp.nov., combined from Plate 22, figs 6, 7, and 9. Dgu—glabellar diverticulum; knb—anterior knob; Su—anterior suture, concave within rim; Gb—lateral glabellar bulge; tr—plectrum.

QUITALIA UNCATA sp.nov.

(Pl. 22, figs 6–10; Pl. 23, figs 1a, 1b; Text-fig. 105)

**Material:** *Quititalia uncata* is relatively rare; about fifteen specimens were examined.

**Holotype:** The cranidium Plate 22, figure 6, CPC 5533, is selected as the holotype because it is the most informative specimen.

**Diagnosis:** The specific diagnosis coincides with the diagnosis of the genus.

**Description:** The thorax is unknown; hence the relative size of the pygidium can only be estimated: 0.5–0.6 of the cephalon seems to be possible, and the thorax had presumably 11–12 segments—one or two more than *Quitacetra arenata*.

The anterior sutures are straight and slightly divergent in front of the eyes; within the rim they turn abruptly adaxially and connect with the margin at the distance of a glabellar width from each other. Within the rim the sutures are concave as in *Quitacetra*. The posterior sutures cut the margin about half way between the occipital lobe and the genal angle, and the posterolateral limbs are acute and small (slightly more than half the occipital lobe). The posterolateral furrows are distinct, and the border narrow.

The palpebral lobes, placed behind the midpoint of the glabella, and about 0.5–0.6 of glabellar length, are narrow and somewhat uplifted and the ocular ridges are distinct; the palpebral furrow is shallow but distinct. The interocular cheek, 0.33 of glabellar width, is quite narrow. The frontal area, almost without space for the brim, is 0.14 of cephalic length, i.e. very short. The plectrum and the rim are an elevated unit, and the plectrum is very short, broad, and separated from the glabella by a deep furrow. The frontal marginal furrow is distinct.

The axial furrows are deep behind, and shallow in front of, the ocular ridges; but at the frontal closure the furrow is deep again. A small knob is seen in front of each ocular ridge, close to the glabellar flank, and there is a pair of short veins comparable with the ocular ridges. Similar structures occur also in *Plectrifer*, *Rhysso-metopus*, and *Rostrifinis*. The glabella, about 0.75 as wide as long, is relatively long, slightly tapering, with obliquely bevelled preocular flanks and straight truncate front. It is carinate and bears two pairs of shallow, simple, and oblique lateral furrows. The glabellar lateral bulges are rather inconspicuous.

The occipital lobe is relatively short, equipped with a median spine and a small elongate node in front of the spine.

The test of the cranidium is minutely punctate and granulose; the granules around the occipital spine have an hapsidial arrangement. Three or four veins radiate from the knobs at the ocular ridges.

In the relatively large and moderately tumid free cheek the marginal furrow is well defined all around, the border is elevated, flat, and expands slightly forward; the falcate genal spine is flat and has a broad basis. The frontal ventral doublure extends apparently to the flank of the plectrum, indicating the presence of a rostral shield about as wide (transversely) as the plectrum itself.

The pygidium is semicircular, its length/width ratio being 0.5; its flanks, however, are less convex than the curve of a circle. In the rear the margin has an acute sinus and is arched, angulate upward (Pl. 23, fig. 1b). The border is convex and narrow and the marginal furrow is distinct but shallow and narrow. The doublure is also narrow. The pleural lobes are weakly convex, subhorizontal in the adaxial part, and gently sloping down from the fulcral line. Three (in the larger pygidium almost four) pairs of pleural ribs are defined by well expressed pleural furrows; interpleural grooves are distinct in smaller pygidia, but less distinct in larger, which develop low knobs on the ribs. The facets are relatively large, the fulcra, at a distance of about 0.75 of shield's width, are as far apart as in *Quitacetra arenata*. A pair of very short marginal spines is present at the anterolateral flanks of the pygidium. The axial lobe is narrow, about 0.27 of shield's width, evenly tapering, with straight flanks, long (the elevated terminus touches the border), and with six annulations.

The annulations are elevated, narrow, transverse crests with indistinct knobs in the middle; the transverse furrows are broad and concave.

The test of the pygidium is minutely punctate.

*Comment on illustrated specimens:*

The holotype cranium, Plate 22, fig. 6, locality D104, is 9·2 mm long; the matrix is bituminous limestone with chert and grains of silica. The minute ornament (granulation and punctation) is barely visible; but the hapsidial arrangement of the ornamental elements on the occipital lobe can be seen; the glabella is carinate.

The cranium, Plate 22, fig. 9, CPC 5536, locality D104, in bituminous limestone, is 9·2 mm long; the glabella is carinate and the glabellar furrows are distinct.

The cranium Plate 22, fig. 10, CPC 5537, locality D59, is immersed in silica; the visible part is 8·4 mm long; it shows the undeformed frontal area.

The free cheek, Plate 22, fig. 7, CPC 5534, locality D59, in chert, is 16·5 mm long from tip to tip; the frontal doublure and part of the genal spine are in shadow; the concave course of the suture within the frontal border is well visible.

The pygidium, Plate 22, fig. 8, CPC 5535, locality D59, in chert, is 5·8 mm long; the anterolateral short spines are intact and the interpleural grooves preserved.

The pygidium, Plate 23, fig. 1, CPC 5538, locality D59, silicified, in impure fragmentary limestone, is 10·0 mm long. Interpleural grooves are preserved on the right pleural lobe; the tips of the anterolateral spines were lost during etching. The angulate upward-arched rear margin is well preserved.

*Occurrence and age:* *Quitulia uncata* sp.nov. comes from the upper levels of the Quita Formation; its age is the Middle Cambrian Zone of *Ptychagnostus punctuosus*, which is also the age of the Formation itself.

QUITALIA sp.nov. aff. UNCATA

(Text-fig. 106)

*Material:* Only pygidia of this form have been found and one of these (CPC 6735) that retains its test is illustrated. In the absence of cranidia open nomenclature is applied.

*Description:* The pygidium is 7·0 mm long and 13·0 mm wide; it is relatively wide, with a width/length ratio of 0·52, and close to *Quitulia uncata*; marginal spines are absent, but the anterolateral margin is angulate at points where *Q. uncata* has



Fig. 106.—*Quitulia* sp.nov., aff. *uncata*, locality D96, CPC 6735, x 5.

produced spines. The axial lobe, 0.3 of shield's width, is relatively wide. Five axial annulations (six in *uncata*) are present, developed as transverse crests separated by broad concave furrows. The axial lobe is long, extending with its antiplectrum to the rear margin (in *uncata* to the border only).

The described pygidium represents, evidently, a species of *Quitatia*, distinct from *Q. uncata*. Notable also is the difference in age: *Quitatia* sp.nov. is about three zones younger than *Q. uncata*.

*Occurrence and age:* *Quitatia* sp.nov. aff. *uncata* occurs in the Steamboat Sandstone in association with *Quitacetra arenata*: the illustrated pygidium comes from locality D96. Its age is the Middle Cambrian Zone of *Leiopyge laevigata* (*laevigata* II, or Zone of *Proampyx agra*).

#### MAPANIIDAE gen.nov. et sp.nov.

(Pl. 23, fig. 2; Text-fig. 107)

Only the fragmentary illustrated cranium, CPC 5539, in chert, has been found. It is small, 2.3 mm long. Evidently immature, it cannot be used in establishing a new taxon.

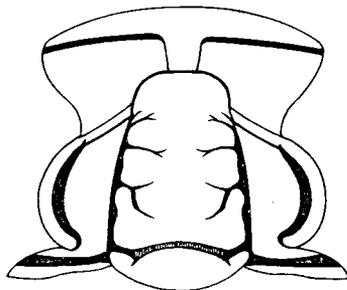


Fig. 107.—Mapaniidae, gen.nov.,  
sp.nov., from Plate 23, fig. 2.

The tapering long glabella, the arrangement of the three pairs of glabellar furrows, and the long frontal area with a narrow low plectrum are reminiscent of *Mapania*; the divergent and sinuate anterior sutures, the very small posterolateral limbs, and the forward arched occipital lobe indicate, however, a separate genus.

*Occurrence and age:* The described cranium comes from locality G103. Its age is the Zone of the Middle/Upper Cambrian passage.

#### Superfamily DAMESELLACEA Kobayashi, 1935

The superfamily Damesellacea is included here in the suborder Ptychopariina, within which it has a well founded independent status. Even a subordinal status within the order Ptychopariida is acceptable; this depends on the general and subjective approach to the classification of the order. The ptychoparioid design of the Drepanurinae is, of course, not evident; but it is well expressed in genera preserving the brim and the rim—in *Parablackwelderia*, *Blackwelderioides*, *Changshania*, *Histiomona* gen.nov., etc. Kobayashi (1962) included in his suborder Damesellina a new superfamily Namanoiacea; it contains several genera of ptychoparioid affinities

which, however, have little in common with the damesellids. If Kobayashi's concept of Namanoiacea is accepted, the name itself becomes a junior synonym of Leiestegiacea Bradley, 1925; in passing, the authorship of Namanoiacea (Namanoiidae) belongs to Lermontova, 1951.

The inclusion of the Damesellina in the order Corynexochida (see Kobayashi, 1962, p. 130) is rather speculative, and the inclusion of the Oryctocephalidae (Corynexochida) in the Damesellacea creates a morphologically artificial taxon.

## Family DAMESELLIDAE

### Subfamily DAMESELLINAE Kobayashi, 1935

#### Genus DAMESELLA Walcott, 1905

The concept of the genus *Damesella* was published by Walcott in 1913. Kobayashi (1941) regards its type species *D. blackwelderi* Walcott as a junior synonym (subjective) of *Cheirurus paronai* Airaghi (1902).

Resser & Endo (1937) described a large number of Middle Cambrian (Taizuan) and early Upper Cambrian (Kushanian, 'Late Middle Cambrian') species of *Damesella*. Several of these, and with good reason, were removed by Kobayashi (1941) from the genus and some others were placed in the synonymy of earlier established species.

*Damesella* and *Blackwelderia* are very close in organization, in time, and in geographic occurrence, and are separable only on the basis of the structure of the cranial front: *Damesella* has a convex and *Blackwelderia* a concave cranial border. Other characters, as for example the presence or absence of ocular ridges, small variations in the size and position of the palpebral lobes, emphasis on glabellar furrows, relative length of the pygidial spines, etc., which are mentioned in published diagnoses and descriptions are irrelevant in differentiating *Damesella* and *Blackwelderia* from each other. In summary, *Damesella* and *Blackwelderia* are Damesellinae with a cranial border, but without a brim, and with a long glabella reaching the marginal furrow; in *Damesella* the cranial border is convex, and in *Blackwelderia*, concave. For example, *Damesella conica* Resser & Endo (1937, pl. 45, fig. 3) and *D. nitida* Resser & Endo (pl. 47, figs 12-17) have a brim separating the glabella from the convex border and should, therefore, be excluded from the genus *Damesella*.

*Damesella torosa* sp.nov. is the only species of its genus found hitherto in Australia. It antedates *Blackwelderia* and its affiliates just as in South-eastern Asia (Chang, 1959, p. 233).

#### DAMESELLA TOROSA sp.nov.

(Pl. 42, figs 4-6; Text-figs 108, 109)

*Material:* Three specimens are described; the cranidium and pygidium are in chert pebbles ('gibbers') weathered out of limestone, and the free cheek in a chert biscuit from a silty sandstone. The gibbers are residuals in place of the weathered rock and not transported from elsewhere.

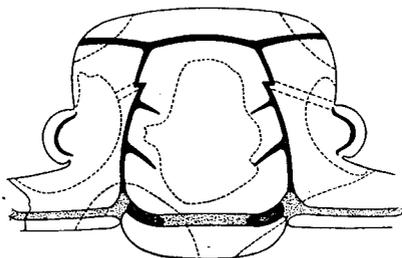


Fig. 108.—*Damesella torosa* sp.nov., from Plate 42, fig. 5.

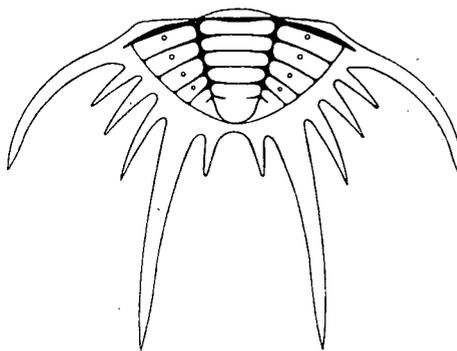


Fig. 109.—*Damesella torosa* sp.nov., from Plate 42, fig. 6.

*Generic position:* The subfamilial classification (Damesellinae) cannot be queried; the character of the pygidium alone is indicative of *Damesella* as well as *Blackwelderia*; the cranidium, however, with the glabella reaching the border, which is convex, indicates a *Damesella* related to *D. paronai* (Airaghi) which also has six pairs of pygidial spines.

*Preservation and specific identity:* The pygidium and the cranidium are fragmentary and it may be doubted whether a definite specific name can be applied; but the preserved parts are sufficient for reconstructions. In the pygidium the anterior axial annulation is almost completely missing, but could be restored because the axial furrows have only one possible position, and its length is indicated by the preserved left pleural spine and the pleural tip; the doublure is exposed, which was hitherto unknown in *Damesella*; axial annulation of the posterior, damaged part is indicated by laterally preserved notches.

In the cranidium (Text-fig. 108) the middle part of the glabella is missing, which is irrelevant; the anterior sutures are just enough preserved to indicate their original position, and, on the left, to indicate the approximate position of the anterior end of the palpebral lobe; its posterior end is less accurately indicated by the right posterolateral limb, whose sutural part is missing. The preserved characters of the cranidium are, consequently, sufficient for a differential diagnosis relative to all published species of *Damesella*.

*Holotype:* The cranidium Plate 42, figure 5, CPC 5692, locality G103b, is selected as the holotype in preference to the pygidium, whose generic classification depends on the characters of the cranidium.

*Diagnosis:* *Damesella torosa* is a coarsely pustulose species with six pairs of pygidial spines; distinguished by the combination of a conical glabella with an expanded frontal lobe, narrow and shallow pygidial pleural furrows, broad and flat pleural ribs, and rather thick and long fifth spines of the pygidium.

*Differential diagnosis:* All known species of *Damesella* have clear ocular ridges, which are vestigial in the new species *torosa*; *Damesella quadrata* Resser & Endo (1937) has an abruptly expanded frontal glabellar lobe comparable with *torosa*, but is distinguished by an almost parallel-sided glabella. Its pygidium is, however,

unknown. As regards the pygidium only *D. paronai* and *D. walcotti* Resser & Endo have also six pairs of spines; but these species are distinguished by deep and wide pleural furrows, which are narrow and shallow in *torosa*. *Damesella conica* Resser & Endo has also six pairs, but its cranidium possesses a narrow brim and is, therefore, rather distinct. Most of the known species of *Damesella* and *Blackwelderia* have seven pairs of spines in the pygidium.

*Description:* The holotype cranidium is 10.6 mm long, including the 2 mm long frontal rim; the interocular cheek is about half the glabellar width and the eyes are situated opposite the second glabellar lobe. The tumid cheeks, culminating as the palpebral lobes (eyes), rise above the glabella in the form of broad cones with gently convex slopes. The frontal rim is moderately convex and subhorizontal; the marginal furrow at its flanks is deeply incised, but in front of the glabella it is broad and shallow. The axial furrows are distinct (but not incised) valleys between the glabella and the cheeks. The occipital furrow is broad and deep, and deepened at its ends. The occipital lobe, about as wide as the rim, is prominent, cuspidate, and has no axial node. The glabella is conical, as wide as long, with slightly convex flanks, with a gently convex, almost subtruncate front, and angular anterolateral corners. The posterior glabellar lobes are tumid, the second lobes are distinct, but the anterior ones are inconspicuous. The frontal glabellar lobe is laterally expanded—a rare character. Three pairs of glabellar furrows are present: the posterior furrows are oblique and deep, the second furrows shallow smooth depressions, and the anterior furrows are short oblique and adaxially directed notches defining the expanded frontal lobe. The ornament consists of coarse scattered pustules on the tumid parts of the test.

The free cheek, Plate 42, figure 4, CPC 5691, is about 14.5 mm long (as preserved). The border is gently convex and widens rearward as in *D. paronai* and in most of the Damesellidae. The genal spine was apparently short, slightly deflected and advanced. The eye was elevated on a low smooth base; a subocular sill (see Text-fig. 116) is absent.

The pygidium Plate 42, figure 6, CPC 5693, is about 7 mm long (restored). It is semicircular, as usual in the Damesellidae. It is fringed by six pairs of spines; the fifth spines are rather thick and long, and the anterior spines are curved and widely divergent. An obscure border is indicated; the doublure is angular, enclosing a voluminous intradoublural space communicating with the rest of the pygidium by a narrow slit. The axis is long, reaches the border, and tapers evenly; apparently four complete and a fifth incomplete annulations are present. Four pairs of flat, distinct pleural ribs without interpleural grooves are defined by shallow and narrow pleural furrows; the anterior pleural furrows are relatively deep and intrude the base of the spine, as seen in all species of the damesellids. The surface is worn, but remnants of pustules are still discernible; furthermore each pleural rib carries a prominent pustule in its middle.

*Occurrence and age:* Locality G103 (a, b), Mungerebar area, the passage beds of the Steamboat Sandstone to the Mungerebar Limestone in the Zone of the Middle Cambrian/Upper Cambrian passage; and in the Mungerebar Limestone at G115 in the Mindyallan Zone of *Erediaspis eretes*.

Genus *BLACKWELDERIA* Walcott, 1905

(Text-fig. 110)

The history of the genus *Blackwelderia* is the same as that of *Damesella* (see above); the differential diagnosis of both these genera is also given in connexion with *Damesella* and *D. torosa* sp.nov. The latest revision of *Blackwelderia*, with a diagnosis, was given by Kobayashi (1942). It includes also *Blackwelderia monkei* (Walcott, 1911), which subsequently became the type of the genus *Blackwelderioides* Hupé, 1955.

It should be noted that the type species, *Blackwelderia sinensis* (Bergeron), has short and evenly long pygidial spines, whereas in all other species the first and the sixth spines are longer than the rest. Quoting Kobayashi (1942), 'setting aside dubious ones, there are three distinct species, namely *B. sinensis*, *B. paronai* and *B. monkei*' in the Kushanian, and one, *B. similis*, in the Taizuan. Of these, *Blackwelderia monkei* is excluded from this genus and placed in *Blackwelderioides* Hupé, 1955.

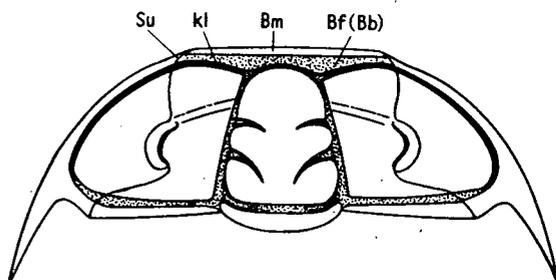


Fig. 110.—*Blackwelderia sinensis* (Bergeron), combined from Bergeron, 1899. Bf (Bb)—marginal furrow and brim; Bm—upturned margin; kl—frontal limit of cephalic pleural lobe; Su—anterior suture turned forward. Note that Bm is produced forward.

It should be noted that *Blackwelderia sinensis* (Bergeron) (Text-fig. 110) has a forward-projected cephalic front—a fact hitherto unnoticed in the literature.

The classification of the complete specimen attributed to *Blackwelderia sinensis* by Kobayashi (1942, pl. 20) should be queried. In this specimen the frontal border and the front of the glabella are absent, preventing any definite generic identification; its free cheek is rather different from the cheek in Walcott (1913, pl. 9, fig. 5c), which has a much shorter (transversely) posterior margin than Kobayashi's specimen. Furthermore, the flowerpot shape of the glabella recalls a *Stephanocare* rather than a *Blackwelderia* or *Damesella*. In the pygidium the spines are flat and falcate, and not constricted at the base, as seen in all pygidia attributed to *B. sinensis* in the literature. Chang (1959, p. 233, footnote) is even more definite in writing that 'Kobayashi's specimen resembles closely *Stephanocare richthofeni* Monke'. Hence the published reconstruction of *Blackwelderia sinensis* (Kobayashi, op. cit., pl. 21, fig. 1, and Harrington et al., p. 0316) is rather problematical.

As regards the specimens included by Kobayashi in the synonymy of *B. sinensis* the following remarks are needed: (1) The cranidia which Monke (1913, pl. 5, figs 1 and 2) refers to *Teinistion sodeni* cannot be interpreted with certainty; the first is probably a *Teinistion*; the second, with its interocular cheeks wider than the glabella and palpebral lobes longer than half the glabella, represent an undescribed genus; (2) of the two pygidia that Resser & Endo (1937, pl. 50, figs 4 and 5) referred tentatively to *sinensis*, the first has a slender axis and extenuated marginal spines and belongs

to a *Blackwelderia* or a *Damesella*, and possibly to *B. sinensis*; but the second with a much wider axis and flat, falcate spines represents another taxon; (3) Kobayashi correctly queries the synonymy of *B. perconvexa* Resser & Endo (pl. 50, figs 6 and 7) with *sinensis*. In *perconvexa* the interocular cheek is as wide as, or even wider than, the glabella, and the posterolateral limbs are much larger than in *sinensis*. (4) *B. tschanghsiengensis* Endo (Endo, in Resser & Endo, 1937, pl. 63, fig. 13) has a short and flat frontal border and is rather distinct (for comparison see under *Blackwelderia gibberina* sp.nov.); the same applies to the second cranidium of this species (loc.cit., pl. 64, fig. 8). The pygidia attributed by Endo to his species cannot be referred to *sinensis*, but are somewhat fragmentary in detail. (5) *B. granosa* Endo was acknowledged by Kobayashi regarding its pygidium only; its cranidia, however, were placed in *sinensis*, but without sufficient reason.

The vertical distribution of the species of *Blackwelderia* in Australia is similar to their distribution in south-eastern Asia (Chang, 1959, p. 233): (1) *Blackwelderia* postdates *Damesella*; (2) *B. sabulosa* sp.nov., *B. sp. A* and *B. sp. B* occur in the Mindyallan Zone of *Cyclagnostus quasivespa* below *Glyptagnostus stolidotus*, and (3) *B. gibberina* sp.nov. and *B. repanda* as well as *Dipyrgotes novella* sp.nov. in the upper Mindyallan *G. stolidotus* Zone.

In China, *B. paronai* and *B. sinensis* have a wider span, being recorded in the 'Blackwelderia Zone' (below) and in the *Drepanura* Zone (above), which is the equivalent of the *G. stolidotus* Zone.

#### BLACKWELDERIA SABULOSA sp.nov.

(Pl. 46, figs 6-8; Pl. 47, figs 1-9; Text-figs 111-113)

*Material*: Some twenty cranidia, twelve pygidia, two free cheeks, and several hypostomata have been examined; five cranidia, two free cheeks, four pygidia and one hypostoma are illustrated. All specimens are silicified tests, embedded partly in silica and partly in limestone.

*Holotype*: The cranidium Plate 46, figures 6 a, b, c, CPC 5724, locality G127 is selected; it is the best preserved specimen.

*Generic classification*: The pygidium of *sabulosa* could be placed in *Damesella* as well as in *Blackwelderia*: neither is the presence or absence of ocular ridges significant in separating *Damesella* and *Blackwelderia*; the flat frontal border eliminates *Damesella*, but occurs in forms attributed to *Blackwelderia* in the literature; furthermore, *Blackwelderia sinensis* (the type of the genus) and *B. sabulosa* sp.nov. share the forward projecting cephalic front—a feature unknown in *Damesella*.

*Diagnosis*: *Blackwelderia sabulosa* sp.nov. is a species with a projecting cephalic front, a pustulose and granulose test, with ocular ridges, with a flat and wide frontal border, with two pairs of glabellar furrows, but without bacculae, and with a pygidium of five axial annulations, four pairs of wide pleural furrows and seven pairs of unequal spines; distinguished by the angular cephalic flanks, keen flanges of the lateral margin and of the genal spines, long genal spines, wide interocular cheeks, short acute subcranial doublures of the free cheeks, and a rapidly tapering glabella.

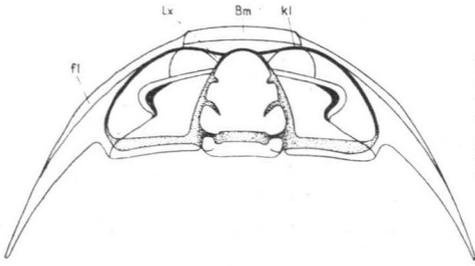


Fig. 111.—*Blackwelderia sabulosa* sp.nov., combined from Plate 46, fig. 6, and Plate 47, figs 3 and 4 (Text-fig. 112). fl—flange (with angulate margin); Bm—forward produced flat rim; kl—frontal limit of cephalic pleural lobes; Lx—anterolateral lobe.

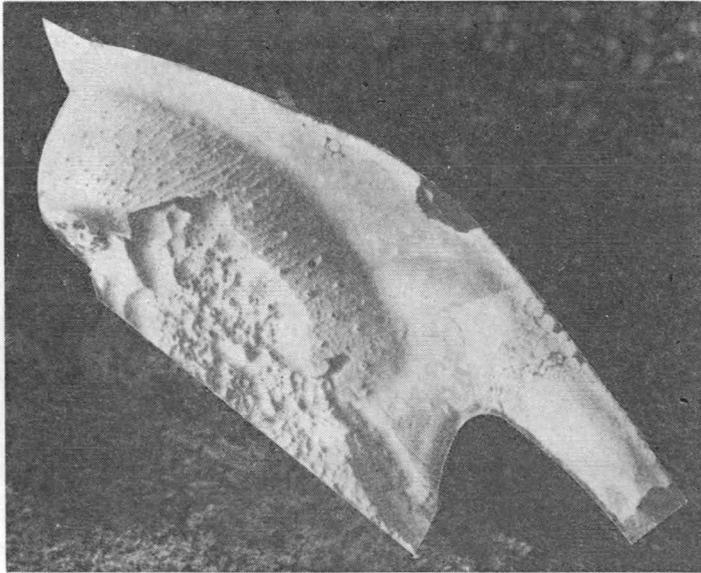


Fig. 112.—*Blackwelderia sabulosa* sp.nov., free cheek, x 3. Same in Plate 47, fig. 4. Note the pointed and attenuated anterior tip.

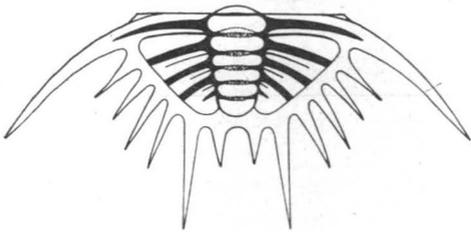


Fig. 113.—*Blackwelderia sabulosa* sp.nov., combined from Plate 47, figs 7-9.

*Differential diagnosis:* No closely related species are known in the literature. *Blackwelderia gibberina* sp.nov. has an almost flat border and bacculae; in *B. tschanghsiengensis* Endo the border appears to be flat but is much shorter than in *sabulosa*. *Blackwelderia sinensis* (Bergeron) lacks also the bacculae (in Bergeron's material; see Text-fig. 110), but is distinct by its longer and less conical glabella and narrower and shorter frontal area with an upturned margin.

*Description:* The cephalon is about semielliptical and, without the spines and the lateral border, almost semicircular in outline. In detail, however, the outline is somewhat angular; its lateral margin at the level of the eyes is angulate. The border is straight in front of, and curved behind, the lateral angularity; furthermore, the cranial front protrudes. No damesellid is known to have angular flanks of the cephalon. The relief of the cephalon is rather pronounced—furrows deep, and lobes tumid; the pleural lobes (cheeks) are dome-like, rise above the glabella, and culminate at the eyes. As usual in the damesellids, the swollen cephalic pleural lobes are produced forward, beyond the glabellar front.

The surface carries large scattered pustules on elevated and tumid parts, and a minute granulation on the midline of the glabella; the free cheeks are venulose, with pustules on the crests of the veins. The slopes of lobes adjacent to the furrows and the furrows themselves are smooth. A rather dense minute third-order granulation occurs on the interocular cheeks.

The free cheek is distinct by its angular margin, as mentioned above; furthermore in its front the margin becomes concave, with projecting tips, and the periphery of the free cheek is depressed to a narrow flange. The border to the free cheek widens rather rapidly rearward, much more than in the known species of *Damesella* and *Blackwelderia*. The genal spines are divergent and long, longer than in any of the previously known forms. In section the spine is biconvex, lenticular, and relatively flat; it is undeflected, but abruptly advanced at the acute but short genal angle. The base of the eye (a part of which is preserved in Pl. 47, fig. 4) is vertical but low, almost smooth (weak radiating veins but no pustules are present), and bears an inconspicuous subocular ledge.

The cranidium is subtrapezoidal in outline. The anterior sutures are first parallel, then converge slightly forward. In the photograph, in plan, the perspective accentuates the convergence of the sutures. For the same reason they appear to converge rearward in frontal view (Pl. 46). The posterior sutures diverge greatly and delineate large triangular, down-geniculated posterolateral limbs.

The interocular cheek (including the palpebral lobe) is as wide as the glabella; the cheek rises evenly at about 18° toward the palpebral lobe. The palpebral lobe is large (about 0.45 of the length of the glabella), flattened and hooked; the palpebral furrow is distinct and wide and the intrapalpebral area between the cusps is slightly swollen. The ocular ridge is distinct in the proximity of the palpebral lobe, but loses its distinction adaxially. The juncture of the ocular ridge with the palpebral lobe is seen in frontal view, just above the suture, and the margin of the lobe overhangs the palpebral part of the suture.

The posterolateral border is narrow and studded with spine-like pustules, and the posterior marginal furrow is wide. The frontal border is relatively large (variable between 0.2 and 0.22 of cephalic length) and divided by a vestigial transverse furrow

into two parts which can be interpreted as rim and brim. No pustules but indistinct large granules are scattered on the rear part of the border.

The occipital lobe is relatively short (about 0.12 of cephalic length), elevated, steep in front, almost straight in the middle, and with swollen lateral and cuspidate lobules; the occipital furrow is wide, distinct, and flanked by the short, deep, and narrow occipital appendiferi (elongate pits).

The conical glabella has almost straight flanks, is slightly wider than long, and tapers relatively rapidly, with the front no more than half the width of the rear. *Blackwelderia sinensis* and *B. paronai* have a wider glabellar front. Two pairs of oblique, short, and deep glabellar furrows are present; the glabellar lobes are distinct but inconspicuous. The front of the glabella is flanked by a pair of inconspicuous anterolateral lobes which are smaller than in *B. gibberina*; similar lobes are present also in *Meropalla auriculata* and *Dipentaspis ratis*.

The specimen Plate 46, figure 8, is the first specimen of the Damesellinae that shows the ventral cephalic structure: a narrow apical doublure can be seen, defined in the rear by the rostral suture; the connective sutures are directed toward the glabellar corners; thus a trapezoidal rostral shield is indicated, in front wider than in the rear.

The hypostoma (Pl. 47, fig. 5) is the same as in *B. sinensis* (see Kobayashi, 1941, p. 43); compared with the width of the glabella the proportions of the hypostoma indicate its relatively small size, reaching rearward to about the anterior ends of the posterior glabellar lobes.

The pygidium, without spines, is subcircular to subtriangular in outline. The axis is long, with five annulations and a short rounded terminus which touches the border. It is a relatively narrow axis, narrower than a pleural lobe without border. The pleural lobe is moderately convex, with flattened ribs and four wide pleural furrows; three vestigial interpleural grooves are developed as raised lines with pustules. The marginal border is narrow, slightly convex, and defined by the scallops of the ends of the pleural ribs, but no defined marginal furrow is present. Seven pairs of extenuated slender spines adorn the margin. The anterior spines are long, curved, and strongly divergent; the sixth spines are also long, but straight; the spines of the second to fourth pair are directed radially and increase in length rearward; the seventh pair is the shortest. The ornament consists of scattered pustules and a finer granulation, especially on the axis. The axial ornament of the pygidium Plate 47, figure 8, is the same as the ornament of the occipital lobe in Plate 47, figure 2.

*Comment on illustrated material:*

The holotype cranidium, Plate 46, fig. 6, CPC 5724, locality G127, is 16 mm long, the frontal border 3.2 mm (0.2 of the total length); the width between the anterior sutures is about 15.5 mm. The tips of the posterolateral limbs are embedded in silica, and remains of irremovable silica are seen on the test itself. Note the pustulose (not granulated) ornament in the front view.

The small cranidium, Plate 46, fig. 7, CPC 5725, locality G127, is 7.5 mm long; the matrix is limestone interwoven with spongy silica. Only the left ocular ridge is indicated.

The cranidium, Plate 47, fig. 1, CPC 5727, locality G127, is 15 mm long. Its frontal lobe is asymmetrical and the flanks of the glabella are somewhat concave, with a shape approaching *Blackwelderia sinensis* in Walcott (1913, pl. 9, fig. 5) and *B. paronai* in Lu (1957, pl. 144, figs 5, 6). The frontal border, about 0.22 of total length, is wider than in the holotype.

The cranidium, Plate 47, fig. 2, CPC 5728, locality G127, is embedded in silica, illustrating the most common mode of the occurrence of fossils. The ornament is perfectly preserved.

The free cheek, Plate 47, fig. 3, CPC 5729, locality G127, is about 31 mm long (as preserved); its frontal part is concealed in silica. The course of the posterior suture, the marginal flange of the spine, and the veins are visible.

The free cheek, Plate 47, fig. 4 (Text-fig. 112), CPC 5730, locality G127, belongs to a large cranidium. The veins carry the pustules; the preserved remnant of the base of the eye is low and provided with an inconspicuous subocular ledge. The preserved front extremity shows the change in the curvature of the margin, and the forward projected tip. The fragment of the axial lobe of a segment of the thorax should not be confused with the remnant of the base of the eye.

The cranidium, Plate 46, fig. 8, CPC 5726, locality G125, is 8 mm long. Note the frontal doublure and the ensuing dorsal and ventral course of the sutures within the frontal border.

The hypostoma, Plate 47, fig. 5, CPC 5731, locality G127, is 12 mm long and belongs to a rather large specimen. The inside view indicates a relatively large anterior border, which, nevertheless, is not long enough to have been in touch with the doublure.

The worn pygidium, Plate 47, fig. 7, CPC 5733, locality G127a, is about 37 mm wide and 18 mm long (without spines).

The pygidium, Plate 47, fig. 8, CPC 5734, locality G127, is 8.1 mm long in its visible part.

The fragmentary and relatively large pygidium, about 12 mm restored, Plate 47, fig. 9, CPC 5735, locality G127, preserves its convexity, the border, and almost complete marginal spines.

The pygidium, Plate 47, fig. 6, CPC 5732, locality G127, is 4.8 mm long without spines and belongs to a relatively small mature specimen.

*Occurrence and age:* The described material of *Blackwelderia sabulosa* sp.nov. was collected in the Mungerebar Limestone at localities G125, G127 and G127a. Other collections: G119?, G124, G126, G130, and G409?. The age is Mindyallan, the Zone of *Cyclagnostus quasivespa*.

#### BLACKWELDERIA GIBBERINA sp.nov.

(Pl. 48, figs 1-3; Text-fig. 114)

*Material:* The material consists of the illustrated specimens—one cranidium and two pygidia, all in dark grey bituminous limestone.

*Holotype:* The cranidium Plate 48, figure 1, CPC 5737, locality W15, is selected as holotype. A pygidium cannot be selected, because it might be confusing on a generic level.

*Generic classification:* The pygidium, although specifically distinctive, is of the kind seen in *Blackwelderia* as well as in *Damesella*, and even in *Blackwelderioides*. In the cranidium, however, the concave frontal border with a slightly upturned and thickened margin, and the presence of bacculae, indicate a *Blackwelderia* related to the type of the genus, *B. sinensis*. Other related species with a granulose test are *B. granosa* Endo and *B. tchanghsiengensis* Endo.

