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MIDDLE CAMBRIAN AGNOSTIDS: SYSTEMATICS AND BIOSTRATIGRAPHY

By

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PART III: PALAEOZOOLOGY

SUMMARY

Biostratigraphy and palaeobiogeography

The zonal distribution of 147 species of Agnostacea is shown in the 'Fundamental Chart'. Westergaard's Swedish scale of zones is used with some small amendments. *Hypagnostus parvifrons* is replaced by *Euagnostus opimus* and the pair of zones of *Ptychagnostus punctuosus* and *Pt. lundgreni-Goniagnostus nathorsti* is developed to three zones of which the middle one, the 'Zone of *Pt. punctuosus* and *G. nathorsti*', is renamed the 'Zone of *Doryagnostus notalibrae*'. The three topmost zones (*Pt. cassis, Leiopyge laevigata* I; *Proampyx agra, L. laevigata* II; and *Holteria arepo, L. laevigata* III) were erected by Öpik (1961b). The panel diagram, Text-figure 1, is condensed from the 'Fundamental Chart' to illustrate the number of species in each of the zones; over 75 species are concentrated in the three zones from *Pt. punctuosus* to *G. nathorsti,* constituting the Undillan Stage. The scale of stages contains four entities: Templetonian, Floran, Undillan, and Boomerangian. The zones and the stages are biostratigraphic operational units of aggregates of species taxa. Of lesser use in stratigraphy are the genera (Text-fig. 1). The biostratigraphic scales of the Northern Hemisphere operating with species of *Paradoxides* can be correlated approximately with the scale of agnostid species; *Paradoxoides* itself vanished before the end of the Epoch. The scale of agnostids is applicable in Scandinavia, Britain, Siberia, northwest Greenland, Newfoundland and New Brunswick, and possibly also in northern Tibet and in China. The omnipresence of some 22-28 species is taken as the main evidence of the pelagic mode of life of agnostids and of a global communication between the Middle Cambrian oceans and seaways.

Morphology and organisation

Agnostids usually occur as disjointed sclerites; most of these are exuviae, but a few belong to secondarily dismembered exoskeletons of dead individuals. Articulated exoskeletons are relatively rare and belong to dead bodies. The enrolled (coiled) skeletons indicate failure of uncoiling which terminated in death. The frequency of remains embedded in a convex-down attitude indicates free fall and moulting above the sea-floor. Conspecific cephala and pygidia in multispecific assemblages can be matched by the method of related points of the acrolobes.

Complete specimens provide information regarding the relative length of tagmata and of the sclerites of the thorax. In the great majority the cephalon is longer than the pygidium; the longest pygidium known is 1.2x the cephalon in length; equality of the shields is rare; pygidia are a little longer than the cephalon. The length of the thorax in relation to the cephalon, depending on the species, is variable between 0.18 and 0.36x; variability within a species remains, however, unknown owing to scarcity of measurable material. The anterior segment of the thorax in all measurable specimens is a little longer than the posterior; the anterior segment, however, owing to the absence of the articulating half-ring is frequently rotated after death out of plane and therefore seems short.

The form of the exoskeleton is semi-ellipsoidal; the dorsum is convex, the ventral side is concave in the living animal. This is a hydrodynamic form advantageous to the streamlined animal in swimming. The shields are semi-elliptical and so is the whole exoskeleton; this is a stabilised shape whose monotony may be lessened by the pygidial marginal spines.

The shape of the axial lobe (Text-fig. 2) provides some taxonomic criteria, such as the shape of the glabellar front, the deflection of the axial furrows at the basal lobes, length and form of the pygidial axis, incidence of effacement in the axial furrows, and the relative length of these furrows.

In agnostids genal and pleural spines are absent; in their thorax only the posterior segment has pointed pleural tips, which are not spines. Paired spines are carried on the fulcra and pairless on the axis. Short fulcral spines are called prongs; retrally directed external prongs cover the articulating sockets and the forward-directed prongs, whose tips rest on the sockets. The prongs are part of the articulating mechanics of the skeleton. The pygidial marginal spines are non-functional external prongs. The external prongs may be developed into spines in the cephalon and the second segment of the thorax in a number of species of the Ptychagnostinae.

Axial (median) spines, when present, are placed on the glabellar rear (in *Goniagnostus* and its subgenera), on the second segment of the thorax, and on the second annulation of the pygidial axis, and are of no particular function; in the spinose group the distribution and the length of fulcral and axial spines are of value in taxonomy.

Homologous elements

The posterior part of the cephalon, the segments of the thorax and the two anterior annulations of the pygidial axial lobe are homologues: the basal lobes in the cephalon are

repeated in the segments of the thorax, and the median part of the axis between the two rows of the post-cephalic basal lobes is the continuation of the glabella; the same applies to the repetition of the posterior part of the cheeks and to the fulcra as annotated in the diagram of *Diplagnostus floralis* (Text-fig. 5).

Appendages (legs) are not preserved, but their presence is indicated by 'muscle scars', notulae, and apodemal pits—the places and points of attachment of tendons in the integument that served to hold the legs. The arrangement is segmental; they are absent on pleurae; the sites are in the cephalic and postcephalic basal lobes and on the pygidial axis. *Doryagnostus magister* serves as an example. The distribution and character of 'muscle spots' in the cephalon is more complicated: for example, tendons in pairs of pits in the transverse glabellar furrow may have suspended the hypostoma; in *Goniagnostus* the lateral glabellar furrows each contain two pits and there is a pair of strong pits (apodemes) close to the glabellar rear.

Five original metameres are fused in the cephalon. There are four in front of the posterior cephalic segment containing the basal lobes; in forms having double basal lobes the anterior pair is interpreted as belonging to the second metamere; the third metamere is marked by the median glabellar node and the lateral glabellar furrows; in front of it the fourth includes the transverse glabellar furrow, and the fifth is the frontal glabellar lobe. The latter carries a pair of large muscle scars in *Galbagnostus* but can be obscured or even obliterated as in *Hypagnostus*.

Merocyclism. In the middle third of the body the periodicity of the sequence of macrosomites and ordinary somites is diadic, as reflected in the external morphology of the exoskeleton; the posterior cephalic segment, which is a segment of the thorax fused to the cephalon, is a macrosomite; the anterior segment of the thorax, lacking extended pleural extremities and an articulating half-ring, is an abbreviated ordinary segment; the next diad comprises the posterior segment of the thorax, a macrosomite, with extended pleurae equipped with articulation facets, articulating half-ring and doublure, frequently with fulcral spines and an axial spine; behind it the anterior annulation of the pygidial axis is normal, and followed by the macrosomite of the second annulation carrying a median node or a spine.

Articulation of the exoskeleton. Coiling (folding) and uncoiling (unfolding) were inherent to agnostids; these were achieved by downward and upward rotation of the cephalon and the pygidium in relation to the thorax and to each other; the rotational play of the segments of the thorax in relation to each other was, however, rather limited because they were interlocked with their pleural terminations; the exoskeleton was (and is) triplicate, and the coiling was performed by clasping the margins of the cephalon and pygidium together, with the thorax standing as the spine of a bound book. The folding was a reflex action in response to an external stimulus.

Agnostids fed on microplankton available in the global marine pelagic realm; water and food were sucked in through the frontal aperture of the hypostoma, the food was retained as a filtrate and the water was ejected by the cephalothoracic aperture as a retrally directed jet by the forward-swimming animal. In the folded state the front was closed, the intake was closed, and the jet was cut out; failure to unfold resulted in suspended animation, starvation, and death.

Mode of life of agnostids

The agnostid trilobites populated the pelagic marine realm—a conclusion based on the following observations: (1) many species occur universally and the scale of the species-zones is of a global validity; (2) agnostid remains occur in all kinds of sediments, which are their burial grounds, whose composition and bathymetry had no influence on life in the pelagic realm; (3) the small size and streamlined body were an advantage in feeding on microplankton; and (4) the absence of eyes remains a problem of their phylogeny but was no disadvantage in feeding day and night.

Systematics

The described species are attributed to two families—the Diplagnostidae (Diplagnostinae) and the Agnostidae. In the Agnostidae three subfamilies are recognised: the Quadragnostinae, the new subfamily Euagnostinae, and the Ptychagnostinae. These taxa are discussed in terms of the 'Tabular Classification of Agnostids' (Öpik, 1967).

The Diplagnostinae received the genera *Pseudoperonopsis* (dormant so far) and the new *Iniospheniscus*. To the Quadragnostinae are added *Itagnostus* nov. (subgenus of *Peronopsis*) and the new genus *Svenax*, and lost by transfer are *Pseudoperonopsis* and *Euagnostus;* the Euagnostinae contain *Euagnostus,* the new genus *Rhodotypiscus,* and the well known *Doryagnostus* (by transfer from the Ptychagnostinae).

The heading 'Hypagnostinae' is employed for an aggregate of species containing some Quadragnostinae, especially *Hypagnostus parvifrons* (the type of its genus and of the Hypagnostinae), as well as forms whose subfamily classification is in need of further consideration.

The Ptychagnostinae are augmented by the new *Aristarius, Aotagnostus, Myrmecomimus, Acidusus, Onymagnostus, Agnostonymus, Zeteagnostus, Criotypus,* and *Allobodochus*—almost duplicating the role of the subfamily. It appears, however, that parcelling the aggregate of the Ptychagnostidae into subfamilies may not be quite successful. *Agnostus pisiformis* (but not the Agnostinae as a whole) and *Onymagnostus* (Ptychagnostinae) are morphologically very close to each other.

The ancestry of agnostids is unknown; the earliest known (from the late Lower Cambrian) display characters seen in *Peronopsis* and *Hypagnostus.*

The Agnostina and the Eodiscina constitute the order Miomera; Eodiscina share with polymerid trilobites several characters that are absent in the Agnostina.

Taxonomics

Diplagnostidae

Diplagnostus floralis sp. nov. is described in full; it is a regular species of its genus. Its annotated reconstruction in Text-figure 5 serves as a guide to the phenomenon of merocyclism and structural homology in the tagmata. *Pseudoperonopsis* Harrington, 1938 (type species: *Peronopsis sallesi,* France and Spain) is described as a diplagnostid; one in the Australian aggregate of five species is *Pseupdoperonopsis perplexa* (Robison) from Utah. *Iniospheniscus* gen. nov., of two named and one unnamed species, is endemic; the type is *I. talis* sp. nov.; prominent characters are the large pygidial axis and the narrow rim. *Baltagnostus* (originally a North American genus) is represented by two endemic species.

Quadragnostinae

Owing to the inferior state of preservation of its type (*Quadragnostus solus*), the concept of the subfamily remains diffuse.

The genus *Peronopsis* is revised on the basis of recent publications concerning its type species, *Peronopsis integra;* excluded from the genus are several forms attributed here to *Quadragnostus* (*quadratus* Tullberg), *Svenax* nov. (*P. pusilla* (Tullberg)), *Pseudoperonopsis; Itagnostus* is a new subgenus of *Peronopsis.* Four new species of *Peronopsis* are described from the Northern Territory, all much older than *P. integra;* the earliest is *P. longinqua* (early Templetonian); the others are a little younger.

The concept of *Acadagnostus* cannot be clarified on the basis of literature; conditionally it is referred to *Acadagnostus scutalis* (Salter), which is described.

Svenax gen. nov. is based on *Agnostus* (= *Peronopsis*) *pusillus*—a Scandinavian species found in Australia.

The name 'Hypagnostinae' Ivshin is a possible junior synonym of Geragnostinae Howell, 1935 because both are diagnosed in similar terms. Nevertheless, *Hypagnostus parvifrons* (the type of its genus) belongs subjectively to the Quadragnostinae ('peronopsids') and other forms in Ivshin's aggregates are of different affinities; so the concept is regarded as unoperational. The originally Swedish species *H. parvifrons* and *H. tjernviki* Westergaard are described; Whitehouse's *H. vortex* and *H. clipeus* are revised; *H. inaequalis* and *H. melicus* are new. Included is also *Tomagnostella.*

Euagnostinae nov.

In the Euagnostinae the pygidial axis is long, tapering, and pointed, and equipped with a rosette (a transverse furrow with a median node) and, among other characters, with a bluntly pointed to rounded glabellar front; the genera are *Euagnostus, Rhodotypiscus,* and *Doryagnostus*

Euagnostus Whitehouse (type: *opimus*) is described from a large supply including two complete exoskeletons; new species are *E. certus, neptis, levifrons,* and *E.? glandifer.* In *Rhodotypiscus nasonis* the glabellar front is rounded and its median node has an extreme retral position. *Doryagnostus* is well known; the Australian *D. magister* Whitehouse is described from numerous complete exoskeletons; new are *D. notalibrae* and *D. solidus;* the thorax in *solidus* is among the largest known in agnostids.

Ptychagnostinae

In previous publications I held that *Triplagnostus* and *Goniagnostus* are subgenera of *Ptychagnostus;* I now regard them as independent genera of the subfamily Ptychagnostinae as defined in the classification adopted in 1967.

Ptychagnostus punctuosus includes the originally Scandinavian subspecies *affinis* and the new subspecies *fermexilis*. *Ptychagnostus atavus* is common, and is accompanied by a rare subspecies—*atavus coartatus*. In two new species (*Pt. idmon* and *Pt. scarifatus*) the cephalic basal lobes are almost confluent with the glabella and the frontal glabellar lobe is relatively narrow.

Acidusus nov., described as a subgenus of *Ptychagnostus*, refers to species with a terminal axial node in the pygidium; spineless and spinose species are present. The new species *Acidusus occultatus* has cephalic fulcral spines and an axial spine; it was described by Whitehouse as *atavus*, but *atavus* is spineless.

Zeteagnostus incautus gen. nov., sp. nov. is distinguished by its rudimentary basal lobes, a terminal node in the pygidial axis, and a very short thorax; the frontal glabellar lobe is very narrow.

Onymagnostus gen. nov., whose type is *O. angulatus* sp. nov., refers to spineless species without a posterior median furrow and a pygidial axial node straddling the rear of the second annulation and the front of the posterior lobe; *Agnostus hybridus* represents *Onymagnostus* in the Northern Hemisphere. In Australia *Agnostus seminula* Whitehouse is also a species of *Onymagnostus*. *O.* (*Agnostonymus*) *semiermis* subgen. nov., sp. nov. is distinguished by its pygidial marginal spines and a rounded glabellar front.

Triplagnostus gibbus, the type of its genus, is stratigraphically significant and is revised on the basis of published data, Swedish specimens, and collections in hand. In *T. gibbus* the basal lobes are simple, pygidial marginal spines are absent, cephalic spines are long, and axial spines are present—one in the posterior segment of the thorax and another in the pygidial axis. The associated subspecies *gibbus posterus* nov. develops double lobes and short fulcral spines in the thorax and becomes abundant in the Zone of *Ptychagnostus atavus*. The subgenus *Triplagnostus* (*Triplagnostus*) includes also species with short pygidial marginal spines; one has single and another double basal lobes (*T. diremptus*). In *T. stramineus* these spines are very long. The species of the subgenus *Triplagnostus* (*Aristarius*) have single basal lobes and overextended pygidial marginal spines. *Aristarius ultimus* sp. nov. is the youngest of the genus, in the Zone of *Goniagnostus nathorsti*.

In species of *Aotagnostus* gen. nov. the glabella rises high retrally, the pygidial axial lobe is relatively short, its second annulation appears gibbose; in three species out of seven, pygidial marginal spines are absent; other spines (fulcral, and axial spines in thorax and pygidium) are prominent.

Species of *Myrmecomimus* gen. nov. have a short bulbous posterior axial lobe in the pygidium, no axial spines, and short fulcral spines only in the cephalon, which resembles *Aotagnostus;* individuals are small, the length of holaspides being between 2.2 and 4.5 mm.

Writers place *Pentagnostus* Lermontova in synonymy with *Peronopsis* or *Triplagnostus;* its pygidial trilobate axial lobe and the slender glabella indicate *Ptychagnostinae;* the generic characters are the rounded glabellar front and a pair of pits at the base of the glabella (as in *Goniagnostus*). *P. anabarensis* Lermontova and *Pentagnostus veles* sp. nov. are found in New South Wales, *Pentagnostus rallus* sp. nov. in the Northern Territory and, apparently, in Siberia. Westergaard's Swedish *Triplagnostus praecurrens* and *T. angermanensis* (from the Zone of *Pt. atavus*) are also attributable to *Pentagnostus; Triplagnostus burgenensis* Rasetti from the Canadian Rocky Mountains seems related to *praecurrens*.

Species of *Goniagnostus* are aggregated in three subgenera: *G.* (*Criotypus*) nov. with *C. oxytorus* as the type; *G.* (*Goniagnostus*), based on *G. nathorsti;* and *G.* (*Allobodochus*) nov., with *G. fumicola* as the type. These subgenera are presumed to be a phyletic sequence beginning with *Criotypus* in the Zone of *Pt. atavus*, followed in the Undillan by *G.* (*Goniagnostus*) and in the Boomerangian and early Upper Cambrian by *Allobodochus*. All known species are variously spinose and distinguished by an axial spine on the rear of the glabella; in *Allobodochus* a tubercle represents that spine. In *Criotypus* cephalic arcuate scrobicules are present and the pygidium contains no axial rosette; in *G.* (*Goniagnostus*) arcuate scrobicules are absent in all species and in the pygidial axis an incipient rosette develops. In *Allobodochus* the rosette becomes a transverse furrow separating the axial rear as a novel lobe.

The earliest representative of *Leiopyge* is *L. praecox* nov. in the zone of *Ptychagnostus punctuosus*, followed in the Zone of *Pt. nathorsti* by *L. cosfordae* sp. nov.; these two are spineless. In the Boomerangian *L. laevigata* and *L. armata* are present as well as the spinose and punctate *L. multifora* sp. nov.

Finally, the genus *Pseudophalacroma* and its species *dubium* are once more described as belonging to the Ptychagnostinae.

INTRODUCTION

This Bulletin presents the taxonomy, temporal stratigraphy, palaeogeography, and ecology of the Middle Cambrian agnostid trilobites beginning with their arrival in the Templetonian and reaching an acme of diversification in Undillan time; agnostids of the latest Middle Cambrian were described earlier (Öpik, 1961b, 1967).

The material described now contains numerous complete specimens which supplied information regarding the morphology and function of the agnostid skeletons so far not attainable with certainty from disjointed sclerites.

The nine named and one unnamed (the initial Templetonian) zones are integrated into four geographically named stages, completing the scale of stages by starting with the Ordian and leading into the early Upper Cambrian; the continuous sequence of stages reads: Ordian, Templetonian, Floran, Undillan, Boomerangian; followed by the early Upper Cambrian Mindyallan and Idamean.

The scale of the zones of the agnostid species is the pivot of the biostratigraphic documentation; it is the time scale A. H. Westergaard introduced in 1946 in Sweden. I have implemented this scale in Australia in the field and in unpublished and published reports for over two decades, but 'on parole', in advance of the descriptions and illustrations of the relevant fossils which are presented here.

Acknowledgement

The photographs reproduced in Plates 1-66 were taken by Mr H. M. Doyle.

PART I: BIOSTRATIGRAPHY AND PALAEOGEOGRAPHY

TEMPORAL DISTRIBUTION OF MIDDLE CAMBRIAN AGNOSTACEA

INTRODUCTION

The temporal, stratigraphic distribution of the Australian Middle Cambrian agnostids is presented in two tables: a table of species which is fundamental, and a table of the vertical distribution of genera; in both tables names are arranged according to the earliest appearance of each taxon.

In the fundamental Table 1 the species are distributed in a time stratigraphic scale of ten agnostid Zones. Each zone is a position in a time scale recognised from its fossils; it is named after a particular species that indicates the span of the zone, and that name serves as a code name for the associated fauna (see Öpik, 1963, pp. 10-14).

The topmost twenty species in the fundamental list have been described already (Öpik, 1961b, 1967). The Australian Middle Cambrian fauna also includes the following forms described and illustrated in terms of open nomenclature: in Öpik (1961b)—*Peronopsis* sp. G, *Diplagnostus* sp. I, *Hypagnostus* sp. F., *Ptychagnostus* sp. P. aff. *nathorsti, Pseudophalacroma* spp. K and L, and *Ptychagnostus* sp. O; in Öpik (1967)—*Peronopsis* aff. *fallax, Linguagnostus* sp. nov. aff. *kjerulfi,* and *Dolichoagnotus?* sp. nov., altogether ten items; these are omitted in Table 1. In the list itself 146 species are recorded, and the sum total of species so far known is therefore 156.

The names of agnostid species in Table 1 are arranged in stratigraphic order descending from the left to the right side columns. The list is accompanied by a diagram of numerical composition of the agnostid zones (Text-fig. 1) as a panel of steps: the earliest below and ascending in the conventional form of presentation of a stratigraphic sequence. The overlap of zones demonstrates the continuity of populations within the sequence; this continuity is visibly tenuous in passing from the Floran into the Undillan at the junction of the *Euagnostus opimus* and *Ptychagnostus punctuosus* zones and once more at the transition between the *Goniagnostus nathorsti* and the *Ptychagnostus cassis* zones.

THE TERMS 'ZONE' AND 'STAGE'

The descriptions of species in the taxonomic part of this monograph conclude with paragraphs headed 'Occurrence and age' and the age is referred to a particular zone or zones. The occurrence is described topologically (see Appendix 2).

In brief the term 'zone' is contemplated here as the designation of a position in a scale of geological time which itself is understood as the sequence of bygone geological (biological and inorganic) events; the scale of zones of species of agnostids refers in particular to bygone biological events. Stratigraphers sometimes employ the same word 'zone' as a term in describing units of extant and tangible strata—fossiliferous or otherwise. Sensible are also phrases like 'fracture zone', climatic zones etc. I understand that the word zone itself has been used as a heading of definitions of many diverse concepts and there is no need to restrict its usage to one of these 'by priority of publication'. In passing, 'zone' is mostly translated as 'belt'; in classical Greek, however, it stands for 'lower girdle of women' and in Latin for 'maiden's girdle'.

'No difference in principle exists between zones and stages; the only difference that matters is purely nomenclatorial: zones derive their names from fossils and stages have geographical names' (Öpik, 1963, pp. 10-11). So, the Boomerangian Stage is the zone of *Leiopyge laevigata,* the Undillan Stage is the zone of *Doryagnostus magister* (or of *Onymagnostus seminula*), and the Floran Stage is at the same time the zone of *Ptychagnostus idmon,* or of *Triplagnostus diremptus,* or of *Pseudoperonopsis ancisa,* or of all at once.

Extended discussions of the concepts of 'zone' as well of 'stage' in stratigraphy are available in my earlier papers (Öpik, 1963, pp. 10-12; 1967, pp. 5-7). In passing, stages and zones, as well as epochs and periods, are constructed and employed as biostratigraphic operational units.

THE STANDING OF THE AGNOSTID SPECIES ZONES AND ZONE SPECIES

In my studies I am operating with the well known scale of Middle Cambrian agnostid species zones published by Westergaard (1946) in Sweden and tested by him on evidence from Norway, Atlantic Maritime Canada, Britain, and also Australia; as a matter of fact, the nomenclature of zones in Table 1 is essentially the same as that employed by A. H. Westergaard. Prior to Westergaard the vertical distribution of agnostids had been studied in Norway by Brögger (1878) and in Sweden by Tullberg (1880); Henningsmoen (1956) in Norway and Hutchison (1962) in Canada (Newfoundland) also adopted Westergaard's scale.

In Australia, Whitehouse (1936, 1939) was the first to identify the presence of species of agnostids described by Tullberg (1880) from the Scandinavian Middle Cambrian. Westergaard's scale of zones was not yet published. With collections in hand I applied the Scandinavian scale in dating and correlation of Cambrian formations in Queensland (Öpik, 1956, p. 15) and again (Öpik, 1960) in a chart accounting for new information but in advance of palaeontological descriptions of the stratigraphically and biogeographically significant material. Soon after, however, followed the publication of the late Middle Cambrian agnostids and other fossils from Queensland (Öpik, 1961b), and the Upper Cambrian transition (Öpik, 1967).

The similarity of the Australian and the Swedish Middle Cambrian agnostid faunas can readily be illustrated. In Table 1, 22 species were described originally from Sweden. Westergaard (op. cit.) listed altogether 90 species; of these some 10 species belong to genera unknown in Australia (*Tomagnostus, Condylopyge,* and *Pleuroctenium*), leaving 80 species in genera also represented in Australia; of these, 22 species (27%) are also Australian. Likewise, not considering the 40 species of nine endemic Australian genera, some 110 species, which make up 20% of the 110.

The following agnostid species occur in the Middle Cambrian in Sweden and in Australia:

	Sweden	*Australia*
Oidalagnostus trispinifer	rare	rare
Hypagnostus cf. *sulcifer*	common	rare
Diplagnostus vestgothicus	rare	rare
Agnostus cf. *neglectus*	common	rare
Hypagnostus brevifrons	common	rare
Ptychagnostus aculeatus	common	rare
Goniagnostus (Allobodochus) spiniger	common	common
Leiopyge armata	common	common
Leiopyge laevigata	common	common
Hypagnostus tjernviki	rare	rare
Hypagnostus (Tomagnostella) nepos	infrequent	rare
Goniagnostus nathorsti	common	common
Onymagnostus stenorrhachis	rare	rare
Svenax pusillus	infrequent	rare
Ptychagnostus punctuosus	common	common
Ptychagnostus punctuosus affinis	common	common
Hypagnostus parvifrons	common	rare
Peronopsis fallax ferox	rare	rare
Ptychagnostus intermedius	rare?	rare
Ptychagnostus atavus	common	common
Triplagnostus gibbus	common	rare
'Peronopsis' or *'Acadagnostus' scutalis*	common	common

Comment that follows elucidates some aspects of the foregoing list.

The frequency of the occurrences of species cannot be described in terms of numbers of specimens, of course; these can be obtained by counting the sites and the number of specimens in each site—but only in collections; also, the supplies consist of disunited shields in the first place. Furthermore, the collections in Sweden were brought together by many persons and during some twelve decades of field exploration whereas the material in hand was collected in about four to five field seasons in a territory larger than that of the Middle Cambrian in Sweden. Admittedly, in the Australian column the designations 'rare' may change with the increase in numbers of sites and of specimens to be recovered from each site. It stands to reason, however, that the description 'common' cannot be degraded to 'rare' although barren strata within a zone, or absence of one or another species in particular sections, or 'bad luck', or an 'unlucky hammer' may accompany the collector of fossils in the field.

Stratigraphically and biogeographically important are the species which are common in Sweden as well as in Australia:

Leiopyge laevigata and *L. armata, Hypagnostus brevifrons, Goniagnostus nathorsti, Ptychagostus punctuosus* and *Pt. atavus*

These occur in Australia and in Sweden in the same superpositional order.

The zone-species *Triplagnostus gibbus* is common in Sweden but is rare in Australia owing to the small number of its known sites. The rest of the species in the Swedish-Australian list conform with the order of zones and, in the absence of one or another zone, species can serve in the identification of the scale position of collections.

CORRELATION OF BIOSTRATIGRAPHIC SCALES

Acadian and Middle Cambrian

In the chart 'Acadian Correlations' (Table 4) the name Acadian, introduced by Dawson in 1867 (1868), was adopted by Walcott (1891,

TABLE 1 (PART 1 OF 3)
FUNDAMENTAL TABLE SHOWING STRATIGRAPHIC DISTRIBUTION OF AGNOSTID SPECIES
(continues on next pages)

STAGES / Species Zones / Species Names	BOOMERANGIAN			UNDILLAN			FLORAN		TEMPLETONIAN		
	L. laevigata III (H. arepo)	L. laevigata II (Pr. agra)	L. laevigata I (Pt. cassis)	G. nathorsti	D. notalibrae (=punctuosus +nathorsti)	Pt. punctuosus	Euagnostus opimus	Pt. atavus	Tripl. gibbus	P. longinqua	
Dolagnostus dilemma	X										
Oidalagnostus trispinifer	X										
Allobodochus fumicola	X										
Grandagnostus velaevis	X										
Hypagnostus cf. sulcifer	X										
Hypagnostus varicosus	X										
Diplagnostus cf. vestgothicus	X										
Agnostus cf. neglectus	X										
Hypagnostus hippalus	X	X									
Hypagnostus willsi		X									
Diplagnostus crassus		X									
Oidalagnostus personatus		X									
Diplagnostus humilis		X									
Tomagnostella cf. nepos		X									
Hypagnostus cf. hunanicus		X									
Ptychagnostus cassis			X								
Ptychagnostus aculeatus			X								
"Peronopsis" scaphoa			X								
Blystagnostus laciniatus			X								
Hypagnostus brevifrons		X	X								
Allobodochus spiniger	X	X									
Leiopyge multifora		X									
Leiopyge nov. aff. armata		X									
Leiopyge armata	X	X									
Leiopyge laevigata	X	X	X								
Leiopyge cosfordae				X							
Myrmecomimus tribulis evanidus				X							
Aristarius ultimus				X							
Acidusus sp. indet. aff. germanus				X							
Acidusus retrotextus				X							
Oedorhachis crenias				X							
Hypagnostus tjernviki				X							
Tomagnostella nepos				X							
Aotagnostus modicus				X							
Goniagnostus verus				X							
Goniagnostus scarabaeus				X	X						
Goniagnostus nathorsti			X	X	X						
Doryagnostus sp. nov. aff. incertus					X						
Doryagnostus solidus					X						
Doryagnostus sp. aff. notalibrae					X						
Doryagnostus notalibrae					X						
Pseudoperonopsis insolita					X						
Hypagnostus inaequalis					X						
Cotalagnostus sp. aff. lens					X						
Baltagnostus robustus					X						
Onymagnostus durusacnitens					X						
Aotagnostus magniceps					X						
Doryagnostus magister				X	X	X					
Onymagnostus seminula				X	X	X					

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p. 248) as a series name to include the faunas of the *Paradoxides* zone; M. Grace Wilmarth (1925, 1938) in lexicons of the USGS refers to Acadian as a proper series-epoch name of the Cambrian. It is also employed by writers as the geographical name for the Middle Cambrian; in French usage (Hupé, 1953, p. 32), for example, this form of reference (Acadian = Middle Cambrian) is employed consistently, with the result that the pre-*Paradoxides* part of the Period became all Lower Cambrian (Géorgien). As is well known the '*Paradoxides* Zone' and the Olenellian (Georgian) are not in contact with each other; they are separated in Acadia by the intervening *Protolenus* sequence which postdates the exit of the olenellids and antedates the arrival of *Paradoxides*. It was identified by Matthew in New Brunswick (at Saint Johns), previously the French Acadie. In modern Canadian literature (Hutchinson, 1952, p. 54) Acadian is used as the name of the Middle Cambrian Epoch.

The *Protolenus* fauna and its sequence answer to the geographic name Hanfordian

TABLE 1 (PART 2 OF 3)
FUNDAMENTAL TABLE SHOWING STRATIGRAPHIC DISTRIBUTION OF AGNOSTID SPECIES
(continues on next pages)

STAGES	BOOMERANGIAN			UNDILLAN			FLORAN		TEMPLETONIAN		
Species Zones / Species Names	L. laevigata III (H. arepo)	L. laevigata II (Pr. agra)	L. laevigata I (Pt. cassis)	G. nathorsti	D. notalibrae (=punctuosus +nathorsti)	Pt. punctuosus	Euagnostus opimus	Pt. atavus	Tripl. gibbus	P. longinqua	
Onymagnostus cf. grandis					X						
Onymagnostus mundus					X						
Onymagnostus cf. stenorrhachis					X						
Svenax vafer					X						
Euagnostus levifrons					X						
Hypagnostus melicus				X	X						
Hypagnostus clipeus				X	X						
Grandagnostus imitans				X	X	X					
Pseudophalacroma dubium	X	X	X	X	X	X					
Aotagnostus culminosus					X	X					
Acidusus germanus					X	X					
Aotagnostus protentus					X	X					
Acidusus occultatus				X		X					
Acidusus acidusus					X	X					
Acidusus navus					X	X					
Myrmecomimus tribulis					X	X					
Pseudoperonopsis perplexa				X	X	X					
Ptychagnostus punct. affinis					X	X					
Ptychagnostus punctuosus punctuosus					X	X					
Goniagnostus nathorsti intersertus					X	X					
Myrmecomimus tribulis mixtus					X	X					
Ptychagnostus sp. nov. D						X					
Myrmecomimus saltus						X					
Doryagnostus incertus						X					
Aotagnostus aotus						X					
Baltagnostus sertulatus						X					
Acidusus sp. aff. occultatus						X					
Aristarius aff. ultimus						X					
Aristarius aristarius						X					
Iniospheniscus? sp. indet.						X					
Euagnostus sp. aff. opimus						X					
Euagnostus neptis						X					
Rhodotypiscus sp. nov. aff. nasonis						X					
Svenax pusillus						X					
Ptychagnostus punctuosus fermexilis						X					
Ptychagnostus mesostatus						X					
Leiopyge praecox						X					
Ptychagnostus (Acidusus) sp. nov.						X					
Criotypus sp. aff. paenerugatus						X					
Ptychagnostus sp. indet. C						X					
Ptychagnostus sp.indet.aff.ponebrevis						X					
Ptychagnostinae,gen.indet., sp.nov.						X					
Iniospheniscus talis						X					
Pseudoperonopsis iniugata						X					
Triplagnostus purus						X					
Criotypus mitigatus						X					
Aotagnostus ponebrevis						X	X				

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(Hanford Brook at Saint Johns); its approximate equivalent is the Australian Ordian Stage (Öpik, 1968a) of the pre-*Paradoxides* Middle Cambrian.

Consequently, the name Acadian as used in our chart describes the major part of the Middle Cambrian, the time of *Paradoxides* and of the arrival of the agnostid faunas; Acadian is, of course, Middle Cambrian, but Middle Cambrian is not all Acadian. Moreover, Middle Cambrian in its present usage is more than the interval of *Paradoxides* because this genus is absent in the uppermost zones of the scale. To conclude, Middle Cambrian can be taken as consisting (1) of the Acadian alone, or (2) of the Hanfordian (post-Olenellian, ante-Paradoxidian) and the Paradoxidian intervals together and (3) with or without the *Leiopyge laevigata* (post-Paradoxidian) top. In passing, *Leiopyge laevigata* and the genus *Leiopyge* occur in the early Upper Cambrian as well. I prefer to operate with the concept of Middle Cambrian as the post-Olenellian Epoch, terminating with the Zone of *Leiopyge*

TABLE 1 (PART 3 OF 3)
FUNDAMENTAL TABLE SHOWING STRATIGRAPHIC DISTRIBUTION OF AGNOSTID SPECIES

STAGES	BOOMERANGIAN			UNDILLAN			FLORAN		TEMPLETONIAN		
Species Names / Species Zones	L. laevigata III (H arepo)	L. laevigata II (Pr. agra)	L. laevigata I (Pt. cassis)	G nathorsti	D. notalibrae (= punctuosus + nathorsti)	Pt. punctuosus	Euagnostus opimus	Pt atavus	Tripl gibbus	P. longinqua	
Onymagnostus angulatus				X	X	X	X				
Diplagnostus floralis						X	X				
Ptychagnostus sp. aff. scarifatus							X				
Ptychagnostus scarifatus							X				
Criotypus sp. nov. aff. lemniscatus							X				
Rhodotypiscus nasonis							X				
Euagnostus opimus							X				
Euagnostus? glandifer							X				
Agnostonymus semiermis							X				
Onymagnostus sp. nov. aff. angulatus							X				
Hypagnostus parvifrons							X	X			
Peronopsis fallax ferox							X	X			
Euagnostus certus						X	X	X			
Triplagnostus diremptus							X	X			
Ptychagnostus idmon							X	X			
Criotypus lemniscatus							X	X			
Pseudoperonopsis ancisa							X	X			
Hypagnostus cf. vortex								X			
Iniospheniscus incanus								X			
Euagnostus sp. indet.								X			
Pseudoperonopsis syrma								X			
Diplagnostus atavorum								X			
Criotypus oxytorus								X			
Criotypus paenerugatus								X			
Criotypus sp. indet.								X			
Triplagnostus stramineus								X			
Aristarius retrocornutus								X			
Zeteagnostus incautus								X			
Ptychagnostus atavus coartatus								X			
Ptychagnostus intermedius								X			
Ptychagnostus sp.indet.B(aff.atavus)								X			
?Ptychagnostus sp.indet.A(aff.atavus)								X			
Triplagnostus scopus								X			
Triplagnostus sp. indet.								X			
Ptychagnostus atavus								X			
Triplagnostus quasigibbus								X			
Triplagnostus fretus								X			
Triplagnostus gibbus posterus							X	X	X		
Triplagnostus gibbus									X		
Peronopsis normata								X	X		
Pentagnostus anabarensis									X		
Pentagnostus veles									X		
Pentagnostus rallus									X		
Linguagnostus? comparabilis									X		
Acadagnostus scutalis									X		
Peronopsis comis									X		
Peronopsis tramitis									X		
Peronopsis prolixa									X		
Peronopsis (Itagnostus) elkedraensis									X	X	
Peronopsis longinqua										X	

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laevigata III, which, in its turn, remains inseparable from the Acadian for practical reasons.

MIDDLE CAMBRIAN STAGES AND ZONES IN AUSTRALIA

The scale of Middle Cambrian stages in our charts is an innovation in Australian stratigraphy in respect of the interval between the termination of the Ordian and the initial Late Cambrian Mindyallan time. Descending from the Mindyallan the stages are Boomerangian, Undillan, Floran, and Templetonian. The first three are proposed herein; the name and concept of the Templetonian are already used in the literature.

The name Boomerangian refers to Boomerang Creek in the northern part of the Burke River Outlier (Öpik, 1961b, text-fig. 2, p. 10; Duchess 4-mile Geological Sheet, Carter & Öpik, 1963); the strata in question have been examined and their fossils described from outcrops at the heads of Boomerang Creek. Other places (Öpik, 1961b, text-fig. 1) are locality T87 (q.v.) in the Tobermory area, and Marion Downs in the Mount Whelan area about the

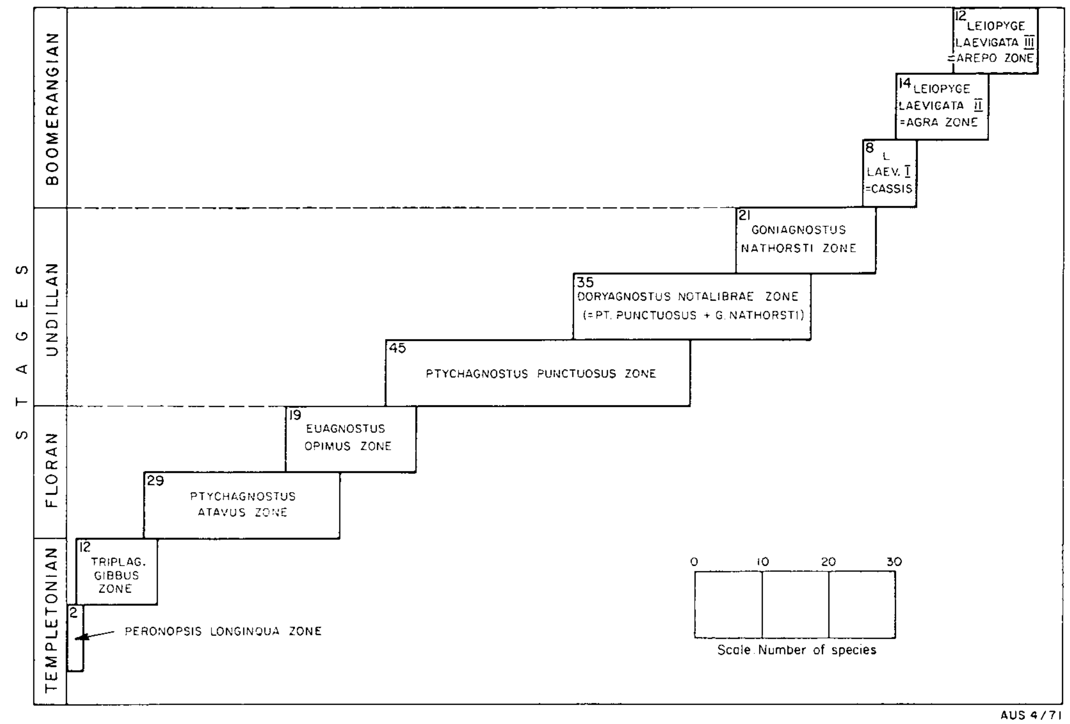


Fig. 1. Distribution of species in the agnostid zones—data extracted from Table 1.

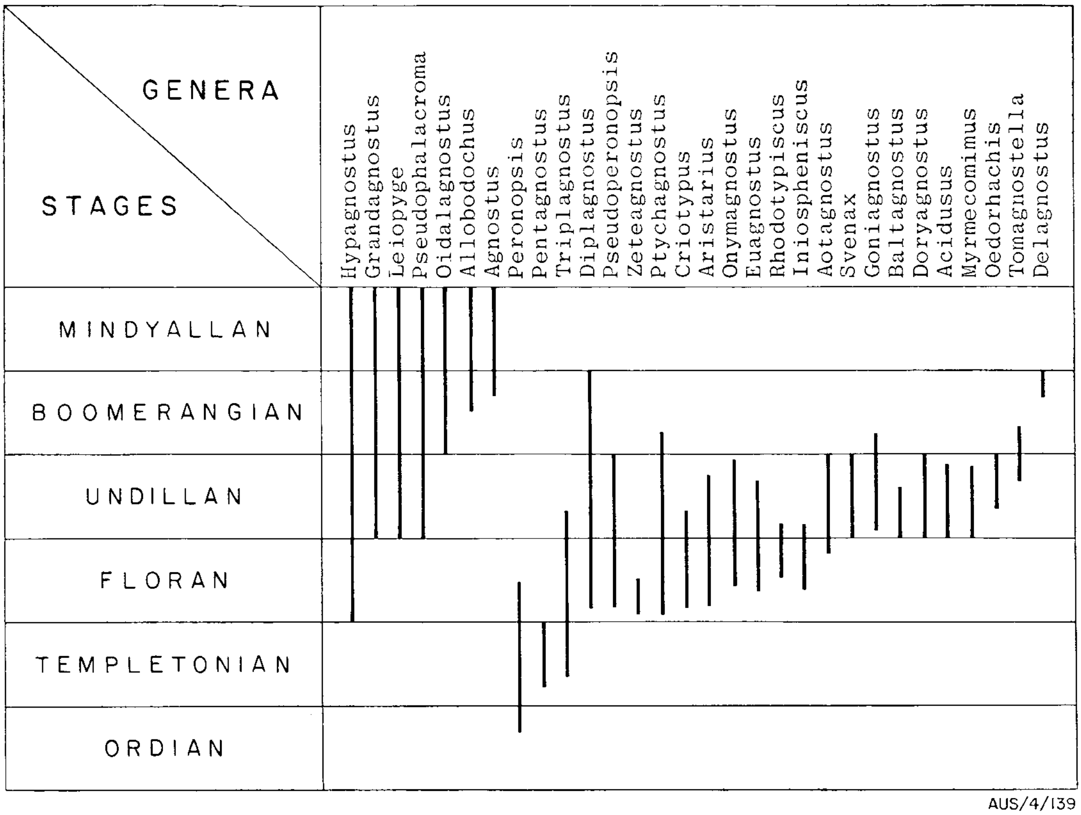
heads of Deadman Creek; of the same age is the Steamboat Sandstone in the southeastern part of the Urandangi and northeastern part of the Glenormiston Sheet areas.

The Boomerangian embraces three zones (*Leiopyge laevigata* I, II, and III) and can be interpreted as the Zone of *Leiopyge laevigata* (but not of the genus *Leiopyge*!); these zones are, however, separable by other faunal components (Öpik, 1961b, text-fig. 15).

The name Undillan refers to the pastoral property Undilla in the Camooweal area. The fossils collected at site M41 (lat. 19°27.5′S, long. 138°38′E) belong to the *Doryagnostus notalibrae* Zone (see below); the *Goniagnostus nathorsti* Zone fossils are exceptionally abundant at site M57, 20 km west of south from Undilla homestead. Other collecting sites of fossils of these two Zones and of the Zone of *Ptychagnostus punctuosus* are entered in the list of localities, Appendix 2. The Undillan—a stage (a scale division) of three zones—is a necessity in biostratigraphic practice: (1) the zone species *Goniagnostus nathorsti* and *Ptychagnostus punctuosus* occur in the middlemost zone together and in good numbers, preventing a clear definition of a 'pure' *punctuosus* and a 'pure' *nathorsti* zone in terms of Westergaard's Swedish scale; at the same time in Norway (Brögger, 1898, table facing p. 34) the overlap of *punctuosus* and *nathorsti* recalls the situation in Australia. In Queensland, however, a long fossil list covers that overlap, with some 20 bi- to trizonal species and another 15 confined to the interval of the overlap. Among the latter species only *Doryagnostus notalibrae* is common enough to serve as a name-giver to the zone—which is identifiable from its total assemblage and by its 'in between' position in the stage. As explained below in the discussion on Table 4, the names 'Zone of *Doryagnostus notalibrae*' or '*notalibrae* Zone' will be used for the interval where *Ptychagnostus punctuosus* and *Goniagnostus nathorsti* occur together. The interval of the three zones of the Undillan answers to the two zones (*punctuosus* Zone and *Ptychagnostus lundgreni-Goniagnostus nathorsti* Zone) of the Scandinavian scale.

The name Floran refers to the grass plain known as Flora Downs, with the Flora Bore, immediately southeast of the junction of Inca Creek and the Buckley River, Mount Isa 1:250 000 Sheet area; there is also a Flora

TABLE 2
STRATIGRAPHIC DISTRIBUTION OF AGNOSTID GENERA



Creek Waterhole, 17 km downstream from that junction; the coordinates, lat. 20°13'S, long. 138°47'E, describe a point on the Flora Downs plain. The strata are siliceous shale and siltstone with chert layers and limestone banks of the Inca Creek Formation. In the scale the Floran Stage intervenes between the Undillan *Ptychagnostus punctuosus* Zone and the Templetonian *Triplagnostus gibbus* Zone below. The Floran includes two zones, *Ptychagnostus atavus*, the earlier, and *Euagnostus opimus*. I introduced the designation Zone of *Euagnostus opimus* (Öpik, 1970) as the Australian alternative to the Swedish scale division known as the zone of *Hypagnostus parvifrons* because in Australia this species is very rare; furthermore in both Scandinavia and Queensland (Table 1) *H. parvifrons* has been reported in *Ptychagnostus atavus* time. Associated with *Euagnostus opimus* are *Rhodotypiscus nasonis, Onymagnostus semiermis, Ptychagnostus scarifatus,* and *Triplagnostus diremptus; T. diremptus* arrived already late in the time of *Pt. atavus*. There are several distinctive polymerid trilobites in the *E. opimus* Zone; among those confined to the zone are six species of *Penarosa* Öpik (1970a) of the Nepeidae. The fauna of the zone is best represented in the Camooweal area (in many places west of Thorntonia) and in the Lawn Hill Sheet area (Öpik *in* Carter & Öpik, 1961). I identified it also in a collection by F. de Keyser, BMR, from the Louie Creek limestone (op. cit., p. 11). In the Flora Downs area *Euagnostus opimus* is present in a collection from site M192 (see p. 176). The earliest zone of the Floran Stage is the Zone of *Ptychagnostus atavus*. Fourteen named species are confined to this zone; seven others pass into the *Euagnostus opimus* Zone, and two (*Peronopsis normata* and *Triplagnostus gibbus posterus*) connect the *atavus* zone with the Templetonian below. In Queensland in *atavus* time arrived the earliest known Diplagnostidae (*Diplagnostus, Pseudoperonopsis,* and *Iniospheniscus*) and *Hypagnostus; Criotypus oxytorus* marks the rise of the *Goniagnostus* stock; *Triplagnostus* is well represented, together with its relative *Aristarius;* the unique *Zeteagnostus incautus* is common. The most abundant species is *Triplagnostus gibbus posterus* (or *gibbusposterus*) whose early finds have been referred to as *T. gibbus* in the literature, and have compromised for a while the stratigraphic significance of *T. gibbus.* In the correlation chart of Queensland (Öpik, 1960) the *'atavus-gibbus'* scale division is all *atavus* (without *gibbus* but with *gibbus posterus*). Finally, in the systematic part in the description of *Acidusus occultatus* (*Pt. punctuosus* Zone material) a misidentification of *Pt. atavus* is rectified.

The name Templetonian was introduced for a 'series' by Whitehouse (1936, 1939); the name of a stage was proposed by Öpik (1957) in consequence of the finds of *Triplagnostus gibbus* in Queensland in strata of the early part of the Inca Formation taken as the top of the Templetonian as well as the top of the *gibbus* zone; the lower part of that zone corresponds to the Beetle Creek sequence with the *Xystridura* fauna. In Queensland, in this sequence, fragments of a *Triplagnostus* and *Peronopsis normata* are present. In Table 1 the agnostid species found in New South Wales are also included in the Templetonian (*Pentagnostus anabarensis* and *P. veles*); as are those in the Sandover Beds in Northern Territory (*Pentagnostus rallus, Linguagnostus comparabilis, Peronopsis comis, P. tramitis, P. prolixa, P.* (*Itagnostus*) *elkedraensis* and *P. longinqua;* of these *longinqua* is older than the rest; *'Acadagnostus'*? or *'Peronopsis' scutalis* is of palaeogeographic significance. *Triplagnostus gibbus* is absent in these parts. The Templetonian Oryctocephalidae from New South Wales, Northern Territory, and Queensland, as described by Shergold (1969), are of the same age. The biostratigraphy of the Templetonian in the Northern Territory cannot be conveniently presented in terms of agnostids; the sequence of species of the Xystridurinae (Öpik, 1975) of some four genus-groups, passing from Ordian into Templetonian time, is relevant.

Stratigraphic distribution of agnostid genera

The biostratigraphy of the genera of agnostids whose species are described in the present paper is summarised in a chart, Table 2. The intervals of time-ranges of the genera in the chart are extracted from the species distribution chart, which shows the earliest arrivals and the last representative of each genus as recorded in Australia so far. Reference is also made to the Ordian Stage, with its record of a *Peronopsis* as yet undescribed; and to the early Upper Cambrian Mindyallan Stage with a prolific fauna of Agnostacea (Öpik, 1967).

The seven genera on the left side of the chart are obviously of a lesser value in stratigraphy, having persisted well into the Upper Cambrian; likewise, in the Mindyallan occurs the genus *Clavagnostus,* which is missing in the Middle Cambrian of Australia but is present in Sweden, Siberia, and America. In the Boomerangian, *Delagnostus* is unique and marks the top of that stage. Congeneric with *Delagnostus dilemma* Öpik (1961b, p. 88) is Phalacromidae gen. et. sp. indet. described by Rosova (1964, p. 20) from the late Middle Cambrian and earliest Upper Cambrian of the northeastern part of the Siberian platform (in the Arctic, east of the Yenissei River).

Some eighteen genera occur in the Undillan; ten are transcurrent, passed on from the Floran or surviving in the Boomerangian; among the rest *Svenax* is extremely rare, *Baltagnostus* is rare and of a short interval, and *Oedorhachis* may have survived in the Mindyallan as the aberrant *Oedorhachis? tridens* Öpik (1967, p. 128). The genera *Aotagnostus, Myrmecomimus,* and *Acidusus* are confined to the Undillan; being endemic they are insignificant in overseas correlations. *Doryagnostus,* however, has a global distribution and, if necessary, the Undillan can be referred to as the 'stage of the genus *Doryagnostus*'.

The Floran 'owns' *Zeteagnostus* and to a lesser degree the combination of *Criotypus, Rhodotypiscus, Iniospheniscus,* and *Triplagnostus.*

In the Templetonian, *Pentagnostus* should be accepted as a characteristic genus.

Outside Australia, in Sweden for example, *Peronopsis* and *Triplagnostus* have been recorded throughout the Middle Cambrian, but in Australia their intervals are relatively short.

To conclude, operational subdivisions of the Middle Cambrian cannot be based on the vertical distribution of genera; in Table 2 the genera are plotted against a sequence of stages which reflects the stratigraphy of species, zones, and numbers of species passing from one zone to another as illustrated in the panel diagram, Text-figure 1. The scale of zones and the scale of stages are applicable in correlations aiming at the discovery of contemporaneous events within narrow limits of error, but with

TABLE 3

RECONCILIATION OF THE STAGE STRATIGRAPHY (WHITEHOUSE, 1939) WITH THE SCALE OF ZONES

A Whitehouse 1939, p. 264 (super-positional order of stages incorrect)	B Stages of column A in terms of agnostid zones (arrangement orderless)	C Whitehouse's divisions (Column A) re-arranged in correct superpositional order of agnostid zones
Anomocare	Euagnostus opimus	Phoidagnostus
Papyriaspis	Pt. punctuosus/G. nathorsti	Amphoton
Phoidagnostus	Leiopyge laevigata	Papyriaspis
Agnostus seminula	Ptychagnostus punctuosus	Agnostus seminula
		Anomocare
Dinesus	Ptychagnostus atavus &	
Eurostina	Triplagnostus gibbus	Dinesus
Amphoton	Goniagnostus nathorsti	

the time ranges of genera alone the correlations will remain diffuse.

THE FIRST QUEENSLAND MIDDLE CAMBRIAN SCALE

An experimental scale of biostratigraphic stages of the Middle Cambrian of Queensland was proposed by Whitehouse as early as 1936-1939. In my papers, 1956-1961, I was unable to arrange the emerging new information in a superpositional order in terms of that scale and operated therefore with a scale of agnostid zones but looking forward for a chance of reconciling the scales with each other; the main obstacle was the *Agnostus seminula* stage of Whitehouse, for which a place could not be found. For a while (Öpik, 1957) even an early part of the *Pt. atavus* zone was erroneously indicated. In the present paper, at last, the position of the *seminula* stage (vide: *Onymagnostus seminula*) became clarified, and placed in the zone of *Ptychagnostus punctuosus*. It is noticeable that Whitehouse in his collections possessed no recognisable specimens of *Ptychagnostus punctuosus* and remained in doubt regarding the position of *seminula* in the sequence. At all events each Whitehouse stage is a recognisable biostratigraphic entity on its own merit, but they were presented originally in an incorrect superpositional order. The corrected order is shown in column C of Table 3. in which the nomenclature is according to Whitehouse. The Whitehouse scale is obsolete now, but it must be consulted in respect of the original labels of material collected by Whitehouse.

DISCUSSION OF, AND REMARKS UPON, THE CORRELATION CHART, TABLE 4

The remarks that follow refer in the first place to the scales included in the 'Chart of Acadian Correlations', Table 4, and the scale of agnostid species and the currently used scales of zones and stages based on sequences of species of *Paradoxides*. Comments are also offered upon the distribution of Acadian faunas around the Arctic Ocean, and the Bohemian and the Mediterranean faunas. The problems of correlation with the Pacific American and with the Chinese Middle Cambrian successions are mentioned.

The Australian scale of agnostid zones of species is a modified version of Westergaard's (1946) Swedish scale. The modifications refer to details but not to changes in the superpositional order of zones. (1) the bipartite Swedish Zone of *Leiopyge laevigata* is tripartite for reasons given by Öpik (1961b). (2) The Swedish Zone of *Ptychagnostus lundgreni* and *Goniagnostus nathorsti*, in the absence of *lundgreni* in Australia, has the simpler code name of *Goniagnostus nathorsti* Zone. (3) In Australia, a separate zone of *'Goniagnostus nathorsti* and *Ptychagnostus punctuous*' (or vice versa) is proposed as a recognisable operational unit—the name 'Zone of *Ptychagnostus punctuosus* and *Goniagnostus nathorsti*' is descriptive but inconveniently long; another shorter form may be *'punctuosus-nathorsti* Zone'; a tentative substitute is the code name *'notalibrae* Zone' in reference to *Doryagnostus notalibrae*, unknown outside Australia. (4) The interval of the Scandinavian Zone of

TABLE 4
CHART OF ACADIAN CORRELATIONS

I AUSTRALIA		II SWEDEN		III ACADIAN STANDARD	IV WALES AND ENGLAND	V SIBERIA	
Zones	Stages	1946-Westergaard-1953				Yarus'es	Zones
Leiopyge laevigata III (Holteria arepo)	Boomerangian	Paradoxides forchhammeri Stage	Leiopyge laevigata	Leiopyge	Leiopyge		Aldanaspis
Leiopyge laevigata II (Proampyx agra)			Exit of Paradoxides	Exit of Paradoxides			Leiopyge laevigata
Leiopyge laevigata I (Ptychagn. cassis)			Paradoxides forchhammeri	Parad. forchhammeri	Paradoxides forchhammeri		Anomocaroides limbatus Anomocaroides
Goniagnostus nathorsti	Undillan		(Paradoxides absent)			Maya Yarus	Centropleura oriens
Dory. notalibrae (=G. nathorsti + Pt. punctuosus)							
Ptychagnostus punctuosus		Paradoxides pardoxissimus Stage	Paradoxides davidis	Paradoxides davidis	Paradoxides davidis		Anopolenus; Paradoxides rugulosus
Euagnostus opimus	Floran		? P.paradoxissimus Paradoxides paradoxissimus				
Ptychagnostus atavus			Par. hicksi	Paradoxides hicksi	MENEVIAN / SOLVAN	Amga Yarus	Par. hicksi -Tomagnostus fissus
Triplagnostus gibbus	Templetonian		Paradoxides paradoxissimus				Tripl. gibbus and Oryctocephalids
Peronopsis longinqua		Paradoxides oelandicus Stage	P. oelandicus et al.	P. bennetti			

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Hypagnostus parvifrons is recognisable in Australia as in Sweden as a scale position; but for reasons already indicated (p. 9), another code name—the *Euagnostus opimus* Zone—is employed in the Australian scale. (5) The designation 'Zone of *Tomagnostus fissus* and *Ptychagnostus atavus*' is replaced by *Ptychagnostus atavus* Zone because no *Tomagnostus* has been found in Australia so far. (6) The Swedish name 'Zone of *Ptychagnostus* (*Triplagnostus*) *gibbus* (inclusive of the limestone layer with *Ctenocephalus exsulans*)' is simplified to Zone of *Triplagnostus gibbus*—*Ctenocephalus* does not occur in Australia. Writers before Westergaard used the name 'Exulans limestone'.

'*Paradoxides* shale' (the lower part of the Alum shale) is the traditional designation of the Middle Cambrian strata in Scandinavia; its biostratigraphy has been presented by early writers in terms of the sequence of species of *Paradoxides* which are used as names of the corresponding beds, which, in turn, were assigned to broad stages with letter symbols and numbers. Brögger (1878) constructed a range chart of fossils found in the *Paradoxides* shale of Norway that contains biostratigraphic data in regard of the species of *Agnostus* (= Agnostacea) and *Paradoxides*, of a lasting stratigraphic value. In Sweden, Tullberg (1880) charted the vertical distribution of known, and of numerous new, species of agnostids in measured sections of the Andrarum alum shale quarries; Tullberg's (op. cit., p. 10) nomenclature refers (1) to the *Paradoxides tessini* and *P. hicksi* 'strata', followed by (2) *P. davidis* strata, (3) *Paradoxides forchhammeri*; and *Solenopleura* strata (Andrarum limestone), and topped by (4) 'Agnosti laevigati' strata; these divisions refer to works of Torell and Linnarsson (references in Tullberg, op. cit.). Tullberg (op. cit., p. 9) tabulated also the superpositional sequence of the assemblages of agnostids interpretable in terms of biostratigraphic zones. Tullberg's stratigraphy remained operational for more than six decades; in Australia Whitehouse (1936, 1939) refers to the scale of Tullberg, and I used Tullberg's information before getting hold of Westergaard's revision (1944) and his final monograph (1946).

Tullberg's and Westergaard's scales in Scandinavia

The scale of stages (Acadian correlation chart, Sweden, Westergaard, 1946) of the *Paradoxides* shale is based on the sequence of Tullberg's '*Paradoxides* strata' but contains amplifications and modification of the traditional form: Westergaard (1) introduced the *Paradoxides oelandicus* Stage (*P. oelandicus* strata of Linnarsson, 1877; *Paradoxides oelandicus* Beds, Westergaard, 1936) which is wanting in the Andrarum sequence; (2) omitted references to *Paradoxides davidis* and *P. hicksi*, which, however, are essential in Acadian and British correlations; (3) defined the stages in terms of sets of agnostid zones; and (4) replaced the species name of *Paradoxides tessini* by its senior objective synonym—*Paradoxides paradoxissimus*. At the same time in a footnote, Westergaard (1946, pp. 7, 8) expressed his dissatisfaction with the *Paradoxides* stratigraphy because of the rarity of specimens and inability to identify their fragments 'with full certainty as to the species', and his satisfaction with the stratigraphic value of the agnostids. Eventually Westergaard (1953) himself dropped the unoperational *Paradoxides* stage nomenclature in favour of the letter symbols *A*, *B*, and *C* but still retained the three biostratigraphic divisions as a set of zones each—facts which escaped the attention of writers. Indeed, the stage names (*Paradoxides oelandicus* excepted) are code names of sets of agnostid zones in the first place, as also indicated in our chart in the column 'Westergaard, 1953'; the data in this column in Table 4 are extracted from the exhaustive tabulation of all known 'non-agnostidean trilobites of the Middle Cambrian of Sweden' in reference to the scale of agnostid zones of 1946 without reviving the nomenclature of the scale of stages. Thus (1) *Paradoxides forchhammeri* is absent at the top of its stage and (2) in the earlier zones of that stage *Paradoxides* and polymerid trilobites are absent; (3) the topmost zone of the *P. paradoxissimus* stage (the *punctuosus* zone) refers to *Paradoxides davidis* and inconclusive finds of *?P. paradoxissimus*; and (4) *Paradoxides hicksi* marks a level about the zone of *Ptychagnostus atavus*. The scale of *Paradoxides* stages, however, may retain its validity when the names of its divisions are taken only as code names (see Öpik, 1963, p. 11) of fossil assemblages and intervals of a time scale. A scale of *Paradoxides* species taxa, on the present state of knowledge, however, cannot cover the whole time span of the Acadian without inevitable gaps. By extrapolation, these can be interpreted as belonging to a stage below or above a *Paradoxides* interval established in a particular section, or area, or region. For example, Henningsmoen (1956, chart, p. 56) displaced in Norway *Goniagnostus nathorsti* down from the *P. forchhammeri* and added it to the top of the *P. paradoxissimus* stage—a variant reflecting Brögger's chart data (1878) of the vertical distribution of trilobites in the Krekling sections; Tullberg (1880, chart, p. 10) in reference to Krekling indicated that *P. tessini* (= *paradoxissimus*) has reached *Ptychagnostus punctuosus* but remains below *Goniagnostus nathorsti*. In all these charts *Paradoxides hicksi* refers to the Zone of *Ptychagnostus atavus*, and *P. davidis* to *Pt. punctuosus*.

The objective synonymy of *Paradoxides tessini* Brongniart, 1822, with the senior, and valid, *Paradoxides paradoxissimus* (Wahlenberg, 1821) was known to Lake (1906-1946, p. 209): 'the specific name *tessini*, originally applied to the same specimen that had been previously called *paradoxissimus*, has no right of priority; but it has the much more important claim of universal use for more than a century'. Westergaard (1944, p. 29) replaced the name of the stratum ('*tessini* beds') by *Paradoxides paradoxissiumus* (= '*tessini*') beds, and later (1953, pl. 8, fig. 2; pp. 34, 35) published a photograph of the type section of the species *paradoxissiumus* Wahlenberg — the recognised type of the genus *Paradoxides* Brongniart.

The Acadian standard

Column III—'Acadian standard' (Atlantic faunal realm, standard sequence, Hutchinson, 1956, p. 305, correlation table)—covers the Middle Cambrian of New Brunswick, Cape Breton Island, and southeastern Newfoundland; the scale of the sequence of species of *Paradoxides* is traditional and has been revised in detail by Howell (1925). The trilobites and their vertical distribution are presented by Hutchinson (1952, 1962); the stratigraphic divisions are zones, but stages are omitted. Howell & Mason (1938), nevertheless, used the British names Menevian and Solvan, and designated the Lower *Paradoxides bennetti* fauna as Bonnetian. Hutchinson (1962) described about forty species of Acadian agnostids from Newfoundland.

Of these species (op. cit., p. 83) *Ptychagnostus atavus* 'has been found in the lowest beds of the *davidis* zone and in the upper part of the *hicksi* zone'; and *Ptychagnostus punctuosus* (op. cit., p. 84) 'occurs sparingly throughout all but the lowest beds of the *davidis* zone and in post-*davidis* zone beds at one locality'. The superpositional order of these two species in Newfoundland is correct, but the intervals of the *Paradoxides* and *Ptychagnostus* zones are out of step with each other. The reasons are the many uncontrollable factors (Öpik, 1961b, pp. 37-38) affecting the degree of accuracy in correlation; empirically, (1) the uncertainty between zones encompasses an average interval of half a zone, but (2) in a sequence of a number of zones, as a rule, the individual errors are not cumulative (Öpik, 1967, p. 5). The occurrence of *Oidalagnostus* (Hutchinson, op. cit., p. 80) in the zone of *Paradoxides forchhammeri*, in the same level as in Sweden and Siberia, is welcome; in Australia it occurs in the Boomerangian and even in the early Upper Cambrian. Hutchinson's Newfoundland record of *Tomagnostus fissus* (*hicksi* zone), *Hypagnostus parvifrons* (*hicksi* and *davidis* zones), *Diplagnostus planicauda bilobatus* (*davidis* and *forchhammeri* zones) and *Doryagnostus incertus* (*davidis* zone) is too limited for a zone-by-zone correlation between Sweden and Acadia, but it seems sufficient for interpolating, if necessary, such scale positions as are not yet documented in terms of common agnostid species.

Among polymerid trilobites in New Brunswick and in Newfoundland two species originally described by C. F. Hartt as *Conocephalites tener* have been recently placed by Sdzuy (1967, p. 111) in his new genus *Badulesia* (Solenopleuropsidae Thoral). Previously Walcott (1884) revised these as species of *Ptychoparia*. Howell (1925, pp. 50-53) referred them to the genus *Liostracus* and established their age as the zone of *Paradoxides bennetti*. Sdzuy (op. cit.) described *Badulesia tenera* (Hartt) from Spain and indicated its occurrence in Asia Minor in material published by Dean & Krummenbacher (1961) from Turkey (Amanos Mountains). Consequently, biogeographic connection in *Paradoxides bennetti* time (= *Paradoxides oelandicus* Stage) prevailed between the American Acadian sequence, northern Spain, and the Amanos in the Near East; and *Badulesia tenera* (= *Pardailhania*) has been also found according the Sdzuy (1957) in the subsurface at Doberlug in Lausitz (about 100 km east-northeast from Leipzig).

Great Britain (England and Wales)

In the British scale (column IV) the traditional designations of Solvan and Menevian as 'beds' are replaced by 'Stages' (Stubblefield, 1956, p. 17). The stage terminology is now replaced by group terms, and the Solvan Group and Menevian Group are united under the name of St Davids Series for local use in Britain (Cowie, Rushton, & Stubblefield, 1972). The Solvan covers 'all Middle Cambrian strata older than the *P. hicksi* zone of Menevian age'. It is generally accepted that the Solvan, in its main part, is a time equivalent of the *Paradoxides oelandicus* stage of Scandinavia and of the *Paradoxides bennetti* zone of Acadia; furthermore, the definition 'older than the *Paradoxides hicksi* zone' implies that it is also older than the zone of *Ptychagnostus atavus,* and that the zone of *Triplagnostus gibbus* (with *Ctenocephalus exsulans*) is the top of the Solvan with *Paradoxides aurora*; hence, the Templetonian Stage and the Solvan are about contemporaneous scale divisions.

The Menevian sequence of species zones of *Paridoxides hicksi* and *davidis,* as indicated by Cobbold & Pocock, are separated from each other by *Paradoxides intermedius* (above *hicksi*) and *P. rugulosus* (below *davidis*). Illing (1916, table II) included some twenty agnostids in his diagrammatic representation of the life-ranges of species common to Scandinavia and to Hartshill (Nuneaton). Well identifiable are (1) the zone of *Ptychagnostus atavus* from the total range of *Paradoxides hicksi* concurrent with *Tomagnostus fissus* and *Ptychagnostus* cf. *intermedius* (closely allied to *Ptychagnostus atavus,* according to Westergaard, 1946, p. 77); (2) next the *'Hartshillia* or Passage fauna', with *Hypagnostus parvifrons* passing up from the zone below; it represents the Swedish *H. parvifrons* zone (= Zone of *Euagnostus opimus,* Australian column); next follows in Hartshill, in Sweden, and in Australia (3) *Ptychagnostus punctuosus* overtaking the arrival of *Goniagnostus nathorsti* in the association of the 'upper *davidis* fauna'; and (4) the presence of *Paradoxides davidis* itself. In terms of the agnostid zones it is probably the latest known datable occurrence of *Paradoxides davidis.* The earliest is in Newfoundland, starting in association with *Ptychagnostus atavus, Hypagnostus parvifrons,* and *Tomagnostus perrugatus,* and passing into the *Ptychagnostus punctuosus* interval, according to Hutchinson (1962, chart). Consequently, the cumulative interval of *Paradoxides davidis* shown in column IV covers a larger part of the Floran and at least the two earliest Undillan zones. According to Hutchinson (op. cit., p. 84) *Ptychagnostus atavus* occurs 'in the lowest beds of the *davidis* zone' and slightly higher than in Sweden; this situation is, of course, also described as the arrival of *P. davidis* late in the *atavus* zone. Likewise in the Manuels Brook Valley, in his bed-by-bed record, Howell (1925, p. 41, bed 94) reported the earliest known occurrence of *P. davidis* some 6 to 7 feet below the latest known *Paradoxides hicksi* (ibid., p. 39, bed 101); in the same section *Ptychagnostus punctuosus* arrives in bed 95—'much the most abundant member of the fauna'. It appears, therefore, that in this 'telescoped' section the *atavus* and *parvifrons* zones cannot be readily separated from each other; moreover, in its latest occurrence *P. davidis* is still associated with *Pt. punctuosus.*

Siberia

The Siberian scales (V, two columns) are extracted from the summary of N. Tchernysheva (1968). The Maya yarus has been subdivided (N. Tchernysheva et al., 1967, 1968) into a lower and an upper subyarus (above *Paradoxides rugulosus*). Jegorova & Savitzky (1969, pp. 53, 57-67) proposed biostratigraphic zones of the Amga and Maya yaruses for the Cambrian sequence in the western Anabar area of the Siberian platform with names selected from the local assemblages of trilobites. The described agnostids are referred to as *Triplagnostus praecurrens, Triplagnostus gibbus, Peronopsis scutalis, P. fallax,* and *P.* aff. *integra.* Among some 35 genera of polymerid trilobites, *Paradoxides, Solenopleura, 'Liostracus', Dolichometopus,* and *Corynexochus* are Acadian (provincial) and *Amphoton, Oryctocephalus,* and *Tonkinella* are extra-Acadian. Pokrovskaya (1958) in describing some 21 species of Middle Cambrian agnostids of Yakutia from the rivers Maya, Lena, Botoma, Olenek, and Amga operated with a variant of the scale (column V): (1) 'the Amga yarus' has the position of the Solvan of column IV; (2) the *Paradoxides hicksi* and *Anopolenus* zones together constitute the Chaya yarus, and (3) the Maya yarus is confined to the later part of the scale beginning with *Centropleura oriens.* Pokrovskaya (op. cit., p. 6) adheres to this scale in her publications of the systematics and biostratigraphy of agnostids and considers the 'old Scandinavian stratigraphic scale' of species of *Paradoxides* of no use in Yakutia. She already operates in her monograph with such 'highlights' as *Tomagnostus fissus, Phoidagnostus bituberculatus, Phalacroma glandiforme, Goniagnostus nathorsti, Hypagnostus exsculptus,* and *Leiopyge laevigata,* and visualises (p. 90) the emergence of a scale of agnostid zones. Soon after, Pokrovskaya (*in*

Tchernysheva et al., 1960, pl. 1) amplified the record with illustrations of Siberian specimens of *Diplagnostus planicauda bilobatus, Linguagnostus gronwalli, Oidalagnostus trispinifer, Ptychagnostus atavus, Triplagnostus gibbus, Clavagnostus repandus, Ciceragnostus cicer,* and *Leiopyge armata,* and the text (op. cit.) records the occurrence of *Doryagnostus incertus* in Yakutia and Kazakhstan. Likewise Tchernysheva (1961, p. 162) has indicated that *Ptychagnostus punctuosus* is one of the common species in the *Anopolenus* zone. With these discoveries the number of agnostid species common to Scandinavia and Siberia is about 35 and N. Tchernysheva (1968) in her table 2 correlated the sequence of the Siberian Middle Cambrian with the 'West European' scale of Westergaard's agnostid zones. In passing, Tchernysheva's (op. cit.) table 1, of 'geological distribution of fossil remains of Middle Cambrian genera of trilobites' accounts for 21 genera of agnostids. As in Australia, some five genera have crossed over into the Upper Cambrian; the whole pattern of genus-ranges is different from the Australian and Scandinavian grids, and all three are similar regarding their inferior resolving power in detailed correlation and stratigraphy.

The fringe of the Arctic Ocean

P. R. Dawes collected and Poulsen (1969) described Middle Cambrian agnostids from northwestern Greenland, in Nyeboe Land on the Lincoln Sea, about lat. 83°N. The fossils are determined as *Eodiscus punctatus, Diplagnostus planicauda bilobatus, Ptychagnostus punctuosus, Ptychagnostus ciceroides, Peronopsis scutalis,* and *Grandagnostus glandiformis,* and dated as representing the *Ptychagnostus punctuosus* Zone and the *Parodoxides forchhammeri* stage. I concur with Poulsen that within the American Atlantic region these fossils indicate a closest affinity to the Middle Cambrian fauna of southeastern Newfoundland, about lat. 47°-48°N and some 4000 km south of Nyeboe Land. The same Acadian agnostids, however, are present much closer in the Siberian platform and its fringing islands: Bennet Island (de Long Islands) is about 2100 km away from Greenland, and North Land Islands are even closer; an early *Paradoxides* fauna is also known in Novaya Zemlya, and *Paradoxides* occurs at the Tana Fiord in the far north of Norway. To speculate, the Arctic Ocean may conceal a region of Middle Cambrian deposits with faunas akin to the Acado-Baltic realm.

Bohemia

The Bohemian Middle Cambrian biostratigraphy and fossils are revised in detail by Snajdr (1958), and it appears that the sequence starting with the zone of *Paradoxides pusillus* postdates the British Solvan Stage and terminates probably in the time of *Hypagnostus parvifrons* (the Zone of *Euagnostus opimus*) or even at the beginning of the *Ptychagnostus punctuosus* interval; thus, the sequence can be dated with the *Paradoxides paradoxissimus* stage but without the Zone of *Triplagnostus gibbus.*

Two species of agnostids of the *Paradoxides pusillus* zone occur in the Acadian: (1) *Condylopyge rex* in Sweden in the *Hypagnostus parvifrons* zone of Westergaard, and in Britain in the *P. hicksi* zone (Illing, 1916), and (2) *Pleuroctenium granulatum* in Newfoundland 'ranging from the upper part of the *bennetti* zone to the upper part of the *davidis* zone' (Hutchinson, 1962, p. 67). The associated *Agnostus* sp. (Snajdr, 1958, pl. 46, fig. 3), a pygidium, represents the genus *Tomagnostus* (aff. *perrugatus*), whose species range from the *gibbus* to the *punctuosus* Zones. The presence of forms of effaced genera (*Phalacroma bibullatum, Skryiagnostus, Phalagnostus*) seems indicative of a *Pt. punctuosus* age, and *Triplagnostus viniciensis* Snajdr is possibly a species of *Onymagnostus* (q.v.). I also appreciate Snajdr's roll of synonyms of *Paradoxides pusillus,* which is the senior synonym of the rather popular name *Paradoxides rugulosus* of writers; at the same time most of the references to *P. rugulosus* in the literature cannot be replaced, according to Snajdr, by the name *pusillus* Barrande.

Germany

In Germany, the Middle Cambrian of the area of Frankenwald (some 150 km west from the outcrop in Bohemia) has been correlated by Sdzuy (1964, p. 218) with the three Swedish stages: (A) the *Paradoxides oelandicus* stage, (B) the *Paradoxides paradoxissimus* stage, and (C) the *Paradoxides forchhammeri* stage; the sequence is much more complete than in Bohemia, whose fauna represents only the *P. paradoxissimus* stage.

In the absence of agnostid species of stratigraphic significance a scale of species zones has not been applied by Sdzuy. Nevertheless, the *Paradoxides forchhammeri* stage fauna (Bergleshof, in Frankenwald) as described by Sdzuy (1966) is quite characteristic and, on the score of its polymerid trilobites, indicates the *Solenopleura brachymetopa* zone (= early Boomerangian) of Sweden. In the Middle Cambrian of Germany and Bohemia the presence of Solenopleuropsidae (-inae) that are absent in Scandinavia testifies to a faunal connection with the Mediterranean; nevertheless, as discussed above (column III, Acadian standard) Solenopleuropsidae are also known in Acadia and should be regarded therefore as constituents of the Acado-Baltic faunal realm together with the Scandinavian faunas.

Mediterranean

The Mediterranean Middle Cambrian faunas have been revised and largely supplemented by Sdzuy (1958; 1961; 1968); their Acadian character rests with species of *Paradoxides*, Conocoryphidae, and Solenopleuropsidae (-inae) as already discussed on the preceding pages. The absence of Ptychagnostinae and the scarcity of agnostids in general prevents the application of the Swedish scale of zones in correlation; present are, for example, *Condylopyge rex* and *Peronopsis fallax* (with subspecies) that range through several zones. A speciality is the genus *Peronopsella* Sdzuy (1968) with representatives in Acadia, Britain, and Germany. Remarkable by its occurrence in Australia and in western North America is *Pseudoperonopsis* (q.v.). In southern France (Howell, 1935), the described eight species seem endemic; these cannot be readily exploited in detail correlation.

America

In North America, outside the Atlantic domain, agnostids of a Scandinavian aspect occur (1) in the Taconic sequence of the State of New York and (2) in the Pacific faunal realm in the west. Rasetti (1967) described from the Taconic specimens of *Ptychagnostus punctuosus* which he attributed to the *Bolaspidella* zone; this discovery indicates an unspecified level within our Undillan Stage; the association with *Leiopyge* indet. is stratigraphically plausible, as in Australia a *Leiopyge* (*L. praecox*, q.v.) is also present in the Zone of *Ptychagnostus punctuosus*. Rasetti's *Ptychagnostus gibbus* (op. cit., p. 28)—probably *Triplagnostus gibbus posterus*—may be signalling the zone of *Ptychagnostus atavus*.

In the Pacific faunal realm agnostids of Scandinavian aspect from Utah have been described by Robison (1964a) and discussed biostratigraphically (1964b). In this second paper Robison operates with genera and refers to Westergaard's scale of *Paradoxides* species and of zones of agnostids. The following remarks refer to Robison's chart (1964b, p. 990): (1) The series name Albertan (= Middle Cambrian) is a junior homonym of the same name employed in the Mesozoic in Canada; it also covers the same interval as the Acadian: before Robison, Shaw (1958, p. 532) employed the name Albertan to the Middle Cambrian with the inclusion of the Dresbachian. (2) In Robison's chart I miss the reference to Rasetti's (1951) *Triplagnostus burgessensis* (close to *T. praecurrens*; see under *Pentagnostus*) and *Peronopsis montis* (see under *Itagnostus elkedraensis*), which are absent in Utah; and (3) the name *Linguagnostus* refers to a single species—*L. perplexus;* it is described here as *Pseudoperonopsis perplexa* (q.v.) from the Undillan Stage in Australia, and indicates correctly the zones of *punctuosus* to *nathorsi* in Utah as well. I think that Robison's correlation with the Scandinavian scale of zones should be accepted in general terms; it is also remarkable that agnostid species of a Scandinavian aspect are participants in a fauna of polymerid trilobites which is strikingly different from the faunas of the Acado-Baltic province.

Resser (1938, 1939a, 1939b) described from the Wasatch Mountains of Utah and Idaho three species: *bonnerensis, brighamensis,* and *lautus,* and referred these to the genus *Agnostus*. These forms are close to *Peronopsis interstricta* (White) in Palmer (1954) and *Peronopsis burgessensis* Rasetti (1951). I hesitate, however, to include them in the genus *Peronopsis* because of their pointed pygidial axial lobe, which is also attenuated in the rear in a manner seen in the Euagnostinae (q.v.). In Montana, however, two species of *Peronopsis* are evident: *Agnostus brevispinus* and possibly *A. robustus* of Deiss (1939); his third species, *'A'. hastatus,* is rather close to *'Acadagnostus' scutalis* (q.v.) as well as to *Agnostus acadicus declivis* Matthew (1886). Consequently, Acadian agnostids are present in Montana. Palmer (1968) described from Alaska the late Middle Cambrian species *Ptychagnostus aculeatus* (Angelin) and *Leiopyge laevigata* (Dalman), of Boomerangian age in Australia; the third form, however, described as *Ptychagnostus punctuosus affinis* (Brögger), seems to represent a new species of the same genus as discussed under *Ptychagnostus punctuosus* below (p. 89).

Poulsen (1960) described from Argentina species of several Acado-Baltic agnostid genera; these species are new and therefore inconclusive in correlation; the age of the fauna is latest Middle Cambrian or even transitional Upper Cambrian as regards its generic composition. To complete the record, Rushton (1963) illustrated from Columbia (South America) an agnostid pygidium (together with a *Paradoxides*) of a *Ptychagnostus* or *Hypagnostus* or even *Tomagnostella* related to *T. nepos,* and Palmer & Gatehouse (1972) described *Peronopsis* cf. *fallax* from Antarctica.

China

In China, Middle Cambrian agnostids, according to Lu (1957), include *Ptychagnostus atavus* and species of *Hypagnostus* of which one (*H.* cf. *hunanicus* Lu) seems present in Australia (Öpik, 1961, p. 64). *Hypagnostus quadratus* Lu (op. cit., pl. 137, figs. 11, 12) has a pygidium recalling *Tomagnostella nepos.* Furthermore, the cephalon of *Ptychagnostus sinicus* Lu (ibid., figs. 17-19) seems akin to *Ptychagnostus idmon* sp. nov. and *Pt. scarifatus* sp. nov. Likewise, I concur with Chu Chao-ling (1965) that the agnostid fauna from the Huzhu district of Tsinghai (= 'Blue Sea'; = Kuku Nor = 'Blue Lake') is of the same age and aspect as the fauna of the Devoncourt Limestone of Queensland and consequently Boomerangian in age. Common species are *Hypagnostus hippalus* Öpik (1961), and possibly *Pseudophalacroma dubium* (Whitehouse); forms attributable to *Allobodochus* nov. and *Diplagnostus planicauda* are also evident. The Huzhu fauna was collected on the northern fringe of the Tibetan upland well west from the Great Wall.

The agnostids described by Resser & Endo (1937) from Manchuria are older than the Huzhu fauna but cannot be dated in terms of our Acadian charts; they are younger than the *Paradoxides oelandicus* stage and came from the Mapan Formation. These agnostids may fall into the *P. paradoxissimus* interval. There are six endemic species, all included in the genus *Agnostus,* and all in need of further study as regards their family affinities and generic characters.

The problem of geographic ubiquity of Middle Cambrian species of agnostids

The zone-species of our charts are found all over the world and so are several species of a subsidiary application in stratigraphy. It stands to reason, however, that they cannot be expected to be omnipresent: some Middle Cambrian marine sequences are devoid of agnostids, or of trilobites, or even of fossils altogether, and hiatuses eliminate faunas and disrupt in places the continuity of populations. Also, a large number of species are rare, or even endemic on extant information. Such faunas contribute nothing towards the problem of ubiquity. Also to be taken into account is the distribution of such genera as *Hypagnostus, Diplagnostus, Oidalagnostus, Ptychagnostus, Leiopyge,* and *Peronopsis;* each of these names covers a taxonomic aggregate of species dispersed over the globe but supposedly close to each other morphologically and phyletically.

The ubiquity of agnostids supplies information regarding some general aspects of Middle Cambrian marine hydrology as well as the mode of life of the agnostids themselves: (1) The epoch was thalassocratic and the seas and oceans remained in communication through open seaways; the existence of regional and even local taxa does not contradict the information supplied by the global distribution of particular species. (2) Uniformity (within limits of thermal conditions) prevailed generally in the marine environment, the communicating seaways included. (3) Marine currents provided for the dispersal of the pelagic agnostids; the mode of life as well as the organisation of the agnostids is discussed in the next chapter.

PART II: MORPHOLOGY, ORGANISATION, MODE OF LIFE

INTRODUCTION: MORPHOLOGICAL TERMINOLOGY

The descriptive morphological terminology employed in this paper was used and defined in earlier reports (Öpik, 1961a, 1961b, 1963, pp. 30-32; 1967, pp. 52-62) and needs no repetition. New terms are *rosette, prongs, fulcral spines,* and *axial spines*. Morphological features are annotated in the following Text-figures: 2, 5, 9, 24, 25, 41, 45.

MODE OF PRESERVATION AND EMBEDDING: DISJOINTED SHIELDS AND INTACT EXOSKELETONS

The mass of the material consists of disjointed shields of exoskeletons dismembered about, or shortly before, the time of embedding; most of it resulted from moulting but some may represent detached parts of dead bodies. Illustrated examples are Plate 1, fig. 4; Plate 2, fig. 1; Plate 22, fig. 1; Plate 25, fig. 1. These illustrations, however, serve the taxonomy in the first place.

The agnostids have a four-piece exoskeleton of cephalon, pygidium, and two segments in the thorax; these are separable along three joints. The disjointed material in the matrix occurs in a disorderly manner; parts belonging to a single individual remain unidentified, but taxonomic units are recognisable in, and describable from, sufficiently well preserved shields.

Among the mass of disjointed skeletal pieces specimens are present which consist of two or even three sclerites in proper articulating contact: (1) the cephalon of *Criotypus lemniscatus* Plate 58, fig. 1, and that of *Onymagnostus durusacnitens* Plate 53, fig. 3, retained their contact with the anterior segment of the thorax; the joint in between is the weakest of the three in the absence of an articulating half-ring in the segment and the corresponding doublure in the cephalon; I presume, therefore, that these specimens are possibly parts of dead bodies which were deprived subsequently of the two posterior sclerites; (2) the pygidium with the thorax of *Triplagnostus fretus* Plate 28, fig. 2, became separated from the cephalon at the weakest joint of the skeleton—an event possible in moulting as well as in a subsequent loss of the cephalon in a dead body; and (3) *Leiopyge armata* Plate 64, figs. 5 and 6, consists of its complete exoskeleton in two parts—the cephalon and the pygidium united with the thorax, and one is overturned relative to the other. This specimen possibly represents an originally coherent body dismembered after death, or an exuvia; the proximity of the parts in the matrix may indicate an event of ecdysis on the sea-floor—an uncommon incident in pelagic animals. Other possibilities are unfinished coiling, or unsuccessful uncoiling of the animal embedded in the soft sediment.

Coiled (enrolled) individuals are very rare among the Australian agnostids; some ten rather ill-preserved specimens of *Hypagnostus* and of *Rhodotypiscus nasonis* have been observed in collections. Unique is the coiled specimen of the ptychagnostid *Pentagnostus veles* Plate 55, fig. 4; it is the skeleton of a dead body and its matrix is shale.

The complete exoskeletons illustrated in this paper, more than 130 individuals, represent a selection of collected remains of dead bodies. In the comments upon species these are described as preserved in a state of articulation, with all the sclerites in proper contact with each other. Some dead individuals settled down on the sea-floor and others possibly died resting on the floor in the still water of the deep. Many complete exoskeletons (for example Pl. 24, fig. 1; Pl. 33, fig. 1; Pl. 34, fig. 1; Pl. 51, fig. 5; Pl. 60, fig. 3; Pl. 62, fig. 3) are embedded dorsum up as evident from the attitude of the anterior segment of the thorax; in living agnostids the anterior segment is held in its position in contact with the cephalon by the fulcral apertures; in the examples (above) this contact, however, is disrupted, the anterior segment is a little rotated and droops down with its anterior edge; in the rear the segment remains supported by the articulating half-ring, which retains its horizontal attitude and is therefore exposed. The rotation of the anterior segment results from the loss of the soft tissue under the sclerite and is possible only in the dorsum-up attitude. Likewise, the anterior segment retained its original position in some perfect exoskeletons, as can be seen for example in Plate 26, fig. 7; Plate 38; Plate 51, fig. 6; Plate 60, fig. 2; the number of such illustrated specimens reflects my searching for the 'best preserved exoskeletons', which are actually rare. As regards the quantity of collected complete skeletons some species are represented by one specimen each, as for example *Criotypus oxytorus* nov., *Triplagnostus stramineus, Ptychagnostus intermedius, Triplagnostus quasigibbus;* whereas of some others (*Dory-*

agnostus magister, Goniagnostus nathorsti, Myrmecomimus tribulis, Triplagnostus gibbus posterus) the supply depends only on the collecting time and is potentially unlimited.

Forms and shapes

The outline

In terms of Raw (1957) the agnostid possesses a 'semiovoid' body; the curvature fore and aft is similar and 'semiellipsoidal' is an appropriate description. The dorsum is convex and the ventral side concave in the living animal. In an agnostid swimming forward the described hydrodynamic shape resulted in a lift in the dorsum direction even at the slow 'agnostid speeds'. The semiellipsoidal design in agnostids is essential in keeping them afloat in the pelagic domain; it is at the same time a fundamental structure of all trilobites and therefore one of the important stabilised morphological characteristics of the class; on the sea-floor the semiellipsoidal shape, once existing, was neither of special advantage nor disadvantage in life.

The shape (the outline) of the shields depends on the relative length and width, and on the curvature of the margins; its visually perceived or statistically defined characters, combined with other characters, are useful in the taxonomy of species and to a lesser degree of supraspecific units. For example, *Onymagnostus angulatus* (Pl. 50, fig. 2) of the Ptychagnostinae differs from other species of the genus in the semielliptical outline of the cephalon; in all other species of *Onymagnostus,* however, no particularly characteristic (diagnostic) shapes are evident. Likewise, in *Iniospheniscus* of the Diplagnostidae the cephalon is almost semielliptical in two species (Pl. 9, figs. 5 and 6; and fig. 8). At the same time, in the species of '*Aspidagnostus* (*vide* Öpik, 1967, p. 115) of the Clavagnostidae the cephalic front is characteristically angulate and pointed, and not arched as in other agnostids. Nevertheless, some species of clavagnostids are also known to have an arched cephalic frontal margin. As regards the curvature of the margins of the shields, the diagrams (text-figures) in this paper are revealing: some curvatures are specific, but others are current in other species, and 'generalised' shapes prevail. In pygidia the monotony is lessened by the incidence of marginal spines and rearward widening of the shield.

The marginal outline is less informative than the shape of the axial lobe surveyed in the next paragraphs and Text-figure 2.

Shapes of the axial lobe

The axis (the axial lobe) of an agnostid exoskeleton is enclosed by the continuous circumaxial furrow; in disjointed shields the description 'axial furrow' or 'dorsal furrow' serves the purpose. In effaced forms vestiges of these furrows serve as keys in interpretations of the systematic position of the species (Öpik, 1967, p. 79) even in instances where the circumaxial furrow cannot be traced in full; hence, diagrams of effaced forms are not included in Text-figure 2.

The characters observable in the shape of the skeletal axis are significant, *inter alia,* in supraspecific and suprageneric taxonomy of agnostids and are evident in forms en grande tenue.

The material in hand consists of a large number of exoskeletons of diverse species of almost all known Middle Cambrian genera and family aggregates. The axial shapes of most of these forms are presented in the text-figures and are not readily comparable with each other at sight; the comparison is facilitated, however, with the aid of the small number of generalised abstract models in Text-figure 2, each supplemented by a comment below. The arrangement of the first five illustrates the influence on the outline produced by the form of the glabella and the diversity of the lateral extent of the basal lobes; the geometry of the rest includes forms which also can be accommodated according to the extent of the basal lobes in the interspaces between the forms of the first five.

In passing, the basal lobes are defined abaxially by mostly sideway-deflected lengths of the axial furrow and are therefore parts of the axis; homologues of cephalic basal lobes are also repeated in the thorax (Text-fig. 5); in some forms the furrow may remain undeflected, as evident in designs V and IX; it is also undeflected in *Zeteagnostus* (q.v.); other examples (Öpik, 1961, p. 88) are *Delagnostus dilemma* and *Phalacroma bibullatum.*

Late Cambrian agnostid material is still deficient in complete exoskeletons. Well known and characteristic, for example, is the course of the axial (circumaxial) furrow in *Glyptagnostus* (*vide* Öpik, 1961); in *Pseudagnostus* the pygidial axial furrows and the axial lobe are suppressed by the deuterolobe, and in

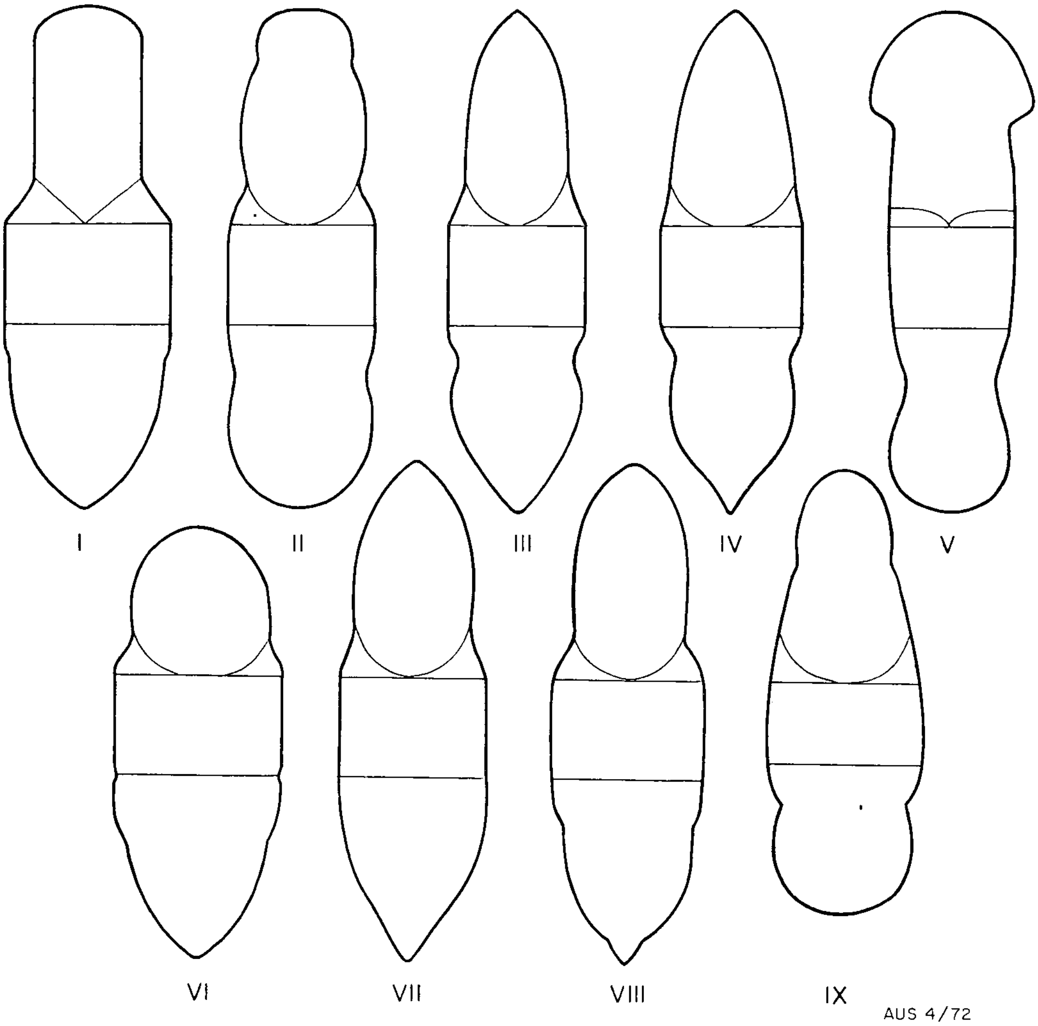

Fig. 2. Shapes of the axial lobe in agnostids; detailed explanation in the text.

Agnostardis the pygidial axis has a rather peculiarly modified structure.

Designs of axial lobes, Text-figure 2:

Design I: Diplagnostus, and the species of *Pseudoperonopsis* in other genera of the Diplagnostidae (*Oedorhachis, Iniospheniscus*) the pygidial axis is expanded variously and the glabellar front rounded; in *Connagnostus* and *Oidalagnostus* (*vide* Öpik, 1967, pp. 130, 135) the pygidial axial furrows are about parallel to each other—a design different from *Diplagnostus.*

Design II: Peronopsis; the diagram recalls I, except for the roundness of the glabellar rear; the outline of the pygidial axis, however, depends on the species (see Text-figs. 9, 11, 12; also 17).

Design III: Triplagnostus; the deflection of the furrows at the basal lobes is less abrupt than in I and II; distinctive is the acuteness fore and aft shared by *Aristarius, Onymagnostus,* and other Ptychagnostinae (IX excepted); design III is also found in *Ptychagnostus* (*atavus, punctuosus*), but with a tendency for even lesser deflection of the furrows at the basal lobes; almost no deflection occurs in *Pt. idmon* and *scarifatus* and none at all in *Zeteagnostus.* In these three forms (Text-figs. 28, 29, and 32) owing to the relative narrowness of the frontal glabellar lobe the axial furrows appear deflected at the front of the posterior glabellar lobe; the same is evident in *Onymagnostus mundus* (Text-fig. 34).

Design IV: Goniagnostus, including *Criotypus* and *Allobodochus.* It is close to III with little or no deflection at the basal lobes; the shape, however, is more pointed than in III. Some deflection is apparent in *Criotypus* (Text-figs. 46 and 47). Of a similar shape is the axis in *Acidusus* (Text-fig. 30).

Design V: Condylopyge (Condylopygidae); this well known agnostid has not been found in Australia. The shape of the axis indicates a form unrelated to others; no deflection at the basal lobes is indicated.

Design VI: Hypagnostus; distinguished by the absence of the frontal part of the circum-axial furrow; the same geometry is known in forms of diverse affinities.

Design VII: Euagnostus (Text-fig. 22), reminiscent of III in having more or less acute closures in front and rear; in the selected *Rhodotypiscus* (Text-fig. 23), the design is different owing to the roundness of the frontal closure, an axial outline seen also in *Acadagnostus scutalis* (Text-fig. 17).

Design VIII: Doryagnostus (Text-figs. 24, 25); the posterior closure is acute as in IV and in *Rhodotypiscus* mentioned in VII; the deflection of the furrows at the basal lobes is as strong as in I and VII.

Design IX: Myrmecomimus (Ptychagnostinae) (Text-fig. 42); the originality of the axial model is caused by the absence of deflection at the basal lobes, bluntness fore and aft, and shortness of the pygidial axis; it is, however, an extreme modification of the ptychagnostid (III and IV) design via *Aotagnostus* (Text-fig. 40), which is acute in the front and bluntly rounded in the rear of the short axis.

The following three forms should be considered also, completing the review of the axial models of agnostids described in this paper:

(1) *Pentagnostus rallus* (Text-fig. 44) and *P. veles.* These are Ptychagnostinae with a pointed axial rear, a rounded (not acute!) front, and strongly deflected furrows at the basal lobes;

(2) *Onymagnostus* (*Agnostonymus*) *semiermis* (Text-fig. 35), also with the front rounded but with a long and slender pygidial axis; and

(3) *Tomagnostella nepos* (Text-fig. 21), reminiscent of *Hypagnostus* (VI) in its cephalon but with a slender pygidial axis in a ptychagnostid style.

Relative length of tagmata in agnostids

Introduction

The relative length of tagmata is calculable from sagittal measurements of the length of the cephalon, the pygidium, and the thorax in complete exoskeletons; many species are based, however, on isolated shields shed by different individuals and of different instars—material containing no information regarding the lengths of thoraces but still exploitable for calculating the length of the pygidium relative to the cephalon and vice versa. This is possible by matching a cephalon and a pygidium equal in width and observing that the pygidium in such a pair will be a little shorter than the cephalon. The measurements should be taken between related points which coincide with each other in coiled exoskeletons; in some forms the matching of the acrolobes of the cephalon and the pygidium is more convenient than the matching of positionally related marginal points. Forms exist also with the pygidium narrower than the cephalon (for example *Triplagnostus scopus,* Plate 27, figs. 5 and 6); in this species the pygidial margin appears congruous with the acrolobe of the cephalon. In passing, the method of matching related points may facilitate the identification of conspecific cephala and pygidia in assemblages of multispecific disjointed shields.

Relative length of the cephalon and pygidium

In plan, the length of the cephalon is the distance between the frontal margin and the margin of the band connecting the basal lobes (the connective band) or the occipital collar; the length of the pygidium is the distance from its rear margin to the front of the axis. The articulating half-ring and furrow are not included because in a properly measurable exoskeleton these are covered by the axial rear of the thorax.