*Differential diagnosis:* In *Blackwelderia sinensis* the pygidial spines are more or less equal in length, the cephalic border is visibly wider and much more concave than in *gibberina*; *B. granosa* has a coarsely granulose surface and rather narrow pygidial pleural lobes; in *B. tchanghsiengensis* the frontal border is as narrow as in *gibberina*, but it is apparently flat; and its pygidium has only three complete axial annulations and well marked interpleural grooves. Furthermore, none of these species possesses ocular ridges, which are present in *gibberina*. The pygidium of *gibberina* with its fifth pair of stronger spines recalls *Damesella brevicaudata* Walcott (1913, pl. 9, fig. 9), which is also granulose and has deep pleural furrows but has a wider, stouter axial lobe. Of the same appearance are the pygidia o

*Damesella damesi* Resser & Endo (1937, pl. 50, figs 20 and 21) in which the pleural furrows terminate in pits as in *gibberina*; Kobayashi placed *D. damesi* in the synonymy of *D. brevicaudata*, but this can be questioned because *brevicaudata* is based on a single pygidium whose associated cranidium remains unknown.

**Diagnosis:** *Blackwelderia gibberina* is a species of strong relief, with a granulose test and bacculae, with ocular ridges and three pairs of glabellar furrows; distinguished by a short and moderately concave frontal border and trifold posterior glabellar furrows forming brackets; in the pygidium interpleural grooves are absent, the five pairs of deep channel-like pleural furrows terminate in pits, the axis consists of five annulations and a bulbous terminus, and of the seven pairs of marginal spines the sixth spines are short.

**Description:** The holotype cranidium is 8.7 mm long. The anterior sutures are slightly convex and converging; within the frontal border they remain dorsal for about a quarter of the width of the border. The posterior sutures are strongly divergent and delineate large, subtriangular posterolateral limbs. The fixed cheeks

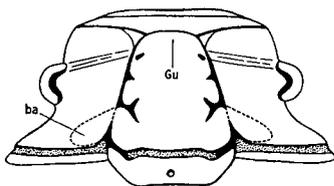


Fig. 114.—*Blackwelderia gibberina* sp.nov., from Plate 46, fig. 1. ba—baccula (—ae); Gu—pre-ocular part of glabella.

are tumid, and culminate at the palpebral lobes as summits well above the glabella: the height of the central part of the cephalon is about 0.7 of the summits. The palpebral lobes are relatively small, about 0.35 of the glabellar length; the interocular cheek in plan is almost as wide as the glabella. The palpebral lobes are placed opposite the second glabellar lobes in a horizontal position but rotation of the front down or up displaces the eyes from the opposition with the second lobes (compare also *Dipyrgotes novella* sp.nov.). The ocular ridge is broad and low, divided in two bands by an incomplete striga, and is well defined in the rear by the extension of the palpebral furrow. The posterior marginal furrow is distinct and the margin itself is conspicuous and studded with pustules. The frontal limit of the cephalic pleural lobe (Text-fig. 111) bulges forward beyond the glabellar front and overhangs the lateral part of the frontal border. The frontal border itself is narrow, about 0.13 of the cranidial length, and slightly concave; its upturned and thickened margin is folded over and passes into a submarginal doublure. The occipital lobe has the shape of a bow and its lateral cusps intrude the marginal border; an occipital node is present. The occipital furrow is broad and shallow in the middle and provided with deep oblique furrows of the appendiferi on its extremities. The axial furrows are deep valleys flanking the glabella. The glabella has straight flanks, is as wide as long, and tapers evenly to about half its posterior width. The posterior glabellar furrows are rather deep, short, oblique, and forked; the adaxial branches of these furrows are a pair of brackets in opposition, not usually seen in the Damesellinae but well developed in the Drepanurinae. The second (S2) furrows are deep and short notches; the third (S3) furrows are small shallow pits not reaching the

axial furrow. The posterior glabellar lobes, angular and swollen, are connected in their frontal part with the large bacculae which are known in *Teinistion* and probably in *B. sinensis*, but not in other species of *Blackwelderia*. In *B. gibberina* the bacculae are inconspicuous subtriangular swellings within the fixed cheek, whereas in *B. sinensis* these lobes are depicted in the literature as oblique ridges. The frontal glabellar lobe slopes down steeply and overhangs slightly the border. A pair of triangular swellings (the anterolateral lobes, Text-fig. 111) separate the front of the glabella from the rather tumid frontal slope of the cephalic pleural lobe.

The ornament consists of a relatively dense granulation on a minutely rough background; flanks and slopes of the furrows are smooth and the posterior margin pustulose.

The associated pygidium Plate 48, figure 2, CPC 5738, is 7.0 mm long and 13.5 mm wide (without spines). It is granulose all over and the ornament is the same as in the holotype cranidium. The axial lobe is slender and long, reaches the border, and consists of five annulations and a short bulbous and rounded terminus. Interpleural grooves are absent; the five pairs of pleural furrows are deep channels terminating in deep pits. The border is distinct although a marginal furrow is absent. The margin carries the usual number of seven pairs of spines. The anterior spines are very long and divergent; the remaining spines are short, including the sixth, which are long in other species of *Blackwelderia* and *Damesella*. But the spines of the fifth pair have a thick base, indicating a size slightly larger than the other spines.

The small pygidium Plate 48, figure 3, CPC 5739, locality G48, is 3.5 mm long and 5.7 mm wide without spines. No cranidia have been found in association with it, and its specific identity is, therefore, not quite certain. It possesses relatively large anterior pleurae, its spines of the sixth pair are weak also, but the axis is relatively wide, about as wide as a pleural lobe.

*Occurrence and age:* *B. gibberina* is a rare species of the Georgina Limestone, found at localities W15, W17, W20, W21, G48, G49, and W66. The age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

BLACKWELDERIA REPANDA sp.nov.

(Pl. 32, fig. 2; Pl. 47, fig. 10)

*Material:* The described and illustrated material consists of one pygidium and one cranidium selected from several fragments; the described specimens are conspecific because their ornament is similar and because the cranidia and pygidia of all other damesellids in the same bed (locality D29, O'Hara Shale) have been also identified.

*Holotype:* The pygidium Plate 47, figure 10, CPC 5736, in hard siliceous shale (chert), locality D29, is selected as the holotype because it can be diagnosed in relation to other known species of *Damesella* and *Blackwelderia*.

*Diagnosis:* *Blackwelderia repanda* sp.nov. is a pustulose species with a straight frontal marginal bar, with subcentral eyes, and with ocular ridges; distinguished by the retroflected rim (bar) and strong pygidial spines of the fifth pair.

*Differential diagnosis:* The pygidium of *B. repanda* is similar to *Damesella brevicaudata* Walcott (1913, pl. 9, fig. 9), which also has large spines of the fifth pair; but *brevicaudata* has five annulations in the axis and no interpleural grooves. The structure of the cephalic front (an elevated straight marginal bar separated from the glabella by a narrow brim or wide marginal furrow) suggests a comparison with *B. sinensis* Bergeron, which is, however, smooth, without pustules, and has a rather different pygidium. *B. gibberina* differs by its almost horizontal frontal border and a pygidium without interpleural grooves. The species of *Dipyrgotes* gen.nov. have a frontal bar, though it is arched forward and not straight, forward placed eyes, and a peculiar pygidium.

*Description:* The cranidium Plate 32, figure 2, CPC 5605, is fragmentary: its posterolateral limbs are missing; a part of the occipital lobe and the occipital furrow are, however, preserved, facilitating the understanding of the proportions. The cranidium is 5.5 mm and the glabella 3.8 mm long, and 4.2 mm wide between the anterior cranial corners. The anterior sutures are slightly convex and converging; the palpebral lobes are 0.4 of glabellar length and placed opposite or slightly behind the glabellar midpoint, and the tips of the lobes are two-thirds of the glabellar width away from the glabella. The eyes are elevated on summits above the level of the glabella; the interocular tumid cheeks slope steeply toward the midline. The ocular ridges are relatively wide and well marked in the rear by the extension of the palpebral furrows. The frontal border has a straight margin and consists of a narrow brim (or extended marginal furrow) with a transversely convex floor and an elevated marginal bar which is retroflected and partly overshadows the brim. A pair of pits in the brim is seen at the anterolateral corners of the glabella; adaxially from these pits the floor slopes up, and the brim becomes narrower owing to the projecting pleural lobes of the cranidium. The glabella tapers forward, its front is rounded, and three pairs of glabellar furrows are developed; the anterior (S3) furrows are small, deep pits at the ends of the ocular ridges. The test is pustulose.

The holotype pygidium Plate 47, figure 10, CPC 5736, is 5.0 mm long (without spines) and 10.0 mm wide (measured between the anterior recesses between the spines). Seven pairs of marginal spines are present, of which the anterior (as usual) and the fifth (not the sixth) pair are large. A border is not indicated; four pairs of pleurae are separated by shallow but distinct interpleural grooves and the four pleural furrows are deep and wide channels. The axial lobe is relatively narrow (narrower than the pleural lobe), long (about 0.85 of pygidial length), and divided into four annulations and a rounded terminus. The test is pustulose and, as in several other damesellids, the base of each spine bears a solitary prominent pustule; three more girdles of such pustules can be seen on the pleural lobes of the same pygidium.

*Occurrence and age:* The described specimens of *Blackwelderia repanda* were collected in the O'Hara Shale at locality D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

BLACKWELDERIA? sp. A

(Pl. 50, fig. 1)

*Material:* The material consists of a single silicified fragmentary pygidium, CPC 5749, 10.5 mm long.

The cranidium is unknown, and even the generic relationship cannot be established; hence, open nomenclature is applied.

The pygidium has a wide, almost parallel-sided axis with five annulations and a short terminus reaching almost the base of the rear spines. The pleural lobes have a steep slope, and no border except for the line marked by the ends of the ribs; the pleural ribs are high and narrow and carry distinct interpleural grooves. Five pairs of deep and wide pleural furrows separate the ribs. Of the seven pairs of marginal spines the first and the sixth are, as usual, long, but apparently the fifth were also larger than the rest. The spines are extenuated and the anterior spines are deflected rearward rather abruptly. The ornament consists of scattered large granules, on the axial annulations and on the base of each spine stands a solitary pustule.

*Occurrence and age:* *Blackwelderia?* sp. A comes from the Mungerebar Limestone, locality G125. The age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

BLACKWELDERIA? sp. B

(Pl. 50, fig. 2)

*Material:* The material consists of a single silicified pygidium, CPC 5750; it is 9.5 mm long and 17.2 mm wide.

Open nomenclature is applied because the cranidium is unknown; the pygidium cannot be attributed to any of the species known in the literature.

The axial lobe narrows rapidly, and consists of five annulations and a pointed terminus; the pleural furrows are shallow and narrow; interpleural grooves are absent, and the five pairs of ribs are broad and flattened. Seven pairs of marginal spines are present, of which the sixth are very large, and the first relatively (or unusually) slender, but the posterior spines are, apparently, very short.

The generic position is doubtful.

*Occurrence and age:* *Blackwelderia?* sp. B comes from the Mungerebar Limestone, locality G127. The age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

Genus DIPYRGOTES nov.

The type of the genus is *Dipyrgotes novella* sp.nov.

*Diagnosis:* *Dipyrgotes* is a genus of the Damesellinae with a concave cephalic frontal border; distinguished by (1) rather wide interocular cheeks, (2) large eyes opposite the anterior part of the glabella, (3) rearward pointing genal spines (not divergent), (4) a depressed border confined to the rear part of the pygidium, and (5) an anterior large, macropleural pygidial segment with two pairs of spines. In the type species (*D. novella*) bacculae are absent.

*Differential diagnosis:* The pygidial structure of *Dipyrgotes* is unique; its macropleural segment suggests some comparison with *Drepanura*, which, however, has a single pair of spines and a rather different cranidium. The concave cephalic border

occurs also in some species of *Blackwelderia*, but the latter has a different pygidium and its eyes are in a different position. The same applies to *Damesella*, in which, moreover, the rim is convex.

DIPYRGOTES NOVELLA sp.nov.

(Pl. 16, fig. 1; Pl. 48, figs 4-6; Pl. 49, figs 1 and 3; Text-figs 115-117)

*Material:* About twenty specimens have been examined; five cranidia, one free cheek, and two pygidia are illustrated. All available material is decorticated, silicified, and embedded in silica. The absence of tests is compensated for by rubber casts of external moulds.

*Holotype:* The pygidium Plate 48, figure 4, CPC 5740, is selected as the holotype, because it displays unique characters of generic significance. A specific diagnosis is omitted because it coincides with the generic diagnosis. The existence of another species is indicated by the free cheek of *Dipyrgotes?* sp. A, Plate 49, figure 2.

*Description:* The relief of the cephalon is very strong, almost grotesque; the furrows are deep and distinct, the angles acute, slopes abrupt, the cephalic pleural lobes vaulted, the glabella arched, the eyes rise like turrets, and the palpebral lobes are acutely bent ridges. The surface is rough, with widely spaced tubercles and fine dense granulation. The outline is semielliptical, its length being about 0.4 of the width. It appears that small cephalons are less convex than large; the illustrations of the smaller specimens, however, are taken in a foreshortened position (to show the border) in which the convexity appears somewhat decreased.

*D. novella* possesses a subtriangular free cheek, bulging slightly outward, with a flat border which is anteriorly rather narrow, but widens rearward and extends into an undeflected almost straight flat spine. The spine is advanced with a genal angle of 45 degrees. Upward the free cheek is drawn out to form a semicylindrical 'turret' with a prominent sill crowned by the narrow base of the eye (subocular band). The function of the subocular sill is unknown.

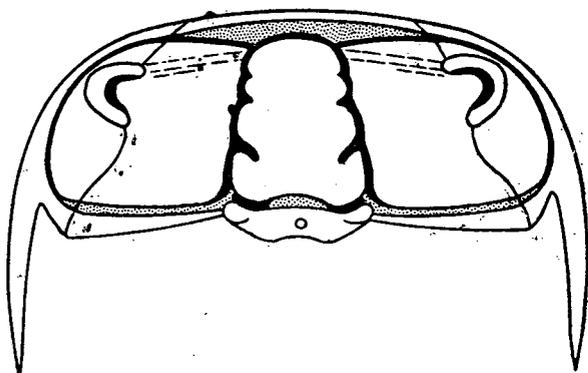


Fig. 115.—*Dipyrgotes novella*, gen.nov., sp.nov., combined from Plate 48, figs 5, 6, and Plate 49, fig 3.

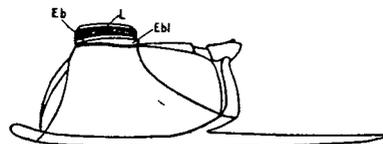


Fig. 116.—*Dipyrgotes novella* sp.nov., lateral view of cephalon, Text-fig. 115. Eb—base of eye; Ebl—subocular sill; L—palpebral lobe.

The almost vertical free cheek (Text-fig. 116) in lateral view creates the impression that the eyes were stalked; but real stalks are absent because the palpebral lobes are placed on the upsloping cheeks, not on separate projections.

The cranium is subtrapezoidal and twice as wide as long. The anterior sutures are converging and almost straight in plan; the posterior sutures are sinuous and divergent. The posterolateral limbs are subtriangular, large, and slope down steeply; the interocular cheeks between the adaxial ends of the palpebral lobes are rather wide, as wide as the glabella. The frontal slope of the cheeks bulges, and is vertical at the base, extending forward even beyond the front of the glabella. The posterolateral marginal furrow is narrow and deep and the posterior border narrow and convex. The palpebral lobes are situated opposite the second glabellar furrows; they are large and long (about 0.4 to 0.5 of the glabella), arcuate (hooked), and elevated; the part of the cheek enclosed between the cusps is swollen and the palpebral furrow is deeply incised. The palpebral lobes are opposite the second glabellar furrows; but they are well elevated above these furrows; even a slight rotation down or up of the front (or rear) of the specimen will displace the lobes (or the furrows) forward or rearward from this opposition. The ocular ridges are weak and erratic, and sometimes not discernible at all. When present (Pl. 49, fig. 1a) they are double.

The occipital lobe is wide in the middle, with cuspidate and narrow flanks, and carries a pair of swollen lateral lobuli. A rather weak occipital node may be present also. The occipital furrow, wide in the middle, narrows laterally and ends in elongate, oblique deep pits similar to the glabellar furrows.

The frontal margin is arcuate forward; the frontal border is concave or even excavated, with a narrow upturned margin.

The axial furrows are deeply sunk between the cheeks and the glabella, but the circumglabellar furrow (in front of the glabella) is less deep.

The glabella has almost straight flanks, is longer than wide (the width is about 0.75 of length), tapers moderately (to about 0.8 of the width of the rear); it is subangular at the anterolateral corners, and gently rounded in front. Three pairs of rather short pit-like glabellar furrows are present; the anterior furrows are rounded pits denting the flanks of the glabella.

The pygidium is subtriangular (spines not considered) and slightly longer than half the width. The axis tapers evenly to an elevated and rounded terminus, the ratio of aft to fore being about 0.5; six complete annulations, and a seventh incomplete, are present. Behind the terminus a low but distinct, triangular, and pointed antiplectrum almost reaches the margin. The pleural lobes are divided by four pairs of pleural furrows; interpleural grooves are absent. Seven pairs of marginal spines are present. The anterior segment is macropleural. It consists of two axial annulations and rather large pleurae each divided by a wide and deep pleural furrow; it carries two marginal spines, of which the anterior is long and falcate, and the other is shorter and straight. The posterior five spines are all directed straight rearward, and the sixth and the first spines are longer than the pygidium itself. The remaining spines are relatively short but uneven in length. The pygidial border is relatively narrow, almost flat, and distinct, but ends abruptly at the macropleural segment.

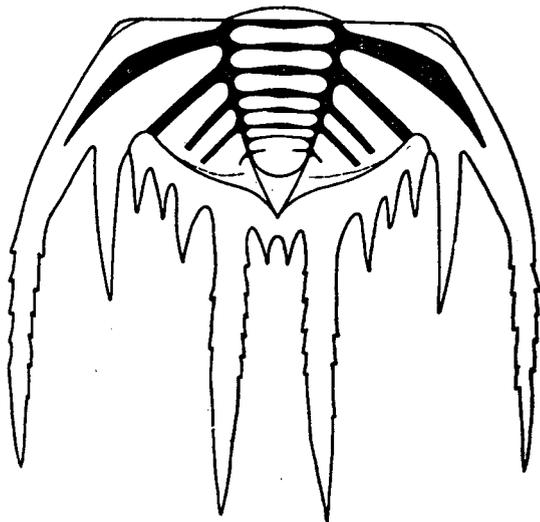


Fig. 117.—*Dipyrgotes novella* sp.nov., combined from Plate 16, fig. 1, and Plate 48, fig. 4.

The ornament consists of scattered large tubercles and dense minute granulation. Chevron terraced lines with angles pointing forward are seen on the larger spines, the edges of which are minutely serrate.

*Comment on illustrated specimens:*

All illustrated material originates from locality D29.

The holotype pygidium, Plate 48, fig. 4, CPC 5740, is 4.0 mm long (without spines); The ornament (coarse granules) is only partly preserved. Specimens with preserved coarse and minute granulation are, however, present in the collection. The similarity of the pygidial and cephalic ornament is the evidence that the described pygidia and cranidia are conspecific. Furthermore, pygidia and cranidia of all other damesellids from locality D29 are known.

The exfoliated and laterally somewhat distorted pygidium Plate 16, fig. 1, CPC 5485, is 4.0 mm long. It appears that the sixth posterior spines were even stronger than in the holotype.

The fragmentary cranidium, Plate 48, fig. 6, CPC 5742, is 4.8 mm long without the anterior border, which is only partly seen in the rubber cast. The ornament, partly preserved on the glabella, is almost perfect on the interocular cheek.

The free cheek, Plate 49, fig. 3, CPC 5745, is about 5.2 mm high. Note the ornament and the 'ledge of the turret'.

The cranidium, Plate 49, fig. 1, CPC 5743, is about 6.8 mm wide between the eyes. It is distorted (shortened), and the border is missing. Note the double ocular ridges and the absence of ocular stalks.

The small cranidium, Plate 48, fig. 5, CPC 5741, is 3.0 mm long; it is less convex than the larger specimens; in the illustration the specimen is rotated front up, and the palpebral lobes appear, therefore, to be slightly behind the second glabellar furrows; the frontal border is well preserved, the glabellar furrows are deep pits; the ocular ridges are indicated.

*Occurrence and age:* *Dipyrgotes novella* is a common species in the 'lower chert bed' of the O'Hara Shale at localities D6, D28, and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

DIPYRGOTES? sp. A

(Pl. 49, fig. 2)

The illustrated free cheek, CPC 5744, 13.5 mm high, is the only available specimen. The cheek is venulose from the subocular sill (see Text-fig. 116) down to the flat border; the spine is undeflected but advanced; the turret is tall and the sill is swollen and oblique. The steep, almost vertical anterior suture indicates a rather forward placed eye, and the posterior suture a large triangular posterolateral limb. The eye itself was apparently shorter than in *D. novella*.

*Occurrence and age:* The free cheek comes from the Georgina Limestone, locality W21 (light grey sandy hard limestone); its age is the Zone of *Glyptagnostus stolidotus*, recognized from the other associated trilobites.

Genus CYRTOPRORA nov.

The type of the genus is *Cyrtoprora intricata* sp.nov.

The generic diagnosis coincides with the diagnosis of the species.

The main generic character is its scroll—the peculiar involute frontal cranial border.

CYRTOPRORA INTRICATA sp.nov.

(Pl. 49, figs 4–6; Text-fig. 118)

*Material:* The illustrated and described material consists of two fragmentary cranidia and a fragment of the interocular cheek with the palpebral lobe; fragments are relatively common.

*Holotype:* The best preserved cranidium Plate 49, figure 4, CPC 5746, in bituminous limestone (Georgina Limestone), locality W15, is selected as the holotype.

*Diagnosis:* *Cyrtoprora intricata* is a species of the Damesellinae with a pustulose test, strong ocular ridges, a glabella longer than wide, and eyes towards the rear; distinguished by its involute frontal border, and symmetrical arrangement of pustules on the glabella.

Some similarity is apparent between *C. intricata* and *Blackwelderia repanda* sp.nov., which both have distinct pits at the anterolateral corners of the glabella; in *B. repanda*, however, the frontal border is only slightly reclined, the eyes are sub-central and the pustules are scattered irregularly.

*Description of the holotype:* The cranidium is 11.8 mm long. The anterior sutures are slightly convex and divergent, almost parallel; the posterior sutures are strongly divergent, and, judging from the position of the palpebral lobes, delineate subtriangular posterolateral limbs, about as long (transversely) as the occipital lobe.

The interocular cheeks slope up steeply with a rearward sweep, and carry on their summits the palpebral lobes. These are placed well in the rear, opposite the posterior glabellar furrows and at the distance from the glabella for about 0.7 of its width in plan. The palpebral lobes are small, about 0.3 of the length of the glabella, but prominent; their anterior tips are continuous with the rather strong ocular ridges; the ridge is defined in the rear by a deep furrow which is the continu-

ation of the palpebral furrow. The occipital lobe is crescentic, arched longitudinally, and lacks a median node. The occipital furrow is rather broad and has deep pits at its ends. The frontal margin is almost straight. The frontal border consists of

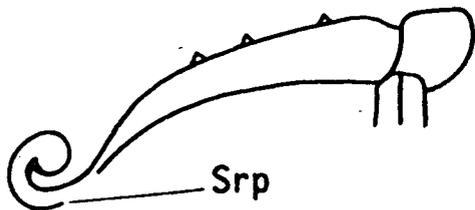


Fig. 118.—*Cyrtoprora intricata*, gen.nov., sp. nov., combined from Plate 49, figs 1 and 5, to show frontal scroll in section. Srp—rostral suture.

a scroll (Text-fig. 118) of a rearward involute fold densely covered with coarse transverse osculating terraced lines. The connexion of the scroll with the test was not evident: it could be suspected that a fragment of another trilobite came to rest accidentally across the frontal margin of the holotype. Hence, a part of the scroll was removed and its structure and connexion with the cranidium established. The test under the cover of the scroll is a transverse channel with delicate terraced lines. The axial furrows are straight and distinct, the glabella is longer than wide, its width in the rear being 0.8 of the length; it tapers forward to about 0.7 of its posterior width, is moderately arched transversely, and slopes in a gentle curve toward the subtruncate front. Three pairs of glabellar furrows are present, developed as deep lateral pits, and decreasing in size toward the front. Two pits are placed also at the anterolateral corners of the glabella.

The test is granulose: on the flanks of the axial furrows and on the occipital lobe a dense minute granulation is apparent which may have been present also on the glabella. Furthermore, large pustules are scattered over all parts of the cranidium; on the median part of the glabella conspicuous pustules are arranged symmetrically in pairs or in transverse rows, reflecting roughly the segmentation. The interocular cheek is densely covered by a delicate transverse osculating striation running down from the palpebral lobe to the axial furrow.

The cranidial fragment, Plate 49, figure 6, CPC 5748, Georgina Limestone (a siliceous lamina in limestone), locality G51, consists of the right flank of the glabella with the glabellar furrows and the occipital lobe, and of the the cheek with the ocular ridge and the palpebral lobe. The interocular cheek measures 10.6 mm from the axial furrow to the edge of the palpebral lobe, the glabella (as preserved) is 7.2 mm and the palpebral lobe 2.2 mm long. The striation on the cheek is well preserved. The abaxial part of the cheek with the palpebral lobe is gently swept rearward and constricted at the base of the lobe; the ocular ridge is sigmoidal.

The cranidium Plate 49, figure 5, CPC 5747, locality W20, Georgina Limestone (a siliceous parting in bituminous limestone), is silicified in a friable matrix and parts have crumbled off. The frontal scroll itself is missing, exposing the frontal channel below the scroll; part of the occipital furrow and the margin of the occipital lobe are also recognizable.

*Occurrence and age:* *Cyrtoprora intricata* has been found in the Georgina Limestone at localities W15, W20, G48, and G51. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

## Genus MERINGASPIS nov.

The type of the genus is *Meringaspis meringaspis* sp.nov.

*Diagnosis:* *Meringaspis* is a genus of the Damesellinae whose species are distinguished by stalked eyes, well developed posterior glabellar furrows, almost obsolete, pit-like, anterior glabellar furrows, and a pygidium with a pointed, triangular, spatulate rear; of the six pairs of slender marginal spines the first and the sixth are large, and the sixth pair arises from the pleural lobes. The glabellar ornament consists of a dense granulation in a Bertillon arrangement. Small bacculae are present.

*Differential diagnosis:* *Meringaspis* possesses a unique pygidial structure which cannot be confused with any other form of the Damesellidae.

Among the Damesellinae *Parablackwelderia spectabilis* (Resser & Endo) recalls *Meringaspis* in having a rounded glabellar front and tall stalked eyes; its pygidium, however, differs little from *Damesella* or *Blackwelderia*. (Hupé (1955, p. 146), Lochman-Balk (in Harrington et al., 1959, p. 0318), and even Kobayashi (1960, p. 352) included *Parablackwelderia* in the Drepanurinae, apparently because of the forward position of the stalked small eyes; but this is a generic character of an otherwise *Blackwelderia*-like form.) In plan (Text-figs 120 and 114) the cranidia of *Meringaspis meringaspis* and *Blackwelderia gibberina* seem similar, but differ in size of the preocular part of the glabella, and of the bacculae, as well as regards the form of the glabellar furrows.

### MERINGASPIS MERINGASPIS sp.nov.

(Pl. 44, fig. 6-9; Pl. 45, figs 1-2; Text-figs 119-121)

*Material:* Three cranidia, one hypostoma, and one pygidium are selected for illustration and description. All specimens, in chert or in siliceous shale, are decorticated, but most of them provide for internal casts and external moulds. The reconstruction of the pygidium (Text-fig. 121) is based on the illustrated pygidium amplified by several more fragmentary specimens. The pygidia and cranidia belong together because (1) all damesellid pygidia and cephalae from the O'Hara Shale are correctly assigned to each other leaving no alternatives for *Meringaspis meringaspis*, and (2) the older forms (*Meringaspis* sp. A and sp. B) have no associates whose pygidia could create confusion.

*Holotype:* The cranidium Plate 44, figure 6, and 45, figure 1, CPC 5713, locality D28, on a bedding plane in chert, is selected as the holotype because it allows for a comparison with *M.* sp. A, which is also a cranidium.

*Diagnosis:* *Meringaspis meringaspis* is distinguished by its straight cranidial front, pit-like anterior glabellar furrows, a long triangular spade-like pygidial rear and elliptical, rounded (not flat) sections of the pygidial spines.

*Description:* The cranidium is subtrapezoidal in outline. The anterior sutures are straight and parallel; they cut the frontal border rather abruptly and change immediately into a ventral course. The posterior sutures are almost straight and divergent, delineating large triangular posterolateral limbs. The interocular cheek slopes adaxially rather steeply, and, together with the free cheeks, carries vertical ocular stalks. The palpebral lobes are relatively small, about 0.25 of glabellar length,

placed in front of the glabellar midpoint, and at a distance of about 0.4 of glabellar width. The ocular ridges are wide and double. The frontal margin is upturned, straight and narrow. The occipital lobe bears a median node, is wider than the glabella, and has forward curving flanks. The occipital furrow is bow-shaped, wide and shallow in the middle, with narrow and deep ends. The axial furrows are valleys between the glabella and the cheeks. The glabella slopes forward in an even arc, and has straight flanks; it is as long as wide and tapers to about 0.6 of its width in the rear; the glabellar front reaches the upturning anterior border, and is rounded. Four pairs of glabellar furrows are present. The posterior furrows are trifid; the branch running obliquely backwards is rather distinct, whereas the anterior branch is rather shallow and barely discernible. The other three pairs of glabellar furrows are small rounded pits not touching the axial furrows; the foremost two pits are close together at the adaxial ends of the ocular ridges.

The ornament consists of a dense and minute granulation, arranged in a relatively simple Bertillon pattern on the glabella, but on the occipital lobe concentrically to the median node. Delicate reticulate veins cover the test in front of the ocular ridges.

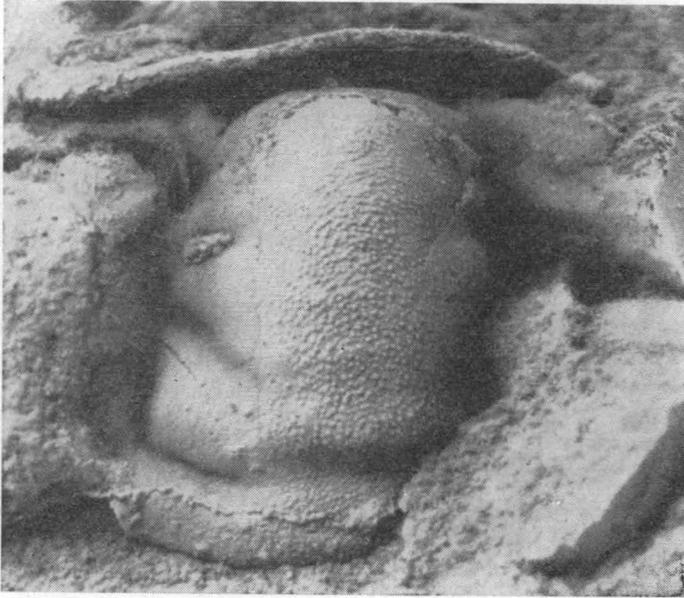


Fig. 119.—*Meringaspis meringaspis* sp.nov., x 12, showing the ornament of the glabella. Same specimen—Plate 44, fig. 7.

The pygidium, disregarding the spines, is triangular and as long as wide. Six pairs of marginal spines are present. The four pairs of minor spines are almost straight and rounded in section; the anterior spines are large, rather slender and curved; the posterior spines are the largest and arise from the pleural platform well off the margin, in a manner seen for example in *Tricrepicephalus*. The anterior spines are visibly the pleural tips of the first pygidial segment, but the others are somewhat

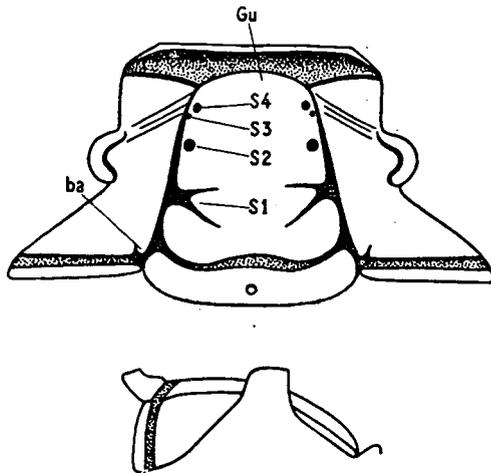


Fig. 120.—*Meringaspis meringaspis* gen. nov., sp. nov., from Plate 45, fig. 1. ba—baccula; Gu—preocular part of glabella; S1-S4—glabellar furrows (pits in S2, S3, and S4).

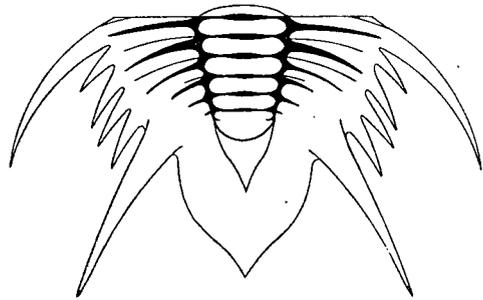


Fig. 121.—*Meringaspis meringaspis* sp. nov., from Plate 45, fig. 2 (and other specimens).

displaced regarding the position of the pleural ribs; it appears even that the second pair of spines belongs also to the anterior segment, which would be a bispinose macropleural segment comparable with *Dipyrgotes* gen. nov. A lateral pygidial border is absent, but behind the posterior spines a concave border is indicated on the posterior tongue. The 'tongue' itself is large and triangular and has sigmoid flanks.

On the pleural lobes four pairs of pleural furrows are present, decreasing rearward in depth and length. Vestigial interpleural grooves are indicated on the crests of the two anterior ribs. The pygidial axis is short—half the length of the pygidium; but it reaches the border and were it not for the posterior 'tongue' would be considered long. It consists of five complete and one (posterior) incomplete annulation and a short rounded terminus. Behind the terminus a low extenuated antiplectrum is indicated. The doublure widens rapidly rearward, bears rather regular terraced lines, and underlies the whole of the posterior 'tongue'.

The ornament consists of an overall minute granulation; furthermore, each pleural rib carries two prominent pustules—one on the base of the spine and another on the tip of the rib itself.

*Comment on illustrated specimens:*

The holotype cranium is 7.2 mm long. It displays the stalks of the eyes rising for about 2 mm above the level of the glabella, the pits replacing the anterior glabellar furrows, the ocular ridges, and the ornament. The posterolateral limbs are missing.

The cranium, Plate 44, fig. 7, CPC 5710, locality D29, in chert, 5.3 mm long, illustrates the ornament; some matrix fills the pit of the second glabellar furrow; the anterior border is unnaturally high, because the floor of the marginal furrow was accidentally removed during preparation.

The cranium Plate 44, fig. 8, CPC 5711, locality D29, an internal cast in chert, is 6.9 mm long. The ornament is preserved, the glabellar pits are less distinct than in the holotype, and the frontal border appears to be rather short, as could be expected in a steinkern.

The hypostoma, Plate 44, fig 9, CPC 5712, locality D29, in chert, and decorticated, is 5·7 mm long. Its minute pustulose ornament is similar to the ornament of the cranidium. The shape, with relatively narrow posterolateral wings, is about the same as in *Damesella* and *Blackwelderia*, and rather different from *Palaeadotes* and *Drepanura*.

The pygidium Plate 45, fig. 2, CPC 5716, in a friable siliceous layer in chert, locality D29, is 7·0 mm long. It is somewhat distorted, and the anterior spines are broken. The posterior 'tongue' is intact, and a part of the doublure with regular terraced lines is exposed.

*Occurrence and age:* *Meringaspis meringaspis* gen.nov. sp.nov. has been found as yet only in the O'Hara Shale ('lower chert bed') at localities D8, D28, and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### MERINGASPIS sp. A

(Pl. 46, figs 2-5)

*Material:* One cranidium and two pygidia are illustrated and described; all specimens are silicified.

#### *Comment on illustrated specimens:*

The cranidium, Plate 46, fig. 2, locality G119, CPC 5718, is 9·5 mm long; the frontal border is relatively short and depressed and the ocular ridges are horizontal (not slanting), prominent, and double. In *M. meringaspis*, however, the ocular ridges are strongly slanting.

The pygidium Plate 46, fig. 5, CPC 5723, locality G119 (silica in limestone), is 6·0 mm long. It differs from *M. meringaspis* in having a bulbous terminus and flattened marginal spines. The extent of the posterior 'tongue', which is broken, remains unknown. The doublure bears regular terraced lines and the spines arise above the margin, which is well exposed.

The pygidium Plate 46, fig. 4, CPC 5722, locality G119 (silica in limestone), is a fragment 7·8 mm long. Flat marginal spines, a steep axial terminus without an antiplectrum and a concave posterior border (fragmentary posterior 'tongue') are evident.

*Occurrence and age:* *Meringaspis* sp. A is widespread in the Mungerebar Limestone and has been recorded at localities G8, G119, G149 and G417. Its age is the Mindyallan Zone of *Erediaspis eretes*.

#### MERINGASPIS sp. B

(Pl. 46, figs 1 and 3)

*Material:* Illustrated are two specimens (one cranidium and one pygidium), which are too fragmentary for a conclusive specific diagnosis.

The silicified cranidium Plate 46, figure 1, locality G131, CPC 5717, is 6·2 mm long. It differs from *Meringaspis meringaspis* sp.nov. in the following characters: (1) the frontal border is arched and not straight; (2) the posterior glabellar furrows are rather oblique; (3) no other glabellar furrows or pits are discernible; (4) the ocular ridges are less slanting than in *M. meringaspis*, indicating a more forward position of the eyes in sp. B; (5) the palpebral lobes are stalked, but are closer to the glabella than in *M. meringaspis*.

The pygidium Plate 46, figure 3, locality G124, CPC 5720, is 4·1 mm long (as preserved); the bulbous terminus recalls *Meringaspis* sp. A.

*Occurrence and age:* *Meringaspis* sp. B comes from the Mungerebar Limestone, localities G10, G115, G124, and G131; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

Genus STEPHANOCARE Monke, 1903

STEPHANOCARE RICHTHOFENI Monke, 1903

(Pl. 44, figs 5 and 6)

*Material:* The described material, all silicified, comprises a cranidium and two free cheeks; less well preserved fragments are also present in some of the collections.

*Stephanocare richthofeni* is the type species of the genus and the only one whose cranidium has been described; others, reviewed by Kobayashi (1941), refer to pygidia only. Monke's contribution remains fundamental; subsequent authors (Woodward, 1905; Walcott, 1913) refer largely to Monke; Kobayashi (1941) produced supplementary information regarding the thorax of *S. richthofeni*, and a reconstruction which is reproduced in Harrington et al. (1959). In this reconstruction the vincular sockets, which are rather strong (Monke, 1903, pl. 9), are greatly reduced and the whole rim is shown as wavy although in reality its frontal slope is wavy but its posterior margin is smooth and straight. In subsequent illustrations and descriptions the glabellar furrows are equally oblique; but, according to Monke, only the posterior furrows are oblique, and the anterior furrows horizontal, as can be seen in Monke's photograph but not in his drawings. As regards the cranial rim (border) Kobayashi (loc. cit., diagnosis, p. 45) writes: 'the outer side of border, which is the doublure, is wavy'. In reality it is not the doublure but the frontal slope of the rim itself; the frontal part of the suture is marginal and the doublure remains with the free cheek and, probably, the rostral shield.

The marginal cephalic 'waves' are vincular sockets to receive the pleural tips of the pygidium and of the thorax of the coiled trilobite. Of all Cambrian trilobites *Stephanocare richthofeni* alone possesses a frontal vincular apparatus; it can be described as perfect and is rivalled only by the Ordovician asaphid *Onchometopus* Schmidt.

*Description of illustrated specimens:*

The cranidium, Plate 44, fig. 5, CPC 5708, locality G153, is 12·8 mm long and one of the largest known. It is fragmentary but displays all essential characters of the species: (1) the surface is densely pustulose; (2) the occipital margin bears spines—eight spines are mentioned by Monke and are also present on an Australian fragment (not illustrated); (3) two pairs of glabellar furrows are present, the anterior short and subhorizontal, the posterior strongly oblique; (4) the occipital furrow is wide, deep, and straight; (5) the glabella is elevated, subconical, and reaches the rim; (6) ocular ridges are absent; (7) the palpebral lobes are opposite the posterior glabellar furrows; (8) the interocular cheek is as wide as half the glabella; (9) the anterior sutures are straight and divergent (and not subparallel; compare Monke, op. cit., pl. 7, fig. 2). The frontal view shows the vincular sockets on the anterior slope of the rim, which itself is narrow and rather high.

The free cheeks Plate 44, fig. 6, CPC 5709, locality G153, are buried in the rock. Both show the vincular sockets, and in the larger (10·8 mm long) the acute genal angle and a part of the genal spine are also visible.

*Occurrence and age:* *S. richthofeni* occurs in the Mungerebar Limestone at locality G153. Its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

STEPHANOCARE sp.nov.

(Text-fig. 122)

The illustrated fragmentary silicified cranidium, CPC 6736, belongs to *Stephanocare* because (1) the glabella has the shape of a flowerpot, (2) the glabella reaches the rim, and show two pairs of lateral furrows, and (3) the rim itself is a transverse

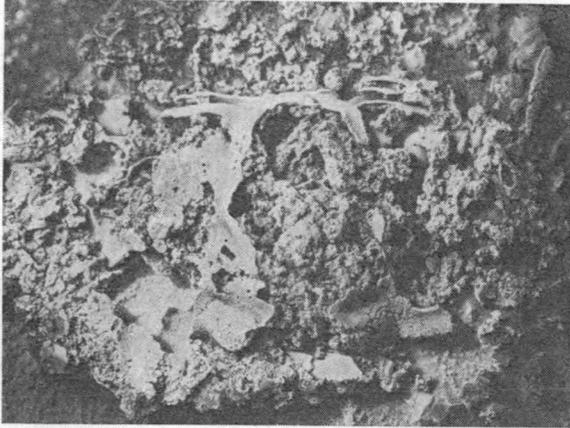


Fig. 122.—*Stephanocare* sp.nov., CPC 6736, x 1.6.

elevated ridge (a narrow fold), as seen in the anterolateral corner of the cranidium. The front of the rim, however, is smooth, without the vincular sockets of *S. richthofeni*. The specimen is 22.5 mm long.

*Occurrence and age:* The fragment comes from the Mungerebar Limestone, locality G132; its age is the Zone of *Cyclagnostus quasivespa*.

Genus DIPENTASPIS nov.

The type species of *Dipentaspis* is *D. dipentaspis* sp.nov.

*Diagnosis:* *Dipentaspis* is a genus of the Damesellidae whose species have (1) an hourglass-shaped cranidium, (2) straight and divergent anterior sutures, (3) relatively small posterolateral limbs, (4) a wide almost flat brimless frontal border produced forward as a trapezoidal projection, (5) the doublure of the free cheeks extended to the midline and separated by a subcephalic suture from the ventral side of the frontal projection, (6) medium-size eyes behind the midpoint of the glabella and relatively close to it, elevated on summits of the cephalic pleural lobes, (7) thick palpebral lobes, (8) a pygidium with five pairs of marginal spines, and a vertical margin below the spines.

*Differential diagnosis:* *Dipentaspis* possesses no unique characters and is based on a combination of characters known in some species of *Blackwelderia*, *Dorypygella* and *Teinistion*; the nearest genera are *Dorypygella* and *Teinistion*, as seen from the following discussion. *Blackwelderia sabulosa* also has a forward produced cephalic front, but its ventral structure is different; furthermore, all known species of *Blackwelderia* have more spines in the pygidium, a different position of the eyes, subparallel anterior sutures, and a trapezoidal cranidium. In *Dorypygella typicalis* the pygidium

has five pairs of spines, but in the cephalon the glabella is rather short and conical, the front is upturned, and the palpebral lobes are rather large. *Teinistion* has an hourglass-shaped cranidium, the doublure of its free cheeks extends to the midline, and the eyes with thick palpebral lobes are behind the midpoint; but its posterolateral limbs are long and narrow, and the pygidium (if a correct pygidium has been assigned to it) has six pairs of spines. Finally, *Dipentaspis* has a cranidium of the same shape as *Teinistion amydiium* sp.nov. and *Histiomona oculosa* sp.nov.; but these forms differ in the structure of the glabella and the frontal border and in the position of the eyes; furthermore, they possess bacculae, which are not evident in *Dipentaspis*.

*Solenoparia tangshihensis* Endo (1944, p. 82, pl. 6, fig. 18), based on a cranidium from the late Middle Cambrian Taizu formation of Manchuria, recalls *Dipentaspis*; Chang (1963) established on it the new genus *Parataizuia*, of the family Ordosiidae Lu. It has, however, a plectrum confluent with the convex rim, a large triangular occipital lobe, and very wide interocular cheeks (as wide as glabella) and cannot be confused with *Dipentaspis*. The pygidium of *Parataizuia* is unknown.

#### DIPENTASPIS DIPENTAS sp.nov.

(Pl. 21, fig. 7; Pl. 43, figs 1-6; Text-figs 123, 124)

*Material:* Most of the specimens occur in sandstone as casts and moulds. Pygidia and free cheeks are abundant; cranidia are less common and fragmentary. Two silicified (etched) free cheeks and one pygidium are also present. One cranidium, three free cheeks, and three pygidia are illustrated.

*Holotype:* The holotype is the silicified pygidium Plate 43, figure 6a, b, CPC 5701, locality D54; it is selected because it is more durable than the friable material in sandstone.

*Diagnosis:* *Dipentaspis dipentas* is distinguished by its pustulose ornament, by the length of its frontal border (about 0.17 of the cephalic length), position of the palpebral lobes (about 0.35 of glabellar width from the glabella), and by the absence of external ocular ridges.

By all these characters *D. dipentas* differs from *D. ratis* sp.nov., which is described below. Several other characters listed in the generic diagnosis, especially regarding the pygidium, may have specific significance, but cannot be included in the present diagnosis because the pygidia of other congeneric forms are unknown.

*Description:* The cephalon, twice as wide as long, has a semicircular outline, except for the genal spines and the trapezoidal projective front. Its relief is rather well expressed and full of contrasts: the border is almost flat, the eyes top sub-conical summits with steep slopes which are vertical at the marginal furrow in front of the eyes; the axial furrows are valleys between the pleural lobes and the glabella is arched longitudinally and transversely. In the rear the posterolateral limbs slope down rather steeply. The surface is coarsely pustulose.

The cranidium is hourglass-shaped, constricted on the level of the eyes. The anterior sutures are straight and divergent; crossing the straight marginal furrow, the sutures turn at an acute angle and remain dorsal for about one-third of the width (transversely) of the frontal border; at a distance of about two-thirds of the length (longitudinally) of the border the sutures pass over into a ventral position. As

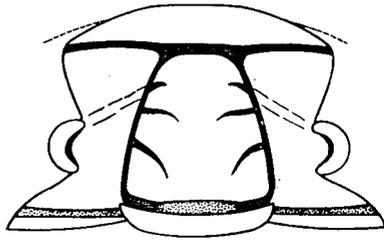
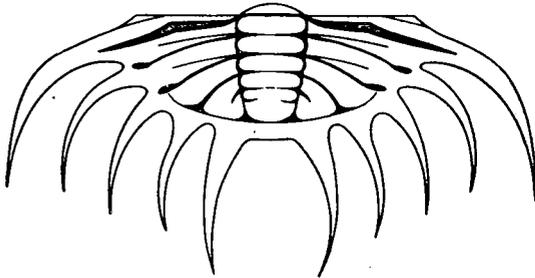


Fig. 123.—*Dipentaspis dipentas* gen. nov., sp. nov., from Plate 21, fig. 7, and Plate 43, figs 1, 3, and 6. Position of vestigial internal ocular ridges is indicated.



seen in Text-figure 123, the cranidium possesses a trapezoidal front extended beyond the points at which the sutures leave the dorsal side. The projected part itself is slightly upturned, but otherwise the border, which is one-sixth (about 0.17) of the cephalon, is almost flat.

The posterior sutures are slightly convex and strongly divergent, and delineate triangular downsloping posterolateral limbs; they are relatively short (transversely), about three-quarters of the occipital lobe, and much shorter than in *Teinistion*.

The posterolateral margin is prominent and the marginal furrow distinct. The palpebral lobes are placed opposite the posterior glabellar furrows and behind the glabellar midpoint, and at a distance of about 0.35 of glabellar width counting from the tip of the anterior cusp of the palpebral lobe. The eyes are consequently close to the glabella. The palpebral lobes, as long as 0.35 of the glabella, are of a medium size. They are strongly arcuate, swollen, thick ridges comparable with *Teinistion* (Monke, 1903, pl. 4, fig. 2a) but not with other damesellids. The edges of the lobes are uplifted and the lobes themselves slope adaxially. Ocular ridges are absent.

The occipital lobe is relatively narrow, with small abaxial lobules, and without a median node; the occipital furrow is wide, and has deep extremities. The glabella is conical, slopes forward in an even curve, and has almost straight flanks and a rounded front; three pairs of shallow glabellar furrows are present. The posterior furrows are oblique, and the second furrows almost horizontal. The third, anterior pair of furrows consists of small lateral indentations. The posterior glabellar lobes are swollen, the others are inconspicuous.

The free cheek has a relatively flat border with a depressed flange; the genal spine is only little advanced, flattened, long, and has a curved tip whose curvature is comparable with the pygidial spines. The frontal doublure of the fixed cheek extends

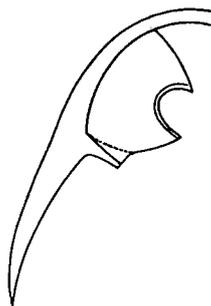


Fig. 124.—*Dipentaspis dipentas*  
sp.nov., from Plate 43, fig. 5.

well to the midline, but the presence neither of a small rostral shield nor of a fused cheek unit could be established. The doublure of the free cheek is much narrower than the external rim, indicating that the frontal doublure is about half the rim's length (longitudinally). A similar structure is apparent in *Teinistion lansi* (Monke, 1903, pl. 4, fig. 7) regarding the extent of the doublure.

The pygidium (without spines) is sub-semicircular to semielliptical in outline; its axial lobe is strongly elevated; the pleural lobes are arched upward and the border (in plan) depressed, but a marginal furrow is absent. Five pairs of long and curved marginal spines arise from the upper edge of the margin; the anterior spines, as usual in most of the damesellids, are the strongest, and the rear spines, seen in the Damesellinae, are absent here. Four pairs of distinct pleural furrows are present, terminating in elongate pits, and the two anterior pairs of the pleural ribs bear weak interpleural grooves. The axial lobe has straight flanks, tapers only slightly, and is narrower than a pleural lobe; the axis consists of five annulations and a short, bluntly rounded terminus.

The surface of the pygidium is pustulose; each axial annulation bears four symmetrically arranged pustules, and on the pleural lobes the pustules are arranged apparently in concentric girdles.

The pygidial doublure is flat, but has a raised inner margin. The pygidium is relatively large, about 0.6 of the length of the cephalon.

*Comment on illustrated material:*

The cranium Plate 43, figs 1a, b, CPC 5696, collection 41621, Frome Broken Hill Pty Ltd, Steamboat Sandstone, is decorticated; the external mould (rubber cast) and the fragmentary internal cast are preserved. It is associated with a pygidium and fragmentary free cheeks. Assuming that these specimens are parts of a single exuvia, the pygidium (without the spines and the articulating half-ring) is about 0.6 of the cephalic length. The cranium itself is 23.0 mm long. The rubber cast (Pl. 43, fig. 2) of the frontal border shows some of the frontal doublure.

The free cheek Plate 43, fig. 5, Text-fig. 127, CPC 5700, locality D96, in friable sandstone, is completely decorticated; its total length is 31 mm. It is most informative regarding the frontal structure: the subcranial doublure is narrow, indicating the course of the suture on the ventral side of the frontal border and of its margin.

The silicified right free cheek, Plate 43, fig. 4, CPC 5699, locality D54, on the discontinuity surface between the Quita Formation (a brecciated limestone bed) and the Steamboat Sandstone (silicified oolites, limestone pellets, quartz sand, calcite matrix, current lamination), is 15.2 mm long as preserved. The posterior part of the base of the eye and the test adjacent to the posterior suture is immersed in silica, and so is the adaxial part of its doublure. The associated left cheek shows the extenuated marginal flange.

The holotype pygidium Plate 43, fig. 6, CPC 5701, locality D54, Steamboat Sandstone (the matrix is described above, with the free cheeks) is 9.5 mm long; it belongs to a specimen larger than the owner of the associated free cheeks.

The pygidium Plate 43, fig. 2, CPC 5697, collection 41621, Frome Broken Hill Pty Ltd, Steamboat Sandstone, is 13.6 mm long and presumably, together with the associated cranidium, forms a single exuvia. The rubber cast shows interpleural grooves on the two anterior ribs.

The pygidium Plate 43, fig. 3, CPC 5698, locality D96, Steamboat Sandstone (friable matrix), is 10.0 mm long; together with its rubber cast and several other associated pygidia it served to restore the marginal spines in Text-figure 123.

*Occurrence and age:* *Dipentaspis dipentas* occurs in the Steamboat Sandstone at localities D54, D95, D96, D99, D101; its age is the Middle Cambrian *Leiopyge laevigata* Zone, ranging through the full span of this triple zone; furthermore, fragments occur in the Middle Cambrian–Upper Cambrian Zone of passage.

#### DIPENTASPIS RATIS sp.nov.

(Pl. 21, fig. 7; Pl. 43, fig. 7; Text-fig. 125)

*Material:* Two cranidia selected from a total of four are illustrated; the matrix is pink fine-grained silty sandstone; tests are not preserved.

*Holotype:* The cranidium Plate 43, figure 7, CPC 5763, locality D95, is selected as the holotype because of its better preservation. It is 15 mm long.

*Diagnosis:* *D. ratis* is distinguished by its smooth test (without pustules), the length of its frontal border (about 0.2 of cephalic length), position of the palpebral lobes (over 0.6 of glabellar width from the glabella), and the presence of distinct

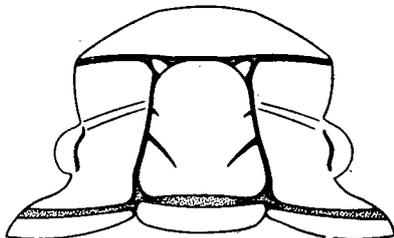


Fig. 125.—*Dipentaspis ratis* sp. nov., from Plate 21, fig. 7, and Plate 43, fig. 7.

ocular ridges. By all these characters *D. ratis* differs from the type of the genus (*D. dipentas*). Furthermore, the glabella in *D. ratis* is slightly shorter, and flanked in front by anterolateral lobes (see Test-fig. 111); only two pairs of indistinct glabellar furrows are discernible.

*Occurrence and age:* *Dipentaspis ratis* is a rare fossil in the upper levels of the Steamboat Sandstone and occurs at localities D95 and D96; its age is the upper part of the Middle Cambrian Triple Zone of *Leiopyge laevigata*.

#### DIPENTASPIS sp.indet.

(Pl. 42, fig. 8)

*Material:* Illustrated is a cranidium, CPC 5695, 5 mm long, in sandstone, selected from several similar fragments. It is very convex and strongly arched longitudinally, with a profile approaching a quadrant of a circle; the frontal border is flat and about 0.17 of total length of the cephalon; the palpebral lobes are rather

long, longer than half the glabella. Open nomenclature is applied because the relatively small size of the specimens and the coarse grains of the matrix prevent study in detail.

*Occurrence and age:* *Dipentaspis* sp. A has been found in the lowermost beds of the Steamboat Sandstone, at locality D54; its age is low in the Middle Cambrian Zone of *Leiopyge laevigata*, which is also present in the same bed.

#### Genus TEINISTION Monke, 1903

The etymology of the name *Teinistion* (neuter) (see Glossary) and its spelling have been explained by Monke; the spelling '*Teiniston*', which is used consistently by Endo in Resser & Endo (1937), appears to be a misunderstanding.

The genus itself is based on *Teinistion lansi* Monke (1903, pl. 4); the type specimen is the cranidium (ibid., pl. 4, fig. 2), which was re-illustrated by Walcott (1913, pl. 9, fig. 1). Monke's plate 9 (squares C4 and C6) contains photographs of cranidia agreeing well with the drawing of the type. Nevertheless, the form of the frontal lobe of the glabella evidently differs; in all drawings it is evenly rounded, whereas in the photographs the glabellar front is truncated or even slightly concave. In the subsequent literature *T. lansi* is shown with a rounded front; furthermore, the presence of glabellar furrows is neglected, although two pairs are present, and described by Monke. Monke's second species—*Teinistion sodeni*—is a good species, but appears to belong to some other genus of the Damesellinae. *Teinistion subconicum* Sun, 1924, however, is a species of the genus, distinguished by a granulose ornament.

Endo in Resser & Endo (1937) established three more species of *Teinistion*: *truncatus* (—um), *obtusus* (—um), and *sulcatus* (—um). One cranidium of *truncatum* (loc. cit., pl. 84, fig. 7) has a truncated glabellar front, and two other (pl. 65, figs 1 and 2) have conical glabellas; nevertheless *truncatum* should be regarded as a *Teinistion*; *obtusum* (pl. 65, figs 6 and 7) has a conical glabella with three pairs of long glabellar furrows and adaxially slanting ocular ridges which indicate a genus different from *Teinistion*; finally, *sulcatum* (pl. 65, fig. 4) has a triangular pointed glabella, horizontal ocular ridges and, apparently, stalked eyes opposite the anterior third of the glabella, and belongs neither to *Teinistion* nor to another known damesellid genus.

Therefore, only three species, *lansi* Monke, *subconicum* Sun, and *truncatum* Endo, can be classified with certainty as *Teinistion*.

Harrington et al. (1959) included *Teinistion* in Emmrichellidae (Emmrichellacea), together with *Dorypygella*, *Changshania*, and *Shantungia*. I concur, however, with Kobayashi (1960) in regarding these genera as members of the Damesellidae, to which they are morphologically similar in cranidial and pygidial characters. Incidentally, from the Emmrichellidae and Emmrichellacea the following genera should be removed: (1) *Eurostina* Whitehouse, a ptychopariid, (2) *Protemnites* Whitehouse, a rather incompletely known ptychopariid, (3) *Probowmania* Kobayashi, a ptychopariid, (4) *Lorenzella* Kobayashi, an agrauloid, (5) *Inouyia* Walcott, incertae familiae, probably affiliated with agrauloids, and (6) *Utia* Walcott, and Utiidae Kobayashi, of doubtful superfamilial affinity. Thus, *Emmrichella* Walcott alone remains in the family.

The characters of *Teinistion* Monke (at the present state of knowledge) can be summarized briefly as follows:

The pygidium is damesellid, with six pairs of marginal spines; the anterior spines are large; the anterior pleural furrow extends into the base of the spine, as seen in all other damesellids; the cranidium is subquadrate, with long and narrow posterolateral limbs owing to the posterior position of the eyes; the reniform palpebral lobes are relatively large and opposite the posterior glabellar furrows; the eyes are elevated above the summits of the adaxially and abaxially sloping cheeks; the ocular ridges are slanting and prominent; the frontal border is wide, upturned, and folded downward; in the type species the frontal margin has a recess; the interocular cheeks may have folds parallel to the ocular ridges; bacculae are present; the glabella is tapering to almost parallel-sided, with a rounded or truncated front and possesses at least two pairs of lateral furrows; the genal spine is undeflected and not advanced.

TEINISTION? AMYDIUM sp.nov.

(Pl. 44, figs 1, 2; Text-fig. 126)

*Material:* Two cranidia in limestone are described and illustrated.

*Holotype:* The holotype is the specimen Plate 44, figure 1, CPC 5704, locality W20.

*Generic classification:* *T.?* *amydium* appears to be affiliated with *T. lansi* because of its subquadrate cranidium, wide frontal border with the upturned margin, and slender glabella; but *amydium* deviates from the concept of *Teinistion*: (1) it has a granulose ornament; but (2) the palpebral lobes are arcuate and not reniform as in *Teinistion*; and (3) the frontal margin is straight, without the rearward recess. The last-mentioned point may be irrelevant because in immature specimens of *T. lansi* the front is also straight, indicating the possibility that in affiliated species such a front may be retained also in maturity. The nearest genus, therefore, is *Teinistion* Monke, but *amydium* probably represents a subgenus, or even a separate but affiliated genus. *Teinistion subconicum* Sun (1924, p. 31, plate 2, fig. 4) is probably related to *amydium* in having a granulose surface, but is distinguished by concave glabellar flanks, shorter occipital lobe, and receding frontal margin.

The diagnosis that follows distinguishes *amydium* from the known species of *Teinistion* as well as all species of the known genera of the Damesellinae.

*Diagnosis:* *Teinistion?* *amydium* is a species of the Damesellinae with a subquadrate cranidium, large arcuate palpebral lobes, a straight frontal margin, a deeply excavated frontal border, prominent bacculae and a granulose glabella; distinguished by its rather long and narrow glabella, three pairs of lateral glabellar pits, a large occipital lobe and smooth cheeks.

*Description:* The cranidium is subquadrate, with slightly divergent and almost straight anterior sutures which remain dorsal within the border for a short distance only. The posterior sutures are greatly divergent, delineating long (transversely) and narrow posterolateral limbs. The palpebral lobes are large, placed opposite the middle of the glabella, and about half the glabella in length; the interocular

cheeks between the cusps of the palpebral lobes are about as wide as the glabella and dip steeply adaxially. The eyes are elevated above the level of the glabella on the summits of the cheeks. The slanting ocular ridges are broad and inconspicuous and accompanied in the rear each by an indistinct fold. In front of the ocular ridges the test slopes gently and the pleural lobes of the cranidium extend forward and well beyond the glabellar tip. The frontal border is rather wide, about 0.2 of the cranidial length, and deeply excavated; the margin itself is straight, up-turned, and consists of a simple fold.

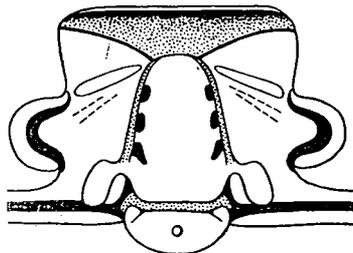


Fig. 126.—*Teinistion? amydium* sp.nov., from Plate 44, figs 1, 2.

The occipital lobe is relatively long (about one-third of the glabella) and bears a low median node and a pair of lobules on the abaxial ends. The occipital furrow is straight, narrow, and deep. The axial furrows are deep valleys between the glabella and the cheeks and are remarkable in having a flat floor; just behind the posterior glabellar pits these furrows are interrupted by the junction of the bacculae with the glabella. The bacculae are relatively small but tumid. The glabella is elongate conical, with slightly convex and steeply sloping flanks, and about as wide as 0.6 of its length. It is a rather narrow glabella. Three pairs of deep pits represent the glabellar furrows. They are in contact with, but do not intrude the axial furrows; the posterior (S1) pits are elongate. No lobes are discernible on the glabella.

The glabella and the occipital lobe are ornamented with scattered rounded granules, but the cheeks are, apparently, smooth.

*Comment on illustrated material:*

The holotype cranidium is 2.7 mm long. Although fragmentary, it shows the left anterior suture, the interocular cheek with the palpebral furrow, and parts of the palpebral lobe, the position of which is necessary for a fair reconstruction of the whole cranidium. The cranidium Plate 44, fig. 2, CPC 5705, locality G50, estimated 3.0 mm long, is rather fragmentary, but shows the left baccula and its connexion with the glabella.

*Occurrence and age:* *Teinistion? amydium* has been found as yet only in the Georgina Limestone at localities G50 and W20. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Genus HISTIOMONA nov.

*Histiomona* is a monotypical genus; its type is *H. oculosa* sp.nov.

The generic diagnosis coincides with the diagnosis of its type species, which is given below. It is a genus of the Damesellidae combining in a peculiar manner some characters of *Blackwelderia* and *Teinistion*. The arcuate palpebral lobes, the

concave frontal border, comparable with *B. paronai*, and the relatively narrow (sagittally) occipital lobe are like *Blackwelderia*; the posterior position of the palpebral lobes, prominent bacculae, long glabella, and somewhat subquadrate cranium recall *Teinistion*. The measured cranidia (6.5 mm and 9.0 mm) are too big to be immature instars of another and already described damesellid.

A new species of *Histiomona* has been collected in the early Upper Cambrian part of the Skewthorpe Formation at Cambridge Gulf (Text-fig. 1) in the extreme north of Western Australia (see Öpik, 1956, p. 53). Its pygidium recalls *Meringaspis*, but its rear border is not extended into a 'tongue'.

HISTIOMONA OCULOSA sp.nov.  
(Pl. 44 figs 3 4; Text-fig. 127)

*Material:* The described material consists of two cranidia found in the same piece of limestone from locality W15.

*Holotype:* Is the smaller but better preserved cranidium Plate 44, figure 4, CPC 5707, 6.5 mm long. The second (larger) specimen, Plate 44, figure 3, CPC 5706, is 9.0 mm long and flattened, but is illustrated to show the granulose ornament and the glabellar furrows, which in the holotype are masked by the convexity of the glabella.

The diagnosis that follows results from a comparison with all known species of the Damesellinae and Dorypygellinae; a differential diagnosis is unnecessary except for the comparison given under the heading of the genus.

*Diagnosis:* *Histiomona oculosa* is a species of the Damesellinae with a cephalon of a relatively low relief, well developed bacculae, wide and concave frontal border, narrow interocular cheeks (half the glabella), and a long glabella; distinguished by the very large palpebral lobes (0.6 of glabellar length), parallel-sided glabella, and a granulose ornament restricted to the median part of the glabella.

*Description:* The cranidium has a relatively low relief; it is subquadrate except for the arcuate palpebral lobes and posterolateral limbs. The anterior sutures are straight, diverge slightly, and remain, within the frontal border, dorsal for a short distance only. The posterior sutures are greatly divergent and delineate narrow

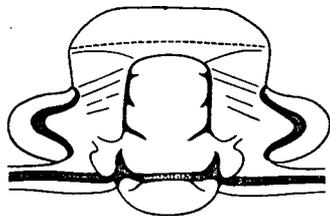


Fig. 127.—*Histiomona oculosa*  
gen.nov., sp.nov., from Plate 44,  
fig. 4.

and long posterolateral limbs, as seen also in *Teinistion*. The palpebral lobes are very large, about 0.6 of glabellar length, broad, abruptly arcuate, and flat; the palpebral furrows are deep and narrow. The interocular cheek between the cusps of the palpebral lobe is about as wide as the glabella and slopes gently adaxially;

the cheek part between the cusps is swollen; the eyes are elevated only slightly above the level of the glabella. The ocular ridges are slanting, broad, and only slightly elevated; the slope in front of the ocular ridges is gentle, the cranidial pleural lobes are not separated by a furrow from the frontal border. The frontal border is rather wide, about 0.4 of glabellar length, concave, and provided with a doublure, the extent of which, however, is unknown. The occipital lobe is relatively flat, about as long as a third of the glabella, and possesses a pair of inconspicuous lateral lobules. The occipital furrow is narrow and ends laterally in deep pits.

The axial furrows are straight shallow valleys between the glabella and the cheeks, but are interrupted just behind the posterior glabellar furrows by the junction of the glabella with the bacculae. The bacculae are elongate, tumid, and provided with a short anterolateral extension (probably a caecal duct). The glabella has straight flanks, and is bluntly rounded in front. It is a relatively long glabella, with a base of about 0.75 of its length. Among other genera of the Damesellinae a glabella longer than wide is known in *Teinistion* only. The posterior (L1) lobes of the glabella are slightly swollen, but the other lobes are not discernible. Three pairs of short and oblique glabellar furrows are present, terminating in deep pits. The anterior (S3) furrows are, however, rather weak.

The ornament consists of a low and relatively dense granulation on the median part of the glabella and the occipital lobe; the rest of the surface is shiny and apparently smooth.

*Occurrence and age:* *Histiomona oculosa* sp. nov. is a rare trilobite in the Georgina Limestone, found as yet only at locality W15; its age is the Zone of *Glyptagnostus stolidotus*.

#### DAMESELLINAE gen. nov. A, sp. indet.

(Pl. 42, fig. 7)

The illustrated fragmentary pygidium, CPC 5694, an external cast in a chert biscuit, is 2.0 mm long on the midline. Its left flank shows four undivided pleural ribs and very long, straight, granulose, and diverging spines apparently corresponding to the two posterior pairs of pleural ribs. Between the spines the border is flat and depressed, with a pair of falcate cusps separated by a semicircular recess of the margin. The axial lobe is wide, but not defined, in the rear, merging with the tumid confluent rear part of the pleural lobes. The axial furrows are distinct anteriorly but fade out rearward. The test is minutely and densely granulose and on the spines the granules are arranged in oblique lines.

The spines themselves are unusually long: an isolated fragment, probably the extension of a spine of the same pygidium, is 10 mm long, both ends broken. A part of it is seen in the illustration.

The fragment is insufficient to restore the outline of the pygidium.

*Occurrence and age:* The fragment was found in the top of the Steamboat Sandstone, passing into the Mungerebar Limestone, at locality G103; its age is the passage from the Middle to the Upper Cambrian. One fragment has been found also in the Mungerebar Limestone (Zone of *Erediaspis eretes*), locality G119.

DAMESELLINAE gen.nov. B, sp.nov.

(Pl. 43, fig. 3)

*Material:* Only the illustrated fragmentary cranium, CPC 5690, in limestone, has been found as yet.

*Description:* The specimen is 12.2 mm long and 20.0 mm wide; the test is preserved and exposed from inside. The anterior sutures are moderately convergent; the palpebral lobes are slightly elevated, horseshoe shaped, and placed in the rear, opposite the posterior glabellar furrows; the palpebral lobes are as long as about 0.3 and the interocular cheek about 0.75 of the glabella. The ocular ridges are narrow, well elevated, and slanting owing to the rearward position of the eyes. The axial furrows are deep, the glabella has straight and tapering flanks. The glabellar lobes are tumid and the three pairs of glabellar furrows are distinct. The posterior furrows are forked, and the adaxial longitudinal branches face one another as 'brackets' similar to *Palaeadotes* gen.nov. The test is minutely granulose and provided with widely spaced and symmetrically arranged large tubercles.

*Generic classification:* The fragment represents a new genus of the Damesellidae, but is insufficient for a proper diagnosis and naming. The rearward position of the palpebral lobes and the symmetrical arrangement of the larger tubercles indicate a possible affiliation with *Cyrtoprora* gen.nov. The nameless form is, however, distinguished by its tapering glabella and low seated palpebral lobes.

*Stratigraphic significance:* The unnamed form is Middle Cambrian, and belongs to the Zone of *Ptychagnostus (Goniagnostus) nathorsti*; fragments of pygidia of even older Damesellidae are also known from the *P. punctuosus* Zone; these are related to *Dipentaspis*. So, (1) Damesellidae existed already well within the Middle Cambrian, and (2) taxonomically inconclusive fragments of damesellids without a control by diagnostic fossils are inaccurate stratigraphically.

*Occurrence and age:* The fragment was found in the area of the Camooweal 1 : 250,000 Sheet at locality M65, a small outlier of Mail Change Limestone and V-Creek Limestone on the right bank of the O'Shannassy River, surrounded by outcrops of the Age Creek Formation. The fossil belongs to the V-Creek Limestone. The age is the Zone of *Ptychagnostus (Goniagnostus) nathorsti*, as determined from the associated trilobites.

Subfamily DREPANURINAE Hupé, 1953

Genus DREPANURA Bergeron, 1899

The genus *Drepanura* is based on the species *D. premesnili* Bergeron, 1899. The holotype and all associated material consist of pygidia only. Monke (1903, pl. 5, figs 5-19) identified correctly Bergeron's species from a number of pygidia and described also its cranidia and free cheeks. In the subsequent literature the cranidia are subject to no confusion, except for minor diversity in interpretations. As regards the free cheeks, the adult *D. premesnili* has no genal spine, but a small deflected spine is present in immaturity. In all cheeks illustrated by Monke the anterior process

is deflected in a manner, seen in *Blackwelderia sabulosa* sp.nov., that indicates the presence of a slightly forward-projecting cephalic front, which has been considered in the reconstruction by Kobayashi (1941, pl. 2).