According to Kobayashi (1939, p. 75) the cephalic and pygidial shields are subequal in size, and 'in some forms the pygidium is somewhat larger than the cephalon'; Moore (*in* Harrington et al., 1959, p. 0160) describes the Agnostida as 'trilobites with subequal cephalon and pygidium'; and Öpik (1967, p. 79) as trilobites 'with the cephalon and pygidium equal in size'. Descriptive of agnostids are also the terms isopygous, macropygous, and the obsolete ordinal name Isopygia.

The survey of the exoskeletons published now and of the published illustrations by writers regarding the relative length of the pygidium and the cephalon produced the following results: (1) The great majority of agnostids are heteropygous with the pygidium shorter than the cephalon; the cephalon is as long as the pygidium together with one-half, or the full length, of the posterior segment of the thorax; (2) a small number of agnostids are isopygous, having the pygidium and cephalon equal in length: for example, some species of *Onymagnostus* gen. nov.; and within the same genus are forms whose pygidium is longer than the cephalon (*Onymagnostus* sp. nov. aff. *angulatus*, and *O. mundus* sp. nov.). In the next examples the length of the cephalon is given in terms of the length of the pygidium; in *Triplagnostus scopus* sp. nov. (Pl. 27, figs. 5 and 6) it is 1.2x, the shortest pygidium found so far; in *Triplagnostus fretus* it is 1.17x; in *Aotagnostus magniceps* 1.13x; in *Aotagnostus modicus* (Pl. 35, fig. 1), 1.1x; in *Ptychagnostus punctuosus* (Pl. 38), the cephalon is as long as the pygidium with its articulating half-ring; in *Leiopyge multifora* (Pl. 65, fig. 3), the shields are equal in length.

These data supplement the descriptions of such species as are represented by complete and well preserved exoskeletons; specimens of this kind, however, are rare and therefore not quite conclusive regarding the taxonomic value of the relative measurements of their pygidia and cephala. The relative size of shields is close to constant within a species, but numerous species possess similar values; and species of the same genus may differ in this character. It seems therefore that no supraspecific significance can be attributed to the size data obtained from the small quantity of measurable material available so far.

Relative length of the thorax and of its segments

Method of measuring. The length of the thorax as a unit as well as its segments separately is conveniently measured exsagittally along the lateral (basal) nodes of the axis or along a line close to these nodes and crossing the adaxial parts of the pleurae and the commissure (the hinge-line) separating the pleurae from each other; this method is applicable to the largest possible number of exoskeletons and supplies comparable numerical data of a similar meaning in different specimens. The cephalon, of course, is measured sagitally.

Length of the thorax relative to the cephalon (Text-fig. 3)

Inequality of the length of the thorax in agnostids is a fact; this length within a species taxon possesses stability, but the accuracy of measurements is influenced by small deformations which cannot be evaluated; larger deformities render the material unsuitable for measuring; but it is also evident that a thorax of a certain length may occur in different species of the same or of other suprageneric units; hence, the length of the thorax remains a valuable but subsidiary taxonomic character.

The relative rarity of measurable complete exoskeletons impedes generalisations of the taxonomic value of the length data. The available material, however, illuminates graphically a subtle but significant aspect of the morphology and organisation of the agnostids.

The information regarding the length of the thorax in this paper refers to some 130 specimens; the micrometer lens data have been also checked with magnified photographs; the numerical data are included in the descriptions of the species and in the comments to the illustrated specimens; likewise, measurements were taken from many specimens left in the collections.

In the graph, Text-figure 3, the vertical lines describe the length ranges of the thorax within each of the taxonomic supraspecific units; these are enumerated at the bottom of the graph by numbers 1 to 17. The meaning of the number corresponding to each line is given below the diagram, including the number of species taxa in each line; for simplicity no data of individual species and their names are indicated in the diagram. The distribution of the lines is, of course, arbitrary; Nos. 1-8 represent the field of low values not crossing the 0.3 level and embracing the species of the Ptychagnostinae; the Agnostinae (No. 9), I presume, are somehow related to the ptychagnostids via *Onymagnostus* (No. 8), but this affinity is not reflected in the length of the thorax, which reaches the value of 0.35. The Condylopygidae (No. 10) are unrelated to the Ptychagnostinae and Agnostinae and the line stands alone for taxonomic/morphological reasons. There is no apparent unity in the field of Nos. 11-17 of taxa referable to diverse family units. Some forms whose thorax is known but with no material at hand are not included in the graph but are considered in the text below.

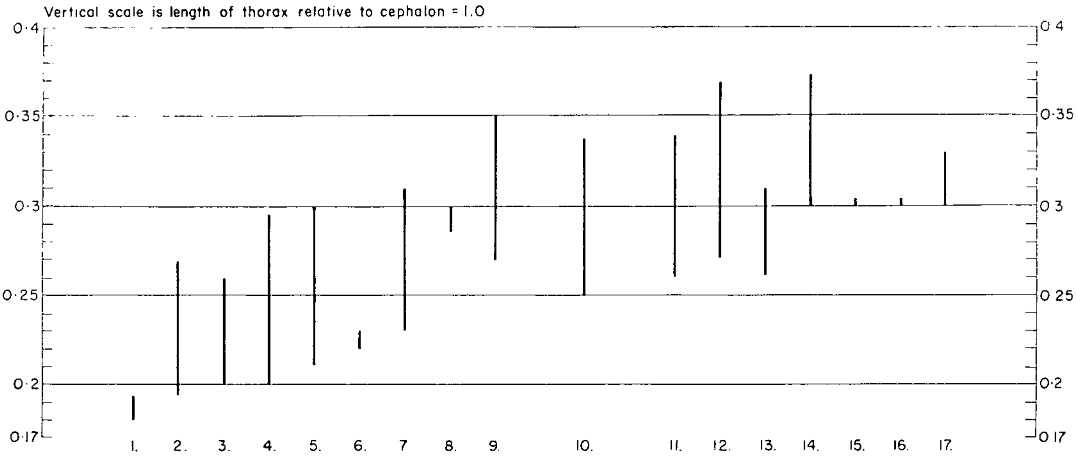

Fig. 3. Length of the thorax relative to the cephalon in agnostids known from the complete exoskeleton; detailed explanation in the text.

Line 1. *Zeteagnostus incautus,* only one species of its genus; data refer to measurements in several specimens; some variability and unaccountable deformation are involved; the interval, however, is small (0.18-0.19x the cephalon).

Line 2. Six species of *Aotagnostus;* the length of the thorax in each is taxonomically significant.

Line 3. *Myrmecomimus,* with four units (species and subspecies); the specimens are very small, so measurements of the thorax, but not of the cephalon, contain inaccuracies.

Line 4. *Triplagnostus* (six species) and its subgenus *Aristarius* (three species) differ in the length of thorax; *Triplagnostus gibbus* has the shortest; it is only a little longer (0.23) in *T. gibbus posterus.*

Line 5. *Ptychagnostus* and its subgenus *Acidusus,* ten species altogether; on the basis of the length of the thorax the subgenera are possibly separable from each other; the *Acidusus* interval is 0.25-0.3; in *Ptychagnostus* 0.23 to 0.27 is indicated.

Line 6. *Leiopyge* (four species) and *Pseudophalacroma* (one species) are unrelated to each other; the values are low.

Line 7. *Criotypus* (two species) and *Goniagnostus* (four species); the longest thorax (not less than 0.32x the cephalon) belongs to *C. lemniscatus,* followed (down the line) by *G. scarabaeus* (0.27), *verus* (0.25), *Criotypus oxytorus* (0.24), *G. nathorsti intersertus* and *G. nathorsti* (0.23).

Line 8. *Onymagnostus* (six species); the interval is very short (0.29-0.3); in *O. durusacnitens* the value possibly a little greater (about 0.32).

Line 9. The Agnostinae: the number of published measurable exoskeletons is very small; the base of the line belongs to *'Agnostus' captiosus* Lazarenko (1966) and *Innitagnostus inexpectans* (Kobayashi) as seen in Öpik's (1967, pl. 2, fig. 11) specimen; in *Agnostos hedini* Troedsson (1937) it is 0.3, in *'Proagnostus' bulbus* about 0.33, and in *Homagnostus obesus* (*vide* Westergaard, 1922) about 0.34-0.35.

Line 10. The Condylopygidae, of two genera and a small number of species, have a rather wide range in the lengths of thorax.

Line 11. *Hypagnostus,* data for species published in this paper; the highest value (0.34) belongs to *H. melicus;* it is lowest (about 0.26) in *H. vortex;* the rest (*clipeus,* 0.28-0.29; *inequalis,* 0.28-0.3; and *tjernviki,* 0.3) are close to each other. Similar is *H. parvifrons* (0.3) and close to the specimen in Westergaard's (1964) Pl. 4, fig. 31—a cephalon with ith thorax attached. Possibly a little shorter (about 0.28) is the thorax in *H. parvifrons* from Utah (Robison, 1964, pl. 81, fig. 6).

Line 12. Peronopsinae: includes *Itagnostus* nov., *Acadagnostus,* and *Peronopsis* of writers (essentially the group of *P. fallax*). In *P. integra* (the type of its genus) it is 0.33-0.35, but the deformed material allows of no accuracy; the highest value (0.37) belongs to *Peronopsis fallax* (*vide* Brögger, 1878, pl. 6, fig. 1), and lowest (0.28) to *Itagnostus elkedraensis* (q.v.); *Peronopsis* ex greg. *fallax* Jegorova (1969, pl. 6) with 0.33-0.34 is close to the top. The Australian forms described in this paper are *P. fallax ferox* (0.33), *comis* (0.32-0.33), *normata* (0.3), and *Acadagnostus scutalis* (0.3).

Line 13. The Euagnostinae I: *Euagnostus,* four species; *Rhodotypiscus,* one species. The lowest mark (0.26) refers to *Euagnostus levifrons;* the rest falls into the interval 0.29-0.32; the number of exoskeletons is relatively small.

Line 14. The Euagnostinae II: *Doryagnostus,* three species; *Doryagnostus magister* (0.3) remains stable in abundant exoskeletons; *D. notalibrae,* also 0.3, is rare; the highest value (0.37) is attained in *D. solidus.*

Line 15. The Diplagnostidae: species of four genera are represented by measurable exoskeletons: *Diplagnostus,* 2 species; *Pseudoperonopsis,* 5 species; *Baltagnostus,* 1 species; *Iniospheniscus,* 1 species. In nearly all forms the value is 0.3, with small alterations owing to accidental deformation; an exception is *Pseudoperonopsis insolita* (0.32).

Line 16. *Glyptagnostos reticulatus* (0.3).

Line 17. The Pseudagnostinae: the number of published exoskeletons is remarkably small in comparison with the large number of named species. In *Pseudagnostus cyclopyge* (*vide* Jaekel, 1909, text-fig. 20) and in *Rhaptagnostus acutifrons* Troedsson (1937) the thorax is 0.3x the cephalon; in *Pseudagnostus rotundatus* Lermontova (*vide* N. Tchernysheva et al., 1960, pl. 2, fig. 7), the value is close to 0.34; *Agnostus securiger* Lake about 0.33; and *Machairagnostus tmetus* about 0.28.

No place in Text-figure 3 is given to *Grandagnostus imitans* (q.v.); its thorax (about 0.23) is too short for a peronopsid; it recalls some Ptychagnostinae, but the structure of its exoskeletons remains a matter of further contemplation.

Some other agnostids not included were measured in the graph: (1) *Tomagnostus,* with 0.3, can be placed with Diplagnostidae or the Ptychagnostinae; (2) in *Phalacroma bibullatum* the value is 0.27 but of no significance regarding its classification; (3) the value is remarkably low in *Leiagnostus* (about 0.22), in *Phalagnostus orbiformis* Ivshin (1960, p. 168) (0.16), which has a relatively large cephalon; and *Sphaeragnostus* (0.13) has the shortest known thorax. In the well known *Geragnostus* and *Trinodus* and their relatives the thorax is large, about 0.34-0.35x the cephalon in length.

Relative length of the segments of the thorax

The inequality of the segments in a thorax of an agnostid is a fact; the posterior segment is the shorter of the two, as already observed by Jaekel (1909, p. 382). A measurable example is the cephalon with its thorax attached of *Doryagnostus solidus* sp. nov., Plate 6, fig. 1, and Text-figure 25, in which the intersegmental joint is clear and the test almost intact; the thorax is shifted a little retrally from the cephalon, exposing its part of the cephalothoracic aperture—the thoracic recess (Robison, 1964, p. 514). The exsagittal length of the anterior segment is 0.2x the cephalon, and the posterior segment 0.17x; the whole thorax is 0.37x the cephalon in length; the relative length of the segments is 6:5. A similar inequality of the segments is also evident in *Doryagnostus magister* (Pl. 20, figs. 1, 3, 4), and in *Criotypus oxytorus* (Pl. 57, figs. 1 and 2, and diagrammatically in Text-fig. 46). In passing, the inequality of the segments has not been consistently shown in the diagrams. The inequality is also visible in photographs of specimens whose thorax is undisturbed and exposed in plan in *Itagnostus elkedraensis* (Pl. 3, figs. 1-3), *Peronopsis comis* (Pl. 2, fig. 4), *Ptychagnostus atavus* (Pl. 43, fig. 1), and several more. But in specimens whose anterior segment has been rotated as in *Goniagnostus nathorsti* (Pl. 60, fig. 3), it seems shorter than the posterior segment, which retains its horizontal attitude.

Spines and fulcral prongs

Prongs and fulcra

Prongs are short paired spines (points) on the left and right fulcral hinges (Text-figs. 5 and 23). The prongs (*ht,* pygidial prong or 'nesting prong', Text-fig. 23) of the anterior edges are invisible from above in complete exoskeletons because they nest in sockets under the external prongs (*th*) that are exposed on the dorsum. This hinge structure of the fulcra is visible for example in *Ptychagnostus punctuosus* (Pl. 38): the right pygidial nesting prong is exposed because its component in the rear of the posterior segment is broken off. The pygidial nesting prongs are evident in the illustrations of *Euagnostus opimus* (Pl. 13, fig. 5), *Leiopyge multifora* (Pl. 65, fig. 3) and *Pseudophalacroma dubium* (Pl. 67, figs. 1, 2) and in several more isolated pygidia. The nesting prongs of the front of the anterior segment are visible owing to its displacement in the holotype of *Onymagnostus mundus* (Pl. 51, fig. 6); note that the position is the corner of the segment because in the anterior segment of agnostids the pleural part outside the fulcra is undeveloped. The external prongs are illustrated in cephala and commonly described as 'posterolateral cephalic spines'. An excellent illustration of sockets under the posterolateral cephalic spines (prongs) in *Peronopsis interstricta* is given by Robison (1964, pl. 82, fig. 2). To conclude, the articulation of the agnostid skeleton is controlled by the 'point-and-socket' mechanics of the fulcra—the same as the ball-and-socket of the polymerid trilobites.

There are three pairs of fulcra in agnostids, consisting of three pairs of nesting, and three pairs of external, spine-like, prongs.

Fulcral spines

The external fulcral prongs (1) remain short in species of several genera and even suprageneric aggregates, and (2) are extended as slender spines in numerous species of some genera of the Ptychagnostinae this modification involves the cephalic posterolateral prongs (spines) and the external fulcral points of the posterior segment of the thorax; the same morphological group also includes forms with long cephalic spines and relatively short, inconspicuous spines in the second segment.

As regards the anterior segment of the thorax, no species is known to possess spines developed from the external fulcral prongs at the posterolateral corners of its sclerite; as seen, for example, in *Doryagnostus solidus* (Pl. 6, fig. 1), these prongs are very small, much smaller than the cephalic posterolateral prongs (almost spines); the anterior segment invariably lacks an articulating half-ring, and the pleurae are clipped short at the fulcra. This structure is once more considered in the discussion of merocyclism in the agnostids (p. 31). In polymerid trilobites fulcral points (prongs, spines) are evident in *Acanthomicmacca* Hupé, 1953 (=*Micmacca walcotti* Matthew, 1899, pl. 4, fig. 5) in the cranidium and thorax, and also in *Corynexochus plumula* Whitehouse (*vide* Öpik, 1967, p. 178, text-fig. 57).

Axial spines

The axial spines are azygous and differ therefore from the fulcral prongs and spines, which occur in pairs on the margins of the sclerites; the axial spines arise from the midline. The largest possible number of axial spines in ptychagnostids is three—one on the rear of the glabella, another on the second segment, and the third on the second annulation of the pygidial axis. Low nodes occur in the same position in many other, spineless, agnostids. In many forms a low median node is also evident on the anterior segment of the thorax, as for example in *Triplagnostus gibbus* (Pl. 23, fig. 1), or *T. gibbus posterus* (Pl. 24, fig. 3), and *Criotypus lemniscatus* (Pl. 58, fig. 1), but it is never an extended spine. It is absent for example in *Grandagnostus imitans, Hypagnostus clipeus,* and *H. melicus,* in *Myrmecomimus,* and possibly in *Aotagnostus.*

The pygidial marginal median spine described by Brögger (1876, p. 65, pl. 6, fig. 1a) in *Agnostus fallax tricuspis* is also, by its position, an axial spine; a similar axial spine is also present in several forms of the Diplagnostidae (*Oidalagnostus, Oedorhachis*) and Clavagnostidae (*Aspidagnostus*): *Utagnostus tricuspidatus* Robison (1964) is remarkable for its long posterolateral (fulcral) cephalic spines in an *Aspidagnostus* style combined with an acute glabellar rear (*vide* Öpik, 1967, pp. 117 and 121). In the well known Condylopygidae the number of axial spines is much larger than in the Ptychagnostinae (Agnostidae): in the rear of the glabella, one on the anterior segment, and three axial spines on the pygidium. The Condylopygidae are unrelated to other families of agnostids (Öpik, 1967, p. 74) and will not be considered further in this paper.

The attitude of spines

The fulcral spines of the cephalon and the thorax in a horizontally stretched agnostid are elevated above the pleura and deflected sideways; at the same time the pleurae are geniculated down at the fulcra—structures preventing the spines from contacting the tergites in articulation. Consequently, the fulcral spines could not hinder the flexibility of the skeleton along the joints between the sclerites.

TABLE 5
DISTRIBUTION OF SPINES IN THE PTYCHAGNOSTINAE

	FULCRAL PRONGS AND SPINES			AXIAL SPINES		
	Cephalon	Thorax second segment	Pygidial marginal	Glabellar rear	Thorax second segment	Pygidial axis 2nd lobe
Triplagnostus:						
quasigibbus	short	prongs	0	0	short	short
gibbus	long	prongs	0	0	long	short
gibbus posterus	long	short	0	0	long	long
diremptus	long	short	short	0	long	short
fretus	long	short	short	0	short	long
scopus	long	long?	short?	0	?	long
stramineus	very long	very long	very long	0	very long	very long
Aristarius:						
retrocornutus	very long	prongs	long	0	very long	long
aristarius	very long	long?	very long	0	very long	long
ultimus	long	long	long	0	long	0?
Aotagnostus:						
aotus	long	short	0	0	short	short
ponebrevis	long	prongs	0	0	long?	short
protentus	very long	long	short	0	long	long
magniceps	long	prongs	long	0	?	long
culminosus	long	long	short	0	long	long
modicus	long	long	0	0	?	?
Myrmecomimus:						
tribulis	short	prongs	0	0	0	0
Ptychagnostus (Acidusus):						
acidusus	prongs	prongs	0	0	0	0
navus	prongs	prongs	0	0	0	0
retrotextus	short	prongs	0	0	short	short
germanus	short	prongs	0	0	short	short
occultatus	medium	prongs	0	0	long	long
Leiopyge:						
armata	long	long	medium	0	0	0
multifora	medium	long	0	0	0	0
Goniagnostus (Criotypus):						
oxytorus	very long	very long	very long	short	long	long
lemnniscatus	prongs	prongs	short	short	long	short
Goniagnostus (Goniagnostus):						
nathorsti	prongs	prongs	short	short	long	long
scarabaeus	long	long	medium	short	long	long
verus		long	short	short	long	long

'0' (Zero) stands for 'absent';

Prongs are the shortest spines, without extension into the medium length.

The length of the spines refers to an estimated gradational scale; in several specimens the length of one or another spine can be numerically expressed as a ratio to the length of the thorax or of another element of an individual skeleton; but generalisations are hazardous because the scarcity of measurable material leaves open the variability of length within a species.

'Short', for example, is the fulcral spine in the second segment of the thorax in *Triplagnostus gibbus* posterus (Pl. 24, fig. 3) and in the cephalon of *Myrmecomimus tribulis* (Pl. 36, fig. 1, Text-fig. 42). *'Medium'* stands for 'medium long'; and

'Long' are spines about as long as or even longer than the thorax.

'Very long', for example, as in *Triplagnostus stramineus* (Text-fig. 39) or in *Criotypus oxytorus* (Text-fig. 46).

The axial spines of the thorax and the pygidium are usually straight and rise relatively steeply retrally, and the spine of the second segment will not contact the dorsum of an up-and-down flipping pygidium. The short spine in the rear of the glabella (Pl. 60, fig. 5; Text-fig. 45), about horizontal, but clearly elevated above the anterior segment of the thorax, may have served as a protective cover to the cephalothoracic aperture; but the aperture is unprotected in any other agnostid.

Functions of spines

The species of the 'spineless' agnostids outnumber greatly the spiny representatives of the ptychagnostids; all agnostids, however, populated the same pelagic environment together, as evident from the association of the remains of spineless and spiny forms. Nevertheless, the possession of spines may have forced upon the ptychagnostids some particular ways of behaviour not shared by other forms. The long spines protected the dorsum, the flanks, and the rear from a too close contact with aggressors of about the same size as the agnostid itself, but not from larger enemies; the ventral side remained, of course, unprotected. When coiling, the spines changed direction rapidly: the pygidial marginal spines swept forward, protecting the front of the cephalon, and were supported by the down- and forward-pointing pygidial axial spine; the spines of the second segment of the thorax, normally overshadowing the pygidium, were pointing down freely. Moreover, the spines moved like whips in the reflex action of sudden coiling. The long spines in the rear and the flanks supported the animal in gliding through the water and the axial spines kept it on its course.

The phenomenon of spinosity, therefore, can be perceived as an adaptation by the 'lucky few' species to the requirements of life in the sea; nevertheless, the spines remain an extreme manifestation of the inherited somatic merocyclism rather than a novel response to the pelagic mode of life.

Taxonomy by spines

The data useful in taxonomy are collected in Table 5; only species represented by complete exoskeletons are tabulated, because the exoskeleton alone shows the structure of the second (spinose) segment of the thorax; no such skeleton is available for *Criotypus lemniscatus,* but the disjointed material allows for the reconstruction in Text-figure 47. Twenty-nine species are tabulated; three species of *Myrmecomimus,* which are omitted, have the same spinosity as *M. tribulis*. Species of *Pentagnostus, Onymagnostus, Zeteagnostus,* and *Ptychagnostus* have only short prongs, none of which extended into spines; taxonomically, these are 'spineless Ptychagnostinae'.

Taxonomically significant is the presence of the axial spine in the rear of the glabella in the species of *Goniagnostus* and the absence of such a spine in all other Agnostidae. Significant for the subgenus *Aristarius* (of *Triplagnostus*) are the very long spines; *Myrmecomimus* has only a single (cephalic) pair of spines, and the species *Triplagnostus quasigibbus* is distinguished within its genus by the shortness of all its spines. In *Acidusus* spines are present in three and absent in two species; *Leiopyge* also includes spinose and spineless forms, and the characters of the spinosity of *Goniagnostus* vary from species to species. At all events, the gift of spines is distributed in unequal shares among the species of the ptychagnostids.

The group of species with unmodified fulcral prongs includes all Quadragnostinae, Agnostinae, Euagnostinae, the Diplagnostidae as tabulated by Öpik (1967), and the following Ptychagnostinae: *Pentagnostus, Onymagnostus, Ptychagnostus, Zeteagnostus, Leiopyge praecox* and *L. cosfordae.* Long fulcral spines are also absent in *Goniagnostus nathorsti, Criotypus lemniscatus,* and some species of *Acidusus* and *Leiopyge* that are included in the next group of forms possessing axial spines.

In passing, pygidial marginal spines are incidental in species of diverse genera; being paired and external these spines represent unfunctional fulcra of a segment of the pygidium; this accepted, these spines mark the posterior edge of that segment.

Homologous structural elements in the agnostid tergite

The structural elements are: (1) the rear of the glabella—the skeletal element between the basal lobes; (2) the basal lobes; (3) the posterolateral portion of the cheeks; (4) the posterolateral spines (the external fulcral prongs); and (5) the furrows. These elements are illustrated and annotated in Text-figure 5, a diagram of *Diplagnostus floralis* sp. nov.; *Diplagnostus floralis* is employed here for a recapitulation of the annotated diagram of *Diplagnostus humilis* Whitehouse (Öpik, 1961b, p. 71 and text-fig. 25)—the first presentation of homologues in the skeleton of an agnostid; in that diagram, however, the reconstruction of the pleural tips, owing to the inferior preservation of the specimen, was incorrect.

The rear occipital and pleuro-occipital position of the cephalon contains all elements that are present in each of the segments of the thorax and can be viewed itself as a segment incorporated in the cephalon; likewise, in the frontal lobe of the pygidial axis, the homologues of the basal lobes and of the glabellar rear are evident; the forward-swinging pleurae of the second segment of the thorax correspond to the posterior slice of the cheeks and a portion of the cephalic rim; the same swing is also clear in the pleural furrows of the anterior segment. The rear of the glabella and its homologues in the thorax differ in shape and relief from each other, but all that matters is the mid-axial position between the basal lobes. The glabellar rear in the anterior segment is, for example, quite clear in *Pseudoperonopsis ancisa,* Plate 11, fig. 6. Furthermore, the lateral lobes in the second pygidial annulation are also interpreted as basal lobes in our diagram of *Diplagnostus floralis.*

The axial furrows (circumaxial furrow, Text-fig. 2) define the axial lobe and separate the basal lobes from the pleurae; they are a fundamental element in all trilobites. The pleural furrows in the agnostid thorax (*F* in Text-fig. 5) are homologues of the posterior part of the cephalon separating the cheeks (*GN*) from the posterior section of the rim including the prongs (*th*); as in the rear of the cephalon the curves of the pleural furrows are deflected sideways and forward. These furrows are pleural by their position and by analogy with the pleural furrows in the polymerid trilobites. In the polymerids, however, these furrows are deflected backward. Otherwise, the phenomenon of the 'occipital similarity' (Öpik, 1961b, p. 125) prevails in the agnostids as well as in polymerids.

APPENDAGES (LEGS), MUSCLE SCARS, NOTULAE, AND APPENDIFERI (APODEMS) IN AGNOSTIDS

Specimens with preserved legs remain undiscovered; nor are footprints and tracks on bedding planes attributable to agnostids known: their absence is in line with the pelagic existence of these trilobites, but cannot be taken alone as proof of a pelagic life, or of a legless constitution.

Muscle scars, notulae, and apodemal pits, which are observable in pairs in segmental order, indicate the number of segments (*vide* Öpik, 1967, p. 67) in agnostid skeletons and occur in exceptional preservation (Öpik, op. cit., pl. 65, figs. 3-7) in some Upper Cambrian forms; they are also observable in the Middle Cambrian species as illustrated in the text-figures in this paper. The terminology is explained by Öpik (1963, p. 32). The 'muscle spots' etc. are part of the prosopon—the external manifestation of markings produced by organs which are in contact with the integument; these markings are passed on also to the exuviae of the skeletal instars. The markings indicate the locations of the attachments of the limbed tendons in the cuticle.

The 'muscle spots' are relatively large and may possess notulae (*vide* Öpik, 1967, text-fig. 45), or are simple (ibid., fig. 43), or only notulae are evident (ibid., figs. 25 and 28). Each cephalic basal lobe of *Aspidagnostus stictus* (ibid., fig. 29) possesses a notula. The diagram of *Doryagnostus magister* (Text-fig. 24) illustrates the muscle scars in the basal lobes in the cephalon and in the thorax—three pairs together, recurrent in all agnostids—as well as in the pygidial axis; the number of these varies, in different forms, between five and eleven (Öpik, 1967, p. 67). Furthermore, the glabella contains four more segments as discussed in the next section; collating information from rare material, these also bear muscle scars interpretable in terms of four pairs of appendages.

Published information regarding muscle spots in the cephalon (in the glabella) is so far restricted to a small number of examples. Among those most informative are *Galbagnostus galba* studied by Whittington (1965, text-fig. 2, pl. 3, figs. 3 and 7) and *'Trinodus' elspethi* (also a *Galbagnostus*) by Cooper (1953, pl. 1, fig. 8); other examples are *Xestagnostus legirupa* and *X. rasilis* (Öpik, 1967, pl. 64, figs. 4 and 5; pl. 65, figs. 3, 4). with an arrangement of muscle spots very different from *Galbagnostus*. In *Xestagnostus* the glabellar field of muscle spots ends at the transverse glabellar furrow, which probably marks also the front of the hypostoma: in a number of agnostids (for example, Öpik, 1963, pl. 2, fig. 12) a pair of pits in the transverse furrow held ligaments suspending the hypostoma by its front. In *Goniagnostus* (and its subgenera *Criotypus* and *Allobodochus*) the lateral glabellar furrows (Text-fig. 45) consist of two pits (notulae) each, and a pair of apodemal pits is clear at the front of the basal lobes; these apodemes carried probably a pair of appendages stronger than others. Such pits are evident also in *Pentagnostus veles* and *P. rallus* (Text-figs. 43 and 44) and are also indicated in *Triplagnostus diremptus* (Pl. 26, fig. 1). The lateral glabellar furrows (plain, or with the pits) are placed over the deep lateral notches of the hypostoma (Robison, 1972, fig. 1), but apodemes remain clear of the hypostomal rear.

In *Galbagnostus galba* (Billings) Whittington (1965, p. 306), six pairs of cephalic muscle scars are present: (1) a pair out of line and on the edge of the glabella (number 4 in Whittington's text-fig. 2); by its position it possibly did not carry legs but may have been connected with hypostomal functions; and (2) a pair of clear scars and a tiny median node on the frontal part of the glabella which is not separated by a transverse furrow but corresponds probably to the frontal glabellar lobe of other agnostids.

THE NUMBER OF METAMERES IN THE CEPHALON AND THE POSITION OF THE GLABELLAR MEDIAN NODE

Five metameres are recognisable in the agnostid cephalon; the count begins with the posterior segment (No. 1) and ends with the frontal glabellar lobe (No. 5); this order is chosen because it reserves a place in front of the glabella for a No. 6, which, however, is not evident in the studied material; nevertheless the 'lateral preglabellar lobes' in a unique specimen of the Upper Cambrian *Innitagnostus inexpectans* described by Öpik (1963, p. 36; pl. 2, figs. 10 and 12) remain an unsolved problem. In the cheeks no trace of segmentation exists, the rear excepted; there is evidence for pleural structure of the posterior (No. 1) segment as discussed in the section on 'Homologous structural elements in the agnostid tergite' (p. 28).

The metameres are enumerated in Text-figures 5, 9, 12, 24, 25, 27, 35, 43, and 45.

The positions of two metameres are observable at a glance: these are the front glabellar lobe (No. 5) and the posterior segment of the cephalon; the locations of the three metameres in between, within the posterior glabellar lobe, are interpretable from the following structures:

(a) The transverse glabellar furrow marks the front of metamere No. 4 behind it; this furrow is the vestige of an articulating furrow which in the skeleton of trilobites stands in front of, and is fused to. the sclerite behind the furrow; consequently, the transverse furrow is not part of the frontal lobe;

(b) the lateral glabellar furrows, or even indentations, mark the front of a metamere (No. 3);

(c) the basal lobes when simple are attributable to the posterior (No. 1) cephalic segment, which resembles a segment of the thorax; the same applies to the posterior basal lobes where the lobes are double. The posterior basal lobes stand immediately behind the deflection angle of the axial furrows as seen in Text-figure 2 (the shape of the axial lobe, q.v.);

(d) in cephala with double basal lobes the anterior lobes are taken as rudiments of the original metamere No. 2, whose pleurae are amalgamated in the cheeks;

(e) the median glabellar node is the mark of the original metamere No. 3. Its position in relation to the midpoint of the posterior glabellar lobe is relevant in taxonomy; only one median node occurs in a glabella but its position is, or may be, different in different taxa; its expression and form are also variable; it is an elevated rounded point, or elongate, or even a low ridge, etc.

The median glabellar node is an axial protuberance and, presumably, a homologue of axial spines of the thorax and the node or spine of the second annulation of the pygidial axis; this accepted, the third somite in the glabella is interpretable as a macrosomite.

The node can stand on the rear border of the original somite, or in its centre, or in front of the centre, or even cover with its base the full length of the somite—possibilities reflected in its position in actual fossils. These are primary reasons for the variability in the positions of the median glabellar node.

Secondary changes in the external position of the median node arose in the course of evolution: the posterior glabellar lobe is the integument of coalescent somites; during the process of fusion the original length of the participants was changing; the increase of one segment was accompanied by a shortening of another, resulting in the concurrent change of the position of the node.

The reasoning so far is based on data observable in the Middle Cambrian agnostids described in the present paper; in the comment that follows, a selection of forms is briefly discussed regarding the morphological manifestation of characters and phenomena leading to the conclusion that the agnostid cephalon contains five original metameres; in the quoted text-figures the metameres are numbered to facilitate the presentation.

(A) The diagram of *Diplagnostus floralis* (Text-fig. 5) is annotated in several aspects; the median node is here a long ridge and metamere No. 3 is very long; metamere No. 2 is discernible but short.

(B) In *Peronopsis integra* (Text-fig. 9) the node is about central in the posterior glabellar lobe; in the species attributed here to *Peronopsis* the node is off centre to the rear but remains, presumably, within the limits of the original middle somite (No. 3). No. 5 (preglabellar lobe) is clear; No. 1 is indicated by the basal lobes; No. 4 is represented by the transverse glabellar furrow and its rear is marked in *P. tramitis* (Text-fig. 3) by the rather short lateral glabellar furrows. No. 2 metamere, however, remains indiscernible for lack of a prosopon.

(C) *Doryagnostus solidus* (Text-fig. 25) shows two pairs of lateral glabellar furrows; of these the anterior pair belongs to metamere No. 3 (with the median node in central position) and the posterior pair is attributable to the second metamere; the transverse glabellar furrow is straight, but in another species, *D. notalibrae* (Pl. 19, fig. 2), it is deformed by a median projection of the No. 4 segment.

(D) In *Ptychagnostus atavus* (Text-fig. 27), the frequently elusive metamere No. 2 is clear, with its presumably rudimentary anterior pair of basal lobes; the front of segment No. 1 is indicated by the abaxial deflection of the cephalic axial furrows. The median node is about central.

(E) In *Onymagnostus* (*Agnostonymus*) (Text-fig. 35) the cephalic metameres are about as clear as in *Ptychagnostus atavus;* No. 4 is long, No. 3 short, and No. 2 also relatively large. The anterior basal lobes are variable in length and the median node in some specimens is off centre to the front.

(F) In *Pentagnostus rallus* (Text-fig. 44), the glabellar median node stands at the posterior limit of metamere No. 3; the separation of No. 2 from No. 1 is reflected in the bipartition of the basal lobes.

(G) In *Goniagnostus* (*Criotypus*) *lemniscatus* (Text-fig. 45), the metameres in the rear are abbreviated in plan; in profile, however, the posterior part is strongly elevated and relatively voluminous, compensating for the short dimensions in plan. The defective material prevents the location of the median node in *lemniscatus*; it is, however, evident in *Goniagnostus nathorsti* (Pl. 60, figs. 1 and 3), on the glabellar posterior culmination and in plan between the anterior basal lobes. If the positions of the original metameric contacts were vertical planes and if the verticality is still conserved in the glabella of *Goniagnostus*, then the node in question belongs to the second and not to the third segment from the rear; it is possible, however, that elements of the original somite No. 3, on the evidence of the position of its median node, were transferred secondarily rearward to override the space of the second somite.

(H) In the illustrations of two aberrant forms (*Rhodotypiscus nasonis* and *Ptychagnostus punctuosus*) the numbering of metameres is omitted because of the erratic position of the median node in these forms.

In *Rhodotypiscus nasonis* (Text-fig. 23), the glabellar median node is far in the rear in a position attributable to metamere No. 2; in related genera (*Euagnostus* and *Doryagnostus*) the node is in a 'normal' position within the limits of metamere No. 3. Nevertheless in *Rh. nasonis* the five metameres are clear.

Ptychagnostus punctuosus is a name covering three subspecies and several other modifications—probably unnamed subspecies; the median node is subcentral in Plate 40, fig. 4; in Plate 40, fig. 6 it is a ridge straddling the junction of metameres 3 and 4; in Plate 39, fig. 2 the node stands on the level of the glabellar lateral furrows; in Plates 38 and 39, fig. 1, a node is placed well in front of the same furrow. Some of these cephala have double and others triple basal lobes. Westergaard's (1946, pl. 11, figs. 26-35; pl. 12, figs. 1-7) paradigm contains similar variants, with the addition of a cephalon (pl. 11, fig. 30) with two nodes, and another (pl. 12, fig. 5) with a prominent median ridge and large simple basal lobes.

Merocyclism of the agnostid skeleton

According to Raw (1953, 1956), a periodicity (merocyclism) of segmentation is apparent in polymerid trilobites and phyletically connects pre-existing annelids with the subsequent trilobites; Raw, however, overlooked the agnostids. The phenomenon of merocyclism refers to the presence of macrosomites followed by one or more less prominent (normal) segments, forming together a cycle. Macrosomites are prominent by their size, or spinosity, or organs that are not evident in the ordinary (normal) segments. In agnostids, the cycles are diadic in the middle third of the body, where to each macrosomite follows a normal segment. In *Diplagnostus floralis* (Text-fig. 5) three diads are recognisable: (1) the posterior part of the cephalon, a macrosomite, is followed by the anterior segment of the thorax, which is 'subnormal' without pleural tips and without articulating doublure and half-ring; (2) the posterior segment of the thorax is a macrosomite with well developed pleural terminations possessing articulation facets followed by the ordinary segment of the anterior pygidial axial annulation and undifferentiated pleurae; and (3) the macrosomite of the second axial annulation is recognisable as such from its median node or even a spine, which is omnipresent in agnostids. The marginal spines are probably the external prongs of the posterior edge of this segment. The diadic merocyclism is not evident in the Condylopygidae, which are structurally different from the rest of the agnostids and in need of a supplementary study of their prosopon.

The macrosomites and the three diads are rather clear in the spinose Ptychagnostinae, as for example in *Goniagnostus scarabaeus* (Text-fig. 49) and *Criotypus* (Text-fig. 46): in these the axial spines belong to the macrosomites; the cephalic segment and the second segment of the thorax are marked by three spines each, and the second annulation of the pygidial axis also belongs to a tri-spinose macrosegment if the pair of the pygidial marginal spines as mentioned above represent the fulcral spines of the same somite.

In the majority of agnostid species the second segment of the thorax lacks the accentuating spines; in these the remaining characters of a macrosomite are the long fully developed free pleurae.

A cyclic structure may originally have existed also in the agnostid cephalon: the posterior cephalic metamere (No. 1) is recognisable as a macrosomite; in front of it metamere No. 2 is ordinary and, as such, is often reduced in size and possesses no clear prosopon of its own. The middle segment (No. 3) is apparently a macrosomite characterised by its median node, which can be equated to an axial spine. Consequently, No. 3 and No. 2 together may constitute a meracyclic diad. The two foremost, No. 4 and No. 5 (the frontal glabellar lobe) are alone equipped with alimentary ducts (see Öpik, 1961a, text-figs. 2-4, p. 414) and by the same token should be acceptable as macrosomites. Consequently, the cephalon in front of its posterior macrosegment consists of a diad and two more macrosomites; or the anterior part of the glabella comprises a set of three macrosomites.

The articulate agnostid exoskeleton

Summary

The manner of articulation and coiling has been studied in polymerids and is known sufficiently well; in agnostids, however, the mechanics of articulation differ in several particular aspects from that of the polymerids though in functional terms it is the same as in other trilobites. In a holaspid agnostid: (1) only four sclerites are evident, connected by three joints; (2) no structure reminiscent of hinges is known in the axial furrows at the adaxial ends of the joints; (3) abaxially, as generally in trilobites, each joint terminates at the geniculation with fulcra which operate as hinges; consequently three pairs of hinges exist in the agnostid exoskeleton; (4) a hinge consists of an external retrally-pointing prong ('spine') with a socket at its reverse side, and another, forward-pointing prong of the rear sclerite, invisible from above, covered by the external prong and nesting in its socket; (5) the fulcral hinges allow for rotation down from the normal (horizontal) position of the exoskeleton, and up to recover the horizontality; the upward rotation is, of course, stopped by the external prongs; (6) the joint is the horizontal axis of the rotation; (7) the rotation is performed by the three tagmata—the cephalon, the pygidium, and the thorax—whose segments rotate within very narrow limits or not at all; and (8) the ultimate rotation results in enrollment described as a triplication of the exoskeleton.

Explanatory discussion

The following rotational events are possible in the coherent exoskeleton: (a) in a static position of the thorax the pygidium and the cephalon may rotate simultaneously, or separately, or in turns; (b) in a static position of the cephalon the thorax and the pygidium may rotate as a unit or in combination with the independent rotation of the pygidium; (c) the pygidium being static the thorax can rotate together with the cephalon; and consequently (d) the floating or swimming animal possessed the ability to move its body in waves, in changing its level in the water and changing the directions when leaning over to one or another flank in groping for edible plankton (see p. 34).

The middle joint opened readily in moulting, but at other times its play was rather limited by the structure of the facets of the posterior free pleurae; these swing forward and under the pleural tips of the anterior segment. The left facet is exposed in the thorax of *Doryagnostus* (Pl. 18, fig. 5), which lost the fulcral prong covering the facet; this prong is intact in Plate 6, fig. 1 as a part of the marginal flange in the anterior segment. Moreover, the facet is limited against the pleural furrow by a low ridge acting, presumably, as a pleural stop. The facets with pleural stops are manifest also in the silicified segments of *Hypagnostus parvifrons* and *Peronopsis interstricta* (Robison, 1964, pl. 81, fig. 8, and pl. 82, fig. 6) and also in the posterior segment of *Trino-*

dus elspethi (Hunt, 1967, pl. 22, fig. 10). The facets and the stops are also visible in the segment of *Aotagnostus culminosus* (Pl. 33, fig. 7; Text-fig. 41).

The amplitude of the rotational play about the middle joint was very narrow, if present at all: this may be illustrated by the specimen of *Doryagnostus notalibrae,* Plate 21, fig. 1, in which the articulating facet is partly and narrowly exposed owing to some displacement of the sclerites rather than to rotation in situ. In discussing the preservation of the complete exoskeleton (q.v.), attention is paid to the post-mortem rotation of the anterior segment, involving the exposure of the articulating half-ring in consequence of the decay of the supporting tissue and disruption of the contact of the thorax with the cephalon. In passing, the overlap of the pleurae (anterior over the one behind) and the articulating half-ring under the axial lobe in its front, and the strict juxtaposition of the margins of the fixed pleurae along the joint proper, are well known in all trilobites and consistent with the streamlined and forward-moving animal. To conclude, the two segments of the thorax in the living agnostid were locked together so as to eliminate almost completely the rotational play in relation to each other—as can be seen, for example, in the lateral view of *Hypagnostus parvifrons mammillatus* (Brögger, 1878, pl. 5, fig. 3d); in coiled exoskeletons (see below) the thorax has, therefore, the appearance of the spine of a hingewise bound book.

The foremost joint connecting the thorax with the cephalon is also equipped with 'prong-over-prong' hinges limiting, or even excluding, the possibility of an upward rotation of the tergites but allowing for a wide arc in rotation downward. Moreover, the absence of an articulating half-ring in the front of the thorax enhanced the flexibility of the coupling of the somites themselves; another factor contributing to the freedom of play at the anterior joint is the absence of free pleurae beyond the fulcral prongs which mark the geniculation of the anterolateral corners of the pleurae of the anterior segment. The movement, however, stops when, in the process of coiling, the frontal parts of the pleural flanks meet the geniculated margins in the rear of the cephalic shield.

In coiling, the thorax with the pygidium attached rotates down about an arc of ninety degrees and assumes a hanging position close to that seen in the lateral view of *Hypagnostus parvifrons* in Rasetti's (1948, pl. 45, fig. 21) specimen.

The posterior hinges connecting the thorax and the pygidium, because of the structure of the fulcra, allow in their turn a free rotation of the pygidium, also about an arc of ninety degrees downward from the horizontal, or forward from the 'hanging' thorax; consequently, the pygidium has rotated (in two steps) about 180 degrees when clasping margin to margin with the cephalon to accomplish the coiling. At the same time the 'shutter gap' between the edges of the posterior free pleurae and of the free pygidial front (Text-fig. 5; *Myrmecomimus tribulis,* Pl. 36, figs. 1, 2), acting as shears, will be shut; moreover, the articulating facets at the frontal wings of the pygidium are concave (see Öpik, 1967: numerous examples), and receive the curved edge of the pleurae of the posterior segment, ensuring a perfect closure of the flanks of the enrolled tergite. Notably (Text-fig. 5) the edge of the anterior pleura in its turn fits in the concave (fluted) facet at the tip of the posterior pleura.

In a coiled exoskeleton the pygidium and the cephalon are not necessarily clasped together edge to edge; as a matter of structure, the doublures of the shields contact each other in the closure of the exoskeleton. Consequently in forms having a different form of shield the closure will be perfect. For example, in *'Phalacroma' glandiforme* (see Westergaard, 1946, pl. 15, figs. 13a-13d) the closure is perfect between shields of unequal form. Consequently, the relatively narrow pygidium in *Triplagnostis scopus* nov. (Pl. 27, figs. 5, 6) cannot prevent the animal from achieving the necessary tight closure in coiling. The whole process of 'coiling and uncoiling' consists in folding and unfolding of a triptych of three hinging units; the convexity of these tagmata leads to the allusion of a roll or coil. It stands to reason that the events of coiling described above in relation to the horizontal cephalon can be viewed also relative to a horizontal pygidium or thorax, and that the tagmata most probably rotated simultaneously to clasp or to part the edges.

The coiling, presumably, was a reflex action, to protect in the first place the soft ventral side and the appendages from an attack; the contracted muscle relaxed slowly after a while and the normal uncoiled attitude was resumed without haste—or even not at all: failures in uncoiling resulting in a prolonged state of suspended animation are documented by finds of enrolled exoskeletons of diverse forms. These are not exuviae but individuals buried alive (Rasetti, 1952, p. 887) preserved as empty shells filled with calcite. Numbers of such known finds are small, much smaller than of polymerid trilobites, ostracods, brachiopods, and pelecypods.

The articulation mechanics as described above refers to observations on a relatively small number of well preserved Middle Cambrian exoskeletons and skeletal parts. It is possible, however, that some species existed of a structure different from *Doryagnostus, Goniagnostus, Peronopsis,* etc. For example, the Ordovician *Geragnostus clusus* Whittington (1963, text-fig. 3, p. 51) is shown without hinges except for the cephalic prongs gripping over rounded anterolateral corners of the anterior segment of the thorax. It seems therefore that articulation was served only by the two articulating half-rings and doublures and that the sclerites possessed a wide rotational freedom, being held together essentially by the somites alone.

Jaekel (1909, text-figs. 1-6) illustrated a coiled specimen of an agnostid—his *Metagnostus erraticus* [in Harrington et al. (1959, p. O178) *Metagnostus* Jaekel is quoted as a synonym of *Trinodus* McCoy—a subjective decision, because the holotype of *T. agnostiformis* (the type species of the genus) as revised by Whittington (1950, pl. 68, figs. 1-3) is a fragmentary cephalon incapable of a conclusive interpretation]. *Metagnostus erraticus* is an Ordovician form with affinities to *Geragnostus longicollis* (Raymond) as described and illustrated by Whittington (1965), as well as *'Trinodus' elspethi* (Raymond) in terms of Hunt (1967) and earlier writers. Jaekel's line drawing of the coiled *M. erraticus* and Whittington's photographs of *Geragnostus longicollis* (op. cit., pl. 1, figs. 6, 9, and 10) display similarity in the structure of the coiled exoskeletons, especially of the thorax, whose two segments retain their original relative attitudes, without the thorax being plicated at the hinges. Jaekel's interpretation of the articulation mechanism of the exoskeleton (op. cit., figs. 2 and 3), however, takes no account of the fulcral apparatus, which, of course, remained unnoticed until many years later. Also wanting was information regarding the structure of the free pleurae, in the absence of properly preserved material. In passing, Jaekel's figure 5 is complete with the cephalic recess (see Robison, 1964, p. 514). Its counterpart, the thoracic recess (see Hunt, op. cit., pl. 22, fig. 46, and Cooper, op. cit., pl. 1, fig. 8) remained unnoticed or was not preserved in Jaekel's specimen.

Agnostids—filter feeders

The pelagic agnostids fed on microbios, which was available in the surface waters of the sea; one may speculate that the nourishment was not collected at sight by the eyeless feeders but was sucked in together with ample amounts of water, presumably continuously, day and night. The peculiar hypostoma (Robison, 1972) lying under the posterior lobe of the glabella was equipped with some filter retaining the plankton and ejecting the water by way of the cephalothoracic aperture; also, a feeble jet from the aperture may have contributed to the forward propulsion of the feeding animal. The aperture is best observable in coiled specimens, but remained exposed and open in uncoiled specimens, in which alone the cephalic front was unobstructed by the contact with the pygidial rim and maintained the continuous inflow of the food-carrying water.

The position of the aperture in the foremost and morphogenetically senior skeletal joint seems significant: it was operational even before the parting of the sclerites from each other. The jet came to a standstill in coiled individuals in which the intake of water was locked out. In passing, hypostomata have not been found in coiled specimens (see Rasetti, 1952); the hypostoma, a sclerite, was subject to moulting; but the investigated coiled animals died probably of hunger because of a failure in the activity of the filtering apparatus deprived of its hypostomal support.

It is rather doubtful that the aperture served as a foramen for a prehensile, or permanently anchored, cirrus (a dorsal azygous appendage): its presence in moulting would separate the exuviae of the cephalon and the thorax from each other always, and totally exclude the shedding of complete exoskeletons.

Mode of life of agnostid trilobites—recapitulation

The agnostids were cosmopolitan animals—dwellers in the surface waters of the sea, equipped with voluminous digestive glands and feeding on microbios. Many species of most of the known genera have a worldwide distribution which can be explained by a pelagic mode of life; agnostids are found as fossils in limestone, in sandy and silty limestone, in sandstone, siltstone, shale, and chert, in bituminous as well as clean sediments. It stands to reason that pelagic animals are not influenced by a euxinic or any other regime at depth (Öpik, 1961a, p. 418; 1961b, p. 130; 1963, p. 27; 1967, p. 38). The remains of agnostids, however, gravitated down to the burial grounds on the floor of the seas, epicontinental and shallow or oceanic and deep; the upper layers of these seas constituted, of course, the continuous pelagic domain. Cambrian oceanic deposits are unknown so far, but by inference they should contain among other fossils also material of agnostid skeletons of taxa already known from epicontinental and marginal formations.

The remains of agnostids are quite numerous in some black (bituminous) shale sequences deposited in euxinic conditions that cannot be considered as biotopes of agnostids. Relevant is the comparison of the faunas of the Inca Formation and the Currant Bush Limestone of the Undilla Basin (Öpik, 1956; 1957, p. 15; 1960, p. 100). These formations are contemporaneous and linked together in a climbing and interbedded contact. They share a diversified fauna of agnostids that are described in the present paper, but differ from each other in respect of other fossils, especially of polymerid trilobites: these are present and even conspicuous in the Currant Bush Limestone and its shale lentils in association with the agnostids, but totally absent in the Inca Formation, in its shale, siltstone, chert, and limestone lentils. I presume therefore that the regime in the Currant Bush depositional area was reasonably hospitable down to the bottom of the sea and different from the environment of the euxinic, inimical, quiescent waters below the surface of the Inca seaways. The agnostid, however, populated the aerated, euphotic and wind-agitated pelagic realm above the stagnant deep. Being eyeless the agnostids were unable to catch their food at sight; I presume that they fed on microbios, taking it in with, and filtering it from, water which passed out through a 'water exhaust' enclosed in the sleeve of the cephalothoracic aperture. Consequently the blindness was no handicap and cannot be regarded as a sign of life in the darkness of the deep, or of mud.

The agnostids were floaters in the first place, but also swimmers adapted to forward propulsion as well as for changing direction in space. Their body is streamlined as in small polymerid trilobites, and of a mobility comparable with the quite alert recent water beetles. Consistent with the streamlined habit is also the retral inclination of spines in the spinose forms. The only forward-pointing structures are the tips of the pleurae of the posterior segment of the thorax (Robison, 1964, p. 515; 1972); these, however, are placed under the margins of the pleurae of the anterior segment and therefore incapable of being deflected sideways by the pressure of water during the forward progression of the animal. Robison (1973) also 'believes that agnostids must have spent most of their life enrolled'. Feeding, disposal of waste, moulting, mating, growth etc., however, are inconsistent with a 'normal' enrolled existence; prolonged enrollment is probably a sign of suspended animation terminating in death. The notion of pelagic ubiquity remains also in force if the concept of drifting algal masses populated by agnostids is accepted; such marine vegetation is, however, unknown in the Cambrian and its existence cannot be deduced from the organisation of the skeleton of agnostids.

Writers have proposed several models of the mode of life of agnostids (reviewed by Robison, 1972); of these the pelagic existence alone is tenable, as is accepted by Robison himself.

PART III: PALAEOZOOLOGY

PROVENANCE OF COLLECTIONS

In the taxonomic descriptions the collecting sites are documented by locality numbers (for example M412) and the specimens are also marked by the same number; the locality numbers are also printed (with some rare omissions) on the sheets of the 4-mile geological series maps (= 1:250 000 sheets) produced by the Bureau of Mineral Resources in Canberra.

Appendix 1 lists the names of the species and their occurrence by way of the site numbers. This is an alphabetical list; the 'contents' serves as a systematic list and indicates the page numbers in the text.

Appendix 2 describes the topology of the collections; the data are (1) the positions of the mapped site numbers; (2) the geographic coordinates of each site; and (3) the name of the formation and the lithology (in brief) as evident from the map or from the record in the field. Moreover, the agnostid species in the collections are listed, but the names of polymerid trilobites are reserved. Some of these have been described already by Öpik (1961b, 1967, 1970, 1975) and Shergold (1969).

In Appendix 2, most of the collections are listed under the names of the 1:250 000 Sheet areas, whose boundaries are marked in the index map (Text-fig. 4). Included in the index map are also several quadrangles within which Middle Cambrian undescribed agnostids are known to be present: Brunette Downs, Alroy, and Ranken, represented in collections by Templetonian forms of *Peronopsis, Acadagnostus,* and *Pentagnostus*. In the Huckitta area the same Templetonian agnostid fauna is present, and in limestone of the Arthur Creek Beds the *Euagnostus opimus* Zone and possibly the Undillan are evident. In the Hay River area I observed in the field the presence of late Undillan and possibly early Boomerangian agnostids in emergent limestone ridges and in a shale.

Finally, in South Australia in the Gidgealpa Wells (see Index Map) about 3 km below the surface and below Mindyallan trilobites (see Öpik, 1967, p. 33), agnostids of Boomerangian and Undillan age are present in limestone.

The topographical descriptions of the collecting sites are amplified by references to formations and the character of the matrix containing the remains of the agnostids. The formations have been briefly described and named by Öpik (1956, 1960). The contacts of the formations are climbing and a time scale on the basis of their sequence remains unattainable: for example, the Inca Formation in the Mount Isa area covers the Floran and the early Undillan, which in the north were times of limestone and dolomite deposition; in the Mount Isa area the V-Creek Limestone rests on the Inca, which is here a temporal equivalent of the Currant Bush Limestone (and Louie Creek Limestone) of the northern terrain. The limestone of site M195 with its late Undillan agnostids is the only known occurrence of the Currant Bush Limestone lithology within the Mount Isa area.

The zone position of the agnostid species as listed in the site descriptions is reflected in the fundamental and integral Table 1. It stands to reason that the reference to zones is not a topological characteristic but a connotation of the time of the biological and inorganic (depositional) events at a particular site.

SUPRAGENERIC SYSTEMATICS

The genera of agnostids described in the present paper are placed in two families, the Diplagnostidae and the Agnostidae, in terms of the morphological classification adopted by Öpik (1967) in his 'Tabular Classification of Agnostids'. This classification is amplified now by the new subfamily Euagnostinae, whose column should be placed in the Agnostidae between the subfamilies Quadragostinae and Ptychagnostinae and receive from the first named the genus *Euagnostus* and from the second *Doryagnostus,* and augmented by the new genus *Rhodotypiscus*.

Pseudoperonopsis should be deleted from the Quadragnostinae and placed in the Diplagnostinae of the Diplagnostidae. In the 'Tabular Classification', criterion I includes the character 'constriction of the acrolobes'; this character is also evident now in the species of the genus *Peronopsis;* consequently *Peronopsis* is to be removed from the column of the Quadragnostinae, of forms with unconstricted acrolobes; this operation may justify the revival of the subfamily Peronopsinae Westergaard, 1936, believed to be a synonym of Quadragnostinae Howell, 1935. Noticeable is also my remark (op. cit., p. 69) regarding the resemblance of *Peronopsis fallax* and *Diplagnostus* as expressed by the dashed part of the line separating the Quadragnostinae and the Diplagnostidae in the 'Table'. In passing, *Onymagnostus durusacnitens* and *Pseudophala-*

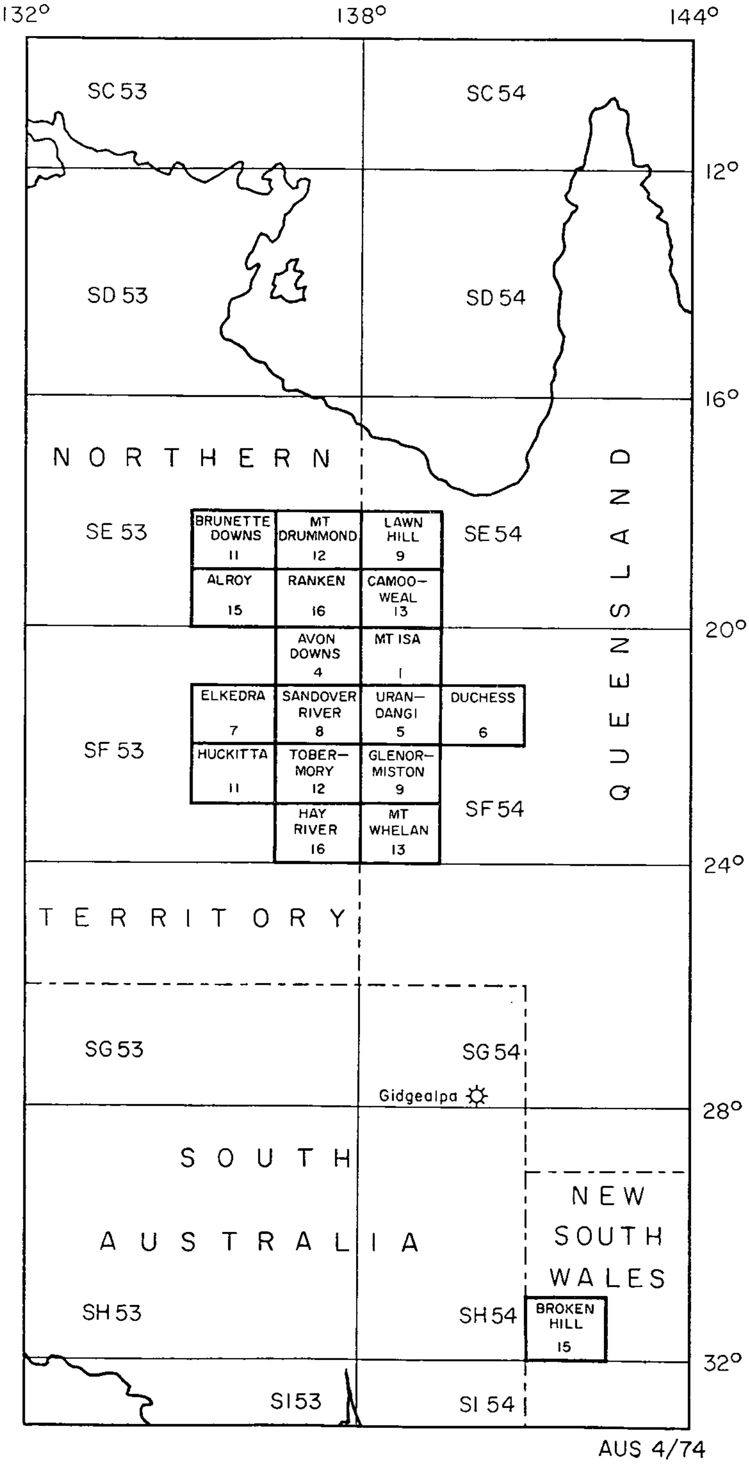

Fig. 4. Index map of the 1:250 000 Sheet areas of the provenance of the described taxa discussed in Appendix 2.

croma dubium (op. cit., p. 62) also have a constricted pygidial acrolobe.

The problem of the classification of *Agnostus pisiformis* in connection with the new genus *Onymagnostus* of the Ptychagnostinae remains open: *Agnostus pisiformis* is the type of the subfamily Agnostinae, M'Coy 1849, and its transfer to the Ptychagnostinae will render the latter a synonym; I prefer to retain the status quo of these genera as belonging to different subfamilies, although the transfer of *Onymagnostus* under the Agnostinae could be another and rather artificial possibility, in preserving the extant nomenclature. At all events *Onymagnostus* stands as a valid genus and cannot be taken as a synonym of *Agnostus* in consideration of the revision of *Agnostus pisiformis* by Henningsmoen (1958, pl. 5, figs. 1-12).

The Ptychagnostinae receive nine new genera, eight of which are proposed on the evidence of complete exoskeletons. The new material described here suggests modifications to the nomenclature discussed earlier (Öpik, 1961b) when *Triplagnostus* and *Ptychagnostus* were regarded as synonyms and *Goniagnostus* was taken as a subgenus of *Ptychagnostus*. In the present paper these names designate separate genera and include new subgenera as well. I regard subgenera as independent taxa which are equal to genera in the classificatory grid; I assign them to genera in consideration of affinities just as genera are attributed to subfamilies or families. The subfamily Ptychagnostinae is contemplated here as an aggregate of a number of multispecific and one or two unispecific genera, including also some forms of the subfamilies Triplagnostinae Kobayashi, 1939 and Leiopyginae Harrington, 1938 (see Öpik, 1967, p. 90). In the review that follows, genera are arranged in groups ('parcels') leading to a potential splitting of the Ptychagnostinae into a set of 'subfamilies'—a procedure calling for an automatic emergence of a family Ptychagnostidae; the same material allows also for different combinations of genera into different parcels and different aggregates of such parcels. The increase of the number of taxonomic names within the ptychagnostids, however, promises neither gains in taxonomy nor better means in determination of their remains for stratigraphic use; the stratigraphy by genera is quite inaccurate and by subfamilies even more so.

Some characters of taxonomic value are discussed in the previous section: the shape of the axial lobe, spines, the relative length of tagmata, and the position of the median glabellar node.

The 'parcels':

I. *Triplagnostus,* of two subgenera (*Triplagnostus* and *Aristarius*) and of twelve named species.

II. *Aotagnostus* (six named species) and *Myrmecomimus* (two species with subspecies).

III. *Ptychagnostus* (of about ten named species-taxa); *Ptychagnostus* (*Acidusus*) with six named species.

IV. *Zeteagnostus* (one species).

V. *Onymagnostus* (of six named species); *Onymagnostus* (*Agnostonymus*) (three species).

VI. *Pentagnostus* (three species).

VII. *Goniagnostus,* of three subgenera (*Goniagnostus, Criotypus, and Allobodochus*), eleven species together.

VIII. *Leiopyge;* described here are five Middle Cambrian species, of which three are new; an early Upper Cambrian form is *Leiopyge cos* Öpik, 1967.

Delagnostus (Öpik, 1961b), *Tomagnostella* Kobayashi, and *Pseudophalacroma dubium* cannot be placed in any of the defined 'parcels', but the evidence favours the subfamily Ptychagnostinae. The Australian Upper Cambrian forms (Öpik, 1967) *Ptychagnostus serus* and *Agnostogonus incognitus* also comply with the concept of the same subfamily.

The ancestry of the agnostids remains unknown; the known (Öpik, 1967, pp. 72-74) begins in the Middle Cambrian with the Condylopygidae, Ptychagnostinae, and Diplagnostidae—forms with already fused glabellar metameres but retaining a clear prosopon of five original somites (see p. 29); an ancestral agnostid can be visualised therefore as possessing a properly segmented cephalon. The earliest known agnostids, however, described from 'about the youngest fossil-bearing Lower Cambrian sediments in eastern North America' by Rasetti & Theokritoff (1967, p. 189) contribute 'nothing to the problem of the origin of the agnostid trilobites'. The authors discuss the morphology of these forms in terms of offshoots of *Peronopsis* and *Hypagnostus* and I accept this interpretation. Moreover, in these agnostids the pygidial and cephalic relief is effaced to a degree even more advanced than in the Middle Cambrian *Peronopsis fallax* and *Peronopsis integra,* for example. Of course, a

TABLE 6
DIFFERENTIAL CHARACTERS OF AGNOSTIDS AND EODISCIDS

AGNOSTINA	EODISCINA
1. Two segments in all species.	Two or three segments.
2. Eyes and sutures absent in all species; no ocular ridges.	Oculate with sutures 'proparian' and (secondarily) eyeless and sutureless (as in polymerids).
3. Scrobiculate cheeks and pygidial pleural lobes.	Scrobiculate cephalic rim in some species.
4. Cephalothoracic aperture.	No aperture (as in polymerids).
5. Repetition of basal lobes in the segments of the thorax.	No basal lobes (as in polymerids).
6. Unsegmented (unfurrowed) cheeks and pygidial pleural lobes. 7. Fused posterior lobe of the pygidial axis.	Furrowed pygidial pleural lobes and segmented pygidial axis in a polymerid style.
8. No cephalic genal spines; fulcral spines evident.	Genal spines probably in *Eodiscus;* fulcral spines in *Pagetia.*

case of a phyletic increase in relief and a reversal of the process of effacement can be inspected in the peronopsids—as exemplified by the *Goniagnostus* stock (see Öpik, 1961b, p. 76; 1967, p. 74), a phenomenon which has no bearing on the problem of the origin of the Agnostids.

The parentage of agnostids is unknown; unknown also are such trilobites as can be regarded as descendants of agnostids before or after their disappearance in Ordovician time. In the system of trilobites the suborders Agnostina and Eodiscina constitute the Order Miomera; if the Eodiscina were unknown the agnostids should remain as a separate aggregate of species without any apparent connection with the rest of the species of their class; the eodiscids, however, possess structures indicating a clear affinity with the polymerid trilobites at the rank of Orders.

The taxonomic affinity between the Agnostina and Eodiscina rests with the following criteria: (1) the small size of the exoskeleton; (2) the number of segments in the thorax (less than four); (3) the incidence of forms with long fulcrul spines in the second segment; (4) relatively large pygidia; and (5) incidence of effacement of external relief. See Table 6.

CLASSIFICATION OF THE TAXA

The names of the taxa in their systematic order are given in the Contents; a repetition of that roll of names would be redundant here.

The names of species are arranged stratigraphically in Table 1—'the Fundamental Chart'; the quantitative zonal distribution of species is given in the panel diagram, Text-figure 1, which contains no taxonomics; the numerical data are extracted from Table 1.

Described and illustrated are 129 species; of these 70 are new and named; presumed new but unnamed are 27; redescribed (revised) are 32 species—10 in Australian and 22 in overseas literature but all found in Australia. Moreover, the first 20 species in Table 1 have been described earlier (Öpik, 1961b, 1967), and among these, 6 forms were originally described from overseas; consequently 28 overseas (universal) species have been identified. The total number of Middle Cambrian agnostids found so far in Queensland, Northern Territory, and New South Wales is 153. The total for Australia, however, should be larger, accounting for the faunas in Tasmania, Victoria, and South Australia (in wells at Gidgealpa); and agnostid-bearing Middle Cambrian strata are also known in Northern Territory in limestones of the Lucy Creek area and in the Hay River area (west of Toko Range).

The number of genera (including subgenera) is 32; of these, 13 are new (4 universal and 9 endemic); the total number of universal genera is 23.

Superfamily **AGNOSTACEA**

Family **DIPLAGNOSTIDAE** Whitehouse, 1936

Subfamily **DIPLAGNOSTINAE**

The concept of the Diplagnostinae and its genera has been discussed by Öpik (1967). Once more, the position of *Tomagnostus* in this subfamily remains in doubt because some of its characters recall the Ptychagnostinae; *Tomagnostus,* however, is absent in Australia.

The constriction of the acrolobes is a common character in the diplagnostids; but it is

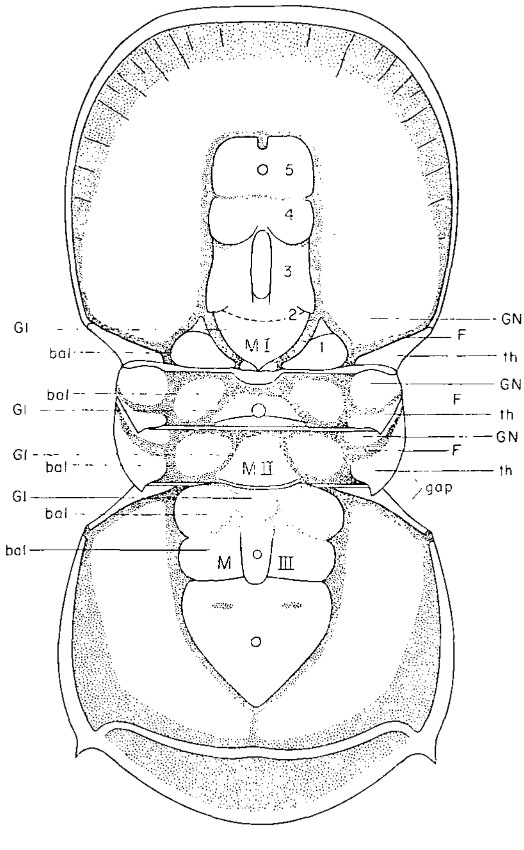

Fig. 5. Exoskeleton of *Diplagnostus floralis* in reference to merocyclism and to the homologous structural elements of the agnostid tergite. M I, M II, and M III—macrosomites; 1-5—segments (metameres) of the cephalon; bal—basal lobes in the cephalon and repeated in the thorax and pygidium; Gl—glabellar rear and its homologues in the thorax and pygidium; F—pleural furrow; GN—cheek (gena) and its homologues; gap—'shutter gap' (a necessity in coiling); th—external prongs.

also evident in some species of *Peronopsis* (for example, *P. longinqua* sp. nov.) and in some species of *Onymagnostus* nov. Species of the following genera of the Diplagnostinae are described here: *Diplagnostus, Oedorhachis, Pseudoperonopsis, Baltagnostus, Iniospheniscus* nov. and *Linguagnostus*. All except *Iniospheniscus* occur also in the Northern Hemisphere. *Linguagnostus comparabilis* is the earliest known diplagnostid—one of the earliest arrivals among the agnostids in Australia. The Diplagnostinae were revised by Öpik (1967).

Genus **Diplagnostus** Jaekel, 1909

Diplagnostus floralis sp. nov.

(Pl. 7, figs. 1-6; Text-fig. 5)

Material: Illustrated are one complete specimen with a broken pygidium, two cephala, three pygidia, and two more cephala in a piece of limestone, all in a light grey fine-grained limestone; these are selected from a larger collection from a single bed.

Holotype: The specimen Plate 7, fig. 5, CPC 14014, with the cephalon, thorax, and part of the pygidium, is selected as the holotype because it eliminates all doubt regarding the 'associated pygidium'.

Diagnosis: Diplagnostus floralis is a regular species of its genus with a zonate pygidium, a narrow rim, wide marginal furrow in both shields, and an acute glabellar rear; the distinguishing characters are: the constriction of the acrolobes, the absence of a preglabellar median furrow, erratic and weak scrobicules in its cheeks, the concave flanks of the glabella; a rearward narrowing pygidial acrolobe concurrent with a rapid widening of the lateral marginal furrows and the collar on the floor of the posterior part of the marginal furrow, a small node in the centre of the posterior lobe of the axis; furthermore, the frontal glabellar lobe is ornate, with a centrally placed small node.

Differential diagnosis: In most of the species of *Diplagnostus* the glabellar rear is acute as in *floralis*; it is, however, broad and blunt in *Diplagnostus crassus* Öpik (1967, pl. 54, fig. 4), which has moreover a scrobiculate test and completely bilobed frontal lobe. The neotype of *D. planicauda bilobatus* Kobayashi, a cephalon (Westergaard, 1946, pl. 8, fig. 16), and the cephalon of *D. floralis* have a similar appearance, but in *planicauda bilobatus* the rim is wide and the marginal furrow narrow and the glabellar flanks are straight; in the pygidium of *bilobatus* the acrolobe is unconstricted and the lateral marginal furrow narrow; a similar structure, different from *floralis,* belongs to *D. planicauda* (Angelin) Westergaard (op. cit., pl. 8, fig. 23). *D. planicauda vestgothicus* (Wallerius) Westergaard (ibid., figs. 25-29) and Öpik (1961b, pl. 19, figs. 13a, b), is scrobiculate in its cephalon and equipped with a preglabellar median furrow, unconstricted acrolobes, and a very narrow pygidial marginal furrow. *Diplagnostus humilis* (Whitehouse, 1936) redescribed by Öpik, (1961b, p.

72, pl. 19, figs. 15a, b) has its collar also on the floor of the marginal furrow but differs in the shape of the cephalon and pygidium; its acrolobes have no stricture and the posterior axial lobe has the median node well in its rear and not central as in *floralis;* scrobicules are absent in the cephalon but a preglabellar median furrow is evident and the pygidial axis is almost in contact with the collar behind it. The new species *Diplagnostus atavorum* is scrobiculate and differs also in the position of the glabellar median node and in other cephalic structures. Finally, *Diplagnostus nordengi* Hutchinson (1962, p. 78) 'included with some hesitation in *Diplagnostus*' by its author, may not be a diplagnostid after all.

Description: Diplagnostus floralis may have attained a length of 8.5-9.0 mm. The acrolobes are moderately constricted and semioval in shape. The margin in the front of the cephalon is slightly obtuse but evenly curved on the sides; the rim is upturned and very narrow and the floor of the wide marginal furrow is crossed in some specimens by radiating straight rugae. The preglabellar median furrow is absent; the frontal lobe, obtusely rounded in front, has a short and shallow sulcus, and a central node which is weak and may be missing in some specimens. The posterior lobe of the glabella is constricted in the middle and its median node is a crest declining retrally in relief; a pair of swellings behind the transverse furrow are apparently large muscle spots, frequently seen also in *Pseudagnostus.* A shallow transcurrent depression (a furrow) connects the tips of the basal lobes and divides the posterior glabellar lobe into two unequal parts.

The rear tip of the glabella is extended into a short acute node. The basal lobes consist of a larger triangular and swollen part with an anterior depressed extension, and can be described as being double. The thorax, about 0.27-0.3x the cephalon in length, has a well developed relief, including a prominent median node on its anterior segment.

In the pygidium the lateral margins are convex, the marginal spines are short and deflected, and the posterior margin is well arched rearward. The rim is evenly narrow and elevated and the marginal furrow, well defined, widens rapidly rearward. The collar contacts the rim at the marginal spines, mostly sags evenly retrally on the floor of the marginal furrow, and in some specimens is bow-shaped with a forward directed projection in the middle. The pygidial axis is relatively flat, distinctly lobate, and transversely furrowed. The median axial node is long, extending over the two anterior lobes, and is crossed by a shallow depression—the anterior transverse furrow. The articulating recess in the axial front is distinct, but the articulating half-ring is inconspicuous. The axis itself is constricted slightly about its second annulation, then widens slightly, and contracts to a triangular rear with flanks straight and converging to an acute tip. The axis does not reach the marginal furrow, and a postaxial furrow is present. On the posterior lobe a pair of short, transverse depressions occur sporadically (see comment below), and a central node is also present. One more node may be present also on the crest of the second axial annulation. There are altogether five small axial nodes on the whole: one on the frontal glabellar lobe, another on the glabellar rear, the third on the thorax, and two on the pygidial axis.

The test is apparently ornamented by a fine and dense granulation.

Some variability in structure is also evident, as mentioned in the comment below.

Comment on illustrated specimens

All specimens have been recovered from a limestone bed, locality M191a.

The holotype (Pl. 7, fig. 5) is 5.0 mm long as preserved; its cephalon is 2.8 mm long. The central node on the frontal glabellar lobe is prominent; a tiny node is also present on the crest of the pygidial axial node, and a stronger one on the axial ring of the anterior segment of the thorax. The tagmata are undisturbed, preserving their contacts in readiness for articulation.

The cephalon Plate 7, fig. 3, CPC 14012, is about 3.1 mm long; radiating rugae cross the floor of the marginal furrow; the node on the frontal glabellar lobe is vestigial; as in the holotype the anterior tips of the basal lobes are depressed (double basal lobes).

The cephalon Plate 7, fig. 4, CPC 14013 is 2.8 mm long (like the holotype); the test appears minutely granulose.

The pygidium Plate 7, fig. 2, CPC 14011, is 2.8 mm long (including the articulating half-ring); the axial lobe is narrower than those of the next two pygidia; the central node on the posterior axial lobe is preserved; the surface of the pleural lobes is corroded—a frequent defect in Diplagnostidae.

The pygidium Plate 7, fig. 6, CPC 14015, is 3.5 mm long and the largest collected, belonging to a specimen some 8.5 mm long. The axis is medium in width.

The pygidium Plate 7, fig. 1, CPC 14010, is 3.1 mm long; its axis is the widest among the three illustrated pygidia. In the posterior lobe a pair of elongate depressions (possibly notulae or the third transverse furrow) is evident.

Occurrence and age: Diplagnostus floralis occurs in the Inca Formation in limestone and in chert, shale, and siltstone at several sites, in the early part of the Undillan Zone of *Ptychagnostus punctuosus*; the species occurs also earlier, in the Currant Bush Limestone, late in the Floran Zone of *Euagnostus opimus.*

Diplagnostus atavorum sp. nov.
(Pl. 22, fig. 2)

Material: Illustrated is one cephalon, CPC 14102, the holotype, in silty shale of the Inca Formation, locality M192. It is slightly defective with an irregular fracture and the left cheek overriding the axial furrow at, and the flank of, the front glabellar lobe; this lobe is in reality transverse subrectangular and not subcircular as seen in the illustration; furthermore the fracture imitates a preglabellar median furrow, which is not present in undistorted cephala. About six such cephala are present in a piece of silty shale, CPC 14362, locality M425; all are about the size of the holotype.

Diagnosis: Diplagnostus atavorum has a scrobiculate (pitted) cephalon with well developed arcuate scrobicules, no preglabellar median furrow, a transverse subrectangular frontal glabellar lobe without a sulcus, an angular glabellar rear with a node on its tip, a very narrow upturned rim, and a broad and deep marginal furrow—a combination of characters not seen together in any other known species of the genus; particularly diagnostic of the species is the small glabellar node behind the midpoint of the posterior glabellar lobe (in other species it is an elongate ridge in the middle of that lobe).

Differential diagnosis: Of the other known species the test is scrobiculate in *Diplagnostus planicauda vestgothicus* (Wallerius) Westergaard (1946, p. 62, pl. 8, figs. 25-29) whose marginal furrow is very narrow, the frontal lobe sulcate, and the acrolobe in front of the glabella divided by a median furrow.

Occurrence and age: Diplagnostus atavorum occurs sporadically in the Inca Formation; its age is the early Floran Zone of *Ptychagnostus atavus.*

Genus Oedorhachis Resser, 1938

Oedorhachis crenias sp. nov.
(Pl. 8, figs. 1-5)

Material: The examined material contains three pygidia and five cephala; two of each are illustrated.

Holotype: The pygidium Plate 8, fig. 1, CPC 14017 is selected as the holotype.

Diagnosis: Oedorhachis crenias is a regular species of its genus distinguished by a small frontal glabellar lobe, a trispinose pygidial margin combined with a zonate rim, and a moderately expanded posterior lobe of the pygidial axis, which is pointed and touches the rim.

Differential diagnosis: In the type species of the genus, *Oedorhachis typicalis* Resser, the rear of the pygidium is angular but without a median spine and the posterior pygidial lobe is almost circular. In *Oedorhachis tridens* Öpik (1967, p. 128) a strong median spine is evident, but the rim is not zonate and the rear axial lobe is also subcircular. *Oidalagnostus? dubius* Westergaard (1946, p. 67, fig. 8) is apparently also an *Oedorhachis* with a trispinose pygidial rim, but its pygidial axis is blunt, not pointed, in the rear.

Description: Oedorhachis crenias is a relatively large agnostid attaining a length of some 9-10 mm, and equal to the holotype of *O. typicalis.* The cephalic rim is very narrow and upturned, the marginal furrow is a broad channel; the cheeks are scrobiculate and the caeca extend across the furrow to the rim as in *Pseudagnostus* cf. *idalis* (Öpik, 1967, pl. 63, fig. 4). The acrolobe is unconstricted and rather steep about the periphery. A shallow and narrow preglabellar furrow divides the acrolobe in front of the glabella. The frontal glabellar lobe is short and a median sulcus is absent. The transverse glabellar furrow, well defined laterally, appears shallow in the middle. The glabella as a whole is boat-shaped, widest behind the transverse furrow and narrowing rearward to its angulate, even acute rear. The lateral furrows of the posterior glabellar lobe are short but deep and the median node has the form of a low crest. The basal lobes are short and triangular.

In the pygidium the lateral margins are evenly convex, the rear margin is moderately arched, and the whole shield, slightly wider than long, appears subrectangular. The rim on the sides is narrow and the marginal spines are short and deflected. Between the spines the rim projects rearward and culminates in a short, flat, triangular median spine behind the inconspicuous collar (the rim is zonate). The marginal furrow is broad and deep and invades the base of the lateral spines. The acrolobe is unconstricted, slightly angular opposite the marginal spines and divided by the tip of the axial lobe, which bears a low terminal node. The articulating half-ring is a narrow transverse ridge separated from the axial front by a broad furrow.

The axis is very long; its acute tips intrude the marginal furrow. The two anterior axial annulations are low in relief and are defined by a transcurrent furrow interrupted in the middle by the long median node, whose tip (apparently a short retral spine) extends beyond the margin of the second annulation. The posterior lobe of the axis, widened laterally and suboval to about elliptical, is triangular in its posterior half. The test is thin and shiny.

Comment on illustrated specimens

The first four illustrated specimens come from a single bed of dark bituminous limestone, locality M24.

The holotype pygidium is 4.2 mm long; it is preserved as an external mould and its cast. The rim is zonate, the median spine is short, the median axial node prominent, but the anterior axial annulation is diffuse.

The pygidium Plate 8, fig. 3, CPC 14018, is about 3.8 mm long; the median node is long, the anterior axial lobe and the articulating half-ring are preserved and the terminal node is visible.

The fragmentary cephalon Plate 8, fig. 4, CPC 14019, is 3 mm long as preserved; the cheeks are corroded; the associated small cephalon is about 1.6 mm long. The rearward taper of the glabella is evident.

The cephalon Plate 8, fig. 5, CPC 14020, in a chert pod in dolomite, from locality M136, is 2.5 mm long; it is exploited in the description of the 'undeformed cephalon'.

Occurrence and age: Oedorhachis crenias is a rare fossil of the V-Creek Limestone, localities M24, M136, and M462 (CPC 14363); its age is the Undillan Zone of *Goniagnostus nathorsti*.

Genus **Pseudoperonopsis** Harrington, 1938

The type species of *Pseudoperonopsis* is *Agnostus sallesi* Munier-Chalmas & Bergeron. Howell (1935) placed *sallesi* in *Peronopsis,* and (*in* Harrington et al., 1959) listed *Pseudoperonopsis* as a synonym of *Peronopsis*. Öpik (1967, p. 76) observed the similarity of the zonate pygidial rim of *Pseudoperonopsis sallesi* and *Peronopsis ferox;* Sdzuy (1961) regarded *sallesi* as a subspecies of *ferox* (*Peronopsis ferox sallesi*).

According to Howell (1935, p. 226) the original description and illustrations of *Agnostus sallesi* are inaccurate, and Sdzuy (op. cit., p. 523) concurs. Of the two specimens published by Howell (op. cit., pl. 22, figs. 17 and 18) only the second (fig. 18) is sufficiently well preserved for taxonomic interpretations; it is a plesiotype kept in the University of Montpellier; even better preserved are the specimens from Spain attributed to *sallesi* by Sdzuy (op. cit., pl. 2, figs. 1-8). Consequently the concept of the species *Agnostus sallesi* is based not on the original type specimen, but on a subsequently published plesiotype (Howell, op. cit.) and the name *sallesi* attributed to it is a reasonable but subjective inference. The diagnosis of the genus *Pseudoperonopsis* compiled on the evidence of the illustrations of *Peronopsis fallax sallesi* (Munier-Chalmas & Bergeron, 1889) Sdzuy (1961, p. 523, pl. 2, figs. 1-8) refers to the following characters: (1) The glabellar rear is wedge-like and acute (rounded in *Peronopsis fallax*); (2) the pygidial axis is short, 0.6-0.7x the shield length and abruptly tapering in its posterior third to an acute apex; (3) the marginal furrow is a wide channel and the rim narrow in the cephalon and pygidium; (4) the rim between the marginal spines is zonate (reminiscent of some specimens of *Peronopsis fallax,* q.v.).

The diagnostic characters indicate a species of the Diplagnostinae (Diplagnostidae) distinguished by a zonate rim; in *Diplagnostus* and *Linguagnostus* the rim is plain, and the collar, stretching also from spine to spine, stands on the confine of the acrolobe or on the floor of the marginal furrow as in *Diplagnostus floralis* sp. nov.

The zonate rim in *Peronopsis ferox* has been already discussed (Öpik, 1967, p. 69); the idea of a possible derivation of *Diplagnostus* (Diplagnostidae) from an early peronopsid, as a matter of speculation, finds some structural support from such forms as *Peronopsis longinqua* sp. nov. The diagnosis presented here refers in the first place to *Agnostus sallesi* in terms of Sdzuy (op. cit.); it is also applicable as the diagnosis of the genus *Pseudoperonopsis* Harrington, 1938, when amplified with the provision of the zonate rim as an unstable structure.

Five species occur in Australia: *Pseudoperonopsis perplexa* (Robison); *P. iniugata* nov.; *P. ancisa* nov.; *P. syrma* nov.; and *P. insolita* nov.

In passing, the genus name *Pseudoperonopsis* is employed here pending a material revision of the holotype of *Agnostus sallesi.*

Pseudoperonopsis perplexa (Robison, 1964)

(Pl. 10, figs. 2-7)

Linguagnostus perplexus Robison (1964, p. 527, pl. 80, figs. 30, 31; pl. 81, figs. 1-3) is here transferred to the genus *Pseudoperonopsis* Harrington, 1938, on the grounds of its similarity to the type species. *Agnostus sallesi* = *Peronopsis sallesi* = *Peronopsis fallax sallesi* in terms of Sdzuy is discussed in the preceding description of the genus. The characters common to *sallesi* and *perplexa* are the shape of the pygidial axis, the zonate pygidium with the collar on the inner edge of the rim between the marginal spines, and the shape of the glabella; the species *perplexa* differs in its less acute glabellar rear, longer pygidial axis, and well expressed sulcus in the glabellar front. In *Linguagnostus kjerulfi* Brögger (1878, pl. 5, fig. 7b) and Westergaard (1946, pl. 8, fig. 32; pl. 9, figs. 2 and 3) the pygidial margin is upturned and rimless, the collar (zone) stands in front of the marginal furrow, and the glabella is boat-shaped; some *Pseudoperonopsis* (*ancisa* and *iniugata*), but not *perplexa,* have the same glabellar shape.

The Australian specimens of *Pseudoperonopsis perplexa* cannot be distinguished from the type material from Utah except for their different state of preservation; even the pygidial border furrow exhibits the 'faint wrinkles normal to margin of furrow' (Robison, op. cit., p. 527), as seen in our Plate 10, fig. 2.

These radiating caeca on the floor of the marginal furrows in *Pseudoperonopsis perplexa* (and in the cephalon of *Diplagnostus floralis*) indicate a glandular anatomy akin to the Pseudagnostinae (Öpik, 1967, pl. 63, fig. 4, pl. 64, figs. 4 and 5); moreover the presence of peripheral caeca in the pygidium of a diplagnostid is evidence of their presence in the acrolobe itself, as seen in *Oidalagnostus personatus* (op. cit., p. 135).

Comment on illustrated specimens

The first three specimens came from the V-Creek Limestone, locality M409.

The specimen Plate 10, fig. 2, CPC 14031, is 7.0 mm long, crushed and decorticated. In the frontal lobe, which is about 0.3x the glabella in length, a median sulcus is absent; the thorax is about 0.3x the cephalon in length; delicate radiating caeca are preserved in the marginal furrow of the pygidium as in Robison's (op. cit.) specimens; the collar on the inner edge of the rim between the spines is weak.

The exoskeleton Plate 10, fig. 3, CPC 14032, is 4.5 mm long as preserved. The cephalic margin in its anterior half is semicircular; a sulcus is evident in the front of the anterior glabellar lobe, which itself is deformed by a crease.

The pygidium Plate 10, fig. 4, CPC 14033, is 3.0 mm long; the postaxial median furrow is indicated; the front of the axis has a well developed recess, a relatively wide articulating furrow, and an elevated half-ring.

The next three specimens were obtained from locality D74, Quita Formation, Urandangi area.

The pygidium Plate 10, fig. 5, CPC 14034, is 2.8 mm long; it is undeformed, the test is more or less preserved, but the collar on the inner edge of the posterior rim is worn off. A weak postaxial median furrow is evident.

The cephalon Plate 10, fig. 6, CPC 14035, is 3.0 mm long; the cephalic narrow rim is upturned and the frontal glabellar sulcus is clear.

The cephalon Plate 10, fig. 7, CPC 14036, is 2.8 mm long; it is the cast of the external surface. The angular glabellar rear is intact; faint traces of radiating caeca are preserved in the marginal furrow; the frontal lobe is short, about 0.26x the glabella in length.

Occurrence and age: Pseudoperonopsis perplexa occurs in the Quita Formation (D74) in the Zone of *Ptychagnostus punctuosus;* it is widespread in the V-Creek Limestone (M409; M59; M139; M212; M214; M234; M247; M408; M410) in the zone of *Doryagnostus notalibrae* (= Zone of *Goniagnostus nathorsti* + *Ptychagnostus punctuosus*); and in the same formation (M195) in the zone of *Goniagnostus nathorsti* (after the disappearance of *Pt. punctuosus*); consequently, *Pseudoperonopsis perplexa* occurs in all zones of the Undillan Stage.

Pseudoperonopsis syrma sp. nov.

(Pl. 11, fig. 7; Text-fig. 6a)

Material: Illustrated is one complete exoskeleton, the holotype CPC 14043.

Diagnosis: Pseudoperonopsis syrma sp. nov. is distinguished by its forward contracting parabolic cephalon, very short frontal glabellar lobe, large triangular basal lobes, wedge-like acute glabellar rear, and crescentic train-like posterior pygidial rim which is subangular in the midline; the collar is developed as a delicate raised ridge along the confine of the rim against the marginal furrow.

The train of the rim, half of which is lined by the doublure, is a feature essential in recognition of the species; it is, however, rarely exposed or preserved.

Differential diagnosis: A posterior pygidial rim with a crescentic train is also found in *Pseudoperonopsis insolita* nov., which, however, cannot be confused with *P. syrma* as evident from the differential diagnosis of *insolita.* In *Pseudoperonopsis ancisa* the frontal glabellar lobe is large and no train is apparent in the pygidial posterior rim.

Description: The holotype is 5.6 mm long; the pygidium is very little shorter than the cephalon; the thorax is 0.3x the cephalon in length and therefore shorter than in *Pseudoperonopsis perplexa;* the tagmata have preserved their original positions, ready for articulation. The acrolobes are slightly constricted and contract forward (in the cephalon) and rearward (in the pygidium) in width. The marginal furrows of the shields are very wide.

In the cephalon the outline is about parapolic but with a truncated frontal margin in its middle; the rim is very narrow and elevated. The preglabellar median furrow is short and shallow; the frontal glabellar lobe is short, about 0.25x the glabella in length, and a median sulcus is absent. The posterior glabellar lobe has a pair of obscure lateral indentations, a central elongate median node, and a long wedge-like rear. The basal lobes are prominent, large and triangular, nesting with their anterior tips in lateral recesses of the glabellar flanks.

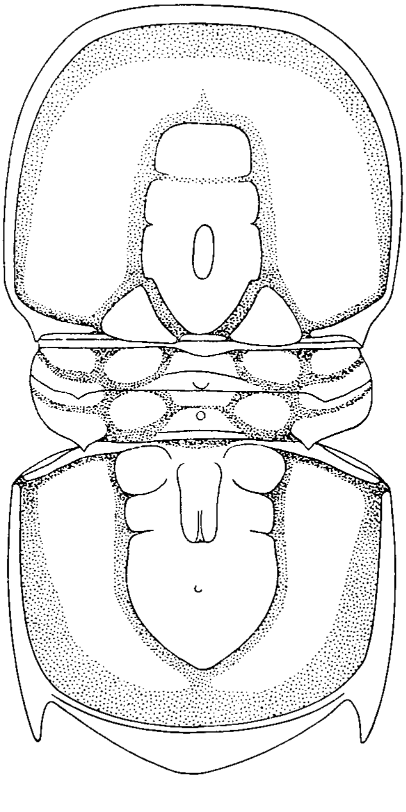

Fig. 6a. *Pseudoperonopsis syrma.*

In the pygidium the rim is narrow but widens behind the marginal spines into a crescentic train which is angular in the rear and provided with a faint collar on its concave front. The pygidial axis, about 0.7x the shield in length, is distinctly trilobate, but the lateral furrows remain short of crossing the midline; the second lobe is laterally contracted; its median node, rising from the middle of the anterior lobe, gains in prominence retrally and develops a tip with a median cleft reminiscent of *Peronopsis tramitis* and *P. longinqua.* The posterior axial lobe is slightly expanded in the middle and then contracts to a point; it is separated from the marginal furrow by a short, broad, shallow postaxial furrow.

Occurrence and age: The holotype of *Pseudoperonopsis syrma* is embedded in a piece of silty siliceous shale of the Inca Formation found at the Buckley River crossing of the Barkly Highway, Mount Isa area; associated is *Ptychagnostus atavus;* the species is also sparsely represented in collection M425 of the same formation; its age is the Undillan Zone of *Ptychagnostus atavus.*

Pseudoperonopsis ancisa sp. nov.

(Pl. 11, figs. 5-6)

Material: Illustrated are two exoskeletons selected from a small supply of isolated shields.

Holotype: The exoskeleton Plate 11, fig. 6, CPC 14042, is selected as the holotype.

Diagnosis: Pseudoperonopsis ancisa is a form with a plain and trainless pygidial posterior rim and a boat-shaped glabella contracting to a bluntly angular rear; it is distinguished by a large frontal glabellar lobe.

Differential diagnosis: In the simplimarginate *P. iniugata* as well as in *P. syrma* the frontal glabellar lobe (0.26 and 0.25 respectively) is shorter than in *ancisa,* with 0.32x the glabellar length; furthermore in *iniugata* the median glabellar node is vestigial; in *syrma* the pygidial train is distinctive. *Pseudoperonopsis perplexa* has also a short frontal glabellar lobe, shorter than in *P. ancisa,* and its pygidial posterior rim is zonate and not as plain as in *ancisa.*

Description: The holotype of *Pseudoperonopsis ancisa* is 7.3 mm long and flattened in siltstone. The cephalon is the larger shield, as long as the pygidium and half the thorax (same in *syrma*), and the thorax is 0.3x the cephalon in length; the rim in the cephalon is flat and narrow and in the pygidium it is quite wide; the marginal furrows are broad channels and the pygidial acrolobe, narrowing retrally, is a little constricted about its middle. In the cephalon the boat-shaped glabella narrows rearward to an angulate rear with convex flanks; the frontal glabellar lobe, as long as 0.32-0.33x the glabella in length, is visibly wider than long; a frontal sulcus seems absent and the preglabellar furrow is vestigially shallow and short. The median node is elongate and placed about the middle of the posterior glabellar lobe.

In the thorax a relatively prominent semicircular axial node is present in the frontal part of the anterior segment. In the pygidium the marginal spines are strong and attenuated and the posterior margin between the spines is 'cut round', lacking the angulate train seen in *Pseudoperonopsis syrma*. The pygidial axis is relatively short (0.7x the shield length) and its anterior lobe is prominently wide. The transverse axial furrows are distinct and the tip of the axial node is entire, without the cleft seen in *P. syrma*. The holotype comes from locality M376, and belongs to the Zone of *Euagnostus opimus*.

The other illustrated exoskeleton, Plate 11, fig. 5, CPC 14041, locality M199, in shale of the Inca Formation, and the Zone of *Ptychagnostus atavus*, is a little older than the holotype, and also smaller. It is 5.2 mm long and flattened—an intaglio of furrows and lobes. It differs from the holotype by its longer pygidial axis of 0.78x the shield length—a character of some instability in *Pseudoperonopsis*.

Occurrence and age: Pseudoperonopsis ancisa is a rare species of the Inca Formation and less rare in a shale in a formation attributed to the Currant Bush Limestone (M376, Lawn Hill area). Its age is late in the Zone of *Ptychagnostus atavus* and passing into the zone of *Euagnostus opimus;* simply, its age is Floran.

Pseudoperonopsis iniugata sp. nov.

(Pl. 11, figs. 1-4; Text-fig. 6b)

Material: Illustrated are one complete exoskeleton and three isolated pygidia from three different sites.

Holotype: The complete exoskeleton Plate 11, fig. 1, CPC 14037, V-Creek Limestone, locality M128, is selected as the holotype; it is the only available complete exoskeleton.

Diagnosis: Pseudoperonopsis iniugata is distinguished by the following combination of characters: (1) the marginal furrows in both shields are relatively narrow, even for a species of the *Diplagnostinae*; (2) the pygidial rim, moderately wide, is collarless—it is a simplimarginate pygidium; (3) the glabella is boat-

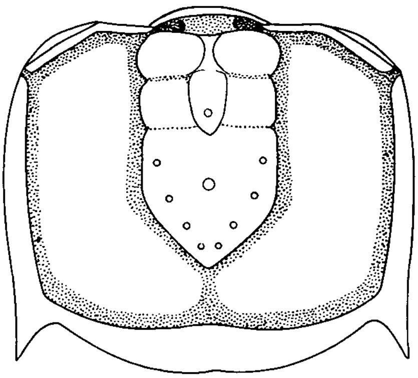

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Fig. 6b. *Pseudoperonopsis iniugata,* **pygidium.**

shaped and tapers slightly rearward to a bluntly pointed apex; and (4) the lateral margins of the cephalon are parallel and the anterior margins evenly curved, as an arc of a circle.

Differential diagnosis: A boat-shaped glabella belongs also to *Linguagnostus* and *Linguagnostus? comparabilis* sp. nov., which are, however, of a different structure. *'Linguagnostus' grönwalli* Kobayashi (see N. Tchernysheva et al., 1960, pl. 1, fig. 5) is also a simplimarginate diplagnostid, but its generic position (*Linguagnostus?* or *Pseudoperonopsis?* or a separate genus?) remains a matter of further enquiry. The closest form is, however, *Pseudoperonopsis ancisa* sp. nov.

Description: The descriptive data given in the diagnosis are supplemented in the comment on illustrated specimens.

Comment on illustrated specimens

The holotype (Pl. 11, fig. 1) is 5.0 mm long; all furrows are wide and deep, having lost the lining of the relatively thick test; the pre-glabellar median furrow is short and deep; the semicircular anterior glabellar lobe is short (about 0.26x the glabella); the median glabella-node is vestigial; the posterior, triangular basal lobes are small, and the anterior are depressed, elongate, and almost vestigial.

The pygidium Plate 11, fig. 4, CPC 14040, locality M191a, is 2.0 mm long; its test is preserved and the furrows are therefore less prominent than in the holotype; detail structures are shown in Text-figure 6b.

The pygidium Plate 11, fig. 3, CPC 14039, locality D74, is 2.4 mm long; a small node is superimposed on the median axial node, but not as clearly as in the holotype or in the next specimen.

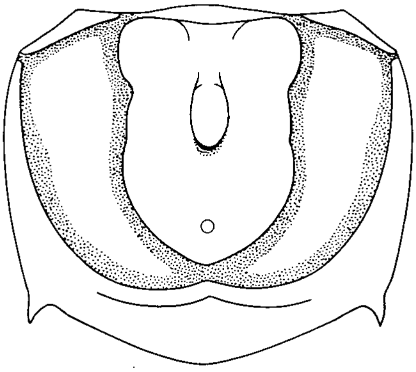

Fig. 7. *Pseudoperonopsis insolita*, **pygidium.**

The pygidium Plate 11, fig. 2, CPC 14038, locality D74, is also 2.4 mm long; the posterior margin is straight in the middle.