Woodward (1905), Walcott (1913), Hupé (1955), Lu (1957), and Tchernysheva et al. (1960) have attributed the correct pygidium to *D. premesnili*; but Kobayashi (loc.cit.) has attached to the correct cephalon the thorax and the pygidium of another trilobite; this reconstruction is reproduced in Harrington et al. (1959, p. 0318, fig. 235), and attributed in the caption of the illustration erroneously to Bergeron, but in the text to Kobayashi, which is correct. The thorax and pygidium of the reconstruction were published earlier by Endo (1939, p. 7, pl. 1, fig. 7); the pygidium is subcircular with five pairs of pleural furrows and a long axis with five annulations; *D. premesnili*, however, has a subtriangular pygidium with about three pairs of indistinct pleural furrows and a short axis with three annulations.

The characters of the cranium of *Drepanura premesnili* can be summarized briefly as follows: (1) the frontal border is straight, very narrow, and slightly upturned; (2) the palpebral lobes are relatively small, opposite the frontal lobe of the glabella and very close to it, so that the interocular cheeks are exceptionally small, almost disappearing; (3) the posterolateral limbs are subtriangular and extremely large; (4) the glabella tapers strongly and has a subtruncate front; (5) two pairs of simple glabellar furrows, and in some specimens a weak third pair, are present.

The characters of *D. premesnili* are the characters of the genus; several species related to *D. premesnili* have been subsequently established by Resser & Endo (1937), and their synonymy has been discussed by Kobayashi (1941). *Drepanura kettleri* Monke, hitherto regarded as the second properly described species of the genus, is transferred here to *Palaeadotes* gen.nov.

*Drepanura premesnili* and its affiliates have not been found as yet in Australia. The name 'Drepanura Zone' as used in the literature refers to *Drepanura premesnili*.

#### Genus PALAEADOTES nov.

The type of *Palaeadotes* is *P. dissidens* sp.nov.

*Diagnosis:* *Palaeadotes* is a genus of the Drepanurinae whose species are distinguished by (1) a subrectangular glabella with somewhat converging or parallel flanks, (2) two to three pairs of glabellar furrows of which the posterior are trifid, with longitudinal branches opposing each other, (3) distinct interocular cheeks, (4) eyes on elevated summits opposite the glabellar middle, (5) a pygidium with five to six pairs of marginal spines, (6) long and slender anterior spines, (7) a depressed complete pygidial border, and (8) pleural lobes with distinct pleural furrows. Furthermore, the pygidial doublure known from *P. italops* sp.nov. has, apparently, a structure unique among trilobites.

*Differential diagnosis:* *Drepanura* Bergeron is the only known genus related to *Palaeadotes*; in *Drepanura*, however, the glabella tapers strongly, the posterior glabellar furrows are simple, the eyes are not elevated and are placed opposite the frontal glabellar lobe and close to the glabella, the interocular cheeks are diminutive, the anterior pygidial spines are broad, the pygidial border is incomplete, stopping at the anterior spines, and the pleural furrows are short and weak.

*Species of Palaeadotes:* Australian species are (1) *P. dissidens* sp.nov. (2) *P. aff. dissidens*, and (3) *P. italops* sp.nov.; Chinese are (4) *Drepanura kettleri* Monke and (5) an undescribed form, known from the thorax and pygidium only (Endo, 1939; Kobayashi, 1941, pl. 1, fig. 7); Swedish is (6) *Drepanura eremita* Westergaard (1947).

Monke, and later Kobayashi, assigned to *P. kettleri* pygidia of a species of Damesellinae or Dorypygellinae, probably immature pygidia of *Dorypygella typicalis* Walcott; it is, however, probable that the 'undescribed form' (5) represents the true pygidium of *kettleri*, which is rather similar to *P. dissidens*. If this is correct, all species (except for *italops*) have the pygidial axis slender, long, and multiannulated (five to six annulations); in *italops* the axis is short and with four annulations only, indicating some resemblance with *Drepanura premesnili*.

All species of *Palaeadotes* have the same stratigraphical age (Kushmanian, or *Agnostus pisiformis* Zone, or Mindyallan).

The name *Drepanura* was previously applied to the Queensland forms by Öpik (1960, p. 106; 1961, p. 39), as the name of the genus nearest to the then undescribed *Palaeadotes*.

Regarding the specific differences the following brief notes should suffice: *P. kettleri* (Monke) has a slightly tapering glabella and recalls therefore *P. dissidens* sp.nov. But in *kettleri* the interocular cheeks are narrower, and the trifidity of the posterior glabellar furrows is barely indicated. *P. eremita* (Westergaard) has an almost parallel-sided glabella, as seen also in *P. italops* sp.nov.; but its pygidium, with a long axis (*italops* has the axis short) and abruptly extenuated spines, is rather different. Furthermore, none of the hitherto described forms of the Drepanurinae possess the interpleural grooves seen in the pygidia of the Australian species.

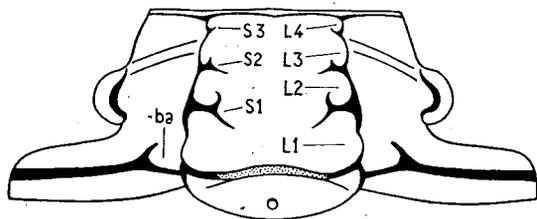


Fig. 128.—*Palaeadotes dissidens* gen.nov., sp. nov., combined from Plate 50, figs 4-6. ba—baccula; S1-S3—glabellar furrows; L1-L4—glabellar lobes; the anterior (L4) lobe is diminutive.

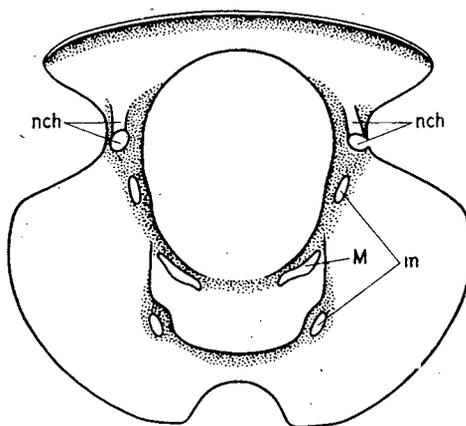


Fig. 129.—*Palaeadotes dissidens* sp.nov., hypostoma, from Plate 50, fig. 3. M—macula; m—muscle? scars; nch—lateral notch (on the right) and lateral tube (on the left).

PALAEADOTES DISSIDENS sp.nov.  
(Pl. 50, figs 3-8; Text-figs 128-129)

*Material:* Three cranidia, one hypostoma, and two pygidia are selected for description; specimens in limestone and in chert are both represented; compressed (shale) specimens are also available but add nothing regarding the species. All material consists of fragments, but they are complementary, allowing for the accurate reconstruction of the cranidium (Text-fig. 128); pygidia are in no need of reconstruction.

*Holotype:* The pygidium Plate 50, figure 8, CPC 5756, locality G50, is selected as the holotype; cranidia and pygidia are equally diagnostic specifically and generically, but a pygidium facilitates the comparison with *Drepanura premesnili* Bergeron, whose type is also a pygidium.

*Diagnosis:* *Palaeadotes dissidens* is distinguished by a slightly tapering glabella with anterior glabellar furrows placed right forward and a diminutive frontal glabellar lobe, by relatively wide interocular cheeks and parallel-sided posterolateral limbs, combined with a pygidium which has a long and slender axis of five annulations, a distinct depressed border with deep distal pits of the interpleural grooves, which rapidly peter out in the adaxial direction; the spines of the sixth pair are longer than the rest of the minor spines.

Differences from *P. italops* are indicated in its diagnosis; furthermore, a differential diagnosis is given in the description of the genus.

*Description:* The cranidium is broadly trapezoidal, disregarding the posterolateral limbs. The anterior sutures are straight and moderately converging; the posterior sutures diverge diametrically and, cutting the posterior margin almost at a right angle, delineate large band-like posterolateral limbs. The posterolateral limbs are divided in two about equal parts by the marginal furrows, which are forked adaxially at the bacculae. The interocular cheeks, about as wide as half the glabella, rise toward the palpebral summit slightly above the level of the glabella. The ocular ridges are slightly curved and slanting and the convex test in front of them slopes gently forward. The palpebral lobes, opposite the glabellar middle, are slightly less than 0.4 (about 0.37) of glabellar length. The cranidial front is straight and provided with a rather narrow upturned border. The occipital lobe, almost crescentic, has a median node and a pair of indistinct lobuli on the cusps. The occipital furrow, shallow in the middle, narrows and deepens laterally. The axial furrows are distinct but unevenly deep: shallow or almost disappearing at the junction of the bacculae with the posterior glabellar lobes, they become especially deep in front of the junction and at the posterior glabellar furrows. The bacculae themselves are fairly large, triangular, and moderately swollen.

The glabella tapers forward to about 0.8 of its posterior width. Arched transversely, it slopes forward with increasing convexity. A median carina, seen in exceptionally well preserved specimens, may be present. The four pairs of lateral glabellar lobes are distinct and tumid. The posterior lobes (L1) are large and concave on the flanks; the second lobes (L2) are reniform and half the size of the posterior lobes; the third lobes (L3) are narrow and only slightly tumid; the foremost lobes (L4) are tiny swellings of the abrupt anterolateral corners of the glabella. The glabellar front is subtruncate and provided with a median recess. Three pairs of

glabellar furrows are present: the posterior (S1) furrows are deep and trifid, with curved branches, the right branch clockwise, the left anticlockwise; one branch (the shorter) is directed forward, and the other (posterior and longer) is oblique. The left and right furrows face each other in the manner of brackets. The furrows of the second pair (S2) are short and may have a short forward-directed branch each, notching the glabellar lobe. The foremost furrows (S3) are rather short and oblique. Notable is the position of the anterior glabellar furrows well in front of the ocular ridges: such a position is unknown in ptychoparioids, but occurs in some dolichometopids.

As regards position, the posterior furrows are opposite the cranidial midpoint and the second furrows about the midpoint of the anterior half of the cranidium, indicating a normal structure of the glabella behind the ocular ridges; the extreme forward position of the third furrows indicates, however, a strong reduction of the frontal part of the cephalon. The cranidial ornament consists of widely spaced rounded granules on a minutely rough, granulose background which is recognizable under a lens only. The hypostoma is described below, under 'Comment on illustrated material'.

The pygidium, without spines, is semicircular; it is relatively flat, but its lobes, furrows, and border are well developed. Seven pairs of marginal spines are present; all spines are flat blades; the anterior spines are narrow (when compared with *Drepanura premesnili*), long and directed rearward; the spines of the remaining six pairs are turned also abruptly rearward, and are relatively long; the spines of the sixth pair are longer than the others (which is common in the Damesellidae) but remain about one-third of the length of the anterior spines. The pygidial border is depressed, slightly concave, and surrounds the shield completely; angular pits reaching the margin between the spines separate the pleural ribs within the border. These pits are the distal ends of the interpleural grooves which die out rapidly in the adaxial direction. Such a structure of the interpleural grooves is rather unusual; one expects them to peter out in the opposite direction. Five pairs of evenly deep and long pleural furrows reach the border (but not the margin); the ribs in between are relatively broad and flat. The axis is narrow (about 0.2 of pygidial width), slender, and long, reaching the border; it consists of five annulations and a somewhat bulbous terminus which may be extended into a low antiplectrum.

The inner edge of the doublure marks the border and may be reflected externally as a paradoublural line in some specimens.

The pygidial ornament is similar to the cranidial ornament. Also, each axial annulation bears a pair of low pustules; symmetrically arranged solitary pustules occur on the base of each spine, and more of them are seen, arranged in two concentric girdles on the pleural lobes.

*Comment on illustrated specimens:*

The fragmentary cranidium, Plate 50, fig. 5, CPC 5753, locality G50, in bituminous limestone is 5.2 mm long and has preserved its test. The anterior glabellar furrows and the median carina are distinct; notable are the deep pits in the occipital furrow and the concave flanks of the posterior glabellar lobes.

The fragmentary cranidium Plate 50, fig. 4, CPC 5752, locality W20, in a chert layer in limestone, is 9.0 mm long. The ocular ridge and the adaxial end of the posterior suture indicate the position and size of the palpebral lobe; the junction of the baccula with the posterior glabellar lobe is well indicated.

The cranidium Plate 50, fig. 6, CPC 5754, in a siliceous parting in limestone, 10.2 mm long, has preserved the posterolateral limb, but otherwise is distorted and abraded.

The holotype pygidium, Plate 50, fig. 8, CPC 5756, locality G50, is 8.7 mm long without spines; only the articulating half-ring is missing; the test is preserved; associated with it is a segment of the same species with a falcate pleural tip.

The pygidium Plate 50, fig. 7, CPC 5755, locality W20, in limestone, is 6.5 mm long; parts are missing, but the test is preserved. The edge of the doublure is strongly imprinted and the posterior annulation of the axis is obscure.

The hypostoma Plate 50, fig. 3, CPC 5751, in chert, locality W20, is 5.3 mm long. Its frontal part and anterior wings are immersed in silica, and Text-figure 129 was, therefore, reconstructed with the aid of the hypostoma of *P. italops*, Plate 51, figs 1 and 2. In outline it compares with the hypostoma of *Drepanura premesnili* (Monke, 1913, pl. 8, fig. 10 and attributed to *Stephanocare*; Walcott, 1913, pl. 10, fig. 2e) which also has greatly expanded posterolateral wings. The expansion of the posterolateral (posterior) wings and the sinus in between give some resemblance to a lichid hypostoma. The median, suboval body, divided into a larger anterior and a smaller posterior lobe, has the appearance usual in Cambrian trilobites; the maculae are distinct, slightly angulate, and elevated ridges. The anterior margin is clean-cut, indicating the existence of a hypostomal suture. The frontal border is concave, indicating probably a steep inclination of the hypostoma down and back in its original position. The lateral notch (Text-fig. 129, left side) is a tubular perforation serving, apparently, as a passage for the antennule; the mode of preservation may suggest, however, that instead of a tube, a fold with a narrow slit was present (same Text-fig., right side). In either case, the hypostoma in the process of moulting had to slide off the appendages, or the appendages had to be extracted from the tubes. The median body is flanked by two pairs of muscle (?) scars, one in front, and another in the rear of the maculae. These scars represent pits on the inner surface. The tubular perforations and the two pairs of scars indicate an organization hitherto unknown in trilobites. The symmetrical distribution of the perforations, scars and maculae may or may not indicate a metamerism of the hypostoma; but certainly, the hypostoma was the sternite of four cephalic somites.

The ornament consists of coarse osculating raised lines without hapsidia; transverse on the median body, the lines are arranged concentrically on the wings and the doublure.

*Occurrence and age:* *Palaeadotes dissidens* occurs in the Georgina Limestone at localities W15, W17, W18, W20, W21, G48, G50, G51, W66, W259, and in the Mungerebar Limestone at McCabe Knob. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### PALAEADOTES aff. DISSIDENS

(Text-figs 130, 131)

*Material:* Two specimens, the cranidium CPC 6737, 7.0 mm long, and the pygidium, CPC 6742, about 10 mm restored, without spines, in limestone from locality G10 are illustrated, selected from a large number of even less well preserved specimens collected at divers localities.

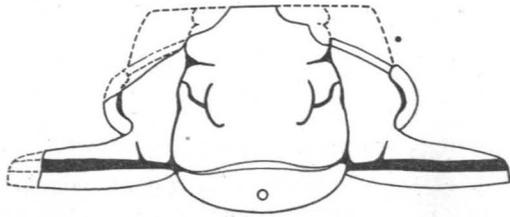


Fig. 130.—*Palaeadotes* aff. *dissidens*,  
from Text-figure 131.

In the cranidium the palpebral lobes are closer to the glabella, and somewhat more in the rear, than in *P. dissidens* and the glabella is ornamented by transverse lines which are seen only on the hypostoma of other species of *Palaeadotes*. The pygidium has a long axial lobe like that of *dissidens*, but it is wider than the slender lobe of *dissidens*.

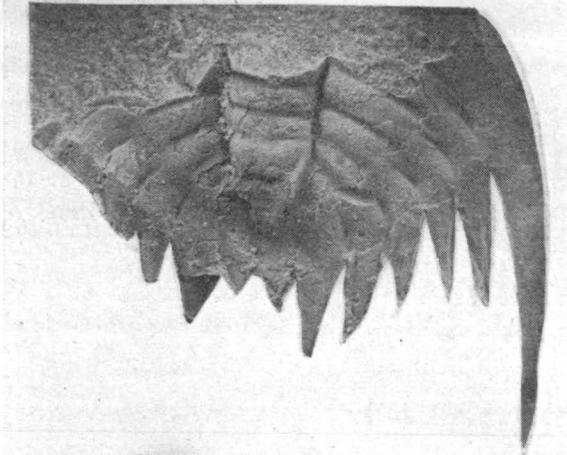
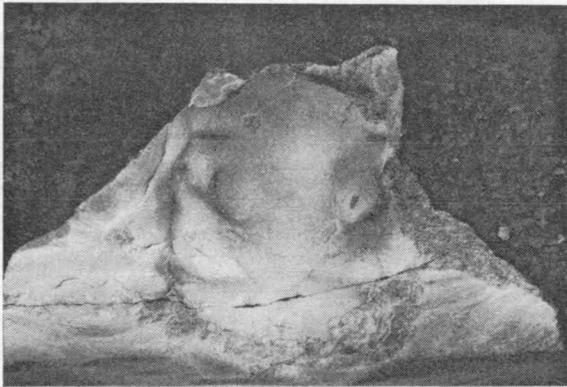


Fig. 131.—*Palaeadotes* aff. *dissidens*,  
locality G10. Cranidium, CPC 6737,  
x 5; pygidium CPC 6742, x 3.

*Occurrence and age:* *Palaeadotes* aff. *dissidens* is found in the Mungerebar Limestone at localities G10, G127, G128, G131, and G153, that is, in the Mindyallan Zone of *Cyclagnostus quasivespa*.

PALAEADOTES ITALOPS sp.nov.

(Pl. 16, fig. 2; Pl. 50, figs 9-12; Pl. 51, figs 1-4; Text-figs 132-133)

*Material:* The illustrated material (four cranidia, two hypostomata, and two pygidia) has been selected from a large number of similar fragments. The matrix is chert, or siliceous shale or friable siliceous silt with irregular grains and inclusions of chert; hence the selection was guided not only by the completeness of specimens, but also by their accessibility for developing by mechanical means.

*Holotype:* The holotype is the pygidium Plate 50, figure 12, CPC 5760; it is selected for convenience of comparison with the holotypes of *P. dissidens* sp.nov. and *Drepanura premesnili* Bergeron.

*Diagnosis:* *Palaeadotes italops* is distinguished by a subrectangular glabella with a relatively large frontal lobe, very narrow and steep interocular cheeks, triangular posterolateral limbs, and by a pygidium with a short and tapering axis of four annulations, a wide border, and diminutive posterior marginal spines.

In all the characters mentioned in the diagnosis it differs from *P. dissidens*; a general differential diagnosis is given in the description of the genus.

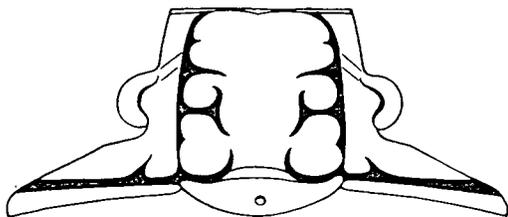


Fig. 132.—*Palaeadotes italops* sp.nov.,  
from Plate 16, fig. 2, and Plate 50, figs  
9-11.

*Description:* In the cranidium the anterior sutures are straight, slightly converging (as in *P. dissidens*), but relatively close to the glabella; the posterior sutures diverge strongly, and delineate large triangular posterolateral limbs with rounded tips. The interocular cheeks are rather narrow (about 0.25 of the glabella) and slope up steeply toward the palpebral lobes, which are about 0.33 of the glabellar length. The marginal furrow is forked adaxially, enclosing the triangular baccula. The cranial front is straight and has a faint upturned border. The occipital lobe bears a low node.

The glabella is almost rectangular; arched transversely, it is straight ('horizontal') longitudinally until its front begins sloping down at the third (L3) glabellar lobe and attains a vertical attitude. The glabellar lobes are distinct and swollen; the posterior lobes are almost isolated by the rear branches of the trifold glabellar furrows and a pair of forward-directed shallow indentations arising from the occipital furrow. The longitudinal branches of the posterior glabellar furrows face one another as brackets; the anterior glabellar furrows are placed more to the rear and the frontal lobe is larger than in *P. dissidens*. The cranial ornament consists of a relatively dense granulation and the granules are uneven in size.

The hypostoma is similar to that of *P. dissidens* (q.v.).

The pygidium, without spines, is semicircular, with a relatively wide border and distinct interpleural grooves which almost reach the axial furrows. The pleural furrows are distinct but shallow. Seven pairs of marginal spines are present: the

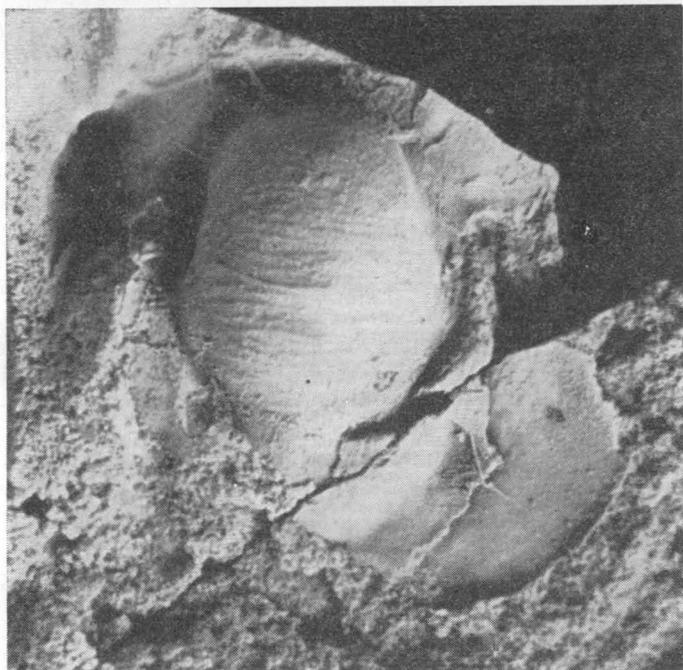


Fig. 133.—*Palaeadotes italops*, hypostoma, x 12, to show the ornament. Same specimen Plate 51, fig. 2.

anterior spines are long, narrow, and falcate; the spines of the posterior (seventh) pair are rather short and close together, as seen in some fragments. The pygidial axis is rather short (half of the pygidial length), tapering, with four annulations and a rounded terminus. The pygidial ornament consists of granules of divers size; isolated larger pustules are also present. The doublure is very wide, and its inner edge coincides with the tip of the axis, with the adaxial margin of the border and the fulcral point. On the ventral side the doublure is divided in two parts by a thread-like concentric ridge which starts at the fulcral points and passes about halfway between the posterior margin and the axial tip; the adaxial part bears terraced lines, but the doublure outside the concentric ridge is smooth. Such a structure is absent in *Drepanura premesnili* (Monke, 1903, pl. 9) and has not been hitherto observed in trilobites.

*Comment on illustrated specimens:*

The fragmentary cranidium, Plate 16, fig. 2, CPC 5486, locality D29, in friable siliceous matrix, belongs to a specimen about 8 mm long and about 18 mm wide between the posterolateral tips. It shows the elevated palpebral lobe, the ocular ridge, the posterolateral limb, the posterior part of the glabella, and the occipital lobe. It is supplemented by the cranidium Plate 50, fig. 9, CPC 5757, from the same locality and bed, and in a similar matrix; this specimen is 6.0 mm long; the left palpebral lobe, the ocular ridge, the whole glabella, half of the occipital lobe, the right posterolateral limb with the bacculae, and the granular ornament are preserved in it. These two specimens together represent all parts of the cranidium.

The fragmentary cranidium Plate 50, fig. 11, CPC 5759, locality D29, in solid chert, is 6.6 mm long. It is not compressed, and retained its original convexity and ornament.

The fragmentary cranidium Plate 50, fig. 10, CPC 5758, locality D29, in granular silica is 7.6 mm long; the posterior tip of the palpebral lobe, the course of the posterior suture, and the ornament are preserved.

The hypostoma Plate 51, fig. 2, CPC 5762, locality D29, in friable matrix with chert, is 5·0 mm long. Its test is preserved, showing the transverse ornamental osculating lines; the doublure of the wing is exposed. Another hypostoma (Pl. 51, fig. 1, CPC 5761, D29) is 4·5 mm long; its flank is angulate.

The holotype pygidium, Plate 50, fig. 12, CPC 5760, in hard granular silica and chert, locality D28, has an axis 2·2 mm long. The distal parts of the spines are not exposed; the ornament is preserved.

The fragmentary pygidium (exposed from the ventral side) Plate 51, fig. 3, CPC 5763, locality D29, is 10·7 mm long. The test is silicified. A prominent concentric ridge, arising at the fulcrum, divides the doublure into an adaxial part with concentric terraced lines, and an abaxial, which merges with the doublure of the spines.

*Occurrence and age:* *P. italops* is a common species in the O'Hara Shale, at localities D6, D28, and D29 in the 'lower chert bed'; it occurs also in the Georgina Limestone at W20, and in the Mungerebar Limestone at G12, in the Mindyallan Zone of *Glyptagnostus stolidotus*; in the Mungerebar Limestone it is rare in beds of the Zone of *Cyclagnostus quasivespa* e.g. at locality G127.

#### Superfamily RAYMONDINACEA

#### Family RAYMONDINIDAE Clarke, 1924

#### Genus BRASSICICEPHALUS Lochman, 1940

#### BRASSICICEPHALUS sp.indet.

(Pl. 36, figs 7, 8)

*Material:* Two cranidia are illustrated, selected from a small number (about six) of less well preserved specimens.

The material is insufficient for a comparison with known species.

Generically, our specimens agree in all aspects (in dorsal, frontal, and lateral views) with the type of the genus—*B. pulchellus* Lochman (1940, pl. 3, figs 1, 4 and 5).

The cranidium Plate 36, Figure 7, CPC 5636, is 2·0 mm long, somewhat flattened and fractured; the cranidium CPC 5637, Figure 8, is 1·6 mm long; the glabella has preserved its convexity, but a part of the occipital lobe is missing, and it appears therefore depressed. The marginal frontal furrow is distinct only on the sides, the tips of the posterolateral limbs are advanced, and the posterolateral marginal furrow swings forward; the glabella is semicylindrical, the furrows are deep and the brim is convex. The palpebral lobes are placed in front of the glabellar midpoint—more forward than in *B. pulchellus*.

*Brassicicephalus* is an early Upper Cambrian genus in America as well as in Australia.

*Occurrence and age:* *Brassicicephalus* sp.indet. occurs in the O'Hara Shale ('lower chert bed') at locality D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Family CEDARIIDAE Raymond, 1937

Genus HENADOPARIA nov.

The type of *Henadoparia* is *H. integra* sp.nov.

The diagnostic characters of the genus are the same as of its type species.

Dr A. R. Palmer (U.S. Geological Survey) in a verbal communication indicated that *Henadoparia integra* resembles in several aspects *Cedaria woosteri* (Whitfield; see Shimer & Shrock, 1944-55), a little known early Upper Cambrian species of Minnesota. Subsequently I examined specimens of *C. woosteri* in the collections of the University of Minnesota (by courtesy of Prof. Preston Cloud) and conclude that this species is very close to *H. integra* indeed. In *woosteri*, however, the genal angles are rounded, whereas in *integra* they are acute.

From *Cedaria* and other cedariids *Henadoparia* differs by the fusion of the sutures and the rather weak and sporadic development of the 'cedariform' course of the vestiges of the posterior sutures.

*Familial classification:* The subordinal classification (Ptychopariina) of *Henadoparia* is evident and rests with the ptychoparioid design of its cephalon (a short and tapering glabella, well developed frontal area that consists of a brim and convex rim (border), and large posterolateral limbs). The position of the eyes, however, close to the glabella, prevents it from being included in the superfamily Ptychopariacea. An affiliation with the Cedariidae is, however, apparent via '*Cedaria*' *woosteri* (Whitfield). Superficially *Henadoparia* resembles some of the Middle Cambrian blind ptychoparioids like *Dasometopus* Resser (Westergaard, 1950) and *Meneviella* Stubblefield as regards the general plan of the cephalon and the prominence of the caecal veins. These genera are placed in the polyphyletic superfamily Conocoryphacea which comprises all blind (eyeless) ptychopariids. Some of these possess sutures which are near-marginal. *Henadoparia*, however, is sighted, its sutures are fused but not transformed into lateral sutures, and it is also much younger than the Conocoryphacea; it cannot be related, therefore, to a superfamily the species of which lost the eyes in the Lower and Middle Cambrian.

Externally similar but much younger than *Henadoparia* are *Loganopeltis* Rasetti, 1943, and *Loganopeltoides* Rasetti, 1945; the history of their sutures, however, is too peculiar (Rasetti, 1948) to be connected directly with *Henadoparia*.

HENADOPARIA INTEGRATA sp.nov.

(Pl. 37, figs 1-5; Text-fig. 134)

*Material:* The illustrated material consists of three cephalons with their counterparts and one cheek fragment selected from a large number of specimens; one pygidium is tentatively assigned to *H. integra*: the matrix is friable to hard silica.

*Holotype:* The cephalon Plate 37, figure 1, CPC 5642, locality D6, in hard silica, is selected as the holotype, being the least flattened specimen.

*Diagnosis:* The diagnostic characters of *H. integra* are as follows: (1) the cephalon is lunate with rearward-swept trigonal genal angles (spines); (2) the border is convex and distinct; (3) the lateral and posterior borders meet at the genal tip; (4) the sutures are fused; (5) the eyes (sighted) are close to the glabella and relatively

small; (6) the glabella is conical, with three pairs of glabellar furrows; (7) the cephalic doublure is continuous and a rostral shield is absent; (8) externally the doublure is indicated by a raised peripheral paradoublural line; (9) the cranial frontal area is elliptical and wide; (10) the posterolateral limbs are very large and apparently have weak cedariform tips; (11) the test is granulose, pitted and venulose; and (12) veins prevail on the free cheeks and granulation on the posterolateral limbs.

The Cedariidae mentioned by Öpik (1956, p. 22) refer in the first place to the occurrence of *Henadoparia integra*.

*Description:* Complete cephalata have been found; dismembered cephalata, isolated free cheeks, and cranidia are absent; irregularly broken cephalata are, however, common. The cephalic sutures are fused, but are indicated by 'lines'; the posterior

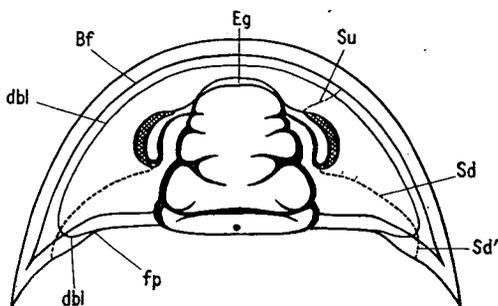


Fig. 134.—*Henadoparia integra* gen. nov., sp. nov., from Plate 37, figs 1 and 3. Bf—marginal furrow; dbl—paradoublural line; Eg—parafrontal band; fp—fulcrum; Su—line of fused anterior suture; Sd—line of fused posterior suture; Sd'—part of posterior suture open in some specimens. The more common shape of glabella is seen in Plate 37, fig. 3.

sutural lines are visible in several specimens, whereas the anterior lines may be absent, or only one of them may be discernible. In most of the specimens the sutural lines fade out before reaching the border; in a single fragment (Pl. 37, fig. 4) the posterior sutural line appears to reach the rear margin in a cedariform curve, and in one or two specimens this line reaches the margin in an even curve. Hence, in *Henadoparia integra* functional sutures are absent, the sutural lines are vestiges of once functional sutures, and the cranidium and the free cheeks are fused into a unit. The fusion of the sutures was no obstacle to moulting. The length of the cephalata has a range from 2.5 to 6 mm, indicating a sequence of instars of complete cephalata. The cephalic doublure bears no trace of sutures and a rostral shield is absent, as seen in several (not illustrated) fragmentary cephalata.

The cephalon is lunate, slightly wider than twice the length, with rearward swept acute genal angles (or broad and short triangular genal spines). It is moderately and evenly convex and sloping toward the border. The border is convex (thickened) and its margin rounded (not angular) and slightly upturned. The marginal furrow is broad and deep; it joins the posterolateral furrow at an acute angle and extends almost to the genal tip. Parallel to the margin, along the inside edge of the marginal furrow, an elevated, low, and rounded concentric ridge represents the paradoublural line; at the genal angle this line crosses the rear posterolateral furrow, turns adaxially, and intercepts the posterior margin at the fulcral point: so the paradoublural line indicates the position of the edge of the pleural doublure, which in all trilobites, and in all parts of any trilobite, terminates at the fulcrum. The vestiges of the anterior sutures diverge widely (at an obtuse angle), indicating a wide elliptical cranial frontal

area. The posterior sutural lines are also strongly divergent, delineating rather large posterolateral limbs reaching the base of the genal spines. The interocular cheeks are swollen and narrow, about 0.2–0.22 of glabellar width, and the palpebral furrows are distinct. The palpebral lobes are 0.25 of glabellar length and placed somewhat anterior to the glabellar midpoint. The eye is elevated, conical, slightly askew and retains its visual surface which is separated from the cheek by a low base. The ocular ridges are prominent, slanting and confluent with the palpebral lobes.

The rim and the brim are about equal in length and are together about 0.25 of glabellar length.

The occipital lobe is relatively short, evenly wide, and bears a small median node. The axial furrows are evenly defined around the glabella. The glabella tapers forward to about 0.5 of its width in the rear, and is obtusely rounded in front; in some specimens a parafrontal band may be present. Three pairs of glabellar furrows are present; the posterior furrows are forked and the glabellar lobes are tumid.

The glabella and the border are minutely granulose; the interocular cheeks are granulose and venulose; the brim is finely venulose and granulose; the free cheeks are irregularly pitted, conspicuously venulose, and the veins themselves are granulose; the posterolateral limbs are granulose and the granules are arranged in a venulose pattern. The different characters of the ornament of the free cheek and the posterolateral limb accentuate by their contrast the fused posterolateral sutural line.

The pygidium Plate 37, figure 5, CPC 5646, locality D29, is assigned tentatively to *Henadoparia integra* because (1) it cannot be assigned to another form of the fauna, (2) no other pygidia are available, and (3) it is comparable with pygidia of *Cedaria*. It is 2.8 mm long, subtriangular, with acute anterolateral corners; the border is wide and flat, the pleural lobes bear three pairs of flat ribs without interpleural grooves; the slender pygidial axis reaches the border and consists of five annulations and a rounded terminus.

*Comment on illustrated specimens:*

The holotype cephalon is 4.0 mm long, preserved in hard granular silica; the test is preserved, the specimen and its counterpart both are available. The posterior suture is indicated by a line separating the pitted venulose free cheek from the more pustulose posterolateral limb; the distal end of the line is almost open, but disappears before reaching the margin. The interocular cheek is venulose, the occipital node is preserved. The glabella is minutely granulose.

The fragmentary cephalon Plate 37, fig. 2, CPC 5643, locality D6, in hard silica (a small splinter of silica), is 5.0 mm long. The glabellar furrows are distinct; the vestigial anterior suture is barely visible, but is absent on the border; the posterior suture is indicated only by the different ornaments of the free cheek and the posterolateral limb.

The cephalon Plate 37, fig. 3, CPC 5644, locality D6, a tiny chip of hard silica, is 3.0 mm long; the glabella is partly corroded; the vestiges of the right anterior and of the posterior sutures are well visible; the ornament contrast between the free cheek (venulose, veins with pustules) and the posterolateral limb (pustules) is emphatic; the visual surface of the right eye is preserved.

The fragment (a left cephalic corner) Plate 37, fig. 4, CPC 5645, locality D29, in friable silica, is 4.2 mm long along the lateral border. It illustrates the fact that the cephalon of *Henadoparia* did not break along the vestigial sutures. The fulcral point and the trace of the doublure touching the margin at the fulcrum are well indicated. The line of the vestigial suture is barely discernible; it appears to reach the posterior margin in a cedariform curve (Text-fig. 134).

*Occurrence and age:* *Henadoparia integra* sp.nov. is a common fossil of the O'Hara Shale ('lower chert bed') at localities D6 and D29; it is rare in the Georgina Limestone, at localities W1 and W20. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

### Superfamily LIOSTRACINACEA

#### Family LIOSTRACINIDAE Raymond, 1937

The Liostracinidae are trilobites of the suborder Ptychopariina; but they cannot be placed in a known superfamily of that suborder and should be regarded, therefore, as suae superfamiliae. The characters of the superfamily are the same as of the family, whose type is *Liostracina* Monke, 1903.

Harrington et al. (1959, p. 0246) included the Liostracinidae in the superfamily Emmrichellacea Kobayashi, and Tchernysheva et al. (1960, p. 88) in the Utiacea Kobayashi. *Utia* itself, however, belongs to the Emmrichellacea according to Harrington et al.

Tchernysheva's classification will not be discussed further because the discussion of the Emmrichellacea that follows applies to both classifications. Emmrichellacea, -idae, and -inae, and the genus *Emmrichella* all refer to a single species, *Ptychoparia* (subgenus *Emmrichella*) *theano* Walcott (1905; 1913; vide 1913). It is distinguished by small posterolateral limbs and large palpebral lobes placed opposite the posterior part of the glabella. Only one specimen, the type, is known and it is rather fragmentary. Walcott and later Sun (1924) included in this subgenus some more species, in all of which the palpebral lobes are smaller than in *theano* and placed about the midpoint of the glabella; these are certainly Ptychopariacea and are in no need of a separate superfamily.

Hence, only *Emmrichella theano* represents the superfamily Emmrichellacea and *E. theano* itself for the purpose of its suprageneric classification should be re-studied materially in the first place.

All other genera of the 'Emmrichellacea' belong to divers superfamilies as follows: *Probowmania*, *Eurostina*, and *Protelmmites* are Ptychopariacea; *Teinistion*, *Dorypygella*, *Changshania*, and *Shangtungia* Damesellacea; *Lorenzella* Agraulidae(?); *Utia* Utiidae incertae superfamiliae, and *Inouyia* Ptychopariina incertae familiae. Finally, the Liostracinidae are regarded here as a family of the superfamily Liostracinacea of the Ptychopariina as revised herein.

The cranial design of the Liostracinidae is already apparent in the Siberian *Eleganolimba fibrata* Pokrovskaja (1959, p. 98, pl. 9, fig. 13). Its frontal area is long and wide, the anterior sutures are widely divergent, the palpebral lobes are in the rear, the interocular cheeks are very wide, and it possesses long and distinct bacculae. It differs from *Liostracina* but recalls *Doremataopsis* gen.nov. by the absence of a median preglabellar furrow, and by the magnificent development of forked caecal veins. It is found in the upper part of the Lenaic stage, considered high in the Lower Cambrian, but according to Öpik (1961, p. 99) possibly early Middle Cambrian. *Eleganolimba* should be considered the oldest known genus of the Liostracinidae.

The family Liostracinidae contains the following genera:

*Eleganolimba* Pokrovskaja, 1959 (suae subfamiliae)

Subfamily Liostracininae

*Liostracina* Monke, 1903

*Lynaspis* gen.nov.

Subfamily Doremataspidinae subf. nov.

*Doremataspis* gen.nov.

Subfamily LIOSTRACININAE Raymond, 1937

Genus LIOSTRACINA Monke, 1903

(Text-fig. 135)

The genus *Liostracina* is monotypical, with *L. krausei* Monke as the type (Text-fig. 135). The genus has been discussed also by Walcott (1913), Resser & Endo (1937), Raymond (1937), Endo (1944), and Kobayashi (1962).

The cranial characters of the genus are: (1) general ptychoparioid design in dorsal aspect; (2) the small steeply adaxially sloping palpebral lobes placed in the rear and far apart; (3) the long, slightly tapering, narrow, and prominent glabella; (4) the presence of the median preglabellar furrow; (5) the presence of prominent bacculae flanking the glabellar rear; and (6) the relatively short posterolateral limbs.

The ventral structure is distinctive: according to Monke (op.cit. pl. 3, fig. 12) a frontal submarginal doublure is present; furthermore, the doublure of the free cheek (ibid., fig. 14) is relatively long.

As regards other characters it should be noted that (1) the posterolateral limbs in *L. krausei* appear short in plan, because they are strongly geniculate downward (Monke, op.cit., pl. 9, fig. 2, underlined, in quadrangle 7c; this is the type specimen);

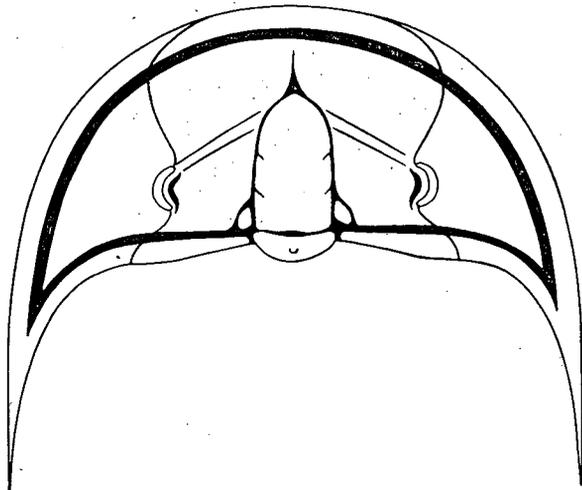


Fig. 135.—*Liostracina krausei* Monke, after Monke (1903, plate 3, figs 10 and 14).

(2) the anterior sutures are assumed by Monke and all subsequent commentators to be subparallel; the free cheek however (Monke, pl. 3, fig. 14) indicates that they are in reality divergent, as shown in Text-figure 135.

In the type of *L. krausei* (Monke, pl. 3, fig. 10, and pl. 9) the anterior cranial corners are unfortunately covered by the matrix, or broken, and the course of the sutures is, therefore, obscure.

The test of *Liostracina krausei* is minutely granulose.

In passing, *Liostracina* (?) *pauper* Resser & Endo, a Middle Cambrian species, lacks the bacculae and has a short brim, and is, therefore, generically distinct. The same applies to *L. (?) paupiformis* Endo (1944, p. 78, pl. 4, fig. 17).

The cranial characters of the species *Liostracina krausei* Monke (from Yen-tsy-yai) are (1) a relatively wide rim and a deep but rather narrow marginal furrow, (2) unadvanced falcate genal spines, (3) obscure ocular ridges, (4) a shallow preglabellar median furrow not reaching the frontal furrow, and (5) a more or less angular glabellar front. No Queensland species possesses these characters.

Walcott (1913, pl. 14, figs 2 and 2a) illustrated as *L. krausei* (from near Yen-chuang) two cranidia in which the median furrow reaches the marginal furrow; consequently their specific identity is not obvious and needs some further study. Resser & Endo (1937, pl. 61) illustrated specimens of *L. krausei* from two different localities: the cranidia in figure 11 (near Hsi-ai) conform with Walcott's, and in figure 12 (near Chin-chia-cheng-tzu) with Monke's material. A wide rim, long preglabellar median furrow, but subparallel anterior sutures are seen in a cranidium illustrated by Lu (1957, pl. 143, fig. 5).

In Australia, undescribed Liostracinidae occur also in the Mindyallan of the Northern Territory in the Alice Springs region. At Ross River, in an oolitic gastropod limestone, a species of *Liostracina* is common which in its cranial character is rather close to *L. krausei* Monke (s. str.), but is distinct by its blunt glabellar front.

The anatomy of the cephalon of *Liostracina* as seen in Australian material deserves a special comment: the median preglabellar furrow combined with the bacculae ('basal lobes') recalls agnostids; the forked, and not simply double, ocular ridges are known to me only in *Nepea* (see Öpik, 1963b), and the adaxial (unforked) part of the ridges is accentuated in the rear by a deep furrow each; furthermore, the doublure expands rearward rather rapidly; the lateral margin is vertical and angular, and the visual surface of the eye is retained by the exuvia of the free cheek.

#### LIOSTRACINA VOLENS sp.nov.

(Pl. 35, figs 1-5; Text-fig. 136)

*Material:* Three cranidia and two free cheeks are illustrated; the cranidia were selected from a large number of examined specimens. Free cheeks are rare and no pygidia are available. Unnumbered cranidia—Plate 59, figure 10 and Plate 50, figure 12.

*Holotype:* The cranidium Plate 35, figure 1, CPC 5621, is selected as the holotype because it is a mould showing the external characters.

*Diagnosis:* *Liostracina volens* is a species with a rather narrow rim, a wide and concave marginal furrow, a well defined median preglabellar furrow, prominent ocular ridges, prominent bacculae, rounded glabellar front, strong occipital node, and a smooth test; it is distinguished from other species by the combination of these characters.

*Description:* The cephalon is lunate, more than twice as wide as long, with rearward-swept broad genal spines. The convexity is moderate, the slope outward is gentle, and the eyes are placed on low summits of the cheeks.

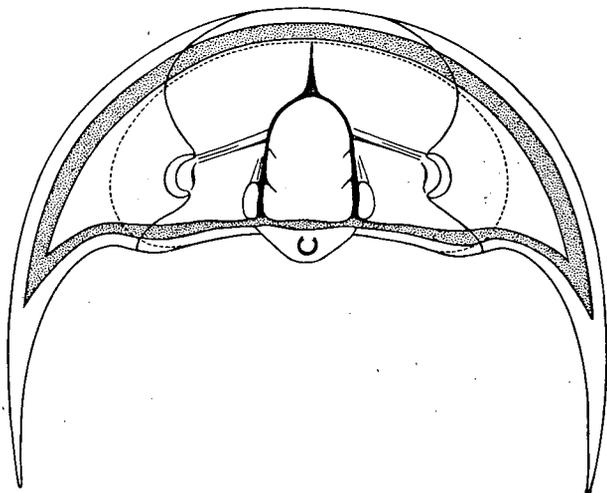


Fig. 136.—*Liostracina volens* sp.nov., from Plate 35, figs 1, 4, and 5.

The free cheeks are relatively large and have a vertical and angular margin. The genal spines have a very broad base and a slightly advanced angle and are intruded by the junction of the marginal furrows. The eyes have a low constricted base and are apparently holochroal.

The posterior sutures diverge in sinuous curves and cut the rear halfway between the glabella and the lateral margin. The anterior sutures diverge at the eyes and converge forward in even curves and intercept the margin about opposite the glabellar flanks; the sutures remain marginal in front and meet in the middle.

The posterolateral limbs are triangular and moderately geniculate; the fulcra are placed at about 0.6 of the occipital width from the axial furrows.

The frontal area, transversely elliptical, about 0.37 of cephalic length, and bilobate, slopes moderately and is slightly convex. The median preglabellar furrow, deep and wide at the glabella, narrows forward and peters out just before reaching the marginal furrow; this furrow is broad, concave, and well defined in the rear by the paradoublural line; the rim is narrow, convex, elevated, and rather steep in its rear. In flattened specimens the paradoublural line is obscure.

The small reniform palpebral lobes, slightly less than 0.3 of glabellar length, and placed behind the glabellar midpoint, are inclined steeply and defined by shallow palpebral furrows; the ocular ridges are prominent, indistinctly forked in the middle and defined posteriorly by a distinct furrow. The interocular cheek slopes toward the bacculae and is about 0.85 of glabellar width.

The bacculae are tumid, placed close to the glabellar base, elongate and long (about 0.3 of glabellar length), and continue forward as low ridges.

The occipital furrow is distinct but relatively shallow; the occipital lobe, triangular and arched transversely, bears a prominent node and is connected with the posterolateral margin—a structure not commonly seen in trilobites. The axial furrows are well defined and surround the glabella without interruption or change in depth.

The glabella is prominent, with steep flanks, slightly less than half the cephalic length, tapering, and possesses a rounded (not angular) front. Two pairs of oblique, short, shallow glabellar furrows are usually present, but difficult to see owing to the steepness of the glabellar flanks.

The test is smooth.

*Comment on illustrated specimens:*

All specimens are from the O'Hara Shale ('lower chert bed'), locality D29.

The holotype cranidium is 3.5 mm long, and preserved as the mould of the external surface. The matrix is hard siliceous shale. Well visible are the narrow rim, the wide marginal furrow defined in the rear by the paradoublural line, the pointed preglabellar median furrow, the double ocular ridges, uplifted palpebral lobes, and the occipital node.

The exfoliated cranidium in friable silica Plate 35, fig. 3, CPC 5623, is 2.4 mm long. The glabellar furrows are indicated.

The exfoliated cranidium in friable silica Plate 35, fig. 2, CPC 5622, is 2.7 mm long. The course of the anterior suture is well visible; the flattened specimen shows the shape of the posterolateral limbs.

The free cheek, Plate 35, fig. 4, CPC 5624, in friable silica, is 6.5 mm long from tip to tip. It is externally exfoliated, showing the widening of the doublure, the angular margin, and the strong terraced lines. In front the doublure extends beyond the midline, indicating that a rostral shield, as well as a median suture, is absent. The visual surface is retained by the cheek.

The free cheek Plate 35, fig. 5, CPC 5625, in friable silica, is 6.0 mm long. The test is preserved and exposed from the ventral side, showing the flat doublure with its terraced lines and angular margin.

*Occurrence and age:* *Liostracina volens* sp.nov. comes from the O'Hara Shale ('lower chert bed'), localities D6, D28, and D29, and is quite common. It has also been recorded in the Georgina Limestone, locality W1. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

LIOSTRACINA NOLENS sp.nov.

(Pl. 35, figs 6, 7)

*Material:* The material consists of two cranidia from the Georgina Limestone, locality W1.

*Holotype:* The better preserved cranidium Plate 35, figure 6, CPC 5626, is the holotype.

*Diagnosis:* *L. nolens* sp.nov. is a species with a narrow brim, and a wide and deep channel-like marginal frontal furrow; distinguished by an almost parallel-sided glabella with a bluntly rounded front, wide interocular cheeks (as wide as the glabella), and a granulose surface supplemented by well developed caecal veins on the brim.

*Differential diagnosis:* *L. nolens* shares with *L. volens* a similar frontal structure (narrow rim, wide marginal furrow) but differs in the shape of the glabella, the greater width of the interocular cheeks, and relatively coarse ornament (*L. volens* is smooth).

*Description:* The holotype cranium is 2.5 mm long. The bacculae are sub-circular and prominent, and their extensions, the ridges along the glabellar flanks, are relatively prominent. The ocular ridges are forked in the abaxial part. The caecal veins on the brim are wavy and the main veins arise from the frontal slope of the ocular ridges. The glabella is ornamented; the granulation on it is arranged in acutely curved lines with the convexity directed forward. On the rather steep glabellar flanks the posterior glabellar furrows are indicated as weak notches.

The cranium Plate 35, figure 7, CPC 5627, locality W1, is 2.4 mm long; it is somewhat deformed; the bacculae are more prominent than in the holotype.

*Occurrence and age:* *L. nolens* has been found only in the Georgina Limestone at localities W1, W20, and G50; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Genus LYNASPIS nov.

*Lynaspis* is monotypical, with *L. noakesi* sp.nov. as its type.

*Diagnosis:* *Lynaspis* is a genus of the Liostracinidae related to *Liostracina* and distinguished by its concavo-convex brim, distinct glabellar furrows, and the absence of a cranial rim.

*Differential diagnosis:* *Lynaspis* is similar to *Liostracina* in having a preglabellar median furrow, bacculae, and widely spaced eyes, but differs by the rimless structure of its frontal area and other characters which are pointed out in the description of the type species.

#### LYNASPIS NOAKESI sp.nov.

(Pl. 35, fig. 8; Text-fig. 137)

*Material:* The material consists of two cranidia in dark grey bituminous limestone from two localities (W1 and W20).

*Holotype:* The illustrated cranium, CPC-5628, locality W20, is the holotype.

*Diagnosis:* The generic diagnosis refers to the main characters of *L. noakesi*; furthermore, its glabella is short (as long as the frontal area) and the interocular cheeks are rather wide (about 1.1 of glabellar width), much shorter and wider than in any of the known species of *Liostracina*.

*Description:* The holotype cranium is 4.4 mm long, and fragmentary; but the part preserved allows for a restoration of the whole shield. The palpebral lobes are small, about 0.25 of glabellar length, the ocular ridges are rather prominent, double (forked), and defined in the rear in their adaxial part by a deep furrow each. The bacculae are large and prominent.

The frontal area is rather broad, transverse, elliptical, and consists of two sub-equal parts; the frontal part is concave and defined in its rear by a faint paradoublural line, and the posterior part is bilobed by the preglabellar furrow into two separate convex fields.

The glabella tapers slightly, has a bluntly rounded front and bears three pairs of glabellar furrows, of which the posterior ones are forked. The frontal area is faintly venulose, but the test is otherwise smooth.

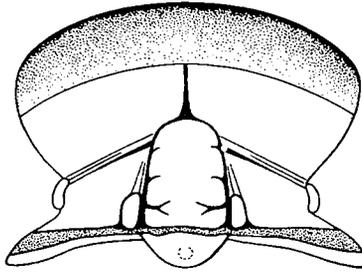


Fig. 137.—*Lynaspis noakesi* gen. nov., sp.nov., from Plate 35, fig. 8.

*Occurrence and age:* *Lynaspis noakesi* is a rare species of the Georgina Limestone, found at localities W1 and W20; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Subfamily DOREMATASPIDINAE nov.

*Diagnosis:* Doremataspidinae are Liostracinidae without the median preglabellar furrow, but with a very large (long and wide) rostral shield.

The existence of a rostral shield in the Liostracininae has not yet been established; if, however, it is present, it should be a small piece because of the near-midline extent of the doublure of the free cheeks, as seen in *Liostracina krausei* Monke and in *L. volens* sp.nov.

#### Genus DOREMATASPIS gen.nov.

The type of *Doremataspis* is *D. ornata* sp.nov.; it is a monotypical genus.

*Diagnosis:* *Doremataspis* is a genus of Liostracinidae distinguished by relatively large palpebral lobes placed opposite the posterior half of the glabella on conical summits of the cephalic pleural lobes; by a wide and thick rim, small posterolateral limbs, wide frontal doublure, and the absence of a preglabellar median furrow. Furthermore, its anterior sutures are widely divergent, and in the free cheeks a ridge separates the adaxial part of the doublure from the concave doublure of the border.

The diversified and vivid ornament combined with the absence of the preglabellar median furrow in *D. ornata* may distract attention from other characters that are relevant in its familial classification. These characters indicate the family Liostracinidae and are the bacculae, the rear position of the eyes, the falcate genal spines, the short glabella, the large elliptical frontal area, and the slanting ocular ridges. The large rostral shield is mentioned in the diagnosis of the subfamily.

A differential diagnosis is superfluous.

#### DOREMATASPIS ORNATA sp.nov.

(Pl. 16, assoc. with figs 1-3; Pl. 35, fig. 9; Pl. 36, figs 1-6; Pl. 45, fig. 1; Text-figs 138, 139)

*Material:* The illustrated material consists of two incomplete cephala, four cranidia, and one isolated free cheek. These are the best preserved specimens selected from a larger number of fragments, as well as specimens which could not be cleaned from the matrix. A pygidium is tentatively assigned to *D. ornata*.

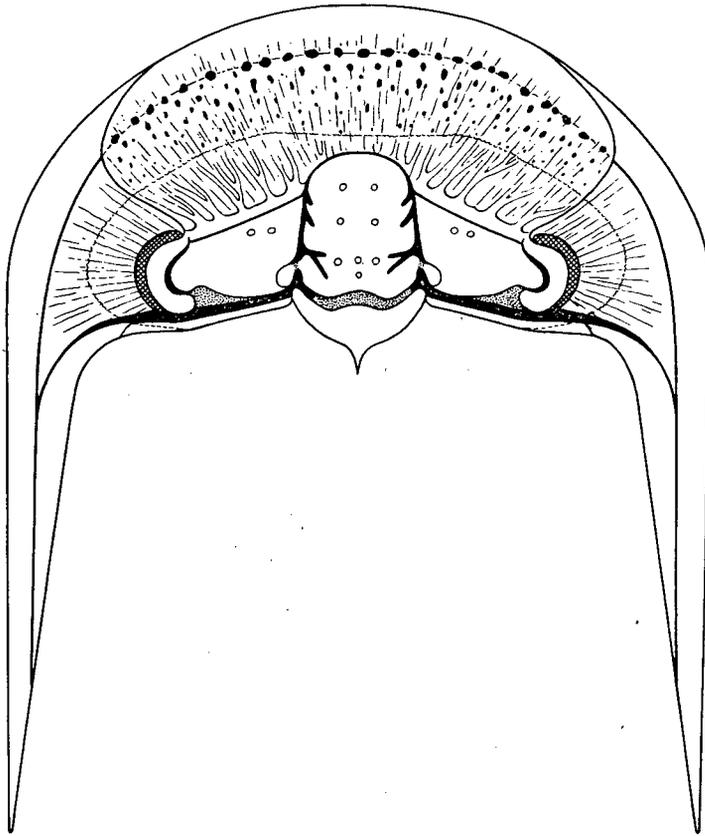


Fig. 138.—*Doremataspis ornata* gen.nov., sp.nov., from Plate 36, figs 2 and 4.

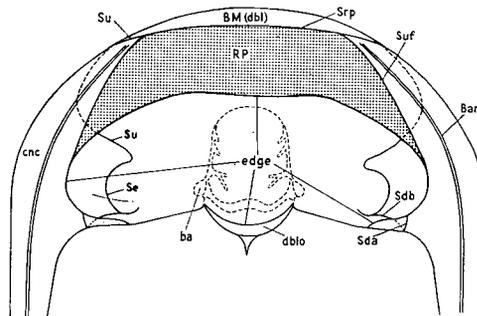


Fig. 139.—*Doremataspis ornata* sp.nov., ventral view of cephalon, from Plate 36, figs 2, 3 and 5. ba—baccula; Bar—ridge on doublure; BM(dbl)—frontalcranial doublure; cnc—concave part of doublure; dblo—occipital doublure; edge—edge of the doublure; RP—rostral shield; Sda—ventral part of posterior suture cutting doublure; Sdb—dorsal part of posterior suture; Se—palpebral suture; Su—anterior suture; Suf—connective suture (ventral); Srp—rostral suture.

*Holotype:* The cranidium Plate 36, figure 4, CPC 5633, is selected as the holotype. It is fragmentary, but durable (in chert), and shows the external characters. The cephalon Plate 36, figure 2 shows details of the ventral anatomy. No single specimen provides for a complete description of the cephalon.

*Diagnosis:* The essential diagnostic characters are given in the description of the genus; this is supplemented by the specific description, especially regarding the proportions of parts and the external ornament. No confusion is possible with the species of *Liostracina*, *Lynaspis*, or any other trilobite.

*Description:* The cephalon is semicircular to lunate, with long genal spines having a broad falcate base. The margins of the spines and the free cheeks are straight until, about the front level of the eyes, they make a subangular turn, and continue in even curves toward the cephalic front. At the subangular turning point the border is widest. The relief is strong, dominated by three summits: the rear of the glabella and the occipital lobe with its spine, and the two conical summits carrying the eyes, which are also placed in the rear. Longitudinally, the glabella is moderately arched and, together with the brim, it slopes forward.

The free cheeks are relatively steep, with a subhorizontal slightly convex border.

The posterior sutures diverge diametrically, cut the margin near the base of the spines, and delineate small blade-like posterolateral limbs. The fulcral points are placed, as in most trilobites, in line with the palpebral lobes less than halfway from the occipital lobe to the lateral margin. The posterolateral border is narrow and the posterolateral marginal furrows are narrow and deep.

The anterior sutures diverge greatly, about  $110^{\circ}$ – $120^{\circ}$ , in gentle curves before reaching the border; within the border they swing adaxially and intercept the margin about opposite the eyes, but the points of interception cannot be accurately established; here the sutures change to a ventral course and join in the middle as a rostral suture which separates the frontal doublure from the rostral shield.

The frontal area, consisting of a brim and a rim, is transverse elliptical (the widest part of the cranidium) and long, about 0.9 of the glabella. The rim is thickened, with a rounded margin, a slightly concave doublure, and relatively flat; a deepened marginal furrow is absent, but an angular change of slope between the steeper brim and the subhorizontal or even rearward sloping rim marks the position of the furrow. The brim is about twice the length of the rim. The paradoublural line is distinct, dividing the brim into an anterior part which is pitted and venulose, and a posterior which is only venulose. No trace of a median preglabellar furrow is present.

The interocular cheeks are as wide as the glabella and slope evenly toward the axis. Abaxially (between the cusps of the palpebral lobes) they are tumid but deeply depressed in the rear.

The palpebral lobes, about 0.5 of glabellar length, are larger than in other species of the *Liostracinidae*; they are shaped like human ears curved in the rear and pointed in front. Placed opposite the posterior half of the glabella with tips on the level of the occipital furrow, the palpebral lobes hang over the posterolateral limbs. The eyes, retained by the moults of the free cheeks, are slightly stalked in side view. The ocular ridges are prominent and slanting.

The occipital lobe is subtriangular and produced forward in the middle; it carries a curved almost erect marginal spine. The occipital furrow, shallow in the middle, is provided with deep oblique pits at the ends.

The axial furrows are V-shaped valleys between the pleural lobes and the glabellar flanks. The glabella is prominent, arched transversely, tapers moderately to a bluntly rounded front, and is short, about 0.46 (less than half) of the cephalon. Three pairs of short oblique lateral furrows are present, and the posterior furrows are forked in some specimens. The posterior glabellar lobes are flanked by the bacculae. These are small, rounded, close to the glabella, and connected with it by low swellings crossing the axial furrows.

The ornament consists of a dense and minute background granulosity. The rim is also pustulose, but this ornament is not quite the same in every specimen; scattered pustules occur on the brim; on the glabella low pustules, arranged metamericly and symmetrically (in pairs and/or in threes), are seen in better preserved specimens; symmetrically arranged pustules are also present on the interocular cheeks.

The free cheeks and the brim are delicately venulose. On the brim forking prominent veins arise in a manner seen in *Eleganolimba* Pokrovskaja. These veins reach the paradoublure line, which is marked by minute intercaecal pits; in front of the line the brim is densely venulose and pitted; the pits are arranged in radiating lines and increase in size toward the front; the pits are largest in the marginal furrow. The rear of the rim is also venulose.

The pygidium, Plate 36, figure 6, locality D29, CPC 5635, is 3.0 mm long. It is elongate semielliptical, and has a wide concave border and a broad doublure. Four pairs of pleurae bear deep and narrow pleural furrows and are separated by distinct interpleural grooves. The axial lobe is relatively short, with four annulations, and tapers evenly to the almost pointed terminus. The test is granulose, similar to the cephalic test of *D. ornata*.

*Ventral structure* (Text-fig. 139): *D. ornata* possesses a very wide cephalic doublure. The ventral side of the doublure beneath the border is concave and bears no terraced lines. On the free cheeks including the genal spines an angulate ridge (or bar) separates the adaxial part of the doublure from its peripheral part; only the adaxial part bears regular terraced lines. The ridge itself corresponds by its position to an external raised line; a furrow is absent. The doublure of the brim carries also regular terraced lines, the number of which is about six or seven. At the connective sutures the ends of the terraced lines of the brim swing rearward, and of the cheeks forward.

The connective sutures are far apart in the rear, starting at the level of the anterior tips of the eyes and halfway between the eyes and the lateral border. They are almost straight and converge forward, intercepting the rostral suture at points about opposite the anterior tips of the palpebral lobes. Hence, a rather long and wide rostral shield is cut out of the doublure by the sutures. This shield is crescentic, but truncate in the front.

*Comment on illustrated specimens:*

All specimens are from the O'Hara Shale ('lower chert bed'); one is from locality D6, another from D28, and the rest from D29 (not specially indicated below).

The holotype cranidium, an external mould in hard chert, is 3.0 mm long. The posterolateral limbs are missing and the casting latex missed the occipital spine; the palpebral lobe, the border with its doublure, and the ornament are well preserved; the pustules on the rim are low.

The cranidium Plate 36, fig. 1, CPC 5630, in hard silica, is 2.8 mm long. The occipital spine, the divergent anterior sutures, and the pustules and veins on the rim are distinct.

The cranidium Plate 35, fig. 9, CPC 5629, in friable silica, is 3.2 mm long. The damaged margin shows the frontal doublure; the paradoublural line is well developed.

The cranidium Plate 45, fig. 1, CPC 5715, locality D28, associated with the holotype of *Meringaspis meringaspis*, is 3.0 mm long. It is an external mould in chert.

The cephalon Plate 36, fig. 2, CPC 5631, in friable silica, is 3.2 mm long without the occipital spine. Most of the silicified dorsal test has crumbled away and the doublure, the rostral shield, and the connective sutures are exposed. This specimen is exceptionally informative on the ventral structure for a Cambrian trilobite.

The fragmentary cephalon (damaged by fire) Plate 36, fig. 3, CPC 5632, locality D6, belongs to a specimen about 3.5 mm long; the length of the fragment (glabella and occipital lobe) is 2.0 mm. The posterolateral limb is outlined; the border part of the doublure is concave (the convex side up) and separated by a ridge from its adaxial part. The ridge extends to the tip of the genal spine. The subangular turn of the margin on the level of the palpebral lobes is clearly expressed. The posterior part of the left connective suture is visible.

The fragmentary free cheek Plate 36, fig. 5, CPC 5634, in friable silica, is 6.0 mm long; the cornea is retained by the mould, and discernible. The doublure is exposed and shows the straight course of the connective suture.

*Occurrence and age:* *Doremataspis ornata* is common in the O'Hara Shale ('lower chert bed') at localities D29, D28, and D6. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

### Superfamily NORWOODIACEA

#### Family NORWOODIIDAE Walcott, 1916

#### Genus NORWOODELLA Resser, 1938

#### NORWOODELLA? DUBITALIS sp.nov.

(Pl. 39, fig. 6)

*Material:* The material consists of four small cranidia on a single piece of limestone with chert; all specimens are partly immersed in silica, and more or less fragmentary.

*Holotype:* The illustrated cranidium, CPC 5665, 1.4 mm long, is the holotype.

*Diagnosis:* *Norwoodella? dubitalis* is a species of the Norwoodiidae with a densely granulated test, inflated large fixed cheeks, a convex and downsloping brim, and a narrow almost vestigial rim; distinguished by its rather conical glabella, three pairs of strong pit-like glabellar furrows, and small forward-placed palpebral lobes which are far apart from the glabella.

*Generic classification and differential diagnosis:* The familial classification (Norwoodiidae) of *dubitalis* is borne out by its proparian structure and the similarity with *Norwoodella saffardi* (Walcott, 1916, pl. 27, fig. 1d) and *N. simplex* (Walcott; op.cit. pl. 27, figs 3, 3a). *N. dubitalis*, however, is distinguished (1) by wider interocular cheeks, (2) by the strongly tapering glabella, and (3) rather deep glabellar furrows. Any of these characters alone would be specific, and the combination

may indicate a separate subgenus, or even a separate genus of the Norwoodiidae. Since *Norwoodella* is well known from complete specimens, equally complete material of *dubitalis* is needed to decide unequivocally its generic classification.

*Description:* The main characters are already given in the diagnosis and the differential diagnosis. In the illustration the rim is not evident because of the strong convexity of the frontal area. On the left, the posterior end of the palpebral lobe is preserved. The anterior sutures are slightly convergent. The axial furrows are deep and broad and the glabella appears sunk between the inflated cephalic pleural lobes.

*Occurrence and age:* *Norwoodella? dubitalis* has been found only in the Mungerebar Limestone at locality G429; its age is the Mindyallan Zone of *Erediaspis eretes*.

#### Superfamily NEPEACEA Whitehouse, 1939 (Lochman-Balk, 1959)

The superfamily Nepeacea is regarded here as consisting of two families, the Nepeidae Whitehouse, 1939, and the Menomoniidae Walcott, 1916. As indicated in the discussion of the Menomoniidae the genus *Bolaspidella* Resser should be transferred to the Nepeidae.

#### Family NEPEIDAE Whitehouse, 1939

The concept of the Nepeidae, including its type, *Nepea narinosa* Whitehouse, has been discussed recently by Öpik (1963); the morphogenesis of Middle Cambrian nepeids (to be published later) indicates that in immaturity the nepeids resemble the mature menomoniid *Biaverta reineri* sp.nov. Furthermore, the menomoniid affiliation of the Nepeidae is suggested by the cephalic structure (large downsloping to vertical posterolateral limbs, deep glabellar furrows, forward-placed eyes, and forward-projecting cephalic pleural lobes) and the multisegmented thorax.

#### Genus FERENEPEA nov.

The type of the genus is *Ferenepea hispida* sp.nov.

*Diagnosis:* Nepeidae with a small boss and small eyes and with the glabella projected forward beyond the ocular ridges (as in *Ascionepea* gen.nov.) but distinguished by a convex, narrow, prominent rim with a vertical frontal slope.

*Differential diagnosis:* The cranial rim is similar to *Nepea* (see Öpik, 1963), but in *Nepea* the boss is very large (0.8 of glabellar length or over), the palpebral lobes are long (0.6 of glabellar length), and the ocular ridges arise at the anterolateral corners of the glabella, which is not projected forward.

#### FERENEPEA HISPIDA sp.nov.

(Pl. 39, figs 7, 8; Pl. 40, fig. 1; Text-fig. 140)

*Material:* Two cranidia and one free cheek unit are illustrated; the cranidia are selected from a large number of specimens; the preservation of the free cheeks as an unbroken unit is exceptional.

*Holotype:* The cranium Plate 39, figures 7a, b, CPC 5666, is selected as the holotype because its internal cast and the external mould are preserved.

*Diagnosis:* Essential diagnostic characters of *F. hispida* are included in the generic diagnosis. Furthermore, the obscurity of the bacculae (which are much stronger in other species of nepeids), the coarse ornament, the pustulose margin of the occipital lobe, and the large distance of the eyes from the glabella are diagnostic of the species.

*Description:* The cephalon is longer than half its width in plan, strongly vaulted, voluminous; its flanks are vertical and the flanks of the genal spines are also almost vertical. All furrows and lobes are well accentuated and deep. The anterior sutures are slightly convex, subparallel, and marginal in front; the sutures are continuous along the margin, and neither a rostral shield nor a median suture is present; this condition is common to all nepeids. The posterior sutures, running down and rearward, turn upward opposite the ends of the posterolateral furrows in a cedariform course and cut the margin at an acute angle.

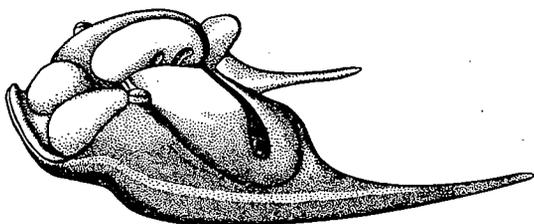


Fig. 140.—*Ferenepia hispida* gen.nov., sp.nov., reconstruction of cephalon, from Plate 39, fig 7, and Plate 40, fig. 1. The pustulose ornament is omitted.

The free cheeks are united in front and remain so in exuvia. The continuous cephalic border has a step-like marginal furrow and long falcate genal spines.

The anterolateral margins are arched upward and the frontal cephalic margin is also arched upward, but to a lesser degree; consequently, the cephalic margin possesses three arcs, as seen also, for example, in some dalmanitids.

The posterolateral limbs are very large, with ends geniculated steeply downward; the posterolateral furrows are incised deeply, expand abaxially, and end well before reaching the suture. The posterolateral border is narrow, elevated, and passes into the base of the falcate spine; intergenal spines, which are very long in *Nepea narinosa* Whitehouse, are totally absent in *Ferenepia hispida*.