Occurrence and age: The holotype of *Pseudoperonopsis iniugata* comes from the Zone of *Doryagnostus notalibrae*. The other specimens are slightly older, of the Zone of *Ptychagnostus punctuosus*; M191b refers to a limestone lentil of the Inca Formation, and D74 a dolomite of the Quita Formation. Consequently it is an early and middle Undillan form.

Pseudoperonopsis insolita sp. nov.
(Pl. 12, figs. 1-3; Text-fig. 7)

Material: The three illustrated specimens constitute the whole available paradigm.

Holotype: The cephalon Plate 12, fig. 1, CPC 14044, is selected as the holotype because of its association with the pygidium (same plate, fig. 2); both shields are equal in size and therefore are not sclerites of a single exuvia.

Diagnosis: Pseudoperonopsis insolita is distinguished by the following characters: (1) the cephalon is rimless, its margin is upturned, and the marginal furrow is a concave broad channel; (2) the preglabellar median furrow is deeply impressed; (3) in the pygidium the axis is long, broad, and tumid; (4) the pygidial posterior rim between the marginal spines is a down-sloping crescent angular in the midline and (5) possesses along the middle of its anterior border a low bow-shaped collar.

Differential diagnosis: The combination of characters included in the diagnosis, and each character apart from the crescentic rim, exclude the possibility of a confusion with any of the known species of the Diplagnostinae; the crescentic rim, however, may indicate an otherwise unrecognisable connection with the older *Pseudoperonopsis syrma* sp. nov. The generic status of *insolita* as a species of *Pseudoperonopsis* is suggested on the evidence of its angulate glabellar rear, the structure of its cephalic border, and the zonate rim of its pygidium.

Description: The cephalon and the pygidium are very complex for a diplagnostid, and the cephalon alone could be mistaken for a *Pseudagnostus*. The cephalic outline is close to a circle; the cheeks are quite tumid and divided in front by the well impressed median furrow; scattered scrobicular pits are present in one and absent in the other cephalon. The frontal glabellar lobe is semielliptical; its front is angulate; the median glabellar node is placed in front of the midpoint of the posterior glabellar lobe or level with a pair of indentations of the flanks. The basal lobes are small and swollen.

In the thorax the lobes are tumid, a median node is evident on the anterior segment; the middle of the axis of the second segment is divided by a deep transverse furrow. In the pygidium the marginal spines are short and deflected; the rim with its collar projects forward, not quite meeting the tip of the axis; the anterior axial lobe is large (long); the second lobe is ill defined but recognisable from the median node; and a small median node is placed in the rear of the posterior lobe. The train of the rim seems short in the projection of the picture; but it slopes down and its length along the slope is 0.25x the shield. The pygidial acrolobe is slightly constricted.

Comment on illustrated specimens

The holotype cephalon is 2.0 mm long; its test is partly preserved; the upturned margin and the acute glabellar rear indicate a diplagnostid.

The pygidium Plate 12, fig. 2, CPC 14045, is also 2.0 mm long (as the holotype, in a close association); some matrix is left on its front, but was removed later for the preparation of Text-figure 7.

The cephalon and attached thorax Plate 13, fig. 3, CPC 14053, are together 3.7 mm long; the cephalon alone measures 2.6 mm.

Occurrence and age: Pseudoperonopsis insolita comes from the V-Creek Limestone, locality M212. Its age is the Undillan Zone of *Doryagnostus notalibrae*.

Genus **Baltagnostus** Lochman, 1944

The type species of *Baltagnostus* is *Proagnostus? centrensis* Resser, 1938.

Öpik (1961b, p. 69) classified *Baltagnostus* as a genus of the Diplagnostidae; Robison (1964) lists the names of the species attributable to the genus, and two more species were added by Rasetti (1967).

In brief, the glabella in *Baltagnostus* is angular in the rear, the glabellar frontal lobe is semicircular to transverse-subrectangular as in *Diplagnostus* and *Iniospheniscus;* the pygidial axis is long and the collar on the rim between the marginal spines is prominent in *centrensis*. In *Baltagnostus eurypyx* Robison (1964), however, the collar on the pygidial rim is weak, and it is even absent in Rasetti's (1967) *Baltagnostus angustilobus* and *stockportensis*.

In *Pseudoperonopsis,* depending on the species, the rim can be also zonate to plain, as in *Baltagnostus*. These two genera are quite close to eath other but differ in the relative length of the pygidial axis: (1) in *Pseudoperonopsis* the axis is short, and (2) in *Baltagnostus* the axis terminates at the marginal furrow; (3) in *Baltagnostus sertulatus* nov., however, the growth of the axis is retarded and it does not reach the furrow. Further comparison remains inconclusive because of the inferior state of preservation of the material of the type species of these genera, *Pseudoperonopsis sallesi* and *Baltagnostus centrensis*.

The Argentinian *Baltagnostus hospitus* and *B. mendozensis* of Poulsen (1960) have simplimarginate pygidia.

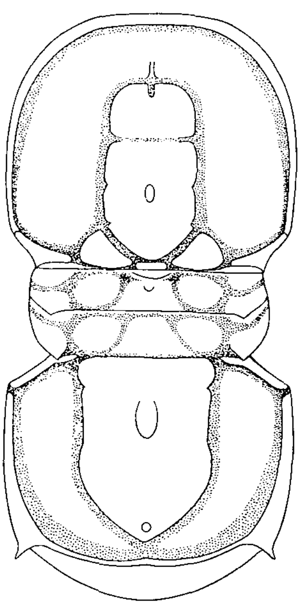

Fig. 8. *Baltagnostus robustus.*

Baltagnostus robustus sp. nov.

(Pl. 12, figs. 4 and 5; Text-fig. 8)

Material: Illustrated are two exoskeletons associated in a piece of limestone, locality M212. Ill preserved isolated shields have been observed in collections from several sites.

Holotype: The exoskeleton Plate 12, fig. 5, CPC 14048, has the better preserved glabella and is selected as the holotype.

Diagnosis: Baltagnostus robustus sp. nov., a species with a broad and ill subdivided, well fused pygidial axis, is distinguished by its subdued collar on the pygidial rim between the marginal spines.

Differential diagnosis: In *Baltagnostus sertulatus* sp. nov. the collar on the pygidial rim is prominent and in the pygidial axis the transverse furrows are present; in *Baltagnostus centrensis* (Resser, 1938, pl. 10, fig. 18) and its probable synonym *B. maryvillensis* (Resser, op. cit., pl. 9, figs. 39, 40) the axis is relatively slender and its transverse furrows are well impressed; in *B. eurypyx* Robison (1964, p. 80, fig. 15) the tip of the axis is somewhat blunt (pointed in *robustus*) and the axial median node is central (in front of the centre in *robustus*); the same is seen in *Baltagnostus angustilobus* and *stockportensis* Rasetti (1967). In the species of *Pseudoperonopsis* the axis is relatively short and clearly lobate, and the cephalic rim is very narrow.

Description: Baltagnostus robustus as a whole is a small species of the Diplagnostidae, recognisable as such from its acute glabellar rear and the zonate rim of the pygidium; the cephalon is only a little longer than the pygidium and the thorax is 0.3x the cephalon in length. The lateral margins of the cephalon converge forward gently, are strongly curved anterolaterally, and the frontal margin is gently arched; the margin of the pygidium is curved evenly because the curvature between the marginal spine is stronger than the arch of the cephalic front. The width of the border in the cephalon is moderate and its rim is relatively wide as compared with *Pseudoperonopsis* (for example, *perplexa*). In the pygidium the rim is wider than in the cephalon and expands rearward; the marginal spines are short and a little deflected; the collar between the spines and along the frontal limit of the rim is inconspicuous but clear. The shields are convex, the glabella and the pygidial axis are prominent—it is a stocky agnostid.

The cheeks are smooth, scrobicules and rugae are absent; in the holotype a short vestigial preglabellar furrow seems indicated, but is absent in the second specimen. The frontal glabellar lobe, about 0.32x the glabella in length, and somewhat rectangular, bears a short and shallow sulcus. In the posterior glabellar lobe the flanks are close to parallel, but its lateral lobes bulge slightly abaxially and the lateral furrows are developed as indentations. The median node is subcentral (a little in front of the midpoint) and marks the culmination in the sagittal profile. The glabellar rear is acute and the basal lobes triangular and relatively large.

The pygidial axis is very wide, about half the shield, wider than in *B. centrensis*, but close to *B. sertulatus* nov., *B. eurypyx* Robison, and *Pseudoperonopsis perplexa*. Its flanks, about parallel in the anterior half, converge in gentle curves rearward to the acute tip. The median axial node is relatively prominent, with a short retroflexed free tip.

Comment on illustrated specimens

The holotype of *Baltagnostus robustus* is 4.0 mm long; the glabellar front is sulcate; the small pygidial marginal spines are preserved.

The exoskeleton Plate 12, fig. 4, CPC 14047, is 4.4 mm long; it is a mould in limestone and the glabellar front is somewhat diffuse. The little node at the tip of the pygidial axis is visible; the test is corroded.

Occurrence and age: Baltagnostus robustus occurs sparsely in the V-Creek Limestone; its age is the Undillan Zone of *Doryagnostus notalibrae*.

Baltagnostus sertulatus sp. nov.

(Pl. 12, figs. 6-9)

Material: The illustrated material comprises two cephala and three pygidia; the matrix is a silty dolomite.

Holotype: The pygidium Plate 12, fig. 6, CPC 14059, is the largest and is therefore selected as the holotype.

Diagnosis: Baltagnostus sertulatus is distinguished by the combination of a relatively narrow border (rim and marginal furrow) in the cephalon with a broad pygidial axis and a prominent collar on the rim between the marginal spines.

Differential diagnosis: Of the known species of *Baltagnostus* only the type, *B. centrensis*, has as prominent a collar as *B. sertulatus*, but in *centrensis* the cephalic border is wide, the axis slender, and the collar straight (sagging in *sertulatus*).

Description: The cephalon is broadly semi-elliptical in outline; the rear of the glabella is angular and its posterior lobe has a pair of lateral indentations, but apparently no median node. The lateral margins of the pygidium are slightly convex, but otherwise parallel to each other, and the posterior margin is arched retrally as seen also in *B. centrensis*. The marginal furrow is wide and defined clearer against the narrow rim rather than the acrolobe.

The pygidial axis is long and has a terminal node on its apex; the transverse furrows are shallow but transcurrent; the two anterior lobes have a moderate relief and the median node on the second lobe is quite prominent. The collar runs along the inner border of the rim and contacts the marginal spines; these are short and somewhat curved.

Comment on illustrated specimens

The holotype pygidium, CPC 14059, is 2.0 mm long. The front of the axial lobe shows a recess.

The pygidium Plate 12, fig. 9, CPC 14052, is 1.5 mm long; its terminal node is preserved; on its right an immersed cephalon shows the angulate rear of its glabella and the triangular basal lobes.

Plate 12, fig. 8, CPC 14051, shows a cephalon and a pygidium; the pygidium is 1.5 mm and the cephalon is 1.3 mm long. In the pygidium the right marginal spine is intact.

The cephalon Plate 12, fig. 7, CPC 14050, is about 1.2 mm long; it is associated with the previous specimen.

Occurrence and age: Baltagnostus sertulatus is known from a stratum of nodular dolomite, Quita Formation, locality D74. Its age is the Undillan Zone of *Ptychagnostus punctuosus*.

Genus **Iniospheniscus** nov.

The type species of *Iniospheniscus* is *I. talis* sp. nov.

Diagnosis: Iniospheniscus comprises species of the Diplagnostidae with a relatively narrow cephalic rim, blunt glabellar front, and angulate glabellar rear, and with a simple to vestigially zonate pygidial rim; distinguished by the long and very broad pygidial axis having the posterior lobe expanded and carrying a long and strong median node on the anterior annulations; the pygidial acrolobe is constricted.

Differential diagnosis: Iniospheniscus is placed in the family Diplagnostidae on the evidence of the following characters: (1) the angulate glabellar rear and the blunt front of the glabella; and (2) the wide, expanded pygidial axis. The posterior lobe of the pygidial axis is also wide in the diplagnostid *Oedorhachis*

Resser, but its cephalic rim is very wide (narrow in *Iniospheniscus*) and its general aspect is that of *Diplagnostus*. Reminiscent of *Iniospheniscus* is also *Diplorrhina triplicata* Hawle & Corda (the type of its genus) as revised by Pek & Vanek (1971, p. 272, pl. 1, fig. 1). It is a diplagnostid with a blunt glabellar rear, and a very wide pygidial border and moderately expanded posterior lobe of the axis; the annulation of the axis and its long median node alone conform with *Iniospheniscus talis* sp. nov. *Diplorrhina cuneifera* is illustrated by Harrington et al. (1959, p. 0185, fig. 126 (5)) under the name of *Peronopsis integra* with an almost acute glabellar rear—a traditional misinterpretation going back to Barrande (1852, pl. 49). Finally, in *Armagnostus megalaxis* Howell (1937, p. 1162) the posterior pygidial axial lobe recalls *Iniospheniscus,* but there are no transverse furrows and its median node is small and inconspicuous; the cephalon attributed to *A. megalaxis* is rather unlike *Iniospheniscus.* No synonymy emerges from these comparisons.

Diagnosis and differential diagnosis of spines: Two species of *Iniosphensicus, talis* nov. and *incanus* nov., are described and named here; in the following text (1) characters common to both species are indicated, and (2) the specific characters presented.

(1) *Common characters:* The outline of the shields is semielliptical, with lateral margins in the cephalon converging forward and in the pygidium rearward; the frontal glabellar lobe is short and its front is blunt, and about straight; the median glabellar node is inconspicuous and placed in front of the midpoint of the posterior glabellar lobe; the occipital part of the glabella is angulate; the cephalic border (rim and marginal furrow together) is relatively narrow and clear. In the pygidium the border is relatively narrow and its marginal spines are small; the pleural lobes are narrow; the axis is broad and expanded in its posterior lobe; it is also long and its tip contacts the marginal furrow; the anterior axial annulation is an elevated bar; the median axial node is prominent; the rim between the spines is vestigially zonate. The acrolobes are a little constricted in the pygidium and the cephalon; the test is granulose.

(2) *Diagnostic characters: Iniospheniscus talis* possesses a weak to almost obliterated preglabellar median furrow and the flanks of the angular occipital part of the glabella are not straight but slightly convex outward and the cheeks close to the border are weakly and occasionally scrobiculate; in the pygidium the transverse furrows are well impressed and a pair of short furrows is evident in the anterior part of the posterior lobe; the posterior axial lobe is widest about its middle, with flanks converging retrally in abrupt curves and meeting as an angular tip.

Iniospheniscus incanus possesses no preglabellar median furrow and the flanks of the angular occipital part of its glabella are straight or almost so; the cheeks are not scrobiculate; in the pygidium the transverse furrows are shallow, and no third pair of furrows is evident; the axial lobe is constricted about the second annulation; the posterior lobe is moderately expanded, and its flanks meet in gentle curves at the tip; furthermore, the axis is relatively slender in comparison with the roughly pentagonal and broad axis of *Iniospheniscus talis.*

Iniospheniscus talis sp. nov.

(Pl. 7, fig. 6; Pl. 9, figs. 1-6)

Material: Illustrated are three cephala and five pygidia selected from a total of about twenty isolated shields from five different sites.

Holotype: The pygidium Plate 9, fig. 1, CPC 14021, is selected as the holotype in preference to a cephalon because pygidia are most suitable in identifying the species. The diagnosis is given at the end of the description of the genus.

Description: Iniospheniscus talis may have attained a length of 7 to 8 mm; as a whole its exoskeleton is broadly elliptical, as evident from the semi-elliptical shape of its shields. The cephalic marginal furrow is very narrow; the rim is also narrow and convex, as for example in *Diplagnostus floralis* whose marginal furrow, however, is much wider than in *I. talis.* The frontal glabellar lobe is transverse rectangular (as generally in the diplagnostids) and about 0.25-0.27x the glabella in length. The neck on the posterior glabellar lobe is low and elongate and stronger in front than in the rear. The scrobicules, when present, are straight radiating lines along the periphery of the cephalic acrolobe, which itself is slightly constricted. The basal lobes are simple. The pygidial rim is narrow on the flanks but relatively wide in the rear and arched retrally. It is zonate with a ridge between the marginal spines as seen in Plate 9, fig. 4; it is a feeble structure and can be overlooked easily. The marginal spines are sideways-deflected tiny points. The marginal furrow is evenly narrow all around the shield and the acrolobe is gently constricted.

The axial node is conspicuous and stout; the two transverse anterior furrows and lobes of the axis are strong and the anterior lobe and the axial node merge to form a T-shaped structure; the node may also extend forward onto the anterior lobe. The definition of the posterior (third) lateral furrows is variable even in a single specimen: in the holotype pygidium the right furrow is deep and the left is shallow.

Comment on illustrated specimens

All specimens without indication of geographic origin were collected from a single stratum of limestone, locality M191, Mount Isa Sheet area.

The holotype pygidium (Pl. 9, fig. 1) is 3.1 mm long. It is slightly deformed and its original semielliptical rearward contracting shape is therefore obscured. During preparation the drill removed a part of the median node and almost obliterated the left pair of the third transverse furrows. The pygidial posterior rim is zonate close to the marginal spines.

The pygidium Plate 9, fig. 2, CPC 14022, in chert (spiculate), is 2.5 mm long; it is from a burned collection, some 4 to 6 km northeast from Yelvertoft Dip, on Inca Creek (about site M164). It is associated with *Diplagnostus floralis* nov. and *Aotagnostus aotus* nov., and identical in age with M191. The test is crushed, but its granulose ornament, even on the rim, is well preserved, and so is the semielliptical shape.

The pygidium Plate 9, fig. 4, CPC 14024, in limestone is 2.5 mm long; its rearward converging lateral margins are undeformed and the zonate condition of the rim between the marginal spines is evident.

The pygidium Plate 9, fig. 3, CPC 14023, is 2.0 mm long; the acrolobe is constricted; the collar—the elevated edge on the inner border of the rim—extends from spine to spine. It comes from the Currant Bush Limestone, site M64, and is associated with *Aotagnostus aotus* and *Ptychagnostus punctuosus*.

The cephalon Plate 9, fig. 5, CPC 14025, is 2.4 mm, and the associated pygidium 2.00 mm, long. In the cephalon the preglabellar furrow is faint, the periphery of the acrolobe is scrobiculate, and a pair of short lateral glabellar furrows is indicated; the frontal lobe is 0.25x the glabella in length. In the pygidium the anterior lobe is accentuated and the axial tip is short of reaching the marginal furrow.

The cephalon Plate 9, fig. 6, CPC 14026, is 3.5 mm long; its frontal glabellar lobe is 0.27x the glabella in length.

The cephalon Plate 7, fig. 6, CPC 14016, associated with a pygidium of *Diplagnostus floralis*, is 2.6 mm long; the preglabellar median furrow and a faint sulcus in the glabellar front are indicated; the tiny node on the glabellar angular tip is clear.

Occurrence and age: Iniospheniscus talis sp. nov. occurs in the Inca Formation and the Currant Bush Limestone; its age is the early Undillan Zone of *Ptychagnostus punctuosus*.

Iniospheniscus incanus sp. nov.

(Pl. 9, figs. 8, 9)

Material: Two shields (one pygidium and one cephalon) are illustrated, selected from a small number of specimens.

Holotype: The pygidium Plate 9, fig. 9, CPC 14029, is selected as the holotype; the cephalon is the less characteristic shield—being close to the cephalon of *Iniospheniscus talis*, the type species.

Diagnosis and differential diagnosis: These are included in the description of the genus.

Description: The cephalon Plate 9, fig. 8, CPC 14028, is 3.1 mm long; it is semielliptical, the rim is elevated and convex; and apparently a little wider than *I. talis*; the marginal furrow is deep and narrow; no scrobicules are evident and the preglabellar furrow is absent. The glabella tapers forward a little and its subrectangular frontal lobe is 0.26x the glabella in length; the median node is very low; the angular glabellar rear is tipped by a low node; the basal lobes are simple and trigonal. The acrolobe is weakly constricted on the level of the glabellar frontal lobe.

The holotype pygidium is 2.3 mm long; also semielliptical, its rim is elevated, narrow on the flanks, and wide and flat in the rear; its inner edge—the pygidial collar—is slightly excavated and extends onto the adaxial margins of the spines; these are short and deflected sideways. The marginal furrow is visibly wide on the flanks, especially at the constriction of the acrolobe. The axis is slightly waisted at the level of the second transverse annulation; the posterior lobe is expanded (less than in *I. talis*) and contracts from about its middle to the narrow but rounded tip, touching the furrow behind it. The two transverse furrows are shallow; the anterior annulation, however, is prominent as the horizontal bar of the 'T' over the prominent oval median node.

A piece of rock with specimens of *Iniospheniscus incanus* associated with the type material is included in the collection of types as CPC 14028.

The test is densely granulose.

Occurrence and age: Iniospheniscus incanus is a rare fossil in siltstone of the Inca Formation; localities M265 and M145 (two pygidia CPC 14364 not illustrated; see under *Peronopsis fallax ferox*, Plate 4, fig. 7); its age is the early Floran Zone of *Ptychagnostus atavus*.

Iniospheniscus? sp. indet.
(Pl. 9, fig. 7)

The illustrated exoskeleton, CPC 14027—a preparation of its mould (external) by means of a needle—is about 8.5 mm long as preserved; the cephalon is 2.7 mm long and the thorax 0.3x the cephalon in length. The pygidial border is lost; considering that the cephalon should be as long as the pygidium together with the posterior segment of the thorax the lost border (rim and marginal furrow) was relatively wide in the midline.

In the cephalon the rim is narrow and the marginal furrow relatively wide and deep. The frontal lobe of the glabella, 0.26x its length, is as short as in *Iniospheniscus talis* and the posterior part of the glabella is angulate with flanks convex outward; the basal lobes are simple. In the pygidium the acrolobe is constricted, the pleural lobes are extremely narrow and are separated in the rear by the axial lobes. The axis itself is very broad and prominent and expanded posteriorly. The median node is prominent and stout and merged with the anterior annulation forming a T-shaped structure as in *Iniospheniscus talis*.

The generic classification (*Iniospheniscus?*) remains inconclusive: narrow pleural lobes are present also in *Agnostascus gravis* Öpik (1967, p. 147) and the cephalic marginal furrow is wider than in *Iniospheniscus talis* but also much wider than in *Agnostascus*; consequently *Iniospheniscus?* may represent a separate genus sharing characters of *Iniospheniscus, Agnostascus,* or some other forms of an unnamed subfamily of the Diplagnostidae (see Öpik, op. cit., p. 147: 'subfamiliae suae').

Occurrence and age: The exoskeleton designated as *Iniospheniscus?* sp. indet. has been obtained from the V-Creek Limestone, locality M243; its age is the early Undillan Zone of *Ptychagnostus punctuosus.*

Genus **Linguagnostus** Kobayashi, 1939

The type species of *Linguagnostus* is *Agnostus kjerulfi* Brögger, 1878; the type specimens, a cephalon and the lectotype pygidium, are re-illustrated by Westergaard (1946, pl. 8, figs. 31, 32); he also illustrated (pl. 9, figs. 1-3) two pygidia and one cephalon from Sweden. *Linguagnostus grönwalli* Kobayashi, 1939, of which a complete specimen is shown by N. Tchernysheva et al. (1960, pl. 1, fig. 4), is an aberrant form with a nonzonate pygidium, but it cannot be convincingly accommodated in this or any other genus of Diplagnostidae. Close to *L. kjerulfi* is, however, *Linguagnostus tricuspis* (Lermontova) Ivshin (1960, p. 149), whose pygidium is zonate.

Linguagnostus? comparabilis sp. nov.
(Pl. 10, fig. 1)

Material: Only one cephalon, the holotype, CPC 14030, is available; it is preserved as an external mould in silty shale.

Diagnosis: Linguagnostus? comparabilis is distinguished by the combination of the elongate semielliptical cephalon without a preglabellar furrow, a relatively large frontal glabellar lobe without a median sulcus, and a low rounded median node placed behind the midpoint of the posterior glabellar lobe. Its glabellar rear is acute, but with convex flanks. In the absence of a pygidium the generic classification is queried.

Differential diagnosis: The outline of the cephalon, its narrow upturned rim, wide marginal furrow, and the boat-shaped and retrally narrowing glabella indicate a species related to the type species of the genus—*L. kjerulfi* (Brögger) Westergaard (1946, pl. 8, fig. 31), which, however, has a sulcate frontal glabellar lobe, a preglabellar median furrow, an elongate median glabellar node, and a rather acute and even extenuated glabellar rear. The glabella is slightly shorter and the frontal lobe larger in *L.? comparabilis* than in *kjerulfi* and other species of the genus. Different from *comparabilis* is also the glabellar structure in the much younger *Linguagnostus* aff. *kjerulfi* (Öpik, 1967, p. 127). A glabella similar to *L.? comparabilis* is also apparent in *Pseudoperonopsis iniugata* sp. nov. (q.v.) and *P. ancisa.*

Occurrence and age: Linguagnostus comparabilis comes from the Sandover Beds, locality N32, of the Northern Territory. The age is late Templetonian, the Zone of *Triplagnostus gibbus.*

Family **AGNOSTIDAE** McCoy, 1849
Subfamily **QUADRAGNOSTINAE**

As is well known the name Quadragnostinae refers to *Quadragnostus solus* Howell, 1935. *Agnostus quadratus* Tullberg (1880), redescribed by Westergaard (1946) as *Peronopsis quadratus,* is also a *Quadragnostus*; the long, pointed, and low pygidial axis in *solus* and in *quadratus* is, however, quite different from *Peronopsis integra* and justifies the independence of *Quadragnostus* and *Peronopsis.* Hence, the subfamily name Peronopsinae Westergaard (1936, p. 28) is only dormant but not invalid.

Remarkable is the similarity of the pygidia of *Quadragnostus solus,* the pygidia of Matthew's *Agnostus acadicus* (see Text-fig. 16) and Tullberg's (op. cit., pl. 2, fig. 25b) illustration of *Agnostus quadratus,* suggesting the possible synonymy of *Quadragnostus* (1935) and the junior *Acadagnostus* (1939) of Kobayashi.

Genus **Peronopsis** Hawle & Corda, 1847

The type species of *Peronopsis* is *Battus integer* Beyrich, 1845. Subsequent authors, however, following Barrande (1852) reverted to the senior name (*Agnostus*), and the designation *Agnostus integer* prevailed in the literature for almost nine decades; the dormant name *Peronopsis* was revived by Howell (1935) and by Westergaard (1936).

Species of *Peronopsis* (*fallax, fallax ferox,* etc.) have been recorded from all corners of the Middle Cambrian globe; the whole material, however, needs re-examination as regards its species and even genus taxonomy.

Concept of genus Peronopsis *(compiled herein)*

(1) The border in the cephalon and pygidium is wide, and widest in the pygidium; (2) the cephalon is about as long as the pygidium and the posterior segment of the thorax taken together; (3) the thorax is 0.3-0.35x the cephalon in length—a large thorax; (4) axial spines are absent; cephalic and pygidial marginal spines are short; fulcral points in the thorax are small angular prongs; (5) the glabella is bilobate and the basal lobes (Text-fig. 2, II) are simple; (6) the preglabellar median furrow is vestigial or even absent in most species; (7) the glabellar rear is rounded and its median node is inconspicuous. In the pygidium (8) the axis is long; (9) the median axial node is low to moderate in relief; (10) the anterior axial lobe and the transverse furrow can be distinct but this relief is variable and can be also vestigial; (11) the posterior axial node is laterally expanded and its flanks are convex; (12) the pygidial acrolobe is more or less constricted, as well as unconstricted.

Characteristic of *Peronopsis* is the combination of the characters integrated in the concept; single characters and restricted selections of characters are less reliable in identification of a *Peronopsis.*

I am hesitant to evaluate the generic classification of all species attributed to *Peronopsis* in the existing literature; acceptable are nevertheless *Agnostus bonnerensis* Resser, 1938; *Peronopsis segmenta* Robison, 1964; *Peronopsis* cf. *gaspensis* Rasetti, 1948; *Diplorrhina normata* Whitehouse, 1936; *Peronopsis fallax* (Linnarsson) and its subspecies; and *Peronopsis brunfloensis* Westergaard, 1946. *Peronopsis scaphoa* Öpik, 1961b, however, belongs to another, unnamed genus and should be excluded from *Peronopsis.*

New are the Australian species *Peronopsis longinqua, P. prolixa, P. tramitis,* and *P. comis.* Finally a new subgenus *Peronopsis* (*Itagnostus*) is proposed for *Agnostus elkedraensis* Etheridge Jr; and *Peronopsis pusilla* (Tullberg) is referred to the new genus *Svenax.*

Some considerations regarding *Peronopsis* are also given in the discussions of *Euagnostus* Whitehouse and *Pseudoperonopsis* Harrington, 1938.

Peronopsis integra (Beyrich, 1845)
(Text-fig. 9)

Snajdr (1958) published a larger number of specimens and designated one of these as the neotype; after Snajdr's selection of the neotype, Pek & Vanek (1971) designated from Beyrich's collections a pygidium as a lectotype of the species *integra* Beyrich, 1845; a lecto-

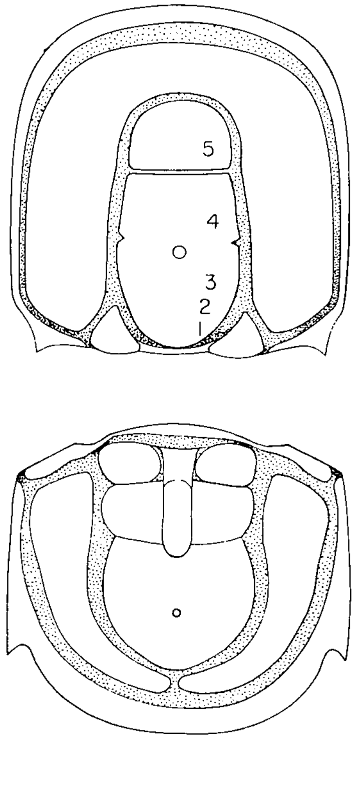

Fig. 9. *Peronopsis integra,* **reconstructed.**

type is the evidence for the existence of a paradigm of one or more syntypes as well; it stands to reason that the whole paradigm should be discussed on the occasion of the selection of the lectotype—a procedure of some finality. The published material is tectonically deformed but it was possible to prepare a diagram (Text-fig. 9) combining several illustrations including the 'neotype' (op. cit., pl. 3, fig. 2); it is, of course, inaccurate in detail but in general correct and corresponds to the following description.

The frontal margin of the cephalon is moderately arched forward and the lateral margins subparallel; the rim and the marginal furrow are broad anteriorly, gradually narrowing rearward; the cheeks in the absence of a preglabellar median furrow are confluent in front of the glabella; the glabella is parallel-sided, relatively long and broad, and its rear is rounded; the frontal glabellar lobe tends to be rectangular; the posterior has a pair of short lateral furrows and a median node about its middle. The basal lobes are triangular and swollen. The pygidium seems slightly shorter than the cephalon; the lateral pygidial margins are parallel, and the rear margin, starting from the marginal spines, is rounded; these spines are triangular, broad, and retral. The acrolobe in some specimens appears slightly constricted about the middle, and the pleural lobes are separated in the rear by the postaxial median furrow. The rim is wide about the marginal spines and visibly widens behind them.

The pygidial axis is long (not quite reaching the marginal furrow), prominent, and broad; two anterior annulations are defined by lateral notches and shallow transverse furrows; the second annulation carries an elevated node—as the culmination of a low median ridge which extends, apparently, to the front of the axis. The posterior axial lobe is slightly expanded in the middle.

Occurrence and age: Peronopsis integra, as described here, is a Middle Cambrian Bohemian species and is unknown elsewhere. According to Snajdr (op. cit.) it belongs in the Zone of *Paradoxides gracilis.* The associated fauna, in my opinion, indicates a position within the interval from late *Ptychagnostus atavus* to early *Pt. punctuosus* Zones.

Peronopsis fallax (Linnarsson)
subsp. **P. fallax ferox** (Tullberg, 1880)
(Pl. 4, figs. 4-7)

Material: Illustrated are two pygidia and two cephala selected from several others, all in a single piece of limestone from locality M208; some seven exoskeletons, about twenty pygidia, and ten cephala flattened in shale have also been identified in two collections. The exoskeletons and shields in shale and siltstone are flattened and preserved as intaglios; none is illustrated, but two are included in the collection of types (CPC 14365 and CPC 14366). In these the thorax, 0.33-0.34x the cephalon in length, has been measured. In the associated intaglios of *Pseudoperonopsis* the thorax (0.3) is smaller.

Remarks: Peronopsis fallax and its retinue of three subspecies has been revised by Westergaard (1946, pp. 37-38) on the basis of Linnarsson's and Tullberg's type material; Kobayashi (1939) earlier listed some eight subspecies and varieties, added two more, and transferred from *P. fallax* two forms to other genera and elevated two to species rank. Finally Öpik (1967, pp. 69, 76, 82) commented upon the relationship of *Peronopsis fallax* with *Diplagnostus* and *Pseudoperonopsis* that is discussed once more under the heading of the latter in this paper. *Peronopsis fallax* together with its subspecies, according to Westergaard (op. cit., p. 98), cover a sequence of seven Middle Cambrian zones; *P. fallax (fallax)* itself is recorded from four earlier zones (late Templetonian and Floran in our terms) and *fallax ferox* falls into the Undillan. Consequently *P. fallax* and its subspecies are of no service in a refined dating of collections and strata. Moreover, the variability within these taxa (Westergaard, 1936, p. 28) results in arbitrary identifications.

Generic classification: Agnostus fallax Linnarsson was attributed to the genus *Peronopsis* by Westergaard (1936) and this classification has been generally accepted. The structure of the cephalon (the rounded glabellar rear, the frontal confluence of the cheeks, small and simple basal lobes) and of the pygidium (marginal spines, wide border, broad and long axis and its clearly impressed transverse furrows) are indeed characters of *Peronopsis;* the posterior lobe of the axis, however, is not expanded laterally—a specific feature separating *fallax* and its relations from most other species of *Peronopsis;* furthermore, the pygidial acrolobe is unconstricted in *fallax fallax,* whereas in *ferox* as in many other species of *Peronopsis, integra* included, a stricture is apparent. Notable in *P. fallax* is the incidence of specimens with a visibly zonate pygidial rim (Westergaard, 1946, pl. 2, figs. 19, 24), although the earliest forms (Westergaard, 1936, pl. 1, figs. 9, 13) are simplimarginate. The zonate structure is rather prominent in a form from Siberia (N. Tchernysheva, 1960, pl. 1, fig. 8); it is attributed to *Peronopsis fallax,* but its cephalon (ibid., fig. 7) indicates a diplagnostid. In passing, the Diplagnostidae descended possibly from a *fallax*-like *Peronopsis* (Öpik, 1967, pp. 69, 74) via *Pseudoperonopsis,* but *fallax* is not the only route.

Description: The cephala attributed here to *Peronopsis fallax ferox* have a narrow rim and a similar marginal furrow, slightly narrower than in Westergaard (1946, pl. 3, fig. 1), and the anterior glabellar lobe seems also slightly longer than in the Swedish specimen; the median glabellar node, however, has a similar subcentral position in both. The illustrated pygidia resemble the lectotype of *P. fallax ferox* (Westergaard, op. cit., pl. 2, fig. 27) as well as the other specimen (ibid., pl. 3, fig. 2): the axis is broad, its flanks are parallel, the two anterior annulations and transverse furrows are well visible, the median node is prominent, and no median postaxial furrow is evident behind the rounded to subangulate axial rear; the axis is relatively short. The marginal spines are short, the marginal furrow is spacious, and the acrolobe is slightly constricted in all specimens. The only difference is evident in the structure of the pygidial rim between the marginal spines: it is zonate in the lectotype and plain in the Australian specimens.

Comment on illustrated specimens

The pygidium Plate 4, fig. 6, CPC 13992, associated with a small fragmentary cephalon of the same species, is slightly less than 2.4 mm long; the transverse furrows and the two anterior axial lobes are distinct; the axial lobe is narrower than in the next specimen; the constriction of the acrolobe is accompanied (as usual) by a widening of the marginal furrow.

The pygidium Plate 4, fig. 5, CPC 13991 is 2.5 mm long. The axial lobe is relatively broad, broader than in the preceding specimen; the annulations and the anterior axial furrows are well developed and the median axial node terminates as a low spine; the tip of the axis bears a low terminal node.

The larger of the two cephala, Plate 4, fig. 4, CPC 13990, is 2.5 mm long; the glabellar rear is rounded, and the median node is subcentral. The described specimens came from a pink and sandy limestone of the Inca Formation, locality M208.

Two exoskeletons, Plate 4, fig. 7, CPC 13993, are 5 and 6 mm long respectively; the thorax is about 0.33x (estimated from the length of the anterior segment) the cephalon. Associated are two cephala of *Hypagnostus* sp. (*parvifrons*?); among numerous isolated shields of these agnostids on the same bedding plane, pygidia of *Iniospheniscus incanus* and an exoskeleton of *Triplagnostus gibbus posterus* are present. Shale of the Inca Formation, locality M145.

Occurrence and age: Peronopsis fallax ferox occurs in the Inca Formation, in limestone lentils (M208) and in siliceous shale, localities M145, M265, and M425; these belong to a later part of the Floran Zone of *Ptychagnostus atavus;* furthermore it is rare in the shale (siltstone), locality M149, in the late Floran Zone of *Euagnostus opimus.*

Peronopsis normata (Whitehouse, 1936)
(Text-fig. 10)

Whitehouse (1936, p. 89, pl. 9, figs. 1, 2) described the agnostid in question as a *Diplorrhina*—a name considered a synonym of *Peronopsis* by Snajdr (1958). The holotype of *P. normata* has been recently reillustrated in Hill et al. (1971, pp. 20-21, pl. 10, fig. 10). It is an exoskeleton about 6.0 mm long; the pygidial rim projects forward in the middle and the pygidial acrolobe appears a little constricted.

Text-figure 10 is a combination from numerous more or less flattened cephala and pygidia in a rough piece of shale, CPC 14367, collection M434. The description that follows is also culled from this material.

The frontal glabellar lobe, almost suboval, is about 0.3x the glabella in length; the posterior lobe with its convex flanks is suboval in shape; a pointed small node is observable on the glabellar rear in two or three shields, and the median node stands behind the midpoint of the posterior lobe. The basal lobes are short. In the pygidium the acrolobe is constricted; the median projection of the rim is erratic and the marginal spines are short. The thorax of the holotype is 0.3x the cephalon in length, and the cephalon is as long as the pygidium and the posterior segment of the thorax.

In the pygidial axis two pairs of short lateral furrows and a relatively prominent median node with a simple tip are present and a small knob stands about the middle of the posterior axial lobe.

Peronopsis integra (Text-fig. 9) has a stouter glabella with parallel flanks, transcurrent furrows in the pygidial axis, and no median projection of the rim. *Peronopsis prolixa* sp. nov. is probably related to *P. normata.*

Occurrence and age: Peronopsis normata (Whitehouse) occurs in all outcrops of the

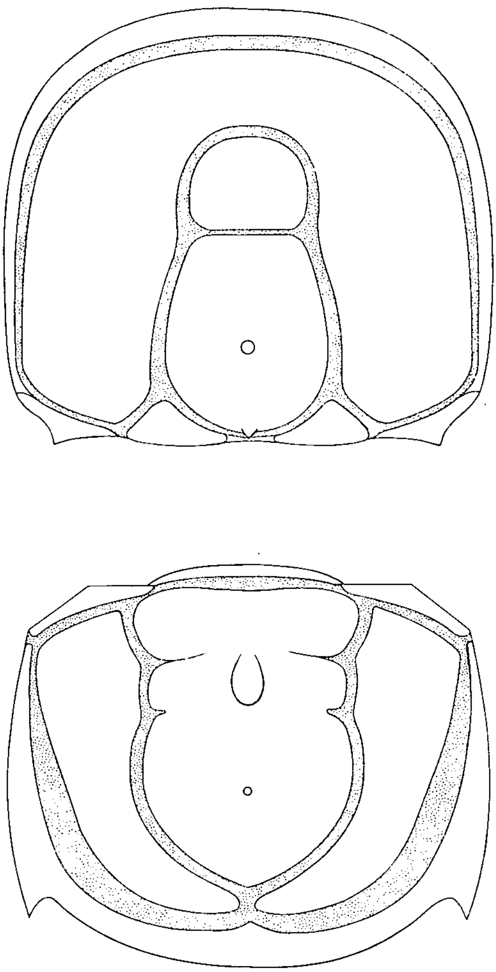

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Fig. 10. ***Peronopsis normata,*** **reconstructed from disassembled shields.**

Beetle Creek Formation of Queensland; its age is Templetonian, but older than the Zone of *Triplagnostus gibbus;* it is also present (CPC 14368, not illustrated) at M179, in a limestone attributed to the Currant Bush Limestone, where its age is the Floran Zone of *Ptychagnostus atavus.*

Peronopsis longinqua sp. nov.

(Pl. 1, figs. 1-3; Text-fig. 11)

Material: Illustrated are one cephalon and two pygidia, selected from several other shields, in a white relatively soft mudstone.

Holotype: The cephalon Plate 1, fig. 1, CPC 13974, is selected as the holotype (see under *P. prolixa*).

Diagnosis: The design of the cephalon of *longinqua,* the trilobation of the pygidial axis and the expanded rear of the pygidial axial lobe, the constriction of the acrolobes, and the presence of marginal spines are characters of the genus *Peronopsis*; *Peronopsis longinqua* is distinguished within the genus by (1) its very wide cephalic marginal furrow and rim, and narrow pygidial rim; (2) the elliptical shape of the glabella and a semielliptical small frontal lobe; (3) the stout posterior lobe of the pygidial axis reaching the marginal furrow; and (4) the very wide pygidial marginal furrow. Furthermore, on the frontal glabellar lobe a tiny central node is apparent; no node is evident on the posterior glabellar lobe; the pygidial marginal furrow intrudes the base of the marginal spine; and the pygidial axial

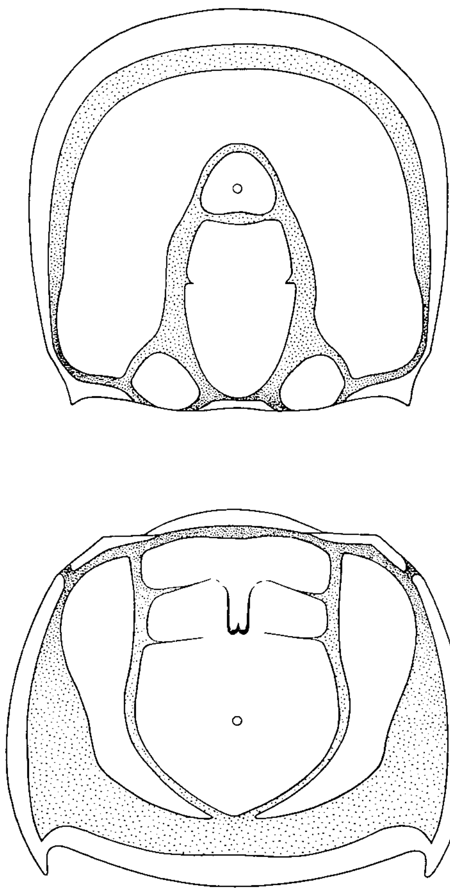

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Fig. 11. *Peronopsis longinqua.*

node is cleft and has a double tip. Examples of occurrence of such structures are rare: a node on the frontal glabellar lobe is present in *Diplagnostus floralis* sp. nov.; the base of the marginal spine is furrowed in *Aspidagnostus inquilinus* and *Oidalagnostus personatus* (Öpik, 1967, pp. 121, 135); a double tip of the pygidial axial node has been previously recorded in *Pseudagnostina vicaria* (op. cit., p. 159) and is visible in the illustrations of *Xestagnostus* (ibid., pl. 64, fig. 1; pl. 65, fig. 7b).

The double tip is also present in *Pseudoperonopsis syrma* (Text-fig. 6a), in *Peronopsis prolixa* sp. nov., and in *P. tramitis* sp. nov. It can be described as an acute cleft in the rear tip of the axial node of the second pygidial annulation. This structure is most easily detectable in photographs of whitened internal casts. The cleft may be filled with matrix and remain undetectable altogether. Its presence or absence is therefore inconclusive in species taxonomy pending forthcoming discoveries of this delicate structure by writers.

Differential diagnosis: No species of *Peronopsis* can be confused with *longinqua;* the nearest is *P. prolixa* sp. nov., but its cephalic structure is quite different and the pygidial marginal spines are much larger. The general aspect of *longinqua* (and *prolixa*) created by the wide marginal furrow and the stricture of the acrolobe is reminiscent of a *Pseudagnostus,* but the deuterolobe of the latter precludes confusions in identification.

At all events species of *Peronopsis* with wide marginal pygidial furrow, constricted acrolobes, and cleft pygidial axial node evoke the notion of some affinity with the Diplagnostidae rather than Agnostidae.

Description: The diagnosis of *P. longinqua* is descriptive and is amplified as follows. The glabellar rear is narrowly rounded, the posterior lobe has a pair of almost imperceptible lateral indentations, and the basal lobes are swollen and relatively large. The glabella is relatively short on account of the long cephalon with the wide border; and the frontal lobe, about 0.27x the glabellar length, seems small indeed in relation to the cephalic length. In the pygidium the axial lobe at its widest is 0.5x the shield's width; transverse furrows are shallow but transcurrent or almost so. The incurved marginal spines are short and delicate and the margin between the spines is only moderately arched rearward. The test is probably granulose.

Comment on illustrated specimens

The holotype cephalon (Plate 1, fig. 1), is 3.0 mm long; its anterolateral part is defective—crushed by a fossil fragment.

The pygidium Plate 1, fig. 3, CPC 13976 is 3.3 mm long. The posterior part of the rim is lost, but the marginal edge is retained in the matrix; the subcentral node on the rear lobe of the axis is small but distinct; the rim seems weakly zonate as visible at the preserved right marginal spine; the median node on the second annulation is damaged, but the bilobation of its tip is still visible.

The pygidium Plate 1, fig. 2, CPC 13975 is 2.7 mm long; the tip of the median node is double.

Occurrence and age: Peronopsis longinqua occurs in the Sandover Beds of the Northern Territory at locality N63; it is associated with *Xystridura filifera* and its age is early Templetonian.

Peronopsis prolixa sp. nov.

(Pl. 1, fig. 4; Text-fig. 12)

Material: The illustrated specimens are contained in a piece of indurated silty shale, with some ten shields attributable to *P. prolixa;* associated are shields of *Peronopsis (Itagnostus) elkedraensis, Peronopsis tramitis, 'Acadagnostus' scutalis, Pentagnostus rallus,* and *Oryctocephalus.*

Holotype: The pygidium Plate 1, fig. 4 (at the upper right of the illustration), CPC 13977 is selected as the holotype; the cephalon on its left is taken as of *P. prolixa* because it cannot be assigned to any other pygidium and species in the collection; further comment follows the differential diagnosis.

Diagnosis: Peronopsis prolixa is distinguished by its pygidium having the acrolobe constricted, and the rim and marginal furrow rather wide; its marginal spines are fairly large and the median node is double at its tip; in the concomitant cephalon the border (rim and marginal furrow) is very narrow and the frontal glabellar lobe is long and has an angular front.

Differential diagnosis: The cephalon attributed to *P. prolixa* recalls *P. normata,* but in *normata* the frontal glabellar lobe is about circular and the lateral margins of the shield converge forward (subparallel and curving in *prolixa*); the pygidial spines in *normata* are relatively short and its border is narrower than in *prolixa.*

The combination of the shields as diagnosed above awaits confirmation by a complete exoskeleton; as evident in Text-figure 12, the shapes of the acrolobes in the cephalon disagree with the shape of the pygidial acrolobe completely. With this incongruity in mind, I selected a pygidium and not a cephalon for the holotype.

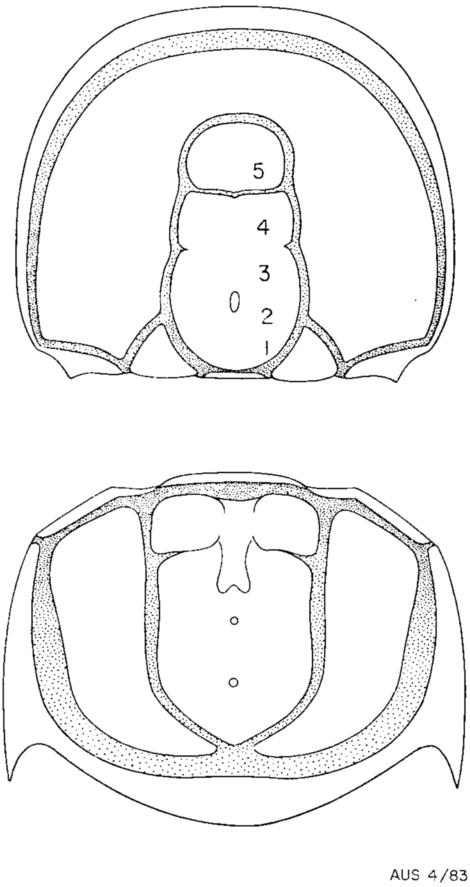

Fig. 12. *Peronopsis prolixa.* **1-5 indicate metameres of the cephalon.**

Description: In *Peronopsis prolixa* the frontal glabellar lobe is long, about 0.35x the glabellar length, and its front is not rounded but angular; the posterior glabellar lobe has slightly convex flanks, tapers forward, and bears a faint node in its rear half. The basal lobes are small (smaller than in *longinqua* and *tramitis*), and close in size to *P. normata.* In the pygidium the rim is relatively wide, and evenly wide in the rear, not projecting forward in the midline. The axis is broad, its posterior lobe is expanded and the bluntly pointed tip contacts the marginal furrow; the transverse furrows are shallow lateral notches connected across the axis by vestigial depressions, and only the anterior annulation shows some relief decreased by the flattening of the test. A small node is discernible slightly behind the midpoint of rear lobe.

Comment on illustrated specimens

The holotype pygidium is about 3.0 mm long; it is flattened and defective posterolaterally but is sufficient for the reconstruction (Text-fig. 12).

The cephalon associated with the holotype is 3.4 mm long; it is shorter than, but as wide as, the associated pygidium. Shields of such sizes are correlative in *Peronopsis* and may belong either to a single exuvia, or to exuviae of two individuals of equal size.

Occurrence and age: The described specimens come from the Sandover Beds of Northern Territory, locality N32; the age is late Templetonian, the Zone of *Triyplagnostus gibbus;* isolated pygidia and cephala have been noted in other collections from the same formation, and of a similar age.

Peronopsis tramitis sp. nov.

(Pl. 2, figs. 1-3; Text-fig. 13)

Material: The illustrated specimens represent a selection from eight pygidia and 14 cephala from two pieces of indurated siliceous siltstone, collection N35.

Holotype: The pygidium Plate 2, fig. 2, CPC 13979 is selected as the holotype.

Diagnosis: Peronopsis tramitis is distinguished by the combination of the following characters: (1) the cephalic margin is evenly rounded and the outline approaches the larger segment of a circle; (2) the frontal lobe of the glabella is transverse elliptical to subcircular; (3) the glabellar rear is narrowly rounded; (4) the posterior pygidial lobe is only slightly expanded, or almost parallel-sided; (5) the frontal axis annulation is defined by the transcurrent anterior transverse furrow, but the second annulation remains confluent with the rest of the axis; furthermore, the pygidial axis behind the median node (which is cleft) has two median nodes; (6) the rim in the pygidium is widened and gently projects forward; (7) the axis is relatively narrow, narrower than in other species.

Differential diagnosis: In other species the cephalic outline is subrectangular with a more abrupt anterolateral curvature; the glabellar rear is usually broadly rounded (*P. longinqua* excepted); the glabella in *longinqua* is elliptical (oval in *tramitis*); the almost parallel-sided posterior axial lobe with its weak lateral expansion contrasts with the well expanded lobe in other species of *Peronopsis*; peculiar also is the relief of the anterior pygidial annulations; usually both anterior annulations are of similar relief, effaced together, but in *tramitis* only the second annulation is effaced. The two nodes on the posterior axial lobe are unique; as a rule, only one node occurs in agnostids. The cleft tip of the median node of *P. tramitis* is shared by *P. longinqua* and *P. prolixa* and can be regarded as a token of kinship. *Peronopsis tramitis* is probably related to several oriental species—mostly of the same age. *Peronopsis rakuroensis* (Kobayashi, 1935, pl. 21, fig. 2) is basically similar to *tramitis* but differs in the shape of the cephalon, smaller basal lobes, and stronger glabellar median node; Saito's (1934, pl. 25, fig. 9) *'Agnostus chinensis'* has a zonate pygidial rim (as in *P. fallax*) and *Agnostus comis* Resser & Endo (in Endo & Resser, 1937, pl. 30, fig. 16) has two pairs of transverse furrows in the pygidial axis. As regards *Agnostus chinensis* Dames (in Richthofen, 1883) Kobayashi's suggestion (*Pseudagnostus* and *Homagnostus*; Upper Cambrian) should be accepted.

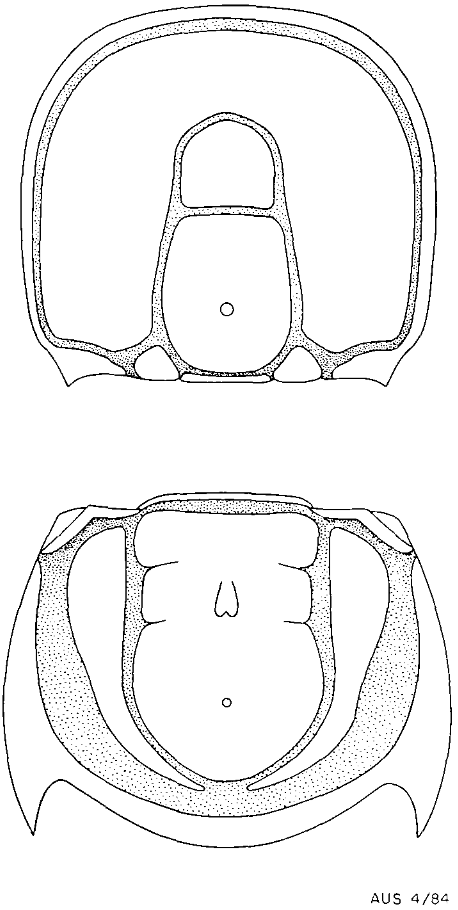

Fig. 13. *Peronopsis tramitis.*

Description: In *Peronopsis tramitis* the border of the cephalon is moderately wide, wider than in *P. prolixa* and much narrower than in *P. longinqua.* The frontal glabellar lobe, variable around 0.3x the glabellar length, is transverse elliptical to almost subcircular. The posterior glabellar lobe tapers forward and shows one pair of short and shallow lateral indentations, and its relatively prominent median node is placed slightly behind the midpoint. The basal lobes are large and triangular. The lateral margins of the pygidium are somewhat convex to the tips of the marginal spines, which are slightly recurved and broad; the margin between the spines is arched moderately rearward. The pygidial rim attains its maximal width on the midline forming a gentle forward projection; the inner edge of the rim is angular and abrupt, but the rim remains collarless. The acrolobe is gently constricted, but the stricture in some specimens can be almost imperceptible. The pygidial axis, about 0.32x the shield width, is narrower than in other species of the genus. The rear of the axis—an almost rectilinear triangle—does not reach the marginal furrow, and a broad and short postaxial median furrow separates the pleural lobes from each other.

Comment on illustrated specimens

The holotype pygidium, collection N35, is 4.0 mm long (without articulating half-ring)—a relatively large individual some 9.5 mm long. It is moderately flattened preserving the relief of the anterior axial lobe and the transverse furrow behind it. The inner edge of the posterior part of the rim is angular.

In Plate 2, fig. 1, CPC 13978, locality N35, the central cephalon is 3.5 mm long; most of its narrow rim is lost, except for a small remnant in the anterolateral sector sufficient for a restoration of the whole rim. The pygidium below shows the cleft median node, which is also preserved in the pygidium half buried under the cephalon. The pygidium above the cephalon has an accidental protuberance in its posterior axial lobe—produced by a fragment of another fossil under that pygidium. In every one of these pygidia the two tiny median nodes of the axis are discernible under a stronger (x15) magnifier.

The two cephala Plate 2, fig. 3, CPC 13980, are associated with the holotype pygidium and have circular orbits as seen in cephala in collection N32. In the explanation of Plate 2 these cephala are referred to as cf. *tramitis* for the following reasons: (1) in the larger cephalon, 3.8 mm long, the frontal glabellar lobe is 0.36x the glabella in length and larger than the cephala in Plate 2, fig. 1; and (2) the smaller cephalon, 2.5 mm long, has the marginal furrow somewhat wider than the cephalon in Plate 2, fig. 1. In the photograph it is foreshortened, but otherwise it is a regular *tramitis* cephalon.

Occurrence and age: Peronopsis tramitis comes from the Sandover Beds of Northern Territory; its age is late Templetonian, the Zone of *Triplagnostus gibbus;* collection N35 is so dated by the associated polymerid trilobites. The species occurs also at locality N32, where its shields are rare and of an inferior preservation.

Peronopsis comis sp. nov.

(Pl. 2, fig. 4)

Material: Illustrated and described is a complete exoskeleton, the holotype CPC 13981, collection N36; it is 5.3 mm long. It is a rubber cast; the matrix is brown indurated siltstone.

Diagnosis: Peronopsis comis is distinguished by the following combination of characters: (1) the cephalon is subquadrate (a common shape in *Peronopsis*); (2) the frontal glabellar lobe is rounded and long, 0.36x the glabella; (3) the glabellar rear is narrowly rounded; (4) the pygidial axis is long, expanded laterally, pointed and reaching the marginal furrow; (5) the frontal axial lobe is well defined by the transcurrent transverse furrow (as in *Peronopsis tramitis,* whose cephalon, however, is subcircular and the pygidial axis almost parallel sided); (6) the pygidial acrolobe is weakly constricted; (7) the rim in the cephalon and pygidium is prominently wide and, apparently, flat; (8) short pygidial marginal spines (excluding confusion with *P. (Itagnostus) elkedraensis,* whose cephalon in variants reminds one of *P. comis*); (9) the glabellar median node is very small and, in the rear, more retral than in other species; and (10) the pygidium is shorter than the cephalon. The thorax is 0.32-0.33x the cephalon in length (calculated from the length of the anterior segment) and is longer than in *Acadagnostus scutalis.*

The differential diagnosis and descriptive data are included in the diagnosis.

Occurrence and age: The holotype comes from collection N36, of the Sandover Beds of the Northern Territory; its age is Templetonian; isolated cephala and pygidia have also been observed in the 'Alexandria Beds', locality NT27.

Subgenus **Peronopsis (Itagnostus)** nov.

The type species of the subgenus is *Agnostus elkedraensis* Etheridge Jr, 1902; Whitehouse (1936) attributed it to *Diplorrhina* and Kobayashi (1939) to *Peronopsis.* The concept of the subgenus and its differential diagnosis are included in the description of *elkedraensis.* In brief, species attributable to *Itagnostus* have a long, undivided pygidial axis expanded laterally in its posterior half, no marginal spines, and no postaxial median furrow. The subgeneric classification is intended to express a presumed affinity between *Itagnostus* and *Peronopsis (Peronopsis)* but also as a step in retaining the concept of the subgenus *Peronopsis* in a form based on *Peronopsis integra.*

Peronopsis (Itagnostus) elkedraensis (Etheridge Jr, 1902)

(Pl. 3, figs. 1-5; Text-fig. 14)

Material: Illustrated are three complete shields and a cluster consisting of three more specimens; associated with Figures 1 and 2 are two more complete shields and numerous cephala, pygidia, and thoraces.

Whitehouse (1936, p. 88, pl. 9, figs. 3, 4) selected one of Etheridge's specimens of *Agnostus*

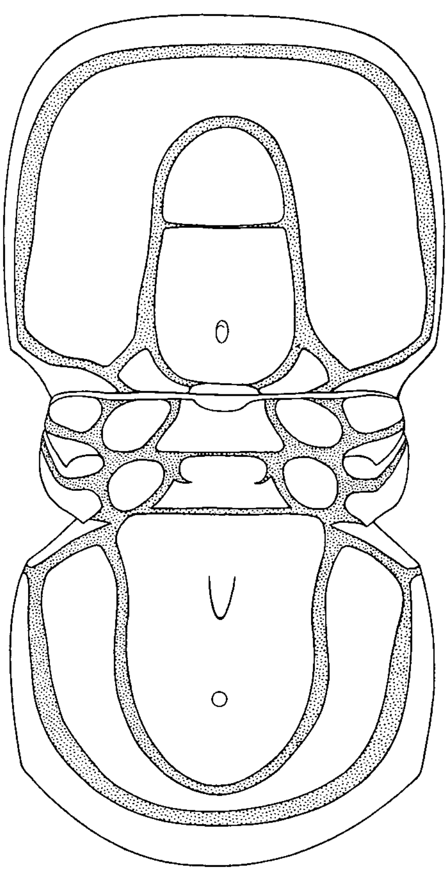

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Fig. 14. *Peronopsis (Itagnostus) elkedraensis.*

elkedraensis as the lectotype (op. cit., fig. 3) and placed the species in the genus *Diplorrhina,* taken here (see *Peronopsis normata*) as a subjective synonym of *Peronopsis.*

The concept of Itagnostus

Peronopsis elkedraensis and the related *Peronopsis montis* (Matthew, 1899) constitute a group of species different from the group of *P. integra*: (1) by the absence of pygidial spines, and (2) by the almost complete effacement of the transverse furrows in the pygidial axis, obscuring its lobes. Furthermore, the postaxial furrow, strong in the *P. integra* group, is missing in *P. elkedraensis.* Nevertheless, the general structure of the cephalon, the laterally expanded posterior pygidial axial lobe, and the stricture of the pygidial axial lobe are characters unifying *Itagnostus elkedraensis* with *Peronopsis.*

Peronopsis montis Matthew (1899, pl. 1, fig. 6) resembles *elkedraensis,* but its glabellar node is subcentral (retral in *elkedraensis*) and it has no posterolateral angularity of the pygidial rim. It appears also that in Rasetti's (1951, pl. 25, figs. 11-14) specimens of *montis* from the Canadian Rocky Mountains the pygidial axis is weakly lobate and shows vestigial lateral transverse furrows. Close to *elkedraensis* is also the Korean agnostid which Saito (1934, pl. 25, figs. 10, 11) attributed to *Agnostus chinensis* Dames. Its pygidial axis is long, undivided by transverse furrows, and the rim is expanded posterolaterally but apparently spineless. On its right a chip of the rim is lost, leaving behind a 'quasi spine' cut out of the rim by a fracture. The horizon according to Saito is 'Ptychoparia beds'—a temporal equivalent of the Sandover Beds (Öpik, 1956; 1957, p. 44) with *P.* (*Itagnostus*) *elkedraensis.* Finally, *Agnostus robustus* Deiss (1939, p. 70) seems also close to *I. elkedraensis* and *I. montis.*

Description: The cephalon is as wide as long, but owing to the unaccountable deformation, aberrations are frequent. The rim is moderately wide and the marginal furrow deep and narrow; in outline the cephalon appears rounded to subrectangular with a stronger anterolateral curvature of the margin. The frontal lobe of the glabella is large (0.36x the glabella) and semielliptical (pl. 3, fig. 1), with forward arched front; the posterior glabellar lobe tapers slightly forward, is devoid of lateral indentations, and carries its median node well back from the midpoint; the glabellar rear is rounded and the basal lobes are small and, apparently, swollen. The thorax is 0.29-0.3x the cephalon in length, with a moderate, normal relief.

In the pygidium the lateral margins seem to converge slightly rearward and pass behind the posterolateral angularity into the evenly curved posterior margin. The rim widens rearward and is apparently of a low convexity; the marginal furrow is relatively wide and deep. The axial lobe is long, broad, constricted at the level of the median axial node, expands rearward, and terminates in a blunt point at a short distance from the marginal furrow. The node on the posterior axial lobe is prominent and placed behind the midpoint of the lobe. The acrolobes are slightly constricted.

Comment on illustrated specimens

The two complete exoskeletons Plate 3, figs. 1 and 2 have been recovered from a piece of pale yellow, silty shale, in parts mottled and siliceous, together with three other complete specimens and a large number of cephala, pygidia, and thoraces of the same species; associated are *Pagetia significans* and fragments of *Xystridura davidsoni* at locality N32.

The exoskeleton Figure 2, CPC 13984, is 5.0 mm long; its counterpart has been also recovered. The thorax is about 0.26x the cephalon in length; the glabellar node is exaggerated through flattening; vestiges of transverse pygidial axial furrows can be seen; no postaxial furrow exists, but there is a longitudinal fracture behind the axial tip; the stricture of the acrolobe is moderate.

The exoskeleton Figure 1, CPC 13983, is 4.8 mm long. Its thorax is about 0.3x the cephalon in length; the glabella and the quite prominent pygidial axial lobe are undeformed; transverse furrows of the pygidial axis are totally absent; the median node on the posterior pygidial lobe is clear; a postaxial delicate furrow, or only a fracture in its position, is visible. The frontal glabellar lobe is undistorted.

The exoskeleton Plate 3, fig. 3, CPC 8399, collection N35, indurated brown siltstone, is about 5.4 mm long; it is associated with an exoskeleton of *Oryctocephalites gelasinus* Shergold (1969, pl. 5, fig. 3). The thorax is 0.3x the cephalon in length and the posterior segment is, as in the other specimens, shorter than the anterior one. The frontal glabellar lobe is almost circular; the median node on the posterior pygidial lobe is quite prominent, and the rim is expanded and angulate. A postaxial furrow is absent.

The cephalon Plate 3, fig. 5, CPC 13986, collection N31 in chert, is 3.8 mm long; it belongs to a large specimen some 9 mm long; it is fractured and a fracture imitates the preglabellar furrow. The forward tapering glabella with the semielliptical frontal lobe and the median node in the rear are characters of the species.

In the cluster of three specimens Plate 3, fig. 4, CPC 13985, locality N32, light brown siliceous shale, the length of each is about 5.0 mm; the shields are flattened and deformed: the glabellar rear appears angular and not rounded as in other specimens. The tagmata are in their original position (as in the other specimens); these are shields of dead animals and not exuviae.

Occurrence and age: Peronopsis (Itagnostus) elkedraensis occurs abundantly in the Sandover Beds of the Northern Territory; its age is the Templetonian Zone of *Triplagnostus gibbus* (the related American *montis* is of a similar age).

?Peronopsis (?Itagnostus) sp. indet.

(Pl. 22, fig. 5)

The material consists of a single pygidium, CPC 14105, 2.3 mm long; its axial lobe is plump, reminiscent of *Itagnostus elkedraensis* (Pl. 3, figs. 1-3). A median node is absent, no transverse furrows are indicated, and the pleural lobes behind the axial tip are confluent in the absence of a postaxial furrow; marginal spines are also absent. Similar also is the pygidium of *Agnostus acadicus* Dawson (Text-fig. 15; see also *Acadagnostus*) and some shields of Lower Cambrian agnostids described by Rasetti (1967, pl. 20, figs. 4, 22, and 27). In the absence of a cephalon the affinity of this form remains obscure, and the application of the name *?Peronopsis* (*?Itagnostus*) is also doubtful.

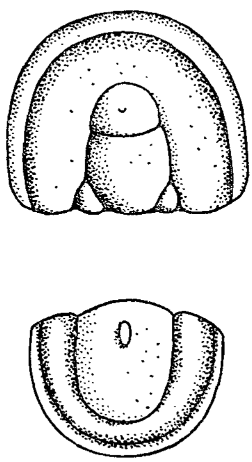

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Fig. 15. *Acadagnostus acadicus,* **facsimile of** *Agnostus acadicus* **Hartt** *in* **Dawson, 1868.**

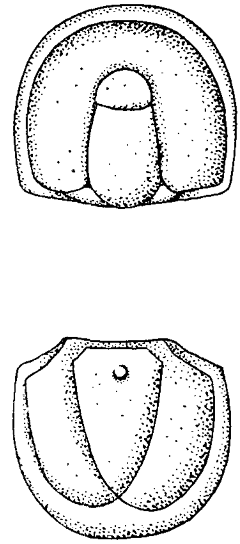

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Fig. 16. *Agnostus acadicus,* **var.** *declivis,* **after Matthew, 1886.**

Occurrence and age: The specimen comes from the Inca Formation, locality M281; its age is the Floran Zone of *Ptychagnostus atavus.*

Genus **Acadagnostus** Kobayashi, 1939

The name *Acadagnostus* is applicable only to its type species—*Agnostus acadicus* Hartt, edited by Dawson (1868, p. 655, fig. 229). The original illustration (fig. 229) comprises one cephalon and one pygidium reproduced here in facsimile, Text-figure 15. Walcott (1884, pl. 2, figs. 2-2c) illustrated the originals but added to *acadicus* two disparate pygidia which are quite different from *acadicus* in terms of Hartt in Dawson; Walcott's illustrations of the correct shields were reprinted by Shimer & Shrock (1944-1949, pl. 251, figs. 11, 12). Neither of the two original syntypes has been designated, to my knowledge, as a lectotype and after Walcott's (1884) revision no material restudy has been published. As a matter of fact, the type specimen (the holotype) of *Agnostus acadicus* is the cephalon as illustrated by Hartt in Dawson (op. cit.); the pygidium cannot be selected as a lectotype because its description starts with the phrase 'Pygidium of this species(?) etc.'

The concept of *Agnostus acadicus* in the current literature is based on an agnostid different from the original syntypes: Matthew

(1886, pl. 7, figs. 5a, 5b) attributed to *Agnostus acadicus* one cephalon and one pygidium, as equal syntypes, which are reprinted here in facsimile, Text-figure 16; these shields may or may not be conspecific. Moreover, the cephalon is visibly different from the illustrated type cephalon of *A. acadicus*, but similar to the cephalon of *Agnostus acadicus*, var. *declivis* (Text-fig. 16). In passing, the pair of nodes at the anterolateral corners of the pygidial axis and accentuated in Harrington et al. (1959, p. 0183, fig. 124 (2)) are no part of the axis but seem perhaps to be the deformed fulcral points.

Kobayashi (1939), while establishing the genus *Acadagnostus*, illustrated in the 'Table showing the classification of Agnostida' Matthew's syntypes and accepted these as *Agnostus acadicus* Hartt.

Westergaard (1946, p. 36) regarded *Acadagnostus* as a synonym of *Peronopsis*; Hutchinson (1962, p. 68) retained *Acadagnostus* (*sensu* Kobayashi) as a subgenus of *Peronopsis*, and (p. 73) attributed to it *Agnostus scutalis* Salter (q.v.).

In summary, the status of *Acadagnostus acadicus* (Hartt, 1868) (1) depends on its cephalon—the holotype by monotypy; (2) *Agnostus acadicus declivis* Matthew, 1885, is a possible synonym of *acadicus* Hartt as indicated by the similarity of its cephalon to Hartt's holotype; (3) the pygidium either of *Agnostus acadicus* or of *acadicus declivis* should be regarded for the time being as assignable to the species *acadicus*; consequently, the concept of the genus *Acadagnostus* Kobayashi is inconclusive and remains objectively incomplete. Subjectively, the arbitrary selection of the pygidia by Matthew (1885) may or may not be operational; in these the pygidial axis is narrow and tapers retrally—a distinction from *Peronopsis*. The same structure of the axis is also present in *Agnostus scutalis* Salter, which is described next as a species of *Acadagnostus* (*vide* Hutchinson, 1962, p. 69).

The possibility of *Acadagnostus* being a junior synonym of *Quadragnostus* is indicated in the discussion of the subfamily Quadragnostinae.

'Acadagnostus' scutalis (Salter, 1872)

(Pl. 2, fig. 5; Text-fig. 17)

The illustrated specimen CPC 13982 is 9.0 mm long, collection F5. Its convexity is preserved, but the test, silicified and in a siliceous matrix, is slightly corroded.

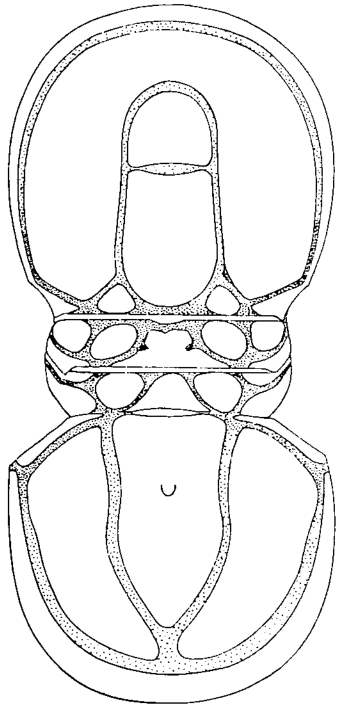

Fig. 17. *'Acadagnostus' scutalis.*

The specimen is attributed to *Agnostus scutalis* Salter in consideration of the following combination of characters: (1) the margins of the cephalon and pygidium are evenly curved, and pygidial marginal spines are absent; (2) the frontal glabellar lobe is relatively long and the basal lobes are small; (3) the pygidial axis is narrow, tapering, and pointed, and a post-axial median furrow is present; and (4) the acrolobes are unconstricted. It is, however, apparent that the pygidial axis is relatively long, longer than in most specimens of *Agnostus exaratus tenuis* (Illing, 1915) but close to Westergaard's (1946, pl. 4) specimens. Relatively long also is the axis in the pygidia of *P. scutalis* described by Hutchinson (1962) from Newfoundland. It seems at first that the pygidial rim in our specimen is narrower than in other specimens attributed to *scutalis* by writers, but the outer edge of the rim is not quite clear—apparently collapsed over the doublure.

The species *Agnostus scutalis* Salter was originally described from a paradigm of six specimens (Hicks, 1872, pl. 5, figs. 9-14) and its subsequent history was clarified by Westergaard as late as 1946: (1) two specimens (figs. 9 and 10) were identified by Lake (1906) as belonging to *Ptychagnostus punctuosus*; and (2) Lake (op. cit., pl. 1, fig. 8) illustrated the complete specimen of Salter's *scutalis* fig. 12 and replaced its name with the name *Agnostus exaratus* Grönwall, 1902—a subjective procedure which in the absence of a designated holotype or lectotype selected from Salter's paradigm cannot be regarded as binding. For the sake of objectivity, this specimen (Salter *in* Hicks, 1872, pl. 1, fig. 12; Lake, 1906, pl. 1, fig. 8) is selected here as the lectotype of *Agnostus scutalis.*

Occurrence and age: 'Acadagnostus' scutalis (Salter) occurs sporadically in the Sandover Beds and 'Alexandria Beds' of Northern Territory; it has been also reported from Queensland (Öpik, 1956; 1957, p. 43) in the Beetle Creek Formation. Its age is Templetonian (the Zone of *Triplagnostus gibbus*).

Genus **Svenax** nov.

Svenax pusillus (Tullberg, 1880)

(Pl. 6, figs. 3-5)

The type species of *Svenax* is *Agnostus pusillus* Tullberg (1880, p. 36; fig. 30); the holotype is a pygidium. Tullberg (op. cit., p. 13) placed *pusillus* in the division of his *Longifrontes,* but described it as a species *incertae sedis*. Kobayashi (1939, p. 113) included it in *Acadagnostus*. Westergaard (1946, p. 42) described it as *Peronopsis pusilla* (Tullberg), of the Zone of *Ptychagnostus punctuosus;* he re-illustrated the holotype, supplemented by two cephala and four pygidia.

Genus *Svenax* is represented by two species —*S. pusillus* (Tullberg) and *S. vafer* sp. nov.

Diagnosis: Svenax recalls a *Peronopsis* as regards the absence of the preglabellar median furrow and the shape of the glabella; it is distinguished by its depressed glabellar frontal lobe and especially by its pygidial axis, which is short, abruptly pointed, and provided with a node at its tip.

Differential diagnosis: Svenax is reminiscent of some species of *Hypagnostus* and *Tomagnostella,* with a laterally expanded glabella between the two pairs of glabellar furrows; a terminal axial node occurs also, for example, in *Tomagnostella nepos* (q.v.), in *Hypagnostus correctus, H. durus* Öpik (1967, p. 84, pl. 52, figs. 5, 6), and *H. hippalus* Öpik, 1961; but in these and similar forms the shape of the pygidial axis is different from *Svenax* and the frontal glabellar lobe is absent. Nevertheless, *Svenax vafer* sp. nov. may bear affinity with *Hypagnostus melicus* sp. nov., as is discussed in the descriptions of these two forms.

Description of Svenax pusillus

The shields of *Svenax pusillus* in hand are small—averaging 2 mm in length, and smaller than the Swedish ones of 3.3-3.4 mm (Westergaard, op. cit., p. 42). The small size of the cephala explains the weakness of their scrobicules, which are quite strong in the larger Swedish cephala; moreover, in these the scrobicules are variously impressed and can also be weak (Westergaard, pl. 4, fig. 14). The weakness of scrobicules is the only character in which our specimens differ from the Swedish ones.

In the cephalon the rim and the marginal furrow are very narrow; the frontal glabellar lobe is depressed and of low relief, reminiscent of *Hypagnostus parvifrons,* but it is enclosed by the circumlabellar furrow, which is unknown in *Hypagnostus*. The posterior glabellar lobe is relatively prominent, rounded in the rear, expanded in the middle, and notched by two pairs of short lateral furrows; its median node is weak and closer to the midpoint than in Westergaard's (op. cit., pl. 4, fig. 14) cephalon. The pygidial rim is of low convexity, narrow, spineless, and widens slightly rearward. The axis is short (0.7x the shield length) and elegantly constricted about the anterior transverse furrow; it expands rearward past the midpoint and finally its almost straight posterior flanks converge in an acuminate tip with the terminal node. The transverse furrows are shallow; the anterior axial lobes are low and the second lobe is equipped with an elongate median node.

Description of illustrated specimens

The cephalon Plate 6, fig. 3, CPC 14003, is 2.2 mm long; the cheeks are scrobiculate, but the scrobicules are shallow—shallower than in the larger cephala illustrated by Westergaard; the posterior glabellar lobe has two pairs of lateral furrows; the delicate furrow around the anterior glabellar lobe is well visible. The test is preserved but corroded.

The cephalon Plate 6, fig. 4, CPC 14004, is 2.1 mm long; most of its test is lost.

The pygidium Plate 6, fig. 5, CPC 14005, is 2.2 mm long; the postaxial median furrow is shallow.

Occurrence and age: The described specimens of *Svenax pusillus* come from a sandy dolomite bed, Quita Formation, locality D74; the age is the early Undillan Zone of *Ptychagnostus punctuosus*. In Sweden (Westergaard, op. cit.,

p. 98) it belongs to the same zone. Howell (1925, p. 38) recorded *Agnostus* cf. *pusillus* in association with *Pt. punctuosus* in Newfoundland.

Svenax vafer sp. nov.

(Pl. 6, fig. 6)

Material: Two pygidia.

Holotype: The holotype, CPC 14006, is illustrated.

Diagnosis: In *Svenax vafer* the posterior lobe of the pygidial axis is relatively narrowed (in *S. pusillus* the flanks of that lobe are convex and the lobe is wide), and the transverse furrows and the anterior annulations are effaced; the middle sector of the marginal furrow is effaced or vestigial and the rim in that sector is about confluent with the acrolobe, and no postaxial median furrow is evident.

Differential diagnosis: S. vafer differs from the type species (*S. pusilla*) by its diagnostic characters.

Description: The holotype and the associated second pygidium (CPC 14006) are 2.0 mm long. The axial lobe is short and acute and its apical node is quite prominent; posterolateral spines are absent; in the second pygidium (as long as the holotype) the marginal furrow is visible as a vestige delineating a median projection of the rim with its tip meeting the top of the axial lobe—a structure reminiscent of *Hypagnostus melicus* sp. nov.

Occurrence and age: The two described pygidia of *Svenax vafer* are preserved in separate pieces of a grey laminated limestone of the V-Creek Limestone, locality M409. The age is the early part of the Undillan Zone of *Doryagnostus notalibrae;* it is slightly younger than *S. pusillus.*

Subfamily 'HYPAGNOSTINAE' Ivshin, 1953 (=QUADRAGNOSTINAE partim)

In an earlier discussion (Öpik, 1967, p. 82) the Hypagnostinae is characterised as heterogeneous in regard to its generic and specific composition. Nevertheless, it refers in the first place to the genus *Hypagnostus* and its type species *H. parvifrons,* and is therefore a regular taxon. It is characterised by the effacement of the anterior glabellar lobe—a phenomenon observable in some species attributable to different family (subfamily) aggregates; consequently the generic composition of the subfamily proposed by Ivshin remains a matter of further study; moreover, the status of the subfamily depends also on the general systematics of the related suprageneric aggregates as reflected in views of writers. At all events, the name Hypagnostinae indicates a subfamily of the Family Agnostidae; but the genus *Hypagnostus* itself can be also included in a subfamily of an earlier date of publication (Quadragostinae, or Peronopsinae, or Spinagnostinae, etc.) and the Hypagnostinae in a synonymy list of one of such subfamilies.

Remarks regarding the species included by writers in, and descriptive of, the concept of the genus *Hypagnostus* are given in the following pages. The problem of the concept hinges in the first place on the effacement of the frontal glabellar lobe—a character recognisable at a glance.

In brief the term 'effacement' in agnostids and in other trilobites describes a partial and selective or even total obliteration of furrows in an exoskeleton as compared with the prosopon en grande tenue. The incidence of effacement is generally no indication of loss of vital organs or of fundamental changes in the somatic anatomy of the animal. The external obliteration of the frontal glabellar lobe may result (1) from the effacement of the furrows defining that lobe externally, as is presumed in *Hypagnostus parvifrons;* the somatic frontal lobe (an organ) is present but may or may not be expressed as a tumidity of the sclerite; (2) from the decrease in length of the somatic, and hence of the skeletal, frontal lobe, as presumed in *Tomagnostella nepos* or (3) from a total reduction of the frontal lobe (organ)—a possibility indicated by Öpik (1961a, p. 414, text-fig. 3) in *Hypagnostus exsculptus,* whose lobe is replaced by caecal veins. It is, however, feasible that the deep-seated lobe (organ) is masked by the alimentary caeca, which are placed high and in contact with the cuticle. At the same time pygidia attributed to *Hypagnostus* differ in design and should be considered in the concept of the genus. At all events a re-study of published specimens is in order before embarking on the hazards of a new generic nomenclature.

Genus **Hypagnostus** Jaekel, 1909

A number of described species commonly included in *Hypagnostus* are transferred in this paper to *Tomagnostella;* thus restricted, the genus *Hypagnostus* refers to its type species *H. parvifrons* and morphologically similar forms.

The combination of the following characters is diagnostic of *Hypagnostus*: (1) the pygidial axis is broad and pointed in the rear and relief of the two anterior segments is not developed; (2) the transverse furrows separating the lobes are short and lateral only, or even vestigial externally; (3) the posterior glabellar lobe is short, rounded in the rear, and well defined by the axial furrows and the transverse furrow in front; (4) the frontal glabellar lobe may be effaced or indicated by a swelling of low relief without the circumaxial furrow. Also, the basal lobes are simple and the acrolobes are unconstricted. In Australia the following twelve species have been identified so far: *Hypagnostus vortex* and *H. clipeus* by Whitehouse; *H. parvifrons* (Linnarsson), *H. tjernviki* (Westergaard), *H. brevifrons* (Angelin); *H. inaequalis* nov., *H. melicus* nov., and the earlier described *H. willsi, H. hippalus, H. varicosus* (all Öpik, 1961b), and *H. correctus* and *durus* (Öpik, 1967).

The species *varicosus* and *durus,* on the grounds of their pygidia, may be removed from *Hypagnostus,* each representing, possibly, a separate genus; *H. brevifrons* can be placed in *Cyclopagnostus* Howell; *H. tjernviki,* of which only a cephalon and a pygidium and a single exoskeleton are known so far, may represent its own genus.

The Chinese (Lu, 1957) *hunanicus* and *quadratus* have properly lobate pygidia and are closer to *Tomagnostella* than to *Hypagnostus.*

Spinagnostus (and Spinagnostidae) Howell, 1935, appears similar to *Hypagnostus* but should retain an independent status. As revised in Harrington et al. (1959, p. 0182), *S. franklinensis* Howell has genal spines, a short, narrow, and tapering glabella devoid of a transverse furrow, a short, undivided, and almost parallel-sided pygidial axis, and broad pygidial marginal spines. A pygidium similar to *Spinagnostus* is also present in *Eoagnostus* Resser & Howell, 1938, as described by Rasetti (1967); the cephalon of *Eoagnostus* retains its transverse glabellar furrow but the furrow surrounding the frontal lobe is effaced; it belongs to the Spinagnostidae according to Rasetti.

Westergaard (op. cit., p. 43) suggests that '*Hypagnostus* arose from *Peronopsis*'; this should be accepted also for *Cotalagnostus* (*C. lens* in the first place); the event of the passage from one structure to another resulted in the effacement of the circumglabellar lobe of *Peronopsis.* No particular species of *Peronopsis* can be named as an ancestor of *Hypagnostus,* nor, even more, of one of its species. It is, however, feasible that *Hypagnostus parvifrons* retained a pygidial structure of the kind seen in *Peronopsis* (*Itagnostus*) *elkedraensis* (similarity of the axial lobes and absence of marginal spines), or in *Peronopsis normata* (forward projecting rim), whose posterior glabellar lobe has also convex flanks. *Hypagnostus clipeus,* however, may have inherited its tapering and pointed pygidial axis from an *Acadagnostus* or even from *Euagnostus.* The species placed in *Tomagnostella* are of a different (ptychagnostid) parentage. The temporal sequence of the species in question is consistent with their inferred phyletics: (1) the earliest known species of *Hypagnostus* appeared in the time of *Ptychagnostus atavus* and postdate *Peronopsis* (*Itagnostus*) *elkedraensis* and *Acadagnostus scutalis;* (2) *Hypagnostus clipeus* postdates *Acadagnostus* and *Euagnostus*; and (3) the species of *Tomagnostella,* all of late Middle Cambrian age, postdate the earlier diversification of the Ptychagnostinae.

Hypagnostus parvifrons (Linnarsson, 1869)
(Pl. 6, figs, 7, 8)

The Australian material attributable to *H. parvifrons* consists of the cephalon Plate 6, fig. 7, and the complete shield fig. 8, associated with another smaller complete shield and several isolated cephala and pygidia.

Westergaard (1946) in revising *H. parvifrons* designated a cephalon (op. cit., p. 116, pl. 4, p. 29) as the lectotype of Linnarsson's species. Its rim expands forward, the glabellar node stands in front of the midpoint, the glabella is slightly shorter than half the cephalon, the glabellar front is not quite rounded but slightly truncate, and the frontal lobe is developed as a barely perceptible vestigial swelling. In the pygidium associated with the holotype (ibid., fig. 28) the rim expands rearward and projects forward in the middle; the axis is long, pointed, and slightly expanded in the middle, the furrows defining the two anterior lobes are only lateral vestiges, and the lobes themselves are lacking in any relief. These characters are also evident in our complete specimen Plate 6, fig. 8, CPC 14008, a silicified test, 5.5 mm long, flattened in chert (from locality M265); its age is the Zone of *Ptychagnostus atavus.* This specimen differs, however, from the Swedish material of *H. parvifrons* by stronger emphasis of the median glabellar, and pygidial, nodes and the scrobiculation of the cheeks consisting of scattered shallow peripheral pits. This scrobiculation is nevertheless much weaker than in *Hypagnostus parvifrons cicatricosus* Westergaard (op. cit., p. 46, pl. 5, fig. 1), which exhibits even arcuate scrobicules; *cicatricosus* and *parvifrons* are connected by 'intermediate stages'; our specimen may be also an 'intermediate' form closest to *parvifrons* (*parvifrons*) rather than to *cicatricosus*. The node close to the pygidial tip in our specimen is low but exaggerated by whitening; its position is the same as in *H. clipeus* (Text-fig. 18). The thorax of our specimen is of the same size and structural detail as Westergaard's (op. cit., pl. 5, fig. 31), which is also reproduced in Harrington et al. (1959, p. 0185).

The cephalon Plate 6, fig. 7, CPC 14007, is undeformed, 2.2 mm long, in limestone from locality M180; its frontal glabellar lobe is indicated, the node on the glabella seems weaker than in the previous specimen, and its test is punctate. Its age is the Zone of *Euagnostus opimus*—the zone after the *atavus* zone.

The material of *Hypagnostus parvifrons* here described constitutes all that has been found so far of that species in Australia. Its rarity explains why until now in reference to the Zone of *Hypagnostus parvifrons* its nominate species was considered by me as being 'conspicuous by its absence'. Moreover, it is a bi-zonal species also in Sweden (Westergaard, op. cit., p. 45) and in western Utah (Robison, 1964). For all these reasons the designation 'Zone of *Hypagnostus parvifrons*', an adoption from Westergaard (1946) was replaced (Öpik, 1970a) in the scale of Middle Cambrian zones by the designation 'Zone of *Euagnostus opimus*'.

Occurrence and age: Hypagnostus parvifrons is an extremely rare species of the Inca Formation and Currant Bush Limestone and occurs in the Zones of *Ptychagnostus atavus* and *Euagnostus opimus* of the Floran Stage.

Hypagnostus cf. **vortex** Whitehouse, 1936
(Pl. 6, fig. 9)

Hypagnostus vortex Whitehouse (1936, pl. 9, figs. 7, 8, p. 103) is based on a cephalon, figure 7 (the holotype) and an associated pygidium, figure 8. These specimens are flattened and slightly worn and possibly dilated in shale. Nevertheless it is apparent that *H. vortex* cannot be confused with *H. parvifrons* because its pygidial rim has not the median projection forward as seen in *parvifrons;* the rim is the same as in the much younger *H. clipeus*, whose glabellar node, however, is placed forward from the subcentral position seen in *vortex*.

The illustrated complete specimen, CPC 14009, is 4.0 mm long and smaller than the original types. The pygidium published by Whitehouse has a relatively long axis and is close to 3.0 mm in length; this difference in size may account for the shorter axis in our specimen.

Description: The cephalic rim is convex and narrow but the marginal furrow is a wide channel, wider than in other species of the genus; the cheeks are scrobiculate with scattered pits; in the glabella the frontal lobe is a vestigial swelling, and the median node is a narrow elongate ridge. The thorax, as long as about 0.22-0.27x the cephalon, is very short (about the same as in the Swedish material of *Hypagnostus parvifrons*) — much shorter than in *Hypagnostus clipeus*. In the pygidium the rim widens evenly rearward, the marginal furrow is moderately wide, the axis is constricted about the second transverse furrow, and the pointed tip has a terminal node. The postaxial furrow is faint.

Occurrence and age: According to Whitehouse the two described shields of the type material of *Hypagnostus vortex* were found in association with *Ptychagnostus atavus;* the specimen of cf. *vortex* described here comes from collection M281; three more specimens came from M265; the matrix is siliceous shale of the Inca Formation, and the associated agnostids indicate the Floran Zone of *Ptychagnostus atavus*.

Hypagnostus clipeus Whitehouse, 1939
(Pl. 5, fig. 1, 7: Text-fig. 18)

Whitehouse (1939, pl. 25, figs. 25 and 26, p. 263, one text-figure) attributed two specimens to *H. clipeus*: (1) the specimen figure 26 (paratype), a distorted complete test with a long and slender pygidial axis reminiscent of *Tomagnostella nepos* (q.v.), and the holotype, figure 25, a complete specimen about 7.0 mm long. The glabella of the holotype is oval (more oval than in the diagram, op. cit., p. 263) and in the pygidium the postaxial furrow is evident (also evident in the diagram), although the text mentions its absence—apparently a lapsus calami. Whitehouse's material was collected at the V-Creek Crossing (our site M409). Westergaard (1946, p. 45) indicated that *clipeus* differs in its pygidial structure from *H. parvifrons* (in *clipeus* the pygidial rim is evenly wide but in *parvifrons* the rim 'projects forward at the axial line'). This, as well as other characters indicated below, prevent the confusion of *clipeus* with *parvifrons*.

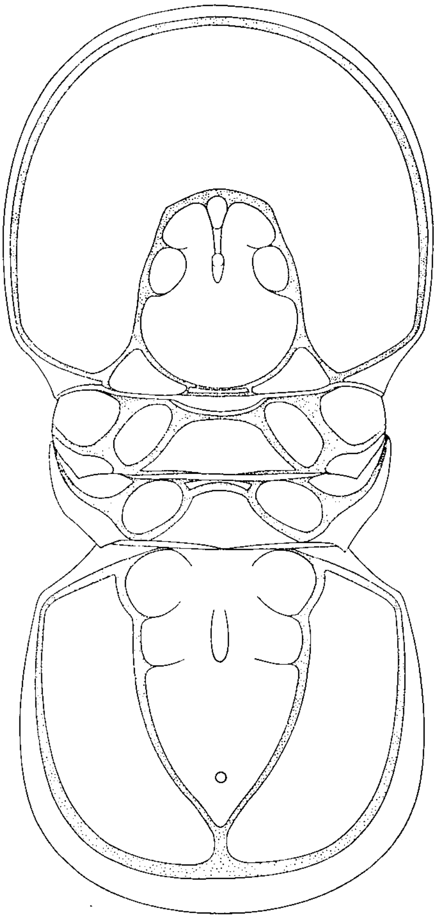

Fig. 18. *Hypagnostus clipeus.*

Description (supplementary): The illustrated and described complete specimen, CPC 13994, from locality M409 (the type locality), is about 6.0 mm long; it is selected from a set of four similar shields. The cephalon is very convex, with a depth of about 0.3x its length; its margin is evenly curved, the border is narrow, and the glabella, slightly less than half the cephalon in length, is oval. In some cephala the frontal glabellar lobe may be visible. The characters so far are also apparent in *Hypagnostus parvifrons.* The glabellar node, however, is advanced more forward than in *parvifrons.* The thorax, about 0.35x the cephalic length, is relatively large, visibly larger than in *H. parvifrons* (Westergaard, op. cit., pl. 4, fig. 31) where it is about 0.23x, and larger than in the Australian form (Pl. 6, fig. 8) with about 0.27-0.28x the cephalon.

The pygidium is a little shorter, and less convex, than the cephalon. Its outline is about 'subquadrate', and widest in the posterior half; the rim widens rearward and the marginal furrow is narrow. The axis narrows rearward, is pointed and sometimes slightly extenuated posteriorly. The transverse furrows are weakly impressed and short. The axial node is low; close to the rear top of the axis a small node is visible especially on internal casts. The pygidial axis gains in relative length during growth; the pygidium Plate 5, fig. 7, CPC 14000, locality M41, is 3.8 mm long, of an exoskeleton about 9.0 mm in length, and its axial tip almost touches the marginal furrow. As a whole, the pygidium resembles *Euagnostus opimus* (q.v.) which, however, has marginal spines.

The test is punctate.

The illustrated specimen has lost the test of the glabella and surrounding parts of the cheeks; the cast in limestone shows two pairs of semicircular swellings (muscle spots) separated by a ridge extending from the median node to an acuminate frontal protuberance.

Hypagnostus inaequalis sp. nov.

(Pl. 5, figs. 2-4; Text-fig. 19)

Material: The material consists of the three illustrated exoskeletons from a single piece of limestone.

Holotype: The exoskeleton Plate 5, fig. 3, CPC 13996, is the largest and best preserved specimen and is therefore selected as the holotype.

Diagnosis: Hypagnostus inaequalis has a glabella shorter than half the cephalon, a relatively short pygidial axis, and short, almost incipient pygidial marginal spines, and is distinguished by its large cephalic border with a broad marginal furrow, a frontal recess in the cephalic acrolobe, and a narrowly rounded tip of the tapering pygidial axis.

Differential diagnosis: Several species of *Hypagnostus* have a relatively short pygidial axis; among these, *H. denticulatus* Westergaard (1946, p. 49, pl. 5, figs. 30-33) is exceptional in having pygidial marginal spines (longer than in *inaequalis*), and its axis is pointed and extenuated and of a structure resembling the Ptychagnostinae (see under *Tomagnostella*). The pygidial margin in *Hypagnostus truncatus* (Brögger), forma 3 of Westergaard (op. cit., p. 47, pl. 5, fig. 23), is angular (with undeveloped spines?), but its axis is acute and the glabella in the associated cephala is longer than half the cephalon. In

Hypagnostus clipeus Whitehouse the cephalic border is narrow; and in *H. vortex* Whitehouse the border is wide, but the pygidial axis is different; furthermore, in these forms marginal pygidial spines and a frontal recess are absent. In passing, the frontal recess in the acrolobe of *Euagnostus opimus* and incipient marginal spines in *E. neptis* may indicate some degree of affinity between *H. inaequalis* and *Euagnostus*.

Description: Hypagnostus inaequalis is represented by small exoskeletons, the largest being 7.2 mm long. The cephalon and the pygidium are equal in length and of similar circular shape; the thorax is about 0.28-0.3x the cephalon in length. In the cephalon the rim is narrow, the marginal furrow is wide and its floor is convex; the pygidial rim is relatively wide and of a low convexity. The glabella, 0.45x the cephalon, is relatively short and oval and its median node, a little in front of the glabellar midpoint, is relatively prominent. The

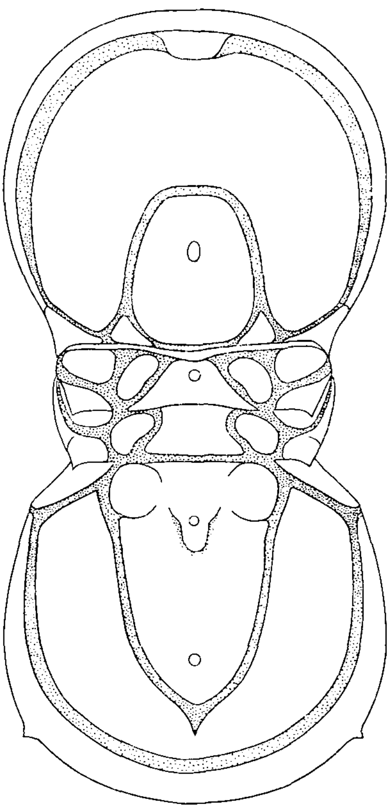

Fig. 19. *Hypagnostus inaequalis.*

basal lobes are triangular and short and the cephalic spines are triangular blades. It is also possible that a preglabellar median furrow is impressed on the mould and also indicated externally in the form of the flaring recess of the acrolobe.

In the pygidium the marginal spines are very short indeed; the axis, 0.7x the shield's length, is slender, and transverse furrows are apparently absent; the median node on the second lobe is quite prominent and its tip seems to possess an obscure cleft; the node in the posterior axial lobe is small and in a quite retral position, a short distance from the axial tip.

Comment on illustrated specimens

The holotype is 7.2 mm long; the collapsed glabella retains its outline and convexity; the pygidium is intact; the postaxial furrow is externally absent; the recess in front of the acrolobe is prominent. The test is thick.

The exoskeleton Plate 5, fig. 2, CPC 13995, is about 7.0 mm long—a little shorter than the holotype—and the frontal recess of the acrolobe is somewhat flattened. The glabella, the left cephalic spine, and the right basal lobe are intact. The pygidial axis is deformed along its right flank and has lost some of its rear; a part of the postaxial furrow is exposed.

The exoskeleton Plate 5, fig. 4, CPC 13997 is 4.8 mm long and smaller than the others. The pygidial axis, owing to the deformation, became pointed, but the node close to the rear of its posterior lobe is still visible, even clearer than in the holotype; the test is lost and the postaxial furrow impressed in the matrix is exposed.

Occurrence and age: Hypagnostus inaequalis comes from the V-Creek Limestone, locality M202; its age is the Undillan Zone of *Doryagnostus notalibrae.*

Hypagnostus melicus sp. nov.

(Pl. 4, figs. 1-2; Pl. 5, fig. 6; Text-fig. 20)

Material: The description is based on one complete exoskeleton, one isolated cephalon, and one pygidium; another complete shield and three pygidia have been identified in collections.

Holotype: The complete exoskeleton Plate 5, fig. 6, CPC 13999, in limestone, locality M462.

Diagnosis: Hypagnostus melicus sp. nov. has a vestigial frontal lobe of the glabella, a thick punctate test, and a narrow cephalic rim; it is distinguished by its long lanceolate pygidial axis reaching the median part of the rim. The convexity of the shields is low to moderate.

Differential diagnosis: The forward-projected median part of the rim is a structure shared with *Hypagnostus parvifrons* and even more so with *Hypagnostus parvifrons mammillatus* (Brögger), as evident from Westergaard (1946, pl. 5, fig. 4) and Hutchinson (1962, pl. 6, figs. 10a and b); the shields of these forms, however, are very convex to extremely convex and the pygidial axis lacks the elegant lanceolate shape of *melicus*. The cephalon of *H. melicus*, Plate 4, fig. 1, resembles to some extent a cephalon attributed by Westergaard (op. cit., pl. 6, fig. 25) to *Cotalagnostus lens claudicans*, but the pygidia of *claudicans* are close to *H. parvifrons*.

A variant of the pygidial design seen in *melicus* is also apparent in the effaced to semi-effaced *Svenax vafer* sp. nov.