The palpebral lobes, 0.2 of glabellar length, and therefore tiny, are placed rather forward, just behind the anterior 0.2 of the glabella. The palpebral furrows are faint but distinct and curve outward in the rear.

The interocular cheeks are very wide, about 1.4 of glabellar width. The ocular ridges are transverse (not slanting) and double, being forked in the proximity of the glabella.

In front of the ocular ridges the pleural cephalic lobes are tumid, sloping adaxially and toward the border. The frontal marginal furrow is narrow and deep; the rim is narrow, cord-like, prominent, arched upward and slightly forward.

The occipital lobe, about 0.25–0.3 of glabellar length, slopes forward and attenuates laterally; the tenuous ends of the occipital lobe merge with the pleuro-occipital border. The occipital furrow is well incised, arched forward, and bears pits at its

ends similar to the glabellar furrows. The axial furrows are V-shaped valleys between the glabella and the pleural lobes; they pass without interruption into the furrows which flank the boss; the circumglabellar furrow is also defined. The circular boss, about 0.4–0.43 of the glabellar length, occupies the space between the glabellar front and the rim.

The glabella is relatively short, about half the cephalic length, tapers moderately, is bluntly rounded in front, slightly longer than wide, is well arched transversely, and has rather steep flanks. Three pairs of short, oblique, pit-like glabellar furrows are present and the lobes between them are well defined. Indistinct bacculae, visible only in casts, flank the posterior lobes of the glabella.

The surface is densely and coarsely pustulose on a background of a minute granulation. The pustules on the margin of the occipital lobe are rather conspicuous, but no pustules are present on the posterior half of the boss.

*Comment on illustrated specimens:*

All specimens come from the O'Hara Shale ('lower chert bed') and are embedded in friable silica.

The holotype cranium is 3.0 mm long, and undistorted. Externally (Pl. 39, fig. 7b) the pustules are dominant, but the background granulation is readily discernible; the rim, the posterolateral margins, and especially the occipital lobe are prominently pustulose, but half the boss is bare; the ocular ridges are partly masked by the pustules. The right palpebral lobe is intact. On the internal cast (Fig. 7a) the pustules are thinner, indicating a relatively thick test, the ocular ridges are clearer (and double) and the weak bacculae are indicated.

The cranium Plate 39, fig. 8, CPC 5667, an internal cast, is 3.0 mm long. Its frontal part is deformed and the glabella appears slightly broader than in the holotype.

The free cheek unit Plate 40, fig. 1, CPC 5668, corresponds to a cranium 3.0 mm long. The arcs of the margin, the marginal course of the frontal part of the suture, and the cedariform posterior suture are graphic.

*Occurrence and age:* *Ferenepea hispida* sp.nov. occurs in all three zones of the Mindyallan stage: in the Mungerebar Limestone, at locality G119, in the Zone of *Erediaspis eretes*, and at localities G10, G127 and G150, in the Zone of *Cyclagnostus quasivespa*; in the Georgina Limestone at localities W1 and W301, and in the O'Hara Shale ('lower chert bed') at D6, D28 and D29, in the Zone of *Glyptagnostus stolidotus*. It is most abundant in the O'Hara Shale.

FERENEPEA PILARIS sp.nov.

(Pl. 40, fig. 2)

*Material:* About ten cranidia are present in the collections, from which the best preserved, CPC 5669, locality G8, is selected as the holotype, and illustrated.

*Diagnosis:* *F. pilaris* is distinguished by its relatively large palpebral lobes, overall pustulose boss, interocular cheeks about 1.1 of glabellar width, and the trapezoidal outline of the cranium.

*Differential diagnosis:* *F. pilaris* is close to the type species *F. hispida*, from which it differs in all the characters mentioned in the diagnosis; further comparison is included in the description of *pilaris*.

*Description:* The holotype cranium is 3.2 mm long. It is trapezoidal in outline, with the posterolateral limbs curving evenly down from the palpebral lobes. The interocular cheeks are about 1.1 of glabellar width (1.4 in *F. hispida*); the palpebral lobes are 0.4 of glabellar length (0.2 in *hispida*), and placed opposite the rear of the anterior half of the glabella. The bacculae are distinct, and ocular ridges obscure. The test is pustulose, including the rear of the boss (in *hispida* the posterior part of the boss is bare).

*Occurrence and age:* *Ferenepea pilaris* sp.nov. is a rare fossil of the Mungerebar Limestone and is found at localities G8; G417 and G119. Its age is the Mindyallan Zone of *Erediaspis eretes*.

#### Genus ASCIONEPEA nov.

The type of the genus is *Ascionepea janitrix* sp.nov.

*Diagnosis:* Nepeidae with a small boss and small eyes and with the glabella projected forward beyond the ocular ridges, as in *Ferenepea* gen.nov., but distinguished by a flat and downsloping vestigial or even obsolete cranial rim.

*Differential diagnosis:* *Ascionepea* differs from *Nepea* Whitehouse in having the palpebral lobes and the boss much smaller; in *Nepea* the cranial rim is convex, narrow, and vertical in front. A *Nepea*-like border is also present in *Ferenepea* gen.nov.

#### ASCIONEPEA JANITRIX sp.nov.

(Pl. 40, fig. 3)

*Material:* The illustrated material consists of one cranium; in the same rock specimen two more adult and several immature cranidia are present.

*Holotype:* The illustrated cranium, CPC 5670, is the holotype.

*Diagnosis:* The essential diagnostic characters of *A. janitrix* are included in the diagnosis of the genus; supplements are given in the description.

*Differential diagnosis:* The differential diagnosis is given in the descriptions of the genus *Ascionepea* and of *A. anitys* sp.nov.

*Description:* The holotype cranium is 2.4 mm long and preserved as a mould in chert. It is moderately vaulted, except for the large tumid and steeply downsloping posterolateral limbs. The anterior sutures are parallel, then turn abruptly, remain marginal, and meet in front. The palpebral lobes are oblique, semicircular, about 0.2 of glabellar length and defined by shallow palpebral furrows. The interocular cheeks are as wide as 1.25 of glabellar width.

The anterior border is flat and downsloping; an elevated rim is absent, and the marginal furrow is indicated only by a slight change of slope between the tumid frontal area and the flat border. The ocular ridges are transverse, double, and their prominence decreases abaxially. The glabella tapers to an evenly rounded front which bears a weak median indentation. The boss is elongate, longer than wide, and pustulose all over. Three pairs of oblique, short, pit-like glabellar furrows are present and the posterior lobes are flanked by large, circular, but low bacculae.

The ornament consists of scattered low pustules on a background of minute granulation. The occipital lobe bears a short vertical submarginal spine, which is not preserved in the holotype.

*Morphogenesis:* It appears that the boss becomes discernible in cranidia over 0.6 mm long.

*Occurrence and age:* *Ascionepea janitrix* was found in a chert biscuit at locality G103 from the topmost and locally silty bed of the Steamboat Sandstone; the age is the Zone of Middle Cambrian–Upper Cambrian passage.

ASCIONEPEA ANITYS sp.nov.  
(Pl. 40, figs 4–6; Pl. 46, fig. 4)

*Material:* The illustrated material consists of three cranidia selected from a larger number of mostly fragmentary specimens.

*Holotype:* The largest cranidium Plate 40, figure 6, CPC 5673, locality G429, is selected as the holotype.

*Diagnosis (and differential diagnosis:)* *Ascionepea anitys* sp.nov. is distinguished by the absence of a marginal cranidial furrow, by its minute palpebral lobes (less than 0.2 of glabellar length), and by the interocular cheeks of about 1.5 of glabellar width. *A. janitrix* has a vestigial marginal furrow, palpebral lobes 0.2 of glabellar length, and narrower interocular cheeks (1.25 of glabella).

*Description:* The holotype cranidium is 2.4 mm long, and silicified in limestone. The frontal margin is arched forward, the brim is convex, sloped moderately, and bears a distinct circular boss. The pustulose ornament is worn off and indicated by tiny holes.

The cranidium Plate 40, figure 4, CPC 5671, locality G119, is 2.2 mm long and silicified in chert. The boss is less distinct than in the holotype, and the ocular ridges are double, forking in the proximity of the glabella. The diminutive left palpebral lobe is preserved.

The cranidium Plate 40, figure 5, CPC 5672, locality G8, silicified in chert, is 1.5 mm long; it is apparently immature and its boss is therefore not yet fully developed. The right palpebral lobe is preserved.

The convexity of the cranidium is apparent in Plate 46, figure 4.

The test in the described specimens is preserved, but slightly worn—the palpebral ridges are not obliterated. Consequently the minute holes in the test indicate the character of the dense ornament: it consisted of relatively fine pustules.

*Occurrence and age:* *A. anitys* occurs in the Mungerebar Limestone in many localities (G8, G9, G114, G119, G427, G429); its age is the Mindyallan Zone of *Erediaspis eretes*.

ASCIONEPEA sp. aff. ANITYS  
(Pl. 40 fig. 7)

A fragmentary cranidium, 3.0 mm long, CPC 5674, silicified in chert, is illustrated. It is distinguished by its relatively coarse pustulose ornament and rather strong furrows flanking the boss. It represents, apparently, a separate species, but is too fragmentary for a proper description.

*Occurrence and age:* The illustrated specimen comes from the Mungerebar Limestone, locality G119; the species occurs also at G114 and G150; its age is the Mindyallan Zone of *Erediaspis eretes*.

#### Family MENOMONIIDAE Walcott, 1916

The Menomoniidae are represented in Australia by the Mindyallan *Biaverta* gen.nov.

The genera *Menomonion* Walcott, *Dresbachia* Walcott, and *Densonella* Shaw, 1952 (= *Millardia* Walcott, 1916) constitute the core of the Menomoniidae; *Paramenomonion* Chu, 1959, included by its author in the Menomoniidae, is regarded by Kobayashi (1960) as a genus of the Damesellidae (subfamily Paramenomonioninae); the classification of *Paramenomonion* remains, however, inconclusive.

Three more genera are included in the Menomoniidae by Harrington et al. (1959): *Coenaspis* Resser, *Deiracephalus* Resser, and *Bolaspidella* Resser. It appears that *Coenaspis* (Resser, 1938, pl. 16, fig. 9) has very little similarity with any of the menomoniids and should be regarded as a ptychoparioid of an uncertain superfamilial position; *Deiracephalus* (see Shaw, 1952) should be regarded as *suae familiae*, and *Bolaspidella* accommodated in the Nepeidae. *Bolaspidella lucieae* Poulsen (1960), for example, possesses the main characters of a nepeid (a cedariform suture, very large posterolateral limbs, forward-placed palpebral lobes, coarse granules and pustules); it is distinguished by the absence of the bacculae, and the preglabellar boss. Bacculae, however, are well developed in *Bolaspidella? tuberculata* Rasetti (1963).

The menomoniid characters of *Biaverta* are discussed under that genus.

#### Genus BIAVERTA nov.

The type of the genus is *Biaverta biaverta* sp.nov.

*Diagnosis:* *Biaverta* is a genus of the Menomoniidae without eyes and without palpebral lobes, but with ocular ridges indicating the original position of the eyes opposite the glabellar front; the free cheeks have long genal spines, the glabellar flanks are concave, and depressed alae are present. In the type species the cranial rim in maturity develops into an elevated retroverted crescent; in immature specimens, however, and in the earlier *B. reineri* sp.nov. the rim is depressed and low.

The ventral structure of the cephalon implies the presence of a median suture disuniting the free cheeks.

The menomoniid characters of *Biaverta* are: the large, inflated pleural lobes of the cephalon, deep furrows and forward-extended axial furrows, the depressed brim, and the forward position of the eyes.

The nearest menomoniid genus is *Densonella* Shaw, 1952 (*Millardia* Walcott), distinct by its large stalked eyes and the absence of genal spines. Disregarding the eyes, *Densonella* and *Biaverta* have a similar appearance, especially in frontal view, as seen from *Millardia optata* (Hall) (Walcott, 1916, pl. 28, fig. 4b) and *M. avitas* Walcott (Lochman, 1940, pl. 4, fig. 39). *Knechtelia* Lochman 1950 is a menomoniid whose frontal area has a structure similar to *Biaverta*.

The genus *Menomonina* and the concept of the family Menomoniidae are based on *Conocephalites calymenoides* Whitfield, 1878. The species name *calymenoides* hints at a possible affiliation of the early Upper Cambrian menomoniids and the post-Cambrian calymenids. The reality of such an affiliation is, however, doubtful, although they share some characters in a combination not seen in other trilobites. In *Biaverta* the 'calymenoid' appearance results from the constricted glabellar lobes, the expansion of the glabellar rear, the concave brim and elevated rim, and the presence of alae (*Pharostoma* spots, accepting that *Pharostoma* itself is a calymenid). The blindness of *Biaverta* and the rather forward-placed eyes in other menomoniids indicate, however, an organization which has departed from the more primitive ptychoparioids; the calymenids, however, have retained the 'premenomoniid', ptychoparioid design. Hence, it is fair to assume that the Menomoniidae and the Calymenidae are affiliated on a subordinal or ordinal rank, but are otherwise not connected phylogenetically; the analogy in habit is, therefore, the result of an independent repetition and not of a direct inheritance of menomoniid characters in the Ptychopariida *Calymene* and *Pharostoma*. Harrington et al. (1959) included the calymenids in the order Phacopida—a somewhat perplexing classification.

*Phylogeny (within the genus)*: The temporal sequence of the species of *Biaverta*, and their close morphological similarity, suggests that the earlier *B. reineri* is parental of the subsequent *B. biaverta*. This is supported by the fact that in immaturity *B. biaverta* lacks the retroverted rim of the adults and resembles mature specimens of *B. reineri*.

BIAVERTA BIAVERTA sp.nov.

(Pl. 37, fig. 6; Pl. 38, figs 1-9; Text-fig. 141)

*Material*: The described material comprises eleven cranidia and two free cheeks, of which one free cheek is not illustrated. The morphological uniformity of a large number of examined cranidia from the 'lower chert bed' of the O'Hara Shale indicates a homogeneous population.

*Holotype*: The cranidium Plate 37, figure 6, CPC 5647, a mould of the external surface, is selected as the holotype because the ornament in it is perfectly preserved.

*Diagnosis*: *Biaverta biaverta* is a species distinguished by its elevated and retroverted crescentic cranidial rim and by its rather diversified cranidial ornament of pustules and pits, and smooth free cheeks.

*Differential diagnosis*: *B. biaverta* differs from the second described species of the genus (*B. reineri*) by the characters indicated in the diagnosis.

*Description*: The reconstruction of the cephalon (Text-fig. 141) is pieced together on the basis of several cranidia, and the free cheek Plate 38, figure 5. The cephalon is rather voluminous because of the abrupt downward geniculation of its flanks, involving the free cheeks and the abaxial part of the cranidium, which are vertical and therefore not well visible in plan. The line of this geniculation gains in accent toward the rear, as seen for example in Plate 38, figure 6, and reaches the posterolateral furrow at a distance of about the width of the occipital lobe. No fulcral points, however, could be detected; hence it is probable that *Biaverta biaverta* is a trilobite without pleural fulcra.

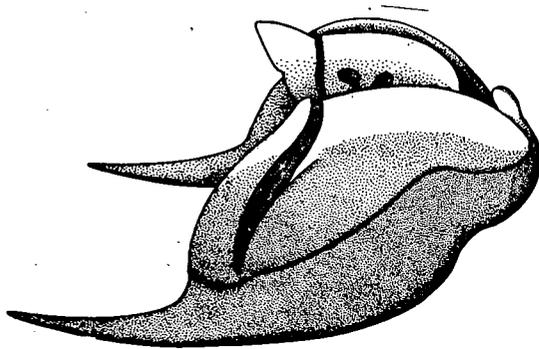


Fig. 141.—*Biaverta biaverta* gen.nov.,  
sp.nov., from Plate 37, fig. 6, and  
Plate 38, figs 2 and 5.

Eyes and palpebral lobes are absent except for the unique cranidium Plate 38, figure 1, which has preserved the rudiment of its right palpebral lobe; it is placed in advance of the glabellar front—a character of the Menomoniidae.

In spite of the absence of palpebral lobes posterior and anterior sections of the sutures can be distinguished; the division is indicated by the adaxially convex notch which indicates approximately the original position of the lost palpebral lobes. The posterior sutures are relatively straight and cut the rear in a gentle curve; they delineate very large hanging posterolateral limbs with a prominent retral swing. The anterior sutures (Pl. 38, fig. 3) converge moderately, curve abruptly at the anterolateral corners, and meet in the upward arched front, separating from it the foremost parts of the free cheeks, which are divided by a median furrow. The free cheek is equipped with a retral undeflected and slightly curved spine which accentuates the opisthoparian character of the trilobite; the free cheek has neither a border nor a marginal furrow, and its flank is slightly convex outward. Its margin is keen and arched upward anterolaterally. In the absence of fulcra the margin of the posterolateral limb swings in a sigmoidal curve rearward and downward to the base of the genal spine. The posterolateral furrows are very deep; they are widest in their middle and stop abruptly before reaching the suture. The posterolateral borders are elevated, narrow, rounded to subangular, but become flat and expanded abaxially.

The pleural lobes (cheeks) of the cranidium bypass the glabella and reach the frontal margin at the flanks of the rim; ocular ridges are relatively well expressed; they are straight, transverse, and arise at the anterolateral corners of the glabella, but in some specimens are arched forward as well. The length of the frontal area is variable between 0.32 and 0.4 of glabellar length. It consists of a deeply depressed brim with an almost flat floor, and an elevated rearward-arched and inclined thick lip-like lunate rim provided with a frontal recess. In older specimens this lip is large and retroverted, concealing much of the brim; but in younger cranidia it is smaller and the brim is partly visible in plan.

The occipital lobe, 0.3 of glabellar length, is elevated in the rear and narrows abaxially, where it almost merges with the posterolateral border. A small occipital node may occur in some specimens. The rather deep and narrow occipital furrow bears at its ends a pair of elongate and deep pits. The axial furrows are deep channels with vertical flanks and flat floors; in the rear, opposite the posterior glabellar lobe,

the furrows are wide and carry the alae; these are lunate, depressed, and each is surrounded abaxially by a very narrow but deep furrow, separating it from the pleural lobes. In front, the apparent extensions of the axial furrows diverge in gentle curves and reach the margin; of course, there are no true axial furrows beyond the glabella, which is defined by a circumglabellar furrow, vestigial in adult specimens, but well expressed in immature specimens.

The glabellar flanks converge forward in the posterior part, but become parallel after about two thirds of the glabellar length, or a little less; the glabella is moderately long, being 0.6 of the cephalic length; the glabellar front is transverse, almost truncate, and bilobed by a median notch. The anterior flanks are rather steep, as is the front; the glabella is arched gently longitudinally and strongly transversely, rising above the level of the cheeks.

Two pairs of glabellar furrows are developed as deep pits; the anterior furrows are lateral notches, but the posterior are larger and widen adaxially into circular pits. Two posterior pairs of glabellar lobes are present; the posterior lobes are round knobs isolated by a shallow depression connecting the glabellar furrow with the occipital furrow.

The ornament of *B. biaverta* is rather diversified in distribution and in character: the rim is densely granulose; the glabella is pustulose (scattered pustules) on the background of a low granulosity; the occipital lobe and the posterolateral border are pustulose; the adaxial parts of the pleural lobes are pustulose and pitted and the pits have convex rims producing a vermiculate pattern; outside the geniculation lines the pits are absent and a minute granulosity is apparent, which disappears rapidly before reaching the sutures; and the free cheeks are smooth. Terraced lines are absent, even on the doublure.

Little is known regarding the ventral structure of the cephalon. The lateral doublure is quite wide; at the front the doublure is relatively narrow with a median rounded, forward-directed recess, whose function is obscure: it could be the frame of a small rostral shield.

*Morphogenesis:* Cranidia of *Biaverta biaverta* ranging in length between 0.75 and 0.6 mm have been examined; it is apparent that the smallest of them represent the early meraspis, and the larger the holaspis stage. It appears that the main morphogenetic events are (1) the initiation and gradual development of the rim, (2) the relative decrease (arrested growth) in length of the brim, and (3) the development of the alae. The palpebral lobes are absent even in the smallest specimens.

*Comment on illustrated specimens:*

All specimens (except for the last) are collected at locality D29, O'Hara Shale ('lower chert bed').

The holotype cranidium Plate 37, fig. 6, CPC 5647, is 3.0 mm long and belongs to an adult. It is an external mould in friable silica. Note the diversity of the ornament, the depressed alae, the notch in the glabellar front, and the geniculation of the cheek.

The free cheek Plate 38, fig. 5, CPC 5652, in friable silica, is about 6.0 mm long. Its frontal part (in shadow) is complete.

The fragmentary cranidium Plate 38, fig. 1, CPC 5648, is 3.5 mm long; it is an external mould in solid (translucent) chert. The ornament is well preserved. It is an abnormal cranidium: the right ocular ridge swings forward and terminates at the palpebral lobe; consequently this specimen is unique in having preserved one eye, or its rudiment.

The cranidium Plate 38, fig. 3, CPC 5650, is 2.0 mm long; it is an external mould in chert; in it the anterolateral corner is intact, showing the relatively abrupt curve of the suture passing into the frontal margin. The brim is wide, and not concealed by the rim—a condition seen in young specimens.

The cranidium Plate 38, fig. 4, CPC 5651, is 2.4 mm long; it is an internal cast in friable silica. Only the left ala is distinct; note the ocular ridges and the glabellar furrows.

The cranidium Plate 38, fig. 2, CPC 5649, is 2.0 mm long, in a tiny splinter of friable silica. Note the steep front of the glabella with the vertical notch.

The fragment Plate 38, fig. 9, CPC 5659, is about 2.4 mm long (glabella and occipital lobe together); the matrix is part friable, and part hard chert. It shows the relatively straight suture and the shape of the occipital lobe; the distal end of the posterolateral furrow peters out before reaching the suture.

A cluster of small cranidia of *Biaverta biaverta* and agnostids, Plate 38, fig. 8, CPC 5658, 5657, 5655, in friable silica. The smallest cranidium of *biaverta* is 1.3 mm long; it shows the rather small, juvenile, undeveloped rim.

The small cranidium Plate 38, fig. 7, CPC 5654, is only 0.8 mm long; the matrix is friable silica. The glabella, glabellar furrows, geniculation of the cheeks, and straight suture are almost the same as in larger specimens; but the rim is not prominent in this early meraspid stage.

The fragmentary cranidium Plate 38, fig. 6, CPC 5653, Georgina Limestone (sandy grey limestone), locality W21, is about 5.5 mm long. The geniculation of the cheek is angular and abrupt; the ornament is worn (in part during preparation).

A free cheek (not illustrated) CPC 6741, in hard chert, locality D6, shows its anterior part, including the frontal doublure on which the presence of a median ventral suture is evident.

*Occurrence and age:* Cranidia of *Biaverta biaverta* sp.nov. are quite common in the O'Hara Shale ('lower chert bed') at localities D6, D28, and especially D29. It occurs also, but is rare, in the Georgina Limestone at localities W21 and W17, and in the Mungerebar Limestone at McCabe Knob. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### BIAVERTA REINERI sp.nov.

(Pl. 39, figs 1-5)

*Material:* The illustrated material comprises five cranidia selected from a larger number of fragmentary specimens.

*Holotype:* The best preserved cranidium, Plate 39, fig. 1, CPC 5660, locality G119, is selected as the holotype.

*Diagnosis:* *B. reineri* sp.nov. is distinguished by its depressed cranial rim and its ornament of a subdued low granulation.

*Differential diagnosis:* *B. reineri* is rather similar to *B. biaverta*, which, however, has a crescentic retroverted rim and a strong and diversified ornament.

*Description:* The cranidium is strongly arched longitudinally and transversely, with steeply downsloping, even vertical flanks. The posterolateral limbs are rather large, with a strong retral swing. The posterior border widens abaxially and the posterior marginal furrow is blind, petering out before reaching the suture. Palpebral ridges and palpebral lobes are absent, but the position of the palpebral lobes opposite the glabellar front is indicated by the ocular embayment in the course of the sutures. The cephalic pleural lobes are projected well forward, flanking the depressed frontal area; it consists of the somewhat convex rim and the downsloping trapezoidal

brim. The glabella is elevated above the pleural lobes, relatively long, with slightly concave flanks and a subtruncate front. Three pairs of short glabellar furrows are present: the anterior furrows are almost imperceptible notches, the middle are deep lateral pits, and the posterior are deep and curved, almost isolating the knob-like posterior glabellar lobes. Small alae are present at these lobes. The occipital lobe bears a pair of dents in its anterior slope.

The ornament is an inconspicuous low and dense granulation, preserved on the holotype.

*Comment on illustrated specimens:*

The holotype cranium, locality G119, preserved in a cavity in chert, and silicified, is 2.8 mm long. Its test is intact, the ornament preserved, and the left suture is fully exposed, showing the absence of the palpebral lobe. The left side of the glabella with its lateral furrows is free; the dent in the occipital lobe is distinct. Parts of the test are covered with irremovable spongy silica.

The cranium Plate 39, fig. 3, CPC 5662, locality G119, silicified, rests on a silicified pygidium of *Meringaspis* sp. The glabella is free but a part of the posterolateral border is missing. Alae (at the base of the glabella on the left) are present.

The cranium Plate 39, fig. 5, CPC 5664, locality G8, etched limestone, in a maze of sponge spicules (*Chancelloria*), trilobite fragments, and small phosphatic brachiopods, is 3.0 mm long.

The cranium Plate 39, fig. 2, CPC 5661, locality G417, is 3.3 mm long. The rim is distinct.

The cranium Plate 39, fig. 4, CPC 5663, locality G8 is 2.0 mm long. In spite of extreme silicification its characters (except for the ornament) are distinguishable.

*Occurrence and age:* *B. reineri* sp.nov. occurs in the Mungerebar Limestone at localities G8, G114, G117, G119, and G417; its age is the Mindyallan Zone of *Erediaspis eretes*. It is also present at G12, low in the Zone of *Glyptagnostus stolidotus*.

## Superfamily AULACODIGMATACEA

### Family AULACODIGMATIDAE, nov.

The type genus of the family is *Aulacodigma* gen.nov.

The diagnosis of the family is based essentially on its type genus; it should be noted, however, that the different course of the posterior sutures in the two described species of *Aulacodigma* may indicate the existence of two separate but related genera in the family; this diversity prevents the inclusion in the familial diagnosis of details regarding the course of these sutures. Furthermore, the family includes two blind genera: *Anopocodia* gen.nov. and *Ajirikina* Kryskov, 1963.

*Anopocodia* is blind and sutureless, as described below; *Ajirikina bulakensis* Kryskov (1963, p. 279, pl. 1, figs 21–23) is close to *Aulacodigma* in the main features of the cephalon, including the sutures, and the number of segments (eight) in the thorax, but it has no eyes and its pygidium is pointed in the rear. Kryskov placed *Ajirikina* in the Conocoryphidae—apparently because of its blindness. *Ajirikina bulakensis* comes from south Kazakhstan; its age is early Upper Cambrian, about the Zone of *Glyptagnostus reticulatus* or perhaps *G. stolidotus*.

*Diagnosis:* The Aulacodigmatidae are classified as a family of the suborder Ptychopariina (in the sense of Harrington et al., 1959). The Aulacodigmatidae refer to species having a short glabella and a relatively long frontal area, a preglabellar boss, subcentral eyes remote from the glabella and free cheeks retaining the cornea,

relatively small posterolateral limbs, isoteliform anterior sutures, and a small number (about 8–9) of segments in the thorax. These characters refer to sighted forms; secondarily blind forms, however, are also known.

The family Aulacodigmatidae cannot be placed in any known superfamily of the ptychoparioids, and is regarded, therefore, as *suae superfamiliae*. An affiliation with the Nepeacea and/or with the Menomoniidae may be suspected, but in the absence of intermediate forms cannot be substantiated. The small number of segments in the thorax and the cedariform posterior sutures in *Aulacodigma* may also indicate some general, vague relationship with *Cedaria* and *Norwoodia*, which, however, possess a rather different cephalic structure.

The structure of the thorax of *Aulacodigma*, with its eight segments, strong facets, globose articulating half-rings, and the axial annulations extending into the pleural furrows, can be described as corynexochoid (dolichometopoid)—a surprising but paradoxical organization as regards the current ordinal classification of trilobites.

#### Genus AULACODIGMA nov.

The type of the genus is *Aulacodigma quasispinale* sp.nov.

The characters of the genus are: (1) the relatively large, transverse, subtrapezoidal cephalon; (2) the thorax of eight segments; (3) a pygidium of a medium size (about 0.4 of the cephalon); (4) the rather narrow doublure; (5) the absence of a cephalic and pygidial border; (6) the 'isoteliform' anterior sutures meeting in a dorsal pointed ogive and (7) passing into a subcephalic median suture; (8) the cedariform course of the posterior sutures; (9) the subcentral eyes remote from the glabella; (10) the exuvia of the free cheek retaining the visual surface; (11) the broad transverse channels of the interocular cheeks (interocular channels); (12) the relatively short glabella with the vestiges of two axial spines (in the type species); (13) the frontal boss defined on the flanks and in the rear (but not in the front) by deep furrows; (14) the advanced, deflected, and transmarginal genal spines; (15) the pair of small spines on the tips of the posterolateral limbs in front of the marginal furrows; (16) the extenuated ends of the axial annulations of the thorax extending into the pleural furrows.

Two species have been named: *Aulacodigma quasispinale* sp.nov. (the type), and *A. illimbatum* sp.nov.

*Diagnosis of A. quasispinale* sp.nov.: The posterior sutures diverge diametrically, then pass around the tips of the posterolateral marginal furrows in an even broad arc delineating relatively small posterolateral limbs; the anterior sutures are subparallel before curving toward the midline; the glabella bears two vestigial axial spines; the cephalic front is straight; the test is minutely granulose.

*Diagnosis of A. illimbatum* sp.nov.: The posterior sutures diverge obliquely rearward and cut across the tips of the posterolateral marginal furrows in a short arc delineating medium-size triangular posterolateral limbs; the anterior sutures converge in front of the eyes; the glabella lacks vestigial axial spines; the cephalic front recedes rearward; the test is visibly granulose; furthermore, the cephalon and cranidium are shorter (wider) than in *A. quasispinale*.

The age of both species is the Mindyallan Zone of *Glyptagnostus stolidotus*, but the collecting sites are geographically separate, and *A. illimbatum* probably post-dates *A. quasispinale*.

*A. quasispinale* and *A. illimbatum* are probably distinct subgenerically, but a decision is reserved because the thorax and pygidium of *illimbatum* are as yet unknown. The significant difference consists in the relatively small size of the posterolateral limbs and diametrically divergent course of the posterior sutures of *A. quasispinale* as compared with *illimbatum*, which has larger triangular posterolateral limbs and oblique posterior sutures.

*Peculiarities of the organization:* The interocular channels of *Aulacodigma* have a structure analogous to the structure of the posterolateral furrows and the pleural furrows of the thorax; it is therefore probable that a homology exists in the sense that these channels represent the pleural furrows of a cephalic segment; accepting this, the ocular ridges are the propleural and the ridges along the posterior border of the channels the opisthopleural caecal veins. Furthermore, it can be speculated that the channels represent dilated ocular strigae (see Öpik, 1961), or, in reverse, that the ocular strigae of other trilobites are reduced original pleural furrows. If so, the double ocular ridges known in many Cambrian trilobites (Öpik, op. cit., p. 425) belong to a single segment. The idea of a restitution of pleural furrows in the cephalon of an Upper Cambrian trilobite would be paradoxical; it is less paradoxical to assume that *Aulacodigma* belongs to a stock retaining a lesser grade of cephalization as compared with the rest of the trilobites. The ptychoparioid design of its cephalon combined with a thorax of a corynexochid design may indicate a common ancestry of these orders as well as testify once more that the known record of the trilobites is still rather incomplete.

Notable also are the sporadic vestigial glabellar spines, which refer to an unfinished process of cephalization, whereas the course of the anterior sutures and the retention of the visual surface in moults of the free cheek is unusual in Cambrian, but common in post-Cambrian trilobites.

*Aulacodigma*, therefore, in retaining a pair of cephalic pleural furrows lags behind all other members of its class, but is ahead of its time as regards the organization of its eyes, its dorsal sutural ogive, and the median subcephalic suture.

#### AULACODIGMA QUASISPINALE sp.nov.

(Pl. 40; figs 8, 9; Pl. 41, figs 1-10; Text-fig. 142)

*Material:* The described and illustrated material comprises two complete specimens, one fragment of the thorax, one free cheek and eight cranidia; these specimens are taken from two sites, separated by some 150 miles. The material from the south-western site (locality W20), containing complete specimens, represents a population embedded on a single surface; the north-eastern site (locality D29), the 'lower chert bed' of the O'Hara Shale, contains an abundance of fragmentary material confined to the thickness of about five inches of rock; this must also represent a population, but the bed may correspond to a span of time somewhat larger than the bedding plane at the first site.

*Holotype:* The complete specimen Plate 40, figure 9, CPC 5676, is selected as the holotype because it shows all essential characters of the species; it has only seven segments in the thorax, and is therefore immature; but in the other complete specimen (Pl. 40, fig. 8) with eight segments, the cephalon is worn and some of its features are vague.

*Diagnosis:* The specific and differential diagnoses are given in the description of the genus (above) together with the diagnoses of *Aulacodigma illibatatum*.

*Description:* *Aulacodigma quasispinale* is a small trilobite, of the size of an agnostid. The body is broad, convex, and has well accentuated furrows and lobes. The cephalon is transverse subtrapezoidal, relatively large, as long as six segments of the thorax, and the pygidium is subtriangular and medium in size, as long as three posterior segments. The thorax has convex and serrate flanks and narrows only little, and the axial furrows are subparallel.

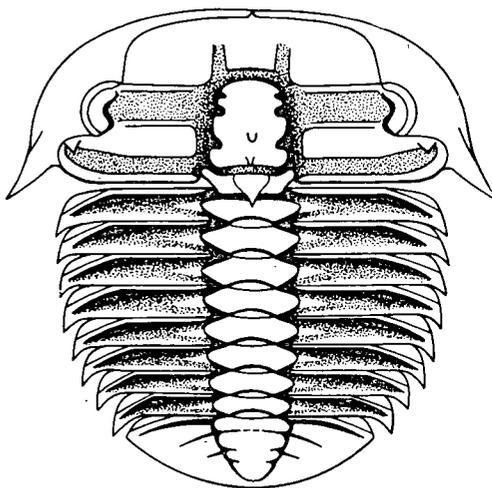


Fig. 142.—*Aulacodigma quasispinale* gen. nov., sp. nov., combined from Plate 40, figs 8 and 9 and several other cephalia.

The cephalon lacks a border and a marginal furrow; it is relatively flat in the middle, but has a convex and steeply downsloping periphery, with an upward arched and transversely straight frontal margin. The free cheek is relatively small and tumid, with a transmarginal, short, advanced, and strongly deflected genal spine; the eye is borne on a base and the cheek retains the visual surface after moulting. The anterior sutures, subparallel in front of the eyes, curve abruptly toward the middle, and, describing a low ogive, meet on the dorsal side at the margin and pass into the median subcephalic suture. In one specimen (Pl. 41, fig. 2) the sutures start to converge at the eyes. The posterior sutures diverge diametrically, then in a hairpin curve around the tips of the marginal furrows turn rearward and reach the margin almost at the base of the genal spines. The posterolateral limbs are relatively short (transversely) and moderately geniculate. The posterior marginal furrows are wide and deep channels not reaching the tips of the posterolateral limbs and not touched by the sutures; anterior to the end of each furrow a short cranidial posterolateral

spine can be seen in better preserved specimens. The posterolateral border is narrow and steep and bears a hump at the fulcral point, placed from the axial furrow at a distance as wide as the occipital lobe.