Description: In *Hypagnostus melicus* the rim in the cephalon is very narrow and a match to the wire-like convex marginal furrow—a fine and deep incision. The frontal lobe (Pl. 4, fig. 1) is a different swelling with a pair of lateral caecal ducts at its rear flanks; it is a glandular arrangement seen in *Hypagnostus*

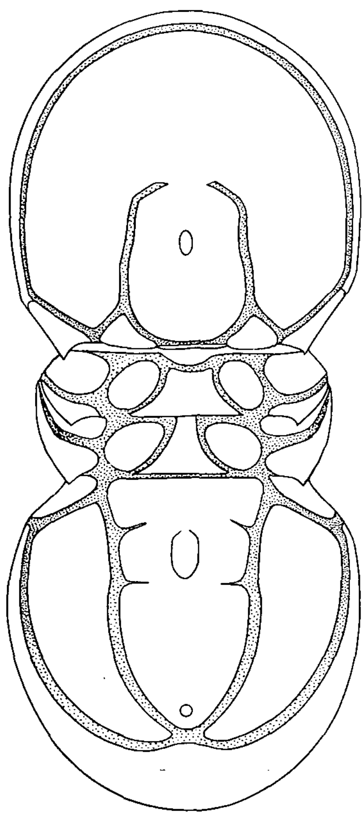

Fig. 20. *Hypagnostus melicus.*

parvifrons cicatricosus Westergaard (op. cit. pl. 5, fig. 1) and in several other forms of *Hypagnostus*, as well as in diplagnostids and ptychagnostids (Öpik, 1961a, p. 414). The posterior glabellar lobe, as long as half the cephalon, has convex flanks and a low angularity of the front, defined by the transverse furrow which is interrupted in the middle, and a low elongate node is placed in front of the midpoint.

The thorax is large, 0.38-0.4x the cephalic length and even larger than in *H. clipeus*.

The rim of the pygidium widens rearward; in the holotype it is wider (longer in the midline) than in others—a sign of some variability within the species. The flanks of the pygidial axis are concave in the middle, widen slightly, and converge in gentle curves at the rear tip. Transverse furrows are not evident externally, but on casts (as in the holotype) lateral shallow furrows mark the anterior annulations. The second annulation has the usual elongate node, and a low node is present close to the tip of the axis.

Comment on illustrated specimens

In the holotype, Plate 5, fig. 6, the shields are disarranged, but measurable, and its correct length is 6.5 mm; the cephalon is fractured and collapsed but the outline of the preglabellar lobe is visible; in the pygidium the axis lost some of its test and shows the transverse furrows disconnected in the middle.

The cephalon Plate 4, fig. 1, CPC 13987, locality M30, in limestone, is 3.3 mm long; the test (punctate) is preserved; a pair of major caecal ducts arise at the rear of the frontal lobe, passing into branches of low relief.

The pygidium Plate 4, fig. 2, CPC 13988, locality M30, associated with the cephalon (above), is 3.3 mm long; the test is preserved and the rim behind the axis is narrower than in the holotype.

Occurrence and age: Hypagnostus melicus sp. nov. occurs in the V-Creek Limestone, localities M462, M30, M41, M136, and M25; the age is Undillan, the Zone of *Goniagnostus nathorsti* and the Zone of *Doryagnostus notalibrae.*

Hypagnostus tjernviki Westergaard, 1946

(Pl. 5, fig. 5)

The illustrated specimen CPC 13998, locality M462, is 3.1 mm long as preserved; it was the first one found in Australia.

Westergaard (1946, p. 49, text-fig. 2) also had in his collection only one pygidium (the holotype) and attributed to the species a quite small cephalon; no other material is known of this species.

The pygidium has parallel lateral margins passing with angularities into the well rounded rear margin. The rim is anteriorly very narrow, but widens rapidly rearward to form a flat and broad crescent; the marginal furrow is well incised but narrow and joins the axial furrow at the rear of the flanks of the axial lobe. Owing to the large size of the axial lobe and the course of the marginal furrows the pleural lobes are exceptionally narrow and short. The axial lobe, as wide as 0.5x the width of the shield, has parallel flanks and a round rear intruding the crescent of the rim; a weak elongate median node is apparent in the anterior part of the axis; lateral furrows are absent.

The cephalon is slightly fractured longitudinally. Its margin is rounded, and the rim narrow. The glabella (the posterior glabellar lobe) is short, about 0.45x the cephalon, and a vestigial anterior glabellar lobe is apparent. Some differences from Swedish specimens are present: (1) the pygidial margin in the holotype curves evenly, without lateral angularities; (2) the axial node is circular, and not elongate; and (3) the preglabellar median furrow in the Swedish cephalon corresponds to a mere fracture in our specimen, and its glabella is longer, probably on account of its well developed anterior lobe, which is, however, confluent with the posterior.

If the cephalon illustrated by Westergaard belongs to a specimen having the structure of the holotype pygidium then two antipodal species may have existed having almost identical pygidia. I think also that the pygidial structure in *Hypagnostus tjernviki* and *Hypagnostus parvifrons* and its allies is rather dissimilar, casting doubt regarding the generic classification of the former.

Occurrence and age: The illustrated specimen attributed to *Hypagnostus tjernviki* comes from sites M462 and M89 in the V-Creek Limestone and the Undillan Zone of *Goniagnostus nathorsti*; in Sweden it is younger by one zone (the *Leiopyge laevigata* Zone).

Genus **Cotalagnostus** Whitehouse, 1936

Cotalagnostus sp. aff. **lens** Grönwall, 1902

(Pl. 4, fig. 3)

The illustrated pygidium, CPC 13989, locality M41, V-Creek Limestone, is 3.4 mm long. Its axis is long, reaching with its acute tips close to the marginal furrow, prominent and relatively broad; its lobes are indicated only by vestigial lateral furrows, and the median node is very small. The rim is downsloping and narrow; marginal spines are absent. The general aspect indicates a species of *Cotalagnostus* but in the absence of a cephalon this generic classification remains inconclusive. In passing, Whitehouse (1936, p. 93, pl. 9, fig. 11) described a fragmentary cephalon from Queensland as *Cotalagnostus* aff. *kushanensis* (Walcott) from the Inca Formation; it seems, however, the cephalon of an undescribed species of *Hypagnostus*. To conclude, the two specimens so far recorded are insufficient evidence of the occurrence of *Cotalagnostus* in Australia.

The age of the described pygidium is the Zone of *Doryagnostus notalibrae.*

Genus **Tomagnostella** Kobayashi, 1939

Kobayashi (1939, p. 150) selected *Agnostus exsculptus* Angelin, 1851 (currently regarded as *Hypagnostus*) as the type species of his new genus; the lectotype of *Hypagnostus exsculptus,* however, was designated and illustrated seven years later by Westergaard (1946, p. 50, pl. 6, figs. 35a, b). It is a cephalon with regular and deep scrobicules; the glabellar front is angular and the glabella is expanded in the middle; a median deep scrobicule is developed in the position of the preglabellar median furrow. Westergaard also attributed three pygidia to *exsculptus* but queried their specific identification. In these pygidia the axis is long, slender, and pointed in the rear; it is also trilobate in a ptychagnostid style. The best preserved pygidium (op. cit., pl. 6, fig. 5) differs little from pygidia attributed to *Hypagnostus nepos* (Brögger). The remaining two pygidia differ in having the tip of the axis depressed; these may belong to a separate species whose cephalon, also attributed to *exsculptus,* is illustrated in Westergaard's (op. cit.) plate 6, fig. 1; it is distinguished by a straight (not angular) transverses glabellar front. In passing, not the lectotype but this cephalon represents *Tomagnostella exsculpta* in Harrington et al. (1959, p. 0186).

Diagnosis (compiled herein): *Tomagnostella* embraces agnostid species with a short glabella (short of the frontal glabellar lobe) distinguished by a long trilobate pygidial axis whose middle annulation is constricted and the posterior lobe is semielliptical and pointed in the rear; in the type species (*Hypagnostus exsculptus* Angelin) the glabellar front is angular ('trigonal'), as it is in *Hypagnostus sulcifer* and

H. nepos, which possess the pygidial structure as above; attributable to *Tomagnostella* are also forms with a straight glabellar front.

Differential diagnosis: Tomagnostella is based in the first place on the structure of its pygidial axis. In *Hypagnostus,* the frontal glabellar lobe is subdued or even effaced, but the pygidia attributed to *Hypagnostus* have a peronopsid appearance; in *Tomagnostella,* however, the pygidial design is ptychagnostid. Furthermore, in *Hypagnostus* the anatomy of the axial part of the glabella under the test of the anterior glabellar lobe remains unreduced, but in *Tomagnostella* (*Hypagnostus exsculptus*), according to Öpik (1961a, p. 413-414), the anterior part of the glabella (the frontal lobe) is replaced by pleural glands (caeca).

Suprageneric classification

Westergaard (1946, p. 44) regarded *Tomagnostella* as a synonym of *Hypagnostus,* although he recognised the ptychagnostid character of its pygidium and the general resemblance of full-grown specimens of *Tomagnostella exsculpta* and *Ptychagnostus convexus* (a species of *Onymagnostus* nov.). Kobayashi (1939) exempted *Tomagnostella* from *Hypagnostus* but placed it in the Tomagnostinae without a reference to the character of the pygidium; I prefer the subfamily Ptychagnostinae on the evidence of the pygidial structure exemplified in *Tomagnostella nepos,* which is described below: moreover, in *Hypagnostus* a different, 'peronopsid' pygidium is evident. Regarding the systematics and structure of the Tomagnostinae see Öpik (1963, p. 34, and 1967, p. 81).

The known species of *Tomagnostella* occur mainly in the late Middle Cambrian (*nathorsti* and *laevigata* Zones) and one is early Upper Cambrian in age. To speculate, *Tomagnostella* may represent a separate stock of agnostids with an originally short glabella.

Species attributable to Tomagnostella:

The following species studied by Westergaard (1946) have the characteristic pygidium, and all were traditionally included in *Hypagnostus*: *H. exsculptus* (with its subspecies *germanus*), *H. nepos, H. denticulatus,* and *H. sulcifer* (with its subspecies *integer*); the pygidia of *germanus* and *integer* and of *H. scrobiculatus* are unknown yet. A pygidium attributed by Westergaard (op. cit., pl. 6, fig. 14) to *sulcifer* has a subcentral node on the posterior axial lobe and belongs to some other species: it may represent a regular ptychagnostid, and another (ibid., fig. 11) belongs to an indeterminate *Ptychagnostus*; the pygidium (ibid., fig. 13) should be accepted as *sulcifer.* Furthermore, attributable to *Tomagnostella* are the early Upper Cambrian *Hypagnostus durus* Öpik (1967) and possibly the Middle Cambrian *H. willsi* Öpik (1961b); *Hypagnostus hippalus* Öpik (ibid.) is a *Tomagnostella* with the pygidium effaced.

The oldest recorded species is *Tomagnostella scrobiculata* (Westergaard) followed by *T. nepos*; outside Scandinavia *nepos* has been found in Queensland, and *T. exsculpta* in northeastern Siberia (Pokrovskaya, 1958). Borovikov & Kryskov (1963) described from the early Upper Cambrian of Kazakhstan under the name *Hypagnostus kendectasicus* a species with a *Tomagnostella*-like cephalon and a pygidium with a very short, narrow, and parallel-sided axis; it may represent a separate genus.

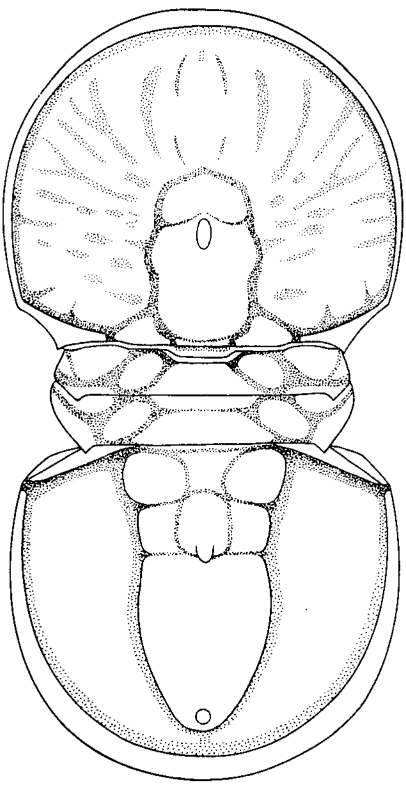

Fig. 21. *Tomagnostella nepos.*

Tomagnostella nepos (Brögger, 1878; Westergaard, 1946)
(Pl. 67, fig. 5: Text-fig. 21)

The type specimen of *Agnostus parvifrons* var. *nepos* Brögger (1878, Pl. 6, fig. 1) is a complete exoskeleton; the illustration is inexact, but the form is identifiable with the aid of its Latin diagnosis. Brögger is the original author; Westergaard, however, is the author of the species taxon *nepos,* having disposed of the noncommittal designation 'var.' (variety) (Westergaard, 1946, p. 48).

The examined Australian material comprises some six complete exoskeletons as well as several isolated cephala and pygidia; the largest exoskeleton, CPC 14361 about 7.6 mm long, is illustrated; it comes from site M195.

The cephalon and the pygidium are equal in size. The cephalon is quite close to the holotype of *Tomagnostella exsculpta* (Westergaard, 1946, pl. 5, fig. 35), whose glabella, however, is large and the scrobicules very strong; in *nepos* (op. cit., pl. 5, fig. 7, cephalon, and figs. 6 and 8, pygidia) the glabella is smaller and the scrobicules are weak or absent. *T. nepos* is therefore the best choice for the material in hand.

The specimen Plate 67, fig. 5, is unevenly distorted, but its test is mostly preserved. The cephalic scrobicules consist of scattered weak grooves and dark lines exaggerated in Text-figure 21. The cephalic rim is narrow and the glabella slightly shorter than in Westergaard's specimen. The glabellar front is angular, the forward placed node is elongate, and the glabella in front of the node is slightly narrower than the rest; in the rear it is broadly rounded and laterally expanded in the middle. The pygidial rim is narrow but widens slightly rearward; there is a pair of posterolateral marginal angulations, seen also in Westergaard's pygidia mentioned above. The axial lobe is long, almost reaching the border; its posterior tip is rounded and carries a relatively prominent terminal node. The two transverse furrows of the axis are distinct; the axis is narrowest about the middle lobe, which has a median node drawn out into a blunt and short spine. The thorax, 0.34x the cephalon in length, has no axial spines or nodes, the fulcral spines are short, and its middle axial part is relatively wide; it is reminiscent of the thorax of such Ptychagnostinae as *Onymagnostus mundus* (Text-fig. 34), *Myrmecomimus* (Text-fig. 42) or *Leiopyge cosfordae* (Text-fig. 52), but also of non-spinose Agnostidae in general.

Occurrence and age: Tomagnostella nepos Westergaard occurs sporadically in the upper part of the V-Creek Limestone in association with *Goniagnostus nathorsti, G. scarabaeus,* and their associates; it is present in collections M57 (CPC 14370) and M195; its age is the late Undillan Zone of *Goniagnostus nathorsti,* as in Sweden.

Genus **Grandagnostus** Howell, 1935
Grandagnostus imitans, Öpik, 1961
(Pl. 22, fig. 4)

The illustrated exoskeleton CPC 14104 is 7.5 mm long; it comes from the V-Creek Limestone, locality M41—the original site and stratum of the type material (Öpik, 1961b, pp. 65-67). Its collapsed test shows characters supplementing the original description: (1) the test, including the thorax, is punctate; (2) the pygidial posterolateral margin shows a pair of tiny angulations — the 'beds' of marginal spines; and (3) the thorax is very short, about 0.23x the cephalon in length. In passing, it is still longer than in *Grandagnostus maja* (Pokrovskaya, 1958, p. 50; pl. 4, fig. 10), whose thorax is 0.2x the cephalon.

The age of *Grandagnostus imitans* is Undillan.

Subfamily **EUAGNOSTINAE** nov.

The type genus of the subfamily Euagnostinae is *Euagnostus* Whitehouse, originally a monotypical genus based on the species *opimus.*

Diagnosis: The known species of Agnostidae assigned to the subfamily Euagnostinae have the following common characters: (1) a preglabellar median furrow, which can be incomplete or fading in some forms; (2) a bluntly pointed (angulate) or even rounded glabellar front; (3) a rounded glabellar rear; (4) a pygidial axis with short lateral or transverse furrows; (5) tapering to a pointed tip in its posterior half which does not reach the border but is followed by a median furrow; (6) a transverse depression close to the axial end, with a central node or knob (rosette, or the knob-and-rosette structure). All known species are forms en grande tenue, but with short cephalic spines and without a median spine in the thorax. The concept of the subfamily comprises the diagnosis of its genera and species.

The aggregate consists of ten named species distributed over three genera as follows: *Euagnostus opimus, E. certus* nov., *E. neptis* nov., *E. levifrons* nov., *E. glandifer* nov., and *E.* sp. aff. *opimus*; *Rhodotypiscus* gen. nov., with *R. nasonis* nov. and *R.* sp. nov. aff. *nasonis*; *Doryagnostus incertus, D. magister, D. notalibrae* nov., *D. solidus* nov., *D.* nov. aff. *incertus,* and *D.* aff. *notalibrae.*

The difference between Euagnostinae and other subfamilies of the Agnostidae (Ptychagnostinae and Quadragnostinae) is discussed in the description of the genera *Euagnostus* and *Rhodotypiscus*. The subfamily classification of *Euagnostus* has been hitherto inconclusive, and *Doryagnostus* had a place in the Ptychagnostinae.

Differential diagnosis of the Euagnostinae (a recapitulation)

As a subfamily of the Agnostidae the Euagnostinae can be placed as a separate column between the Quadragnostinae and the Ptychagnostinae in the 'Tabular classification of Agnostids' of Öpik (1967, facing page 66). The axial lobe of Euagnostinae (*Euagnostus*) is of a different shape from Quadragnostinae (*Peronopsis*) (VII and II respectively, Text-fig. 2); in two species of the Euagnostinae (*Rhodotypiscus nasonis* and *Doryagnostus solidus*) the frontal glabellar lobe is about as blunt as in *Peronopsis*—a character which may become confusing if taken for a sign of a taxonomic affinity. The axial lobe of *Euagnostus, Rhodotypiscus* (Text-fig. 23), and *Doryagnostus* (Text-fig. 24) resembles, however, *Triplagnostus* (III, Text.-fig. 2)—an indication of an affinity of the subfamilies Euagnostinae and Ptychagnostinae. The glabellar front in *Rhodotypiscus* is unusually blunt, but the position of the glabellar node in the rear and the structure of the pointed pygidial axis are characters found in the ptychagnostids. The pygidial axial rosette, which is weak in *Euagnostus* and prominent in *Rhodotypiscus* and *Doryagnostus* (Text-fig. 24), emerges once more independently in *Goniagnostus* and, fortified, in *Allobodochus* while remaining absent in the rest of the known Agnostidae; the rosette is a sign of an affinity originating in a similar but separate development in the organisation.

Genus **Euganostus** Whitehouse, 1936

The type species of *Euagnostus* is *E. opimus* Whitehouse (1936, p. 87); Whitehouse (1939, p. 260) mentioned also the occurrence of another form as *Euagnostus* sp. in the V-Creek Limestone, and consequently younger than the type species. Whitehouse (1936) placed *Agnostus exaratus* Grönwall tentatively in *Euagnostus interstrictus* White as being 'most similar to *E. opimus*'; in these species and in *opimus* the pygidial axis tapers to a point—a structure possible in different agnostid stocks. *A. exaratus*—Illing's (1959) substitute name for *Acadagnostus scutalis* (q.v.)—has a rounded glabellar front different from the pointed front of *opimus,* no pygidial marginal spines, and a different pygidial shape. Nevertheless, *Acadagnostus* Kobayashi (1939) should be studied once more regarding its possible connection with the senior *Euagnostus* (1936). A similar study is needed regarding *Agnostus interstrictus,* whose placing in *Peronopsis* by Palmer (1954; Robison, 1964) is even less acceptable than in *Acadagnostus.*

The species of *Euagnostus* are listed in the description of the subfamily Euagnostinae; furthermore, from siltstone (and chert), locality M59, of the *Ptychagnostus punctuosus* Zone a pygidium (CPC 14371) reminiscent of

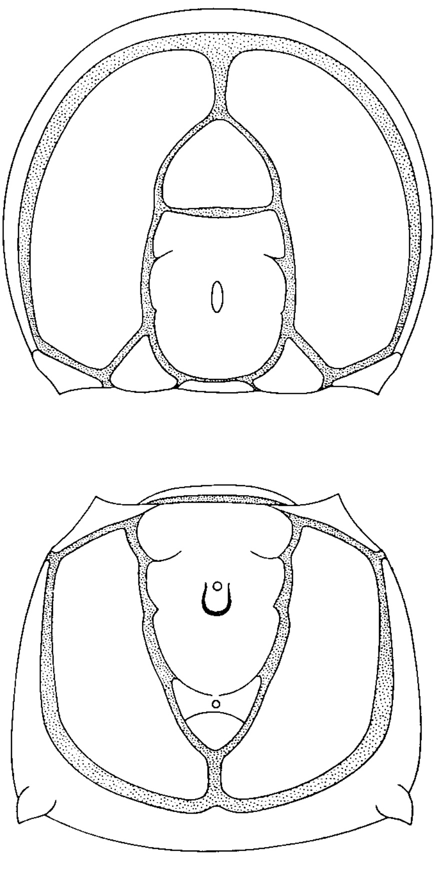

Fig. 22. *Euagnostus opimus.*

E. opimus has been obtained; it differs, however, from *E. opimus* by its visibly rearward converging lateral margins.

Diagnosis (herein compiled): In addition to the characters of the subfamily Euagnostinae the species of the genus *Euagnostus* are distinguished by a moderately tapering glabella, a rearward expanding and wide pygidial rim with short to rudimentary marginal spines, and a well fused pygidial axis with more or less even (not baroque) flanks converging to the acute apex; its rosette (knob-and-rosette structure) has externally an inconspicuous relief. The deep furrows are externally relatively narrow, but very wide in casts owing to the thickness of the test.

Euagnostus opimus Whitehouse, 1936

(Pl. 13, figs. 1-8; Pl. 14, figs. 1-4; Text-fig. 22)

Material: Illustrated are (1) the holotype pygidium of *Euagnostus opimus* Whitehouse (1936, pl. 8, fig. 11) and the associated cephala (ibid., fig. 10), courtesy of Dr F. W. Whitehouse; Dr P. Jell kindly prepared the rubber casts on my request from the originals, which are kept in the collections of the University of Queensland, Brisbane; (2) two complete specimens, two pygidia, and two cephala supplementing the original types; and (3) four cephala and one pygidium each deviating in a different manner from the rest of the material and attributable to *opimus* as its possible variants; in these cephala the large frontal glabellar lobe and its pointed tip are diagnostic of *E. opimus*.

Diagnosis: Whitehouse, op. cit., p. 87. In brief, the species of *E. opimus* is recognisable from the combination of the following characters: (1) the frontal emargination (recess) of the cephalic acrolobe; (2) the tumid large and well defined frontal glabellar lobe, 0.3-0.37x the glabella in length; (3) the externally shallow preglabellar median furrow; (4) the pygidial axis, tapering to a point and with gently curving flanks; (5) the short thorax, about 0.25-0.26x the cephalic length.

Differential diagnosis: The frontal glabellar node is small in *E. certus* sp. nov. and almost effaced in *E. neptis* sp. nov. whose preglabellar median furrow is effaced also. In these two species the thorax is also longer than in *E. opimus*. The pygidial axes in *E. opimus* and in *E. neptis* are similarly shaped, and different from *certus*.

In all species of *Euagnostus* the test is thick, especially along the furrows; the pygidial spines are small, and the rosette on the rear of the axis is inconspicuous: it is easily lost in corroded tests.

Description: Euagnostus opimus is a fairly large agnostid attaining some 10 mm in length. The cephalon and pygidium are about equal and the thorax is short, about 0.25-0.26x the cephalon; it is shorter than in *Euagnostus certus* sp. nov.

The cephalon in its outline is a larger segment of a circle; its border is quite wide with a convex rim and deeply impressed marginal furrow, and closely similar to *Doryagnostus incertus*. The preglabellar median furrow, shallow externally and deeper in internal casts, flares forward widely and forms an emargination of the front of the acrolobe which remains higher than the expanded floor of the marginal furrow. The cheeks are smooth, except for faint arcuate scrobicules observable in some specimens.

The glabella is relatively long and prominent, especially in the posterior, almost bulbous half of its rear lobe; as a whole it tapers forward moderately and is slightly expanded about the median node; this node itself is elongate and placed behind the middle of the rear lobe; a pair of oblique lateral furrows is present about half way between the node and the transverse furrow. The glabellar rear is well rounded and even globose. The frontal glabellar lobe is semielliptical, tumid, surrounded by deep furrows and has an angular to pointed front, and is large but variable, some 0.33-0.37x the glabellar length. The basal lobes are relatively small but prominent and swollen; the connective band (occipital band, Robison, 1964; occipital collar, Öpik, 1967) is narrow, arched, and separated from the basal lobes by shallow furrows. The cephalic spines are short and curved.

The pygidium appears almost rectangular; the lateral margins, however, are slightly convex and diverge rearward, the posterior margin between the spines is arched moderately rearward, and the marginal spines are very short and swollen, partly arising from the rim and not direct from the very margin itself, and are placed well in the rear. The shoulders are thick and the fulcral prongs are prominent and forward inclined, almost horn-like, points. The rim is barely convex, flatter than the cephalic rim. The marginal furrow, externally deep and of variable width, is lined by a rather solid part of the test and without that test is manifest as a broad channel seen in the holotype. The postaxial median front is simliar in structure. The axial furrows are externally narrow and deep and fortified by a lining of thickened test. The axis is long and tapers to a pointed apex but is variable in shape; mostly triangular, its flanks in some specimens can appear subparallel about the second axial lobe. The transverse furrows are quite shallow but clearly define the lobes; these are low and the anterior lobe is the widest. The median node is moderate in relief and is confined to the second lobe. The rear of the axis is slightly drawn out; the rosette-and-knob structure is perceptible in whitened tests, and the knob (or node) is placed from the apex at a distance of 0.2x the length of the axis. The front of the axis is straight, without an articulating recess; the articulating furrow is narrow and provided with a pair of lateral elongate pits; the articulating half-ring (Pl. 13, fig. 6) is elevated, bow-shaped, and has a retral projection.

The test is thick and punctate.

Comment on illustrated specimens

The holotype pygidium, Plate 13, fig. 2, is 3.5 mm long; its identification features (small marginal spines, strong marginal furrow, axis tapering to a point) are sufficiently well preserved; moreover, on the rubber cast itself the rosette-and-knob structure of the rear of the axis (see Text-fig. 33), which is anyway of low relief in *opimus,* is visible in suitable illumination. It is exfoliated and the marginal furrow, having lost its thick test, appears very wide in the cast.

The cephalon associated with the holotype (Whitehouse, 1936, pl. 8, fig. 10) is 4.0 mm long in the rubber cast (Plate 13, fig. 1). The preglabellar median furrow is exaggerated because the test is lost on its floor, but is still preserved on the flanks of the furrow; the depth of the furrow in the picture is actually reduced by the double thickness of the test; the frontal glabellar lobe is 0.35x the glabella in length. The median node is lost. The complete exoskeleton Plate 13, fig. 7, CPC 14057, Currant Bush Limestone, locality M124 is 6.5 mm long; it is crushed, but the emargination (recess) of the front of the acrolobe is evident; the preglabellar median furrow, owing to the preserved test, is shallow; the median node in front of the midpoint of the posterior glabellar lobe deviates from the central position seen in other cephala. The marginal furrow, having its test preserved, is narrower than in the exfoliated holotype. In the cephalon some of the matrix is left in the frontal part of the furrow because it is removable only with the test. The frontal lobe (flattened) is 0.33x the glabella. Locality M124 is situated in the area of outcrops which produced the original types.

The next four specimens came from locality M180, from strata attributed to the Currant Bush Limestone. In these specimens the test is intact.

The pygidium Plate 13, fig. 6, CPC 14056, is 2.8 mm long. The axis is relatively slender. Of the associated pygidia the largest is 4.0 mm and the smallest 1.6 mm long; the axis is short and gibbose.

The pygidium Plate 13, fig. 5, CPC 14055, is 3.2 mm long. The marginal spines are of the same structure as in the holotype; the fulcral prongs are rather prominent and inclined forward. The rosette-and-knob structure of the axis in the two described and other associated pygidia is seen in Text-figure 22.

The next two cephala have retained the test, which is punctate; they are both about 4.3-4.4 mm long.

The cephalon Plate 13, fig. 3, CPC 14053, is undeformed; the frontal recess of the acrolobe is clear; the preglabellar median furrow is visible as a shallow depression; the frontal glabellar lobe is 0.37x the glabella in length.

The cephalon Plate 13, fig. 4, CPC 14054, is slightly sheared (askew to left). The frontal recess is weak; the preglabellar median furrow visible at the glabellar tip changes forward into a broad flare as in the holotype; the frontal lobe is 0.33x the glabella. Arcuate scrobicules are faintly indicated off the anterolateral confines of the frontal glabellar lobe.

The next four cephala and one pygidium are attributed to *E. opimus,* but this assignment can be queried; they occur in association with other described specimens of *opimus.*

The cephalon Plate 13, fig. 8, CPC 14058, locality M123, is 4.0 mm long; its test is preserved, the frontal lobe is 0.37x the glabella in length, and the preglabellar median furrow is very deep; a variant of *E. opimus* is therefore suspected.

The cephalon Plate 14, fig. 2, CPC 14060, locality M180, is 3.0 mm long; it is the only known specimen with a visibly scrobiculate test; its frontal lobe is 0.34x the glabella in length.

The cephalon Plate 14, fig. 3, CPC 14061, from M180, is 2.5 mm long. Its marginal furrow is narrow and a glabellar node is absent; its frontal lobe is 0.37x the glabellar length; it may belong to a different species.

The cephalon Plate 14, fig. 4, CPC 14062, from M180, about 3.1 mm long, has a slender glabella, probably the result of lateral compression; the frontal lobe is 0.36x the glabellar length.

The complete exoskeleton Plate 14, fig. 1, CPC 14059, locality M180, is 8.0 mm long; the matrix is laminated silty limestone. The test is slightly sheared, flattened and creased. At first it could be mistaken for *Onymagnostus semiermis* (Pl. 54, figs. 7, 8), but the frontal emargination of the cephalic acrolobe, the pointed glabellar front, the simple basal lobes, and the undeveloped axial transverse furrows are characters of *Euagnostus opimus.*

The complete exoskeleton CPC 14372 (not illustrated), in siltstone, site M192, is 6.2 mm long.

Occurrence and age: Euagnostus opimus occurs in the Currant Bush Limestone M123 and

124, and in limestone attributed to it (M180), and is rare in the shale and siltstone of the Inca Formation (M176, M412, and M192); it designates the Floran Zone of *Euagnostus opimus,* the substitute name for the *Hypagnostus parvifrons* Zone in Scandinavian terms.

Euganostus sp. aff. **opimus**

(Pl. 15, fig. 4)

The illustrated and sole available cephalon, CPC 14071, locality M65, is 4.5 mm long. It has retained its test and the original convexity. In general, it tallies with the cephala of *Euagnostus opimus* except for the following peculiarities: (1) the glabella has a somewhat oval outline; (2) the transverse glabellar furrow fades out abaxially; and (3) the median node is placed in front of the midpoint of the posterior glabellar lobe.

In cephala attributed to *Euagnostus opimus* the flanks of the glabella are about straight, the transverse furrow is evenly deep, and the median node is central. In the exoskeleton Plate 13, fig. 7, the median node is more advanced—a derivation from other specimens of *E. opimus.* In the absence of a pygidium the identity of *Euagnostus* sp. aff. *opimus* remains inconclusive: *Doryagnostus* seems also an alternative, as for example *D. notalibrae* (Pl. 19, fig. 2) whose glabella, however, is less oval and a little more slender than the glabella of *Euagnostus* sp. aff. *opimus.*

Occurrence and age: Euagnostus sp. aff. *opimus* comes from a sandy limestone (an interbed in the Age Creek Formation), M65; the age is the Undillan Zone of *Doryagnostus notalibrae.*

Euagnostus certus sp. nov.

(Pl. 14, figs. 6-9; Pl. 42, fig. 6)

Material: Illustrated are two complete specimens and three cephala; the earliest known pygidium is mentioned in the comment (below); cephala and pygidia occur in several sites but are in an inferior state of preservation.

Holotype: The complete specimen Plate 14, fig. 6, CPC 14064 in limestone, locality M124 is selected as the holotype.

Diagnosis: Euagnostus certus nov. is distinguished by its small frontal glabellar lobe (0.25-0.28x the glabella in length), evenly curved front of the cephalic acrolobe (it is not emarginate), and pygidial axis with parallel flanks in its anterior half.

Differential diagnosis: In *Euagnostus opimus* and *E. neptis* the frontal glabellar lobe is visibly longer than in *E. certus* and the pygidial axis tapers more or less evenly rearward.

Description: The shape of the shields, the thickness of the test, the structure of the deep furrows, the position of the median nodes on the glabella and the pygidial axis, and the weakly developed rosette-and-knob are the same as in *E. opimus* (q.v.). The pygidial marginal spines are retral and slightly longer than in the other species and appear as extensions of the lateral rim in the whole width. The thorax, about 0.3x cephalic length, is slightly longer than in *E. opimus* and shorter than *E. neptis.*

Comment on illustrated specimens

The two complete specimens come from the Currant Bush Limestone, locality M124. The holotype is 4.7 mm long; the preglabellar median furrow is visible on the right side of a fracture which should not be taken for the furrow. The test is thick and partly preserved on the cephalon.

The complete specimen Plate 14, fig. 7, CPC 14065, associated with the holotype (in the same bedding plane, and same piece of limestone) is 6.0 mm long; the tagmata retain their original arrangement (ready for articulation); the glabellar node is visible just behind the larger 'node' which is the cast of a hole in the test; the preglabellar furrow is partly masked by a longitudinal fracture.

The cephalon Plate 14, fig. 9, CPC 14067, locality M191a, is 2.2 mm long; it is aberrant in having a rounded glabellar front.

The cephalon Plate 14, fig. 8, CPC 14066, locality M191(a), limestone of the Inca Formation, is 2.2 mm long; it is the youngest known specimen (Zone of *Ptychagnostus punctuosus*).

One pygidium, CPC 14373 (not illustrated), 3.0 mm long, has been found in limestone attributed to the Currant Bush Limestone, locality M179; its age is the Zone of *Ptychagnostus atavus.*

The cephalon associated with *Ptychagnostus atavus coartatus* in Plate 42, fig. 6, is about 3.0 mm long. Its glabellar structure is close to *Euagnostus opimus;* it differs, however, from *opimus* in having a narrow border and externally a deep preglabellar median furrow with a modest frontal flare. The test is minutely punctate. The narrow border, especially with the very narrow marginal furrow, renders the generic classification somewhat inconclusive; a form of *Onymagnostus* gen. nov. remains a possible alternative.

Occurrence and age: Euagnostus certus occurs in the Currant Bush Limestone (locality M124), in some other sites in strata attributed to that formation (M179; M180; M183), and in the Inca Formation (M425); it covers the range of three zones (*P. atavus, Euagnostus opimus,* and *P. punctuosus*).

Euagnostus neptis sp. nov.
(Pl. 15, fig. 1)

Material: The examined material consists of some ten complete specimens; one of these, CPC 14068, is illustrated and selected as the holotype.

Diagnosis: In *Euagnostus neptis* the frontal glabellar lobe is depressed and almost flat and the furrow surrounding it is very shallow; the preglabellar median furrow is also very shallow, close to vestigial; the pygidial marginal spines are very small and visible only under a magnifier; the rosette-and-knob structure in the rear of the pygidial axis is rather weak but still discernible in whitened specimens.

Differential diagnosis: At first the cephalon can be interpreted as of *Hypagnostus*, retaining the vestige of the frontal glabellar lobe in the manner of *Hypognostus parvifrons;* it is, however, surrounded by a proper furrow recognisable on the internal side as a faint U-shaped ridge—a structure unknown in *Hypagnostus*. The border in the cephalon and pygidium, the furrows, and the shape of the axis are about the same as in *Euagnostus opimus*, whose exoskeleton, however, indicates a form en grande tenue, without any effacement of relief.

Description: The anterior glabellar lobe has a pointed front and is large, about 0.32x the glabella in length; the median node on the posterior glabellar lobe is elongate and prominent and stands in front of the midpoint, farther forward than in the other species. The thorax is relatively large, about 0.3x the cephalon in length; in the pygidium the axial median node is quite prominent. The internal structure of the frontal glabellar lobe, defined by a low U-shaped ridge (externally a furrow), can be seen on a specimen associated with the holotype; another complete specimen, CPC 14374, 10.6 mm long displays the U-furrow and the preglabellar median furrow faintly impressed; another specimen, CPC 14375, about 7.5 mm long, is similar.

Occurrence and age: The holotype and the associated specimens of *Euagnostus neptis* come from a single bed of the V-Creek Limestone, locality M243; its age is the Undillan Zone of *Ptychagnostus punctuosus*.

Euagnostus levifrons sp. nov.
(Pl. 15, figs. 2, 3)

Material: The described material consists of a damaged exoskeleton and one isolated pygidium, in limestone.

Holotype: The exoskeleton, Plate 15, fig. 3, CPC 14070, locality M409, is the holotype.

Diagnosis: Euagnostus levifrons sp. nov. is distinguished by the total absence of a preglabellar median furrow, combined with a well defined glabella and a slender subtrigonal and pointed pygidial axis.

Differential diagnosis: In *Euagnostus opimus* the preglabellar median furrow is externally shallow, but well impressed on the internal cast; in *E. neptis* the frontal glabellar lobe is depressed and the preglabellar median furrow, although vestigial, is still present; and *E. certus* nov. is distinguished by its short frontal glabellar lobe and distinct preglabellar median furrow. Reminiscent of *E. levifrons* is *Agnostus acadicus* var. *declivis* Matthew (1886, pl. 7, figs. 6a and 6b), attributed to *Acadagnostus* by Kobayashi (1939, p. 113); its glabella, however, is short and the pygidial rim narrow (Text-fig. 16); it is unrelated to *Acadagnostus acadicus* (q.v.) both in its correct sense, and in the sense of subsequent interpreters. Somewhat similar is also *'Acadagnostus' scutalis* (q.v.), which differs by its parallel sided glabella.

Description: The holotype exoskeleton has been damaged in a fire, having lost the median part of its pygidial axis. The specimen is 6.2 mm long. In the frontal margin of the cephalic acrolobe a recess is apparent, but it is much weaker than in the other species of *Euagnostus*. The glabella tapers moderately; the frontal lobe, about 0.34x the glabella in length, is larger than in other species of the genus, and the posterior lobe with its lateral expansion about the middle differs little from *Euagnostus opimus*; its median node is low and central. No trace of a preglabellar median furrow is detectable on the matrix of the cast.

In the pygidium the rim widens retrally and seems to possess a posterolateral angulation in the position of the absent marginal spine. The rear of the axis is a little attenuated, the relief of the rosette is weak, and its knob is placed close to the rear, at a distance of 0.2x the axial length from its tip. The shape of the axis differs little from *Euagnostus neptis*. In the thorax, which is about 0.3x the cephalon in length, the lateral axial lobules of the posterior segment are semi-effaced.

The pygidium Plate 15, fig. 2, locality M41, CPC 14069, is 3.5 mm long. The posterolateral angulations of the margin are distinct and the postaxial median furrow does not seem to reach the marginal furrow. In passing, Whitehouse (1939, p. 260) mentioned the occurrence of *Euagnostus* sp. at the road crossing of V-Creek—the site M409 as recorded here. *Occurrence and age: Euagnostus levifrons* sp. nov. is a rare fossil of the V-Creek Limestone; its age is the Undillan Zone of *Doryagnostus notalibrae.*

Euagnostus? glandifer sp. nov.

(Pl. 14, fig. 5; Pl. 22, fig. 3)

Material: The material attributed to the species *glandifer* consists of the two illustrated shields.

Holotype: The cephalon Plate 22, fig. 3, is the holotype, specimen CPC 14103, from locality M180.

Diagnosis: Euagnostus? glandifer has a narrow cephalic rim, a slender glabella, and is distinguished by its depressed and laterally expanded, acorn-shaped frontal glabellar lobe, which is visibly wider than the anterior part of the posterior glabellar lobe. The characters of the pygidium are not included in the diagnosis because a complete exoskeleton alone can provide for evidence of the conspecific nature of the two shields.

Differential diagnosis: The species in hand cannot be attributed to the Ptychagnostinae or the Quadragnostinae; nevertheless it belongs to the family Agnostidae and shares characters with *Euagnostus* such as the frontal recess in the cephalon and the position of the elongate glabellar median node. In the pygidial axis the presence or absence of a rosette cannot be established owing to deformation. The acorn shape of the frontal glabellar lobe is unique; nevertheless, in the specimen of *Rhodotypiscus nasonis* Plate 16, fig. 5, a slight expansion of the frontal glabellar lobe recalls *glandifer.* The name of the genus is queried because *glandifer,* with more material, may demand a generic name of its own. At all events, the concepts of *Euagnostus* cannot depend on the characters of *glandifer.*

Description: The cephalon is 3.8 mm long, with an evenly and moderately convex acrolobe; the rim is narrow and strongly convex, and the marginal furrow is deep and narrow. The posterolateral spines (the left is lost), rising from a narrow base, have developed needle-like tips. The circumglabellar furrow is deep at the flanks of the posterior lobe, shallow at the anterior lobe, and almost faint at the frontal closure; faint also is the preglabellar median furrow, which terminates at the flaring recess in the acrolobe. The basal lobes are triangular, tumid but relatively short. The glabella is slender; its rear is rounded, even obtuse; the median node, a long, narrow, low crest, seems to consist of two parts. The transverse furrow is shallow in the middle; the frontal glabellar lobe is 0.33x the glabellar length.

The pygidium is 2.8 mm long. Its rim is relatively narrow; its marginal spines are short and connected with a low crest on the lateral parts of the rim. The tip of the pointed axial lobe, owing to deformation, appears a little obtuse; the front part of the posterior lobe is laterally expanded. The transverse furrows are weak; the axis is constricted about the second annulation and the anterior annulation is the widest. The median node is clear and raised posteriorly. The acrolobes in both shields are unconstricted; the test is indistinctly punctate.

Occurrence and age: Euagnostus? glandifer comes from locality M180 (limestone attributed to the Currant Bush Limestone, about the Northern Territory boundary in the Lawn Hill Sheet area); it is associated with *Euagnostus opimus;* its age is the Floran Zone of *Euagnostus opimus.*

Genus Rhodotypiscus nov.

The type species of *Rhodotypiscus* is *Rh. nasonis* nov.

Diagnosis: The following combination of selected characters of the type species is diagnostic of the genus *Rhodotypiscus*: (1) the subrectangular cephalon with rounded anterolateral margins (reminiscent of some species of *Peronopsis*) and a glabella with parallel flanks; (2) the retral position of the glabellar median node, close to the posterior pointed culmination of *Triplagnostus*; (3) narrow cephalic and pygidial border usual in Ptychagnostinae and Agnostinae; (4) the trilobate pygidial axis—as in *Euagnostus* and *Doryagnostus;* and (5) the rosette-and-knob structure of the axial rear as in *Euagnostus*, but as prominent as in *Doryagnostus magister* and *Goniagnostus nathorsti.* As a whole *Rhodotypiscus* strikes the eye as a blend of structures found in peronopsids, as well as in *Doryagnostus* and in *Goniagnostus.* Reminiscent of *Rhodotypiscus* is *Doryagnostus solidus* sp. nov. (q.v.).

It is possible that *Peronopsis taitzuhoensis* Lu (1957, pl. 137, 4 and 5), and even more *P.* cf. *taitzuhoensis* Lu sensu Chien (1961, pl. 1, fig. 3), are related to *Rhodotypiscus.*

Rhodotypiscus nasonis sp. nov.

(Pl. 16, figs. 1-5; Pl. 59, fig. 1; Text-fig. 23)

Material: An ample supply of specimens in limestone, siltstone and shale, and in chert has been

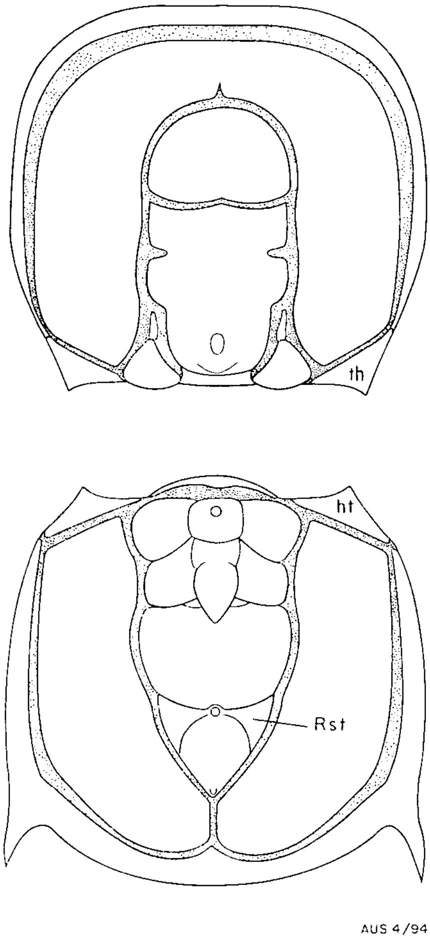

Fig. 23. *Rhodotypiscus nasonis.* **th—cephalic prong; ht—pygidial prong; Rst—rosette.**

studied; the illustrated paradigm comprises three complete exoskeletons, two cephala, and one pygidium.

Holotype: The complete test Pl. 16, fig. 1, CPC 14072, is selected as the holotype.

Diagnosis: The diagnostic characters of *Rhodotypiscus nasonis* are evident from the generic description.

Differential diagnosis: Rh. nasonis is the sole named species of its genus; its difference from the species of related genera (*Euagnostus, Doryagnostus*) is indicated in the generic description, and in the description that follows below.

Description: Rhodotypiscus nasonis is a relatively large agnostid, attaining a length of 10-11 mm. In the cephalon the margin is strongly curved anterolaterally and its outline is subrectangular, unlike the circular curvature of *Euagnostus* and *Doryagnostus;* the rim is narrow and prominent with an abrupt, angular inner edge against the deep and narrow marginal furrow. The front of the acrolobe is straight, or slightly retral, or even a little emarginate, but less than *Euagnostus opimus,* and the preglabellar median furrow is very short. The glabella, about 0.7x the cephalon in length, is prominent and has slightly concave flanks; the frontal lobe is large, 0.36 to 0.38x the glabella in length, with front rounded or a little angular in the middle. In the posterior lobe the lateral furrows are short and deep and tend to join in a shallow depression across the glabella. Behind the furrows the flanks are visibly expanded laterally. In profile the glabella rises rearward in a concave slope to culminate in a low conical summit at the rear; in front of the summit and close to it, but down the slope, stands the inconspicuous median glabellar lobe (Pl. 59, fig. 1). The basal lobes are triangular and swollen but extend forward as depressed attenuated tongues which are separated from the swollen main part by a shallow furrow; consequently, it is difficult to decide whether the basal lobes are simple or double. The tips of a basal lobe nest in recesses of the posterior glabellar flank —a structure known in various agnostids (e.g. *Innitagnostus innitens* (Öpik, 1967, p. 99, pl. 58, fig. 2).

In the pygidium the marginal outline seems more circular than in the cephalon, but the abrupt increase of its curvature at the spines corresponds to the anterolateral curvature of the cephalon; the rim is narrow but widens slightly about the marginal spines. These spines are long (longer than in *Euagnostus*), about as long as in *Doryagnostus*, and in a similar position relative to the moderately arched posterior margin. The marginal furrow is also narrow. The postaxial median furrow is deep and narrow. The axis is slender and as baroque as in *Doryagnostus*. The anterior axial lobe is broad and defined by oblique furrows crossing the crest of the axis; the second axial lobe is narrow, but ill defined by the second transverse furrow; the median node rises retrally and terminates as a short spine. The posterior axial lobe expands behind the axial spine and almost evenly contracts to its pointed tip. The knob of the rosette is placed from the axial tip at the distance of 0.27x the axial length; it is small but rather conspicuous, and set deep in the transverse depression at the contact of the curves facing each other; behind the rosette the attenuated extremity of the axis gains in tumidity as a lobe in its own right: the axial structure of *Rh. nasonis* is confusingly similar to *Doryagnostus;* it differs from *Goniagnostus* as regards its weaker relief of lobes and transverse furrows, and the more retral position of the rosette. The thorax is about 0.3x the cephalon in length. The test is thick and punctate.

Comment on illustrated specimens

The holotype, in limestone, locality M124, is 6.4 mm long; there is an incomplete short preglabellar median furrow; in the posterior glabellar lobe the lateral furrows are connected by a transcurrent depression. In the pygidium the axis seems slender because its right side is pressed down and its flank is invisible from above. The test is preserved; a pygidial marginal spine is prominent.

The complete (but disturbed) specimen CPC 14076, Plate 16, fig. 5 in hard siltstone (almost chert) of the Inca Formation, locality M412, is as a whole about 9.0 mm long; it is an internal cast; some of its features are diffuse, especially the rosette-and-knob structure; the frontal glabellar lobe is wide in the rear; the glabellar median node is preserved.

The complete specimen Plate 16, fig. 4, CPC 14075, in shale of the Inca Formation, locality M412, has an original length of 7.0 mm; it is irregularly flattened; a short preglabellar median furrow is evident.

The cephalon Plate 16, fig. 2, CPC 14073, in hard siltstone (or chert) of the Inca Formation, locality M412, is almost 4.0 mm long. The inner edge of the rim is abrupt; the posterior glabellar summit and the node in front of it are well preserved; the glabellar median furrow is very short, and the frontal glabellar lobe wide.

The cephalon Plate 59, fig. 1, CPC 14317, is 4.2 mm long; the matrix is shale of the Inca Formation, locality M176. The glabellar median node and the posterior summit are strong and the full length of the right basal lobe is visible; the front of the acrolobe is emarginate.

The pygidium Plate 16, fig. 3, CPC 14074, in limestone, locality M124, is 3.0 mm long; its test is intact. The axis, 0.77x the shield's length, is undeformed and the rosette is prominent; there is also an odd median node on the very front of the axis.

Occurrence and age: Rhodotypiscus nasonis occurs in the Inca Formation (very abundant in M176, M412); in a siltstone probably attributable to the Inca Formation (M376); in the Currant Bush Limestone (M124, M150, M176) and in strata attributed to that formation (M180, M183); also in the Age Creek Formation (M160) and in some more places. It is a common species of the Floran Zone of *Euagnostus opimus.*

Rhodotypiscus sp. nov. aff. **nasonis**

(Pl. 17, figs. 1, 2)

The illustrated exoskeleton, CPC 14077, has a length of 7.00 mm (corrected for the loss of a segment of the thorax); it is deformed—the left side of the acrolobe overrides the flank of the pygidial axis. It differs from *Rhodotypiscus nasonis* by the rounded strawberry shape of the frontal glabellar lobe, the shorter pygidial axis (0.7x the shield's length), and the rather retral position of the node of the rosette, which itself is also inconspicuous. The structure of the occipital part of the glabella, which could not be satisfactorily dematricated in the mould, remains unknown.

Occurrence and age: The specimen comes from the V-Creek Limestone, locality M243; its age is the Undillan Zone of *Ptychagnostus punctuosus.*

Genus **Doryagnostus** Kobayashi, 1939

The type species of *Doryagnostus* is *Agnostus incertus* Brögger (1878, p. 70, pl. 6, fig. 4). Kobayashi repeated Brögger's drawing in his 'Table showing the classification of Agnostida' and placed *D. incertus* (Brögger) in the subfamily Triplagnostinae. Kobayashi (1939b, p. 579) subsequently indicated that *Ceratagnostus* Whitehouse (1939) is a junior synonym of *Doryagnostus;* this synonymy, accepted also by Westergaard (1946, p. 82), cannot be contested. It is, however, a subjective synonymy because the type of *Ceratagnostus* is *C. magister* Whitehouse, and not *incertus* Brögger. According to Westergaard (op. cit., p. 83) the species *magister* is also a synonym of *incertus* Brögger, which name therefore replaces *magister* in the current Australian literature. Westergaard regarded *Doryagnostus* as a genus of the Ptychagnostinae, which coincides (subjectively) with the Triplagnostinae of Kobayashi. Öpik (1961b, p. 77; 1967, table facing page 66) employed the same classification for *Doryagnostus.*

In retrospect, *Doryagnostus incertus* was classified with the ptychagnostids (1) because it could not be accommodated in any of the other known subfamilies; (2) because the absence of axial spines and the design of the cephalon suggest a comparison with *'Triplagnostus'* (here *Onymagnostus*) *hybridus* and its allies; (3) because the resemblance of the structure of the pygidial axial rear (the rosette-and-knob) between *Doryagnostus* and *Goni-*

agnostus was taken for a sign of a close affinity; and (4) because this axial structure was interpretable as an exclusive innovation of the *Ptychagnostus* stock, developed in *Goniagnostus*. The external manifestation of the rosette-and-knob structure is, however, polyphyletic as discussed elsewhere. In brief, it occurs in three independent stocks: (1) in the *Euagnostinae* including *Doryagnostus*; (2) in late Middle to Upper Cambrian *Goniagnostus*; and (3) in the Upper Cambrian *Glyptagnostus* and *Agnostardis* (Öpik, 1963).

The concept of the genus Doryagnostus

(1) The outline of the cephalon is a larger arc of a circle (as in *Euagnostus*, but not in *Rhodotypiscus*);

(2) The preglabellar median furrow is long (as in *Euagnostus* but not in *Rhodotypiscus*);

(3) The glabellar frontal lobe is bluntly pointed (as in *Euagnostus*);

(4) The posterior glabellar lobe has parallel flanks (as in *Rhodotypiscus*);

(5) The pygidial marginal spines are long and retral (as in *Rhodotypiscus* but not *Euagnostus*);

(6) The transverse furrows and lobes of the pygidial axis are weak (as in *Euagnostus* and *Rhodotypiscus*, and different from the well expressed lobes and furrows in the ptychagnostids).

(7) The pygidial axis, constricted about the second lobe and attenuated in the rear which carries the transverse rosette, has a baroque appearance and is close to *Rhodotypiscus*.

The known species of *Doryagnostus* are: *Agnostus incertus* Brögger; *Ceratagnostus magister* Whitehouse; *Doryagnostus notalibrae* sp. nov., and *Doryagnostus solidus* sp. nov.; an undescribed species seems also present in Utah, represented by a cephalon (Robison, 1964, pl. 79, fig. 11) attributed to *Ptychagnostus hybridus* and a pygidium (ibid., fig. 8) of *?Ptychagnostus* sp.

Doryagnostus incertus (Brögger, 1878)

The holotype of *D. incertus*, by monotypy, is *Agnostus incertus* Brögger (1878, pl. 6, fig. 4, p. 70); Westergaard (1946, p. 83) lists the citations and elucidates the structure of this species on the basis of Swedish specimens (op. cit., pl. 12, figs. 20-23; pl. 13, figs. 1-3) and states (op. cit., p. 84) that *'Ceratagnostus magister* Whitehouse is in all probability synonymous with *D. incertus*'. I accepted this synonym in my earlier reports and fossil lists pending a revision of the Australian material. In brief, (1) *Doryagnostus magister* (Whitehouse) is a valid species and not a synonym of *incertus;* (2) *incertus* is not present in Australia; (3) *incertus* is confined to the Zone of *Ptychagnostus punctuosus*; and (4) *magister* in Australia arrives in the *P. punctuosus* zone and is most abundant in the Zone of *Ptychagnostus nathorsti* and is, therefore, a bi-zonal species.

Diagnosis of the species incertus (compiled herein, on the basis of the illustrations published by Brögger and by Westergaard): pygidial marginal spines rather short, slightly deflected, and advanced forward to, or even slightly beyond, the transverse level, passing through the tip of the axis; the pygidium is as wide as long. These are holaspid characters; the pygidial length is taken without the articulating half-ring (from the front of the axis); the taxonomic value of these characters emerged from the comparison with *D. magister*.

Differential diagnosis: In all specimens of *Doryagnostus magister* the pygidial spines are large, undeflected, curved, and placed visibly behind the transverse level of the axial tips, and the pygidium is wider than long. In passing, the position of the marginal spines in the pygidia attributed to *D. incertus* from Newfoundland (Hutchinson, 1962, pl. 10, figs. 10, 11) is about the same as in *D. magister* and not *D. incertus* (Brögger).

Doryagnostus sp. nov. aff. **incertus**
(Pl. 17, fig. 3)

The sole, and illustrated, pygidium, CPC 14078, in limestone, is 4.3 mm long. It resembles *D. incertus* (Brögger), especially the pygidium illustrated by Westergaard (1946, pl. 13, fig. 3) in its subpentagonal outline, advanced position of the marginal spines, and the general outline of the axis; it differs, however, by the total absence of the transverse depression in the axial rear.

The axis is very long (0.84x the shield's length), about as long as in the holotype of *D. incertus* (Brögger, 1878, pl. 6, fig. 4) and the marginal spines are also not deflected but retral.

Occurrence and age: The pygidium described as *Doryagnostus* sp. nov. aff. *incertus* came from V-Creek Limestone, locality M41; its age is late in the Undillan Zone of *Doryagnostus notalibrae*.

Doryagnostus magister (Whitehouse, 1939)
(Pl. 17, figs. 4-6; Pl. 18, figs. 1-5; Pl. 20, figs. 1-4; Text-fig. 24)

Material: Illustrated are six exoskeletons, four pygidia, and two cephala, selected from a large supply of specimens.

Holotype: The specimen published as such by Whitehouse (1939, pl. 25, fig. 27).

Diagnosis: The diagnosis of the species *Doryagnostus magister* is given above as the differential diagnosis of the species *incertus* Brögger.

Differential diagnosis: The main part of the differential diagnosis of *D. magister* is found in the diagnosis of *D. incertus*; further comment is given under *Doryagnostus notalibrae* sp. nov. and *D. solidus* sp. nov.

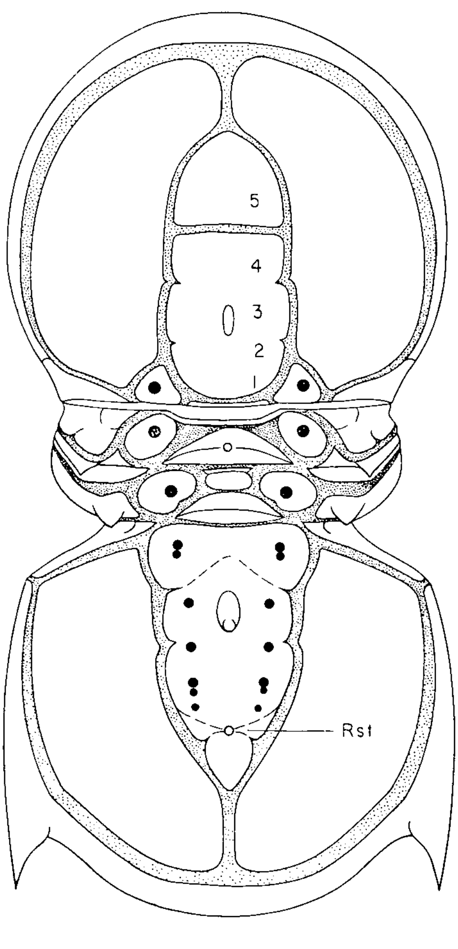

Fig. 24. *Doryagnostus magister.* **1-5 indicate metameres of the cephalon; Rst—rosette.**

Description: Doryagnostus magister is a large agnostid, attaining some 15 mm in length; the pygidium and the cephalon are equidimensional and so are the glabella and the pygidial axis; the thorax is medium in size, about 0.3x the cephalon in length. The cephalic spines are triangular and short, the glabellar median node, close to the midpoint of the rear glabellar lobe, is low and more or less elongate; axial spines are absent; the pygidial axial node is moderately elevated and confined to the second axial annulation; the axis is 0.7x the shield's length, and the pygidial marginal spines are prominent and retral. All furrows are well impressed, and the lobes are clearly defined. The test is punctate. *Doryagnostus magister* is a species en grande tenue. In outline the cephalon is a larger segment of a circle, but arched slightly forward in front; the rim is moderately wide, of a low convexity, and the marginal furrow deep. The preglabellar median furrow, relatively deep and narrow, flares in front, but the flare remains narrow and even absent. On the cheeks external scrobicules are absent but occasionally are indicated internally as radiating dark lines and spots (Pl. 18, fig. 4).

The frontal glabellar lobe, variable in length between 0.34 and 0.37x the glabella, has in its posterior part slightly convex to subparallel flanks which converge forward to a pointed tip; in immature specimens the frontal lobe is shorter (0.3) and in one specimen (Pl. 20, fig. 1) it is even 0.4x the glabella. The transverse glabellar furrow is externally straight but sometimes, especially in internal casts (Pl. 20, fig. 2) it can be bow-shaped, but to a lesser degree than in *Doryagnostus notalibrae* sp. nov.; laterally the furrow is deeper than in the middle. The posterior glabellar lobe has two pairs of lateral notches but the posterior notches are erratic. In its middle, between the notches, the glabella is slightly expanded. The glabella has a rounded rear. The pygidial axis has a baroque appearance; the anterior lobe is the widest and defined by a pair of oblique furrows which fade out toward the midline; the second lobe is narrower and the furrows behind it are very short; the third (posterior) lobe consists of two parts separated by a broad, laterally flaring depression with a central node (the rosette-and-knob structure); the anterior part is slightly expanded laterally and rounded in the rear; the posterior, attenuated part is a small triangular and pointed lobe; the rosette and the terminal lobe are depressed in relation to the anterior part of the axis. The relief of the transverse depression and the attenuated end lobe is variable; it is stronger than in *Euagnostus* but remains quite close to *Rhodotypiscus* and *Doryagnostus incertus*. Complete specimens of *Doryagnostus magister* are recognisable at a glance, and so are its isolated pygidia; isolated cephala superficially inspected, however, can be confused with *Euagnostus* and even *Onymagnostus*. The variability is evident from the comment that follows below.

Comment on illustrated specimens

The following two specimens came from a dolomitic nodular bed, Quita Formation, Urandangi area, locality D74, the Zone of *Ptychagnostus punctuosus*.

The cephalon Plate 17, fig. 5, CPC 14080, is 4.0 mm long and almost undeformed; the test is corroded and partly silicified. The frontal glabellar lobe is 0.36x the glabella in length.

The pygidium Plate 17, fig. 6, CPC 14081, is 3.0 mm long. The marginal spines are quite long, but slightly deflected.

The next ten specimens have been collected from the V-Creek Limestone (M195 excepted) from several different sites, of two different horizons: collections M409, M410, and M24 came from a lower horizon containing *Ptychagnostus punctuosus* and *Goniagnostus nathorsti* together; collections M57 and M195 represent a higher horizon together with *Goniagnostus nathorsti* alone.

The complete test Plate 17, fig. 4, CPC 14079, M409, is 4.7 mm long; it is a not quite mature holaspis having a slender and short pygidial axis 0.65x the shield's length; in larger holaspides it is 0.7x. The next four specimens are arranged by increase in length.

The complete holaspis Plate 20, fig. 1, CPC 14091, M57, is 7.0 mm long; its test is preserved; the tagmata are in proper contact and ready for articulation. The preglabellar median furrow flares in front; the transverse glabellar furrow is straight; the axis has its rear well attenuated and depressed, about as in *D. incertus* of Westergaard (op. cit., pl. 12, fig. 22). The length of the pygidium is about 0.88x its width.

The test Plate 20, fig. 4, CPC 14094, M409, is 9.0 mm long; the margin of the cephalon is slightly arched forward visibly more than in the published specimens of *incertus;* the frontal glabellar lobe, 0.37x the glabellar length, is relatively long; the preglabellar median furrow has a frontal flare; the pygidial marginal spines arise about half-way between the axial tip and the rim. The tagmata preserve their articulation order.

The exoskeleton Plate 20, fig. 2, CPC 14092, M57, is 9.0 mm long; specimens of this size are more common than smaller and larger individuals when 'the best' state of preservation is considered. The cephalon is decorticated and shows a small recess in the rear of the frontal glabellar lobe; in *D. magister* this structure is rare (see also *Doryagnostus notalibrae* nov.). The size of the frontal glabellar lobe, 0.34x the glabella in length; is normal for *magister*.

The large test Plate 20, figs. 3, 3a, CPC 14093, M409, is 14.4 mm long; all parts are in articulation order. A fracture partly obscures the frontal part of the preglabellar median furrow; the transverse glabellar furrow is short, the length of the pygidium is 0.84x its width. The lateral axial lobes (basal lobes) of the thorax are somewhat mammillate as can be seen in the semilateral view (fig. 3a).

The pygidium Plate 18, fig. 1, CPC 14082, M57, is 3.5 mm long, and almost undeformed; the marginal spines arise partly from the surface of the rim, as in *Euagnostus opimus*. The rosette with its transverse depression crossing the rear of the glabella is well preserved.

The pygidium Plate 18, fig. 2, CPC 14083, M57, is 3.5 mm long; its lateral margins are less convex than in other specimens and the axis retains the slenderness of immaturity.

The pygidium Plate 18, fig. 3, CPC 14084, associated with *Oedorhachis crenias,* M24, is 4.6 mm long; it also has a slender axis and the marginal spines each in a different and abnormal position.

The completely flat test, not illustrated, CPC 14376, M195 (attributed to the Currant Bush Limestone on lithology), is 9.0 mm long, and an example of preservation in a thin shale lamina.

The cephalon Plate 18, fig. 4, CPC 14085, M410, is 5.6 mm long; it is the inner surface of the test preserving the radiating scrobicules as dark lines and spots; scrobiculate and rugose exteriors are unknown in *magister* but recorded in *incertus* (Westergaard, op. cit. Pl. 12, fig. 21).

The isolated thorax Plate 18, fig. 5, CPC 14086, M409, is about 2.0 mm, and belongs to a specimen about 14 mm long. The two segments are held together by the interlocking fulcra; a part of the articulating facet of the posterior segment is exposed on the left. The test is punctate.

Occurrence and age: Doryagnostus magister is a rather common agnostid of the V-Creek Limestone, and occurs also in the Split Rock Sandstone and in the Quita Formation, all in Queensland; it occurs over the whole range of the Undillan Stage (the Zones of *Ptychagnostus punctuosus* to *Goniagnostus nathorsti*).

Doryagnostus notalibrae sp. nov.

(Pl. 19, figs. 1-4; Pl. 21, figs. 1-3)

Material: Illustrated are five cephala (one with its thorax) and two pygidia selected from some twenty shields from several sites.

Holotype: The pygidium Plate 19, fig. 1, CPC 14087, is selected as the holotype because it is more characteristic than the cephalon in the absence of a complete specimen.

Diagnosis: Doryagnostus notalibrae is distinguished by its long pygidial axis (0.8x the shield's length) with a weakly differentiated end lobe and rosette and with the marginal spines on level with the axial tip; and by the cephalon having a triangular glabellar frontal lobe and a bow-shaped transverse glabellar furrow congruous with the front of the posterior and the rear of the frontal glabellar lobes.

Differential diagnosis: D. notalibrae differs from *D. magister* in all characters included in the diagnosis; in *D. magister* the pygidial axis is less fused and shorter (0.7x the shield's length), the end lobe is depressed, the transverse furrow and the rosette are more conspicuous, and the marginal spines are in a more retral position. In *D. solidus* and in *D. notalibrae* these spines are in the same position relative to the axial tip, but otherwise these species cannot be confused with each other. The structure of the pygidial rosette is reminiscent of *Euagnostus*; but the structure of the rim and the laterally expanded axis of *notalibrae* are characters of *Doryagnostus* rather than *Euagnostus*.

Description: The cephalon is broadly semi-elliptical, slightly elongate and with a somewhat forward arched frontal margin; the rim is moderately wide and barely convex, and wider than the marginal furrow. The preglabellar median furrow is well impressed and expands forward in a trumpet-like flare. The periphery of the cephalic acrolobe is often scrobiculate. The frontal glabellar lobe is triangular to subconical and pointed in front and emarginate in the rear at the midline; the transverse glabellar furrow is bow-shaped and so is the front of the posterior glabellar lobe, protruding forward and filling the recess in front of it. The posterior, stout glabellar lobe, moderately arched in profile, is well rounded in the rear, bears a small node in its middle, and two pairs of short indentations on its flanks. The basal lobes are triangular, small, and tumid, and the posterolateral spines are triangular short curved plates.

In the pygidium the rim is relatively narrow and slopes outward, and the marginal spines, of a moderate size, are slightly hooked. The postaxial furrow is distinct but shallow. The axial furrows are narrow and well incised; the transverse furrows are indicated as two pairs of lateral notches; the anterior axial lobe is trapezoidal and widest in front; the second lobe is narrower and carries a relatively short median node; the posterior lobe first expands and then tapers rearward to its pointed tip. The end lobe is only slightly but clearly attenuated; the transverse depression of the rosette is shallow, its knob is low, and the triangular end lobe is only slightly swollen, or even not at all.

Some variability of characters is also evident: (1) in the transverse glabellar furrow the median projection of the posterior lobe is sometimes unclear in smaller specimens; at the same time the bow shape occurs also in *Doryagnostus magister* and therefore cannot be taken alone as a reliable species character; (2) specimens with a somewhat slender pygidial axis have been observed in the collection M212; and (3) the anterior axial lobe can be defined more clearly than in the holotype.

Comment on illustrated specimens

The following three specimens have retained their original form; the matrix is a large pod of calcite, locality M89.

The holotype pygidium, Plate 19, figs. 1-1a, has lost a part of its left marginal spine; at the front of the axis a pair of small knobs (muscle spots) close to the midline is visible.

The cephalon Plate 19, figs. 2-2a, CPC 14088, is 4.4 mm long; and equals the holotype pygidium. The preglabellar median furrow is flaring almost from the glabellar tip onward. The frontal lobe is relatively large, about 0.33x the glabella in length, along the midline; the front of the posterior lobe is bow-shaped. In lateral view the cephalic spine is well visible.

The cephalon Plate 19, figs. 3-3a, CPC 14089, is 4.7 mm long; the largest available, it belongs to a specimen some 11.3 mm long. The triangular frontal glabellar lobe is 0.32x the glabella in length; the acrolobes are scrobiculate along the marginal furrow, as can be seen in lateral view (Fig. 3a).

The cephalon Plate 19, fig. 4, CPC 14090, locality M212, in marly limestone, is 3.8 mm long. The frontal flare of the preglabellar median furrow is rather wide.

The cephalon Plate 21, fig. 3, CPC 14097, locality M214, in marly limestone, is 1.7 mm long; it has an exceptionally broad and flaring preglabellar median furrow.

The two following specimens are associated in a piece of limestone, locality M212.

In the specimen Plate 21, fig. 1, CPC 14095, the cephalon is 4.2 mm long and the thorax 0.3x the cephalon in length; the frontal glabellar lobe is 0.32x the glabella in length.

The pygidium Plate 21, fig. 2, CPC 14096, is 5.6 mm long—an exoskeleton about 13 mm long is indicated; it is fractured and collapsed along the axial furrows.

Occurrence and age: Doryagnostus notalibrae occurs in the V-Creek Limestone (M89; M212;

M214; M247); its age is the Undillan Zone of *Goniagnostus nathorsti* associated with *Ptychagnostus punctuosus* which is the same as the Zone of *Doryagnostus notalibrae.*

Doryagnostus sp. aff. **notalibrae**

(Pl. 21, figs. 5-6)

The illustrated and only available material consists of one cephalon (CPC 14099) and one pygidium (CPC 14100) in limestone; the cephalon, 4.4 mm long, has a slightly narrower glabella than the cephalon of *notalibrae* Plate 19, fig. 2. In the pygidium Pl. 21, fig. 6, which is 5.0 mm long, and of an individual almost 12 mm in length, the axis is visibly shorter and its transverse furrows are also clearer than in *notalibrae* (Plate 21, fig. 1).

Occurrence and age: Doryagnostus sp. aff. *notalibrae,* from the locality M161 of the Currant Bush Limestone and of the Undillan Zone of *Ptychagnostus punctuosus,* is a little older than *D. notalibrae* itself.

Doryagnostus solidus sp. nov.

(Pl. 6, figs. 1-2; Pl. 21, fig. 4; Text-fig. 25)

Material: Illustrated are one complete shield, one cephalon with its thorax, and one isolated pygidium; *D. solidus* is a rare form, but its isolated cephala and pygidia are present in several collections.

Holotype: The only available complete specimen, Plate 21, fig. 4, CPC 14098, locality M139, is the holotype.

Diagnosis and differential diagnosis: In *Doryagnostus solidus* the pygidial axis (0.7x the shield's length) and the position of the marginal spines behind the level of the tip of the axis are about the same as in *Doryagnostus notalibrae,* but different from *Doryagnostus incertus*; the species is, however, distinguished from other known species of its genus by (1) its very shallow, even faint preglabellar furrow without a frontal flare, (2) the large and rather bluntly pointed frontal glabellar lobe reminiscent of *Rhodotypiscus nasonis,* (3) short pygidial marginal spines with drawn-out points, (4) the relatively narrow (transversely) anterior axial lobe of the pygidial axis, (5) the shallow transverse depression of the rosette and the weakly developed relief of the end lobe, and (6) its thorax—the largest known in its subfamily.

Doryagnostus solidus cannot be placed in *Rhodotypiscus,* in which the cephalon has a different shape and a peculiar glabella with its extremely retral culmination.

Description: The holotype is a complete exoskeleton about 11.3 mm long; its posterior segment of the thorax is partly overridden by the displaced pygidium. All furrows are narrow, and relief of the lobes is well developed; the preglabellar median furrow is faint. The frontal glabellar lobe is about 0.4x (0.39) the glabella in length; the posterior, stout lobe has parallel flanks and the median node is small. The pygidium in the holotype is as long as the cephalon; the axis is quite well fused, but the anterior lobe is stronger in some specimens than in others. The knob of the rosette is prominent but the transverse depression is shallow.

Comment on illustrated material

The holotype is described above. The specimen Plate 6, fig. 1, CPC 14001, locality M139, a cephalon and thorax together, belongs to an individual some 12.0 mm long, the test of the cephalon is creased and the glabella twisted; the preglabellar median furrow is faint; the posterolateral spines have drawn-out tips similar to the pygidial marginal spines. The thorax (0.38-0.4x the cephalon) is preserved exceptionally well; the left posterior fulcral point of the anterior segment repeats the structure of the cephalic spine. The same specimen is annotated in Text-figure 25.

The pygidium Plate 6, fig. 2, CPC 14002, locality M409, is 3.7 mm long; its right marginal part is lost; a pair of notulae is visible on the anterior axial lobe, and notulae are evident on the posterior lobe close to the axial furrows.

Occurrence and age: Doryagnostus solidus occurs in the V-Creek Limestone at the sites M139, M409, and probably some other places; collection M139 yielded two described specimens associated with several isolated shields. It is a rare form. The age is the Undillan Zone of *Doryagnostus notalibrae.*

Subfamily **PTYCHAGNOSTINAE** Kobayashi, 1939

(Possible synonyms: Leiopyginae Harrington, 1939; Hastagnostidae Howell, 1937)

The species of the Subfamily Ptychagnostinae are 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 pygidial axis, frequent occurrence of cephalic rugae, granular ornament, and occasional occurrence of a frontal glabellar sulcus. This diagnosis needs the following amplifications: (1) the glabellar front is rounded in species of *Pentagnostus* and in *Agnostonymus semiermis* nov.; (2) in species of the genus *Myrmecomimus* nov. the pygidial axis is short and rounded in its rear; (3) in the cephalon the axial furrows

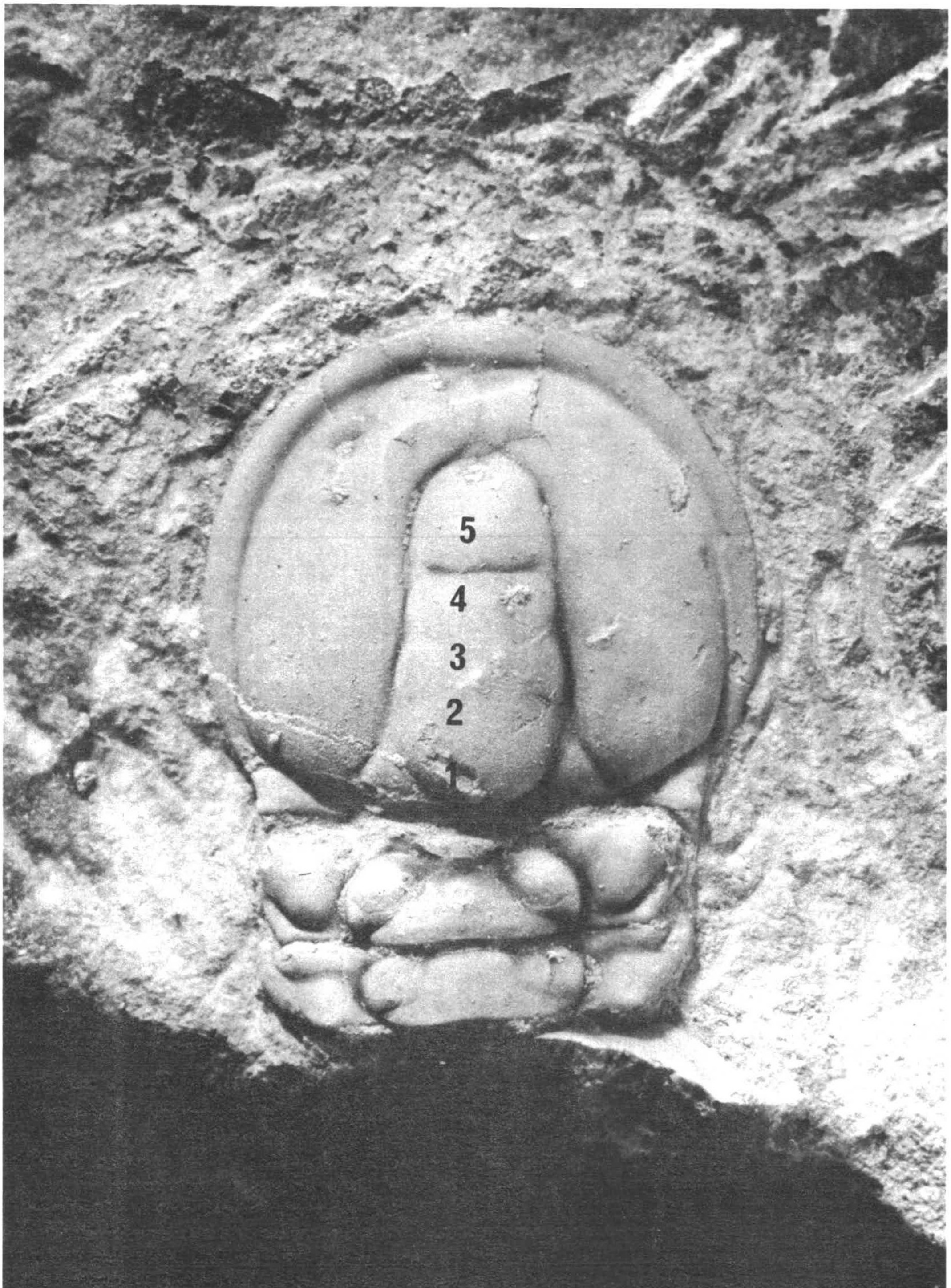

Fig. 25. *Doryagnostus solidus,* **enlarged photograph of Plate 6, fig. 1; 1-5 are metameres of the cephalon.**

are only slightly deflected at the basal lobes (IX, Text-fig. 2); and (4) numerous species are equipped with axial and fulcral spines (see under 'taxonomy by spines', Table V), but others are not.

The type of the Ptychagnostinae is *Ptychagnostus* Jaekel, 1909, whose type species is *Agnostus punctuosus* Angelin; it is a species without extended spines.

At this point remarks are needed concerning the subjective synonymy of Hastagnostidae Howell (1937) and Ptychagnostidae Kobayashi (1939) and the seniority of Howell's name emergent in Harrington et al. (1959, p. 0179), where the genus *Ptychagnostus* is included in the Hastagnostidae. As observed earlier (Öpik, 1961b, pp. 53 and 25) *Hastagnostus* belongs to the Agnostidae and the name Hastagnostidae is its junior synonym; *Hastagnostus augustus* Howell (op. cit., pl. 3, fig. 4; Howell *in* Harrington et al., op. cit., fig. 116-5) has a rounded pygidial axial rear —a character justifying the generic name and possibly the subfamily name of Hastagnostinae as different from the Ptychagnostinae in our interpretation. The small size of the frontal glabellar lobe and the absence of a postaxial pygidial median furrow in *Hastagnostus augustus* invoke a comparison with *Onymagnostus mundus* sp. nov., but the different structure of the pygidial axis prevents any conclusion on the generic affinity of these forms. At all events, the family, subfamily, and genus nomenclature adheres only to the holotype of *Hastagnostus augustus.*

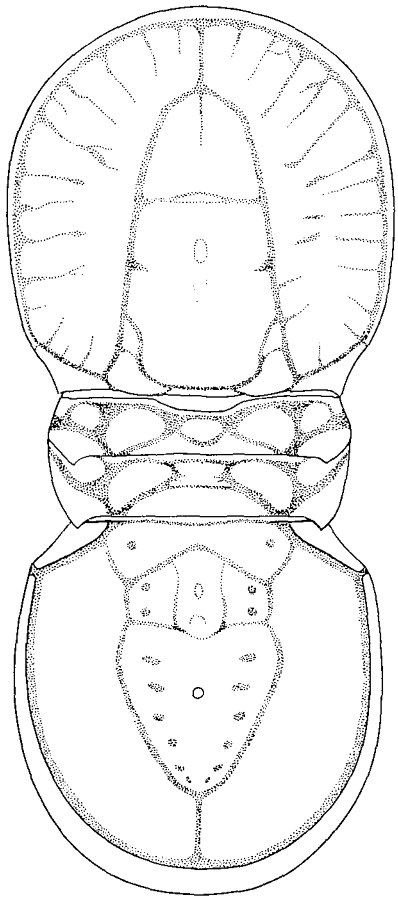

Fig. 26. *Ptychagnostus punctuosus punctuosus.*

Genus **Ptychagnostus** Jaekel, 1909

Jaekel defined *Ptychagnostus* as a genus of the subfamily Agnostinae with double basal lobes and radial folds or irregular knolls on the cheeks and mostly on the pleural lobes of the pygidium. He included inter alia what became known as *Glyptagnostus reticulatus,* which possesses the structure of the pygidial pleural lobes mentioned in the definition.

With Jaekel's concept in mind, Öpik (1961b) included *Ptychagnostus* in the subfamily Glyptagnostinae Whitehouse, 1936. Kobayashi (1939), however, in proposing the Subfamily Ptychagnostinae as different from the Glyptagnostinae added clarity to the classification of these agnostids; later (Öpik, 1967, p. 63) I placed the Ptychagnostinae in the Family Agnostidae and *Glyptagnostus*(-inae) in the Diplagnostidae. Westergaard (1946) placed *Ptychagnostus* in the Subfamily Agnostinae as Jaekel did; moreover, he regarded *Triplagnostus* as a subgenus of *Ptychagnostus*; and Öpik (1961b, 1967) suggested also the status of a subgenus for *Goniagnostus* Howell.

Here, *Ptychagnostus, Triplagnostus,* and *Goniagnostus* are taken as genera equal in status and each is augmented by subgenera.

Diagnosis of Ptychagnostus *and its subgenera*

In all species of the genus *Ptychagnostus* the cheeks are rugose, the basal lobes are double (rarely triple), the median glabellar node is about central to subcentral.

In the subgenus *Ptychagnostus* (*Ptychagnostus*) axial spikes are absent, fulcrul spines are undeveloped. The median node on the posterior pygidial axial lobe has a subcentral position. An exceptional species is *Ptychagnostus cassis* Öpik (1961b, p. 77) with its extended cephalic spines; its basal lobes are double (described erroneously as simple) and the pygidium regular.

In the subgenus *Ptychagnostus (Acidusus)* nov., the posterior pygidial axial lobe has a node on its tip, axial spines may occur in the thorax and in the pygidial axes, and fulcral spines in the cephalon.

Differential diagnosis: See *Triplagnostus, Zeteagnostus, Onymagnostus,* and *Goniagnostus.*

Ptychagnostus punctuosus punctuosus (Angelin, 1851)

(Pl. 38, fig. 1; Pl. 39, figs. 1-7, 9, 10; Pl. 40, fig. 1; Text-fig. 26)

Introduction

Westergaard (1946, p. 78) redescribed *Ptychagnostus punctuosus* from Sweden and discussed its geographic distribution (Sweden, Norway, Borneholm, and Newfoundland); Howell (1944, 1945) published a complete specimen from Newfoundland, and Hutchinson (1962, p. 84) illustrated eleven shields from the same island. Rasetti (1967, p. 28) recorded and illustrated *Pt. punctuosus* from the Taconic sequence of the State of New York and, finally, Palmer (1968, p. 28, pl. 4, figs. 26, 27) attributed two shields from Alaska to *Pt. punctuosus affinis;* but in its cephalon (fig. 26) the dimples of the cheeks, the arcuate scrobicules, the retral position of the median glabellar node, and the relatively large posterolateral spines indicate a species different from *punctuosus*; likewise the pygidium (fig. 27) seems to have a node well to the rear of the axis.

The occurrence of *Ptychagnostus punctuosus* as a zone species in Australia (Queensland) has been reported by Öpik (1956; 1957, pp. 14, 15), but hitherto no illustrations have been published.

Brögger (1878) in describing *Agnostus punctuosus* (op. cit., p. 67, pl. 5, figs. 12a, 12b) established two varieties—*A. punctuosus* var. *affinis* (q.v.) and var. *bipunctata*—and indicated in his table of the stratigraphic distribution of fossils the presence of otherwise not described varieties (var.). *A. punctuosus affinis* (op. cit., p. 68, pl. 5, figs. 2a, 2b) has been acknowledged in the literature, especially by Westergaard (1946), but *bipunctata* (op. cit., pl. 5, fig. 2c), whose only distinctive character is a pair of notulae on the anterior pygidial axial lobe, remains with *punctuosus (punctuosus)* or possibly with *punctuosus affinis.*

Remarks: The traditional subspecies nomenclature is unwieldy; but the subspecies taxa, for practical reasons, can be replaced by a species nomenclature: (1) *Ptychagnostus punctuosus* may designate pygidia not associated with cephala; (2) *P. affinis* is applicable in the presence of smooth cephala; these two are concurrent forms and the simplified nomenclature has no influence in stratigraphy; (3) *P. fermexilis* nov. (q.v.) is identifiable on the evidence of isolated shields.

The repetition of the name *(punctuosus punctuosus)* in taxonomic descriptions and discussions is appropriate in respect of the two other subspecies, *P. punctuosus affinis* (Brögger) and *P. punctuosus fermexilis* nov.

Westergaard (op. cit., pl. 12, figs. 3, 3a) designated as the lectotype a cephalon selected from Angelin's syntypes; it is about 5.0 mm long, with a frontal glabellar lobe bluntly angulate in front and 0.37x the glabella in length; a recess is also apparent in its rear; the glabella at its widest is very close to 0.5x its length; and the ornament (granulation on caeca, and even on parts of the glabella) is well developed. The cephalon with the triple basal lobe (pl. 12, fig. 1), and another cephalon (pl. 11, fig. 34) differ little from the lectotype. Two pygidia (pl. 11, fig. 35; and pl. 12, fig. 2) conform to the lectotype; the rest of the specimens in Westergaard's paradigm (op. cit., pl. 12, figs. 4-7), however, represent variants attributable to *punctuosus punctuosus* because of their ornament.

The review of the Swedish type material is appropriate for an understanding of the Australian specimens attributable to *Ptychagnostus punctuosus punctuosus,* but some reservations are still called for: (1) the Swedish and the Australian collections represent separate populations geographically remote from each other, and (2) the length of the shields is different. The largest in Australian collections are about 3.5 mm against 5.0-5.5 mm in Westergaard's paradigm; according to Westergaard (op. cit., p. 78) the postaxial median furrow becomes effaced in pygidia more than 4 mm long; the pygidial axis is also the longest in the large pygidia. Furthermore, the combination of the lectotype cephalon with a pygidium suggested in the review is inferred on the evidence of Australian, in the absence of Swedish, complete specimens; Brögger's (1878, pl. 6, figs. 12a, 12b) specimens from Sweden (Scania) may be parts of a dismembered complete exoskeleton, but the glabella is slender and the pygidial axis strongly attenuated in its posterior half, and therefore not assignable to *P. punctuosus punctuosus*.

The shields, the pygidia in the first place, vary in convexity, which is of no taxonomic significance.

Diagnosis: Ptychagnostus punctuosus punctuosus is the type of its genus; its shields are about subcircular to slightly subelliptical, with evenly curving margins and narrow borders; the cephalic acrolobe is rugose, but arcuate scrobicules are absent; the median glabellar node is usually placed in front of the lobe's midpoint and even in front of the lateral furrows; the posterior glabellar lobe is relatively wide (about 0.5x the glabellar length). In the pygidium the axial node is low; the posterior axial lobe has slightly concave flanks and a shallow transverse depression; the diagnostic combination of characters above is augmented by the ornament, consisting of rounded and crowded granules (hollow swellings) on the cephalon and the pygidium.

Differential diagnosis: The cephalon in *P. punctuosus punctuosus* is ornamented—the main difference from *punctuosus affinis*; the simulataneous occurrence of both subspecies in several sites casts doubt on the validity of their taxonomic separation (Hutchinson, 1962, p. 84); the validity, however, is supported by the abundant occurrence of *punctuosus punctuosus* alone at locality D74 in Queensland, signalling the reality of a pure population of that subspecies. The difference from *Ptychagnostus punctuosus fermexilis* subsp. nov. is given in the description of that form. *Ptychagnostus aculeatus* (Angelin) is also heavily granulose, but its glabellar median node has a retral position, the pygidial lateral margins are parallel, and the posterior pygidial axial lobe has a narrow elevated keel (Westergaard, op. cit., p. 80), which according to Öpik (1961b, p. 80) may be a spine arising from the rear of the second axial lobe. In Westergaard's specimens (op. cit., pl. 12, figs. 9, 10) the spine is lost, but its long scar indicates that the anterior part of the spine is fused to the test below it.

Description: Descriptive data necessary for the identification of the subspecies are given in the diagnosis, in the differential diagnosis, and in the comment on the illustrated specimens.

The cephalon is the largest shield, about as long as the pygidium and half a segment of the thorax taken together. In the cephalon the combination of ornamental granules separated by narrow interspaces and distributed on the periphery of the acrolobe on the caeca reminds one of the reticulate pattern of *Glyptagnostus*. The frontal sulcus varies in length, but remains shallow. The transverse glabellar furrow is expanded in the middle, accounting for the recess in the rear of the frontal glabellar lobe. The position and length of the median node of the posterior glabellar lobe are variable: fundamentally it is a ridge culminating on its anterior or posterior end as a rounded node, or possessing an even elevation. The basal lobes are usually double, or even triple; one or the other may be triple or remain almost undissected. The pygidial axis is invariably divided by the two incised transverse furrows into three lobes; the median node on the second annulation is low, and in the middle of that segment a small, superimposed, node occurs sporadically. The subcentral node on the posterior lobe is sometimes flanked by a pair of longitudinal lines. Notulae are visible only in exceptionally well preserved tests and are shown in Text-figure 26. The articulating device (Pl. 39, fig. 7) resembles a *Glyptagnostus* or a *Pseudagnostus* rather than another agnostid. *Ptychagnostus punctuosus punctuosus* has an exoskeleton en grande tenue, and only in larger specimens (*teste* Westergaard) is the postaxial median furrow subject to a gradual effacement.

Comment on illustrated specimens

The complete exoskeleton Plate 38, CPC 14190, and Plate 39, fig. 1, CPC 14191, locality Q6, Quita Formation, in fine-grained sandy limestone, is 6.4 mm long. It is undeformed, retaining the original convexity; the glabellar front is angular, the shallow sulcus on the frontal lobe dissects the lobe completely; the frontal lobe is 0.35x the glabella in length and has a recess in its rear. The right side basal lobe is triple. The posterior lobe of the pygidial axis is carinate. The thorax, 0.27x the cephalon in length, is close to *atavus* and larger than in *intermedius*.

The two immature specimens that follow come from the V-Creek Limestone, locality M409.

The specimen Plate 39, fig. 10, CPC 14200, is 3.5 mm long; it is an early holaspis. The ornament is worn or possibly weakly developed; the pygidial axis is short, but the node on the posterior lobe is prominent.

The exoskeleton Plate 39, fig. 9, CPC 14199, is 2.5 mm long. It is a late meraspis with the posterior segment of the thorax still fused to the pygidium. The ornament on the cheeks is prominent and the node on the second axial lobe is advanced and strong.

The pygidium Plate 39, fig. 6, CPC 14196, locality M174, V-Creek Limestone, is 3.5 mm long. The posterior axial lobe shows a transverse depression, the central node on the second segment is clear, and notulae are evident, six pairs on the posterior lobe. The fulcral points are prominent.

The pygidium Plate 39, fig. 7, CPC 14197, locality M214, V-Creek Limestone, is 3.4 mm long. The structure of the articulating device (narrow and arched half-ring, deep articulating furrow, and recess in the axial front) is clear. The central node on the second lobe lost its tip.

The cephalon Plate 40, fig. 1, CPC 14201, locality M59, in chert of the Inca Formation, is 3.5 mm long. It is a laterally deformed internal cast. The median glabellar node is narrow and long and the duplication of the basal lobes is vestigial.

The next four specimens have been selected from an abundant supply at locality D74, Quita Formation; the matrix is a sandy dolomite; the tests are corroded but the ornament is still distinguishable in all specimens.

The cephalon Plate 39, fig. 3, CPC 14193, is 2.8 mm long. The glabellar front is angulate, and the frontal lobe is 0.37x the glabella in length. A cephalon of *Aotagnostus protentus* nov. is associated.

The cephalon Plate 39, fig. 4, CPC 14194, is 2.5 mm long; the angulation of the glabellar front is obscure; the frontal glabellar lobe, 0.37x the glabella in length, shows the recess in its rear.

The cephalon Plate 39, fig. 2, CPC 14192, is 3.5 mm long; the glabellar front is asymmetrical and pointed; the basal lobes are unusually prominent; the lateral glabellar furrows are forked; the glabella at its widest is 0.5x its length.

The pygidium Plate 39, fig. 5, CPC 14195, is 3.5 mm long as preserved. The posterior lobe is depressed and the postaxial furrow peters out retrally.

Occurrence and age: Ptychagnostus punctuosus punctuosus occurs in the V-Creek Limestone, Quita Formation, and Inca Formation; the vertical distribution of the sites from which specimens are illustrated here is as follows: (1) in ascending order, M59, Q6, and D74, the zone of *Ptychagnostus punctuosus;* and higher up, (2) M409, M174, and M214, the Zone of *Doryagnostus notalibrae.*

Ptychagnostus punctuosus affinis (Brögger, 1878)

(Pl. 39, fig. 8; Pl. 40, figs. 2-7)

Material: Illustrated are two complete specimens and four isolated cephala.

Remarks: In *Ptychagnostus punctuosus affinis* the pygidium is visibly granulose and the cephalon smooth, but in *punctuosus punctuosus* both the shields are ornamented; it appears also that the pygidial ornament in *affinis* is finer than in the nominate subspecies. Nevertheless with the pygidia alone, and in the absence of cephala, the two subspecies cannot always be distinguished; but an error of this kind has no stratigraphic significance because they have a similar temporal distribution. Supplementary data regarding the subspecies *affinis* are given in the comment on illustrated specimens; the literature is discussed in connection with *punctuosus punctuosus.*

Comment on illustrated specimens

The complete test Plate 40, fig. 2, CPC 14202, locality M410, V-Creek Limestone, is 5.5 mm long. The granulation of the pygidial acrolobe is finer and the granules are therefore spaced wider than in *punctuosus punctuosus;* in the cephalon a minute and scattered granulation seems present in the rear of the cheeks; the scrobicules, in the absence of the masking granulation, are well visible; the glabellar median node is weak and in an advanced position (as in *punctuosus punctuosus*); the glabella at its widest is also 0.5x its length, but the frontal glabellar lobe, about 0.4x the glabella in length, is somewhat large; its front seems pointed, but the pointed part belongs to the posterior flare of the preglabellar median furrow, which is also the flare of the sulcus.

The complete specimen Plate 39, fig. 8, CPC 14198, about locality M166, Currant Bush Limestone, is 11.0 mm long; it belongs to a collection singed in a fire. It is remarkably similar, even regarding the mode of deformation, to the exoskeleton from Newfoundland in Shimer & Shrock (1944-1955, pl. 251, fig. 20); it is also the first identified Australian specimen of the subspecies. The scrobicules are exceptionally strong; in the pygidial axis a pair of notulae is visible, and the second axial lobe has a central node on the crest of the main median node. The granulation of the pygidial pleural lobes is relatively dense. The counterpart was lost in the fire.

The next two cephala and one pygidium are from a limestone of the Quita Formation, locality D69.

The cephalon Plate 40, fig. 3, CPC 14203, is 2.5 mm long; the frontal lobe is 0.4x the glabella in length, the median node is elongate and the basal lobes strong; the glabella at its widest is 0.5x its length.

The small cephalon (cf. *affinis*) Plate 40, fig. 4, CPC 14204, is about 1.9 mm long. The subcentral position of the median glabellar node, which is combined with a lesser node close behind, reminds one of a Swedish cephalon of *punctuosus affinis* (Westergaard, op. cit., pl. 11, fig. 30); the glabella is narrow, 0.44x its length, as in *punctuosus fermexilis* (q.v.), whose test, however, is ornamented.

The cephalon Plate 40, fig. 6, CPC 14206, locality M234, V-Creek Limestone, is 3.0 mm long; it is crushed and dilated. The median node is long, and the basal lobes are well exposed.

The pygidium Plate 40, fig. 7, CPC 14207, locality D69, is 3.6 mm long. Its ornament is finer than usual, indicating a local aberration; as for example, with a cephalon as above. Associated with it are several small but very deformed complete tests with a similar weak pygidial ornament.

The cephalon Plate 40, fig. 5, CPC 14205, locality M191a, limestone of the Inca Formation, is 2.3 mm long. It is deformed and corroded about the glabella and the cheeks. The basal lobes are strong.

Occurrence and age: Ptychagnostus punctuosus affinis occurs scattered in the V-Creek limestone and the Inca Formation, and is relatively frequent in the Quita Formation; its age is Undillan. The succession of sites from which specimens are illustrated is as follows (in ascending order): M191a, the oldest and about the same age as M59 with *punctuosus punctuosus*; M166, D69; these belong to the Zone of *Ptychagnostus punctuosus,* and M234 and M410 to the Zone of *Doryagnostus notalibrae.*

Ptychagnostus punctuosus fermexilis subsp. nov.

(Pl. 41, figs. 1-5)

Material: The illustrated material consists of two cephala and three pygidia selected from a larger number of specimens, locality D155, and one cephalon from Q6.

Holotype: The cephalon Plate 41, fig. 3, CPC 14213, is selected as the holotype.

Diagnosis and differential diagnosis: The subspecies *punctuosus fermexilis* is similar to *punctuosus punctuosus* in having the cephalon and the pygidium ornamented by a relatively coarse granulation; it is distinguished by the slenderness of its glabella and by the prominence of the central node on the second lobe of the pygidial axis. Furthermore, the postaxial median furrow is short and the periphery of the pygidial acrolobe is free from granulation.

Descriptive remarks: The glabella is elegantly slender, as wide as 0.43-0.45x, and the frontal lobe 0.4x, the glabella in length. In *Pt. punctuosus punctuosus* and *affinis,* these are 0.5 and 0.35-0.37 respectively. Less diagnostic is the shape of the pygidial axis: the width of its posterior lobe is around 0.5-0.54x, and in *punctuosus punctuosus* 0.52-0.6x the length of the axis.

Comment on illustrated specimens

All specimens (the last excepted) are selected from the collection D155, a bituminous limestone attributed to the Inca Formation.

The holotype cephalon, Plate 41, fig. 3, is 2.5 mm long. The glabella at its widest is 0.43x, and the frontal lobe 0.4x the length of the glabella.

The pygidium Plate 41, fig. 2, CPC 14212, is 3.1 mm long; the subcentral node on the second axial lobe is prominent, some granulation is present on the axis, the postaxial furrow is short, and the periphery of the acrolobe is smooth. A pair of longitudinal depressions is apparent on the posterior axial lobe.

The pygidium Plate 41, fig. 4, CPC 14214, is 2.7 mm long; its articulating device is exposed.

The cephalon and pygidium Plate 41, fig. 1 (presumably shields of an individual) are numbered CPC 14210 and 14211. The cephalon, 1.75 mm long, has a prominent median glabellar node, a long median sulcus on the frontal lobe, and clearly subdivided basal lobes. The associated pygidium, about 1.6 mm long, has a very slender axis (owing to deformation?), prominent nodes on the middle and posterior lobes, and a short and fading postaxial furrow.

The cephalon Plate 41, fig. 5, CPC 14215, locality Q6 (not D155 as above) is 2.5 mm long. The glabella at its widest is 0.45x the length; ornament is prominent.

Occurrence and age: Ptychagnostus punctuosus fermexilis occurs in the Quita Formation and also in the Inca Formation, at site D155, where it is not accompanied by other subspecies of *Pt. punctuosus.* Its age is the Undillan Zone of *Ptychagnostus punctuosus.*

Ptychagnostus sp. nov. D

(Pl. 40, figs. 9, 10)

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

Description: The cephalon Plate 40, fig. 9, CPC 14209, is 3.5 mm long and flattened in shale. The front glabellar lobe, 0.4x the glabella in length, is as long as in *Ptychagnostus atavus* and longer than *Pt. punctuosus;* other characters, however, indicate an affinity with *Ptychagnostus punctuosus,* as follows: (1) the median glabellar node is advanced; (2) the left basal lobe is triple—as also seen in some specimens of *punctuosus*; (3) the scrobicules are absent; and (4) the general aspect of the cephalon is the same as in *Pt. punctuosus affinis,* Plate 40, fig. 2. The test of the cephalon is minutely granulose.

The pygidium Plate 40, fig. 10, CPC 14209a, is 3.5 mm long, and is less deformed than the cephalon. The test appears minutely granulose —reminiscent of *Ptychagnostus intermedius* (q.v.) and different from *punctuosus*; the general aspect of the pygidium is the same as in *atavus* and *punctuosus* but the posterior axial lobe has a slight transverse depression and a small node (whose tip is lost) in front of its median node—structures of *punctuosus.*

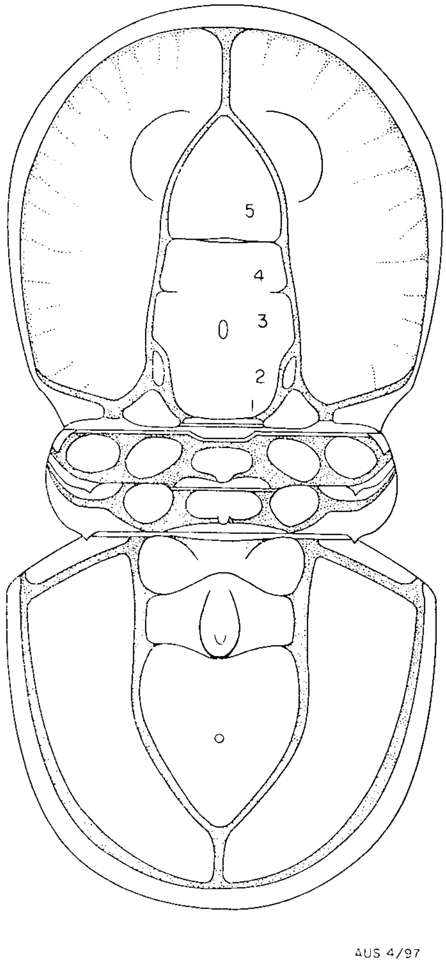

Fig. 27. *Ptychagnostus atavus.* **1-5 indicate metameres of the cephalon.**

All considered, the form can be regarded as belonging to a species taxon intermediate between *atavus* and *punctuosus affinis* in terms of a 'practically continuous evolutional series' (Westergaard, 1946, p. 79). In Australia *Ptychagnostus atavus* and the *Pt. punctuosus* aggregate of forms are separated from each other by the Zone of *Euagnostus opimus,* on present knowledge devoid of transitional forms; the stratigraphic discontinuity of the 'series' here, however, cannot be taken as a taxonomic character.

Occurrence and age: Ptychagnostus sp. nov. D comes from shale of the Inca Formation, collection M263, in association with *Aristarius aristarius, Aotagnostus aotus,* and *Diplagnostus floralis,* indicating the earliest part of the Undillan Zone of *Ptychagnostus punctuosus.*

Ptychagnostus atavus (Tullberg, 1880)
(Pl. 29, fig. 7; Pl. 42, figs. 7, 8; Pl. 43, figs. 1-4; Text-fig. 27)

Westergaard (1946, pp. 76-77, pl. 11, figs. 8-23, and (?) figs. 24 and 25) described in detail Tullberg's *Agnostus atavus* including its inherent variability and the 'variability' dependent on the properties of the matrix (limestone and shale). Westergaard also established the position of *Pt. atavus* in the sequence, above and after *Triplagnostus gibbus;* in the literature before 1946 the interpretation in reverse was prevalent.

Whitehouse (1936, p. 85, pl. 8, figs. 8, 9) described as *Triplagnostus atavus* agnostids belonging to another species which is discussed here under *Acidusus occultatus;* a cephalon of *atavus* has been also illustrated by Whitehouse (ibid., pl. 10, fig. 1 part). In eastern Siberia Lermontova (1940, p. 127, pl. 35, figs. 11, 12) identified the same species, and a complete specimen is illustrated in N. Tchernysheva (1960, pl. 1, fig. 10); and Hutchinson (1962, p. 83, pl. 8, figs. 16-22; pl. 9, figs. 1-8) described *Pt. atavus,* including its morphogeny, from Newfoundland. Finally Lu (1957, pl. 137, figs. 14-16) attributed to *atavus* a *Ptychagnostus* from China; the frontal annulation of its pygidial axis, however, has a pair of tumid and disunited lateral lobes, and in the second lobe the base of a spine (and not of an elongate node) seems to be present.

According to Hutchinson (op. cit., p. 56 and p. 83) *Pt. atavus* occurs in the zones of *Paradoxides hicksi* and *P. davidis,* and in the latter zone is listed together with *Ptychagnostus punctuosus* and *Doryagnostus incertus.*

I note that *Ptychagnostus atavus* has been found in association with *?incertus* at two localities, but neither form is mentioned from a locality with *Ptychagnostus punctuosus.* Furthermore, N. Tchernysheva's (op. cit.) Siberian specimen of *Pt. atavus,* collected from the *Anopolenus* zone (*?P. davidis* zone) seems considerably younger than *Ptychagnostus atavus* in Australia and Sweden. According to Hutchinson (op. cit., p. 83), *Pt. atavus* 'has been found associated with *Paradoxides davidis* and *Hypagnostus parvifrons* in the lowest beds of the *davidis* zone and the upper part of the *hicksi* zone'. In Australia *Hypagnostus parvifrons* (q.v.) is also associated with *Ptychagnostus atavus,* but the zone of *parvifrons* (in Swedish terms) is post-*atavus* and corresponds to the *Euagnostus opimus* zone—an interval separating *Pt. atavus* from *Pt. punc-*

tuosus. Consequently, the Australian and Newfoundland *Pt. atavus* faunas may not be exactly contemporaneous for an accurate correlation of the sequences, apparently because the *Paradoxides* and the agnostid zones are out of phase, being divisions of two different scales.

Diagnosis: Ptychagnostus atavus is a species en grande tenue with an ornamentless (smooth) test, an inconspicuous median glabellar node placed close to, or sometimes behind, the midpoint of the posterior glabellar lobe, and a tiny node about the midpoint of the posterior axial lobe of the pygidium. The variability in the following characters should be considered in identification of the species: (1) the frontal glabellar lobe may have sporadically a sulcus, not observed yet in Australian specimens; (2) the cheeks are usually scrobiculate, but with various degrees of emphasis; (3) arcuate scrobicules are frequently absent; (4) the lateral margins of the pygidium usually contract retrally, but evenly convex margins are also possible.

Differential diagnosis: Ptychagnostus punctuosus differs by its characteristic ornament and by the distribution of that ornament on the tagmata; *Ptychagnostus aculeatus* (Angelin) discussed by Westergaard (1946) and by Öpik (1961b) has no pygidial marginal spines, but is structurally quite remote from *Pt. atavus*. The difference of *Pt. atavus* from *Pt. idmon* sp. nov. and *scarifatus* sp. nov. is evident from the differential diagnosis of these forms; *Ptychagnostus cassis* has extended cephalic spines: see Öpik (1961b, p. 77). The Australian specimens attributed to *Pt. atavus* differ from the Swedish ones on two points: (1) the thorax is a little shorter in the only known complete Swedish exoskeleton (Westergaard, op. cit., pl. 11, fig. 23), and (2) the node on the posterior glabellar lobe is consistently central but it is behind the centre as well as central in Sweden. Consequently two separate populations of *Ptychagnostus atavus* existed, one in Sweden and another in Australia.

Description: The descriptive data are given in the comment that follows below.

Comment on illustrated specimens

All specimens are selected from shale of the Inca Formation. Pygidia of *Pt. atavus* in limestone are illustrated in Plate 25, fig. 1.

The cephalon Plate 43, fig. 3, CPC 14228, from M192, is 2.5 mm long; the matrix is hard, brown and porous (leached) siliceous siltstone. The basal lobes are visibly double; it is almost a replica of the cephalon in Westergaard's figure 23; neither a sulcus in the glabellar front, nor arcuate scrobicules are evident.

The next five specimens came from a silty shale, locality M425.

The cephalon Plate 42, fig. 8, CPC 14225, is 3.4 mm long; the left flank of the glabella is overridden by the cheek, and the whole is askew to the right. The radial scrobicules are very weak, but the arcuate scrobicules are indicated (Westergaard, fig. 12).

The cephalon Plate 42, fig. 7, CPC 14224, is 4.0 mm long; it is flattened (collapsed) and the rim on the flanks is lost on the left and overridden by the cheek on the right side; also the left side of the glabella is covered by the cheek; the cephalon is therefore unnaturally long; in general, however, including the scrobicules, it is close to Westergaard's figure 18—a deformed (short) cephalon.

The pygidium Plate 43, fig. 4, CPC 14229, is 3.0 mm long. A weak node in a subcentral position on the posterior axial lobe is apparent; the outline of the shield and its axis is the same as in Westergaard's figure 23, but quite different from Westergaard's figure 10.

The complete, white, test Plate 43, fig. 1, CPC 14226, in white matrix is 6.6 mm long. It collapsed asymmetrically, as evident from the short distance of the median glabellar node from the right axial furrow; this distance from the left furrow is correct, and the glabella is of the proper tapering shape; the subcentral node on the pygidial posterior axial lobe is visible owing to whitening. Scrobicules are preserved on the fringe of the left cheek; the right side arcuate scrobicule, almost obliterated by comparison, is indicated. The postaxial median furrow is faint (close to a fracture).

The complete, white, test Plate 43, fig. 2, CPC 14227 is 7.3 mm long; it is also asymmetrically deformed, with the right cheek overriding the left flank of the glabella and the left arcuate scrobicule impinged on the flank of the frontal glabellar lobe. This specimen is close to Westergaard's figure 23. The thorax is about 0.26-0.27x the cephalon in length.

The cephalon Plate 29, fig. 7, CPC 14390, is 2.7 mm long, in siltstone, locality M265.

Occurrence and age: Ptychagnostus atavus occurs in shale, silty shale, chert, and limestone of the Inca Formation and is present in the following collections: M169 (limestone), M170, M188, M208 (limestone), M263, M265, M281, M425, M433, and M434; the species is relatively common at M425 but otherwise it is rare and has to be searched for. The age is the Floran Zone of *Ptychagnostus atavus*.

Ptychagnostus atavus coartatus subsp. nov.
(Plate 42, figs. 5, 6)

Material: Two cephala are illustrated, selected from sporadic specimens observed in rock samples: pygidia are unknown or not identifiable because of their similarity to *atavus* itself.

Holotype: The cephalon, CPC 14222, Plate 42, fig. 5.

Diagnosis: Ptychagnostus atavus coartatus has well developed and long double basal lobes, rather weak caeca, and a narrow glabella, and is distinguished by the parallelism of the flanks of the posterior glabellar lobe.

Differential diagnosis: In *Pt. atavus atavus* the glabellar flanks converge forward and the caeca are clearer than in the subspecies *coartatus.*

Comment on illustrated specimens

The holotype cephalon, CPC 14222, locality M192, is about 2.3 mm long; the scrobicules are weakly indicated; the preglabellar median furrow terminates in a flare; the frontal glabellar lobe, about 0.38-0.4x the glabella in length, is longer than in *atavus.* The test is minutely granulose.

The cephalon Plate 42, fig. 6, CPC 14223, is 3.8 mm long; the frontal lobe is 0.4x the glabella, which is slightly deformed and creased. It is associated with a cephalon of *Euganostus certus* (q.v.)—the earliest known specimen of that species.

Occurrence and age: Ptychagnostus atavus coartatus is a rare form in the Inca Formation; its age is the Floran Zone of *Ptychagnostus atavus.*

Ptychagnostus intermedius (Tullberg, 1880)

(Pl. 41, fig. 8)

The illustrated exoskeleton, CPC 14218, in silty shale, locality M170, is 5.5 mm long; it has been singed in a fire. The cephalon and the pygidium are about the same as in *Pt. atavus* and the basal lobes are also double. The test, however, is granulose (smooth in *atavus*) and the thorax, about 0.22x the cephalon, is much shorter than in Australian and Swedish exoskeletons of *Pt. atavus.*

Westergaard (op. cit., p. 76, pl. 11, figs. 19-21) revised the syntypes of *intermedius*—two cephala and one pygidium in shale—and observed their fine granulose ornament but dismissed it as 'an adventitious feature due to the coating of calcite'; and seeing that *atavus* and *intermedius* cannot be 'definitely distinguished' from each other, Westergaard considered *intermedius* as a synonym of *atavus.* (In passing, *atavus* has 'page priority' over *intermedius,* both being published in the same paper.) This synonymy is subjective, of course.

The specimen in hand represents a species different from *Ptychagnostus atavus* but seems rather close to *intermedius;* a final decision regarding its specific identity, however, is reserved here in the absence of supporting exoskeletons in published Swedish material.

Illing's (1916, pl. 28, fig. 12) *Agnostus* cf. *intermedius* is unrelated to *Ptychagnostus* and represents a species of *Onymagnostus* (q.v.).

Occurrence and age: The described exoskeleton of *Ptychagnostus intermedius* comes from the Inca Formation; its age is the Floran Zone of *Ptychagnostus atavus.*

Ptychagnostus idmon sp. nov.

(Pl. 43, figs 5-8; Text-fig. 28)

Material: Illustrated are three cephala and one pygidium selected from a number of less well preserved shields, all in limestone.

Holotype: The cephalon Plate 43, fig. 5, CPC 14230, locality M208, is selected as the holotype; it is associated with the pygidium Plate 43, fig. 7, which, unless another allied species is present—and there is no indication of this in the identifiable fragments—must belong to *idmon.*

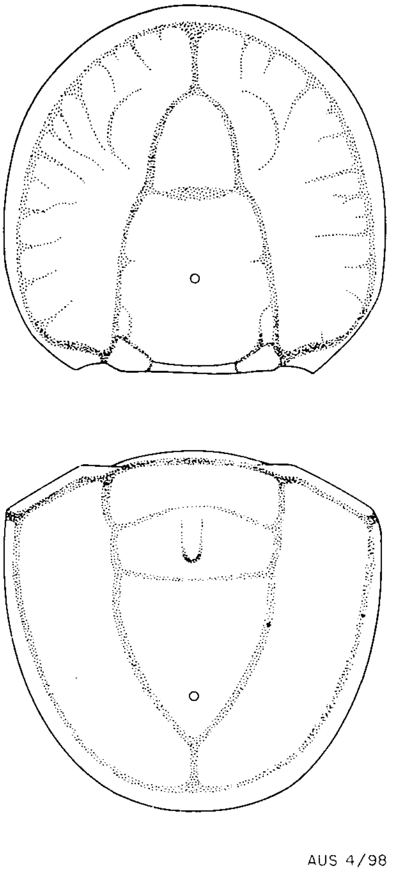

Fig. 28. *Ptychagnostus idmon.*

Diagnosis: Ptychagnostus idmon is distinguished by the change of direction of the axial furrows in their passage from the slender frontal lobe to the flanks of the stout posterior glabellar lobe; and by the structure of the double basal lobes, whose anterior part is almost confluent with the glabella. The pygidial axial node is low and short, and the node on the posterior axial lobe is placed well to its rear.

Differential diagnosis: Ptychagnostus idmon differs from other species in its glabellar structure (the narrow frontal and broad posterior lobe and the change of the direction of the axial furrows behind the transverse furrow); with its double basal lobes it remains nevertheless a regular *Ptychagnostus*; the glabellar structure, however, is the same as in *Ptychagnostus* (*Zeteagnostus*) *incautus* (q.v.), whose basal lobes are only vestiges fully incorporated in the glabellar rear.

Description: In the cephalon the border is very narrow; the cheeks are scrobiculate, but the arcuate scrobicules are erratic (a pair, or a single, or even absent), and divided by the preglabellar median furrow. The frontal glabellar lobe, about 0.37x the glabella in length, is pointed and slender, and in its posterior half has subparallel to slightly convex flanks. The posterior glabellar lobe is the widest, expanding visibly behind the transverse glabellar furrow; there is also a pair of short lateral indentations and a subcentral low median node. The glabella rear is rounded; the basal lobes are double; the anterior part of a lobe is narrow, inconspicuous, and separated from the glabella by a rather shallow furrow; it rests in a recess of the glabellar flank and remains confined by the continuous axial furrow; the posterior part is triangular, swollen, small, and surrounded by furrows; its posterolateral tip extends abaxially from the line of the glabellar flank. The posterolateral spines are short.

The pygidium is semielliptical, with an evenly curving margin and a narrow border. The axis is trilobate with transcurrent transverse furrows; on the second lobe the median node is low and short. The posterior lobe is slightly expanded in front and triangular, with slightly convex flanks converging to an acute tip; a small node is placed in the rear of the posterior lobe; its distance from the tip is 0.25x the lobe's length. The test is granulose; the granules are low and rounded—much finer than, but still reminiscent of, *Ptychagnostus punctuosus.*

Comment on illustrated specimens

The two following specimens were obtained from a limestone bank of the Inca Formation.

The holotype cephalon is 2.3 mm long; on the left the basal lobes are exposed and the anterior lobe is nesting in, but not quite fused with, the glabella. The cephalon is associated with a pygidium of *Peronopsis fallax.*

The pygidium Plate 43, fig. 7, CPC 14232, M208, is 2.2 mm long; it may even belong to the holotype cephalon (pygidia are usually slightly shorter than the cephalon). The second transverse furrow is transcurrent and not interrupted by the tip of the median node, which is quite low.

The next two specimens came from the Currant Bush Limestone, locality M176, upper part of the outcrop.

The cephalon Plate 43, fig. 6, CPC 14231, is 2.8 mm long. It is collapsed and creased and its scrobicules are therefore accentuated. The basal lobes are well exposed and their posterolateral tips are beyond, and out of the line of, the glabellar flanks.

The small and immature cephalon Plate 43, figs. 8 and 8a, CPC 14233, is 1.2 mm long; it is very convex and without scrobicules. It seems very close to *Pt. (Zeteagnostus) incautus* (q.v.) but its basal lobes are developed properly.

Occurrence and age: Ptychagnostus idmon occurs in the Inca Formation (M208, M149) and in the Currant Bush Limestone; usually rare it is common in M149. It is a bi-zonal Floran species: collection M208 belongs to the Zone of *Ptychagnostus atavus* and collection M149 and M208 to the Zone of *Euagnostus opimus.*

Ptychagnostus scarifatus sp. nov.

(Pl. 44, figs. 1-5; Pl. 58, fig. 2; Text-fig. 29)

Material: Illustrated are three cephala and one pygidium, selected from ten shields in a single bed of limestone, locality M176.

Holotype: The cephalon Plate 44, figs. 2 and 3, CPC 14235, is selected as the holotype; it has lost its test, but shows the structure of the basal lobes and is undeformed.

Diagnosis: Ptychagnostus scarifatus, a regular species of its genus, is distinguished by its glabellar frontal lobe being slightly but distinctly narrower than the frontal part of the posterior lobe, and by confluence of the tips of the basal lobes with the glabella; in the pygidium the median node on the second annulation reaches the transverse furrow, the anterior axial lobe is undivided, and the node on the posterior lobe is placed behind its midpoint, at about 0.55 to 0.6x the length of that lobe.

Differential diagnosis: In *Ptychagnostus idmon* the frontal lobe is narrower, the posterior lobe

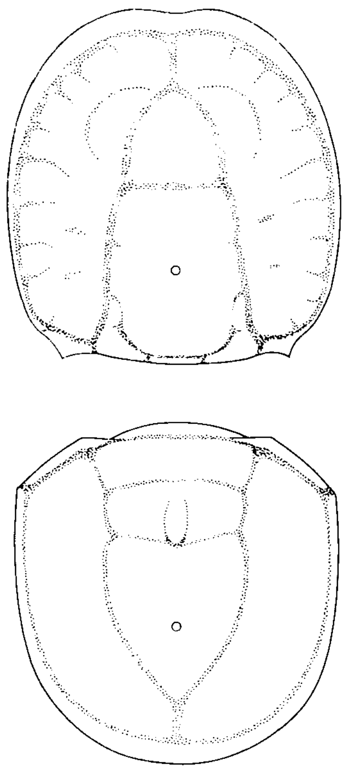

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Fig. 29. *Ptychagnostus scarifatus.*

behind the transverse furrow visibly wider, and the axial median node shorter, than in *scarifatus*; the node on the posterior axial lobe in *idmon* has also a more retral position, but the anterior axial lobe has a similar structure in both these forms. *Ptychagnostus atavus* has the frontal lobe as wide as the posterior lobe, fully developed double basal lobes, lateral lobules in the anterior axial annulation, and a quite prominent median node on the second annulation. It should be noted that defective specimens of *Ptychagnostus scarifatus* can be confused with the older *Pt. atavus* and become a source of erroneous stratigraphic interpretations.

Description: In the cephalon the rim in the midline projects slightly rearward and the projection can be supplemented by a recess in the frontal margin. The glabella is relatively broad and its lateral indentations (the usual pair) are inconspicuous and very short. The scrobicules are moderate to strong, but slightly irregular.

In the pygidium the rim is narrow, the furrows are distinct, and the postaxial furrow is present. In the axis the lobes are separated from each other by transcurrent furrows; the posterior lobe, slightly dilated about its middle, contracts retrally to an acute apex. The shields, especially the pygidium, are strongly arched longitudinally and transversely. The ornament detected on the pygidium consists of delicate lines in a Bertillon pattern too fine for illustration.

Comment on illustrated specimens

The holotype cephalon is 2.5 mm long; its front is emarginate and the almost fused basal lobes are exposed; a short sulcus (cleft) is evident in the glabellar front. Associated is a pygidium of *Triplagnostus diremptus.*

The pygidium Plate 44, fig. 5, CPC 14237, is 2.3 mm long; the median node reaches the transverse furrow; the anterior axial lobe is not subdivided.

The cephalon Plate 44, fig. 4, CPC 14236, is 3.0 mm long; it is fractured but retains its convexity. The frontal glabellar lobe is narrower than the posterior lobe; the anterior part of the basal lobe is ill defined adaxially; the arcuate scrobicules are rather weak. The frontal emargination is unclear.

The cephalon Plate 44, fig. 1, CPC 14234, is 3.0 mm long; it is moderately compressed and the glabellar rear is collapsed at a fracture (an open cleft); the frontal glabellar lobe is narrower than the posterior lobe, the scrobicules are well impressed, and of the frontal emargination the retral projection of the inner edge of the rim is present. The basal lobes have unequal relief.

The cephalon associated with *Criotypus lemniscatus,* Plate 58, figs. 2 and 3, is 3.5 mm long; it is flattened in shale and the collapsed basal lobes are clear.

Occurrence and age: Ptychagnostus scarifatus has been found in the Currant Bush Limestone, locality M176; it is also present below that limestone at the same locality in shale of the Inca Formation; its age is the Floran Zone of *Euagnostus opimus.*

Ptychagnostus sp. aff. **scarifatus**

(Pl. 44, fig. 6)

The illustrated pygidium, CPC 14238, locality M176, and associated with *Ptychagnostus scarifatus* and *Pt. idmon,* is 2.5 mm long. It is very convex ('superconvex') and distinguished by its wide and flat rim.

Ptychagnostus mesostatus sp. nov.

(Pl. 40, fig. 8; Pl. 41, figs. 6 and 7)

Material: The material, all illustrated, consists of one complete exoskeleton and one isolated pygidium, each from a different locality and formation.

Holotype: The complete exoskeleton Plate 41, figs. 6 and 7, CPC 14216-7, is the holotype.

Diagnosis: Ptychagnostus mesostatus is distinguished by the combination of the following characters: (1) the posterior glabellar lobe has parallel flanks; (2) arcuate scrobicules are present; and (3) the pygidium is granulose all over.

Differential diagnosis: Ptychagnostus intermedius is different in having a tapering glabella and a much finer granulation; *Pt. atavus* is similar only regarding its incidental arcuate scrobicules; and in *Ptychagnostus punctuosus* and its subspecies arcuate scrobicules are unknown, the glabella is tapering, and the ornament is coarse.

Description: The preglabellar median furrow is short, not reaching the border; the frontal glabellar lobe, about 0.37x the glabella in length, is about triangular and sulcate in front. A median glabellar node is not evident except for a slight gibbosity about the middle of the posterior lobe. The basal lobes are triplicate as incidentally in *Pt. punctuosus.* The glabella, as wide as 0.42-0.43x its length, has a shape reminiscent of a *Triplagnostus* rather than a *Ptychagnostus.* In the pygidium the granulation is dense and visible under a low magnification, but in *intermedius* a magnification of about x10 is necessary. The pygidial median axial node is large and prominent, the anterior axial lobe shows a pair of tumid lateral lobules and in the posterior, converging flanks of the axis are straight. The thorax, as long as about 0.26x the cephalon, is larger than in *intermedius,* but about the same as in *atavus* and *punctuosus.*

Comment on illustrated specimens

The holotype, in friable siliceous siltstone with chert, Inca Formation, locality M59, is 5.2 mm long. The fracture in the frontal glabellar lobe is accidental; a piece of the cephalon, recovered from the mould, was cemented in its place, but another piece is lost. The preglabellar median furrow is short and the basal lobe triple. The arcuate scrobicules are well visible and the glabellar front is sulcate.

The pygidium Plate 40, fig. 8, CPC 14208, locality M64, Current Bush Limestone, is 2.8 mm long. The test is deformed. It is granular all over, but the granulation is finer than in the holotype and the shape of the shield and its axis recall *Pt. punctuosus affinis;* in *affinis,* however, the ornament is relatively coarse.

Occurrence and age: Ptychagnostus mesostatus has been found in the Inca Formation and possibly in the Currant Bush Limestone and Quita Formation; its age is the Undillan Zone of *Ptychagnostus punctuosus.*

?**Ptychagnostus** sp. indet. A (aff. **atavus**)

(Pl. 42, figs. 3, 4)

The illustrated cephalon, the only available specimen, CPC 14221, is 3.8 mm long. The characters of a *Ptychagnostus* are: (1) the triple and long basal lobes (see *Ptychagnostus punctuosus,* Text-fig. 26), (2) the short triangular cephalic prongs (spines), (3) the dimpled cheeks with the arcuate scrobicules, and (4) the blunt and spineless glabellar rear. Unique, however, is the structure of the glabella at the basal lobes; the glabellar flanks are slight without lateral recesses to accommodate the basal lobes—a structure of a *Glyptagnostus* (Öpik, 1961a, text-fig. 15) hitherto unknown in the Ptychagnostinae. The glabella is deformed (collapsed in the midline and fractured in the rear) but these defects have not influenced the shape of the basal lobes.

The generic name is queried in the absence of other supporting specimens, and the species remains unnamed for the same reason.

Occurrence and age: ?Ptychagnostus sp. indet. A has been obtained from a piece of siltstone with chert of the Inca Formation, collection M427; its age is the Floran Zone of *Ptychagnostus atavus.*

Ptychagnostus sp. indet. B (aff. **atavus**)

(Pl. 49, figs. 1-4)

Material: Illustrated are two cephala and two pygidia, in limestone from a single locality.

Description: The cephala and the pygidia, taken alone, as well as a paradigm, possess the diagnostic characters of *Ptychagnostus*: no extended spines are evident, pygidial marginal spines are absent, a subcentral node is present on the posterior axial lobe, the glabella tapers forward, has a median node behind the midpoint of its posterior lobe, and double basal lobes. The species differs from *Ptychagnostus atavus* by its smooth cheeks, neither rugose nor scrobiculate, by the posterior position of the glabellar median node, and by the prominence of the node on the second axial lobe in the pygidium.

The cephalon Plate 49, fig. 4, CPC 14266, is 3.7 mm long; its frontal glabellar lobe seems narrower than in the next.

The cephalon Plate 49, fig. 2, CPC 14264, is 2.6 mm long; the cephalic spine on the right corner seems long because some matrix has been left around it as a necessary support. The frontal glabellar lobe is broad and the glabellar rear is well rounded.

The pygidium Plate 49, fig. 3, CPC 14265, is 3.5 mm long; the test is crushed but the prominent axial node and the small node in the middle of the posterior lobe are preserved; the spineless rim is narrow.

The pygidium Plate 49, fig. 1, CPC 14263, is 4.0 mm long. The anterior lobe of the axis and the articulating half-ring, which are defective in the other pygidium, are preserved.

Occurrence: The described shields of *Ptychagnostus* have been found in limestone of the Inca Formation, locality D150; the age is the Floran Zone of *Ptychagnostus atavus.*

Ptychagnostus sp. indet. C

(Pl. 42, figs. 1, 2)

Illustrated are two pygidia which are apparently conspecific; they cannot be attributed to a named species and no cephalon attributable to these pygidia is known.

The pygidium Plate 42, fig. 1, CPC 14219, is 3.0 mm long; the matrix is shale of the Inca Formation, collection M263. The rim is narrow, there are two nodes on the second axial lobe (as in *Ptychagnostus punctuosus*) but their relief is rather low, and the axis is relatively short and broad. The articulating device is simple. Associated in the photograph is a pygidium of *Aotagnostus aotus.*

The pygidium Plate 42, fig. 2, CPC 14220, in impure limestone of the Quita Formation, locality D69, is 2.2 mm long; its test is silicified, but worn. It is smaller than the other specimens, its axis is also less expanded, and the postaxial median furrow seems incomplete.

The general aspect of these pygidia recalls *Ptychagnostus idmon* and *Pt. scarifatus* and, owing to the absence of ornamentation, to a lesser degree *Pt. punctuosus.*

Occurrence and age: Ptychagnostus pygidia of the kind described here are rare in collections from the Inca Formation, Currant Bush Limestone, and Quita Formation; the age is early in the Undillan Zone of *Ptychagnostus punctuosus.*

PTYCHAGNOSTINAE, gen. indet., sp. nov.

(Pl. 49, fig. 5)

The illustrated pygidium, CPC 14267, is 4.0 mm long, of an exoskeleton some 9 to 10 mm in length. The structure of the axis is typical of the subfamily Ptychagnostinae; the subcentral position of the node on the posterior axial lobe suggests a form related to *Triplagnostus* or even *Criotypus,* but not *Acidusus*; the stump of the axial spine and right side marginal spine exclude the genus *Ptychagnostus.* An undescribed, new species is indicated by the narrowness of the rim, forward position of the possibly sideways deflected marginal spines, and the prominently broad pygidial axis.

Occurrence and age: Limestone of the Inca Formation, locality D154; the age is the Zone of *Ptychagnostus punctuosus* (early part) or late in the Zone of *Euagnostus opimus.*

Subgenus **Ptychagnostus (Acidusus)** nov.

The type of *Acidusus* is *A. acidusus* sp. nov.

Diagnosis and concept of the subgenus: Ptychagnostus and *Acidusus* share (1) the forward-tapering glabella, (2) the double basal lobes, and (3) a pygidium without marginal spines; the distinguishing character of *Acidusus* is its terminal pygidial axial node (sting, knob).

In the species of *Ptychagnostus* and in the majority of the Ptychagnostinae a node is present about, or behind, the middle of the posterior pygidial lobe. In *Tomagnostella* and in *Zeteagnostus* the node is terminal, but these genera (q.v.) are structurally different from *Ptychagnostus* and *Acidusus.* A terminal node is also prevalent in the Agnostinae, and Pseudagnostinae of the Upper Cambrian; it has the same position as the spine of *Pagetia,* as discussed below under *Acidusus acidusus.* The node in a more forward position in the majority of the ptychagnostids and peronopsids may or may not be a homologue of the terminal node, and an explanatory hypothesis regarding these matters has been put forward by Öpik (1967, p. 61). The structure of the axial pygidial node in *Acidusus* resembles *Onymagnostus, Aotagnostus,* and *Goniagnostus* (clear in Pl. 61, fig. 2) in having its base extended onto the anterior part of the posterior lobe that is also weakly indicated in *Ptychagnostus* and *Triplagnostus* (see *Acidusus* aff. *occultatus,* Text-fig. 31). Eight species are attributed here to *Ptychagnostus* (*Acidusus*) as listed below in four separate groups; the first six species are arranged according to the increase in the number of spines.

Group A—species without axial spines and without extended cephalic spines:

1. *Acidusus acidusus,* whose cephalon (apart from the pygidium) can be confused with *Ptychagnostus punctuosus affinis*;
2. *Acidusus navus,* with a cephalon reminiscent of *Ptychagnostus atavus.*

Group B—species with an axial spine in the thorax and extended cephalic spines:

3. *Acidusus retrotextus*;
4. *Acidusus germanus*.

Group C—species with an axial spine on the thorax and the pygidium.

5. *Acidusus occultatus*;
6. *Acidusus* sp. aff. *occultatus*.

Group D—incompletely known forms:

7. *Acidusus* sp. indet. aff. *germanus*; one distorted exoskeleton.
8. *Acidusus* sp. nov., one cephalon and one pygidium; the pygidium has marginal spines which otherwise are unknown in *Ptychagnostus;* each shield may belong to a separate species.

The species of Groups B and C are reminiscent of *Triplagnostus* in their spinosity; but the glabella of *Triplagnostus* has parallel flanks and the posterior pygidial axial lobe has a node about its middle.

The same aggregate of four spinose species can be regarded, if necessary, as a separate subgenus of *Ptychagnostus,* or even of *Acidusus.*

The defective specimen of *Acidusus* sp. aff. *occultatus* (q.v.) is structurally informative and may represent a form quite different from *occultatus* itself.

The ptychagnostid described by Robison (1964, pl. 79, fig. 15) as *Ptychagnostus richmondensis* (Walcott) suggests an *Acidusus* of our group A (without axial spines); *Pt. richmondensis* itself, as revised by Palmer (1954, pl. 12, fig. 4), is a species with very long cephalic spines and without a pygidial axial spine; these forms are not evident in Australia and their subgeneric classification within *Ptychagnostus* remains inconclusive. Robison's (1964, pl. 79, fig. 12) complete specimen in the paradigm of *Ptychagnostus richmondensis* represents an unnamed species of *Goniagnostus* without pygidial marginal spines (see comment on *richmondensis* under *Goniagnostus*).

Ptychagnostus (Acidusus) acidusus sp. nov. (Pl. 46, figs. 2-4)

Material: The available material consists of a complete exoskeleton and one isolated pygidium from a single limestone bed.

Holotype: The complete exoskeleton, Plate 46, figs. 2 and 3, CPC 14248.

Diagnosis: Ptychagnostus (*Acidusus*) *acidusus* is a species with short triangular cephalic prongs and without axial and pygidial marginal spines distinguished by its narrowly blunt and sulcate glabellar front, deep cephalic scrobicules, and pygidial pleural lobes ornamented with crowded granules and pits; each cephalic fulcral prong is tipped by a small spine-like point.

Differential diagnosis: The general design of *Acidusus acidusus* is reminiscent of *Ptychagnostus punctuosus affinis,* especially regarding the development of the cephalic scrobicules; in *Pt. punctuosus,* however, the glabellar node is placed well forward, the node on the posterior axial lobe of the pygidium is subcentral, no terminal node exists, and the ornament of the pygidial pleural lobes consists of a coarser granulation without pits. In *Acidusus navus* the frontal glabellar lobe is long and pointed, its scrobicules are shallow but regular, and the posterior pygidial axial lobe is obese and rounded in the rear. Finally *Acidusus retrotextus* has also a narrowly blunt and sulcate glabellar front, but its cephalic spines are extended and needle-like, the scrobicules are shallow, the second segment of the thorax has an axial spine, and its pygidial rim is distinctive in its broadness.

Description: The holotype exoskeleton is 7.0 mm long; the cephalon is about 10 percent longer than the pygidium, and the thorax, 0.25-0.27x the cephalon in length, is therefore relatively short. The cephalic rim is very narrow, even less than half the pygidial rim. The cheeks are rugose, the scrobicules are deeply impressed and irregularly discontinuous, and some scattered dimples are also apparent; the preglabellar median furrow is unevenly deep and is like a chain of scrobicular dimples rather than an even furrow. The axial furrows are deep and straight, evenly flanking the basal lobes and the tapering glabella; the frontal glabellar lobe, 0.36x the glabella in length, is not pointed but narrowly blunt in front and its median sulcus is short. The lateral glabellar furrows are broad and deep and the furrows separating the basal lobes from the glabella are also well impressed; the median node is small but distinct, placed between the tips of the basal lobes and well behind the midpoint of the posterior glabellar lobe. The basal lobes are long and double, but the duplication is expressed by a transverse constriction rather than a deep furrow. The cephalic spines are triangular, short, and have drawn-out tips. The test of the cephalon is minutely and densely granulose.

In the thorax a low axial node with a reclined tip stands on the anterior segment; the fulcral points are shorter than the cephalic spines and no axial spine is present on the second segment: the structure of the thorax is the same as in *Ptychagnostus* and in the majority of Agnostacea as well.

In the pygidium the rim is slightly convex and relatively wide even in its anterior part; the shoulders are strong, with forward-directed short fulcral prongs. The axis is long (0.8x the shield length) and its ptychagnostoid trilobation is well expressed by the deep transverse furrows. The anterior axial lobe is tripartite and the lateral, slanting parts of the anterior furrow are deeply sunk, as in *Acidusus occultatus* (Text-fig. 30). The second transverse furrow, laterally horizontal, surrounds in the middle the rear of the stout median node, which extends onto the anterior part of the posterior lobe; this extension is shorter than in *Acidusus occultatus* and much shorter than in *Aotagnostus* and *Onymagnostus*; the rear of the median node is crowned by a small node. The posterior lobe has about five pairs of notulae and its terminal node is prominent and reclined, reminiscent of, and probably homologous with, the terminal spine of *Pagetia,* as well as of *Serrodiscus spinulosus* Rasetti (1967, pl. 2, fig. 3) or *Analox bipunctata* (Rasetti, 1966, pl. 2, fig. 1). The postaxial furrow is shallow and the rear of the pygidium is emarginate. The test of the axis of the pygidium seems smooth, but its pleural lobes are rough with a combination of granules and punctation. The axis is notulate.

The pygidium Plate 46, fig. 4, CPC 14249, is 2.4 mm long. Its rim in the rear is deformed and the emargination is obscure.

Occurrence and age: Acidusus acidusus has been found in the V-Creek Limestone, locality M234; its age is the Undillan Zone of *Doryagnostus notalibrae.*

Ptychagnostus (Acidusus) navus sp. nov.

(Pl. 46, fig. 1)

Holotype: The illustrated complete exoskeleton, CPC 14247, locality M214, is the holotype; no other specimens attributable to the species have been collected.

Diagnosis: Ptychagnostus (*Acidusus*) *navus* is a species with short triangular cephalic prongs and without axial and pygidial marginal spines; distinguished by the combination of a cephalon having a pointed and relatively long frontal glabellar lobe and regular but shallow pinnate scrobicules; and a pygidium having an obese posterior axial lobe rounded in the rear and no postaxial median furrow.

Differential diagnosis: Acidusus navus and *A. acidusus* are similar regarding the absence of spines with the exception of the short cephalic spines; for this reason they share a structurally identical thorax. In *A. acidusus,* however, the front of the glabella is blunt, the frontal glabellar lobe is shorter, the scrobicules are different, and the posterior pygidial lobe is pointed in the rear. The cephalic structure in *A. navus* seems close to *Ptychagnostus atavus* and related forms, but the pygidial axial structure is reminiscent of the Late Cambrian *Innitagnostus inexpectans* (Kobayashi) as illustrated by Palmer (1962, pl. 1, figs. 6 and 9) and Öpik (1963, pl. 2, figs. 10, 11, and text-fig. 6). Among the Ptychagnostinae the pygidial axis is also rounded in the species of *Myrmecomimus.*

Description: The holotype of *Ptychagnostus* (*Acidusus*) *navus* is 6.3 mm long; the test is intact and the cephalon and the thorax are in contact ready for articulation; the second segment and the pygidium are, however, slightly displaced, apparently after the dead body came to rest on the sea-floor. The cephalon cannot be distinguished conclusively from *Ptychagnostus atavus*; the glabella, about 0.8x the shield length, is longer than in the Australian specimens (Text-fig. 27) of *atavus* but differs little from the Swedish ones illustrated by Westergaard (1946). The frontal glabellar lobe, 0.42x the length of the glabella, is relatively long. The rim is narrow and convex, the scrobicules are shallow and pinnate, more regularly than in most of the cephala of *atavus.* The glabellar median node, placed slightly behind the midpoint of the posterior lobe, is small; the basal lobes are tumid, long and double, but the dividing transverse furrow is shallow. The thorax, about 0.25x the cephalon, is of the same age as in *Ptychagnostus atavus;* no axial spine is present, the fulcral points are angular short projections—diminutive replicas of the cephalic spines—and the posterior segment has an angular rear margin filling the articulation recess in the front of the pygidial axis—a frequent structure in such agnostids, with or without the axial spine, as are provided with the recess.

In the pygidium the rim is convex and relatively wide—about twice the cephalic rim; the shoulders are thick and separated from the rim by the extension of the marginal furrow; the pleural lobes are moderately convex. The pygidial axis, 0.75x the shield length, is prominent and strong in relief. The anterior axial annulation has tumid flanks and is narrow in the middle owing to the retral articulating recess and forward-projected second lobe—in the manner seen also in *Ptychagnostus* (*Acidusus*) aff. *occultatus* (q.v.). The second axial lobe is transversely hexagonal and bounded by the deep transverse furrows of two oblique (slanting) branches; the hexagon itself is tripartite, with a stout median axial node which is topped in the rear by a small knob. The posterior axial lobe, obese and about oval, carries close to its tip the terminal node, which is rather small: the test is relatively thick and conceals the node which should be stronger in cast.

The ornament in the cephalon consists of a minute granulation; it is also minute (almost imperceptible) on the axial lobe of the pygidium, but more prominent on the rim and the pleural lobes; the punctation seen in *Acidusus acidusus* is, however, absent here.

Occurrence and age: Ptychagnostus (*Acidusus*) *navus* is a fossil of the V-Creek Limestone, locality M214; its age is the Zone of *Doryagnostus notalibrae*.

Ptychagnostus (Acidusus) retrotextus sp. nov.
(Pl. 46, fig. 5)

Holotype: The illustrated complete specimen, CPC 14250, is the holotype; this specimen is unique.

Diagnosis: Acidusus retrotextus has scrobiculate cheeks, extended (but relatively short) cephalic spines, a slender axial spine on the second segment of the thorax, no axial spine in the pygidium, a prominent terminal node, and a blunt and sulcate glabellar front; it is distinguished by its strongly tapering glabella, small basal lobes, and wide pygidial rim.

Differential diagnosis: Acidusus germanus nov. also has no pygidial axial spine and its other spines are the same as in *A. retrotextus*; but in *germanus* the glabellar front is pointed, the basal lobes are strong and the pygidial rim is narrow; furthermore, its scrobicules in all specimens are weaker than in *retrotextus*. *A. occultatus* differs from *A. retrotextus* and *A. germanus* by its pygidial axial spine; its scrobicules are about as strong as in *retrotextus*, but the basal lobes are rather prominent. The glabellar front is also blunt in *Acidusus acidusus*, but it is spineless and possesses a distinctive pygidial ornament.

Description: The holotype of *Acidusus retrotextus* is 6.0 mm long. The pygidium and the thorax are in proper contact, but the cephalon is slightly displaced. Some small parts of the test are preserved—it is a very thin test. The cephalon is circular. The cephalic rim, of which a part is preserved in front, is extremely narrow and the pygidial rim is exceptionally wide and moderately convex. The thorax, about 0.25-0.27x the cephalon in length, is close in size to other species of *Acidusus*, and the cephalon is about 7 percent longer than the pygidium.

In the cephalon the scrobicules are narrow, starting from dimples at some distance from the glabella, and the preglabellar median furrow is distinct but narrow. The glabella, rather wide in the rear, tapers evenly forward to a narrow, bluntly rounded and sulcate front. The frontal glabellar lobe is 0.4x the glabella in length; the median glabellar lobe, well behind the midpoint of the posterior lobe, is small; the basal lobes are short, laterally bounded by the straight axial furrows and seemingly double. The cephalic spines are extended into delicate needles. The axial spine in the thorax is lost, but its presence is evident from the stump.

In the pygidium the axis, 0.65x the shield length, is relatively short, but its tip is quite close to the marginal furrow, and the shallow postaxial median furrow is therefore short. The second axial lobe is evenly arched upward and extends in the middle onto the anterior part of the posterior lobe; the median axial node is small and crowns the extension. The terminal node, close to the posterior tip of the axis, is conspicuous. The surface seems smooth, but obscure traces of a minute granulation and punctae are detectable on parts of the decorticated shields.

Occurrence and age: Ptychagnostus (*Acidusus*) *retrotextus* comes from the V-Creek Limestone, locality M416. The age is of the Undillan Zone of *Goniagnostus nathorsti*.

Ptychagnostus (Acidusus) germanus sp. nov.
(Pl. 47, figs. 1-6)

Material: The material in hand consists of eleven complete specimens and numerous isolated shields, all from a single bed of limestone; illustrated are two complete, specimens, two cephala, and three pygidia.

Holotype: The best preserved exoskeleton, Plate 47, fig. 1, CPC 14251, is selected as the holotype.

Diagnosis: Acidusus germanus is a species with extended but short cephalic spines and an axial spine on the second segment of the thorax, but without a pygidial axial spine; distinguished by the combination of a pointed glabella, very weakly scrobiculate to almost smooth cheeks, and a relatively narrow pygidial rim.

Differential diagnosis: Acidusus germanus and *A. retrotextus* are similar regarding the number and length of spines and the absence of the pygidial axial spine; but in *A. retrotextus* the glabellar front is bluntly rounded and sulcate, the scrobicules are clear, and the pygidial rim is much wider than in *A. germanus.* The cephalon of *A. germanus* is generally similar to *A. navus,* whose cephalic spines, however, are short, and the thorax and pygidium are rather different; apart from the spines and the terminal node, *A. germanus* resembles *Ptychagnostus atavus.*

Description: In *Acidusus germanus* the cephalon, in general terms, is structurally close to *A. navus,* but the pygidium to *A. acidusus*; complete specimens of these three forms cannot therefore be confused with each other; but cephala of *A. germanus* and *navus* and pygidia of *A. germanus* and *A. acidusus* can be confused. Nevertheless preserved isolated shields are sufficiently disparate and can be identified.

Acidusus germanus is relatively small, attaining a length of 6 to 7 mm. The cephalic rim is very narrow and convex; in the pygidium the rim is wider—of a moderate width; the cephalon is about 10 percent longer than the pygidium and the thorax 0.26-0.28x the cephalon. The scrobicules are weak (weaker than in *Acidusus navus*) and almost undistinguishable in several cephala. The glabella tapers forward from a relatively wide rear (wider than in *navus*) and is pointed; the frontal glabellar lobe, variable from 0.37-0.4x the glabella in length, remains slightly shorter than in *navus* and the median node is also a little more retral. The basal lobes are long, prominent, and double (as in *navus*). The cephalic spines are extended (and different from the short triangular projections of *navus*), attenuated, and a little longer than a segment of the thorax. In the pygidium of *germanus* the axis, 0.7-0.75x the shield length, is slightly shorter than in *A. acidusus,* but it is spineless in both, and quite similar in shape. The terminal node is low and inconspicuous (a 'sting' in *A. acidusus*) and the pygidial rear is evenly arched in plan and without an emargination. The pygidial ornament consists of a dense and minute granulation reminiscent of *Acidusus navus.* The pygidial axial median node is prominent and straddles the second transverse furrow; when lost (Pl. 47, fig. 2) its scar can be mistaken for the base of an axial spine because of the similarity with such a scar in *Acidusus occultatus,* which has an axial spine.

Comment on illustrated material

All specimens were collected from the V-Creek Limestone, locality M214.

The holotype is 4.5 mm long. The left cephalic spine and the stump of the axial spine of the thorax are preserved; the median pygidial axial node is quite prominent and the terminal node is low and almost invisible. The scrobicules are very weak.

In the exoskeleton Plate 47, fig. 2, CPC 14252, the cephalon is 3.0 mm long—the whole was about 6.5 mm. The basal lobes are long and double and tumid with a shallow dividing furrow in between. The base of the median axial node in the pygidium intrudes the frontal part of the posterior lobe.

Of the two cephala Plate 47, fig. 6 and Plate 61, fig. 4, the smaller (CPC 14256) is 2.5 mm long; its right spine is preserved; in the larger cephalon (a mould in the matrix) the scrobicules are visible. A pygidium of *Goniagnostus nathorsti* is associated.

The pygidium Plate 47, fig. 4, CPC 14254, is 2.6 mm long; its articulating half-ring is exposed; the terminal node is a low swelling. Of the two pygidia, Plate 47, figs. 3 and 5, CPC 14253, 14255, the larger is 2.3 mm and the smaller (immature) 1.7 mm long; the terminal node is clear, especially in the mould; minute granulation is apparent.

Occurrence and age: Ptychagnostus (Acidusus) germanus comes from a single site, M214 of the V-Creek Limestone; its age is the Undillan Zone of *Doryagnostus notalibrae.*

Ptychagnostus (Acidusus) occultatus sp. nov.

(Pl. 48, figs. 1-2; Text-fig. 30)

Material: Illustrated are three exoskeletons, selected from, and associated with, numerous isolated shields.

Holotype: The complete specimen in limestone Plate 48, fig. 1, CPC 14257, is selected as the holotype; the two other specimens, in a friable silty calcareous matrix, are preserved less well.

Diagnosis: Acidusus occultatus is characterised by the combination of a cephalon with well developed scrobicules and dimples, pointed glabellar front, tumid and clearly double basal lobes, relatively long cephalic spines, an axial spine in the thorax, and a visibly prominent terminal node; and is distinguished by possessing a median axial spine in the pygidium.

Differential diagnosis: Acidusus occultatus is generally similar to *A. germanus,* but in the latter the scrobicules are weak or even vestigial, the basal lobes are divided less clearly, the cephalic spines are shorter, the terminal node is low, and the median axial node is not extended into a spine. It seems to me that specimens attributed to *Triplagnostus atavus* by Whitehouse (1936, pl. 8, figs. 8 and 9) from the Yelvertoft area belong to *Acidusus occultatus*: in one of these (fig. 9) the stump of the pygidial axial spine is indicated (see also Hill et al., 1971, pl. 9, fig. 6).

Description: The holotype has lost a chip off its front, and its pygidium is a little displaced; its original length should be about 6.0 mm. The cephalon is the largest shield, about 12 percent longer than the pygidium, and the thorax is about 0.27x the cephalon in length. The cephalic rim, as in other species of *Acidusus,* is very narrow and convex, but the pygidial rim is broad, but less so than in *A. retrotextus.*

In the cephalon the scrobicules are well impressed and begin adaxially as dimples. The

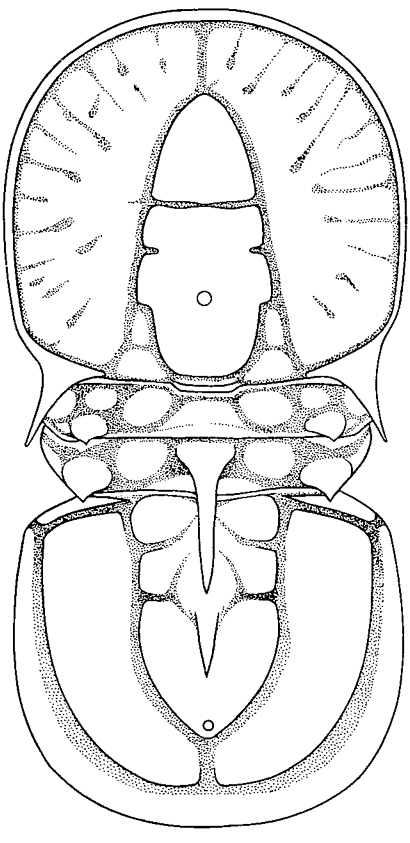

Fig. 30. *Ptychagnostus (Acidusus) occultatus.*

frontal glabellar lobe, 0.4x the glabella in length, has convex flanks and a pointed tip without a sulcus; the median glabellar node stands behind the midpoint of the posterior lobe; the strong basal lobes are divided by deep transverse furrows; the cephalic spines are longer than in other species of the subgenus, as evident from the broken right spine of the holotype. The length of the axial spine in the thorax is unknown, but its stump is quite strong. In the pygidium the axis has a well developed relief and is 0.7-0.72x the shield length. The anterior axial lobe is bipartite, with tumid lateral lobules connected in front and separated in the rear by the acute forward projection of the second lobe; the base of the axial spine straddles the rear of the second and the front of the posterior lobe, and the spine itself is visible in the next specimen; in the holotype the spine left its impression on the middle of the posterior lobe. The terminal node is almost as prominent as in *Acidusus acidusus.* The cephalic and the pygidial test is minutely granulose.

Of the two complete specimens Plate 48, fig. 2, CPC 14258, the largest is 5.4 mm long; details of the structure are obscured by the granulosity of the silty matrix, but a large part of the pygidial axial spine is preserved.

Occurrence and age: The described material of *Ptychagnostus (Acidusus) occultatus* comes from limestone and siltstone of the Inca Formation, locality M60, of the Zone of *Ptychagnostus punctuosus*; two cephala and two pygidia (CPC 14377) are also present in a piece of limestone (V-Creek Limestone), collection M57, Zone of *Goniagnostus nathorsti.*

Ptychagnostus (Acidusus) sp. aff. **occultatus**

(Pl. 48, fig. 3; Text-fig. 31)

Material: The material consists of one complete but defective exoskeleton, one cephalon, and one pygidium.

Description: The illustrated specimen of *A.* aff. *occultatus,* CPC 14259, is 6.8 mm long. It is defective and a species name is therefore reserved. The posterior glabellar lobe, almost all of the thorax, and the median axial node of the pygidium are lost, and the lost parts cannot be visualised, but the following structures are evident: (1) the frontal glabellar lobe has a bluntly angular front; (2) each basal lobe has a central dimple—a quite unique feature among agnostids; (3) the anterior pygidial axial lobe is bipartite, completely divided by the attenuated forward projection of the second axial lobe; and (4) the

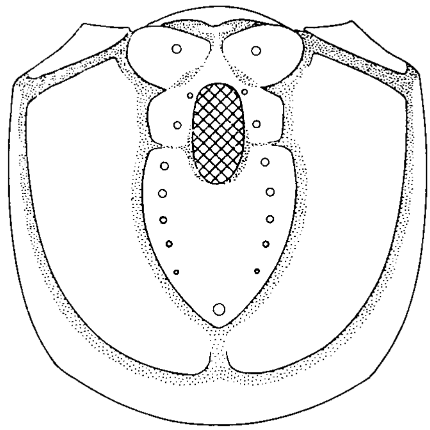

Fig. 31. *Ptychagnostus (Acidusus)* **sp. aff.** *occultatus.* **Central part of the test is lost.**

pygidial margin is posterolaterally angulate, indicating 'potential' marginal spines. The cephalic scrobicules with dimples and the prominent terminal node bear some resemblance to *Acidusus retrotextus,* which also has the wide pygidial rim. About eight pairs of axial notulae (Text-fig. 31) seem present and the postaxial median furrow is rather shallow. The base of the pygidial median node extends well rearward as in *Onymagnostus* and *Aotagnostus.*

Occurrence and age: The specimen described as *Ptychagnostus* (*Acidusus*) sp. aff. *occultatus* comes from the Inca Formation, locality M60; it is associated with *Acidusus occultatus*; the age is the Undillan Zone of *Ptychagnostus punctuosus.*

Ptychagnostus (Acidusus) sp. indet. aff. **germanus**

(Pl. 48, fig. 4)

The illustrated exoskeleton, locality M411 (top of the sequence), CPC 14260, is 4.6 mm long. It possesses a small node on the tip of its pygidial axis—a characteristic feature of *Acidusus*; no axial spine is evident on the pygidial axis and the cephalic spines as preserved are relatively prominent and may or may not have been attenuated into an extended point; the absence of an axial spine in the thorax is also inconclusive. Furthermore, the basal lobes are not preserved and the test is deformed in a manner preventing further comparison. Nevertheless, the structure of the pygidium recalls *Acidusus germanus.*

Occurrence and age: The described exoskeleton has been obtained from the V-Creek Limestone from strata assignable to the Undillan Zone of *Goniagnostus nathorsti.*

Ptychagnostus (Acidusus) sp. nov.

(Pl. 48, figs. 5 and 6)

Material: Illustrated are one pygidium and one cephalon, from the same zone but different formations; these shields may or may not be conspecific; the 'sp. nov.' in the title refers to the pygidium in the first place.

Description: The pygidium Plate 48, fig. 6, CPC 14262, locality D155, Inca Formation, is 2.2 mm long; *Acidusus* is indicated by the small node on the tip of the posterior axial lobe, and the novelty of the species is concluded from the combination of the spineless axial median node with the marginal spines; no such spines are known in other species of *Acidusus* or *Ptychagnostus.*

The cephalon Plate 48, fig. 5, CPC 14261, in limestone of the Quita Formation, locality D55, is 2.8 mm long. Its large double basal lobes, evenly forward tapering and pointed glabella and the relatively strong, triangular, but not extended, cephalic spines as well as scrobicules are indicative of *Ptychagnostus*; the design of the cephalon resembles *Acidusus germanus,* whose cephalic spines, however, are long.

The age of the two shields is the Undillan Zone of *Ptychagnostus punctuosus.*

Genus **Zeteagnostus** nov.

The type species of *Zeteagnostus* is *Z. incautus* nov.

Diagnosis: The characters of the genus are (1) the trapezoidal retrally dilated posterior glabellar lobes, (2) the rudimentary and simple basal lobes in holaspides, (3) the very short thorax, and (4) the position of the terminal node on the tip of the axis.

Differential diagnosis: Zeteagnostus cannot be confused with another genus of the Ptychagnostinae and is regarded therefore as a separate genus; nevertheless, its affinity with *Ptychagnostus idmon* sp. nov. and *Pt. scarifatus* nov. seems indicated by the similar shape of the glabella.

Zeteagnostus incautus sp. nov.

(Pl. 28, figs. 1, 5; Pl. 44, figs. 7-9; Pl. 45, figs. 1-4; Text-fig. 32)

Material: Illustrated are four exoskeletons and five isolated shields, selected from an abundant supply of specimens.

Holotype: The cephalon Plate 45, fig. 1, CPC 14242, is selected as the holotype; it is relatively large and conveniently associated with a smaller but complete holaspid test.

Diagnosis: The diagnosis is given under the heading of the genus, and is amplified by the descriptive data and the comment on illustrated specimens.

Comparison: The structure of the glabella and the pygidium of *Z. incautus* and *Ptychagnostus idmon* sp. nov. is quite similar; in particular, the narrow frontal and the expanded posterior glabellar lobes common to both, and not seen in other species, indicate a close kinship. In *Ptychagnostus idmon,* however, the double basal lobes and the scrobiculate cheeks prevent any confusion of the two species. At the same time, *Ptychagnostus idmon,* associated in the *atavus* zone with *Z. incautus,* survives the latter in passing on into the next, younger zone of *Euagnostus opimus.* Consequently *Zeteagnostus incautus, Ptychagnostus idmon,* and *Ptychagnostus atavus* appeared simultaneously in a temporal as well as in a phyletic sense. The phyletic relationships of these forms remain, however, inconclusive and speculative: *Z. incautus* arose either from a form with simple basal lobes, or as an offshoot of the *idmon* lineage in an initial process of effacement of the lobes. The morphogeny is also ambiguous: the cephalon of *Z. incautus* in immaturity (P. 45, fig. 2) possesses simple and clearly defined basal lobes, which in adults (in the holotype, for example) are fused with the glabella.

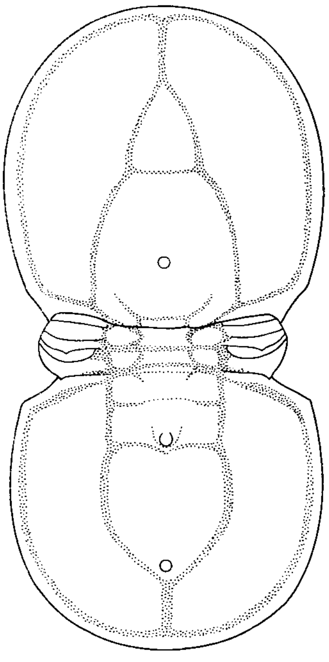

Fig. 32. *Zeteagnostus incautus.*

Description: Zeteagnostus incautus is a small agnostid attaining a length of 4.5-5.0 mm. Undeformed, its shields are evenly convex; flattened cephala are circular, and unflattened the shape is almost imperceptibly elongate elliptical to oval. The cephalon is as long as the pygidium and thorax taken together; the thorax is also short, 0.18-0.2x the cephalon in length. Spines, except for the posterolateral spines of the cephalon, are absent.

In the cephalon the rim is convex and narrow and has a small retral projection opposite the preglabellar median furrow accompanied by a slight frontal emargination—structures observable also in *Ptychagnostus scarifatus* sp. nov.; the cheeks are smooth, scrobicules are absent.

In the glabella the frontal lobe is pointed, triangular, and narrow, and 0.35x the glabella in length. The posterior lobe is trapezoidal, with a rear twice the frontal width; the rather inconspicuous basal lobes are incorporated in the glabella and laterally defined by the axial furrows; the abaxial tips of the basal lobes are not extended sideways. In immature cephala the simple basal lobes and the glabella are clearly separate, but in holaspides the separating furrows fade out before reaching the glabellar flank, and an indistinct pair of swellings is sometimes visible in the position of the anterior basal lobes. The median glabellar node is small and placed well behind the midpoint of the posterior lobe, as can be seen in Plate 44, fig. 8; occasional grains of the matrix, however, may obscure the node (as in Pl. 45, fig. 1).

In the pygidium the rim is slightly wider than in the cephalon and is not crossed at the anterolateral angles by the shoulder furrows—a structure of some rarity in agnostids. The axis is clearly trilobate, the median node on the second annulation is small, and there is a tiny node close to the pointed axial tip—in a position seen in the species of *Acidusus.* The postaxial median furrow is distinct.

In immature cephala of *Ptychagnostus idmon* the test is as smooth as in *Z. incautus,* but the abaxial tips of the basal lobes are extended laterally and at variance with the structure of *Z. incautus.*

Comment on illustrated specimens

All described and illustrated specimens, and indeed all available material of *Zeteagnostus incautus,* were obtained from the Inca Formation.

The holotype cephalon, collection M281, is 2.1 mm long. The silicified test is slightly flattened in shale so that the posterolateral spines and the feeble basal lobes are exposed. The posterior glabellar lobe shows in its anterior half a pair of shallow, short, oblique lateral furrows. The associated small holaspid test is 3.0 mm long. The pygidial axis has almost parallel flanks.

The exoskeleton Plate 44, fig. 9, CPC 14241, in shale, collection M281, is 3.7 mm long. The glabellar median node is relatively prominent and the posterior lobe of the pygidial axis is isolated.

The pygidium Plate 45, fig. 3, CPC 14244, in silty shale, collection M281, is 2.0 mm long and corresponds in size to the holotype cephalon. The continuity of the rim and the shoulder as well as of the marginal furrow and the shoulder furrow is well visible.

The cephalon and pygidium Plate 45, fig. 2, CPC 14243 are embedded in porous siltstone, locality M192. The cephalon is 1.2 mm long, and the shields are, presumably, parts of a single exuvia. It is an immature specimen with a short pygidial axis and quite well delineated simple basal lobes.

The next two specimens come from a fine-grained limestone, locality M423.

The cephalon Plate 44, fig. 8, CPC 14240, is 1.7 mm long. The test is smooth and the rim slightly projects in the midline retrally.

The complete test Plate 44, fig. 7, CPC 14239, is 4.3 mm long. The pygidial axis seems relatively long, and close to its tip a terminal node is indicated.

The exoskeleton Plate 45, fig. 4, associated with *Criotypus paenerugatus* (CPC 14245), locality M265, friable siltstone, is about 3.8 mm long; the node on the axial tip is well visible.

Occurrence and age: Zetagnostus incautus is quite common and widely distributed in the Inca Formation. Its age is the Floran Zone of *Ptychagnostus atavus*; the species is therefore instrumental in identification of that zone in view of the rarity of *atavus* itself.

Genus **Onymagnostus** nov.

The type species of *Onymagnostus* is *O. angulatus* nov.

Diagnosis: The species of the Ptychagnostinae aggregated under the name of *Onymagnostus* have no axial, fulcral, or extended cephalic spines and are distinguished by the combination of a slender and long pygidial axis 0.8-0.85x the shield length with the median node straddling the rear of the second and the front of the posterior lobe; in most of the known species a postaxial median furrow is absent; in *O.* (*Agnostonymus*) *semiermis* subgen. nov., sp. nov. pygidial marginal spines are present.

Differential diagnosis: In the recent literature the seven species listed below are referred to as *Ptychagnostus,* or *Triplagnostus,* or *Ptychagnostus* (*Triplagnostus*); the species of *Triplagnostus,* however, are disparate, having a parallel-sided posterior glabellar lobe, extended fulcral and long axial spines, and a different pygidial axis. In *Ptychagnostus,* as in *Onymagnostus,* axial spines are present, and the fulcral spines are short, but the structure of the pygidial axis is still quite different; nevertheless, *Onymagnostus* can be regarded as a subgenus of *Ptychagnostus* if necessary; but the species of *Ptychagnostus* (*Ptychagnostus*) and those of *Pt.* (*Onymagnostus*) require each a separate generic diagnosis. A straddling pygidial axial node occurs also in *Aotagnostus* and in *Ptychagnostus* (*Acidusus*). Attributable to *Onymagnostus* are the following already described species: *Agnostus hybridus* Brögger, *Agnostus stenorrhachis* Grönwall, *Ptychagnostus* (*Triplagnostus*) *convexus* Westergaard, *Ptychagnostus grandis* Hutchinson, *Agnostus laevigatus ciceroides* Matthew (with three simultaneous synonyms, according to Hutchinson, 1962, p. 85), and *Agnostus altus* Grönwall (a junior synonym of *ciceroides,* according to Hutchinson, op. cit.). The seventh species taxon is *Agnostus pulchellus* Illing (1916)—a possible synonym of *hybridus* (according to Westergaard, op. cit., p. 71); and the eighth is *Agnostus seminula* Whitehouse. Six of these are forms en grande tenue, and three (*Pt. convexus, A. ciceroides* and its variants, and *A. altus*) are more or less effaced; *ciceroides* is effaced in a style reminiscent of *Leiopyge laevigata* as discussed recently by Hutchinson (op. cit., p. 85). *O. ciceroides* and *altus* were included by Kobayashi (1939, p. 129) in the genus *Cotalagnostus* Whitehouse, and the subfamily Leiopyginae. The cephala of *ciceroides* in the paradigm of Hutchinson (op. cit., pl. 10), which includes also the holotype (pl. 9, fig. 20), reveal characters of the Ptychagnostinae; the complete exoskeleton some 20 mm in length (pl. 10, fig. 8), is effaced but interpretable as an image of *Onymagnostus mundus* sp. nov. (q.v.) In the effaced forms, the rearward extension of the pygidial median axial node seems much shorter. Finally, the effaced forms (*convexus, ciceroides,* and *altus*) are unsuitable for contemplating the diagnosis because of their effacement, but are nevertheless interpretable generically by comparison with species en grande tenue.

In passing, Hutchinson (1962, pl. 8, figs. 3, 4) illustrated two pygidia of *stenorrhachis* having a postaxial median furrow, and Westergaard (op. cit., p. 71) mentions the same in occasional specimens of *hybridus*; it appears therefore that the absence of the postaxial median furrow is not absolutely diagnostic for the genus.

Agnostus cf. *intermedius* Illing (1916, p. 408) from the zone of *Paradoxides hicksi* (about the Zone of *Hypagnostus parvifrons*), considered by Westergaard (1946, p. 77) under *Ptychagnostus atavus,* represents an unnamed species of *Onymagnostus*; (1) the basal lobes are simple; (2) there is no postaxial pygidial furrow; and (3) the cephalon and the pygidium are equal in length. The frontal glabellar lobe, about 0.33x the glabella in length, recalls *Onymagnostus mundus,* but no further comparison is possible owing to the imperfect preservation of the English specimen.

In the present paper the following species are described: *Onymagnostus angulatus* nov., *O.* aff. *angulatus, O. mundus* nov., *O. durusacnitens* nov., *O. seminula* (Whitehouse) and *Onymagnostus* (subgen. *Agnostonymus*) *semiermis* nov.; moreover, specimens attributed to *Onymagnostus stenorrhachis* (Grönwall) and *O. grandis* (Hutchinson) occur in Queensland and are described here.

Onymagnostus angulatus nov. is selected as the type species of the genus for the following reasons: (1) *O. semiermis* with is rounded, blunt glabellar front and pygidial marginal spines is a solitary aberrant form; (2) *O. mundus* and *O. seminula* are stratigraphically late and rare species and probably epigons of the stock; (3) *Agnostus gibbus hybridus* is the earliest named species; its original (Brögger, 1878) is in need of a material revision and the identification of that species in the literature refers to specimens from Sweden (Westergaard, op. cit., pl. 9, figs. 25, 26); (4) *O. stenorrhachis* is also in need of a revision in view of its pygidia from Newfoundland having a postaxial median furrow.

Onymagnostus angulatus sp. nov.

(Pl. 50, figs. 1-8; Pl. 51, figs. 1-3)

Material: Illustrated are (1) two exoskeletons and two pygidia and one cephalon (selected from about 20 shields) from the *Euagnostus opimus* zone; (2) one cephalon and three pygidia from the next younger Zone of *Ptychagnostus punctuosus,* and (3) one cephalon and one pygidium (the youngest available), from the *punctuosus* to *Goniagnostus nathorsti* interval, and structurally approaching *Onymagnostus hybridus* (Brögger, 1878; in terms of Westergaard, 1946).

Holotype: The cephalon Plate 50, fig. 2, CPC 14269, associated with a pygidium is selected as the holotype; it is supplemented for the purpose of the diagnosis by the associated pygidium, Plate 50, fig. 1.

Diagnosis: Onymagnostus angulatus has a pointed frontal glabellar lobe, prominent but indistinctly duplicated basal lobes, and a slender pygidial axis widest across its anterior lobe, and is distinguished by its semielliptical cephalon, and pygidial rim angulate and widened in the position of marginal spines, which are not present; the cephalon is widest in its rear.

The diagnosis refers to the oldest material from the Zone of *Euagnostus opimus*; the younger and modified forms are discussed in the comment on the illustrated specimens.

Differential diagnosis: The angulate glabellar front in the holotype is clearly different from the obtuse front of *Onymagnostus* (*Agnostonymus*) *semiermis,* which possesses also distinctive pygidial marginal spines; an angulate pygidial margin is apparent in a pygidium attributed to *Onymagnostus convexus* (Westergaard, 1946, pl. 10, fig. 10), but in another pygidium the rim is evenly narrow and the cephala are semieffaced; nevertheless, notable in the cephala is the semielliptical outline and the occasional duplication of the basal lobes (ibid., fig. 9). *Onymagnostus convexus,* from the Zone of *Ptychagnostus atavus,* is older than *O. angulatus. Agnostus gibbus* var. *hybrida* Brögger, 1878, Westergaard's (op. cit., pl. 10, figs. 1 and 2) *Triplagnostus hybridus* (Brögger), has parallel glabellar flanks and an evenly narrow pygidial rim without a trace of angulation and is therefore different from *O. angulatus*; it belongs in the Zone of *Ptychagnostus punctuosus.* A cephalon and pygidium, however (Westergaard, op. cit., pl. 9, figs. 25 and 26), from the older Zone of *Hypagnostus parvifrons,* are more in line with *O. angulatus,* but the cephalon is widest across the middle, the posterior lobe of the pygidium is only little narrower than the axial front, and the rim, although flat, is not angulate; its anterior axial lobe is undivided. Our specimen Plate 50, fig. 5, attributed to *O. angulatus,* resembles these shields, but its anterior axial lobe is divided (tripartite) and visibly the widest. In passing, Robison (1964, p. 523, pl. 79, figs. 10 and 13, and 11 and 14) described from Utah two cephala and two pygidia of *Ptychagnostus hybridus*; of the cephala, one (fig. 10) is close to Westergaard's (op. cit., pl. 9, fig. 25) and in the other (fig. 11) the posterior glabellar lobe has parallel flanks.

Description: Onymagnostus angulatus is a relatively large agnostid, attaining 10.0 mm in length. Its shields are very convex, especially the pygidium, and the axial lobes are only slightly elevated above the transverse arc of the acrolobes; the cephalon and the pygidium are equal in length (in other Ptychagnostinae the pygidium is shorter than the cephalon).

The cephalon is widest in the rear; its lateral margins converge forward in even curves and close in front completing a half of an elongate broad ellipse. The cephalic rim is narrow and almost flat and the marginal furrow very narrow but distinct, as is the preglabellar median furrow. The cheeks are smooth, but faint arcuate scrobicules occur occasionally. The glabella tapers slightly forward and its posterior lobe is expanded about the middle; a pair of lateral very short furrows is evident, and the median node is placed in front of the midpoint of the posterior glabellar lobe. The frontal lobe is 0.36x the glabella in length; its shape is variable, pentagonal as in the holotype, or with convex flanks joining in a relatively blunt or angulate front. The basal lobes consist of the main, posterior part, which is very tumid to mammillate, and a narrow and depressed anterior part.

The thorax has very prominent axial nodes resembling the basal lobes and is 0.3x the cephalon in length.

In the pygidium the rim is slightly convex in the anterior part of the shield; it flattens retrally and widens to form the posterolateral angluations in place of the marginal spines, and in the rear it is flat and narrow again. In specimens from the *Ptychagnostus punctuosus* zone the angulation is sometimes weak, and in one illustrated pygidium (Pl. 50, fig. 5) the margin is even: in this the axis, about 0.78x the shield length, is also shorter than in the rest of the pygidia.

The pygidial axis is long (0.8 to 0.85x the shield) and elegantly slender. Its anterior, clearly tripartite lobe is the widest; the second lobe carries the prominent median node, whose posterior prominent part crosses over to the rear lobe and is integrated with its test; the second transverse furrow circumscribes this part of the node—the culmination of the shield. A small and low knob is superimposed on the median node on the transverse level of the furrow. The posterior axial lobe is often depressed in the middle and there is a subcentral small node. A postaxial median furrow is absent.

Comment on illustrated specimens

1. Specimens from the Zone of *Euagnostus opimus*

The holotype cephalon, locality M123, Currant Bush Limestone, is 3.5 mm long; arcuate scrobicules are present but almost imperceptible. The anterior glabellar lobe is 0.36x the glabella in length; its front is angulate; the anterior basal lobes are small and depressed. In the pygidium partly covered by the cephalon the rim is flat and angulate posterolaterally.

The pygidium Plate 50, fig. 1, CPC 14268, associated with the holotype cephalon, is 4.0 mm long; the rim is flat and its margin angulate. The posterior axial lobe has a shallow transverse depression and the anterior lobe, wider than the posterior, is tripartite with a pair of lateral lobules.

The exoskeleton Plate 50, fig. 8, CPC 14275, in shale of the Inca Formation, locality M412, is 10.0 mm long. The cephalon is semielliptical, but the frontal lobe, 0.37x the glabella in length, is less angulate than in the holotype, and the test is fractured and deformed.

The exoskeleton Plate 50, fig. 3, CPC 14270, locality M160, Age Creek Formation, is 9.0 mm long; the matrix is chert in dolomite. The frontal glabellar lobe has about the same shape as in the previous specimen; the thorax is 0.3x the cephalon in length. The pygidial rim is partly immersed in silica; but after photographing, its angular posterolateral part on the right side was liberated from the matrix.

2. Specimens from the Zone of *Ptychagnostus punctuosus*

The matrix is bituminous limestone, Currant Bush Limestone, locality M64.

The cephalon Plate 50, fig. 4, CPC 14271, is 2.5 mm long; its semielliptical outline is less pronounced than in the holotype; the glabellar front is angulate; the posterior glabellar lobe is more expanded about its middle than in the holotype; scrobicules are absent.

The pygidium Plate 50, fig. 7, CPC 14274, is 3.5 mm long; the rim is flat, relatively narrow but still angulate at the position where marginal spines should be expected; the axis seems shorter than in the older specimens.

The pygidium Plate 50, fig. 5, CPC 14272, is 3.0 mm long; the anterior and posterior axial lobes are almost equal in width; the articulating device (crescentic half-ring and narrow articulating furrow) is basic and different from the agnostid device of *O. semiermis*.

The pygidium Plate 50, fig. 6, CPC 14273, is 3.5 mm long; the rim is evenly wide (without angulation) as in *Onymagnostus hybridus*

(Brögger) but the anterior axial lobe is tripartite with a pair of lateral lobules.

3. Specimens from the Zone of *Ptychagnostus punctuosus* (associated with *Goniagnostus nathorsti*)

The cephalon Plate 51, fig. 1, CPC 14276, from the V-Creek Limestone, locality M409, is 2.8 mm long; its outline, with evenly curved lateral margins and the maximal width across the middle, visibly deviates from the holotype.

The pygidium Plate 51, fig. 2, CPC 14277, also from locality M409, is 4.5 mm long; it is undeformed and very convex. The rear of the axis is less pointed than in the holotype, and the angulation of the rim is moderate; the articulating device is basic.

The cephalon Plate 51, fig. 3, CPC 14278, from the V-Creek Limestone, locality M416, is 2.8 mm long; its outline is semielliptical, but the basal lobes are simple. It is the youngest known specimen attributed to *O. angulatus,* of the Zone of *Ptychagnostus nathorsti.*

Occurrence and age: Onymagnostus angulatus occurs in the Currant Bush Limestone, in the Inca Formation, in the Age Creek Formation, and in the V-Creek Limestone; its age is the Floran Zone of *Euagnostus opimus,* and the Undillan Zones of *Ptychagnostus punctuosus* and *Doryagnostus notalibrae.*

Onymagnostus sp. nov. aff. **angulatus**

(Pl. 51, figs. 4, 5)

In this form the pygidium is larger than the cephalon.

Illustrated are an exoskeleton and a pygidium, in limestone, locality M180; several isolated shields have been also collected, but the inferior preservation prevents a conclusive specific interpretation.

The exoskeleton Plate 51, fig. 5, CPC 14280, is 10 mm long; its test is preserved. The rim in both shields is convex; the acute frontal glabellar lobe is 0.4x the glabella in length. The cephalon is the shorter shield, about 0.9x the length of the pygidium; but the cephalon and the anterior segment together equal the pygidium in length, in contrast to the prevalence of the cephalon over the pygidium in the majority of agnostids. The pygidial axis is very long, close to 0.9x the shield length; a pair of elongate muscle spots are evident in its posterior lobe, and a tiny median node in between.

The pygidium Plate 51, fig. 4, CPC 14279, is 3.8 mm long. The anterior axial lobe is tripartite (as in the exoskeleton) and on the margin a pair of small, almost imperceptible projections represent the undeveloped marginal spines.

The described specimens are strongly convex and the slope of the acrolobe behind the pygidial axis is rather steep. A postaxial median furrow is absent. The test is smooth.

Occurrence and age: Onymagnostus sp. nov. aff. *angulatus* occurs in strata attributed to the Currant Bush Limestone; its age is the Floran Zone of *Euagnostus opimus.*

Onymagnostus durusacnitens sp. nov.

(Pl. 53, figs. 2-4; Text-fig. 33)

Material: Illustrated are a cephalon with the attached anterior segment of the thorax, and one pygidium; another pygidium and a deformed complete exoskeleton have been identified in the collection, all from a single limestone bed, M41.

Holotype: The pygidium Plate 53, fig. 2, CPC 14287, is selected as the holotype in preference to the cephalon; the characters of pygidia are diagnostic in the first place.

Diagnosis: Onymagnostus durusacnitens has a thick test with externally shallow furrows which are well impressed on internal moulds; with straight flanks of the evenly and moderately tapering glabella; a very convex pygidium with steeply sloping flanks of the acrolobe, especially at the rear of the shield. The anterior annulation of the pygidial axis is tripartite (with lateral lobules) and its second transverse furrow is obliterated externally. It is distinguished by its forward widening cephalic rim and the constriction of the pygidial acrolobe.

Differential diagnosis: The cephalon of *O. durusacnitens* resembles *O. seminula,* whose

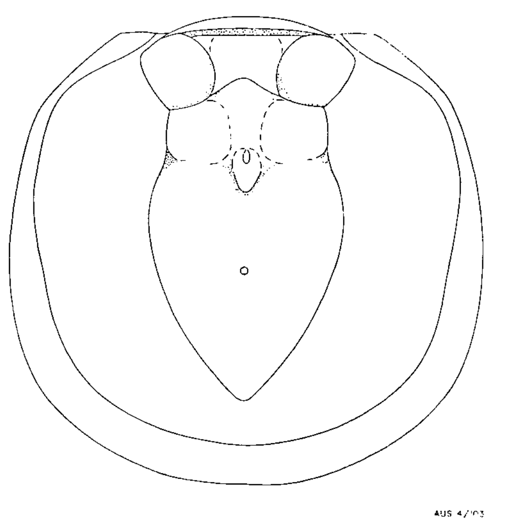

Fig. 33. *Onymagnostus durusacnitens.*

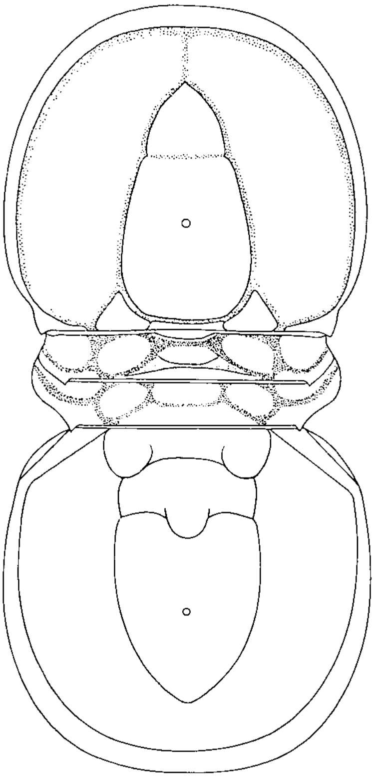

Fig. 34. *Onymagnostus mundus.*

test, however, is thin and furrows clear, and the pygidial acrolobe, as in all known species of *Onymagnostus,* is unconstricted.

Description: The cephalic rim is slightly convex, almost flat, and relatively wide in front; the marginal furrow is distinct but very narrow; the frontal glabellar lobe, about 0.34x the glabella in length, is bluntly pointed; the basal lobes are small with the anterior part almost fused to the glabella. The cephalic spines (the right prong is visible in Plate 53, fig. 3) have an attenuated tip and are more conspicuous than in other species of *Onymagnostus.* In the thorax the fulcral points of the anterior segment are very short and so are the opposed fulcra connecting the thorax and the pygidium. In the pygidium the axis is 0.8x the shield length, the median node is provided with a small knob and is itself relatively small, and a postaxial furrow is absent.

Comment on specimens included in the paradigm

The holotype pygidium is 3.7 mm long in plan; its convexity is preserved and the height at the culmination (about the median node) is 0.5x the shield length. The acrolobe is constricted.

The cephalon in Plate 53, fig. 3, CPC 14288, is 3.5 mm long; the punctuation of the test is visible in parts, including the thorax. The cephalon is very convex, and owing to the thickness of the test the furrows are shallow; the basal lobe in its anterior part is almost confluent with the glabella. Some of the matrix adheres to the test; it is not removable without damaging the test. The combination of the cephalon with the anterior segment in situ is discussed under the heading 'mode of life'.

The exoskeleton Plate 53, fig. 4, CPC 14289, is 5.0 mm long; its pygidial axis is lost and the anterior segment of the thorax is represented by the outline of its left pleura. The slope is very steep in the pygidial rear. In the cephalon some of the test is lost over the left axial furrow and part of the transverse glabellar furrows, which are deep and clear on the internal cast. The shields are equal in length.

Occurrence and age: Onymagnostus durusacnitens occurs in a single bed of the V-Creek Limestone at M41 and M30; it is a rare species. Its age is the Zone of *Doryagnostus notalibrae.*

Onymagnostus mundus sp. nov.
(Pl. 51, fig. 6; Pl. 52, figs. 1 and 2;
Text-fig. 34)

Material: Illustrated are two complete exoskeletons from different localities; several cephala and pygidia have been also identified in collections.

Holotype: The specimen Plate 51, fig. 6, CPC 14281, is selected as the holotype; it is undeformed, but is still a little defective; the missing part of the pygidial axis is evident in the other specimen.

Diagnosis: Onymagnostus mundus is distinguished by its small subtriangular and short frontal glabellar lobe 0.31-0.32x the glabella in length; by the shape of the posterior glabellar lobe—broad in the rear and tapering forward, with convex flanks—and by the convex flanks of the posterior lobe of the pygidial axis. Furthermore, the pygidial axis and shoulders are not interrupted by the shoulder furrow, which is continuous with the marginal furrow, and the cephalon is widest across its middle.

Differential diagnosis: The general aspect of *O. mundus* reminds one of *Ptychagnostus* (= *Onymagnostus*) *ciceroides* (Matthew)—the large exoskeleton illustrated by Hutchinson (1962, pl. 10, fig. 8); it is, however, semi-effaced, its rim is visibly narrower than in *mundus,* and the pygidial median node is small; the marginal and shoulder furrow is, nevertheless, continuous in both species—a sign of an incipient effacement in *mundus* as well. The glabellar structure of *mundus* is not unlike *Zeteagnostus incautus,* but the basal lobes are well developed and its pygidial axis and thorax cannot be confused with *Zeteagnostus.* The pygidial rim is posterolaterally slightly expanded, indicating a possible affinity with the earlier *O. angulatus*; in *angulatus,* however, the frontal glabellar lobe is large, the shoulder furrow cuts the rim, the pygidial median node is strong, and the semielliptical outline of the cephalon is quite distinctive.

Description: Onymagnostus mundus, slightly less than 10 mm in length, is an agnostid of a medium size and en grande tenue. The shields are equal in length and quite convex, the pygidium more than the cephalon. The rim of the shields is moderately wide, slightly convex in the cephalon and in the anterior part of the pygidium and flatter in the pygidial rear; the marginal furrows are deep and narrow and the axial furrows, including the preglabellar median furrow, are clearly incised but narrow (in the holotype), but more conspicuous in flattened shields. No scrobiculation is evident in the cephalic acrolobe. The frontal glabellar lobe is pointed, subtriangular, with convex flanks and visibly narrower than the posterior glabellar lobe; there is a faint indication of a pair of lateral furrows, and the median node, in front of the midpoint, is low and small. The glabellar rear is well rounded, arched longitudinally and transversely, and the basal lobes are simple, triangular, and swollen. The thorax, about 0.28-0.3x the cephalon in length, has a well developed relief.

In the pygidium the axis is long (0.8x the shield length) and less slender than in other species (even stout). The anterior axial lobe is faintly tripartite and visibly wider than the posterior lobe; the median node on the second annulation seems shorter (shorter than in *O. angulatus*); the flanks of the posterior lobe are convex down to the axial tip, and a subcentral node is also evident. A postaxial median furrow is absent.

Comment on illustrated specimens

All collected specimens came from the V-Creek Limestone.

The holotype, locality M212, is 7.5 mm long. The original convexity is preserved and the tagmata retain the arrangement ready for articulation. Some of the median part of the glabella is lost but the base of the median glabellar node is preserved; a sliver of the pygidial axis is also missing.

The complete exoskeleton Plate 52, figs. 1 and 2, CPC 14282, locality M247, is 9.4 mm long. It is flattened and unevenly deformed and the furrows are accentuated more than in the undeformed holotype; the parts lost in the holotype, however, are preserved, and so is the illustrated counterpart of this specimen.

Occurrence and age: Onymagnostus mundus is a rare fossil of the V-Creek Limestone, collections M212, M247, and M418 (isolated shields only). Its age is the Zone of *Doryagnostus notalibrae.*

Onymagnostus seminula (Whitehouse, 1939)

(Pl. 52, figs. 3-5; Pl. 53, fig. 1)

Introduction (geographic position and age): The species *Agnostus seminula* refers to a single specimen (Whitehouse, 1939, pl. 25, fig. 24; p. 254); its generic position (*Onymagnostus*) could be established here on the basis of the adequate illustration of the holotype given by Hill et al. (1971, pl. Cm. 13, fig. 1). The geographic position described in the caption to this figure is, however, misleading: (1) the site is indeed 11.5 miles northeast from Yelvertoft Dip (cattle dip) as published by Whitehouse (op. cit.) but not from 'Yelvertoft Homestead' of that caption; (2) the reference 'at Dingo Creek Crossing, Paradise Goldfields road' indicates a distance of 20 miles from the Dip; and (3) the Crossing is a site of a Templetonian fauna.

The age of *Agnostus seminula* is, according to Whitehouse (op. cit., p. 266), the '*Agnostus seminula* Stage' of an undefined position in the Middle Cambrian. The site—18.5 km from Yelvertop Dip—is marked on the Camooweal 4-mile sheet with M166, which refers to the large limestone bank (a plateau) north of the Thorntonia/Paradise Goldfields road junction. I assigned this limestone to the Currant Bush Limestone and to the Zone of *Ptychagnostus punctuosus* on the evidence of the occurrence at M166 of *Aotagnostus aotus* (q.v.) and of the specimen of *Pt. punctuosus affinis* shown in Plate 39. fig. 8 (see also under *Triplagnostus purus*).

Summing up, *Agnostus* (here: *Onymagnostus*) *seminula* was found originally in a limestone of the Zone of *Ptychagnostus punctuosus*; see 'Table of Reconciliation of the stage stratigraphy' (Whitehouse, 1939) with the scale of zones. The age given by Öpik (1970a, p. 4) as *Pt. atavus* zone is erroneous.

Material: Three complete specimens and one isolated pygidium are illustrated and described.

Diagnosis: The distinguishing characters of *Onymagnostus seminula* are the relatively long frontal glabellar lobe (0.34-0.38x the glabella in length), straight and slightly converging glabellar flanks, and relatively short pygidial median axial node; furthermore, the frontal annulation of the axis is undivided and the pygidial margin has an even course without a trace of an angulation.

Differential diagnosis: Onymagnostus seminula and *O. mundus* resemble each other generally; in *O. mundus,* however, the frontal glabellar lobe is visibly shorter than in *seminula* and the flanks of the posterior glabellar lobe are convex (straight in *seminula*).

Description: In *Onymagnostus seminula* the rim of the shields is relatively narrow and convex; in the cephalon scrobicules are absent and the basal lobes are simple; the glabellar flanks are straight past the middle of its frontal lobe; the median glabellar node is low and can be overlooked easily. The thorax, ca. 0.3x the cephalon, is average in length. In the pygidium the shoulder furrows cut across the rim, which is continuous in *O. mundus.* The pygidial axis is long (0.8-0.83x the shield) and a postaxial furrow is absent.

Comment on specimens

The holotype of *Onymagnostus seminula* (see Hill et al., op. cit.) is about 7.4 mm long. The test is fractured and the pygidial axis seems narrow because its left margin is pressed down into the axial furrow; the pygidial rim is still preserved.

The following specimens belong to the V-Creek Limestone.

The exoskeleton CPC 14284, Plate 52, fig. 4, locality M212, is 6.2 mm long; its test is thin but mostly preserved; the axial part of the anterior segment of the thorax is lost; the pygidium is fractured and the anterior part of the axis has collapsed. These deformations affected the shape of the axis.

The pygidium Plate 52, fig. 5, CPC 14285, locality M41, is 3.8 mm long; the undivided anterior annulation of the axis is clear; the axis itself is deformed through collapse. The associated immature shields of agnostids represent two different but undeterminable ptychagnostids.

The exoskeleton Plate 52, fig. 3, CPC 14283, locality M462, is 5.6 mm long; it is undeformed but otherwise identical with the holotype; the pygidial axis is slender and its rim is somewhat wider than the rim of the cephalon. The axial lobe of the pygidium is about 0.36x the width of the acrolobe measured across the tip of the median node; the same should be accepted also for the holotype.

The exoskeleton Plate 53, fig. 1, CPC 14286, locality M462, is 5.0 mm long as preserved, having lost the posterior segment of its thorax. The glabellar median node is clear and the flanks of the posterior lobe of the pygidial axis are more convex than in the specimen above, from the same locality.

Occurrence and age: Onymagnostus seminula is a rare species and has been found as complete exoskeletons; the illustrated specimens are Undillan in age; the material from M41 and M212 belongs to the Zone of *Doryagnostus notalibrae*; the specimens from M462, from the Zone of *Goniagnostus nathorsti* are the youngest known; the age of the holotype (the Zone of *Ptychagnostus punctuosus*) is discussed above in the introduction.

Onymagnostus cf. **grandis** (Hutchinson, 1962)

(Pl. 53, fig. 6)

The whole material consists of the illustrated cephalon, CPC 14291; it is 4.0 mm long and incomplete posterolaterally. The structure of the cephalon is almost identical with the cephala of *Ptychagnostus grandis* Hutchinson (1962, pl. 8, figs. 7-9) whose pygidia (ibid., figs. 6, 10, and 11) indicate a species of the genus *Onymagnostus* nov.; the median glabellar node is indistinct in the type material but visible in our specimen. The cephalic rim is narrow and almost flat; the cheeks are rugose and the veins fan out from a pair of ducts starting at the rear of the frontal lobe; the glabella tapers forward and the frontal glabellar lobe, about 0.37x the glabella in length, has convex flanks and a pointed front; the basal lobes are small and their anterior parts are almost fused to the glabella, and the test is punctate.

The Australian specimen is qualified as cf. *grandis* because the holotype is not a cephalon but a pygidium (Hutchinson, op. cit.) resembling *Onymagnostus stenorrhachis;* the Queensland pygidium attributed here to *O. stenorrhachis* (Pl. 53, fig. 5), however, is wanting in characters of the holotype of *grandis.*

Occurrence and age: The described cephalon attributed to *Onymagnostus grandis* (Hutchinson) is a fossil of the V-Creek Limestone, locality M30; its age is the Zone of *Doryagnostus notalibrae.*

Onymagnostus cf. **stenorrhachis** (Grönwall, 1902)

(Pl. 53, fig. 5)

The illustrated pygidium, CPC 14290, locality M41, is 4.0 mm long. The species *stenorrhachis* is indicated by the following characters: (1) the anterior lobe is tripartite and its lateral lobules are clear, and (2) the rim is narrow and the margin is even, without any trace of angulations. The posterior lobe is, however, less slender than in the holotype (Grönwall, 1902, pl. 1, fig. 16) or in pygidia illustrated by Westergaard (1946, pl. 10, fig. 4) and Hutchinson (1962, pl. 8, figs. 4, 5).

Occurrence and age: The pygidium attributed to *Onymagnostus stenorrhachis* has been obtained from the V-Creek Limestone, locality M41. Its age is the Undillan Zone of *Doryagnostus notalibrae.*

Subgenus **Onymagnostus (Agnostonymus)** nov.

The type species of *Agnostonymus* is *Onymagnostus semiermis* nov.

Diagnosis: In *Agnostonymus* the glabellar front is rounded and the pygidial margin has a pair of posterolateral spines.

Differential diagnosis: In *Onymagnostus* (*Onymagnostus*) the glabellar front is pointed and the pygidial margin is spineless.

Onymagnostus (Agnostonymus) semiermis sp. nov.

(Pl. 54, figs. 1-8; Text-fig. 35)

Material: Illustrated are three cephala and two pygidia, from a single limestone bed, and two exoskeletons in shale; specimens from several other sites are also available, including about seven complete tests in shale (M176).

Holotype: The cephalon Plate 54, fig. 2, CPC 14293, is selected as the holotype; it is supplemented by the associated pygidia and the combination of such cephala and pygidia in complete exoskeletons.

Diagnosis: *Onymagnostus semiermis* has smooth to erratically scrobiculate cheeks, and a long and slender pygidial axis with weakly expressed lateral lobules in its anterior lobe, which is the widest; distinguished by the rounded (not pointed) glabellar front and spinose pygidial margin. The basal lobes are double.

Differential diagnosis: In other species attributed to *Onymagnostus* marginal pygidial spines are absent and the glabellar front is pointed. These structures apart, *O. semiermis* and *O. stenorrhachis* (Grönwall) share the slender pygidial axis, the subdivided anterior axial lobe, and the scrobiculation of the cheeks (dimpled in Swedish specimens: Westergaard, 1946, pl. 10, fig. 4; furrowed in Canadian ones: Hutchinson, 1962, pl. 8, fig. 1). *Onymagnostus angulatus* sp. nov. has no marginal spines, but the angulation of its pygidial rim is a structure transitional between the spinose margin of *semiermis* and the evenly curved margin seen in the rest of the species included in the genus *Onymagnostus*; another transitional form is described under *O.* aff. *semiermis.* The rounded glabellar front is at variance with the majority of the Ptychagnostinae and is therefore a possible reason for another generic name or at least for speculations regarding a possible kinship with *Peronopsis* and its allies. Such a front occurs in three more species and is discussed under the heading of *Pentagnostus* (q.v.). Finally, the spinose pygidial margin, the absence of the postaxial median furrow and the aspect of the posterior glabellar lobe of *O.* (*A.*) *semiermis* are foreshadowing the features of the much younger *Agnostus pisiformis* of the Agnostinae.

Description: *Onymagnostus* (*Agnostonymus*) *semiermis* is a fairly large form, attaining a length of over 10 mm; the pygidium and the cephalon are equal in length and the thorax is 0.29-0.3x the cephalon. The shields are quite strongly convex and of a similar shape. The cephalon is wider than long, with an evenly

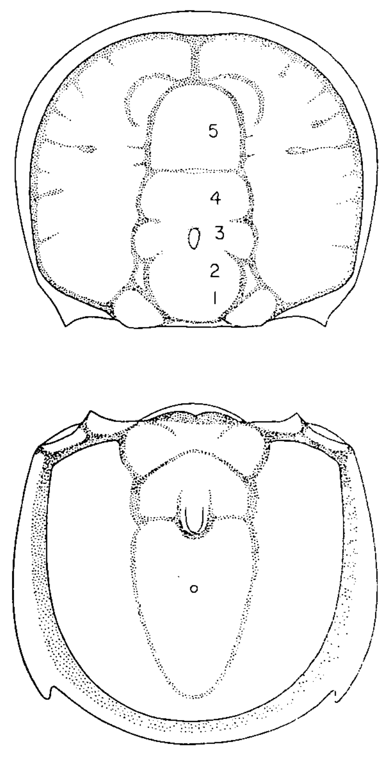

Fig. 35. *Onymagnostus (Agnostonymus) semiermis.* **1-5 indicate metameres of the cephalon.**

curving margin; the rim is convex and the marginal furrow is deep and narrow. The preglabellar median furrow is deep and narrow; the cheeks are smooth or even scrobiculate and arcuate scrobicules are also present; the scrobicules, however, are faint and even invisible in average specimens. The cephalic spines are short.

The glabella is well subdivided; its frontal lobe is long, about 0.4-0.42x the glabella, semielliptical and not pointed or angulate, but well rounded in front. The posterior glabellar lobe tapers forward slightly, and has a pair of well impressed short lateral furrows; in the middle it is expanded into a pair of tumid lateral lobes; its rear is elevated, tumid, and well rounded posteriorly. The median node is placed about the middle of the posterior glabellar lobe. The basal lobes are long, nesting with their anterior tips in angular recesses of the glabellar flanks behind the middle lateral lobes; the basal lobes are also composite (double): the posterior part is large, prominent and even mammillate, but the frontal is low and narrow; the dividing furrow is oblique and shallow; these structures resemble *Innitagnostus innitens* (Öpik, 1967, p. 99).

In the pygidium the rim is about as wide as in the cephalon and widened slightly at the marginal spines; these are short and follow the curvature of the lateral pygidial margin; behind the spines the margin is narrowest. The acrolobe between the border and the pygidial axis slopes down steeply, bringing the pygidial rim and the axial tip in plan close to each other. The axis is slender, long (0.85x the shield length), and the posterior lobe is narrow, 0.37-0.7x the width. The posterior lobe has slightly concave flanks in its rear, a small median node in its middle, and in some specimens a transverse depression. A postaxial furrow is absent. The anterior axial lobe is undivided; the median (main) node on the second annulation is stout and extends well beyond the transverse furrow. The articulating device resembles *Ptychagnostus punctuosus*; the half-ring projects retrally in the middle, the articulating furrow is relatively wide, but the axial front is straight without a recess.

Comment on illustrated specimens

The matrix of the following five specimens is limestone, locality M150.

The holotype cephalon (a test) is 3.5 mm long. The scrobicules are weak but visible.

The cephalon Plate 54, fig. 1, CPC 14292, is 3.9 mm; the arcuate scrobicules are barely visible; the frontal lobe is 0.41x the glabella in length.