The frontal area is long, about 0.6 of glabellar length (in plan) and no trace of a division into a brim and a rim can be seen. In the middle there is a subrectangular boss, well defined and steep in the rear and flanked by distinct but shallow longitudinal furrows; these furrows and the boss fade out forward. The palpebral lobes are relatively large, elevated and flat, placed opposite the anterior half of the glabella; they are about 0.6, and the intact eyes about 0.65–0.68, of glabellar length. The eyes are far apart, the interocular cheek being wider than the glabella, variable around 1.3 to 1.5 of its width. In immature specimens it is less, about 1.0 to 1.1. The interocular cheeks are depressed transverse channels, with steep margins and flat floors merging with the axial furrows. The anterior border of the channel is marked by the narrow ocular ridge, which continues in the palpebral lobe; the posterior margin also carries a ridge, but it is less distinct than the anterior ocular ridge. The occipital lobe is rather prominent, with narrow flanks bent forward and a somewhat onion-shaped upright short conical median spine. The occipital furrow is distinct and deepened at its oblique ends. The axial furrows are rather wide and deep and surround the glabella completely. The glabella is short, about half the cephalon, with an almost straight forward-sloping and mostly carinate crest, but arched transversely and with flanks about vertical and convex outward. About as wide as long, the glabella tapers to a rounded to subtruncate front. Two low nodes (vestigial spines) are present on the rear of the crest: either node may be missing, or both can be subdued and almost indiscernible. Three pairs of short but deep glabellar furrows are developed as notches; the posterior furrows are rather oblique, and the two posterior glabellar lobes are conspicuous. The cephalic doublure is very narrow and convex and carries terraced lines. The ornament consists of a dense and minute granulation, destroyed in many specimens by silicification.

The thorax consists of eight segments with falcate recurving short pleural spines, well developed articulating facets and broad and long channel-like pleural furrows. The free parts of the pleurae are relatively short, the fulcral lines being placed each at a distance of the width of the axial lobe from the axial furrows. The shape of the axial annulations and of the occipital lobe is the same; the ends of the annulations are pointed and extend well into the adaxial parts of the pleural furrows; the articulating joints are placed about half-way between the midline and the outer ends of the annulations. The axis is prominent, rising above the flat interfulcral parts of the pleural lobes; the articulating half-rings are relatively long and globose.

The pygidium is transverse semielliptical, without a border, and with about two pairs of pleural ribs. The pygidial axial lobe reaches almost the margin, has convex flanks, tapers rapidly to an almost pointed terminus, and consists of one complete and two incomplete annulations.

Some variability is also apparent: during growth the distance of the eyes from the glabella increases; the interocular channels are mostly transverse and straight, but can be slightly slanting and curved; the shape and elevation of the boss are variable; the frontal lobe of the glabella may be subtruncate to evenly rounded; and the glabellar nodes (vestigial spines) are erratic.

*Comment on illustrated specimens:*

The first five specimens come from the Georgina Limestone, locality W20 (the south-western site) and are collected from a single siliceous bedding plane; the specimens are silicified.

The holotype is 4.7 mm long; the test is worn in parts, and a part of the pygidium is missing; on the right side the cephalic doublure is exposed as a deep channel; the spines on the posterolateral tips in front of the marginal furrow are preserved.

The complete specimen Plate 40, fig. 8, CPC 5675, is 5.5 mm long, including the pygidium, the outline of which is preserved. The tips of the pleurae are well outlined as cavities exposing the doublure.

The fragmentary thorax Plate 41, fig. 1, CPC 5677, together with the attached pygidium, is 2.0 mm long. The subglobose articulating half-rings are exposed.

The cephalon Plate 41, fig. 2, CPC 5678, is 2.5 mm long. The eyes are intact, but the margin is flattened, simulating a border, which in reality is absent. The specimen is a mould (embedded dorsum down)

The cephalon Plate 41, fig. 4, CPC 5680, a mould (embedded dorsum down) is 2.2 mm long. The eyes are intact, the ocular ridges are obscure.

The following seven specimens are taken from the 'lower chert bed' of the O'Hara Shale (the north-eastern site), locality D29 (one cephalon (Pl. 45, fig. 5) is from locality D6).

The free cheek Plate 41, fig. 3, CPC 5679, is about 2.3 mm long from tip to tip; the visual surface of the eye is preserved, and the ocelli are visible under strong magnification.

The cranium Plate 41, fig. 6, CPC 5682, is about 1.7 mm long. The tip of the left posterolateral limb is broken; the interocular channels are transverse and deep, and the right palpebral lobe is intact.

The cranium Plate 41, fig. 7, CPC 5683, is 1.6 mm long; the interocular channels are slanting and extend behind the palpebral lobe. The posterior node on the glabella is distinct.

The cephalon Plate 41, fig. 5, CPC 5681, is 1.6 mm long. The doublure is exposed, the frontal ogive of the cranium is preserved, but is obscured by a grain of rock in the hollow doublure. The boss is relatively small and has converging flanks.

The cephalon Plate 41, fig. 8, CPC 5684, is 1.3 mm long. The two median tubercles (vestigial glabellar spines) are distinct.

The cephalon Plate 41, fig. 10, CPC 5686, is 1.1 mm long. It is immature, but displays all essential characters.

The cephalon Plate 41, fig. 9, CPC 5685, is 0.9 mm long; the cranial ogive is apparent in the frontal view, but slightly distorted; in entirely intact specimens the cephalic front is arched more upward. The associated agnostid cephalon belongs to *Agnostardis amplinatis*.

*Occurrence and age:* *Aulacodigma quasispinale* sp.nov. has been found in the Georgina Limestone at localities W20, W15, W17, W66, G49, and G51; and in the O'Hara Shale ('lower chert bed') at localities D6, D28, and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

AULACODIGMA ILLIMBATUM sp.nov.

(Pl. 42, figs 1, 2; Text-fig. 143)

*Material:* Only four specimens have been collected; besides the two illustrated cephalons, another fragmentary cephalon and one cranium are available.

*Holotype:* The cephalon Plate 42, figure 1, CPC 5688, is selected as the holotype because of its excellent preservation.

*Diagnosis:* The diagnosis and the differential diagnosis are given in the description of the genus, to facilitate comparison with *A. quasispinale*.

*Description:* The following description is brief, because it is unnecessary to repeat the generic characters, which are evident from the description of *Aulacodigma quasispinale*.

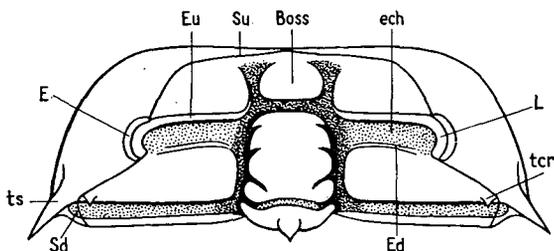


Fig. 143.—*Aulacodigma illimbatum* sp.nov., from Plate 42, fig. 1. Boss—frontal boss; ech—interocular channel; Ed—posterior ocular ridge; E—visual surface (eye); Eu—ocular ridge; L—palpebral lobe; Sd—posterior suture (cedariform); Su— anterior suture (isoteloid); tcr—cranial posterolateral spine; ts—genal spine (transmarginal).

The cephalon and cranium of *A. illimbatum* are both slightly wider (relatively shorter) than in *A. quasispinale*. The frontal margin is arched upward and rearward; a lateral border is indicated at the base of the spine, but it cannot be regarded as a true border because it is produced only by the tumidity of the base of the genal spine rising above the marginal slope. The genal angle is relatively narrow (transversely) and the spine is delicate as compared with *A. quasispinale*. The anterior sutures converge in front of the eyes and the median point of the ogive is relatively inconspicuous. The posterior sutures diverge first as straight lines, then recurve, cutting across the tips of the marginal furrow. The posterolateral limbs are triangular and relatively large, and each bears a tiny spine overlapping the anterior edge of the marginal furrow. The preglabellar boss is rather prominent, semi-globose, but still ill defined in its front. The palpebral lobes are half as long as the glabella, and slightly shorter than in *A. quasispinale*, and the interocular cheeks are only slightly wider than the glabella. The interocular channels are slightly curved and slanting, and the anterior and posterior ocular ridges are distinct.

The occipital lobe bears a short and almost upright spine. The glabella has almost straight flanks and a subtruncate frontal lobe. Median glabellar spines are absent; the glabellar lobes are inconspicuous, and so are the three pairs of short lateral glabellar furrows. The test is pustulose; the ornament is relatively coarse on the fixed cheeks and less coarse on the glabella and the frontal area.

*Comment on illustrated specimens:*

The holotype cephalon, Plate 42, fig. 1, CPC 5688, Pomegranate Limestone, locality B537, is 2 mm long. The ocular ridge and the ridge along the posterior margin of the interocular channel are distinct; note the spine at the anterior tip of the posterolateral limb.

The cephalon Plate 42, fig. 2, CPC 5689, Pomegranate Limestone, locality B525, is 1.9 mm long. The specimen is somewhat distorted, the interocular channels are arched forward, the front is flattened and shows the ogive. The genal spine is visibly transmarginal.

*Occurrence and age:* *Aulacodigma illimbatum* has been found only in the Pomegranate Limestone at Wills Creek, at localities B525 and B537; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

## Family AULACODIGMATIDAE?

### Genus ANOPOCODIA nov.

*Anopocodia* is monotypical, with *A. globiceps* as its type.

The familial classification is questionable because of the rather simplified organization of the trilobite, lacking the facial sutures and eyes. The elongate glabella, deep axial furrows, the forward position of the boss, which almost reaches the margin, and absence of a cephalic border suggest an affiliation with *Aulacodigma*; if this is accepted, *Anopocodia* evolved by the effacement of the glabellar furrows and all features of the cephalic pleural lobes seen in *Aulacodigma*—a speculation in need of further proof.

Among the sighted trilobites the pustulose *Lorenzella? convexa* Resser & Endo (1937, pl. 55, fig. 18; pl. 65, figs 26 and 27) bears also some similarity with *Anopocodia*. Kobayashi (1960, p. 389) included *L? convexa* in his new genus *Cyclolorenzella*, which belongs, in his opinion, to the Agrauidae. Consequently *Anopocodia* can be interpreted as a blind *Cyclolorenzella* as well as a blind and effaced *Aulacodigma*. The presence of palpebral lobes (eyes) in *L? convexa* is not evident in the illustrated fragmentary cranidia (Resser & Endo, op. cit.) and its reconstruction (Kobayashi, op. cit., text-fig. 9k) shows a course of sutures not compatible with the type of *Cyclolorenzella* (ibid., fig. 9j). Hence, the generic classification of *L? convexa* is in need of revision.

### ANOPOCODIA GLOBICEPS sp.nov.

(Pl. 16, figs 4, 5; Text-fig. 144)

*Material*: The material consists of two cephalae only.

*Holotype*: The specimen Plate 16, figure 5, CPC 5489, is selected as the holotype because it is embedded in hard rock, whereas the matrix of the second specimen (Pl. 16, fig. 4, CPC 5488) is friable silica. This specimen is about 0.5 mm long.

A specific diagnosis cannot be compiled because it is a unique form; it differs from all known species of trilobites by the absence of eyes and sutures, and of the border, and by the presence of a semiglobose boss between the glabella and the frontal margin. As indicated in the discussion of the familial classification *Lorenzella? convexa* Resser & Endo may be related to *Anopocodia globiceps*; but *convexa* has a conspicuously pustulose test and is, therefore, specifically distinct from the smooth *globiceps*.

*Description*: *Anopocodia globiceps* is a minute trilobite, with cephalae about 0.65 mm long and 1.0 mm wide. The cephalic margin is evenly convex, a marginal furrow is absent, but the posterolateral furrows are distinct, and the fulcral points are placed about halfway between the occipital lobe and the genal angles. The cephalon is vaulted, with a steeply sloping periphery and rather tumid adaxially sloping cheeks (pleural lobes) which show neither sutures nor any trace of eyes. The occipital lobe bears a short marginal spine and the occipital furrow is narrow but distinct. The axial furrows are deep valleys between the cheeks and the glabella. In its rear the glabella is almost parallel-sided, but tapers in its frontal part rather rapidly. No brim is present, but between the glabellar front and the margin a circular boss,

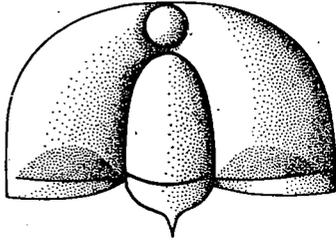


Fig. 144.—*Anopocodia globiceps* gen.nov., sp.nov., from Plate 16, fig. 5.

about 0.3 of glabellar length, is well defined by deep furrows. The cephalic doublure is very narrow and convex. It is continuous and bears no signs of ventral sutures. The test is smooth.

*Occurrence and age:* *Anopocodia globiceps* sp.nov. has been found only in the O'Hara Shale ('lower chert bed') at locality D29; it escapes detection easily because of its small size. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### Suborder PTYCHOPARIINA superfamiliae incertae

#### Family PLACOSEMATIDAE nov.

The type of the family is *Placosema* gen.nov.

The Placosematidae are brimless Ptychopariina with an ovate glabella reaching the marginal furrow, with converging anterior sutures and small subcentral eyes. The new family Placosematidae is necessary to accommodate genera which cannot be placed in any of the hitherto established families without substantially changing their concepts.

It is possible that *Albansia* Howell, 1937 and *Albansia? montanensis* Howell & Duncan (1939) (see Lochman & Duncan, 1944) are also placosematids; these fossils, however, are insufficiently preserved for a conclusive comparison with *Placosema*.

#### Genus PLACOSEMA nov.

The type of the genus is *Placosema caelatum* sp.nov.

*Diagnosis:* The species of *Placosema* are distinguished by (1) a convex and steeply sloping cranidium with extremely deep axial, circumglabellar, occipital, and posterior marginal furrows; (2) an ovate and transversely moderately arched and about equidimensional glabella which reaches the frontal border; (3) subcentral palpebral lobes of medium length; (4) interocular cheeks about as wide as 0.5 of the glabellar width; (5) a rather narrow but high and steeply sloping or vertical frontal border, straight in plan, with a flat face; and (6) converging convex anterior sutures running in more or less even curves from the palpebral lobes to the lower edge (margin) of the rim.

*Comparison:* It is, apparently, accidental that *Placosema* is associated with two species of *Meropalla* gen.nov., which also have a flat and high frontal rim. Otherwise these two genera are disparate and belong to different families and even superfamilies. Two species are described: *Placosema caelatum* sp.nov., and *P. adnatum* sp.nov.

PLACOSEMA CAELATUM sp.nov.

(Pl. 20, figs 2-4)

*Material:* The available material consists only of silicified cranidia and one incomplete free cheek. The cheek and two cranidia are selected for description.

*Holotype:* The cranidium Plate 20, figure 2, CPC 5518, locality G127, Mungerebar Limestone, is selected as the holotype because all its parts are accessible for observation.

*Diagnosis:* *Placosema caelatum* is distinguished by its very deep frontal marginal furrow; for the differential diagnosis see *Placosema adnatum* sp.nov.

*Description:* The cephalon is broadly semielliptical and strongly arched in both directions, with steeply sloping free cheeks and extrafulcral posterolateral limbs. All furrows are deeply incised, relatively narrow, and of about the same width. The posterior marginal furrows, however, peter out before crossing the sutures, the palpebral furrows are relatively shallow, and the two pairs of glabellar furrows present are rather shallow. The anterior sutures are convex, and converge forward; without a change in direction the sutures cross the rim and intercept the margin at a short distance from the anterolateral corners of the cranidium; in the front the sutures unite and remain marginal. The posterior sutures diverge strongly, are slightly convex and delineate large triangular posterolateral limbs. The interocular cheeks are slightly convex, as wide as 0.45-0.5 of the glabella and slope toward the palpebral lobes, which remain well below the level of the cheeks. The palpebral lobes are medium-sized, about 0.35-0.4 of glabellar length and placed opposite the cranial centre, or opposite the second quarter of the glabella counting from the rear, and opposite the posterior glabellar furrows. The ocular ridges are faint and narrow. The frontal border, looking from above, is a straight narrow bar with a rounded crest and coincides with the steep frontal slope of the glabella. The border is arched upward, without abaxial geniculations, and has a high and almost flat face carrying terraced lines. The occipital lobe is long (sagittally) in the middle and intrudes the rear of the glabella; at the flanks a pair of notches separates the rather narrow forward-curving lateral cusps of the occipital lobe.

The glabella reaches the marginal frontal furrow, which is confluent in the middle with the circumglabellar furrow; the glabella is slightly shorter than wide (as long as about 0.85 of its width), ovate, with convex flanks; it is widest in the posterior third, subtruncate in front, and somewhat elevated above the general transverse arc of the cephalon. In the rear the glabella has a broad median recess, accentuated by the low tumidity of the posterior glabellar lobes.

The test is apparently smooth; scattered low rounded granules may have been present but are obliterated by silicification. The presence or absence of a genal spine cannot be established with the material in hand.

It is probable that the 'indeterminable Pygidium No. 1' (q.v.) is the pygidium of *Placosema caelatum*.

*Comment on illustrated specimens:*

The holotype cranidium is 4.8 mm in horizontal attitude, and its sagittal chord about 5.4 mm long; between the tips of the posterolateral limbs it measures 9.8 mm; the glabella is 3.5 mm long and 3.8 mm wide. A thin layer of irremovable silica covers parts of the glabella. At the frontal margin a transverse line and a shallow furrow above it are present.

The free cheek Plate 20, fig. 4, CPC 5520, locality G124, shows the widening border; the genal angle is, however, immersed in silica.

The cranidium Plate 20, fig. 3, CPC 5519, locality G119, in silica, is the largest available; it is 6.1 mm long, and the glabella is 3.7 mm long and 4.0 mm wide. The ocular ridge is distinct and glabellar furrows are clearly indicated; in the illustration the front is tilted up, showing in perspective the slope of the frontal face, but the rim itself is also thicker than in other specimens.

*Occurrence and age:* *Placosema caelatum* occurs in the Mungerebar Limestone at localities G8, G119, G124, G125, G126, G127, G130, G137, and G417; its age is the Mindyallan Zones of *Erediaspis eretes* (G8, G119, G417) and of *Cyclagnostus quasivespa* (G124, G125, G126, G127, G130, G137).

PLACOSEMA ADNATUM sp.nov.

(Pl. 19, fig. 6; Pl. 20, fig. 1)

*Material:* The available material consists of three cranidia, of which two are illustrated.

*Holotype:* The silicified specimen Plate 20, figure 1, from the Georgina Limestone, locality G51, CPC 5517, is the holotype; the other specimens are partly flattened and fractured and less suitable for description.

*Diagnosis:* *Placosema adnatum* sp.nov. is a species of *Placosema* in which the frontal marginal furrow is almost effaced, and the glabella is slightly constricted in its anterior part.

*Differential diagnosis:* In *P. caelatum* the frontal marginal furrow is deep and narrow; furthermore, in *adnatum* the palpebral lobes are smaller, the interocular cheeks slightly wider, and the posterior glabellar recess weaker than in *caelatum*.

*Description:* The holotype cranidium is 5.7 mm long; it is rather friable, and some parts of it were lost during the etching and carving by a needle. The generic diagnosis can serve as a general description of the specimen, supplemented by the specific and differential diagnosis, but some additional data are also necessary. The glabella is well rounded in front (and not subtruncate as in *caelatum*) and has a slight constriction in its anterior third; the palpebral lobes are about 0.3–0.32 of glabellar length and the interocular cheek is 0.6 of the width of the glabella. A recess in the rear of the glabella is absent, but the occipital lobe is notched as in *caelatum*. The ocular ridge is low but distinct, and the test is smooth. The rim appears wide from above because in the illustration the specimen is tilted, showing the face of the rim in perspective. The border slopes down steeply, following the general arcuate slope of the cranidium.

The second cranidium Plate 19, figure 6, CPC 5516, locality G12, in sandy limestone, is 5.7 mm long; the test is thick and smooth, the ocular ridge is well developed on the cast, and the posterior edge of the glabella has a weak recess which is not seen in the holotype.

*Occurrence and age:* *Placosema adnatum* has been found in the Georgina Limestone at locality G51, and in the Mungerebar Limestone at locality G12, in the Mindyallan Zone of *Glyptagnostus stolidotus*; it also occurs at locality G124 of the Mungerebar Limestone in the Zone of *Cyclagnostus quasivespa*.

Family POLYCYRTASPIDIDAE nov.

Genus POLYCYRTASPIS nov.

The type of the genus is *Polycyrtaspis flexuosa* sp.nov. The genus is monotypical and the characters of the genus and of the family are evident from the description of the type species.

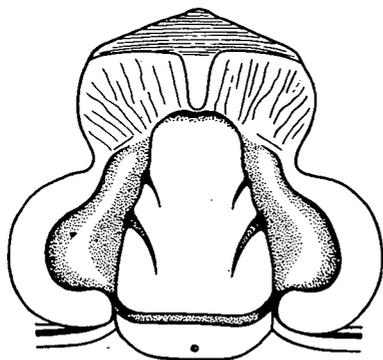


Fig. 145.—*Polycyrtaspis flexuosa*, gen. nov., sp.nov., from Plate 9, figs 1 and 2.

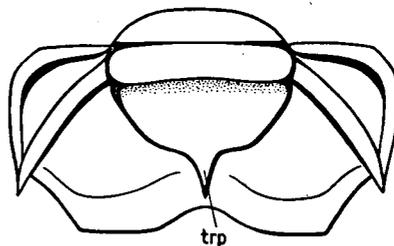


Fig. 146.—*Polycyrtaspis flexuosa* sp.nov., pygidium, from Plate 9, fig. 3. trp—antiplectrum.

POLYCYRTASPIS FLEXUOSA sp.nov.

(Pl. 9, figs 1-4; Text-figs 145, 146)

*Material* : Two cranidia are illustrated, selected from a large number of cranidia which are all more less fragmentary ; a hypostoma and a pygidium tentatively assigned to *P. flexuosa* are also described.

*Holotype* : The cranidium Plate 9, figure 1, CPC 5420, is selected as the holotype because of its large size.

*Diagnosis* : *Polycyrtaspis flexuosa* is distinguished from the known species of the Ptychopariina by its oversized palpebral lobes (and eyes), a pyriform glabella with deep lateral pits, an angulate front, and very small posterolateral limbs.

*Description* : The cranidium is relatively long, somewhat subtriangular, moderately convex, and evenly arched sagittally. Its curved lines and accentuated furrows and lobes, the pyriform glabella, and the extremely large palpebral lobes create a unique and easily recognizable design. It is still a ptychoparioid design, recognizable from the long frontal area, venulose brim, and tapering glabella. The large eyes placed close to the glabella exclude, however, the superfamily Ptychopariacea and other known Ptychopariina.

The anterior sutures are evenly curved and convex outward, but within the rim they are relatively straight and converge to the midline, meeting in a flat ogive ; its frontal peak is bent down, and the sutures meet at the marginal tip. The rim is elevated, relatively flat, triangular, and covered with transverse terraced lines. The marginal furrow is distinct, with a steep frontal slope, and interrupted in the middle

by a prominent narrow plectrum reaching the glabellar front. The brim is transversely suboval, almost flat, and covered by radiating veins. The whole frontal area is long, about 0·6 of glabellar length.

The posterior sutures diverge diametrically ; between the rear of the palpebral lobe and the suture below it a narrow slit indicates the rearward-looking part of the eye enclosed by the palpebral suture (above) and the adaxial part of the posterior suture (below). The posterolateral limbs are very small, but their tips are not preserved.

The palpebral lobes are very long (over 0·8 of glabella), flat, horizontal, and broad, and their posterior tips, reaching beyond the occipital furrow, are ear-like, elevated. The ocular ridges are inconspicuous and rather oblique. The cusps of the palpebral lobes are close to the glabella, enclosing the interocular cheeks, which are developed into elongate sinuate swellings. The occipital lobe is relatively short and the occipital node is placed behind its centre. The occipital furrow is shallow, but its ends are deep and narrow pits. The axial furrows are exceptionally deep, but the circumglabellar furrow is normal, shallow. The glabella is pyriform, expanded in the rear, narrow anteriorly, and rounded in front. The glabellar front itself is somewhat bilobed. Two pairs of oblique glabellar furrows are present, with deep pits at the abaxial ends. The test is apparently smooth.

The pygidium and the hypostoma are described below.

*Comment on illustrated specimens:*

The holotype is 10·1 mm long, and slightly flattened; the matrix is chert, the posterolateral limbs are not exposed, and some of the silica could not be removed from the rear of the axial furrows.

The specimen Plate 9, fig. 2, CPC 5421, is 3·2 mm long; the matrix is friable silica, and the specimen is apparently not deformed. The test is preserved, the glabellar furrows are externally inconspicuous, and the palpebral lobes are raised above the small posterolateral limbs.

The pygidium Plate 9, figs 3a, b and Text-figure 146, CPC 5422, is 1·3 mm long. The axial lobe is broad and short; it consists of a single annulation and a large terminus with a prominent and narrow antiplectrum. The pleural lobes are depressed and have a pair of prominent oblique narrow ribs extended into short lateral marginal spines. The lateral border is elevated and narrow, but behind the spines the border is ill defined and the pygidial periphery is concave. The posterior margin is broadly sinuate; the doublure is very wide. Two pygidia have been found altogether. The pygidium is assigned to *P. flexuosa* on the assumption that an 'unusual' pygidium should correspond to an 'unusual' cranidium.

The hypostoma Plate 9, fig. 4, CPC 5423, is 3·0 mm long; it is incomplete—some of its frontal margin is missing. The median lobe is moderately convex, pyriform, and extenuated in the rear into a narrow ogive reaching the border; the lateral border is narrow and constricted in the anterior half and expanded in the rear; the extremities of the anterior wings have a deep pit each; the anterior margin is arched downward. This hypostoma cannot be attributed to any of the Mindyallan trilobites except *Polycyrtaspis* because (1) the median lobe reflects the pyriform shape of the glabella, and (2) the constriction in the anterior part of the hypostoma indicates that the anterior cusps of the palpebral lobes are close to the glabella.

*Occurrence and age:* The illustrated specimens of *P. flexuosa* came from the O'Hara Shale ('lower chert bed'), locality D29 ; other localities are D6 and D28. Fragments of cranidia have been observed in the Georgina Limestone (locality W20). The age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

PTYCHOPARIINA superfamiliae incertae

Genus TOWNLEYELLA nov.

The genus is monotypical, with *T. townleyi* sp.nov. as its type.

*Diagnosis* : The combination of following characters identifies the genus *Townleyella* : (1) small eyes remote from the glabella, and in a forward position ; (2) rather tumid interocular cheeks vaulted above the depressed palpebral lobes ; (3) tapering glabella with almost isolated posterior lobes ; (4) relatively large bacculae ; (5) abaxially widening posterior border ; (6) advanced tips of posterolateral limbs (and probably advanced genal spines) ; and (7) densely granulose test.

*Suprageneric classification* : The cranidial design of *Townleyella* is ptychoparioid, that is, the glabella is tapering and relatively short, the frontal area consists of a brim and a rim, the eyes are relatively small and remote from the glabella, and the posterolateral limbs are large and triangular. The presence of bacculae, the deep glabellar furrows, and the almost isolated posterior glabellar lobes allow of no conclusive familial classification ; neither can a separate family be established, because only the cranidium is known as yet. Some similarity with *Calymenidius* Rasetti is apparent ; but *Calymenidius* has no brim, no bacculae, only two pairs of glabellar furrows, and narrower interocular cheeks, and is, therefore, rather distinct from *Townleyella*.

TOWNLEYELLA TOWNLEYI sp.nov.

(Pl. 8, figs 4, 5 ; Text-fig. 147.)

*Material* : Two cranidia are illustrated, selected from six available specimens.

*Holotype* : The specimen Plate 8, figure 4, CPC 5416, locality D29, is preserved the best and is the holotype.

*Diagnosis* : The summary of the generic characters given in the description of the genus serves as the specific diagnosis.

*Description* : The holotype cranidium is 2.5 mm long (without spine) and the largest specimen about 3 mm long. It is subtrapezoidal, with an almost straight frontal rim, slightly arched upward and rearward.

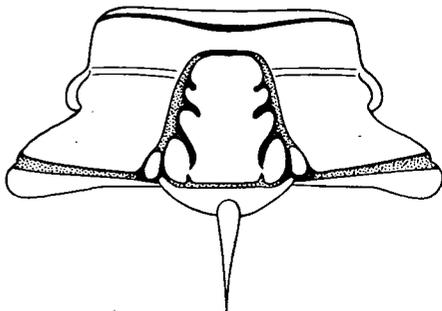


Fig. 147.—*Townleyella townleyi* gen.nov., sp. nov., from Plate 8, fig. 4.

The anterior sutures are slightly convergent (almost parallel) within the brim, but within the rim they turn abruptly toward the midline and intercept the frontal margin at a rather short but not accurately definable distance from the anterolateral

corners. The posterior sutures are relatively straight and divergent and delineate moderately large triangular posterolateral limbs. The posterior border broadens outside the fulcaral points; its tip is rounded and advanced forward, indicating a somewhat advanced position of the genal spine (or of the genal corner). The frontal area is moderately long (about 0.35 of glabella), and the brim and the rim on the midline are about equal in length. The brim is slightly convex and downsloping, the rim is upturned, bow-shaped, and defined by the shallow but distinct marginal furrow. The palpebral lobes are small, slightly less than 0.3 of glabellar length, and placed opposite the midpoint of the anterior half of the glabella. The eyes are far apart, the interocular cheek being 1.2 to 1.3 of glabellar width on the mid-level of the palpebral lobes. The ocular ridges are rather distinct and transverse (horizontal). The interocular cheeks are prominent and tumid, with summits elevated above the glabella, and sloping down toward the palpebral lobes, which have the appearance of ledges at the foot of the convex slope of the cheeks. The occipital lobe is relatively short (longitudinally), with drawn out and forwardswept ends which are almost confluent with the bacculae; these are relatively prominent and as long as the posterior glabellar lobes. The occipital spine is slender and long; the occipital furrow is straight and narrow. The axial furrows are wide, deep, and surround the glabella. The glabella tapers forward to about 0.5 of its width in the rear and is as wide as long, with straight flanks, subtruncate, but with well rounded anterolateral corners. Three pairs of deep glabellar furrows are present. The posterior furrows are long and oblique, almost reaching the rear of the glabella and separating the elongate and swollen posterior lobes; the S2 furrows are oblique and short, and the anterior furrows short lateral notches.

The test is densely pustulose.

*Comment on illustrated specimens:*

The holotype cranium is embedded in friable silica; the test and the left palpebral lobe are preserved; the palpebral lobe is inconspicuous, overshadowed by the tumid cheek.

The cranium Plate 8, fig. 5, CPC 5417, in hard siliceous shale, is 2.0 mm long (without the occipital lobe). Its right palpebral lobe is just visible.

*Occurrence and age:* *Townleyella townleyi* gen.nov. et sp.nov. has been found in the O'Hara Shale ('lower chert bed') at localities D6 and D29. Fragments occur also in the Georgina Limestone, locality W20. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

PTYCHOPARIINA familiae incertae

Genus LIOSTRACINOIDES Raymond, 1937

LIOSTRACINOIDES? sp.

(Pl. 10, fig. 9)

*Material:* One cranium, CPC 5436, 2.6 mm long, in chert, O'Hara Shale ('lower chert bed'), locality D6, is illustrated, selected from several equally imperfect specimens.

*Generic and familial classification:* Our form differs from *Liostracinoides vermontensis* Raymond in having a differently shaped glabella. In *L. vermontensis* the glabella is tapering, with a rounded front, and two pairs of glabellar furrows; the

posterior furrows isolate 'a small pair of almost triangular basal lobes' (Raymond, 1937, p. 1092). In the Australian form, however, the glabella is subpentagonal, broad, its front is angular, and it has no glabellar furrows and, consequently, no 'basal lobes'. An affiliation with *vermontensis* is indicated by the following characters: the general ptychoparioid design, deep axial furrows surrounding the glabella; the preglabellar median furrow, a rather short occipital lobe with pointed ends, and small palpebral lobes placed about opposite the glabellar midpoint and about half the glabellar width from the axial furrows.

The preglabellar median furrow is the essential feature that suggests the possibility of an affiliation of *L. vermontensis* with *Liostracina* Monke and the family Liostracini-*dae* Raymond. Without that furrow *L. vermontensis* could be placed with the ptychopariids, or solenopleurids, or tricepicephalids, without causing changes in the concepts of these family groups. But a preglabellar median furrow occurs sporadically in forms of various families (*Lioparia* Lorenz = *Liaoyangaspis* Chang, 1959; *Mesotaphraspis* Whittington & Evitt) and not exclusively in the Liostracini-*dae*. *Liostracina* and its affiliates, as described in this paper, cannot accommodate *Liostracinoidea vermontensis* or the Australian form, which, therefore, are regarded as *incertae familiae*.

*Occurrence and age:* *Liostracinoidea* sp. indet. is a rare fossil found only in the O'Hara Shale ('lower chert bed') at localities D6 and D29. Its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### TRILOBITA INCERTAE SEDIS

LARVA, gen. indet. et sp. indet.

(Pl. 36, figs 9-12)

*Material:* The specimens Plate 36, Figures 10, 11, and 12 are clustered on a single piece of limestone, locality G48.

*Description:* The whole shield is 0.6 mm long in figure 10 (CPC 5639) and 0.65 mm in figure 11 (CPC 5640); these specimens represent protaspides of a late degree in which cephalon and pygidium are separated axially, but their pleural lobes remain fused and an articulating joint is not, therefore, developed.

The exoskeleton has the form of half an elongate ellipsoid split along its longer axis; the pygidium is the small part, 0.3 of the total length. Its tapering axial lobe is defined anteriorly by the axial furrows, which fade out rearward; no segmentation and no border is present. In the cephalon the glabella, which expands forward slightly, is laterally defined by deep axial furrows, but its frontal part is confluent with the convex shield; within this confluent part an indistinct swelling without definable limits may belong to the glabellar front. The occipital furrow is shallow and the occipital lobe bears a median node placed well forward. The trilobite is blind; it has neither eyes nor palpebral lobes, and facial sutures are absent.

The cephalon Figure 9 (CPC 5638), is 0.7 mm long; it is sutureless and blind, the axial furrows are very deep, and the posterolateral marginal furrows are distinct. The glabella has a pair of lateral notches; but, as in the protaspis, its front is confluent with the rest of the shield.

The fragmentary cephalon Figure 12 (CPC 5641), 0·8 mm long, has apparently three pairs of short lateral glabellar furrows.

The two isolated cephalata represent, presumably, early meraspids of the same form as the protaspis.

No trilobite larva to compare with Larva gen. et sp. indet., and no comparable sutureless trilobites are known to facilitate a conclusive classification of these objects. The cephalic structure reminds one of *Shumardia*, whose larvae are, however, very different indeed. Somewhat closer are the larvae of *Norwoodella* (Hu, 1963), which differ in having eyes and a completely outlined tapering glabella. Finally, the blind *Anopocodia globiceps* gen.nov., sp.nov., in cephalata of the same size (0·65 mm), has a well outlined glabella and a boss and cannot be therefore compared with the Larva. gen. indet., sp. indet.

*Occurrence and age:* Larva gen. et sp. indet. has been found in the Georgina Limestone at localities G48 and G50; the age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

### UNIDENTIFIED FREE CHEEKS

#### *Free Cheek No. 1*

(Pl. 51, fig. 12)

The illustrated free cheek, CPC 5774, in silica, is 4·0 mm long from tip to tip. It belongs to a trilobite with a brim and a rim and rather large eyes opposite the posterior part of the glabella and rather close to it. The border is flat; the test is granulose and heavily venulose. The posterior marginal furrow is almost all within the cheek, indicating that the posterolateral limbs are minute and partly overshadowed by the eye. It is possible that this cheek No. 1 belongs to *Polycyrtaspis flexuosa* sp.nov.; in *P. flexuosa*, however, the anterior sutures are convex and not straight as in the cheek No. 1.

*Occurrence and age:* The free cheek No. 1 comes from the O'Hara Shale ('lower chert bed'), locality D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

#### *Free Cheek No. 2*

(Pl. 51, fig. 11)

Only two specimens, both from the same locality and bed, have been found as yet. The illustrated specimen, CPC 5773, is 25·3 mm long. The cheek is rather swollen, without a border, and the genal spine, circular in section, is curved and stout. The posterolateral marginal furrow is very shallow.