The cephalon Plate 54, fig. 3, CPC 14294, is 4.0 mm long; scrobicules are absent; the left basal lobe is intact and its main, posterior part is prominent.

The pygidium Plate 54, figs. 5 and 6, CPC 14296, is 3.5 mm long. It is undeformed and the acrolobe behind the axis slopes steeply down; the articulating half-ring is well exposed; the tiny node about the middle of the posterior lobe is visible.

The pygidium Plate 54, fig. 4, CPC 14295, is 2.5 mm long. The posterior lobe of the axis has a depression in the middle and the marginal spines are short.

The matrix of the next two exoskeletons is shale (Inca Formation), locality M176. The specimens are complete but flattened.

The exoskeleton Plate 54, fig. 8, CPC 14298, is 9.0 mm long. The glabellar front is rounded (blunt) and a short sulcus seems indicated; the left pygidial marginal spine is clear; the frontal glabellar lobe is about 0.4x the glabella in length.

The exoskeleton Plate 54, fig. 7, CPC 14297, is 10.5 mm long; the left flank of the glabella is creased and the left half of the glabella is therefore narrower than the right, as can be seen from the position of the median node. The thorax is about 0.3x the cephalon, and the pygidium equals the cephalon in length. The outline of the pygidium is undeformed, but the cephalon seems dilated in the rear and its shape is about semielliptical. The arcuate scrobicules and some rugosity of the cheeks are weakly reflected in the latex cast. In the thorax the median, axial, part of the second segment is divided longitudinally by a furrow and in the anterior segment there is a prominent lobe ('glabella') between the 'basal lobes' (see Text-fig. 5). The thorax in *O. mundus* is similar.

Occurrence and age: Onymagnostus (*Agnostonymus*) *semiermis* sp. nov. occurs in the Currant Bush Limestone (M150, M176) and in strata assigned to it (M180, M376), and in shale of the Inca Formation (M176; M412); its age is the Floran Zone of *Euagnostus opimus*.

Genus **Triplagnostus** Howell, 1935

The type species of *Triplagnostus* by original designation is *Agnostus gibbus* Linnarsson, 1869. The diagnosis compiled by Howell is adequate, but incomplete because at that time (1935) the species *A. gibbus* was insufficiently known. The diagnosis (Howell, 1935, p. 14) reads:

'Agnostians with well developed dorsal furrows, glabellas, and pygidial axes, with the anterior lobe of the glabella pointed in front and the cheeks divided by a medial furrow, with the pygidial axis long and bluntly pointed at the rear, and with distinct furrows on the glabella and the axis. In the known species the test is smooth and the flange of the pygidium does not bear spines, and these features are probably characteristic of the genus.

'The genotype is *Agnostus gibbus* Linnarsson, from the Middle Cambrian of Sweden. The forms described by Matthew from New Brunswick as *Agnostus gibbus acutilobus* and *Agnostus gibbus partitus,* and the form described by Brögger from Norway as *Agnostus gibbus hybrida,* are also referred to this genus. All these forms are of Medial Cambrian age.

'*Triplagnostus* is known to have ranged through most of Paradoxidian time. Its species are characteristic members of *Paradoxides* faunas on both sides of the North Atlantic. One new form believed to belong to the genus is characteristic of one of the latest *Paradoxides* faunas of New Brunswick.'

Agnostus partitus and *Agnostus acutilobus* have been described as new species by Matthew (1886 for 1885, p. 68, pl. 7, figs. 2a and 2b; and p. 73, pl. 7, fig. 10, respectively). *A. partitus,* as published, refers to a cephalon with a small frontal lobe and acute glabellar rear; the pygidium attributed to it is apparently of a peronopsid with marginal spines; *A. acutilobus,* according to Matthew (op. cit., p. 74) resembles *A. gibbus hybridus* Brögger (which should be accepted), and is a species of *Onymagnostus* nov.

Triplagnostus lomondensis Howell, 1935, is a species of the Ptychagnostinae, but its generic classification remains inconclusive. Assuming that its cephalon (op. cit., fig. 7) has short triangular spines and that the pygidial axial node (ibid., fig. 8) is low and spineless, it should be transferred to *?Ptychagnostus.* In the pygidium described by Hutchinson (1952, p. 70, pl. 1, fig. 5) as cf. *lomondensis* no axial spine is present.

Westergaard (1946, p. 70, pl. 9, figs. 18-20 and 22-24) established in *Ptychagnostus (Triplagnostus) gibbus* the presence of: (1) cephalic spines of varying length, (2) an axial spine on the second segment of the thorax, and (3) a 'coarse short spine on the second axial ring of the pygidium', and indicated that 'by spinosity the species is distinct from other Scandinavian forms referable to *Triplagnostus*'. Furthermore, in the thorax (ibid., figs. 20 and 23) short fulcral projections are evident in the second segment. The test is not smooth, but minutely granulose in Swedish specimens (Öpik, 1961b, p. 76), which also possess a small subcentral node on the posterior axial lobe of the pygidium. Also, *T. gibbus*—the type species of its genus—has simple basal lobes and no pygidial marginal spines; but species with double basal lobes and with marginal spines exist, and are described now from Australia. Finally, all known species attributable to *Triplagnostus* as revised here are forms en grande tenue, and effaced forms are not evident in its stock. The phylogenetic derivation of *Leiopyge laevigata* (Westergaard, 1946, p. 74) from *Ptychagnostus (Triplagnostus) elegans* and *elegans laevissimus* Westergaard remains a tenable conclusion, because these forms are species of *Leiopyge* and not of *Triplagnostus.*

In passing, earlier discussions (for example, Öpik, 1961b, p. 76) regarding *Triplagnostus* and *Leiopyge* refer to Westergaard's comprehensive concept of *Triplagnostus* but without *Triplagnostus gibbus* itself.

Diagnosis (compiled herein): The species attributed to *Triplagnostus* are distinguished by a glabella with a pointed front, with a parallel-sided as well as slightly tapering glabellar lobe, extended cephalic spines, and axial spines on the posterior segment of the thorax and on the pygidial axis; with the median glabellar node in a posterior position and without an axial spine in the glabellar rear.

Furthermore, depending on the species, (1) scrobicules can be absent, but when present, are weak; (2) basal lobes can be simple or double; (3) pygidial marginal spines are absent but also present in different lengths; (4) the fulcral points of the segments of the thorax are short angular projections or short reclined spines; (5) the pygidial axis is pointed, and 0.7x (or slightly less) the shield length; (6) the posterior axial lobe has a small subcentral node or knob; and (7) the test is minutely granulose.

The diagnostic character, the parallel-sided posterior glabellar lobe, holds for *Triplagnostus gibbus posterus;* in other forms, however, the glabellar flanks converge slightly and this convergence is frequently accentuated in flattened tests.

Differential diagnosis: The two names *Leiopyge* Hawle & Corda 1847 and *Ptychagnostus* Jaekel 1909 were established prior to *Triplagnostus* Howell, 1935; *Leiopyge* is quite disparate and cannot be regarded as a synonym of *Triplagnostus*: the species of the Ptychagnostinae *elegans* Tullberg, *elegans laevissima* Westergaard, *lundgreni Tullberg,* and *lundgreni nanus* Grönwall were revised by Westergaard (1946) and placed in *Triplagnostus,* but are transferred here to *Leiopyge.* Westergaard also included in *Triplagnostus* the species *hybridus* and its allies which are placed herein, and discussed, under the new genus *Onymagnostus*; finally, *Triplagnostus praecurrens* (Westergaard) and *T. angermanensis* are accommodated in *Pentagnostus* (q.v.). All these are non-spinose forms.

Likewise, *Triplagnostus trapezoidalis* Bognibova (*in* N. Tchernysheva, 1971, p. 91) and *T. ademptus* Pokrovskaya & Jegorova (*in* Savitsky et al., 1972, p. 61) are novel species of *Pentagnostus*.

Ptychagnostus (*Ptychagnostus*) refers to spineless species having a tapering glabella with a subcentral median node and is therefore diagnostically different from *Triplagnostus*; nevertheless the latter can be regarded as a subgenus of *Ptychagnostus* because the spinose and spineless species of *Acidusus* (q.v.) are described here also as a subgenus of *Ptychagnostus*. In *Acidusus*, however, the tapering glabella and the terminal node at the tip of the pygidial axis indicate a structure incompatible with *Triplagnostus*. The species of the new genus *Aotagnostus* (q.v.) are spinose but otherwise different and cannot be confused with *Triplagnostus*. Finally, *Goniagnostus* and related forms with lateral pits in the glabella rear and a terminal axial spine of the glabella are discussed separately and can be distinguished from *Triplagnostus* at a glance.

Described are the following species of *Triplagnostus*:

A. Subgenus *Triplagnostus* (*Triplagnostus*) (glabella parallel-sided)
   1. Species without pygidial marginal spines:
      Triplagnostus gibbus gibbus—basal lobes simple.
      Triplagnostus gibbus posterus nov.—basal lobes double.
      Triplagnostus. quasigibbus nov. — basal lobes double.
      Triplagnostus sp. indet. (pygidium only).
   2. Species with pygidial marginal spines:
      Triplagnostus fretus nov.—basal lobes simple.
      Triplagnostus scopus nov.
      Triplagnostus diremptus nov.—basal lobes double.
      Triplagnostus purus (Whitehouse).
      Triplagnostus stramineus nov. — basal lobes simple; spines very long.

B. Subgenus *Aristarius* nov.: glabella trigonal; pygidial spines extended; basal lobes simple.
   Triplagnostus (*Aristarius*) *retrocornutus* nov.
   Triplagnostus (*Aristarius*) *aristarius* nov.
   Triplagnostus (*Aristarius*) *ultimus* nov.
   Triplagnostus (*Aristarius*) aff. *ultimus* nov.

Geologically the oldest is *Triplagnostus gibbus gibbus*, of the *T. gibbus* zone; in the next zone of *Ptychagnostus atavus* five species —*T. gibbus posterus, T. quasigibbus, T. purus, T. retrocornutus,* and *T. stramineus*—have been found, and *T. gibbus posterus* survives to reach the beginning of the *Ptychagnostus punctuosus* Zone; *T. diremptus* is known only in the *Euagnostus opimus* Zone; *T. aristarius* is rare in the early *Ptychagnostus punctuosus* Zone, and so is *ultimus* in the Zone of *Goniagnostus nathorsti*. The species in the list above are grouped together according to the increase in spinosity.

Triplagnostus gibbus (Linnarsson, 1869)

According to Westergaard (1936, p. 29) *Agnostus gibbus* has been established on specimens 'which may be syntypes', and 'this form has never been fully described and depicted' and its obvious spinosity has been 'overlooked by Linnarsson and subsequent authors'. In his final revision of *gibbus*, Westergaard (1946) ignored the 'may be syntypes' and depicted material from four Swedish sites different from Linnarsson's original localities without designating a lectotype or a neotype for the species.

I identify the species *Triplagnostus gibbus* (Linnarsson, 1869) on the evidence of Westergaard (1946, pl. 9, figs. 17-20 and 20-24)—a paradigm of morphological uniformity taken as representing the subspecies *T. gibbus gibbus*, restricted to the division designated the Zone of *Triplagnostus gibbus* (Westergaard, op. cit., p. 8); this form occurs also in Australia in a similar stratigraphic position. Furthermore, I describe another Australian subspecies, *Triplagnostus gibbus posterus*, of a longer age range, known for more than three decades and attributed hitherto to the Swedish *T. gibbus* (*gibbus*).

Triplagnostus gibbus gibbus (Linnarsson)

(Pl. 23, figs. 1-3; Text-fig. 36)

Material: Illustrated are three specimens selected from a larger number of isolated shields; complete specimens are rare.

Diagnosis (compiled herein): *Triplagnostus gibbus gibbus* belongs to the group of forms having no marginal pygidial spines and is distinguished by its simple (undivided) basal lobes and extended but relatively short spines.

Differential diagnosis: Triplagnostus gibbus posterus differs by its double basal lobes and spines longer than in *gibbus gibbus*; *T. quasigibbus* also has double basal lobes, but its spines are shorter. Whitehouse (1936, p. 84, pl. 8, figs. 6 and 7; pl. 10, fig. 2) assigned to *Triplagnostus gibbus* Australian forms with clearly double basal lobes discussed here under *T. gibbus posterus*—a plausible identification based on antedating Westergaard's revisions of 1936 and 1946. The Swedish specimens (Westergaard, 1946, pl. 9, figs. 17-20 and 22-24; but apparently not fig. 21) have simple basal lobes, but their cephalic spines are shorter than in the Australian ones; the cephalon fig. 21, however, is scrobiculate and dimpled, has arcuate scrobicules and there is a pair of pits at the tips of the basal lobes; it resembles *Triplagnostus diremptus* sp. nov., Plate 26, fig. 6, whose basal lobes, however, are double. The Swedish specimens have also attained a length almost twice the Australian ones—a difference of two populations geographically remote from each other.

I also have examined a small number of Swedish specimens of large shields of *Triplagnostus gibbus* from the 'limestone layer with *Ctenocephalus exsulans*' (*vide* Westergaard, op. cit., p. 8). In these the granulation of the test is finer than in Australian ones; moreover, the basal lobes in some specimens display certain complications: the basal lobe itself is a subtrigonal boss, but seems to have a narrow and flat to slightly swollen extension forward, in the position of the anterior basal lobes of *Triplagnostus gibbus posterus*.

In *Ptychagnostus gibbus* described by Rasetti (1967, p. 28, pl. 10, figs. 1-8) the basal lobes are somewhat short and double and in the pygidium the posterior axial lobe is relatively short—only slightly longer than the anterior two lobes taken together.

The subspecific identity of the Siberian specimen of *Triplagnostus gibbus* (Tchernysheva et al., 1960, pl. 1, fig. 11), an exoskeleton about 4.5 mm long, remains inconclusive. So do the specimens of *Triplagnostus gibbus* by Savitsky et al. (1972, pl. 5, figs. 1-6), who mentioned (ibid., p. 60) the presence of small marginal pygidial spines (ibid., fig. 2), and the shape of the frontal glabellar lobe is also different from a regular *gibbus*; the thorax seems also shorter (0.24-0.25x the cephalon) than in Westergaard's (op. cit., pl. 9, fig. 20) specimen; the structure of the basal lobes is not clear in these illustrations of the Siberian specimens.

Description: General descriptive data are given in the diagnosis of the genus supplemented in the diagnosis of the subspecies. Furthermore, the rim in both the shields is weakly convex, very narrow in the cephalon and only slightly wider in the pygidium. No rugosity has been observed in the cheeks, and scrobicules are absent. The frontal glabellar lobe, about 0.4x the glabella in length, is pointed and a sulcus is absent. The lateral furrows in the posterior lobe are clear but short, the median node is low, sometimes elongate and, placed behind the midpoint, marks the culmination of the glabellar profile; the glabellar rear is tumid, rounded, and a little contracted in the rear to accommodate the basal lobes. These lobes are tumid, triangular, and attenuated in front. The cephalic spines are as long as, or a little longer than, the thorax, whose fulcral points

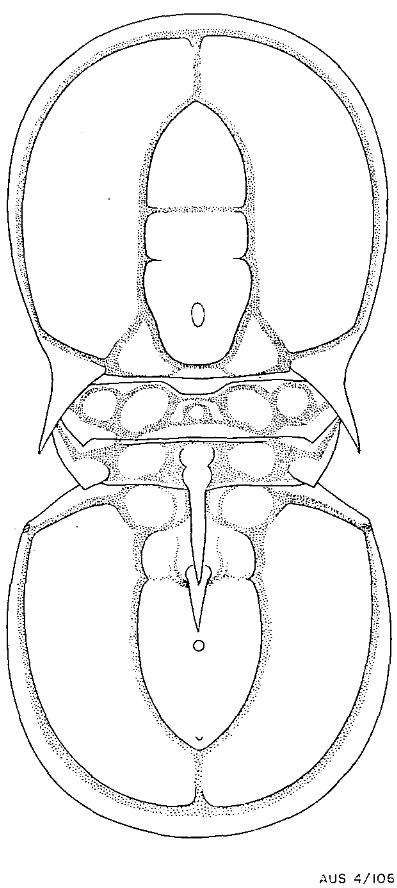

Fig. 36. *Triplagnostus gibbus gibbus.*

in the second segment are short angular projections (spines in *T. gibbus posterus*). In the only hitherto known complete specimen (Westergaard, 1946, pl. 9, fig. 20) the thorax is about 0.26x, and in Plate 23, fig. 1 not less than 0.27x, the cephalon in length, and larger than the 0.22-0.23x in *gibbus posterus*. In the pygidium, the two anterior lobes together are visibly shorter than the posterior lobe of 0.7x the axis in length; the posterior lobe carries a small central knob or node, which occurs also in the Swedish specimens, in which it has been hitherto overlooked. The test is granulose, and the ornament in the pygidium is clearer than in the cephalon.

Comment on illustrated specimens

The illustrated specimens of *Triplagnostus gibbus gibbus,* in a piece of siltstone of the Inca Formation, come from locality M433 (at Beetle Creek).

The cephalon in the exoskeleton Plate 23, fig. 1, CPC 14106, is 2.6 mm long. The test is silicified and minutely granulose, the basal lobes are undivided (simple) and swollen. The asymmetry of the frontal glabellar lobe is an individual monstrosity. The thorax is not less than 0.27x the cephalon in length but seems shorter because the anterior segment has overridden the frontal part of the second segment. Associated are three more cephala of a similar stricture.

The pygidium Plate 23, fig. 2, CPC 14107, is 2.5 mm long; its posterior axial lobe is somewhat trigonal, its median node is clear, and the test granulose.

The pygidium Plate 23, fig. 3, CPC 14108, is 2.8 mm long. The posterior axial lobe has slightly convex flanks and the postaxial median furrow seems shallow. The granulosity of the test is stronger than in the other specimens.

Occurrence and age: Triplagnostus gibbus gibbus has been found in Australia only in two localities, M433 and M430, in the lowermost part of the Inca Formation; the strata with that species at site M433 top the Beetle Creek Formation, distinguished by its fauna of polymerid trilobites, especially *Xystridura,* and rare agnostids including fragmentary shields of a *Triplagnostus*. The age of the described material is late Templetonian (late Zone of *Triplagnostus gibbus*) passing above into the zone of *Ptychagnostus atavus*.

Triplagnostus gibbus posterus subsp. nov.

(Pl. 23, figs. 4 and 5; Pl. 24, figs. 1-5; Pl. 25, figs. 1-3; Pl. 27, fig. 2)

Material: Illustrated are four exoskeletons and five isolated shields selected from a countless supply of specimens; some ten shields are clustered in Plate 25, fig. 1.

Holotype: The complete exoskeleton Plate 23, fig. 4, CPC 14109, is selected as the holotype.

Diagnosis: Triplagnostus gibbus posterus has no pygidial marginal spines and is distinguished by the following characters: (1) double basal lobes, (2) long cephalic spines, (3) very long axial spines, and (4) short but clear recurved fulcral spines in the second segment of the thorax.

Differential diagnosis: The subspecies *gibbus posterus* differs from *T. gibbus gibbus* by the characters enumerated in the diagnosis above; its difference from *Triplagnostus quasigibbus* nov., which also has no pygidial marginal spines, is evident from the description of the latter. Whitehouse (1936, p. 84, pl. 8, figs. 6 and 7; pl. 10, fig. 2) attributed to *Triplagnostus gibbus* (Linnarsson) cephala with double basal lobes associated with pygidia without marginal spines; those specimens belong to *Triplagnostus gibbus posterus* of this Bulletin. Öpik (1956; 1957, p. 15) on the evidence of similar material indicated in a chart the overlap of the Zones of *gibbus* and *atavus,* and in another chart (Öpik, 1960), operates with an '*atavus-gibbus*' zone. In these, however, the name *gibbus* in association with *atavus* means now *Triplagnostus gibbus posterus*—a form concurrent with *T. gibbus gibbus* and *Ptychagnostus atavus. T. gibbus posterus* survived even in the early part of the *Ptychagnostus punctuosus* time.

Description: Triplagnostus gibbus posterus can be described generally in terms of the genus, amplified by the data given in the diagnosis, and in the comment on the illustrated specimens. The identification of the subspecies in defective or incompletely dematricated specimens is, however, unsafe and the correct result depends on the following data: (1) in the pygidium the absence of marginal spines and the presence of an extended axial spine (or its stump) must be evident; (2) in the cephalon the duplication of the basal lobes and the extended spines (or stumps of such spines) should be ascertained; and (3) consideration should be given to the possibility of confusing *T. gibbus posterus* with *T. diremptus* that can arise in the absence of supporting pygidia.

These warnings are necessary because *Triplagnostus gibbus posterus* is of no significance in the refined stratigraphy of zones but its erroneous identification under the name of another species may become perchance a source of stratigraphic misinterpretations.

Comment on illustrated specimens

The two following specimens from locality M433 represent *T. gibbus posterus* associated with *T. gibbus gibbus*.

The larger cephalon Plate 23, fig. 5, CPC 14110, is 3.1 mm long; the cephalic spines, less than half the glabella in length though still longer than in *gibbus gibbus,* are shorter than in specimens from the *Ptychagnostus atavus* zone; the basal lobes are double also in the associated smaller cephalon, with their anterior tips clearly separated from the larger, posterior part.

The holotype exoskeleton, Plate 23, fig. 4, CPC 14109, is 5.6 mm long; it is fractured and unevenly flattened, with the glabella and the pygidial axis pressed down from their original elevated position. The basal lobes are double (as above) and the fulcral prongs are extended into short recurved prickles. The test is indistinctly granulose. The cephalon is about 1.1x the length of the pygidium and the thorax 0.22-0.23x the cephalon. In the complete test of *T. gibbus* (Westergaard, 1946, pl. 9, fig. 20) the thorax is larger —about 0.26x. The holotype is the oldest known complete test of *T. gibbus posterus* nov.

The exoskeleton Plate 27, fig. 2, CPC 14126, collection M263, silty shale of the Inca Formation (earliest part of the *Ptychagnostus punctuosus* Zone), is the youngest known specimen (the oldest complete is the holotype). It is 7.2 mm long. The test is flattened and deformed, with the frontal lobe and pygidial axis dilated and posterior glabellar lobe twisted. The axial spines are very long, and the recurved fulcral prongs in the second segment are prominent; the rim of the cephalon and pygidium is somewhat narrow.

The next specimens have been selected from collections of the Inca Formation, Zone of *Ptychagnostus atavus.*

The exoskeleton Plate 24, fig. 3, CPC 14112, locality M425, is 5.8 mm long; the test is silicified and fragile and its matrix is friable siltstone. The left basal lobe is deformed, the other is intact and double. A prominent axial node is present on the anterior segment of the thorax, and the node on the posterior axial lobe of the pygidium is well visible. The cephalon is almost 1.2x the length of the pygidium.

The exoskeleton Plate 24, figs. 1 and 2, CPC 14111, locality M425 (as above), is 6.0 mm long. The cephalic spines are half the glabella in length. The latex casts of the axial spines curled after the extraction of the cast.

Of the two cephala Plate 25, fig. 2, CPC 14116, locality M425, the larger is 2.5 mm long. In these the posterior glabellar lobe tapers slightly forward and the smaller cephalon has a relatively slender glabella.

The matrix is limestone in the next specimens.

The cephalon Plate 25, fig. 3, CPC 14117, locality M169, is 3.2 mm long. The test is preserved and granulose; the glabella is deformed and pressed down between the cheeks and tilted to the left, displacing the node from its median position. The basal lobes are clearly double, each consisting of two bosses.

A cluster of isolated shields Plate 25, fig. 1, CPC 14115, locality M169, contains some ten cephala, the largest about 1.7 mm long, and about six pygidia, belonging to *Triplagnostus gibbus posterus;* associated are three pygidia of *Ptychagnostus atavus* and two shields of a *Pseudoperonopsis.*

The cephalon Plate 24, fig. 5, CPC 14114, locality M208, is 2.5 mm long. It has retained its test and flattened a little. The spines with tips diving into the matrix seem short, the transverse glabellar furrow is shallow, and so is the transverse furrow in the double basal lobes. The constriction of the posterior glabellar lobe indicates a variant of the main form.

Associated with the cephalon above, the pygidium Plate 24, fig. 4, CPC 14113, is 2.7 mm long. It has preserved its original convexity.

Occurrence and age: Triplagnostus gibbus posterus is the most common and abundant agnostid in the Inca Formation, and of a long stratigraphic span: (1) it appears late in the Zone of *Triplagnostus gibbus,* (2) is most prolific in the Zone of *Ptychagnostus atavus,* and (3) after that zone is rare, but reaches the beginning of the Zone of *Ptychagnostus punctuosus.*

Triplagnostus quasigibbus sp. nov.

(Pl. 27, fig. 1)

Material: The illustrated exoskeleton, CPC 14125, is the holotype and the only available specimen.

Diagnosis: Triplagnostus quasigibbus is a species with double basal lobes and without pygidial marginal spines, distinguished by the following characters: (1) the posterior glabellar lobe tapers a little forward; (2) the cephalic and axial spines are extended but short; (3) the fulcral points in the second segment of the thorax are spineless angular projections; (4) the rim in the cephalon and especially in the pygidium is extremely narrow; (5) the postaxial median furrow is vestigial; and (6) the ornament consists of a dense and relatively coarse granulation.

Differential diagnosis: Triplagnostus quasigibbus shares with *T. gibbus posterus* the spineless pygidial margin and the double basal lobes, but differs in respect of all other diagnostic characters.

Description: The holotype is 7.0 mm long with a thorax about 0.23-0.24x the cephalon in length. The left basal lobe, which is intact, is short and its posterior part is a rather small boss. The cephalic spines have lost their tips, which may have reached the posterior margin of the anterior segment of the thorax as can be seen from the imprint of the spine on the right pleura. In the pygidium the subcentral node on the posterior axial lobe is inconspicuous and almost lost in the dense granulosity of the ornament, and the postaxial furrow is indicated only by a short depression behind the axial tip.

Occurrence and age: The holotype of *Triplagnostus quasigibbus* has been found in silty shale of the Inca Formation, locality M265; its age is the Floran Zone of *Ptychagnostus atavus.*

Triplagnostus sp. indet.

(Pl. 27, fig. 3)

The illustrated pygidium, the only available shield, CPC 14127, is 2.2 mm long. It is flattened, but otherwise well preserved. Marginal spines are absent, as in *Triplagnostus gibbus gibbus, T. gibbus posterus,* and *T. quasigibbus*; in these, however, the pygidial axis is longer, broader, and pointed. In the illustrated specimen of *Triplagnostus* sp. indet. the rear of the axis is bluntly rounded, tapering and slightly attenuated; it is short, about 0.65x the shield length. The axial spine is strong but is incomplete; its tip may have reached the rear of the axis.

Occurrence and age: Triplagnostus sp. indet. (the pygidium) comes from the Inca Formation, locality M425; its age is the Floran Zone of *Pychagnostus atavus.*

Triplagnostus fretus sp. nov.

(Pl. 28, figs. 1-6)

Material: Illustrated are one exoskeleton, one cephalon, a thorax with the pygidium attached, and three pygidia, all in silty shale, from a supply of some fifty shields.

Holotype: The exoskeleton Plate 28, fig. 1, locality M281, CPC 14130, is selected as the holotype.

Diagnosis: Triplagnostus fretus is a species with simple basal lobes, a slender pygidial axial lobe behind the main annulation, and a thick base to the pygidial axial spine; distinguished by its short trigonal pygidial marginal spines, deflected sideways.

Differential diagnosis: Triplagnostus fretus differs from *T. gibbus gibbus* (which also has simple basal lobes) by its pygidial marginal spines; in *Aristarius retrocornutus* the cephalon (Pl. 29, figs. 4 and 6) resembles *fretus* in design but its glabella is trigonal and its frontal glabellar lobe, about 0.42x the glabella in length, is longer and also pointed; in *fretus* it is 0.38-0.40x and the flanks are convex. In *Triplagnostus diremptus* (q.v.) the pygidial spines are also very short but its basal lobes are double. Finally, *Goniagnostus purus* Whitehouse (1939), whose holotype is a pygidium with short spines, is discussed separately.

Description: Triplagnostus fretus sp. nov. is a species en grande tenue of a medium size, attaining a length of 7.0-8.0 mm. Its cephalon is longitudinally and transversely the larger shield, about 1.2x the pygidium in length; its thorax, 0.23x the cephalon in length, is average for the genus. The cephalic rim is narrow and convex, and the pygidial rim is little wider and relatively flat.

In the cephalon the cheeks have neither scrobicules nor rugae; the preglabellar median furrow flares a little in front; the posterior glabellar lobe has almost parallel flanks and rather weak lateral furrows; the frontal lobe, 0.4x the glabella in length, is pointed. The median glabellar node is placed in the rear as in other species of the genus. The basal lobes are simple, tumid, and large, as seen also in *T. gibbus gibbus.* The cephalic spines, about 0.5x the glabella in length and much shorter than in *Triplagnostus stramineus,* are slender but with a quite strong base. In the thorax, the prongs are recurved, short, and prominent, and about as strong as in *T. gibbus posterus* or *stramineus* nov.

In the pygidium the marginal spines are trigonal, short, and deflected. The axial lobe is long (as in other species of the genus), and variable between 0.75-0.78x the shield length; the anterior transverse furrow is rather deep and the anterior lobe is tripartite with strong lateral lobules; the second axial lobe consists in its larger median part of the stout median node—the base of the slender axial spine. The postaxial median furrow is usually clear, but in one specimen it appears vestigial.

Comment on illustrated specimens

Five of the six illustrated specimens have been obtained from a piece of silt shale, Inca Formation, collection M281.

The holotype is 5.5 mm long. The pygidium is deformed a little and the tip of its axial lobe has lost the rounded shape seen in undeformed specimens. The left marginal spine is visible but has lost some of its test; the axial node is stout and the axial spine is indicated by its stump. In the cephalon the basal lobes are defective; the cephalic spine, arising from a rather stout base, is attenuated and about half the cephalon in length. In the thorax (see also the next specimen) the pointed fulcral prongs of the posterior segment grip the fulcral points of the pygidium. The glabellar median node is placed well in the rear (as in *T.*

gibbus) and the small node (knob) about the centre of the posterior pygidial axial lobe is evident. The cephalon, 1.2x the pygidium in length, is relatively large, larger than in the *Triplagnostus gibbus* and *gibbus posterus*.

The pygidium in Plate 28, fig. 2, CPC 14131, is 3.2 mm long; the marginal spines seem small, retaining only the middle part of the test; in the thorax the stump of the axial spine is slender and the fulcral prongs are short spines. The total length of the exoskeleton should be about 7.0 mm.

The cephalon Plate 28, fig. 5, CPC 14134, is 2.8 mm long; its triangular, large and simple left basal lobe is intact.

The pygidium Plate 28, fig. 3, CPC 14132, is 3.0 mm long; the right marginal spine (trigonal in shape) is clear; the axial rear is as blunt as that in the next specimen.

The pygidium Plate 28, fig. 4, CPC 14133, is a little longer than 3.0 mm; the marginal spines are visibly trigonal. The axial rear is bluntly rounded, and the postaxial median furrow is small.

The pygidium Plate 27, fig. 4, CPC 14128, locality M265, is 2.5 mm long; it is almost flat, the axial node excepted; the missing part of the axial spine possibly left its imprint in the test, with the tip extending close to the rear of the axis.

Occurrence and age: Triplagnostus fretus occurs in the Inca Formation, in siltstone and shale, at localities M281, M265, and M188; its age is the Floran Zone of *Ptychagnostus atavus*; it is unknown in younger strata.

Triplagnostus purus (Whitehouse, 1939)

Whitehouse (1939, pp. 258-259, pl. 25, figs. 21-23) described this species under the name of *Goniagnostus purus* in consideration of its pygidial marginal spines; at the same time he recognised its similarity to *Triplagnostus*. The species *purus* was, nevertheless, taken by its author 'as a very early member of *Goniagnostus*, having recently branched off from the group of *Triplagnostus gibbus* and not yet acquired all the typical features of *Goniagnostus*'.

Latex casts (courtesy Dr P. Jell) of Whitehouse's specimens figures 21 and 23 were at hand in revising the taxonomy of *T. purus*.

The holotype of *purus* is the pygidium, fig. 23, so designated by Whitehouse. The shield with its articulating half-ring is 3.2 mm long, its axial lobe is about 0.7x the shield length, the two transverse furrows are clear, the anterior annulation is tripartite with prominent lateral lobules and the second carries the stump of the axial spine. The axis is constricted about the second annulation, the posterior axial lobe is expanded laterally, and its flanks meet in even curves at the tip, which is not quite blunt but angular. The marginal spines are short and moderately deflected. According to Whitehouse (op. cit., p. 259) the species, but for the spines, is hardly to be distinguished from *Triplagnostus gibbus*. The test is smooth.

Diagnosis (compiled herein): *Triplagnostus purus* possesses short pygidial marginal spines and is distinguished by its smooth test and evenly curved flanks of the posterior axial lobe.

Furthermore, the cephalon (ibid., fig. 22) associated with the holotype pygidium also belongs to the genus *Triplagnostus*: the glabella is pointed in front, its median node stands well to the rear and the basal lobes (obscured in the illustration) are narrow and acutely triangular and presumably simple. This cephalon, however, has not been located in the collections. The other illustrated cephalon (ibid., fig. 21), also associated with the holotype of *purus*, belongs to *Ptychagnostus punctuosus affinis*.

Differential diagnosis: Triplagnostus diremptus sp. nov. and *T. fretus* sp. nov. have short pygidial marginal spines. In *T. diremptus* (Pl. 26, figs. 2-4) the pygidial test is granulose (*purus* is smooth), the axis is 0.73-0.77x the shield length (0.7 in *purus*) and the axis is slightly constricted in the rear (flanks are convex in *purus*) about the median node and is a little extenuated and swollen behind the constriction. In *Triplagnostus fretus* (Pl. 28) the pygidial axis is also longer (0.75-0.77) than in *purus* and of a different shape.

Occurrence and age: Whitehouse (op. cit., p. 259) quotes: 'from the *Agnostus seminula* Stage in limestone eleven and a half miles north of Yelvertoft Dip'; the age is the Undillan Zone of *Ptychagnostus punctuosus*—the same as of *Onymagnostus seminula*.

Triplagnostus diremptus sp. nov.

(Pl. 22, fig. 1; Pl. 26, figs. 1-6; Pl. 44, fig. 3)

Material: Illustrated are three cephala and six pygidia and a cluster of shields; a complete exoskeleton, in the same cluster, is described.

Holotype: The cephalon Plate 26, fig. 1, CPC 14118, is the selected holotype.

Diagnosis: Triplagnostus diremptus has a granulose test; a pair of pits in the flanks of the glabella about the front of the basal lobes; a pair of extended cephalic spines and axial spines on the second segment of the thorax and in the pygidium, as usual in the genus; the species is distinguished by the combination of a cephalon with double basal lobes and a pygidium with short marginal spines, and a slightly constricted and attenuated posterior of the pygidial axial lobe.

Differential diagnosis: Double basal lobes are also evident in *Triplagnostus gibbus posterus,* which, however, has no pygidial marginal spines; moreover, the duplication of its basal lobes is less clear than in *diremptus* and pits at the basal lobes are absent. Marginal pygidial spines are also present in *Triplagnostus fretus* nov. and in *T. purus* Whitehouse; in *T. fretus* the basal lobes are simple and the pygidial axis is not constricted. The cephalon of *T. purus* is insufficiently known, but its differential pygidial characters are discussed in its description.

Description: Triplagnostus diremptus is a species en grande tenue and may have attained a length of 7 to 8 mm. The cephalon is about 1.2x the pygidium in length and the thorax, about 0.2x the cephalon, is short. The rim in the shields is narrow and convex. The cheeks are usually smooth without scrobicules, but in one cephalon, Plate 26, fig. 6, shallow arcuate scrobicules and dimples are indicated. The frontal glabellar lobe is pointed and its flanks are evenly convex. The posterior lobe is a little expanded behind the lateral furrows, which are clear and short; in profile the glabella rises rearward in a concave curve and culminates behind the median node. The basal lobes are clearly subdivided into a posterior semiglobose ('full') boss and an anterior trigonal narrow swelling. The cephalic spines are about 0.5x the glabella in length as seen in Plate 22, fig. 1. The pygidium in its outline is close to a larger arc of a circle; the marginal spines are short and deflected and, in flattened shields, may be trigonal. The marginal furrow is narrow and deep and the acrolobe rises steeply at its margin over the furrow. The pygidial axis is relatively long, variable between 0.73 and 0.78x the shield length, and is narrowest about the middle annulation. Behind the middle of the posterior axial lobe stands the clear median node (knob), and about it the axis is laterally and slightly constricted and attenuated, and behind the constriction also a little tumid. A rosette is absent and the whole structure of the axis resembles *Goniagnostus nathorsti intersertus* (Pl. 61, fig. 7).

Comment on illustrated specimens

The following three specimens were obtained from locality M123, Currant Bush Limestone.

The holotype cephalon is 2.7 mm long; large stumps of the spines are preserved and the lateral glabellar furrows are strong. The associated pygidium is 1.6 mm long; it is fractured and parts of the rim with spines are lost, but the granulation of the test is clear, and stronger than in the cephalon.

The pygidium Plate 26, fig. 2, CPC 14119, is 1.6 mm long. The left marginal spine is intact and the node on the posterior axial lobe is prominent; behind the midpoint of that lobe, whose rear is attenuated, the axis is 0.73x the shield length (in larger shields it is longer).

The pygidium Plate 26, fig. 4, CPC 14121, is 2.1 mm long. The marginal spines are preserved, the axial rear is attenuated, the axis is 0.77x the shield length; the anterior axial lobe is tripartite and relatively narrow transversely. The ornament (granulation) is overemphasised by excessive whitening.

The pygidium Plate 26, fig. 3, CPC 14120, Currant Bush Limestone, locality M150, is 3.6 mm long, and larger than the other pygidia; it belongs to an exoskeleton about 7.5 mm long.

The pygidium Plate 44, fig. 2, associated with the holotype of *Ptychagnostus scarifatus,* Currant Bush Limestone, locality M176, is 3.0 mm long.

The complete exoskeleton (not illustrated) CPC 14378, in shale of the Inca Formation, locality M149, is 4.3 mm long; the cephalon is 1.2x the pygidium in length and the thorax about 0.2x the cephalon; the pygidial marginal spines are preserved, the basal lobes are double, and the second segment of the thorax is equipped with an axial spine.

The cluster of shields in silty shale of the Inca Formation, CPC 14379, locality M149, represents a part of a bedding plane; visible are pygidia with attenuated axial rear and marginal spines (some are flattened) and cephala with posterolateral spines. All these specimens belong to the Zone of *Euagnostus opimus.*

The next two specimens belong to the latest part of the Zone of *Ptychagnostus atavus.*

The cephalon Plate 26, fig. 5, CPC 14122, in porous siltstone of the Inca Formation, locality M192, is 2.8 mm long. The double basal lobes are strong; the crest of the glabellar rear is apparently a fold in the test resulting from lateral deformation. In the anterolateral corners of the posterior glabellar lobe a pair of circular impressions represent by their symmetrical position and shape a pair of muscle scars (or notulae) and their prominence seems an individual trait of that specimen.

The cephalon Plate 26, fig. 6, CPC 14123, in limestone of the Inca Formation, locality M208, is 2.6 mm long. Its very weak scrobiculation is visible under whitening and in oblique illumination; but otherwise it does not differ from the holotype cephalon.

Occurrence and age: Triplagnostus diremptus is a species of the Floran Stage; it makes its appearance in shale and limestone of the Inca Formation (M192 and M208 respectively) late in the Zone of *Ptychagnostus atavus;* it is infrequent in the Currant Bush Limestone (M123, M150, M176) but very abundant in shale of the Inca Formation, locality M149, in the Zone of *Euagnostus opimus*.

Triplagnostus scopus sp. nov.

(Pl. 27, figs. 5 and 6)

The material consists of the illustrated exoskeleton CPC 14129, the holotype, in shale of the Inca Formation, locality M265.

Diagnosis: Triplagnostus scopus is a species with a parallel-sided (regular *Triplagnostus*) glabella, simple basal lobes, and pygidial marginal spines; it is distinguished by its long frontal glabellar lobe, long and broad pygidial axial lobe, and relatively small pygidium.

Differential diagnosis: T. stramineus nov. and *T. fretus* also have simple basal lobes and pygidial marginal spines; in *T. stramineus*, however, the frontal glabellar lobe (0.41x the glabella in length) is shorter than in *scopus* (0.45); the pygidial axis is in *stramineus* relatively short (0.7x the shield length) against 0.83 in *scopus*. In *T. fretus* the frontal glabellar lobe is also relatively short (0.4x the glabella) and the pygidial axis is about 0.75x. In these three species of spinose *Triplagnostus* the pygidium is narrower than the cephalon, in *scopus* more than in the others; in *scopus* the pygidium is still a little wider than the cephalic acrolobe. In a coiled state the margins of the shields may not coincide with each other because the closure is effected by the contact of the doublures.

Description: The exoskeleton of *T. scopus* is 7.0 mm long; the cephalon is as long as 1.2x the pygidial length; the pygidium is about as wide as the cephalic acrolobe; the thorax is about 0.23x the cephalon in length (less than 0.24 in terms of Text-fig. 2). The cephalon is about circular, its rim is evenly narrow and smooth, without scrobicules or rugosity. In the glabella the frontal lobe is visibly large, with a bluntly pointed tip and convex flanks, and different from *T. stramineus*. The median glabellar node stands far back, as in *Triplagnostus gibbus* (Text-fig. 36); the basal lobes are long and simple and a fracture simulates a duplication in the right lobe. The fulcral spines are relatively long—a little longer than the thorax, as evident from the imprint of the bent left spine.

In the thorax the fulcral points in the anterior segment are wanting in spines; in the second segment, however, the fulcral spines are prominent, more than in *Triplagnostus gibbus posterus* (Pl. 24, fig. 3) but less than in *Goniagnostus* (Text-figs. 49 and 50). In the anterior segment an axial node (almost a short spine), and in the second segment the usual axial spine, are manifest. The longest axial spine (half of it is preserved) is that in the second annulation of the pygidial axis.

In the pygidium the rim, still narrow, is about twice the cephalic rim; the marginal spines seem not extended, although they may have lost some of their length. A postaxial median furrow is not evident; the axial lobe is relatively narrow about its middle annulation; the flanks of its posterior broad lobe are convex and meet in the rear at a bluntly angulate tip. The silicified test seems smooth or, possibly, indistinctly granulose; the latex cast (Pl. 27, fig. 6) is granulose all over.

The specimen is complete; the missing parts of the spines remained in the matrix; the deformation is the result of compaction of the sediment. It appears that the exoskeleton is the last integument of the particular individual.

Occurrence and age: The described specimen of *Triplagnostus scopus* came from a silty shale of the Inca Formation, locality M265; its age is the Floran Zone of *Ptychagnostus atavus*.

Triplagnostus stramineus sp. nov.

(Pl. 26, fig. 7; Text-fig. 37)

The material consists of the holotype exoskeleton CPC 14124, in shale of the Inca Formation, locality M265.

Diagnosis: Triplagnostus stramineus has a parallel-sided glabella, simple basal lobes, and pygidial marginal spines; it is distinguished by its triangular glabellar frontal lobe, retrally tapered pygidial axial lobe of a moderate length, and exceptionally long cephalic and pygidial marginal spines.

Differential diagnosis: No other known *Triplagnostus* has spines as long as *T. stramineus*; in the related *T. scopus* nov. the pygidial axis is visibly longer and its posterior lobe is broad and its flanks are convex and different from the almost triangular axis of *scopus*; the frontal glabellar lobe in *stramineus* is also shorter and more acute in front than in *scopus*; finally, *scopus* lacks a postaxial median furrow, clear in *stramineus*. In *Triplagnostus fretus* nov. a postaxial median furrow is also present; its spines, however, are short, the pygidial axial lobe is about oval, and the frontal glabellar lobe is much shorter than in *stramineus*. Long spines are present also in the species of *Triplagnostus* (*Aristarius*) (Text-figs. 38, 39) but in these the trigonal glabella is distinctive; nevertheless, pygidia resemble *T. stramineus*.

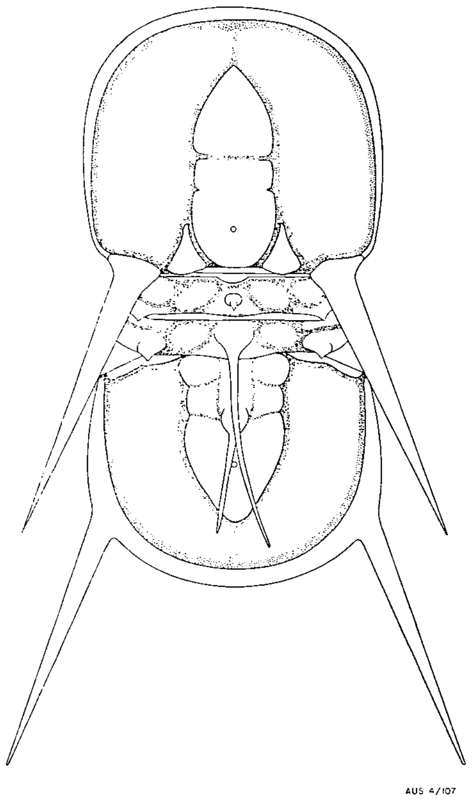

Fig. 37. *Triplagnostus stramineus.*

Description: The holotype of *stramineus* is 6.5 mm long; it is flattened but complete, having preserved its spines on the right side, and the axial spines (in parts as imprints on the test) as shown in Text-figure 37.

It is a species completely en grande tenue, rivalled only by *Goniagnostus* (*Criotypus*) *oxytorus* with its occipital spine and the extended posterior fulcral spines in the thorax.

The cephalon is the larger shield, about 1.2x the pygidium in length; the thorax is 0.24x the cephalon in length, and about as long as in *Aristarius retrocornutus* and *ultimus*, with 0.25 and 0.23 respectively.

The frontal glabellar lobe, 0.41-0.42x the glabella in length, about as wide as long, and pointed in front, has convex posterior flanks and seems a little wider than the posterior lobe behind it. The median glabellar node is small but prominent and placed about the middle of the posterior half of the posterior lobe, whose rear is broadly rounded and does not cover the occipital collar. The basal lobes are triangular and simple, with laterally projected abaxial corners.

In the pygidium the rim is wider than the narrow rim of the cephalon, and in the rear, between the marginal spines, there is an outer flange possibly resulting from the collapse of the test over the doublure. The marginal spines are as long as the pygidium, straight and deflected sideways, but are shorter than the cephalic spines, which are as long as the thorax and pygidium together. The pygidial axis, 0.7x the shield length, is narrowly blunt (not quite pointed) at its tip and moderately contracted about its second annulation; the anterior annulation is the widest, and tripartite with clear lateral lobules. The axial spine, rising from the tip of the median node after collapsing, may have reached the rear of the axis. The posterior axial lobe has convex anterior flanks and tapers retrally.

In the thorax the axial spine is long and delicate and the fulcral spines in the second segment are short angular prongs.

The test is minutely granulose.

Occurrence and age: The holotype of *Triplagnostus stramineus* is embedded in a shale with chert of the Inca Formation, locality M265; its age is the Floran Zone of *Ptychagnostus atavus.*

Subgenus **Triplagnostus (Aristarius)** nov.

The type species of the subgenus *Aristarius* is *Triplagnostus* (*Aristarius*) *aristarius* sp. nov.

The name *Aristarius* designates species of *Triplagnostus* with a trigonal glabella, extended pygidial marginal spines, and simple basal lobes. The basal lobes are simple also in *Triplagnostus gibbus gibbus*, but in *gibbus* the pygidial margin is spineless. The total absence of spines in the pygidium of *gibbus* may be regarded as a character taxonomically more significant than the shortness of the spines in *fretus*, whose cephalic structure, however, resembles *gibbus*.

Three species, *retrocornutus* (Zone of *Pt. atavus*), *aristarius* (Zone of *Pt. punctuosus*), and *ultimus* (Zone of *G. nathorsti*), resemble each other in having a similar elongate, trigonal, and pointed glabella, suggesting a phyletic chain of forms distinguished by modifications of the structure of the pygidial axis. This chain itself is, however, broken by stratigraphic (faunal, but not depositional) gaps and by the absence of intermediate forms in collections in hand.

Triplagnostus (Aristarius) retrocornutus sp. nov.

(Pl. 29, figs. 1-6)

Material: Illustrated are one defective exoskeleton, two cephala, and three pygidia; six more shields have been noted in the same collection.

Holotype: The exoskeleton, Plate 29, fig. 1, CPC 14135, is selected as the holotype.

Diagnosis: Aristarius retrocornutus has a trigonal glabella with slightly convex flanks of the frontal glabellar lobe; it is distinguished by very long and deflected pygidial marginal spines and a relatively strong pygidial axial spine on the second annulation. The length of the frontal glabellar lobe is 1.3-1.4x its width in the rear.

Differential diagnosis: In *Aristarius aristarius* the pygidial axial spine is short; in *Aristarius ultimus* no axial spine is evident in the pygidium.

Description: Aristarius retrocornutus, as evident from the largest shields available, reached a sagittal length of some 8.3 mm without, and 11.0 mm to the level of the tip of, the pygidial marginal spines. The cephalon is only slightly longer than the pygidium and the thorax is 0.25x the length of the cephalon. In *Triplagnostus stramineus* the cephalon is visibly larger and the thorax (0.22) shorter than in *retrocornutus*; in *Aristarius ultimus* the thorax is about as long as in *retrocornutus.*

The glabella tapers forward but less abruptly than in *A. aristarius,* whose frontal glabellar lobe has straight flanks; the length of the lobe is about the same in both species (0.42-0.43x the glabella); the median glabellar node is distinct and the glabellar rear in plan is semioval; in profile it slopes down from the culmination in an even arc not overhanging the occipital collar.

In the pygidium the margin in front of the spines is more or less straight, and behind the spines it is an arc of a circle; the rim is relatively wide and greatly expanded at the base of the marginal spines, which are strongly deflected sideways. The pygidial axis in undeformed shields (Pl. 29, fig. 5) has somewhat convex flanks in the posterior lobe, and the median node on the second annulation is prominent and bulbous and extended into a long spine which when collapsed may have reached beyond the middle of the posterior axial lobe.

No ornament seems to be present: the test appears smooth.

Comment on illustrated specimens

All specimens came from siltstone (silty shale) with chert pods of the Inca Formation, locality M265.

The holotype exoskeleton, in chert, is 6.9 mm long; more than half is well enough preserved for a study of the whole; fractures obscure the structure of its pygidial axis. This specimen is essential (1) in identification of isolated shields of the species, and (2) in establishing the difference between *A. retrocornutus* and the concurrent *Triplagnostus stramineus.* The glabella tapers evenly forward; the flank of the frontal lobe is convex; and the pygidial marginal spine is deflected sideways.

The cephalon Plate 29, fig. 6, CPC 14140, is 2.6 mm long; it supplements the holotype regarding the shape of the glabella and its frontal lobe.

The cephalon Plate 29, fig. 4, CPC 14138, associated with a smaller cephalon, is 2.5 mm long; it is flattened and the glabella is pressed down relative to the cheeks; the gentle slope of the glabellar rear is retained exposing the occipital collar.

The pygidium Plate 29, fig. 2, CPC 14136, is 4.0 mm long, of an exoskeleton about 8.0 mm long; the axis is deformed and tilted to the left, but a part of its axial spine is preserved; the postaxial median furrow is shallow and incomplete; the marginal spines are curved.

The pygidium Plate 29, fig. 5, CPC 14139, is 3.0 mm long; the axis is collapsed, the axial spine is lost, but the shield is otherwise undeformed; the postaxial median furrow is clear; the marginal spines arise from a rather wide base; the node on the posterior axial lobe is inconspicuous.

The small pygidium Plate 29, fig. 3, CPC 14137, is about 2.2 mm long; the median axial node is bulbous and carries a delicate spine; the latex failed to cast the whole of the spine, and the extracted part of the cast curled subsequently. The marginal spines are straight.

Occurrence and age: Aristarius retrocornutus is a rare fossil of the Inca Formation; its age is the Floran Zone of *Ptychagnostus atavus.*

Triplagnostus (Aristarius) aristarius sp. nov.

(Pl. 30, figs. 1-3; Text-fig. 38)

Material: Illustrated are one cephalon and one pygidium selected from some ten cephala and four pygidia—all in a single piece of silty shale (the chips are deposited in the collection with the figured specimens).

Holotype: The cephalon Plate 30, figs. 2 and 3, CPC 14142, 3, is selected as the holotype.

Diagnosis and differential diagnosis: In *Aristarius aristarius* the glabella has straight flanks converging evenly and meeting at the acute front (as in *A. ultimus*) and the pygidium bears a short axial spine (in *ultimus* the median axial node is spineless). The difference

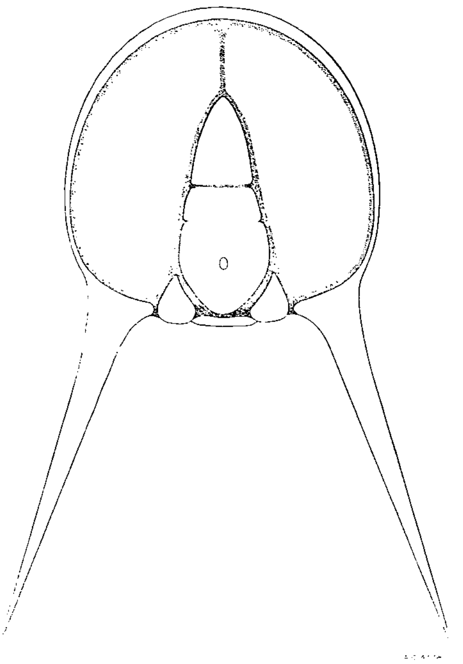

Fig. 38. *Triplagnostus (Aristarius) aristarius.*

from *A. retrocornutus* is discussed under that species.

Description: The holotype cephalon is about 3.3 mm long, the largest cephalon 4.0, and the smallest 1.0 mm long. The glabella is slender, trigonal and pointed in front, and subangular to narrowly rounded in the rear between the simple, triangular, and swollen basal lobes—a shape rather uncommon in Ptychagnostinae, in which the rear is generally broadly rounded. The frontal glabellar lobe, about 0.42-0.43x the glabella in length, is visibly slender—as long as about 1.45x its width in the rear (1.1 in *ultimus*); the median glabellar node marks the culmination of the glabellar profile about the level of the tips of the basal lobes; from here the glabella slopes down in a gentle arc, leaving the occipital collar exposed in plan. The rim is narrow and the outline of the cephalon is close to a circle. The illustrated pygidium Plate 30, fig. 1, CPC 14141, is 3.0 mm long; the pygidial rim is wider than in the cephalon, and the marginal spines, about as long as the shield, diverge at an angle of about 50-55 degrees. The pygidial axis, about 0.73-0.74x the shield length, is pointed in the rear; the flanks of the posterior axial lobe are slightly convex, and a small node is placed a little behind the lobe's midpoint. In the second lobe the median node is moderately prominent and its base is extended for a short distance onto the anterior part of the posterior lobe; the median node carries a short spine on its rear.

The test is smooth.

Occurrence and age: Triplagnostus (Aristarius) aristarius is a fossil of the Inca Formation and has been found in a shale, locality M263; its age is Undillan—early in the Zone of *Ptychagnostus punctuosus.*

Triplagnostus (Aristarius) ultimus sp. nov.

(Pl. 30, fig. 5; Pl. 31, figs. 1 and 2; Text-fig. 39)

Material: Illustrated are one exoskeleton and two pygidia; two more pygidia are available.

Holotype: The exoskeleton Plate 31, fig. 1, CPC 14146, is selected as the holotype.

Diagnosis: Aristarius ultimus is a regular species of its subgenus regarding spinosity and the trigonal shape of the glabella, distinguished by a relatively short frontal glabellar lobe about 0.4x the glabella in length and about as long as 1.1x its rear width, and by the spineless median node of the pygidial axis.

Differential diagnosis: Aristarius ultimus resembles *A. aristarius* and *A. retrocornutus* regarding the trigonality of the glabella but differs from these by the smaller size of the frontal glabellar lobe (as long as 1.1x its rear width) and by the absence of an axial pygidial spine; in *A. retrocornutus* the length of the frontal glabellar lobe is 1.3-1.4x its rear width, and in *A. aristarius* 1.45x.

Description: In the cephalon of the holotype the glabella, including the basal lobes, tapers evenly forward, but its frontal lobe has slightly convex flanks; the basal lobes are simple and relatively short; the transverse glabellar furrow appears shallow. In the thorax the second segment has a strong axial spine but no extended

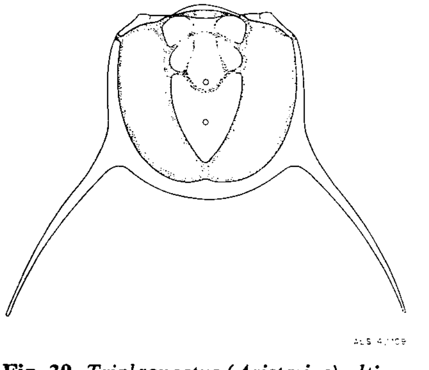

Fig. 39. *Triplagnostus (Aristarius) ultimus.*

fulcral spines. The thorax is about 0.23x the cephalon in length.

In the pygidium the rim is widened at the broad bases of the deflected and divergent marginal spines. The axis in the two illustrated unflattened pygidia is in plan as long as 0.78x the shield length and longer than in the holotype; the acrolobe in the rear of the pygidium in the holotype is, however, flattened and lost its slope, increasing the relative length of the shield by deformation.

The pygidial axis is appropriately trigonal; its anterior annulation is wide and has a pair of prominent lateral lobules; the second lobe, sagittally twice as long as its flanks, carries a rearward rising broad (*gibbus*) swell (the strong median node) straddling the frontal part of the posterior lobe and terminating as a blunt and low node. The posterior pygidial axial lobe tapers rearward with slightly convex flanks, is somewhat constricted in the middle and attenuated behind the constriction. Its rear is acute. The test is very thin and smooth.

Comment on illustrated specimens

All specimens come from limestone, locality M57.

The holotype exoskeleton is 6.3 mm long; singed in fire, it is defective; still, traces of the left cephalic and of the pygidial spines are discernible; the proximal part of the reclined axial spine of the thorax is preserved; the pygidial median node is spineless, and the pygidium is a little flattened. The cephalon is as long as the pygidium and the posterior segment of the thorax taken together.

The singed pygidium Plate 30, fig. 5, CPC 14145, is 2.5 mm long; the subcentral node on the posterior axial lobe is preserved, and the scar left from the median node of the second segment extends onto the anterior part of the posterior lobe.

The pygidium Plate 31, fig. 2, CPC 14147, is 2.4 mm long; the axis is slightly attenuated in the rear and the gibbose median node on the second axial lobe is spineless.

Occurrence and age: Aristarius ultimus is a rare fossil of the V-Creek Limestone, found in its upper part at locality M57; its age is the Undillan Zone of *Goniagnostus nathorsti*.

Triplagnostus (Aristarius) aff. **ultimus**

(Pl. 30, fig. 4)

The illustrated exoskeleton, CPC 14144, is 8.5 mm long; it is a mould of a flattened test in shale dematricated with a needle.

The characters of the subgenus *Aristarius* are as follows: (1) the basal lobes are simple; (2) the cephalic spines are very long, as long as the glabella; (3) the axial spine of the thorax is as long as the pygidium; and (4) long but ill preserved pygidial marginal spines are evident. Structures, however, which should be diagnostic for the species are inconclusive. The frontal glabellar lobe is about 0.43x the glabella in length and is longer than in *ultimus*; the axis of the pygidium is deformed and has lost relief and definition of its transverse furrows and its two anterior lobes; and the median axial node seems spineless in *Aristarius ultimus* as well as *Triplagnostus stramineus*. In passing, each spine collapsed along a longitudinal fracture and the seemingly angular section of the axial spine is the result of collapse.

The glabella, however, is deformed in several ways and its original shape remains conjectural; the posterior lobe tapers forward and the frontal lobe is dilated and split longitudinally; consequently *Aristarius* remains doubtful but *Triplagnostus* acceptable.

Occurrence and age: The exoskeleton of *Aristarius* aff. *ultimus* has been obtained from a small outlier of a pink shale of the Inca Formation, locality M434; it is associated with *Myrmecomimus* cf. *saltus* and an *Aotagnostus* (pygidium with spines); these fossils indicate the Undillan Zone of *Ptychagnostus punctuosus*.

Genus **Aotagnostus** nov.

The type species of *Aotagnostus* is *A. culminosus* nov.

Diagnosis: Aotagnostus refers to species of Ptychagnostinae en grande tenue which, depending on the species, attain in holaspides a length of 3.5 to 10 mm. The glabella is prominent, with a very tumid posterior lobe whose low median node is placed about or mostly behind its middle; the pygidial axis is also high and gibbose. The distinguishing characters are: (1) long and strong cephalic fulcral spines; (2) fulcral spines and an axial spine on the second segment of the thorax; (3) strong and gibbose median pygidial node on the second axial lobe and the anterior part of the posterior lobe, tipped by a spine; (4) relatively short retrally tapering posterior pygidial axial lobe sloping down behind the median node, and pointed in the rear; and (5) five segments in the pygidial axis (the two anterior lobes and three pairs of muscle spots in the posterior lobe) in *A. culminosus* as reported earlier (Öpik, 1967, p. 67) and about seven in *A. protentus*.

The described species of *Aotagnostus* fall into two separate groups: (1) species with pygidial marginal spines—*A. culminosus, A. protentus,* and *A. magniceps;* these have double basal lobes. *Ptychagnostus akanthodes* Robison, as discussed below, is also a species of this group; (2) species without pygidial marginal spines—*A. aotus, A. ponebrevis,* and *A. modicus.* These groups of convenience in the taxonomic procedure may or may not be regarded as subgenera of the genus *Aotagnostus* depending on the chance of preservation or of discovery of the marginal spines in doubtful material.

Differential diagnosis: The general aspect is reminiscent of *Myrmecomimus* nov., in which, however, only cephalic spines are present and the pygidial second and posterior axial lobes are fused into a bulb. The spinosity is significant in combination with other characters because it is present also in several other ptychagnostids, as for example in *Triplagnostus;* the extension of the pygidial axial node onto the posterior axial lobe occurs in *Onymagnostus* nov., *Ptychagnostus* (*Acidusus*) nov., *Ptychagnostus aculeatus* (Angelin) Westergaard (1946, p. 79), and *Ptychagnostus akanthodes* Robison (1964, p. 523). In *Onymagnostus* (q.v.) spines are absent and the pygidial axis is long; *Pt. aculeatus* (discussed in connection with *Onymagnostus*) is unrelated to *Aotagnostus;* in *Pt. akanthodes,* however, the pygidial axis has the same structure as in *Aotagnostus* and its spinosity recalls *A. culminosus; Pt. akanthodes* is distinguished by its scrobiculate cheeks, forward-placed pygidial marginal spines, and ornamented test.

It is probable that the cephalon of an agnostid described by Whitehouse (1936, pl. 8, fig. 14) under the name of *Solenagnostus acuminatus* belongs to a species of *Aotagnostus* nov. The genus *Solenagnostus* Whitehouse (op. cit.) has *Agnostus longifrons* Nicholas (1916, pl. 39, fig. 1) as its type species; *A. longifrons,* however, is either a *Pytchagnostus* with simple basal lobes, or a *Triplagnostus* (as generally assumed) of unknown spinosity. Consequently, *Aotagnostus* and *Solenagnostus* are not synonyms. The species name *acuminatus* Whitehouse adheres to its type only: (1) it is a deformed cephalon; (2) the specific identification of solitary cephala of *Aotagnostus* is inconclusive; and (3) no pygidium has been described. The type cephalon is nevertheless quite large (apparently 6.5 mm long, and has a very long frontal glabellar lobe indicating a species of the *Aotagnostus protentus* group of forms. The problem of *Solenagnostus* has been discussed in detail by Öpik (1961b, p. 78).

Six new species are described: *Aotagnostus aotus, A. ponebrevis, A. magniceps, A. protentus, A. culminosus,* and *A. modicus.* As regards age, *ponebrevis* appears, and is rare, in the *Euagnostus opimus* Zone; it is abundant in the early *Ptychagnostus punctuosus* Zone, together, but not mixing, with *A. aotus. A. culminosus* arrives in the upper half of the *Pt. punctuosus* Zone, survives that species, and reaches the *Goniagnostus nathorsti* Zone. *A. magniceps* and *protentus* are associated with *Pt. punctuosus* and *G. nathorsti; A. magniceps* is very rare. *A. modicus* is associated with *G. nathorsti* after the disappearance of *Pt. punctuosus.* Consequently, *Aotagnostus* is a genus of the Undillan Stage.

Aotagnostus aotus sp. nov.

(Pl. 32, figs. 1-7)

Material: Illustrated are two holaspid and two meraspid exoskeletons and a cluster of three shields.

Holotype: The exoskeletons Plate 32, figs. 1 and 2, CPC 14151, locality M263, is selected as the holotype.

Diagnosis: Aotagnostus aotus is a species without pygidial marginal spines, with long cephalic spines and short fulcral spines in the thorax and a delicate axial spine in the second segment of the thorax and a very short spine on the tip of the pygidial median node; it is distinguished by its moderately short pygidial axis (0.67-0.7x the shield length), laterally expanded posterior pygidial axial lobe, and relatively narrow rim in the pygidial rear.

Differential diagnosis: The species of *Aotagnostus* having pygidial marginal spines (*A. culminosus, A. protentus,* and *A. magniceps*), as well as spineless *A. modicus* are discussed under their own headings and are omitted here. *Aotagnostus aotus* and *A. ponebrevis,* however, resemble each other quite closely and are also contemporaneous participants of the faunal assemblage of *Diplagnostus floralis* nov. and *Iniospheniscus talis* nov., and are discussed here in some detail. *A. ponebrevis* differs from *A. aotus* (1) by its shorter pygidial axis (0.6x the shield length, or slightly less), (2) by the triangular shape of the posterior pygidial lobe, (3) by the widening of the rim in the pygidial rear, and (4) by the more pronounced convergence of the flanks of the posterior glabellar lobe. Furthermore, *Aotagnostus ponebrevis* constitutes a population of morphological uniformity at site M191, as does *Aotagnostus aotus* in collection M263. These sites are separated from each other by some seventy kilometres and no barrier of any significance: both sites represent the Inca Formation of a uniform depositional environment. The existence of two geographically separate populations of different species taxa is an indication of their biological disparity; nevertheless, the occurrence of intermediate forms remains a possibility and a matter of further collecting; and *Aotagnostus aotus* and *A. ponebrevis* have been found together in a single piece of chert at locality M164.

Description: As a whole, *Aotagnostus aotus* is a relatively small to medium en grande tenue agnostid known from specimens reaching a length of 7.0 mm. Its axial relief, especially in the pygidium, is strong; the thorax, about 0.18-0.2x the cephalon in length, is short; the rim in both shields is narrow; and all furrows, including the preglabellar and postaxial median furrows, are narrow and deep. The cephalic spines are long, reaching the pygidial front and arising from a broad base filling the space between the basal lobes and the posterolateral corners of the cephalon; the spine on the second segment of the thorax is delicate and may have extended over the front of the pygidium; the fulcral spines of the second segment are relatively short, just gripping the fulcral points of the pygidium.

In the cephalon the frontal glabellar lobe is pointed, triangular with slightly convex flanks, slightly wider than the front of the posterior lobe, and as long as about 0.4x the glabella. The posterior glabellar lobe tapers forward from a well rounded rear which, bulging retrally, extends slightly beyond the basal lobes; these lobes are small, simple, and tumid. The median glabellar node is placed in the middle of the posterior lobe and marks the culmination of its profile. In the pygidium the axis is somewhat short, about 0.65-0.67x the shield length; its anterior lobe is tripartite with a pair of lateral lobules and the anterior transverse furrow arched forward. The second lobe is large and prominent; its rear margin, deformed by the V-shaped second transverse furrow, extends to the midpoint of the posterior axial lobe; in profile, the second lobe rises rearward and culminates in a short tip. The posterior axial lobe has convex flanks and a relatively prominent median knob in the middle of its posterior half.

The test is smooth to minutely granulose; the granulosity in Plate 32, figs. 1 and 2 seems over-exaggerated by whitening and reflects, apparently, the texture of the matrix.

Variability: (1) The posterior axial lobe in the pygidium can be acute triangular (Pl. 42, fig. 1), or slender (Pl. 42, fig. 7), or convex along its flanks (Pl. 42, fig. 2), or rounded (Pl. 32, figs. 3, 4); and (2) the rim in the rear of the pygidium varies in width within narrow limits but remains narrower than in *Aotagnostus ponebrevis*.

Comment on illustrated specimens

The four specimens that follow have been selected from collection M263, friable siltstone of the Inca Formation; they are decorticated, showing a relief stronger than the exterior of the tests from locality M166.

The holotype is 4.7 mm long. The cephalic spines are broken but the left stump is visibly strong; the spine on the second segment of the thorax is delicate, recurved, and has lost its point; the fulcral spines on the same segment lost their short points, and the tip of the pygidial median node is also broken; a scratch is evident behind that node and in front of the node on the posterior axial lobe. The pygidial axis is 0.67x the shield length. The basal lobes are short but tumid.

An exoskeleton in close association with the holotype is 3.3 mm long; its pygidial axis, 0.7x the shield length is a little longer than in the holotype.

The larger pygidium Plate 32, fig. 7, CPC 14155, is 2.5 mm long and the smaller about 2.0 mm long. The piece of rock, some 4 x 5 cm in size, contains 15 shields of *A. aotus*. In the larger pygidium the axial node is narrower than in the holotype and the posterior axial lobe is also relatively slender.

The small exoskeleton Plate 32, fig. 6, CPC 14154, is 2.0 mm long; it is a meraspis with a single free segment overridden by the cephalon. The second segment of the thorax is fused with the pygidium; the future axial spine is indicated by a node. The axis is rather narrow.

The next two specimens, in Currant Bush Limestone, locality M166, have been singed in a fire; the test is preserved; the external relief is of a lesser contrast than in the decorticated material described above.

The exoskeleton Plate 32, figs. 3 and 4, CPC 14152, is 5.6 mm long; the frontal glabellar lobe seems wide, the flanks of the posterior glabellar lobe and of the pygidial axis are only slightly tapering. The axial lobe, 0.65x the shield length, seems shorter than in the holotype; the median node is well elevated, but its tip being fused to the matrix could not be extracted; such a tip is indicated in decorticated specimens.

The small complete specimen Plate 32, fig. 5, CPC 14153, associated with the exoskeleton above, is 2.1 mm long; it is a meraspis with one free segment in the thorax. The pygidial rim encloses the pleural ends of the not yet liberated second segment of the thorax.

Occurrence and age: Aotagnostus aotus is abundant in M263, in the siltstone of the Inca Formation, and in chert in association with *Iniospheniscus* (Plate 9, fig. 2); it occurs also in limestone (Currant Bush Limestone) at sites M64 and M166; its age is in the Undillan Zone of *Ptychagnostus punctuosus.*

Aotagnostus ponebrevis sp. nov.
(Pl. 31, figs. 3-7)

Material: Illustrated are one complete exoskeleton, one isolated cephalon, and one pygidium, all in limestone.

Holotype: The exoskeleton Plate 31, figs. 5-7, CPC 14150, is selected as the holotype.

Diagnosis: Aotagnostus ponebrevis resembles *Aotagnostus aotus* in having no pygidial marginal spines, short fulcral points, and a delicate axial spine in the second segment of the thorax as well as a short spine on the pygidial median node; it is distinguished by its relatively short pygidial axis, about 0.56-0.6x the shield length, by its crescentic pygidial rim expanded in the rear, and by the relatively long frontal glabellar lobe 0.42-0.44x the glabella in length.

Differential diagnosis: The differential diagnosis is given in the description of *Aotagnostus aotus;* also, in *A. aotus* the frontal glabellar lobe is shorter than in *ponebrevis.*

Description: The holotype is 4.0 mm long with its tagmata in their original arrangement; the cephalon is the largest shield, about 1.1x the length of the pygidium, the thorax, about 0.23-0.24x the cephalon, is short, but still longer than in *A. aotus;* the stump of the axial spine on the second segment is preserved. All furrows and lobes are well developed—it is a species en grande tenue. In profile (Pl. 31, fig. 6) the posterior glabellar lobe is high and tumid, culminating at its median node and bulging retrally over the posterior margin of the shield and well above the tumid cheeks; the pygidial axis is also prominent, but the pleural pygidial lobes are less tumid than the cheeks; the posterior segment is arched and the stump of its axial spine is reclined; the shutter gap (see Text-fig. 5) is clear.

In the cephalon the rim is very narrow and convex, the frontal glabellar lobe is swollen, pointed, widest across its middle and visibly wider than the front of the posterior lobe; the median glabellar node is small and in plan often placed behind the midpoint, and in profile about that point. The basal lobes are apparently simple, triangular, elongate, and close to the glabella in a manner seen in *Myrmecomimus* (q.v.); the cephalic spines (only stumps preserved in the holotype) are long and strong and, arising from a rather broad base, are attenuated to acute tips.

In the pygidium the rim is wider than in the cephalon, and widens rearward to a crescent with a distinct median forward projection opposite the terminal flare of the postaxial median furrow. The anterior axial lobe is tripartite with low lateral furrows, the tip of the axial median node extends over the second transverse furrow exposed in the holotype, which lost its spine; the base of the spine extends into the posterior axial lobe for a short distance only—visibly shorter than in other specimens, as for example in *Aotagnostus magniceps* (Pl. 33, fig. 8). The node on the posterior axial lobe is very small and placed half way from the rear of the median axial node to the axial tip.

The cephalon Plate 31, fig. 3, CPC 14148, is 2.5 mm long, and belongs to a specimen about 5.0 mm long—larger than the holotype; its cephalic spines are clear; the test is smooth.

The pygidium Plate 31, fig. 4, CPC 14149, is 2.0 mm long; its pygidial axis is intact, supplementing the holotype.

The holotype (Pl. 31, figs. 5-7) is 4.0 mm long; it is exposed on a very small chip of limestone and illustrated from above, including a latex cast, and from the right flank in profile.

Occurrence and age: All illustrated specimens have been obtained from a limestone bank of the Inca Formation, locality M191. The age is the initial part of the Zone of *Ptychagnostus punctuosus*; specimens have been found also at several other sites of the same formation, as for example, in chert, M164, in association with *Aotagnostus aotus*; and in limestone of Quita Formation, D69, in association with *Diplagnostus floralis.* The earliest specimen of *Aotagnostus ponebrevis* is known from site M192, in association with *Euagnostus opimus.*

Aotagnostus sp. indet. aff. **ponebrevis**
(Pl. 32, fig. 9)

The illustrated pygidium, CPC 14165, is 2.5 mm long. Its margin is spineless as in *A. aotus* and *A. ponebrevis*; the axis is stout and relatively long, 0.65x the shield length, as in *A. aotus*; the lateral lobules of the anterior axial lobe are prominent and the preserved base of the median axial node indicates a strong reclined spine; the crescentic rim resembles *A. ponebrevis.* The described combination of characters indicates a form disparate from other species of the genus.

Occurrence and age: The described pygidium comes from an ellipsoidal limestone of the Inca Formation, locality M191b, close to but not identical with the limestone of site M191. The age is probably the same as of *Aotagnostus ponebrevis* (early Undillan) but fossils supporting that age are absent.

Aotagnostus magniceps sp. nov.

(Pl. 33, fig. 8)

Material and holotype: The species *A. magniceps* is based on the illustrated, and only available exoskeleton—the holotype, CPC 14164.

Diagnosis: Aotagnostus magniceps is a species with marginal pygidial spines and attenuated posterior axial lobe in the pygidium, distinguished by the rearward position of the marginal spines, which also are relatively long, and by the absence of fulcral spines in the second segment of the thorax. Furthermore, the frontal glabellar lobe is long and broad and the second pygidial axial transverse furrow remains divided by the median node. The cephalon is visibly larger (wider and longer) than the pygidium.

Differential diagnosis: In other species of *Aotagnostus* with pygidial spines (*culminosus* and *protentus*), these spines are shorter and placed more forward than in *A. magniceps*, and the fulcral spines are present and long. The pygidial axis is also attenuated in *A. protentus* but is shorter than in *magniceps*. The frontal lobe in *A. culminosus* is shorter and smaller, and in *protentus* narrower than in *A. magniceps*.

Description: The holotype of *Aotagnostus magniceps* is 6.0 mm long as preserved; the cephalon is the larger shield, about 10 percent longer than the pygidium. In the cephalon the rim is extremely narrow and so is the deep marginal furrow; in the pygidium the rim is visibly wider, widens rearward, and is widest at the marginal spines; in other species of the genus the pygidial rim is narrower than in *magniceps*. The cheeks and the pygidial pleural lobes are moderately convex; the lobes of the glabella are tumid, and the posterior lobe culminates at its median node placed behind the midpoint. The frontal lobe, about 0.43x the glabella in length, is about oval. The cephalic spines (the left spine is intact) are about as long as the thorax, and arise from the whole posterolateral margin (as in all species of the genus). The thorax is disarranged, about 0.25x the cephalon in length, and has lost its axial spine (if such was present); the fulcral points of the posterior segment are clear—short angulations only. The basal lobes seem double.

In the pygidium the lateral margins are slightly convex, much less than in other species. Owing to the retral position of the marginal spines the posterior margin is only slightly arched in plan. The pygidial axis, about 0.72x the shield length, is longer than in other species of *Aotagnostus*. The anterior axial lobe is tripartite and its lateral lobules are prominent; it starts at the front of the second lobe and its base extends well beyond the second lateral transverse furrow into the front part of the posterior axial lobe; but the axial spine itself is lost; its strong gibbose base indicates a prominent spine. The posterior lobe is constricted, tapers to a rounded tip, and its median knob is placed well in the rear. Five or six pairs of notulae (knobs) are evident behind the spine on the posterior lobe of the axis.

Occurrence and age: The holotype of *Aotagnostus magniceps* comes from the V-Creek Limestone, locality M139; its age is the Undillan Zone of *Doryagnostus notalibrae*.

Aotagnostus protentus sp. nov.

(Pl. 33, figs. 1-6; Pl. 39, fig. 3)

Material: Illustrated are two exoskeletons, one exoskeleton without pygidium, two cephala, and two pygidia—seven specimens from five sites.

Holotype: The exoskeleton Plate 33, fig. 1, CPC 14157, is the holotype.

Diagnosis: Aotagnostus protentus has short pygidial marginal spines and well developed fulcral spines in the cephalon and in the second segment, and axial spines in the second segment and in the pygidium, whose posterior axial lobe is attenuated and a little constricted in the middle; the species is distinguished by its relatively long and slender frontal glabellar lobe (0.42-0.44x the glabella in length) and a relatively short pygidial axis.

Differential diagnosis: Aotagnostus aotus, A. ponebrevis, and *A. modicus* have no pygidial marginal spines and different structures in the pygidial axis and the glabella—each in its own manner. In *A. magniceps* and *A. culminosus* pygidial marginal spines are present; in *magniceps* the rearward position and length of these spines prevent any confusion; also fulcral extended spines are absent in the thorax of *magniceps* but present in *protentus*.

In *A. culminosus* the frontal glabellar lobe is relatively short (0.37-0.4x) and the posterior axial lobe in the pygidium is not attenuated but has convex flanks and a more or less plump shape; *A. protentus* and *A. culminosus* are concurrent species and the differences from each other therefore should not be overlooked.

Description: Descriptive data are given above in the diagnosis and the differential diagnosis; two different forms of *Aotagnostus protentus* can be distinguished as regards the length of the skeletal spines: (1) forms with long spines found in the strata of the Zone of *Doryagnostus notalibrae* and (2) forms with shorter spines prevalent in the earlier Zone of *Ptychagnostus punctuosus*; specimens which have lost their spines cannot be attributed to either of these groups because of their similarity in other characters, namely the relative length and form of the frontal glabellar lobe and the shape of the pygidial axis. The holotype (Pl. 33, fig. 1) is defective as regards its broken spines. The description is continued in the comment that follows below.

Comment on illustrated specimens

The first four specimens came from the V-Creek Limestone (Zone of *Doryagnostus notalibrae*).

The incomplete exoskeleton Plate 33, fig. 2, CPC 14158, locality M194, is to the tip of its axial spine 7.5 mm long; the cephalon above is 4.0 mm long, and its frontal glabellar lobe is 0.44x the glabella in length. The matrix is translucent laminated chert. The axial spine is as long as the glabella, and the left cephalic spine has a very wide base and is more than twice the length of the thorax; the imprint of the anterior half of the right fulcral spine is longer than the thorax. The chert contains also *Goniagnostus scarabaeus,* an *Onymagnostus,* and *Myrmecomimus.*

The holotype (Pl. 33, fig. 1, locality M409) is an external mould in limestone, 8.4 mm long. The frontal glabellar lobe is about 0.42x the glabella in length; the cheeks are weakly scrobiculate; the wide base of the right cephalic spine and a fairly long part of the left spine are preserved. The pygidial spines are small and deflected, the stump of the pygidial axial spine is strong, but the rest of it remains in the matrix of the mould.

The pygidium Plate 33, fig. 6, CPC 14162, locality M212 (V-Creek Limestone), is 3.1 mm long without the attached segment. The axial lobe as in the holotype is 0.7x the shield length; the delicate marginal spines are clear.

The small exoskeleton Plate 33, fig. 3, CPC 14159, also from M212, a mould in limestone, is 3.5 mm long. The right pygidial marginal spine is preserved; owing to the immaturity of the specimen the pygidial axial lobe is relatively short—0.6x the shield length. The retral position of the glabellar node is rather unusual for an *Aotagnostus.*

The next described three specimens came from the Quita Formation (southeast of Urandangi Sheet) of the Zone of *Ptychagnostus punctuosus.*

The pygidium Plate 33, fig. 4, CPC 14160, locality D74, is 4.0 mm long. The axial lobe is 0.72x the shield length; its posterior lobe is less attenuated and less pointed than in later specimens (Pl. 33, fig. 6; the holotype, Pl. 33, fig. 1) but preserves the characteristic shape of its species, different from the concurrent *Aotagnostus culminosus,* Plate 34, figs. 2-4.

The cephalon Plate 39, fig. 3, also from D74 and from the same bed as the pygidium, is 2.8 mm long; its frontal lobe is slender and close to 0.41x—a little shorter than in the holotype; the posterolateral spines are much shorter than in Plate 33, fig. 2.

The cephalon Plate 33, fig. 5, CPC 14161, locality D69, is 4.2 mm long; its frontal glabellar lobe is 0.45x the glabella in length—the longest among the illustrated specimens; but the cephalic spines are relatively short.

Occurrence and age: Aotagnostus protentus appears in the Quita Formation (D74, D69, and some other sites) in the Undillan Zone of *Ptychagnostus punctuosus* and continues onward into the Zone of *Doryagnostus notalibrae*; it is frequent in V-Creek Limestone, M409, M212, M194, and many more sites.

Aotagnostus culminosus sp. nov.

(Pl. 33, fig. 7; Pl. 34, figs. 1-8; Text-figs. 40, 41)

Material: The described material consists of two exoskeletons, one segment of the thorax, two cephala, and three pygidia.

Holotype: The complete exoskeleton Plate 34, fig. 1, CPC 14166 locality M234, is the holotype.

Diagnosis: Aotagnostus culminosus is a species with short pygidial marginal spines, well developed cephalic, fulcral, and axial spines, double basal lobes, and a pygidial axis of moderate length (in holaspides 0.68-0.72x the shield length); it is distinguished by its moderately long frontal glabellar lobe (0.37-0.4x the glabella in length) and convex flanks of the posterior lobe of the pygidial axis.

Differential diagnosis: Aotagnostus culminosus and *A. protentus* are structurally close to each other, but in *protentus* the frontal glabellar lobe is longer, the posterior lobe of the pygidial axis has concave flanks and is attenuated, and its spines in the cephalon and in the thorax are visibly longer than in *culminosus;* in the early form of *protentus,* however, the cephalic spines are only slightly longer than in *culminosus.*

Description: Data descriptive of *Aotagnostus culminosus* are included in its diagnosis and in comment that follows below. The species may have attained some 10 mm in length; scrobiculation of the cheeks occurs sporadically (Pl. 34, fig. 8); the frontal glabellar lobe varies in shape, with almost straight to convex flanks. The basal lobes are often deformed, but are double and reminiscent of *Myrmecomimus tri-*

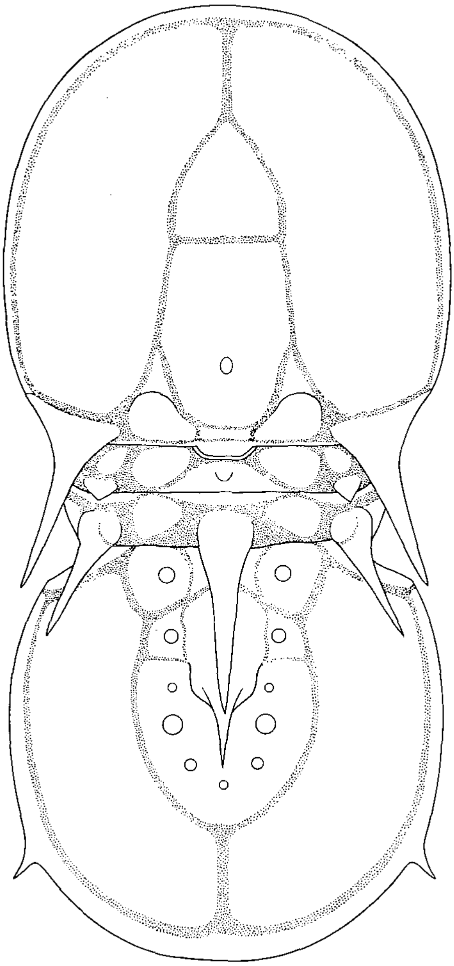

Fig. 40. *Aotagnostus culminosus.*

bulis (Text-fig. 42). The thorax, about 0.25-0.27x the cephalon in length, is possibly longer than in *Aotagnostus protentus.* The pygidial axis, owing to the convexity of the flanks of its posterior lobe, seems plump when compared with *A. magniceps* and *protentus.* The second axial annulation (Pl. 34, figs. 2-4) is very tumid, the axial spine is straight, straddles the second transverse furrow, and is extended into a needle-like tip.

Comment on specimens

The holotype exoskeleton, locality M234, is 9.0 mm long; the right pygidial marginal and the cephalic spines are preserved; other spines are indicated by their stumps; the missing parts are restored in Text-figure 40. The frontal glabellar lobe is 0.37x the glabella, and the pygidial axis is 0.25-0.27x the cephalon in length.

The exoskeleton Plate 34, fig. 5, CPC 14168, locality M409, is 9.0 mm long. The chip of the cephalon with the glabellar frontal lobe has been cemented in its original position, but another chip is lost. The shape of the frontal lobe with convex posterior flanks represents a frequent variation; the test is smooth and shiny; the axial pygidial lobe is 0.7x the shield length.

The posterior segment of the thorax Plate 33, fig. 7, CPC 14163, locality M212, is 3.5 mm wide. The axial and the right fulcral spines are clear; the articulating half-ring is exposed. The free pleurae (Text-fig. 41) in the posterior segment are equipped each with a facet separated from the pleural furrow by a ridge acting as a pleural stop of the anterior pleura; the edge of that pleura rests on the facet which for that purpose is concave (fluted). See also under the heading 'The articulate agnostid exoskeleton' (p. 32).

The cephalon Plate 34, fig. 7, CPC 14170, locality M212, is 3.2 mm long; it is undeformed and has the basal lobes preserved; these appear double.

The next two specimens are associated in a single bed, locality M411.

The cephalon (not illustrated) CPC 14380 is 4.2 mm long; its frontal lobe is 0.4x the glabella in length, and has convex flanks; the left side basal lobe is double.

The pygidium Plate 34, fig. 6, CPC 14169, is 3.3 mm long; its axis is about 0.72x the shield length.

The cephalon Plate 34, fig. 8, CPC 14171, locality M234, is 4.0 mm long; the cheeks are rugose.

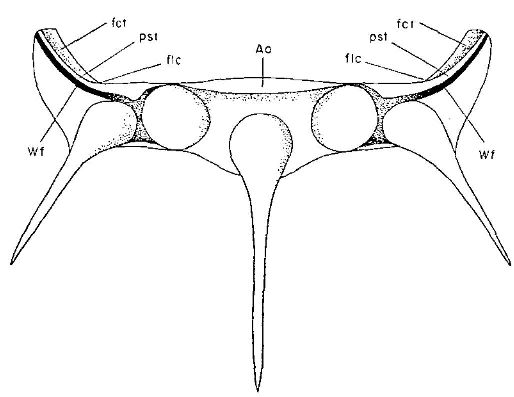

Fig. 41. ***Aotagnostus culminosus,* second (posterior) segment of the thorax shown in Plate 33, fig. 7. Aa—axial articulating half-ring; fct—facet; pst—pleural stop; flc—fulcrum and geniculation; Wf—pleural furrow.**

The pygidium (not illustrated) CPC 14381, locality M212, about 2.1 mm long, has its axial muscle spots preserved (shown in Text-fig. 40).

The pygidium Plate 34, figs. 2-4, CPC 14167, dolomitic limestone of the Quita Formation, locality D74, is 3.8 mm long; the second axial lobe is very tumid, the axial spine straddles the transverse furrow, and is straight and reclined; but the latex failed to fill the cavity of the slender needle-like tip of the spine.

Occurrence and age: Aotagnostus culminosus occurs frequently in the V-Creek Limestone; it is common at localities M409, M411 (lower part of the section), M212, M234, M204; it is also present but rare in the Quita Formation, Locality D74.

Its age is Undillan, the Zones of *Ptychagnostus punctuosus* and *Doryagnostus notalibrae.*

Aotagnostus modicus sp. nov.

(Pl. 35, figs. 1-3)

Material: Illustrated are two exoskeletons and one isolated cephalon; the rest of the material consists of two isolated pygidia and one more cephalon. The test is preserved, but the specimens are crushed and defective; the matrix is a grey hard limestone.

Holotype: The exoskeleton Plate 35, fig. 1, CPC 14172, is selected as the holotype.

Diagnosis: Aotagnostus modicus has no pygidial marginal spines but a relatively long pygidial axis and a forward-tapering posterior glabellar lobe followed by an oval and laterally expanded frontal glabellar lobe; the glabella is therefore prominently narrow at its transverse furrow; the median node is placed about the middle of the posterior glabellar lobe.

Differential diagnosis: Pygidial marginal spines are also absent in *A. ponebrevis* and *A. aotus.* In the first the pygidial axis is very short and the rim in the rear is expanded, but *A. modicus* has a visibly longer pygidial axis and an evenly narrow rim. In *Aotagnostus aotus* the pygidial rim is also narrow but its axis is still short. The difference in the cephalic structure is evident from a comparison of the undeformed exoskeleton of *Aotagnostus aotus* in limestone (Pl. 32, figs. 1 and 2) with *A. modicus*: in *A. aotus* the front of the posterior glabellar lobe is about 0.8x, and in *modicus* about 0.65-0.7x, its maximal width. The frontal lobe in *A. aotus,* oval as it is, is less expanded than in *modicus.* In other species the glabellar median node stands behind the midpoint of its posterior lobe.

Description: Aotagnostus modicus has attained a length of 8.0 mm, which may not be, however, its maximal size. The cephalon, as usual, is as long as the pygidium and the posterior segment of the thorax together, and the thorax is about 0.25x the cephalon in length. The rim in both shields is narrow, especially in the cephalon, and convex. The cephalic spines are about half the glabella in length, but the length of the axial spines in the thorax and pygidium cannot be established. The fulcral spines in the second segment were extended, as seen from the base of the right spine in the holotype. The frontal glabellar lobe, an oval acute in front, is as wide as long and 0.4x the glabella in length. The transverse glabellar furrow is deep, about as deep as in *A. ponebrevis.*

The posterior glabellar lobe is widest in the middle and its rear is well rounded, elevated and arched over the collar in the rear; the median node is distinct, placed close to the centre of the lobe as in *A. aotus,* and a little more forward than in other species of the genus. The basal lobes are simple but ill preserved and laterally enclosed by the straight axial furrows.

In the pygidium the axis is 0.7-0.72x the shield length; the second transverse furrow has oblique (not horizontal) lateral sections; the anterior furrow is, as usual, arched forward and the second axial lobe is therefore transverse elliptical; the base of the axial spine extends only a little into the posterior lobe, less than in other species. The posterior pygidial axial lobe has convex flanks and is swollen in its anterior half. The axial rear is narrowly rounded and a low node is apparent close to the midpoint of the posterior lobe.

The test is smooth.

Comment on illustrated specimens

The holotype exoskeleton is 5.6 mm long. The long cephalic spine and the simple basal lobe are preserved on the left side. The frontal glabellar lobe is 0.4x the glabella, and the pygidial axis 0.72x the shield in length.

The exoskeleton Plate 35, fig. 2, CPC 14173, is 6.8 mm long. The stump of the axial spine in the thorax is preserved, and the thorax is about 0.25x the cephalon in length.

The cephalon Plate 35, fig. 3, CPC 14174, is 3.3 mm long. Its frontal glabellar lobe is wider than in the two specimens above. Short lateral glabellar furrows are evident.

Occurrence and age: Aotagnostus modicus is a rare fossil of the V-Creek Limestone, found at a single locality, M142, in one bed high in the sequence of that formation; its age is the Undillan Zone of *Goniagnostus nathorsti* (after the disappearance of *Ptychagnostus punctuosus*).

Genus **Myrmecomimus** nov.

The type species of *Myrmecomimus* is *M. tribulis* nov.

Diagnosis: Myrmecomimus refers to very small species of Ptychagnostinae with holaspides less than 5 mm in length having tumid and prominent frontal and posterior glabellar lobes, a bulbous but short posterior axial lobe in the pygidium, and relatively low cheeks and pygidial pleural lobes; these structures create a habit recognisable at a glance and distinct from all known agnostids. Furthermore (1) the rim in the cephalon and pygidium is very narrow and convex; (2) axial and pygidial marginal spines are absent; (3) the pygidial axis is short, about 0.6 and rarely 0.7x the shield length; (4) the anterior axial transverse furrow is very deep, the anterior axial lobe is tripartite with distinct lateral lobules, depressed to the level of the thorax and structurally a replica of the axial part of the rear segment of the thorax; (5) the second and third axial lobes are fused into a prominent bulbous unit with a median node on the second lobe and the second transverse furrow impressed on the arc of the bulb.

Differential diagnosis: The general structure of the glabella and the pygidial axis, especially of the second axial lobe, indicate an affinity with the Ptychagnostinae; a related genus is *Aotagnostus* nov., an aggregate of five new species distinguished in the first place by the strong cephalic, fulcral, and axial spines in the thorax and pygidium as well as by the absence of the bulbosity of the pygidial axis.

The following species of *Myrmecomimus* are described: *M. tribulis* and its two subspecies—*tribulis mixtus* and *tribulis evanidus*—and *M. saltus*.

M. tribulis is a species en grande tenue, but in the other forms some effacement of the preglabellar and postaxial median furrows and the second axial furrow is evident. All are frequent to abundant, but only holaspides occur. The smallest observed exoskeleton is about 2.2 mm and the largest 4.5 mm long.

Myrmecomimus appears first in the Zone of *Ptychagnostus punctuosus* and disappears together with that species early in the time of *Goniagnostus nathorsti.*

Myrmecomimus tribulis sp. nov.

(Pl. 36, figs. 1-4; Text-fig. 42)

Material: Illustrated are four complete exoskeletons in limestone, selected from a larger supply of complete specimens and isolated shields.

Holotype: The exoskeleton Plate 36, figs 1, 1a, and 2, CPC 14179, is selected as the holotype, preserved with its mould cast in rubber.

Diagnosis: Myrmecomimus tribulis tribulis, a form en grande tenue, is distinguished by the complete preglabellar and postaxial furrows, clearly outlined second pygidial axial lobe, and the relatively prominent median node on that lobe; furthermore, its test is smooth.

Differential diagnosis: The differences from *M. saltus, M. tribulis mixtus,* and *M. tribulis evanidus* are discussed in the descriptions of those forms.

Description: The general appearance of *M. tribulis* is described in the diagnosis of the genus. The cephalon is slightly longer than the pygidium, and about as wide as long and widest across its middle; the shape is about

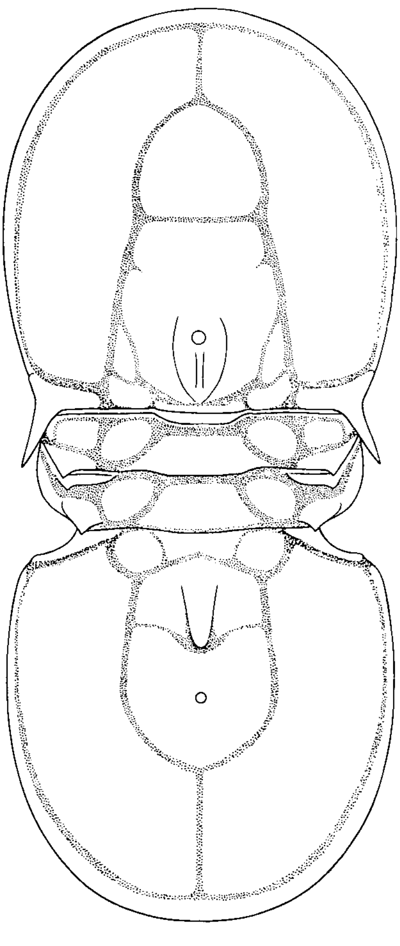

Fig. 42. *Myrmecomimus tribulis.*

oval with a weakly forward arched front. The glabella tapers forward; the frontal lobe, 0.37-0.4x the glabella in length, is oval, widest across its middle, and slightly wider than the front of the posterior lobe. The transverse glabellar furrow is deep and straight, and the low median node is placed behind the mid-point of the posterior glabellar lobe. Posteriorly, the glabella is rounded to broadly angular and slopes down abruptly; in some specimens it is also carinate behind the median node. The basal lobes are long and double and laterally confined by the straight axial furrows as in *Aotagnostus culminosus* (q.v.). The cephalic spines have attenuated needle-like tips and structurally resemble undeveloped spines of an *Aotagnostus* or *Triplagnostus*.

The thorax, slightly less than 0.3x the cephalon in length, has no axial spines or nodes, and its fulcral projections are inconspicuous.

The pygidium is slightly shorter than wide; it is shorter than, but as wide as, or even a little wider than, the cephalon. The second axial transverse furrow is strongly impressed in the middle and shallow laterally, where the anterior and the middle lobe are almost continuous. The anterior transverse furrow in the axis is evenly and deeply impressed and divides the axis into two main lobes, almost obscuring its still recognisable trilobation of a ptychagnostid. The median node is broad and long, pointed, and elevated in the rear over the transverse furrow. The pygidial shoulders are concave (arched retrally) and the facets are also concave and almost vertical.

Comment on illustrated specimens

All specimens were collected at locality M212, from the V-Creek Limestone.

The holotype exoskeleton is 3.2 mm long. The basal lobes are double; the cephalic spines are fairly long and attenuated. In the other exoskeleton associated with the holotype the frontal glabellar lobe appears very large and long (its photograph is out of plan); in this specimen the lobe in plan is 0.4x and in the holotype 0.37x the glabella in length. The attenuated tips of the cephalic spines are visible in fig. 1; the white tips, of calcite filling, are extracted by the latex.

The exoskeleton Plate 36, fig. 3, CPC 14180, is 2.8 mm long; its cephalon is slightly compressed laterally.

The exoskeleton Plate 36, fig. 4, CPC 14181, is 3.8 mm long; the acrolobe in front of the glabella is crushed and the preglabellar median furrow is unclear. The glabellar rear is carinate behind the median node. The tripartition of the anterior axial lobe is well exposed.

Occurrence and age: Myrmecomimus tribulis is a common but inconspicuous fossil of the V-Creek Limestone; it appears in the Undillan Zone of *Ptychagnostus punctuosus* and attained abundance in the Zone of *Doryagnostus notalibrae*.

Myrmecomimus tribulis mixtus subsp. nov.

(Pl. 36, figs. 5, 6; Pl. 37, figs. 1-4)

Material: Illustrated are three exoskeletons, one cephalon, and one pygidium.

Holotype: The complete exoskeleton Plate 37, fig. 1, CPC 14184, is selected as the holotype of the subspecies.

Diagnosis and differential diagnosis: In specimens attributable to *M. tribulis mixtus* the pygidial axis has the second lobe, its median node, and the transverse furrows developed as in *tribulis tribulis*; the postaxial and the preglabellar median furrows, however, strong in the latter, are weak in *mixtus* and the postaxial furrow is even effaced in many specimens. In the glabella of *mixtus* the frontal lobe across its middle is visibly wider (up to 1.35x) than the front of the posterior lobe; the frontal lobe itself is oval and has in some specimens its front almost pointed. In *tribulis evanidus* the glabellar structure is reminiscent of *mixtus,* but the second pygidial axial furrow is rather shallow and the median axial node is reduced in size.

Description: The diagnostic characters excepted, the subspecies *tribulis mixtus* is describable in terms of *M. tribulis tribulis*; the separation of these two subspecies is sometimes arbitrary because in *tribulis* the relative width of the frontal glabellar lobe is variable and signs of effacement of the median furrows are also observable.

Comment on illustrated specimens

All specimens except for the last came from the V-Creek Limestone.

The holotype, Pl. 37, fig. 1, locality M409 is 3.7 mm long; the preglabellar median furrow (note the fracture to its left) is very shallow; of the postaxial median furrow only the rear part with the weak flare at its end is clear; the anterior glabellar lobe is 1.36x the width of the front of the posterior lobe; the basal lobes are long and double but the dividing furrow is shallow; the lateral lobules of the anterior axial lobe are prominent; the test is preserved and is apparently minutely granulose. The three tagmata are preserved in articulation readiness.

The pygidium Plate 36, fig. 6, CPC 14183, associated with the holotype, is 1.9 mm long; it belongs to an exoskeleton about 4.4-4.5 mm in length. The shoulders outside the fulcra are concave, as in all species of the genus indicating concave and almost vertical facets. The test is smooth. The specimen is deformed and its axis is askew to the right.

The next two specimens were selected from a larger collection, locality M411 (close to the water level of the creek and the base of the section; about 30 m higher the described material of *M. tribulis evanidus* was collected.).

The complete specimen Plate 37, fig. 2, CPC 14185, is 4.0 mm long; the pygidium is deformed; only the distal part of the pygidial postaxial furrow is evident. In the cephalon the trace of the preglabellar median furrow is visible close to the rim; the preglabellar lobe is as wide as about 1.3x the front of the posterior lobe; the basal lobes are double. The test is smooth.

The cephalon Plate 36, fig. 5, CPC 14182, locality M411, is 1.9 mm long; the preglabellar median furrow is complete but shallow.

The complete specimen Plate 37, figs. 3 and 4, CPC 14186, is 4.4 mm long; the matrix is siltstone with chert of the Inca Formation, locality M59; the age is the Zone of *Ptychagnostus punctuosus* (antedating *Goniagnostus nathorsti*). The preglabellar median furrow is clear; the frontal glabellar lobe is almost pointed and, as in *tribulis tribulis,* only little wider than the front of the posterior lobe.

In Plate 37, fig. 4 the open shutter gap (see Text-fig. 5) is well exposed; the pygidial facet is vertical and concave; the edge of the free pleura of the posterior segment of the thorax is convex to fit the concavity of the facet in coiling.

Occurrence and age: The subspecies *Myrmecomimus tribulis mixtus* occurs in the Inca Formation and the V-Creek Limestone; its age is the Zone of *Ptychagnostus punctuosus,* including its association with *Goniagnostus nathorsti* (i.e. the Zone of *Doryagnostus notalibrae*).

Myrmecomimus tribulis evanidus subsp. nov.
(Pl. 35, figs. 4-7)

Material: Illustrated are one exoskeleton, two isolated pygidia, and a cephalon and pygidium of a disarranged exoskeleton; some more isolated shields are associated with these specimens, all from a single limestone bed.

Holotype: The exoskeleton Plate 35, fig. 6, CPC 14177, is selected as the holotype.

Diagnosis: Myrmecomimus tribulis evanidus is distinguished by the total absence of the preglabellar and postaxial pygidial median furrows, and by a vestigial second axial transverse furrow; furthermore, the axial bulb consisting of the fused second and posterior lobes is elongate, oval and relatively long (0.7x the cephalon in length), and the basal lobes in the cephalon are long, broad at base, and indistinctly divided (double).

Differential diagnosis: The cephalic structure especially of the glabella is about the same as in *M. tribulis mixtus* and the two can be confused, but their pygidia are different; in *tribulis mixtus* the second transverse furrow is not effaced and the median node is as strong as in *tribulis tribulis* itself. It appears that *evanidus* differs from the two subspecies by a more advanced effacement of the axial median furrows and the pygidial axis. The subspecies category of *evanidus,* therefore, is an expression of its presumed close affiliation with *tribulis* and *tribulis mixtus.* The dissimilarity of *tribulis mixtus* and *Myrmecomimus saltus* (which is also partially effaced) is discussed with the latter.

Comment on illustrated specimens

All specimens were obtained from the V-Creek Limestone, from the top of the section M411 and about 30 m above the bed with *Myrmecomimus tribulis mixtus.*

The holotype is 4.0 mm long; the basal lobes are strong and swollen but the furrow dividing the posterior and anterior part of the lobe is shallow; the vestigial second pygidial transverse furrow is indicated. The pygidium associated with the holotype is 2.0 mm long. The axial bulb is elongate and its median node is clear; the axis itself, 0.7x the shield length, is the longest known in a *Myrmecomimus.* The same figure (0.7) occurs frequently in other species of the Ptychagnostinae, in which, however, its meaning is not the same as in *Myrmecomimus,* as explained in the description of that genus.

The cephalon associated with a pygidium Plate 35, fig. 4, CPC 14175, is 2.0 mm long; the pygidium is slightly shorter, of course. The cephalon is deformed, but very similar to the cephalon of *M. tribulis mixtus* in Plate 36, fig. 5. In the pygidium the rear of the axis is narrowly overridden by the acrolobe; the second transverse furrow in the pygidial axis is almost obliterated; the articulating half-ring is relatively prominent, the shoulders are concave (arched retrally) and the fulcral prongs are inclined forward. A very fine, almost latent granulosity of the test is indicated under strong magnification.

The exoskeleton Plate 35, fig. 5, CPC 14176, in limestone, locality M411 (top of the sequence), is 4.5 mm long. The thorax is about 0.21-0.22x the cephalon in length.

The pygidium Plate 35, fig. 7, CPC 14178, is 2.2 mm long—of an exoskeleton about 4.7 mm in length; the test is very thin; the second transverse furrow is completely effaced and the median axial node is small and low; the axis, 0.75x the shield length, is actually shorter—it gained in length through the deforming oblique fracture.

Occurrence and age: Myrmecomimus tribulis evanidus has been collected from the V-Creek

Limestone at the top of the section, site M411; its age is Undillan—the beginning of the Zone of *Goniagnostus nathorsti* (about the disappearance of *Ptychagnostus punctuosus*); it is also the youngest known *Myrmecomimus*, emphasising the evanescence of the genus.

Myrmecomimus saltus sp. nov.

(Pl. 37, figs. 5-8)

Material: Illustrated are four complete exoskeletons in hard siltstone; the collection contains complete exoskeletons and a number of isolated shields.

Holotype: The specimen Plate 37, figs. 7 and 8, CPC 14189, is selected as the holotype; a part of its glabellar rear is lost but otherwise it is undeformed.

Diagnosis: Myrmecomimus saltus is a species with effaced postaxial and preglabellar median furrows, globose frontal glabellar lobe, and vestigial second transverse furrow in the pygidial axis, and is distinguished by the small size of its double basal lobes, vestigial median pygidial node, and granulose test.

Differential diagnosis: The degree of effacement in *M. saltus* is about the same as in *M. tribulis evanidus*; in *evanidus*, however, the basal lobes are strong, the frontal glabellar lobe oval, the pygidial axial node has retained some relief, and the test is practically smooth. Regarding the effacement, *M. tribulis evanidus* acquired it independently of the stratigraphically earlier *M. saltus*, which is apparently the earliest known species of the genus.

Remarks: A second collection of *Myrmecomimus saltus*, from the Inca Formation, locality M434, yielded one complete exoskeleton (CPC 14382, not illustrated) in shale and a number of cephala and pygidia in two pieces of chert with siltstone (CPC 14383). These shields have preserved their original convexity; in the pygidia the axial bulb is even more prominent than in the described material, and in some of the shields the postaxial and preglabellar furrows are indicated. Of the associated agnostids, *Aotagnostus aotus* indicates an early part of the Zone of *Ptychagnostus punctuosus*.

Comment on illustrated specimens

All illustrated specimens were obtained from siltstone and chert of the Inca Formation, locality M289.

The holotype, Pl. 37, figs. 7 and 8 is 2.6 mm long, a relatively small individual. The basal lobes are visibly double, the test in the acrolobes granulose, the frontal glabellar lobe equidimensional, and a vestige of the postaxial median furrow seems present. In lateral view the posterior glabellar lobe, having lost its top, is low.

The exoskeleton Plate 37, fig. 6, CPC 14188, is 3.5 mm long; it is larger and has also the axial bulb more obese than the holotype.

The exoskeletons Plate 37, fig. 5, CPC 14187, are each 4.0 mm long and the largest available; in the less deformed the pygidial axial bulb is rather obese, and its median node seems completely effaced; in the upper specimen the posterolateral cephalic spines, preserved with their tips, are very short, much shorter than in *M. tribulis*.

Occurrence and age: Myrmecomimus saltus is a species of the Inca Formation, of sites M289 and M434. Its age is Undillan, early in the Zone of *Ptychagnostus punctuosus*.

Genus **Pentagnostus** Lermontova, 1940

The type species of *Pentagnostus* by monotypy and original designation is *P. anabarensis* Lermontova (1940, p. 127, pl. 35, figs. 10-10d). The genus has been accepted by Harrington et al. (1959, p. 0185) and included in the family Spinagnostidae: N. Tchernysheva et al. (1960) placed it in the synonymy of *Peronopsis* as another alternative. *Triplagnostus* (Tchernysheva, 1961, table 1; Pokrovskaya, 1961, p. 261) occurs also in the literature; Öpik (1967, pp. 77, 78) in discussing these classifications placed *Pentagnostus* in the subfamily Ptychagnostinae.

The cephalon and pygidium of *Pentagnostus anabarensis* in Harrington et al. (op. cit.) after Lermontova (1940, pl. 35, figs. 10c, 10d) is handy for an understanding of the characters of the genus and its suprageneric classification: (1) in the pygidium the axis is trilobate with two transcurrent transverse furrows, and a median node on the second annulation which is projected forward in the middle; the posterior lobe, expanded about its middle, contracts with the convex flanks to a bluntly pointed apex; (2) the rim in both shields is narrow and flat or almost so; the structure of the pygidium and the rim is that of a *Ptychagnostus* and different from *Peronopsis* and its allies. In passing, in smaller pygidia the postaxial median furrow is incipient and in larger ones it is strong; (3) in the cephalon the frontal glabellar lobe is fairly long (0.38-0.4x the glabella in length), semioval and rounded (not acute) in front, the posterior lobe has parallel flanks, and the preglabellar furrow, when present, remains short and weak; the basal lobes according to Lermontova (op. cit., p. 128) are small and triangular. The blunt glabellar front is interpretable as an 'obvious' character of *Peronopsis* or a related genus. In brief, *Pentagnostus* is acceptable as a genus distinguished by the combination of a ptychagnostid pygidium and a cephalon with a parallel-sided glabella and a rounded (not pointed) glabellar front. Attributable to *Pentagnostus* are *Agnostus gibbus praecurrens* Westergaard, 1936 = *Triplagnostus praecurrens* (Westergaard, 1946) and *T. praecurrens* in terms of N. Tchernysheva (1961, p. 46, pl. 1, figs. 1-14). Younger than the other species is *Ptychagnostus (Triplagnostus) angermanensis* Westergaard, 1946, from the *atavus* zone; it has a pair of apodemal pits at the adaxial tips of the basal lobes, seen also in the new Australian species *Pentagnostus rallus* and *P. veles,* and in *Goniagnostus.*

The parallel-sided glabella of *Pentagnostus* is shared by *Triplagnostus,* but in the latter the glabellar front is acuminate and its assortment of spines is absent in *Pentagnostus.* Finally, in *Onymagnostus semiermis* the front of the anterior glabellar lobe is rounded (acuminate in all the other species of that genus), but its pygidial structure, especially the retrally extended median axial node, is not seen in *Pentagnostus.*

The geographic and palaeogeographic distribution of known species of *Pentagnostus* is as follows: in Australia one species (*P. rallus*) occurs abundantly in the Northern Territory, two (*P. anabarensis* and *P. veles*) in western New South Wales, and none in Queensland; in Siberia (Yakutia) two species, of which *P. anabarensis* occurs in New South Wales and *P. rallus* in the Northern Territory. The synonymy of *Triplagnostus burgessensis* Rasetti (1951) and *praecurrens,* as suggested by Öpik (1956; 1957, p. 44) is still in need of further investigation.

Two Siberian species (*trapezoidalis* and *ademptus*) were originally described as belonging to *Triplagnostus;* and Siberian specimens of *Triplagnostus (Pentagnostus) praecurrens* are described by Jegorova & Savitzky (1969) and by N. Tchernysheva (1971).

Pentagnostus anabarensis Lermontova, 1940

(Pl. 54, fig. 9)

The illustrated complete exoskeleton, CPC 14299, is 5.8 mm long as preserved; the deformation of its thorax and the pygidial rear considered, the real length is not less than 6.0 mm. The matrix is shale and the test is flattened; for this reason the cephalic rim appears narrow: its peripheral part is exposed and the inner part is flat and is dragged down together with the marginal furrow. As in the type material of *Pentagnostus anabarensis,* in the cephalon scrobicules are absent, the glabellar front is rounded, the flanks of the posterior lobe are parallel, and its median node is placed about the middle. The frontal glabellar lobe is long, about 0.4x the glabellar length, and the basal lobes are triangular and simple; the left basal lobe together with the glabellar rear is deformed, but the right side is intact. The preglabellar median furrow is weak and short, not reaching the front of the acrolobe. In the pygidium marginal spines are absent, as evident in the counterpart of the specimen; the axis is bulky and a knob or small node is superimposed on the median axial node, as can be seen also in the illustrations (Lermontova, op. cit., and Harrington et al., 1959, p. 0185). The Australian and the Siberian specimens, being visibly different regarding the matrix, deformation, and defects, are morphologically not separable as different species.

Pentagnostus anabarensis and *Pentagnostus praecurrens* (Westergaard) are similar in having no scrobiculate cheeks and simple basal lobes, but in *praecurrens* (Westergaard, 1936, pl. 1, figs. 21, 23) the pygidial axis is different; it is less prominent and its rear lobe less expanded than in *anabarensis.*

Occurrence and age: The illustrated Australian specimen comes from New South Wales, Mount Wright area (see Öpik, 1968, p. 146) from a shale of an unnamed formation* attributable to the Templetonian (late in the Zone of *Triplagnostus gibbus*); in Siberia it is a species of the Amga Stage (in the early part of that stage and about the same age as in Australia).

Pentagnostus veles sp. nov.

(Plate 55, figs. 1-5; Text-fig. 43)

Material: Illustrated are two complete exoskeletons and one isolated pygidium; the collection includes also one isolated cephalon and one immature pygidium.

Holotype: The exoskeleton Plate 55, figs. 1-3, CPC 14300, is the holotype.

Diagnosis: Pentagnostus veles is distinguished by the following combination of characters: (1) the cheeks are dimpled and scrobiculate, and arcuate scrobicules are clear; (2) the basal lobes are double and a pair of pits is present in the glabella close to their frontal tips; (3) the glabella is relatively narrow; (4) the post-

* J. H. Shergold (pers. comm., 1977) believes this may be the Coonigan Formation (Warris, 1967; Rose & Brunker, 1969; Cooper, 1975).

axial furrow is complete; and (5) pygidial marginal spines are clear.

Differential diagnosis: Pentagnostus rallus sp. nov. is of the same age as *P. veles* but its glabella is broader, the scrobiculation (dimples) weaker, the postaxial furrow is missing, and pygidial marginal spines are diminutive or even absent.

Description: In *Pentagnostus veles* the rim in both shields is relatively narrow (narrower than in *rallus*), and *veles* has a slender glabella and pygidial axis, more slender than *rallus* in flattened specimens (Text-figs. 43 and 44). The frontal lobe, 0.4x the glabella in length, is the same as in other species of *Pentagnostus* with the exception of *P. angermanensis* (Westergaard, 1946, p. 70), in which it is 0.32x. The median node is inconspicuous and placed behind the midpoint of the posterior glabellar lobe. The preglabellar median furrow is short (deep and complete in *angermanensis*) and the basal lobes are double (simple and large in *angermanensis*). The pits at the basal lobes are small and deep. In the pygidium the marginal spines are of medium length, the postaxial median furrow is complete (missing in *P. rallus* and *angermanensis*); the anterior axial lobe is tripartite, and the posterior appears slightly attenuated in its rear half. The test in *P. veles* is minutely and weakly granulose.

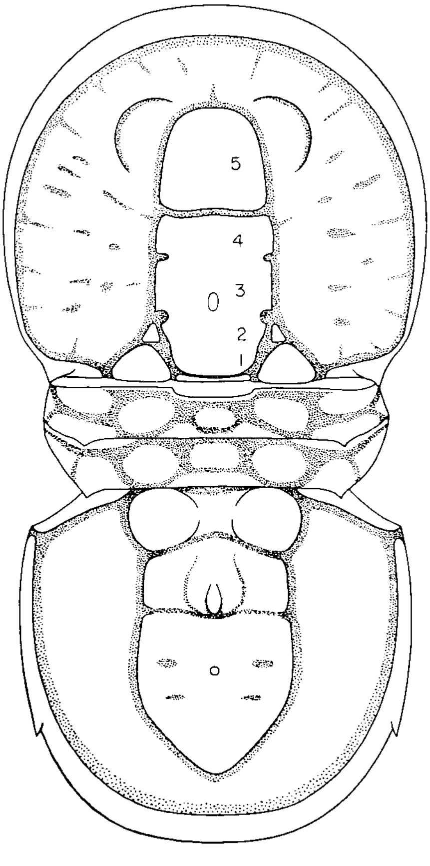

Fig. 43. *Pentagnostus veles.* **1-5 indicate metameres of the cephalon.**

Comment on illustrated specimens

All specimens have been obtained from a single bed of shale in a relatively small outcrop.

The holotype exoskeleton is 7.2 mm long. It is flattened and the pygidium is distorted; the cephalon is slightly wider than long—and hence close to its original shape except for the left flank having the border and the cheek distorted together; the same defect is evident also in the pygidium. The test is thin, apparently silicified, and fractured into a mosaic of irregular shreds; the pits at the tips of the basal lobes are partly filled by matrix; the median pygidial node is distorted but its tip seems preserved.

In the exoskeleton Plate 55, fig. 4, CPC 14301, the cephalon is 3.6 mm long (longer than in the holotype) indicating a total length of about 8.0 mm. The pygidial axis is reflected on the left side of the glabella and the left cheek; on the left side the ventral ridge of the marginal pygidial furrow is intact and the imprint of the marginal spine is visible. In the cephalon (which is the right way up) the pits at the glabellar rear are free of matrix.

The pygidium Plate 55, fig. 5, CPC 14302, is 3.2 mm long; the postaxial median furrow is clear, and the node on the posterior axial lobe is visible. The front of the axis has the recess, and the articulating furrow is somewhat wide.

Occurrence and age: Pentagnostus veles comes from New South Wales, Mount Wright area, from a shale of an unnamed formation* attributable to the Templetonian (late in the Zone of *Triplagnostus gibbus*).

Pentagnostus rallus sp. nov.
(Pl. 56, figs. 1-7; Text-fig. 44)

Material: Illustrated are one exoskeleton and seven shields selected from an unlimited supply of specimens; these are more or less flattened in silty shale; less flattened material is rare in chert and in indurated siltstone.

Holotype: The complete exoskeleton Plate 56, figs. 1 and 2, CPC 14303, from locality N32 is selected as the holotype.

Diagnosis: Pentagnostus rallus has almost smooth to weakly dimpled and scrobiculate

* See footnote to *Pentagnostus anabarensis*

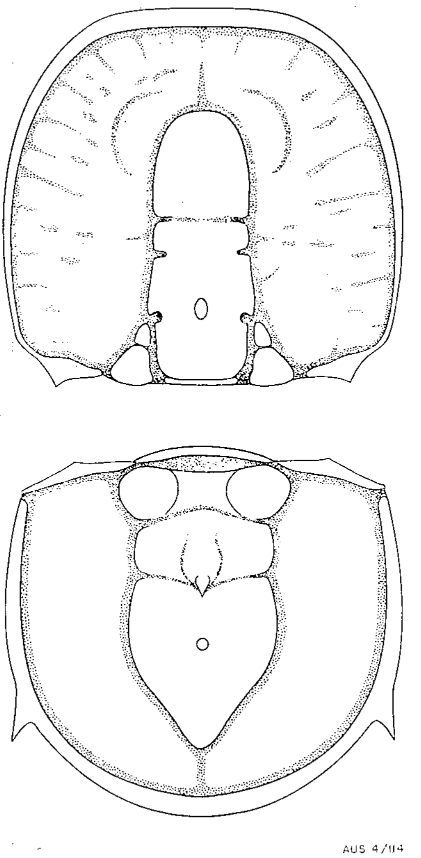

Fig. 44. *Pentagnostus rallus.*

cheeks, double basal lobes and a pair of pits at their tips in the glabellar flanks, and a somewhat wide glabella and pygidial axis, and is distinguished by the absence of the pygidial postaxial median furrow; pygidial marginal spines are diminutive or can be absent.

Differential diagnosis: P. rallus and *veles* are very similar; their difference is discussed under the latter and is evident from Text-figures 43 and 44. Also close is *P. praecurrens* (Westergaard, 1936; 1946), which, however, is unscrobiculate and has simple basal lobes; N. Tchernysheva's (1961, p. 46, pl. 1, figs. 7-14) *'Triplagnostus praecurrens'*, however, seems to represent *P. rallus* in Siberia. Most probably (op. cit., fig. 10) its basal lobes are double also.

Description: Pentagnostus rallus is a medium-sized agnostid some 8 mm in length; it is elliptical in shape, twice as long as wide; the cephalon is slightly longer than in the pygidium. The rim in its shield is relatively wide (wider than in *P. veles*) and of a low convexity, almost flat. The preglabellar median furrow is shallow and short, the cheeks are smooth to dimpled, and the arcuate scrobicules are shallow and frequently even obscure. The flanks of the glabella are about straight and parallel half way up the frontal lobe; this lobe, 0.4x the glabella in length, is well rounded in front. The node on the posterior glabellar lobe is placed close to the lobe's midpoint; a pair of short lateral furrows is also present. The basal lobes are double but the duplication is often obscure in creased test; a pair of pits marks the frontal end of the basal lobes; in undistorted cephala these pits appear as lateral indentations of the glabellar flanks. The posterolateral cephalic spines are short prongs.

The thorax, 0.3x the cephalon in length, has no axial spine and the fulcral spines are only short projections, of the same length as in *P. praecurrens* (Westergaard, 1946, pl. 9, fig. 9).

In the pygidium the margin is even, but in some specimens (Text-fig. 44) short incipient marginal spines are observable; a postaxial median furrow is absent in larger, but is discernible in small pygidia about 1.5 mm and less in length (examples occur in chips deposited in the collection with the illustrated specimens). The anterior axial lobe is tripartite but the lateral lobules remain inconspicuous; the median node on the second segment is broad and long and pointed in the rear; the transverse furrows are well impressed and the second furrow is almost straight and remains clear behind the median node. In the posterior lobe the median node is small and there are one or two pairs of elongate notular depressions.

Comment on illustrated specimens

All specimens belong to the Sandover Beds, Northern Territory; the collection numbers (N31, N35) are cited only for specimens which are not from locality N32.

The holotype exoskeleton is 6.8 mm long and flattened; the cephalon is fractured longitudinally and dilated in its rear, creating the impression of a tapering glabella which in fact should have parallel flanks; the rim is flat, having lost its low convexity; the pits at the tips of the basal lobes, owing to the flattening, are well exposed; the basal lobes are double, as evident from the internal cast (fig. 1), which also shows the shallow dimples in the cheeks and the arcuate scrobicules.

Of the two cephala Plate 56, fig. 3, CPC 14304, the lower (complete) is 2.8 mm long; its rim is preserved, but the basal lobes are deformed, not showing their duplication clearly; it is exposed in the upper specimen which also has a strong median glabellar node.

The cephalon Plate 56, fig. 7, collection N31, CPC 14308, is 3.0 mm long. It preserves the original convexity; the glabella is parallel-sided, the pit (on the left) owing to the steep slope of the glabella is almost invisible; the rim is distorted but its low convexity is apparent.

The pygidium Plate 56, fig. 6, CPC 14307, is 2.7 mm long; diminutive marginal spines are evident.

The pygidium Plate 56, fig. 5, CPC 14306, is 2.9 mm long; the median axial node is prominent and a pair of elongate notulae is visible on the posterior axial lobes.

The pygidium Plate 56, fig. 4, associated with a cephalon of *Peronopsis* (*Itagnostus*) *elkedraensis*, CPC 14305, is 2.9 mm long; the rim is intact, marginal spines are absent, and the posterior axial lobe shows two pairs of notular impressions.

Occurrence and age: Pentagnostus rallus occurs in the Sandover Beds of the Northern Territory; it is very abundant at locality N32 and has been identified in several other collections. Its age is late in the Templetonian Zone of *Triplagnostus gibbus*. Disguised under the name of *Triplagnostus praecurrens* it has been described from the early part of the Amga Stage of Yakutia (Siberia).

Genus **Goniagnostus** Howell, 1935

Introduction

Agnostus nathorsti Brögger (1878, pl. 5, fig. 1) is the type species of the genus; the holotype is an exoskeleton from Krekling; and Tullberg (1880) illustrated another from Sweden. The first published photograph (a cephalon and a pygidium), also from Krekling, are Howell's (1935, figs. 1 and 2). Whitehouse (1939) followed with exoskeletons of *Goniagnostus* from Queensland. Westergaard (1946, pp. 80-82, pl. 12) described *G. nathorsti* from Sweden and once more *G. spiniger* (q.v.) and remarked that 'the spinosity itself may not be of specific value'. Finally, Pokrovskaya (1958) in describing several species of *Goniagnostus* from Siberia observed in cephala the appendiferal pits and the occipital axial spine and characters of the spinosity in the exoskeletons (op. cit., diagnosis of the genus, p. 59).

Concepts and diagnoses of the genus Goniagnostus *and its subgenera*

The species of *Goniagnostus* are Ptychagnostinae with a pointed glabella and a pointed pygidial axis which is trilobite and its circumglabellar (axial) furrows (IV in Text-fig. 2) are only a little deflected at the basal lobes.

The species of *Goniagnostus* are described here in terms of three subgenera: *Goniagnostus* (*Criotypus*) subgen. nov., *G.* (*Goniagnostus*) Howell, and *G.* (*Allobodochus*) subgen. nov. These subgenera can each be regarded as a separate genus-taxon; but the subgeneric status is convenient in presenting the presumed phylogeny within the stock of *Goniagnostus,* as discussed below.

The mutual affinity of the subgenera *Goniagnostus, Criotypus,* and *Allobodochus* is evident from their identical structure of the posterior glabellar lobe (Text-fig. 45). This structure is also a relevant diagnostic characteristic of the genus *Goniagnostus*.

The midmost glabella (mG) is free of muscle spots and appendiferi but carries a retrally directed axial spine on its rear (in *Allobodochus* it is apparently a short tubercle); the culmination in the rear probablv represents the displaced median node. Against the depressed glabellar flanks (the outer glabella) the prominent midmost glabella is defined by a clear change of slope or (in *Allobodochus*) by delicate furrows.

The flanks of the posterior glabellar lobe (the outer glabella) contain the basal lobes, the appendiferal pits, and the pair of lateral glabellar furrows. The lateral furrows consist of two pits each—a pecularity of *Goniagnostus*. But the apodemal pits at the tips of the basal lobes, placed in front of the basal lobes in all species of the genus, are also evident in *Pentagnostus* and in *Triplagnostus diremptus* sp. nov. Moreover, such pits are also clear in *Tomagnostus perrugatus* (Grönwall) of Westergaard (1946, pl. 8, fig. 7) and in other species of that genus. Consequently, these apodemal pits are diagnostic in combination with other characters in different species; they are absent in *Ptychagnostus punctuosus* and *Pt. atavus*, in most species of *Triplagnostus,* and in all of *Acidusus* and of *Aotagnostus*.

The cheeks are rugose (scrobiculate)—as is usual in agnostids (vide Öpik, 1961a); the presence of arcuate scrobicules in *Criotypus* and their absence in *Goniagnostus* and *Allobodochus* is of a taxonomic significance within *Goniagnostus*.

The pygidial axial lobe is trilobate, its two anterior lobes are tripartite and the posterior axial lobe carries a knob close to, or behind, its middle; a rosette (see Text-fig. 24) is developed in *Goniagnostus* and *Allobodochus,* but absent in *Criotypus*. The spinosity is variable (see Table 5); the test is granulose.

The genus arrived with species of the subgenus *Criotypus* in the Zone of *Ptychagnostus atavus* and reached the early Upper Cambrian with *Goniagnostus* (*Allobodochus*) *nodibundus* (Öpik, 1967), surviving through the sequence of four stages (Floran, Undillan, Boomerangian, and Mindyallan). The general integumental design of *Goniagnostus* is subject to modifications in the course of time, allowing for three separate subgeneric aggregates as follows:

A. Subgenus *Criotypus* nov. The type species is *Criotypus oxytorus* nov.; the other, also new species are *Criotypus mitigatus, C. lemniscatus, C. paenerugatus, C.* sp. nov. aff. *lemniscatus, C.* sp. aff. *paenerugatus*, and *C.* sp. indet. The distinguishing characters are: (1) the posterior pygidial axial lobe is slightly attenuated; its transverse depression is shallow (almost imperceptible) and its median knob stands behind, but close to, the midpoint; consequently no rosette is present; (2) arcuate scrobicules are evident; and (3) the spinosity is different in different species. *Criotypus* is the earliest known subgenus of *Goniagnostus.*

B. Subgenus *Goniagnostus* (*Goniagnostus*) Howell, 1935. The characters are: (1) the rosette (the transverse depression and node in the posterior pygidial axial lobe) is clear but variable in emphasis even in a single species, and so is the attenuation in the rear of that lobe; (2) arcuate scrobicules are absent but all other rugae and scrobicules are strong; and (3) different species differ regarding the spinosity. The species are: (1) *Goniagnostus nathorsti* (Brögger), (2) *G. scarabaeus* Whitehouse (1939), (3) *G. longispinus* Pokrovskaya (1958)—a possible synonym of *scarabaeus,* and (4) *G. verus* nov. These species are Undillan in age.

C. Subgenus *Allobodochus* nov. Its type species is *Goniagnostus* (*Allobodochus*) *fumicola* (Öpik, 1961b). Other species are *Goniagnostus spiniger* (Westergaard) and *Goniagnostus nodibundus* (Öpik 1967). The characters are: (1) the delicate furrows separating the midmost glabella from the outer glabellar flanks; (2) the posterior part of the pygidial axis is isolated from the axial lobe by the rosette; the isolated (secondary) lobe recalls *Glyptagnostus* and the axial lobe is now quadrilobate (a trilobate axis is normal in the Ptychagnostinae); a similar structure but of lesser relief is also the rosette in the Euagnostinae (*Rhodotypiscus, Doryagnostus*); and (3) the test is granulose, stronger than in other species of the subgenus. Moreover, it seems that in *Allobodochus* an extended axial spine on the glabellar rear seen in *Criotypus* and *Goniagnostus* is replaced by a short tubercle.

A. fumicola and *A. spiniger* are late Middle Cambrian (Boomerangian) and *A. nodibundus* is early Upper Cambrian (Mindyallan) in age.

Differential diagnosis: Goniagnostus cannot be confused with *Ptychagnostus* (*Ptychagnostus*), *Onymagnostus, Zeteagnostus, Myrmecomimus,* or *Leiopyge;* the spinose species of *Ptychagnostus* (*Acidusus*) may recall superficially a *Goniagnostus* but are distinguished by their terminal axial node. *Triplagnostus* and *Aotagnostus,* however, are in need of special comment: (1) *Triplagnostus* is recognisable from the parallel flanks of the glabella, the absence of pits in the lateral glabellar furrows, and the absence of the spine on the glabellar rear; the pygidia in all species of *Triplagnostus,* however, and of *Goniagnostus* (*Criotypus*) have a similar design; (2) *Aotagnostus* is also spinose, but differs from *Goniagnostus* in the structure of the cephalon and the pygidial axis: glabellar apodemal pits are absent, the glabellar furrows are weak, and the relief of its pygidial axis is dominated by the prominence of its second lobe. Finally, in the description of *G.* (*Criotypus*) *lemniscatus,* its semblance with *Tomagnostus* is discussed: briefly, the prosopon of the cephalic caeca in *Criotypus* and in some forms attributed to *Tomagnostus* looks identical only because it reflects the general model of the glandular system of Agnostidae and Diplagnostidae; the glabellar structure of *Criotypus,* however (Text-fig. 45), is the same as of *Goniagnostus.*

In passing, *Agnostus aculeatus* Angelin (Westergaard, 1946; Öpik, 1961b) a *Goniagnostus* according to Kobayashi (1939) and *Ptychagnostus* (*Ptychagnostus*) according to Westergaard (op. cit.) has a cephalon of a *Goniagnostus* and is a separate genus; it is discussed in connection with *Onymagnostus* (q.v.).

Phylogeny of the Goniagnostus *stock*

Goniagnostus (subgenus *Criotypus*) and *Ptychagnostus* emerged simultaneously in the Zone of *Ptychagnostus atavus* and a little after the arrival of *Triplagnostus* and *Pentagnostus*; the known species of these genera constitute separate stocks whose common parental form remains in obscurity. To speculate, the axial spines, the terminal pygidial axial 'sting' of *Acidusus,* the composition of the glabella consisting of a frontal and a posterior lobe, and

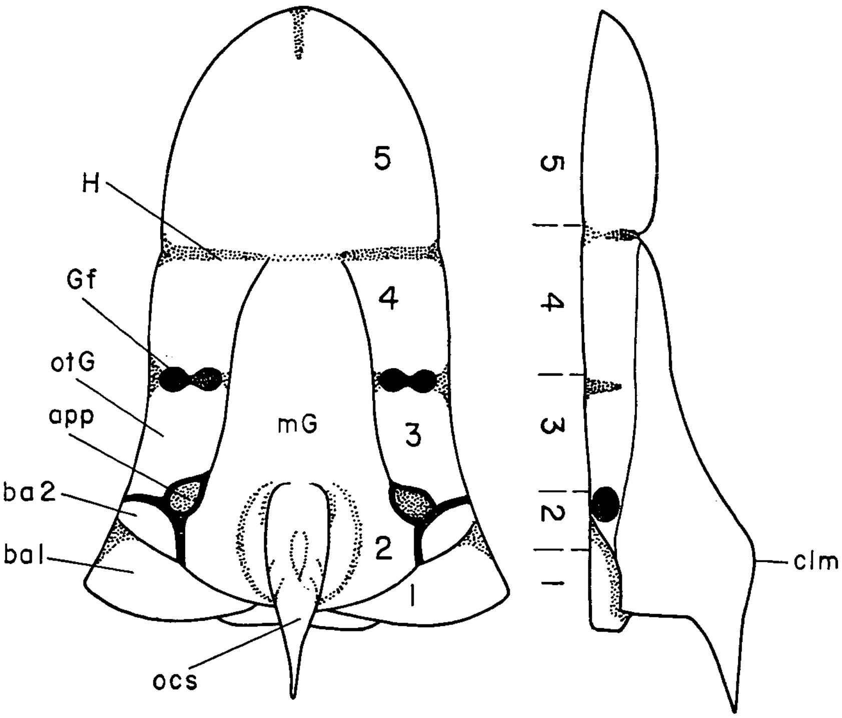

Fig. 45. The structure of the cephalic axial lobe in *Goniagnostus (Criotypus), G. (Goniagnostus)* **and** *G. (Allobodochus).* **5—frontal glabellar lobe; 1-5—metameres of the glabella (and cephalon); mG—the midmost glabella; otG—the outer glabella (left and right); H—anterior transverse furrow; Gf—lateral glabellar furrow and its pits; app—posterior appendiferal pits; ba2—anterior basal lobe; bal—posterior basal lobes; ocs—occipital spine; clm—glabellar culmination.**

the thorax of two segments, all indicate a source close to the eodiscids and pagetiids, and a problem of the general phylogeny of agnostids that cannot be formulated clearly.

The phyletic succession of the subgeneric agregates of *Goniagnostus* is evident from their temporal succession beginning with *Criotypus,* passing to *Goniagnostus* (*Goniagnostus*) and terminating with the sophisticated *Allobodochus.* In the cephalon the obliteration of the arcuate scrobicules marks the change from *Criotypus* to *G.* (*Goniagnostus*)—a presumably irreversible event affecting the otherwise conservative cephalic structure; the simple trilobate pygidial axis of *Criotypus* maintained in the early forms of *Goniagnostus nathorsti* is, apparently, gradually modified in developing the attenuation of the posterior pygidial axial lobe and its transverse depression of the rosette; and finally this transverse depression gains in emphasis to manifest itself as a secondary transverse axial furrow of a quadrilobate axis. The modifications of the spinosity are not quite in step with the directed transformation of the pygidial axis: the cephalic spines are long in the early *Criotypus oxytorus,* short in *C. lemniscatus* and in *Goniagnostus nathorsti,* but long in its 'twin' species *G. scarabaeus* and in *Allobodochus.* It seems that the length of all spines fluctuates within the stock and contributes to the characteristics only of the species.

Subgenus **Goniagnostus (Criotypus)** nov.

Goniagnostus (Criotypus) oxytorus sp. nov.

(Pl. 57, figs. 1, 2; Text-fig. 46)

Material: Available is an exoskeleton, the holotype, CPC 14309, from locality M425.

Diagnosis: Criotypus oxytorus is distinguished by its very long cephalic spines and long retral and curved pygidial marginal spines placed well in the rear of the shield; furthermore, its fulcral spines in the second segment of the thorax are also very long and the basal lobes are undivided; the test is granulose, and the granulosity is especially prominent in the pleural lobes of the pygidium.

Moreover, in terms of Text-figure 2, the axial furrows are deflected at the basal lobes quite abruptly in *C. oxytorus* and in the other species of the subgenus, visibly more than in the subgenus *Goniagnostus* (see design IV, Text-fig. 2).

Differential diagnosis: In *Criotypus lemniscatus* and *C. paenerugatus* the cephalic spines are short trigonal prongs and the basal lobes are double; the pygidial spines in *C. lemniscatus* are short and placed more forward than in *C. oxytorus.*

In *Goniagnostus (Goniagnostus) scarabaeus* Whitehouse (Text-fig. 49) the pygidial marginal spines are also curved and placed in the rear, but are deflected sideways. Rearward placed marginal pygidial spines are also present in *Aotagnostus magniceps* and long fulcral spines in the thorax are known in *Aotagnostus culminosus* and *A. protentus;* consequently, similar spinosity occurs in divers genera of Ptychagnostinae.

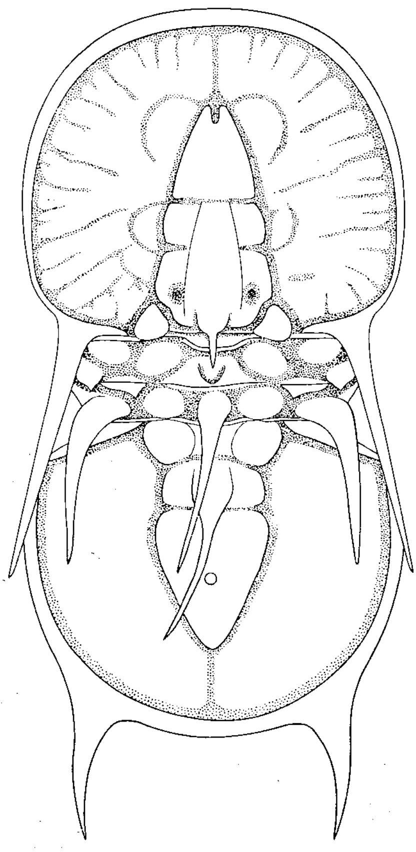

Fig. 46. *Goniagnostus (Criotypus) oxytorus.*

Description: Goniagnostus (Criotypus) oxytorus is a species completely en grande tenue with three paired and three azygous axial long spines—nine altogether. The holotype exoskeleton is 6.2 mm long and flattened in shale. The cephalon is a little longer than the pygidium and the thorax is about 0.24x the cephalon in length.

In the cephalon the rim is narrow and convex, but the wider pygidial rim seems almost flat and is expanded at the base of the marginal spines; the marginal furrows, as in all Ptychagnostinae, are narrow and deep. The cheeks are prominently rugose and scrobiculate; the preglabellar median furrow, the arcuate scrobicules, and the sulcus in the glabellar front merge together at the glabellar tip.

The frontal glabellar lobe, 0.4x the glabella in length, is trigonal and a little longer than wide. The axial furrows are straight from the tip in front to the basal lobes, where they are deflected sideways. In the posterior glabellar lobe the lateral furrows (Gf, Text-fig. 45) are relatively short and deep with pits close to each other. Owing to the corrosion of the test and the flattening, the separation is unclear in the photograph. The apodemal pits (app, Text-fig. 45) in the glabellar rear and off the axial furrows are preserved as hollow cones (not funnels) with retrally inclined axes; in the glabellar rear a median crest is extended into an axial spine, whose tip is lost in the matrix. The relief of the midmost glabella is obliterated, but its anterior part behind the transverse furrow is discernible. The basal lobes are simple and trigonal. The cephalic spines are as long as the glabella and extend rearward to about the middle of the pygidium.

The axial spines, one in the thorax and another in the pygidium, have lost their distal parts, though their extent is evident from their imprints in the test.

The pygidium (save the spines) is a large arc of a circle in outline. Its marginal spines are well in the rear and close to the midline. The pygidial axis, 0.75x the shield length, is trilobate; its anterior lobe is tripartite with clear lateral lobules; the second lobe is narrow (as usual in the Ptychagnostinae); the third (posterior) lobe is acute, almost imperceptibly attenuated in its rear half, and is equipped with a centrally placed quite prominent node (or knob). A rosette is absent.

Occurrence and age: Goniagnostus (Criotypus) oxytorus is a rare fossil of the Inca Formation; of the Floran *Ptychagnostus atavus* zone.

Goniagnostus (Criotypus) mitigatus sp. nov.
(Pl. 57, fig. 3)

Material: The material consists of a single cephalon, the holotype, CPC 14310.

Diagnosis and differential diagnosis: The diagnosis of *Criotypus oxytorus* nov. is applicable to the new species; in *C. mitigatus,* however, the anterior glabellar lobe, 0.4x the glabella in length, is shorter than in *oxytorus,* the spine in the glabellar rear is relatively small, the relief of the scrobiculation is mitigated and the arcuate scrobicules are vestigial, but clearer on the left than on the right cheek; it is nevertheless enough to prevent the application of the name *Goniagnostus* (*Goniagnostus*); compare *G.* (*Goniagnostus*) *verus,* Plate 33, fig. 2.

Occurrence and age: The cephalon of *C. mitigatus* was recovered from limestone, locality M191a; its age is early Undillan in the Zone of *Ptychagnostus punctuosus.*

Goniagnostus (Criotypus) lemniscatus sp. nov.
(Pl. 58, figs. 1-8; Pl. 59, fig. 1; Text-figs. 45, 47)

Material: The illustrated part of the paradigm consists of six cephala and six pygidia; available, but not illustrated, are also two cephala and two isolated posterior segments of the thorax. No complete exoskeleton has been found, but the available sclerites are sufficient for a description of the whole. About 70 shields have been examined.

Holotype: The cephalon with the anterior segment of the thorax attached (Plate 58, fig. 1), CPC 14311, is selected as the holotype; it is flattened in shale and has some defects; but it is supplemented by other cephala described in the comment on the illustrated specimens.

Diagnosis: Criotypus lemniscatus sp. nov. is distinguished by the following combination of characters: (1) the cephalic and pygidial marginal spines are short; (2) the basal lobes are double; (3) the test has no ornament (no granulation); and (4) the flanks of the frontal glabellar lobe converge more abruptly than the flanks of the posterior lobe. Furthermore, its thorax, about 0.32x the cephalon in length, is longer than in *C. oxytorus* (about 0.24) and in other known species of *Goniagnostus.*

Differential diagnosis: Criotypus oxytorus is different in having extremely long spines, simple basal lobes, a granulose test, and more evenly converging, almost straight glabellar

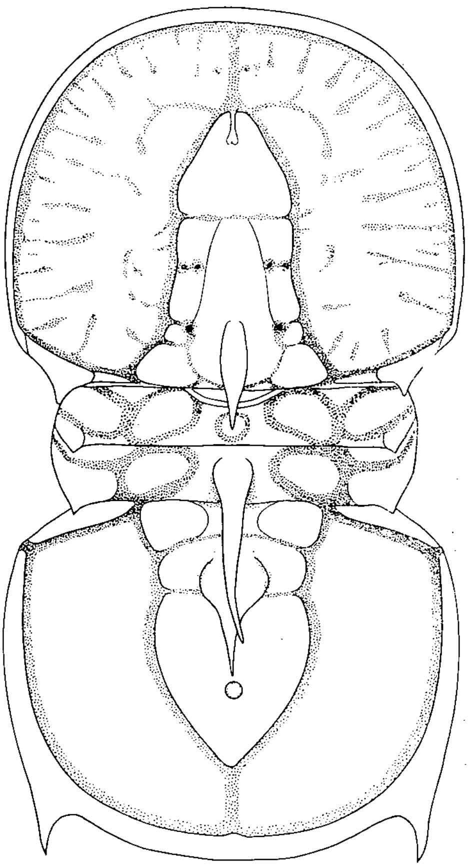

Fig. 47. *Goniagnostus (Criotypus) lemniscatus.*

flanks; *Criotypus paenerugatus* (q.v.) has double basal lobes but its glabella has a shape different from *C. lemniscatus* and the cheeks have only vestigial scrobicules or none at all.

The resemblance between *G.* (*Criotypus*) *lemniscatus* and *Tomagnostus* rests with two structures; (1) the combination consisting of the arcuate scrobicules, preglabellar median furrow and the frontal glabellar sulcus merging at the glabellar tip, as seen for example in *Agnostus corrugatus* Illing (1916, pl. 29, fig. 8) or in *T. perrugatus* (Grönwall) Westergaard (1946, pl. 8, fig. 3); and (2) the presence of apodemal pits in the glabellar rear seen in the cephalon attributed to *perrugatus* by Westergaard (ibid., fig. 7). I have commented earlier upon the scrobicules (Öpik, 1967, p. 72) as a 'fundamental feature of agnostid anatomy' and as a problem of the family classification of the Tomagnostinae (op. cit., p. 81).

The apodemal pits found so far in three genera (*Pentagnostus, Goniagnostus,* and *Tomagnostus*) are probably over-developed muscle spots (notulae) and constitute a problem of agnostid anatomy requiring further study and supplementary observations. The following characters of *Criotypus lemniscatus* alienating it from the Tomagnostinae indicate its affinity to the Ptychagnostinae and *Goniagnostus*: (1) the occipital spine and the posterior glabellar culmination (Text-fig. 45); (2) the axial spinosity in the thorax; (3) the triangular and pointed anterior glabellar lobe; and (4) the median (longitudinal) prominence of the midmost glabella.

Description: Goniagnostus (*Criotypus*) *lemniscatus* is a relatively large agnostid not less than 10 to 11 mm long in maturity. Its shields are a little wider than long, with evenly curving margins and narrow and moderately convex rims in uncompressed specimens; the thorax, about 0.3x the cephalon in length, is longer than in *G.* (*C.*) *oxytorus, Goniagnostus* (*Goniagnostus*) *nathorsti,* and *G.* (*G.*) *scarabaeus.* The cephalon is presumably longer than the pygidium, but in the absence of a complete exoskeleton the ratio is unknown. The three axial spines (occipital, thoracic, and pygidial) are extended but relatively short, the cephalic prongs are short and triangular, and the pygidial marginal spines short: the style of spinosity in *C. lemniscatus* is the same as in *Goniagnostus nathorsti.*

In the cephalon the cheeks are rugose and scrobiculate; the frontal part of the glabella is flanked by a pair of semicircular arcuate scrobicules in the same manner as in *C. oxytorus*; the adaxial ends of the scrobicules are dimples but isolated dimples are few; the arcuate scrobicules in some specimens (for example, Pl. 58, fig. 8) are broken up partly into dimples.

The structure of the glabella is explained in Text-figure 45. The frontal lobe, 0.4x the glabella in length (but variable a little), has convex flanks; the flanks of the posterior glabellar lobe are a little convex; the sulcus in its front is variable in its depth. The transverse glabellar furrow is laterally deep and very shallow in the middle—at the front of the midmost glabella; the lateral glabellar furrows of two pits each are deep and end abruptly against the midmost glabella. The culmination in the glabellar rear rises high and narrow, being compressed laterally. The occipital spine behind the summit of the culmination is a delicate retral spike, apparently shorter than in *C. oxytorus* and about as long as in *C. paenerugatus* and *G. nathorsti* and *scarabaeus.* The apodemal pits are placed at the adaxial frontal tips of the basal lobes and in touch with the midmost glabella—a position similar to the adaxial ends of the lateral glabellar furrows. The basal lobes are large and tumid and divided by a slanting furrow into an anterior smaller and a posterior larger boss.

In the thorax the axial node on the anterior segment is also evident in several other Ptychagnostinae and other agnostids. The axial spine on the second segment is slender and the fulcral points are sharp but not extended.

In the pygidium the posterior axial lobe is attenuated and its rear more or less pointed; there is also a shallow transverse depression about the prominent median node; the rear part behind the node and depression is slightly tumid (Pl. 58, fig. 5)—a structure recalling the rosette of *Rhodotypiscus* (q.v.)—and foreshadowed the quadrilobation of *Allobodochus.*

The test is thin and smooth without the granulation seen in *C. oxytorus* as well as in several other Ptychagnostinae.

Comment on illustrated specimens

The cephalon Plate 58, fig. 8, CPC 14316, Currant Bush Limestone, locality M150, is 3.7 mm long. It is undeformed but has lost almost all of its thin test. The median part of the posterior glabellar lobe (the midmost glabellar) is a slightly elevated ridge (Text-fig. 45).

The next six specimens were obtained from shale of the Inca Formation, sinkhole M176.

The holotype cephalon with half the thorax attached, Pl. 58, fig. 1, CPC 14311, is 4.6 mm long and the cephalon alone 4.0 mm long. The glabellar rear is tilted to the left and defective. The basal lobes are double; the frontal sulcus seems shallow and in the anterior segment of the thorax a quite prominent axial node is evident. The anterior segment is long, about 0.17-0.18x the cephalon in length and longer than in *Criotypus oxytorus* with 0.13x. The whole thorax of *lemniscatus* should be about 0.32x the cephalon, taking into account the shortness of the posterior segment. The adaxial ends of the scrobicules are dimples. The whole exoskeleton should be about 9 mm long.

The cephalon Plate 58, fig. 4, CPC 14313, is 3.8 mm long. Its frontal glabellar sulcus is clear.

The cephalon Plate 58, figs. 2 and 3, CPC 14312 (associated with a cephalon of *Ptychagnostus scarifatus*) is 3.8 mm long. The frontal glabellar sulcus and the apodemal pits are clear; the occipital part of the glabella and the basal lobes are displaced but in the rubber cast the down-bent occipital spine is visible.

The piece of shale Plate 59, fig. 1, CPC 14317, contain two pygidia of *Goniagnostus* (*Criotypus*) *lemniscatus,* the larger being 4.2 mm long; the posterior axial lobe is attenuated, its median node is clear, and short marginal spines are evident. In the same piece of shale the mould of the second segment with its axial spine, as described in the text, is evident; also the cephalon whose glabella is depicted in Text-fig. 45. The associated cephalon of *Rhodotypiscus nasonis* is described (p. 81).

Of the two pygidia Plate 58, fig. 5, CPC 14314, the larger is 4.0 mm long; it lacks the postaxial median furrow. The axial rear is more attenuated in the smaller than in the larger pygidium.

The larger pygidium in Plate 58, figs. 6 and 7, CPC 14315, is 4.5 mm long, of an exoskeleton 10 to 11 mm in length. The axial spine is extended but not really long; it seems almost complete in the rubber cast of the smaller fragmentary shield.

Occurrence and age: Goniagnostus (Criotypus) lemniscatus occurs in the Inca Formation (collections M176, M412, and M425) and in the Currant Bush Limestone (M176 and M150). The age of M425 is the Floran Zone of *Ptychagnostus atavus;* it contains two cephala only, which are not illustrated; one is associated with the *Triplagnostus gibbus posterus* of Plate 24, fig. 3. All other material belongs to the Zone of *Euagnostus opimus.*

Goniagnostus (Criotypus) sp. nov. aff. **lemniscatus**

(Pl. 59, figs. 2 and 3)

Material: The material consists of the two illustrated cephala.

Description: The cephalon Plate 59, fig. 2, locality M123, CPC 14318, in limestone, is 2.5 mm long; its test is preserved. Its characters are (1) the tumidity of the frontal glabellar lobe, (2) weak rugae and scrobicules, and (3) vestigial arcuate scrobicules.

The cephalon Plate 59, fig. 3, locality M412, in chert, CPC 14319, is 3.5 mm long. The left side of the glabella is overridden by the cheek, and some of the culmination of the glabella is lost. The scrobicules are combined with dimples, the arcuate scrobicules are almost imperceptible, and the basal lobes are apparently simple. The right cephalic spine is very short, and is not an extension of the margin; its base is a swelling superimposed on the rim, seen also in *Criotypus lemniscatus* (Pl. 58, fig. 1).

Occurrence and age: Criotypus sp. nov. aff. *lemniscatus* is a rare fossil of the Currant Bush Limestone (M123) and the Inca Formation (chert, M412). Its age is the Floran Zone of *Euagnostus opimus.*

Goniagnostus (Criotypus) paenerugatus sp. nov.

(Pl. 45, fig. 5; Pl. 59, figs. 4-6)

Material: Illustrated are three cephala selected from a total of eight; no pygidia have been collected.

Holotype: The cephalon Plate 59, figs. 4 and 5, CPC 14320, is the largest available and selected therefore as the holotype.

Diagnosis: Criotypus paenerugatus is distinguished by the following combination of characters: (1) rugae are absent and the scrobicules when present are rather weak; (2) the glabella is trigonal with slightly convex flanks; (3) the basal lobes are double; and (4) the cephalic spines are short triangular prongs.

Differential diagnosis: Criotypus paenerugatus has about the same glabella as *C. oxytorus,* from which it differs by its double basal lobes and short spines; in *Criotypus lemniscatus* the basal lobes are double and the cephalic spines short, but its cheeks are rugose, the scrobicules strong, and the glabellar shape is different from *C. paenerugatus.*

Description: The holotype cephalon of *Criotypus paenerugatus,* the largest available, indicates an exoskeleton some 7 mm long. The cephalon (as usual) is wider than long with an even marginal curvature; the rim is narrow and convex; the cheeks are faintly, or not at all, scrobiculate; the arcuate scrobicules indicate the subgenus *Criotypus.* The preglabellar median furrow is distinct. The glabella as a whole appears triangular and the frontal lobe, with more or less convex flanks, is acute; its tip may bear a trace of a median sulcus. The lateral furrows in the posterior glabellar lobe are short and deep; each consists of two pits, as seen in the cephalon Plate 49, fig. 5. The apodemal pits are clear and the basal lobes are double; the posterior part of the lobe is prominent, as a tumid boss; the occipital spine is a delicate needle. The test under stronger magnification seems minutely granulose.

Comment on illustrated specimens

The matrix of the described specimens is siltstone, Inca Formation.

The holotype, locality M425, is 3.1 mm long and preserved with its counterpart. The cast in the matrix shows the left arcuate scrobicule and weak peripheral scrobicules which are not evident in the rubber cast of the exterior; the latter shows the deformed culmination and the proximal part of the terminal axial spine. The midmost glabella is clear.

The cephalon Plate 45, fig. 5, CPC 14246, locality M265, is 2.4 mm long; the glabella is creased; in its front the sulcus is indicated; the imprint of the occipital spine about 0.3 mm long is clear. Associated is *Zeteagnostus incautus*. The transverse fracture in the rock is about at the contact of the siltstone with a pod of chert.

The cephalon Plate 59, fig. 6, CPC 14321, collection M281, is 2.5 mm long. Its frontal lobe is less acute than in the two other specimens.

An unillustrated cephalon from locality M425 is 2.8 mm long, its rear is damaged and the glabella dilated; in the lateral glabellar furrows the paired pits are clear.

Occurrence and age: Criotypus paenerugatus is a rare fossil of the Inca Formation, found in collections M425, M265, and M281. Its age is the Floran Zone of *Ptychagnostus atavus*.

Goniagnostus (Criotypus) sp. aff. **paenerugatus**

(Pl. 32, fig. 8)

The illustrated and only cephalon, associated with shields of *Aotagnostus aotus* (CPC 14156), is 1.7 mm long; its double basal lobes and short triangular spines recall *C. lemniscatus* and *C. paenerugatus*. Its cheeks are scrobiculate, but arcuate scrobicules are absent —as in *Goniagnostus* (*Goniagnostus*) *nathorsti* for example. The glabella is triangular, the apodemal pits and the lateral furrows deep, and of its occipital spine a large stump is preserved. The surface is granulose.

Occurrence and age: The matrix is a friable siltstone of the Inca Formation, locality M263; the age is the early part of the Undillan Zone of *Ptychagnostus punctuosus*.

Goniagnostus (Criotypus) sp. indet.

(Pl. 59, fig. 7)

The illustrated fragmentary cephalon, CPC 14322, in limestone, is about 2.0 mm long; it is so defective that its specific identity cannot be determined. Its rugosity, well impressed scrobicules, and sulcus recall *Criotypus oxytorus* as well as *C. lemniscatus*, but its granulose test, excluding the latter from further consideration, favours *C. oxytorus* as a guess.

Another associated cephalon, deposited in the collection with the one illustrated, is also rather defective.

Occurrence and age: Criotypus sp. indet. has been obtained from locality D150 of the Inca Formation, Burke River Outlier. Its age is Floran, either late in the Zone of *Ptychagnostus atavus* or in that of *Euagnostus opimus*.

Subgenus **Goniagnostus (Goniagnostus)** Howell, 1935

The subgenus name (*Goniagnostus*) is introduced because of the new subgenera *Criotypus* and *Allobodochus;* the characters of all these subgenera are given under the general title of genus *Goniagnostus*.

The following species belong to the subgenus *Goniagnostus*:

1. *G. nathorsti* (Brögger, 1878); described originally from Scandinavia; it occurs in Australia and has been recorded from Siberia by Pokrovskaya (1958), but this needs confirmation; Matthew (1897, pl. 1, fig. 2) illustrated a pygidium whose identity is doubtful. Insufficiently documented is also the presence of *G. nathorsti* in England (Illing, 1916).
2. *Goniagnostus scarabaeus* Whitehouse, 1939; an Australian species revised here.
3. *Goniagnostus verus* sp. nov.
4. *Goniagnostus nathorsti intersertus* subsp. nov.
5. *Goniagnostus longispinus* Pokrovskaya (1958), and *G. longispinus latirhachis* Pokrovskaya. In these the axial spinosity has been described by their author.
6. *Goniagnostus confluens* (Matthew) revised by Howell (1935); the pygidium attributed to this species may belong to a *Tomagnostus*.
7. *Goniagnostus scanensis* Westergaard (1946). It belongs to the Ptychagnostinae but its cephalon is unknown and the generic classification remains therefore inconclusive. Remarkable also is the specimen Robison (1964, pl. 79, fig. 18) attributed to *Ptychagnostus richmondensis*; it represents a regular species of *Goniagnostus* distinguished by the absence of pygidial marginal spines (see also under *Acidusus*).

Goniagnostus (Goniagnostus) nathorsti (Brögger, 1878)

(Pl. 47, fig. 6; Pl. 60, figs. 1-5; Pl. 61, figs. 1, 3-6; Text-fig. 48)

Material: Illustrated are four exoskeletons, three cephala, and three pygidia, selected from an abundant supply of specimens.

Holotype: The complete exoskeleton of *Agnostus nathorsti* Brögger (1878, p. 68, pl. 5, fig. 1) is the holotype by monotypy.

Diagnostic characters of the species: Goniagnostus nathorsti is distinguished by its short cephalic and pygidial marginal spines; furthermore, its pygidial axis is relatively broad (about as wide as the glabellar rear) and the glabella tapers more or less evenly forward.

The term 'short cephalic spines' is condensed from the descriptive phrase: 'short triangular projections at the posterolateral corners of the cephalon'. The tip of such a spine is acute and

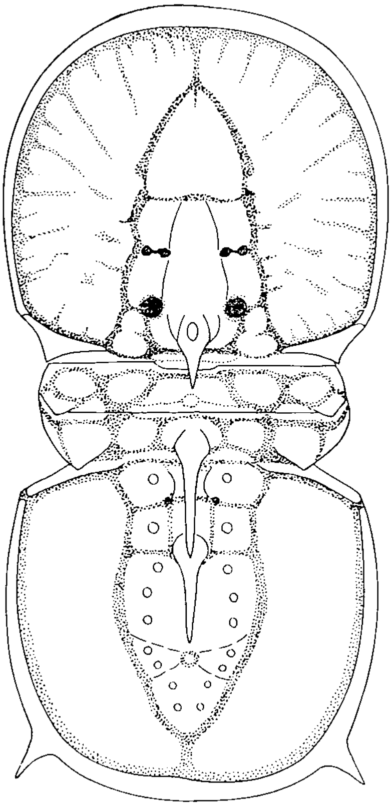

Fig. 48. *Goniagnostus (Goniagnostus) nathorsti.*

even attenuated, and is observable in well preserved and properly dematricated specimens. The other descriptive terms 'long spines' or 'extended spines' are self explanatory. In brief, cephalic spines of any kind in agnostids are homologues of the fulcral spines in the thorax as discussed under 'Morphology' (p. 25).

In other species (*Goniagnostus scarabaeus* Whitehouse and *G. longispinus* Pokrovskaya, 1958) the cephalic spines are long; in *G. scarabaeus* the pygidial marginal spines are 'medium' but still longer than in *nathorsti.*

The holotype and the shields published by Westergaard (1946) conform to the diagnostic characters as given above; our diagnosis, however, needs a revision of the holotype and associated material regarding the following structures unobserved in the Scandinavian but evident in the Australian forms: (1) the presence of an axial spine in the second segment of the thorax; I have observed such isolated segments in material from Krekling but a positive or negative confirmation based on the specimen is most desirable; (2) the presence of an occipital spine, which is an elusive structure even in Australian material; it is, however, indicated in a cephalon published by Westergaard (1946, pl. 12, fig. 14). I take it as supporting the general definition of the genus *Goniagnostus* (p.); and (3) the basal lobes are triangular according to Brögger (op. cit., p. 68), but their structure is complicated—composite (knobbly) in Australian as well as Swedish (Westergaard, op. cit., pl. 12, fig. 14) cephala.

As regards the shape of the pygidia, it is somewhat variable in Swedish as well as Australian material and similar variants are evident; the pygidial axis, however, seems shorter in most of the Australian than the Scandinavian representatives of *Goniagnostus nathorsti,* which anyway belong to two contemporaneous populations separated from each other by some 15 000 km.

The population of *Goniagnostus nathorsti* in Queensland is best represented in locality M57, in the upper part of the V-Creek Limestone. The rock is an impure silty limestone and even marl, of which less than 3 m is seen. Isolated shields and complete exoskeletons of *Goniagnostus* are present in abundance. I have not found in this collection a single specimen of *Goniagnostus scarabaeus*; thus, *G. nathorsti* and *scarabaeus* are species which may occur separately, as well as together as local populations in collection M469.

As regards preservation, however, all specimens are variously deformed through compaction of the sediment, obscuring the original convexity of the shields.

The occurrence of *Goniagnostus nathorsti* in Australia has been recorded already by Whitehouse (1939, p. 259, pl. 25, fig. 20) as cf. *nathorsti* (Brögger).

Description: Goniagnostus (*Goniagnostus*) *nathorsti* is represented in Australian collections by relatively small specimens reaching a length of some 7 to 8 mm. The cephalon, usually about as long as the pygidium and half the length of the posterior segment of the thorax, is the larger shield, but specimens with both shields almost equal in length have been observed. The rim in both shields is narrow and convex and, as usual, is wider in the pygidium than in the cephalon; the thorax is about 0.27-0.28x the cephalon in length. The shields are a little wider than long, with evenly curved margins. The spinosity is moderate; the cephalic, occipital, pygidial marginal, and fulcral spines in the thorax are not extended, but the axial spines, one in the thorax and another in the pygidium, are relatively long.

The cheeks are prominently rugose and scrobiculate; the scrobicules radiate from dimples, and scattered dimples are also present; arcuate scrobicules are absent. The preglabellar median furrow connects the marginal furrow with a flare.

The glabella is triangular, but its flanks are not quite straight but a little convex, and the frontal part of the posterior lobe seems expanded and even angulate. The frontal glabellar lobe, 0.4-0.42x the glabella in length, is acutely trigonal with slightly convex flanks and in some specimens is provided with a short and shallow sulcus; a recess occurs occasionally in the rear of the frontal lobe. The transverse glabellar furrow is shallow in the middle at the front of the midmost glabella—a structure explained in Text-figure 45 (*Criotypus lemniscatus*). The midmost glabella is confined between the lateral glabellar furrow and the posterior apodemal pits and its relief is low; in exceptional preservation (Pl. 60, figs. 1, 3) the lateral glabellar furrows are composite; each consists of a pair of apodemal pits and the adaxial pits appearing as homologues of the posterior, larger apodemes.

The glabellar culmination is marked by a low node and behind it the retral axial spine (Pl. 60, fig. 5) extends over the anterior part of the segment of the thorax, over the occipital collar and the frontal recess of the thorax; when well preserved the spine appears as an extension of a crest behind the median node.

The basal lobes nest in recesses of the posterior part of the glabella; they are composite and knobbly, and the left and right lobes can be different in appearance, as seen in a cephalon published by Westergaard (1946, pl. 12, fig. 14).

The pygidia are variable in shape, but none has been found as elongate as in the illustration of the holotype (Brögger, op. cit., pl. 5, fig. 1); but a similarity with the pygidium from Krekling (Howell, 1935, fig. 2) and the Swedish pygidia (Westergaard, op. cit., figs. 15 and 16 but not fig. 13) is evident; the short pygidial marginal spines are usually deflected but also retral as in Plate 60, fig. 1. The pygidial axis is variable, 0.75-0.8x the shield length; the flanks of the posterior lobe are convex, and the axis itself is usually broad, but can also be relatively slender, but not as slender as in *Goniagnostus scarabaeus*. In a slender axis (Pl. 61, figs. 5 and 6) the posterior attenuation and the transverse depression in the rosette are clearer than in the plump ones. The anterior axial lobe is tripartite, with tumid lateral lobules and a median lobule; in the second lobe the median node is a prominent rearward upsloping ridge passing into the axial spine; the base of the spine straddles the second transverse furrow but intrudes the posterior lobe for a short distance only.

The test is granulose; this ornament is usually stronger in the pygidium than in the cephalon, and absent or subdued in the axis of the exoskeleton; but it can be present all over the cephalon, as seen in Plate 60, fig. 4.

Comment on illustrated specimens

The five specimens (four exoskeletons and one cephalon) described below have been obtained from locality M57, the top of the V-Creek Limestone.

The exoskeleton Plate 61, fig. 1, CPC 14328, is 6.8 mm long; it is fractured and has been singed in a fire. Its cephalic spines are short and the pygidial marginal spines are short and deflected; the stumps of the occipital and axial spines are clear; the triangular fulcral spines are prominent but short; the node on the posterior axial lobe seems too large owing to over-whitening of the specimen with magnesia; the sulcus in the front of the glabella is shallow. The ornament on the pleural lobes of the pygidium is visibly stronger than on the cheeks. The rear of the posterior axial lobe is deformed and the transverse depression is obscure. The pygidial axis, 0.8x the shield length, is quite long.

The exoskeleton Plate 60, fig. 3, CPC 14325, is 6.9 mm long. The glabellar flanks are somewhat convex; a frontal sulcus seems absent; the glabellar culmination is marked by a low node; the axial (occipital) spine is indicatd by its stump; the left basal lobe is double (knobbly); the pygidial axis, about 0.73x the shield length, is short but broad; the ornament is weak.

The exoskeleton Plate 60, fig. 1, CPC 14323, is 6.3 mm long. The glabella is deformed on its left, but the frontal sulcus is indicated; the median node on the culmination and behind it the stump of the occipital spine are visible. A slender axial spine on the second segment of the thorax is partly preserved. The pygidial axial rear is attenuated and its rosette is clear.

The exoskeleton Plate 60, fig. 2, CPC 14324, is 6.3 mm long. The left lateral glabellar furrow consists of two clear pits. The left basal lobe is weakly subdivided, but the right lobe is triple with a small intervening swelling between the two main bosses. The occipital collar is exposed. The pygidial axis, 0.76x the shield length, is broad, attenuated in the rear, and provided with a transverse depression.

The cephalon Plate 60, fig. 5, CPC 14327, is 2.6 mm long; the preparation displays the glabellar culmination and the occipital spine behind it.

The cephalon Plate 60, fig. 4, CPC 14326, locality M416 (top of the V-Creek Limestone) is 3.3 mm long to the tip of the occipital spine; a low crest connects the spine with the median node. The frontal sulcus is indicated; the posterior part of the basal lobe is large; the test is granulose all over (the glabella included).

Two pygidia, selected from a large supply in collection M57, are described next.

The pygidium Plate 61, fig. 6, CPC 14333, is 2.8 mm long; the axis, 0.75x the shield length is attenuated, and the rosette (transverse depression with the node) is clear.

The pygidium Plate 61, fig. 5, CPC 14332, is 2.5 mm long; the rosette is clear; it differs from fig. 6 by a slightly more retral position of the node in the posterior axial lobe.

The pygidium Plate 61, fig. 4 (also Pl. 47, fig. 6), CPC 14331, V-Creek Limestone, locality M214, is 3.0 mm long. The axial tip is blunted by fractures. The median axial node (the base of the axial spine) straddles the posterior transverse furrow; a pair of pits (possibly apodemes) are visible in the anterior transverse furrow close to the anterior of the median axial node.

The cephalon Plate 61, fig. 3, CPC 14330, is 3.0 mm long. The matrix is red sandstone (Split Rock Sandstone, Barkly Highway), east of Waroona Creek, locality M276, Camooweal area. The cephalic spines are short.

Occurrence and age: Goniagnostus (Goniagnostus) nathorsti in Australia is a fossil of the V-Creek Limestone, Split Rock Sandstone, and Roaring Siltstone (Öpik, 1961b, p. 84). It occurs first in association with *Ptychagnostus punctuosus*; after the disappearance of the latter, *G. nathorsti* becomes rather frequent, even abundant, and marks the *G. nathorsti* Zone. Briefly, it is absent in the early Undillan and prevails in the two later zones of that stage.

Goniagnostus (Goniagnostus) nathorsti intersertus subsp. nov.

(Pl. 61, fig. 7)

Material: One exoskeleton, the holotype, CPC 14334, is illustrated; the collection contains also the counterpart of the holotype, another exoskeleton, and one isolated cephalon, all in one piece of singed limestone.

Diagnosis: Goniagnostus nathorsti intersertus is a form with evenly tapering glabella and a broad pygidial axis distinguished by the absence of a rosette and of the transverse depression and attenuation in the rear of the pygidial axis and by somewhat extended pygidial marginal spines.

Differential diagnosis: G. nathorsti intersertus is similar to such specimens of *nathorsti* as have a weak transverse depression in the pygidial axis, as for example Plate 61, fig. 1; in these, however, the rear of the pygidial axis is attenuated and the marginal pygidial spines are short. The extended marginal pygidial spines in the subspecies *intersertus* recall also *Goniagnostus scarabaeus,* whose glabella, however, is less trigonal and the pygidial axis even more slender and is equipped with a rosette. The simplicity of the pygidial structure is about the same as in *Criotypus lemniscatus* (p. 147), but even in this species some attenuation of the pygidial axis rear is evident.

Description: The holotype exoskeleton is 5.1 mm long (in the counterpart); the cephalic spines are, apparently, extended (in the counterpart) and longer than in the main form of *nathorsti*; the basal lobes are knobbly (double); the pygidial pleural lobes are minutely granulose and the cephalic test is smooth.

The exoskeleton associated with the holotype is 7.0 mm long; its cephalon is 1.1x the pygidium in length.

Occurrence and age: The matrix is a splintery dark bituminous limestone, collected at about M118, west of M64, and attributed to the top of the Currant Bush Limestone; its age is Undillan, the Zone of *Ptychagnostus punctuosus* (about the arrival of *Goniagnostus nathorsti*).

Goniagnostus (Goniagnostus) scarabaeus Whitehouse, 1939

(Pl. 61, figs. 2 and 8; Pl. 62, figs. 1 and 2; Text-fig. 49)

Material: Illustrated are three exoskeletons from different sites, and one isolated cephalon; three more specimens (one cephalon and two exoskeletons) provided some supplementary morphological information and are included in the paradigm without being themselves illustrated. The revision of *G. scarabaeus* as presented here is based on the collection from locality M462, of about ten exoskeletons and fifteen isolated shields; no other species of *Goniagnostus* is present and the supply in hand indicates therefore the presence of a local pure population of *G. scarabaeus.* In passing, a single cephalon of *G. scarabaeus* has been observed in association with *Goniagnostus verus* sp. nov.

Holotype: Whitehouse (1939, p. 25, fig. 19) illustrated a single exoskeleton and designated it as the holotype.

The distinguishing characters of *Goniagnostus scarabaeus* are: (1) the moderately extended and slightly curved pygidial marginal spines seen in

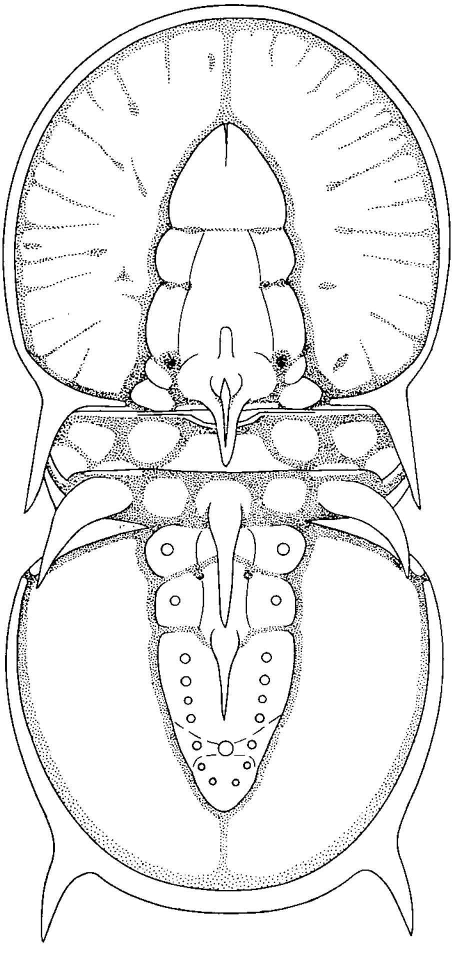

Fig. 49. *Goniagnostus (Goniagnostus) scarabaeus.*

the illustration of the holotype; (2) the relatively slender pygidial axis; and (3) the broad and moderately tapering glabella and the convex flanks of its frontal lobe. These characters are included in the original descriptive diagnosis (Whitehouse, op. cit., p. 260) and are sufficient to identify the species.

An enlarged photograph of the holotype has been published by Hill et al. (1971, pl. 9, fig. 8); it seems that some of its surface has crumbled off; nevertheless the characters of the species as described here are recognisable with the aid of Whitehouse's original illustrations and description.

Differential diagnosis: Goniagnostus scarabaeus Whitehouse, 1939, differs from *G. nathorsti* (Brögger, 1878) by its stronger spines (cephalic, fulcral, and pygidial), and shapes of the glabella and the pygidial axis; it is quite probable that the agnostid attributed by Pokrovskaya (1958, pl. 5, figs. 13-15) to *G. nathorsti* represents *G. scarabaeus* in Siberia; and that material described by her as *G. longispinus* sp. nov. contains also *scarabaeus*-like exoskeletons.

Description: Goniagnostus scarabaeus has attained a length around 10 mm as seen in the holotype, which is the largest known exoskeleton. The cephalon is slightly longer than the pygidium and the thorax is about 0.27x the cephalon in length. The cephalon and pygidium are more or less semielliptical in outline, but the 'subquadrangular' shapes occur in larger specimens (Whitehouse, op. cit., p. 260). The rim in the cephalon is narrow (as in all Ptychagnostinae) and in the pygidium it is a little wider. The spinosity of rim spines is well expressed, the cephalic spines are about half the glabella in length, the axial (occipital) spine extends to the middle of the thorax, and the axial spines (in the thorax and pygidium) are of only moderate length. The fulcral spines are prominent, with a wide and tumid base, divergent and curved, and with tips reaching the level of the anterior transverse furrow of the pygidial axial lobe; the pygidial marginal spines are placed well rearward (a resemblance to *Criotypus oxytorus*), extended, and as curved as the fulcral spines.

In the cephalon the scrobicules are well impressed and dimpled adaxially but can also be shallow occasionally. The frontal glabellar lobe is subtrigonal with convex flanks, mostly acute and sulcate in front. The posterior lobe tapers moderately forward, and its flanks are expanded between the transverse and lateral furrows. Each lateral furrow has a pair of apodemal pits and is quite deep; the posterior apodemal pits are visibly deep; the midmost glabellar ridge (see Text-fig. 45) is clear and the occipital spine attenuated. The basal lobes are double but occasionally almost confluent on one or other side of the glabella.

In the pygidium the axis is about 0.8x the shield length and in its posterior lobe the transverse depression, the node, and the attenuation of the rosette are clear; the axial tip is narrowly rounded. About nine pairs of muscle spots are discernible on the pygidial axis.

The pygidial pleural lobes are densely granulated; the cephalic test seems smooth to almost imperceptibly granulose.

Comment on illustrated and not illustrated specimens

All specimens came from the V-Creek Limestone. The following specimens have been selected from collection M462.

The exoskeleton Plate 61, fig. 8 and Plate 62, fig. 1, CPC 14335, is 7.0 mm long. The characteristic pygidial marginal spines are as clear as in the holotype; the proximal part of the left cephalic spine and the axial spines in the thorax and pygidium are represented by stumps; the left fulcral spine in the displaced posterior segment of the thorax is partly concealed by the matrix; after photographing, both spines were dematricated and appear almost intact as shown in Text-fig. 49. These spines can be mistakenly interpreted as falcate pleural tips (see text-fig. in Whitehouse, op. cit., p. 260). The muscle spots in the pygidial axis are low swellings; a pair of pits is evident at the flanks of the median axial node in the anterior transverse furrow. In the cephalon the scrobicules are shallow, the basal lobes are double.

The cephalon Plate 61, fig. 2, CPC 14329, without the occipital spine is about 3.0 mm and with the occipital spine 3.5 mm long; the node and the crest are quite prominent; the cephalic spines are long but not specially dematricated. The scrobicules are normal and well impressed.

In the incomplete exoskeleton, collection M195, CPC 14384, not illustrated (a cephalon with attached thorax), the cephalon is 2.8 mm long; the thorax is 0.27x the cephalon in length; its fulcral spines are preserved.

The unillustrated exoskeleton CPC 14385, 6.5 mm long, is almost undeformed but a larger part is about as long as 0.4-0.5x the glabella.

The exoskeleton Plate 62, fig. 2, CPC 14336, locality M247, is 7.3 mm long; the scrobicules are deep and terminate adaxially in dimples; the characteristic marginal pygidial spine (subsequently dematricated) is preserved on the right side; the granulosity of the pygidial pleural lobes is prominent and the cephalic test seems smooth. The tagmata are in perfect articulation contact.

The exoskeleton (not illustrated) CPC 14386, locality M409, is 5.0 mm long; singed in a fire, it lost some of its parts. The frontal sulcus is prominent.

Occurrence and age: Goniagnostus (Goniagnostus) scarabaeus comes from the V-Creek Limestone; it arrives in the Undillan Zone of *Doryagnostus notalibrae* about the end of the lifetime of *Ptychagnostus punctuosus* (at M409) and survives it into the Zone of *Goniagnostus nathorsti.*

Goniagnostus (Goniagnostus) verus sp. nov.

(Pl. 62, figs. 3-5; Pl. 63, figs. 1 and 2; Text-fig. 50)

Material: Illustrated are two exoskeletons, two cephala, and one pygidium; these are selected from a total of some 15 exoskeletons and 45 isolated shields—all in a single layer of limestone. The material in hand can be regarded as a supply from a local population to the species; it is associated with the contemporaneous *Goniagnostus scarabaeus* Whitehouse, represented by a single cephalon as mentioned in the concluding comment.

Holotype: The exoskeleton Plate 62, fig. 3, CPC 14337, is selected as the holotype.

Diagnosis: Goniagnostus verus is a species with a relatively broad glabella and a slender pygidial axis and prominent fulcral spines in the second segment of the thorax, distinguished by the combination of long cephalic and very short pygidial marginal spines and by the absence of a node and of a carina in the occipital culmination in front of the occipital spine.

Differential diagnosis: In *Goniagnostus nathorsti* and *G. scarabaeus* a node and an occipital carina are present; in *G. nathorsti* the cephalic spines are short, the fulcral spines are not extended, and the pygidial axis is broad; in *G. scarabaeus* the pygidial marginal spines are extended, but its pygidial axis is also relatively slender.

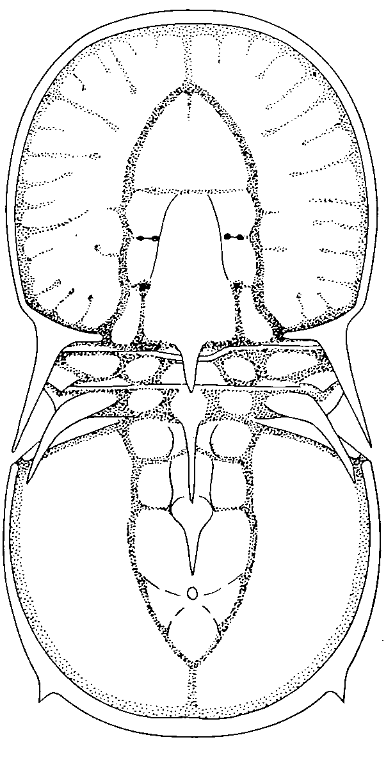

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Fig. 50. *Goniagnostus (Goniagnostus) verus.*

Description: Goniagnostus verus is a relatively small agnostid: the shortest exoskeleton in the collection is 3.0 mm and the longest about 7.0 mm; isolated shields indicate lengths about 8.0 mm. The cephalon is as long as the pygidium and about one-half of the posterior segment of the thorax; the thorax is 0.23-0.25x the cephalon in length.

In the cephalon the scrobicules begin as dimples and the rugae are prominent. The frontal glabellar lobe, about 0.4x the glabella in length, is bluntly pointed and its frontal sulcus is shallow but distinct; the lobe itself is trigonal but its flanks can be slightly concave in the middle as seen in undeformed cephala (Pl. 63, fig. 2). The posterior glabellar lobe has subparallel flanks, which, however, are angulate in front and contracted about the posterior apodemal pits. The described shape of the glabella (concave flanks of the frontal lobe and the posterior contraction) is apparently characteristic of the species. The lateral glabellar furrows are deep, with a pair of apodemal pits each, and the midmost glabellar ridge is distinct. In profile, the posterior glabellar lobe rises up in a concave slope to a prominent culmination without a perceptible median node and without a crest. The occipital spine extends over the anterior segment of the thorax and rises rearward in conformity with the glabellar profile; it is a delicate structure and is bent (hanging) down in some specimens. The basal lobes are knobby—double as well as close to simple even in one and the same shield.

In the pygidium the axis is visibly slender, resembling *G. scarabaeus* and especially some specimens of *Goniagnostus nathorsti* (Pl. 61, figs. 5 and 6) whose marginal spines are also short; properly preserved isolated pygidia of *G. verus* are, however, granulose all over, but in *G. nathorsti* the axis is smooth.

The test of *G. verus* is granulose; even the cephalon (Pl. 63, fig. 2) is granulose all over.

Comment on illustrated and other exploited material

The matrix is limestone, locality M195.

The holotype exoskeleton is 6.0 mm long; the fulcral spines in the second segment of the thorax were lost during dematrication; the short pygidial marginal and long cephalic spines are evident.

The exoskeleton Plate 62, fig. 5, CPC 14339, 6.4 mm long, is a little deformed; the frontal sulcus is indicated.

The flattened cephalon Plate 63, fig. 1, CPC 14340, is about 3.0 mm long. The absence of a median glabellar node and of an occipital carina is evident; the axial spine on the glabellar rear is relatively long.

The cephalon Plate 63, fig. 2, CPC 14341, is about 3.2 mm long. It is uncompressed; the frontal glabellar sulcus, the left cephalic spine, the proximal part of the occipital spine, the apodemal pits (paired in the lateral furrows), and the tips of the axial lobes and the occipital aperture are clear; the test is granulose all over.

The pygidium Plate 62, fig. 4, CPC 14338, is about 2.7 mm long. Notulae are evident on each of the anterior annulations; the rosette is clear.

The following material included in the collection of types contains specimens exploited in the description of *Goniagnostus verus*:

(1) An exoskeleton CPC 14387: it is 3.5 mm long and has preserved the diagnostic structures of the species. It is associated with a 2.2 mm-long cephalon attributable to *Goniagnostus scarabaeus* on evidence of the occipital structure (median node and crest, as in Pl. 61, fig. 8).

(2) An exoskeleton CPC 14388: it is 5.6 mm long, and the occipital cephalic and fulcral spines are preserved; associated is another, defective, exoskeleton and isolated cephala and pygidia.

(3) The exoskeleton of *Tomagnostella nepos* CPC 14389, is associated with two exoskeletons of *G. verus.*

(4) The illustrated specimen of *Tomagnostella nepos* Plate 67, fig. 5, CPC 14361, is associated with a mould of *G. verus* displaying its spinosity in full, as shown in Text-fig. 50; it is 5.0 mm long.

Occurrence and age: Goniagnostus (Goniagnostus) verus has been collected so far from a single locality in a limestone (attributed to the Currant Bush Limestone), M195. Its age is the late Undillan Zone of *Goniagnostus nathorsti.*

Subgenus **Goniagnostus (Allobodochus)** nov.

Goniagnostus fumicola (Öpik, 1961) is herein designated as the type species of *Allobodochus.*

Goniagnostus (Allobodochus) spiniger (Westergaard, 1946)

(Plate 63, figs. 3-8)

The holotype of *spiniger,* by original designation, is the cephalon published by Westergaard, and supplemented by a pygidium (Westergaard, 1946, pl. 12, figs. 18 and 19).

According to Westergaard (op. cit., p. 82) the species was published by him in 1931 under the name of *Agnostus nathorsti spiniger;* the full description with illustrations, generic identification, and the rank of species followed in 1946.

The occurrence of *Goniagnostus spiniger* in Australia has been mentioned previously by Öpik (1967, p. 90). The fragmentary pygidium described by Öpik (1961b, p. 84, pl. 21, fig. 1, and text-fig. 30) as *Ptychagnostus* (*Goniagnostus*) sp. P aff. *nathorsti* most probably belongs also to *spiniger;* its reconstruction (ibid., text-fig. 30) postulates short marginal spines, which, however, are not preserved in the specimen itself.

Description

The three following specimens are in limestone from T87, Tobermory Sheet area, NT. The age is Boomerangian, the Zone of *Leiopyge laevigata.*

The cephalon Plate 63, fig. 5, CPC 14343, is 4.3 mm long; a part of it is lost, but the rest is uncompressed, preserving the evenly curved margin seen in the holotype (Westergaard, 1946, pl. 12, fig. 18). The middlemost glabellar ridge is prominent, abutting in front against the shallow middle part of the transverse glabellar furrow, and is posteriorly confined by the glabellar furrows and basal lobe as in the holotype and in *G.* (*Criotypus*) *lemniscatus* (Text-fig. 45); the frontal glabellar lobe is typical—pointed and narrower than the glabella behind it. The glabellar culmination is defective; the glabellar rear, however, retains its steep and retral slope exposing the occipital collar (as in the holotype). The preglabellar median furrow is clear and straight.

The cephalon Plate 63, figs. 3 and 4, CPC 14342, is 4.0 mm long; it is flattened and dilated and has therefore lost the original curvature of the margin. The scrobiculation of the cheeks does not differ from the preceding specimen and the holotype, but the flanks of the glabella are angular in front and behind the glabellar lateral furrows—more than in the preceding specimen, which is closer to the holotype. In the very rear of the glabella a small projection is left over from a faint median keel. The apodemal pits are clear and in position seen in Text-figure 45. The basal lobes are large, tumid, and simple, and the cephalic spines are typically long. The test is granulose.

The pygidium Plate 63, fig. 6, CPC 14344, is 4.7 mm long; it is fragmentary, having lost its marginal spines. It differs from the holotype in having the flanks in the posterior axial lobe slightly convex (in the holotype the flanks are straight); in the rosette the transverse furrow is well defined, the node on its floor is visible, and behind it the secondary triangular lobe is tumid; the axis is quadrilobate. The test is granulated more strongly than in the cephalon.

For the specimens above, the locality is T87, Tobermory 1:250 000 Sheet area, Northern Territory. The age is Boomerangian, the Zone of *Leiopyge laevigata.*

The cephalon and the pygidium that are described below have been selected from the Steamboat Sandstone, D54 (Öpik, 1967, part 2, p. 14); other localities are D96 and G106 (op. cit., part 1, p. 90). The matrix is friable reddish sandstone and the sandgrains mask detail structures of the fossils; the tests are leached. The age is Boomerangian, the Zone of *Leiopyge laevigata.*

The cephalon Plate 63, fig. 7, CPC 14345, is 3.5 mm long; its rugosity and a part of its left spine are recognisable.

The pygidium Plate 63, fig. 8, CPC 14346, is 4.0 mm long; the axis is trigonal with straight flanks, the transverse depression is clear and long spines are indicated.

Concluding remarks: The available material of *Goniagnostus* (*Allobodochus*) *spiniger* remains inconclusive regarding the presence or absence of an occipital spine.

Genus **Leiopyge** Hawle & Corda, 1847

The type species of *Leiopyge,* as originally designated by Corda, is *Battus laevigatus* Dalman, 1828; Westergaard (1946, pp. 87-89, pl. 13, figs. 18-27; pl. 16, fig. 9) in revising the species and its genus illustrated three syntypes from the Dalman paradigm and selected as the lectotype a cephalon (op. cit., pl. 13, fig. 21).

The Australian material of *Leiopyge laevigata* has been described and the systematics of *Leiopyge* discussed by Öpik (1961b, pp. 85-87; and 1967).

Regarding the systematics of the species attributed and attributable to *Leiopyge* the following remarks should be considered: (1) the subfamily Ptychagnostinae for these species is indicated by their morphology; (2) within the genus effacement of external features, in various degrees, is prevalent and effaced forms cannot serve in constructing comprehensive suprageneric concepts, but should be classified according to concepts based on forms en grande tenue; and (3) the genus name *Leiopyge* Hawle & Corda 1847 has nomenclatorial priority over other generic names of the Ptychagnostinae (Öpik, 1961b, p. 85) and will prevail in lists of subjective synonyms. In passing, the spelling *Leiopyge* and not *Lejopyge* is employed here for the following reasons: (1)

the word is classical Greek in Latin translation, and (2) 'i' (iota) cannot be expressed by 'j' which is unknown in Latin and Greek alphabets.

The notion of the derivation of *Leiopyge* by a process of gradual progressive effacement from *Triplagnostus* in general terms is no taxonomic character because *Triplagnostus,* as revised in this paper, and *Leiopyge* belong to two different stocks of the Ptychagnostinae; nevertheless, Westergaard's (1946) conception of the phyletic series beginning with *'Triplagnostus' elegans* over *'T'. elegans laevissimus* and passing to *Leiopyge laevigata* should be accepted, with the inclusion of *'T'. lundgreni* and *'T.' lundgreni nanus* as well. These forms are excluded from *Triplagnostus* and regarded here as belonging to the genus *Leiopyge* itself; the phyletics of this stock, however, has been veiled in the literature by the liberal and unqualified reference of these forms to *Triplagnostus.*

Concept of the genus Leiopyge (compiled herein)

Diagnostic of *Leiopyge* is the combination of the following characters: (1) The glabella is elongate, oval, tapering evenly forward, and pointed in front; its flanks are gently convex; the confining axial furrows, when not effaced, are continuous without change in direction at the ends of the transverse glabellar furrow. (2) The basal lobes in all known species are simple. (3) The median glabellar node is very small. (4) The preglabellar median furrow is present, or vestigial, or absent depending on the grade of effacement. (5) The cheeks are smooth or sporadically rugose, but the incidence of rugosity seems independent of the grade of effacement. (6) In the pygidium the axis is trilobate and pointed in the rear, but the axial furrows behind the anterior pygidial annulation in effaced forms can be vestigial or even obliterated; the same applies to the transverse furrows and the postaxial median furrow. (7) The median node on the second axial lobe is low and small, and vestigial in effaced forms. (8) The median node on the posterior axial lobe is mostly absent, but when discernible is placed in front of or behind the midpoint of that lobe. (9) As a generality, the cephalon is as long as the pygidium and the posterior segment of the thorax taken together; the thorax is short, 0.22-0.26x the cephalon in length, depending on the species. (10) The cephalon is strongly and the pygidium moderately convex. (11) The glabella and the pygidial axis are only a little elevated above the general arch of the acrolobes; but (12) in effaced forms this relief is lost with the exception of the glabellar rear and the front of the pygidial axis in proximity to, and homology with, the thorax, which is not subject to effacement; retained are the fulcral points, the basal lobes, the circumoccipital furrow, and the shoulder furrow (in the pygidium). (13) Axial spines and fulcral spines developed from prongs are absent in most of the species; in spinose species the fulcral spines are extended and an axial spine is present in the second segment of the thorax; the rears of the glabella and of the pygidial axis have no spines. (14) The process of effacement is progressive in individuals; in early instars (Text-fig. 51) of *Leiopyge praecox* the cephalic furrows and lobes are clear, but become obliterated in subsequent instars; a similar progressive effacement is apparent also in the temporal sequence of species as a phylogenetic trend; this, however, is not demonstrable in detail because similar grades of effacement are out of step in concurrent lineages. (15) The effacement is confined to the integument; no other organs, however, are involved: for example, the caecal prosopon may be absent but the caecal apparatus remains functional as seen in *Leiopyge laevigata,* Plate 64, figs. 1 and 2.

The original diagnosis of *Leiopyge* by Hawle & Corda (1847, p. 51) is in need of no amendment, nor is the extended diagnosis by Robison (1964, p. 521); an abridged diagnosis is also given by Howell (*in* Harrington et al., 1959, p. 0178). In these the effacement is regarded as the paramount character of the genus. It is consequently a restrictive diagnosis and if so applied, forms with clear furrows (*elegans* and *lundgreni*) included in the concept of the genus may be taken as species of an unnamed subgenus of *Leiopyge.*

Among the genera postdating the name *Leiopyge* (1847), *Onymagnostus* nov. as regards the outline of the glabella recalls *Leiopyge,* but has a different pygidial structure and has not been involved in a process of progressive effacement. The vestigial structures of the pygidial axis observed in *Leiopyge armata* (p. 161) and the spinosity of its exoskeleton, especially the extended fulcral spines of the second segment of its thorax, recall for example an *Aristarius.*

Within the spineless stock of *Leiopyge* a high degree of effacement evolved twice in two separate lineages and at different times: in the main and conspicuous lineage (from *L. elegans* to *laevigata*) the effacement was attained late in the Middle Cambrian; in the 'lesser' lineage, however, it is manifest in *Leiopyge praecox* some two zones earlier. To speculate, the lesser lineage maintained its continuity in the species of the genus *Pseudophalacroma* (p. 163).

Leiopyge armata and *L. multifora* nov. seem to indicate a separate lineage conserving an ancestral spinosity.

Leiopyge praecox sp. nov.

(Pl. 66, figs. 1-7; Pl. 41, fig. 1; Text-fig. 51)

Material: Illustrated are four cephala and two pygidia; the total number of examined shields is ten—all from a single bed of limestone.

Holotype: The cephalon Plate 66, fig. 1, CPC 14353, is the largest available and selected as the holotype.

Diagnosis: Leiopyge praecox is a spineless species in an advanced grade of effacement, distinguished by its subdued basal lobes, by its circumglabellar furrow confined to its rear, erased or rarely vestigial glabellar median, and pygidial axial median node, and a faint cephalic, and a relatively broad pygidial rim.

Differential diagnosis: Structurally the nearest species is *Leiopyge laevigata,* which, however, is effaced in a lesser degree, showing vestiges of the axial furrows, conspicuous basal lobes, and median nodes, and whose pygidial rim is narrower than in *L. praecox.* Stratigraphically, *Leiopyge praecox,* of the Zone of *Ptychagnostus punctuosus,* is the earliest effaced species of its genus, visibly more effaced than the younger *Leiopyge laevigata* — both representing inpendent lineages.

In the small (1.1 mm long) and immature cephalon Text-figure 51, the furrows are not yet effaced and the glabellar median node (more forward than in *L. laevigata*) resembles large cephala of *'Triplagnostus' elegans* (Tullberg) Westergaard (1946, pl. 10, figs. 11, 13, 17); the pygidial rim in *Leiopyge elegans* and in its relation *L. lundgreni* is much narrower than in *Leiopyge praecox.*

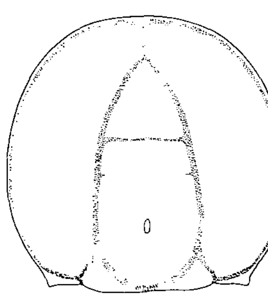

Fig. 51. *Leiopyge praecox.*

Finally, *Leiopyge praecox* resembles also *Pseudophalacroma crebrum* Pokrovskaya (1958) and *Pseudophalacroma dubium* (Whitehouse, 1936) regarding the structure of the cephalon and the pygidial rim, but differs from these in the shape of the pygidium; moreover, *P. crebrum* still shows the outline of the pygidial axis and *P. dubium* possesses the cephalic and pygidial median nodes which are not evident in *praecox.* At all events these characters are specifically diagnostic and only the different pygidial shapes separate the genera from each other.

Description: Leiopyge praecox attained a length of not less than 8.0 mm, as indicated by the size of its holotype. In the cephalon, which is strongly convex, almost circular to slightly oval, the rim is extremely narrow and the marginal furrow faint; the surface is smooth and featureless except for a vestige of the preglabellar median furrow and the circumglabellar furrow which does not extend forward beyond the tips of the basal lobes; these lobes are low and small; the cephalic spines are inconspicuous triangular posterior extensions of the rim. The connective band in the rear of the cephalon is narrow and almost vertical and the arc of the cephalic aperture in it is low (collapsed in Pl. 66, fig. 4).

In the pygidium the outline is close to circular, the rim is moderately wide and convex, and the marginal furrow deep; it joins the shoulder furrows at the anterodorsal corners without cutting the rim. The acrolobe is convex (less than the cephalon), a little constricted about the middle, and its margin overhangs the adaxial part of the marginal furrow. Of the axial furrows only the foremost parts are retained; the rest of the acrolobe is featureless.

A clear ornament is not evident in the test except for an almost imperceptible and erratic granulation reflecting the punctation of the parietal surface of the cephalic test and indicated in its turn by the dense papillosity of the mould of that surface.

Comment on illustrated specimens

The holotype cephalon is 4.0 mm long, indicating an exoskeleton about 8.0 mm in length. The test is thin and partly preserved; its parietal punctation is reflected in the papillosity of the internal mould; in the illustration the vestigial glabellar node is brought to light. The rim is distinct but extremely narrow; the preglabellar median furrow with its frontal flare shows up from under the test; the left acrolobe shows some stylolite scratches.

The cephalon Plate 6, figs. 3 and 4, CPC 14355, is 3.5 mm long; the test on the right side seems rugose; in the view from the rear (fig. 4) the low relief of the basal lobes is apparent.

The cephalon Plate 66, fig. 2, CPC 14354, is 1.9 mm long; the basal lobes seem clear.

The cephalon Text-figure 51 and Plate 41, fig. 1, associated with *Ptychagnostus punctuosus fermexilis*, is 1.1 mm long; it is discussed in the differential diagnosis.

The pygidium Plate 66, figs. 6 and 7, CPC 14357, is 2.2 mm long; in rear view the overhang of the margin of the acrolobe over the marginal furrow is evident; the articulating half-ring and furrow are short (longitudinally).

The pygidium Plate 66, fig. 5, CPC 14356, is 2.5 mm long.

Occurrence and age: The described material of *Leiopyge praecox* has been found in the Inca Formation, at locality D155; its age is the early Undillan Zone of *Ptychagnostus punctuosus* (before the arrival of *Goniagnostus nathorsti*).

Leiopyge cosfordae sp. nov.

(Pl. 65, figs. 1 and 2; Text-fig. 52)

Material: The examined material consists of eight exoskeletons and about twelve isolated shields all in a single bed of limestone.

Holotype: The holotype is the illustrated exoskeleton, CPC 14350.

Diagnosis: Leiopyge cosfordae is a species without axial and pygidial marginal spines, with very short cephalic and fulcral prongs, with the pygidial axis attenuated in its rear and a wide pygidial rim; distinguished by its generally effaced habit but retaining the contours of its lobes defined by the delicate, faintly engraved, full set of furrows.