*Occurrence and age:* The specimens come from the Mungerebar Limestone, locality G124; the age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

### UNIDENTIFIED PYGIDIA

#### *Pygidium No. 1*

(Pl. 51, figs 5, 6)

Two pygidia (fig. 5—CPC 5767, 2·5 mm long; fig. 6—CPC 5768, 2·0 mm long) are illustrated. More than twice as wide as long, the outline is about a segment of a circle; the axial lobe is stout, elevated, of two annulations and a long terminus

reaching the margin. Four pairs of rearward-swept pleural ribs and six pairs of marginal spines are discernible. Below the spines, and concealed by them, the margin is a vertical band passing at a right angle into the doublure.

Pygidium No. 1 belongs, probably, to *Placosema caelatum* sp.nov., with which it is associated.

*Occurrence and age:* Pygidium No. 1 occurs in the Mungerebar Limestone at localities G8, G119, and G144; the age is the Mindyallan Zone of *Erediaspis eretes*.

#### *Pygidium No. 2*

(Pl. 51, fig. 7)

Three pygidia of this kind have been recorded. The illustrated pygidium, CPC 5769, locality G119, is 4.0 mm long. Slightly concave along the margin, it lacks a border and a marginal furrow. The pleural ribs expand abaxially, are swept rearward, and almost reach the margin. The rear margin is broadly sinuate. The axial lobe is broad, stout, relatively short, of two annulations and a bluntly rounded terminus. These pygidia occur in association with cranidia of *Iniotoma iniotoma*, to which no pygidia have been assigned as yet. If this type of pygidium belongs to *Iniotoma*, it cannot be retained in the family Asaphiscidae, or even in the Asaphiscacea.

*Occurrence and age:* Pygidium No. 2 is found in the Mungerebar Limestone at localities G8, G119 and G429. Its age is the Mindyallan Zone of *Erediaspis eretes*.

#### *Pygidium No. 3*

(Pl. 51, fig. 9)

Only one specimen, CPC 5771, has been found. It is relatively large, 6.5 mm long. Elongate, semielliptical, its pleural lobes are quite flat, borderless, and concave along the margin. A depression at the posterolateral part indicates, probably, the presence of down-bent lateral spines; only one pair of frontal pleural ribs can be discerned. The axial lobe is high and convex, with four annulations; these are ornate with crenellated posterior edges. The terminus is bluntly pointed. The doublure is wide, marked externally by the paradoublure line. The test is, apparently, punctate.

*Occurrence and age:* Pygidium No. 3 comes from the Mungerebar Limestone, locality G118; its age is the Mindyallan Zone of *Erediaspis eretes*.

#### *Pygidium and Thorax No. 4*

(Pl. 51, fig. 13)

The specimen, CPC 5775, is 32 mm long. The axial lobe is narrow, but the pleurae are very wide and have well defined narrow pleural furrows. The pleural tips are extended into rearward-curved spines. The transverse elliptical pygidium is as long as 4.5-5 segments of the thorax. Four pairs of rearward-swept ribs are present on the pleural lobes; the axial lobe is short and has five annulations. The doublure of the pygidium and the thorax is quite narrow. The specimen apparently belongs to the Aphelaspidae.

*Occurrence and age:* A piece of chert derived from O'Hara Shale, found in Bronzewing Creek, Duchess Area, locality D116; the age is either Mindyallan or Idamean.

*Pygidium* No. 5

(Pl. 51, fig. 8)

Only the illustrated fragmentary specimen, CPC 5770, is available. It is 5.0 mm long, its axial lobe is relatively short and prominent and consists of four annulations and a pointed terminus followed by a long and low antiplectrum. The relatively flat pleural lobe carries three curved ribs almost reaching the rimless margin. The rear is slightly sinuate. The ornament consists of a minute and dense granulation. The general aspect recalls *Dikelokephalinidae*.

*Occurrence and age:* The specimen comes from the O'Hara Shale locality D29; its age is the Mindyallan Zone of *Glyptagnostus stolidotus*.

Suborder ASAPHINA Salter, 1864

Superfamily ASAPHACEA

Family ASAPHIDAE Burmeister, 1843

Subfamily GRIPHASAPHINAE nov.

The new subfamily contains a single genus—*Griphasaphus* nov.

*Diagnosis:* Asaphidae with palpebral furrows, triangular posterolateral limbs, and an occipital node; distinguished by a parallel-sided short pygidial axis.

In all hitherto known asaphids the pygidial axis tapers rearward and has concave flanks.

Genus GRIPHASAPHUS nov.

The type and only known species of the genus is *Griphasaphus griphus* sp. nov.

The following generic diagnosis is also the diagnosis of the species *G. griphus*; an abridged diagnosis is already given with the subfamily Griphasaphinae subf. nov.

The distinctive single characters of *Griphasaphus*, that are not present in other asaphids, are: (1) the truncated cranidial front, (2) the frontal recess of the glabella, (3) the subtriangular posterolateral limbs, and (4) the parallel-sided pygidial axis with five annulations only. These characters are combined with the presence of palpebral furrows and ocular ridges, paradoublural lines, an elongate and constricted glabella without glabellar furrows and without a node, a wide cephalic and pygidial border, the presence of an occipital node, and the absence of Panderian organs. All these characters occur in other asaphids, but in different combinations.

*Comparison:* The late Upper Cambrian *Eoasaphus superstes* (Linnarsson; see Westergaard, 1922; 1939) has also the small number of five axial annulations in the pygidium, but differs in having an angulate cranidial front, defined glabellar and occipital furrows, etc. Palpebral furrows, and rarely ocular ridges, are noted in several early Ordovician asaphids, but are uncommon generally; examples are *Plesiomegalaspis planilimbata* (Angelin), *Borogothus stenorhachis* (Angelin), and *Hunnebergia retusa* Tjernvik (1956). An occipital node is present in *Ogygiocaris*

Angelin (Henningsmoen, 1960); all these forms also possess paradoublural lines. An elongate and constricted glabella without glabellar furrows is common, as for example in *Isoteloides*, *Lannacus*, and *Megalaspides*; in the first two the cephalic and pygidial borders are also depressed and concave. Other genera with this kind of glabella are *Ptychopyge*, *Asaphellus*, *Niobella*, *Asaphelina*, and several more.

*Griphasaphus griphus* is the oldest known asaphid; although several Ordovician forms contain some of its characters, none can be regarded as a direct descendant. Notable is the effaced appearance of *griphus*; its pygidium is completely fused and the glabella has no furrows. Its Middle Cambrian ancestors, as yet unknown, should also be Asaphacea, but with less fused tagmata. The less effaced Ordovician forms can be derived from such ancestors, but not from species like *G. griphus* that have a flush relief of the shield.

In the subsequent asaphids the cranial front is pointed or rounded, but never truncated as in *Griphasaphus*. This truncation may be a sign of the presence of a rostellum—a remnant of the rostral shield (see *Auritama* gen.nov.).

#### GRIPHASAPHUS GRIPHUS sp.nov.

(Pl. 33, fig. 4; Pl. 34, figs 1-7; Text-fig. 148)

*Material*: Numerous silicified fragments are available; unsilicified cranidia are present in a piece of limestone from locality G125.

*Holotype*: The largest of the unsilicified cranidia, Plate 33, figure 4, CPC 5613, is selected as the holotype.

The diagnostic characters are given above, in the description of the genus.

*Description*: The cephalon is parabolic to semicircular in outline, relatively flat and evenly sloping from the glabella to the gently concave border. The free cheek has no marginal furrows; its genal spine is falcate and pointed. A delicate concentric paradoublural ridge marks the edge of the border and of the doublure and extends across the anterior suture to the anterolateral flank of the glabella. The anterior sutures curve evenly outward from the palpebral lobes and then, from about the midline of the border, to the frontal margin, where they become marginal and meet, truncating the front of the cranidium. This truncation of the front is

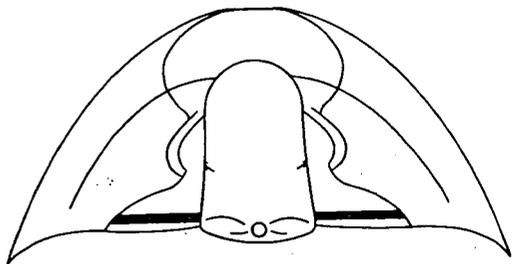


Fig. 148.—*Griphasaphus griphus*, gen. nov., sp.nov., combined from Plate 34.

unknown in other asaphids; in these the sutures meet at an angle or an extenuated prong, or less commonly in an even curve. The posterior sutures diverge strongly, cutting the posterior margin at an acute angle in the middle of the posterolateral

margin. Owing to the straight course of the sutures the posterolateral limbs are subtriangular and distinctive. The palpebral lobes, close to the glabella as in all asaphids, are narrow, moderately arcuate, and somewhat hooked, defined by shallow palpebral furrows which reach the glabella; the ocular ridges are inconspicuous. The palpebral lobes are as long as about 0.35 of the glabella, and opposite its midpoint. The interocular cheek is gently tumid and, together with the palpebral lobe, about 0.4 of the glabellar width. The frontal border of the cranium is rather large, about 0.25 of the glabellar length; the cranial posterolateral border is narrow and elevated and its furrow is wide and shallow.

The occipital lobe is rather short and ill defined because of the almost total absence of an occipital furrow—a general feature in asaphids. An occipital node, however, is present; it is absent in most of the asaphids, but present in *Ogygiocaris* (see Henningsmoen, 1960). The axial furrows are indicated only by the change of slope between the glabella (axial lobe) and the cephalic pleural lobes. The glabella is long, its width being 0.62 to 0.65 of its length, and widest in the rear. In maturity it is evenly rounded in front, but has a faint frontal recess in immature specimens, and is slightly constricted in the middle. The only sign of glabellar furrows is a slight rugosity in some specimens. A glabellar median node is absent.

The ventral structure includes a convex doublure that gradually expands forward, following the expanding dorsal border; the position of the adaxial ends of the paradoublural line at the anterolateral flanks of the glabella indicates a frontal recess in the doublure to fit the hypostoma, as is usual in asaphids. A median frontal suture is indicated by cleancut edges of the doublure in isolated free cheeks. The terraced lines are conspicuous and regular, but Panderian organs are absent in the cephalon. The test is smooth, without any ornamental features. The pygidium is large; it was probably as long as, or slightly shorter than, the cephalon. It is almost semi-circular with an evenly rounded margin without a recess in the rear. Two pairs of rather indistinct pleural ribs are indicated in the frontal part of the pygidium; the border is wide, depressed, and gently concave; a border furrow is absent, but a weak paradoublural line is discernible (Pl. 34, fig. 7), running from the fulcral points to the posterolateral flank of the axial terminus: consequently the doublure is also rather wide. The axial lobe is narrow (0.2 of anterior width) and relatively short (about 0.6 of the total length), with almost parallel flanks and with five weakly expressed annulations and a rounded terminus. The axial furrows are distinct but shallow.

*Comment on illustrated specimens:*

The holotype cranium (unsilicified, Plate 33, fig. 4, locality G125) is 7.9 mm long. Its frontal margin is slightly damaged, creating the impression of being straight.

The cranium Plate 34, fig. 1, CPC 5614, associated with the holotype, is 6.0 mm long. Its front is intact and rounded.

The cranium Plate 34, fig. 3, CPC 5616, associated with the holotype, is only 3.1 mm long, and immature; its frontal margin is truncate and the glabellar front shows a shallow recess. A vague indication of a vestigial plectrum may be only the result of an accidental deformation.

The cranium Plate 34, fig. 5, CPC 5618, locality G124, silica in limestone, is 14.2 mm long. It shows the constricted glabella, the left palpebral lobe, and parts of the frontal border. The right posterolateral limb is almost complete, but masked by some irremovable silica.

The fragment of the posterior left part of the cranium Plate 34, fig. 4, CPC 5617, locality G124 shows the course of the distal part of the posterior suture.

The free cheek Plate 34, fig. 2, CPC 5615, locality G124, silica in chert and limestone, 13.3 mm long, has preserved the genal spine; no Panderian organ is present. Associated free cheeks show on the dorsal surface the delicate paradoublural line.

The pygidium Plate 34, fig. 6, CPC 5619, locality G124, silica in limestone, is 7.5 mm long; the recess in the rear is accidental, produced during the etching and mechanical removal of the siliceous matrix.

The pygidium Plate 34, fig. 7, CPC 5620, locality G124, silica in chert, is 10.0 mm long, with a 6.6 mm axis; it is uncompressed and shows the wide border.

*Occurrence and age:* *Griphasaphus griphus* occurs in the Mungerebar Limestone at localities G119, G124, G125, G127; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

## Class CRUSTACEA

Subclass OSTRACODOIDEA Ivanova, 1960

Order BRADORIIDA Raymond, 1935

The ordinal name 'Archaeocopida n. order Sylvester-Bradley, 1961', replaces the name Bradoriida Raymond, 1935. The material exploited by Sylvester-Bradley is exactly the same as revised by Raymond, 1935, and even by Ulrich & Bassler, 1931. Hence, no new order, but the new name Archaeocopida, was introduced by Sylvester-Bradley. To quote the 'Treatise' 'nothing precludes substitution of a new name for an old one', meaning the nomenclature of classes and orders, but the acceptance of such new names is neither obligatory nor commendable. The same applies to 'Leperditicopida Scott, n. order', 1953. The nomenclatorial priority adheres to Leperditiida Pokorny, 1935, and Pokorny, not Scott, remains the author of the scientific concept of the order.

Consideration should be given to the classification suggested by Ivanova (1960). The nomenclature employed by her is in good taste and the concepts are illuminating. The classification is as follows: 'Class Crustacea; Subclass Ostracodoidea (new name, and concept); Order Bradoriida Raymond, 1935; Order Leperditiida Pokorny, 1935; Order Ostracoda Latreille, 1806'.

In this experimental classification the Bradoriida are neither subordinate to Ostracoda nor the Ostracoda to the Bradoriida, but their probable affiliation within a subclass finds its expression.

Externally, the Bradoriida bear similarities with the Ostracoda, and even more so with the Leperditiida; but the anatomy of the bradoriid animal itself is totally unknown. No evidence is available to justify the assumption that its body was reduced in the manner of living ostracodes; most probably the bradoriids possessed the full number of tagmata, as is suggested by the posterior gap of *Aristaluta*, which may have served as the passage for the abdomen and the telson. The unsatisfactory preservation of the known material of the Bradoriida, however, prevents any further interpretations and speculations as regards their organization.

The chemical composition of the shell of the Bradoriida is still unknown; traditionally, it is described as 'calcareo-corneous', and even 'chitin' has been mentioned. It is apparently calcareous but contains also some calcium-phosphate.

Family BEYRICHONIDAE Ulrich & Bassler, 1931

The familial reference (Beyrichonidae) is only tentative. It is applied here in the first place to *Aristaluta*, which has a border and anterodorsal nodes, and sulci; according to Ulrich & Bassler (op.cit., p. 42) there is no gap in the carapace of the Beyrichonidae, but this needs confirming. In *Svealuta* no gap is present, the closure of the valves is complete, but the well developed border and the anterior position of the nodes and sulci still indicates some affiliation with *Bradoria* and *Aristaluta*.

Genus SVEALUTA Öpik, 1961

SVEALUTA cf. PRIMORDIALIS (Linnarsson)

(Pl. 2, fig. 2)

Only one fragmentary left valve, CPC 5362, is available and illustrated. It is 6.4 mm long; the border is preserved only at the posterior angle, and the species, therefore, cannot be identified. The large tumid semiglobose anterior node suggests *S. primordialis*, but there is also a swelling at the posterior angle defined by a shallow sulcus which is not seen in *primordialis*.

*Occurrence and age:* The fragment comes from the Mungerebar Limestone, locality G131; its age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

Genus ARISTALUTA Öpik, 1961

ARISTALUTA SPICATA sp.nov.

(Pl. 2, figs 3, 4; Text-fig. 149)

*Material:* The available and illustrated material consists of a right and a left valve.

*Holotype:* The right valve Plate 2, figure 3, CPC 5363 is selected as holotype; its front is damaged, but the node and the sulci are well preserved.

*Diagnosis:* *Aristaluta spicata* sp.nov. is distinguished by its prominent and pointed anterodorsal node and a pair of sulci defining the base of that node, and by the subcircular outline of the carapace.

*Differential diagnosis:* In *Aristaluta gutta* Öpik, 1961, the anterodorsal node is less prominent and a sulcus is present in a mid-dorsal position that is absent in *A. spicata*; the outline of the carapace of *A. gutta* is leperditoid.

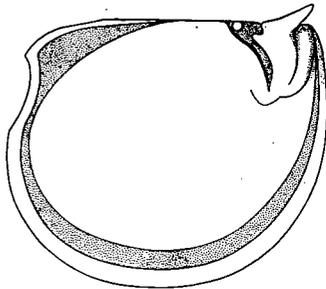


Fig. 149.—*Aristaluta spicata* sp. nov., from Plate 2, fig. 3.

*Description:* The holotype and the left valve (Pl. 2, fig. 4, CPC 5364) are equal in size, about 1·8 mm long and 1·7 mm high. The border is prominent, convex, and well defined by the marginal furrow; a doublure is present. The presence of a gap at the posterior extremity cannot be proved because the valves are somewhat flattened, and because no complete and uncompressed carapace is available; in the border at the posterior extremity, however, a recess is present, the edges of which appear flaring, and the posterodorsal part is not angulate but rounded, as seen in *A. gutta*; hence a gap was probably present.

The test is smooth and shiny.

*Occurrence and age:* *Aristaluta spicata* comes from the Mungerebar Limestone, locality G9; its age is the Middle Cambrian/Upper Cambrian Zone of passage.

## VERMES

Problematica (castings, burrows) occur in the Mungerebar Limestone at localities G113, G114, G127, G151, G400 and G437. Almost every locality has its own kind of burrows, which however are rather uninformative. The localities above represent all three zones of the Mindyallan.

### *Castings No. 1*

(Pl. 2, fig. 1)

The castings No. 1 (CPC 5361) occur as patchy accumulations on an even bedding plane in limestone. They are stained brown and silicified. Some appear striate longitudinally; the length of an individual dropping varies from 2 to 3 cm; having been apparently plastic they are flattened and each follows the relief of its substratum of other castings which cross each other irregularly in all directions. The animal itself is unknown; it was, perhaps, a swimmer resting for a while and digesting its meal.

*Occurrence and age:* Several patches of these castings were collected in the Mungerebar Limestone at locality G127; the age is the Mindyallan Zone of *Cyclagnostus quasivespa*.

### *Burrows No. 2*

(Text-fig. 14)

The illustrated burrows come from locality G400 (Mungerebar-Mindyalla area, map, Text-fig. 3), left bank of the Georgina River. The rock is a relatively coarse-grained dolomite—a rather unusual sediment for bearing, as well as preserving, burrows. When these burrows were made it was an unconsolidated dolomite sand. It is difficult to imagine the food the animals were searching for in the dolomite precipitate, devoid of any trace of life except the burrowing animals themselves.

The diameters of the burrows are of all sizes up to 1·5 cm. and all are found in a single bed near its upper bedding plane. It is a relatively large outcrop of dolomite cleft into blocks by joints and protruding through the sand of the flood plain of the Georgina River.

*Occurrence and age:* The dolomite is apparently an interbed in the upper part of the Mungerebar Limestone; its age is the Mindyallan *Glyptagnostus stolidotus* Zone. Direct evidence for the formation and age are not present; the locality is, however, within the belt of outcrops of the *stolidotus* Zone; south from G400, and hence higher in the sequence, at G140 in a dolomitic limestone *Acrothele* occurs; an identical rock with *Acrothele* and *Blackwelderia* is seen at localities G161 and G409 at McCabe Knob.

## GLOSSARY

### (Explanation of New Names of Fossils)

- abundans* (*Cermataspis*): Lat., 'abundant'.
- Acrodirotes*: Fem., Greek, 'high in the neck', alluding to the prominent occipital lobe.
- Adelogonus*: Masc., Greek, 'obscure in origin'.
- adnatum* (*Placosema*): Lat., 'attached' (refers to the fused rim).
- advena* (*Mindycrusta*): Lat., 'newcomer'.
- Aedotes*: Fem., Greek, 'distinguished by modesty', referring to the small size of the fossil.
- Agelagma*: Neuter, Greek, 'detached from the herd'; agma—splinter; agele—herd; refers to the main occurrence of the lonchocephalids in North America.
- Agnostascus*: Masc., Greek, 'unknown bag', alludes to the shape of the pygidial axial lobe.
- Agnostoglossa*: Fem., Greek, 'unknown tongue'.
- Agnostogonus*: Masc., Greek, 'unknown origin'.
- agrestis* (*Idolagnostus*): Lat., 'rustic', 'of the fields'; compare *dryas*.
- Ammagnostus*: Masc., Greek, 'sandy *Agnostus*'; alludes to the granulose ornament.
- ampullatus* (*Pseudagnostus*): Lat., 'with a bottle', alludes to the shape of the pygidial axial lobe.
- amydium* (*Teimistion*): Greek, 'without ship'; alludes to the meaning of *Teimistion* (q.v.).
- anitys* (*Ascionepea*): Greek, 'rimless' ('no rim').
- Anopocodia*: Fem., Greek, 'eyeless head'.
- apicula* (*Oxyagnostus*): Lat., 'little bee', alludes to the shape of the pygidial axis with a terminal 'sting'.
- arenata* (*Quitacetra*): Lat., 'sprinkled with sand', alludes to the occurrence in sandstone.
- artilmbatus* (*Agnostus*): Lat., 'having a narrow border'.
- Ascionepea*: Fem., Greek, askia—'no shade' and *Nepea* (a genus of trilobites), 'casting no shadow', alluding to the occurrence in the tropics.
- asper* (*Lophoholcus*): Lat., 'rough', in reference to the accentuated relief.
- aspis* (*Paracoosia*): Greek 'shield'.
- Aulacodigma*: Neuter, Greek, 'channel pattern', alluding to the interocular channels.
- auriculata* (*Meropalla*): Lat., 'with little ears' (palpebral lobes).
- aurita* (*Auritama*): Lat., 'equipped with handles'.
- Auritama*: Fem., Lat., 'ear' and 'vessel', alluding to the field name 'jughandles', in reference to the arcuate palpebral lobes.
- baccata* (*Idamea*): Lat., 'set with pearls', alluding to the ornament.
- bassa* (*Agnostoglossa*): Lat., 'low, depressed', alludes to the low tumidity of its acrolobes.
- Biaverta*: Fem., Lat., 'double saddle bag'; alludes to the shape of the cephalon.
- biaverta* (*Biaverta*): see above.
- bidens* (*Meteoraspis*): Lat., 'with two teeth'—the short pygidial spines.
- bigenensis* (*Triadaspis*): Lat., 'of a twofold origin', alluding to the similarity to both *Aspidagnostus* and *Oidalagnostus*.
- bisectus* (*Clavagnostus*): Lat., 'divided in two halves', alludes to the preglabellar median furrow.
- bulgosus* (*Pseudagnostus*): Lat., 'bulging'.
- caelatum* (*Placosema*): Lat., 'vaulted', 'arched'.
- caseyi* (*Leichneyella*) after J. N. Casey, leader of the Georgina Geological Party.
- Cermataspis*: Fem., Greek, 'small shield', small 'piece of a shield'.
- compacta* (*Mindycrusta*): Lat., 'compact'.
- Connagnostus*: Masc. Greek; konnos, 'beard', alludes to the pygidial axial lobe having the appearance of a bearded mask.
- correctus* (*Hypagnostus*): Lat., 'corrected', alludes to an earlier misidentification.
- cos* (*Leiopyge*): Lat., 'stone'.
- crassus* (*Diplagnostus*): Lat., 'robust'.
- Cyrtoprora*: Fem., Greek, 'scroll prow', refers to the involute cranial rim.
- declivis* (*Aedotes*): Lat., 'steep', with steep slopes.
- dipentus* (*Dipentaspis*): Greek, 'two fives'; see *Dipentaspis*.
- Dipentaspis*: Fem., Greek, 'twice-five shield', alludes to the five pairs of pygidial marginal spines.
- Dipyrgotes*: Fem., Greek, 'two turrets', alludes to the turret eyes.
- discretus* (*Plurinodus*), Lat., 'separated' (from all other associated agnostids).
- dissidens* (*Palaeadotes*): Lat., 'dissident', not agreeing with *Drepanura*.
- Doremataspis*: Fem., Greek, 'gift shield'.
- dubitalis* (*Norwoodella?*): Lat., 'doubtful'.
- durus* (*Hypagnostus*): Lat., 'enduring', 'lasting', alluding to the longevity of its genus.
- dryas* (*Idolagnostus*): Greek, 'dryad', but also 'of the woods'; see also *agrestis*.
- enodis* (*Alomataspis*): Lat., 'smooth', 'nodeless'.
- Erediaspis*: Fem., 'Eredia's shield' After the Portuguese navigator Emanuel Godinho de Eredia, who reached the north coast of Australia in 1601.
- eretes* (*Erediaspis*): Greek, 'rower', 'oarsman', alluding to the long pygidial spines.
- erista* (*Solenopleura?*): Greek, 'contested', 'matter of contention'.

*euryaxis* (*Ammagnostus*): Greek, 'broad axial lobe'.  
*evexus* (*Grandagnostus*): Lat., 'rounded', 'tumid'.  
*expansa* (*Auritama*): Lat., 'broad'.  
*extricans* (*Idamea*): Lat., 'disentangling' (the concept of *Idamea*).  
*fastosa* (*Acrodirotes*): Lat., 'proud', 'arrogant'.  
*Ferenepea*: Fem., Lat., 'almost *Nepea*'.  
*flexuosa* (*Polycyrtaspis*): Lat., 'full of curves'.  
*georginae* (*Blountia*): Lat., genitive, 'of the Georgina River'.  
*gibberina* (*Blackwelderia*): Lat., 'little humpback', refers to the high glabella.  
*globiceps* (*Anopocodia*): Lat., 'globe head', in reference to the frontal boss.  
*gravis* (*Agnostascus*): Lat., 'heavy'.  
*Griphasaphus*: Masc. Greek, 'riddle' and '*Asaphus*'.  
*griphus* (*Griphasaphus*): Greek, 'riddle', 'puzzle'.  
*Hadragnostus*: Masc. Greek, 'bulky' and *Agnostus*, as regards the glabella and the pygidial axial lobe.  
*Henadoparia*: Fem., Greek, 'unit cheek', alluding to the cephalon fused into a single shield.  
*hispidia* (*Ferenepea*): Lat. 'bristly', with a pustulose ornament.  
*Histiomona*: Fem., Greek, histion, sail as in *Teinistion* (q.v.), and mona (mone) a suffix denoting quality.  
*idalis* (*Pseudagnostus*): Lat., abbreviated from 'ida(me)lis', alluding to the Idamean aboriginal tribe.  
*Idolagnostus*: Masc., Greek and Latin, 'idol unknown', alludes to the glabella having the shape of an effigy.  
*illimbatum* (*Aulacodigma*): Lat., 'deprived of the rim'.  
*immodulata* (*Modocia*): Lat., 'not according to measure'.  
*incognitus* (*Agnostogonus*): Lat., 'unknown'.  
*Iniotoma*: Fem., Greek, 'occiput dissected' in reference to the abbreviated occipital furrow.  
*iniotoma* (*Iniotoma*): see above.  
*Innitagnostus*: Masc. Lat.-Greek; see *innitens*.  
*innitens* (*Innitagnostus*): Lat., 'frosted', alludes to the minutely granulose surface without lustre.  
*inquilinus* (*Aspidagnostus*): Lat., 'sojourner'.  
*instans* (*Aedotes*): Lat., 'standing by', referring to its abundant occurrence.  
*integra* (*Henadoparia*): Lat., 'whole', 'undivided', with fused sutures.  
*integriceps* (*Ammagnostus*): Lat., 'entire head' alludes to the absence of the preglabellar median furrow.  
*Interalia*: Fem., Lat., 'among others'.  
*intricata* (*Cyrtopora*): Lat., 'intricate', in reference to the involute rim (scroll).  
*italops* (*Palaeadotes*): Greek, 'bullface' (see Text-fig. 132, upside down).  
*janitrix* (*Ascionepea*): Lat., 'usherette', for example, ushering in the Upper Cambrian.  
*Lampropeltis*: Fem., Greek, 'shiny shield'.  
*las* (*Hadragnostus*): Greek, 'stone'.  
*laticeps* (*Agelagma*): Lat., 'broad-headed'.  
*Leichmeyella*: Fem., from Leichney, maiden name of J. N. Casey's mother (see under '*caseyi*').  
*lenis* (*Glyptagnostus*): Lat., 'smooth', 'mild', without rugae.  
*Lispagnostus*: Masc. Greek, 'smooth' and '*Agnostus*', as distinct from the blistered *Glyptagnostus*.  
*Lophoholcus*: Masc., Greek, 'crest and furrow', alludes to the strong relief of the cephalon.  
*lunatula* (*Peichiashania*): 'equipped with a crescent' (the flat rim).  
*Lynaspis*: Fem., from Lyndon C. Noakes, geologist, author's companion in the field in Queensland.  
*Meringaspis*: Fem., Greek, 'bristle shield', refers to the spiny pygidium.  
*meringaspis* (*Meringaspis*): see above.  
*Meropalla*: Fem., Greek, 'part of a ball', refers to the globose cephalon.  
*mestus* (*Pseudagnostus*): Greek, 'well fed', 'full', referring to the tumid pygidial acrolobe.  
*Metopotropis*: Fem., Greek, 'forehead with keel', in reference to the tropidium.  
*Mindycrusta*: Fem., combined from 'Mindyalla', and 'crusta' (as in Crustacea).  
*mindycrusta* (*Mindycrusta*): see above.  
*mitis* (*Ammagnostus*; *Plectrifer*): Lat., 'humble'.  
*mutans* (*Aedotes*): Lat., 'changing'.  
*neuter* (*Rhyssometopus*): Lat. 'neuter', referring to the arbitrary subgeneric classification.  
*Nilegna*: Fem., anagram to commemorate N. P. Angelin (Angelin spelled in reverse).  
*nitens* (*Lampropeltis*): Lat., 'shiny'.  
*noakesi* (*Lynaspis*): see *Lynaspis*.  
*nobilis* (*Peratagnostus*): Lat., 'noble', 'of nobility' in the sense of a long ancestry.  
*nodibundus* (*Prychagnostus*): Lat., 'very nodose'.  
*volens* (*Liostracina*): Lat., 'unwilling'; see also *volens*.  
*Nomadinis*: Masc., Greek, 'descendant (inis) of nomads'.  
*notostena* (*Mindycrusta*): Greek, 'back narrow', with a narrow pygidial axis.  
*novella* (*Dipyrgotes*): Lat., 'novelty'.  
*oculosa* (*Histiomona*): Lat., 'with large eyes'.  
*offula* (*Onchonotellus*): Lat., 'little thing', 'bit'.

*ornata* (*Doremataspis*): Lat., 'ornate'.  
*Oxyagnostus*: Masc., Greek; oxys—'sharp', 'pointed', alludes to the shape of the rear of the pygidial axis.  
*Palaeadotes*, Fem., Greek, from Palaeades Dalman, 1827—another name of trilobites.  
*pelta* (*Peichiashania*): Greek, 'shield'.  
*Peratagnostus*: Masc., Greek; peras—'end' in the sense of 'the last' of the Quadragnostinae.  
*personatus* (*Oidalagnostus*): Lat., 'having a mask', alludes to the bearded mask-like pygidial axis.  
*pilaris* (*Ferenepea*): Lat., 'of a ball', having a globose preglabellar boss.  
*Placosema*: Neuter, Greek, plax—'plate', 'tablet'; sema—'token'.  
*Plectrifer*: Masc., Lat., 'plectrum carrier'.  
*plectrifer* (*Plectrifer*): see above.  
*Plurinodus*: Masc., Lat., 'many nodes', alludes to *Trinodus*.  
*Polycyrtaspis*: Fem., Greek, 'manifold curved shield'.  
*princeps* (*Rhyssometopus*): Lat., 'chief'.  
*priscilla* (*Saukia*): Lat., 'ancient'.  
*pristinus* (*Nomadinis*): Lat., 'ancient'.  
*psammius* (*Ammagnostus*): Greek, 'sandy'.  
*pyriceps* (*Lobocephalina*): Lat., 'pear head', refers to the pear-shaped glabella.  
*quadrans* (*Meropalla*): Lat., of a quarter part (the cephalon is one quarter of a sphere).  
*quadratum* (*Agelagma*): Lat., 'square'.  
*quasispinale* (*Aulacodigma*): Lat., 'simulating a backbone' in the structure of the axis of the thorax.  
*quasivespa* (*Cyclagnostus*): Lat., 'simulating a wasp', alludes to the shape of the pygidial axial lobe.  
*Quitacetra*: Fem., combined from the geographic name Quita (creek, area), and cetra (Lat.), 'small shield'.  
*Quitalia*: Fem., combined from the geographic name Quita (creek, area), and—alia (Lat.) 'another'.  
*rasilis* (*Xestagnostus*): Lat., 'scraped smooth'.  
*ratis* (*Dipentaspis*): Lat., 'raft', in reference to the shape of the cranidium (see under *Teinistion*).  
*reineri* (*Biaverta*): After Dr E. Reiner (see Öpik, 1960, p. 90.)  
*repanda* (*Blackwelderia*): Lat., 'rearward bent', in reference to the frontal border.  
*Rhyssometopus*: Masc., Greek, 'wrinkled forehead', alludes to the field name 'wrinklefront'.  
*rhyssometopus* (*Rhyssometopus*): see above.  
*Rostrifinis*: Masc., Lat., 'beak end', referring to the frontal cusp.  
*rostrifinis* (*Rostrifinis*): see above.  
*rugiceps* (*Rhyssometopus*): Lat., 'wrinkled head'.  
*sabulosa* (*Blackwelderia*): Lat., 'sandy', referring to the granulosity of the test.  
*serena* (*Interalia*): Lat., 'serene'.  
*sericatus* (*Pseudagnostus*): Lat., 'having a silky lustre'.  
*serus* (*Ptychagnostus*): Lat., 'late'.  
*sigmata* (*Nilegna*): Lat., 'with sigmas' (sigmate palpebral lobes).  
*solus* (*Adelogonus*): Lat., 'single', 'lonely'.  
*spicata* (*Aristaluta*): Lat., equipped with a point.  
*stictus* (*Aspidagnostus*): Greek, Lat., 'pricked', with scrobicular pits.  
*Teinistion*: Neuter, Greek, 'spread sail', 'canvas', Monke, 1903., p. 117. The new names (q.v.) *amydium*, *Histiomona* and *ratis* allude to this name.  
*tiro* (*Rostrifinis*): Lat., 'beginner', the earliest known species of its genus.  
*torosa* (*Damesella*): Lat., 'bulging'.  
*Townleyella*: Fem., from the geologist K. A. Townley, the Editor of this Bulletin and author's companion in the field in Queensland.  
*townleyi* (*Townleyella*): see above.  
*tranans* (*Olenoides*): Lat., 'swimming by'.  
*travesi* (*Metopotropis*): after the geologist D. M. Traves, author's travelling companion in northern Australia.  
*Triadaspis*: Fem., Greek, 'shield in triads', referring to the trifold division of each part of the axial lobe.  
*tridens* (*Oedorhachis*): Lat., 'trident', alludes to the three marginal spines in the pygidium.  
*trilunata* (*Auritama*): Lat., 'with three crescents' (the cranial rim and the two palpebral lobes).  
*uncata* (*Quitalia*): Lat., 'hooked', referring to the pygidial spines.  
*venerabilis* (*Connagnostus*): Lat., 'venerable'.  
*vetusta* (*Saratogia*): Lat., 'ancient'.  
*vicaria* (*Pseudagnostina*): Lat., 'deputy'.  
*volens* (*Liostracina*): Lat., 'willing'; see also *nolens*.  
*Xestagnostus*: Masc., Greek, 'polished *Aagnostus*'.  
*zonatus* (*Connagnostus*): Greek, Lat., having a zonate pygidium.

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