Differential diagnosis: The wide pygidial rim recalls *Leiopyge praecox,* which is, however, much more effaced than *L. cosfordae; Leiopyge laevigata* is also well effaced but its pygidial rim is narrow; *L. armata* and *L. multifora* are distinct by their spinosity. Finally, *Leiopyge elegans* (Tullberg) (Westergaard, 1946, pl. 10, figs. 11-20) resembles *L. cosfordae* regarding the axial design (including the attenuation of the pygidial axis), but its furrows are deeper, the pygidial axis is longer, and the pygidial rim is very narrow. In passing, *Leiopyge praecox* and *L. cosfordae* belong to diverse lineages because the latter is effaced visibly less than the stratigraphically older *L. praecox*.

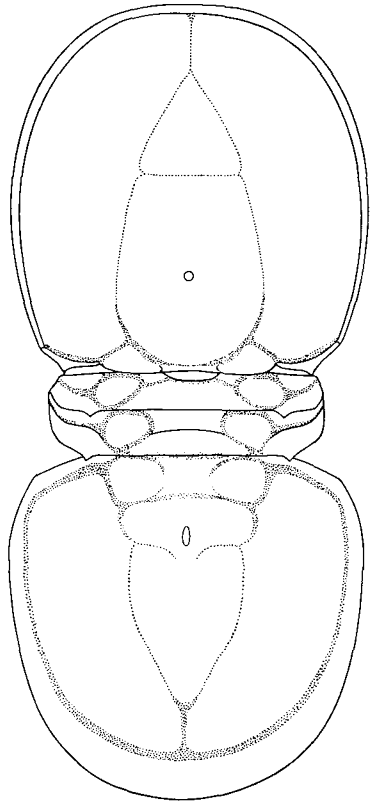

Fig. 52. *Leiopyge cosfordae.*

Description: The holotype of *Leiopyge cosfordae* is 6.0 mm and the largest exoskeleton in the collection is 8.0 mm long. The cephalon is as long as the pygidium together with half the length of the posterior segment of the thorax; this seems a discrepancy in respect of the usually observed length (cephalon = pygidium with a segment); the pygidial rim, however, is exceptionally wide (about twice the normal for the Ptychagnostinae) and the discrepancy resolves as follows: the cephalon is as long as a segment of the thorax, together with the pygidium with one-half its rim. The thorax is about 0.22-0.23x the cephalon in length.

The margins of the shields are evenly rounded, the cephalon is prominently tumid, stronger than the pygidial acrolobe. The marginal furrows in the shields are clear and moderately deep but the furrows defining the lobes are generally narrow and shallow.

In the cephalon the rim is convex and thread-like narrow; the cheeks are smooth except for indistinct peripheral scrobicules; the preglabellar median furrow is faint. The glabella is elongate oval and pointed in front and its flanks are gently and evenly convex. The frontal glabella lobe is about 0.37x the glabella in length and the transverse glabellar furrow is evident on the internal cast. The circumoccipital furrow is clear and the glabellar rear is evenly tumid; the median node, a little behind the midpoint of the posterior glabellar lobe, is very small but distinct. The basal lobes are simple, triangular, swollen, and defined by well impressed furrows. The cephalic spines are small triangular blades hiding in the shadows of the tumid rear of the acrolobe.

In the pygidium the rim at the anterolateral corners is continuous with the shoulders; the axis, 0.7x the shield length, seems short on account of the width of the rim. The anterior axial lobe is well defined and even its lateral lobules are indicated; the second lobe is also clear but its median node is suppressed; the posterior axial lobe is slightly attenuated in its posterior third; the position of its median node, however, cannot be established owing to the corrosion of the surface in all examined specimens. The postaxial median furrow is shallow but complete. The test is minutely punctate but otherwise smooth.

Occurrence and age: Leiopyge cosfordae is known only from locality M195, in limestone attributed to the Currant Bush Limestone; its age is the late Undillan Zone of *Goniagnostus nathorsti* (after the disappearance of *Ptychagnostus punctuosus*).

Leiopyge laevigata (Dalman, 1828)

(Pl. 64, figs. 1-3)

The illustrated cephalon, CPC 14347, in limestone supplements the earlier description of Australian material (Öpik, 1961b, pp. 85-87; pl. 21, figs. 5-9) of *Leiopyge laevigata;* the cephalon is about 4.0 mm long. In the internal cast (decorticated and dorsum up) in limestone (Pl. 64, fig. 3) the cheeks are smooth without rugosity and scrobicules; the whitened parietal surface of the test (Pl. 64, fig. 1) is also free of rugae and scrobicules but bears the rather faint intaglio of the glabella, including the pointed frontal lobe which is sulcate in front, muscle spots, and the median node in the posterior lobe. The frontal lobe with its sulcus conforms to the structure of *Leiopyge elegans* illustrated by Westergaard (pl. 10, fig. 13). The same parietal surface has been also photographed without whitening in figure 2. In it the glandular (caecal) system, the confines of the glabella, the median node, and the dark muscle spots are preserved in dark and light coloration but without any relief (see Westergaard, op. cit., p. 134, pl. 13, fig. 35). A median line beginning with the 'preglabellar median furrow' and passing rearward beyond the median node indicates a bi-partition of the cephalon by a median supporting mesentery of soft tissue. The described anatomy in *L. laevigata* is normal in agnostids (see Öpik, 1961a), effaced and en grande tenue.

Occurrence and age: The described cephalon of *Leiopyge laevigata* has been found in a limestone attributed to the Devoncourt Limestone (Öpik, 1961a, p. 48), locality T87, collection 41618; its age is the Boomerangian Zone of *Leiopyge laevigata.*

Leiopyge armata (Linnarsson, 1869)

(Pl. 64, figs. 5 and 6; Text-fig. 53)

The original name of the form is *Agnostus laevigata* var. *armata.* Westergaard (1946, pp. 89 and 90) interpreted it as a subspecies of *laevigata;* I regard *Leiopyge armata* here as a well defined species taxon whose spinosity is inherited from a less effaced spinose form or a novel modification within the spineless lineage of *Leiopyge laevigata.*

Isolated shields of *Leiopyge armata* from Australia (Queensland) have been described by Öpik (1961b, p. 87) and its occurrence in Tasmania is noted.

Leiopyge armata is distinguished by its spinosity; the cephalic and the fulcral spines in the second segment of the thorax are extended, pygidial marginal spines are present, but of varying length, and axial spines are absent. An exoskeleton resembling *armata* with a short spine on the second segment of the thorax and without fulcral spines is illustrated by N. Tchernysheva et al. (1960, pl. 1, fig. 18) but without naming or explanation; in the text (p. 60) it is mentioned without a species name as an example of the genus *Leiopyge.* Its cephalon, about 1.2x the pygidium in length, is quite unusual regarding its relative size. The specific identity of this Yakutian(?) exoskeleton remains open.

The illustrated exoskeleton, CPC 14349, Plate 64, figs. 5 and 6, is complete but consists of two disunited parts embedded side by side and overturned in relation to each other. As a whole, it is 7.2 mm long. In the cephalon the rim is narrow, the spines are extended, the circumoccipital furrow, the median node, and the basal lobes are typical; peripheral scrobicules and the preglabellar median furrow are

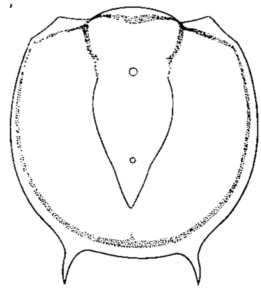

Fig. 53. *Leiopyge armata.*

discernible as vestiges. The thorax is about 0.25x the cephalon in length; the fulcral spines are evident from their stumps but an axial spine is absent.

In the pygidium the rim is wider than in the cephalon, its marginal spines are moderately long and the margin between the spines slopes downward. In the axis the two anterior lobes are slightly indicated and the median axial node is small; behind the node the confining axial furrows are visible as faint dark lines; the posterior axial lobe is discernible; in its anterior half the flanks are convex and the rear is attenuated, and the median node is also visible about the onset of the attenuation. The design of the whole axis can be described as the ghost of a *Goniagnostus* axis, and the rather retral position of the marginal spines recalls *Goniagnostus* (*Criotypus*) *oxytorus.*

Occurrence and age: The described exoskeleton of *Leiopyge armata* was obtained from a bituminous limestone (attributed to the Devoncourt Limestone), locality W36; its age is the Boomerangian Zone of *Leiopyge laevigata.*

Leiopyge sp. nov. aff. **armata**

(Pl. 64, fig. 4)

The only available and illustrated specimen, CPC 14348, is a 2.0 mm-long and well preserved pygidium united with its thorax. In the absence of a cephalon I reserve the naming of the species.

In the pygidium marginal spines are absent as in *Leiopyge laevigata* and *L. multifora;* in the posterior segment of the thorax extended fulcral spines are indicated by prominent stumps, as in *L. armata* and *L. multifora,* but this segment has also a median axial spine unknown in other described species. To conclude, this form is distinguished by the combination of a trispinose posterior segment of the thorax with a spineless pygidium.

Occurrence and age: This unnamed form of *Leiopyge* has been obtained from a bituminous limestone (attributed to the Devoncourt Limestone), locality W36; its age is the Boomerangian Zone of *Leiopyge laevigata.*

Leiopyge multifora sp. nov.

(Pl. 65, figs. 3 and 4; Text-fig. 54)

Material: The available material consists of the two illustrated specimens.

Holotype: The exoskeleton Plate 65, fig. 3, CPC 14351, is the holotype.

Diagnosis: Leiopyge multifora is distinguished by (1) its elongate shield, (2) absence of an external cephalic rim, (3) subdued basal lobes, (4) a spinosity restricted to the extended cephalic and fulcral spines in the second segment of the thorax (Text-fig. 54), and absence of pygidial marginal, and axial spines, and (5) the conspicuous punctation of the test.

Differential diagnosis: Leiopyge multifora cannot be confused with another species; the spinosity recalls *L. armata,* but in the latter the pygidial marginal spines, which are absent in *multifora,* are distinctive. The elongate shields resemble *Pseudophalacroma dubium* (Whitehouse, Öpik, 1961b, p. 93)—a species whose systematic position on account of this similarity should be re-assessed. In passing, Öpik (1961b, pp. 47 and 93) tentatively referred the holotype of *L. multifora* to *Pseudophalacroma dubium.*

Description: The holotype of *Leiopyge multifora* is 7.2 mm long; its thorax is defective and not even reflected in the counterpart; in the pygidium the acrolobe and the rim are disrupted along the marginal furrow and out of their original position, which seems preserved in Plate 65, fig. 4. The narrow doublure exposed in the front of the cephalon should not be mistaken for the rim, which is absent. The median glabellar node is placed well in the rear, and of the furrows the circumglabellar part alone is discernible. In the pygidium the rim is relatively wide and convex; in the axis the anterior lobe is indicated, the median axial node is rather weak, and the node in the posterior axial lobe has about the same position as in *L. armata* (Text-fig. 53). The punctation of the test is well exposed but some of the pits are still plugged by the matrix.

In the specimen Plate 65, fig. 4, CPC 14352, the pygidium is about 4.0 mm long and a little larger than in the holotype. In the thorax an axial spine is absent but the stout base of the right fulcral spine is preserved. In the pygidium the margin of the acrolobe overhangs the marginal furrow and even the inner slope of the rim, decreasing its exposed width, which itself seems also narrower than in the holotype.

Occurrence and age: The described specimens of *Leiopyge multifora*, in bituminous limestone (attributed to the Devoncourt Limestone) locality W36, belong to the Boomerangian Zone of *Leiopyge laevigata*.

Genus **Pseudophalacroma** Pokrovskaya, 1956

Pseudophalacroma is placed here in the subfamily Ptychagnostinae in respect of the structure of its pygidial axis and presumed to constitute a lineage of effaced forms related probably to *Leiopyge;* close to *Pseudophalacroma* is *Leiopyge praecox* sp. nov., which belongs to the Ptychagnostinae, but of a lineage different from *Leiopyge laevigata;* likewise *Leiopyge multifora* and *Pseudophalacroma dubium* differ from each other regarding the structure of the cephala and spinosity but have similar pygidia, in a similar veiling grade of effacement.

The genus *Pseudophalacroma* has been discussed in some detail by Öpik (1961b, pp. 90-94) and classified with the Agnostacea incertae familiae; later on (Öpik, 1967, p. 77) it was placed in the subfamily Quadragnostinae as a form with a wide pygidial border (op. cit., 'Tabular classification'), but with the proviso

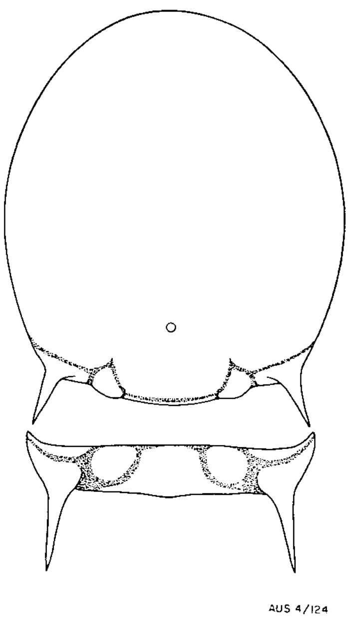

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Fig. 54. *Leiopyge multifora.*

of its constricted pygidial acrolobe. A similar constriction is also apparent in *Peronopsis integra* and in the new *Peronopsis longinqua* and *prolixa* and in *Peronopsis normata* (Whitehouse), which are Quadragnostinae with a wide pygidial border. At the same time a constricted acrolobe became evident in forms attributed to the Ptychagnostinae, in *Onymagnostus durusacnitens* sp. nov. and in *Leiopyge praecox* which combines the constriction of the acrolobe with a border wider than in other ptychagnostids.

The type species of *Pseudophalacroma* is *P. crebrum* Pokrovskaya (1958, pp. 79-80) attributed to the subfamily Leiopyginae (a subjective synonym of Ptychagnostinae according to Öpik, 1967, p. 90). The species is based on three exoskeletons, with the following characters: the cephalon, about as long as the pygidium with the thorax together, is effaced; it has a thread-like narrow rim, no median node; its basal lobes are simple and the glabellar rear defined by the circumoccipital part of the axial furrows. The thorax is short, about 0.22x the cephalon in length. In the pygidium the rim is wide (resembling *Pseudophalacroma dubium*, Pl. 67, fig. 4), but the vestigial axis is characteristically short (shorter than in *dubium*), and a postaxial median furrow seems indicated. The shape of the pygidial axial lobe in *Pseudophalacroma crebrum* (Pokrovskaya, loc. cit., fig. 6) is characteristically ptychagnostid and resembles, for example, *Ptychagnostus scarifatus* (Text-fig. 29). *Pseudophalacroma crebrum* is a Siberian (Yakutian) late Middle Cambrian species.

Pseudophalacroma dubium (Whitehouse, 1936)

(Pl. 67, figs. 1-4)

Material: Illustrated are three shields, in limestone, from two collections, Q6 and D55; the first contains six pygidia and two cephala, and the second one pygidium and one cephalon. These collections have been obtained from the Quita Formation, and from the Zone of *Ptychagnostus punctuosus;* these specimens are stratigraphically older than the holotype (Whitehouse, 1936) and the material described by Öpik (1961b, pp. 93-94)—all from the Zone of *Leiopyge laevigata*.

It is possible that the two pygidia now described are not conspecific because one is larger and more elongate than the other; furthermore, different shapes are also evident in the earlier described pygidia (Öpik, op. cit., pl. 22, figs. 5-10) attributed to *P. dubium*, and in two more, designated as sp. K and sp. L. at the same time the number of each kind is rather small and therefore insufficient for a conclusive study of the composition of the material regarding the species as well as the variability of each of the components. The cephala are even less informative, being about the same in *Pseudophalacroma* and *Leiopyge praecox*.

Description: The cephalon Plate 67, fig. 4, CPC 14360, collection Q6, is 2.8 mm long; it is strongly and evenly convex, and elliptical to suboval, a little longer than wide. The rim is convex but thread-like narrow; the spines are small triangular prongs, the basal lobes are distinct but low, and the glabellar rear is for a short distance enclosed in the axial (circumoccipital) furrow; of the connective band the edge is exposed but the rest (as in *Leiopyge praecox*) slopes down into the matrix. The median glabellar node is vestigial, almost imperceptible; it is more prominent in previously described cephala from the Devoncourt Limestone.

The pygidium Plate 67, fig. 3, CPC 14359, also from Q6 and associated with the cephalon, is 2.6 mm long. Its rim is wide, widening in the rear, and wider than in *Leiopyge praecox*. The axis is defined by external furrows only in its anterior part, but otherwise indicated as a low swelling; the thick test is lost in parts, exposing the pointed rear of the axis and the imprint of the postaxial median furrow in the matrix. The design of the axis indicates the Ptychagnostinae, and recalls *Leiopyge armata* (Text-fig. 53) and in combination with the wide rim *Leiopyge cosfordae* nov.

The pygidium Plate 67, figs. 1 and 2, CPC 14358, collection D55, is 5.3 mm long—indicating an exoskeleton as long as about 12 mm. The test is intact and the preservation is exquisite. The rim is very wide, about as wide as in *Pseudophalacroma* sp. L (Öpik, 1961b, pl. 22, fig. 12), which, however, possesses a relatively prominent median axial node; the axis, more than a 'ghost', is long and slender as in regular Ptychagnostinae and visibly longer than in *Pseudophalacroma crebrum* Pokrovskaya (1958, pl. 3, figs. 4-6) and close to the axis of the pygidium from Q6; muscle spots are indicated on the two anterior lobes and some 9-10 pairs of small muscle spots seem present on the axis; a small median node is clear, about 0.22x the length of the axis from its tip. The postaxial median furrow is indicated and its imprint on the matrix should be strong. The articulating device is agnostoid, the acrolobe is constricted, as already described in *Pseudophalacroma,* and the test is punctate.

Occurrence and age: The described shields attributed to *Pseudophalacroma dubium,* from the Quita Formation, belong to the Zone of *Ptychagnostus punctuosus*; it appears, therefore, that the age of *Pseudophalacroma dubium* spans the Undillan and the Boomerangian Stages of the Middle Cambrian.

REFERENCES

ANGELIN, N. P., 1851 (1851-1854)—Palaeontologica Scandinavica; *vide* Westergaard, 1910.

BARRANDE, J., 1852—SYSTEME SILURIEN DU CENTRE DE LA BOHEME, 1.

BOGNIBOVA, R. T., 1971—in TCHERNYSHEVA, N. E. (Ed.).

BOROVIKOV, L. I., & KRYSKOV, L. N., 1963—Kembriiskiye otlozhenia gorakh Kendyktas (yushnyi Kazakhstan). *Trudy VSEGEI,* N.S. 94, 266-80.

BRÖGGER, W. C., 1878—Om paradoxides skiferne ved Krekling. *Nyt. Mag. Naturvedensk, Oslo,* 24(1), 18-88.

CARTER, E. K., BROOKS, J. H., & WALKER, K. R., 1961—The Precambrian mineral belt of northwestern Queensland. *Bur. Miner. Resour. Aust. Bull.* 51.

CARTER, E. K., & ÖPIK, A. A., 1961—Lawn Hill—4-mile Geological Series. *Bur. Miner. Resour. Aust. explan. Notes,* SE.54-9.

CARTER, E. K., & ÖPIK, A. A., 1963—Duchess, Queensland—4-mile Geological Series. *Bur. Miner. Resour. Aust. explan. Notes,* SF.54-6.

CASEY, J. N., & GILBERT-TOMLINSON, Joyce, 1956—Cambrian geology of the Huckitta-Marqua region, Northern Territory. *In* RODGERS, J. (Ed.), part 2, 55-74.

CHAPMAN, F., 1911—New or little-known Victorian fossils in the National Museum. *Proc. Roy. Soc. Vic.,* 23, 305-24.

CHIEN TI-YUAN, 1961—Cambrian trilobites from Sandu and Duyun, southern Kweichow. *Acta palaeont. Sinica,* 9(2), 81-129.

CHU CHAO-LING, 1965—Some Middle Cambrian trilobites from Huzhu, Tsinghai. *Acta palaeont. Sinica,* 13(1), 145-9.

COBBOLD, E. S., & POCKOCK, R. W., 1934—The Cambrian area of Rushton (Shropshire). *Phil. Trans. Roy. Soc.,* B, 223.

COOPER, B. N., 1953—Trilobites from the Lower Champlainian formations of the Appalachian Valley. *Geol. Soc. Am. Mem.* 55.

COWIE, J. W., RUSHTON, A. W. A., & STUBBLEFIELD, C. J., 1972—Cambrian. *Geol. Soc. London spec. Rep.* 2.

DAMES, W., 1883—Kambrische Trilobiten von Liao-Tung. *In* RICHTHOFEN, 1883.

DAWSON, J. W., 1868—ACADIAN GEOLOGY. London.

DEAN, W. T., & KRUMMENBACHER, R., 1961—Cambrian trilobites from the Amanos Mountains, Turkey. *Palaeontology,* 4, 71-81.

DEISS, C., 1939—Cambrian stratigraphy and trilobites of northwestern Montana. *Geol. Soc. Am. spec. Pap.* 18.

DE KEYSER, F., & COOK, P. J., 1972—Geology of the Middle Cambrian phosphorites and associated sediments of northwestern Queensland. *Bur. Miner. Resour. Aust. Bull.* 138.

ENDO, R., & RESSER, C. E., 1937—The Sinian and Cambrian formations and fossils of Manchoukuo. *Manchurian Sci. Mus. Bull.* 1.

ETHERIDGE, R., Jr, 1902—Official contributions to the palaeontology of South Australia, No. 13, *S. Aust. parl. Pap.,* pp. 3-4.

FLEMING, P. J. G., 1973—Bradoriids from the *Xystridura* Zone of the Georgina Basin, Queensland. *Geol. Surv. Qld Publ.* 356 (*palaeont. Pap.* 31).

GRÖNWALL, K. A., 1902—Bornholms Paradoxoides lag og deres fauna. *Danm. geol. Undersøg.,* ser. 2(13).

HARRINGTON, H. J., 1938—Sobre las faunas del Ordoviciano inferior del norte Argentina. *Mus. de la Plata, Rev.* n. ser., 109-289.

HARRINGTON, H. J., ET AL., 1959—TREATISE ON INVERTEBRATE PALAEONTOLOGY: O(1) TRILOBITA. *Univ. Kansas Press.*

HARTT, C. F., 1868—*In* DAWSON, J. W.

HAWLE, T., & CORDA, A. T., 1847—Prodrom einer Monographie der böhmischen Trilobiten.

HENNINGSMOEN, G., 1952—Early Middle Cambrian fauna from Rogaland, SW Norway. *Norsk. geol. tidskr.,* 30, 13-32.

HENNINGSMOEN, G., 1956—The Cambrian of Norway. *In* RODGERS, J. (Ed.), 1, 45-57 .

HENNINGSMOEN, G., 1958—The Upper Cambrian faunas of Norway with descriptions of non-olenid invertebrate fossils. *Norsk. geol. tidskr.,* 38(2), 179-96.

HICKS, H., 1872—On some undescribed fossils from the Menevian group. *Quart. J. geol. Soc. London,* 28, 179.

HILL, D., ET AL. (Editors), 1971—Cambrian fossils of Queensland. *Qld palaeontogr. Soc.,* Pls 1-15.

HOWELL, B. F., 1925—The faunas of the Cambrian *Paradoxides* beds at Manuels, Newfoundland. *Bulls. Am. Paleont.,* 11, 43.

HOWELL, B. F., 1935—Cambrian and Ordovician trilobites from Hérault, southern France. *J. Paleont.,* 9(3), 222-38.

HOWELL, B. F., 1935a—New Middle Cambrian agnostian trilobites from Vermont. *J. Paleont.,* 9(3), 218-21.

HOWELL, B. F., 1935b—Some New Brunswick Cambrian agnostids. *Bull. Wagner Inst. Sci. Philad.,* 10(2), 13-15.

HOWELL, B. F., 1937—Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. *Bull. geol. Soc. Am.,* 48, 1147-1210.

HOWELL, B. F., & MASON, J. F., 1938—Correlation of Middle Cambrian faunas of North America. *J. Paleont.,* 12(3), 295-7.

HUNT, A. S., 1967—Growth variation and instar development of an agnostid trilobite. *J. Paleont.,* 41(1), 203-9.

HUPE, P., 1953—Contribution à l'étude du Cambrien inférieur et du Précambrien III de l'anti-Atlas Marrocain. *Serv. géol. Maroc. Notes Mem.* 103.

HUTCHINSON, R. D., 1952—The stratigraphy and trilobite faunas of the Cambrian sedimentary rocks of Cape Breton Island, Nova Scotia. *Geol. Surv. Canada Mem.* 263.

HUTCHINSON, R. D., 1956—Cambrian stratigraphy, correlation, and paleogeography of eastern Canada. *In* RODGERS, J. (Ed.), 2, 289-314.

HUTCHINSON, R. D., 1962—Cambrian stratigraphy and trilobite faunas of southwestern Newfoundland. *Geol. Soc. Canada Bull.* 88.

ILLING, V. C., 1916—The paradoxidian fauna of a part of the Stockingford shales. *Quart. J. geol. Soc. London,* 71, 386-450.

IVSHIN, L. L., 1953—Srednekembrijskiye trilobity Kazakhstana, 1. *Acad. Sci. Kazakh. SSR, Alma-Ata.*

IVSHIN, N. K., 1960—*In* KHALFIN, L. L. (Ed.).

JAEKEL, O., 1909—Ueber die Agnostiden. *Z. deutsch. geol. Gesell.,* 61, 380-401.

JEGOROVA, L. I., 1960—*In* JEGOROVA, L. I., & SAVITSKY, V. E.

JEGOROVA, L. I., & SAVITSKY, V. E., 1969—Stratigrafiya i biofatsii Kembriya Sibirskoi platformy (Zapadnoye Prianabarye). *Trudy SNIIGGIMS,* 43, 1-408, Nyedra Press.

KHALFIN, L. L. (Ed.), 1960—Biostratigrafiya paleozoya Sayano-Alytaiskoi gornoi oblasti. 1 —Nizhni paleozoi. *Trudy SNIIG,* 19.

KOBAYASHI, T., 1935—Cambrian faunas of South Chosen. *J. Fac. Sci. Imp. Univ. Tokyo,* 4(2).

KOBAYASHI, T., 1939—On the agnostids (part I). *J. Fac. Sci. Imp. Univ. Tokyo,* ser. 2 5(5), 60-108.

KRYSKOV, L. N., 1963—*In* BOROVIKOV, L. I., & KRYSKOV, L. N.

LAKE, P., 1906-1946—A monograph of the British Cambrian trilobites. *Palaeontogr. Soc. London.*

LAZARENKO, N. P., 1966—Biostratigrafiya i nyekotorye novye trilobity verkhnego Kembriya Olenekskogo podnyatiya i Kharaulakhskikh gor. *Uchgonye zapiski,* II, 33-78. *NTTGA, Leningrad.*

LINNARSSON, J. G. O., 1869—Om Vestergötlands cambriska och siluriska aflagringar. *Vet. Akad. Handl.* 8(2).

LINNARSSON, G., 1877—Om faunan i lagren med *Paradoxides ölandicus. Geol. For. Stockholm Forhandl.,* 3(40), 12, 1-24.

LOCHMAN, Christina, 1944—*In* LOCHMAN, Christina, & DUNCAN, D.

LOCHMAN, Christina, & DUNCAN, D., 1944—Early Upper Cambrian faunas of central Montana. *Geol. Soc. Am., spec. Pap.* 54.

LOTZE, F. & SDZUY, K., 1961—Das Kambrium Spaniens. *Akad. Wiss., Lit., Mainz. math.-naturw. Kl., Abh.,* Parts I-III.

LU YEN-LAO, 1957—Trilobita; *in* INDEX FOSSILS OF CHINA, 3, 240-94. *Inst. Palaeont. Acad. Sinica.*

MATTHEW, G. F., 1885—The faunas of the St John group. *Trans. Roy. Soc. Canada,* 1(4), 99-124.

MATTHEW, G. F., 1886—Illustrations of the fauna of the St. John Group, continued. *Trans. Roy. Soc. Canada,* 3(4).

MATTHEW, G. F., 1895—The Protolenus Fauna. *Trans. N.Y. Acad. Sci.,* 14, 101-83.

MATTHEW, G. F., 1899—Studies on Cambrian faunas. *Trans. Roy. Soc. Canada,* ser. 2, 5(4).

NICHOLAS, T. C., 1916—Notes on the trilobite fauna of the Middle Cambrian of the St Tudwal's Peninsula. *Quart. J. geol. Soc. London,* 71.

ÖPIK, A. A., 1956—Cambrian geology of Queensland, 1-24; Cambrian geology of Northern Territory, 25-54; Cambrian palaeogeography of Australia, 239-84; *in* RODGERS, J. (Ed.).

ÖPIK, A. A., 1960—Cambrian and Ordovician geology [of Queensland]. *J. geol. Soc. Aust.,* 7, 89-114.

ÖPIK, A. A., 1961a—Alimentary caeca of agnostids and other trilobites. *Palaeontology,* 3(4), 410-38.

ÖPIK, A. A., 1961b—The geology and palaeontology of the headwaters of the Burke River, Queensland. *Bur. Miner. Resour. Aust. Bull.* 53.

ÖPIK, A. A., 1963—Early Upper Cambrian fossils from Queensland. *Bur. Miner. Resour. Aust. Bull.* 64.

ÖPIK, A A., 1966—The early Upper Cambrian crisis and its correlation. *J. Proc. Roy. Soc. N.S.W.,* 100, 9-14

ÖPIK, A. A., 1967—The Mindyallan fauna of northwestern Queensland. *Bur. Miner. Resour. Aust. Bull.* 74, 2 vols.

ÖPIK, A. A., 1968—The Ordian stage of the Cambrian and its Australian Metadoxididae. *Bur. Miner. Resour. Aust. Bull.* 92, 133-69.

ÖPIK, A. A., 1970a—Nepeid trilobites of the Middle Cambrian of northern Australia. *Bur. Miner. Resour. Aust. Bull.* 113.

ÖPIK, A. A., 1970b—*Redlichia* of the Ordian (Cambrian) of Northern Australia and New South Wales. *Bur. Miner. Resour. Aust. Bull.* 114.

ÖPIK, A. A., & others, 1957—The Cambrian geology of Australia (Reprinted from RODGERS. J., Ed.). *Bur. Miner. Resour. Aust. Bull.* 49.

PALMER, A. R., 1954—An appraisal of the Great Basin Middle Cambrian trilobites described before 1900. *U.S. geol. Surv. prof. Pap.* 264-D, 55-86.

PALMER, A. R., 1962—*Glyptagnostus* and associated trilobites in the United States. *U.S. geol. Surv. prof. Pap.* 374-F, 1-79.

PALMER, A. R., 1968—Cambrian trilobites of east-central Alaska. *U.S. geol. Surv. prof. Pap.* 559-N, 1-115.

PALMER, A. R., & GATEHOUSE, C. G., 1972—Early Middle Cambrian trilobites from Antarctica. *U.S. geol. Surv. prof. Pap.* 456-D.

PEK, I., 1972—*Peronopsis integra* (Beyrich, 1845), the youngest agnostid trilobite from the Cambrian of Central Bohemia *Vestn. ostr. ustavu geol.*, 47, 105-6.

PEK, I., & VANEK, J., 1971—Revision of the genus *Peronopsis* Hawle & Corda, 1847, and *Diplorrhina* Hawle & Corda, 1847 (Trilobita) from the Middle Cambrian of Bohemia. *Vestn. ostr. ustavu geol.*, 46, 263-76.

POKROVSKAYA, N. V., 1958—Angnostidy Srednyego Kembriya Yakutii, chast 1. *Trudy geol. Inst. Acad. Sci. USSR*, 16.

POKROVSKAYA, N. V., 1960—*In* TCHERNYSHEVA, N. (Ed.).

POKROVSKAYA, N. V., 1961—O yarusnom rastchlenenii Kembria. Symposium, the Cambrian System, its palaeogeography and the problem of its lower boundary; *20th Int. geol. Congr.*, 3.

POKROVSKAYA, N. V., & JEGOROVA, G. I., 1972—*In* SAVITZKY ET AL.

POULSEN, Chr., 1960—Fossils from the late Middle Cambrian *Bolaspidella* zone of Mendoza, Argentina. *Mat. Fys. Dan. Vid. Selsk.* 32(11), 1-40.

POULSEN, V., 1969—An Atlantic Middle Cambrian fauna from North Greenland. *Lethaia*, 2(1), 1-14.

RASETTI, F., 1948—Middle Cambrian trilobites from the Levis Conglomerate of Quebec. *J. Paleont.*, 22(3), 315-39.

RASETTI, F., 1951—Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smiths. misc. Coll.*, 116(5).

RASETTI, F., 1952—Ventral cephalic structures in Cambrian trilobites. *Am. J. Sci.*, 250, 885-98.

RASETTI, F., 1967—Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. *Smiths. misc. Coll.*, 152(4).

RASETTI, F., & THEOKRITOFF, G., 1967—Lower Cambrian agnostid trilobites of North America. *J. Paleont.*, 41(1), 189-96.

RAW, F., 1953—The external morphology of the trilobite. *J. Paleont.*, 27(1), 82-129.

RAW, F., 1957—Origin of Chelicerates. *J. Paleont.*, 31(1), 139-92.

RESSER, Ch. E., 1938a—Middle Cambrian fossils from Pend Oreille Lake, Idaho. *Smith. misc. Coll.*, 97(3).

RESSER, Ch. E., 1938b—The Cambrian System (restricted) of the southern Appalachians. *Geol. Soc. Am., spec. Pap.* 15.

RESSER, Ch. E., 1939a—The Spence-Shale and its fauna. *Smiths. misc. Coll.*, 97(12).

RESSER, Ch. E., 1939b—The *Ptarmigania* strata of the northern Wasatch Mountains. *Smiths. misc. Coll.*, 98(24).

RESSER, Ch. E., & ENDO, R., 1937—*See* ENDO, R., & RESSER, Ch. E.

RICHTHOFEN, F. F. VON, 1883—CHINA. Ergebnisse iegener Reisen und darauf gegründete Studien. *Verlag von Dietrich Reimer, Berlin.* Vol. 4, Palaeontology.

ROBISON, R. A., 1964—Late Middle Cambrian faunas from western Utah. *J. Paleont.*, 38(3), 510-66.

ROBISON, R. A., 1972a—Hypostoma of agnostid trilobites. *Lethaia*, 5, 239-48.

ROBISON, R. A., 1972b—Mode of life of agnostid trilobites. *24th int. geol. Cong.*, sec. 7, 33-40.

RODGERS, J. (Ed.), 1956—Symposium: El sistema Cambrico, su palaeogeografia y el problema de su base. *20th int. geol. Cong., Mexico.*

ROSOVA, A. V., 1964—Biostratigrafiya i opisaniye trilobitov srednyego i verkhnyego Kembriya severo-zapada Sibirskoi Platformy. *Nauka Press, Moscow.*

ROSS, R. J., Jr, 1958—Trilobites in a pillow lava of the Ordovician Valmy Formation, Nevada. *J. Paleont.*, 32(3), 559-70.

RUSHTON, A. W. A., 1966—The Cambrian trilobites from the Purley Shales of Warwickshire. *Palaeontogr. Soc. Monogr.*, 511, vol. 120.

RUSSELL, R. T., & TRUEMAN, N. A., 1971—The geology of the Duchess phosphate deposit, northwestern Queensland, Australia. *Econ. Geol.*, 66, 1186-214.

SAITO, K., 1934—Older Cambrian Trilobita and Conchostraca from northwestern Korea. *Jap. J. Geol. Geogr.*, 11(3-4), 211-38.

SALTER, J. W., 1872—*In* HICKS, H.

SAVITSKY ET AL., 1972—Kembrig Sibirskoi platformy. *Sib. Inst. Geol. Geophys. Miner., Trudy*, 130.

SDZUY, K., 1958—Neue Trilobiten aus dem Mittelkambrium von Spanien. *Senck. Leth.*, 39(3-4), 235-53.

SDZUY, K., 1961—*In* LOTZE, F., & SDZUY, K.

SDZUY, K., 1966—Das Kambrium des Frankenwaldes. 2: Die Bergleshof-Schichten und ihre Trilobiten Fauna. *Senck. Leth.*, 47(1), 57-86.

SDZUY, K., 1967 (=1968)—Trilobites del Cambrico Medio de Asturias. *Trab. Geol.*, 1, 77-133. Oviedo.

SHAW, A. B., 1958—Stratigraphy and structure of the St Albans area, northwestern Vermont. *Bull. geol. Soc. Am.*, 69, 519-68.

SHERGOLD, J. H., 1969—Oryctocephalidae (Trilobita: Middle Cambrian) of Australia. *Bur. Miner. Resour. Aust. Bull.* 104.

SHIMER, H. W., & SHROCK, R. A., 1944-1955—INDEX FOSSILS OF NORTH AMERICA. *N.Y., McGraw-Hill.*

SMITH, K. G., VINE, R. R., FORMAN, D. J., & JENSEN, A. R., 1962—Hay River, Northern Territory, 1:250 000 Geological Series, Sheet SF/53-16. *Bur. Miner. Resour. Aust.*

SNAJDR, M., 1958—The trilobites of the Middle Cambrian of Bohemia. *Roz. czl., geol. Ust.*, 24.

STRAND, T., 1929—The Cambrian beds of the Mjøsen district in Norway. *Norsk geol. tidskr.*, 10, 307-65.

STUBBLEFIELD, C. J., 1956—Cambrian palaeogeography in Britain; *in* RODGERS, J. (Ed.), I, 1-43.

TCHERNYSHEVA, N. E., 1961—Stratigrafiya Kembriya Aldanskoi antiklizy i paleontologicheskoye obosnovaniye vydeleniya amginskugo yarusa. *Trudy VSEGEI*, n.s., 49.

TCHERNYSHEVA, N. E., 1967—Stratotipitcheskij razrez maiskogo yarusa stenyego Kembriya. *Byull. nauchno-teckhn. Inform.*, 7, 38-12. ONTI-VIEMS.

TCHERNYSHEVA, N. E., 1968—Biostratigrafia srednyego Kembriya SSSR. *Trudy VSEGEI: Problemy Stratigrafii i Paleogeografii* (reprint).

TCHERNYSHEVA, N. E. (Ed.), 1971—Amginskey yarus Alteya-Sayanskoi Oblasti. *Sib. Inst. Geol. Geophys. Miner., Novosibirsk, Trudy* III.

TCHERNYSHEVA, N. E. (Ed.) ET AL., 1960—ARTHROPODA, TRILOBITOMORPHA AND CRUSTACEA. *Osnovy Palaeontologii, Acad. Sci. USSR*, Moscow.

TCHERNYSHEVA, N. E. (Ed.) ET AL., 1965—Kembrijskaya Sistema; *in* STRATIGRAFIYA *SSSR* (Fourteen volumes). *Nyedra Press, Moscow.*

TROEDSSON, G. T., 1937—On the Cambro-Ordovician faunas of western Quruq Tagh, Tien shan. *Palaeont. sinica*, n.s., 2, 1-24.

TULLBERG, S. A., 1880—Agnostus-Arterna de Kambriska Aflagringarne vid Andrarum. *Sver. geol. Unders. Avh.*, ser. C, 42.

WALCOTT, C. D., 1884—On the Cambrian faunas of North America, preliminary studies. *U.S. geol. Surv. Bull.* 10.

WALLCOTT, C. D., 1891—Correlation papers: Cambrian. *U.S. geol. Surv. Bull.* 81.

WESTERGAARD, A. H., 1910—Index to N. P. Angelin, Palaeontologia Scandinavica. *Lunds Fysiogr. Sellsk. Handl.*, N.F. 21, 2.

WESTERGAARD, A. H., 1922—Sveriges olenidskiffer. *Avh. sver. geol. Unders.* ser. C, 18, 1-205.

WESTERGAARD, A. H., 1936—*Paradoxides oelandicus* beds of Öland. *Avh. sver. geol. Unders.*, ser. C, 394 (Arsbok, 30, 1), 1-66.

WESTERGAARD, A. H., 1944—Borrningar genom skaanes Alunskiffer. *Avh. sver. geol. Unders.*, ser. C, 459 (Arsbok 38, 1).

WESTERGAARD, A. H., 1946—Agnostidea of the Middle Cambrian of Sweden. *Avh. sver. geol. Unders.* Ser., C477 (Arsbok 40, 1).

WESTERGAARD, A. H., 1953—Non-agnostidean trilobites of the Middle Cambrian of Sweden, III. *Avh. sver. geol. Unders.*, ser. C, 526 (Arsbok 46, 2).

WHITEHOUSE, F. W., 1936—The Cambrian faunas of northeastern Australia, Part I. stratigraphic outline; Part II, Trilobita (Miomera). *Mem. Qld Mus.*, 11, 59-112.

WHITEHOUSE, F. W., 1939—Idem., Part III: the polymerid trilobites. *Mem. Qld Mus.*, 11(3), 179-282.

WHITTINGTON, H. B., 1950—Sixteen Ordovician genotype trilobites. *J. Paleont.*, 24, 531-65.

WHITTINGTON, H. B., 1963—Middle Ordovician trilobites from Lower Head, western Newfoundland. *Bull. Mus. Comp. Zool., Harvard Univ.*, 129(1).

WHITTINGTON, H. B., 1965—Trilobites of the Ordovician Table Head Formation, western Newfoundland. *Bull. Mus. Comp. Zool., Harvard Univ.*, 132(4), 275-442.

WILMARTH, M. Grace, 1925—The geologic time classification of the United States Geological Survey compared with other classifications accompanied by the original definitions of Era, Period and Epoch terms. *U.S. geol. Surv. Bull.* 769 (with index).

WILMARTH, M. Grace, 1938—Lexicon of geologic names of the United States, Part 1, A-L. *U.S. geol. Surv. Bull.* 896.

APPENDIX 1: CHECK LIST OF SPECIES OF AGNOSTACEA, AND COLLECTING SITES

'Acadagnostus' scutalis	F5
Acidusus acidusus	M234
Acidusus germanus	M214
Acidusus sp. indet. aff. *germanus*	M411
Acidusus navus	M214
Acidusus occultatus	M57, M60, M424
Acidusus sp. aff. *occultatus*	M60
Acidusus retrotextus	M416
Acidusus sp. nov.	D155
Agnostonymus semiermis	M150, M176, M180, M376, M412
Allobodochus spiniger	D54, D96, G106, T87
Aotagnostus aotus	M64, M164, M166, M263, D69
Aotagnostus culminosus	M204, M212, M234, M409, M410, M411, M418, D74
Aotagnostus magniceps	M139
Aotagnostus modicus	M142
Aotagnostus ponebrevis	M164, M191, M192
Aotagnostus sp. indet. aff. *ponebrevis*	M191b
Aotagnostus protentus	M25, M194, M212, M289, M409, D69, D74
Aristarius aristarius	M263
Aristarius retrocornutus	M265
Aristarius ultimus	M57
Aristarius aff. *ultimus*	M434
Baltagnostus robustus	M212
Baltagnostus sertulatus	D66, D74
Cotalagnostus sp. aff. *lens*	M30
Criotypus lemniscatus	M150, M176, M192, M412, M425
Criotypus sp. nov. aff. *lemniscatus*	M123, M192, M412
Criotypus mitigatus	M191a
Criotypus oxytorus	M425
Criotypus paenerugatus	M265, M281, M425
Criotypus sp. aff. *paenerugatus*	M263
Criotypus sp. indet.	D150
Diplagnostus atavorum	M192, M425
Diplagnostus floralis	M59, M154, M191a, M263, M424, M434, D69
Doryagnostus sp. nov. aff. *incertus*	M41
Doryagnostus magister	M24, M25, M41, M57, M117, M118, M130, M142, M194, M195, M202, M213, M247, M408, M409, M410, M411, M416, M418, M462, D74
Doryagnostus notalibrae	M89, M212, M214, M247
Doryagnostus sp. aff. *notalibrae*	M161
Doryagnostus solidus	M139, M409, M418
Euagnostus certus	M124, M179, M180, M183, M191a, M425
Euagnostus? glandifer	M180, M376
Euagnostus levifrons	M41, M409
Euagnostus neptis	M243
Euagnostus opimus	M123, M124, M150, M160, M176, M192, M376, M412
Euagnostus sp. aff. *opimus*	M65
Euagnostus sp. indet.	M425
Goniagnostus nathorsti	M57, M117, M142, M214, M276, M409, M410, M411, M416
Goniagnostus nathorsti intersertus	labelled as from west of M64; the site is probably between M130 and M118
Goniagnostus scarabaeus	M118, M194, M195, M247, M409, M462
Goniagnostus verus	M195
Goniagnostus (Allobodochus)	see *Allobodochus*
Goniagnostus (Criotypus)	see *Criotypus*
Goniagnostus (Goniagnostus)	see *Goniagnostus*

Grandagnostus imitans	M30, M41, M89, M214, M234, M409, M416, M418
Hypagnostus clipeus	M142, M213, M247, M409, M418
Hypagnostus inaequalis	M161, M202
Hypagnostus melicus	M24, M25, M30, M41, M136, M139, M416, M462
Hypagnostus parvifrons	M180, M265
Hypagnostus tjernviki	M89, M462
Hypagnostus cf. *vortex*	M281
Iniospheniscus incanus	M145, M265
Iniospheniscus talis	M64, M164, M191a, M263
Iniospheniscus? sp. indet.	M243
Itagnostus elkedraensis	NAE, N32, N35, N63
?Itagnostus sp. indet.	M281
Leiopyge armata	W36 (D11, D13A, D15, D18, D21, D26, G103)
Leiopyge sp. nov. aff. *armata*	W36
Leiopyge cosfordae	M195
Leiopyge laevigata	T87, D7/15, D18, D55, G102, G103, G104, G106, G107
Leiopyge multifora	W36
Leiopyge praecox	D59, D155
Linguagnostus? comparabilis	N32
Myrmecomimus saltus	M289, M434
Myrmecomimus tribulis	M25, M212, M411
Myrmecomimus tribulis evanidus	M411
Myrmecomimus tribulis mixtus	M59, M60, M139, M194, M234, M409, M411
Oedorhachis crenias	M24, M136, M462
Onymagnostus angulatus	M64, M123, M160, M409, M412, M416
Onymagnostus sp. nov. aff. *angulatus*	M180
Onymagnostus durusacnitens	M30, M41, M118
Onymagnostus cf. *grandis*	M30
Onymagnostus mundus	M212, M247, M416, M418
Onymagnostus seminula	M41, M166, M212, M462
Onymagnostus cf. stenorrhachis	M41
Onymagnostus (Agnostonymus)	see *Agnostonymus*
Pentagnostus anabarensis	Mount Wright area, New South Wales
Pentagnostus rallus	Loc. N32, collections N31-N35, Sandover River area, Northern Territory
Pentagnostus veles	Mount Wright area, New South Wales
Peronopsis comis	N36
Peronopsis fallax ferox	M145, M149, M208, M265, M281, M425
Peronopsis longinqua	N63
Peronopsis normata	M179, M433, M434
Peronopsis prolixa	N32
Peronopsis tramitis	N35
Peronopsis (Itagnostus)	see *Itagnostus*
Pseudoperonopsis ancisa	M199, M376
Pseudoperonopsis iniugata	M128, M191a, D69 (cf.), D74
Pseudoperonopsis insolita	M212
Pseudoperonopsis perplexa	M57, M59, M139, M202, M204, M212, M214, M234, M247, M263, M289, M408, M409, M410, M411, M418, M434 (cf.), D74
Pseudoperonopsis syrma	Buckley River crossing of Barkly Highway; M425
Pseudophalacroma dubium	D55, Q6 (=D74), D19B, D7/15, D11, D18, T87
Ptychagnostinae, gen. indet., sp. nov.	D150, D154
Ptychagnostus atavus	M169, M192, M198, M207, M208, M281, M265, M425, M430, M433, M434
Ptychagnostus atavus coartatus	M192, M425
Ptychagnostus idmon	M149, M176, M208
Ptychagnostus intermedius	M170
Ptychagnostus mesostatus	M59, M64
Ptychagnostus punctuosus affinis	M59, M60, M64, M166, M191a, M204, M234, M410, M411, M424(?), D69, D86

Ptychagnostus punctuosus fermexilis	D155, Q6 (D74)
Ptychagnostus punctuosus punctuosus	M41, M59, M174, M212, M214, M409, M411, D66, D74, Q6
Ptychagnostus scarifatus	M176
Ptychagnostus sp. aff. *scarifatus*	M176
?Ptychagnostus sp. indet. A (aff. *atavus*)	M427
Ptychagnostus sp. indet. B (aff. *atavus*)	D150
Ptychagnostus sp. indet. C	M263, D69
Ptychagnostus sp. nov. *D*	M263
Ptychagnostus (Acidusus)	see *Acidusus*
Rhodotypiscus nasonis	M123, M124, M150, M160, M176, M180, M183, M376, M412
Rhodotypiscus sp. nov. aff. *nasonis*	M243
Svenax pusillus	D66, D74
Svenax vafer	M409
Tomagnostella nepos	M57, M195, M204
Triplagnostus diremptus	M123, M149, M150, M176, M192, M208, M376
Triplagnostus fretus	M188, M265, M281
Triplagnostus gibbus gibbus	M430, M433
Triplagnostus gibbus posterus	M145, M169, M170, M188, M192, M198, M208, M263, M265, M281, M423, M425, M430, M433
Triplagnostus purus	presumably M166
Triplagnostus quasigibbus	M265
Triplagnostus scopus	M265
Triplagnostus stramineus	M265
Triplagnostus sp. indet.	M425
Triplagnostus (Aristarius)	see *Aristarius*
Zeteagnostus incautus	M169, M192, M199, M265, M281, M423, M425

APPENDIX 2: DESCRIPTION OF LOCALITIES

The geographic and geological data presented in this Appendix are extracted from the cards of the catalogue already mentioned by Öpik (1967, vol. 2, p. 5).

Species of Agnostacea are listed, but the names of the concurrent species of polymerid trilobites (Ptychopariidae, Solenopleuridae, Anomocaridae, Dolichometopidae, etc.) are reserved.

CAMOOWEAL 1:250 000 Sheet area

The Middle Cambrian sequence of the Undilla Basin in the Camooweal Sheet area is complete except for the following hiatuses:

(1) Strata and fossils of the *Ptychagnostus atavus* time are absent in the northeast (M150, M176).

(2) In the same area east of M130 the zones containing *Goniagnostus nathorsti* are absent.

(3) The sequence of the Basin ends with the exit of *Goniagnostus nathorsti* in the Split Rock Sandstone.

M24 19°25.9'S, 138°34.4'E
Outcrops along left bank of Douglas Creek; collection from about 1.0-1.5 km north from spring. Flaggy, dark, smelly limestone with layers of calcite. V-Creek Limestone.

Doryagnostus magister
Hypagnostus clipeus
Hypagnostus melicus
Oedorhachis crenias
Zone of *Goniagnostus nathorsti*

M25 19°28'S, 138°33.2'E
Thinly laminated hard siliceous limestone with aphanitic nodules; at Bull Creek. V-Creek Limestone.

Aotagnostus protentus
Doryagnostus magister
Hypagnostus melicus
Myrmecomimus tribulis
Zone of *Doryagnostus notalibrae*

M30 19°27.8'S, 138°37.5'E
Sandy micaceous limestone—mostly ellipsoids. V-Creek Limestone.

Cotalagnostus sp. aff. *lens*
Hypagnostus melicus
Onymagnostus cf. *grandis*
Onymagnostus durusacnitens
Zone of *Doryagnostus notalibrae*

M41 19°27.5'S, 138°37'E
Soft laminated grey sandy limestone with ellipsoids of hard limestone; above it a limestone layer with chert biscuits. V-Creek Limestone.

Doryagnostus magister (in biscuits)
Doryagnostus sp. nov. aff. *incertus*
Euagnostus levifrons
Grandagnostus imitans
Hypagnostus melicus
Onymagnostus cf. *stenorrhachis*
Onymagnostus durusacnitens
Onymagnostus seminula
Ptychagnostus punctuosus punctuosus
Zone of *Doryagnostus notalibrae*

M54 19°37'S, 138°38'E
Grey impure marly limestone with harder ellipsoids, in the stream bed at Undilla homestead. V-Creek Limestone.
Doryagnostus magister
Hypagnostus clipeus
Zone of *Goniagnostus nathorsti*

M57 19°47.5'S, 138°39'E
In a small tributary of Douglas Creek at the foot of the Bagoor Plateau. V-Creek Limestone.
Aristarius ultimus
Acidusus occultatus
Doryagnostus magister
Goniagnostus nathorsti
Pseudoperonopsis perplexa
Tomagnostella nepos
Zone of *Goniagnostus nathorsti*

M64 19°32.6'S, 138°51.3'E
Interbedded bituminous, pale grey laminated, aphanitic limestones, some oolitic beds and chert. Current Bush Limestone. The collection refers to a stretch of 500 m of strata dipping gently SSW.
Aotagnostus aotus
Doryagnostus indet.
Euagnostus neptis
Goniagnostus nathorsti intersertus (W of M64)
Hypagnostus sp. indet.
Onymagnostus angulatus
Ptychagnostus mesostatus
Ptychagnostus punctuosus affinis
Pseudoperonopsis indet.
Early in the Zone of *Ptychagnostus punctuosus*

M65 19°24'S, 138°32'E
A downfaulted limestone block—a narrow enclave in the dolomites of the Age Creek Formation on the right bank of the O'Shanassy River.
Euagnostus sp. aff. *opimus*

M89 19°27'S, 138°32'E
About the Douglas Creek/Bull Creek fork, close to locality M418; in the bank of a small channel; grey impure limestone; a lens or an extended pod of calcite with some chert concretions; the collection is from the calcite. V-Creek Limestone.
Doryagnostus notalibrae
Euagnostus cf. *certus*
Euagnostus neptis
Goniagnostus nathorsti
Grandagnostus imitans
Hypagnostus clipeus
Hypagnostus tjernviki
Onymagnostus sp. indet.
Pseudoperonopsis perplexa
Zone of *Doryagnostus notalibrae*

M117 19°35′S, 138°45′E
Close to the right bank of One Mile Creek (a tributary of Harris Creek), about 13 km east to north from Undilla homestead; some 40 m is exposed in the face of a hill; on its top rests a sheet of Age Creek thick-bedded oolitic dolomitic rock. V-Creek Limestone.

Doryagnostus magister
Goniagnostus nathorsti
Grandagnostus imitans
Pseudoperonopsis perplexa
Zone of *Doryagnostus notalibrae*

M118 19°34′S, 138°48′E
Grey impure limestone. V-Creek Limestone.
Doryagnostus magister
Goniagnostus scarabaeus
Grandagnostus imitans
Hypagnostus clipeus
Onymagnostus durusacnitens (a pygidium)
Zone of *Doryagnostus notalibrae*

Note: on the map the locality number is not clear, and can be mistaken for 78, but M78 is used for a different site (Morsten homestead, and A-Bore). The limestone of M118 is replaced to the east by the thin ironstone layer at M130.

M123 19°31′S, 138°47.6′E
A north-facing, low-angle cuesta, about 30 m high; grey and off-pink limestone with shaly partings, oolitic in places; chert layers. Collection is from lowermost 3-5 m. Currant Bush Limestone.

Criotypus sp. nov. aff. *lemniscatus*
Euagnostus opimus
Onymagnostus angulatus
Rhodotypiscus nasonis
Triplagnostus diremptus
Zone of *Euagnostus opimus*

M124 19°31.6′S, 138°47.4′E
A low-angle cuesta, about 30 m high; in its upper part some 20-21 m of dolomitic sandy limestone with slumps; in the lower, fossiliferous 8 m, grey bituminous limestone with oolitic and aphanitic layers; chert. Currant Bush Limestone.

Euagnostus certus
Euagnostus opimus
Rhodotypiscus nasonis
Zone of *Euagnostus opimus*

M128 19°31′S, 138°47.5′E
Bank of a stream. Below, impure (marly) limestone with aphanitic layers; higher up, harder beds. V-Creek Limestone.

Aotagnostus culminosus
Doryagnostus magister
Pseudoperonopsis iniugata in the upper part
Zone of *Doryagnostus notalibrae*

M130 19°33.5′S, 138°48.5′E
A conspicuous solitary butte, 20-21 m high on a broad socle of limestone; the top is red sandstone (Split Rock); it rests on a thin impure ironstone layer representing the V-Creek Limestone; strata below (shale with chert over limestone) belong to the Currant Bush Limestone. Collection is from the ironstone.

Aotagnostus culminosus
Doryagnostus magister
Pseudoperonopsis perplexa
Ptychagnostus indet.
Some polymerid trilobites
Split Rock: Zone of *Goniagnostus nathorsti*
Ironstone; Zone of *Doryagnostus notalibrae*
Currant Bush: Zone of *Ptychagnostus punctuosus*

M136 19°31′S, 138°39.8′E
Massive dolomite; at its southern edge, thin-bedded dolomite with chert. Age Creek Formation.

Oedorhachis crenias
Polymerids, Eocrinoidea
Zone of *Goniagnostus nathorsti*

M139 19°40.5′S, 138°45.5′E
Western slope of the Harris Creek valley; laminated grey marly limestone. V-Creek Limestone.

Aotagnostus magniceps
Doryagnostus solidus
Hypagnostus melicus
Myrmecomimus tribulis mixtus
Onymagnostus indet. (?*seminula*)
Pseudoperonopsis indet. (?*perplexa*)
Zone of *Doryagnostus notalibrae*

M142 19°49.8′S, 138°49.2′E
Laminated grey, and marly limestone. V-Creek Limestone.

Aotagnostus modicus
Doryagnostus magister
Goniagnostus nathorsti
Hypagnostus clipeus
Zone of *Doryagnostus notalibrae*

M145 19°38.5′S, 138°53.5′E
In Cattle Creek. Inca siltstone and shale, mottled; salt licks.

Iniospheniscus incanus
Hypagnostus cf. *vortex*
Peronopsis fallax ferox
Ptychagnostus indet.
Triplagnostus gibbus posterus
Zone of *Ptychagnostus atavus*

M149 19°35.5′S, 138°56.7′E
A cluster of buttes on a socle of dolomitic limestone, right bank of West Thornton River.

(1) The buttes: Inca siltstone, shale and some chert, about 20 m.

Aotagnostus ponebrevis
Criotypus lemniscatus
Euagnostus opimus
Hypagnostus sp. indet.
Pseudoperonopsis syrma
Ptychagnostus idmon
Rhodotypiscus nasonis
Triplagnostus diremptus
Zone of *Euagnostus opimus*

(2) The socle: dolomitic limestone (Thorntonia) with about 40% of nodular chert.

Pagetia
Xystridura

M150 19°38.3′S, 138°56′E
A terraced hill of limestone, 6.5 km S from Thorntonia homestead. At the eastern Bank of West Thornton River. Siltstone, shale and chert of the Incas are absent. Currant Bush Limestone.

(1) The uppermost 11 m consists of colour-banded aphanitic limestone with intervening 2 m of breccia.
Aotagnostus cf. *aotus* at top

(2) Next comes 1.5 m of dark, smelly fossiliferous limestone.
Criotypus lemniscatus
Euagnostus opimus
Onymagnostus (Agnostonymus) semiermis
Rhodotypiscus nasonis
Triplagnostus diremptus
Zone of *Euagnostus opimus*

(3) Below follows 5.5 m of limestone with chert and oolitic layers and a breccia at the base.

(4) At the base is 15+ m of dolomitic limestone (Thorntonia Limestone, Templetonian).

M160 19°23.5′S, 138°35.5′E
Dolomite with chert layers and biscuits, less than 0.5 m amid S to SSW-dipping barren dolomite beds of Age Creek Formation.

Euagnostus opimus
Onymagnostus angulatus
Onymagnostus (Agnostonymus) semiermis
Rhodotypiscus nasonis
Zone of *Euagnostus opimus*

M161 19°27′S, 138°37′E
Grey thin-bedded limestone and bituminous limestone with some chert. Lithologically, the transition from Currant Bush to V-Creek is apparent.

Aotagnostus aotus
Doryagnostus sp. aff. *notalibrae*
Euagnostus cf. *certus*
Hypagnostus cf. *inaequalis*
Onymagnostus angulatus
Pseudoperonopsis indet. *(?ancisa)*
?Rhodotypiscus nasonis
Zone of *Euagnostus opimus* passing into Zone of *Ptychagnostus punctuosus*

M166 19°59.3′S, 138°54′E
Flaggy, grey, smelly limestone with a S-facing terraced slope of about 30 m of strata formation. Currant Bush Limestone or possibly a bank in the Inca.

Aotagnostus aotus
Onymagnostus seminula
Ptychagnostus punctuosus affinis
In the D-Tree Creek valley the next older fauna is found, in chert.
Zone of *Doryagnostus notalibrae*

M167 19°51′S, 138°55′E
Hanging Rock waterfall at the head of the West Thornton River. Point x marks a lateritic mesa; the overhanging rock of the waterfall consists of lateritic Polland Shale; its base is 0.6 m of a conglomerate of chert and siltstone of the Incas, followed by about 1.2 m of Inca bedrock.

Triplagnostus gibbus posterus
Zone of *Ptychagnostus atavus*

M169 19°49′S, 138°55.4′E
A butte of strata of about 20 m of the Inca Formation: lateritic siltstone and shale with an intervening 3 m of limestone (Pl. 25, fig. 1).
In the siltstone:

Ptychagnostus atavus
Triplagnostus gibbus posterus
In the limestone:
Euagnostus cf. *certus*
Pseudoperonopsis cf. *ancisa*
Ptychagnostus atavus
Triplagnostus gibbus posterus
Zeteagnostus incautus
Zone of *Ptychagnostus atavus*

M170 19°48′S, 138°55.4′E
A mesa about 50 m high with its core a mass of chert (Precambrian); shale (siltstone) of Inca Formation (about 30 m) with slumps, is partly dislocated by faulting.

Ptychagnostus intermedius
Triplagnostus gibbus posterus
Zone of *Ptychagnostus atavus*

M171 19°47.5′S, 138°55′E
Deep Creek, right bank. Sequence is dislocated by faulting. Laminated impure limestone over siltstone; large rocky surfaces. Horizontal surfaces with stylolites cut across inclined (dislocated) strata (postdating the faulting—Deep Creek Fault).

Ptychagnostus punctuosus

M174 19°47′S, 138°53′E
About 3 km west from Deep Creek crossing; marly laminated limestone with harder laminated interbeds; it is close to M173—a bituminous limestone with chert and with aphanitic limestone. V-Creek Limestone.

Ptychagnostus punctuosus
Aotagnostus protentus
Doryagnostus magister
Myrmecomimus tribulis
Zone of *Ptychagnostus punctuosus* (passing up into *Doryagnostus notalibrae?*)

M176 19°33′S, 138°54.5′E
A sinkhole and its fringe. Section totals 18-20 m. Currant Bush Limestone.

(1) On the fringe: 7.5 m of bituminous well-bedded limestone, about 4.5 m visible.

(2) In the sinkhole: 7.5 m of limestone as above but sandy and micaceous in parts, with aphanitic layers.

(3) Below (2): 3 m of soft fissile yellow shale, siltstone with chert layers; abrupt lower contact (Inca Shale).

(4) Then over 6 m of dolomitic limestone (Thorntonia).

In limestone:

Onymagnostus (Agnostonymus) semiermis
Ptychagnostus idmon
Ptychagnostus scarifatus
Rhodotypiscus nasonis
Triplagnostus diremptus
Zone of *Euagnostus opimus*

In shale (bed 3):

Onymagnostus (Agnostonymus) semiermis
Pseudoperonopsis ancisa
Ptychagnostus scarifatus
Rhodotypiscus nasonis

M177 About 0.8 km W of M176
There is an intraformational limestone breccia at the track. See M150.

M265 19°58.5′S, 138°55′E
Northern slope of Inca Creek valley; lateritic siltstone, shale, and chert; large slabs in collapsed outcrops and rubble. Inca Formation.

Aristarius retrocornutus
Criotypus paenerugatus
Hypagnostus parvifrons
Iniospheniscus incanus
Peronopsis fallax ferox
Ptychagnostus atavus
Triplagnostus fretus
Triplagnostus gibbus posterus
Triplagnostus scopus
Triplagnostus stramineus
Triplagnostus quasigibbus
Zeteagnostus incautus
Zone of *Ptychagnostus atavus*

M276 19°59′S, 138°30′E
Dark red sandstone over thick-bedded Mail Change Limestone exposed in a quarry. Split Rock Sandstone.

Goniagnostus nathorsti
Zone of *Goniagnostus nathorsti*

(Remains of agnostids occur in several sites of Split Rock Sandstone, but their unsatisfactory state of preservation makes them indeterminable)

M408 19°41′S, 138°41.2′E
Quartpot Well on Quartpot Creek; material is in and from the well. Laminated dark grey marly limestone with black spots on bedding planes (unaltered fresh V-Creek rock).

Doryagnostus magister
Myrmecomimus tribulis mixtus
Pseudoperonopsis perplexa
Zone of *Goniagnostus nathorsti*

M409 19°35.5′S, 138°43.6′E
V-Creek crossing, including V-Creek canyon; outcrops in the creek bed; left bank cliff downstream, and ravines east of crossing. Blueish limestone with oolitic bands in the cliff; laminated fissile grey impure limestone with hard interbeds. V-Creek Limestone.

Aotagnostus culminosus
Aotagnostus protentus
Doryagnostus magister
Doryagnostus solidus
Euagnostus levifrons
Goniagnostus nathorsti
Goniagnostus scarabaeus
Grandagnostus imitans
Hypagnostus clipeus
Hypagnostus parvifrons mammillatus (pyg. fragments)
Myrmecomimus tribulis
Myrmecomimus tribulis mixtus
Onymagnostus angulatus
Pseudoperonopsis perplexa
Ptychagnostus punctuosus
Svenax vafer
Zone of *Doryagnostus notalibrae*

M410 19°35′S, 138°44.5′E
In the V-Creek/Harris Creek fork overlooking Patchwork Waterhole (a rock hole). Grey marly laminated limestone with step-forming hard banks. Collection is from the ‘hard banks’. About 30 m exposed. V-Creek Limestone.

Aotagnostus culminosus
Doryagnostus magister
Hypagnostus clipeus
Myrmecomimus tribulis
Pseudoperonopsis perplexa
Ptychagnostus punctuosus affinis
Zone of *Doryagnostus notalibrae*

M411 19°40.5′S, 138°40.5′E
V-Creek Limestone on Harris Creek, at the Top Harris Waterhole; in the canyon and on the right bank with its terraced and dissected slope of the valley. Total exposed is some 35 m of limestone.

In canyon, in laminated friable marly beds (marked “L.B.” in collection):

Aotagnostus culminosus
Doryagnostus magister
Myrmecomimus tribulis
Myrmecomimus tribulis mixtus
Pseudoperonopsis perplexa
Ptychagnostus punctuosus
Ptychagnostus punctuosus affinis
Zone of *Doryagnostus notalibrae*

In valley, close to the top (marked “U.B.55” in collection):

Pt. (Acidusus) sp. indet. aff. *germanus*
Doryagnostus magister
Goniagnostus nathorsti
Myrmecomimus tribulis evanidus
Zone of *Goniagnostus nathorsti*

M412 19°31′S, 138°53′E
Chummy Bore, 6.5 km W of Thorntonia. Siltstone. shale(mottled) with chert. Inca Formation.

Criotypus lemniscatus
Criotypus sp. nov. aff. *lemniscatus*
Euagnostus opimus
Onymagnostus angulatus
Onymagnostus (Agnostonymus) semiermis
Rhodotypiscus nasonis
Zone of *Euagnostus opimus*

De Keyser & Cook (1972, p. 27; map and legend) allotted the name 'Chummy Bore Formation' to the sequence at M412 and placed it below the Split Rock Sandstone and above the V-Creek Limestone. But the Chummy Bore Formation rests on Thorntonia Limestone and is a lateral and synchronous deposit of strata described from M123, M124, M150 (part), M149, M160, M176, and represents an early (lower) part of the Currant Bush Limestone. There is no Split Rock Sandstone and no V-Creek Limestone present in this particular area. Compare also M130.

M416 19°32.8′S, 138°35.7′E
11.2 km from Undilla, 2 km W from Douglas Creek. Flaggy marly limestone. V-Creek Limestone.

Acidusus retrotextus
Doryagnostus magister
Goniagnostus nathorsti
Grandagnostus imitans
Hypagnostus melicus
Onymagnostus mundus
Onymagnostus angulatus
Pseudoperonopsis perplexa
Zone of *Doryagnostus notalibrae*

M418 19°27.5′S, 138°33′E
On Douglas Creek, some 6 km upstream from the O'Shanassy River junction. V-Creek Limestone.

Aotagnostus culminosus
Doryagnostus magister
Doryagnostus solidus
Goniagnostus nathorsti
Grandagnostus imitans
Hypagnostus clipeus
Myrmecomimus tribulis
Onymagnostus mundus
Pseudoperonopsis perplexa
Zone of *Doryagnostus notalibrae*

MOUNT ISA 1:250 000 Sheet area

Biostratigraphically the Middle Cambrian sequence in the Whistlers Creek/Buckley River area is as complete as in the Camooweal area; east of that river most of the *Goniagnostus nathorsti* and parts of the *Ptychagnostus punctuosus* strata may be lost to erosion. In the minor outliers (M263, M433, M434) the youngest fauna belongs to the *Ptychagnostus punctuosus* (early Undillan) time; in the outliers a hiatus may represent the time of *Euagnostus opimus*. See under M192.

M59 20°10′S, 138°45′E
West of Plain Creek. Siliceous shale (siltstone) and chert. Inca Formation.

Aotagnostus indet.
Diplagnostus indet. (possibly *floralis*)
Euagnostus sp. indet.
Pseudoperonopsis perplexa
Ptychagnostus mesostatus
Ptychagnostus punctuosus affinis
Myrmecomimus tribulis mixtus
Zone of *Ptychagnostus punctuosus*

M60 20°02′S, 138°46′E
At ruins of Old Yelvertoft, about the fork of Plain Creek and Carleton Creek. Light grey sandy limestone; a bank in the Inca Formation.

Acidusus occultatus
Acidusus sp. aff. *occultatus*
Myrmecomimus tribulis mixtus
Pseudoperonopsis perplexa
Ptychagnostus punctuosus affinis
Zone of *Ptychagnostus punctuosus*

M164 20°02′S, 138°49′E
Inca Creek valley. Chert layers in siltstone (shale) of the Inca Formation. Chert with sponge spicules (spiculite, spongiolite).

Aotagnostus aotus
Aotagnostus ponebrevis
Diplagnostus floralis
Iniospheniscus talis
Zone of *Ptychagnostus punctuosus*

M188 20°06′S, 138°48.5′E
Along the Barkly Highway. Siltstone of the Inca Formation. Abundant pebbles on the surface.

Peronopsis fallax ferox
Pseudoperonopsis sp. (?*syrma*)
Ptychagnostus atavus
Triplagnostus fretus
Triplagnostus gibbus posterus
In a playa nearby, chert of the Beetle Creek Formation is present in a small emergent outcrop.
Zone of *Ptychagnostus atavus*

M191 20°14′S, 138°47′E
A bank of flaggy limestone of the Inca Formation, about 5-6 m thick. The fossils from the NE end of the bank are marked 191a; at the SW end an outcrop of grey ellipsoidal limestone is referred to as 191b.

Aotagnostus ponebrevis
Aotagnostus sp. indet. aff. *ponebrevis* in 191b
Criotypus mitigatus
Diplagnostus floralis
Euagnostus certus
Iniospheniscus talis
Pseudoperonopsis iniugata
Ptychagnostus punctuosus affinis
Zone of *Ptychagnostus punctuosus*

M192 20°15′S, 138°49′E
Flora Downs area, on Sherrin Creek. Siltstone with chert layers, Inca Formation.

Collection (1):
Aotagnostus ponebrevis
Criotypus lemniscatus
Euagnostus opimus
Hypagnostus sp.
Onymagnostus (Agnostonymus) semiermis
Triplagnostus diremptus
Zone of *Euagnostus opimus*

Collection (2):
Ptychagnostus atavus
Ptychagnostus atavus coartatus
Triplagnostus gibbus posterus
Zeteagnostus incautus
Zone of *Ptychagnostus atavus*

M193 20°14′S, 138°51.5′E
Bits of siltstone and chert of the Inca Formation at the foot of a Pilpah Sandstone ridge.
Aotagnostus (aotus or *ponebrevis)*
Iniospheniscus talis
Ptychagnostus punctuosus affinis
A litter of pebbles with fragments of *Redlichia*
Zone of *Ptychagnostus punctuosus*

No M number 20°15′S, 138°58′E
Buckley River crossing. Siltstone of the Inca Formation; angular debris in river bed.
Pseudoperonopsis syrma
Ptychagnostus atavus
Triplagnostus gibbus posterus
Zone of *Ptychagnostus atavus*

M194 20°01′S, 138°42′E
Forty-mile Plain, at the foot of the Umberella Range. Laminated translucent angular chert bits, probably residual, from dissolved limestone. ?V-Creek or Inca Formation.
Aotagnostus protentus
Doryagnostus magister
Goniagnostus scarabaeus
Myrmecomimus tribulis mixtus
Onymagnostus indet.
Zone of *Doryagnostus notalibrae*

M195 20°01′S, 138°41.5′E
Forty-mile Plain. Limestone in large slabs and monolithic blocks on black soil; lutitic, partly brecciated, grey, with near-shaly partings. Attributed to Currant Bush Limestone.
Doryagnostus magister
Goniagnostus scarabaeus
Goniagnostus verus
Leiopyge cosfordae
Tomagnostella nepos
Zone of *Goniagnostus nathorsti*

M198 20°07′S, 138°35′E
On Whistlers Creek, upstream from M199. Siltstone, Inca Formation. About 150 m of siltstone is exposed (Öpik, 1960, p. 101).
Peronopsis fallax ferox
Ptychagnostus atavus
Triplagnostus gibbus posterus
Zone of *Ptychagnostus atavus*

M199 20°08′S, 138°14.5′E
Whistlers Creek; a rockhole. Inca siltstone and some chert in a free face, 10 m high.
Pseudoperonopsis ancisa
Ptychagnostus atavus
Ptychagnostus cf. *idmon*
Triplagnostus gibbus posterus
Zeteagnostus incautus
Pagetia, fragments of *Fouchouia,* and a nepeid
Zone of *Ptychagnostus atavus*

M202 20°11′S, 138°35′E
Impure grey bedded limestone; small outcrops. V-Creek Limestone.
Doryagnostus magister
Hypagnostus inaequalis
Pseudoperonopsis perplexa
Zone of *Ptychagnostus punctuosus,* passing up into the Zone of *Doryagnostus notalibrae*

M204 20°14′S, 138°34′E
Flaggy grey laminated limestone. V-Creek Limestone.
Aotagnostus culminosus
Doryagnostus magister
Myrmecomimus tribulis
Pseudoperonopsis perplexa
Peronopsis indet.
Ptychagnostus punctuosus affinis
Tomagnostella nepos
Zone of *Doryagnostus notalibrae*

M207 20°17′S, 138°41′E
Pilpah Sandstone with a capping of conglomerate 3-12 m thick and a veneer of siliceous shale (Beetle Creek Formation) with a mass of *Xystridura.* Pebbles of Inca chert and shale contain:
Ptychagnostus atavus
Triplagnostus gibbus posterus

M208 20°18′S, 138°40′E
A limestone bank in the Inca Formation.
Peronopsis fallax ferox
Ptychagnostus atavus
Ptychagnostus idmon
Triplagnostus diremptus
Triplagnostus gibbus posterus
Late in Zone of *Ptychagnostus atavus*

M212 20°15′S, 138°38′E
Grey flaggy limestone with a laminated pink bed. Large collection. V-Creek Limestone.
Aotagnostus culminosus
Aotagnostus protentus
Baltagnostus robustus
Diplagnostus cf. *planicauda bilobatus*
Doryagnostus notalibrae
Myrmecomimus tribulis
Onymagnostus mundus
Onymagnostus seminula
Pseudoperonopsis insolita
Pseudoperonopsis perplexa
Ptychagnostus punctuosus
Zone of *Doryagnostus notalibrae*

M213 20°14′S, 138°17.5′E
Pink laminated limestone with grey nodules and regular layers of chert; fossils also in chert. V-Creek Limestone.
In chert:
Acidusus cf. *occultatus*
Doryagnostus magister
Hypagnostus clipeus
Myrmecomimus tribulis mixtus
Pseudoperonopsis indet.
Zone of *Doryagnostus notalibrae*

M214 20°18.5′S, 138°38′E
Grey laminated limestone. V-Creek Limestone.
Acidusus germanus
Acidusus navus
Doryagnostus notalibrae
Goniagnostus nathorsti
Grandagnostus imitans
Pseudoperonopsis perplexa
Ptychagnostus punctuosus
Zone of *Doryagnostus notalibrae*

M234 20°11.5′S, 138°27′E
Grey and pink limestone interbeds in soft impure limestone. V-Creek Limestone.
Acidusus acidusus
Aotagnostus culminosus
Grandagnostus imitans
Myrmecomimus tribulis mixtus
Pseudoperonopsis perplexa
Ptychagnostus punctuosus affinis
Zone of *Doryagnostus notalibrae*

M243 20°17′S, 138°35′E
At fork of Whistlers Creek and Buckley River channels. Grey limestone beds and soft impure limestone interbedded. V-Creek Limestone.
Euagnostus neptis
Iniospheniscus? sp. indet.
Pseudoperonopsis perplexa
Rhodotypiscus sp. nov. aff. *nasonis*
Also *Opsidiscus* and Ptychopariidae
Zone of *Ptychagnostus punctuosus*

M247 20°15′S, 138°34′E
In Whistlers Creek bed at No. 7 Bore, Barkly Downs. Grey laminated limestone with ellipsoids and thin interbeds. V-Creek Limestone.
Doryagnostus magister
Doryagnostus notalibrae
Goniagnostus scarabaeus
Hypagnostus clipeus
Myrmecomimus sp. indet.
Onymagnostus mundus
Pseudoperonopsis perplexa
Zone of *Doryagnostus notalibrae*

M263 20°36′S, 139°20′E
Site is about 3 km long and cut by the Templeton River in two parts. Siltstone and shale of the Inca Formation are exposed in small rolling folds. The youngest strata (a soft yellow and pink siltstone) in floaters and angular rubble have been collected at a crossing on the eastern bank of the river. The eastern (meridional) edge of the outcrops may indicate a fault against the basement in the east.
Aotagnostus aotus
Aristarius aristarius
Criotypus sp. aff. *paenerugatus*
Diplagnostus floralis
Iniospheniscus talis
Pseudoperonopsis perplexa
Ptychagnostus sp. indet. C
Triplagnostus gibbus posterus
Zone of *Ptychagnostus punctuosus*

M281 20°03′S, 138°48′E
At Two Miles Waterhole, slabs of siltstone and chert of the Inca Formation in creek bed; outcrops downstream and upstream.
Criotypus paenerugatus
Hypagnostus vortex
Peronopsis fallax ferox
?Peronopsis (?Itagnostus) sp. indet.
Ptychagnostus atavus
Triplagnostus fretus
Triplagnostus gibbus posterus
Zeteagnostus incautus
Zone of *Ptychagnostus atavus*

M289 20°02′S, 138°54.5′E
Siltstone, chert, limestone of the Inca Formation.
Aotagnostus protentus
Myrmecomimus saltus
Pseudoperonopsis perplexa
Ptychagnostus indet.
Zone of *Ptychagnostus punctuosus*

M423 20°10′S, 138°35′E
At the Wire Yard waterhole, right bank of Whistlers Creek. Flaggy grey limestone—a bank of the Inca Formation. In creek bed siltstone is exposed.
Euagnostus cf. *certus*
Triplagnostus gibbus posterus
Zeteagnostus incautus
A ptychopariid
Zone of *Ptychagnostus atavus*

M424 20°02′S, 138°47′E
'New Tank' at Yelvertoft. Friable siltstone—fine-grained sandstone, stratified to banded; calcareous.
Acidusus occultatus
Diplagnostus floralis
Hypagnostus sp. indet.
Ptychagnostus punctuosus (?affinis)
Zone of *Ptychagnostus punctuosus*

M425 20°12.5′S, 138°51.5′E
At NE corner of Flora Downs and separated by a fault from outcrops of Pilpah Sandstone. Siltstone, chert, and siliceous shale of the Inca Formation. A site of abundant agnostids.
Criotypus lemniscatus
Criotypus oxytorus
Criotypus paenerugatus
Diplagnostus atavorum

Euagnostus certus
Hypagnostus sp. indet.
Peronopsis fallax ferox
Pseudoperonopsis syrma
Ptychagnostus atavus
Ptychagnostus atavus coartatus
Triplagnostus gibbus posterus
Triplagnostus sp. indet.
Zeteagnostus incautus
Zone of *Ptychagnostus atavus*

M427 20°23.5′S, 138°44.5′E
Apparently an old bajada over Templetonian outcrops; outcrops are probably upstream in the enclave valley in the Ogilvie Range. One pebble contains:
Pseudoperonopsis sp. indet.
Ptychagnostus atavus
Ptychagnostus sp. indet. A (aff. *atavus*)
In the collection this pebble is wrongly marked 'M207'

M430 20°18′S, 138°53.5′E
Low rocky outcrops and rubble of siliceous shale with chert. Inca Formation. Two assemblages of agnostids:
(1)
Peronopsis fallax ferox
Pseudoperonopsis aff. *iniugata*
Ptychagnostus atavus
Triplagnostus gibbus posterus
Zone of *Ptychagnostus atavus*
(2)
Triplagnostus gibbus gibbus
Triplagnostus gibbus posterus
Late in Zone of *Triplagnostus gibbus*

M433 20°36′S, 139°19′E
This site number covers (1) the Beetle Creek Formation at Beetle Creek, with *Peronopsis normata;* (2) in the mesa nearby, the Beetle Creek sequence is crowned by 15-17 m of siltstone and shale of the Inca Formation; in its lower part *Triplagnostus gibbus* and *T. gibbus posterus* are present; the higher beds contain *Ptychagnostus atavus, Triplagnostus gibbus posterus, Pseudoperonopsis* sp. indet., and fragments of a *Criotypus*. The lowermost strata (1-3 m, variable) contain *Redlichia* and silicified stromatolites resting on the floor of basement rocks.
From the Zone of *Redlichia chinensis* and up to the Zone of *Ptychagnostus atavus*.

M434 20°44′S, 139°19.5′E
Siltstone and chert strata of the Beetle Creek Formation are well exposed; *Peronopsis normata* is frequent. Shale-siltstone litter with *Ptychagnostus atavus* is rare. Younger strata are apparent in downfaulted blocks. (1) a pink smooth shale in a small outcrop yielded *Myrmecomimus saltus, Aotagnostus aotus,* and *Aristarius* aff. *ultimus;* (2) angular bits of chert contain *Diplagnostus floralis, Pseudoperonopsis* cf. *perplexa,* and *Myrmecomimus* cf. *tribulis mixtus*. From Templetonian up into the Zone of *Ptychagnostus punctuosus*.

M462 20°03′S, 138°35′E
Bank of a small creek channel; grey flaggy limestone, about 100 m from Whistlers Bore. V-Creek Limestone.
Doryagnostus magister
Goniagnostus nathorsti
Goniagnostus scarabaeus
Hypagnostus melicus
Hypagnostus tjernviki
Oedorhachis crenias
Onymagnostus seminula
Zone of *Goniagnostus nathorsti*

DUCHESS 1:250 000 Sheet area

(The Burke River Outlier)

The topological data given below refer to sites of the Inca Formation and one site of Thorntonia Limestone. The phosphate and phosphatic deposits of the Inca Formation contain (according to Russell & Trueman, 1971) agnostids and other trilobites of Templetonian age, as well as several forms of Bradoriida (Fleming, 1973).

Öpik (1961) described agnostids and other fossils of late Middle Cambrian (Boomerangian) age, and later (*in* Carter & Öpik, 1963) described Upper Cambrian fossils from other sites west of the Burke River. See also Öpik (1960, p. 101).

D148 21°50′S, 139°58.3′E
Mount Murray; a table top and a chain of four hills. Siliceous siltstone and shale with chert and smelly bituminous limestone layers.
Triplagnostus sp. indet.
Zone of *Ptychagnostus atavus*

D149
1.5-2 km NW from Mount Murray (D148). A low cliff; siltstone and sandy shale (almost a laminated sandstone).
Ptychagnostinae indet.

D150 21°47′S, 139°53′E
About 2 km N of Mount Murray. Dark grey smelly limestone with layers of chert and siltstone.
Criotypus sp. indet.
Ptychagnostus sp. indet. B (aff. *atavus*)
Ptychagnostinae gen. indet., sp. nov. (as in D154)
?Zone of *Euagnostus opimus*

D153 21°45′S, 139°59′E
An enclave of dolomitic limestone with chert (Thorntonia Limestone) emergent through its unconformable mantle of Inca siltstone (with Ptychagnostinae).

D154 21°45′S, 139°59′E
East from and close to D153. Grey limestone interbeds in siltstone (siliceous shale).
Euagnostus indet.
Ptychagnostinae, gen. indet., sp. nov.

D155 21°44′S, 139°59′E
About 2.5 km from the D153 enclave. Dark grey smelly limestone; light grey limestone; chert and siliceous shale layers. Inca Formation.
Leiopyge praecox
Ptychagnostus punctuosus fermexilis
Ptychagnostus (Acidusus) sp. nov.
Zone of *Ptychagnostus punctuosus*

URANDANGI 1:250 000 Sheet area

Agnostids found at D95 and D96 are listed in Öpik (1967, vol. 2, p. 14): the Floran and the time of *Goniagnostus nathorsti* are represented by hiatuses.

D54 21°57′S, 139°04′E
Steamboat Sandstone at Quita Bore, left bank of Quita Creek.
Allobodochus spiniger
Zone of *Leiopyge laevigata* (over strata of the Zone of *Ptychagnostus punctuosus*).

D55 21°58′S, 139°07′E
Limestone in creek gully between two tall mesas.
Ptychagnostus (Acidusus) sp. nov. (Pl. 48, fig. 5)
Pseudophalacroma dubium
Zone of *Ptychagnostus punctuosus*

D57
In the SW periphery of the hill D69. Quita Creek Limestone.
Leiopyge praecox
Zone of *Ptychagnostus punctuosus*

D63 21°57′S, 139°09.5′E
About 3 km SE from D74. Pallid lateritic material, derived from Blazan Shale.
Pseudophalacroma cf. *dubium*
Pseudophalacroma cf. sp. K (Öpik, 1961, p. 22, fig. 11)
Blazan strata rest on the Precambrian basalt as well as on *Redlichia*-bearing chert in sandstone and on Thorntonia Limestone
Zone of *Ptychagnostus punctuosus*

D66 21°55.5′S, 139°07′E
About 2 km N of point D74. Grey limestone (Quita area).
Baltagnostus sertulatus
Hypagnostus aff. *brevifrons*
Pseudoperonopsis sp. indet.
Svenax pusillus
Zone of *Ptychagnostus punctuosus*

D69 21°54′S, 139°07′E
Outlier of rocks of the Quita Formation resting on dolomitic limestone (Thorntonia) and separated by a well exposed disconformity; it is a terraced hill of platy limestone on top, and siliceous shale and platy calcareous chert below, totalling 30-35 m thickness.
Aotagnostus aotus
Aotagnostus protentus
Diplagnostus floralis
Pseudoperonopsis cf. *iniugata*
Ptychagnostus punctuosus affinis
Zone of *Ptychagnostus punctuosus*

D74 21°56′S, 139°07.5′E
A cluster of elongate mesas; the section in the east-facing eastern mesas is, from the top:
(1) 3 m of laterite
(2) 7.5 m of red, pallid, and mottled lateritic shale, unfossiliferous
(3) 1.5 m of conglomerate
(4) 9 m of fissile fine-grained sandstone with *Quitacetra arenata* Öpik, 1967. Quita Creek Formation-early Boomerangian
(5) Dolomitic limestone, ellipsoids in sandy friable matrix; very fossiliferous
(6) Fissile friable sandstone
(7) Platy sandy aphanitic limestone with chert.

Units 5 to 7 total over 12 m of exposure. The following fossils come from unit 5:
Aotagnostus culminosus
Aotagnostus protentus
Baltagnostus sertulatus
Doryagnostus magister
Myrmecomimus sp. indet.
Pseudoperonopsis iniugata
Pseudoperonopsis perplexa
Ptychagnostus punctuosus
Svenax pusillus
Zone of *Ptychagnostus punctuosus*

Q6
Close to D74, from about bed 7 in the section. Quita Creek Formation.
Ptychagnostus punctuosus punctuosus
Ptychagnostus punctuosus fermexilis
Pseudophalacroma dubium

D86 21°53′S, 139°05.5′E
1-1.5 km WNW from point D69. On the uneven rough surface of the outcrop of dolomitic limestone (Thorntonia) rests unconformably a very small residual of brown siliceous shale, about 5 cm thick and 1 m across.
Euagnostus sp. indet.
Ptychagnostus punctuosus affinis
Some phosphatic brachiopods, *Hyolitus and Stenotheca*
Zone of *Ptychagnostus punctuosus*

No number 21°21.5′S, 139°05′E
Yellow hard siliceous dolomitic beds of the Quita Formation, in a creek bed.
Aotagnostus culminosus
Pseudoperonopsis sp. indet.
Ptychagnostus punctuosus affinis

GLENORMISTON and MOUNT WHELAN 1:250 000 Sheet areas

The biostratigraphy of the Middle Cambrian and the agnostids are treated by Öpik (1967, Vol. 2). Middle Cambrian sites in the Glenormiston area are G101, G103, G104, G106, G107, G116, G123, G133; those in the Mount Whelan area are W36, W250, W255.

W36 23°02.5′S, 138°40′E
Black, somewhat bituminous limestone (Devoncourt). The list by Öpik (1967, vol. 2, p. 13) now reads:
Diplagnostus crassus
Hypagnostus brevifrons
Leiopyge armata
Leiopyge laevigata
Leiopyge multifora
Leiopyge sp. nov. aff. *armata*
Oidalagnostus personatus

LAWN HILL 1:250 000 Sheet area

(extends into MOUNT DRUMMOND area, Northern Territory)

In the Lawn Hill Sheet area and the adjacent part of the Mount Drummond area the sequence is continuous from the Ordian and Templetonian up into the Floran Zone of *Euagnostus opimus*. No evidence of strata and faunas of Undillan age has been found.

M183 18°36′S, 138°02′E
Dark grey limestone. Currant Bush (=Louie Creek) Limestone.
Euagnostus opimus
Euagnostus certus
Rhodotypiscus nasonis

M376 18°36.5′S, 138°03′E
Mottled siltstone and shale in banks and in the bed of a small stream; moderately contorted. ?Inca Formation as part of Currant Bush (=Louie Creek) Limestone.
Euagnostus certus
Euagnostus opimus
Onymagnostus (Agnostonymus) semiermis
Onymagnostus angulatus
Pseudoperonopsis ancisa
Rhodotypiscus nasonis
Triplagnostus diremptus
Zone of *Euagnostus opimus*

NEW SOUTH WALES

Mount Wright area

Shale 10 km NW from Mount Wright (31°12.5′S, 172°20′E). See locality 4D in BMR Bulletin 159. The Oryctocephalidae from the same site have been described by Shergold (1969).
Pentagnostus anabarensis Lermontova
Pentagnostus veles sp. nov.

NORTHERN TERRITORY

T87 22°54′S, 137°41′E
Tobermory 1:250 000 Sheet area, Marqua Beds. The outcrop is at a road cutting the escarpment of Cambrian rocks. Öpik (1961, p. 48) referred to it informally as 'Devoncourt' limestone. It rests on Templetonian followed by Ordian strata, including chert with *Redlichia chinensis*. The rock at T87 is a dark blue sandy limestone; its age is Boomerangian. The amplified list of fossils reads:
Allobodochus spiniger
Agnostus cf. *neglectus*
Delagnostus dilemma
Holteria arepo
Hypagnostus ?brevifrons
Hypagnostus hippalus
Hypagnostus cf. *sulcifer*
Leiopyge laevigata
Mapania dicella
Mapania synophrys
Pseudophalacroma dubium

N32
Sandover Beds, siltstone and shale; see BMR Bull. 121 (text-fig. 1, Site B).
'Acadagnostus' scutalis
Linguagnostus comparabilis
Pentagnostus rallus
Peronopsis (Itagnostus) elkedraensis
Peronopsis prolixa

F5 21°32′S, 135°50′E
Position is only approximate. Sandover beds, siltstone.
'Acadagnostus' scutalis

N31, N33-36
Sandover Beds (Argadargada Pebbles). Geography is given in BMR Bulletin 121 (text-fig. 1; p. 13).
'Acadagnostus' scutalis
Pentagnostus rallus
Peronopsis comis
Peronopsis prolixa
Peronopsis tramitis
Peronopsis (Itagnostus) elkedraensis

N63 21°37′S, 135°23′E
About the Ammaroo Discovery Well; soft pallid siltstone. The stratigraphic position is discussed in BMR Bulletin 121 (text-fig. 1, site 9A).
Peronopsis longinqua
Peronopsis (Itagnostus) elkedraensis

M179 18°38′S, 137°56′E
Mount Drummond 1:250 000 Sheet area; southern bank of Lancewood Creek. Limestone and marly limestone of the Currant Bush (=Louie Creek) Limestone.
Euagnostus certus
Peronopsis normata
Peronopsis sp. indet.
Zone of *Ptychagnostus atavus*

M180 18°38′S, 137°57.5′E
Mount Drummond 1:250 000 Sheet area; on Lancewood Creek. Grey limestone and marly limestone. Currant Bush (=Louie Creek) Limestone.
Euagnostus certus
Euagnostus glandifer
Euagnostus opimus
Hypagnostus parvifrons
Onymagnostus (Agnostonymus) semiermis
Onymagnostus sp. nov. aff. *angulatus*
Rhodotypiscus nasonis
Zone of *Euagnostus opimus*

GLOSSARY

EXPLANATION OF NEW NAMES OF TAXA

Acidusus	Masc., Greek: 'spiked being', alluding to the tip of the pygidial axis.
Agnostonymus	Masc., Greek, transposition from *Onymagnostus* (q.v.).
Allobodochus	Masc., Greek: 'another lobe-bearer', meaning the secondary lobe in the rear of the pygidial axis.
ancisa	(*Pseudoperonopsis*), Lat.: 'cut round' (in the rear of the pygidial margin).
angulatus	(*Onymagnostus*), Lat.: meaning the angulate pygidial margin.
Aotagnostus	Masc., Greek: see *aotus*.
aotus	(*Aotagnostus*), Greek: 'the choicest of its kind'.
Aristarius	Masc., Lat.: 'beard of a grain' (e.g. barley); alludes to spines.
atavorum	(*Diplagnostus*), Lat., genitive pl. of *atavus* (associated with *Ptychagnostus atavus*).
certus	(*Euagnostus*), Lat.: 'definite, sure'.
coartatus	(*Ptychagnostus atavus*), Lat.: 'contracted'.
comis	(*Peronopsis*), Lat.: 'comely'.
comparabilis	(*Linguagnostus*), Lat., comparable with species of the same genus.
cosfordae	(*Leiopyge*): named for Mrs Wendy Cosford, who proof-read all my publications in the last 15 years.
crenias	(*Oedorhachis*), Greek: 'from a spring' (collected at the spring M24).
Criotypus	Masc., Greek: 'ram's blow mark'; alludes to the arcuate scrobicules (*krios*—ram; *typos*—blow).
culminosus	(*Aotagnostus*), Lat.: 'having many summits'.
diremptus	(*Triplagnostus*), Lat.: 'separated'.
durusacnitens	(*Onymagnostus*), Lat.: 'hard and shiny'.
evanidus	(*Myrmecomimus*), Lat.: 'vanishing'.
fermexilis	(*Ptychagnostus punctuosus*), Lat.: 'nearly slender'.
floralis	(*Diplagnostus*): Austral. geogr.—found about Flora Downs, Queensland.
fretus	(*Triplagnostus*), Lat.: 'reliable'.
germanus	(*Acidusus*), Lat.: 'genuine'.
glandifer	(*Euagnostus*), Lat.: 'acorn-bearer'.
idmon	(*Ptychagnostus*), Greek: 'skilled, knowing'; also the Argonaut Idmon.
inaequalis	(*Hypagnostus*), Lat.: 'uneven'.
incanus	(*Iniospheniscus*), Lat.: after Inca Creek.
incautus	(*Zeteagnostus*), Lat.: 'careless, unwary, unguarded'.
Iniospheniscus	Masc., Greek, diminutive; *inion*—'nape of the neck'; *sphen*—'a chip'.
iniugata	(*Pseudoperonopsis*), Lat.: 'yokeless', alluding to the absence of the pygidial collar.
insolita	(*Pseudoperonopsis*), Lat.: 'uncommon'.
intersertus	(*Goniagnostus nathorsti*), Lat.: 'placed in between'.
Itagnostus	Masc., Greek: *itos*—'passable'.
lemniscatus	(*Criotypus*), Lat.: 'adorned with ribbons'; from Greek *lemniskos*—'a ribbon, band'.
levifrons	(*Euagnostus*), Lat.: 'smooth in front' (no preglabellar median furrow).
longinqua	(*Peronopsis*), Lat.: 'distant, remote'.
magniceps	(*Aotagnostus*), Lat.: 'big head'.
melicus	(*Hypagnostus*), Lat.: 'musical, lyrical'; alludes to the occurrence at Whistlers Creek.
mesostatus	(*Ptychagnostus*), masc., Greek: 'standing in the middle' (between *Pt. punctuosus* and *Pt. atavus*).
mitigatus	(*Criotypus*), Lat.: 'mild'.
mixtus	(*Myrmecomimus tribulis*), Lat.: 'mixed' (in the sense of the combination of character).

modicus	(*Aotagnostus*), Lat.: 'moderate'.
multifora	(*Leiopyge*), Lat.: 'with many holes'.
mundus	(*Onymagnostus*), Lat.: 'neat, elegant'.
Myrmecomimus	Masc., Greek: *myrmex*—'ant'; *mimus*—'imitator'; simulating ants.
nasonis	(*Rhodotypiscus*), Lat.: in respect of Publius Ovidus Naso.
navus	(*Acidusus*), Lat.: 'zealous'.
neptis	(*Euagnostus*), Lat.: 'grand-daughter' (compare *Tomagnostella nepos*).
notalibrae	(*Doryagnostus*), Lat.: 'mark of the constellation Libra'; alludes to the shape of the transverse glabellar furrow; also an allusion to its position in the midmost zone of the Undillan Stage.
occultatus	(*Acidusus*), Lat.: 'hidden' (previously mistaken for *Pt. atavus*).
Onymagnostus	Masc., Greek: *onyma*—'name' + agnostus.
oxytorus	(*Criotypus*), Greek: 'prickly'.
paenerugatus	(*Criotypus*), Lat.: 'nearly rugose'.
ponebrevis	(*Aotagnostus*), Lat.: 'short behind', referring to the pygidial axis.
posterus	(*Triplagnostus gibbus*) Lat.: 'the next, subsequent'.
praecox	(*Leiopyge*), Lat.: 'premature'.
prolixa	(*Peronopsis*), Lat.: 'expanded'.
protentus	(*Aotagnostus*), Lat.: 'stretched'.
quasigibbus	(*Triplagnostus*), Lat. 'simulating *gibbus*'.
rallus	(*Pentagnostus*), Lat.: 'thin, of fine texture'.
retrocornutus	(*Aristarius*), Lat.: 'rear-horned'.
retrotextus	(*Acidusus*), Lat.: 'rear-fringed'.
Rhodotypiscus	Masc. diminutive, Greek: 'rose-mark', referring to the rosette in its pygidium.
robustus	(*Baltagnostus*), Lat.: 'robust'.
saltus	(*Myrmecomimus*), Lat.: genitive of *saltus*—'of the glade' (refers to site of discovery).
scarifatus	(*Ptychagnostus*), Lat.: 'scratched up', scrobiculate.
scopus	(*Triplagnostus*), Latin ex Greek: 'shooting target'.
semiermis	(*Agnostonymus*), Lat.: 'half-armed'.
sertulatus	(*Baltagnostus*), Lat. diminutive: 'with a garland'.
solidus	(*Doryagnostus*), Lat.: 'solid'.
stramineus	(*Triplagnostus*), Lat.: 'straw made'.
Svenax	abbreviated combination of Sven Axel, first names of Tullberg; masc., indeclinable.
syrma	(*Pseudoperonopsis*), Greek: 'robe with a train', alluding to the extended rim in the pygidial rear.
talis	(*Iniospheniscus*), Lat.: 'of such remarkable kind'.
tramitis	(*Peronopsis*), Lat.: 'of the by-way'.
tribulis	(*Myrmecomimus*), Lat.: 'fellow-tribesman'.
ultimus	(*Aristarius*), Lat.: 'the last' (of the genus).
vafer	(*Svenax*), Lat.: 'artful'.
veles	(*Pentagnostus*), Lat.: 'light-armed'.
verus	(*Goniagnostus*), Lat.: 'genuine'.
Zeteagnostus	Masc., Greek: stem *zete,* the name of the Argonaut Zetes (searcher).

INDEX OF SELECTED ITEMS

Prepared by Carol Ryan

(for taxonomic nomenclature, see *Contents,* pp. iv-vii

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